When forms meet genes: revision of the scleractinian genera Micromussa and Homophyllia (Lobophylliidae) with a description of two new species and one new genus

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Abstract

The scleractinian family Lobophylliidae is undergoing a major taxonomic revision thanks to the combination of molecular and morphological data. In this study, we investigate the evolutionary relationships and the macro- and micromorphology of six nominal coral species belonging to two of the nine molecular clades of the Lobophylliidae, clades A and B, and of Symphyllia wilsoni, a lobophylliid species analyzed from a molecular point of view for the first time. Sequence data from mitochondrial DNA (COI and the intergenic spacer between COI and l-rRNA), and nuclear DNA (histone H3 and ITS region) are used to generate robust molecular phylogenies and a median-joining haplotype network. Molecular results are strongly in agreement with detailed observations of gross- and fine-scale morphology of skeletons, leading to the formal revision of the genera Micromussa and Homophyllia and the description of two newly discovered zooxanthellate shallow-water species, Micromussa pacifica sp. nov. Benzoni & Arrigoni and Micromussa indiana sp. nov. Benzoni & Arrigoni, and a new genus, Australophyllia gen. nov. Benzoni & Arrigoni. In particular, Acanthastrea lordhowensis and Montastraea multipunctata are moved into Micromussa, A. hillae is synonymized with A. bowerbanki and is transferred to Homophyllia, and a revised diagnosis for both genera is provided. Micromussa pacifica sp. nov. is described from the Gambier Islands with its distribution spanning New Caledonia and eastern Australia. Despite a superficial resemblance with Homophyllia australis, it has distinctive macro- and micromorphological septal features. Micromussa indiana sp. nov., previously identified as M. amakusensis, is here described from the Gulf of Aden and the southern Red Sea as a distinct species that is genetically separated from M. amakusensis and is morphologically distinct from the latter due to its smaller corallite size and lower number of septa. Finally, molecular trees show that S. wilsoni is closely related, but molecularly separated from clades A and B, and, also based on a unique
combination of corallite and sub-corallite characters, the species is moved into *Australophyllia* gen. nov. These findings confirm the need for using both genetic and morphological datasets for the ongoing taxonomic revision of scleractinian corals.

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### Introduction

In the last decade the increasing use of molecular tools and novel morphological analyses have shed new light on the evolution and systematics of scleractinian corals (Stolarski, 2003; Fukami et al., 2004a, 2008; Wallace et al., 2007; Budd and Stolarski, 2009, 2011; Gittenberger et al., 2011; Stolarski et al., 2011; Huang et al., 2012a, b; Kitano et al., 2014; Kitahara et al., 2016). The integration of genetics and morphology has provided new hypotheses about the evolutionary history of scleractinian corals, and has led to a revolution in their taxonomy at all ranks (Stolarski and Janiszewska, 2001; Budd et al., 2010, 2012; Stolarski et al., 2011; Benzioni et al., 2012a, b; Kitahara et al., 2012b; Huang et al., 2014a).

The family Lobophylliidae Dai & Horng, 2009 is an ecologically important group in tropical Indo-Pacific coral reefs (Veron and Pichon, 1980; Scheer and Pillai, 1983; Veron, 1993, 2000). Based on morphological characters, it currently comprises 12 extant genera and 52 zooxanthellate species and is widely distributed from the Red Sea and eastern Africa to French Polynesia (Veron, 2000; Dai and Horng, 2009; Budd et al., 2012; Benzioni, 2013; Hoogenboom et al., 2015). To date, based on mitochondrial and nuclear phylogenies, this taxon corresponds to a monophyletic lineage consisting of nine main genus-level molecular clades, clades A to I sensu Arrigoni et al. (2014a), which are mostly in disagreement with the taxonomy of lobophylliids that until recently has been based solely on macromorphology (Arrigoni et al., 2012, 2014a). Indeed, all polytypic genera described in Veron (2000) analyzed so far, i.e. *Acanthastrea* Milne Edwards & Haime, 1848, *Echinophyllia* Klunzinger, 1879, *Lobophyllia* de Blainville, 1830, *Micromussa* Veron, 2000, *Oxypora* Saville Kent, 1871, and *Symphyllia* Milne Edwards & Haime, 1848, are not monophyletic (Arrigoni et al., 2014a). Furthermore, the phylogenetic position and taxonomy of two monospecific genera, *Echinomorpha* Veron, 2000 and *Homophyllia* Brüggemann, 1877, were still uncertain (Budd et al., 2012) because they have previously not been investigated at a molecular level, while the monotypic genus *Moseleya* has already been molecularly characterized (Huang et al., 2011).

Recent work has integrated molecular findings with novel macro- and micromorphological skeleton data, leading to the identification of a new set of informative characters useful for revising the family taxonomy and systematics (Budd and Stolarski, 2009; Budd et al., 2012; Arrigoni et al., 2014b, 2015). In particular, micromorphological characters such as the height, spacing, and shape of septal teeth; the distribution and shape of granules on septal faces; and the structure of the area between teeth (Budd and Stolarski, 2009, 2011) are now known to be informative and diagnostic for the Lobophylliidae (Budd and Stolarski, 2009; Budd et al., 2012; Arrigoni et al., 2014b, 2015) as in other coral families (Hoeksema, 1989; Benzioni et al., 2007, 2012a; Gittenberger et al., 2011; Budd and Stolarski, 2011; Janiszewska et al., 2011, 2013, 2015; Budd et al., 2012; Schmidt-Roach et al., 2014; Huang et al., 2014a, b). Therefore, the family Lobophylliidae is currently undergoing a revision that started with the phylogenetic re-classification of the genera *Australomussa* Veron, 1985, *Parascolymia* Wells, 1964, and *Sclerophyllia* Klunzinger, 1879, as a result of the aforementioned integrated morpho-molecular approach (Arrigoni et al., 2014b, 2015).

In a recent study, unexpected genetic affinities were found between the Lobophylliidae species included in the sister clades A and B sensu Arrigoni et al. (2014a).
Fig. 1. Lobophylliidae included in this study. A) Holotype of Micromussa amakusensis MTQ G32485 from Japan; B) Micromussa indiana sp. nov. (referred to as Micromussa cf. amakusensis in text) from the Gulf of Aden MNHN-IK-2012-14232; C) Holotype of Acanthastrea lordhowensis MTQ G57483 from Australia; D) Micromussa multipunctata (previously Montastraea) RMNH Coel 40090 from Malaysia; E) Micromussa pacifica sp. nov. (referred to as Homophyllia cf. australis in text) MNHN IK-2012-16046 from New Caledonia; F) Homophyllia australis IRD HS3524 from New Caledonia; G) Homophyllia bowerbanki (previously Acanthastrea) IRD HS3287 from New Caledonia; H) Homophyllia bowerbanki (previously Acanthastrea hillae) AM MH043 from Australia; I) Australophyllia wilsoni (previously Symphyllia) from Australia; J) Acanthastrea cf. hemprichii (referred in the text as Acanthastrea cf. hillae) UNIMIB BA115 from the Gulf of Aden.
Fig. 2. Lobophylliidae included in this study in situ. A) Micromussa amakusensis from Japan; B) Micromussa indiana sp. nov. (referred to as Micromussa cf. amakusensis in text) same specimen shown in 1B; C) Micromussa lordhowensis (previously Acanthastrea) from Lord Howe, Australia; D) Micromussa multipunctata (previously Montastrea) same specimen shown in 1D; E) Micromussa pacifica sp. nov. (referred to as Homophyllia cf. australis in text), same specimen shown in 1F; F) Homophyllia australis, same specimen shown in 1E; G) Homophyllia bowerbanki (previously Acanthastrea), same specimen shown in 1I; H) Homophyllia bowerbanki (previously A. hillae) IRD HS3066 from New Caledonia; I) Australophyllia wilsoni from Australia; J) Acanthastrea cf. hemprichii (referred in the text as A. cf. hillae) same specimen shown in 1H.
Clade A

Clade A is composed of *Micromussa amakusensis* (Veron, 1990) (Figs 1A, 2A) and *Montastraea multipunctata* (Hodgson, 1985) (Figs 1D, 2D). The latter was formally assigned to the Lobophylliidae but its genetic placement represents a taxonomic issue that calls for a formal revision because it is not related to the type species *Montastraea cavernosa* (Linnaeus, 1767) (Huang et al., 2011; Arrigoni et al., 2014a). Nevertheless, no detailed morphological studies have, to date, been conducted on this species. The poorly studied type species *Micromussa amakusensis* has been recorded throughout the Indo-Pacific, from the studied type species to date, been conducted on this species. The poorly nevertheless, no detailed morphological studies have, to date, been conducted on this species. The poorly studied type species *Micromussa amakusensis* has been recorded throughout the Indo-Pacific, from the

Clade B

Clade B sensu Arrigoni et al. (2014a) currently contains *Acanthastrea bowerbanki* Milne Edwards & Haime, 1857 (Figs 1G, 2G) and *A. hillae* Wells, 1955 (Figs 1H, 2H). At a molecular level, *A. bowerbanki* and *A. hillae* are not closely related to the type species *A. echinata* (Dana, 1846), which is recovered in clade E sensu Arrigoni et al. (2014a), and the establishment of a new genus to accommodate species in clade B is thus tentative. The sister-relationship between the two species is corroborated also by remarkable morphological similarities (Chevalier, 1975; Veron and Pichon, 1980; Veron, 1992, 2000; Wallace et al., 2009). Their coralla are similar in growth form and mode of budding, while their corallites are among the largest of all species currently assigned to *Acanthastrea* (Veron and Pichon, 1980; Veron, 2000). Furthermore, *A. bowerbanki* and *A. hillae* show a partially overlapping geographic distribution, mainly in the Central Pacific (Veron and Pichon, 1980; Veron, 1993, 2000; Wallace et al., 2009), where they are generally uncommon throughout the tropics but more abundant in high latitude and marginal reef localities (Veron, 1993). *Acanthastrea hillae* has been also reported from the Western Indian Ocean but these records are doubtful (Veron, 2000). For this reason, material from Yemen assigned to this species based on macromorphology was also included in this study (Figs 1J, 2J).

The monotypic genus *Homophyllia* has a complicated nomenclatural history (Vaughan and Wells, 1943; Wells, 1964; Veron and Pichon, 1980; Veron, 2000; Budd et al., 2012). Previously considered a junior synonym of *Lobophyllia* (Matthai, 1928; Vaughan and Wells, 1943) and *Scolymia* (Veron and Pichon, 1980; Veron, 2000), it was restored by Budd et al. (2012) following novel morphological evidence proposed by Budd and Stolarski (2009). Budd et al. (2012) showed that the micromorphology and the microstructure of the monostomatous species *Homophyllia australis* (Milne Edwards & Haime, 1849) (Figs 1F, 2F) are clearly distinguished from those of the solitary species *Scolymia lacera* (Pallas, 1766) and *Parascolymia vitiensis* (Brüggemann, 1877) (Budd and Stolarski, 2009; Budd et al., 2012; Arrigoni et al., 2014b). Nevertheless, despite the increasing amount of genetic data concerning the Lobophylliidae (Arrigoni et al., 2014a, 2014b, 2015, 2016), no molecular information is available for *H. australis*. In this study we analyzed a large collection of specimens encompassing the whole range of morphological variability shown by Veron and Pichon (1980), thus including specimens with typical morphology (Budd and Stolarski, 2009: fig 2K; Veron and Pichon, 1980: figs 408, 410, 420; Figs 1F, 2F) and other specimens with thinner and less numerous septa identified as *H. cf. australis* (Veron and Pichon, 1980: figs 412, 424; Figs 1E, 2E).

Symphyllia wilsoni

*Symphyllia wilsoni* Veron, 1985 (Figs II, 2I) is a relatively poorly known species, which is distributed from south to southwestern Australia (Veron, 2000)
and ascribed to the genus Symphyllia by reason of its massive coralla with large meandering valleys. However, as remarked by Veron (2000), this species presents some odd macromorphological characters, such as small skeletal features compared to those of its congeners and septa resembling those of the genus Acanthastrea. Although several Symphyllia representatives, including the type species, were included in molecular analyses and found in clade I sensu Arrigoni et al. (2014a), S. wilsoni has previously not been examined and is therefore included in our analyses in order to ascertain its status.

The present study aims to provide a robust molecular phylogeny reconstruction of six nominal species included in clades A and B, and of S. wilsoni. We analyze material from different geographic localities spanning the known range of intraspecific morphological variability and several types of sequence data: the mitochondrial DNA regions cytochrome c oxidase subunit I (COI) as well as the non-coding intergenic spacer region between COI and large ribosomal RNA subunit, and the nuclear markers ribosomal internal transcribed spacers 1 and 2 (ITS region) and the histone H3 gene. Furthermore, we investigate gross- and fine-scale morphology of skeletons of each coral species, including material from each type locality, except for M. multipunctata, which was sampled from the northernmost tip of Borneo (Waheed et al., 2015).

Material and methods

Coral sampling and identification

A total of 87 coral specimens ascribed to Acanthastrea bowerbanki, A. echinata, A. hillae, A. lordhowensis, Homophyllia australis, Micromussa amakusensis, Montastraea multipunctata, and Symphyllia wilsoni, were collected while SCUBA diving between 1 and 35 m depth from different localities in the Indian and Pacific Ocean and analyzed from both molecular and morphological point of view (S1). Furthermore, the lectotype of M. diminuta and the holotype of A. minuta were used in the morphological analysis. Samples of A. bowerbanki, A. hillae, A. lordhowensis, H. australis, and S. wilsoni were sampled from their type locality, Australia, as well as M. amakusensis from Japan. Each coral sample was photographed underwater and then collected, tagged, and approximately 1 cm² of the entire specimen was broken off and put in CHAOS solution (not an acronym; 4 M guanidine thiocyanate, 0.1% N-lauroyl sarcosine sodium, 10 mM Tris pH 8, 0.1 M 2-mercaptoethanol) to dissolve the tissue or fixed in 95% ethanol for further molecular analyses. The remaining corallum was immersed in sodium hypochlorite for 48 hours to remove all tissues, rinsed in freshwater and air-dried for identification and microscope observations (Figs 1, 2). Specimens were identified at species level based on their morphological structures following Milne Edwards and Haime (1848), Wells (1964), Veron and Pichon (1980, 1982), Hodgson (1985), Veron (1985, 1990, 2000), Wallace et al. (2009), and Pichon et al. (2010), as well as referring to illustrations of holotypes in their original descriptions. Voucher samples were deposited at the University of Milano-Bicocca (UNIMIB, Milano, Italy), the Australian Museum (AM, Sydney, Australia), the Institut de Recherche pour le Développement (IRD, Nouméa, New Caledonia), the Seto Marine Biological Laboratory at the Kyoto University (SMBL, Kyoto, Japan), the University of Miyazaki (Miyazaki, Japan), Naturalis Biodiversity Center (RMNH, Leiden, the Netherlands), and the Museum of Tropical Queensland (MTQ, Townsville, Australia).

DNA preparation, amplification, and sequence analyses

Total genomic DNA was extracted using the DNeasy Blood and Tissue kit (Qiagen Inc., Hilden, Germany) from coral tissue preserved in ethanol or using a phenol-chloroform-based method with a phenol extraction buffer (100 mM Tris pH 8, 10 mM EDTA, 0.1% SDS) from specimens conserved in CHAOS solution (Fukami et al., 2004a; Huang et al., 2011). For all coralline samples, we amplified and directly sequenced one mitochondrial marker (COI) and two nuclear markers (histone H3 and ITS region). The COI gene, histone H3, and ITS region were amplified using the primer pairs MCOIF and MCOIR and the protocol proposed by Benzoni et al. (2011), H3F and H3R (Colgan et al., 1998), ITS4 (White et al., 1990) and A18S (Takabayashi et al., 1998) and the protocol published by Benzoni et al. (2011), respectively. Furthermore, for species included in clade A sensu Arrigoni et al. (2014a), IGR was amplified using MNC1F and MNC1R primers (Fukami et al., 2004b; Huang et al., 2009) and the protocol described by Arrigoni et al. (2016). All PCR products were purified with Illustra ExoStar (GE Healthcare, Buckinghamshire, UK) and directly sequenced in both strands using an ABI 3130x1 Genetic Analyzer (Applied Biosystems, Carlsbad, CA,
Fig. 3. Bayesian phylogeny reconstruction of the family Lobophylliidae for the analysis of the concatenated data set of COI, histone H3, and ITS region. Numbers above branches indicate nodal support by means of Bayesian posterior probabilities (> 0.8), Maximum Likelihood SH-like support (> 0.7), and Maximum Parsimony bootstrap support (> 50). Lower values of support not shown. Clades within Lobophylliidae are coloured and labelled A to I according to Arrigoni et al. (2014a). Specimens analyzed in this study are in bold.
USA). Chromatograms were manually corrected for misreads, if necessary, and forward and reverse strands were merged into one sequence file using CodonCode Aligner 3.6.1 (CodonCode Corporation, Dedham, MA, USA). In particular, chromatograms of products obtained with ITS4 and A18S primers did not show any intra-individual polymorphisms or double peaks, thereby allowing direct sequencing of this region. All newly obtained sequences were deposited in EMBL, and accession numbers are listed in S1.

Sequence alignments were generated using the E-INS-i option in MAFFT 7.130b (Katoh et al., 2002; Katoh and Standley, 2013) under default parameters. For phylogenetic analyses, sequences of COI, histone H3, and ITS region were concatenated into one partitioned dataset. Three methods, maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI), were employed to reconstruct the phylogenetic relationships within the Lobophylliidae. For MP analysis, tree searches were generated in PAUP* 4.0b10 (Swofford, 2003) using heuristic searches with 10000 random additions. Branch support was estimated with the bootstrap confidence levels using 1000 replicates. Prior to the model-based phylogenetic analyses, the best-fit model of nucleotide substitution was identified for each gene partition separately by means of the Akaike Information Criterion calculated with MrModeltest 2.3 (Nylander, 2004). The following substitution models were suggested: the GTR + I + G for ITS region, the HKY + G + I for COI, and the K80 + I for histone H3. ML topologies were calculated with PhyML (Guindon and Gascuel, 2003) under the substitution models proposed by MrModeltest 2.3 (Nylander, 2004). The SH-like test replicates was performed employing MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001). Two simultaneous runs of four Markov Monte Carlo chains were conducted for 3 x 10^7 generations, sampling every 100 generations to ensure independence of the successive samples. Results were analyzed for stationarity and convergence using Tracer 1.6 (Rambaut and Drummond, 2009), with a burn-in of 25% of sampled generations. Additionally, ML phylogenetic reconstructions for each separate COI, histone H3, and ITS region were obtained using PhyML (Guindon and Gascuel, 2003) under the substitution models proposed by MrModeltest 2.3 (Nylander, 2004). The SH-like test replicates was performed to assess the branch support of ML trees. Within clade A sensu Arrigoni et al. (2014a), Network 4.6.1.2 (http://www.fluxus-technology.com) was used to construct a median-joining haplotype network (Bandelt et al., 1999) for the IGR dataset. This method is especially applicable to non-recombinant DNA sequences, such as mitochondrial DNA, and combines all minimum spanning trees into a single network. Alignment was converted to the Roehl format using DnaSP (Librado and Rozas, 2009), invariable sites were removed and sites with gaps were not considered.

**Morphological analyses**

Scleractinian coral skeletons of the sequenced lobophylliids were analyzed both at macro- and micromorphological levels using light microscopy and Scanning Electron Microscopy (SEM), respectively, in order to find morphological characters supporting the molecular phylogeny reconstructions. Images of coral skeletons were taken with a Canon G5 digital camera as well as with a Leica M80 microscope equipped with a Leica IC80HD camera. For scanning electron microscope (SEM) imaging, skeleton fragments were ground to produce a flat edge, mounted on stubs using silver glue, sputter-coated with conductive gold film, and examined using a Vega Tescan Scanning Electron Microscope at the University of Milano-Bicocca. At least five different corallites per species were examined at micromorphological level. For a glossary of skeletal terms we followed Budd et al. (2012) and we also adopted their character names, ID numbers (in brackets), and state names. In addition to samples deposited in the institutions mentioned earlier, we analyzed specimens and type material from the Environment Protection Authority, Sana’a and Socotra, Yemen (EPA S), the Muséum National d’Histoire Naturelle (MNHN, Paris, France), the Natural History Museum (NHMK, London, UK, formerly British Museum of Natural History, BMNH), the Queensland Museum (QM, Brisbane, Australia), the Marine Science Institute, University of the Philippines (UP, Manila, the Philippines), and the Western Australian Museum (WAM, Perth, Australia).

**Results**

**Molecular phylogenetic and haplotype network analyses**

New sequence data of COI, histone H3, and ITS region, generated in this study from 87 coral samples representing 11 species, were combined with published sequences of the families Lobophylliidae, Merulinidae Verrill, 1865, Diploastreaeidae Chevalier & Beau-
vais, 1987, and Montastraeidae Yabe & Sugiyama, 1941, resulting in an alignment composed of 50 nominal species. *Plesiastrea versipora* was selected as outgroup because of its divergence from the Lobophylliidae, Merulinidae, Diploastreidae, and Montastraeidae (Fukami et al., 2008; Benzoni et al., 2011; Huang et al., 2011; Budd et al., 2012). The final concatenated dataset of aligned sequences of the three molecular fragments had a total length of 1939 bp (COI: 580 bp, histone H3: 318 bp, ITS region: 1041 bp). The ITS region was the most variable, with 191 variable sites (148 positions parsimony-informative PI), the COI gene fragment showed 87 bp variable sites (57 positions PI), and the histone H3 sequences featured 90 bp variable sites (84 positions PI).

The three single gene trees did not show any supported topological conflicts, although the resolution differed notably among the three topologies (Figs S3-S5). Nevertheless, each of the analyzed specimens belonged to the same molecular clade in all of the three phylogenetic reconstructions. Bayesian, maximum likelihood, and maximum parsimony topologies were highly concordant and node support values were high across the ingroup and outgroup.

The phylogram based on the concatenated (COI, histone H3, and ITS region) molecular datasets was broadly consistent with previously published phylogeny reconstructions (Huang et al., 2011; Arrigoni et al., 2014a, 2014b, 2015), confirming the Lobophylliidae and Merulinidae as monophyletic taxa (Fig. 3). All of the nine main genus-level lineages proposed by Arrigoni et al. (2014a) for the Lobophylliidae were highly supported by all methods of phylogeny reconstruction. Clades A and B were sister taxa of each other. Both were well resolved and strongly supported (Bayesian posterior probability score Pp = 1, ML SH-like support Ss = 1, MP bootstrapping support Bs = 99 for both clades). A close-up of the phylogenetic relationships among and within clades A and B is shown in Fig. S6. Clade A contained three nominal species: the type species of the genus *Micromussa*, *M. amakusensis*, along with *Montastraea multipunctata* and *A. lordhowensis*. The monophyly of the latter two species was highly supported whereas *M. amakusensis* was split into two main lineages. In particular, the colonies of *M. amakusensis* from the type locality Japan were grouped together and sister to *Montastraea multipunctata*, with the exception of the uncertain position of one sample SMBL Cni-11051. In contrast, specimens of *M. cf. amakusensis* from Yemen formed a monophyletic lineage with strong support (Pp = 1, Ss = 1, Bs = 95) that was sister to the group containing *M. amakusensis* from Japan and *Montastraea multipunctata*. Within clade A, we found a well-supported basal group (Pp = 1, Ss = 1, Bs = 99) composed of all of the specimens identified as *Homophyllia cf. australis* (Figs 1E, 2E). This lineage was not closely related to the one including the specimens of *H. australis* that showed the typical morphology (Figs 1F, 2F) which formed a well-supported group (Pp = 0.9, Ss = 0.89, Bs = 83) within clade B. *Homophyllia australis* was instead sister to the well-supported lineage (Pp = 0.95, Ss = 0.94, Bs = 90) composed of *A. bowerbanki* and *A. hillae*. The latter two species could be distinguished using these three molecular markers as the average genetic distance between these two species was 2.3 ± 0.3%, and fully overlapped with
the intraspecific distances within *A. bowerbanki* and *A. hillae* that are 2.1 ± 0.3% and 2.4 ± 0.4%, respectively. Finally, all of the analyzed colonies of *A. echinata* grouped within clade E, together with the Indian Ocean specimen of *A. cf. hillae* (Fig. 1J, 2J) and published sequences of *A. rotundoflora*, *A. subechinata*, and *A. hemprichii*, although the genetic boundaries at species level within this clade remain unclear. Surprisingly, within this family a novel clade was detected that comprised *S. wilsoni* exclusively with a very strongly supported lineage monophyly (Pp = 1, Ss = 1, Bs = 99), that was deeply divergent from clade I, which contains the genera *Lobophyllia*, *Parascolymia*, and all of the other *Symphyllia* species analyzed so far. *Symphyllia wilsoni* fell at the base of the sister clades A and B.

The final alignment of IGR data consisted of 1608 bp, of which 52 positions were variable. Haplotype network analysis of clade A, as inferred from the mtDNA IGR locus, was highly concordant with the phylogeny reconstruction of clade A based on COI, histone H3, and ITS region (Fig. 4). A total of nine haplotypes were detected and five main clusters, corresponding to the five lineages found using the other markers, were revealed. These clusters were separated by a minimum of eight substitutions (between *M. amakusensis* from Japan and *A. lordhowensis*) and no haplotypes were shared between two or more clusters. In particular, we found two closely related haplotypes specific to *M. amakusensis* from Japan and differing by three base changes, two closely related haplotypes for *M. amakusensis* from Japan and differing by three base changes, two closely related haplotypes for *M. amakusensis* from Japan and differing by three base changes, two closely related haplotypes for *Montastrea multipunctata* separated by one substitution, two closely related haplotypes specific to *A. Lordhowensis* showing one mutation event, a single haplotype for all eight specimens of *H. cf. australis*, and two closely re-
related haplotypes for *M. amakusensis* from Yemen differing by one base changes. Notably, *M. amakusensis* from Japan and *M. cf. amakusensis* from Yemen were distantly related and separated by 35 - 39 substitutions.

**Macromorphology**

The examined lobophylliid species presented a wide array of corallum macromorphology and corallite organization. *Homophyllia australis* (Figs 1F, 2F, 10, 11, 12A) and *H. cf. australis* (Figs 1E, 2E, 8, 9, 12D) were solitary forming large and predominantly monocentric coralla. *Micromussa amakusensis* (Figs 1A, 2A, 7A), *M. cf. amakusensis* (Figs 1B, 2B, 5, 6, 7D), *A. lordhowensis* (Figs 1C, 2C, S5, S6), Montastraea multipunctata (Figs 1D, 2D, S9, S10), *A. hillae* (Figs 1H, 2H, S13A, C, E, G), *A. cf. hillae* (Figs 1J, 2J), *A. bowerbanki* (Figs 1G, 2G, S13B, D, F, H) and *S. wilsoni* (Figs 1I, 2I, 13) were colonial species forming encrusting to massive coralla. Corallite organization was cerioid in *M. amakusensis* (Fig. 1A), *M. cf. amakusensis* (Fig. 1B), and *A. lordhowensis* (Fig. 1C); plocoid in *Montastrea multipunctata* (Fig. 1D); cerioid to sub-meandroid in *A. hillae* (Fig. 1H) and *A. bowerbanki* (Fig. 1G); and mainly meandroid in *S. wilsoni* (Fig. 1I).

In all the examined species, both intracalicular and extracalicular budding occurred (Table 1). Although polystomatous coralla were observed in both *Homophyllia australis* and *H. cf. australis*, a more pronounced tendency to polystomatism was observed in the examined series of the latter (Figs 8C–I, 9D–H, S11). Both intracalicular (Fig. 8C) and extracalicular (Fig. 8F–I) modes of budding were observed in *H. cf. australis*.
specimens where the former occurred, adjacent centers were linked by lamellar linkage (Fig. 8C).

Circumoral budding and associated corallite polymorphism was not observed in any of the examined taxa (Table 1). However, in specimens identified as *A. bowerbanki* a larger central corallite was observed (Figs S13B, D, F, H, S14B, D, F, H) following Veron (2000) (Table 1). Veron (2000, vol. 3, p. 26) remarked that in colonies of this species “a central corallite is usually conspicuous”, but he did not mention this character for *A. hillae*. However, a larger corallite undergoing intracalicular budding was observed roughly at the center of the holotype of this species (Fig. S13A) as well as in the holotype of *A. bowerbanki* (Fig. S13B) and in some specimens illustrated by Veron and Pichon (1980: figs 441, 443).

The only species with meandroid corallite arrangement was *S. wilsoni* (Table 1) (Figs 11, 13A–B). Although these were generally uniserial and discontinuous, in some cases a biserial condition was almost attained. In fact, in this species centers within a series were linked by a thick lamellar process which in some cases seemed to actually split the columella in two, giving it a bilateral symmetry (Fig. 13C). *Symphyllia wilsoni* was also the only species among those we examined or (to our knowledge) in the Lobophylliidae to form monticules (Fig. 13A, E–F) resembling the hydnophores typical of the merulinid genus *Hydnophora* Fischer von Waldheim, 1807 and of the agariciid *Pavona varians* Verrill, 1864. These monticules formed “where sections of common wall between corallites intersect and develop into conical mounds” (Veron, 2000: vol. 2, p. 346).

With reference to the ranges set by Budd et al. (2012), calices were large (>15 mm) in *A. bowerbanki*, *A. hillae*, *A. cf. hillae*, *H. australis*, and *H. cf. australis*, medium (8–15 mm) in *S. wilsoni*, *M. amakusensis*, *M. cf. amakusensis*, and *A. lordhowensis*, and small to me-
and elongated polyps). In the plocoid $M$. mul-
taternity while 4 cycles were found in $M$. multipunctata
and resembled those of the typical $M$. amakusensis, in
the species with medium sized corallites, $M$. amakusensis
and $M$. cf. amakusensis (Figs 1A, 7A and Figs 1B, 7D, respectively). The latter displayed a
more variable corallite diameter and outline (Fig. 5).

In fact, although some coralla can display corallites with a
larger diameter and more regular shape (Fig. 5C–D) and
resembled those of the typical $M$. amakusensis, in
these specimens the within corallum variability for
these characters was remarkable (Fig. S13D, F, H). Similarly, this character showed an
to a more regular outline (Fig. S7E). Such intraspecific
irregular free septa and a similar spacing of septa (6 –
from round to oval in larger corallites although smaller
corallites can be more irregular (Figs S9, S10).

With respect to the number of septa, Acanthastrea
lordhowensis, Microsmussa cf. amakusensis, and
Montastraea multipunctata had 3 – 4 cycles of septa
while 4 cycles were found in $M$. amakusensis. More
than 4 cycles were observed in all the other examined
species. All examined species shared the presence of
irregular free septa and a similar spacing of septa (6 –
11 per 5 mm).

Costosepta were unequal in relative thickness be-
tween those of the first two orders and those of the third
order in $M$. cf. amakusensis, Montastraea multipunc-
tata, $H$. australis, $A$. hillae, $A$. cf. hillae, and $S$. wilsoni,
while in the remainder of the examined species cos-
tosepta were unequal to slightly unequal (Table 1),
showing a certain intraspecific variability of this char-
acter. Notably, the thickness of costosepta in $A$. bower-
banki was only slightly unequal in the holotype (Fig.
S13B) and in some of the other examined specimens
(Fig. S13D, F, H). Similarly, this character showed an
obvious variability also in the examined specimens of
$A$. hillae (Fig. S13A, C, E, G). In $S$. wilsoni the unequal
costosepta thickness was particularly obvious especially
within the series of corallites where thicker septa
reach and fuse with the lamellar process uniting the
centers (Fig. 13B–C). As a result, thicker costosepta al-
ternated with series centers in this species.

The columella was trabecular, spongy and smaller
than 1/4 of the diameter of the calice in all species
except $M$. amakusensis and Montastraea multipunc-
tata, where it was consistently larger (Table 1). The
dimension of the columella (relative to the calice width)
was quite variable in $S$. wilsoni where it was
smaller in series of corallites (Fig. 13B, D) and larger
in monocentric corallites (Fig. 13B).

**Micromorphology**

Despite the above-mentioned macromorphological
variability of skeletal structures (Table 1), all the ex-
ained taxa shared similar micromorphology and, in
particular, have septal teeth with an elliptical base at
mid-septum and irregular tooth tips.

Septal tooth height was medium (0.3 – 0.6 mm) in
$M$. amakusensis, $M$. cf. amakusensis, $A$. lordhowensis,
Montastraea multipunctata, and $S$. wilsoni; medium
to high in $A$. cf. hillae; and high (> 0.6 mm) in $H$. australis, $H$. cf. australis, $A$. hillae, and $A$. bowerbanki
(Table 1) (Fig. 14). Both Wells (1955), in his original
description of $A$. hillae, and later Chevalier (1975) re-
marked that in this species septal teeth tend “to be
relatively small near tops of walls and increasing
greatly in height toward the columella, especially in
the case of the longer septa but decreasing again at the
inner ends of the septa” (Wells, 1955) (Fig. S13A). We
observed the same variation in septal teeth height in
the septa of the first and second cycle in all examined
specimens of $A$. hillae (e.g. Fig. S13C, E, G). Although
the same was not observed in the holotype of $A$. bow-
erbanki, which have thinner septa than the holotype of
$A$. hillae, this peculiar within-septum tooth height
variation was observed in several specimens of this
species (Fig. 5D, F, H), although it was less obvious in
specimens with thinner septa (Fig. 5H). The same pat-
tern in septal teeth height variation was consistently
observed in all examined specimens of $H$. australis
(Fig. 10B–D, F–H), but not in those of $H$. cf. australis
(Figs 8, 10E–F), in which septal teeth of the first two
cycles decreased in height from the wall to the colum-
ella. In $A$. lordhowensis, although septal teeth were
of uniform height within septa, a certain degree of in-
traspecific variation of this character was observed
with some specimens having more developed teeth
(Fig. S7C, F) than others (Fig. S7D–E).

Although septal tooth size varied between cycles of
septa (being larger in those of lower orders and smaller
in those of higher orders) their shape was consistently
uniform within the same species in all cases except $A$. 
cf. hillae (Table 1). Tooth spacing was wide (> 1.0 mm) in *H. australis*, *A. hillae*, and *A. bowerbanki* (Fig. 14L–Q) and medium (0.3 – 1.0 mm) in all the other species. Inter-area structure was smooth in all species (Table 1). Septal side granulation was weak, rounded, and uniformly distributed in *H. australis*, *A. hillae*, and *A. bowerbanki* (Fig. 14P–R); weak, rounded, and scattered in *S. wilsoni* (Fig. 14S); weak, rounded and enveloped by thickening deposits in *A. cf. hillae* (Fig. 14T); strong, pointed and scattered in *M. amakusensis, M. cf. amakusensis, A. lordhowensis, Montastraea multipunctata*, and *H. cf. australis* (Fig. 14F–J) (Table 1).

A peculiar micromorphology was observed in *S. wilsoni* where columnellae in series of corallites were separated, as described above, by ridges formed by the fusion of thicker septa with the lamellar process uniting centers. SEM observations had revealed the presence of clusters of granules arranged over this lamellar process in a saddle-like fashion (Fig. 13H–J).
Discussion

As a result of the evaluation above, a number of formal taxonomic actions are undertaken hereafter (Fig. 15), including the description of two new species, *Micromussa pacifica* sp. nov. (so far *Homophyllia cf. australis*) and *Micromussa indiana* sp. nov. (so far *Micromussa cf. amakusensis*), and one new genus, *Australophyllia* gen. nov., to accommodate *S. wilsoni*. *Acanthastrea hillae* is considered a junior synonym of *Acanthastrea bowerbanki* and this species is formally moved into *Homophyllia*. Finally, *Montastrea multipunctata* and *A. lordhowensis* are moved to the genus *Micromussa*, whereas *M. minuta* is moved to *Acanthastrea* and *M. diminuta* to *Goniopa*. For detailed descriptions and systematic account we refer to the Appendix. The genus *Micromussa* is characterized by medium tooth spacing (0.3 – 1.0 mm) and by strong, pointed and scattered septal side granulation, whereas *Homophyllia* shows wide tooth spacing (> 1.0 mm) and weak, rounded, and uniformly distributed septal side granulation (Fig. 14). Conversely, *Australophyllia* shows medium tooth spacing (0.3 – 1.0 mm), weak, rounded, and scattered septal side granulation, and munticules.

In this study we explored the molecular phylogeny and proposed a new taxonomy for seven nominal scleractinian coral species ascribed to the Lobophylliidae (Fig. 15), corroborating the molecular data with the morphological data supported molecular findings, reveal the case of *Goniopa* sp. nov. Therefore, the previous lack of direct comparison of skeletal morphology from Indian Ocean and Pacific Ocean material (Veron, 2000; Pichon et al., 2010) has perpetrated this error and underestimated the increasingly clear peculiarities of the Indian Ocean coral fauna (Arrigoni et al., 2012; Obura, 2012; Reijnen et al., 2014). However, once type material, specimens collected from type localities, and a large reference collection from Yemen were compared, the macromorphological differences between these species became obvious. Recent works have revealed several other cases of deep genetic divergence between Indian and Pacific populations in some species ascribed to other families, such as *Blastomussa merleti* (Arrigoni et al., 2012), *Coelastrea aspera* and *C. palauensis* (Huang et al., 2014b), *Favites halicora* (Arrigoni et al., 2012), *Goniopa somaliensis* (Kitano...
et al., 2014), Pocillopora spp. (Pinzon et al., 2013), and Stylophora pistillata (Stefani et al., 2011; Keshawmurthy et al., 2011; Flot et al., 2011). Such evidence strongly argues against the concept of “geographic subspecies” proposed by Veron (1995) in order to explain the wide variety of geographic variations in some nominal species living both in the Indian and Pacific Ocean.

Micromussa lordhowensis represents one of the various cases of Acanthastrea mis-assignment highlighted by Arrigoni et al. (2014a, 2015). As shown by these authors, Acanthastrea, as interpreted until Veron (2000), was the most polyphyletic genus in the family Lobophylliidae based on mitochondrial and nuclear phylogeny reconstructions. In the present study, M. lordhowensis was studied for the first time from a phylogenetic perspective and transferred to Micromussa as it was found to be unrelated to the genus type, A. echinata (Fig. 3), but closely related to the other species in Micromussa. Furthermore, morphological analyses confirmed that M. lordhowensis displays the septal size, shape, and granulation typical of all Micromussa species rather than the smoother septal sides ornamentation of Acanthastrea (see also Arrigoni et al., 2015). In the original description of M. multipunctata, Hodgson (1985) stated that, despite some characteristics shared with the other species of Montastraea (now exclusively a monospecific Atlantic genus, see Budd et al. (2012)), M. multipunctata is unusual on the basis of growth form, polyp shape, and notably septal dentations. Indeed this species is also different from all the others species examined in this study due to its plocoid corallite organization. Nevertheless, the molecular results presented in this study show that M. multipunctata clearly belongs to the lineage composed of the other four Micromussa species (Fig. 3). Moreover, this species shares a similar septal teeth micromorphology with the other Micromussa species having, for example, the same type of strong septal sides and tips granulation (Fig. 12).

The other new species of Micromussa described in this study, M. pacifica sp. nov., represents a different case altogether. This solitary species has been confused for a long time with the largely sympatric Homophyllia australis (Veron and Pichon, 1980). Superficially, these two species are indeed impressively similar, especially in the field, although a closer observation of the skeletal features allowed separating them effectively, a distinction fully confirmed by the molecular results.

Clade B

The genus Homophyllia was resurrected by Budd et al. (2012) following recent morphological observations on H. australis and Parascolymia vitiensis (Budd and Stolarski, 2009). The authors demonstrated that these two Pacific species are clearly unrelated based on the septa granulation, the area between teeth, and the thickening deposits (Budd and Stolarski, 2009; Budd et al., 2012). The phylogeny reconstruction proposed in this study confirms that H. australis belongs to the Lobophylliidae and that it is not related to P. vitiensis (Fig. 3), thus
supporting the taxonomic changes proposed by Budd et al. (2012). The combination of morpho-molecular data solves a long-standing taxonomic riddle concerning the placement of these two species (Matthai, 1928; Vaughan and Wells, 1943; Wells, 1964; Veron and Pichon, 1980; Veron, 2000) and represents an excellent example of concordance between genetics and novel morphological characters (Stolarski and Roniewicz, 2001; Budd et al., 2010).

Two variable, though consistently different, morphs of the solitary species *Homophyllia australis* were distinguished in the examined material and the molecular analyses supported our initial separation of the large set of specimens included in our analyses in two different clades, namely the typical *H. australis* in clade B and *M. pacifica* sp. nov. in clade A (Fig. 3). With reference to the characters defined by Budd et al. (2012), both morphs have large calices (Figs 8, 10, 12A, D), more than 4 cycles of septa with those of the fifth cycle or higher free (Fig. 12B, E), similar septal spacing and a trabecular and spongy columella (Figs 8, 10) of similar size relative to calice width. However, calices in *H. australis* can attain larger dimensions (Fig. S12) and reach up to 6 cycles of septa while in

Fig. 8. *Micromussa pacifica* sp. nov. (referred to as *Homophyllia cf. australis* in text) (Specimens in A–F included in the phylogeny reconstruction in Fig. 3). A) Top and B) Side view of MNHN IK-2012-16046; C) IRD HS3359 polystomatous specimen, image shows detail of the linkage (dashed line); D) MNHN IK-2012-16045 polystomatous specimen; E) Side view of IRD HS3327; F) Top view of MNHN IK-2012-16043; G–I) Show top, side and lateral corallite view, respectively, of MNHN IK-2012-16044 a specimen with two calices from the Gambier Islands. White arrows indicates a budding calice.
M. pacifica sp. nov. the largest calices are smaller and a maximum of 5 cycles of septa were observed (Fig. S11). A more pronounced tendency to polystomatism was observed in M. pacifica sp. nov. than in the typical H. australis. Moreover, in H. australis septa are markedly unequal in thickness and height in all examined specimens (Figs 10, 12A-C, S12) while in M. pacifica sp. nov. septa are slightly unequal (Figs 8, 12D-F, S11) with only some cases of unequal septa observed (Figs 9A, S11), and while in the former septal teeth height increases from mid-septum towards the columella in the first two cycles, in the latter this variation is not observed. Finally, the medium septal tooth spacing and the strong, pointed and scattered septal granulation, typical of all the species recovered in clade A with Micromussa clearly distinguish M. pacifica sp. nov. from the typical H. australis having large spacing and weak, rounded, uniformly distributed granulation. The two forms co-occur in the field (e.g. in New Caledonia and in Western Australia) and their similar
macromorphology is likely to have misled previous authors in detecting more subtle differences at the septal level. For example, Veron and Pichon (1980) included specimens of *M. pacifica* sp. nov. (e.g. fig. 428) and of *H. australis* (e.g. fig. 430) in the same series.

Doubts on the identification of Acanthastrea-like specimens with large polyps as *Acanthastrea hillae* or *H. bowerbanki* can be found in the literature. Chevalier (1975) having examined the type material of both species remarked “Acanthastrea hillae *parait très proche, peut-être même identique à A. bowerbanki*” (*A. hillae* seems very close, maybe even identical to *A. bowerbanki*). However, he also noted the differences in thickness of septa and development of septal teeth that we have also observed in our examination of the holotypes of both species despite their similar coralite size (Fig. S13A, B). Veron (2000) indicated the presence of a central larger coralite as a diagnostic character for *H. bowerbanki* but he does not mention this for *A. hillae*. However, the holotypes of both species

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**Fig. 10.** Top (A, C, E, G) and side (B, D, F, H) views of *Homophyllia australis* (specimens included in the phylogeny reconstruction in Fig. 3. A) IRD HS3441, top view; B) Side view of the same corallum as in A; C) IRD HS3470, top view; D) Side view of the same corallum as in C; E) IRD HS3545, top view; F) Side view of the same corallum as in E; G) IRD HS3524, top view; H) side view of the same corallum as in G. Black arrows point to the large septal teeth of the first cycle of septa.
have a central larger corallite undergoing intracaliccular budding (Fig. S13A, B). Conversely, Veron and Pi-chron (1980) in their treatment of *A. hillae*, noted a “superficial resemblance between some coralla of this species and *Moseleya latistellata* which also has a central corallite, similar type of budding and corallites of similar size and shape”. They further separated both species on the basis of the different septal teeth and presence of paliform lobes. In the present study we examined a large series of specimens spanning the range of the morphological variability that separates the holotypes of *H. hillae* and *A. bowerbanki*, thus including specimens with thicker (Fig. S13C) and thinner (Fig. S13D) septa, as well as specimens with more obvious larger central corallites (Fig. S13D) and lack thereof (Fig. S13E). All these were recovered in the same well-supported clade in clade B (Fig. 3) and no differences in any of the morphological characters considered (other than relative costosepta thickness) were observed. We conclude that in absence of evi-
dence of morphological and molecular characters that allow the separation of the two nominal species, *H. bowerbanki* is a senior synonym of *A. hillae*, and therefore has preference. Furthermore, based on the placement of this species in clade B together with *H. australis*, rather than in clade E with the type species of *Acanthastrea*, and the consistent micromorphological affinities between the two species (Table 1), we formally move *A. hillae* into the genus *Homophyllia* as a junior synonym of *H. bowerbanki*.

As a result of the morphological and molecular investigations presented in this study, the once monospecific genus *Homophyllia* now includes two species, *H. australis*, the predominantly solitary type species, and the colonial *H. bowerbanki* (Fig. 15). Although previous authors noted the pronounced septal sides granulation of both species (Veron and Pichon, 1980), the strikingly different corallum shape likely kept them from considering this skeletal feature as phylogenetically informative, thus solitary and colonial species were maintained in different genera. A similar situation has also been recently reported for another lobophyllid genus, *Sclerophyllia*, originally consisting of a monostomatous species (Klunzinger, 1879). The genus was recently revised based on molecular and morphological evidence and is currently composed of a solitary and a colonial species (Arrigoni et al., 2015). This result is not entirely unexpected, because in the scleractinian family Fungiidae, monostomatous and polysomatous species were traditionally also classified in different genera despite close phylogenetic relations (Hoeksema 1989, 1991, 1993). Molecular analyses have resulted in a new classification of this family, in which this distinction does not matter anymore, such as among species of the genera *Cycloseris* and *Pleuractis* (Gittenberger et al., 2011; Benzoni et al., 2012).

Despite superficial macromorphological similarities between *H. bowerbanki* and *Acanthastrea* species, mainly the size and arrangement of corallites and the number of septa (Veron and Pichon, 1980), consistent
differences in septal tooth micromorphology were evidenced between these species (Budd and Stolarski, 2009; Arrigoni et al., 2015). Furthermore, a deep genetic divergence separates the clade including *H. bowerbanki* from the lineage leading to the species of *Acanthastrea* (Fig. 3; Arrigoni et al., 2014a, 2014b, 2015). Indeed, some large specimens of *Acanthastrea*, like the colonies of *A. hemprichii* included in molecular and morphological analyses of the present study (Figs 1J, 2J), can look similar to *H. bowerbanki* and *A. hillae* (Figs 1G-H, 2G-H) and were therefore preliminarily identified as such in the field. However, none of the specimens from the Indian Ocean identified as *A. hillae* in the present study actually belong to *A. hillae*. Thus, it is possible that the supposed presence of this species in the Indian Ocean (Veron, 2000) is actually derived from erroneous identifications of *A. hemprichii*. Veron (2000, vol. 3, p. 28) himself reports that “records from the western Indian Ocean are doubtful”. If this is the case, the geographic distribution of the genus *Homophyllia* would be restricted to the western Pacific, encompassing tropical, sub-tropical, and temperate conditions. Moreover, the two species of *Homophyllia* are predominantly sub-tropical, being uncommon within
their range but relatively frequent in sub-tropical locali-
ties, such as Japan, New Caledonia, and south-western
Australia (Veron and Marsh, 1988; Veron, 1993, 2000;
Wallace et al., 2009). For example, in Australia they are
rare on the Great Barrier Reef but are relatively com-
mon south to Moreton Bay (Veron and Pichon, 1980;
Veron and Marsh, 1988; Wallace et al., 2009).

Clade J

The most unexpected result of the present study is the
recovery of *Australophyllia wilsoni*, formerly assigned
to *Symphyllia*, as a distinct lineage within the Lobo-
phylliidae. The multi-locus phylogeny reconstruction
and each of the three single gene topologies are con-
cordant in supporting this unique assignment al-
though the best resolution is obtained using the con-
catenated data set (Figs 3, S3-S6). Considering the
concatenated COI-histone H3-ITS region data set, the
interclade genetic distances between *A. wilsoni* and
the other eight clades go from the smallest values with
clad A (3.2 ± 0.4%) and clade B (3 ± 0.4%) to the
largest one with clade G (9.6 ± 0.7%) (S2), while all of
the other distances vary between 5.6 and 6.2. These

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**Fig. 14.** Scanning Electron Microscopy images of the septal teeth (A–E, K–O) and granules (F–J, P–T) of the examined Lobophylliidae recovered in clade A (A–J), clade B (K–M, P–R), clade J (N, S), clade E (O, T) (see Fig. 3 for clades and colour codes). A, F) *Micromussa amakusensis*; B, G) *Micromussa indiana* sp. nov. (referred to as *Micromussa cf. amakusensis* in text); C, H) *Micromussa lordhowensis* (previously *Acanthastrea*) AM 1642; D, I) *Micromussa multipunctata* (previously *Montastrea*) RMNH Coel 40090; E, J) *Micromussa pacifica* sp. nov. (referred to as *Homophyllia* cf. *australis* in text); K, P) *Homophyllia australis* IRD HS3311; L, Q) *Homophyllia bowerbanki* (previously *Acanthastrea*) AM 4629; M, R) *Homophyllia bowerbanki* (previously *A. hillae*) AM MH019; N, S) *Australophyllia wilsoni* (previously *Symphyllia*) AM WIL1; O, T) *Acanthastrea cf. hemprichii* (referred in the text as *A. cf. hillae*) UNIMIB BA115.
distances completely overlap with the pairwise interclade distances for the other clades, thus confirming the genetic distinctiveness of *A. wilsoni* within its family.

In the original description of *A. wilsoni*, Veron (1985) placed the species in the genus *Symphyllia* considering the massive or sub-massive flattened colony and a general resemblance of the meandroid corallite arrangement to that of this genus, although corallites are smaller than those of any other *Symphyllia* species (Veron, 2000). Despite a superficial appearance of the macro morphology of the colony to some merulinds, such as *Platygyra* and *Oulophyllia*, Veron (1985) included *A. wilsoni* within the Mussidae (now an exclusively Atlantic taxon, see Budd et al. (2012)) because of the size of septal dentations and the thick and fleshy aspect of living polyps. Our molecular analyses demonstrate that the species belongs to the Lobophylliidae but that it is not closely related to any of the known extant lobophylliid genera, showing a sister relationship with the group composed by *Micromussa* and *Homophyllia* (Fig. 3). These genetic findings are also supported by a combination of several macro and micromorphological characters illustrating the uniqueness of *A. wilsoni* among the other taxa examined in the present study (Table 1), and among the lobophylliids in general, also due to the presence of monticules and the morphology of the columella in series of calices.

Another interesting feature of *A. wilsoni* is represented by its geographic distribution. The species is restricted to the temperate waters of south-west Australia, recorded from Shark Bay to Geographe Bay along the coasts of Western Australia and thence east to Bremer Bay in south Australia (Veron, 1985, 1993, 2000; Veron and Marsh, 1988). It is usually found in shallow water on kelp-dominated coastal exposed rock surfaces (Veron, 1985, 1993; Veron and Marsh, 1988). This peculiar distribution range mostly overlaps that of another distinctive species, *Coscinaraea marshalli*, and it is also similar to that of the south-eastern Australian species *Coscinaraea meneili*, otherwise it is unlike that of any other known extant coral species (Veron and Pichon, 1980; Veron and Marsh, 1988; Veron, 1993, 2000).

**Taxa outside clades A, B, and J**

For *Goniopora diminuta* and *Acanthastrea minuta*, no molecular and micromorphological data are available and, to our knowledge, few specimens are deposited at museums. We examined the lectotype of the former species and the holotype of the latter one (Fig. S15). The present macromorphological observations allowed us to clarify that neither species actually belongs to *Micromussa*.

The lectotype of *G. diminuta* (MTQ G 55851, Veron, 2002, figs 235–237, Fig. S15A, B, D) is in fact a specimen of the poritid genus *Goniopora*, most likely a *G. somaliensis*. The corallites in this specimen show the typical septal structure and fusion of the genus *Goniopora* Blainville, 1830, a columella made of a single
vertical process and the presence of five pali around it (Fig. S15B). Moreover, the observation of the skeletal structure in longitudinal section shows the typical porous mesh of trabeculae and synapticulae observed in poritiids (Fig. S15D). The size of the calices (3 – 4 mm) and the pattern of septal fusion resemble those observed in the holotype of Goniopora somaliensis Vaughan, 1907 (Fig. S15C). In situ images of this species in Veron (2000, vol. 39, figs 2–4) show, as also remarked by the author, a lack of the “thick fleshy tissue over the skeleton” typical of the lobophylliids. However, as no image showing the appearance of the holotype before collection was published it cannot be ascertained if these images actually correspond to the same specimen. On the basis of the skeletal morphology described above, this species is, therefore in the present revision not included in the genus Micromussa but in the genus Goniopora.

The holotype of Acanthastrea minuta (Moll & Best, 1984, RMNH Coel. 15275, Fig. S15E, F) shows all the characters of the genus Acanthastrea, to which it is restored, rather than those of Micromussa and thus it is not included in Micromussa in the present study. This specimen has a well-developed spinose coenosquem, less than six septa per 5 mm in terms of septal spacing, and less than six teeth per septum (Fig. S15F). Veron (2000) moved this species to the genus Micromussa likely due to the small diameter of the calices. However, the image of the skeleton published by Veron (2000, vol. 3: 8) shows a specimen with a different morphology from that of the holotype with very unequual costosepta in relative thickness. On the basis of these observations the species is returned to the genus Acanthastrea.

The material from the Indian Ocean identified as Acanthastrea cf. hilliae on the basis of macromorphology (Figs 1H, 2H) was recovered in clade E together with all the Acanthastrea species, including the genus type species (Fig. 3). Despite a similar macromorphology to A. hilliae and H. bowerbanki for all the characters examined in this study, including the size of calices and the number of septa (Table 1), the SEM observations allowed us to ascertain that septal granulation in the examined material is weak, rounded, enveloped by thickening deposits and, thus, different from that of all the species recovered in clades A and B (Fig. 14O, T). This suggests that Acanthastrea specimens with large calices may indeed have been previously misidentified as A. hilliae as in the case of the specimen shown by Veron & Pichon (1980, figs 442 and 444). As no specimens of A. hilliae have been collected in the Indian Ocean so far, either for this study or in the examined museum collections (namely at the MTQ, MNHN, or RMNH), the records for this species outside the Pacific Ocean are considered dubious and might be referred as A. cf. hemprichii until further morpho-molecular studies will clarify their status.

Final remarks

A growing volume of work dealing with taxonomy and systematics of scleractinian corals have demonstrated that the use of both genetic and morphological analyses is an indispensable approach to understand and clarify the evolution of these invertebrates (Benzon et al., 2007, 2010, 2012a, 2012b; Budd et al., 2010, 2012; Gittenberger et al., 2011; Stolarski et al., 2011; Kitahara et al., 2012a, 2012b; Schmidt-Roach et al., 2014; Huang et al., 2014b; Arrigoni et al., 2014c; Terraneo et al., 2014). In this study we combine robust molecular analyses based on multiple DNA regions with detailed observations of morphology at colony, corallite, and sub-corallite scales. The present work increases the current knowledge of taxonomy and biodiversity of the family Lobophylliidae and, more generally, highlights the importance of analyzing both genetics and morphology. The inclusion of as many species as possible and from different localities, as done here for M. amakusensis, in a molecular phylogenetic framework is a necessary step towards a comprehensive reconstruction of coral evolutionary history as an increasing number of previously unstudied taxa exhibit unexpected phylogenetic placements that have been misunderstood and ignored by traditional systematics (Fukami et al., 2004a, 2008; Kitahara et al., 2010, 2012a, 2012b; Stolarski et al., 2011; Huang et al., 2011, 2014b; Arrigoni et al., 2014a; Kitano et al., 2014). We strongly encourage the examination of specimens from multiple localities, ideally including the entire geographic distribution range of a species and above all the type locality, in order to define the intraspecific morphological variation and evaluate the possible presence of cryptic or previously overlooked species. Finally, we recommend also the inclusion of microstructural data to the presented molecular and micromorphological observations in future works as they were demonstrated to be useful and diagnostic in previous systematic revisions (Budd et al., 2012; Kitahara et al., 2012b; Huang et al., 2014a; Arrigoni et al., 2014c; Janiszewska et al., 2015).
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Online Supplementary Information

S1. List of the material examined in this study from a molecular point of view. For each specimen we list code, identification, sampling locality, collector, and molecular markers used for the genetic analyses.

S2. Pairwise comparisons of genetic distance within and between clades of the family Lobophylliidae. Standard deviations listed on the upper right hand portions for each set of comparisons.

S3. ML tree based on mitochondrial COI dataset. Node values are ML SH-like support (> 0.7).

S4. ML tree based on nuclear histone H3 dataset. Node values are ML SH-like support (> 0.7).

S5. ML tree based on ITS region dataset. Node values are ML SH-like support (> 0.7).

S6. Close-up of phylogenetic relationships among and within clades A and B from the phylogenetic tree reported in Fig. 3 and based on the combined COI, H3, and ITS region dataset.

S7. Coralla of Micromussa lordhowensis (previously Acanthastrea) examined in this study showing the range of intra-specific macromorphological variability of corallite shape, septal fusion and thickness. A) Holotype, MTQ G57483; B) AM 5098*; C) AM 5050*; D) AM AU055; E) AM AU008; F) AM 1642*. * = specimens included in the phylogeny reconstruction in Fig. 3 (clade A).

S8. Intra-specific variability in situ of specimens of Micromussa lordhowensis (previously Acanthastrea) examined in this study. A) Two adjacent colonies with different colouration; B) A colony with brown and white rounded polyps and brown peristome; C) A colony with green and white rounded and irregular polyps and white peristome; D) A colony with brown and white rounded and irregular polyps and green peristome; E) A colony with green and white elongated polyps; F) Detail of a colony with grey and white irregular polyps and grey peristome; G) A colony with brown and white elongated and red peristome; H) A colony with green and white irregularly shaped polyps and wide red peristome.

S9. Coralla of Micromussa multipunctata (previously Montastraea) examined in this study. A) RMNH Coel 24241; B) RMNH Coel 40077*; C) RMNH Coel 40078* (same colony as in Fig. S11C); D) RMNH Coel 40099*. * = specimens included in the phylogeny reconstruction in Fig. 3 (clade A).

S10. Intra-specific variability in situ of specimens of Micromussa multipunctata (previously Montastraea) examined in this study. A) A colony from Malaysia with “a chocolate-brown coenosarc colouration” described as the most typical by Hodgson (1985); B) A large colony from Malaysia with bright red and white polyps; C) Same colony as in Fig. IC with orange retracted polyps; D) RMNH Coel 40078 from Malaysia, same colony as in Fig. S10C with bright red polyps.
SI1. Coralla of some of the specimens of *Micromussa pacifica* sp. nov. (referred to as *Homophyllia cf. australis* in text) examined in this study showing the intra-specific macromorphological variability of this species. Specimen code close to the images. All specimens are included in the phylogeny reconstruction in Fig. 3 (clade A).

SI2. Coralla of some of the specimens of *Homophyllia australis* examined in this study showing the intra-specific macromorphological variability of this species. Specimen code close to the images. All specimens are included in the phylogeny reconstruction in Fig. 3 (clade B).

SI3. Coralla of *Homophyllia bowerbanki* (previously *Acanthastrea bowerbanki* (B, D, F, H) and *Acanthastrea hillae* (A, C, E, G)) examined in this study showing the overlapping range of macromorphological variability between the two nominal species. A) Holotype of *Acanthastrea hillae*, UQF 179; B) Holotype of *Acanthastrea bowerbanki*, MNHN850; C) IRD HS3531*; D) IRD HS3285*; E) AM MH043*; F) IRD HS3446*; G) AM AU184 (left hand side corallum) growing adjacent to *Homophyllia australis* (single larger corallite on the right); H) AM AU249, same colony in Fig. 10H. White arrows point at the two columellae of the bicentric calice central to the corallum in both holotypes. Black arrows point at the prominent septal teeth of the first cycle of septa towards the columella.* = specimens included in the phylogeny reconstruction in Fig. 3 (clade B).

SI4. Intra-specific variability *in situ* of specimens of *Homophyllia bowerbanki* (previously *Acanthastrea bowerbanki* and *Acanthastrea hillae*) examined in this study. A) AM AU183, mottled green and red colony growing adjacent to *Homophyllia australis* (on the right); B) IRD HS3286, dark brown and white mottled colouration with a prominent central polyp; C) Orange and green colony at Noddy Island, Admiralty Group, Australia (31°30.060’S; 159°3.823’E, 16/12/2015); D) Brown and white coloured colony with a prominent central polyp at Lord Howe Island, Australia (31°30.695’S; 159°3.426’E, 16/12/2014); E) Beige and white colony with irregularly shaped polyps at Lord Howe Island, Australia (31°32.996’S; 159°3.796’E, 17/12/2014); F) AM AU174, green, brown and white colony with large polyps roughly arranged around a central rounder one, Noddy Island, Admiralty Group, Australia (17/12/2015); G) A large colony with brown polyps and white peristome at Balls Pyramid, Lord Howe Island, Australia (31°45.402’S, 159°14.253’E, 18/12/2014) (Picture by T.H. Sinclair-Taylor); H) AM AU249, large bright orange colony with a prominent central polyp (Picture by T.H. Sinclair-Taylor).

SI5. Lectotype of *Micromussa diminuta* Veron, 2000 (A–B, D), holotypes of *Goniopora somaliensis* (C) and *Acanthastrea minuta* Moll & Borel-Best, 1984 (E–F). A) MTQ G55851, whole specimen; B) Corallites showing the typical septal fusion and the pali of the genus *Goniopora*; C) USNM 21989, detail of the corallites; D) Longitudinal section of the corallites of the same specimen as in A and B showing the porous nature of septa and corallite walls resulting from the fusion of trabeculae and synapticulae typically observed in *Goniopora*; E) RMNH Coel 15275; F) Close up of a corallite showing the typical shape of costoseptal teeth of the genus *Acanthastrea*. White arrows point at the single process forming the columella which is surrounded by pali.
Appendix

Systematics

Family Lobophylliidae Dai & Horng, 2009

Genus *Micromussa* Veron, 2000

Type species: *Acanthastrea amakusensis* Veron, 1990

Revised diagnosis. Solitary or colonial with encrusting to submassive and massive coralla. Budding intracalicular and extracalicular. Corallites monomorphic. Corallite integration discrete. Monticules absent. Calice width small-medium, medium (4 – 15 mm) and large (> 15 mm). Septa in 3 – 4 cycles (24 – 36 septa) or more of four cycles (≥ 48 septa). Free septa irregular. Between 6 and 11 septa per 5 mm. Costosepta slightly unequal to unequal in relative thickness. Columellae trabecular and spongy, > or < 1/4 of calice width. At midcalice tooth base elliptical-parallel and tooth tip irregular. Septal teeth height medium (0.3 – 0.6 mm) but can be high (> 0.6 mm) in *M. pacifica* sp. nov. Tooth space medium (0.3 – 1.0 mm). Interarea smooth. Granules strong, pointed, scattered on septal face. Tooth shape equal between first and third order septa. Tooth size equal between midcalice and inner end in the first two cycles of septa.

Remarks. The main characters differentiating *Micromussa* from *Homophyllia* are the shape and distribution of granules (Table 1) which are strong, pointed, and scattered in the former genus and weak, rounded, uniformly distributed in the latter.

Species included.

*Micromussa amakusensis* (Veron, 1990) (Figs 1A, 2A, 7A–C, 14A, F) *Acanthastrea amakusensis* Veron, 1990 p. 137, figs 42–44, 82


Type material. The holotype G57483 (Figs 1C, S8A) from Lord Howe Island, Australia is deposited at the MTQ.

Examined material. **Australia** – (coll. A.H. Baird): AM 1596, AM 1597, Solitary Islands, Sandon Reef, 0.5m, 30/09/2012; AM 1598, Solitary Islands, Sandon Reef, 0.5m, 30/09/2012; AM 1642, Solitary Islands, Sandon Reef, 0.5m, 02/10/2012; AM 5019, AM 5023, AM 5038, Solitary Islands, Bubble Cave, 12m, 08/07/2014; AM 5050, Solitary Islands, Bubble Cave, 12m, 08/07/2014; AM 5063, AM 5079, AM 5085, AM 5098, AM 5099G, AM 5099R, Solitary Islands, Anemone Bay, 12m, 08/07/2014; AM MH042, Lord Howe Island, Admiralty Group, 20/03/2013, 14m, coll. M. Hoogenboom; MTQ (Moreton Bay collection, coll. C.C. Wallace, I. Fellegara, P. Muir): G56540, Moreton Bay, Peel Island, 1m, 01/12/2001; G6628, Moreton Bay; MTQ (AIMS monograph coral collection, coll. M. Pichon and J.E.N. Veron): G57483 (holotype), Lord Howe Island, 1m; G58513, Lord Howe Island; BM(NH).1983.9.212; (coll F. Benzoni): AM AU008, Mutton Bird Bay (30°18.237'S; 153°9.041'E), 06/12/2014; AM AU009, Mutton Bird Bay (30°18.237'S; 153°9.041'E), 06/12/2014; AM AU014, Minnie Waters pools (29°46.732'S; 153°10.189'E), 07/12/2014; AM AU044, SW Solitary, 08/12/2104; AM AU048, SW Solitary, 08/12/2104; AM AU055, Split Island (30°14.494'S; 153°10.780'E), 08/12/2104; AM AU060, Split Island (30°14.494'S; 153°10.780'E), 08/12/2104; AM AU120, N Solitary Bubble (29°55.644'S;153°23.359'E), 10/12/2014; AM...


Micromussa multipunctata (Hodgson, 1985) comb. nov. (Figs 1D, 2D, 14D, I, S7, S8) Montastrea multipunctata Hodgson, 1985, figs 1–8, 9; Veron (2000) vol. 3, p. 221, figs 4–7

Type material. Four syntypes (UP C-783, UP C-786, UP C-787, UP C-788) from Tambuli Reef, Mactan Island, Cebu, Philippines are deposited at the UP.

Examined material. Malaysia, North Sabah – RMNH (coll. B.W. Hoeksema): Coel. 40077, station TMP20, Banggi Outer NE Reef (07°22.54´N, 117°22.25´E), 8m, 14/09/2012; Coel. 40078, station TMP20, Banggi Outer NE Reef (07°22.54´N, 117°22.25´E), 9m, 14/09/2012; Coel. 40099, station TMP19, Outer Latoan Patch (07°22.54´N, 117°22.25´E), 8m, 14/09/2012; Philippines – RMNH Coel. 24241 Mactan Island, Cebu, 1-5m, 01/05/1981; UP P1L02161, Talim Point, Batangas, Philippines, 6.6m, 22/08/2009, coll. D. Huang.

Distribution. From the Coral Triangle to the northern central Pacific (Veron, 2000).


Type material. The holotype (MNHN IK-2012-14232, Figs 1B, 2B, 5A–B) from Al Mukallah, Yemen is deposited at MNHN.


Etymology. The name refers to the currently known geographic distribution of this species, restricted to the Indian Ocean.

Description. Colonial with encrusting coralla. Budding intracalicular and extracalicular. Corallites irregularly polygonal in outline. Calice width 5 – 10 mm, diameter variable between calices of the same corallum. Septa in 3 – 4 cycles (24 – 36 septa), those of the first two cycles (the second sometimes incomplete) reach the columella, those of the other cycles, often incomplete, are free. Costosepta are unequal in relative thickness (Fig. 5B). Columellae trabecular and spongy < 1/4 of calice width (Fig. 5C). Septal teeth height medium (0.3 – 0.6 mm). Interarea smooth. Granules strong, pointed, scattered on septal face.

Holotype. The specimen is an irregularly shaped fragment of a colony, it measures 12 x 8.5 x 2 cm and has an encrusting growth form (Fig. 5A). The corallites are irregularly polygonal in outline and their largest diameter ranges from 0.5 to 1 cm (Figs 1B, 5B). Up to 4 cycles of septa are visible in the largest corallites, while only the first three are present in smaller corallites, sometimes the second and the third ones incomplete (Fig. 5B). Septa of the first 2 cycles reach the columella. Columellae are trabecular and measure from 1 to 2.5 mm in diameter. In vivo, the colony had a greenish colour with bright red peristome (Fig. 2B).

Remarks. Within the genus, this species is distinguished from M. amakusensis which has slightly larger corallites, 4 cycles of more regularly arranged septa the first 3 of which reach a larger columella (Fig. 7A) (> 1/4 of calice width) made of more numerous processes (Fig. 7A, C). Septal teeth are more regularly spaced along the septum in M. amakusensis (Fig. 7B).
than in *M. indiana* (Fig. 7E). The latter has smaller corallites and less numerous septa than *M. lordhowensis* and is readily told apart from *M. multipunctata* which is plocoid, and from *M. pacifica* sp. nov. which has much larger and predominantly solitary coralla with more numerous septa (Table 1).

**Colour.** The peristome has a different colour from the rest of the polyp all the combinations of bright red, orange, brown, green, grey and white have been observed (Fig. 6).

**Ecology.** This species is found between 2 and 10 m depth in protected environments where it grows on hard substrates often in proximity of pockets of sediment. The thin colonies are often infested by polychaetes, boring bivalves, cirripeds and gall crabs (*e.g.* the holotype in Fig. 5A).

**Distribution.** Southern Red Sea, North-western Gulf of Aden, Socotra Island, Oman, Kenya.

### Micromussa pacifica Benzioni & Arrigoni sp. nov.

(Figs 1E, 2E, 8, 9, 12D–F, 14E, J, S9)

*Scolymia australis* Veron & Pichon 1980 in part, figs 425–426, 428–429; Veron, 2000 in part, vol. 3 pp. 70–71, figs 1, 6

**Type material.** The holotype (MNHN IK-2012-16043, Figs 8F, 9D, S11) and a paratype (MNHN IK-2012-16044, Fig. 8G–I), both from Taravai Island, Gambier Islands, French Polynesia are deposited at MNHN.

**Examined material.** *Australia* – RMNH Coel. 16306, Erith Island, Murray Pass, May 1974; AM AU133, Lord Howe Island (31°31.076’S; 159°3.929’E), 14/12/2014, coll. F. Benzioni; AM AU141, Lord Howe Island (31°33.224’S; 159°4.480’E), coll. F. Benzioni, 15/12/2014; *New Caledonia* – MNHN IK-2012-16045, Loyalty Islands, Ouvéa Island, Bagata (20°37.448’S; 166°16.252’E), 21/02/14, coll. F. Benzioni, BIBELOT Expedition; MNHN IK-2012-16046, Loyalty Islands, Ouvéa Island (20°25.426’S; 166°29.098’E), 22/02/14, coll. F. Benzioni, BIBELOT Expedition; IRD HS3202, Cap Begat (21°21.242’E; 165°52.142’E), 19/04/2012, coll. F. Benzioni; IRD (BIBELOT Expedition, Loyalty Islands, coll. F. Benzioni): HS3327, Loyalty Islands, Maré Island, south of Cap Machan (21°24.967’S; 167°49.152’E), 15/02/14; HS3359, Maré Island, Tadine Bay (21°35.283’S; 167°51.258’E), 15/02/14; HS3471, Lifou Island, Cap Ainé Martin (20°46.857’S; 167°02.272’E), 20/02/14; HS3527, Astrolabe Reef, Oues Reef (19°52.194’S; 165°33.375’E), 24/02/2014; HS3528, Astrolabe Reef, Oues Reef (19°52.194’S; 165°33.375’E), 24/02/2014; *French Polynesia, Gambier Islands* – MNHN IK-2012-14249, coll. M. Seurat, 15/09/1902; MNHN (Tara Oceans Expedition, coll. F. Benzioni): IK-2012-16043, Taravai Island (23°08.72’S; 135°03.09’W), 08/07/2011; IK-2012-16044, Taravai Island (23°08.72’S; 135°03.09’W), 08/07/2011; UNIMIB (Tara Oceans Expedition, coll. F. Benzioni): GA130, NE Lagoon pinnacles (23°04.12’S; 134°55.83’W), 05/07/2011; GA150, Taravai Island (23°08.72’S; 135°03.09’W), 08/07/2011; GA186, Tekava Island (23°10.13’S; 134°51.51’W), 10/07/11; *French Polynesia, Austral Islands* – MTQ (International collection): G64026, Rapa Island, Taravoi; G64051, Rapa Island, Baie Aurei; G64052, Rapa Island, Baie Aurei.

**Etymology.** The name refers to the geographic distribution of this species, restricted to the central and western Pacific Ocean.

**Description.** Solitary (Fig. 8A–B) to polystomatous (Fig. 8C) or forming coralla up to 3 corallites (Fig. 8D–I). Budding intracallicular (Fig. 8C) and extracallicular (Fig. 8F–I). Corallites round in outline. Calice width 15 – 25 mm. Septa in 4 – 5 cycles (≥ 48 septa), those of the first three cycles reach the columella, those of the fourth fuse with those of the third just before reaching the columella, and those of the fifth or more are free and often incomplete (Fig. 8D–E). Costosepta slightly unequal to unequal in relative thickness (Fig. 8D). Columellae trabecular and spongy, < 1/4 of calice width (Fig. 8D–F). Septal teeth height medium (0.3 – 0.6 mm) but can be high (> 0.6 mm) in some specimens. Tooth space medium (0.3–1 mm). Intereaerea smooth. Granules strong, pointed, scattered on septal face.

**Holotype.** The specimen includes two corallites growing on a slab of dead tabular *Acropora* (Figs 8F, S9). The largest corallite is rounded in shape and it measures 2.3 cm in diameter, the smaller one, budding from the former extracallicularly, is oval in shape and is 0.9 cm in diameter (shown by the arrow in Fig. 8F). The living colony included a third even smaller corallite (Fig. 9D) which was sampled for molecular analyses. The largest corallite presents 5 cycles of septa, the fourth one incomplete. Septa of the first 3 cycles reach the columella which is trabecular and 3.5 mm in diameter. *In vivo*, the colony had bright red peristome (Fig. 9D).

**Remarks.** Within the genus, this species is readily distinguished from all the others by the size of corallites and number of corallites and septa. The macromorphology and the *in situ* appearance of this species are closer to those of *H. australis*, with similar corallum shape.
and number of septa, than to any other congener within *Micromussa*. However, *H. australis* has overall larger corallites and wider septal tooth spacing. Septal teeth are between 2 to 4 mm apart in *H. australis* (Fig. 12B–C) and between 0.5 and 2.5 mm apart in *M. pacifica* (Fig. 12E–F). In fact, the character which perhaps is most useful for telling the two species apart is the increase in tooth size between midcalice and inner end in the first two cycles of septa observed in *H. australis* (arrows in Fig. 10B–C) but not in the new species. In particular, the tallest septa on primary septa in *H. australis* can reach up to 4 mm while (e.g. Fig. 10D) while they reach an observed maximum of 2.5 mm in *M. pacifica* (e.g. Fig. 8E).

**Colour.** The peristome has a different colour from the rest of the polyp all the combinations of bright red, orange, brown, green, grey and white have been observed (Fig. 9). In situ, this species and *H. australis* can co-occur (for example, in New Caledonia and Australia) and are found in the same habitats. They can be told apart by the more uniform within polyp colouration in the former (Fig. 9), and the more frequent and abundant presence of white areas in the peristome and, especially, over the septa in the latter (Fig. 11).

**Ecology.** This species is found between 10 and 40 m depth in protected environments with high sedimentation as well as in the deeper parts of outer reef slopes. The holotype and other specimens were growing on hard substrate coming from coral rubble consisting of fragments of dead tabular *Acropora* (Fig. S11).

**Distribution.** French Polynesia (Gambier and Austral Islands), New Caledonia (Grand Terre and Loyalty Islands), and eastern Australia.

**Remarks.** Two specimens of this species were sampled in the Gambier Islands in 1902 by M. Seurat, then director of the Biological Research Laboratory in Rikitea (1902-1904), and deposited in the MNHN general collection (IK-2012-14249). They had been previously identified as *Mussa costata* Dana, 1846 and *Scolymia* ? by different authors.

**Genus Homophyllia** Brüggemann, 1877

Type species: *Homophyllia australis* (Milne Edwards & Haime, 1849)

**Revised diagnosis.** Solitary or colonial with encrusting to submassive and massive coralla. Budding mainly intracalicular, extracalicular budding is also observed. Corallites monomorphic although central larger and rounder corallites are often observed in colonial coralla. Corallite integration discrete. Monticules absent. Calice width large (> 15 mm). Septa in more than four cycles (≥ 48 septa). Free septa irregular. Between 6 and 11 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy, < 1/4 of calice width. At midcalice tooth base elliptical-parallel and tooth tip irregular. Septal teeth height high (> 0.6 mm). Tooth space wide (> 1 mm). Interarea smooth. Granules weak, rounded, uniformly distributed on septal face. Tooth shape equal between first and third order septa. Tooth size increases between midcalice and inner end in the first two cycles of septa.

**Remarks.** The main characters differentiating *Homophyllia* from *Micromussa* are the shape and distribution of granules (Table 1) which are weak, rounded, uniformly distributed in the former genus and strong, pointed, and scattered in the latter.

**Species included.**

*Homophyllia australis* (Milne Edwards & Haime, 1849) (Figs 1F, 2F, 10, 11, 12A–C, 14K, P, S10)

*Caryophyllia australis* Milne Edwards & Haime, 1849 p. 320, pl. 8 fig. 2

*Scolymia* cf. *vitiensis* (Bruggemann, 1877) Veron & Pichon (1980) fig. 412


*Scolymia (= Homophyllia) australis* (Milne Edwards & Haime, 1849) Budd & Stolarski (2009) figs 2K, 4K, 5A, 6K, 7E, 7K, 11H

**Type material.** Two syntypes NHMUK 1840.11.30.77 and NHMUK 1840.11.30.79 from South Australia. Original designation Brüggemann, 1877: 310.

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Genus Australophyllia. Bennett & Arrigoni gen. nov. Type species: Australophyllia wilsoni (Veron, 1985) comb. nov.
Etymology. The name refers to the peculiar and narrow geographic distribution of this genus.

Diagnosis. Colonial with submassive to massive coralla. Budding intracalicular and extracalicular. Corallites monomorphic. Corallite uniserial and discrete. Monticules present. Calice width medium (4 – 15 mm). Septa in more than four cycles (≥ 48 septa). Free septa irregular. Between 6 and 11 septa per 5 mm. Costosepta unequal in relative thickness. Adjacent corallite centers discontinuous with lamellar linkage. Columellae trabecular and spongy, < 1/4 of calice width in series although it can be larger in monocentric corallites. At midcalice tooth base elliptical-parallel and tooth tip irregular. Septal teeth height medium (0.3 – 0.6 mm). Tooth space medium (0.3 – 1 mm). Interarea smooth. Granules weak, rounded, scattered on septal face. Tooth shape equal between first and third order septa. Tooth size equal between midcalice and inner end in the first two cycles of septa.

Remarks. The main characters differentiating Australophyllia from the other genera in this study are the uniserial corallites, which are discrete in all the other examined taxa, the discontinuous corallite centre linkage as opposed to the absence of linkage in the other taxa. Moreover, in Australophyllia and the granules on septal sides are weak, rounded, scattered while they are strong, pointed, and scattered in Micromussa, weak, rounded, uniformly distributed in Homophyllia, and weak, rounded, enveloped by thickening deposits in Acanthastrea (Table 1).

Species included (monotypic genus).
Australophyllia wilsoni (Veron, 1985) comb. nov. (Figs 11, 21, 13, 14N–S)
Symphyllia wilsoni (Veron, 1985) pp. 169-170, figs 18-22; Veron, 2000, vol. 3, p. 53, figs 2–4

Type material. The holotype (Z910) from Rat Island, Houtman Abrolhos Islands, Western Australia is deposited at the WAM. Two paratypes (Z911, Z912) are deposited at the WAM.

Examed material. Western Australia – (coll. D.P. Thomson): AM WIL1, Hall Bank, 09/04/2013, 9m; AM WIL2, Hall Bank, 09/04/2013, 9m; AM WIL3, Hall Bank, 09/04/2013, 9m; AM WIL4, AM WIL5; RMNH Coel. 22399, West Australia, Abrolhos Islands, 2m, 03/04/1976; WAM 168-84 (holotype), Rat Island, Houtman Abrolhos Islands, Western Australia, 8m, 1983, coll. J.E.N. Veron; paratype (WAM 169-84), Port Denison, Western Australia, 9m, 1982, J.E.N. Veron; paratype (WAM 170-84), Port Denison, Western Australia, 12m, 1982, coll. J.E.N. Veron.

Distribution. This species is restricted to Southwestern Australia and thrives in temperate conditions.

Genus Acanthastrea Milne Edwards & Haime, 1848
Type species: Astraea echinata (Dana, 1846)

Species included.
Acanthastrea minuta Moll & Borel-Best, 1984 (Fig. S15E, F)
Acanthastrea minuta Moll & Borel-Best, 1984 p. 53, fig. 12

Type material. The holotype (RMNH 15275, Fig. S13E, F) from north Bone Tambung, Spermonde Archipelago, South Sulawesi, Indonesia is deposited at the RMNH.

Family Poritidae Gray, 1842
Genus Goniopora de Blainville, 1830
Species included.
Goniopora diminuta (Veron, 2000) (Fig. S15A, B, D)

Type material. The lectotype (MTQ G55851, Fig. S15A, B, D) from southern Sri Lanka is deposited at the MTQ. This species was described in Veron (2000) without designating type material and type locality, rendering it as nomen nudum. Subsequently, it was re-described in Veron (2002) with the designation of a ‘holotype’ (MTQ G55851). Following ICZN (2011: 164), the Veron (2000) publication was validated as an available taxonomic work. The species named in Veron (2000) is therefore valid, but the type specimen designated in Veron (2002) is not (Wallace et al., 2012). Therefore this specimen is herein regarded as lectotype.