



Phylogenetic position of the reef-builder *Madrepora carolina* and the genus *Thalamophyllia* (Anthozoa, Scleractinia): new additions for the family Agariciidae

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Abstract

The family Madreporidae Ehrenberg, 1834 (Anthozoa, Scleractinia), includes some of the most important mesophotic and deep-sea habitat-forming species of stony corals. However, molecular data are completely lacking for some of its species, preventing the test of their phylogenetic position. The integration of molecular and morphological data in scleractinian taxonomy has revealed the presence of several para- or polyphyletic lineages, which in most cases are still waiting for a revision. Here, using a genomic approach that couples nuclear ultraconserved and exon loci and complete mitochondrial genome features, we investigate the phylogenetic position of three *Madrepora* Linnaeus, 1758 species - sequenced for the first time - and the genus *Thalamophyllia* Duchassaing, 1870. The latter has been historically assigned to the family Caryophylliidae Dana, 1846, but recent molecular studies have found it more closely related to the phylogenetically distant family Agariciidae Gray, 1847. Here, we present congruent nuclear and mitochondrial results placing the species *Madrepora carolina* (Pourtalès, 1871) and the genus *Thalamophyllia* inside the family Agariciidae. Specifically, both taxa present the canonical mitochondrial gene order - shared with the family Agariciidae and the majority of stony corals - while lacking the specific gene transpositions characteristic of the families Madreporidae and Caryophylliidae, respectively. The genus *Thalamophyllia* and the species *M. carolina* are, therefore, formally moved to the family Agariciidae, and *M. carolina* is accommodated in a new genus (*Pseudomadrepore* Vaga & Quattrini gen. nov.). The results of this study uncover another case of macromorphological skeletal convergence in the order, while untangling the relationship of some deep-water scleractinian taxa.

Keywords *Pseudomadrepore* · Madreporidae · Western Central Atlantic · Deep sea · Mitochondrial genome · Ultraconserved elements

Introduction

The advent of molecular studies has revolutionized the systematics of scleractinian (Anthozoa, Scleractinia) corals (Romano and Palumbi 1996; Romano and Cairns 2000; Fukami et al. 2008; Stolarski et al. 2011; Huang et al. 2011), previously based only on observations of skeletal macromorphology (Vaughan and Wells 1943; Wells 1956). Over the past two decades, molecular phylogenetic studies have highlighted pervasive morphological plasticity

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(Todd 2008) and convergence (Flot et al. 2011; Benzoni et al. 2012; Vaga et al. 2024a) at various taxonomical levels within Scleractinia. Such plasticity has historically hampered a correct and robust classification of stony corals based solely on morphological traits. The phylogenetic relationships within and among several scleractinian lineages have now been resolved by integrating morphological and genetic data (e.g., Huang et al. 2014; Kitano et al. 2014; Arrigoni et al. 2014, 2016; Cowman et al. 2020). Yet, many lineages - especially deep-water and azooxanthellate (i.e., that do not rely on the symbiosis with Symbiodiniaceae) - are still known to be para- or polyphyletic (e.g., family Caryophylliidae Dana 1846 [Kitahara et al. 2010, 2012; Seiblit et al. 2022]), and await a systematic revision (Kitahara et al. 2016; Campoy et al. 2020).

The genus *Madrepora* Linnaeus, 1758, recently re-assigned to the monogeneric family Madreporidae Ehrenberg, 1834 (Addamo et al. 2024), has had an especially challenging taxonomic history with hundreds of species synonymized or moved into different genera (Hoeksema and Cairns 2025). At present, seven extant species are recognized, of which three occur in the Atlantic Ocean - i.e., *Madrepora oculata* Linnaeus, 1758, *Madrepora piresae* Kitahara, Capel & Zilberberg, 2024, and *Madrepora carolina* (Pourtalès, 1871).

Overall, all *Madrepora* species are considered important mesophotic and deep-water framework engineers (Roberts 2009; Capel et al. 2024) with wide bathymetric ranges (Hoeksema and Cairns 2025). Interestingly, *M. piresae* has been recently described from specimens collected off the coast of Brazil, initially identified as *M. oculata* (Capel et al. 2024). This result points to possible cryptic diversity within the genus.

Madrepora carolina is a species widespread in the Western Central Atlantic and commonly found in mesophotic and deep waters (from 50 to 800 m depth), where it can form large and bushy colonies (Fig. 1A, B) (Cairns 1979, 2000; Santodomingo et al. 2013; Hoeksema and Cairns 2025). Albeit frequently collected and known to play an important ecological role, no molecular data were previously available for this species; thus, its phylogenetic position has never been examined.

The innovative use of phylogenomic approaches has aided in unraveling the evolutionary history of coral taxa (e.g., Quattrini et al. 2018; Quek et al. 2020, 2023). Among these novel approaches, nuclear ultraconserved elements (UCEs) and exon loci have been successfully used to investigate relationships within many groups of Anthozoa (Cowman et al. 2020; Erickson et al. 2021; Morrissey et al. 2023). This wide range of markers has proved to be more effective than single nuclear and mitochondrial markers in resolving



Fig. 1 In situ and museum specimen pictures of *Madrepora carolina*. **A** In situ picture of a specimen collected in Puerto Rico (USNM 1689184) courtesy of the Schmidt Ocean Institute; **B** in situ picture of multiple colonies on the MS-AL shelf including sample USNM 1676158; **C** on deck picture of a pink colony from the MS-AL shelf

(USNM 1676109); **D**, **E** detailed calicular view (stack image) and colony fragment of USNM 10254 (not used for molecular analyses); **F** image of *M. carolina* syntype (*Lophohelia carolina* Pourtalès, 1871) observed at the Museum of Comparative Zoology (MCZ) at Harvard

both shallow and deep nodes in phylogeny reconstructions (McFadden et al. 2022). Moreover, features of the complete mitochondrial (mt) genome (e.g., GC content, gene order) have been investigated and, in some instances, found to be taxonomically informative for certain scleractinian lineages/families (Seiblitze et al. 2022; Capel et al. 2024; Vaga et al. 2024a). The mt gene order has already been found to be an informative character frequently used to define different lineages in several groups of animals (revised in Boore and Brown 1998). Inside the order Scleractinia, a specific mt gene rearrangement - inverted order for the *cox2* and *cox3* genes - was initially found in *Madrepora oculata* (Lin et al. 2012) and later confirmed to be pervasive and exclusive of the family Madreporidae (Capel et al. 2024). Similarly, the mt genomes of species belonging to the family Caryophylliidae (“true” Caryophylliidae *sensu* Seiblitze et al. 2022) are characterized by a three-gene transposition (*cob*, *nad2*, and *nad6*) not detected in any other Scleractinia lineage to date (Seiblitze et al. 2022; Vaga et al. 2022).

Herein, using nuclear UCEs and exons and complete mt genomes, we found that the species *Madrepora carolina* is nested within the family Agariciidae Gray 1847 (suborder

Refertina Okubo 2016), which is phylogenetically distant from the family Madreporidae (suborder Vacatina Okubo 2016). *M. carolina* was found as a sister lineage to the genus *Thalamophyllia* Duchassaing 1870, which was previously thought to belong to the family Caryophylliidae (although also previously recovered as closely related to Agariciidae - see Barbeitos et al. 2010). Analyses of the complete mt genomes of *M. carolina* and *Thalamophyllia* show that they do not present the mt gene rearrangements characteristic of Madreporidae and Caryophylliidae species, respectively. In the light of these results, we propose that *M. carolina* and the genus *Thalamophyllia* belong to the family Agariciidae. Thus, to accommodate *M. carolina* within agariciids, we describe a new genus named *Pseudomadrepore* Vaga & Quattrini.

Material and methods

Specimen collection and morphological analyses

A combination of freshly collected and historical museum specimens was used for this study - 13 and 11

Table 1 Species name, museum catalog number (USNM=Smithsonian National Museum of Natural History, former United States National Museum), collection site details, coloration of the alive colonies (only for the *Madrepora carolina* specimens), and nuclear data information included in this study. *Indicates historical museum

specimens. ^Indicates specimens collected during the expedition FKt230417. Specimens without superscript symbols were collected during two expeditions aboard the NOAA Ship *Pisces* (PC-22-02 and PC-23-02). PR, Puerto Rico; LA, Louisiana; AL, Alabama; TX, Texas; MS, Mississippi

Species	Museum voucher	Latitude	Longitude	Depth (m)	Locality	Coloration	UCEs loci
<i>Agaricia agaricites</i> [^]	USNM 1689220	17.88	-67.02	19	La Parguera, PR	n/a	1464
<i>Agaricia fragilis</i> [*]	USNM 1552755	27.89	-93.30	58	Louisiana	n/a	1739
<i>Agaricia undata</i> [^]	USNM 1689185	17.88	-67.02	82	La Parguera, PR	n/a	1408
<i>Dactylotrachus cervicornis</i> [*]	NIWA 118911	-30.22	-178.35	n/a	South Pacific	n/a	1062
<i>Helioseris cucullata</i> [*]	USNM 1552950	27.81	-93.05	58	Louisiana	n/a	1568
<i>Madrepore arbuscula</i> [*]	USNM 96752	-5.30	133.01	212	Indonesia	n/a	756
<i>Madrepore carolina</i> [*]	USNM 72589	25.28	-83.96	127	Florida	n/a	606
<i>Madrepore carolina</i> [*]	USNM 87787	27.74	-91.13	129	Green Canyon, LA	n/a	1526
<i>Madrepore carolina</i>	USNM 1666284	29.81	-87.27	90	MS-AL Shelf	White	415
<i>Madrepore carolina</i> [*]	USNM 1665786	28.01	-93.48	85	McNeil, TX	Pink	1521
<i>Madrepore carolina</i>	USNM 1676109	29.80	-87.27	93	MS-AL Shelf	Pink	1112
<i>Madrepore carolina</i>	USNM 1676157	29.59	-87.35	96	MS-AL Shelf	White	251
<i>Madrepore carolina</i>	USNM 1676158	29.59	-87.35	96	MS-AL Shelf	White	331
<i>Madrepore carolina</i>	USNM 1676341	29.33	-87.77	100	MS-AL Shelf	White	544
<i>Madrepore carolina</i>	USNM 1676365	29.36	-87.74	98	MS-AL Shelf	White	388
<i>Madrepore carolina</i>	USNM 1676396	29.32	-87.78	102	MS-AL Shelf	White	483
<i>Madrepore carolina</i> [^]	USNM 1689165	18.38	-67.41	331	Desecheo Ridge, PR	White	1503
<i>Madrepore carolina</i> [^]	USNM 1689184	18.38	-67.41	324	Desecheo Ridge, PR	White	1590
<i>Madrepore carolina</i>	USNM 1693353	29.26	-88.34	88	MS-AL Shelf	White	584
<i>Madrepore carolina</i>	USNM 1693390	29.39	-88.02	76	MS-AL Shelf	White	680
<i>Madrepore minutiseptum</i> [*]	USNM 98549	-14.22	-178.17	235	Futuna Islands	n/a	1706
<i>Thalamophyllia gasti</i> [*]	USNM 98473	43.17	5.37	23	Marseille, France	n/a	1476
<i>Thalamophyllia riisei</i> [*]	USNM 94743	25.38	-77.85	77	Bahamas	n/a	785
<i>Thalamophyllia tenuescens</i> [*]	MNHN-IK-2012-17602	-22.57	167.60	233	New Caledonia	n/a	1624

total specimens, respectively (complete list and details in Table 1). Four individuals (two *M. carolina* and two *Agaricia* Lamarck, 1801 species) were collected from Desecheo Ridge and La Parguera, Puerto Rico (Fig. 1A) during the Schmidt Ocean Institute expedition FKt230417 entitled: “Health diagnostics of deep-sea coral” onboard the R/V *Falkor (too)*. Nine individuals of *M. carolina* were collected in July 2022 and July 2023 from the Mississippi-Alabama continental shelf (herein referred to as the MS-AL shelf) (Fig. 1B) during two expeditions aboard the NOAA Ship *Pisces* (PC-22-02 and PC-23-02) as part of the Mesophotic and Deep Benthic Communities (MDBC) restoration projects being carried out pursuant to the Deepwater Horizon Oil Spill Natural Resource Damage Assessment, Open Ocean Trustee Implementation Group Final Restoration Plan 2 (OOTIG 2019) (see Fig. 2 for collection localities). In situ pictures were taken by the remotely operated vehicle (ROV) *Mohawk* on the *Pisces* and the ROV *SuBastian* on the R/V *Falkor (too)*. All samples were deposited at the Smithsonian National Museum of Natural History and preserved in 95% ethanol (voucher numbers detailed in Table 1). The historical museum specimens selected for this study, including four *Madrepora* specimens and three *Thalamophyllia* species, are all preserved in 70% ethanol (except for

USNM 1665786, which is preserved in 95% ethanol). Stack microscopy images were taken using an Olympus DSX100 optical microscope (Olympus Corporation, Tokyo, Japan). Microarchitectural features were examined with a scanning electron microscope (SEM) (FEI Apreo FESEM) from a dry preserved specimen of *M. carolina* (USNM 62065, Cozumel Island, 20°25'N/86°13'W, 274 m). These specimens were mounted on stubs and sputter-coated with conductive gold film. Specifically, we mainly focused on the examination of the internal and external features of the septa following the observations made by Kitahara et al. (2012).

DNA extractions, library preparation, and sequencing

Total genomic DNA extraction of the specimens analyzed in this study was performed either using the DNeasy Blood and Tissue kit (Qiagen) following the manufacturer's animal tissue protocol or using the high-throughput AutoGen (Holliston, Massachusetts, USA) extraction device, which uses a phenol-chloroform-based extraction method. DNA purification was performed for samples that did not yield good DNA quality using the Genomic DNA Clean and Concentrator kit (Zymo Research). DNA integrity was assessed in a 1%

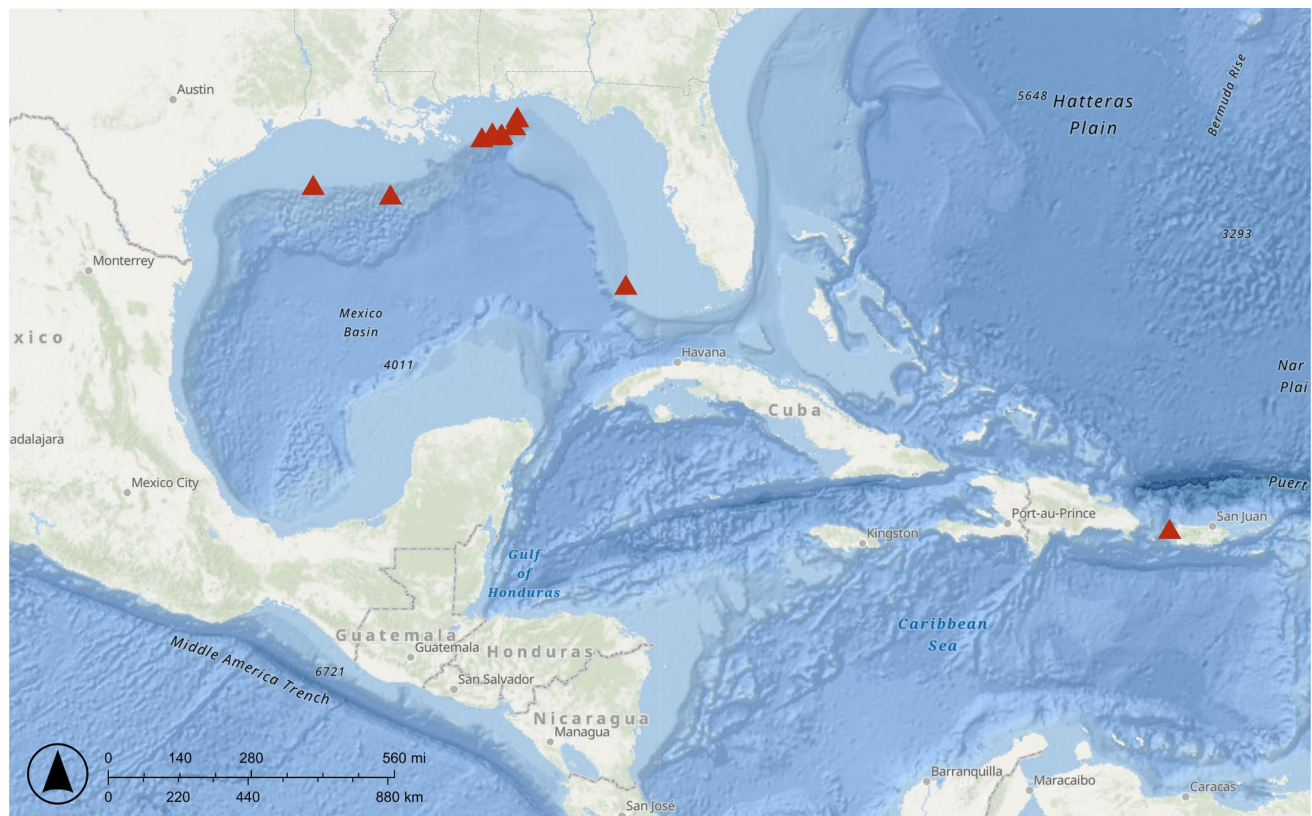


Fig. 2 Collection localities of *Madrepora carolina* specimens included in this study (red triangles). The map was created using ArcGIS Online (<https://www.arcgis.com/index.html>)

agarose gel electrophoresis. The NEBNext Ultra II DNA Library Prep Kit was used with some modifications as in Quattrini et al. (2024). DNA concentration before and after library preparation was quantified on a Qubit 2.0 fluorometer (Thermo Fisher Scientific) High Sensitivity Assay, and size distributions were assessed on an Agilent TapeStation. For two historical museum specimens (i.e., USNM 87787 and USNM 72589) the MyBaits protocol v IV (Arbor BioSciences, Ann Arbor, MI) was used to target and enrich UCEs and exons with the hexacoral/scleractinian combined baits set developed by Quattrini et al. (2018), Cowman et al. (2020), and Quek et al. (2020). Samples were sequenced on an Illumina NovaSeq 6000 (150 bp PE reads) at the Oklahoma Medical Research Foundation Genomics Core.

Mitochondrial genome analyses

Quality control and adapter removal of demultiplexed sequencing data were performed with Trimmomatic (Bolger et al. 2014). Trimmed sequences were assembled into contigs using SPAdes v 3.15 (Bankevich et al. 2012), and mt contigs were selected using command line BLASTn (Altschul et al. 1990) against a set of reference scleractinian mt genomes. Annotation - using translation Table 4 (Mold, Protozoan, Coelenterate) - and circularity were performed and manually verified using Geneious Prime 2024.0.5 (Biomatters Ltd., Auckland, New Zealand). The boundaries of all genes were then confirmed using BLAST against the NCBI nucleotide database. Base pair differences between complete mitogenomes were calculated through Geneious Prime 2024.0.5.

Nuclear phylogenomic analyses

Assembled reads were processed using the Phyluce pipeline (Faircloth 2016). At this stage, previously published genomic data of scleractinian species spanning both suborders were included in the analyses, and five Corallimorpharia species were used as outgroup (see Supplementary Table 1). 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 (Quattrini et al. 2018; Cowman et al. 2020; 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), and a data matrix of locus alignments was created using “phyluce_align_get_only_loci_with_min_taxa” in which

each locus had 50% species occupancy. The 50% threshold was used as it provides a good balance between data completeness and the number of loci retained for phylogenetic reconstruction. Each locus alignment was then concatenated, and the partition charset was created using “phyluce_align_format_nexus_files_for_raxml.” Finally, “phyluce_align_get_informative_sites” was applied to calculate the number of parsimony informative sites. The concatenated alignment was used to perform a partitioned phylogenomic analysis using maximum likelihood (ML) in IQ-TREE v2.1 (Nguyen et al. 2015). The best-fit models for each locus and best partition scheme were selected (-m MFP + MERGE) by ModelFinder (Kalyaanamoorthy et al. 2017) as implemented in IQTREE v 2.1. Ultrafast bootstrap approximation (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).

Results

Nuclear data

A total of 2489 UCEs and exon loci (out of 2490 total loci included in the scleractinian bait set) across all targeted specimens were recovered from the assembled contigs. The alignment included 77 scleractinian specimens, 24 sequenced for this study, and five corallimorpharians as outgroups. The number of loci recovered from each newly sequenced specimen ranged from 251 to 1739 per sample (mean: 1020 ± 529 loci). The final 50% matrix (resulting ML tree shown in Fig. 3) included a concatenated alignment of 977 UCE and exon loci with an alignment length of 171,002 bp of which 41.7% were phylogenetically informative.

The ML phylogeny has 86% of the nodes with support equal to or higher than 95% in both UFBoot and SHaLRT values (Fig. 3). *Madrepora minutiseptum* Cairns & Zibrowius, 1997 and *Madrepora arbuscula* (Moseley, 1880) were retrieved as sister species and grouped with the other previously sequenced *Madrepora* spp. (SHaLRT = 100, UFBoot = 100), while all newly collected specimens of *Madrepora carolina* grouped inside the family Agariciidae, which was confirmed to be monophyletic (SHaLRT = 100, UFBoot = 100) (Fig. 3). The family Agariciidae was subdivided into two reciprocally monophyletic lineages, one including *Thalamophyllia* spp. and *M. carolina* (SHaLRT = 100, UFBoot = 100) and the other including the remaining tested agariciids (SHaLRT = 100, UFBoot = 100). The *Thalamophyllia* species and *M. carolina* were retrieved as reciprocally monophyletic. At the same time, the lineage including all the *M. carolina* specimens is fully supported, while the lineage including the three *Thalamophyllia*

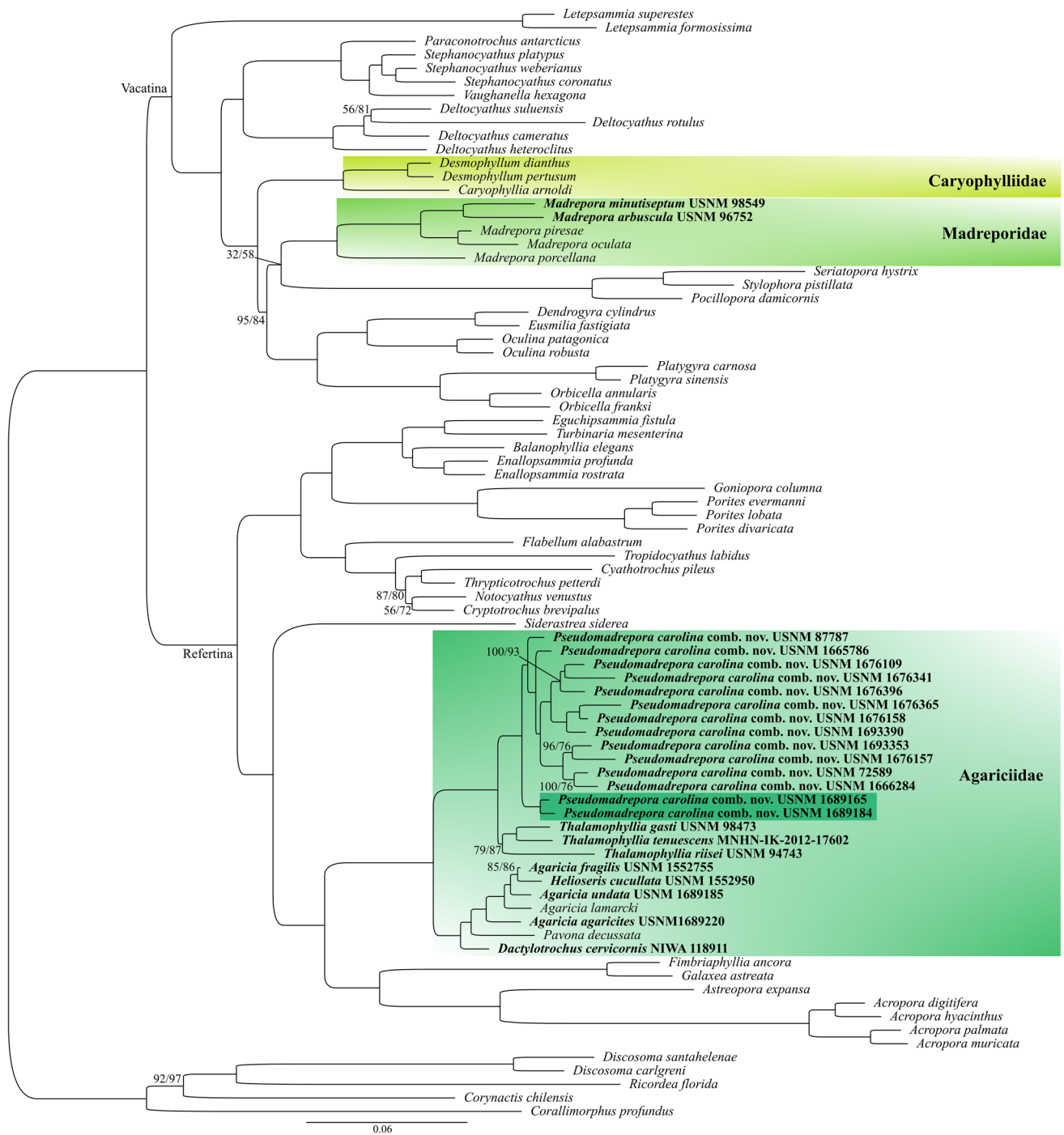


Fig. 3 Maximum likelihood phylogeny based on nuclear UCEs and exon loci (50% taxon occupancy - 171,002 bp). Nodes without numbers indicate that both SHaLRT and UFBoot values are >95. The families Agariciidae, Caryophylliidae, and Madreporidae are high-

lighted by colored boxes. Species sequenced for this study are in bold. The darker green box inside the family Agariciidae indicates the two *Pseudomadrepore carolina* comb. nov. (formerly *Madrepore carolina*) specimens from Puerto Rico

species was less supported (SHaLRT = 79, UFBoot = 87). Inside the *M. carolina* group, the two specimens from Puerto Rico were retrieved as sister to the specimens collected from the MS-AL shelf, Texas, and Florida (SHaLRT = 100, UFBoot = 100).

Mitochondrial data

The average coverage of mitochondrial genomes ranged from 26.2 to 364.4 X (Table 2). The complete mt genomes from *Thalamophyllia gastii* (Döderlein, 1913),

Table 2 Species, museum catalogue number, and mt data information for the species included in this study for which the complete mt genome was retrieved. PR, Puerto Rico; MS, Mississippi; AL, Alabama. *Pseudomadrepورا carolina* comb. nov. = former *Madrepورا carolina*

Species	Museum voucher	Mt assembly coverage (X)	Mt genome length (bp)	Mt genome GC content (%)
<i>Pseudomadrepورا carolina</i> comb. nov. (MS-AL shelf)	USNM 1676109	72.0	18,055	39.9
<i>Pseudomadrepورا carolina</i> comb. nov. (MS-AL shelf)	USNM 1666284	26.2	18,055	39.9
<i>Pseudomadrepورا carolina</i> comb. nov. (PR)	USNM 1689184	364.4	18,066	39.9
<i>Madrepورا minutiseptum</i>	USNM 98549	264.9	15,821	30.4
<i>Thalamophyllia gasti</i>	USNM 98473	167.8	18,459	40.2
<i>Thalamophyllia riisei</i>	USNM 94743	56.5	18,182	39.9

Thalamophyllia riisei (Duchassaing & Michelotti, 1860), three specimens of *Madrepورا carolina* (two from the MS-AL shelf and one from Puerto Rico), and *Madrepورا minutiseptum* (GenBank accession numbers PV815617-22) were assembled and circularized. The coverage, length, and GC content of each genome can be found in Table 2. The two *M. carolina* from the MS-AL shelf have identical mt genomes with no base pair differences. In contrast, the mt genome of the *M. carolina* from Puerto Rico is slightly longer (11 bp) and presents 49 bp differences from the MS-AL shelf counterparts. *Thalamophyllia* spp. and *M. carolina* mt genomes show the canonical mt gene order for Scleractinia (i.e., shared by the majority of scleractinian species - see Seiblitiz et al. [2022]), while *M. minutiseptum* has an inverted order of the *cox2* and *cox3* genes, a feature shared with all the other *Madrepورا* species studied so far (Capel et al. 2024) (Fig. 4). No mt genomes in this study contain the *cox1* gene intron (i.e., LAGLII homing endonuclease). Similarly to other Refertina corals, *Thalamophyllia* spp. and *M. carolina* mt genomes show rather long intergenic regions (IGRs) (up to 617 bp between *cytb* and *nad2* in *T. gasti*) that result in an overall longer mt genome compared to their Vacatina counterparts.

Taxonomic account

Order Scleractinia Bourne, 1900.

Suborder Refertina Okubo, 2016

Family Agariciidae Gray, 1847

Type genus: *Agaricia* Lamarck, 1801

Diagnosis (amended from Kitahara et al. 2012): Solitary or colonial. Corallum always attached. Colony shape branching, massive, columnar, encrusting, foliose, reptoid, bushy, or flabellate formed by intratentacular or extratentacular budding. Wall septothecate or synapticulothecate, the latter usually becoming solid or absent. Septa rarely porous, formed by a continuous middle rapid accretion zone flanked by perpendicular to slightly oblique bundles of fibers (thickening deposits). Septal margins usually beaded. Septal faces with scale-like microtexture and bearing rows of granules or menianes, both composed of RAD. Endothecal dissepiments mostly absent. Columella trabecular or absent.

Genera included: *Agaricia* Lamarck, 1801, *Dactylotrachus* Wells, 1954, *Gardineroseris* Scheer & Pillai, 1974, *Helioseris* Milne Edwards & Haime, 1849, *Leptoseris* Milne Edwards & Haime, 1849, *Pavona* Lamarck, 1801,

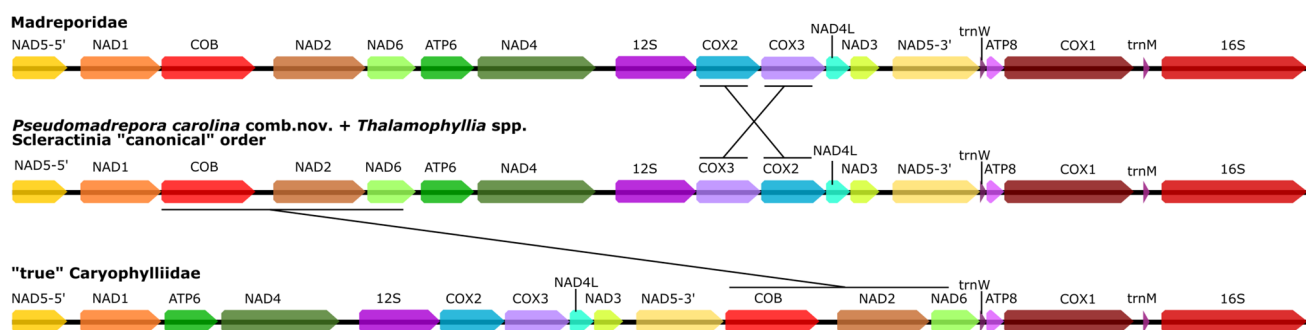


Fig. 4 Mitochondrial gene maps of species belonging to (from top to bottom): (i) the family Madreporidae, (ii) the majority of Scleractinia lineages (including *Pseudomadrepورا carolina* comb. nov. - formerly *Madrepورا carolina* - and *Thalamophyllia* spp.), and (iii) the “true”

Caryophylliidae group. Scaling is approximate. Protein-coding, tRNA, and rRNA genes are abbreviated as in the text. Blank regions between genes represent intergenic spacers

Pseudomadrepora Vaga & Quattrini gen. nov., *Thalamophyllia* Duchassaing, 1870

Genus *Thalamophyllia* Duchassaing, 1870

Type species: esmophyllum rusei Duchassaing & Michelotti, 1860; = *Thalamophyllia riisei* (Duchassaing & Michelotti, 1860) (type by monotypy).

Species included: Thalamophyllia gasti (Döderlein, 1913); *Thalamophyllia gombergi* Cairns, 1979; *Thalamophyllia riisei* (Duchassaing & Michelotti, 1860); *Thalamophyllia senaria* Kitahara & Cairns, 2021; *Thalamophyllia tenuescens* (Gardiner, 1899); *Thalamophyllia wirtzi* Ocaña et al., 2015.

Diagnosis (amended from Kitahara & Cairns, 2021): Colonial, forming reptoid colonies by extratentacular budding from thin common basal coenosteum. Base monocyclic or polycyclic. Corallites ceratoid. Pali and columella absent. Fossa deep, endotheca absent.

Distribution: Western Central Atlantic, Mediterranean Sea, Western Pacific; 4–1317 m depth.

Genus *Pseudomadrepora* Vaga & Quattrini gen. nov.

Figures 1 and 5

ZooBank: <http://zoobank.org/133EADDA-C3BB-462E-90D7-6835AECAE23F>

Type species: Pseudomadrepora carolina (Pourtalès, 1871) comb. nov.

Etymology: The generic name *Pseudomadrepora* is a combination of the Greek prefix *pseudo* (fake) with the well-known genus *Madrepora* that together allude to the morphological resemblance of the two genera. Genre: Feminine.

Common name: “Pourtalès’ fan coral” by Messing (1987)

Species included: Pseudomadrepora carolina (Pourtalès, 1871) comb. nov.

Types: Lophohelia carolina Portalès, 1871 = *Pseudomadrepora carolina* comb. nov. (Pourtalès, 1871) (Syntype MCZ:IZ:CNID-2754 - two labels are present: 2754 and 2764 [see Fig. 1F]). *Lophohelia exigua* Portalès, 1871 = *Pseudomadrepora carolina* comb. nov. (Pourtalès, 1871) (Syntype MCZ:IZ:CNID-2778). *Type locality* - Cuba, off Havana. Precise location and depth unknown.

Diagnosis (adapted from Cairns 2000 diagnosis of *Madrepora carolina*): Colonial, forming bushy or flabellate colonies with extratentacular and sympodial branching. Corallites 3.5–5.5 mm in diameter, flared distally, and projecting well above the branch coenosteum. In large colonies, corallites tend to occur on only one side of the colony. Coenosteum white, finely granular, and faintly striate. Cl-2 present near the calicular edge. Septa hexamerally arranged in 3 cycles according to the formula: $S1 > S2 > S3$. S1 highly exsert and dimorphic in size, i.e., two opposing pairs of S1 are wider than the remaining two S1. S3 rudimentary. Fossa deep. Columella absent. Tissue of alive specimens can be of a bright pink color.

Remarks: Despite the outstanding morphological similarity of *Pseudomadrepora carolina* comb. nov. to the genus *Madrepora* (to which it was before ascribed), phylogenetic results unequivocally place this species in the family Agariciidae. Moreover, its microstructural features - i.e., scale-like organization of the septal faces, and septa formed by middle rapid accretion zone flanked by slightly oblique bundles of fibers (see Fig. 5) - provide additional support for grouping *P. carolina* comb. nov. with the Agariciidae. *Pseudomadrepora* Vaga & Quattrini gen. nov. can be distinguished from other agariciid genera by the complete absence of columellar elements and by its branching (bushy or flabellate) colonies. It can also be distinguished from

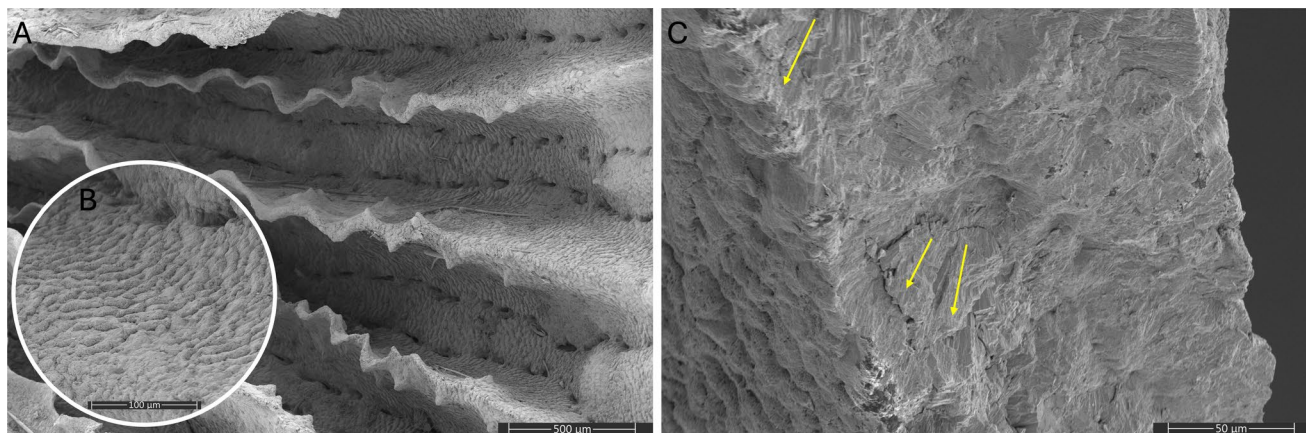


Fig. 5 Microstructural features of *Pseudomadrepora carolina* comb. nov. (USNM 62065, Cozumel Island, 20°25'N/86°13'W, 274 m). **A** View of the septa with details of the scale-like; **B** microtexture of the

septal faces. **C** Detail of the middle part of the septum with bundles of fibers (thickening deposits) occurring slightly oblique in the septum (yellow arrows)

Madrepora species by its larger and flared corallites, absence of columella, and its dimorphic S1 (see Fig. 4 in Capel et al. 2024). Moreover, it is the only species within Agariciidae and Madreporidae that forms colonies in which corallites can occur on only one side of the colony. Some colonies showed a bright pink coenosarc at the time of collection (see Table 1 and Fig. 1C), a characteristic already observed by R. H. Hubbard - label written on specimens USNM 80977 collected from Tobago (depth 91 to 152 m). The coloration does not seem to be restricted to a certain geographical area (it occurs in distant parts of the Western Central Atlantic) or to a certain depth; moreover, it is unknown what is causing the coloration. Additional specimens' observations and study of the substrate and/or diet might help in understanding the significance of this coloration.

Distribution: Western Atlantic from Bermuda to Brazil; 53–801 m depth.

Discussion

The mitochondrial genome

Pseudomadrepore carolina comb. nov. and *Thalamophyllia* spp. mt genomes have lengths and GC content that match those of other refertinan corals (from ~17.0 to ~19.5 kbp and ~36.2 to ~40.5% GC [e.g., Lin et al. 2011; Kitahara et al. 2014; Capel et al. 2016; Terraneo et al. 2018; Vaga et al. 2024a]), while *Madrepore minutiseptum* has length and GC content that match those of vacatinan corals (~14.9 to ~17.8 kbp and ~29.1 to ~36.7% GC [e.g., Chen et al. 2008; Seiblitiz et al. 2022], with some exceptions - see family Micrabaciidae in Seiblitiz et al. [2020]). Thus, the general characteristics of *P. carolina* comb. nov. and *Thalamophyllia* spp. complete mt genomes corroborate their placement within the suborder Refertina. Data of mt genomes for multiple specimens of the same species are still extremely rare in Scleractinia. However, previous studies have reported a maximum of 15 bp differences for the mt genome of different populations within the same scleractinian species and up to 63 bp differences in cryptic species inside the genus *Plesiastrea* Milne Edwards & Haime, 1848 (Juszkiewicz et al. 2022; Seiblitiz et al. 2022) or as low as only 1 bp difference between two separate species (Capel et al. 2024). Addamo et al. (2016) found 99.88% percentage of identity between the scleractinian species *Desmophyllum dianthus* (Esper, 1794) and *Desmophyllum pertusum* (Linnaeus, 1758) (as *Lophelia pertusa*). The number of bp differences and percentage of identity (49 bp and 99.73%, respectively) between the mt genome of *P. carolina* comb. nov. from Puerto Rico and MS-AL shelf might thus point to cryptic diversity within *P. carolina* comb. nov. Although

the *cox1* intron (i.e., LAGLIDADG type homing endonuclease) has previously been observed in other scleractinians (Celis et al. 2017; Chuang et al. 2017), it was not found in the agariciid mt genomes. The pervasiveness of this homing endonuclease among scleractinian lineages is still mostly unknown but gains and/or losses have been documented across Scleractinia and more broadly across Hexacorallia (Fukami et al. 2007; Quattrini et al. 2023).

The number of discovered mt genome rearrangements within Scleractinia has been rapidly increasing in the past decade (Chen et al. 2008; Emblem et al. 2011; Lin et al. 2012; Stolarski et al. 2021; Li et al. 2023; Vaga et al. 2024a), a character being currently used as additionally informative to untangle the systematics of some challenging groups (Seiblitiz et al. 2022; Capel et al. 2024; Vaga et al. 2024b). The two-gene inversion (inverted *cox3* and *cox2* order - see Fig. 4) found in *M. minutiseptum* has already been reported in *M. oculata*, *M. piresae*, and *Madrepore porcellana* (Moseley, 1880) (Lin et al. 2012) (reads assembly did not retrieve the complete mt genome for *Madrepore arbuscula*) and hypothesized to be exclusive of the family Madreporidae (Capel et al. 2024). In contrast, the same inversion was not found in *P. carolina* comb. nov., which have the canonical scleractinian gene order shared by Agariciidae representatives (Medina et al. 2006). *Thalamophyllia* spp. also have the canonical gene order and not the three-gene transposition characteristic of the “true” Caryophylliidae family, to which the genus was previously assigned. These results, together, further confirm the systematic position of *P. carolina* comb. nov. and *Thalamophyllia* spp. proposed in this study.

Phylogenetic results

Nuclear phylogeny recovered all *Thalamophyllia* spp., including the type species of the genus *T. riisei*, as well as *Pseudomadrepore carolina* comb. nov. grouped within the family Agariciidae, and phylogenetically distant from the family Caryophylliidae and Madreporidae to which they were respectively previously ascribed. Based on concurring mitochondrial and nuclear results, the genus *Thalamophyllia* is formally moved into the family Agariciidae. Indeed, previous molecular studies, based on few mitochondrial and nuclear ribosomal markers, had shown a close relationship between these two lineages (Romano and Cairns 2000; Barbeitos et al. 2010; Stolarski et al. 2011; Kitahara et al. 2012, 2016; Campoy et al. 2020), but due to a lack of definitive proof, the genus was never formally transferred from the family Caryophylliidae (but see Kitahara and Cairns 2021). *Thalamophyllia* is only the second genus (together with *Pseudomadrepore* Vaga & Quattrini gen. nov. from the present work) included in the family Agariciidae to be exclusively composed of azooxanthellate species. Before the study by Kitahara et al. (2012) that placed the genus *Dactylotrachus* Wells, 1954 inside Agariciidae, the family was

composed only of colonial and zooxanthellate genera. Subsequently, Hoeksema (2012) described an azooxanthellate *Lep-toseris* (*L. troglodyta* Hoeksema, 2012), but no molecular data is available for it. The three *Thalamophyllia* species included in this study were retrieved in a monophyletic clade but without strong support, which raises questions about the validity of the genus. However, the other three extant and valid *Thalamophyllia* species - *Thalamophyllia gombergi* Cairns, 1979, *Thalamophyllia senaria* Kitahara & Cairns, 2021, and *Thalamophyllia wirtzi* Ocaña et al., 2015 (see Hoeksema and Cairns 2025) could not be included in the analyses as specimens were not available to us.

In the presented phylogeny, the two *P. carolina* comb. nov. specimens collected near Puerto Rico formed a separate lineage sister to the rest of the specimens from the MS-AL shelf, Texas, and Florida, which are instead found intermingled and not differentiated by location. Considering that the Caribbean specimens were collected at greater depth (> 300 m) than those from the MS-AL shelf (between 80 and 130 m) (see Table 1), this result, together with the differences found in the mt genomes, might suggest the presence of population structure in the species between regions and/or depths. Indeed, segregation by distance or by depth has been repeatedly observed in different coral taxa (e.g., Quattrini et al. 2022; Sturm et al. 2023) with important repercussions for conservation strategies. The inclusion of more specimens in future studies from additional locations and depths will be fundamental to shed light into the presence of population structure for the species *P. carolina* comb. nov. or possible cryptic species diversity.

Macromorphological convergence

Pseudomadrepورا carolina comb. nov. and species of the family Madreporidae represent a case of extreme macromorphological convergence, already observed in other scleractinian taxa (Huang et al. 2009; Benzoni et al. 2012; Vaga et al. 2024a). Morphological convergence and plasticity have historically hindered the systematics of several scleractinian taxa, problems that are being currently overcome by the use of an integrative morpho-molecular approach (Huang et al. 2011; Arrigoni et al. 2014; Kitahara et al. 2016). Convergent morphologies are thought to be a possible result of exposure to similar conditions and environments - and implies the presence of conserved molecular pathways in evolutionary distinct lineages. However, the role and function of many scleractinian characters (e.g., columella) are mainly unknown thus, future studies focused on the ecology and physiology of stony corals are needed to shed light on their functional significance.

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Declarations

Conflict of interest The authors declare no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for animal testing, animal care, and use of animals were followed by the authors.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities.

Data availability Complete mitochondrial genomes were deposited in the GenBank repository (accession numbers PV815617-22). Raw read data were uploaded to the Sequence Read Archive under the BioProjects# PRJNA1277317 and PRJNA1277313 - under the umbrella Mesophotic and Deep Benthic Community restoration project# PRJNA1135238 and the umbrella Smithsonian Institution DNA Barcoding Network project# PRJNA81359, respectively. BioSample# SAMN49105786-90, SAMN49106435-53. SRA# SRR34005811-5, SRR34027636-54. Accession numbers of already published and deposited in GenBank sequences used to build the alignments are listed in Supplementary Information 1.

Author contribution CFV and AMQ conceived and designed the study. SH contributed with specimens and resources. CFV and LJM conducted molecular work. CFV analyzed the data. CFV, SDC, MVK, and AMQ interpreted the results. CFV wrote the original draft. All authors edited and approved the final manuscript.

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