

Research Article

Mushroom Soft Corals (Octocorallia: Coralliidae) From Seamounts in the Tropical Northwestern Pacific: Morphology and Phylogenetic Analysis Reveal a New Genus and Six New Species

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Mushroom soft corals in the subfamily Anthomastinae are among the most remarkable octocorals found in the deep sea, characterized by their capitate or mushroom-shaped red colonies and large autozooids. To date, their species diversity remains largely unknown due to limited research, and their phylogenetic relationships have yet to be explored. Based on samples collected from four seamounts in the tropical Northwestern Pacific, we establish a new genus and six new species within Anthomastinae: *Neoanthomastus stellatus* gen. et sp. nov., *Neoanthomastus elongatus* gen. et sp. nov., *Anthomastus sphaericus* sp. nov., *Anthomastus tongi* sp. nov., *Pseudoanthomastus ornatus* sp. nov., and *Pseudoanthomastus applanatus* sp. nov. We transfer four species of *Anthomastus* with the siphonozooids extending into the stalk to the new genus *Neoanthomastus*, and four additional species of *Anthomastus* to *Pseudoanthomastus*. A dichotomous key to all five known genera and 43 species of Anthomastinae is provided. Meanwhile, we utilize the concatenated nucleotides of 13 mitochondrial protein-coding genes (PCGs), the full-length coding regions of the mitochondrial *MutS* gene (*mtMutS*) and the barcodes of partial *mtMutS* to elucidate the phylogenetic relationships among all the five genera (*Anthomastus*, *Bathyalcyon*, *Heteropolypus*, *Pseudoanthomastus*, and *Neoanthomastus* gen. nov.) and available species of Anthomastinae. The phylogenetic trees constructed from the three types of sequences suggest a hierarchical relationship where *Neoanthomastus* gen. nov. and *Pseudoanthomastus* form a clade that clusters with *Bathyalcyon*, which in turn with *Heteropolypus*, and finally with *Anthomastus*, all with high nodal supports. We also identify a second species in octocorals that lack the unique *mtMutS*. The study reveals a high diversity of mushroom soft corals and underscores the need for further systematic and zoogeographic research.

Keywords: *anthomastus*; anthomastinae; deep sea; mitochondrial DNA; *mtMutS*; new taxa

1. Introduction

Octocorals are among the dominant megafaunal taxa in hard-bottom environments, ranging from shallow waters to the deep sea, and are particularly abundant and diverse on seamounts (e.g., [1]). They exhibit remarkable planar structures or three-dimensional “trees,” function as framework

builders and provide habitats for a variety of invertebrates and fishes (e.g., [2]). Among octocorals, mushroom soft corals which belong to the subfamily Anthomastinae Verrill, 1922, are a remarkable group characterized by their typically capitate or mushroom-shaped colonies with relatively large autozooids and small siphonozooids [3]. Guided by molecular phylogenetics, McFadden, Van Ofwegen, and Quattrini

[4] transferred Anthomastinae from the family Alcyoniidae Lamouroux, 1812 to Coralliidae Lamouroux, 1812, a family that includes precious corals and bubblegum corals.

Anthomastinae currently comprises four genera and 37 species, which are found at water depths ranging 126–4298 m worldwide. Among these, *Anthomastus* Verrill, 1878, contains 20 species; *Bathyalcyon* Versluys, 1906 has only one species; both *Heteropolypus* Tixier-Durivault, 1964 [5], and *Pseudoanthomastus* Tixier-Durivault and d'Hondt, 1974 [6, 7], each contain eight species [3, 8–12]. To date, the phylogenetic relationships among Anthomastinae have not been reconstructed. Additionally, the taxonomic features used to distinguish genera and species need to be reevaluated following both morphological and phylogenetic analyses, while some species require redescription to clarify important characteristics, such as sclerites.

Although the species diversity of Anthomastinae comprises approximately one-third of that of Coralliidae (120 species), it remains the least taxonomically studied group when compared to precious corals and bubblegum corals. The Western Pacific hosts the highest diversity, with 15 species identified, including eight species found in the Southwestern Pacific off New Caledonia [9, 13–15]. To date, only two species have been reported from the tropical Northwestern Pacific: *Bathyalcyon robustum* Versluys, 1906, and *Anthomastus nanhaiensis* Li and Xu [11]. During surveys of the seamount benthos in the tropical northwestern Pacific, we discovered six new species of Anthomastinae, two of which represent a new genus. For the first time, we reconstructed the phylogenetic relationships among all five genera and the available species of Anthomastinae using mitochondrial sequences. We also compared the strengths of various alternatives for phylogenetic inference. Based on our phylogenetic analysis and examination of generic features, we transfer four species of *Anthomastus* to the new genus *Neoanthomastus* and four species of *Anthomastus* to *Pseudoanthomastus*.

2. Material and Methods

2.1. Specimen Collection. Specimens were collected from four seamounts of the Caroline Plate in the tropical Northwestern Pacific, informally designed as “M4,” “M5,” “M6,” and “M7,” by the remotely operated vehicle (ROV) submersible *FaXian* during the research cruises of the R/V *KeXue* in 2017 and 2019. The specimens were photographed in situ prior to sampling by the ROV. Immediately after collection, tissues from the tentacles or stalks were excised and stored at -80°C for DNA extraction, while the colonies were photographed and subsequently fixed in 95% ethanol. All type and voucher specimens are deposited in the Marine Biological Museum of the Chinese Academy of Sciences (MBMCASs) in Qingdao, China.

2.2. Morphological Examination. General morphology and anatomy were examined using a stereo-dissecting microscope. Sclerites were isolated from various tissues (including autozoid tentacles, anthocodia wall, pharynx, capitulum surface and interior, stalk surface and interior) by digestion in sodium hypochlorite. To investigate the ultrastructure, sclerites were air dried, mounted on carbon double-sided adhesive tape, and coated for the scanning electron

microscope (SEM). SEM scans were obtained using a Hitachi S-3400N SEM at 15 kV with the optimal magnification selected for each sclerite. Approximately 40 sclerites from each tissue type were photographed and measured. The morphological terminology primarily follows Bayer, Grasshoff, and Verseveldt [16], while the systematics adheres to McFadden, Van Ofwegen, and Quattrini [4].

2.3. DNA Extraction and Sequencing. Total DNA was extracted from the polyps of mushroom soft corals using the DNeasy Blood and Tissue Kit (Qiagen, Germany). The concentration of total isolated DNA was determined with a Qubit Fluorometer (Thermo Scientific, USA), and the quality of the extracted DNA was visualized by electrophoresis on a 1% agarose gel stained with SYBR Safe DNA gel stain (Thermo Scientific, USA).

A paired-end library with an insert size of 300 bp was prepared from total genomic DNA using the VAHTS Universal Plus DNA Library Prep Kit for Illumina V2 (Illumina, USA) following the manufacturer's instruction. This library was sequenced on the Illumina NovaSeq 6000 platform (2×150 bp paired-end reads) (Illumina, USA) at Berry Genomics Co., Ltd. (Beijing, China).

2.4. Assembly and Annotation of the Mitochondrial Genomes. Adapters and components with a quality score below 15 (Phred33 format) were removed from the raw reads using Trimmomatic version 0.36 [17]. The cleaned reads were assembled using the MitoFlex assembler version 0.2.9, which automatically selects mitochondrial genomes from the assembled scaffolds [18]. Annotations of the mitochondrial genomes were conducted on the MITOS web server [19]. The boundaries of the 14 mitochondrial protein-coding genes (PCGs) and 2 rRNAs were determined by aligning them with the homologous genes of soft corals in the Anthomastinae.

2.5. Phylogenetic Analyses. For octocorals, PCGs of mitochondrial genomes evolved at an extremely low rate, with the exception of the mitochondrial *MutS* gene (*mtMutS*) [20]. However, losses of *mtMutS* occasionally occur in the octocorallians, which poses a challenge in assigning the placements of these taxa in the phylogenetic tree based on the rapidly evolving *mtMutS*. To address this dilemma, both the full-length coding regions of *mtMutS* and the concatenated nucleotides of 13 PCGs (excluding *mtMutS*) were utilized for phylogenetic analysis. Furthermore, to include more closely related species in the phylogenetic tree, the barcodes of partial *mtMutS* sequences available for Anthomastinae in GenBank were also employed for phylogenetic inference. The details of the sequences used for phylogenetic analysis are summarized in Table 1.

For the phylogenetic analysis based on 13 PCGs, the nucleotide sequences of these genes were aligned separately using MAFFT v7.471 [21]. Poorly aligned regions were removed with trimAI v1.2 utilizing the “automated1” parameter set [22]. The resulting alignments were concatenated into a single matrix, comprising 10,967 nucleotides to infer phylogenetic relationships using three methods: Maximum Parsimony, Maximum Likelihood, and Bayesian inference. The phylogenetic tree was constructed using the Maximum Parsimony

TABLE 1: Sequences utilized for phylogenetic analysis.

Species	Specimen registration number	GenBank accession number of mtgenome	GenBank accession number of <i>mtMutS</i>
<i>A. cf. canariensis</i>	CMF-2022	—	ON109700.1
<i>A. grandiflorus</i>	—	OL616289_1	OL616289_1
<i>A. cf. grandiflorus</i>	AMQ 2013	—	KC984603.1
<i>A. muscarioides</i>	MNHN:JK-2012-10	—	ON109689
<i>A. nanhaiensis</i>	MBM286430	PV175348	PV175348
<i>A. sphaericus</i>	MBM286336	PV153459	PV153459
<i>A. sphaericus</i>	MBM286337	PV153460	PV153460
<i>A. sphaericus</i>	MBM286338	PV153461	PV153461
<i>A. tongi</i> sp. nov.	MBM286425	PV173764	—
<i>Anthomastus</i> sp.	USNM 1081145	KM015353_1	KM015353_1
<i>Anthomastus</i> sp.	USNM 1171062	KM015352_1	KM015352_1
<i>Anthomastus</i> sp.	HI 035	—	MT655177.1
<i>Anthomastus</i> sp.	USNM 1116820	—	MT655176.1
<i>Anthomastus</i> sp.	SW3155	—	KP324390.1
<i>Anthomastus</i> sp.	WHOI p4	—	KX008392.1
<i>Anthomastus</i> sp.	ANT22	OL616209_1	OL616209_1
<i>B. robustum</i> delta	LII-09-028	—	KC984604.1
<i>B. robustum</i>	MBM286427	PV173767	PV173767
<i>B. robustum</i>	MBM286428	PV173768	PV173768
<i>B. robustum</i>	NIWA 12618-1	PV175346	PV175346
<i>B. robustum</i>	NIWA 12618-2	PV175347	PV175347
<i>H. ritteri</i>	—	—	DQ302816.1
<i>H. sol</i>	—	—	ON109690.1
<i>Heteropolypus</i> sp.	NIWA 69654	PV153462	PV153462
<i>Heteropolypus</i> sp.	NIWA 82615	PV153463	PV153463
<i>Heteropolypus</i> sp.	NIWA 121406	PV153464	PV153464
<i>Heteropolypus</i> sp.	NIWA 126895	PV153465	PV153465
<i>Heteropolypus</i> sp.	NIWA 69654	—	KX008402.1
<i>Heteropolypus</i> sp.	NIWA 85040	—	KX008403.1
<i>Heteropolypus</i> sp.	NIWA 85662	—	KX008404.1
<i>N. elongatus</i>	MBM286421	PV175375	PV175375
<i>N. stellatus</i>	MBM286422	PV175376	PV175376
<i>P. applanatus</i>	MBM286426	PV175377	PV175377
<i>P. ornatus</i>	MBM286335	PV175378	PV175378
<i>Pseudoanthomastus</i> sp.	ANT288	OL616264_1	—
<i>Pseudoanthomastus</i> sp.	ANT287	OL616265_1	OL616265_1
<i>Pseudoanthomastus</i> sp.	USNM 160657	—	OM798842.1
<i>Pseudoanthomastus</i> sp.	AT41-18-025	—	OM798843.1
<i>Pseudoanthomastus</i> sp.	AT41-18-027	—	OM798844.1
<i>Anthomastinae</i> sp. n.	ANT85	—	OL616208.1
<i>Corallium japonicum</i>	—	AB595189_1	AB595189_1
<i>C. rubrum</i>	—	AB700136_1	AB700136_1
<i>Pleurocorallium elatius</i>	—	AB700134_1	AB700134_1
<i>P. konojoi</i>	—	AB595190_1	AB595190_1
<i>Paragorgia coralloides</i>	—	KF785800_1	KF785800_1
<i>P. papillata</i>	MBM286350	—	MW139970.1
<i>P. rubra</i>	Y30157	—	KX505989.1
<i>Sibogagorgia cauliflora</i>	—	KM015354_1	KM015354_1

Note: New sequenced species are given in bold; — means no data available.

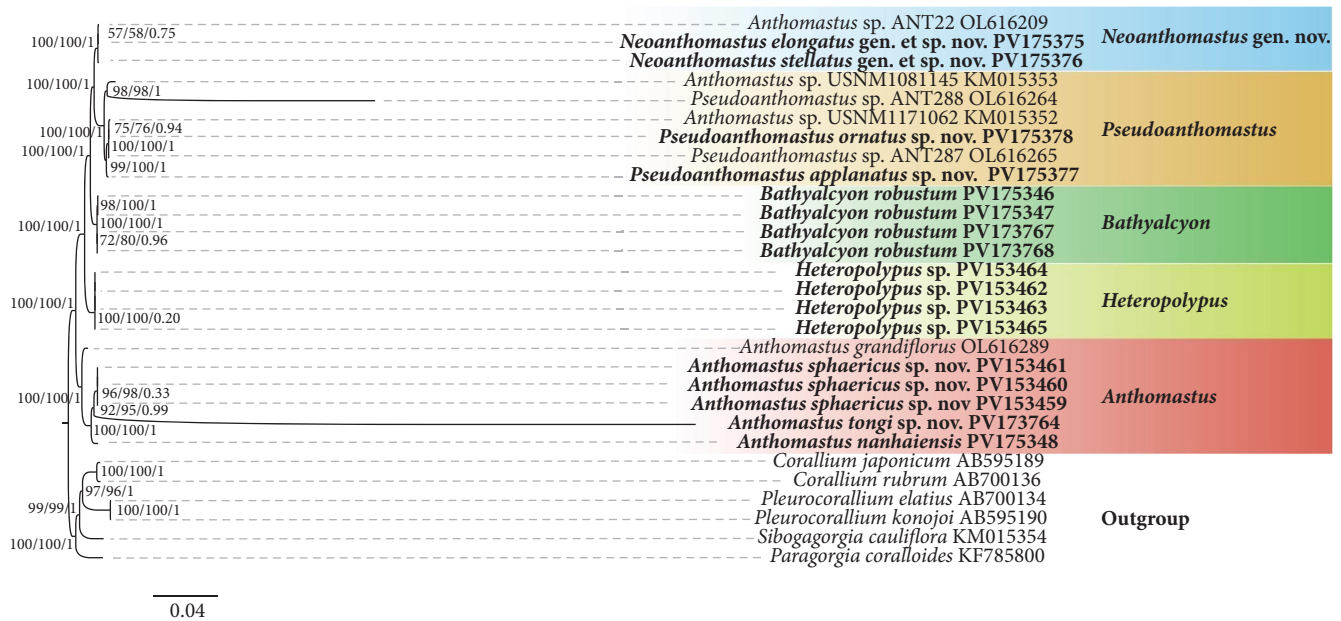


FIGURE 1: A phylogenetic tree of the species within Anthomastinae constructed from the concatenated nucleotides sequences of 13 PCGs in mitochondrial genomes (*mtMutS* not included). SH-aLRT, ultrafast bootstrap values, and posterior probabilities are indicated near the nodes of each branch. The species names in bold represent the sequences generated in this study. The genera outside of Anthomastinae within Coralliidae are used as outgroups. PCGs, protein-coding genes.

method implemented in MEGA X [23]. Gaps were treated as missing data, and the phylogeny was assessed using the bootstrap method with 1000 sampling replications. The PhyloSuite pipeline was employed to conduct Maximum Likelihood analysis and Bayesian inference [24]. Within this pipeline, the optimal partitioning schemes and evolutionary models were determined using PartitionFinder 2, which utilizes the greedy algorithm and the AICc criterion [25]. The “all” and “MrBayes” modes were employed to determine the partitioning schemes and models for Maximum Likelihood and Bayesian analyses, respectively. Subsequently, tree constructions were conducted using the methods of Maximum Likelihood and Bayesian inference methods. The Maximum Likelihood phylogeny was inferred using IQ-TREE software, applying the models selected for each identified partition (Table S1) with 20,000 ultrafast bootstraps [26]. The Bayesian tree was constructed using MrBayes 3.2.6 [27], and the model for each component region (Table S1) was selected based on the recommendations of PartitionFinder2. Four independent runs of four Markov Chain Monte Carlo (MCMC) chains were conducted. Each chain was run for 8 million generations, with the first 25% discarded as burn-in.

For the phylogenetic analysis utilizing the sequences of full-length *mtMutS* and *mtMutS* barcodes, the alignment blocks, after trimming, were 2988 and 650 nucleotides in length, respectively. The optimal models for Maximum Likelihood and Bayesian analyses were selected using ModelFinder ([28]; Table S1). All other procedures for tree construction were consistent with those used for the sequence matrix of 13 PCGs.

2.6. Calculation of Genetic Distances. To confirm the species and genus delimitations of Anthomastinae proposed in this

study, we calculated the genetic distances between and within different genera and species using Mega X with the Kimura 2-Parameter model for the concatenated 13 PCGs of mitochondrial genomes [23]. Because *Pseudoanthomastus* sp. (OL616264) and *A. tongi* sp. nov. exhibited exceptionally high evolutionary rates for the 13 PCGs compared with other species in Anthomastinae (Figure 1), these two taxa were excluded from the analysis.

3. Results

3.1. Loss of *mtMutS* in *Octocorallia*. By the tblastn search, *mtMutS* was not detected in *A. tongi* sp. nov. According to the phylogenetic tree constructed from 13 PCGs, the loss of *mtMutS* in *Pseudoanthomastus* sp. (OL616264) and *A. tongi* sp. nov. occurred independently. Both species exhibited exceptionally high evolutionary rates compared to other species in Anthomastinae (Figure 1).

3.2. Phylogenetic Analysis. Both phylogenetic trees, based on 13 PCGs and the full-length *mtMutS*, clustered the species of Anthomastinae into five clades, corresponding to the five genera of Anthomastinae depicted in this study. In both trees, *Neoanthomastus* gen. nov. and *Pseudoanthomastus* form a clade that is the sister group to *Bathyalcyon*. This trio then clusters with *Heteropolypus*, which is ultimately sister to *Anthomastus*. The topologies of these five genera in both trees are consistent, exhibiting high nodal support (Figures 1 and 2, Figures S1 and S2). It is noteworthy that *A. tongi* sp. nov. and *Pseudoanthomastus* sp. (OL616264), both of which lack *mtMutS* in their mitochondrial genomes, are positioned within the *Anthomastus* and *Pseudoanthomastus* clades, respectively, in both the Maximum Likelihood and Bayesian trees. However, they cluster together in the Maximum Parsimony tree

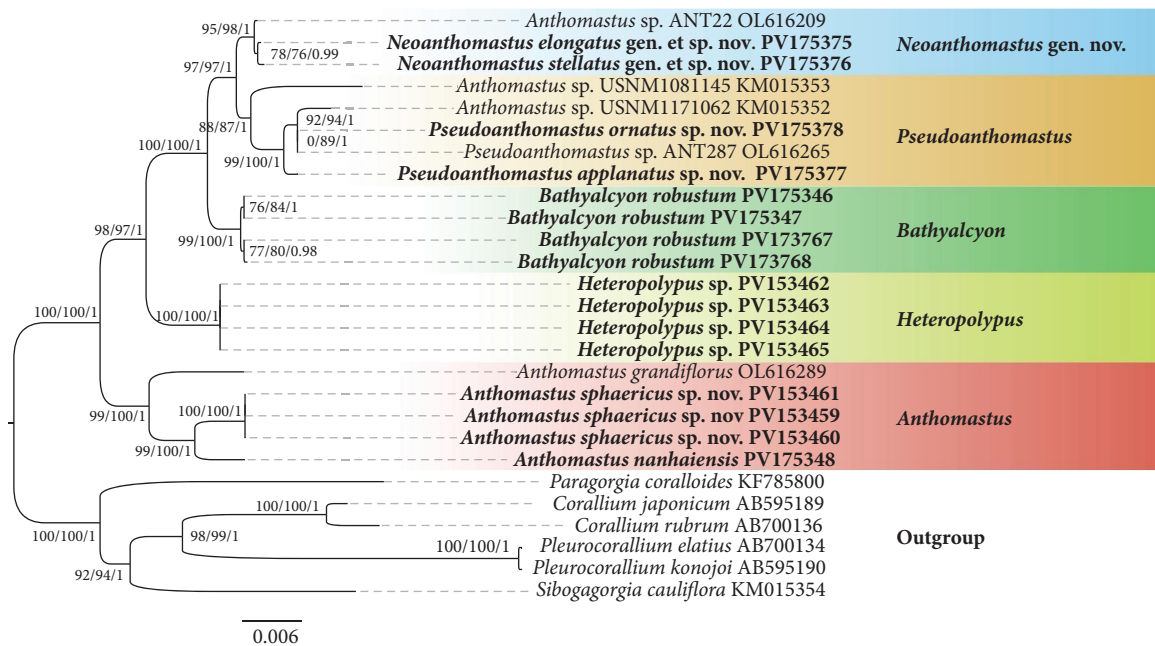


FIGURE 2: A phylogenetic tree of the species within Anthomastinae constructed using full-length *mtMutS* sequences. SH-aLRT, ultrafast bootstrap values, and posterior probabilities are indicated near the nodes of each branch. The genera outside of Anthomastinae within Coralliidae are used as outgroups.

constructed using 13 PCGs (Figure 1, Figure S1). For the tree constructed using partial *mtMutS*, the topology nearly agrees with that generated from 13 PCGs or full-length *mtMutS*, except that *A. muscarioides* clustered with the outgroups (Figure 3, Figure S3). This incongruence may arise from the limited length of the *mtMutS* barcodes or the rapid evolutionary rates in certain species, which did not provide sufficient information to generate a reliable phylogeny, as indicated by the low support values on the nodes.

3.3. Genetic Distances. The intergenus genetic distances in Anthomastinae ranged from 0.92% (between *Neoanthomastus* gen. nov. and *Bathyalcyon*) to 3.02% (between *Pseudoanthomastus* and *Anthomastus*). This range was greater than the intragenus genetic distances, which varied from 0 (within *Heteropolypus*) to 0.83% (within *Anthomastus*) (Table S2).

For intraspecies analysis, genetic distances were calculated exclusively within *Anthomastus*. This decision was made because each species in the other four genera had only a single mitochondrial sequence available, or some species had not been identified to the species level (e.g., *Heteropolypus* sp.). The interspecies genetic distances within *Anthomastus* ranged from 0.84% to 1.45%, while the intraspecies genetic distance for *A. sphaericus* was zero (Table S3). The interspecies genetic distances in *Pseudoanthomastus* ranged from 0.03% to 1.19% (Table S4). For *Neoanthomastus*, the interspecies genetic distances ranged from 0.10% to 0.11% (Table S5). These results support the species identities established in this study; however, defining a reliable barcode gap for species identification in Anthomastinae will require additional intraspecies genetic information in future research.

3.4. Systematics. Class Octocorallia Haeckel, 1866 [29]

Order Scleractyonia McFadden, van Ofwegen and Quattrini, 2022

Family Coralliidae Lamouroux, 1812 [30]

3.4.1. Subfamily Anthomastinae Verrill, 1922. Anthomastinae Verrill, 1922:40; Bayer, 1993:5; d'Hondt and d'Hondt, 2020:247–248.

3.4.1.1. Diagnosis (Modification Based on [3]). Coralliidae usually capitate, mushroom-shaped or occasionally encrusting-shaped colonies, typically divided into capitulum and stalk. Polyps dimorphic. Autozooids sterile is relatively large and not very numerous. Siphonozooids scattered on capitulum, stalk or anthocodial wall, fertile, and minute. Tentacular sclerites commonly multiradiates, rods, plates, clubs, and crosses. Pharyngeal sclerites predominately platelets or rodlets. Sclerites also containing needles, sticks, double stars, double spheroids, and irregular forms.

3.4.2. Genus Anthomastus Verrill, 1878 [31–33]. *Anthomastus* Verrill, 1878:376; Molodtsova, 2013:491–492; d'Hondt and d'Hondt, 2020:250.

Anthomastus s. s. Bayer, 1993:6.

(in part) *Anthomastus* Studer, 1901:26–27; Kükenthal, 1910:57–58; Jungersen, 1927:5; Deichmann, 1936:52.

3.4.2.1. Diagnosis (Modified From [8], With Italics Indicating Modifications). Colonies hemispherical to capitate with dome-shaped capitulum gradually passing via an inconspicuous stalk into the holdfast, or mushroom-shaped with a conspicuous stalk. Polyps dimorphic, with sclerites. Autozooids

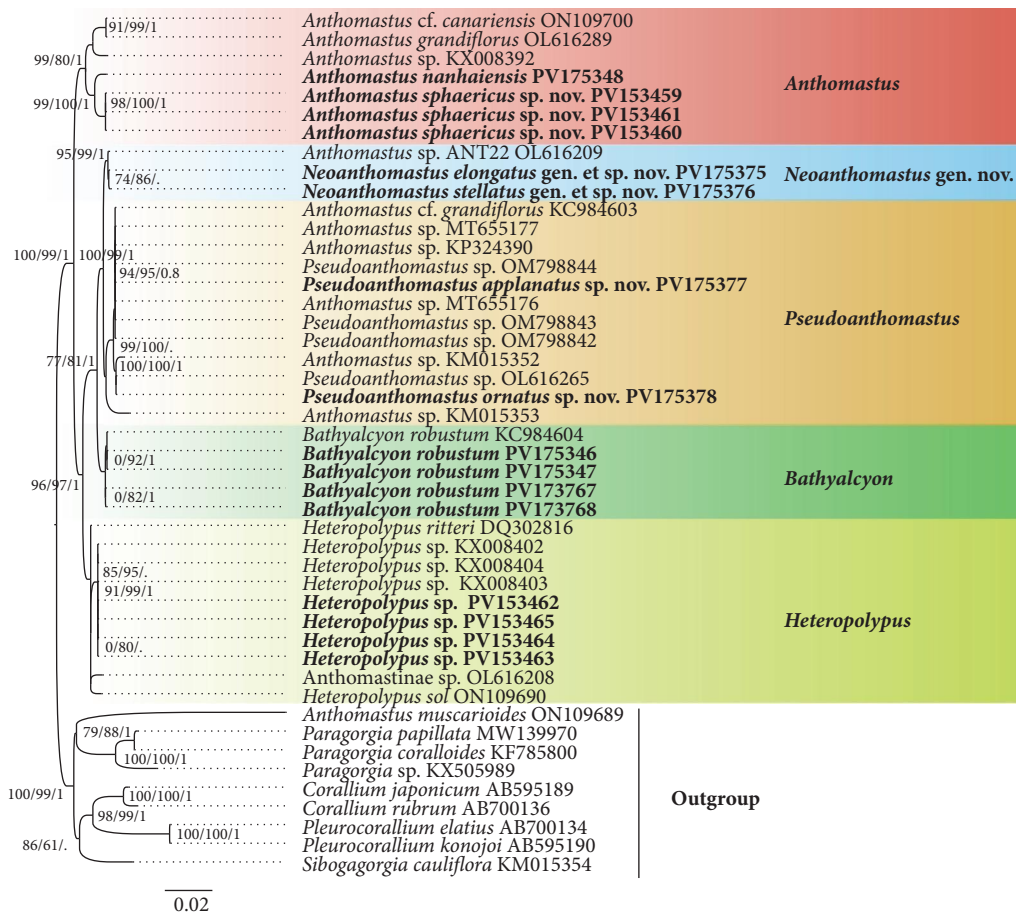


FIGURE 3: A phylogenetic tree of Anthomastinae based on the partial *mtMutS*. SH-aLRT, ultrafast bootstrap values, and posterior probabilities are indicated near the nodes of each branch. Bootstrap values are displayed if they exceed 60%, and posterior probabilities are shown only if they reach 0.6. The genera outside of Anthomastinae within Coralliidae are used as outgroups.

arranged over the capitulum, sterile, retractile, and relatively large. Sclerites equally developed at dorsal and ventral sides of autozooids. Anthocodial armature usually more developed at the base of autozooid tentacles. Siphonozooids *restricted in capitulum*, fertile, and numerous. Sclerites containing needles, rods, *multiradiates*, warted clubs, plates, spindles, and *tuberculated double spheroids*. Pharyngeal sclerites predominately platelets, *rodlets*, or *absent*. Tentacular sclerites predominately rods, plates, and crosses.

3.4.2.2. Remarks. *Anthomastus* is the first established and most commonly studied genus of mushroom soft corals among octocoral taxonomists and related researchers. Consequently, many specimens have been misidentified, and some species have even been incorrectly assigned to the wrong genus. For instance, Molodtsova [8] questioned the generic assignment of *A. zealandicus*, *A. aberrans*, and *A. agaricoides*, and corrected the misidentification of *A. grandiflorus* made by Ditlevsen [34], Martin and Britayev [35], and Watling et al. [36]. This is also reflected in our phylogenetic trees where *Anthomastus* is inferred to be polyphyletic as *Anthomastus* cf. *grandiflorus* (KC984603) and several unidentified species of *Anthomastus* are grouped within the *Pseudoanthomastus* and *Neoanthomastus* gen. nov. clades. According to these

trees, *Anthomastus* is considered a primitive genus of Anthomastinae by having predominately rods in tentacles, predominantly platelets or rodlets in pharynx, and siphonozooids located in capitulum. The pharyngeal and tentacular sclerites have been used to distinguish *Anthomastus* and *Pseudoanthomastus*. In this study, we restrict *Anthomastus* to include only those species whose siphonozooids are confined to the capitulum, and establish the new genus *Neoanthomastus* for species whose siphonozooids extend into the stalk. Consequently, the four species *Anthomastus giganteus*, *A. hicksoni*, *A. purpureus*, and *A. tahinodus* are transferred to *Neoanthomastus* gen. nov. as *N. giganteus* (Tixier-Durivault, 1954) [37] comb. nov., *N. hicksoni* (Bock, 1938) [38] comb. nov., *N. purpureus* (Koren and Danielssen, 1883) [39] comb. nov., and *N. tahinodus* (d'Hondt, 1988) [40] comb. nov., respectively. In addition, we define the pharyngeal sclerites as “predominately platelets, rodlets, or absent”, as some species (e.g., *A. bathyproctus*, *A. cyanae*, *A. megacephalus*, *A. muscarioides*, and *A. sphaericus*) possess rodlets predominately or exclusively in their pharynx, while *A. bayeri* is devoid of sclerite from the pharynx [3, 8, 9, 13, 14].

Anthomastus agassizii and *A. zealandicus* possess multi-radiates in tentacles, a characteristic feature of *Pseudoanthomastus* rather than *Anthomastus* [13, 14, 41]. Therefore, we transfer both species to the genus *Pseudoanthomastus* as

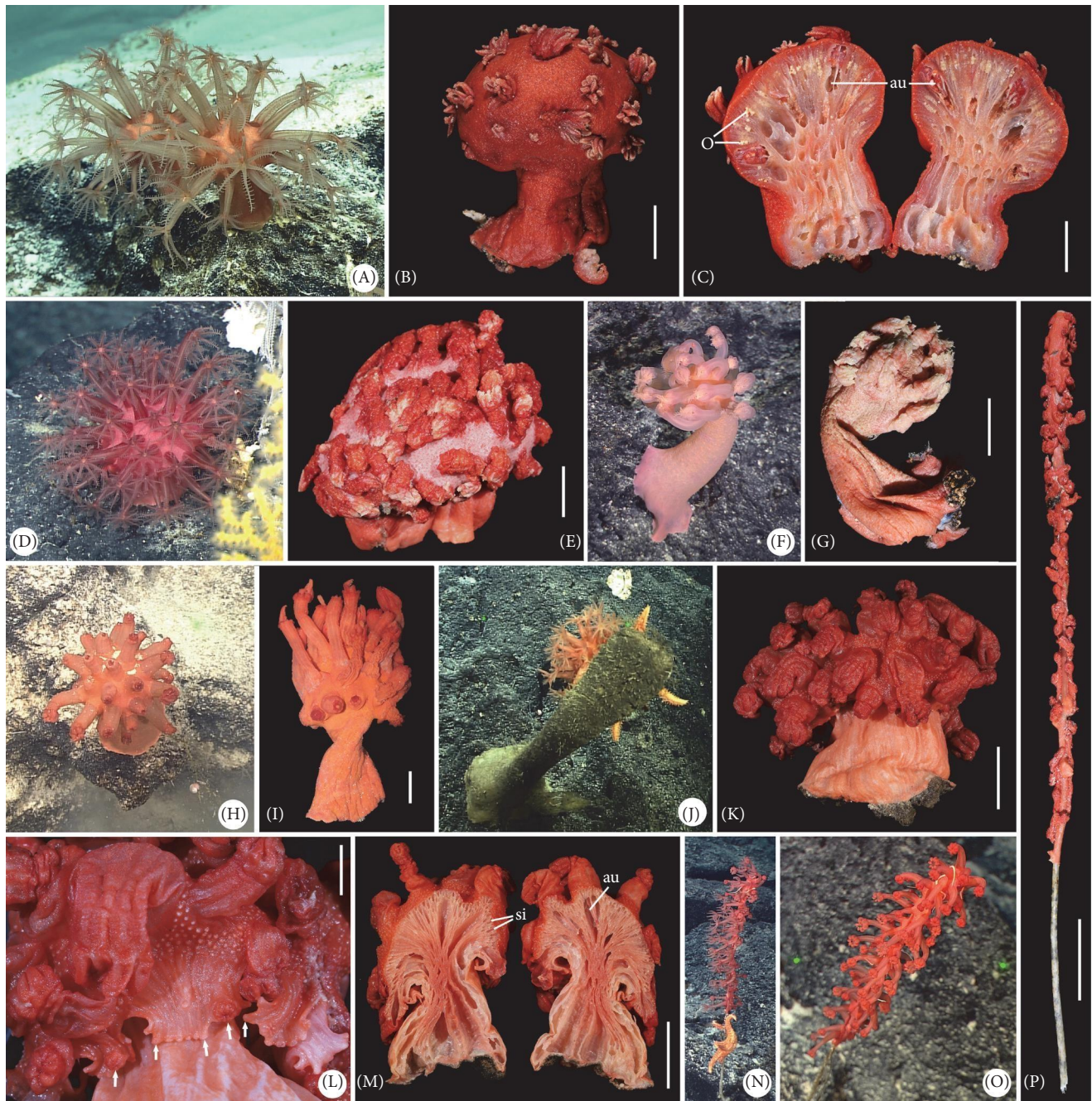


FIGURE 4: Morphology of *Neoanthomastus* gen. nov. and six new species of Anthomastinae. (A–C) *A. sphaericus* sp. nov., same specimen in situ (A) and in preservation (B, C). (D, E) *A. tongi* sp. nov. in situ and in preservation. (F, G) *N. stellatus* gen. et sp. nov. in situ and in preservation. (H, I) *N. elongatus* gen. et sp. nov. in situ and in preservation. (J–M) *P. ornatus* sp. nov., same specimen in situ (J) and in preservation (K–M), arrows indicate small autozooids of capitulum margin. (N–P) *P. applanatus* sp. nov., same specimen in situ (N, O) and in preservation (P). au, autozooids; o, oocytes; si, siphonozooids. Scale bars = 10 mm (B, C, E), 20 mm (G, I, K, M), 5 mm (L), and 50 mm (P).

P. agassizii (Verrill, 1922) [41] comb. nov. and *P. zealandicus* (Benham, 1928) [42] comb. nov. The colony shape of *A. aberrans* and *A. paradoxus*, two encrusting-shaped species, resembles that of *P. applanatus* sp. nov. described below. Their anthocodial walls contain multiradiates and thorny clubs, characteristics typical of *Pseudoanthomastus* [14, 43]. Consequently, these species are also transferred to *Pseudoanthomastus* as *P. aberrans* (Thomson and Henderson,

1906) [43] comb. nov. and *P. paradoxus* (d'Hondt in d'Hondt and d'Hondt, 2018) [14] comb. nov.

3.4.3. *Anthomastus sphaericus* sp. nov. Figures 4A–C, 5, and 6.

3.4.3.1. *Material Examined*. Holotype: MBM286336, collected on August 20, 2017 from the station FX-Dive 136

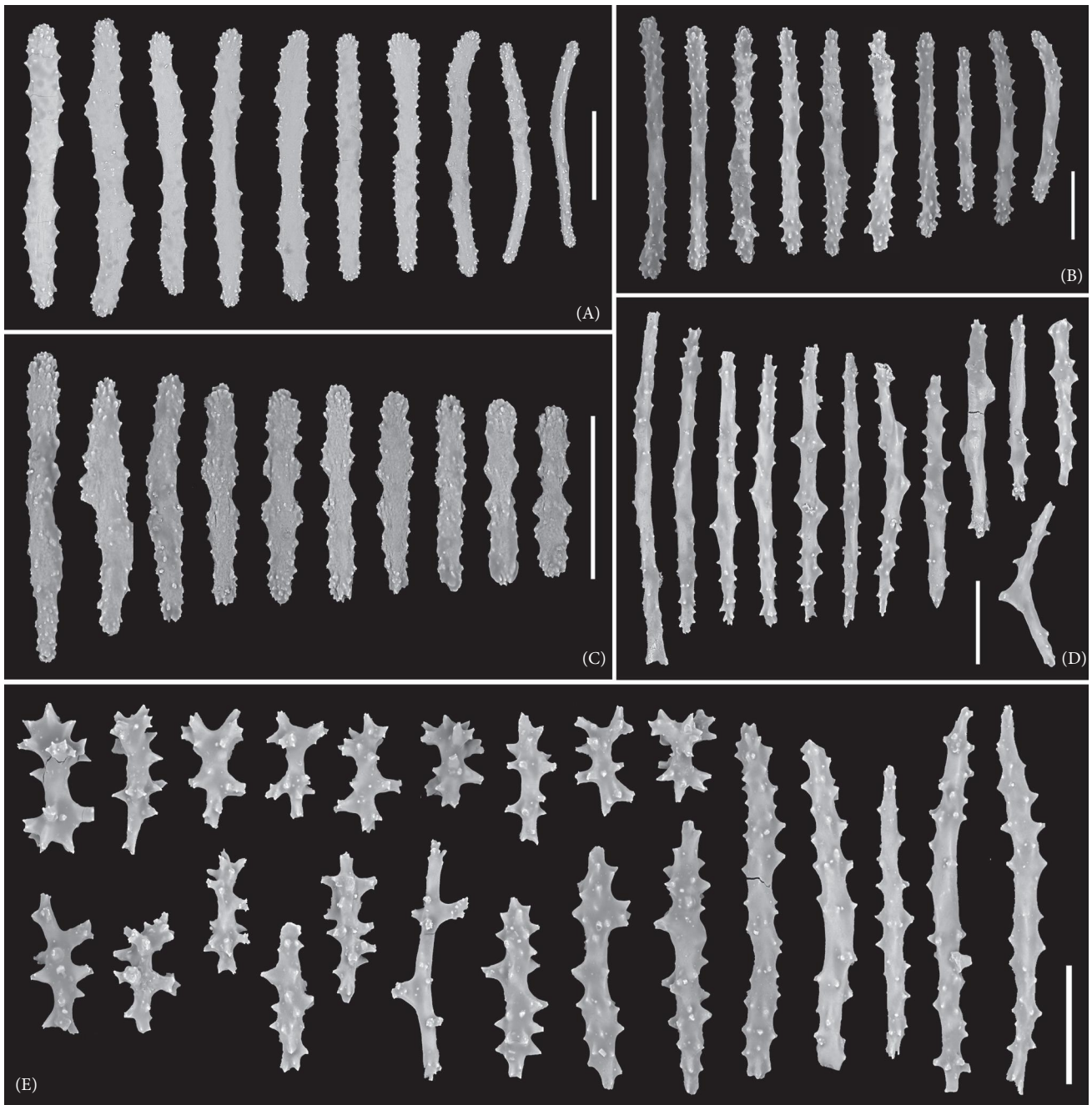


FIGURE 5: Sclerites from the holotype of *A. sphaericus* sp. nov. (A) Sclerites from tentacles of autozooids. (B) Sclerites from anthocodial wall. (C) Sclerites from pharynx. (D) Sclerites from interior of stalk. (E) Sclerites from surface of stalk. Scale bars = 0.1 mm.

(10°28.54'N, 140°05.64'E) of M4 seamount with water depth of 1435 m. Paratypes: MBM286337 and MBM286338, each with one specimen, collected together with the holotype.

3.4.3.2. Description of Holotype

3.4.3.2.1. Colony Form and Size. In life, animal attached to hard substrate (Figure 4A). Colony capitate, 50 mm long. Stalk short, about 22 mm long and 19 × 10 mm wide, emerging from a membranous and spreading holdfast. Capitulum projecting from stalk, nearly spherical, 42 × 33 mm in width

and 28 mm long (occupying 56% of total colony length), and bearing 27 autozooids (Figure 4B,C).

3.4.3.2.2. Polyps. Polyps dimorphic. Autozooids sterile, arranged evenly over capitulum, and most not completely retracted into capitulum, leaving tentacles and sometimes upper anthocodia outside capitulum surface. Autozooids up to 8 mm long and 6 mm wide. Tentacles 5–7 mm long with 15–21 pairs of pinnules. Siphonozooids fertile, inconspicuous, scattered among autozooids, and about 0.5 mm wide.

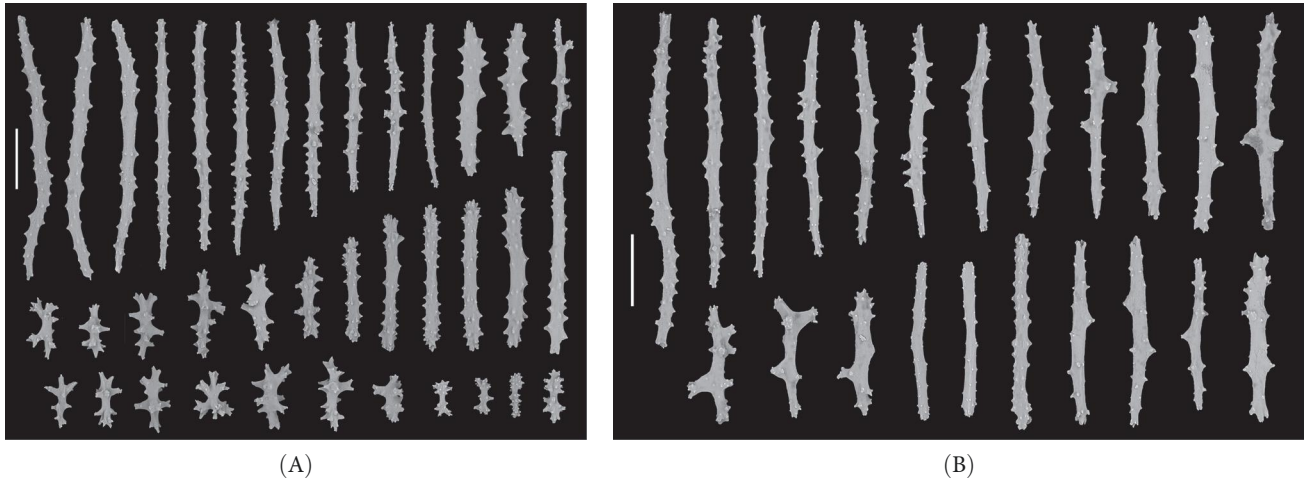


FIGURE 6: Sclerites from the holotype of *A. sphaericus* sp. nov. (A) Sclerites from surface of capitulum. (B) Sclerites from interior of capitulum. Scale bars = 0.1 mm.

3.4.3.2.3. Sclerites. Tentacular sclerites nearly all tuberculated rods measuring 0.24–0.35 mm long (Figure 5A). Anthocodial sclerite type same to that of tentacle, mostly 0.24–0.39 mm long; these sclerites not arranged en chevron, and crown not developed (Figure 5B). Pharyngeal sclerites exclusively slightly flattened rodlets ranging 0.11–0.19 mm long (Figure 5C). Sclerites from the stalk interior predominately rods to needles, slightly tuberculated, and ranging 0.20–0.42 mm long (Figure 5D). Sclerites from the stalk surface predominately multiradiates ranging 0.08–0.15 mm long; tuberculated spindles and rods ranging 0.20–0.30 mm long (Figure 5E). Sclerites of the capitulum surface predominately tuberculated needles ranging 0.28–0.44 mm long; spiny rods ranging 0.18–0.34 mm long; multiradiates ranging 0.06–0.15 mm long (Figure 6A). Sclerites of the capitulum interior predominately tuberculated needles ranging 0.28–0.47 mm long; tuberculated to spiny rods ranging 0.22–0.30 mm long; multiradiates large, rare, and ranging 0.17–0.18 mm long (Figure 6B).

3.4.3.2.4. Color. Colony dark red in preservation. Autozooids pinkish in situ (Figure 4A–C).

3.4.3.3. Variation. Both paratypes with same colony shape as holotype. Paratype MBM286337 measuring 46 mm long with capitulum 40 × 36 mm in diameter and 28 mm long, capitulum bearing 34 autozooids, and stalk 22 × 12 mm in diameter and 18 mm long. Paratype MBM286338 measuring 31 mm long with capitulum 30 × 25 mm in diameter and 22 mm long, capitulum bearing 20 autozooids, and stalk 23 × 14 mm in diameter and 9 mm long.

3.4.3.4. Etymology. The Greek adjective *sphaericus* (spherical) refers to the spherical capitulum of the species.

3.4.3.5. Distribution and Habitat. Found only from M4 seamount in the tropical Northwestern Pacific, where the water depth was 1435 m and temperature about 2.9°C. In situ, the species attached to hard substrate.

3.4.3.6. Remarks. *Anthomastus sphaericus* sp. nov. matches well with the generic definition of *Anthomastus*, in which it resembles *A. bathyproctus* in having rodlets in pharynx and predominately rods in tentacles. The two species differ distinctly in the colony shape and anthocodial sclerites: *A. sphaericus* sp. nov. has capitate colony with spherical capitulum and short stalk and has nearly all rods in anthocodial wall; while *A. bathyproctus* has mushroom-shaped to obconic colony with capitulum completely retractile into digitiform stalk and has multiradiates, double stars, and clubs in anthocodial wall [3].

Among the members with unknown pharyngeal sclerites, *A. sphaericus* sp. nov. resembles *A. agaricoides*, *A. antarcticus*, *A. canariensis*, and *A. globosus* in spherical capitulum. However, the new species differs from *A. agaricoides* by its short and broad stalk (vs. cylindrical and slender), red colony, autozooids and siphonozooids (vs. purplish red colony, yellowish white autozooids and white siphonozooids, respectively), and probably larger tentacular sclerites; from *A. antarcticus* by more autozooids (20–34 vs. very few), and red autozooids and siphonozooids (vs. yellowish); from *A. canariensis* by larger colony size (31–50 mm vs. 10 mm long) and more autozooids (20–34 vs. 12 or 13 in number); from *A. globosus* by possessing sclerites provided with conical protuberances rather than rounded ones in those of *A. globosus*, larger colony size (31–50 mm vs. 15 mm long) and more autozooids (20–34 vs. 16 in number).

Anthomastus sphaericus sp. nov. showed no intraspecific genetic variation in the concatenated 13 PCGs of mitochondrial genomes. It formed sister clades with *A. tongi* sp. nov. in the case only four of 14 known *Anthomastus* species were available for phylogenetic reconstruction (Figure 1; Table S2).

3.4.4. *Anthomastus tongi* sp. nov. Figures 4D,E, 7, and 8.

3.4.4.1. Material Examined. Holotype: MBM286425, collected on June 5, 2019 from the M6 seamount station FX-Dive 217 (10°6.92'N, 140°14.58'E) with water depth of 790 m.

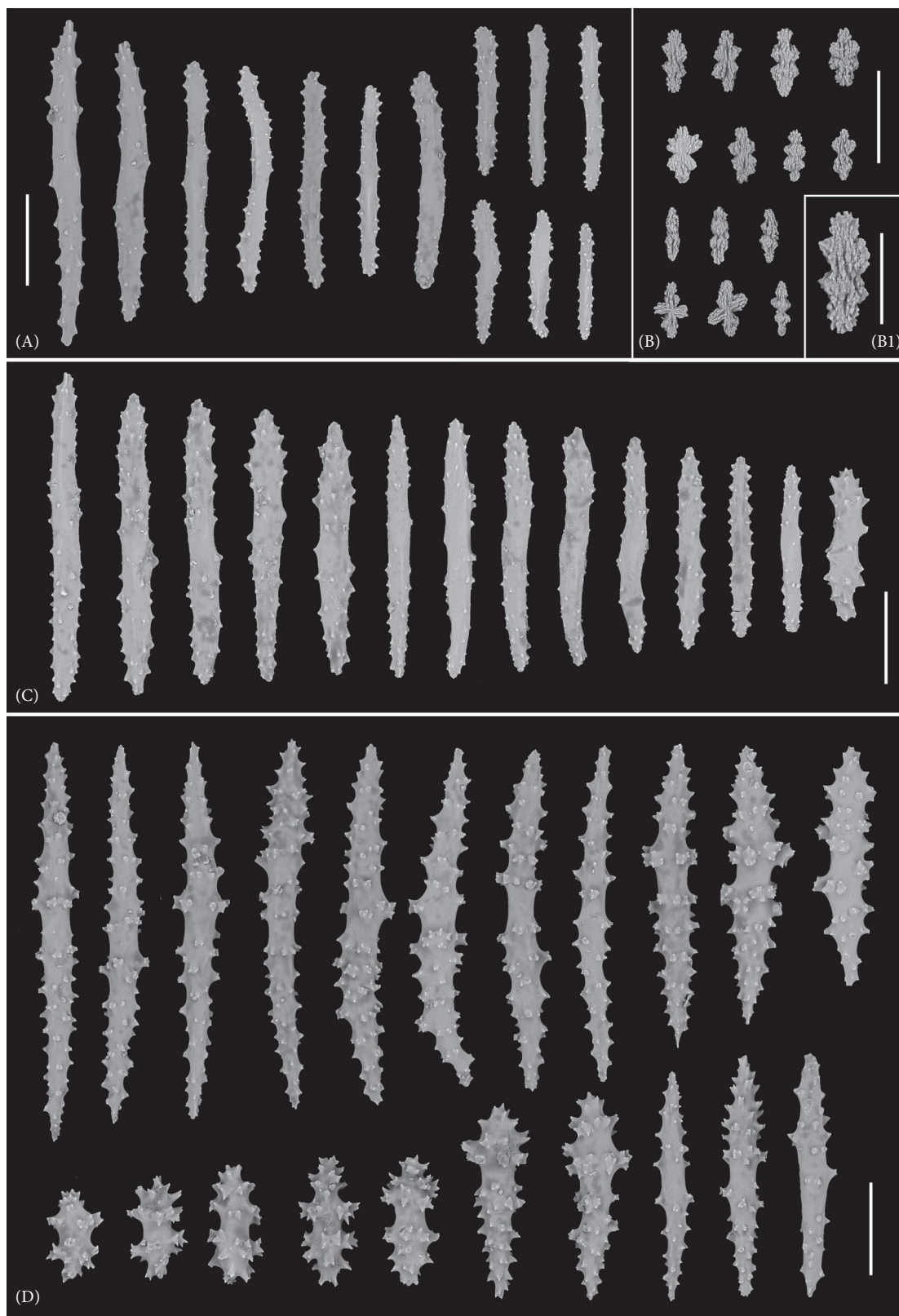


FIGURE 7: Sclerites of *A. tongi* sp. nov. (A) Sclerites from tentacles of autozooid. (B, B1) Sclerites from pharynx. (C) Sclerites from anthocodial wall. (D) Sclerites from surface of capitulum. Scale bars = 0.1 mm (A–D) and 0.05 mm (B1).

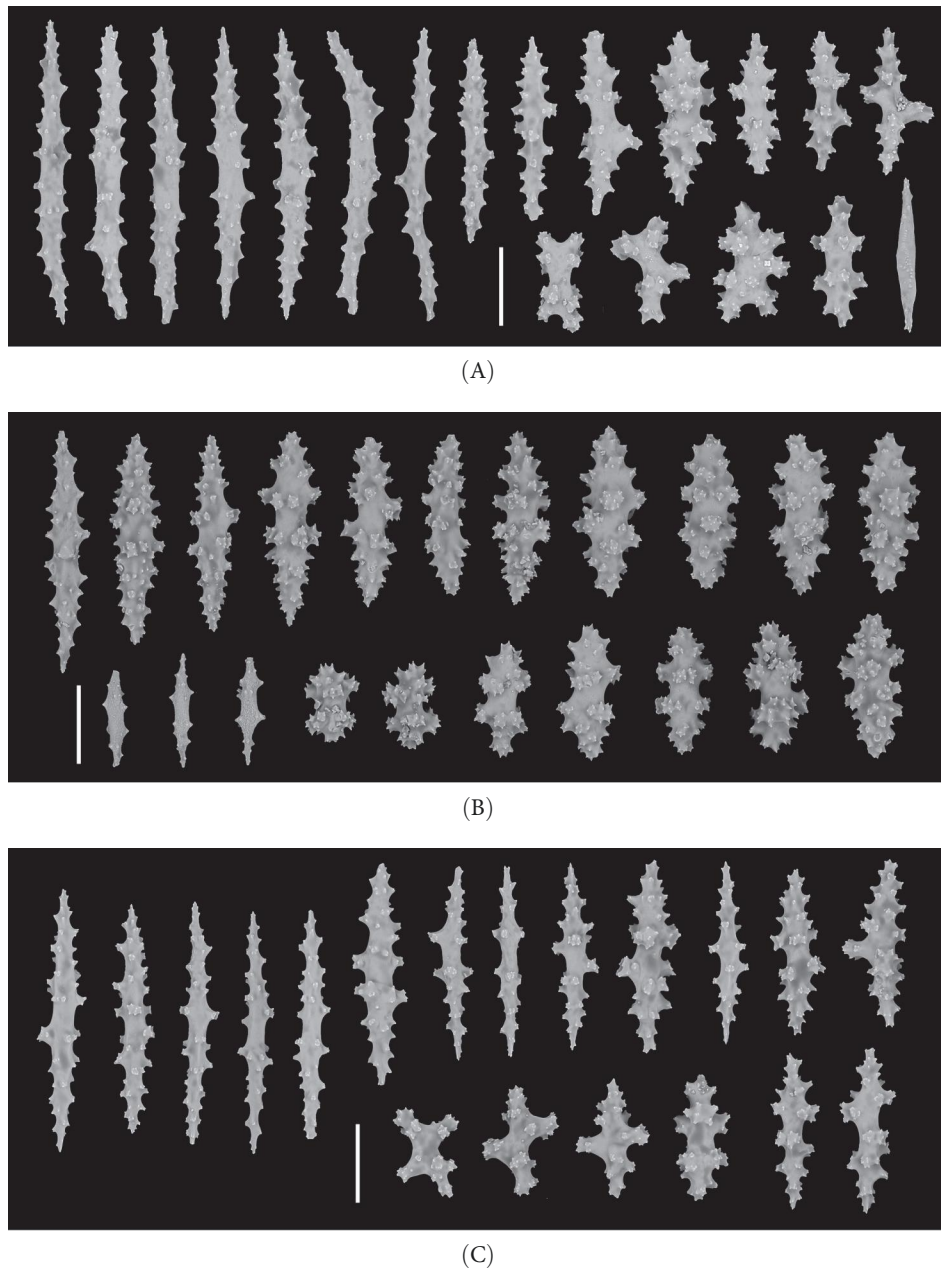


FIGURE 8: Sclerites of *A. tongi* sp. nov. (A) Sclerites from interior of capitulum. (B) Sclerites from surface of stalk. (C) Sclerites from interior of stalk. Scale bars = 0.1 mm (A–C).

3.4.4.2. Description of Holotype

3.4.4.2.1. Colony Form and Size. In life, animal attached to hard substrate, with autozooids expanded and pinnules visible (Figure 4D). Colony capitate, 42 mm long, hemispherical. Stalk short, about 14 mm long and about 22 mm in diameter, emerging from a membranous and spreading holdfast. Capitulum projecting from stalk, nearly spherical, about 42 mm in diameter and 28 mm long (occupying 67% of total colony length), and bearing 90 autozooids (Figure 4E).

3.4.4.2.2. Polyps. Polyps dimorphic. Autozooids sterile, arranged evenly over capitulum, not retracted, leaving tentacles and anthocodia outside capitulum. Autozooids up to 15 mm long and 6 mm wide. Tentacles up to 4 mm long with

more than 20 pairs of pinnules. Siphonozooids fertile, inconspicuous, scattered among autozooids, and measuring 0.2–0.3 mm wide.

3.4.4.2.3. Sclerites. Tentacular sclerites predominately tuberculated rods, straight to slightly curved, measuring 0.13–0.35 mm long (Figure 7A). Pharyngeal sclerites predominately platelets, ranging 0.06–0.08 mm long, and occasionally cross with similar size (Figure 7B,B1). Anthocodial sclerite type same to that of tentacle, mostly 0.17–0.36 mm long; these sclerites not arranged en chevron, and crown not developed (Figure 7C). Sclerites of capitulum surface predominately tuberculated spindles ranging 0.25–0.43 mm long; less commonly squat tuberculated rods ranging 0.10–0.13 mm long;

occasionally tuberculated clubs ranging 0.21–0.23 mm long (Figure 7D). Sclerites of capitulum interior predominately ordinarily to highly tuberculated spindles, ordinarily tuberculated ones slender, having small and simple protuberances, and ranging 0.37–0.39 mm long; highly tuberculated ones dumpy, having large and highly ramified protuberances, and ranging 0.18–0.24 mm long; occasionally smooth spindles and irregular forms having protuberances and size similar to those of highly tuberculated spindles (Figure 8A). Sclerites of stalk surface predominately dumpy and highly tuberculated spindles, usually ranging 0.15–0.26 mm long; occasionally slender and slightly tuberculated spindles ranging 0.12–0.14 mm long, and double stars ranging 0.10–0.11 mm long (Figure 8B). Sclerites of stalk interior similar to those of capitulum interior, predominately tuberculated spindles, ranging 0.16–0.30 mm long; irregular forms ranging 0.13–0.15 mm long (Figure 8C).

3.4.4.2.4. *Color*. Colony red both in life and in preservation (Figure 4D,E).

3.4.4.3. *Etymology*. Named for the Chinese distinguished biologist Dizhou Tong (1902–1979), in honor of his contribution to the experimental embryology and clone technology in China.

3.4.4.4. *Distribution and Habitat*. Found only on M6 seamount located on the Caroline Ridge in the tropical northwestern Pacific, where the water depth was 790 m, temperature about 5.1°C. In situ, *A. tongi* sp. nov. attached to hard substrate.

3.4.4.5. *Remarks*. *Anthomastus tongi* sp. nov. is the second octocoral species lacking *mtMutS*, like *Pseudoanthomastus* sp. [20]. Morphologically, *A. tongi* sp. nov. matches well with the definition of *Anthomastus* and mostly resembles *A. nanhaiensis* by having platelets in pharynx, predominately rods in tentacles and capitate colony. They differ distinctly by double spheroids which are absent in *A. tongi* sp. nov. but are abundant in the capitulum and stalk of *A. nanhaiensis* (see [11]).

3.4.5. *Neoanthomastus* gen. nov.

3.4.5.1. *Diagnosis*. Mushroom-shaped, capitate colonies with domeshaped capitulum separated from a conspicuous and often cylindrical stalk. Polyps dimorphic, with sclerites. Autozooids arranged over capitulum, sterile, large, not very numerous, retractile but not completely retracted. Sclerites equally developed around autozooids. Anthocodial armature more developed near base of tentacles. Siphonozooids scattered over both capitulum and stalk, fertile, conspicuous, feebly armored, and numerous. Sclerites multiradiates, rods, spindles, and needles. Pharyngeal sclerites predominately rodlets. Tentacular sclerites predominately rods, spindles, and multiradiates.

3.4.5.2. *Type Species*. *Neoanthomastus stellatus* gen. et sp. nov., here designated.

3.4.5.3. *Etymology*. Composite of the Greek prefix *neos* (new) and the generic name *Anthomastus*. Gender masculine.

3.4.5.4. *Remarks*. Morphologically, *N. stellatus* sp. nov. and *N. elongatus* sp. nov. mostly resemble members of *Pseudoanthomastus* by having predominately rodlets in pharynx and diverse sclerites in tentacles. In all the phylogenetic trees constructed in this study, the two new species of *Neoanthomastus* are grouped together and then sister to *Pseudoanthomastus* (Figures 1–3). The genetic distance between the two new species and *Pseudoanthomastus* is 1.20%, much larger than the intragenus genetic distances of *Pseudoanthomastus* (0.58%) as well as all the other intragenus genetic distances of Anthomastinae (0%–0.83%) (Table S2). The molecular result supports the usage of pharyngeal and tentacular sclerites as the most important characters of Anthomastinae and highlights also the taxonomic significance of the location of siphonozooids on stalk in generic separation. The location of siphonozooids on stalk has just been recognized for species separation in *Anthomastus*. *Bathyalcyon* as a peculiar genus has only a single autozooid, where siphonozooids occupy the wall [3, 11, 44]. Therefore, we establish the new genus *Neoanthomastus* to accommodate *N. stellatus* sp. nov. and *N. elongatus* sp. nov. with siphonozooids extending to stalk. *A. giganteus*, *A. hicksoni*, *A. purpureus* (original combination *Sarcophyton purpureus*), and *A. tahinodus* also possess siphonozooids extending to stalk. Thus, we assign them into the new genus: *Neoanthomastus giganteus* (Tixier-Durivault, 1954) [37] comb. nov., *Neoanthomastus hicksoni* (Bock, 1938) [38] comb. nov., *Neoanthomastus purpureus* (Koren and Danielssen, 1883) [39] comb. nov., and *Neoanthomastus tahinodus* (d'Hondt, 1988) [40] comb. nov.

3.4.6. *Neoanthomastus stellatus* gen. et sp. nov. Figures 4F,G and 9.

3.4.6.1. *Material Examined*. Holotype: MBM286422, collected on May 30, 2019 from the station FX-Dive 212 (10°3.57'N, 140°10.95'E) of M5 seamount with water depth of 1221 m.

3.4.6.2. *Description of Holotype*

3.4.6.2.1. *Colony Form and Size*. In life, animal attached to hard substrate, colony mushroom-shaped including a convex capitulum and an elongate stalk (Figure 4F). Preserved colony 105 mm long with capitulum bearing 22 autozooids. Capitulum convex, 39 mm in width and 45 mm long, occupying 43% of total colony length. Stalk cylindrical and elongated, ~60 mm long, measuring 18 mm in diameter at middle narrowest part. Holdfast round in life, irregular in preservation, and measuring ~30 × 48 mm in width (Figure 4G).

3.4.6.2.2. *Polyps*. Polyps dimorphic. Autozooids sterile, scattered evenly over whole capitulum, mostly contracted slightly; the largest ones approximately 20 mm long and 6 mm wide. Tentacles contracted, up to 7 mm long. Siphonozooids fertile, conspicuous and numerous, scattered among whole colony, visible as minute red protuberances, of various sizes and maximum about 2.0 mm wide.

3.4.6.2.3. *Sclerites*. Tentacular sclerites exclusively tuberculated rods, straight to curved, often expanded at one or both ends, and ranging 0.12–0.26 mm long (Figure 9A).

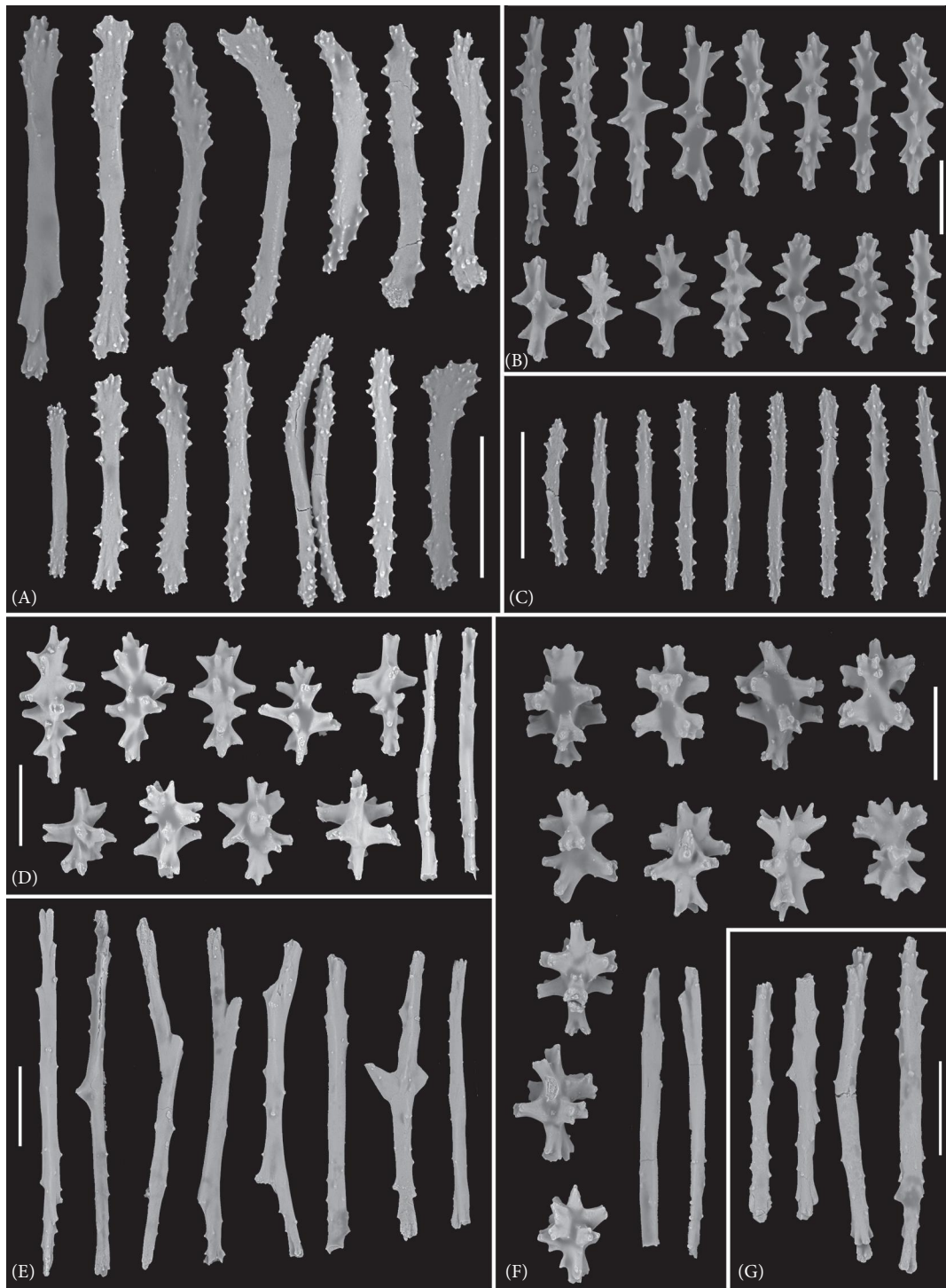


FIGURE 9: Sclerites of the holotype of *N. stellatus* sp. nov. (A) Sclerites from tentacles of autozooids. (B) Sclerites from anthocodial walls. (C) Sclerites from pharynx. (D) Sclerites from surface of capitulum. (E) Sclerites from interior of capitulum. (F) Sclerites from surface of stalk. (G) Sclerites from interior of stalk. Scale bars = 0.1 mm.

Anthocodial sclerites predominately spiny rods to multiradiates with blunt protuberances, ranging 0.14–0.31 mm long; sclerites not arranged en chevron, and crown not developed (Figure 9B). Pharyngeal sclerites exclusively tuberculated

rods, 0.12–0.17 mm long (Figure 9C). Sclerites of capitulum surface predominately multiradiates ranging 0.11–0.19 mm long; occasionally slightly tuberculated rods ~0.30 mm long (Figure 9D). Sclerites of capitulum interior exclusively rods,

nearly smooth, with few but large protuberances or bifurcate, and ranging 0.33–0.45 mm long (Figure 9E). Sclerites of stalk surface predominately multiradiates ranging 0.11–0.14 mm long; occasionally smooth rods ~0.31 mm long (Figure 9F). Sclerites of stalk interior exclusively slightly tuberculated rods ranging 0.25–0.36 mm long (Figure 9G).

3.4.6.2.4. Color. Colony surface pink both in vivo and in ethanol preservation; inner colony white with sclerite aggregation area reddish (Figure 4F,G). Sclerites translucent to reddish under transmitted light.

3.4.6.3. Etymology. The Latin adjective *stellatus* (stellate) refers to the stellated siphonozooids on the stalk.

3.4.6.4. Distribution and Habitat. Found on M5 seamount located on the Caroline Ridge in the tropical Northwestern Pacific, where the water depth was 1221 m, temperature about 3.8°C. In situ, *N. stellatus* sp. nov. attached to hard substrates and inhabited by a crustacean amphipod.

3.4.6.5. Remarks. *Neoanthomastus stellatus* sp. nov. resembles *N. tahinodus* [40] comb. nov. (original combination *A. tahinodus*) by having an elongated and cylindrical stalk, siphonozooids scattered among the whole stalk, and sclerites with blunt protuberances. The new species differs from *N. tahinodus* comb. nov. by possessing exclusively rods in the tentacles (vs. with also multiradiates), the sclerite types in anthocodial wall (spiny rods to multiradiates vs. only multiradiates), and the distribution of autozooids (scattered evenly over capitulum vs. mostly on the periphery of capitulum with central capitulum clear).

3.4.7. *Neoanthomastus elongatus* gen. et sp. nov. Figures 4H,I and 10.

3.4.7.1. Material Examined. Holotype: MBM286421, collected on June 8, 2019 from the station FX-Dive 220 (10°4.93'N, 140°15.52'E) of M7 seamount with water depth of 1094 m.

3.4.7.2. Description of Holotype

3.4.7.2.1. Colony Form and Size. In life, animal attached to hard substrate, colony mushroom-shaped including a convex capitulum and an elongate stalk. Autozoooid tentacles retracted into anthocodiae when disturbed (Figure 4H). Preserved colony about 150 mm long with capitulum bearing 29 autozooids. Capitulum convex, about 55 mm in width and 90 mm long, occupying 60% of total colony length. Stalk cylindrical and elongated, ~60 mm long, measuring 19 mm in diameter at middle narrowest part. Holdfast round in life, irregular in preservation, and measuring ~25 × 40 mm in width (Figure 4I).

3.4.7.2.2. Polyps. Polyps dimorphic. Autozooids sterile, scattered evenly over whole capitulum, most slightly contracted, with a few retracted into capitulum; the largest one up to 60 mm long and 12 mm wide. Tentacles contracted, maximum 15 mm long and 5 mm wide, with about 25 pairs of pinnules; pinnules up to 2.5 mm long. A few small and developing autozooids occurred in the lowest part of capitulum. Siphonozooids fertile, conspicuous and numerous, scattered among whole colony, visible as minute red protuberances,

and usually 0.5 mm wide, smaller than distance between two of them.

3.4.7.2.3. Sclerites. Tentacular sclerites predominately tuberculated rods with small protuberances, ranging 0.13–0.41 mm long; less commonly multiradiates to highly tuberculated rods with blunt protuberances, mostly elongate, ranging 0.05–0.12 mm long (Figure 10A). Anthocodial sclerites predominately multiradiates with blunt protuberances, and ranging 0.06–0.10 mm long; tuberculated rods with blunt protuberances, and ranging 0.15–0.26 mm long; sclerites not arranged en chevron, and crown not developed (Figure 10B). Pharyngeal sclerites exclusively tuberculated rodlets ranging 0.11–0.16 mm long (Figure 10C). Sclerites of capitulum surface predominately tuberculated rods to spindles ranging 0.13–0.27 mm long; multiradiates ranging 0.07–0.08 mm long (Figure 10D). Sclerites of capitulum interior predominately tuberculated rods to spindles, ranging 0.15–0.33 mm long; occasionally multiradiates (Figure 10E). Sclerites from stalk surface predominately multiradiates ranging 0.07–0.09 mm long; tuberculated spindles ranging 0.13–0.21 mm long (Figure 10F). Sclerites from stalk interior exclusively tuberculated rods ranging 0.17–0.34 mm long (Figure 10G).

3.4.7.2.4. Color. Colony surface pink both in vivo and in ethanol preservation; inner colony white with sclerite aggregation area reddish (Figure 4H,I). Sclerites translucent to reddish under transmitted light.

3.4.7.3. Etymology. The Latin adjective *elongatus* (elongate) refers to the long colony of the species.

3.4.7.4. Distribution and Habitat. Found only on M7 seamount located on the Caroline Ridge in the tropical Northwestern Pacific, where the water depth was 1094 m and temperature about 4.4°C.

3.4.7.5. Remarks. *Neoanthomastus elongatus* sp. nov. resembles *N. tahinodus* comb. nov. (original combination *A. tahinodus*) and *N. stellatus* sp. nov. by having an elongated and cylindrical stalk, siphonozooids scattered around the whole stalk, and sclerites with blunt protuberances. The new species differs from *N. tahinodus* comb. nov. by the presence of exclusively multiradiates in anthocodial wall (vs. with multiradiates and rods), and autozooids scattered evenly over capitulum (vs. mostly on the periphery of capitulum with central capitulum clear); from *N. stellatus* sp. nov. by having multiradiates and rods in the anthocodial wall (vs. exclusively multiradiates).

3.4.8. *Pseudoanthomastus* Tixier-Durivault and d'Hondt, 1974 [5–7, 45, 46]. *Pseudoanthomastus* Tixier-Durivault and d'Hondt, 1974:1384; Molodtsova, 2013:498–500; d'Hondt and d'Hondt, 2020:250.

(in part) *Pseudoanthomastus* Pasternak, 1981:41–42.

(in part) *Anthomastus* Studer, 1901:26–27; Kükenthal, 1910:57–58; Deichmann, 1936:52; Tixier-Durivault and d'Hondt, 1973; d'Hondt, 1988:265.

3.4.8.1. Diagnosis (Modified From [8], With Italics Indicating Modifications). Mushroom-shaped, capitate colonies with domeshaped capitulum sharply separated from a conspicuous stalk, or occasionally encrusting-shaped with holdfast

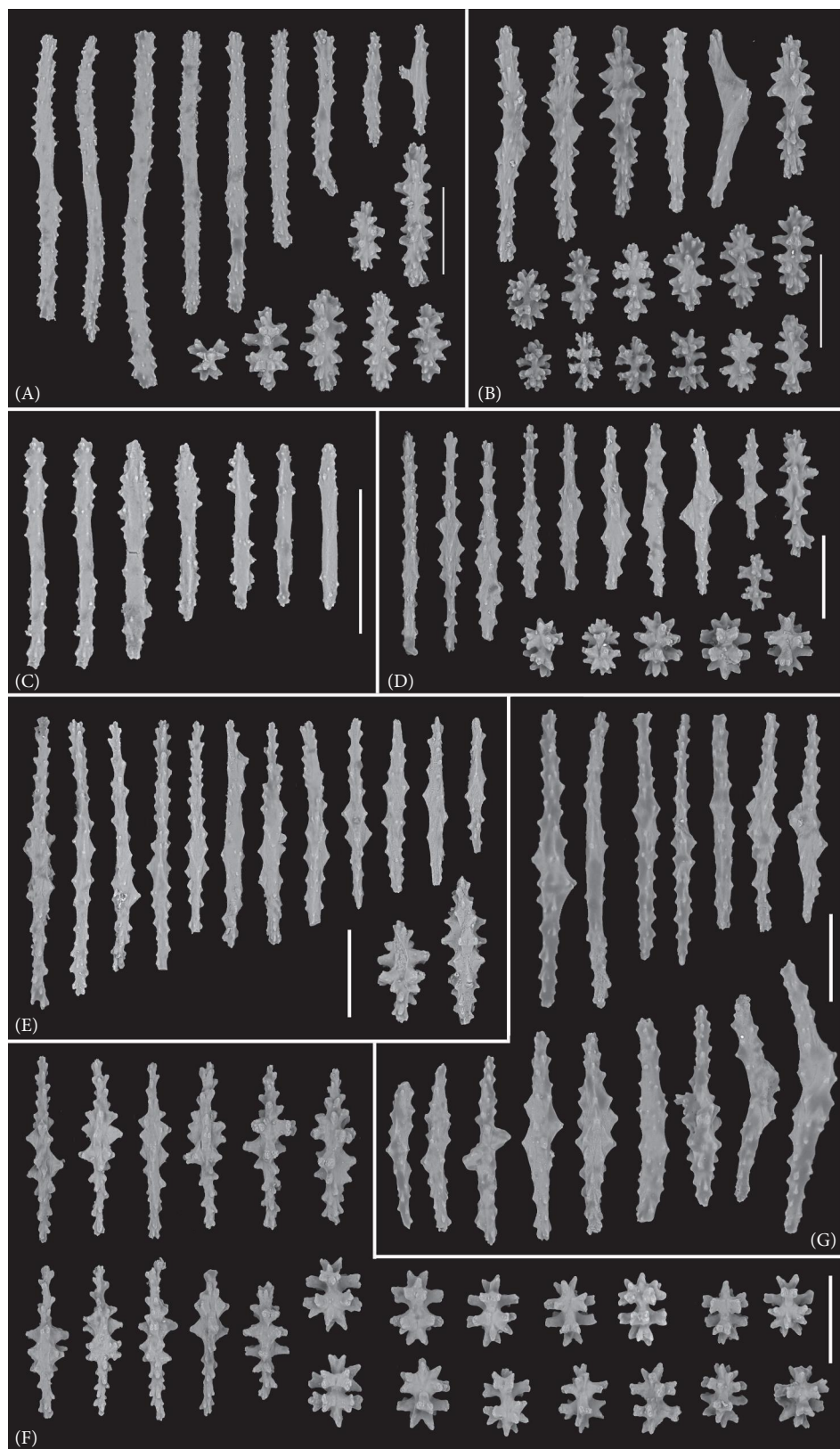


FIGURE 10: Sclerites of the holotype of *N. elongatus* sp. nov. (A) Sclerites from tentacles of autozoid. (B) Sclerites from anthocodial wall. (C) Sclerites from pharynx. (D) Sclerites from surface of capitulum. (E) Sclerites from interior of capitulum. (F) Sclerites from surface of stalk. (G) Sclerites from interior of stalk. Scale bars = 0.1 mm.

wrapped substrate. Polyps dimorphic, with sclerites. Autozooids sterile, large, retractile but rarely completely retracted, and arranged over capitulum. Sclerites equally developed around autozooids. Anthocodial armature more developed near base of tentacles. Siphonozooids fertile, usually conspicuous, feebly armored, numerous, and scattered among autozooids. Sclerites multiradiates, warted clubs, thorny clubs with head formed of distally pointed tubercles, rods, spindles and crosses. Pharyngeal sclerites predominately rodlets or spindles. Tentacular sclerites predominately needles, rods, clubs, and multiradiates.

3.4.8.2. Remarks. The genus *Pseudoanthomastus* Tixier-Durivault and d'Hondt, 1974 [6, 7], differs from other four genera of Anthomastinae by the predominant rodlets in pharyngeal sclerites, highly diverse tentacular sclerites, and the siphonozooids confined to capitulum ([8]; remarks on *Neoanthomastus* gen. nov.). *P. applanatus* sp. nov. mostly resemble *P. aberrans* [43] comb. nov. and *P. paradoxus* (d'Hondt in [14]) comb. nov. by having the peculiar encrusting-form colony shape. It is assigned into *Pseudoanthomastus* by having spindles in pharynx (a sclerite type more resemble rodlets in pharynx of *Pseudoanthomastus* than platelets in pharynx of *Anthomastus* and *Heteropolypus*), and thorny clubs and multiradiates in tentacles (the character of *Pseudoanthomastus* rather than *Anthomastus*). The assignment is supported by molecular result that *P. applanatus* sp. nov. is clustered within the *Pseudoanthomastus* clade in all the phylogenetic trees (Figures 1–3). To accommodate the three encrusting-shaped species, we extend the definition of *Pseudoanthomastus* in colony shape and pharyngeal sclerites.

3.4.9. *Pseudoanthomastus ornatus* sp. nov. Figures 4J–M and 11.

3.4.9.1. Material Examined. Holotype: MBM286335, collected on August 24, 2017 from the station FX-Dive 140 (10°31.50'N, 140°11.00'E) of M4 seamount with water depth of 1429 m.

3.4.9.2. Description of Holotype

3.4.9.2.1. Colony Form and Size. Colony mushroom-shaped. In life, animal attached to dead sponge, with a sea star living nearby; colony including a dome-shaped capitulum with large autozooids and a stout stalk. Autozoid tentacles expanded in situ and contracted when disturbed (Figure 4J). Preserved colony 74 mm long with capitulum bearing 50 autozooids. Capitulum 82 × 49 mm in width and 42 mm long, occupying ~57% of total colony length. Stalk stout, ~32 mm long, 34 × 20 mm in narrowest width at the upmost part, and downward expanding into a holdfast that measures 45 × 35 mm in width (Figure 4K).

3.4.9.2.2. Polyps. Polyps dimorphic, confined to capitulum. Autozooids sterile, arranged over whole capitulum, most partly contracted, up to 26 mm long and 13 mm wide (Figure 4J–M). Tentacles contracted, up to 9 mm long when expanded. A row of small and developing autozooids occurred in the rim of the capitulum (Figure 4L). Siphonozooids fertile; conspicuous and numerous, visible as minute white protuberances, scattered among autozooids; usually 0.35–0.5 mm wide, smaller than distance between two of them (Figure 4L,M).

3.4.9.2.3. Sclerites. Tentacular sclerites mainly thorny clubs, 0.10–0.22 mm long; multiradiates, 0.03–0.04 mm long; tuberculated rods, straight to curved, 0.26–0.30 mm long; needles, 0.34–0.48 mm long (Figure 11A). Pharyngeal sclerites predominately spiny rodlets with prominent spines on one half, and ranging 0.10–0.16 mm long; rarely crosses (Figure 11B). Anthocodial sclerites mainly rods, 0.19–0.45 mm long; thorny clubs, 0.09–0.23 mm long; multiradiates, 0.06–0.11 mm long; sclerites not arranged en chevron, and crown not developed (Figure 11C). Sclerites of the capitulum surface double stars, 0.06–0.08 mm long; needles, 0.30–0.52 mm long (Figure 11D). Sclerites of capitulum interior predominately needles, 0.30–0.55 mm long (Figure 11E). Sclerites from the stalk surface double stars to multiradiates, 0.05–0.11 mm long; needles, 0.25–0.47 mm long (Figure 11F). Sclerites from the stalk interior exclusively needles, 0.36–0.51 mm long (Figure 11G).

3.4.9.2.4. Color. Colony surface red with capitulum darker than stalk both in vivo and in ethanol preservation; inner colony whitish to reddish (Figure 4J–M). Sclerites translucent to reddish under transmitted light.

3.4.9.3. Etymology. The Latin adjective *ornatus* (ornate) refers to the bright-colored and beautiful colony of the species.

3.4.9.4. Distribution and Habitat. Found only on M4 seamount located on the Caroline Ridge in the tropical Northwestern Pacific, where the water depth was 1429 m, temperature about 3.2°C. In situ, *P. ornatus* sp. nov. attached to a dead sponge rod that was also inhabited by a sea star (Echinodermata: Asteroidea: Goniasteridae).

3.4.9.5. Remarks. *Pseudoanthomastus ornatus* sp. nov. matches well with the definition of *Pseudoanthomastus* by having siphonozooids restricted in capitulum, predominately rodlets in pharynx, and diverse tentacular sclerites. It mostly resembles *P. fisheri* in having mushroom-shaped colony and double stars in capitulum and stalk. However, *P. ornatus* differs from *P. fisheri* by its pharyngeal rodlet shape (prominently spiny rods on one half vs. flattened spiny rods with expanded end) and diverse tentacular sclerites (thorny clubs, multiradiates, rods and needles vs. flattened rods). In addition, *P. ornatus* has a larger colony size (74 mm vs. maximum 23 mm long), and larger (26 mm long and 13 mm wide vs. 5 mm long and 3–4 mm wide) and higher number of autozooids (50 vs. ca. 25) [47]. In all the phylogenetic trees constructed, *P. ornatus* is located within the *Pseudoanthomastus* clade and clustered with *Pseudoanthomastus* sp. (OL616265). They might represent the same species considering the genetic distance of the concatenated 13 PCGs between them is only 0.0287 (Figures 1–3, Figures S1–S3; Table S4).

3.4.10. *Pseudoanthomastus applanatus* sp. nov. Figures 4N–P and 12.

3.4.10.1. Material Examined. Holotype: MBM286426, collected on June 6, 2019 from the station FX-Dive 218 (10°8.12'N, 140°14.48'E) of M6 seamount with water depth of 1242 m.



FIGURE 11: Sclerites of *P. ornatus* sp. nov. (A) Sclerites from tentacles of autozooid. (B) Sclerites from pharynx. (C) Sclerites from anthocodial wall. (D) Sclerites from surface of capitulum. (E) Sclerites from interior of capitulum. (F) Sclerites from surface of stalk. (G) Sclerites from interior of stalk. Scale bars = 0.1 mm.

3.4.10.2. Description of Holotype.

3.4.10.2.1. *Colony Form and Size.* In life, colony elongated, composed of a thin capitulum and stalk, the latter wrapped and stretching along a dead sponge (Figure 4N,O). Preserved colony 336 mm long, with width reduced gradually from 23 mm in upper to 5 mm in lower (Figure 4P).

3.4.10.2.2. *Polyps.* Polyps dimorphic, confined to capitulum. Autozooids sterile, 68 in number, arranged over the whole capitulum, expanded in situ and contracted when disturbed, most partly retracted in preservation, up to 18 mm long and 9 mm wide, with tentacles up to 9 mm long (Figure 4N–P). A row of small and undeveloped autozooids occurred in rim of capitulum. Siphonozooids numerous, scattered among autozooids, visible as minute protuberances, and about 0.5 mm wide.

3.4.10.2.3. *Sclerites.* Tentacular sclerites mostly tuberculated rods (0.23–0.57 mm long), thorny clubs (0.09–0.20 mm long), and multiradiates (0.09–0.13 mm long); rarely needles (0.37–0.49 mm long) and plates (0.10–0.11 mm long) (Figure 12A). Anthocodial sclerites mostly spiny rods (0.34–0.49 mm long), thorny clubs (0.16–0.30 mm long); rarely spindles (0.13–0.18 mm long) and multiradiates (0.08–0.11 mm long); these sclerites not arranged en chevron, and crown not developed (Figure 12B). Pharyngeal sclerites exclusively rodlets, ranging 0.11–0.17 mm long (Figure 12C). Sclerites from capitulum mostly spiny rods (0.25–0.48 mm long), thorny spindles (0.13–0.24 mm long), and multiradiates (0.06–0.12 mm long); rarely clubs (0.12–0.18 mm long), and crosses (0.09–0.15 mm long) (Figure 12D). Sclerites from stalk mostly thorny spindles (0.10–0.21 mm long) and multiradiates (0.07–0.11 mm long) (Figure 12E).

3.4.10.2.4. *Color.* Colony red both in vivo and in ethanol preservation (Figure 4N–P). Sclerites light reddish to transparent under transmitted light.

3.4.10.3. *Etymology.* The New Latin adjective *applanatus* (applanate) refers to the applanate capitulum and stalk of the species.

3.4.10.4. *Distribution and Habitat.* Found only on M6 seamount located on the Caroline Ridge in the tropical Northwestern Pacific, where the water depth was 1242 m, temperature about 3.6°C. In situ, *P. applanatus* covered up a dead sponge rod that was also inhabited by a sea star and several ophiuroid individuals.

3.4.10.5. *Remarks.* *Pseudoanthomastus applanatus* sp. nov. mostly resemble *P. aberrans* [43] comb. nov. and *P. paradoxus* (d'Hondt in [14]) comb. nov. by having a peculiar encrusting-shaped colony. However, the new species differs from *P. aberrans* comb. nov. by the presence of thorny clubs in capitulum (vs. absence); and from *P. paradoxus* comb. nov. by having much higher number of incompletely retractile autozooids (68 vs. 17 completely retractile autozooids). In addition, the spindles of autozooids in the new species are covered with small protuberances, while they are larger protuberances in *P. paradoxus* comb. nov. [9, 14, 43, 48].

3.4.11. Key to Genera and Species of Anthomastinae

1. Autozooid tentacular sclerites less diverse, predominately rods, plates and crosses.....*Anthomastus* (5)
Autozooid tentacular sclerites more diverse, including rods, clubs, spindles, multiradiates, plates and crosses.....2
2. Pharyngeal sclerites predominately platelets.....*Heteropolypus* (18)
Pharyngeal sclerites predominately rodlets.....3
3. Single large autozooid.....*Bathyalcyon robustum*
Autozooids few in number.....4
4. Siphonozooids restricted in capitulum.....*Pseudoanthomastus* (25)
Siphonozooids located in capitulum and stalk.....*Neoanthomastus* gen. nov. (38)
5. Pharyngeal sclerites absent.....*A. bayeri*
Pharyngeal sclerites present.....6
6. Pharyngeal sclerites predominately platelets.....7 [also refer to 15]
Pharyngeal sclerites predominately rodlets or not known.....10
7. Tentacular sclerites predominately rods and excluding plates.....8
Tentacular sclerites more diverse and including plates.....9
8. Double spheroids present in capitulum and stalk; sclerites absent in anthocodial wall.....*A. nanhaiensis*
Double spheroids absent; anthocodial wall predominately rods.....*A. tongi* sp. nov.
9. Autozooids arranged over whole capitulum; spindles present and rods absent in tentacles and anthocodial wall.....*A. grandifloras*
Autozooids arranged over the distal 3/4 of capitulum; rods present and spindles absent in tentacles and anthocodial wall.....*A. gyratus*
10. Pharyngeal sclerites predominately rodlets.....11 [also refer to 15]
Pharyngeal sclerites not known.....15
11. Tentacles with numerous squat rods.....12
Tentacles lack squat rods.....13
12. Tentacular sclerites composed of also needles, rods and spindles.....*A. megacephalus*

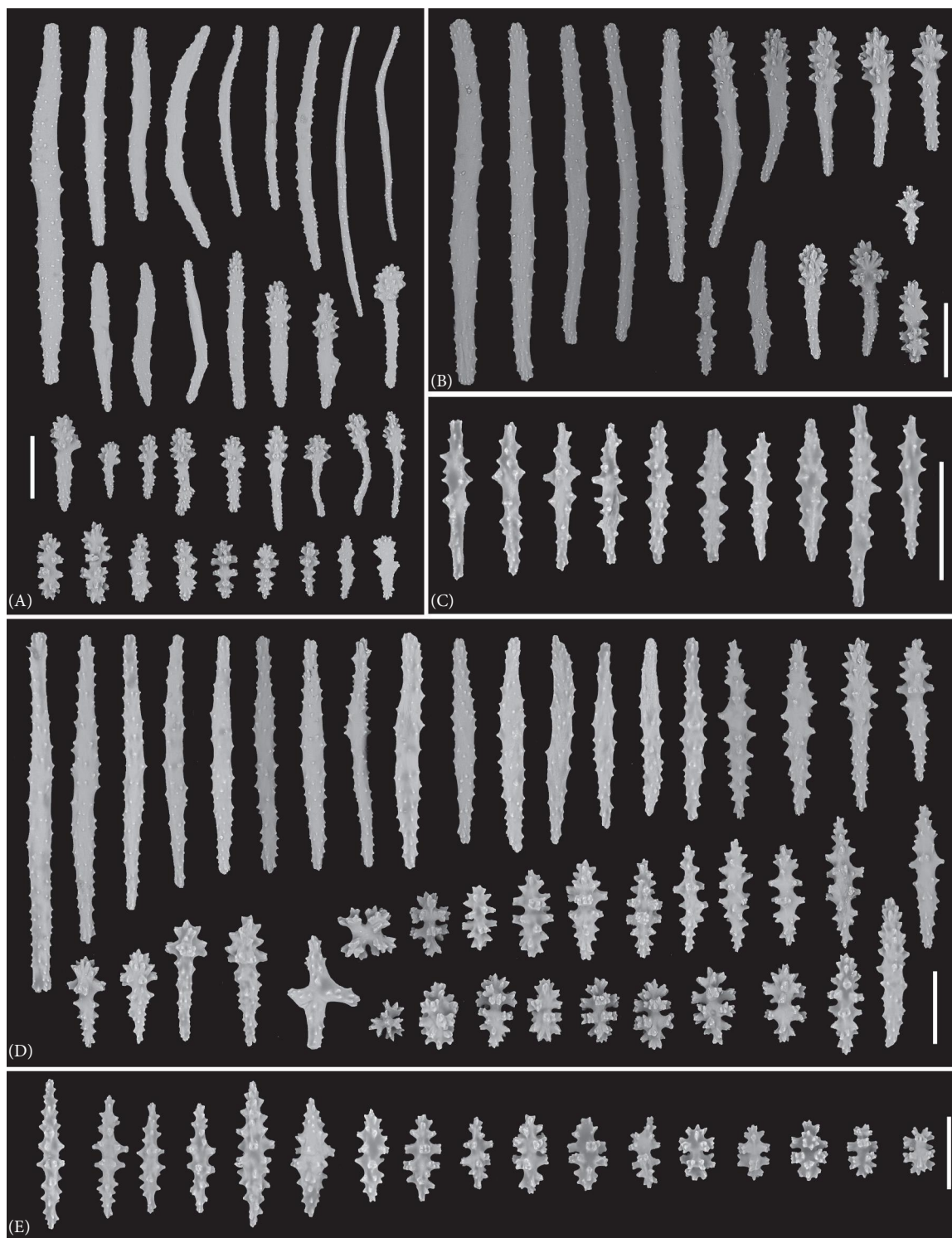


FIGURE 12: Sclerites of *P. applanatus* sp. nov. (A) Sclerites from autozooid tentacles. (B) Sclerites from anthocodial wall. (C) Sclerites from pharynx. (D) Sclerites from capitulum. (E) Sclerites from stalk. Scale bars = 0.1 mm.

- Tentacular sclerites composed of exclusively squat rods..... *A. muscarioides*
13. Sclerites scanty throughout colony; tentacular sclerites predominately highly tuberculated rods with ends usually furcated.....
.....*A. cyanae*
Sclerites abundant; tentacular sclerites predominately slightly tuberculated rods.....
.....14
14. Capitulum completely retractile into stalk; stalk digitiform to anchor colony in soft substrate.....
.....*A. bathyproctus*
Capitulum spherical; stalk short.....
..... *A. sphaericus* sp. nov.
15. Colony ≤ 15 mm long.....
.....16
Colony ≥ 35 mm long.....
.....17
16. Sclerites from capitulum and stalk generally with many rounded protuberances.....
..... *A. globosus*
Sclerites from capitulum and stalk generally with conical protuberances.....
.....*A. canariensis*
17. Sclerites almost uniform throughout colony, including rods, irregular forms (might be multiradiates) and clubs; siphonozooids white.....
.....*A. agaricoides*
Sclerites from tentacles, anthocodial wall and stalk varied; siphonozooids yellowish.....
.....*A. antarcticus*
18. Plates present in autozooid tentacles.....
.....19
Plates absent in autozooidtentacles.....
.....21
19. Rods present in tentacles.....
..... *H. sol*
Rods absent in tentacles.....
.....20
20. Plates with a diagonal keel present in tentacles.....
.....*H. roseus*
Plates with a diagonal keel absent in tentacles...
.....*H. annae*
21. Clubs present in tentacles.....
.....22
Clubs absent in tentacles.....
.....23
22. Spindles present in tentacles.....
..... *H. steenstrupi*
Spindles absent in tentacles.....
..... *H. rylovi*
23. Capitulum flattened.....
.....*H. ritteri*
- Capitulum convex.....
.....24
24. Mesozooids scattered on capitulum.....
..... *H. japonicus*
Mesozooids arranged at upper part of capitulum.....
.....*H. insolitus*
25. Colony encrusting-shaped
.....26
Colony capitate or mushroom-shaped.....
.....28
26. Spindles from autozooids slightly tuberculated; autozooids > 60 in number, incompletely retractile...
.....27
Spindles from autozooids moderately tuberculated; autozooids 17 in number, completely retractile...
.....*P. paradoxus* comb. nov.
27. Thorny clubs absent in capitulum.....
..... *P. aberrans* comb. nov.
Thorny clubs present in capitulum.....
.....*P. applanatus* sp. nov.
28. Clubs present in autozooids.....
.....29
Clubs absent in autozooids.....
.....*P. agassizii* comb. nov.
29. High number of clubs present or not currently known in autozooids.....
.....30
Low number of clubs in autozooids.....
.....*P. mariejoeseae*
30. Double stars present in surface of capitulum and stalk.....
.....31
Double stars absent or not known.....
.....32
31. Pharyngeal sclerites predominately flattened spiny rodlets with one or both ends expanded; tentacular sclerites predominately flattened rods; colony and autozooids relatively small.....
..... *P. fisheri*
Pharyngeal sclerites predominately spiny rodlets with large spines on one half; tentacular sclerites diverse; colony and autozooids relatively large.....
..... *P. ornatus* sp. nov.
32. Siphonozooids present in whole capitulum.....
.....33
Siphonozooids absent in the lower capitulum...
.....*P. paravenustus*
33. Spindles present.....
.....34
Spindles absent.....
.....37
34. Colony relatively < 30 mm long.....
.....35
Colony relatively 60 mm long.....
..... *P. tixierdurivaultae*
35. Capitulum flatened.....
..... *P. agaricus*

- Capitulum spherical or hemispherical.....36
36. Capitulum spherical; Sticks absent; colony color varied.....*P. pseudovenustus*
 Capitulum hemispherical; sticks present; colony cream-white.....*P. gloriosus*
37. Anthocodial sclerites including clubs and arranged en chevron; colony pinkish white to very pale red-orange.....*P. venustus*
 Anthocodial sclerites without clubs and not arranged en chevron; colony carmine.....*P. zealandicus* comb. nov.
38. Colony < 60 mm; stalk not elongated.....39
 Colony ≥ 90 mm; stalk elongated.....40
39. Capitulum spherical with 15–35 autozooids; siphonozooids on the upper 2/3 of stalk; anthocodia rich in sclerites; colony purple.....*Neanthomastus purpureus* comb. nov.
 Capitulum flattened with 5 autozooids; siphonozooids on the upper 1/3 of stalk; anthocodia with few sclerites; colony red.....*N. hicksoni* comb. nov.
40. Siphonozooids on the whole stalk; multiradiates, rods and spindles with blunt protuberances; colony red to pink.....41
 Siphonozooids on the upper 1/3 of stalk; multiradiates to spindles with sharp protuberances; colony creamy white.....*N. giganteus* comb. nov.
41. Tentacular sclerites composed of rods and multiradiates.....42
 Tentacular sclerites composed of exclusively rods.....*N. stellatus* sp. nov.
42. Multiradiates and rods present in anthocodial wall; autozooids absent in central capitulum.....*N. tahinodus* comb. nov.
 Only multiradiates present in anthocodial wall; autozooids scattered evenly over capitulum.....*N. elongatus* sp. nov.

4. Discussion

4.1. Strengths of Different Alternatives for Phylogenetic Inference in Anthomastinae. The *mtMutS* gene is unique to Octocorallia. The loss of *mtMutS* in octocorals has ever been identified in *Pseudoanthomastus* sp. (OL616264) [20]. By the tblastn search, we detected a second species lack of *mtMutS*, viz., *A. tongi* sp. nov. Using 13 PCGs to construct phylogenetic trees, *A. tongi* sp. nov. and *Pseudoanthomastus* sp. (OL616264) occurred in different clades in both Maximum Likelihood and Bayesian analyses. Their branches were significantly longer than those of other

species, indicating faster evolutionary rates compared to other species (Figure 1). However, these two species clustered together in the Maximum Parsimony tree (Figure S1). This finding supports the hypothesis that *mtMutS* is involved in DNA repair, leading to slower evolutionary rates [20]. Since the Maximum Parsimony method assumes that all lineages evolve at the same rate [49], it is plausible that *A. tongi* sp. nov. and *Pseudoanthomastus* sp. (OL616264) are more susceptible to the effects of long-branch attraction, resulting in their erroneous grouping. Moreover, the topology derived from the Maximum Parsimony method was not supported by morphological analysis. It is likely that the loss of *mtMutS* in *Pseudoanthomastus* sp. (OL616264) and *A. tongi* sp. nov. occurred independently.

Our phylogenetic analysis based on the commonly used partial *mtMutS* for Octocorallia exhibited obscure relationships with low nodal support. This indicates that partial *mtMutS* is unqualified to elucidate the phylogenetic relationships among species. In contrast, the full-length *mtMutS* is more effective in elucidating the phylogenetic relationships among Anthomastinae species. The phylogenetic analysis based on the 13 PCGs (excluding *mtMutS*) exhibits a topology very similar to that derived from the full-length *mtMutS*, with both analyses demonstrating high nodal support. The PCGs can serve as a powerful marker to resolve the phylogenetic relationships among species of Anthomastinae and Octocorallia as well, especially considering that *mtMutS* may be absent in certain species.

4.2. Evolution of Main Characters and Genera of Anthomastinae. The genera and species of mushroom soft corals in Anthomastinae are primarily distinguished by the sclerite types of various tissues, the location of polyps, and the shape, size, and color of colony. Among these characters, the pharyngeal and tentacular sclerites are regarded as the most important ones in delineating genus and species [8]. This view is also supported by current molecular phylogenetic analyses. The pharyngeal sclerites in Anthomastinae are composed of platelets or rodlets similar to those of other taxa within the family Coralliidae, particularly precious corals. They are much smaller in size and can be easily distinguished from sclerites of other tissues. Our phylogenetic analysis suggests that pharyngeal platelets are likely a primitive character, while rodlets evolved independently twice within Anthomastinae. Tentacular sclerites in the basal *Anthomastus* clade of Anthomastinae are composed of predominately rods. From this clade, tentacular sclerites of all the other four diversified genera evolved by incorporating needles, spindles, clubs, and multiradiates. Our study emphasized the taxonomic significance of the location of siphonozooids on stalk for generic differentiation. Siphonozooids are found exclusively in the capitulum of *Anthomastus*, *Heteropolypus*, and *Pseudoanthomastus*. In contrast, they extend to both capitulum and stalk in *Neanthomastus* gen. nov. and are present in autocodia wall of the derived *Bathyalcyon*.

The phylogenetic trees constructed from 13 PCGs, full-length *mtMutS* and the barcodes of partial *mtMutS* support the independence of the five genera within Anthomastinae (Figures 1–3, Figures S1–S3). *Anthomastus* cf. *grandiflorus*

(KC984603) and several unidentified species of *Anthomastus* are grouped within the clades of *Pseudoanthomastus* and *Neoanthomastus* gen. nov. suggesting that these may be mis-identifications. Molodtsova [8] indicates that many reports of *A. grandiflorus* are, in fact, members of *Pseudoanthomastus*. Our phylogenetic analysis suggests that *Anthomastus* is a primitive genus within Anthomastinae, characterized by the predominately rods in tentacles, predominately platelets or rodlets in pharynx, and siphonozooids located in capitulum. Subsequently, *Heteropolypus* originated from *Anthomastus* with pharyngeal platelets and diverse tentacular sclerites occurred. The ancestor of *Neoanthomastus*, *Pseudoanthomastus*, and *Bathyalcyon* originated from *Heteropolypus*, where pharyngeal platelets evolved into rodlets, and *Pseudoanthomastus* likely retained other ancestral characters. In some species of *Anthomastus*, pharyngeal rodlets originated from platelets again independently. *Bathyalcyon* emerged from an ancestor in which many smaller autozooids were reduced to a single large autozoid, accompanied by siphonozooids occupying anthocodial wall. *Neoanthomastus* gen. nov. originated from an ancestor similar to *Pseudoanthomastus*, with siphonozooids occupying stalk. Nonetheless, further study is necessary to confirm these evolutionary processes.

As there is no key to the genera and species of mushroom soft corals except a tabular key to the species of *Heteropolypus* provided by Dautova [10], we propose a dichotomous key to all five known genera and 43 species of Anthomastinae to facilitate identification.

5. Conclusions

Mushroom soft corals, precious corals, and bubblegum corals represent the three main groups of Coralliidae. Among these, mushroom soft corals are the least studied, and their species diversity and phylogenetic relationships are far beyond known. Here, we describe a new genus *Neoanthomastus* gen. nov. and six new species of Anthomastinae based on samples from four seamounts in the tropical North-western Pacific and propose eight new combinations. Based on the newly obtained sequences, we reconstructed the first phylogenetic relationships among mushroom soft corals by using the concatenated nucleotides of 13 mitochondrial PCGs, the full-length coding regions of *mtMutS* and the barcodes of partial *mtMutS*, respectively. Our investigation demonstrates that the full-length *mtMutS* is as effective as the 13 PCGs in inferring the phylogenetic relationships among the genera and species of Anthomastinae. In contrast, the partial *mtMutS* is inadequate for revealing these relationships among species. Our molecular phylogenetic analyses support the independence of the five genera within Anthomastinae, with *Neoanthomastus* gen. nov. recovered as the most derived group and sister to *Pseudoanthomastus*, while *Anthomastus* represents the earliest lineage within Anthomastinae. *A. tongi* sp. nov. is identified as the second octocoral species lacking the *mtMutS*, and the loss of *mtMutS* in *A. tongi* sp. nov. and *Pseudoanthomastus* sp. (OL616264) occurred independently. This study enhances our understanding of species diversity and inter-generic phylogeny among mushroom soft corals and emphasizes

the necessity for global diversity assessments and interspecific phylogenetic investigations as well as the integrated studies on the main groups within Coralliidae.

Data Availability Statement

The voucher specimens described in this study are available at MBMCAS. The molecular sequences newly obtained for this study have been deposited in GenBank. The registration number of specimens and the GenBank accession number of sequences are listed in Table 1. The registration of *Anthomastus sphaericus* sp. nov., *A. tongi* sp. nov., *Neoanthomastus* gen. nov., *Neoanthomastus stellatus* sp. nov., *N. elongatus* sp. nov., *Pseudoanthomastus ornatus* sp. nov., *P. applanatus* sp. nov., and the publication in Zoobank are as follows, respectively: urn:lsid:zoobank.org:act:DF86B1F4-91C3-496C-B5B4-3C2CC7B82112, LSIDurn:lsid:zoobank.org:act:BB095367-F443-4288-8CFF-CE706F752383, urn:lsid:zoobank.org:act:B2AED882-2750-430F-96AC-2200AEFF9582, LSIDurn:lsid:zoobank.org:act:6A3D35B1-32A3-468E-8F98-5A0346DF889E, LSIDurn:lsid:zoobank.org:act:9D53B89E-74F9-4DB3-984F-8A171AC82C67, LSIDurn:lsid:zoobank.org:act:4B6EF854-F48E-4620-9C3F-EFEC9C15C54D, LSIDurn:lsid:zoobank.org:act:0E1343D2-AD59-4FCF-95CA-97CC15180CF8, and urn:lsid:zoobank.org:pub:561D76F8-A0EA-4B7C-850C-5870B12EDA2D.

Conflicts of Interest

The authors declare no conflicts of interest.

Author Contributions

Yang Li conceived the research, studied the morphology, and participated in the sampling, molecular analysis, and funding. Junyuan Li conducted and performed the molecular analysis. Kuidong Xu conducted the sampling and secured the funding. All authors discussed the results and contributed to the final manuscript.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. (*Supporting Information*)

The supporting information for this article includes three figures (Parsimony trees elucidating phylogenetic relationships of genera and species within Anthomastinae based on the concatenated nucleotides of 13 PCGs, the full-length *mtMutS*, and the partial *mtMutS*, respectively) and five tables (for phylogenetic analysis and calculation of genetic distances). These can be found at the end of the article or online at: Figure S1. A Parsimony tree of species in Anthomastinae based on the concatenated nucleotides of 13 PCGs (*mtMutS* not included) in mitochondrial genomes. For each node, support values of Maximum Parsimony (the first number), Maximum Likelihood (the second number), and Bayesian inference (the third number) are shown. Dashes (–) indicate nodes that are not supported in corresponding analyses. Bootstrap values are only shown if they are larger than 60% and posterior possibilities are displayed only if the values reach 0.6. The genera outside Anthomastinae within Coralliidae are used as outgroup. Figure S2. A Parsimony tree of species in Anthomastinae based on the full-length *mtMutS*. For each node, support values of Maximum Parsimony (the first number), Maximum Likelihood (the second number), and Bayesian inference (the third number) are shown. Dashes (–) indicate nodes that are not supported in corresponding analyses. Bootstrap values are only shown if they are larger than 60% and posterior possibilities are displayed only if the values reach 0.6. The genera outside of Anthomastinae within Coralliidae are used as outgroups. Figure S3. A Parsimony tree of the species in Anthomastinae based on the partial *mtMutS*. For each node, support values of Maximum Parsimony (the first number), Maximum Likelihood (the second number), and Bayesian inference (the third number) are shown. Dashes (–) indicate nodes that are not supported in corresponding analyses. Bootstrap values are only shown if they are larger than 60% and posterior possibilities are displayed only if the values reach 0.6. The genera outside of Anthomastinae within Coralliidae are used as outgroups. Table S1. The best models and partitioning schemes for Bayesian and Maximum Likelihood analysis. Table S2. Estimates of evolutionary divergence between and within genera measured by Kimura 2-parameter distances (%) based on 14 protein-coding genes of mitochondrial genomes. Table S3. Estimates of evolutionary divergence between and within the species in *Anthomastus* measured by Kimura 2-parameter distances (%) based on 14 protein-coding genes of mitochondrial genomes. Table S4. Estimates of evolutionary divergence between and within the species in *Pseudoanthomastus* measured by Kimura 2-parameter distances (%) based on 14 protein-coding genes of mitochondrial genomes. Table S5. Estimates of evolutionary divergence between and within the species in *Neoanthomastus* measured by Kimura 2-parameter distances (%) based on 14 protein-coding genes of mitochondrial genomes.

References

- [1] K. Stocks, "Seamount Invertebrates: Composition and Vulnerability to Fishing," in *Seamounts: Biodiversity and Fisheries*, eds. T. Morato and D. Pauly, (University of British Columbia, Vancouver, Canada, 2004): 17–24.
- [2] L. Buhl-Mortensen and P. B. Mortensen, "Distribution and Diversity of Species Associated With Deep-Sea Gorgonian Corals off Atlantic Canada," in *Cold-Water Corals and Ecosystems*, (Springer-Verlag, Heidelberg, Berlin, 2005): 849–879.
- [3] F. M. Bayer, "Taxonomic Status of the Octocoral Genus *Bathyalcyon* (Alcyoniidae: Anthomastinae), With Descriptions of a New Subspecies From the Gulf of Mexico and a New Species of *Anthomastus* From Antarctic Waters," *Precious Corals and Octocoral Research* 1 (1993): 3–13.
- [4] C. S. McFadden, L. P. Van Ofwegen, and A. M. Quattrini, "Revisionary Systematics of Octocorallia (Cnidaria: Anthozoa) Guided by Phylogenomics," *Bulletin of the Society of Systematic Biologists* 1, no. 3 (2022): 8735.
- [5] A. Tixier-Durivault, "Stolonifera et Alcyonacea," *Galathea Report* 7 (1964): 43–58.
- [6] A. Tixier-Durivault and M.-J. d'Hondt, "Nouvelles Recoltes d'Octocoralliaires a Madagascar," *Tethys* 5, no. 2-3 (1973): 251–266.
- [7] A. Tixier-Durivault and M.-J. d'Hondt, "Les Octocoralliaires de la Campagne Biacores," *Bulletin du Muséum National d'histoire Naturelle, Paris, Series* 252 (1974): 1361–1433.
- [8] T. N. Molodtsova, "Deep-Sea Mushroom Soft Corals (Octocorallia: Alcyonacea: Alcyoniidae) of the Northern Mid-Atlantic Ridge," *Marine Biology Research* 9, no. 5-6 (2013): 488–515.
- [9] M.-J. d'Hondt and J.-L. d'Hondt, "Catalogue et Distribution géographique des Anthomastinae (Octocorallia, Alcyonacea, Alcyoniidae) Notes Sur Quelques Alcyonaires 'Capites'," *Bulletin de la Société Zoologique de France* 145, no. 3 (2020): 247–293.
- [10] T. N. Dautova, "New Species of Deep-Sea *Heteropolypus* Soft Corals (Anthozoa: Octocorallia) From the Kurile Islands, Sea of Okhotsk (Northwest Pacific), With Summary Data on Distinctive Characters of the Known Species of the Known Species of the Genus," *European Journal of Taxonomy* 806, no. 1 (2022): 128–147.
- [11] Y. Li and K. Xu, "*Anthomastus nanhaiensis* New Species and *Bathyalcyon robustum* Versluys, 1906, Two Mushroom Soft Corals (Octocorallia: Coralliidae) From Zhenbei Seamount in the South China Sea," *Raffles Bulletin of Zoology* 71 (2023): 1–12.
- [12] C. S. McFadden, R. Cordeiro, K. Samimi-Namin, G. Williams, and L. van Ofwegen, "World List of Octocorallia. Anthomastinae Verrill, 1922," 2025, <https://www.marinespecies.org/aphia.php?p=taxdetails&id=1510270>, Accessed through: World Register of Marine Species at: 1922.
- [13] M.-J. d'Hondt and J.-L. d'Hondt, "*Anthomastus cyanae* n. sp., Nouvel Octocoralliaire Alcyonacea Vivant à l'entour des Sources Hydrothermales du Pacifique Est, et Remarques Sur le Genre *Bathyalcyon*," *Bulletin de la Société Zoologique de France* 142, no. 4 (2017): 157–184.
- [14] M.-J. d'Hondt and J.-L. d'Hondt, "*Anthomastus* et *Pseudoanthomastus* (Octocorallia, Alcyoniidae) de Nouvelle-Calédonie et d'autres Provenances," *Bulletin de la Société Zoologique de France* 143, no. 3 (2018): 75–142.
- [15] M.-J. d'Hondt and J.-L. d'Hondt, "Note Sur Quelques Espèces d'*Anthomastus* et Autre Anthomastinae (Octocoralliaires, Alcyoniidae); Description de *Pseudoanthomastus gloriosus* n. sp." *Bulletin de la Société Linnéenne de Bordeaux* 1, no. 2 (2019): 103–118.
- [16] F. M. Bayer, M. Grasshoff, and J. Verseveldt, *Illustrated Trilingual Glossary of Morphological and Anatomical Terms Applied to Octocorallia* (Brill, E.J./Dr. Backhuys, 1983).
- [17] A. M. Bolger, M. Lohse, and B. Usadel, "Trimomatic: A Flexible Trimmer for Illumina Sequence Data," *Bioinformatics* 30, no. 15 (2014): 2114–2120.

- [18] J. Li, W. Li, A. Wang, and Y. Zhang, "MitoFlex: An Efficient, High-Performance Toolkit for Animal Mitogenome Assembly, Annotation and Visualization," *Bioinformatics* 37, no. 18 (2021): 3001–3003.
- [19] M. Bernt, A. Donath, F. Jühling, et al., "MITOS: Improved de Novo Metazoan Mitochondrial Genome Annotation," *Molecular Phylogenetics and Evolution* 69, no. 2 (2013): 313–319.
- [20] V. Muthye, C. D. Mackereth, J. B. Stewart, and D. V. Lavrov, "Large Dataset of Octocoral Mitochondrial Genomes Provides New Insights Into mt-*MutS* Evolution and Function," *DNA Repair* 110 (2022): 103273.
- [21] K. Katoh and D. M. Standley, "MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability," *Molecular Biology and Evolution* 30, no. 4 (2013): 772–780.
- [22] S. Capella-Gutiérrez, J. M. Silla-Martínez, and T. Gabaldón, "TrimAl: A Tool for Automated Alignment Trimming in Large-Scale Phylogenetic Analyses," *Bioinformatics* 25, no. 15 (2009): 1972–1973.
- [23] S. Kumar, G. Stecher, M. Li, C. Knyaz, K. Tamura, and F. U. Battistuzzi, "MEGA X: Molecular Evolutionary Genetics Analysis Across Computing Platforms," *Molecular Biology and Evolution* 35, no. 6 (2018): 1547–1549.
- [24] D. Zhang, F. Gao, I. Jakovlić, et al., "PhyloSuite: An Integrated and Scalable Desktop Platform for Streamlined Molecular Sequence Data Management and Evolutionary Phylogenetics Studies," *Molecular Ecology Resources* 20, no. 1 (2020): 348–355.
- [25] R. Lanfear, P. B. Frandsen, A. M. Wright, T. Senfeld, and B. Calcott, "PartitionFinder 2: New Methods for Selecting Partitioned Models of Evolution for Molecular and Morphological Phylogenetic Analyses," *Molecular Biology and Evolution* 34, no. 3 (2016): msw260.
- [26] L.-T. Nguyen, H. A. Schmidt, A. von Haeseler, and B. Q. Minh, "IQ-TREE: A Fast and Effective Stochastic Algorithm for Estimating Maximum-Likelihood Phylogenies," *Molecular Biology and Evolution* 32, no. 1 (2014): 268–274.
- [27] F. Ronquist and J. P. Huelsenbeck, "MrBayes 3: Bayesian Phylogenetic Inference Under Mixed Models," *Bioinformatics* 19, no. 12 (2003): 1572–1574.
- [28] S. Kalyanamoorthy, B. Q. Minh, T. K. F. Wong, A. von Haeseler, and L. S. Jermin, "ModelFinder: Fast Model Selection for Accurate Phylogenetic Estimates," *Nature Methods* 14, no. 6 (2017): 587–589.
- [29] E. Haeckel, *Generelle Morphologie der Organismen*, 2 (Verlag von Georg Reimer, Berlin, Germany, 1866).
- [30] J. V. F. Lamouroux, "Extrait d'un Mémoire sur la Classification des Polypiers Coralligènes Non Entièrement Pierreux," *Nouveau Bulletin Scientifique de la Société Philosophique* 3 (1812): 181–188.
- [31] E. Deichmann, "The Alcyonaria of the Western Part of the Atlantic Ocean," in *Memoires of the Museum of Comparative Zoology*, 53, (Harvard College, 1936): 1–317.
- [32] H. F. E. Jungersen, "Anthomastus. Danish Ingolf-Expedition," *Copenhagen* 5, no. 11 (1927): 1–14.
- [33] A. E. Verrill, "Notice of Recent Additions to the Marine Fauna of the Eastern Coast of North America, No. 2," *American Journal of Science and Arts* 16, no. 95 (1878): 371–378.
- [34] H. Ditlevsen, "Annelids. I," *Danish Ingolf-Expedition* 4, no. 4 (1917): 1–71.
- [35] D. Martin and T. A. Britayev, "Symbiotic Polychaetes: Review of Known Species," *Oceanography and Marine Biology: An Annual Review* 36 (1998): 217–340.
- [36] L. Watling, S. C. France, E. Pante, and A. Simpson, "Biology of Deep-Water Octocorals," *Advances in Marine Biology* 60 (2011): 41–122.
- [37] A. Tixier-Durivault, "Les Octocoralliaires d'Afrique du Sud. (I. Alcyonacea)," *Bulletin du Muséum National d'histoire Naturelle, Paris, Series 2* 26, no. 4 (1954): 526–533.
- [38] S. Bock, "The Alcyonarian Genus *Bathyalcyon*," *K Sven Vetenskapsakad Handl* 16 (1938): 1–54.
- [39] J. Koren and D. C. Danielssen, "Nye Alcyonider, Gorgonider og Pennatulider Tilhørende Norges Fauna," (1883): 1–38, *Bergens Museum Skrifter* 2 (1883): 1–38.
- [40] M.-J. d'Hondt, "Anthomastus tahinodus n. sp., Octocoralliare Alcyonacea du Nord-est de Tahiti," *Bulletin du Muséum National d'histoire Naturelle, Paris, Series 4* 10, no. 2 (1988): 265–276.
- [41] A. E. Verrill, "Report of the Canadian Arctic Expedition 1913–18. Volume VIII: Mollusks, Echinoderms, Coelenterates, etc. Part G: Alcyonaria and Actiniaria. F.A. Acland, Ottawa, Canada," (1922).
- [42] W. B. Benham, "On Some Alcyonarians From New Zealand Waters," *Transactions and Proceedings of the New Zealand Institute* 59 (1928): 67–84.
- [43] J. A. Thomson and W. D. Henderson, "An Account of the Alcyonarians Collected by the Royal Indian Marine Survey Ship 'Investigator' in the Indian Ocean. I," The alcyonarians of the deep sea. Trustees of the Indian Museum, University of Aberdeen, 1–128 (1906).
- [44] J. Versluys, "*Bathyalcyon robustum* Nov. Gen. Nov. Spec. Ein Neuer Alcyonier der Siboga-Sammlung," *Zoologischer Anzeiger* 30 (1906): 549–553.
- [45] F. A. Pasternak, *Benthos of Submarine Mountains Marcus-Necker and Adjacent Pacific Regions* (P.P. Shirshov Institute of Oceanology, Academy of Sciences of the USSR, Moscow, Russia, 1981): 40–55.
- [46] T. Studer, "Alcyonaires Provenant des Campagnes de l'Hirondelle," *Resultats des Campagnes Scientifiques, Monaco* 20 (1901): 1–64.
- [47] F. M. Bayer, "Descriptions and Redescriptions of the Hawaiian Octocorals Collected by the U.S. Fish Commission Steamer 'Albatross. (I. Alcyonacea, Stolonifera and Telestacea)," *Pacific Science* 6, no. 2 (1952): 126–136.
- [48] W. Kükenthal, "Zur Kenntnis der Gattung Anthomastus Verr. Beiträge Zur Naturgeschichte Ostasiens. Herausgegeben von Dr. F. Doflein. Abhandlungen der Math.-Phys. Klasse Der K. Bayer," *Akademie der Wissenschaften I I*, no. 9 (1910): 1–15.
- [49] J. Felsenstein, "Cases in Which Parsimony or Compatibility Methods Will Be Positively Misleading," *Systematic Biology* 27, no. 4 (1978): 401–410.