



3. Coral Taxonomy: Lobophylliidae Dai and Horng 2009

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We hitherto explored the history of taxonomy, why it is so important, the rudiments of hard coral skeletons upon which their evolutionary trajectories were founded, and the early- to mid-2010s' attempts to definitively rank the family Lobophylliidae into monophyletic clades comprising all the descendants from a common ancestor, after molecular studies had emphasised the polyphyly of most extant scleractinian classifications. The discovery of ancient deep-water Basal and the dichotomy of Complexa and Robusta deepened the uncertainty, where molecular analyses would one day unearth delineating simple pure character attributes (sPu) that would enhance resolution when combined with DNA sequence analyses. Classifications remain in flux and thus all historic nomenclature is associated with a year, whereas unfamiliar terms are clarified in Appendix I. Herein the seminal studies of Arrigoni and collaborators from 2016 and 2019 bring us up to speed with contemporary phylogenetically-discriminating molecular, macromorphological, and microstructural analyses, while parts 1. and 2. remain indispensable background.

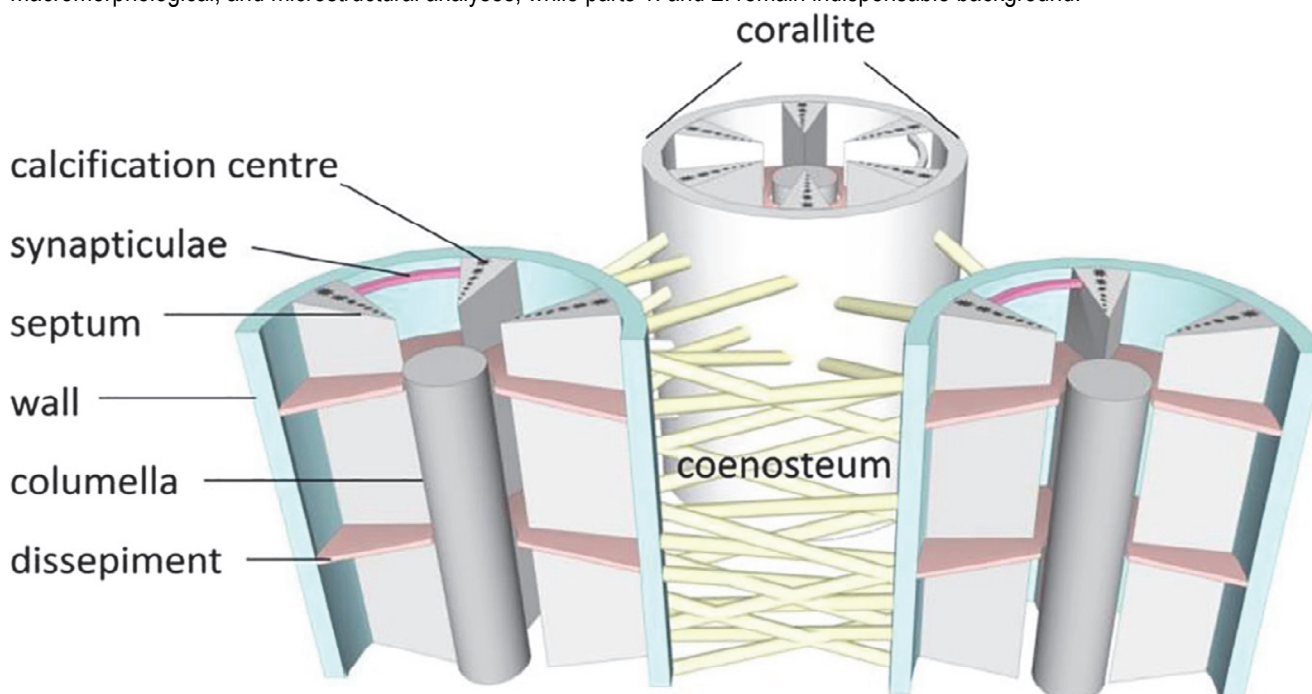


Fig 0. A diagram illustrating some common skeletal features courtesy of Zhao et al. 2021 and The Creative Commons Attribution Licence 4.0.

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Fig 1a. Living colonies of four Lobophylliidae and their skeletal coralla featuring their corallites: [A] Japanese *Micromussa amakusensis*; [B] tentatively *Micromussa* cf. *amakusensis* elevated to the new species *Micromussa indiana* from Yemen's Gulf of Aden; [C] Australia's *Acanthastrea lordhowensis*, and [D] Malaysia's *Micromussa multipunctata* (formerly: *Montastraea multipunctata*). Photography courtesy of Arrigoni et al. 2016 and the Creative Commons Attribution Licence 4.0.

The family Lobophylliidae comprises large polyp Scleractinia that are ecologically and economically significant in the Indo-Pacific yet their congeners extend to the Red Sea and from French Polynesia to eastern Africa. With 12 extant genera and 52 species in 2016 (Arrigoni et al. 2016), sequence analyses of nuclear and mitochondrial genes recommended reclassifications into the monophyletic clades A to J that contradicted established ranks discerned using merely fossil and skeletal attributes (Arrigoni et al. 2012; Arrigoni et al. 2014a). Hence the polyphyly of the lobophylliid genera *Acanthastrea*, *Echinophyllia*, *Lobophyllia*, *Micromussa*, *Oxypora*, and *Symphyllia* were highlighted in 2014 (Arrigoni et al. 2014a). Furthermore, molecular informatics had yet to be generated for the genera *Echinomorpha* and *Homophyllia* (Budd et al. 2012) while Huang and allies ranked *Moseleya* in clades XIX+XX by 2011.

Traditional and contemporary taxonomy have advanced side-by-side insofar as molecular and morphological congruency appears mandatory for definitive phylogenetic trees (Budd et al. 2010). For example, microstructures like septal tooth height, shape, distribution, adjoining topologies (interareas), and their granulose surfaces (Budd & Stolarski 2009; Budd & Stolarski 2011) are now considered phylogenetically-discriminating (Budd & Stolarski 2009; Budd & Stolarski 2011; Budd et al. 2012; Arrigoni et al. 2014b; Arrigoni et al. 2015). So were the *Australomussa* and *Parascolymia* revisions of Arrigoni and collaborators in 2014(b) and 2015, while ancestral commonalities were identified amongst the postulated monophyletic lobophylliid clades A and B (Arrigoni et al. 2014b).

Clade A included *Micromussa amakusensis* and *Montastraea multipunctata* which was absorbed by Lobophylliidae despite its non-affinity with *Montastraea cavernosa* (Huang et al. 2011; Arrigoni et al. 2014a) whilst its micromorphology remained undetermined. *M. amakusensis* type species are an epitome of clade A, whilst they remain common throughout the Indo-Pacific (Fig 1a.; Arrigoni et al. 2016).

Japanese *Micromussa amakusensis* and *Acanthastrea lordhowensis* appear somewhat alike in situ yet the former has larger

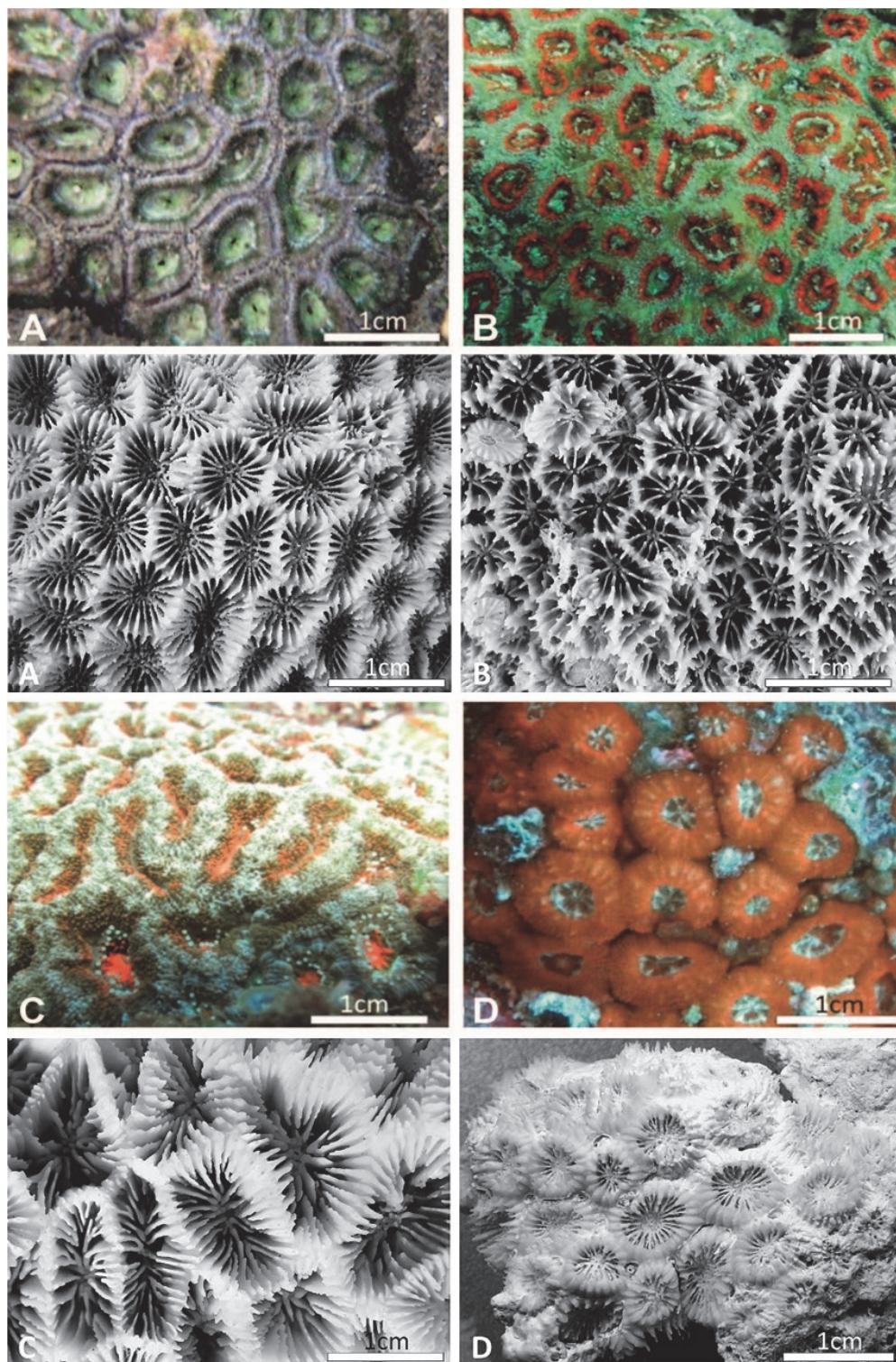
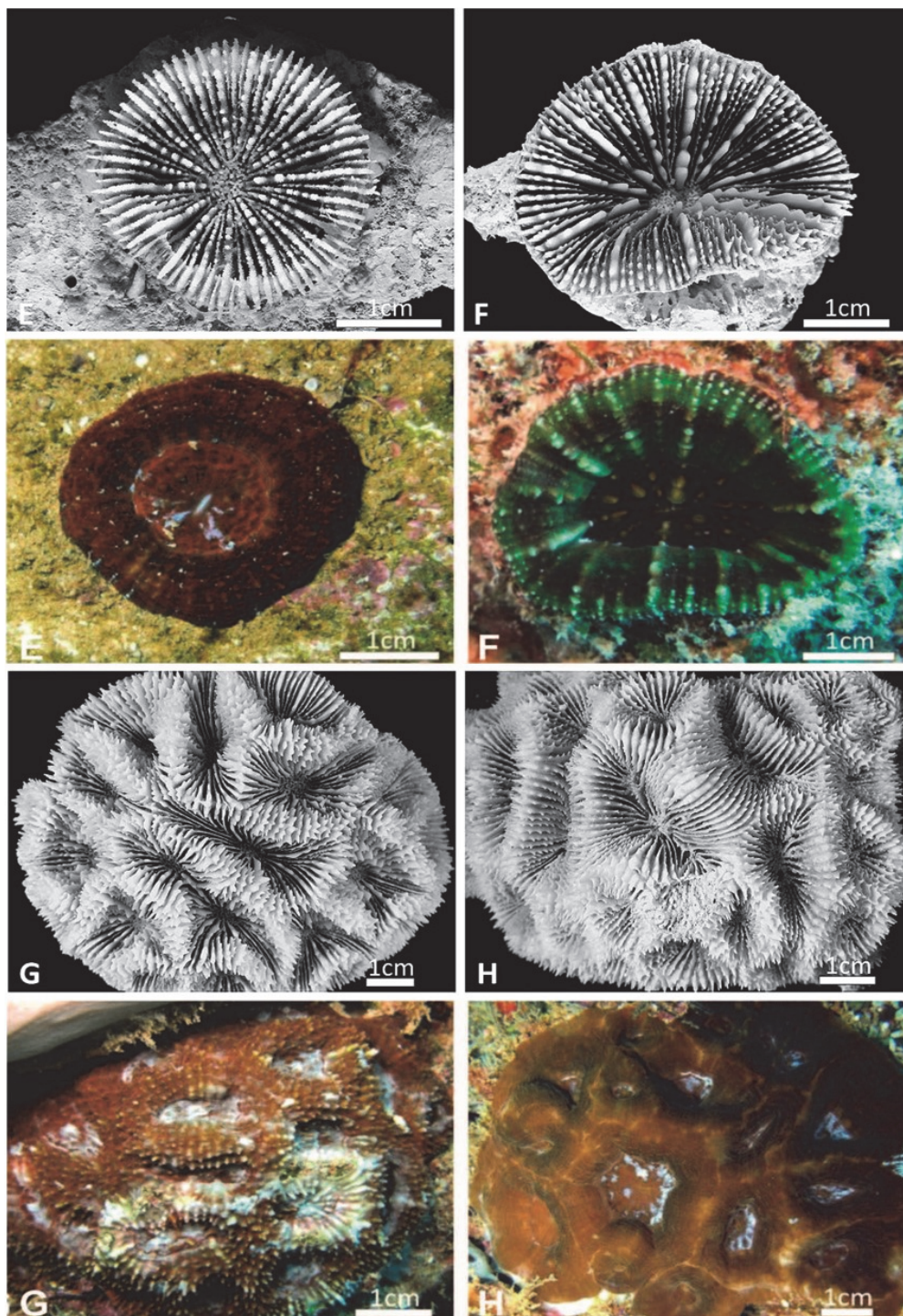


Fig 1b. Skeletal coralla featuring their corallites and living polyps/colonies of four Lobophylliidae: [E] the new species, *Micromussa pacifica* formerly New Caledonia's *Homophyllia* cf. *australis*; [F] *Homophyllia australis* from New Caledonia; [G] New Caledonian *Homophyllia bowerbanki*, previously *Acanthastrea bowerbanki*, and [H] Australian *Homophyllia bowerbanki*, hitherto *Acanthastrea hillae*. Photography courtesy of Arrigoni et al. 2016 and the Creative Commons Attribution Licence 4.0.



less evenly arranged corallites while the latter has fewer septa. Nevertheless, the genus *Micromussa* was erected to nest all previously ascribed species of *Acanthastrea* with sub-5-mm corallites to the exclusion of *A. lordhowensis* in 2000 (Fig 1a.). To this end, *Acanthastrea minuta* was absorbed into *Micromussa* as *M. minuta* and the new Sri Lankan species *M. diminuta* was described (Veron 2000).

Clade B comprises *Acanthastrea bowerbanki* and *A. hillae* where molecular analyses indicate they are distinct from the pre-2014 species type, *A. echinata* which was reclassified in clade E (Arrigoni et al. 2014a), and thus a new species type and genus was advocated for clade B in 2016. Primarily central Pacific but more common at higher latitudes, *A. bowerbanki* and *A. hillae* (Veron 1992; Veron 1993; Veron 2000; Wallace et al. 2009) are remarkably morphologically alike (Arrigoni et al. 2016) with almost identical corallum configurations, growth, and corallite budding (Chevalier 1975, cited in Arrigoni et al. 2016; Veron 1992; Veron 2000; Wallace et al. 2009) which were amongst the largest polyps of all *Acanthastrea*-assigned corals in 2016 (Fig 1b.; Arrigoni et al. 2016). *Acanthastrea hillae* may have been spotted in the western Indian Ocean (Veron 2000) while samples from micromorphologically assigned Yemeni *A. hillae* were included in the morpho-molecular analyses of Arrigoni and colleagues from 2016.

The taxonomic history of *Homophyllia* has renounced several synonyms. Previously a junior affiliate of *Lobophyllia* (Matthai 1928, cited in Arrigoni et al. 2016; Vaughan & Wells 1943, cited in Arrigoni et al. 2016) and *Scolymia* (Veron 2000); *Homophyllia* was resurrected by Budd and colleagues in 2012 following Budd & Stolarski's morphological study from 2009. Corallum micro-morphology and -structure clearly discerned *Homophyllia australis* from its tentative congeners: *Scolymia lacera* and *Parascolymia vitiensis* (Fig 1b.; Budd & Stolarski 2009; Budd et al. 2012; Arrigoni et al. 2014b), whilst molecular analyses had yet to be carried out on *H. australis* in 2016. Hence an extensive range of morphological and molecular analyses were exploited to elucidate the ancestry of this species (Arrigoni et al. 2016).

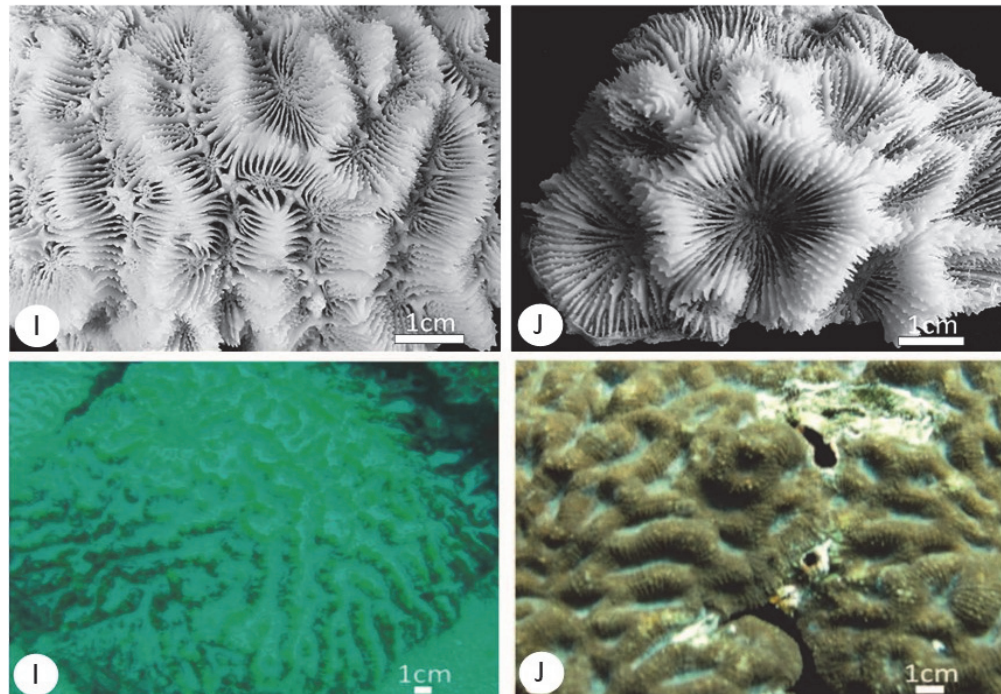
Largely temperate Australia's *Symphyllia wilsoni* were assigned this genus by virtue of their deep coralla and wandering valleys (Arrigoni et al. 2016), yet Veron had highlighted uncharacteristically small skeletal features and septa more akin to those of

Acanthastrea in 2000 (Fig 1c.). Molecular analyses had positioned several members of this genus in clade I (Arrigoni et al. 2014a) while hitherto unexamined *S. wilsoni* was subjected to extensive morpho-molecular studies in 2016 (Arrigoni et al. 2016).

Such approaches were exploited to delineate the lobophylliid genera *Acanthastrea*, *Echinophyllia*, *Lobophyllia*, *Micromussa*, *Oxypora*, and *Symphyllia* from their known geographic limits. Analyses of their mitochondrial DNA markers encoding their 580-base pair (bp) subunits of cytochrome c oxidase I (COI) and their 1,608-bp non-coding intergenic spacer regions (IGR) between COI and their large ribosomal RNA subunits, were combined with their 1,041-bp intranuclear sequences of ribosomal internally transcribed spacers 1 and 2 (ITS1 and ITS2) and 318-bp oligomers from their histone H3 genes. Macro- and micro-skeletal topologies were examined from each species including coralla from regional types but investigations of *Montastraea multipunctata* were restricted to samples from Borneo (Fig 1a.; Arrigoni et al. 2016).

Corallum macromorphology was evaluated using brightfield microscopy whereas a scanning electron microscope (SEM) facilitated microstructural analyses of fragments mounted and sputter-coated with a conductive gold film. Arrigoni and allies' sequence data for 11 Lobophylliidae were aligned with those of previous studies to discern 50 putative species. *Plesiastrea versipora*'s significant divergence from the lobophylliid families Diploastraeidae, Merulinidae, and Montastraeidae made for a comparative and corroborating outgroup (Fukami et al. 2008; Benzoni et al. 2011; Huang et al. 2011; Budd et al. 2012). Molecular analyses affirmed the monophyly of the families Lobophylliidae and Merulinidae which concurred with all previous studies where Arrigoni and collaborators had differentiated nine genera in 2014(a; Arrigoni et al. 2016). The study resolved the sister clades A and B where the former comprised tentative and dichotomous *Micromussa amakusensis* accompanied by monophyletic *Montastraea cf. multipunctata* and *Acanthastrea cf. lordhowensis*. Japanese *Micromussa amakusensis* was grouped with all but one isolate of *Montastraea multipunctata* while Yemeni *M. cf. amakusensis* belonged to a Japanese-congenic monophyletic clade. Genotyping indicated clade A comprised a major lineage of *Homophyllia cf. australis* while traditional morphological studies placed dissimilar *H. australis* in clade B with strong ties with their sister taxa *Acanthastrea bowerbanki* and *A. hillae* (Fig 2.; Arrigoni et al. 2016). This

Fig 1c. Skeletal coralla featuring their corallites and in situ living colonies of the lobophylliids: Australian *Australophyllia wilsoni*, formerly *Symphyllia wilsoni* [I] and *Acanthastrea cf. hemprichii* (synonym: *Acanthastrea cf. hillae*) [J] sampled from the Gulf of Aden. Photography courtesy of Arrigoni et al. 2016 and the Creative Commons Attribution Licence 4.0.



lends credence to the view that colonies have evolved independently to become geographically, geno-, and pheno-typically distinct (Veron 1995, cited in Arrigoni et al. 2016; Ramirez-Portilla et al. 2022).

Of the analysed strains of *Acanthastrea echinata*, all grouped within clade E along with *A. cf. hillae* from the Indian Ocean and *A. cf. hemprichii*, *A. rotundoflora*, and *A. subechinata* ranked using the sequence data from previous studies hence species boundaries were ill-defined. Remarkably, the five strains of *Symphyllia wilsoni* had to be revised into the new monophyletic clade J that diverged before the clade A and B split, which are pheno- and genotypically distant from other *Symphyllia* species and the genera *Lobophyllia* and *Parascolymia* that make up more ancient clade I (Fig 2.; Arrigoni et al. 2016).

The scale bars of phylogenetic trees reveal genetic distance expressed as the number of bp substitutions which are natural mutations that assist demarcation of species and higher classifications. Haplotype network analyses of the mitochondrial DNA IGR locus suggested no fewer than eight bp separated *A. lordhowensis* and Japanese *M. amakusensis* while two strains of this species from the same region differed by only three bp. The haplotypic variation between two Yemeni *M. amakusensis*, two *M. multipunctata*, and two other *A. lordhowensis* was as little as one substitution. Moreover, there was nil genetic distance between all isolates of *H. cf. australis*, whereas disparities of 35 to 39 bps separated the haplotypes of *M. cf. amakusensis* from Japan and Yemen.

Corallite configurations and diameters are extensively divergent within species of Lobophylliidae. Figure 1. features photographs of this family's in situ wild colonies/polyps and skeletons. *Micromussa multipunctata*'s coralla are unique insofar as they manifest as disorganised non-boundary-sharing plocoid corallites (Fig 1a. D), whereas those of non-colonial (solitary) *Homophyllia australis* and *Micromussa pacifica* contrast with massive or encrusting *Symphyllia wilsoni*, *Homophyllia bowerbanki* (synonym: *A. bowerbanki*), *Homophyllia bowerbanki* (synonym: *A. hillae*), *Micromussa amakusensis*, *M. indiana*, *M. lordhowensis*, and *M. multipunctata* (Fig 1b.

Table 1. Lobophylliidae				
Macromorphological Attribute/Peculiarity	Clade A			
	<i>Micromussa amakusensis</i>	New <i>Micromussa indiana</i> (Syn: <i>M. cf. amakusensis</i>)	<i>Micromussa lordhowensis</i> (Syn: <i>A. lordhowensis</i>)	<i>Micromussa multipunctata</i> (Syn: <i>M. multipunctata</i>)
Corallite Budding from within Calice (Intercalicular)	+	+	+	+
Corallite Budding from Outside of Calice (Extracalicular)	+	+	+	+
Budding from Locality of Mouth Resulting in Various Polyp Forms (Circumoral)	-	-	-	-
Integration of Corallite in Corallum	Discrete	Discrete	Discrete	Discrete
Width of Calice or Valley	Medium	Medium	Medium	Small to Medium
Septa per Corallite Expressed in Cycles	4	3 to 4	3 to 4	3 to 4
Autonomous Septa	Irregular	Irregular	Irregular	Irregular
Septa per 5 millimetres of Corallite Circumference (Spacing)	6 to 11	6 to 11	6 to 11	6 to 11
Septa (s) and/or Corallite Wall (C) Thickness (Costoseptal)	Unequal to Quasi-Unequal	Unequal	Unequal to Quasi-Unequal	Unequal
Measured as Cs1 and Cs2 versus Cs3 Cycles				
Central Septal and Columella Confluence	-	-	-	-
Structure of Columella	Trabeculate & Spongy	Trabeculate & Spongy	Trabeculate & Spongy	Trabeculate & Spongy
Comparative Columella to Calice Diameter	>1 / 4	<1 / 4	<1 / 4	>1 / 4
Microstructural Attribute/Peculiarity				
Mid-Septal Tooth Base	Elliptical to Parallel	Elliptical to Parallel	Elliptical to Parallel	Elliptical to Parallel
Tooth Tips	Irregular	Irregular	Irregular	Irregular
Tooth Height (S1)	Medium	Medium	Medium	Medium
Tooth Spacing (S1)	Medium	Medium	Medium	Medium
Granule Shape and Arrangement	Defined, Pointy, & Scattered	Defined, Pointy, & Scattered	Defined, Pointy, & Scattered	Defined, Pointy, & Scattered
The Structure of Septum Between Teeth (Interarea)	Smooth	Smooth	Smooth	Smooth
Shape of Teeth Expressed as Cs3 ÷ Cs1	Equal	Equal	Equal	Equal

Table 1. The manifestations of skeletal macromorphological and microstructural features of lobophylliid clade A. Former names are bracketed as synonyms (Syn) where A. and M. refer to *Acanthastrea* and *Montastraea*. “New” describes a clade, species, or genus erected in the study of Arrigoni and collaborators from 2016, while “cf.” was used as a tentative classification to describe in situ wild colonies whose species was refuted or substantiated. See figure 20. of Part 1. Corallum phenotypes consistent with Budd et al. 2012 and adapted from data presented by Arrigoni et al. 2016.

Table 2. Lobophylliidae				
Macromorphological Attribute/Peculiarity	Clade B			
	<i>Homophyllia australis</i>	<i>Homophyllia bowerbanki</i> (Syn: <i>A. bowerbanki</i>)	<i>Homophyllia bowerbanki</i> (Syn: <i>A. hillae</i>)	New <i>Micromussa pacifica</i> (<i>H. cf. australis</i>)
Corallite Budding from within Calice (Intercalicular)	+ Polycentric Corallum	+	+	+ Polycentric Corallum
Corallite Budding from Outside of Calice (Extracalicular)	+ Polycentric Corallum	+	+	+ Polycentric Corallum
Budding from Locality of Mouth Resulting in Various Polyp Forms (Circumoral)	-	-	-	-
Integration of Corallite in Corallum	Discrete	Discrete	Discrete	Discrete
Width of Calice or Valley	Large	Large	Large	Large
Septa per Corallite Expressed in Cycles	>4	>4	>4	>4
Autonomous Septa	Irregular	Irregular	Irregular	Irregular
Septa per 5 millimetres of Corallite Circumference (Spacing)	6 to 11	6 to 11	6 to 11	6 to 11
Septa (s) and/or Corallite Wall (C) Thickness (Costoseptal)	Unequal	Unequal to Quasi-Unequal	Unequal	Unequal to Quasi-Unequal
Measured as Cs1 and Cs2 versus Cs3 Cycles				
Central Septal and Columella Confluence	-	-	-	-
Structure of Columella	Trabeculate & Spongy	Trabeculate & Spongy	Trabeculate & Spongy	Trabeculate & Spongy
Comparative Columella to Calice Diameter	<1 / 4	<1 / 4	<1 / 4 Uniserial Corallite	<1 / 4
Microstructural Attribute/Peculiarity				
Mid-Septal Tooth Base	Elliptical to Parallel	Elliptical to Parallel	Elliptical to Parallel	Elliptical to Parallel
Tooth Tips	Irregular	Irregular	Irregular	Irregular
Tooth Height (S1)	High	High	High	High
Tooth Spacing (S1)	Wide	Wide	Wide	Medium
Granule Shape and Arrangement	Slight, Oblique, & Uniform	Slight, Oblique, & Uniform	Slight, Oblique, & Uniform	Defined, Pointy, & Scattered
The Structure of Septum Between Teeth (Interarea)	Smooth	Smooth	Smooth	Smooth
Shape of Teeth Expressed as Cs3 ÷ Cs1	Equal	Equal	Equal	Equal

Table 2. The skeletal macromorphological and microstructural features of lobophylliid clade B. Former names are bracketed as synonyms (Syn) where A. and H. refer to *Acanthastrea* and *Homophyllia*. “New” describes a clade, species, or genus erected in the study of Arrigoni and collaborators from 2016, while “cf.” was used as a tentative classification to describe in situ wild colonies whose species was refuted or substantiated. Corallum phenotypes consistent with Budd et al. 2012 and adapted from data presented by Arrigoni et al. 2016.

E & F).

Tables 1. to 3. summarise the species-delineating skeletal traits of the family Lobophylliidae that expedited revisions, and the erection of two new species, one genus, and one clade in combination with molecular analyses, whilst figures 2., 3., and 4. illustrate a definitive phylogenetic tree featuring micrographs of each group’s epitomising macromorphological and microstructural phenotypes, SEMs of the septal teeth of each species, and a graphic representation of the findings of Arrigoni and colleagues from 2016.

Micromussa amakusensis, *M. indiana*, and *M. lordhowensis* have wall-sharing cercoid corallites whereas *Austalophyllia wilsoni* remain discontinuously uni-, bi-, or multi-serial and meandroid, whilst intermediate corallites manifest in the coralla of both strains of *Homophyllia bowerbanki* (Fig 1b. G & H; Fig 1c. I). All studied lobophylliid corallites undergo intra- and extra-calicular budding; however, the coralla of *Homophyllia australis* and *Micromussa pacifica* are prone to polystomatism where solitary corals develop more than one mouth which is more prevalent in the latter. A lamellar linkage is formed between columella during the polystomatous intracalicular budding of these two species (Fig 5.). Circumoral budding was not observed in any of the examined lobophylliids yet a conspicuous quasi-central enlarged corallite was formed in both examples of *Homophyllia bowerbanki* akin to *Acanthastrea* cf.

hemprichii (Fig 1c. J; Arrigoni et al. 2016).

The profoundly meandroid coralla of *Austalophyllia wilsoni* are unique amongst this study's Lobophylliidae insofar as each valley was formed from the centres of multiple corallites whose columellae were adjoined and appeared to be divided by peculiar wide lamellar processes that conferred bilateral symmetry (Fig 6. A & C). Species of *Hydnophora* of the family Merulinidae and *Pavona varians* of the family Agariciidae form hydnoophores akin to *Austalophyllia wilsoni*'s monticules which are conical peaks arising from abutting corallite walls as indicated by the white arrow in plate A, and the SEMs of E to G of figure 6. (Arrigoni et al. 2016).

A theca is a corallite- or corallum-enveloping sheath, while corallite walls are formed by several means that safeguard the contiguity of the postero-septal margin. The rear of each septum may be linked by dissepiments in parathecal; septa thicken and

Table 3. The skeletal macromorphological and microstructural features of clades E and J of Lobophylliidae. Former names are bracketed as synonyms (Syn) where A. and S. refer to *Acanthastrea* and *Symphyllia*. "New" describes a clade, species, or genus erected in the study of Arrigoni and collaborators from 2016, whilst "cf." was used as a tentative classification to describe in situ wild colonies whose species was refuted or substantiated. Corallum phenotypes consistent with Budd et al. 2012 and adapted from data presented in Arrigoni et al. 2016.

fuse in septothecal; costosepta are adjoined by perpendicular bridging remnants of the original marginothecal corallite wall in trabeculothecal, or septa are interwoven by perpendicular synaptical rods in synapticalothecal (Fig 0.; Budd & Storlarski 2011).

Budd and colleagues categorised the diameters of calices into large, medium, and medium to small which corresponded to >15, 8 to 15, and 9 to 3 mm respectively (Budd et al. 2012), where those of *Acanthastrea cf. hemprichii*, *Homophyllia australis*, the two *H. bowerbanki*, and *Micromussa pacifica* were large, while the calices of *Austalophyllia wilsoni*, *Micromussa amakusensis*, *M. indiana*, and *M. lordhowensis* were medium, and *Micromussa multipunctata*'s were medium to small (Arrigoni et al. 2016).

The largest calice dimensions of the colonial lobophylliids in this study bud from within the coralla of *Homophyllia australis* whilst the medium calices of *Micromussa amakusensis* were larger than their respective putative congeners: *H. cf. australis* and *M. cf. amakusensis*, which assisted their reclassification to *Micromussa pacifica* and *M. indiana* (Fig 1a. A; Fig 7.). However, corallite contour and diameter are highly variable in *M. indiana* sometimes manifesting as larger and more even configurations that resemble *M. amakusensis*, whereas these dimensions in *Micromussa lordhowensis* can exceed those of both. Such corallites may be elongate, form irregular polygons, or be more conventional, whilst comparatively consistent small irregular, larger round, or oval plocoid corallites develop in the coralla of *Micromussa multipunctata* (Arrigoni et al. 2016).

Septal growth is cyclic where those from successive rounds are twice as many and thinner (Cairns 2001) while the ends of delicate "free" septa that fall short of the centre are sometimes evident between substantial costa- and upper columella-adjointing costosepta (Appendix I; Figs 7. & 8.; Cairns 2001; Budd & Storlarski 2011). 3 to 4 cycles form the septa of *Micromussa indiana*'s, *M. lordhowensis*', and *M. multipunctata*'s corallites which contrast with the 4 of *M. amakusensis*. More than 4 cycles were observed in all other examined lobophylliids while septal spacing ranged from 6 to 12 for every 5 mm of corallite circumference, whereas free irregular septa were present in all (Arrigoni et al. 2016).

Costoseptal thicknesses were unequal and fell midway between the combined first and second cycles and the third in *Acanthastrea cf. hemprichii*, *Austalophyllia wilsoni*, *Homophyllia australis*, *H. bowerbanki* (Syn: *Acanthastrea hillae*), *Micromussa indiana*, and *M. multipunctata*, while these features remained mismatched or marginally-mismatched in the other *H. bowerbanki*, *M. amakusensis*, *M. lordhowensis*, and *M. pacifica*. However, conspecific widths continued to differ where *H. bowerbanki*'s (Syn: *Acanthastrea bowerbanki*'s) were somewhat the same yet were conspicuously variate amongst the strains of *H. bowerbanki* (Syn: *A. hillae*) and meandroid *Austalophyllia wilsoni*, where a series of valley-constrained corallites are separated by prominent fused dividing septa unified with centre-coalescing lamellar processes, while the inner extremities of such septa became saddle-like (Fig 6. A, C, & H to F; Arrigoni et al. 2016).

Spongy trabeculate columellae of less than a quarter of calice diameters manifest in all investigated lobophylliids except *Micromussa multipunctata* and *M. amakusensis* where they were consistently wider. Nevertheless, the columellae of *Austalophyllia wilsoni* were reduced in their meandroid valleys but were larger in their sporadic monocentric corallites (Fig 6. B; Arrigoni et al. 2016).

The microstructures shared amongst the examined Lobophylliidae are numerous yet included elliptical mid-septum tooth bases and their variable tips. The height of septal teeth decreases with each successive cycle. *Homophyllia australis*, *H. bowerbanki* (Syn: *Acanthastrea bowerbanki*), *H. bowerbanki* (Syn: *Acanthastrea hillae*), and *Micromussa pacifica* had elevated septal tooth heights of 0.6 mm, where those of *Austalophyllia wilsoni*, *Micromussa amakusensis*, *M. indiana*, *M. lordhowensis*, and *M. multipunctata*

Table 3. Lobophylliidae	Clade E	New Clade J
Macromorphological Attribute/Peculiarity	<i>Acanthastrea</i> cf. <i>hemprichii</i> (A. cf. <i>hillae</i>)	New Genus <i>Austalophyllia</i> <i>wilsoni</i> (Syn: <i>S. wilsoni</i>)
Corallite Budding from within Calice (Intercalicular)	+	+
Corallite Budding from Outside of Calice (Extracalicular)	+	+
Budding from Locality of Mouth Resulting in Various Polyp Forms (Circumoral)	-	-
Integration of Corallite in Corallum	Discrete	Discrete
Width of Calice or Valley	Large	Small to Medium
Septa per Corallite Expressed in Cycles	>4	>4
Autonomous Septa	Irregular	Irregular
Septa per 5 millimetres of Corallite Circumference (Spacing)	6 to 11	6 to 11
Septa (s) and/or Corallite Wall (C) Thickness (Costoseptal)	Unequal	Unequal
Measured as Cs1 and Cs2 versus Cs3 Cycles	-	Intermittent
Central Septal and Columella Confluence	-	Intermittent
Structure of Columella	Trabeculate & Spongy	Trabeculate & Spongy
Comparative Columella to Calice Diameter	<1 / 4	<1 / 4
Microstructural Attribute/Peculiarity		
Mid-Septal Tooth Base	Elliptical to Parallel	Elliptical to Parallel
Tooth Tips	Irregular	Irregular
Tooth Height (S1)	Medium to High	Medium
Tooth Spacing (S1)	Medium to Wide	Medium
Granule Shape and Arrangement	Slight, Oblique, Arising from Thickened Deposits	Slight, Oblique, & Scattered
The Structure of Septum Between Teeth (Interarea)	Smooth	Smooth
Shape of Teeth Expressed as Cs3 + Cs1	Unequal	Equal

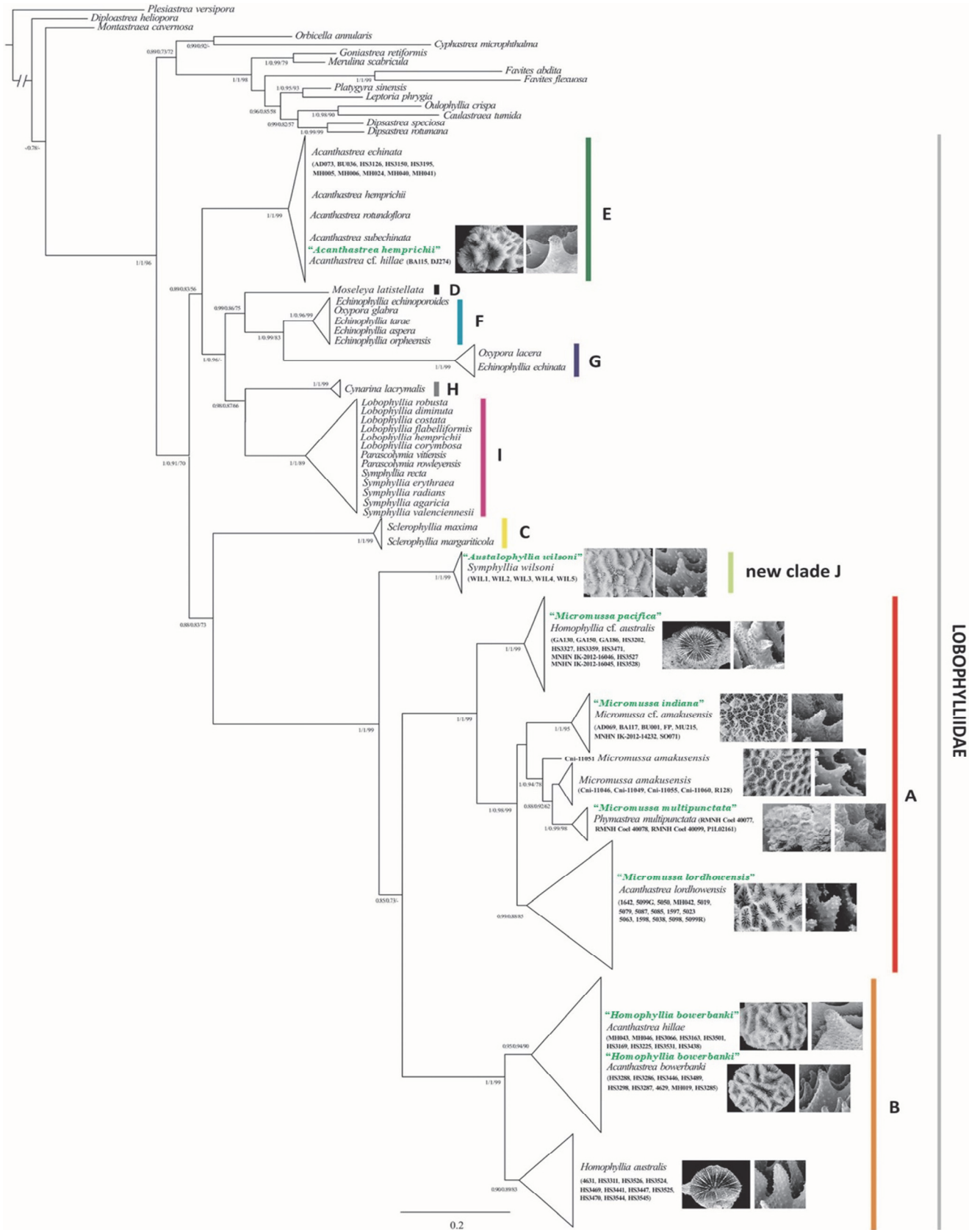


Fig 2. The revised phylogenetic tree of each species type in the family Lobophylliidae constructed by Arrigoni and allies and published in 2016. Discerned using combined sequence analyses of the DNA markers: mitochondrial cytochrome c oxidase subunit I (COI) and the non-coding intergenic spacer region (IGR) between COI and the large ribosomal RNA subunit, together with intranuclear ribosomal internally transcribed spacers 1 and 2 (ITS) and the histone H3 gene. The current study's reclassifications are highlighted in green, whilst strain identifiers are emboldened. Comprises phylogenetically discerning group type corallite macromorphology and septal tooth microstructures, whereas Arabic clade descriptors remain consistent with those of Arrigoni and collaborators from 2014a. Nodes supported by Bayesian posterior probabilities (>0.8)/maximum likelihood SH-like support (>0.7)/maximum parsimony bootstrap support (>50 percent of 1,000). For scale bar consult: Appendix I. Adapted from the tree and analyses of Arrigoni et al. 2016 courtesy of the Creative Commons Attribution Licence 4.0.

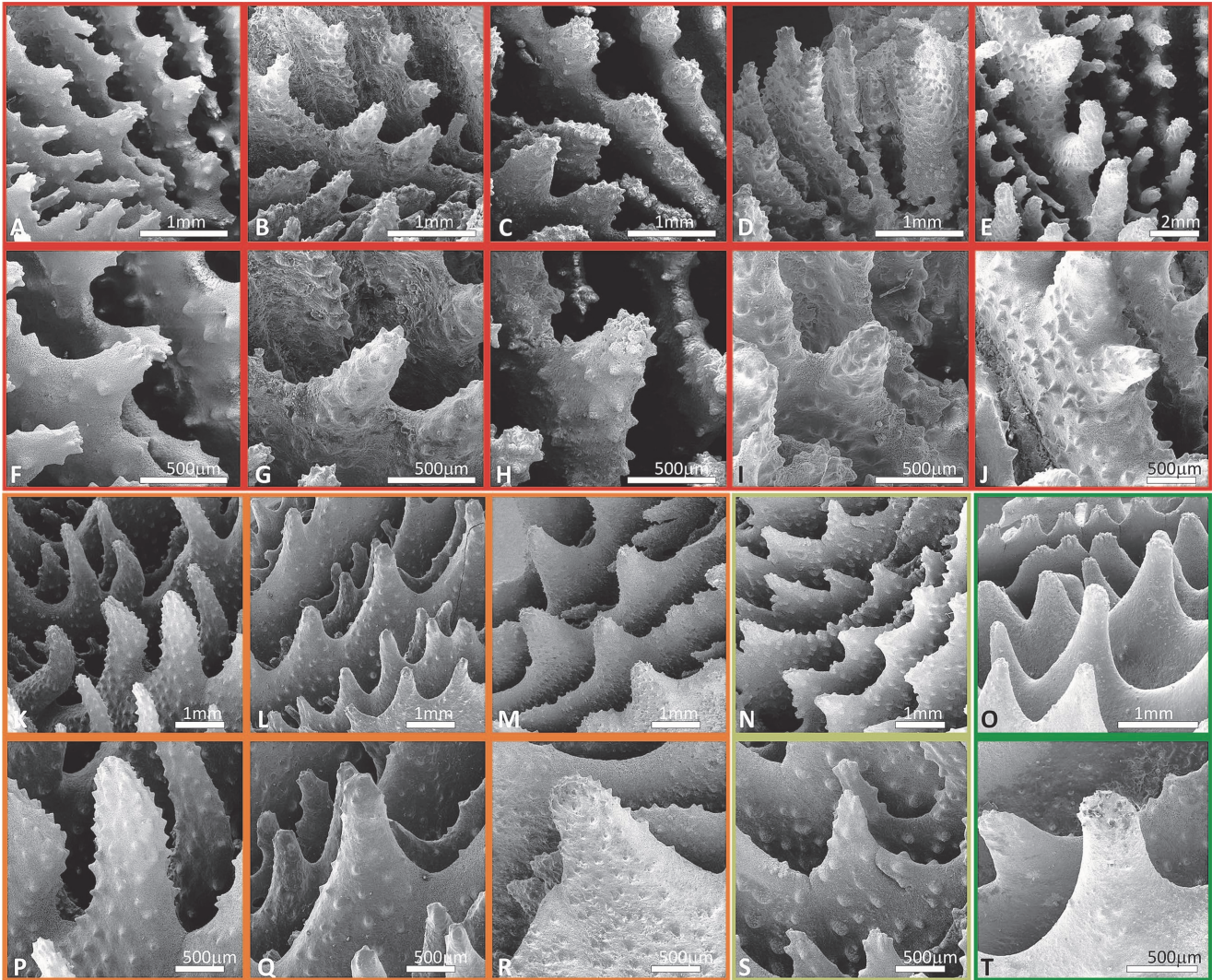


Fig 3. Scanning electron micrographs (SEMs) of the microstructures of the septal teeth of the investigated lobophylliids where those beneath are magnifications of those above, and borders differentiate **clade A**; **clade B**; **clade E**, and **clade J**: [A & F] *Micromussa amakusensis*; [B & G] the new species *Micromussa indiana* frequently described herein as *Micromussa cf. amakusensis*; [C & H] *Acanthastrea lordhowensis* reclassified as *Micromussa lordhowensis*; [D & I] revised *Micromussa multipunctata* previously *Montastraea multipunctata*; [E & J] the new species *Micromussa pacifica* ascending from corals formerly referred to as *Homophyllia cf. australis*; [P & K] *Homophyllia australis*; [L & Q] reclassified *Homophyllia bowerbanki* hitherto *Acanthastrea bowerbanki*; [M & R] *Acanthastrea hillae* revised to *Homophyllia bowerbanki*; [N & S] teeth of the new genus *Australophyllia wilsoni* that absorbed *Symphyllia wilsoni*, and [O & T] *Acanthastrea cf. hillae* redesignated *Acanthastrea cf. hemprichii* (Fig 4.). Micrographs and analyses courtesy of Arrigoni et al. 2016 and the Creative Commons Attribution Licence 4.0.

ranged from 0.3 to 0.6 mm. Chevalier (1975, cited in Arrigoni et al. 2016) remarked that the septal tooth height of *H. bowerbanki* (Syn: *Acanthastrea hillae*) increased towards the columella but was comparatively diminished at septal extremities which concurred with Wells observations from 1955. An identical trend was noted by Arrigoni and collaborators in primary and secondary septa which was lacking in the haplotype *H. bowerbanki* (Syn: *Acanthastrea bowerbanki*) where septa are relatively thinner. Analogous variances in septal teeth occurred in solitary *Homophyllia australis* but not in *Micromussa pacifica* where the teeth on primary and secondary septa were tallest above the corallite periphery and decreased towards the centre (Figs 8. & 9.). The septal teeth of *Micromussa lordhowensis* remained comparatively even although conspecific prominence varied (Arrigoni et al. 2016).

Septal tooth interareas were smooth, and their shapes were consistent amongst all studied lobophylliids excluding *Acanthastrea cf. hemprichii* and *Homophyllia australis* whose primary septa were adorned with paliform lobes (Fig 9. H). Tooth spacing exceeded 1 mm in *Homophyllia australis*, *H. bowerbanki* (Syn: *Acanthastrea hillae*), and *H. bowerbanki* (Syn: *Acanthastrea bowerbanki*), yet ranged from 0.3 to 1.0 mm in the other Lobophylliidae. Lateral septal granulations were slight, rounded, and uniformly distributed in *Homophyllia australis*, *H. bowerbanki* (Syn: *Acanthastrea hillae*), and *H. bowerbanki* (Syn: *Acanthastrea bowerbanki*), while they were slight, rounded, and scattered in *Australophyllia wilsoni*, but they were ill-defined, oblique, and arose from thickened deposits in *Acanthastrea cf. hemprichii* (Fig 3.). Irrespective, the septal granulations of *Micromussa amakusensis*, *M. indiana*, *M. lordhowensis*, *M. multipunctata*, and *M. pacifica* were prominent, pointed, and scattered. The fused and enlarged corallite-dividing septa that formed saddle-shaped structures on their inner extremities appeared peculiar to the series of corallites found in the valleys of meandroid *Australophyllia wilsoni* (Fig 6.; Arrigoni et al. 2016).

Micromussa minuta was reclassified as *Acanthastrea minuta* and ranked within clade E, whereas *M. diminuta* was absorbed into the outgroup genus, *Goniopora* as *G. diminuta* in addition to the conspicuous revisions and erections of tables 1. to 3. (Fig 4.).

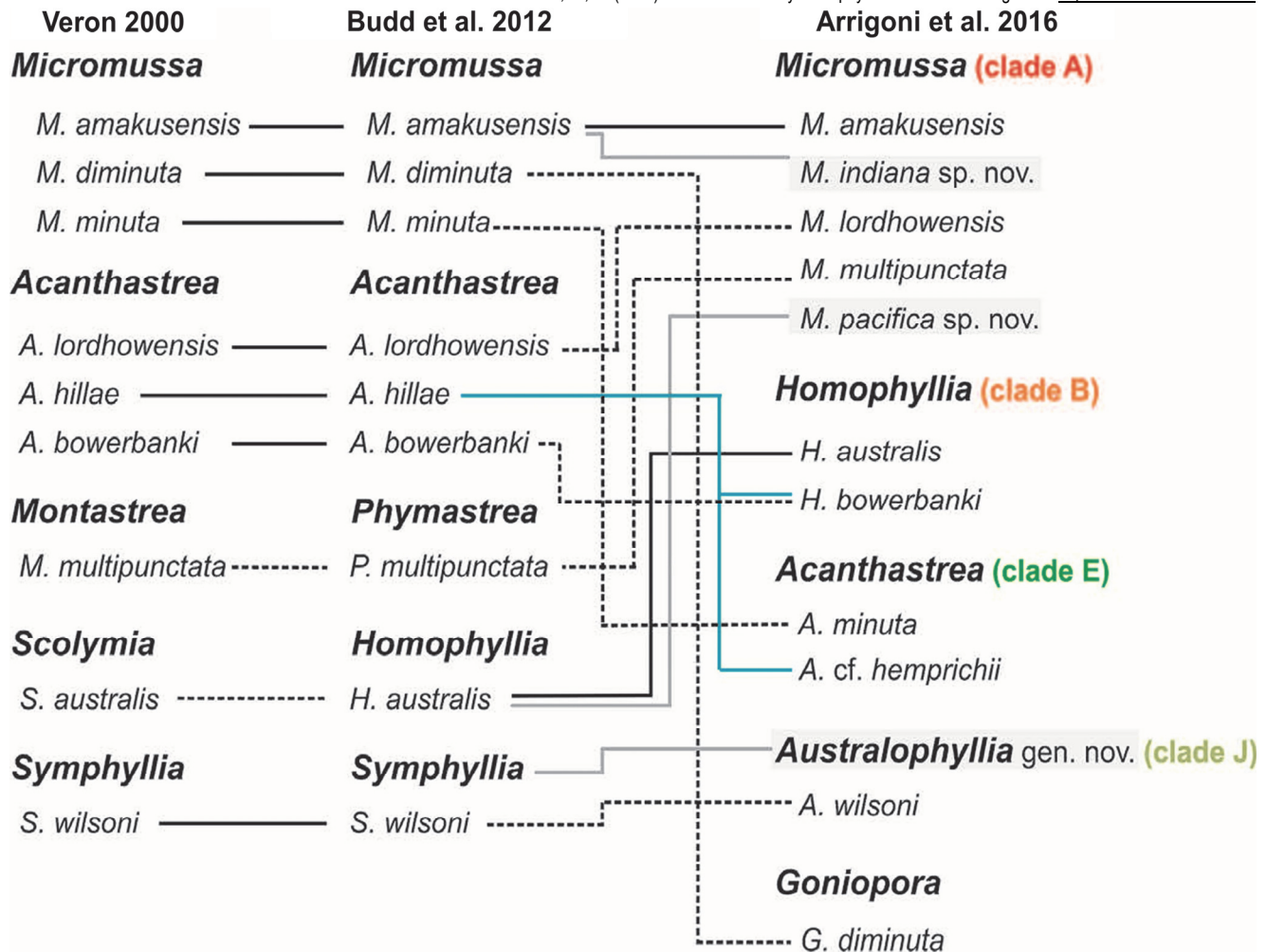


Fig 4. The revised classifications of Lobophylliidae corroborated by the morpho-molecular analyses of Arrigoni and colleagues from 2016 where upheld species are connected with a solid black line, absorption into a different genus is expressed by a dotted black line, accepted synonyms are linked with a solid blue line, and grey lines indicate the species to which the nucleic acid markers were previously assigned now attributed to a different species. Consult table 3. of Part 1. Analyses courtesy of Arrigoni et al. 2016 and the Creative Commons Attribution Licence 4.0.

Notwithstanding the unique divergent growth form, polyp outline, and plocoid corallites of *Micromussa multipunctata*, the molecular and microstructural analyses firmly positioned this species alongside its *Micromussa* congeners in an A subclade (Fig 1a. D; Fig 3. D & I). *Homophyllia australis* and *Micromussa pacifica* are solitary and superficially alike, geographically proximal, and share ancestral lineage (sympatric); however, the findings of extensive morphological and molecular evaluations advocated the creation of the latter in clade A (Arrigoni et al. 2016) and refuted the relation of definitive *H. australis* with *Parascolymia vitiensis* and positioned this species within clade B (Budd et al. 2012). *Acanthastrea hillae* was formally reclassified as *Homophyllia hillae* as a junior synonym of *Homophyllia bowerbanki* of clade B. These two latter revisions are noteworthy insofar as they unequivocally rank a solitary and colonial species in one genus (Arrigoni et al. 2016). Additionally, intracalicular mono- or poly-stomatous budding is no longer regarded as phylogenetically-discriminating and thus cannot impede cladistics (Gittenberger et al. 2011; Benzoni et al. 2012).

All of the wild in situ specimens identified as *Acanthastrea hillae* from the Indian Ocean appeared to be misidentifications of *Acanthastrea cf. hemprichii* (Veron 2000) and thus *A. hillae* may not grow in this region which would constrain species of *Homophyllia* to the temperate, sub-, and -tropical environs of the western Pacific (Arrigoni et al. 2016). Both species are comparatively rare, yet occur more frequently in Japan's, New Caledonia's, and south-western Australia's subtropics (Veron & Marsh 1988; Veron 1993; Veron 2000; Wallace et al. 2009).

A surprising development was the erection of monospecific clade J that comprises the new genus *Australophyllia* as *A. wilsoni* whose strains diverged before their sister genera *Homophyllia* and *Micromussa* (Arrigoni et al. 2016). This species tends to be limited to the kelp forests and rocky outcrops of temperate south-eastern and -western Australia (Veron 1985; Veron 1993; Veron 2000; Veron & Marsh 1988) alongside species of the genus *Coscinaraea* (Veron & Pichon 1980; Veron & Marsh 1988; Veron 1993; Veron 2000).

Exhaustive morphological studies that excluded molecular data suggested that neither *Micromussa diminuta* nor *M. minuta* were members of *Micromussa* where one strain of the former was most likely *Goniopora somaliensis* while *M. diminuta* was repositioned within *Goniopora*. Equally, *Acanthastrea minuta* was resurrected from *Micromussa minuta* (Arrigoni et al. 2016).

Strains assumed to be *Acanthastrea cf. hillae* were discerned from their tentative congeners *Homophyllia bowerbanki* by their lateral septal granulation that was slight, oblique, and arose from thickened deposits, which were putatively recovered in *Acanthastrea* of clade E as *A. cf. hemprichii* (Fig 3. O & T). Such corals cannot be definitively ranked without corroborating molecular evidence.

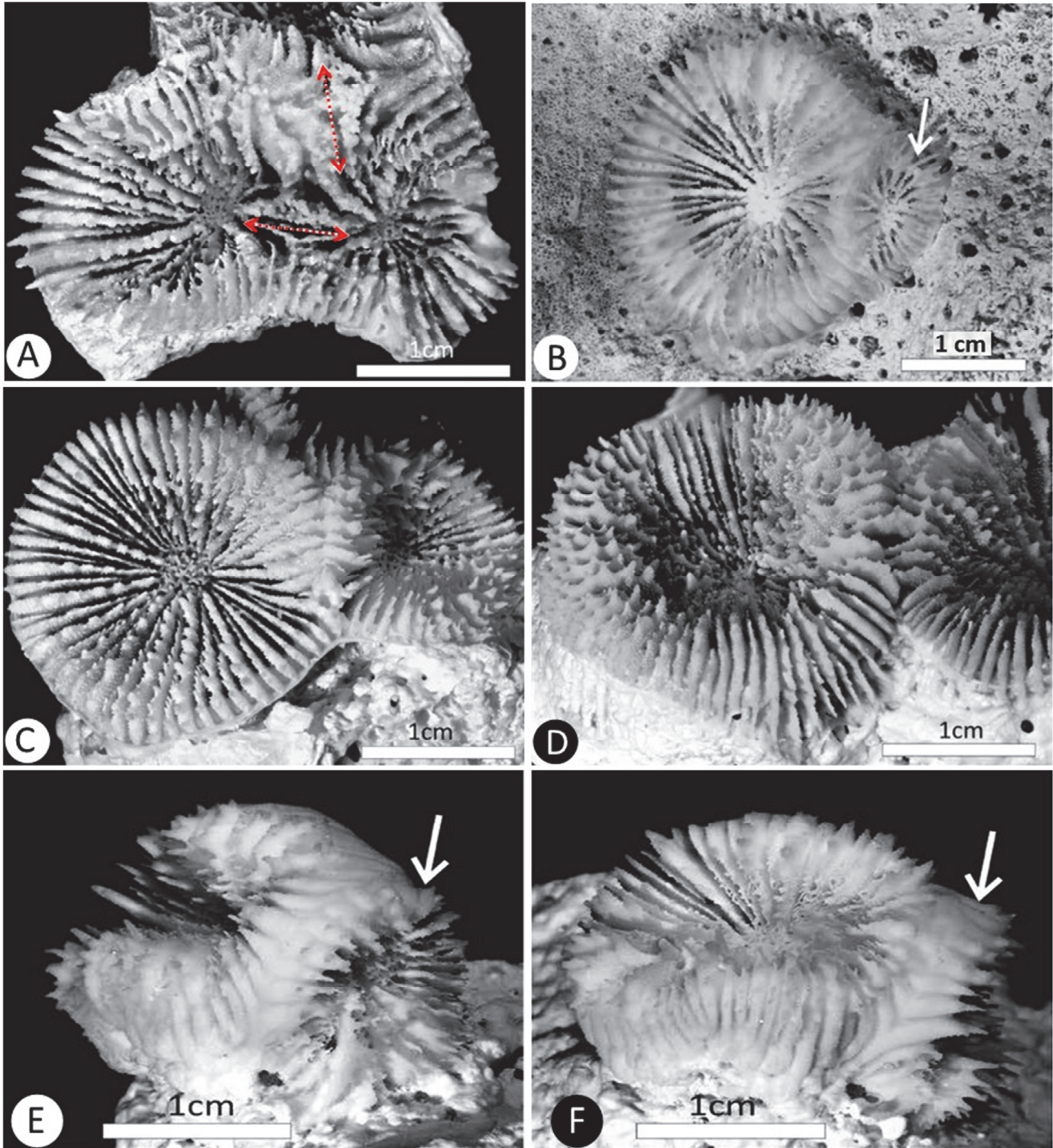


Fig 5. Two kinds of polystomatous budding in *Homophyllia australis* and *Micromussa pacifica* where solitary corals develop more than one mouth. Red dotted arrows highlight lamellae linkages. Images courtesy of Arrigoni et al. 2016 and the Creative Commons Attribution Licence 4.0.

This research emphasised the indispensability of rigorous macro- and micro-morphological and -structural analyses that enhance the precision of molecular techniques (Budd et al. 2012; Kitahara et al. 2012b; Huang et al. 2014a; Arrigoni et al. 2014b; Janiszewska et al. 2015) and the inclusion of conspecific specimens from geographically distant reefs as they may unearth cryptic and sympatric speciation, and obviate misidentifications derived from phenotypic plasticity (Arrigoni et al. 2016).

Distinct species of coral can be visually indistinguishable (cryptic) and even divers with decades of experience find in situ identification beset with uncertainty, which is only intensified by epigenetic variation. *Paraechinophyllia variabilis* is a cryptic lobophylliid that grows in the Red Sea, the reefs of Mayotte Island and Madagascar in the Indian Ocean, Yemeni's Gulf of Aden, and Australian, New Caledonian, and Papua New Guinean waters that appears identical to *Echinophyllia aspera* or *E. orpheensis*, which was first unearthed and classified by Arrigoni and collaborators in 2019 by analysing the fossil record and six concatenated genetic markers. Strains of *Paraechinophyllia variabilis* arose in the Pliocene three million years ago (MYA), yet their ancestors deeply diverged from *Echinophyllia* and *Oxypora* in the early Miocene 21.5 MYA which split some eight MY later. The original divergence of *P. variabilis* was untangled by molecular evaluation and merely calice relief which exemplifies how a single morphological attribute can be phylogenetically-discriminating and that merely nominal phenotypic variance may transpire over millions of years (Fig 10.;

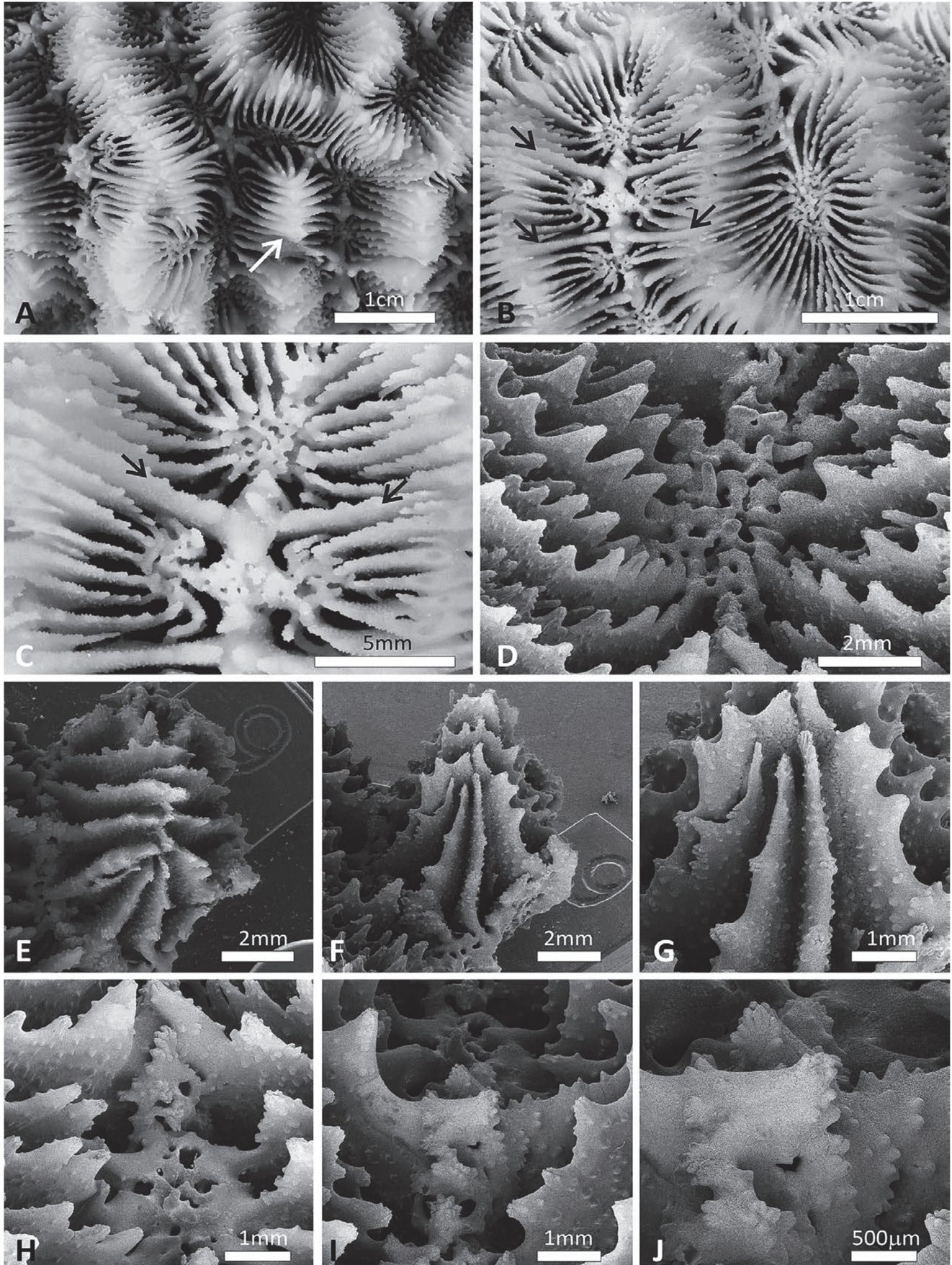


Fig 6. [A] the extensively meandroid corallite configuration of *Austalophyllia wilsoni* featuring conical mounds of monticules formed on the boundary of corallite walls highlighted with a white arrow; [B & C] illustrating a multicorallite valley whose integral walls form thickened lamellae indicated by black arrows; [D] exemplifying a columella-nestling deep valley; [E to F] SEMs of monticules with septal granulation [G]; [H] magnified columella with the extremities of thickened lamellar processes to its rear; [I] columella-separating saddle-like junction of thickened lamellae, and granulation [J]. Photography and micrographs courtesy of Arrigoni et al. 2016 and the Creative Commons Attribution Licence 4.0.

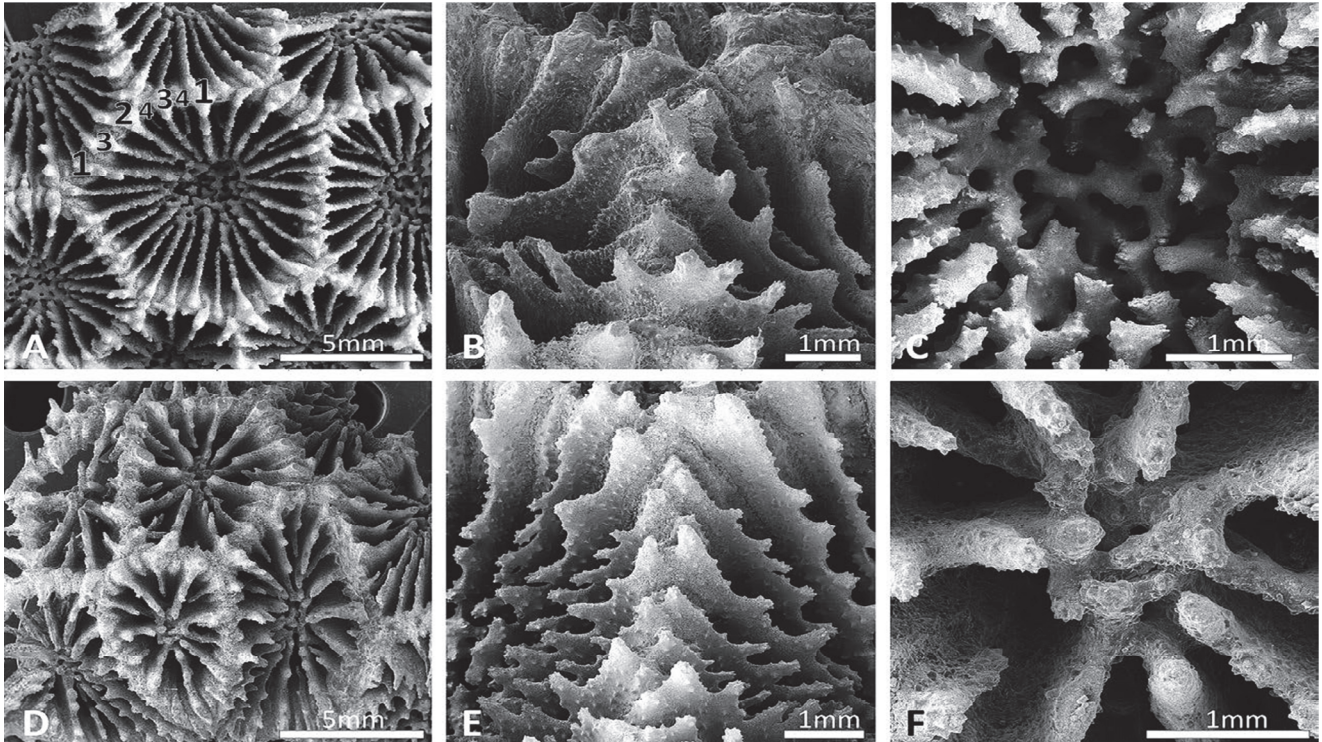


Fig 7. [A] the calices of *Micromussa pacifica* featuring septal cycles 1 to 4; [D] the smaller calices of *M. Indiana*; [B & E] SEMs of the septa on their calice boundaries, and [C & F] overhead SEMs of their respective columellae. Consult figure 20. of Part 1. Images courtesy of Arrigoni et al. 2016 and the Creative Commons Attribution Licence 4.0.

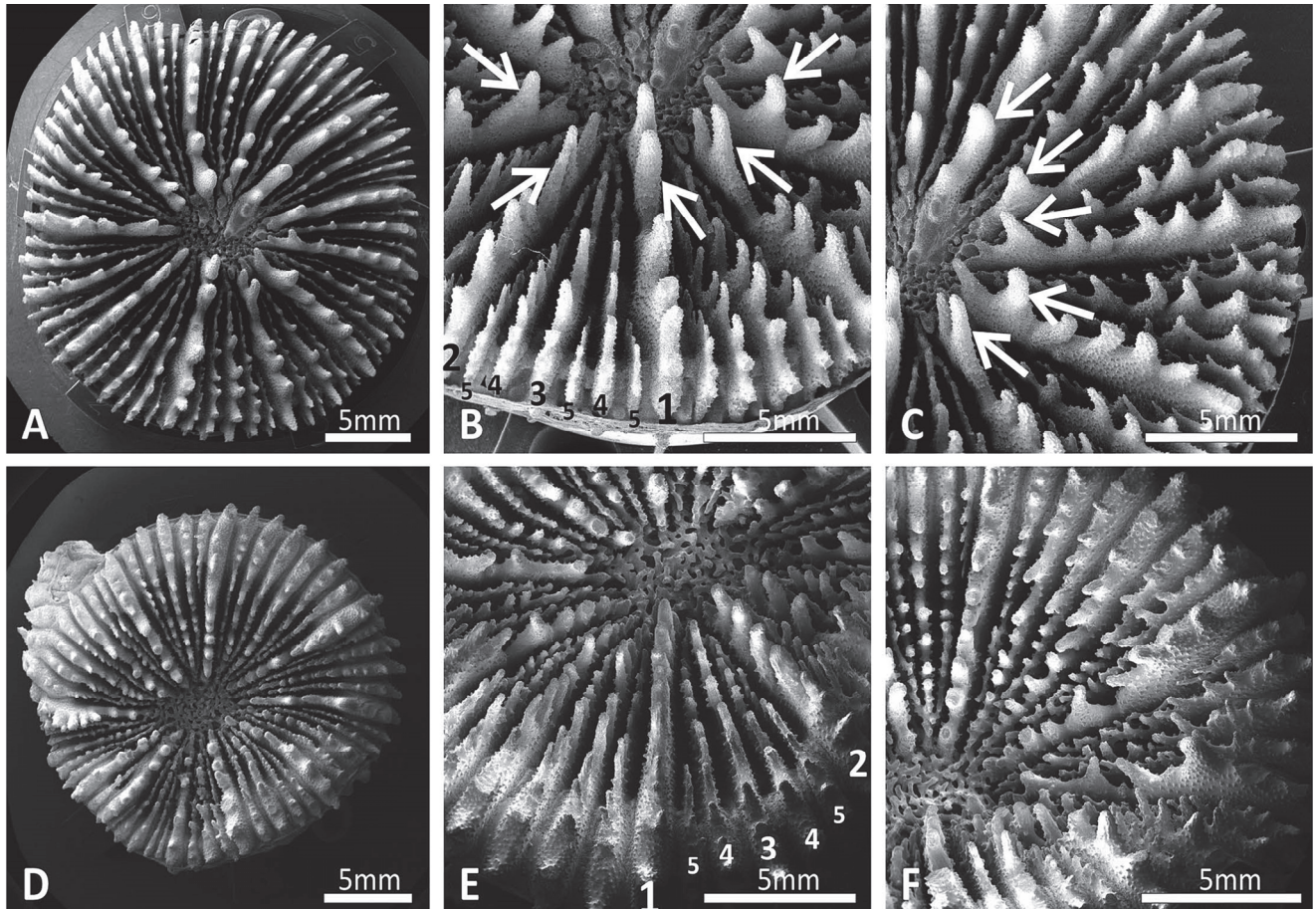
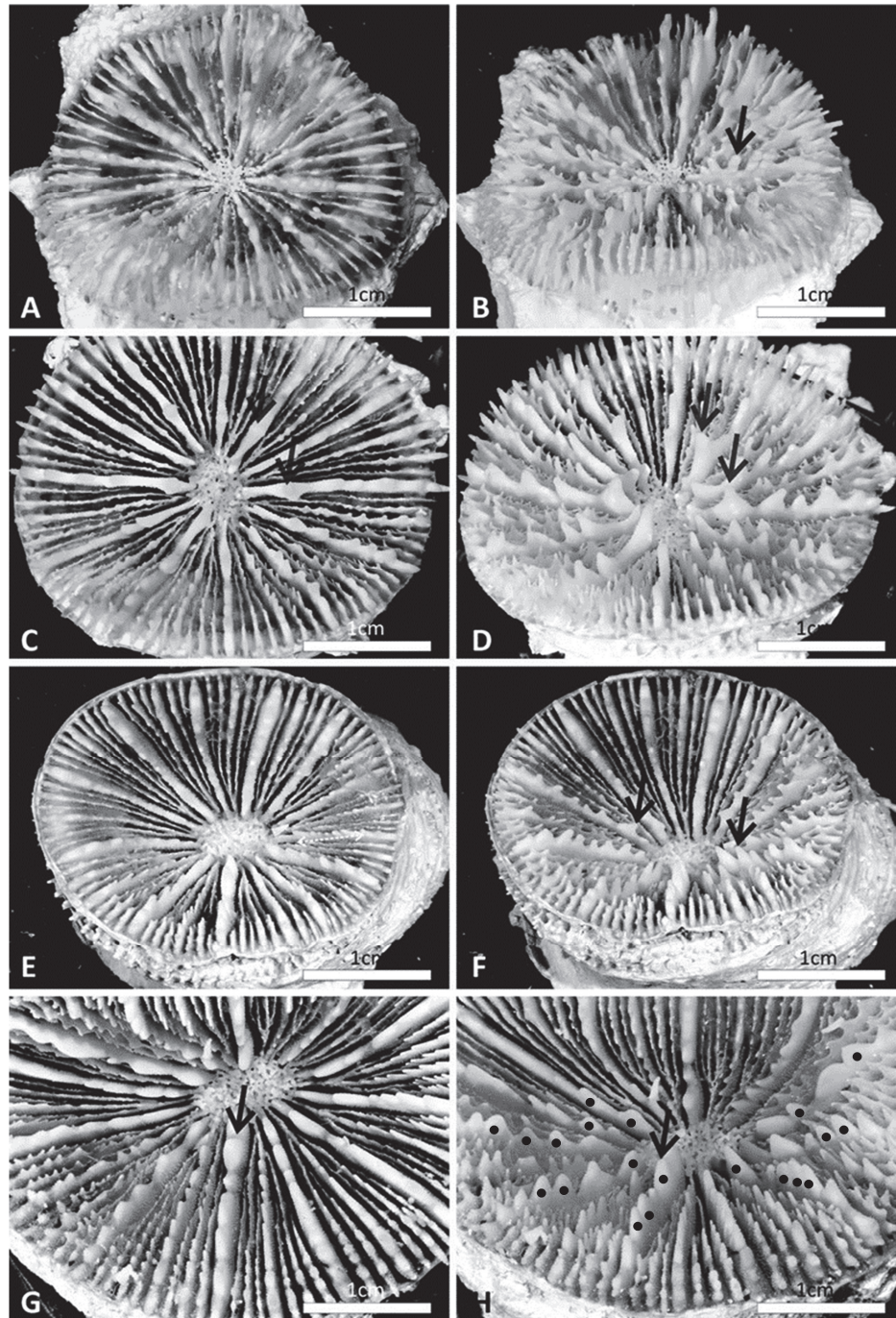


Fig 8. The skeletal macromorphologies of the solitary corallites of *Homophyllia australis* [A to C] and *Micromussa pacifica* [D to F]. [B & C] larger inner septal teeth of *Homophyllia australis*; [B & E] septal cycle. Images courtesy of Arrigoni et al. 2016 and the Creative Commons Attribution Licence 4.0.

Arrigoni et al. 2019).

Conspecific morphological variations nullify the objectivity of traditional taxonomy and blur species boundaries (Veron &

Fig 9. Solitary corallites of *Homophyllia australis* exemplifying the prominent septal teeth of the first cycle, increments in tooth height towards the upper columella, and first and second order paliform septal teeth/lobes marked with black circles [H]. Images courtesy of, and adapted from, Arrigoni et al. 2016 and the Creative Commons Attribution Licence 4.0.



Pichon 1976) which is exacerbated by introgressive hybridisation whereby genetic material is bidirectionally shared between species which creates viable and fertile crosses even amongst reef teleosts (Combosch & Vollmer 2015; Suzuki et al. 2016; Harrison et al. 2017). Cryptic speciation appears rife amongst the genera *Acropora* (Ladner 2012; Richards et al. 2016), *Pocillopora* (Souter 2010; Pinzon et al. 2013, cited in Arrigoni et al. 2019; Schmidt-Roach et al. 2013; Gelin et al. 2017), *Seriatopora* (Bongaerts et al. 2010; Warner et al. 2015), and *Stylophora* (Flot et al. 2011; Stefani et al. 2011).

The family Lobophylliidae sustained major taxonomic reshuffling throughout the early to mid-2010s (Arrigoni et al. 2019). The genera *Australomussa* and *Parascolumia* were absorbed by *Lobophyllia* (Arrigoni et al. 2014) and *Sclerophyllia* was resurrected (Arrigoni et al. 2015). *Homophyllia* and *Micromussa* acquired recruits while the new genus *Australophyllia* was positioned within novel clade J, and *Micromussa indiana* and *M. pacifica* were first described (Arrigoni et al. 2016). Nevertheless, sequence analyses of COI, ITS, histone H3 and the observation of 46 corallite and subcorallite morphologies facilitated the revision of the entire family in 2016. However, there was insufficient data to define *Echinophyllia* and *Oxypora* (Huang et al. 2016), while a subsequent morpho-molecular study erected a nascent lobophylliid genus and uncovered *Echinophyllia gallii* and *E. bulbosa* in the Indian Ocean whose bulb-like ornamentation adorns its primary septa (Arrigoni et al. 2016a).

Numerous field samples including one of each of the 54 extant lobophylliid species together with yet to be genotyped *Echinophyllia patula*, *Lobophyllia hataii*, *L. hassi*, and *Oxypora crassispinosa* were collected from the Red Sea, the southern and western Indian Ocean, and the northwestern Gulf of Aden. Concatenations of six molecular markers from their nuclear and mitochondrial genomes were evaluated for single nucleotide substitutions, while 46 skeleto-morphological traits assisted the elucidation of ancestries of the family Lobophylliidae on a comprehensive phylogenetic tree (Fig 10.; Arrigoni et al. 2019).

The study amplified, sequenced, and aligned [1] the barcoding sequences of the mitochondrial cytochrome oxidase subunit I gene (COI); [2] the encoding region of the 12 svedberg (S) mitochondrial ribosomal ribonucleic acid (rRNA) gene; [3] the 3 prime (') end of the adenosine triphosphate (ATP) synthase (ATPase) subunit 6 gene along with the 5' end of the nicotinamide adenine dinucleotide hydrogen (NADH) dehydrogenase subunit 4 gene (ATP6-NAD4); [4] the 3' end of the NADH dehydrogenase subunit 3 gene combined with the 5' end of the NADH dehydrogenase subunit 5 gene (NAD3-NAD5); [5] the histone H3 gene; and [6] the collective sequences of the 3' end of the 18S rRNA gene; the entire internally transcribed spacer 1 gene (ITS1), the 5.8S rDNA-integral ITS2 segment, and the 5' end of the 28S rRNA gene's internally transcribed spacer (ITS; Arrigoni et al. 2019).

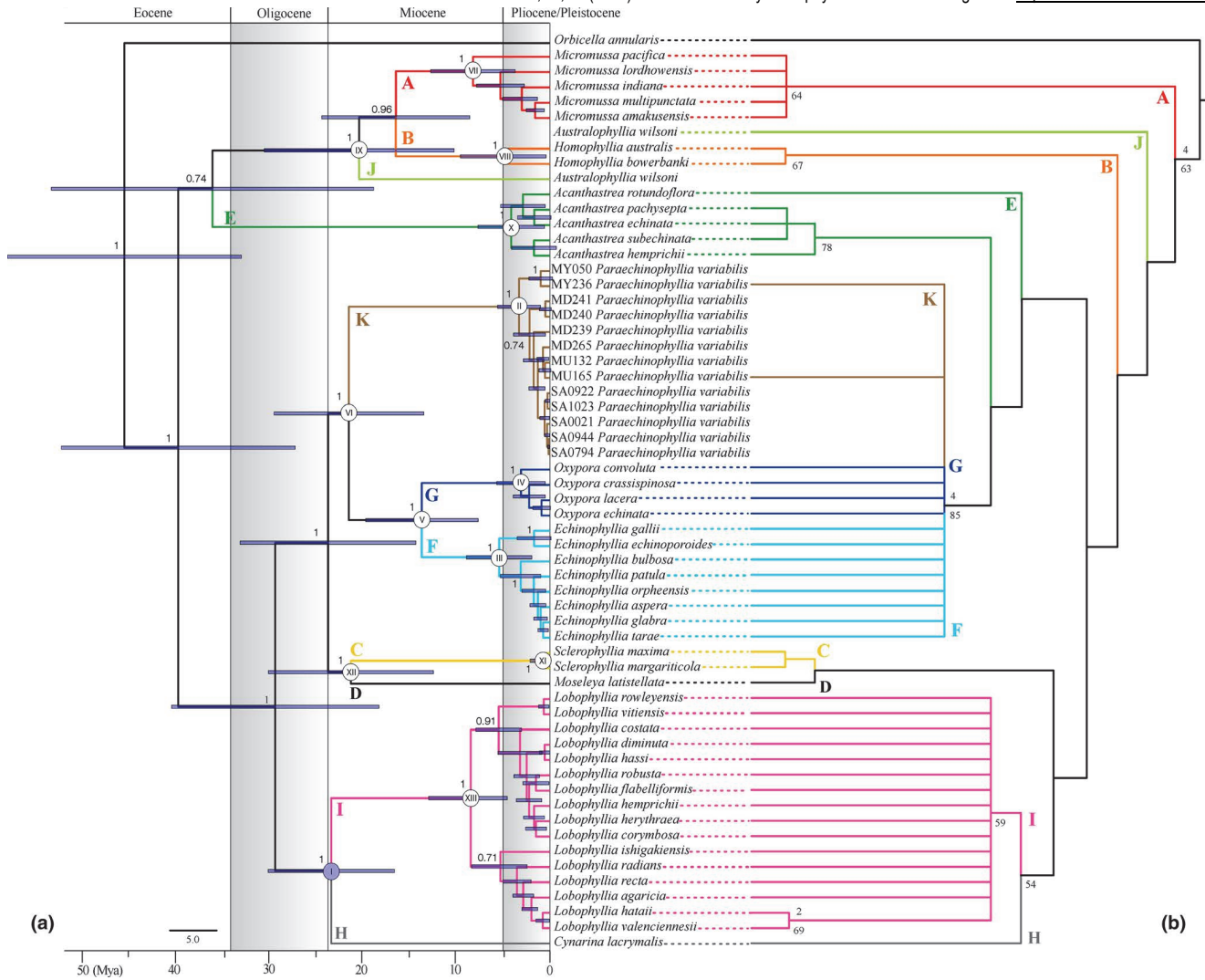


Fig 10. The phylogenetic tree of Arrigoni and allies from 2019 featuring a palaeontological timeline and the definitive clade and species ranks of the family Lobophylliidae like nascent *Paraechinophyllia variabilis* of novel clade K, where “I” encircled by violet represents *Lobophyllia*’s emergence some 19 to 31 MYA. Colours consistent with clades A to J as defined by Arrigoni and allies in 2014(a) and Huang and collaborators in 2016. (a) phylogeny inferred from the analyses of the six concatenated molecular markers and the fossil record; (b) ancestral lineages derived from skeletomorphological studies. Analyses and tree courtesy of Arrigoni et al. 2019 and the Creative Commons Attribution Licence 4.0.

Comparative sequence analyses of the COI, histone H3, ITS1, and ITS2 genes have revealed the evolutionary relationships of Lobophylliidae (Arrigoni et al. 2014a; Arrigoni et al. 2014; Arrigoni et al. 2015; Arrigoni et al. 2016), and the nucleic acid markers ATP6-NAD4 have delineated the species boundaries of the genera *Echinophyllia* and *Oxyphora* (Arrigoni et al. 2016); notwithstanding, this study was the first to phylogenetically compare the sequences of the genes of 12S rRNA and NAD3-NAD5. 207 alignments of the six concatenated molecular biomarkers were combined with those of 123 published sequences (Arrigoni et al. 2019).

20 macromorphological, 13 micromorphological, and 13 microstructural features of *Echinophyllia aspera*, *Oxyphora lacera*, and other tentative species of cf. *Echinophyllia* were examined for the discerning skeletal topographies established by Budd and collaborators in their study of Mussidae published in 2012, and implemented in Huang and colleagues’ revisions of and Diploastraeidae, Merulinidae, and Montastraeidae in 2014, while the same attributes were used in the above and the current study to affirm Lobophylliidae’s canonical taxa in 2016 and 2019 (Arrigoni et al. 2016; Arrigoni et al. 2019). These 46 morphological characters could not at first discern the newly discovered and established cryptic genus *Paraechinophyllia* until the experimenters searched for clade-pervasive simple pure character attributes (sPu) which are not present in other clades (Arrigoni et al. 2019).

Orbicella annularis was used as a phylogenetically corroborating outgroup (Arrigoni et al. 2019) while the genus *Symphyllia* remains a junior synonym of *Lobophyllia* (Huang et al. 2016). The present-day wealth of bioinformatics coupled to the sophistication of statistical and gene sequence analyses account for variables too numerous to include, yet they generate conclusive outcomes with unparalleled likelihoods.

Each molecular marker inferred dissimilar evolutionary trajectories yet consistently ranked species into the same clade, albeit remarkably, 13 samples from putative species of *Echinophyllia* were not retrieved in clade E but were assigned novel *Paraechinophyllia variabilis* and clustered into the new monospecific clade K. However, this clade’s sister taxa were more challenging to delineate insofar as the trees generated from ITS1/2 or histone H3 markers inferred *Moseleya*, whereas those of COI or NAD3-NAD5 endorsed *Australophyllia*, *Homophyllia*, and *Micromussa*. Nevertheless, *Paraechinophyllia* was separated from *Moseleya* and *Homophyllia* by respective pairwise intergenic distances of 2.35 and 4.63 that robustly overlapped with all other lobophylliids

Fig 11. Strains of novel *Paraechinophyllia variabilis* of relatively newly established clade K from the Indian Ocean, the Red Sea, and Yemen, exhibiting extraordinary phenotypic plasticity (Fig 12.). Images courtesy of Arrigoni et al. 2019 and the Creative Commons Attribution Licence 4.0.

(Appendix I). Samples from strains of *Paraechinophyllia variabilis* collected off Mayotte Island were distinct, yet were sisters of those from nearby Madagascar, Yemen, and the Red Sea.

The lineages discerned using a combination of molecular markers and the fossil-record are featured to the left of figure 10. (a). Combined molecular analyses of 21 key nucleotide alignments suggested strains of *P. variabilis* were distinct from the genera *Echinophyllia* and *Oxypora* that emerged three to five MYA, and *Moseleya* and *Sclerophyllia* which is the youngest lobophylliid genus at less than one MY old. Nonetheless, *Lobophyllia* is the most ancient yet barely exceeds eight (Arrigoni et al. 2019).

The morphological reconstruction of figure 10. (b) largely reflects the molecular and fossil ancestries supporting seven out of the 11 clades with at least moderate likelihood for *Micromussa* of clade A, *Homophyllia* of clade B, and *Lobophyllia* of clade I, yet *Paraechinophyllia* of clade K, *Echinophyllia* of F, and clade G's *Oxypora* were of mutual monophyletic descent with 92 percent confidence (Arrigoni et al. 2019).

Acanthastrea rotundiflora diverged before its congeners of clade E which were sister taxa to morphologically alike *Echinophyllia*, *Oxypora*, and *Paraechinophyllia* which were epitomised by extensive coenosteum composed of spinose costae (Nothdurft & Webb 2007), organically unified corallites, a lack of epitheca, and columellae that were equal to or more than $\frac{1}{4}$ of the diameters of their calices. Merely three skeletal features varied amongst clades F, G, and K where calice relief was small (<3 mm) in the former two and medium (3 to 6 mm) in the latter. Trabeculate compact columellae composed of one to three aragonite threads and distinct paliform teeth manifest in *Oxypora*, whereas spongy trabeculate columellae and ill-defined paliform lobes form in *Echinophyllia* and *Paraechinophyllia* (Fig 9.; Arrigoni et al. 2019).

Several previously recognised lobophylliid micro-textures and -structures were observed in *Paraechinophyllia* (Huang et al. 2016) like trabeculate bundles of fibres that form broadening bands of aragonite (Figs 13. & 14.; Frankowiak et al. 2016). Rapid accretion deposits (RADs) are analogous in the skeletal frameworks of *Echinophyllia*, *Oxypora*, and *Paraechinophyllia* which form clustered projections extending into the latero-septal façades of lower cycle septa of consolidated morphotypes, that may reflect septal tooth development, whereas mid-septum waves or straight sections of RADs occur in the primary and secondary cycles of delicate corallites (Fig 13.; Arrigoni et al. 2019).

Echinophyllia aspera, *E. orpheensis*, and *Paraechinophyllia variabilis* are sympatric inasmuch as they are mutually photically, bathymetrically, and reef zone-adapted, while strains of *Oxypora lacera* were absorbed into *Echinophyllia* by virtue of their 44 nucleotide alignments. Even so, *E. lacera* and *P. variabilis* share compact trabeculate columellae consisting of one to three threads. The current study's molecular analyses endorsed the reclassification of *Echinophyllia echinata* to *Oxypora echinata* with the aim of attaining monophyly in clades F and G (Fig 10. Arrigoni et al. 2019).

Visual likeness makes for a poor estimate of speciation insofar as outward transformation is not a prerequisite for the genetic mutations that create new species, and homoplasy whereby unrelated organisms acquire identical features is not uncommon amongst corals. Species cannot interbreed due to geographic separation, physical variances that preclude mating, sperm/egg incompatibility or genotypic disparities that lead to non-productive crosses (Knowlton 1993; Palumbi 1994). Nebulousness pervades the latter two in several classified species including those of corals, whereas simultaneous morphological stability and molecular speciation may be particularly advantageous for extremophiles (Schonrogge et al. 2002, cited in Arrigoni et al. 2019). Moreover, evolution remains driven by ecological niche diversification (Rissler & Apodaca 2007, cited in Arrigoni et al. 2019).

Echinophyllia aspera, *E. glabra*, *E. lacera*, *E. orpheensis*, and *Oxypora crassispinosa* are gonochoric broadcasters (Baird et al.

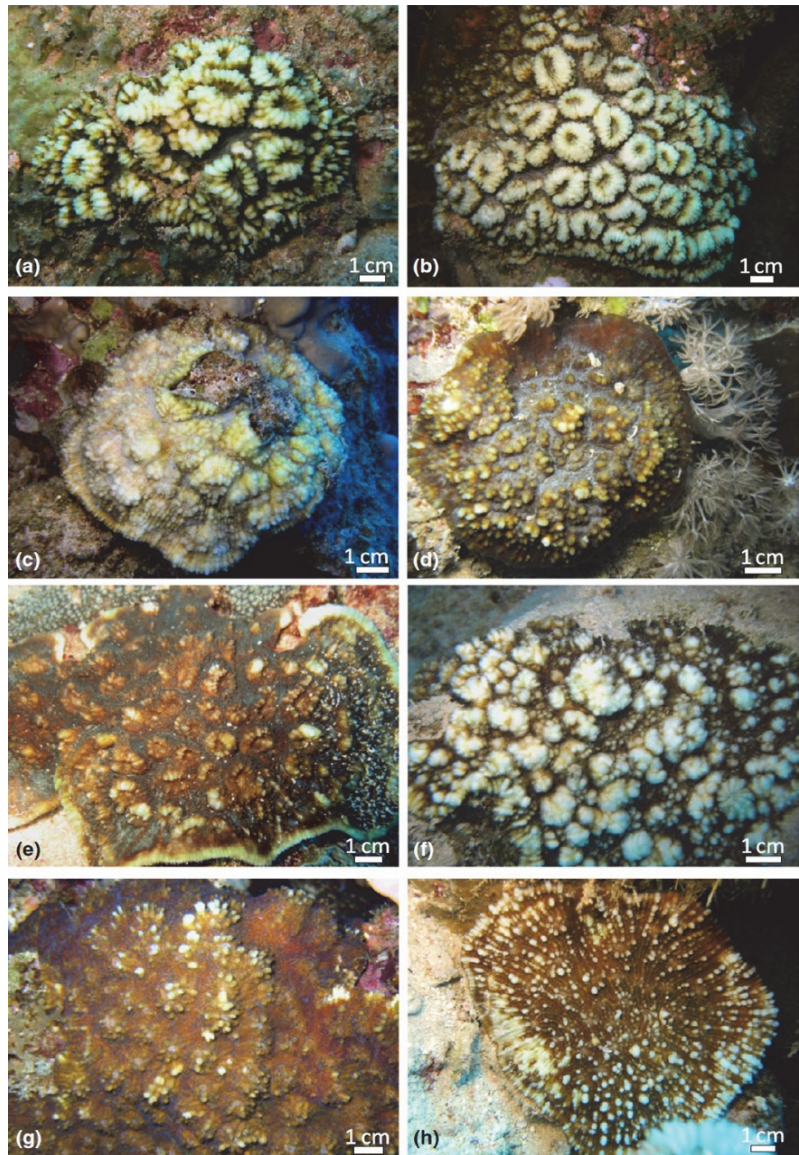


Fig 12. The corallites of various strains of novel *Paraechinophyllia variabilis* of comparatively newly formed clade K from the Indian Ocean, the Red Sea, and Yemen, exemplifying skeletal morphological plasticity. Images courtesy of Arrigoni et al. 2019 and the Creative Commons Attribution Licence 4.0.

2009, cited in Arrigoni et al. 2019; Bouwmeester et al. 2019, cited in Arrigoni et al. 2019), where precise procreative windows (Vize et al. 2005; Levitan et al. 2011) and temporal gamete viability prohibit interspecific hybridisation (Levitan et al. 2011).

Examinations of histological mounts that preserve flesh in a lifelike form remain absent from the coral taxonomist's toolbox, but they have been exploited to phylogenetically rank other members of the phylum Cnidaria (Fautin 2009). Studies of embryogenesis profess that distinct blastula to gastrula metamorphoses appear familiarly and generically discriminating (Okubo 2016), whereas spawning windows have exposed covert species of *Acropora* (Rosser 2015) and *Pocillopora* (Pinzon et al. 2013, cited in Arrigoni et al. 2019; Schmidt-Roach et al. 2013). Furthermore, habitat-attuned interspecific strains and their zooxanthellae are genotypically divergent in the genera *Seriatopora* (Bongaerts et al. 2010; Warner et al. 2015) and *Pocillopora* (Schmidt-Roach et al. 2013).

Their competency at cohabiting alongside their visually indistinguishable peers may have longstanding ecological implications insofar as the phenotypic inertia of cryptic species may spell maladaptation to environmental change (Arrigoni et al. 2019). The numerous niches offered by each reef zone where organisms compete fiercely for space, are hotbeds of natural selection (Bickford et al. 2007), whilst molecular approaches continue to unearth inconspicuous coral taxa (Kitahara et al. 2016, cited in Arrigoni et al. 2019).

The phenotypic commonalities of *Echinophyllia aspera*, *E. orpheensis*, and *Paraechinophyllia variabilis* may be extraordinary synapomorphy, where ancestral traits are retained and shared amongst the descendants of a common ancestor, yet such attributes are often modified, whereas evolutionary stasis is commonplace in organisms that become optimally niche-adapted. The microstructures and biomineralization patterns in some species of *Acropora* have not changed for 48 MY (Stolarski et al. 2016) whilst extinct corals were very different to their modern-day counterparts (Wallace 1999, cited in Arrigoni et al. 2019; Wallace & Rosen 2006; Santodomingo et al. 2015). Strains of *Paraechinophyllia variabilis* from Mayotte Island and Madagascar were more akin to *Echinophyllia orpheensis*, while Gulf of Aden examples looked like *E. aspera*. Nevertheless, those from the Red Sea retain common elements of both, which is redolent of genotypic and ecological impacts, whilst the skeletal accretion patterns of these three species appear to have been conserved (Arrigoni et al. 2019), since they diverged over 20 MYA.

Numerous species of coral appear peculiar to the north and western limits of the Indian Ocean (Obura 2012) which may represent a secondary focus of scleractinian heterogeneity akin to that of the Coral Triangle (Hoeksema 2007, cited in Arrigoni et al. 2019; Huang et al. 2015; Huang et al. 2018), and the northern Mozambique Channel and the Red Sea (Obura 2012; Veron et al. 2015, cited in Arrigoni et al. 2019) where strains of *Paraechinophyllia variabilis* are known to reside (Arrigoni et al. 2019).

Besides ancient plate tectonic-derived geological upheavals like the splitting and coalescence of landmasses and the creation of shallow water ecosystems ripe for coral inhabitation (Arrigoni et al. 2019), volcanic activity solubilises coral-nutrient minerals and trace elements which likely underpinned primordial scleractinian biodiversity like it does today.

The experimenters concluded that a lack of morphologically-discriminating features should not forestall species classification when corroborated by robust molecular analyses (Arrigoni et al. 2019).

That concludes our delve into the taxonomic reshuffling of the family Lobophylliidae. Revisions were required in several other scleractinian families to accomplish monophyly which are discussed next along with other conspicuous examples, while we expand our skillset in this fascinating yet frequently considered "dry" discipline which may at times contradict the most adept at coral identification.

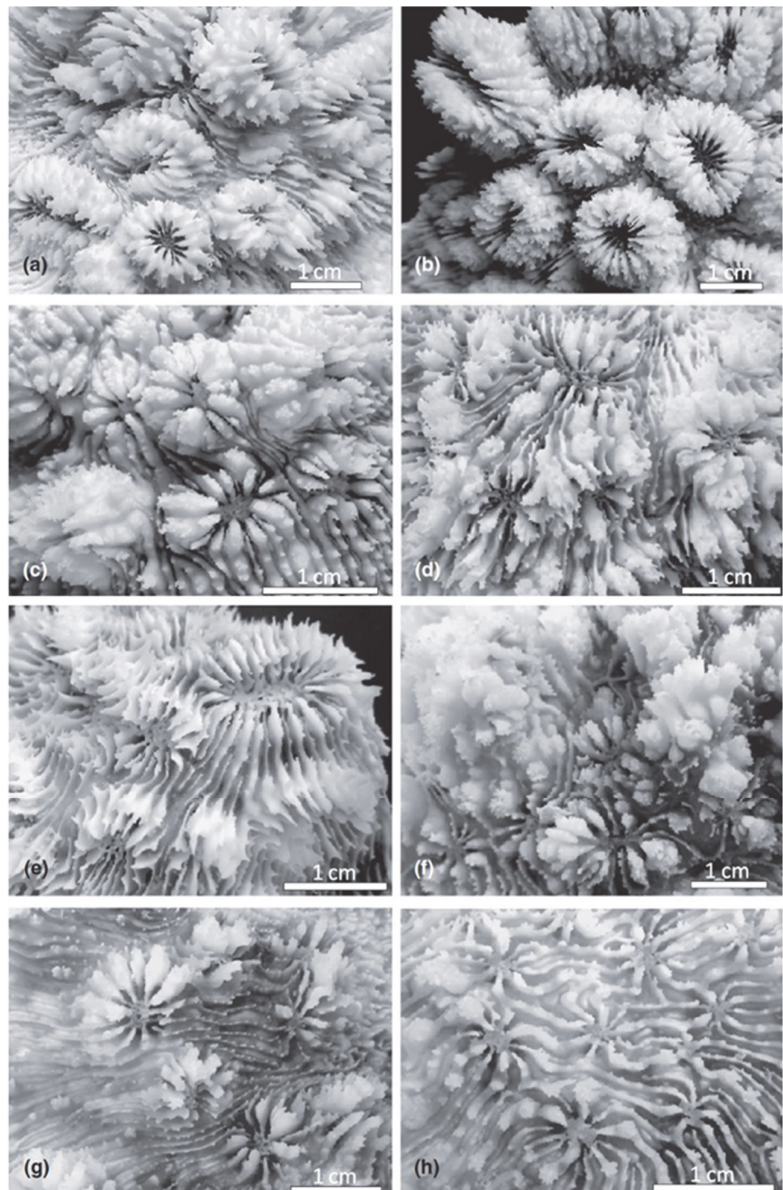




Fig 13. An ultra-high magnification SEM of two centres of rapid skeletal accretion interspersed with organic phases previously referred to and considered trabeculate rods and their associated fibres. Consult figure 2. of Nothdurft and Webb 2007 and Part 1. SEM courtesy of Arrigoni et al. 2019 and the Creative Commons Attribution Licence 4.0.

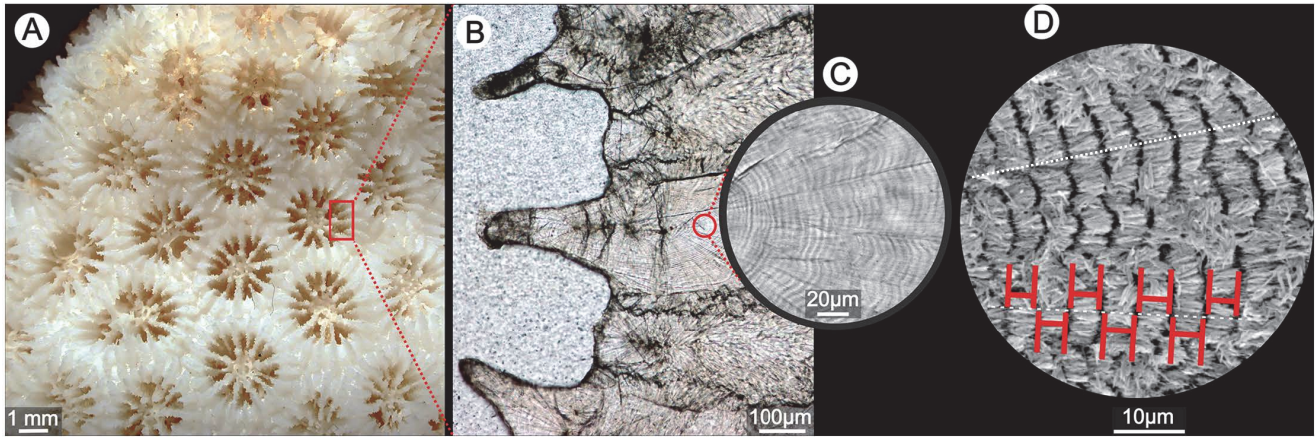


Fig 14. The thickening skeletal deposits of *Goniastrea stelligera*: [A] a corallite from which a thin section was crafted (red box); [B] brightfield micrograph of light and dark deposits; [C] SEM of a fibre (white dotted line) where organic layers are deposited at the beginning and end of each zone (red H). Photography and micrographs courtesy of Frankowiak et al. 2016 and the Creative Commons Attribution Licence.

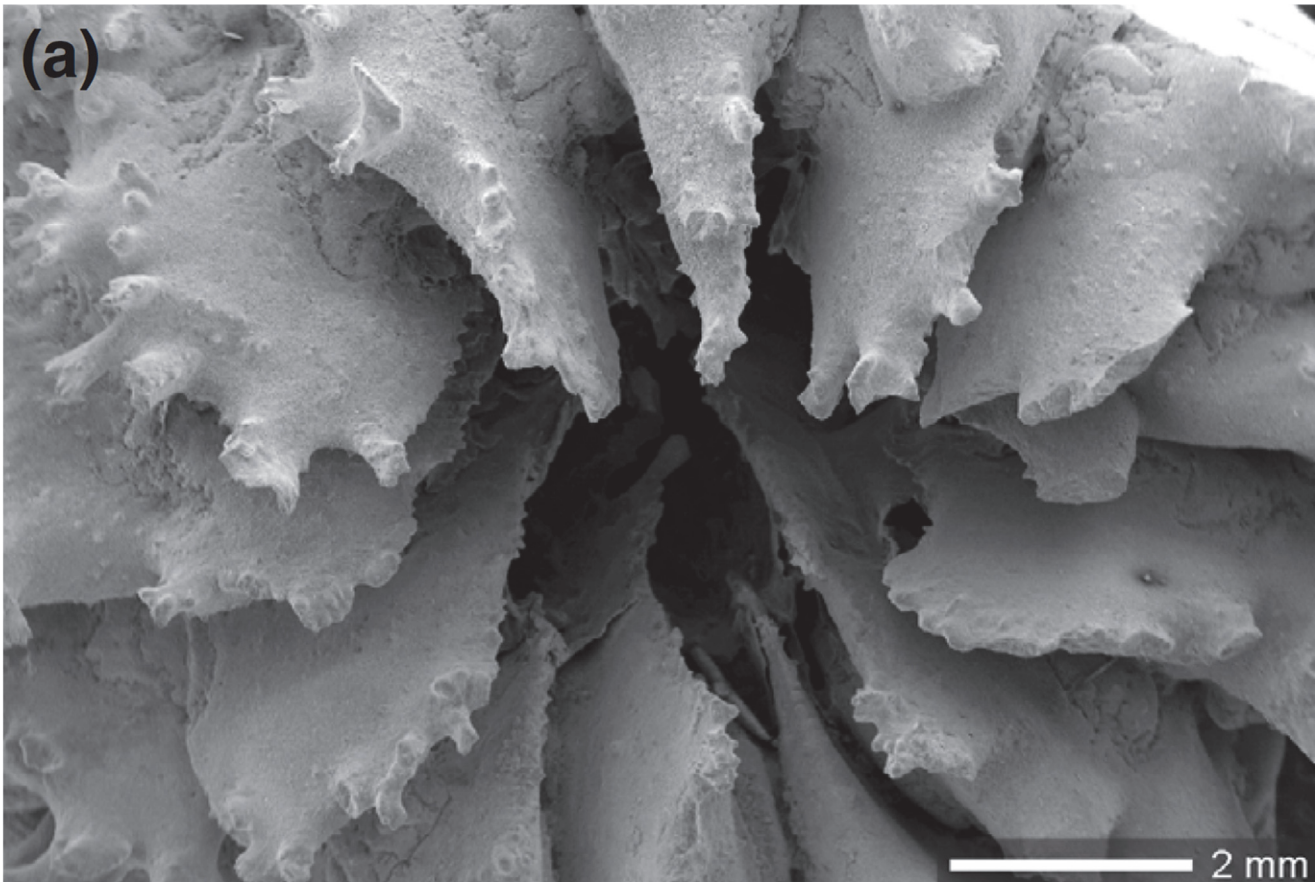


Fig 15. A SEM of a corallite of novel *Paraechinophyllia variabilis*, courtesy of Arrigoni et al. 2019 and the Creative Commons Attribution Licence 4.0.

Aslett 2024

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Appendix I Glossary

Allele refers to different forms of a gene.

Animal Pole is a surface zone of an egg which marks the most mitotically active yolk-diminished region.

Bootstrap replicates are equal-sized multiple sequence aligned fictional substitute nucleic acids with confidences proportional to percentage identity.

Canonical, substantiated, acknowledged.

Cercoid corallites share walls.

Clade describes a monophyletic group of organisms comprising all the descendants from a common ancestor (**Cladistics**).

Coenosteum is the part of the skeleton that adjoins the corallites of colonial species (Fig 0.).

Congeners refers to close relatives (**Congeneric**).

Costa is a radial structure outside the corallite wall which may be autonomous or integral to a costoseptum.

Costoseptum is a fan-shaped radial element that adjoins an outer costa to a conspicuous inner septum unified with the upper

columella.

Cryptic Speciation has occurred when distinct localised species appear identical.

The cells of a **Diploid** organism have a chromosome from each parent ($2n$), whereas the copy number of **Haploid** organisms is $1n$. Eukaryotic DNA is wrapped around histone proteins to prevent tangling, and **Epigenetic Modification** either acetylates or methylates their tails, which either grants or precludes access to the gene which forestalls transcription.

Fenestrate refers to perforations or transparencies.

gen nov. is a newly discovered and named genus.

Haplotype is a conjunction of haploid and genotype that refers to alleles or nucleic acid sequences residing on the same chromosome that were inherited simultaneously from one parent.

Hermatypic and Ahermatypic Corals - the terms hermatypic and ahermatypic have been misused. Irregularities such as sea fans possessing rigid skeletons are constructive, but they may or may not contain "algal" symbionts and do not contribute to reef substratum. Ahermatypes may have large or small polyps and do not contain zooxanthellae. Scleractinia are "true" reef builders but may be azooxanthellate or contain "algal" symbionts. Scleractinia and hermatype are not interchangeable. Hermatypic corals contain zooxanthellae and are constructive. Ahermatypes are azooxanthellate and non-constructive. This clear definition also applies to non-Scleractinia (Schuhmacher & Zibrowius 1985).

Heterotrophs cannot utilise inorganic carbon for growth so they must dine on organic plant- or animal-derived nourishment. Their sources include glucose, yet several microscopic taxa retain the capacity to transform inorganic compounds which are frequently used as substrates for chemical reactions.

Heterozygous refers to different forms of a gene carried by a diploid ($2n$) organism usually from each parent on opposing chromosomes where each one of an individual's $1n$ gametes carry one kind of **Allele**.

Eukaryotic DNA is wrapped around **Histone** proteins to prevent tangling, and **Epigenetic Modification** either acetylates or methylates their tails which either grants or precludes access to the gene which forestalls transcription.

Homoplasmy and **Convergent Evolution** are synonymous insofar as they refer to the development of similar or identical traits in unrelated organisms.

Homozygous refers to the same form of a gene carried by a diploid ($2n$) organism usually from each parent on opposing chromosomes where each one of an individual's $1n$ gametes carry the same kind.

Intergenic Distance refers to the combined regulatory noncoding DNA between a gene and its up- and down-stream neighbours.

Interspecific Hybridisation creates a subpopulation with a distinct genotype.

Introgression facilitates the dissemination of genes between species arising from recurring hybridisation and backcrossing over long periods of time.

Meiocyte is a cell generated by meiosis which is contextually synonymous with **Gamete** within which diploid chromosome copy number is halved (**Haploid**).

Multiseriate describes things that are arranged in a series or row.

Ontogeny/Ontogenesis describes the development of an organism from the moment of fertilisation to a mature adult.

Ontology is used contextually to describe the intra- and extra-cellular metabolic pathways associated with an organism's day-to-day housekeeping, homeostatic, and reproductive processes.

Paliform septal Lobes are typically hemispherical **Exsert** upper-margin protuberances that may in some cases crown the upper columella. See figure 9. H.

Paralogues are two copies derived from a single ancestral gene residing at two distal loci in the same genome.

Paraphyly refers to a group of organisms that evolved from a common ancestor that lacks all descendants.

Phenetics, Numerical Taxonomy, or Taximetrics classifies organisms according to their physical features irrespective of their putative evolutionary trajectories.

Phenotypic Plasticity foregoes the accepted developmental and evolutionary paradigms and expedites swift morphological responses to environmental change.

Phenotypic traits are an organism's observable characteristics which include how it interacts with its environment, that originate from its epigenotype and genotype.

Phylogenetic Tree "is a graphic representation of the interrelations and evolutionary history of a group of organisms, indicating the relative order of successive divisions of the line of descent, coincident with speciation events" (Wallace et al. 1996).

Synonymous **Plesiomorphy** and **Symplesiomorphy** refer to the sharing of an inherited attribute by all members of a clade which does not differentiate that clade from others.

Plocoid corallites do not share walls which are separated by conspicuous coenosteum.

Scale Bars of Phylogenetic Trees refer to relative evolutionary distance expressed as the developmental/mutagenic substitutions of nucleotides.

sp. nov. is a newly discovered and named species.

Svedberg (S) is a sedimentation coefficient that relates to particle-size and settlement-rapidity during centrifugation. 1 svedberg is equal to 10^{-13} seconds (100 femtoseconds) which is a non-SI unit used to describe the size of nucleic acids or proteins (Stryer 1995).

Symbiosis is the coexistence of two or more closely associated organisms that acquire mutual benefit.

Sympatric Speciation is the evolution of a new species from a single ancestor inhabiting the same region.

Synapomorphies are modified forms of an ancestral attribute that are exclusively shared amongst all descendants.

Synapomorphy refers to a phylogenetically-discriminating empirical attribute that differentiates a monophyletic clade (Hennig 1957, cited in Arrigoni et al. 2019).

Synapticulae are perpendicularly coordinated corallite wall-forming rods that interweave the postero-septal margin.

Syntenic means “threaded together” and refers to several intrachromosomal genes traced using somatic cell hybridisation (Russell 1998).

Trabeculae were thought septum-forming discrete vertical rods associated with radially arranged fibres while they are now known to be smooth centres of rapid aragonite deposition that craft numerous skeletal features (Nothdurft & Webb 2007).

The terms **Zooxanthellate** and **Azooxanthellate** refer to organisms with and without **Symbiotic** “algal”-partners.

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A marine aquarium, reef tank, and saltwater fish system guide, handcrafted by a coral reef expert.