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Overview of the genus *Sympodium* Ehrenberg, 1834 (Octocorallia, Alcyonacea, Xeniidae), with the description of new species, revealing regional endemism

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Abstract

The oldest existing type material for any of the xeniid soft corals, *Sympodium caeruleum* Ehrenberg, 1834, is re-described. An integrated analysis of molecular and morphological characters of Indo-Pacific Xeniidae support the description of seven new species of that genus. The extent of interspecific morphological variation within the genus is extensive; colonies arise from an encrusting membrane of variable thickness that can be either mat-like or may have ribbon-like extensions or irregularly shaped low mounds. The polyps can either arise separately from the membrane or may be arranged into clusters of polyps that bud off at different levels to form small branched groups. The sclerites of all species are uniformly ellipsoid platelets, abundant throughout the colony. The genetic results suggest that *Sympodium* species demonstrate restricted geographic ranges and regional endemism, with distinct genotypes (molecular operational taxonomic units) each mostly found at a single Indo-Pacific location. The results emphasize the importance of integrating classical taxonomy with a re-examination of original old type material and molecular phylogenetic analyses, in order to delineate species boundaries and to recognize biodiversity patterns.

Key words: Indo-Pacific Ocean, new species, molecular phylogeny, MOTUs, taxonomy, sclerite microstructure

Introduction

The soft coral genus *Sympodium* was established by Ehrenberg (1834), based on material collected in the Red Sea during the early 1820s. Initially, this genus was assigned to the family Halcyonina, but later Milne Edwards and Haime (1857) transferred it to the family Cornulariidae. Ehrenberg's study assigned two Red Sea species to the genus: *S. caeruleum* Ehrenberg, 1834 and *S. fuliginosum* Ehrenberg, 1834. The former species has retained its taxonomic status while the latter one was transferred by Kükenthal (1904) to *Anthelia* Lamarck, 1816, and synonymized with *A. glauca* Lamarck, 1816. While revising the genus, Kükenthal (1916) relocated *Sympodium* to the family Xeniidae, and simultaneously transferred no fewer than 31 *Sympodium* species described by then to several other octocoral genera. His revision retained only two species in their originally assigned genus: *S. caeruleum* Ehrenberg, 1834 and *S. tamatavense* Cohn, 1908. Clearly, Kükenthal's study highlighted the confusion over the taxonomic characters that justify assignment of a species to *Sympodium*. The most recent taxonomic diagnosis of the genus *Sympodium,* provided by Fabricius and Alderslade (2001), describes it as being an Indo-Pacific zooxanthellate soft coral whose colonies consist of a basal membrane or ribbon-like stolons from which small retractile polyps arise. They further indicate that the basal membrane can be thick, even featuring irregularly shaped mounds, and that the sclerites are corpuscle-like platelets or spheroids, as commonly found among other genera of the family Xeniidae.

Since its original description *S. caeruleum* has been reported from Indo-Pacific reefs ranging from the western Indian Ocean to the Pacific (May 1898: Tumbatu (Zanzibar); Thomson & Mackinnon 1906: Coetivy (Seychelles) and Egmont (Chagos Archipelago); Thomson & Dean 1931: Indonesia; Roxas 1933: Philippines; Tixier-Durivault 1966 and Verseveldt 1973: Madagascar; Utinomi 1977: Ryukyu Archipelago (Japan); Malyutin 1992: Coetivy

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(Seychelles); Benayahu 1993: South Africa; McFadden *et al*. 2014a: Sulawesi (Indonesia); McFadden *et al*. 2014b: Palau (sequences deposited in GenBank as *S. caeruleum*). In addition, this species has been recorded from several areas of the Red Sea (Gohar 1940: Ghardaqa; Reinicke 1997: northern Gulf of Aqaba and Sudan; Haverkort-Yeh *et al*. 2013: Saudi Arabia). In contrast, *S. tamatavense* has not been reported since its initial description from a type locality in Madagascar. Two unidentified *Sympodium* species have been recorded from the temperate region of Japan (Koido *et al*. 2019).

The original description and several subsequent taxonomic studies of *S. caeruleum* describe it as a membranous colony growing over the hard substrate, with polyps that can fully retract within the membranous basal coenenchyme. In addition, they refer to the presence of small disc-like sclerites and to living colonies being light gray in color, often with a bluish tinge, probably due to the sclerites whose granular surface-microstructure can be seen under SEM (Reinicke 1997). The latter study also discusses the spelling variations noted in the relevant taxonomic literature (*S. coeruleum vs*. *S. caeruleum*).

Previous revisionary studies conducted on the family Xeniidae, genera *Ovabunda* (see Hálasz *et al*. 2014, McFadden *et al*. 2017), *Conglomeratusclera* and *Caementabunda* (Benayahu *et al*. 2018), *Xenia* (see Hálasz *et al*. 2019), and *Unomia* (Benayahu *et al*. 2021) have demonstrated the importance of integrating both classical taxonomy and genetic data for such a purpose. The current study sought to revisit the genus *Sympodium*, including examination of the type of *S. caeruleum* as well as relevant material from several Indo-Pacific locations, most of which was suitable for genetic analyses. These analyses have established several distinct molecular operational taxonomic units (MOTUs) within the genus, some of which were already recognized prior to the current study (McFadden *et al*. 2019). Here, the type specimen of *S. caeruleum* is re-described, and the genetic results of the other specimens in congruence with morphological differences support the description of seven new species of the genus. We also address the question of whether *Sympodium* species demonstrate restricted geographic ranges and regional endemism. Our results further emphasize the significance of the integration of classical taxonomy with a re-examination of original old type-material, along with molecular phylogenetic analyses, in order to elucidate the true biodiversity of the Indo-Pacific soft corals.

Materials and methods

The study examined the original type specimen of *S. caeruleum* deposited at the Zoologisches Museum Berlin (ZMB), along with material from the Steinhardt Museum of Natural History at Tel Aviv University (SMNHTAU), Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie, Leiden, RMNH), Zoologisches Museum Hamburg (ZMH), Queensland Museum (QM), Western Australian Museum (WAM), U.S. National Museum of Natural History, Washington D.C. (USNM), and Florida Museum of Natural History (UF).

Morphological studies

Morphological features (shape and dimensions) of the preserved colonies were recorded. Similarly, the retractability of the polyps was noted and, where possible, the number of rows of pinnules and number of pinnules on the aboral side of the tentacles were counted under a dissecting microscope. The length of the polyp body and the tentacles, as well as the dimension and shape of the pinnules, were recorded as appropriate (see also Halász *et al*. 2019).

To examine the sclerites, the tissue samples were treated with 10% sodium hypochlorite followed by repeated rinses in distilled water. Wet preparations of the clean sclerites were examined under a Nikon Eclipse 80i light microscope at X200–400 magnification (see also Aharonovich & Benayahu 2011). SEM mounts were prepared with each stub containing numerous sclerites. The samples were coated with Pd/Au and viewed under a Quanta 200 FEG (Field Emission Gun) ESEM operated at 5–20 kV or Au coated and viewed under a Hitachi TM-1000 ESEM.

Molecular phylogenetic analyses

For any specimens that had not been sequenced previously, DNA was extracted from EtOH-preserved tissue samples using a DNeasy Blood & Tissue Kit (Qiagen, Inc.). Fragments of the mitochondrial *mtMutS* and *COI* (+*igr1*) genes and nuclear *28S rDNA* were amplified by polymerase chain reaction (PCR) and sequenced using published primers and protocols (McFadden *et al*. 2014a). New sequences were added to an alignment of ~170 xeniid taxa (plus three outgroups) analyzed previously by McFadden *et al*. (2019) and Benayahu *et al*. (2021) (Table 1), and realigned using the L-INS-i method in MAFFT (Katoh *et al*. 2005). mothur v1.42 (Schloss *et al*. 2009) was used to delimit

TABLE 1. *Sympodium* specimens and sequences included in the phylogenetic analysis. MOTU: molecular operational taxonomic unit; CASIZ: California Academy of Sciences; RMNH: Naturalis Biodiversity Center, Leiden; UF: Florida Natural History Museum; USNM: National Museum of Natural History, Smithsonian Institution; SMNHTAU: Steinhardt Museum of Natural History, Tel Aviv University.

				GenBank Accession No.		
Species	MOTU	Museum Acc.	Collection Location	**mutS**	**COI**	**28S**
Sympodium arbusculum **sp. n.**	38	SMNHTAU_Co_31143	Kenya	MZ359157	MZ359181	NA
Sympodium arbusculum **sp. n.**	38	SMNHTAU_Co_31153	Kenya	MZ359158	MZ359182	NA
Sympodium arbusculum **sp. n.**	38	SMNHTAU_Co_31163	Kenya	MZ359159	MZ359183	MZ359642
Sympodium arbusculum **sp. n.**	38	SMNHTAU_Co_31173	Kenya	MZ359160	NA	NA
Sympodium arbusculum **sp. n.**	38	SMNHTAU_Co_31495	Kenya	MZ359161	MZ359184	MZ359643
Sympodium arbusculum **sp. n.**	38	SMNHTAU_Co_31512	Kenya	MZ359162	MZ359185	NA
Sympodium arbusculum **sp. n.**	38	SMNHTAU_Co_31590	Kenya	MZ359163	MZ359186	NA
Sympodium arbusculum **sp. n.**	38	SMNHTAU_Co_32919	Tanzania	MZ359164	MZ359187	MZ359644
Sympodium arbusculum **sp. n.**	38	SMNHTAU_Co_36015	Madagascar	MK030390	MK039213	MK030496
Sympodium arbusculum **sp. n.**	38	SMNHTAU_Co_36017	Madagascar	MK396682	MK396729	MK400138
Sympodium caeruleum	21	UF 14223	Red Sea, Saudi Arabia	MZ359165	MZ359188	NA
Sympodium caeruleum	21	UF 9544	Red Sea, Saudi Arabia	MZ359166	MZ359189	MZ359645
Sympodium caeruleum	21	USNM 1201969	Red Sea, Saudi Arabia	MK030388	MK039210	MK030493
Sympodium caeruleum	21	USNM 1201982	Red Sea, Saudi Arabia	MK396692	KC864962	MK400150
Sympodium caeruleum	21	SMNHTAU_Co_34185	Red Sea, Israel	JX203815	GU356009	JX203758
Sympodium epiphytum **sp. n.**	37	SMNHTAU_Co_35977	Madagascar	MZ359167	NA	MZ359653
Sympodium epiphytum **sp. n.**	37	SMNHTAU_Co_36010	Madagascar	MK030389	MK039212	MK030495
Sympodium epiphytum **sp. n.**	37	SMNHTAU_Co_36062	Madagascar	MZ359168	MK396731	MK400140
Sympodium gibbaeum **sp. n.**	46	SMNHTAU_Co_36032	Madagascar	MZ359169	MK039215	MK030498
Sympodium gibbaeum **sp. n.**	46	SMNHTAU_Co_36121	Madagascar	MZ359170	NA	MK400146
Sympodium hexagonatus **sp. n.**	44	QM G330076	Western Australia	MZ359171	MK039214	MK030497
Sympodium sp.	69	CASIZ 184551	Sulawesi, Indonesia	MZ359172	MZ359190	MZ359646
Sympodium sp.	41	RMNH Coel. 41526	Palau	MZ359173	KF955271	KF915548

......continued on the next page

TABLE 1. (Continued)

Species	MOTU	Museum Acc.	Collection Location	GenBank Accession No.		
				mutS	**COI**	**28S**
Sympodium subtilis **sp. n.**	68	SMNHTAU_Co_38092	Danjo Is., Japan	MZ359174	MZ359191	MZ359647
Sympodium subtilis **sp. n.**	68	SMNHTAU_Co_38103	Danjo Is., Japan	MZ359175	MZ359192	MZ359648
Sympodium subtilis **sp. n.**	68	SMNHTAU_Co_38104	Danjo Is., Japan	MZ359177	MZ359194	MZ359650
Sympodium subtilis **sp. n.**	68	SMNHTAU_Co_38204	Danjo Is., Japan	MZ359176	MZ359193	MZ359649
Sympodium vegrandis **sp. n.**	54	SMNHTAU_Co_35751	Green I., Taiwan	MK030391	MK039216	MK030499
Sympodium vegrandis **sp. n.**	54	SMNHTAU_Co_37888	Green I., Taiwan	MZ359178	NA	MZ359651
Sympodium yonaguniensis **sp. n.**	36	SMNHTAU_Co_35117	Yonaguni I., Japan	MZ359179	MK039211	MK030494
Sympodium yonaguniensis **sp. n.**	36	SMNHTAU_Co_35164	Yonaguni I., Japan	MZ359180	MZ359195	MZ359652
Sympodium yonaguniensis **sp. n.**	36	SMNHTAU_Co_35754	Green I., Taiwan	MK030392	MK039217	MK030500

molecular operational taxonomic units (MOTUs) based on an average genetic distance (uncorrected p) threshold of 0.003, which has been shown in previous studies to yield a high concordance with morphospecies designations (McFadden *et al*. 2014b).

Preliminary phylogenetic analyses of each gene region using PhyML (Guindon & Gascuel 2003) revealed congruence of gene trees, therefore all three genes were concatenated for further analyses. JModeltest (Darriba *et al*. 2012) was used to identify the best model of evolution for each gene region based on the Aikake Information Criterion (AIC). Maximum likelihood analyses were run using RAxML v8 (Stamatakis 2014) with 1000 rapid bootstrap replicates, which allows a search for the best-scoring tree and bootstrapping in a single run; the GTR+I+G substitution model was applied to all three gene partitions. A partitioned analysis was run using MrBayes v. 3.2.1 (Ronquist *et al*. 2012), applying a HKY+I+G model separately to *mtMutS* and *COI* partitions, and a GTR+I+G model to *28S rDNA*. MrBayes was run for 3,000,000 generations (until standard deviation of split partitions < 0.01) with a burn-in of 25% and default Metropolis coupling parameters.

Results

Systematics

Order Alcyonacea Lamouroux, 1812

Family Xeniidae Ehrenberg, 1828

Sympodium Ehrenberg, 1834

Type species *Sympodium caeruleum* Ehrenberg,1834: 285

Klunzinger 1877: 42; May 1898: 46–51; Wright & Studer 1889: 270–271; Cohn 1908: 241–242; Kükenthal 1916: 453; Hickson 1931: 174–175; Roxas 1933: 106–107; Macfadyen 1936: 23; Gohar 1940: 106–107; Tixier-Durivault 1966: 371; Reinicke 1997: 22–23.

Diagnosis. Colonies encrusting. The encrusting part is a membrane of variable thickness. It can be either mat-like or with ribbon-like extensions; when thicker, it features irregularly shaped low mounds. Polyps monomorphic, commonly retractile, mostly found over the entire surface of the colony, but some parts of the encrusting membrane have very few polyps. Commonly, the polyps arise individually from the membrane or the mounds and can be either spaced or closely set. In the latter case, they can appear as clusters comprising polyps that bud off at different levels to form small branched groups. The sclerites are ellipsoid platelets, abundant throughout the colony. They reach up to ca. 0.03 mm maximal diameter, with each composed of densely packed calcite rods. The tips of the rods are distinct on the surface of the sclerites and commonly provide a granular microstructure. Zooxanthellate.

Sympodium arbusculum sp. n.

Figs. 1, 2, 3A

Material. Madagascar. **Holotype**: SMNHTAU_Co_36017, Ankaréa (12°50.054'S, 48°34.563.3'E), 6–9 m, 29 November 2012, coll. Y. Benayahu; **Paratypes**: SMNHTAU_Co 38226, five colonies, same details as the holotype; SMNHTAU_Co_36015, same details; Tanzania, SMNHTAU_Co_32919, Shundo (4°52'53"S, 39°18'10"E), 0–25 m, 10 December 2004, coll. Y. Benayahu; Kenya. SMNHTAU_Co_31143, off Mombasa, Turning Buoy, 10 m, 16 February 2001, coll. Y. Benayahu & S. Perkol-Finkel; SMNHTAU_Co_31153, same details; SMNHTAU_Co_31163, off Mombasa, Simon's Corner, 20–26 m, 20 February 2001, coll. Y. Benayahu & S. Perkol-Finkel; Kenya, SMNHTAU_Co_31173, off Mombasa, Shelly Beach, 10–12 m, 20 February 2001, coll. Y. Benayahu & S. Perkol-Finkel; SMNHTAU_Co_31495, off Likoni, Shelly Reef (4°06.4'S, 39°41'S), 19 m, 9 March 2002, coll. Y. Benayahu; SMNHTAU_Co_31512, off Likoni, Wall (4°06.4'S, 39°42'E), 15–27 m, 2 February 2002, coll. Y. Benayahu; SMNHTAU_Co_31590, off Likoni, Shelly Reef (4°06.4'S, 39°41'E), 19 m, 9 March 2002, coll. Y. Benayahu.

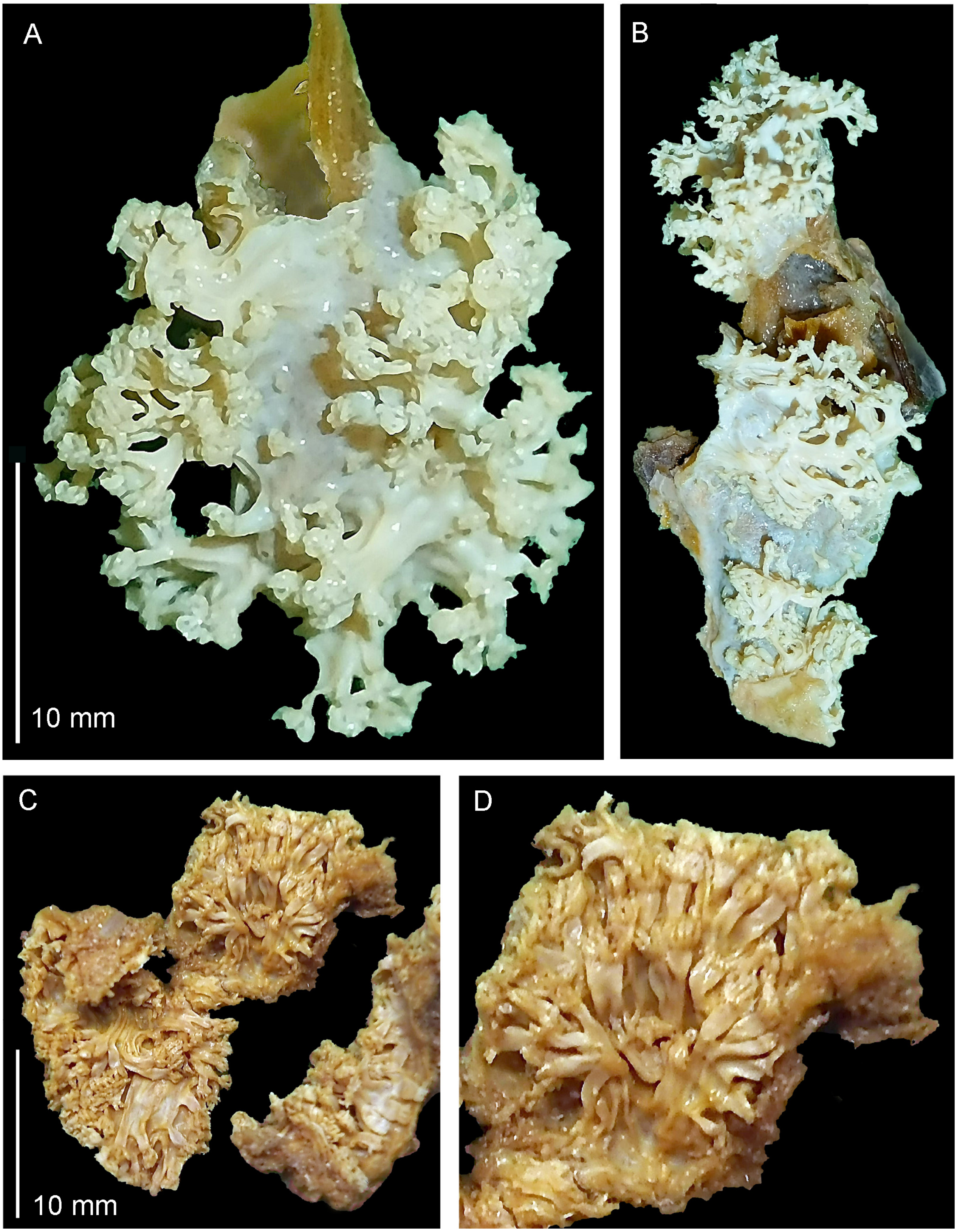

FIGURE 1. *Sympodium arbusculum* **sp. n.**: morphology of type material. (A) Holotype (SMNHTAU_Co_36017) with polyps budding off on different levels from the encrusting membrane, occasionally dichotomously, forming small branched groups of polyps. (B) Paratype (SMNHTAU_Co_38226) featuring clusters of expanded polyps. (C) Paratype (SMNHTAU_Co_36015) comprises eight fragments, two shown here. (D) Polyps of the paratype (SMNHTAU_Co_36015) whose polyps bud off in a distinct dichotomous manner, forming small groups of polyps.

Description. The holotype is an encrusting colony attached by a membrane to calcareous fragments, and measures 1.9 x 1.5 cm (Fig. 1A). Its soft basal membrane is thin, <1 mm thick. Clusters of non-retractile polyps bud off at different levels, occasionally dichotomously, to form small branched groups of polyps (Fig. 1A). Occasionally, individual polyps arise from the membrane between the clustered polyps. The polyps that are the most expanded are up to 4 mm long and the tentacles are up to 1 mm long. The poor preservation state of the sample prevents a precise pinnule count, but it is estimated to be a single row with up to 10 slender and pointed pinnules on either side of the tentacle.

The sclerites of the holotype are ellipsoid platelets, abundant throughout the colony, 0.010–0.011 x 0.015–0.017 mm in diameter (Fig. 2A). They are composed of tightly packed calcite rods whose tips provide a uniform granular appearance to the sclerite surface (Fig. 2B)

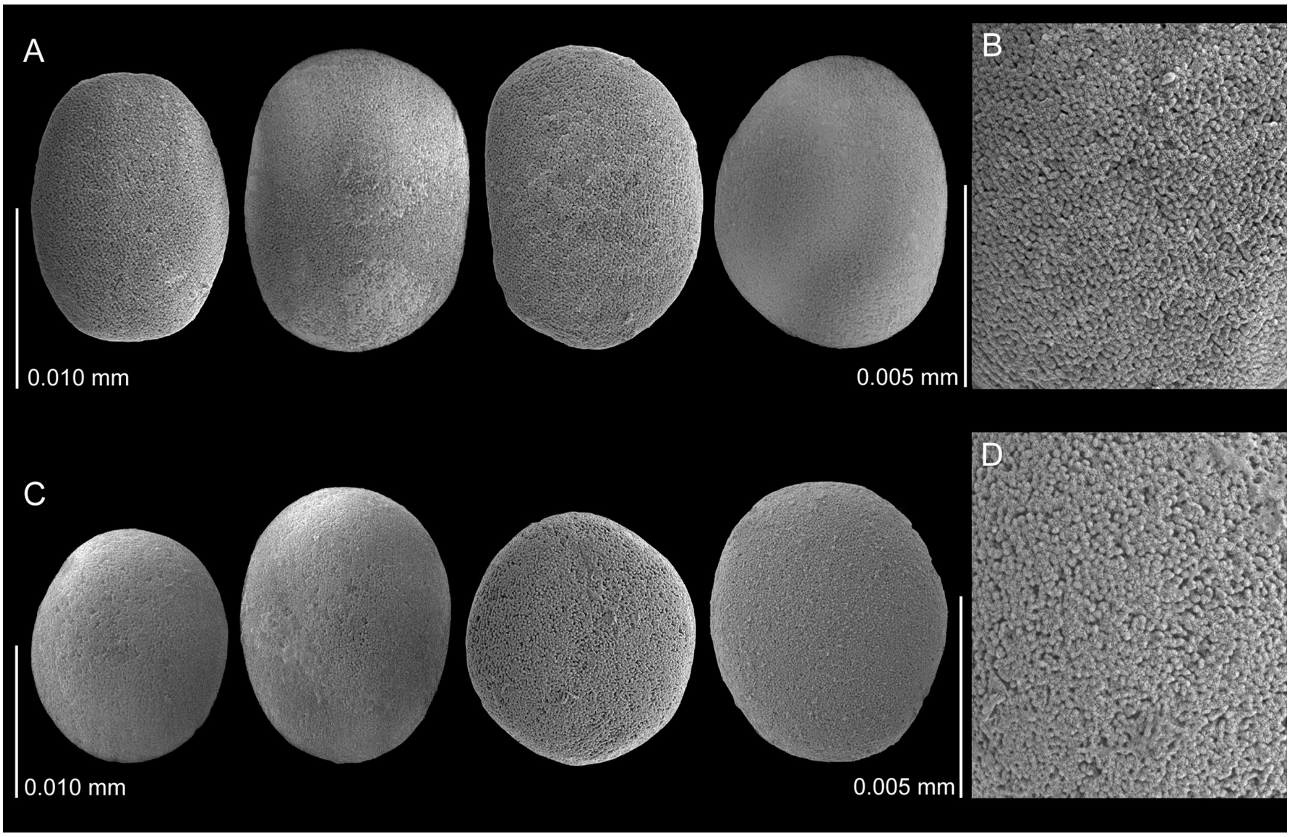

FIGURE 2. Scanning electron micrographs of sclerites of *Sympodium arbusculum* **sp. n.** Holotype (SMNHTAU_Co_36017): (A) Ellipsoid platelets. (B) Tips of calcite rods provide a uniform granular appearance to the sclerite surface. Paratype (SMNHTAU_Co_36015): (C) Ellipsoid platelets. (D) Tips of calcite rods provide a uniform granular appearance to the sclerite surface.

Color. The ethanol-preserved colony is light cream..

Etymology. The species' name is derived from the Latin 'arbuscula', bush, referring to the clustered arrangement of polyps.

Variation. The paratype SMNHTAU_Co_38226 comprises four colonies that vary in size: the smallest colony measures 1.0 x 0.5 cm and the largest one 3.5 x 1.5 cm (Fig. 1B: one of the paratypes). Groups of polyps comprising these paratypes range in number of polyps from 4 to 18, and are up to 20 mm long from the basal membrane to the tip of the uppermost polyp. The paratype SMNHTAU_Co_36015 comprises eight colonies or fragments that resemble the holotype, except in size. The dichotomous arrangement of the polyps is visible (Fig. 1C, D). Both the dimensions of the paratypes' sclerites (Fig. 2C) and their surface microstructure (Fig. 2D) correspond to those of the holotype (Fig. 2A, B).

Remarks. The morphology of the colonies, and in particular the arrangement of the non-retractile polyps in clusters, is considered to be diagnostic of the species. The holotype was sequenced and subsequently assigned to MOTU38 (McFadden *et al*. 2019).

Living features. The live brownish colonies feature clusters of expanded polyps (Fig. 3A).

Distribution. Kenya, Madagascar, Tanzania.

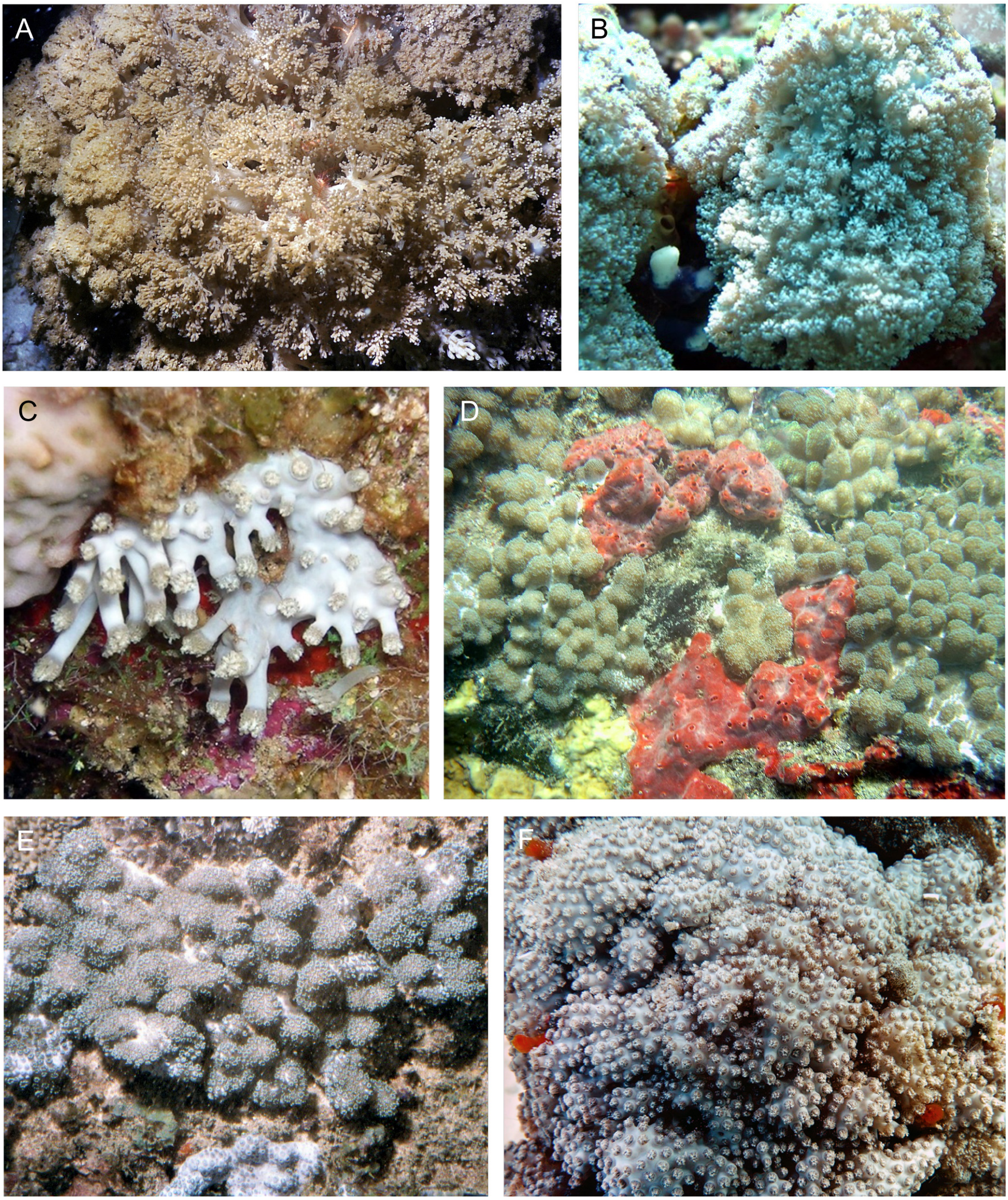

FIGURE 3. Live colonies of *Sympodium* species on the reef. (A) *S. arbusculum* **sp. n.**: colonies with clusters of expanded polyps. (B, C) *S. caeruleum* Ehrenberg, 1834; membrane-like colonies with expanded polyps. (D, E) Patches of *Sympodium gibbaeum* **sp. n.** colonies with expanded polyps over the mounds. (F) *S. hexagonotus* **sp. n.** holotype colony featuring distinct mounds with expanded polyps.

Sympodium caeruleum **Ehrenberg, 1834**

Figs. 3B–C, 4, 5

Sympodium caeruleum Ehrenberg 1834: 61

Sympodium caeruleum Ehrenberg, 1834; Dana, 1846: 609; Hickson 1931: 174; Gohar 1940: 107–108, pl. VIII; Benayahu 1990: 118 (listed only); Reinicke 1995: 56–57, figs. 1, 12; Reinicke 1997: 23, figs 7a–b, Plate 9, 13; McFadden *et al*. 2011 (listed only); Haverkort-Yeh *et al*. 2013 (listed only); McFadden *et al*. 2019 (listed only).

Sympodium cœruleum: Milne Edwards & Haime 1857: 111; Gray, 1869: 120; Wright & Studer, 1889: 271 (listed only).

S. coeruleum: Kükenthal 1904: 39–41, plate 4, fig. 3; pl. 5, figs. 13, 14; Kükenthal 1913: 2 (listed only); Kükenthal 1916: 456.

? *Sympodium cöruleum*: Klunzinger 1877: 42–43, Plate 3, Fig. 5.

Not *Sympodium caeruleum*: May 1899: 51–52; Thomson & Henderson: 1906: 408; Thomson & Mackinnon, 1910: 168; Thomson & Dean 1931: 21; Roxas 1933: 107, pl. 3 fig. 4; Macfadyen 1936: 23; Tixier-Durivault 1966: 371–372, fig. 334; Verseveldt 1973: 168–169; Utinomi: 1977: 7–8, plate II, fig. 5; Benayahu 1993: 6 (listed only); Malyutin 1992: 2 (listed only): Janes 2013: 198 (listed only); McFadden *et al*. 2014a: Table 1.

Material examined. Syntypes: Egypt. ZMB Cni 240 (several colonies), northern Red Sea, Gulf of Suez, Sinai, At-Tur, coll. H. H. R. Hartmeyer. **Additional material**: Egypt. ZMH C 3245, same details; SMNHTAU_Co_ 9897, northern Red Sea Gulf of Suez, Abu Durbah (28° 28’ 25”N, 33° 19’ 51”E), 1 October 1972, coll. L. Fishelson; SMNHTAU_Co_ 9898, same details; SMNHTAU_Co_ 25585, same details; SMNHTAU_Co_ 25397, northern Red Sea, southern tip of Sinai Peninsula, 2–5 m, 8 November 1981, coll. Y. Benayahu; SMNHTAU_Co_ 25641, northern Red Sea, southern tip of Sinai Peninsula, Shaab al Utaf (27°45’ 23.6”N, 34°10’10.4”E), 3 m, 15 August 1987, coll. Y. Benayahu; SMNHTAU_Co_ 26022, northern Red Sea, southern tip of Sinai, 27 March 1987, coll. Y. Benayahu; SMNHTAU_Co_ 26024, northern Red Sea, Straits of Tiran, 18 m, 27 March 1988, coll. Y. Benayahu; SMNHTAU_Co_ 26031, northern Red Sea, Gulf of Suez, Shag Rock (27°47’00.0”N 33°53’00.0”E), 25 m, 7 October 1987, coll. Y. Benayahu; SMNHTAU_Co_ 26032, northern Red Sea, Gulf of Suez, Shag Rock (27°47’00.0”N 33°53’00.0”E), 8 October 1987, coll. Y. Benayahu; SMNHTAU_Co_ 26033, northern Red Sea, southern tip of Sinai Peninsula, Shaab al Utaf (27°45’23.6”N, 34°10’10.4”E), 10 m, 5 October 1988, Coll. Y. Benayahu; Israel. SMNHTAU_Co_ 7953, northern Red Sea, Gulf of Aqaba, Eilat, 1 June 1971, coll. L. Fishelson; SMNHTAU_Co_ 34184, northern Red Sea, Gulf of Aqaba, Eilat, Princess Coral Reef (29°29.77’N, 34°54.53’E), 22.9–24.4 m, 26 July 2007, coll. Y. Benayahu; SMNHTAU_Co_ 34185, same details; SMNHTAU_Co_ 34919, northern Red Sea, Gulf of Aqaba, Eilat, Oil Jetty (29.52993°N, 34.93535°E), 13 m, 30 November 2008, coll. D. Aharonovich; SMNHTAU_Co_35020; northern Red Sea, Gulf of Aqaba, Eilat, the reef across the Interuniversity Institute for Marine Sciences, Israel (29°30′N, 034°55′E), 10–12m, 19 February 2008, coll. D. Aharonovich; SMNHTAU_Co_35028, northern Red Sea, Gulf of Aqaba, Eilat, Oil Jetty (29.52993°N, 34.93535°E), 13 May 2008, 12 m, coll. D. Aharonovich; SMNHTAU_Co_35030 same details; SMNHTAU_Co_35032 same details; SMNHTAU_Co_ 35044, northern Red Sea, Gulf of Aqaba, Eilat, Coral Beach Nature Reserve (29.50993°N, 34.92.39°E), 20 m, 18 January, 2011, coll. A. Halász; SMNHTAU_Co_ 37045, northern Red Sea, Gulf of Aqaba, Eilat, Oil Jetty (29.52993°N, 34.93535°E), 10 m, 9 November 2011, coll. A. Halász; SMNHTAU_Co_ 37046, northern Red Sea, Gulf of Aqaba, Eilat, Oil Jetty (29.52993°N, 34.93535°E) , 15 m, 9 November 2011, coll. A. Halász; SMNHTAU_Co_ 37047, northern Red Sea, Gulf of Aqaba, Eilat, Princess Coral Reef, (29°29.77’N, 34°54.53’E), 25 m, 8 November 2011, coll. A. Halász; SMNHTAU_Co_ 37048, northern Red Sea, Gulf of Aqaba, Eilat, Oil Jetty (29.52993°N, 34.93535°E), 10 m, 9 November 2011, coll. A. Halász; SMNHTAU_Co_ 37688, Northern Red Sea, Gulf of Aqaba, Eilat, Princess Coral Reef (29°29.77’N, 34°54.53’E), 5 m, 20 March 2018, coll. R. Liberman. Saudi Arabia. USNM1201982, Al Lith, Marmar Reef (19° 50’N, 39°56’E), 5 m, April 2011, coll. R. Haverkort-Yeh; USNM1201969, Dora Reef (19°49’N, 39 °53’E), 6 m, April 2011, coll. R. Haverkort-Yeh; UF 9544, Yanbu, Shi’b Sufflami (23.543467°N, 38.22791°7E), 4 March 2014, coll. G. Paulay; UF 14223, Jeddah (21.7127°N, 39.0803°E), 24.4 m, 26 October 2018, coll. C. McFadden.

Description. The syntypes, ZMB Cni 240, consist of several small encrusting membrane-like colonies firmly attached to an irregular calcareous fragment measuring approximately 10 x 6 cm (Fig. 4A). The largest colony is 2.5 x 2 cm and the others are smaller, approximately 1 cm^2. Certain parts of the colonies are extended into small crevices of the fragment. The membrane overgrowing the substrate is 1–1.5 mm thick. Some of the polyps are fully retracted while others are partly expanded (Fig. 4B). The polyp body is up to 10 mm long and the tentacles up to 5 mm long. The pinnules are arranged in 3 rows, with 5–8 pinnules in the outermost row. They are short, approximately 1 mm long and 0.5 mm wide, with almost no space between adjacent ones.

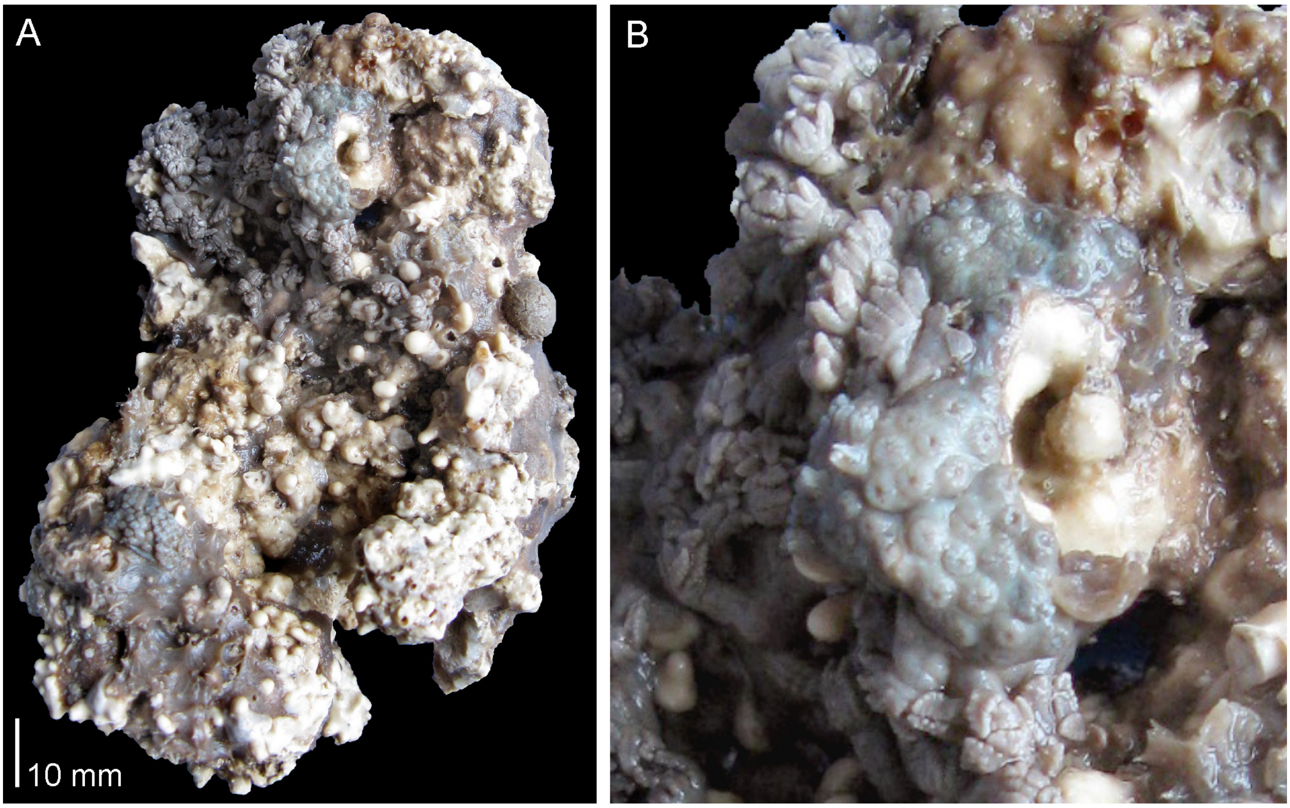

FIGURE 4. *Sympodium caeruleum* Ehrenberg, 1834. Syntypes (ZMB 240): (A) Colonies attached to a calcareous substrate. (B) View of expanded and retracted polyps.

The sclerites of the syntypes are ellipsoid platelets, highly abundant throughout the colony, measuring 0.010–0.012 x 0.014–0.017 mm in diameter (Fig. 5A). They are composed of calcite rods, uniform in diameter of ca. 0.001 mm; the tips of the rods are perpendicular to the surface of the sclerite, giving it a granular appearance (Fig. 5B).

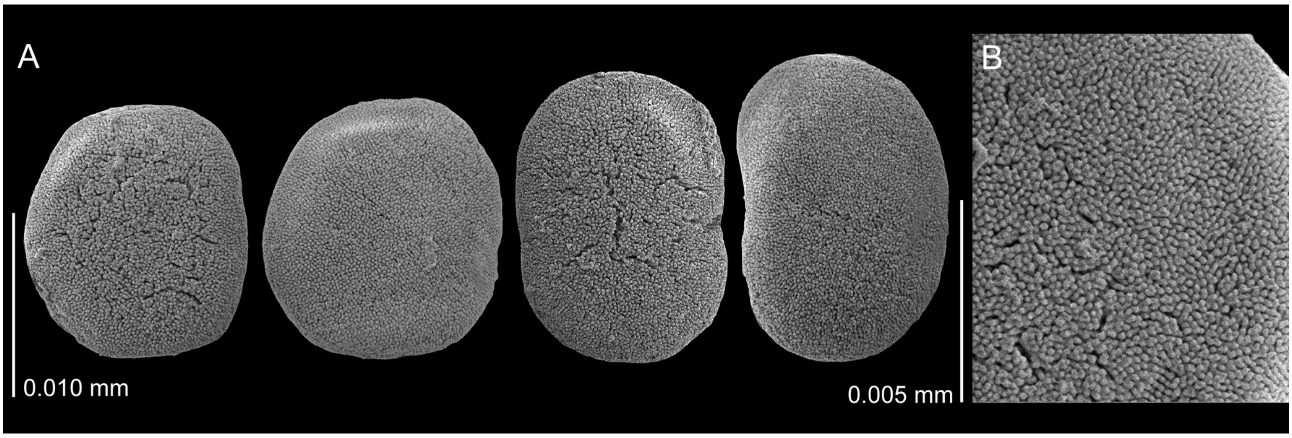

FIGURE 5. Scanning electron micrographs of sclerites of *Sympodium caeruleum* Ehrenberg, 1834. Syntypes (ZMB 240): (A) Ellipsoid platelets. (B) Tips of calcite rods provide a uniform granular appearance to the sclerite surface.

Color. The ethanol-preserved syntypes are gray.

Variation. The morphological features of the sequenced colony (SMNHTAU_Co_ 34185) resemble those of the syntypes, and it similarly grows over a calcareous fragment by means of a thin spreading membrane. The pinnules are arranged in 2–3 rows, with 6–7 pinnules in the outermost one. Some pinnules are retracted, however the few expanded ones are up to 1 mm in length. Similarly, other Red Sea colonies that were sequenced (USNM1201982 and USNM 1201969) resemble the syntypes, except in size.

Color. All the ethanol-preserved samples are gray.

Remarks. The morphology of all the additional *S. caeruleum* colonies collected from the Red Sea (Israel, Egypt, and Saudi Arabia) corresponds to the syntypes, but they may differ in size and in the density of the polyps emerging from the spreading membrane. All of the sequenced colonies (SMNHTAU_Co_ 34185, USNM 1201982, USNM 1201969, UF 9544 and UF 14223) were assigned to MOTU21 (McFadden *et al*. 2019). Based on the current findings, it is suggested that this species is the only representative of the genus present in the Red Sea.

Living features. The live colonies feature a membrane-like morphology with expanded polyps, whose color presents a bluish or light greyish-white tinge (Figs. 3B–C).

Distribution. Red Sea.

Sympodium epiphytum sp. n.

Figs. 6, 7

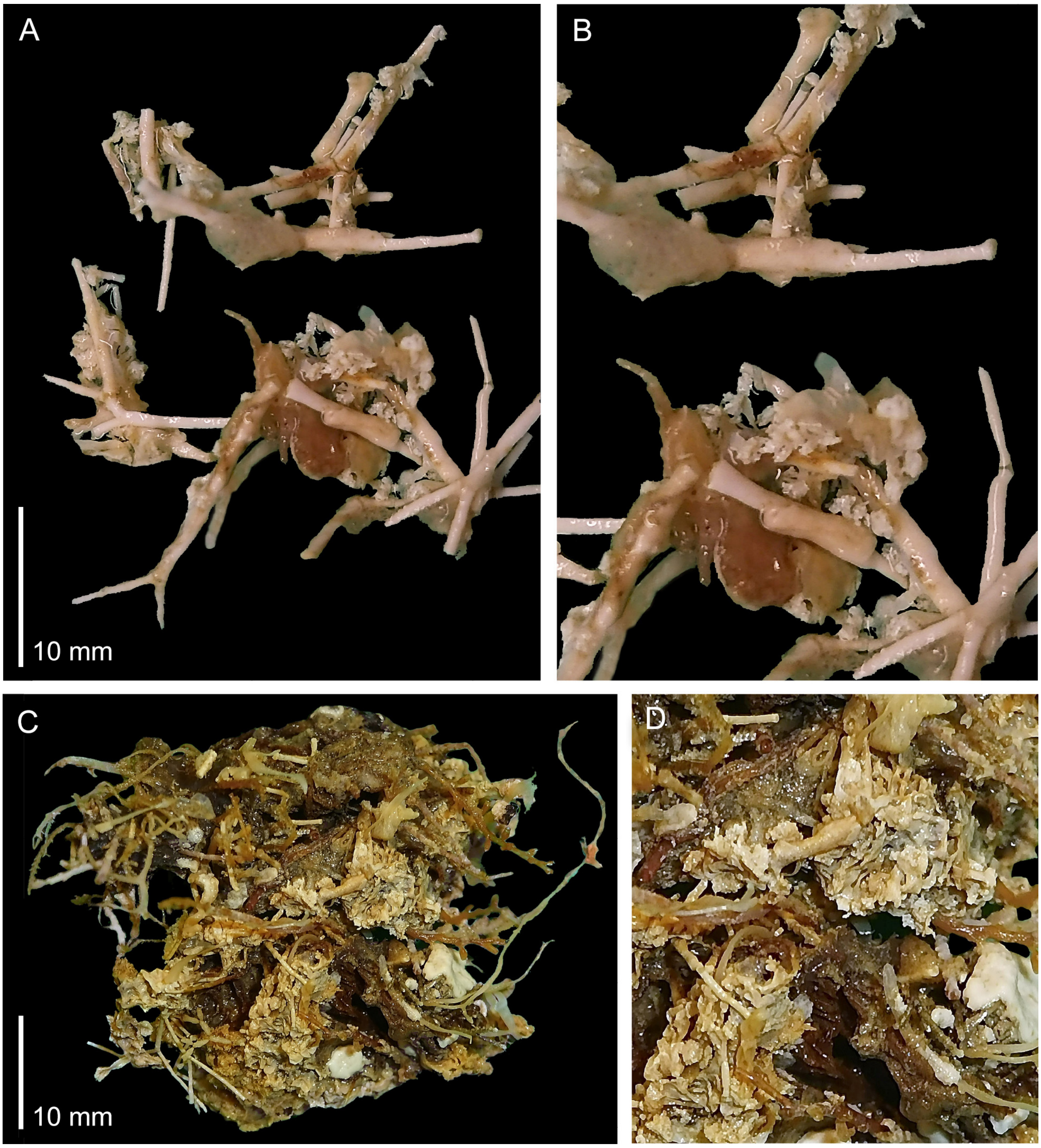

FIGURE 6. *Sympodium epiphytum* **sp. n.**: morphology of type material. (A) Syntypes (SMNHTAU_Co_36010) are encrusting colonies growing on thin branched algal fragments. (B) Several syntypes interconnected by a thin spreading membrane. (C) Paratype (SMNHTAU_Co_35977) growing on algal material. (D) Higher magnification of several paratype colonies.

Material. Madagascar. **Syntypes**: SMNHTAU_Co_36010, Ankaréa (12°50.054'S, 48°34.563.3'E), 24–26 m, 29 November 2012, coll. Y. Benayahu; **Paratypes:** SMNHTAU_Co_35977, Riva Be (12°59.126' S, 48°34.453'E), 8–10 m, 27 November 2012, coll. Y. Benayahu; SMNHTAU_Co_ 36062, 4 Fréres (12°59.655'S, 48°29.248'E), 4–15 m, 1 December 2012, Coll. Y. Benayahu.

Description. The syntypes comprise several small encrusting colonies up to only 5 x 5 mm. They are densely growing on thin branched algal material which easily fragments (Fig. 6A). Some of the colonies are connected by their thin spreading membrane, and therefore it is not practical to separate a single colony as a holotype. The small size of the syntypes is also reflected by the fact that each comprises only 4–12 polyps (Fig. 6B). The polyps are expanded and their body measures up to 2.5 mm. The tentacles are approximately 1 mm long and feature one row of 7–9 pinnules on either side. The pinnules are slender and pointed, up to 0.25 mm long.

The sclerites of the syntypes are ellipsoid platelets, highly abundant throughout the colony, measuring 0.011–0.012 x 0.015–0.017 mm in diameter (Fig. 7A). They are composed of calcite rods whose tips mostly provide a granular appearance to the sclerite surface (Fig. 7B).

Color. The ethanol-preserved colonies are cream.

Etymology. The species' name is derived from the ancient Greek "epiphúton", one [plant] that grows upon another plant (epí, "on top of") + (phutón, "plant"), via epi- ("above, over") + - phyte ("plant"). It denotes the nature of the colonies found growing on algal material.

Variation. The paratypes SMNHTAU_Co_35977 (not shown) and SMNHTAU_Co_ 36062 (Fig. 6C) are similarly attached to algal fragments. Some of the colonies are larger than those of the syntypes, up to 8 x 8 mm (Fig. 6D). Their sclerites are similar to those of paratype SMNHTAU_Co_36062 (Fig. 7C), with a surface that features calcite rods (Fig. 7D) that are more densely packed than those of the holotype (Fig. 7B).

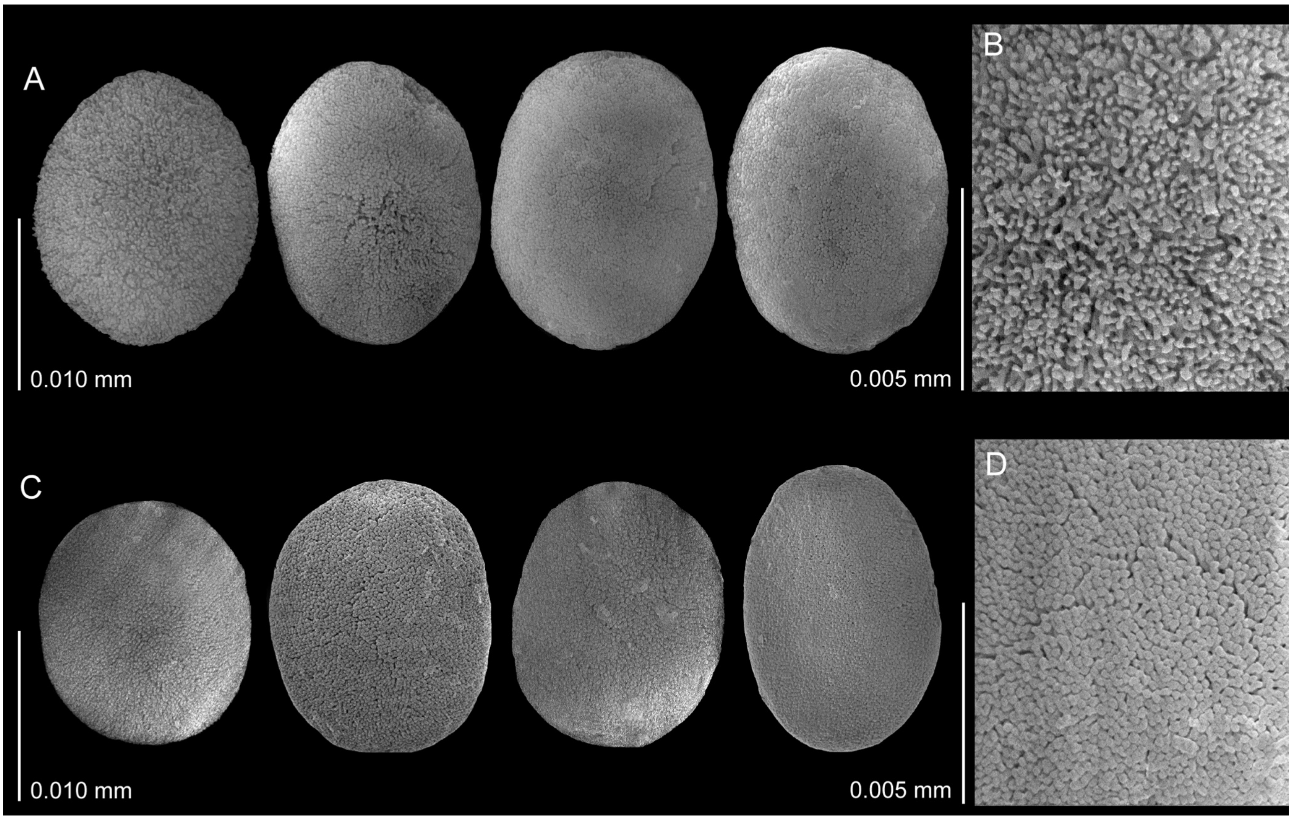

FIGURE 7. Scanning electron micrographs of sclerites of *Sympodium epiphytum* **sp. n.**: Syntypes (SMNHTAU_Co_36010): (A) Ellipsoid platelets. (B) Tips of calcite rods provide a uniform granular appearance to the sclerite surface. Paratype (SMNHTAU_Co_35977): (C) Ellipsoid platelets. (B) Tips of calcite rods provide a uniform granular appearance to the sclerite surface**.**

Remarks. The epiphytic nature of the colonies is suggested to be diagnostic for this species The syntypes and a paratype were sequenced and subsequently assigned to MOTU37 (McFadden *et al*. 2019).

Distribution. Madagascar.

Sympodium gibbaeum **sp. n.**
Figs. 3D, E, 8, 9

Material. Madagascar. **Holotype**: SMNHTAU_Co_36121, Nose Be (13°29.032'S, 47°58.721'E), 2–14 m, 3 December 2012, coll. Y. Benayahu. **Paratypes**; SMNHTAU_Co_ 38227, ten fragments, same details as the holotype, SMNHTAU_Co_36032, Ankaréa (12°49.978'S, 48°34.504'E), 26–28 m, 30 November 2012, coll. Y. Benayahu.

Description. Encrusting colony with densely packed knob-like mounds (Fig. 8A). The holotype measures 3.2 x 1.5 cm, the mounds are 8–10 mm high and the spreading membrane in between is about 1 mm thick. The polyps are uniformly spaced throughout the surface of the colony; those of the upper part of the mounds are fully retracted, leaving distinct round pits of about 1 mm in diameter (Fig. 8A). The polyps of the periphery of the lobes are partly expanded, up to 1.2 mm long, with tentacles up to 0.5 mm long. Most of the pinnules are retracted, but there appears to be a single row of 3–5 pinnules on either side of the tentacle.

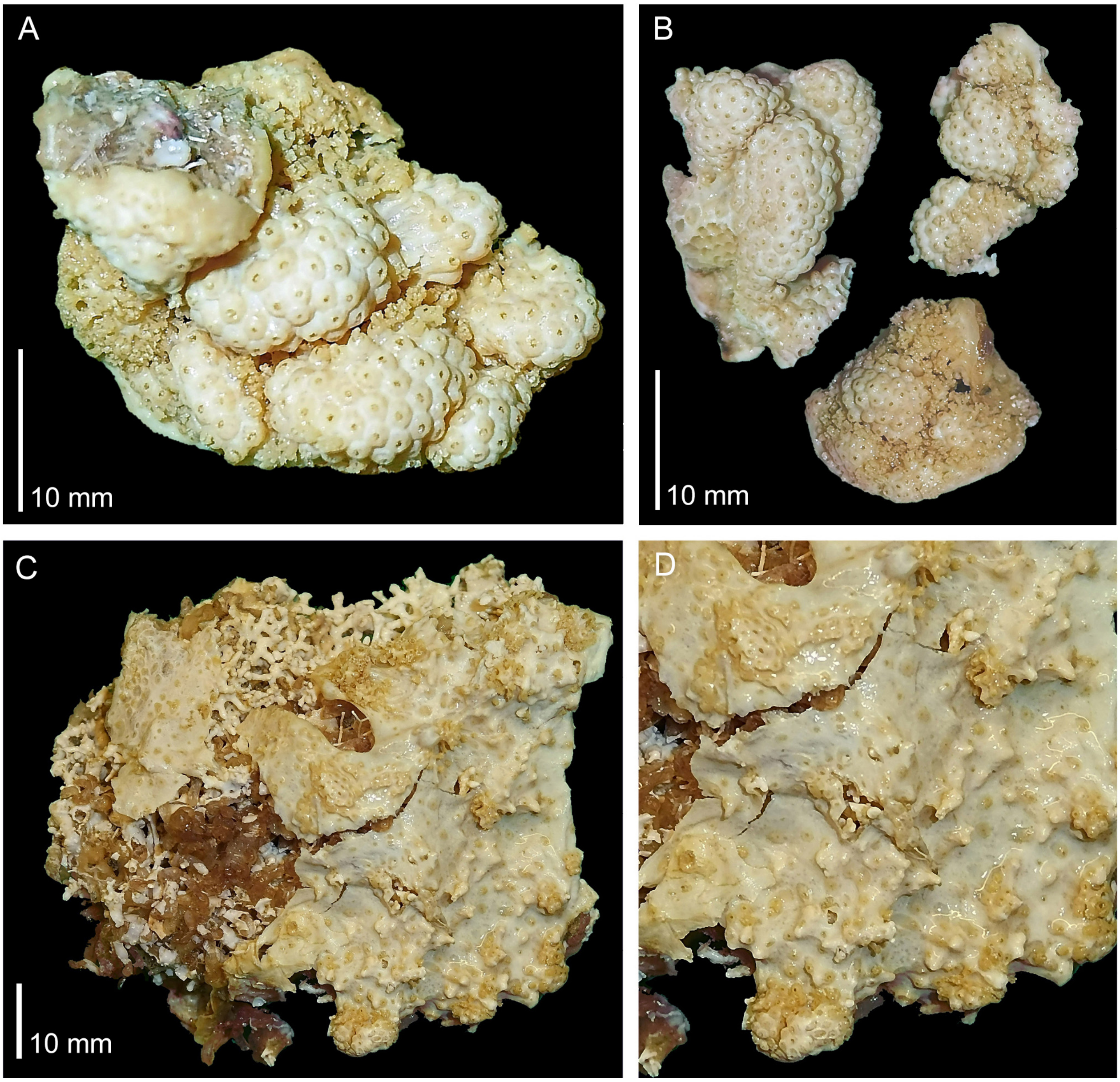

FIGURE 8. *Sympodium gibbaeum* **sp. n.**: morphology of type material colonies. (A) Holotype (SMNHTAU_Co_36121) featuring densely packed knob-like mounds with polyps retracted on top of mounds and partially expanded between them. (B) Paratype colonies (SMNHTAU_Co_38227) with expanded and retracted polyps on top of mounds. (C) Paratype (SMNHTAU_Co_36032) is an encrusting membranous colony with individual separated polyps and with some low mounds bearing polyps. (D) Higher magnification of part of the paratype (SMNHTAU_Co_36032) showing polyp location on both the encrusting membrane and the low mounds.

The sclerites of the holotype are ellipsoid platelets, abundant throughout the colony, and measure 0.014–0.016 x 0.016–0.019 mm in diameter (Fig. 9A). They are composed of packed calcite rods whose tips appear to bend over at the surface (Fig. 9B).

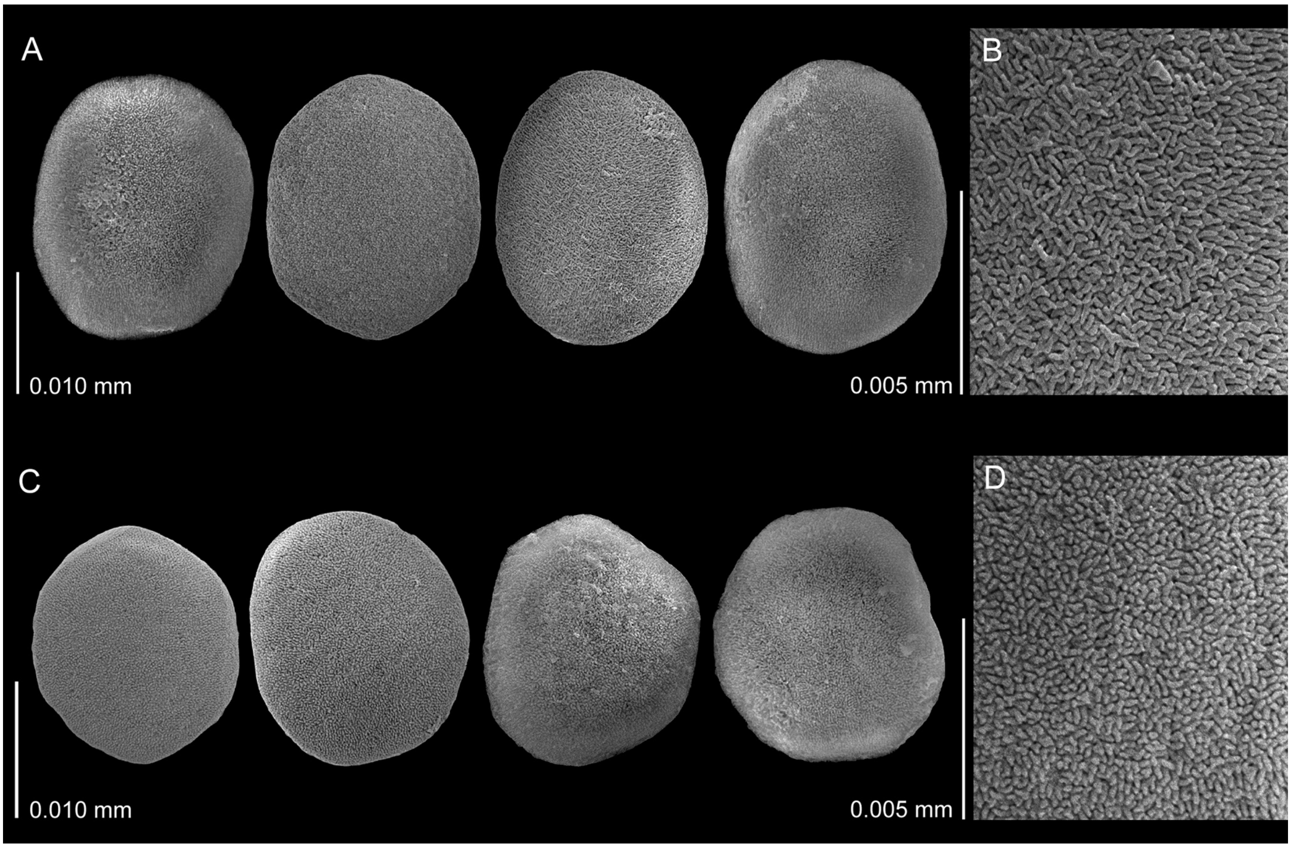

FIGURE 9. Scanning electron micrographs of sclerites of *Sympodium gibbaeum* **sp. n.** Holotype (SMNHTAU_Co_36121): (A) Ellipsoid platelets. (B) Tips of calcite rods provide a uniform granular appearance to the sclerite surface, some of the tips are oblique. Paratype (SMNHTAU_Co_36032): (C) Ellipsoid platelets. (B) Tips of calcite rods provide a uniform granular appearance to the sclerite surface, some of the tips are oblique or parallel to the surface.

Color. The ethanol-preserved colony is light cream.

Etymology. The species' name, *gibbaeum,* is derived from the Latin "gibbosus" meaning hunchback, referring to the mounds of the colony.

Variation. The paratype SMNHTAU_Co_38227 (Fig. 8B) resembles the holotype, but is smaller. The paratype SMNHTAU_Co_36032 (Fig. 8C) comprises a delicate membranous colony featuring several low mounds. The spreading membrane is 1–2 mm thick with some individual polyps set apart, leaving 4–10 mm gaps with no polyps but the few low mounds do bear polyps (Fig. 8D). The sclerites of the paratype SMNHTAU_Co_38227 (Fig. 9C) resemble those of the holotype, but their outline can be more angular and their surface microstructure presents an oblique-to-parallel orientation of the calcite rods (Fig. 9B).

Remarks. The morphology of the colonies, featuring mounds, mostly with a round outline, is considered diagnostic for the species. The morphological differences between the holotype (Fig. 9A) and the paratypes (Fig. 9B–D) are suggested to represent intraspecific variation. The ethanol-preserved holotype (SMNHTAU_Co_36121) and a paratype (SMNHTAU_Co_36032) were sequenced and subsequently assigned to MOTU46 (McFadden *et al.* 2019).

Living features. The live colonies feature distinct mounds with expanded polyps, also presenting some color variation such as green-beige or gray (Fig. 3D, E).

Distribution. Madagascar.

Sympodium hexagonotus sp. n.

Figs. 3F, 10, 11.

Material. Australia. **Holotype:** QM G330076, Ningaloo Reef, inside Norwegian Bommies, Western Australia, Australia (22°37'17.6"S, 113°38'32.6"E), Lagoon (Patch Reef), 5–6 m, 19 May 2009, coll. M. Ekins & M. Bryce; **Paratypes**: QM G339750, four fragments same details as the holotype.

WAM Z29359, same details as the holotype.

Description. The holotype measures 25 x 33 mm (Fig. 10A), and features mounds covered with densely packed polyps. The spreading membrane is about 1 mm thick and the mounds are about 10 mm high. Only a few polyps are significantly expanded while the majority are in various states of retraction. The expanded polyps are up to 1.5 mm long and their tentacles are approximately 0.5 mm long with a single row of 7–8 pinnules on either side of the tentacle.

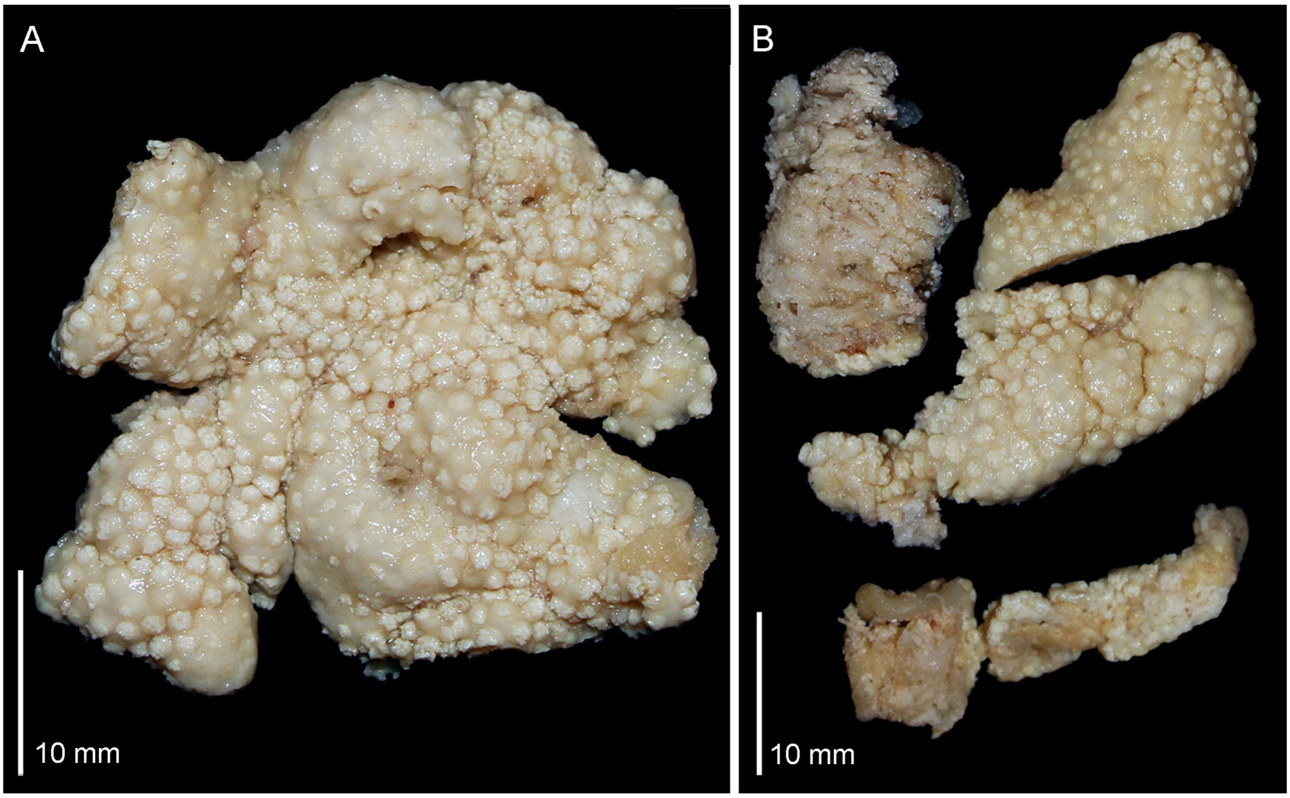

FIGURE 10. *Sympodium hexagonotus* **sp. n.**: morphology of type material colonies. (A) Holotype (QM G330076) featuring mounds with mostly retracted polyps. (B) Paratype fragments (QM G339750).

The sclerites of the holotype are ellipsoid platelets, mostly hexagonal in shape. They are opalescent and abundant throughout the colony, measuring 0.010–0.028 x 0.008–0.023 mm in diameter (Fig. 11A). The sclerites are composed of calcite rods whose tips provide a uniform granular appearance to the sclerite surface. They are arranged in dense patches with some space in between (Fig. 11B).

Color. The ethanol-preserved holotype is cream.

Etymology. The species' name, *hexagonotus* in Greek, means a six-sided polygon, referring to the unique shape of the sclerites.

Remarks. The paratypes resemble the holotype except for their size. The morphology of the colonies is characterized by both mounds and the hexagonal sclerites whose diameter is the largest recorded to date among the congeners (0.028 mm). The ethanol-preserved holotype (QM G330076) was sequenced and subsequently assigned to MOTU44 (McFadden *et al*. 2019).

Living features. The live colonies feature distinct mounds and are bluish/cream in color (Fig. 3F)

Distribution. Western Australia

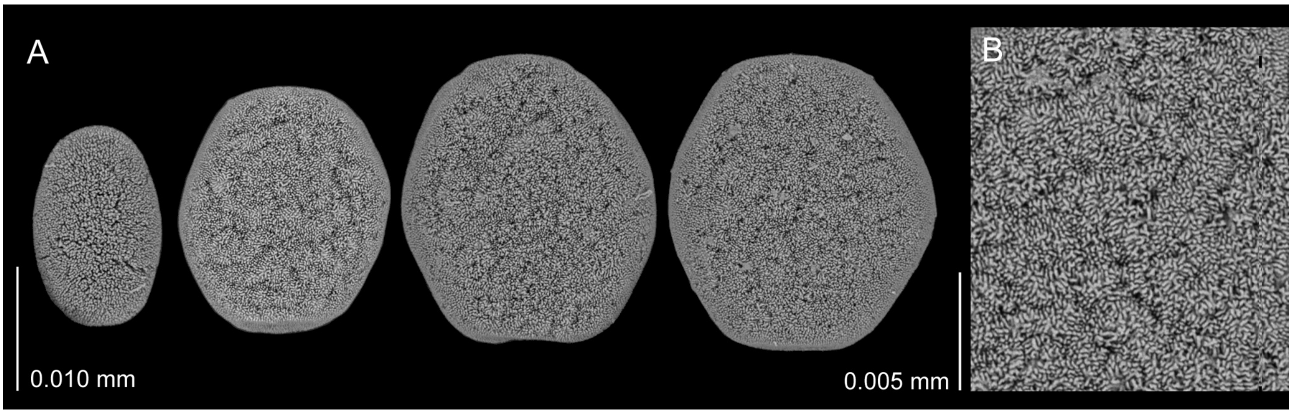

FIGURE 11. Scanning electron micrographs of sclerites of *Sympodium hexagonotus* **sp. n.** Holotype (QM G330076): (A) Ellipsoid platelets with hexagonal outline. (B) Tips of calcite rods provide a granular appearance to the sclerite surface but organized in patches with space in between.

Sympodium subtilis sp. n.

Figs. 12, 13, 14A

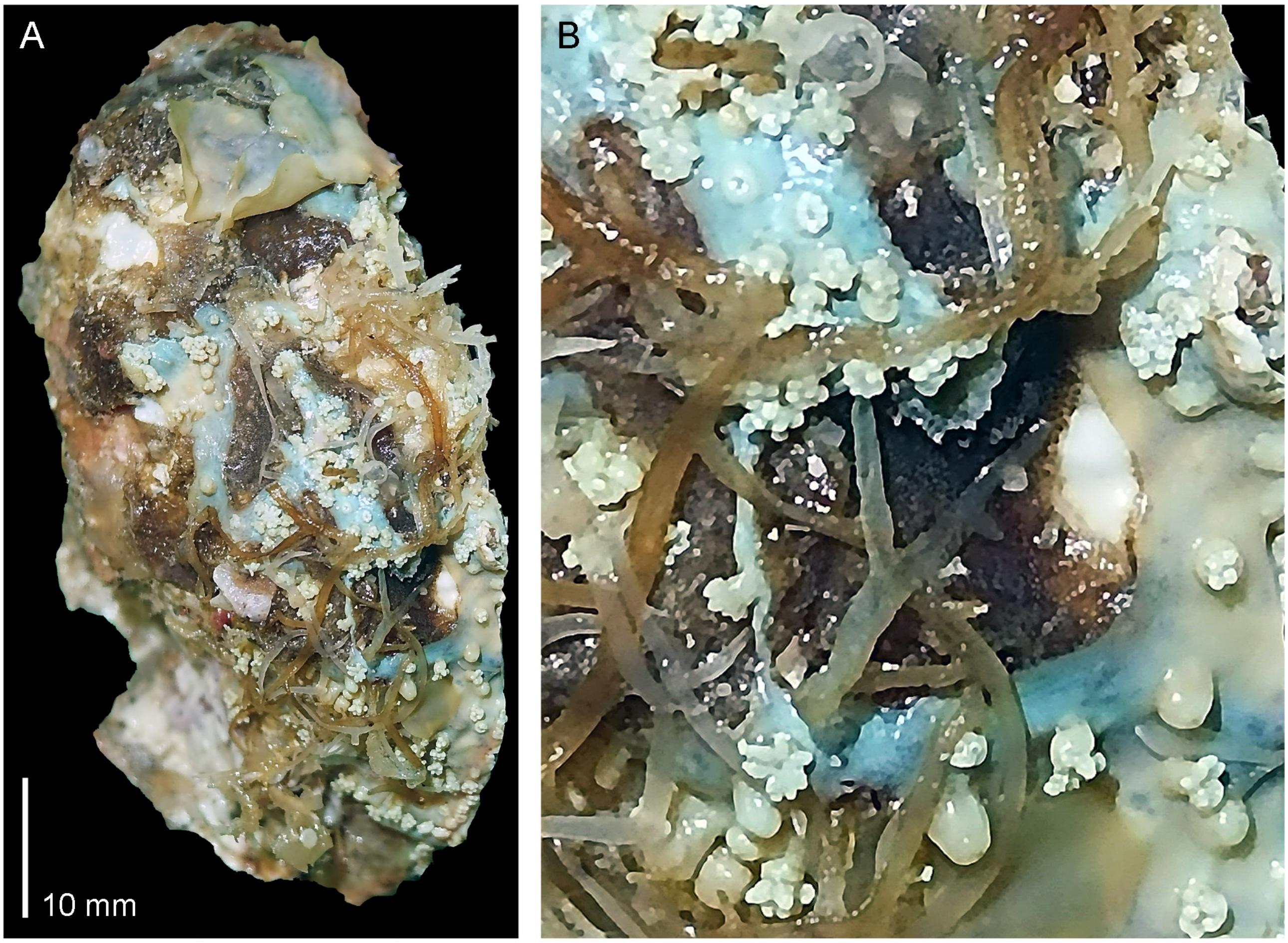

FIGURE 12. *Sympodium subtilis* **sp. n.**: morphology of type material colonies. (A) Syntypes (SMNHTAU_Co_38204) encrusting colonies with delicate membrane growing on a bivalve shell. (B) Higher magnification of portion of syntypes showing both expanded and retracted polyps on spreading membrane.

Material. Japan. **Syntypes**: SMNHTAU_Co_38204, Nagasaki, Danjo Islands, south of Arasesaki, Ojima, NW side (32.051168°N, 128.391857°E), 23 September 2018, 10–20 m, coll. C. McFadden; **Paratypes:** SMNHTAU_

Co_38092 Nagasaki, Danjo Islands, Ojima, SE side (32.038886°N, 128.387278°E), 22 September 2018, 10–20 m, coll. C. McFadden (molecular sample only); SMNHTAU_Co_38103 Nagasaki, Danjo Islands, rocks west of Yorijima (32.024824°N, 128.364289°E), 23 September 2018, 10–20 m, coll. C. McFadden (molecular sample only); SMNHTAU_Co_38104, same details.

Description. The syntypes comprise several irregular encrusting colonies with a delicate thin spreading membrane (<0.5 mm) attached to a bivalve shell (Fig. 12A). The largest colony has a surface area of ca. 15 mm^2. In addition, there are a few small colonies measuring 3–5 mm^2. It was not possible to separate a single colony as a holotype without compromising its integrity and therefore syntypes were assigned. The polyps emerge from the membrane 1–5 mm apart and exhibit various degrees of retraction (Fig. 12B). The few expanded polyps are up to 1.5 mm long and their tentacles are approximately 0.5 mm long. The pinnules are either totally or partially contracted, with a single row of 3–5 pinnules on either side of the tentacle.

The sclerites of the syntypes are ellipsoid platelets, abundant throughout the colony and measuring 0.010–0.012 x 0.013–0.015 mm in diameter (Fig.13A). They are composed of densely packed calcite rods whose tips provide a uniform granular appearance to the sclerite surface (Fig. 13B).

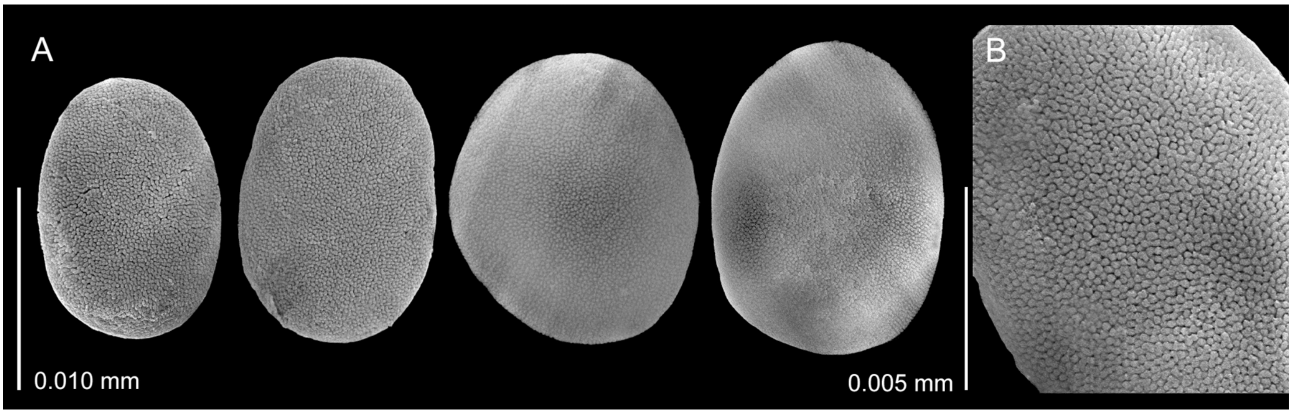

FIGURE 13. Scanning electron micrographs of sclerites of *Sympodium subtilis* **sp. n.** Syntypes (SMNHTAU_Co_38204): (A) Ellipsoid platelets. (B) Tips of calcite rods provide a uniform granular appearance to the sclerite surface.

Color. The ethanol-preserved syntypes are light gray, almost white.

Etymology. The species' name, *subtilis* from the Latin meaning delicate, refers to the delicate encrusting membrane of the species.

Variation. The paratype SMNHTAU_Co_38104 is a small colony measuring only a few mm in size, but otherwise resembles the holotype.

Living features. The live colonies feature polyps arranged in groups (Fig. 14A).

Distribution. Japan.

Remarks. The colonies are characterized by a remarkably thin and delicate spreading membrane which is suggested to be diagnostic for this species. The ethanol-preserved syntypes and paratypes were sequenced and subsequently assigned to MOTU68.

***Sympodium vegrandis* sp. n.**

Figs. 14B–C, 15, 16

Material. Taiwan. **Holotype:** SMNHTAU_Co_35751, Green Island, Iron Artificial Reef (22°38'33"N, 121°28'31"E), 20–26 m, 9 September 2012, coll. Y. Benayahu; **Paratype**: SMNHTAU_Co_37888, Green Island, Lighthouse End (22°40'32.04"N, 121°27'44.58"E), 20–26 m, October 2019, coll. Y. Benayahu.

Description. The syntypes comprise 25–30 small encrusting colonies attached to a fluffy sponge fragment (Fig. 15A). Each features up to 15 polyps and measures approximately 2 x 4 mm. There are also a few individual polyps on the sponge surface (Fig. 15 B). Some colonies reveal a round outline (Fig. 15B) while in others their thin spreading membrane (<0.5 mm) forms an elongate, ribbon-like extension, bearing polyps. All of the colonies in the aggregation are designated as syntypes because it is not possible to separate a single colony as a holotype without compromising its integrity. The majority of the polyps are variously retracted. The few fully expanded polyps are up to 1.5 mm long and their tentacles are approximately 0.5 mm long. There is a single row of 3–4 pinnules on either side of the tentacles, which are almost fully retracted.

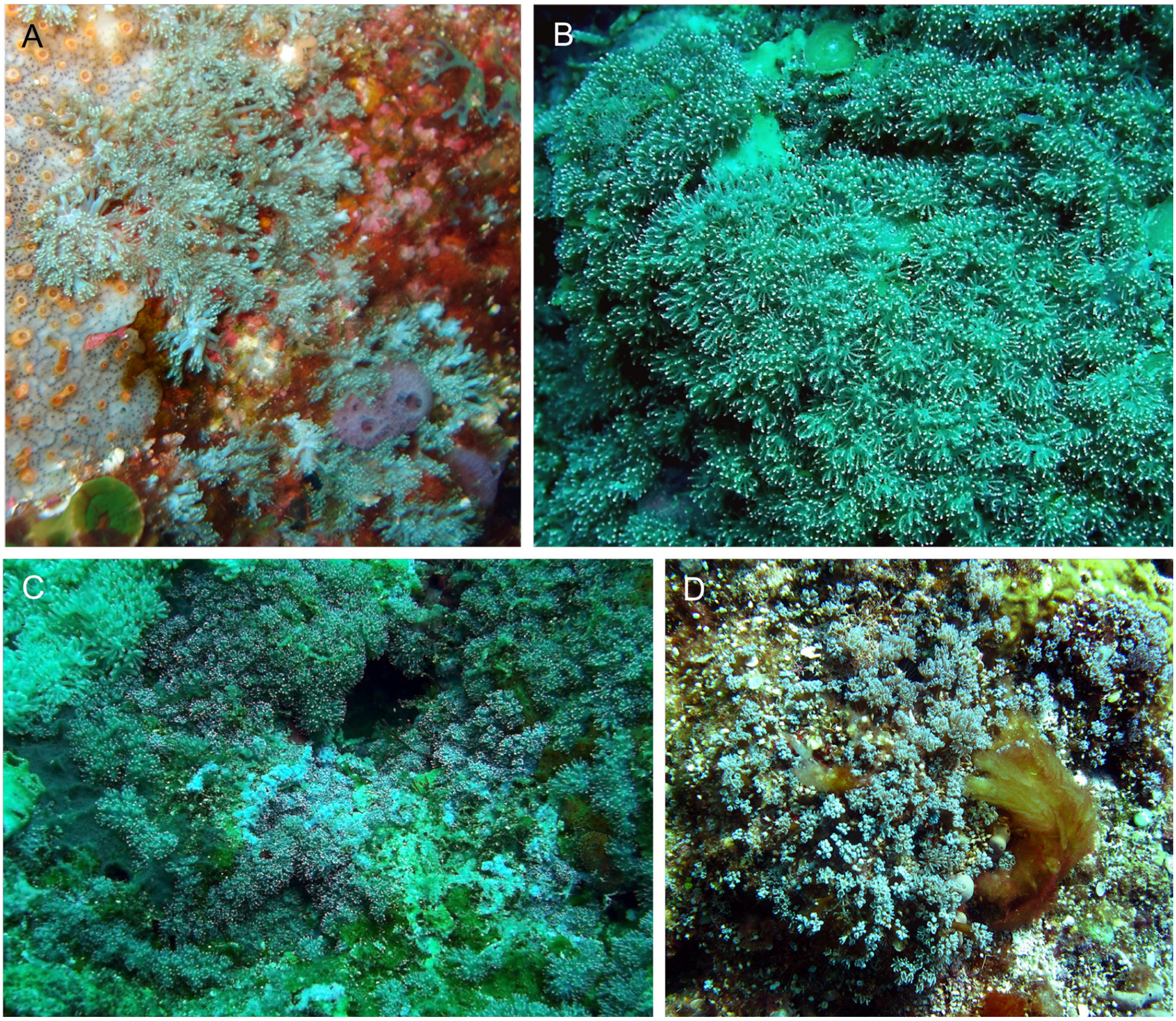

FIGURE 14. Live colonies of *Sympodium* species on the reef. (A) Colonies of *S. subtilis* **sp. n.** with expanded polyps. (B, C) Colonies of *S. vegrandis* **sp. n.** (D, E) Colonies of *S. yonaguniensis* **sp. n.**

The sclerites of the syntypes are ellipsoid platelets, measuring 0.009–0.010 x 0.012–0.015 mm in diameter (Fig. 16A). They are composed of calcite rods whose tips provide a uniform granular appearance to the sclerite surface (Fig. 16B).

Color. The ethanol-preserved syntypes are light cream.

Etymology. The species' name, *vegrandis* in Latin, meaning small, diminutive, refers to the size of the colonies.

Variation. The paratype resembles the syntypes.

Remarks. The colonies are characterized by their minute size and sclerites whose diameter is the smallest recorded to date among the congeners. The syntypes uniquely exhibit single (not clustered) polyps that are probably juvenile recruits. The ethanol-preserved syntypes and paratype were sequenced and subsequently assigned to MOTU54 (McFadden *et al*. 2019).

Living features. The aggregated live colonies exhibit a distinct bluish/green color (Fig. 14 B, C)

Distribution. Taiwan (Green Island).

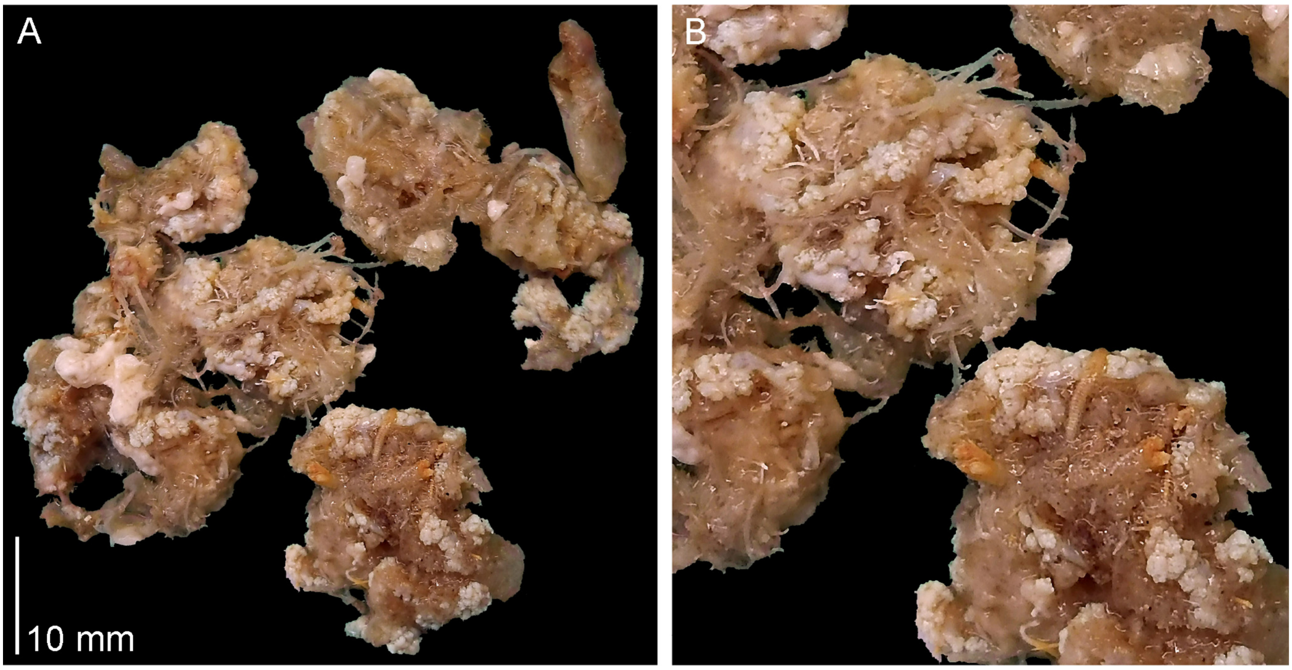

FIGURE 15. *Sympodium vegrandis* **sp. n.**: morphology of type material colonies. (A) Syntypes (SMNHTAU_Co_35751) are small colonies attached to a sponge, with several shown here. (B) Higher magnification of syntypes featuring mostly retracted polyps and a few expanded ones. The encrusting membrane also displays stolon-like extensions bearing polyps.

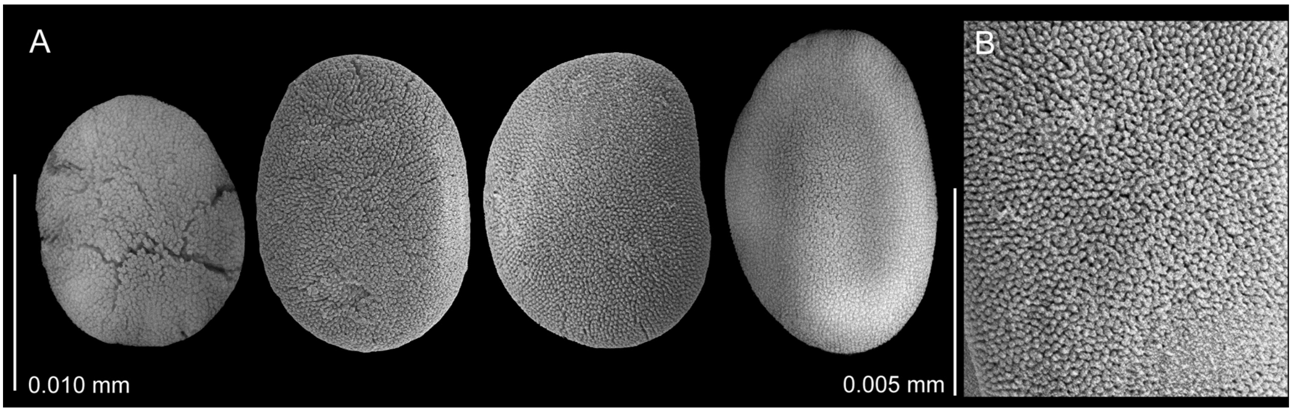

FIGURE 16. Scanning electron micrographs of sclerites of *Sympodium vegrandis* **sp. n.** syntypes (SMNHTAU_Co_35751): (A) Ellipsoid platelets. (B) Tips of calcite rods provide a uniform granular appearance to the sclerite surface.

Sympodium yonaguniensis **sp. n.**

Fig. 14D, Fig. 17, Fig. 18

Material. Japan. **Holotype.** SMNHTAU_Co_35117, Ryukyu Archipelago, Yonaguni Is., Umabanazaki Point, 8–12 m, 3 July, 2010, Coll. Y. Benayahu; **Paratypes**. SMNHTAU_Co_38228, same details, 11 fragments, SMNHTAU_Co_35164 Ryukyu Archipelago, Yonaguni Is., West Point, 16–22 m, 5 July, 2010, 6 fragments, Coll. Y. Benayahu; Taiwan. SMNHTAU_Co_35754 Green Is. Iron Artificial Reef (22°38’33”N, 121°28’31”E), 20–26 m, 5 September 2012.

Description. The holotype is an encrusting and soft colony with irregular upper surface, measuring 5 x 32 mm and up to 3 mm thick (Fig. 17A). Some polyps emerge individually and others in small groups of 3–5, forming low mounds up to 2–4 mm in diameter. Almost all the polyps are retracted and the few that are either partly or mostly expanded measure up to 2 mm, with tentacles up to 1 mm long. Most of the pinnules are retracted and only the few partly retracted ones can be seen under the dissecting microscope.

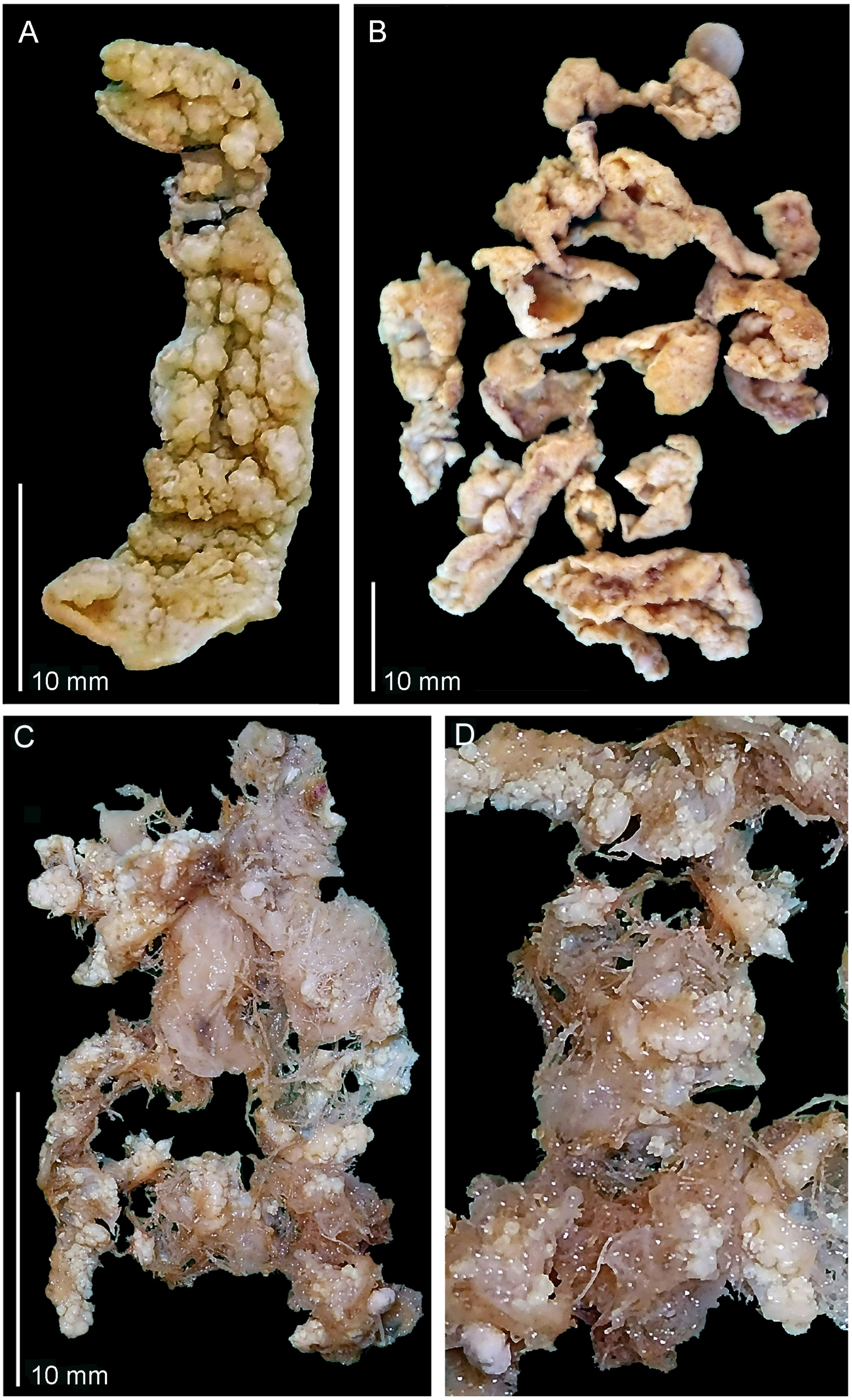

FIGURE 17. *Sympodium yonaguniensis* **sp. n.**: morphology of type material colonies. (A) Holotype (SMNHTAU_Co_35117) featuring irregular upper surface with some polyps emerging individually and others in groups; almost all are retracted. (B) Paratype colonies (SMNHTAU_Co_38228); five shown here. (C) Paratype (SMNHTAU_Co_35754) comprises small colonies growing on turf algae and a sponge. (D) Higher magnification of the paratype showing partly retracted polyps of colonies.

The sclerites of the holotype are ellipsoid platelets, abundant throughout the colony, measuring 0.012–0.016 x 0.010–0.012 mm in diameter (Fig. 18A). They are composed of densely packed calcite rods whose tips provide a granular appearance to the sclerite surface (Fig. 18B).

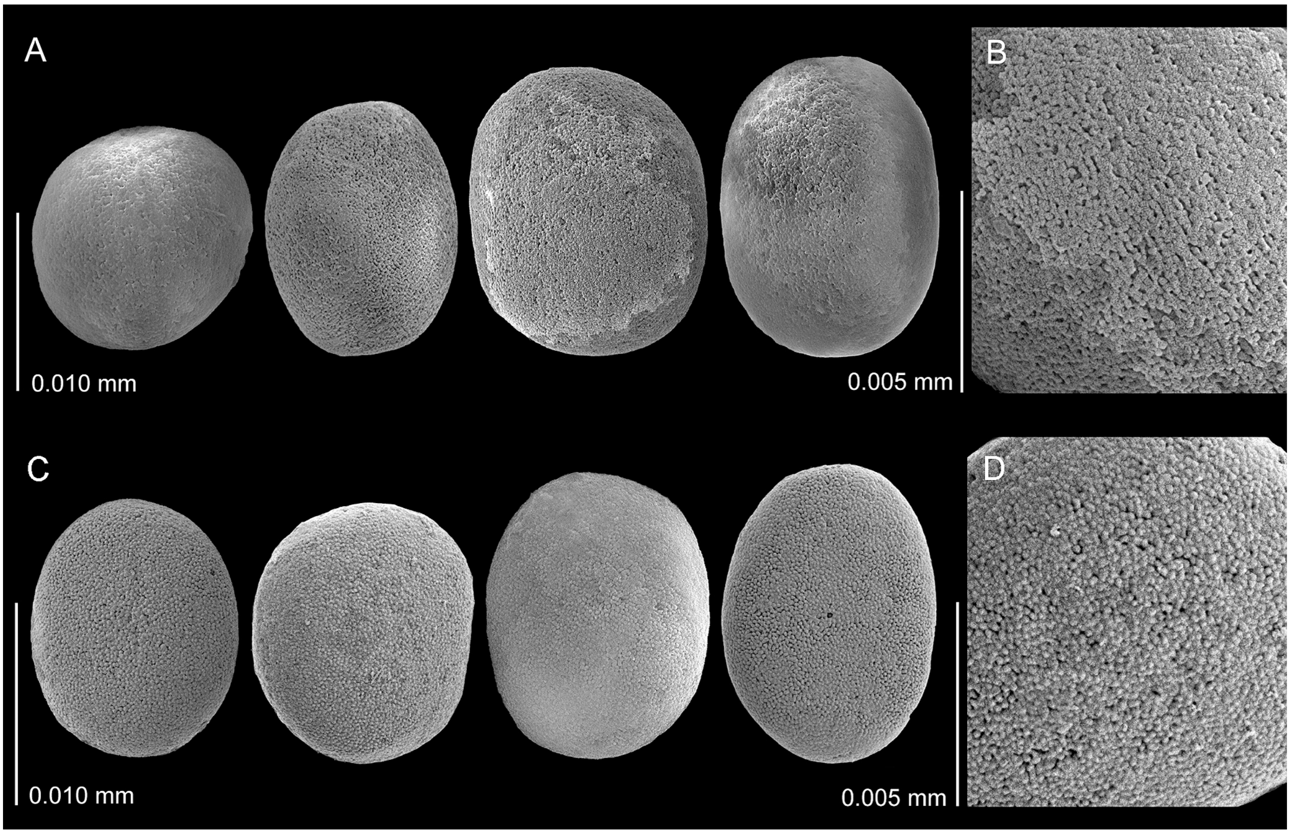

FIGURE 18. Scanning electron micrographs of sclerites of *Sympodium yonaguniensis* **sp. n.** holotype (SMNHTAU_Co_ 35117): (A) Ellipsoid platelets. (B) Tips of calcite rods provide a uniform granular appearance to the sclerite surface. Paratype (SMNHTAU_Co_35754): (C) Ellipsoid platelets. (D) Tips of calcite rods provide a uniform granular appearance to the sclerite surface.

Color. The ethanol-preserved colony is light cream.

Living features. The live colonies present clusters of brown-gray expanded polyps over the reef substrate (Fig. 14D).

Etymology. The species is named after Yonaguni Island, the type locality of the species.

Variation. The paratypes SMNHTAU_Co_38228 (Fig, 17B), SMNHTAU_Co_35164 and SMNHTAU_Co_ 35754 (Figs. 17C, D), are smaller than the holotype, but otherwise resemble the holotype.

Remarks. The morphological features of the colony, specifically the relatively thick encrusting membrane and the polyps emerging in groups from low mounds, are considered to be diagnostic for this species. The ethanol-preserved holotype and paratypes (SMNHTAU_Co_35164, SMNHTAU_Co_35754) were sequenced and subsequently assigned to MOTU36 (McFadden *et al*. 2019).

Distribution. Japan: Ryukyu Archipelago, Yonaguni Island; Taiwan: Green Island.

Molecular Results

Maximum likelihood and Bayesian analyses recovered the same relationships among *Sympodium* taxa, supporting the monophyly of each of the eight species described above (Fig. 19). There was strong support for a clade composed of *S. caeruleum*, *S. gibbaeum* **n. sp.** and *S. hexagonatus* **n. sp.**; and somewhat weaker support for a sister relationship between *S. vegrandis* **n. sp.** and *S. subtilis* **n. sp.** Where multiple species occurred at the same location (Madagascar: *S. arbusculum*, *S. epiphytum*, *S. gibbaeum*; Green Is.: *S. vegrandis*, *S. yonaguniensis*), sympatric congeners were not sister taxa but instead belonged to different clades within the genus (Fig. 19).

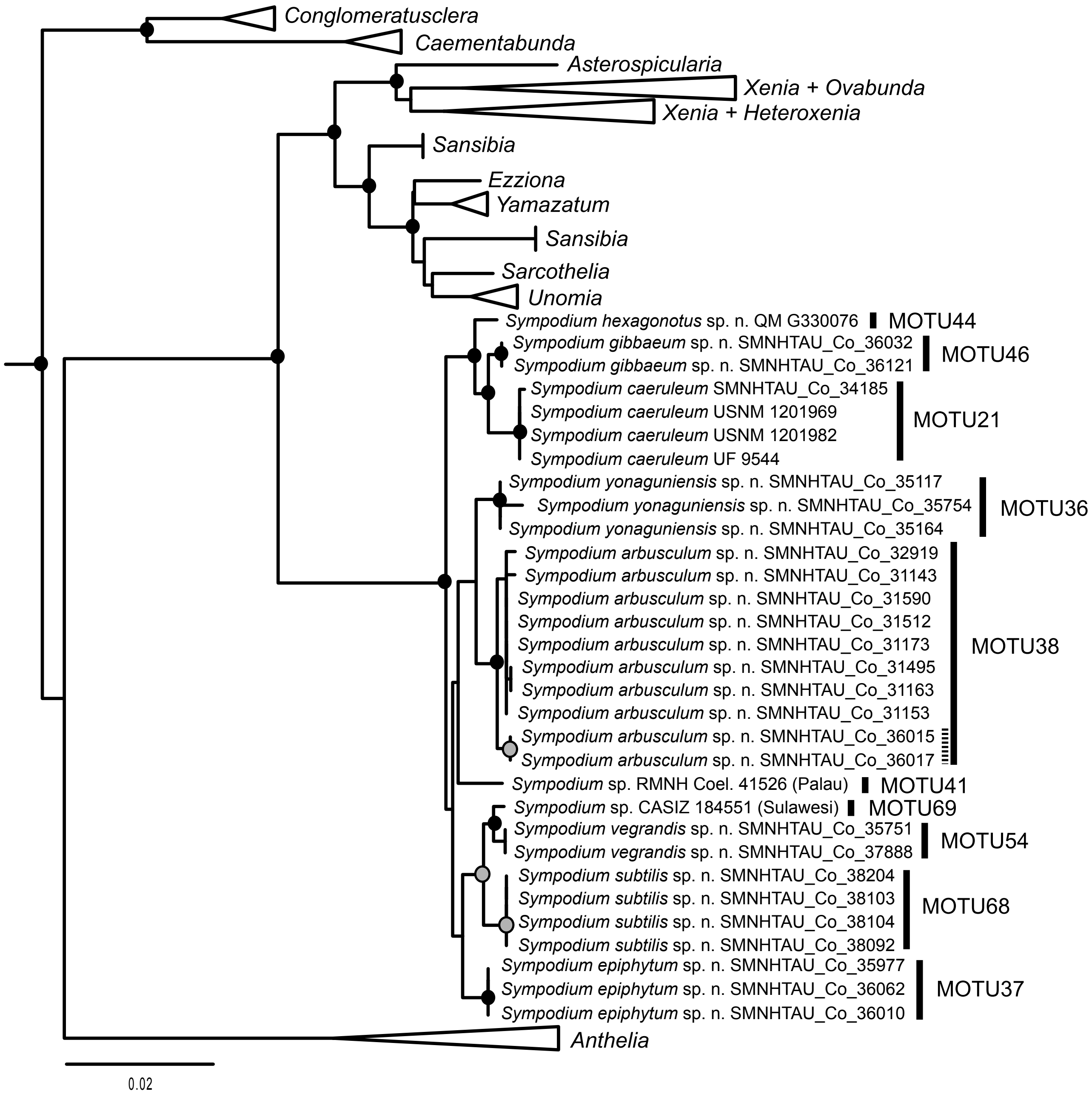

FIGURE 19. Maximum likelihood (ML) tree for concatenated *mtMutS*, *COI* and *28S rDNA* gene regions (1981 bp). Clades of Xeniidae genera other than *Sympodium* have been collapsed to facilitate readability. Black circles: ML bootstrap value (b.s.) >70%, Bayesian posterior probability (p.p) >0.95; gray circles: b.s. >70%, p.p. < 0.95. Dashed vertical line indicates specimens of *S. arbusculum* **sp. n.** from Madagascar that belonged to a distinct MOTU in some analyses.

A genetic distance threshold of 0.003 (concatenated alignment of *mtMutS*, *igr1*, *COI* and *28S rDNA*) delimited 11 MOTUs, including *S. caeruleum* (MOTU21 of McFadden *et al.* 2019); *S. hexagonotus* (MOTU44); *S. yonaguniensis* (MOTU36); *S. vegrandis* (MOTU54); *S. gibbaeum* (MOTU46); *S. subtilis* (newly assigned MOTU68); RMNH Coel. 41526, a previously sequenced specimen from Palau (MOTU41) (McFadden *et al.* 2014b); and CASIZ 184551, a specimen from Sulawesi (newly assigned MOTU69) (McFadden *et al.* 2014a). *S. arbusculum* was divided among three MOTUs, with the two specimens from Madagascar (SMNHTAU_Co_36015, 36017) separated from those from Kenya and Tanzania. Several of the Kenyan specimens of *S. arbusculum* fell into a third MOTU with *S. epiphytum* (MOTU37), although this result is most likely an artifact of missing data for *28S rDNA* for those individuals, and those two taxa are not sisters in the phylogenetic analyses (Fig. 19). Analysis of *igr1+COI* alone (767 bp) differentiated eight MOTUs (0.003 threshold), supporting the distinctions of all species except *S. gibbaeum* which was lumped with *S. caeruleum*, and placing CASIZ 184551 in MOTU54 with *S. vegrandis*. *28S rDNA* (757 bp) suggested 10 MOTUs (0.007 threshold), separating the *S. arbusculum* specimens from East Africa and Madagascar into two separate MOTUs, but also lumping CASIZ 184551 with *S. vegrandis*. *mtMutS* (457 bp) was the least variable and informative locus, lumping all species but *S. yonaguniensis* and *S. hexagonatus* into a single MOTU (0.003 threshold), but separating CASIZ 184551 from *S. vegrandis*.

Discussion

Since the original description of *S. caeruleum* by Ehrenberg (1834), traditional taxonomic studies have indicated that it has a broad distribution throughout the Indo-Pacific reef system (e.g. Utinomi 1977, Verseveldt 1973, Reinicke 1997 and references therein). In contrast, the current genetic analysis and the taxonomic results suggest that this species' occurrence is confined to the Red Sea. Specimens matching *S. caeruleum* morphologically and genetically (MOTU21) were sampled from the Red Sea in both Israel and Saudi Arabia, but nowhere else in the Indo-Pacific. All material sampled from outside of the Red Sea belonged to the other seven taxa of *Sympodium* newly described here. Table 2 summarizes the morphological characteristics of all *Sympodium* species described in this paper and their respective MOTUs. The geographic distributions of those new taxa further suggest high rates of endemism in this genus, as only two species were sampled at more than a single location. *S. yonaguniensis* was collected at Yonaguni Island (Ryukyu Archipelago, Japan) and Green Island (Taiwan), two sites that are separated by only about 250 km. *S. arbusculum* was found in Kenya, Tanzania and Madagascar, although the phylogenetic and MOTU analyses both suggest some genetic differentiation between the Madagascar and East African populations that could potentially represent different species. Whether or not CASIZ 184551 from Sulawesi belongs to *S. vegrandis*, a species otherwise found only at Green Island (Taiwan), also requires further study.

The preliminary taxonomic examination of the material in the current study erroneously assigned several samples to xeniid genera other than *Sympodium,* with some specimens remaining unidentified. A later and more complete taxonomic identification was facilitated by a subsequent molecular analysis of a geographically diverse collection of the family Xeniidae (McFadden *et al*. 2019). That study demonstrated distinct molecular operational taxonomic units (MOTUs) within the family, each mostly found at a single Indo-Pacific location. The current study formally describes several of those already recognized MOTUs as well as new ones that correspond to the genus *Sympodium.* Following the current genetic analyses, the taxonomic assignment of the material was revised in congruence with the morphological characters required for species delineation. In addition to the seven new species described, phylogenetic analyses of existing sequence data suggest that one additional species occurs in Palau (RMNH Coel. 41526; MOTU41), and that CASIZ 184551 from Sulawesi (MOTU 69) might also represent a distinct species. Neither of those specimens could be obtained for examination at the present time.

Both our classical taxonomy and molecular analyses confirmed that only the Red Sea samples should be assigned to *S. caeruleum*. This finding raises serious reservations concerning the validity of the taxonomic findings published since the original description of *S. caeruleum,* which have indicated that this species has a broad distribution throughout the Indo-Pacific reef system (e.g. Utinomi 1977, Verseveldt 1973, Reinicke 1997 and references therein). The present study focused mainly on fresh material that could be subjected to genetic analyses and did not include old samples from the Red Sea or elsewhere, which await future studies.

The past taxonomic records of *S. caeruleum* from the non-Red Sea regions, despite being dubious, all refer to encrusting colonies featuring a basal membrane, retractile polyps, and the presence of minute oval disc sclerites (e.g. May 1898: 51–52, Kükenthal 1904: 39, Thomson & Dean 1931: 21, Roxas 1933: 107, Tixier-Durivault 1966: 371–372, Utinomi 1977: 7–8). The present results confirm that these general morphological characters are shared by all of the newly-described *Sympodium* species, but certain variable morphological characters are suitable for species delineation. For example, the colonies of *S. arbusculum* **sp. n.** feature clusters of dichotomously arranged polyps (Fig. 1), while those of both *S. gibbaeum* **sp. n.** and *S. hexagonotus* **sp. n.** are encrusting with knob-like mounds (Figs. 8, 10). Likewise, all the other new species are also encrusting, with each featuring some diagnostic morphological characters (i.e. *S. epiphytum* **sp. n**: growth on algal material, Fig. 6; *S. subtilis* sp. n.:thin and delicate encrusting membrane, Fig. 12; *S. vegrandis* **sp. n.**: minute colony size, Fig. 15 and *S. yonaguniensis*: rough surface texture, Fig. 17). It should be noted that all of the currently examined *S. caeruleum* colonies feature an encrusting spreading membrane, as described originally by Ehrenberg (1834) and subsequently in other Red Sea studies (Gohar 1940, Reinicke 1997).

TABLE 2. Morphological characteristics of *Sympodium* species. In bold most diagnostic features. MOTU indicates respective molecular operational taxonomic unit within the genus.

Species	Colony morphology	Polyps	Sclerites	MOTU
S. arbusculum **n. sp.**	**slightly arborescent clusters of polyps** arise from membrane, <1 mm thick	non-retractile, up to 10 pinnules in a single row	ellipsoid platelets, 0.010–0.011 x 0.015–0.017 mm	38
S. caeruleum	**polyps arise separately from membrane**, 1–1.5 mm thick	retractile, 3 rows of pinnules, 5–8 pinnules in the outermost row	ellipsoid platelets, 0.010–0.012 x 0.014–0.017 mm	21
S. epiphytum **n. sp.**	polyps arise separately from membrane, 1 mm thick and **attached to algae**	retractile, 7–9 pinnules in a single row	ellipsoid platelets, 0.011–0.012 x 0.015–0.017 mm	37
S. gibbaeum **n. sp.**	**polyps arranged on densely packed knob-like mounds** that arise from a membrane, 1 mm thick	retractile, 3–5 pinnules in a single row	ellipsoid platelets, 0.014–0.016 x 0.016–0.019 mm	46
S. hexagonotus **n. sp.**	**polyps arranged on densely packed knob-like mounds** that arise from a membrane, 1 mm thick	retractile, 7–8 pinnules in a single row	**hexagonal platelets,** 0.010–0.028 x 0.008–0.023 mm	44
S. subtilis **n. sp.**	polyps arise separately from membrane, **0.5 mm thick**	retractile, 3–5 pinnules in a single row	ellipsoid platelets, 0.010–0.012 x 0.013–0.015 mm	68
S. vegrandis **n. sp.**	polyps arise separately from membrane, **<0.5 mm thick, with occasional stolon-like extensions**	retractile, 3–4 pinnules in a single row	ellipsoid platelets, 0.009–0.010 x 0.012–0.015 mm	54
S. yonaguniensis **n. sp.**	polyps arise from membrane separately or in groups of 3–5, **up to 3 mm thick with irregular low mounds**	retractile (number of pinnules undetermined)	ellipsoid platelets, 0.012–0.016 x 0.010–0.012 mm	36

Similar to most earlier xeniid descriptions, the taxonomic literature on *S. caeruleum* refers to their sclerites as minute discs, typical of *Xenia* species (e.g. Macfadyen 1936, Gohar 1940, Fabricius & Alderslade 2001). Such sclerites were hand illustrated by Tixier-Durivault (1966: Fig. 334) and SEM-imaged by Reinicke (1997). The current findings indicate that all *Sympodium* species possess numerous sclerites throughout the colony, composed of ellipsoid platelets comprising densely packed calcite rods whose tips provide a granular appearance to the sclerite surface (Figs. 2, 5, 7, 9, 11, 13, 16, 18). The sclerite size range is quite uniform, with the smallest ones found in *S. vegrandis* **sp. n.** (Fig. 16: 0.009–0.010 x 0.012–0.015 mm) and the largest in *S. hexagonatus* **sp. n.** (Fig. 11: 0.010–0.028 x 0.008–0.023 mm). The granular sclerite surface is shared by all species with some variation, as exhibited by *S. arbusculum* (Fig. 2B) and *S. hexagonatus* (Fig. 11). Interestingly, *S. hexagonatus* features angular sclerites (Fig. 11A) that occasionally can also be found in *S. gibbaeum* (Fig. 9). Several xeniid genera revised in recent years similarly demonstrate a quite uniform sclerite microstructure within any given genus (*Ovabunda*: Hálasz *et al*. 2014, *Xenia*: Hálasz *et al*. 2019, *Caementabunda*: Benayahu *et al*. 2018 and *Unomia*: Benayahu *et al*. 2021), with the exception of *Conglomeratusclera* (see Benayahu *et al*. 2018). It should also be noted that a granular surface microstructure occurs in several xeniid genera, therefore this cannot be considered a diagnostic character for genus- or species-level identification (Halász *et al*. 2019, Benayahu *et al*. 2021).

Morphological characters of the polyps such as dimensions of the polyp body and tentacles, numbers of rows of pinnules, pinnules per row and the amount of free space between them have been widely used for species delineation of xeniids (e.g. Hálasz *et al*. 2014, 2019 and references therein). Similarly, some studies have described these characters for *Sympodium* material that has been examined (Gohar 1940, Verseveldt 1973, Reinicke 1997). However, since the *Sympodium* polyps, including their pinnules, commonly retract, quantifying these morphometric characters is often not feasible. In this study we have nonetheless presented these parameters where possible.

To date, in our ongoing examination of historic octocoral collections we have not come across any additional *Sympodium*-like material; however, the existence of such material is not excluded. In this regard it should be noted that Thomson & Henderson (1906: 408) identified *S. caeruleum* from Zanzibar, contending that it has no trace of "calcareous bodies", which is a puzzling note. Our attempts to find the depository of the type colony of *S. tamatavense* Cohn, 1908 failed (type locality Madagascar), and, therefore, we could not compare it to any of the currently described new species from this region. It should be noted that a soft coral colony was identified and described as *S. tamatavense* by Tixier-Durivault (1966: 373–375). However, the sclerite drawings indicate that the specimen is actually *Cladiella* sp., in light of the diagnostic dumbbell sclerites depicted (Fig. 336).

The current study demonstrates that when seeking to revise those xeniid octocorals for which it is challenging to assign Latin binomials, assessing MOTUs from genetic analysis of fresh material offers a highly valuable approach (see also McFadden *et al*. 2019). Similarly, the search for historical type material and its re-description, along with collection of relevant fresh material from the type locality, facilitates validation of the congruence between morphospecies and MOTUs. Such studies are critical for any biodiversity-related studies and conservation initiatives.

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