SYSTEMATICS AND PHYLOGENY

# Shedding new light on old algae: Matching names and sequences in the brown algal genus *Lobophora* (Dictyotales, Phaeophyceae)

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**Abstract** The existence of massive cryptic diversity in algae makes linking DNA-based lineages to existing taxa exceedingly difficult. A better integration of historical collections into modern taxonomic research is therefore highly desirable. Using the brown algal genus *Lobophora* as a test case, we explore the feasibility of linking taxonomic names to clades in modern phylogenies. Despite *Lobophora* being a pantropical genus with probably more than 100 species, traditionally only a handful of species have been recognized. In this study we reevaluated the identity of 17 historical taxa thought to belong to *Lobophora* by attempting DNA amplification of herbarium material as well as specimens recently collected from the type localities (epitypes). In an attempt to assign them to Molecular Operational Taxonomic Units, the obtained sequences were integrated in a global *Lobophora* phylogeny based upon data derived from more than 650 specimens. Our results indicate that although five sequences were obtained from type specimens, exclusive reliance on information preserved in type specimens is problematic. Epitype material proved a more successful way forward, but this route often comes with a considerable degree of uncertainty, especially in tropical regions where the extent of sympatry among *Lobophora* lineages is often considerable. More problematic from a broader perspective is the fact that for 35% of historical taxa, either the type could not be traced or permission was not granted to extract DNA from the types. Such a low accessibility rate may reduce our reliance on type material and jeopardize future efforts to integrate historical taxa into a framework of a modern DNA-based taxonomy.

**Keywords** *Aglaozonia*; *Dictyota*; DNA; herbarium; *Lobophora*; *Pocockiella*; *Ralfsia*; *Stypopodium*; type material; types; *Zonaria*

**Supplementary Material** The Electronic Supplement (Tables S1–S3; Fig. S1; Appendix S1) is available in the Supplementary Data section of the online version of this article at http://ingentaconnect.com/content/iapt/tax; alignments and gene trees are available from TreeBase: http://purl.org/phylo/treebase/phylows/study/TB2:S19589

## INTRODUCTION

Molecular systematics has profoundly altered our view of algal diversity. At lower taxonomic levels, DNA sequence data unveiled the existence of massive cryptic or pseudo-cryptic algal diversity (Maggs & al., 2007; De Clerck & al., 2013), which severely reduced the utility of morphology as the only criterion for species delimitation (Sáez & Lozano, 2005; Cianciola & al., 2010; Leliaert & al., 2014; Verbruggen, 2014). As a side effect, cryptic diversity also makes linking DNA-delimited species

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to formally described taxa exceedingly difficult. Saunders & McDevit (2012b) and De Clerck & al. (2013) described a growing tendency in phycology in which formal algal taxonomy is moving to a more informal system whereby clade-, specimen- or strain-based identifiers are used to communicate biological information. A better integration of historical collections into modern taxonomic research is therefore a pressing need (Hind & al., 2014). Strategies that have been proposed include both generating DNA sequences from type collections and designating epitypes from which sequence data can be readily obtained (Tautz & al., 2003). Although obviously DNA sequence information from the type specimen itself would be favored, it remains to be evaluated how successful this approach is across a broad range of taxa.

A number of case studies have successfully generated DNA sequences from type material of marine macroalgae (e.g., Hughey & al., 2001; Brodie & al., 2007; Gabrielson, 2008a, b; Hughey & Gabrielson, 2012; Saunders & McDevit, 2012a; Hind & al., 2014; Hughey & al., 2014; Sauvage & al., 2014). The focus of these studies has been largely to pinpoint the identity of the types of one or a few species only. A more encompassing study, such as establishing the identity of all types of a specific genus, has not yet been attempted. Moreover, most studies have focused on red and green seaweeds, while obtaining DNA of sufficient quality from brown algae is widely regarded as more challenging (Phillips & al., 2001; Varela-Álvarez & al., 2006; McDevit & Saunders, 2009).

The brown algal genus *Lobophora* J.Agardh forms an excellent test case to investigate the feasibility of integrating sequences from type material in algal taxonomy. *Lobophora* is a morphologically variable genus, ranging from crustose species tightly attached to the substratum, to erect, fan-shaped or dichotomously branched species. The internal structure is composed of 3 to 25 cell layers. A distinctly larger central layer of the medulla is considered a diagnostic vegetative character for the genus. Recent studies have demonstrated that the genus is far more diverse than traditionally assumed (Sun & al., 2012; Vieira & al., 2014; Schultz & al., 2015; Steen & al., 2015). For decades three species were recognized, of which *L. variegata* (J.V.Lamour.) Womersley ex E.C.Oliveira was by far the most commonly reported; the other species being *L. dichotoma* (Simons) P.C.Silva and *L. papenfussii* (W.R.Taylor) Farghaly. Even though a number of additional species were recently described based on morphological criteria only (*Lobophora indica* (M.U.Rao) V.Krishnam. & Baluswami, *L. minima* V.Krishnam. & Baluswami, *L. rickeri* Kraft; Krishnamurthy & Baluswami, 2000; Kraft, 2009), the true magnitude of the diversity was uncovered only by the application of DNA sequence data. For example, in a study focusing on the Asian and Australian *Lobophora* diversity, Sun & al. (2012) recognized nine Molecular Operational Taxonomical Units (MOTUs) of which four were formally described. Subsequently, Vieira & al. (2014) and Schultz & al. (2015) described 10 and 3 new species from New Caledonia and the Western Atlantic Ocean, respectively. At present, 21 *Lobophora* species are flagged as currently accepted in AlgaeBase (Guiry & Guiry, 2015), but it is expected that this number presents only the tip of the iceberg (Vieira, 2015).

Even though the realization of a huge taxonomic deficit (i.e., percentage of the estimated total diversity that currently remains undescribed) in *Lobophora* resulted in an upsurge of newly described species, so far none of these studies has made an attempt to integrate historic taxa, which were described mostly in the 19th century and traditionally regarded as synonyms of *L. variegata*. These names, however, cannot be simply dismissed on an *ad hoc* basis, and it is probable that some of these taxa are conspecific with recently described species, over which they would have priority. Because of the high levels of cryptic diversity, the identity of historic specimens is difficult to ascertain and should preferably be addressed using molecular approaches.

The present study aims to investigate the feasibility of integrating historical collections into modern, DNA-based, algal systematics, at the scale of a higher taxon, and taking the genus *Lobophora* as a case study.

## ■ MATERIALS AND METHODS

**Type material. —** We identified all published taxa (Table 1; Fig. 1) which are either currently regarded or suspected to belong to *Lobophora* (Papenfuss, 1943; Womersley, 1967). Type material of these species was traced in various herbaria and authorization for removing fragments, necessary for molecular and morphological analyses, was requested. To avoid taxonomic confusion due to homonymy we refer to the basionyms of all the types.

**Taxon sampling. —** Taxon sampling consisted of 598 *Lobophora* specimens, 307 of which were sampled in the course of this study. Sampling was carried out from the intertidal down to 90 m deep by snorkeling, scuba diving or box-dredging. *Lobophora* specimens were obtained from more than 40 countries (Fig. 1; Appendix 1). Voucher specimens were preserved in silica gel for DNA extraction and dried as herbarium specimens. In some cases, subsamples were preserved in a 5% formaldehyde solution with seawater for anatomical examination, and dehydrated in silica gel for DNA extraction. Vouchers are deposited in BOL, GENT, LAF, MICH, PC, TFC and UNB. Among the recent collections are specimens from the type localities of five species regarded as *Lobophora* synonyms: *Aglaozonia pacifica* Setch., *A. canariensis* Sauv., *Dictyota variegata* J.V.Lamour., *Pocockiella dichotoma* Simons, *Zonaria nigrescens* Sond. (Fig. 1; Appendix 1).

**DNA extraction, amplification, sequencing and sequence alignments. —** Total genomic DNA of historic type specimens was extracted using a DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany). A standard CTAB-extraction method (De Clerck & al., 2006) was used to extract DNA from recently collected material. Genomic DNA of type specimens was subsequently purified with a Wizard DNA Clean-Up System (Promega, Madison, Wisconsin, U.S.A.) following the manufacturer's instructions. Sequences were generated for one mitochondrial (*cox3*) and two chloroplast genes (*psbA*, *rbcL*). In order to obtain sequences from type specimens, we designed primers (Electr. Suppl.: Table S1) to generate short

**Table 1.** Species and their respective types associated with *Lobophora*.

| | | | | Molecular analyses | | | | | | | Taxonomic criteria | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Basionym | Type locality | Loan requested | Type collections | Type | DNA | *cox3* | *psbA* | *rbcL* | Morphology | Anatomy | Type locality | DNA | Morphology | Current name in *Lobophora* |
| *Dictyota variegata* J.V.Lamour. 1809 | Antilles | ● | CN C7F100 | H | ● | | ● | | Fig. 3A–F | Fig. 4A–F | ● | ● | ● | *L. variegata* (J.V.Lamour.) Womersley ex E.C.Oliveira |
| *Zonaria collaris* C.Agardh 1820 | Jamaica, West Indies | ○ | LD 48006, 47966, 47967[a] | – | | | | | Fig. 3AC | – | | | | – |
| *Zonaria nigrescens* Sond. 1845 | Western Australia, Australia | ○ | MEL 16822[a] | E | ● | ● | ● | ● | Fig. 3S, T | – | ● | | ● | *L. sonderi* C.W.Vieira & al. |
| *Stypopodium fissum* Kütz. 1859 | [Embouchure de la rivière de Gabon, Equatorial Guinea] | ● | L 937-273-354 | H | ● | | | | Fig. 3AA | Fig. 4U, V | | | | – |
| *Stypopodium laciniatum* Kütz. 1859 | Canary Islands, Spain | ● | L 937-55-255 | H | ● | | | | Fig. 3AB | Fig. 4W, X | | | | – |
| *Zonaria latissima* Sond. ex Kütz. 1859 | Eritrea | ● | L 937-46-235 | H | ● | | | | Fig. 3AD | Fig. 4Y, Z | | | | – |
| *Zonaria obscura* Dickie 1875 | Mangaia, Cook Islands | ● | BM 563329 | H | ● | | | ● | Fig. 3AE | – | ● | ● | ● | *L. obscura* (Dickie) C.W.Vieira & al. |
| *Zonaria isselii* Picc. & Grunow 1884 | Massawa, Eritrea | ● | W 19388, 19389, 19390, 19393 | L | ● | | | ● | Fig. 3I | Fig. 4I, J | | ● | | *L. isselii* (Picc. & Grunow) C.W.Vieira & al. |
| *Lobophora nigrescens* J.Agardh 1894 | Dromana Bay, Victoria, Australia | ● | LD 48307 | H | ● | | | | Fig. 3U–Z | pub. | | ● | | *L. nigrescens* J.Agardh |
| *Ralfsia ceylanica* Harv. ex E.S.Barton 1903 | Minicoy, Lakshadweep, India | ● | BM 562896 | H | ● | | | | Fig. 3Q | Fig. 4Q, R | ● | | ● | *L. ceylanica* (Harv. ex E.S.Barton) C.W.Vieira & al. |
| *Aglaozonia canariensis* Sauv. 1905 | Punta del Hidalgo, Tenerife, Canary Islands, Spain | ○ | PC[b] | N | ● | ● | ● | ● | Fig. 3J | Fig. 4K, L | ● | | | *L. canariensis* (Sauv.) C.W.Vieira & al. |
| *Aglaozonia pacifica* Setch. 1922 | Papeete, Tahiti | ● | UC/JEPS 5057a | E | ● | ● | ● | ● | Fig. 3K, L | Fig. 4M, N | ● | | | *L. pacifica* (Setch.) C.W.Vieira & al. |
| *Pocockiella papenfussii* W.R.Taylor 1946 | Bikini Atoll, Marshall Islands | ● | MICH WRT46-232 | I | ● | ● | | | Fig. 3G, H | Fig. 4G, H | | ● | | *L. papenfussii* (W.R.Taylor) Farghaly |
| *Pocockiella dichotoma* Simons 1966 | Kosi Bay, Kwazulu-Natal, South Africa | ● | BOL 150036 | E | ● | ● | ● | ● | Fig. 3M–P | Fig. 4O, P | ● | | ● | *L. dichotoma* (Simons) P.C.Silva |
| *Lobophora indica* (M.U.Rao) V.Krishnam. & Baluswami 2000 | Krusadai Island, India | ○ | KIA 1520[b] | – | | | | | – | – | | | | *L. ceylanica* (Harv. ex E.S.Barton) C.W.Vieira & al. |
| *Lobophora minima* V.Krishnam. & Baluswami 2000 | Neil Island, Andaman Islands, India | ○ | KIA 4320[b] | – | | | | | – | – | | | | – |
| *Lobophora rickeri* Kraft 2009 | Wistari Reef, southern Great Barrier Reef, Queensland, Australia | ○ | MELU KA00335[c] | E | ● | ● | ● | ● | pub. | pub. | ● | | | *L. rickeri* Kraft |

Solid circles: types that were granted for loan and DNA extraction; empty circles: [a]no permission was granted to extract DNA from the type; [b]the type could not be located; [c]the type was not requested on loan since it is preserved in formalin. Abbreviations: E, epitype; H, holotype; I, isotype; L, lectotype, N, neotype; pub., see figures in the original publication.

fragments, 100–200 bp for *cox3*, *psbA* and *rbcL* genes. Often multiple primer combinations were tested. PCR and sequencing conditions are detailed in Table S1 (Electr. Suppl.). The E-Gel Agarose Gel Electrophoresis (Life Technologies, Carlsbad, California, U.S.A.) 2% Agarose was used to select and isolate PCR fragments of interest. If needed, a nested PCR was performed to further amplify the isolated fragments. The following precautions to avoid contamination and produce reproducible and authentic results were used when working with herbarium specimens: physical isolation of all benchwork, two DNA extraction controls for each sample and PCR negative controls (see Saunders & McDevit, 2012a).

A total of 300 *cox3*, 222 *rbcL* and 190 *psbA* sequences were newly generated in this study. The datasets were complemented by 278 *cox3*, 148 *rbcL* and 90 *psbA Lobophora* sequences from GenBank (Appendix 1). Sequences were aligned using MUSCLE (Edgar, 2004) implemented in eBioX v.1.6beta (Barrio & al., 2009; available at http://www.ebioinformatics.org).

**Species delimitation. —** Since traditional morphology-based species delimitation often yields inaccurate estimates of seaweed diversity (Leliaert & al., 2014), we defined species exclusively based on DNA sequence data. To do so we applied the Maximum Likelihood implementation of the GMYC model (Pons & al., 2006; Reid & Carstens, 2012) on the *cox3* dataset. This approach has previously been applied to define *Lobophora* species from New Caledonia (Vieira & al., 2014). Application of the ML-GMYC on *cox3* yielded results highly similar to other delimitation methods such as the Bayesian implementation of the GMYC model (Reid & Carstens, 2012) and Automatic Barcode Gap Discovery (Puillandre & al., 2012) for the same marker *cox3*. In addition, a comparison of species delimitation results based on the mitochondrial *cox3* gene with chloroplast-encoded *rbcL* and *psbA* genes yielded virtually identical results (Vieira & al., 2014). GMYC analyses under a single-threshold were conducted in R (R Development Core Team, 2013) using the package "Splits". The *cox3* ultrametric tree, used to conduct the GMYC species delineation, was constructed using Bayesian analyses in BEAST v1.8.2 (Drummond & al., 2012). A GTR+I+Γ substitution model was identified as the best-fitting model for *cox3*, based on the Akaike information criterion (AIC) using jModelTest v.2 (Darriba & al., 2012). BEAST analyses were run under a relaxed molecular clock in combination with a Yule tree prior. Other priors were set to default. In order to check for convergence of the MCMC chains, we performed two independent runs for $10^7$ generations each, starting from random trees and sampling every $10^4$ generations. MCMC output files of the independent runs were inspected in Tracer v.1.5 (Rambaut & Drummond, 2007) for acceptable effective sample sizes (ESS > 200). A burn-in of 25% was applied once log-likelihood values had stabilized. Maximum clade credibility trees and posterior probability for the nodes were calculated using the post-burn-in trees using TreeAnnotator v.1.8.2 (included in the BEAST package).

**Phylogenetic reconstruction. —** ML analyses of *cox3* (610 bp), *psbA* (919 bp) and *rbcL* (1360 bp) were conducted separately for each gene using RAxML under a GTR+CAT model (RAxML v.8.1.21; Stamatakis, 2014). The robustness of the resulting phylogenies was tested using 1000 replicates of a rapid bootstrap heuristic (Stamatakis, 2006). No apparent topological conflict was detected in supported nodes between the respective gene trees. Alignments and gene trees are available from TreeBase: TB2:S19589.

A concatenated alignment of the *cox3* (610 bp)+*psbA* (919 bp)+*rbcL* (1360 bp) genes was created. The matrix was 80% filled at the gene level. A selection of *Dictyota* J.V.Lamour., *Padina* Adans. and *Zonaria* C.Agardh species was used as outgroup taxa (Appendix 1). A maximum likelihood (ML) species tree was generated from the concatenated

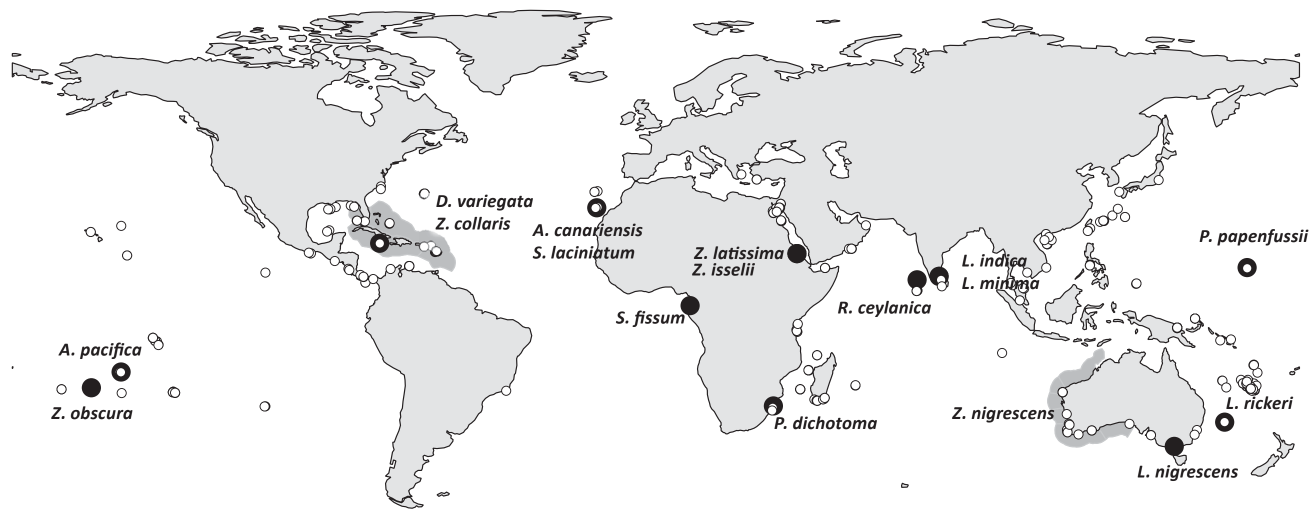


**Fig. 1.** Distribution of *Lobophora* with indication of the localities of 17 *Lobophora* types described prior to 2012 for which no molecular data are available (black circles) and of the sampling localities of recently collected specimens for which molecular data are available (white circles). Type localities of *D. variegata* and *Z. nigrescens*, the Caribbean and Western Australia, respectively, are shown in grey because they are only known on a regional level.

alignment, partitioned by gene and codon position. ML analyses were conducted using RAxML under a GTR+CAT model (Stamatakis, 2014). The robustness of the resulting phylogenies was tested using 1000 replicates of a rapid bootstrap heuristic (Stamatakis, 2006).

**Sequence similarity searches. —** For short sequences obtained from type specimens, sequence similarity searches were performed using BLAST (Altschul & al., 1990) against all available *Lobophora* sequences.

**Morphological analyses. —** Morphological observations of *Lobophora* species included analyses of the external and internal morphology of the specimens. External observations consisted in the description of the general appearance, growth form, size and color of the thallus. For the internal morphology, longitudinal and transverse sections were made of the middle portions of the thallus using a portable medical freezing microtome (Labonord). Alternatively, cross sections by hand were made for some type material and some Caribbean specimens. When possible, a total of 45 measurements were made for each species. Photographs of the sections were taken with a digital camera (Olympus Camedia C-5050 5.0 Megapixel) attached to a compound microscope (Olympus BH-2). All available type specimens were examined for generic confirmation and morphologically compared to the new collections.

## ■ RESULTS

We identified 17 names that are currently accepted or that have been related at some point in their taxonomic history to *Lobophora* and for which no molecular data are available (Table 1; Fig. 1). We failed to obtain the types of *L. indica* and *L. minima*, which should be housed at the Centre for Advanced Studies in Botany, University of Madras. In addition, we did not receive authorization to remove a fragment for DNA extraction for the following types: *Pocockiella dichotoma*, *Zonaria collaris* C.Agardh and *Zonaria nigrescens*. Because of the fragmentary status of the type specimen of *Aglaozonia pacifica* we did not perform molecular analyses. The type of *L. rickeri* is preserved in formaldehyde, largely impeding molecular analyses (but see Campos & Gilbert, 2012), and was therefore not requested on loan. Finally, out of the nine type specimens, we were able to amplify and sequence DNA fragments from five (*D. variegata*, *L. nigrescens* J.Agardh, *P. papenfussii*, *Z. isselii* C.Agardh and *Z. obscura* Dickie; Electr. Suppl.: Fig. S1). Of four species (*A. canariensis*, *A. pacifica*, *P. dichotoma*, *Z. nigrescens*) we obtained sequences from material collected from type localities.

**Sequence similarity and phylogenies. —** Affinities of gene sequences from types were assessed using BLAST searches and phylogenetic trees. Results of the BLAST analyses are given in Electr. Suppl.: Table S2. The GMYC analysis based on the mitochondrial *cox3* marker resulted in delimitation of 109 MOTUs (see Vieira & al., in prep. for further details). Phylogenetic analyses of both single-gene phylogenies and the concatenated phylogeny corroborated the BLAST results, clustering the types with species with which they had the highest similarity (Fig. 2). Out of the five types, *D. variegata* and *Z. obscura* turned out to be identical to an undescribed Caribbean lineage (*Lobophora* sp75) and to *L. crassa* C.W.Vieira & al., respectively (Fig. 2; Electr. Suppl.: Table S2). *Pocockiella papenfussii* was resolved as a singleton sister to an unnamed lineage (*Lobophora* sp23; 98% similarity; *cox3*; Electr. Suppl.: Table S2). The clade *Lobophora* sp23–*P. papenfussii* is sister to *L. densa* C.W.Vieira & al.. Likewise, *Z. isselii* is also resolved as a singleton sister to a clade composed of six species including *L. abscondita* C.W.Vieira & al. (97% similarity; *rbcL*), respectively (Fig. 2, Electr. Suppl.: Table S2). *Lobophora nigrescens* was identical to *L. australis* Z.Sun & al. (100% and 98% similarity; *psbA* and *cox3*). Phylogenetic results confirmed that the newly collected specimens that we associated with *P. dichotoma* based on morphological similarities belong to the genus *Lobophora*. It came out as a distinct species with strong node support (Fig. 2). Specimens collected near the type localities of *A. canariensis* clustered with *L. payriae* N.E.Schultz & al. *Lobophora rickeri* is sister to *L. undulata* C.W.Vieira & al., while *Aglaozonia pacifica* is sister to the clade comprising *L. undulata*, *L. rickeri* and 3 unnamed lineages (*Lobophora* sp18, sp19, sp48; Fig. 2). Placement of the type sequences within *Lobophora* phylogenetic tree overall yielded strong bootstrap support values (>90) except for the node uniting *P. papenfussii* with *Lobophora* sp23 (<60). The clade *P. papenfussii*–*Lobophora* sp23 is, nevertheless, sister to *L. densa* with a node support of 100.

**Morphology. —** All the types examined displayed the characters used to circumscribe *Lobophora*, i.e., a multilayered thallus composed of an outer cortex and inner medulla with the central layer of medullary cells being distinctly larger. Illustrations, descriptions and measurements of morphological characters are given in Figs. 3 and 4 and Table 2.

**Neo- and epitypification. —** For the type material for which molecular data could not be obtained, but for which we acquired specimens from the type localities that corresponded morphologically to the original description, we designated neo- or epitypes. Epitypes were designated for six species: *A. pacifica*, *L. nigrescens*, *L. rickeri*, *P. dichotoma*, *R. ceylanica* and *Z. nigrescens*, and a neotype was designated for *A. canariensis*.

## ■ DISCUSSION

A series of recent papers (Sun & al., 2012; Vieira & al., 2014; Schultz & al., 2015; this study) gradually refined the idea of *Lobophora* being not a species-poor genus, with one widespread species, *L. variegata*, but a highly diverse genus. Currently, 21 species of *Lobophora* are accepted, but the real species diversity is significantly higher. Here, we made an attempt to link the names of 17 taxa, most of them traditionally considered synonyms of *L. variegata* (Table 1), to lineages discovered through gene sequencing. We were able to obtain DNA sequence data from five type specimens. For seven species for which no DNA sequences from authentic type materials could be obtained, specimens were collected at type

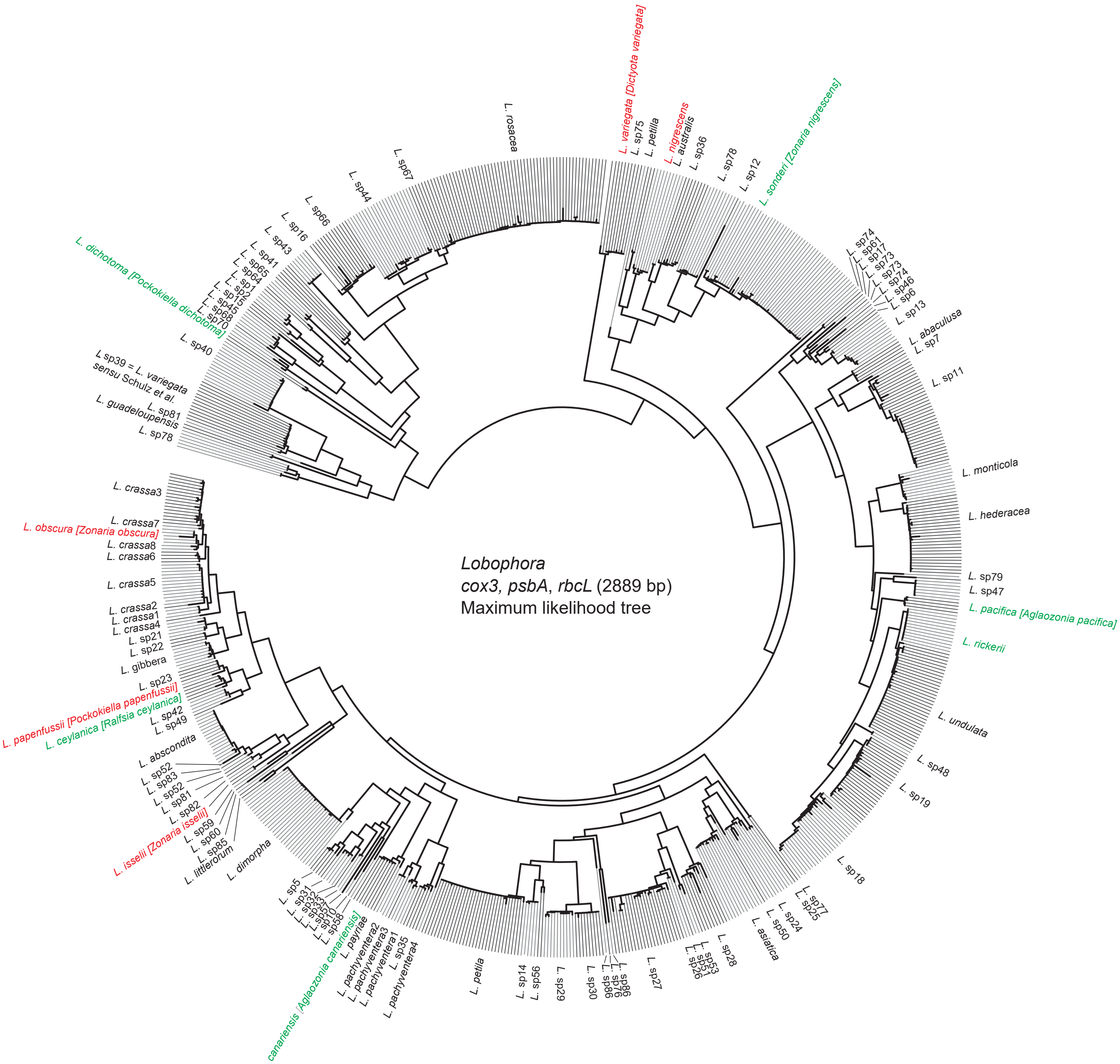


**Fig. 2.** Maximum likelihood phylogenetic tree based on the concatenated alignment of the *cox3* (610 bp)+*psbA* (919 bp)+*rbcL* (1360 bp) dataset. The holotypes are indicated in red font and the epitypes and a neotype in green font.

**Fig. 3.** External morphology of: **A & B,** *Lobophora variegata* holotype[1] and new specimens from **C,** Bahamas (*LAF6912*), **D,** Florida Keys (*LAF6914*), ▶ **E,** Guadeloupe (*IRD11140*), **F,** St. Kitts and Nevis (*LAF6947*); **G,** *L. papenfussii* holotype; **H,** *Lobophora papenfussii* isotype; **I,** *Zonaria issellii* type; **J,** *Aglaozonia canariensis* neotype (*ODC2383*); **K,** *Aglaozonia pacifica* holotype and **L,** epitype[2]; **M,** *Pocockiella dichotoma* holotype and **N,** epitype (*LMD1006*), **O,** *P. dichotoma* holotype close-up and **P,** epitype close-up (*LMD1006*); **Q,** *Ralfsia ceylanica* holotype; **R,** *Lobophora densa* holotype (*IRD7885*); **S,** *Zonaria nigrescens* holotype[3] and **T,** isotype[3]; **U,** *Lobophora nigrescens* sensu Sun & al. (2012) (*JFC0286*)[4], **V,** *L. nigrescens* sensu Sun & al. (2012) (*JFC0215*)[4], **W,** *L. nigrescens* sensu Sun & al. (2012) (*IRD7920*), **X,** *L. nigrescens* sensu Sun & al. (2012) (*IRD7920*); **Y,** *L. nigrescens* holotype[5] and **Z,** isotype[5]; **AA,** *Stypopodium fissum* type; **AB,** *S. laciniatum* type; **AC,** *Zonaria collaris* type; **AD,** *Z. latissima* type; **AE,** *Z. obscura* type; **AF,** *Lobophora crassa* (*CV3040*). — Photo credits: Courtesy of: [1]Chantal Billard of the J.V.F. Lamouroux Herbarium (CN, France), [2]M. Zubia, [3]the staff of the National Herbarium of Victoria (MEL, Melbourne, Australia), [4]H. Verbruggen, [5]Patrik Froden of the Botanical Museum (LD, Sweden).


A
2 cm
B
4 cm
C
2.5 cm
D
2.5 cm
E
1 cm
F
1.5 cm
G
4 cm
H
2 cm
I
1 cm
J
2 cm
K
1 cm
L
1 cm
M
2 cm
N
4 cm
O
0.5 cm
P
0.5 cm
Q
0.5 cm
R
2 cm
S
3 cm
T
3 cm
U
3 cm
V
4 cm
W
0.5 cm
X
0.5 cm
Y
2 cm
Z
4 cm
AA
3 cm
AB
1.5 cm
AC
1 cm
AD
4.5 cm
AE
1 cm
AF
2 cm

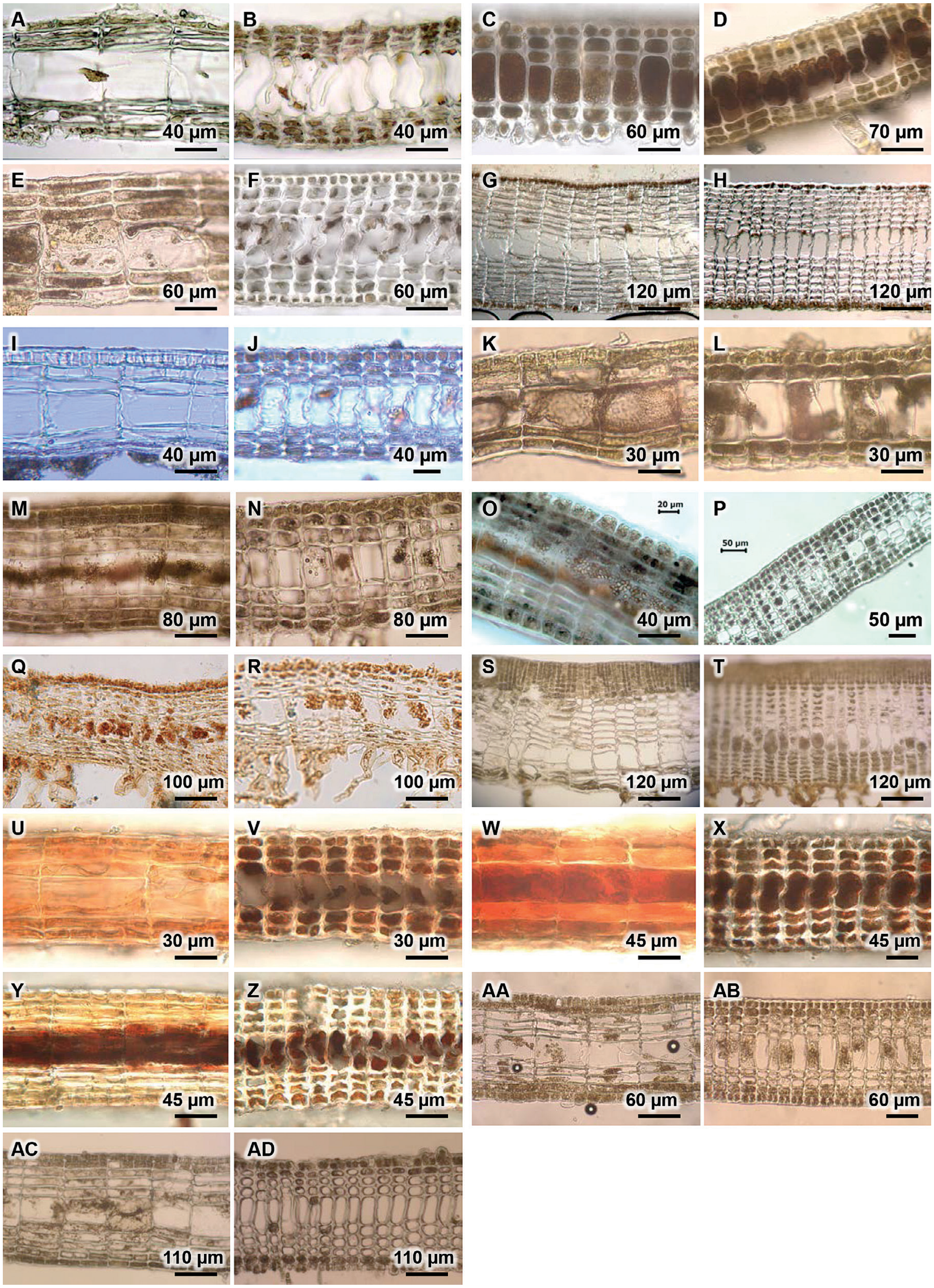


**Fig. 4.** Anatomy of: **A,** *Lobophora variegata* holotype longitudinal section (LS) and **B,** transverse section (TS), **C,** *L. variegata* TS (Florida Keys, *LAF6914*), **D,** *L. variegata* TS (Bahamas, *LAF6912*), **E,** *L. variegata* TS (Guadeloupe, *IRD11140*), **F,** *L. variegata* TS (St. Kitts and Nevis, *LAF6947*); **G,** *L. papenfussii* isotype LS and **H,** TS; **I,** *L. isselii* LS and **J,** TS; **K,** *Aglaozonia canariensis* neotype (*ODC2383*) LS and **L,** TS; **M,** *L. pacifica* epitype (UPF026) LS and **N,** TS; **O,** *L. dichotoma* epitype (*LMD1006*) LS and **P,** TS; **Q,** *Ralfsia ceylanica* holotype LS and **R,** TS; **S,** *Lobophora densa* (*IRD7885*) LS and **T,** TS; **U,** *Stypopodium fissum* holotype LS and **V,** TS; **W,** *S. laciniatum* holotype LS and **X,** TS; **Y,** *Zonaria latissima* holotype LS and **Z,** TS; **AA,** *Lobophora nigrescens* sensu Sun & al. (2012) (*IRD7920*) LS and **AB,** TS; **AC,** *L. crassa* (*CV3040*) LS and **AD,** TS.

**Table 2.** Comparison of morphological and anatomical characters of *Lobophora* type specimens.

| | *L. pacifica* (Setch.) C.W.Vieira[d] (This study) | *L. canariensis* (Sauv.) C.W.Vieira[f] (This study) | *L. dichotoma* (Simons) P.C.Silva[d] (Simons, 1966) | *L. papenfussii* (W.R.Taylor) Farghaly[a] (Taylor, 1950) | *L. papenfussii* (W.R.Taylor) Farghaly[b] (This study) | *L. rickeri* Kraft[a] (Kraft, 2009) | *L. variegata* (J.V.Lamour.) Womersley ex E.C. Oliveira[a] (This study) | *L. variegata* (J.V.Lamour.) Womersley ex E.C. Oliveira[e] (This study) | *L. minima* V.Krishnam. & Baluswami[c] (Krishnamurthy & Baluswami, 2000) | *L. ceylanica* (Harv. ex E.S.Barton) C.W.Vieira & al.[a] (Barton, 1903) | *S. fissum* Kütz.[a] (This study) | *S. laciniatum* Kütz.[a] (This study) | *L. isselii* (Picc. & Grunow) C.W.Vieira & al.[a] (This study) | *Z. latissima* Sond. ex Kütz.[a] (This study) | *L. sonderi* C.W.Vieira & al.[e] (Vieira & al., 2014) | *L. obscura* (Dickie) C.W.Vieira & al.[e] (Vieira & al., 2014) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Thickness | | | | | | | | | | | | | | | | |
| Average | 186±17 | 102±8 | 130±8 | NA | 347±23 | 221±17 | 126±7 | 152±19 | 80 | >200 | 90±10 | 138±13 | 133±18 | 145±20 | 211±8 | 205±17 |
| Min–Max | 168–202 | 80–112 | 117–140 | 385–640 | 308–388 | 110–500 | 112–140 | 124–197 | 80 | 200– | 80–100 | 125–150 | 115–150 | 125–165 | 168–252 | 160 -250 |
| Number of cells | | | | | | | | | | | | | | | | |
| Average | 8 | 5 | 9 | NA | 16 | 10 | 7 | 6 | 4 | NA | 7 | 7 | 7 | 9 | 10 | 10 |
| Min–Max | 6–9 | 5 | 8–9 | 17–23 | 14–17 | 8–9 | 7 | 5–7 | 3–4 | 12– | 6–7 | 7 | 6–7 | 9 | 8–12 | 10 |
| Number of dorsal cells | | | | | | | | | | | | | | | | |
| Average | 4 | 2 | 4 | NA | 8 | 5 | 3 | 3 | 2 | NA | 3 | 3 | 3 | 4 | 5 | 5 |
| Min–Max | 3–4 | 2 | 4 | 8 – 11 | 7–8 | 4–5 | 3 | 2–3 | 1–2 | 7– | 3 | 3 | 3 | 4 | 4–6 | 5 |
| Number of ventral cells | | | | | | | | | | | | | | | | |
| Average | 4 | 2 | 4 | NA | 7 | 3 | 3 | 3 | 1 | 5 | 3 | 3 | 3 | 4 | 4 | 4 |
| Min–Max | 3–4 | 2 | 3–4 | 8 – 11 | 6–8 | 3–4 | 3 | 2–3 | 1 | 4–5 | 2–3 | 3 | 2–3 | 4 | 3–5 | 4 |
| Medulla length | | | | | | | | | | | | | | | | |
| Average | 71±10 | 79±12 | 41±3 | NA | 36±4 | 81±12 | 80±5 | 81±6 | 75 | 50 | 58±8 | 58±8 | 58±8 | 58±8 | 99±16 | 81±12 |
| Min–Max | 60–80 | 60–100 | 36–46 | 57–70 | 28–40 | 68–92 | 74–92 | 68–94 | 75 | 50 | 50–75 | 50–75 | 50–75 | 50–75 | 64–120 | 68–92 |
| Medulla height | | | | | | | | | | | | | | | | |
| Average | 54±7 | 45±6 | 24±3 | NA | 82±12 | 62±9 | 53±5 | 70±11 | 30 | 40 | 30 | 35 | 43±8 | 40 | 57±10 | 60±9 |
| Min–Max | 47–60 | 30–54 | 20–30 | NA | 60–100 | 52–70 | 40–60 | 50–94 | 30 | 40 | 30 | 35 | 35–50 | 40 | 28–76 | 52–70 |
| Medulla width | | | | | | | | | | | | | | | | |
| Average | 30±6 | 33±4 | 29±2 | NA | 77±5 | 30±3 | 27±3 | 33±10 | 30 | NA | 23±3 | 23±3 | 23±3 | 23±3 | 27±3 | 30±3 |
| Min–Max | 24–36 | 30–40 | 25–32 | NA | 68–84 | 27–33 | 24–32 | 23–43 | 30 | NA | 20–25 | 20–25 | 20–25 | 20–25 | 20–32 | 27–33 |
| Dorsal height | | | | | | | | | | | | | | | | |
| Average | 70±13 | 30±3 | 55±4 | NA | 141±11 | 81±3 | 37±3 | 16±3 | 35 | NA | 40 | 50 | 50 | 58±8 | 81±9 | 65±3 |
| Min–Max | 57–83 | 26–34 | 50–62 | NA | 124–175 | 78–84 | 30–40 | 13–25 | 35 | NA | 40 | 50 | 50 | 50–75 | 68–100 | 61–67 |
| Ventral height | | | | | | | | | | | | | | | | |
| Average | 57±3 | 27±3 | 50±5 | NA | 124±14 | 47±3 | 37±3 | 17±2 | 18 | NA | 25±5 | 50 | 40±10 | 58±8 | 72±9 | 62±3 |
| Min–Max | 53–60 | 20–32 | 40–58 | NA | 100–152 | 43–49 | 30–40 | 13–21 | 18 | NA | 30–40 | 50 | 30–50 | 50–75 | 48–92 | 59–65 |
| Thallus | | | | | | | | | | | | | | | | |
| Growth–form | crustose | Prostrate | stipitate | crustose | crustose | crustose | stipitate | stipitate, ruffled | NA | crustose | stipitate | stipitate | NA | stipitate | stipitate | crustose |
| Color | dark brown | orange-brown | brown | dark green to dark brown | dark green to dark brown | NA | dark orange brown | dark orange brown to dark green | NA | dark brown | dark brown | dark brown | dark brown | dark brown | dark brown | dark brown |

NA: data not available. Measurements based on [a]holotype, [b]isotype, [c]original illustrations, [d]epitype, [e]new collections, [f]neotype. *Zonaria collaris* C.Agardh is not presented since no data are available.

localities, from which DNA data was obtained. Integrating these sequences in a global dataset covering a large part of the distribution of *Lobophora* allowed us to confirm the status of *L. variegata*, *L. dichotoma* and *L. papenfussii*. These species were traditionally regarded as separate species. Seven species are reinstated (*Aglaozonia canariensis*, *A. pacifica*, *Lobophora nigrescens*, *Ralfsia ceylanica* Harv. ex E.S.Barton, *Zonaria isselii*, *Z. nigrescens*, *Z. obscura*), while five species (*Lobophora australis*, *L. crassa*, *L. densa*, *L. indica*, *L. payriae*) are reduced to taxonomic synonyms. Below we concisely detail the major taxonomic changes resulting from this study. We refer to the Electr. Suppl.: Appendix S1 for full details.

In line with the study of Schultz & al. (2015), we conclude that *Lobophora variegata* is most likely restricted to the Caribbean Sea. Schultz & al. (2015) proposed to assign the name *L. variegata* to specimens identified from Bermuda and St. Croix, a decision based on morphological similarities. In our study, however, these specimens cluster with *L.* sp39 and not with the sequence generated from the type specimen of *L. variegata* (Fig. 2). The latter is resolved in a clade with specimens from the Bahamas, Florida Keys, Grand Cayman, Guadeloupe, Jamaica and St Kitts and Nevis. This information consequently supersedes the epitypification by Schultz & al. (2015). Our analyses also disclose that *L. papenfussii* (W.R.Taylor) Farghaly, originally described from Bikini Atoll, is a distinct species, closely related to *Ralfsia ceylanica* (= *L. densa*, see further). Although *L. papenfussii* somehow resembles the latter in external morphology (Fig. 3G, H, Q, R; Table 2), sections of the isotype do not show the numerous superficial cell layers diagnostic for *L. densa* (Figs. 4G, H, Q–T). A third species which has traditionally been recognized is *L. dichotoma*, described from Kosi Bay, South Africa (Simons, 1966). *Lobophora dichotoma* presents a very characteristic and atypical morphology. As shown in Fig. 3M–P, *L. dichotoma* has dichotomous, strap-shaped branches very similar to other Dictyotales genera such as *Dictyota*, *Stoechospermum* Kütz. and *Zonaria*. Morphological comparisons of newly collected specimens from Ribbon Reef, Sodwana Bay, 70 km south of Kosi Bay (type locality), with *Lobophora dichotoma* holotype material (BOL!) indicated that they are the same species (Figs. 3M–P, 4O, P). Molecular and anatomical data of newly collected specimens confirm that this species belongs in *Lobophora*. Furthermore, molecular analyses resolved *L. dichotoma* as one of the earliest diverging lineages (Fig. 2).

Sequences and morphological examination of type material of *Zonaria isselii*, described from Massawa, Eritrea and considered a taxonomic synonym of *Lobophora variegata* by Papenfuss (1943), confirm that *Z. isselii* is a distinct *Lobophora* species (Figs. 3I, 4I, J). We therefore reinstate *Z. isselii* Picc. & Grunow (in Piccone, 1884), and propose a new combination. Molecular analyses also disclosed that *Z. obscura* corresponds to *L. crassa* Z.Sun & al. (Sun & al., 2012), which was shown to be a complex of at least four MOTUs (Vieira & al., 2014). The original morphological description of *Z. obscura* fits the description of *L. crassa* (Sun & al., 2012; Vieira & al., 2014; Fig. 3AF), over which it has priority. We propose the resurrection of *Z. obscura* Dickie and a new combination.

*Aglaozonia canariensis* was originally described from the Canary Islands and considered a synonym of *Lobophora variegata* by Papenfuss (1943). Morphological (external and internal) features of newly collected specimens (Figs. 3J, 4K, L) from Punta del Hidalgo, Tenerife, Canary Islands (Spain), match the original description of *A. canariensis* (Sauvageau, 1905). Molecular results confirmed the correct generic identity of *A. canariensis* in *Lobophora* as advocated by Papenfuss (1943). Sequences of the recently described species *L. payriae* by Schultz & al. (2015), however, are identical to those of *L. canariensis*. The former is consequently reduced to a synonym. *Ralfsia ceylanica* was described from Lakshadweep (formerly the Laccadive Islands), India and considered a synonym of *L. variegata* by Papenfuss (1943). It is a crustose species with a thick and unique anatomy (Figs. 3Q, 4Q, R). Two species of *Lobophora*, *L. densa* (Figs. 3R, 4S, T) and *L. indica*, morphologically resemble *R. ceylanica*. *Lobophora densa* was reported from the Maldives, 330 km south of Minicoy, Lakshadweep, India, and *L. indica* from the southeastern coast of India (Krishnamurthy & Baluswami, 2000). Based on morphological similarities and geographic proximity between these three species, we regard these species as synonyms.

*Lobophora nigrescens* J.Agardh (Agardh, 1894) and *Zonaria nigrescens* Sond. (Sonder, 1845) were regarded by Womersley (1967) as taxonomic synonyms of *L. variegata*. Both taxa were described from Australia, the former from "Dromana Bay" (Victoria) and the latter from Western Australia (exact locality unknown). Sun & al. (2012) reinstated *L. nigrescens* J.Agardh based on specimens from Sydney (New South Wales) and Seaford (South Australia). The name *Z. nigrescens* Sond. was not considered as a potential legitimate name for the species. Comparison between *L. nigrescens* J.Agardh (Fig. 3Y, Z) and *Z. nigrescens* Sond. (Fig. 3S, T) show that they are distinct morphological species and that *L. nigrescens* sensu Sun & al. (2012) (Fig. 3U–X; Sun & al., 2012: figs. 4–8) matches the description of *Z. nigrescens* Sond. (Fig. 3S, T), and *L. nigrescens* J.Agardh (Fig. 3Y, Z) that of *L. australis* (Sun & al., 2012: figs. 9–13). We compared the morphology of the type of *Z. nigrescens* Sond., with recently collected specimens from Western Australia. Molecular analyses revealed the presence of at least eight MOTUs in Western Australia. Since among these species only *L. nigrescens* sensu Sun & al. (2012) showed a clear morphological resemblance to *Z. nigrescens*, we propose the reinstatement of *Z. nigrescens*. Transfer to *Lobophora* requires a new name for *Zonaria nigrescens* Sond.

*Lobophora rickeri* was described from the southern Great Barrier Reef, Queensland (Australia) and Lord Howe Island, New South Wales (Australia). Because all specimens from Lord Howe Island matched a single species, we assigned these new collections to *L. rickeri*. *Lobophora rickeri* is epitypified by material newly collected on Lord Howe Island (GWS022754).

*Zonaria collaris* C.Agardh (Agardh, 1820), *Stypopodium fissum* Kütz., *S. laciniatum* Kütz. and *Z. latissima* Sond. ex Kütz. (Kützing, 1859) have not been included for further taxonomic treatment because at present we do not have sufficient data, lacking DNA or additional type locality material.

In this study we used *Lobophora* as a case study to investigate how feasible it is to integrate historical collections into modern, largely DNA-based, algal systematics. We aimed to reassess the taxonomic identity of old types associated with the brown algal genus *Lobophora* and to give to those names a molecular identity. Because of the high species diversity and relatively small number of types, *Lobophora* was selected as a case study to assess whether or not matching type names to modern day sequences is a feasible and worthy endeavor. The first obstacle in completing this task was the accession of the types and the authorization to perform destructive sampling necessary for molecular and anatomical analyses. We were able to access two-thirds of the types requested. The second obstacle was to obtain sequences from types that are, in our case study, up to 206 years old. Using a PCR-based approach, we were able to amplify short fragments of DNA from five types. Although we could probably have increased our success rate slightly by generating lineage-specific primers, successful molecular results rely heavily on the preservation quality of the type material, which is beyond the control of the investigator. A second strategy consisted of obtaining new collections from type localities and morphological comparisons to perform epitypification, and molecular identification of some types. Finally, by means of molecular analyses of types, epitypes and neotype, we were able to reintegrate 11 of the 17 types associated with *Lobophora*. Unfortunately, four *Lobophora* types (*Zonaria collaris*, *Stypopodium fissum*, *S. laciniatum*, *Z. latissima*) remain of uncertain taxonomic identity. At present, according to the rules of the *ICN* there is no option to dismiss or reject those taxa.

Great progress has been made in molecular biology and sequencing technology over the last three decades, which in principle allows us to obtain sequences from herbarium specimens. A number of studies, including this one, were at least partially successful in this endeavor (e.g., Hughey & al., 2001; Brodie & al., 2007; Gabrielson, 2008a, b; Saunders & McDevit, 2012a). So far such initiatives have not been attempted on a large scale, assessing the feasibility of sequencing all types of certain higher taxon. Although containing a relatively small number of old types only, our work was not entirely successful, despite the time and effort spent. However, our effort appears derisory in comparison with the amount of work that will be required with other algal genera such as *Ceramium* Roth, *Cladophora* Kütz., *Nitzschia* Hassall, *Polysiphonia* Grev. or *Scenedesmus* Meyen that have hundreds of types, which in the case of microscopic algae are often preserved as microscope slides.

The alternative approach which consists of sequencing specimens collected at type localities evidently yields a significantly higher success rate, but is unfortunately not entirely free of problems. Especially in areas characterized by a high number of sympatric species, considerable uncertainty is often associated with the selection of a specimen which could serve as an epitype. This problem is only confounded by protologues which are often very vague on the morphological characteristics as well as the type locality itself ("Antilles", "Western Australia"). This uncertainty is illustrated here for the type of *D. variegata*. Schultz & al. (2015) selected a specimen from St. Croix as epitype, while our sequence of an original Lamouroux specimen links *D. variegata* to another Caribbean species (*Lobophora* sp75).

In summary, although attempts to match names of old species to contemporary genetic species are great and noble, they are unfortunately not a panacea, leading inescapably to leave some names unconnected to DNA-based species. Instead of ignoring the problem, taxonomists should become conscious of the need to take measures to prevent old species names from becoming ineffective at fulfilling their "unique identifier" function. For this reason, we may consider the possibility of introducing the concept of Lists of Available Names (LAN) in botanical nomenclature, analogous to the provisions of the *International Code of Zoological Nomenclature* (Art. 79). A LAN, a list of names proposed by a team of taxonomic experts in consultation with the Commission, provides a means to restrict availability of names (Segers & al., 2012). Since names not included in the LAN are no longer considered, it helps stabilizing nomenclature by removing names that cannot be linked to a taxonomic identity. At present, the *ICN* does not offer this possibility, creating a backlog of names that are dragged along with little added value to modern taxonomic research. Especially in groups, such as algae, in which the sheer volume of heterotypic synonyms and names of uncertain affinity, which outnumber the currently accepted species by a factor of 3–5 to 1 (De Clerck & al., 2013), the adoption of a LAN could be an effective tool to restore the role of taxa as anchors to which biological or other information is attached.

## ■ NOMENCLATURAL CHANGES

Based on our analysis of *cox3*, *psbA* and *rbcL* gene sequences we propose the following taxonomic changes and typification. Additional details on the taxonomic history of the taxa are provided in the Electr. Suppl.: Appendix S1.

***Lobophora isselii*** (Picc. & Grunow) C.W.Vieira, De Clerck & Payri, **comb. nov.** ≡ *Zonaria isselii* Picc. & Grunow in Nuovo Giorn. Bot. Ital. 16: 297, pl. VII figs. 1–4; pl. IX fig. 1. 1884 – **Lectotype (designated here):** ERITREA, Massawa, 1870, *Issel sub Piccone 58* (W No. W19388!)

***Lobophora obscura*** (Dickie) C.W.Vieira, De Clerck & Payri, **comb. nov.** ≡ *Zonaria obscura* Dickie in J. Linn. Soc., Bot. 15: 31. 1875 – Holotype: Cook Islands, Mangaia, *W.W. Gill s.n.* (BM barcode BM00563329!)

= *Lobophora crassa* Z.Sun, P.E.Lim & H.Kawai in Phycologia 51: 507–508. 2012 – Holotype: China, Hainan, Xidao Island, on exposed reef face, 16 Dec 2008, *J. Yao & Z. Sun s.n.* (SAP barcode SAP109518 n.v.).

***Lobophora canariensis*** (Sauv.) C.W.Vieira, De Clerck & Payri, **comb. nov.** ≡ *Aglaozonia canariensis* Sauv. in Bull. Stat. Biol. Arcachon 8: 79. 1905 – **Neotype (designated here):** Spain, Punta del Hidalgo, Tenerife, Canary

Islands, May 2015, *O. De Clerck ODC2383* (PC barcode PC0063044).

= *Lobophora payriae* N.E.Schultz, C.W.Schneid. & F.Rousseau, in Eur. J. Phycol. 50: 17. 2015 – Holotype: offshore west of High Point, Bermuda Is., Bermuda, 35–36 m, 24 Aug 2010, *C.W. Schneider BDA0433* (MICH!).

*Note*. – Since the holotype of *Aglaozonia canariensis* is missing in PC (Bruno de Reviers, pers. comm.), we selected a neotype for this name collected at the locality of the original type.

***Lobophora pacifica*** (Setch.) C.W.Vieira, De Clerck & Payri, **comb. nov.** ≡ *Aglaozonia pacifica* Setch. in Univ. Calif. Publ. Bot. 12: 90, pl. 7–22. 1926 – Holotype: French Polynesia, Barrier reef off Papeete, May 1922, *W.A. Setchell 5057a* (UC barcode UC 261174!) – **Epitype (designated here):** French Polynesia, Fa'aa: Vicinity of Papeete, Moorea, Feb 2014, *M. Zubia UPF026* (PC barcode PC0063045).

*Note*. – Since only a very small fragment of the holotype remains in UC, no morphological or molecular analyses were performed on the type material of *Lobophora pacifica*. The type material associated with this name is demonstrably ambiguous and cannot be critically identified. Consequently, an epitype collected at the type locality was selected.

***Lobophora dichotoma*** (Simons) P.C.Silva in Univ. Calif. Publ. Bot. 79: 598. 1996 ≡ *Pocockiella dichotoma* Simons in Bothalia 9: 169, fig. 1. 1966 – Holotype: South Africa, 'n Guma Rocks, Kosi Bay, Sep 1961, *Meyer sub Simons 625* (BOL barcode BOL150036!) – **Epitype (designated here):** South Africa, Ribbon Reef, Sodwana Bay, Oct 2013, *J.J. Bolton, R.A. Anderson & L. Mattio D1006* (BOL barcode BOL150668).

*Note*. – *Lobophora dichotoma* presents a very characteristic and atypical morphology, which differentiates it from any other *Lobophora* species. Although the internal morphology of *Pocockiella dichotoma* accurately fits the generic description of *Lobophora*, the external appearance does not. The holotype at BOL is not available for DNA sequencing. Consequently, we selected an epitype collected close to the type locality that morphologically resembled *L. dichotoma* type.

***Lobophora ceylanica*** (Harv. ex E.S.Barton) C.W.Vieira, De Clerck & Payri, **comb. nov.** ≡ *Ralfsia ceylanica* Harv. ex E.S.Barton in J. Linn. Soc., Bot. 35: 477, pl. 13 fig. 1–4. 1903 – Holotype: India, Sri Lanka. *Ferguson 59* (BM barcode BM000562896!) – **Epitype (designated here):** Maldives, Baa Atoll, May 2009, *C. Payri IRD4605* (PC barcode PC0063012).

= *Lobophora densa* C.W.Vieira, De Clerck & Payri in J. Phycol. 50: 1109–1110. 2014 – Holotype: Ilots du Passage, Chesterfield Islands, New Caledonia, growing on dead coral on outer slope at −50 m, 20 Jul 2008, *C. Payri IRD7885* (PC barcode PC0063012!).

= *Lobophora variegata* var. *indica* M.U.Rao in Desikachary & Raja Rao, Taxonomy of Algae: 772. 1980 ≡ *L. indica* (M.U.Rao) V.Krishnam. & Baluswami in Indian Hydrobiol. 3: 47. 2000 – Holotype: no. *534* (Marine algal herbarium, Andhra University, Waltair, India, n.v.).

*Note*. – Since we could not obtain sequences from the type of *Ralfsia ceylanica* and due to cryptic diversity, the type material associated with this name is demonstrably ambiguous and cannot be critically identified. It is therefore necessary to select an epitype, which is consistent with the original description and material of this name.

***Lobophora sonderi*** C.W.Vieira, De Clerck & Payri, **nom. nov.** ≡ *Zonaria nigrescens* Sond. in Bot. Zeitung (Berlin) 3: 50. 1845, non *L. nigrescens* J.Agardh 1894 – **Lectotype (designated here):** Australia, Western Australia, *L. Preiss s.n.* (MEL barcode MEL 16822!).

*Note*. – Because the name *Lobophora nigrescens* J.Agardh exists, we are not able to transfer Sonder's epithet into *Lobophora*. Consequently, a nomen novum in *Lobophora* is hereby proposed for *Zonaria nigrescens* Sond.

***Lobophora nigrescens*** J.Agardh, Analecta Algol., cont. 1: 23, pl. I fig. 7, 8. 1894 – Holotype: Australia, Dromana, *J. Br. Wilson 15B* (LD barcode LD48307!)

= *Lobophora australis* Z.Sun, Gurgel & H.Kawai in Phycologia 51: 505. 2012 – Holotype: Australia, Coobowie, South Australia, 9 Oct 2009, *H. Kawai s.n.* (SAP barcode 109517 n.v.).

***Lobophora rickeri*** Kraft, Algae of Australia 2: 210, 336. 2009 – Holotype: Australia, Wistari Reef, Southern Great Barrier Reef, Queensland, Nov 1982, *R.W. Ricker & G. Norbury KA-00355* (MELU n.v.) – **Epitype (designated here):** Australia, Lord Howe Island, *G.W. Saunders GWS022754* (UNB).

*Note*. – Because the holotype of *Lobophora rickeri* at MELU was kept in formaldehyde, impeding DNA sequencing, and due to cryptic diversity, the type material associated with this name is demonstrably ambiguous and cannot be critically identified. It is therefore necessary to select an epitype, which is consistent with the original description and material of this name.

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**Appendix 1.** List of taxa used in this study.

Taxon, collector and collection number, location of voucher, country of origin, GenBank accession numbers (*cox3*, *psbA*, *rbcL*).

***Lobophora abaculusa*** C.W.Vieira, Payri & De Clerck, *C. Payri IRD11067* (NOU), New Caledonia, KM487894, –, KM488178; *C. Payri IRD277* (NOU), New Caledonia, KM487893, KM488036, KM488180; *C. Payri IRD7641* (NOU), New Caledonia, KM487895, –, KM488177; *C. Payri IRD7651* (NOU), New Caledonia, KM487897, KM488035, KM488176; *C. Vieira IRD11127* (NOU), New Caledonia, KM487896, KM488034, KM488179; ***Lobophora abscondita*** C.W.Vieira, Payri & De Clerck, *C. Payri IRD7919* (NOU), New Caledonia, –, KM488064, KM488129; *C. Payri PAP509* (NOU), Papua New Guinea, KU353162*, KU352935*, KU353030*; *C. Payri PAP513* (NOU), Papua New Guinea, KU353163*, KU352936*, KU353031*; *C. Vieira CV3058* (NOU), New Caledonia, –, KM488065, –; *C. Vieira CV3060* (NOU), New Caledonia, –, KM488061, –; *C. Vieira CV3076* (NOU), New Caledonia, –, KM488062, KM488128; *C. Vieira CV3088* (NOU), New Caledonia, KM487773, –, –; *C. Vieira CV3091* (NOU), New Caledonia, KM487774, –, –; *C. Vieira CV3096* (NOU), New Caledonia, KM487775, KM488067, KM488131; *C. Vieira CV3097* (NOU), New Caledonia, KM487776, –, KM488132; *C. Vieira CV3098* (NOU), New Caledonia, KM487778, –, –; *C. Vieira IRD10198* (NOU), New Caledonia, –, KM488063, KM488130; *C. Vieira IRD11057* (NOU), New Caledonia, KM487777, KM488068, KM488134; *C. Vieira IRD11122* (NOU), New Caledonia, –, KM488066, KM488133; ***Lobophora asiatica*** Z.Sun, J.Tanaka & H.Kawai, *C. Vieira CV3068* (NOU), New Caledonia, KM487806, KM488073, KM488194; *H. Kudo PALBB025* (Yamagata University), Palau, –, –, AB096897; *J. Costa & al. HV03588* (MELU), Australia, KU353337*, –, –; *J.J. Bolton & al. LMD1598* (BOL), South Africa, –, –, KU353136*; *J. Yao & Z. Sun KU-d5130* (SAP), China, AB665365, –, AB665270; *J. Yao & Z. Sun Sun1* (KU), China, KU353338*, –, KU353137*; *P.E. Lim KU-d3965* (SAP), Malaysia, AB665368, –, AB665273; *T. Hanyuda NNW16* (SAP), Japan, –, –, AB548390; *T. Kitayama KU-d7621* (SAP), China, AB665366, –, AB665271; *T. Van Nguyen & O. De Clerck NVT052* (GENT), Viet Nam, KU353339*, –, –; *Z. Sun s.n.* (SAP 109520), Japan, AB665367, –, AB665272; ***Lobophora canariensis*** (Sauv.) C.W.Vieira, De Clerck & Payri,

**Appendix 1.** Continued.

*L. Charles & al. 0143229* (PC), Guadeloupe, KR260356 , –, –; *L. Charles & al. 0143233* (PC), Guadeloupe, KR260351 , –, –; *L. Le Gall & al. 0143228* (PC), Guadeloupe, KR260357 , –, –; *O. De Clerck ODC2202* (GENT), Tenerife, KU353276*, KU352871*, KU353057*; *O. De Clerck ODC2376* (GENT), Tenerife, KU353275*, KU352870*, KU353058*; *O. De Clerck ODC2383* (GENT), Tenerife, KU353274*, KU352872*, KU353059*; *T.R. Popolizio BDA1280* (CWS), Bermuda, KR260349 , –, –; ***Lobophora ceylanica*** (Harv. ex E.S.Barton) C.W.Vieira, De Clerck & Payri, *C. Payri IRD4605* (NOU), Maldives, KM487800, –, KM488136; *C. Payri IRD4677* (NOU), Maldives, KU353188*, –, KM488137; *C. Payri IRD4882* (NOU), Maldives, KM487801, –, KM488138; *C. Payri IRD7885* (NOU), New Caledonia, KM487799, –, KM488135; *M. Zubia JN040* (NOU), Juan de Nova Island, KU353187*, –, KU353028*; ***Lobophora dichotoma*** (Simons) P.C.Silva, *E. Coppejans MAD1928* (PC), Madagascar, –, KU352969*, –; *J.J. Bolton & al. LMD1006* (BOL), South Africa, KU353394, KU352970*, KU353000*; ***Lobophora dimorpha*** C.W.Vieira, Payri & De Clerck, *C. Payri & al. IRD2634* (NOU), Vanuatu, –, –, KU353157*; *C. Vieira CV3044* (NOU), New Caledonia, KM487887, KM488081, KM488190; *C. Vieira CV3053* (NOU), New Caledonia, KM487866, KM488078, KM488191; *C. Vieira CV3054* (NOU), New Caledonia, KM487872, KM488079, KM488192; *C. Vieira CV3099* (NOU), New Caledonia, KM487869, –, –; *C. Vieira CV3126* (NOU), New Caledonia, KM487874, –, –; *C. Vieira CV3127* (NOU), New Caledonia, KM487880, –, –; *C. Vieira CV3128* (NOU), New Caledonia, KM487885, –, –; *C. Vieira CV3129* (NOU), New Caledonia, KM487881, –, –; *C. Vieira CV3130* (NOU), New Caledonia, KM487871, –, –; *C. Vieira CV3131* (NOU), New Caledonia, KM487867, –, –; *C. Vieira CV3132* (NOU), New Caledonia, KM487875, –, –; *C. Vieira CV3136* (NOU), New Caledonia, KM487876, –, –; *C. Vieira CV3137* (NOU), New Caledonia, KM487868, –, –; *C. Vieira CV3138* (NOU), New Caledonia, KM487882, KM488076, KM488187; *C. Vieira CV3139* (NOU), New Caledonia, KM487883, KM488083, KM488186; *C. Vieira CV3140* (NOU), New Caledonia, KM487877, –, KM488185; *C. Vieira CV3143* (NOU), New Caledonia, KM487878, –, –; *C. Vieira CV3144* (NOU), New Caledonia, KM487870, –, –; *C. Vieira CV3145* (NOU), New Caledonia, KM487889, –, –; *C. Vieira CV3146* (NOU), New Caledonia, KM487879, –, –; *C. Vieira CV3148* (NOU), New Caledonia, KM487886, –, –; *C. Vieira CV3233* (NOU), New Caledonia, –, KM488082, KM488188; *C. Vieira IRD10218* (NOU), New Caledonia, KM487873, –, –; *C. Vieira IRD10219* (NOU), New Caledonia, KM487884, –, –; *C. Vieira IRD10220* (NOU), New Caledonia, KM487888, KM488080, KM488193; *C. Vieira IRD10227* (NOU), New Caledonia, KM487890, KM488077, KM488189; ***Lobophora gibbera*** C.W.Vieira, Payri & De Clerck, *C. Vieira CV3256* (NOU), New Caledonia, KM487796, –, KU353002*; *C. Vieira CV3257* (NOU), New Caledonia, KM487798, –, KU353003*; *C. Vieira IRD11058* (NOU), New Caledonia, KM487795, KM488070, KM488139; *C. Vieira IRD11125* (NOU), New Caledonia, KM487797, –, KU353004*; *J.L. Menou & C. Payri IRD275* (NOU), New Caledonia, KM487794, KM488069, EU579954; *M. Zubia EUR262* (BOL), Europa Island, KU353164*, –, –; ***Lobophora guadeloupensis*** N.E.Schultz, F.Rousseau & L.Le Gall, *E. Vassard & al. 0143254* (PC), Guadeloupe, KR260345 , –, –; *F. Rousseau & al. 0143243* (PC), Guadeloupe, KR260344, –, –; ***Lobophora hederacea*** C.W.Vieira, Payri & De Clerck, *C. Payri IRD7621* (NOU), New Caledonia, KM487819, –, KM488163; *C. Payri IRD7880* (NOU), New Caledonia, KM487821, KM488051, KM488165; *C. Vieira CV3106* (NOU), New Caledonia, KM487824, –, –; *C. Vieira CV3163* (NOU), New Caledonia, KM487830, –, –; *C. Vieira CV3165* (NOU), New Caledonia, KM487828, –, –; *C. Vieira CV3167* (NOU), New Caledonia, KM487831, –, –; *C. Vieira CV3168* (NOU), New Caledonia, KM487832, KM488056, KM488164; *C. Vieira CV3169* (NOU), New Caledonia, KM487833, KM488057, KM488171; *C. Vieira CV3170* (NOU), New Caledonia, KM487834, –, KM488170; *C. Vieira CV3171* (NOU), New Caledonia, KM487825, –, –; *C. Vieira CV3172* (NOU), New Caledonia, KM487826, –, –; *C. Vieira CV3173* (NOU), New Caledonia, KM487835, –, –; *C. Vieira CV3174* (NOU), New Caledonia, KM487836, –, –; *C. Vieira CV3175* (NOU), New Caledonia, KM487820, –, –; *C. Vieira CV3184* (NOU), New Caledonia, KM487837, –, –; *C. Vieira CV3234* (NOU), New Caledonia, –, KM488055, KM488167; *C. Vieira IRD10189* (NOU), New Caledonia, KM487827, KM488048, KM488174; *C. Vieira IRD10190* (NOU), New Caledonia, KM487823, KM488049, KM488169; *C. Vieira IRD10191* (NOU), New Caledonia, KM487822, KM488053, KM488172; *C. Vieira IRD10192* (NOU), New Caledonia, KU353245*, KM488052, KM488173; *C. Vieira IRD10193* (NOU), New Caledonia, –, KM488050, KM488166; *C. Vieira IRD10225* (NOU), New Caledonia, KM487829, –, –; *C. Vieira IRD11124* (NOU), New Caledonia, –, KM488054, KM488168; ***Lobophora littlerorum*** C.W.Schneid., N.E.Schultz & L.Le Gall, *L. Charles & al. 0533605* (PC), Guadeloupe, KR260347 , –, –; *L. Charles & al. 0533606* (PC), Guadeloupe, KR260348 , –, –; ***Lobophora monticola*** C.W.Vieira, Payri & De Clerck, *C. Payri IRD7640* (NOU), New Caledonia, KM487812, –, –; *C. Payri IRD7878* (NOU), New Caledonia, KM487817, KM488046, KM488162; *C. Payri IRD7882* (NOU), New Caledonia, KM487818, KM488047, KM488159; *C. Payri IRD7889* (NOU), New Caledonia, KU353244*, –, –; *C. Payri IRD7897* (NOU), New Caledonia, KM487813, –, –; *C. Vieira IRD10199* (NOU), New Caledonia, KM487815, –, –; *F. Houlbreque IRD10200* (NOU), New Caledonia, KM487816, –, KM488160; *J.L. Menou & C. Payri IRD7631* (NOU), New Caledonia, KM487814, –, KM488161; ***Lobophora nigrescens*** J.Agardh, *H. Kawai s.n.* (SAP 109517), Australia, AB665369, –, AB665258; *H. Verbruggen & L. Tyberghein HV2431* (GENT), Australia, KU353377*, KU352864*, –; *H. Verbruggen & L. Tyberghein HV2438* (GENT), Australia, KU353375*, –, –; *H. Verbruggen & L. Tyberghein HV2476* (GENT), Australia, KU353376*, KU352863*, –; *L. Tyberghein & H. Verbruggen LT0286* (GENT), Australia, KU353378*, –, –; *W.J. Lee & E.C. Yang SAL36* (NCUE), Australia, –, DQ866944, DQ866924; *G.W. Saunders GWS025025* (UNB), Australia, KU353373*, –, –; *S. Berrin & al. HV03610* (MELU), Australia, KU353374*, –, –; ***Lobophora obscura* 1** (Dickie) C.W.Vieira, De Clerck & Payri, *H. Kawai KU-d3692* (SAP), U.S.A., AB665370, –, AB665260; *H. Kawai KU-d3694* (SAP), U.S.A., AB665371, –, AB665261; *Z. Sun KU-d9520* (SAP), Japan, AB665373, –, AB665264; ***Lobophora obscura* 2** (Dickie) C.W.Vieira, De Clerck & Payri, *C. Vieira IRD10187* (NOU), New Caledonia, KM487780, KM488072, –; ***Lobophora obscura* 3** (Dickie) C.W.Vieira, De Clerck & Payri, *C. Payri & A.D.R. N'Yeurt IRD1394* (NOU), Solomon Islands, –, –, KU353014*; *C. Payri IRD10233* (NOU), Papua New Guinea, KU353174*, KU352949*, KU353009*; *C. Payri IRD10237* (NOU), Papua New Guinea, KU353179*, KU352950*, KU353008*; *C. Payri IRD10238* (NOU), Papua New Guinea, KU353175*, –, –; *C. Payri IRD11137* (NOU), Papua New Guinea, KU353176*, –, KU353011*; *C. Payri IRD11138* (NOU), Papua New Guinea, KU353180*, –, –; *C. Payri IRD11158* (NOU), Papua New Guinea, KU353172*, KU352946*, KU353015*; *C. Payri PAP185* (NOU), Papua New Guinea, KU353178*, KU352947*, KU353010*; *C. Payri PAP662* (NOU), Papua New Guinea, KU353177*, KU352948*, KU353013*; *C. Payri PCT41* (NOU), Papua New Guinea, KU353169*, –, KU353012*; *F. Leliaert PNGMAD3528* (GENT), Papua New Guinea, KU353168*, –, –; *F. Leliaert PNGMAD4020* (GENT), Papua New Guinea, KU353167*, –, –; *F. Leliaert PNGMAD4072* (GENT), Papua New Guinea, KU353170*, –, –; *F. Leliaert PNGMAD4083* (GENT), Papua New Guinea, KU353171*, –, –; *H. Verbruggen PHV419* (MELU), Papua New Guinea, KU353173*, –, –; *J. Yao & Z. Sun s.n.* (SAP 1096518), China, AB665372, –, AB665262; ***Lobophora obscura* 4** (Dickie) C.W.Vieira, De Clerck & Payri, *C. Payri IRD7884* (NOU), New Caledonia, KM487779, –, KM488141; ***Lobophora obscura* 5** (Dickie) C.W.Vieira, De Clerck & Payri, *C. Vieira CV3089* (NOU), New Caledonia, KM487789, –, KM488143; *C. Vieira CV3092* (NOU), New Caledonia, KM487787, KM488071, KM488144; *C. Vieira CV3093* (NOU), New Caledonia, KM487793, –, –; *C. Vieira CV3094* (NOU), New Caledonia, KM487782, –, –; *C. Vieira CV3115* (NOU), New Caledonia, KM487781, –, –; *C. Vieira CV3116* (NOU), New Caledonia, KM487790, –, –; *C. Vieira CV3117* (NOU), New Caledonia, KM487788, –, –; *C. Vieira CV3119* (NOU), New Caledonia, KM487785, –, –; *C. Vieira CV3120* (NOU), New Caledonia, KM487783, –, –; *C. Vieira CV3121* (NOU), New Caledonia, KM487786, –, –; *C. Vieira CV3122* (NOU), New Caledonia, KM487791, –, –; *C. Vieira CV3123* (NOU), New Caledonia, KM487792, –, –; *C. Vieira IRD10188* (NOU), New Caledonia, KM487784, –, KM488142; ***Lobophora obscura* 6** (Dickie) C.W.Vieira, De Clerck & Payri, *J.J.Bolton & al. LMD1671* (BOL), South Africa, –, KU352942*, KU353005*; *J.J. Bolton & al. LMD1685* (BOL), South Africa, –, KU352943*, KU353006*; *L. Le Gall MAD2138* (PC), Madagascar, LN831819, –, –; *T. Schils & al. MUS2098* (GENT), Oman, –, KU352944*, KU353007*; ***Lobophora obscura* 7** (Dickie) C.W.Vieira, De Clerck & Payri, *T. Van Nguyen & O. De Clerck NVT093* (GENT), Viet Nam, KU353166*, KU352951*, KU353019*; ***Lobophora obscura* 8** (Dickie) C.W.Vieira, De Clerck & Payri, *C. Payri IRD7992* (NOU), French Polynesia, –, –, KU353016*; *C. Payri IRD8157* (NOU), French Polynesia, –, KU352952*, KU353018*; *C. Payri IRD8918* (NOU), French Polynesia, KU353181*, KU352954*, –; *C. Payri IRD8919* (NOU), French Polynesia, KU353183*, KU352945*, KU353017*; *C. Payri IRD8920* (NOU), French Polynesia, KU353184*, –, –; *C. Payri IRD8921* (NOU), French Polynesia, KU353182*, KU352953*, KU353020*; ***Lobophora pachyventera* 1** Z.Sun, P.-E.Lim, J.Tanaka & H.Kawai, *H. Kawai KU-d3577* (SAP), China, AB665378, –, AB665267; *J. Yao & Z. Sun KU-d5110* (SAP), China, AB665376, –, AB665265; *J. Yao & Z. Sun KU-d5112* (SAP), China, AB665377, –, AB665266; *W.J. Lee & I. -K. Hwang TAHL20* (NCUE), Taiwan, –, DQ866942, DQ866930; ***Lobophora pachyventera* 2** Z.Sun, P.-E.Lim, J.Tanaka & H.Kawai, *C. Payri & al. IRD2635* (NOU), Vanuatu, –, –, KU353046*; *C. Payri IRD7881* (NOU), New Caledonia, KM487803, KM488059, KM488127; *C. Vieira CV3095* (NOU), New Caledonia, KM487802, KM488058, KM488126; ***Lobophora pachyventera* 3** Z.Sun, P.-E.Lim, J.Tanaka & H.Kawai, *J. Tanaka & Z. Sun s.n.* (SAP 109519),

**Appendix 1.** Continued.

Japan, AB665379, –, AB665268; ***Lobophora pachyventera*** **4** Z.Sun, P.-E.Lim, J.Tanaka & H.Kawai, *P.E. Lim KU-d5184* (SAP), Malaysia, AB665380, –, AB665269; ***Lobophora pacifica*** (Setch.) C.W.Vieira, De Clerck & Payri *C. Payri CP08407* (NOU), French Polynesia, KU353241*, –, KU353094*; *C. Payri CP08432* (NOU), French Polynesia, KU353242*, –, KU353097*; *C. Vieira IRD11120* (NOU), New Caledonia, KM487838, –, KU353096*; *C. Vieira IRD11121* (NOU), New Caledonia, KM487839, –, KU353095*; *M. Zubia UPF026* (PC), French Polynesia, KX581361*, –, KX581362*; ***Lobophora petila*** C.W.Vieira, Payri & De Clerck, *C. Payri IRD11139* (NOU), Papua New Guinea, KU353302*, –, –; *C. Payri IRD7657* (NOU), New Caledonia, –, –, KM488197; *C. Payri IRD7877* (NOU), New Caledonia, KM487808, –, –; *C. Payri IRD9831* (NOU), Papua New Guinea, KU353313*, –, –; *C. Payri IRD9832* (NOU), Papua New Guinea, KU353317*, –, –; *C. Payri IRD9833* (NOU), Papua New Guinea, KU353312*, –, –; *C. Payri IRD9834* (NOU), Papua New Guinea, KU353311*, –, –; *C. Payri IRD9835* (NOU), Papua New Guinea, KU353314*, –, –; *C. Payri IRD9836* (NOU), Papua New Guinea, KU353318*, –, –; *C. Payri IRD9837* (NOU), Papua New Guinea, KU353324*, –, –; *C. Payri IRD9838* (NOU), Papua New Guinea, KU353301*, –, –; *C. Payri IRD9839* (NOU), Papua New Guinea, KU353309*, –, –; *C. Payri IRD9840* (NOU), Papua New Guinea, KM487807, KU352930*, –; *C. Payri IRD9841* (NOU), Papua New Guinea, KU353308*, –, –; *C. Payri IRD9842* (NOU), Papua New Guinea, KU353307*, –, –; *C. Payri IRD9843* (NOU), Papua New Guinea, KU353306*, –, –; *C. Payri IRD9844* (NOU), Papua New Guinea, KU353305*, –, –; *C. Payri IRD9845* (NOU), Papua New Guinea, KU353315*, –, –; *C. Payri PAP557*b (NOU), Papua New Guinea, KU353310*, –, –; *C. Payri PAP950* (NOU), Papua New Guinea, KM487810, KU352931*, –; *F. Leliaert PNGMAD3160* (GENT), Papua New Guinea, KU353321*, –, –; *F. Leliaert PNGMAD3173* (GENT), Papua New Guinea, KU353319*, –, –; *F. Leliaert PNGMAD3825* (GENT), Papua New Guinea, KU353320*, –, –; *F. Leliaert PNGMAD4033* (GENT), Papua New Guinea, KU353322*, –, –; *H. Verbruggen PHV385* (MELU), Papua New Guinea, KU353323*, –, –; *H. Verbruggen PHV394* (MELU), Papua New Guinea, KU353304*, –, –; *H. Verbruggen PHV440* (MELU), Papua New Guinea, KU353316*, –, –; *H. Verbruggen PHV551* (MELU), Papua New Guinea, KU353303*, –, –; *H. Verbruggen PHV773* (MELU), Papua New Guinea, KU353300*, –, –; *H. Verbruggen PHV900* (MELU), Papua New Guinea, KM487809, KM488060, KM488196; ***Lobophora rickeri*** Kraft, *G.W. Saunders GWS022463* (UNB), Vanuatu, –, –, KU353065*; *G.W. Saunders GWS022754* (UNB), Australia, KU353237*, KU352893*, KU353062*; *G.W. Saunders GWS023034* (UNB), Australia, KU353236*, KU352896*, KU353068*; *G.W. Saunders GWS023070* (UNB), Australia, KU353235*, KU352897*, KU353069*; *G.W. Saunders GWS023071* (UNB), Australia, KU353234*, KU352894*, KU353063*; *G.W. Saunders GWS023104* (UNB), Australia, KU353231*, –, –; *G.W. Saunders GWS023108* (UNB), Australia, KU353232*, –, –; *G.W. Saunders GWS023129* (UNB), Australia, –, KU352895*, KU353128*; *G.W. Saunders GWS023132* (UNB), Australia, KU353233*, –, KU353064*; *G.W. Saunders GWS023589* (UNB), Australia, KU353238*, –, KU353070*; *G.W. Saunders GWS025798* (UNB), Philippines, –, –, KU353067*; *M. Zubia ARV317* (NOU), Reunion, –, –, KU353066*; ***Lobophora rosacea*** C.W.Vieira, De Clerck & Payri, *C. Payri IRD253* (NOU), New Caledonia, –, KM488019, KM488094; *C. Payri IRD7876* (NOU), New Caledonia, KM487910, KM488016, KM488108; *C. Payri IRD7879* (NOU), New Caledonia, KM487938, –, KM488109; *C. Payri IRD7888* (NOU), New Caledonia, –, KM488015, KM488093; *C. Payri IRD7918* (NOU), New Caledonia, –, KM488018, KM488112; *C. Vieira CV3056* (NOU), New Caledonia, –, KM488014, KM488104; *C. Vieira CV3063* (NOU), New Caledonia, –, KM488003, KM488102; *C. Vieira CV3065* (NOU), New Caledonia, –, KM488004, KM488113; *C. Vieira CV3070* (NOU), New Caledonia, KM487911, KM488011, KM488105; *C. Vieira CV3071* (NOU), New Caledonia, KM487908, KM488012, KM488095; *C. Vieira CV3072* (NOU), New Caledonia, KM487916, KM488005, KM488102; *C. Vieira CV3073* (NOU), New Caledonia, KM487904, –, –; *C. Vieira CV3085* (NOU), New Caledonia, KM487939, –, –; *C. Vieira CV3101* (NOU), New Caledonia, KM487940, –, –; *C. Vieira CV3105* (NOU), New Caledonia, KM487923, –, –; *C. Vieira CV3107* (NOU), New Caledonia, KM487929, –, –; *C. Vieira CV3108* (NOU), New Caledonia, KM487898, –, –; *C. Vieira CV3111* (NOU), New Caledonia, KM487931, –, –; *C. Vieira CV3112* (NOU), New Caledonia, KM487927, –, –; *C. Vieira CV3166* (NOU), New Caledonia, KM487926, –, –; *C. Vieira CV3176* (NOU), New Caledonia, KM487935, –, –; *C. Vieira CV3177* (NOU), New Caledonia, KM487925, –, –; *C. Vieira CV3178* (NOU), New Caledonia, KM487917, –, –; *C. Vieira CV3179* (NOU), New Caledonia, KM487918, –, –; *C. Vieira CV3180* (NOU), New Caledonia, KM487919, –, –; *C. Vieira CV3183* (NOU), New Caledonia, KM487930, –, –; *C. Vieira CV3185* (NOU), New Caledonia, KM487924, –, –; *C. Vieira CV3188* (NOU), New Caledonia, KM487922, –, –; *C. Vieira CV3189* (NOU), New Caledonia, KM487921, –, –; *C. Vieira CV3190* (NOU), New Caledonia, KM487932, –, –; *C. Vieira CV3191* (NOU), New Caledonia, KM487933, –, –; *C. Vieira CV3194* (NOU), New Caledonia, KM487934, –, –; *C. Vieira CV3195* (NOU), New Caledonia, KM487920, –, –; *C. Vieira IRD10196* (NOU), New Caledonia, KM487914, KM488008, KM488099; *C. Vieira IRD10201* (NOU), New Caledonia, KM487942, –, –; *C. Vieira IRD10203* (NOU), New Caledonia, KM487941, –, –; *C. Vieira IRD10205* (NOU), New Caledonia, KM487900, KM488022, KM488106; *C. Vieira IRD10206* (NOU), New Caledonia, KM487899, KM488007, KM488114; *C. Vieira IRD10207* (NOU), New Caledonia, KM487905, KM488009, KM488107; *C. Vieira IRD10208* (NOU), New Caledonia, –, KM488010, –; *C. Vieira IRD10209* (NOU), New Caledonia, KM487915, KM488021, KM488110; *C. Vieira IRD10210* (NOU), New Caledonia, KM487906, KM488024, KM488100; *C. Vieira IRD10211* (NOU), New Caledonia, KM487901, KM488006, KM488098; *C. Vieira IRD10212* (NOU), New Caledonia, KM487907, KM488013, KM488103; *C. Vieira IRD10213* (NOU), New Caledonia, KM487909, KM488017, –; *C. Vieira IRD10215* (NOU), New Caledonia, KM487912, KM488023, KM488096; *C. Vieira IRD10216* (NOU), New Caledonia, –, –, KM488092; *C. Vieira IRD10226* (NOU), New Caledonia, KM487903, KM488002, –; *C. Vieira IRD11126* (NOU), New Caledonia, KM487913, KM488020, KM488111; *F. Houlbreque IRD10204* (NOU), New Caledonia, KM487928, –, –; *J.L. Menou & al. IRD7662* (NOU), New Caledonia, KM487902, –, –; *L. Mattio & al. IRD7659* (NOU), New Caledonia, KM487937, –, –; *L. Mattio & al. IRD7913* (NOU), New Caledonia, KM487936, –, –; *L. Mattio & al. IRD7914* (NOU), New Caledonia, KU353403*, –, –; *L. Mattio & al. IRD7915* (NOU), New Caledonia, KU353410*, –, –; *O. De Clerck ODC1571* (GENT), Kenya, KU353411*, –, –; ***Lobophora sonderi*** C.W.Vieira, De Clerck & Payri, *C. Payri IRD7920* (NOU), New Caledonia, KM487750, KM488032, KM488121; *C. Payri IRD7921* (NOU), New Caledonia, –, KM488031, KM488124; *C. Vieira CV3051* (NOU), New Caledonia, –, KM488028, KM488123; *C. Vieira CV3055* (NOU), New Caledonia, KM487770, KM488029, KM488117; *C. Vieira CV3074* (NOU), New Caledonia, KM487771, KM488026, KM488120; *C. Vieira CV3079* (NOU), New Caledonia, KM487764, –, –; *C. Vieira CV3192* (NOU), New Caledonia, KM487754, –, –; *C. Vieira CV3193* (NOU), New Caledonia, KM487753, –, –; *C. Vieira CV3196* (NOU), New Caledonia, KM487757, –, –; *C. Vieira CV3197* (NOU), New Caledonia, KM487767, –, –; *C. Vieira CV3198* (NOU), New Caledonia, KM487766, –, –; *C. Vieira CV3199* (NOU), New Caledonia, KM487765, –, –; *C. Vieira CV3200* (NOU), New Caledonia, KM487758, –, –; *C. Vieira CV3201* (NOU), New Caledonia, KM487752, –, –; *C. Vieira CV3202* (NOU), New Caledonia, KM487762, –, –; *C. Vieira CV3203* (NOU), New Caledonia, KM487759, –, –; *C. Vieira CV3204* (NOU), New Caledonia, KM487761, –, –; *C. Vieira CV3205* (NOU), New Caledonia, KM487760, –, –; *C. Vieira CV3206* (NOU), New Caledonia, KM487763, –, –; *C. Vieira CV3252* (NOU), New Caledonia, –, KM488027, –; *C. Vieira IRD10194* (NOU), New Caledonia, KM487751, –, –; *C. Vieira IRD10195* (NOU), New Caledonia, KM487755, KM488025, KM488116; *C. Vieira IRD10197* (NOU), New Caledonia, KM487769, KM488033, KM488118; *C. Vieira IRD10214* (NOU), New Caledonia, KM487768, KM488030, KM488122; *C. Vieira IRD11123* (NOU), New Caledonia, KU353363*, –, KM488119; *G.W. Saunders GWS024839* (UNB), Australia, –, –, KU353151*; *G.W. Saunders GWS035587* (UNB), Australia, –, –, KU353150*; *H. Kawai KU-d271* (SAP), Australia, AB665374, –, –; *L. Mattio & al. IRD482* (NOU), New Caledonia, KM487756, –, –; *L. Tyberghein & H. Verbruggen LT0083* (GENT), Australia, KU353364*, KU352858*, KU353154*; *L. Tyberghein & H. Verbruggen LT0368* (GENT), Australia, –, KU352860*, –; *N. Phillips LNIG* (UNB), Australia, –, –, EF990239; *G.W. Saunders GWS024408* (UNB), Australia, –, –, KU353153*; *G.W. Saunders GWS025462* (UNB), Australia, KU353368*, –, –; *H. Kawai KU-d6625* (SAP), Australia, AB665375, –, AB665257; *H. Verbruggen & L. Tyberghein HV2505* (GENT), Australia, KU353365*, KU352859*, –; *J. Costa & V. Marcelino JFC0214* (MELU), Australia, KU353369*, –, –; *J. Costa & V. Marcelino JFC0215* (MELU), Australia, KU353371*, –, –; *J. Costa & V. Marcelino JFC0253* (MELU), Australia, KU353372*, –, –; *J. Costa & V. Marcelino JFC0286* (MELU), Australia, KU353370*, –, –; *L. Tyberghein & H. Verbruggen LT0326* (GENT), Australia, KU353366*, –, KU353152*; *L. Tyberghein & H. Verbruggen LT0348* (GENT), Australia, KU353367*, –, –; *L. Tyberghein & H. Verbruggen LT0455* (GENT), Australia, –, KU352857*, –; *M.E. Ramirez LAF6887* (LAF), Chile, –, –, KU364181; ***Lobophora variegata*** (J.V.Lamour.) Womersley ex E.C.Oliveira *A. Carlile LAF6912* (LAF), Bahamas, KU364222*, KU364269*, KU364182*; *D. Ott & T. Sanderson MW11719* (MICH), Bahamas, –, KU352855*, KU352999*; *H. Verbruggen HV939* (GENT), Jamaica, KU353160*, –, –; *O. Camacho LAF6914* (LAF), Florida Keys (U.S.A.), KU364223*, KU364270*, KU364183*; *R. Gray MW11793* (MICH), Bahamas, –, KU352856*, KU352998*, *C. Payri IRD11140* (NOU), Guadeloupe, KX061443*, KX061444*, KX061445*; ***Lobophora undulata*** C.W.Vieira, De Clerck & Payri, *C. Payri IRD11068* (NOU), New Caledonia,

**Appendix 1.** Continued.

KM487851, –, KM488150; *C. Payri IRD11069* (NOU), New Caledonia, KM487852, –, KM488154; *C. Payri IRD7669* (NOU), New Caledonia, KU353240*, KM488042, KM488157; *C. Payri IRD7671* (NOU), New Caledonia, KM487859, –, –; *C. Vieira CV3059* (NOU), New Caledonia, –, KM488044, KM488148; *C. Vieira CV3078* (NOU), New Caledonia, KM487847, –, –; *C. Vieira CV3090* (NOU), New Caledonia, KM487846, –, –; *C. Vieira CV3102* (NOU), New Caledonia, KM487845, –, –; *C. Vieira CV3103* (NOU), New Caledonia, KM487850, –, –; *C. Vieira CV3104* (NOU), New Caledonia, KM487844, –, –; *C. Vieira CV3110* (NOU), New Caledonia, KM487853, –, –; *C. Vieira CV3113* (NOU), New Caledonia, KM487854, –, –; *C. Vieira CV3150* (NOU), New Caledonia, KM487848, –, –; *C. Vieira CV3151* (NOU), New Caledonia, KM487855, KM488045, KM488153; *C. Vieira CV3152* (NOU), New Caledonia, KM487856, KM488041, KM488152; *C. Vieira CV3153* (NOU), New Caledonia, KM487860, –, KM488156; *C. Vieira CV3155* (NOU), New Caledonia, KM487862, –, –; *C. Vieira CV3156* (NOU), New Caledonia, KM487857, –, –; *C. Vieira CV3157* (NOU), New Caledonia, KM487858, –, –; *C. Vieira CV3158* (NOU), New Caledonia, KM487841, –, –; *C. Vieira CV3159* (NOU), New Caledonia, KM487843, –, –; *C. Vieira CV3160* (NOU), New Caledonia, KM487861, –, –; *C. Vieira CV3161* (NOU), New Caledonia, KM487849, –, –; *C. Vieira CV3164* (NOU), New Caledonia, KM487863, –, –; *C. Vieira CV3181* (NOU), New Caledonia, –, KM488040, KM488147; *C. Vieira CV3182* (NOU), New Caledonia, –, KM488039, KM488155; *C. Vieira IRD10202* (NOU), New Caledonia, KM487842, KM488043, KM488149; *C. Vieira IRD11054* (NOU), New Caledonia, –, KM488038, KM488151; *M.E. Ramirez LAF6756* (LAF), Chile, KU364217, –, –; *M.E. Ramirez LAF6885* (LAF), Chile, KU364220, KU364267, KU364179; *M.E. Ramirez LAF6886* (LAF), Chile, KU364221, KU364268, KU364180; ***Lobophora* sp1** *C. Payri IRD11065* (NOU), New Caledonia, –, –, KM488088; *C. Payri IRD276* (NOU), New Caledonia, –, –, KM488087; *J.L. Menou IRD7670* (NOU), New Caledonia, KM487944, –, KM488089; *Z. Sun & T. Hanyuda d7715* (KU), Japan, KU353384*, –, KU352990*; ***Lobophora* sp2** *C. Payri IRD259* (NOU), New Caledonia, –, –, EU579956; *C. Payri IRD7638* (NOU), New Caledonia, KM487943, KM488000, KM488086; ***Lobophora* sp3** *C. Payri IRD7887* (NOU), New Caledonia, KM487865, KM488075, KM488184; ***Lobophora* sp4** *C. Vieira IRD10230* (NOU), New Caledonia, KM487811, KM488074, KM488125; ***Lobophora* sp5** *C. Payri IRD7883* (NOU), New Caledonia, KM487804, KM488084, KM488181; *F. Leliaert PNGMAD3496* (GENT), Papua New Guinea, KU353352*, –, –; *H. Verbruggen PHV241* (MELU), Papua New Guinea, KM487805, KM488085, KM488182; *H. Verbruggen PHV567* (MELU), Papua New Guinea, KU353353*, –, KM488183; *J. Tanaka & Z. Sun d5811* (KU), Japan, KU353351*, –, KU353052*; ***Lobophora* sp6** *C. Vieira IRD11052* (NOU), New Caledonia, KM487892, KM488037, KM488145; *C. Payri GAM13*CP215 (NOU), French Polynesia, KU353257*, KU352883*, KU353127*; ***Lobophora* sp7** *C. Payri IRD7676* (NOU), New Caledonia, KM487891, –, KM488175; ***Lobophora* sp10** *M. Zubia JN046* (NOU), Juan de Nova Island, KU353273*, –, KU353049*; ***Lobophora* sp11** *C. Payri GAM13*CP502 (NOU), French Polynesia, –, KU352915*, –; *C. Payri GAM13*CP575 (NOU), French Polynesia, KU353272*, KU352922*, KU353079*; *C. Payri IRD8763* (NOU), French Polynesia, –, KU352920*, KU353081*; *C. Payri IRD8764* (NOU), French Polynesia, KU353266*, KU352923*, KU353087*; *C. Payri IRD8765* (NOU), French Polynesia, KU353264*, –, KU353091*; *C. Payri IRD8766* (NOU), French Polynesia, KU353265*, KU352925*, KU353090*; *C. Payri IRD8768* (NOU), French Polynesia, KU353271*, KU352921*, KU353082*; *C. Payri IRD8770* (NOU), French Polynesia, KU353259*, KU352917*, KU353086*; *C. Payri IRD8772* (NOU), French Polynesia, KU353267*, KU352914*, KU353092*; *C. Payri IRD8773* (NOU), French Polynesia, KU353260*, KU352926*, KU353085*; *C. Payri IRD8774* (NOU), French Polynesia, KU353263*, KU352924*, KU353083*; *C. Payri IRD8775* (NOU), French Polynesia, KU353262*, –, KU353084*; *C. Payri IRD8776* (NOU), French Polynesia, KU353270*, KU352916*, KU353088*; *C. Payri IRD8787* (NOU), French Polynesia, KU353258*, KU352912*, KU353089*; *C. Payri IRD8795* (NOU), French Polynesia, KU353261*, KU352913*, KU353078*; *C. Payri IRD8797* (NOU), French Polynesia, KU353268*, KU352918*, KU353093*; *C. Payri IRD8798* (NOU), French Polynesia, KU353269*, KU352919*, KU353080*; ***Lobophora* sp12** *G.W. Saunders GWS025592* (UNB), Australia, –, –, KU353061*; ***Lobophora* sp13** *C. Payri GAM13*CP378 (NOU), French Polynesia, KU353256*, –, –; *C. Payri GAM13*CP433 (NOU), French Polynesia, KU353252*, KU352879*, –; *C. Payri GAM13*CP577 (NOU), French Polynesia, KU353251*, KU352877*, KU353103*; *C. Payri IRD8762* (NOU), French Polynesia, KU353254*, KU352878*, KU353101*; *C. Payri IRD8788* (NOU), French Polynesia, KU353255*, KU352880*, KU353102*; *C. Payri IRD8799* (NOU), French Polynesia, KU353253*, KU352881*, KU353105*; *C. Payri IRD8800* (NOU), French Polynesia, –, KU352882*, KU353104*; ***Lobophora* sp14** *H. Verbruggen HV03051* (GENT), Israel, KU353278*, –, –; *H. Verbruggen HV03408* (GENT), Egypt, KU353279*, KU352962*, KU353047*; *O. De Clerck IRD11156* (NOU), Egypt, KU353280*, KU352961*, KU353045*; *T. Sauvage & al. LAF5673* (LAF), Egypt, KU364193, KU364235, –; *T. Sauvage & al. LAF5748* (LAF), Egypt, KU364195, KU364238, KU364155; ***Lobophora* sp15** *C. Payri & A.D.R. N'Yeurt IRD1382* (NOU), Solomon Islands, –, –, EU579953; ***Lobophora* sp16** *E. Coppejans HEC15982* (GENT), Sri Lanka, KU353418*, –, –; *G. Richards & H. Ford MW0709* (MICH), Oman, KU353426*, KU352982*, KU353142*; *G. Richards & H. Ford MW1009* (MICH), Oman, KU353427*, KU352979*, KU353140*; *G. Richards & H. Ford MW1909* (MICH), Oman, KU353423*, KU352983*, KU353143*; *H. Verbruggen & al. TZ0752* (GENT), Tanzania , KU353420*, –, –; *H. Verbruggen & al. TZ0809* (GENT), Tanzania, KU353421*, –, KU353139*; *H. Verbruggen & al. TZ0847* (GENT), Tanzania, KU353422*, KU352978*, KU353138*; *H. Verbruggen & al. TZ538* (GENT), Tanzania, –, KU352977*, –; *O. De Clerck ODC1511* (GENT), Kenya, KU353419*, –, –; *T. Schils & al. DHO0052* (GENT), Oman, KU353424*, –, –; *T. Schils & al. DHO0214* (GENT), Oman, KU353425*, KU352981*, KU353141*; *T. Schils & al. MAS2155* (GENT), Oman, –, KU352980*, –; ***Lobophora* sp17** *S. Andrefouet IRD11050* (NOU), French Polynesia, KU353247*, KU352874*, KU353099*; *S. Andrefouet IRD11051* (NOU), French Polynesia, KU353246*, KU352873*, KU353100*; ***Lobophora* sp18** *C. Vieira CV3258* (NOU), New Caledonia, KM487840, –, KU353074*; *H. Kudo PALBB062* (Yamagata University), Palau, –, –, AB096896; *H. Verbruggen & al. JFC0025* (MELU), Australia, KU353223*, –, –; *H. Verbruggen & al. JFC0136* (MELU), Australia, KU353221*, –, –; *H. Verbruggen HV03056* (GENT), Israel, KU353228*, –, –; *J. Costa & al. HV03585* (MELU), Australia, KU353217*, –, –; *J. Costa & al. HV03591* (MELU), Australia, KU353222*, –, –; *J. Costa & al. JFC0096* (MELU), Australia, KU353224*, –, –; *J. Costa & al. JFC0121* (MELU), Australia, KU353216*, –, –; *J. Costa & S. Berrin JFC0071* (MELU), Australia, KU353219*, –, –; *L. Mattio IRD11073* (NOU), Mayotte, –, –, KU353072*; *M. Zubia JN091* (NOU), Juan de Nova Island, KU353225*, –, KU353075*; *S. Berrin & al. HV03621* (MELU), Australia, KU353220*, –, –; *S.M. Boo PDI002* (CNUK), Japan, –, AY528843, –; *T. Sauvage & al. LAF5802* (LAF), Egypt, KU364196, KU364239, 0; *T. Sauvage & al. LAF5803* (LAF), Egypt, KU364197, KU364240, KU364156; *T. Sauvage & al. LAF5851* (LAF), Egypt, KU364198, KU364241, KU364157; *T. Sauvage & al. LAF5856* (LAF), Egypt, KU364199, KU364242, KU364158; *T. Sauvage & al. LAF5978* (LAF), Egypt, KU364200, KU364243, KU364159; *T. Sauvage HV02912* (GENT), Israel, KU353226*, KU352910*, KU353077*; *T. Sauvage HV02919* (GENT), Israel, KU353227*, KU352911*, KU353076*; *V. Marcelino & al. HV03652* (MELU), Australia, KU353218*, –, –; *V. Marcelino & al. HV03653* (MELU), Australia, KU353215*, –, –; *W.J. Lee & al. ZoD1* (CNUK), Japan, –, AY5284411, AY527199; *Z. Sun MBMD00101* (–), Japan, KU353214*, –, KU353073*; ***Lobophora* sp19** *C. Payri & al. IRD2636* (NOU), Vanuatu, –, –, KU353107*; *C. Payri & al. IRD2638* (NOU), Vanuatu, KU353203*, –, KU353106*; *C. Payri GAM13*CP329 (NOU), French Polynesia, KU353206*, KU352904*, KU353116*; *C. Payri IRD8771* (NOU), French Polynesia, KU353205*, KU352900*, KU353121*; *C. Payri IRD8778* (NOU), French Polynesia, KU353201*, KU352902*, KU353124*; *C. Payri IRD8779* (NOU), French Polynesia, KU353213*, KU352905*, KU353120*; *C. Payri IRD8783* (NOU), French Polynesia, KU353210*, KU352909*, KU353123*; *C. Payri IRD8784* (NOU), French Polynesia, KU353202*, KU352898*, KU353115*; *C. Payri IRD8785* (NOU), French Polynesia, KU353208*, KU352899*, KU353119*; *C. Payri IRD8790* (NOU), French Polynesia, KU353204*, KU352901*, KU353117*; *C. Payri IRD8791* (NOU), French Polynesia, KU353211*, KU352908*, KU353122*; *C. Payri IRD8792* (NOU), French Polynesia, KU353212*, KU352907*, KU353118*; *C. Payri IRD8793* (NOU), French Polynesia, KU353207*, KU352906*, –; *C. Payri IRD8794* (NOU), French Polynesia, KU353209*, KU352903*, KU353060*; ***Lobophora* sp20** *S. Andrefouet IRD11053* (NOU), Saudi Arabia, –, –, KU353098*; *T. Sauvage & al. LAF5652* (LAF), Egypt, KU364192, KU364234, KU364153; *T. Sauvage & al. LAF5678* (LAF), Egypt, –, KU364236, –; *T. Sauvage & al. LAF5700* (LAF), Egypt, KU364194, KU364237, KU364154; *T. Sauvage & al. LAF6145* (LAF), Egypt, KU364201, KU364244, –; ***Lobophora* sp21** *B. Wysor & N. Hammerman LAF6599* (LAF), Panama, –, KU364251, KU364166; *B. Wysor LAF6600* (LAF), Panama, KU364206, KU364252, KU364167; *C. Fernandez-Garcia LAF6618* (LAF), Mexico, KU364208, KU364254, KU364169; *C. Fernandez-Garcia LAF6619* (LAF), Mexico, KU364209, KU364255, KU364170; *H. Verbruggen & T. Tyberghein MX0096* (GENT), Mexico, KU353165*, KU352955*, KU353001*; ***Lobophora* sp22** *C. Fernandez-Garcia & A. Planas LAF6617* (LAF), El Salvador, KU364207, KU364253, KU364168; *C. Fernandez-Garcia & A. Planas LAF6623* (LAF), Costa Rica, KU364212, KU364258, KU364173; *C. Fernandez-Garcia LAF6621* (LAF), Nicaragua, KU364211, KU364257, KU364172; ***Lobophora* sp23** *M. Zubia GLO038* (NOU), Glorioso Islands, –, –, KU353027*; *M. Zubia GLO079* (NOU), Glorioso Islands, –, KU352941*, KU353026*;

**Appendix 1.** Continued.

*M. Zubia GLO180* (NOU), Glorioso Islands, KU353185*, KU352940*, KU353025*; *M. Zubia GLO308* (NOU), Glorioso Islands, KU353186*, KU352939*, –; ***Lobophora* sp24** *J. Yao & Z. Sun KU-d5139* (SAP), China, AB665382, –, AB665274; *E. Coppejans HEC16695* (GENT), Thailand, KU353341*, –, –; *E. Coppejans HEC16814* (GENT), Thailand, KU353340*, –, –; *J. Tanaka & Z. Sun KU-d4615* (SAP), Japan, AB665384, –, AB665276; *J. Tanaka & Z. Sun KU-d5812* (SAP), Japan, AB665386, –, AB665278; *J. Yao & Z. Sun Sun2* (KU), China, KU353342*, –, KU353135*; *L. Mattio IRD11070* (NOU), Mayotte, –, –, KU353134*; ***Lobophora* sp25** *F. Rousseau & al. MAD0063* (PC), Madagascar, LN831820, –, –; *R.A. Anderson RA559* (BOL), South Africa, KU353335*, –, –; ***Lobophora* sp26** *M. Zubia EUR021* (BOL), Europa Island, KU353331*, –, –; *M. Zubia EUR077* (BOL), Europa Island, KU353332*, –, –; ***Lobophora* sp27** *A. Engelen IRD10231* (NOU), Curaçao, KU353334*, –, –; *C. Bouchon IRD11055* (NOU), Saint Barthelemy, –, –, KU353113*; *C.W. Schneider & al. KW160* (CWS), Florida, KR260336 , –, –; *H. Verbruggen HV939b* (GENT), Jamaica, –, KU352929*, –; *H. Verbruggen HV954* (GENT), Jamaica, KU353333*, –, –; *L. Le Gall & al. 0143238* (PC), Guadeloupe, KR260319 , –, –; *L. Le Gall & al. 0143239* (PC), Guadeloupe, KR260317 , –, –; *L. Le Gall & al. 0143240* (PC), Guadeloupe, KR260318 , –, –; *O. Camacho & S. Fredericq LAF4483* (LAF), U.S.A., KU364191, KU364233, KU364152; *O. Camacho & S. Fredericq LAF6460* (LAF), U.S.A., KU364204, KU364249, KU364164; *O. Camacho & S. Fredericq LAF7001* (LAF), U.S.A., KU364226, KU364273, KU364186; *S. Draisma KU-d9471* (SAP), Netherlands, AB665389, –, AB665281; *T.R. Popolizio BDA1441* (CWS), Bermuda, KR260340 , –, –; *T.R. Popolizio & E.D. Salomaki STX0085* (CWS), Saint Croix, KR260331 , –, –; *T.R. Popolizio & E.D. Salomaki STX0100* (CWS), Saint Croix, KR260330 , –, –; ***Lobophora* sp28** *C. Payri IRD10242* (NOU), Papua New Guinea, KU353328*, –, –; *G.W. Saunders GWS025837* (UNB), Philippines, –, –, KU353112*; *G.W. Saunders GWS025866* (UNB), Philippines, KU353326*, –, KU353111*; *H. Verbruggen HV03432* (GENT), Egypt, KU353327*, KU352927*, KU353109*; *H. Verbruggen HV03441* (GENT), Egypt, KU353329*, KU352928*, KU353108*; *H. Verbruggen HV03489* (GENT), Egypt, KU353330*, –, –; *P.E. Lim KU-d5187* (SAP), Malaysia, AB665388, –, AB665280; *T. Sauvage & al. LAF6234* (LAF), Egypt, –, KU364245, KU364160; ***Lobophora* sp29** *C. Payri IRD9853* (NOU), Papua New Guinea, KU353298*, –, KU353035*; *C. Payri PAP089* (NOU), Papua New Guinea, KU353291*, –, KU353033*; *C. Payri PAP098* (NOU), Papua New Guinea, KU353292*, –, KU353038*; *C. Payri PAP446* (NOU), Papua New Guinea, KU353296*, KU352957*, KU353034*; *C. Payri PAP646* (NOU), Papua New Guinea, KU353299*, –, –; *C. Payri PAP802*a (NOU), Papua New Guinea, KU353293*, –, –; *H. Verbruggen PHV369* (MELU), Papua New Guinea, KU353290*, –, –; *H. Verbruggen PHV594* (MELU), Papua New Guinea, KU353295*, KU352956*, KU353037*; *H. Verbruggen PHV646* (MELU), Papua New Guinea, KU353297*, KU352958*, KU353036*; *H. Verbruggen PHV825* (MELU), Papua New Guinea, KU353294*, –, –; ***Lobophora* sp30** *C. Payri PAP538* (NOU), Papua New Guinea, KU353285, KU352960*, KU353040*; *C. Payri PAP578* (NOU), Papua New Guinea, KU353284*, KU352959*, KU353039*; *C. Payri PAP619* (NOU), Papua New Guinea, KU353287*, –, KU353041*; *C. Payri PAP621* (NOU), Papua New Guinea, KU353286*, –, –; *F. Leliaert PNGMAD3655* (GENT), Papua New Guinea, KU353288*, –, –; *F. Leliaert PNGMAD3735* (GENT), Papua New Guinea, KU353289*, –, –; *F. Leliaert PNGMAD3755* (GENT), Papua New Guinea, KU353281*, –, –; *F. Leliaert PNGMAD3918* (GENT), Papua New Guinea, KU353283*, –, –; *F. Leliaert PNGMAD4097* (GENT), Papua New Guinea, KU353282*, –, –; ***Lobophora* sp31** *C. Payri IRD8914* (NOU), French Polynesia, KU353347*, KU352887*, KU353055*; *C. Payri IRD8915* (NOU), French Polynesia, KU353348*, KU352888*, KU353054*; *C. Payri MQ11157* (NOU), French Polynesia, KU353349*, –, –; *C. Payri MQ11158* (NOU), French Polynesia, KU353350*, KU352886*, KU353056*; ***Lobophora* sp32** *C. Payri IRD8916* (NOU), French Polynesia, KU353346*, KU352885*, KU353053*; ***Lobophora* sp33** *C. Payri IRD10232* (NOU), Papua New Guinea, KU353345*, KU352890*, KU353051*; *C. Payri IRD10234* (NOU), Papua New Guinea, KU353344*, KU352889*, KU353050*; ***Lobophora* sp35** *J.J. Bolton & al. LMD1617* (BOL), South Africa, KU353198*, KU352868*, KU353044*; *J.J. Bolton & al. LMD1618* (BOL), South Africa, KU353195*, KU352869*, KU353043*; *M. Zubia JN234* (NOU), Juan de Nova Island, KU353194*, –, KU353042*; *R.A. Anderson RA505* (BOL), South Africa, KU353197*, –, –; *R.A. Anderson RA672* (BOL), South Africa, KU353196*, –, –; ***Lobophora* sp36** *E. Coppejans MAD1674* (PC), Madagascar, LN831822, –, –; *E. Coppejans MAD1787* (PC), Madagascar, LN831823, –, –; *E. Coppejans MAD1815* (PC), Madagascar, LN831824, –, –; *E. Coppejans MAD1991* (PC), Madagascar, LN831825, –, –; *F. Rousseau & al. MAD0382* (PC), Madagascar, LN831821, –, –; *J.J. Bolton & al. LMD1356* (BOL), South Africa, KU353355*, KU352865*, –; *J.J. Bolton & al. LMD1616* (BOL), South Africa, KU353354*, KU352866*, KU353129*; *R.A. Anderson RA1007* (BOL), South Africa, KU353356*, –, –; ***Lobophora* sp37** *E. Coppejans & O. De Clerck HEC15767* (GENT), Portugal, KU353359*, –, –; *O. De Clerck ODC2278* (GENT), Portugal, KU353358*, –, –; *O. De Clerck ODC2286* (GENT), Portugal, KU353360*, –, –; *O. De Clerck ODC2364* (GENT), Tenerife, KU353362*, KU352861*, KU353156*; *O. De Clerck ODC2385* (GENT), Tenerife, KU353361*, KU352862*, KU353155*; *R.A. Anderson RA1050* (BOL), South Africa, KU353357*, –, –; ***Lobophora* sp39** *C. Bouchon IRD11056* (NOU), Saint Barthelemy, –, KU352965*, KU353130*; *C. Payri IRD11062* (NOU), Clipperton Island, KU353393*, –, –; *C.W. Schneider & C.E. Lane BDA0336* (CWS), Bermuda, KR260365 , –, –; *O. De Clerck & al. ODC2201* (GENT), Tenerife, KU353390*, KU352967*, KU353133*; *O. De Clerck ODC2371* (GENT), Tenerife, KU353391*, KU352966*, KU353131*; *O. De Clerck ODC2384* (GENT), Tenerife, KU353392*, KU352968*, KU353132*; *S. Fredericq LAF6658* (LAF), Mexico, –, –, KU364174; *S. Fredericq LAF6661* (LAF), U.S.A., KU364213, KU364261, KU364175; *T.R. Popolizio BDA0873* (CWS), Bermuda, KR260369 , –, –; *T.R. Popolizio BDA1667* (CWS), Bermuda, KR260363 , –, –; *T.R. Popolizio & E.D. Salomaki STX0156* (CWS), Saint Croix, KR260367 , –, –; ***Lobophora* sp40** *H. Kawai d10456* (KU), Greece, KU353385*, –, KU353159*; *H. Verbruggen & al. HV03239* (GENT), Greece, KU353388*, –, –; *H. Verbruggen & al. HV03287* (GENT), Greece, KU353389*, –, –; *H. Verbruggen & O. De Clerck HV03174* (GENT), Greece, KU353387*, KU352964*, KU353158*; *O. Camacho & S. Fredericq LAF3708* (LAF), U.S.A., KU364187, KU364227, KU364146; *O. Camacho & S. Fredericq LAF4092* (LAF), U.S.A., KU364188, KU364229, KU364147; *O. Camacho & S. Fredericq LAF4329* (LAF), U.S.A., –, –, KU364148; *O. Camacho & S. Fredericq LAF4445* (LAF), U.S.A., KU364190, KU364232, KU364151; *O. Camacho & S. Fredericq LAF6459* (LAF), U.S.A., KU364203, KU364248, KU364163; *O. Camacho & S. Fredericq LAF6461* (LAF), U.S.A., KU364205, KU364250, KU364165; *O. Camacho LAF6787* (LAF), U.S.A., KU364219, KU364266, KU364178; *O. De Clerck ODC2063* (GENT), Greece, KU353386*, KU352963*, KU353110*; *T.R. Popolizio BDA1321* (CWS), Bermuda, KR260316 , –, –; ***Lobophora* sp41** *C. Payri IRD9859* (NOU), Papua New Guinea, KU353399*, KU352975*, KU352991*; *C. Payri PAP002* (NOU), Papua New Guinea, KU353395*, KU352974*, KU352993*; *F. Leliaert PNGMAD3467* (GENT), Papua New Guinea, KU353398*, –, –; *H. Kudo PALNG021* (Yamagata University), Palau, –, –, AB096899; *H. Verbruggen PHV046* (MELU), Papua New Guinea, KU353397*, KU352973*, KU352994*; *H. Verbruggen PHV891* (MELU), Papua New Guinea, KU353396*, KU352976*, KU352992*; ***Lobophora* sp42** *H. Verbruggen & al. TZ0751* (GENT), Tanzania , –, KU352938*, KU353021*; *M. Zubia JN177* (NOU), Juan de Nova Island, KU353190*, –, KU353024*; *M. Zubia JN183* (NOU), Juan de Nova Island, KU353191*, –, KU353022*; *M. Zubia JN209* (NOU), Juan de Nova Island, KU353192*, –, KU353023*; ***Lobophora* sp43** *G.W. Saunders GWS024843* (UNB), Australia, KU353404*, –, –; *G.W. Saunders GWS025444* (UNB), Australia, KU353406*, –, –; *J. Costa & al. JFC0105* (MELU), Australia, KU353409*, –, –; *J. Costa & al. JFC0124* (MELU), Australia, KU353407*, –, –; *J. Costa & S. Berrin JFC0053* (MELU), Australia, KU353405*, –, –; *J. Costa & S. Berrin JFC0067* (MELU), Australia, KU353408*, –, –; ***Lobophora* sp44** *E. Coppejans MAD1788* (PC), Madagascar, LN831826, –, –; *E. Coppejans MAD1956* (PC), Madagascar, LN831827, –, –; *H. Verbruggen HV2780* (GENT), Brazil, KU353413*, KU352984*, KU353145*; *J.J. Bolton & al. LMD1576* (BOL), South Africa, KU353415*, KU352987*, KU353146*; *J.J. Bolton & al. LMD1597* (BOL), South Africa, KU353414*, KU352985*, –; *J.J. Bolton & al. LMD1670* (BOL), South Africa, KU353416*, KU352986*, KU353144*; *J. Nivia & C. Fernandez-Garcia LAF6738* (LAF), Costa Rica, KU364216, KU364264, KU364176; *L. Le Gall MAD2183* (PC), Madagascar, LN831828, –, –; *O. Camacho & S. Fredericq LAF6997* (LAF), U.S.A., KU364224, KU364271, KU364184; *O. Camacho LAF6655* (LAF), Panama, –, KU364259, –; *O. Camacho LAF6786* (LAF), U.S.A., KU364218, KU364265, KU364177; *S. Fredericq LAF4331* (LAF), Panama, KU364189, KU364231, KU364150; *S. Fredericq LAF6660* (LAF), U.S.A., –, KU364260, –; *S. Fredericq LAF6680* (LAF), U.S.A., KU364214, KU364262, –; *S. Fredericq LAF6692* (LAF), U.S.A., KU364215, KU364263, –; ***Lobophora* sp45** *E. Coppejans MAD1641* (PC), Madagascar, LN831831, –, –; *F. Rousseau & al. MAD0109* (PC), Madagascar, LN831829, –, –; *F. Rousseau & al. MAD0110* (PC), Madagascar, LN831830, –, –; *L. Le Gall MAD2068* (PC), Madagascar, LN831832, –, –; *O. De Clerck ODC1647* (GENT), Kenya , KU353382*, KU352854*, KU352988*; ***Lobophora* sp46** *M. Zubia EUR235* (BOL), Europa Island, KU353250*, –, –; ***Lobophora* sp47** *M. Zubia EUR275* (BOL), Europa Island, KU353243*, –, –; ***Lobophora* sp48** *C. Payri IRD4579* (NOU), Maldives, KU353229*, –, KU353071*; *C. Payri IRD4580* (NOU), Maldives, KU353230*, KU352892*, KM488146; ***Lobophora* sp49** *E. Coppejans HEC16690* (GENT), Thailand, KU353189*, –, –; ***Lobophora* sp50** *F. Leliaert PNGMAD3045* (GENT), Papua New Guinea, KU353336*, –, –; ***Lobophora***

**Appendix 1.** Continued.

**sp51** *H. Kawai KU-d1727* (SAP), Japan, AB665387, –, AB665279; ***Lobophora*** **sp52** *H. Kawai KU-d1733* (SAP), Japan, AB665381, –, AB665263; *M. Zubia GLO095* (NOU), Glorioso Islands, –, KU352932*, KU353032*; ***Lobophora*** **sp53** *J. Tanaka & Z. Sun KU-d5807* (SAP), Japan, AB665385, –, AB665277; *T. Sauvage & al. LAF6248* (LAF), Egypt, –, KU364246, KU364161; ***Lobophora*** **sp55** *H. Verbruggen HV03494* (GENT), Egypt, KU353325*, –, –; ***Lobophora*** **sp56** *J. Yao & Z. Sun KU-d5119* (SAP), China, AB665383, –, AB665275; *E. Coppejans HEC16632* (GENT), Thailand, –, KX581363*, KX581364*; ***Lobophora*** **sp57** *C. Payri IRD8767* (NOU), French Polynesia, KU353343*, KU352884*, KU353048*; ***Lobophora*** **sp58** *C. Fernandez-Garcia LAF6620* (LAF), Panama, KU364210, KU364256, KU364171; ***Lobophora*** **sp59** *O. De Clerck IRD11157* (NOU), Egypt, KU353200*, KU352867*, –; ***Lobophora*** **sp60** *M. Zubia EUR104* (BOL), Europa Island, KU353199*, –, –; ***Lobophora*** **sp61** *F. Leliaert PNGMAD3999* (GENT), Papua New Guinea, KU353193*, –, –; ***Lobophora*** **sp64** *F. Rousseau & al. 0143252* (PC), Guadeloupe, KR260361 , –, –; *P.E. Lim d5186* (KU), Malaysia, KU353428*, –, KU352995*; ***Lobophora*** **sp65** *O. Camacho LAF6430* (LAF), Columbia, KU364202, KU364247, KU364162; ***Lobophora*** **sp66** *T. Schils & al. DHO20407* (GENT), Oman, KU353417*, –, –; ***Lobophora*** **sp67** *J. Yao & Z. Sun MBMD00616* (–), China, KU353402*, –, KU353149*; *J. Yao & Z. Sun Sun3* (–), China, KU353400*, –, KU353147*; *Z. Sun Sun4* (–), China, KU353401*, –, KU353148*; ***Lobophora*** **sp68** *E. Coppejans HEC16059* (GENT), Sri Lanka, KU353381*, KU352853*, –; ***Lobophora*** **sp69** *Z. Sun d4842* (KU), Japan, KU353383*, –, KU352989*; ***Lobophora*** **sp70** *C. Payri IRD8789* (NOU), French Polynesia, KU353380*, KU352972*, KU352997*; *M. Zubia ARV634* (NOU), Reunion, KU353379*, KU352971*, KU352996*; ***Lobophora*** **sp73** *C. Payri IRD8769* (NOU), French Polynesia, KU353249*, KU352876*, KU353125*; ***Lobophora*** **sp74** *C. Payri IRD8796* (NOU), French Polynesia, KU353248*, KU352875*, KU353126*; ***Lobophora*** **sp76** *M. Zubia ARV652* (NOU), Reunion, KU353277*, –, –; ***Lobophora*** **sp77** *O. Camacho & S. Fredericq LAF3989* (LAF), U.S.A., –, KU364228, –; *O. Camacho & S. Fredericq LAF6999* (LAF), U.S.A., KU364225, KU364272, KU364185; ***Lobophora*** **sp78** *F. Rousseau & C. Payri FRA0105* (PC), Guadeloupe, –, –, EU579955; *O. Camacho LAF4330* (LAF), Panama, –, KU364230, KU364149; ***Lobophora*** **sp79** *L. Mattio IRD11071* (NOU), Mayotte, –, KU352891*, KU353114*; ***Lobophora*** **sp80** *H. Kudo PALNGl020* (Yamagata University), Palau, –, –, AB096898; ***Lobophora*** **sp81** *M. Zubia GLO075* (NOU), Glorioso Islands, –, KU352933*, –; ***Lobophora*** **sp82** *C. Payri PAP866* (NOU), Papua New Guinea, KU353161*, KU352934*, –; ***Lobophora*** **sp83** *M. Zubia GLO051* (NOU), Glorioso Islands, –, KU352937*, KU353029*; ***Lobophora*** **sp84** *S. Arai CHICHI* (SAP), Japan, AB358938, –, AB358935; ***Lobophora*** **sp86** *T.R. Popolizio & E.D. Salomaki STX0024* (CWS), Saint Croix, KR260360 , –, –.