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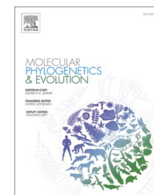

A hybrid-capture approach to reconstruct the phylogeny of Scleractinia (Cnidaria: Hexacorallia)

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ABSTRACT

A well-supported evolutionary tree representing most major lineages of scleractinian corals is in sight with the development and application of phylogenomic approaches. Specifically, hybrid-capture techniques are shedding light on the evolution and systematics of corals. Here, we reconstructed a broad phylogeny of Scleractinia to test previous phylogenetic hypotheses inferred from a few molecular markers, in particular, the relationships among major scleractinian families and genera, and to identify clades that require further research. We analysed 449 nuclear loci from 422 corals, comprising 266 species spanning 26 families, combining data across whole genomes, transcriptomes, hybrid capture and low-coverage sequencing to reconstruct the largest phylogenomic tree of scleractinians to date. Due to the large number of loci and data completeness (less than 38% missing data), node supports were high across shallow and deep nodes with incongruences observed in only a few shallow nodes. The “Robust” and “Complex” clades were recovered unequivocally, and our analyses confirmed that Micrabaciidae Vaughan, 1905 is sister to the “Robust” clade, transforming our understanding of the “Basal” clade. Several families remain polyphyletic in our phylogeny, including Deltocyathiidae Kitahara, Cairns, Stolarski & Miller, 2012, Caryophylliidae Dana, 1846, and Coscinaraeidae Benzoni, Arrigoni, Stefani & Stolarski, 2012, and we hereby formally proposed the family name Pachyseridae Benzoni & Hoeksema to accommodate *Pachyseris* Milne Edwards & Haime, 1849, which is phylogenetically distinct from Agariciidae Gray, 1847. Results also revealed species misidentifications and inconsistencies within morphologically complex clades, such as *Acropora* Oken, 1815 and *Platygyra* Ehrenberg, 1834, underscoring the need for reference skeletal material and topotypes, as well as the importance of detailed taxonomic work. The approach and findings here provide much

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promise for further stabilising the topology of the scleractinian tree of life and advancing our understanding of coral evolution.

1. Introduction

Stony corals (Cnidaria: Hexacorallia: Scleractinia) comprise some of the most well-studied marine organisms in the world, yet a thoroughly supported molecular phylogeny of this iconic lineage remains elusive due to the scarcity of phylogenetically informative markers (Budd et al., 2010; Fukami, 2008; Kitahara et al., 2016; but see Quattrini et al., 2018; Quek et al., 2020). Prior to the molecular revolution in the 1990s, scleractinian evolution was inferred from morphological characteristics, some of which were presented as character states in cladistic analyses (Wells, 1966; Cairns, 1984; Hoeksema, 1989; Pandolfi, 1992; Veron, 1986, 1995, 2000; Wallace, 1999; Cairns, 2001). However, the apparent extensive overlap between intraspecific and interspecific morphological variation, together with phenotypic plasticity, has confounded coral taxonomy and systematics (Todd, 2008; Budd et al., 2010). Recent applications of more advanced molecular techniques have improved our understanding of the scleractinian phylogeny markedly, providing unprecedented insight into the evolutionary history of the clade (Fukami et al., 2004, 2008; Kitahara et al., 2010b; Cowman et al., 2020; Quattrini et al., 2020).

Molecular sequence data first transformed our understanding of evolutionary relationships in Scleractinia at the turn of the century, when mitochondrial 16S ribosomal RNA data provided the first evidence of two distinct groups subsequently named by Romano and Palumbi (1996, 1997) as the “Robust” and “Complex” clades (see also Chen et al., 1995; Romano and Cairns, 2000). Approximately a decade later, Fukami et al. (2004, 2008) used nuclear and mitochondrial gene trees to demonstrate a deep evolutionary divergence between Pacific and Atlantic lineages despite extensive similarities of macromorphological characteristics for many taxa, such as Faviidae Milne Edwards & Haime, 1857, Lobophylliidae Dai & Horng, 2009, and Merulinidae Milne Edwards & Haime, 1857. The integration of molecular and morphological data has led to many other significant changes across the scleractinian tree of life in the last two decades, including the designation of new families, the elevation of genus and species names out of synonymy, and the description of new species (Benzoni et al., 2007, 2010, 2012a, 2012b, 2014; Wallace et al., 2007; Kitahara et al., 2010a; 2012, 2013; Huang et al., 2011, 2014a, 2014b, 2016; Gittenberger et al., 2011; Arrigoni et al., 2012, 2014a, 2014b, 2014c, 2014d, 2021; Kitano et al., 2014; Luzon et al., 2017; Juszkiewicz et al., 2022).

Increasingly, the accessibility of molecular markers and analytical advances in phylogenetic methods have spawned several “supertree” and “supermatrix” phylogenies that include more extensive species sampling (Kerr, 2005; Huang, 2012; Huang and Roy, 2015; Kitahara et al., 2016; Hartmann et al., 2017; Gault et al., 2021). These phylogenetic reconstructions have addressed questions spanning different biological disciplines, ranging from conservation prioritisation to ancestral state reconstruction. Nevertheless, these trees were based on a small number of mitochondrial or ribosomal genes (Chen et al., 1995; Romano and Palumbi, 1996, 1997; Medina et al., 1999; Berntson et al., 1999; Chen et al., 2000). Consequently, most of them are plagued by extensive polytomies and inconsistent topologies, with varying levels of support at important higher-level nodes. Furthermore, mitochondrial genes are particularly problematic in Anthozoa because of the slow rates of evolution and substitution saturation (Shearer et al., 2002; Hellberg, 2006; Huang et al., 2008; Pratlong et al., 2017). Earlier studies have demonstrated incongruences between mitochondrial and nuclear phylogenies, such as the phylogenetic position of corallimorpharians (Medina et al., 2006; Kitahara et al., 2014; Lin et al., 2014), and the monophyly of octocorals (Kayal et al., 2013; Zapata et al., 2015). Ribosomal-based phylogenies have also resulted in inconsistent inferences among anthozoans (e.g. Chen et al., 1995; Song and Won, 1997; Berntson et al., 1999).

High-throughput sequencing (HTS) has greatly accelerated our understanding of anthozoan evolution, such as resolving the phylogenetic position of ceriantharians and corallimorpharians, as well as the monophyly of Anthozoa (Zapata et al., 2015; Lin et al., 2016; Kayal et al., 2018; Quattrini et al., 2020; McFadden et al., 2021; see also McFadden et al., 2022). The application of HTS techniques is most common and diverse in Scleractinia (Quek and Huang, 2022), having been used to investigate mitochondrial evolution (Seiblitz et al., 2020, 2022), delimit species boundaries, identify cryptic species (Arrigoni et al., 2020; Oku et al., 2020; Juszkiewicz et al., 2022), and infer broad phylogenetic relationships (Kayal et al., 2018; Quek and Huang, 2019; Quattrini et al., 2020). Among the different methods, hybrid capture-based approaches have emerged as a frontrunner for phylogenomic reconstructions due to their versatility and applicability across various scales of divergence times (Faircloth et al., 2012; Erickson et al., 2021). Currently, there are two sets of baits designed for scleractinians, one targeting scleractinians (Quek et al., 2020), and the other targeting all hexacorals (Cowman et al., 2020; refined from Quattrini et al., 2018).

Recent phylogenomic studies of Scleractinia using hybrid-capture techniques have given insight into the evolution of these marine invertebrates. For example, using a refined hexacoral bait set, Cowman et al. (2020) found incongruent relationships between molecular data and morphological grouping of *Acropora* Oken, 1815 (*sensu* Wallace, 1999) (see also Richards et al., 2013). *Acropora* is a diverse genus for which inferring species-level relationships can be challenging due to possible convergent evolution, interspecific hybridisation and phenotypic plasticity (van Oppen et al., 2001; Richards et al., 2010, 2013). Nevertheless, Cowman et al. (2020) identified six lineages within *Acropora*, highlighting the potential for the phylogenomic approach to help clarify evolutionary relationships within challenging taxonomic groups. Similarly, Grinblat et al. (2021) used the same bait set across the “Robust” family Fungiidae Dana, 1846 in a biogeographic study, identifying multiple cryptic lineages of *Herpolitha limax* (Esper, 1792), *Ctenactis echinata* (Pallas, 1766) and *Fungia fungites* (Linnaeus, 1758). More broadly, Quattrini et al. (2020; see also McFadden et al., 2021) reconstructed a time-calibrated Anthozoa phylogeny using a bait set combination (Quattrini et al., 2018; Cowman et al., 2020), placing the origin of Scleractinia at 383 Ma (95% confidence interval 324–447 Ma). Furthermore, they correlated paleoclimatic changes with diversification rates and skeletal trait evolution through deep time, providing some insights into the future of anthozoans and reefs under imminent climate change. Indeed, hybrid-capture techniques have proven to be an invaluable tool for broad taxonomic sampling and phylogenomic reconstructions.

In this study, we reconstructed a broad phylogeny of the Scleractinia clade to test longstanding questions in coral evolution and systematics. Our main goals were to validate previous scleractinian trees inferred from a relatively small number ($\leq$12) of molecular markers (e.g. Fukami et al., 2008; Kitahara et al., 2016), to resolve the relationships among major scleractinian families and genera, and to identify clades that require further taxonomic revisions or fine-tuning of recent revisions. We also attempted time-calibrated Bayesian analyses to infer the chronogram of Scleractinia, focusing on understanding the effects of different fossil age priors and their combinations on divergence time estimates. Overall, our study analysed a total of 422 terminals, comprising *in silico* samples of nine genomes, 47 transcriptomes, and 28 low-coverage sequenced samples, in conjunction with 338 samples sequenced using hybrid capture, of which 318 were newly sequenced in this study.

2. Material and methods

2.1. Sample collection, library preparation and sequencing

In total, 327 specimens were collected from both intertidal and subtidal habitats in Singapore, Australia and the Red Sea (Table S1), but some were eventually removed due to uncertain taxonomic identity. Specimen vouchers were deposited at the Lee Kong Chian Natural History Museum, King Abdullah University of Science and Technology and the Western Australian Museum. DNA extraction and library preparation protocols were previously described by Quek et al. (2020). Briefly, high quality genomic DNA (gDNA) was extracted and purified using E.Z.N.A Mollusc DNA Kit (Omega Bio-tek) with a modified elution step and Zymo Genomic DNA Clean and Concentrator respectively. Purified gDNA was then sonicated using Bioruptor Pico (Diagenode) with a target mode size of 200 bp, and dual-indexed libraries were prepared using KAPA HyperPrep Kit (KK8502; KAPA Biosystems) with a double size selection using Agencourt AMPure XP beads (Beckman Coulter). Hybrid capture was then conducted following the manufacturer's protocol (MyBaits, Arbor Biosciences) with baits either from Quek et al. (2020) or combined from Quek et al. (2020) and Cowman et al. (2020). Libraries were pooled in batches of 23–24 libraries per capture reaction, with 100 ng of library used per sample. Four separate Illumina HiSeq 4000 lanes were used for sequencing, with 96, 93, 94 and 46 samples in each respective lane (Table S1). Two samples that were poorly sequenced from the first round of sequencing were re-sequenced in the fourth round of sequencing. Raw data from this study were deposited in GenBank SRA under PRJNA865877.

Apart from hybrid capture, 28 samples underwent untargeted whole-genome sequencing, which had comparatively lower coverage. DNA was extracted from these samples using either the DNeasy Blood and Tissue Kit (Qiagen) or the Gentra Puregene Tissue Kit (Qiagen) (Table S2). In the case of *Enallopsammia rostrata* (Pourtalès, 1878) and *Truncatoflabellum vigintifarium* Cairns, 1999, extracts were also purified using the Genomic DNA Clean and Concentrator kit (Zymo Research). Library preparation was performed with the TruSeq DNA Nano (Illumina) and DNA shearing was performed in a Covaris ultrasonicator. For *Cyathotrochus pileus* (Alcock, 1902) and *Dendrophyllia* sp., the library target insert size was 550 bp, while in the other samples, it was 350 bp. Sequencing was performed by pooling eight samples per MiSeq run, and three samples had underwent additional NextSeq sequencing(Table S2). Other samples sequenced but not included in this study were omitted from Table S2. Specimens are deposited either at Muséum National d'Histoire Naturelle, Center for Marine Biology of the University of São Paulo or National Institute of Water and Atmospheric Research (New Zealand). Data from these runs were not deposited in GenBank, but may be made available upon request to I.G.L. Seiblitz or M.V. Kitahara.

2.2. Locus identification for hybrid capture

To increase taxon sampling based on hybrid capture, we downloaded raw sequences from samples (n = 20) in Quek et al. (2020) and carried out the following bioinformatic pipeline in conjunction with sequenced samples from this study. Adapters and poor-quality bases were trimmed from raw reads using fastp v0.20.0 under default settings (Chen et al., 2018). Trimmed sequences were then funnelled into HybPiper v1.3.1 (Johnson et al., 2016) using the bait file from Quek et al. (2020; https://doi.org/10.5281/zenodo.3590246), with paralogs and single-copy exons extracted for downstream analyses.

Cross-contamination between samples in hybrid-capture studies is a recurring problem (e.g. Hugall et al., 2016; Bank et al., 2017; Quek et al., 2020). Therefore, we adopted the following strategy to identify and filter for cross-contaminant sequences. Cross-contamination was highlighted from paralogous sequences extracted by HybPiper v1.3.1 (Johnson et al., 2016). To distinguish between true paralogy and cross-contamination, we took an approach similar to Bank et al. (2017). The k-mer coverage for each paralogous locus assembled was first obtained from the HybPiper output. If the k-mer coverage determined by SPAdes v3.14.0 (Bankevich et al., 2012) was at least 10-fold higher than that of the other paralogous contig(s) assembled, we removed the contig(s) that was likely the result of cross-contamination. Furthermore, coverage for extracted regions was determined by mapping trimmed reads to both paralogous and single-copy sequences extracted using BWA-MEM under default settings (Li, 2013). Mean coverage was then calculated using Qualimap v2.2.1 (Okonechnikov et al., 2016), and sequences with mean coverage less than 30 were removed.

2.3. In silico data analyses

To further increase taxon sampling and validate the versatility of our pipeline, we adopted two strategies based on *in silico* methods. Genome and transcriptome data were combined with hybrid-capture samples by first downloading nine and 47 genomes and transcriptomes respectively (Table S1). HiSeq 2500 reads were then simulated from both assembled genomes and transcriptomes using art_illumina v2.5.8 (Huang et al., 2012) based on settings modified (*-l* 150, *-f* 20, *-m* 250, *-s* 10) from Faircloth et al. (2012).

To determine if data and samples from low-coverage sequencing could also be combined in downstream phylogenomic analyses, we assembled the reads of 28 of these samples (Seiblitz et al., 2020, 2022, and samples above) using SPAdes v3.14.0 (Bankevich et al., 2012) under default settings. Reads were then simulated following those of assembled genomes and transcriptomes. Simulated reads were put through HybPiper v1.3.1 (Johnson et al., 2016), with orthologs and paralogs extracted and filtered as above.

2.4. Phylogenetic analyses

Phylogenomic inferences were conducted via two tree phylogenetic optimality criteria: maximum likelihood (ML) and Bayesian inference (BI). To prepare the supermatrices for phylogenomic inference, each locus was aligned by MAFFT v7.310 with the alignment algorithm selected automatically (Katoh et al., 2002; Katoh and Standley, 2013). Poorly-aligned regions were trimmed using trimAL v1.4 using the heuristic setting (Capella-Gutiérrez et al., 2009).

To determine if missing data had marked effects on phylogenomic reconstruction, four different concatenated supermatrices were prepared: 25-percent taxon-occupancy matrix (409 loci), 50-percent taxon-occupancy matrix (325 loci), 75-percent taxon-occupancy matrix (158 loci), and all-loci matrix (449 loci). Subsequently, ML phylogenies were reconstructed by RAxML-NG (Stamatakis et al., 2005; Kozlov et al., 2019), partitioned by loci according to the best model selected by ModelTest-NG (Darriba et al., 2020). Each tree was reconstructed using 10 random and 10 parsimony starting trees each, and bootstrap supports were calculated based on 200 pseudoreplicates.

As most incongruences among the four ML phylogenies were limited to shallow nodes, the all-loci supermatrix that garnered the highest average ML bootstrap was used for BI analyses in ExaBayes v1.5 (Aberer et al., 2014). Four independent runs were performed, each computed with four coupled Markov chain Monte Carlo (MCMC) chains, sampling every 500 generations over 2 million generations. Convergence was ascertained based on average standard deviation of split frequencies (ASDSF less than 5%). Following a burn-in of the first 25% sampled generations, a majority-rule consensus tree was generated across the four runs.

2.5. Divergence time estimation

The all-loci matrix and tree topology obtained from the ML analysis of the all-loci matrix were trimmed to species level. Divergence time estimations were performed using BEAST v2.6.3 (Bouckaert et al., 2014, 2019). The data matrix was partitioned by locus, with the best model of

evolution determined by ModelTest-NG. Nine calibration points were analysed, with all except the root constrained by lognormal distribution with hard lower bound (age of fossil) and soft upper bound described by log mean and standard deviation of 2.0 and 0.85 respectively: *Acropora* (66 Ma; Budd and Wallace, 2008; Richards et al., 2013); *Flabellum* Lesson, 1831 (77.9 Ma; Felix, 1909; Stolarski et al., 2011); Acroporidae Verrill, 1901 (100.5 Ma; Wallace, 2012; Huang et al., 2018); *Hydnophora* Fischer von Waldheim, 1807 (124 Ma; Baron-Szabo, 1997); Dendrophylliidae Gray, 1847 (127.2 Ma; Wanner, 1902; Stolarski et al., 2011); *Montastraea* Blainville, 1830 (137.5 Ma; Koby, 1896; Budd and Coates, 1992); *Caryophyllia* Lamarck, 1801 (160.4 Ma; Geyer, 1954; Lauxmann, 1991; Stolarski et al., 2011); Fungiidae (218.6 Ma; Smith, 1927); maximum age of root (520 Ma; Hou and Bergström, 2003; Li et al., 2007; Quattrini et al., 2020). Both the monophyly of Scleractinia and Corallimorpharia were further constrained (e.g. Lin et al., 2016; Wang et al., 2017). Other priors contained model specifications for each locus as determined previously, and include a relaxed clock model with a birth–death tree.

Using all calibration points, four separate Markov chain Monte Carlo (MCMC) runs of 10 million generations each were conducted with a sampling interval of every 1000 generations. Convergence between runs was not evident for the entire analysis and no level of burn-in would produce sufficient posterior samples (Table S3). Therefore, we analysed each one of the above scleractinian calibrations independently, plus the root calibration as stated above. Four separate MCMC runs of 50 million generations were conducted with a sampling interval of 1000. The posterior effective sample size ($ESS_{posterior}$) values were tabulated and ranked after discarding a burn-in of 10%, with the best performance across runs observed in the Fungiidae-calibrated tree (Table S3). We then identified the remaining calibration points that fell within the divergence times estimated in the Fungiidae-calibrated analysis, which were *Hydnophora*, *Montastraea*, Caryophylliidae, and *Flabellum*.

Based on these five calibration points, we prepared four separate matrices for divergence time estimations. In the first matrix, we included only Fungiidae and *Hydnophora* as priors, along with the root, due to *Hydnophora*-calibrated tree having the second highest $ESS_{posterior}$ value. Following this, we applied the Fungiidae calibration point with each of the remaining three calibration points in decreasing order of $ESS_{posterior}$ values (Table S3). Four runs of 250 million generations each with a sampling interval of 1000 were performed. A burn-in of 75% was specified following convergence checking in Tracer v1.7 (Rambaut et al., 2018).

3. Results

3.1. Hybrid capture and in silico data

After the removal of samples that were either poorly sequenced or had uncertain species identification (n = 9), we analysed a total of 422 terminals in the final phylogeny reconstruction, comprising 266 species spanning 26 families. As expected, the number of loci recovered for corallimorpharians was much lower compared to corals (see Quek et al., 2020), with less than 50 loci recovered regardless of data origin ($\mu = 37 \pm$ SD 9). Among the three strategies adopted for locus identification, with the exclusion of corallimorpharians, *in vitro* methods clearly outperformed *in silico* methods among scleractinians. Specifically, in ascending order of loci recovered, low-coverage sequencing samples recovered a mean of 77 (±SD 56) loci, with *Anthemiphyllia patera* Pourtalès, 1878 represented by only five loci. Data mined from transcriptomes ($\mu = 160 \pm$ SD 55) and genomes ($\mu = 268 \pm$ SD 67) recovered comparatively more loci, with hybrid capture ($\mu = 311 \pm$ SD 54) outperforming all *in silico* methods (Fig. S1).

3.2. Phylogenetic analyses

From the initial 452 loci targeted by Quek et al. (2020), 449 were available for phylogenetic inferences following quality filtering. The alignment lengths of the concatenated matrices in order of increasing levels of missing data as defined in Quek and Huang (2019) were: (1) 67,735 bp with 15.55% missing data for the 75-percent taxon-occupancy matrix; (2) 127,966 bp with 25.74% missing data for the 50-percent taxon-occupancy matrix; (3) 156,856 bp with 31.99% missing data for the 25-percent taxon-occupancy matrix; and (4) 175,718 bp with 37.67% missing data for the all-loci matrix.

Among the four different ML trees reconstructed, topologies were very similar at all deep nodes, with incongruences observed only in shallow nodes. Likewise, the BI phylogeny also largely corresponded with the all-loci matrix ML phylogeny reconstruction (Figs. 1, 2). Furthermore, bootstrap support generally increased with increasing alignment lengths: (1) 75-percent taxon-occupancy matrix (mean = 86 ± SD 22); (2) 50-percent taxon-occupancy matrix (mean = 90 ± SD 18); (3) 25-percent taxon-occupancy matrix (mean = 91 ± SD 17); and (4) all-loci matrix (mean = 92 ± SD 16).

As expected, both the “Robust” and “Complex” clades were recovered unequivocally with both ML and BI analyses (Fig. 1). Relationships among families and genera also largely mirrored previous analyses (e.g. Kitahara et al., 2016). However, there were differences, such as Micrabaciidae being sister group to the “Robust” clade, instead of the sister to both “Robust” and “Complex” clades (see also Quattrini et al. 2020; McFadden et al. 2021). In addition, several non-monophyletic families were recovered, including Deltocyathiidae (see Kitahara et al., 2013), Caryophylliidae (see Seiblitz et al., 2022) and Coscinaraeidae.

Within the “Complex” clade, our reconstruction found a number of interesting relationships, such as the placement of *Alveopora* Blainville, 1830 as sister to *Montipora* Blainville, 1830 and, *Coeloseris* Vaughan, 1918 and *Pachyseris* Milne Edwards & Haime, 1849 as being closely related to members of the Euphylliidae. Furthermore, the non-monophyly of *Pavona* Lamarck, 1801 within the Agariciidae highlighted inconsistencies between currently accepted classification and phylogenomic reconstructions. In addition, we confidently placed *Bernardpora* Kitano & Fukami, 2014 as sister to *Porites* Link, 1807, and corroborated evidence for the “*Porites lobata* species complex” (*sensu* Forsman et al., 2009), here comprising *P. lobata*, *P. lutea*, *P. deformis*, *P. australiensis* and *P. cylindrica* (Fig. 1). Finally, *Deltocyathus magnificus* Moseley, 1876 was found to be sister to members of Turbinoliidae Milne Edwards & Haime, 1848, with the remaining two *Deltocyathus* Milne Edwards & Haime, 1848 species nested within the “Robust” clade as previously suggested by Kitahara et al. (2010, 2013) and Stolarski et al. (2011).

Within the “Robust” clade, we placed *Leptastrea* Milne Edwards & Haime, 1849 as sister to *Heliofungia* Wells, 1966 within Fungiidae with strong statistical support. The distant relationship between Plerogyridae Rowlett, 2020 and Plesiastreidae Dai & Horng, 2009 was also unexpected, along with relationships within Fungiidae such as *Sandalolitha robusta* (Quelch, 1886) being nested within *Podabacia* Milne Edwards & Haime, 1849, *Danafungia horrida* (Dana, 1846) as sister to *Lithophyllon undulatum* Rehberg, 1892 and congener *D. scruposa* (Klunzinger, 1879) as sister to *Fungia* Lamarck, 1801. We further clarified relationships between members of the Merulinidae, which ranks among the most taxonomically challenging group, along with the Caryophylliidae. Taxa of interest within the Merulinidae include *Dipsastraea* Blainville, 1830, *Favites* Link, 1807, and *Goniastrea* Milne Edwards & Haime, 1848, all of which were not monophyletic. Finding *Merulina* Ehrenberg, 1834 nested within *Goniastrea* was also unexpected.

3.3. Divergence time estimation

In the analyses including all calibration points (Table S3), while the $ESS_{posterior}$ stood at 538.8, the ESS for the most recent common ancestor (MRCA) age (ESS_{MRCA}) were less than 25, with the exception of Fungiidae ($ESS_{MRCA} = 207.1$). Among all the single-calibration estimations, the Fungiidae-calibrated analysis outperformed all the other analyses

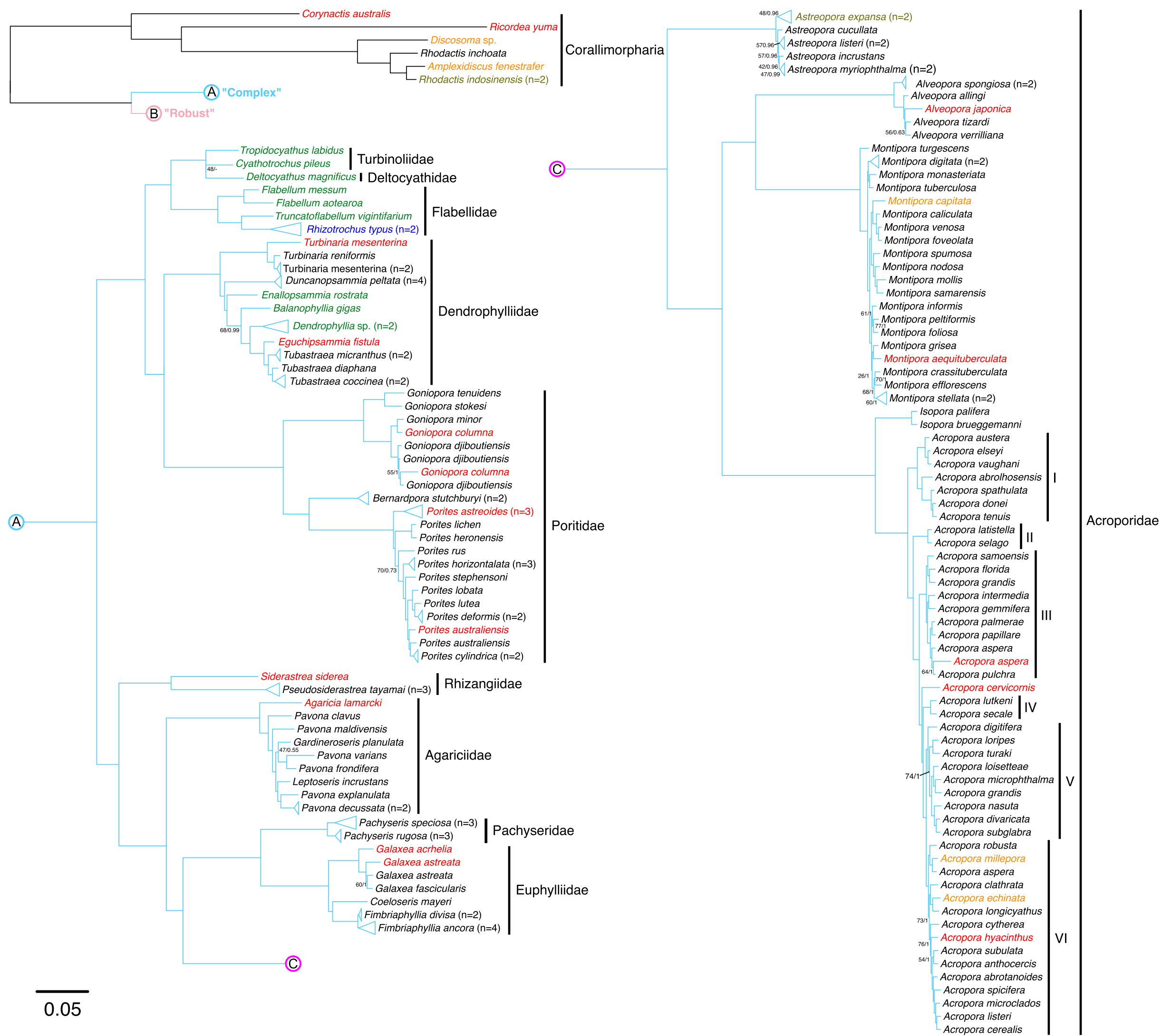

Fig. 1. Maximum likelihood phylogeny of scleractinian corals with corallimorpharians as outgroup, focusing on the "Complex" clade. Bootstrap support and Bayesian posterior probabilities were both greater than 80 and 0.9 respectively, unless otherwise stated. Taxon names coloured to show the different data types: hybrid capture (black), genome simulations (orange), low-coverage sequencing simulations (green), transcriptome simulations (red), hybrid capture and transcriptome simulations (olive), low-coverage sequencing and transcriptome simulations (blue), and genome and transcriptome simulations (purple).

($ESS_{posterior}$ = 684)—ranked in descending order, *Hydnophora* ($ESS_{posterior}$ = 667.5), *Montastraea* ($ESS_{posterior}$ = 570.2), and Acroporidae ($ESS_{posterior}$ = 349.9), with the others having a $ESS_{posterior}$ less than 300 (Table S3). The estimations with a step-wise inclusion of calibrations, based on the Fungiidae-calibrated tree, also fared poorly. While the tree with all five calibrations plus root performed well ($ESS_{posterior}$ = 474.2), the remaining ESS_{MRCA} ranged between 46 and 71 only. All time-calibrated phylogenies were deposited at Zenodo (https://doi.org/10.5281/zenodo.7677093).

4. Discussion

The phylogenomic tree reconstructed in this study is the largest thus far in terms of taxon sampling of scleractinians with representatives across a majority of extant lineages. The paucity of phylogenomic data on scleractinians was apparent prior to the present analysis, with the highest taxonomic coverage previously presented by Cowman et al. (2020) with 99 samples but from only three families (see also Quattrini et al., 2020; McFadden et al., 2021). The relationships among all family-level clades here are very similar to the 12-gene tree of Kitahara et al. (2016), despite a stark contrast in the number and type of markers analysed. Nevertheless, our study highlights the value of using phylogenomics in future reconstructions, due to the higher resolving power and node support afforded by large data matrices, and to resolve affinities within problematic lineages (e.g. *Leptastrea*, discussed below). Our comprehensive phylogeny has also uncovered several topological differences for a number of subfamilial taxa with previous molecular phylogenies reconstructed based on mitochondrial and ribosomal genes (e.g. Fukami et al., 2008; Kitahara et al., 2010b, 2016). Furthermore, unlike the aforementioned large phylogenies, bootstrap and posterior probabilities are high across all nodes, regardless at shallow or deep levels (Figs. 1, 2). We recognise that large phylogenomic studies like ours can incur considerable costs which may be prohibitive in more resource-limited settings. Many recent studies continue to rely on a small number of loci to resolve taxonomy and build large phylogenies with satisfactory results (e.g. Campoy et al., 2020; Chen et al., 2022; Arrigoni et al., 2023). Therefore, we suggest that hybrid-capture phylogenomics may be most cost-effective for testing recalcitrant species complexes (Grinblat et al., 2021; Ramírez-Portilla et al., 2022), precise time calibration for ancestral trait reconstruction (Quattrini et al., 2020), or resolving uncertain evolutionary relationships (Cowman et al., 2020; this study).

Fig. 2. Maximum likelihood phylogeny of scleractinian corals with corallimorpharians as outgroup, focusing on the "Robust" clade. Bootstrap support and Bayesian posterior probabilities were both greater than 80 and 0.9 respectively, unless otherwise stated. Taxon names coloured to show the different data types: hybrid capture (black), genome simulations (orange), low-coverage sequencing simulations (green), transcriptome simulations (red), hybrid capture and transcriptome simulations (olive), low-coverage sequencing and transcriptome simulations (blue), and genome and transcriptome simulations (purple).

The inclusion of transcriptome and genome data in hybrid-capture analyses have been applied across the tree of life, including anthozoans (Quattrini et al., 2018, 2020), bees (Bossert et al., 2019), lepidopterans (Breinholt et al., 2018), and wasps (Bank et al., 2017). Within scleractinians, the inclusion of transcriptome and genome data is particularly useful, considering difficulties in obtaining samples from some taxa. For example, this study focuses largely on samples from the Indo-Pacific realm, without the inclusion of new samples from the Atlantic Ocean. By capitalising on available transcriptomes, such as for *Pseudodiploria strigosa* (Dana, 1846) and *Porites astreoides* Lamarck, 1816, we have been able to incorporate distinct lineages for analyses at a global scale. Notably, the phylogenetic positions of taxa mined from genome and transcriptome simulations are concordant with recent phylogenomic studies, such as *Porites astreoides* being the earliest diverging *Porites* (Quek and Huang, 2019). Despite leveraging *in silico* methods, we highlight that the sampling in this study remains geographically limited due to the exclusion or limited representation of taxa from regions such as East Africa, Indian Ocean, and parts of the Pacific Ocean. Future studies may consider building upon the phylogeny reconstruction based on techniques used in this study to further our understanding of coral evolution at the global scale.

Among samples for which both a genome and transcriptome have been used (i.e. *Orbicella faveolata* (Ellis & Solander, 1786) and *Montastraea cavernosa* (Linnaeus, 1767)), we recover them as clades between the two samples (Fig. 2). However, in a small number of taxa the inclusion of transcriptome data reveals inconsistencies. For example, transcriptome data from *Platygyra* show one *P. sinensis* (Milne Edwards & Haime, 1849) representative forming a clade with *P. carnosa* Veron, 2000, rather than with the other *P. sinensis* sampled via hybrid capture. This could be an artefact of sampling, since transcriptomic data is derived from expressed transcripts, whereas genome and hybrid-capture data are more similar, being derived from complete sequences with both exons and introns instead. Alternatively, the short branches within *Platygyra* suggests that there is limited phylogenetic signal within that clade (see Miller and Babcock, 1997; Miller and Benzie, 1997; Mangubhai et al., 2007; Huang et al., 2009, 2011). It is also possible that the sample identified as *P. carnosa* does not belong to a species that is distinct from *P. sinensis*, given that the former has been described with features similar to other *Platygyra* species, including *P. sinensis*. In fact, *Platygyra carnosa* has been described as being massive in colony shape,

with cerioid to submeandroid corallites and thin, acute walls; the only diagnostic feature is its fleshy polyps (Veron, 2000, 2002). Close examination of their type material—MTQ G55795 at Museum of Tropical Queensland, and MNHN IK-2010–417 at Muséum national d'Histoire naturelle, respectively—confirms the similarity. Nevertheless, the majority of taxa represented by transcriptome data fell within expectations on the phylogeny reconstruction (Figs. 1, 2), suggesting that the inclusion of transcriptomic data is unlikely to be of critical concern except at the shallowest branches. Crucially, we could not rule out the possibility that specimens may have been misidentified, supporting the need for reference skeletal material, topotypes and detailed taxonomic work on such collections following this study (Bonito et al., 2021).

As expected, samples based on low-coverage sequencing simulations yield the fewest loci (Fig. S1). Despite the small number of loci, the novel pipeline developed in this study to combine all three types of data has resulted in a phylogeny that is remarkably similar to previous reconstructions (Kitahara et al., 2016; Quattrini et al., 2020). To illustrate this, all three samples from Micrabaciidae identical to that of Quattrini et al. (2020) have been recovered as the earliest diverging clade within the "Robust" corals, contradicting molecular phylogenies that confidently and consistently recovered Micrabaciidae as a member of the "Basal" clade (Stolarski et al., 2011; Campoy et al., 2020; but see Seiblitz et al., 2020). There remain limited characteristics that could be considered autapomorphic for the "Robust" clade, apart from a developmental trait in the embryo—forming a hollow sphere or having a well-developed blastocoel (Okubo et al., 2013). However, this trait is also present in the "Complex" species *Pavona decussata* (Dana, 1846). Nevertheless, based on the shorter phylogenetic genetic distance between the "Basal" and "Complex" clades, both Micrabaciidae and Gardineriidae Stolarski, 1996 were placed in the new taxon Refertina with the "Complex" corals (Okubo, 2016), even though their embryonic stages have not been examined. It is however clear that Micrabaciidae is a unique family, being the only extant group to possess thickening deposits comprising irregular meshwork of minute fibres organised into small (1–2 μm thick), chip-like bundles (Janiszewska et al., 2011, 2013, 2015). Results here support its position as sister group to the rest of the "Robust" corals.

With a number of low-coverage genome sequencing datasets available (reviewed in Quek and Huang, 2022), the potential for large phylogenies to be reconstructed with currently available data is noteworthy. Future studies could also adapt the pipeline described in this study to other types of sequencing data (e.g. hybrid-capture data based on alternative sets of bait, and restriction site-associated DNA sequencing, or RAD-seq) to determine the feasibility of the inclusion of other types of sequencing data. This would reduce the prohibitive expenses associated with large-scale phylogenomic studies.

Leveraging the power of molecular data, global efforts by taxonomists have revolutionised our understanding of the phylogeny and systematics of scleractinians. Still, with larger phylogenomic reconstructions, our perspective on scleractinian evolution continues to evolve in tandem. While most families sampled here are recovered as monophyletic (Figs. 1, 2; Kitahara et al., 2016), there remain several families that require additional taxonomic revisions. For example, Caryophylliidae remain one of the few polyphyletic families within the Scleractinia (Romano and Palumbi, 1996; Romano and Cairns, 2000; Kitahara et al., 2013, 2016; but see Seiblitz et al., 2022). Similarly, *Deltocyathus magnificus* (Deltocyathiidae) is nested within Turbinoliidae, consistent with Kitahara et al. (2016). Finally, the families Coscinaraeidae and Psammocoridae Chevalier & Beauvais, 1987 were previously recovered as monophyletic (Benzoni et al., 2007, 2010, 2012b), but with a more comprehensive taxonomic sampling, the monophyly of Coscinaraeidae has been challenged (Fig. 2; Kitahara et al., 2016).

Specifically in the "Complex" clade, in agreement with the phylotranscriptomic reconstruction by Richards et al. (2020), we recovered *Alveopora* as sister to *Montipora*, contrary to mitochondrial and ribosomal phylogenies that placed *Alveopora* as sister to *Astreopora* Blainville, 1830 (Fukami et al., 2008; Kitahara et al., 2010b, 2014; Kitano et al., 2014). Morphological evidence supporting the sister relationship between *Alveopora* and *Montipora* is based primarily on the shared morphological feature of well-developed synapticular rods which grow horizontally and inwards from nodes in the corallite wall (Richards et al., 2020). While present, horizontal synapticular growth is much less well-developed in *Astreopora*.

Similarly, *Coeloseris mayeri* Vaughan, 1918 and *Pachyseris* were historically classified under Agariciidae based on morphology (e.g. Vaughan and Wells, 1943; Veron and Pichon, 1980), although the former lacks certain micromorphological features common to other agariciids (Kitahara et al., 2012). *Pachyseris*, in fact, is currently classified as Scleractinia *incertae sedis*, being more closely related to Euphylliidae Milne Edwards & Haime, 1857 (Kitahara et al., 2012). Similar to *Pachyseris*, *C. mayeri* was recovered closer to euphylliids than to agariciids, with Arrigoni et al. (2017) recovering *C. mayeri* as sister to the euphylliids: *Galaxea astreata* (Lamarck, 1816) and *Euphyllia glabrescens* (Chamisso & Eysenhardt, 1821). *Coeloseris* has recently been moved into Euphylliidae formally (Arrigoni et al., 2023). These results were in agreement with previous morphological analyses by Kitahara et al. (2012) showing the lack of the Agariciidae autapomorphies, such as the presence of long menianae on septal faces where low but pointed granulae are rather found, like in other Euphylliidae species. Consistently, we have here recovered a similar topology, with *Pachyseris* being sister to Euphylliidae, and *C. mayeri* nested within Euphylliidae and sister to *Fimbriaphyllia* Veron & Pichon, 1980.

Since *Pachyseris* is a distinct clade and, according to Article 16.2 of the International Code of Zoological Nomenclature, the family name Pachyseridae has already been used informally while still taxonomically unavailable (Mizerek et al., 2016; Coleman et al., 2019; Bridge et al., 2020; Cárdenas et al., 2020), we hereby formally propose the family name Pachyseridae Benzoni & Hoeksema, with *Pachyseris* Milne Edwards & Haime, 1849, as the type and only genus (by original designation). The family characters are the same as those of the type genus, whose type species, *P. rugosa* (Lamarck, 1801), was redescribed most recently by Terraneo et al. (2014). *Pachyseris* was separated from the Agariciidae because of its distinct phylogenetic position, and was temporarily placed in Scleractinia *incertae sedis* (Terraneo et al., 2014).

Within *Acropora*, we could not directly compare our results with the topology in Cowman et al. (2020) due to the small number of overlapping taxa ($n = 12$). Notably, we recovered seven major clades instead of six—the additional clade represented by the Caribbean species *Acropora cervicornis* (Lamarck, 1816), which is sister group to clades IV, V and VI (*sensu* Cowman et al., 2020)—with several similarities between the two topologies. First, *A. austera* (Dana, 1846) belongs to the earliest diverging clade of *Acropora*, labelled as clade I *sensu* Cowman et al. (2020) (see also Richards et al., 2016) (Fig. 1). We note that *A. tenuis* (Dana, 1846) is also placed within this clade, corresponding to Mao et al. (2018) who suggested that *A. tenuis* has been genetically isolated from the other acroporids based on whole genome data (see also van Oppen et al., 2001). Unexpectedly, we recovered *A. abrolhosensis* Veron, 1985, *A. elseyi* (Brook, 1892) and *A. spathulata* (Brook, 1891) in clade I, which occurred in more terminal clades in Richards et al. (2016). In clade II *sensu* Cowman et al. (2020), we similarly recovered *A. latistella* (Brook, 1892) as a member of the second diverging lineage, sister to *A. selago* (Studer, 1879) (Fig. 1). In the third lineage (clade III *sensu* Cowman et al., 2020), there were no overlapping taxa *per se*, albeit one *A.* aff. *intermedia* was included in their phylogeny, with ours identified as *A. intermedia* (Brook, 1891) that overlapped between the two studies. Members of clade IV *sensu* Cowman et al. (2020) were not present in our study but are likely to be closest to *A. lutkeni* Crossland, 1952 and *A. secale* (Studer, 1878) here based on Wallace (1999). Three intersecting members between the two studies—*A. digitifera* (Dana, 1846), *A. turaki* Wallace, 1994 and *A. divaricata* (Dana, 1846)—in clade V *sensu* Cowman et al. (2020) were also recovered as part of a similar clade here. Finally, in clade VI *sensu* Cowman et al. (2020), *A. spicifera* (Dana,

1846), *A. abrotanoides* (Lamarck, 1816), *A. cytherea* (Dana, 1846) and *A. listeri* (Brook, 1893) were recovered in the terminal clade within *Acropora* (Fig. 1). We further recovered *A. longicyathus* (Milne Edwards, 1860) and *A. echinata* (Dana, 1846) as sister taxa in this study (Fig. 1). Within this hyperdiverse clade, there is direct experimental, molecular or genetic evidence for hybridisation, polyploidy and gene duplication events (Kenyon, 1997; Willis et al., 2006; Richards et al., 2008; Mao et al., 2018; Mao and Satoh 2019; Mao, 2020; Hobbs et al., 2022), along with rapid speciation (Wallace and Rosen, 2006; Richards et al., 2013), convergent evolution (Richards et al., 2010) and phenotypic plasticity (Todd, 2008; Million et al., 2022). These factors potentially interact to confound interpretations of evolutionary history. While genome-wide markers such as those applied here should reduce the effect of bias amongst markers, progressing our understanding of species relationships in *Acropora* requires well-replicated phylogeographic studies that are linked to taxonomically sound skeletal reference specimens and type material (Cowman et al., 2020; Bonito et al., 2021; e.g. Juszkiewicz et al., 2022), and where possible, reproductive studies (Ramírez-Portilla et al., 2022). Only with such integrated taxonomic approaches (Kitahara et al., 2016) will it be possible to disentangle discrepancies between species and gene trees and interpret species relationships confidently.

Consistent with previous molecular analyses, the non-monophyly of *Pavona* Lamarck, 1801 (Agariciidae) was reliably recovered (Kitahara et al., 2012; Luck et al., 2013; Waheed et al., 2015; Terraneo et al., 2017). We also observed several differences when compared to Terraneo et al. (2017). For example, *Leptoseris incrustans* (Quelch, 1886) is more closely related to *P. decussata* and *P. explanulata* (Lamarck, 1816) than to *Gardineroseris planulata* (Dana, 1846), which forms a sister clade with *P. frondifera* (Lamarck, 1816) and *P. varians* (Verrill, 1864) instead. Given the inconsistencies between phylogenies reconstructed within this enigmatic family, we recommend future taxonomic revisions capitalise on phylogenomic methods for evolutionary reconstructions.

Within Poritidae Gray, 1840, our results are consistent with a recent revision by Kitano et al. (2014) based on COI sequences. Interestingly, Kitano et al. (2014) recovered *Bernardpora stutchburyi* (Wells, 1955) as sister to *Porites*—a result consistent with phylogenomic analyses (Fig. 1)—whereas Kitahara et al. (2016) recovered *Bernardpora* to be sister to *Goniopora* de Blainville, 1830 instead, despite having more molecular markers. This could be due to alignment uncertainty in large phylogenies or conflicting signals between gene trees in concatenated analyses (see Philippe et al., 2011). Within *Porites*, we recovered a phylogeny consistent with Forsman et al. (2009, 2020) and Quek and Huang (2019), with a "*Porites lobata* species complex" comprising five species in this study (*P. lobata* Dana, 1846, *P. lutea* Milne Edwards & Haime, 1851, *P. deformis* Nemenzo, 1955, *P. australiensis* Vaughan, 1918 and *P. cylindrica* Dana, 1846; Fig. 1). Evidently, both nuclear internal transcribed spacer (ITS) and RAD-seq data (Forsman et al., 2009; 2020; Terraneo et al., 2019a, 2019b, 2021) were unable to resolve the complex.

In the "Robust" clade, *Nemenzophyllia* Hodgson & Ross, 1982, *Blastomussa* Wells, 1968, *Plerogyra* Milne Edwards & Haime, 1848 and *Physogyra* Quelch, 1884 formed a clade based on mitochondrial and ribosomal reconstructions (Benzoni et al., 2014; Kitahara et al., 2016; Arrigoni et al., 2017). As Benzoni et al. (2014) further stated, more work is required on skeleton macro- and micromorphology from candidates within the family before proposing a family-level classification. To date, no published account exists of any morphological character that could be considered an autapomorphy of the family Plerogyridae despite its formal establishment. An exception can be made when a new family consists of a single monophyletic genus, such as Pachyseridae with *Pachyseris* in the present study. Similar to Kitahara et al. (2016), Benzoni et al. (2014) recovered *Plerogyra* and *Physogyra* as sister to Plesiastreidae. However, we recovered a distinct phylogenetic relationship, with both members represented in Plerogyridae as the earliest diverging clade from Fungiidae, Coscinaeridae, Psammocoridae, Oulastreidae Vaughan, 1919 and Caryophylliidae (Fig. 2). Nevertheless, our study lacked representatives from Meandrinidae Gray, 1847 and Oculinidae Gray, 1847, which are potentially important in clarifying the phylogenetic positions of *Plerogyra* and *Physogyra* (see Kitahara et al., 2016; Arrigoni et al., 2017).

Diverging before Fungiidae, Psammocoridae and Coscinaraeidae, Oulastreidae consists of a single extant accepted species: *Oulastrea crispata* (Lamarck, 1816). In this study, we designated two samples as Oulastreidae sp. 1 and sp. 2 due to their phylogenetic position and molecular affinity in morphology to *Oulastrea crispata*. Based on Kitahara et al. (2016), *Heterocyathus sulcatus* (Verrill, 1866) is sister to *O. crispata*, similar to Arrigoni et al. (2017) with *Heterocyathus* sp. sister to *O. crispata*, a result which we replicated with the exception of Oulastreidae sp. 2 in between the two tips. Given the complicated taxonomy of caryophylliids, under which *H. sulcatus* is currently ascribed to, the massive undertaking to revise members of Caryophyllidae would likely be aided by phylogenomic techniques (Seiblitz et al., 2022).

Recently, some species of *Leptastrea* underwent a taxonomic revision by Arrigoni et al. (2020), but their phylogenetic position within Scleractinia was uncertain. Molecular phylogenies based on varied markers have consistently recovered *Leptastrea* as being closely related to or nested within Fungiidae (Romano and Palumbi, 1996; Fukami et al., 2008; Kitahara et al., 2010b, 2016). Here, our analyses placed *Leptastrea* as sister to *Heliofungia* with maximum support, resolving their phylogeny for the first time. Nevertheless, only one species of *Leptastrea* (n = 3) was included in this study, and more taxonomic work is needed to unravel the intriguing phenomenon of this "faviid" (*sensu* Veron, 2000) nested among mushroom corals. Morphologically, all Fungiidae share "fulturae" (i.e., compound synapticulae connecting adjacent septa) as a synapomorphy (Gill, 1980; Hoeksema, 1989), which previously supported the inclusion of *Cycloseris explanulata* (van der Horst, 1922) and *C. wellsi* (Veron & Pichon, 1980) in that family, while they were previously considered most closely affiliated with members of Psammocoridae and Coscinaraeidae, respectively (Benzoni et al., 2007, 2012a).

Gittenberger et al. (2011) had revised members of Fungiidae using two genes: COI and ITS, distinguishing three major clades within the family, of which only one was supported by morphological examination. While several genera they examined were recovered as monophyletic (i.e. *Ctenactis* Verrill, 1864, *Podabacia* and *Danafungia* Wells, 1966), our phylogenomic reconstruction suggests otherwise (Fig. 2). In particular, *Podabacia* and *Sandalolitha* Quelch, 1884 were recovered as sister clades by Gittenberger et al. (2011), but our analyses nested *Sandalolitha* within *Podabacia* instead. There are also several topological differences between the trees, such as *Danafungia horrida* being more closely related to *Lithophyllon* Rehberg, 1892 rather than being in a monophyletic group with *D. scruposa*. Nonetheless, we did not include several other fungiid genera, such as *Cycloseris* Milne Edwards & Haime, 1849, *Halomitra* Dana, 1846, *Pleuractis* Verrill, 1864 and *Zoopilus* Dana, 1846, which could affect the topology within this family. Finally, as with many scleractinians, cryptic species complexes are increasing acknowledged as a critical factor to consider in light of the molecular phylogeny (e.g. Forsman et al., 2009, 2017, 2020; Bongaerts et al., 2021; Feldman et al., 2022). For example, Oku et al. (2020) recently found a cryptic lineage within *Fungia fungites*. A targeted, comprehensive revision of Fungiidae is still needed, and phylogenomics has the potential to resolve species relationships within the family.

Having earned the moniker "Bigmessidae" due to difficulty in its classification based on morphological characters (Budd, 2009; Huang et al., 2011), members within Merulinidae were revised extensively in a global effort based on a few standard molecular markers in conjunction with morphological traits (Huang et al., 2009, 2011, 2014a, 2014b; Budd et al., 2012). Consistent with Huang et al. (2014a, 2014b), we showed *Paragoniastrea* Huang, Benzoni & Budd, 2014 to be phylogenetically distinct from *Goniastrea*, and *Coelastrea* Verrill, 1866 from other *Dipsastraea*. Similar to Huang et al. (2014a), we also recovered *G. retiformis* (Lamarck, 1816) as phylogenetically distinct from *G. favulus* (Dana, 1846), *G. pectinata* (Ehrenberg, 1834) and *G. edwardsi* Chevalier,

1971, which also form a clade with *Merulina ampliata* (Ellis & Solander, 1786), *M. scabricula* Dana, 1846 and *M. cylindrica* (Milne Edwards & Haime, 1849). Several genera still require revision despite the extensive work from the present phylogenomic and past phylogenetic analyses, including but not limited to *Favites*, *Pectinia* Blainville, 1825 and *Dipsastraea* (but see Arrigoni et al., 2021). We expect ongoing efforts to continue within this clade, which could be catalysed by robust phylogenetic sampling based on hybrid-capture techniques.

There have been many disparate estimates of divergence times based on mitochondrial and ribosomal genes (Stolarski et al., 2011, 2021; Park et al., 2012; Huang and Roy, 2015; Kitahara et al., 2016; Campoy et al., 2020). However, McFadden et al. (2021) composed a phylogenomic reconstruction across broad taxonomic groups of anthozoans using hybrid capture that recovered a robust and well-supported time-calibrated anthozoan phylogeny. Despite our best efforts, we could not secure a reliable, time-calibrated phylogeny across most divergence dating analyses. Fossils are invaluable for calibration of node ages within a phylogeny, but the lack of relevant fossils, and both sampling and phylogenetic uncertainties can obfuscate accurate estimations (Forest, 2009; Sauquet, 2013; Guindon, 2020). Furthermore, other priors such as statistical distributions for age bounds of clades based on fossils (Ho and Phillips, 2009; Parham et al., 2012; Nowak et al., 2013), clock models (Ho, 2009; Sauquet, 2013; Crisp et al., 2014), and nucleotide substitution models and associated partitions (Schenk and Hufford, 2010; but see Du et al., 2019) also affect the resulting output. For large phylogenomic analyses such as ours, immense computational burden is imposed. We emphasise that additional molecular data might not result in more accurate estimates due to theoretical bounds set by fossil constraints (Dos Reis et al., 2018). Instead, it might be more helpful to further expand the taxonomic sampling and carefully subsample gene sets for detailed analysis. This would also apply to several Atlantic reef coral genera, which have received very little attention in molecular studies and contain unresolved species problems, such as some genera in the family Faviidae (e.g. *Mycetophyllia* Milne Edwards & Haime, 1848 and *Scolymia* Haime, 1852).

5. Conclusions

Phylogenomics harnesses the information present in genomes to better resolve both shallow and deep relationships among taxa, circumventing the issues plaguing phylogenies reconstructed based on mitochondrial and/or ribosomal genes only, particularly in taxonomic revisions that are typically riddled with polytomies. In this study, we have reconstructed a comprehensive phylogenomic tree for scleractinians and demonstrated the urgent need for taxonomic revisions in several clades. We do so with a much higher degree of confidence across all branches, applying novel techniques to augment taxon sampling based on previous genomic data. The approach and findings here provide much promise for further stabilising the topology and our understanding of the scleractinian tree of life.

CRediT authorship contribution statement

Z.B. Randolph Quek: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization. **Sudhanshi S. Jain:** Investigation, Data curation, Writing – review & editing. **Zoe T. Richards:** Resources, Data curation, Writing – review & editing, Funding acquisition. **Roberto Arrigoni:** Investigation, Data curation, Writing – review & editing. **Francesca Benzoni:** Data curation, Writing – review & editing. **Bert W. Hoeksema:** Data curation, Writing – review & editing. **Jose I. Carvajal:** Resources, Data curation, Writing – review & editing. **Nerida G. Wilson:** Resources, Data curation, Writing – review & editing. **Andrew H. Baird:** Data curation, Writing – review & editing. **Marcelo V. Kitahara:** Resources, Data curation, Writing – review & editing, Funding acquisition. **Isabela G.L. Seiblitz:** Resources, Data curation, Writing – review & editing. **Claudia F. Vaga:** Resources, Data curation, Writing – review & editing. **Danwei Huang:** Conceptualization, Methodology, Investigation, Data curation, Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2023.107867.

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