CONTRIBUTIONS TO ZOOLOGY (2023) 1–42

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Phylogenetics and taxonomy of the scleractinian coral family Euphylliidae

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Published with license by Koninklijke Brill NV | DOI: 10.1163/18759866-BJA10041
 | ISSN: 1383-4517 (print) 1875-9866 (online)

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RECEIVED: 25 NOVEMBER 2022 | REVISED AND ACCEPTED: 9 FEBRUARY 2023
EDITOR: R. VONK

Abstract

The family Euphylliidae consists of reef-building zooxanthellate scleractinian corals distributed across the Indo-Pacific. Seven extant genera comprising a total of 22 valid species are currently recognised. Recent studies have re-organised the taxonomy of the family at the genus level based on molecular and morphological data, including a comprehensive revision of *Euphyllia* and the resurrection of *Fimbriaphyllia*. Here, three mitochondrial loci (COI, 12S rRNA, and 16S rRNA) were sequenced and morphological examinations were conducted at three scales (macro/micromorphology and microstructure of the skeleton, and polyp morphology) to study the phylogeny and taxonomy of Euphylliidae. We analysed a total of 11 valid species collected from seven Indo-Pacific localities. The monotypic genus *Coeloseris*, currently in Agariciidae, was also investigated since previous molecular data suggested a close relationship with the Euphylliidae. Molecular and morphological phylogenetic trees were broadly concordant in the definition of genus-level clades. All analysed genera, i.e., *Ctenella*, *Euphyllia*, *Fimbriaphyllia*, *Galaxea*, and *Gyrosmilia*, were reciprocally monophyletic based on molecular results. *Coeloseris* was nested within the family and, therefore, is formally moved into Euphylliidae. Updated morphological diagnoses are provided for each investigated genus. This study further demonstrated that a phylogenetic classification of scleractinian corals can be achieved by applying a combined morpho-molecular approach. Finally, we encourage phylogenetic and taxonomic studies of the euphylliid taxa not yet analysed molecularly, such as the monotypic genera *Montigyra* and *Simplastrea*.

Keywords

coral reefs – hard corals – Indo-Pacific Ocean – integrative systematics – mitochondrial markers – morphology

Introduction

The taxonomy of scleractinian corals (Cnidaria: Anthozoa: Scleractinia) has been traditionally conducted based on the examination of macroscopic skeletal characters (e.g., Milne Edwards & Haime, 1857; Duncan, 1884; Matthai, 1928). Although some authors have also attempted to include microstructural characteristics in their observations (Ogilvie, 1896; Vaughan & Wells, 1943; Alloiteau, 1952; Wells, 1956; Chevalier & Beauvais, 1987), these early criteria have been applied mainly to extinct taxa without support from additional approaches (Stolarski & Roniewicz, 2001). Starting from the late 1990s, the advent of

molecular phylogenies has challenged the traditional systematics of the order Scleractinia Bourne, 1900, showing that the classical macromorphology-based classifications were unreliable (Romano & Palumbi, 1996, 1997; Romano & Cairns, 2000; Chen et al., 2002; Le Goff-Vitry et al., 2004; Fukami et al., 2004, 2008; Huang et al., 2009; Stolarski et al., 2011). The re-evaluation of coral biomineralization processes and skeletal growth, as well as the discovery of new micromorphological characters have subsequently integrated and corroborated the growing amount of genetic data (Stolarski, 2000; Cuif et al., 2003; Stolarski, 2003; Cuif & Dauphin, 2005; Budd & Stolarski, 2009, 2011; Janiszewska et al., 2015). The integrated morpho-molecular approach provided the backbone for formal taxonomic revisions of multiple families and genera (Fukami et al., 2000; Wallace et al., 2007; Benzoni et al., 2007, 2010, 2012; Gittenberger et al., 2011; Budd et al., 2012; Kitahara et al., 2012a, 2012b; Kitano et al., 2014; Schmidt-Roach et al., 2014; Huang et al., 2014, 2016; Capel et al., 2020; Oku et al., 2020; Juskiewicz et al., 2022; Seiblitz et al., 2022).

Although we are in a fervid period for coral taxonomy thanks to a combined use of multiple lines of evidence, several taxa are still defined exclusively based on traditional macromorphology (Kitahara et al., 2016). The present study partially fills this gap for the family Euphylliidae Milne Edwards & Haime, 1857. This group currently comprises 22 extant valid species ascribed to seven genera, namely *Ctenella* Matthai, 1928, *Euphyllia* Dana, 1846, *Fimbriaphyllia* Veron & Pichon, 1980, *Galaxea* Oken, 1815, *Gyrosmilia* Milne Edwards & Haime, 1851, *Montigyra* Matthai, 1928, and *Simplastrea* Umbgrove, 1939 (Budd et al., 2012; Luzon et al., 2017, 2018; Hoeksema & Cairns, 2023). All representatives are colonial and zooxanthellate (Veron, 2000). They are widely distributed on shallow-water reefs of the Indo-Pacific (Veron, 2000; Veron et al., 2015; DeVantier & Turak, 2017), although some species of *Euphyllia* and *Galaxea* have also been documented in the mesophotic zone (>40 m depth) (e.g., Bridge et al., 2011; Blyth-Skyrme et al., 2013; Eyal et al., 2016; Muir et al., 2018; Montgomery et al., 2019).

The family has a long-standing history of taxonomic instability (table 1). It was originally proposed as Euphylliaceae at the rank of "*agèle*" by Milne Edwards & Haime (1857) to include 12 genera, seven of which are extant taxa, namely *Euphyllia*, *Eusmilia* Milne Edwards & Haime, 1848, *Gyrosmilia*, *Plerogyra* Milne Edwards & Haime, 1848, *Dendrogyra* Ehrenberg, 1834, *Dichocoenia* Milne Edwards & Haime, 1848, and *Pectinia* Blainville, 1825. The former four genera, together with *Physogyra* Quelch, 1884, were then accommodated in the subfamily Euphylliinae Alloiteau, 1952 (= Euphylliidae Milne Edwards & Haime, 1857) within the large family Meandrinidae Gray, 1847 by Alloiteau (1952). Subsequent monographs did not retain Euphylliidae as valid taxon and classified these genera into several families, such as Caryophylliidae Dana, 1846, Eusmilidae Milne Edwards & Haime, 1857, Meandrinidae Gray, 1847, Oculinidae Gray, 1847, and Pectiniidae Vaughan & Wells, 1943 (Vaughan & Wells, 1943; Wells, 1956; Veron & Pichon, 1980; Chevalier & Beauvais, 1987). Finally, Veron (2000) used Euphyllidae Veron, 2000 to accommodate *Euphyllia*, *Catalaphyllia* Wells, 1971, *Nemenzophyllia* Hodgson & Ross, 1982, *Plerogyra*, and *Physogyra*, while *Gyrosmilia* and *Eusmilia* were ascribed to Meandrinidae (Veron, 2000). Molecular phylogenetic analyses generated novel information to disentangle this taxonomic instability (e.g., Fukami et al., 2008; Kitahara et al., 2010, 2016). *Euphyllia*, the type genus of the family, clustered with *Ctenella*, *Fimbriaphyllia*, and *Galaxea* in clade V *sensu* Fukami et al. (2008) within the "Complex" group (Fukami et al., 2008; Huang, 2012; Kitahara et al., 2016;

TABLE 1 Historical changes in the systematics of the genera ascribed to Euphylliidae.

Genus	Milne Edwards & Haime (1857)	Vaughan & Wells (1943)	Alloiteau (1952)	Chevalier & Beauvais (1987)	Veron (2000)	Budd et al. (2012)	This study
Acrhelia	Oculinaceae*	Galaxeinae (Oculinidae)	Galaxeinae (Meandriidae)*	Galaxeidae*	Junior synonym of *Galaxea*	Junior synonym of *Galaxea*	Junior synonym of *Galaxea*
Coeloseris	–	Agariciidae	NM	Agariciidae	Agariciidae	Agariciidae	Euphylliidae
Ctenella	–	Eusmiliinae (Caryophylliidae)	Meandriinae (Meandriidae)	Meandrinidae	Meandrinidae	Euphylliidae	Euphylliidae
Euphyllia	Euphylliaceae	Eusmiliinae (Caryophylliidae)	Euphylliinae (Meandriidae)	Eusmilidae	Euphyllidae	Euphylliidae	Euphylliidae
Fimbriaphyllia	–	–	–	subgenus of *Euphyllia*	subgenus of *Euphyllia*	subgenus of *Euphyllia*	Euphylliidae**
Galaxea	Stylinaceae	Galaxeinae (Oculinidae)	Galaxeinae (Meandriidae)	Galaxeidae	Oculinidae	Euphylliidae	Euphylliidae
Gyrosmilia	Euphylliaceae	Eusmiliinae (Caryophylliidae)	Euphylliinae (Meandriidae)	Eusmilidae	Meandrinidae	Euphylliidae	Euphylliidae
Montigyra	–	Faviinae (Favidae)	Faviidae	Trachyphyllidae	Meandrinidae	Euphylliidae	Euphylliidae
Simplastrea	–	Galaxeinae (Oculinidae)	Galaxeinae (Meandriidae)	NM	Oculinidae	Euphylliidae	Euphylliidae

Abbreviations and symbols: – = examined taxonomic reference predates the taxon original description; NM = not mentioned in the study; * = *Acrhelia* accepted as *Acrohelia*; ** = Luzon et al. (2017, 2018) elevated *Fimbriaphyllia* to valid genus.

Akmal et al., 2017; Luzon et al., 2017, 2018). Conversely, in the "Robust" group, *Dendrogyra*, *Dichocoenia*, *Eusmilia*, and *Meandrina* were nested together in clade XII *sensu* Fukami et al. (2008), corresponding to Meandrinidae (Fukami et al., 2008; Barbeitos et al., 2010; Budd et al., 2012; Kitahara et al., 2016). Within the "Robust" clade, *Blastomussa* Wells, 1968, *Nemenzophyllia*, *Physogyra*, and *Plerogyra* were recovered in clade XIV *sensu* Fukami et al. (2008) and transferred to Plerogyridae Rowlett, 2020 (see Fukami et al., 2008; Huang, 2012; Arrigoni et al., 2012; Benzoni et al., 2014; Kitahara et al., 2016; Akmal et al., 2017; Rowlett, 2020). Based on this data set, *Ctenella* and *Galaxea* were moved to Euphylliidae by Budd et al. (2012), while *Gyrosmilia*, *Montigyra*, and *Simplastrea* were also transferred to the family despite the absence of molecular evidence. The last taxonomic change within Euphylliidae concerned the elevation of *Euphyllia* (*Fimbriaphyllia*) from subgenus to genus (Luzon et al., 2017, 2018). The authors demonstrated that *Fimbriaphyllia* is distinct from *Euphyllia* based on a combination of molecular, morphological (macromorphology and polyp structure), and reproductive (sexuality and reproductive mode) data (Luzon et al., 2017, 2018). Finally, Rowlett (2020) formally moved *Catalaphyllia* to Merulinidae Verrill, 1865, a taxonomic action that may have been inspired by molecular results of previous studies (Barbeitos et al., 2010; Kitahara et al., 2016).

Here, we studied the phylogenetics of Euphylliidae by analyzing 32 newly collected specimens from the Indo-Pacific belonging to four euphylliid genera. In addition, two specimens of *Coeloseris* Vaughan, 1918, a monotypic genus currently ascribed to Agariciidae Gray, 1847 (Veron, 2000; Waheed et al., 2015a), were collected and investigated. Indeed, previous molecular data indicated that the genus is sister to a lineage including *Euphyllia glabrescens* (Chamisso & Eysenhardt, 1821) and *Galaxea astreata* (Lamarck, 1816) (Arrigoni et al., 2017), while morphological observations by Kitahara et al. (2012b) indicated that *Coeloseris mayeri* Vaughan, 1918 lacks the main morphological characters shared by all extant agariciid genera. We sequenced three mitochondrial loci and investigated a total of 23 morphological characters, including skeletal macromorphology, micromorphology/microstructure, and polyp structure. Molecular and morphological phylogeny reconstructions of Euphylliidae were generated and compared. Based on our results, a revised taxonomic account of all analysed genera is provided.

Materials and methods

Sampling and identification

A total of 32 specimens representing 11 species of Euphylliidae were sampled while SCUBA diving between 1 and 35 m depth from seven localities in the Indian and Pacific Ocean, including the Red Sea coast of Saudi Arabia, Djibouti, Yemen (Socotra Island and Hadramaut province), Mayotte Island, Maldives, Papua New Guinea, and New Caledonia (supplementary table S1). The obtained species represent four out of the seven currently recognised genera of Euphylliidae, namely *Euphyllia*, *Fimbriaphyllia*, *Galaxea*, and *Gyrosmilia*. Additionally, two specimens of *Coeloseris mayeri* were collected and analysed to evaluate the potential molecular and morphological affinities of this genus to Euphylliidae. Each coral colony was photographed underwater and a fragment was collected and tagged. Approximately 2 cm^2 of the collected tissue was fixed in absolute ethanol or conserved 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) (Sargent et al., 1986). The remaining material was immersed in sodium hypochlorite for 48 hours to remove soft

tissues, rinsed in freshwater, and air-dried for identification and microscope observations of the cleaned corallum. Species level identification was based, when possible, on original descriptions and type material. Newly collected specimens were deposited at Institute de Recherche pour le Développement (IRD, Nouméa, New Caledonia), King Abdullah University of Science and Technology (KAUST, Thuwal, Saudi Arabia), and University of Milano-Bicocca (UNIMIB, Milan, Italy). Thin sections and skeletal fragments attached to microscope stubs are housed at Institute of Paleobiology, Polish Academy of Sciences (ZPAL, Warsaw, Poland).

Molecular analyses

Total genomic DNA was extracted using the DNeasy® Blood and Tissue kit (Qiagen Inc., Hilden, Germany) from coral tissues preserved in ethanol or using a phenol-chloroform-based method with a phenol extraction buffer (100 mM Tris-Cl pH 8, 10 mM EDTA, 0.1% SDS) from samples conserved in CHAOS solution (Fukami et al., 2004; Huang et al., 2011). DNA sequence data was collected for three mitochondrial gene fragments: the barcoding portion of the cytochrome c oxidase gene (COI), the small subunit of ribosomal RNA (12S rRNA), and the large subunit of ribosomal RNA (16S rRNA). The three markers were selected because they proved to be informative for testing the monophyly of scleractinian taxa in previous studies (e.g., Fukami et al., 2008; Kitahara et al., 2010; Stolarski et al., 2011; Kitahara et al., 2012b). We used the primers LCO1490–HCO2198 (Folmer et al., 1994) for COI, ANTMT12SF–ANTMT12SR (Chen & Yu, 2000) for 12S rRNA, and LP16SF–LP16SR (Le Goff-Vitry et al., 2004) for 16S rRNA. PCR protocols from Stolarski et al. (2011) were followed. All PCR products were purified with Illustra ExoStar (GE Healthcare, Buckinghamshire, UK) and directly sequenced using an ABI 3130xl Genetic Analyzer (Applied Biosystems, Carlsbad, CA, USA). Sequences obtained in this study were deposited in NCBI under accession numbers OQ301692–OQ301709 (COI), OQ303739–OQ303765 (12S rDNA), and OQ301759–OQ301783 (16S rDNA) (supplementary table S1).

For the phylogenetic analyses, our newly generated sequences were aligned with Euphylliidae sequences from previous studies (Romano & Palumbi, 1996; Romano & Cairns, 2000; Chen et al., 2002; Fukami et al., 2008; Barbeitos et al., 2010; Lin et al., 2011; Niu et al., 2016; Akmal et al., 2017; Chuang et al., 2017) and several other representatives of the "Complex" clade downloaded from GenBank (supplementary table S2). We did not include COI sequences of euphylliids published by Luzon et al. (2017, 2018), notably including some species not analysed in this study such as *Fimbriaphyllia paraancora* (Veron, 1990) and *Fimbriaphyllia yaeyamensis* (Shirai, 1990), because the COI regions targeted by Luzon et al. (2017, 2018) and in our study overlapped only by about 50 bp. The sequence of the corallimorpharian *Discosoma nummiforme* Rüppell & Leuckart, 1828 (accession number KP938434) was selected as outgroup following Fukami et al. (2008) and Lin et al. (2014). Multiple alignments were carried out using MAFFT v.7.130b (Katoh & Toh, 2008; Katoh et al., 2009; Katoh & Standley, 2016) and the iterative refinement method e-ins-i. General statistics concerning the three genetic markers were calculated with DnaSP v.5.10.01 (Rozas et al., 2003; Librado & Rozas, 2009).

Sequence data sets from each locus were analysed individually as well as in a concatenated matrix. Phylogenetic analyses were conducted under three optimality criteria, namely maximum likelihood (ML), Bayesian inference (BI), and maximum parsimony (MP). ML phylogeny hypotheses were obtained using RAxML v.8 (Stamatakis, 2014) and the

graphical front-end raxmlGUI v.2.0.8 (Edler et al., 2021). The GTRGAMMA substitution model was applied and the branch support was assessed by 1,000 rapid bootstrap replicates. Prior to BI analyses, the most suitable nucleotide substitution models were selected for each locus using jModelTest v.2.1.9 (Guindon & Gascuel, 2003; Posada, 2008; Darriba et al., 2012), testing for 24 models, and choosing the best model based on the Akaike Information Criterion (AIC). The software selected the GTR + G for COI, the GTR + I + G for 12S rRNA, and the HKY + G for 16S rRNA. Under these evolution models, MrBayes v.3.2.6 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003; Ronquist et al., 2012) was used for each data set to generate four Markov chains of 10 million iterations in two runs, logging one tree per 100 generations. MCMC convergence among runs was assessed using Tracer v.1.7 (Rambaut et al., 2018), and the first 20,001 trees were discarded as burn-in. For both ML and BI analyses, the obtained phylogenetic trees were visualised using FigTree v.1.4.4 (Rambaut & Drummond, 2009). MP tree searches were run using TNT v.1.5 (Goloboff, 1999; Goloboff et al., 2008). Tree searches were performed with 10,000 random addition sequence replicates, each employing 100 cycles of sectorial searches, ratcheting, drifting, and tree fusing. Clade stability was determined through 10,000 bootstrap replications and a final strict consensus was obtained.

Morphological analyses

Observations at macromorphological level were made using a Leica M80 microscope (Wetzlar, Germany) equipped with a Leica IC80HD camera (Wetzlar, Germany). For the analysis at micromorphological/microstructural scale, specimens were observed intact, as broken and etched samples, or as thin sections (about 30 μm thick). Transverse broken sections of septa were exposed for 20 s of etching in 0.1% formic acid solution, rinsed with distilled water, and air-dried following the procedure described by Stolarski (2003). Once dried, the samples were mounted on stubs and sputter-coated with conductive platinum film. Thin sections were observed and photographed with a Nikon Eclipse 80i (Tokyo, Japan) transmitted light microscope, whereas intact and broken/etched skeleton samples were observed with a Philips XL 20 (Amsterdam, the Netherlands) scanning electron microscope (SEM) at the Institute of Paleobiology, Polish Academy of Sciences (Warsaw, Poland).

The survey of morphology targeted a total of 23 characters of the coral skeletal structure at three distinct scales, namely macromorphology (n = 18), micromorphology/microstructure (n = 3), and polyp structure (n = 2) (supplementary table S3). We usually investigated a single specimen belonging to each collected euphylliid species and to *Coeloseris mayeri* (supplementary table S4). Macromorphology and polyp structure was also observed for *Ctenella chagius* Matthai, 1928 (holotype BMNH 1928.3.1.61, British Museum of Natural History, London, UK – now NHMUK, Natural History Museum in London). Additionally, we selected *Gardineroseris planulata* (Dana, 1846) as outgroup. The analysed macromorphological characters were identical to those studied by Huang et al. (2014, 2016), with the exclusion of three characters, namely "monticules", "development of septal lobes", and "epitheca", that were not applicable or informative for Euphylliidae. Additionally, we adjusted the following characters to accommodate for states that are displayed by some taxa of Euphylliidae: "relative costosepta thickness" (character 13) with three ordered states – unequal, slightly unequal, equal; "columella linkage" (character 14) with three ordered states – absent, discontinuous (lamellar), continuous (trabecular);

"columella structure" (character 15) with four unordered states – lamellar, trabecular/compact (1–3 threads), trabecular/spongy (> 3 threads), reduced to inner septa margin processes. For macromorphology, we followed the glossary of skeletal terms in Budd et al. (2012). Concerning micromorphology/microstructure, we followed Kitahara et al. (2012b) and investigated three characters: "microtexture of septal faces" (character 19) with six unordered states – no distinct shingles, shingles not clear, shingles arranged into unique meandering "persian lamb fur" pattern, granular/occasional shingles, delicately grainy (low but pointed granulae arranged in rows parallel to septal margin), delicately granular, small-sized shingles; "microstructure of thickening deposits (TDs)" (character 20) with six unordered states – bundles of fibers not well delineated perpendicular to septal surface, bundles of fibers typically perpendicular to septal surface, bundles of fibers perpendicular/slightly oblique to the septal surface, well delineated bundles of fibers perpendicular/slightly oblique to the septal surface, fibers arranged into snake-like bundles (consequence of continuous growth of shingles), in some (axial) septa regions fibers arranged into elongated bundles (consequence of continuous growth of shingles); "arrangement of septal rapid accretion deposits (RADs)" (character 21) with three unordered states – closely spaced, closely spaced (zig-zag mid-septal zone), closely spaced (often not well delineated RADs). It is noteworthy that the large number of states of characters 19 and 20 may result in less weight of these two characters in the phylogenetic analysis. Several euphylliid species and genera have been traditionally identified based on differences of their polyps rather than corallite structures because they usually display distinct large polyps with elongate tentacles that are extended in daytime while the skeletal macroscopic features are devoid of much variability (Chevalier, 1971; Shirai, 1980; Veron & Pichon, 1980; Veron, 1990, 2000; Turak et al., 2012; Luzon et al., 2017, 2018). Following Luzon et al. (2017, 2018), we investigated the polyp structure with two different characters: "tentacles at daytime" (character 22) with three ordered states – retracted, partially/fully extended, fully extended; "tentacle shape" (character 23) with two unordered states – simple, complex.

The matrix composed of 23 morphological characters (see supplementary data S1) was used for phylogenetic analyses and included a total of 12 species of Euphylliidae and *Coeloseris mayeri*. *Pachyseris speciosa* was selected as outgroup based on our molecular phylogenetic tree and previous genetic studies (e.g., Fukami et al., 2008; Kitahara et al., 2016). MP phylogenetic analysis was run using TNT v.1.5 (Goloboff, 1999; Goloboff et al., 2008), under the same settings described for the molecular phylogeny reconstructions. Tree searches were performed with 10,000 random addition sequence replicates, each employing 100 cycles of sectorial searches, ratcheting, drifting, and tree fusing. Clade stability was determined through 10,000 bootstrap replications and a final strict consensus was obtained.

Results

Specimen identification

On the basis of the skeleton morphology and the examination of type material and relevant taxonomic studies (e.g., Chevalier, 1971; Pillai & Scheer, 1976; Veron & Pichon, 1980; Scheer & Pillai, 1983; Veron, 1990; Sheppard & Sheppard, 1991; Veron, 2000), the collected material was identified as following: *Coeloseris mayeri* (n = 2, from New Caledonia and Papua New Guinea), *Euphyllia cristata* Chevalier, 1971 (n = 3, from New Caledonia and

Papua New Guinea), *Euphyllia glabrescens* (n = 4, from Maldives, New Caledonia, and Papua New Guinea), *Fimbriaphyllia ancora* (Veron & Pichon, 1980) (n = 3, from Papua New Guinea), *Fimbriaphyllia divisa* (Veron & Pichon, 1980) (n = 3, from Mayotte Island and New Caledonia), *Fimbriaphyllia paradivisa* (Veron, 1990) (n = 3, from Saudi Arabia, Red Sea coast), *Galaxea acrhelia* Veron, 2000 (n = 1, from Papua New Guinea), *Galaxea astreata* (n = 3, from Saudi Arabia, Red Sea coast, Socotra Island, and Papua New Guinea), *Galaxea fascicularis* (Linnaeus, 1767) (n = 4, Saudi Arabia, Red Sea coast, Djibouti, Yemen, and Papua New Guinea), *Galaxea horrescens* (Dana, 1846) (n = 3, from New Caledonia and Papua New Guinea), *Galaxea paucisepta* Claereboudt, 1990 (n = 2, from New Caledonia), and *Gyrosmilia interrupta* (Ehrenberg, 1834) (n = 3, from Saudi Arabia, Red Sea coast) (figs. 1–2, supplementary table S1).

Molecular analyses

The combined matrix of the three sequenced mitochondrial loci included 56 terminals for a total of 1,982 bp (supplementary tables S1–S2), of which 586 bp, 883 bp, and 513 bp referred to CO1, 12S rRNA, and 16S rRNA, respectively. It was composed of 464 variable positions (23.4%) of which 298 were parsimony-informative (15%). Specifically, the CO1 alignment included 180 mutations, resulting in 147 polymorphic sites (25%) of which 107 were parsimony-informative (18.2%). The 12S rRNA locus exhibited a total of 257 mutations, with 210 variable positions (23.7%) of which 132 were parsimony-informative (14.9%). The 16S rRNA data set showed 129 mutations and 107 polymorphic positions (20.8%), including 59 parsimony-informative sites (11.5%).

The molecular phylogeny reconstruction inferred from the concatenated data set (CO1 + 12S rRNA + 16S rRNA) indicated that the examined Euphylliidae (clade V *sensu* Fukami et al. 2008) and *Coeloseris* formed a monophyletic clade with high or moderate branch supports (BI posterior probability BIpp = 1, ML bootstrap support MLbs = 100, MP bootstrap support MPbs = 85) within the "Complex" scleractinian corals (fig. 3). The family lineage was sister to the one grouping *Pachyseris* (clade IV *sensu* Fukami et al. 2008) with high branch supports (BIpp = 1, MLbs = 100, MPbs = 93). The Euphylliidae lineage included a total of six main groups: group V–A *sensu* Luzon et al. (2017, 2018) included the three analysed species of *Fimbriaphyllia*, namely *F. ancora*, *F. divisa*, and *F. paradivisa* (BIpp = 1, MLbs = 99, MPbs = 90); group V–B *sensu* Luzon et al. (2017) was composed of all analysed species of *Galaxea*, namely *G. acrhelia*, *G. astreata*, *G. fascicularis*, *G. horrescens*, and *G. paucisepta* (BIpp = 1, MLbs = 92, MPbs = 78); group V–C *sensu* Luzon et al. (2017, 2018) clustered the two analysed species of *Euphyllia*, namely *E. cristata* and *E. glabrescens* (BIpp = 1, MLbs = 98, MPbs = 91); group V–D *sensu* Luzon et al. (2017, 2018) included *Ctenella* and was sister to group V–E composed of the three studied samples of *Gyrosmilia* (BIpp = 0.97, MLbs = 100, MPbs = -); group V–F clustered the two analysed samples of *Coeloseris* (BIpp = 1, MLbs = 100, MPbs = 99). Within the three polytypic genera examined, namely *Euphyllia*, *Fimbriaphyllia*, and *Galaxea*, the different species were indistinguishable based on the presented phylogenetic tree. The phylogenetic relationships among the six euphylliid genera remained unresolved, with the only exception of the sister relationship between *Ctenlla* and *Gyrosmilia* showing moderate branch supports (BIpp = 1, MLbs = 96, MPbs = –).

The three single-locus phylogeny reconstructions broadly resolved the same families and genera obtained using the combined matrix (supplementary figs. S1–S3) but not their phylogenetic relationships. In all phylogenetic trees, Euphylliidae including *Coeloseris*

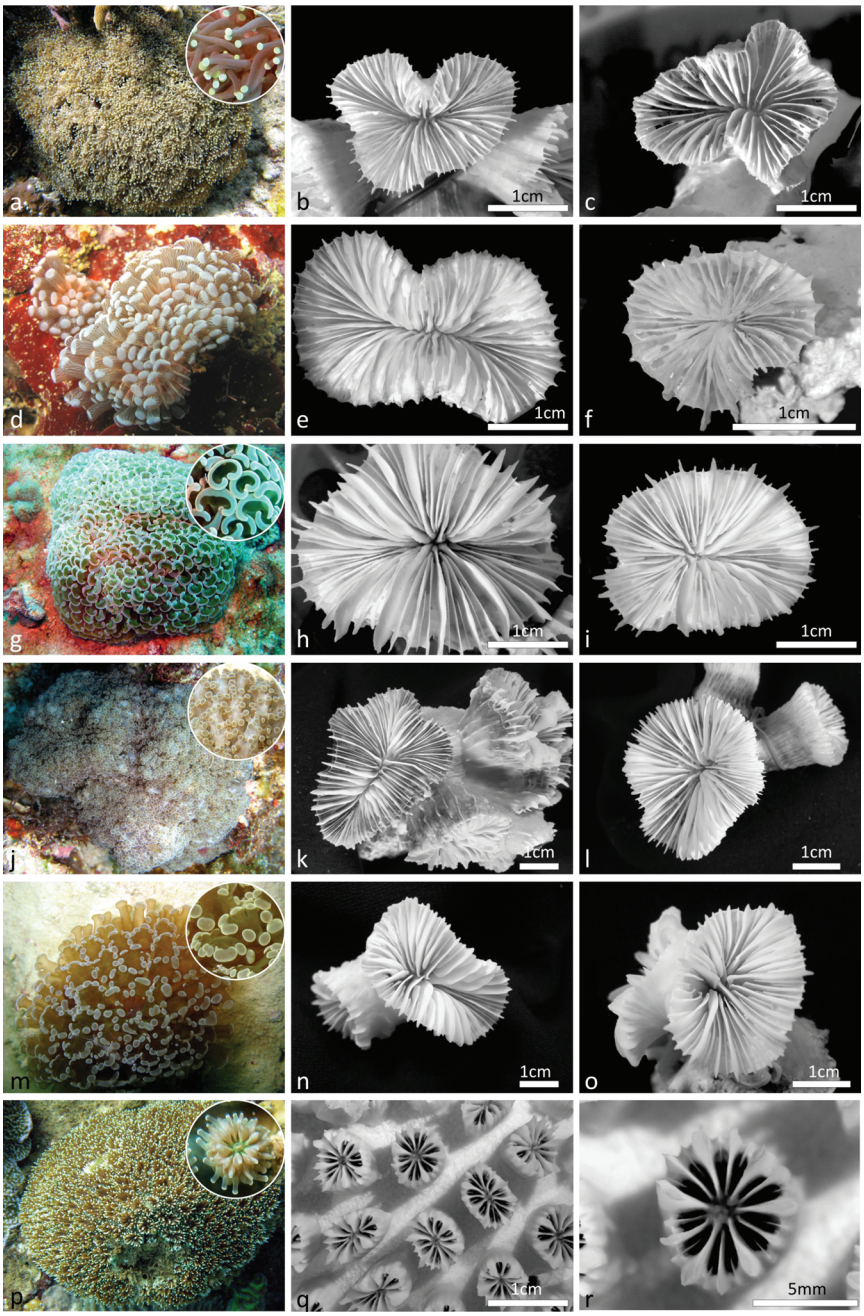

FIGURE 1 *In situ* (a, d, g, j, m, p, close-up of the tentacles in the inset) and skeleton (b–c, e–f, h–i, k–l, n–o, q–r) images of the taxa examined in this paper. *Euphyllia glabrescens*, Papua New Guinea: (a, c) UNIMIB PFB634, Nusalomon Island, Kavieng, (b) UNIMIB PFB435, Nusa Island, Kavieng. *Euphyllia cristata*, Kavieng, Papua New Guinea: (d–e) UNIMIB PFB688, Albatross Passage, (f) UNIMIB PFB825. *Fimbriaphyllia ancora*, Kavieng, Papua New Guinea: (g) UNIMIB PFB756, (h) UNIMIB PFB427, Nago Island, (i) UNIMIB PFB635, Nusalomon Island. *Fimbriaphyllia divisa*, New Caledonia: (j–k) IRD HS3588, Ilôt Ndié, Pines Island, (l) IRD HS3683, Ilot Reynard, Chesterfield Islands. *Fimbriaphyllia paradivisa*, Hindiyah, Saudi Arabia: (m–n) KAUST SA1809, (o) KAUST SA1808. *Galaxea fascicularis*, Ghoubet el Kareb, Djibouti: (p–r) UNIMIB–TO DJ324.

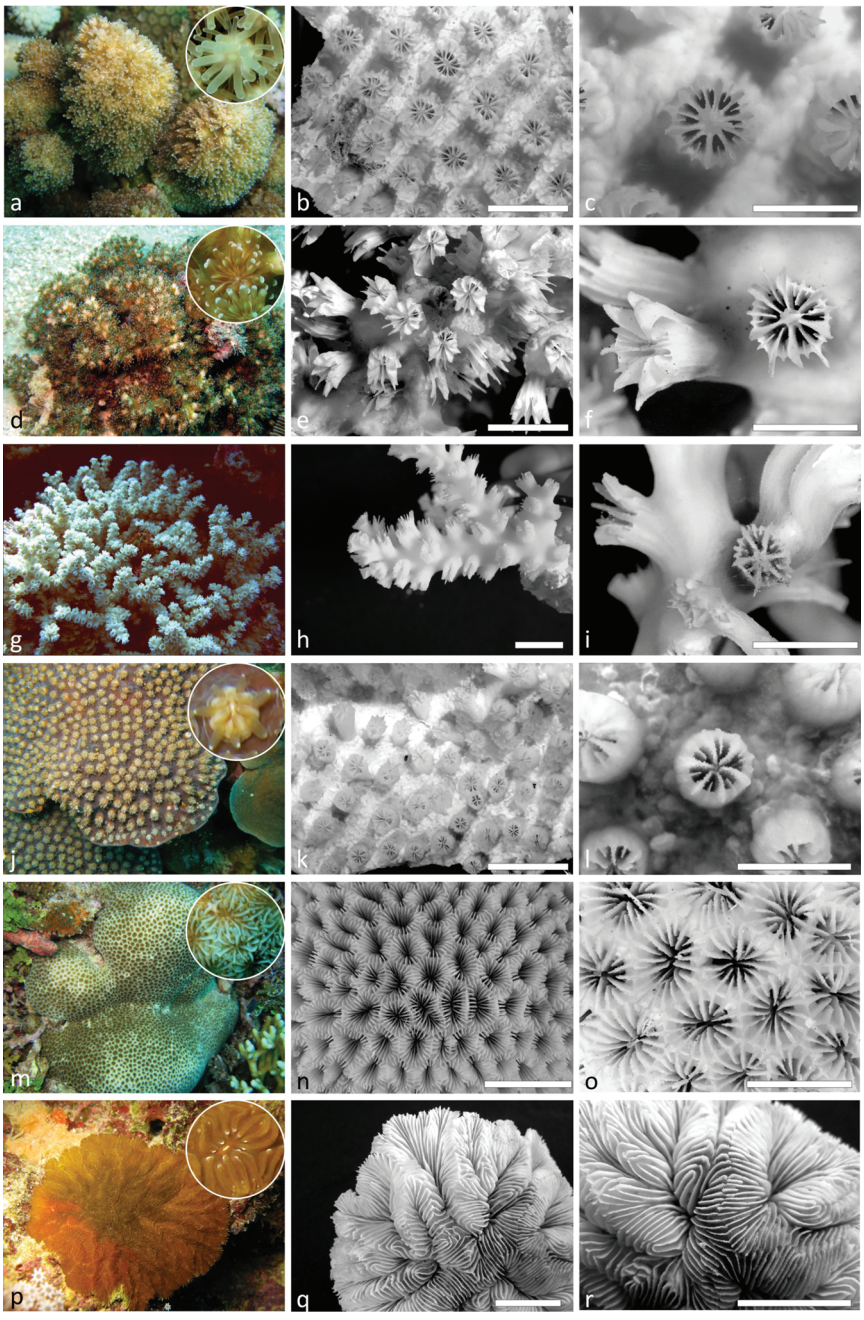

FIGURE 2 *In situ* (a, d, g, j, m, p, close-up of the tentacles in the inset) and skeleton (b–c, e–f, h–i, k–l, n–o, q–r) images of the taxa examined in this paper. *Galaxea astreata*: (a, c) UNIMIB–TO MY001, Ile Blanche, Mayotte Island, (b) UNIMIB–TO DJ042, Oblal, Djibouti, (c) UNIMIB–TO DJ325, Ghoubet el Kareb, Djibouti. *Galaxea acrhelia*: (d–f) UNIMIB PFB166, Masas Island, Madang, Papua New Guinea. *Galaxea horrescens*: (g–h) IRD HS4121, Chesterfield Islands, New Caledonia, (i) UNIMIB PFB478, Usien Island, Kavieng, Papua New Guinea. *Galaxea paucisepta*, Prony Bay, New Caledonia: (j–l) IRD HS2895. *Coeloseris mayeri*: (m, o) UNIMIB PFB127, Masas Island, Madang, Papua New Guinea, (n) IRD HS1768, Cap Goulvain, New Caledonia. *Gyrosmilia interrupta*: (p–r) KAUST SA0001, Al Lith, Saudi Arabia.

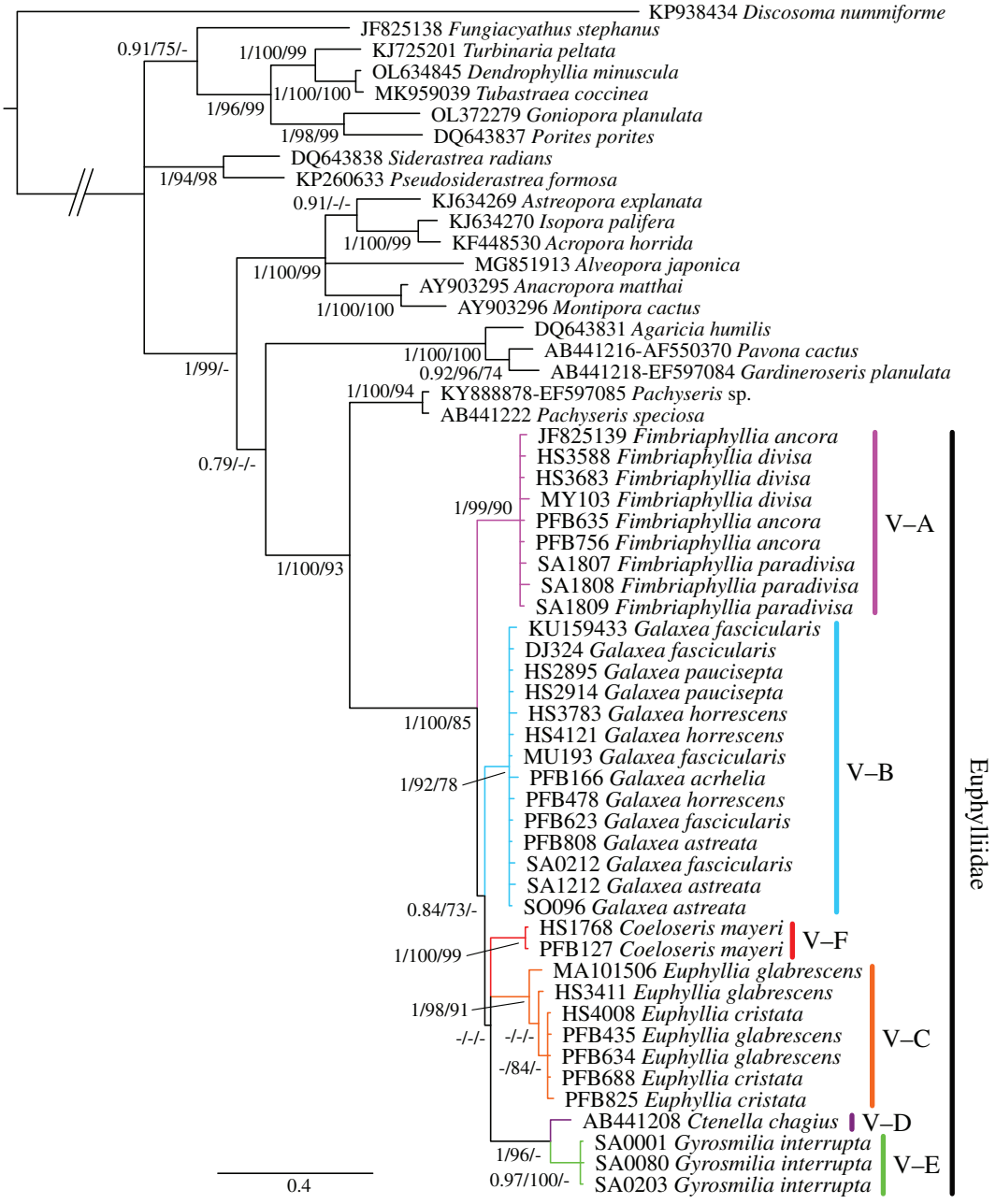

FIGURE 3 Bayesian inference molecular phylogeny reconstruction of Euphylliidae based on three mitochondrial loci (COI, 12S rRNA, and 16S rRNA). Numbers at nodes indicate Bayesian posterior probabilities (≥0.70), maximum likelihood bootstrap supports (≥70), and maximum parsimony supports (≥70), respectively. Colours and clade names refer to Luzon et al. (2017, 2018).

was resolved as a monophyletic lineage with high branch supports (BIpp = 1/1/1, MLbs = 98/100/95, MPbs = 97/99/95 for COI, 12S rRNA, and 16S rRNA, respectively). Its sister clade was represented by *Pachyseris* in both COI and 12S rRNA analyses and Acroporidae in the 16S

rRNA phylogeny hypothesis. It is noteworthy that the 16S rRNA alignment did not include any sequences of *Pachyseris* because no 16S rRNA sequences of this genus were available on GenBank at the time of the analyses. Within Euphylliidae, the phylogeny reconstructions inferred from 12S rRNA and 16S rRNA recovered *Fimbriaphyllia* (group V–A *sensu* Luzon et al. 2017, 2018), *Galaxea* (group V–B *sensu* Luzon et al. 2017, 2018), *Euphyllia* (group V–C *sensu* Luzon et al. 2017, 2018), *Gyrosmilia* (group V–E), and *Coeloseris* (group V–F) as monophyletic lineages with low to high branch supports. No sequences of *Ctenella* were available on GenBank for these two mitochondrial loci. The COI phylogenetic tree resolved *Fimbriaphyllia* (group V–A *sensu* Luzon et al. 2017, 2018), *Euphyllia* (group V–C *sensu* Luzon et al. 2017, 2018), and *Coeloseris* (group V–F) as distinct clades, while all *Galaxea* sequences formed a large unresolved polytomy within Euphylliidae. In addition, our sequences of *Gyrosmilia* and the GenBank sequence of *Ctenella* (accession number AB441208) were nested together in a single group (BIpp = 0.98, MLbs = 74, MPbs = 54).

Morphological analyses

The phylogeny reconstruction of Euphylliidae based on 23 morphological characters recovered the five analysed species of *Galaxea* in a single clade, albeit with very low branch support (MPbs = 33) (fig. 4). The sister lineage of *Galaxea* was represented by a clade (MPbs = 93) including *Euphyllia* and *Fimbriaphyllia*. Within this lineage, the three studied species of *Fimbriaphyllia* formed a monophyletic group with low branch support (MPbs = 64), while the two species of *Euphyllia* resulted in an unresolved position. A group including *Gyrosmilia* and *Ctenella* (MPbs = 14) was sister to the lineage leading to *Galaxea*, *Euphyllia*, and *Fimbriaphyllia*. Finally, *Coeloseris* was basal to all euphylliid genera.

From a morphological point of view, *Galaxea* displayed several unique characters among euphylliids, including an extensive coenosteum (≥ corallite diameter), a vesicular coenosteum structure, a mostly not confluent continuity of costosepta, a trabecular compact (1–3 threads) columella structure, and a columella size ≥ ¼ relative to calice width (although *G. paucisepta* did not) (figs. 1Q, R, 2B, C, E, F, H, I, K, L, 5, 6). *Gyrosmilia* (figs. 2Q, R, 7) and *Ctenella* possessed identical states for 15 macromorphological characters and differed only on the basis of their columella (linkage, structure, and size). Similarly, *Euphyllia* (figs. 1B, C, E, F, 8) and *Fimbriaphyllia* (figs. 1H, I, K, L, N, O, 9) shared identical macromorphology and were distinguished only by their columella. All euphylliid genera and *Coeloseris* (figs. 2N, O, 10) had regular free septa and abundant endotheca while *Pachyseris*, the sister taxon of Euphylliidae, showed absent or poorly developed free septa and sparse endotheca. Looking at micromorphology/microstructure, septal faces of *G. acrhelia*, *G. astreata*, and *G. fascicularis* showed shingles arranged into unique, meandering "persian lamb fur" pattern (figs. 5B, C, F, 6B, E) (septal faces, internal part of the wall; see also Stolarski, 2003). In these three *Galaxea* species, septal margin was straight or slightly undulated, composed of closely spaced (but not well delineated) RAD regions, with well delineated bundles of TD fibers that formed parallel to each other and oblique to the septal surface packages (figs. 5D, E, K, L, M, N, 6C, D). Conversely, in small corallites of both *G. horrescens* and *G. paucisepta* shingles was not clear or delicately granular (figs. 5L–N, 6F–I). In *Gyrosmilia*, septal surface was delicately granular, with margin straight or slightly undulated that was composed of closely spaced (zig-zag mid-septal) RAD zone (fig. 7). Bundles of TD fibers were not well delineated, perpendicular to septal surface

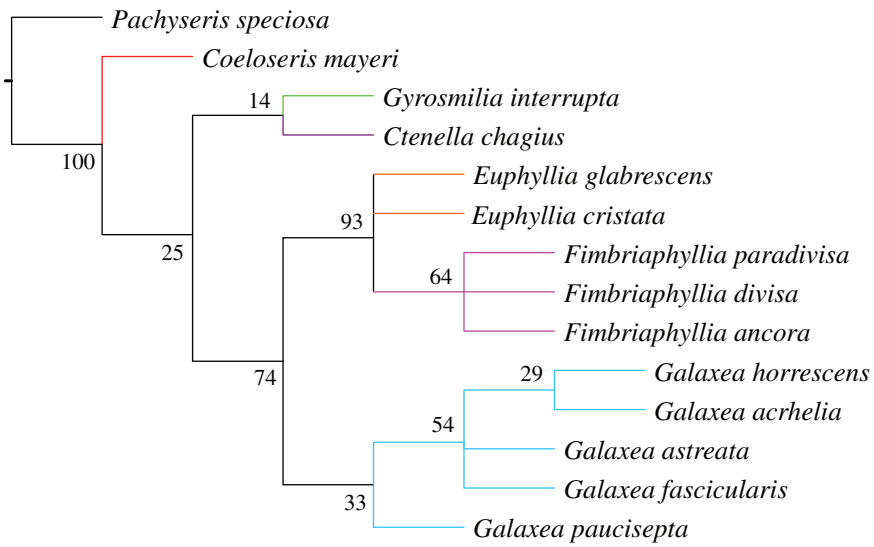

FIGURE 4 Maximum parsimony morphological phylogeny reconstruction of Euphylliidae based on 23 characters at three levels (macromorphology, micromorphology/microstructure, and polyp structure). Numbers at nodes indicate maximum parsimony bootstrap supports.

(fig. 7B). The two collected species of *Euphyllia* exhibited an identical texture of the septal margin that corresponded to a straight or zig-zag mid-septal (RAD) zone in transversely sectioned septa (figs. 8A, B, G, H, I). In *E. glabrescens*, septal faces and other intercalicular spaces showed small-sized shingles (fig. 8C) or granular textures (figs. 8D, E), while shingles were not clear in *E. cristata* (figs. 8G, H, I). *Fimbriaphyllia* was distinct from *Euphyllia* on the basis of delicately grainy septal faces, with low but pointed granulae arranged in rows parallel to septal margin (figs. 9A, B, F, J, K). Moreover, in the three investigated species of *Fimbriaphyllia* septal margins were undulated and composed of weakly individualised (figs. 9B, C, K, L) or closely spaced RAD regions (fig. 9G). In transversely sectioned septa, these textures corresponded to zig-zag mid-septal (RAD) zone and not well delineated bundles of TD fibers. Like other euphylliids, *Coeloseris* showed delicately granular septal faces, with septal margin straight composed of sometimes separated but closely spaced RAD region (figs. 10B, D) that, in transversely sectioned septa, resulted in not well delineated bundles of TD fibers.

Based on the polyp structure, *Euphyllia* (figs. 1A, D) and *Fimbriaphyllia* (figs. 1G, J, M) were easily distinguishable because, although tentacles of both genera were fully extended at daytime, the polyp shape was simple in the former genus and complex in the latter genus, with variably and distinctively shaped tentacles (see also Luzon et al., 2017, 2018). *Coeloseris* (fig. 2M) was the only analysed genus with polyp retracted at daytime while the remaining euphylliid genera, namely *Gyrosmilia* (figs. 2P, 11C, D), *Ctenella*, and *Galaxea* (figs. 1P, 2A, D, G, J, 11A, B), possessed simple polyps that were either partially or fully extracted at daytime.

Taxonomy

According to the molecular and morphological here and previous studies (Fukami et al., 2008; Lin et al., 2011; Budd et al., 2012; Kitahara et al., 2012b, 2016; Akmal et al., 2017; Luzon

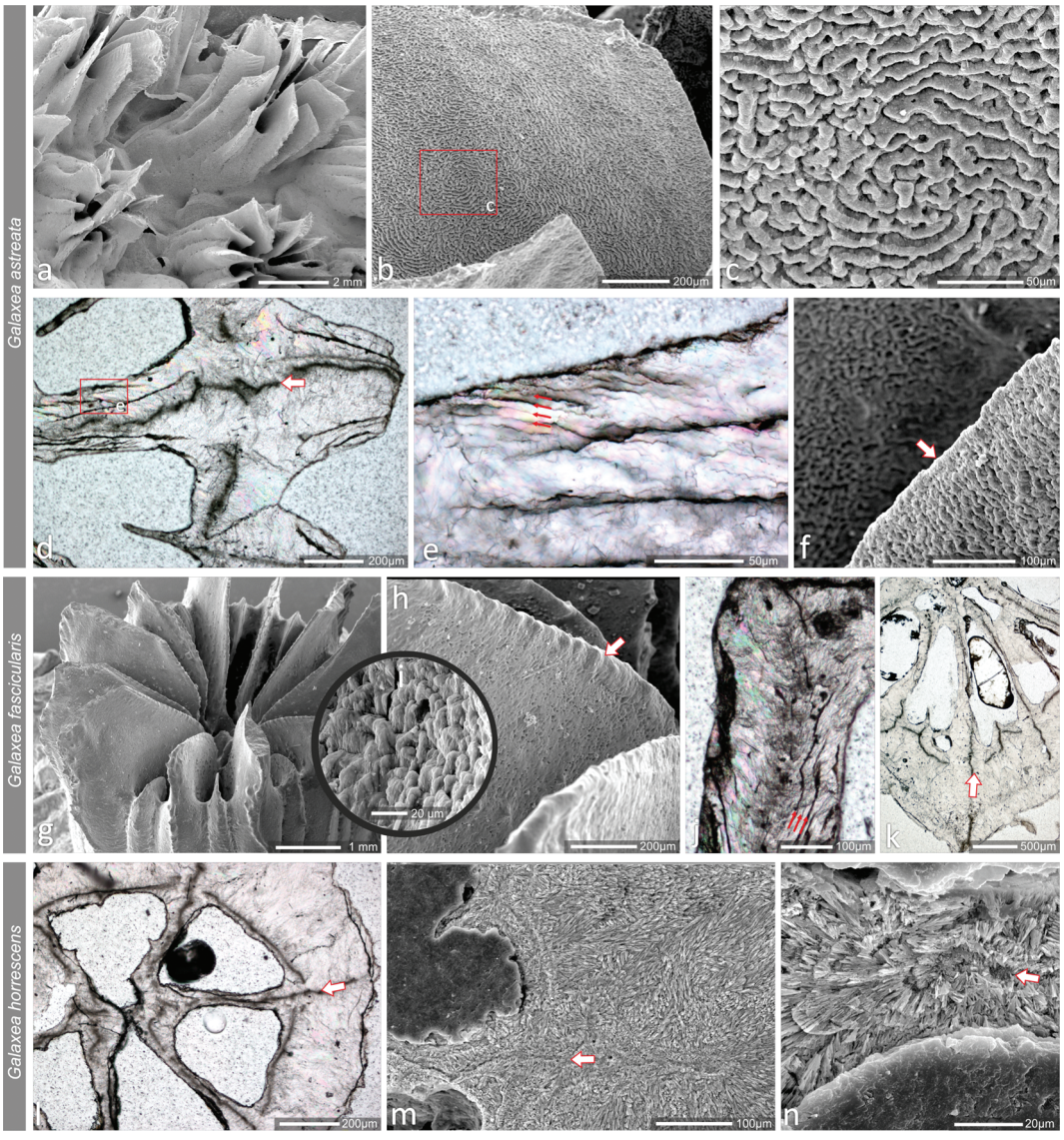

FIGURE 5 Micromorphological and microstructural skeletal characteristics of *Galaxea* (part 1). (a–f) *G. astreata* (UNIMIB PFB808/ ZPAL H.25/145, KAUST SA1212/ ZPAL H.25/144), (g–k) *G. fascicularis* (KAUST SA0212/ ZPAL H.25/146), (l–n) *G. horrescens* (UNIMIB PFB478/ ZPAL H.25/147). Septal faces with shingles arranged into unique, meandering "persian lamb fur" pattern (especially in b, c, f). Septal granulae low and widely spaced. Septal margin straight or slightly undulated, composed of closely-spaced not well delineated RAD regions (f, h; white-red-outline arrows). Such textures correspond to straight or zig-zag mid-septal (RADs) zone in transversely sectioned septa (d, k, l, m, n) and well delineated bundles of TD fibers that often form parallel to each other and oblique to the septal surface packages (e, i). In small corallites of *G. horrescens*, development of shingles is not clear. a–c, f–i: SEM images of corallum surface; m–n: SEM images of etched sections; d, e, j, k, l: transmitted light optical images.

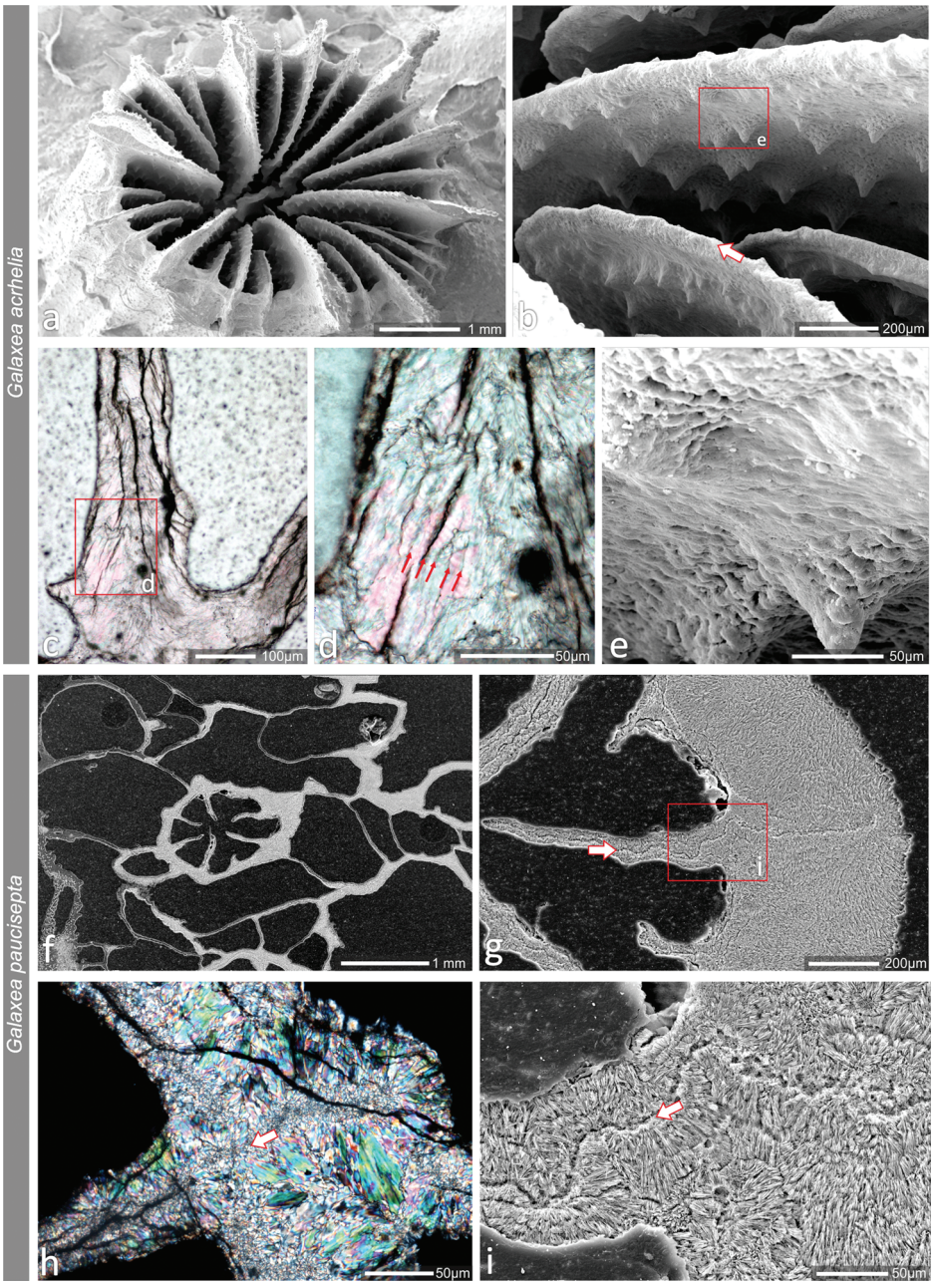

FIGURE 6 Micromorphological and microstructural skeletal characteristics of *Galaxea* (part 2). (a–e) *G. acrhelia* (UNIMIB PFB166/ ZPAL H.25/148), (f–i) *G. paucisepta* (IRD HS2895/ ZPAL H.25/149). In *G. acrhelia*, septal faces show shingles arranged into "persian lamb fur" pattern (b, e). Septal granulae relatively well developed. Septal margin straight or slightly undulated, composed of closely-spaced RAD regions (b; white-red-outline arrows). Such texture corresponds to straight mid-septal (RADs) zone in transversely sectioned septa (c, d) and well delineated bundles of TD fibers that form parallel to each other and oblique to the septal surface packages (c, d, red arrows). Small in diameter corallites of *G. paucisepta*, development of shingles is not clear; RADs or septa straight or zig-zag (h, i). a, b, e: SEM images of corallum surface; f, g, i: SEM images of etched sections; c, d, h: transmitted light optical images (h, polarised light).

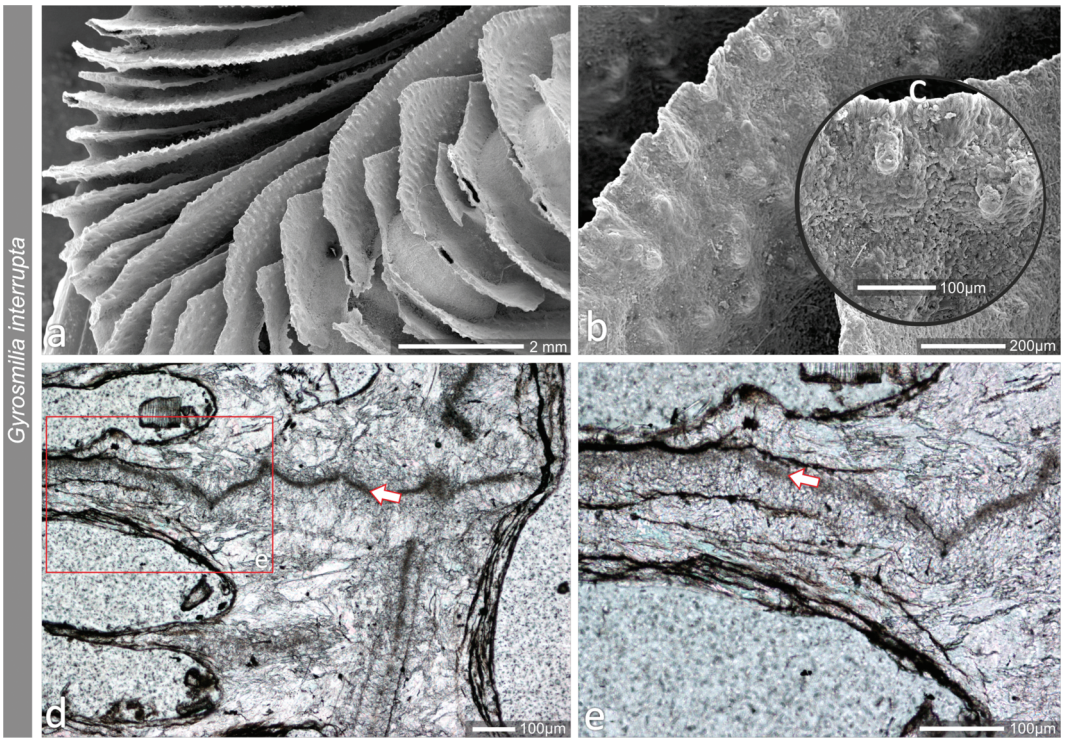

FIGURE 7 Micromorphological and microstructural skeletal characteristics of *Gyrosmilia* (*G. interrupta*, KAUST SA0080/ ZPAL H.25/150). Septal faces with low spines forming rows parallel to septa margin; septal surface between with delicately granular textures (b, c). Septal margin straight or slightly undulated (b), composed of closely-spaced RAD regions. RAD arrangement corresponds to straight or zig-zag mid-septal (RADs) zone in transversely sectioned septa (d, e). Bundles of TD fibers do not differentiate into distinct packages of fibers (b). a–c: SEM images of corallum surface; d, e: transmitted light optical images.

et al., 2017, 2018; Wepfer et al., 2020), a taxonomic account of Euphylliidae is herein provided. We present morphological diagnoses of the family and of the genera that were analysed in this study. *Coeloseris* is herein formally transferred to Euphylliidae. *Montigyra* and *Simplastrea* are conservatively maintained within the Euphylliidae according to Budd et al. (2012) as no phylogenetic data are available.

Order Scleractinia Boume, 1900

Family Euphylliidae Milne Edwards & Haime, 1857

Synonyms: Galaxeinae Vaughan & Wells, 1943; Euphylliinae Alloiteau, 1952; Euphyllidae Veron, 2000; Euphylliidae Veron, 2002.

Type genus: *Euphyllia* Dana, 1846.

Diagnosis: Colonial. Budding extracalicular and, typically, intracalicular. Corallites monomorphic; discrete or uni- or multi serial. Coenosteum bay be fused walls, extensive (≥ corallite diameter), or phaceloid. Coenosteum vesicular if present. Calice of width variable (< 4 mm, 4–15 mm, or > 15 mm) and relief medium to high (≥ 3 mm). Costosepta mostly not confluent if present. Number of septa variable (< 3 cycles, 3 cycles, or ≥ 3 cycles). Free septa regular. Septal spacing variable (< 6 septa, 6–11 septa, or > 11 septa per 5 mm). Costosepta may be equal or unequal in relative thickness. If present, columellae may be lamellar, trabecular compact (1–3 threads),

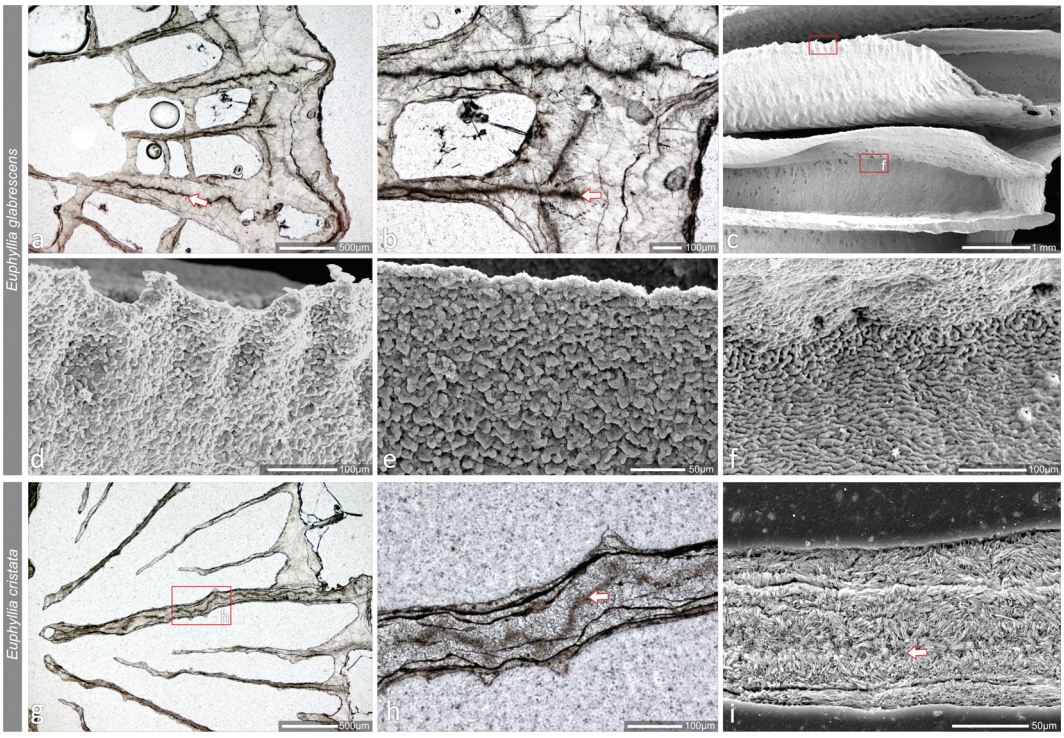

FIGURE 8 Micromorphological and microstructural skeletal characteristics of *Euphyllia*. (a–f) *E. glabrescens* (UNIMIB PFB435/ ZPAL H.25/151), (g–i) *E. cristata* (UNIMIB PFB825/ ZPAL H.25/152). In *E. glabrescens*, septal faces and other intercalicular space show small-sized shingles (c) or granulae (d, e) textures. Septal margin straight (e) or slightly undulated (d), composed of closely-spaced RAD regions. This texture corresponds to straight or zig-zag mid-septal (RADS) zone in transversely sectioned septa (a, b). Bundles of TD fibers do not differentiate into distinct packages of fibers (b). In *E. cristata* RADS of septa straight or zig-zag (g–i); no distinct shingles. c–f: SEM images of corallum surface; i: SEM images of etched sections; a, b, g, h: transmitted light optical images.

or reduced to inner septa margin processes, of sizes variable relative to calice width (< 1/4 or ≥ 1/4), with linkage absent or continuous. Paliform lobes absent. Endotheca abundant (vesicular). Microtexture of septal faces variable (delicately granular, delicately grainy with low but pointed granulae arranged in rows parallel to septal margin, shingles absent or small-sized or arranged into unique, meandering "persian lamb fur" pattern). Bundles of TD fibers variable (not well delineated perpendicular to septal surface, well delineated perpendicular/slightly oblique to septal surface, in some axial septa regions arranged into elongated bundles as consequence of continuous growth of shingles). RADS closely spaced, sometimes zig-zag mid-septal or not well delineated. Polyp tentacles retracted, partially/fully extended, or fully extended at daytime, of shape simple or complex.

Genera included: *Euphyllia* Dana, 1846; *Coeloseris* Vaughan, 1918; *Ctenella* Matthai, 1928; *Fimbriaphyllia* Veron & Pichon, 1980; *Galaxea* Oken, 1815; *Gyrosmilia* Milne Edwards & Haime, 1851; (?) *Montigyra* Matthai, 1928; (?) *Simplastrea* Umbgrove, 1939.

Taxonomic remarks: Euphylliidae was firstly established by Milne Edwards & Haime (1857) as Euphylliaceae at the lower-level rank of "*agèle*". Therefore, subsequent descriptions,

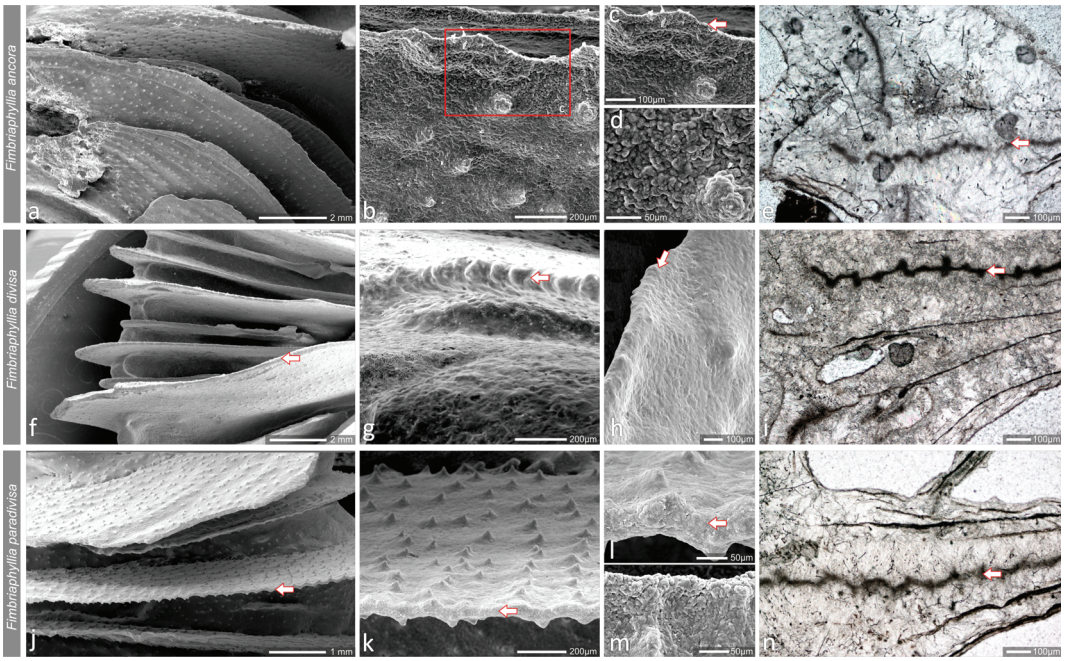

FIGURE 9 Micromorphological and microstructural skeletal characteristics of *Fimbriaphyllia*. (a–e) *F. ancora* (UNIMIB PFB804/ ZPAL H.25/153), (f–i) *F. divisa* (UNIMIB–TO MY103/ ZPAL H.25/154), (j–n) *F. paradivisa* (KAUST SA1807/ ZPAL H.25/155). Septal faces covered with low but pointed granulae arranged in rows parallel to septal margin (a, b, f, j, k). Between granulae, septal surface only delicately grainy. Septal margin undulated composed of weakly individualised (b, c, k, l) or very closely-spaced RAD regions (g). Such texture corresponds to zig-zag mid-septal (RADs) zone in transversely sectioned septa (e, i, n; white-red-outline arrows) and not well delineated bundles of TD fibers. Left 1st–3rd columns: SEM images of corallum surface; 4th column: transmitted light optical images.

including Euphylliinae Alloiteau, 1952, Euphyllidae Veron, 2000, and Euphylliidae Veron, 2002, are either junior synonym or misspelling (see ICZN, 2011). Galaxeinae Vaughan & Wells, 1943 was originally established as a sub-family of Oculinidae by Vaughan & Wells (1943) but, since its type genus *Galaxea* is nested within to Euphylliidae, Galaxeinae is herein considered a junior synonym of Euphylliidae. Following the molecular results of Fukami et al. (2008), Euphylliidae was formally re-organised at the genus level by Budd et al. (2012) to include only members of clade V *sensu* Fukami et al. (2008), namely *Euphyllia*, *Galaxea*, and *Ctenella*. The authors also transferred to Euphylliidae three genera that were not genetically analysed but considered to be morphologically similar to euphylliids, namely *Gyrosmilia*, *Montigyra*, and *Simplastrea*. Subsequently, Luzon et al. (2017, 2018) resurrected *Fimbriaphyllia* as a valid genus of Euphylliidae, restoring the monophyly of *Euphyllia*. In our study, we showed that *Gyrosmilia* clustered within Euphylliidae. Additionally, we found *Coeloseris* included within Euphylliidae based on both molecular and morphological data, confirming previous evidence by Kitahara et al. (2012b) and Arrigoni et al. (2017). As such, *Coeloseris* is herein transferred to Euphylliidae.

Morphological remarks: All investigated genera of Euphylliidae are characterised by extracalicular budding, absent polymorphism, regular free septa, absent paliform

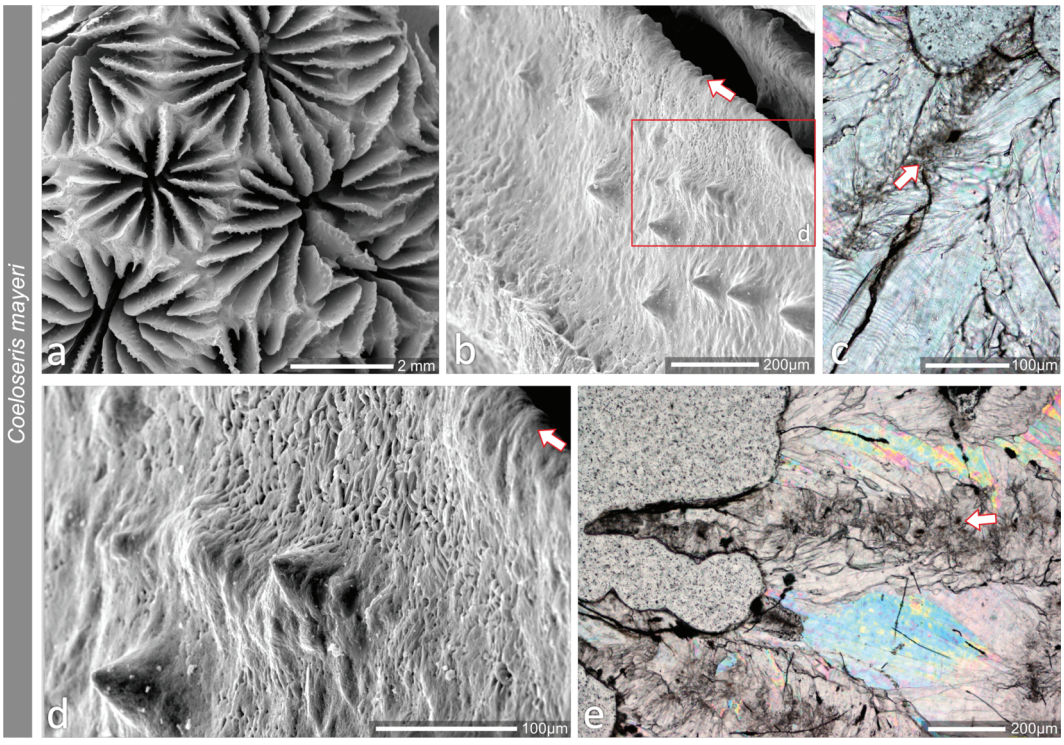

FIGURE 10 Micromorphological and microstructural skeletal characteristics of *Coeloseris* (*C. mayeri*, USNM 68296/ ZPAL H.25/156). Septal faces covered with low but pointed granulae (b, d) arranged in rows more or less parallel to distal and axial septal margin. Between granulae, septal surface only delicately grainy. Septal margin straight composed of sometimes separated but closely-spaced RADs regions (b, d; white-red-outline arrows). Such texture corresponds to straight mid-septal (RADS) zone in transversely sectioned septa (c, e) and not well delineated larger bundles of TD fibers. a, b, d: SEM images of corallum surface; c, e: transmitted light optical images.

lobes, and abundant endotheca. The states of the remaining 13 macromorphological characters are variable among genera. It is noteworthy to highlight that *Pachyseris speciosa*, belonging to the genus that represents the sister taxon of Euphylliidae in the molecular phylogenetic tree of Scleractinia (see Kitahara et al., 2016), possesses absent or poorly developed free septa and sparse endotheca. The two species of Agariciidae studied here, namely *Gardineroseris planulata* and *Pavona cactus*, show sparse endotheca, slightly unequal costosepta in relative thickness, and discontinuous columella linkages that are not found in the investigated euphylliids. From a micromorphological/microstructural perspective, the most distinct euphylliid subclade is represented by *Galaxea* species, which consistently form well developed shingles (or scale-like structures) arranged into unique, meandering "persian lamb fur" pattern on skeletal structures (septal faces, internal part of the wall; see also Stolarski, 2003). Noteworthy, less distinct shingles occur also in some species of *Euphyllia*, e.g., *E. glabrescens*, and in some examined specimens of the euphylliid sister taxon *Pachyseris* (*P. speciosa*). This character was found also in herein examined agariciids, i.e., *G. planulata* and *P. cactus*, and previously noted also in juvenile stages of other agariciids, i.e., *Dactylotrochus* and *Leptoseris* (Kitahara et al.,

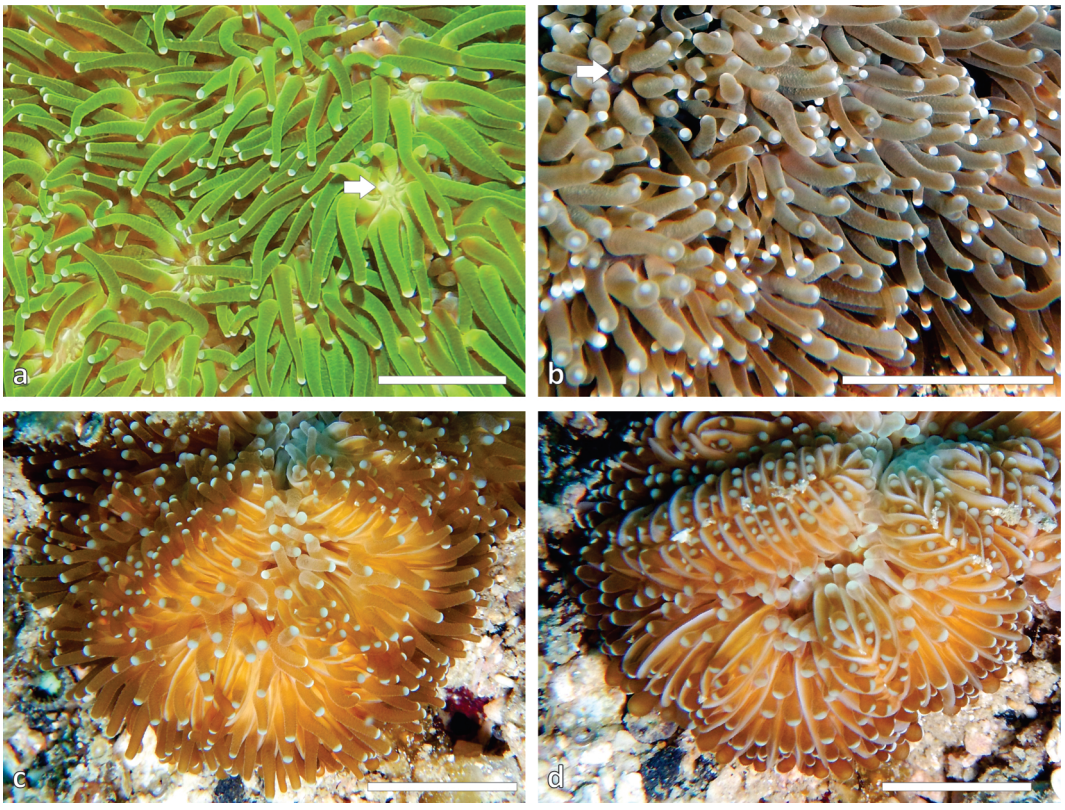

FIGURE 11 Extended tentacles of (a) *Galaxea fascicularis*, (b) *Galaxea astreata*, (c–d, same colony) *Gyrosmilia interrupta*, all from Nosy Sakatia, Madagascar. White arrows point at polyp mouths. Scale bars: 1 cm.

2012b). Shingles of unique morphology are particularly strongly developed in acroporids (Stolarski et al., 2016). The occurrence of shingles may point to a common theme in the histological organisation of calicoblastic tissues in euphylliids and the mentioned euphylliid sister/outgroups, but with distinct and strong expression in some groups (*Galaxea*-group or acroporids). The investigated euphylliid taxa show a tendency to develop granulae in rows parallel to the septal margins (clearly visible in *Fimbriaphyllia*). This character is particularly well developed in agariciids where occasionally the rows of granulae may merge to form lists or meninae on septal faces as in *Leptoseris* (e.g., *L. fragilis*) and *Dactylotrochus* (Kitahara et al. 2012b). The occurrence of granulae or merged granulae (menianae in some agariiciids), developed as structures parallel to septal margins, may point to a common biomineralization pattern, i.e., synchronous formation of rows of RADs on lateral septal faces in the agariciid-euphylliid evolutionary lineage (noted also by Cuif et al., 2003). All euphylliids investigated here, and *Pachyseris*, but also agariciids and acroporids, develop closely spaced, often not well delineated RADs on the septal margin.

Distribution: Euphylliidae is widely distributed on tropical and sub-tropical photic and mesophotic reefs of the Indo-Pacific, and absent in the eastern Pacific (Veron, 2000; Loya et al., 2019).

***Euphyllia* Dana, 1846**

(figs. 1A–F, 8)

Synonyms: *Euphyllia* (*Euphyllia*) Dana, 1846; *Leptosmilia* Milne Edwards & Haime, 1848;

Plocophyllia Reuss, 1868; *Euphyllia* (*Euphyllia*) Veron & Pichon, 1980.
Type species: *Caryophyllia glabrescens* Chamisso & Eysenhardt, 1821; holotype: not traced (illustrated in Chamisso & Eysenhardt, 1821: plate XXXIII, figs. 1a, 1b); type locality: Ratak Chain (Marshall Islands).

Original description: 'Quite simple, or segregato-gemmate, rarely free: zoophytes hemispherical. Tentacles oblong, subequal. Coralla having the calices subturbinate, either circular or much compressed, sometimes meandering; lamellae nearly or quite entire; cell very narrow at bottom.' (Dana, 1846: 157).

Diagnosis: Colonial. Budding intracalicular and extracalicular. Corallites monomorphic and discrete. Colonies phaceloid. Calice of relief high (> 6 mm) and width large (> 15 mm). Septa in ≥ 4 cycles (≥ 48 septa). Free septa regular. Septa spacing wide (> 11 septa per 5 mm). Costosepta unequal in relative thickness. Columellae reduced to inner septa margin processes, with size small relative to calice width (< 1/4), with linkage absent. Paliform lobes absent. Endotheca abundant (vesicular). Septal faces with shingles absent or small-sized. Bundles of TD fibers typically perpendicular to septal faces or not well delineated. Closely spaced (zig-zag mid-septal zone) RADs. Polyp tentacles fully extended at daytime, of shape simple.

Species included: *Euphyllia glabrescens* (Chamisso & Eysenhardt, 1821); *Euphyllia baliensis* Turak, Devantier & Erdman, 2012; *Euphyllia cristata* Chevalier, 1971; *Euphyllia paraglabrescens* Veron, 1990.

Taxonomic remarks: Dana (1846) originally introduced *Euphyllia* to include a total of 13 species. For detailed explanations on the determination of *E. glabrescens* as the type species of the genus see Vaughan (1918: 81) and Matthai (1928: 173). As with other euphylliid genera, *Euphyllia* has been historically transferred to several families based on skeletal macromorphology (see table 1; Milne Edwards & Haime, 1857; Vaughan & Wells, 1943; Alloiteau, 1952; Wells, 1956; Veron & Pichon, 1980; Chevalier & Beauvais, 1987; Veron, 2000). This historical taxonomic uncertainty was initially solved by a first comprehensive molecular phylogenetic tree of scleractinian corals showing that *Euphyllia* clustered within clade V *sensu* Fukami et al. (2008), together with *Ctenella* and *Galaxea* (Fukami et al., 2008). On the basis of these molecular results, Budd et al. (2012) re-organised the family Euphylliidae to include the members of clade V *sensu* Fukami et al. (2008). Subsequently, Luzon et al. (2017, 2018) found that representatives of *Euphyllia* were split in two main molecular lineages (see also Fukami et al., 2008; Lin et al., 2011; Akmal et al., 2017). Using a combination of molecular, morphological (skeleton and polyp morphology), and reproductive data, Luzon et al. (2017) revised *Euphyllia* to consist of four species, namely *E. glabrescens*, *E. baliensis*, *E. cristata*, and *E. paraglabrescens*, and moved the other five species of *Euphyllia* into *Fimbriaphyllia*. Our molecular and morphological results confirmed and strongly supported the study by Luzon et al. (2017, 2018).

Although we were not able to trace the holotype of *E. glabrescens*, the type species of *Euphyllia*, we did not designate a neotype because we did not perform a comprehensive search in all relevant museums and we cannot exclude that the holotype is deposited somewhere. Despite much of the Chamisso's collection is deposited in the Museum für Naturkunde (ZMB, Berlin, Germany), the type of the species could not be located there. To identify our specimens, we referred to the original illustration of *E. glabrescens* in Chamisso & Eysenhardt (1821: pl. XXXIII, figs. 1a, 1b).

Morphological remarks: Within Euphylliidae, the genus shares several macromorphological characters with *Fimbriaphyllia*, for example a phaceloid

coenosteum, large calice relief (> 15 mm), and wide septa spacing (> 11 septa per 5 mm). Nevertheless, the two genera can be told apart by their columella, which is reduced to inner septa margin processes, with a small size relative to calice width (< 1/4), and with absent linkage in *Euphyllia*. Micromorphologically, while *Euphyllia* exhibits closely spaced (zig-zag mid-septal zone) RADs similar to *Fimbriaphyllia* and *Gyrosmilia*, it is distinguished from these two genera by having septal faces with shingles absent or small-sized. Finally, *Euphyllia* and *Fimbriaphyllia* are the only euphylliids having polyps always fully extended at daytime but their polyp shapes easily distinguish the two genera, as also described and discussed in detail by Luzon et al. (2017, 2018). *Euphyllia* displays a simple polyp shape while representatives of *Fimbriaphyllia* have tentacles with complex shapes (see also Veron, 2000).

Distribution: Euphyllia is widely distributed on the reefs of the Indian and Pacific Oceans, occurring from the Arabian Sea and East Africa as far east as Marshall Islands in the Northern Hemisphere and Tonga and American Samoa in the Southern Hemisphere (Lamberts, 1983; Best et al., 1989; Sheppard & Sheppard, 1991; Veron, 2000; Obura, 2012; Richards & Beger, 2013; Huang et al., 2015; Veron et al., 2015; Waheed et al., 2015b; DeVantier & Turak, 2017; Montgomery et al., 2019). Records of *E. glabrescens* from the Red Sea (Berumen et al., 2019) remain uncertain and mainly based on accounts of the skeleton macro-morphology devoid of tentacles images or detailed description. It is indeed possible that records of *Euphyllia* in the Red Sea actually referred to *Fimbriaphyllia*. For example, the historical record by Scheer & Pillai (1983: Plate 37, Fig. 3) is based on material showing the same corallum and septa morphology as the material of *Fimbriaphyllia paradivisa* we collected and examined from the south Red Sea (fig. 1M–O). Conversely, records of Red Sea *Fimbriaphyllia*, especially from mesophotic depths, are numerous and well-illustrated showing the typical complex morphology of the extended tentacles in this genus (e.g., Eyal et al., 2016: Fig. 2), albeit still mostly classified as *Euphyllia* (e.g., Rinsky et al., 2022).

Coeloseris Vaughan, 1918

(figs. 2M–O, 10)

Synonyms: *Xishasiderastrea* Zou, 1975.

Type species: *Coeloseris mayeri* Vaughan, 1918; syntypes: USNM 45546, USNM 45547, USNM 45548, USNM 68296, USNM 85762, USNM M 546581 (National Museum of Natural History, Smithsonian Institution, Washington, DC, USA); type locality: Murray Island (Australia).

Original description: 'Corallum of massive growth-form. Calices polygonal, separated by simple, imperforate walls, which are secondarily thickened by vesicular endothecal dissepiments. Asexual reproduction by subequal fission. Septa imperforate, margins subentire, microscopically dentate. Synapticulae present, but rare; when present they are near the wall. No columella. This species is separable from the massive species of *Pavona* by the fewness of its synapticulae and the absence of columella.' (Vaughan, 1918: 139).

Diagnosis: Colonial. Budding intracalicular and extracalicular. Corallites monomorphic and discrete. Fused walls. Calice of width small (< 4 mm) and relief medium (3–6 mm). Septa in 3 cycles (24–36 septa). Free septa regular. Septal spacing narrow (< 6 septa per 5 mm). Costosepta equal in relative thickness. Columellae absent. Paliform lobes absent. Endotheca abundant (vesicular). Septal faces delicately granular. Bundles of TD fibers well delineated, perpendicular/slightly oblique to septal surface. Closely spaced RADs. Polyp tentacles retracted at daytime, of shape simple.

Species included: *Coeloseris mayeri* Vaughan, 1918.

Taxonomic remarks: *Coeloseris* is a monotypic genus described from Murray Island (Australia) by Vaughan (1918). The genus has been traditionally considered a member of Agariciidae given a superficial macromorphological resemblance with *Pavona* Lamarck, 1801 (see table 1; Matthai, 1928; Vaughan & Wells, 1943; Alloiteau, 1952; Wells, 1956; Veron & Pichon, 1980; Chevalier & Beauvais, 1987; Veron, 2000; Waheed et al., 2015a). Kitahara et al. (2012b) showed that *Coeloseris* differed from all extant agariciid genera as it lacks the main diagnostic micromorphological/microstructural characters of the family such as long menianes, scale-like organisation of tectura (thickening desposits outside the rapid accretion deposits of the wall), and beaded septa margins. Subsequently, a molecular study based on 18S rDNA suggested that *C. mayeri* was closely related to two species of *Euphyllia* and *Galaxea* and not related to the molecular lineage of Agariciidae (Arrigoni et al., 2017). Here, we confirmed both previous molecular and morphological results and formally transferred *Coeloseris* to Euphylliidae.

Morphological remarks: Kitahara et al. (2012b) showed that *Coeloseris* lacks the main micromorphological/microstructural features that are typical of all extant members of Agariciidae. Indeed, like other euphylliid genera, *Coeloseris* shows delicately granular septal faces, with septal margin straight, composed of a sometimes separated but closely spaced RAD region that, in transversely sectioned septa, result in not well delineated bundles of TD fibers. Additionally, the present study indicates that an abundant endotheca, a character shared among all representatives of Euphylliidae, is present in *Coeloseris* while the two investigated agariciid species *Gardineroseris planulata* and *Pavona cactus* possess a sparse endotheca. From a macromorphological perspective, *Coeloseris* is easily distinguishable among euphylliids considering its growth form, small width of calice (< 4 mm), and narrow septal spacing (< 6 septa per 5 mm). Concerning the polyp morphology, *Coeloseris* is the only euphylliid genus displaying retracted tentacles at daytime.

Distribution: Coeloseris is widely distributed on the reefs of the central Indo-Pacific, occurring from the Andaman and Nicobar Islands and western Sumatra to as far east as Marshall Islands in the Northern Hemisphere and American Samoa in the Southern Hemisphere (Pillai, 1983; Best et al., 1989; Jonker & Johan, 1999; Veron, 2000; Kenyon et al., 2010; Richards & Beger, 2013; Huang et al., 2015; Veron et al., 2015; DeVantier & Turak, 2017; Montgomery et al., 2019). Records from Kenya and South Africa are doubtful (Lemmens, 1993; Riegl, 1993).

***Ctenella* Matthai, 1928**

Type species: *Ctenella chagius* Matthai, 1928; holotype: BMNH 1928.3.1.61; paratypes: BMNH 1928.3.1.60, BMNH 1928.4.18.591; type locality: Chagos.

Not: *Ctenella* C. Carré & D. Carré, 1993 (phylum Ctenophora), junior homonym; invalid name.

Original description: 'Encrusting, massive or explanate, light. Growth-size small. Base of attachment broad or pedunculate. Valley sinuous, continuous or discontinuous at places, up to 14 mm. in width, depth up to 10 mm. Colline swollen to varying extent (up to 8 mm.) by endothecal deposition, ridged or with rounded edge. Septa in 1 cm. up to 20, of which up to 8 meeting columella, with margins vertical (sometimes curving to right or left) and entire, sides granular or spinulose, those of opposite sides of colline either alternating or continuous over colline. Columella lamellar, comparatively thin but solid, usually continuous (occasionally discontinuous) along middle of valley, and with sharp somewhat wavy ridge above. *Ctenella* has some

resemblance to *Pectinia,* since the septa have vertical *entire* margins and granular or spinulose sides, and since the columella is lamellar, comparatively thin but solid, usually continuous along the middle of the valley with a sharp wavy ridge above. But in *Ctenella* each septum does not appear to be composed of a pair of lamellae, as is often the case in *Pectinia,* the valleys do not attain to the same width, colline is never grooved, and the corallum is not massive or heavy' (Matthai, 1928: 171).

Diagnosis: Colonial. Budding intracalicular and extracalicular. Corallites monomorphic and uni- or multi serial. Fused walls. Calice of width medium (4–15 mm) and relief medium (3–6 mm). Septa in ≥ 4 cycles (≥ 48 septa). Free septa regular. Septal spacing medium (6–11 septa per 5 mm). Costosepta equal in relative thickness. Columellae lamellar, with size small relative to calice width (< 1/4), with linkage continuous. Paliform lobes absent. Endotheca abundant (vesicular). Polyp tentacles partially/fully extended at daytime, of shape simple.

Species included: *Ctenella chagius* Matthai, 1928.

Taxonomic remarks: Matthai (1928) established *Ctenella* to include two species, *C. chagius* and *Ctenella laxa* Matthai (1928). To date, the latter species is considered as a taxon *inquirendum* (Hoeksema & Cairns, 2023). On the basis of meandroid colony and lamellar columella, *Ctenella* has been historically considered a member of either Meandrinidae or Eusmiliidae (junior synonym of Meandrinidae) (see table 1; Vaughan & Wells, 1943; Alloiteau, 1952; Wells, 1956; Chevalier & Beauvais, 1987; Veron, 2000). With sequences from mitochondrial markers COI and cytB, Fukami et al. (2008) showed that *C. chagius* belonged to clade V *sensu* Fukami et al. (2008). Following the molecular phylogenetic tree of Fukami et al. (2008), Budd et al. (2012) assigned all members of clade V *sensu* Fukami et al. (2008), thus including *Ctenella*, to Euphylliidae. Although *Ctenella* was not collected for this study, we included this taxon in both molecular and morphological phylogeny reconstructions by using the COI sequence of *C. chagius* published by Fukami et al. (2008) (accession number AB441208) and investigating macromorphology of the holotype of *C. chagius* (BMNH 1928.3.1.61) and the polyp structure. Both analyses corroborated *Ctenella* as a member of Euphylliidae and showed a sister relationship with *Gyrosmilia*.

Morphological remarks: Ctenella displays 15 out of the 18 investigated macromorphological characters identical to *Gyrosmilia* of which one shared character, i.e., uni-or multi serial corallites, is unique within the family. Nevertheless, a lamellar columella, with continuous linkage, unambiguously tells apart *Ctenella* from *Gyrosmilia* and it has narrower valleys. No micromorphological/microstructural characters have been investigated for *Ctenella* in this study.

Distribution: Ctenella is restricted to the reefs of Chagos Archipelago and Mauritius (Rosen, 1971; Sheppard et al., 1983; Veron, 2000; Pillay et al., 2002; Obura, 2012).

Fimbriaphyllia Veron & Pichon, 1980

(figs. 1G–O, 9)

Synonyms: *Botryphyllia* Shirai, 1980; *Euphyllia* (*Fimbriaphyllia*) Veron & Pichon, 1980.

Type species: *Euphyllia* (*Fimbriaphyllia*) *ancora* Veron & Pichon, 1980; holotype: BMNH 1983.9.27.6 (illustrated in Veron & Pichon, 1980: figs. 623, 628); paratype: GL 4152 (Queensland Museum, Brisbane, Australia; see Veron & Wallace, 1984: 473–474); type locality: Jewell Reef, Great Barrier Reef (Australia).

Original description: 'Coralla are flabelloid to flabello-meandroid depending mainly on size. Small, flabelloid coralla initially develop a crescentic form from which irregular branches

develop. Larger coralla are dome-shaped with long sinuous to straight valleys which are usually interconnected. The width of the valleys varies greatly, depending on environmental conditions and the corallum size. Large coralla, which are mostly restricted to protected, partly turbid water, usually have narrow valleys. Coralla in early stages of development have wide valleys, usually with fluted margins. They are in the process of relatively rapid lateral growth and hence valleys are wide and thecae often greatly thickened by dissepiments. The development of the septa is also variable and also depends on environmental conditions and corallum size. Large coralla and those from turbid biotopes have small, relatively regular septa which are only slightly exsert and which are usually in three regular orders with an abortive fourth order. Small coralla and those from more exposed biotopes have more irregular septa. Some may be exsert up to 1 cm, others only fine ridges with orders often difficult to distinguish. All septa are glabrous or finely dentate and frequently have finely serrated margins. The larger septa extend to, or nearly to, the valley axis or calice centre and have vertical or subvertical inner margins which may be folded or curved towards the centres. Some septa have broad inner margins which may become slightly dentate. There are no columellae. The development of the costae varies greatly depending on the degree to which the septa are exsert and the degree of development of the exothecal dissepiments. In some coralla, the costae appear only as fine striations, in others they are lobed or form spines which, as with *E. glabrescens*, may develop into buds. Some coralla show pronounced development of endothecal dissepiments but this is usually restricted to small coralla or those growing in exposed biotopes where lateral growth is pronounced (Veron & Pichon, 1980: 352, 354).

Diagnosis: Colonial. Budding intracalicular and extracalicular. Corallites monomorphic and discrete. Colonies phaceloid. Calice of relief high (> 6 mm) and width large (> 15 mm). Septa in ≥ 4 cycles (≥ 48 septa). Free septa regular. Septal spacing wide (> 11 septa per 5 mm). Costosepta unequal in relative thickness. Columellae absent. Paliform lobes absent. Endotheca abundant (vesicular). Septal faces delicately grainy, with low but pointed granulae arranged in rows parallel to septal margin. Bundles of TD fibers not well delineated, perpendicular to septal surface. Closely spaced (zig-zag mid-septal zone) RADs. Polyp tentacles fully extended at daytime, of shape complex.

Species included: *Fimbriaphyllia ancora* (Veron & Pichon, 1980); *Fimbriaphyllia divisa* (Veron & Pichon, 1980); *Fimbriaphyllia paraancora* (Veron, 1990); *Fimbriaphyllia paradivisa* (Veron, 1990); *Fimbriaphyllia yaeyamensis* (Shirai, 1980).

Taxonomic remarks: Based on colony growth form, Veron & Pichon (1980) established two subgenera within the genus *Euphyllia*, namely *Euphyllia* and *Fimbriaphyllia*. Originally, the subgenus *Fimbriaphyllia* included *E.* (*Fimbriaphyllia*) *ancora* and *E.* (*Fimbriaphyllia*) *divisa*, while the subgenus *Euphyllia* was composed of *E.* (*Euphyllia*) *cristata* and *E.* (*Euphyllia*) *glabrescens* (Veron & Pichon, 1980). Subsequently, Veron (2000) maintained two distinct groups within the genus *Euphyllia*, separating the phaceloid species from the flabello-meandroid ones. Molecular data showed that the species traditionally ascribed to *Euphyllia* were separated in two major lineages (Fukami et al., 2008; Lin et al., 2011; Akmal et al., 2017; Luzon et al., 2017, 2018). Luzon et al. (2017, 2018) demonstrated that these two groups can be distinguished based on the polyp morphology and reproductive traits and not on the colony growth form. As such, Luzon et al. (2017, 2018) resurrected *Fimbriaphyllia* as a valid genus to be composed of five species, namely *F. ancora*, *F. divisa*, *F. paraancora*, *F. paradivisa*, and *F.*

yaeyamensis. Our morpho-molecular results are in agreement with those presented by Luzon et al. (2017, 2018) and previous molecular phylogeny reconstructions (Fukami et al., 2008; Lin et al., 2011; Akmal et al., 2017).

Morphological remarks: Fimbriaphyllia has been traditionally confused with *Euphyllia* because of their macromorphological resemblance. The morphological characters that separate the two genera are described in the morphological remarks section of *Euphyllia*, with a particular focus on the columella structure and polyp shape as diagnostic characters. Additionally, septal faces are delicately grainy, with the low but pointed granulae arranged in rows parallel to septal margin, which is a unique micromorphological/microstructural feature within the family Euphylliidae.

Distribution: Fimbriaphyllia is widely distributed on the reefs of the Indian and Pacific Oceans, occurring from the Red Sea and East Africa as far east as Marshall Islands in the Northern Hemisphere and Fiji in the Southern Hemisphere (Veron, 2000; Glynn et al., 2007; Obura, 2012; Richards & Beger, 2013; Huang et al., 2015; Veron et al., 2015; Eyal et al., 2016; DeVantier & Turak, 2017; Berumen et al., 2019; Montgomery et al., 2019).

Galaxea Oken, 1815

(figs. 1P–R, 2A–L, 5, 6, 11A–B)

Synonyms: *Acrhelia* Milne Edwards & Haime, 1849; *Acrohelia* Milne Edwards & Haime, 1857; *Organites* Link, 1907.

Type species: *Madrepora fascicularis* Linnaeus, 1767; holotype: not traced; type locality: Indian Ocean (O. indico, see Linnaeus, 1767).

Original description: 'tamm nur eine einfache, kurze Röhre, oft viele unten wie in eine Mittels punct verbunden.' (Oken, 1815: 71).

Diagnosis: Colonial. Budding exclusively extracalicular. Corallites monomorphic and discrete. Coenosteum extensive (≥ corallite diameter) and vesicular. Calice width small to medium (≤ 15 mm) and relief medium to high (≥ 3 mm). Costosepta mostly not confluent. Septa in ≤ 3 cycles (≤ 36 septa). Free septa regular. Septal spacing narrow to medium (≤ 11 septa per 5 mm). Costosepta unequal in relative thickness. Columellae trabecular and compact (1–3 threads), with size variable to calice width, with linkage absent. Paliform lobes absent. Endotheca abundant (vesicular). Microtexture of septal faces variable, delicately granular or with shingles arranged into unique, meandering "persian lamb fur" pattern. Bundles of TD fibers typically perpendicular to septal surface or in some (axial) septa regions arranged into elongated bundles (consequence of continuous growth of shingles). Closely spaced (often not well delineated) RADS. Polyp tentacles partially/fully extended at daytime, of shape simple.

Species included: *Galaxea fascicularis* (Linnaeus, 1767); *Galaxea acrhelia* Veron, 2000; *Galaxea alta* Nemenzo, 1979; *Galaxea astreata* (Lamarck, 1816); *Galaxea cryptoramosa* Fenner & Veron, 2000; *Galaxea horrescens* (Dana, 1846); *Galaxea longisepta* Fenner & Veron, 2000; *Galaxea pauciradiata* (Blainville, 1830); *Galaxea paucisepta* Claereboudt, 1990.

Taxonomic remarks: *Galaxea* was originally introduced by Oken (1815) and, to date, includes a total of nine extant valid species. According to ICZN opinion 417 (ICZN, 1956), names proposed by Oken (1815) were rejected for nomenclatural purposes, so authority of this taxon was assigned to Milne Edwards & Haime (1851), the second authors who used the name. Subsequently, Potts (1995) proposed an application to conserve *Galaxea* Oken (1815) and ICZN opinion 2061 (ICZN, 2004) ruled that *Galaxea* Oken (1815) was conserved despite the rejection of Oken's (1815) work. The genus has been traditionally included within either Oculinidae or Galaxeinae (see table 1; Vaughan & Wells, 1943; Alloiteau, 1952;

Wells, 1956; Scheer & Pillai, 1983; Chevalier & Beauvais, 1987; Sheppard & Sheppard, 1991; Veron, 2000). Fukami et al. (2008) showed that *Galaxea* clustered within clade V *sensu* Fukami et al. (2008) and, since Budd et al. (2012) assigned all members of clade V *sensu* Fukami et al. (2008) to Euphylliidae, the genus was transferred to this family. Subsequent molecular phylogeny reconstructions of scleractinian corals, including the one presented in this study, confirmed this assignment and the monophyly of the genus (Kitahara et al., 2010, 2016; Luzon et al., 2017; Wepfer et al., 2020). Our morphological phylogenetic tree recovered the five analysed species of *Galaxea* as a single linage that was sister to the group including *Euphyllia* and *Fimbriaphyllia*, corroborating the genetic results. Furthermore, we confirmed that *Acrhelia* Milne Edwards & Haime, 1849 is a junior synonym of *Galaxea* since our specimens of *G. horrescens*, the type species of *Acrhelia*, clustered within the lineage of *Galaxea* in both molecular and morphological analyses.

We were not able to trace a holotype of the type species of *Galaxea*, namely *G. fascicularis*, because it was not designated. Linneus (1767) just referred to pre-linnean names in previous works and mentioned the Indian Ocean as distribution range. We did not designate a neotype because we suggest that this action should be done in a taxonomic revision of the genus in which all species and their synomyms are compared. Since a recent phylogenomic study suggested that *G. fascicularis* may include several distinct species from different localities across the Indo-Pacific (Wepfer et al., 2020), for the identification of our newly-collected material we referred to Veron (2000), which illustrated specimens of *G. fascicularis* from both the Indian and Pacific Ocean.

Morphological remarks: Galaxea is macromorphologically distinguishable from other extant euphylliids by displaying several characters that are unique within the family, such as an extensive coenosteum (≥ corallite diameter), a vescicular coenosteum structure, a mostly not confluent continuity of costosepta, a trabecular compact (1–3 threads) columella structure, and a columella size ≥ ¼ relative to calice width (with the notable exception of *G. paucisepta*). Although not present in *G. horrescens* and *G. paucisepta*, the other investigated *Galaxea* species possess septal faces with shingles arranged into unique, meandering "persian lamb fur" pattern and bundles of TD fibers typically perpendicular to the septal surface or that in some (axial) septa regions are arranged in elongated bundles (as a consequence of the continuous growth of the shingles).

Distribution: Galaxea is widely distributed on the reefs of the Indian and Pacific Oceans, ranging from the Red Sea and East Africa to as far east as the Marshall Islands in the Northern Hemisphere and French Polynesia in the Southern Hemisphere (Best et al., 1989; Sheppard & Sheppard, 1991; Veron, 2000; Glynn et al., 2007; Pichon & Benzoni, 2007; Obura, 2012; Richards & Beger, 2013; Huang et al., 2015; Veron et al., 2015; DeVantier & Turak, 2017; Berumen et al., 2019; Montgomery et al., 2019).

Gyrosmilia Milne Edwards & Haime, 1851

(figs. 2P–R, 7, 11C–D)

Type species: *Manicina interrupta* Ehrenberg, 1834; holotype: ZMB Cni749; type locality: Red Sea.

Original description: 'polypier composé, se multipliant par fissiparité; polypiérites restant unis en séries, lesquelles sont soudées entre elles par leurs murailles; columelle nulle; les centres calicinaux distincts; cloisons minces, entiéres, glabres, serrées; l'endothéque n'occupant que les parties inférieures des loges.' (Milne Edwards & Haime, 1851: 55).

Diagnosis: Colonial. Budding intracalicular and extracalicular. Corallites monomorphic and uni- or multi serial. Fused walls. Calice of width medium (4–15 mm) and relief medium (3–6 mm). Septa in more than 4 cycles (≥ 48 septa). Free septa regular. Septal spacing medium (6–11 septa per 5 mm). Costosepta equal in relative thickness. Columella absent. Paliform lobes absent. Endotheca abundant (vesicular). Septal faces delicately granular. Bundles of TD fibers not well delineated, perpendicular to septal surface. Closely spaced (zig-zag mid-septal zone) RADS. Polyp tentacles partially/fully extended at daytime, of shape simple.

Species included: *Gyrosmilia interrupta* (Ehrenberg, 1834).

Taxonomic remarks: *Gyrosmilia* was formally introduced by Milne Edwards & Haime (1851) to include a single species, namely *G. interrupta*. The monospecific genus can be easily distinguished by its unique morphology, forming meandroid small colonies with collines and absent columella (Matthai, 1928; Scheer & Pillai, 1983; Sheppard & Sheppard, 1991). As such, the validity of *Gyrosmilia* has never been questioned by subsequent authors and, given a general resemblance to *Euphyllia*, the two genera have been traditionally placed together at the family level, with a few exceptions (see table 1; Milne Edwards & Haime, 1857; Vaughan & Wells, 1943; Alloiteau, 1952; Wells, 1956; Scheer & Pillai, 1983; Chevalier & Beauvais, 1987; Sheppard & Sheppard, 1991; Veron, 2000). Recently, Budd et al. (2012) transferred the genus to Euphylliidae. In this study, we showed that *Gyrosmilia* clustered within this family and was sister to *Ctenella* in both molecular and morphological phylogenetic trees.

Morphological remarks: As discussed in the morphological remarks section of *Ctenella,* the macromorphology of *Gyrosmilia* is similar to the one of *Ctenella* and the two genera differ by their columella that is absent in *Gyrosmilia*. Like in *Euphyllia* and *Fimbriaphyllia*, RADS in *Ctenella* correspond to a straight or zig-zag mid-septal (RADS) zone in transversely sectioned septa and bundles of TD fibers are not well delineated, perpendicular to the septal surface. The septal surface with delicately granular textures distinguishes the genus from *Euphyllia* and *Fimbriaphyllia*.

Distribution: Gyrosmilia is restricted to the reefs of the Red Sea and south-western Indian Ocean, occurring in East Africa coast (including Tanzania, Kenya, Mozambique, and South Africa) to as far east as the Mascarene Archipelago (Rosen, 1971; Faure, 1977; Rosen, 1979; Scheer & Pillai, 1983; Sheppard, 1987; Sheppard & Sheppard, 1991; Veron, 2000; Obura, 2012; Veron et al., 2015; DeVantier & Turak, 2017; Berumen et al., 2019).

(?) *Montigyra* Matthai, 1928

Type species: *Montigyra kenti* Matthai, 1928; holotype: BMNH 95.10.9.88; type locality: Lacepede Islands (Western Australia).

Original description: 'Massive, growth-size medium, calicinal surface convex. Valley continuous, comparatively wide and deep. Colline discontinuous, in the form of monticules varying in length. Septa evenly thin, upper half or two-thirds of principal ones more or less vertical, lower half or one-third broadening towards columella and appearing somewhat like paliform lobes. Septal margins finely dentate in upper half or two-thirds, teeth increasing in length in lower half or one-third, sides granular. Columella in the form of centres usually connected by 1–3 lamellae. This genus resembles *Trachyphyllia* and *Callogyra* in growth-size and in septal characters. Although walls are fused as in *Callogyra,* the collines thus formed are discontinuous, much thinner and not grooved. It differs from both genera in the columellar

centres being usually connected by lamellae and not so well developed. Like *Trachyphyllia* and *Callogyra, Montigyra* is also an Indo-Pacific genus.' (Matthai, 1928: 255).

Species included: *Montigyra kenti* Matthai, 1928.

Taxonomic remarks: *Montigyra* is a monotypic genus known from a single specimen from Western Australia (Matthai, 1928). It has been historically considered a member of different families (see table 1; Matthai, 1928; Wells, 1956; Chevalier & Beauvais, 1987; Veron, 2000). Recently, Budd et al. (2012) transferred the genus to Euphylliidae as being closely related to *Gyrosmilia* and this taxonomic action is herein maintained since we did not investigate the genus.

Distribution: Montigyra is known only from Lacepede Islands, Western Australia (Matthai, 1928; Veron, 2000).

(?) *Simplastrea* Umbgrove, 1939

Type species: *Simplastrea vesicularis* Umbgrove, 1939; holotype: RMNH.COEL9362 (Naturalis Biodiversity Center, Leiden, the Netherlands – formerly Rijksmuseum van Natuurlijke Historie); type locality: Onrust Island, Bay of Jakarta (Indonesia).

Original description: 'Corallites separated by a vesicular coenenchyma. Septa extending outside the calicular walls to meet either a septocosta of an adjacent corallite or a lamen of the choenenchyma. Corallite walls formed by vertical lamina of the coenenchyma and of a discontinuous broken appearance. Septal edges subentire. Columella trabecular. Dissepimenta present, no synapticulae. The coral seems close to *Physogyra* from which it may be distinguished especially by the occurence of a kind of pseudo-corallite walls.' (Umbgrove, 1939: 24).

Species included: *Simplastrea vesicularis* Umbgrove, 1939.

Taxonomic remarks: *Simplastrea* is a monotypic genus described on the basis of a single likely fossil specimen from Indonesia (Umbgrove, 1939). It was originally included in Eusmiliidae Milne Edwards & Haime, 1857 and, subsequently, transferred to other families in conjunction with *Galaxea*, to whom it morphologically resembles the most (see Table 1; Vaughan & Wells, 1943; Alloiteau, 1952; Wells, 1956; Veron & Pichon, 1980; Veron, 2000). Lastly, Budd et al. (2012) considered *Galaxea* and *Simplastrea* as genera belonging to Euphylliidae based on molecular evidence available for the former one. In this study, *Simplastrea* was not collected and its placement within Euphylliidae proposed by Budd et al. (2012) is hence maintained.

Distribution: Simplastrea is known only from the reefs of Indonesia and Papua New Guinea (Umbgrove, 1939; Veron, 2000). The species was described from Onrust Island in Jakarta Bay (Umbgrove, 1939) but has not been reported from this locality since then (van der Meij et al., 2010). The reef conditions around this island, which is located nearshore and close to Jakarta, have degraded in the last decades (Cleary et al., 2006, 2008, 2014).

Discussion

In this study, we sequenced three mitochondrial markers and investigated 23 morphological characters for several members of the scleractinian corals Euphylliidae. We demonstrated that genetic and morphological phylogenetic trees are largely in agreement in delineating genera within the family. Based on morpho-molecular results, *Coeloseris* was formally transferred to Euphylliidae. We provided a taxonomic account of all extant genera ascribed to the family which now includes a total of 23 extant species ascribed to eight genera, namely *Coeloseris*, *Ctenella*, *Euphyllia*,

Fimbriaphyllia, *Galaxea*, *Gyrosmilia*, *Montigyra*, and *Simplastrea*.

The taxonomic revisions of Euphylliidae, referred as clade V *sensu* Fukami et al. (2008), based on molecular and/or morphological criteria proposed by Budd et al. (2012) and Luzon et al. (2017, 2018) have disentangled some long-standing taxonomic uncertainties, such as the inclusion of *Ctenella*, *Galaxea*, and *Gyrosmilia* among euphylliids and the resurrection of *Fimbriaphyllia* as a valid genus. On the basis of these two studies, Euphylliidae and its genera are now monophyletic entities. Within Euphylliidae, Luzon et al. (2017, 2018) identified four molecular lineages corresponding to the four euphylliid genera that they analysed: *Fimbriaphyllia* in group V–A, *Galaxea* in group V–B, *Euphyllia* in group V–C, and *Ctenella* in group V–D. Using largely distinct molecular loci, our molecular results confirmed the presence of the same four linages and found two additional clades represented by *Gyrosmilia* in group V–E and *Coeloseris* in group V–F. Notably, the phylogenetic relationships among the six main lineages remained largely unresolved using three loci (CO1, 12S rRNA, and 16S rRNA) and the morphological data set, preventing us to reconstruct ancestral state evolution of the investigated morphological characters within the family. The recent development of hybrid-capture baits for scleractinian corals may be a promising tool to generate a well-resolved phylogeny hypothesis of Euphylliidae (Quattrini et al., 2018; Cowman et al., 2020; Quek et al., 2020; Quek & Huang, 2021).

The monotypic *Gyrosmilia* was transferred to Euphylliidae by Budd et al. (2012) in the absence of genetic data and, based on our molecular results, we demonstrated the validity of this taxonomic assignment. Additionally, although only CO1 is available for *Ctenella* (Fukami et al., 2008) and our morphological phylogenetic analysis showed a low supported sister relationship between *Gyrosmilia* and *Ctenella*, the molecular data suggested a sister relationship between the two genera and additional future studies are in need to disentangle this potential evolutionary relationship. The two taxa are indeed distinguished based only on their columella that is absent in *Gyrosmilia* and lamellar with continuous linkage in *Ctenella*. This close relationship is interesting under an evolutionary and biogeographical perspective since both *Gyrosmilia* and *Ctenella* are endemic to the Indian Ocean (Veron, 2000). The two species live in sympatry in Mauritius while *Gyrosmilia* occurs also in the Red Sea, East Africa coasts and Madagascar, while *Ctenella* extends only to Chagos Archipelago (Rosen, 1971; Faure, 1977; Rosen, 1979; Sheppard et al., 1983; Sheppard, 1987; Sheppard & Sheppard, 1991; Veron, 2000; Pillay et al., 2002; Veron et a., 2015; DeVantier & Turak, 2017; Berumen et al., 2019). The discovery of a single genetic lineage including these two Indian Ocean genera suggests that they share a common evolutionary origin and, more in general, strengthens the evolutionary distinctiveness of the Indian coral fauna (Obura, 2012, 2016; Kusumoto et al., 2020).

The sole taxonomic action undertaken in this study is the formal assignment of *Coeloseris* to Euphylliidae. Based on traditional macromorphology-based taxonomy, the genus has been consistently considered a member of Agariciidae (e.g., Matthai, 1928; Vaughan & Wells, 1943, 1956; Veron & Pichon, 1980; Chevalier & Beauvais, 1987; Veron, 2000) but recent morphological and molecular evidence has questioned this taxonomic assignment. Firstly, Kitahara et al. (2012b) investigated micromorphology/microstructure of all extant agariciid genera and observed that they possessed similar main features, such as septal menianes or granules arranged parallel to septal edge, with the exception of *Coeloseris*. Secondly, based on 18S rDNA, *Coeloseris* did

not cluster with the other agariciids but was found to be closely related to *Galaxea* and *Euphyllia* by Arrigoni et al. (2017). In our study, we confirmed both previous studies and showed that *Coeloseris* formed the novel group V–F within Euphylliidae. Moreover, macromorphological observations indicated that endotheca is abundant in *Coeloseris* and all euphylliids while it is sparse in *Pachyseris* and the investigated members of agariciids, namely *Gardineroseris planulata* and *Pavona cactus*. As such, both molecular and morphological data indicated that *Coeloseris* is a member of Euphylliidae and does not belong to the Agariciidae lineage.

Two out the eight extant genera ascribed to Euphylliidae, namely *Montigyra* and *Simplastrea*, have yet to be placed on the phylogeny. Both genera are extremely poorly studied, probably as a consequence of their restricted geographic distributions and/or rarity. *Montigyra* is among the most enigmatic and least studied scleractinian corals. It is known from a single specimen collected by W. Saville-Kent from Western Australia that was used by Matthai (1928) to describe the genus and the only species ascribed to it, namely *M. kenti*. Despite a very easily recognizable and unique macromorphology of the colony, the genus has never been found elsewhere and neither in subsequent field works conducted in Western Australia and, therefore, may be extinct (Veron & Marsh, 1988; Veron, 1993, 2000; Richards et al., 2014; Jones, 2016; Richards, 2108). *Montigyra* was originally described as a meandroid representative of Astraeidae Dana, 1846 and, subsequently, it was transferred to different families, such as Faviidae Gregory, 1900, Trachyphyllidae Wells, 1956, and Meandrinidae (see table 1; Matthai, 1928; Wells, 1956; Chevalier & Beauvais, 1987; Veron, 2000). Recently, Budd et al. (2012) interpreted the genus as closely related to *Gyrosmilia* and moved both taxa to Euphylliidae in the absence of morpho-molecular data. Although our molecular phylogenetic tree confirmed that *Gyrosmilia* belongs to Euphylliidae, we did not provide any novel information on *Montigyra* and, as such, we maintained *Montigyra* within Euphylliidae according to Budd et al. (2012). Similar to *Montigyra*, *Simplastrea* is a monotypic and poorly known genus of scleractinian corals. It was described by Umbgrove (1939) on the basis of a single specimen collected by J. Verwey in Jakarta Bay, Indonesia. The genus has not been recorded since in this region probably because of its rarity and a general decline in species richness in Jakarta Bay due to long-term anthropogenic stressors (Djohani, 1994; Tomascik et al., 1993; DeVantier & Turak, 2007; van der Meij et al., 2010). Subsequently, *Simplastrea* has been recorded in Papua New Guinea (Veron, 2000). The macromorphology of *Simplastrea* superficially resembles that of *Galaxea* and, for this reason, the two genera have been historically placed together at the family level (Vaughan & Wells, 1943; Alloiteau, 1952; Wells, 1956; Veron & Pichon, 1980; Veron, 2000). Budd et al. (2012) transferred both *Galaxea* and *Simplastrea* to Euphylliidae on the basis of previous molecular phylogenies that showed *Galaxea* to be clustered within the clade of Euphylliidae (Fukami et al., 2008; Kitahara et al., 2010).

In conclusion, there are still critical gaps in our knowledge of the systematics and phylogeny of Euphylliidae. A first aspect is the inclusion in a molecular phylogenetic context of euphylliid taxa for which no sequences are available to date, such as two genera, namely *Montigyra* and *Simplastrea*, and some species of *Galaxea* and *Euphyllia*, for which genetic resources will elucidate their evolutionary relationships among euphylliids. A second opportunity is the investigation of reproductive traits of euphylliid taxa that lack of this information. While in this study we focused

only on molecular and morphological data, Luzon et al. (2017, 2018) showed that an additional source of information useful for exploring the systematics of Euphylliidae may be represented by reproductive data. Luzon et al. (2017, 2018) found that the distinction between *Euphyllia* and *Fimbriaphyllia* was also supported by their sexuality and reproductive mode since *E. glabrescens* is a hermaphroditic brooder while species of *Fimbriaphyllia* are gonochoric broadcast spawners (Baird et al., 2009, 2021). In our study, we found a sister relationship between *Gyrosmilia interrupta*, which is known to be a gonochoric spawner (Bouwmeester al., 2016), and *Ctenella chagius*. Unfortunately, to our knowledge, no information about the reproductive traits is available for the latter species (e.g., Sheppard et al., 1983; Luzon et al., 2017, 2018; Baird et al., 2021) and, as such, we cannot evaluate whether the close morpho-molecular affinity between *Gyrosmilia* and *Ctenella* is supported or not by their sexuality and reproductive mode. Similar to *Ctenella chagius*, reproductive traits are unknown for several other euphylliid species and we encourage to investigate them to be able to trace the evolution of these features along the phylogenetic tree of Euphylliidae. A third research opportunity is the study of species boundaries within *Euphyllia*, *Fimbriaphyllia*, and *Galaxea* using phylogenomics and referral to type material. The use of phylogenomic tools has increased our ability to molecularly distinguish closely related species (Miller et al., 2007; Faircloth et al., 2012) and recent genomic-based studies have demonstrated that the actual scleractinian coral diversity may be largely hidden and underestimated (e.g., Johnston et al., 2017; Arrigoni et al., 2020; Cowman et al., 2020; Bongaerts et al., 2021; Wepfer et al., 2020; Grinblat et al., 2021; Terraneo et al., 2021). For example, Wepfer et al. (2020) provided a high-resolution phylogenomic hypothesis of *Galaxea* across the Indo-Pacific, showing that most extant species described based on macromorphology are polyphyletic. Phylogenomic approaches may be applied also to the other two euphylliid genera that are not monotypic, namely *Euphyllia* and *Fimbriaphyllia*, with the aim to investigate their species richness.

Acknowledgements

The authors are grateful to the three anonymous reviewers for their important comments and suggestions. We deeply thank D Huang (NUS) for his constructive comments on the first manuscript draft. We thank Lueter C (ZMB) for information provided about the holotype of *Caryophyllia glabrescens*. New Caledonia data and specimens were obtained during the ird CORALCAL1 (http://dx.doi.org/10.17600/7100020), CORALCAL2 (http://dx.doi.org/10.17600/8100050), CORALCAL3 (http://dx.doi.org/10.17600/9100010), CORALCAL4 (http://dx.doi.org/10.17600/12100060), BIBELOT (http://dx.doi.org/10.17600/14003700), and CORALCAL5 (http://dx.doi.org/10.17600/15004300) expeditions on the RV Alis. Material from Madagascar was collected during the MAD (http://dx.doi.org/10.17600/16004700) expedition on the RV Antea. For New Caledonia and Madagascar, we are grateful to the chief scientists and cruise organisers C. Fauvelot (IRD) and H. Magalon (ULR) for invitation to join and valuable help with sampling authorisations. The MADANG expedition specimens were obtained during the "Our Planet Reviewed" Papua Niugini expedition (http://dx.doi.org/10.17600/12100070) organised by Muséum National d'Histoire Naturelle (MNHN), Pro Natura International (PNI), Institut de Recherche pour le Développement (IRD), and University of Papua New Guinea (UPNG), Principal Investigators Philippe Bouchet and Sarah Samadi. The organizers acknowledge

funding from the Total Foundation, Prince Albert II of Monaco Foundation, Fondation EDF, Stavros Niarchos Foundation, and Entrepose Contracting, and in-kind support from the Divine Word University (DWU). Material from Kavieng, PNG, was sampled during the KAVIENG Expedition (https://doi.org/10.17600/14004400). The expedition operated under a permit delivered by the Papua New Guinea Department of Environment and Conservation. Permissions relevant for KAUST to undertake the research have been obtained from the applicable governmental agencies in the Kingdom of Saudi Arabia. For sampling in the Red Sea, we wish to thank the captain and crew of the mv Dream-Master, the KAUST Coastal and Marine Resources Core Lab, and A Gusti (KAUST). We are grateful to E Dutrieux, CH Chaineau (Total SA), R Hirst, M Abdul Aziz (YLNG), and M Pichon (MTQ) for allowing and supporting research in Yemen. We are grateful to E Karsenti (EMBL) and E Bougois (Tara Expeditions), the OCEANS Consortium for allowing sampling during the Tara Oceans expedition in Djibouti and Mayotte. We thank the commitment of the following people and additional sponsors who made this singular expedition possible: CNRS, EMBL, Genoscope/CEA, VIB, Stazione Zoologica Anton Dohrn, UNIMIB, ANR (projects POSEIDON/ANR-09-BLAN-0348, BIOMARKS/ANR-08-BDVA-003, PROMETHEUS/ANR-09-GENM-031, and TARA-GIRUS/ANR-09-PCS-GENM-218), EU FP7 (MicroB3/No.287589), FWO, BIO5, Biosphere 2, agnès b., the Veolia Environment Foundation, Region Bretagne, World Courier, Illumina, Cap L'Orient, the EDF Foundation EDF Diversiterre, FRB, the Prince Albert II de Monaco Foundation, Etienne Bourgois, the Tara schooner, and its captain and crew. Tara Oceans would not exist without continuous support from 23 institutes (http://oceans.taraexpeditions.org). This article is contribution number 142 of the Tara Oceans Expedition 2009–2012.

Supplementary material

Supplementary material is available online at: https://doi.org/10.6084/m9.figshare.22067939

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