Received: 13 December 2023 | Revised: 6 March 2024 | Accepted: 16 March 2024
DOI: 10.1111/zsc.12657

Zoologica Scripta | WILEY

ORIGINAL ARTICLE

Untangling deep-sea corals systematics: Description of a new family, Stephanocyathidae (Anthozoa, Scleractinia), through a genomic approach

Claudia Francesca Vaga[1,2,3] | **Isabela Galvao de Lossio e Seiblitz**[2,3] | **Katia Cristina Cruz Capel**[2,4] | **Andrea M. Quattrini**[1] | **Jaroslaw Stolarski**[5] | **Stephen D. Cairns**[1] | **Marcelo Visentini Kitahara**[1,2,3]

[1]Department of Invertebrate Zoology, Smithsonian Institution, Washington, DC, USA

[2]Center for Marine Biology, University of São Paulo, São Sebastião, Brazil

[3]Graduate Program in Zoology, Department of Zoology, Institute of Biosciences, University of São Paulo, São Paulo, Brazil

[4]Invertebrate Department, National Museum of Rio de Janeiro, Federal University of Rio de Janeiro, Rio de Janeiro, Brazil

[5]Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland

Correspondence
Claudia Francesca Vaga and Marcelo Visentini Kitahara, Department of Invertebrate Zoology, Smithsonian National Museum of Natural History, 10th and Constitution Ave NW, Washington, DC 20560, USA.
Email: claudia.vaga90@gmail.com and mvkitahara@yahoo.com.br

Funding information
Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 142149/2018-7 and 305274/2021-0; Fundação de Amparo à Pesquisa do Estado de São Paulo, Grant/Award Number: 2014/01332-0 and 2021/06866-6

Abstract

Once considered the most speciose mostly azooxanthellate scleractinian group, the family Caryophylliidae is found to be highly polyphyletic based on molecular data and is undergoing a process of systematic revision. High-throughput sequencing methods coupled with morphological analyses have facilitated revision of several scleractinian lineages, including the aforementioned family. In previous studies that relied on few mitochondrial and nuclear markers, the caryophylliid genera *Stephanocyathus* and *Vaughanella* were phylogenetically recovered in separate clades from the lineage that includes the type genus of the family, *Caryophyllia*, which is considered the 'true' Caryophylliidae. To help untangle the relationship among taxa of this family, here a new deep-sea scleractinian family (Stephanocyathidae Vaga, Cairns & Kitahara fam. nov.) is proposed based on phylogenomic reconstructions coupled with molecular features, specifically gene order, of the complete mitochondrial genome. Evolutionary reconstructions were based on both mitochondrial and nuclear ultraconserved elements (UCEs) and exon loci data sets and confirmed the divergent position of the genera *Stephanocyathus* and *Vaughanella*. The new family shows a specific gene transposition in the mitochondrial genome, not present in the 'true' caryophylliid lineage, but instead already observed for the species *Paraconotrochus antarcticus*, recovered as sister taxon of the here proposed new family. Although its phylogenetic position is unknown, the genus *Ericiocyathus* is also added to the new family, based on macromorphological similarities. This study represents a step forward in our understanding of deep-sea corals relationships and provide further information (e.g., mitochondrial gene order) that will aid in future efforts of assessing the systematic of caryophylliid lineages.

KEYWORDS
deep sea, mitochondrial genome, Scleractinia, systematics, ultraconserved elements

1 | INTRODUCTION

Since the onset of molecular studies, scleractinian coral systematics has been under revision and several families have been recovered as para- or polyphyletic (e.g., Arrigoni et al., 2014; Fukami et al., 2008; Huang et al., 2011; Kitahara et al., 2016). Among the latter, species of the family Caryophylliidae Dana, 1846, once considered the most morphologically diverse and speciose family composed mostly—but not only—by azooxanthellate species, have been recovered in at least nine unrelated clades in both the 'Complex'/Refertina and 'Robust'/Vacatina main coral groups (e.g., Campoy et al., 2020; Kitahara et al., 2010, 2016). Consequently, to unify molecular and morphological data, the taxonomy/systematics of the family has been under revision using integrative approaches. Within this effort, studies based on microstructural analyses and phylogenetic results from few nuclear and mitochondrial markers have reassigned: (i) the monospecific caryophylliid genus *Dactylotrochus* Wells, 1954 to the refertinan family Agariciidae Gray, 1847 (Kitahara, Stolarski, et al., 2012)—the former becoming the first azooxanthellate, solitary and deep-sea agariciid—and, concurrently, (ii) the early diverging vacatinan clade composed solely of the 'caryophylliid' *Deltocyathus* Milne Edwards & Haime, 1848 species to the newly established monogeneric family Deltocyathidae Kitahara, Cairns, et al. (2012).

More recently, the more thorough usage of high-throughput sequencing methods—for example target enrichment and genome skimming—has enabled the access and handling of vast amounts of molecular data (Goodwin et al., 2016; Kulkarni & Frommolt, 2017; Quattrini et al., 2023). Coupling nuclear ultraconserved elements (UCEs) and exon loci and complete mitochondrial (mt) genomes, a recent study showed that all sequenced components of the caryophylliid clade comprising the type genus of the family (i.e., *Caryophyllia* Lamarck, 1801), have a specific mt genome rearrangement (i.e., a transposition of the gene block containing *cob*, *nad2* and *nad6* genes between *nad5 5′* and *trnW* different from the canonical scleractinian mt gene order—gene block located between *nad1* and *atp6*) not present in any other sequenced scleractinian taxa (Seiblitz et al., 2022; Vaga et al., 2022). The aforementioned studies recovered the genera *Crispatotrochus* Tenison-Woods, 1878, *Desmophyllum* Ehrenberg, 1834, *Premocyathus* Yabe & Eguchi, 1942 and *Solenosmilia* Duncan, 1873 grouping with *Caryophyllia* in a monophyletic clade that is phylogenetically independent from all the other 'caryophylliid' clades recovered so far. Together, these results suggested that mt genome rearrangements can have taxonomic significance (also shown in other groups of animals such as crabs (Zhang et al., 2020), scale worms (Zhang et al., 2018), and black corals (Brugler & France, 2007)) and that the family Caryophylliidae is smaller than previously thought. Within the two suborders of Scleractinia, mitochondrial rearrangements have been found to occur more frequently in vacatinans than in refertinan corals: (i) duplicated *trnW* in *Seriatopora* Lamarck, 1816 and *Stylophora* Schweigger, 1820 (Chen, Chiou, et al., 2008; Chen, Dai, et al., 2008); (ii) transposition of *trnM* in *Paraconotrochus* Cairns & Parker, 1992 (Stolarski et al., 2021); (iii) inverted order of the *cox3* and *cox2* genes in *Madrepora* Linnaeus, 1758 (Lin et al., 2012); (iv) transposition of the genes *cob*, *nad2*, and *nad6* in Caryophyllidae (sensu Seiblitz et al., 2022); and (v) transposition of the genes *cox2* and *cox3* in Deltocyathidae (Vaga et al., 2024). Besides the caryophylliids transposition, at least another rearrangement (i.e., inverted gene order in *Madrepora*) appears to be family specific (Capel et al., 2024).

The caryophylliid genera *Vaughanella* Gravier, 1915 and *Stephanocyathus* Seguenza, 1864 comprise five and 16 solitary and azooxanthellate extant species, respectively (Hoeksema & Cairns, 2023). For taxonomic purposes, the genus *Stephanocyathus* is divided into three sub-genera based on the presence, size and number of costal spines/tubercles (i.e., *Acinocyathus* Wells, 1984, *Odontocyathus* Moseley, 1880, and *Stephanocyathus*). Similar in gross morphology, *Vaughanella* and *Stephanocyathus* are mainly distinguished by their mode of life: the former always attached to the substrate through a reinforced pedicel and a fairly well-developed encrusting base; and, the latter, being free-living in the adult stage (e.g., Cairns, 1995; Kitahara & Cairns, 2021). Due to their fairly large dimensions for a solitary species and widespread distribution, these species, in particular the ones ascribed to *Stephanocyathus*, are among the most frequently sampled and readily identified deep-sea scleractinians.

Historically assigned to the family Caryophylliidae, both genera have been recovered from previous studies as sister taxa occupying an early divergent position in the vacatinan clade (Kitahara et al., 2016; Quek et al., 2023; Stolarski et al., 2011 [only *Stephanocyathus* included]; but see Campoy et al., 2020). Kitahara and Cairns (2021) proposed 'Clade B', which is composed of a lineage of early diverging genera—that is *Aulocyathus*, *Conotrochus*, *Faustinotrochus*, *Lochmaeotrochus*, *Stephanocyathus* and *Vaughanella*—within vacatinan scleractinians previously assigned to the family Caryophylliidae. However, some of their 'Clade B' genera were included based either only on shared morphological features (Kitahara & Cairns, 2021)—that is *Aulocyathus* and *Lochmaeotrochus*—or on previous phylogenies resulting only from few mitochondrial and nuclear markers (e.g., 16S and 28S; Stolarski et al., 2011) or from a supertree algorithm (Kerr, 2005; Kitahara et al., 2016). Moreover, unlike previous studies, Campoy et al. (2020; using COX1, 16S, 18S and 28S) recovered this lineage as early diverging inside the Refertina clade. Thus, due to the lack of extensive molecular data that often improves resolution in phylogenetic reconstructions, Clade B was not elevated to the family rank.

Herein, based on newly sequenced complete mt genomes and nuclear (>120,000 bp from UCE/exon loci) data sets from *Stephanocyathus* (*Odontocyathus*) *coronatus* (de Pourtalès, 1867), *Stephanocyathus* (*Odontocyathus*) *weberianus* (Alcock, 1902), *Stephanocyathus* (*Stephanocyathus*) *platypus* (Moseley, 1876) and *Vaughanella hexagona* Kitahara & Cairns, 2021, we propose a new scleractinian family in the Robust/Vacatina clade. *S.* (*O.*) *weberianus* was recently synonymized with *S.* (*O.*) *coronatus* by Kitahara & Cairns (2021: 428); however, we kept these species separated to test their relationship with the new set of genomic data. We explored the phylogenetic position of the new family through phylogenomic reconstructions using both nuclear and mitochondrial data sets and mitogenome features. Furthermore, based on similar macromorphological characteristics, we also included the genus *Ericiocyathus* Cairns & Zibrowius, 1997 in the new family, although its phylogenetic placement remains unknown.

2 | MATERIALS AND METHODS

2.1 | DNA extractions, library preparation and sequencing

Specimens were identified to the species level following Cairns (1995) and Kitahara and Cairns (2021). Total genomic DNA extraction of the four specimens analysed in this study (details in Table 1, additional information in Table S1) was performed using the DNeasy Blood and Tissue kit (Qiagen) following the manufacturer's animal tissue protocol. DNA purity and integrity were assessed on a spectrophotometer (Nanodrop, Thermo Fisher Scientific) and in a 1% agarose gel electrophoresis, respectively. Libraries were prepared using the TruSeq DNA Nano library preparation kit (Illumina) with 350 bp insert target size and with modifications in index adapter concentration and number of PCR cycles as proposed by Seiblitz et al. (2022). DNA concentration before and after library preparation was quantified on a Qubit 2.0 fluorometer (Thermo Fisher Scientific), and size distributions were assessed on a Bioanalyzer (Agilent). Illumina sequencing was performed either on a MiSeq (300 bp PE reads) at the Genome Investigation and Analysis Laboratory of the Centro de Facilidades para a Pesquisa (GENIAL CEFAP, USP) or on a NovaSeq 6000 (150 bp PE reads) at the Human Genome and Stem Cell Research Center (CEGH-CEL, USP) (details in Table 1).

TABLE 1 Species, museum catalogue numbers, sequencing platforms and nuclear and mitochondrial data information included in this study.

Species	Museum catalogue number	Illumina platform	# contigs	# nuclear UCEs/exon loci recovered	Average mt assembly coverage	Mt genome length (bp)	Mt genome GC content (%)
Stephanocyathus (*O.*) *coronatus*	MNHN-IK-2012-3821	MiSeq	152,843	675	69.3	15,713	36.7
Stephanocythus (*O.*) *weberianus*	MNHN-IK-2016-2484	NovaSeq	403,737	1432	165.9	15,713	36.7
Stephanocyathus (*S.*) *platypus*	NIWA-125128	NovaSeq	388,570	1188	240.0	15,713	36.7
Vaughanella hexagona	MNHN-IK-2012-17586*	NovaSeq	249,365	637	17.2	15,713	36.7

Note: MNHN and NIWA represent the *Muséum National d'Histoire Naturelle* (Paris, France) and the National Institute for Water and Atmospheric Research (Wellington, New Zealand), respectively. The asterisk (*) indicates paratype material.

2.2 | Mitochondrial genome analyses

Quality control of sequencing data was performed with Trimmomatic (Bolger et al., 2014). Trimmed sequences were assembled into contigs using SPAdes v 3.1 (Bankevich et al., 2012; with the careful parameter) and mitochondrial contigs were selected using command line BLASTn against a set of reference coral mitogenomes. Mitochondrial genes were annotated using MITOS2 online tool (Bernt et al., 2013) with the genetic code 4 (mold) and RefSeq 89 Metazoa. Annotation and circularity were manually verified using Geneious Prime 2022.2.1 (Biomatters Ltd. Auckland, New Zealand). Boundaries of all genes were then confirmed using BLAST against either the NCBI nucleotide database or non-redundant protein sequences database. Base pair differences between complete mitogenomes were calculated through Geneious Prime 2022.2.1. Once mitogenomes were fully annotated, they were included in a phylogenetic reconstruction together with 66 published mitogenomes (see Table S1). Sequence alignments of protein coding, transfer RNA and ribosomal RNA genes were performed with MUSCLE 3.8.425 (Edgar, 2004). Alignments were visually inspected for ambiguous sites and successively concatenated resulting in a final alignment of 13,872 bp.

2.3 | Bioinformatic processing, assembly and alignment of UCE

For the processing of nuclear data, the resulting contigs files from the SPAdes assembler were used. Assembled reads were processed using the phyluce pipeline (Faircloth, 2016). At this stage, previously published genomic and transcriptomic scleractinian data—and Corallimorpharia species as outgroup taxa—were included in the analyses (see Table S2). UCEs and exon loci were identified through genome skimming using the program 'phyluce_assembly_match_contigs_to_probes' that matched a combined scleractinian bait set (Cowman et al., 2020; Quattrini et al., 2018; Quek et al., 2020) to the assembled contigs with a minimum coverage of 70% and a minimum identity of 70%. Loci were then extracted into separate FASTA files using 'phyluce_assembly_get_fastas_from_match_counts' and aligned with default parameters using 'phyluce_align_seqcap_align' in MAFFT (Katoh et al., 2002). Loci were internally trimmed with 'phyluce_align_get_gblocks_trimmed_alignments_from _untrimmed' that uses GBlocks (Castresana, 2000). Multiple data matrices of locus alignments were created using 'phyluce_align_get_only_loci_with_min_taxa', in which each locus had either 50% or 75% species occupancy, and 'phyluce_align_get_informative_sites' was applied to calculate the number of parsimony informative sites. Finally, each locus alignment was then concatenated, and the partition charset explicit using 'phyluce_align_format_nexus_files_for_raxml'.

2.4 | Phylogenomic analyses

For both the mitochondrial and the nuclear data sets, a partitioned phylogenomic analysis was conducted using maximum likelihood (ML) in IQ-TREE v 2.1 (Nguyen et al., 2015). The best-fit models and best partition scheme for the nuclear loci, and the best-fit models for mitochondrial genes were selected by ModelFinder (Kalyaanamoorthy et al., 2017) as implemented in IQ-TREE v 2.1. Ultrafast bootstrap approximantion (UFBoot) (-B 1000; Hoang et al., 2018) was conducted as well as the SH-like approximate likelihood ratio test (-alrt 1000; Anisimova et al., 2011). Both phylogenetic reconstructions were rooted with Corallimorpharia.

3 | RESULTS

3.1 | Nuclear data

For the nuclear data set, a total of 2483 loci (out of 2490) across all targeted specimens were recovered from the assembled contigs (Nuclear UCEs and exon loci sequences were deposited as a Targeted Locus Study [TLS] at GenBank under the BioProject PRJNA1079249, BioSamples # SAMN40034314-7, accession numbers KIFQ00000000-KIFT00000000). The final alignment included 69 scleractinian species, four of which were sequenced for this study, and five corallimorpharians that were used as outgroups. The number of loci recovered from each species ranged from 90 to 1649 per sample (mean: 780 ± 365 loci), with a range between 637 and 1432 loci for the newly sequenced species (Table 1). The 50% and 75% taxon occupancy matrices resulted in identical and well-supported maximum likelihood (ML) topologies (75% taxon occupancy ML tree in Appendix S1). The final 50% matrix (resulting ML topology shown in Figure 1) included a concatenated alignment of 635 UCEs and exon loci with an alignment length of 122,610 bp, of which 41.9% were informative.

The ML phylogeny has 91% of the nodes with support equal or higher than 95% in both SHaLRT and UFBoot values (Figure 1). *Paraconotrochus*, *Stephanocyathus* and *Vaughanella* species were recovered with maximum support (SHaLRT = 100, UFBoot = 100) as a clade sister of the family Deltocyathidae (SHaLRT = 100, UFBoot = 100) and

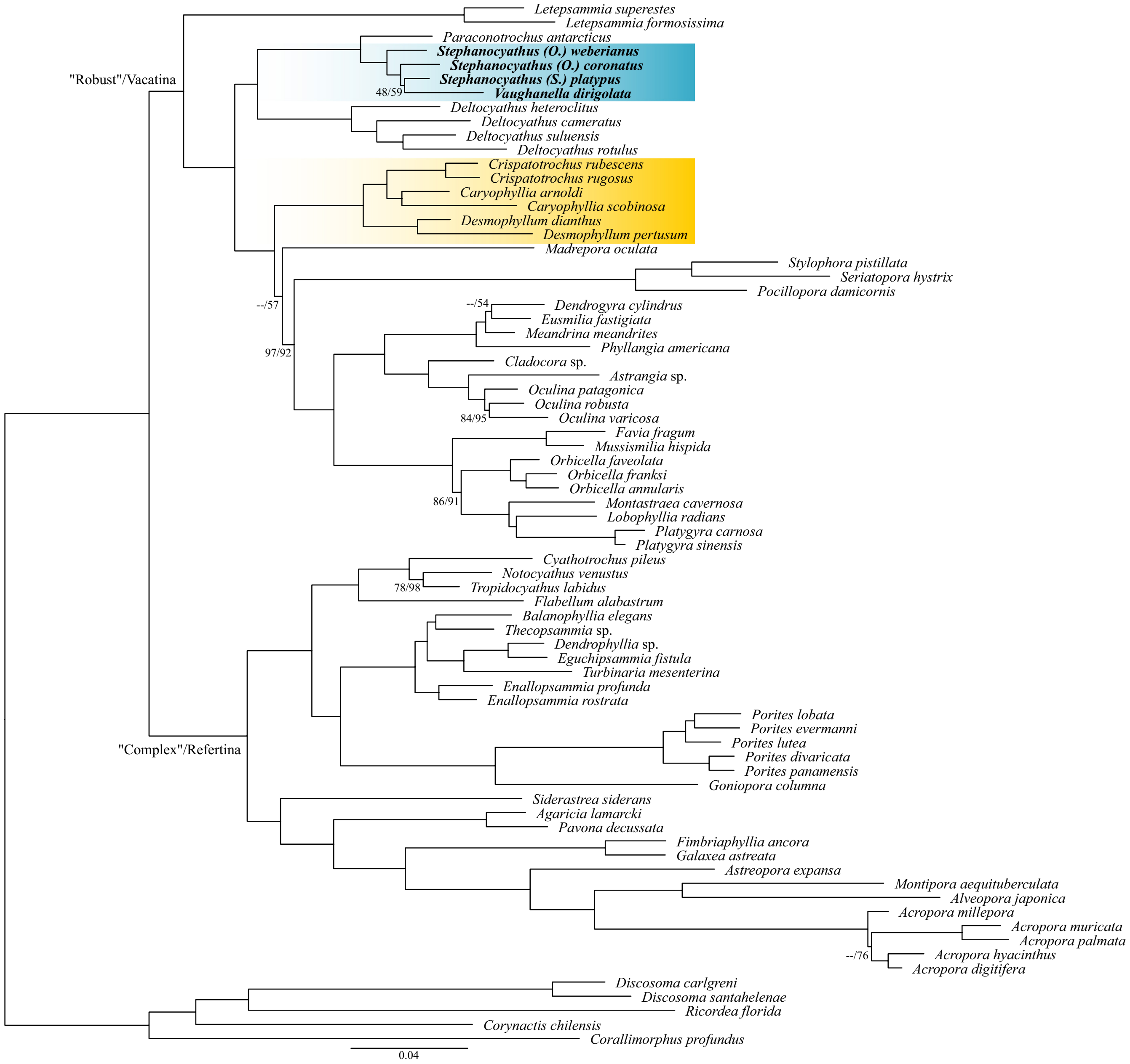

FIGURE 1 Maximum likelihood phylogeny based on the nuclear data set (50% taxon occupancy—122,610 bp). Nodes without numbers indicate SHaLRT and UFBoot values >95. Light blue box indicates the new family Stephanocyathidae Vaga, Cairns and Kitahara fam. nov. Yellow box indicates the 'true' Caryophylliidae clade. Species sequenced for this study are in bold.

early diverging within the Robust/Vacatina clade, well separated from the 'true' Caryophylliidae clade (sensu Seiblitz et al., 2022). Specifically, *P. antarcticus* was recovered as sister species to *Stephanocyathus* and *Vaughanella*. The two *Stephanocyathus* (*O.*) species were recovered as paraphyletic with *V. hexagona* embedded in the clade.

3.2 | Mitochondrial data

The average coverage of mitochondrial genomes ranged from 17.2 to 165.9× (Table 1). The complete mt genomes of *Stephanocyathus* (*O.*) *coronatus*, *Stephanocyathus* (*O.*) *weberianus*, *Stephanocyathus* (*S.*) *platypus* and *V. hexagona* (GenBank accession numbers PP180009-PP180012) are circular and very similar to each other, with equal length (15,713 bp) and GC content (36.7%). Numbers of base pair differences between the four recovered mt genomes are specified in Table 2 and are found both in protein coding genes and intergenic regions. *Stephanocyathus* and *Vaughanella* mitogenomes, similarly to *P. antarcticus* (Stolarski et al., 2021), do not present the *cox1* gene intron previously observed in other scleractinians (Celis et al., 2017;

TABLE 2 Number of mt genome base pair differences between *Stephanocyathus* (*O.*) *coronatus*, *Stephanocyathus* (*O.*) *weberianus*, *Stephanocyathus* (*S.*) *platypus* and *Vaughanella hexagona*.

	S.* (*O.*) *coronatus	***S.* (*O.*) *weberianus***	***S.* (*S.*) *platypus***	***V. hexagona***
S. (*O.*) *coronatus*				
S. (*O.*) *weberianus*	21			
S. (*S.*) *platypus*	11	21		
V. hexagona	18	25	16	

Chuang et al., 2017) and, thus, do not have the LAGLIDADG type homing endonuclease encoded within it (found in some scleractinian *cox1* intron—Fukami et al., 2007; Quattrini et al., 2023). All four mt genomes have a transposition of the gene *trnM*, which is placed between the *nad4* and 12S rDNA, while in the scleractinian canonical mt genome order, the *trnM* is found between the *cox1* and 16S rDNA (Figure 3). This specific mt gene transposition has already been detected in *P. antarcticus* (Stolarski et al., 2021). The intergenic regions (IGR) are all rather short (<200 bp), the only longer one (341 bp) being between the *cox1* and 16S rDNA.

In the mt genome ML phylogeny, 90% of the nodes had support higher than 95% in both SHaLRT and UFBoot values (Figure 2). *Paraconotrochus*, *Stephanocyathus* and *Vaughanella* species were recovered as a clade within the 'Robust'/Vacatina clade (SHaLRT = 100, UFBoot = 100) as sister to all remaining vacatinan corals. The specific position of *P. antarcticus* in relation to *Stephanocyathus* and *Vaughanella* species mirrors what resulted from the nuclear phylogenetic reconstruction. The position of the family Deltocyathidae, which divides the aforementioned species from the remaining vacatinan clades, is poorly supported (Figure 2). However, the 'true' Caryophylliidae group was recovered as a well-separated clade (SHaLRT = 100, UFBoot = 100).

3.3 | Taxonomic account

Order Scleractinia Bourne, 1900

Suborder Vacatina Okubo, 2016

Family Stephanocyathidae fam. nov. Vaga, Cairns & Kitahara (Figure 4)

Type genus

Stephanocyathus Seguenza, 1864.

Etymology

Named after the designated type genus *Stephanocyathus*.

Genera included

Ericiocyathus Cairns & Zibrowius, 1997; *Stephanocyathus* Seguenza, 1864; and *Vaughanella* Gravier, 1915.

Diagnosis

Corallum solitary, robust, trochoid when attached but patellate to bowl-shaped when unattached. Septotheca costate. In some species C1 (or C1-2) bear spines or tubercles. Paliform lobes present before all but last (or last and penultimate) septal cycle. Columella papillose or formed by a solid fusion of axial septal edges.

Remarks

The family is composed of solitary taxa characterized by slightly different macromorphology. Albeit *Ericiocyathus* lacks any molecular data, the genus is transferred to the new family due to its closest resemblance with *Stephanocyathus* as described by Cairns and Zibrowius (1997). The septotheca is costate in all the genera. Long C1 spines are only known in some *Stephanocyathus* species, while the genus *Ericiocyathus* is recognized by having a series of delicate, elongated spines along the entire length of C1 and C2 (Cairns & Zibrowius, 1997). All genera are free-living, except for *Vaughanella*, whose components are attached to the substrate by a robust pedicel (Cairns & Kitahara, 2012). Representatives of this family are distributed worldwide but they are known only from waters deeper than 200 m with the deepest records being at more than 3000 m (see Kitahara & Cairns, 2021).

Micromophological characteristics of the skeleton of Stephanocyathidae Vaga, Cairns & Kitahara fam. nov. are common to all their representatives: distal edges of septa are straight/slightly undulated and rather smooth. Illustrated examples (e.g., Stolarski, 2003: *Stephanocyathus*) show that septal edges consist of densely packed, individualized rapid accretion deposits (RAD); in transverse, etched sections RADs are recognizable as densely packed hollow-out regions; lateral sides of septa are covered with granulations typically with rounded tips; thickening deposits consist of bundles of fibres arranged approximately perpendicularly to the septal surface.

Comparisons

The family Caryophylliidae has been historically defined by the character of its representatives of having completely smooth margins of septa that reflected a simple microstructural organization of the skeleton (Vaughan & Wells, 1943). However, this is an overly generic character that led to

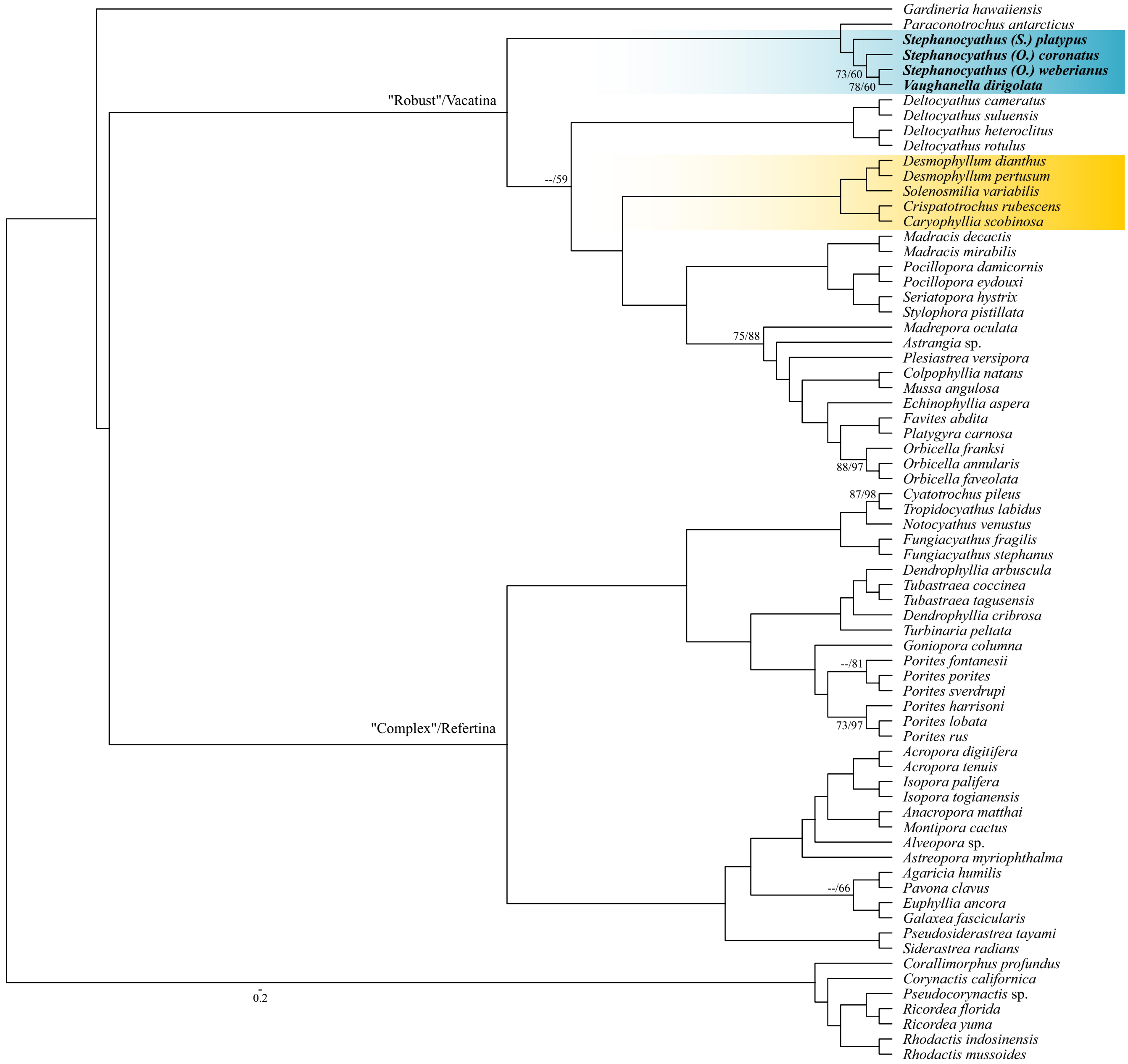

FIGURE 2 Maximum likelihood phylogeny based on the mitochondrial data set (13,872 bp). Nodes without numbers indicate SHaLRT and UFBoot values >95. Light blue box indicates the new family Stephanocyathidae Vaga, Cairns and Kitahara fam. nov. Yellow box indicates the 'true' Caryophylliidae clade. Species sequenced for this study are in bold.

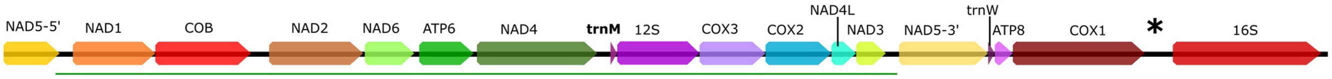

FIGURE 3 Mitochondrial gene map of the species *Stephanocyathus* (*O.*) *coronatus*, *Stephanocyathus* (*O.*) *weberianus*, *Stephanocyathus* (*S.*) *platypus* and *Vaughanella hexagona*. Protein coding, tRNA and rRNA genes were abbreviated as in the text. Blank regions between genes represent intergenic spacers. The NAD5 intron is indicated by the green underline. The transposed gene (trnM) is marked in bold and an asterisk (*) indicates the canonical position of this gene for Scleractinia.

the inclusion in the family of a wide variety of species and genera. While representatives of Stephanocyathidae Vaga, Cairns & Kitahara fam. nov. present smooth margins of septa, they can be differentiated by other traditional caryophylliid lineages using the combination of characters detailed in the diagnosis. The most closely related taxa to Stephanocyathidae Vaga, Cairns & Kitahara fam. nov. following our analysis are *Paraconotrochus antarcticus* and the

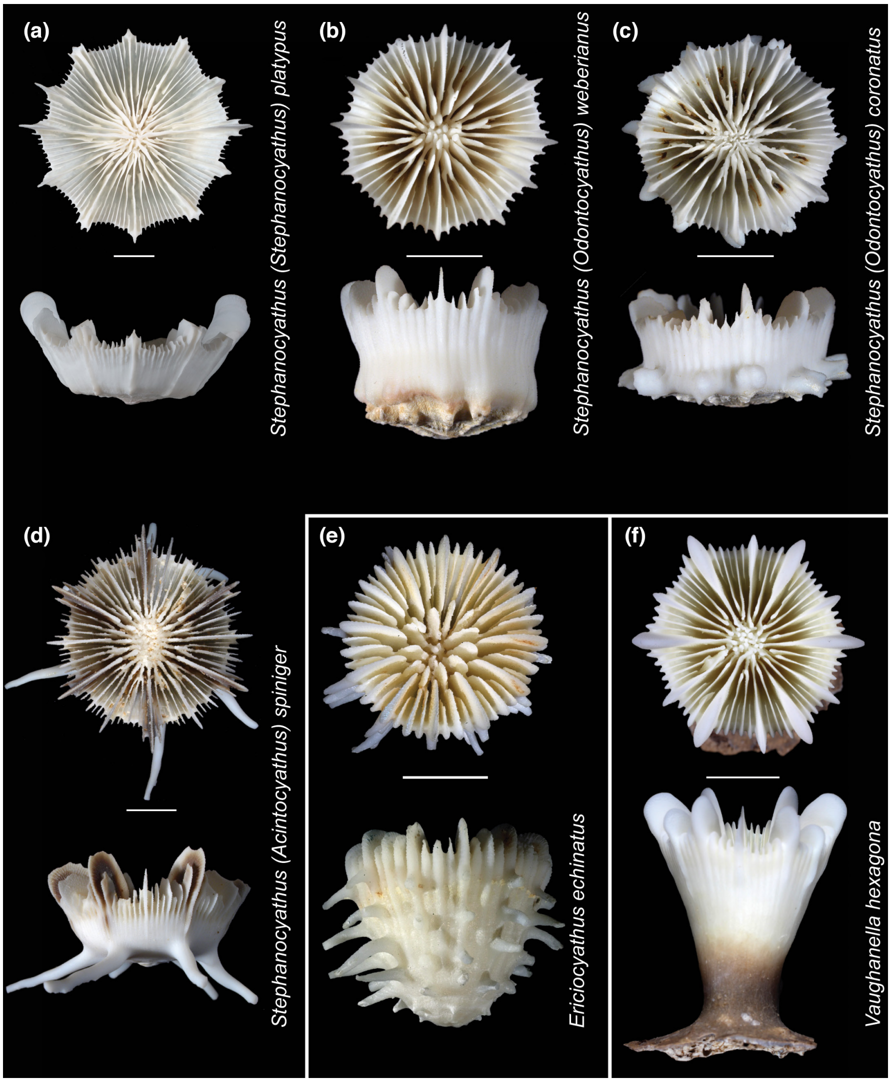

FIGURE 4 Calicular (top) and lateral view (bottom) of some representatives of the three genera included in the newly described family. (a) *Stephanocyathus* (*S.*) *platypus*, (b) *Stephanocyathus* (*O.*) *webarianus*, (c) *Stephanocyathus* (*O.*) *coronatus*, (d) *Stephanocyathus* (*A.*) *spiniger*, (e) *Ericiocyathus echinatus* and (f) *Vaughanella hexagona*. Scale bars: a, 1 cm; b, c, e, f, 2 cm; d, 0.5 cm.

family Deltocyathidae. Species belonging to the latter are easily differentiated from Stephanocyathidae Vaga, Cairns & Kitahara fam. nov. by having a more discoidal corallum (vs. patellate to bowl-shaped) and by having only S1 independent (vs. all septa being independent except for S2 and S3 in some species). Regarding *P. antarcticus*, it presents a thicker theca, smooth or with low granulated ridges (vs. costate in Stephanocyathidae Vaga, Cairns & Kitahara fam. nov.). The corallum is usually trochoid to turbinate (vs. patellate to bowl-shaped) and always free.

Resurrecting Stephanocyathus (*Odontocyathus*) *weberianus* (Alcock, 1902): *S.* (*O.*) *weberianus* was synonymized to *Stephanocyathus* (*Odontocyathus*) *coronatus* based on a large collection that casted doubts on the differentiation of the two species (Kitahara & Cairns, 2021). However, part of the molecular results presented herein advocates that it is a valid species (i.e., not synonymous to *Stephanocyathus* [*Odontocyathus*] *coronatus*). Therefore, the previous morphological differences used to differentiate both species (i.e., [based on Cairns, 1995]: (i)—costal tubercles [12] in *S.* (*O.*) *coronatus* is complexly ornamented and in *S.* (*O.*) *weberianus* [12–18] are simple and usually worn; (ii)—base of *S.* (*O.*) *coronatus* is usually convex, whereas in *S.* (*O.*) *weberianus* is flat; (iii)—corallum of *S.* (*O.*) *coronatus* is higher in the proportion to its diameter; (iv)—*S.* (*O.*) *coronatus* usually have only four septal cycles [48 septa], and that of *S.* (*O.*) *weberianus* usually have additional S5; and (v)—S3-5 of *S.* (*O.*) *coronatus* are less exsert in relation to their S1-2 than in *S.* (*O.*) *weberianus*) are still valid.

4 | DISCUSSION

4.1 | The mitochondrial genomes

The mt genomes from *S.* (*O.*) *coronatus*, *S.* (*O.*) *weberianus*, *S.* (*S.*) *platypus* and *V. hexagona* (details in Table 1) have a length that match those of other vacatinan taxa (from ~14.9 to ~17.8 kbp; e.g., Chen, Dai, et al., 2008; Seiblitz et al., 2022) but a GC content most similar to refertinans

(~36.2 to ~40.5%; e.g., Kitahara et al., 2014), while vacatinan GC content range from ~29.1 to ~35.1%. A higher mt genome GC content has already been detected in other vacatinans such as of *Caryophyllia* (Seiblitz et al., 2022) and *Deltocyathus* (Vaga et al., 2024), as well as in the 'Basal' clade—sensu Stolarski et al. (2011) (but see Quattrini et al., 2020; Seiblitz et al., 2020). The mt genome of *Paraconotrochus antarcticus*—recovered as sister species of the *Stephanocyathus* and *Vaughanella* clade—is longer (i.e., 17,562 bp; Stolarski et al., 2021) mostly due to an IGR of 2187 bp between the *cox1* and the 16S rDNA, which is absent from the other mt genomes from vacatinan species presented in this study. Such significant differences in species belonging to closely related lineages are seldom found in Scleractinia and hexacorals in general. Nevertheless, *P. antarcticus* is a unique and puzzling scleractinian species that was recently discovered to deposit a two-component calcite-aragonite skeleton (Stolarski et al., 2021). Future genomic data of this species will confirm these mitochondrial characteristics and its phylogenetic position inside the order. Results presented here and data from *Deltocyathus* mt genomes (Vaga et al., 2024) show that longer intergenic regions, and highly divergent in the case of *Deltocyathus* species, are found corresponding to the 'canonical' position of the transported genes. This result could point at a possible mechanism of increased base pair substitution rates and/or increased insertion rates after the rearrangement occurred. However, data from additional species are necessary to better investigate this feature and its implications.

Notably, *Stephanocyathus* and *Vaughanella* mt genomes have the *trnM* located between *nad4* and 12S rDNA genes (Figure 3), while the scleractinian 'canonical' position of *trnM* is between *cox1* and 16S rDNA genes. The same transposition was known before only for the mt genome of *P. antarcticus* (Stolarski et al., 2021). Some scleractinian mt genome transpositions have been hypothesized to be specific to certain lineages (i.e., they are synapomorphic), thus acquiring taxonomic significance (Capel et al., 2024; Lin et al., 2012; Seiblitz et al., 2022; Vaga et al., 2024). Given the early divergent position of the new family here described, and the fact that several genera recovered as closely related in previous studies are still missing complete mt data, it is still uncertain whether this transposition is specific to this clade, or if it is more widely present across different lineages.

4.2 | Phylogenetic position of Stephanocyathidae Vaga, Cairns & Kitahara fam. nov.

Both the nuclear and mitochondrial phylogenies recovered the clade comprising *Stephanocyathus* and *Vaughanella* as distinctly separated from the family Caryophylliidae ('true' Caryophylliidae (Seiblitz et al., 2022)). However, while the mt genome-based phylogeny recovered Stephanocyathidae Vaga, Cairns & Kitahara fam. nov.—together with *P. antarcticus*—as sister to the remaining vacatinan lineages, the nuclear phylogeny placed them as sister to the family Deltocyathidae (sister clade), with the two clades as an early diverging vacatinan lineage. Missing data from several species of a specific group can lead to inconsistent topologies (e.g., Liu et al., 2015), thus, a future inclusion of additional early diverging scleractinian lineages will clarify the relationship of Stephanocyathidae Vaga, Cairns & Kitahara fam. nov. with other vacatinan clades, as well as to *P. antarcticus*.

Coupling nuclear and mt genome phylogenetic reconstructions with mitochondrial gene order, this study confirmed the placement of Stephanocyathidae Vaga, Cairns & Kitahara fam. nov. as an independent and early diverging clade within the Vacatina. This result—discordantly only from Campoy et al. (2020) that recovered this lineage as pertaining to the order Refertina—agrees with previous studies that, based on nuclear and mitochondrial markers, consistently recovered *Paraconotrochus*, *Stephanocyathus* and/or *Vaughanella* species as separate lineages from the 'true' Caryophylliidae clade (Daly et al., 2003; Kitahara et al., 2016; Quattrini et al., 2020; Romano & Cairns, 2000; Stolarski et al., 2011).

4.3 | The Stephanocyathus/Vaughanella species complex

Together, *Stephanocyathus* and *Vaughanella* comprise 21 extant species (Hoeksema & Cairns, 2023) but, for this study, only four species were successfully sequenced and analysed. We attempted the sequencing of another three species spanning across the two genera (i.e., *S.* (*S.*) *regius*, *S.* (*A.*) *spiniger* and *V. multipalifera*) but either extraction or library preparation repeatedly failed even when using: (i) different specimens of the same species, (ii) different DNA extraction/purification kits and (iii) modifications in the DNA shearing settings and number of PCR cycles for the library preparation of samples with degraded DNA (see Seiblitz et al., 2022 for details). DNA extractions from some deep-sea scleractinian genera (e.g., *Leptopenus*) often fail or do not perform well regardless of the use of somewhat fresh or museum material (*authors' personal observations*, C. F. Vaga, M. V. Kitahara and I. G. L. Seiblitz). Nevertheless, some representatives of *Stephanocyathus* and *Vaughanella* are within the commonly collected scleractinians in the deep sea and, therefore, additional molecular data might be produced from freshly collected material for the herein-described family in the future. Sequencing the subgenus *Stephanocyathus* (*Acinocyathus*) is of particular interest. In a previous phylogenetic study *Stephanocyathus* (*A.*) *spiniger* was recovered in a separate lineage from *S.* (*O.*) *weberianus* and *S.* (*O.*) *coronatus* (Stolarski et al., 2011) and could therefore belong to a different scleractinian group.

Stephanocyathus (*O.*) *weberianus* has been recently synonymized with *S.* (*O.*) *coronatus* based on a large set of specimens of the latter sampled from New Caledonia. According to Kitahara and Cairns (2021), the examination of more than 400 specimens suggested that some of the morphological characters used to differentiate both species overlap. However, both the nuclear and mitochondrial phylogenies did not recover *S.* (*O.*) *weberianus* and *S.* (*O.*) *coronatus* as monophyletic. Moreover, the mitochondrial genomes of the two *Stephanocyathus* species show a significant number of base pair differences (Table 2), comparable to the differences found between *S.* (*S.*) *platypus* and *S.* (*O.*) *weberianus* already considered distinct species. Currently, complete mt genomes are available for a limited number of scleractinian species and rarely for multiple specimens of the same species, thus a widely accepted genetic distance threshold to differentiate scleractinian genera and/or species using complete mitochondrial genome sequences has not been established to date, and it would be probably 'lineage' specific. Nevertheless, Seiblitz et al. (2022) compared multiple complete mt genomes of geographically distant specimens of *Desmophyllum pertusum*—already suggested to be a cryptic species complex (Le Goff-Vitry et al., 2004)—and found a maximum of 15 base pair differences. Thus, mitochondrial characteristics corroborate the hypothesis suggested by the phylogeny reconstruction that *S.* (*O.*) *coronatus* and *S.* (*O.*) *weberianus* may, in fact, be distinct species. *Stephanocyathus* (*O.*) *weberianus* is therefore herein resurrected resulting in a species known to occur in the western Pacific and New Caledonia. The two species can be separated by the following characters (see Cairns, 1994; Kitahara & Cairns, 2021): (i) *S.* (*O.*) *coronatus* invariably has only 12 costal tubercles corresponding to each C1-2 whereas *S.* (*O.*) *weberianus* has 12–18 smaller tubercles; and (ii) *S.* (*O.*) *coronatus* has more exsert S1-2.

In both the nuclear and mitochondrial phylogenies *V. hexagona* was recovered embedded in the *Stephanocyathus* lineages and, specifically, as sister species of either *S.* (*S.*) *platypus* (Figure 1) or *S.* (*O.*) *weberianus* (Figure 2). This result mirrors previous studies that show *Vaughanella* as closely related to *Stephanocyathus* (Kitahara et al., 2016; Romano & Cairns, 2000), specifically with the former recovered as a paraphyletic lineage, intermingled with *Stephanocyathus* species (Campoy et al., 2020; Stolarski et al., 2011). *Stephanocyathus* and *Vaughanella* share similar macromorphology of the calicular elements (Figure 4), and species have been historically divided into these two genera based on their relationship with the substrate in adult stage: free in *Stephanocyathus*; and attached to the substrate in *Vaughanella* (Cairns, 1995; Kitahara & Cairns, 2021). While such an easily observable trait makes a misidentification of the specimens highly improbable, it is probably not a taxonomically informative feature. In fact, several scleractinian genera house both free-living and attached species—for example *Trochocyathus*, *Balanophyllia*, *Flabellum* (see Kitahara & Cairns, 2021) and *Cycloseris* (Benzoni et al., 2012; Gittenberger et al., 2011)—thus this morphological feature is not necessarily a genus-level defining characteristic. Molecular data from the type taxon and additional species will determine whether *Vaughanella* needs to be synonymized to *Stephanocyathus*.

4.4 | The genus *Ericiocyathus*

The monospecific genus *Ericiocyathus* Cairns & Zibrowius, 1997 was described from dry museum material collected in 1909 from the Philippines (holotype and all paratypes available at the Smithsonian National Museum of Natural History—NMNH). These specimens had been previously identified as *Trochocyathus* (*Aplocyathus*) sp. and, therefore, included in the family Caryophylliidae. No ethanol-preserved specimens are available for this genus. Thus, its placement inside caryophylliids was firstly due to its resemblance to *Trochocyathus*. Unfortunately, fresh *Ericiocyathus* specimens have never been collected on recent expeditions and, therefore, its phylogenetic position remains obscure. Nevertheless, considering the recent efforts of revision of the family Caryophylliidae (see Kitahara, Stolarski, et al., 2012; Kitahara, Cairns, et al., 2012; Seiblitz et al., 2022) and the reassessed closest resemblance between *Ericiocyathus* and *Stephanocyathus* (Cairns & Zibrowius, 1997) we tentatively transfer it to the new family here designated.

ACKNOWLEDGEMENTS

We would like to thank Amana Garrido for the library preparation of the *Stephanocyathus* (*S.*) *platypus* specimen. We would also like to thank Nina Ramos for her help in producing images of *S.* (*S.*) *platypus*. This manuscript is a contribution of NP-BioMar, USP. The authors would like to thank the *Muséum national d'Histoire naturelle* (MNHN, France) for specimens, as well as the Genome Investigation and Analysis Laboratory of the University of São Paulo (Genial CEFAP—USP) and the Human Genome and Stem Cell Research Center (CEGH-CEL, USP), where library preparation and sequencing took place. This work was supported by the São Paulo Research Foundation (FAPESP grants #2014/01332-0 and #2021/06866-6 to MVK) and by The Brazilian National Council for Scientific and Technological Development (CNPq #305274/2021-0 to MVK and #142149/2018-7 to CVF). CFV would also like to thank the Smithsonian Fellowship Program and the Invertebrate Zoology Coral Endowment Fund at the Smithsonian National Museum of Natural History.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

ORCID

Claudia Francesca Vaga https://orcid.org/0000-0002-7431-7452

REFERENCES

Alcock, A. (1902). Diagnoses and descriptions of new species of corals from the "Siboga-expedition". *Tijdschrift der Nederlandse Dierkundige Vereeniging (ser. 2)*, *7*, 89–115.

Anisimova, M., Gil, M., Dufayard, J. F., Dessimoz, C., & Gascuel, O. (2011). Survey of branch support methods demonstrates accuracy, power, and robustness of fast likelihood-based approximation schemes. *Systematic Biology*, *60*, 685–699. https://doi.org/10.1093/sysbio/syr041

Arrigoni, R., Terraneo, T. I., Galli, P., & Benzoni, F. (2014). Lobophylliidae (Cnidaria, Scleractinia) reshuffled: Pervasive non-monophyly at genus level. *Molecular Phylogenetics and Evolution*, *73*, 60–64. https://doi.org/10.1016/j.ympev.2014.01.010

Bankevich, A., Nurk, S., Antipov, D., Gurevich, A. A., Dvorkin, M., Kulikov, A. S., Lesin, V. M., Nikolenko, S. I., Pham, S., Prjibelski, A. D., Pyshkin, A. V., Sirotkin, A. V., Vyahhi, N., Tesler, G., Alekseyev, M. A., & Pevzner, P. A. (2012). SPAdes: A new genome assembly algorithm and its applications to single-cell sequencing. *Journal of Computational Biology*, *19*(5), 455–477. https://doi.org/10.1089/cmb.2012.0021

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

Bernt, M., Donath, A., Jühling, F., Externbrink, F., Florentz, C., Fritzsch, G., Pütz, J., Middendorf, M., & Stadler, P. F. (2013). MITOS: Improved de novo metazoan mitochondrial genome annotation. *Molecular Phylogenetics and Evolution*, *69*(2), 313–319. https://doi.org/10.1016/j.ympev.2012.08.023

Bolger, A. M., Lohse, M., & Usadel, B. (2014). Trimmomatic: A flexible trimmer for Illumina sequence data. *Bioinformatics*, *30*, 2114–2120. https://doi.org/10.1093/bioinformatics/btu170

Bourne, G. C. (1900). Chap. 6. The Anthozoa. In E. R. Lankester (Ed.), *A treatise on zoology. Part II. The porifera and Coelenterata* (pp. 1–84). Adam & Charles Black.

Brugler, M. R., & France, S. C. (2007). The complete mitochondrial genome of the black coral *Chrysopathes formosa* (Cnidaria: Anthozoa: Antipatharia) supports classification of antipatharians within the subclass Hexacorallia. *Molecular Phylogenetics and Evolution*, *42*(3), 776–788. https://doi.org/10.1016/j.ympev.2006.08.016

Cairns, S. D. (1994). Scleractinia of the temperate North Pacific. *Smithsonian Contributions to Zoology*, *557*, 1–150.

Cairns, S. D. (1995). The marine fauna of New Zealand: Scleractinia (Cnidaria: Anthozoa). *New Zealand Oceanographic Institute. Memoir*, *103*, 1–210.

Cairns, S., & Kitahara, M. (2012). An illustrated key to the genera and subgenera of the recent azooxanthellate Scleractinia (Cnidaria, Anthozoa), with an attached glossary. *ZooKeys*, *227*, 1–47. https://doi.org/10.3897/zookeys.227.3612

Cairns, S. D., & Parker, S. A. (1992). Review of the recent Scleractinia (stony corals) of South Australia, Victoria and Tasmania. *Records of the South Australian Museum. Monograph Series*, *3*, 1–82, pls. 1–18.

Cairns, S. D., & Zibrowius, H. (1997). *Cnidaria Anthozoa: Azooxanthellate Scleractinia from the Philippine and Indonesian regions* (Vol. *172*, pp. 27–244). Mémoires du Muséum National d'Histoire Naturelle.

Campoy, A. N., Addamo, A. M., Machordom, A., Meade, A., Rivadeneira, M. M., Hernandez, C. E., & Venditti, C. (2020). The origin and correlated evolution of symbiosis and coloniality in scleractinian corals. *Frontiers in Marine Science*, *7*, 461. https://doi.org/10.3389/fmars.2020.00461

Capel, K. C., Zilberberg, C., Carpes, R. M., Morrison, C. L., Vaga, C. F., Quattrini, A. M., Zb Quek, R., Huang, D., Cairns, S. D., & Kitahara, M. V. (2024). How long have we been mistaken? Multi-tools shedding light into the systematics of the widespread deep-water genus *Madrepora* Linnaeus, 1758 (Scleractinia). *Molecular Phylogenetics and Evolution*, *191*, 107994.

Castresana, J. (2000). Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution*, *17*(4), 540–552. https://doi.org/10.1093/oxfordjournals.molbev.a026334

Celis, J. S., Edgell, D. R., Stelbrink, B., Wibberg, D., Hauffe, T., Blom, J., Kalinowski, J., & Palazzo, A. F. (2017). Evolutionary and biogeographical implications of degraded LAGLIDADG endonuclease functionality and group I intron occurrence in stony corals (Scleractinia) and mushroom corals (Corallimorpharia). *PLoS One*, *12*(3), e0173734. https://doi.org/10.1371/journal.pone.0173734

Chen, C., Chiou, C. Y., Dai, C. F., & Chen, C. A. (2008). Unique mitogenomic features in the scleractinian family Pocilloporidae (Scleractinia: Astrocoeniina). *Marine Biotechnology*, *10*, 538–553. https://doi.org/10.1007/s10126-008-9093-x

Chen, C., Dai, C. F., Plathong, S., Chiou, C. Y., & Chen, C. A. (2008). The complete mitochondrial genomes of needle corals, *Seriatopora* spp. (Scleractinia: Pocilloporidae): An idiosyncratic *atp8*, duplicated *trnW* gene, and hypervariable regions used to determine species phylogenies and recently diverged populations. *Molecular Phylogenetics and Evolution*, *46*(1), 19–33. https://doi.org/10.1016/j.ympev.2007.09.013

Chuang, Y., Kitahara, M. V., Fukami, H., Tracey, D., Miller, D. J., & Chen, C. A. (2017). Loss and gain of group I introns in the mitochondrial cox1 gene of the Scleractinia (Cnidaria; Anthozoa). *Zoological Studies*, *56*, 9. https://doi.org/10.6620/ZS.2017.56-09

Cowman, P. F., Quattrini, A. M., Bridge, T. C. L., Watkins-Colwell, G. J., Fadli, N., Grinblat, M., Roberts, T. E., McFadden, C. S., Miller, D. J., & Baird, A. H. (2020). An enhanced target-enrichment bait set for Hexacorallia provides phylogenomic resolution of the staghorn corals (Acroporidae) and close relatives. *Molecular Phylogenetics and Evolution*, *153*, 106944. https://doi.org/10.1016/j.ympev.2020.106944

Daly, M., Fautin, D. G., & Cappola, V. A. (2003). Systematics of the Hexacorallia (Cnidaria: Anthozoa). *Zoological Journal of the Linnean Society*, *139*, 419–437. https://doi.org/10.1046/j.1096-3642.2003.00084.x

Dana, J. D. (1846). *Zoophytes. United States Exploring Expedition during the years 1838–1842* (Vol. *7*, pp. 1–740). Lea and Blanchard, 61 pls. (1846: 1–120, 709–720; 1848: 121–708, 721–740; 1849: atlas pls. 1–61).

de Pourtalès, L. F. (1867). Contributions to the fauna of the Gulf stream at great depths. *Bulletin of the Museum of Comparative Zoology at Harvard College, in Cambridge*, *1*(6), 103–120.

Edgar, R. C. (2004). MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, *32*(5), 1792–1797. https://doi.org/10.1093/nar/gkh340

Faircloth, B. C. (2016). PHYLUCE is a software package for the analysis of conserved genomic loci. *Bioinformatics*, *32*(5), 786–788. https://doi.org/10.1093/bioinformatics/btv646

Fukami, H., Chen, C. A., Budd, A. F., Collins, A., Wallace, C., Chuang, Y. Y., Chen, C., Dai, C.-F., Iwao, K., Sheppard, C., & Knowlton, N. (2008). Mitochondrial and nuclear genes suggest that stony corals are monophyletic but most families of stony corals are not (order Scleractinia, class Anthozoa, phylum cnidaria). *PLoS One*, *3*, e3222. https://doi.org/10.1371/journal.pone.0003222

Fukami, H., Chen, C. A., Chiou, C. Y., & Knowlton, N. (2007). Novel group I introns encoding a putative homing endonuclease in the mitochondrial cox1 gene of scleractinian corals. *Journal of Molecular Evolution*, *64*, 591–600. https://doi.org/10.1007/s00239-006-0279-4

Gittenberger, A., Reijnen, B. T., & Hoeksema, B. W. (2011). A molecularly based phylogeny reconstruction of mushroom corals (Scleractinia: Fungiidae) with taxonomic consequences and evolutionary implications for life history traits. *Contributions to Zoology*, *80*, 107–132.

Goodwin, S., McPherson, J. D., & McCombie, W. R. (2016). Coming of age: Ten years of next-generation sequencing technologies. *Nature Reviews Genetics*, *17*(6), 333–351. https://doi.org/10.1038/nrg.2016.49

Gravier, C. (1915). Note préliminaire sur les Madréporaires recueilles au cours des croisières de la Princesse-Alice et de l'Hirondelle II, de inclusivement. *Bulletin de l'Institut Océanographique de Monaco*, *304*, 1–22.

Gray, J. E. (1847). An outline of an arrangement of stony corals. *Annals and Magazine of Natural History*, *19*, 120–128.

Hoang, D. T., Chernomor, O., von Haeseler, A., Minh, B. Q., & Vinh, L. S. (2018). UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution*, *35*, 518–522. https://doi.org/10.1093/molbev/msx281

Hoeksema, B., & Cairns, S. (2023). *World register of marine species. At VLIZ*. https://www.marinespecies.org

Huang, D., Licuanan, W. Y., Baird, A. H., & Fukami, H. (2011). Cleaning up the 'Bigmessidae': Molecular phylogeny of scleractinian corals from Faviidae, Merulinidae. Pectiniidae and Trachyphylliidae. *BMC Evolutionary Biology*, *11*, 37. https://doi.org/10.1186/1471-2148-11-37

Kalyaanamoorthy, S., Minh, B. Q., Wong, T. K. F., von Haeseler, A., & Jermiin, L. S. (2017). ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods*, *14*(660), 587–589. https://doi.org/10.1038/nmeth.4285

Katoh, K., Misawa, K., Kuma, K., & Miyata, T. (2002). MAFFT: A novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research*, *30*(14), 3059–3066. https://doi.org/10.1093/nar/gkf436

Kerr, A. M. (2005). Molecular and morphological supertree of stony corals (Anthozoa: Scleractinia) using matrix representation parsimony. *Biological Reviews*, *80*(4), 543–558. https://doi.org/10.1017/S1464793105006780

Kitahara, M. V., & Cairns, S. D. (2021). Azooxanthellate Scleractinia (cnidaria, Anthozoa) from New Caledonia. *Mémoires du Muséum National d'histoire Naturelle*, *215*, 1–722.

Kitahara, M. V., Cairns, S. D., Stolarski, J., Blair, D., Miller, D. J., & DeSalle, R. (2010). A comprehensive phylogenetic analysis of the scleractinia (Cnidaria, Anthozoa) based on mitochondrial CO1 sequence data. *PLoS One*, *5*(7), e11490. https://doi.org/10.1371/journal.pone.0011490

Kitahara, M. V., Cairns, S. D., Stolarski, J., & Miller, D. J. (2012). Deltocyathiidae, an early-diverging family of robust corals (Anthozoa, Scleractinia). *Zoologica Scripta*, *42*(2), 201–212. https://doi.org/10.1111/j.1463-6409.2012.00575.x

Kitahara, M. V., Fukami, H., Benzoni, F., & Huang, D. (2016). The new systematics of Scleractinia: Integrating molecular and morphological evidence. In S. Goffredo & Z. Dubinsky (Eds.), *The cnidaria, past, present and future* (pp. 41–59). Springer International Publishing.

Kitahara, M. V., Lin, M. F., Foret, S., Huttley, G., Miller, D. J., & Chen, C. A. (2014). The "naked coral" hypothesis revisited–evidence for and against scleractinian monophyly. *PLoS One*, *9*(4), e94774. https://doi.org/10.1371/journal.pone.0094774

Kitahara, M. V., Stolarski, J., Cairns, S. D., Benzoni, F., Stake, J. L., & Miller, D. J. (2012). The first modern solitary Agariciidae (Anthozoa, Scleractinia) revealed by molecular and microstructural analysis. *Invertebrate Systematics*, *26*, 303–315. https://doi.org/10.1071/IS11053

Kulkarni, P., & Frommolt, P. (2017). Challenges in the setup of large-scale next-generation sequencing analysis workflows. *Computational and Structural Biotechnology Journal*, *15*, 471–477. https://doi.org/10.1016/j.csbj.2017.10.001

Lamarck, J. B. (1801). *Système des animaux sans vertèbres, ou tableau général des classes, des ordres et des genres de ces animaux; Présentant leurs caractères essentiels et leur distribution, d'apres la considération de leurs rapports naturels et de leur organisation, et suivant l'arrangement établi dans les galeries du Muséum d'Histoire Naturelle, parmi leurs dépouilles conservées; Précédé du discours d'ouverture du Cours de Zoologie, donné dans le Muséum National d'Histoire Naturelle l'an 8 de la République* (p. 432). Published by the author and Deterville, viii +.

Lamarck, J. B. (1816). *Histoire naturelle des animaux sans vertèbres* (p. 568). Tome second, Verdière.

Le Goff-Vitry, M. C., Pybus, O. G., & Rogers, A. D. (2004). Genetic structure of the deep-sea coral *Lophelia pertusa* in the northeast Atlantic revealed by microsatellites and internal transcribed spacer sequences. *Molecular Ecology*, *13*, 537–549. https://doi.org/10.1046/j.1365-294X.2004.2079.x

Lin, M. F., Kitahara, M. V., Tachikawa, H., Fukami, H., Miller, D. J., & Chen, C. A. (2012). Novel organization of the mitochondrial genome in the deep-sea coral, *Madrepora oculata* (Hexacorallia, Scleractinia, Oculinidae) and its taxonomic implications. *Molecular Phylogenetics and Evolution*, *65*(1), 323–328. https://doi.org/10.1016/j.ympev.2012.06.011

Linnaeus, C. (1758). *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis* (Vol. *1*, 10th revised ed., p. 824). Editio decima, reformata.

Liu, L., Xi, Z., Wu, S., Davis, C. C., & Edwards, S. V. (2015). Estimating phylogenetic trees from genome-scale data. *Annals of the New York Academy of Sciences*, *1360*(1), 36–53. https://doi.org/10.1111/nyas.12747

Milne Edwards, H., & Haime, J. (1848). Recherches sur les polypiers. Mémoire 2. Monographie des turbinolides. *Annales Des Sciences Naturelles, Zoologie, Series 3*, *9*, 211–344, pls. 7–10.

Moseley, H. N. (1881 [1880]). Report on certain hydroid, alcyonarian, and Madreporarian corals procured during the voyage of H.M.S. challenger, in the years 1873–1876. Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–76. *Zoology*, *2*(part 7), 1–248, pl. Hydrocorallinae 1-14, Helioporidae 1-2, Madreporaria 1-16.

Nguyen, L. T., Schmidt, H. A., von Haeseler, A., & Minh, B. Q. (2015). IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, *32*, 268–274. https://doi.org/10.1093/molbev/msu300

Quattrini, A. M., Faircloth, B. C., Dueñas, L. F., Bridge, T. C., Brugler, M. R., Calixto-Botía, I. F., DeLeo, D. M., Forêt, S., Herrera, S., Lee, S. M. Y., Miller, D. J., Prada, C., Rádis-Baptista, G., Ramírez-Portilla, C., Sánchez, J. A., Rodríguez, E., & McFadden, C. S. (2018). Universal target-enrichment baits for anthozoan (Cnidaria) phylogenomics: New approaches to long-standing problems. *Molecular Ecology Resources*, *18*(2), 281–295. https://doi.org/10.1111/1755-0998.12736

Quattrini, A. M., Rodríguez, E., Faircloth, B. C., Cowman, P. F., Brugler, M. R., Farfan, G. A., Hellberg, M. E., Kitahara, M. V., Morrison, C. L., Paz-García, D. A., Reimer, J. D., & McFadden, C. S. (2020). Palaeoclimate ocean conditions shaped the evolution of corals and their skeletons through deep time. *Nature Ecology & Evolution*, *1-8*, 1531–1538. https://doi.org/10.1038/s41559-020-01291-1

Quattrini, A. M., Snyder, K. E., Purow-Ruderman, R., Seiblitz, I. G. L., Hoang, J., Floerke, N., Ramos, N. I., Wirshing, H. H., Rodriguez, E., & McFadden, C. S. (2023). Mito-nuclear discordance within Anthozoa, with notes on unique properties of their mitochondrial genomes. *Scientific Reports*, *13*(1), 7443. https://doi.org/10.1038/s41598-023-34059-1

Quek, Z. B. R., Jain, S. S., Neo, M. L., Rouse, G. W., & Huang, D. (2020). Transcriptome-based target-enrichment baits for stony corals (Cnidaria: Anthozoa: Scleractinia). *Molecular Ecology Resources*, *20*(3), 807–818. https://doi.org/10.1111/1755-0998.13150

Quek, Z. R., Jain, S. S., Richards, Z. T., Arrigoni, R., Benzoni, F., Hoeksema, B. W., Carvajal, J. I., Wilson, N. G., Baird, A. H., Kitahara, M. V., Seiblitz, I. G. L., Vaga, C. F., & Huang, D. (2023). A hybrid-capture approach to reconstruct the phylogeny of Scleractinia (Cnidaria: Hexacorallia). *Molecular Phylogenetics and Evolution*, *186*, 107867. https://doi.org/10.1016/j.ympev.2023.107867

Romano, S. L., & Cairns, S. D. (2000). Molecular phylogenetic hypotheses for the evolution of scleractinian corals. *Bulletin of Marine Science*, *67*(3), 1043–1068.

Schweigger, A. F. (1820). *Handbuch der Naturgeschichte der skelettlosen ungegliederten Thiere* (pp. 1–802). Im Verlag der Dyk'schen Buchhandlung.

Seguenza, G. (1864). Disquisizioni paleontologiche intorno ai corallarii fossili delle rocce Terziarie del distretto di Messina. *Memorie della Reale Accademia delle Scienze di Torino, Serie II*, *21*, 399–458, pls. 1–5, 459–560, pls. 6–15.

Seiblitz, I. G., Capel, K. C. C., Stolarski, J., Quek, Z. B. R., Huang, D., & Kitahara, M. V. (2020). The earliest diverging extant scleractinian corals recovered by mitochondrial genomes. *Scientific Reports*, *10*(1), 20714. https://doi.org/10.1038/s41598-020-77763-y

Seiblitz, I. G. L., Vaga, C. F., Capel, K. C. C., Cairns, S. D., Stolarski, J., Quattrini, A. M., & Kitahara, M. V. (2022). Caryophylliids (Anthozoa, Scleractinia) and mitochondrial gene order: Insights from mitochondrial and nuclear phylogenomics. *Molecular Phylogenetics and Evolution*, *175*, 107565. https://doi.org/10.1016/j.ympev.2022.107565

Stolarski, J. (2003). Three-dimensional micro-and nanostructural characteristics of the scleractinian coral skeleton: A biocalcification proxy. *Acta Palaeontologica Polonica*, *48*(4), 497–530.

Stolarski, J., Coronado, I., Murphy, J. G., Kitahara, M. V., Janiszewska, K., Mazur, M., Gothmann, A. M., Bouvier, A. S., Marin-Carbonne, J., Taylor, M. L., Quattrini, A. M., McFadden, C. S., Higgins, J. A., Robinson, L. F., & Meibom, A. (2021). A modern scleractinian coral with a two-component calcite-aragonite skeleton. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(3), e2013316117. https://doi.org/10.1073/pnas.2013316117

Stolarski, J., Kitahara, M. V., Miller, D. J., Cairns, S. D., Mazur, M., & Meibom, A. (2011). The ancient evolutionary origins of Scleractinia revealed by azooxanthellate corals. *BMC Evolutionary Biology*, *11*, 316. https://doi.org/10.1186/1471-2148-11-316

Vaga, C. F., Seiblitz, I. G. L., Capel, K. C. C., & Kitahara, M. V. (2022). The mitochondrial genomes of *Crispatotrochus rubescens* and *Crispatotrochus rugosus* (Hexacorallia; Scleractinia): New insights on the phylogeny of the family Caryophylliidae. *Molecular Biology Reports*, *49*(12), 12269–12273. https://doi.org/10.1007/s11033-022-08029-1

Vaga, C. F., Seiblitz, I. G. L., Stolarski, J., Capel, K. C. C., Quattrini, A. M., Cairns, S. D., Huang, D., Quek, R. Z. B., & Kitahara, M. V. (2024). 300 million years apart: The extreme case of macromorphological skeletal convergence between deltocyathids and a turbinolid coral (Anthozoa, Scleractinia). *Invertebrate Systematics*. In press.

Vaughan, T. W., & Wells, J. W. (1943). Revision of the suborders, families and genera of the Scleractinia. *Special Paper of the Geological Society of America*, *44*, 1–394. https://doi.org/10.1130/SPE44-P1

Wells, J. W. (1954). Bikini and nearby atolls: 2. Oceanography (biologic). Recent corals of The Marshall Islands. *Geological Survey Professional Paper*, *260-1*, 385–486, pls. 94–185.

Wells, J. W. (1984). Notes on Indo-Pacific scleractinian corals. Part 10. Late Pleistocene ahermatypic corals from Vanuatu. *Pacific Science*, *38*(3), 205–219.

Zhang, Y., Gong, L., Lu, X., Jiang, L., Liu, B., Liu, L., Lü, Z., Li, P., & Zhang, X. (2020). Gene rearrangements in the mitochondrial genome of *Chiromantes eulimene* (Brachyura: Sesarmidae) and phylogenetic implications for Brachyura. *International Journal of Biological Macromolecules*, *162*, 704–714. https://doi.org/10.1016/j.ijbiomac.2020.06.196

Zhang, Y., Sun, J., Rouse, G. W., Wiklund, H., Pleijel, F., Watanabe, H. K., Chen, C., Qian, P. Y., & Qiu, J. W. (2018). Phylogeny, evolution and mitochondrial gene order rearrangement in scale worms (Aphroditiformia, Annelida). *Molecular Phylogenetics and Evolution*, *125*, 220–231. https://doi.org/10.1016/j.ympev.2018.04.002

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Vaga, C. F., Seiblitz, I. G. d. L. e., Capel, K. C. C., Quattrini, A. M., Stolarski, J., Cairns, S. D., & Kitahara, M. V. (2024). Untangling deep-sea corals systematics: Description of a new family, Stephanocyathidae (Anthozoa, Scleractinia), through a genomic approach. *Zoologica Scripta*, *00*, 1–14. https://doi.org/10.1111/zsc.12657