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Taxonomic classification of the reef coral family Lobophylliidae (Cnidaria: Anthozoa: Scleractinia)

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Lobophylliidae is a family-level clade of corals within the 'robust' lineage of Scleractinia. It comprises species traditionally classified as Indo-Pacific 'mussids', 'faviids', and 'pectiniids'. Following detailed revisions of the closely related families Merulinidae, Mussidae, Montastraeidae, and Diploastraeidae, this monograph focuses on the taxonomy of Lobophylliidae. Specifically, we studied 44 of a total of 54 living lobophylliid species from all 11 genera based on an integrative analysis of colony, corallite, and subcorallite morphology with molecular sequence data. By examining coral skeletal features at three distinct levels – macromorphology, micromorphology, and microstructure – we built a morphological matrix comprising 46 characters. Data were analysed via maximum parsimony and transformed onto a robust molecular phylogeny inferred using two nuclear (histone H3 and internal transcribed spacers) and one mitochondrial (cytochrome c oxidase subunit I) DNA loci. The results suggest that micromorphological characters exhibit the lowest level of homoplasy within Lobophylliidae. Molecular and morphological trees show that *Symphyllia*, *Parascolymia*, and *Australomussa* should be considered junior synonyms of *Lobophyllia*, whereas *Lobophyllia pachysepta* needs to be transferred to *Acanthastrea*. Our analyses also lend strong support to recent revisions of *Acanthastrea*, which has been reorganized into five separate genera (*Lobophyllia*, *Acanthastrea*, *Homophyllia*, *Sclerophyllia*, and *Micromussa*), and to the establishment of *Australophyllia*. *Cynarina* and the monotypic *Moseleya* remain unchanged, and there are insufficient data to redefine *Oxypora*, *Echinophyllia*, and *Echinomorpha*. Finally, all lobophylliid genera are diagnosed under the phylogenetic classification system proposed here, which will facilitate the placement of extinct taxa on the scleractinian tree of life.

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INTRODUCTION

The reclassification of modern reef (i.e. zooxanthellate) corals is underway, supported by various molecular and morphological approaches (e.g. Gittenberger, Reijnen & Hoeksema, 2011; Benzoni *et al.*, 2012a,b; Arrigoni *et al.*, 2014a; Kitano *et al.*, 2014). The present study is the third in a series of monographs that considers species traditionally placed in the suborder Faviina *sensu* Vaughan & Wells (1943) and Wells (1956), or Faviina + Meandriina *sensu* Veron (1995). The series formally establishes a revised taxonomic classification that is based on new molecular results (Fukami *et al.*, 2008; Huang *et al.*, 2011; Arrigoni *et al.*, 2012, 2014b,c, 2015, 2016a), and focuses on the family and genus levels. It treats eight extant families – Meandrinidae Gray, 1847, Oculinidae Gray, 1847, Rhizangiidae d'Orbigny, 1851, Merulinidae Verrill, 1865, Mussidae Ortmann, 1890, Faviidae Gregory, 1900 (including Trachyphylliidae Verrill, 1901), Anthemiphylliidae Vaughan, 1907, and Pectiniidae Vaughan & Wells, 1943 – mostly nested within the 'robust' group and shown to be nonmonophyletic (Fukami *et al.*, 2008; Kitahara *et al.*, 2010; Stolarski *et al.*, 2011; Huang, 2012; Huang & Roy, 2013, 2015). A few genera conventionally classified within these families have been found to belong in the 'complex' clade (e.g. *Ctenella* Matthai, 1928, and *Galaxea* Milne Edwards & Haime, 1857).

The first monograph of this series by Budd *et al.* (2012) moved these 'complex' genera into the family Euphylliidae Alloiteau, 1952. More importantly, the authors reorganized four of the 'robust' families (Merulinidae, Mussidae, Faviidae, and Pectiniidae) using the molecular phylogeny of Fukami *et al.* (2008). Aided by detailed observations and phylogenetic analyses of coral morphology at the corallite and subcorallite scales (38 characters) in 67 species (Budd & Stolarski, 2009, 2011), Budd *et al.* (2012) redefined Mussidae (clade XXI *sensu* Fukami *et al.*, 2008) to incorporate Mussinae (Atlantic 'mussids') and Faviinae (Atlantic 'faviids'). At the genus level, *Isophyllastrea* Matthai, 1928, was synonymized with *Isophyllia* Milne Edwards & Haime, 1851a, and one new genus *Pseudodiploria* Fukami, Budd & Knowlton, 2012, was established.

Budd *et al.* (2012) also moved all the members of clade XVII (*sensu* Fukami *et al.*, 2008), comprising the Indo-Pacific genera within Merulinidae, Faviidae (plus *Orbicella* Dana, 1846, in the Atlantic), Pectiniidae, and Trachyphylliidae (*sensu* Vaughan & Wells, 1943) into Merulinidae, and resurrected the genera *Dipsastraea* de Blainville, 1830 (= Indo-Pacific '*Favia*'), *Phymastrea* Milne Edwards & Haime, 1848a (= Indo-Pacific '*Montastraea*'), *Parascolymia* Wells, 1964, and *Homophyllia* Brüggemann, 1877 (= Indo-Pacific '*Scolymia*'). The phylogenetically distinct *Diploastrea heliopora* (Lamarck, 1816) (clade XV; Indo-Pacific) and *Montastraea cavernosa* (Linnaeus, 1767) (clade XVI; Atlantic) were separated into two families monotypic for extant taxa – Diploastraeidae Chevalier & Beauvais, 1987, and Montastraeidae Yabe & Sugiyama, 1941, respectively. Finally, the Indo-Pacific 'mussids' and 'pectiniid' genera, *Echinomorpha* Veron, 2000, *Echinophyllia* Klunzinger, 1879, and *Oxypora* Saville Kent, 1871 (clades XVIII–XX *sensu* Fukami *et al.*, 2008), were placed in the family Lobophylliidae Dai & Horng, 2009 (= Lobophylliidae Budd *et al.*, 2012; see also Licuanan, 2009; Fig. 1). Morphological phylogenetic analyses were able to recover the redefined Mussidae and Lobophylliidae as monophyletic groups, but not Merulinidae.

The second monograph by Huang *et al.* (2014b) formally revised genera in the families Merulinidae, Montastraeidae, and Diploastraeidae by characterizing their corallite and subcorallite morphologies (44 characters, 84 species), performing a morphological phylogenetic analysis, and comparing the results with previously published molecular phylogenetic results (Huang *et al.*, 2011; Arrigoni *et al.*, 2012). In particular, *Pectinia* de Blainville, 1825, was subdivided into *Pectinia* and *Physophyllia* Duncan, 1884; *Goniastrea* Milne Edwards & Haime, 1848a, was

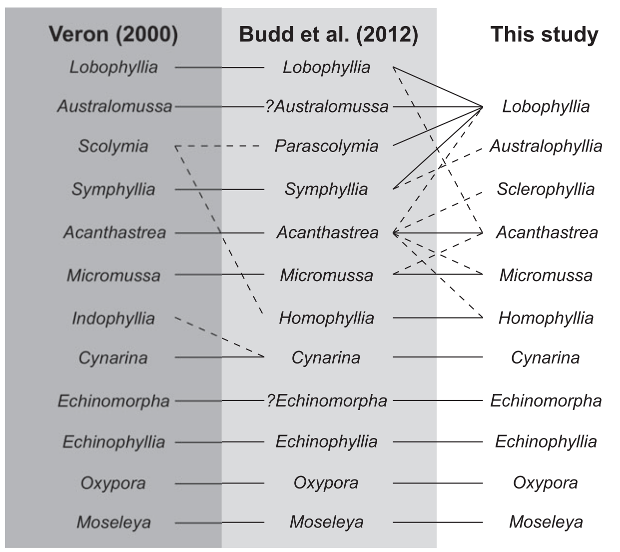


Figure 1. Comparisons amongst recent classifications of genera in Lobophylliidae. Continuous lines track generic synonyms, whereas dotted lines indicate movements of species amongst genera. See Stolarski & Roniewicz (2001) for comparisons with Vaughan & Wells (1943), Wells (1956), Alloiteau (1952), and Chevalier & Beauvais (1987).

subdivided into *Goniastrea* and *Coelastrea* Verrill, 1866 (see also Huang *et al.*, 2014a); *Dipsastraea* de Blainville, 1830, was subdivided into *Dipsastraea* and *Favites* Link, 1807, with *Barabattoia* Yabe & Sugiyama, 1941, regarded as a junior synonym; and *Phymastrea* was synonymized with *Favites*, with some members redistributed into *Astrea* Lamarck, 1801, and *Paramontastraea* Huang & Budd in Huang *et al.*, 2014b. Phylogenetic analyses of Merulinidae, Montastraeidae, and Diploastraeidae showed that morphological and molecular trees were generally congruent at the genus level, with Merulinidae finally recovered as a clade.

Here, we present a detailed species-level analysis of 44 Lobophylliidae species (clades XVIII–XX *sensu* Fukami *et al.*, 2008) based on three DNA markers, 46 corallite and subcorallite characters, and also reconstruct ancestral morphological states for genus-level clades. Our results recover Lobophylliidae as a monophyletic lineage and show once again that morphological and molecular trees are mostly congruent at the genus level. Finally, we provide an account of all 11 genera and 54 species in the family, formally revising parts of the lobophylliid classification where necessary to formulate a taxonomy supported by a rich set of phylogenetic data. Specifically, we present differential diagnoses for taxa, and where possible, identify explicit apomorphies for taxonomic identification. Based on our results, *Australomussa* Veron, 1985, *Parascolymia* Wells, 1964, and *Symphyllia* Milne Edwards & Haime, 1848a, are considered junior synonyms of *Lobophyllia* de Blainville, 1830, *Acanthastrea* Milne Edwards & Haime, 1848a, is reorganized into five genera (*Acanthastrea*, *Lobophyllia*, *Sclerophyllia* Klunzinger, 1879, *Micromussa* Veron, 2000, and *Homophyllia*); and three genera previously assigned to the traditional family Pectiniidae (*Echinomorpha*, *Echinophyllia*, and *Oxypora*), as well as *Cynarina* Brüggemann, 1877, remain unchanged (Fig. 1).

As in previous monographs of this series, aside from formally revising and recognizing diagnostic characters of families and genera, one vital aim is to develop informative morphological characters that can be applied to the fossil record and used to trace the evolutionary history of reef corals through geological time.

MATERIAL AND METHODS

Taxa studied

We analysed 44 species within clades XVIII–XX, including 32 species that have been positively placed on the molecular phylogeny of Arrigoni *et al.* (2014c). These represent all 11 Lobophylliidae genera, incorporating the 12 genera listed by Budd *et al.* (2012). We also included *Homophyllia hillae* (Wells, 1955) as a separate taxon although it has recently been synonymized under *Homophyllia bowerbanki* (Milne Edwards & Haime, 1857) (Arrigoni *et al.*, 2016a); our study presented a fine opportunity to test the relatedness between them.

Taxonomy at the species level was based primarily on Veron (2000, 2002), along with new species described thereafter. We were able to locate and photograph nearly all of the name-bearing type specimens of genera and species within Lobophylliidae, many of which are figured here. Specimens that are not name-bearing and figured for the first time are indicated as hypotypes.

Veron (2000) described 103 new scleractinian species without designating type material or type localities, rendering them as *nomina nuda*. These were redescribed in Veron (2002) and a 'holotype' was designated for each species. Following ICZN (2011: 162–166), the Veron (2000) publication was validated as an available taxonomic work. The species named in Veron (2000) are therefore valid, but the type specimens designated in Veron (2002) are not (see Wallace, Done & Muir, 2012). Nine of these species are in Lobophylliidae. Based on Veron (2000, 2002), it is clear that Dr J. E. N. Veron used more than one specimen when describing each species, e.g. at least two for *Lobophyllia flabelliformis* Veron, 2000 (Veron, 2002: 136, figs 250–253; ICZN, 2011: 164) and three for *Oxypora convoluta* Veron, 2000 (Veron, 2002: 114, figs 216–220; ICZN, 2011: 165). Each of these specimens should be regarded as part of a syntype series. Therefore, we regard Dr Veron's intent as being for the nine Lobophylliidae 'holotypes' in Veron (2002) to be lectotypes chosen subsequent to the original descriptions of the syntype series based on Veron (2000).

Geographical distributions of genera were obtained from Veron (2000), with updates from Veron *et al.* (2009, 2011, 2015). Other distributional data referred to are specifically cited.

Molecular characters

Most DNA sequences were derived from published data of Arrigoni *et al.* (2012, 2014b,c, 2015, 2016a) and Huang *et al.* (2011) (Appendix S1). For the remaining species, genomic DNA was extracted from 95% ethanol-preserved tissue samples using a DNeasy Blood and Tissue kit (Qiagen Inc., Valencia, CA, USA) following the manufacturer's protocols. Three molecular markers were obtained, namely the nuclear histone H3 (Colgan *et al.*, 1998), nuclear internal transcribed spacers 1 and 2 (ITS; including 5.8S rDNA; Takabayashi *et al.*, 1998a,b), and mitochondrial cytochrome c oxidase subunit I (Fukami *et al.*, 2004a,b). PCR protocols followed Benzoni *et al.* (2011) and Sanger sequencing was carried out by Macrogen Inc. (Seoul, South Korea). New sequences generated from this study were deposited in GenBank (Appendix S1).

Sequences for 40 taxa (including *Homophyllia hillae*) were organized into three separate data matrices using MESQUITE 3.02 (Maddison & Maddison, 2015). Alignments were carried out using the E-INS-i option with default parameters in MAFFT 7.205 (Katoh *et al.*, 2002; Katoh & Toh, 2008; Katoh, Asimenos & Toh, 2009; Katoh & Standley, 2013). The three data sets were concatenated and partitioned by gene.

Morphological characters

Coral skeletal morphological traits for 44 taxa (including *H. hillae*) were examined to construct a morphological matrix in MESQUITE consisting of 46 characters (Table 1; Appendices S2 and S3). Three types of characters – macromorphology, micromorphology, and microstructure – were studied. Observations of macromorphology were made using a stereomicroscope to visualize the coarse structure of the colony, calice, septa, columella, wall, and coenosteum (Vaughan & Wells, 1943; Wells, 1956; Beauvais *et al.*, 1993; Johnson, 1998; Wallace, 1999; Budd & Smith, 2005; Huang *et al.*, 2009). Micromorphology was examined using scanning electron microscopy at no more than 200× magnification to visualize the structure and distribution of septal teeth, area between teeth (interarea), and septal face granulations (Hoeksema, 1989; Beauvais *et al.*, 1993; Cuif & Perrin, 1999; Cuif *et al.*, 2003; Budd & Smith, 2005; Budd & Stolarski, 2009, 2011). Microstructure was examined by cutting, impregnating (with epoxy), and transverse-sectioning each calice (thickness ~30 μm), and visualizing the rapid accretion and thickening deposits within the wall, septa and columella under a stereo or light microscope at < 100× magnification (Alloiteau, 1952; Chevalier & Beauvais, 1987; Beauvais *et al.*, 1993; Stolarski & Roniewicz, 2001; Cuif *et al.*, 2003; Stolarski, 2003; Nothdurft & Webb, 2007; Budd & Stolarski, 2009, 2011; Brahmi *et al.*, 2010; Cuif, 2010). These characters were used by Budd *et al.* (2012; see especially their Appendix S3) in their revision of Mussidae, and Huang *et al.* (2014a,b) in their analyses of Merulinidae.

The 46 characters studied here were identical to those used in Huang *et al.* (2014a,b), with the addition of two characters that were informative amongst the subjects of this study. First, many lobophylliid species possessed teeth that varied in shape between the first- and third-order septa (S1 and S3 respectively, Budd *et al.*, 2012; Huang *et al.*, 2014b), so we included the character 'S1/S3 tooth shape' with two states, equal or unequal (character 28). Second, in some species the size of the teeth differed between those on the costa rising over the wall and those on the septum (Budd *et al.*, 2012; Huang *et al.*, 2014b). Therefore, the character 'wall/septum tooth size' with two states, equal or unequal (character 29), was analysed.

Phylogenetic analyses

We applied three phylogenetic tree optimality criteria on the molecular data set (Appendix S3). First, maximum likelihood (ML) trees were inferred using RAxML 8.0.9 (Stamatakis, Ludwig & Meier, 2005; Stamatakis, 2006, 2014; Stamatakis, Hoover & Rougemont, 2008) with the default GTRGAMMA model and 50 random starting trees. Clade supports were obtained using 1000 bootstrap pseudoreplicates (Felsenstein, 1985). Second, for Bayesian analyses, we determined the most suitable model of molecular evolution for each gene partition using jModelTest 2.1.5 (Guindon & Gascuel, 2003; Posada, 2008; Darriba *et al.*, 2012), testing for a total of 24 models based on the Akaike information criterion. Bayesian inferences were carried out in MrBayes 3.2.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003; Ronquist *et al.*, 2012). Four Markov chains of 12 000 000 generations were implemented in two runs, logging one tree per 100 generations. The first 20 001 trees from each run were discarded as burn-in following the examination of Markov chain Monte Carlo (MCMC) convergence using TRACER 1.6 (Rambaut *et al.*, 2014). Finally, under the maximum parsimony (MP) framework, tree searches were performed in TNT 1.1 (Goloboff, 1999; Nixon, 1999; Goloboff, Farris & Nixon, 2008) with 10 000 random addition sequence replicates, each employing 100 cycles of sectorial searches, ratcheting, drifting, and tree fusing. Gaps were treated as missing data. Clade stability was determined through 10 000 bootstrap replications.

For the morphological phylogenetic analysis, we performed the above MP tree searches and 10 000 bootstrap pseudoreplicates on the 46-character data matrix (Appendix S3) using TNT. We also employed TreeRot 3 (Sorenson & Franzosa, 2007) to evaluate Bremer support (Bremer, 1988; see also Grant & Kluge, 2008) for each node. For this computation, tree searches were carried out in PAUP* 4.0b10 (Swofford, 2003) using 1000 random addition replicates for each constrained analysis, with a rearrangement limit of 200 000 per replicate.

For both data sets, we included *Orbicella annularis*, *Goniastrea retiformis*, and *Merulina ampliata* (clade XVII) as outgroups, based on the large body of

Table 1. List of parsimony-informative characters and states

					Source char. no.		Molecular tree			Morphology tree		
No.	Type	Character	States	Parsimony model	M1	M2	Steps	CI	RI	Steps	CI	RI
2	Macromorphology	Extracalicular budding	0 = absent 1 = present	Unordered	2	2	6	0.167	0.667	6	0.167	0.667
3	Macromorphology	Polymorphism	0 = absent 1 = present	Unordered	3	3	4	0.250	0.400	5	0.200	0.333
5	Macromorphology	Corallite integration	0 = discrete (1–3 centres) 1 = uni- or multiserial 2 = organically united	Ordered	4	5	7	0.286	0.808	8	0.250	0.800
6	Macromorphology	Coenosteum amount	0 = fused walls 1 = limited (includes double wall) 2 = moderate (< corallite diameter) 3 = extensive (≥ corallite diameter) 4 = phaceloid	Unordered	6	6	14	0.286	0.583	9	0.444	0.828
8	Macromorphology	Calice width	0 = small (< 4 mm) 1 = medium (4–15 mm) 2 = large (> 15 mm)	Ordered	7	8	5	0.400	0.850	4	0.500	0.905
9	Macromorphology	Calice relief	0 = low (< 3 mm) 1 = medium (3–6 mm) 2 = high (> 6 mm)	Ordered	8	9	6	0.333	0.857	4	0.500	0.935
10	Macromorphology	Continuity of costosepta	0 = not confluent 1 = confluent	Unordered	9	10	6	0.167	0.583	4	0.250	0.750
11	Macromorphology	Number of septa	0 = < 3 cycles (< 24) 1 = 3 cycles (24–36) 2 = ≥ 4 cycles (≥ 48)	Ordered	10	11	6	0.333	0.846	5	0.400	0.889
12	Macromorphology	Free septa	0 = absent 1 = irregular 2 = regular	Ordered	11	12	2	0.500	0.000	2	0.500	0.000
13	Macromorphology	Septa spacing (per 5 mm)	0 = < 6 1 = 6–11 2 = > 11	Ordered	12	13	3	0.667	0.917	4	0.500	0.846
14	Macromorphology	Relative costosepta thickness	0 = unequal 1 = equal	Unordered	13	14	1	1.000	1.000	1	1.000	1.000
15	Macromorphology	Columella linkage	0 = continuous (trabecular linkage) 1 = discontinuous (lamellar linkage)	Unordered	14	15	1	1.000	1.000	1	1.000	1.000

16	Macromorphology	Columella structure	0 = lamellar 1 = trabecular, compact (1–3 threads) 2 = trabecular, spongy (> 3 threads)	Unordered	15	16	4	0.250	0.400	2	0.500	0.800
17	Macromorphology	Columella size (relative to calice width)	0 = < 1/4 1 = ≥ 1/4	Unordered	16	17	2	0.500	0.875	2	0.500	0.889
18	Macromorphology	Development of paliform lobes	0 = absent 1 = weak or moderate 2 = well developed	Ordered	21	18	6	0.333	0.500	5	0.400	0.700
19	Macromorphology	Development of septal lobes	0 = absent 1 = weak or moderate 2 = well developed	Ordered	21	19	–	–	–	1	1.000	1.000
20	Macromorphology	Epitheca	0 = absent 1 = reduced 2 = well developed	Ordered	18	20	8	0.250	0.813	9	0.222	0.794
21	Macromorphology	Endotheca	0 = sparse 1 = low-moderate (tabular) 2 = abundant (vesicular)	Ordered	19	21	2	1.000	1.000	2	1.000	1.000
22	Micromorphology	Tooth base outline (midcalice)	0 = elliptical-parallel 1 = elliptical-perpendicular 2 = circular	Unordered	35	22	1	1.000	1.000	1	1.000	1.000
24	Micromorphology	Tooth tip orientation (midcalice)	0 = parallel 1 = perpendicular 2 = multiaxial threads 3 = multiaxial bulbs	Unordered	38	24	3	1.000	1.000	3	1.000	1.000
25	Micromorphology	Tooth height (S1)	0 = low (< 0.3 mm) 1 = medium (0.3–0.6 mm) 2 = high (> 0.6 mm)	Ordered	39	25	3	0.667	0.950	3	0.667	0.950
26	Micromorphology	Tooth spacing (S1)	0 = narrow (< 0.3 mm) 1 = medium (0.3–1 mm) 2 = wide (> 1 mm)	Ordered	40	26	5	0.400	0.850	4	0.500	0.900
27	Micromorphology	More than 6 teeth per septum	0 = absent 1 = present	Unordered	–	27	2	0.500	0.889	1	1.000	1.000
28	Micromorphology	S1/S3 tooth shape	0 = equal 1 = unequal	Unordered	45	–	1	1.000	1.000	1	1.000	1.000
29	Micromorphology	Wall/septum tooth size	0 = equal 1 = unequal	Unordered	47	–	1	1.000	1.000	1	1.000	1.000
30	Micromorphology	Granule distribution	0 = aligned 1 = uniform 2 = scattered	Unordered	43	28	1	1.000	1.000	1	1.000	1.000

Table 1. *Continued*

No.	Type	Character	States	Parsimony model	Source char. no.		Molecular tree			Morphology tree		
					M1	M2	Steps	CI	RI	Steps	CI	RI
31	Micromorphology	Granule shape	0 = weak (rounded) 1 = strong (pointed) 2 = irregular	Unordered	43	29	3	0.667	0.889	3	0.667	0.889
32	Micromorphology	Interarea	0 = horizontal bands 1 = smooth 2 = palisade	Unordered	44	30	2	0.500	0.941	2	0.500	0.944
35	Microstructure	Abortive septa	0 = absent 1 = weak 2 = strong	Ordered	24	33	2	1.000	1.000	2	1.000	1.000
37	Microstructure	Paratheca	0 = absent 1 = partial 2 = dominant (= parathecal)	Ordered	26	35	2	1.000	1.000	2	1.000	1.000
38	Microstructure	Thickening deposits/ structure	0 = microfibrous 1 = thick fibrous 2 = concentric rings (extensive stereome)	Ordered	28	36	1	1.000	1.000	1	1.000	1.000
39	Microstructure	Costa centre clusters	0 = not distinct 1 = weak 2 = strong	Ordered	29	37	2	0.500	0.875	2	0.500	0.875
40	Microstructure	Distance between costa clusters	0 = <0.3 mm 1 = 0.3–0.6 mm 2 = > 0.6 mm	Ordered	30	38	3	0.667	0.875	2	1.000	1.000
41	Microstructure	Costa medial lines	0 = absent 1 = weak 2 = strong	Ordered	31	39	2	0.500	0.833	2	0.500	0.833
42	Microstructure	Septum centre clusters	0 = not distinct 1 = weak 2 = strong	Ordered	29	40	1	1.000	1.000	1	1.000	1.000
43	Microstructure	Distance between septum clusters	0 = < 0.3 mm 1 = 0.3–0.5 mm 2 = > 0.5 mm	Ordered	30	41	3	0.667	0.900	3	0.667	0.900

M1, monograph 1 (Budd *et al.*, 2012); M2, monograph 2 (Huang *et al.*, 2014b); CI, consistency index (Kluge & Farris, 1969); RI, retention index (Farris, 1989).

evidence supporting the distinction of these species from Lobophylliidae (Fukami *et al.*, 2008; Huang *et al.*, 2011; Arrigoni *et al.*, 2012; Huang, 2012; Huang & Roy, 2013, 2015; Marcelino *et al.*, 2013).

We reconstructed the morphological evolution of Lobophylliidae species by mapping the 46 characters onto both the ML molecular phylogeny and the most parsimonious morphological trees using MESQUITE. Ancestral states were inferred using the MP criterion on both sets of trees, but furthermore with the Mk1 likelihood model (Lewis, 2001) for the molecular tree. Character transformations allowed inference of state changes leading to genus-level clades, and apomorphies (i.e. derived characters) were recognized only when present on both molecular and morphological tree topologies.

To determine morphological traits that were diagnostic of clades, we evaluated the consistency index (CI; Kluge & Farris, 1969) and retention index (RI; Farris, 1989) for each character on the molecular and morphological trees. Character comparisons were based only on the RI because the CI does not account for autapomorphies, which do not contribute to the tree topology (Farris, 1989). We omitted characters from these calculations if they were not informative on either tree.

Museum abbreviations

FEBRAS, Museum of the Zhirmunsky Institute of Marine Biology, Far East Branch, Russian Academy of Sciences, Vladivostok, Russia; GLAHM, Hunterian Museum and Art Gallery, University of Glasgow, UK; IRD, Institut de recherche pour le développement, Nouméa, New Caledonia; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MNHN, Muséum national d'Histoire naturelle de Paris, France; MTQ, Museum of Tropical Queensland, Townsville, Australia; NHMUK, Natural History Museum, London, UK; QM, Queensland Museum, Brisbane, Australia; RMNH, Naturalis Biodiversity Center, Leiden, The Netherlands (formerly Rijksmuseum van Natuurlijke Historie); SU, Silliman University, Dumaguete, Negros Oriental, Philippines; SUI, Paleontology Repository of the University of Iowa, Iowa City, Iowa, USA; TIU, Tôkohu Imperial University, Sendai, Japan; UF, Florida Museum of National History, University of Florida, Gainesville, Florida, USA; UNIMIB, University of Milano-Bicocca, Milan, Italy; UP, Marine Science Institute, University of the Philippines, Quezon City, Philippines; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; WAM, Western Australian Museum, Perth, Australia; ZMB, Museum für Naturkunde, Berlin, Germany (formerly Zoologisches Museum Berlin); ZMUC, Zoologisk Museum, University of Copenhagen, Denmark; ZRC, Zoological Reference Collection, Lee Kong Chian Natural History Museum, National University of Singapore, Singapore.

RESULTS

The molecular phylogenetic analyses recovered trees that are broadly concordant amongst the three optimality criteria used. Lobophylliidae is a strongly supported monophyletic group, garnering ML and MP resampling scores of 100 and 90, respectively, and a Bayesian posterior probability of 1 (Fig. 2A). The ten subclades, A to J, defined by Arrigoni *et al.* (2014b,c, 2015, 2016a) were also found in all of our analyses, with strong support for the seven multispecific clades (ML bootstrap ≥ 80/posterior probability = 1.00/MP bootstrap ≥ 98). Three internal nodes each grouping two subclades are well supported – A + B (ML bootstrap/posterior probability/MP bootstrap = 81/0.96/64), F + G (95/1/92), and H + I (87/1.00/93). *Australophyllia wilsoni* (Veron, 1985), a phylogenetically unique species in subclade J examined by Arrigoni *et al.* (2016a), is consistently recovered as sister group to subclades A + B (100/1/100). *Lobophyllia pachysepta* Chevalier, 1975, is the earliest branching species of subclade E and is considered as part of the maximally supported subclade. However, nearly all of the remaining deep branches have very low support (bootstrap < 50), and are not concordant across the three optimality criteria.

Whilst all the subclades are well supported, only a few of them contain relationships that are stably resolved. On the one hand, the sister relationship between *H. bowerbanki* and *H. hillae* in subclade B is well supported (93/1.00/63), and the internal topology of *Micromussa* species in subclade A is consistent and moderately supported. On the other hand, the placement of *Echinomorpha*, *Echinophyllia*, and *Oxypora* species in both subclades F and G is tentative, as the majority of presumed members were not sampled. For subclade I, except for the sister grouping of *Parascolymia rowleyensis* and *Parascolymia vitiensis* (100/1/99), most of the remaining species are not resolved. These include current members of *Lobophyllia*, *Acanthastrea*, and *Symphyllia*, as defined by Arrigoni *et al.* (2014b).

The morphological phylogenetic analysis based on the 47-taxon by 46-character data set found 17 most parsimonious trees each with a length of 108. The strict consensus tree is shown in Figure 2B. Results of the bootstrap resampling and Bremer support analyses show that Lobophylliidae is a strongly supported clade (MP bootstrap = 95/Bremer support = 5). Seven of the ten molecular subclades (A–J,

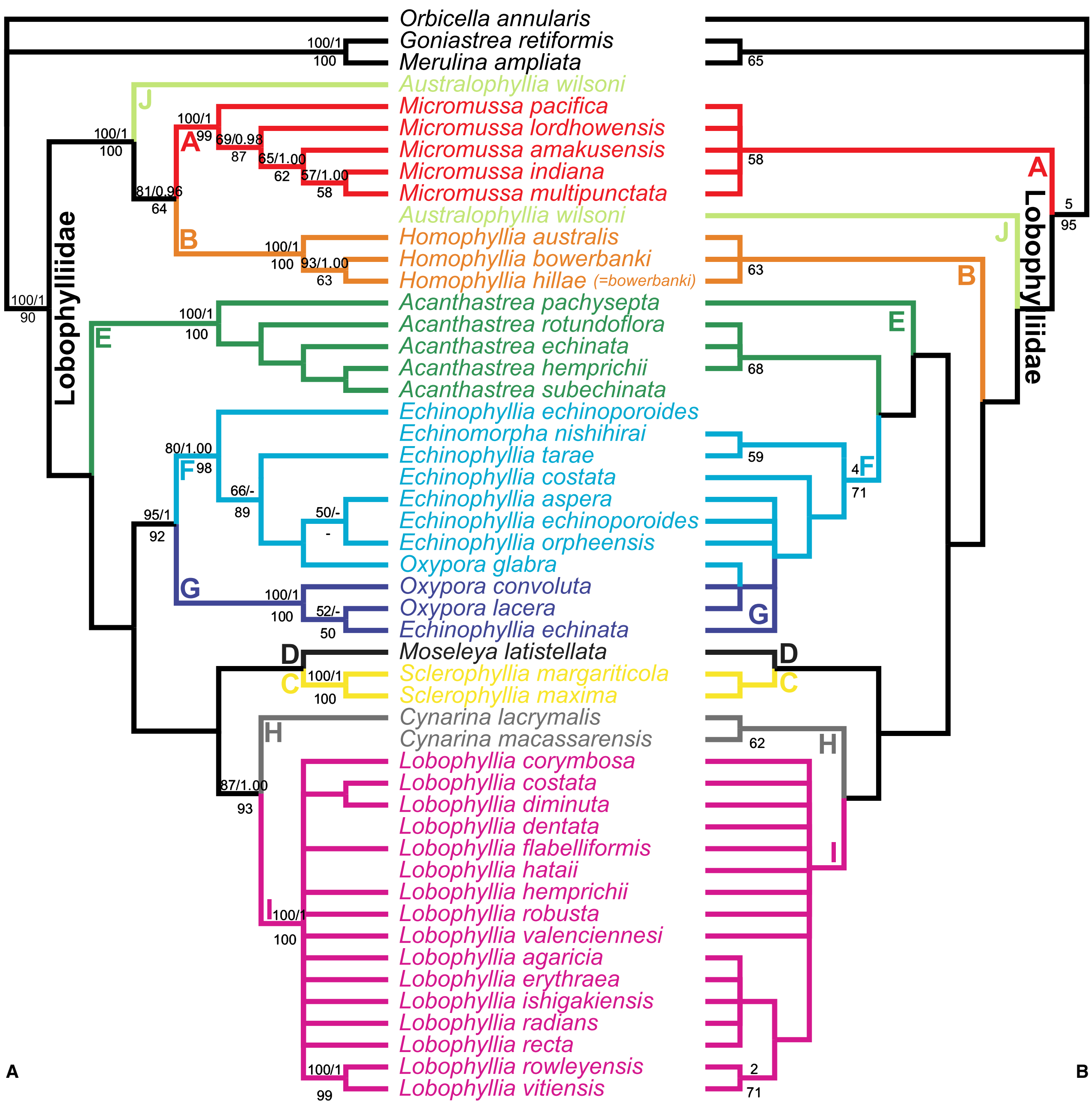


Figure 2. Phylogenetic reconstructions of the reef coral family Lobophylliidae with Merulinidae as outgroup. Molecular subclades within Lobophylliidae are differentiated by colour (Arrigoni *et al.*, 2015). (A) strict consensus of 18 maximum parsimony trees based on histone H3, internal transcribed spacers, and cytochrome c oxidase subunit I. Numbers adjacent to branches show support values (upper: maximum likelihood bootstrap ≥ 50, Bayesian posterior probability ≥ 0.9; lower: maximum parsimony bootstrap ≥ 50). (B) strict consensus of 17 maximum parsimony trees based on 46 morphological characters, with numbers indicating support (upper: Bremer decay index ≥ 2; lower: maximum parsimony bootstrap ≥ 50).

except E, F, and G *sensu* Arrigoni *et al.*, 2014c) are present on the morphological phylogeny, with at least moderate support for three of the eight multi-specific clades. These supported groups are subclades A (58/1), B (63/1), and H (62/1). Subclades C and I are in all of the most parsimonious trees, but not supported by the bootstrap analysis.

In contrast to the molecular trees, *L. pachysepta* is sister group to the clade E + F + G rather than clustering with subclade E. The molecular clades F and

G, which comprise species of the paraphyletic genera *Echinophyllia* and *Oxypora*, are also not found on the morphological tree. *Oxypora* is monophyletic based on morphological data, but *Echinophyllia* remains paraphyletic, with *Echinophyllia tarae* + *Echinomorpha nishihirai* forming the earliest branching group (59/1) in the well-supported F + G clade (71/4). Similar to the molecular trees, however, other internal nodes clustering the subclades have low support.

The character analyses showed that 36 of the 46 characters are informative for building the morphological tree (i.e. variable, with all states shared by more than one taxon), representing 86% of macromorphological characters, 91% of micromorphological characters, and 57% of microstructural characters (Table 1).

Similar to these proportions, micromorphological traits exhibited higher RI values (mean RI = 0.952 ± SD 0.058) compared with macromorphological (mean RI = 0.712 ± SD 0.271) or microstructural (mean RI = 0.935 ± SD 0.071) characters when data were transformed onto the molecular phylogeny. The difference overall is statistically significant (Kruskal–Wallis test, $K = 11.04$, $P = 0.0040$), with macromorphology scoring significantly lower RIs than micromorphology (Wilcoxon test, $P = 0.0040$) and microstructure (Wilcoxon test, $P = 0.0169$).

For the character transformations on the most parsimonious morphological trees, micromorphology also has the lowest level of homoplasy (mean RI = 0.968 ± SD 0.045) compared with macromorphology (mean RI = 0.785 ± SD 0.253) and microstructure (mean RI = 0.951 ± SD 0.070) (Table 1). These represent significant differences overall (Kruskal–Wallis test, $K = 10.06$, $P = 0.0065$), with macromorphology giving significantly lower RI values than micromorphology (Wilcoxon test, $P = 0.0055$) and microstructure (Wilcoxon test, $P = 0.0289$). On both sets of phylogenies, the differences in RI between micromorphological and microstructural characters are not significant (Wilcoxon test, $P \geq 0.6689$).

Using the most parsimonious transformations on both sets of trees, five characters (two macromorphological, two micromorphological, and one microstructural) are found to be unambiguous synapomorphies of Lobophylliidae. They are spinose coenosteum (character 7), discontinuous columellae amongst adjacent corallites with lamellar linkage (character 15), elliptical-parallel tooth base at midcalice (character 22), parallel or multiaxial bulbous tooth tip (character 24), and thickening deposits in concentric rings with extensive stereome (character 38). There are as many synapomorphies for macromorphology as micromorphology, but this belies the homoplastic nature of many macromorphological characters, including extracalicular budding (character 2), corallite polymorphism (character 3), and paliform lobes (character 18).

Lobophylliidae synapomorphies aside, many characters exhibiting the lowest levels of homoplasy (RI = 1) are diagnostic of the subclades. For macromorphology, septal lobes (character 19) are present only in subclade H, and endotheca (character 21) is abundant only in subclade I. For micromorphology, tooth tip form a multiaxial bulb (character 24) in F + G, with ≤ 6 teeth per septum (character 27) in E + F + G, unequal S1/S3 tooth shape (character 28) in the most inclusive clade excluding subclades A and B, unequal wall/septum tooth size (character 29) in H + I, and uniformly distributed granules (character 30) in subclade B. The only microstructural trait diagnostic of subclades is weak costa centre clusters (character 39), a synapomorphy for F + G.

Indeed, our analyses of the RI and number of phylogenetically informative characters indicate that micromorphological characters have the highest level of congruence between the molecular and morphological trees. Nevertheless, all of the examined synapomorphies at the major clade (XVIII–XX) and subclade (A–J) levels are taxonomically informative and thus form the basis for the diagnoses of Lobophylliidae and its constituent genera (for transformations of family and genus synapomorphies on the morphological phylogeny, see Appendix S4).

DISCUSSION

This monograph completes the broad-based revision of major clades XV–XXI (*sensu* Fukami *et al.*, 2008). On the one hand, the tasks that this work aims to perform are made easier by the precedence set by the first two monographs focusing on the other four families (Mussidae, Merulinidae, Montastraeidae, and Diploastraeidae), and also because the remaining pool of understudied taxa has shrunk. On the other hand, we are still faced with serious conundrums, such as the close evolutionary relationships amongst distantly classified genera and species, as well as the lack of informative characters that can resolve every node on the morphological phylogeny.

As with the work on Merulinidae, the nesting of Pectiniidae genera within the Pacific 'mussids' needed to be verified prior to this study with additional data and analyses since the relationship was unveiled by Fukami *et al.* (2004b, 2008). Subsequent authors had grouped these taxa in Lobophylliidae Dai & Horng, 2009 (Licuanan, 2009; Budd *et al.*, 2012), but they did not present new supporting data. Although Arrigoni *et al.* (2012) added data for *Echinophyllia aspera* (Ellis & Solander, 1786), their work was not principally focused on lobophylliid genera. The comprehensive analysis of the family by Arrigoni *et al.* (2014c) nearly doubled the sampling of the subclade comprising *Echinophyllia* and *Oxypora* (F + G *sensu* Arrigoni *et al.*, 2014c), and even included the recently described *Echinophyllia tarae* Benzoni, 2013.

The present study adds *Oxypora convoluta* Veron, 2000, to the molecular analysis, which now covers eight of the 13 species in *Echinophyllia* and *Oxypora* that are unequivocally nested within Lobophylliidae. Five species remain to be sampled, yet it is already clear that the evolutionary history of these two genera is complex. Species are not split by genus identity into the two subclades F and G. Rather, *Echinophyllia echinata* joins *Oxypora lacera* (Verrill, 1864) and *Ox. convoluta* in subclade G, whereas *Ox. glabra* Nemenzo, 1959, is in subclade F with the rest of the *Echinophyllia* species (Fig. 2A). This stands in marked contrast to the morphological phylogeny, which groups *Echinophyllia tarae* with *Echinomorpha nishihirai* (Veron, 1990) in the sister clade to the rest of *Echinophyllia* and *Oxypora* (Fig. 2B). Not surprisingly, *Oxypora* species form a monophyletic group – as a result of their compact columellae (one to three threads) and absence of distinct paliform (uniaxial) lobes – nested within a paraphyletic *Echinophyllia*. Complete sampling of *Oxypora*, by targeting the uncommon *Oxypora crassispinosa* Nemenzo, 1979, in the central Indo-Pacific and the rare *Oxypora egyptensis* Veron, 2000, in the Red Sea (Veron, 2000) may provide clues to the evolution of this enigmatic group. We will also need to probe subcorallite morphology for finer-scale differences between members of subclades F and G. Presently, the conflict between molecular and morphological data stems wholly from convergent macromorphological features that group *Oxypora* species together, as all the subcorallite characters observed thus far are invariable amongst *Echinophyllia* and *Oxypora* species. We expect that studies with greater sampling to better characterize intra- and interspecific variation will help uncover phylogenetically informative traits at the micromorphological and microstructural levels.

Another major disagreement between the molecular and morphological results concerns the placement of *L. pachysepta* Chevalier, 1975. This phaceloid/flabello-meandroid coral is sister species to the E + F + G clade on the morphological tree but is sister species to subclade E on the molecular tree, as shown here for the first time. It possesses several macromorphological traits that suggest a strong affinity to other *Lobophyllia* species (*sensu* Veron, 2000), including the phaceloid corallum, large (>15 mm) and high (>6 mm) calices. Whereas most of the subcorallite traits of *L. pachysepta* are identical to those amongst *Acanthastrea* species in subclade E, its wide tooth spacing (>1 mm) and weak septum centre clusters prohibit a closer relationship with *Acanthastrea* as suggested by the molecular phylogeny. Further analyses of the morphology of this rogue species may lead to a stable placement. Nevertheless, its inclusion within subclade E has strong support from genetic data, which we rely on for redefining *Acanthastrea* to include *L. pachysepta*.

It is worth noting that the remaining seven molecular subclades are recovered in the present study, often with strong support in either or both molecular and morphological reconstructions. Many of these groupings have been replicated several times before by Arrigoni *et al.* (2012, 2014b,c, 2015, 2016a), and provide support for the genus definitions given here. Subclades A, B, C, H, and I are multispecific groups that delimit the genera *Micromussa*, *Homophyllia*, *Sclerophyllia*, *Cynarina*, and *Lobophyllia*, respectively. Subclade I is of major taxonomic significance here, as *Lobophyllia*, *Australomussa*, *Parascolymia*, and *Symphyllia* (*sensu* Veron, 2000) have been indistinguishable genetically (Arrigoni *et al.*, 2014b,c). Our analyses integrating morphological data unequivocally support the placement of these taxa under the senior synonym, *Lobophyllia* de Blainville, 1830, with the inclusion of *Acanthastrea ishigakiensis* Veron, 1990, in this genus. Subclades D and J, represented respectively by *Moseleya* Quelch, 1884, and *Australophyllia* Benzoni & Arrigoni in Arrigoni *et al.*, 2016a, are monotypic.

The phylogenies reconstructed here have resolved genus-level taxa amongst lobophylliids, but they are by no means complete in elucidating the evolutionary history of every genus. On the molecular tree, sister–group relationships are supported for the genus pairs of *Micromussa*–*Homophyllia*, *Cynarina*–*Lobophyllia*, and *Echinophyllia*–*Oxypora*, as well as the trio of *Micromussa*–*Homophyllia*–*Australophyllia*. However, the other internal nodes are generally not supported, and the morphological tree also does not support the monophyly amongst *Micromussa*, *Homophyllia*, and *Australophyllia*. Clearly, the morphological traits used here are insufficient in supporting this topology or any alternatives. The taxonomic sampling of these three genera is nearly complete, and only *Micromussa regularis* (Veron, 2000) remains to be placed specifically. Therefore, we need to examine their morphology in greater detail in order to estimate the relationships amongst *Micromussa*, *Homophyllia*, and *Australophyllia*.

Our character analyses do hint at the scale at which we should focus when seeking to resolve the tree topology amongst lobophylliid genera. Both the RI and number of phylogenetically informative characters indicate that micromorphological characters exhibit the lowest level of homoplasy (Table 1), so we can expect relatively few convergent traits when examining shapes of teeth along the wall, septa, columella, and septal face granulations. The intergeneric variability of these characters first considered by Budd & Stolarski (2009) illustrates this point, although their taxon sampling was sparse. Subsequently, Arrigoni *et al.* (2014b, 2015, 2016a) demonstrated the utility of these micromorphological features for the definition and description of subclades A, B, C, and J. Our analyses show that micromorphological characters, such as shape of the tooth tip (multiaxial bulb in *Echinophyllia* + *Oxypora*), number of teeth per septum (≤ 6 in *Echinophyllia* + *Echinomorpha* + *Oxypora*), and variability of tooth size between wall and septum (unequal in *Cynarina* + *Lobophyllia*), are informative above the genus level. By contrast, fewer microstructural characters vary within Lobophylliidae, and macromorphology exhibits significantly higher levels of homoplasy.

At the family level, Budd *et al.* (2012) mapped 38 morphological characters onto the Fukami *et al.* (2008) molecular tree (67 species) and recognized that the shapes of teeth along the septal margin and granules on the septal face best distinguished families. Huang *et al.* (2014b) later transformed 44 characters onto the Huang *et al.* (2011) molecular tree (77 species) and the reconstructed morphological phylogeny (78 species) to find five subcorallite characters – both micromorphological and microstructural – to be synapomorphic for Merulinidae. Consistently, we find three subcorallite characters to be synapomorphic for Lobophylliidae, although two macromorphological characters are also synapomorphies. Here we synthesize these traits that also form part of the suite of features that are diagnostic of the families studied thus far (see also Budd & Stolarski, 2009, 2011).

Merulinidae Verrill, 1865 (clade XVII): irregular perpendicular or multiaxial septal tooth tips at midcalice, irregularly shaped granules, weak costa centre clusters, ≤ 0.6 mm separating costa clusters, and ≤ 0.5 mm separating septum centre clusters.

Mussidae Ortmann, 1890 (clade XXI): exclusively intracalicular budding, stout, blocky teeth with regular pointed septal tooth tips and circular tooth bases at midcalice, horizontal bands extending between teeth, aligned pointed granules, and septothecal or parathecal walls.

Montastraeidae Yabe & Sugiyama, 1941 (clade XVI): exclusively extracalicular budding, stout, blocky teeth with regular pointed septal tooth tips and elliptical-perpendicular tooth bases at midcalice, and septothecal walls with weak abortive septa.

Diploastraeidae Chevalier & Beauvais, 1987 (clade XV): exclusively extracalicular budding, regular pointed septal tooth tips and elliptical-parallel tooth bases at midcalice, synapticulothecal walls, and thickening deposits in concentric rings with extensive stereome.

Lobophylliidae Dai & Horng, 2009 (clades XVIII–XX): intracalicular budding, spinose coenosteum, irregular lobate or bulbous septal tooth tips at midcalice, parathecal walls (if walls present), thickening deposits in concentric rings with extensive stereome, weak to strong costa centre clusters, ≥ 0.3 mm separating costa clusters, weak to strong costa medial lines, and ≥ 0.3 mm separating septum centre clusters.

Primary microstructural characters such as the coarse arrangements of rapid accretion centres and thickening deposits have successfully supported morpho-molecular coral phylogenies. However, recent studies further suggest that different scleractinian clades may exhibit distinct fine-scale patterning of thickening deposits (Janiszewska *et al.*, 2011; Stolarski *et al.*, 2011). We have consistently observed microtuberculate texturing on skeletal surfaces of examined lobophylliids that corresponds to slender bundles of fibres constituting the thickening deposits (Fig. 3). These preliminary observations should be extended to other closely related taxa to assess potential clade-specific biomineralization control of the fibres and their consequent taxonomic value.

The resolution of families and genera in the least inclusive clade including XV and XXI (*sensu* Fukami *et al.*, 2008) has preoccupied numerous systematists with nearly a decade of work. The problem was first outlined in detail by Fukami *et al.* (2008; see also Kitahara *et al.*, 2010), which led to the development of morphological characters that support the major clades and subclades (Budd & Stolarski, 2009, 2011). Thus far, about 20 published papers written by over three dozen contributors, focusing on the phylogeny and classification of this clade, have helped stabilize its taxonomy (Dai & Horng, 2009; Fukami & Nomura, 2009; Huang *et al.*, 2009, 2011, 2014a,b; Benzoni *et al.*, 2011; Carlon *et al.*, 2011; Arrigoni *et al.*, 2012, 2014b,c, 2015, 2016a,b; Budd *et al.*, 2012; Kongjandtre *et al.*, 2012; Schwartz, Budd & Carlon, 2012; Benzoni, 2013; Isomura, Nozawa & Fukami, 2014; this study). However, a number of taxa remain to be revised because of data limitation, including *Australogyra*, *Boninastrea*, *Erythrastrea*, *Mycedium*, *Pectinia*, and *Physophyllia* of Merulinidae, as well as *Echinomorpha*, *Echinophyllia*, and *Oxypora* of Lobophylliidae. New palaeontological, morphological, and genomic data to infer their positions on the phylogeny, resolve deeper relationships, and support time-calibrated reconstructions will set

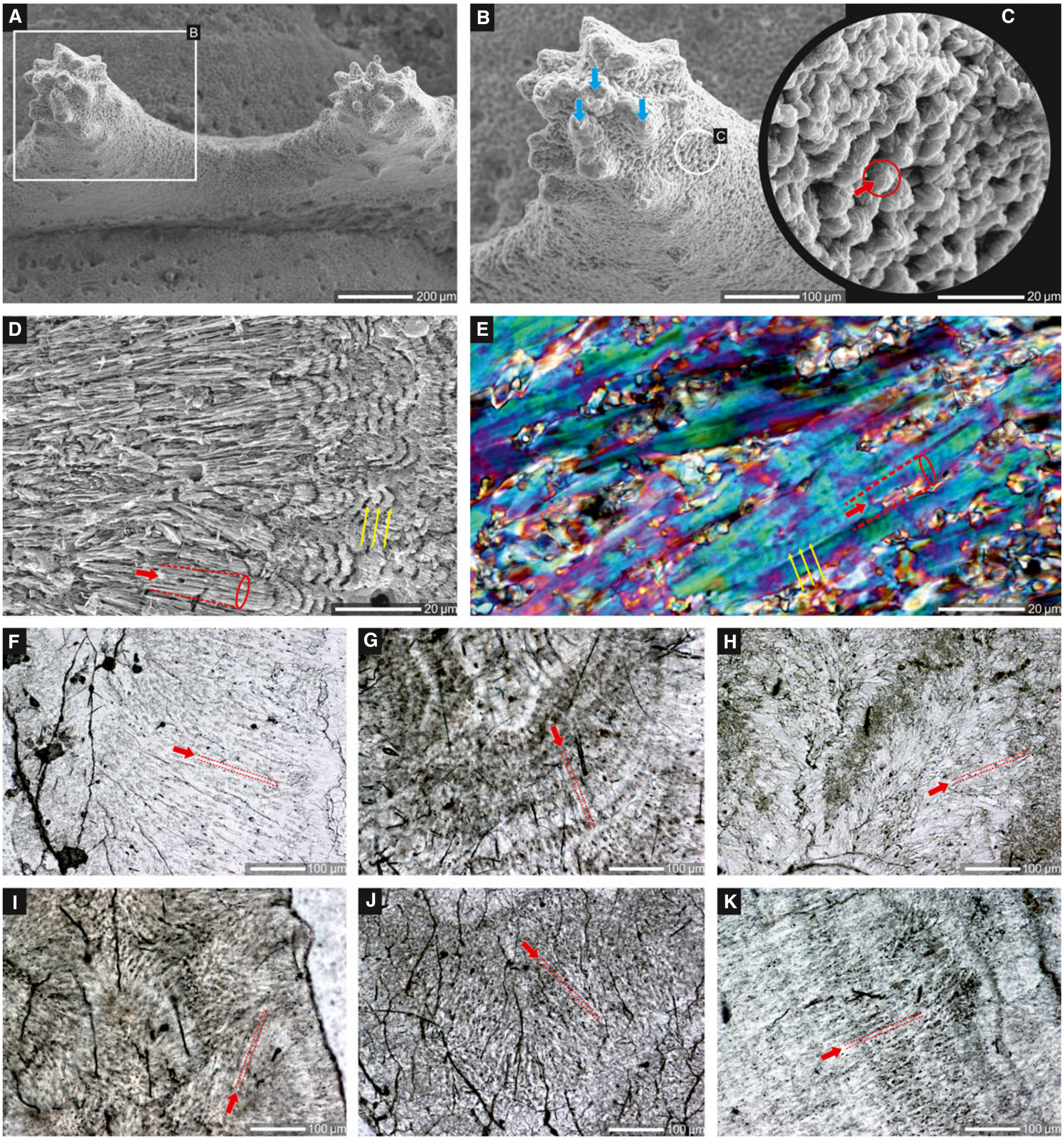


Figure 3. Micromorphology and microstructure of thickening deposits in Lobophylliidae. (A–E) *Acanthastrea echinata* (Dana, 1846); UNIMIB PFB201, Duad Island, Papua New Guinea. Microtuberculate texture was observed on surfaces of skeletal structures: overall (scanning electron microscopy; A); enlarged view of septal teeth that, in addition to granulations corresponding to centres of rapid accretion (blue arrows; B), shows micrognulation texture (red arrow and circle; C). Tips of these microtubercules correspond to slender bundles of fibres (red arrow and dashed lines) that form thickening deposits (regular growth bands marked with yellow arrows; polished and etched section, D; transverse thin section under polarized light, E). (F–K) the same microstructure of thickening deposits was observed in other lobophylliids (red arrow and dashed lines), suggesting clade-specific biomineralization control of formation. Similar structural organisation of thickening deposits may be affected by early diagenetic and/or bioerosional processes. (F) *Homophyllia bowerbanki* (Milne Edwards & Haime, 1857); MTQ MH019, Lord Howe Island, Australia. (G) *Homophyllia hillae* (Wells, 1955) (= *Homophyllia bowerbanki*); MTQ MH046, north Noddy Island, Lord Howe Island, Australia. (H) *Cynarina lacrymalis* (Milne Edwards & Haime, 1849a); IRD HS1604, Banc Gail, New Caledonia. (I) *Lobophyllia costata* (Dana, 1846); UNIMIB GA024, Gambier Islands, French Polynesia. (J) *Echinophyllia orpheensis* Veron & Pichon, 1980; MTQ 6821, Little Pioneer Bay, Orpheus Island, Palm Islands, Australia. (K) *Oxypora lacera* (Verrill, 1864); UNIMIB DJ155, Djibouti.

the stage for extinct taxa to be integrated on the coral tree of life.

SYSTEMATIC ACCOUNT

Family Lobophylliidae Dai & Horng, 2009: 59

Type genus
Lobophyllia de Blainville, 1830: 321.

Diagnosis (apomorphies in italics)
Colonial in nearly all species. Budding intracalicular, and may also be extracalicular. Corallites monomorphic or polymorphic; discrete, uniserial, or organically united. Monticules mainly absent. Walls may be fused, separated to various degrees, or colonies may be phaceloid or flabello-meandroid. *Coenosteum spinose if present*. Calice width medium to large ($\geq$ 4 mm), with varying relief. Costosepta may be confluent. Septa in varying cycles and abundances. Free septa irregular. Septa spaced $\leq$ 11 septa per 5 mm. Costosepta unequal in relative thickness. Columellae mainly trabecular and spongy (> 3 threads), of varying sizes, and *discontinuous amongst adjacent corallites with lamellar linkage*. Paliform (uniaxial) or septal (multiaxial) lobes may be weakly or moderately developed. Epitheca varies in development. Endotheca low-moderate (tabular) or abundant (vesicular).

Tooth base at midcalice elliptical-parallel. Tooth tip at midcalice irregular; *tip orientation parallel or forming multiaxial bulb*. Tooth height medium to high ($\geq$ 0.3 mm). Tooth spacing medium to wide ($\geq$ 0.3 mm), with varying numbers of teeth per septum. Tooth shape may vary between first- and third-order septa. Tooth size may vary between wall and septum. Granules mainly scattered on septal face; weak (rounded), strong (pointed), or irregular. Interarea smooth or palisade.

Walls formed by dominant paratheca and partial septotheca. *Thickening deposits in concentric rings with extensive stereome.* Costa centre clusters weak or strong; $\geq$ 0.3 mm between clusters; medial lines weak or strong. Septum centre clusters weak or strong; $\geq$ 0.3 mm between clusters; medial lines weak. Perpendicular crosses absent. Columella centres clustered.

Genera included
1. *Lobophyllia* de Blainville, 1830: 321.
2. *Acanthastrea* Milne Edwards & Haime, 1848a, vol. 27: 495.
3. *Australophyllia* Benzoni & Arrigoni in Arrigoni *et al.*, 2016a.
4. *Cynarina* Brüggemann, 1877: 305.
5. *Echinomorpha* Veron, 2000, vol. 2: 333.
6. *Echinophyllia* Klunzinger, 1879: 69.
7. *Homophyllia* Brüggemann, 1877: 310.
8. *Micromussa* Veron, 2000, vol. 3: 8.
9. *Moseleya* Quelch, 1884: 292.
10. *Oxypora* Saville Kent, 1871: 283.
11. *Sclerophyllia* Klunzinger, 1879: 4.

Taxonomic remarks
Lobophylliidae was established by Dai & Horng (2009: 59) for six of the 13 genera in Mussidae *sensu* Veron (2000) and two of the five genera in Pectiniidae *sensu* Veron (2000). Licuanan (2009: 135) followed this scheme for the corals of the north-western Philippines. These taxa constitute the molecular clades XVIII, XIX, and XX designated by Fukami *et al.* (2008) (for a list of all available lobophylliid *nomina*, valid and synonymized, see Appendix S5).

For Mussidae *sensu* Veron (2000; see also Vaughan & Wells, 1943; Wells, 1956), Dai & Horng (2009) dealt only with the fauna in Taiwan (i.e. *Lobophyllia* de Blainville, 1830: 321, *Acanthastrea* Milne Edwards & Haime, 1848a, vol. 27: 495, *Australomussa* Veron, 1985: 171, *Cynarina* Brüggemann, 1877: 305, *Scolymia* Haime, 1852: 279, and *Symphyllia* Milne Edwards & Haime, 1848a, vol. 27: 491), so the remaining seven genera were not included in the new family. The Atlantic taxa, represented by four of these seven genera, *Mussa* Oken, 1815: 73, *Isophyllia* Milne Edwards & Haime, 1851a, vol. 5: 87, *Mussismilia* Ortmann, 1890: 292, and *Mycetophyllia* Milne Edwards & Haime, 1848a, vol. 27: 491, were placed in Mussidae by Budd *et al.* (2012) owing to the deep divergence between the Atlantic (clade XXI *sensu* Fukami *et al.*, 2008) and Indo-Pacific fauna (Fukami *et al.*, 2004b, 2008), and the status of *Mussa* as type genus of Mussidae Ortmann, 1890: 315. *Blastomussa* Wells, 1968: 276, was placed in family *incertae sedis* (Budd *et al.*, 2012) because it is genetically distinct from lobophylliids and mussids, and most closely related to *Physogyra*, *Plerogyra*, and *Nemenzophyllia* (clade XIV; Fukami *et al.*, 2008; Benzoni *et al.*, 2014). Also in family *incertae sedis* is *Indophyllia* Gerth, 1921: 405, now considered an extinct genus after *Indophyllia macassarensis* Best & Hoeksema, 1987: 394, was transferred into *Cynarina* by Budd *et al.* (2012). *Micromussa* Veron, 2000, vol. 3: 8, the final Mussidae genus (*sensu* Veron, 2000), was placed in Lobophylliidae by Budd *et al.* (2012).

Further actions influenced the final generic composition of Lobophylliidae prior to the present study. *Scolymia*, one of the six genera that initially defined the family (Dai & Horng, 2009), was moved into Mussidae because its type, *Madrepora lacera* Pallas, 1766: 298 (see Vaughan, 1901: 6), is an Atlantic species (Budd *et al.*, 2012). Its two Indo-Pacific members were redistributed into *Homophyllia* Brüggemann, 1877: 310, and *Parascolymia* Wells, 1964: 379. The two Pectiniidae genera (*sensu* Veron, 2000) initially assigned to Lobophylliidae by Dai & Horng (2009), *Echinophyllia* Klunzinger, 1879: 69, and *Oxypora* Saville Kent, 1871: 283, were joined by *Echinomorpha* Veron, 2000, vol. 2: 333 (Budd *et al.*, 2012). *Moseleya* Quelch, 1884: 292, formerly in Faviidae *sensu* Veron (2000) was also placed in Lobophylliidae (Huang *et al.*, 2011; Budd *et al.*, 2012). *Sclerophyllia* Klunzinger, 1879: 4, was resurrected based on new molecular and morphological data collected for *Sclerophyllia margariticola* Klunzinger, 1879: 4, whose sister congener is *Acanthastrea maxima* Sheppard & Salm, 1988: 276 (Arrigoni *et al.*, 2015). Arrigoni *et al.* (2014b) found *Australomussa* and *Parascolymia* to be genetically indistinguishable, and therefore considered the former to be a junior synonym of the latter. Finally, based on a morpho-molecular approach Arrigoni *et al.* (2016a) formally revised *Homophyllia* and *Micromussa* with the inclusion of *H. bowerbanki* (Milne Edwards & Haime, 1857), *Micromussa lordhowensis* (Veron & Pichon, 1982), and *Micromussa multipunctata* (Hodgson, 1985), as well as the new species *Micromussa indiana* Benzoni & Arrigoni, and *Micromussa pacifica* Benzoni & Arrigoni. The authors also established *Australophyllia* Benzoni & Arrigoni, to accommodate the highly divergent *A. wilsoni*.

Drawing upon the morphological and molecular phylogenies inferred in this study (Fig. 2), as well as prior work carried out by Budd *et al.* (2012) and Arrigoni *et al.* (2012, 2014b,c, 2015, 2016a), we classify Lobophylliidae species into 11 genera. The major change over the most recent proposals by Arrigoni *et al.* (2014b, 2015) is the placement of all members of subclade I (*sensu* Arrigoni *et al.*, 2014c) in *Lobophyllia*; our results show neither genetic nor morphological separation amongst *Lobophyllia*, *Parascolymia*, and *Symphyllia*. Furthermore, they support the transfers of *Ac. ishigakiensis* Veron, 1990: 132, into *Lobophyllia*, and *L. pachysepta* Chevalier, 1975: 269, into *Acanthastrea*, which we carry out here. *Lobophyllia* thus becomes the most species-rich genus in Lobophylliidae but with relatively limited genetic differentiation amongst species (see Arrigoni *et al.*, 2014b: fig. 9, 2014c: fig. 1).

Lobophylliidae is widely distributed on reefs of the Indo-Pacific, and absent in the eastern Pacific.

Morphological remarks

There are five synapomorphies defining Lobophylliidae (bootstrap support of 95 and decay index of 5): (1) coenosteum spinose (likelihood of 1 based on the Mk1 model); (2) columellae discontinuous amongst adjacent corallites with lamellar linkage (likelihood 1.00); (3) tooth base at midcalice elliptical-parallel (likelihood 1.00); (4) tooth tip orientation parallel or forming multiaxial bulb (likelihood 1.00); and (5) thickening deposits in concentric rings with extensive stereome (likelihood 1.00). These comprise two macromorphological, two micromorphological, and one microstructural features. All of these characters strongly support the monophyly of Lobophylliidae and are monomorphic within the clade. Furthermore, the subcorallite characters unequivocally distinguish Lobophylliidae from Merulinidae, which has circular tooth base at midcalice, tooth tip orientated perpendicular to the septum or as multiaxial threads, and thickening deposits that are thick fibrous.

Mussidae (clade XXI) is an exclusively Atlantic clade, and in contrast to Lobophylliidae, has costate coenosteum, regular (pointed) midcalice tooth tip, transverse septal crosses (as clusters or carinae), and no extensive stereome thickening (Budd *et al.*, 2012).

Genus *Lobophyllia* de Blainville, 1830: 321 (Fig. 4)

Synonyms

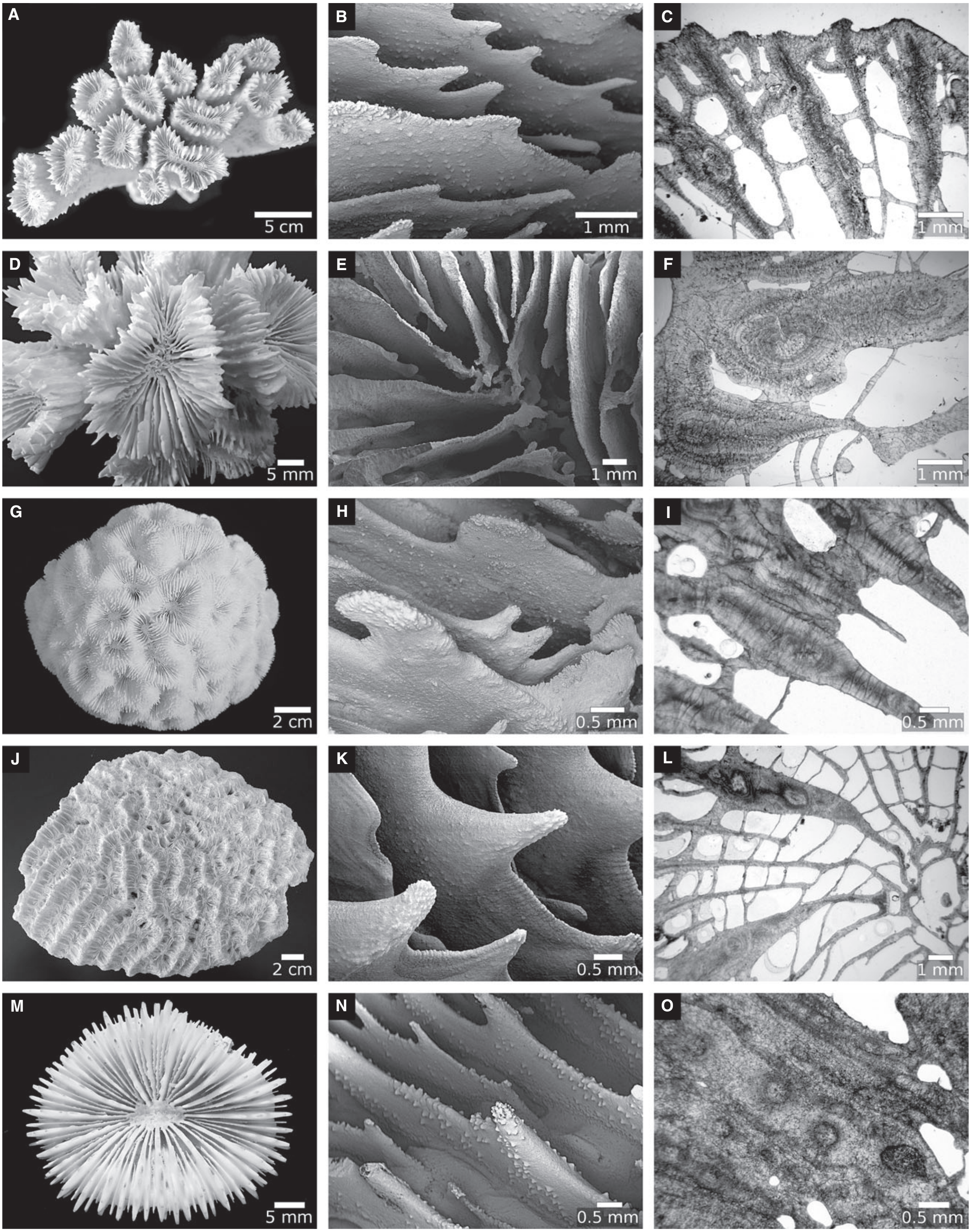
Australomussa Veron, 1985: 171 (type species: *Australomussa rowleyensis* Veron, 1985: 171, figs 23–25; original designation, Veron, 1985: 171); *Palauphyllia* Yabe, Sugiyama & Eguchi, 1936: 44 (type species: *Lobophyllia hataii* Yabe *et al.*, 1936: 44, pl. 26: fig. 3, pl. 28: figs 6, 7; original designation, Yabe *et al.*, 1936: 44); *Parascolymia* Wells, 1964: 379 (type species: *Scolymia vitiensis* Brüggemann, 1877: 304; original designation, Wells, 1964: 379); *Symphyllia* Milne Edwards & Haime, 1848a, vol. 27: 491 (type species: *Meandrina sinuosa* Quoy & Gaimard, 1833: 227, pl. 18: figs 4, 5 = *Mussa nobilis* Dana, 1846: 187, pl. 8: fig. 10 = *Mussa recta* Dana, 1846: 186, pl. 8, figs 11, 11a; Matthai, 1928: 229; original designation, Milne Edwards & Haime, 1848a, vol. 27: 491).

Type species

Madrepora corymbosa Forskal, 1775: 137; subsequent designation, Matthai, 1928: 210.

Original description

Animaux actiniformes, pourvus d'une grande quantité de tentacules cylindriques, plus ou moins longs, sortant de loges coniques, à ouverture subcirculaire, quelquefois même alongées et sinueuses, partagées en un grand nombre de sillons par des lamelles tranchantes, laciniées, situées à l'extrémité des branches, en général peu nombreuses et fasciculées, composant un polypier calcaire, fixe, turbiné, strié longitudinalement à l'extérieur et très-lacuneux à l'intérieur. (de Blainville, 1830: 321)


A
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N
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O
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Subsequent descriptions
Quoy & Gaimard, 1833: 193; Milne Edwards & Haime, 1848a, vol. 27: 491; Milne Edwards & Haime, 1849a, vol. 11: 244; Milne Edwards & Haime, 1850, vol. 5: xxxii; Matthai, 1928: 208–210; Crossland, 1935: 502; Wells, 1936: 117; Yabe *et al.*, 1936: 42–43; Vaughan & Wells, 1943: 194–195; Alloiteau, 1952: 630; Crossland, 1952: 142; Wells, 1956: F417; Nemenzo, 1959: 128; Chevalier, 1975: 231; Ditlev, 1980: 79; Veron & Pichon, 1980: 266; Scheer & Pillai, 1983: 145; Wood, 1983: 195–196; Veron, 1986: 412; Chevalier & Beauvais, 1987: 723–724; Veron & Hodgson, 1989: 267; Sheppard, 1990: 6; Sheppard & Sheppard, 1991: 116; Latypov & Dautova, 1998: 60–61; Veron, 2000, vol. 3: 38; Latypov, 2006: 343; Latypov 2014: 355.

Diagnosis (apomorphies in italics)
Colonial; submassive or massive. Budding intracalicular, and may also be extracalicular. Corallites monomorphic or polymorphic; discrete or *uniserial*. Monticules absent. Walls may be fused, or colonies may be phaceloid or flabello-meandroid. Calice width large (> 15 mm), with high relief (> 6 mm). Costosepta may or may not be confluent. Septa in ≥ 4 cycles (≥ 48 septa). Free septa irregular. Septa spaced < 6 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy (> 3 threads), < 1/4 of calice width, and discontinuous amongst adjacent corallites with lamellar linkage. Internal lobes absent. Epitheca reduced if present. *Endotheca abundant (vesicular)* (Fig. 4A, D, G, J, M).

Tooth base at midcalice elliptical-parallel. Tooth tip orientation parallel. Teeth tall (> 0.6 mm); widely spaced (> 1 mm), with > 6 teeth per septum. Tooth shape unequal between first- and third-order septa. Tooth size unequal between wall and septum. Granules scattered on septal face; weak (rounded). Interarea palisade (Fig. 4B, E, H, K, N).

Walls formed by dominant paratheca and partial septotheca. Thickening deposits in concentric rings with extensive stereome. Costa centre clusters strong; > 0.6 mm between clusters; medial lines weak. Septum centre clusters weak; > 0.5 mm between clusters; medial lines weak (Fig. 4C, F, I, L, O).

Species included
1. *Lobophyllia corymbosa* (Forskal, 1775: 137); holotype: ZMUC ANT-000526 (dry specimen); type locality: Red Sea; phylogenetic data: molecular and morphology.
2. *Lobophyllia agaricia* (Milne Edwards & Haime, 1849a, vol. 11: 255); holotype: MNHN scle913 (dry specimen); type locality: unknown; phylogenetic data: molecular and morphology.
3. *Lobophyllia costata* (Dana, 1846: 179, pl. 7: figs 2, 2a, 2b); holotype: USNM 43 (dry specimen); type locality: Tahiti, Society Islands; phylogenetic data: molecular and morphology.
4. *Lobophyllia dentata* Veron, 2000, vol. 3: 46, figs 1–4 (see also Veron, 2002: 134, figs 248, 249; ICZN, 2011: 164); lectotype (designated herein): MTQ G55826 (dry specimen); type locality: Milne Bay, Papua New Guinea (4 m depth); phylogenetic data: morphology only.
5. *Lobophyllia diminuta* Veron, 1985: 165, figs 16, 17; holotype: WAM Z913 (also WAM 167–84; Griffith & Fromont, 1998: 236) (dry specimen); type locality: northern Swain Reefs, Australia (2 m depth); phylogenetic data: molecular and morphology.
6. *Lobophyllia erythraea* (Klunzinger, 1879: 10, pl. 1: fig. 10, pl. 9: fig. 9); holotype: ZMB Cni 2171 (dry specimen); type locality: 'Kosseir' (specimen label), Egypt, Red Sea; phylogenetic data: molecular and morphology.
7. *Lobophyllia flabelliformis* Veron, 2000, vol. 3: 48, figs 1–5 (see also Veron, 2002: 136, figs 250–253; ICZN, 2011: 164); lectotype (designated herein): MTQ G55827 (dry specimen); type locality: Milne Bay, Papua New Guinea (7 m depth); phylogenetic data: molecular and morphology.

Figure 4. *Lobophyllia* de Blainville, 1830, may have fused walls, or may be phaceloid/flabello-meandroid, with large (> 15 mm) and high-relief (> 6 mm) calices, septa in ≥ 4 cycles (≥ 48 septa), and abundant (vesicular) endotheca. Septal teeth are tall (> 0.6 mm) and widely spaced (> 1 mm), unequally shaped between first- and third-order septa, unequally sized between wall and septum, with palisade interarea. Walls formed by dominant paratheca and partial septotheca, with strong costa centre clusters. (A–C) *Lobophyllia corymbosa* (Forskal, 1775), type species of *Lobophyllia*; macromorphology, holotype ZMUC ANT-000526 (A; photo by M. V. Sørensen); micromorphology (scanning electron microscopy; B) and microstructure (transverse thin section; C), hypotype UF 566, Guam. (D–F) *Lobophyllia costata* (Dana, 1846); macromorphology (D), micromorphology (E), and microstructure (F), holotype USNM 43, Tahiti. (G–I) *Lobophyllia ishigakiensis* (Veron, 1990); macromorphology, holotype MTQ G32484, Kabira Bay, Ishigaki Island, Japan (G); micromorphology (H), and microstructure (I), hypotype IRD HS3127, New Caledonia. (J–L) *Lobophyllia recta* (Dana, 1846); macromorphology (J) and microstructure (L), syntype USNM 9, Wake Island, North Pacific Ocean; micromorphology, hypotype USNM 91129, Halmahera, Moluccas, Indonesia (K). (M–O) *Lobophyllia vitiensis* (Brüggemann, 1877); macromorphology, holotype NHMUK 1862.2.4.49, Fiji (M; photo by H. Taylor); micromorphology (N) and microstructure (O), hypotype USNM 83332, New Caledonia.

8. *Lobophyllia grandis* Latypov, 2006: 347, fig. 80-3 (= *Lobophyllia* sp. 1: Latypov & Dautova, 1998: 64, pl. 14: fig. 3); holotype: FEBRAS 1/95279 (dry specimen); type locality: Bai Thanh Bay, Khanh Hoa, Vietnam (2.5 m depth); phylogenetic data: none.
9. *Lobophyllia hassi* (Pillai & Scheer, 1976: 66, pl. 29: figs 2, 3); holotype: X2:88-6, Hessian State Museum, Darmstadt, status unknown; type locality: Rasdu Atoll, Maldives; phylogenetic data: none.
10. *Lobophyllia hataii* Yabe *et al.*, 1936: 44, pl. 26: fig. 3, pl. 28: figs 6, 7; holotype: TIU 56623 (dry specimen); type locality: Palau; phylogenetic data: morphology only.
11. *Lobophyllia hemprichii* (Ehrenberg, 1834: 325); holotype: ZMB Cni 648 (dry specimen); type locality: Red Sea; phylogenetic data: molecular and morphology.
12. *Lobophyllia ishigakiensis* (Veron, 1990: 132, figs 38–41, 80, 81); holotype: MTQ G32484 (dry specimen); type locality: Kabira Bay, Ishigaki Island, Japan (10 m depth); phylogenetic data: molecular and morphology.
13. *Lobophyllia radians* (Milne Edwards & Haime, 1849a, vol. 11: 255); holotype: MNHN scle920 (dry specimen); type locality: 'Océan Indien' (specimen label); phylogenetic data: molecular and morphology.
14. *Lobophyllia recta* (Dana, 1846: 186, pl. 8, figs 11, 11a); syntype: USNM 9 (dry specimen); type locality: Wake Island, North Pacific Ocean; phylogenetic data: molecular and morphology.
15. *Lobophyllia robusta* Yabe & Sugiyama in Yabe *et al.*, 1936: 44, pl. 32: figs 2–4; holotype: TIU 40468 (dry specimen); type locality: Misaki, Shikoku, Japan; phylogenetic data: molecular and morphology.
16. *Lobophyllia rowleyensis* (Veron, 1985: 171, figs 23–25); holotype: WAM Z907 (also WAM 171-84; Griffith & Fromont, 1998: 235) (dry specimen); paratypes: WAM Z908, Z909 (also WAM 172-84, 173-84; Griffith & Fromont, 1998: 235) (two dry specimens); type locality: Legendre Island, Dampier Archipelago, Western Australia (17 m depth); phylogenetic data: molecular and morphology.
17. *Lobophyllia serrata* Veron, 2000, vol. 3: 41, figs 5, 6 (see also Veron, 2002: 133, figs 246, 247; ICZN, 2011: 164); lectotype (designated herein): UP MSI-3007-CO (dry specimen); type locality: Calamian Islands, Palawan, Philippines (10 m depth); phylogenetic data: none.
18. *Lobophyllia valenciennesi* (Milne Edwards & Haime, 1849a, vol. 11: 256) (see Article 58.14 of the International Code of Zoological Nomenclature); holotype: MNHN scle927 (dry specimen); type locality: Singapore; phylogenetic data: molecular and morphology.
19. *Lobophyllia vitiensis* (Brüggemann, 1877: 304); holotype: NHMUK 1862.2.4.49 (dry specimen); type locality: Fiji; phylogenetic data: molecular and morphology.

Taxonomic remarks

Lobophyllia was first described by de Blainville (1830: 321) for seven species: (1) *Lobophyllia glabrescens* (De Chamisso & Eysenhardt, 1821: 369); (2) *Lobophyllia angulosa* (Pallas, 1766: 299); (3) *Lobophyllia aurantiaca* (=*Lobophyllia aurea* Quoy & Gaimard, 1833: 195); (4) *Lobophyllia fastigiata* (Pallas, 1766: 301); (5) *Lobophyllia corymbosa* (Forskal, 1775: 137); (6) *Lobophyllia sinuosa* (Lamarck, 1816: 229); and (7) *Lobophyllia carduus* (Ellis & Solander, 1786: 153). The first, second, and fourth are the type species of *Euphyllia* Dana, 1846: 40, *Mussa* Oken, 1815: 73, and *Eusmilia* Milne Edwards & Haime, 1848b, vol. 27: 467, respectively (Matthai, 1928), whereas the third belongs to *Tubastraea* Lesson, 1829: 93 (Cairns, 2001). The fifth species was thus chosen to be the type species of *Lobophyllia*, and the genus resurrected by Matthai (1928: 208) to incorporate all the Indo-Pacific species of *Mussa* as defined by Milne Edwards & Haime (1857), i.e. *L. corymbosa* (Forskal, 1775: 137), *L. costata* (Dana, 1846: 179; but see Sheppard, 1987) and *L. hemprichii* (Ehrenberg, 1834: 325). A further eight species were described in this genus by Yabe *et al.* (1936; two species), Chevalier (1975; one species), Veron (1985, 2000); four species), and Latypov (2006; one species).

However, our analyses demonstrate that *L. pachysepta* Chevalier, 1975: 269, is more closely related to *Acanthastrea* than to other *Lobophyllia* species, including the type *L. corymbosa*, and thus should be regarded as an *Acanthastrea* species (Fig. 2). Both molecular and morphological trees also show that *Ac. ishigakiensis* Veron, 1990: 132, *Parascolymia*, and nearly all *Symphyllia* species are nested amongst *Lobophyllia* species in subclade I (*sensu* Arrigoni *et al.*, 2014c), supporting the call by Arrigoni *et al.* (2014c) to consolidate these taxa into a single genus. Therefore, *Ac. ishigakiensis*, both *Parascolymia* species, and six *Symphyllia* species are herein transferred into *Lobophyllia*, which now comprises a clade of 19 closely related species. Many of these species form single lineages, but some are paraphyletic, including *L. corymbosa*, *L. hemprichii*, *L. rowleyensis*, and *L. vitiensis* (see Arrigoni *et al.*, 2014b: fig. 9, 2014c: fig. 1).

The holotype of *L. corymbosa*, type species of *Lobophyllia*, is at the ZMUC (ANT-000526), where the types of other species described by Forskal (1775) can also be found today, e.g. lectotype of *Dipsastraea favus* (Forskål, 1775: 132; ZMUC ANT-000466) and syntypes of *Cyphastrea serailia* (Forskål, 1775: 135; ZMUC ANT-000367 to ANT-000373).

Lobophyllia is widely distributed on the reefs of the Indo-Pacific, present from the Red Sea and East Africa to as far east as the Marshall Islands in the Northern Hemisphere (Veron, 2000) and the Pitcairn Islands in the Southern Hemisphere (Glynn *et al.*, 2007).

Morphological remarks

This genus is delimited by two synapomorphies, uniserial corallites (likelihood of 1.00 based on the Mk1 model) and vesicular endotheca (likelihood 1.00). However, a reduction in the number of centres occurs amongst *L. corymbosa*, *L. dentata*, *L. diminuta*, and *L. serrata*. On the one hand, *L. vitiensis* and *L. rowleyensis*, previously in *Parascolymia*, form a clade that is supported by a moderate bootstrap value (71) and decay index (2), with the synapomorphies extracalicular budding (likelihood 1.00) and polymorphic corallites (likelihood 1.00). On the other hand, species that had in the past been separated into the genera *Lobophyllia* and *Symphyllia* (*sensu* Matthai, 1928; Veron, 2000) do not form clades on either the morphological or molecular tree.

Symphyllia has often been compared to *Lobophyllia*, as both possess lamellar linkages between columellar centres (Matthai, 1928; Vaughan & Wells, 1943; Wells, 1956), but the former can be differentiated by its longer, meandering valleys bordered by fused walls (Chevalier, 1975; Wood, 1983; Veron, 1986, 2000). However, this distinction is problematic because *Symphyllia valenciennesi* Milne Edwards & Haime, 1849a, vol. 11: 256 (see Chevalier, 1975), and *L. hataii* Yabe *et al.*, 1936: 44, have shallow and straight valleys that radiate from the colony centre, with the periphery being flabello-meandroid (Veron, 2000). These two species do not group together on the morphological phylogeny (Fig. 2B), but rather form a paraphyletic group with the rest of the *Lobophyllia sensu stricto*, indicating that these characters are not reliable in delimiting species groups within subclade I (*sensu* Arrigoni *et al.*, 2014c).

Cynarina is the sister genus of *Lobophyllia*, but is morphologically distinct from the latter as it is solitary and may be free-living, have weak or moderate development of septal lobes, low-moderate (tabular) endotheca, and strong costa medial lines.

Although *Lobophyllia* is restricted to the Indo-Pacific, it has historically been confused with the Atlantic genus *Mussa* because they share many macromorphological characters (Chevalier, 1975; Veron, 2000). However, the presence of lamellar linkages between columellar centres in *Lobophyllia*, as mentioned above, is a key distinguishing feature (Matthai, 1928). Furthermore, *Mussa* possesses several subcorallite traits that are not found in *Lobophyllia*: circular tooth base, pointed tooth tip, granules aligned on septal face, interarea formed by horizontal bands, parathecal walls with trabeculothecal elements, reduced thickening deposits, and transverse septal crosses (Budd & Stolarski, 2009; Budd *et al.*, 2012).

Genus *Acanthastrea* Milne Edwards & Haime, 1848a: 495 (Fig. 5)

Type species

Acanthastrea spinosa Milne Edwards & Haime, 1848a, vol. 27: 495 = *Astrea dipsacea* Quoy & Gaimard, 1833: 210, pl. 17: figs 1, 2 (see Dana, 1846: 226; Milne Edwards & Haime, 1849b, vol. 12: 145) (= *Astraea echinata* Dana, 1846: 229, pl. 12: figs 1, 1a, b); original designation, Milne Edwards & Haime, 1848a, vol. 27: 495; holotype: MNHN IK-2010-599 (dry specimen); type locality: Tongatapu, Tonga.

Original description

Se sépare de toutes les autres *Astrées* par ses cloisons très-échinulées dont les épines les plus fortes sont les plus extérieures. (Milne Edwards & Haime, 1848a, vol. 27: 495)

Subsequent descriptions

Milne Edwards & Haime, 1849b, vol. 12: 144; Milne Edwards & Haime, 1850, vol. 5: xlii; Milne Edwards & Haime, 1851a, vol. 5: 106; Milne Edwards & Haime, 1857, vol. 2: 501; Klunzinger, 1879: 42; Duncan, 1884: 119–120; Delage & Hérouard, 1901: 632; Vaughan, 1918: 125; Faustino, 1927: 162–163; Yabe *et al.*, 1936: 47; Vaughan & Wells, 1943: 193–194; Alloiteau, 1952: 631; Crossland, 1952: 140–141; Wells, 1956: F417; Chevalier, 1975: 312; Ditlev, 1980: 79; Veron & Pichon, 1980: 252; Nemenzo & Hodgson, 1983: 42; Scheer & Pillai, 1983: 147; Wood, 1983: 195; Veron, 1986: 406; Chevalier & Beauvais, 1987: 724; Sheppard & Salm, 1988: 276; Veron & Hodgson, 1989: 266; Sheppard, 1990: 10; Sheppard & Sheppard, 1991: 112; Veron, 1993: 245; Latypov & Dautova, 1998: 59; Veron, 2000, vol. 3: 12; Claereboudt, 2006: 212; Latypov, 2006: 341; Latypov 2014: 353–354.

Diagnosis

Colonial; submassive or massive. Budding intracalicular and extracalicular. Corallites monomorphic; mainly discrete. Monticules absent. Coenosteum spinose; limited (includes double wall), moderate (< corallite diameter) amount, or colonies may be phaceloid or partly flabello-meandroid. Calice width

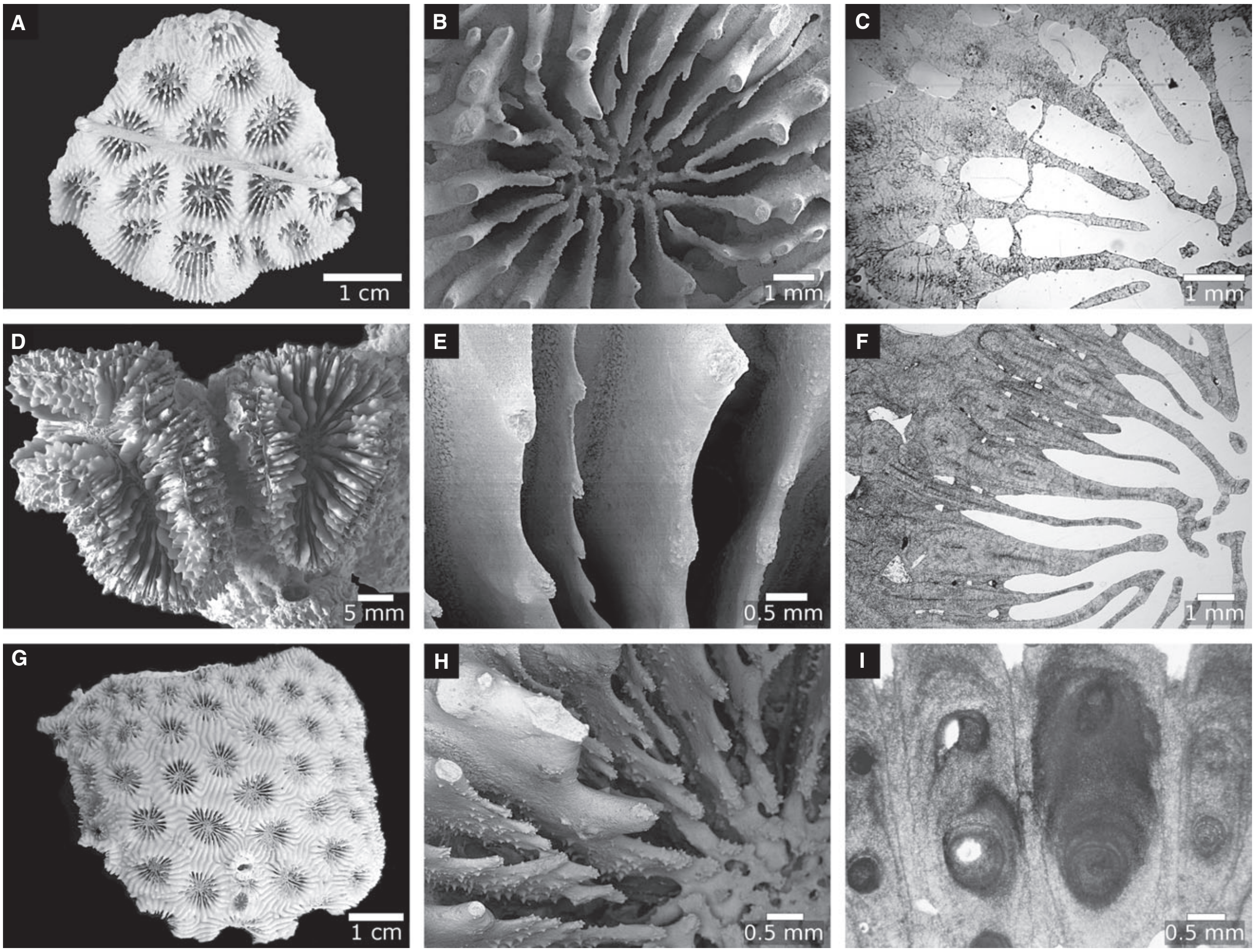

Figure 5. *Acanthastrea* Milne Edwards & Haime, 1848a, generally has discrete corallites, with varying amounts of coenosteum, or may be phaceloid/flabello-meandroid, with medium to large (≥ 4 mm) and medium- to high-relief (≥ 3 mm) calices, and septa in three cycles (24–36 septa). Septal teeth with medium height (0.3–0.6 mm) and medium to wide spacing (≥ 0.3 mm), unequally shaped between first- and third-order septa, equally sized between wall and septum, and smooth interarea. Walls formed by dominant paratheca and partial septotheca, with strong costa and septum centre clusters. (A–C) *Acanthastrea echinata* (Dana, 1846), type species of *Acanthastrea*; macromorphology, *Acanthastrea spinosa* Milne Edwards & Haime, 1848a, holotype of *Acanthastrea* MNHN IK-2010-599, Tongatapu, Tonga (A; photo by A. Andouche); micromorphology (scanning electron microscopy; B) and microstructure (transverse thin section; C), syntype USNM 25, Fiji. D–F, *Acanthastrea pachysepta* (Chevalier, 1975); macromorphology, holotype MNHN IK-2010-660, Chesterfield, Islands, New Caledonia (D); micromorphology (E) and microstructure (F), hypotype USNM 45515, Murray Island, Australia. (G–I) *Acanthastrea rotundoflora* Chevalier, 1975; macromorphology, holotype MNHN IK-2010-675, south-east Fabre Atoll, New Caledonia (G); micromorphology (H) and microstructure (I), hypotype IRD HS3166, New Caledonia.

medium to large (≥ 4 mm), with medium to high relief (≥ 3 mm). Costosepta mostly confluent. Septa in three cycles (24–36 septa). Free septa irregular. Septa spaced < 6 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy (> 3 threads), < 1/4 of calice width, and discontinuous amongst adjacent corallites with lamellar linkage. Internal lobes usually absent. Epitheca reduced. Endotheca low-moderate (tabular) (Fig. 5A, D, G).

Tooth base at midcalice elliptical-parallel. Tooth tip orientation parallel. Tooth height usually medium (0.3–0.6 mm). Tooth spacing medium to wide (≥ 0.3 mm), with ≤ 6 teeth per septum. Tooth shape unequal between first- and third-order septa. Tooth size equal between wall and septum. Granules scattered on septal face; weak (rounded). Interarea smooth (Fig. 5B, E, H).

Walls formed by dominant paratheca and partial septotheca. Thickening deposits in concentric rings with extensive stereome. Costa centre clusters strong; > 0.6 mm between clusters; medial lines weak. Septum centre clusters may be strong; > 0.5 mm between clusters; medial lines weak (Fig. 5C, F, I).

Species included

1. *Acanthastrea echinata* (Dana, 1846: 229, pl. 12: figs 1, 1a, b); syntype: USNM 25 (dry specimen); type locality: Fiji; phylogenetic data: molecular and morphology.
2. *Acanthastrea brevis* Milne Edwards & Haime, 1849b, vol. 12: 146; holotype: MNHN scle851 (dry specimen); type locality: unknown; phylogenetic data: none.
3. *Acanthastrea hemprichii* (Ehrenberg, 1834: 320); holotype: lost; type locality: Red Sea; phylogenetic data: molecular and morphology.
4. *Acanthastrea minuta* Moll & Best, 1984: 53, fig. 12; holotype: RMNH 15275 (dry specimen); type locality: 100 m offshore of north Bone Tambung, Spermonde Archipelago, Indonesia (7 m depth); phylogenetic data: none.
5. *Acanthastrea pachysepta* (Chevalier, 1975: 269, pl. 24: fig. 1); holotype: MNHN IK-2010-660 (dry specimen); type locality: Chesterfield, Islands, New Caledonia (1 m depth); phylogenetic data: molecular and morphology.
6. *Acanthastrea rotundoflora* Chevalier, 1975: 325, pl. 29: fig. 3, pl. 31: fig. 7; holotype: MNHN IK-2010-675 (dry specimen); type locality: south-east Fabre Atoll, New Caledonia (4–5 m depth); phylogenetic data: molecular and morphology.
7. *Acanthastrea subechinata* Veron, 2000, vol. 3: 13, figs 3–5 (see also Veron, 2002: 128, figs 238, 239; ICZN, 2011: 163); lectotype (designated herein): UP MSI-3001-CO (dry specimen); type locality: Calamian Islands, Palawan, Philippines (10 m depth); phylogenetic data: molecular only.

Taxonomic remarks

The genus was first described to contain four monocentric species (i.e. '*Astrées*'; Milne Edwards & Haime, 1848a, vol. 27: 495) that have especially spinose wall septa – *Acanthastrea hirsuta* Milne Edwards & Haime, 1849b, vol. 12: 145, *Acanthastrea spinosa* Milne Edwards & Haime, 1848a, vol. 27: 495, *Acanthastrea brevis* Milne Edwards & Haime, 1849b, vol. 12: 146, and *Acanthastrea grandis* Milne Edwards & Haime, 1849b, vol. 12: 146. These species have mostly been synonymized as *Acanthastrea echinata* (Dana, 1846: 229) (Chevalier, 1975; Veron & Pichon, 1980). It should be noted that the *Ac. spinosa* specimen used by Milne Edwards & Haime, 1848a, vol 27: 495, to establish the genus (MNHN IK-2010-599) should still be considered the type of *Acanthastrea*.

By the time of Veron (2000), 12 *Acanthastrea* species were recognized as valid, including five described by Veron (1990, 2000) and Veron & Pichon (1982). Molecular phylogenetic analyses by Fukami *et al.* (2008) then showed that the genus was polyphyletic, with representatives in clades XVIII, clustering with *Micromussa amakusensis* (Veron, 1990: 137), and XX (*sensu* Fukami *et al.*, 2008). Kitahara *et al.* (2010) obtained a similar result, but extensive sampling by Arrigoni *et al.* (2014c) further showed that *Acanthastrea* is distributed amongst four major subclades (B, C, E, and I, *sensu* Arrigoni *et al.*, 2014c). Arrigoni *et al.* (2015) then swiftly moved *Ac. maxima* Sheppard & Salm, 1988: 276, into the revived *Sclerophyllia* Klunzinger, 1879: 4. Finally, Arrigoni *et al.* (2016a) synonymized *Acanthastrea hillae* Wells, 1955, under *Acanthastrea bowerbanki* Milne Edwards & Haime, 1857, and moved the species into *Homophyllia*. *Acanthastrea lordhowensis* Veron & Pichon, 1982, was also transferred into *Micromussa*, whereas *Micromussa minuta* (Moll & Best, 1984) was moved into *Acanthastrea* based on detailed examination of the holotype (Arrigoni *et al.*, 2016a).

Our molecular and morphological trees support these changes, and also the further transfers of *Ac. ishigakiensis* Veron, 1990: 132, into *Lobophyllia* (Fig. 2), and *Ac. regularis* Veron, 2000, vol. 3: 16, into *Micromussa*. Arrigoni *et al.* (2014c) suggested that *Ac. faviaformis* Veron, 2000, vol. 3: 24, should be transferred into the merulinid genus *Dipsastraea* de Blainville, 1830, and our examination of the lectotype (designated herein) shows that its macromorphological characters are scored identically to *Dipsastraea* spp. (Appendix S2). Here we formally carry out the genus reassignment – *Dipsastraea faviaformis* (Veron, 2000) comb. nov.

The molecular phylogeny here groups *L. pachysepta* Chevalier, 1975: 269, and the remaining *Acanthastrea* species together in subclade E (Fig. 2A), although they form a paraphyly on the morphological phylogeny (Fig. 2B) owing to the disparately large corallites and phaceloid/flabello-meandroid colonies of *L. pachysepta*. Based on the molecular tree and subcorallite characters that are nearly identical between this rogue species and *Acanthastrea* – differing only in tooth spacing and distinctiveness of septum centre clusters – we move *L. pachysepta* into the present genus. The resulting classification thus comprises seven *Acanthastrea* species.

Acanthastrea is widely distributed on the reefs of the Indo-Pacific, present from the Red Sea and East Africa to as far east as the Marshall Islands in the Northern Hemisphere (Veron, 2000) and the Gambier Islands in the Southern Hemisphere (Glynn *et al.*, 2007).

Morphological remarks
The genus is paraphyletic on the morphological phylogeny (Fig. 2B). On the molecular tree, *Acanthastrea* possesses several symplesiomorphies, including extracalicular budding, discrete corallites, columellae < 1/4 of calice width, reduced epitheca, parallel tooth tip at midcalice, strong costa centre clusters, weak costa medial lines, and > 0.5 mm between septum centre clusters. These traits distinguish *Acanthastrea* from its sister clade of *Echinophyllia* + *Oxypora*. Excluding *Ac. pachysepta*, the genus is moderately supported on the morphological tree (bootstrap support of 68), with limited/moderate coenosteum amount and strong septum centre clusters as synapomorphies. Several characters separate *Acanthastrea* from taxa previously associated with the genus that are in subclades A (*Micromussa*), B (*Homophyllia*), C (*Sclerophyllia*), and I (*Lobophyllia*), including septa spacing, epitheca and endotheca development, number of teeth per septum, S1/S3 tooth shape, and wall/septum tooth size.

Acanthastrea has historically been confused with the merulinid genus *Favites* Link, 1807: 162, as they are superficially alike and the inner edge of the septum possesses similar teeth (Chevalier, 1975). When Matthai (1914) synonymized *Favites* with *Favia* Oken, 1815: 67, the *Acanthastrea* species (i.e. *Ac. hirsuta* and *Astraea hemprichii*) were also transferred into *Favia*, although these actions were almost immediately reversed as Vaughan (1918) revived both *Favites* and *Acanthastrea*. The latter is easily distinguished from *Favites* by its sparser septa (three cycles; 24–36 septa; < 6 septa per 5 mm), lamellar linkage between columellae, absence of paliform lobes, reduced epitheca and endotheca, less numerous septal teeth which are parallel to the septa at midcalice, smooth interarea, thickening deposits in concentric rings with extensive stereome, wider separation between centre clusters, and the lack of transverse crosses.

Genus *Australophyllia* Benzoni & Arrigoni in Arrigoni *et al.*, 2016a (Fig. 6)

Type species
Symphyllia wilsoni Veron, 1985: 167, figs 18–22; original designation, Arrigoni *et al.*, 2016a.

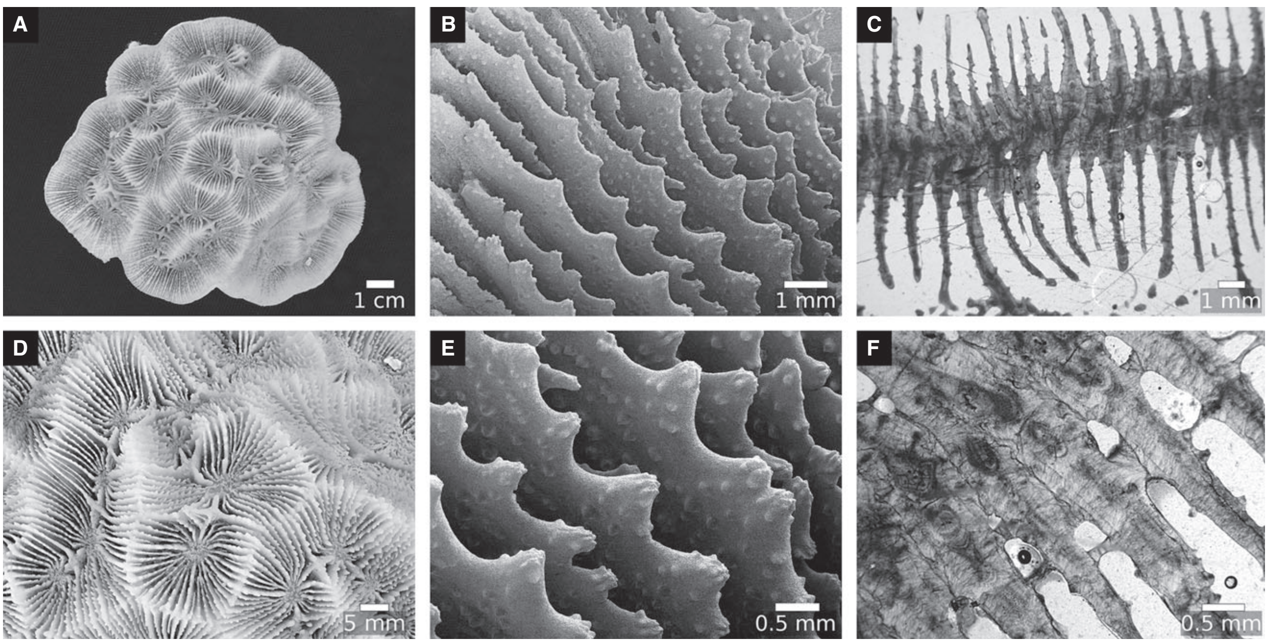

Figure 6. *Australophyllia* Benzoni & Arrigoni in Arrigoni *et al.*, 2016a, has uniserial corallites with fused walls sometimes forming monticules, medium-size (4–15 mm) and medium-relief (3–6 mm) calices, septa in ≥ 4 cycles (≥ 48 septa), and well-developed epitheca. Septal teeth typically with medium height (0.3–0.6 mm) and spacing (0.3–1.0 mm), equally shaped between first- and third-order septa, equally sized between wall and septum, and smooth interarea. Walls formed by dominant paratheca and partial septotheca, with strong costa centre clusters. (A–F) *Australophyllia wilsoni* (Veron, 1985), type and only living species of *Australophyllia*; macromorphology, holotype WAM Z910, Rat Island, Houtman Abrolhos Islands, Western Australia (A, D; photo by WAM); micromorphology (scanning electron microscopy; B, E), hypotype WAM WIL05, Hall Bank, Western Australia; and microstructure (transverse thin section; C, F), hypotype WAM WIL03, Hall Bank, Western Australia.

Diagnosis (apomorphies in italics)
Colonial; submassive or massive. *Budding exclusively intracalicular.* Corallites monomorphic; *uniserial. Monticules may be present.* Walls fused. Calice width usually medium (4–15 mm), with medium relief (3–6 mm). Costosepta mostly confluent. Septa in ≥ 4 cycles (≥ 48 septa). Free septa irregular. Septa spaced six to 11 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy (> 3 threads), < 1/4 of calice width, and discontinuous amongst adjacent corallites with lamellar linkage. Internal lobes usually absent. Epitheca well developed. Endotheca low–moderate (tabular) (Fig. 6A, D).

Tooth base at midcalice elliptical-parallel. Tooth tip orientation parallel. Tooth height medium (0.3–0.6 mm), but may be slightly taller. Tooth spacing medium (0.3–1.0 mm), with > 6 teeth per septum. Tooth shape equal between first- and third-order septa. Tooth size equal between wall and septum. Granules scattered, sometimes distributed uniformly, on septal face; weak (rounded). Interarea smooth (Fig. 6B, E).

Walls formed by dominant paratheca and partial septotheca. Thickening deposits in concentric rings with extensive stereome. Costa centre clusters strong; > 0.6 mm between clusters; medial lines weak. Septum centre clusters weak; > 0.5 mm between clusters; medial lines weak (Fig. 6C, F).

Species included
Australophyllia wilsoni (Veron, 1985: 167, figs 18–22); holotype: WAM Z910 (also WAM 168-84; Griffith & Fromont, 1998: 236) (dry specimen); paratypes: WAM Z911, Z912 (also WAM 169-84, 170-84; Griffith & Fromont, 1998: 236) (two dry specimens); type locality: Rat Island, Houtman Abrolhos Islands, Western Australia (8 m depth); phylogenetic data: molecular and morphology.

Taxonomic remarks
Australophyllia was described by Benzoni & Arrigoni in Arrigoni *et al.* (2016a) to contain the phylogenetically distinct *Symphyllia wilsoni* Veron, 1985, as a newly discovered lineage (subclade J). Instead of grouping with its congenerics or the *Lobophyllia* species (subclade I) as defined in this study, it has been recovered close to *Homophyllia* and *Micromussa* based on molecular (Arrigoni *et al.*, 2016a; Fig. 2A) and morphological data (Fig. 2B). No other species have been found with a closer relationship to *Homophyllia* or *Micromussa* despite near-complete sampling of the members of *Symphyllia sensu* Veron (2000).

Australophyllia is restricted to the reefs of southern and Western Australia (Veron, 2000; Arrigoni *et al.*, 2016a).

Morphological remarks
Three autapomorphies, all macromorphological traits, unambiguously define this monotypic genus: exclusively intracalicular budding, presence of monticules, and uniserial corallites. *Australophyllia* is closely related to *Homophyllia* and *Micromussa*, forming a sister taxon to *Homophyllia* + *Micromussa* based on molecular data (Fig. 2A), but a paraphyletic grade with morphological data, *Micromussa* being the earliest-branching clade (Fig. 2B). As such, it appears to have an intermediate morphology between *Micromussa* and *Homophyllia*, particular with respect to calice width and relief, number of septa, and septal tooth height and spacing, as well as uniformity of granule distribution. It shares all other morphological traits (excluding the autapomorphies) with *Homophyllia*, therefore positioning it between *Micromussa* and *Homophyllia* in the grade.

Although it superficially resembles *Symphyllia* (= *Lobophyllia*), in which *Au. wilsoni* was placed, it can be distinguished easily by the presence of monticules (or broken walls), smaller calices and septa spacing, well-developed epitheca, low–moderate endotheca, lower septal teeth and narrower tooth spacing, similar tooth shape between first- and third-order septa, and comparable tooth size between wall and septum, as well as smooth interarea.

GENUS *CYNARINA* BRÜGGEMANN, 1877: 305 (FIG. 7)

Synonyms
Acanthophyllia Wells, 1937: 242 (type species: *Caryophyllia deshayesiana* Michelin, 1850: 238, pl. 2; original designation, Wells, 1937: 242); *Protolobophyllia* Yabe & Sugiyama, 1935: 381 (type species: *Antillia japonica* Yabe & Sugiyama, 1931: 128, pl. 37: figs 1–5, pl. 38: figs 1, 2; original designation, Yabe & Sugiyama, 1935: 382); *Rhodocyathus* Bourne, 1905: 191 (type species: *Rhodocyathus ceylonensis* Bourne, 1905: 191, pl. 1: figs 1, 1A; original designation, Bourne, 1905: 191).

Type species
Cynarina savignyi Brüggemann, 1877: 305 = *Caryophyllia carduus* Audouin, 1826: 233, pl. 4: figs 2.1, 2.2, 2.3 (= *Caryophyllia lacrymalis* Milne Edwards & Haime, 1849a, vol. 11: 238; Milne Edwards & Haime, 1848c, vol. 10, pl. 8: figs 1, 1a); original designation, Brüggemann, 1877: 305; syntypes: NHMUK 1858.2.12.3, 1869.2.25.39, one unlabelled lot (eight dry specimens; Wells, 1964); type locality: Gulf of Suez, Red Sea.

Original description

Agreeing in all respects with *Scolymia*, except that the coral is free when adult, turbinate, and covered with a thick epitheca. From *Antillia* it differs in having the costae roughly spinose; the free edges of the larger septa lacero-dentate, the septal teeth increasing in size from within outwards, the calicular fossa very shallow; the calice circular in the adult, compressed in the young (the reverse being the case in *Antillia*). From *Homophyllia* it is likewise distinguished by the structure of its costae, septa, and fossa; besides, *Homophyllia* is always fixed by its base, and shows a very thin, appressed epitheca, whereas the latter is thick and only loosely adherent in *Cynarina*. (Brüggemann, 1877: 305)

Subsequent descriptions

Klunzinger, 1879: 3–4; Wells, 1964: 376; Chevalier, 1975: 292; Ditlev, 1980: 76; Veron & Pichon, 1980: 238; Scheer & Pillai, 1983: 144–145; Wood, 1983: 193; Veron, 1986: 396; Chevalier & Beauvais, 1987: 723; Veron & Hodgson, 1989: 266; Sheppard, 1990: 6; Sheppard & Sheppard, 1991: 112; Veron, 1992: 148; Latypov & Dautova, 1998: 55–56; Veron, 2000, vol. 3: 82; Latypov, 2006: 338; Latypov, 2014: 350.

Diagnosis (apomorphies in italics)

Solitary. Budding intracalicular. Corallites monomorphic; discrete. Calice width large (> 15 mm), with high relief (> 6 mm). Septa in ≥ 4 cycles (≥ 48 septa). Free septa irregular. Septa spaced < 6 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy (> 3 threads), < 1/4 of calice width. *Septal (multiaxial) lobes weakly or moderately developed.* Epitheca reduced. Endotheca usually low–moderate (tabular), but may be abundant (Fig. 7A, D).

Tooth base at midcalice elliptical-parallel. Tooth tip orientation parallel. Teeth tall (> 0.6 mm); widely spaced (> 1 mm), with > 6 teeth per septum. Tooth shape unequal between first- and third-order septa. Tooth size unequal between wall and septum. Granules scattered on septal face; weak (rounded). Interarea palisade (Fig. 7B, E).

Walls formed by dominant paratheca and partial septotheca. Thickening deposits in concentric rings with extensive stereome. Costa centre clusters strong; > 0.6 mm between clusters; *medial lines strong*. Septum centre clusters weak; > 0.5 mm between clusters; medial lines weak (Fig. 7C, F).

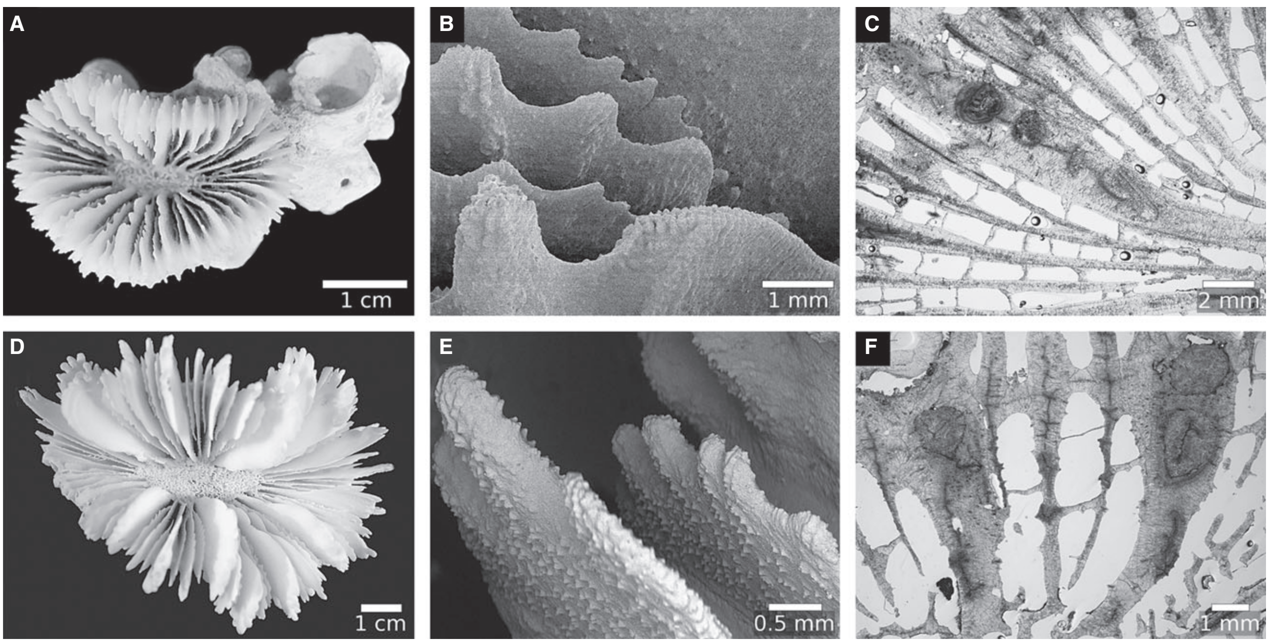

Figure 7. *Cynarina* Brüggemann, 1877, is solitary, with discrete corallites, large (> 15 mm) and high-relief (> 6 mm) calices, septa in ≥ 4 cycles (≥ 48 septa), and weak/moderate septal lobes. Septal teeth are tall (> 0.6 mm) and widely spaced (> 1 mm), unequally shaped between first- and third-order septa, unequally sized between wall and septum, with palisade interarea. Walls formed by dominant paratheca and partial septotheca, with strong costa centre clusters and medial lines. (A–F) *Cynarina lacrymalis* (Milne Edwards & Haime, 1849a), type species of *Cynarina*; macromorphology, *Cynarina savignyi* Brüggemann, 1877, syntype of *Cynarina* NHMUK (unlabelled lot), Gulf of Suez, Red Sea (A; photo by N. Santodomingo); micromorphology (scanning electron microscopy; B) and microstructure (transverse thin section; C), hypotype USNM 93865, Madang, Papua New Guinea; macromorphology (D), micromorphology (E), and microstructure (F), hypotype USNM 93862, Madang, Papua New Guinea.

Species included

1. *Cynarina lacrymalis* (Milne Edwards & Haime, 1849a, vol. 11: 238; Milne Edwards & Haime, 1848c, vol. 10, pl. 8: figs 1, 1a); holotype: MNHN status unknown; type locality: 'les Philippines?' (Milne Edwards & Haime, 1849a, vol. 11: 239); phylogenetic data: molecular and morphology.
2. *Cynarina macassarensis* (Best & Hoeksema, 1987: 394, figs 5–7); holotype: RMNH 22189 (dry specimen); paratypes: RMNH 22190–22192 (seven dry specimens); type locality: Samalona, Spermonde Archipelago, Indonesia (21–36 m depth); phylogenetic data: morphology only.

Taxonomic remarks

Cynarina was established by Brüggemann (1877: 305) for a new species *Cynarina savignyi* Brüggemann, 1877: 305, which was collected from the Gulf of Suez and deposited at the British Museum (now NHMUK). Brüggemann (1877: 306) stated on the description of *Cyn. savignyi* that, 'of this species, the Museum contains a considerable series of specimens; yet I have taken the description from a single example, because this is the only one which is fully adult and at the same time beautifully regular in its septal apparatus'. Indeed, we found eight specimens at NHMUK that were examined by Brüggemann (1877), and the largest of which fits his description and should be considered the holotype of the species (Fig. 7A). However, Brüggemann (1877: 305) was less specific in his description for the genus, and clearly used all of the specimens available to him at that time. Therefore we regard all eight specimens (NHMUK 1858.2.12.3, 1869.2.25.39, and one unlabelled lot) as syntypical material for the genus.

Cynarina savignyi was named after J. C. Savigny, who discovered and figured the species as *Caryophyllia carduus* in Audouin (1826: 233, pl. 4: figs 2.1, 2.2, 2.3). The latter species name had already been used in *Madrepora carduus* Ellis & Solander, 1786: 153, pl. 35 (= *Madrepora lacera* Pallas, 1766: 298), an Atlantic species, whereas *Cyn. savignyi* was a junior synonym of *Caryophyllia lacrymalis* Milne Edwards & Haime, 1849a, vol. 11: 238, which remained the only valid species in *Cynarina* until Budd *et al.* (2012) transferred *Indophyllia macassarensis* Best & Hoeksema, 1987: 394, into the genus. Our morphological analysis support this placement as *Cyn. lacrymalis* and *Cynarina macassarensis* form a clade (Fig. 2B), but molecular sampling is needed to verify this result.

Cynarina has been affiliated with *Lobophyllia* and *Symphyllia* in the past. Matthai (1928) considered the solitary forms represented by *Scolymia* Haime, 1852: 279, *Homophyllia* Brüggemann, 1877: 310, *Sclerophyllia* Klunzinger, 1879: 4, and *Cynarina* to be early monocentric stages of the colonial *Lobophyllia*, and placed them in tentative synonymy under the latter. Wells (1937) followed this line of reasoning when he synonymized *Scolymia* under *Mussa* Oken, 1815: 73, *Homophyllia* under *Lobophyllia* de Blainville, 1830: 321, and *Sclerophyllia* + *Cynarina* under *Symphyllia* Milne Edwards & Haime, 1848a, vol. 27: 491. Vaughan & Wells (1943) and Wells (1956) preserved this scheme but placed *Cynarina* under *Lobophyllia* instead. Subsequently, Wells (1964) resurrected all of the solitary taxa above except for *Sclerophyllia*. The latter, together with *Rhodocyathus* Bourne, 1905: 191, and *Protolobophyllia* Yabe & Sugiyama, 1935: 381, were considered as synonyms of *Cynarina* (Wells, 1964; Veron & Pichon, 1980). However, the most recent phylogenetic analysis by Arrigoni *et al.* (2015), supported by our results here (Fig. 2), indicated that *Sclerophyllia* is a distinct genus and it has since been resurrected (see below).

Acanthophyllia Wells, 1937: 242, was described as a fully solitary coral that, in comparison with *Cynarina*, possesses even larger lobate teeth, much bigger over the wall than near the columella. Although this separation was maintained by Wells (1964), Veron & Pichon (1980) studied the holotype of its type species *Acanthophyllia deshayesiana* and detected only minor differences in internal lobe development between *Acanthophyllia* and *Cynarina*, tentatively listing *Acanthophyllia* as a junior synonym. Here, we also find septal tooth size and septal lobe development to be comparable between the two taxa, thus supporting the generic synonymy presented by Veron & Pichon (1980). Some exceptional specimens identified as *Cyn. lacrymalis* by Wells (1964, pls 20, 21) that were collected from Gubbins Reef in Australia and Banc Gail in New Caledonia have more rounded tooth tips and well-developed septal lobes. These peculiar corals have superficial affinities to Caryophylliidae and are in need of more detailed examinations.

Cynarina is widely distributed on the reefs of the Indo-Pacific, present from the Red Sea and East Africa to as far east as the Marshall Islands in the Northern Hemisphere and Samoa in the Southern Hemisphere (Veron, 2000).

Morphological remarks

Two synapomorphies have been recovered for the moderately supported *Cynarina* clade (bootstrap support of 62): weakly or moderately developed septal (multiaxial) lobes (likelihood of 1.00 based on the Mk1 model) and strong costa medial lines (likelihood 1). The sister relationship between *Cynarina* and *Lobophyllia* recovered here is unsurprising given their previous affiliation, and the inclusive clade is indeed supported by the synapomorphy of unequal tooth size between the wall and septum (likelihood 0.90). They can however be distinguished easily based on *Cynarina*'s synapomorphies, as well as its solitary form and low–moderate (tabular, instead of vesicular) endotheca.

Within Lobophylliidae, in which species are predominantly colonial, *Cynarina* is the only genus that is exclusively solitary. *Lobophyllia vitiensis* (Brüggemann, 1877: 304), *Homophyllia australis* (Milne Edwards & Haime, 1849a, vol. 11: 239), and *Mi. pacifica* Benzoni & Arrigoni in Arrigoni *et al.*, 2016a, are typically monostomatous but can sometimes form polystomatous coralla (Arrigoni *et al.*, 2014b; e.g. NHMUK 1840.11.30.79, syntype of *Caryophyllia australis*). The congeneric of the monostomatous *Sclerophyllia margariticola* Klunzinger, 1879: 4 – *Scl. maxima* (Sheppard & Salm, 1988: 276) – is colonial.

Genus *Echinomorpha* Veron, 2000 (2): 333 (Fig. 8)

Type species
Echinophyllia nishihirai Veron, 1990: 130, figs 35–37, 79; original designation, Veron, 2000, vol. 2: 333.

Original description
This genus has only one species, see *Echinomorpha nishihirai*. (Veron, 2000, vol. 2: 333)

For *Echinomorpha nishihirai*, 'Characters: Colonies or individuals are thin and delicate. They may have only one corallite or have a prominent central corallite and widely spaced peripheral corallites. Septo-costae radiate from the central corallite like spokes from a wheel. Colour: Uniform or mottled dark browns or greens.' (Veron, 2000, vol. 2: 333)

Diagnosis (apomorphy in italics)
Colonial, but often solitary; laminar. Budding intracalicular. Corallites polymorphic; organically united and lacking distinct calical walls. Monticules absent. Coenosteum spinose; extensive amount (≥ corallite diameter). Calice width large (> 15 mm), with medium relief (3–6 mm). Costosepta mostly confluent in colonies. *Septa in ≥ 4 cycles (≥ 48 septa).* Free septa irregular. Septa spaced < 6 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy (> 3 threads), ≥ 1/4 of calice width, and discontinuous amongst adjacent corallites with lamellar linkage. Paliform (uniaxial) lobes weakly developed. Epitheca absent. Endotheca low–moderate (tabular) (Fig. 8).

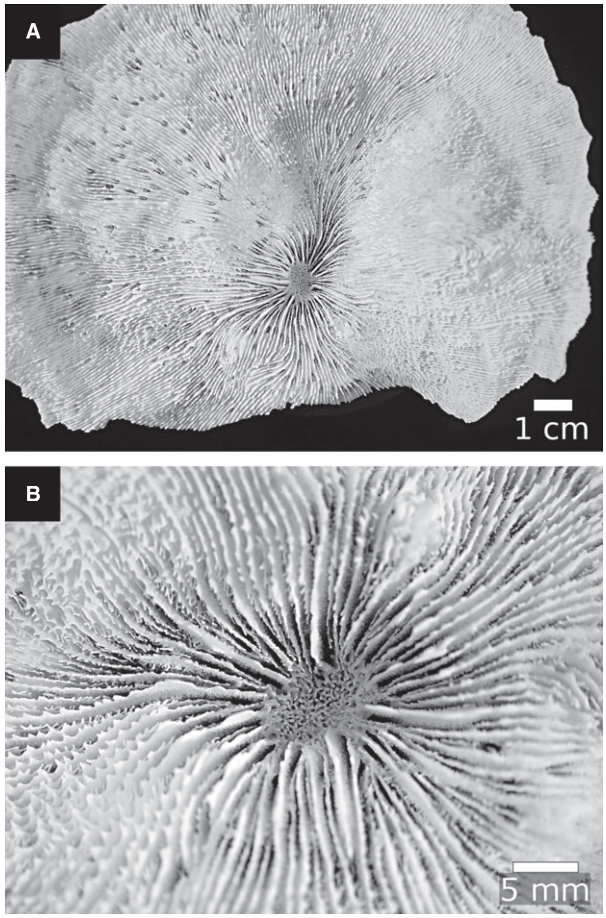

Figure 8. *Echinomorpha* Veron, 2000, may be solitary; colonies contain organically united and polymorphic corallites, with large (> 15 mm) and medium-relief (3–6 mm) calices, septa in ≥ 4 cycles (≥ 48 septa), large (≥ 1/4 of calice width) spongy columellae, and weak paliform (uniaxial) lobes. (A, B) *Echinomorpha nishihirai* (Veron, 1990), type and only living species of *Echinomorpha*; macromorphology, holotype MTQ G32483, Okinawa Island, Ryukyu Islands, Japan.

Species included
Echinomorpha nishihirai (Veron, 1990: 130, figs 35–37, 79); holotype: MTQ G32483 (dry specimen); type locality: Okinawa Island, Ryukyu Islands, Japan; phylogenetic data: morphology only.

Taxonomic remarks
Echinomorpha is a monotypic genus that was described recently (Veron, 2000, vol. 2: 333). Its sole member previously belonged to the closely related *Echinophyllia*. Although no genetic material was available to place the genus on the molecular phylogeny, we analysed the macromorphological data for *Echinomorpha nishihirai* (Veron, 1990: 130). Our

results show that it is nested within the *Echinophyllia* + *Oxypora* clade and is the sister taxon to *Echinophyllia tarae* Benzoni, 2013: 63. There is low support for the latter relationship, but the former is supported by a high bootstrap value of 71 and decay index of 4. Owing to the sparse taxonomic sampling amongst *Echinomorpha*, *Echinophyllia*, and *Oxypora* (subclade F + G *sensu* Arrigoni *et al.*, 2014c) in this study, we refrain from prescribing formal changes for these taxa.

Echinomorpha is restricted to the reefs of the central Indo-Pacific between Japan and Indonesia (Veron, 2000).

Morphological remarks
Echinomorpha possesses the autapomorphy of septa in ≥ 4 cycles (≥ 48 septa), and is unique amongst the closely related genera of *Echinomorpha*, *Echinophyllia*, and *Oxypora* in subclade F, which generally have fewer septa. Subcorallite and genetic characters for *Echinomorpha nishihirai* have not been examined, but all the observed macromorphological traits suggest that it may be the sister species of *Echinophyllia tarae*, which differs only in having a raised central corallite rim and paliform crown, and lacking the above autapomorphy (Benzoni, 2013).

GENUS *ECHINOPHYLLIA* KLUNZINGER, 1879: 69 (FIG. 9)

Synonym
Oxyphyllia Yabe & Eguchi, 1935a: 377 (type species: *Madrepora aspera* Ellis & Solander, 1786: 156, pl. 39; original designation, Yabe & Eguchi, 1935a: 377).

Type species
Madrepora aspera Ellis & Solander, 1786: 156, pl. 39; subsequent designation, Wells, 1936: 111.

Original description
Polypar zusammengesetzt, blattartig, dünn, unten radiär gerippt, oben mit zerstreuten mehr weniger vorstehenden Kelchen ohne deutliche Mauern, mit wohl entwickelten um die Kelchcentren radiären stark gezähnten Septen; die Kelch durch stark gezähnte subparallele Rippen oder Septa verbunden. Columella deutlich, Unterseite gerippt, mit oder ohne Epithek. (Klunzinger, 1879: 69)

Subsequent descriptions
Crossland, 1935: 503; Wells, 1936: 110–111; Vaughan & Wells, 1943: 197; Alloiteau, 1952: 631–632; Wells, 1955: 5; Wells, 1956: F419; Nemenzo, 1959: 119; Chevalier, 1975: 356–357; Pillai & Scheer, 1976: 67; Ditlev, 1980: 80; Veron & Pichon, 1980: 297–298; Scheer & Pillai, 1983: 152; Wood, 1983: 197–198; Veron, 1986: 372; Chevalier & Beauvais, 1987: 725–726; Sheppard, 1990: 16; Veron, 1993: 231; Latypov & Dautova, 1998: 43; Veron, 2000, vol. 2: 322; Claereboudt, 2006: 203; Latypov, 2006: 326; Latypov, 2014: 336.

Diagnosis
Colonial; laminar. Budding intracalicular; peripheral budding may be present. Corallites may be polymorphic; organically united and lacking distinct calical walls. Monticules absent. Coenosteum spinose; extensive amount (≥ corallite diameter). Calice width medium to large (≥ 4 mm), with low to medium relief (≤ 6 mm). Costosepta mostly confluent. Septa in ≤ 3 cycles (≤ 36 septa). Free septa irregular. Septa spaced ≤ 11 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy (> 3 threads), ≥ 1/4 of calice width, and discontinuous amongst adjacent corallites with lamellar linkage. Paliform (uniaxial) lobes weakly or moderately developed. Epitheca absent. Endotheca low–moderate (tabular) (Fig. 9A, D, G).

Tooth base at midcalice elliptical-parallel. Tooth tip forming multiaxial bulb. Tooth height medium (0.3–0.6 mm). Tooth spacing medium (0.3–1.0 mm), with ≤ 6 teeth per septum. Tooth size equal between wall and septum. Granules scattered on septal face; weak (rounded). Interarea smooth (Fig. 9B, E, H).

Walls formed by dominant paratheca and partial septotheca. Thickening deposits with extensive stereome. Costa centre clusters weak; > 0.6 mm between clusters; medial lines strong. Septum centre clusters weak; 0.3–0.5 mm between clusters; medial lines weak (Fig. 9C, F, I).

Species included
1. *Echinophyllia aspera* (Ellis & Solander, 1786: 156, pl. 39); holotype: GLAHM 104004 (dry specimen); type locality: 'Oceano Indiæ orientalis' (Ellis & Solander, 1786: 156); phylogenetic data: molecular and morphology.
2. *Echinophyllia costata* Fenner & Veron in Veron, 2000, vol. 2: 330, figs 1–3 (see also Veron, 2002: 110, figs 209–212; ICZN, 2011: 163); lectotype (designated herein): MTQ G55809 (dry specimen); type locality: Banai Island, Sulawesi, Indonesia (22 m depth); phylogenetic data: morphology only.
3. *Echinophyllia echinata* (Saville Kent, 1871: 283, pl. 23: fig. 3); holotype: NHMUK 1855.12.7.155 (dry specimen); type locality: San Cristobal, Solomon Islands; phylogenetic data: molecular and morphology.

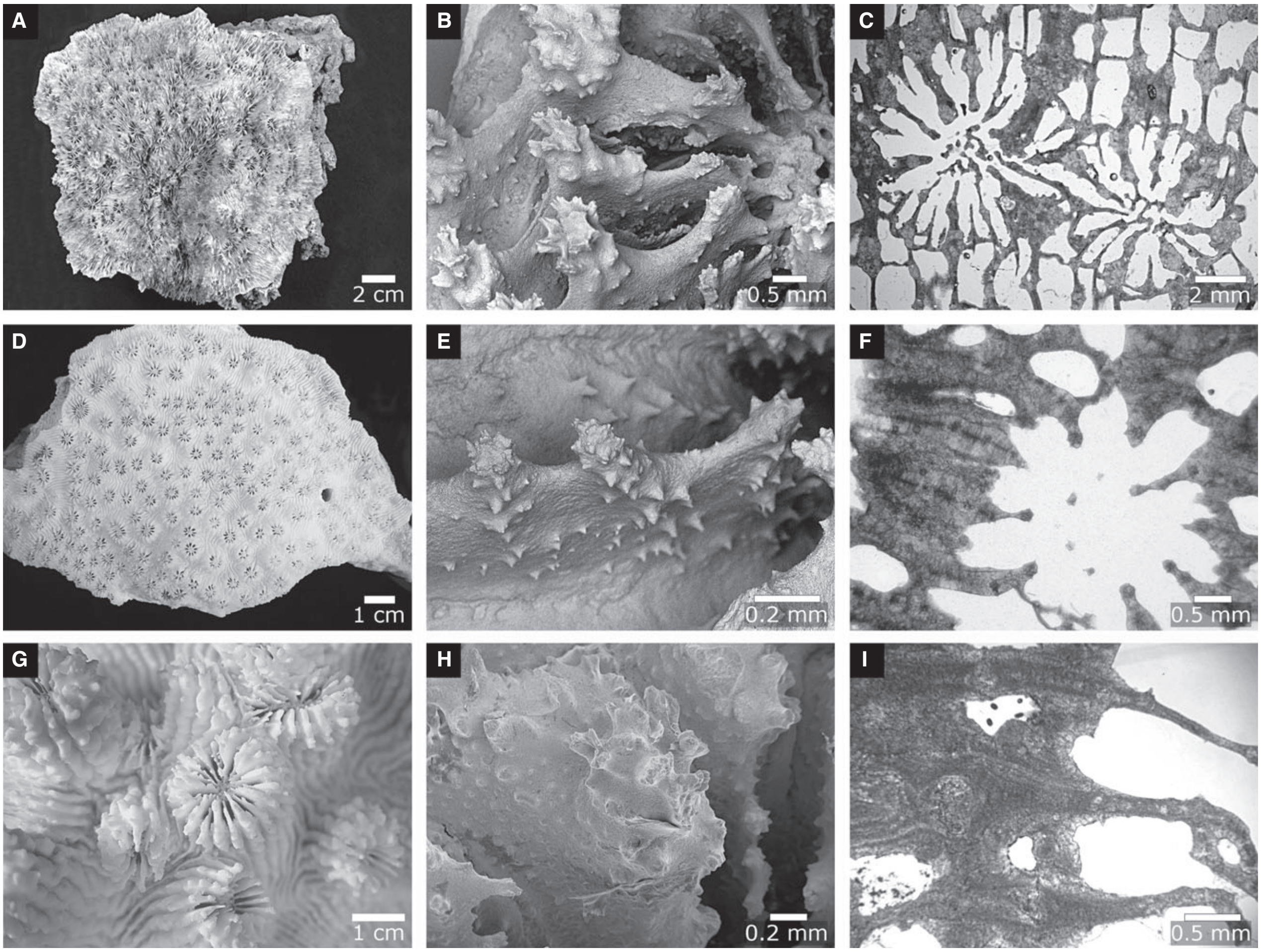

Figure 9. *Echinophyllia* Klunzinger, 1879, has organically united and sometimes polymorphic corallites, extensive coenosteum (≥ corallite diameter), septa in ≤ 3 cycles (≤ 36 septa), large (≥ 1/4 of calice width) spongy columellae, and weak/moderate paliform (uniaxial) lobes. Septal teeth with medium height (0.3–0.6 mm) and spacing (0.3–1.0 mm), equally sized between wall and septum, and smooth interarea. Walls formed by dominant paratheca and partial septotheca, with strong costa medial lines. (A–C) *Echinophyllia aspera* (Ellis & Solander, 1786), type species of *Echinophyllia*; macromorphology, holotype GLAHM 104004 (A; photo by K. G. Johnson); micromorphology (scanning electron microscopy; B) and microstructure (transverse thin section; C), hypotype USNM 45075, Bikini Atoll, Marshall Islands. (D–F) *Echinophyllia echinoporoides* Veron & Pichon, 1980; macromorphology, holotype NHMUK 1983.9.27.4, Whitsunday Islands, Australia (D); micromorphology (E) and microstructure (F), hypotype UNIMIB PFB379, Madang, Papua New Guinea. (G–I) *Echinophyllia orpheensis* Veron & Pichon, 1980; macromorphology, holotype MTQ G57510, south Pioneer Bay, Orpheus Island, Palm Islands, Australia (G); micromorphology (H) and microstructure (I), hypotype USNM 93798, Madang, Papua New Guinea.

4. *Echinophyllia echinoporoides* Veron & Pichon, 1980: 310, figs 539–545, 806; holotype: NHMUK 1983.9.27.4 (dry specimen); type locality: Whitsunday Islands, Australia; phylogenetic data: molecular and morphology.
5. *Echinophyllia orpheensis* Veron & Pichon, 1980: 302, figs 522–534, 803, 804; holotype: MTQ G57510 (dry specimen); type locality: south Pioneer Bay, Orpheus Island, Palm Islands, Australia (10 m depth); phylogenetic data: molecular and morphology.
6. *Echinophyllia patula* (Hodgson & Ross, 1981: 173, fig. 3); holotype: UP C-538 (dry specimen); type locality: Maribago, Mactan Island, Cebu, Philippines (35 m depth); phylogenetic data: none.
7. *Echinophyllia pectinata* Veron, 2000, vol. 2: 331, fig. 4 (see also Veron, 2002: 112, figs 213–215; ICZN, 2011: 163); lectotype (designated herein): UP MSI-3004-CO (dry specimen); type locality: Calamian Islands, Palawan, Philippines (25 m depth); phylogenetic data: none.

8. *Echinophyllia tarae* Benzoni, 2013: 63, figs 2–8, 9a, b, 10b, d; holotype: MNHN IK-2012-8000 (dry specimen); type locality: Taravai Island, Gambier Islands, French Polynesia (10 m depth); phylogenetic data: molecular and morphology.

Taxonomic remarks

The genus was established by Klunzinger (1879: 69) for the type species *Madrepora aspera* Ellis & Solander, 1786: 156, as well as *Trachypora lacera* Verrill, 1864: 53, under the family 'Fungidae' (Klunzinger, 1879: 59). It was thought to be closely related to *Halomitra* Dana, 1846, *Mycedium* Milne Edwards & Haime, 1851b, vol. 15: 130, and *Echinopora* Lamarck, 1816: 252, of which only the first genus is indeed in Fungiidae Dana, 1846: 283. The latter two are nested within Merulinidae Verrill, 1865: 146 (Budd *et al.*, 2012; Huang *et al.*, 2014b). Prior to this, *Ma. aspera* was actually grouped with *Tra. lacera* Verrill, 1864: 53, in the genus *Trachypora* Verrill, 1864: 53 (= *Oxypora* Saville Kent, 1871: 283), which was an attempt to distinguish these species from *Halomitra* and *Echinopora*.

The association of *Echinophyllia*, or its junior synonym *Oxyphyllia* Yabe & Eguchi, 1935a: 377, with the fungiids persisted when Wells (1935) grouped it with *Oxypora*, *Tridacophyllia* de Blainville, 1830: 327 (= *Pectinia* de Blainville, 1825: 201), *Mycedium*, and *Physophyllia* Duncan, 1884: 118, in Tridacophylliidae Thiel, 1932: 96, which was originally placed in Fungida (see Yabe & Eguchi, 1935b). Furthermore, *Oxyphyllia* (= *Echinophyllia*) was placed in Echinoporidae Verrill, 1901: 132, together with *Echinopora* and *Mycedium* by Yabe *et al.* (1936). However, Wells (1935) stated that *Physophyllia*, and by familial association, *Echinophyllia* is not in Fungiidae, and furthermore that there are no true synapticulae – a major synapomorphy of Fungiidae – in any of these genera.

When Pectiniidae was established by Vaughan & Wells (1943: 196) within Faviida for the five Tridacophylliidae genera above, there was little doubt that *Echinophyllia* was distinct from fungiids (but see Matthai, 1948), which were characterized by fenestrate septa. Since then, this classification had become convention (e.g. Wells, 1956; Nemenzo, 1959; Chevalier, 1975; Wood, 1983; Veron, 2000) until the challenge posed by molecular data first revealed by Fukami *et al.* (2004b). Through extensive genetic sampling of *Echinophyllia* in recent years, consensus that *Echinophyllia* and *Oxypora* are sister genera (subclade F + G *sensu* Arrigoni *et al.*, 2014c) nested within the Lobophylliidae clade (XIX *sensu* Fukami *et al.*, 2008) is emerging. The remaining three living genera in Pectiniidae are nested within Merulinidae (clade XVII *sensu* Fukami *et al.*, 2008), and thus Pectiniidae has been synonymized (Budd *et al.*, 2012; see also Huang *et al.*, 2011, 2014b; Arrigoni *et al.*, 2012).

The placement of *Echinophyllia* in Pectiniidae was long held and appeared stable, so the rare note that it resembled an outgroup was particularly prominent. Chevalier (1975) observed that the septal tooth ornamentation is strong and similar to those in 'Mussidae' (= Lobophylliidae), becoming more irregular distally. Our character analysis supports this observation, with *Echinophyllia* displaying similar tooth base and tip outline as other lobophylliids, but with the apex enlarging into a multiaxial bulb by branching into multidirectional tips.

Echinophyllia is widely distributed on the reefs of the Indo-Pacific, present from the Red Sea and East Africa to as far east as the Marshall Islands in the Northern Hemisphere (Veron, 2000) and the Gambier Islands in the Southern Hemisphere (Glynn *et al.*, 2007; Benzoni, 2013).

Morphological remarks

There are no unambiguous apomorphies for *Echinophyllia* on either the molecular or morphological tree. Three *Oxypora* species are nested amongst five *Echinophyllia* species in subclade F + G (*sensu* Arrigoni *et al.*, 2014c) on the molecular phylogeny (Fig. 2A), and these genera are not reciprocally monophyletic on the morphological tree (Fig. 2B). The clade comprising these three genera is well supported with a bootstrap value of 71 and decay index of 4, and is defined by four synapomorphies: (1) organically united corallites (likelihood of 0.86 based on the Mk1 model); (2) extensive coenosteum (≥ corallite diameter) (likelihood 0.75); (3) columellae ≥ 1/4 of calice width (likelihood 0.92); and (4) loss of epitheca (likelihood 0.84).

The sister relationship between *Echinophyllia* and *Oxypora* is further supported by the presence of alveoli, which are small pits on the exotheca forming at points of insertion of new septocostae (Chevalier, 1975; Wood, 1983; Veron, 1986, 2000; Benzoni, 2013). In *Oxypora*, these pits may penetrate to the undersurface of the colony to form slit-like pores (Vaughan & Wells, 1943; Wells, 1956; Veron & Pichon, 1980; Dai & Horng, 2009). This distinction appears to be merely superficial as they cannot be distinguished based on molecular data or subcorallite morphology. Furthermore, the current *Echinophyllia–Oxypora* dichotomy belies the peculiar affinities of some constituent species. On the one hand, *Echinophyllia echinata* (Saville Kent, 1871: 283) and *Echinophyllia tarae* Benzoni, 2013: 63, are morphologically similar to *Echinomorpha nishihirai* – initially placed in *Echinophyllia* (Veron, 1990) – mainly because they all possess a prominent central (polymorphic) corallite (Benzoni, 2013). On the other hand, this affinity is not supported by either molecular or morphological data. More comprehensive taxonomic and genetic sampling of subclade F + G, especially of *Oxypora* species, would be necessary to resolve these genera.

Mycedium was thought to be a closely related species to *Echinophyllia*, and Wells (1954) remarked that the former can only be distinguished by its more inclined orientation of calices on laminar colonies. Detailed examinations of subcorallite morphology by Huang *et al.* (2014b) and the present study suggest that multiple characters separate them, including tooth base outline, tooth tip orientation, and thickening deposits, as well as costa and septum centre clusters.

GENUS *HOMOPHYLLIA* BRÜGGEMANN, 1877: 310 (FIG. 10)

Type species
Caryophyllia australis Milne Edwards & Haime, 1849a, vol. 11: 239; Milne Edwards & Haime, 1848c, vol. 10, pl. 8: fig. 2; original designation, Brüggemann, 1877: 310.

Original description
Coral neatly turbinate, with a narrow, somewhat expanded base. Outside of wall covered almost to the edge with a thin closely adherent epitheca, through which the costæ are distinctly perceptible. Costæ crowded, perfectly equal, prominent, minutely denticulate. Calicle circular, deep. Edges of septa with crowded, narrow, subequal teeth. Columella very small, rounded in outline, coarsely trabecular. (Brüggemann, 1877: 310)

Subsequent descriptions
Wells, 1956: F417; Wells, 1964: 378; Ditlev, 1980: 76; Chevalier & Beauvais, 1987: 723; Arrigoni *et al.*, 2016a.

Diagnosis (apomorphies in italics)
Colonial, but may be solitary in *H. australis*; colonies submassive or massive. Budding intracalicular, and may also be extracalicular. Corallites typically monomorphic; discrete. Monticules absent. Walls fused. Calice width large (> 15 mm), with high relief (> 6 mm). Costosepta mostly confluent. Septa in ≥ 4 cycles (≥ 48 septa). Free septa irregular. Septa spaced six to 11 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy (> 3 threads), < 1/4 of calice width, and discontinuous amongst adjacent corallites with lamellar linkage. Internal lobes usually absent. Epitheca well developed. Endotheca low–moderate (tabular) (Fig. 10A, D, G).

Tooth base at midcalice elliptical-parallel. Tooth tip orientation parallel. *Teeth tall (> 0.6 mm)*; widely spaced (> 1 mm), with > 6 teeth per septum. Tooth shape equal between first- and third-order septa. Tooth size equal between wall and septum, but the teeth at midcalice may be larger than those at the columellar end of the septum. *Granules distributed uniformly on septal face*; weak (rounded). Interarea smooth (Fig. 10B, E, H).

Walls formed by dominant paratheca and partial septotheca. Thickening deposits in concentric rings with extensive stereome. Costa centre clusters strong; > 0.6 mm between clusters; medial lines weak. Septum centre clusters weak; > 0.5 mm between clusters; medial lines weak (Fig. 10C, F, I).

Species included
1. *Homophyllia australis* (Milne Edwards & Haime, 1849a, vol. 11: 239; Milne Edwards & Haime, 1848c, vol. 10, pl. 8: fig. 2); syntypes: NHMUK 1840.11.30.77, 1840.11.30.79 (two dry specimens); type locality: Port Lincoln, South Australia; phylogenetic data: molecular and morphology.
2. *Homophyllia bowerbanki* (Milne Edwards & Haime, 1857, vol. 2: 503, pl. D6: fig. 1); holotype: MNHN scle850 (dry specimen); type locality: Australia; phylogenetic data: molecular and morphology.

Taxonomic remarks
Homophyllia was established by Brüggemann (1877: 310) to contain *Caryophyllia australis* Milne Edwards & Haime, 1849a, vol. 11: 239, the type and only one of two species to have been assigned to the genus until Arrigoni *et al.* (2016a) transferred into it a species previously in *Acanthastrea*. *Heterocyathus incrustans* (Dennant, 1906: 161), a junior synonym of the facultatively zooxanthellate *Heterocyathus sulcatus* (Verrill, 1866: 48), was provisionally placed in *Homophyllia* when it was first described (Cairns, 2009).

The validity of *Homophyllia* had been undermined for a considerable part of its taxonomic history. Matthai (1928) and Wells (1937) thought that it was an early monocentric stage of *Lobophyllia* and therefore synonymized *Homophyllia* under the latter. Vaughan & Wells (1943) did not question this scheme but Wells (1956) recognized it as a genus distinct from *Lobophyllia*. Based on the similarity between *Ca. australis* Milne Edwards & Haime, 1849a, vol. 11: 239, and *Scolymia vitiensis* Brüggemann, 1877: 304, Veron & Pichon (1980) placed both of them in *Scolymia* Haime, 1852: 279. *Homophyllia* and *Parascolymia* Wells, 1964: 379, respectively contained these species, and were thus synonymized under *Scolymia*. The authors were also not convinced that these two species were distinct, emphasising that ‘*H.*

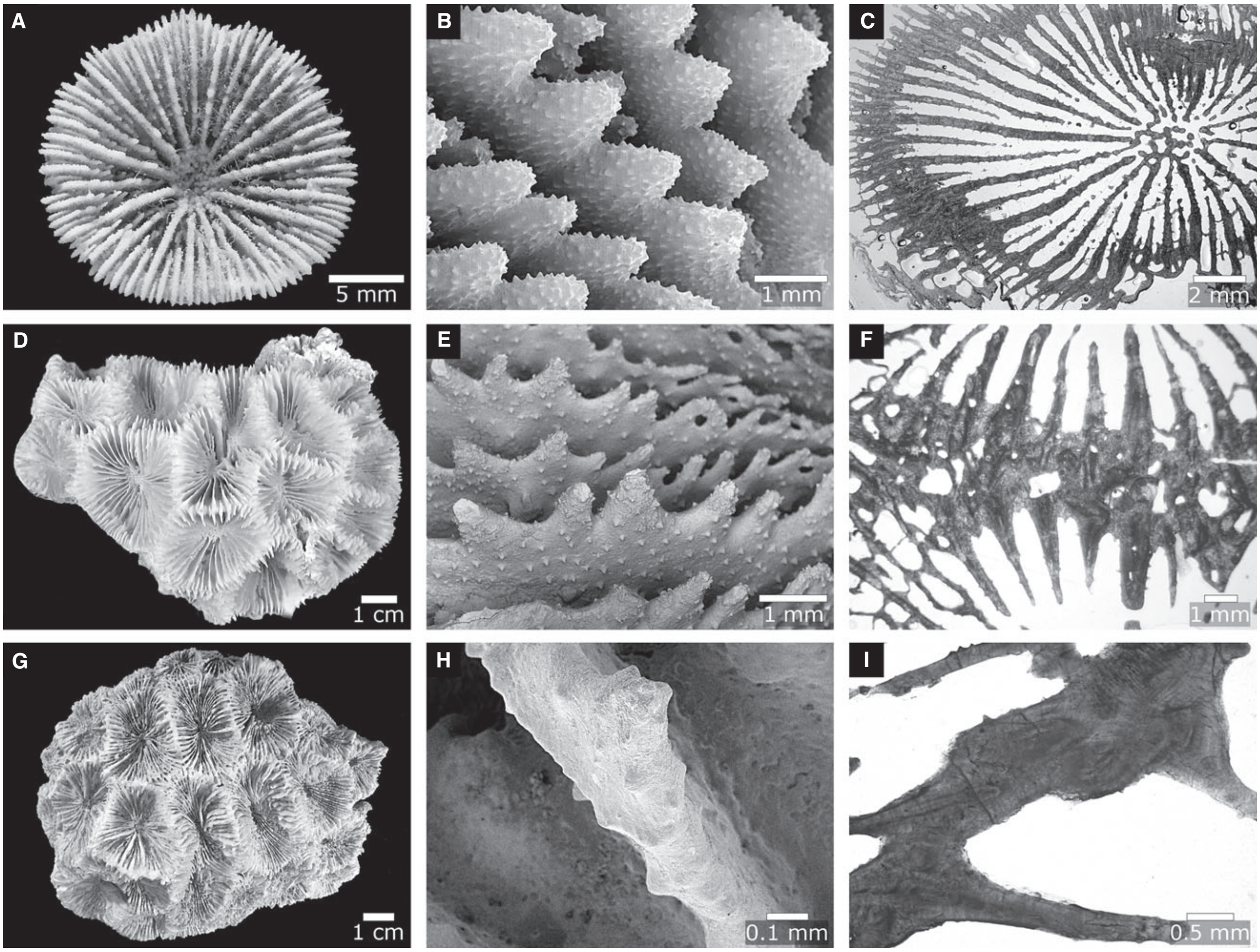

Figure 10. *Homophyllia* Brüggemann, 1877, has discrete corallites with fused walls, large (> 15 mm) and high-relief (> 6 mm) calices, septa in ≥ 4 cycles (≥ 48 septa), and well-developed epitheca. Septal teeth are tall (> 0.6 mm) and widely spaced (> 1 mm), equally shaped between first- and third-order septa, equally sized between wall and septum, with uniformly distributed granules, and smooth interarea. Walls formed by dominant paratheca and partial septotheca, with strong costa centre clusters. (A–C) *Homophyllia australis* (Milne Edwards & Haime, 1849a), type species of *Homophyllia*; macromorphology, syntype NHMUK 1840.11.30.77, Port Lincoln, South Australia (A; photo by H. Taylor); micromorphology (scanning electron microscopy; B) and microstructure (transverse thin section; C), hypotype USNM 85709, Sir Joseph Banks Group, South Australia. (D–F) *Homophyllia bowerbanki* (Milne Edwards & Haime, 1857); macromorphology, holotype MNHN scle850, Australia (D); micromorphology (E) and microstructure (F), hypotype IRD HS3285, New Caledonia. (G–I) *Homophyllia hillae* (Wells, 1955) (=*Homophyllia bowerbanki*); macromorphology, holotype QM F17943, Moreton Bay, Australia (G); micromorphology (H) and microstructure (I), hypotype USNM 91198, Lord Howe Island, Australia.

australis and *Scolymia* (= *Parascolymia*) *vitiensis* may be the same species, the former being a cold water ecomorph or geographic subspecies of the latter' (Veron & Pichon, 1980: 244). Nevertheless, they have remained as valid species to date, and were considered as the only Indo-Pacific members of *Scolymia* (Wood, 1983; Veron, 1986, 2000), whose type species *Ma. lacera* Pallas, 1766: 298 (see Vaughan, 1901: 6), is an Atlantic species.

The deep divergence between the Atlantic (clade XXI *sensu* Fukami *et al.*, 2008) and Indo-Pacific corals (Fukami *et al.*, 2004b, 2008) revealed by genetic data meant that the two Indo-Pacific members of *Scolymia* had to be redistributed into *Homophyllia* and *Parascolymia* (Budd *et al.*, 2012). A more recent molecular analysis indicated that *Ac. bowerbanki* Milne Edwards & Haime, 1857, vol. 2: 503, and *Ac. hillae* Wells, 1955: 15, are indistinguishable and form a sister group to *H. australis*, so *Ac. hillae* became a junior synonym of *H. bowerbanki* (Arrigoni *et al.*, 2016a). Our analyses lend support to this classification (Fig. 2).

Homophyllia is present on the reefs of the western Indian Ocean (Sheppard & Sheppard, 1991) and central Indo-Pacific, to as far east as the Marshall Islands in the Northern Hemisphere (Veron, 2000) and the Austral Islands in the Southern Hemisphere (Glynn *et al.*, 2007).

Morphological remarks
The *Homophyllia* clade comprising two species is moderately supported on the morphological tree (Fig. 2B) with a bootstrap value of 63, as well as the synapomorphies of tall teeth (> 0.6 mm) (likelihood of 0.99 based on the Mk1 model) and granules distributed uniformly on the septal face (likelihood 1.00). It is the sister genus to *Micromussa* based on molecular characters (Fig. 2A), but forms a paraphyletic group with *Micromussa* and *Australophyllia* on the basis of morphological traits (Fig. 2B). *Homophyllia* is easily distinguished from these closely related genera by its larger and deeper calice, greater tooth height and spacing, and uniformly distributed granules.

Homophyllia australis may be unique amongst congeneric and closely related allogeneric species in being predominantly solitary, but polystomatous specimens have been observed and collected (Veron, 1986, 2000; Arrigoni *et al.*, 2016a), including even one of its two syntypes, NHMUK 1840.11.30.79. In these cases, corallites may no longer be considered monomorphic as diagnosed for the genus. We also note that several coralla of *H. bowerbanki* contain a central corallite that is slightly larger than usual.

GENUS *MICROMUSSA* VERON, 2000 (3): 8 (FIG. 11)

Type species
Acanthastrea amakusensis Veron, 1990: 137, figs 42–44, 82; original designation, Veron, 2000, vol. 3: 8.

Original description
Colonies are submassive or encrusting and usually flat. Corallites are cerioid or subplocoid, either circular or angular in shape and up to 8 millimetres diameter. Septa are thickened at the corallite wall, and have conspicuous teeth. Colonies may have fleshy tissue over the skeleton, but skeletal structures remain visible. Tentacles are extended only at night. (Veron, 2000, vol. 3: 8)

Subsequent descriptions
Claereboudt, 2006: 226; Arrigoni *et al.*, 2016a.

Diagnosis (apomorphies in italics)
Colonial; encrusting or massive. Budding intracalicular and extracalicular. Corallites monomorphic; discrete. Monticules absent. Coenosteum spinose; *usually limited (includes double wall)*. Calice width medium (4–15 mm), with medium relief (3–6 mm). Costosepta mostly not confluent. Septa typically in three cycles (24–36 septa), although *Mi. pacifica* may contain more than 36 septa. Free septa irregular. Septa spaced six to 11 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy (> 3 threads), < 1/4 of calice width, and discontinuous amongst adjacent corallites with lamellar linkage. Internal lobes usually absent. Epitheca well developed. Endotheca low–moderate (tabular) (Fig. 11A, D).

Tooth base at midcalice elliptical-parallel. Tooth tip orientation parallel. Tooth height medium (0.3–0.6 mm). Tooth spacing medium (0.3–1.0 mm), with > 6 teeth per septum. Tooth shape equal between first- and third-order septa. Tooth size equal between wall and septum. Granules scattered on septal face; *strong (pointed)*. Interarea smooth (Fig. 11B, E).

Walls formed by dominant paratheca and partial septotheca. Thickening deposits in concentric rings with extensive stereome. Costa centre clusters strong; 0.3–0.6 mm between clusters; medial lines weak. Septum centre clusters weak; > 0.5 mm between clusters; medial lines weak (Fig. 11C, F).

Species included
1. *Micromussa amakusensis* (Veron, 1990: 137, figs 42–44, 82); holotype: MTQ G32485 (dry specimen); type locality: Amakusa Islands, Japan (10 m depth); phylogenetic data: molecular and morphology.
2. *Micromussa indiana* Benzoni & Arrigoni in Arrigoni *et al.*, 2016a; holotype: MNHN IK-2012-14232 (dry specimen); type locality: Al Mukallah, Yemen (5 m depth); phylogenetic data: molecular and morphology.
3. *Micromussa lordhowensis* (Veron & Pichon, 1982: 138 = *Acanthastrea* sp. Veron & Done, 1979: 219 = *Acanthastrea* sp. Veron & Pichon, 1980: 264, figs 455, 456); holotype: MTQ G57483 (dry specimen); type locality: North Bay, Lord Howe Island, Australia (2 m depth); phylogenetic data: molecular and morphology.
4. *Micromussa multipunctata* (Hodgson, 1985: 284, figs 1–8, 9A); syntypes: UP C-783, C-786, C-787, C-788 (four dry specimens); type locality: Tambuli Reef, Mactan Island, Cebu, Philippines (6 m depth); phylogenetic data: molecular and morphology.
5. *Micromussa pacifica* Benzoni & Arrigoni in Arrigoni *et al.*, 2016a; holotype: MNHN IK-2012-16043 (dry specimen); type locality: Mangareva, Gambier Islands, French Polynesia (15 m depth); phylogenetic data: molecular and morphology.

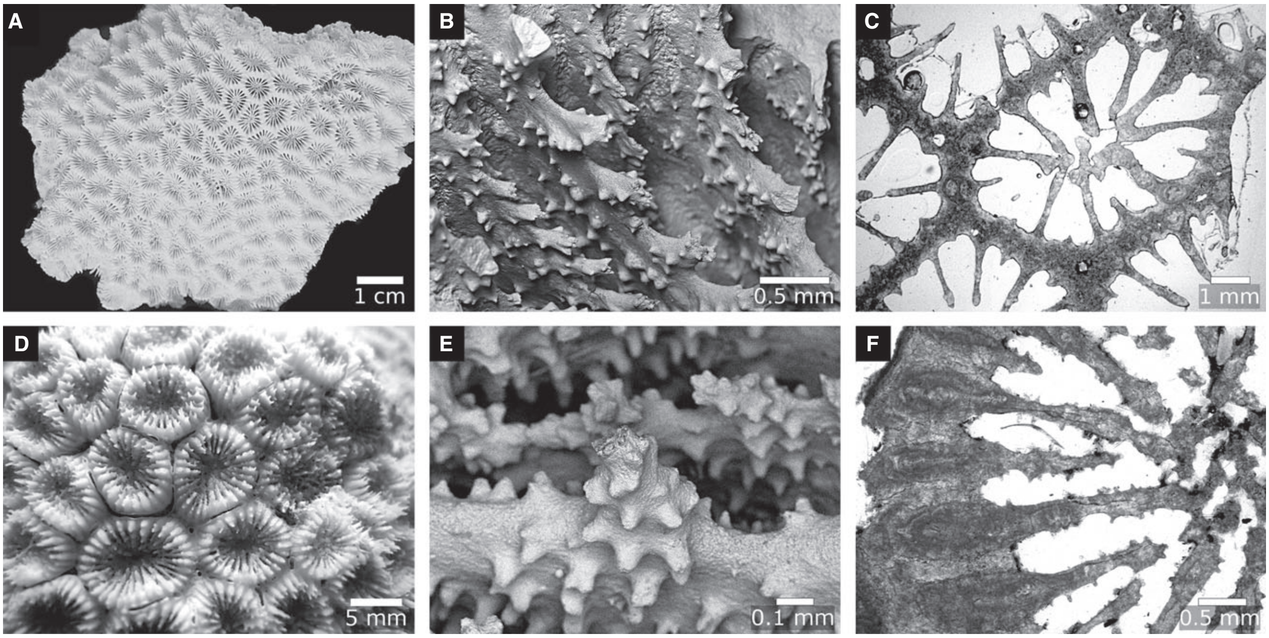

Figure 11. *Micromussa* Veron, 2000, has discrete corallites with double walls, medium-size (4–15 mm) and medium-relief (3–6 mm) calices, septa in three cycles (24–36 septa), and well-developed epitheca. Septal teeth with medium height (0.3–0.6 mm) and spacing (0.3–1.0 mm), equally shaped between first- and third-order septa, equally sized between wall and septum, strong (pointed) granules, and smooth interarea. Walls formed by dominant paratheca and partial septotheca, with strong costa centre clusters. (A) *Micromussa amakusensis* (Veron, 1990), type species of *Micromussa*; macromorphology, holotype MTQ G32485, Amakusa Islands, Japan. (B, C) *Micromussa indiana* Benzoni & Arrigoni in Arrigoni *et al.*, 2016a; micromorphology (scanning electron microscopy; B) and microstructure (transverse thin section; C), hypotype UF 457, Oman. (D–F) *Micromussa multipunctata* (Hodgson, 1985); macromorphology (D), micromorphology (E), and microstructure (F), hypotype UP P1L02161, Talim Point, Batangas, Philippines.

6. *Micromussa regularis* (Veron, 2000, vol. 3: 16, figs 1–4; see also Veron, 2002: 130, figs 240–242; ICZN, 2011: 163); lectotype (designated herein): MTQ G55818 (dry specimen); type locality: Milne Bay, Papua New Guinea (3 m depth); phylogenetic data: none.

Taxonomic remarks
Micromussa was established recently by Veron (2000, vol. 3: 8) to contain the designated type *Acanthastrea amakusensis* Veron, 1990: 137, as well as *Ac. minuta* Moll & Best, 1984: 53, and a new species *Micromussa diminuta* Veron, 2000, vol. 3: 9. No data exist for the latter two species, but detailed observations by Arrigoni *et al.* (2016a) indicate that *Ac. minuta* should not have been moved into *Micromussa*, while *Mi. diminuta* actually belongs to *Goniopora*. Molecular analyses have also demonstrated that *Acanthastrea lordhowensis* Veron & Pichon, 1982: 138, and *Montastrea multipunctata* Hodgson, 1985: 284, are closely related to *Mi. amakusensis* (Arrigoni *et al.*, 2014b,c, 2015, 2016a; see also Fig. 2A). Specifically, *Montastrea multipunctata* is closely related to *Mi. amakusensis* and *Mi. indiana*, whereas *Ac. lordhowensis* and *Mi. pacifica* are basal to the three species; these have all been placed in *Micromussa* (Arrigoni *et al.*, 2016a).

Both our molecular and morphological analyses support the clade grouping these five species (Fig. 2), whose macromorphological characters are also shared with *Acanthastrea regularis* Veron, 2000, vol. 3: 16 (Appendix S2). We note that subcorallite morphology and molecular data have not been sampled for the latter species. Superficially, it resembles *Favites valenciennesi* (Milne Edwards & Haime, 1849b, vol. 12: 124), although possessing thicker walls and more exsert septal teeth. Based parsimoniously on the characters examinable for the holotype, it is clear *Ac. regularis* has no affinity to *Acanthastrea*, and is herein transferred into *Micromussa*. Consequently, the described diversity of this genus currently stands at six species.

Micromussa is widely distributed on the reefs of the Indo-Pacific, present from the southern Red Sea (Arrigoni *et al.*, 2016a) to as far east as the Marshall Islands in the Northern Hemisphere and Fiji in the Southern Hemisphere (Veron, 2000).

Morphological remarks

Two unambiguous synapomorphies support the *Micromussa* clade (bootstrap value of 58) – limited coenosteum (likelihood of 0.92 based on the Mk1 model) and strong (pointed) granules on the septal face (likelihood 0.98). *Micromussa* is the sister genus to *Homophyllia* based on molecular characters (Fig. 2A), but forms a paraphyletic group with *Homophyllia* and *Australophyllia* when analysed using morphological data (Fig. 2B). *Micromussa* is easily distinguished from these closely related genera by their less numerous septa (24–36), costosepta that are not confluent, shorter distance between costa centre clusters (0.3–0.6 mm), and the two synapomorphies.

GENUS *MOSELEYA* QUELCH, 1884: 292 (FIG. 12)

Type species

Moseleya latistellata Quelch, 1884: 293; type by monotypy.

Original description

Corallum compound, flattened, or slightly and broadly convex. Young calicles developing by calicinal marginal budding around a very large median calicle, which has very numerous septal orders, the calicles becoming polygonal and deep at the centre. Epitheca very slight; wall very thin and almost rudimentary, but developed so as to give a distinct simple line of separation to the calicles on the surface, often interrupted, seen in section in a very rudimentary state separating the calicinal centres. Costæ very distinct, thin, and finely denticulate. Septa often confluent and continuous from centre to centre in the line of union between adjoining calicles, very thin and close, finely tooth above, and having the teeth subequal or slightly larger near the centre. Endothecal dissepiments vesicular, very abundantly developed, leaving but a very small portion of the septa free exteriorly, seen in transverse section forming nearly concentric lines, and more or less complete tabulæ at the centre. A false columella present, seen exteriorly to be formed by the trabeculate and vermiform nature of the innermost upper part of the septa, entirely or almost absent in transverse section, where the septa are seen to meet almost at a point. (Quelch, 1884: 292–293)

Subsequent descriptions

Duncan, 1884: 130–131; Quelch, 1886: 110–111; Delage & Hérouard, 1901: 633; Vaughan & Wells, 1943: 170; Wells, 1955: 6; Wells, 1956: F407; Veron, Pichon & Wijsman-Best, 1977: 201–203; Ditlev, 1980: 73; Wood, 1983: 171, 174; Veron, 1986: 534; Chevalier & Beauvais, 1987: 720; Sheppard, 1990: 10; Veron, 1993: 315; Latypov, 1995: 82; Veron, 2000, vol. 3: 269; Latypov, 2006: 174–175; Latypov, 2014: 189.

Diagnosis (apomorphies in italics)

Colonial; submassive or massive. Budding intracalicular and extracalicular. Corallites may be polymorphic; discrete. Monticules absent. *Walls fused.* Calice width large (> 15 mm), with high relief (> 6 mm). Costosepta mostly confluent. Septa in ≥ 4 cycles (≥ 48 septa). Free septa irregular. Septa spaced < 6 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy (> 3 threads), < 1/4 of calice width, and discontinuous amongst adjacent corallites with lamellar linkage. *Paliform (uniaxial) lobes weakly or moderately developed if present.* Epitheca reduced. Endotheca usually low–moderate (tabular), but may be abundant (Fig. 12A, D).

Tooth base at midcalice elliptical-parallel. Tooth tip orientation parallel. Teeth tall (> 0.6 mm). Tooth spacing medium (0.3–1.0 mm), with > 6 teeth per septum. Tooth shape unequal between first- and third-order septa. Tooth size equal between wall and septum. Granules scattered on septal face; irregular in shape. Interarea palisade (Fig. 12B, E).

Walls formed by dominant paratheca and partial septotheca. Thickening deposits in concentric rings with extensive stereome. Costa centre clusters strong; > 0.6 mm between clusters; medial lines weak. Septum centre clusters weak; > 0.5 mm between clusters; medial lines weak (Fig. 12C, F).

Species included

Moseleya latistellata Quelch, 1884: 293; holotype: NHMUK 1886.12.9.158 (dry specimen); type locality: Wednesday Island, Torres Strait, Australia (15 m depth); phylogenetic data: molecular and morphology.

Taxonomic remarks

The genus was established by Quelch (1884: 292) based on material collected from the HMS Challenger expedition at Torres Strait, Australia. It was named in honour of Henry Nottidge Moseley, a British naturalist on the expedition, and placed within a new subfamily Moseleyinæ. It is the senior homonym of the grenadier fish *Moseleya* Goode & Bean, 1895, named after the same Challenger naturalist, but which has been replaced by *Coryphaenoides* Gunnerus, 1765. *Moseleya latistellata* Quelch, 1884: 293, remains the only species to have been described in this genus, and is the type by monotypy.

Vaughan & Wells (1943: 170) transferred *Moseleya* into Faviidae Gregory, 1900, and subsequent authors have followed suit (Wells, 1956; Veron *et al.*, 1977; Wood, 1983; Veron, 1986, 2000; Veron & Marsh, 1988). However, the first molecular data for *Mos. latistellata* presented by Huang *et al.* (2011) showed that it is nested in the clade XIX + XX

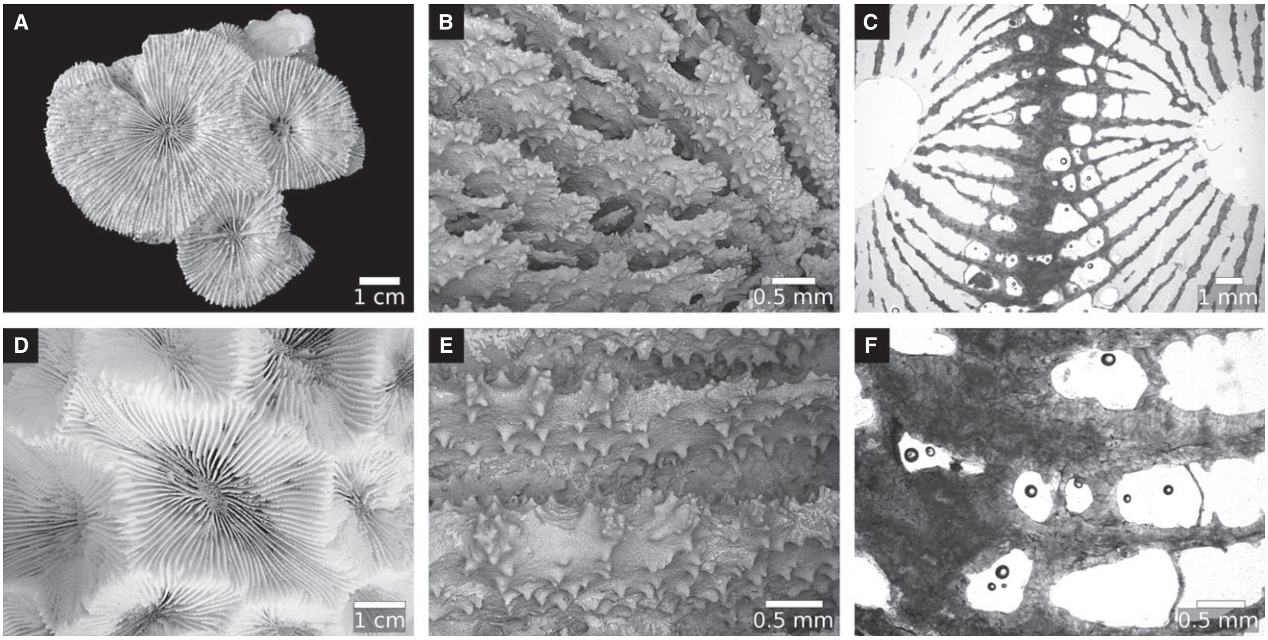

Figure 12. *Moseleya* Quelch, 1884, has discrete corallites that may be polymorphic, with fused walls, large (> 15 mm) and high-relief (> 6 mm) calices, and septa in ≥ 4 cycles (≥ 48 septa). Septal teeth are tall (> 0.6 mm) with medium spacing (0.3–1.0 mm), unequally shaped between first- and third-order septa, equally sized between wall and septum, and palisade interarea. Walls formed by dominant paratheca and partial septotheca, with strong costa centre clusters. (A–F) *Moseleya latistellata* Quelch, 1884, type and only living species of *Moseleya*; macromorphology, holotype NHMUK 1886.12.9.158, Wednesday Island, Torres Strait, Australia (A; photo by H. Taylor); micromorphology (scanning electron microscopy; B, E) and microstructure (transverse thin section; C, F), hypotype MTQ G61909, Magnetic Island, Queensland, Australia; macromorphology, hypotype MTQ G39700, Thursday Island, Queensland, Australia (D).

(*sensu* Fukami *et al.*, 2008), later classified as Lobophylliidae Dai & Horng, 2009. Budd *et al.* (2012) then formally transferred the genus into Lobophylliidae in the first monograph of the present series. Analyses with expanded taxon sampling have continually supported this classification (Huang, 2012; Arrigoni *et al.*, 2012, 2014b,c, 2015; Huang & Roy, 2013, 2015; Fig. 2A), and so have independent analyses using morphological data (Huang *et al.*, 2014b; Fig. 2B).

Moseleya is restricted to reefs of the central Indo-Pacific between southern Taiwan and northern Australia (Veron, 2000).

Morphological remarks

There are two autapomorphies that unambiguously define this monotypic genus. *Moseleya* has fused walls and weakly or moderately developed paliform (uniaxial) lobes, although this is sometimes absent. These traits clearly distinguish *Moseleya* from the closely related *Sclerophyllia*, with which it forms a poorly supported clade based on molecular and morphological data. Other characters that are present in *Moseleya* but not in *Sclerophyllia* include confluent costosepta, reduced epitheca, and medium tooth spacing (0.3–1.0 mm).

Moseleya can easily be mistaken for a Pacific 'faviid' (Merulinidae) as it possesses relatively thin walls and costosepta, and has indeed been placed in Faviidae since Vaughan & Wells (1943: 170) until as recently as Veron (2000, vol. 3: 269; see also Wells, 1955). However, it possesses several key traits that place it firmly within Lobophylliidae, including irregular tooth tip at midcalice that are orientated parallel to the septum, unequal tooth shape between the first- and third-order septa, as well as > 0.6 and > 0.5 mm separating the costa and septum centre clusters, respectively.

Genus *Oxypora* Saville Kent, 1871: 283 (Fig. 13)

Synonym

Trachypora Verrill, 1864: 53 (type species: *Trachypora lacera* Verrill, 1864: 53; original designation, Verrill, 1864: 53); *non Trachypora* Milne Edwards & Haime (1851a, vol. 5: 158).

Type species
Trachypora lacera Verrill, 1864: 53; subsequent designation, Wells, 1936: 122.

Original description

This name is proposed in place of *Trachypora* of A. E. Verrill (Bulletin Mus. Comp. Zoology, Cambridge, U. S. p. 53, 1863), which has been already adopted by Milne-Edwards for a genus of the Cyathophylliidæ. He separates it from *Echinopora* on account of the echinate and coarsely costate character of the lower surface of the corallum. (Saville Kent, 1871: 283–284)

Subsequent descriptions
Quelch, 1886: 129; Delage & Hérouard, 1901: 641; Yabe & Eguchi, 1935b: 431; Wells, 1936: 122; Yabe *et al.*, 1936: 53; Vaughan & Wells, 1943: 197–198; Crossland, 1952: 158; Wells, 1956: F419; Nemenzo, 1959: 121; Chevalier, 1975: 383–384; Ditlev, 1980: 81; Veron & Pichon, 1980: 313–314; Scheer & Pillai, 1983: 153–154; Wood, 1983: 198–199; Veron, 1986: 378; Chevalier & Beauvais, 1987: 726; Veron & Hodgson, 1989: 265; Sheppard, 1990: 16; Sheppard & Sheppard, 1991: 109; Latypov & Dautova, 1998: 46; Veron, 2000, vol. 2: 334; Claereboudt, 2006: 206; Latypov, 2006: 330; Latypov, 2014: 340.

Diagnosis
Colonial; laminar. Budding intracalicular. Corallites may be polymorphic; organically united and lacking distinct calical walls. Monticules absent. Coenosteum spinose; extensive amount (≥ corallite diameter). Calice width medium (4–15 mm), with low relief (< 3 mm). Costosepta mostly confluent. Septa in < 3 cycles (< 24 septa). Free septa irregular. Septa spaced < 6 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and compact (one to three threads), ≥ 1/4 of calice width, and discontinuous amongst adjacent corallites with lamellar linkage. Internal lobes absent. Epitheca absent. Endotheca low–moderate (tabular) (Fig. 13A, D).

Tooth base at midcalice elliptical-parallel. Tooth tip forming multiaxial bulb. Tooth height medium (0.3–0.6 mm). Tooth spacing medium (0.3–1.0 mm), with ≤ 6 teeth per septum. Tooth size equal between

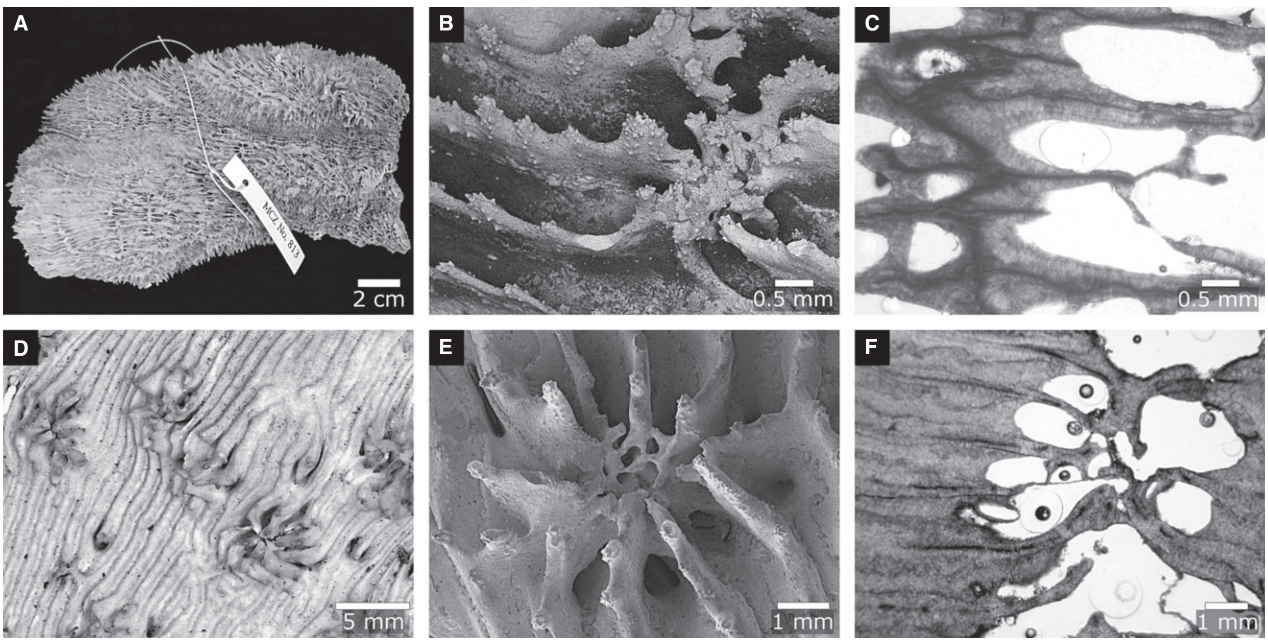

Figure 13. *Oxypora* Saville Kent, 1871, has organically united and sometimes polymorphic corallites, extensive coenosteum (≥ corallite diameter), septa in < 3 cycles (< 24 septa), and large (≥ 1/4 of calice width), compact columellae. Septal teeth with medium height (0.3–0.6 mm) and spacing (0.3–1.0 mm), equally sized between wall and septum, and smooth interarea. Walls formed by dominant paratheca and partial septotheca, with strong costa medial lines. (A–C) *Oxypora lacera* (Verrill, 1864), type species of *Oxypora*; macromorphology, syntype MCZ IZ 44065, Singapore (A; photo by A. J. Baldinger); micromorphology (scanning electron microscopy; B) and microstructure (transverse thin section; C), hypotype UNIMIB BU004, Burum, Yemen. (D–F) *Oxypora glabra* Nemenzo, 1959; macromorphology, holotype UP C-300, Paniquian Island, Puerto Galera, Philippines (D; photo by K. S. Luzon); micromorphology (E) and microstructure (F), hypotype USNM 92395, Auluptagel Island, Palau.

wall and septum. Granules scattered on septal face; weak (rounded). Interarea smooth (Fig. 13B, E).

Walls formed by dominant paratheca and partial septotheca. Thickening deposits with extensive stereome. Costa centre clusters weak; > 0.6 mm between clusters; medial lines strong. Septum centre clusters weak; 0.3–0.5 mm between clusters; medial lines weak (Fig. 13C, F).

Species included

1. *Oxypora lacera* (Verrill, 1864: 53); syntypes: MCZ IZ 44065, IZ 44066 (two dry specimens); type locality: Singapore; phylogenetic data: molecular and morphology.
2. *Oxypora convoluta* Veron, 2000, vol. 2: 340, figs 1–4 (see also Veron, 2002: 114, figs 216–220; ICZN, 2011: 165); lectotype (designated herein): MTQ G55792 (dry specimen); type locality: Ras Mohammed National Park, Sharm al-Sheikh, Sinai Peninsula, Egypt (20 m depth); phylogenetic data: molecular and morphology.
3. *Oxypora crassispinosa* Nemenzo, 1979: 12, pl. 4: fig. 2; holotype: SU CRS-023; type locality: San Plavo Reef, San Carlos City, Negros Occidental, Philippines (18 m depth); phylogenetic data: none.
4. *Oxypora egyptensis* Veron, 2000, vol. 2: 341, fig. 5 (see also Veron, 2002: 116, figs 221–223; ICZN, 2011: 165); lectotype (designated herein): MTQ G55784 (dry specimen); type locality: eastern Sinai Peninsula, Egypt (15 m depth); phylogenetic data: none.
5. *Oxypora glabra* Nemenzo, 1959: 122, pl. 18: fig. 2; holotype: UP C-300 (dry specimen); type locality: Paniquian Island, Puerto Galera, Philippines; phylogenetic data: molecular and morphology.

Taxonomic remarks

Oxypora was established by Saville Kent (1871: 283) to replace *Trachypora* Verrill, 1864: 53, which was represented by *Tra. lacera* Verrill, 1864: 53, but had already been used by Milne Edwards & Haime (1851a, vol. 5: 158) for a Devonian tabulate coral (Wells, 1936). Saville Kent's proposal was probably unknown to Klunzinger (1879), who placed *Tra. lacera* in *Echinophyllia* Klunzinger, 1879: 69 (Quelch, 1886). Partly as a result of this affiliation, *Oxypora* was grouped by Wells (1935) with *Echinophyllia*, *Tridacophyllia* de Blainville, 1830: 327 (= *Pectinia* de Blainville, 1825: 201), *Mycedium*, and *Physophyllia* Duncan, 1884: 118, in Tridacophylliidae Thiel, 1932: 96, which was originally placed in Fungida (see Yabe & Eguchi, 1935b). *Trachypora lacera* was later designated as the type of *Oxypora* by Wells (1936), validating it as a separate genus from *Echinophyllia*.

Oxypora was placed in the newly established Pectiniidae by Vaughan & Wells (1943: 196), along with the five Tridacophylliidae genera above. Until relatively recently, this classification remained stable (e.g. Wells, 1956; Nemenzo, 1959; Chevalier, 1975; Wood, 1983; Veron, 2000). Molecular-based phylogenies have indicated that *Pectinia*, *Mycedium*, and *Physophyllia* are in the Merulinidae clade, distinct from the sister groups comprising *Echinophyllia* and *Oxypora* (subclade F + G *sensu* Arrigoni *et al.*, 2014c) that are nested within Lobophylliidae (clade XIX *sensu* Fukami *et al.*, 2008; Arrigoni *et al.*, 2014b,c, 2015, 2016a). Consequently, Pectiniidae has been synonymized (Budd *et al.*, 2012; see also Huang *et al.*, 2011, 2014b; Arrigoni *et al.*, 2012).

Oxypora is widely distributed on the reefs of the Indo-Pacific, present from the Red Sea and East Africa to as far east as the Marshall Islands in the Northern Hemisphere and Samoa in the Southern Hemisphere (Veron, 2000).

Morphological remarks

There are no unambiguous apomorphies for *Oxypora*, although compact columellae (one to three threads) and the absence of distinct paliform (uniaxial) lobes are synapomorphies on the morphological phylogeny. The three representatives analysed here are nested within the clade dominated by *Echinophyllia* (subclade F + G *sensu* Arrigoni *et al.*, 2014c), as a polyphyletic group on the molecular tree (Fig. 2A), and as a monophyly on the morphological tree (Fig. 2B). Together with *Echinomorpha*, these genera form a well-supported clade with a bootstrap value of 71 and decay index of 4, and are defined by four synapomorphies: (1) organically united corallites (likelihood of 0.86 based on the Mk1 model); (2) extensive coenosteum (≥ corallite diameter) (likelihood 0.75); (3) columellae ≥ 1/4 of calice width (likelihood 0.92); and (4) loss of epitheca (likelihood 0.84).

Historically, the affiliation between *Oxypora* and *Echinophyllia* has been extremely close. The latter was synonymized under the former by Crossland (1952), who found no morphological traits to separate the two genera. Chevalier (1975) also placed *Ox. glabra* Nemenzo, 1959: 122, under *Echinophyllia* based on a specimen from New Caledonia. This resulted in *Ox. lacera* (Verrill, 1864: 53) being the sole species classed in *Oxypora* during that time. Interestingly, the position of *Ox. glabra* on the molecular phylogeny (Fig. 2A) does show that *Ox. glabra* is more closely related to all *Echinophyllia* species except *Echinophyllia echinata*, which forms a clade with *Ox. lacera* and *Ox. convoluta* Veron, 2000, vol. 2: 340. The close relationship between *Echinophyllia* and *Oxypora* is further supported by the presence of alveoli, which are small pits on the exotheca forming at points of insertion of new septocostae (Chevalier, 1975; Wood, 1983; Veron, 1986, 2000; Benzoni, 2013). As explained above for *Echinophyllia*, the unexpected split of this group into the molecular clades F and G, not accompanied by consistent morphological variation, indicates that the *Echinophyllia–Oxypora* dichotomy ought to be tested with more comprehensive taxonomic and genetic sampling of *Oxypora*.

Genus *Sclerophyllia* Klunzinger, 1879: 4 (Fig. 14)

Type species
Sclerophyllia margariticola Klunzinger, 1879: 4, pl. 1: fig. 12; type by monotypy.

Original description
Polypar mit sehr entwickelter Epithek, an der Basis breit, aufgewachsen, im Alter nicht frei, nieder, ziemlich breit. Rippen in der Nähe des Kelchrandes wohl entwickelt, oben mit einigen Dörnchen, weiter herab durch die Epithek ganz verdeckt. Septa debordirend, breit, zahlreich; die grösseren dick, sehr grob und ungleich gezähnt, auch innen und unten. Die Columella hat die Tendenz, compact zu werden. Auch die Interseptalräume der Kelche zeigen die Neigung, sich auszufüllen mit compacter Substanz. (Klunzinger, 1879: 4)

Subsequent descriptions
Delage & Hérouard, 1901: 622; Arrigoni *et al.*, 2015: 155.

Diagnosis (apomorphy in italics)
Colonial or solitary; colonies submassive or massive. Budding intracalicular and extracalicular in colonies. Corallites monomorphic; discrete. Monticules absent. Coenosteum spinose; limited amount (includes double wall) in colonies. Calice width large (> 15 mm), with high relief (> 6 mm). Costosepta mostly not confluent. Septa in ≥ 4 cycles (≥ 48 septa). Free septa irregular. Septa spaced < 6 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy (> 3 threads), < 1/4 of calice width, and discontinuous amongst adjacent corallites with lamellar linkage. Internal lobes usually absent; paliform (uniaxial) lobes weakly developed if present. *Epitheca well developed.* Endotheca low–moderate (tabular) (Fig. 14A, D).

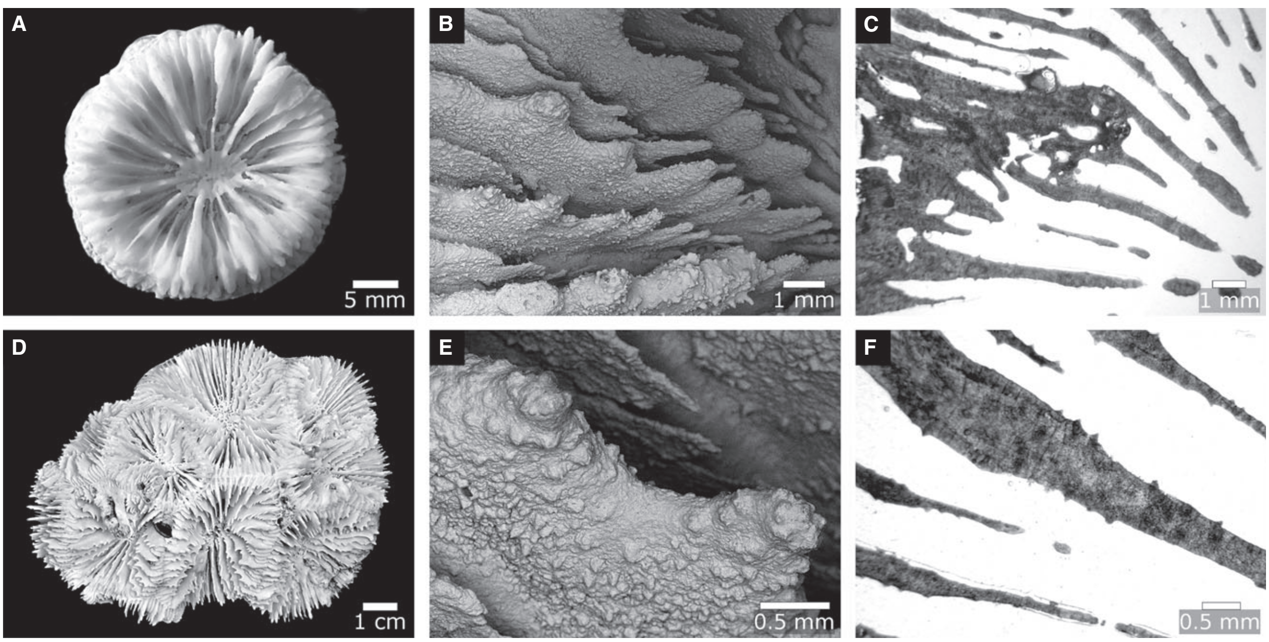

Figure 14. *Sclerophyllia* Klunzinger, 1879, is solitary or colonial, with discrete corallites, double walls in colonies, large (> 15 mm) and high-relief (> 6 mm) calices, septa in ≥ 4 cycles (≥ 48 septa), and well-developed epitheca. Septal teeth are tall (> 0.6 mm) and widely spaced (> 1 mm), unequally shaped between first- and third-order septa, equally sized between wall and septum, and palisade interarea. Walls formed by dominant paratheca and partial septotheca, with strong costa centre clusters. (A) *Sclerophyllia margariticola* Klunzinger, 1879, type species of *Sclerophyllia*; macromorphology, syntype ZMB Cni 2181, Egypt, Red Sea. (B–F) *Sclerophyllia maxima* (Sheppard & Salm, 1988); micromorphology (scanning electron microscopy; B, E) and microstructure (transverse thin section; C, F), hypotype UNIMIB MU161, Yemen; macromorphology, holotype NHMUK 1986.11.17.2, Muscat, Oman (D).

Tooth base at midcalice elliptical-parallel. Tooth tip orientation parallel. Teeth tall (> 0.6 mm); widely spaced (> 1 mm), with > 6 teeth per septum. Tooth shape unequal between first- and third-order septa. Tooth size equal between wall and septum. Granules scattered on septal face; irregular in shape. Interarea palisade (Fig. 14B, E).

Walls formed by dominant paratheca and partial septotheca. Thickening deposits in concentric rings with extensive stereome. Costa centre clusters strong; > 0.6 mm between clusters; medial lines weak. Septum centre clusters weak; > 0.5 mm between clusters; medial lines weak (Fig. 14C, F).

Species included

1. *Sclerophyllia margariticola* Klunzinger, 1879: 4, pl. 1: fig. 12; lectotype: ZMB Cni 2181; type locality: 'Koseir' (specimen label), Egypt, Red Sea; phylogenetic data: molecular and morphology.
2. *Sclerophyllia maxima* (Sheppard & Salm, 1988: 276, figs 4, 5); holotype: NHMUK 1986.11.17.2 (dry specimen); type locality: Muscat, Oman (14 m depth); phylogenetic data: molecular (see also Arrigoni *et al.*, 2015) and morphology.

Taxonomic remarks

The genus was described by Klunzinger (1879: 4) for the solitary and monocentric species *Scl. margariticola* Klunzinger, 1879: 4, first collected from the Red Sea in Egypt. It was later found in Djibouti by Gravier (1907, 1911; see also Vaughan, 1907) but, soon after, synonymized under *Lobophyllia* (Matthai, 1928) and *Symphyllia* (Wells, 1937, 1956; Vaughan & Wells, 1943) as monocentric juvenile stages of these colonial genera. *Sclerophyllia*, *Rhodocyathus* Bourne, 1905: 191, and *Protolobophyllia* Yabe & Sugiyama, 1935: 381, were subsequently considered a junior synonym of *Cynarina* by Wells (1964) and Veron & Pichon (1980). Specifically, they regarded *Cyn. lacrymalis* (Milne Edwards & Haime, 1849a, vol. 11: 238) and *Scl. margariticola* to be the same species.

However, the most recent phylogenetic analyses performed by Arrigoni *et al.* (2015) and the present study based on both molecular and morphological data (Fig. 2), have demonstrated that *Scl. margariticola* is a distinct species most closely related to a species restricted to the Arabian Peninsula, *Ac. maxima* Sheppard & Salm, 1988: 276, and not the widespread *Cyn. lacrymalis*. The monophyly of *Scl. margariticola* + *Ac. maxima*, also known as subclade C (*sensu* Arrigoni *et al.*, 2014c), is well supported, and thus *Sclerophyllia* has been resurrected to incorporate these two species (Arrigoni *et al.*, 2015).

Sclerophyllia is restricted to reefs of the Arabian Peninsula and Arabian Sea (Sheppard & Sheppard, 1991; Veron, 2000; Arrigoni *et al.*, 2015).

Morphological remarks

The well-developed epitheca is an unambiguous synapomorphy (likelihood of 1.00 based on the Mk1 model) recovered for the *Sclerophyllia* clade. The two members of this genus share all the micromorphological characteristics analysed here, including those illustrated by Arrigoni *et al.* (2015), i.e. high elliptical septal teeth parallel to the septum, irregular lobate tips, wide tooth spacing (> 1 mm), granules scattered on the septal face, and a palisade interarea.

Sclerophyllia is closely related to *Moseleya*. They form a monophyletic group on the morphological tree and a paraphyletic grade on the molecular tree (Fig. 2). However, they are separated based on the more common presence of weak to moderate paliform lobes, reduced epitheca, and smaller tooth spacing in *Moseleya*. Monostomatous *Sclerophyllia* specimens are always of the species *Scl. margariticola*. The only other lobophylliid taxon that is exclusively monostomatous is *Cynarina*.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the supporting information tab for this article:

Appendix S1. List of species and GenBank sequence data used for the molecular analyses.
Appendix S2. List of specimens examined and the morphological data.
Appendix S3. Nexus data file containing the aligned molecular and morphological data matrices used in this study, as well as inferred trees (including phylograms) obtained from all phylogenetic analyses.
Appendix S4. Parsimony-optimized character transformations on the morphological phylogeny for synapomorphies of Lobophylliidae and its constituent genera.
Appendix S5. List of all available lobophylliid *nomina*.