

## Lobophora (Dictyotales, Phaeophyceae) from the western Indian Ocean: diversity and biogeography

Vieira Christophe <sup>1,2,\*</sup>, Rasoamanendrika Faravavy A. <sup>3</sup>, Zubia Mayalen <sup>4</sup>, Bolton John J. <sup>5</sup>, Anderson Robert J. <sup>5</sup>, Engelen Aschwin H. <sup>6</sup>, D'Hondt Sofie <sup>2</sup>, Leliaert Frederik <sup>2,7</sup>, Payri Claude <sup>8</sup>, Kawai Hiroshi <sup>1</sup>, De Clerck Olivier <sup>2</sup>

<sup>1</sup> Kobe University Research Center for Inland Seas, Rokkodai, Kobe 657-8501, Japan

<sup>2</sup> Phycology Research Group and Center for Molecular Phylogenetics and Evolution, Ghent University, Krijgslaan 281 (S8), B-9000 Ghent, Belgium

<sup>3</sup> University of Antsirana, Antsirana, Madagascar

<sup>4</sup> Université de la Polynésie française, UMR Ecosystèmes Insulaires Océaniques, LabEx CORAIL, BP6570, Faa'a, 98702 Tahiti, French Polynesia

<sup>5</sup> Department of Biological Sciences, University of Cape Town, Rondebosch 7701, South Africa

<sup>6</sup> Centro de Ciências Do Mar Do Algarve (CCMAR), University of Algarve, 8005 139 Faro, Portugal

<sup>7</sup> Meise Botanic Garden, Meise 1860, Belgium

<sup>8</sup> UMR ENTROPIE (IRD, UR, UNC, Ifremer, CNRS), Institut de Recherche pour le Développement, B.P. A5 Nouméa Cedex, Nouvelle-Calédonie 98848, France

\* Corresponding author : Christophe Vieira, email address : [cvcarp@gmail.com](mailto:cvcarp@gmail.com)

### Abstract :

The brown algal genus *Lobophora* (Dictyotales, Phaeophyceae) is an important ecological component of tropical marine systems. Although still scantily sampled, 35 species of *Lobophora* were discovered previously from the western Indian Ocean. This study updates previous diversity estimates by incorporating recent collections from Madagascar, Mozambique, and the Red Sea, considerably improving our knowledge of *Lobophora* diversity and biogeography in this region. Eight additional species are identified from the western Indian Ocean, raising the total number of *Lobophora* species to 43. Fifteen species are new to science and described herein. With ca. 40% of the global diversity, the western Indian Ocean is second only to the Central Indo-Pacific. Of the species identified to date, 29 appear to be restricted to the western Indian Ocean, three are shared with the Atlantic (four including *L. lessepsiana* introduced to the western Mediterranean Sea) and 12 have a wider distribution in the Indo-Pacific. The western Indian Ocean supports a high diversity with ca. 67% of its *Lobophora* restricted to this region, which is comparable to the Central Indo-Pacific (62%) and the Caribbean (61%). The presence of several putative endemic species in the western Indian Ocean islands and the Red Sea illustrates that these provinces played an important role in *Lobophora* species diversification within the western Indian Ocean by producing locally new species. The small number of species shared between the western Indo-Pacific and Atlantic indicates that this oceanic boundary – associated with the temperate Agulhas marine province, and the Benguela current and upwelling – acts as an effective dispersal barrier.

---

## Highlights

► Diversity of genus *Lobophora* is reassessed in the western Indian Ocean. ► A total of forty-three species are recognized. ► Twenty-nine species appear endemic to the western Indian Ocean. ► Fifteen species are described as new.

**Keywords** : Madagascar, Mozambique molecular phylogenetics, Red Sea, seaweeds, South Africa, taxonomy

## 56 **1. Introduction**

57 The brown algal genus *Lobophora* J.Agardh (Dictyotales, Phaeophyceae) is an  
58 important ecological component of tropical and sub-tropical marine systems (Puk et  
59 al., 2020; Vieira, 2020; Vieira et al., 2014; Vieira et al., 2020b). Beginning in 2012, a  
60 renewed interest in the taxonomy of the genus has resulted in a spectacular increase in  
61 species discovery and descriptions. This progress resulted largely from the use of  
62 molecular data in combination with morphological and ecological observations.  
63 Initially, sampling effort primarily targeted localities in the Pacific (e.g., Japan (Sun et  
64 al., 2012), New Caledonia (Vieira et al., 2014), Papua New Guinea (Vieira et al.,  
65 2019), Palau (Puk et al., 2020)) and the Atlantic Ocean (e.g., the Caribbean Sea  
66 (Camacho et al., 2019; Schultz et al., 2015; Vieira et al., 2020b), Macaronesia (Vieira  
67 et al., 2020a) and the Mediterranean Sea (Vieira et al., 2018)). While global diversity  
68 of the genus was also assessed (Vieira et al., 2017; Vieira et al., 2016), the sampling  
69 effort in many regions remained limited and most likely resulted in an  
70 underestimation of the actual species diversity in several regions. Greater sampling  
71 effort is required in the Central Indo-Pacific (CIP), Eastern Indo-Pacific, Eastern  
72 Pacific, Southern Atlantic and the Indian Ocean, in order to better document  
73 *Lobophora* species diversity. As the number of newly discovered species grew rapidly  
74 in the last few years, it also became clear that the name *L. variegata* (J.V.Lamour.)  
75 Womersley ex E.C.Oliveira had been incorrectly used for a wide variety of species.  
76 Recent studies indicate that *L. variegata* is likely restricted to the Greater Caribbean  
77 (Vieira et al., 2020b).

78 This study focuses on the western Indian Ocean, defined here as the marine region  
79 encompassing six provinces *sensu* Spalding et al. (2007): Agulhas (A in Fig. 3),  
80 western Indian-Ocean *sensu stricto* (*s.s.*) (B), Somali/Arabian (C), Red Sea and Gulf  
81 of Aden (D), West and South Indian Shelf (E) and Central Indian Ocean Islands (F).  
82 The Bay of Bengal and Andaman provinces were not included in this study because  
83 of the absence of recent data. While Spalding et al. (2007) excluded the Agulhas  
84 province from the western Indian Ocean and placed it in the Temperate Southern  
85 Africa realm instead, we chose to include Agulhas in this study because of the  
86 imprecise limit of the tropical Indian Ocean seaweed flora, as a result of the overlap  
87 of tropical and temperate elements along a considerable part of the North Agulhas  
88 province (Bolton et al., 2004).

89 Complementing previous taxonomic efforts on the genus *Lobophora* in the western  
90 Indian Ocean (Steen et al., 2015; Vieira et al., 2017; Vieira et al., 2016), additional  
91 sampling was carried out in Madagascar, Mozambique and the Red Sea. We  
92 summarize current knowledge of *Lobophora* diversity and discuss the biogeography  
93 in this marine region at the junction between the Indo-Pacific and Atlantic Oceans.  
94 New species identified from the Western Indian Ocean are herein described.

95

## 96 **2. Material and Methods**

### 97 *2.1. Sampling localities*

98 Sampling was conducted in Madagascar, Mozambique and the Red Sea. Specimens  
99 were collected either by snorkeling between 0 and 10 m depths or by SCUBA to 35 m  
100 depth in: Antsiranana Bay, northern Madagascar (November 2018); Inhambane and  
101 Zavora, Mozambique (April-May 2018); Masra Shagra, Egypt (June 2019); from  
102 Cesare and Rosh Hanikra, Tchelet Island, Israel (July-August 2017) (Table A.1). A

103 total of 52, 28 and 37 specimens were sampled from Madagascar, Mozambique and  
104 the Red Sea, respectively. Specimens were preserved in silica gel for molecular  
105 analyses, and herbarium specimens were mounted and later deposited in either the  
106 Herbarium of the University of Antsirananana, Madagascar or the Herbarium of Meise  
107 Botanic Garden, Meise, Belgium (BR). Type specimens were deposited at Meise  
108 Botanic Garden, Meise, Belgium (BR), at the Institut de Recherche pour le  
109 Développement (IRD), Nouméa, Nouvelle-Calédonie (NOU) or at Université de  
110 Polynésie Française, Tahiti, Fa'a, French Polynesia (UPF), registered in the Index  
111 Herbariorum (Thiers, 2020). Less recent samples of GENT collections (Ghent  
112 University, Belgium) from East Africa were also examined.

## 113 *2.2. Molecular and morphological analyses*

114 Total genomic DNA was obtained from silica gel-dried tissue samples using a  
115 cetyl-trimethyl ammonium bromide (CTAB) extraction method. Sequences were  
116 generated from the mitochondrial encoded cytochrome c oxidase III gene (*cox3*)  
117 following Vieira et al. (2014), and from two chloroplast genes (*psbA*, *rbcL*) for the  
118 new lineages identified with *cox3*. New sequences were added to the datasets from  
119 Vieira et al. (2020a) including all *Lobophora* species for which sequences are  
120 available, and aligned using MUSCLE (Edgar, 2004). Bayesian inference and  
121 maximum likelihood phylogenetic trees were generated with *cox3*, *psbA* and *rbcL*  
122 following Vieira et al. (2016). Morphological observations included analyses of the  
123 external and internal structures following Vieira et al. (2014).

124

## 125 **3. Results**

### 126 *3.1. Molecular phylogenetic analyses*

127 A total of 122 sequences (72 *cox3*, 24 *psbA*, 26 *rbcL*) were generated from 72  
128 specimens (Table S2). Specimens collected in this study positioned in 19 well-  
129 supported lineages in both ML and BI trees (Figs 1, 2, A.1-6), including seven  
130 previously described species: *L. boussoleae* C.W.Vieira & C.Payri, *L. dagamae*  
131 C.W.Vieira, *L. dichotoma* (Simons) P.C.Silva, *L. dispersa* O.Camacho, Freshwater &  
132 Fredericq, *L. endeavouriae* C.W.Vieira, *L. isselii* (Picc. & Grunow) C.W.Vieira, De  
133 Clerck & C.Payri and *L. lessepsiana* C.W.Vieira; four previously recorded  
134 undescribed lineages: *L. sp20*, *L. sp25*, *L. sp35* and *L. sp45*; and eight new lineages:  
135 *L. obscura*10, *L. sp104*, *L. sp113*, *L. sp114*, *L. sp115*, *L. sp116*, *L. sp117* and *L.*  
136 *sp118*. Taking into consideration previous studies, the 44 western Indian Ocean  
137 lineages identified so far comprise seven singletons (i.e., lineages represented by only  
138 one specimen; *L. sp46*, *L. sp47*, *L. sp59*, *L. sp60*, *L. sp68*, *L. sp76*, *L. sp83*) and seven  
139 doubletons (i.e., lineages represented by two specimens; *L. sp26*, *L. sp48*, *L. sp52*, *L.*  
140 *sp53*, *L. sp70*, *L. sp79*, *L. sp104*). In line with previous studies we equate these  
141 lineages as species (Vieira et al. 2016).

### 142 3.2. Taxonomic results

143 We describe 15 new species of *Lobophora* from the western Indian Ocean, for  
144 which we had enough material and at least two sequenced specimens: *L. africana* sp.  
145 nov., *L. antsirananaensis* sp. nov., *L. bandeirae* sp. nov., *L. erythraea* sp. nov., *L.*  
146 *evanii* sp. nov., *L. flabellata* sp. nov., *L. garyi* sp. nov., *L. gloriosa* sp. nov., *L. henae*  
147 sp. nov., *L. kimiae* sp. nov., *L. madagascariensis* sp. nov., *L. maldivensis* sp. nov., *L.*  
148 *novae* sp. nov., *L. soaresii* sp. nov. and *L. zmaragdina* sp. nov. (Taxonomic treatment  
149 section; Table 1; Figs 4-6, A.7). In addition, we provide more detailed descriptions of  
150 *L. dichotoma* and *L. isselii* based on South African and Malagasy materials,  
151 respectively (Fig. A.7A-J). Anatomical and morphological data are also provided for

152 the remaining undescribed species from the Western Indian Ocean (Figs 6, A.7, Table  
153 1).

### 154 3.3. Biogeography

155 A total of four species are reported from the Agulhas province, 32 from the  
156 western Indian Ocean *s.s.*, two from the Somali/Arabian region, eight from the Red  
157 Sea, two from the West and South Indian Shelf and three from the Central Indian  
158 Ocean Islands. It should be noted that species reported from the Agulhas province  
159 were found only ca. 20 km south of the Western Indian Ocean/Agulhas provinces  
160 boundary (Fig. 3). The southernmost distribution limit of *Lobophora* inferred from  
161 this study is situated at Mission Rocks, KwaZulu-Natal, South Africa (*L. dagamae*; -  
162 28.276568, 32.505798) (red line in Fig. 3). No molecular data are available so far  
163 from the Bay of Bengal and Andaman provinces. However, *Lobophora minima* was  
164 described from the Andaman province and only reported from that area using  
165 morphological criteria only (Fig. 3). Among the 44 species of *Lobophora* documented  
166 to date from the western Indian Ocean, 29 are restricted to this region, four species  
167 (including *L. lessepsiana*, which is introduced in the eastern Mediterranean Sea) occur  
168 in the Atlantic Ocean and 13 in the broader Indo-Pacific Ocean. A total of nine  
169 species are recorded for South Africa.

170

## 171 4. Discussion

172 This study significantly improves our knowledge of *Lobophora* species  
173 diversity and biogeography in the western Indian Ocean.

### 174 4.1. Diversity

175           With 44 recorded *Lobophora* species, the western Indian Ocean represents the  
176 second most diverse region of the world for this genus, after the Central Indo-Pacific  
177 with 60 species (Vieira et al., 2017). Samples have been collected from 15 “countries”  
178 (*sensu* NCBI country list; <https://www.ncbi.nlm.nih.gov/genbank/collab/country>) in  
179 the western Indian Ocean: Egypt, Europa Island, Glorioso Islands, Israel, Juan de  
180 Nova Island, Kenya, Madagascar, Maldives, Mayotte, Oman, Réunion, Saudi Arabia,  
181 South Africa, Sri Lanka and Tanzania.

182           Of these 44 species, 36 were previously reported from the western Indian  
183 Ocean (Steen et al., 2015; Vieira et al., 2017; Vieira et al., 2016) and eight are newly  
184 reported. A total of 30 species are now formerly described: *L. africana* sp. nov., *L.*  
185 *antsiranensis* sp. nov., *L. asiatica*, *L. bandeirae* sp. nov., *L. boussoleae*, *L.*  
186 *ceylanica*, *L. challengeriae*, *L. dagamae*, *L. dichotoma*, *L. dispersa*, *L. endeavouriae*,  
187 *L. erythraea* sp. nov., *L. evanii* sp. nov., *L. flabellata* sp. nov., *L. garyi* sp. nov., *L.*  
188 *gibbera*, *L. gloriosa* sp. nov., *L. hena* sp. nov., *L. isselii*, *L. kimiae* sp. nov., *L.*  
189 *lessepsiana*, *L. madagascarensis* sp. nov., *L. maldivensis* sp. nov., *L. novae* sp. nov.,  
190 *L. providenceae*, *L. rickeri*, *L. rosacea*, *L. setchellii*, *L. soaresii* sp. nov. and *L.*  
191 *zmaragdina* sp. nov.; and 14 species remain undescribed: *L. sp26*, *L. sp46*, *L. sp47*, *L.*  
192 *sp52*, *L. sp53*, *L. sp59*, *L. sp60*, *L. sp68*, *L. sp70*, *L. sp76*, *L. sp79*, *L. sp83*, *L. sp104*,  
193 and *L. sp118*. Additional material is needed for the description of these remaining  
194 species.

195           Species diversity patterns across the western Indian Ocean still reflect uneven  
196 sampling across the region with a greater effort in the western Indian Ocean *s.s.* A  
197 more detailed perspective of the diversity in this region will require additional  
198 sampling in the following provinces: Somali/Arabian, Red Sea, West and South



199 Indian Shelf, Central Indian Ocean Islands, as well as in the Bay of Bengal and  
200 Andaman provinces where no data are yet available.

201         We provide the first report of *L. isselii* outside of the Red Sea. Type material  
202 was examined and sequenced from Massawa, Egypt by Vieira et al. (2016), which  
203 resulted in the transfer of *Zonaria isseli* to the genus *Lobophora*. The short *rbcL*  
204 fragments sequenced from the type collections (W19388, W19390) formed a distinct  
205 lineage with no correspondence to available data in Vieira et al. (2016). Specimens  
206 from northern Madagascar unequivocally matched *L. isselii* Type material sequences,  
207 indicating that the species may be distributed across the East African coast.  
208 *Lobophora isselii* specimens collected from Madagascar conformed to the original  
209 description (Piccone and Grunow *in* Piccone, 1884), morphologically, anatomically  
210 and ecologically by growing encrusted on mollusk shells, but also on rocks, and live  
211 and dead corals (Figs 4K, L, A.7B).

212         Our overall knowledge of seaweed diversity in the western Indian Ocean is  
213 fragmentary and often reflects the level of taxonomic effort. Countries such as India,  
214 Kenya, Madagascar, Mauritius, South Africa and Tanzania have received greater  
215 attention with a known diversity ranging between 400 to 800 species (Fig. 3; Bolton  
216 et al., 2012; Bolton et al., 2007; Bolton and Stegenga, 2002; Bolton et al., 2003; Oza  
217 and Zaidi, 2001; Vieira et al., 2021), while the known diversity in neighboring  
218 countries such as Somalia, Mozambique and seas surrounding the Arabian peninsula  
219 is half that (Bolton et al., 2007). The situation is similar for patterns of species  
220 diversity in the genus *Lobophora* in the western Indian Ocean, based on previous  
221 literature and this study. At present the diversity documented from these under-  
222 sampled regions is very low, with two to three species reported from the  
223 Somali/Arabian, Central Indian Ocean Islands and West and South Indian Shelf

224 provinces (Fig. 3). *Lobophora indica* (M.U.Rao) V.Krishnam. & Baluswami,  
225 described from Neil Island (Andaman Islands, India), is the only species so far  
226 reported from the Andaman province, but no molecular data is yet available for this  
227 species.

#### 228 4.2. Distribution

229 The southernmost distribution limit of *Lobophora* (red line in Fig. 3) occurs in  
230 the northern part of the Agulhas Province, ca. 20 km south of the boundary with the  
231 western Indian Ocean *s.s.* according to Spalding et al. (2007), in the vicinity of Saint  
232 Lucia 135 km south of the Mozambique border. Despite many sampling campaigns,  
233 no *Lobophora* species have been collected further south in the Agulhas province.  
234 Samples in herbaria (BOL, GENT, PMB) have sometimes been labeled as *Lobophora*  
235 from sites further south of Mission Rocks within the Agulhas province, but  
236 corresponded to other Dictyotales genera (e.g. *Distromium*). This distribution limit  
237 corresponds to the major biogeographic transition from a tropical Indian Ocean to a  
238 temperate South African seaweed flora (Bolton et al., 2004; Sink et al., 2005) and  
239 marks the minimum thermal tolerance (*ca.* 20°C minimum monthly mean) of  
240 *Lobophora* species from the western Indo-Pacific, as also observed on the East coast  
241 of North America (Vieira et al., 2020b).

242 Distribution patterns indicate climate affinities (i.e., subtropical and tropical  
243 affinities) among the *Lobophora* species from western Indian Ocean. Thirteen species  
244 present clear tropical-fringe or subtropical affinities, with minimum low temperatures  
245 of *ca.* 20°C, in the southern (South Africa, Réunion) and northern hemispheres (Red  
246 Sea): *L. dagamae* (Macaronesia, South Africa), *L. dichotoma* (Mozambique, South  
247 Africa, southern Madagascar), *L. dispersa* (Mozambique, South Africa, southern  
248 Madagascar, North Greater Caribbean), *L. lessepsiana* (North Red Sea), *L. rickeri*

249 (Australia, Réunion), *L. erythraea* (North Red Sea), *L. flabellata* (South Africa,  
250 southern Madagascar), *L. sp53* (North Red Sea), *L. sp59* (North Red Sea), *L. sp70*  
251 (Réunion), *L. sp104* (South Africa) and *L. sp118* (North Red Sea). The only  
252 subtropical species present in both hemispheres are those that crossed to the Atlantic  
253 (*L. dagamae*, *L. dispersa*). Seven species are distributed in subtropical and tropical  
254 waters: *L. asiatica* (Australia, China, Japan, Malaysia, New Caledonia, South Africa,  
255 Vietnam), *L. boussoleae* (Egypt, Malaysia, Papua New Guinea, Philippines), *L.*  
256 *endeavouriae* (Australia, Egypt, Israel, Japan, Juan de Nova, Mayotte, New  
257 Caledonia, Papua New Guinea), *L. obscura6* (Oman, southern Madagascar, South  
258 Africa), *L. kimiae* (South Africa, northern Madagascar), *L. sp45* (Kenya,  
259 Mozambique, southern Madagascar) and *L. sp52* (Glorioso, Japan). The remaining 24  
260 species are restricted to tropical waters.

261 A mixture of subtropical and tropical species characterizes the South African  
262 *Lobophora* flora. Except for *L. sp104*, restricted to South Africa, the subtropical  
263 species can be found in southern Madagascar (*L. dichotoma*, *L. flabellata*, *L.*  
264 *dispersa*), Juan de Nova (*L. novae*) and in the Atlantic (*L. dagamae*, *L. dispersa*). The  
265 other species are found in tropical localities such as in northern Madagascar (*L.*  
266 *kimiae*), Oman (*L. zmaragdina*; and also southern Madagascar). In this regard, South  
267 Africa is a region of overlap between the Atlantic and Indian Ocean, and between  
268 tropical and subtropical *Lobophora* species. Similar conclusions were made on the  
269 transitional overlap (Subtropical Natal Province) between the tropical and subtropical  
270 regions for rocky intertidal and shallow subtidal communities (Bolton et al., 2004;  
271 Porter et al., 2013; Sink et al., 2005). Southern Madagascar shares more species of  
272 *Lobophora* in common with South Africa (five species; *L. dichotoma*, *L. dispersa*, *L.*  
273 *obscura6*, *L. kimiae*, *L. flabellata*) than with northern Madagascar (one species; *L.*

274 *kimiae*) stressing the importance of thermal affinities in structuring *Lobophora*  
275 species distribution. Biogeographic links among similar climate but disjunct regions  
276 have been shown in other groups across the three main seaweed classes within the  
277 Indian Ocean, e.g., in *Sargassum* (Fucales, Phaeophyceae; Mattio et al., 2015),  
278 *Laurencia* (Ceramiales, Rhodophyceae; Francis et al., 2017), *Pseudocodium*  
279 (Bryopsidales, Ulvophyceae; De Clerck et al., 2008), supported by molecular data.

280         Given the current sampling, only one species, *L. setchellii*, displays a broad  
281 distribution, spanning three oceans (Vieira et al., 2020b; Fig. 7). However, Vieira et  
282 al. (2020b) advised undertaking additional molecular analyses to elucidate if this  
283 broad distribution is the result of multiple introductions (broad human or natural  
284 dispersal) or if this cosmopolitan species constitutes a species complex and is similar  
285 to *L. obscura*, which is widespread across the Indo-Pacific but absent from the  
286 Atlantic. Note that *Lobophora variegata*, widely reported from many world regions in  
287 the past, was not identified from the western Indian Ocean, further confirming its  
288 restriction to the Caribbean Sea (Vieira et al., 2020b).

289         This high percentage of *Lobophora* species restricted to the western Indian  
290 Ocean (see below; Fig. 7) is evidence for a floristic distinction common to many other  
291 seaweed floras, which often differ markedly from those in other Indian Ocean  
292 countries (Bolton et al., 2007). Compared to other groups of seaweeds (Bolton et al.,  
293 2007), *Lobophora* from the western Indian Ocean shares closest links with the rest of  
294 the Indo Pacific, but presents limited affinities with the Atlantic (see below; Fig. 7).  
295 However, we know almost nothing about *Lobophora* diversity in West Africa. John et  
296 al. (2003) reported three forms of *L. variegata* (erect, semi-erect and closely adherent  
297 forms) from the tropical West Africa sub-region, which most likely correspond to  
298 several different species non-conspecific with *L. variegata*. While Bolton et al. (2007)

299 found similarities among seaweed floras in southeastern African countries (Kenya,  
300 Tanzania, Madagascar, South Africa), and specificities such as the Kenyan flora,  
301 which produces a distinct grouping of seaweed floras, our dataset is at present  
302 inadequate to further discuss affinities of *Lobophora* species among these countries.

### 303 4.3. Endemism

304 A total of 29 species are geographically restricted to the western Indian Ocean  
305 *s.l.*, which represents *ca.* 65% of the regional diversity documented so far (Fig. 7). In  
306 relation to the total number of species, this level is comparable – although slightly  
307 higher – to the Greater Caribbean (11 of the 18 species) and the Central Indo-Pacific  
308 (37 of the 60 species) (Vieira et al., 2017; Vieira et al., 2020b).

309 While *Lobophora* species from the eastern African coast are broadly  
310 distributed (except for *L. sp104* restricted to South Africa) across the western Indian  
311 Ocean (Fig. 7), a total of 15 species are geographically restricted to the western Indian  
312 Ocean islands: *L. sp52* and *L. sp83* in Glorioso Islands; *L. sp79* in Mayotte; *L. sp26*,  
313 *L. sp46*, *L. sp47* and *L. sp60* in Europa Island; *L. antsiranensis*, *L. evanii*, *L. garyi*,  
314 *L. hena*, *L. madagascarensis*, and *L. soaresii* in Madagascar; *L. maldivensis* in the  
315 Maldives; and *L. sp76* in Réunion. A more comprehensive sampling in the western  
316 Indian Ocean may allow concluding if these numbers reflect high endemism  
317 characteristic of western Indian Ocean islands.

318 Eight species were found in the Red Sea, including five restricted to this  
319 region (*L. lessepsiana*, *L. sp53*, *L. sp59*, *L. sp118*). *Lobophora lessepsiana* is the only  
320 species found to date across the Red and Mediterranean Seas as a result of migration  
321 via the Suez Canal from the Red Sea (Vieira et al., 2018). *Lobophora endeavouriae*  
322 and *L. isselii* are the only species distributed in the Red Sea and in the western Indian  
323 Ocean.

#### 324 4.4. Oceanic dispersal barrier

325           Only ~9% (four species including one Lessepsian migrant species) of the  
326 species from the western Indian Ocean *s.l.* are shared with the Atlantic (Figs 3, 7), and  
327 ~30% (13 species) with the Central Indo-Pacific (Figs 3, 7). These data emphasize the  
328 role of oceanic dispersal barriers in *Lobophora* distributions. One species, *L.*  
329 *lessepsiana*, crossed the Suez Canal from the Red Sea to the Mediterranean Sea  
330 (Vieira et al., 2018), and the other three species (*L. dagamae*, *L. dispersa*, *L.*  
331 *setchellii*) that cross the Atlantic/Indian Ocean boundary are all sister to Indo-Pacific  
332 species and present subtropical affinities. This limited number of species distributed  
333 across the western Indo-Pacific and Atlantic Oceans indicates that environmental  
334 factors such as the Benguela and Agulhas currents and the Benguela upwelling  
335 system, which is associated with an abrupt drop in mean sea surface temperature west  
336 of the southern tip of South Africa (Teske et al., 2008), have acted as efficient  
337 historical and modern dispersal barriers. Note, however, that while the drop in mean  
338 sea surface temperature is a relatively recent geological phenomenon (>1 Mya;  
339 Romero et al., 2003), time divergence between these Atlantic/Indian Ocean species  
340 pairs are of older dates ranging between ~5-20 Mya (Vieira et al., 2017).

341           While the western Indian Ocean Islands may support numerous endemic  
342 *Lobophora* species, connectivity is also prominent among western Indian Ocean  
343 Islands with the rest of the western Indian Ocean (*ca.* 40% of western Indian Ocean  
344 species) (Fig. 7).

345           The distribution of 13 species across the Indian Ocean, between the western  
346 Indian Ocean *s.l.* and the Central Indo-Pacific, indicates connectivity between these  
347 regions (Figs 3, 7). Only one species is shared with Australia, *L. rickeri* indicating  
348 that long-dispersal events between Australia and the western Indian Ocean are rare.

349 Disjunct geographic distribution between distant subtropical regions across the Indian  
350 Ocean have been reported in other seaweeds, such as *Pseudocodium*, also supported  
351 by molecular data (De Clerck et al., 2008).

#### 352 4.5. Evolution and historical biogeography

353 From our current understanding of diversity and species' ranges, *Lobophora*  
354 species diversity in the western Indian Ocean is the result of repeated establishments  
355 from the Central Indo Pacific, followed by local diversification (Vieira et al. 2017), a  
356 pattern that has been inferred for other seaweed groups, including the red alga  
357 *Portieria* (Leliaert et al., 2018). In turn, the western Indian Ocean supplied the Central  
358 Indo-Pacific (>10 species; Vieira et al. 2017) as well as the Atlantic, through the  
359 limited number of species that managed crossing the Atlantic/Indian Ocean boundary  
360 (Vieira et al., 2017; Vieira et al., 2020b), and colonized the Atlantic and diversified  
361 regionally. The high level of "endemism" (29 species; ca. 65% of western Indian  
362 Ocean diversity) may be to a large extent due to isolation by distance on western  
363 Indian Ocean islands and in the Red Sea.

364

### 365 5. Taxonomic treatments

366 5. 1. *Lobophora africana* C.W.Vieira & M.Zubia, sp. nov. (Figs 5A, 6A)

367 **Description:** Thallus coarse, predominantly decumbent, light to dark brown in color,  
368 up to 11 cm wide and 5 cm tall, 304-436  $\mu\text{m}$  thick, attached to the substratum by  
369 ventral rhizoids. Margins entire. Structure with 14-19 cell layers: a single-cell-layered  
370 medulla, a dorsal cortex of 7-10 cell layers, and a ventral cortex of 5 to 8 cell layers.

371 TYPE: Juan de Nova, North West of Juan de Nova Island, 13 Dec 2013, *Zubia 5560*  
372 (UPF, holotypus) 5663 (UPF, isotypus).

373 **Representative DNA sequences:** KU353190 (*cox3*, from the holotype) and  
374 KU353024 (*rbcL*, from the holotype).

375 **Etymology:** The specific epithet *africana* pertains to its African origin.

376 **Diagnostic characters:** The species was distinctive from sympatric species in the  
377 decumbent growth habit, coarse thallus, light to dark brown color, ecological habit  
378 growing on hard substrates, and the distinctive DNA sequences.

379 **Distribution and habitat:** Juan de Nova and Tanzania. Growing on hard substrate at  
380 15-20 m depth.

381 **Additional collections examined:** Juan de Nova. North West of Juan de Nova Island,  
382 14 Dec 2013, *Maya JN209* (UPF).

383 **Remarks:** This species corresponds to *Lobophora* sp42 of Vieira et al. (2016)

384 5. 2. *Lobophora antsirananaensis* C.W.Vieira & F.A.Rasoamanendrika, sp. nov. (Figs  
385 4A, 5B, 6B)

386 **Description:** Thallus procumbent to decumbent, up to 6 cm wide and 3.5 cm tall, 55-  
387 73  $\mu\text{m}$  thick, dark orange in color with darker concentric lines, attached to the  
388 substratum by ventral rhizoids. Margins entire. Structure with 5-6 cell layers: a single-  
389 cell-layered medulla, a dorsal cortex of 2-3 cell layers, and a ventral cortex of 2 cell  
390 layers.

391 **TYPE:** Madagascar, Antsiranana Bay, Orangea, 21 Nov 2018, *Vieira and*  
392 *Rasoamanendrika BR5010179404610V* (BR, holotypus), *BR5010175853719V* (BR,  
393 isotypus).

394 **Representative DNA sequences:** MW510173 (*cox3*, from the holotype), MW510999  
395 (*psbA*, from the holotype) and MW511032 (*rbcL*, from the holotype).

396 **Etymology:** The specific epithet *antsirananaensis* pertains to the Type locality,  
397 Antsiranana, meaning in its native language “the place where salt is produced”.



398 **Diagnostic characters:** The species was distinctive from sympatric species in the  
399 decumbent growth habit, thallus thickness, dark orange color with darker concentric  
400 lines, ecological habit growing in seagrass beds on other seaweeds, and the distinctive  
401 DNA sequences.

402 **Distribution and habitat:** Madagascar. Growing on other macroalgae in seagrass  
403 beds down to 1 m depth.

404 5. 3. *Lobophora bandeirae* C.W.Vieira, De Clerck & Leliaert, sp. nov. (Figs 5C, 6C)

405 **Description:** Thallus forming small rosette, brown in color with concentric lines, up  
406 to 10 cm wide and 7 cm tall, 98-100  $\mu\text{m}$  thick, attached to the substratum by basal  
407 rhizoids. Margins entire. Structure with 7 cell layers: a single-cell-layered medulla  
408 and dorsal and ventral cortices of 3 cell layers.

409 TYPE: Mozambique, Inhambane, Tofo, Marble Arch, 30 Apr 2018, *De Clerck and*  
410 *Leliaert BR5010109465490V* (BR, holotypus).

411 **Representative DNA sequences:** MW996659 (*cox3*, from the holotype) and  
412 MW996679 (*psbA*, from the specimen BR5010109445478V).

413 **Etymology:** The specific epithet *bandeirae* derives from the Mozambican phycologist  
414 Salomão Bandeira.

415 **Diagnostic characters:** The species was distinctive from sympatric species in  
416 forming dense rosette and the distinctive DNA sequences.

417 **Distribution and habitat:** Kenya, Madagascar, Mozambique. Growing on hard  
418 substrate down to 20 m depth.

419 **Additional collections examined:** Kenya. Mombasa, Nyali, Mc Kenzie Point, 4 Apr  
420 2008, *De Clerck ODC1647* (BR).

421 Madagascar. Anosy, Phare Flacourt, 29 Apr 2010, *Anderson, Coppejans, de Reviers,*  
422 *Le Gall, Rousseau and Tsarahevitra MAD0109, MAD0110* (PC); Anosy, Baie des

423 Gallions, 12 May 2010, *Anderson, Coppejans, de Reviere, Le Gall, Rousseau and*  
424 *Tsarahevitra MAD1641* (PC); Anosy, Sainte Luce, 4 Jun 2010, *Anderson, Coppejans,*  
425 *de Reviere, Le Gall, Rousseau and Tsarahevitra MAD2068* (PC).

426 Mozambique. Inhambane, Tofo, Crocodile Rock, 29 Apr 2018, *De Clerck and*  
427 *Leliaert BR5010109419561V* (BR); Zavora, Witches Hat, 5 May 2018, *De Clerck and*  
428 *Leliaert BR5010109228484V, BR5010109445478V, BR5010109063313V* (BR);  
429 Zavora, Deep Reef South, 6 May 2018, *De Clerck and Leliaert BR5010109193379V*  
430 (BR); Zavora, Great Wall South, 9 May 2018, *De Clerck and Leliaert*  
431 *BR5010109662462V* (BR).

432 **Remarks:** This species corresponds to *Lobophora* sp45 of Vieira et al. (2016)

433 5. 4. *Lobophora dichotoma* (Simons) P.C.Silva (Fig. 4C, 5E, Fig. A.7J, K)

434 **References:** Simons (1966): Fig. 1, Silva et al. (1996), Vieira et al. (2016): Figs. 3M-  
435 P, 4O-P.

436 **Basionym:** *Pocockiella dichotoma* Simons (1966).

437 **TYPE:** South Africa, Kwazulu-Natal, Kosi Bay, Ingwavuma *Meyer sub Simons*  
438 *150036* (BOL, holotypus); South Africa, Ribbon Reef, Sodwana Bay, Oct 2013,  
439 *Bolton, Anderson and Mattio 150668* (BOL, epitypus).

440 **Diagnosis:** Thallus erect, either fan shaped entire to multi-lobed up to 3.5 cm wide  
441 and 3 cm tall, or dichotomous with strap-shaped branches up to 10 cm tall, 117-140  
442 µm thick, green to light brown in color with white margin. Attached to substratum by  
443 multicellular brown rhizoids forming a stupose mat. One individual can present both  
444 morphotypes. Structure with 8-9 cell layers: a single-cell-layered medulla, a dorsal  
445 cortex of 7-8 cell layers, and a ventral cortex of 6-8 cell layers.

446 The species was distinctive from sympatric species in its dichotomous strap-shaped  
447 branches and the distinctive DNA sequences.

448 **Representative DNA sequences:** KU353394 (*cox3*, from the epitype); KU353000  
449 (*psbA*, from the epitype) and KU352970 (*rbcL*, from the epitype).

450 **Distribution and habitat:** Madagascar, Mozambique, South Africa. Growing on hard  
451 substrate down to 20 m depth.

452 **Additional specimens examined.** South Africa. Sodwana Ribbon Reef, Bangha Nek,  
453 24 Mar 2013, *Bolton, Anderson and Mattio LMD1006* (BOL); KwaZulu Natal,  
454 Mabibi, 18 Jan 2016, *De Clerck, Anderson, Boothroyd, and Rothman KZN16-316*  
455 (BOL); KwaZulu Natal, Island Rock, 18 Jan 2016, *De Clerck, Anderson, Boothroyd,*  
456 *Rothman KZN16-328, KZN16-330* (BOL).

457 Mozambique. Inhambane, Tofo, 1 May 2018, *De Clerck and Leliaert MOZ18-100*  
458 (GENT).

459 **Remarks:** This species corresponds to *Lobophora* sp36 of Vieira et al. (2016).

460 5. 5. *Lobophora erythraea* C.W.Vieira, sp. nov. (Figs 5F, 6D)

461 **Description:** Thallus predominantly procumbent, light brown in color, 190-232 µm  
462 thick, attached to the substratum by basal rhizoids. Margins entire. Structure with 8-9  
463 cell layers: a single-cell-layered medulla, a dorsal cortex of 4-3, and a ventral cortex  
464 of 4 cell layers.

465 **TYPE:** Saudi Arabia, Aqaba Golf, Magna, 29 Sep 2013, *Andrefouët 201604* (NOU,  
466 holotypus).

467 **Representative DNA sequences:** KU353098 (*rbcL*, from the holotype).

468 **Distribution and habitat:** Egypt, Saudi Arabia. Growing on bedrock, dead corals,  
469 basal dead parts of corals such as *Porites* and *Millepora*.

470 **Etymology:** The specific epithet erythraea pertains to its Erythrean (Red Sea) origin.

471 **Diagnostic characters:** The species was distinctive from sympatric species in the  
472 procumbent growth habit, light brown color, thallus thickness, ecological habit  
473 growing on hard substratum, and the distinctive DNA sequences.

474 **Additional specimens examined.** Egypt. Marsa Shagra, 6-12 Jun 2019, *Engelen*  
475 *AZO04, AZO54, AZO76* (GENT).

476 **Remarks:** this species corresponds to *Lobophora* sp20 of Vieira et al. (2016).

477 5. 6. *Lobophora evanii* C.W.Vieira & F.A.Rasoamanendrika, sp. nov. (Figs 4F, 5G,  
478 6E)

479 **Description:** Thallus fan shaped, predominantly procumbent, up to 3 cm wide and 2.5  
480 cm tall, 90-135  $\mu$ m thick, homogenously vivid orange in color. Attached to the  
481 substratum by basal ventral rhizoids. Margin entire. Structure with 5-8 cell layers: a  
482 single-cell-layered medulla, and dorsal and ventral cortices of 2-3 cell layers.

483 **TYPE:** Madagascar, Antsiranana Bay, Orangea, 21 Nov 2018, *Vieira and*  
484 *Rasoamanendrika*, *BR5010179403583V* (BR, holotypus), *BR5010175852682V*,  
485 *BR5010175851654V*, *BR5010175850626V*, *BR5010175849880V* (BR, isotypi).

486 **Representative DNA sequences:** MW510212 (*cox3*, from the holotype), MW511014  
487 (*psbA*, from the holotype) and MW511027 (*rbcL*, from the holotype).

488 **Distribution and habitat:** Madagascar. Growing on dead coral branches, live corals  
489 (e.g., brain corals), soft-corals, bedrock.

490 **Etymology:** The specific epithet *evanii* derives from the name of the first author's  
491 son, Evan Vieira.

492 **Diagnostic characters:** The species was distinctive from sympatric species in the  
493 procumbent growth habit, vivid orange color, thallus thickness and the distinctive  
494 DNA sequences.

495 5. 7. *Lobophora flabellata* C.W.Vieira, De Clerck, R.J.Anderson & J.J.Bolton, sp.

496 nov. (Figs 4G, 5H, 6F, A.7A)

497 **Description:** Thalli in dense erect blades, up to 11 cm tall, 186-246 µm thick,  
498 medium to dark brown with darker irregular concentric lines. Fronds composed of  
499 several lobes, stipitate, anchored by an obvious holdfast. Margins entire. Structure  
500 with 11-15 cell layers: a single-cell-layered medulla, a dorsal cortex of 5-8 cell layers,  
501 a ventral cortex of 5-6 cell layers.

502 **TYPE:** South Africa, Bhanga Nek, South end of Saxon reef, 3 Oct 2013, *Bolton,*  
503 *Anderson and Mattio 201535* (NOU, holotypus), *201536* (NOU, isotypus).

504 **Representative DNA sequences:** KU353355 (*cox3*, from the holotype) and  
505 KU352865 (*psbA*, from the holotype).

506 **Etymology:** The specific epithet is from the Latin flabellate, ‘fan-shaped’, referring to  
507 the shape of the thallus.

508 **Diagnostic characters:** The species is distinguished from sympatric species by the  
509 dense erect blades, medium to dark brown thallus color with darker irregular  
510 concentric lines.

511 **Distribution and habitat:** Madagascar, South Africa. Growing on sand between 0-20  
512 m depth.

513 **Additional collections examined:** Madagascar. Lavanono, 17 May 2010, *Anderson*  
514 *et al.* MAD1787 (GENT); Pointe d'Ambero, Anosy, 5 May 2010, *Anderson et al.*  
515 MAD0382 (GENT); Pointe d'Ambero, Anosy, 14 May 2010, *Anderson et al.*  
516 MAD1674 (GENT); Rocher de l'Albatros, Beloha, 18 May 2010, *Anderson et al.*  
517 MAD181 (GENT); Lagon de Baravo, Tulear, 28 May 2010, *Anderson et al.*  
518 MAD1991 (GENT).

519 South Africa. KwaZulu Natal, Sodwana Bay, Ribbon Reef, 24 Mar 2011, *Anderson*  
520 RA1007 (PC); KwaZulu Natal, Mabibi, 12 Jan 2016, *De Clerck KZN16-139* (BOL);  
521 KwaZulu Natal, Sodwana Bay, 9-Mile Reef, 14 Jan 2016, *De Clerck and Rothman*  
522 *KZN16-190* (BOL); KwaZulu Natal, Sodwana Bay, Island Rock, 14 Jan 2016, *De*  
523 *Clerck and Rothman KZN16-205* (BOL); KwaZulu Natal, Mabibi, 17 Jan 2016, *De*  
524 *Clerck, Anderson, Boothroyd and Rothman KZN16-263* (BOL); KwaZulu Natal,  
525 Mabibi, 18 Jan 2016, *De Clerck, Anderson, Boothroyd, and Rothman KZN16-317*  
526 (BOL).

527 5. 8. *Lobophora garyi* C.W.Vieira & F.A.Rasoamanendrika, sp. nov. (Figs 4H, 5I,  
528 6G)

529 **Description:** Thallus predominantly decumbent to crustose, up to 3.5 cm wide and 3  
530 cm tall, 68-85  $\mu\text{m}$  thick, brown to light green radial gradient in color speckled with  
531 darker small spots, attached to the substratum by basal ventral rhizoids. Margins  
532 entire. Structure with 5 cell layers: a single-cell-layered medulla, and dorsal and  
533 ventral cortices of 2 cell- layers.

534 **TYPE:** Madagascar, Antsiranana Bay, Baie de Tonnerre, 20 Nov 2018, *Vieira and*  
535 *Rasoamanendrika BR5010179402555V* (BR, holotypus), *BR5010175848852V*,  
536 *BR5010175847824V* (BR, isotypi).

537 **Representative DNA sequences:** MW510172 (*cox3*, from the holotype), MW511006  
538 (*psbA*, from the holotype) and MW511031 (*rbcL*, from the holotype).

539 **Distribution and habitat:** Madagascar. Growing on dead coral branches, down to 1  
540 m depth.

541 **Etymology:** The specific epithet *garyi* derives from the name of the first author's son,  
542 Gary Vieira.

543 **Diagnostic characters:** The species was distinctive from sympatric species in the  
544 decumbent to crustose growth habit, brown to light green radial color speckled with  
545 darker small spots, thin thallus, growing on dead coral branches, and the distinctive  
546 DNA sequences.

547 *5. 9. Lobophora gloriosa* C.Vieira & M.Zubia, sp. nov. (Figs 4I, 5J, 6H)

548 **Description:** Thallus coarse, predominantly decumbent, up to 7 cm wide and 7 cm  
549 tall, 410-503  $\mu\text{m}$  thick, medium to light brown in color with lighter margins, attached  
550 to the substratum by basal rhizoids. Margins entire. Structure with 21-22 cell layers: a  
551 single-cell-layered medulla, a dorsal cortex of 11-12 cell layers, and a ventral cortex  
552 of 8- 9 cell-layers.

553 **TYPE:** Glorioso Islands, Grande Glorieuse 7-15 Dec 2008, *Zubia 5561* (UPF,  
554 holotypus), *5664*, *5665* (UPF, isotypi).

555 **Representative DNA sequences:** KU353185 (*cox3*, from the holotype), KU352940  
556 (*psbA*, from the holotype) and KU353025 (*rbcL*, from the holotype).

557 **Distribution and habitat:** Glorioso Islands, Maldives. Growing on hard substrate  
558 between 0-15 m depth.

559 **Etymology:** The specific epithet *gloriosa* pertains to the Type locality.

560 **Diagnostic characters:** The species was distinctive from sympatric species in the  
561 decumbent growth habit, coarse thallus, light brown color, and the distinctive DNA  
562 sequences.

563 **Additional specimens examined.** Glorioso Islands. Grande Glorieuse, 7-15 Dec  
564 2008, *Zubia GLO038* (UPF).

565 Maldives. Baa Atoll, 28 May 2009, *Payri IRD4590* (NOU).

566 **Remarks:** this species corresponds to *Lobophora* sp23 of Vieira et al. (2016).

567 5. 10. *Lobophora hena* C.W.Vieira & F.A.Rasoamanendrika, sp. nov. (Figs 4J, 5K,  
568 6I)

569 **Description:** Thallus small, crustose to decumbent, overlapping, up to 2.5 cm wide  
570 and 2.5 cm tall, 38-63  $\mu\text{m}$  thick, light brown in color with lighter margins, attached to  
571 the substratum by ventral rhizoids. Thalli overlapping forming a mat. Margins entire.  
572 Structure with 3-5 cell layers: a single-cell-layered medulla, and dorsal and ventral  
573 cortices of 1-2 cell layers.

574 **TYPE:** Madagascar, Antsiranana Bay, Baie de Tonnerre, 20 Nov 2018, *Vieira and*  
575 *Rasoamanendrika BR5010179401527V* (BR, holotypus) *BR5010175846797V*,  
576 *BR5010175862698V*, *BR5010175861660V*, *BR5010175860632V*,  
577 *BR5010175859896V* (BR, isotypi).

578 **Representative DNA sequences:** MW510224 (*cox3*, from the holotype), MW511011  
579 (*psbA*, from the isotype *BR5010175846797V*) and MW511034 (*rbcL*, from the  
580 holotype).

581 **Distribution and habitat:** Madagascar. Growing on dead corals, bedrock and  
582 epiphytic on calcareous red algae, down to 1 m depth.

583 **Etymology:** The specific epithet *hena* derives from the name of the first author's  
584 daughter, Gaïa, Hena Vieira.



585 **Diagnostic characters:** The species was distinctive from sympatric species in the  
586 crustose to decumbent growth habit, light brown color, thin thallus, overlapping thalli,  
587 growing on hard substratum, and the distinctive DNA sequences.

588 5. 11. *Lobophora isselii* (Picc. & Grunow) C.W.Vieira, De Clerck & Payri (Figs  
589 4K,L, 5L, 6J, A.7B)

590 **References:** Piccone (1884): Fig 1-4, (Vieira et al., 2016): Figs 4I, J.

591 **Basionym:** *Zonaria isselii* Picc. & Grunow (1884)

592 **Diagnosis:** Thallus predominantly crustose, up to 3 cm wide and 2 cm tall, 93-150  
593  $\mu\text{m}$  thick, orange-brown in color speckled with small dark brown spots, attached to  
594 the substratum by basal rhizoids. Margin entire. Structure with 5-7 cell layers: a  
595 single-cell-layered medulla, a dorsal cortex of 2-3 cell layers, and a ventral cortex of 2  
596 cell layers.

597 **TYPE:** Eritrea, Massawa, 1870, *Issel sub Piccone 19388* (W, lecto.).

598 **Distribution and habitat:** Eritrea, Madagascar. Grows on rock, mollusks shells, dead  
599 and live corals (Fig. 4F, Q, R).

600 **Diagnostic characters:** The species was distinctive from sympatric species in the  
601 crustose growth habit, orange-brown color speckled with small dark brown spots,  
602 growing on rocks, corals and mollusks shells, and the distinctive DNA sequences.

603 **Additional specimens examined.** Madagascar. Antsiranana Bay, Mer d'Emeraude,  
604 23 Nov 2018, *Vieira MADA18ALG061, MADA18ALG063, MADA18ALG067,*  
605 *MADA18ALG068, MADA18ALG069, CWV2674* (BR).

606 5. 12. *Lobophora kimiae* C.W.Vieira & F.A.Rasoamanendrika, sp. nov. (Figs 4M,  
607 5M, 6K)

608 **Description:** Thallus predominantly procumbent, up to 3 cm wide and 2.5 cm tall,  
609 98-110  $\mu\text{m}$  thick, light brown in color, attached to a veneer of coarse mobile sand on  
610 rocky substrate by scattered ventral rhizoids. Margins entire. Structure with 5 cell  
611 layers: a single-cell-layered medulla, and dorsal and ventral cortices of 2 cell layers.

612 **TYPE:** Madagascar, Antsiranana Bay, Mer d'Emeraude, 21 Nov 2018, *Vieira and*  
613 *Rasoamanendrika BR5010179400490V* (BR, holotypus) *BR5010175858868V* (BR,  
614 isotypus).

615 **Representative DNA sequences:** MW510228 (*cox3*, from the holotype), MW511018  
616 (*psbA*, from the isotype) and MW511045 (*rbcL*, from the isotype).

617 **Distribution and habitat:** Madagascar, South Africa. Growing on hard and soft  
618 substrate, sand and rocks on shallow habitats, in seagrass beds, down to 1 m depth.

619 **Etymology:** The specific epithet *kimiae* derives from the name of the first author's  
620 wife, Yi Sun Kim.

621 **Diagnostic characters:** The species was distinctive from sympatric species in the  
622 procumbent growth habit on coarse mobile sand veneer, light brown color, and the  
623 distinctive DNA sequences.

624 **Additional specimens examined.** Madagascar. Antsiranana Bay, Orangea, 21 Nov  
625 2018, *Vieira and Rasoamanendrika MADA18ALG103, MADA18ALG111,*  
626 *MADA18ALG119* (BR); Fort Dauphin, Plage monseigneur Anosy, 28 Apr 2010,  
627 *Anderson et al. MAD0063* (PC).

628 South Africa. KwaZulu-Natal, Sodwana Bay, Quarter Mile Reef, 10 Apr 2009,  
629 *Anderson RA559* (PC).

630 **Remarks:** This species corresponds to *Lobophora* sp25 of Vieira et al. (2016).

631 5. 13. *Lobophora madagascariensis* C.W.Vieira & F.A.Rasoamanendrika, sp. nov.

632 (Figs 4N, 5N, 6L)

633 **Description:** Thallus predominantly crustose, coarse, up to 5 cm wide and 3 cm tall,  
634 255-310 µm thick, green khaki in color with grayish radial lines, attached to the  
635 substratum by basal mound of rhizoids. Margins entire. Structure with 15-17 cell  
636 layers: a single-cell-layered medulla, a dorsal cortex of 8-10, and a ventral cortex of  
637 5-6 cell layers.

638 **TYPE:** Madagascar, Antsiranana Bay, Baie de Tonnerre, 20 Nov 2018, *Vieira and*  
639 *Rasoamanendrika* BR5010179399824V (BR, holotypus), BR5010175857830V,  
640 BR5010175856802V, BR5010175855775V, BR5010175854747V (BR, isotypi).

641 **Representative DNA sequences:** MW510194 (*cox3*, from the holotype), MW510997  
642 (*psbA*, from the specimen MADA18ALG029) and MW511040 (*rbcL*, from the  
643 specimen MADA18ALG029).

644 **Etymology:** The specific epithet madagascariensis pertains to the Type locality.

645 **Diagnostic characters:** The species was distinctive from sympatric species in the  
646 crustose growth habit, green khaki color with grayish radial lines, coarse thallus, and  
647 the distinctive DNA sequences.

648 **Distribution and habitat:** Madagascar. Growing on bedrock, dead corals and the  
649 basal part of massive corals such as *Porites*.

650 **Additional specimens examined.** Madagascar. Antsiranana Bay, Baie de Tonnerre,  
651 20 Nov 2018, *Vieira* CWV2663, CWV2671 (BR).

652 5. 14 *Lobophora maldivensis* C.W.Vieira & Payri, sp. nov. (Figs 5O, 6M)

653 **Diagnosis:** Thallus predominantly decumbent, up to 5 cm wide and 4 cm tall, 164-  
654 260 µm thick, homogeneous dark green in color, attached to substratum by the basal  
655 part, distal part of the thallus tightly adhering or free. Structure with 8-9 cell layers: a

656 single-cell-layered medulla, a dorsal cortex of 8-4 cell layers, and a ventral cortex of 4  
657 cell layers.

658 **TYPE:** Maldives, Baa Atoll, Hithaadhoo, 28 May 2009, *Payri 201540* (NOU,  
659 holotypus), *201541* (NOU, isotypus).

660 **Representative DNA sequences:** KU353229 (*cox3*, from the holotype), KU352892  
661 (*psbA*, from the holotype) and KU353071 (*rbcL*, from the holotype).

662 **Etymology:** The specific epithet *maldivensis* pertains to the Type locality.

663 **Diagnostic characters:** The species was distinctive from sympatric species in the  
664 decumbent growth habit, homogeneous dark green color, and the distinctive DNA  
665 sequences.

666 **Distribution and habitat:** Maldives. Creeping over hard substratum in shallow area  
667 of coral reef (3m depth) mixed with other benthic organisms.

668 **Remarks:** This species corresponds to *Lobophora* sp48 of Vieira et al. (2016).

669 *5. 15. Lobophora novae* C.W.Vieira & M.Zubia, sp. nov. (Figs 4P, 5P, 6N, A.7C)

670 **Description:** Thallus flabellate, predominantly procumbent, undulated longitudinally,  
671 up to 5 cm wide and 3.5 cm tall, 60-144  $\mu\text{m}$  thick, olive-green in color with light to  
672 dark green radial stripes and speckled with dark spot forming in same individuals  
673 irregular concentric lines, attached to the substratum by basal ventral rhizoids. Margin  
674 entire. Structure with 5-7 cell layers: a single-cell-layered medulla, and dorsal and  
675 ventral cortices of 2-3 cell layers.

676 **TYPE:** Juan de Nova, South-East of Juan de Nova Island, 15 Dec 2013, *Zubia 5562*  
677 (UPF, holotypus).

678 **Representative DNA sequences:** KU353194 (*cox3*, from the holotype) and  
679 KU353042 (*rbcL*, from the holotype).

680 **Etymology:** The specific epithet novae pertains to the Type locality, Juan de Nova  
681 Island, which was named after the Portuguese-Galician explorer João da Nova (1460-  
682 1509) who came across the island in 1501.

683 **Diagnostic characters:** The species is distinguished from sympatric species by its  
684 olive-green hue, striped with lighter radial lines, speckled with dark spots and  
685 undulated thallus, and the distinctive DNA sequences.

686 **Distribution and habitat:** Juan de Nova, Mozambique, South Africa. Growing on  
687 hard substrate at 20 m depth.

688 **Additional specimens examined.** South Africa. Bhanga Nek, 5 Oct 2013, *Bolton,*  
689 *Anderson and Mattio LMD1617* (NOU); Bhanga Nek, 5 Oct 2013, *Bolton, Anderson*  
690 *and Mattio LMD1618* (NOU); KwaZulu-Natal, Sodwana Bay, 10 Jan 2007, *Anderson*  
691 *RA505* (PC); KwaZulu-Natal, Sodwana Bay, 2 Feb 2010, *Anderson RA672* (PC);  
692 KwaZulu-Natal, Mabibi, 18 Jan 2016, *De Clerck KZN16-321* (BOL).

693 Mozambique. Inhambane, Tofo, Crocodile Rock, 29 Apr 2018, *De Clerck MOZ18-*  
694 *041* (BR); Inhambane, Tofo, Marble Arch, 30 Apr 2018, *De Clerck MOZ18-071*  
695 (BR).

696 **Remarks:** This species corresponds to *Lobophora* sp35 of Vieira et al. (2016).

697 5. 16. *Lobophora soaresii* C.W.Vieira & F.A.Rasoamanendrika, sp. nov. (Figs 4Q,  
698 5Q, 6O)

699 **Description:**

700 Thallus predominantly decumbent, up to 6 cm wide and 4 cm tall, 215-285 µm thick,  
701 heterogeneous green to brown color patterns with clearer radial and concentric lines,  
702 attached to the substratum by basal ventral rhizoids. Margins entire. Structure with  
703 13-16 cell layers: a single-cell-layered medulla, a dorsal cortex of 6-8, and a ventral  
704 cortex of 6-7 cell layers.

705 **TYPE:** Madagascar, Orangea small pass, Antsiranana Bay, Madagascar, 21 Nov  
706 2018, *Vieira and Rasoamanendrika* BR5010179424632V (BR, holotypus).

707 **Representative DNA sequences:** MW510175 (*cox3*, from the holotype) and  
708 MW510995 (*psbA*, from the holotype) and MW511036 (*rbcL*, from the holotype).

709 **Etymology:** The specific epithet *soaresii* pertains to the Type locality, Diego-Suarez  
710 Bay or Antsiranana Bay, which was named after the Portuguese navigator and  
711 explorer Diogo Soares de Albergaria (1460-1509) who visited Madagascar in 1543.

712 **Diagnostic characters:** The species is distinguished from sympatric species in the  
713 crustose growth habit, heterogeneous green to brown color patterns with clearer radial  
714 and concentric lines, thallus thickness and the distinctive DNA sequences.

715 **Distribution and habitat:** Madagascar. Growing on bedrock epiphytic on other  
716 macroalgae.

717 **Additional specimens examined.** Madagascar. Antsiranana, Southern part of Diego-  
718 Suez bay, 22 Oct 2016, Payri *NOU205228* (NOU).

719 *5. 17. Lobophora zmaragdina* C.W.Vieira, & C.Payri, sp. nov. (Figs 4R, 5R, 6P)

720 **Description:** Thallus predominantly crustose, coarse, up to 5 cm wide and 3 cm tall,  
721 190-260  $\mu\text{m}$  thick, green in color with grayish radial lines, attached to the substratum  
722 by ventral rhizoids. Margins entire. Structure with 11 cell layers: a single-cell-layered  
723 medulla, dorsal and ventral cortices of 5 cell layers.

724 **TYPE:** Madagascar, Sainte Marie, Pointe Tafondro, 19 Oct 2016, *Payri 205163*  
725 (NOU, holotypus).

726 **Representative DNA sequences:** MW223530 (*cox3*, from the specimen MUS2098),  
727 MW996680 (*psbA*, from the holotype) and MW996688 (*rbcL*, from the holotype).

728 **Etymology:** The specific epithet *zmaragdina* comes from the Latin adjective  
729 ‘*zmaragdina*’ meaning emerald-green in reference to the thallus visual aspect.

730 **Diagnostic characters:** The species is distinguished from sympatric species in the  
731 crustose growth habit, green color with grayish radial lines, thallus thickness and the  
732 distinctive DNA sequences.

733 **Distribution and habitat:** Madagascar, Oman, South Africa. Growing on hard  
734 substratum mixed with other organisms, in shallow habitats.

735 **Additional specimens examined.** South Africa. Bhangarock, 7 Oct 2013, *Bolton,*  
736 *Anderson, Mattio LMD1671* (NOU); Saxon Reef, 8 Oct 2013, *Bolton, Anderson,*  
737 *Mattio LMD1685* (NOU).

738 Madagascar. Anosy, Saint Luce, 5 Jun 2010, *Anderson, Coppejans, de Reviers, Le*  
739 *Gall, Rousseau and Tsarahevitra MAD2138* (PC); Antsiranana Bay, Orangea small  
740 pass, 22 Nov 2018, *Vieira and Rasoamanendrika MADA18ALG281* (BR).

741 Oman. Bandar Khayran, 28 Oct 2004, *MUS2098* (BR).

742

## 743 **6. Conclusions**

744 This study considerably improves our knowledge of *Lobophora* diversity and  
745 biogeography in the western Indian Ocean by incorporating collections from  
746 Madagascar, Mozambique and the Red Sea in published global datasets. The diversity  
747 of *Lobophora* is now re-evaluated to 44 species in the western Indian Ocean,  
748 compared to the 36 species based on previous literature. However, our sampling effort  
749 remains uneven across the western Indian Ocean, suggesting that this region  
750 potentially harbors a greater diversity. The Andaman, Bay of Bengal, Central Indian  
751 Ocean, Somali/Arabian and West and South Indian Shelf provinces in particular  
752 deserve further attention. This second most diverse marine region for the genus  
753 *Lobophora* worldwide contains a high regional endemism. The western Indian Ocean  
754 islands and the Red Sea appear to have played a major role in this regional

755 diversification. Finer geographical-scale study will clarify the evolutionary processes  
756 that generate diversity within the western Indian Ocean.



757 **Acknowledgements**

758 Part of the sampling for this study took place within the framework of the  
759 capacity-building program “Gestion des collections et des données biologiques”  
760 organized in Antsiranana, Madagascar, by the Royal Museum for Central Africa,  
761 Belgium. The authors thank the Royal Museum for Central Africa, Belgium, for  
762 financing the fieldwork. This work makes use of resources and facilities provided by  
763 UGent as part of the Belgian contribution to EMBRC-ERIC (FWO GOH3817N). We  
764 gratefully acknowledge the following expeditions, cruises and institutions: Atimo  
765 Vatae expedition to South Madagascar (Principal Investigator, Philippe Bouchet), part  
766 of a cluster of Mozambique-Madagascar expeditions funded by the Total Foundation,  
767 Prince Albert II of Monaco Foundation, and Stavros Niarchos Foundation under “Our  
768 Planet Reviewed”, a joint initiative of Muséum National d’Histoire Naturelle  
769 (MNHN) and Pro Natura International (PNI) in partnership with Institut d’Halieutique  
770 et des Sciences Marines, University of Toliara (IH.SM) and the Madagascar bureau of  
771 Wildlife Conservation Society (WCS); EATSA & MaTaMo1 expeditions funded by  
772 the Belgian Directorate-General for Development Cooperation through the CEBioS  
773 Programme, partim GTI, The King Léopold III Fund for Nature Exploration and  
774 Conservation, and the Research Foundation – Flanders. CV is an International  
775 Research Fellow of the Japan Society for the Promotion of Science. We acknowledge  
776 the program Biorecie (Biodiversity, Resources and Conservation of Eparses Islands)  
777 thanks to which samples were previously collected in the Eparses Islands.

778

779 **Funding:** This work was supported by the Belgian Development Cooperation through  
780 a framework agreement project (2013-2018) with the Royal Museum for Central  
781 Africa and Ghent University (Ghent, Belgium) with infrastructure funded by

782 European Marine Biological Resource Centre Belgium/Research Foundation -  
783 Flanders Project [grant number GOH3817N]; the Portuguese national funds from  
784 FCT - Foundation for Science and Technology through project UIDB/04326/2020.  
785 CV postdoctoral fellowship and research was supported by Ghent University (grant  
786 number BOF16/PDO/141). The Japan Society for the Promotion of Science (JSPS) is  
787 acknowledged for additional financial support including a Kakenhi Grant-in-Aid for  
788 Science (grant number 19F19796).  
789  
790

791 **References**

- 792 Bolton, J., Bhagooli, R., Mattio, L., 2012. The Mauritian seaweed flora: diversity and  
 793 potential for sustainable utilisation. *University of Mauritius Research Journal*  
 794 18, 6-27.
- 795 Bolton, J., Leliaert, F., De Clerck, O., Anderson, R., Stegenga, H., Engledow, H.,  
 796 Coppejans, E., 2004. Where is the western limit of the tropical Indian Ocean  
 797 seaweed flora? An analysis of intertidal seaweed biogeography on the east  
 798 coast of South Africa. *Marine Biology* 144, 51-59.
- 799 Bolton, J., Oyieke, H., Gwada, P., 2007. The seaweeds of Kenya: checklist, history of  
 800 seaweed study, coastal environment, and analysis of seaweed diversity and  
 801 biogeography. *South African Journal of Botany* 73, 76-88.
- 802 Bolton, J., Stegenga, H., 2002. Seaweed species diversity in South Africa. *South*  
 803 *African Journal of Marine Science* 24, 9-18.
- 804 Bolton, J.J., De Clerck, O., John, D.M., 2003. Seaweed diversity patterns in sub-  
 805 Saharan Africa, in: Decker, C., Griffiths, C., Prochazka, K., Ras, C.,  
 806 Whitfield, A. (Eds.), *Proceedings of the Marine Biodiversity in Sub-*  
 807 *Saharan Africa: The Known and the Unknown*, Cape Town, ZA.
- 808 Camacho, O., Fernández-García, C., Vieira, C., Gurgel, C.F.D., Norris, J.,  
 809 Freshwater, D.W., Fredericq, S., 2019. The systematics of *Lobophora*  
 810 (Dictyotales, Phaeophyceae) in the western Atlantic and eastern Pacific  
 811 oceans: eight new species *Journal of Phycology* 55, 611–624.
- 812 De Clerck, O., Verbruggen, H., Huisman, J.M., Faye, E.J., Leliaert, F., Schils, T.,  
 813 Coppejans, E., 2008. Systematics and biogeography of the genus  
 814 *Pseudocodium* (Bryopsidales, Chlorophyta), including the description of *P.*  
 815 *natalense* sp. nov. from South Africa. *Phycologia* 47, 225-235.
- 816 Edgar, R.C., 2004. MUSCLE: multiple sequence alignment with high accuracy and  
 817 high throughput. *Nucleic Acids Research* 32, 1792-1797.
- 818 Francis, C., Bolton, J.J., Mattio, L., Mandiwana-Neudani, T.G., Anderson, R.J., 2017.  
 819 Molecular systematics reveals increased diversity within the South African  
 820 *Laurencia* complex (Rhodomelaceae, Rhodophyta). *Journal of Phycology* 53,  
 821 804-819.
- 822 Guindon, S., Dufayard, J.F., Lefort, V., Anisimova, M., Hordijk, W., Gascuel, O.,  
 823 2010. New algorithms and methods to estimate Maximum-Likelihood  
 824 phylogenies: assessing the performance of PhyML 3.0. *Systematic Biology*  
 825 59, 307-321.
- 826 John, D.M., Lawson, G.W., Ameka, G.K., 2003. The marine macroalgae of the  
 827 tropical West Africa sub-region. *Nova Hedwigia Beihefte* 125, 1-217.
- 828 Leliaert, F., Payo, D.A., Gurgel, C.F.D., Schils, T., Draisma, S.G., Saunders, G.W.,  
 829 Kamiya, M., Sherwood, A.R., Lin, S.M., Huisman, J.M., Le Gall, L.,  
 830 Anderson, R.J., Bolton, J.J., Mattio, L., Zubia, M., Spokes, T., Vieira, C.,  
 831 Payri, C.E., Coppejans, E., D'hondt, S., Verbruggen, H., De Clerck, O., 2018.  
 832 Patterns and drivers of species diversity in the Indo-Pacific red seaweed  
 833 *Portieria*. *Journal of Biogeography* 45, 2299-2313.
- 834 Mattio, L., Bolton, J.J., Anderson, R.J., 2015. Contribution to the revision of the  
 835 genus *Sargassum* (Fucales, Phaeophyceae) in Madagascar using  
 836 morphological and molecular data. *Cryptogamie, Algologie* 36, 143-169.
- 837 Oza, R.M., Zaidi, S., 2001. A revised checklist of Indian marine algae. Central Salt  
 838 and Marine Chemicals Research Institute, Bhavnagar, India.

- 839 Piccone, A., 1884. Contribuzioni all'algologica Eritrea. Nuovo Giornale Bot. Ital. 16,  
840 281-332, pls. VII-IX.
- 841 Porter, S., Branch, G., Sink, K., 2013. Biogeographic patterns on shallow subtidal  
842 reefs in the western Indian Ocean. *Marine Biology* 160, 1271-1283.
- 843 Puk, L.D., Vieira, C., Roff, G., De Clerck, O., Mumby, P.J., 2020. Cryptic diversity in  
844 the macroalgal genus *Lobophora* (Dictyotales) reveals environmental drivers  
845 of algal assemblages. *Marine Biology* 167, 1-15.
- 846 Romero, O., Mollenhauer, G., Schneider, R.R., Wefer, G., 2003. Oscillations of the  
847 siliceous imprint in the central Benguela Upwelling System from MIS 3  
848 through to the early Holocene: the influence of the Southern Ocean. *Journal of*  
849 *Quaternary Science* 18, 733-743.
- 850 Schultz, N.E., Lane, C.E., Le Gall, L., Gey, D., Bigney, A.R., De Reviers, B.,  
851 Rousseau, F., Schneider, C.W., 2015. A barcode analysis of the genus  
852 *Lobophora* (Dictyotales, Phaeophyceae) in the western Atlantic Ocean with  
853 four novel species and the epitypification of *L. variegata* (J.V. Lamouroux)  
854 E.C. Oliveira. *European Journal of Phycology* 50, 1-20.
- 855 Silva, P.C., Basson, P.W., Moe, R.L., 1996. Catalogue of the benthic marine algae of  
856 the Indian Ocean. *University of California Publications in Botany* 79, 1259.
- 857 Simons, R.H., 1966. A new species of the Dictyotales from South Africa. *Bothalia* 9,  
858 169-171.
- 859 Sink, K., Branch, G., Harris, J., 2005. Biogeographic patterns in rocky intertidal  
860 communities in KwaZulu-Natal, South Africa. *African Journal of Marine*  
861 *Science* 27, 81-96.
- 862 Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M.,  
863 Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., 2007. Marine  
864 ecoregions of the world: a bioregionalization of coastal and shelf areas.  
865 *Bioscience* 57, 573-583.
- 866 Steen, F., Vieira, C., Leliaert, F., Payri, E.C., De Clerck, O., 2015. Biogeographic  
867 affinities of Dictyotales from Madagascar: a phylogenetic approach.  
868 *Cryptogamie, Algologie* 36, 129-141.
- 869 Sun, Z., Hanyuda, T., Lim, P.-E., Tanaka, J., Gurgel, C.F.D., Kawai, H., 2012.  
870 Taxonomic revision of the genus *Lobophora* (Dictyotales, Phaeophyceae)  
871 based on morphological evidence and analyses *rbcL* and *cox3* gene sequences.  
872 *Phycologia* 51, 500-512.
- 873 Teske, P.R., Papadopoulos, I., Newman, B.K., Dworschak, P.C., McQuaid, C.D.,  
874 Barker, N.P., 2008. Oceanic dispersal barriers, adaptation and larval retention:  
875 an interdisciplinary assessment of potential factors maintaining a  
876 phylogeographic break between sister lineages of an African prawn. *BMC*  
877 *Evolutionary Biology* 8, 341.
- 878 Thiers, B., 2020. Index Herbariorum: A global directory of public herbaria and  
879 associated staff, New York Botanical Gardens Virtual Herbarium, New York,  
880 NY, US. Available at: <http://www.givd.info> .
- 881 Vieira, C., 2020. *Lobophora*–coral interactions and phase shifts: summary of current  
882 knowledge and future directions. *Aquatic Ecology* 54, 1-20.
- 883 Vieira, C., Aharonov, A., Paz, G., Tsiamis, K., Engelen, A., Einav, R., De Clerck, O.,  
884 2018. Diversity and origin of the genus *Lobophora* in the Mediterranean Sea  
885 including the description of two new species. *Phycologia* 58, 163-168.
- 886 Vieira, C., Camacho, O., Sun, Z., Fredericq, S., Leliaert, F., Payri, C., De Clerck, O.,  
887 2017. Historical biogeography of the highly diverse brown seaweed

888 *Lobophora* (Dictyotales, Phaeophyceae). Molecular Phylogenetics and  
889 Evolution 110, 81-92.

890 Vieira, C., Camacho, O., Wynne, M.J., Mattio, L., Anderson, R., Bolton, J.J., Sansón,  
891 M., D'Hondt, S., Leliaert, F., Fredericq, S., Payri, C., De Clerck, O., 2016.  
892 Shedding new light on old algae: matching names and sequences in the brown  
893 algal genus *Lobophora* (Dictyotales, Phaeophyceae). Taxon 65, 689-707.

894 Vieira, C., D'hondt, S., De Clerck, O., Payri, C.E., 2014. Toward an inordinate  
895 fondness for stars, beetles and *Lobophora*? Species diversity of the genus  
896 *Lobophora* (Dictyotales, Phaeophyceae) in New Caledonia. Journal of  
897 Phycology 50, 1101-1119.

898 Vieira, C., De Clerck, O., Millet, L., Payri, C.E., 2019. Description of 10 new  
899 *Lobophora* species from the Bismarck Sea (Papua New Guinea). Phycological  
900 Research 67, 228-238.

901 Vieira, C., Henriques, F., D'hondt, S., Neto, A.I., Almada, C.H., Kaufmann, M.,  
902 Sansón, M., Sangil, C., De Clerck, O., 2020a. *Lobophora* (Dictyotales) species  
903 richness, ecology and biogeography across the North-eastern Atlantic  
904 archipelagos. Journal of Phycology 56, 346-357.

905 Vieira, C., Morrow, K.M., D'Hondt, S., Camacho, O., Engelen, A.H., Payri, C., De  
906 Clerck, O., 2020b. Diversity, ecology, biogeography and evolution of the  
907 prevalent brown algal genus *Lobophora* in the Greater Caribbean sea,  
908 including the description of five new species. Journal of Phycology 56, 592-  
909 607.

910 Vieira, C., N'Yeurt, A.D.R., Rasoamanendrika, A.F., D'Hondt, S., Tran, L.-A.T., Van  
911 den Spiegel, D., Hiroshi, K., De Clerck, O., 2021. Marine macroalgal  
912 biodiversity of northern Madagascar: morpho-genetic systematics and  
913 implications of anthropic impacts for conservation. Biodiversity and  
914 Conservation 30, 1501–1546.

915

916

**Table 1.** Morphological and anatomical characters of newly described species of *Lobophora* (Dictyotales, Phaeophyceae) the western Indian Ocean.

	<i>L. africana</i>	<i>L. antsirananaensis</i>	<i>L. erythraea</i>	<i>L. evanii</i>	<i>L. bandeirae</i>	<i>L. flabellata</i>	<i>L. garyi</i>	<i>L. gloriosa</i>
<b>Thickness (<math>\mu\text{m}</math>)</b>								
<b>Average + SD</b>	358.5 $\pm$ 34.8	64.3 $\pm$ 5.0	208.8 $\pm$ 13.8	112.0 $\pm$ 14.8	99.0	220.0 $\pm$ 16.6	76.5 $\pm$ 5.8	456.0 $\pm$ 37.8
<b>Min-Max</b>	304 - 436	55 - 73	190 - 232	90 - 135	98 - 100	186 - 246	68 - 85	410 - 503
<b>Number of cells</b>								
<b>Average + SD</b>	15.4 $\pm$ 1.6	5.2 $\pm$ 0.4	8.8 $\pm$ 0.4	6.9 $\pm$ 1.1	7.0	12.3 $\pm$ 1.1	5.0 $\pm$ 0.0	21.7 $\pm$ 0.5
<b>Min-Max</b>	14 - 19	5 - 6	8 - 9	5 - 8	7	11 - 15	5	21 - 22
<b>Number of dorsal cells</b>								
<b>Average + SD</b>	8.0 $\pm$ 1.1	2.2 $\pm$ 0.4	4.0 $\pm$ 0.0	2.9 $\pm$ 0.3	3.0	6.1 $\pm$ 0.8	2.0 $\pm$ 0.0	11.9 $\pm$ 0.3
<b>Min-Max</b>	7 - 10	2 - 3	4	2 - 3	3	5 - 8	2	11 - 12
<b>Number of ventral cells</b>								
<b>Average + SD</b>	6.5 $\pm$ 0.8	2.0 $\pm$ 0.0	3.8 $\pm$ 0.4	2.5 $\pm$ 0.5	3.0	5.3 $\pm$ 0.4	2.0 $\pm$ 0.0	8.8 $\pm$ 0.4
<b>Min-Max</b>	5 - 8	2	3 - 4	2 - 3	3	5 - 6	2	8 - 9
<b>Medulla length (<math>\mu\text{m}</math>)</b>								
<b>Average + SD</b>	80.6 $\pm$ 10.2	61.5 $\pm$ 11.4	90.4 $\pm$ 5.0	64.0 $\pm$ 9.6	62.0	82.6 $\pm$ 17.2	87.5 $\pm$ 6.8	91.5 $\pm$ 3.9
<b>Min-Max</b>	64 - 100	50 - 75	82 - 94	55 - 80	62	64 - 120	78 - 95	86 - 97
<b>Medulla height (<math>\mu\text{m}</math>)</b>								
<b>Average + SD</b>	81.3 $\pm$ 11.8	20.0 $\pm$ 2.0	68.2 $\pm$ 8.5	39.5 $\pm$ 7.0	33.0	45.9 $\pm$ 15.2	27.8 $\pm$ 2.8	64.1 $\pm$ 8.5
<b>Min-Max</b>	60 - 100	18 - 23	52 - 80	30 - 50	33	20 - 70	23 - 30	51 - 72
<b>Medulla width (<math>\mu\text{m}</math>)</b>								
<b>Average + SD</b>	33.8 $\pm$ 3.2	32.0 $\pm$ 5.7	28.0 $\pm$ 2.4	27.5 $\pm$ 4.0	24.0	24.0 $\pm$ 3.0	23.5 $\pm$ 1.4	24.3 $\pm$ 2.8
<b>Min-Max</b>	30 - 40	25 - 38	24 - 30	23 - 33	24	20 - 28	23 - 25	22 - 28
<b>Dorsal height (<math>\mu\text{m}</math>)</b>								
<b>Average + SD</b>	161.1 $\pm$ 19.8	24.8 $\pm$ 3.0	73.2 $\pm$ 4.7	39.5 $\pm$ 4.2	36.0	90.6 $\pm$ 8.1	25.8 $\pm$ 3.1	235.2 $\pm$ 8.5
<b>Min-Max</b>	140 - 208	20 - 30	66 - 80	33 - 45	36	74 - 102	23 - 30	222 - 249
<b>Ventral height (<math>\mu\text{m}</math>)</b>								
<b>Average + SD</b>	116.1 $\pm$ 21.0	19.5 $\pm$ 2.3	67.4 $\pm$ 4.7	33.0 $\pm$ 8.5	33.0	83.5 $\pm$ 6.3	23.0 $\pm$ 2.0	188.8 $\pm$ 9.6
<b>Min-Max</b>	80 - 152	15 - 23	50 - 80	15 - 43	33	70 - 100	20 - 25	176 - 202
<b>Thallus</b>								
<b>Growth-form</b>	decumbent	procumbent to decumbent	decumbent	procumbent	erect	erect	decumbent to crustose	decumbent
<b>Color</b>	dark brown	dark orange	dark brown	orange	brown	dark brown	brown to light green	medium brown
<b>Max width (cm)</b>	11	6	-	3	10	11	3.5	7
<b>Max height (cm)</b>	5	3.5	-	2.5	7	-	3	7
<b>References</b>	This study	This study	This study	This study	This study	This study	This study	This study

	<i>L. henae</i>	<i>L. isselii</i>	<i>L. kimiae</i>	<i>L. madagascariensis</i>	<i>L. maldivensis</i>	<i>L. novae</i>	<i>L. soaresii</i>	<i>L. zmaragdina</i>
<b>Thickness (µm)</b>								
<b>Average + SD</b>	48.5 ± 8.5	104.0 ± 8.6	105.3 ± 4.5	296.0 ± 17.1	199.0 ± 25.6	101.4 ± 26.1	265.0 ± 20.3	225.0
<b>Min-Max</b>	38 - 63	93 - 115	98 - 110	255 - 310	164 - 260	60 - 144	215 - 285	190 - 260
<b>Number of cells</b>								
<b>Average + SD</b>	3.9 ± 0.7	5.7 ± 0.5	5.0 ± 0.0	15.8 ± 0.6	8.7 ± 0.5	5.8 ± 0.5	14.3 ± 0.8	11.0
<b>Min-Max</b>	3 - 5	5 - 6	5	15 - 17	8 - 9	5 - 7	13 - 16	11
<b>Number of dorsal cells</b>								
<b>Average + SD</b>	1.7 ± 0.5	2.7 ± 0.5	2.0 ± 0.0	8.8 ± 0.6	3.7 ± 0.5	2.8 ± 0.4	7.0 ± 0.5	5.0
<b>Min-Max</b>	1 - 2	2 - 3	2	8 - 10	3 - 4	2 - 3	6 - 8	5
<b>Number of ventral cells</b>								
<b>Average + SD</b>	1.2 ± 0.4	2.0 ± 0.0	2.0 ± 0.0	5.9 ± 0.3	4.0 ± 0.0	2.1 ± 0.2	6.3 ± 0.5	5.0
<b>Min-Max</b>	1 - 2	2	2	5 - 6	4	2 - 3	6 - 7	5
<b>Medulla length (µm)</b>								
<b>Average + SD</b>	66.0 ± 5.8	87.5 ± 4.0	64.5 ± 6.0	29.0 ± 2.2	89.2 ± 9.4	74.6 ± 14.0	99.0 ± 7.4	72.0
<b>Min-Max</b>	60 - 75	83 - 93	60 - 75	25 - 30	74 - 100	60 - 92	90 - 110	67 - 77
<b>Medulla height (µm)</b>								
<b>Average + SD</b>	20.8 ± 4.4	41.0 ± 5.2	41.0 ± 3.9	47.5 ± 10.3	60.3 ± 14.2	37.7 ± 14.4	58.5 ± 20.6	64.5
<b>Min-Max</b>	13 - 28	30 - 45	33 - 45	35 - 65	40 - 100	20 - 70	30 - 95	49 - 80
<b>Medulla width (µm)</b>								
<b>Average + SD</b>	31.5 ± 5.2	30.5 ± 3.3	32.5 ± 4.7	74.0 ± 11.9	26.4 ± 4.2	27.4 ± 4.4	29.0 ± 7.4	38.0
<b>Min-Max</b>	25 - 38	25 - 33	28 - 40	60 - 90	30 - 32	24 - 38	20 - 40	36 - 40
<b>Dorsal height (µm)</b>								
<b>Average + SD</b>	16.8 ± 2.9	37.8 ± 6.6	34.0 ± 2.4	148.0 ± 8.6	67.4 ± 11.8	35.9 ± 9.9	119.0 ± 11.7	99.0
<b>Min-Max</b>	13 - 20	25 - 45	30 - 38	135 - 160	50 - 90	20 - 50	95 - 135	86 - 112
<b>Ventral height (µm)</b>								
<b>Average + SD</b>	11.0 ± 4.4	25.3 ± 1.4	30.3 ± 4.2	100.5 ± 13.8	71.3 ± 6.3	27.8 ± 5.8	87.5 ± 20.6	76.0
<b>Min-Max</b>	8 - 20	23 - 28	25 - 38	75 - 115	62 - 80	20 - 44	50 - 115	76 - 77
<b>Thallus</b>								
<b>Growth-form</b>	decumbent to crustose	crustose	procumbent	crustose	decumbent	procumbent	crustose to decumbent	crustose
<b>Color</b>	light brown	orange-brown	light brown	green with gray radial lines	dark green	olive-green	green to brown with gray radial lines	green with gray radial lines
<b>Max width (cm)</b>	2.5	3	3	5	5	5	6	5
<b>Max height (cm)</b>	2.5	2	2.5	3	4	3.5	4	3
<b>References</b>	This study	This study	This study	This study	This study	This study	This study	This study

921  
922

## Figure captions

923 **Figure 1.** Specimen-level phylogeny of the genus *Lobophora* (Dictyotales, Phaeophyceae).  
924 Phylogenetic tree reconstructed using Bayesian method based on *cox3* sequences. The values shown at  
925 each node represent posterior probabilities. A black filled circle represents full support. Four species  
926 did not have *cox3* sequences and were identified based on *psbA* and *rbcL* (*L. asiatica*, *L. rickeri*, *L.*  
927 *sp79*, *L. sp83*).

928 **Figure 2.** Phylogenetic tree of *Lobophora* (Dictyotales, Phaeophyceae) species. Maximum likelihood  
929 phylogenetic tree based on a concatenated alignment including *cox3*, *psbA* and *rbcL* sequences.

930 **Figure 3.** Species diversity map of *Lobophora* (Dictyotales, Phaeophyceae) within the western Indian  
931 Ocean. Marine provinces are based on Spalding et al. (2007). The table on the left lists the 44 species  
932 of *Lobophora* documented to date from the western Indian Ocean per province. Red line indicates the  
933 southernmost limit of *Lobophora* distribution along the Southeastern African coast. White filled circles  
934 indicate type localities of previously and newly described species. Total numbers of marine seaweeds  
935 for the western Indian Ocean countries are provided under the country's name, when the data is  
936 available in the literature; <sup>a</sup> Bolton and Stegenga (2002), <sup>b</sup> Bolton et al. (2003), <sup>c</sup> Bolton et al. (2007), <sup>d</sup>  
937 Vieira et al. (2021), <sup>e</sup> Guiry and Guiry (2011) in Bolton et al. (2012), <sup>f</sup> Oza and Zaidi (2001).

938 **Figure 4.** Habit photographs of some *Lobophora* (Dictyotales, Phaeophyceae) species from the western  
939 Indian Ocean. *Lobophora antsirananaensis* sp. nov. from Antsiranana Bay, Madagascar, voucher  
940 MADA18ALG116 (A); *L. ceylanica* from Juan de Nova Island, voucher JN040 (B); *L. dichotoma* from  
941 Kwazulu Natal, South Africa, voucher KZN16-273 (C); *L. dispersa* from Bhanga Nek, South Africa,  
942 voucher LMD1597 (D); *L. endeavouriae* from Saint Marie, Madagascar, voucher MD138 (E); *L. evanii*  
943 sp. nov. from Antsiranana Bay, Madagascar, voucher MADA18ALG101 (F); *L. flabellata* sp. nov.  
944 from Mozambique (G); *L. garyi* sp. nov. from Antsiranana Bay, Madagascar, voucher  
945 MADA18ALG031 (H); *L. gloriosa* sp. nov. from Grande Glorieuse, Glorioso Islands, voucher  
946 GLO0180 (I); *L. henaie* sp. nov. from Antsiranana Bay, Madagascar, voucher MADA18ALG080 (J); *L.*  
947 *isselii* from Antsiranana Bay, Madagascar, on dead coral, voucher MADA18ALG567 (K), and on  
948 mollusks shells, voucher MADA18ALG563 (L); *L. kimiae* sp. nov. from Antsiranana Bay,  
949 Madagascar, voucher MADA18ALG111 (M); *L. madagascariensis* sp. nov. from Antsiranana Bay,  
950 Madagascar, voucher MADA18ALG033 (N); *L. sp47* from Europa Island, voucher EUR275 (N); *L.*  
951 *novae* from Madagascar, voucher MD648 (O), and Juan de Nova, voucher JN234 (P); *L. soaresii* sp.



952 nov. from Antsiranana Bay, Madagascar, voucher MADA18ALG275 (Q); *L. zmaragdina* sp. nov. from  
953 Antsiranana Bay, Madagascar, voucher MD064 (R).

954 **Figure 5.** *Ex situ* photographs of some *Lobophora* species from the western Indian Ocean. *Lobophora*  
955 *africana* sp. nov. from Juan de Nova Island, voucher JN177 (A); *L. antsirananaensis* sp. nov. from  
956 Antsiranana Bay, Madagascar, voucher MADA18ALG112 (B); *L. bandeirae* sp. nov. from Inhambane,  
957 Mozambique, voucher BR5010109465490V (C); *L. ceylanica* from Juan de Nova Island, voucher  
958 JN040 (D); *L. dichotoma* from Bhanga Nek, South Africa, voucher KZN16-316 (E); *L. erythraea* sp.  
959 nov. from Glorioso Island, voucher IRD11053 (F); *L. evanii* sp. nov. from Antsiranana Bay,  
960 Madagascar, voucher MADA18ALG101 (G); *L. flabellata* sp. nov. from Bhanga Nek, South Africa,  
961 voucher LMD1616 (H); *L. garyi* sp. nov. from Antsiranana Bay, Madagascar, voucher  
962 MADA18ALG031 (I); *L. gloriosa* sp. nov. from Grande Glorieuse, Glorioso Islands, voucher  
963 GLO0180 (J); *L. henaie* sp. nov. from Antsiranana Bay, Madagascar, voucher MADA18ALG038 (K); *L.*  
964 *isselii* from Antsiranana Bay, Madagascar, voucher MADA18ALG569 (L); *L. kimiae* sp. nov. from  
965 Antsiranana Bay, Madagascar, voucher MADA18ALG111 (M); *L. madagascariensis* from Antsiranana  
966 Bay, Madagascar, voucher MADA18ALG033 (N); *L. maldivensis* sp. nov. from Baa Atoll, Maldives,  
967 voucher IRD4579 (O); *L. novae* sp. nov. from Bhanga Nek, South Africa, voucher LMD1617 (P); *L.*  
968 *soaresii* sp. nov. from Antsiranana Bay, Madagascar, voucher MADA18ALG275 (Q); *L. zmaragdina*  
969 sp. nov. from Bhanga Nek, South Africa, voucher LMD1671 (R). Scale bar equals 1 cm.

970 **Figure 6.** Transverse (up) and longitudinal (down) sections of thallus of *Lobophora* species from the  
971 western Indian Ocean.

972 *Lobophora africana* sp. nov. from Juan de Nova, voucher JN177 (A); *L. antsirananaensis* sp. nov.,  
973 voucher MADA18ALG116 (B); *L. bandeirae* sp. nov., voucher BR5010109465490V (C); *L. erythraea*  
974 sp. nov. from Aqaba Golf, Saudi Arabia, voucher IRD11053 (D); *L. evanii* sp. nov., voucher  
975 MADA18ALG101 (E); *L. flabellata* sp. nov., voucher LMD1616 (F); *L. garyi* sp. nov., voucher  
976 MADA18ALG031 (G); *L. gloriosa* sp. nov., voucher GLO0180 (H); *L. henaie* sp. nov., voucher  
977 MADA18ALG080 (I); *L. isselii*, voucher MADA18ALG569 (F); *L. kimiae* sp. nov., voucher  
978 MADA18ALG111 (G); *L. madagascariensis* sp. nov., voucher MADA18ALG033 (HJ). Unless  
979 indicated, scale bar equals 100  $\mu$ m.

980 **Figure 6 (continued).** Transverse (up) and longitudinal (down) sections of thallus of *Lobophora*  
981 species from the western Indian Ocean. *L. maldivensis* sp. nov., voucher IRD4579 (M); *L. novae* sp.

982 nov. from Juan de Nova, voucher JN234 (N); *L. soaresii* sp. nov., voucher MADA18ALG275 (O); *L.*  
983 *zmaragdina* sp. nov., voucher MD064 (P). Unless indicated, scale bar equals 100 µm.

984 **Figure 7.** Longitudinal range of *Lobophora* (Dictyotales, Phaeophyceae) species from the western  
985 Indian Ocean.

986

## 987 **Appendix**

988 **Table A.1.** Voucher information and GenBank accession data for material of *Lobophora* from the  
989 western Indian Ocean used in this study. In bold the specimens sequenced in this study.

990 **Fig. A.1.** Phylogenetic tree of the genus *Lobophora*, based on *cox3* sequences, using Bayesian method,  
991 generated with MrBayes v3.2. The values shown at each node represent posterior probabilities. Four  
992 species did not have *cox3* sequences and were identified based on *psbA* and *rbcL* (*L. asiatica*, *L.*  
993 *rickeri*, *L. sp79*, *L. sp83*).

994 **Fig. A.2.** Phylogenetic tree of the genus *Lobophora*, based on *psbA* sequences, reconstructed with the  
995 maximum likelihood method using a best fit substitution model and a SPR branch swapping algorithm  
996 in PhyML 3.0 (Guindon et al., 2010). The values shown at each node represent the bootstrap values.

997 **Fig. A.3.** Phylogenetic tree of the genus *Lobophora*, based on *psbA* sequences, using Bayesian method,  
998 generated with MrBayes v3. The values shown at each node represent posterior probabilities.

999 **Fig. A.4.** Phylogenetic tree of the genus *Lobophora*, based on *rbcL* sequences, reconstructed with the  
1000 maximum likelihood method using a best fit substitution model and a SPR branch swapping algorithm  
1001 in PhyML 3.0 (Guindon et al., 2010). The values shown at each node represent the bootstrap values.

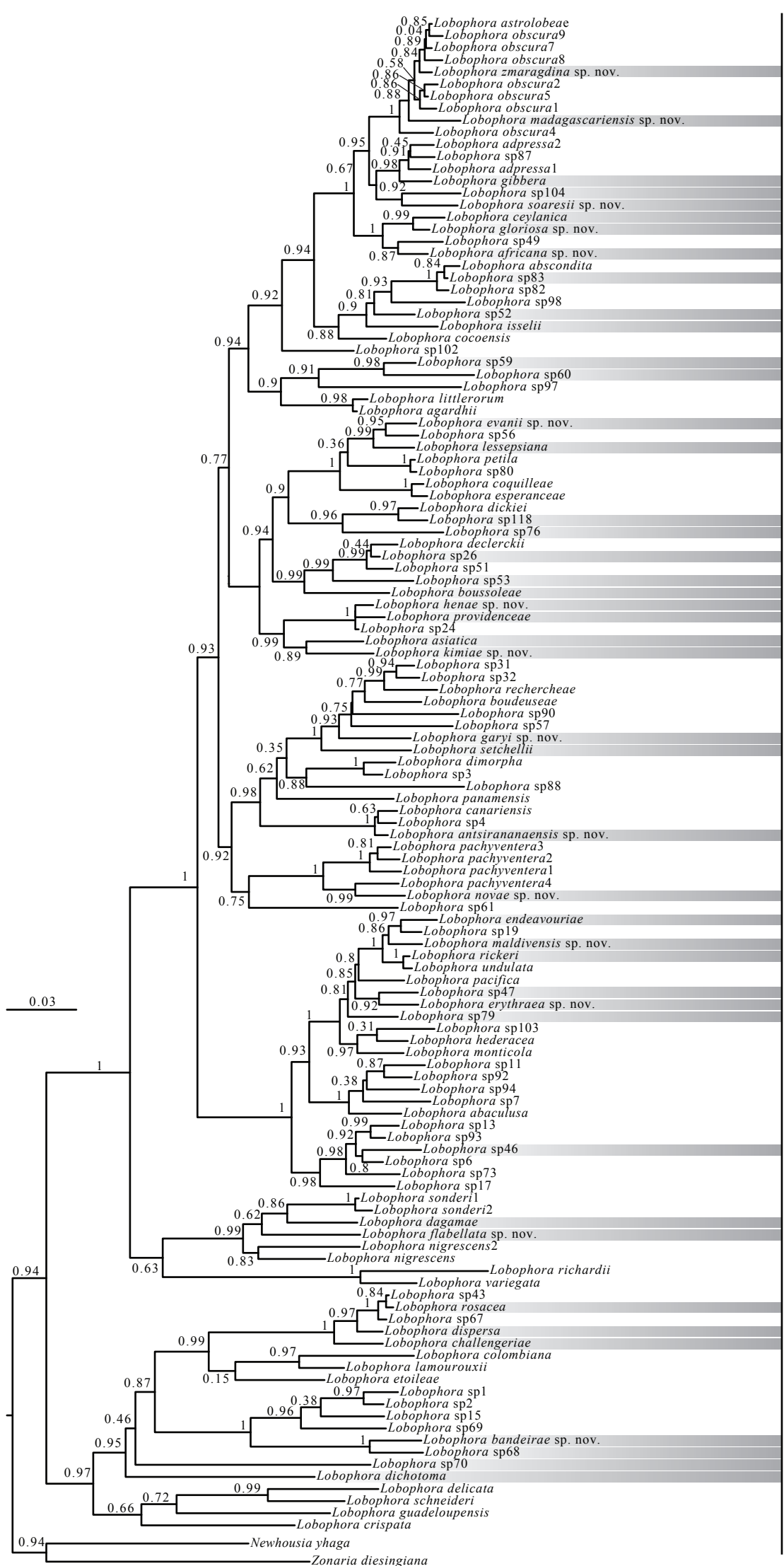
1002 **Fig. A.5.** Phylogenetic tree of the genus *Lobophora*, based on *rbcL* sequences, using Bayesian method,  
1003 generated with MrBayes v3.2. The values shown at each node represent posterior probabilities.

1004 **Fig. A.6..** *Lobophora* species tree generated from a concatenated alignment including *cox3*, *psbA* and  
1005 *rbcL* using Bayesian Bayesian method, generated with MrBayes v3.2. The values shown at each node  
1006 represent posterior probabilities.

1007 **Fig. A.7.** Photographs of *Lobophora* spp. from the western Indian Ocean. Habit photographs of  
1008 *Lobophora flabellata* from Mozambique forming large patches (A); *L. isselii* from Antsiranana Bay,  
1009 Madagascar, on live corals, voucher MADA18ALG568 (B); *L. novae* from Juan de Nova forming  
1010 dense beds (C); *L. sp26* from Europa Island, voucher EUR077 (D); *L. sp46* from Europa Island,  
1011 voucher EUR235 (E); *L. sp47* from Europa Island, voucher EUR275 (F); *L. sp52* from Grande  
1012 Glorieuse, Glorioso Islands, voucher GLO0095 (G); *L. sp60* from Europa Island, voucher EUR104

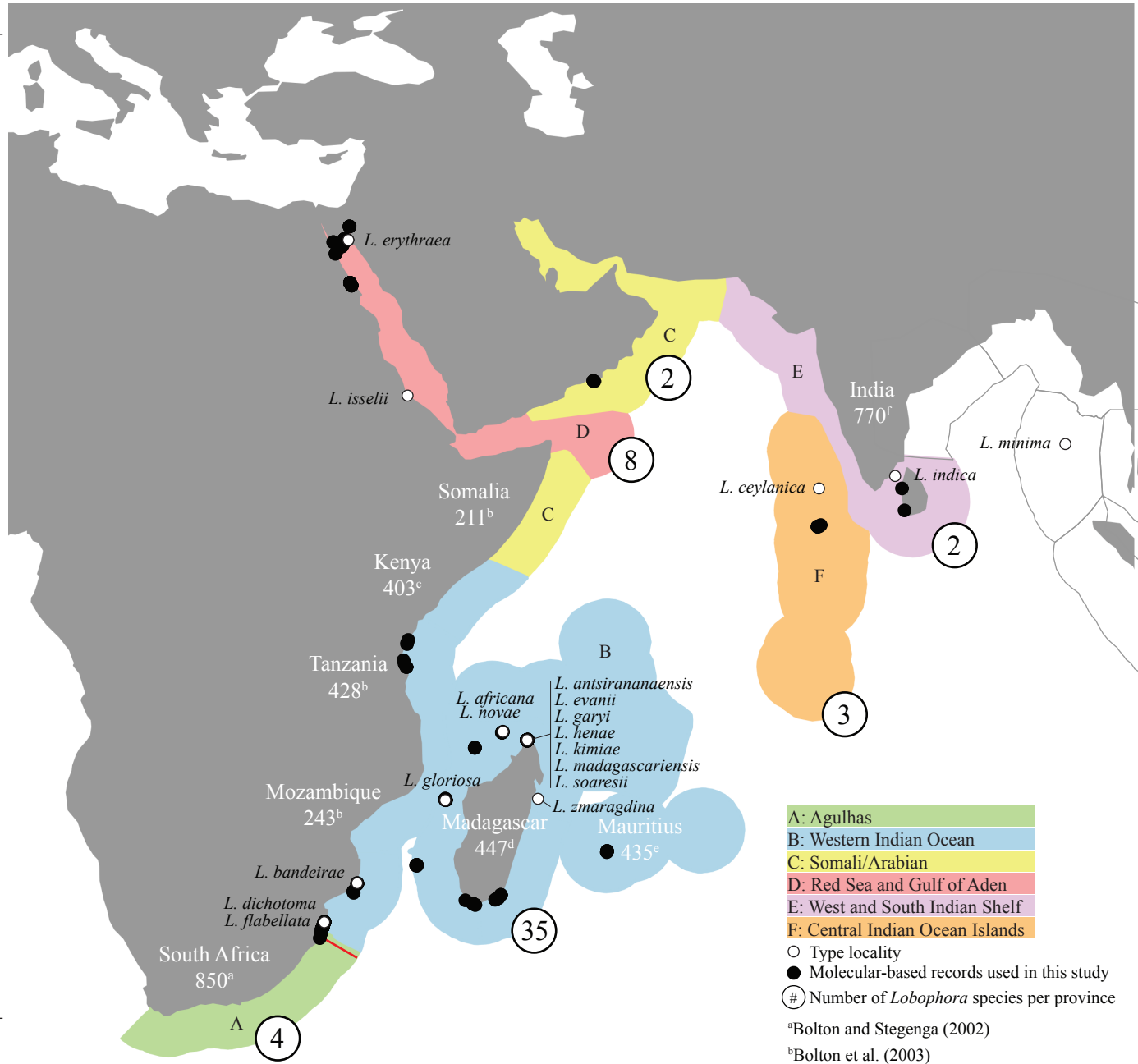
1013 (H); *L. sp83* from Grande Glorieuse, Glorioso Islands, voucher GLO0051 (I). Ex situ photographs of *L.*  
1014 *dichotoma* from KwaZulu-Natal, South Africa, voucher KZN16-316 (J) and voucher KZN16-330 (K);  
1015 *L. sp26* from Europa Island, voucher EUR077 (L); *L. sp52* from Glorioso Island, voucher GLO095  
1016 (M); *L. sp59* from Marsa Alam, Egypt, voucher IRD11157 (N); *L. sp60* from Europa Island, voucher  
1017 EUR104 (O); *L. sp76* from Réunion, voucher AVR656 (P); *L. sp79* from Mayotte, voucher LYD10-  
1018 102 (Q); *L. sp83* from Glorioso Island, voucher GLO051 (R). Scale bar equals 1 cm.





	Atl.	A	B	C	D	E	F	CIP
<i>L. africana</i>			●					
<i>L. antsirananaensis</i>			●					
<i>L. asiatica</i>								●
<i>L. bandeirae</i>			●					
<i>L. boussoleae</i>					●			●
<i>L. ceylanica</i>			●				●	●
<i>L. challengeriae</i>			●	●		●		●
<i>L. dagamae</i>	●		●					
<i>L. dichotoma</i>		●	●					
<i>L. dispersa</i>	●		●					●
<i>L. endeavouriae</i>			●		●			
<i>L. erythraea</i>					●			
<i>L. evanii</i>			●					
<i>L. flabellata</i>		●	●					
<i>L. garyi</i>			●					
<i>L. gibbera</i>								●
<i>L. gloriosa</i>			●				●	
<i>L. hena</i>			●					●
<i>L. isselii</i>			●		●			
<i>L. kimiae</i>			●					
<i>L. lessepsiana</i>	●				●			
<i>L. madagascariensis</i>			●					
<i>L. maldivensis</i>							●	
<i>L. novae</i>		●	●					
<i>L. providenceae</i>			●					●
<i>L. rickeri</i>			●					●
<i>L. rosacea</i>			●					●
<i>L. setchellii</i>	●		●					●
<i>L. soaresii</i>			●					
<i>L. zmaragdina</i>				●				
<i>L. sp26</i>			●					
<i>L. sp46</i>			●					
<i>L. sp47</i>			●					
<i>L. sp52</i>			●					●
<i>L. sp53</i>					●			●
<i>L. sp59</i>			●		●			
<i>L. sp60</i>			●					
<i>L. sp68</i>						●		
<i>L. sp70</i>			●					●
<i>L. sp76</i>			●					
<i>L. sp79</i>			●					
<i>L. sp83</i>			●					
<i>L. sp104</i>		●						
<i>L. sp118</i>					●			

Atl.: Atlantic  
 CIP: Central Indo-Pacific  
 No molecular data for *L. indica* and *L. minima*



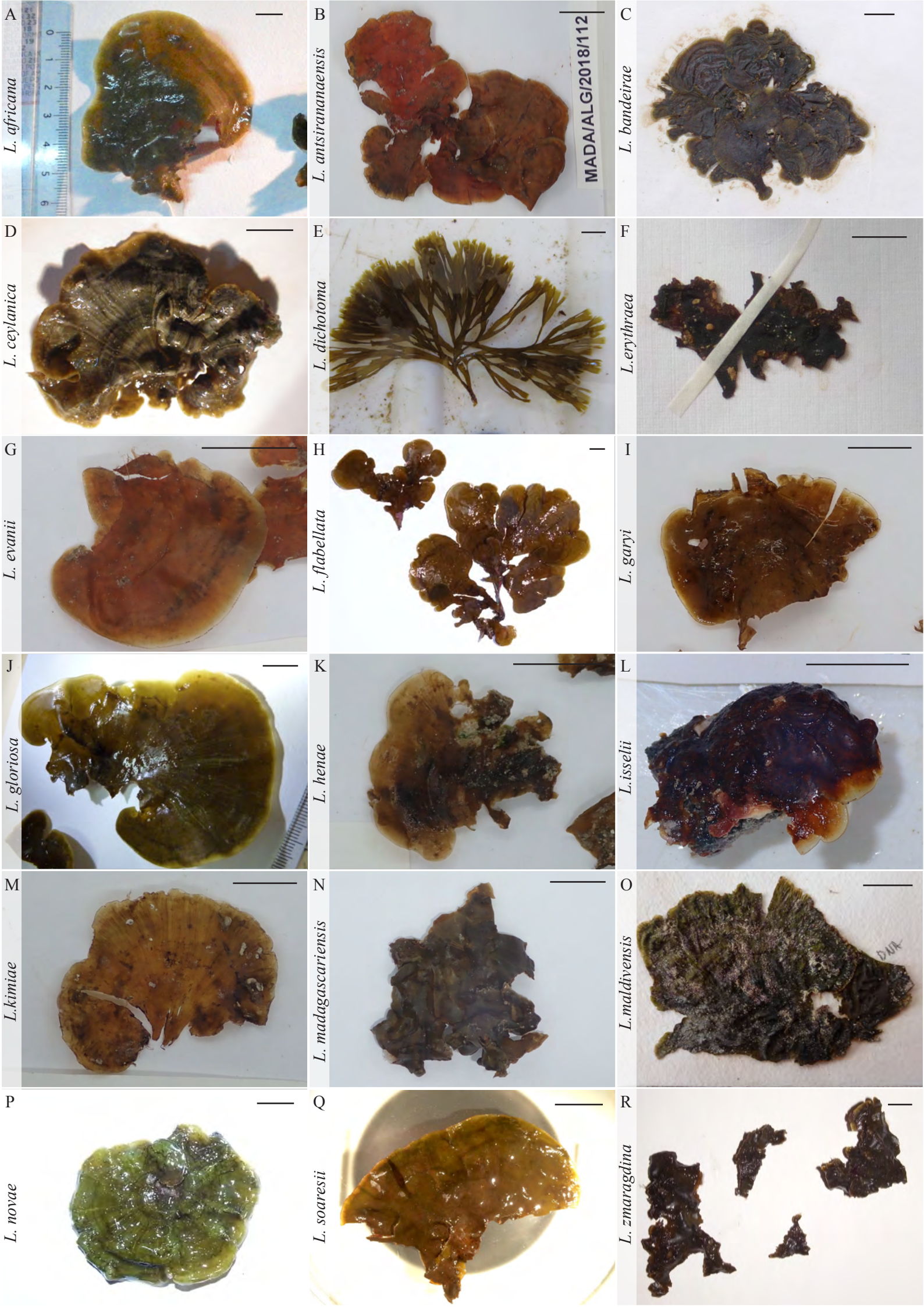
- A: Agulhas
- B: Western Indian Ocean
- C: Somali/Arabian
- D: Red Sea and Gulf of Aden
- E: West and South Indian Shelf
- F: Central Indian Ocean Islands

- Type locality
- Molecular-based records used in this study
- # Number of *Lobophora* species per province
- <sup>a</sup>Bolton and Stegenga (2002)
- <sup>b</sup>Bolton et al. (2003)
- <sup>c</sup>Bolton et al. (2007)
- <sup>d</sup>Vieira et al. (2021)
- <sup>e</sup>Guiry and Guiry (2011) in Bolton et al. (2012)
- <sup>f</sup>Oza and Zaidi (2001)

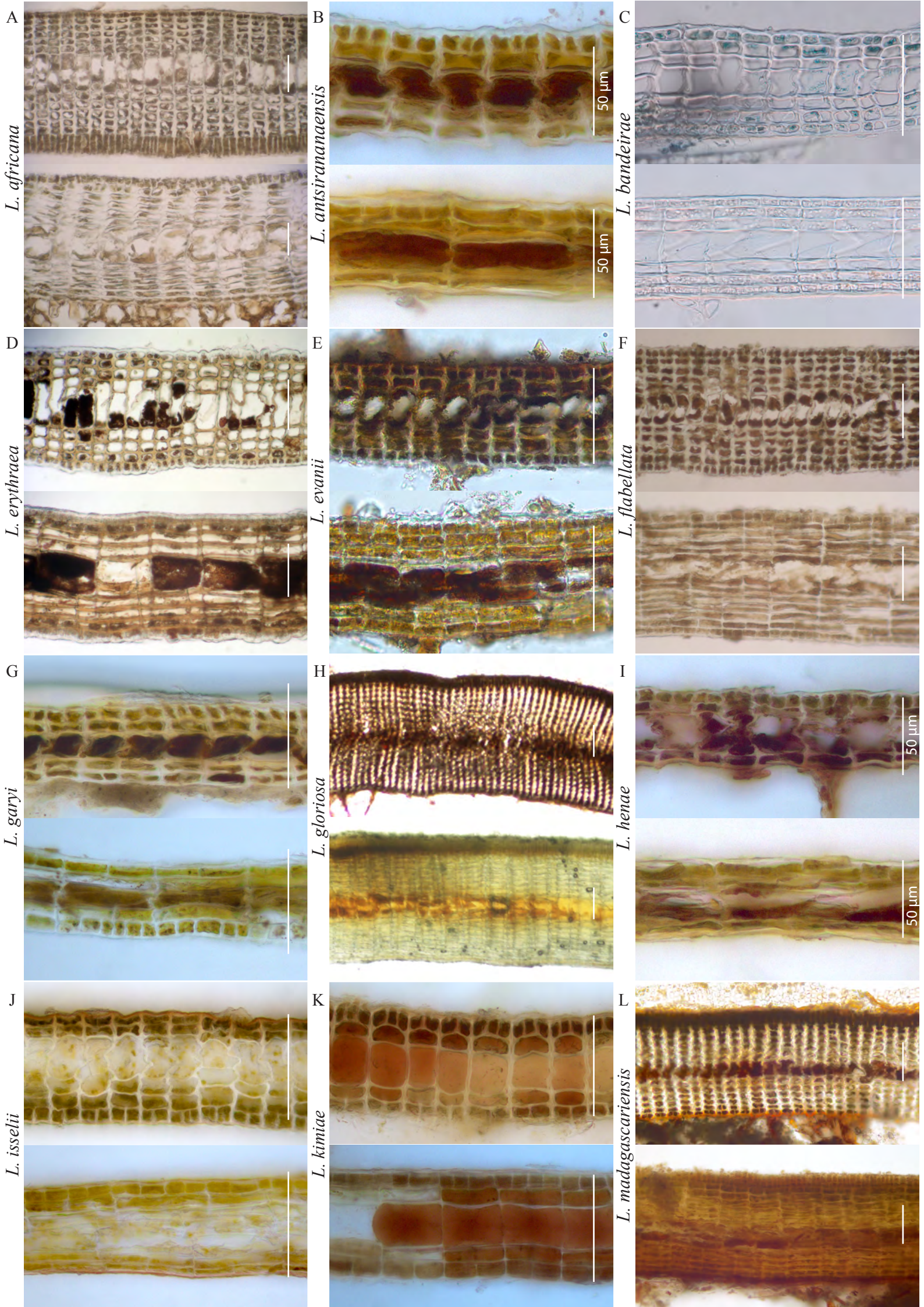




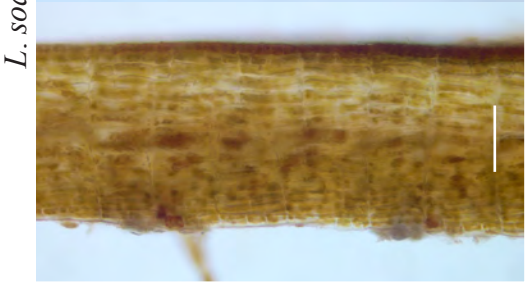
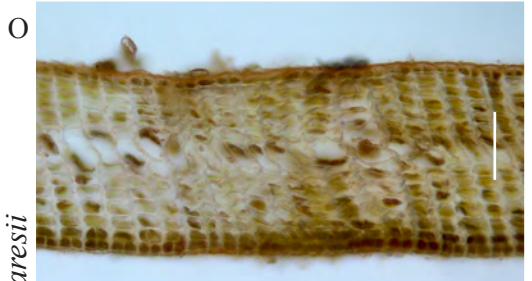
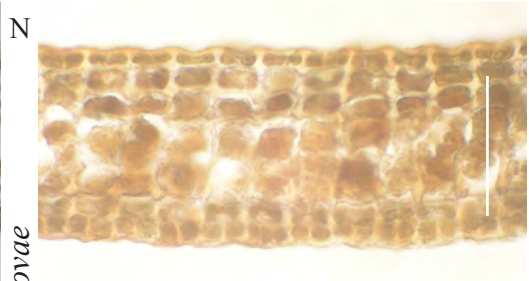
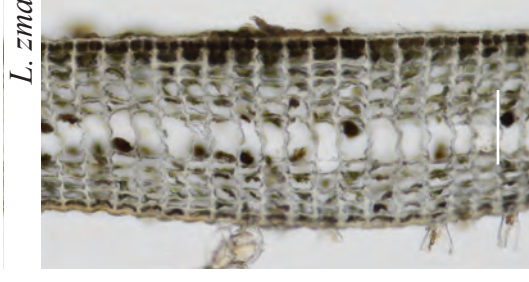
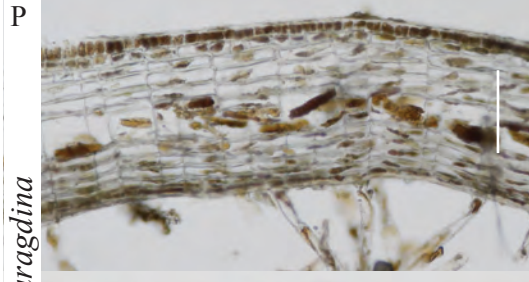
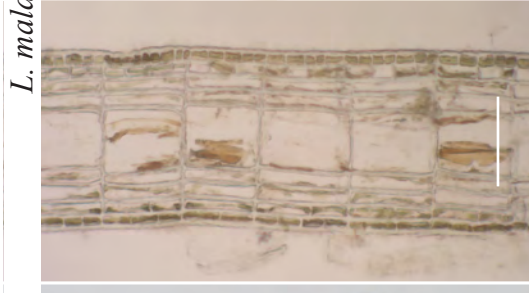


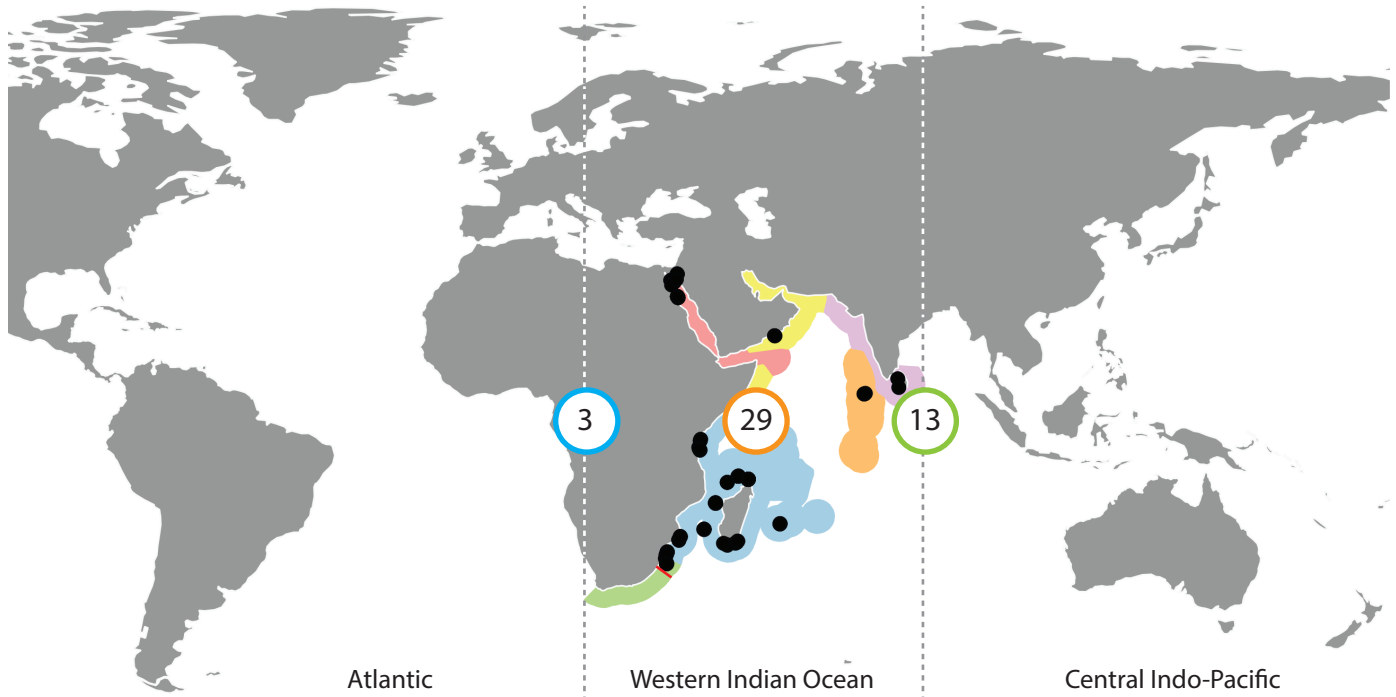












Atlantic

Western Indian Ocean

Central Indo-Pacific

3

29

13

