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Phylogenomics reveals high black coral diversity in the Red Sea supporting the resurrection of the family Stichopathidae (Hexacorallia: Antipatharia)

SILVIA VICARIO^{1,2*}, TULLIA I. TERRANEO², GIOVANNI CHIMIENTI³, NICOLAS OURY^{1,2}, JEREMY HOROWITZ⁴, LAURA MACRINA^{1,2}, FEDERICA BARRECA², FABIO MARCHESE², MICHAEL L. BERUMEN^{1,2}, CARLOS M. DUARTE^{1,2}, AMEER A. EWEIDA^{5,6}, VINCENT PIERIBONE⁷, MOHAMMED QURBAN⁸, HILDEGARD WESTPHAL^{9,10}, CECILE FAUVELOT^{11,12}, MATTIE RODRIGUE⁷ & FRANCESCA BENZONI^{1,2*}

¹Marine Science Program, Biological and Environmental Science and Engineering Division (BESE), King Abdullah University of Science and Technology (KAUST), Thuwal 23955-6900, Kingdom of Saudi Arabia

 nicolas.oury@kaust.edu.sa;  <https://orcid.org/0000-0002-5386-4633>

 laura.macrina@kaust.edu.sa;  <https://orcid.org/0000-0003-1863-0134>

 michael.berumen@kaust.edu.sa;  <https://orcid.org/0000-0003-2463-2742>

 carlos.duarte@kaust.edu.sa;  <https://orcid.org/0000-0002-1213-1361>

²Red Sea Research Center, King Abdullah University of Science and Technology (KAUST), Thuwal 23955-6900, Kingdom of Saudi Arabia

 tulliaisotta.terranEO@kaust.edu.sa;  <https://orcid.org/0000-0003-2806-4471>

 federica.barreca@kaust.edu.sa;  <https://orcid.org/0000-0002-8240-1806>

 Fabio.marchese@kaust.edu.sa;  <https://orcid.org/0000-0001-8384-3019>

³Department of Biosciences, Biotechnology and Environment, University of Bari Aldo Moro, Bari, Italy

 giovanni.chimienti@uniba.it;  <https://orcid.org/0000-0003-2581-3430>

⁴Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

 HorowitzJ@si.edu;  <https://orcid.org/0000-0002-2643-5200>

⁵Marine Conservation Program, NEOM, Kingdom of Saudi Arabia

 ameer.abdulla@gmail.com

⁶Center of Carbonate Research, Department of Marine Geosciences, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149, U.S.A.

⁷OceanX 37W 39th St, New York, NY, U.S.A.

 vincent@oceanx.org;  <https://orcid.org/0000-0002-5836-5454>

 mattie.rodrique@gmail.com;  <https://orcid.org/0000-0003-2307-0274>

⁸National Center for Wildlife Development, Kingdom of Saudi Arabia

 mqurban@mewa.gov.sa;  <https://orcid.org/0009-0000-2467-1106>

⁹Leibniz Centre for Tropical Marine Research (ZMT), Bremen, Germany

 hildegard.westphal@leibniz-zmt.de;  <https://orcid.org/0000-0001-7324-6122>

¹⁰Department of Geosciences, Bremen University, Bremen, Germany

¹¹UMR ENTROPIE (UR-IRD-IFREMER-CNRS-UNC), Nouméa, 98800, New Caledonia

 cecile.fauvelot@ird.fr;  <https://orcid.org/0000-0003-0806-1222>

¹²Laboratoire d'Océanographie de Villefranche, LOV (Sorbonne Université, CNRS), 06230, Villefranche-sur-mer, France

*Corresponding authors:  silvia.vicario@kaust.edu.sa;  <https://orcid.org/0000-0001-9983-6833>

 francesca.benzoni@kaust.edu.sa;  <https://orcid.org/0000-0001-8906-1309>

Abstract

Antipathidae Ehrenberg, 1834 is the largest family within the order Antipatharia (commonly known as black corals), and includes corals distributed worldwide from shallow to deep waters. With over 124 nominal species, Antipathidae comprises taxa with diverse morphologies, whose taxonomic boundaries, diversity, and distribution remain poorly resolved due to morphological convergence, limited sampling, and discordance between genetic and morphological evidence. Here, we integrated phylogenomic analyses from target-capture of ultraconserved elements (UCEs) and exon loci with detailed morphological analyses for a total of 107 black coral specimens, including 70 collected from the Red Sea between 3 and 623 m water depth, 18 from the Indo-

Pacific and Atlantic Oceans between 3 and 26 m water depth, and 19 specimens from museum collections, five of which representing type material. Moreover, previously published UCE data from 77 specimens was included in the analysis. Our results supported the resurrection of the family Stichopathidae Roule, 1905 to accommodate the genera *Cirripathes* de Blainville, 1830 and *Stichopathes* Brook, 1889, formerly assigned to Antipathidae. We described three new genera, *Multilobopathes* **gen. nov.**, *Papillopathes* **gen. nov.**, and *Opreskopathes* **gen. nov.**, to accommodate species previously assigned to *Antipathes* Pallas, 1766, including newly discovered taxa from the Red Sea. *Antipathes lentipinna* is reassigned to *Multilobopathes lentipinna* (Brook, 1889) **comb. nov.**, *Antipathes grandis* to *Papillopathes grandis* (Verrill, 1928) **comb. nov.**,

Antipathes caribbeana, *Antipathes umbratica*, and *Antipathes rubusiformis* are reassigned to *Opreskopathes caribbeana* (Opresko, 1996), *Opreskopathes umbratica* (Opresko, 1996), and *Opreskopathes rubusiformis* (Warner & Opresko, 2004) **comb. nov.**, respectively. Finally, four new species, *Multilobopathes ornatus* **sp. nov.**, *Multilobopathes intricatus* **sp. nov.**, *Multilobopathes densispinosus* **sp. nov.**, and *Stichopathes arenicola* **sp. nov.**, are described from the Red Sea. Our results provide the first step towards a comprehensive revision of the diversity and distribution of the order Antipatharia.

Key words: Anthozoa, UCE, Systematic revision, Antipathidae

Introduction

Collection-based biodiversity studies are essential to understand patterns of distribution and evolution in marine organisms (Brown 2013; McFadden *et al.* 2019). Such studies require a range of factors from genes to communities, including regional species richness, species distributions, and molecular relationships (Margules *et al.* 2002; Jenkins & Köhler 2024; O'Hara *et al.* 2025). However, one of the main challenges in the exploration of marine biodiversity is the significant bias in sampling efforts towards shallow, more easily accessible waters (Hendriks *et al.* 2006; Bridge *et al.* 2013; Brandt *et al.* 2016), leading to limited understanding of marine habitats below the reach of SCUBA diving (Danovaro *et al.* 2017). Consequently, knowledge of the diversity and evolution of many marine groups, especially those that are most taxonomically diverse in deeper habitats, like black corals, remains incomplete (Danovaro *et al.* 2010; Costello & Chaudhary 2017; Tapia-Guerra *et al.* 2021).

Black corals (Hexacorallia: Anthozoa: Antipatharia) are sessile colonial invertebrates with a cosmopolitan distribution (Wagner *et al.* 2012; Gaino *et al.* 2013), occurring from shallow waters to depths exceeding 8,500 m (Pasternak 1977; Molodtsova 2006; Wagner *et al.* 2012). In tropical and subtropical regions, they are more diverse and abundant at mesophotic depths (40–200 m) (Bo *et al.* 2019; Terrana *et al.* 2024; Vicario *et al.* 2024a), where, along with octocorals and stony corals, they form three-dimensional structures on the seafloor, similar in complexity to shallow-water coral reefs (Ragnarsson *et al.* 2017; Chimienti *et al.* 2025; Macrina *et al.* 2025).

Despite their ecological significance, antipatharians remain poorly understood in terms of global distribution and biodiversity. Addressing current knowledge gaps relies on the precise species delimitation (Costello *et al.* 2017; Vences *et al.* 2024), the definition of diagnostic morphological characters, and comprehensive sampling across taxa and regions. However, morphological characters traditionally used for black coral classification are subject to convergent evolution and homoplasy, and morphologically similar taxa might be phylogenetically divergent (*e.g.*, Bo *et al.* 2012; Brugler *et al.* 2013; Barrett

et al. 2020; Terrana *et al.* 2024; Vicario *et al.* 2024a). Molecular phylogenetics has repeatedly highlighted the incongruence of morphology-based Antipatharia taxonomy and systematics (*e.g.*, Brugler *et al.* 2013; Bo *et al.* 2018; Horowitz *et al.* 2020; 2022), yet a comprehensive taxonomic revision of the order has not been undertaken, as opposed to, among cnidarians, the order Scleractinia (Kitahara *et al.* 2016) or the class Octocorallia (McFadden *et al.* 2022). Six out of nine families of black corals are polyphyletic and progress in addressing these issues has been limited by the lack of resolution of traditional molecular markers, the lack of type material genetic data, and an overall insufficient number of sequenced specimens from few localities.

One of the regions that are still relatively understudied is the Red Sea (Berumen *et al.* 2013; Cochran *et al.* 2024), a narrow and young basin known for its high marine biodiversity and significant rates of endemism at the outskirts of the larger Indo-Pacific (DiBattista *et al.* 2016a; 2016b, Berumen *et al.* 2019). Red Sea organisms have adapted to survive in warm conditions from shallow to deep waters, where temperatures stabilize at 21°C below 200 m depth (Sofianos & Johns 2007; Roder *et al.* 2013), and the environment is characterized by oligotrophy, hypersalinity, limited oxygen availability and favourable conditions for calcifying organisms (Roder *et al.* 2013; Qurban *et al.* 2014).

The assessment of black coral fauna inhabiting the Red Sea has only recently gathered momentum (Chimienti *et al.* 2022; 2025; Vicario *et al.* 2024a; 2024b), revealing that antipatharians in the basin are abundant and diverse. Based on the sequencing of three mitochondrial regions, Vicario *et al.* (2024a) identified 11 genera across five antipatharian families—Antipathidae Ehrenberg, 1834; Aphanipathidae Opresko 2004; Myriopathidae Opresko 2001; Pteridopathidae Horowitz, 2026; Schizopathidae Brook, 1889—and provided the first molecular assessment of the order in the northern Red Sea and Gulf of Aqaba covering 4–627 m depth.

The family Antipathidae was the most abundantly sampled, and the most diversified one, and remains to date the most species-rich globally, including nine genera and 124 accepted species, and accounting for the 40.9% of the order's species diversity (Daly *et al.* 2007; Bo 2008). This family was the first to be described within the order Antipatharia, and historically included taxa with a wide range of morphologies, including branched and unbranched colony forms, and a remarkable diversity of spine shapes and surface ornamentations (Opresko 2001). An early attempt to subdivide the family Antipathidae was made by Roule (1905), who proposed the family “Stichopathidès” (Stichopathidae) to accommodate the unbranched genera *Stichopathes* Brook, 1889 and *Cirripathes* de Blainville, 1830, which he observed as morphologically distinct from the branched forms of Antipathidae. However, Roule's classification was overlooked by subsequent authors, and the family Stichopathidae was eventually synonymized with Antipathidae, and forgotten in the taxonomic literature since its original description. Although subsequent revisions by Opresko (2001–2006) reallocated several

Antipathidae taxa to newly established families and genera, the group remains morphologically heterogeneous, poorly defined, and taxonomically challenging.

From a systematic perspective, the morphological traits historically used to delineate taxa within Antipathidae have proven to be of limited phylogenetic value (Bo *et al.* 2012; 2018). Molecular studies have revealed the polyphyletic nature of the family, indicating that no clear genetic boundaries exist among several of its genera as currently described (*e.g.*, Brugler *et al.* 2013; Horowitz *et al.* 2022; 2023; Vicario *et al.* 2024a). Most notably, the family's type species, *Antipathes dichotoma* Pallas, 1766, appears to be more closely related to taxa in the family Aphanipathidae than to other members of Antipathidae (*e.g.*, Bo *et al.* 2018; Horowitz *et al.* 2024). Moreover, single-stem genera within Antipathidae, namely, *Cirripathes*, *Pseudocirripathes* Bo & Bavestrello, 2009, and *Stichopathes* are also polyphyletic (*e.g.*, Brugler *et al.* 2013; Horowitz *et al.* 2022; Vicario *et al.* 2024a). In fact, species of the genera *Cirripathes* and *Stichopathes* are closely related to branched species within the Antipathidae, while *Pseudocirripathes* species are closer to branched species in the Aphanipathidae (*e.g.*, Bo *et al.* 2012; Brugler *et al.* 2013; Terrana *et al.* 2024). This suggests that unbranched forms have independently evolved across different lineages several times over the evolutionary history of the order, and that this character alone is insufficient to diagnose a genus. Despite all these lines of evidence, a comprehensive taxonomic revision of the family is still pending.

In recent years, the use of genome-wide sequencing methods has been increasingly employed to solve long lasting taxonomic uncertainties in Anthozoans (Quattrini *et al.* 2018; 2020; McFadden *et al.* 2021), and in the order Antipatharia (Barrett *et al.* 2020; Horowitz *et al.* 2022; 2023). In this context, target capture enrichment of ultraconserved elements (UCEs) and exons represents a valuable option, supporting comprehensive evolutionary analyses ranging from deep divergences to fine-scale phylogenies (Horowitz *et al.* 2022; Bridge *et al.* 2023; Macrina *et al.* 2026), and allowing to retrieve good quality data also when working with highly degraded DNA (Blaimer *et al.* 2016; Ruane & Austin 2017), such as those obtained from museum specimens (including type material) not originally preserved for genetic studies (Hawkins *et al.* 2016; McCormack *et al.* 2016; Ruane & Austin 2017; Connelly *et al.* 2024).

This study provides a first broad molecular assessment of the order Antipatharia based on UCEs. The resulting phylogenomic analysis supports the resurrection of the family Stichopathidae, corroborated by molecular data from its type species, *Stichopathes pourtalesi* Brook, 1889 and morphological data. We provide a revised diagnosis for the family, describe three new genera and four new species, and reallocate five species previously assigned to the genus *Antipathes* Pallas, 1766 to the newly described genera based on morphological and/or molecular analyses of type material. This work is based on an extensive collection of a total of 107 specimens, including 70 gathered from broad latitudinal and bathymetric ranges

in the Saudi Arabian Red Sea, 18 from three localities in the Indo-Pacific Ocean (Madagascar, Réunion Island, and French Polynesia), two from one locality in the Atlantic Ocean (Cabo Verde), as well as 17 museum the Natural History Museum, UK (NHMUK), and the Museum of Comparative Zoology (MCZ) at Harvard University, Cambridge, MA. Together these specimens encompass ten ecoregions worldwide.

Materials and Methods

Coral sampling and collection

A total of 70 black coral specimens were collected from the Saudi Arabian Red Sea, from 3 to 623 m depth, between 2020 and 2023, including photic (< 40 m; $N = 31$), mesophotic (40 to 200 m; $N = 31$), and aphotic (> 200 m; $N = 6$) depths (Fig. 1, Table S1). Additionally, 20 colonies were collected in shallow waters at three localities in the Indo-Pacific Ocean, namely Madagascar ($N = 11$; from 2 to 13 m depth), Réunion Island ($N = 4$; from 14 to 26 m depth), and French Polynesia ($N = 3$; from 10 to 12 m depth), and one locality in the Atlantic Ocean, Cabo Verde ($N = 2$, from 14 to 15 m depth) (Fig. 1, Table S1). Sampling in the Saudi Arabian Red Sea took place during different oceanographic expeditions, namely the Red Sea Deep Blue (RSDB) in October 2020, the Red Sea Decade (RSDE), and Relationships Cultivation (RC) expeditions from February to June 2022, conducted aboard the R/V *OceanXplorer* (Marshall Islands), and the M193 REPLENISH expedition in September–October 2023 aboard the R/V *Meteor* (Germany; Lüdmann *et al.* 2023). The collection of black coral colonies and *in situ* imaging methods, including SCUBA diving, ROV, and submersible operations that occurred aboard the R/V *OceanXplorer* are detailed in Vicario *et al.* (2024a). Onboard the R/V *Meteor*, ROV surveys and specimen collection were conducted using the *MARUM-Squid* ROV of Bremen University, a light work-class ROV (SAAB Seaeye, UK) rated to 2,000 m depth. The ROV was equipped with a SULIS Z70 camera (\$K UHD, 30 fps, 12x optical zoom), and an HD Lookdown camera for quasi-vertical seafloor monitoring, and an IMECO TIGERSHARK camera (14 megapixels) for high-resolution still imaging. Two Imenco Dusky Shark line lasers projected parallel beams at 10 cm spacing for size reference. Specimens were collected using a Schilling Orion 7P hydraulic manipulator.

Additionally, black coral colonies were collected via SCUBA diving in October 2020 as part of the RSDB expedition in the Gulf of Aqaba and northern Red Sea, between September 2021 and November 2023 from the northern and central Saudi Arabian Red Sea, in July 2022 in Cabo Verde during the mission DISCOVER aboard the R/V *ANTEA*, (France) in August 2023 from French Polynesia during the mission ICONIC aboard the R/V *ANTEA*, and in March 2024 from Réunion Island and Madagascar. The collected colonies were processed aboard the research vessels or immediately upon returning to shore if collected during single-day sampling trips. The apical portion (~10 cm) of each colony branch was

preserved in 99% ethanol for subsequent DNA extraction and molecular analyses. The remaining portion of the colony (if available) was air-dried.

Our collection also comprises subsamples from 17 black coral specimens housed at the NMNH, one at the NHMUK, and one at the MCZ (Fig. 1), encompassing both type and non-type material collected between 1879 and 2018 from various ecoregions worldwide (Fig. 1). These specimens were preserved either dry or in 70–95% ethanol. Metadata for these specimens is provided in Table S1.

Morphological analyses

The preparation of newly collected specimens for imaging and morphological analyses followed the protocols outlined in Vicario *et al.* (2024a). The skeletal elements of the specimens housed at the NMNH were coated with a 30–40 nm layer of gold 60% and palladium 40% and imaged using a Zeiss EVO MA 15 Scanning Electron Microscope (SEM). Measurements of spines and polyps were conducted as described in Terrana *et al.* (2020). Specifically, ‘spine height’ was measured as the distance between the apex and the center of the spine base, and ‘spine spacing’ was taken between the tips of adjacent spines in the same axial row. The ‘number of spine rows’ was determined in frontal view, counting only the rows in which the spine bases were visible. ‘Polyp transversal diameter’ was measured from the distal to the proximal lateral tentacle, and ‘polyp spacing’ was measured from the edge of the distal lateral tentacles of one polyp to the edge of the proximal lateral tentacles of the adjacent one. Diameters of the stem, branches, and branchlets (herein defined as the highest order branches) were measured including the spines, except when measurements were taken from SEM images, in which case spines were not considered. Measurements were performed using ImageJ 1.53t (Schneider *et al.* 2012).

Coral identification

Identification at the species level was based on colony, polyp, and skeletal morphological traits, following original descriptions, type material, and taxonomic literature including Dana 1846; Brook 1889; Schultze 1896; Roule 1902; Cooper 1903; 1909; Roule 1905; van Pesch, 1910; 1914; Verrill 1928; Opresko 1996; 2009; Warner & Opresko 2004; Terrana *et al.* 2024. Type specimens of *Antipathes*, *Cirrhipathes*, and *Stichopathes* preserved in the collections of the NMNH and Naturalis Biodiversity Center (RMNH, Leiden, the Netherlands) were examined and photographed during museum visits to support the identification of collected material. In addition, type material of *Antipathes rubusiformis* Warner & Opresko 2004 and *Stichopathes pourtalesi* was inspected and imaged at the NHMUK and MCZ, respectively.

DNA extraction, purification and quantification

Genomic DNA from ethanol-preserved coral samples was extracted using the DNeasy® Blood and Tissue Kit (Qiagen Inc. Hilden, Germany) following the manufacturer’s guidelines. To address the presence of

inhibitory compounds commonly found in black corals, which can affect subsequent library preparation, the extracted DNA was further purified using a Monarch® PCR & DNA Cleanup Kit (5 µg) (New England Biolabs, Ipswich, MA, USA) following the manufacturer’s protocol. The concentration of purified DNA was quantified using a Qubit dsDNA High Sensitivity Assay Kit (Thermo Fisher Scientific, Waltham, MA, USA) with a Qubit® fluorometer (Thermo Fisher Scientific, Waltham, MA, USA). DNA quality was assessed using a Nanodrop™ 2000 C spectrophotometer (Thermo Fisher Scientific, Wilmington, DE, USA).

UCE sequencing and bioinformatics processing

DNA extracts were sent to Arbor Biosciences (ANN Arbor, MI, USA) or the iGenSeq platform (ICM, Paris, France) for library preparation and target enrichment of UCE/exon loci using the hexa-v2-scleractinia bait set (Cowman *et al.* 2020). Libraries were then PE150 sequenced with an Illumina NovaSeq 6000 (Illumina, San Diego, CA) following the protocols detailed in Quattrini *et al.* (2018). Library preparation for samples USNM 1106208, USNM 1122627, USNM 1665782, USNM 43443, USNM 1484548 were prepared at half the recommended reaction volume using the New England Biolabs (Ipswich, MA, USA) Next Ultra II FS DNA Library Prep kit with incubation times of either 7.5 or 8.5 mins for enzymatic shearing. Bead cleanups were performed using KAPA pure beads (Roche Diagnostics, Indianapolis, IN, USA) and an Opentrons robot with a bead ratio of 0.8X (Long Island City, NY, USA). Using Y-yoke adapter sequences, samples were indexed with unique combinations of iTru i5 and i7 barcode indices before pooling (Glenn *et al.* 2019). Sequencing was performed on an Illumina NovaSeq X Plus at the Oklahoma Medical Research Foundation Genomics Facility with other samples to obtain 10M paired-end (PE) reads (150 bp) per sample.

Raw sequences reads from 107 newly generated and 77 publicly available UCE sequences from the NCBI Sequence Read Archive (<https://www.ncbi.nlm.nih.gov/sra>) from Horowitz *et al.* (2022; 2023) and Quattrini *et al.* (2018; 2023) underwent quality assessment using FastQC v0.11.8 (<http://www.bioinformatics.babraham.ac.uk/projects/fastqc/>) and MultiQC v1.9 (Ewels *et al.* 2016) both before and after the removal of adapter contamination and low-quality bases. This pre-processing step was carried out using cutadapt v2.1 (Martin 2011), available in the wrapper script Trim Galore! v0.6.10 (http://www.bioinformatics.babraham.ac.uk/projects/trim_galore/). Subsequently, trimmed reads were *de novo* assembled using SPAdes v3.15.5 (Bankevich *et al.* 2012). Post-trimming analyses were performed following the guidelines outlined in the Phyluce documentation, available online at <https://phyluce.readthedocs.io/en/v1.6.8/tutorial-one.html>.

Phylogenomic analyses

Phylogenomic analyses were conducted by running Maximum Likelihood (ML) analyses on three distinct datasets. To infer higher-level phylogenetic relationships

within the order Antipatharia, we first reconstructed a phylogenomic tree using a dataset encompassing all families within the order. The dataset included a total of 67 specimens, comprising previously published data from 60 specimens and seven newly produced (Table S2). The recovered loci were aligned and filtered into a 50% sample occupancy matrix. The resulting phylogeny was rooted to Leiopathidae Haeckel, 1896. Based on the results of the previous phylogenomic reconstruction (see above) a second analysis focusing on specimens identified as belonging to clade aff. Antipathidae 1 was performed. This dataset comprised 124 specimens, including 19 previously published and 105 newly generated for this study (five of which were also included in the previous dataset). The recovered loci were aligned and filtered into 55% and 70% sample occupancy matrices. The phylogenomic reconstructions were rooted to *Blastopathes medusa* Horowitz, 2020.

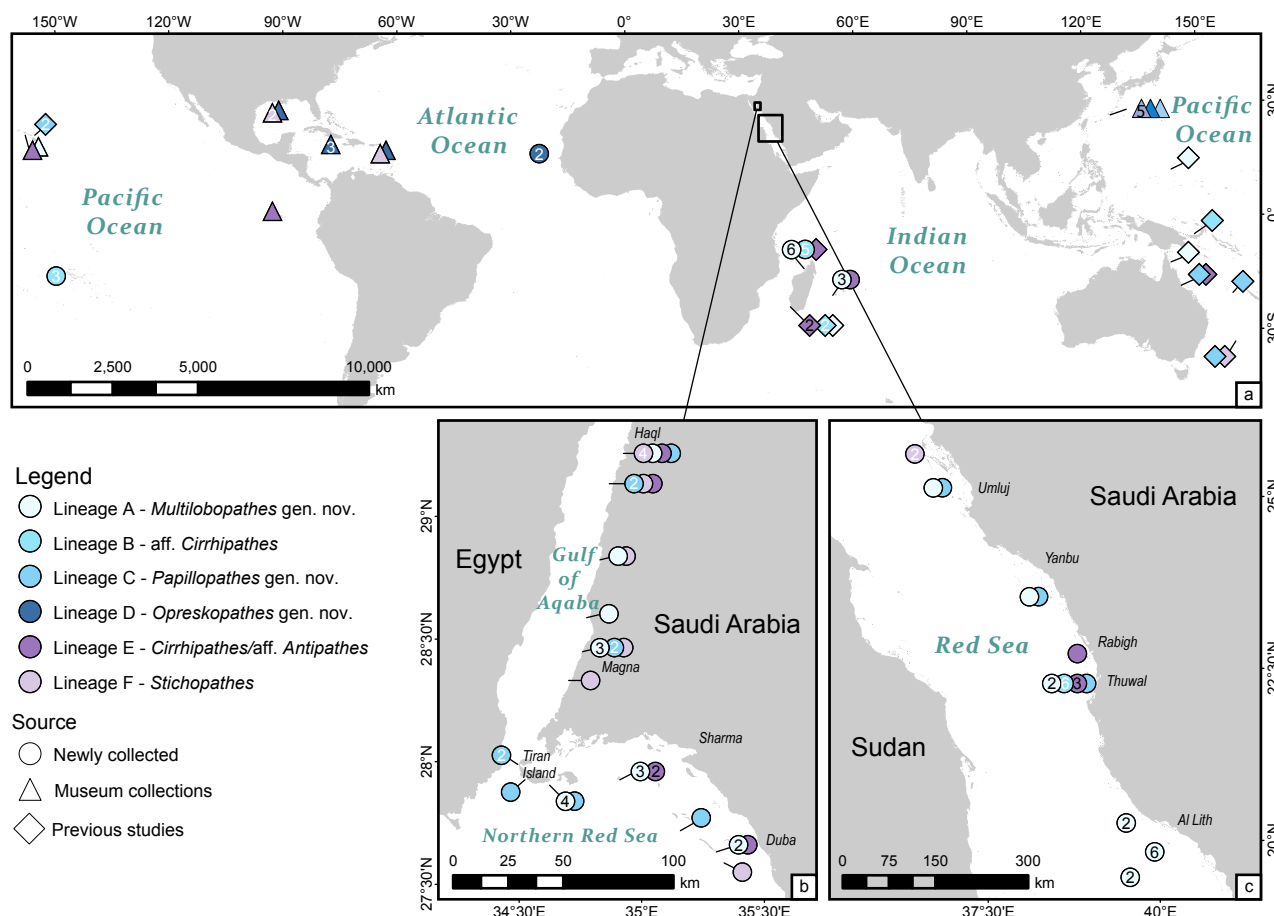
Using the 43 loci successfully recovered from the lectotype of *Stichopathes pourtalesi*, the type species of the genus *Stichopathes*, we conducted a separate phylogenetic analysis to verify its phylogenetic position. The recovered loci were extracted and aligned alongside homologous loci from 63 representative taxa within the

clade aff. Antipathidae 1 to ensure direct comparability. The resulting phylogenomic reconstruction was rooted to *Blastopathes medusa*.

For each analysis, filtered loci were combined into a single partitioned alignment. ML phylogenetic reconstructions were conducted using IQTREE v2.0.5 (Nguyen *et al.* 2015) and 1,000 ultrafast bootstrap replicates (Minh *et al.* 2020). ModelFinder (Kalyaanamoorthy *et al.* 2017) was used to determine the optimal model scheme for each UCE/exon partition. Ultrafast bootstrap support approximation, gene concordance factor (gCF), and site concordance factors (sCF) were calculated across the phylogeny using IQ-TREE v2.0.5. Specifically, gCF quantifies the proportion of decisive gene trees supporting a given branch (Lanfear & Hahn 2024), while sCF measures the proportion of informative sites supporting the corresponding quartet topology. Raw sequence data are deposited in the NCBI Sequence Read Archive database (BioProject IDs PRJNA1348881, PRJNA1043120, PRJNA644402).

Mitochondrial markers amplification and sequencing

To complement the UCE dataset, and to provide single



marker publicly available genetic data for future comparative studies, two mitochondrial genetic markers were amplified for newly collected taxa: *trnW-IGR-nad2* (*IgrW*) and *nad5-IGR-nad1* (*IgrN*). Polymerase chain reactions (PCRs), purification, and Sanger sequencing followed the protocol described in Vicario *et al.* (2024a). Additionally, the cytochrome *c* oxidase subunit I (COI) marker was recovered from the UCE assemblies. For each sample, the contigs assembled *de novo* with SPAdes v3.15.5 (see “UCE sequencing and bioinformatics processing”) were searched against a set of antipatharian COI reference barcodes using BLASTn (discontiguous megablast; BLAST v2.16.0; Camacho *et al.* 2009). Hits with an aligned length >200 bp and >80% identity were retained, and the single longest matching region per sample was extracted as the COI sequence using samtools faidx v1.16.1 (Danecek *et al.* 2021). To place the newly recovered sequences in a broader context, 215 publicly available antipatharian COI sequences were downloaded from GenBank. The combined dataset of 256 sequences was aligned with MAFFT v7.505 (Katoh & Standley 2013). The alignment was inspected and trimmed to remove poorly aligned terminal regions. A ML phylogenetic tree was inferred with IQ-TREE v2.0.5 (Nguyen *et al.* 2015) under the best-fit model selected by ModelFinder (Kalyaanamoorthy *et al.* 2017), with node support assessed by 1,000 ultrafast bootstrap replicates (Hoang *et al.* 2018). All newly generated sequences were deposited in GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>), with accession numbers listed in Table S2.

Results

Antipatharia morphological identification

Based on morphological characters, examination of type material, and original descriptions, the 124 Antipatharia specimens included in this study (105 unpublished, and 19 previously published) were assigned to the genera *Antipathes*, *Cirrhopathes*, and *Stichopathes*. Of these, 19 newly collected specimens from the Red Sea were assigned to three valid species (Table S1), while for 35 specimens that were retrieved from museum collections or previously published, we kept their original identification and confirmed it when possible (Table S1).

For the remaining 23 newly collected specimens that closely resembled nominal species but could not be confidently identified due to either a lack of available type material or considerable distance between the collection site and the type locality, the “cf” qualifier was used (Table S1). These included *Stichopathes* cf. *contorta*, *S.* cf. *desaturata*, and *S.* cf. *maldivensis*. Finally, 48 newly collected specimens representing 12 morphospecies did not match previous original descriptions of nominal species and were provisionally designated as *Antipathes* sp. 1, *Cirrhopathes* spp. 1–5, and *Stichopathes* spp. 1–7 (Table S1).

Phylogenomic results

Three datasets have been generated to investigate phylogenomic relationships within the order Antipatharia, with particular focus on the family-level clade aff. Antipathidae 1 and the placement of the genus *Stichopathes*.

Dataset 1: Family-level relationships within the order Antipatharia (Fig. 2)

This first dataset including 67 representatives of all families within the order Antipatharia yielded a total of 265,710,933 raw reads, and between 41,847 and 28,456,527 raw reads per sample (Table S2). After quality control and adapter trimming, an average of $4,002,586 \pm 5,857,197$ SD high-quality reads per sample was retained (Table S2). Reads were *de novo* assembled with SPAdes, producing contigs with an average length of 500.7 ± 358.4 SD base pairs (Table S2). Target enrichment recovered 230 to 1,474 loci per sample (Table S2), with an average of 683.10 ± 202.70 SD unique loci per sample. The recovered loci were aligned and filtered into a 50% sample occupancy matrix, that comprised 778 loci resulting into a concatenated alignment of 190,863 bp. The alignment had an average of 92.0 ± 49.1 SD parsimony informative sites per locus.

The best-fit substitution model selected through ModelFinder for this dataset was TIM2+F+I+G4. The resulting ML tree recovered strong support for the division of Antipatharia into 16 major clades (Fig. 2) fully supported by ultrafast bootstrap, gene concordance factor and site concordance factor supports (Fig. S1). Of these, five clades included material assigned to the family Aphanipathidae ($N = 9$), while a single clade was recovered for each of the families Myriopathidae ($N = 10$), Stylopathidae Opresko, 2006 ($N = 3$), Pteridopathidae ($N = 4$), Ameripathidae Opresko & Horowitz, 2024 ($N = 2$), Schizopathidae Brook, 1889 ($N = 13$), Cladopathidae Kinoshita, 1910 ($N = 2$), and Leiopathidae ($N = 2$) (Figs. 2, S1). However, including more samples representing these families might reveal their polyphyly (Brugler *et al.* 2013; Horowitz *et al.* 2022). Material currently assigned to the family Antipathidae ($N = 22$) was instead retrieved across five well-supported, highly divergent clades: aff. Antipathidae 1, aff. Antipathidae 2, aff. Antipathidae 3, aff. Antipathidae 4/Aphanipathidae (including material originally assigned to both Antipathidae and Aphanipathidae), and Antipathidae (Fig. 2). Notably, material assigned to the type species of the family Antipathidae, *Antipathes dichotoma*, clustered within Antipathidae (Fig. 2), suggesting that it should represent the true position of the family and that other clades including material identified as *Antipathes* are in need of revision.

The aff. Antipathidae 1 clade clustered specimens traditionally assigned to *Antipathes*, *Cirrhopathes*, and *Stichopathes* (Fig. 2), while aff. Antipathidae 2 clustered material identified as *Blastopathes* Horowitz, Brugler, Bridge & Cowman, 2020. aff. Antipathidae 3 included specimens identified as *Antipathes* (Fig.

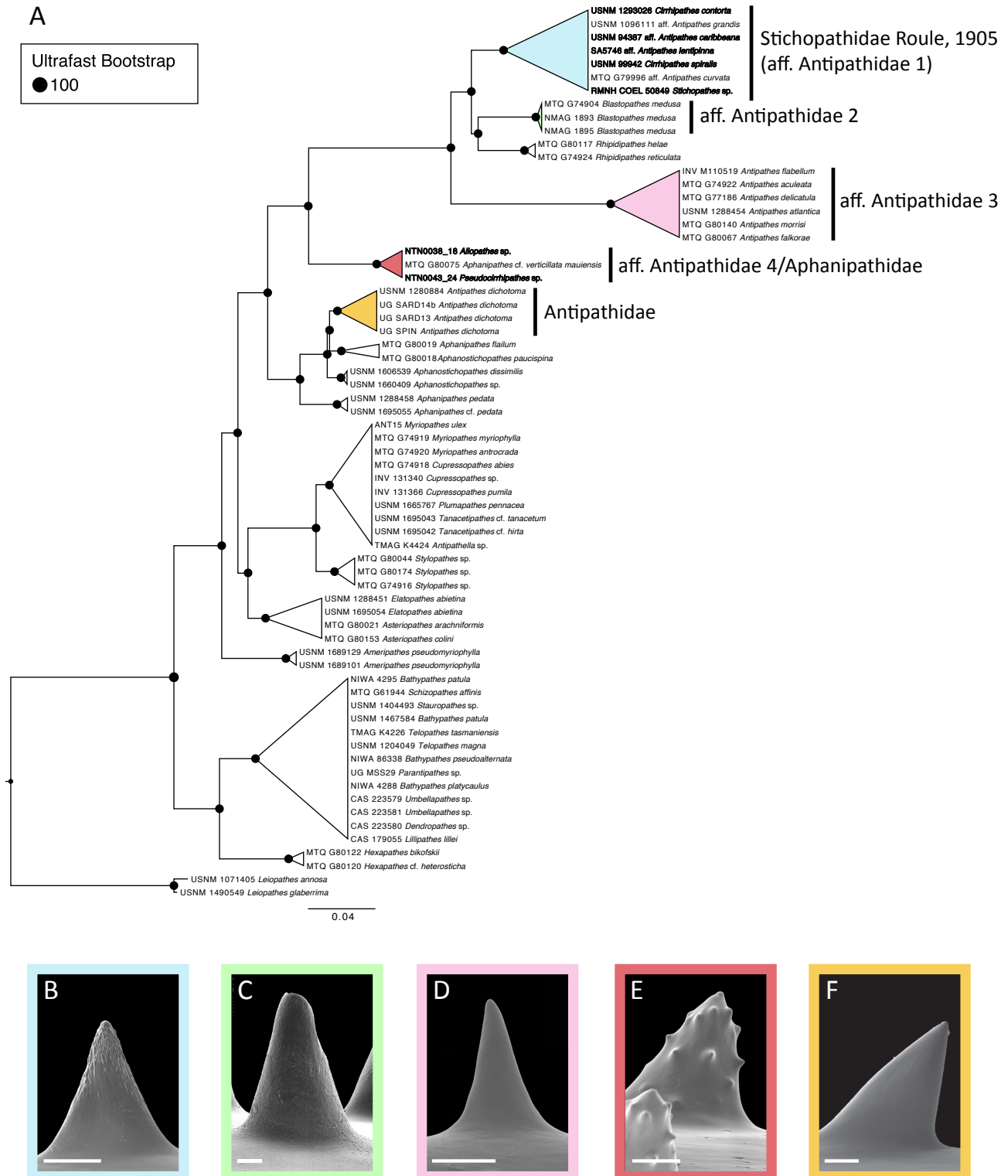


FIGURE 2. (A) IQTree Maximum Likelihood phylogenomic tree of 67 Antipatharia specimens inferred from a concatenated alignment of 778 UCE and exon loci (50% sample occupancy matrix). Colored triangles represent lineages containing specimens of the family Antipathidae. White triangles indicate lineages not including specimens belonging to the family Antipathidae. Sequences in bold are newly produced. Node circles represent ultrafast bootstrap supports. Panels (B-F) report Scanning Electron Microscopy pictures of specimens spines (scale bars: 50 μ m). Color-codes correspond to lineages as per (A). (B) Polypar spine of RMNH.COEL.50849 in distal section, (C-F) polypar spine on terminal branch of: (C) MTQ G74906, (D) NHMT-R2E2064.4, (E) NTN0038_18, and (F) USNM 1280884. The spine images in panels C and D are sourced from Fig. 6A in Horowitz *et al.* (2020) and Fig. 3h in Terrana *et al.* (2024), respectively. A version of the tree showing ultrafast bootstraps, gene concordance factor, and site concordance factor supports is provided in Fig. S1

2), and aff. Antipathidae 4/Aphanipathidae comprised material assigned to *Allopathes* Opresko & Cairns, 1994, *Pseudocirripathes*, and *Aphanipathes* Brook, 1889.

Dataset 2: Complete phylogenomic reconstruction within the family-level clade aff. Antipathidae 1 (Fig. 3)

The second dataset included all specimens bearing papillose spines and having a non-pinnulate corallum, characters that have been found diagnostic of clade aff. Antipathidae 1. This yielded a cumulative total of 518,645,335 raw reads, with between 33,928 and 45,345,421 raw reads per sample (Table S2). After quality control and adapter trimming, an average of $4,141,980 \pm 5,743,444$ SD high-quality reads per sample was retained. Reads were *de novo* assembled with SPAdes, producing contigs with an average length of 326.54 ± 83.92 SD base pairs. Target enrichment recovered 162 to 1,181 loci per sample (Table S2), with an average of 624.40 ± 135.30 SD unique loci per sample. The recovered loci were aligned and filtered into 55% (Fig. 3, S2) and 70% (Fig. S3) sample occupancy matrices. The 55% matrix comprised 493 loci concatenated into an alignment of 151,446 base pairs. The alignment had an average of 83.9 ± 27.0 SD parsimony informative sites. The 70% matrix retained 142 loci for a final alignment length of 46,840 base pairs, with an average of 83.3 ± 26.5 SD parsimony informative sites.

The resulting phylogenomic reconstructions were conducted with the 55% and 70% matrices using IQTree, with the best substitution model being TPM3+F+I+G4 for both. The phylogeny reconstructed using the 55% matrix recovered higher support values. Hereafter, we discuss only results for the 55% matrix (Fig. 3, S2; but see Fig. S3 for the phylogenomic reconstruction with the 70% data matrix). Six well-defined genus-level lineages (A–F), all supported by 100% Ultrafast Bootstrap values (Fig. 3), high site concordance factors (sCF > 50; except lineage E, sCF > 34), and moderate to high gene concordance factors (gCF > 50 for lineages B and D; gCF > 10 for lineages A, C, E, and F; Fig. S2) were identified, comprising a total of 32 well supported lineages (nine within lineage A, three within B, four within lineage C, five within lineage D, seven within lineage E, and four within lineage F). Specimens identified as *Stichopathes* based on the genus' diagnostic morphological characters were distributed across 14 lineages (cl. A1, A2, A5, A6, A9, C14–C16, D20, D21, F29–F32). Similarly, material morphologically identified as *Cirripathes* was recovered in eight well-supported lineages (lineages B10–B12, E22–E24, E27, E28). Finally, *Antipathes* specimens were distributed among nine lineages (lineages A3, A4, A7, A8, C13, D17–D19, E25, E26) (Fig. 3). Collectively, these results indicate that the three genera *Antipathes*, *Cirripathes* and *Stichopathes* are polyphyletic. Although the type material of *S. pourtalesii* could not be confidently analysed within this dataset (but see dataset 3), a specimen collected near the *S. pourtalesii*

type locality (USNM 1222140) and showing diagnostic morphological features consistent with the type (Fig. 8) (thus being a potential topotype), clustered within lineage F32. This suggests that other lineages currently including material identified as *Stichopathes* but not closely related to this lineage, represent distinct taxa in need of formal taxonomic reassessment (namely cl. A1, A2, A5, A6, A9, C14–C16, D20, D21).

The type material of the type species of the genus *Cirripathes* (*C. spiralis* (Linnaeus, 1758)) is currently considered lost. However, in the present analysis, a specimen housed at the NMNH and identified as *C. spiralis* (USNM 99942), displaying morphological characters consistent with the original description, was recovered within lineage E27. Consequently, material morphologically assigned to *Cirripathes* but clustering in distinct genus-level lineages (cl. B10–B12) (Fig. 3) is herein provisionally referred to as aff. *Cirripathes* to reflect uncertain placements.

The genus-level lineage A, which included *Stichopathes* cf. *maldivensis* (cl. A1), *S. cf. flagellum* (cl. A2), *Antipathes lentipinna* Brook, 1889 (cl. A3), *A. fruticosa* Gray, 1857, *A. griggi* Opresko, 2009 (cl. A4), *Stichopathes* spp. (cl. A5–A6, A9), *Antipathes* sp. (cl. A7), and *A. cf. spinulosa* (cl. A8), was not closely related to either the *Stichopathes* lineage (cl. F32; Fig. 3) or the *Antipathes* lineage (Antipathidae; Fig. 2). This phylogenetic placement, combined with consistent morphological characters (see morphological results), supports the formal establishment of an undescribed genus.

The genus-level lineage C, comprising material ascribed to *Antipathes grandis* (cl. C13), *Stichopathes* cf. sp. 1 (cl. C14), *S. cf. desaturata* (cl. C15), and *S. sp. 3* (cl. C16) (Fig. 3), was neither closely related to the *Stichopathes* lineage (cl. F32; Fig. 3) nor to the *Antipathes* lineage (Antipathidae; Fig. 2). Therefore, this result and consistent morphological characters (see morphological results) within the lineage in exam, support the establishment of a new genus.

A further distinct genus-level lineage (D) including material morphologically identified as *Antipathes* and *Stichopathes*, included *A. caribbeana* Opresko, 1996 (cl. D17), *A. umbratica* Opresko, 1996 (cl. D18), *A. rubusiformis* (cl. D19), *S. sp. 1* (cl. D20), *S. sp. 2* (cl. D21) was not closely related to the lineages including their respective type species. This group is hereafter ascribed to a new genus (Fig. 3).

The distinct lineage E comprised material currently assigned to both *Cirripathes* and *Antipathes* (cl. E22–E28) (Fig. 3). Specimens attributed to *Cirripathes* were distributed across multiple divergent lineages, including *C. sp. 1* (cl. E22), previously published material identified as *C. contorta* van Pesch, 1910 and *C. densiflora* Silberfeld, 1909 together with a newly generated sequence from the Red Sea (*C. sp.*, cl. E23), and additional NMNH material previously identified as *C. anguina* (Dana, 1846), *C. contorta*, *C. cf. contorta* and *C. propinqua* Brook, 1889 (cl. E24) (Fig. 3). *Cirripathes spiralis*, the genus type species, clustered in lineage E27, while *C. sp. 2* (cl. E28) consisted exclusively of newly

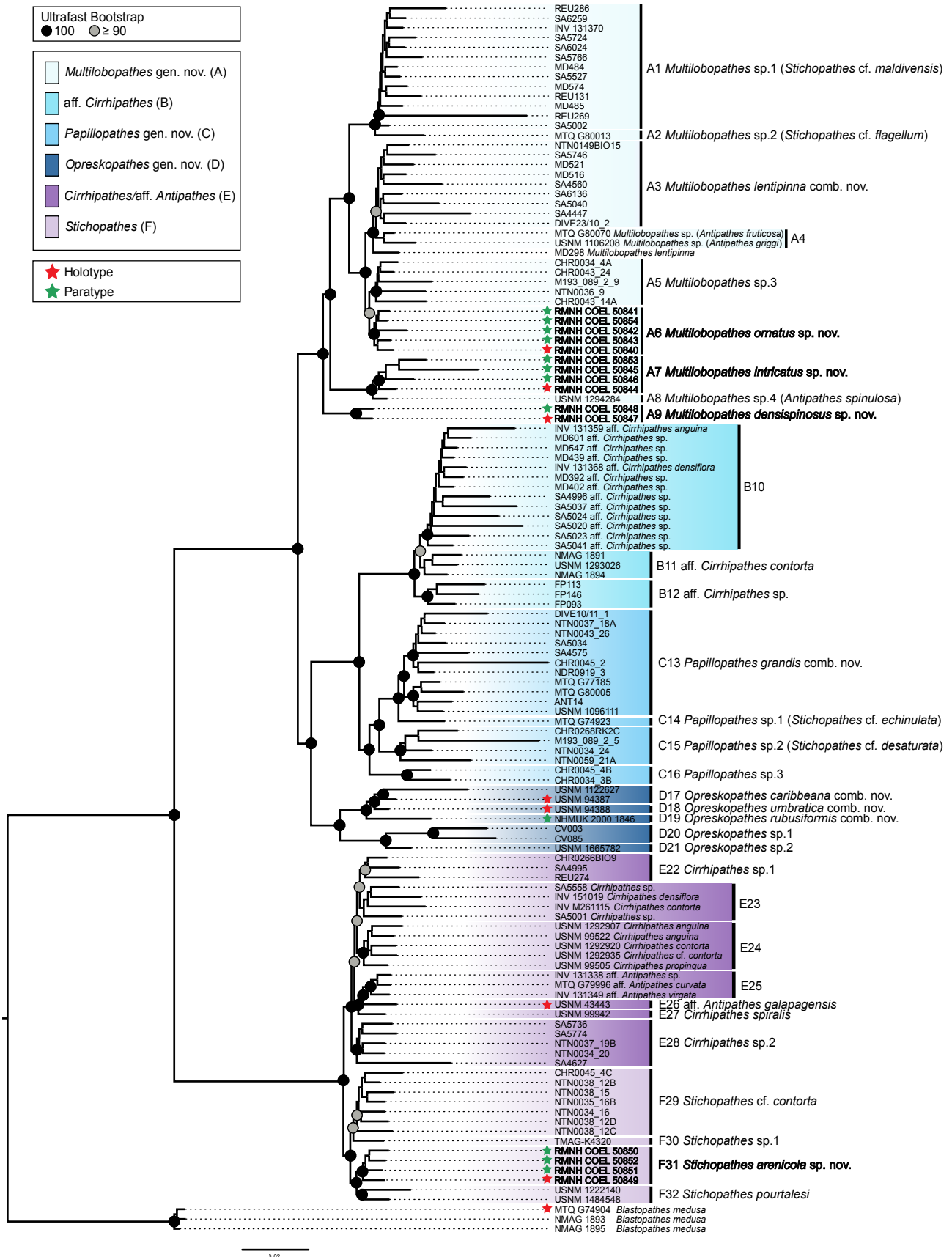


FIGURE 3. IQTree Maximum Likelihood phylogenomic tree of 123 Stichopathidae specimens inferred from a concatenated alignment of 493 UCE and exon loci (55% sample occupancy matrix). Node circles represent ultrafast bootstrap supports. The star symbol after the specimen name represent type material. The newly described species from this study are reported in bold. Names shown in brackets indicate the original species-level identifications prior to the present taxonomic revision. A version of the tree showing ultrafast bootstraps, gene concordance factor, and site concordance factor supports is provided in Fig. S2.

sequenced Red Sea material (Fig. 3). Notably, material identified as *Antipathes* spp. was also recovered in two sister lineages within this lineage: lineage E25, which included previously published specimen identified as *A. curvata* van Pesch, 1910, *A. cf. virgata*, and *A. sp.*, and lineage E26, which contained the specimen of the holotype of *A. galapagensis* Deichmann, 1941 (Fig. 3). However, *A. dichotoma* (the type species of *Antipathes*) was recovered far outside these lineages, meaning that the taxonomy of these species warrants re-evaluation. Accordingly, all specimens previously identified as *Antipathes* spp. within this lineage are herein provisionally referred to as aff. *Antipathes* (Fig. 3).

Lastly, the genus-level lineage F, comprising material ascribed to *Stichopathes*, included *S. cf. contorta* (cl. F29), *S. sp.* (cl. F30), *S. sp. 7* (cl. F31), and *S. pourtalesi* (cl. F32) (Fig. 3).

Dataset 3: Confirmation of the placement of *Stichopathes* (Fig. S4)

A third dataset was produced to verify the position of the lectotype of the type species of the genus *Stichopathes*, i.e., *S. pourtalesi*. This included representative taxa within the clade aff. Antipathidae 1 (Table S2) and yield a cumulative total of 365,179,254 reads for the dataset, with the total number of raw reads generated per sample ranging from 468,195 to 45,345,421 (Table S2). After quality control and adapter trimming, an average of $5,016,319.02 \pm 7,740,479.18$ SD high-quality reads per sample was retained. Reads were *de novo* assembled with SPAdes, producing contigs with an average length of 336.6 ± 80.3 SD base pairs. The resulting analysis comprised 32 loci shared across all samples, into a 9,809 bp alignment. The alignment had an average of 53.8 ± 36.9 SD parsimony informative sites.

The best-fit substitution model for this analysis was K2P+R3. In this analysis, *S. pourtalesi* was recovered within the family-level clade aff. Antipathidae 1, supporting the resurrection of the family Stichopathidae and the reassignment of the genera *Stichopathes* and *Cirripathes* from Antipathidae (which true position is now within clade Antipathidae) to this family. Precisely, the sequence of the lectotype of *S. pourtalesi* (MCZ 90342) fell sister to a clade comprising specimens identified as *Stichopathes* spp., *Cirripathes* spp. and *Antipathes* spp. Support values were high for deep nodes but decreased at shallow nodes (Fig. S4), making the precise placement of the type species within a sublineage less reliable.

Mitochondrial COI phylogenetic reconstruction

To complement the phylogenomic dataset with a widely comparable barcoding marker, the COI was recovered from the UCE assemblies for 41 of the 117 samples (including at least two sequences per newly described species) and analysed together with 215 publicly available antipatharian COI sequences. At the family level, the resulting ML tree (Fig. S5) was largely congruent with the UCE phylogeny (Fig. 2), recovering the family-level

clade aff. Antipathidae 1 (Stichopathidae) as distinct from Antipathidae. The only notable topological inconsistency concerned Pteridopathidae, which in the COI tree was sister to the complex comprising aff. Antipathidae 1, aff. Antipathidae 2, aff. Antipathidae 3, and aff. Antipathidae 4/Aphanipathidae, whereas in the UCE phylogeny (Fig. 2) and in previous studies (e.g., Brugler *et al.* 2013; Horowitz *et al.* 2026) it was recovered as sister to Myriopathidae and Stylopathidae.

Within the family Stichopathidae support at deeper nodes was generally limited and the genus-level lineages were only partly resolved. Lineages A, B, C and D were recovered as a single clade (Fig. S5), whereas lineages E and F) formed separate clades (Fig. S5). Despite this reduced resolution, the COI data corroborated the polyphyly of *Antipathes*, *Cirripathes*, and *Stichopathes* recovered from the UCE analyses.

Morphological results

Examination of spine morphology across the five clades comprising taxa assigned to Antipathidae, as recovered in the phylogenomic reconstruction from dataset 1 (Fig. 2A), revealed diagnostic differences. Representatives of aff. Antipathidae 1 displayed papillose spines (Fig. 2B), while specimens assigned to aff. Antipathidae 2 and 3 were characterized by smooth spines (Fig. 2C, 2D). Specimens within aff. Antipathidae 4/Aphanipathidae (Fig. 2E) exhibited spines bearing tubercles and arranged in verticills (Fig. 2E), while Antipathidae (Fig. 2F) were distinguished by smooth triangular spines.

Building on the phylogenomic partitioning retrieved from the second dataset (Fig. 3), we integrated detailed morphological examination of genus-level lineages within the aff. Antipathidae 1 (Fig. 2A) lineage (A–F) (Fig. 3) to define their diagnostic traits. All lineages share the presence of papillose spines (Fig. 2B), but each is distinguished by the following unique features. The genus-level lineage A is distinguished from all the other lineages within aff. Antipathidae 1 by having secondary spines, papillose spines with apices modified on at least part of the colony, occasional presence of tubercles, a reduced interpolypar space, and a uniserial arrangement of polyps (Figs. 9, 11–22, Table 1). In addition, four species-level lineages within the genus-level lineage A (lineages A5–A7, A9), did not correspond to any currently described nominal species.

Lineage B comprised specimens tentatively assigned to aff. *Cirripathes* spp. (Fig. 3), which share the unique combination of unbranched colonies, conical, blunt and papillose spines on larger diameter sections, and polyps distributed around the stem (Figs. 23, 24, Table 1).

Specimens within the genus-level lineage C are distinct from other lineages in having simple and papillose spines combined with a uniserial arrangement of polyps (Figs. 25–27, Table 1).

Specimens within the genus-level lineage D are the only ones having extremely developed papillae resembling tubercles, and the uniserial arrangement of polyps (Figs. 28, 29, Table 1).

Material assigned to the lineage E consistently exhibited polyps occurring on multiple sides of the axis, at least in parts of the colony. However, this feature alone did not provide sufficient diagnostic evidence to justify the recognition of a separate genus (Table 1).

Lastly, in addition to molecular considerations related to the position of the lectotype of *S. pourtalesi*, examination of an NMNH specimen (USNM 122240) revealed morphological characters consistent with *S. pourtalesi*. Figure 8 present a comparison of polyp and spine arrangement between the lectotype MCZ 90342 and the schizoparalectotype MCZ 90343 (from Bo & Opresko 2015) and the NMNH specimen. Both show triangular spines with faint, fusiform papillae restricted to the spine apex, uniserial polyp arrangement, and polyps with a large transverse diameter (up to 1.7 mm in the re-diagnosis and up to 2.2 mm in the specimen examined here) (Table 1). Taken together, these lines of evidence supported the recognition of the genus-level lineage F as *Stichopathes*. Additionally, one lineage (cl. F31) within the genus-level lineage F did not correspond to any currently described nominal species.

Systematic account

Family Stichopathidae Roule, 1905

Stichopathides Roule 1905: pp. 38, 53

Antipathidae (in part), van Pesch 1914: pp. 21–23

Antipathidae (in part), Pax 1932: pp. 409–411; 444, 445

Antipathidae (in part), Opresko 2009: pp. 277–290

Antipathidae (in part), Terrana *et al.* 2020: pp. 8, 25, 37

Revised diagnosis

Corallum unbranched or branched, not pinnulate. Spines triangular, conical, or cylindrical; simple, forked or multilobed; papillose and rarely tuberculated. Polypar spines usually larger than abpolypar spines. Secondary spines can occur. In unbranched colonies, polyps either arranged uniserially, distributed in irregular rows on one side on the colony, or distributed all around the stem. In branched colonies, polyps uniserially arranged, on old branches can occur on multiple rows. In preserved material, polyps generally rounded, 0.5–2.5 mm in transverse diameter, interpolypar space 0–0.60 mm.

Type genus *Stichopathes* Brook, 1889

Included genera. *Stichopathes*, *Cirrhopathes* de Blainville, 1830, *Multilobopathes* **gen. nov.**, *Papillobathes* **gen. nov.**, *Opreskopathes* **gen. nov.**

Comparative diagnosis. The family Stichopathidae differs from other families within Antipatharia based on the combination of non-pinnulate corallum, consistently papillose spines, and polyps up to 2.5 mm in transverse diameter.

The families Ameripathidae Opresko & Horowitz, 2024, Myriopathidae, Pteridopathidae, Cladopathidae Kinoshita, 1910, and Schizopathidae are distinct from Stichopathidae by having a pinnulate corallum. In addition to sharing pinnulate branching, Ameripathidae

differs from the resurrected family by its triangular spines, which are smooth or with knob-like protuberances, and transversely elongated polyps (Horowitz *et al.* 2024). Myriopathidae is characterized by acicular, bifid, trifid or dendritic spines, with smooth or with fine-elongated papillae (Opresko 2001), and polyps not exceeding 1 mm in transverse diameter. Pteridopathidae is characterized by spines with conical tubercles and polyps up to 1 mm (Horowitz *et al.* 2026). Cladopathidae is distinguished by polyps with a transverse diameter of 2 mm or more, and smooth spines (Opresko 2003a). Schizopathidae differs in its large transversely elongated polyps (1.5–12 mm), and triangular and smooth spines (Opresko 2002). The family Stylopathidae differs in having conical, simple and smooth spines, transversely elongated polyps, and a corallum that is mostly pinnulate (Opresko 2006). Among non-pinnulate families, Leiopathidae can be distinguished by having spines with a smooth surface (Wagner & Opresko 2015), differently from the papillose spines typical observed in Stichopathidae.

Aphanipathidae is distinguished by acicular or cylindrical spines with distinct tubercles or occasionally smooth surfaces (Opresko 2004). In contrast, taxa within the Stichopathidae possess spines that are consistently papillose, only occasionally bearing tubercles.

Polyps preserved in ethanol of taxa within the Stichopathidae are generally rounded in shape, though some species exhibit transversely compressed polyps. Morphologically, these polyps resemble those of Aphanipathidae, being subequal or slightly elongated along either axis, with short, blunt, and subequal tentacles, a key trait distinguishing Aphanipathidae from Antipathidae. However, in the absence of *in situ* images to assess tentacle conditions, distinguishing this family from Aphanipathidae based solely on polyp morphology remains inconclusive. Following the present revision, Antipathidae *sensu lato* can be distinguished from Stichopathidae by the absence of papillose spines: depending on the clade, Antipathidae spines are either smooth or tuberculate and arranged in verticils. (Fig. 2; see Remarks for a detailed morphological characterization of each Antipathidae clade).

Remarks. We propose the resurrection of the family Stichopathidae to accommodate the genera *Stichopathes*, *Cirrhopathes*, three new genera formally described hereafter, namely *Multilobopathes* **gen. nov.**, *Papillobathes* **gen. nov.**, *Opreskopathes* **gen. nov.**, five species previously assigned to *Antipathes*, namely, *Multilobopathes lentipinna* **comb. nov.**, *Papillobathes grandis* **comb. nov.**, *Opreskopathes caribbeana* **comb. nov.**, *Opreskopathes umbratica* **comb. nov.**, *Opreskopathes rubusiformis* **comb. nov.**, and four new species, *Multilobopathes ornatus* **sp. nov.**, *Multilobopathes intricatus* **sp. nov.**, *Multilobopathes densispinosus* **sp. nov.**, and *Stichopathes arenicola* **sp. nov.** (Table 1).

The family Antipathidae comprises a heterogeneous assemblage of forms with branched and unbranched colonies, none bearing pinnules, and polyps typically rounded or slightly elongated (Opresko 2001; Horowitz

et al. 2024). Spine morphology is highly variable, including triangular, cylindrical, or conical shapes (Opresko 2001; Wagner 2015; Horowitz et al. 2024), simple, forked, multilobed or bearing knobs (Horowitz et al. 2024); with surfaces that may be smooth, papillose, or tuberculate. Phylogenomic analyses reveal that this morphological variation is structured across distinct clades, each diagnosable by specific spine characters. Specifically, branched and unbranched colonies bearing consistently papillose, simple, forked, or multilobed spines previously assigned to Antipathidae, are now recovered within the resurrected Stichopathidae (Fig. 2). Branched and unbranched forms with tuberculate spines extending from base to apex and arranged in verticils, including *Pseudocirripathes*, *Allopathes*, and *Aphanipathes verticillata* (aphanipathid) form a distinct clade (aff. Antipathidae 4/Aphanipathidae) (Fig. 2). The remaining clades bear smooth spines: Antipathidae (*A. dichotoma*; triangular spines, polyps 2–2.4 mm; Opresko 2003b), aff. Antipathidae 3 (small smooth spines on branched *Antipathes* colonies, except *Antipathes falkorae* Horowitz, 2022 which has slight papillae restricted to the tips of spines), and aff. Antipathidae 2 (*Blastopathes*, with clusters of branches arising from singular locations Horowitz et al. 2020).

Of the nine genera previously assigned to the family Antipathidae, only three, *Antipathes*, *Cirripathes*, and *Stichopathes*, include at least one described species characterized by papillose spine surface. The status of the genus *Pteropathes* Brook, 1889 remains uncertain in this context. Neither the original descriptions of *P. fragilis* Brook, 1889 nor *P. simpsoni* Summers, 1910 provided details on spine ornamentation. The illustration of *P. fragilis* lacks evidence of surface features, and re-examination of its holotype (USNM 100397) confirms smooth, extremely elongated spines, letting us suppose its exclusion from the resurrected family. For *P. simpsoni*, the presence or absence of spine ornamentation remains unknown.

Distribution. Indian Ocean, Pacific Ocean, Atlantic Ocean

Genus *Stichopathes* Brook, 1889

Cirripathes (*Stichopathes*) van Pesch 1914: p. 105

Revised diagnosis. Corallum unbranched. Spines triangular, conical, simple, bilobed or multilobed; papillose. Polypar spines height 0.08–0.50 mm; five to eight longitudinal rows of spines in lateral view. No secondary spines. Polyps in a single row on one side of the corallum; five to eight polyps/cm.

Type species. *Stichopathes pourtalesi* Brook, 1889

Species in the genus: *Stichopathes abyssicola*, *S. aggregata*, *S. alcocki*, *S. bispinosa*, *S. bournei*, *S. ceylonensis*, *S. contorta*, *S. desaturata*, *S. diversa*, *S. echinulata*, *S. eustropha*, *S. filiformis*, *S. flagellum*, *S. gracilis*, *S. gravieri*, *S. indica*, *S. longispina*, *S. luetkeni*, *S. maldivensis*, *S. occidentalis*, *S. papillosa*, *S. pourtalesi*,

S. regularis, *S. richardi*, *S. saccula*, *S. semiglabra*, *S. setacea*, *S. seychellensis*, *S. solorensis*, *S. spinosa*, *S. variabilis* *S. arenicola* **sp. nov.**

Remarks. In his 1889 description, Brook classified all whip black coral species with a single row of polyps along the axis under the genus *Stichopathes*, regardless of spine shape and ornamentation. Phylogenetic analyses, including the one presented here and those from other studies (e.g., Horowitz et al. 2022; Vicario et al. 2024a), have demonstrated that this trait appears in multiple, sometimes unrelated, lineages. Instead, spine morphology and ornamentation, combined with the arrangement of the polyps, provide more reliable taxonomic markers for distinguishing these groups. Following the present revision, several species currently assigned to the genus may no longer conform strictly to the emended diagnosis, potentially fitting the diagnoses of the newly described genera *Multilobopathes* **gen. nov.**, *Papillopathes* **gen. nov.**, and *Opreskopathes* **gen. nov.** However, in the absence of molecular data from type material or topotypes of the nominal *Stichopathes* species, we conservatively refrain from formally transferring any species at this time. Species that morphologically correspond to the newly described genera are discussed in the “Remarks” sections of the respective genera, where candidate transfers are flagged for future investigation (candidate species reassignments are summarised in Table S3).

Species assigned to *Stichopathes* included in this study

Stichopathes cf. *contorta*.; lineage F29 in Fig. 3; Fig. 4.

Material examined (Table S1): CHR0045_4C, Red Sea, Gulf of Aqaba, 123 m; NTN0035_16B, Red Sea, Gulf of Aqaba, 103 m; NTN0038_15, Red Sea, Gulf of Aqaba, 134 m; NTN0038_12B, Red Sea, Gulf of Aqaba, 142 m; NTN0034_16, Red Sea, Gulf of Aqaba, 166 m; NTN0038_12D, Red Sea, Gulf of Aqaba, 141 m; NTN0038_12C, Red Sea, Gulf of Aqaba, 141 m.

Description of material examined: Colonies unbranched (Fig. 4A). After a few centimeters from the base, some colonies exhibit a contorted growth pattern before forming up to five spirals, while others maintain a straight axis before transitioning directly into a coiled arrangement (Fig. 4A). The basal stem diameter reaches up to 0.9 mm. In distal skeletal portions (0.32–0.65 mm diameter), spines are tall, triangular and laterally compressed, or conical, and are either simple or with faint lobes at the apex (Fig. 4D, E, G, H). Papillae are rounded at the apex, and elongated towards the bottom, extending over two-third of the entire surface of the spine (Fig. 4G, H). Spines are 0.11–0.22 tall, 0.13–0.18 wide, distanced 0.44–0.92 mm apart, with five to nine longitudinal spines in lateral view. Abpolypar spines are 0.08–0.13 mm tall, and 0.10–0.14 mm wide.

In proximal portions of the corallum, polypar spines are triangular, simple, occasionally with poorly developed

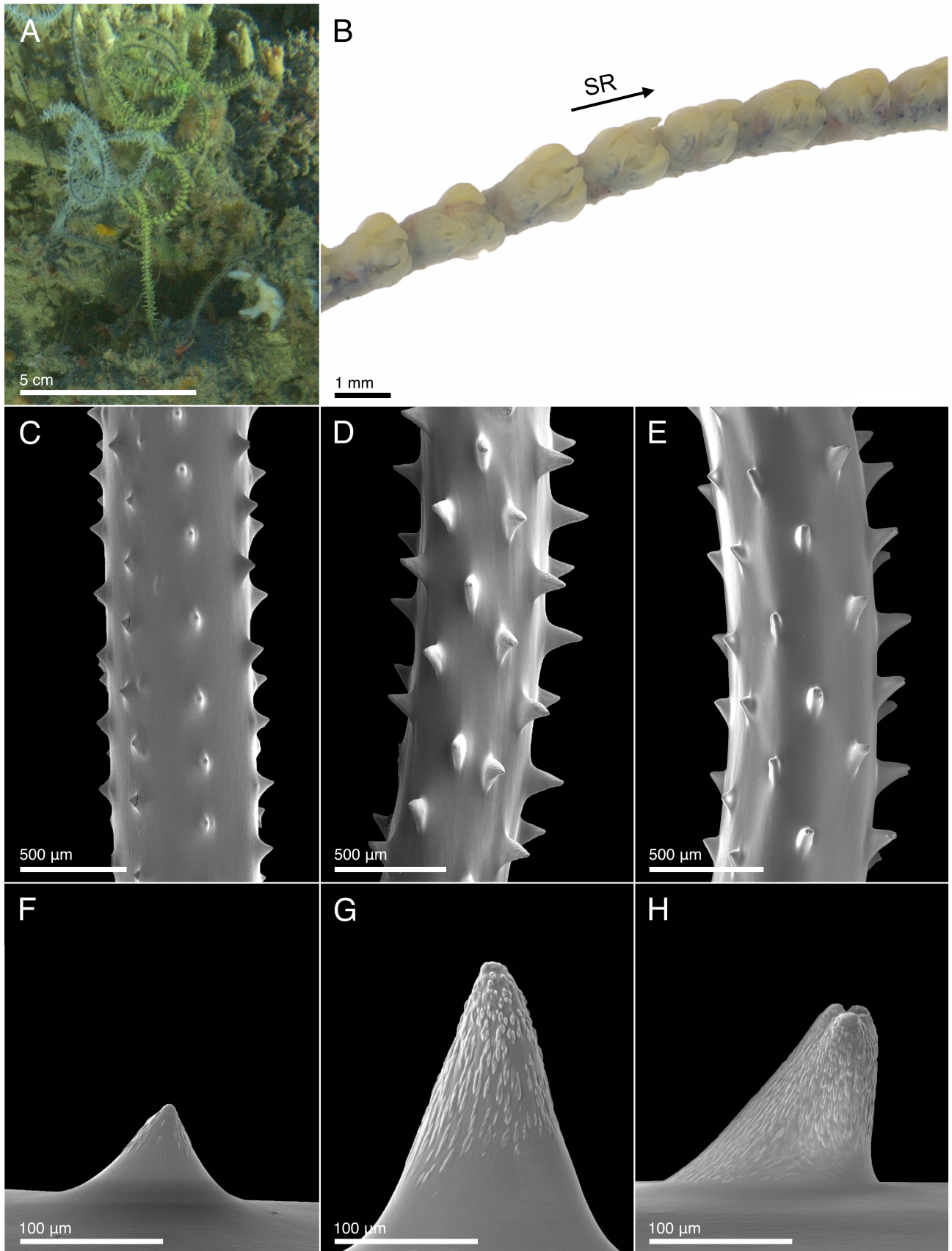


FIGURE 4. *Stichopathes* cf. *contorta*. (A) *In situ* image of specimen NTN0038_15; (B) close-up of polyps of specimen NTN0038_15; (C) spine arrangement on proximal section of specimen NTN0038_15; (D) spine arrangement on distal section of specimen NTN0038_15; (E) spine arrangement on distal section of specimen NTN0038_12C; (F) close-ups view of spines of the proximal section of specimen NTN0038_15; (G) close-up view of spines of the distal section of specimen NTN0038_15; (H) close-up view of spines of the distal section of specimen NTN0038_12C. SR: single row.

apical lobes (Fig. 4C, F). Papillae are faint, elongated, extending up to half of the spine surface (Fig. 4F). Spines are 0.075–0.13 mm tall, 0.11–0.13 mm wide, distanced 0.32–0.48 mm apart, and five longitudinal rows are present in lateral view. No difference between polypar and abpolypar spines was detected. Secondary spines are never observed.

Coenchine is white in color, occasionally pale yellowish after preservation (Fig. 4B). Polyps are arranged in a single, regular row on one side of the corallum, following its curves and spirals (Fig. 4B). Polyps are 0.50–1.4 mm in transverse diameter, spaced 0.15–0.40 mm, with seven to eight polyps/cm.

Remarks. Among whip corals characterized by a single row of polyps along one side of the corallum, papillose spines with a modified apex in at least part of the colony, and the absence of secondary spines, are *Stichopathes gracilis*, *Stichopathes papillosa*, *Stichopathes contorta*, *Stichopathes diversa* and *S. pourtalesi*. *Stichopathes diversa* is described as having stout, cylindrical spines, a feature that is not observed in the specimens examined here. The holotype of *S. gracilis* was thoroughly re-examined by Bo & Opresko, 2015, who described the colony as curved but not spiral, with polyps measuring 1.5–2.0 mm in transverse diameter. The spines were reported as triangular and compressed, papillose on the upper half, with a simple apex or bearing small lobes. In contrast, the specimens examined in this study exhibit

conical spines and polyps whose transverse diameter does not exceed 1.4 mm.

Stichopathes papillosa was originally described by Thomson & Simpson (1905) as having a spiral growth form, polyps approximately 1 mm in transverse diameter, and papillose spines with notched tips. Two spine morphologies were reported: conical spines at the proximal portion of the colony, and flattened, triangular spines at the distal part. While this spine pattern aligns with that of our specimens, notable differences are observed in spines height and in the number of longitudinal rows. *S. papillosa* has spines measuring 0.28–0.34 mm in height and exhibits 12–14 longitudinal rows of spines on one side, whereas our specimens display shorter spines (0.12–0.22 mm) and fewer longitudinal rows (five to nine). *S. pourtalesi* differs in having papillae that are only weakly developed in the distal portions of the skeleton, appearing as faint fusiform projections (Bo & Opresko 2015). In contrast, the specimens examined here show spines in the distal regions with distinctly developed, abundant papillae. Moreover, *S. pourtalesi* spines are generally smaller (0.14–0.17 mm) and directed distally, whereas in our material they are larger (up to 0.22 mm) and oriented perpendicularly to the corallum axis. Lastly, *S. contorta* is the species that most closely resembles the Red Sea specimens. The colony exhibits an upward growth pattern that forms several spirals. Polyps measure approximately 1 mm in transverse diameter (Terrana

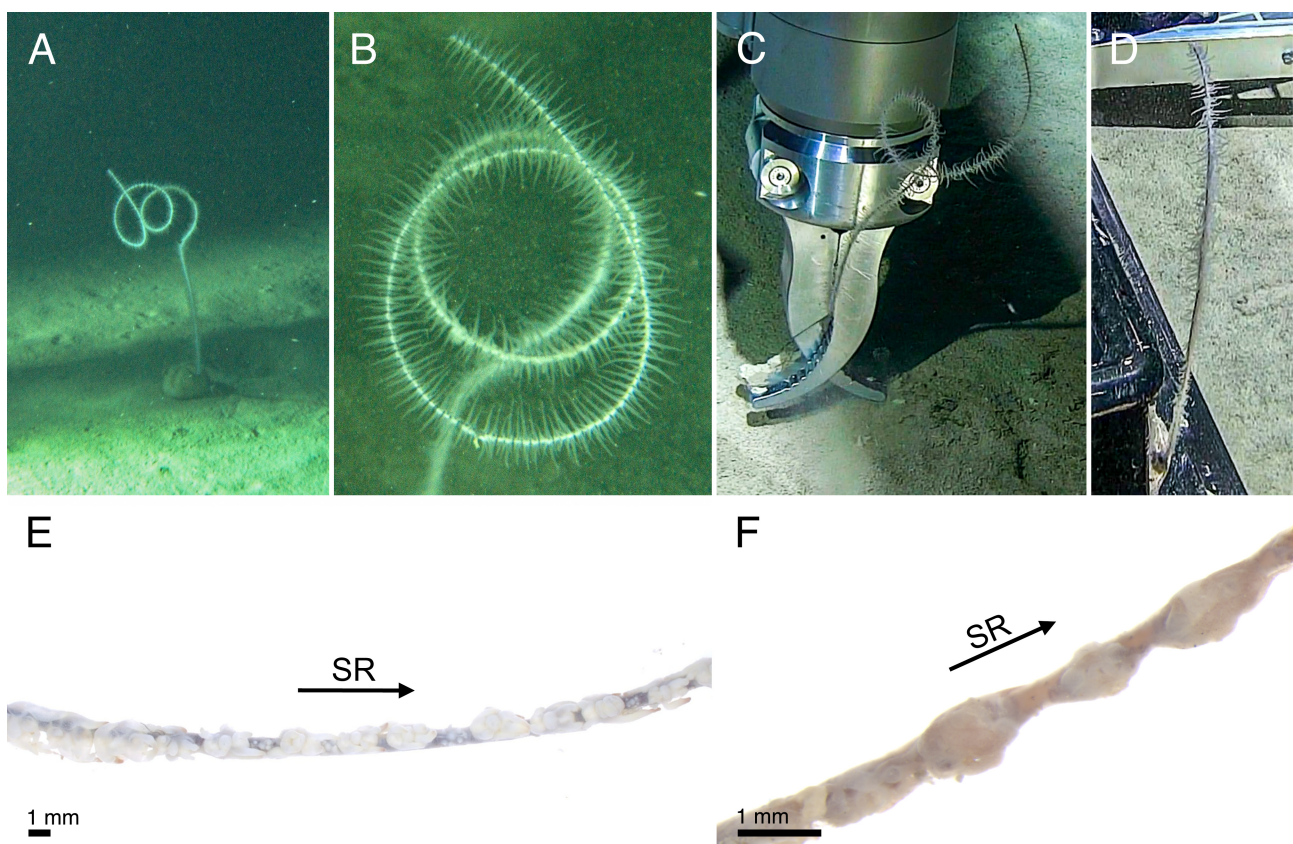


FIGURE 5. *Stichopathes arenicola* sp. nov. (A) *In situ* image of holotype RMNH.COEL.50849; (B) close-up view of polyps of holotype RMNH.COEL.50849; (C) *in situ* image of paratype RMNH.COEL.50851; (D) *in situ* image of paratype RMNH.COEL.50852; (E) close-up view of ethanol-preserved polyps of holotype RMNH.COEL.50849; (F) close-up view of ethanol-preserved polyps of paratype RMNH.COEL.50851. SR: single row

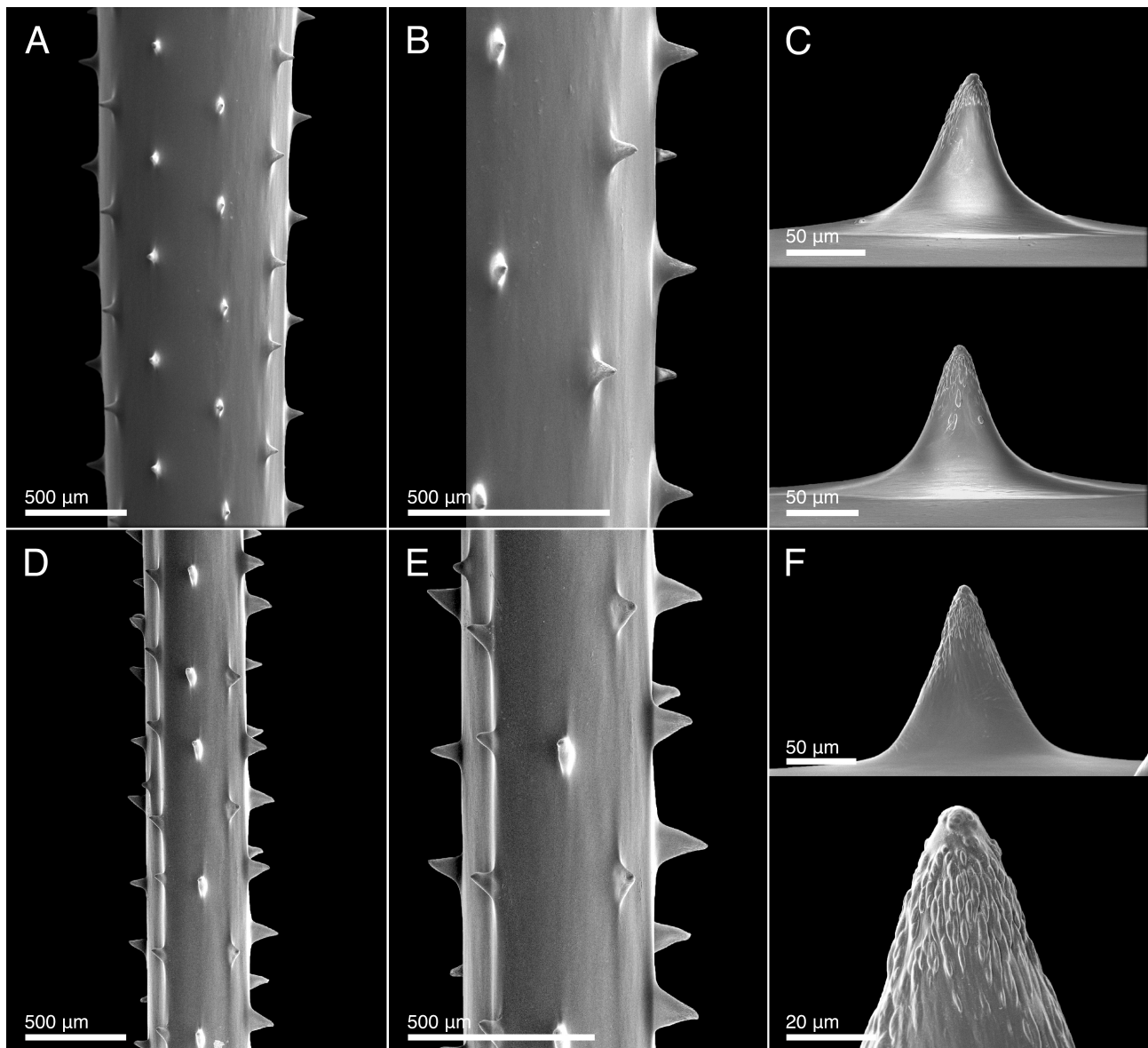


FIGURE 6. Proximal and distal spines of the holotype of *Stichopathes arenicola* sp. nov. RMNH.COEL.50849. (A, B) spines arrangement of proximal section at different magnifications; (C) close-up view of polypar spines in the proximal section; (D, E) spines arrangement of distal section at different magnifications; (F) close-up view of polypar spines in the distal section.

et al. 2024). The spines are conical and papillose, with notched and slightly knobbed apices (Terrana *et al.* 2024), reaching up to 0.22 mm in height on the polypar side and 0.08 mm on the abpolypar side, with seven longitudinal rows of spines on each side (Terrana *et al.* 2024). Due to these morphological similarities, the Red Sea specimens are tentatively assigned to *Stichopathes* cf. *contorta*.

Distribution. Red Sea, Sri Lanka, French Polynesia; 103–166 m depth.

Stichopathes arenicola sp. nov. Vicario & Chimienti
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Lineage F31 in Fig. 3; Figs. 5–7.

Material examined (Table S1). **Holotype:** RMNH.COEL.50849 (Figs. 5A, B, E, 6), Red Sea, South Sila Island, 27.600183°N, 35.335483°E, 493 m, 10 October 2020 (collection code NTN0029_7). **Paratypes:** RMNH.COEL.50851 (Figs. 5C, F, 7A, B, E, F), Red Sea, Gulf of Aqaba, 28.345306°N, 34.697935°E, 623 m, 31 May 2022 (collection code CHR0291BIO11); RMNH.COEL.50852 (Figs. 5D, 7C, G), Red Sea, South of Al Wajh, 25.654922°N, 36.475183°E, 393 m, 20 April 2022 (collection code CHR0249BIO4); RMNH.COEL.50850 (Fig. 7D, H), Red Sea, South of Al Wajh, 25.582282°N, 36.560506°E, 406 m, 20 April 2022 (collection code CHR0251BIO1).

Type locality. Red Sea.

Diagnosis. Corallum unbranched, with or without distal loose coils. Spines triangular, acute, perpendicular to the corallum, and papillose. Papillae rounded on

the tip of the spine and elongated over the upper half of the spine. Distal, polypar spines 0.09–0.13 mm tall, 0.10–0.14 mm wide, 0.47–0.78 mm apart. Abpolypar spines 0.06–0.08 mm tall and 0.08–0.09 mm wide. Five to eight longitudinal rows of spines in lateral view. Proximal spines isomorphic, 0.07–0.09 mm tall, 0.09–0.10 mm wide, and 0.48–0.62 mm apart, with five to six longitudinal rows in lateral view. Secondary spines absent. Polyps in a single row on one side of the corallum, with elongated sagittal tentacles. Polyps 1–2 mm in transverse diameter, interpolypar distance of 0.2–0.5 mm, and five–eight polyps/cm.

Holotype description. The holotype is a 65 cm long colony settled on a sea urchin skeleton, collected from a sandy-bottom environment (Fig. 5A). The corallum is unbranched, straight for the initial 29 cm, after which it develops into two loose spiral loops (Fig. 5A, B). Proximal diameter is 1.54 mm and distal diameter is 0.60 mm.

Spines are triangular, simple, acute, perpendicular to the corallum, and papillose (Fig. 6A, B, D, E). Papillae are rounded and distinct near the apex, while elongated forms extend to the upper half of the spine surface or slightly beyond on lateral sides, where they coalesce (Fig. 6C, F). Secondary spines are absent.

In the distal portion of the colony (0.43 mm in diameter), the spines are 0.11–0.13 mm tall, 0.11–0.14 mm wide, 0.47–0.61 mm apart, with two spines/mm. Abpolypar spines are 0.06–0.08 mm tall, 0.08–0.09 mm wide and 0.64–0.87 mm apart. Six longitudinal rows of spines are visible in lateral view (Fig. 6D, E).

In the proximal region of the colony (diameter 0.96 mm), the spines are 0.08–0.10 mm tall, 0.09–0.10 mm wide, 0.48–0.54 mm apart, with three spines/mm. No clear difference between polypar and abpolypar spines is observed. Six longitudinal rows of spines are visible in lateral view (Fig. 6A, B).

Polyps are white *in vivo*, arranged uniserially, with transparent, elongated sagittal tentacles (Fig. 5B), which are not visible in the ethanol-preserved portion (Fig. 5E). Polyps are 1.7–2.0 mm in transverse diameter, though smaller polyps occasionally intercalate, measuring approximately 0.74–0.94 mm. Interpolypar spacing is 0.23–0.37 mm, resulting in five polyps/cm (Fig. 5E).

Description of paratypes

Paratype RMNH.COEL.50851. Complete, unbranched colony, 71 cm long, with basal plate, collected from a sandy-bottom environment. The colony is mostly straight, forming a loose coil in the middle portion (Fig. 5C). Proximal diameter is 1.3 mm and distal diameter is 0.09 mm.

In the distal section (0.43 mm in diameter), polypar spines are triangular, simple, perpendicular to the corallum, and papillose (Fig. 7B, F). Papillae are rounded on top, while they become elongated down to half-spine length (Fig. 7F). Polypar spines are 0.08–0.09 mm tall, 0.09–0.10 mm wide, 0.74–0.78 mm apart, with two spines/mm. Abpolypar spines are 0.07–0.08 mm tall, 0.10–0.11 wide

and 0.76–0.80 mm apart. Seven longitudinal rows are visible in lateral view (Fig. 7B, F).

In the proximal section (0.63 mm in diameter), spines are triangular, simple and acute (Fig. 7A, E). Papillae are elongated, distinct, and confined at the top of the spine. Spines are isomorphic, 0.08–0.09 mm tall, 0.09–0.10 mm wide, 0.55–0.62 mm apart, with three spines/mm. Six longitudinal rows of spines are present in lateral view (Fig. 7A). Polyps are white, arranged uniserially, with long sagittal tentacles. They are up 1–1.5 mm in transverse diameter, 0.2–0.5 mm apart, with seven to eight polyps/cm (Fig. 5F).

Paratype RMNH.COEL.50850. Complete, unbranched colony, 29 cm long, with proximal diameter of 1 mm and distal diameter of 0.55 mm. The corallum is straight, attached to a biogenic substrate, and was collected from a sandy-bottom environment. Polypar spines in the distal section of the colony (0.40 mm in diameter) are triangular, simple, acute and perpendicular to the corallum (Fig. 7D, H). Papillae are rounded or elongated, distinct and scattered near the apex, with elongated forms extending to mid-spine where they become faint and indistinct. Polypar spines are 0.09 mm tall, 0.10–0.11 mm wide, 0.62–0.65 apart, with three spines/mm (Fig. 7D, H). Abpolypar spines are 0.08 mm tall, 0.9–0.11 mm wide and 0.58–0.64 mm apart. Five longitudinal rows are present in lateral view (Fig. 7D).

Polyps are white *in vivo*, arranged uniserially, with long sagittal tentacles. Polyps transverse diameter is 1–1.3 mm, interpolypar space 0.16–0.24 mm, with eight polyps/cm.

Paratype RMNH.COEL.50852. Complete, unbranched colony with a straight corallum, 12 cm long, proximal diameter of 0.62 mm, and distal diameter of 0.52 mm (Fig. 5D). The colony is attached to a biogenic substrate and was collected from a sandy-bottom environment. Distal spines (axis diameter: 0.33 mm) are triangular, simple, acute, and perpendicular to the corallum (Fig. 7C). Papillae are rounded or elongated, distinct and scattered, with elongated forms extending to mid-spine (Fig. 7G). Polypar spines are 0.10 mm tall, 0.11–0.13 mm wide, 0.60–0.62 mm apart, with two or three spines/mm. Abpolypar spines are 0.07–0.08 mm tall, 0.11–0.12 mm wide, 0.58–0.63 mm apart. Seven longitudinal rows of spines are visible in lateral view. Polyps are white *in vivo*, uniserially arranged, with long sagittal tentacles. Transverse diameter, interpolypar space, and density could not be measured due to bad preservation of the polyps.

Remarks. Among whip black coral species with uniserial polyp arrangement and triangular, papillose spines bearing a simple apex throughout the corallum, *S. desaturata*, *S. echinulata*, and *S. filiformis* are morphologically comparable. Re-examination of the holotype of *S. filiformis* (USNM 100373) revealed distinct spine size and shape between the two species. *S. filiformis* has triangular, elongated, laterally compressed, and blunt spines, 0.18–0.20 mm tall, and 0.15–0.16 mm wide in a 0.30 mm diameter section. Papillae are elongated or irregularly shaped, sparsely distributed and

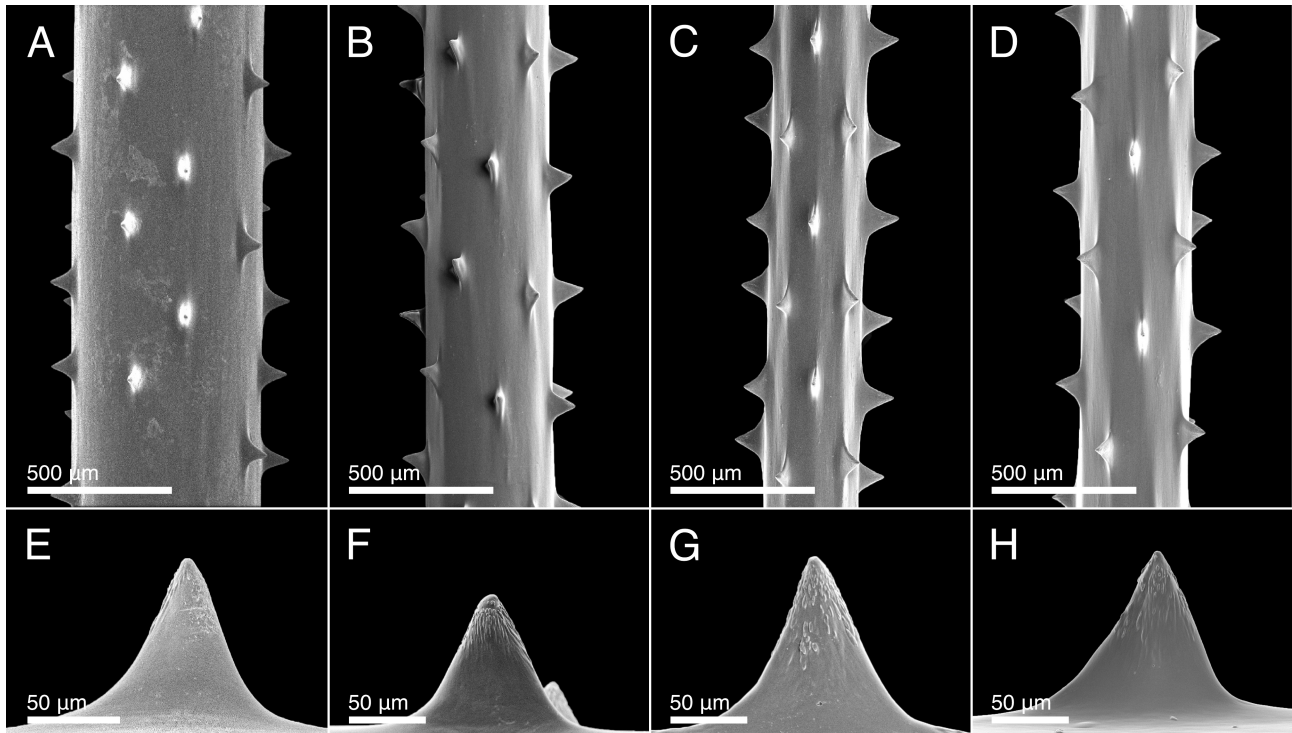


FIGURE 7. Spines arrangement of paratypes of *Stichopathes arenicola* sp. nov. (A) spine arrangement of proximal section of paratype RMNH.COEL.50851; (B) spine arrangement of distal section of paratype RMNH.COEL.50851; (C) spine arrangement of distal section of paratype RMNH.COEL.50852; (D) spine arrangement of distal section of paratype RMNH.COEL.50850; (E) close-up view of polypar spines in the proximal section of paratype RMNH.COEL.50851; (F) close-up view of polypar spines in the distal section of paratype RMNH.COEL.50851; (G) close-up view of polypar spines in the distal section of paratype RMNH.COEL.50852; (H) close-up view of polypar spines in the distal section of paratype RMNH.COEL.50850.

scattered across the distal half of the spine. Instead, in *S. arenicola* **sp. nov.** spines are consistently triangular, acute, vertically directed, and up to 0.13 mm tall in coral sections of similar diameter.

S. echinulata differs from the species in exam by having well-developed papillae that extend over two-third to the full spine surface, 10–12 longitudinal rows of spines in lateral view (vs. 5–8 in *S. arenicola* **sp. nov.**), polypar spines that are distally inclined (vertically directed in *S. arenicola* **sp. nov.**), and 0.16–0.19 mm tall. Pictures of the skeletal spines of the holotype (USNM 100371) are shown in Wagner *et al.* (2015). *S. desaturata* is distinguished by a consistently irregularly sinuous corallum, and polyps never exceeding 1.0 mm in transverse diameter, which is not observed in *S. arenicola* **sp. nov.** Additionally, the polypar spines in *S. desaturata* can be triangular or conical, occasionally laterally compressed, with papillae covering up to two-thirds or the full surface, unlike in *S. arenicola*, where spines are consistently triangular and papillae never extends below the upper half of the spine surface. From a phylogenetic standpoint, *S. desaturata* groups within Lineage A alongside *Papilopathes* (*Antipathes*) *grandis* **comb. nov.** (Terrana *et al.* 2024), corresponding to Lineage C in this study, while *S. arenicola* **sp. nov.** belongs to Lineage F, indicating distant evolutionary placement.

Etymology. The specific name *arenicola* is derived from the Latin words *arena* (sand) and *-cola* (dweller or

inhabitant), referring to this species' preference for sandy or muddy bottoms.

Habitat and ecology. Specimens of this species were collected exclusively from deep waters of the Red Sea, at depths ranging from 393 to 623 m. Colonies typically inhabit sandy or muddy bottoms where they are settled on small, hard substrates such as sea urchin tests, rocks, or coral rubble.

Stichopathes pourtalesi (Brook, 1889); lineage F32 in Fig. 3; Fig. 8. Lectotype: MCZ 90342; type locality: Montserrat. Material molecularly examined, lectotype, MCZ 90342; type locality: Western-Central Atlantic Ocean, Montserrat.

Other material examined (Table S1): USNM 1222140 (Fig. 8D, E, F), USA, Gulf of Mexico, 85 m; USNM 1484548, USA, Gulf of Mexico, 110 m.

Description of material examined. Colonies unbranched and broken into several fragments. In skeletal portions measuring 0.44–0.48 mm in diameter spines are triangular, simple, papillose, with faint elongated papillae that extend up to half the spine surface (Fig. 8E, F). Spines on thicker skeletal sections (0.77 mm diameter) are simple, bilobed and rarely multilobed, with much more developed and distinct elongated papillae extending over two-thirds of the spine surface. Polypar spines are 0.090–0.14 mm

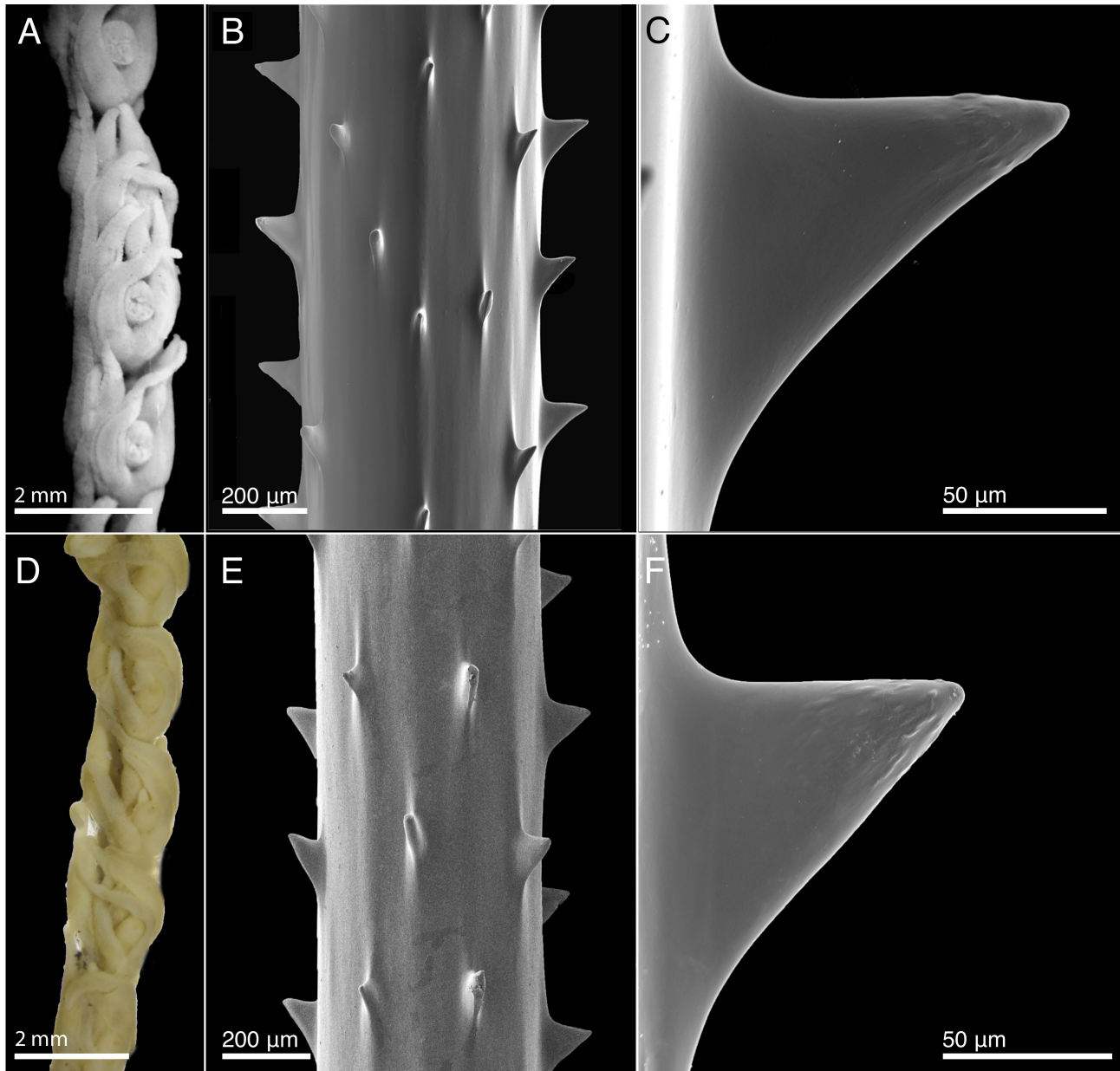


FIGURE 8. *Stichopathes pourtalesi*. (A) Polyps of lectotype of *S. pourtalesi* (MCZ 90342) modified from Bo & Opresko 2015, (B, C) Stem section showing spine arrangement and size, and spine detail of the schizoparalectotype (MCZ 90343) modified from Bo & Opresko 2015, (D) Polyps of *S. pourtalesi* (USNM 1222140), (E, F) Stem section and spine detail of *S. pourtalesi* (USNM 1222140).

tall, 0.10–0.17 mm wide, distanced 0.58–0.78 mm apart, with six–eight longitudinal spines in lateral view (Fig. 8E, F). Abpolypar spines are 0.075–0.10 mm tall, and 0.09–0.13 mm wide. Secondary spines are not observed. Polyps are arranged in a single, regular row on one side of the corallum (Fig. 8D). Polyps have long distal tentacles, they are 1.7–1.9 mm in transverse diameter, spaced 0–0.2 mm apart, with five–six polyps/cm.

Remarks. A detailed comparison of whip black coral species exhibiting a single row of polyps along one side of the corallum, papillose spines with a modified apex in at least part of the colony, and the absence of secondary spines, is reported in the remarks section of *S. cf. contorta*. The morphological characters observed in

the specimens examined here fit the re-description for the type material of *Stichopathes pourtalesi* (Bo & Opresko 2015). A comparative plate illustrating the lectotype (MCZ 90342), the schizoparalectotype (MCZ 90343) from Bo & Opresko (2015), and the specimens examined in this study (USNM 1222140) is presented in Fig. 8. Furthermore, a phylogenomic reconstruction of representatives of the family Stichopathidae, including the sequence of the lectotype MCZ 90342, is shown in Fig. S4. In this analysis, the sequence of the lectotype is sister to lineages E (*Cirrhopathes* / aff. *Antipathes*) and F (*Stichopathes*). Although support values were high for deep nodes, they decreased toward shallower nodes (Fig. S4), rendering the precise placement of the type species within a sublineage

uncertain. Nevertheless, the consistent morphological characters between the specimens examined here and the type material strongly support the interpretation that lineage F32 corresponds to *S. pourtalesi*, and consequently lineage F can be confidently assigned to *Stichopathes*.

Genus *Multilobopathes* Vicario & Chimienti gen. nov.

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Antipathes (in part), Brook 1889: p. 103

Antipathes (in part), van Pesch 1914: pp. 52, 69, 71

Antipathes (in part), Opresko 2009: pp. 285–287

Antipathes (in part), Terrana *et al.* 2020: pp. 13–15

Diagnosis. Colonies unbranched, branched, not pinnulate. Polypar spines triangular or conical in distal regions, conical or cylindrical in middle and proximal regions; spines simple, forked, or multilobed, papillose throughout, with rounded or elongated papillae; tubercles occasionally present. Polypar spines height 0.08–0.55 mm; 6–14 longitudinal rows of spines in lateral view. Secondary spines present in proximal and middle regions, rare or absent distally. Polyps uniserial along one side of the axis; in older basal branches, multiple rows may occur. Polyps densely arranged, with little to no interpolypar spacing (>0 –0.3 mm); transverse diameter 0.60–2.0 mm; 5–13 polyps/cm.

Type species. *Antipathes lentipinna* Brook, 1889 accepted as *Multilobopathes lentipinna* (Brook, 1889) **comb. nov.**

Species in the genus: *Multilobopathes lentipinna*, *Multilobopathes ornatus*, *Multilobopathes intricatus*, *Multilobopathes densispinosus*.

Remarks. *Multilobopathes* **gen. nov.** is distinguished from other genera within the order by papillose spines that are simple, forked, or multilobed in distal regions and forked or multilobed in middle and proximal regions; the presence of secondary spines; and reduced interpolypar spacing (>0 –0.3 mm).

Other genera with similar external morphology include *Papillopathes* **gen. nov.** and *Opreskopathes* **gen. nov.**, both of which include branched and unbranched forms. However, they differ from *Multilobopathes* in having exclusively simple spines and lacking secondary spines.

A multilobed spine apex and the presence of secondary spines are features shared by some species currently ascribed to *Antipathes* and *Stichopathes* taxa. Among these, *Stichopathes diversa*, *S. maldivensis*, *S. bispinosa*, and *S. alcocki* exhibit morphological characteristics consistent with *Multilobopathes*, and further examination of type material, or material from their type localities is needed to clarify their taxonomic placement.

Of the *Antipathes* species with papillose spines, eight (*A. spinulosa*, *A. fruticosa*, *A. aculeata*, *A. griggi*, *A. arborea*, *A. curvata*, and *A. galapagensis*) exhibit a multilobed or notched spine apex. Among these, *A. curvata*,

A. arborea, and *A. galapagensis* lack secondary spines. For the remaining species, future molecular analyses of type material, or topotypes where types are unavailable, will be necessary to determine their placement within *Multilobopathes*.

Etymology. From the Latin “*multi*” meaning “many”, and “*lobo*” meaning “lobe” denoting the multilobed characteristic of the spines in at least a portion of the colony. Gender: masculine

Distribution. Red Sea, Madagascar, Réunion Island, Hawaii, Guam, Australia (Coral Sea), Japan (Okinawa); 2–227 m depth.

Species assigned to *Multilobopathes*:

Multilobopathes sp. 1; lineage A1 in Fig. 3; Fig. 9.

Material examined (Table S1): SA5527, Red Sea, Farasan banks, 12 m; SA5724, Red Sea, Shushah Island, 10 m; SA6024, Red Sea, Al-Lith, 3.5 m; SA5766, Red Sea, Shushah Island, 16 m; SA6259, Red Sea, Al-Lith, 9.6 m; SA5002, Red Sea, Thuwal, Rose Reef, 6 m; MD484, Madagascar, Nosy Be, Banc des Gorgones, 13 m; MD485, Madagascar, Nosy Be, Banc des Gorgones, 13 m; MD574, Madagascar, Nosy Be, Sakatia Beachfront Villa, 2.5 m; REU131, Réunion Island, Pointe au sel, 25 m; REU286, Réunion Island, Tour de Boucan, 18 m; REU269, Réunion Island, Cap LaHoussaye, 14 m.

Description of material examined. Colonies are unbranched, straight or sinuous, with a thick corallum, up to 3 m tall (Fig. 9A–E). On distal sections ranging 2.0–3.7 mm in diameter, spines are tall, conical or cylindrical, papillose; papillae are predominantly elongated, covering most of the spine surface, although rounded papillae may occur near the spine apex (Fig. 9F–K). Tubercles are present at the apex and on one (Fig. 9H) or both sides of the spines (Fig. 9K). Polypar spines are 0.45–0.55 mm tall, 0.21–0.29 mm wide and irregularly spaced. Abpolypar spines are conical, with less developed papillae and tubercles compared to polypar spines. They are 0.24–0.31 mm tall and 0.20–0.22 mm wide. Although irregular, approximately 12–14 longitudinal rows of spines are visible in lateral view (Fig. 9F, I). Secondary spines are present, varying in shape (triangular, conical, or cylindrical), irregularly arranged between primary spines and more abundant in thicker regions of the corallum.

Two colour morphotypes observed: orange-brown (more common) (Fig. 9A, C–E) and pale green (Fig. 9B). Polyps are uniserially arranged on one side of the axis (Fig. 9C–E), sometimes forming a slight spiral along the corallum. Polyps show a prominent oral cone, 1.5–2.0 mm in transverse diameter, with no interpolypar space, resulting in 5–6 polyps/cm.

Remarks. Among whip-like black corals bearing papillose, cylindrical or conical primary spines and secondary spines, are *Stichopathes alcocki*, *S. bispinosa*, *S. diversa*, and *S. maldivensis*. In both *S. alcocki* and *S. diversa*, the original descriptions do not report spine tuberculation, a diagnostic feature consistently observed

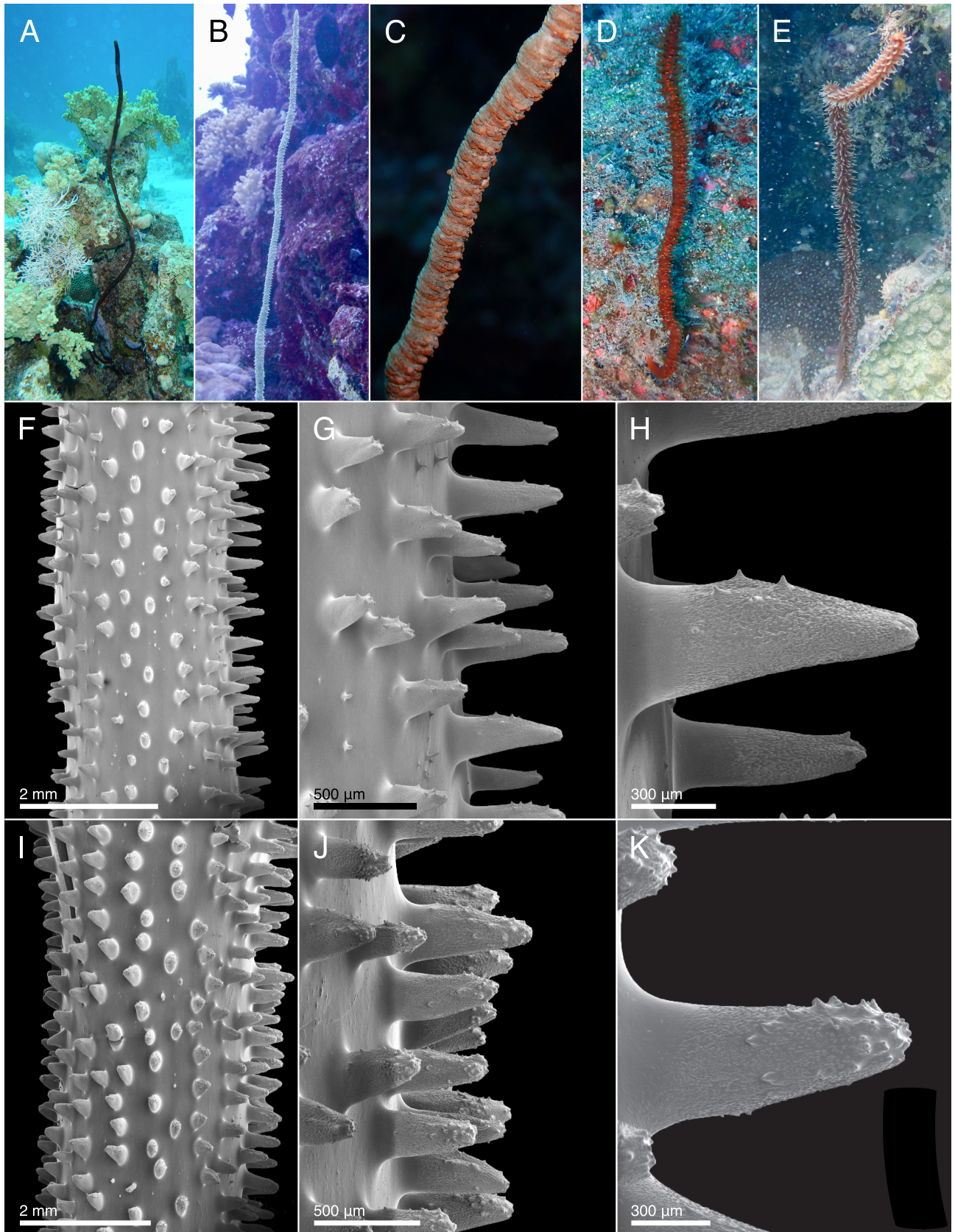


FIGURE 9. *Multilobopathes* sp. 1. *In situ* images showing morphologies from the Saudi Arabian Red Sea, Madagascar and Réunion Island. (A) SA5724; (B) SA6259; (C) SA5766; (D) REU286; (E) MD574. Spines arrangement and close-up views of spines on distal section of SA5724 (F-H). Spines arrangement and close-up views of spines on distal section of SA6259 (I-K).

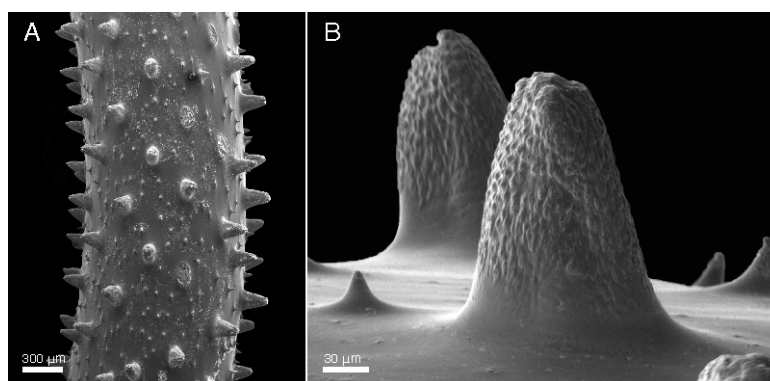


FIGURE 10. *Cirrhipathes? diversa* schizoholotype USNM 100372. (A) Spines arrangement; (B) close-up view of spines.

in the Red Sea material examined here. This is further confirmed by re-examination of the holotype of *S. diversa* (USNM 100372), which lacks tubercles on the spine surfaces (Fig. 10).

Multilobopathes sp.1 closely resembles specimens identified as *Stichopathes* cf. *maldivensis* in Terrana *et al.* (2020), as well as specimens assigned to lineage D in Bo *et al.* (2012) and *Stichopathes?* sp. in Wagner (2015). The holotype of *S. maldivensis* is presumed to be lost, and Cooper's (1903) original description is limited, referring to a straight, unbranched colony with a stout basal diameter (4 mm). The spines were described as bluntly conical (approximately 0.3 mm tall), with rough surfaces, likely indicative of papillae, and knobbed apices. Secondary spines were noted as irregularly distributed, and polyps as uniserial, though no further details on polyp morphology was provided. All of these features, except for the knobbed apex, are consistent with the specimens analysed in this study. However, in some distal portions of our material, early-stage tubercles occur apically and may appear knobbed under low magnification. Currently, *S. maldivensis* remains the only valid species with a straight, unbranched corallum exhibiting this combination of spine characteristics.

Another comparable species is *Cirrhipathes* (?) *flagellum*, originally described by Brook (1889) as a long, straight, unbranched colony with a stout basal diameter (~6 mm), though no polyp information was available due to poor preservation. Re-examination of the skeletal elements of the schizoholotype (USNM 100367) revealed spine shape, size, and ornamentation consistent with the present material, including conical to cylindrical spines with papillose surfaces and well-developed tubercles. In both, tubercles are prominent; however, in *Cirrhipathes* (?) *flagellum*, they are primarily restricted to one side and the frontal face, while in the current specimens, tubercles may occur in a similar distribution or extend across all surfaces including the apex. Spine size (e.g., polypar spines ~0.5 mm tall) is also consistent with our specimens.

Due to the lack of polyp information, Brook did not assign the species to a confirmed genus. To resolve its uncertain placement and avoid homonymy with *Stichopathes flagellum* Roule (1905), the species was later

renamed as *Stichopathes bispinosa* by Summer (1910). However, this synonymy remains unresolved (Terrana *et al.* 2020). Summer (1910) re-described *S. bispinosa* as having a stout, sinuous stem that tapers gradually and forms large spirals, a uniserial arrangement of flat, closely spaced polyps with short, thick tentacles, traits partially overlapping with our material. In contrast, the Red Sea specimens exhibit straight or slightly sinuous colonies, never coiled, and spine details in Summer's drawings show subtle differences from those observed here.

Given the uncertainty surrounding the synonymy, the limited detail in original descriptions, and the lack of available type material for *S. maldivensis*, the identification of the present specimens remains tentative.

Distribution. Red Sea, Madagascar, Réunion Island; 2–29 m depth.

Multilobopathes lentipinna (Brook, 1889) **comb. nov.**; lineage A3 in Fig. 3; Figs. 11,12; holotype: NHMUK1973.9.20.1; type locality: Red Sea. Material morphologically examined, schizoholotype, USNM 92586, Saudi Arabia, Jiddah, depth NA.

Other material examined (Table S1): SA4447, Red Sea, North of Duba, 4 m; DIVE23/10_2, Red Sea, Gulf of Aqaba, 30 m; SA4560, Red Sea, Gulf of Aqaba, 22 m; SA5040, Red Sea, Thuwal, Tahala Reef, 20 m; SA5746, Red Sea, Shushah Island, 9 m; SA6136, Red Sea, Al-Lith, 10 m; NTN0149BIO15, Red Sea, Yanbu, 68 m; MD298, Madagascar, Nosy Be, Nosy Sakatia, 9.5 m; MD516, Madagascar, Nosy Be, Nosy Kombu, 7 m; MD521, Madagascar, Nosy Be, Nosy Kombu, 6 m.

Description of material examined. Colonies are branched, bushy, with an irregular branching pattern spreading in all directions. In large colonies, the branches are densely arranged, forming a distinctly three-dimensional structure with branchlets radiating outward in multiple directions. In some parts of the colony, branchlets may be uniserially arranged. The largest colony observed exceeded 3 m in width (Fig. 11A). Smaller colonies are more common (Fig. 11C) and are typically found attached to hard substrates or beneath overhangs. These smaller colonies display a more sparsely branched, bushy growth

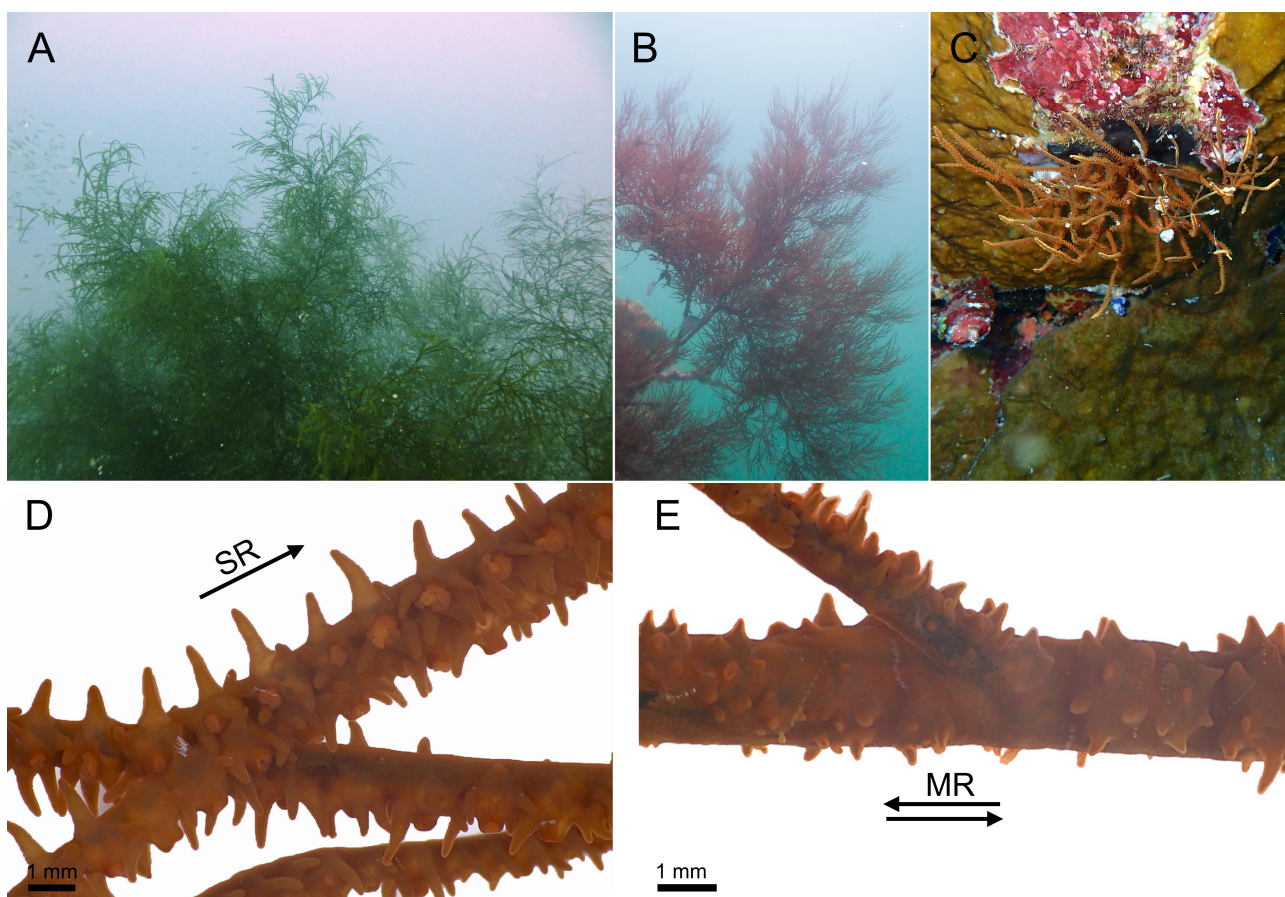


FIGURE 11. *Multilobopathes lentipinna*. In situ images showing different morphologies from the Saudi Arabian Red Sea and Madagascar (A) SA5040; (B) MD521; (C) SA6136; (D) ethanol-preserved polyps on branchlets of specimen SA5040; (E) ethanol-preserved polyps on branch of specimen SA5040. SR: single row, MR: multiple rows

form with irregularly arranged branches and branchlets spreading vertically (Fig. 11C).

Spines on the distal portions of branchlets (0.35–0.50 mm in diameter) are predominantly triangular and laterally compressed, although conical shapes can also occur (Fig. 12G–L). Spines may be simple, forked (Fig. 12J–L), or multilobed (Fig. 12G–I), often with a coronate arrangement of the lobes. Papillae are elongated and may cover the entire spine surface. Polypar spines are 0.10–0.21 mm tall, 0.06–0.12 wide, spaced 0.20–0.51 mm apart, with five to seven longitudinal rows of spines in lateral view. Abpolypar spines are 0.09–0.12 tall, and 0.06–0.12 mm wide. Secondary spines are rare but can occasionally occur (Fig. 12G). On thicker branches (0.75–2.2 mm in diameter), spines are conical and become increasingly stout on thicker axes (Fig. 12A–C). These spines are often multilobed, with either a coronate arrangement of apical lobes or a jagged appearance where lobes may extend along the spine surface. Spines are papillose, with papillae covering most or all of the spine surface; papillae are rounded at the apex and more elongated towards the base. Secondary spines can occur in these regions (Fig. 12G) but are not always present. Polypar spines are 0.09–0.18 mm tall, 0.07–0.12 wide, spaced 0.25–0.50 mm apart, with six–nine longitudinal rows of spines in lateral view. On thick branches abpolypar spines

usually cannot be distinguished from polypar spines. On thinner branches they are 0.08–0.10 tall, and 0.08–0.10 mm wide.

Polyps and coenhome are predominantly dark red or brownish. Polyps are uniserially arranged on branches and branchlets (Fig. 11D), while on thicker branches they are irregularly distributed around the stem (Fig. 11E). They are 0.9–1.3 mm in transverse diameter, close to each other with interpolypar space 0–0.3 mm, resulting in seven–twelve polyps/cm.

Remarks. Among previously described branched species of Antipatharia with papillose spines bearing forked or multilobed apices in at least some parts of the colony are *Multilobopathes lentipinna* **comb. nov.**, *Antipathes griggi*, *Antipathes spinulosa*, *Antipathes fruticosa*, *Antipathes arborea*, *Antipathes curvata*, and *Antipathes galapagensis*. Comparisons of these species are discussed in detail in the remarks section of *M. intricatus* **sp. nov.** and in Opresko (2009). Examination of the schizoholotype of *M. lentipinna* **comb. nov.** (USNM 92586) confirmed the same diagnostic spine characters observed in the topotypes and additional material from Madagascar here examined. On thicker branches, the holotype presented conical, stout, multilobed spines with a coronate arrangement of the lobes. Spines were papillose, 0.12–0.17 mm tall and 0.08–0.10 mm wide.

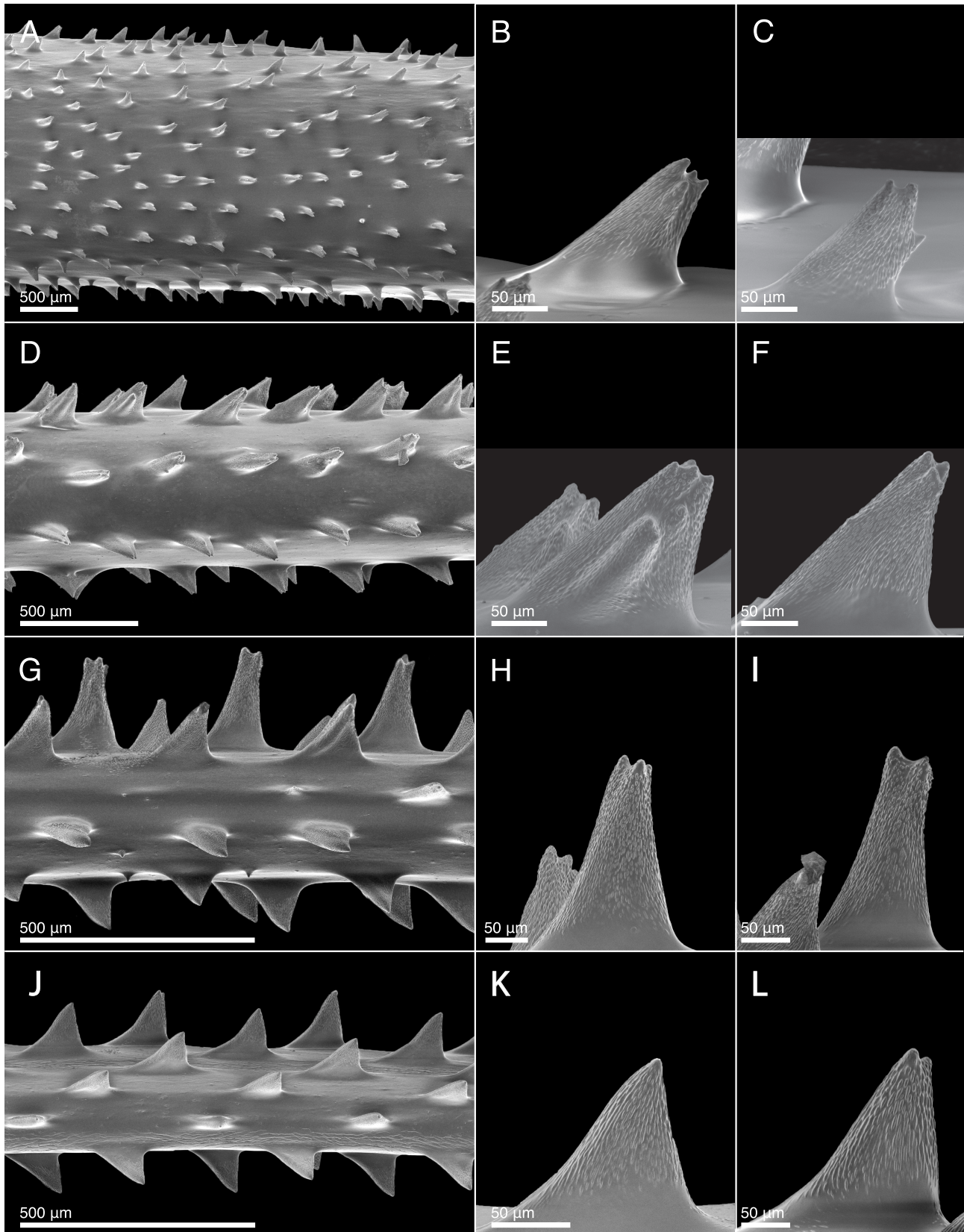


FIGURE 12. Spines arrangement of *Multilobopathes lentipinna* SA5040. (A, D) spines arrangement on two distinct branches of different diameter; (B, C, E, F) close-up views of polypar spines on two distinct branches of different diameter; (G, J) spines arrangement on two distinct branchlets; (H, I, K, L) close-up views of polypar spines on distinct branchlets.

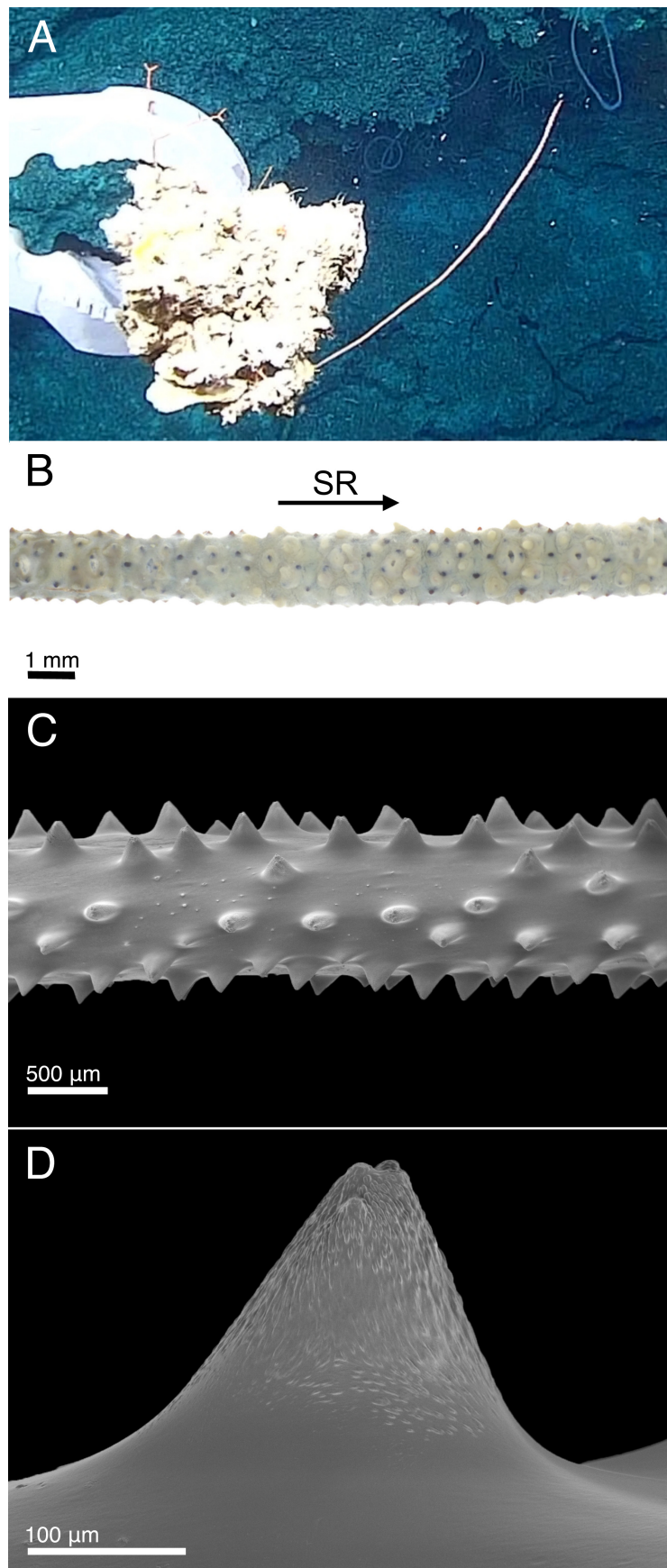


FIGURE 13. *Multilobopathes* sp. 3 CHR0043_14 (A) *In situ* image of the colony; (B) Ethanol-preserved polyps on the stem; (C) spine arrangement on the stem; (D) close-up view of polypar spine on the stem. SR: single row.

Spine morphology varied with branchlet diameter: thinner branches bear triangular spines that are simple or forked, whereas thicker branches have laterally compressed triangular spines with multilobed apices arranged coronately. Spines are 0.13–0.27 mm tall, 0.09–0.13 mm wide, and are spaced 0.23–0.50 mm apart, with six to eight longitudinal rows visible in lateral view. Images of the holotype spines are provided in Opresko (2009).

Distribution. Red Sea, Mozambique, Madagascar; 4–68 m depth.

Multilobopathes sp.3; lineage A5 in Fig. 3, Fig. 13.

Material examined (Table S1): CHR0034_4A, Red Sea, North of Duba, 92.8 m; M193_089_2_9, Red Sea, Al Wajh, 93.0 m; CHR0043_24, Red Sea, Gulf of Aqaba, 116.4 m; NTN0036_9, Red Sea, Gulf of Aqaba, 186.1 m.

Description of material examined. Colonies are unbranched, straight (Fig. 13A), or slightly sinuous. On distal sections ranging 0.6–0.75 mm in diameter, spines are bilobed or multilobed, forming a distinct crown-like structure (Fig. 13C, D). Spines are conical, papillose, papillae are predominantly elongated, covering most of the spine surface (Fig. 13C, D). Polypar spines are 0.16–0.24 mm tall, 0.12–0.22 mm wide, and distanced 0.46–0.80 mm apart. Abpolypar spines are conical, 0.08–0.17 mm tall and 0.11–0.20 mm wide. 6–11 longitudinal rows are visible in lateral view. Secondary spines can be present, arranged between primary spines and more abundant in thicker regions of the corallum (Fig. 13C). Polyps are uniserially arranged on one side of the axis (Fig. 13B). Polyps are 0.7–1.5 mm in transverse diameter, spaced 0–0.3 mm apart, resulting in 7–11 polyps/cm.

Distribution. Red Sea; 93–186 m depth.

Multilobopathes ornatus Chimienti & Vicario **sp. nov.**
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Lineage A6 in Fig. 3; Figs. 14–16

Material examined (Table S1). **Holotype:** RMNH.COEL.50840 (Figs. 14A, 15), Red Sea, Gulf of Aqaba, 29.264073°N, 34.928625°E, 94 m, 21 October 2020 (collection code NTN0037_16). **Paratypes:** RMNH.COEL.50843 (Figs. 14C, E, F; 16A–D), Red Sea, off Tiran Island, 27.909091°N, 34.627748°E, 121 m, 27 June 2022 (collection code NDR0920_10); RMNH.COEL.50854 (Fig. 14B), Red Sea, off Tiran Island, 27.909094°N, 34.627749°E, 119 m, 27 June 2022 (collection code NDR0920_11); RMNH.COEL.50842 (Fig. 16I–L), Red Sea, Gulf of Aqaba, 28.47947°N, 34.76997°E, 101 m, 13 November 2020 (collection code CHR0044_2A); RMNH.COEL.50841 (Fig. 16E–H), Red Sea, off Tiran Island, 27.90931°N, 34.62771°E, 95.5 m, 4 November 2020 (collection code CHR0034_2B).

Type locality. Red Sea.

Diagnosis. Corallum unbranched, forming tight coils or spirals from the base or from the central portion of the colony.

Distal spines triangular, simple, bilobed or multilobed, half to fully papillose. Papillae elongated, numerous and often coalescent. Polypar spines 0.10–0.20 mm tall and 0.11–0.15 mm wide, 0.43–0.75 mm apart, with two–three spines/mm and seven–nine longitudinal rows of spines in lateral view. Abpolypar spines smaller than polypar ones, 0.06–0.13 mm tall and 0.08–0.15 mm wide.

Central spines triangular to conical, bi- or multilobed, half to fully papillose. Polypar spines 0.14–0.15 mm tall and 0.12–0.14 mm wide, 0.59–0.61 mm apart, with two spines/mm and five longitudinal rows of spines in lateral view.

Proximal spines conical and stout, multilobed, half to fully papillose; lobes can extend along the spine surface. Papillae rounded or elongated, numerous and often coalescent. Polypar spines 0.16–0.24 mm tall and 0.11–0.21 mm wide, 0.48–0.80 mm apart, with two–three spines/mm and seven–nine longitudinal rows of spines in lateral view. Secondary spines present.

Polyps arranged in a single row along one side of the corallum, following the outer curvature of the coils. Polyps 0.65–1.1 mm in transverse diameter, very close to each other, with an interpolypar distance of 0.0–0.3 mm, and a density of 10–13 polyps/cm.

Holotype description. The holotype is a 37 cm long colony lacking the basal plate (Fig. 14A). The corallum is slender, unbranched, with four coils. It tapers gradually from a proximal diameter of 1.2 mm to 0.52 mm at the distal end.

Spine morphology varies along the colony. The distal portion of the colony (0.47 mm in diameter) shows spines triangular, exhibiting apex simple, bilobed, or occasionally multilobed (Fig. 15C, F, I, L). They are papillose, with numerous rounded papillae confined at the apex, and elongated forms covering two-thirds to the entire surface of the spine often coalescing. Polypar spines are 0.10–0.11 mm tall and 0.11–0.12 mm wide, 0.34–0.63 mm apart. Abpolypar spines are slightly smaller, 0.06–0.09 mm tall and 0.08–0.10 mm wide. There are two to three spines/mm and up to eight longitudinal rows are visible in lateral view. Secondary spines are absent in this section. The middle portion of the corallum (axis diameter: 0.52 mm) bears polypar spines that are conical, with a multilobed apex forming a distinct crown-like structure with three to six apical lobes (Fig. 15B, E, H, K). Abpolypar spines remain triangular, distally inclined, and simple. Spine ornamentation is similar to the one from the distal spines. Polypar spines are 0.14–0.15 mm tall and 0.12–0.14 mm wide, 0.59–0.61 mm apart. Abpolypar spines are 0.08–0.10 mm tall and 0.11 mm wide. There are two spines/mm, and six longitudinal rows are visible in lateral view. In the proximal portion (axis diameter: 1.1 mm) spines are stout, conical, and multilobed (Fig. 15A, D, G, J). In some cases, the lobes resemble tubercles and may be particularly prominent and numerous, up to 12, with occasional lateral development extending down the

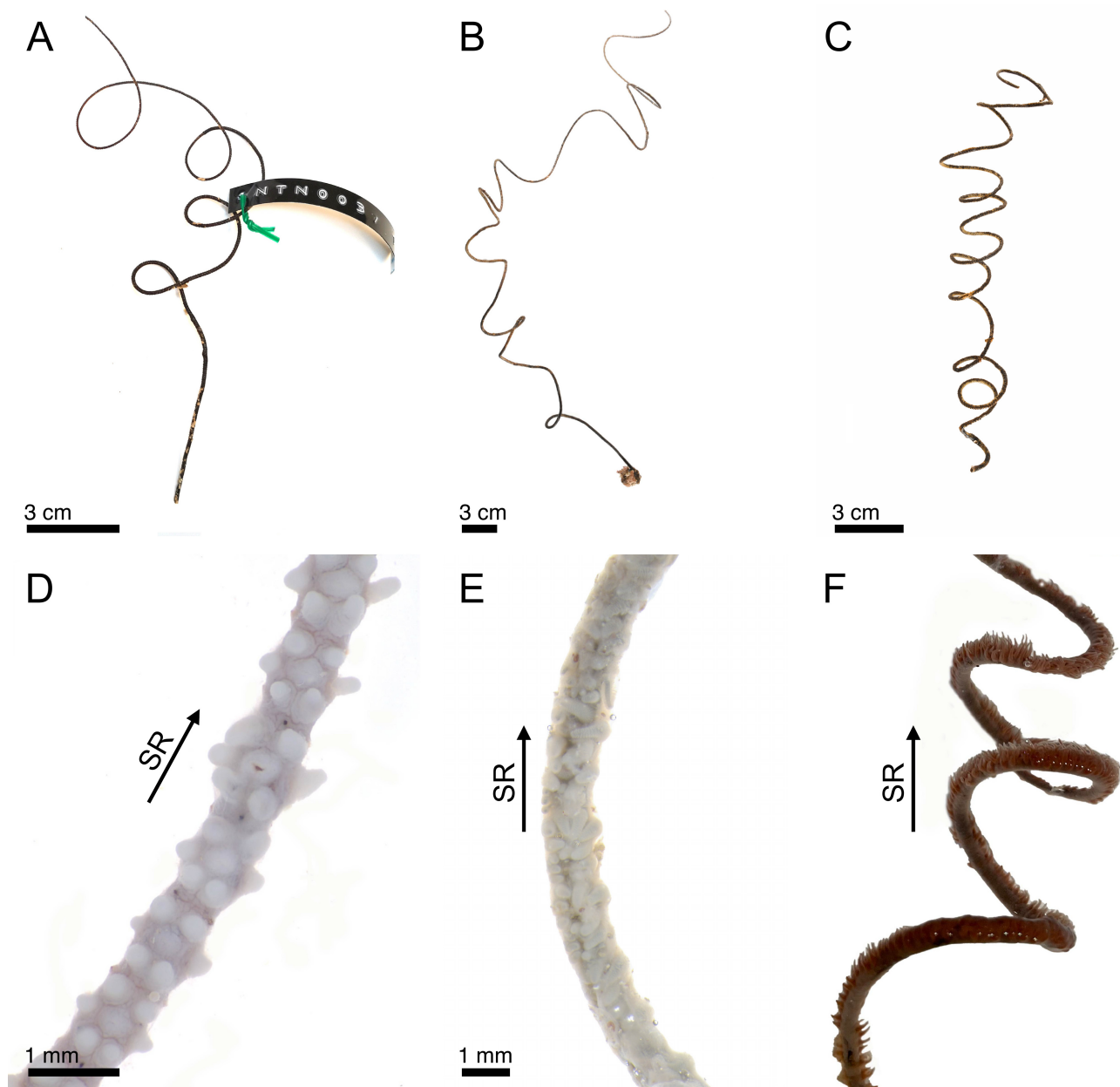


FIGURE 14. *Multilobopathes ornatus* sp. nov. (A) Dry colony of holotype RMNH.COEL.50840; (B) Dry colony of paratype RMNH.COEL.50854; (C) Dry colony of paratype NDR0920-10; (D) Close-up view of ethanol-preserved polyps of holotype NTN0037_17; (E) Close-up view of ethanol-preserved polyps of paratype RMNH.COEL.50843; (F) Close-up view of polyps right after collection of paratype RMNH.COEL.50843. SR: single row

sides of the spine (Fig. 15J). Papillae are elongated, with distribution and coalescence similar to that of more distal regions. Polypar spines are 0.13–0.15 mm tall and 0.14–0.15 mm wide, with three spines/mm and six to seven longitudinal rows visible in lateral view. Secondary spines are abundant throughout, appearing triangular to conical, and may be either smooth or papillose.

Polyps are arranged uniserially on one side of the axis. In ethanol-preserved material, both the coenenchyme and polyps appear white. Polyps show a transverse diameter of 0.82–0.94 mm, and an interpolypar distance of 0–0.1 mm, resulting in a density of approximately ten polyps/cm (Fig. 14D).

Description of the paratypes

Paratype RMNH.COEL.50843: Unbranched colony of 48.7 cm in length with eight tight coils (Fig. 14C); proximal stem diameter 2.4 mm (Fig. 14C). Distal spines (axis diameter: 0.67 mm) are conical and elongated (Fig. 16E), simple or bifid/trilobed (Fig. 16F–H), with lobes occasionally projecting laterally in the transverse plane (Fig. 16F–H). Spines are densely papillose on two-thirds of their surface; papillae are elongated and coalesce. Polypar spines are 0.18–0.19 mm tall, 0.12–0.14 mm wide, with two spines/mm and spaced 0.66–0.72 mm apart. Secondary spines are present. Proximal spines (axis diameter: 1.7 mm) are robust, conical, with blunt

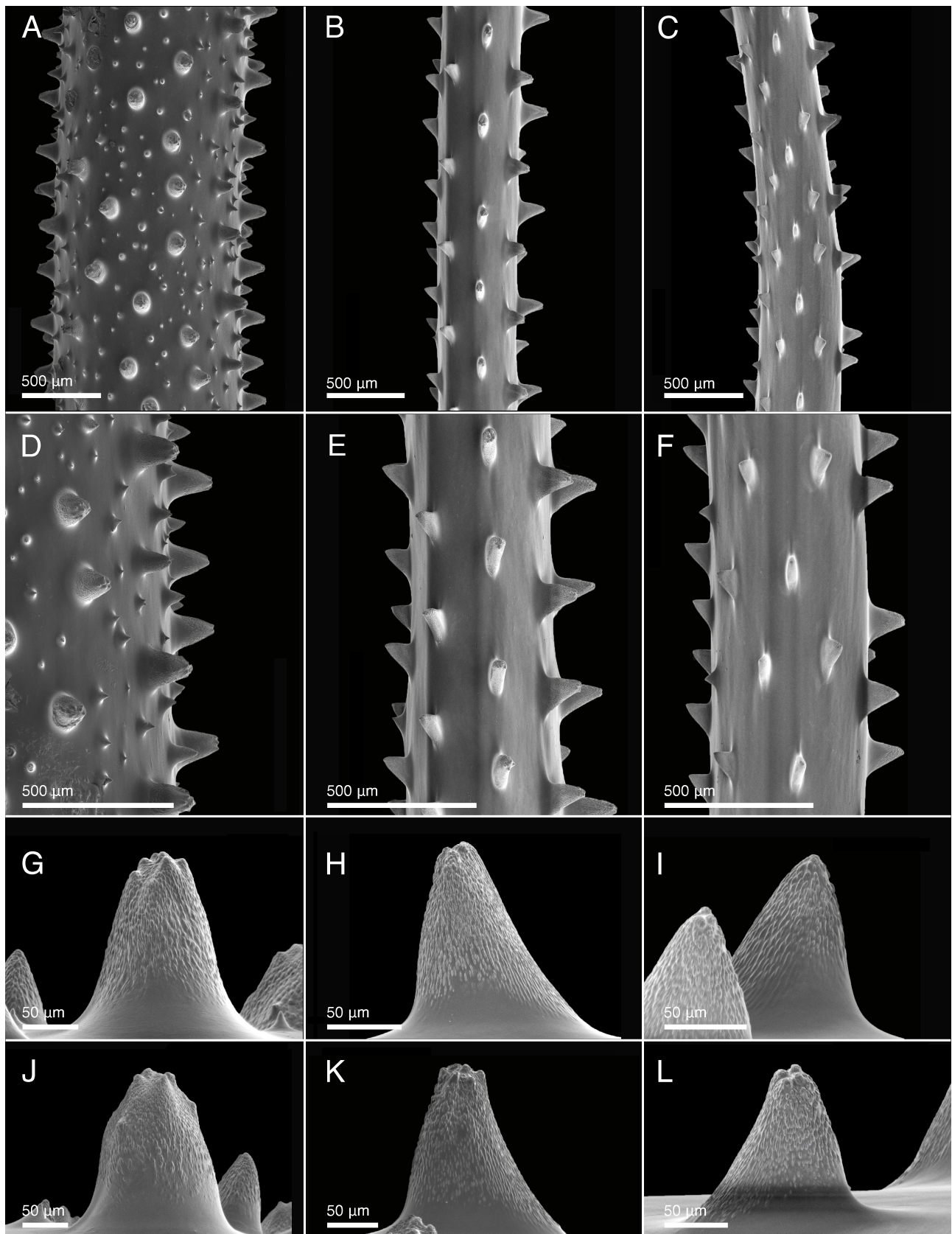


FIGURE 15. Proximal, middle, and distal skeleton of the holotype of *Multilobopathes ornatus* sp. nov. (RMNH.COEL.50840). (A, D) basal section at different magnifications; (B, E) middle section at different magnifications; (C, F) apical section at different magnifications; (G, J) close-up views of polypar spines in the basal section; (H, K) close-up views of polypar spines in the middle section; (I, L) close-up views of polypar spines in the apical section.

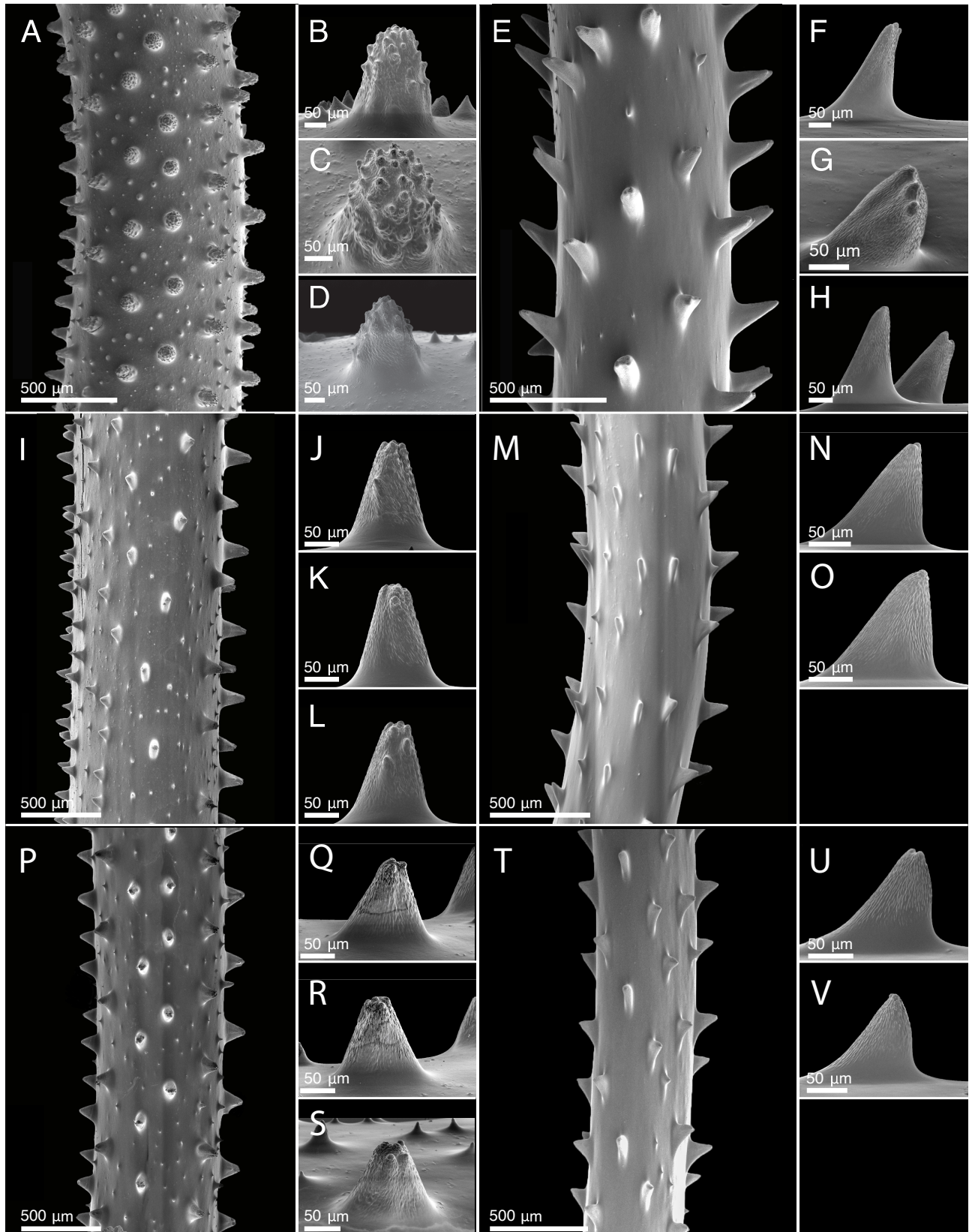


FIGURE 16. Paratypes of *Multilobopathes ornatus* sp. nov. RMNH.COEL.50843 (A) spine arrangement on proximal section; (B–D) close-up view of spines on proximal section; (E) spine arrangement on distal section; (F–H) close-up view of spines on distal section. RMNH.COEL.50841 (I) spine arrangement on proximal section; (J–L) close-up view of spines on proximal section; (M) spine arrangement on distal section; (N, O) close-up view of spines on distal section. RMNH.COEL.50842 (P) spine arrangement on proximal section; (Q–S) close-up view of spines on proximal section; (T) spine arrangement on distal section; (U, V) close-up view of spines on distal section.

apices (Fig. 16A). Lobes are highly developed, forming tubercle-like structures covering the apex and extending to the spine's midsection (Fig. 16B–D). Papillae are rounded and extend from apex to base. Polypar spines are 0.21–0.22 mm tall, 0.18–0.20 mm wide, with two spines/mm and spaced 0.63–0.67 mm apart, arranged in eight longitudinal rows in lateral view. Secondary spines are abundant, triangular and papillose.

Polyps and coenenchyme are dark red *in vivo* (Fig. 14F), turning white upon preservation in ethanol (Fig. 14E). They are arranged in a single row on one side of the stem, 0.85–0.98 mm in transverse diameter, spaced 0–0.1 mm apart, resulting in 10–12 polyps/cm (Fig. 14E, F).

Paratype RMNH.COEL.50854: Complete, unbranched colony with a sinuous, loosely coiled stem and irregular undulations (Fig. 14B). The colony is 32.5 cm tall, with a stem diameter of 1.8 mm in proximity of the base. Distal spines (axis diameter: 0.54 mm) are conical, elongated, simple or multilobed. Lobes can form a coronate arrangement, or they may also be projected on one side of the spine. Spines are densely papillose over two-thirds or the whole surface, with papillae elongated and coalescent. Polypar spines are 0.19–0.20 mm tall, 0.14–0.15 mm wide, and spaced 0.43 mm apart, with three spines/mm and eight longitudinal rows seen in lateral view. Proximal spines (axis diameter: 1.65 mm) are stout, conical, blunt and multilobed. Lobes are highly developed and numerous, they resemble tubercles and occasional extend down the sides of the spine. Papillae are mostly rounded, however elongated forms occur, extending down on the whole surface. Polypar spines are 0.23–0.24 mm tall, 0.19–0.21 mm wide, spaced 0.48–0.68 mm apart, with two or three spines/mm and ten longitudinal spine rows visible in lateral view. Secondary spines are present. Polyps are dark red *in vivo*, turning white upon preservation in ethanol. Polyps are uniserially arranged, 0.73–0.83 mm in transverse diameter, spaced 0–0.2 mm apart, resulting in 12–13 polyps/cm.

Paratype RMNH.COEL.50842: Complete colony measuring 29.7 cm, with four spirals; the first, more loosely coiled, arises 4 cm from the base, followed by three tighter coils. Distal spines (axis diameter: 0.50 mm) are triangular, with acute apex, simple or occasionally bilobed, and densely papillose with elongated, coalescing papillae (Fig. 16T–V). Polypar spines are 0.10–0.11 mm tall, 0.11–0.12 mm wide, spaced 0.60–0.66 mm apart, with three spines/mm and eight or nine longitudinal rows per lateral view. Small secondary spines are occasionally present (Fig. 16T). Proximal spines (axis diameter: 0.78 mm) are stout, conical, with broad bases and blunt apices bearing up to six lobes in a crown-like arrangement, rarely extending laterally (Fig. 16P). Rounded papillae cover the top of the spines, while elongated papillae develop almost until the end of the spine (Fig. 16Q–S). Polypar spines are 0.11–0.12 mm tall, 0.12–0.14 mm wide, spaced 0.41–0.50 mm apart, with two spines/mm and seven longitudinal rows in lateral view. Secondary spines are abundant over the entire surface.

Polyps are 0.65–0.77 mm in transverse diameter, 0–0.1 mm apart, with 10–11 polyps/cm.

Paratype RMNH.COEL.50841: Complete colony, 14 cm tall, with two tight spirals beginning 7 cm from the base. Distal spines (axis diameter: 0.58 mm) are triangular to conical, simple or bilobed, papillose over most of their surface, with elongated, coalescing papillae. Polypar spines are 0.12–0.13 mm in height, 0.11–0.12 mm wide, spaced 0.62–0.75 mm apart, with three spines/mm and nine longitudinal rows in lateral view (Fig. 16M). Few secondary spines are present. Proximal spines (axis diameter: 0.91 mm) are stout conical and blunt, with up to five apical lobes and occasionally one–two lateral ones (Fig. 16I–L). Papillae are rounded at the top of the spines, also covering the apical lobes, while elongated forms extend till the spine base. Polypar spines are 0.13–0.14 mm tall, 0.12 mm wide, spaced 0.41–0.57 mm apart, with two or three spines/mm and six or seven longitudinal rows in lateral view. Secondary spines are distributed across the entire surface.

Polyps are 0.87–1.1 mm in transverse diameter, 0–0.1 mm apart, with 9–10 polyps/cm.

Remarks. As discussed in the remarks for *Multilobopathes* **gen. nov.**, among the known whip-like black corals only *Stichopathes maldivensis* and *Cirrhopathes? diversa* exhibit the combination of a uniserial polyp arrangement on one side of the axis, the presence of secondary spines, and modifications to the apices of the primary spines. *S. maldivensis* is characterized by a straight, uncoiled corallum, whereas *M. ornatus* consistently exhibits a coiled or spiralled stem. Additionally, *M. ornatus* differs from *S. maldivensis* in possessing conical or triangular spines with simple or bilobed apices in at least a portion of the colony, a character not reported in the original description of *S. maldivensis*. Furthermore, the polypar spines of *M. ornatus* do not exceed 0.24 mm in height, in contrast to the larger spines of *S. maldivensis*, which reach up to 0.3 mm.

The spine morphology, arrangement, ornamentation, and size in the proximal portion of *M. ornatus* closely resemble those observed in *C.? diversa*. Re-examination of the schizoholotype of *C.? diversa* (USNM 100372) confirmed the presence of stout, bluntly cylindrical spines with apices bearing minimal knob-like projections (Fig. 10). However, in *M. ornatus*, the spines in the middle-proximal section are conical and robust, terminating in a blunt, multilobed apex that forms a distinct crown-like structure (Fig. 10). Notably, neither the examined material nor Brook's (1889) original description of *C.? diversa* mention the presence of conical or triangular spines with simple or bilobed apices, morphological traits that are clearly observed in the distal to mid-distal portions of *M. ornatus* and further support its recognition as a distinct species.

Etymology. The species name derives from the Latin word *ornatus*, meaning “adorned” or “decorated”. The name refers to the ornamentation of the spines in the proximal part of the colony, which bear multiple lobes and give the spines a distinctive and elaborate appearance.

Distribution. Red Sea; 94–121 m depth.

Multilobopathes intricatus Vicario **sp. nov.**

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Lineage A7 in Fig. 3; Figs. 17–19

Material examined (Table S1). **Holotype:** RMNH.COEL.50844 (Figs. 17A, C, E, G, 18), Red Sea, Al-Lith, 19.82391°N, 39.91861°E, 19 m, 15 August 2023 (collection code SA6266). **Paratypes:** RMNH.COEL.50853 (Figs. 17B, D, F, H, 19), Red Sea, Al-Lith, 19.84469°N, 39.9347°E, 31.5 m, 15 August 2023 (collection code SA6250); RMNH.COEL.50846, Red Sea, Al-Lith, 19.84469°N, 39.9347°E, 27.5 m, 15 August 2023 (collection code SA6255); RMNH.COEL.50845 Red Sea, Al-Lith, 19.84469°N, 39.9347°E, 26.3 m, 15 August 2023 (collection code SA6254).

Type locality. Red Sea.

Diagnosis. Colonies branched, bramble-like to bushy, with irregularly curved branches. Branches in all directions with thin and flexible terminal branchlets. Spines on distal portion of branchlets triangular, simple, occasionally forked, 0.08–0.11 mm tall, and 0.08–0.13 mm wide. Spines on proximal portion of branchlets conical, elongated, simple, forked or multilobed, 0.09–0.12 mm tall and 0.09–0.13 mm wide. Spines on branches conical, multilobed, 0.11–0.14 mm tall and 0.10–0.13 mm wide. Spines papillose; with elongated papillae on half to 2/3 of the spine. Polypar spines larger than abpolypar ones. Polyps orange *in vivo*, uniserial, 0.57–0.86 mm in transverse diameter, 0.06–0.17 mm apart with 10–13 polyps/cm.

Holotype description. The holotype (RMNH.COEL.50844) is a colony portion 7.5 cm tall and 9.3 cm wide (Fig. 17A, E). The holdfast and the lower part of the main branch were not sampled. Branching is up to the 6th order. Colony is bushy, with branches irregularly curved spreading in all directions, and with thin, flexible and elongated terminal branchlets measuring up to 3 cm in length. Pattern of binary division is visible across multiple branching levels, although not consistent throughout the colony. The proximal portion is 1.31 mm in diameter, while distal branchlets are 0.19–0.37 mm in diameter.

On the distal portion of a branchlet of 0.20 mm in diameter, polypar spines are triangular, simple, or rarely forked, have a papillose surface, with elongated papillae that coalesce, extending till half of the surface of the spines. Polypar spines are 0.079–0.091 mm tall, 0.087–0.10 mm wide (Fig. 18C, F, I, L), with three-four spines/mm and distanced 0.30–0.43 mm apart. Abpolypar spines are simple, 0.07 mm tall, and 0.07–0.09 mm wide. Five longitudinal rows are observed in lateral view. On the proximal portion of a distinct branchlet of 0.30 mm, polypar spines are conical, elongated, bifurcated or multilobed, with lobes mostly projecting on one side of the spine. Spines are papillose, with elongated papillae on most of the surface. Polypar spines are 0.11–0.12 mm tall, 0.092–0.097 wide, with five spines/mm and spaced 0.16–0.24 mm apart (Fig. 18B, E, H, K). Abpolypar spines are simple, 0.09–0.10 mm tall, and 0.09–0.10 mm

wide. The spines are arranged in axial rows, with six rows visible in lateral view, while the distance between the tips of two adjacent spines ranges between 0.30 and 0.43 mm. Secondary spines not present on branchlets.

On a branch measuring 0.80 mm in diameter, spines are conical with elongated papillae extending on two-third of the surface of the spine (Fig. 18A, D, G, J). The papillae are densely distributed and often coalescent. Spines show several distal lobes, often near the apex even though jagged appearance might occur (Fig. 18G). Spines 0.11–0.13 mm tall, 0.10–0.12 wide, with three spines/mm and 0.40–0.44 mm apart, with no clear distinction between polypar and abpolypar spines. Seven rows of spines are visible in lateral view. In this portion of the colony, a few small secondary spines are present.

Both coenenchyme and polyps display an orange-brown coloration *in vivo* (Fig. 17A, C). Polyps are uniserially arranged, 0.57–0.86 mm in transverse diameter and 0.12–0.17 mm apart, with 10–11 polyps/cm (Fig. 17G).

Description of the paratypes

Paratype RMNH.COEL.50853: Bushy colony lacking a basal plate, measuring 12.5 cm in height and 14.5 cm in width (Fig. 17B, D, F). Branchlets 0.24–0.29 mm in diameter; branches larger, with the most basal portion sampled measures 1.55 mm. Distal portion of branchlets of 0.18–0.21 mm in diameter have triangular spines, simple or forked, bearing elongated papillae till half surface of the spine (Fig. 19C, F, I). Polypar spines are 0.083–0.094 mm tall, 0.093–0.13 mm wide, with three spines/mm and distanced 0.42–0.48 mm apart. Six longitudinal rows in lateral view (Fig. 19C). On the proximal portion of a distinct branchlet of 0.23 mm in diameter, polypar spines are conical, forked, or multilobed, have a papillose surface, with elongated papillae that coalesce, extending till two-thirds of the surface of the spines. Polypar spines are 0.10–0.11 mm tall, 0.090–0.10 mm wide (Fig. 19B, E, H), with three spines/mm and 0.30–0.43 mm apart. They are arranged in five longitudinal rows in lateral view (Fig. 19B). Spines on a branch measuring 0.80 mm in diameter are stout, conical, and multilobed. These lobes are highly developed, and typically form a coronate arrangement, although they may also be projected on one side of the spine (Fig. 19A, D, G). Polypar spines 0.13–0.14 mm tall, 0.12–0.13 mm wide, with two-three spines/mm, irregularly arranged and distanced, but nine longitudinal rows are tentatively visible in lateral view (Fig. 19A). Polyps orange-brown *in vivo*, uniserial, 0.57–0.86 mm in transverse diameter and 0.12–0.17 mm apart, with 11 polyps/cm (Fig. 17D, H).

Paratype RMNH.COEL.50846: Complete colony, 11 cm tall and 9 cm wide. Branchlets 0.26–0.35 mm in diameter, with the proximal stem 1.11 mm in diameter. On the distal portion of a 0.16 mm diameter branchlet, spines are triangular, elongated, simple or bifurcated, and papillose. Papillae elongated, coalescent, covering two-third or the whole surface. Polypar spines 0.10–0.11 mm tall, 0.10–0.12 mm wide, with three spines/mm and

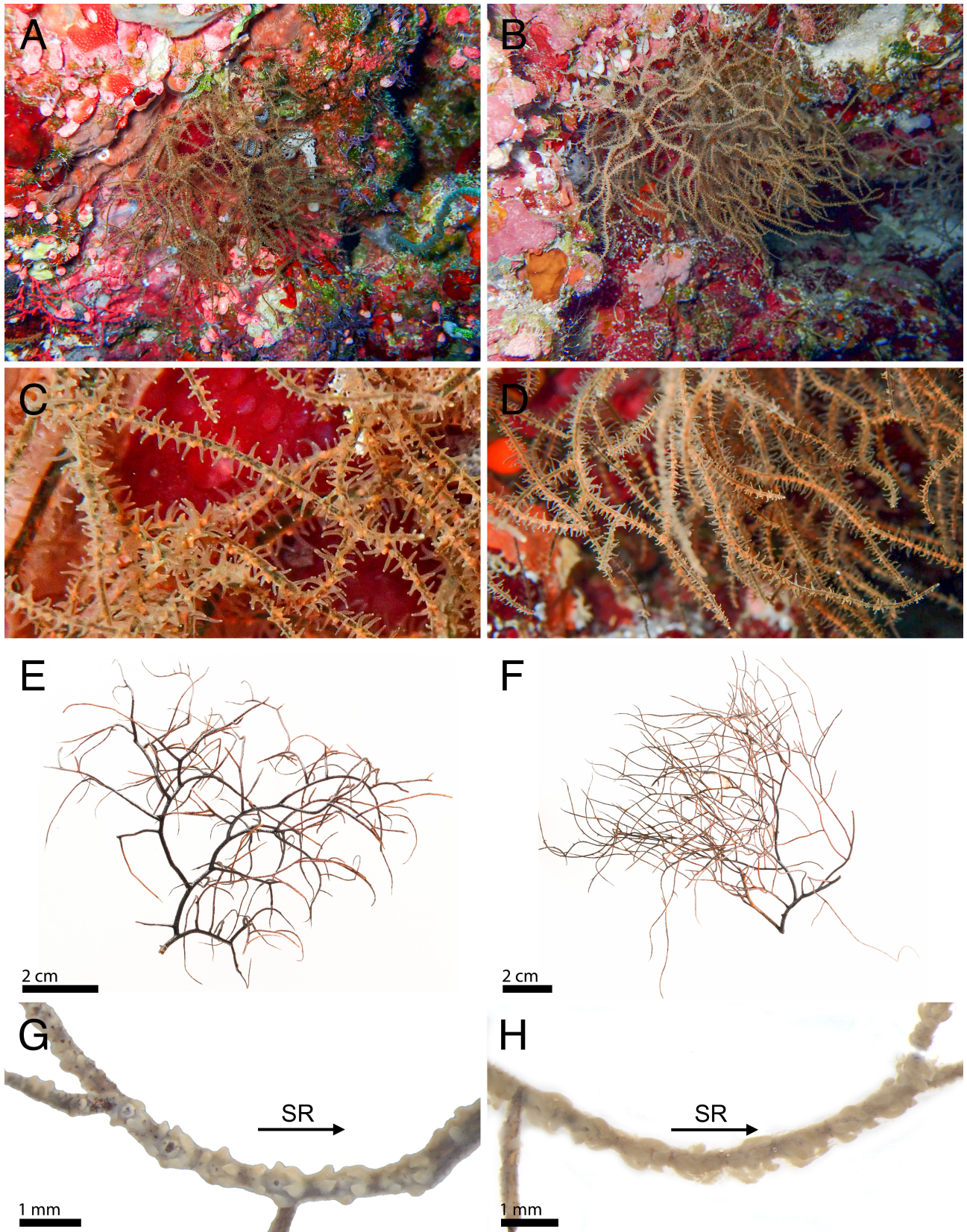


FIGURE 17. *Multilobopathes intricatus* sp. nov. (A) *In situ* image of holotype RMNH.COEL.50844; (B) *In situ* image of paratype RMNH.COEL.50853; (C) Close-up of polyps of holotype RMNH.COEL.50844; (D) Close-up view of polyps of paratype RMNH.COEL.50853; (E) Dry colony of holotype RMNH.COEL.50844; (F) Dry colony of paratype RMNH.COEL.50853; (G) Close-up view of ethanol-preserved polyps of holotype RMNH.COEL.50844; (H) Close-up view of ethanol-preserved polyps of paratype RMNH.COEL.50853. SR: single row.

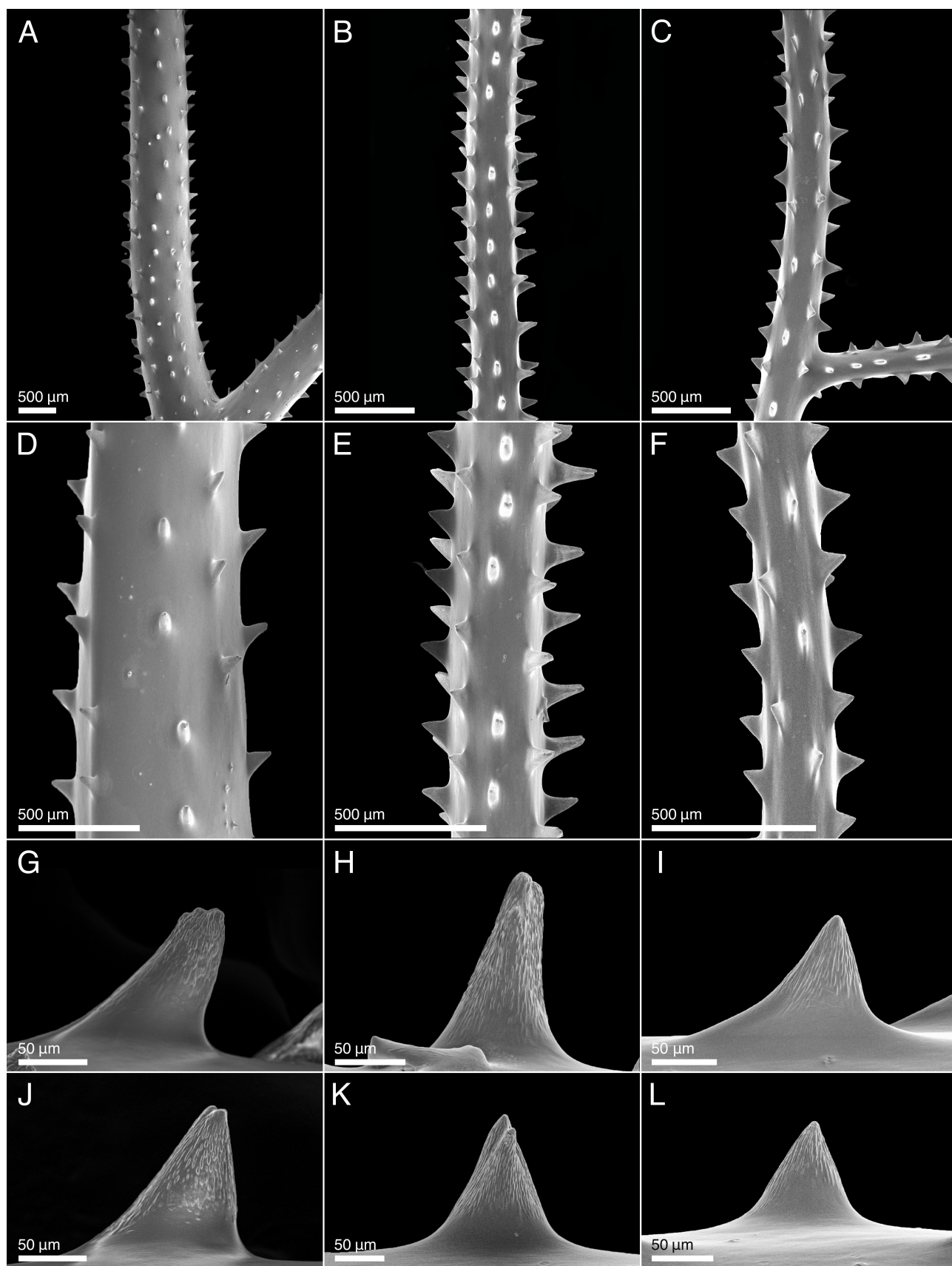


FIGURE 18. Spines on branch, and branchlet fragments of the holotype RMNH.COEL.50844 of *Multilobopathes intricatus* sp. nov. (A, D) spine arrangement on branch at different magnifications; (B, E) spine arrangement on proximal section of a branchlet at different magnification; (C, F) spine arrangement on distal section of a branchlet at different magnification; (G, J) close-up view of spines of the branch section; (H, K) close-up view of polypar spines on proximal section of a branchlets; (I, L) close-up view of polypar spines on distal section of a branchlets.

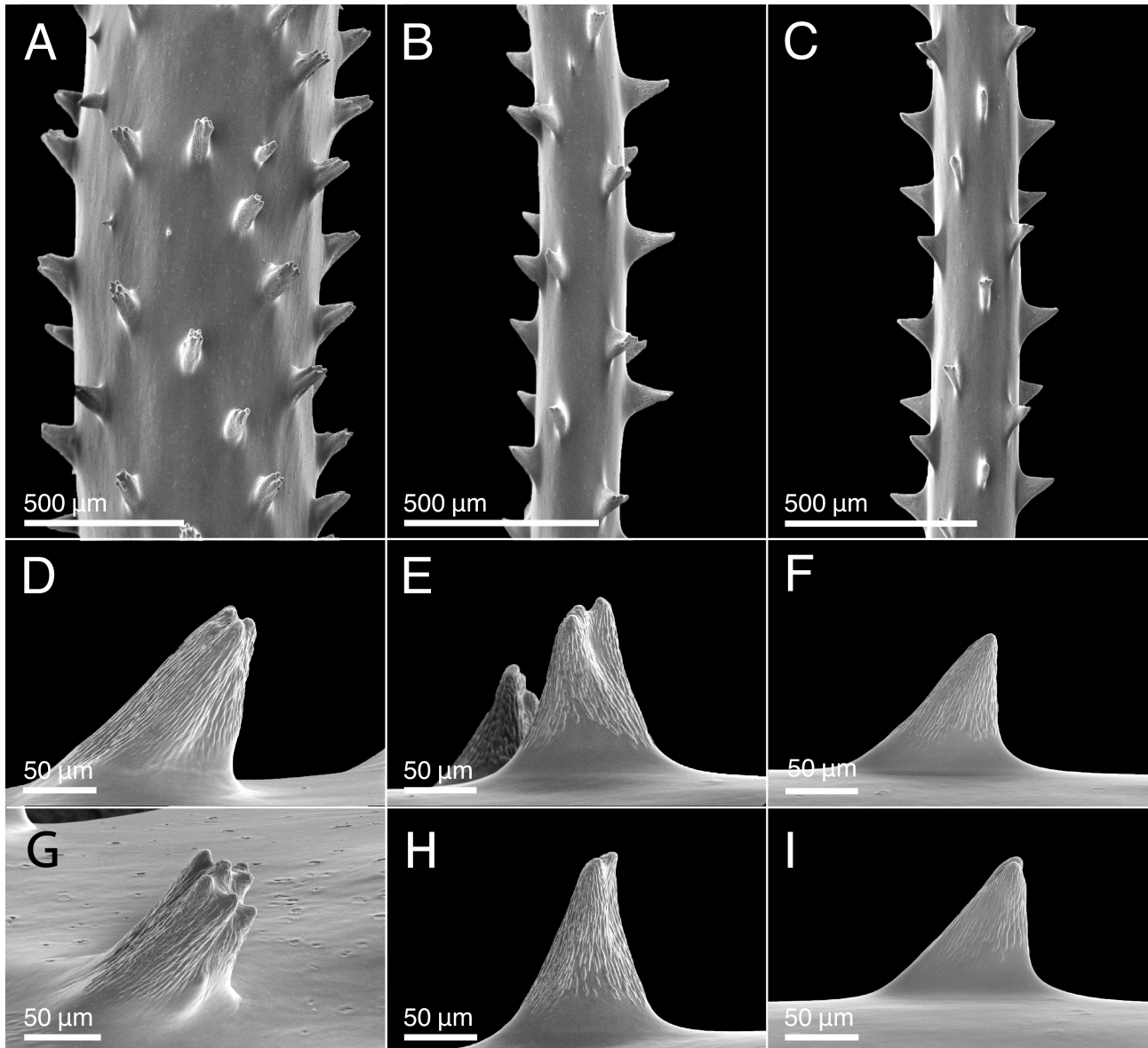


FIGURE 19. Spines of paratypes of *Multilobopathes intricatus* sp. nov. RMNH.COEL.50853 (A) spine arrangement on branch; (B) spine arrangement on proximal section of a branchlet; (C) spine arrangement on distal section of a branchlet; (D, G) close-up view of spines on branch; (E, H) close-up view of spines on proximal section of a branchlet; (F, I) close-up view of spines on distal section of a branchlet.

0.46–0.53 mm apart. Spines on the proximal portion of a branchlet measuring 0.40 mm in diameter are conical, mostly simple, but occasionally forked, and with elongated papillae the coalescence till two-third of the spine surface. Spines are 0.09–0.10 mm tall, 0.11–0.13 mm wide, with three-four spines/mm and spaced 0.42–0.49 mm apart. Polyps are orange-brown *in vivo* and uniserial arranged. Due to degradation of the polyps following ethanol preservation, size measurements could not be assessed.

Remarks. Among the previously described branched species of Antipatharia characterized by papillose spines with forked or multilobed apices in at least some portions of the colony are *Multilobopathes lentipinna* **comb. nov.**, *Antipathes griggi*, *Antipathes spinulosa*, *Antipathes fruticosa*, *Antipathes arborea*, *Antipathes curvata*, and *Antipathes galapagensis*.

A. fruticosa, *M. lentipinna*, and *A. griggi* differ from *M. intricatus* in exhibiting distally directed branching (see Opresko 2009, Figs. 1, 5), in contrast to the more irregular, multidirectional branching pattern observed in the latter. *A. galapagensis* can be distinguished by its tall, bushy corallum with pinnately arranged branchlets and polyps irregularly distributed along the stem and branches, features not observed in *M. intricatus*.

A. arborea differs by its arborescent growth form, reaching up to 90 cm in height, and by its larger polyps, with a transverse diameter of approximately 1.3 mm (Dennis M. Opresko pers. obs.). In contrast, *M. intricatus*, exhibits a bushy morphology and polyps smaller than 0.86 mm in transverse diameter. As the species under examination, *A. curvata* displays a bushy colony morphology. However, a re-examination of the schizoholotype of the species

(USNM 100416) reveals spines inclined distally at 35–40°, densely arranged on branches ~0.55 mm in diameter (spacing: 0.19–0.28 mm), with papillae confined to the upper portion of the spine that fade progressively towards the middle, transitioning into a faintly striated texture. In contrast, *M. intricatus* exhibits spines that are mostly vertically oriented and more spaced (0.40–0.68 mm) on branches of comparable size, and sharp papillae extending up to the full spine surface. Moreover, the polyps in *A. curvata* reach up to 1.3 mm in transverse diameter, notably larger than those observed in *M. intricatus*.

The species most similar in external appearance to *M. intricatus* is *A. spinulosa*. However, the spines in *A. spinulosa* reach up to 0.34 mm in height (Opresko 2009), whereas the tallest spines in *M. intricatus* are approximately half that size.

Molecular data of type material of the species *M. lentipinna*, *A. curvata*, and *A. galapagensis* confirm that these species are not related to the current one (Fig. 3).

Etymology. The specific name *intricatus* is derived from the Latin, meaning “entangled” or “complex”. It refers to the intricately branched colony morphology characterized by irregularly curved branches spreading in multiple directions.

Distribution. Red Sea; 20–31 m depth.

Multilobopathes densispinosus Vicario & Terraneo **sp. nov.**

urn:lsid:zoobank.org:act:B0677D39-EA93-4ACE-B536-9C49F3C3D507

Lineage A9 in Fig. 3; Figs. 20–22

Material examined (Table S1). **Holotype:** RMNH.COEL.50847 (Figs. 20A, D, F, 21), Red Sea, North of Al Lith, 20.252046°N 39.50635°E, 206 m, 27 February 2022 (collection code NTN0124BIO19). **Paratype:** RMNH.COEL.50848 (Figs. 20B, C, E, G, 22), Red Sea, North of Al Lith, 20.252080°N 39.50416°E, 227 m, 27 February 2022 (collection code CHR0202BIO13).

Type locality. Red Sea.

Diagnosis. Corallum unbranched, sinuous or forming loose spirals. Distal spines conical or triangular, simple or forked, and papillose. Papillae rounded or slightly elongated, distinct, covering up to two-thirds of the spine surface. Polypar spines 0.09–0.11 mm tall and 0.11–0.13 mm wide. Abpolypar spines 0.07–0.08 mm tall and 0.10–0.13 mm wide. Proximal spines are conical, forked or multilobed. Papillae rounded or slightly elongated, covering up to the whole surface. Polypar spines 0.12–0.14 mm tall and 0.15–0.17 mm wide. Abpolypar spines 0.07–0.11 mm tall and 0.10–0.13 mm wide. Secondary spines abundant. Polyps arranged unilaterally, 0.87–1.2 mm in transverse diameter, 0–0.2 mm apart, with nine–eleven polyps/cm.

Description of the holotype: The holotype is a complete, unbranched colony, 98 cm long, attached to a hard substrate via a basal holdfast (Fig. 20A). The corallum is slender and flexible, with a predominantly

horizontal orientation and irregular curvatures that may reflect environmental influences (Fig. 20A). The corallum has a proximal diameter of 2 mm and a distal diameter of 0.09 mm.

Spines on the distal corallum (0.51 mm in diameter) are triangular and simple (Fig. 21E–H), though occasional forked spines are present. Spines are papillose from the apex to near the base, bearing rounded papillae near the tip and elongated papillae towards the base. These papillae are distinct and moderately protrude from the spine surface without coalescing (Fig. 21G, H). Polypar spines are 0.10–0.11 mm tall, 0.10–0.13 mm wide. Abpolypar spines are 0.07–0.08 mm tall and 0.10–0.13 mm wide. There are three–four spines/mm and they are irregularly placed and distanced, without clear longitudinal rows. Secondary spines are scattered, lacking any form of ornamentation (Fig. 21E, F). Their density is 21.9 secondary spines/mm². In some curved portions of the colony, only secondary spines are present on one side.

In the middle portion of the colony (1.6 mm in diameter), spines are conical and predominantly bi- or trilobed (Fig. 21A–D). Papillae are rounded or slightly elongated, coalescent, and protrude from the spine surface, extending from the apex to about two-thirds of its length (Fig. 21C, D). Polypar spines are 0.12–0.14 mm tall and 0.15–0.16 mm wide, while abpolypar spines are consistently reduced, being 0.074–0.09 mm tall and 0.11–0.13 mm wide. There are two–three spines/mm. Secondary spines are extremely abundant, especially on the abpolypar side, with a density of 85 secondary spines/mm² (Fig. 21A, B).

Polyps are white, with elongated sagittal tentacles (Fig. 20D). The coenenchyme is thin, allowing the dark coloration of the underlying skeleton to be visible (Fig. 20D). In the proximal part polyps are arranged alternately on one side of the axis (Fig. 20D), while in the distal sections they are uniseriably arranged on the same side (Fig. 20F, G). Polyps 0.87–1.2 mm in transverse diameter, with eight or nine polyps/cm. Interpolypar space up to 0.1 mm.

Description of the paratype

Paratype RMNH.COEL.50848: Complete colony with basal plate, 99 cm long. The colony is unbranched, growing vertically for approximately 30 cm before forming a loose distal spiral and extending horizontally (Fig. 20B, C). Proximal and distal stem diameters are 1.8 mm and 1.1 mm, respectively.

In the distal section (0.65 mm in diameter) spines are triangular, simple and acute (Fig. 22E–H). Papillae are rounded and extend over two-thirds of the spine surface (Fig. 22G, H). They are distinct on the apical and lateral surfaces but become faint below the upper half of the spine. Polypar spines are 0.09–0.11 mm tall and 0.13–0.14 mm wide, with three–four spines/mm and arranged in nine–ten longitudinal rows. Secondary spines are absent. In the middle section (1.4 mm in diameter) polypar spines are conical and faintly bi- and trilobed (Fig.

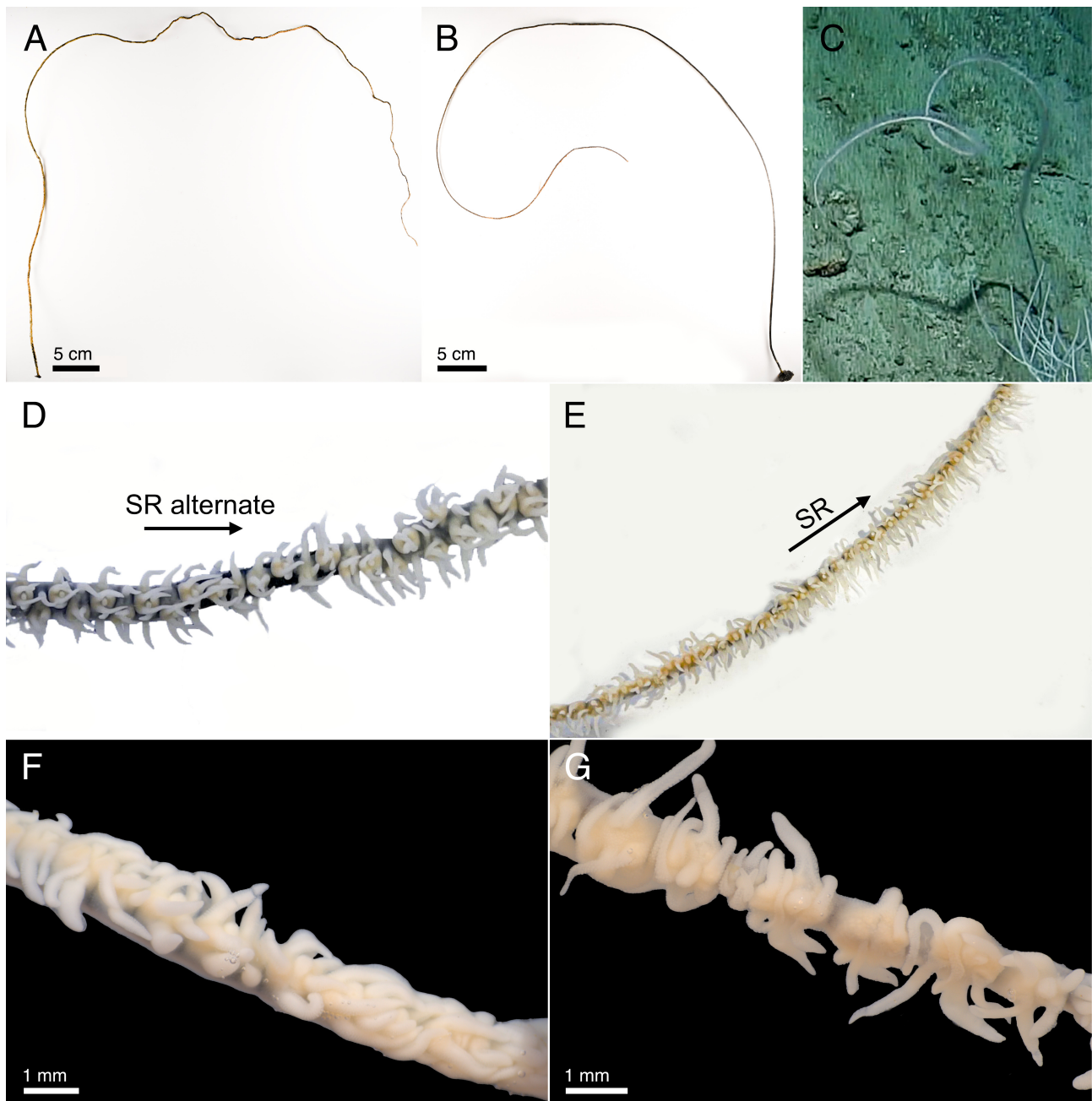


FIGURE 20. *Multilobopathes densispinosus* sp. nov. (A) Dry colony of the holotype RMNH.COEL.50847; (B) Dry colony of the paratype RMNH.COEL.50848; (C) *In situ* colony of the paratype RMNH.COEL.50848; (D) Polyps arrangement on the middle-proximal portion of the holotype right after collection; (E) Polyps arrangement on the middle portion of the paratype right after collection; (F) Polyps arrangement on the apical section of the holotype preserved in ethanol; (G) Polyps arrangement on the apical section of the paratype preserved in ethanol. SR: single row

22A–D). Papillae are rounded or occasionally elongated, extremely developed, covering the entire spine surface and often coalescing to the point of appearing as a single structure (Fig. 22C, D). Polypar spines are 0.12–0.13 mm tall, 0.16–0.17 mm wide, with four-six spines/mm and irregularly arranged. Secondary spines are abundant (Fig. 22A, B). Polyps are white *in vivo*, uniserially arranged, 1–1.1 mm in traverse diameter, spaced up to 0.1 mm, resulting in eleven polyps/cm (Fig. 20E, G).

Remarks: Among previously described whip-like black coral species, eight are known to exhibit secondary

spines: *Cirrhopathes? diversa*, *Cirrhopathes gardineri*, *Cirrhopathes secchini*, *Stichopathes alcocki*, *Stichopathes bispinosa*, *Stichopathes bournei*, and *Stichopathes maldivensis*. Of these, only *Stichopathes maldivensis*, *Cirrhopathes? diversa* and *Cirrhopathes gardineri* show modifications of the spine apex. The latter can be excluded from further comparison due to its irregular polyp arrangement along the corallum, which contrasts with the mostly uniserial pattern observed in the present material. Brook (1889) originally described *Cirrhopathes? diversa* as having stout, cylindrical spines with blunt

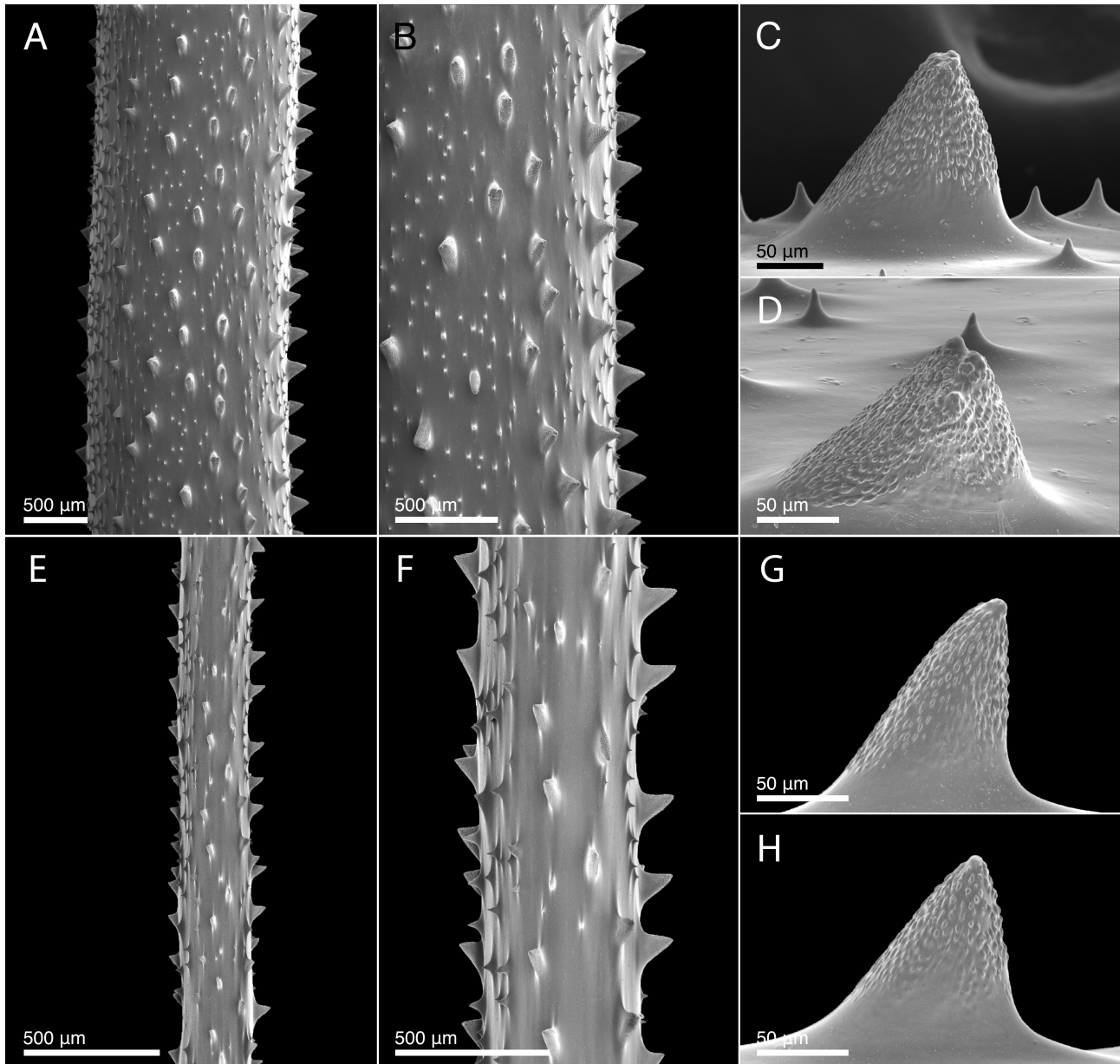


FIGURE 21. Spines arrangement in the middle and distal sections of the holotype RMNH.COEL.50847. *Multilobopathes densispinosus* sp. nov. (A, B) spines arrangement of middle section at different magnifications; (C, D) close-up view of polypar spines in the middle section; (E, F) spines arrangement of distal section at different magnifications; (G, H) close-up view of polypar spines in the distal section.

apices. The re-examination of the type specimen (USNM 100372) confirmed that the primary spines are stout and cylindrical, but the apex is ornamented with multiple knob-like projections, and secondary spines are densely distributed over the corallum surface (Fig. 10).

Although the type specimen of *S. maldivensis* is presumed lost, Brook (1889) described its spines as stout, bluntly conical, with rough surfaces and a knobbed apex. The conical and triangular shape of the spines in the present species and their multilobed nature do not match those of any previously described species, including *S. maldivensis* and *C. ? diversa*, and therefore preclude its assignment to any of these taxa.

Etymology. The specific name *densispinosus* is derived from the Latin words *densus* meaning “dense”

and *spinosus* meaning “spiny”. This refers to the species’ characteristic dense arrangement of secondary spines.

Distribution. Red Sea; 206–227 m depth.

aff. *Cirrhopathes*

Lineages B10–B12 in Fig. 3; Figs. 23, 24

Material examined (Table S1): SA4996, Red Sea, Thuwal, Long Reef, 8 m; SA5020, Red Sea, Thuwal, Rose Reef, 8 m; SA5023, Red Sea, Thuwal, Rose Reef, 8 m; SA5024, Red Sea, Thuwal, Rose Reef, 8.0 m; SA5037, Red Sea, Thuwal, Tahala Reef, 23 m; SA5041, Red Sea, Thuwal, Tahala Reef, 20 m; MD392, Madagascar, Nosy

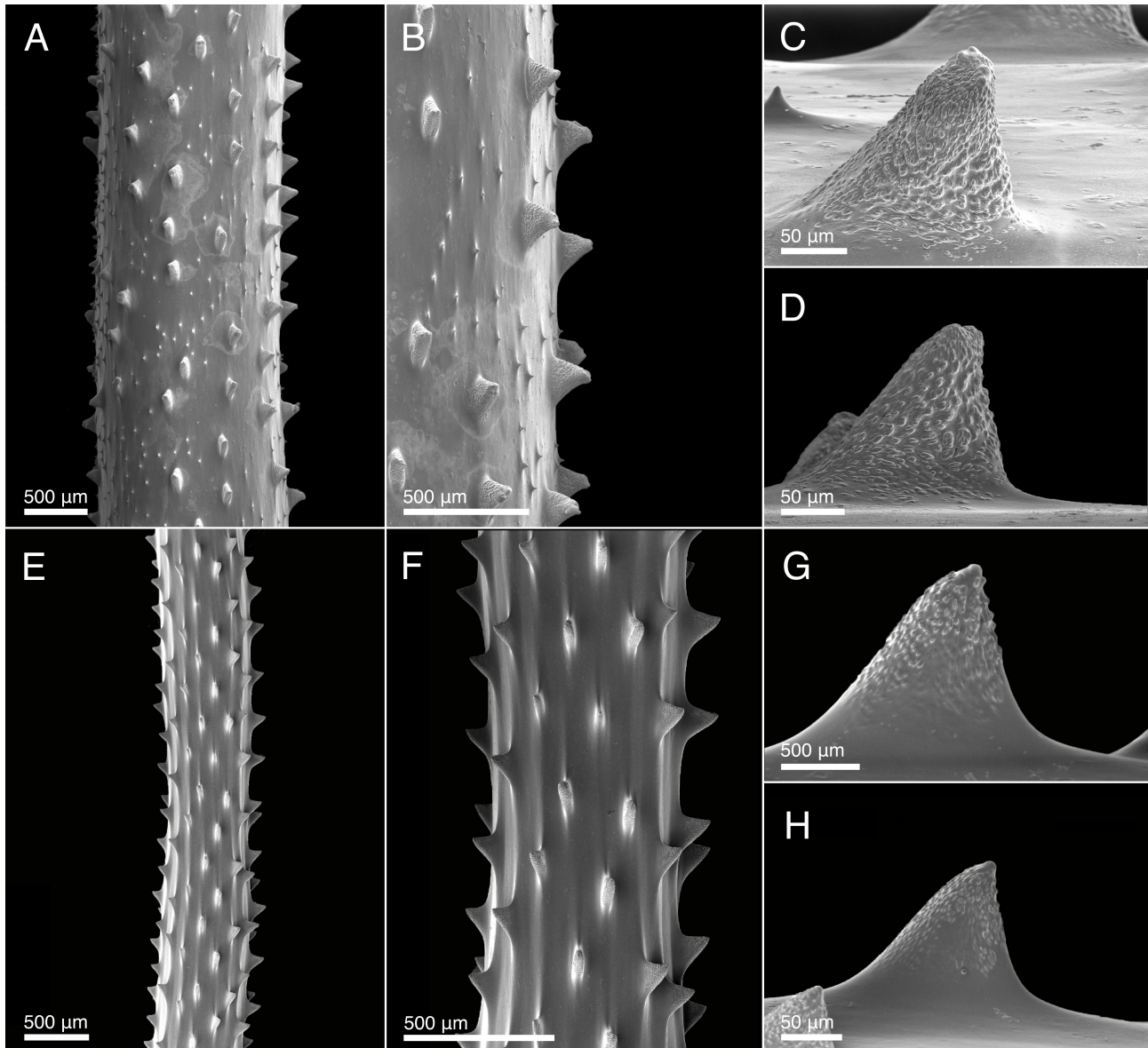


FIGURE 22. Spines arrangement in the middle and distal fragments of the paratype RMNH.COEL.50848. *Multilobopathes densispinosus* sp. nov. (A, B) spines arrangement of middle section at different magnifications; (C, D) close-up view of polypar spines in the middle section; (E, F) spines arrangement of distal section at different magnifications; (G, H) close-up view of polypar spines in the distal section.

Be, Nosy Tanga, 6 m; MD402, Madagascar, Nosy Be, Nosy Tanga, 8 m; MD439, Madagascar, Befotaka Bay, 7.8 m; MD547, Madagascar, Nosy Be, Nosy Sakatia, 9 m; MD601, Madagascar, Nosy Sakatia, 6.9 m; USNM 1293026, Japan, Okinawa, 46 m; FP093, French Polynesia, Sociétés, Tetiaroa, 12 m; FP113, French Polynesia, Sociétés, Bora Bora, 10 m; FP146, French Polynesia, Sociétés, Bora Bora, 10 m.

Description of material examined: Colonies unbranched, with straight, sinuous, or occasionally contorted growth forms (Fig. 23A–F). Spines on distal sections of the colonies are triangular or conical, laterally compressed, simple with mostly acute apex (Fig. 24B, D, F, H). They are papillose up to 2/3 of the spine surface, with rounded papillae at the top and elongated forms towards the bottom. Spines are 0.12–0.19 mm tall, 0.10–

0.13 mm wide, distanced 0.17–0.8 mm apart, and up to 10 longitudinal rows of spines are seen in lateral view. On sections ranging 1.6–2.8 mm in diameter, spines are conical, blunt, simple, and exhibit a half to fully papillose surface adorned with well-developed papillae, rounded on top and elongated towards the bottom (Fig. 24A, C, E, G). They are 0.12–0.25 mm tall, 0.13–0.17 mm wide and spaced 0.2–0.7 mm apart. Spines are distributed in irregular rows, but approximately up to 18 longitudinal rows of spines are seen in lateral view. Secondary spines are not present, though newly formed spines often show a narrow cylindrical shape (Fig. 24).

In situ colonies exhibit several distinct phenotypes. Their coenchime can be grey, light green, dark green, or brown, with polyps being orange, green or yellow (Fig. 23). Distal polyps tend to be arranged in multiple irregular



FIGURE 23. aff. *Cirrhipathes* spp. (A–F) *In situ* images showing the range of phenotypes.

rows, leaving one side of the axis free of polyps, while middle and proximal polyps are distributed in multiple irregular rows all around the stem sometimes without leaving one side of the axis free (Fig. 23). Polyps are 0.6–2.1 mm in transverse diameter, with 8–12 polyps/cm.

Distribution. Red Sea, Madagascar, Japan (Okinawa), Papua New Guinea, French Polynesia; 5–46 m depth.

***Papilopathes* Chimienti & Vicario gen. nov.**

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Antipathes (in part), Verrill 1928: pp. 7, 9,

?*Antipathes* (in part), Grigg 1965: pp. 244–260

Antipathes (in part), Grigg & Opresko 1977: 242–261

? *Antipathes* (in part), Zou & Zhou 1984: p. 104

Antipathes (in part), Wagner *et al.* 2010: pp. 275–287

Antipathes (in part), Gress *et al.* 2020: pp. 1–6

Antipathes (in part), Morgulis *et al.* 2022: p. 38

Diagnosis. Corallum unbranched or branched. Spines triangular or conical; simple with acute apex in distal sections, blunter in the middle and proximal sections. Spines papillose up to 2/3 of the spine surface; papillae generally elongated. Polypar spine height 0.06–0.12 mm; 5–9 longitudinal rows in lateral view. Secondary spines absent. Polyps arranged uniserially, 0.34–1.17 mm in transverse diameter, 0.20–0.63 mm apart; 7–14 polyps/cm.

Type species. *Antipathes grandis* Verrill, 1928 accepted as *Papilopathes grandis* (Verrill, 1928) **comb. nov.**

Species in the genus. *Papilopathes grandis* (Verrill, 1928) **comb. nov.**

Remarks. *Papilopathes* gen. nov. is distinguished from other genera within the order Antipatharia by the

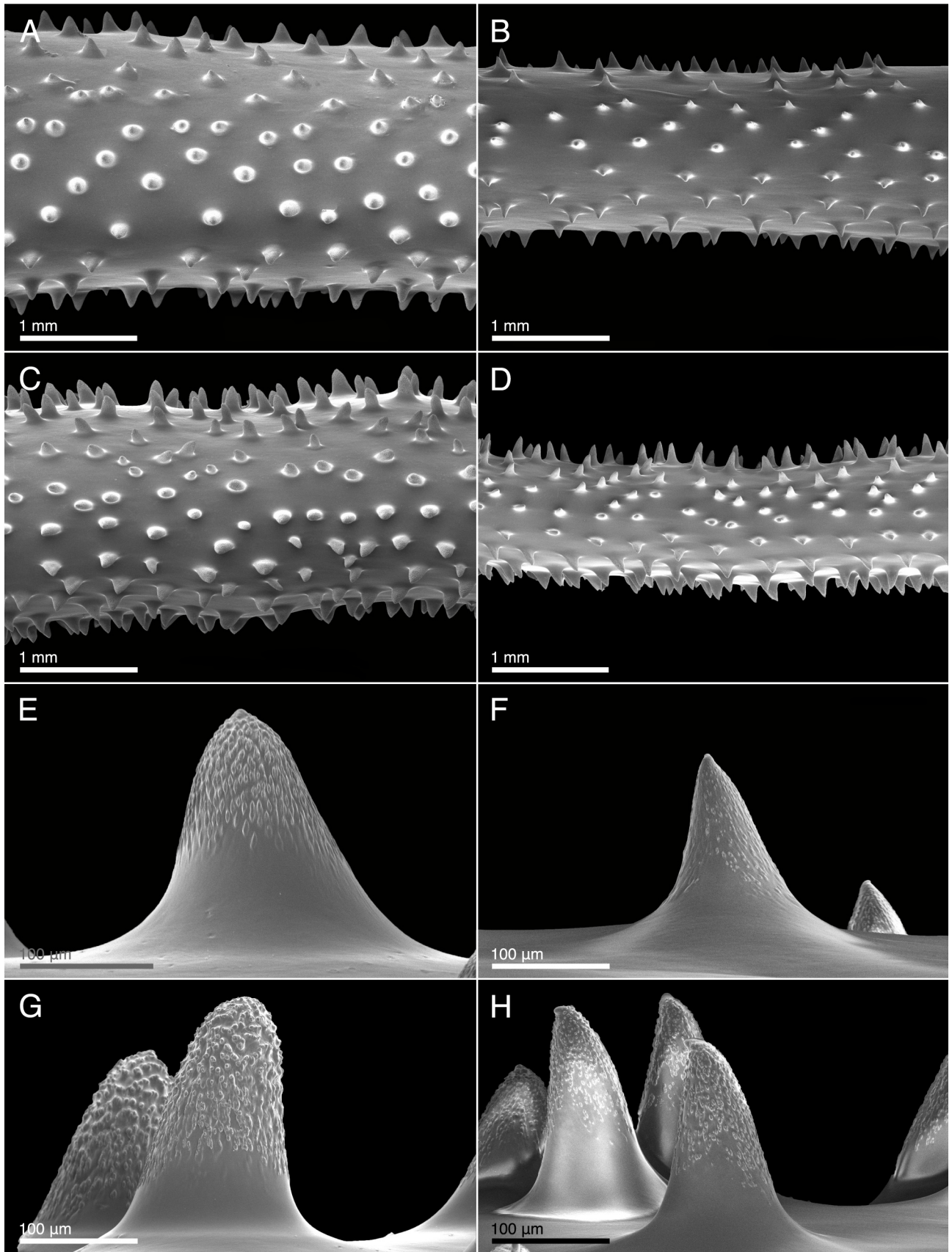


FIGURE 24. Examples of spines of aff. *Cirrhipathes* spp. Spine arrangement of proximal sections of corallum and close-up view of polypar spines (A, E) SA4996; (C, G) SA5023; spines arrangement of distal sections of corallum and close-ups view of polypar spines (B, F) SA4996; (D, H) SA5023.

combination of unbranched or branched colony forms and simple papillose spines.

Among genera that include both branched and unbranched forms, *Multilobopathes* **gen. nov.** differs from *Papillopathes* by having spines with apices that may be simple, forked, or multilobed, and by the presence of secondary spines in at least part of the colony. In contrast, *Papillopathes* consistently exhibits simple spines and lacks secondary spines. The two genera also differ in polyp size and spacing: *Papillopathes* has smaller polyps (0.34–1.1 mm in transverse diameter) compared to *Multilobopathes* **gen. nov.** (0.65–2 mm), and a larger interpolypar spacing (0.20–0.63 mm vs 0–0.3 mm).

Papillopathes **gen. nov.** differs from *Opreskopathes* **gen. nov.** in the morphology of the papillae, which in *Opreskopathes* **gen. nov.** are so developed that they nearly resemble tubercles. In addition, spine height in

Opreskopathes **gen. nov.** reaches up to 0.40 mm, more than twice the height of the tallest spines observed in *Papillopathes* **gen. nov.**

Etymology. From the Latin *papilla*, “small protuberance”, indicating the papillose characteristic of the spines. Gender: masculine

Distribution. Red Sea, Madagascar, Australia (Coral Sea), Hawaii; 11–123 m depth.

Species assigned to *Papillopathes* included in this study

Papillopathes grandis (Verrill, 1928) **comb. nov.**; lineage C13 in Fig. 3; Fig. 25. Holotype: BPBM 102; type locality: Hawaii. Material morphological examined, schizoholotype, USNM 1072629, Hawaii, Maui Island,

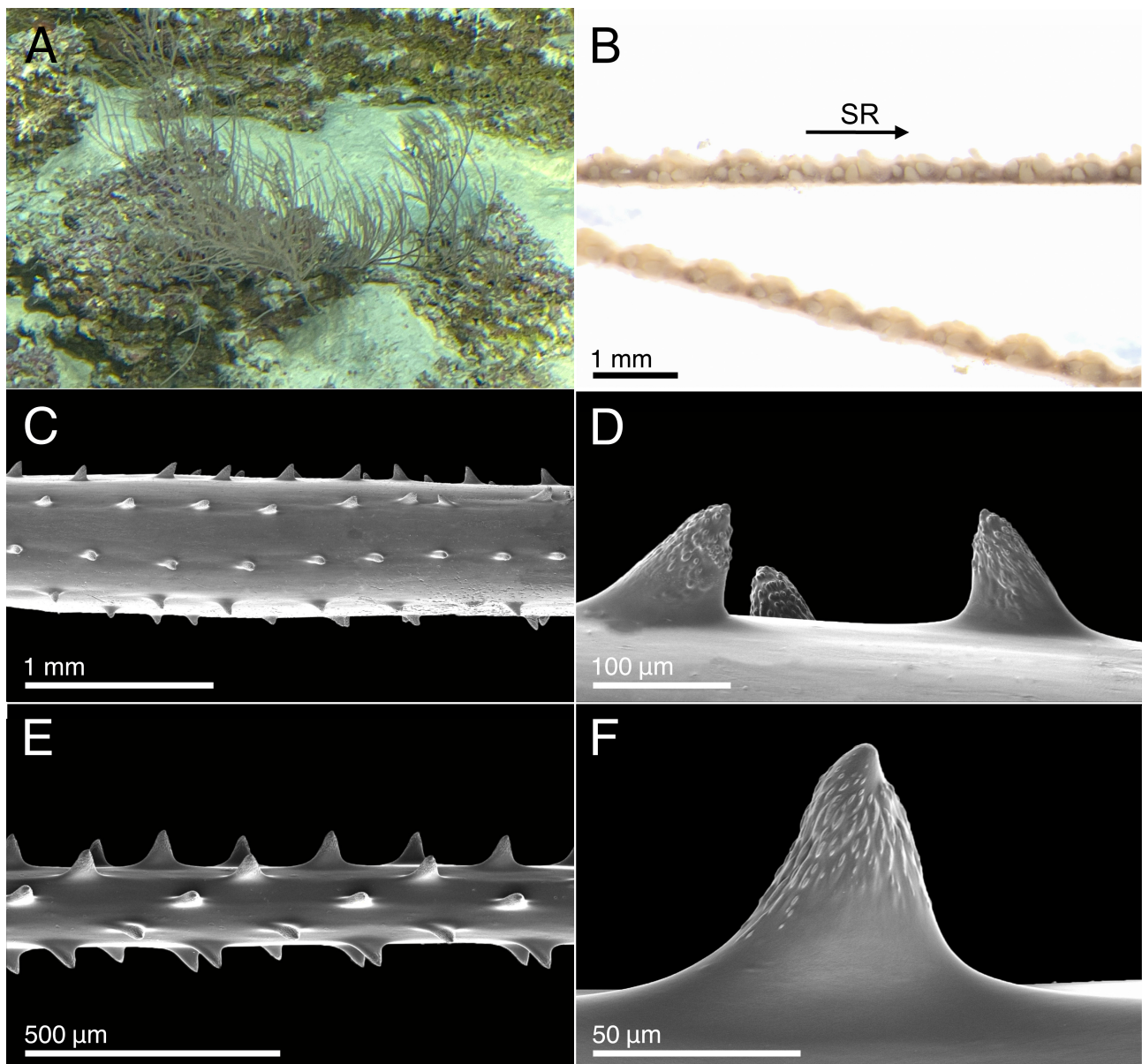


FIGURE 25. *Papillopathes grandis* NDR0919_3. (A) *In situ* image of the colony; (B) Ethanol-preserved polyps arrangement on branchlets; (C) spine arrangement on branch; (D) close-up view of polypar spine on branch; (E) spine arrangement on branchlet (F) close-up view of polypar spine on branchlet. SR: single row.

depth NA, material morphological and molecular examined, topotype, USNM 1096111, Hawaii, Keyhole Pinnacle, Auau Channel, depth 81 m.

Other material examined (Table S1): SA4575, Red Sea, Gulf of Aqaba, depth 1–30 m; DIVE10/11_1, Red Sea, Strait of Tiran, 27 m; SA5034, Red Sea, Thuwal, Tahala Reef, 24 m; NTN0043_26, Red Sea, North of Duba, 80 m; NTN0037_18A, Red Sea, Gulf of Aqaba, 73 m; NDR0919_3, Red Sea, Gulf of Aqaba, 101 m; CHR0045_2 Red Sea, Gulf of Aqaba, 116 m.

Description of material examined. Colonies are sparsely or densely branched, up to the 10th order (Fig. 25A). Branches are distally directed, with elongated and flexible terminal branchlets that are typically arranged uniserially (Fig. 25A); however, in some colonies, branchlets may be irregularly disposed around the main branches. Branch diameter ranges 0.80–3.10 mm, while terminal branchlets are 0.30–0.80 mm in diameter and can reach up to 15 cm in length. Spines on branchlets are conical and laterally compressed, occasionally triangular in shape, with a simple, acute apex (Fig. 25E, F). Polypar spines are 0.06–0.10 mm tall, 0.07–0.10 mm wide, and are spaced 0.19–0.41 mm apart. The spine surface is covered with papillae up to 2/3 of the surface; papillae are predominantly elongate, though rounded forms may occur near the apex (Fig. 25F). Abpolypar spines are smaller than polypar ones, ranging from 0.05–0.08 mm in height and 0.06–0.10 mm in width. From five to nine longitudinal rows of spines are visible in lateral view. On larger branches, spines are conical but not laterally compressed, retaining a simple, acute apex (Fig. 25C, D). They are 0.08–0.13 mm tall, 0.09–0.13 mm wide, and 0.31–0.73 mm apart. Abpolypar spines are smaller, being 0.05–0.11 mm tall. Five to eight longitudinal rows of spines are visible in lateral view. Secondary spines are absent. Colonies color *in vivo* is red or white (Fig. 25A). Polyps are arranged in a single row on branchlets (Fig. 25B), occasionally occurring on two or more sides of the larger branches. Polyps are 0.44–0.82 mm in transverse diameter and 0.27–0.40 mm apart, resulting in a density of 9–12 polyps/cm.

Remarks. Based on corallum growth and spine morphology, three nominal species resemble the Red Sea *P. grandis* specimens: *Opreskopathes caribbeana* **comb. nov.**, *Antipathes pseudodichotoma*, and *Antipathes regularis*. The latter two share a similar growth pattern with the Red Sea colonies, but their original descriptions lack sufficient detail for a comprehensive comparison. *A. regularis* was described from a single branch fragment, preventing a full assessment of colony architecture. While spine shape is comparable, the description does not include information on spine size and surface ornamentation. *A. pseudodichotoma* was described from two broken branches that both exhibit pseudodichotomous branching, a feature not observed in the Red Sea specimens. Moreover, the original description lacks any description of spine shape or ornamentation.

Among the three, *O. caribbeana* **comb. nov.** most closely resembles the Red Sea material, as already detailed in Wagner *et al.* (2010), sharing long and narrow

terminal branchlets (sometimes uniserially arranged) and similar size for both spines and polyps. However, it can be distinguished by the ornamentation of the spines: in *O. caribbeana*, papillae are notably thick and resemble protruding tubercles, whereas in the Red Sea specimens they are less prominent. In addition, molecular data from the holotype of *O. caribbeana* **comb. nov.** support its placement in the genus *Opreskopathes* **gen. nov.**, confirming its distinction from the Red Sea material.

Distribution. Red Sea, Madagascar, Australia (Coral Sea), Hawaii; 11–116 m depth.

Papillopathes sp. 2; lineage C15 in Fig. 3; Fig. 26

Material examined (Table S1): NTN0059_21A Red Sea, Strait of Tiran, 106 m; CHR0268RK2C, Red Sea, Yanbu, 94 m; M193_089_2_5, Red Sea, Al Wajh, 111 m (Fig. 26); NTN0034_24, Red Sea, Gulf of Aqaba, 57 m.

Description of material examined. Unbranched colonies with several spirals arising either from the basal or central part of the colony (Fig. 26A).

Spines on the distal half of the corallum (sections 0.23–0.36 mm in diameter) are triangular or conical, perpendicular to the corallum, and papillose (Fig. 26B, C). Papillae are elongated, covering at least 2/3 of the spine surface (Fig. 26C). Depending on the examined region, they may appear distinct or partially coalescent. Polypar spines in this region are 0.09–0.12 mm tall and 0.08–0.11 mm wide, spaced 0.35–0.50 mm apart, with six to eight longitudinal rows visible in lateral view (Fig. 26B). Abpolypar spines are shorter than polypar ones, being 0.04–0.06 mm tall (Fig. 26D).

Spines on the proximal half of the corallum are conical, similar to the distal ones in both size and ornamentation. Papillae are rounded. No secondary spines were observed in any part of the colony. Polyps are arranged in a single row along one side of the corallum and follow the direction of the colony's spiral contortion. Polyp transverse diameters range 0.35–0.70 mm, with an interpolypar distance of 0.20–0.44 mm and 10–14 polyps/cm.

Remarks. Among whip-like antipatharians presenting one row of polyps on one side, showcasing spines papillose with a consistent simple apex, are *Stichopathes alcocki*, *Stichopathes bispinosa*, *Stichopathes bournei*, *Stichopathes desaturata*, *Stichopathes echinulata*, *Stichopathes filiformis*, *Stichopathes semiglabra*, *Stichopathes saccula*, *Stichopathes luetkeni*, *Stichopathes occidentalis*, *Stichopathes regularis*, and *Stichopathes spinosa*. Of these, *S. occidentalis* and *S. luetkeni* differ from Red Sea specimens by the characteristics of the papillae, which are so thick that almost resemble tubercles. The species *S. alcocki*, *S. bispinosa*, and *S. bournei* can also be excluded by the presence of secondary spines. *S. regularis* is characterized by a verticillated arrangement of the spines, which is not observed in the Red Sea specimens. *S. spinosa* was scantily described by Silberfeld (1909) and no information about the ornamentation of the spines is available. In his brief description, the author states that

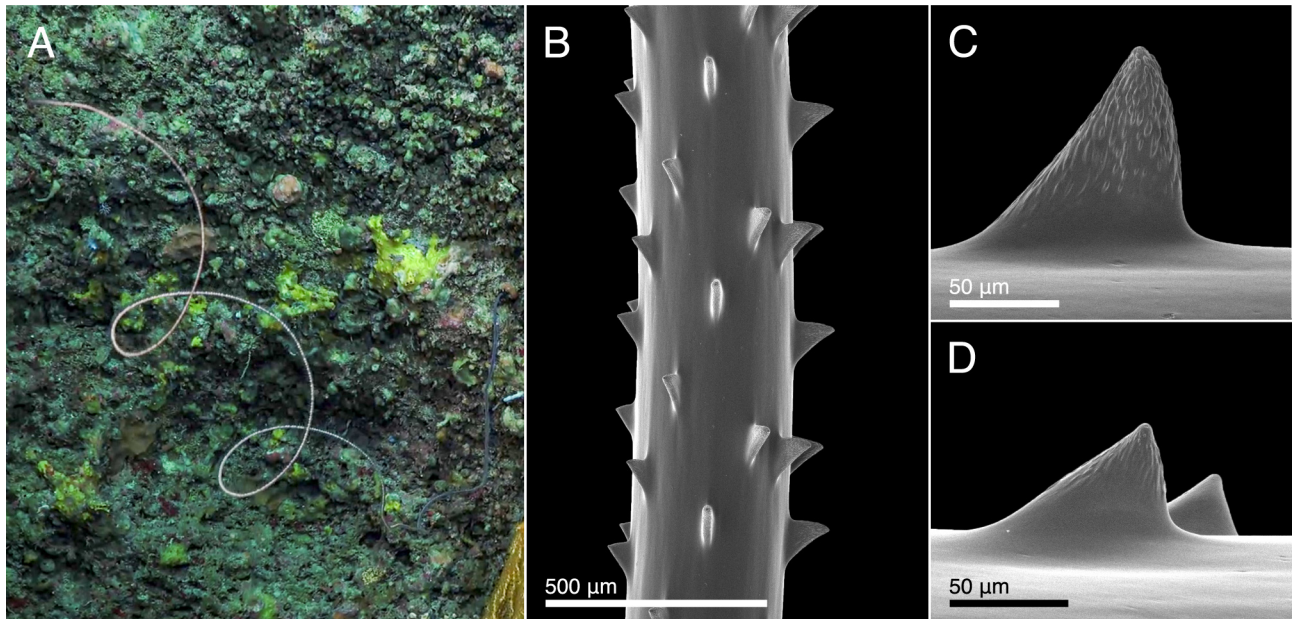


FIGURE 26. *Papillopathes* sp. 2 (*Stichopathes* cf. *desaturata*) M193_089_2_5. (A) *In situ* image of the colony; (B) spine arrangement on distal section; (C) close-up view of polypar spine on distal section; (D) close-up view of abpolypar spine on distal section.

the spines on the lower part of the stem are around 0.30 mm tall, while the spines of the Red Sea specimens show a maximum size of 0.12 mm. *S. semiglabra* and *S. saccula* closely resemble the Red Sea specimens in terms of spine characteristics. A re-examination of the syntype of *S. semiglabra* (ZMA.COEL.3460) revealed that the spines on the distal portion of the corallum (axis diameter: 0.3 mm) are triangular, papillose, 0.13–0.15 mm in height and 0.13–0.15 mm in width, with polyps measuring 0.65–0.70 mm in transverse diameter. These features exclude a match with our material. In comparison, a re-examination of the holotype of *S. saccula* (ZMA.COEL.3459) revealed polyps 1.5–2.0 mm in transverse diameter, with five to seven polyps/cm, whereas in our specimens the polyps never exceed 0.70 mm in transverse diameter. A re-examination of the schizotype of *S. filiformis* (USNM 100373) revealed elongated, laterally compressed triangular spines, with papillae sparsely scattered across the surface, and polypar spines 0.18–0.20 mm tall on a branch section of 0.30 mm in diameter. *S. echinulata* also differs from the specimens under examination. A re-examination of its schizoholotype (USNM 100371) showed polypar spines 0.16–0.19 mm tall, distanced 0.63–0.76 mm apart, and ten to twelve longitudinal rows of spines in lateral view, all characters that differ with the Red Sea specimens. Lastly, *S. desaturata* is the species that most resemble the Red Sea material. Terrana *et al.* (2024) based on ITS1 molecular data, showed that *S. desaturata* is closely related to *Papillopathes* (*Antipathes*) *grandis* **comb. nov.** This relationship is confirmed in our phylogenetic reconstruction (Fig. 3), where *Papillopathes* sp. 2 (*S. cf. desaturata*) is sister to *P. grandis* **comb. nov.** Moreover, spines height, spines distance, polyps transverse diameter, polyps density

and interpolypar spacing of the specimens in exam fall in the range report for *S. desaturata*. However, slight differences are observed in spines morphology, since the spines are more conical and distally directed in the Red Sea specimens, whereas they tend to be more vertically oriented in *S. desaturata*. Additionally, Red Sea colonies form several spirals, occasionally resulting in tightly coiled structures, while *S. desaturata* exhibits a more irregularly contorted axis. These differences, however, are not considered robust enough to distinguish between the two species. A comparative analysis including the molecular data from the holotype of *S. desaturata* would be essential to confirm the taxonomic identity of the Red Sea specimens, and eventually to transfer *S. desaturata* to the genus *Papillopathes*.

Distribution. Red Sea, French Polynesia; 57–120 m depth.

Papillopathes sp.3; lineage C16 in Fig. 3, Fig. 27

Material examined (Table S1): CHR0045_4B Red Sea, Gulf of Aqaba, 123 m; CHR0034_3B, Red Sea, North of Duba, 93 m.

Description of material examined. Colonies are unbranched, straight, forming a loose spiral at the apical part (Fig. 27A). On distal sections ranging 0.38–0.55 mm in diameter, spines are simple, acute, conical, or triangular, papillose, papillae are predominantly elongated but rounded close to the apex, covering half to 2/3 of the spine surface (Fig. 27C, D, E). Polypar spines are 0.078–0.098 mm tall, 0.086–0.10 mm wide, and distanced 0.45–0.60 mm apart. Abpolypar spines are smaller, 0.050–0.071 mm tall and 0.066–0.097 wide. 6–10 longitudinal rows are

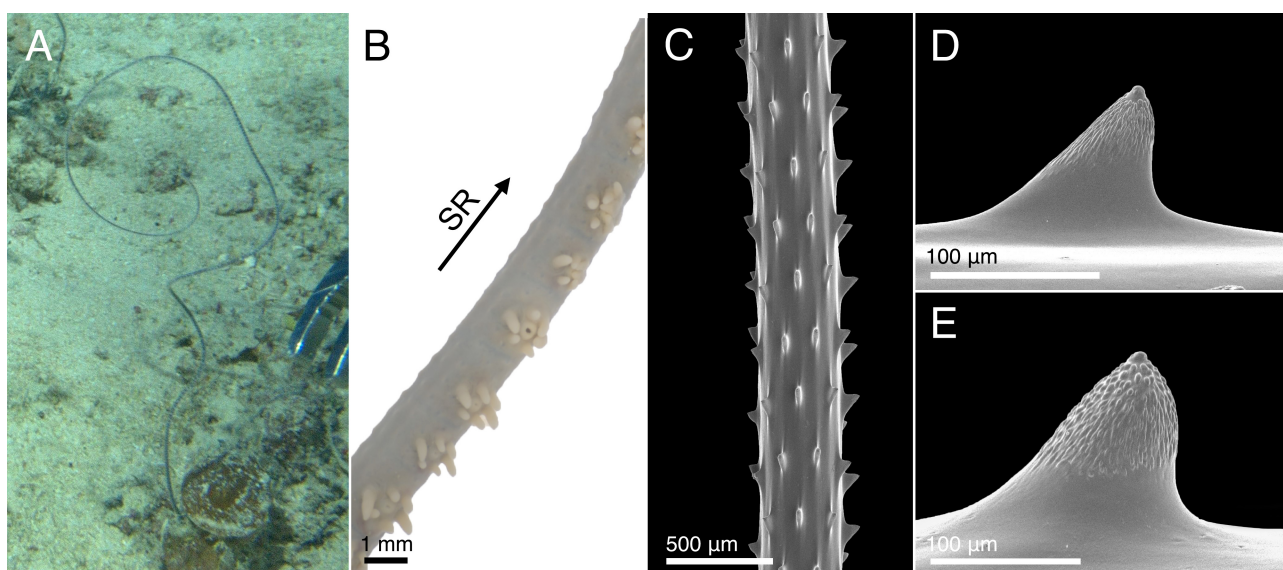


FIGURE 27. *Papillopathes* sp.3 CHR0034_3B. (A) *In situ* image of the colony; (B) Ethanol-preserved polyps arrangement on stem; (C) spine arrangement on the apical portion of the stem; (D) close-up view of polypar spine on apical portion of the stem; (E) spine arrangement on middle portion of the stem. SR: single row.

visible in lateral view (Fig. 27C). Polyps are uniserially arranged on one side of the axis (Fig. 27B). Polyps are 0.7–1.0 mm in transverse diameter, spaced 0.50–0.93 mm apart, resulting in seven–eight polyps/cm.

Distribution. Red Sea; 93–123 m depth

***Opreskopathes* Vicario gen. nov.**

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Antipathes (in part), Opresko 1996: pp. 289–299

Antipathes (in part), Warner & Opresko 2004: pp. 169–174

Antipathes (in part), Wagner *et al.* 2010: pp. 283

Antipathes (in part), Bo *et al.* 2012: p. 5

Diagnosis. Colonies unbranched or branched. Spines triangular laterally compressed, or conical; simple acute or blunt apex. Spines papillose up to two-thirds of their surface; papillae prominently rounded, distinct and protruding, sometimes resembling tubercles. Polypar spines height 0.08–0.40 mm; 5–11 longitudinal rows of spines in lateral view; secondary spines absent. Polyps arranged in a single row along the stem or occasionally in an alternating pattern on one side of the corallum. In branched colonies and on older branches, polyps may be distributed around the entire corallum. Polyps transverse diameter 0.5–1.5 mm, interpolypar space 0–0.8 mm, 6–8 polyps/cm.

Type species. *Antipathes caribbeana* Opresko, 1996 accepted as *Opreskopathes caribbeana* (Opresko, 1996) **comb. nov.**

Species in the genus. *Opreskopathes caribbeana* (Opresko, 1996) **comb. nov.**, *Opreskopathes umbratica* (Opresko, 1996) **comb. nov.**, *Opreskopathes rubusiformis* (Warner & Opresko, 2004) **comb. nov.**

Remarks. *Opreskopathes* gen. nov. is distinguished

from other genera by prominently rounded or conical and distinct protruding papillae on the skeletal spines, a key diagnostic feature of the genus. This characteristic, along with the examination of both morphological traits and molecular data from type material, led to the reassignment of *Antipathes caribbeana*, *Antipathes umbratica* and *Antipathes rubusiformis* to *Opreskopathes* gen. nov.

Among Antipatharia species exhibiting papillose ornamentation, *Stichopathes occidentalis* Gray, 1860, and *Stichopathes luetkeni* Brook, 1889, display similarly pronounced papillae. Future molecular studies of the type material may clarify whether these species also belong to *Opreskopathes* gen. nov.

Etymology. The name *Opresko*, is chosen in honor of Dr. Dennis Opresko, recognizing his extensive contribution to the study of the taxonomy and diversity of black corals worldwide. Gender: feminine

Distribution. Cabo Verde, Caribbean Sea (Jamaica, Netherlands Antilles), Gulf of Mexico; 20–79 m depth.

Species assigned to *Opreskopathes* included in this study

Opreskopathes caribbeana (Opresko, 1996) **comb. nov.**; lineage D17 in Fig. 3. Holotype: USNM 94387 (Fig. 28A–C); type locality: Jamaica. Material morphological and molecular examined, holotype, USNM 94387 (Fig. 28A–C), Caribbean Sea, Jamaica, Discovery Bay, depth 38m. Other material examined: USNM 1122627, Netherlands Antilles, Saba Island, 60 m.

Opreskopathes umbratica (Opresko, 1996) **comb. nov.**; lineage D18 in Fig. 3. Holotype: USNM 94388 (Fig. 28D, E); type locality: Bahamas. Material morphological and molecular examined, holotype, USNM 94388, Bahamas, Eleuthera Island, depth 30m.

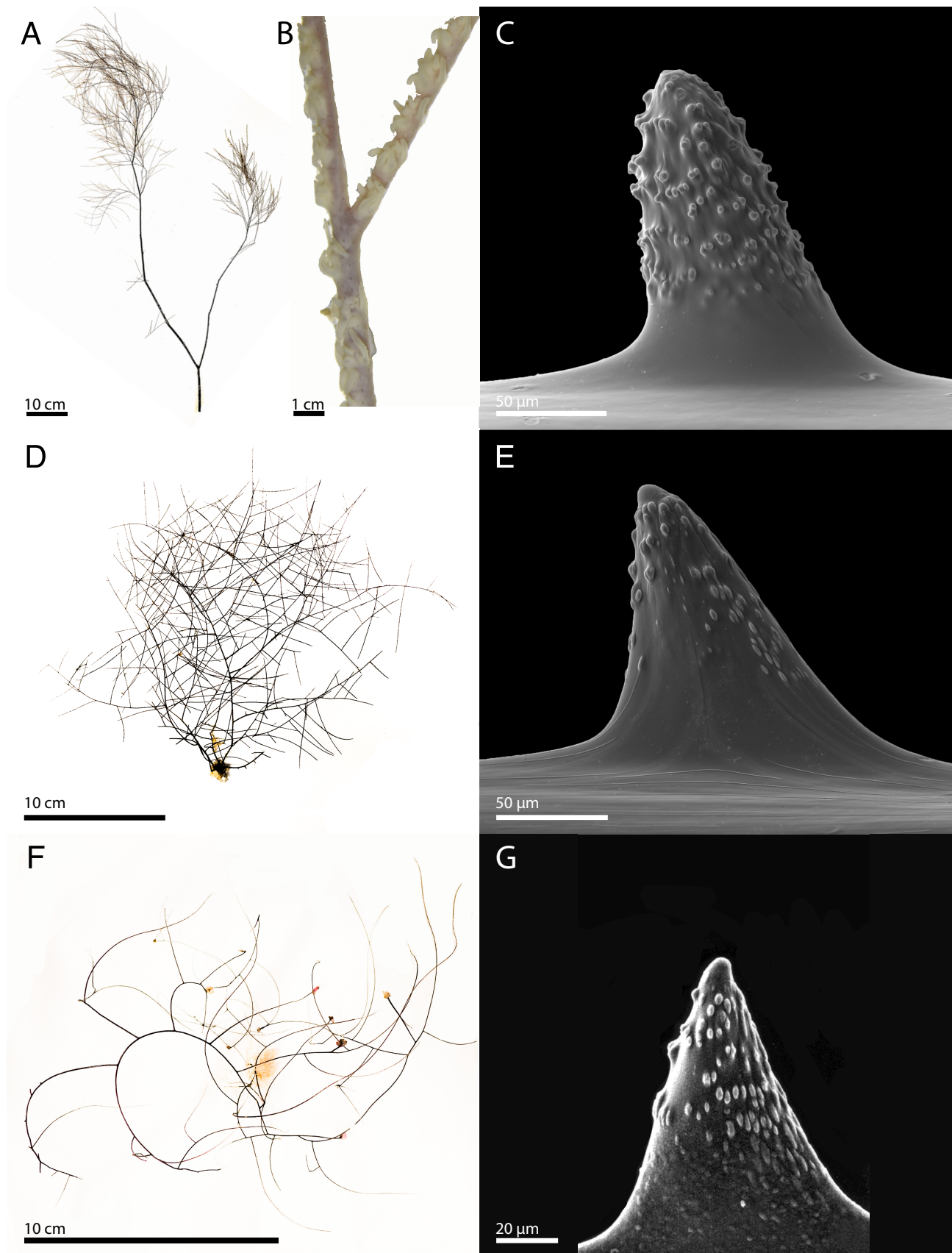


FIGURE 28. *Opreskopathes* **gen. nov.** (A) Dry colony of *O. caribbeana* **comb. nov.** holotype USNM 94387; (B) Ethanol-preserved polyps arrangement of *O. caribbeana* **comb. nov.** holotype USNM 94387; (C) Close-up view of polypar spine of *O. caribbeana* **comb. nov.** holotype USNM 94387; (D) Dry colony of *O. umbratica* **comb. nov.** holotype USNM 94388; (E) Close-up view of polypar spine of *O. umbratica* **comb. nov.** holotype USNM 94388; (F) Dry colony of *O. rubusiformis* **comb. nov.** paratype NHMUK 2000.1846; (G) Close-up view of polypar spine of *O. rubusiformis* **comb. nov.** holotype NHMUK.2000.1844 modified from Warner & Opresko 2004.

Opreskopathes rubusiformis (Warner & Opresko, 2004) **comb. nov.**; lineage D19 in Fig. 3. Holotype: NHMUK.2000.1844 (Fig. 28F); type locality: Jamaica. Material molecular examined, paratype, NHMUK.2000.1846 (Fig. 28G), Jamaica, Rio Bueno, depth 20–30 m.

Opreskopathes sp.1; lineage D20 in Fig. 3, Fig. 29

Material examined (Table S1): CV003, Cabo Verde, Sal island, Tres grutas, 15 m; CV085, Cabo Verde, Sal island, Palmeira, 14 m.

Description of material examined. Colonies unbranched, straight or slightly curved near the distal end (Fig. 29A). On the distal portion, polypar spines are triangular, laterally compressed, vertically directed, and simple (Fig. 29B, C). Spines are papillose, with distinct rounded papillae covering the upper half of the surface, and elongated, coalescing papillae developing basally (Fig. 29B, C). Papillae are strongly developed, projecting prominently from the spine surface (Fig. 29B, C). Polypar spines are 0.24–0.40 mm tall, 0.16–0.21 mm wide, irregularly spaced. Abpolypar spines are 0.26–0.30 mm tall and 0.14–0.18 mm wide. 9–11 longitudinal rows are tentatively counted in lateral view (Fig. 29B).

Polyps and coenenchyme orange in color (Fig. 29A).

On the apical portion of the colony, polyps are regularly arranged in a single row; in the middle and basal portions, polyps are unilaterally arranged, forming a single, somewhat irregular row along one side of the axis (Fig. 29A). Polyps are densely packed with minimal to no interpolar spacing. Polyps preserved in ethanol were degraded, preventing measurement of polyp transverse diameter and interpolar distance.

Distribution. Cabo Verde; 14–15 m depth.

Opreskopathes sp.2; lineage D21 in Fig. 3.

Material examined (Table S1): USNM 1665782, USA, Gulf of Mexico, 79 m.

Description of material examined. Although the colony and spines are not well preserved, the available material retains diagnostic features. The colony is unbranched and fragmented in the preserved material; however, a coiled growth pattern is evident. On a section of the stem measuring 0.6 mm in diameter, polypar spines are triangular, simple, distally inclined, and papillose. Papillae development on the lateral surfaces of the spines is asymmetric: one side bears well-developed, rounded or conical papillae that project prominently from the spine surface, while the opposite side displays less developed, coalescent papillae. Polypar spines are 0.14–0.15 mm

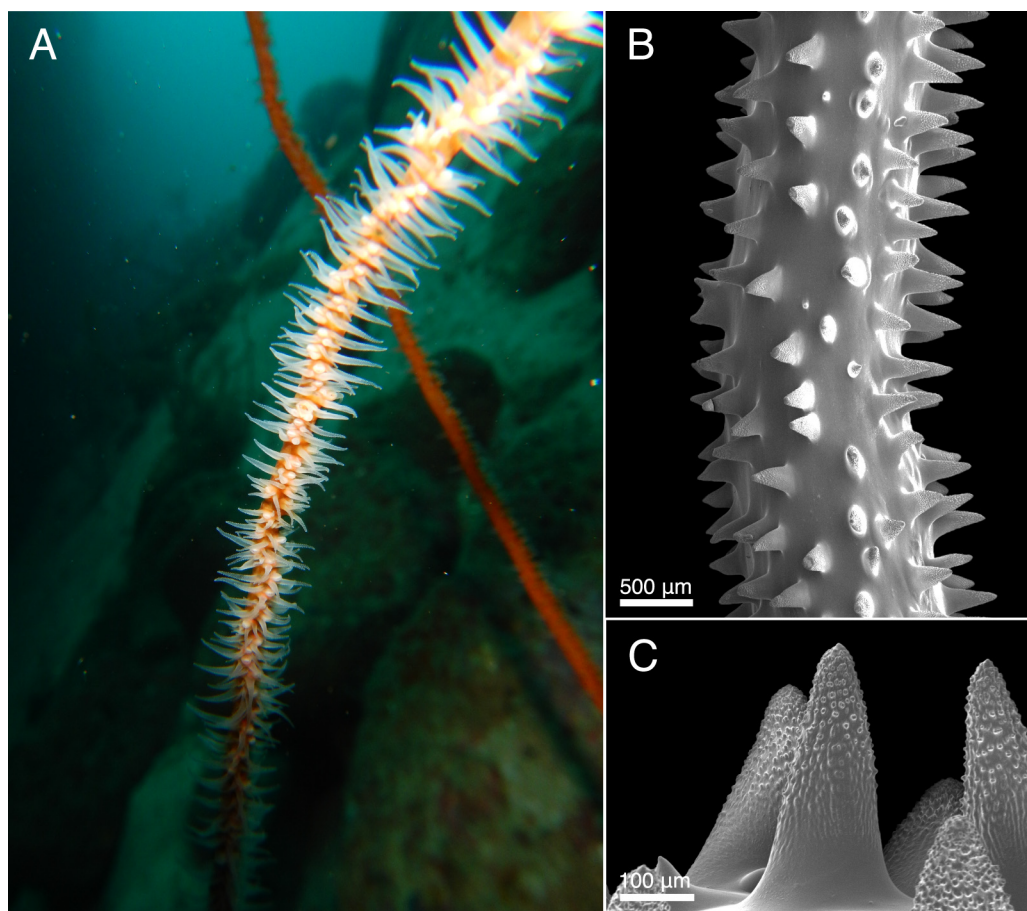


FIGURE 29. *Opreskopathes* sp.1 CV003. (A) *In situ* image of the colony; (B) spine arrangement on the apical portion of the stem; (C) close-up view of polypar spine on apical portion of the stem.

TABLE 1. Summary of the diagnostic morphological characters of the genera within the family Stichopathidae.

Family		Stichopathidae Roule, 1905				
Lineage	A	B	C	D	E	F
Genus	<i>Multilobopathes</i> gen. nov.	aff. <i>Cirripathes</i>	<i>Papillopathes</i> gen. nov.	<i>Opreskopathes</i> gen. nov.	<i>Cirripathes</i> / aff. <i>Antipathes</i>	<i>Stichopathes</i>
Type species	<i>Multilobopathes lentipinna</i>		<i>Papillopathes grandis</i>	<i>Opreskopathes caribbeana</i>	<i>Cirripathes spiralis</i>	<i>Stichopathes pourtalesi</i>
Type locality	Red Sea		Hawaii	Jamaica	Indian Ocean	Montserrat
Colony form	Unbranched and branched	Unbranched	Unbranched and branched	Unbranched and branched	Unbranched and branched	Unbranched
Polyps arrangement	One row one side	Multiple rows multiple sides/ one side free	One row one side	One row irregular / multiple rows, one side free	Multiple rows, one side free of polyps	One row one side
Polyps transverse diameter (mm)	0.6–2.0	0.6–2.1	0.3–1.1	0.5–1.5	0.5–2.5	0.8–2.0
Interpolypar space (mm)	>0–0.3	Irregular	0.2–0.9	>0–0.8	>0–0.4/ irregular	>0–0.5
Spine surface	Papillose	Papillose	Papillose	Prominently papillose	Papillose	Papillose
Spine apex	Simple, forked or multilobed	Simple	Simple	Simple	Simple or multilobed	Simple or multilobed
Secondary spines	Yes	No	No	No	No	No

tall, 0.12–0.13 wide and distanced 0.38–0.42 mm apart. Abpolypar spines are 0.09–0.10 mm tall, 0.08–0.10 mm wide. 10–11 longitudinal rows in lateral view. Polyps in ethanol preserved material are white, arranged uniserially, transverse diameter is 1.1–1.5 mm, spaced 0–0.2 mm apart, resulting in 7–8 polyps/cm.

Distribution. Gulf of Mexico; 79 m depth.

Cirripathes, de Blainville, 1830

Antipathes (in part), Dana 1846: pp.576, 577

Antipathes (in part), Gray 1857: pp. 290, 291

Antipathes (in part), Pourtales 1880: p. 114

Cirripathes (*Cirripathes*), Brook 1889: pp. 38, 81 [emended diagnosis]

Eucirripathes van Pesch 1914: p. 23 [new name for *Cirripathes* Brook emend.; diagnosis here adopted for *Cirripathes* sensu de Blainville]

Diagnosis. Colony unbranched or at most bearing insignificant branches. Polyps in one or more longitudinal rows; rounded, with tentacles grouped. In some parts of the colony, polyps arranged around the entire axis or leaving one side of the axis free.

Type species. *Cirripathes spiralis* (Linnaeus, 1758)

Species in the genus: *Cirripathes anguina*, *C. contorta*, *C. densiflora*, *C. gardineri*, *C. hainanensis*, *C. indica*, *C. musculosa*, *C. nana*, *C. propinqua*, *C. rumphii*, *C. secchini*, *C. sinensis*, *C. spiralis*, *C. translucens*.

Remarks: The phylogenetic position of *Cirripathes* is here anchored by the recent designation of a neotype for the type species *C. spiralis* (Bo *et al. in review*), which falls within lineage E, specifically sublineage E27, of the present analysis. However, specimens morphologically assigned to *Cirripathes* are distributed across two phylogenetically divergent clades, lineages B and E, indicating that the genus as currently defined is not monophyletic. Given the position of *C. spiralis*, clade B represents a morphologically and phylogenetically distinct entity requiring the erection of a new genus, which is deferred pending the availability of additional morphological and molecular data necessary to establish robust diagnostic characters. Moreover, in the absence of molecular data from type material or topotypes of the nominal *Cirripathes* species, all currently described *Cirripathes* species are conservatively retained within the genus. Furthermore, *Cirripathes* in lineage E clusters as sister to branched aff. *Antipathes* clades. This relationships raises the question of whether a future emended diagnosis of *Cirripathes* should be broadened

to include branched colony forms. Candidate species reassignments are summarised in Table S3.

Discussion

This study represents the most comprehensive genomic and morphological analysis of the family Antipathidae conducted to date. Through extensive sampling and phylogenomic analyses, we have bridged critical knowledge gaps in the taxonomy, biodiversity, and distribution of black corals, providing a robust framework for the first systematic revision of the group after the seminal revisions by Opresko (2001–2006).

By integrating morphology, phylogenomics, type material, and original descriptions, we have formally resurrected the family Stichopathidae and revised its morphological diagnosis. The genera *Stichopathes* and *Cirripathes* are moved to Stichopathidae, together with three newly established genera. Finally, we reassigned five species formerly placed within *Antipathes* to these new genera and described four new species.

By integrating our genomic backbone with detailed morphological analyses of numerous specimens, we showed that spines morphology and ornamentation provide a basis for reclassifying species previously attributed to the Antipathidae into distinct family-level taxa. We identified genus level diagnostic characters within the Stichopathidae, such as spines morphology, presence or absence of secondary spines, polyps size, and interpolypar distance, confirming that the traditionally used branching pattern is not reflective of genus level boundaries (e.g., Bo *et al.* 2012; Opresko *et al.* 2020).

A long-forgotten family in the historical literature

Significant changes to the classification of Antipatharia began in the late 1800s, with two main taxonomic frameworks gradually taking shape. Brook (1889) was among the first authors to reclassify the order, recognizing three families, and dividing the family Antipathidae into two subfamilies, Antipathinae and Schizopathinae, based on polyp morphology (Fig. 30). Within Antipathinae, he further distinguished two subtribes according to the corallum branching pattern: the Indivisae, comprising *Cirripathes* and *Stichopathes* with their unbranched stems, and the Ramosae, including branched genera (Fig. 30). A few years later, Schultze (1896) revisited Brook's system. While retaining the division at the subfamily level, he proposed a new criterion for lower-level classification, focusing on the number of mesenteries. This led him to reorganize the Antipathidae into three subfamilies and to establish the Dekamerota, which incorporated Brook's Indivisae and Ramosae without altering the generic subdivision (Fig. 30). Building upon these earlier works, Roule (1905), in his *Description des Antipathaires et Cériantaires*, undertook a critical reassessment of Antipatharia taxonomy. In his manuscript, he first synthesized the key diagnostic morphological

characters, then reviewed the prevailing classification schemes and the taxonomy of the specimens he examined. In his concluding remarks (pp. 36–38), Roule endorsed Schultze's framework over Brook's, arguing that the number of mesenteries provided a more reliable and consistent basis for taxonomic classification, as it was used for distinguishing Antipatharia from other anthozoans. By adopting Schultze's approach, Roule maintained the division into Dekamerota and Dodekamerota but elevated these categories to the rank of suborders. As a result, he introduced several new families. The genus *Leiopathes*, represented the new family Leiopathidae, in the suborder Dodekamerota. Within the suborder Dekamerota, within the Ramosae group, Roule distinguished three families, the Antipathidae, the Parantipathidae, and the Schizopathidae, while in the Indivisae group he established the family Stichopatidae to accommodate *Stichopathes* and *Cirripathes* based on the unbranched morphology of their corallum (Fig. 30).

The first author after Roule who comprehensively reviewed the classification attempts of earlier authors was van Pesch (1914). In his work, he grouped all Antipatharia species within a single family, the Antipathidae. He agreed with Schultze on the use of primary and secondary mesenteries as informative taxonomic characters. Consequently, he combined Schultze's Dekamerota and Dodekamerota, distinguished by the presence of secondary mesenteries, into a single subfamily, the Heterotaniales, which contrasted with the Hexamerota, characterized by primary mesenteries (Fig. 30). van Pesch further refined the classification at lower taxonomic ranks by using internal anatomical features as additional criteria, and noting that branching pattern was not a reliable character for classification, that ultimately led him to merge the Indivisae (*Cirripathes* and *Stichopathes*) and the Ramosae (branched genera) into a single subtribe (Fig. 30).

Since that moment, the unbranched genera *Stichopathes* and *Cirripathes* continued to be assigned to the family Antipathidae (Fig. 30). While our work confirmed van Pesch's observation regarding the limited systematic value of black coral colony branching patterns, it also supports the resurrection of the family Stichopathidae, based on distinctive features of the spine ornamentation and phylogenetic evidence. Furthermore, some species previously assigned to *Antipathes* have been reassigned to Stichopathidae, reflecting a necessary re-evaluation of historical classifications that relied predominantly on colony morphology.

Phylogenomic considerations

Historically, phylogenetic relationships within the order Antipatharia have been inferred using mitochondrial and nuclear markers (e.g., Lapian *et al.* 2007; Brugler *et al.* 2013). While informative at higher taxonomic levels, these markers often lack the resolution needed to distinguish relationships at the genus or species level (Brugler *et al.* 2013). The recent development of next-generation

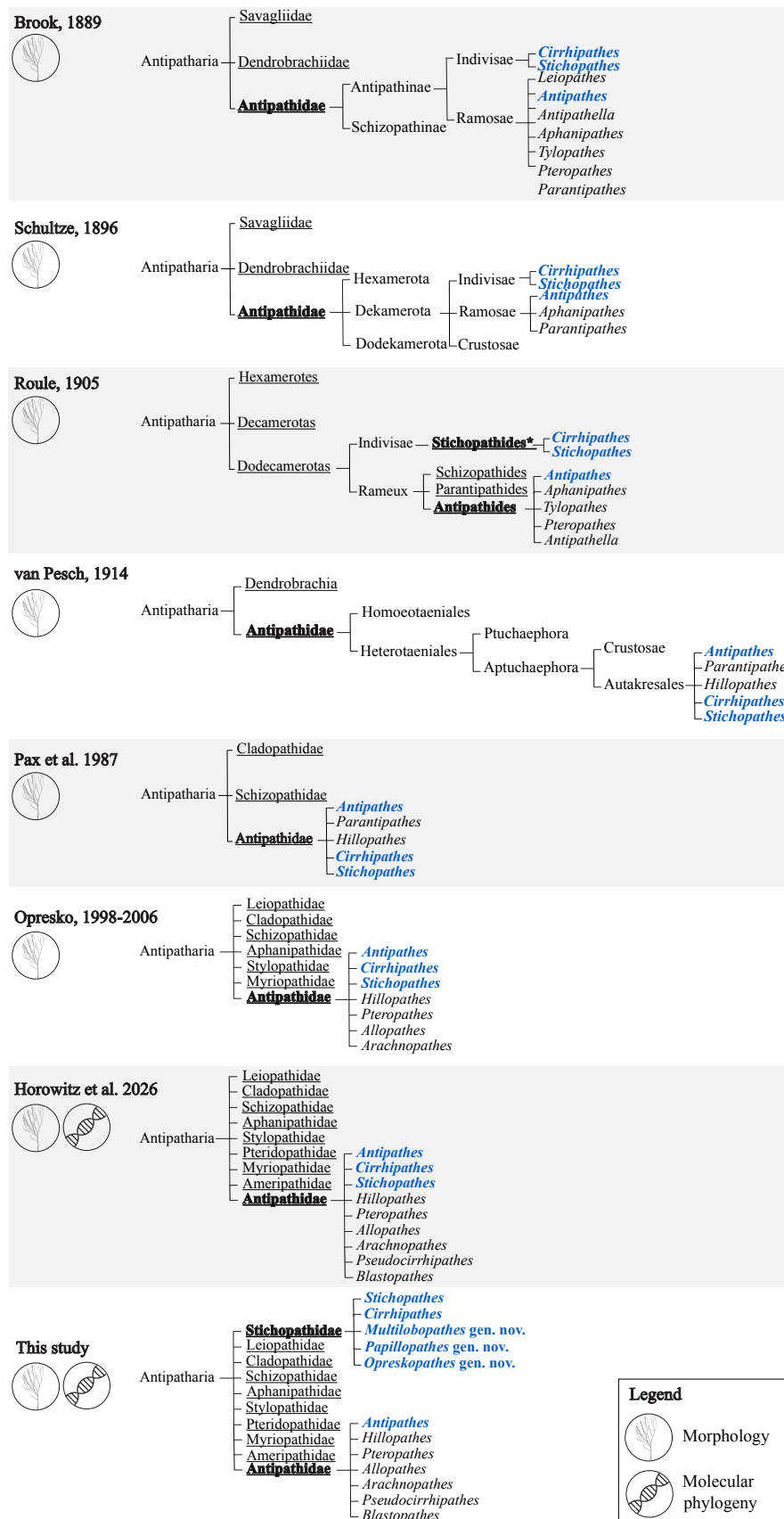


FIGURE 30. Schematic timeline of the classification of the order Antipatharia with a focus on taxonomic changes of the families Antipathidae and Stichopathidae. The placement of genera historically included in Antipathidae is shown across major taxonomic studies, highlighting their reassignments through time. Family-level taxa are underlined; Antipathidae and Stichopathidae are both underlined and in bold. Genera transferred to the family Stichopathidae and the genus *Antipathes* (some of whose valid species were moved to the resurrected family) are indicated in blue. For each study, the type of data used to establish the classification (morphological or molecular) is noted.

sequencing technologies, coupled with reduced costs for targeted enrichment, has now enabled the scientific community to apply high-resolution phylogenomic approaches more broadly. For example, Vicario *et al.* (2024a) provided the first comprehensive assessment of Antipatharia in the northern Saudi Arabian Red Sea using three mitochondrial markers, but their analyses were limited in their ability to resolve relationships among closely related taxa. In the present study, we expand on that dataset by using UCEs, to achieve a higher level of phylogenomic resolution (Quattrini *et al.* 2018; Cowman *et al.* 2020; McFadden *et al.* 2022; Oury *et al.* 2023). A direct comparison between the mitochondrial reconstruction from Vicario *et al.* (2024a) and the UCE-based phylogeny from the current work, shows that Lineage I in Figure 2 of Vicario *et al.* (2024a) corresponds to the family Stichopathidae in the present analysis. To facilitate integration with existing mitochondrial frameworks, *COI*, *IgrW* and *IgrN* barcoding sequences were generated for at least two representatives of all newly collected and described taxa, complementing those already available from Vicario *et al.* (2024a) (Table S2; Fig. S5). As expected from the known low resolution of COI in anthozoans (*e.g.*, Brugler *et al.* 2013), the COI phylogenetic reconstruction (Fig. S5) recovered structure only at the family level, with Stichopathidae clearly distinct from the other Antipathidae lineages. Within Stichopathidae, COI could not discriminate among genus-level lineages: *Multilobopathes* **gen. nov.**, aff. *Cirripathes*, *Papillopathes* **gen. nov.**, and *Opreskopathes* **gen. nov.** were intermixed in one clade, while *Stichopathes*, *Cirripathes* and aff. *Antipathes* grouped in a separate clade. We nonetheless provide these barcodes to make at least family-level molecular data publicly accessible and comparable with the broader anthozoan literature. In contrast, the UCE phylogenomic reconstruction recovered 32 distinct lineages, 25 of which correspond to unique morphotypes, demonstrating the higher resolution of UCEs.

Despite the significant improvement in phylogenetic resolution provided by UCEs, a few lineages in our dataset remain only partially resolved. Notably, lineages A4, B10, E22, E23, E24, E25, and E28 each contain multiple putative species or morphologies that cannot be confidently delineated based on our current sampling and morphological evidence alone. This lack of resolution may result from insufficient sampling across regions, limited representation of intraspecific variation, or the presence of cryptic diversity.

To address these challenges, it will be essential to expand the sampling effort across latitudes and depths, as extended taxon sampling has been shown to improve the accuracy and resolution of phylogenetic trees (McFadden *et al.* 2022; Quek *et al.* 2023). In addition, the development of an Antipatharia-specific bait set would substantially increase the number of informative UCE loci captured and improve phylogenetic resolution among closely related black coral species. Moreover, integrating genome-wide single nucleotide polymorphisms (SNPs) analysis can provide finer-scale insights into population

structure, gene flow, and species boundaries, especially when morphological traits alone are ambiguous (Leaché *et al.* 2014; Derkarabetian *et al.* 2019; Oury *et al.* 2025; Terraneo *et al.* 2025). By combining increased sampling with high-resolution SNP analyses, future studies can more robustly delimit species within these unresolved lineages and reveal patterns of diversification.

Bathymetric and biogeographic patterns of black corals diversity

The distribution of marine organisms is strongly influenced by depth, geography, and environmental conditions, which together shape how species diversify and adapt across regions (Wiens & Donoghue 2004; Bowen *et al.* 2013). An analysis of depth-related patterns in 83 black coral species (Horowitz *et al.* 2023) indicated that their diversification began on the continental slope (250–1000 m), with later radiations into both shallower shelf waters (<250 m) and deeper abyssal zones (>1000 m). According to this study, the resurrected family Stichopathidae, corresponding to a portion of Lineage A1a in Horowitz *et al.* (2023), diversified around 183 million years ago through an onshore transition. The same work proposes that this lineage's rapid expansion onto the shelf may have been facilitated by reduced competition during periods of elevated temperatures and atmospheric pCO₂, which likely limited the presence of coral with calcium-carbonate skeletons (Horowitz *et al.* 2023).

In our study, the comprehensive exploration of Red Sea black corals across a wide latitudinal and bathymetric gradient revealed a clear pattern of geographic and bathymetric partitioning. Among the 32 lineages identified, six were depth generalists, occurring across a range of depths and in different environmental and topographic settings (Fig. S6). In contrast, the majority of lineages were depth specialists, with 14 lineages restricted to shallow waters (<40 m), 10 to mesophotic depths (40–200 m), and two to deep-sea zones (>200 m) (Fig. S6), suggesting adaptation to specific depth-related environmental conditions. These findings challenge the traditional view of the order Antipatharia as an almost exclusively deep-water group (Cairns 2007), showing instead that many depth-specialist lineages occur in shallow habitats where black corals can be abundant, diverse, and ecologically significant. Our results also confirmed that the mesophotic zone functions as a centre of diversity for black corals (Bo *et al.* 2019; Tapia-Guerra *et al.* 2021; Vicario *et al.* 2024a; Chimienti *et al.* 2025) and support the idea that some species of black corals have adapted to particular depth ranges, reflecting the depth-differentiation hypothesis (Rex & Etter 2010). According to this hypothesis, species divergence can occur more rapidly across short vertical distances than across large horizontal ones, particularly in taxa exposed to steep environmental gradients (Etter *et al.* 2005; Quattrini *et al.* 2015; Betters *et al.* 2023). This framework is particularly relevant in the Red Sea, where extreme salinity, temperature, and oxygen conditions create a unique selective environment for marine life

(Berumen *et al.* 2019). Below 200 m, the Red Sea's waters stabilize at approximately 21°C (Sofianos & Johns 2007), in contrast to the typical 12–4°C range in mesophotic and deep-sea coral environments elsewhere (Roberts *et al.* 2006). These unusual conditions are further compounded by oligotrophic waters, low oxygen availability, geographic isolation (Mitchell *et al.* 2021), limited water exchange, and distinct geological conditions (Rohling *et al.* 1998; Eladawi *et al.* 2017). The discovery of novel black coral lineages is consistent with broader patterns of high endemism and gradient-driven differentiation for marine taxa in the basin (Berumen *et al.* 2019; Arrigoni *et al.* 2019; Terraneo *et al.* 2019; Macrina *et al.* 2026).

In our study, by integrating data spanning the Red Sea and Indian, Pacific, and Atlantic Oceans, we recovered 16 lineages that appear restricted to specific biogeographic regions (excluding singletons for which further sampling is needed) (Fig. S6). Of these, nine lineages appeared to be unique to the Red Sea (cl. A5–A7, A9, C15, C16, E28, E29, E31) (Fig. S6). Such apparent regional restriction aligns with growing evidence that many coral species, spanning scleractinian corals (Underwood *et al.* 2020; Figueiredo *et al.* 2022; Bridge *et al.* 2023) and octocorals (Untiedt *et al.* 2021; McFadden *et al.* 2025) have more restricted geographic ranges than previously assumed, likely due to limited larval dispersal capabilities (Paulay & Meyer 2006; McFadden *et al.* 2025). To establish whether these lineages are Red Sea endemics or whether their apparent restriction in distribution reflects sampling gaps, targeted surveys in neighbouring regions, and in the Indian Ocean in particular, will be essential. Beyond the Red Sea, we also identified three lineages restricted to the North Pacific (cl. A4, B11, E24), one in the South Pacific (lineage B12), and three in the Atlantic Ocean (cl. D17, D20, F32) (Fig. S6). Notably, the genus *Opreskopathes* **gen. nov.** appears, based on current data, to be confined to the eastern and western Atlantic (Fig. S6).

The only species in our dataset showing a broad geographic distribution was *P. grandis* (cl. C13) (Gress *et al.* 2020), which occurred from the Red Sea to Madagascar, Australia and Hawaii (Fig. S6). Whether this range reflects its real distribution or unresolved cryptic diversity remains unclear, particularly given the potential for environmental plasticity leading to convergent colony growth forms. Its broad distribution could be an example of a complex of cryptic species where further genetic analyses at finer scales could reveal multiple, geographically restricted lineages (Fig. S6) (Quattrini *et al.* 2019; McFadden *et al.* 2025).

On top of biogeography and depth distribution, habitat complexity and topographic heterogeneity can play an additional role in structuring black coral communities (Tapia-Guerra *et al.* 2021; Amaro *et al.* 2025). Certain lineages showed strong habitat preferences, which may reflect both ecological requirements and evolutionary history. For example, the newly described species *M. intricatus* (cl. A7), was exclusively found in low-light environments such as under overhangs and within caves likely to reduce competition with light-dependent organisms, to optimize exposure to water flow for

enhanced prey capture, or helping their anchorage and feeding efficiency (Grigg 1965; Wagner *et al.* 2012; Bo *et al.* 2019; Braga-Henriques *et al.* 2022; Chimienti *et al.* 2025). Similarly, *Stichopathes* cf. *contorta* (cl. 29) was frequently observed at mesophotic depths, attached to biogenic substrates like algal nodules or consolidated hardgrounds. These habitats, often shared with octocorals and scleractinians, provide structurally complex environments that may facilitate larval settlement and reduce interspecific competition. In contrast, *Stichopathes arenicola* **sp. nov.** (cl. 31) was restricted to aphotic depths, inhabiting flat, low-complexity sandy plains, where colonies were anchored to small rocks, shell fragments, or urchin skeletons, with little to no other visible benthic fauna nearby.

Reassessment of the role of morphology in Antipatharia taxonomy: insights from genomic data

This study contributes to the partial taxonomic revision of the genera *Antipathes* and *Stichopathes* by assigning nine species to newly described or existing genera. However, several taxonomic uncertainties remain, and this work unveiled areas for future research to be addressed. At the family level, our phylogenetic reconstruction confirms that Antipathidae *sensu lato* is polyphyletic (Brugler *et al.* 2013; Horowitz *et al.* 2020) with the type species of the family, *A. dichotoma* clustering with aphanipathids species (Horowitz *et al.* 2026). Accordingly, clades aff. Antipathidae 2, 3 and 4 represent distinct lineages requiring further investigation. Indeed, informed taxonomic decisions for these lineages will require additional data, including molecular sequence of type specimens, and broader taxon sampling to fill species gaps. In this context, a formal petition has been submitted to the ICZN to designate *Antipathes flabellum* Pallas, 1766 as the new type species of the genus *Antipathes*, replacing *A. dichotoma* (Case number 3909) (Horowitz *et al.* 2026). If approved, this action would place the nominal genus *Antipathes* within clade aff. Antipathidae 3 (Fig. 2), which would then become the nominal Antipathidae.

Beyond the family-level, several genus-level lineages also require further resolution before formal taxonomic decisions can be undertaken. Lineage E (*Cirrhopathes*/aff. *Antipathes*) exemplifies this complexity, including several well-supported species complexes (lineages E22–E28), for which no strong unifying morphological character was retrieved which would justify their placement as a single genus. The only apparent shared trait is polyp arrangement, where, at least in some parts of the colony, one side of the stem remains free of polyps. Within this complex, lineages E22–24, E27–E28 group *Cirrhopathes*-like specimens characterized by polyps arranged irregularly along the stem while consistently leaving one side free of polyps. Conversely, lineages E25 and E26 cluster species with branched colony forms. Specifically, they include aff. *A. curvata* (MTQ G79996), aff. *A. cf. virgata* (INV 131338), and aff. *A.*

galapagensis (USNM 43443), the latter representing the type specimen. *Antipathes galapagensis* exhibits polyps primarily arranged in a single row (side by side), occasionally occurring in two opposite rows on thicker branches. *Antipathes curvata* was originally described by van Pesch (1914) with polyps in an unrecognizable mass due to preservation, though he noted they were mostly found on one side of the colony. The specimen included here (MTQ G79996) presents polyps irregularly arranged in a single row. Similarly, the specimen identified as *A. cf. virgata* by Terrana *et al.* (2020) was described with polyps generally in one row, though on thicker branches they occur on both sides, consistently leaving one side of the stem free of polyps. When arranged in a single row, they may twist around the branch, while on thicker axes, they are more evenly distributed.

While polyp arrangement appears to be a potential unifying trait for this lineage, we refrain from making taxonomic decisions until a more consistent and well-supported morphological pattern emerges as more specimens and taxa are added in future works. Two hypotheses can be considered: (1) further sampling and genomic sequencing may reveal common morphological characteristics supporting the classification of these lineages within a single new genus, or (2) additional analyses may instead indicate that each lineage within this complex represents a distinct genus.

A genus requiring more attention is *Cirrhipathes*. This genus currently comprises 15 species, all from the Indian or Pacific Ocean, but one (*C. secchini* Echeverria, 2002) from the Atlantic Ocean. The type material of the type species of the genus, *C. spiralis*, is currently considered lost. For this reason, a neotype for *C. spiralis* has recently been designated (Bo *et al. in review*). The specimen falls within lineage E27 presented in our analysis, thereby anchoring the genus *Cirrhipathes* to that clade in our paper. In the present phylogenetic reconstruction, colonies fitting the original description of the genus *Cirrhipathes* are split into two distinct lineages, aff. *Cirrhipathes* (cl. B10–B12) and *Cirrhipathes*/aff. *Antipathes* (cl. E22–E24, E27–E28) (Fig. 3). *Cirrhipathes spiralis* is unbranched, forms tight spirals, bears blunt conical spines with apical lobes, and has polyps arranged in one to several rows (Bo *et al. in review*). Our analysis included a specimen from NMNH (USNM 99942) identified as *C. spiralis*, which clustered within lineage E27 and closely corresponded to the neotype description. This specimen displays a spiral growth form, tall papillose cylindrical spines with some knob-like projections, and polyps irregularly arranged, leaving the inner side of the spiral free of polyps. By contrast, colonies in the genus-level lineage aff. *Cirrhipathes* (cl. B10–B12) lack a spiral growth form, never develop cylindrical spines with knobbed apices, and show polyps arranged around the corallum or leaving one side free, but not in a single row. While these differences are consistent with generic-level distinction, we refrain from formally erecting a new genus for the clade encompassing lineages B10–B12 pending a more comprehensive sampling of the group, which will be necessary to establish robust diagnostic characters and

circumscribe the taxon appropriately. Additionally, a genus-wide revision of *Cirrhipathes* should explicitly include examination of both the proximal and distal regions of the colonies, as these portions often differ substantially in shape and surface ornamentation (Terrana *et al.* 2020). Failure to account for this intra-colony variation may lead to taxonomic misidentifications, underestimation of morphological diversity, and overestimation of species.

Conclusions

This work represents a step towards a revised taxonomy of the order Antipatharia and a better understanding of its diversity, distribution, and evolutionary history. Particularly, by integrating genomic data, morphological analyses, and the examination of type material across a large collection spanning localities worldwide and a broad bathymetric range, we have laid the foundation for addressing the polyphyly of the family Antipathidae. The resurrection of the family Stichopathidae and eventually the formal description of three new genera represent necessary and fundamental steps towards the end goal of a comprehensive revision of the order. However, while the formal resurrection of Stichopathidae was addressed in the present manuscript, the formal description of the other family-level lineages identified here will be part of a future community-wide effort. Our sampling across the Red Sea revealed a pronounced pattern of bathymetric partitioning and a high proportion of potential endemic lineages, reframing the basin as a hotspot for black coral diversification and highlighting the mesophotic zone as a key reservoir of diversity warranting conservation attention. While this study represented an initial step, future research should aim to clarify species boundaries within *Cirrhipathes*, and to revise the status of additional species currently assigned to *Antipathes* and *Stichopathes*, moving towards a comprehensive revision. Achieving this goal will require the revision of existing type material and targeted sampling in type localities where original material is unavailable, in order to resolve long-standing taxonomic ambiguities.

CRedit authorship contribution statement

SV: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Software, Validation, Visualization, Writing—original draft, Writing—review and editing.

TIT: Conceptualization, Investigation, Supervision, Validation, Writing—review and editing.

GC: Conceptualization, Investigation, Validation, Writing—review and editing.

NO: Investigation, Supervision, Validation, Methodology, Writing—review and editing.

JH: Formal analysis, Investigation, Validation, Writing—review and editing.

LM: Investigation, Writing—review and editing.

FBa: Investigation, Writing—review and editing.

FM: Investigation, Writing—review and editing.
 MLB: Funding acquisition, Project administration, Writing—review and editing.
 CMD: Funding acquisition, Project administration, Resources, Writing—review and editing.
 AAE: Funding acquisition, Project administration, Resources, Writing—review and editing.
 VP: Data curation, Funding acquisition, Project administration, Resources, Writing—review and editing.
 MQ: Funding acquisition, Project administration, Resources, Writing—review and editing.
 HW: Funding acquisition, Project administration, Writing—review and editing.
 CF: Funding acquisition, Project administration, Writing—review and editing.
 MR: Data curation, Resources, Writing—review and editing.
 FBe: Conceptualization, Data curation, Formal Analysis, Investigation, Supervision, Validation, Funding acquisition, Project administration, Resources, Writing—review and editing.

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Declaration of Competing Interest

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

Data accessibility

The sequence data supporting this study's finding are available in GenBank of NCBI. The associated **BioProject** numbers are PRJNA1348881, PRJNA1043120, PRJNA644402**BioSample** and GenBank accession numbers for *IgrN*, *IgrW* and *COI* are listed in Table S2.

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All data collected onboard during the Red Sea Decade Expedition (RSDE), including data collected by sensors, acoustic mapping devices, and images collected by ROVs and submersibles, are property of the National Center for Wildlife (NCW). The videos, images, and audio media obtained during the course of the RSDE are credited to the NCW, Kingdom of Saudi Arabia.

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Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper.

Supplementary_Data_1_Table_S1

Supplementary_Data_2_Table_S2

Supplementary_Materials.docx