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Morphological and Phylogenomic Insights Into Hidden Diversity in Coralliidae With Description of a New Species *Paraminabea xishaensis* sp. nov. From the South China Sea

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ABSTRACT

The family Coralliidae (Octocorallia) includes ecologically and economically important octocorals that build rigid, three-dimensional skeletal frameworks from shallow reefs to the deep sea. Despite extensive morphological study, species boundaries remain difficult to delimit because of morphological convergence, phenotypic plasticity, and the limited resolution of commonly used molecular markers. During benthic surveys in the Xisha Islands, South China Sea, we discovered a new coralliid species, *Paraminabea xishaensis* sp. nov. The new species resembles *P. aldersladei* in overall colony form but can be distinguished by a consistent suite of diagnostic sclerite characters, most notably stalk sclerites with a continuous transverse groove and the presence of six- to eight-radiate forms approaching double stars; autozooid and siphonozooid pores were not apparent. Phylogenomic analyses based on 2903 ultraconserved element (UCE) loci recover *P. xishaensis* sp. nov. as sister to *P. aldersladei* with strong support within a family-wide UCE phylogeny framework of Coralliidae, consistent with its recognition as a distinct species. The phylogeny further recovers five deeply divergent and internally coherent lineages within Coralliidae: *Sphaerasclera*, *Paraminabea*, a clade comprising *Sibogagorgia*, *Paragorgia*, *Hemicorallium*, *Corallium*, and *Pleurocorallium*, *Minabea*, and Anthomastinae. This phylogenomic framework provides a comparative baseline for future studies that incorporate expanded sampling and genome-derived single-copy orthologs to investigate adaptive evolution, mitonuclear discordance, and ecological diversification across Coralliidae.

1 | Introduction

Coralliidae (Octocorallia: Scleralcyonacea) represents a family of ecologically and economically important octocorals whose rigid, calcitic axial skeletons contribute to the formation of complex three-dimensional habitats across depths ranging from shallow reefs to the deep sea. These habitat-forming species enhance benthic complexity and provide structural refuges for diverse associated fauna [1]. Despite their ecological and evolutionary significance, relationships within Coralliidae remain incompletely resolved. Extensive morphological convergence, phenotypic plasticity, and the limited resolving power of traditional

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molecular markers—particularly mitochondrial mtMutS and nuclear 28S rDNA—have obscured both species boundaries and higher-level relationships [2–4]. The unusually slow mitochondrial substitution rate in Anthozoa [5] further constrains phylogenetic inference based on mtDNA, leaving the natural classification of the family unsettled.

Early molecular phylogenies based on mtMutS and 28S markers provided only partial resolution within the family, often yielding weakly supported or topologically unstable relationships [6]. Reduced-representation sequencing approaches such as MIG-seq and RAD-seq have since improved resolution among closely related species [7, 8]. However, while these methods perform well at shallow evolutionary scales, their stochastic locus recovery and high rates of dropout limit comparability across deep divergences. In contrast, analyses of ultraconserved elements (UCEs) capture thousands of orthologous nuclear loci that couple conserved cores with variable flanking regions, enabling simultaneous resolution of both ancient and recent splits [9–11]. Recent UCE-based phylogenomic studies have established a robust evolutionary framework for Octocorallia, revealing extensive incongruence between morphology-based taxonomy and molecular phylogeny, and providing new insight into the evolution of skeletal mineralization and character homoplasy across the subclass [12, 13]. Yet, within Coralliidae, genome-scale data remain sparse, and the phylogenetic placement of several genera—including *Paraminabea*—has not been rigorously tested.

The genus *Paraminabea* [14] is morphologically distinctive yet taxonomically problematic. All known species are azooxanthellate, inhabiting mesophotic to upper-bathyal depths throughout the Indo-West Pacific. Colonies are digitate or lobate, with dimorphic polyps and highly variable sclerite assemblages that complicate morphological diagnosis [15, 16]. Previous molecular datasets have been insufficient to test the monophyly of *Paraminabea* or clarify its relationships with related genera such as *Corallium* and *Pleurocorallium* [6]. As a result, both its intrageneric diversification and evolutionary placement within Coralliidae remain unresolved.

The Xisha Islands, situated in the central South China Sea, represent a biogeographically pivotal transition zone between the Indo-Malayan biodiversity hotspot and the northwestern Pacific. Their mesophotic reefs and complex current systems may promote endemism and cryptic diversification, yet octocorals from this region remain poorly documented compared with scleractinians. Previous regional studies have reported multiple *Paraminabea* species in the western Pacific and Japanese waters [6, 17], suggesting that the South China Sea may harbor additional, undescribed diversity.

During recent benthic surveys in the Xisha Islands, we collected several azooxanthellate colonies that closely resemble *Paraminabea aldersladei* in overall appearance but differ in colony architecture and sclerite composition. We also obtained additional specimens representing several Coralliidae species from the East and South China Seas to provide broader taxonomic context and to support phylogenetic analyses. We hypothesize that the Xisha colonies represent a distinct evolutionary lineage within *Paraminabea*, and that analyses of UCE-based nuclear markers will help resolve their phylogenetic placement within the family. By integrating detailed morphological comparisons with genome-scale phylogenomic data, this study offers new perspectives on the evolutionary diversification of *Paraminabea*, refines the systematic framework of the Coralliidae, and establishes a genomic foundation for future investigations of octocoral evolution and taxonomy.

2 | Materials and Methods

2.1 | Sample Collection and Morphological Analysis

Specimens of *P. xishaensis* sp. nov. were collected by SCUBA diving from the Xisha Islands, South China Sea during surveys conducted in 2024. Additional specimens of *Sphaerasclera*, *Paraminabea*, *Minabea*, and *Anthomastus* were obtained from the East and South China Seas by SCUBA diving and fishery bycatch (Table 1). In situ ecological photographs were taken using a

TABLE 1 | Sampling stations of the family Coralliidae used in this study.

Species	Sample ID	Sampling site	Coordinates	Sampling date
	XS001	Beijiao Atoll, Xisha Islands, China	21°05′7.00″N, 109°06′14.00″E	August 30, 2024
	XS002	Beijiao Atoll, Xisha Islands, China	21°05′7.00″N, 109°06′14.00″E	August 30, 2024
Paraminabea xishaensis sp. nov.	XS003	Huaguang Atoll, Xisha Islands, China	16°13′4.5″N, 111°35′54.8″E	May 26, 2025
	XS004	Huaguang Atoll, Xisha Islands, China	16°13′4.5″N, 111°35′54.8″E	May 26, 2025
	XS005	Huaguang Atoll, Xisha Islands, China	16°13′4.5″N, 111°35′54.8″E	May 26, 2025
Sphaerasclera sp.	DHM01	East China Sea	22°15′00″N, 117°25′00″E	April 15, 2025
Paraminabea rubeusa	ZH003	Zhuhai, Guangdong, China	22°3′13.87″N, 114°0′34.78″E	October 17, 2024
	ZH005	Zhuhai, Guangdong, China	22°6′37.07″N, 114°2′39.19″E	June 23, 2025
Paraminabea hongkongensis	ZH001	Zhuhai, Guangdong, China	22°3′31.11″N, 113°59′1.03″E	October 14, 2024
	ZH002	Zhuhai, Guangdong, China	22°6′37.07″N, 114°2′39.19″E	October 14, 2024
Minabea cf. *phalloides*	NHM01	South China Sea (fishery bycatch)	19°37′44″N, 113°57′54″E	April 8, 2025
Anthomastus cf. *muscarioides*	NH001	South China Sea (fishery bycatch)	19°37′44″N, 113°57′54″E	April 8, 2025

Nikon D850 digital camera with underwater housing. All specimens were preserved in 99% ethanol immediately after collection. Portions of the specimens were isolated and preserved in absolute ethanol for molecular studies. Colony morphology and anatomical structures were examined under a stereo dissecting microscope following standard octocoral protocols [18]. Sclerites were isolated by dissolving tissues in a saturated sodium hypochlorite solution, rinsed thoroughly in distilled water, air-dried, and then observed under a scanning electron microscope (SEM). Cleaned and air-dried sclerites were mounted on aluminum stubs using conductive carbon tape and sputter-coated with an ~10 nm gold–palladium layer. SEM images were acquired using a Zeiss Sigma field-emission scanning electron microscope operated at 20 kV accelerating voltage, a working distance of 10 mm, and high-vacuum mode. Morphological features were examined using the secondary electron detector at magnifications ranging from 200× to 2000×. Morphological terminology follows Bayer and Verseveldt [19]. Type material is deposited in the Institute of Marine Drugs, Guangxi University of Chinese Medicine (GXTCMU).

2.2 | DNA Extraction and Sequencing

Genomic DNA was extracted from 99% ethanol-preserved tissues using the TIANamp Marine Animals DNA Kit (Tiangen, China) following the manufacturer's protocol. Approximately 20–30 mg of tissue was briefly rinsed to remove residual ethanol, digested with Proteinase K, and purified using silica spin columns, with genomic DNA eluted in 50–100 μL of elution buffer and stored at −20°C. DNA quantity and quality were assessed using NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific, USA) and Qubit 4.0 fluorometer (Thermo Fisher Scientific, USA). For library preparation, ~0.2 μg of genomic DNA per specimen was fragmented to an average size of ~ 350 bp using a Covaris LE220R-plus (Covaris, USA), followed by end repair, A-tailing, adapter ligation, and PCR amplification. Libraries were purified with AMPure XP beads (Beckman Coulter, USA), assessed on an Agilent 5400 system (Agilent Technologies, USA). After phosphorylation and circularization, DNA nanoballs were generated by rolling circle amplification and sequenced on a DNBSEQ-T7 platform (MGI, China) at Novogene (Beijing, China) using 150-bp paired-end reads, yielding ~40 million clean reads per specimen.

2.3 | UCEs Recovery and Phylogenetic Analyses

Genomic data for Coralliidae were compiled from two sources: newly sequenced specimens generated in this study and publicly available datasets downloaded from the Sequence Read Archive (SRA). All SRA datasets were downloaded as raw sequencing reads and processed using the same trimming, locus recovery, alignment, and filtering pipeline as the newly sequenced specimens. Based on WoRMS (Coralliidae Lamouroux, 1812; AphiaID 125280), the family currently comprises 16 recognized genera, of which 13 are represented in our phylogenomic dataset, corresponding to 81.3% genus-level coverage. Two *Parasphaerasclera* species were designated as the outgroup based on their phylogenetic position inferred in McFadden et al. [12].

Raw reads were first quality-trimmed with fastp v1.0.1 [20] under default parameters. Target loci were recovered in silico as UCEs and exon regions from shotgun sequencing data using sequences from a previously published octocoral bait set [21] (29,181 probes targeting 3023 loci) as reference in GeneMiner2 [22], rather than for experimental hybridization enrichment.

In GeneMiner2, UCE locus recovery follows a reference-guided analytical framework, similar to that implemented in HybPiper [23], in which reads corresponding to target loci are first identified using k-mer based filtering, thereby restricting subsequent assembly to the intended genomic regions prior to contig construction. Filtered reads were assembled independently for each locus using a reference-guided, local de novo assembly strategy implemented in GeneMiner2; no whole-sample or genome-wide de novo assembly was conducted. For each target locus, GeneMiner2 constructs local de Bruijn graphs from locus-specific reads and applies a greedy extension procedure that prioritizes paths supported by read depth, consistency in k-mer positions relative to the reference, and strand orientation. Putative contigs are subsequently evaluated by mapping high-quality internal read segments to assess assembly reliability. GeneMiner2 was run with the parameters -kf 27 (k-mer length used for read filtering and locus identification), –min-depth 2 (minimum read depth required for locus retention, following depth-handling logic analogous to the single-cell mode in SPAdes), and -c 0.70 (consensus threshold for base calling), with the k-mer setting chosen to balance locus recovery and per-locus missing data.

Recovered loci were aligned independently by locus and subsequently filtered using AMAS [24] to construct concatenated data matrices retaining loci present in at least 80% of the sampled taxa. Maximum-likelihood (ML) phylogenies were reconstructed with IQ-TREE v3.0.1 [25] with initial data partitions defined by locus and best-fit substitution models and partition-merging schemes selected using ModelFinder [26] under the greedy search strategy (-m MFP + MERGE). Node support was assessed using 10,000 ultrafast bootstrap replicates (UFBoot) [26] and 10,000 SH-like approximate likelihood ratio test (SH-aLRT) replicates [27]. Final trees were visualized and annotated using the Interactive Tree Of Life (iTOL) v7.

3 | Results

3.1 | Morphology of *P. xishaensis* sp. nov.

Class Octocorallia Haeckel, 1866

Order Scleralcyonacea McFadden, Van Ofwegen & Quattrini, 2022

Family Coralliidae Lamouroux, 1812

Genus *Paraminabea* Williams & Alderslade, 1999

Paraminabea Williams & Alderslade, 1999:337-364

Type species *Paraminabea indica* (Thomson & Henderson, 1905), by subsequent designation (Thomson & Henderson, 1905:274–275) *Bellonella indica* Thomson & Henderson, 1905

Diagnosis [14] Colonies unbranched and hemispherical to digitiform: low and dome-shaped to elongate and finger-like. Polyps dimorphic. Sclerites of surface and interior of colony densely set: mostly barrels and six or eight-radiates with spindles, rods,

tuberculate spheroids; seven-radiates or double stars sometimes occurring. Color red, orange, yellow or pinkish-white to cream-white.

Paraminabea xishaensis sp. nov.

Figures 1A-C, 2, and 3A–E.

Holotype: GXTCMU-2024-XS001, shallow coral reef, Beijiao Atoll, Xisha Islands (= Paracel Islands, 21°05′6. 41″N, 109°06′ 14.09″E, 18 m, South China Sea, coll. X-M Liu, 29 August 2024.

Paratype: GXTCMU-2024-XS002, shallow coral reef, Beijiao Atoll, Xisha Islands, China, 21°05′7. 00″ N, 109°06′14.00″ E, 12 m, South China Sea, coll. X-M Liu, 30 August 2024. GXTCMU-2025-XS003, GXTCMU-2025-XS004, GXTCMU-2025-XS005, shallow coral reef, Huaguang Atoll, Xisha Islands, 16°13′4.5″ N, 111°35′54.8″ E, 20 m, South China Sea, coll. Li You, 26 May 2025.

Diagnosis: Digitiform, yellow or orange colonies, stalk short, polyps dimorphic, autozooids are indistinct; sclerites are predominantly subspheroidal, barrel-shaped, elongate fusiform, and radiate, with some exhibiting a continuous transverse groove along the waist. The nomenclatural act has been registered in ZooBank under the following LSID: urn:lsid:zoobank.org:act:2E509FE0-CCDD-4636-8A66-C4559A826D4E.

Description: The holotype is a complete specimen, 31 mm long, with a basal diameter of 10 mm and tapering distally to 5 mm at the tip. Colonies digitiform, tapering distally. Inhabit areas such as overhangs and caves (Figure 1A–C). Stalk restricted to the proximal one-sixth of the colony. Polyparium restricted to the distal five-sixths. Polyps dimorphic. The colony is tightly contracted and consequently the siphonozooids are not visible on the surface; these can only be observed in the longitudinal section of the colony. After preservation in ethanol, the colony is orange in color, and the sclerites appear orange-red under the

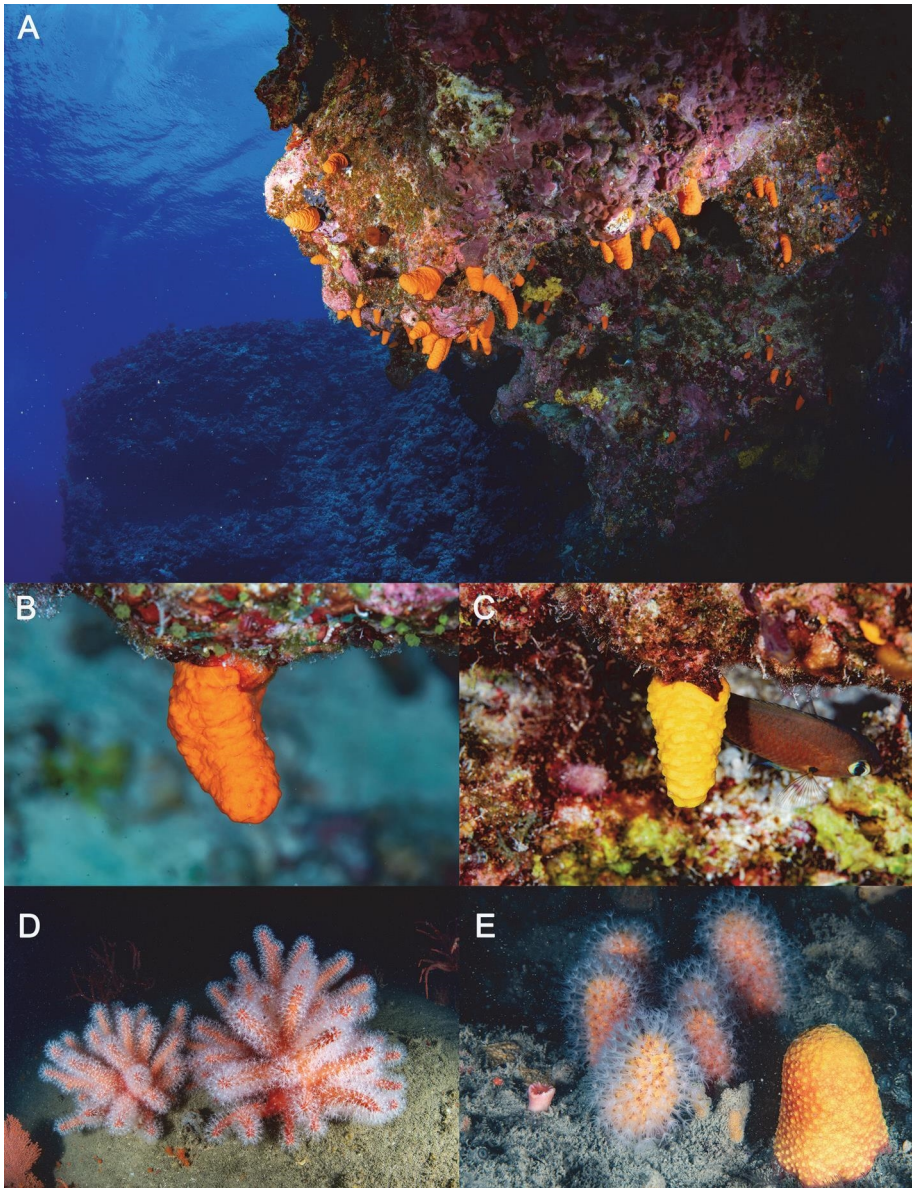

FIGURE 1 | In situ photos of *Paraminabea* species. (A) *P. xishaensis* sp. nov. showing the habitat; (B) *P. xishaensis* sp. nov. (XS004) orange color pattern; (C) *P. xishaensis* sp. nov. (XS005) yellow color pattern; (D) *P. rubeusa* (ZH003); (E) *P. hongkongensis* (ZH002).

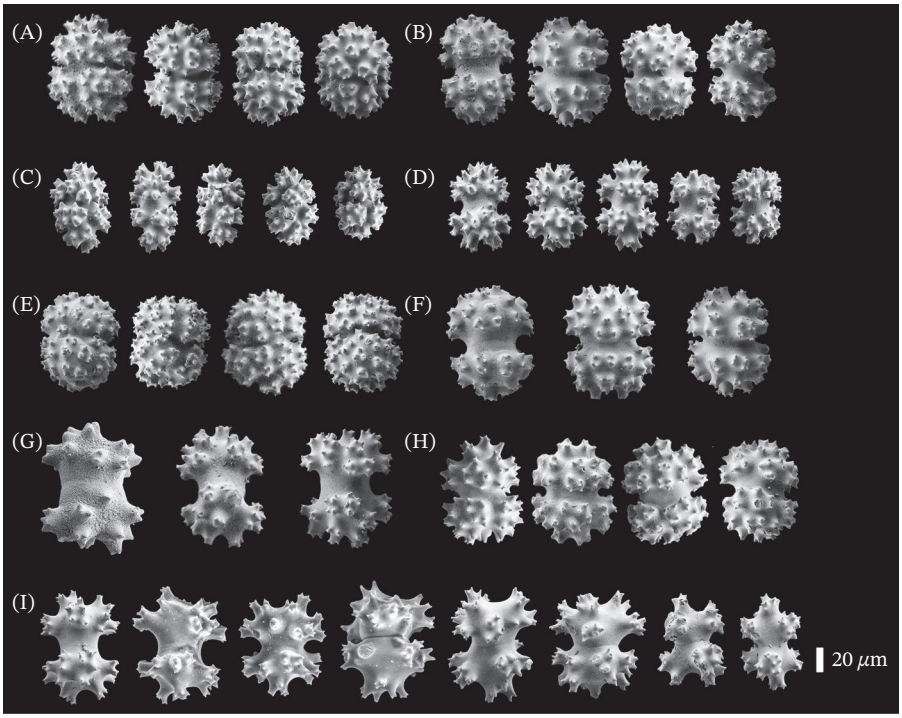

FIGURE 2 | Sclerites of *Paraminabea xishaensis* sp. nov. holotype (GXTCMU-2024-XS001) under SEM. (A, B) Interior of the polyparium, (C, D) surface of the polyparium, (E–G) interior of the stalk, (H–I) surface of the stalk. Scale bar represents 20 μm.

microscope. The sclerites are densely distributed throughout the surface and interior of the colony. Sclerites from the polyparium (Figure 2A–D) and stalk (Figure 2E–I) are variable. The interior sclerites of the polyparium consist of sub-spheroidal forms, ~0.08 mm in length, with a very short waist (Figure 2A), together with robust barrel shaped sclerites about 0.07 mm long (Figure 2B). On the surface of the polyparium, sclerites are predominantly elongate and fusiform, reaching about 0.10 mm in length and densely covered with stout, radially arranged spines (Figure 2C); in addition, 6–8-radiate sclerites measuring 0.05 mm in length are also present (Figure 2D). The sclerites in the stalk interior resemble those of the polyparium (Figure 2E,F) but also include double-star forms, about 0.07 mm in length, with an elongated waist and relatively blunt spine-like processes (Figure 2G). On the stalk surface, robust barrel shaped sclerites (Figure 2H) (0.05 mm long) occur together with radiate sclerites bearing large, knob-like processes, each process long and bluntly spinose, reaching up to 0.05 mm in length. Some sclerites exhibit a continuous transverse groove along the waist (Figure 2I). The overall morphology of the holotype is shown in Figure 3A.

In longitudinal section, the outer layer of the colony exhibits several broad, sac-like autozooidal gastric cavities, each containing mature gonads, together with narrow, elliptical siphonozooidal cavities. The inner region contains numerous medullar canals that are smaller than the autozooidal cavities but larger than the siphonozooidal cavities, and these canals are not interconnected.

Variation of paratypes: The four paratypes are highly similar to the holotype in overall morphology, size, and sclerite structure, with the main difference being in coloration (Figure 3B–E).

Coloration: The colonies are orange or yellow and the polyps are white, sclerites are orange. Coloration of colonies is retained after preservation in alcohol.

Etymology: Named after the typical location Xisha Islands.

Habitat: Colonies usually grow inverted in vertical reef cavities or depressions, often associated with sponges and azooxanthellate corals.

Distribution: Known only from the coral reef of Xisha Islands.

Remarks: There are 11 described species of *Paraminabea*. *P. xishaensis* sp. nov. most closely resembles *P. aldersladei* [28] in overall colony form and general sclerite composition. However, it differs in having stalk sclerites with a distinct transverse continuous groove on the waist (length 0.15–0.20 mm), a feature absent in *P. aldersladei*. In addition, the autozooids of *P. aldersladei* [14] are surrounded by conspicuous siphonozooids forming minute pores 0.03–0.10 mm in diameter, whereas such structures are not discernible in *P. xishaensis* sp. nov.

The new species, *P. xishaensis* sp. nov., can be readily distinguished from all congeners by its colony growth form and sclerite forms. In terms of colony architecture, *P. arborea* [14], *P. indica* [29], and *P. rubeusa* [15] exhibit branched colonies, whereas *P. acronocephala* [28] and *P. goslineri* [28] possess dome-shaped colonies. The remaining congeners, including *P. aldersladei* [28], *P. robusta* [30], *P. cosmarioidea* [28], *P. kosiensis* [28], *P. hongkongensis* [31], and *P. inflata* [32], display digitiform colonies. The new species also exhibits a digitiform growth form but differs markedly in its sclerite. The sclerites of *P. kosiensis* are elongate spindles, while *P. hongkongensis* and *P. inflata* possess cruciform sclerites. *P. cosmarioidea* is characterized by rotund barrel-shaped sclerites bearing small, densely packed tuberculations, and *P. robusta* displays sclerites with tuberculate spheroids. In comparison, both *P. xishaensis* sp. nov. and *P. hongkongensis* possess sclerites that exhibit a continuous transverse groove along the waist; however, the latter lacks the sub-spheroidal sclerites.

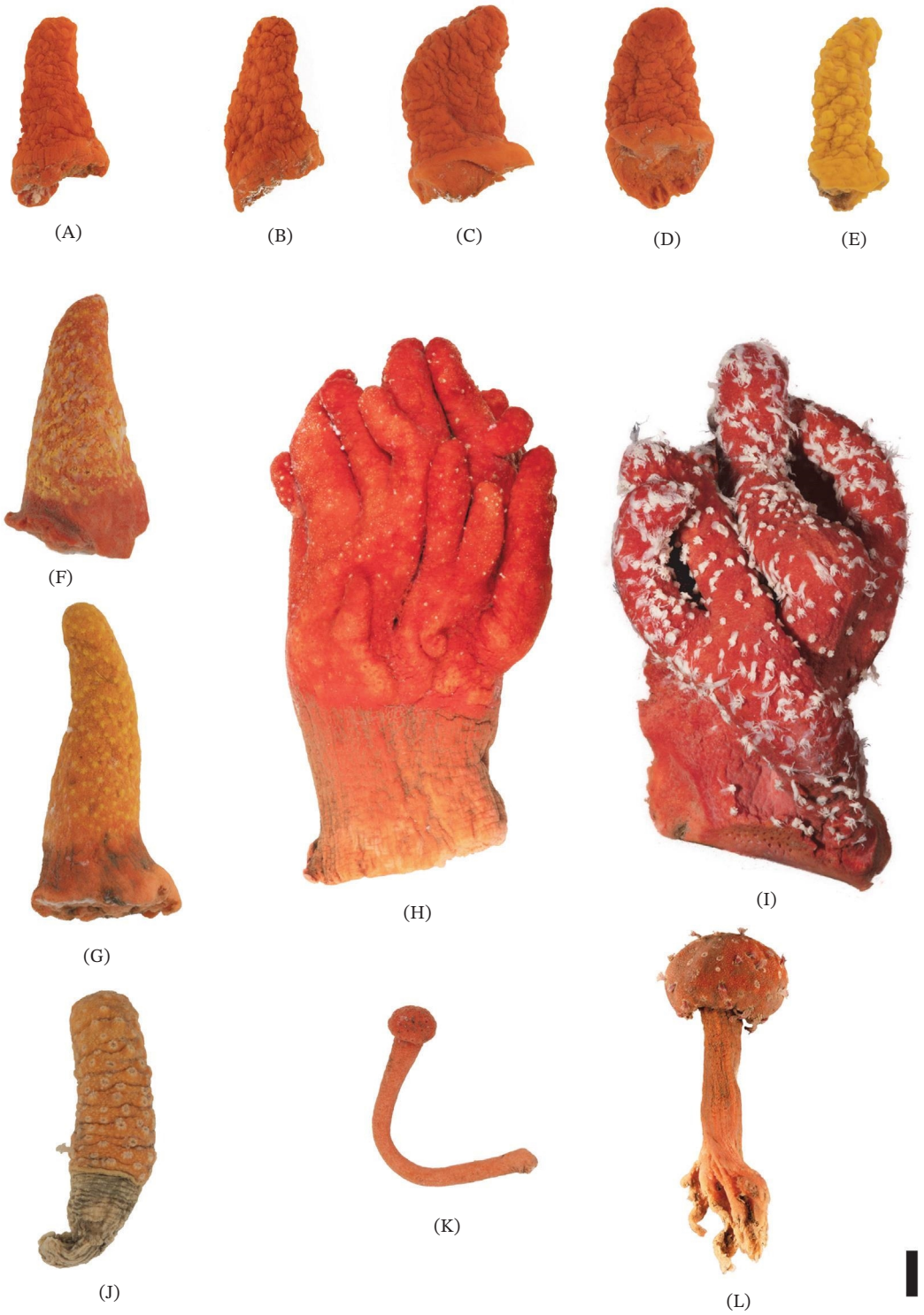

FIGURE 3 | Colony morphology of Coralliid specimens after preservation in ethanol. (A) *Paraminabea xishaensis* sp. nov., holotype (GXTCMU-2024-XS001); (B) *Paraminabea xishaensis* sp. nov., paratype (GXTCMU-2024-XS002); (C) *Paraminabea xishaensis* sp. nov., paratype (GXTCMU-2025-XS003); (D) *Paraminabea xishaensis* sp. nov., paratype (GXTCMU-2025-XS004); (E) *Paraminabea xishaensis* sp. nov., paratype (GXTCMU-2025-XS005); (F) *Paraminabea hongkongensis* (ZH001); (G) *Paraminabea hongkongensis* (ZH002); (H) *Paraminabea rubeusa* (ZH003); (I) *Paraminabea rubeusa* (ZH005); (J) *Minabea* cf. *phalloides* (NH001); (K) *Sphaerasclera* sp. (DHM01); (L) *Anthomastus* cf. *muscarioides* (NHM01). Scale bar represents 10 mm.

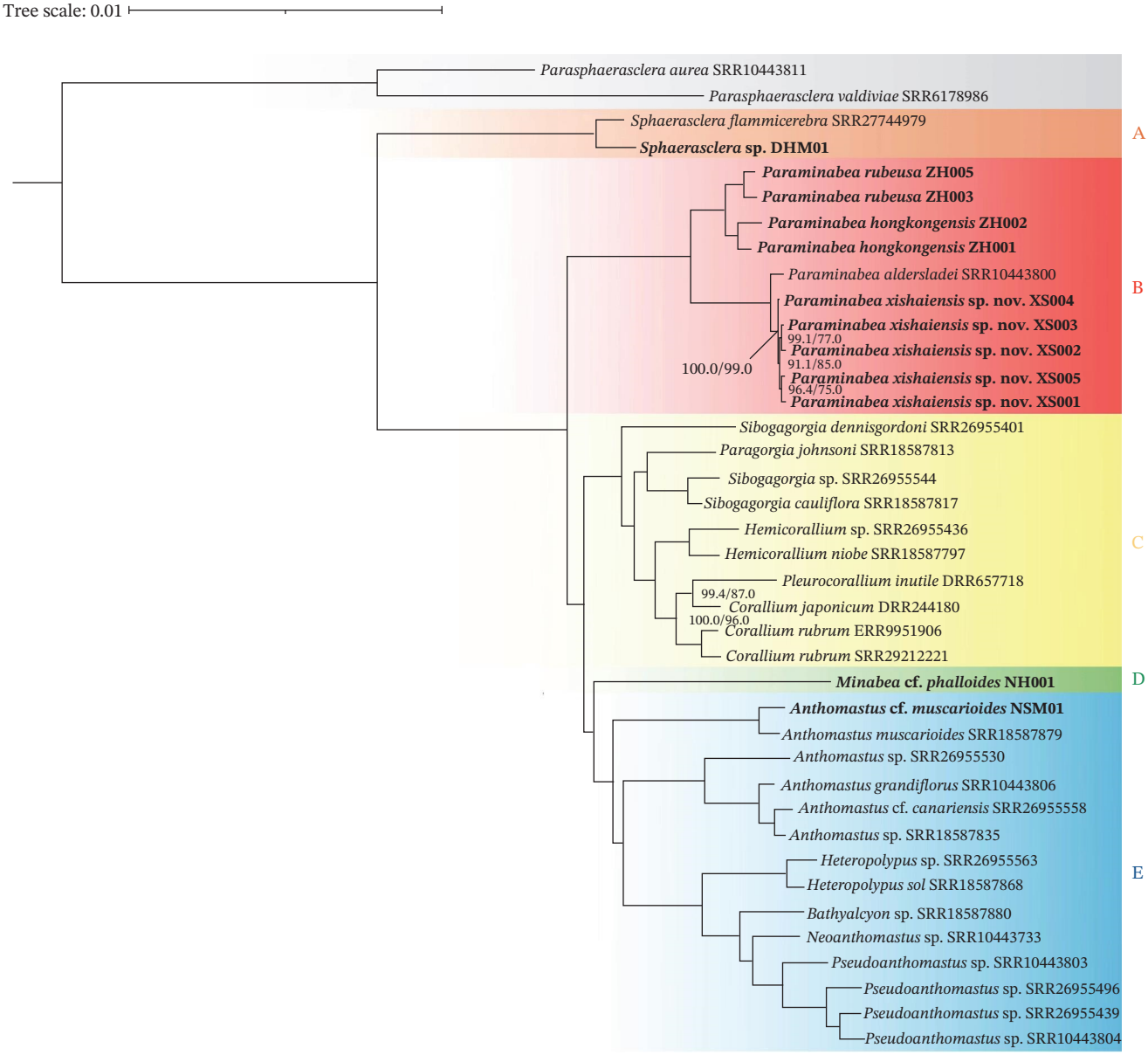

FIGURE 4 | Maximum-likelihood phylogeny of Coralliidae inferred from 1792 concatenated ultraconserved element (UCEs) loci (80% taxon occupancy; 239,271 bp). Node support is shown as ultrafast bootstrap (UFBoot) and SH-like approximate likelihood ratio test (SH-aLRT) values (UFBoot/SH-aLRT). The topology recovers five deeply divergent and internally coherent clades within Coralliidae: clade A, *Sphaerasclera*; clade B, *Paraminabea*; clade C, comprising *Sibogagorgia*, *Paragorgia*, *Hemicorallium*, *Corallium*, and *Pleurocorallium*; clade D, *Minabea*; and clade E, Anthomastinae (*Anthomastus*, *Bathyalcyon*, *Heteropolypus*, *Neoanthomastus*, *Pseudoanthomastus*). Clade labels (A–E) are shown adjacent to the corresponding lineages and color matched to the clade highlighting in the phylogeny. Support values of 100.0/100.0 are omitted for clarity.

3.2 | Phylogenomic Analysis of UCEs

We recovered 2,903 UCE loci from 39 specimens, including 12 newly sequenced in this study and 27 retrieved from the SRA. The newly generated dataset included two *P. rubeusa* (ZH003 and ZH005) (Figure 1D and Figure 3H,I), two *P. hongkongensis* (ZH001 and ZH002) (Figure 1E; Figure 3F,G), five *Paraminabea xishaensis* sp. nov. (XS001–XS005) (Figure 3A–E), one *Anthomastus* cf. *muscarioides* (NH001) (Figure 3L), one *Sphaerasclera* sp. (DHM01) (Figure 3K), and one *Minabea* cf. *phalloides* (NHM01) (Figure 3J). Each sample yielded 375–2774 loci, with a mean of 2302 ± 485 loci per sample. The 80% taxon-occupancy matrix comprised 1792 loci (239,271 bp), of which 18.2% (43,488 bp) were parsimony-informative.

The ML phylogeny is shown in Figure 4. Within Coralliidae, *Sphaerasclera* (clade A), represented by *Sphaerasclera flammicerebra* and *Sphaerasclera* sp. (DHM01), was recovered near the base of the ingroup topology and as sister to all remaining ingroup taxa (bootstrap = 100). Within *Paraminabea* (clade B), *P. xishaensis* sp. nov. was recovered as a distinct lineage closely related to *P. aldersladei*, whereas *P. rubeusa* and *P. hongkongensis* each formed monophyletic lineages. Clade C, comprising *Sibogagorgia*, *Paragorgia*, *Hemicorallium*, *Corallium*, and *Pleurocorallium*, formed a cohesive and well-supported clade (bootstrap = 100). Clade D (*Minabea*) was recovered as an independent and strongly supported lineage (bootstrap = 100) positioned between clades C and E in the inferred topology. Clade E (Anthomastinae)

formed a monophyletic group (bootstrap = 100) comprising *Anthomastus*, *Bathyalcyon*, *Heteropolypus*, *Neoanthomastus*, and *Pseudoanthomastus*.

4 | Discussion

4.1 | Taxonomic Status of *P. xishaensis* sp. nov

Morphological evidence supports the recognition of *P. xishaensis* sp. nov. as a distinct species, and UCE-based phylogenomic analyses provide concordant support for its placement relative to closely related congeners. Morphologically, the new species closely resembles *P. aldersladei* in overall colony form, polyp dimorphism, and the presence of barrel-shaped and subspheroidal sclerites; however, the most prominent characteristic is that the radial sclerites of the stalk possess continuous transverse grooves and longer radial warts—an otherwise unreported feature among congeners—as well as smaller fusiform sclerites and a more orderly arrangement of subspheroidal forms. Phylogenomically, *P. xishaensis* sp. nov. is consistently recovered as sister to *P. aldersladei* in the UCE-based ML tree with strong support (bootstrap = 100). Although internal branch lengths within this clade are short, as is typical of UCEs datasets for closely related taxa, the two lineages are separated by a clearly resolved branch, indicating a consistent phylogenomic signal supporting lineage independence. All five sequenced specimens of *P. xishaensis* sp. nov. (XS001–XS005), collected from two reef sites within the Xisha Islands separated by more than 200 km, form a strongly supported monophyletic group (bootstrap = 100). Within this monophyletic lineage, node support values show some variation and branches are short, resulting in a shallow internal phylogenetic structure; however, this structure shows no correspondence with sampling locality, and the overall topology remains stable in supporting its delimitation as a single evolutionary lineage. Taken together, the recovery of geographically separated specimens as a single, well-supported phylogenomic lineage, combined with clear and consistent morphological diagnostic characters, provides robust integrative evidence for delimiting *P. xishaensis* sp. nov. as a distinct species.

4.2 | Phylogenomic Framework and Subfamilial Structure of Coralliidae

The UCE-based phylogeny provides a genome-scale framework for Coralliidae and clarifies several relationships that have remained uncertain in morphology-based and single-gene studies [4, 33]. Our analyses recover five deeply divergent yet internally coherent lineages, corresponding to five clades: clade A, *Sphaerasclera*; clade B, *Paraminabea*; clade C, comprising *Sibogagorgia*, *Paragorgia*, *Hemicorallium*, *Corallium*, and *Pleurocorallium*; clade D, *Minabea*; and clade E, Anthomastinae. These results suggest that UCEs data can recover both deeper and shallower splits within the family, helping to mitigate the limited phylogenetic signal and instability often associated with mitochondrial and ribosomal markers in octocoral systematics.

Clades A (*Sphaerasclera*) and B (*Paraminabea*) are recovered near the base of the ingroup topology. This placement accords with shared morphological features, including polyp dimorphism and subspheroidal to radiate sclerites, traits that have historically been interpreted as plesiomorphic within the family [4, 34]. The recovered sister relationship between clades A and B provides genome-scale support for treating these skeletal characters as ancestral rather than the result of convergence. Within *Paraminabea* (clade B), *P. xishaensis* sp. nov. is recovered as a distinct lineage closely related to *P. aldersladei*, consistent with the diagnostic morphology and supporting recognition of the new species.

Clade C, comprising *Sibogagorgia*, *Paragorgia*, *Hemicorallium*, *Corallium*, and *Pleurocorallium*, forms a well-supported radiation (bootstrap = 98–100) characterized by the evolution of a rigid axial skeleton and a reduction in polyp dimorphism, in contrast to clades A and B. Within clade C, the sister relationship between *Hemicorallium* and (*Corallium* + *Pleurocorallium*) mirrors topologies recovered in earlier molecular studies [4, 33] and is consistent with a cohesive evolutionary radiation potentially associated with a single origin of axial calcification followed by repeated morphological specialization in deep-sea environments [17].

Clade D, *Minabea* cf. *phalloides*, forms an independent and strongly supported lineage placed between clades C and E in the inferred topology, suggesting a distinct evolutionary trajectory within Coralliidae and raising the possibility that it captures intermediate character combinations between colonial and solitary forms. This study documents *M.* cf. *phalloides* from bottom-trawl collections in the South China Sea and provides the first molecular data for *Minabea*, offering genomic evidence for its placement within Coralliidae [35, 36].

Within clade E (Anthomastinae Verrill, 1922), *Anthomastus muscarioides* is recovered as the earliest-branching lineage in our analysis, followed by *Heteropolypus*, *Bathyalcyon*, *Neoanthomastus*, and *Pseudoanthomastus*, consistent with the topology reported by Li et al. [37]. This arrangement supports the monophyly of Anthomastinae while refining relationships among its constituent genera, and it is compatible with a scenario in which solitary morphology in Anthomastines evolved via paedomorphic reduction rather than through multiple independent origins.

Overall, this phylogenomic framework provides a useful comparative baseline for future five-clade revisions of Coralliidae and offers new context for interpreting the evolution of skeletal architecture within Octocorallia. By integrating genome-scale data with classical morphology, our results allow long-standing, morphology-based hypotheses to be evaluated explicitly on a phylogenetic tree and point to potentially important transitions in colony form, polyp dimorphism, and axial skeletal evolution across the family.

4.3 | Significance and Future Perspectives of UCE-Based Phylogenomics in Coralliidae

The phylogenomic framework established in this study highlights the growing utility of UCEs as a consistent and scalable genomic resource for octocoral systematics. Traditional mitochondrial and nuclear markers, such as MutS and 28S rDNA, have limited power for resolving relationships within Coralliidae due to low substitution rates and incomplete lineage sorting. Reduced-representation approaches such as MIG-seq and RAD-seq are informative for population-level studies but tend to lose efficacy at deeper phylogenetic scales because of locus dropout

and allelic bias. In contrast, UCEs enable stable recovery of orthologous loci across broad evolutionary distances, allowing both shallow and deep divergences to be examined within a single analytical framework. By integrating UCEs data from *Sphaerasclera*, *Paraminabea*, *Corallium*, *Minabea*, and Anthomastinae, the present dataset provides the most comprehensive genomic representation of Coralliidae to date, encompassing 10 of the 13 recognized genera. The remaining genera—*Carotalcyon*, *Mollecorallium*, and *Notodysiferus*—remain morphologically distinctive but phylogenetically unresolved; future inclusion of these taxa using UCEs or low-coverage genome sequencing will be critical for testing alternative hypotheses of subfamilial delimitation.

Methodologically, this work represents the first application of GeneMiner2 [22] to coral phylogenomics. Unlike traditional assembly-based pipelines such as PHYLUCE [38], and similar in overall analytical philosophy to target-guided frameworks such as HybPiper [23], GeneMiner2 implements a reference-guided de Bruijn graph strategy with self-seeding, greedy extension, and parameter-bootstrap validation, supported by a weighted-node model that stabilizes assembly and minimizes substitution and indel errors. These innovations substantially reduce computational time and memory consumption while maintaining comparable levels of locus recovery and alignment quality. The resulting increase in efficiency markedly improves the feasibility of large-scale phylogenomic analyses, even for non-model or archival specimens. This advance parallels recent calls for re-evaluating the untapped potential of short-read sequencing in biodiversity genomics [39], emphasizing that robust phylogenetic resolution can be achieved without dependance on long-read assemblies.

Notably, this study presents the first genomic data for the genus *Minabea*, collected from trawled material in the South China Sea, and provides an initial phylogenomic assessment of its placement within Coralliidae under our UCE-based framework. As more high-quality reference genomes for Coralliidae become available, single-copy orthologous genes can also be efficiently retrieved from shallow genome sequencing data, facilitating comparative analyses of adaptive evolution, mitonuclear discordance, and ecological diversification across the family. Such an integrative genomic framework will bridge population-level and higher-level phylogenetic studies, transforming the current taxonomic structure of Coralliidae into a set of explicit, testable evolutionary hypotheses.

5 | Conclusions

This study combined molecular and morphological aspects into an integrated taxonomic approach and identified a new species, *P. xishaensis* sp. nov. Phylogenomic analyses of 2903 UCEs loci recovered *P. xishaensis* sp. nov. as the sister lineage to *P. aldersladei* and resolved a robust framework for Coralliidae, revealing five divergent clades. The first genomic record of genus *Minabea* further clarifies its taxonomic position and highlights an independent evolutionary trajectory within the family. Methodologically, this study represents the first application of GeneMiner2 to coral phylogenomics, demonstrating that UCEs data can be efficiently extracted and analyzed even from ethanol-preserved or non-model specimens. The resulting high-resolution phylogeny provides a foundation for future comparative genomic studies integrating single-copy orthologs from reference genomes to explore adaptive evolution, mitonuclear discordance, and ecological diversification across Coralliidae, transforming its taxonomy into a testable evolutionary framework.

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Ethics Statement

This work is registered in ZooBank under LSID: urn:lsid:zoobank.org:pub:BDD5F40A-4384-4125-A7AD-C668C961E336.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available upon request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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