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Revisionary systematics of Octocorallia (Cnidaria: Anthozoa) guided by phylogenomics

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Abstract

The anthozoan sub-class Octocorallia includes over 3500 nominal species of soft corals and gorgonian sea fans, many of which serve as critical foundation species in benthic marine ecosystems in shallow waters to the deep sea. Despite their familiarity and ecological impor-tance, the diversity and taxonomy of octocorals remain poorly known. All of the orders, subordinal groups, and a majority of families have been recognized to be poly- or paraphyletic, but poor resolution of the deeper nodes in mitochondrial or single-locus nuclear gene trees have hindered formal revision of the higher-level taxonomy of the group. We used sequence data from target-capture of 739 ultraconserved and exon loci to reconstruct a fully resolved phylogeny for 185 octocoral taxa represent-ing 55 of 63 currently recognized families. We use this phylogeny, sup-plemented with a gene tree for mitochondrial *mtMutS* for an additional 107 taxa, to guide a revision of the families and orders of Octocorallia. We (1) elevate the anthozoan sub-classes Octocorallia and Hexacorallia to the rank of Class; (2) replace the three currently recognized orders of Octocorallia (Alcyonacea, Pennatulacea, Helioporacea) with two new orders reflecting reciprocally monophyletic major clades; and (3) revise all families with the exception of the 15 recognized families of sea pens, which we accommodate within a new superfamily. The revised classification of Octocorallia thus comprises 79 families, including 18 that are newly described and three that have been reinstated or elevated in rank. In addition, two new genera are described and another three reinstated. We leave the family assignment of 46 of 413 genera as *incertae sedis* until further molecular or morphological data can be obtained to confirm their phylogenetic affinities.

1 INTRODUCTION

The anthozoan clade Octocorallia comprises over 3500 species of soft corals, sea fans, and sea pens (Williams

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and Cairns 2019), including some of the ocean's most familiar and ecologically important benthic fauna. Octocorals occur in all marine habitats worldwide. Their diversity is highest in the deep sea (Cairns 2007) where they serve as important foundation species, generating structurally complex three-dimensional "forests" that support many other invertebrate and fish taxa (Krieger and Wing 2002; Buhl-Mortensen et al. 2010; Sánchez 2016; Schweitzer and Stevens 2019; Tsounis et al. 2020). They are also diverse and abundant on tropical coral reefs where they are often the dominant sessile space-occupiers (Tursch and Tursch 1982; Dinesen 1983; Riegl et al. 1995; Fabricius 1997), a trend that may be increasing on some reefs as scleractinian corals decline disproportionately in response to ongoing environmental change (Inoue et al. 2013; Ruzicka et al. 2013; Lenz et al. 2015; Lasker et al. 2020). Nonetheless, despite the abundance, familiarity, and ecological importance of octocorals, their taxonomy remains poorly known, with a majority of taxa not reliably identifiable to the level of species (Fabricius and Alderslade 2001).

Since the early twentieth century, Octocorallia has been divided among anywhere from three (Kükenthal 1919) to eight (Madsen 1944) orders. Following the revision of Bayer (1981a), a three-order classification has been widely adopted, recognizing Pennatulacea (sea pens; 15 families, ~300 species) and Helioporacea (blue corals; two families, 5 extant species) as discrete higher taxa based on their distinctive morphological synapomorphies, and lumping all other octocorals into Alcyonacea. Attempts to divide Alcyonacea (>3000 species in 46 families) into subordinal groups have been largely unsatisfactory. Most gorgonians (i.e., octocorals with an internal skeletal axis) have been assigned to the alcyonacean suborders Calcaxonia Grasshoff, 1999 (axis of solid calcium carbonate) or Holaxonia Studer, 1887 (largely proteinaceous axis with little to no calcified material), which each have been assumed to represent clades. The remaining taxa of Alcyonacea, however, have been treated as non-Linnean "subordinal groups", divided into categories that represent grades of colony morphology rather than clades (Hickson 1930; Bayer 1981a). These include Scleraxonia (colonies with a skeletal axis or axial-like layer formed by sclerites), Alcyoniina (colonies without a skeletal axis and with polyps embedded in a fleshy mass of coenenchyme, i.e., soft corals), Stolonifera (colonies with polyps connected basally by stolons or membranes), and Protoalcyonaria (solitary polyps). The advent of molecular phylogenetics at the turn of the 21st century reinforced the observation that these subordinal groups do not represent clades and also revealed paraphyly among the three octocoral orders (Berntson et al. 2001). In the two decades since, additional molecular phylogenetic studies have revealed that almost all of the recognized families of octocorals are also non-monophyletic (McFadden et al. 2006a; McFadden and van Ofwegen 2012a, 2013, 2017; Pante et al. 2012; Cairns and Wirshing 2015; Kushida and Reimer 2018; Heestand Saucier et al. 2021).

The traditional classification of octocorals into families and sub-orders or orders has been based largely on shared gross morphological characters such as the presence/absence and composition of a skeletal axis and the overall growth form of the colony. Molecular phylogenetic analyses that have revealed the non-monophyly of these higher taxa also imply that these gross morphological characters are labile and subject to widespread homoplasy (McFadden et al. 2006a, 2010). Ancestral state reconstructions confirm that skeletal axes have been gained and lost multiple times throughout Octocorallia (Quattrini et al. 2020). In particular, axes formed by the consolidation of sclerites (taxa historically placed in subordinal group Scleraxonia) have arisen independently in many clades. Simple colony forms in which polyps are connected basally by stolons or membranes (historically subordinal group Stolonifera) have also evolved multiple times and often within clades of otherwise complex growth forms, including cases in which a skeletal axis has apparently been lost (McFadden et al. 2006a). The evidence for phylogenetic relationships and evolutionary gains and losses supported by molecular and phylogenomic studies suggests that reclassification of taxa at and above the rank of family should not be based on these evolutionarily labile traits but instead on alternative—potentially more subtle—morphological characters shared by the taxa that constitute well-supported clades in the molecular phylogeny.

Despite the recognition for over 20 years that a Linnean classification system based on skeletal morphology and colony growth form does not reflect the underlying phylogenetic relationships among Octocorallia, no alternative ordinal-level classification has been proposed. Few families have been fully revised; although, a few new families have been erected and formerly suppressed families have been reinstated to accommodate genera that do not belong in the families to which they have historically been assigned (McFadden and van Ofwegen 2013, 2017; Cairns and Wirshing 2015; Moore et al. 2017; Cairns et al. 2021; Heestand Saucier et al. 2021; Cordeiro et al. 2021; López-González and Drewery 2022). The primary impediment to widespread revision of families and orders has been a lack of phylogenetic resolution of the deeper nodes in the octocoral tree (McFadden et al. 2006a), making it unclear how well family- or ordinal-level clades are supported. Strong support for molecular clades is particularly important to allow the subsequent identification of novel morphological synapomorphies suitable for the diagnosis of higher taxa. With the recent application of phylogenomic approaches to octocoral systematics, most of the deeper nodes in the octocoral tree of life are now fully resolved or strongly supported (Quattrini et al. 2020; McFadden at al. 2021).

Here we use a phylogenomic reconstruction that includes representatives of 55 of the 63 currently defined families and all sub-ordinal groups of octocorals to guide a revision of the orders and most families of Octocorallia exclusive of the sea pens. We supplement the phylogenomic analysis with a taxonomically comprehensive gene tree for the mitochondrial mismatch repair gene (*mtMutS*) to support the taxonomic placement of an additional six families and 107 genera for which phylogenomic data are not yet available. Together these phylogenies support the diagnosis of new, restricted, or expanded families that are both monophyletic and defined by morphological synapomorphies or suites of diagnostic morphological characters.

2 METHODS

2.1 Sample collection and preparation

Specimens have been obtained over the past 30 years, identified by taxonomic experts (including the co-authors), and subsequently deposited in curated museum collections (see Suppl. Table S1 for repositories). DNA was extracted from frozen or ethanol-preserved tissue using either a modified CTAB protocol (McFadden et al. 2006b) or Qiagen DNEasy Blood and Tissue Kit following the manufacturer's recommended protocol. DNA had been stored and kept frozen at –20°C for up to 18 years before being used in this study (Quattrini et al. 2018, 2020). DNA samples were quantified using a Qubit fluorometer, and DNA was checked for quality using a NanoDrop spectrophotometer and agarose gel electrophoresis. Libraries were prepared and target-enriched either by Arbor Biosystems (Ann Arbor, MI) (Quattrini et al. 2020) or in-house following the protocol outlined in Quattrini et al. (2018). Both the anthozoan (Quattrini et al. 2018) and octocoral (Erickson et al. 2021) baitsets were used to target-enrich non-coding (UCEs) and coding regions (exons) of genomes. Pooled (in 8-plex captures), enriched libraries were sequenced on an Illumina HiSeq or NovaSeq (150 bp PE reads). Sequence data from 112 specimens included here were published in prior studies (Quattrini et al. 2018, 2020; McFadden et al. 2021; Erickson et al. 2021; Untiedt et al. 2021), but we added 84 additional specimens to include a larger representation of currently described octocoral families. In total, genomic data for 185 octocorals and 11 hexacorals as outgroup taxa were included in the present study.

2.2 Phylogenomic analyses

Reads were processed using the Phyluce pipeline (Faircloth 2016) with some modifications as outlined in Quattrini et al. (2018). Briefly, reads were cleaned using illumiprocessor (Faircloth 2013) and Trimmomatic v. 0.35 (Bolger et al. 2014) and then assembled using SPAdes v. 3.1 (Bankevich et al. 2012; with the --careful and --cov-cutoff 2 parameters). The *phyluce_assembly_match_contigs_to_probes* command was used to match the octocoral baits (Erickson et al. 2021) to the contigs to identify loci with a minimum coverage of 70% and a minimum identity of 70%. Loci were then extracted using *phyluce_assembly_get_fastas_from_match_counts* and then aligned with MAFFT v7.130b (Katoh and Standley 2013) and edge-trimmed using *phyluce_align_seqcap_align*. To compare with edge-trimmed alignments, we also conducted internal trimming with Gblocks (Castresana 2000; Talavera and Castresana 2007) using *phyluce_align_get_gblocks_trimmed_alignments_from_untrimmed* (b1=0.5, b2=0.5, b3=10, b4=5). Aligned and concatenated data matrices including all loci with at least 60% or 75% of taxa present were generated using the program *phyluce_align_get_only_loci_with_min_taxa*.

Phylogenomic analyses were conducted using maximum likelihood in IQTree v. 2.1 (Nguyen et al. 2015) on the concatenated datasets. We ran analyses on the different datasets using the best model (GTR+F+R10) chosen with ModelFinder (Kalyaanamoorthy et al. 2017) (Table 1). Ultrafast bootstrapping (-bb 1000, Hoang et al. 2018) and the Sh-like approximate likelihood ratio test (-alrt 1000, Anisimova et al. 2011) were both conducted. Trees were rooted to Hexacorallia, including representatives of all orders except Corallimorpharia.

A species tree analysis was also conducted using ASTRAL III, which is statistically consistent under a multispecies coalescent model (Zhang et al. 2018). Gene trees were constructed in IQTree using the best fit model of evolution selected with ModelFinder for each gene. We used the edge-trimmed loci (n=241) that each had 75% of taxa represented. Treeshrink (Mai and Mirarab 2018) was used to remove long branches, and the newick utility, nw_ed, was used to remove branches with <30 % bootstrap support prior to running IQTree. All code can be found in Suppl. File S1.

2.3 Phylogenetic analysis of *mtMutS*

To increase taxonomic coverage at the genus level, we supplemented the phylogenomic analyses with analysis of the mitochondrial mutS-like DNA repair gene

Table 1. Alignment summary data for each dataset used in phylogenetic analyses.

Dataset	Method	# Taxa	# Loci	Mean locus length (bp)	Total align length (bp)	Model	# b.s. values < 95	# b.s. values < 75	Astral Score
60%_edge	IQTree	196	739	1735 ± 1581	1,281,999	GTR+F+R10	10	1	--
60%_internal	IQTree	196	912	479 ± 241	436,851	GTR+F+R10	8	2	--
75%_edge	IQTree	196	241	2035 ± 1634	490,521	GTR+F+R10	17	9	--
75%_internal	IQTree	196	296	507 ± 264	150,052	GTR+F+R10	18	6	--
75%_edge	ASTRAL III	196	241	2035 ± 1634	--	Per gene	--	--	0.81
75%_internal	ASTRAL III	196	296	507 ± 264	--	Per gene	--	--	0.80
mtMutS	IQTree	284	1	688 ± 74	1038	TVM+F+R5	35	14	--

(*mtMutS*), the most widely used marker for DNA barcoding and species-level phylogenetic studies of Octocorallia (McFadden et al. 2010). For the majority of the specimens used in the phylogenomic analysis, we included the *mtMutS* sequence obtained from the same individual. In a few cases in which we were unable to recover *mtMutS* from the target-capture reads or by PCR and Sanger sequencing, we substituted sequences that had been obtained from another individual of the same species collected from the same location. *mtMutS* sequences for an additional 107 specimens of genera and families not included in the phylogenomic analysis were obtained from GenBank (Suppl. Table S1). When possible, we selected sequences linked to vouchered museum specimens whose identity can be independently verified or revisited in future if necessary. We have also indicated taxa for which there are sequence data but no museum vouchers (or the repository and accession number were not provided to GenBank); and, thus, the identity of those taxa cannot be independently verified (Suppl. Table S1).

Translated amino acid sequences were aligned using the FFT-NS-i method in MAFFT v. 5 (Katoh et al. 2005), and the nucleotide alignment was then adjusted manually to reflect the codon alignment. Several taxa for which available *mtMutS* sequences were too short (<250 bp) to be phylogenetically informative were removed from the alignment prior to analysis, as were several taxa with highly divergent *mtMutS* sequences that could not be aligned with confidence. IQTree v. 2.1.2 (Nguyen et al. 2015) was used to construct a maximum likelihood tree using the model of evolution (TVM+F+R5) selected by ModelFinder (Kalyaanamoorthy et al. 2017) with support from 10K ultrafast bootstrap replicates (Hoang et al. 2018) (unconstrained tree). In addition, we ran a second maximum likelihood analysis using the same parameters but with the tree topology constrained to match the topology of the best tree obtained from analysis of the target-enriched loci (60% taxon occupancy, internally-trimmed IQTree) (constrained tree). Constraining the *mtMutS* tree to match the topology of the phylogenomic tree forced several taxa with divergent *mtMutS* sequences that are often subject to long branch attraction (e.g., McFadden and van Ofwegen 2017; Muthye et al. 2022) to be placed in the same position in the *mtMutS* tree as they were found in the phylogenomic analyses. AU (Shimodaira 2002) and SH (Shimodaira and Hasegawa 1999) tests were run in IQTree to test for significant differences between constrained and unconstrained topologies.

3 RESULTS

3.1 Target capture and assembly statistics

The total number of quality trimmed reads obtained (including outgroup taxa) ranged from 303,971 to 28,150,406 PE reads per sample. Trimmed reads were assembled into a mean of 89,643 ± 90,935 SD contigs per sample (range: 4,394 to 467,520) with a mean length of 503 ± 127 bp (Suppl. Table S2). A total of 163 to 2,282 loci out of 3,023 targeted loci were recovered from each individual. The mean number of loci recovered with the octocoral bait set was 1,499 ± 509 SD per sample with a mean length of 1,060 ± 393 bp (range: 351 to 2,944 bp). Alignment lengths ranged from 150,052 to 1,281,999 bp and 241 to 912 loci across 75% and 60% data matrices, respectively (Table 1).

3.2 Phylogenomic results

All phylogenomic analyses recovered similar tree topologies but varied in the strength of support for some nodes (Table 1, Suppl. file S2). Support values were uniformly highest for the phylogeny reconstructed using IQTree and the GTR+G model with the 60% taxon matrix (Fig. 1) and lowest for the ASTRAL species trees (Table 1). Nodes with bootstrap values less than 100% in Fig. 1 were also less strongly supported in all other analyses (Table 1, Suppl. file S2).

All analyses recovered strong support for the division of Octocorallia into two major, reciprocally monophyletic clades (Fig. 1), identified previously as Holaxonia-Alcyoniina and Calcaxonia-Pennatulacea (McFadden et al. 2006a, 2010). Calcaxonia-Pennatulacea included: all members of suborder Calcaxonia with the exception of *Isis hippuris* Linnaeus, 1758; order Pennatulacea; order Helioporacea; the scleraxonian families Spongiodermidae, Briareidae, Parisididae, Coralliidae, and Paragorgiidae; the family Parasphaerascleridae, subfamily Anthomastinae (Alcyoniidae), and alcyoniid genera *Paraminabea* and *Sphaerasclera*, all belonging to subordinal group Alcyoniina; and the stoloniferan family Cornulariidae and genus *Telestula* (Clavulariidae). *Dendrobrachia* (Dendrobrachiidae) and *Ideogorgia* (Keroeididae), both of suborder Holaxonia, and the scleraxonian genus *Erythropodium* (Anthothelidae) also fell into this clade.

The Holaxonia-Alcyoniina clade included: all members of suborder Holaxonia excluding *Dendrobrachia* and *Ideogorgia*; all families of subordinal group Alcyoniina excluding Parasphaerascleridae and the genera of Alcyoniidae listed above; all families and genera of subordinal group Stolonifera with the exceptions of Cornulariidae and *Telestula*; and the scleraxonian families Subergorgiidae, Melithaeidae, and Anthothelidae (excluding *Erythropodium*).

Within Calcaxonia-Pennatulacea, Cornulariidae was the earliest diverging lineage, sister to four well supported clades (S1-S4, Fig. 1). Clade S1 corresponded to clade Actinaxonia (Williams 2019), comprising a monophyletic Pennatulacea sister to the calcaxonian family Ellisellidae. Clade S2 corresponded to Suborder Calcaxonia Grasshoff, 1999 as amended by Williams (2019) and Heestand Saucier et al. (2021) but excluding Chelidonisididae whose position within the Calcaxonia- Pennatulacea clade remains poorly resolved. Clade S2 encompassed five well-supported subclades: a monophyletic family Primnoidae; monophyletic Keratoisididae plus Isidoidae; monophyletic Chrysogorgiidae consisting of genera previously identified as belonging to the MCC ("monophyletic Chrysogorgiidae clade," Pante et al. 2012); monophyletic Mopseidae; and a subclade consisting of family Ifalukellidae plus several additional genera of Chrysogorgiidae. Although the monophyly of each of these subclades was strongly supported, the relationships among them were not, despite all analyses placing the Ifalukellidae clade sister to the rest.

Order Helioporacea and *Dendrobrachia* were united in a small third clade (S3) that was suggested by most but not all analyses to be sister to clade S2. Clade S4 included an eclectic mix of taxa from subordinal groups Scleraxonia, Alcyoniina, and Stolonifera divided among three subclades whose relationships to one another were not well supported. One of these has been identified in previous studies as the *Corallium-Anthomastus* clade (McFadden et al. 2006a, 2010) and included the scleraxonian families Coralliidae and Paragorgiidae along with alcyoniids Anthomastinae, *Paraminabea,* and *Sphaerasclera*. Family Parasphaerascleridae constituted a second subclade whose relationship as sister to the other two subclades was only weakly supported. The final subclade included a well-supported group encompassing Spongiodermidae,

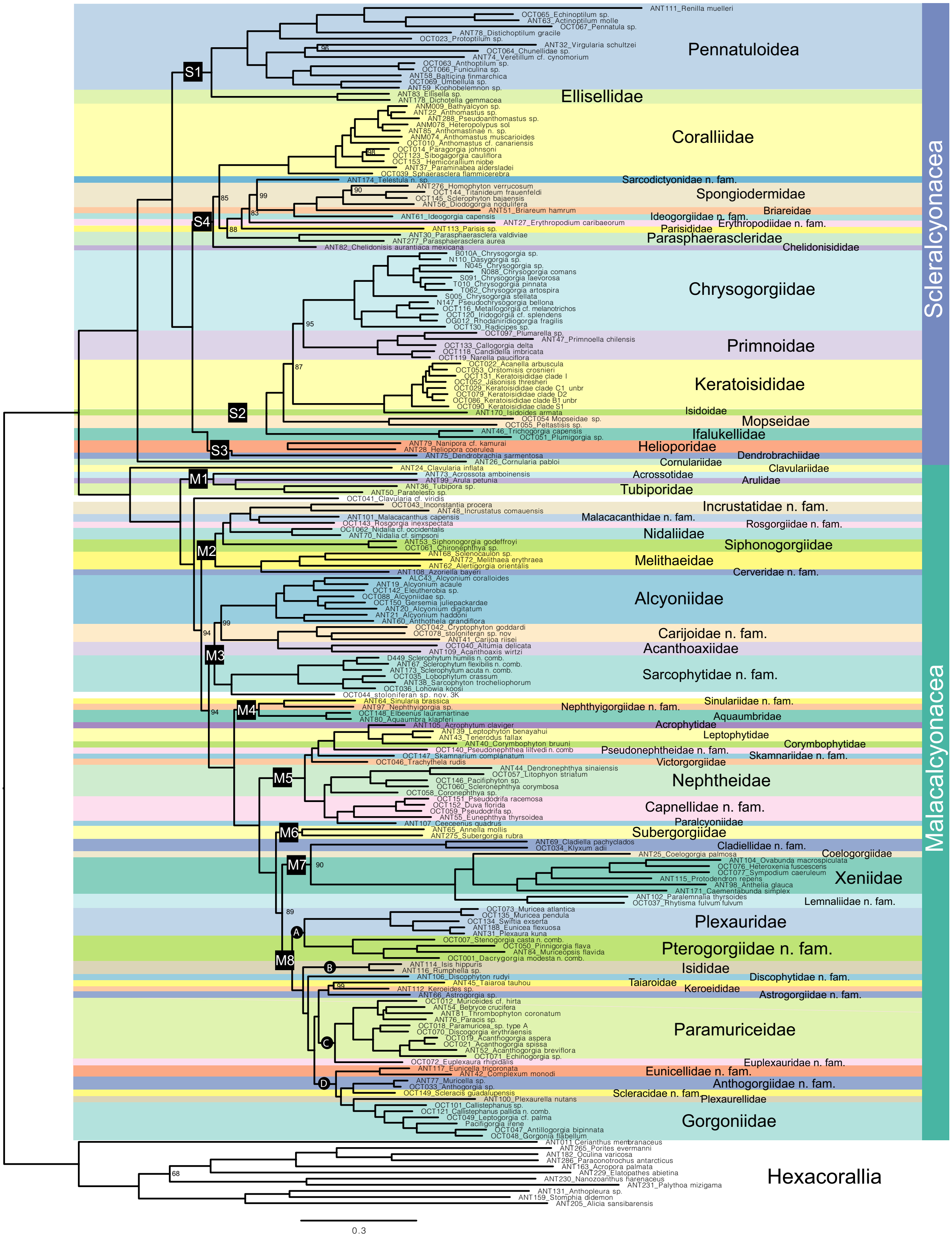


Fig. 1: Maximum likelihood tree of Octocorallia inferred from concatenated alignment of 739 UCE and exon loci (60% taxon occupancy, edge-trimmed). All nodes have 100% support from 1000 ultrafast bootstrap replicates unless otherwise noted. Proposed families and orders are indicated by colored bars; white bars indicate taxa left *incertae sedis*. Numbered squares and circles on branches identify clades discussed in Results.

Briareidae, and *Ideogorgia*, plus three taxa (*Erythropodium, Telestula*, and *Parisis*) whose relationships to that group and to one another remained poorly resolved.

Within Holaxonia-Alcyoniina, the stoloniferan *Clavularia inflata* Schenk, 1896 (Clavulariidae) was sister to all other taxa, which were divided among eight well supported clades (M1-M8) (Fig. 1). Although each of these clades was supported in all analyses, the relationships among them differed, in particular between the maximum likelihood and ASTRAL analyses (Suppl. file S2). Clade M1 included a diverse assortment of Stolonifera, including families Tubiporidae, Acrossotidae, Arulidae, and several genera of Clavulariidae (*Stragulum, Paratelesto*). Clade M2 encompassed a very eclectic mix including: the scleraxonian family Melithaeidae, several genera of Anthothelidae (*Alertigorgia, Solenocaulon*), and *Rosgorgia* (Subergorgiidae); the stoloniferans *Azoriella, Incrustatus,* and *Inconstantia*, all belonging to Clavulariidae; and the family Nidaliidae plus the alcyoniid *Malacacanthus*. Clade M3 united three well supported subclades of mostly Alcyoniidae and stoloniferans. Clade M4 consisted of four taxa of soft corals: *Aquaumbra* (Aquaumbridae), *Elbeenus* (Alcyoniidae), *Nephthyigorgia* (Nidaliidae), and *Sinularia brassica* May, 1898, which did not fall with other members of *Sinularia* in M3. Clade M5 comprised mostly Alcyoniina, including families Acrophytidae, Leptophytidae, Corymbophytidae, Paralcyoniidae, and most of Nephtheidae. *Skamnarium* (Alcyoniidae) and the stoloniferan *Trachythela* (Clavulariidae) also belonged to this clade. The scleraxonian family Subergorgiidae (*Annella* and *Subergorgia*) constituted clade M6.

Clade M7 consisted of two subclades whose sister relationship was not supported by all analyses. One of these subclades included Xeniidae plus *Paralemnalia* (Nephtheidae), *Rhytisma* (Alcyoniidae), *Protodendron* (Alcyoniidae), and the stoloniferan family Coelogorgiidae. The second subclade comprised the Alcyoniidae genera *Cladiella* and *Klyxum*. Species tree analyses placed that subclade within or sister to Holaxonia (Suppl. files S2), a relationship that has also been recovered in mitochondrial gene phylogenies (McFadden et al. 2006a).

The final clade, M8, constituted most of Suborder Holaxonia Studer, 1887. Within this clade we recovered four well supported subclades (M8A-M8D) plus several taxa whose relationships and positions within the clade were unstable. Subclade M8B included just *Isis hippuris* (Isididae) and *Rumphella* (Gorgoniidae), while each of the other three subclades included a mix of species from families Plexauridae, Gorgoniidae, and Acanthogorgiidae. Subclade M8A was largely Plexauridae (Plexaurinae) plus some Gorgoniidae; M8C was primarily Plexauridae (Stenogorgiinae) plus *Acanthogorgia*; and M8D was mostly Gorgoniidae with some Plexauridae and Acanthogorgiidae. Subclades M8C and M8D included the genera *Thrombophyton* and *Complexum*, respectively, both of which lack axes and are classified as Alcyoniidae. *Keroeides* (Keroeididae), *Astrogorgia* (Plexauridae), and two additional genera without axes, *Discophyton* (Alcyoniidae) and *Taiaroa* (Taiaroidae), occupied unsupported positions within clade M8 that varied among analyses. All analyses did, however, group *Keroeides, Astrogorgia,* and *Taiaroa* together.

3.3 Phylogenetic analyses of *mtMutS*

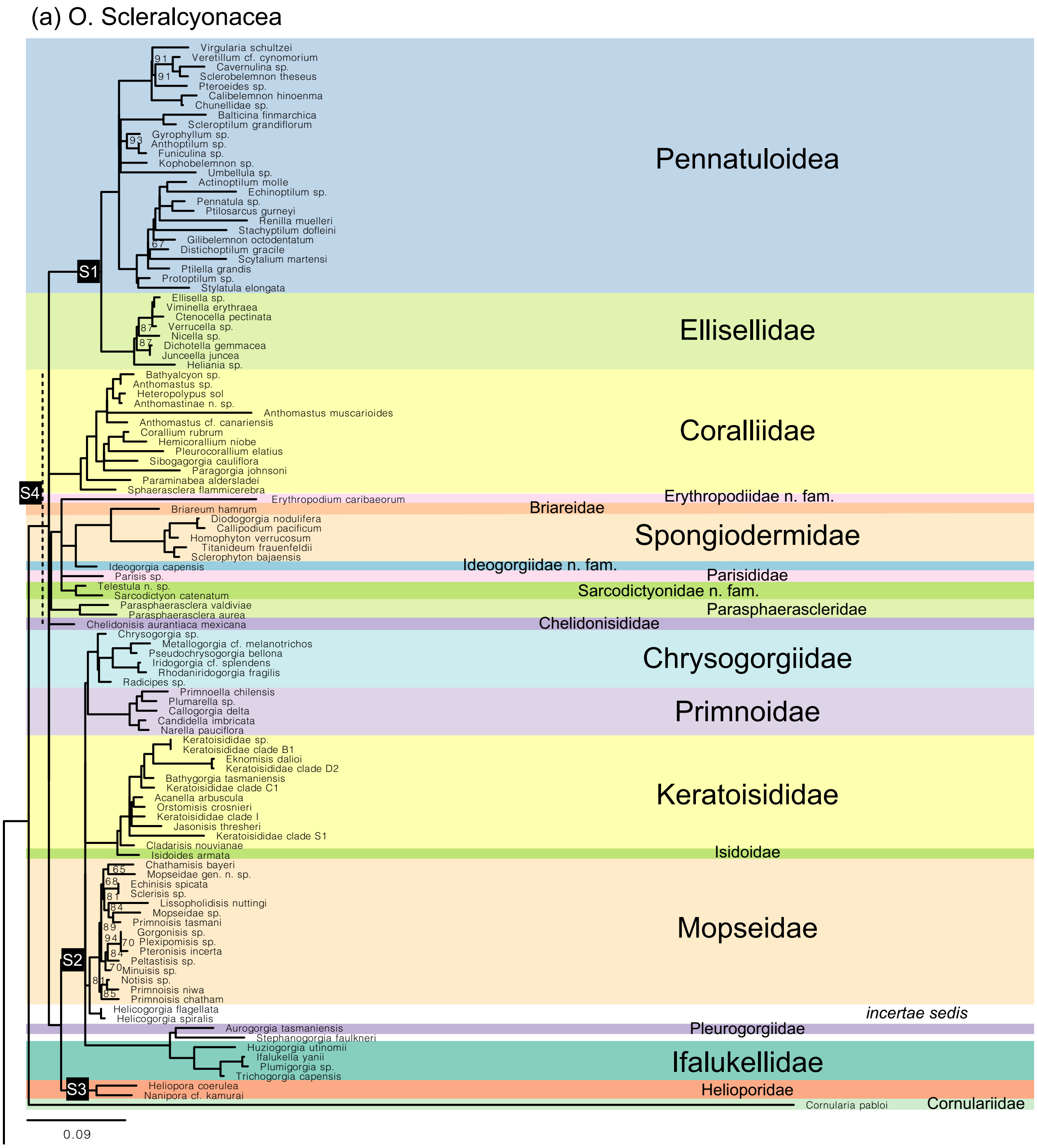
The alignment of *mtMutS* included 284 taxa for a total length of 1038 bp (Table 1). The topology of the unconstrained tree (Suppl. File S2) was significantly different from that of the tree constrained to match the topology recovered from the phylogenomic analysis (Fig. 2). The primary differences between constrained and unconstrained trees were the phylogenetic positions of several taxa with divergent mitochondrial gene sequences whose placement in the unconstrained phylogeny appears to be subject to artifacts of long branch attraction. These included *Cornularia*, which grouped with *Erythropodium,* and *Muricella* + *Anthogorgia,* which grouped with *Clavularia* cf. *viridis,* in the unconstrained tree. In the unconstrained tree, *Subergorgia* and *Annella,* both of which are long branches, did not group together, whereas they did in the tree constrained by the target-enriched phylogeny. *Acanthogorgia aspera* Pourtalès, 1867 did not fall into a clade with the other two *Acanthogorgia* species, and *Euplexaura* grouped with *Acanthogorgia* and *Guaiagorgia* in the unconstrained tree. Relationships among major clades also differed between constrained and unconstrained topologies, although many of these were poorly supported in both analyses. A majority of taxa, however, belonged to the same well-supported clades in both the fully resolved target-enriched phylogeny (Fig. 1) and the unconstrained *mtMutS* phylogeny (Suppl. Files S2). Most of the genera for which only *mtMutS* sequences were available were found in the clades they would be expected to belong to based on their current familial assignment or morphological similarity to taxa included in the phylogenomic analysis. The constrained *mtMutS* phylogeny therefore reflects a consensus view of the relationships among 257 genera and 60 of the 63 currently recognized families of octocorals (Fig. 2).

4 DISCUSSION

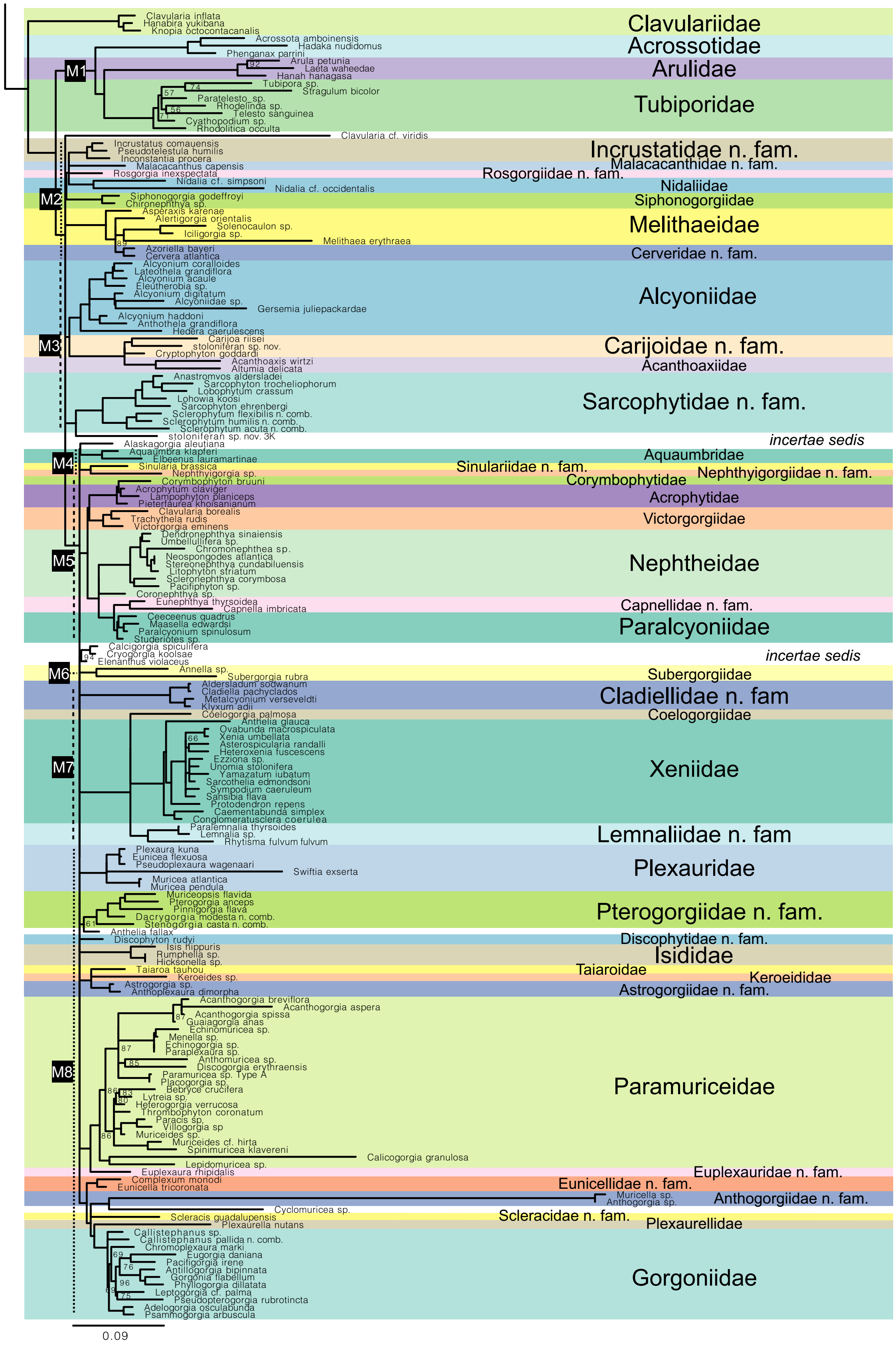
The well-supported phylogeny recovered using UCE and exon loci (Fig. 1) is largely congruent with phylogenies that have been published previously based on analyses of mitochondrial genes alone (*mtMutS*, *COI,* *ND2*) (e.g., McFadden et al. 2006a) or mitochondrial genes combined with *28S rDNA* (Breedy et al. 2012; Brockman and McFadden 2012; McFadden and van Ofwegen 2012a; Cairns and Wirshing 2015). The phylogenomic analyses recovered the same major clades observed previously but with much stronger support for the monophyly of those clades and, in some cases, the relationships among clades. In particular, the reciprocal monophyly of the two major clades (Calcaxonia-Pennatulacea and Holaxonia-Alcyoniina) has been unclear from mitochondrial gene phylogenies that placed Cornulariidae sister to both clades rather than sister to Calcaxonia-Pennatulacea (Brockman and McFadden 2012; McFadden and van Ofwegen 2012a). The phylogenomic analyses strongly support Cornulariidae as a member of Calcaxonia-Pennatulacea. The positions of families Melithaeidae, Leptophytidae, and Acanthogorgiidae have also been unstable in past analyses; all of these taxa occupy very long branches in the mitochondrial gene phylogenies (e.g., McFadden and van Ofwegen 2017; Fig. 2), suggesting that rate variation among lineages may influence the phylogenetic signal from mitochondrial genomes (Muthye et al. 2022).

Although the major clades within Calcaxonia-Pennatulacea and Holaxonia-Alcyoniina (S1-S4, M1-M8) are each strongly supported by the phylogenomic analyses, and most have also received (weaker) support in single-gene analyses (Fig. 2), a few of the relationships among these clades are still not well resolved and differed among the various phylogenetic analyses (Suppl. Files S2). The very short branch lengths along the backbone of Holaxonia-Alcyoniina in particular suggest a rapid and ancient radiation of this clade. A time-calibrated phylogeny of

Fig. 2: Maximum likelihood tree of Octocorallia inferred from 1059 bp alignment of *mtMutS* with tree topology constrained to match the topology of the target-enriched tree (Fig. 1). All nodes have ≥95% support from 10,000 ultrafast bootstrap replicates unless otherwise noted. Proposed families are indicated by colored bars; white bars indicate taxa left *incertae sedis*. Numbered squares and dashed lines along backbone denote taxa included in the clades discussed in Results. (a) Order Scleralcyonacea. (b) Order Malacalcyonacea.



(a) O. Scleralcyonacea



(b) O. Malacalcyonacea

Anthozoa indicates that the major clades of Holaxonia-Alcyoniina evolved 350-200 Ma, and some groups such as Holaxonia experienced increased rates of diversification in the late Triassic (Quattrini et al. 2020). Periods of rapid morphological diversification are often associated with phylogenomic conflict that may lead to difficulties resolving the phylogenetic relationships among major lineages (Parins-Fukuchi et al. 2021).

Ability to infer the relationships among major clades is destabilized by a few taxa on long branches whose positions within the tree varied among analyses. These include *Chelidonisis*; a stoloniferan identified as *Clavularia* cf. *viridis sensu* Dean, 1927; and the *Cladiella-Klyxum* clade of Alcyoniidae. Mitochondrial gene trees suggest that there are other nominal taxa as well as currently undescribed species not included in our phylogenomic analysis that may fall outside of the larger clades (Fig. 2). These "orphan" lineages likely represent either relic species of clades that arose long ago and have experienced high extinction or could be ancient lineages that have never diversified. The very sparse nature of the octocoral fossil record will likely preclude ever distinguishing among these alternative hypotheses. Orphan lineages may also simply reflect inadequate sampling of certain habitats (e.g., mesophotic depths) and inconspicuous groups (e.g., stoloniferans) and a consequent lack of knowledge of the true diversity of poorly known taxa.

4.1 Homoplasies and conserved characters

Ancestral state reconstructions suggest that the most recent common ancestor of Octocorallia lacked a skeletal axis and may or may not have had sclerites (Quattrini et al. 2020; McFadden et al. 2021). Skeletal axes have evolved independently in many different lineages of octocorals and in many different ways, including convergent evolution of largely proteinaceous as well as solid calcium carbonate axes (Quattrini et al. 2020). The development of an axis may be progressive. Several clades exhibit transitions from colonies lacking an axis to gradual consolidation and, in some cases, fusion of coenenchymal sclerites into a rigid axis. Such transitions are exemplified by the *Anthomastus-Corallium* clade. Within that clade, however, the form of the sclerites remains constant, with only the degree to which they are consolidated changing. Similarly, in the Alcyoniidae clade (which includes *Anthothela*), colonies typically exhibit two distinct layers of sclerites, with an outer (surface) layer of sclerites that differ in form from those typically found in the inner layer. Within this clade, there is a continuum of colony forms ranging from those with very sparse or almost no sclerites in the inner layer (*Gersemia*) to taxa in which the sclerites of the inner coenenchyme are numerous and densely packed together to form a medulla (*Anthothela*). This continuum may occur within a single species as exemplified by *Anthothela grandiflora* (Sars, 1856), in which colonies may grow as thin membranes with no medullar layer or produce branches that have a distinct axial medulla (Moore et al. 2017). Jointed skeletal axes in which internodes of either solid (non-scleritic) calcium carbonate or fused sclerites alternate with flexible, proteinaceous nodes have also arisen independently in a number of clades.

The past classification of scleraxonians—taxa with an axis of unconsolidated or consolidated sclerites—has focused on the presence and arrangement of boundary canals that separate the axial medulla from the overlying cortex (Wright and Studer 1889; Aurivillius 1931). Families have been defined based on shared characters such as whether or not canals penetrate the medullar layer and the presence or distinctive arrangement of canals separating the medulla and cortex (e.g., Cairns and Wirshing 2015). Phylogenetic analyses reveal the arrangements of these canals to be homoplasies and suggest instead that the form of the sclerites that constitute the medulla is a more phylogenetically informative character. It is likely that consolidation of sclerites within the coenenchyme necessitates the development of a boundary canal system for fluid transport around an axis and that a limited number of possible canal arrangements have evolved repeatedly concomitant with the evolution of an axis. It is the sclerite composition of the medulla rather than the arrangement of canals within or surrounding it that defines clades of scleraxonians.

Among taxa that lack an axis, colony growth form is both evolutionarily labile and often plastic within a species. Colonies with simple membranous or stoloniferous growth forms, in which polyps are connected basally by thin sheets of tissue or tubular canals, are distributed throughout the octocoral tree of life. In some clades (including both Calcaxonia-Pennatulacea and Holaxonia-Alcyoniina) these simple growth forms seem to be ancestral, with colony form becoming more complex as the clade diversified. In other clades, complex morphologies have apparently been lost in a reversion to simpler forms, as seen in taxa such as *Thrombophyton,* a genus with an encrusting, membranous growth form that belongs to a lineage of holaxonian gorgonians. In some clades, growth form is variable within populations. For instance, in both *Alcyonium coralloides* (Pallas, 1766) and *Anthothela grandiflora*, individual colonies may grow as thin membranes that are capable of giving rise respectively to fleshy lobes or to complex branched structures with a consolidated medulla (McFadden 1999; Moore et al. 2017). Similarly, although there is some evidence that the common ancestor of all extant Octocorallia lacked sclerites (Quattrini et al. 2020), many clades include species in which sclerites have been lost secondarily (Benayahu et al. 2017; Quattrini et al. 2020), and, in some cases, the presence of sclerites in a colony may vary among individuals of a species (e.g., *Xenia umbellata*, Halász et al. 2019).

In light of the apparent lability of axis formation and colony growth morphology, the two characters that have historically been used for the highest levels of classification in Octocorallia, what morphological characters are diagnostic of higher taxa? Although a skeletal axis has evolved independently in many lineages, the underlying mechanism of axis formation and details of its microstructure differ widely among clades but may be conserved within clades. For example, most species formerly classified as Scleraxonia form an axis through consolidation of sclerites. The form of the sclerites in the axis and the degree to which they are consolidated or fused differ among clades, but those characters are constant within clades and are therefore both phylogenetically informative and taxonomically diagnostic. Microstructural differences may also distinguish taxa that share superficially similar axes. Differences in the microstructure of the solid (non-scleritic) skeletal axes of Ellisellidae compared to the other families of Calcaxonia with which they have been classified have long been recognized (Bayer 1955). The microstructure of the ellisellid axis, in which the solid calcareous material is arranged in wedge-shaped sclerodermites rather than concentric lamellae, is, however, shared with Pennatulacea, which is evidence of a sister relationship that has since been validated with molecular data (Williams

2019). Likewise, microstructural differences between the jointed axis of *Isis hippuris*, in which solid calcareous internodes appear to form by fusion of sclerites (Bayer 1955), and the jointed axes of other "isidid" taxa (e.g., Keratoisididae, Mopseidae) that have non-scleritic calcareous internodes are now recognized to be phylogenetically informative: *Isis* is very distant phylogenetically from any of the other taxa with superficially similar jointed axes (Heestand Saucier et al. 2021).

Just as the form of the sclerites found in skeletal axes is phylogenetically informative, the characteristic form or arrangement of the sclerites found in species that lack an axis may also inform higher taxonomic classification. While many taxa share certain basic sclerite forms such as spindles, some sclerite forms are synapomorphies of higher taxa. For example, distinctive radiates that lack complex tubercular ornamentation unite the taxa in *Anthomastus-Corallium*, a clade of otherwise morphologically disparate taxa that have been classified in three families and two suborders. *Chelidonisis,* a genus with a jointed skeleton that was long classified with the similarly jointed Isididae, is clearly distinguishable by the form of its sclerites, which differ from anything found in other former isidids (Heestand Saucier et al. 2021). The distribution and arrangement of sclerites in the colony may also be diagnostic at higher taxonomic levels. The absence of sclerites in the polyps or their arrangement as a collaret and points are examples of characters that unite the taxa in some clades in which colony growth form or axial development are highly variable, such as in Alcyoniidae *sensu stricto*. Characters such as these that may be conserved within one clade and therefore useful for its diagnosis may, however, vary among or even within species in other clades. Additional examples include polyp dimorphism (i.e., presence of siphonozooids in addition to autozooids) and photosymbioses with dinoflagellates. Polyp dimorphism is conserved in higher taxa such as Pennatulacea and the *Anthomastus-Corallium* clade. Within Xeniidae and a few other families, however, some genera have siphonozooids while others lack them, and species in the xeniid genus *Heteroxenia* have even been documented to develop siphonozooids seasonally or ontogenetically (Gohar 1940; Achituv and Benayahu 1990). Likewise, many clades comprise solely zooxanthellate or solely azooxanthellate genera, but in other clades this trait varies among genera (e.g., Nephtheidae, Plexauridae) or, rarely, within genera (e.g., *Eunicella*, Aurelle et al. 2017; *Junceella*, Williams et al. 2010).

Because the majority of morphological characters used to distinguish phylogenetic clades are evolutionarily labile at some taxonomic level, there are very few higher taxa of octocorals for which a single morphological synapomorphy is diagnostic. Examples of such characters include the unique colony morphology of the sea pens, the massive aragonitic skeleton of Helioporidae, the cuticular "theca" of Cornulariidae, and the armored polyps and operculum of Primnoidae. Diagnosis of most other higher taxa relies on unique combinations of character states, some or all of which may be shared with other clades.

4.2 Phylogenetic classification of Octocorallia

From the earliest molecular phylogenies (Berntson et al. 2001), it has been clear that the higher order Linnean classification of Octocorallia, based largely on gross morphology of the colonial growth form, does not reflect the group's phylogeny (reviewed by McFadden et al. 2010). While it has been obvious that many higher taxa are poly- or paraphyletic, limited support for relationships among and within many of the molecular clades has discouraged attempts to revise the ordinal and family-level taxonomy of Octocorallia. Here, we consider that much of the octocoral phylogeny is now resolved and supported well enough to proceed with those revisions. We also recognize, however, that the incomplete taxon sampling of some groups—in particular those families and genera already recognized to be highly polyphyletic—precludes taxonomic placement of all genera and species with certainty. Numerous genera will remain *incertae sedis* until additional molecular or morphological analyses allow confirmation of their phylogenetic affinity.

Within the Linnean classification system all higher taxa are artificial constructs. We espouse the cladistic philosophy that Linnean taxa should reflect monophyly (Hennig 1966), as revealed most clearly by molecular data in this group of organisms. But we are also mindful that, in practice, it is desirable that higher taxa should be identifiable morphologically. There seems to be little value in defining families that encompass such a wide range of morphological variation that they will comfortably accommodate almost any taxon. Conversely, circumscribing taxa so narrowly that the higher-level classification simply repeats the lower levels (i.e., monotypy) defeats the purpose of a hierarchical system of classification. Our proposed familial revision therefore attempts to reflect the underlying phylogenetic structure of the group (as revealed by molecular analyses) while simultaneously identifying diagnostic morphological characters that can be used to classify taxa for which molecular data are not yet available.

To accomplish this goal we have followed the principles of classification outlined by Backlund and Bremer (1998). The primary principle of this system is to preserve the monophyly of higher taxa, with secondary principles of maximizing nomenclatural stability, phylogenetic information, and ease of identification. All of the families we propose here are monophyletic as currently understood from the phylogenetic analyses we present. To the degree possible, we have tried to retain existing family concepts while circumscribing their membership and amending their diagnoses, if necessary, to preserve monophyly. In some cases (e.g., Coralliidae, Tubiporidae, Gorgoniidae), preserving monophyly has required expanding a family concept to encompass taxa that would otherwise need to be defined as monotypic families. For other families that have long been recognized to be highly polyphyletic (e.g., Alcyoniidae, Clavulariidae, Plexauridae), we have narrowed the family concept to restrict it to the clade that includes the type taxon while erecting new families for other clades. In all such cases, however, we have tried to adhere to the secondary principle of ease of identification by defining families as clades of genera that also share one or more diagnostic morphological characteristics. In cases in which sister taxa are sufficiently different morphologically that we have found no clear, diagnostic morphological characters to unite them and distinguish them from other higher taxa, we have opted instead to retain or define monotypic families.

We acknowledge that some gross morphological characters that have traditionally been used to define higher taxa, such as the presence and composition of a skeletal axis or overall colony growth form, represent homoplasies. Development or loss of a skeletal axis and reversion to a stoloniferous or membranous growth form are transitions that are observed within a number of the major clades. In some cases, we have chosen to accommodate such transitions within the definition of a family, particularly when they present a continuum or evolutionary progression of character states within a clade. We believe this decision is preferable to the alternatives of erecting paraphyletic or polyphyletic families or defining so many monotypic families as to make the rank meaningless. Even so, there are some cases in which we have chosen to circumscribe families very narrowly, thereby increasing substantially the number of families recognized from 63 to 79 (Table 2).

5 TAXONOMIC REVISIONS

Phylum Cnidaria Hatschek, 1888
Sub-Phylum Medusozoa Petersen, 1979 [new rank]
    Class Cubozoa Werner, 1973
    Class Hydrozoa Owen, 1843
    Class Myxozoa Grassé, 1970
    Class Scyphozoa Goette, 1887
    Class Staurozoa Werner, 1973

Sub-Phylum Anthozoa Ehrenberg, 1834 [new rank]
    Class Hexacorallia Haeckel, 1896 [new rank]
    Class Octocorallia Haeckel, 1866 [new rank]
        Order Malacalcyonacea [new]
        Order Scleralcyonacea [new]

5.1 Remarks

Phylum Cnidaria is currently divided among six classes in two reciprocally monophyletic clades, Medusozoa and Anthozoa (Daly et al. 2007). Five of those six classes (Hydrozoa, Scyphozoa, Staurozoa, Cubozoa, Myxozoa) are united in clade Medusozoa, distinguished from Anthozoa by a biphasic life cycle (lost in numerous taxa) in which a sessile polypoid stage alternates with a (usually pelagic) medusoid stage. Anthozoa lacks a medusoid stage. Although the true number of species in either clade is uncertain, approximately 7500 extant species of Anthozoa and 5800 Medusozoa have been described (Daly et al. 2007; Chang et al. 2015). Fossil-calibrated molecular phylogenetic analyses place the divergence of Anthozoa and Medusozoa in the pre-Cambrian, perhaps as long ago as 750 Myr (Quattrini et al. 2020, McFadden et al. 2021). The two currently recognized sub-classes of Anthozoa, Hexacorallia and Octocorallia, likewise diverged in the pre-Cambrian (McFadden et al. 2021), as did the classes of Medusozoa (Park et al. 2012; Holzer et al. 2018). To reflect the reciprocal monophyly of clades Medusozoa and Anthozoa and the similarities in divergence times of the major groups within each clade, we elevate both Medusozoa and Anthozoa to the rank of sub-phylum and Hexacorallia and Octocorallia to the rank of class. Cnidaria thus comprises two sub-phyla, Anthozoa and Medusozoa, with two and five classes, respectively.

Phylogenomic analyses support the division of Octocorallia into two reciprocally monophyletic clades, which we designate as orders. These two clades have been recognized in previous molecular phylogenetic studies and have been referred to as Holaxonia-Alcyoniina and Calcaxonia-Pennatulacea, reflecting the majority taxonomic composition of each clade (McFadden et al. 2010). We establish O. Malacalcyonacea for the Holaxonia-Alcyoniina clade and O. Scleralcyonacea for the Calcaxonia-Pennatulacea clade. While Malacalcyonacea includes a majority of taxa previously considered to belong to the subordinal groups Holaxonia and Alcyoniina, it also includes many taxa formerly classified as Stolonifera and Scler-

Table 2. Summary of proposed changes to higher taxonomic levels. Clades are indicated in Figures 1, 2 and in the text. Bold: new or reinstated taxon or new rank. *monogeneric family

Clade	Family	Former Higher Taxon	Proposed Changes
Order Scleralcyonacea			new order (= Calcaxonia-Pennatulacea clade)
S0	Cornulariidae*	Stolonifera	none
S1	Ellisellidae	Calcaxonia	none
S1	**Pennatuloidea**	Pennatulacea	new superfamily for 15 families of sea pens
S2	Chrysogorgiidae	Calcaxonia	restrict to 7 genera of "monophyletic Chrysogorgiidae clade" (sensu Pante et al. 2012)
S2	Ifalukellidae	Calcaxonia	include Huziogorgiidae in Ifalukellidae
S2	Isidoidae*	Calcaxonia	none
S2	Keratoisididae	Calcaxonia	none
S2	Mopseidae	Calcaxonia	none
S2	Pleurogorgiidae	Calcaxonia	none
S2	Primnoidae	Calcaxonia	none
S3	Dendrobrachiidae*	Holaxonia	none
S3	Helioporidae	Helioporacea	include Lithotelestidae in Helioporidae
S4	Briareidae*	Scleraxonia	none
S4	Chelidonisididae*	Calcaxonia	none
S4	Corallidae	Scleraxonia	include Paragorgiidae plus Anthomastinae, *Paraminabea*, *Sphaerasclera* (all formerly Alcyoniidae)
S4	**Erythropodiidae***	Scleraxonia: Anthothelidae	new rank for Erythropodiinae Kükenthal, 1916
S4	**Ideogorgiidae***	Holaxonia: Keroeididae	new monotypic family for *Ideogorgia*
S4	Parasphaerascleridae*	Alcyoniina	none
S4	Parisididae*	Scleraxonia	none
S4	**Sarcodictyonidae**	Stolonifera: Clavulariidae	new family for 2 genera of former Clavulariidae
S4	Spongiodermidae	Scleraxonia	none
Order Malacalcyonacea			new order (= Holaxonia-Alcyoniina clade)
M0	Clavulariidae	Stolonifera	restrict family to *Clavularia, Knopia, Hanabira*
M1	Acrossotidae	Stolonifera	include *Hadaka, Phenganax* (formerly Clavulariidae)
M1	Arulidae	Stolonifera	none
M1	Tubiporidae	Stolonifera	include 9 genera of former Clavulariidae
M2	**Cerveridae**	Stolonifera: Clavulariidae	new family for 2 genera of former Clavulariidae
M2	**Incrustatidae**	Stolonifera: Clavulariidae	new family for 3 genera of former Clavulariidae

M2	**Malacacanthidae***	Alcyoniina: Alcyoniidae	new monotypic family for *Malacacanthus*
M2	Melithaeidae	Scleraxonia	include 3 genera of former Anthothelidae
M2	Nidaliidae	Alcyoniina	restrict to *Nidalia* and 3 other genera
M2	**Rosgorgiidae***	Scleraxonia: Subergorgiidae	new monotypic family for *Rosgorgia*
M2	**Siphonogorgiidae**	Alcyoniina: Nidaliidae	reinstate Siphonogorgiidae Kölliker, 1874 for *Chironephthya*, *Siphonogorgia* (formerly Nidaliidae)
M3	Acanthoaxiidae	Holaxonia	include *Altumia* (formerly Clavulariidae)
M3	Alcyoniidae	Alcyoniina	restrict to *Alcyonium* and 4 other genera plus *Gersemia* (formerly Nephtheidae), *Anthothela* (formerly Anthothelidae)
M3	**Carijoidae**	Stolonifera: Clavulariidae	new family for 2 genera of former Clavulariidae
M3	**Sarcophytidae**	Alcyoniina: Alcyoniidae	new family for 5 genera of former Alcyoniidae
M4	Aquaumbridae	Alcyoniina	include *Elbeenus* (formerly Alcyoniidae)
M4	**Nephthyigorgiidae***	Alcyoniina: Nidaliidae	new monotypic family for *Nephthyigorgia*
M4	**Sinulariidae***	Alcyoniina: Alcyoniidae	new monotypic family for *Sinularia brassica*
M5	Acrophytidae	Alcyoniina	none
M5	**Capnellidae**	Alcyoniina: Nephtheidae	new family for 5 genera of former Nephtheidae
M5	Corymbophytidae*	Alcyoniina	none
M5	Leptophytidae	Alcyoniina	none
M5	Nephtheidae	Alcyoniina	restrict to 9 genera
M5	Paralcyoniidae	Alcyoniina	none
M5	**Pseudonephtheidae***	Alcyoniina: Nephtheidae	new monotypic family for *Pseudonephthea* n. gen.
M5	**Skamnariidae***	Alcyoniina: Alcyoniidae	new monotypic family for *Skamnarium*
M5	Victorgorgiidae	Scleraxonia	include *Trachythela* (formerly Clavulariidae)
M6	Subergorgiidae	Scleraxonia	restrict to *Subergorgia* + *Annella*
M7	**Cladiellidae**	Alcyoniina: Alcyoniidae	new family for 4 genera of former Alcyoniidae
M7	Coelogorgiidae*	Stolonifera	none
M7	**Lemnaliidae**	Alcyoniina: Alcyoniidae, Nephtheidae	new family for 3 genera of former Nephtheidae and Alcyoniidae
M7	Xeniidae	Alcyoniina	include *Protodendron* (formerly Alcyoniidae)
M8	**Anthogorgiidae**	Holaxonia: Acanthogorgiidae	new family for 2 genera of former Acanthogorgiidae

M8	**Astrogorgiidae**	Holaxonia: Plexauridae	new family for 3 genera of former Plexauridae
M8	**Discophytidae***	Alcyoniina: Alcyoniidae	new monotypic family for *Discophyton*
M8	**Eunicellidae**	Alcyoniina, Holaxonia	new family for *Eunicella* (formerly Gorgoniidae) + *Complexum* (formerly Alcyoniidae)
M8	**Euplexauridae***	Holaxonia: Plexauridae	new monotypic family for *Euplexaura*
M8	Gorgoniidae	Holaxonia	include 4 genera of former Plexauridae
M8	Isididae	Calcaxonia, Holaxonia	include 2 genera of former Gorgoniidae
M8	Keroeididae*	Holaxonia	restrict to *Keroeides*
M8	**Paramuriceidae**	Holaxonia: Plexauridae	Paramuriceidae Bayer, 1956 reinstated for Plexauridae (Stenogorgiinae) plus *Acanthogorgia* (formerly Acanthogorgiidae), *Thrombophyton* (formerly Alcyoniidae)
M8	Plexaurellidae	Holaxonia	none
M8	Plexauridae	Holaxonia	restrict to *Plexaura* and 4 other genera
M8	**Scleracidae***	Holaxonia: Plexauridae	new monotypic family for *Scleracis*
M8	**Pterogorgiidae**	Holaxonia: Plexauridae, Gorgoniidae	new family for 7 genera of former Plexauridae and Gorgoniidae
M8	Taiaroidae*	Protoalcyonaria	none

axonia. Scleralcyonacea includes former orders Pennatulacea and Helioporacea, most members of former suborder Calcaxonia, and a morphologically heterogeneous assortment of taxa formerly considered to belong to Alcyoniina, Stolonifera, Scleraxonia, and Holaxonia. Both orders encompass taxa with a wide range of growth morphologies, including those with and without skeletal axes. Most of the taxa in Scleralcyonacea, however, have axes of solid calcium carbonate or, alternatively, sclerites fused together with calcitic material. The etymology of the name is from the Greek *scler* (hard) combined with -alcyonacea, the name of the former order encompassing all octocorals other than sea pens and blue corals. The vast majority of taxa in Malacalcyonacea have either a largely proteinaceous or no skeletal axis, hence the etymology from the Greek *malacos* (soft) and -alcyonacea. Within each of these large and diverse orders we have assigned families to the clades discussed above in Results (S1-S4, M1-M8) (Figs. 1, 2), some of which correspond in part to former suborders. Because many of these distinct clades include a morphologically eclectic mix of families, we have not designated them as formal Linnean suborders that would require a morphological diagnosis.

[Note: in the following accounts, * is used to indicate a genus for which no molecular data are currently available to support taxonomic placement. A glossary of anatomical terms is included in Appendix 1. Depth ranges are loosely defined as shallow (<50 m), moderately deep (50-200 m), and deep (>200 m).]

ORDER SCLERALCYONACEA

Family Cornulariidae Dana, 1846

Type genus. *Cornularia* Lamarck, 1816

Diagnosis. Octocorals without a skeletal axis, with polyps connected basally by tubular stolons. Polyps monomorphic, anthocodia retractile into tubular calyx. Stolons and calyces covered by a thick chitinous envelope (cuticle) forming a kind of theca. Polyps and coenenchyme without sclerites. Azooxanthellate. [modified from López-González et al. 1995]

Distribution. Shallow water, southeastern Atlantic and Mediterranean.

Included genera. *Cornularia* Lamarck, 1816

Remarks. This monotypic family of two known species is unique among octocorals in having the polyps surrounded by a cuticular envelope resembling the theca of a hydroid. Mitochondrial gene phylogenies reconstruct *Cornularia* as the earliest-diverging lineage of octocorals, sister to all extant groups (McFadden and van Ofwegen 2012a). The phylogenomic analysis, however, suggests it is the earliest-diverging member of Scleralcyonacea.

[CLADE S1]

Family Ellisellidae Gray, 1859

Type genus. *Ellisella* Gray, 1858

Diagnosis. Octocorals with a skeletal axis of solid (non-scleritic) calcium carbonate. Calcareous fibers of axis oriented radially and grouped to form sclerodermites, not forming concentric layers. Colonies erect, unbranched or branched (dichotomous, lyrate, flabellate, or reticulate), planar or bushy. Polyps monomorphic, non-retractile but highly contractile. Sclerites similar in all parts of colony, small double-heads (sometimes as asymmetrical clubs), rods or spindles with median waist, symmetrical radiates (capstans). Sclerites usually brightly colored. Usually azooxanthellate, rarely zooxanthellate. [modified from Bayer and Grasshoff 1994]

Distribution. Cosmopolitan in shallow to deep water.

Included genera. *Ctenocella* Valenciennes, 1855; *Dichotella* Gray, 1870; *Ellisella* Gray, 1858; *Heliania* Gray, 1859; *Junceella* Valenciennes, 1855; *Nicella* Gray, 1870; **Phenilia* Gray, 1859; **Riisea* Duchassaing & Michelotti, 1860; *Verrucella* Milne Edwards & Haime, 1857; *Viminella* Gray, 1870.

Remarks. The monophyly of Ellisellidae and its relationship as the sister clade to Pennatulacea has been supported by all molecular data obtained to date (McFadden et al. 2006a). The morphological affinities of these taxa were first noted by Bayer (1955), who remarked on the similarity of the axes of Ellisellidae and Pennatulacea and the differences between Ellisellidae and Primnoidae or Chrysogorgiidae. In the former groups, the calcareous fibers that make up the axis are oriented radially to form sclerodermites, different from the concentric layers that characterize the axis of primnoids and chrysogorgiids. The characteristic forms of the sclerites found in ellisellids are a diagnostic synapomorphy of the family. Although the family appears to be monophyletic, a molecular phylogeny of Ellisellidae based on *mtMutS* revealed that six of the eight recognized genera for which molecular data are available are polyphyletic (Bilewitch et al. 2014). Despite the apparent need for revisions at the genus level and the lack of molecular data for the poorly known, monotypic genera *Riisea* and *Phenilia*, the distinctive sclerite and axial characters support the monophyly of this family.

SUPER-FAMILY PENNATULOIDEA

Diagnosis. Octocorals with or without a skeletal axis, with colony subdivided into a proximal peduncle and distal rachis. Axis, if present, solid (non-scleritic) calcium carbonate. Calcareous fibers of axis oriented radially and grouped to form sclerodermites, not forming concentric layers. Polyps dimorphic, occasionally trimorphic, retractile. Polyps restricted to rachis, distributed evenly over entire surface, biserially, in whorls, only at terminal end, or arising from leaves.

Included families. Anthoptilidae Kölliker, 1880; Balticinidae Balss, 1910; Chunellidae Kükenthal, 1902; Echinoptilidae Hubrecht, 1885; Funiculinidae Gray, 1870; Kophobelemnidae Gray, 1860; Pennatulidae Ehrenberg, 1834; Protoptilidae Kölliker, 1880; *Pseudumbellulidae López-González, 2022; Renillidae Gray, 1870; *Scleroptilidae Jungersen, 1904; *Stachyptilidae Kölliker, 1880; Umbellulidae Kölliker, 1880; Veretillidae Herklots, 1858; Virgulariidae Verrill, 1868. (asterisks = no phylogenomic data available)

Remarks. To date there has been no comprehensive molecular phylogenetic or phylogenomic study of sea pens that has included representatives of all families from both deep and shallow habitats. Separate studies focusing on deepwater taxa (Dolan et al. 2013; García-Cárdenas et al. 2020) and shallow-water Pacific genera (Kushida and Reimer 2018), using mitochondrial markers (*mtMutS, COI, ND2*) and *28S rDNA*, all suggest that several recognized families are polyphyletic and that genera are distributed among 3-4 well supported clades within the superfamily (López-González and Drewery 2022). We consider the taxon sampling in both single-gene and phylogenomic studies to be too sparse so far to confidently guide revisions of the pennatuloid families, and suggest this group would be a fruitful target for further phylogenomic work with more comprehensive taxon sampling.

[CLADE S2]

Family Chrysogorgiidae Verrill, 1883

Type genus. *Chrysogorgia* Duchassaing & Michelotti, 1864

Diagnosis. Octocorals with a skeletal axis of solid (non-scleritic), concentrically layered calcium carbonate. Axial layers usually smooth (not undulated); axis elliptical or circular in cross-section. Axis brittle, with metallic luster, not translucent. Colonies erect, unbranched or branched (sympodial, dichotomous, bottlebrush, pinnate), anchored by an encrusting or root-like and usually strongly calcified holdfast. Polyps monomorphic, non-retractile but contractile, predominantly arranged uniserially on the axis. Sclerites include scales, elongate (often with waist) or irregular and branched; plates; spindles and rods, often flattened. Scales show a circular extinction pattern when viewed with polarized light. Azooxanthellate. [modified from Cairns et al. 2021]

Distribution. Cosmopolitan in deep water.

Included genera. *Chrysogorgia* Duchassaing & Michelotti, 1864; *Iridogorgia* Verrill, 1883; *Metallogorgia* Versluys, 1902; *Pseudochrysogorgia* Pante & France, 2010; *Radicipes* Stearns, 1883; *Ramuligorgia* Cairns, Cordeiro & Xu, 2021; *Rhodaniridogorgia* Watling, 2007

Remarks. Several recent molecular analyses based on combined *mtMutS, COI,* and *18S rDNA* have supported the monophyly of the genera listed above (Pante et al. 2012; Cairns et al. 2021). Three other genera previously placed in Chrysogorgiidae (*Pleurogorgia* Versluys, 1902; *Trichogorgia* Hickson, 1904; *Stephanogorgia* Bayer & Muzik, 1976) are not supported by molecular evidence to belong to this family and have been or are hereby moved to other families or left *incertae sedis.* The phylogenetic placement of additional genera for which molecular data are currently limited or unavailable also remains uncertain. These include *Chalcogorgia* Bayer, 1949; *Distichogorgia* Bayer, 1979; *Flagelligorgia* Cairns & Cordeiro, 2017; *Helicogorgia* Verrill, 1883; and *Xenogorgia* Bayer & Muzik, 1976. Because these genera share certain morphological characters with *Pleurogorgia, Trichogorgia,* and *Stephanogorgia,* it is likely that they will be found not to belong to Chrysogorgiidae (Pante et al. 2012). The *mtMutS* phylogeny (Fig. 2a) does not clearly resolve the phylogenetic position of *Helicogorgia* but suggests that it does not belong to either Chrysogorgiidae *sensu stricto* or to the clade that includes *Pleurogorgia, Trichogorgia,* and *Stephanogorgia*. The phylogenetic position of *Stephanogorgia* also remains uncertain; although it shares a number of morphological characters with Ifalukellidae, the *mtMutS* phylogeny suggests it is sister to Pleurogorgiidae (Fig. 2a). For now, we leave *Stephanogorgia, Helicogorgia,* and the other four genera that lack molecular data as *incertae sedis.*

Family Ifalukellidae Bayer, 1955

Type genus. *Ifalukella* Bayer, 1955

Diagnosis. Octocorals with a skeletal axis of non-calcified protein or solid (non-scleritic), concentrically layered calcium carbonate. Concentric layers nearly smooth, not oriented in a radial pattern. Colonies erect, branched (lyrate, dichotomous, pinnate or irregular lateral), planar or bushy, with large, calcareous holdfast. Polyps monomorphic, retractile. Sclerites absent or sparse, small (<0.1 mm) corpuscles, oval or elongate, usually with a median constriction and irregularly granular sculpture. Zooxanthellate or azooxanthellate. [modified from Bayer 1955]

Distribution. Probably cosmopolitan in shallow to deep water.

Included genera. *Ifalukella* Bayer, 1955; *Huziogorgia* López-González, 2020; *Plumigorgia* Nutting, 1910; ?*Trichogorgia* Hickson, 1904

Remarks. Bayer (1955) established the family Ifalukellidae for two genera of shallow-water, zooxanthellate octocorals with aragonitic axes (Bayer and McIntyre 2001) and small, corpuscular sclerites that are often only very sparsely distributed throughout the colony (Opresko and Bayer 1991). Molecular phylogenetic and phylogenomic analyses have revealed a close relationship between these genera and several species currently or formerly assigned to the genus *Trichogorgia*, leading to the recent reassignment of *T. capensis* (Hickson, 1904) to Ifalukellidae (López-González 2020). In the same paper, López-González (2020) described a new genus, *Huziogorgia*, and family, Huziogorgiidae, for another species of *Trichogorgia, T. utinomii* Cordeiro, 2019. The new family was justified based solely on genetic distances between *H. utinomii* and other species of Ifalukellidae at the mitochondrial *mtMutS* and *COI* loci, rather than on morphological distinctions between the species. As shown clearly by comparison of the phylogeny based on target-enriched nuclear genes (Fig.1) to the *mtMutS* phylogeny (Fig. 2a), genetic distance values alone and for a single locus should not be used to justify decisions about higher levels of taxonomic classification. The *mtMutS* tree reveals numerous instances of genera and species on long branches (i.e., separated by high genetic distances from sister taxa) that are anomalous when compared to the nuclear gene phylogeny, suggesting that lineage-specific rate variation may complicate phylogenetic inference from mitochondrial genes (e.g., McFadden and van Ofwegen 2017; Muthye et al. 2022). *Huziogorgia* appears to belong to a monophyletic group with Ifalukellidae and shares many morphological characters with other members of the clade; therefore, we reassign the genus to Ifalukellidae.

Both *Huziogorgia* and *T. capensis* differ from other Ifalukellidae in lacking sclerites and being azooxanthellate, traits that are variable within and among other families of octocorals. *T. capensis* is further differentiated from the other species by its axis that lacks any calcified elements. While the axes of *Ifalukella* and *Plumigorgia* have been studied in detail and confirmed to be composed of aragonite (Bayer and McIntyre 2001), comparable studies of axis composition have yet to be conducted for *Huziogorgia* or *T. capensis* (Cordeiro 2019). The poorly known genus *Trichogorgia* currently includes species with and without sclerites, with different types of sclerites (scales or spindles), different arrangements of sclerites in the polyps, and different degrees of calcification of the axis (Cordeiro 2019). Molecular data are not available for the type species, *T. flexilis* Hickson, 1904, to confirm if it belongs to this Ifalukellidae clade or if it is closely related to *T. capensis*. Indeed, in the same publication in which *Trichogorgia* (originally assigned to Chrysogorgiidae) was described, Hickson (1904) described *Malacogorgia capensis* and assigned it to its own family, Malacogorgiidae. Kükenthal (1919) reassigned *M. capensis* to *Trichogorgia*, but it may be that the original genus assignment should hold.

Family Isidoidae Heestand Saucier, France & Watling, 2021

Type genus. *Isidoides* Nutting, 1910

Diagnosis. Octocorals with a skeletal axis of solid (non-scleritic), concentrically layered calcium carbonate. Colonies erect, branched (pseudo-dichotomous), planar. Polyps monomorphic, non-retractile, mostly biserially or triserially arranged on the axis. Sclerites smooth, flattened, scale-like rods (finger biscuit-shaped) of relatively uniform size, abundant and tightly packed throughout the surface tissue of the colony, rarely in the pharynx. Cross-shaped sclerites present but few in number. Azooxanthellate. [modified from Heestand Saucier et al. 2021]

Distribution. Deep water, southwestern

Pacific.

Included genera. *Isidoides* Nutting, 1910

Remarks. The phylogenetic position of the monotypic genus *Isidoides* has long been unclear. It was originally placed in Gorgonellidae (= Ellisellidae) by Nutting (1910), who also noted that its sclerites resembled those of some isidids. It was subsequently transferred to Chrysogorgiidae based on the similarity of its sclerites to those of that family (Bayer and Stefani 1988). Its phylogenetic position as sister to Keratoisididae was first recognized by Pante et al. (2012), who subsequently re-described the genus and classified it as *incertae sedis* (Pante et al. 2013). Although they recognized similarities between the form and arrangement of sclerites in *Isidoides* and Keratoisididae, they argued against including it in that family due to its lack of a jointed axis and the relatively large genetic distance separating it from other keratoisidid genera. Heestand Saucier et al. (2021) subsequently placed it in its own monotypic family, Isidoidae. The phylogenomic data support the status of *Isidoides* as the sister taxon to Keratoisididae, and we maintain it as a separate family to reflect the morphological differences between it and the keratoisidid taxa.

Family Keratoisididae Gray, 1870

Type genus. *Keratoisis* Wright, 1869

Diagnosis. Octocorals with a (usually) jointed skeletal axis of hollow or solid internodes of non-scleritic calcium carbonate separated by proteinaceous nodes that lack sclerites and may be flexible in younger parts of the colony. Calcareous fibers of internodes oriented radially and grouped to form sclerodermites, not arranged in concentric layers. Colonies erect, unbranched or branched (e.g., dichotomous, trichotomous, pseudo-dichotomous or lyrate, with branching occurring at nodes or internodes), planar or bushy, attached to hard substrate with a calcium carbonate holdfast or anchored in soft sediment with a root-like holdfast. Polyps monomorphic, non-retractile but contractile. Polyp sclerites needles, spindles, rods, or scales arranged longitudinally or obliquely along the polyp body; one or a cluster of needle-like sclerites protrude between the bases of the tentacles in many, but not all, species. Sclerites of coenenchyme of similar form but smaller. Pharyngeal sclerites usually present, including tuberculated or spiny rodlets and double stars. Azooxanthellate. [modified from Heestand Saucier et al. 2021]

Distribution. Cosmopolitan in deep water.

Included genera. *Acanella* Gray, 1870; *Bathygorgia* Wright, 1885; *Cladarisis* Watling, 2015; *Eknomisis* Watling & France, 2011; *Isidella* Gray, 1857; *Jasonisis* Alderslade & McFadden, 2012; *Keratoisis* Wright, 1869; *Lepidisis* Verrill, 1883; *Orstomisis* Bayer, 1990.

Remarks. The monophyly of Keratoisidinae has long been supported by single-gene phylogenetic reconstructions (primarily using *mtMutS*) and the discovery that most members of this clade share a unique, derived mitochondrial gene order (Brugler and France 2008; Brockman and McFadden 2012). The recent publication of Heestand Saucier et al. (2021) elevates the subfamily to the rank of family, a revision that is supported by our phylogenomic analysis. As suggested by both phylogenomic and molecular phylogenetic evidence (Figs. 1, 2a), Keratoisididae is not the sister clade to the other isidid subfamilies, Mopseinae and Isidinae, each of which has also now been elevated in rank (Heestand Saucier et al. 2021). Morphological distinctions among many of the recognized genera of Keratoisididae are unclear, and the family also includes a number of morphologically distinct clades whose descriptions as new genera are pending (Watling et al., 2022). We use the clade designations of Watling et al.

(2022) to identify the specimens included in the phylogenomic and *mtMutS* phylogenies (Figs. 1, 2a).

Family Mopseidae Gray, 1870

Type genus. *Mopsea* Lamouroux, 1816

Diagnosis. Octocorals with a jointed skeletal axis of internodes of solid (non-scleritic) calcium carbonate separated by proteinaceous nodes that lack sclerites. Calcareous fibers of internodes oriented radially and grouped to form sclerodermites, not arranged in concentric layers. Internodes commonly sculptured with longitudinal ridges, spines or granulations of various sizes. Colonies erect, branched or unbranched (with branching occurring at nodes and internodes, but primarily internodal), planar or bushy. Polyps monomorphic, non-retractile but contractile. Polyp sclerites smooth, tuberculate, or thorny scales or plates (generally broad, but sometimes narrow, thick, and spindle-like) with a distal margin that is dentate, tuberculate, scalloped or thorny, or rarely more or less entire; proximal margin generally with lobes or tuberculate root-like processes; arranged transversely on polyp body; alternatively, narrow or stout spindles, generally flattened, with a simple or complex margin, arranged longitudinally. Anthopomal sclerites scale-like (generally triangular, triradiate, or crescentic), situated intermesentarily and forming simple or complex protective arrangements which enclose the deflated tentacles during contraction. Sclerites of coenenchyme surface derived from unilaterally spinose spindles, sometimes present as irregularly shaped platelets. Azooxanthellate. [modified from Alderslade and McFadden 2012]

Distribution. Moderately deep water in the southern hemisphere.

Included genera. **Acanthoisis* Studer, 1887; **Annisis* Alderslade, 1998; **Australisis* Bayer & Stefani, 1987; **Caribisis* Bayer & Stefani, 1987; *Chathamisis* Grant, 1976; **Circinisis* Grant, 1976; *Echinisis* Thomson & Rennet, 1932; **Florectisis* Alderslade, 1998; *Gorgonisis* Alderslade, 1998; **Iotisis* Alderslade, 1998; *Jasminisis* Alderslade, 1998; **Ktenosquamisis* Alderslade, 1998; *Lissopholidisis* Alderslade, 1998; *Minuisis* Grant, 1976; **Mopsea* Lamouroux, 1816; **Myriozotisis* Alderslade, 1998; *Notisis* Gravier, 1913; **Oparinisis* Alderslade, 1998; **Pangolinisis* Alderslade, 1998; **Paracanthoisis* Alderslade, 1998; *Peltastisis* Nutting, 1910; *Plexipomisis* Alderslade, 1998; *Primnoisis* Studer & Wright, 1887; *Pteronisis* Alderslade, 1998; *Sclerisis* Studer, 1878; **Sphaerokodisis* Alderslade, 1998; **Stenisis* Bayer & Stefani, 1987; **Tenuisis* Bayer & Stefani, 1987; **Tethrisis* Alderslade, 1998; *Zignisis* Alderslade, 1998

Remarks. Although the genera in this family were previously included with Keratoisidinae in family Isididae, phylogenomic (Fig. 1) and phylogenetic analyses (Alderslade and McFadden 2012) suggest that the two clades are not sisters. They share a similar jointed axis but differ in both the form and arrangement of the sclerites found in the polyps and coenenchyme (Alderslade 1998). Most of the mopseid genera are poorly known, and relatively little molecular data are available for them. We were able to include only two taxa in the phylogenomic analysis, but *mtMutS* sequences that are available for an additional ten genera support the monophyly of the family and suggest there is relatively little genetic differentiation among genera (Fig. 2a). Although seven genera (*Annisis, Circinisis, Florectisis, Gorgonisis, Pangolinisis, Plexipomisis, Zignisis*) have previously been separated into sub-family Circinisidinae largely on the basis of differences in the sclerites of the coenenchyme surface (rooted heads or smooth oval scales rather than spindle derivatives), *mtMutS* sequences that are available for three of those genera do not support their separation from the taxa formerly placed in Mopseinae (Fig. 2a). Heestand Saucier et al. (2021) elevated Mopseidae to family rank and included in it all genera of former Mopseinae and Circinisidinae, a revision that is supported by the molecular analyses.

Family Pleurogorgiidae Cairns, Cordeiro & Alderslade, 2021

Type genus. *Pleurogorgia* Versluys, 1902

Diagnosis. Octocorals with a skeletal axis of solid (non-scleritic) calcium carbonate arranged in concentric layers. Axial layers usually smooth (not undulated); elliptical or circular in cross-section. Axis brittle, with metallic luster, not translucent. Colonies erect, unbranched or branching in a secund manner, anchored by a strongly calcified disc-like holdfast. Polyps monomorphic, non-retractile but contractile, arranged uniserially. Sclerites of polyp body wall and coenenchyme in two layers, the lower containing elongate scales and tuberculate, flattened spindles and plates, the upper containing bud plates that may grade into unilaterally foliate spheroids. Tentacular sclerites include smooth and tuberculate scales that may be accompanied by bud plates and some foliate spheroids. Sclerites show a circular or no extinction pattern when viewed with polarized light. Azooxanthellate. [modified from Cairns et al. 2021]

Distribution. Moderately deep to deep water, Indian and southern Pacific Oceans.

Included genera. *Aurogorgia* Cairns, Cordeiro & Alderslade, 2021; **Pleurogorgia* Versluys, 1902

Remarks. Cairns et al. (2021) recently established this family for *Pleurogorgia*, formerly assigned to Chrysogorgiidae, and a new genus, *Aurogorgia*, with which it had been confused. Molecular data for *mtMutS* support the distinction of *Aurogorgia* from Chrysogorgiidae and place it in the same clade as Ifalukellidae. Both *Aurogorgia* and *Pleurogorgia* (for which no molecular data exist) are distinguished from other taxa in the Ifalukellidae clade by a unique sclerite form, termed "bud plates" (Cairns et al. 2021).

Family Primnoidae Milne Edwards, 1857

Type genus. *Primnoa* Lamouroux, 1812

Diagnosis. Octocorals with a skeletal axis of solid (non-scleritic) and continuous calcium carbonate (with only one exception, *Mirostenella*, which has a jointed axis). Cross section of axis reveals undulating concentric layers of calcified material embedded in gorgonin, resulting from a longitudinal (not radial) pattern of calcification; outer axial surface usually longitudinally striate (or grooved). Colonies erect, unbranched, or branched in a variety of manners, usually firmly attached to substrate by a discoidal, calcareous holdfast. Polyps monomorphic, non-retractile, with calyces occurring in a variety of arrangements and orientations, in one case (*Ainigmaptilon*) arranged in clusters on leaf-like structures. Polyps heavily armored with calcareous scales that are usually arranged in an imbricate manner: each calyx has eight triangular opercular scales forming a closeable operculum, a variable number of marginal (buccal or circumopercular) scales (usually eight), and a variable number of rows of longitudinal body wall scales (often eight). Coenenchymal sclerites predominantly imbricate scales, some genera with an inner layer of tuberculate spheroids that compose the walls of the longitudinal canals. Scales show a cruciform extinction pattern when viewed with polarized light. Azooxanthellate. [modified from Cairns and Bayer 2009]

Distribution. Cosmopolitan, mostly in deep water.

Included genera. *Abyssoprimnoa* Cairns, 2015; **Acanthoprimnoa* Cairns & Bayer, 2004; *Aglaoprimnoa* Bayer, 1996; *Ainigmaptilon* Dean, 1926; *Armadillogorgia* Bayer, 1980; *Arntzia* López-González, Gili & Orejas, 2002; **Arthrogorgia* Kükenthal, 1908; *Australogorgia* Cairns & Bayer, 2009; *Callogorgia* Gray, 1858; *Callozostron* Wright, 1885; *Calyptrophora* Gray, 1866; *Candidella* Bayer, 1954; *Convexella* Bayer, 1996; *Dasystenella* Versluys, 1906; *Dicholaphis* Kinoshita, 1907; *Fannyella* Gray, 1872; *Faxiella* Zapata-Guardiola & López-González, 2012; **Helicoprimnoa* Cairns, 2012; *Heptaprimnoa* Cairns, 2012; *Loboprimnoa* Cairns, 2016; *Macroprimnoa* Cairns, 2018; *Metafannyella* Cairns & Bayer, 2009; **Metanarella* Cairns, 2012; **Microprimnoa* Bayer & Stefani, 1989; *Mirostenella* Bayer, 1988; *Narella* Gray, 1870; **Narelloides* Cairns, 2012; *Onogorgia* Cairns & Bayer, 2009; *Ophidiogorgia* Bayer, 1980; *Pachyprimnoa* Cairns, 2016; *Paracalyptrophora* Kinoshita, 1908; *Paranarella* Cairns, 2007; *Parastenella* Versluys, 1906; *Perissogorgia* Bayer & Stefani, 1989; *Plumarella* Gray, 1870; *Primnoa* Lamouroux, 1812; **Primnocapsa* Zapata-Guardiola & López-González, 2012; *Primnoeides* Studer & Wright, 1887; *Primnoella* Gray, 1858; **Pseudoplumarella* Kükenthal, 1915; **Pterostenella* Versluys, 1906; *Pyrogorgia* Cairns & Bayer, 2009; **Scopaegorgia* Zapata-Guardiola & López-González, 2010; *Tauroprimnoa* Zapata-Guardiola & López-González, 2010; *Thouarella* Gray, 1870; *Tokoprymno* Bayer, 1996; *Verticillata* Zapata-Guardiola, López-González & Gili, 2012

Remarks. A recent, comprehensive molecular analysis of family Primnoidae using a combination of four gene regions (*mtMutS, COI, ND2*, and *28S rDNA*) established the phylogenetic relationships among 33 of the 43 described genera (Cairns and Wirshing 2018). Consequently, we included only those genera for which phylogenomic data are newly available in our phylogenetic analyses (Fig. 1, 2a). Based on the unique, diagnostic morphological characters that define this family, there is little reason to question the familial placement of the other 10 genera for which molecular data are still lacking.

[CLADE S3]

Family Dendrobrachiidae Brook, 1889

Type genus. *Dendrobrachia* Brook, 1889

Diagnosis. Octocorals with skeletal axis of non-mineralized protein, lacking a hollow, cross-chambered core. Axis marked by conspicuous ridges and grooves, with more or less numerous and prominent spines along the summit of the ridges. Colonies erect, sparsely branched (irregular but generally bilateral and alternate), planar. Polyps monomorphic, well-spaced on branches and branchlets. Polyps and coenenchyme without sclerites. Azooxanthellate. [modified from Opresko and Bayer 1991]

Distribution. Deep water, Atlantic and Mediterranean.

Included genera. *Dendrobrachia* Brook, 1889

Remarks. Although it had been classified in former suborder Holaxonia as a result of its proteinaceous axis, a previous molecular phylogenetic analysis based on *mtMutS* and *COI* showed that this enigmatic family belongs to O. Scleralcyonacea (Aurelle et al. 2019). Neither of those genes, however, was able to resolve the position of *Dendrobrachia* within that clade. The phylogenomic analyses (Fig. 1) confirm its placement in Scleralcyonacea and suggest that it is sister to Helioporidae.

Family Helioporidae Mosely, 1876

Type genus. *Heliopora* Blainville, 1830

Diagnosis. Octocorals with a rigid skeleton composed of hexagonal crystals of aragonite, with polyp body walls similarly formed of crystalline aragonite rather than fused sclerites. Colonies massive, often lobate or digitate, or with polyps connected basally by calcified stolons. Polyps monomorphic, retractile, distributed evenly over colony surface. Axial polyps sometimes budding laterally to produce secondary polyps. Polyps without sclerites or with radiates in proximal body wall and tentacles. Zooxanthellate or azooxanthellate.

Distribution. Shallow waters of the tropical Indo-Pacific; deep waters of western Atlantic.

Included genera. **Epiphaxum* Lonsdale, 1850; *Heliopora* Blainville, 1830; *Nanipora* Miyazaki & Reimer, 2015

Remarks. The blue coral, *Heliopora*, has long been placed in a monotypic family, Helioporidae, and order, Helioporacea, on account of its distinctive skeleton that differs from all other extant octocorals. Two genera of stoloniferous octocorals with similar skeletons of crystalline aragonite were subsequently assigned to a separate family, Lithotelestidae Bayer & Muzik, 1977, within Helioporacea. Molecular phylogenetic and phylogenomic analyses confirm the monophyly of Helioporacea but also suggest there is nothing particularly phylogenetically distinctive about this clade despite its unique morphology. It is one of many clades within Scleralcyonacea, and the phylogenomic analyses suggest it is sister to Dendrobrachiidae, a family that lacks any calcareous elements. We abolish the order Helioporacea and include these genera with aragonitic skeletons within Scleralcyonacea.

Families Helioporidae and Lithotelestidae have been distinguished primarily by colony growth form. Helioporidae forms massive colonies in which the living tissue is restricted to a thin surface layer, separated by transverse plates from the underlying layers of calcium carbonate. In contrast, colonies of Lithotelestidae consist of thinly encrusting, calcified stolons from which calcified, tubular calyces arise. Such a diversity of colony growth forms is not uncommon in other families of octocorals, and we suggest the two families be united in Helioporidae. It should be noted, however, that molecular data are not available for *Epiphaxum*, the rarely encountered type genus of Lithotelestidae. *Epiphaxum* differs from *Heliopora* and *Nanipora* in several ways, including: having calcitic sclerites in the polyps and prominent longitudinal grooves on the surfaces of the calyces; lacking zooxanthellae; and occurring in deep water of the western Atlantic rather than the shallow tropical Indo-Pacific. Based on the similarity of their aragonitic skeletons, we consider it likely that *Epiphaxum* belongs with the other two genera in Helioporidae, but molecular phylogenetic data will be required to confirm that taxonomic status.

[CLADE S4]

Family Briareidae Gray, 1859

Type genus. *Briareum* Blainville, 1834

Diagnosis. Octocorals without a skeletal axis, with coenenchyme subdivided into outer cortex and inner (basal) medulla. Colonies encrusting, upright with tall digitiform lobes, or forming tangled masses of cylindrical branches that may be hollow. Medulla penetrated by gastrovascular canals but lacking a distinct zone of boundary canals separating it from cortex. Polyps monomorphic, retractile, lacking sclerites, and restricted to the cortex with gastrovascular cavities not penetrating medulla. Sclerites of medulla spindles with high complex tubercles, often branched and fused into clumps. Sclerites of cortex robust spindles with complex tubercles, often high and usually arranged in distinct girdles. Medullar sclerites always magenta. Zooxanthellate. [modified from

Fabricius and Alderslade 2001]
Included genera. *Briareum* Blainville, 1834
Distribution. Shallow tropical waters of the Indo-Pacific and western Atlantic.
Remarks. *Lignopsis* Pérez & Zamponi, 2000 was assigned to Briareidae based on the shared characters of a medulla highly perforated by gastrovascular canals, the absence of a ring of boundary canals between the cortex and medulla, and polyps restricted to the cortex. This genus differs from *Briareum*, however, in a number of ways, including an arborescent, branched growth form, a clear demarcation between cortex and medulla, and sclerites in the form of radiates (capstans) in the cortex and spinose needles in the medulla that are not colored. Moreover, *Lignopsis* is azooxanthellate and has a sub-Antarctic rather than tropical distribution. In the absence of molecular data to confirm its familial placement, for now we consider *Lignopsis* to be *incertae sedis*.

Family Chelidonisididae Heestand Saucier, France & Watling, 2021

Type genus. *Chelidonisis* Studer, 1890
Diagnosis. Octocorals with a jointed skeletal axis of internodes of solid (non-scleritic) calcium carbonate separated by proteinaceous nodes that lack sclerites. Internodes longitudinally grooved, the ridges serrated. Colonies erect, branched (dichotomous, branching from the distal ends of the internodes), planar but occasionally anastomosing to form multiplanar thickets. Polyps monomorphic, non-retractile but contracting to hemispherical or bluntly conical mounds, distributed mostly biserially in the plane of ramification, widely spaced. Coenenchyme thin, sclerites of polyps and coenenchyme predominantly 6-radiates. Azooxanthellate. [modified from Bayer and Stefani 1987]
Distribution. Cosmopolitan in deep water.
Included genera. *Chelidonisis* Studer, 1890
Remarks. *Chelidonisis* has historically been placed in Isididae, a group with which it shares a jointed skeletal axis of solid calcareous internodes separated by proteinaceous nodes. The radiate sclerites found throughout its tissues are, however, unique among isidids and bear a close resemblance to those found in some species of Parasphaerascleridae. The serrated ornamentation of the internodes also distinguishes this genus from all isidids. The phylogenetic position of *Chelidonisis* is highly unstable, and its sister taxon is unclear. Single-gene and phylogenomic analyses all place it on a long branch, loosely affiliated with Parasphaerascleridae and Coralliidae. On the basis of its phylogenetic position and its unique sclerome combined with a jointed axis, Heestand Saucier et al. (2021) assigned *Chelidonisis* to a new, monotypic family, a revision that is supported by the phylogenomic data.

Family Coralliidae Lamouroux, 1812

Type genus. *Corallium* Cuvier, 1798
Diagnosis. Octocorals with or without a skeletal axis of unfused or fused sclerites. Colonies without an axis typically hemispherical to digitiform, capitate with a conspicuous sterile stalk, or (rarely) sparsely branched or lobate; colonies with an axis erect with sparse to profuse branching, usually planar. Polyps dimorphic, with reproductive siphonozooids and feeding autozooids, retractile into coenenchyme or cortex surrounding axis. Polyps lacking sclerites or with spindles, ovals, clubs, or radiates. Sclerites of surface and inner coenenchyme are radiates and spheroids lacking complex tubercles; some species with blunt rods and spindles. Sclerites often brightly colored, usually red. Azooxanthellate (rarely zooxanthellate).
Distribution. Cosmopolitan, mostly in deep water.

Included genera. *Anthomastus* Verrill, 1878; *Bathyalcyon* Versluys, 1906; **Carotalcyon* Utinomi, 1952; *Corallium* Cuvier, 1798; *Hemicorallium* Gray, 1867; *Heteropolypus* Tixier-Durivault, 1964; **Minabea* Utinomi, 1957; *Notodysiferus* Alderslade, 2003; *Paragorgia* Milne Edwards & Haime, 1857; *Paraminabea* Williams & Alderslade, 1999; *Pleurocorallium* Gray, 1867; *Pseudoanthomastus* Tixier-Durivault & d'Hondt, 1974; *Sibogagorgia* Stiasny, 1937; *Sphaerasclera* McFadden & van Ofwegen, 2013.

Remarks. We re-circumscribe this family to include genera that have previously been assigned to three different families (Paragorgiidae Kükenthal, 1916; Sibogagorgiidae Verseveldt, 1942; and Alcyoniidae Lamouroux, 1812) and two different sub-ordinal groups, Scleraxonia and Alcyoniina. The morphological similarities among these seemingly disparate taxa were, however, noted long ago. As discussed by Bayer (1993): "Broch & Horridge (1957: 158)... remarked that 'it is rather astonishing that nobody seems to have observed the evident relationship between *Paragorgia* and *Anthomastus*'...Broch & Horridge concluded that *Bathyalcyon* and *Anthomastus* should be included with *Paragorgia* and *Sibogagorgia* in one family, Paragorgiidae, on the basis of dimorphism and similarity of sclerites. They maintained that *Anthomastus* differs anatomically from *Paragorgia* only in the absence of horny material, a character they considered of negligible importance compared with dimorphism and similarity of sclerites." Other authors have, in turn, remarked on the extreme similarity of sclerite form between Paragorgiidae and Coralliidae (Bayer 1964; Sánchez 2005) with Bayer (1964) noting that it "calls for a thorough investigation of axis formation in these and other genera and a reappraisal of the systematic significance of axial characters in general."

The phylogenomic reconstruction supports the conclusion that the presence of an axis, either of sclerites embedded in gorgonin (*Paragorgia, Sibogagorgia*) or cemented together within a solid calcareous matrix (*Corallium, Hemicorallium, Pleurocorallium*; Debreuil et al. 2011), is less informative phylogenetically than the shared characters of polyp dimorphism and the characteristic forms of the radiates in these taxa. The relationships of the genera within the Coralliidae clade suggest an evolutionary progression from colonies that lack an axis and have simple, unbranched growth forms to those with an axis of unfused sclerites embedded in medullar tissue to those with sclerites cemented together to form a solid axis. This evolutionary progression has proceeded with little genomic differentiation as indicated by the relatively short branch lengths separating species with these very different growth forms (Fig. 1). The degree of genetic divergence among the genera that comprise this clade is comparable to or less than that in a number of other families of octocorals within which colony growth form and axial formation are relatively homogeneous, further supporting our decision to unite them within a single, monophyletic family.

Sphaerasclera is the earliest diverging member of Coralliidae and the only one for which polyp dimorphism has not been confirmed. McFadden and van Ofwegen (2013) discussed the difficulty of detecting siphonozooids in that genus and raised the possibility that they might be present. Sequence data for the *ND2* gene support the placement of *Notodysiferus* in Coralliidae (McFadden et al. 2006a). Although it is zooxanthellate and occurs in shallow water, it nonetheless shares the characteristic sclerite form and polyp dimorphism with other members of the clade (Alderslade 2003). Too few *ND2* sequences are available for other members of the family to determine its sister taxon with any confidence. No molecular data are available for the monotypic genera *Minabea* and *Carotalcyon*, but both of those genera also share the diagnostic morphological characters of Coralliidae (characteristic form of the radiates, polyp dimorphism).

Family Erythropodiidae Kükenthal, 1916 new rank

Type genus. *Erythropodium* Kölliker, 1865

Diagnosis. Octocorals without a skeletal axis, with coenenchyme subdivided into outer cortex and inner (basal) medulla. Colonies thinly encrusting. Basement layer (medulla) separated from cortex by network of large canals. Polyps monomorphic, retractile, restricted to the cortex with gastrovascular cavities not penetrating medulla. Sclerites throughout colony are small derivatives of 6-radiates, often fused into clumps in medulla. Medullar sclerites magenta. Zooxanthellate.

Distribution. Shallow waters of the tropical western Atlantic and western Pacific.

Included genera. *Erythropodium* Kölliker, 1865

Remarks. Kükenthal (1916) included *Erythropodium* in Briareidae, within which he assigned it to sub-family Erythropodiinae, distinct from Briareinae Kükenthal, 1916. Bayer (1956) subsequently re-assigned the genus to Anthothelidae Broch, 1916, a family characterized by medullar and cortical layers separated by a distinct ring or layer of boundary canals that rarely perforate the medulla. Phylogenetic analyses place *Erythropodium* far from any other anthothelids but close to Briareidae. Although it belongs to a clade with *Briareum* and *Callipodium*, two genera with similar encrusting growth forms, in neither of those genera is the medulla separated from the cortex by extensive boundary canals. Moreover, *Erythropodium* lacks the branched spindles with girdles of high tubercles that are characteristic of the other two genera. On the basis of its unique morphological characters and the phylogenetic position it occupies on a long branch whose position is somewhat unstable, we elevate its taxonomic status to that of a monotypic family.

Family Ideogorgiidae new fam.

Type genus. *Ideogorgia* Bayer, 1981

Diagnosis. Octocorals with a proteinaceous skeletal axis, with horn-like central core surrounded by cortex of unfused sclerites embedded in sheaths of gorgonin. Colonies erect, sparsely branched (dichotomous), more-or-less planar. Polyps monomorphic, retractile into prominent calyces or nearly flush with surface, distributed evenly over branches or clustered more densely at branch tips. Polyps lacking sclerites or with blunt rods, smooth or with tuberculated ends. Sclerites of coenenchyme are triradiates; axial cortex with irregularly-shaped, smooth rods. Azooxanthellate.

Distribution. Cold or deep water of southern hemisphere.

Included genera. *Ideogorgia* Bayer, 1981

Remarks. Since its original description, *Ideogorgia capensis* (Hickson, 1904), the type species (and, until recently, only known member) of the genus *Ideogorgia*, has been transferred among families repeatedly. Originally described as an ellisellid, it was placed in Sclerogorgidae (O. Pseudaxonia) by Simpson (1910) before subsequent transfers to Briareidae (Kükenthal 1919), Subergorgiidae (Hickson 1930), and, most recently, Keroeididae Kinoshita, 1910 (Bayer 1981a). Keroeididae includes several poorly known genera of gorgonians whose skeletal compositions are transitional between those of typical holaxonians and scleraxonians. Like Holaxonia, in Keroeididae the axis is largely composed of gorgonin and may have a hollow, cross-chambered core; unlike Holaxonia, sclerites are embedded in the axis and may fill the central core (Fabricius and Alderslade 2001). Only two of the four genera currently considered to belong to Keroeididae have been included in molecular phylogenetic analyses. These analyses suggest the family is not monophyletic since *Keroeides* belongs to Malacalcyonacea and *Ideogorgia* to Scleralcyonacea, where it is sister to Spongiodermidae + Briareidae (Figs. 1, 2a). The structure of the axis and form of the coenenchymal sclerites in *Ideogorgia* are unique among Scleralcyonacea. As a result of its distinct morphology and phylogenetic position, we assign *Ideogorgia* to a new, monotypic family, Ideogorgiidae.

Family Parasphaerascleridae McFadden & van Ofwegen, 2013

Type genus. *Parasphaerasclera* McFadden & van Ofwegen, 2013

Diagnosis. Octocorals without a skeletal axis, colonies digitiform, digitate or lobate, usually with a sterile stalk although this may be indistinct. Polyps monomorphic, fully retractile into coenenchyme, distributed evenly over surfaces of lobes. Polyp sclerites absent. Sclerites of colony surface and interior predominantly radiates and tuberculate spheroids, occasionally rods and crosses. Sclerites brightly colored. Azooxanthellate. [modified from McFadden and van Ofwegen 2013]

Distribution. Shallow water of tropical Indo-Pacific and southern Africa.

Included genera. *Parasphaerasclera* McFadden & van Ofwegen, 2013

Remarks. This family shares a number of morphological characters with *Paraminabea*, including a similarity of colony growth form, absence of polyp sclerites, brightly colored (usually red or yellow) sclerites, and, in some but not all species, radiates of a similar form to those characteristic of Coralliidae. Unlike the members of Coralliidae, however, *Parasphaerasclera* has monomorphic rather than dimorphic polyps. Parasphaerascleridae occupies a poorly resolved position in the phylogeny relative to Coralliidae and other taxa in clade S4 (Fig. 1).

Family Parisididae Aurivillius, 1931

Type genus. *Parisis* Verrill, 1864

Diagnosis. Octocorals with a jointed skeletal axis, with solid calcareous internodes of fused sclerites alternating with proteinaceous nodes containing sclerites. Internodes and nodes of axis longitudinally grooved. Colonies erect, profusely branched (branches arising from internodes), planar or bushy. Polyps monomorphic, non-retractile but contracting to form conical mounds, distributed evenly over surfaces of all branches. Sclerites of polyps, colony surface and fused in internodes are tubercular plates and irregular forms. Sclerites embedded in axial nodes are lobate rods. Azooxanthellate. [modified from Fabricius and Alderslade 2001]

Distribution. Shallow to moderately deep water of the tropical Indo-Pacific.

Included genera. *Parisis* Verrill, 1864

Remarks. *Parisis* has long been assigned to a monotypic family on the basis of its unique skeletal morphology of a jointed axis in which the internodes are composed of fused sclerites and the proteinaceous nodes contain sclerites. Phylogenomic data confirm its placement on a long branch in the octocoral tree, not closely related to any other genera. Although all analyses support its membership in a clade with Spongiodermidae, Briareidae, *Erythropodium, Ideogorgia*, and

Telestula, its sister relationship to any one of those taxa remains poorly resolved.

Family Sarcodictyonidae new fam.

Type genus. *Sarcodictyon* Forbes in Johnston, 1847

Diagnosis. Octocorals without a skeletal axis, polyps connected basally by ribbon-like stolons that may fuse to form membranous expansions. Polyps monomorphic, anthocodiae retractile into calyces that may be short or very tall, evenly distributed over surface of colony. Axial polyps may bud laterally to produce secondary daughter polyps. Stolons and calyces covered by a thin cuticle. Polyp sclerites small, blunt rods with tubercular ornamentation, sparse or arranged in longitudinal rows but not as collaret and points. Sclerites of calyces and stolons are stellate plates, crosses, 6-radiates or irregularly-shaped, branched forms with dense tubercular ornamentation. Azooxanthellate.

Distribution. Cosmopolitan in cold temperate or deep water.

Included genera. *Sarcodictyon* Forbes in Johnston, 1847; *Telestula* Madsen, 1944

Remarks. Morphologically, the members of this family are difficult to distinguish from stoloniferous families belonging to Malacalcyonacea and exemplify the convergent evolution of fairly simple growth forms among Octocorallia. Apart from the very clear phylogenetic distinctions between them, Sarcodictyonidae n. fam. and Incrustatidae n. fam. are particularly difficult to separate. Both families include genera that have tall polyps that may bud laterally to produce secondary polyps and have a sclerite-filled intrusion tissue in their bases (e.g., *Telestula, Pseudotelestula;* Poliseno et al. 2021) as well as genera in which polyps retract into very short calyces and do not produce secondary polyps (e.g., *Sarcodictyon, Incrustatus*). The general form of the sclerites in both families is also similar, including mostly irregular forms derived from spindles or radiates with complex tubercular ornamentation. Unlike some other families of stoloniferous genera, the sclerites in the stolons and lower polyp body wall are never fused. Genera that share these general characteristics can be found in a variety of other families of Malacalcyonacea as well; these include, most notably, *Discophyton* McFadden & Hochberg, 2003 and *Thrombophyton* McFadden & Hochberg, 2003, both of which fall within clades of holaxonian gorgonians. These species appear to represent cases in which simple membranous growth forms have evolved secondarily within clades otherwise characterized by structurally complex colonies with skeletal axes.

Family Spongiodermidae Wright & Studer, 1889

Type genus. *Spongioderma* Kölliker, 1871 (= *Homophyton* Gray, 1866)

Diagnosis. Octocorals with or without a skeletal axis of densely packed sclerites embedded in proteinaceous gorgonin. Axial medulla surrounded by a ring of longitudinal boundary canals; a secondary ring canal system may also separate inner from outer cortex. Colonies encrusting (lacking an axis) or erect, unbranched, sparsely branched, or planar with dichotomous branching. Polyps retractile into calyces that may be flush with the surface, distributed evenly over entire colony. Medullar (axial) sclerites stout rods, often bifurcate, branched, and/or spiny, arranged longitudinally in axis. Sclerites of cortex always include radiates, and may include spindles, ovals and double heads. Azooxanthellate. [modified from Cairns and Wirshing 2015]

Distribution. Shallow to moderately deep water in western Atlantic, eastern Pacific and southern Africa.

Included genera. *Callipodium* Verrill, 1869; *Diodogorgia* Kükenthal, 1919; *Homophyton* Gray, 1866; *Sclerophyton* Cairns & Wirshing, 2015; *Titanideum* Verrill, 1864; **Tripalea* Bayer, 1955

Remarks. Cairns and Wirshing (2015) resurrected this family which had been merged with Anthothelidae. Their combined morphological and molecular analyses support the monophyly of the family and its phylogenetic distinction from other genera formerly assigned to Anthothelidae.

ORDER MALACALCYONACEA

Family Clavulariidae Hickson, 1894

Type genus. *Clavularia* Blainville, 1830

Diagnosis. Octocorals without a skeletal axis, polyps connected basally by ribbon-like stolons or thin membranes and sometimes also by raised stolons. Polyps monomorphic, anthocodiae retractile into clavate calyces that may be very tall. Pinnules free or fused to form broad blade-like expansions of the tentacle (pseudopinnules). Sclerites of tentacles minute rods, platelets or scales. Sclerites of calyces and stolons absent or smooth or tuberculate spindles, often fused into clumps in stolons. Zooxanthellate.

Distribution. Shallow waters of the tropical Indo-Pacific.

Included genera. *Clavularia* Blainville, 1830; *Hanabira* Lau, Stokvis, Imahara & Reimer, 2019; *Knopia* Alderslade & McFadden, 2007

Remarks. The diagnosis of family Clavulariidae is complicated by incomplete knowledge and lack of molecular data for *C. viridis* Quoy & Gaimard, 1833, the type species of *Clavularia*. The family has long been a repository for all octocorals with a stoloniferous growth form, and the genus encompasses most of those species whose sclerites are in the general form of spindles. Molecular evidence has made it clear that both the genus and family are highly polyphyletic, and "clavulariids" are found throughout the octocoral tree of life (McFadden and van Ofwegen 2012a; Benayahu et al. 2017). *C. viridis* is one of several large-polyped, zooxanthellate tropical forms. Species morphologically similar to *C. viridis* such as *C. inflata* Schenk, 1896 form a clade that is sister to the rest of Malacalcyonacea, and for now we restrict the definition of family Clavulariidae to that clade. No molecular data are available, however, for specimens matching Quoy & Gaimard's *C. viridis*. A specimen of *Clavularia* cf. *viridis* that is included in the phylogenomic analysis matches Dean's (1927) interpretation of *Clavularia (Hicksonia) viridis*, but according to Alderslade (pers. comm.) does not match the original type material of Quoy & Gaimard. *Clavularia* cf. *viridis sensu* Dean, 1927 does not belong to the same clade as *C. inflata*, but occupies a poorly resolved position on a long branch within Malacalcyonacea (Fig. 1). Until molecular data for material that matches the type of *C. viridis* becomes available and its phylogenetic position can be confirmed, it is necessary to consider the possibility that the clade we have designated as Clavulariidae might not represent that family.

[CLADE M1]

Family Acrossotidae Bourne, 1914

Type genus. *Acrossota* Bourne, 1914

Diagnosis. Octocorals without a skeletal axis, polyps connected basally by network of tubular or ribbon-like stolons that may fuse to form broad, membranous expansions. Stolons and calyces covered by a thin cuticle. Polyps monomorphic, anthocodia retractile into calyx but not into stolon. Pinnules may be short and conical, fused to form broad blade-like expansions of the tentacle (pseudopinnules), or entirely absent. No sclerites in any part of colony. Zooxanthellate.

Distribution. Shallow waters of the tropical Indo-Pacific.

Included genera. *Acrossota* Bourne, 1914; *Hadaka* Lau & Reimer, 2019; *Phenganax* Alderslade & McFadden, 2011.

Remarks. Acrossotidae is another family that was originally erected for a single species with a unique morphology. *Acrossota* Bourne, 1914 is the only octocoral known to lack pinnules entirely, although in some other taxa such as *Briareum* the pinnules may be greatly reduced and barely visible. *Phenganax* and *Hadaka* are both recently described taxa that share with *Acrossota* a similar, stoloniferous growth form and complete absence of sclerites. Although they have pinnules, the form of the pinnules in both genera is atypical, either fused to form broad blades or reduced to stubby, conical processes. The close (possibly paraphyletic) phylogenetic relationships among the three genera (Lau and Reimer 2019a) support our proposal to broaden the diagnosis of Acrossotidae to include these related forms.

Family Arulidae McFadden & van Ofwegen, 2012

Type genus. *Arula* McFadden & van Ofwegen, 2012

Diagnosis. Octocorals without a skeletal axis, polyps connected basally by thin tubular or ribbon-like stolons. Polyps monomorphic, anthocodiae retractile into cylindrical to clavate calyces. Tentacles fused proximally to form a broad, circular oral membrane. Polyp sclerites rods. Sclerites of calyces and stolons are table-radiates, often fused in stolons. Calyces may also have 6-radiates or rods. Zooxanthellate.

Distribution. Shallow waters of the tropical Indo-Pacific.

Included genera. *Arula* McFadden & van Ofwegen, 2012; *Bunga* Lau & Reimer, 2019; *Hanah* Lau, Stokvis, van Ofwegen & Reimer, 2020; *Laeta* Lau & Reimer, 2019

Remarks. Arulidae was first described in 2012 for a stoloniferous octocoral with a unique polyp structure (oral membrane formed by the fusion of tentacles proximally) and unique sclerite form (table-radiates). Since then three additional genera have been described that share these same morphological synapomorphies and belong to the same molecular clade (Lau and Reimer 2019b).

Family Tubiporidae Ehrenberg, 1828

Type genus. *Tubipora* Linnaeus, 1758

Diagnosis. Octocorals without a skeletal axis, often with sclerites fused to form rigid tubes or branches. Polyps connected basally by network of stolons or membranes, sometimes giving rise to clusters of erect branches forming bushy colonies or to vertical tubes joined by raised stolonic platforms. Polyps monomorphic, retractile, distributed uniformly over surfaces of membranes or stolons. Axial polyps sometimes budding laterally to produce daughter polyps up to fourth order. Polyps lacking sclerites entirely or with spinose spindles or rods arranged as points with or without collaret; tentacular sclerites small rods and spindles or minute corpuscles. Calyces, stolons or membrane with irregular tuberculate rods, spindles or ovals, sometimes branched, inseparably fused and almost always red. Free (unfused) sclerites in the form of tuberculate ovals, spindles, crosses, and radiate-like forms may also be present in polyp, calyces or coenenchyme. Azooxanthellate or zooxanthellate.

Distribution. Shallow to moderately deep waters of the tropical Indo-Pacific.

Included genera. **Bathytelesto* Bayer, 1981; *Cyathopodium* Verrill, 1868; *Paratelesto* Utinomi, 1958; *Rhodelinda* Bayer, 1981; *Rhodolitica* Breedy, van Ofwegen, McFadden & Murillo-Cruz, 2021; **Scyphopodium* Bayer, 1981; **Stereotelesto* Bayer, 1981; *Stragulum* van Ofwegen & Haddad, 2011; *Telesto* Lamouroux, 1812; *Tubipora* Linnaeus, 1758

Remarks. *Tubipora* has long been assigned to a monotypic family reflecting its unique "organ pipe" morphology of individual, calcified polyp tubes connected by horizontal stolonic platforms. Molecular phylogenetic analyses reveal, however, that *Tubipora* belongs to a larger clade that includes species with a wide variety of growth forms, ranging from thinly encrusting or membranous colonies to forms in which tall axial polyps bud laterally to produce bushy colonies with rigid polyp walls. All members of this clade have in common a basal membrane or network of stolons from which the polyps arise, and sclerites in the coenenchyme or calyx that are inseparably fused and usually bright red in color. Most of the genera in this clade are monotypic and poorly known, and molecular data are not available to validate the inclusion of *Bathytelesto*, *Stereotelesto* or *Scyphopodium*. The latter genus differs from the others in the family in having fused sclerites in the stolons and calyces that are white, although some colonies of *Stragulum* also have white rather than red fused sclerites (van Ofwegen and Haddad 2011).

The genus *Telesto* is poorly described, and the characteristics of the type species, *T. aurantiaca* Lamouroux, 1812, require verification. Bayer (1961) noted that *Telesto* included species of two different forms, and subsequently assigned those with colorless, elongate rod-like sclerites in the calyx to *Carijoa* Müller, 1867, a genus that is phylogenetically distant from Tubiporidae (Fig. 1). Bayer also noted that Lamouroux's figure of *T. aurantiaca* bears a resemblance to *T. sanguinea* Deichmann, 1936, sharing with that species body wall sclerites that are red and in the form of irregular oval bodies with tuberculate ornamentation. He also remarked on the morphological similarities between *T. sanguinea* and *Paratelesto*. Based on both morphological evidence and the phylogenetic placement of *T. sanguinea* (Fig. 2b) we include *Telesto* in Tubiporidae while recognizing that the diagnostic characters of the genus require further confirmation.

[CLADE M2]

Family Cerveridae n. fam.

Type genus. *Cervera* López-González, Ocaña, García-Gómez & Núñez, 1995

Diagnosis. Octocorals without a skeletal axis, polyps connected basally by network of flattened stolons. Stolons and calyces covered by a thin periderm. Polyps monomorphic, anthocodia retractile into calyx to form low conical or hemispherical mounds. Polyp sclerites absent or small, discoidal and multiradiate flat plates. No sclerites in stolons. Azooxanthellate.

Distribution. Cold-temperate North Atlantic and Mediterranean, possibly also North Pacific.

Included genera. *Azoriella* López-González & Gili, 2008; *Cervera* López-González, Ocaña, García-Gómez & Núñez, 1995

Remarks. The two stoloniferous genera belonging to this clade have similar colony growth forms. Both are azooxanthellate and found in cold-temperate waters. The form of the sclerites in the polyps of *Azoriella* is unique, but *Cervera* is very similar to genera in the families Acrossotidae and Acanthoaxiidae, with which it shares a complete lack of sclerites. Members of Acrossotidae are, however, zooxanthellate, tropical taxa whose pinnules are modified in various different ways. *Altumia*, belonging to Acanthoaxiidae, is very similar to *Cervera*. The main distinction between them is that *Altumia* has not been reported to have a thin periderm covering the stolons and calyces (Benayahu et al. 2017).

Family Incrustatidae n. fam.

Type genus. *Incrustatus* van Ofwegen, Häusserman & Försterra, 2007

Diagnosis. Octocorals without a skeletal axis, polyps connected basally by ribbon-like stolons or membranes. Polyps monomorphic, retractile into calyces that may be short (flush with membrane) or very tall, evenly distributed over surface of colony or stolonal network. Axial polyps sometimes budding laterally to produce daughter polyps to third order. Polyp sclerites may be absent, sparsely distributed rods, or spindles arranged as collaret and points. Sclerites of calyces and stolons or membranes are spindles, ovals, radiates and irregular forms derived from radiates, all with complex tubercular ornamentation. Azooxanthellate.

Distribution. Cold or deep water of southern and northern hemispheres.

Included genera. *Inconstantia* McFadden & van Ofwegen, 2012; *Incrustatus* van Ofwegen, Häusserman & Försterra, 2007; *Pseudotelestula* Altuna & Poliseno, 2021

Remarks. Phylogenetic analyses unite these three genera in a clade within which it is not possible to resolve the sister relationships among taxa that are equally genetically distant from one another (Poliseno et al. 2021). The range of morphological variation within the family is exemplified by the genus *Inconstantia*, which includes three species that differ greatly in morphology yet are nearly indistinguishable genetically using conventional molecular markers (McFadden and van Ofwegen 2012a). *Inconstantia exigua* McFadden & van Ofwegen, 2012 closely resembles *Incrustatus*, having a membranous growth form, polyps that retract into low mounds that are flush or nearly flush with the colony surface, radiates and ovals of very similar form in the coenenchyme, and few or no sclerites in the polyps. In contrast, *Inconstantia procera* McFadden & van Ofwegen, 2012 resembles *Pseudotelestula* with very tall calyces arising from ribbon-like stolons, and spindles with dense tubercular sculpture in the calyces and stolons. While not as obvious as in *Pseudotelestula*, *I. procera* may also bud secondary polyps from the bases of primary polyps (McFadden and van Ofwegen 2012a: Fig. 8f), but it differs from that genus in lacking sclerites arranged as a collaret and points in the polyps. As discussed under Remarks for that family, Sarcodictyonidae n. fam. in Scleralcyonacea shares many of the same morphological characters as Incrustatidae n. fam., and the taxa are difficult to distinguish despite the very large phylogenetic distance that separates them.

Family Malacacanthidae n. fam.

Type genus. *Malacacanthus* J.S. Thomson, 1910

Diagnosis. Octocorals without a skeletal axis, with a cylindrical stalk into which a hemispherical to globular polyparium can be fully retracted. Stalk covered by a rough, horn-like cuticular envelope. Polyps dimorphic, retractile, distributed evenly over surface of polyparium, absent from stalk. No sclerites in any part of colony. Azooxanthellate.

Distribution. Endemic to cold temperate Agulhas Bioregion, southern Africa.

Included genera. *Malacacanthus* J.S. Thomson, 1910

Remarks. The southern African endemic species *Malacacanthus capensis* (Hickson, 1900) was originally described as a member of the genus *Heteroxenia*, family Xeniidae. It shares with that genus polyp dimorphism (with siphonozooids only present or detectable in large colonies), polyps restricted to a distinct polyparium atop a cylindrical stalk, and, with some *Heteroxenia* species, absence of sclerites. It was later reassigned to Alcyoniidae (Thomson 1921), and in a subsequent re-description left in Alcyoniidae as an “atypical genus” (Williams 1987). It is, however, phylogenetically distant from any other alcyoniids, and sister to the monotypic gorgonian family Rosgorgiidae n. fam. The only other morphologically similar species is the equally enigmatic *Ceratocaulon wandeli* (Jungersen, 1892), which has a similar colony form consisting of a polyparium that is retractile into a stalk covered by a horn-like cuticular envelope. *Ceratocaulon*, however, has monomorphic rather than dimorphic polyps, and Madsen (1944) describes it as having small, discoidal plate-like sclerites throughout the colony, distributed densely in some specimens but virtually absent in others. No molecular data are available for *Ceratocaulon* and for now we leave it as *incertae sedis*, with the suggestion that it might also be found to belong to Malacacanthidae n. fam.

Family Melithaeidae Gray, 1870

Type genus. *Melithaea* Milne Edwards, 1857

Diagnosis. Octocorals with a skeletal axis of consolidated sclerites embedded within a proteinaceous or calcitic matrix. Axis may be jointed, with rigid internodes of sclerites cemented together by calcite alternating with flexible, proteinaceous nodes containing sclerites. Colonies erect, profusely branched (often dichotomous), planar, bushy or tangled, with branches sometimes modified into flat blades or hollow tubes. Branching predominantly from nodes in jointed forms. Polyps monomorphic, retractile into coenenchyme or calyces, distributed over all surfaces of branches, occasionally confined to terminal branchlets or arranged biserially. Axial sclerites needles, spindles or rods that may be stick-like, sinuous and branched, or cigar-shaped with or without a median girdle of tubercles. Polyp sclerites curved spindles, occasionally clubs, arranged as collaret and points; flattened, curved spindles or crescentic scales in tentacles. Sclerites of calyces and cortical coenenchyme tuberculate spindles or ovals, leaf clubs, foliate spheroids, double discs, birotulates, and capstans. Sclerites usually brightly colored. Azooxanthellate or (rarely) zooxanthellate. [modified from Alderslade 2006]

Distribution. Shallow to moderately deep water of the Indo-Pacific. One species in western Atlantic tropics.

Included genera. *Alertigorgia* Kükenthal, 1908; *Asperaxis* Alderslade, 2006; *Iciligorgia* Duchassaing, 1870; *Melithaea* Milne Edwards, 1857; *Solenocaulon* Gray, 1862

Remarks. This is another family in which an evolutionary progression in axial formation may be observed. *Alertigorgia, Iciligorgia* and *Solenocaulon* were all formerly assigned to Anthothelidae, united with other species in which a medulla of unfused sclerites is separated from the cortex by boundary canals. All three of these genera have axes similarly composed of densely packed sclerites in the form of needles and tuberculate rods or spindles. In *Asperaxis*, the axis consists of smooth stick-like sclerites and tuberculate rods and spindles that may be cemented together within a calcite matrix to form solid internodes. These internodes are separated by softer nodes in which the same sclerite forms are embedded in an organic rather than a calcified matrix. The transitions between internodal and nodal regions of the axis are not strongly demarcated and may be only partial (Alderslade 2006). The alternation of highly calcified nodes with flexible, proteinaceous internodes is further developed in *Melithaea*. In that genus, internodes are formed by smooth, cigar-shaped rods cemented together within a calcified matrix. The nodes, which consist of similar rods embedded within a proteinaceous matrix, are clearly delimited from the calcified internodes and are typically conspicuous (swollen and bulbous). *Asperaxis* represents a clear intermediate form between those genera with axes in which the sclerites are merely consolidated within a proteinaceous matrix to the highly calcified and fully jointed axis of *Melithaea*. The phylogenetic relationship between *Melithaea* and *Asperaxis*, whose morphology would appear to be a transitional state between the other genera, needs to be further clarified with phylogenomic data. Although the *mtMutS* phylogeny suggests that *Asperaxis* and *Melithaea* are not sister taxa within the clade (Fig. 2b), the topology of the *mtMutS* tree is likely influenced by the long branch leading to *Melithaea* (Felsenstein 1978), an artifact that is not observed in the phylogenomic analysis.

The genera assigned here to Melithaeidae have in common polyp sclerites arranged as a collaret and points, and curved, flattened scale-like sclerites in the tentacles that have been variously described as "foliaceous crescents" and "dragon-wings". Species within the large and diverse genus *Melithaea* exhibit a wide range of sclerite forms in the cortical coenenchyme, from tuberculate spindles to leaf-clubs and leafy spheroids. While *Melithaea* was formerly divided among five genera distinguished largely by the differences in these cortical sclerites, the presence of transitional forms and lack of evidence for phylogenetic distinctions among groups with different sclerite types has led to their synonymization within a single genus (Reijnen et al. 2014).

Family Nidaliidae Gray, 1869

Type genus. *Nidalia* Gray, 1835

Diagnosis. Octocorals without a consolidated skeletal axis, but with a rigid cylindrical stalk formed by dense layers of longitudinally disposed sclerites surrounding central canals. Colony growth form unbranched or occasionally furcate, with a distinct stalk and hemispherical to globular or palmate polyparium. Polyps monomorphic or dimorphic, retractile into large calyces, distributed over surface of polyparium, absent from stalk. Polyp sclerites curved spindles arranged in a strong collaret and points, with rods, scales and stellate forms in tentacles; short rods, narrow spindles, ovals or figure-eight scales in polyp body and pharynx. Sclerites of stalk are large, tuberculate spindles to ovals. Interior canal walls with shorter and thinner spindles. Azooxanthellate.

Distribution. Shallow to deep waters of tropical Indo-Pacific and Atlantic.

Included genera. **Agaricoides* Simpson, 1905; *Nidalia* Gray, 1835; **Nidaliopsis* Kükenthal, 1906; **Orlikia* Malyutin, 1993

Remarks. Three of the four genera we include in this family are very poorly known, lacking molecular data to confirm their placement. They all share with *Nidalia* an unbranched, stalked growth form with polyps restricted to a distinct polyparium; large spindles or spindle-like sclerites arranged longitudinally in the rigid stalk; and polyps with a strong collaret and points, retractile into large calyces. *Nidaliopsis* differs from the others in having dimorphic polyps, a trait that also varies among genera in some other families such as Sarcophytidae n. fam. Although *Stereacanthia* Thomson & Henderson, 1906 has also been included in Nidaliidae, it is even less well known than these other rare genera. In the absence of any recent documentation or modern descriptions of *Stereacanthia*, we leave this genus *incertae sedis*.

Family Rosgorgiidae n. fam.

Type genus. *Rosgorgia* López-González & Gili, 2001

Diagnosis. Octocorals with a skeletal axis of interlocked, partially fused sclerites embedded in a proteinaceous matrix. Axis (medulla) separated from cortical coenenchyme by ring of boundary canals. Colonies erect, sparsely branched. Polyps retractile, arranged on all sides of branches, occasionally densely crowded. Axial sclerites of two forms: long, smooth and sinuous needles that may fuse to form a network, and tuberculate spindles. Polyp sclerites tuberculate rods, sparsely distributed. Sclerites of cortex tuberculate spindles. Azooxanthellate.

Distribution. Deep water, Antarctic.

Included genera. *Rosgorgia* López-González & Gili, 2001

Remarks. The recently described genus *Rosgorgia* was originally assigned to Subergorgiidae, with which it shares an axis of smooth, sinuous sclerites that may be partially fused. It differs from that family, however, in also having tuberculate spindles incorporated in the axial medulla. The two genera belonging to Subergorgiidae are found in relatively shallow waters of the tropical Indo-Pacific, whereas *Rosgorgia* is known only from Antarctic deep waters. From the phylogenetic analysis it is clear that *Rosgorgia* does not belong to Subergorgiidae, nor is it closely related or morphologically similar to any other species with a skeletal axis. Its closest relative appears to be the southern African endemic *Malacacanthus*, with which it shares few morphological characters. Based on their unique morphological characters as well as their phylogenetic relationships, we consider it appropriate to assign both of those genera to monotypic families.

Family Siphonogorgiidae Kölliker, 1874

Type genus. *Siphonogorgia* Kölliker, 1874

Diagnosis. Octocorals without a consolidated skeletal axis, but with rigid branches formed by dense layers of longitudinally disposed sclerites surrounding central canals. Colony growth form erect or pendant, profusely branched, planar or bushy. Polyps monomorphic, retractile into low or large, shelf-like calyces, distributed evenly over all branches or restricted to terminal branchlets. Polyp sclerites tuberculate spindles arranged in a strong collaret and points, broad flattened rods and curved scales in tentacles, small rods in polyp body wall and pharynx. Sclerites of branch surfaces are large spindles with complex tubercles, arranged longitudinally, smaller spindles and rods in calyces. Interior canal walls with shorter and thinner spindles and rods. Sclerites usually brightly colored. Azooxanthellate.

Distribution. Shallow to moderately deep waters of Indo-Pacific and western Atlantic. One Mediterranean species.

Included genera. *Chironephthya* Studer, 1887; *Siphonogorgia* Kölliker, 1874

Remarks. These two genera have historically been classified together with *Nidalia*, another genus with rigid stalks formed by longitudinally disposed sclerites but with a typically unbranched growth form. While some phylogenetic analyses recover Siphonogorgiidae and *Nidalia* as sister taxa, that relationship is not strongly supported, and the branch lengths between them are long, suggesting an ancient divergence (Fig. 1). For those reasons, we restrict Nidaliidae to the unbranched taxa and resurrect Siphonogorgiidae for *Chironephthya* and *Siphonogorgia*. These two genera are distinguished primarily by the distribution of the polyps (on all branches vs. only on terminal branchlets) and the form of the calyces, which are prominent and shelf-like in *Chironephthya* but relatively small and inconspicuous in *Siphonogorgia*. Molecular phylogenetic analyses suggest, however, that the genera are paraphyletic with no clear genetic distinctions between species with different calyx morphologies (McFadden et al. 2014a) and should probably be synonymized.

[CLADE M3]

Family Acanthoaxiidae van Ofwegen & McFadden, 2010

Type genus. *Acanthoaxis* van Ofwegen & McFadden, 2010

Diagnosis. Octocorals with or without a skeletal axis. Axis, when present, entirely proteinaceous with a narrow, hollow, soft, cross-chambered central core, and prominent spines on its surface. Colonies membranous or erect, sparsely branched. Lacking sclerites in all parts of the colony. Azooxanthellate.

Distribution. Shallow to moderately deep waters of tropical Indo-Pacific and eastern Atlantic.

Included genera. *Acanthoaxis* van Ofwegen & McFadden, 2010; *Altumia* Benayahu, McFadden & Shoham, 2017

Remarks. Acanthoaxiidae was erected for the enigmatic *Acanthoaxis*, a species lacking sclerites and with an entirely proteinaceous skeletal axis. It shares with *Dendrobrachia* spines on the proteinaceous axis and a complete lack of sclerites, but the axis of *Acanthoaxis* has a hollow, cross-chambered core similar to that of the holaxonian gorgonians. Acanthoaxiidae is, however, phylogenetically distant from either *Dendrobrachia* or the holaxonian clade, and appears to represent an independent evolutionary gain of a proteinaceous axis (Quattrini et al. 2020). *Altumia* is the sister to *Acanthoaxis*, and shares with it a complete lack of sclerites. If *Altumia* were to secrete a proteinaceous axis the two genera would be indistinguishable—indeed, upon its discovery it was initially considered that *Acanthoaxis* might be a membranous *Altumia*-like octocoral overgrowing the proteinaceous skeleton of an antipatharian, a hypothesis that was ruled out by the presence of a hollow, cross-chambered core in the axis (van Ofwegen and McFadden 2010). We unite these two genera in a single family and consider that *Acanthoaxis* most likely evolved from an ancestor closely resembling *Altumia*. As discussed in the Remarks for Cerveridae n. fam., *Altumia* can be distinguished from the otherwise very similar genus *Cervera* by the lack of a periderm covering the stolons and polyps.

Family Alcyoniidae Lamouroux, 1812

Type genus. *Alcyonium* Linnaeus, 1758

Diagnosis. Octocorals without a skeletal axis, occasionally with coenenchyme subdivided into outer cortex and inner medulla. When present, medulla formed of tightly packed but not fused sclerites, separated from cortex by ring of boundary canals. Colonies membranous, lobate to digitate, arborescent with a single stalk, or bramble-like without a main stalk. Polyps monomorphic, rarely non-retractile but usually fully retractile into coenenchyme or into conspicuous calyces, distributed evenly throughout colony but sometimes arranged more densely at branch tips or clustered on lobes or branches arising from membranous regions. Polyp sclerites spindles and sticks usually arranged as collaret and points, but sometimes sparse or arranged only as points. Tentacle rachis usually heavily armed with spindles, rods or clubs that may be thorny or spatulate. Sclerites of coenenchyme typically arranged in two layers, outer (surface) layer of radiates, clubs or small spindles or tuberculate rods, interior layer of longer spindles or rods, sometimes sparse, or branched and densely packed to form medulla. Sclerites often brightly colored. Azooxanthellate.

Distribution. Cold temperate or deep water of northern and southern hemispheres.

Included genera. *Alcyonium* Linnaeus, 1758; *Anthothela* Verrill, 1879; **Bellonella* Gray, 1862; *Eleutherobia* Pütter, 1900; *Gersemia* von Marenzeller, 1878; *Hedera* Conti-Jerpe &

Freshwater, 2017; *Lateothela* Moore, Alderslade & Miller, 2017

Remarks. Alcyoniidae and *Alcyonium* have long been taxa defined largely by the absence of characters diagnostic of other families of Alcyoniina (i.e., soft corals that lack axes and have polyps arranged within a usually fleshy mass of coenenchyme). As a result, definitions of this family and genus continued to expand over time as taxa that could not be accommodated in other families were assigned to Alcyoniidae or *Alcyonium* by default. The polyphyletic nature of both of these higher taxa has been recognized since the earliest molecular phylogenetic studies (McFadden et al. 2006a), and several recent revisions have established new genera or families for some former *Alcyonium* and Alcyoniidae (Alderslade 2000; McFadden and van Ofwegen 2013, 2017). The close phylogenetic relationships among *Alcyonium sensu stricto* and several genera traditionally assigned to other families, notably *Gersemia* (Nephtheidae) and *Anthothela* (Anthothelidae) have also been revealed by previous molecular phylogenetic as well as morphological studies (McFadden and van Ofwegen 2013; Williams 2013; Moore et al. 2017).

Those genera that we have included within a monophyletic Alcyoniidae share a general similarity of sclerite form and arrangement. Most species have polyp sclerites arranged as a prominent collaret and points, and the tentacle rachis is heavily armed with spindles, rods or club-like sclerites. The sclerites of the coenenchyme are usually arranged in two distinct layers, with the inner layer consisting only of spindles or rods. In *Anthothela*, these two layers have become further developed into an inner medulla of densely packed, unfused sclerites separated from the outer cortex by boundary canals. Colony growth forms within the family range from thinly membranous to fleshy, lobate or digitate colonies. Transitions among these forms can be observed within genera and even in some species. For example, *Anthothela* includes species with membranous growth forms as well as species such as *A. grandiflora* (Sars, 1856) that start out growing as thin membranes (with no discernible medulla) before giving rise to profuse, tangled branches with a well-defined cortex and medulla (Moore et al. 2017). Similarly, *Alcyonium coralloides* (Pallas, 1766) often grows as a thin membrane from which fleshy lobes may arise at intervals (Groot and Weinberg 1982). Species in Alcyoniidae are united by a general similarity of sclerite form and arrangement rather than uniformity of colony growth form.

The genera included within Alcyoniidae are in need of further revision, in particular *Alcyonium*. That genus is polyphyletic with at least four distinct clades, each of which is sister to another genus in the family (Figs. 1, 2b). The poorly known *Eleutherobia* also comprises a heterogeneous mix of species characterized by different sclerite forms that may not represent a single genus (McFadden and van Ofwegen 2013). No molecular data are currently available for *Bellonella*, another poorly known genus. Although it shares many of the same characters and has been widely confused with both *Alcyonium* and *Eleutherobia*, molecular phylogenetic evidence is needed to confirm its assignment to this family.

Family Carijoidae n. fam.

Type genus. *Carijoa* Müller, 1867

Diagnosis. Octocorals without a skeletal axis, polyps connected basally by network of ribbon-like stolons or membranous expansions. Polyps monomorphic, retractile, distributed over surfaces of membranes or stolons. Axial polyps sometimes budding laterally to produce daughter polyps, giving rise to bushy colonies. Polyp sclerites absent or sparse, smooth rods that may be arranged as collaret and points. Sclerites of calyces and stolons are rods and spindles with sparse tubercular ornamentation, often branched and fusing into clumps, or irregular ovals and radiates with complex tubercular ornamentation. Azooxanthellate.

Distribution. Cosmopolitan in shallow to moderately deep water.

Included genera. *Carijoa* Müller, 1867; *Cryptophyton* Williams, 2000

Remarks. *Carijoa* and the superficially similar genus *Telesto* have been widely confused and synonymized throughout most of the 20th century (McFadden and van Ofwegen 2012a). Like most previous authors, Bayer (1961) treated them as a single genus, but he recognized differences between them and subsequently reinstated *Carijoa* without comment (Bayer 1981a, 1981b). Although the two genera have similar colony growth forms, their scleromes differ. Molecular phylogenetic analyses suggest that *Telesto*, which has irregularly oval sclerites with dense, complex tubercles, belongs to Tubiporidae, phylogenetically distant from *Carijoa*, whose sclerites are predominantly rods and slender spindles with sparse ornamentation. Within *Carijoa*, species differ widely in colony growth form. Some species produce bushy colonies by extensive budding of secondary polyps from very long axial polyps, while other species have low, encrusting growth forms in which most polyps arise directly from a network of stolons attached to the substrate (McFadden and van Ofwegen 2012a). Molecular phylogenetic analyses unite *Cryptophyton goddardi* Williams, 2000 in a clade with *Carijoa* (Figs. 1, 2b), a genus with which it has little in common other than an encrusting, stoloniferous growth form. The coenenchymal sclerites of *C. goddardi* are mostly irregular derivatives of radiates and ovals that are never fused, and the polyps lack sclerites. A recently described second species of *Cryptophyton* has exclusively small, stellate sclerites (Williams 2013), but its relationship to *C. goddardi* has not been confirmed with molecular data, and it is very possible that it belongs to a different genus and family.

Included in our phylogenomic analysis is an undescribed stoloniferous species (OCT078) that is sister to *Carijoa* and quite similar to it morphologically. OCT078 has polyps that are retractile into tall, clavate calyces that arise from a network of narrow stolons; smooth rods that are distributed sparsely in the anthocodia, arranged as a collaret and points; a dense layer of smooth rods, often forked and with sparse, simple ornamentation in the calyx, and tangled clumps of similar sclerites in the stolons. Unlike *Carijoa*, this species does not appear to bud secondary polyps.

Family Sarcophytidae n. fam.

Type genus. *Sarcophyton* Lesson, 1834

Diagnosis. Octocorals without a skeletal axis, colonies lobate, plate-like or capitate with a conspicuous stalk, not highly branched. Polyps monomorphic or dimorphic, fully retractile into thick coenenchyme. Sclerites of polyps rods, spindles, clubs and scales, often arranged as collaret and/or points but sometimes absent. Sclerites of colony surface clubs and spindles; spindles with complex tubercular ornamentation in interior coenenchyme. Zooxanthellate.

Distribution. Shallow waters of the tropical Indo-Pacific.

Included genera. *Anastromvos* Bryce & Wilson, 2019; *Lobophytum* von Marenzeller, 1886; *Lohowia* Alderslade, 2003; *Sarcophyton* Lesson, 1834; *Sclerophytum* Pratt, 1903

Remarks. The members of this family are among the most familiar, diverse and abundant species found on Indo-Pacific coral reefs. They have long been classified in Alcyoniidae along with temperate and cold-water species with which they share similar sclerites and massive, fleshy growth forms that are not highly branched. All species of Sarcophytidae are, however, zooxanthellate; their sclerites are never colored; and the sclerites of the colony surface are almost always well-formed clubs while the colony interior has only tuberculate spindles that may be very large. Four of the five genera in this family (*Anastromvos, Lobophytum, Lohowia, Sarcophyton*) have dimorphic polyps. These four taxa constitute a well-supported clade, although the morphological distinctions and phylogenetic relationships among them are unclear and require further study (McFadden et al. 2006b; Benayahu et al. 2018).

Within Sarcophytidae n. fam., the monomorphic genus *Sinularia* is sister to the dimorphic clade, with the notable exception of *Sinularia brassica* May, 1898. Both phylogenomic and molecular phylogenetic analyses confirm that *S. brassica* does not belong to Sarcophytidae n. fam. (Figs. 1, 2b), and we hereby assign it to a monotypic genus and family. *S. brassica* is, however, the type species of the genus *Sinularia* and as such it should retain that name. For the other 179 nominal species of *Sinularia* that belong to Sarcophytidae n. fam., we reinstate the genus *Sclerophytum* Pratt, 1903, a genus that was originally described to accommodate 13 species that Kükenthal (1906) subsequently synonymized with *Sinularia*. As Pratt (1903) did not assign a type species for *Sclerophytum*, we designate *Alcyonium polydactylum* Ehrenberg, 1834, the oldest of the species she included in *Sclerophytum*, as the type by subsequent designation.

[CLADE M4]

Family Aquaumbridae Breedy, van Ofwegen & Vargas, 2012

Type genus. *Aquaumbra* Breedy, van Ofwegen & Vargas, 2012

Diagnosis. Octocorals without a skeletal axis, colonies arborescent with branches or finger-like lobes arising from a distinct, basal stalk. Colonies soft and flabby, lobes transparent and jelly-like. Polyps monomorphic, non-retractile but contractile, distributed evenly over surfaces of lobes and smaller branches but absent from stalk. Polyp sclerites are rods, needles and curved spindles arranged as robust collaret and points. Sclerites absent from surface of lobes; spindles and rods distributed sparsely in inner coenenchyme. Sclerites colorless. Azooxanthellate. [modified from Breedy et al. 2012]

Distribution. Deep waters of the tropical Pacific and western Atlantic.

Included genera. *Aquaumbra* Breedy, van Ofwegen & Vargas, 2012; *Elbeenus* Alderslade, 2002

Remarks. Aquaumbridae was established for *Aquaumbra klapferi* Breedy, van Ofwegen & Vargas, 2012, an enigmatic soft coral from tropical deep waters with flabby, transparent lobes and no sclerites in the colony surface. Phylogenetic analysis of the mitochondrial *mtMutS* and *ND2* genes suggested it was not closely related to any other families of soft corals, and supported the description of a new family (Breedy et al. 2012). The phylogenomic analyses suggest that *Aquaumbra* is sister to *Elbeenus*, another enigmatic soft coral from moderately deep tropical waters that had been assigned to Alcyoniidae. Based on that sister relationship and the morphological characters it shares with *Aquaumbra* such as soft, transparent lobes, polyp sclerites in a strong collaret-and-points arrangement, and the absence of sclerites in the surface of the lobes, we transfer *Elbeenus* to Aquaumbridae.

Family Nephthyigorgiidae n. fam.

Type genus. *Nephthyigorgia* Kükenthal, 1910
Diagnosis. Octocorals without a skeletal axis, colonies lobate or digitate, often with a short stalk. Polyps monomorphic, retractile into large and conspicuous calyces, distributed evenly over surface of lobes but absent from stalk. Sclerites of polyps are curved spindles arranged as prominent collaret and points. Sclerites of calyces and coenenchyme surface are large spindles with complex tubercles, arranged longitudinally in calyces and forming dense layer on colony surface; sparse in colony interior. Sclerites often colored. Azooxanthellate. [modified from Fabricius and Alderslade 2001]
Distribution. Shallow to moderately deep waters of the tropical Indo-Pacific.
Included genera. *Nephthyigorgia* Kükenthal, 1910
Remarks. Kükenthal (1910) classified *Nephthyigorgia* in Siphonogorgiidae along with *Siphonogorgia* and *Chironephthya*, taxa with which it shares prominent calyces and large spindles arranged densely and mostly longitudinally in the colony surface, giving the colonies a rigid exterior. Utinomi (1958) suppressed Siphonogorgiidae, citing the precedence of Nidaliidae, and assigned *Nephthyigorgia* to subfamily Siphonogorgiinae Kölliker, 1874. Alderslade (2002) predicted that Nidaliidae would be found to be polyphyletic, and suggested that *Nephthyigorgia* and other non-gorgonian-like genera such as *Nidalia* might be better placed in Alcyoniidae. He also noted similarities between *Nephthyigorgia* and *Elbeenus*, remarking that the latter, which he placed in Alcyoniidae, would certainly not fit in Nidaliidae. The phylogenomic analyses do group *Nephthyigorgia* and *Elbeenus* together in clade M4, but they are not sister taxa (Fig. 1). Although they share similar sclerite forms and have polyp sclerites arranged as collaret and points, *Nephthyigorgia* differs considerably from both *Elbeenus* and *Aquaumbra* in having a dense layer of spindles on the colony surface with only sparse sclerites in the colony interior. In contrast, the other two genera lack sclerites in the colony surface except in the stalk (*Elbeenus*); consequently, colonies of *Elbeenus* and *Aquaumbra* are soft and flabby, whereas those of *Nephthyigorgia* are stiff and brittle. Considering these morphological differences and the phylogenetic relationships among the genera, we assign *Nephthyigorgia* to a new, monotypic family.

Family Sinulariidae new fam.

Type genus. *Sinularia* May, 1898
Diagnosis. Octocorals without a skeletal axis, colonies encrusting or with lobes, marginal folds or flat leaves arising from a short stalk, often cup- or funnel-shaped. Polyps monomorphic, retractile, distributed evenly over surface of polyparium, absent from stalk. Polyps with small rods and club-like sclerites, scales in tentacles. Sclerites of colony surface are clubs with very broad heads, typically subdivided into 2-3 toothed prominences; sclerites of colony interior are large spindles with complex tubercles. Zooxanthellate.
Distribution. Shallow waters of the tropical Indo-Pacific.
Included genera. *Sinularia* May, 1898
Remarks. Molecular phylogenetic and phylogenomic analyses have revealed that *Sinularia brassica* May, 1898 does not belong to a clade with other species of *Sinularia*, or even to family Sarcophytidae n. fam. (Figs. 1, 2b). It differs from all members of that family in the form of the club sclerites found in the colony surface, which have very broad heads

that are usually subdivided into two or three distinct prominences, and in having broad, flat scales in the tentacles. The phylogenetic analyses suggest that this species belongs to clade M4 where it is sister to *Nephthyigorgia*, a taxon with which it has little in common morphologically. Accordingly, we place each of those taxa in new, monotypic families, establishing Sinulariidae to accommodate *Sinularia brassica*.

Although the morphologically similar *Sinularia dura* (Pratt, 1903) has been synonymized with *S. brassica* (Benayahu et al. 1995), single-locus molecular studies have revealed genetic variation that suggests *dura* may be a valid species (McFadden et al. 2014a) and that there may be additional cryptic species within the clade.

[CLADE M5]

Family Acrophytidae McFadden & van Ofwegen, 2017

Type genus. *Acrophytum* Hickson, 1900

Diagnosis. Octocorals without a skeletal axis, colonies digitiform or clavate with distinct stalk and polyparium. Polyps monomorphic or dimorphic, retractile, distributed evenly over surface of polyparium, absent from stalk. Polyps with few or no sclerites. Sclerites of colony surface predominantly large spindles and clubs arranged longitudinally in stalk, often forming palisade-like structure around base of polyp. Interior sclerites, if present, of same form as in stalk surface. Colonies often brightly colored in life, losing color in ethanol. Sclerites colorless. Azooxanthellate. [modified from McFadden and van Ofwegen 2017]

Distribution. Endemic to cold temperate Agulhas Bioregion, southern Africa.

Included genera. *Acrophytum* Hickson, 1900; *Lampophyton* Williams, 2000; *Pieterfaurea* Verseveldt & Bayer, 1988

Remarks. Acrophytidae was established recently for several genera endemic to the cold-temperate waters of southern Africa that had previously been included in Alcyoniidae and Nidaliidae. Phylogenetically they are closer to Nephtheidae than to either of those families.

Family Corymbophytidae McFadden & van Ofwegen, 2017

Type genus. *Corymbophyton* McFadden & van Ofwegen, 2017

Diagnosis. Octocorals without a skeletal axis, colonies of small clusters of polyps arising from stolon-like basal membrane. Polyps monomorphic, fused to one another only along proximal half of their length. Sclerites are rods, spindles and bent clubs. Azooxanthellate. [modified from McFadden and van Ofwegen 2017]

Distribution. Endemic to cold temperate Agulhas Bioregion, southern Africa.

Included genera. *Corymbophyton* McFadden & van Ofwegen, 2017

Remarks. Corymbophytidae was established for *Corymbophyton bruuni* (Bayer, 1995), a species endemic to South Africa that was originally assigned to the genus *Protodendron* and family Alcyoniidae. It shares with that genus an unusual growth form in which clusters of polyps that are fused proximally arise from a stolon or membrane. The sclerites of the two genera are, however, quite different. Corymbophytidae is one of four families of southern African endemics, most of which had once been considered to belong to Alcyoniidae. Although these four families form a monophyletic clade (Fig. 1), they share few morphological characters that would unite them in a single family, hence we have made the decision to maintain them for now as separate families as originally proposed (McFadden and van Ofwegen 2017).

Family Capnellidae n. fam.

Type genus. *Capnella* Gray, 1869
Diagnosis. Octocorals without a skeletal axis, colonies arborescent or bushy, with distinct stalk. Polyps arising from branchlets, lobes or catkins, never from main branches or stalk. Polyps monomorphic, non-retractile but contractile, cylindrical to clavate and typically curving inwards. Polyp sclerites in the form of spindles and rods with complex tubercles, unilaterally spinose spindles ("caterpillars"), thorny clubs and leaf clubs. Sclerites of stalk surface and interior are radiates, leaf capstans, spheroids and irregular forms with dense tubercular ornamentation. Azooxanthellate or zooxanthellate.
Distribution. Cosmopolitan in shallow to deep water.
Included genera. *Capnella* Gray, 1869; *Drifa* Danielssen, 1887; *Duva* Koren & Danielssen, 1883; *Eunephthya* Verrill, 1869; *Pseudodrifa* Utinomi, 1961
Remarks. The genera in this family were all previously assigned to Nephtheidae. They differ from most genera in that family by lacking a supporting bundle of sclerites and having unilaterally spinose spindles ("caterpillars") and leaf clubs in the polyps. They are predominantly azooxanthellate and found in cold or deep water at high latitudes, although the zooxanthellate tropical genus *Capnella* is an exception. The northern genera *Drifa*, *Duva,* and *Pseudodrifa* appear to have a paraphyletic relationship and should perhaps be reassigned to a single genus (Fig. 1). In addition, limited molecular phylogenetic data suggest that temperate species from the southern hemisphere that are currently assigned to *Capnella* may belong to a separate genus (McFadden and van Ofwegen 2012b).

Family Leptophytidae McFadden & van Ofwegen, 2017

Type genus. *Leptophyton* van Ofwegen & Schleyer, 1997
Diagnosis. Octocorals without a skeletal axis, colonies encrusting or lobate. Polyps monomorphic, retractile, distributed over entire surface of lobes. Polyps usually (but not always) with sclerites in the tentacles. Sclerites include radiates, spheroids, spindles, rods and club-like forms. Sclerites of colony interior, if present, of same forms as those in colony surface and polyps, no distinction between surface layer and interior. Colonies often brightly colored in life, losing color in ethanol. Sclerites colorless. Azooxanthellate.
Distribution. Endemic to cold temperate Agulhas Bioregion, southern Africa.
Included genera. *Circularius* McFadden & van Ofwegen, 2017; *Leptophyton* van Ofwegen & Schleyer, 1997; *Porphyrophyton* McFadden & van Ofwegen, 2017; *Tenerodus* McFadden & van Ofwegen, 2017
Remarks. Leptophytidae includes several genera of southern African endemics previously assigned to Alcyoniidae and Nephtheidae. Although they are united in a clade with the southern African endemics Acrophytidae and Corymbophytidae, they do not share the colony or sclerite forms characteristic of either of those families and also differ from them in having highly rearranged mitochondrial genomes (McFadden and van Ofwegen 2017).

Family Nephtheidae Gray, 1862

Type genus. *Litophyton* Forskål, 1775 (= *Nephthea* Audouin, 1828)
Diagnosis. Octocorals without a skeletal axis, colonies arborescent, often highly branched or umbellate and with a conspicuous stalk. Polyps arise from terminal branchlets, rarely on main branches or stalk.

Polyps monomorphic, non-retractile, with weak or well-developed supporting bundle of sclerites. Polyp sclerites spindles and rods. Sclerites of branch and stalk surface are spindles and irregular radiate-like forms, few sclerites in colony interior. Sclerites often brightly colored. Zooxanthellate or azooxanthellate.

Distribution. Shallow to moderately deep waters of tropical Indo-Pacific.

Included genera. *Chromonephthea* van Ofwegen, 2005; *Coronephthya* Utinomi, 1966; *Dendronephthya* Kükenthal, 1905; *Litophyton* Forskål, 1775; *Neospongodes* Kükenthal, 1903; *Pacifiphyton* Williams, 1997; *Scleronephthya* Studer, 1887; *Stereonephthya* Kükenthal, 1905; *Umbellulifera* Thomson & Dean, 1931

Remarks. Phylogenetic analyses suggest that the genera of former nephtheids found in cold-temperate waters (Capnellidae n. fam.) belong to a separate clade that is not sister to the Indo-Pacific forms. The tropical genera *Lemnalia* and *Paralemnalia*, long considered to be Nephtheidae, are also phylogenetically distant despite the superficial similarity between the frequently confused genera *Lemnalia* and *Litophyton*. These genera all lack the supporting bundles of sclerites in the polyps that characterize the majority of taxa we retain in Nephtheidae *sensu stricto*. Molecular data are not currently available for three poorly known, monotypic genera that have been assigned to Nephtheidae (*Aspera* Dautova, 2018; *Chondronephthya* Utinomi, 1960; *Daniela* Koch, 1891). These genera all lack supporting bundles of sclerites and appear to be morphologically most similar to taxa such as *Gersemia* and *Eunephthya* that have been transferred to other families; we leave them *incertae sedis* until their phylogenetic relationships can be confirmed.

Family Paralcyoniidae Gray, 1869

Type genus. *Paralcyonium* Milne Edwards & Haime, 1850

Diagnosis. Octocorals without a skeletal axis, colonies with a cylindrical stalk into which a digitiform or branched polyparium can be fully retracted. Polyps monomorphic, distributed on surface and branches of retractile polyparium, absent from stalk. Polyp sclerites platelets, rods and spindles, sometimes forming a supporting bundle. Sclerites of stalk typically long spindles. Azooxanthellate.

Distribution. Cosmopolitan in shallow to moderately deep water.

Included genera. *Ceeceenus* van Ofwegen & Benayahu, 2006; *Dimorphophyton* Williams, 2000; *Maasella* Poche, 1914; **Nanalcyon* Imahara, 2013; *Paralcyonium* Milne Edwards & Haime, 1850; *Studeriotes* Thomson & Simpson, 1909

Remarks. The retractile polyparium is a unique morphological synapomorphy of this family, and all phylogenetic analyses to date have supported its monophyly. The only taxa with a similarly retractile polyparium are *Malacacanthus*, which has a hemispherical rather than digitiform or branched polyparium and lacks sclerites, and *Lanthanocephalus* Williams & Starmer, 2000, an enigmatic, monotypic southern African genus whose phylogenetic affinities remain unknown (McFadden and van Ofwegen 2017).

Family Pseudonephtheidae new fam.

Type genus. *Pseudonephthea* n. gen.

Diagnosis. Octocorals without a skeletal axis, colonies arborescent with profuse branches arising from a conspicuous stalk. Polyps arise from terminal branchlets, absent from main branches and stalk. Polyps monomorphic, non-retractile, supporting bundles absent. Polyp sclerites spindles and rods with high, tubercular ornamentation, arranged more-or-less longitudinally and not forming collaret and points. Sclerites of branch and stalk surface are spindles, small irregular capstans, and radiate-like forms; few sclerites in colony interior. Azooxanthellate.

Distribution. Endemic to cold temperate Agulhas Bioregion, southern Africa.

Included genera. *Pseudonephthea* n. gen.

Remarks. Verseveldt and Williams (1988) described *Litophyton liltvedi* from South Africa, assigning it to Nephtheidae based on its arborescent growth form with non-retractile polyps arranged on terminal branchlets, and to *Litophyton* because the polyps lack either supporting bundles or the leaf-clubs that characterize the otherwise similar genus *Eunephthya*. Williams and Lundsten (2009) subsequently transferred the species to *Gersemia*, a genus of azooxanthellate, cold-water taxa with capstan-like sclerites in the surface of the stalk. Phylogenomic analyses suggest, however, that *G. liltvedi* is not a member of the *Gersemia* clade or of the family Alcyoniidae to which *Gersemia* belongs. Instead, it is sister to several recently described families of former Nephtheidae and Alcyoniidae that are likewise endemic to the temperate Agulhas bioregion of southern Africa (McFadden and van Ofwegen 2017). Although it is tempting to assign all of these southern African endemic taxa to a single monophyletic family, as discussed by McFadden and van Ofwegen (2017) they are morphologically diverse and cannot be united by any one diagnostic character or suite of characters. We assign *G. liltvedi* to a new genus, *Pseudonephthea* n. gen., and monotypic family, Pseudonephtheidae n. fam., to reflect its unique phylogenetic position and morphology. The description of the genus is as for the family. Etymology: from the Greek *pseudo* (false) and *Nephthea*, reflecting the characters it shares with Nephtheidae and its historical misclassification in two different genera formerly belonging to that family.

Family Skamnariidae new fam.

Type genus. *Skamnarium* Alderslade, 2000

Diagnosis. Octocorals without a skeletal axis, colonies pedestal-shaped with a stump-like cylindrical stalk. Polyps monomorphic, retractile, distributed densely over flat summit of stalk. Polyps lacking sclerites. Sclerites of surface and interior of coenenchyme large rods arranged longitudinally. Zooxanthellate.

Distribution. Shallow water of southwestern Australia.

Included genera. *Skamnarium* Alderslade, 2000

Remarks. Alderslade (2000) established the monotypic genus *Skamnarium* for *Alcyonium complanatum* Verseveldt, 1977, an unusual species known only from shallow reef habitats in subtropical western Australia. Morphologically, *Skamnarium* most closely resembles the southern African endemic *Lampophyton* Williams, 2000. It shares with that genus an overall similarity of colony form, absence of sclerites in the polyps, and large sclerites arranged longitudinally in the stalk. As discussed by Alderslade (2000), however, the arrangement of sclerites in the stalk differs between the genera and *Skamnarium* is zooxanthellate whereas *Lampophyton* is not. Although *Skamnarium* is sister to a clade of families endemic to southern Africa, it is not sister to Acrophytidae, the family to which *Lampophyton* belongs (Fig. 1). We hereby remove *Skamnarium* from Alcyoniidae, a family to which it clearly does not belong, and establish a new, monotypic family for this unusual taxon.

Family Victorgorgiidae Moore, Alderslade & Miller, 2017

Type genus. *Victorgorgia* López-González & Briand, 2002

Diagnosis. Octocorals without a skeletal axis. Coenenchyme may be subdivided into outer cortex and inner medulla, with extensive boundary space between medulla and cortex, and large, obvious coelenteric canals in central medulla. Colonies with polyps connected basally by stolons or membranes, or erect, branched (sparse and irregular), more-or-less planar. Polyps monomorphic, retractile into calyces, distributed over all surfaces, crowded at branch tips. Polyp sclerites tuberculate sticks and spindles, arranged as robust collaret and points; "josephinae" clubs in tentacles. Sclerites of calyx, cortex and medulla mainly tuberculate sticks, spindles, clubs. Colonies brightly colored in life (typically magenta or purple), losing color in ethanol. Sclerites colorless. Azooxanthellate.

Distribution. Deep water of Atlantic and Pacific.

Included genera. *Trachythela* Verrill, 1922; *Victorgorgia* López-González & Briand, 2002

Remarks. Both phylogenomic (Fig. 1) and mitochondrial gene analyses (Moore et al. 2017) support the monophyly of a clade that includes the genus *Victorgorgia* as well as *Trachythela rudis* Verrill, 1922 and *Clavularia borealis* Koren & Danielssen, 1883. Those two membranous species share with *Victorgorgia* sclerites that are predominantly large, tuberculate spindles and a very well-developed polyp armature with a collaret and points of large, often bent spindles. Although each of the genera we include in Victorgorgiidae has diagnostic morphological characters, the characteristics of the family overlap considerably with Alcyoniidae. That family also includes genera that are primarily membranous and encrusting as well as ones that may produce branched colonies with a well-developed medulla and cortex separated by boundary canals. The two families would seem to be most readily separated by color: Victorgorgiidae are typically bright purple in life but with colorless sclerites, whereas Alcyoniidae are rarely purple but have brightly colored (usually red or yellow) sclerites. The alcyoniid genus *Hedera* is a notable exception.

[CLADE M6]

Family Subergorgiidae Gray, 1859

Type genus. *Subergorgia* Gray, 1857

Diagnosis. Octocorals with a skeletal axis of interlocked, partially fused sclerites embedded in a proteinaceous matrix. Axis (medulla) separated from cortical coenenchyme by ring of boundary canals. Colonies erect, branched (lateral to dichotomous or reticulate), planar. Polyps monomorphic, retractile, arranged on all or just two sides of branches. Axial sclerites long, smooth and sinuous, branching and fusing to form a network. Polyp sclerites flattened, curved spindles arranged as collaret and points or just points. Sclerites of cortex tuberculate spindles or ovals, small double heads, and double wheels. Azooxanthellate.

Distribution. Shallow to moderately deep waters of the tropical Indo-Pacific.

Included genera. *Annella* Gray, 1859; *Subergorgia* Gray, 1857

Remarks. The two subergorgiid genera, *Annella* and *Subergorgia*, are both on long branches in the phylogenomic (Fig. 1) and *mtMutS* (Fig. 2b) phylogenies. In phylogenetic analyses based on mitochondrial genes alone they rarely group together, perhaps as an artifact of long branch attraction with other taxa (Brockman and McFadden 2012). The phylogenomic analyses, however, recover 100% support for the sister relationship of these two taxa which share similar axial construction and have traditionally been classified together in Subergorgiidae.

[CLADE M7]

Family Cladiellidae n. fam.

Type genus. *Cladiella* Gray, 1869

Diagnosis. Octocorals without a skeletal axis, colonies lobate to digitate, lobes often subdivided but not highly branched. Polyps monomorphic, retractile or non-retractile but highly contractile, evenly distributed over lobe surfaces. Polyp sclerites minute discs, figure-eights or flattened rods. Sclerites of colony surface and coenenchyme double-heads, blunt spindles with conical protuberances, or minute figure-eights and granular rods. Some species may lack sclerites entirely. Zooxanthellate or (rarely) azooxanthellate.

Distribution. Shallow waters of the tropical Indo-Pacific.

Included genera. *Aldersladum* Benayahu & McFadden, 2011; *Cladiella* Gray, 1869; *Klyxum* Alderslade, 2000

Remarks. The taxa in this family, all formerly placed in Alcyoniidae, are united by the characteristic form of the polyp sclerites which are minute discs, often with a waist or depressions resembling a figure-eight. This clade is not closely related to Alcyoniidae, but its phylogenetic position within Malacalcyonacea is uncertain and somewhat unstable. Mitochondrial gene sequences and some phylogenomic analyses have placed Cladiellidae as sister to a clade of holaxonian gorgonians (McFadden et al. 2006a; 2021). Other phylogenomic analyses including the one presented here (Fig. 1) suggest instead that it is sister to the clade of soft corals that includes Xeniidae.

In addition to the three genera listed above, Cladiellidae also includes the species *Metalcyonium verseveldti* Benayahu, 1982. The genus *Metalcyonium* is invalid, however, as it has been synonymized with *Bellonella* Gray, 1862 (Verseveldt and Bayer 1988), a genus to which *M. verseveldti* clearly does not belong. Descriptions of a new genus to accommodate *M. verseveldti* and several related new species are in progress (McFadden et al., unpubl. data).

Family Coelogorgiidae Bourne, 1900

Type genus. *Coelogorgia* Milne Edwards, 1857

Diagnosis. Octocorals without a skeletal axis, with axial polyps arising from stolons attached to hard substrate. Axial polyps alternately bud secondary and tertiary (lateral) polyps, giving rise to highly branched, bushy colonies. Polyps monomorphic, non-retractile. Sclerites throughout colony are spindles with large complex tubercles often arranged in girdles, some granular scales in polyp tentacles. Zooxanthellate.

Distribution. Shallow waters of the tropical Indo-Pacific.

Included genera. *Coelogorgia* Milne Edwards, 1857

Remarks. Phylogenomic and most molecular phylogenetic analyses position *Coelogorgia* as the sister taxon to Xeniidae (Figs. 1, 2b). It shares few morphological characters with that family, however, and its unique growth form supports maintaining its long-time status as a monotypic family.

Family Lemnaliidae n. fam.

Type genus. *Lemnalia* Gray, 1868

Diagnosis. Octocorals without a skeletal axis, colonies membranous, digitiform or arborescent with conspicuous stalk. Polyps evenly distributed on membranes or on distal regions of branches or branchlets, never on stalk or base of colony. Polyps monomorphic, retractile or non-retractile but highly contractile. Polyp sclerites long spindles or sticks, lobate scales in tentacles. Sclerites of branch and stalk surface sticks and spindles, crescents, radiates. Zooxanthellate.

Distribution. Shallow waters of the tropical Indo-Pacific.

Included genera. *Lemnalia* Gray, 1868; *Paralemnalia* Kükenthal, 1913; *Rhytisma* Alderslade, 2000

Remarks. *Lemnalia* and *Paralemnalia* were historically included in Nephtheidae, but all molecular phylogenetic analyses have placed them in a separate clade far removed from that family (McFadden et al. 2006a). Although *Lemnalia* and *Litophyton* have very similar arborescent growth forms and share some sclerite forms, they can be distinguished by the long, thin sticks or spindles with fairly sparse tuberculation that are found in the colony interior, on the surface of the branches, and in the anthocodiae of *Lemnalia*. Although its encrusting colony form is very different from that of *Lemnalia* and *Paralemnalia, Rhytisma* (formerly assigned to Alcyoniidae) shares with those genera a sclerome that includes long spindles in the colony surface and interior, and scales in the tentacles.

Family Xeniidae Ehrenberg, 1828

Type genus. *Xenia* Lamarck, 1816

Diagnosis. Octocorals without a skeletal axis, colonies very soft and often slimy, stoloniferous to membranous, lobate, or upright with a cylindrical stalk, sometimes sparsely branched. Polyps monomorphic or dimorphic, evenly distributed or clustered on membranes or lobes, or restricted to dome-shaped polyparium at the distal end of a stalk. Polyps usually non-retractile and only slightly contractile, but occasionally highly contractile or (rarely) retractile. Sclerites minute corpuscular discs or flattened rods, tiny stellate bodies, or (rarely) spindles, highly variable in number and sometimes entirely absent. Zooxanthellate.

Distribution. Shallow waters of the tropical Indo-Pacific.

Included genera. *Anthelia* Lamarck, 1816; *Asterospicularia* Utinomi, 1951; **Bayerxenia* Alderslade, 2001; *Caementabunda* Benayahu, van Ofwegen & McFadden, 2018; *Conglomeratusclera* Benayahu, van Ofwegen & McFadden, 2018; *Ezziona* Alderslade & Janes, 2017; **Fasciclia* Janes, 2008; **Funginus* Tixier-Durivault, 1987; *Heteroxenia* Kölliker, 1874; **Ingotia* Alderslade, 2001; *Latissimia* Benayahu, Ekins & McFadden, 2022; **Orangaslia* Alderslade, 2001; *Ovabunda* Alderslade, 2001; *Protodendron* Thomson & Dean, 1931; *Quattuoria* Benayahu & McFadden, 2022; *Sansibia* Alderslade, 2000; *Sarcothelia* Verrill, 1928; *Sympodium* Ehrenberg, 1834; *Unomia* Benayahu, van Ofwegen, Allais & McFadden, 2021; *Xenia* Lamarck, 1816; *Yamazatum* Benayahu, 2010

Remarks. A majority of the taxa comprising Xeniidae are united by the characteristic form of the sclerites, which are typically minute (<0.03 mm) corpuscle-like discs distributed in all parts of the colony. Lacking any rigid structures, xeniids typically form small colonies that are very soft. Exceptions include *Anthelia* and *Fasciclia* in which the sclerites are small rods, and *Asterospicularia*, which has small stellate sclerites in addition to the typical minute discs that are restricted to the polyps. The latter genus was originally placed in a monotypic family, but all molecular analyses have supported its position within Xeniidae (McFadden et al. 2006a, 2014b; Fig.1). *Protodendron*, formerly assigned to Alcyoniidae, has a growth form in which only the proximal halves of polyps are joined together in clusters that arise from a membrane, not dissimilar to that of *Fasciclia*. Its sclerites, however, are long spindles, sometimes bent, with small, curved rods in the tentacles (Bayer 1995). These sclerites are atypical of Xeniidae and more closely resemble those of Lemnaliidae and Coelogorgiidae, the sister clades to Xeniidae. Phylogenomic and molecular phylogenetic analyses, however, place *Protodendron* well within Xeniidae.

[CLADE M8]

Family Anthogorgiidae new fam.

Type genus. *Anthogorgia* Verrill, 1868

Diagnosis. Octocorals with a proteinaceous skeletal axis. Axis hollow with wide cross-chambered central core; coenenchyme relatively thick. Colonies erect, profusely branched, forming fans with or without anastomoses, planar. Polyps monomorphic, non-retractile, tall and cylindrical or short and dome-shaped, distributed evenly over branch surfaces; heavily armored polyps may be mistaken for calyces. Polyp sclerites blunt spindles with large tubercles, arranged in chevrons; tentacles with small, bent rods. Sclerites of coenenchyme blunt spindles similar to those of polyps, small capstans, and ovals. Sclerites may be colored. Azooxanthellate. [modified from Fabricius and Alderslade 2001]

Distribution. Shallow to moderately deep waters of the tropical Indo-Pacific.

Included genera. *Anthogorgia* Verrill, 1868; *Muricella* Verrill, 1869

Remarks. *Anthogorgia* and *Muricella* are two very similar genera of sea fans that have been differentiated primarily based on differences in the height and shape of the non-retractile polyps, size of the spindles in the coenenchyme, and the degree of anastomosis of the branches. Both are poorly known, in part because they have historically been confused with other genera such as *Astrogorgia* and *Acanthomuricea* (Grasshoff 1999). They have most recently been classified in Acanthogorgiidae along with other taxa that have conspicuous, non-retractile polyps and sclerites that are predominantly tuberculate spindles. Molecular phylogenetic and phylogenomic analyses place *Acanthogorgia* in Paramuriceidae, a group with which it shares very thin coenenchyme and the presence (in some species) of thornscales or their derivatives. In contrast, *Anthogorgia* and *Muricella* lack thornscales and have relatively thick coenenchyme. With *Scleracis*, they form a sister clade to Plexaurellidae and Gorgoniidae. They differ from those two families, however, in axis construction and sclerome, lacking the radiates and small spindle-derivatives of Gorgoniidae and the butterfly sclerites of Plexaurellidae. Based on those differences and their phylogenetic position, we propose a new family, Anthogorgiidae, to accommodate these two genera. Anthogorgiidae is most similar morphologically to Astrogorgiidae n. fam., but in that family the polyps are retractile into true calyces.

The *mtMutS* phylogeny (Fig. 2b) suggests that *Cyclomuricea*, another genus formerly placed in Acanthogorgiidae, may also belong to Anthogorgiidae. No phylogenomic data are available for that genus, however, and its apparent position as sister to *Anthogorgia* and *Muricella* could be an artifact of long branch attraction, as the latter genera have been shown to have accelerated rates of mitochondrial gene evolution (Muthye et al. 2022). For now, we leave *Cyclomuricea* as *incertae sedis*.

Family Astrogorgiidae n. fam.

Type genus. *Astrogorgia* Verrill, 1886

Diagnosis. Octocorals with a proteinaceous skeletal axis. Axis hollow with cross-chambered central core. Colonies erect, branched (irregular lateral to form open fans, branches not anastomosing), planar. Polyps monomorphic, retractile into low or tall calyces, distributed evenly over branch surfaces or arranged biserially down opposite margins of branches. Polyp sclerites spindles and rods arranged in eight longitudinal groups but not as collaret or points; short rods and granular scales in tentacles. Sclerites of calyces and outer coenenchymal layer exclusively spindles; inner coenenchyme with shorter spindles or rods, often capstan-like. Azooxanthellate. [modified from Fabricius and Alderslade 2001]

Distribution. Shallow waters of the tropical Indo-Pacific.

Included genera. **Acanthomuricea* Hentschel, 1903; *Anthoplexaura* Kükenthal, 1908; *Astrogorgia* Verrill, 1886

Remarks. *Astrogorgia* has previously been classified in Plexauridae (Stenogorgiinae) Bayer, 1981, which superseded Paramuriceidae Bayer, 1956. It differs from Paramuriceidae (as defined herein) in lacking thornscales or their derivatives, and from Plexauridae in having thin coenenchyme, only spindles in the calyces and colony surface, and in the arrangement of sclerites in the polyps that do not form a typical collaret and points. Both molecular phylogenetic and phylogenomic analyses separate *Astrogorgia* from all other clades of holaxonians, and instead unite it in a clade with *Taiaroa* Bayer & Muzik, 1976 and *Keroeides* Wright & Studer, 1887 (Figs. 1, 2b). Although *Keroeides* has a colony growth form that is similar to that of *Astrogorgia*, it has a unique skeletal construction in which sclerites are embedded in a hollow, cross-chambered axis of gorgonin. *Taiaroa* lacks an axis and has solitary polyps. Based on these morphological differences, we consider it appropriate to maintain each of these genera in separate families, and establish a new family, Astrogorgiidae, for *Astrogorgia*. Although no molecular data are available to confirm the phylogenetic placement of *Acanthomuricea*, it is morphologically nearly identical to *Astrogorgia*, distinguished only by the size of the largest spindles (Grasshoff 1999). The two genera are considered by some authors to be synonymous (Fabricius and Alderslade 2001), and we assume they will be found to be close phylogenetically.

mtMutS sequences that are available for the monotypic genus *Anthoplexaura* Kükenthal, 1908 suggest a very close phylogenetic relationship between that genus and *Astrogorgia* (Fig. 2b). *Anthoplexaura dimorpha* Kükenthal, 1908 is a poorly known species originally described as having thick coenenchyme and large, dimorphic polyps that lack sclerites (Kükenthal 1908), characters very different from those of *Astrogorgia*. Fabricius and Alderslade (2001) assert, however, that the report of dimorphic polyps in *A. dimorpha* was erroneous, and suggest it is actually a species of *Astrogorgia* that is parasitized by a hydrozoan. The identity of the *mtMutS* sequence that is available for *A. dimorpha* cannot be verified as it appears never to have been formally published, and the existence or location of voucher material is unknown. Nonetheless, the similarity of this sequence to that of *Astrogorgia* supports the suggestion that *Anthoplexaura* is not a valid genus.

Family Discophytidae n. fam.

Type genus. *Discophyton* McFadden & Hochberg, 2003

Diagnosis. Octocorals without a skeletal axis, colonies encrusting, membranous. Polyps monomorphic, retractile, distributed evenly within thin, membranous coenenchyme. Polyps lacking sclerites. Sclerites of coenenchyme are irregular forms derived from radiates. Azooxanthellate.

Distribution. Shallow, cold waters of the northeastern Pacific.

Included genera. *Discophyton* McFadden & Hochberg, 2003

Remarks. Although it was originally assigned to *Alcyonium* and Alcyoniidae, the enigmatic species *Discophyton rudyi* (Verseveldt & van Ofwegen, 1992) does not appear to be closely related to anything else in the octocoral tree. Like *Thrombophyton*, it falls within the clade of holaxonian gorgonians (M8) and may be a species that has secondarily lost an axis and reverted to a simple, membranous growth form. The two genera are not, however, closely related. There is strong support for *Thrombophyton* belonging to Paramuriceidae, whereas *Discophyton* occupies a relatively long branch in the phylogenomic tree outside of any of the major subclades that comprise clade M8 (Fig. 1). Morphologically, *Discophyton* is most similar to *Incrustatus* (Incrustatidae n. fam.) and *Cryptophyton* (Carijoidae n. fam.), both of which belong to clades whose members have exclusively stoloniferous or membranous growth forms. The form of asexual reproduction exhibited by *Discophyton*, in which colonies undergo continual, programmed fission to form monoclonal aggregations of uniformly-sized, small colonies (McFadden 1991), is unique among octocorals.

Family Eunicellidae new fam.

Type genus. *Eunicella* Verrill, 1869

Diagnosis. Octocorals with or without a skeletal axis. If present, axis proteinaceous with hollow, cross-chambered central core; no mineralization. Colonies without an axis encrusting or lobate. Colonies with an axis erect, sparsely branched, planar. Polyps monomorphic, retractile into coenenchyme or prominent calyces, distributed evenly over surfaces of lobes or branches. Polyp sclerites sparse tuberculate rods or spindles that may be arranged in chevrons to form points. Sclerites of coenenchyme are spindles with prominent girdles of tubercles, ovals, double-heads, or rods. Outer layer of coenenchyme (if present) with clubs or balloon-clubs. Azooxanthellate (rarely zooxanthellate).

Distribution. Shallow to moderately deep waters of eastern Atlantic and Mediterranean.

Included genera. *Complexum* van Ofwegen, Aurelle & Sartoretto, 2014; *Eunicella* Verrill, 1869

Remarks. The genus *Eunicella* was historically classified in Plexauridae (Verrill 1869; Kükenthal 1919; Bayer 1956) but later moved to Gorgoniidae (Bayer 1981a), a family with which it shares small (<0.3 mm) spindles with prominent girdles of tubercles in the inner layer of the coenenchyme. The balloon-club sclerites found in the outer coenenchyme are unique to this genus and distinguish it from all other genera. Bayer (1981a) recognized three distinct types of balloon-clubs, however, which he separated into species-groups in his key. The most common form of balloon-clubs, represented in the type species *E. verrucosa* (Pallas, 1766), are described as having "heads...with low, smooth warts but no whorl of points" (Bayer 1981a). In contrast, three southern African species have "balloon-clubs with 2 or 3 whorls of upwardly directed points" (Bayer 1981a) that have been referred to as "crowns" (Williams 1992). Molecular data from mitochondrial genes suggest that these southern African species belong to a subclade that is nested within the larger clade of species whose balloon-clubs lack crowns (McFadden, unpubl. data). Bayer's third group includes two deep-water species with "head of balloon-clubs smooth, tear-drop-shaped, more-or-less 3-flanged" (Bayer 1981a). Phylogenetic and phylogenomic analyses place those species in an entirely different clade, and for them we describe a new genus (see Pterogorgiidae n. fam.).

The genus *Complexum*, described

recently to accommodate former *Alcyonium* species from the eastern Atlantic, is a close sister taxon to *Eunicella* in molecular phylogenies (van Ofwegen et al. 2014; Figs. 1, 2b). These two genera share little in common morphologically other than a general similarity of the form of the spindles that are found in the inner coenenchyme; these spindles are, however, somewhat larger in *Complexum* than in *Eunicella*. Based on its phylogenetic position within clade M8, *Complexum* is another genus that would appear to be a gorgonian that has lost its skeletal axis and reverted to a membranous or lobate growth form. Although it would perhaps be more appropriate to assign *Complexum* to a separate family, we place it in Eunicellidae to reflect the well-supported sister relationship between these morphologically disparate genera. They have similar geographical distributions, found primarily in the eastern Atlantic along the African coast.

Family Euplexauridae new fam.

Type genus. *Euplexaura* Verrill, 1869

Diagnosis. Octocorals with a proteinaceous skeletal axis. Axis hollow with wide, cross-chambered central core; coenenchyme thick. Colonies erect, branched (irregular lateral to form open fans, branches not anastomosing, sometimes whip-like), usually planar, sometimes bushy. Polyps monomorphic, retractile into coenenchyme or (rarely) prominent calyces, distributed evenly over branch surfaces. Polyp sclerites absent or large spindles, sometimes arranged as strong collaret and points or only points. Sclerites of calyces and outer coenenchyme ovals or spheroids, occasionally plump spindles, with dense, complex tubercles; interior coenenchyme with rods or small spindles with simple tubercles. Azooxanthellate. [modified from Matsumoto and van Ofwegen 2016]

Distribution. Shallow waters of the tropical Indo-Pacific.

Included genera. *Euplexaura* Verrill, 1869

Remarks. Phylogenetic and phylogenomic analyses support the genus *Euplexaura* as the sister taxon to Paramuriceidae (Figs. 1, 2b). Because it does not share the defining characteristics of that family (e.g., thornscales, thin coenenchyme), it seems more appropriate to describe a new, monotypic family for this genus than to try to accommodate it in Paramuriceidae. Indeed, Bayer (1956) did not include *Euplexaura* in Paramuriceidae or in Plexauridae (Stenogorgiinae) in his later revision (Bayer 1981a). It has historically been classified in Plexauridae (Kükenthal 1919; Bayer 1956), a family whose member genera are now recognized to belong to five different phylogenetic clades. While the colony growth form and thick branches of *Euplexaura* are similar to some of the genera we retain in Plexauridae *sensu stricto*, its coenenchymal sclerites are unlike those of that family, and it is not close to them phylogenetically.

Family Gorgoniidae Lamouroux, 1812

Type genus. *Gorgonia* Linnaeus, 1758

Diagnosis. Octocorals with a proteinaceous skeletal axis that may contain non-scleritic carbonate hydroxylapatite (CHAp). Axis hollow, with narrow cross-chambered central core; cortex dense with little or no loculation. Colonies erect, branched (dichotomous, pinnate, reticulate, or forming flattened, leaf-like fronds), planar or bushy, often anchored by a strongly calcified holdfast. Polyps monomorphic, retractile into coenenchyme or low mounds, distributed over all surfaces or arranged biserially on branches. Polyp sclerites flattened rods with smooth, scalloped, indented or lobed margins, arranged as sparse points with or without collaret. Sclerites of coenenchyme are radiates, small (<0.3 mm) spindles with complex tubercles often arranged in regular girdles, and their derivatives (e.g., scaphoids, double-discs, ovals). Sclerites often brightly colored. Zooxanthellate or azooxanthellate.

Distribution. Shallow to moderately deep waters of the Atlantic and eastern Pacific; one genus in central Indo-Pacific.

Included genera. *Adelogorgia* Bayer, 1958; *Antillogorgia* Bayer, 1958; *Callistephanus* Wright & Studer, 1889; *Chromoplexaura* Williams, 2013; *Eugorgia* Verrill, 1868; *Gorgonia* Linnaeus, 1758; *Leptogorgia* Milne Edwards, 1857; **Olindagorgia* Bayer, 1981; *Pacifigorgia* Bayer, 1951; **Phycogorgia* Milne Edwards & Haime, 1850; *Phyllogorgia* Milne Edwards, 1857; *Psammogorgia* Verrill, 1868; *Pseudopterogorgia* Kükenthal, 1919

Remarks. The genera referred to previously as the "monophyletic gorgoniid clade" (MGC) (Cordeiro et al. 2021) all share a number of distinctive morphological features. These include a narrow cross-chambered core and the mineral carbonate hydroxylapatite (CHAp) embedded in the proteinaceous axis; coenenchymal sclerites that are predominantly small (<0.3 mm) spindles, radiates, and their derivatives such as scaphoids and double-discs; and polyp armature consisting of small rods arranged in points with or without a sparse collaret. Molecular phylogenetic and phylogenomic analyses suggest that the MGC genera belong to a larger clade that also includes *Adelogorgia, Psammogorgia, Chromoplexaura* and some species of *Swiftia*, and we broaden the diagnosis of the family to include those taxa. *Adelogorgia*, originally assigned to Gorgoniidae by Bayer (1958) but later moved by him without comment to Plexauridae (Bayer 1981a), has the same basic sclerite forms as *Eugorgia* but with the addition of leaf clubs around the polyp apertures (Breedy and Guzman 2018). It differs from the MGC genera in having a wide, cross-chambered core and apparently also lacking any mineralization of the axis (Breedy and Guzman 2018). *Psammogorgia* also lacks mineralization of the axis and differs from other gorgoniids in having large spindles arranged as a robust collaret and points, and wart clubs in the coenenchyme along with small, irregular spindles and radiates (Breedy and Guzman 2020). The coenenchymal sclerites of *Chromoplexaura* are predominantly radiates and small, plump spindles to ovals, <0.25 mm in length (Williams 2013), and the polyps have tuberculate spindles and rods arranged in points. Notably, Nutting (1909) originally misidentified *Chromoplexaura* (=*Euplexaura*) *marki* as a variant of *Psammogorgia arbuscula* (Kükenthal, 1913). *Chromoplexaura* is also described as being similar to some species of *Swiftia* (Williams 2013; Williams and Breedy 2019).

The genus *Swiftia* Duchassaing & Michelotti, 1864 was assigned to Paramuriceidae by Bayer (1956), and his later key includes the accompanying note "This genus is usually assigned to the family Gorgoniidae... but it seems to have more in common with the paramuriceids and plexaurids than with the gorgoniids" (Bayer 1961). Grasshoff (1977) noted that the position of the genus lies somewhere between Paramuriceidae, Plexauridae, and Gorgoniidae, and recognized three distinct species groups. As revealed clearly by both molecular phylogenetic (Frometa et al. 2021) and phylogenomic analyses (Fig. 1), *Swiftia* is polyphyletic; species attributed to that genus appear in three distinct clades, a situation that has undoubtedly led to the confusion surrounding its taxonomic placement. Specimens identified as *S. exserta* Duchassaing & Michelotti, 1864 (type species of *Swiftia*; Grasshoff's (1977) group 1) belong to Plexauridae *sensu stricto,* while *S. casta* (Verrill, 1883) (type species of *Stenogorgia*

Verrill, 1883) falls in Pterogorgiidae n. fam. The species that belong to the Gorgoniidae clade have been identified as *S. pallida* Madsen, 1970 (Fig. 1), as well as *S. pacifica* (Nutting, 1912), *S. spauldingi* (Nutting, 1909), *S. kofoidi* (Nutting, 1909) and *S. simplex* (Nutting, 1909) (Frometa et al. 2021). These correspond to Grasshoff's (1977) group 2, which included *S. pallida* as well as *S. koreni* (Wright & Studer, 1889) and *S. rosea* (Grieg, 1887), three species that Madsen (1970) considered to be synonyms. *S. koreni* is the type of *Callistephanus* Wright & Studer, 1889, to which we suggest all of the *Swiftia* species belonging to the Gorgoniidae clade should be reassigned. These species have in common tall, conical calyces that are usually arranged alternately on opposite margins of a branch, and sclerites in the coenenchyme that are predominantly radiates.

A recently published molecular phylogenetic analysis based on *mtMutS*, *COI*, and *28S rDNA* suggests that some species of *Thesea* Duchassaing & Michelotti, 1860 may also belong to Gorgoniidae (Carpinelli et al. 2022). Like *Swiftia*, however, this genus appears to be polyphyletic, with other species belonging to Paramuriceidae or, possibly, Euplexauridae n. fam. We leave *Thesea* as *incertae sedis* until phylogenomic and further morphological studies can clarify the defining characters and phylogenetic relationships of the disparate clades it appears to encompass.

Family Isididae Lamouroux, 1812

Type genus. *Isis* Linnaeus, 1758

Diagnosis. Octocorals with a skeletal axis, entirely proteinaceous or jointed with solid calcareous internodes alternating with proteinaceous nodes that lack sclerites. Colonies erect, branched (branches usually short but sometimes long and whip-like or modified into flat blades), planar or bushy. Polyps monomorphic, retractile into thick coenenchyme, densely distributed over branch surfaces. Polyp sclerites absent or sparse, small, flattened rods arranged longitudinally at bases of tentacles. Sclerites of coenenchyme surface are clubs with a whorl of three large warts surrounding a terminal wart; inner layer of coenenchyme with spindles with large tubercles arranged in girdles, also ovals, radiates, and occasionally long rods. Zooxanthellate.

Distribution. Shallow waters of the tropical Indo-Pacific.

Included genera. *Hicksonella* Nutting, 1910; *Isis* Linnaeus, 1758; *Rumphella* Bayer, 1955

Remarks. *Isis hippuris*, type species of Isididae, has long been classified with the other bamboo corals in clade S2, placed in a subfamily (Isidinae) distinct from those exclusively deep-water taxa. Despite the superficial similarity of their jointed skeletal axes, molecular phylogenetic and phylogenomic analyses indicate that *Isis* does not belong to Scleralcyonacea but instead to Malacalcyonacea where it is sister to *Rumphella* and *Hicksonella*, two genera that have been considered to belong to Gorgoniidae (Fig. 1). Bayer (1955) noted that the solid calcareous internodes of the *Isis* axis differ in microstructure from those of other bamboo corals, consisting of calcareous fibers "united in bundles...radiating outward from the central core," and suggested that these "sclerodermites of *Isis* are actually highly modified spicules" (Bayer 1955). This construction is similar to what is seen in *Parisis*, with the main difference between the taxa being the presence of sclerites in the proteinaceous nodes of *Parisis* and their absence in *Isis* (Bayer 1955). Bayer's observations support the phylogenetic evidence that the jointed axis of *Isis* evolved independently of the similarly jointed axes of other octocoral taxa.

Rumphella and *Hicksonella* have a

skeletal axis that differs greatly from that of *Isis*, composed solely of proteinaceous gorgonin without calcareous inclusions. Despite this obvious difference, all three taxa nonetheless share several defining morphological characters. Their growth forms are very similar, with branched or bushy colonies that have thick cylindrical branches into which the polyps can be completely retracted; they have no or relatively few sclerites in the polyps; small clubs in the surface of the coenenchyme; and an inner layer of sclerites consisting of tuberculate forms such as spindles, ovals, or radiates. They are also zooxanthellate, a trait that distinguishes them from the majority of other Indo-Pacific gorgonians. *Hicksonella* and *Rumphella* are separated primarily by the presence in *Hicksonella* of rare, very long rods in the coenenchyme. The limited molecular data available to date suggest there is little genetic differentiation between those two genera, and they should perhaps be synonymized (Alderslade 1986; McFadden et al. 2014a).

Family Keroeididae Kinoshita, 1910

Type genus. *Keroeides* Wright & Studer, 1887

Diagnosis. Octocorals with a scleroproteinaceous skeletal axis, with hollow, cross-chambered central core surrounded by sclerites embedded in dense matrix of gorgonin. Colonies erect, profusely branched, planar or bushy. Polyps monomorphic, retractile into prominent calyces, distributed evenly and well-spaced over branches. Axial sclerites smooth, spindle-shaped, occasionally fused or anastomosing, densely packed around central core; sclerites of outer axial layer tightly bound with gorgonin. Polyps with tuberculate rods arranged as points without collaret; branched rods or scales in tentacles. Sclerites of coenenchyme are large, tuberculate spindles and irregular plates forming a pavement-like surface layer. Azooxanthellate. [modified from Fabricius and Alderslade 2001]

Distribution. Shallow to moderately deep waters of the tropical Indo-Pacific.

Included genera. *Keroeides* Wright & Studer, 1887

Remarks. As discussed above in Remarks for Ideogorgiidae n. fam., Keroeididae was established for gorgonians with an axis morphology transitional between that of typical holaxonians and scleraxonians. *Keroeides* shares with scleraxonians an axis composed of unfused sclerites embedded in gorgonin, but the axis has a hollow, cross-chambered central core like that of holaxonians. This unusual axial form appears to have evolved independently at least twice, as phylogenomic and molecular phylogenetic analyses place *Keroeides* among the holaxonian genera in Malacalcyonacea, while *Ideogorgia*, a genus with a similar axis, belongs to a clade of scleraxonians in Scleralcyonacea (Fig. 1, 2). Genomic data are unavailable at present for two other genera that have been assigned to Keroeididae, *Pseudothelogorgia* van Ofwegen, 1991 and *Thelogorgia* Bayer, 1991. Although they share similar axial construction and sclerite forms with *Keroeides* they differ in other significant ways such as the arrangement of sclerites in the polyps and structure of the calyx. Preliminary phylogenetic analysis of a *mtMutS* sequence for *Pseudothelogorgia* could not resolve its relationship to other taxa in Malacalcyonacea (C. McFadden, unpubl. data). We leave both *Thelogorgia* and *Pseudothelogorgia incertae sedis* until additional data become available to confirm their phylogenetic placement.

Family Paramuriceidae Bayer, 1956

Type genus. *Paramuricea* Kölliker, 1865

Diagnosis. Octocorals with (or rarely without) a proteinaceous skeletal axis. Axis hollow, with wide cross-chambered central core; coenenchyme usually very thin. Colonies erect, unbranched or branched (sparse and whip-like to profuse, often reticulate), planar or bushy. Polyps monomorphic, retractile into prominent calyces or non-retractile but with heavily armored polyp body wall giving the appearance of a cylindrical calyx. Polyps heavily armed with spindles, usually large and often bent or spinose, typically arranged as collaret and points. Calyces with thorn-scales, thornspindles, long spindles or short high-warted sclerites, typically differing in form from coenenchymal sclerites. Sclerites of coenenchyme in two layers: outer layer of thornspindles, thornstars or their derivatives; inner layer of simple or branched spindles. Azooxanthellate.

Distribution. Cosmopolitan, mostly in moderately deep to deep water.

Included genera. **Acanthacis* Deichmann, 1936; *Acanthogorgia* Gray, 1857; *Anthomuricea* Studer, 1887; **Astromuricea* Germanos, 1895; *Bebryce* Philippi, 1841; *Calicogorgia* Thomson & Henderson, 1906; **Dentomuricea* Grasshoff, 1977; *Discogorgia* Kükenthal, 1919; *Echinogorgia* Kölliker, 1865; *Echinomuricea* Verrill, 1869; *Guaiagorgia* Grasshoff & Alderslade, 1997; *Heterogorgia* Verrill, 1868; **Lapidogorgia* Grasshoff, 1999; *Lepidomuricea* Kükenthal, 1919; *Lytreia* Bayer, 1981; **Menacella* Gray, 1870; *Menella* Gray, 1870; *Muriceides* Studer, 1887; *Paracis* Kükenthal, 1919; *Paramuricea* Kölliker, 1865; *Paraplexaura* Kükenthal, 1909; *Placogorgia* Wright & Studer, 1889; *Spinimuricea* Grasshoff, 1992; *Thrombophyton* McFadden & Hochberg, 2003; **Trimuricea* Gordon, 1926; *Villogorgia* Duchassaing & Michelotti, 1864

Remarks. Bayer (1956) established Paramuriceidae to accommodate gorgonian genera that have a proteinaceous axis with a wide, cross-chambered central core surrounded by a thin coenenchyme ("rind"); anthocodial armature of strong points, often with a collaret; and "coenenchymal sclerites spindles only in some but commonly modified strongly as thorn scales or having other forms" (Bayer 1956). He later stated that "[Paramuriceidae] may yet require further subdivision into a restricted Paramuriceidae including only the genera with thorn-scales or comparable sclerites, and a new family including those genera with generalized spicules in the form of spindles or plates but no thorn-scales" (Bayer 1961). Rather than assigning those genera lacking thornscales to a new family, however, he subsequently transferred some of them (e.g., *Cyclomuricea, Muricella*) to Acanthogorgiidae, and reduced Paramuriceidae to the rank of subfamily (as Stenogorgiinae) within Plexauridae (Bayer 1981a). The phylogenomic and molecular phylogenetic analyses (e.g., Wirshing et al. 2005; Vargas et al. 2014), however, validate the clear separation of Stenogorgiinae from Plexaurinae, and do not support them as sister clades. All of the gorgonian genera with thornscales or similarly modified sclerites (thornspindles, thornstars, rooted heads, etc.) belong to this clade, for which we reinstate family Paramuriceidae. Of those genera included in Stenogorgiinae by Bayer (1981a) only *Swiftia* (=*Stenogorgia*) and *Scleracis*—neither of which have thornscales—do not belong to this clade. No or only limited molecular data are available to confirm the phylogenetic affinities of *Thesea* Duchassaing & Michelotti, 1864 (a genus often confused with *Swiftia*, and likewise polyphyletic; Carpinelli et al. 2022), *Pseudothesea* Kükenthal, 1919, *Hypnogorgia* Duchassaing & Michelotti, 1864 (often confused with *Muricea*), or *Filigorgia* Stiasny, 1937 (previously synonymized with *Leptogorgia*). As all of these genera also lack thornscales, it is likely that they will also be found to belong to clades other than Paramuriceidae. We tentatively assign *Filigorgia* to Pterogorgiidae n. fam., and leave the other genera as *incertae sedis*.

Genera not included in Paramuriceidae or Stenogorgiinae by Bayer (1956, 1981a) that are suggested by molecular evidence to belong to this clade include *Acanthogorgia, Anthomuricea, Guaiagorgia* and *Thrombophyton*. The placement of *Acanthogorgia* and *Thrombophyton* within Paramuriceidae is widely supported by both phylogenomic and molecular phylogenetic data (McFadden et al. 2006a). *Thrombophyton* lacks an axis and has a membranous growth form, very different from any of the other taxa in Paramuriceidae. It shares with them, however, a well-developed collaret and points of large spindles, and low calyces formed by sclerites that differ somewhat in form from those of the coenenchyme surface (McFadden and Hochberg 2003). The sclerites of the coenenchyme are predominantly irregular, tuberculate rods, cylinders, and ovals rather than thornscales or their derivatives. Based on its phylogenetic position, *Thrombophyton* would appear to be a paramuriceid that has secondarily lost its axis and reverted to a membranous growth form.

Acanthogorgia differs from other Paramuriceidae in having non-retractile polyps in which the polyp body wall is heavily armed with spindles arranged in chevrons, resembling a cylindrical calyx. Without an introvert (i.e., a region of the body wall lacking sclerites) the polyps are unable to retract into the coenenchyme and can only contract to a limited degree. These body wall spindles are often spinose and may resemble thornspindles; in addition, some species of *Acanthogorgia* have thornscales or thornstars, consistent with their membership in Paramuriceidae (Grasshoff 1973, 1999; Fabricius and Alderslade 2001). Molecular phylogenetic analyses of mitochondrial genes have found *Acanthogorgia* to be polyphyletic, although both identified clades appear to belong to Paramuriceidae (McFadden et al. 2006a). Interestingly, the three species included in our phylogeny are monophyletic in the phylogenomic analysis, but not in the unconstrained *mtMutS* tree (Suppl. files S2). Further taxon sampling is required to determine if the genus is monophyletic or not, and what morphological characters might be associated with different clades.

Phylogenomic data are not available for *Guaiagorgia* or *Anthomuricea*, but *mtMutS* sequences place both genera in Paramuriceidae. However, both of these genera lack the characters most typical of the family. We assign them to Paramuriceidae for now but suggest that phylogenomic data be obtained in future to support that assignment. No molecular data are available for *Acanthacis, Astromuricea, Dentomuricea, Lapidogorgia, Menacella,* or *Trimuricea*, but all of those genera have thornscales or their derivatives, consistent with membership in Paramuriceidae.

Family Plexaurellidae Verrill, 1912

Type genus. *Plexaurella* Kölliker, 1865

Diagnosis. Octocorals with a proteinaceous skeletal axis. Axis with a chambered central core and loculi densely calcified, with calcium carbonate strands longitudinally placed and anastomosing between them. In cross section, concentric loculi filled with Mg-calcite. Holdfast mainly composed of aragonite. Colonies erect, sparsely branched, planar or bushy, branchlets with limited flexibility. Polyps monomorphic, retractile into calyces that are often prominent but sometimes absent, distributed evenly over branch surfaces. Polyps lacking sclerites or with rods, sometimes arranged as collaret and points. Coenenchyme thick and porous, divided in three distinct layers. Surface layer usually thin and filled with six-radiate sclerites or small butterflies with very short arms. Middle layer thick, with the largest sclerites, mainly butterflies, spindles, tri-radiates, four-radiates and/or six-radiates. Axial layer with sclerites similar to those of the middle layer, but smaller and less ornamented, with no intrusion of middle layer sclerites. Zooxanthellate. [modified from Cordeiro et al. 2021]

Distribution. Shallow waters of tropical western Atlantic.

Included genera. *Plexaurella* Kölliker, 1865

Remarks. The axial construction and butterfly sclerites of *Plexaurella* are unlike those of any other genera of holaxonians. Although it has usually been classified in Plexauridae, the first molecular phylogenies revealed its closer genetic affinity to Gorgoniidae (Sánchez et al. 2003). Combined with its unique morphological synapomorphies, its position as a long branch sister to the gorgoniid clade supports the resurrection of Plexaurellidae as a monotypic family (Cordeiro et al. 2021).

Family Plexauridae Gray, 1859

Type genus. *Plexaura* Lamouroux, 1812

Diagnosis. Octocorals with a proteinaceous skeletal axis. Axis hollow with wide, cross-chambered central core; coenenchyme usually thick, commonly loculated; holdfast often heavily calcified with aragonite. Circle of longitudinal canals surrounding axis separates coenenchyme into inner (axial sheath) and outer layers. Colonies erect, sparsely or profusely branched, branches usually thick; planar or bushy. Polyps monomorphic, retractile into coenenchyme or conspicuous calyces, distributed evenly over branch surfaces. Polyp sclerites absent, or straight or curved rods or spindles arranged as points with or without collaret. Sclerites of outer coenenchymal layer spindles, clubs, leaf-clubs, capstans; inner layer with spindles or capstans, often purple; spindles typically >0.3 mm in length. Zooxanthellate or azooxanthellate.

Distribution. Shallow to moderately deep waters of western Atlantic and eastern Pacific tropics.

Included genera. *Eunicea* Lamouroux, 1816; *Muricea* Lamouroux, 1821; *Plexaura* Lamouroux, 1812; *Pseudoplexaura* Wright & Studer, 1889; *Swiftia* Duchassaing & Michelotti, 1864

Remarks. The genera we retain in Plexauridae form a well-supported clade distinct from other holaxonians in both phylogenomic (Fig. 1) and previous molecular phylogenetic analyses (Sánchez et al. 2003; Wirshing et al. 2005; Vargas et al. 2014). This clade includes a subset of the genera classified by Bayer (1981a) in subfamily Plexaurinae. They are distinguished from those we assign to Paramuriceidae by usually having thick coenenchyme (resulting in thick branches) that is subdivided into distinct layers by a ring of circular canals surrounding the axis (Bayer 1961). The sclerites of the inner layer (axial sheath) usually include capstans (*Eunicea* is an exception) in addition to large (>0.5 mm) spindles, and the surface layer usually includes clubs (*Muricea* is an exception).

Phylogenomic analyses place *Swiftia exserta* (Ellis & Solander, 1786), the type species of *Swiftia*, in Plexauridae, separated from other members of that genus. Indeed, *S. exserta* differs from other *Swiftia* in having capstans and long spindles (>0.3 mm) in the outer coenenchymal layer, and predominantly radiates that resemble those of *Plexaura* in the inner coenenchymal layer. As in the other plexaurid genera, longitudinal canals divide the coenenchyme into distinct layers (Goldberg 2001). *S. exserta* also occurs in shallower water than other members of the genus (Goldberg 2001), consistent with the ecological characteristics of the rest of the Plexauridae clade. We propose that those species of *Swiftia* that belong to other clades be re-assigned to different genera. Most were originally described as *Stenogorgia* Verrill, 1883, a genus that was synonymized with *Swiftia* by Deichman (1936). The type species of that genus is, however, *Stenogorgia casta* (Verrill, 1883), which is also morphologically and phylogenetically distinct from other *Swiftia* (Figs. 1, 2b). *Callistephanus* Wright & Studer, 1889 would appear to be the appropriate name for the majority of *Swiftia* species that are phylogenetically allied with Gorgoniidae.

Bayer (1981a) also included in Plexauridae (Plexaurinae) *Anthoplexaura, Euplexaura, Muriceopsis, Plexaurella*, and *Psammogorgia*, genera whose membership in Plexauridae is not supported by molecular data. *Plexaurella* has subsequently been transferred to Plexaurellidae, a monotypic family distinguished by its unique axial construction and sclerite forms (Cordeiro et al. 2021). *Euplexaura* is also morphologically distinctive, and phylogenetic analyses suggest it is sister to Paramuriceidae (Fig. 1). Early molecular phylogenetic analyses revealed that *Muriceopsis* belongs to Pterogorgiidae n. fam. (Sánchez et al. 2003; Wirshing et al. 2005). Phylogenomic data are not available for *Psammogorgia*, but single-locus molecular phylogenetic analyses (Fig. 2b) suggest it is sister to *Adelogorgia*, which belongs to Gorgoniidae. Although *Psammogorgia* does share some morphological characters with Plexauridae (well-developed collaret and points of large spindles, clubs in coenenchyme surface), the coenenchymal spindles are small (<0.3 mm) like those of Gorgoniidae. The only sequence data available for *Anthoplexaura* suggest that it is closely related to *Astrogorgia* (Fig. 2b), as proposed by Fabricius and Alderslade (2001).

Several genera of gorgonians that have been newly described or reinstated in recent years and assigned to Plexauridae lack molecular data and their familial affinities cannot be confirmed at present. These include *Bayergorgia* Williams & López-González, 2005, *Elasmogorgia* Wright & Studer, 1889, and *Mesogligorgia* López-González, 2007. Only mitochondrial gene data are available for *Alaskagorgia* Sánchez & Cairns, 2004 and *Cryogorgia* Williams, 2005. Phylogenetic analyses suggest that *Cryogorgia* is very close genetically to *Calcigorgia* Broch, 1935 while *Alaskagorgia* does not have apparent close affinities to any other holaxonian taxa (Fig. 2b). We consider all of these genera *incertae sedis* until their relationships can be confirmed with phylogenomic data.

Family Pterogorgiidae new fam.

Type genus. *Pterogorgia* Ehrenberg, 1834

Diagnosis. Octocorals with a proteinaceous skeletal axis. Axis hollow with wide, cross-chambered central core. Colonies erect, sparsely to profusely branched (dichotomous, pinnate), planar or bushy; branches may be flattened, oval or triangular in cross-section. Polyps monomorphic, retractile into coenenchyme or into low calyces, distributed evenly over branch surface or arranged biserially in recessed grooves along branch margins. Polyp sclerites small, flattened rods or slender spindles only rarely arranged as collaret and points. Sclerites of coenenchyme always include asymmetrically spiny or curved spindles; capstans, asymmetrical clubs or balloon-clubs, double-heads or plates may also be present. Zooxanthellate or azooxanthellate.

Distribution. Primarily shallow to deep waters of tropical Atlantic. One genus in shallow waters of tropical Indo-Pacific.

Included genera. *Dacrygorgia* n. gen.; *Filigorgia* Stiasny, 1937; *Muriceopsis* Aurivillius, 1931; *Pinnigorgia* Grasshoff & Alderslade, 1997; *Pterogorgia* Ehrenberg, 1834; *Stenogorgia* Verrill, 1883; *Tobagogorgia* Sánchez, 2007

Remarks: Early molecular phylogenetic work on the holaxonian gorgonians revealed a well-supported monophyletic clade composed of genera that had previously been classified in two different families. These included *Pterogorgia* and *Pinnigorgia*—both considered to belong to Gorgoniidae—and *Muriceopsis* of Plexauridae (Sánchez et al. 2003; McFadden et al. 2006a). Subsequent molecular phylogenetic and morphological studies have suggested that *Tobagogorgia* might also belong to this same clade (Aguilar and Sánchez 2007; Sánchez 2007). In a morphological analysis of Gorgoniidae, Sánchez (2007) identified *Muriceopsis, Pinnigorgia,* and *Tobagogorgia* as a clade characterized by having asymmetric, spiny spindles in the surface of the coenenchyme. *Pterogorgia* also has asymmetrical spindles, although they are more similar to the scaphoids characteristic of the gorgoniid genera *Antillogorgia* and *Gorgonia*, with which Sánchez (2007) grouped it. The growth morphology of *Pterogorgia*, with flattened branches and calyces located in grooves along the branch margins, is also unlike that of any other species in this clade. Molecular data from *ITS2* suggest that *Filigorgia* may also belong to Pterogorgiidae n. fam. (Aguilar and Sánchez 2007). Although Sánchez (2007) separated *Filigorgia* into a unique morphological group characterized by very long, slender spindles in the surface layer of the coenenchyme, those spindles are asymmetrically spiny and often slightly curved. We tentatively assign *Filigorgia* and *Tobagogorgia* to Pterogorgiidae based on the preliminary *ITS2* data and possession of asymmetrically spiny spindles in the coenenchyme surface, but their placement has yet to be confirmed by either phylogenomic or mitochondrial gene data.

Our phylogenomic analyses add two additional taxa to Pterogorgiidae n. fam.: *Swiftia casta* (Verrill, 1883) and *Eunicella modesta* Verrill, 1883, both of which have spindles in the coenenchyme that are only slightly asymmetrically spiny or curved. *S. casta* is the type species of *Stenogorgia* Verrill, 1883, a genus that was synonymized with *Swiftia* by Deichmann (1936). As first remarked on by Grieg (1887) and further noted by Bielschowsky (1929) and Madsen (1970), the sclerites in the coenenchyme of *S. casta* are solely spindles, whereas those of *Swiftia exserta* and the other species originally assigned to *Stenogorgia* are predominantly capstans. Moreover, the phylogenetic and phylogenomic results suggest that *S. casta* is phylogenetically distant from any of those species with capstans (Fig. 1, 2b). We reinstate *Stenogorgia* for *S. casta* alone, and suggest that *Callistephanus* Wright & Studer, 1889 be reinstated to accommodate the other species formerly assigned to *Stenogorgia*.

Pterogorgiidae n. fam. also includes *Eunicella modesta* Verrill, 1883, which is phylogenetically far removed from the other species of *Eunicella* for which we have described a new family, Eunicellidae. *E. modesta* and its congener *E. albatrossi* Stiasny, 1941 are morphologically, ecologically, and geographically distinct from all other *Eunicella* species. Both species are found in deep water (475-900 m) in the western Atlantic (Hourigan et al. 2020), whereas all other *Eunicella* inhabit relatively shallow depths (<200 m) in the eastern Atlantic and Mediterranean (Grasshoff 1992). Although they share the characteristic balloon-club sclerites of *Eunicella*, in both *E. modesta* and *E. albatrossi* those balloon-clubs have heads that are smooth and teardrop-shaped without the warts or whorls of points that characterize the balloon-clubs of other species (Bayer 1981a). Based on these differences we establish a new genus to accommodate *E. modesta* and *E. albatrossi*.

Dacrygorgia **n. gen.**

Type species. *Eunicella modesta* Verrill, 1883

Diagnosis. Octocorals with an unmineralized, proteinaceous axis. Colonies erect, sparsely branched, planar. Polyps monomorphic, retractile into low, hemispherical calyces that are crowded on the branch surface. Coenenchymal sclerites are balloon-clubs with smooth, teardrop-shaped heads, arranged densely with heads facing out to give the colony surface a smooth, granulated appearance. Spindles, double-heads, and irregular plates in inner layer of coenenchyme. Anthocodia strongly armed with spindles and rods arranged longitudinally in eight bands. Azooxanthellate.

Included species. *Dacrygorgia modesta* (Verrill, 1883) n. comb.; *Dacrygorgia albatrossi* (Stiasny, 1938) n. comb.

Etymology. From the Greek, *dacryon* (a tear-drop) in combination with *-gorgia* (a suffix commonly used in octocoral names), in reference to the tear-drop shape of the balloon-clubs in this genus. Gender feminine.

Remarks. *Dacrygorgia* n. gen. is easily distinguished from *Eunicella*, the only other genus with similar sclerites, by the smooth, teardrop-shaped heads of the balloon-clubs. The genus is known only from deep water in the western Atlantic, whereas *Eunicella* is distributed in shallow to moderately deep water (<200 m) in the eastern Atlantic and Mediterranean.

Family Scleracidae new fam.

Type genus. *Scleracis* Riess in Kükenthal, 1919

Diagnosis. Octocorals with a proteinaceous skeletal axis, with wide, cross-chambered central core. Colonies erect, branched (lateral and dichotomous), planar. Polyps monomorphic, retractile into low calyces, arranged biserially and irregularly alternate along branch margins. Polyp sclerites sparse, curved rods. Sclerites of coenenchyme in two layers: outer layer of very large, tuberculate spindles or plates forming translucent, glass-like pavement, inner layer of spindles with sparse tubercles. Azooxanthellate.

Distribution. Deep water of tropical western Atlantic.

Included genera. *Scleracis* Riess in Kükenthal, 1919

Remarks. Bayer (1956) included *Scleracis* in Paramuriceidae. *Scleracis* and the superficially similar genus *Paracis* both have a pavement-like layer on the coenenchyme surface formed by large spindles or plates. *Paracis*, however, has thornscales in the calyces like other members of Paramuriceidae, whereas *Scleracis* does not. The phylogenomic analysis suggests that *Scleracis guadalupensis* (Duchassaing & Michelotti, 1860) is the sister to Anthogorgiidae n. fam. Unlike that family, it has polyps that are retractile into low calyces, and its coenenchyme is composed of two distinct layers, with an inner layer of small spindles below the outer pavement of large spindles. We consider these differences substantial enough to assign *Scleracis* to a new, monotypic family, Scleracidae. The other known species of *Scleracis*, *S. petrosa* Deichmann, 1936, has large plate-like sclerites rather than spindles in the outer coenenchyme; no molecular data are available to confirm the sister relationship between this species and *S. guadalupensis*, or the monophyly of the genus.

Family Taiaroidae Bayer & Muzik, 1976

Type genus. *Taiaroa* Bayer & Muzik, 1976

Table 3: Genera whose familial assignment is left as *incertae sedis* due to insufficient molecular or morphological evidence to confirm their phylogenetic placement.

Genus	Authority	most recent taxonomic assignment
Acanthomuricea	Hentschel, 1903	Plexauridae
Alaskagorgia	Sánchez & Cairns, 2004	Plexauridae
Aspera	Dautova, 2018	Nephtheidae
Bayergorgia	Williams & López-González, 2005	Plexauridae
Briareopsis	Bayer, 1993	Anthothelidae
Calcigorgia	Broch, 1935	Acanthogorgiidae
Caliacis	Deichmann, 1936	Plexauridae
Canarya	Ocaña & van Ofwegen, 2003	Clavulariidae
Ceratocaulon	Jungersen, 1892	Alcyoniidae
Chalcogorgia	Bayer, 1949	Chrysogorgiidae
Chondronephthya	Utinomi, 1960	Nephtheidae
Cryogorgia	Williams, 2005	Plexauridae
Cyclomuricea	Nutting, 1908	Acanthogorgiidae
Daniela	Koch, 1891	Nephtheidae
Denhartogia	Ocaña & van Ofwegen, 2003	Clavulariidae
Distichogorgia	Bayer, 1979	Chrysogorgiidae
Elasmogorgia	Wright & Studer, 1889	Plexauridae
Elenanthus	Sanamyan & Sanamyan, 2020	Stolonifera
Flagelligorgia	Cairns & Cordeiro, 2017	Chrysogorgiidae
Helicogorgia	Verrill, 1883	Chrysogorgiidae
Hypnogorgia	Duchassaing & Michelotti, 1864	Plexauridae
Ignis	Dautova, 2018	Haimeidae
Inflatocalyx	Verseveldt & Bayer, 1988	Alcyoniidae
Lanthanocephalus	Williams & Starmer, 2000	Alcyoniidae
Lignopsis	Pérez & Zamponi, 2000	Briareidae
Mesogligorgia	López-González, 2007	Plexauridae
Moolabalia	Alderslade, 2001	Clavulariidae
Pseudocladochonus	Versluys, 1907	Clavulariidae
Pseudogorgia	Utinomi & Harada, 1973	Pseudogorgiidae
Pseudosuberia	Kükenthal, 1916	Briareidae
Pseudothelogorgia	van Ofwegen, 1991	Keroeididae
Pseudothesea	Kükenthal, 1919	Plexauridae
Rolandia	de Lacaze-Duthiers, 1900	Clavulariidae
Scleranthelia	Studer, 1878	Clavulariidae
Sphaeralcyon	López-González & Gili, 2000	Alcyoniidae
Speirogorgia	Williams, 2019	Calcaxonia
Stephanogorgia	Bayer & Muzik, 1976	Chrysogorgiidae
Stereacanthia	Thomson & Henderson, 1906	Nidaliidae
Stereogorgia	Kükenthal, 1916	Anthothelidae
Stereosoma	Hickson, 1904	Clavulariidae
Tesseranthelia	Bayer, 1981	Clavulariidae
Thelogorgia	Bayer, 1991	Keroeididae
Thesea	Duchassaing & Michelotti, 1860	Plexauridae
Trichogorgia	Hickson, 1904	Chrysogorgiidae
Tubigorgia	Pasternak, 1985	Anthothelidae
Verseveldtia	Williams, 1990	Alcyoniidae
Williamsium	Moore, Alderslade & Miller, 2017	Anthothelidae
Xenogorgia	Bayer & Muzik, 1976	Chrysogorgiidae

Diagnosis. Octocorals without a skeletal axis, with solitary polyps. Polyps fastened in soft substrate by numerous filamentous holdfasts, divided into distinct calyx and anthocodia; anthocodia fully retractile into calyx. Calyx covered by thin cuticle. Polyp sclerites thorny spindles and rods forming collaret and points, arranged longitudinally in calyx. Azooxanthellate. [modified from Bayer and Muzik 1976]

Distribution. Deep water of southwestern Pacific.

Included genera. *Taiaroa* Bayer & Muzik, 1976

Remarks. *Taiaroa* remains the only well-documented octocoral with a solitary growth form. Although *Bathyalcyon* and some other species of Anthomastinae have only a single, large autozooid they also have siphonozooids, making them colonial. The phylogenetic position of *Taiaroa* among holaxonian gorgonians, where it appears to be sister to *Keroeides* and *Astrogorgia* (Fig. 1), suggests that this is another species that has secondarily evolved to lose an axis.

Taxa left *incertae sedis*

We leave 46 genera and two families (Haimeidae Wright, 1865; Pseudogorgiidae Utinomi & Harada, 1973) whose phylogenetic positions are still unknown or uncertain as *incertae sedis* (Table 3). The majority of these are rare taxa that have seldom been recorded since their original description, for which material suitable for molecular analysis may not exist. If or when appropriate material becomes available, it is likely that many of these genera will be found to occupy unique positions in the octocoral tree of life meriting additional families. Moreover, a large number of octocoral species remain undescribed, and many environments (e.g., the mesophotic zone) are underexplored, with plenty of scope for the discovery and description of new lineages as yet unrepresented in the phylogeny. Indeed, we included in the phylogenomic analysis several specimens of undescribed octocorals with morphologically simple, stoloniferous growth forms. Two of these (*Clavularia* cf. *viridis*, stoloniferan sp. nov. 3K) occupy unique branches in the phylogeny (Figs. 1, 2b), not genetically or morphologically similar to their sister clades. Upon their formal description, it is likely these taxa will merit status as monotypic families. The *mtMutS* phylogeny also includes additional taxa (i.e., *Calcigorgia, Cryogorgia, Alaskagorgia, Elenanthus, Anthelia fallax, Helicogorgia*) that fall outside of any of the families we have described herein. Their phylogenetic positions require further confirmation from genomic data, but it would not be a surprise if some of them are also found to represent unique family-level clades. Although the octocoral tree of life is still far from fully known, the classification scheme proposed herein provides a phylogenetic framework upon which to build and to begin to understand the evolution of morphological and functional traits within Octocorallia.

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Data availability

Raw Data: SRA Genbank PRJNA822352, BioSample #SAMN27177414-SAMN27177498

New sequences for mtMutS included in phylogenetic analyses: GenBank accessions ON109689- ON109752.

Suppl. files S1: Code used for analyses of target-capture sequence data. https://zenodo.org/record/6545370#.YuF6XezMJjM

Additional supplemental data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.6m905qg29

Suppl. files S2: Treefiles for all phylogenetic analyses listed in Table 1.

Suppl. Table S1: Museum and GenBank accession numbers for all specimens and sequences used in phylogenetic analyses.

Suppl. Table S2. Read and locus statistics for samples used for target-enrichment sequencing.

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Appendix 1. Terms and definitions used in family diagnoses, following (in part) Bayer et al. 1983, Alderslade 1998, and Fabricius and Alderslade 2001. Please refer to Bayer et al. 1983 for definitions of branching patterns and sclerite forms.

anthocodia	the distal part of a polyp, bearing the mouth and the tentacles; this part is able to extend above the colony surface and may be contractile or retractile (used interchangeably with polyp)
anthopoma	protective structure covering the oral region of the polyp during contraction, formed by sclerites on and just below the tentacle bases (see also operculum, collaret and points)
anthostele*	lower part of the polyp (below the introvert) containing the entire gastrodermal canal, into which the upper part of the polyp (anthocodia) may be able to retract; in species lacking a calyx, the anthostele does not protrude above the surface of the coenenchyme
aragonite	mineral polymorph of calcium carbonate
autozooid	polyp with eight well-developed tentacles and mesenteries; the only kind of polyp in monomorphic species, often just termed polyp
axis	internal supporting structure that may be calcareous or proteinaceous or both; the calcareous matter may be scleritic (i.e., formed by sclerites) or non-scleritic
azooxanthellate	lacking photosymbioses with single-celled dinoflagellates
body wall	wall of polyp body enclosing the gastric cavity
boundary canal	gastrodermal canal separating the cortex from the medulla
calcite	mineral polymorph of calcium carbonate
calyx*	tissue surrounding the upper end of an anthostele that protrudes above the colony surface, into which the anthocodia retracts; often reinforced with sclerites of specialized form, although in some species the calyx may lack sclerites entirely (pl: calyces)
capitate	having a disk-shaped or hemispherical polyparium that is broader than the colony stalk (i.e., mushroom-shaped)
carbonate hydroxylapatite (CHAp)	calcium carbonate and phosphate fibrous material found in some axes
coenenchyme	tissue between the polyps, consisting of mesogloea usually with sclerites and penetrated by the network of solenia and the larger gastrodermal canals
collaret	ring of transversely placed sclerites encircling the anthocodia below the tentacles, sometimes referred to as a crown
colony	a group of interconnected, genetically identical polyps
contractile	polyps deflate and tentacles fold inward over the mouth, but the anthocodia does not invaginate or withdraw into the anthostele
cortex	the coenenchymal layer surrounding the medulla and containing the polyps; also used to denote the layer of tissue immediately surrounding a proteinaceous axis (e.g., axial cortex)
cross-chambered central core	hollow center of a proteinaceous axis subdivided by transverse partitions composed of a meshwork of fine organic filaments
cuticle	protective layer of chitinous material surrounding the stolons or polyps
dimorphic	having two polyp types, typically autozooids and siphonozooids
gastrodermal canal	tube in the gastric cavity connected to other parts of the colony by narrower solenia
gorgonian	colloquial term for an octocoral colony with an internal axis

gorgonin	hard, complex scleroprotein, similar to horn, which is a component of some axes
holdfast	base of gorgonian colony attached to the substrate
horny	colloquial, having gorgonin or an axis made of gorgonin
internode	calcareous segment of a jointed axis
introvert	region of the polyp lacking sclerites that allows the anthocodia to retract by invagination into the anthostele
loculus	calcified area or fibre-filled space in a proteinaceous axis that can appear crescentic or lenticular in cross section
medulla	inner supporting layer composed of a dense aggregate of sclerites that can be loose to fused, often but not always forming an axis
mesentery	thin, radial, non-calcareous partitions that join the pharynx to the body wall and subdivide the gastrovascular cavity of the polyp
monomorphic	having only one type of polyp (autozooids)
node	the flexible proteinaceous segment of a jointed axis
operculum	a set of eight triangular, scale-like sclerites that cover the withdrawn tentacles in Primnoidae (see also anthopoma)
peduncle	lower part of a pennatulacean colony, lacking polyps; serves to anchor the colony in sediment
periderm	thin outer layer of protective tissue surrounding stolons or polyps; similar to cuticle
pharynx	tube that connects the mouth to the gastric cavity
pinnules	lateral projections on tentacles
points	eight sets of sclerites in the anthocodia, arranged longitudinally (often as chevrons) at or below the base of each tentacle (see also anthopoma)
polyp	an individual structure that consists of a columnar body with a distal mouth usually surrounded by a ring of tentacles
polyparium	the part of a colony that bears polyps
proteinaceous	having an axis made of gorgonin, sometimes referred to as "horny"
pseudopinnules	finger-like caecae extending from the margins of the tentacle, resembling pinnules that have fused to form a broad, blade-like expanse of tissue
rachis	the upper part of a pennatulacean colony on which the polyps are arranged
retractile	anthocodia of the polyp can withdraw fully into the anthostele by invagination
sclerite	a calcitic skeletal element, often microscopic, embedded in the coenenchyme and polyps (obsolete: spicule)
sclerodermites	the calcareous units (bundles of fibers) that make up a calcified axis; may be arranged radially or in concentric layers
sclerome	inventory of all sclerites and their arrangement in one colony
scleroprotein	insoluble, filamentous, or fibrous structural proteins or gorgonin
siphonozooid	polyp with reduced or no tentacles, commonly with reduced mesenterial filaments; usually much smaller than autozooids, and serve to pump water into the colony
solenia	network of narrow canals lined with gastrodermis that penetrate the coenenchyme and interconnect the gastric cavities of polyps

stalk	basal part of colony below the branches or polyparium; when lacking polyps, referred to as sterile
stolon	a cylindrical tube or flattened, ribbon-like sheet of coenenchyme growing over the substrate and peripherally producing new polyps; stolons may anastomose at junctions to form networks or fuse laterally to form membranes
theca	cup-like sheath of cuticle surrounding the polyp
tubercle	small, rounded projection or protuberance on a sclerite (also called a wart)
whorl	arrangement of polyps that encircle a branch or tubercles that encircle a sclerite
zooxanthellate	having photosymbioses with single-celled dinoflagellates

*Bayer et al. (1983) synonymize the terms anthostele and calyx. Alderslade (1998) discusses the history of the terms and maintains a distinction, restricting anthostele to the entire lower region of the polyp that generally does not extend above the surface of the coenenchyme and into which the upper part of the polyp (anthocodia) may retract. In species in which the upper part of the anthostele does extend above the coenenchyme surface, it is surrounded by a calyx, a layer of tissue that is often reinforced by specialized sclerites (Fabricius and Alderslade 2001). We use the term calyx for any non-retractile structure that protrudes above the coenenchyme surface and into which the anthocodia retracts, regardless of whether or not it is reinforced by sclerites.