Acanthastrea species

2. Coral Taxonomy: Early Disentanglements

Chris Aslett

The first editorial armed the reader with the insight to fully comprehend these early attempts to extricate the ancestries of reef-forming corals, whilst unfamiliar terms are clarified in Appendix I. Shortly after coral taxonomists began to exploit molecular techniques, it became evident a new set of morphological traits were necessary to redress the polyphyly of several scleractinian suborders, families, and genera, like those that were present or could be identified in both the fossil record and in present-day coralla. Remarkably, the canonical suborders Astrocoeniina, Caryophylliina, Dendrophylliina, Fungiina, Meandriina, and Poritiina included members from both Robusta and Complexa clades (Budd et al. 2012) that diverged over two hundred million years ago (MYA; Romano & Palumbi 1996; Fukami et al. 2008; Budd et al. 2010; Kitahara et al. 2010; Kayal et al. 2013; Okubo et al. 2013) where limited molecular analyses suggested that the former radiated from within the latter's family Agariciidae (Fukami et al. 2008; Kitahara et al. 2010). Surprising still, was the discovery of a more ancient Basal clade comprising mostly deepwater azooxanthellates (Kitahara et al. 2010), whose microbial consortium may include nominal "algal" partners (Gong et al. 2023). Multinational teams of taxonomists were thus motivated to make vital inroads into this seemingly insurmountable muddle (Kitahara et al. 2012).

The exceptionally diverse scleractinian family Caryophylliidae has more than 300 extant species (Cairns 2009) with representatives extending from the tropics to the poles (Roberts et al. 2003). Some are intertidal like *Paracyathus darwinensis* whilst others like *Deltocyathus parvulus* may be found at 5,000 m. Ostensibly, the vast majority are azooxanthellates residing at aphotic 200 m, yet several are euphotic hermatypes of which some form stable aposymbiotic morphs (Cairns et al. 1999). *Caryophyllia aspera* is the smallest solitary member with a less than 5-mm calice, whereas some colonies like those of *Lophelia pertusa* may be several metres across. Mitochondrial (Romano & Cairns 2000; Le Goff-Vitry et al. 2004; Kitahara et al. 2010a; Stolarski et al. 2011) and nuclear (Cuif et al. 2003; Barbeitos et al. 2010; Stolarski et al. 2011; Huang 2012, cited in Kitahara et al. 2012) molecular analyses had highlighted significant polyphyly with eight clusters occurring within both Complexa and Robusta with two encircling the genera *Caryophyllia* (Kitahara et al. 2010a) and *Dactylotrochus* (Kitahara et al. 2012). The latter is exceedingly speciose comprising 25 extant obligate zooplanktivorous azooxanthellates that dwell from 44 to 5,080 m whose skeletal features had been recently scrutinised (Kitahara & Cairns 2009), whilst preliminary molecular analyses suggested its members grouped into a convincing monophyletic clade alongside its sister taxon *Anthemiphyllia patera* subspecies *costata* that were the first to diverge from the base of Robusta (Kitahara et al. 2012). Nevertheless, earlier contrasting research suggested that Robusta diverged from within Agariciidae of Complexa (Fukami et al. 2008; Kitahara et al. 2010b) instead of a mutual split. All the same, such artefactual separation is evident when constructing ancestries discerned with mitochondrial cytochrome oxidase 1 (CO1; Kitahara et al 2012). *Dactylotrochus magnificus* was exceptional insofar as it nested in the Complexa family Turbinoliidae (Stolarski et al. 2011). The microstructures of this species are analogous to those of this study's newly erected family Deltocyathiidae; notwithstanding, hitherto and supplementary molecular analyses firmly and consistently positioned this species in Turbinoliidae so it remained an enigma, inasmuch as its patterns of skeletal deposition conflicted with its family's (Figs 1. & 2.; Kitahara et al. 2012).

Part sequences of mitochondrial 16 svedberg (S) rDNA and CO1 together with nuclear 28S rDNA loci were amplified using the polymerase chain reaction (PCR) in accordance with the protocol outlined and published by Stolarski and allies in 2011. Sequence-alignment of concatenated CO1 and 28S rDNA was meant to confer greater resolution when screening a vast assortment of

Keywords: clade; Complexa; coral; Corallimorpharia; Basal; macromorphology; micromorphology; microstructure; phylogenetic tree; Robusta; Scleractinia.

Scleractinia including deep-dwellers and hermatypes. Yet unconventionally, a phylogenetic reconstruction was discerned by segments of 16S rDNA and 28S rDNA (Kitahara et al 2012).

The sequences for *Deltocyathus* were aligned with libraries of scleractinian annotated data sets where those of *D. inusitatus*, *D. magnificus*, *D. sarsi*, and *D. suluensis* were delineated using combined 28S rDNA and CO1, although divergent DNA preservation likely precluded dual analyses for *D. corrugatus* and *D. vaughani* or *D. ornatus* and *D. rotulus* whose sequences only aligned for merely the former or latter respectively. Furthermore, part mitochondrial 16S rDNA would only amplify for *D. magnificus* which is genotypically distinct from its phenotypic counterparts whose genotypes were unrelated to Complexa, where most had stronger affinity with Basal. Their early divergence from Robusta likely reflects this kinship while CO1 analyses clustered all *Deltocyathus* bar *D. magnificus* within Robusta, whereas 28S rDNA clustered them in Basal (Fig 1.). However, amplicons of Basal-genera excluding 28S rDNA, positioned the majority of *Deltocyathus* within Robusta, whilst the researchers remarked that long-branch attraction and nucleotide compositional bias occasionally generates analytical artefacts. Nevertheless, such ambiguity warranted further investigation (Kitahara et al. 2012).

CO1 and 28S rDNA sequence concatenations were aligned with other scleractinian families to yield a 1,215-base pair (bp) matrix covering 22 and 21 zoo- and presumed a-zooxanthellate species, 35 genera, and 15 families. Both molecular and morphological data supported the Complexa families Dendrophylliidae, Flabellidae, Oculinidae, Poritidae, Siderastreidae, and Turbinoliidae and "robust" corals of Anthemiphyllidae, Caryophylliidae, Faviidae, Meandrinidae, Mussidae, Oculinidae, Pectiniidae, Pocilloporidae, and Stenocyathidae (Kitahara et al. 2012).

With the exception of *D. helianthus*, the remaining documented 24 species of *Deltocyathus* are solitary with a discoidal to patellate corallum while the former is unattached which likely settles and develops on mud or fine sand (Appendix I). Most have enlarged costae adorning their calice circumference while their spines are sometimes extraordinarily prominent as is the case for *D. corrugatus* where six to 12 extend beyond the calice periphery. These and their conical or sometimes slightly concave bases lend orientative inertia in surge exposed environments. Stabilising trilateral or rectangular lancets project beyond the calice wall when spines are absent, like they do in *D. rotulus*, whilst the septa of mature *Deltocyathus* are frequently arranged in cycles of four or five totalling 48 or 96. Primary and occasionally secondary are upper columella-adjoining costosepta, whereas S4 and S5 are "free" and lacerated with their lower axial edge fused with their flanking septa. Septal granules are perpendicularly arranged in rows on the upper septal edge, while pali are pillar-like structures composed of centres of rapid accretion (trabeculae; Benzoni et al 2011) that are united with the axial edges of each septum by a deep and narrow notch except for those of the last cycle which epitomise *Deltocyathus* and distinguish it from other caryophylliid genera. Their spongy (papillose) elliptical columellae remain composed of few regularly arranged rods, while pali remain adjoined to all septa in *D. vaughani* (Kitahara et al. 2012).

Table 1. Presenting the species that featured in the phylogenetic analyses of Kitahara and allies from 2012 whose familiar rank was uncertain. Adapted from Kitahara et al. 2012.

Table 1. Family	Genus/Species
Agariciidae	*Pachyseris speciosa*
	Echinopora lamellosa
	Coeloseris species
Faviidae	*Favia fragum*
	Favia stelligera
Merulinidae	*Merulina scabricula*
Mussidae	*Cynarina lacrymalis*
	Cynarina species
	Mussa angulosa
	Mussismilia braziliensis
Oculinidae	*Galaxea fascicularis*
	Madrepora oculata
Pectiniidae	*Echinophyllia aspera*
Siderastreidae	*Psammocora stellata*

Although septal façades are swathed in rows of pointed granulations that sometimes fuse and form ridges at right-angles to the septal plane, most structures are smooth in species of *Deltocyathus* at nominal magnification. Ultra magnification reveals that all surfaces are made up of disorganised crystalline assemblages which are less dense on the apices of septal granules. Patterns of rapid accretion deposits (RADs) and thickening deposits (TDs) are now a common phylogenetically discerning microstructural character, yet these taxonomic approaches were barely established at this time. RADs form a framework of conspicuous concentric centres enriched in and interspersed with organic components which underly rapid accretion fronts that are widened and consolidated by weakly-organic fibrous layers of TDs (Fig 2.). The examined corallites of *Deltocyathus* had septothecal walls formed from the fusion of their posterioseptal margins. Identification of this kind of wall is made by examining mid-septal RADs sandwiched by fibrous bundles of TDs in ultra-thin etched and polished transverse sections from the periphery of a solitary corallum. Nevertheless, such architecture is an ontogenic biomarker insofar as marginotheca develop into trabeculotheca which become septotheca in adults (Stolarski 1995). RADs flanked by TDs manifest as discrete rows of darkened aligned bars in ultra-thin longitudinal septal sections consistent with the original observations of trabeculae reported by Wells in 1956.

The families of most azooxanthellate Scleractinia that were phylogenetically ranked using traditional macromorphology are monophyletic (Stolarski et al. 2011) apart from Caryophylliidae which is the second most speciose. Sequence analyses of this group's 12S rDNA (Barbeitos et al. 2010), 16S rDNA (Romano & Cairns 2000; Le Goff-Vitry et al. 2004), CO1 (Kitahara et al. 2010b), and

Table 2. Featuring historic classifications and those of Budd and allies from 2012 where blocks of colour indicate closely related genera, where the most recent data excludes poorly defined (*incertae sedis*) *Leptastrea* and *Oulastrea* of clade XI, *Cladocora* and *Solenastrea* of clade XIII, and *Blastomussa*, *Parasimplastrea*, and *Plesiastrea* of clade XIV. The findings of Wells from 1956 and Veron's from 2000 as cited in table 2. of Budd et al. 2012 and adapted from Budd et al. 2012.

Table 2. Research		
Well 1956	Veron 2000	Budd et al. 2012
Family Mussidae	**Family Mussidae**	**Family Mussidae**
		Subfamily Mussinae
Mussa [=*Scolmia*]	*Mussa*	*Mussa*
Isophyllia	*Isophyllia* [=*Isophyllastrea*]	*Isophyllia* [=*Isophyllastrea*]
Isophyllastrea	*Mycetophyllia*	*Mycetophyllia*
Mycetophyllia	*Mussismilia*	excusively Atalntic *Scolymia*
Mussismilia	*Lobophyllia*	
Lobophyllia	*Acanthastrea*	**Subfamily Faviinae**
Acanthastrea	*Symphyllia*	excusively Atalntic *Favia*
Symphyllia	*Australomussa*	*Colpophyllia*
Cynarina	*Micromussa*	*Diploria*
Homophyllia	*Cynarina*	**"New"** *Pseudodiploria*
Parascolymia	*Scolymia* [=*Homophyllia* & *Parascolymia*]	Manicina
Blastomussa	Genus Blastomussa	*Mussismilia*
	Genus Indophyllia	
Family Faviidae		**"New" Family Lobophylliidae**
Subfamily Faviinae	**Family Faviidae**	**Clade XIX**
Favia	*Favia*	*Lobophyllia*
Colpophyllia	*Colpophyllia*	*Acanthastrea*
Diploria	*Diploria*	*Symphyllia*
Manicina	*Manicina*	*Australomussa*
Barabattoia	*Barabattoia* [=*Bikiniastrea*]	*Micromussa*
Bikiniastrea	*Caulastrea*	*Cynarina*
Caulastrea	*Favites*	*Homophyllia* includes *Scolymia* from Indo-Pacific
Favites	*Goniastrea*	*Parascolymia* includes *Scolymia* from Indo-Pacific
Goniastrea	*Leptoria*	*Oxypora*
Leptoria	*Oulophyllia*	*Echinophyllia*
Oulophyllia	*Platygyra*	*Echinomorpha*
Platygyra	*Australogyra*	*Moseleya*
Hydnophora	*Erythrastrea*	
Plesiastrea	*Montastrea*	**Monospecific Family Montastraeidae**
	Diploastrea	**Clade XVI**
Subfamily Montastreinae	*Cyphastrea*	*Montastraea cavernosa*
Montastrea	*Echinopora*	
Diploastrea	*Cladocora*	**Family Diploastreidae (clade XV)**
Cyphastrea	*Solenastrea*	*Diploastrea*
Echinopora	*Leptastrea*	
Cladocora	*Oulastrea*	**Family Merulinidae (clade XVII)**
Solenastrea	*Plesiastrea*	*Merulina*
Leptastrea	*Parasimplastrea*	*Boninastrea*
Oulastrea	*Moseleya*	*Paraclavarina*
		Scapophyllia
Subfamily Trachyphylliinae	**Family Trachyphylliidae**	*Hydnophora*
Indophyllia	Trachyphyllia	*Barabattoia*
Trachyphyllia	Pectiniidae	*Caulastraea*
Moseleya	Pectinia	*Favites*
	Mycedium	*Goniastrea*
Family Pectiniidae	Oxypora	*Leptoria*
Pectinia	Echinophyllia	*Oulophyllia*
Mycedium	Echinomorpha	*Platygyra*
Oxypora		*Australogyra*
Echinophyllia	**Family Merulinidae**	*Erythrastrea*
	Merulina	*Cyphastrea*
Family Merulinidae	*Boninastrea*	*Echinopora*
Merulina	*Paraclavarina*	*Dipsastraea* includes *Favia* from Indo-Pacific
Boninastraea	*Scapophyllia*	*Phymastrea* includes *Montastraea* from Indo-Pacific
Clavarina	*Hydnophora*	*Orbicella*
Scapophyllia		*Montastraea annularis*
	Family Oculinidae	*Trachyphyllia*
Family Oculinidae	*Oculina*	*Pectinia*
Galaxea	*Schizoculina*	*Mycedium*
Simplastrea	*Galaxea*	
	Simplastrea	**Family Meandrinidae (clade XII)**
Family Meandrinidae		*Meandrina*
Meandrina	**Family Meandrinidae**	*Dichocoenia*
Dichocoenia	*Meandrina* [=*Goreaugyra*]	*Dendrogyra*
Dendrogyra	*Dichocoenia*	*Eusmilia*
Ctenella	*Dendrogyra*	
	Ctenella	**Family Euphylliidae (clade V)**
Family Caryophylliidae	*Eusmilia*	*Ctenella*
Eusmilia	*Gyrosmilia*	*Gyrosmilia*
Gyrosmilia	*Montigyra*	*Montigyra*
Montigyra		*Galaxea*
		Simplastrea

28S rDNA (Stolarski et al. 2011) revealed significant polyphyly that advocated a taxonomic review of several of its 300 extant species. Solitary present-day azooxanthellate lineages such as species of *Deltocyathus* are interesting insofar as they may be analogues of ancient solitary zooplanktonic-dependent stony corals that evolved into today's reef-forming hermatypes (Kitahara et al. 2012). Squires identified the most ancient fossil of this genus from the Upper Cretaceous which was published in 1958; however, its members appear to have been abundant throughout the Cenozoic: Palaeocene (Durham 1943) and Eocene (Wells 1976), while phenotypically alike colonies were established in the Middle Jurassic (Bajocian; Mariotti 2003). This earlier than previously suggested fossil record is thus congruent with the tree of Kitahara and collaborators from 2012 (Fig 1.). Nevertheless, the affinity of *D. magnificus* with "complex" turbinoliid corals such as *Tropidocyathus lessoni* and *Cyathotrochus pileus* was borne out by its longer 16S rDNA segment and the base compositions of its CO1 and 28S rDNA amplicons, that are enriched in cytosine and diminished in thymine. The skeletons of *D. magnificus* are indistinguishable from other members of this genus at all levels of magnification and sample preparation; however, this species is unique insofar as its corallum is entirely enveloped including its edges in soft tissue which is common in Turbinoliidae, but not in its congeners whose polyps barely extend beyond their calice boundaries. It would represent an extraordinary example of micromorphological and microstructural convergence if this coral's

preliminary rank is confirmed by other means. *D. magnificus* was thus ranked along with other members of its genus in the new family Deltocyathiidae until corroborating analyses position this species within Turbinoliidae. Nonetheless, the study's morphological findings were commensurate with historic, insofar as the new family's species type remains *Turbinolia italica* Michelotti 1838 (Kitahara et al. 2012).

Budd and collaborators embarked on an ambitious journey to define an unequivocal integrated morpho-molecular system to delineate the eight Robusta extant families and their genera conventionally ranked in the suborders Faviina and Meandriina. Initial analyses of mitochondrial genome encoded cytochrome oxidase b (cyt *b*) and cytochrome oxidase I (COI), and nuclear chromosomal β-tubulin and rDNA genes from six of these families highlighted their polyphyly, where Oculinidae comprised mostly azooxanthellates while Faviidae, Meandrinidae, Merulinidae, Mussidae, and Pectiniidae were hermatypic. Contrasting molecular studies discovered that Rhizangiidae were close relatives of polyphyletic Anthemiphylliidae and Oculinidae which radiated from the base of Robusta proximal to Pocilloporidae but were distantly related to Faviina (Kitahara et al. 2010; Budd et al. 2012) and that most members of the comparatively recently erected clades XII, XIII, and XXI were constrained to the Atlantic and adjacent basins (Fukami et al. 2008). Furthermore, Fukami and allies emphasised polyphyly in the genera *Favia*, *Montastraea*, and *Scolymia* in 2004 and 2008 while the leading monograph of Budd and colleagues focussed on delineating the ancestries of the Atlantic and Indo-Pacific families Faviidae and Mussidae of clade XXI (Budd et al. 2012).

Molecular analyses contrasted with conventional morphological data insofar as distinct Atlantic and Indo-Pacific species appeared to be visually indistinguishable (homoplastic) where the Atlantic genera *Favia* (Faviidae) and *Scolymia* (Mussidae) are more closely related to one another than they are to their Indo-Pacific congeners. Clade XXI repudiates the Cenozoic deep diversification and the close relation of its Atlantic and Indo-Pacific affiliates (Veron 1995, cited in Budd et al. 2012; Paulay 1997; Veron 2000, cited in Budd et al. 2012) and is thus of morphological and geographic interest (Budd et al. 2012).

Taxonomists commenced to place a greater emphasis on micromorphological and microstructural analyses at this time (Budd & Stolarski 2009; Budd & Stolarski 2011). The former relies upon scanning electron micrographs (SEMs) to examine the shape of septal teeth and their granulation, whereas the latter's transverse or longitudinal SEMs of formic acid-etched and polished sections highlight disparities in the centres of skeletal deposition and their fibres (Stolarski 2003). Molecular analyses lend greater support for the basal nodes of ancestral trees whereas morphological studies corroborate likelihoods at the tips (Budd et al. 2010; Kitahara et al. 2012).

Budd and collaborators formulated a morphological character matrix combining traditional macromorphological features with contemporary micromorphological and microstructural attributes to test their phylogenetic significance against the 67 species ranked in clades XV to XXI by Fukami and allies in 2008. Their aim was to recover the familiar analogous clades XVII, XIX, and XXI within their newly devised framework (Budd et al. 2012).

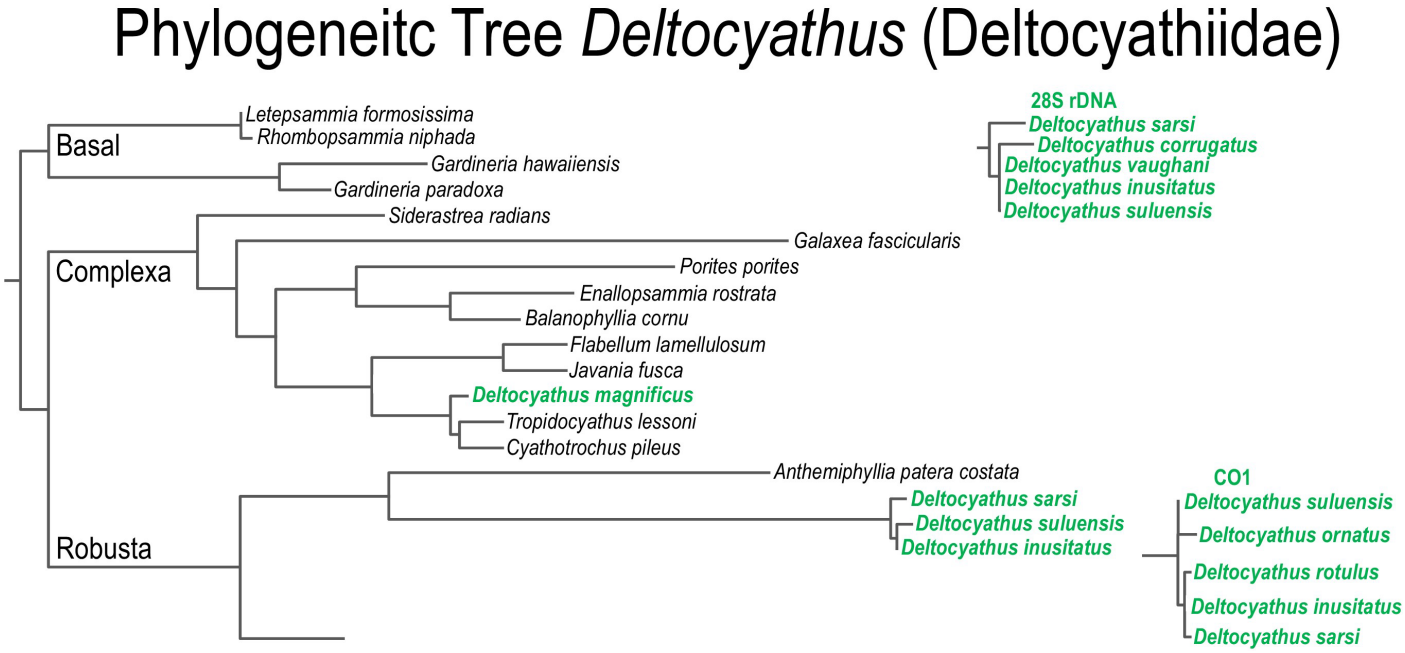


Fig 1. A part representation of the combined molecular tree of Kitahara and allies from 2012 featuring "robust" species of ***Deltocyathus*** of the comparatively newly erected family Deltocyathiidae illustrating the Basal, Complexa, and Robusta divergences as resolved in this study, and atypical ***Deltocyathus magnificus*** of the Complexa family Turbinoliidae. Of note are the clade cluster inconsistencies discerned by comparing sequences from the CO1 or 28S rDNA genes. Adapted from data presented by Kitahara et al. in 2012.

Notwithstanding the primary focus of their initial monograph to revise Mussidae of clade XXI, the experimenters also evaluated clades XV to XX to an end of exposing phylogenetically discriminating synapomorphies, skeletal features, and accretions. The study appraised numerous characterised and established species of faviid and mussid from distinct Atlantic and Indo-Pacific lineages together with an assortment of Merulinidae, Pectiniidae, and Trachyphylliidae (Budd et al. 2012).

38 of the macromorphological skeletal features of 295 specimens were analysed like their intracorallum corallite configurations and intra- and extra-calicular budding, calice size and shape, septal development including cycle and spacing, columellar lobes, wall type, endo- and exo-theca, and coenosteum. Consult figures 20. and 21. of 1. Coral Taxonomy: An Introduction.

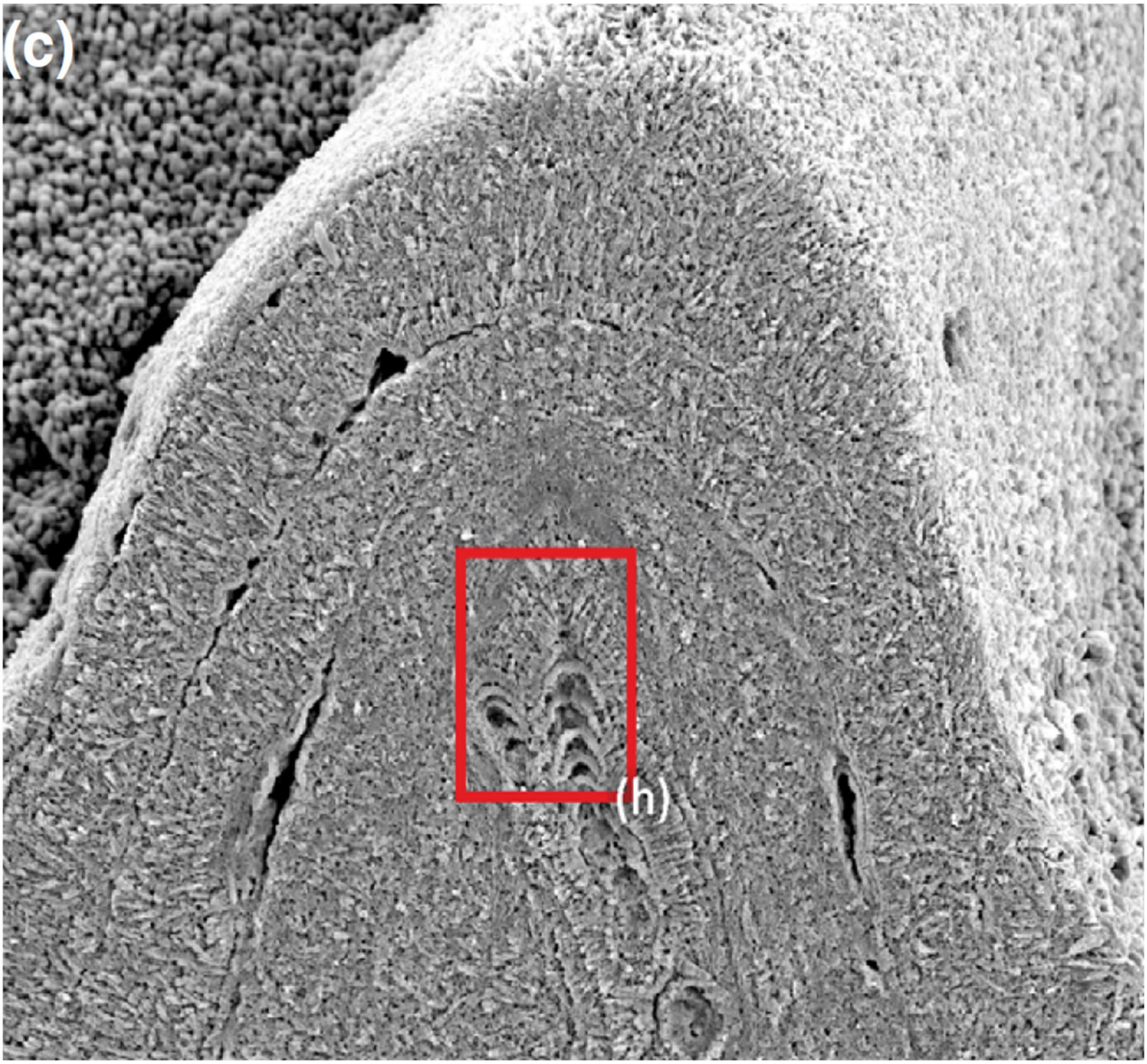


Fig 2. [c] a cross-sectional scanning electron micrograph (SEM) of a septum illustrating layered thickening deposits and concentric centres of rapid accretion interspersed with darker organic phases (h) previously considered trabeculate rods. Equivalent centres form a rapid accretion front (RAF) just beneath the upper surface of an actively growing septum. SEM courtesy of Arrigoni et al. 2019 and the Creative Commons Attribution Licence 4.0.

Corals whose calices do not bud, manifest as solitary corallites whereas a corallum with a prominent central surrounded by at least three smaller is indicative of circumoral budding. Intracalicular budding may result in a series of valley constrained centres with or without walls which are known as organically united. Rows of wall-enclosed corallites may be singular (uniseriate) or multiple (multiseriate) which may meander (meandroid). Separated valleys are flabelloid whereas walls may be single or double (Budd et al. 2012).

Coenosteum is the corallite-adjoining calciferous material which may be composed of radially arranged vertical dividing slabs called costae (costate) that may have spines (spinose). It may also be fashioned from exothecal dissepiment vesicles or unstructured and compact. Corallites may be juxtaposed which lack coenosteum (cercoid) or their coenosteum can range from nominal to extensive (plocoid). Corallites may also be separated spatially to form autonomous branches (phaceloid; Budd et al. 2012).

Calices are measured across their centre to the inner edge of opposing walls while calice height measures the vertical depth of each calice including the septal margin and colline (Appendix I.; Budd et al. 2012). See Part I.

Septa are vertically radiating corallite partitions that are typically arranged in cycles of six. Six stout wall-integral columella-adjoining septa occur in the first and second cycles, with 12 in the third, and 24 in the fourth…and so on (6/6/12/24). Consult figure 21. of Part I. Tertiary cycle septa may or may not reach the centre, and quaternary and above have typically unadjoined inner extremities which are termed “free” septa. Another scoreable septal attribute enumerates how many occur every 5 mm of corallite circumference (Budd et al. 2012).

Costae tend to be septa-contiguous vertical and radially symmetrical extensions that adorn the exterior of the corallite wall that may converge with their neighbours, whereas costal confluence cannot occur in phaceloid or solitary corallites (Budd et al. 2012).

The columella is an axial vertical column that descends into the corallite while its upper surface may be formed from interwoven trabeculate threads that emanate from the ends of lower cycle septa, or it may be laminar which manifests as a centre-unifying fenestrate (perforated) plate. Compact columellae are composed of few trabecular threads whereas spongy are formed from more than three. The columellae of serial corallites may be continuous which are interlaced with trabeculate fibres, or they may be discontinuous and linked by septal lamellar processes (Budd et al. 2012).

Tabular endotheca are horizontal wall-to-wall dissepiment plates that divide the lower cylindrical corallite bore, while small curved and overlapping dissepiments form vesicular endotheca, whereas exotheca is a corallite-wall enveloping sheath (Budd et al. 2012).

Paliform lobes are enlarged rounded septal teeth that vary in height, number, and thickness, whereas mid-septal lobes are formed by multiple axes of rapid accretion (Budd et al. 2012). See figure 9. of Part 3.

3D micromorphological analyses focus on the costoseptal teeth that adorn the growing septal margins and surround the columella, and their lateral granulation that reflects their underlying aragonite deposition. Wells's conception of septal construction from 1956 documented vertical trabeculate rods that were centres of accretion with radially aligned aragonite fibres, which are a series of single threads in simple trabeculate fans and multiple bundles in compound, where each septum can be formed from one or several fans. Tooth size, shape, spacing, and their endogenous calcification were familiarly discerning within the suborder Faviina. Faviidae were epitomised by septa formed from one or two simple trabeculate fans with regular teeth, whereas those of Mussidae developed from numerous large simple fans with lobular dentation. Merulinidae had septa formed from one compound trabeculate fan which commenced with regular teeth and became scattered, spiny, and irregular, whilst Pectiniidae were composed of one compound fan with regular or almost indiscernible teeth (Wells 1956, cited in Budd et al. 2012). The modern view is that dentations are formed from multiple configurations of calcification centres with thickened fibrous concretions (Cuif et al. 1998; Cuif & Perrin 1999; Cuif et al. 2003; Stolarski 2003; Cuif & Dauphin 2005). The shape of mid-septal tooth bases and their tips are scored separately (Budd & Stolarski 2009; Budd & Stolarski 2011) where bases are circular with spinose or conical teeth, elliptical with inline lobate or triangular teeth, or transverse tricone with paddle-like teeth (Cuif & Perrin 1999; Cuif et al. 2003). Tips may be regular or irregular: bulbous, jagged (lacerate; hirsute), lobular, or sharp while tooth height and spacing is gauged mid-septum. Tooth interareas may be shaped from vertical bands, horizontal palisades (rods), or smooth, while granulations are manifestations of transverse calcification that vary in size, shape, and distribution which tend to be evaluated mid-septum (Budd et al. 2012). Nevertheless, divergent intraseptal teeth occur in several solitary Scleractinia (Arrigoni et al. 2016; Arrigoni et al. 2019).

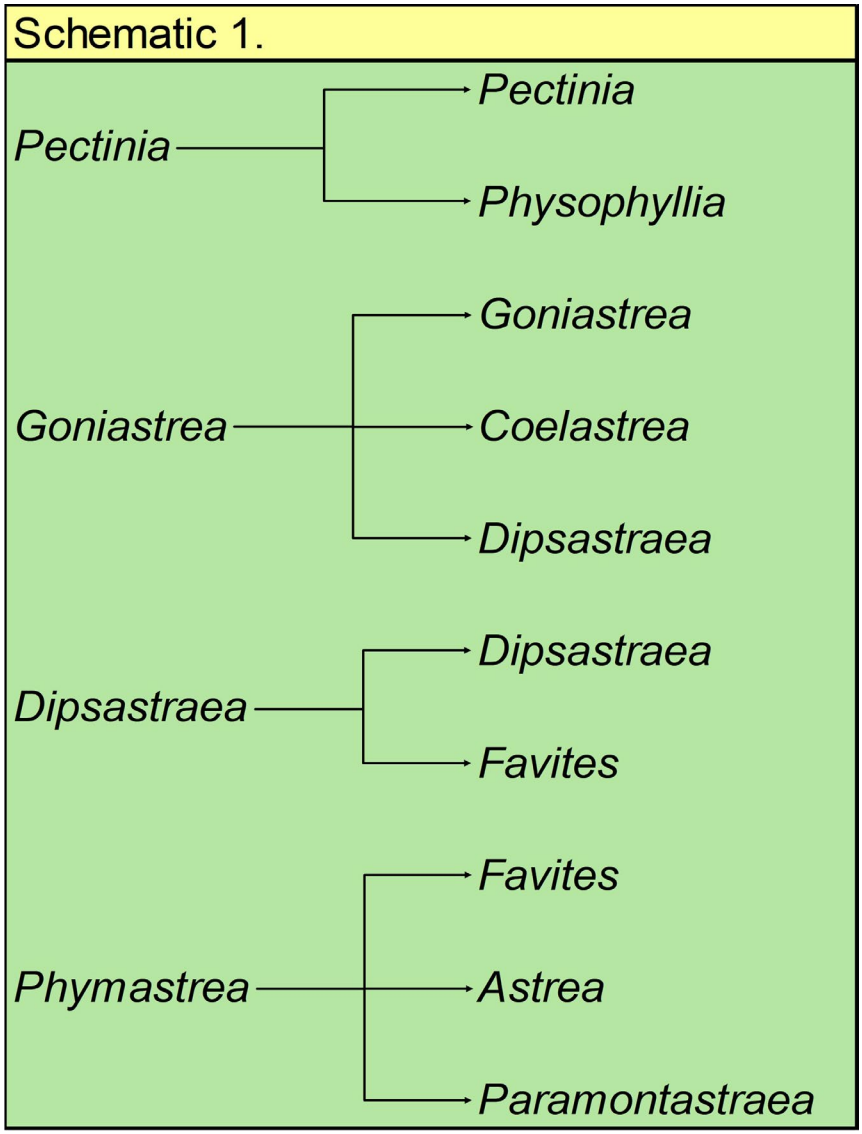
2D microstructural examinations of ultra-thin sections sputter-coated with a platinum or gold film (Kitahara et al. 2012) exploit stereo optical and electronic microscopy to identify patterns of rapid accretion centres, their fibres, and their thickening deposits in septa including costosepta, columella, and corallite walls (Budd et al. 2012), which are formed by various means of adjoining the posterioseptal margin. The rear of each septum is linked by intercostal or epicostal dissepiments in parathecal walls; septa thicken and fuse in septothecal; costosepta are adjoined by perpendicular bridging remnants of the original margino-thecal corallite boundary in trabeculothecal; septa are interwoven by perpendicular synapticulate rods in synapticulothecal, or conventional septa are adjoined by long slender vertical abortive septa that do not protrude into the calice bore (Budd & Storlarski 2011; Budd et al. 2012). Thickening fibrous deposits flank rapid calcification centres which are interspersed with fewer organic phases termed sclerenchyme, stereoplasm, or stereome, which can be microfibrous, occur in layers, or form extensive concentric rings (Fig 2.; Budd et al. 2012).

Phylogenetic character mapping was attained from combined Bayesian sequence analyses of a 607-base pair (bp) region of the scleractinian mitochondrial cytochrome oxidase I gene (*cox1*) with a 776-bp segment of the cytochrome oxidase *b* gene (*cob*), consistent with the study of Fukami and colleagues from 2008. A total of 67 species from clades XV to XXI were evaluated to recreate their tree which comprises genera typically assigned to the families Faviidae, Merulinidae, Mussidae, Pectiniidae, and Trachyphylliidae. Such an approach facilitated the unearthing of synapomorphies after molecular analyses discovered distinct species amongst the macro- and micro-morphologically and microstructurally examined visually indistinguishable specimens, or those with identical physical attributes. Investigations were intentionally skewed towards synapomorphies that differentiated the study's familiar rank Mussidae, and subfamilies Mussinae, and Faviinae, and their three subordinate clades lodging the genera [1] *Colpophyllia* and [2] *Mussismilia* together with [3] *Diploria*, *Favia*, *Manicina,* and *Pseudodiploria*. Scleractinia from clades XVII and XVIII as well as *Diploastrea* and *Heliopora* from clade XV, and clade XVI's *Montastraea cavernosa* constituted a significantly

validating outgroup. The corallite attribute, synapticulothecal walls did not vary between corals of the core analyses and was thus excluded (Budd et al. 2012).

The study erected the family Lobophylliidae with members from clades XVIII to XX, resurrected previously discarded families Montastreidae (clade XVI) and Diploastreidae (clade XV) by elevating the genera *Montastraea* and *Diploastrea*, ranked clade XVII's Pectiniidae and Trachyphylliidae as junior synonyms of Merulinidae (Budd et al. 2012, cited in Huang et al. 2014), and demoted the family Faviidae of clade XXI to the subfamily Faviinae. Mussidae was subdivided into Atlantic clade XXI, and XVIII to XX lobophylliids from the Indo-Pacific. Members of the former family Faviidae were disseminated into Atlantic Mussidae (XXI) and Pacific Merulinidae (XVII). Merulinidae and Trachyphylliidae were first absorbed into Indo-Pacific faviids then designated Merulinidae, whereas Pectiniidae were segregated into Lobophylliidae and Merulinidae. Members of the family Mussidae were subdivided into the subfamilies Faviinae and Mussinae, while all revisions significantly impacted genera (Budd et al. 2012).

Mussismilia was transferred from Mussinae to the subfamily Faviinae while *Diploria* was split into monospecific *Diploria labyrinthiformis*, and *Pseudodiploria strigosa* and *P. clivosa*. *Favia* was shared into Atlantic Mussidae as *Favia* and Indo-Pacific Merulinidae as *Dipsastraea*. *Montastraea* was fragmented as Atlantic *Montastraea* of Montastreidae (XVI) and Atlantic *Orbicella* and Indo-Pacific *Phymastrea* of Merulinidae. *Scolymia* was distributed amongst Atlantic Mussidae and reclassified as the lobophylliids *Parascolymia* and *Homophyllia* consistent with Wells from 1964. *Eusmilia* migrated to Meandrinidae (XII), *Ctenella* and *Galaxea* to Euphylliidae (V), while *Simplastrea* was tentatively ranked in the same family. *Favia leptophylla* was absorbed by *Mussismilia* as *M. leptophylla* whereas *Blastomussa*, *Cladocora*, *Indophyllia*, *Leptastrea*, *Oulastrea*, *Parasimplastrea*, *Plesiastrea*, and *Solenastrea* were unresolvable and thus remained *incertae sedis* while table 2. summarises historic classifications and the current study's revisions (Budd et al. 2012).



Schematic 1. Presenting the revisions of Budd and colleagues' genera from 2012 by Huang and allies published in 2014. Adapted from Huang et al. 2014.

The scleractinian family Agariciidae comprises 47 extant species shared amongst seven genera (Veron 2000a; Glynn et al. 2001; Licuanan & Aliño 2009) with representatives in several shallow-water ecosystems extending to 100 m (Fricke et al. 1987). The genera *Agaricia* and *Helioseris* are only found in the western Atlantic, while *Coeloseris*, *Gardineroseris*, *Pachyseris*, *Pavona*, and *Leptoseris* inhabit the Indo-Pacific, where the latter also grows in the Caribbean. All agariciids were zooxanthellate (hermatypic) which manifest as plating (laminar), frondose, or massive (boulder) colonies like most of the 27 fossil genera assigned to this family, albeit the now extinct, solitary, and likely sunlight-independent genera *Trochoseris* and *Vaughanoseris* endured the Middle to Upper Cretaceous (Wells 1956; Chevalier 1961, cited in Kitahara et al 2012b; Chevalier 1968, cited in Kitahara et al 2012b; Budd & McNeill 1998; Baron-Szabo 2002; Pandey & Fürsich 2005, cited in Kitahara et al 2012b; Baron-Szabo 2008; Pandey et al. 2007, cited in Kitahara et al 2012b).

With the exception of *Pachyseris* (Fukami et al. 2008; Kitahara et al. 2010b), Agariciidae was validated by pioneering sequence analyses of the mitochondrial CO1 gene (Romano & Palumbi 1996; Romano & Cairns 2000; Le Goff-Vitry et al. 2004; Kerr 2005; Fukami et al. 2008; Kitahara et al. 2010a; Kitahara et al. 2010b; Stolarski et al. 2011) which nested the family in Complexa alongside its shallow-water sister taxa Acroporidae and Poritidae. The discovery that the solitary trochoid and sessile sunlight-independent 73 to 852 m-dwelling species *Dactylotrochus cervicornis* (synonym: *Tridacophyllia cervicornis*: Astraeidae) of the family Caryophylliidae had significant affinity with entirely colonial and zooxanthellate Agariciidae, was a surprising development arising from the study of Kitahara and colleagues from 2010(b). Wells had moved *D. cervicornis* to Caryophylliidae in 1954 by virtue of their moderately bifurcating four to eight theca that protrude beyond their calicular periphery, insignificant septal dentation, and their alikeness to the caryophylliid genus type *Desmophyllum* which is more evident in juveniles. These findings lend further credence to the idea that the ancestors of current hermatypes were solitary and azooxanthellate like fossilised species of *Trochoseris*, while

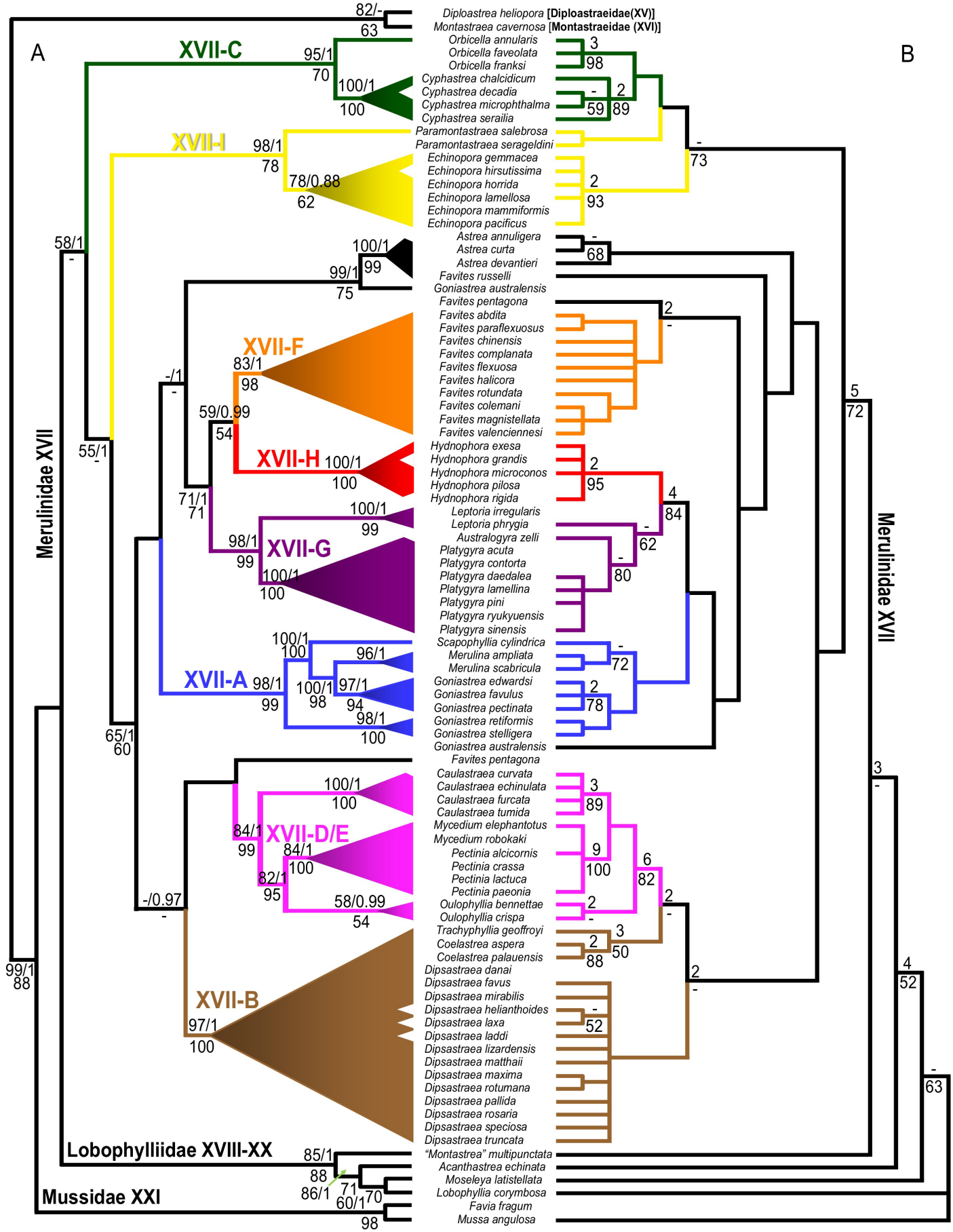


Fig 3. [A] a recreation of the maximum likelihood phylogenetic tree of clade XVII (Merunlinidae) from 2014 where the ancestries of 93 species were discerned by sequence analyses of three nuclear and two mitochondrial genomic markers. Clade VX (Diploastraeidae), clades XVIII to XX (Lobophylliidae), clade XVI (Montastraeidae), and clade XXI (Musidae) were analysed as corroborating outgroups. Colours indicate clade XVII's subclades A to I where values above or below nodes represent maximum likelihood bootstrap ≥50% of 1,000/Bayesian posterior probability ≥0.9 or maximum parsimony bootstrap ≥50%. [B] one of eight maximum parsimony trees supported by 44 morphological characters by Huang and allies in 2014 where numbers above or beneath nodes specify Bremer decay index ≥2 or maximum parsimony bootstrap ≥50%. Adapted from data presented in Huang et al. 2014.

Kitahara and colleagues' comprehensive morpho-molecular analyses legitimised the migration of *Dactylotrochus cervicornis* to Agariciidae in 2012 (Kitahara et al. 2012b).

Meniane are formed from the fusion of a horizontal line of septal granulations whose peak protrudes from and runs along the septal plane that occur in species of *Dactylotrochus* and *Leptoseris* (Kitahara et al. 2012) while successions of horizontal septal granulations are common to most Agariciidae (Cuif et al. 2003). However, early fusional development may manifest as beads in juveniles, whilst tectura and beaded septal margins are also phylogenetically discerning for *D. cervicornis* and Agariciidae (Appendix I). Remarkably, *Coeloseris* were the only Agariciidae whose corallites lacked these features, whose coralla were morphologically distinct from their sisters, and whose genes had yet to be analysed (Table 1.; Kitahara et al 2012).

The aim of Huang and allies' monograph from 2014 was to further delineate the informal classification Bigmessidae (clade XVII Fukami et al. 2008) as an addendum to their preliminary revisions from 2011. See: Part 1. Bigmessidae comprised eight extant families (Vaughan & Wells 1943) traditionally ranked in the order Faviina by Vaughan and Wells in 1943 and Wells in 1956 and later in the orders Faviina and Meandriina by Veron in 1995 (cited in Huang et al 2014). All extant families of Bigmessidae were pervaded with para- and poly-phyly (Fukami et al. 2008; Kitahara et al. 2010b; Stolarski et al. 2011; Huang 2012). Most genera were Robusta but others including *Ctenella* and *Galaxea* were Complexa, hence these two genera were migrated to Euphylliidae while Merulinidae assimilated the remainder of Bigmessidae: Faviidae, Pectiniidae, and Trachyphylliidae in 2012 (Budd et al. 2012; Huang et al. 2014). Huang and allies' 2014 morpho-molecular review upheld or corroborated Budd and colleagues' genera *Australogyra*, *Boninastrea*, *Caulastraea*, *Cyphastrea*, *Diploastrea*, *Echinopora*, *Erythrastrea*, *Favites*, *Hydnophora*, *Leptoria*, *Merulina*, *Montastraea*, *Mycedium*, *Orbicella*, *Oulophyllia*, *Paraclavarina*, *Platygyra*, *Scapophyllia*, and *Trachyphyllia* from 2012, while their revisions are featured in schematic 1. (Huang et al. 2014).

Most genera of Merulinidae were monophyletic apart from *Dipsastraea*, *Favites*, *Goniastrea*, and *Phymastrea* (Huang et al. 2011) while subcorallite characters support subclades A to J (Budd & Stolarski 2011). *Dipsastraea stelligera* is implicated in the polyphyly of this genus because it is a sister taxon of *Goniastrea retiformis* by virtue of its abortive septa, while the walls of other species of *Dipsastraea* are septothecal (Budd & Stolarski 2011). Septal teeth also invalidate the rank of *Dipsastraea stelligera* which are irregular in Indo-Pacific Merulinidae and regular in Atlantic Faviinae (Budd & Stolarski 2009; Budd & Stolarski 2011) which assisted the revisions of the former family in 2012 (Budd et al. 2012). Huang and allies thus ventured to untangle the species of Diploastraeidae, Merulinidae, and Montastraeidae using established subcorallite features and macromorphological evidence comprising 44 skeletal attributes and their previous comprehensive molecular analyses from 2011. To this end, they examined over 400 samples and reconstructed the ancestries of 139 species and 24 genera (Fig 3.; Hung et al. 2014).

Some genera like *Caulastraea* had both septal and paliform lobes which were scored separately instead of adopting the combined descriptor of 'internal lobes' devised by Budd and colleagues in 2012. Likewise, many of this team's morphological traits were subdivided into separately scored attributes and/or refined/redefined in the monograph of Huang and allies from 2014, while several that were noninformative for clade XVII were excluded. Remarkably, all clade XVII merulinids had clusters of rapid accretion separated by ≤0.6 mm within their costae and ≤0.5 mm within their septa. As expected, monticules (hydnophores) were only observed in species of *Hydnophora* (Huang et al. 2014) but occur in agariciid *Pavona varians* and lobophylliid *Symphyllia wilsoni* (Arrigoni et al. 2016), whereas *Symphyllia* did not feature in Huang and allies' tree (Appendix I).

Huang and allies resurrected *Astrea* Lamarck 1801 to absorb *Astrea annuliger*, *A. curta*, *Plesiastrea devantieri* as *A. devantieri*, and *Madrepora rotulosa* as *A. rotulosa*, while they recovered *Coelastrea* Verrill 1866 to rank *C. tenuis* and assimilate *Goniastrea aspera* as *Coelastrea aspera,* and *Favia palauensis* as *C. palauensis*. They erected and described *Paramontastraea* Huang & Budd 2014 to nest *P. salebrosa*, *Favites peresi* as *P. peresi*, and *Montastraea serageldini* as *P. serageldini*. *Barabattoia* became a junior synonym of *Dipsastraea* de Blainville 1830 which assimilated the hitherto assigned species of *Barabattoia*: *Dipsastraea amicorum, D. laddi*, and *D. mirabilis*, whereas *Phymastrea* became a junior synonym of *Favites* Link 1807 which engendered *Favites colemani*, *Favites magnistellata*, and *Favites valenciennesi*. *Favites rotundata* Veron, Pichon and Wijsman-Best 1977 was reverted, while *Astrea* (*Orbicella*) *stelligera* was absorbed by *Goniastrea* Milne Edwards & Haime 1848 as *G. stelligera* (Fig 3.; Huang et al. 2014).

Montastrea de Blainville 1830 originated as the subgenus *Astrea* that referred to extinct fossils, yet its synonym *Heliastraea* Milne Edwards & Haime 1857 was taxonomically favoured into which 45 living and extinct species were ranked including the species type *Madrepora astroites* Forskål 1775 (synonym: *Astrea forskaliana* Milne Edwards & Haime 1849) and *Madrepora cavernosa* Esper 1795 (synonym: *Madrepora cavernosa* Linnaeus 1767). However, this group's species type, *M. astroites* makes *Echinopora* the modern synonym of *Heliastraea* (Wijsman-Best 1980; Veron 2000). Cenozoic to Palaeozoic *Astrea guettardi* Defrance 1826 was one of the earliest fossilised species classified within the newly elevated genus *Montastr**ea*** (Lang & Smith 1935, cited in Huang et al. 2014; Wells 1936). Whereafter, Vaughan and Wells redefined the genus to include its fossilised synonyms *Heliastraea* and *Orbicella* and living Red Sea *Astrea forskaliana*, *Madrepora cavernosa,* and species of *Orbicella* in 1943. *Heliastraea* was de-synonymised by Wells in 1956 which constrained its living counterparts to the Atlantic, while the "*a*" of *Montastr**a**ea* was added by Veron in 2000. Its definition was then expanded to immerse species that bud extracalicularly like Indo-Pacific *Astrea annuligera* Milne Edwards & Haime 1849, *A. curta* Dana 1846, *Montastraea magnistellata* Chevalier 1971, and *Phymastrea valenciennesi* Milne Edwards & Haime 1849 (Chevalier 1971, cited in Huang et al. 2014; Veron et al. 1977; Veron 1986; Veron 2000). However, the boundary of this genus remains somewhat nebulous with that of *Plesiastrea* Milne Edwards & Haime 1848 (Veron et al. 1977). Molecular studies deepened the uncertainty insofar as the polyphyly of *Montastraea* Veron 2000 initially appeared to extend to three clades (Fukami et al. 2008; Kitahara et al. 2010) and later six (Huang et al. 2011; Arrigoni et al. 2012). All were ranked at this juncture in Merulinidae apart from *Montastraea cavernosa* Linnaeus 1767 of clade XVI (Montastraeidae) and *Montastraea multipunctata* Hodgson 1985 tentatively classified in clades XVIII to XX (Lobophylliidae; Huang et al. 2011; Arrigoni et al. 2014a), yet *Montastraea cavernosa* along with

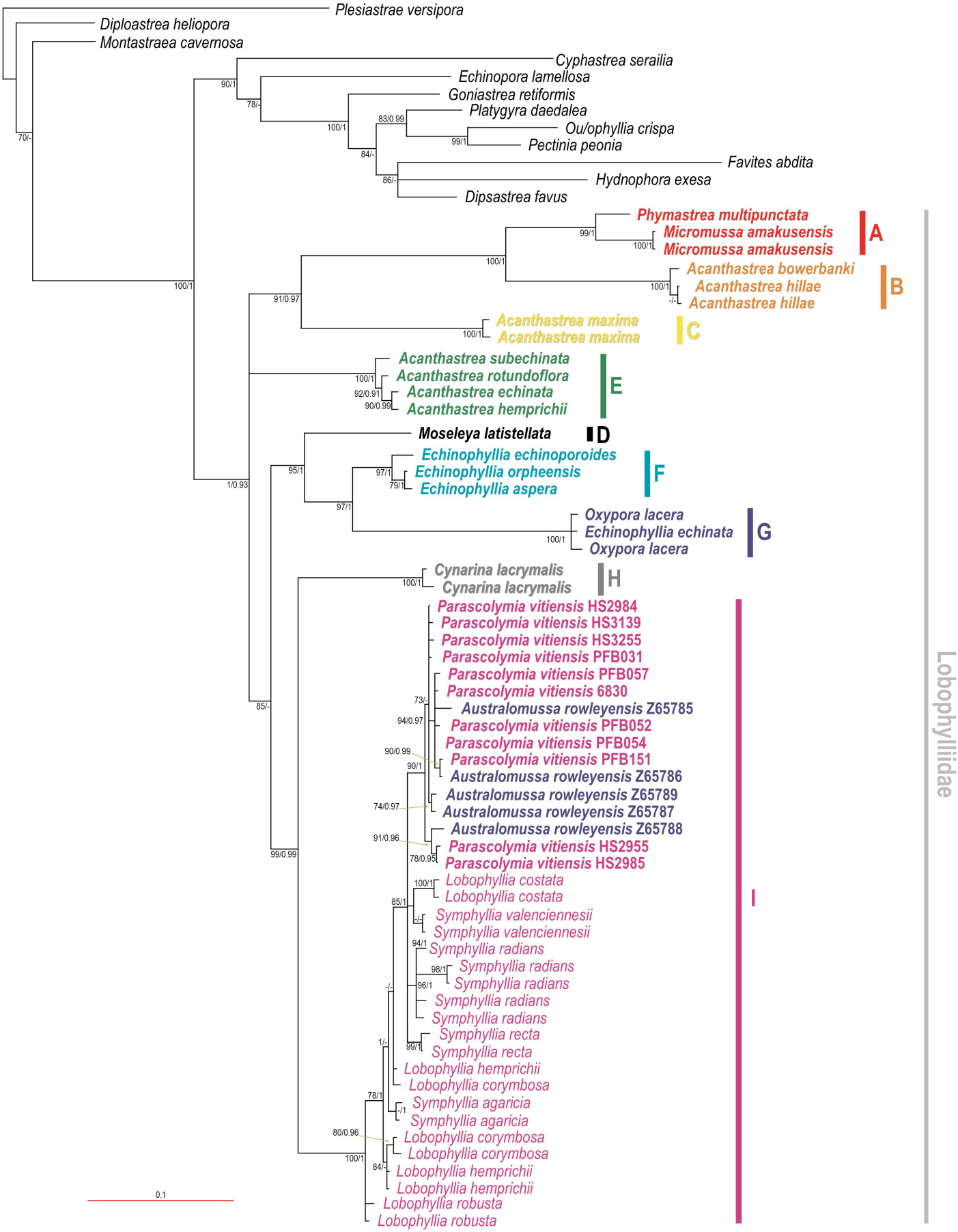


Fig 4. A representation of the tree of Arigoni and allies from 2014(a) substantiating the phylogenetic rank of strains of the clade I lobophylliids *Parascolymia vitiensis* Brüggemann 1877 and recently elevated *Parascolymia rowleyensis* Veron 1985 (junior synonym: *Australomussa rowleyensis*), and the revised/corroborated ancestries of Lobophylliidae (clades A to I) beneath the study's validating outgroups. Comprises node-associated maximum likelihood bootstrap (>70%)/Bayesian posterior probabilities (>0.9). Of note is the distinct ancestries of clades D and E. Adapted from data presented by Arrigoni et al 2014(a).

its sister taxon *Diploastrea heliopora* of clade XV (Diploastraeidae), represent the most ancient divergent lineages amongst clades XV to XXI (Huang et al. 2011; Arrigoni et al. 2012; Budd et al. 2012). However, contrasting molecular evidence positioned

Montastraeidae as a sister to Lobophylliidae, Merulinidae, and Mussidae (Fig 3.; Fukami et al. 2008). Species of *Montastraea* grow on Atlantic reefs off Brazil and West Africa and in the Caribbean (Huang et al. 2014).

Table 3.

Character Macromorphology	*Parascolymia vitiensis*	*Parascolymia rowleyensis* (Jr. syn: *A. rowleyensis*)
1. Intracalicular budding	***Present	Present
2. Extracalicular budding	***Present	Present
3. Circumoral budding	***Present	Present
4. Corallite corallum integration	***Uni- or multi-seriate	Uni- or multi-seriate
7. **Calice/valley width**	**Large (>25 mm)**	**Large (>25 mm)**
9. **Costoseptal continuity**	***Mostly non-confluent**	**Mostly confluent**
10. **Septa cycle**	**4 cycles**	**6 to 7 cycles**
11. Free septa	Present	Present
12. Septal spacing per 5 mm	Wide (<6)	Wide (<6)
13. **Relative costoseptal thickness** (*Cs1+ Cs2) versus (Cs3) cycles	**Unequal**	**Slightly unequal**
14. Corallite central linkage	Discontinuous & lamellar	Discontinuous & lamellar
15. Columella form	Trabeculate & spongy	Trabeculate & spongy
16. **Columella to calice ratio**	**Small (<1/4)**	**Medium to small (≤1/4)**
Micromorphology		
19. Endotheca	Abundant & vesicular	Abundant & vesicular
35. Mid-septal tooth base	Elliptical & parallel	Elliptical & parallel
38. Tooth tips	Irregular lobes	Irregular lobes
39. **Tooth height **S1**	**High (≥1 mm)**	**High (<1 mm)**
40. **Tooth spacing **S1**	**Very wide (>2 mm)**	**Wide (1 to 2 mm)**
43. **Granule shape and distribution**	**Weak enveloped by thickening deposits**	**Strong & scattered**
44. **Interarea superstructure**	**Smooth and palisade**	**Palisade**
45. **Tooth shape** *Cs3÷Cs1	**Unequal**	**Equal**

*Costoseptal Cycle
**Septal Cycle
***Appraised on polycentric corallum

Table 3. The macro- and micro-morphological attributes and scorings for the clade I lobophylliids *Parascolymia vitiensis* Brüggemann 1877 and recently absorbed *Parascolymia rowleyensis* Veron 1985 where features that differ between species are emboldened. Adapted from data and analyses presented by Arrigoni et al. in 2014(a).

The species type *Orbicella minikoiensis* Gardiner 1904 spawned the genus *Diploastrea* Vaughan 1918 which is morphologically indistinguishable from *Astrea heliopora* (Matthai 1914) which has be mistaken numerous times for *Diploastrea*'s species type (Vaughan & Wells 1943; Wells 1956; Chevalier 1975, cited in Huang et al 2014; Veron et al. 1977; Veron 1986; Chevalier & Beauvais 1987, cited in Huang et al. 2014; Budd et al. 2012; Huang et al. 2014). Gardiner's 1904 examinations were restricted to three samples from distinct colonies of *Orbicella minikoiensis* endemic to reefs off Minicoy in India's Lakshadweep. 11 fossils from the Lower Cretaceous were ranked in *Diploastrea* including *D. crassolamellata* Duncan 1863; *D. harrisi* Wells 1932 (Wells 1956), and *D. aequalis* Budd 1992 (Budd et al. 1992, cited in Huang et al. 2014). The deep divergence of *Diploastrea heliopora* Lamarck 1816 amongst clades XV to XXI whose preliminary molecular evidence implies its ancestors emerged some 70 MYA is reflected in the fossil record (Budd et al. 2012); however, extensive morphological studies of living specimens from several distinct geographic regions are required to affirm its taxonomic rank. Living strains of *Diploastrea heliopora* are extraordinary inasmuch as they are the only members of this genus whose rank has stood the test of time since their inception, which is testament to their unique ancestry and physiology which includes synapticulothecal walls, which differentiate them from all species featured in Huang and collaborators' monograph of 2014 (Huang et al. 2014). Nevertheless, Veron adopted Faviidae Wells 1956 in 2000 which was not redressed until Budd and allies' monograph reverted *Diploastrea heliopora* to monospecific Diploastraeidae Chevalier & Beauvais 1987 of clade XV in 2012 (Huang et al. 2014). The evidence of the time inferred Diploastraeidae was sister to Montastraeidae (Huang et al. 2011; Arrigoni et al. 2012; Budd et al. 2012) or Lobophylliidae, Merulinidae, and Mussidae (Fukami et al. 2008) while species of *Diploastrea* are widespread in the Indo-Pacific yet do not extend eastward from Hawaii (Huang et al. 2014).

Integrated morpho-molecular approaches have resolved the longstanding taxonomic disparities of 21 species of *Pocillopora*

Lamarck 1816 (Schmidt-Roach et al. 2012; Schmidt-Roach et al. 2013; Schmidt-Roach et al. 2014) and 23 species of *Psammocora* Dana 1846 (Benzoni 2006; Stefani et al. 2008; Benzoni et al. 2010; Benzoni et al. 2012b). Indo-Pacific Mussidae Ortmann 1890 were migrated to Lobophylliidae Dai and Horng 2009 by Fukami and allies, after their groundbreaking morpho-molecular studies of 2004 and 2008, while their structural traits highlighted their distinct lineages arising from the Atlantic and Indo-Pacific basins (Budd & Stolarski 2009; Budd et al. 2012).

Following Budd and collaborators' monograph of 2012, Lobophylliidae comprised the genera *Acanthastrea* Milne Edwards and Haime 1848, *Cynarina* Brüggemann 1877, *Echinophyllia* Klunzinger 1879, *Homophyllia* Brüggemann 1877, *Lobophyllia* de Blainville 1830, *Micromussa* Veron 2000, *Moseleya* Quelch 1884, *Oxypora* Saville Kent 1871, *Parascolymia* Wells 1964, and *Symphyllia* Milne Edwards and Haime 1848 (Budd et al. 2012). Notwithstanding, molecular data were lacking for *Echinomorpha* Veron 2000 and *Australomussa* Veron 1985 which were ripe for revision. Intra- or extra-calicular budding, corallum configuration, corallite size and shape, septal cycle, tooth shape, distribution, and granulation together with configurations of costoseptal calcification centres and thickening deposits of *Acanthastrea*, *Cynarina*, *Echinophyllia*, *Homophyllia*, *Lobophyllia*, *Micromussa*, *Oxypora*, *Parascolymia*, and *Symphyllia* were scored by Budd and Stolarski in 2009 and Budd and colleagues in 2012 where septal tooth shape and distribution, interarea granulation, and their thickening deposits proved exceptionally phylogenetically discerning for Lobophylliidae (Arrigoni et al 2014a). Arrigoni and allies had presented a phylogenetic tree featuring clades A to I of monophyletic Lobophylliidae whose genera were significantly para- or polyphyletic, which should not be confused with the merulinid clade XVII and its subclades A to I (Fig 4.). Monospecific *Parascolymia* was nested in clade I alongside all molecularly analysed species of *Lobophyllia* and *Symphyllia* including two strains of *L. corymbosa* Forskål 1775 and one of *S. radians* Milne Edwards and Haime 1849 (Arrigoni et al. 2014b), yet *Parascolymia* lacked formal revision (Arrigoni et al. 2014a).

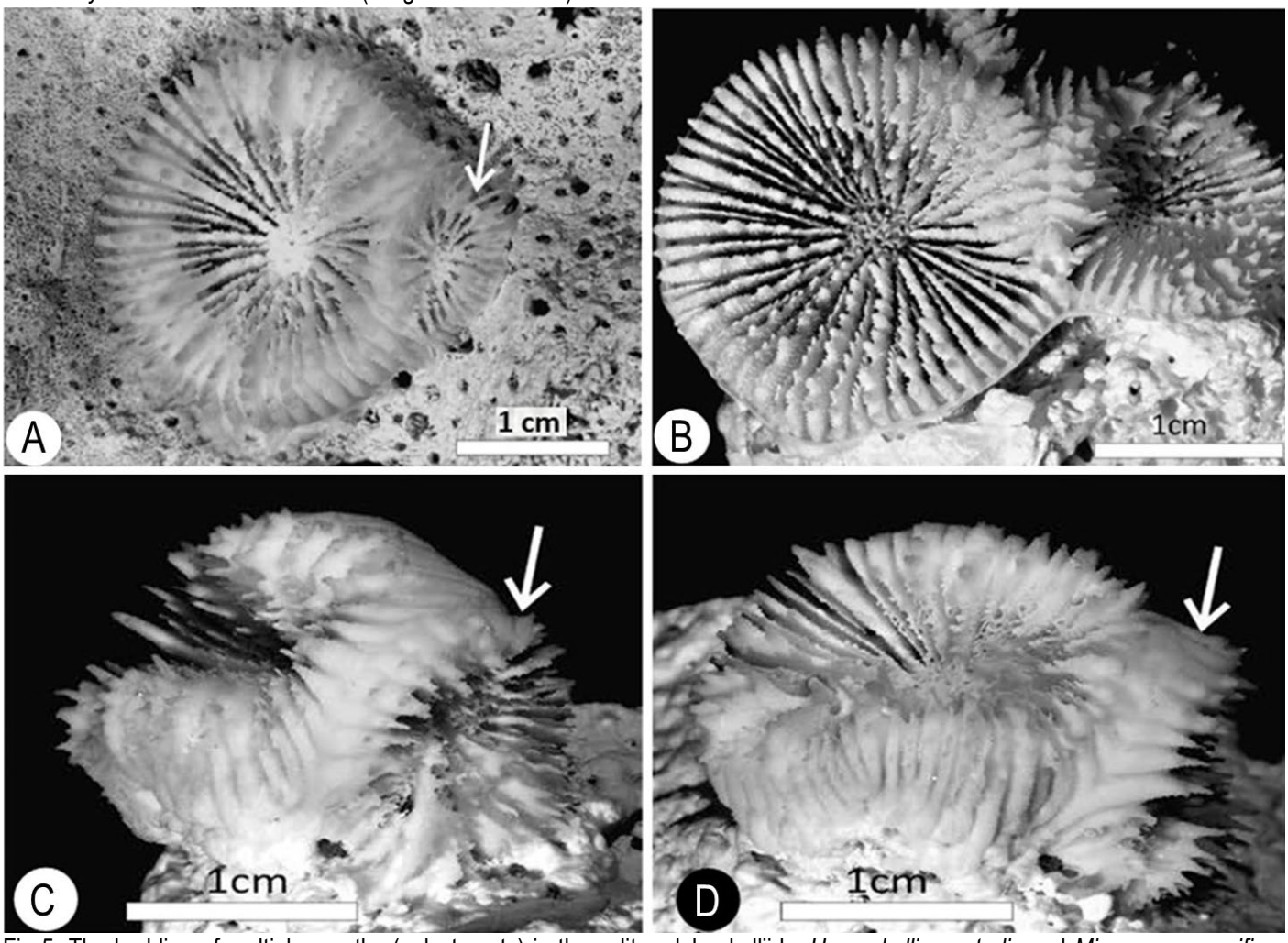


Fig 5. The budding of multiple mouths (polystomaty) in the solitary lobophylliids: *Homophyllia australis* and *Micromussa pacifica*. Images courtesy of Arrigoni et al. 2016 and the Creative Commons Attribution Licence 4.0.

Hermatypic *Australomussa rowleyensis* Veron 1985 were described from Western Australian samples and ranked within Mussidae by virtue of their flattened helmet- or dome-shaped coralla, ~20 mm valleys, thick walls, and extensive columellae (Veron 1985). Veron remarked that that *Australomussa* were morphologically distinct from other genera bar a slight resemblance to *Symphyllia* and *Parascolymia* which they were most alike (Veron 1985); however, the study did not appraise micromorphological attributes (Arrigoni et al. 2014a). Homoplasy is rife amongst Lobophylliidae and Mussidae (Budd & Stolarski 2009; Budd et al. 2012); nevertheless, these studies identified novel familiar- and species-discriminating micromorphological characters which they used to score *Parascolymia vitiensis* Brüggemann 1877 yet *Australomussa rowleyensis* remained undescribed (Arrigoni et al. 2014a). The latter is distributed in the Western Pacific which includes the Coral Triangle (Hoeksema 2007; Veron et al. 2009) which shares territory with the former that appears absent from Western Australia yet extends westward to the Indian Ocean and eastward to the central

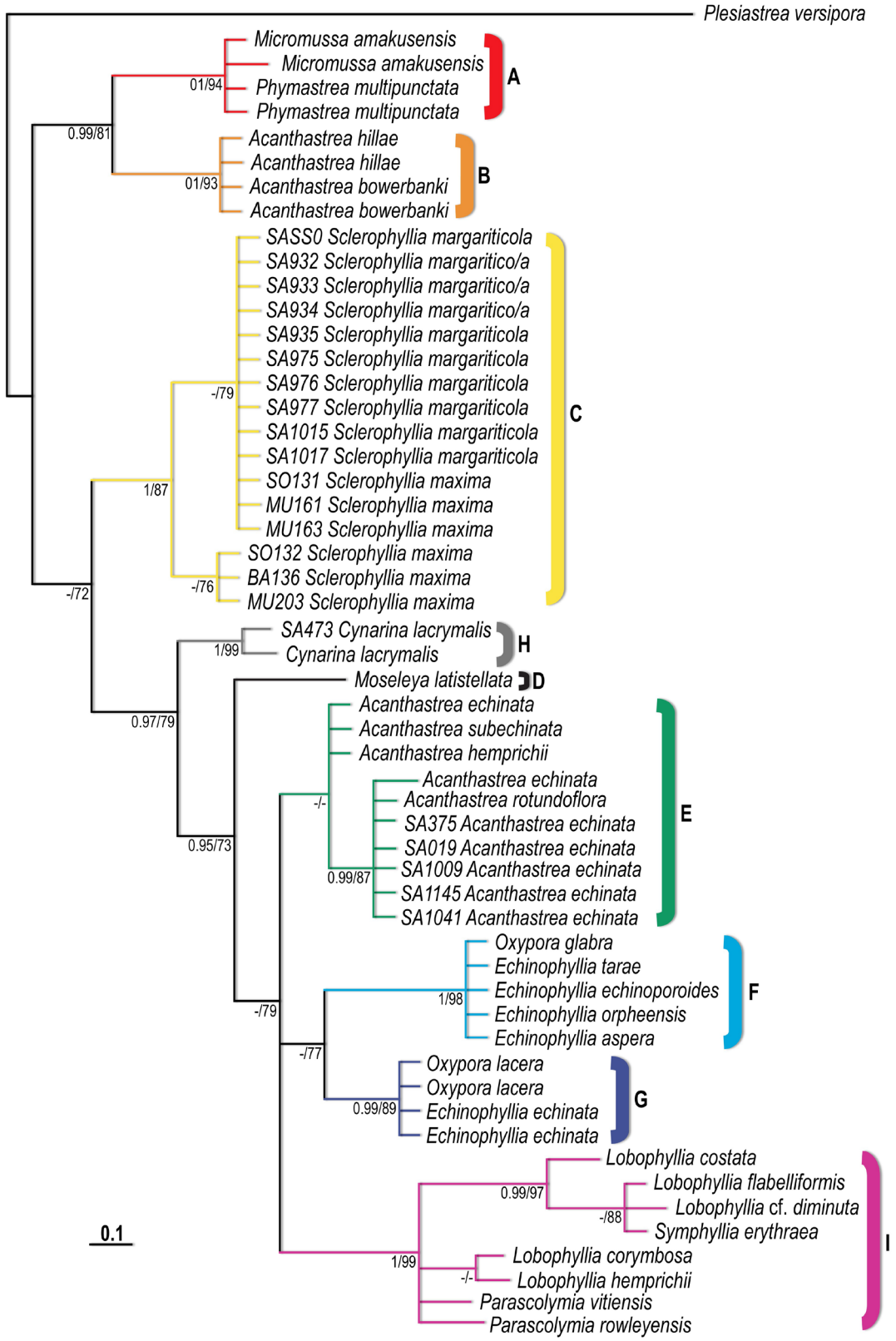


Fig 6. A representation of the phylogenetic tree of Arrigoni and allies from 2015 featuring the ancestries of members of the family Lobophylliidae and contextualising the taxonomic position of strains of resurrected *Sclerophyllia margariticola* and *Sclerophyllia maxima* (formerly: *Acanthastrea maxima*) discerned using Bayesian interference analyses of sequences from the mitochondrial genome-encoded CO1 gene. Numbers associated with nodes specify Bayesian posterior probability higher than 0.95/more than 70% of 1,000 maximum likelihood (ML) bootstraps. The colours of the lobophylliid clades A to I are consistent with Arrigoni et al. 2014b and adapted from data presented in Arrigoni et al. 2015.

Pacific (Veron 2000).

Strains of *A. rowleyensis* have retained their taxonomic nomenclature despite their affinity with *Symphyllia* and *Parascolymia*, whereas the opposite is true for *P. vitiensis*. This species was first designated *Litophyllia vitiensis* Milne Edwards and Haime 1857 (Gardiner 1899; Crossland 1952) and later *Protolobophyllia japonica* Yabe and Sugiyama 1935. However, *Scolymia* Haime 1852 and *Protolobophyllia* Yabe and Sugiyama 1935 were unanimously ranked as junior synonyms of *Lobophyllia* by Matthai in 1928, Wells in 1937, and Vaughan and Wells in 1943, who assumed that solitary monostomatous (single-mouthed) corallites were juveniles of *Lobophyllia* (Arigoni et al. 2014a). Notions such as these are entirely rational considering the polyps of species of *Lobophyllia* can be several inches across. Wells recognised that Atlantic *Scolymia lacera* Pallas 1766 and Indo-Pacific *Scolymia vitiensis* were derived from distinct ancestries after he discovered that specimens of *Protolobophyllia* cf. *japonica* were indeed *Cynarina lacrymalis* Milne, Edwards, and Haime 1848. Wells thus erected *Parascolymia* to absorb *Scolymia vitiensis* as *P. vitiensis* in 1964. Despite this, their typical mono-columella and -centric corallites and the geographic separation paradigm, motivated Veron and Pichon to synonymise *Parascolymia* and *Scolymia* in 1980. All the same, Budd and allies used the morpho-molecular data from Fukami and colleagues and Budd and Stolarski to revert the regionality of Indo-Pacific *Parascolymia* and Atlantic *Scolymia* in 2012 (Fukami et al. 2004; Fukami et al. 2008; Budd & Stolarski 2009; Budd et al. 2012).

The solitary corallites of *P. vitiensis* are often monostomatous yet multi-mouthed polystomatous examples are not uncommon (Chevalier 1975, cited in Arrigoni et al. 2014a; Veron & Pichon 1980) where several mono- and poly-stomatous examples of *P. vitiensis* from New Caledonia and Papua New Guinea whose larger coralla were analogous to those of *A. rowleyensis*, prompted Arrigoni and allies to embark on a thorough morpho-molecular review of these monospecific genera and their species in 2014(a).

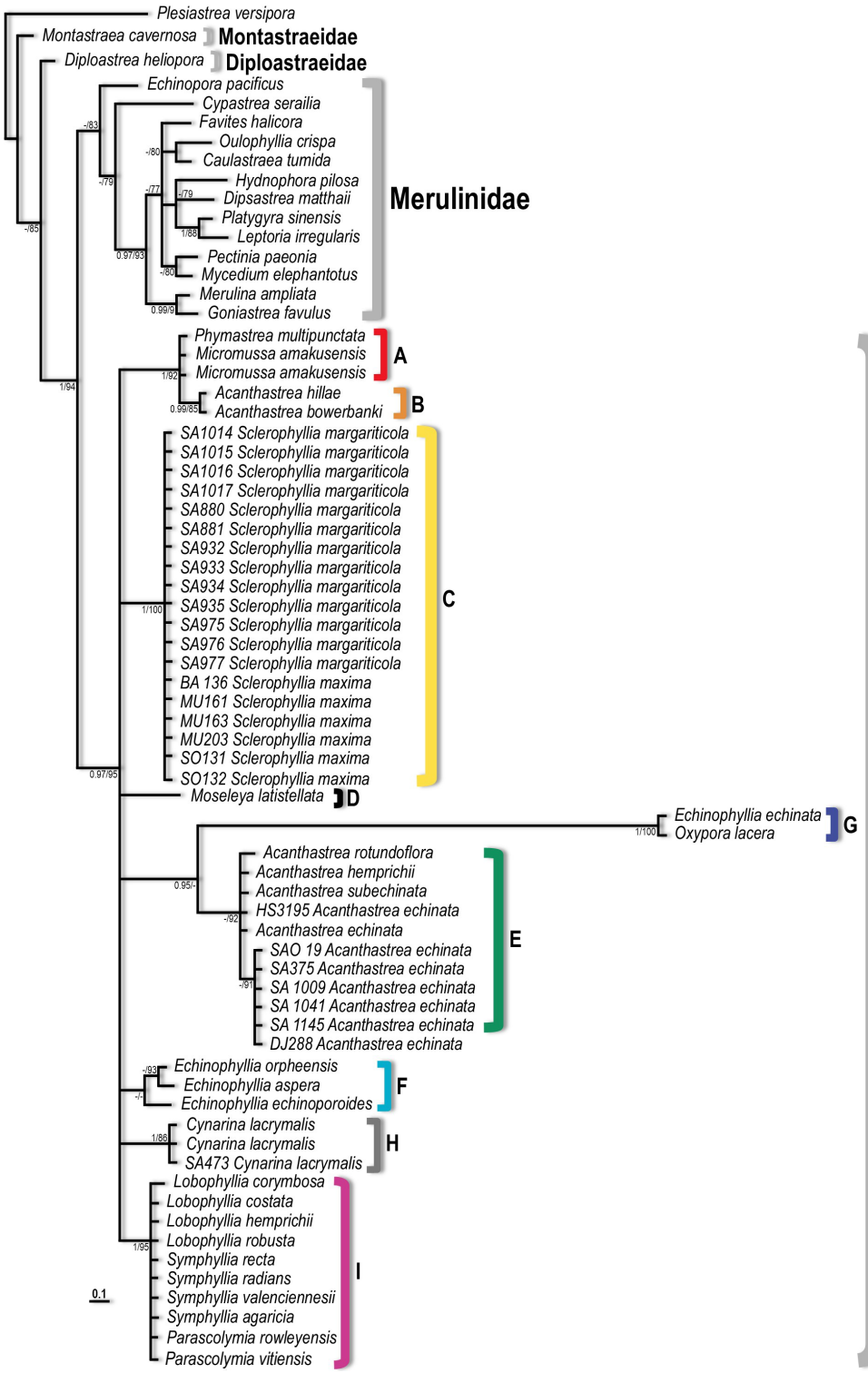


Fig 7. A representation of the phylogenetic tree of Arrigoni and allies from 2015 featuring the ancestries of members of the families Diploastraeidae, Lobophylliidae, Merulinidae, and Montastraeidae which contextualises the taxonomic position of strains of resurrected *Sclerophyllia margariticola* and *Sclerophyllia maxima* (formerly: *Acanthastrea maxima*). Discerned using Bayesian interference analyses of sequences from nucleus-encoded histone H3 genes. Numbers associated with nodes specify Bayesian posterior probability higher than 0.95/more than 70% of 1,000 maximum likelihood (ML) bootstraps. The colours of the lobophylliid clades A to I are consistent with Arrigoni et al. 2014b and adapted from data presented in Arrigoni et al. 2015.

A concatenated matrix of DNA comprising 580 bps of the barcoding regions of mitochondrial cytochrome oxidase subunit I (CO1) and 951 and 318 bps from nuclear-encoded ribosomal internally transcribed spacers (ITSs) and histone H3 proteins, were amplified, sequenced, aligned, and compared with bioinformatics. The former two biomarkers had been used to comprehensively revise Lobophylliidae by a related team published in the same year (Arrigoni et al. 2014b), whilst Huang and collaborators had discovered that the latter demonstrated merit as a tool for discerning the basal nodes of related Merulinidae Verrill 1865 in 2011 and in 2014(b). Molecular approaches have proven invaluable for delineating the ancestries of several polyphyletic groups which assisted their revision into monophyletic clades (Huang et al. 2008; Souter 2010; Gittenberger et al. 2011; Huang et al. 2011; Benzoni et al. 2012a; Richards et al. 2013; Arrigoni et al. 2014b) that confer maximum likelihood support for entire lineages. Furthermore, the macro- and micro-morphologies of all Lobophylliidae Dai and Horng 2009 were examined to facilitate mapping the entire family on a definitive phylogenetic tree with the aim of elucidating the lineages of *Australomussa rowleyensis* Veron 1985 and *Parascolymia vitiensis* Brüggemann 1877. The invariant molecular analyses of these species motivated the researchers to formally ranked *Australomussa* as a junior synonym of *Parascolymia* resulting in a nomenclative shift to *P. rowleyensis*. Nonetheless, the coralla of *P. vitiensis* and *P. rowleyensis* are significantly different, insofar as they vary by 10 of the 21 morphological attributes established by Budd and allies in 2012 which warranted their demarcation as discrete species (Fig 4.; Table 3.). This study therefore emphasised the value of integrated morpho-molecular approaches for the modern taxonomist (Arrigoni et al. 2014a).

P. vitiensis manifests in both solitary and colonial morphs and undergoes both intra- and extra-calicular budding. Flattened or moderately concaved colonies are formed by circumoral budding which results in polymorphic corallites whose integration is uni- or multi-seriate. The colonies of *P. rowleyensis* are formed by circumoral budding, yet thereafter, intra- and extra-calicular budding occur. Both species have analogous corallite and corallum configurations while the enlarged quasi-central corallite that spawns the colony remains conspicuous in juveniles (Table 3.; Arrigoni et al. 2014a).

Monophyly now pervades most species of clade I excluding polyphyletic *Lobophyllia corymbosa* Ehrenberg 1834 and *L.*

hemprichii Ehrenberg 1834. All the merulinid subclades established by Budd and Stolarski and Huang and allies in 2011 were corroborated bar D/E whose evolutionary histories were significantly unrelated, whilst apart from clade F, Bayesian inference (BI) and maximum likelihood (ML) analyses of CO1 and rDNA supported most of the clades established by Arrigoni and colleagues in 2014(b; Fig 4.). ITS regions varied significantly amongst species which enhanced tip resolution whilst they offered robust support for principal nodes. Nevertheless, the rank of *Acanthastrea ishigakiensis* Veron 1990 remained poorly defined by virtue of its strong affinity with *Symphyllia recta* (Arrigoni et al. 2014a).

Several of the solitary genera of Lobophylliidae like *Acanthophyllia* Wells 1937, *Cynarina* Bruggemann 1877, *Homophyllia* Bruggemann 1877, *Indophyllia* Gerth 1921, *Protolobophyllia* Yabe and Sugiyama 1935, *Rhodocyathus* Bourne 1905, and *Sclerophyllia* Klunzinger 1879 may be invalid (Matthai 1928, cited in Arrigoni et al. 2015; Wells 1964; Veron & Pichon 1980). Many are both mono- and poly-stomatous whilst the polyps of *Cynarina* and *Homophyllia* only ever have one mouth (Budd et al. 2012). Nevertheless, the valid lobophylliid genus *Parascolymia* manifests as monocentric and polystomatous coralla or forms colonies (Chevalier 1975, cited in Arrigoni et al. 2015; Veron & Pichon 1980; Arrigoni et al. 2014a; Arrigoni et al. 2015).

Monospecific *Sclerophyllia* Klunzinger 1879 was initially described from several living samples collected off Al-Qusayr in Egypt's northern Red Sea. Solitary *Sclerophyllia margariticola* has elliptical or circular monocentric 3-to-4-cm corallites which are two times wider than the height of the corallum with 60 to 96 septa arranged in 5 cycles with broader primary, secondary, or tertiary. Each corallite has an elliptical columella formed from bundles of anastomose trabeculae that actively grow and fuse (Klunzinger 1879, cited in Arrigoni et al. 2015). Gravier collected samples in Djibouti in 1907 and 1911 from which he described *Sclerophyllia margariticola* (cited in Arrigoni et al 2015). *S. margariticola* was documented by Montanaro-Gallitelli in 1943 which according to Wells was a misidentification (cited in Arrigoni et al. 2015; Wells 1964) whilst numerous studies had concluded that *Sclerophyllia* was a junior synonym of *Symphyllia* (Matthai 1928, cited in Arrigoni et al. 2015; Wells 1937, cited in Arrigoni et al. 2015; Vaughan & Wells 1943) and later *Cynarina* (Veron & Pichon 1980; Wells 1964) which was not recovered in the monographs of Veron or Budd and collaborators from 2000 and 2012 (Veron 2000; Budd et al. 2012). Hence this genus has remained ostensibly invalid since Gravier's survey and description in 1911 (Arrigoni et al. 2015).

Table 4.

Character Macromorphology	*Cynarina lacrymalis*	*Sclerophyllia margariticola*	*Sclerophyllia maxima* (Syn: *Acanthastrea maxima*)	*Acanthastrea echinata*
1. Intracalicular budding	***	***	**Present**	**Present**
2. Extracalicular budding	***	***	**Present**	**Present**
3. Circumoral budding	***	***	**Present**	**Present**
4. Corallite corallum integration	***	***	**Discrete**	**Discrete**
7. **Calice/valley width**	**Large**	**Large**	**Large**	**Medium**
9. **Costoseptal continuity**	***	***	**Mostly non-confluent**	**Mostly confluent**
10. **Septa cycle**	**5 cycles**	**6 cycles**	**5 cycles**	**3 cycles**
11. Free septa	Present	Present	Present	Present
12. Septal spacing per 5 mm	Wide	Wide	Wide	Wide
13. **Relative costoseptal thickness** (*Cs1+ Cs2) versus (Cs3) cycles	**Unequal**	**Slightly unequal**	**Unequal**	**Equal**
14. Corallite central linkage	**Lamellar**	***	**Trabecular**	**Lamellar**
15. Columella form	**Trabeculate & spongy**	**Trabeculate & spongy**	**Trabeculate & spongy**	**Trabeculate & Compact**
16. **Columella to calice ratio**	**<1/4**	**<1/4**	**<1/4**	**1/2**
Micromorphology				
21. Internal lobes	**Septal**	**Well-developed**	**Absent**	**Absent**
35. Mid-septal tooth base	Elliptical & parallel	Elliptical & parallel	Elliptical & parallel	Elliptical & parallel
38. Tooth tips	Irregular lobes	Irregular lobes	Irregular lobes	Irregular lobes
39. **Tooth height **S1**	**High**	**High**	**High**	**Medium**
40. **Tooth spacing **S1**	Very wide	Very wide	Very wide	Very wide
43. **Granule shape and distribution**	**Well-formed & Scattered**	**Strong & scattered**	**Strong & scattered**	**Weak enveloped by thickening deposits**
44. **Interarea superstructure**	**Smooth and palisade**	**Palisade**	**Smooth and palisade**	**Quasi-Palisade & Smooth**
45. **Tooth shape** *Cs3÷Cs1	**Unequal**	**Unequal**	**Unequal**	**Equal**

*Costoseptal Cycle
**Septal Cycle
***Appraised on polycentric corallum

Table 4. The macro- and micro-morphological scores of *Cynarina lacrymalis*, *Sclerophyllia margariticola, Sclerophyllia maxima* (formerly: *Acanthastrea maxima*), and *Acanthastrea echinata* where variant attributes are emboldened. Adapted from data presented by Arrigoni et al 2015.

Coastal specimens of *Acanthastrea maxima* were collected off Balhaf, Al Mukallah, and Socotra Island in Yemen's Gulf of Aden from 2007 to 2010, whereas *Acanthastrea echinata*, *Cynarina lacrymalis*, and *Sclerophyllia margariticola* were collected from various Red Sea reefs extending from the Gulf of Aqaba to Thuwal in Saudi Arabia in 2013 (Arrigoni et al. 2015).

Skeletal features were examined for the ontogenic biomarkers described by Klunzinger in 1879 (cited in Arrigoni et al. 2015), Sheppard and Salm in 1988, Sheppard and Sheppard in 1991, and Pichon and collaborators in 2010, while molecular analyses focussed on sequences associated with mitochondrial cytochrome c oxidase's subunit I (COI), the non-coding intergenic spacer region (IGR) between COI and the large ribosomal RNA subunit (l-rRNA), and nuclear loci encoding histone H3 proteins and regions of the internally transcribed spacer 2 (ITS2; Arrigoni et al. 2015).

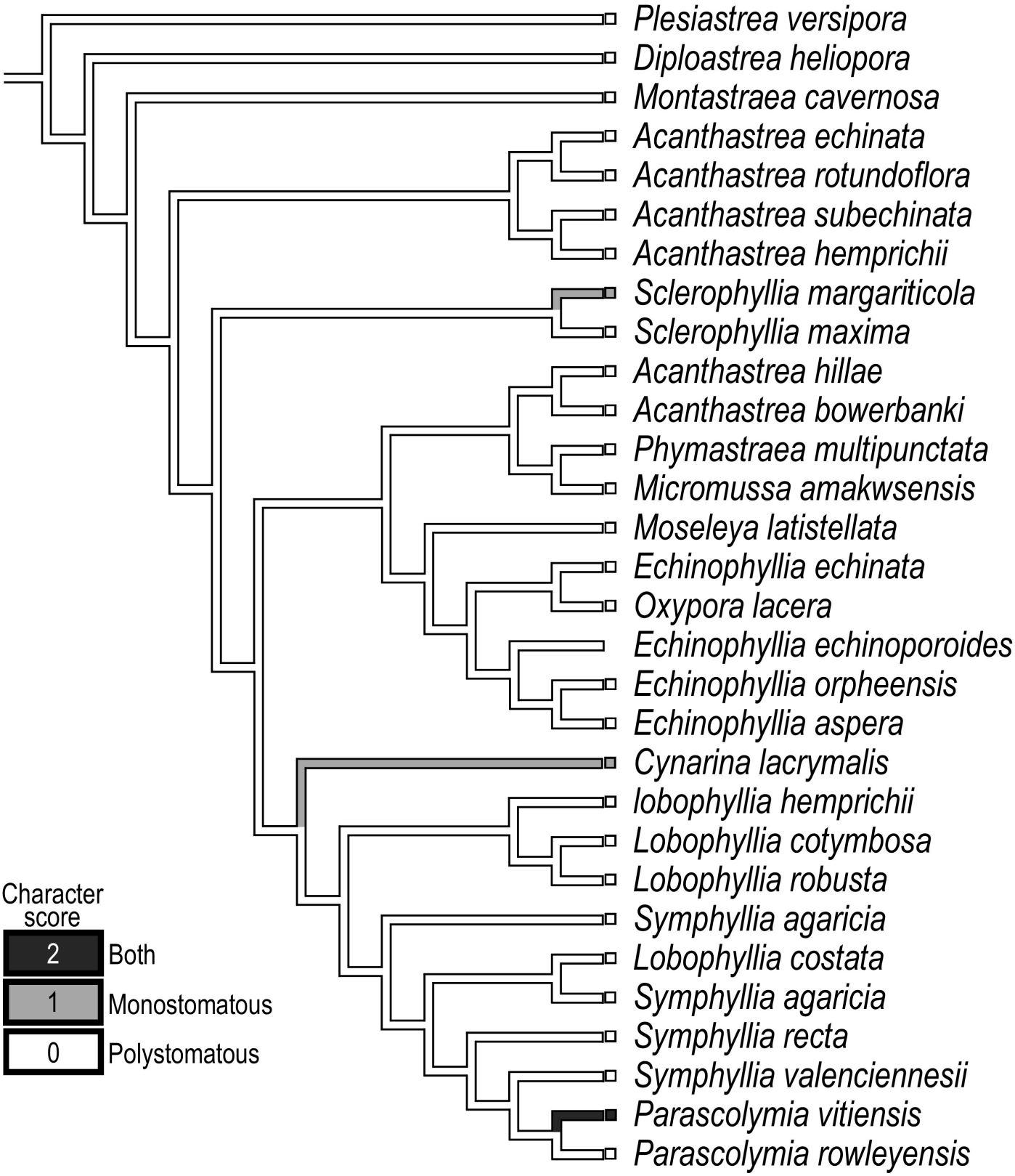


Fig 8. A representation of the tree of Arrigoni and collaborators from 2015 illustrating the heritable trait of multiple mouths within Lobophylliidae, where a corallite with one or more than one mouth is referred to as mono- or poly-stomatous. Adapted from data presented in Arrigoni et al. 2015.

The sisterhood of clades E and G was highlighted in the nuclear tree of histone H3 that was absent from the lineages discerned using mitochondrial CO1 which offered superior resolution for clades D to G and I (Figs 6. & 7.). As we have come to expect from the world-renowned teams headed by Arrigoni and others such as Budd and Huang, far from simply ascertaining the ancestries of strains of *Symphyllia margariticola* and their close relatives and mapping them onto a graphic representation of their taxonomic position within Lobophylliidae, the experimenters also took the family's representatives with available data for their COI, histone H3, and rDNA loci and the tentative ancestral trait of "multiple mouths" which is conspicuous in solitary species, and generated a maximum likelihood parsimonious tree to an astonishing end (Fig 5. & 8.). As exploited by Fukami and colleagues in 2008 and featured in Budd and allies' monograph of 2012, *Diploastrea heliopora* Lamarck 1816, *Montastraea cavernosa* Linnaeus 1767, and *Plesiastrea versipora* Lamarck 1816 made for corroborating outgroups. Polystomaty was scored for colonies as 0 to the exclusion of *Cynarina lacrymalis*, *Parascolymia vitiensis*, and *Sclerophyllia margariticola*, as 1 for solitary monostomatous *C. lacrymalis* and *S.*

margariticola, and as 2 for poly- or mono-stomatous *Parascolymia vitiensis* (Fig 8.; Arrigoni et al. 2015).

The researchers mapped the ancestral lineages of Lobophylliidae using part sequences of histone H3 and CO1 where the former's reconstruction was robustly monophyletic. Notwithstanding, there was merely nominal support for Merulinidae while Montastraeidae were basal with respect to their sisters Diploastreidae and Merulinidae. Most of the nine lobophylliid genera featured in Arrigoni and allies' tree discerned using concatenated sequences from COI and rDNA from 2014(a; Fig 4.) were recovered using histone H3 with minimal to adequate nodal support. *Acanthastrea maxima* and *Sclerophyllia margariticola* cluster in monophyletic lobophylliid clade C, which are remarkably haplotypically alike. Moreover, *S. margariticola* and *A. maxima* bore little relation to most of clade E's *Acanthastrea* including the species type, *A. echinata* and *Cynarina lacrymalis* of clade H (Fig 7.). The CO1 tree had merely minimal support for clade E yet substantiated the trend between clades C, E, and H. Notably, clade G's *Echinophyllia echinata and Oxypora lacera* are basally divergent from their sisters of clade E which evolve several MY later in the H3 tree as opposed to their grouping using sequences of CO1 which infers they evolved around the same epoch as clade E with their other *Echinophyllia* and *Oxypora* sisters of clade F (Fig 6.). Nevertheless, CO1 sequences are predisposed to generating artefacts arising from long-branch attraction and nucleotide compositional bias (Kitahara et al. 2012), yet the ancestral relationships between clades D and H as well as clades E, F, G, and I are better resolved in the mitochondrial tree (Fig 7.; Arrigoni et al. 2015), which traces "the egg's" maternal lineage.


Lobophyllia cf. *hemprichii*

Haplotype network analyses (HNA) of the ITS2 and IGR loci ascertained the bp substitution-based relative evolutionary distance between *A. maxima* and *S. margariticola*. The IGR loci unearthed four haplotypes: two differed by only two bps amongst the six samples of *A. maxima* whereas two varied by merely three mutations out of the 13 samples of *S. margariticola*, while the same analyses separated these species by only four bps. ITS2's HNA revealed separation of two to nine bps between *A. maxima*'s strains, whereas the evolutionary distance between *S. margariticola*'s haplotypes was merely two to three, with a seven bp disparity between species (Arrigoni et al. 2015).

The solitary coralla of *S. margariticola* are polymorphic where juveniles tend to be round, albeit oval, cyathiform, or even quasi-triangular polyps are not uncommon. The columella-crowning conspicuous paliform lobes of some are evident beneath their living flesh while their polyps envelope the entire corallum including the margin of their substratum-adjoining holdfast. With large calices exceeding 15 mm consistent with the scoring protocol of Budd and colleagues from 2012, the largest documented example to date had a diameter of 35 mm. Four complete septal cycles radiate within calices with a partial fifth, whereas Klunzinger observed up to six in larger specimens collected in the late 19th century, which were all remarkably, accreted onto pearl oystershells (Klunzinger 1879, cited in Arrigoni et al. 2015). Thicker primary, secondary, and tertiary septa contrast with thinner "free" quaternary, while the extremities of the penultimate are curved toward the last which fuse with the base of the upper columella. 4 to 5 well-spaced septa are precipitated for every 5 mm of corallite circumference while extensively developed costae extend 5 to 6 mm below the wall. Earlier cycle costae are thicker resulting in irregular costosepta. With more than three trabeculae, their columellae are spongy and of variable width, even so, they do not exceed ¼ of the diameter of each calice. They have extensively concreted epitheca while their internal septal lobes are comparatively diminished but may be iconically paliform (Arrigoni et al. 2015).

The flattened or massive coralla of colonial *Acanthastrea maxima* are generated by circumoral budding which is accompanied by intra- and extra-calicular, where a larger central corallite typically dominates juveniles. Strains of this species do not form serial calices, whereas discretely integrated corallites lack separating coenosteum which fuses their walls. Be that as it may, corallite boundaries are seldom observed enclosed within a double wall. Calice diameters are typically large, albeit those that are medium sized, sometimes surround the quasi-central principal corallite. The distal boundaries of inclined corallites on corallum peripheries are predisposed to expansion, while their costae and septa remain incontiguous. There are five orders of septal cycles with thicker primary, secondary, and tertiary together with "free" quaternary, whose extremities curve towards and fuse with those of the previous cycle which unify with the upper columella. Costosepta are rarely confluent while the centres of corallites remain linked by lamellar processes. Spongy trabeculate columellae are ¼ of calice widths while internal lobes remain absent and epitheca are well-developed (Arrigoni et al. 2015).

The bases of *Sclerophyllia margariticola*'s mid-septal teeth are elliptical and aligned in parallel with lobular tips. The prominent teeth of S1 are uncommonly spaced at 2 mm apart whose shape is irregular, whilst those of lower cycles tend to be larger. Lateral septal granulations are strong and scattered, whereas interareas remain smooth or palisade. The upper margins of their septa plateau, whereas costoseptal cycles 1 and 3 bear uneven teeth (Table 4.; Arrigoni et al. 2015).

The tooth bases of *Acanthastrea maxima* are elliptical which run in parallel down the length of each septum, while their tips are lobate and irregular. The teeth of their first cycle are elevated and distributed at 2 mm apart like *S. margariticola*'s. Tooth shapes are irregular which are more sizeable on lower cycle septa, whilst their lateral granulation is strong and scattered. Interareas are palisade whereas the upper margins of primary and secondary septa are flattened, while asymmetry pervades the teeth of the third and first costoseptal cycle (Table 4.; Arrigoni et al. 2015).

Thanks to the morpho-molecular evidence, the experimenters were able to resurrect *Sclerophyllia* Klunzinger 1879 and *Sclerophyllia margariticola* Klunzinger 1879 and migrate *Acanthastrea maxima* as *Sclerophyllia maxima* Sheppard and Salm 1988. The molecular reconstruction of the character trait polystomatous budding suggests that it is a pervasive and heritable attribute within Lobophylliidae while the lineages of *Cynarina lacrymalis* and *Sclerophyllia margariticola* attest that the development of a

single mouth has occurred separately at least twice in their evolutionary histories (Fig 8.; Arrigoni et al. 2016).

The most conspicuous difference between the members of bispecific clade C is that *S. margariticola* and *S. maxima* are solitary or colonial which like poly- or mono-stomatous budding were previously considered generically-discriminating (Gittenberger et al. 2011; Benzoni et al. 2012a; Arrigoni et al. 2016), while internal lobes are absent in *S. maxima*. Their molecular analyses were indiscernible with merely nominal intergenic distances whilst they remain remarkably micromorphologically alike. The upper margins of their early cycle septa are peculiarly flattened unlike *Acanthastrea*'s species type, *A. echinata* whose are round, while eight of the 14 conventionally scored macromorphological and four of the seven micromorphological attributes separated the hitherto congeners *S. maxima* and *A. echinata*. The lateral septal granulations of *Sclerophylllia* are strong and scattered, whereas they are weak and enveloped in thickening deposits in the latter. Previously synonymised monostomatous *Sclerophyllia margariticola* and *Cynarina lacrymalis* bear a striking resemblance, yet closer inspection reveals they differ in the cycle, spacing, and thickness of their septa and costosepta. Besides, the septal teeth of the latter are wider and better developed (Arrigoni et al. 2015).

The genus *Sclerophyllia* is endemic to the Gulf of Aden, the Arabian Sea, the Gulf of Oman, the Persian Gulf, and the waters of the Red Sea, where *S. margariticola* has only been spotted in the latter, while comparatively rare *S. maxima* are only found in the remaining territories (Klunzinger 1879, cited in Arrigoni et al. 2015; Carpenter et al. 1997, cited in Arrigoni et al. 2016; Claereboudt 2006, cited in Arrigoni et al. 2015; Pichon et al. 2010). The exceptionally narrow strait of Bab al Mandab is likely responsible for forestalling species migrations between the Red Sea and the Gulf of Aden over the last 5 MY (Siddal et al. 2003); nevertheless, the prevailing paradigm concludes corals are "standalone" entities that evolve in isolation which become phenotypically, genotypically, and geographically diverse (Veron 1995, cited in Arrigoni et al. 2016; Ramirez-Portilla et al. 2022).

The comprehensive molecular as well as micromorphological studies of Arrigoni and colleagues reported in 2016(a) facilitated the resolution of two closely related genera: *Echinophyllia* and *Oxypora* for which genotypic investigations were hitherto lacking. Two iconic species, *E. echinoporoides* and *O. convoluta* were nested in a cluster comprising *E. aspera*, *E. orpheensis*, *E. tarae*, and *O. glabra*, while *E. echinata* and *O. lacera* were molecularly alike. Their findings erected Red Sea-endemic *E. bulbosa* and *E. gallii* that can be found off Maldivian atolls and in the waters of Mayotte (Arrigoni et al. 2016a).

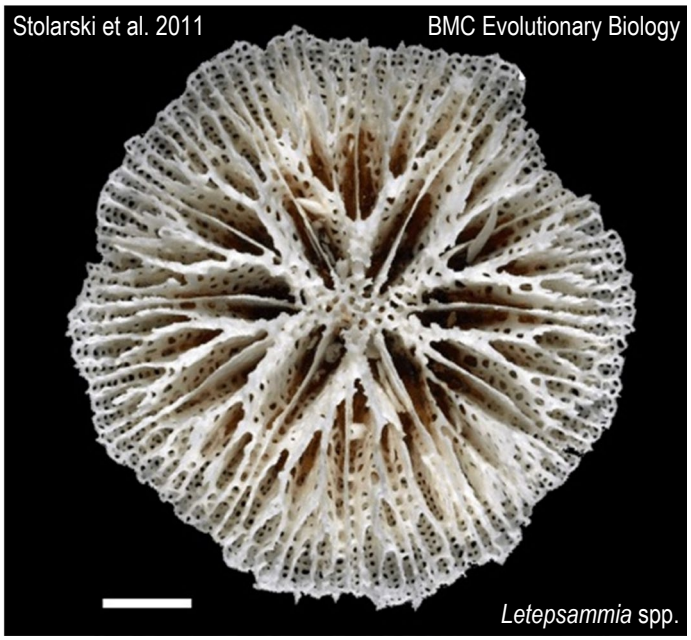
The family Dendrophylliidae is extraordinary insofar as its members are solitary or colonial, zooxanthellate or azooxanthellate, and inhabit shallow- or deep-water. Notwithstanding, this family was considered monophyletic in the absence of molecular analyses. Extensive morpho-molecular studies were thus carried out on 11 dendrophylliid genera and 30 species where the phylogenetic reconstruction exploited two mitochondrial and one nuclear locus, which assisted comparative micro-morphological and -structural examinations. The study affirmed the monophyly of the family yet unearthed significant para- or polyphyly in bi- or multi-specific genera apart from *Tubastraea*. The research thus highlighted evolutionary convergence, homoplasy, and intraspecific variation that remained undetected by conventional means. All genera remained micro- and macro-morphologically alike which in isolation hampered cladistics, yet *Tubastraea* were epitomised by conspicuous shingle-like TDs parallel to their skeletal outlines (Arrigoni et al. 2014c).

Fig 9. Corallivorous nudibranchs (*Phestilla melanobrachia*) upon a recently consumed deep-water azooxanthellate Dendrophylliidae (Scleractinia: Hexacorallia).

The scleractinian family Micrabaciidae has distinctive TDs composed of various configurations of ultra-microscopic spicule-like bundles that form a surface meshwork (Janiszewska et al. 2011), whereas their septa develop from porous wedge-like corallite wall incursions which appear iconically flower-like from above when they coalesce with those of the previous cycle. Costae alternate with septa around the corallite circumference (Janiszewska et al. 2013) while all such skeletal attributes separate this family from other Scleractinia (Janiszewska et al. 2015). Gardineriidae and Micrabaciidae form a convincing Basal clade whose ancestors began to emerge in the Ordovician (Stolarski et al. 2011). However, their earliest fossil record is 96 MYO from the Lower Cretaceous (Cenomanian) with 20 species of *Micrabacia* from the Mesozoic (Vaughan & Wells 1943). They were extensively distributed and prolific around North America and Europe yet appeared to wane in the Paleo- and -Eocene (Squires 1967) and were absent by the Oligocene. Even so, they reappeared in the Miocene as species of *Stephanophyllia* while *Leptopenus*, *Letepsammia*, and *Rhombopsammia* are their modern-day counterparts (Squires 1967; Cairns 1989). Squires suggested that the Micrabaciids of today may not be descended from species of *Micrabacia* (Squires 1967), albeit fossils do not comprise DNA, the features of their corallites remain remarkably conserved in extant and extinct genera. The study's aim was to complement the description of Micrabaciidae using informative fossilised *Stephanophyllia* from the Cenozoic (Janiszewska et al. 2015).

Corallite form and configuration are shared amongst extinct *Stephanophyllia elegans* Bronn 1837 and all living Micrabaciidae. However, ultra-magnification reveals variations in their thickening and rapid accretion deposits (TDs and RADs) which are most analogous. The microstructural analyses of fossils are enhanced by electron backscatter diffraction (EBSD), X-ray dispersion

fluorescence, cathodoluminescence (CL) microscopy, and Raman spectrometric mapping, which detects a tiny percentage of emissions with distinctive wavelengths scattered from a high-intensity laser to decipher developmental disparities in aragonite concretions (Janiszewska et al. 2015; Horiba 2019).



Diagenetic calcite recrystallisation typically perturbs the aragonite polymorphs of fossilised corals which demands careful interpretation when making direct comparisons with living specimens. However, Raman maps and CL microscopy revealed that the skeletons of *S. elegans* were entirely composed of aragonite and that the typical artefacts of calcite banding were absent from the primary frameworks of fossils from Korytnica. X-ray dispersion suggested that the ratios of magnesium (Mg) to calcium (Ca) and strontium (Sr) to Ca were 1 and 15 respectively (Janiszewska et al. 2015) which are indicative of ancient sea surface temperatures (SSTs) and seawater composition. Modern scleractinian aragonite comprises from 0.07 to 3.5 percent Mg (Bingman 1997; Holmes-Farley 2003a; Holmes-Farley 2003d; Holmes-Farley 2003e) with Sr to Ca ratios of ~9 to 12 (Stolarski et al. 2011), which are comparable to those of fossilised *S. elegans*. Biogenic crystals preserve some organic molecules in extant and extinct specimens, where scanning X-ray microscopy and mapping of 2D micro-fluorescence detected sulphur in RADS and TDs likely from the mucosal sulphated polysaccharides (Janiszewska et al. 2015) of mucin glycoproteins, where strontium ions (Sr^{2+}) likely neutralise sulphate repulsion through the formation of relatively stable, ionically bonded, and neutrally-charged strontium sulphate ($SrSO_4$; Clode & Marshall 2002; Holmes-Farley 2003d).

The thickening septal deposits of Miocene and Pliocene *Stephanophyllia* are composed of long, thin, juxtaposed fibres that thatch septa as opposed to the chip-like bundles of spicules that enmesh those of Recent micrabaciids. These two kinds of TDs are peculiar to this family which divided and continues to divide them from other extinct and present-day stony corals. Remarkably, the same structures were observed in fossils collected from several worldwide locations (Janiszewska et al. 2015) which may suggest that geographic separation in ancient seas was less of an evolutionary catalyst than it is today. Variances in the orientations of septal TDs were evident amongst the fossilised outgroup genera: *Flabellum*, *Porites*, and *Thecocyathus* preserved in Korytnica clay, where the fibres of the latter two were perpendicular to the corallum surface yet they were sub-parallel in the former which coalesced as scales. Analogous attributes are also observed in their current species (Janiszewska et al. 2015).

The microstructures of *Stephanophyllia* from the Neogene were distinct from all previous Micrabaciidae and any other corals. Furthermore, the two kinds of TDs described here for modern and ancient micrabaciids may indicate there is room for taxonomic revision. Despite the deep Basal divergence of Gardineriidae and Micrabaciidae, the former is macromorphologically and microstructurally distinct from the latter, while several solitary Scleractinia from the Mid-Triassic share the skeletal features of Gardineriidae, but those of Micrabaciidae are different to any other corals that grew in the Jurassic or Triassic which do not have even a hint of their rudimentary beginnings. A lack of common features or those that may be considered synapomorphies suggests that the ancestors of these families diverged several MY earlier, or that they arose from distinct lineages. The scleractinian dearth of the Ordovician and Middle Permian Palaeozoic (Scrutton & Clarkson 1991; Ezaki 1998) lends credence to the notion that their emergence was significantly more ancient (Stolarski et al. 2011). It has been suggested that either calciferous skeletons have been transitory on evolutionary timescales (Fautin & Lowenstein 1994) or that the substrates of the Palaeozoic were not conducive to fossil formation or these layers remain geologically undiscovered (Ezaki 1998; Janiszewska et al. 2015). Fossils of *Stephanophyllia* do not materialise until the Lower Cretaceous which may have evolved from a soft-bodied hexacorallian ancestor that became skeletonised which may have coincided with their ascent to shallow-water (Janiszewska et al. 2015).

Huang and allies' monograph published in 2016 was dedicated to Scleractinia conventionally ranked in the suborders Faviina and Meandriina or simply Faviina, whose morpho-molecular analyses revised species of the predominantly Robusta families: Anthemiphylliidae Vaughan 1907; Faviidae Gregory 1900; Meandrinidae Gray 1847; Merulinidae Verrill 1865; Mussidae Ortmann 1890; Oculinidae Gray 1847; Pectiniidae Vaughan and Wells 1943, Rhizangiidae d'Orbigny 1851, and Trachyphylliidae Verrill 1901 (Fukami et al. 2008; Kitahara et al. 2010; Stolarski et al. 2011; Huang 2012, cited in Huang et al. 2016; Huang & Roy 2015) where Faviina is also ordinal. Nonetheless, some of the genera of these families like *Ctenella* Matthai 1928 and *Galaxea* Milne Edwards and Haime 1857 are Complexa affiliates which were migrated to Euphylliidae Alloiteau 1952 in 2012 (Budd et al 2012; Huang et al. 2016). Huang and allies formally reorganised 84 species within Diploastraeidae, Merulinidae, and Montastraeidae in 2014 using their own morpho-molecular data and those of Huang and collaborators from 2011 and Arrigoni and colleagues from 2012. See Part I.

Taxonomic studies now aim to define the lineages of species by organising them into monophyletic clades comprising only and all the descendants of a common ancestor, which bear Arabian characters or Roman numerals. The researchers re-evaluated 44 species from clades XVIII to XX (Fukami et al. 2008) previously ranked in the family Lobophylliidae. The study constructed morphological and molecular trees clustering the lineages of subclades A to J commensurate with the findings of comparative DNA marker and corallite character analyses (Fig 10.; Huang et al. 2016).

Molecularly indistinguishable *Australomussa* Veron 1985, *Parascolymia* Wells 1964, and *Symphyllia* Milne Edwards and Haime 1848 of subclade I (Arrigoni et al. 2014b; Arrigoni et al. 2014c) were reclassified as junior synonyms of *Lobophyllia* de Blainville 1830 and thus became species of *Lobophyllia* which also absorbed *Acanthastrea ishigakiensis* as *L. ishigakiensis*. *Acanthastrea* Milne Edwards and Haime 1848 were shared amongst *Acanthastrea*, *Homophyllia*, *Lobophyllia*, *Micromussa* Veron 2000, and *Sclerophyllia* Klunzinger 1879, whilst *Cynarina* Bruggemann 1877 was upheld with the pectiniid genera *Echinomorpha*, *Echinophyllia*, and *Oxypora* (Huang et al. 2016).

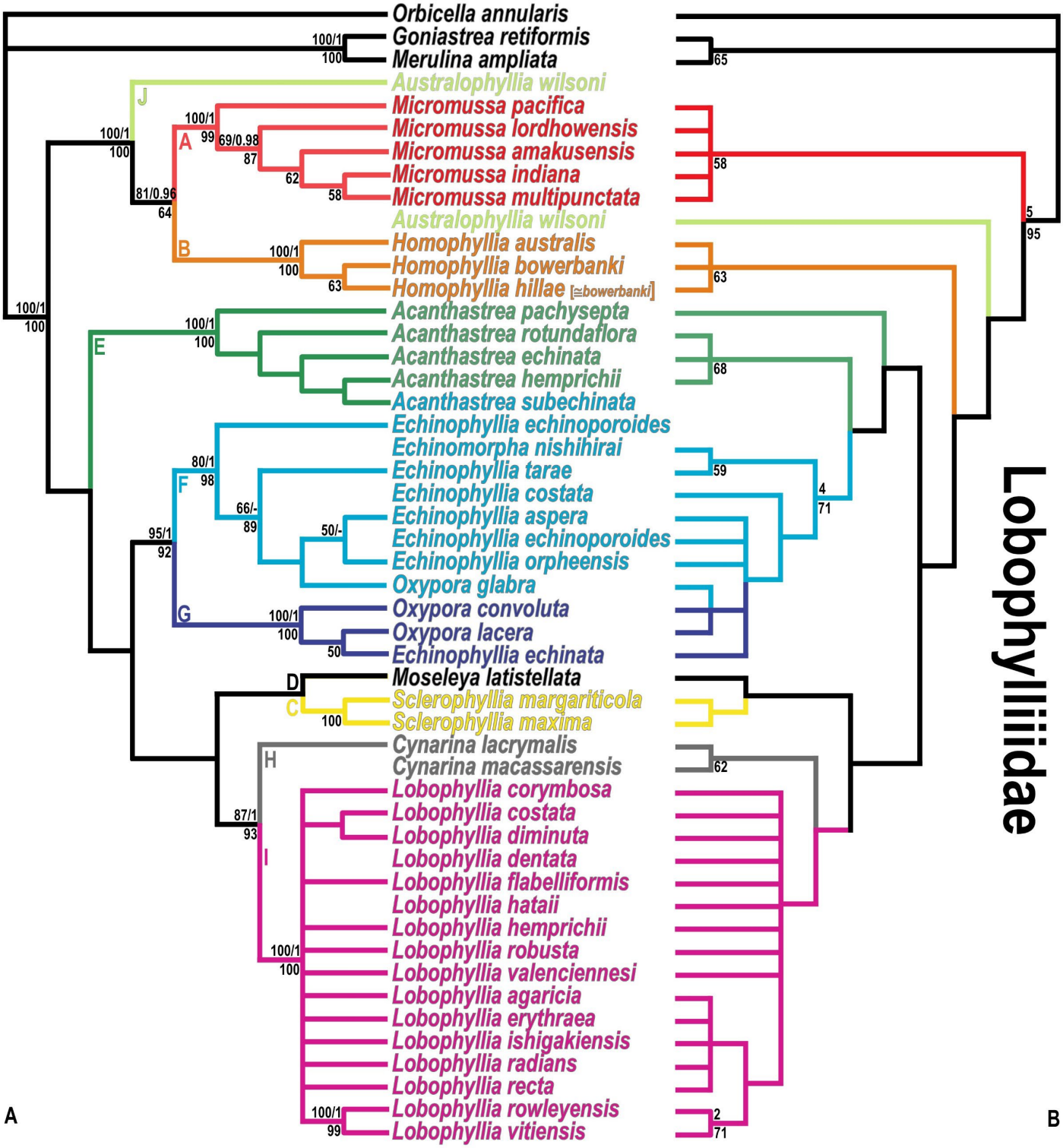


Fig 10. A representation of the evolutionary histories of the family Lobophylliidae where subclades A to J are coloured according to Arrigoni et al. 2015, with the overhead basally divergent corroborating merulinid outgroup: *Goniastrea retiformis*, *Merulina ampliata*, and *Orbicella annularis* of clade XVII. [A] a strict consensus of 18 maximum parsimony trees ascertained using the combined DNA sequence analyses of part histone H3, internally transcribed spacers 1 and 2 comprising 5.8 rDNA, and cytochrome c oxidase subunit I. Values above nodes specify maximum likelihood bootstrap ≥50% of 1,000/Bayesian posterior probability ≥0.9 whilst maximum parsimony bootstrap ≥50% is indicated beneath. [B] a strict consensus of 17 maximum parsimony trees delineated using 46 morphological attributes with at least minimal node support, where Bremer decay index ≥2 and maximum parsimony bootstrap ≥50% are featured above and beneath resolvable nodes. Adapted from data presented in Huang et al. 2016.

Geographic distributions were obtained from Veron 2000 (cited in Huang et al. 2016) as well as Veron and allies from 2009, 2011 (cited in Huang et al. 2016), and 2015 which were supplemented by surveys of the day (Huang et al. 2016).

Part sequences of nuclear DNA encoding histone H3, internally transcribed spacers 1 and 2 (ITS1; ITS2) including 5.8S rDNA, and informative sequences of mitochondrial cytochrome c oxidase subunit I (COI) were amplified and aligned from 44 species to yield a robust ancestral tree, whereas the morphological phylogenetic reconstruction of 47 taxa was of lower resolution with nominal node support (Fig 10. B). These findings re-emphasise the proficiency of combined morpho-molecular approaches.

Acanthastrea pachysepta (formerly: *Lobophyllia pachysepta* Chevalier 1975) grouped alongside its sister subclades E, F, and G in the morphological tree as opposed to clustering within E of the molecular tree. The skeletal attributes of this species shared common elements with *Lobophyllia* and *Acanthastrea*; however, the molecular data strongly recommended that *Lobophyllia pachysepta* be recombined as *Acanthastrea pachysepta.* Subclade D *Moseleya* Quelch 1884 and J *Australophyllia* Benzoni and Arrigoni 2016 remained monospecific (Arrigoni et al. 2016). The current study's nucleic acid analyses were first performed on *Oxypora convoluta* Veron 2000 which left merely five species of the lobophylliid genera *Echinophyllia* and *Oxypora* to be sampled and appraised, yet their ancestries were not straightforward. Para- and mono-phyletic *Echinophyllia* and *Oxypora* are shared between the multi-generic subclades F and G, where morphology inferred a deep basal divergence of *Echinomorpha nishihirai* and *E. tarae* Benzoni 2013 from subclade F. Studies of comparatively scarce Indo-Pacific *Oxypora crassispinosa* Nemenzo 1979 and rarely seen Red Sea *Oxypora egyptensis* Veron 2000 may assist clarification of the intricate evolutionary trajectories of this group. Pairs of sister genera were conspicuous in the molecular tree like *Micromussa* and *Homophyllia* of subclades A and B as well as *Cynarina* and *Lobophyllia* of subclades H and I, together with the trio *Australophyllia*, *Homophyllia*, and *Micromussa* of subclades J, B, and A. Nevertheless, the internal nodes for these parings are not supported, whilst the trinity's monophyly is not upheld in the morphological tree.

The researchers remarked that further work was required to define the ancestries of *Echinophyllia* and *Oxypora* and the interrelations of *Australophyllia*, *Homophyllia*, and *Micromussa* insofar as morphological analyses was still wanting with regard to finer scale phylogenetically-discerning and node-resolving skeletal traits. Moreover, *Micromussa regularis* Veron 2000 had yet to be ranked (Fig 10. A & B; Huang et al. 2016).

Fig 11. An iconic image posted on the Aquarium Advice forum under: "When acans attack!" The cf. *Acanthastrea* (Faviina: cf. Lobophylliidae) fragment on the left has released mesenterial filaments to digest the cf. *Favia* (Faviina: cf. Faviinae) "frag" to the right. Courtesy of Jimbo7 © 2010.

Micro- and macro-morphological features are the least and the most homoplastic while microstructures barely diverge within Lobophylliidae. Synapomorphy is rife amongst the sub-corallite micro-morphological and -structural features of Merulinidae and Lobophylliidae with two macromorphological. Despite over 20 studies extricating the lineages of these and related clades, several genera remained unresolved like *Australogyra*, *Boninastrea*, *Echinomorpha*, *Erythrastrea*, *Mycedium*, *Pectinia*, and *Physophyllia* (Huang et al. 2016).

Devoted teams of taxonomists continue to unravel the scleractinian conundrum, while next we divulge the evolutionary trajectories of the LPS family Lobophylliidae to a definitive end.

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.

Aposymbiosis describes symbiotic organisms that live autonomously.

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

Solitary **Calceolid** coralla are shaped like the front of a slipper (Oxford Reference 2024).

Canonical means substantiated or acknowledged.

Carina is a linear series of rapid accretion clusters.

Cercoid corallites lack coenosteum and share walls.

Solitary **Ceratoid** coralla are horn shaped with apical angles of less than 20° (Oxford Reference 2024).

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

Coenosteum is the part of the skeleton that adjoins the corallites of colonial species.

Colline are corallite-separating skeletal ridges composed of coenosteum (Riddle 2007).

Congeners refers to congeneric relatives.

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.

Solitary **Cylindrical** coralla are ellipsoidal with parallel-sides while those that are slightly S-shaped are **Scolecoid** (Oxford Reference 2024).

Cyathiform means goblet shaped.

The cells of a **Diploid** organism have a chromosome from each parent (2_n), whereas the copy number of **Haploid** organisms is 1_n.

Solitary **Discoid** coralla are shaped like buttons (Oxford Reference 2024).

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 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 (2_n) organism usually from each parent on opposing chromosomes where each one of an individual's 1_n 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.

Homoplasy and **Convergent Evolution** are synonymous insofar as they refer to the development of similar or identical traits in distinct species.

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

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**).

Meniane are sharp ridges formed from the fusion of consecutive septal granulations that run horizontally on either side of septal façades that occur in species of *Dactylotrochus* and *Leptoseris* (Agariciidae; Kitahara et al. 2012).

Monticules (**Hydnophores**) are conical peaks arising from abutting corallite walls.

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.

Pali are intracalicular pillar-like structures composed of rapid accretion centres hitherto regarded as trabeculate rods.

Paliform septal **Lobes** are typically hemispherical **Exsert** upper-margin protuberances that may in some cases crown the upper columella. See Part III's 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.

Solitary **Patellate** coralla have low profiles with apical angles equal to, or those that exceed, 120° (Oxford Reference 2024).

The corallites of **Phaceloid** skeletons form distinct branches which lack coenosteum.

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 mutagenic nucleotide substitutions.

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 1995a).

Symbiosis is the coexistence of two or more closely associated organisms which 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 phylogenetically-discriminating empirical attributes that epitomise a monophyletic clade (Hennig 1957, cited in Arrigoni et al. 2019).

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

Syntenic means "threaded together" which refers to several intrachromosomal genes traced using somatic cell hybridisation (Russell 1998).

Tectura are thickening deposits (TDs) that lie outside the corallite wall's front of rapid accretion that may aggregate into scale-like structures that are evident in most Agariciidae (Kitahara et al. 2012).

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).

Solitary **Trochoid** coralla are conical with apical angles of 40^{o} (Oxford Reference 2024).

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

References

Arrigoni, R., Benzoni, F., Huang, D., Fukami, H., Chen, C., A., Berumen, M., L., Hoogenboom, M., Thomson, D., P., Hoeksema, B., W., Budd, A., F., Zayasu, Y., Terraneo, T., I., Kitano, Y., F. & Baird, A., H. (2016) When forms meet genes: revision of the scleractinian genera Micromussa and Homophyllia (Lobophylliidae) with a description of two new species and one new genus. Contributions to Zoology. 85, 387-422.

Arrigoni, R., Berumen, M., L., Chen, C., A., Terraneo, T., I., Baird, A., H., Payri, C. & Benzoni, F. (2016a) Species delimitation in the reef coral genera Echinophyllia and Oxypora (Scleractinia, Lobophylliidae) with a description of two new species. Mol. Phylogenet. Evol. 105, 146-159.

Arrigoni, R., Berumen, M., L., Stolarski, J., Terraneo, T., I. & Benzoni, F. (2019) Uncovering hidden coral diversity: a new cryptic lobophylliid scleractinian from the Indian Ocean. Cladistics. 35, 301-328.

Arrigoni, R., Berumen, M., L., Terraneo, T., I., Caragnano, A., Bouwmeester, J. & Benzoni, F. (2015) Forgotten in the taxonomic literature: resurrection of the scleractinian coral genus Sclerophyllia (Scleractinia, Lobophylliidae) from the Arabian Peninsula and its phylogenetic relationships. Systematics and Biodiversity. 49, 140-163.

Arrigoni, R., Kitano, Y., F., Stolarski, J., Hoeksema, B., W., Fukami, H., Stefani, F., Galli, P., Montano, S., Castoldi, E. & Benzoni, F. (2014c) A phylogeny reconstruction of the Dendrophylliidae (Cnidaria, Scleractinia) based on molecular and micromorphogical criteria, and its ecological implications. Zoologica Scripta. 43, 661-688.

Arrigoni, R., Richards, Z., T., Chen, C., A., Baird, A., H. & Benzoni, F. (2014d) Taxonomy and phylogenetic relationships of the coral genera Australomussa and Parascolymia (Scleractinia, Lobophylliidae). Contributions to Zoology. 83, 195-215.

Arrigoni, R., Richards, Z., T., Chen, C., A., Baird, A., H. & Benzoni, F. (2014a) Phylogenetic relationships and taxonomy of the coral genera Australomussa and Parascolymia (Scleractinia, Lobophylliidae). Contributions to Zoology. 83, 195-215.

Arrigoni, R., Stefani, F., Pichon, M., Galli, P. & Benzoni, F. (2012) Molecular phylogeny of the Robust clade (Faviidae, Mussidae, Merulinidae, and Pectiniidae): an Indian Ocean perspective. Molecular Phylogenetics and Evolution. 65, 183-193.

Arrigoni, R., Terraneo, T., I., Galli, P. & Benzoni, F. (2014b) Lobophylliidae (Cnidaria, Scleractinia) reshuffled: pervasive non-monophyly at genus level. Molecular Phylogenetics and Evolution. 73, 60-64.

Barbeitos, M., Romano, S. & Lasker, H., R. (2010) Repeated loss of coloniality and symbiosis in scleractinian corals. Proceedings of the National Academy of Science. 26, 11877-11882.

Baron-Szabo, R., C. (2002) Scleractinian Corals of the Cretaceous. A Guide to Cretaceous Forms with Descriptions, Illustrations, and Remarks on their Taxonomic Position. Baron-Szabo, Knoxville, TN, USA.

Baron-Szabo, R., C. (2008) Corals of the K/T-boundary: scleractinian corals of the suborders Dendrophylliina, Caryophylliina, Fungiina, Microsolenina, and Stylinina. Zootaxa. 1952, 1-244.

Benzoni, F. (2006) Psammocora albopicta sp. nov., a new species of scleractinian coral from the Indo-West Pacific (Scleractinia; Siderastreidae). Zootaxa 1358: 49-57.

Benzoni, F., Arrigoni, R., Stefani, F. & Pichon, M. (2011) Phylogeny of the coral genus Plesiastrea (Cnidaria, Scleractinia). Contributions to Zoology. 80(4), 231-24.

Benzoni, F., Arrigoni, R., Stefani, F. & Stolarski, J. (2012a) Systematics of the coral genus Craterastrea (Cnidaria, Anthozoa, Scleractinia) and description of a new family through combined morphological and molecular analyses. Systematics and Biodiversity. 10, 417-433.

Benzoni, F., Arrigoni, R., Stefani, F., Reijnen, B., T., Montano, S. & Hoeksema, B., W. (2012) Phylogenetic position and taxonomy of Cycloseris explanulata and C. wellsi (Scleractinia: Fungiidae): lost mushroom corals find their way home. Contributions to Zoology. 81, 125-146.

Benzoni, F., Stefani, F., Pichon, M. & Galli, P. (2010) The name game: morpho-molecular species boundaries in the genus Psammocora (Cnidaria, Scleractinia). Zoological Journal of the Linnean Society. 160, 421-456.

Bingman, C. (1997) Calcium Carbonate for CaCO3/CO2 Reactors: More Than Meets the Eye. http://web.archive.org/web/20010210225056/http://www.animalnetwork.com/fish2/aqfm/1997/aug/bio/default.asp

Budd, A., F. & McNeill, D., F. (1998) Zooxanthellate scleractinian corals from the Bowden Shell Bed, SE Jamaica. Contributions to Tertiary and Quaternary Geology. 35, 49-65.
Budd, A., F. & Stolarski, J. (2009) Searching for new morphological characters in the systematics of scleractinian reef corals: comparison of septal teeth and granules between Atlantic and Pacific Mussidae. Acta Zoologica. 90, 142-165.
Budd, A., F. & Stolarski, J. (2011) Corallite wall and septal microstructure in scleractinian reef corals: Comparison of molecular clades within the family Faviidae. J Morphol. 272, 66-88.
Budd, A., F., Fukami., H., Smith, N. & Knowlton, N. (2012) Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). Zoological Journal of the Linnean Society. 166, 465-529.
Budd, A., F., Romano, S., L., Smith, N., D. & Barbeitos, M., S. (2010) Rethinking the phylogeny of scleractinian corals: A review of morphological and molecular data. Integr Comp Biol. 50, 411-427. http://www.doi.org/10.1093/icb/icq062
Budd, A., F., Stemann, T., A. & Stewart, R., H. (1992) Eocene Caribbean reef corals: a unique fauna from the Gatuncillo Formation of Panama. Journal of Paleontology. 66. 570-594.
Cairns, S., D. (1989) A revision of the ahermatypic Scleractinia of the Philippine Islands and adjacent waters, Part 1: Fungiacyathidae, Micrabaciidae, Turbinoliinae, Guyniidae, and Flabellidae. Smithsonian Contributions to Zoology. 486, 1-136
Cairns, S., D. (2009) Online appendix: Phylogenetic list of 711 valid Recent azooxanthellate scleractinian species, with their junior synonyms and depth ranges. In: J. M. Roberts, A. Wheeler, A. Freiwald & S. D. Cairns (Eds) Cold Water Corals: The Biology and Geology of Deep-Sea Corals Habitats. Cambridge University Press. http://www.lophelia.org/pdf/Cold-water_Corals_Online_Appendix_000.pdf
Cairns, S., D., Hoeksema, B., W. & van der Land, J. (1999) Appendix: list of extant Stony Corals. Atoll Research Bulletin. 459, 13-46.
Carpenter, K., E., Harrison, P., L., Hodgson, G., Alsaffar, A., H. & Ajhazeem, H. (1997) The corals and coral reefs of Kuwait. Kuwait: Inst Scientific Research and Environment Public Authority.
Chevalier, J., P. & Beauvais, L. (1987) Ordre des scléractiniaires: XI. Systématique. Traité de zoologie. Tome III. Cnidaires: Anthozoaires. Grassé, P., P & Doumenc, D. (eds.). Masson, Paris. pp 679–764.
Chevalier, J., P. (1961) Recherches sur les madréporaries et les formations récifals miocènes de la Mediterranée occidentale. Memoirs of the Geological Society of France. 93, 1-562.
Chevalier, J., P. (1968) Expédition francaise sur les récifs coralliens de la Nouvelle Calédonie. Fond Singer-Polignac. I, 1-155.
Chevalier, J., P. (1971) Les scléractiniaires de la Mélanésie française (Nouvelle Calédonie, Iles Chesterfield, Iles Loyauté, Nouvelles Hébrides). Première partie. Expédition Française sur les Récifs Coralliens de la Nouvelle Calédonie. 5, 1-307.
Chevalier, J., P. (1975) Les Scléractiniaires de la Mélanésie Française (Nouvelle-Calédonie, Iles Chesterfield, Iles Loyauté, Nouvelles Hébrides). Expédition Francaise Sur les Récifs Coralliens de la Nouvelle-Calédonie, Deuxieme Partie. 7, 1-407.
Claereboudt, M., R. (2006) Coral Reefs and Reef Corals of the Gulf of Oman. Al-Roya Publishing, Muscat.
Clode, P., L. & Marshall, A., T. (2002) Low temperature X-ray microanalysis of calcium in a scleractinian coral: evidence of active transport mechanisms. Journal of Experimental Biology. 205(22), 3543-3552.
Cohen, A., L., Owens, K., E., Layne, G., D. & Shimizu, N. (2002) The Effect of Algal Symbionts on the Accuracy of Sr/Ca Paleotemperatures from Coral. Science. 296(5566), 331-333.
Cuif, J-P. & Dauphin, Y. (2005) The two-step mode of growth in the scleractinian coral skeletons from the micrometre to the overall scale. Journal of Structural Biology. 150, 319–331.
Cuif, J-P. & Perrin, C. (1999) Micromorphology and microstructure as expressions of scleractinian skeletogenesis in Favia fragum (Esper, 1795) (Faviidae, Scleractinia). Zoosystema. 21, 137-156.
Cuif, J-P., Dauphin, Y. & Gautret, P. (1998) Compositional diversity of soluble mineralizing matrices in some recent coral skeletons compared to fine-scale growth structures of fibers: discussion of consequences for biomineralization and diagenesis. International Journal of Earth Sciences. 88, 582-592.
Cuif, J-P., Lecointre, G., Perrin, C., Tillier, A. & Tillier, S. (2003) Patterns of septal biomineralization in Scleractinia compared with their 28S rRNA phylogeny: a dual approach for a new taxonomic framework. Zoologica Scripta. 32, 459-473.
Durham, J., W. (1943) Pacific Coast Cretaceous and Tertiary corals. Journal of Paleontology. 17, 196-202.
Ezaki, Y. (1998) Palaeozoic Scleractinia: progenitors or Extinct Experiments? Paleobiology. 24, 227-234.
Fautin, D., G. & Lowenstein, J., M. (1994) Phylogenetic relationships among scleractinians, actiniarians, and corallimorpharians (Coelenterata: Anthozoa). Proceedings of the Seventh International Coral Reef Symposium. 2, 665-670.
Fricke, H., W., Vareschi, E. & Schlichter, D. (1987) Photoecology of the coral Leptoseris fragilis in the Red Sea twilight zone (an experimental study by submersible). Oecologia. 73, 371-381. http://www.doi.org/10.1007/BF00385253
Fukami, H., Budd, A., F., Paulay, G., Solé-Cava, A., Chen, C., A., Iwao, K.& Knowlton, N. (2004) Conventional taxonomy obscures deep divergence between Pacific and Atlantic corals. *Nature.* 427, 832-835.
Fukami, H., Chen, C., A., Budd, A., F., Collins, A., Wallace, C. et al. (2008) Mitochondrial and nuclear genes suggest that stony corals are monophyletic but most families of stony corals are not (Order Scleractinia, Class Anthozoa, Phylum Cnidaria). PLOS ONE. 3.
Gittenberger, A., Reijnen, B., T. & Hoeksema, B., W. (2011) A molecularly based phylogeny reconstruction of mushroom corals (Scleractinia: Fungiidae) with taxonomic consequences and evolutionary implications for life history traits. Contributions to Zoology. 80, 107-132.
Glynn, P., W., Maté, J., L. & Stemann, T., A. (2001) Pavona chiriquiensis, a new species of zooxanthellate scleractinian coral (Cnidaria: Anthozoa: Agariciidae) from the eastern tropical Pacific. Proceedings of the Biological Society of Washington. 10, 210-225.
Gravier, C. (1907) Note sur quelques coraux des recifs du Golfe de Tadjourah. Bulletin du Museum d'Histoire Naturelle, 13, 339-343.
Gravier, C., J. (1911) Les recifs de coraux et les madreporaires de la baie de Tadjourah (Golfe d'Aden). Masson: Annales de l'Institut Oceanographique.
Gong, S., Liang, J., Jin, X., Xu, L., Zhao, M. & Yu, K. (2023) Unfolding the secrets of microbiome (Symbiodiniaceae and bacteria) in cold-water coral. Environmental Microbiology. 11(5). https://doi.org/10.1128/spectrum.01315-23
Hennig, W. (1957) Systematik und Phylogenese. In: Hannemann, H.-J. (Ed.), Berichtuber die Hundertjahrfeier der Deutschen Entomologischen Gesellschaft Berlin. Akademie Verlag, Berlin. pp 50-71.
Hoeksema, B., W. (2007) Delineation of the Indo-Malayan Centre of Maximum Marine Biodiversity: The Coral Triangle. Biogeography, Time and Place: Renema, W. (ed.). Distributions, Barriers and Islands. pp. 117-178
Holmes-Farley, R. (2003a) Aquarium Chemistry: Magnesium in Reef Aquaria. AdvancedAquarist.com. Volume 11. https://www.advancedaquarist.com/2003/10/chemistry
Holmes-Farley, R. (2003d) Aquarium Chemistry: Strontium and the Reef Aquarium. AdvancedAquarist.com. https://www.advancedaquarist.com/2003/11/chemistry
Holmes-Farley, R. (2003e) Aquarium Chemistry: Magnesium and Strontium in Limewater. AdvancedAquarist.com. https://www.advancedaquarist.com/2003/12/chemistry
Horiba (2019) What is Raman Spectroscopy? Horiba.com. https://www.horiba.com/en_en/raman-imaging-and-spectroscopy/
Huang, D. & Roy, K. (2013) Anthropogenic extinction threats and future loss of evolutionary history in reef corals. Ecology and Evolution. 3, 1184-1193.
Huang, D. & Roy, K. (2015) The future of evolutionary diversity in reef corals. Philosophical Transactions of the Royal Society B-Biological Sciences. 370,

20140010.
Huang, D. (2012) Threatened reef corals of the world. PLoS ONE. 7, e34459.
Huang, D., Arrigoni, R., Benzoni, F., Fukami, H., Knowlton, N., Smith, N., D., Stolarski, J., Chou, L., M. & Budd, A., F. (2016) Taxonomic classification of the reef coral family Lobophylliidae (Cnidaria: Anthozoa: Scleractinia). Zoological Journal of the Linnean Society. 178, 436-481.
Huang, D., Benzoni, F., Fukami, H., Knowlton, N., Smith, N., D. & Budd, A., F. (2014) Taxonomic classification of the reef coral families Merulinidae, Montastraeidae, and Diploastraeidae (Cnidaria: Anthozoa: Scleractinia). Zoological Journal of the Linnean Society. 171, 277-355.
Huang, D., Licuanan, W., Y., Baird, A., H. & Fukami, H. (2011) Cleaning up the 'Bigmessidae': molecular phylogeny of scleractinian corals from Faviidae, Merulinidae, Pectiniidae and Trachyphylliidae. BMC Evolutionary Biology. 11, 37.
Huang, D., Meier. R,, Todd, P., A. & Chou, L., M. (2008) Slow mitochondrial COI sequence evolution at the base of the metazoan tree and its implications for DNA barcoding. Journal of Molecular Evolution. 66, 167-174.
Janiszewska, K., Jaroszewicz, J. & Stolarski, J. (2013) Skeletal ontogeny in basal scleractinian micrabaciid corals. Journal of Morphology. 274, 243-257.
Janiszewska, K., Stolarski, J., Benzerara, K., Meibom, A., Mazur, M., Kitahara, M., V. & Cairns, S., D. (2011) A unique skeletal microstructure of the deep-sea micrabaciid scleractinian corals. Journal of Morphology. 231, 191-203.
Janiszewska, K., Stolarski, J., Kitahara, M., V., Neuser, N., D. & Mazur, M. (2015) Microstructural disparity between basal micrabaciids and other Scleractinia: new evidence from Neogene Stephanophyllia. Lethaia. http://www.doi.org/10.1111/let.12119
Kayal, E., Roure, B., Philippe, H., Collins, A., G. & Lavrov, D., V. (2013) Cnidarian phylogenetic relationships as revealed by mitogenomics. BMC Evol Biol. 13, 5.
Kerr, A., M. (2005) Molecular and morphological supertree of stony corals (Anthozoa: Scleractinia) using matrix representation parsimony. Biological Reviews of the Cambridge Philosophical Society. 80, 1-16. http://www.doi.org/10.1017/S1464793105006780
Kitahara, M., V, Stolarski, J., Cairns, S., D., Benzoni, F., Stake, J., L. & Miller, D., J. (2012b) The first modern solitary Agariciidae (Anthozoa, Scleractinia) revealed by molecular and microstructural analysis. Invertebrate Systematics. 26, 303-315.
Kitahara, M., V. & Cairns, S., D. (2009) Revision of the genus Deltocyathus (Cnidaria, Scleractinia), with a description of a new species from New Caledonia. Zoosystema. 31, 233-249.
Kitahara, M., V., Cairns, S., D. & Miller, D., J. (2010a) Monophyletic origin of the Caryophyllia (Scleractinia; Caryophylliidae), with description of six new species. Systematics and Biodiversity. 8, 91-118. http://www.doi.org/10.1080/14772000903571088
Kitahara, M., V., Cairns, S., D., Stolarski, J. & Miller, D., J. (2012) Deltocyathiidae, an early diverging family of Robust corals (Anthozoa, Scleractinia). Zoologica Scripta. 42, 201-212.
Kitahara, M., V., Cairns, S., D., Stolarski, J., Blair, D. & Miller, D., J. (2010) A comprehensive phylogenetic analysis of the Scleractinia (Cnidaria, Anthozoa) based on mitochondrial CO1 sequence data. PLOS ONE. 5.
Kitahara, M., V., Cairns, S., D., Stolarski, J., Blair, D. & Miller, D., J. (2010b) A comprehensive phylogenetic analysis of the Scleractinia (Cnidaria, Anthozoa) based on mitochondrial CO1 sequence data. PLoS ONE. 5, e11490.
Kitahara, M., V., Cairns, S., D., Stolarski, J., Miller, D., J. (2012a) Deltocyathiidae, an early-diverging family of Robust corals (Anthozoa, Scleractinia). Zoologica Scripta. 42, 201-212.
Klunzinger, C., B. (1879) Die Korallenthiere des Rothen Meeres, 3. Theil: Die Steinkorallen. Zweiter Abschnitt: Die Asteraeaceen und Fungiaceen, Berlin: Gutmann.
Lang, W., D. & Smith, S. (1935) Cyathophyllum caespitosum Goldfuss, and other Devonian corals considered in a revision of that species. Quarterly Journal of the Geological Society. 91, 538-590.
Le Goff-Vitry, M., C., Rogers, A., D. & Baglow, D. (2004) A deep-sea slant on the molecular phylogeny of the Scleractinia. Molecular Phylogenetics and Evolution. 30, 167-177.
Licuanan, W., Y. & Aliño, P., M. (2009) Leptoseris kalayaanensis (Scleractinia: Agariciidae), a new coral species from the Philipines. The Raffles Bulletin of Zoology. 57, 1-4.
Mariotti, N. (2003) Nerone, Central Apennines, Italy). Geobios. 36, 603-623.
Matthai, G. (1914) A revision of the Recent colonial Astræidæ possessing distinct corallites. Transactions of the Linnean Society of London. 17, 1-140.
Matthai, G. (1928) A monograph of the recent meandroid Astraeidae. Catalogue of the Madreporarian Corals in the British Museum (Natural History). 7, 1-288..
Montanaro-Gattinelli, E. (1943) Coralli costruttori delle scogliere emerse di Massaua e Gibuti. Roma: Reale Accademia d'Italia.
Nothdurft, L. D. & ·Webb, G., E. (2007) Microstructure of common reef-building coral genera Acropora, Pocillopora, Goniastrea and Porites: constraints on spatial resolution in geochemical sampling. Facies. 53, 1-26. http://www.dio.org/10.1007/s10347-006-0090-0
Okubo, N., Mezaki, T., Nozawa, Y., Nakano, Y., Lien, Y-T., et al. (2013) Comparative Embryology of Eleven Species of Stony Corals (Scleractinia). PLoS ONE 8(12), e84115. http://www.doi.org/10.1371/journal.pone.0084115
Oxford Reference (2024) Solitary Corallum Definitions for Calceloid, Caratoid, Discoid, Patellate, Scolecoid, and Trochoid. https://www.oxfordreference.com/display/10.1093/oi/authority.20110803100517268
Pandey, D., K. & Fürsich, F., T. (2005) Jurassic corals from southern Tunisia. Zitteliana. A 45, 3-34.
Pandey, D., K., Fursich, F., T., Baron-Szabo, R., M. & Wilmsen, M. (2007) Lower Cretaceous corals fromthe Koppeh Dagh, NE-Iran.Zitteliana. A47, 3-52.
Paulay, G. (1997) Diversity and distribution of reef organisms. Life and death of coral reefs. Birkeland, C. (ed.). Chapman & Hall, New York. pp 298-353.
Pichon, M., Benzoni, F., Chaineu, C., H. & Dutriex, E. (2010) Field Guide to the hard corals of the southern coast of Yemen. Biotope Parthenope, Paris.
Ramirez-Portilla, C., Baird, A., H., Cowman3, P., F., Quattrini, A., M., Harii, S., Frederic Sinniger, F. & Flot, J-F. (2022) Solving the Coral Species Delimitation Conundrum. *Syst. Biol.* 71(2), 461-475. http://www.dio.org/10.1093/sysbio/syab077
Richards, Z., T., Wallace, C., C. & Miller, D., J. (2013) Molecular phylogenetics of geographically restricted Acropora species: Implications for conservation. Molecular Phylogenetics and Evolution. 69, 837-851.
Richter, D., K., Immenhauser, A. & Neuser, R., D. (2008) Electron Backscatter Diffraction (EBSD) documents randomly oriented c-axes in moonmilk calcite fibres - evidence for biologically induced precipitation. Sedimentology. 55, 487-497.
Riddle, D. (2007) Stony Coral Identification Primer for Aquarists, Part One. AdvancedAquarist. Com. https://reefs.com/magazine/stony-coral-identification-primer-for-aquarists-part-one/
Roberts, J., M., Long, D., Wilson, J., B., Mortensen, P., B. & Gage, J., D. (2003) The cold-water coral Lophelia pertusa (Scleractinia) and enigmatic seabed mounds along the northeast Atlantic margin: are they related? Marine Pollution Bulletin. 46, 7-20.
Romano, S., L. & Cairns, S., D. (2000) Molecular phylogenetic hypotheses for the evolution of scleractinian corals. Bulletin of Marine Science. 67, 1043-1068.
Romano, S., L. & Palumbi, S., R. (1996) Evolution of scleractinian corals inferred from molecular systematics. Science. 271. 640-642. http://www.doi.org/10.1126/science.271.5249.640
Russell, P., J. (1998) Genetics Fifth Edition. Russell, P., J., Buck, E & Dhillon, A. (eds.). The Benjamin/Cumming Publishing Company Inc., Melo Park, CA, USA. p 183; G 8.
Schmidt-Roach, S., Lundgren, P., Miller, K., J., Gerlach, G., Noreen, A. & Andreakis, N. (2012) Assessing hidden speciesdiversity in the coral Pocillopora damicornis from Eastern Australia. Coral Reefs. 32, 1-12.
Schmidt-Roach, S., Miller, K., J. & Andreadkis, N. (2013) Pocillopora aliciae: a new species of scleractinian coral (Scleractinia, Pocilloporidae) from subtropical

Eastern Australia. Zootaxa. 3626, 576-582.
Schmidt-Roach, S., Miller, K., J., Lundgren, P. & Andreakis, N. (2014) With eyes wide open: a revision of species within and closely related to the Pocillopora damicornis species complex (Scleractinia; Pocilloporidae) using morphology and genetics. Zoological Journal of the Linnean Society. 170, 1-33.
Schuhmacher, H. & Zibrowius, H. (1985) What is hermatypic? Coral Reefs. 4, 1-9.
Scrutton, C., T. & Clarkson, E., N., K. (1991) A new scleractinian-like coral from the Ordovician of the Southern Uplands, Scotland. Palaeontology. 34, 179-194.
Sheppard, C., R., C. & Salm, R., V. (1988) Reef and coral communities of Oman, with a description of a new coral species (Order Scleractinia, genus Acanthastrea). Journal of Natural History 22, 263-279.
Sheppard, C., R., C. & Sheppard, A., L., S. (1991) Corals and coral communities of Saudi Arabia. Fauna of Arabia. 12, 1-170.
Souter, P. (2010) Hidden genetic diversity in a key model species of coral. Marine Biology. 157, 875-885.
Squires, D., F. (1958) The Cretaceous and Tertiary corals of New Zealand. New Zealand Geological Survey, Paleontology Bulletin. 29, 107.
Squires, D., F. (1967) The evolution of the deep-sea coral family Micrabaciidae. Studies in Tropical Oceanography. 5, 502-510.
Stefani, F., Benzoni, F., Pichon, M., Cancelliere. C. & Galli, P. (2008) A multidisciplinary approach to the definition of species boundaries in branching species of the coral genus Psammocora (Cnidaria, Scleractinia). Zoologica Scripta. 37, 71-91.
Stolarski, J. (1995) Ontogenetic development of the thecal structures in Caryophylliinae scleractinian corals. Acta Palaeontologica Polonica. 40, 19-44.
Stolarski, J. (1996) Gardineria - a scleractinian living fossil. Acta Palaeontologica Polonica. 41, 339-367.
Stolarski, J. (2003) Three-dimensional micro- and nanostructural characteristics of the scleractinian coral skeleton: a biocalcification proxy. Acta Paleontol Polo. 48, 497–530.
Stolarski, J., Kitahara, M., V., Miller, D., J., Cairns, S., D., Mazur, M. & Meibom, A. (2011) An ancient evolutionary origin of Scleractinia revealed by azooxanthellate corals. BMC Evolutionary Biology. 11, 316. http://www.doi.org/10.1186/1471-2148-11-316
Stryer, L. (1995a) Biochemistry 4th Edition. Stryer, L. (ed.). W. H. Freeman and Company, New York. pp 653-682.
Vaughan, T., W. & Wells, J., W. (1943) Revision of the suborders, families, and genera of the Scleractinia. Geological Society of America, Special Paper. 44, 1-363.
Veron, J. E., N., Devantier, L., M., Turak, E., Green, A., L., Kininmonth, S., Stafford-Smith, M. & Peterson, N. (2009) Delineating the Coral Triangle. Galaxea, Journal of Coral Reef Studies. 11, 91-100.
Veron, J., E., N. & Pichon, M. (1980) Scleractinia of Eastern Australia. Part 3, Families Agariciidae, Siderastreidae, Fungiidae, Oculinidae, Merulinidae, Mussidae, Pectiniidae, Caryophylliidae, Dendrophyliidae. Australian Institute of Marine Science Monograph Series. 4, 1-422.
Veron, J., E., N. (1985) New Scleractinia from Australian coral reefs. Records of the Western Australian Museum. 12, 147-183.
Veron, J., E., N. (1986) Corals of Australia and the Indo-Pacific. Angus & Robertson, Sydney.
Veron, J., E., N. (1995) Corals in space and time. Veron, J., E., N. (ed.). UNSW Press, Sydney.
Veron, J., E., N. (2000) Corals of the World. Townsville: Australian Institute of Marine Science.
Veron, J., E., N. (2000a) Corals of the World. Volume 2. Australian Institute of Marine Science, Townsville.
Veron, J., E., N., DeVantier, L., M., Turak, E., Green, A., L., Kininmonth, S., Stafford-Smith, M., G. & Peterson, N. (2009) Delineating the Coral Triangle. Galaxea. 11, 91-100.
Veron, J., E., N., DeVantier, L., M., Turak, E., Green, A., L., Kininmonth, S., Stafford-Smith, M., G. & Peterson, N. (2011) The Coral Triangle. Coral reefs: an ecosystem in transition. Dubinsky, Z. & Stambler, N. (eds.). Springer, Dordrecht. pp 47-55.
Veron, J., E., N., Odorico, D., M., Chen, C., A. & Miller, D., J. (1996) Reassessing evolutionary relationships of scleractinian corals. Coral Reefs. 15, 1-9.
Veron, J., E., N., Pichon, M. & Wijsman-Best, M. (1977) Scleractinia of eastern Australia. Part II. Families Faviidae, Trachyphylliidae. Australian Institute of Marine Science, Townsville.
Veron, J., Stafford-Smith, M., DeVantier, L. & Turak, E. (2015) Overview of distribution patterns of zooxanthellate Scleractinia. Frontiers in Marine Science. 1, 81.
Wallace, R., A., Sanders, G., P. & Ferl, R., J. (1996) Biology: The Science of Life, Fourth Edition, HaperCollins Publishers Inc. New York, USA. G-22; pp 384-385.
Wells, J., W. (1936) The nomenclature and type species of some genera of Recent and fossil corals. American Journal of Science. 31, 97-134
Wells, J., W. (1937) Coral studies. I Two new species of fossil corals. II Five new genera of the Madreporaria. Bulletins of American Paleontology, 23, 238-253.
Wells, J., W. (1956) Scleractinia. Treatise on invertebrate paleontology by Lawrence, F., K., S. Moore, R., C. (ed.). Geological Society of America and University of Kansas Press. F328– F444.
Wells, J., W. (1964) The recent solitary mussid scleractinian corals. Zoologische Mededelingen. 39, 375-384.
Wells, J., W. (1976) Eocene corals from Eua, Tonga. Geological Survey Professional Paper. 640-G, G1-G13.
Wijsman-Best, M. (1977) Indo-Pacific coral species belonging to the subfamily Montastreinae Vaughan & Wells, 1943 (Scleractinia-Coelenterata) Part I. The genera Montastrea and Plesiastrea. Zoologische Mededelingen Leiden. 52, 81-97.

Hashtags: #coralreefs #coralconservation #reefrestoration #MarineConservation #coralreefconservation #oceanconservation #thecompletereefaquarist #reefconservation #reefaquarium
A marine aquarium, reef tank, and saltwater fish system guide, handcrafted by a coral reef expert.