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Revisiting the type of *Cespitularia stolonifera* Gohar, 1938 leads to the description of a new genus and a species of the family Xeniidae (Octocorallia, Alcyonacea)

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Abstract

Because of the problematical identity and status of the type of the xeniid soft coral genus *Cespitularia* Milne-Edwards & Haime, 1850, the species *C. stolonifera* Gohar, 1938 is revised. Examination of the type colonies has led to the establishment of the new genus *Unomia* gen. n. which is described and depicted. This genus features a stalk, commonly divided into branches featuring a diffuse polypiferous part consisting of distal clustered polyps and proximal individual ones on the stalk or the basal membranous part of the colonies. The sclerites are ellipsoid platelets composed of dendritic calcite rods whose tips are distinct on the surface of the platelets. Freshly collected material from Venezuelan reefs where the species is invasive was subjected to molecular phylogenetic analysis, the results of which substantiate the taxonomic assignment of the new genus under *U. stolonifera* **comb. n.** A new species, *U. complanatis,* from Japan and Green Island (Taiwan) is described and further illustrates the extent of the interspecific morphological variation within the genus. The results reveal that the biogeographic distribution of *Unomia* **gen. n.** includes Pacific Ocean reefs in addition to the previously reported invaded Caribbean reefs.

Key words: Pacific Ocean, Venezuela, new genus, molecular phylogeny, taxonomy, sclerite microstructure

Introduction

Members of the octocoral family Xeniidae are common on Indo-Pacific coral reefs and have been the focus of a substantial number of recent taxonomic and phylogenetic studies (e.g., Alderslade 2001; Janes, 2008, 2013; McFadden *et al*. 2014a, 2019; Benayahu *et al*. 2018a; Halász *et al*. 2014, 2015, 2019). These octocorals play a significant ecological role on many Indo-Pacific reefs, as well as contributing to the octocoral species richness there (e.g., Benayahu 2010: Japan; Haverkort-Yeh *et al*. 2013: Saudi Arabia; Janes *et al*. 2013: Lembeh, Indonesia; Schleyer *et al*. 2016: Reunion Is.; Schleyer and Benayahu 2018: Mayotte Is.; Schleyer *et al*. 2018: Glorieuses Is.; Benayahu *et al*. 2018b: Dongsha Atoll, Taiwan; Bryce *et al*. 2018: western Australia; Koido *et al*. 2019: Japan). Studies have also shown that xeniids introduced from the aquarium trade have become invasive in Venezuela (Ruiz-Allais *et al*. 2014) and Brazil (Mantelatto *et al*. 2018), where they outcompete indigenous species and have subsequently expanded their native distribution beyond the Indo-Pacific region.

Studies on xeniid taxonomy have considered the morphological features of the polyps to be species-diagnostic, in particular the number of rows of pinnules on the tentacles and the number of pinnules in the outermost row (e.g., Reinicke 1997; Halász *et al*. 2014, 2019 and references therein). In contrast, other studies have demonstrated that these characters are not informative for delineation of species in the genera *Ovabunda* Alderslade, 2001 (Halász *et al*. 2015, McFadden *et al*. 2017), *Caementabunda* Benayahu *et al*. 2018, and *Conglomeratusclera* Benayahu *et al*. 2018. The literature on this family also considers features such as colony shape, colony dimensions, and coloration, as well as polyp retractability and pulsation in the live state to be species-diagnostic (e.g., Reinicke 1997; Halász *et al*. 2014, 2015, 2019).

The use of scanning electron microscopy (SEM) has illuminated the diverse microstructural features of xeniid

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sclerites, and, consequently, several new taxa have been described (e.g., Benayahu 1990, 2010; Alderslade 2000, 2001; Janes 2008; Aharonovich and Benayahu 2011; Benayahu *et al*. 2018a; Halász *et al*. 2014, 2019). Notably, several phylogenetic studies support the hypothesis that distinct sclerite microstructures justify establishing taxonomic boundaries within the Xeniidae (Haverkort-Yeh *et al*. 2013; McFadden *et al*. 2014a; Benayahu *et al*. 2018a; Halász *et al*. 2019). The literature thus indicates that integrating morphological with molecular phylogenetic analyses is necessary in order to delimit the taxonomic boundaries within this family.

The confusion in the literature concerning the diagnosis of the xeniid genus *Cespitularia* Milne-Edwards & Haime, 1850 has been discussed by Benayahu *et al*. (2018a). In that study, examination of type colonies led to the designation of *Cespitularia coerulea* May, 1898 as *Conglomeratusclera* **gen. n.** and *Cespitularia simplex* Thomson & Dean, 1931 as *Caementabunda* **gen. n.** These two genera each feature a different and unique sclerite microstructure, thus highlighting the significance of that trait for generic assignment within the Xeniidae. In addition, freshly collected material of both genera subjected to molecular phylogenetic analysis substantiated the taxonomic description of these two new genera (Benayahu *et al*. 2018a).

Doubt regarding both the diagnosis of *Cespitularia* and the validity of the other species assigned to that genus (Cordeiro *et al*. 2020) motivated us to further revisit the relevant type material. The current study therefore re-examined the type of *C. stolonifera* Gohar, 1938, along with other related material. This resulted in the description of a new genus substantiated by both morphological and molecular analyses, as well as description of a new species of that genus. Consequently, we reconsider some of the morphological traits currently used for xeniid taxonomic delineation and emphasize the importance of including molecular phylogenetic analysis for this purpose.

Materials and methods

The study examined preserved type specimens of *C. stolonifera* deposited at the British Museum of Natural History (BMNH) and additional material from both the Naturalis Biodiversity Center, formerly Rijksmuseum van Natuurlijke Historie, Leiden (RMNH) and the Steinhardt Museum of Natural History at Tel Aviv University (ZMTAU). Morphological features of the preserved colonies were recorded, including dimensions, branching and shape of the polypary. 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 dimensions and shape of the pinnules, were similarly recorded (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 from both polyps and the colony base were examined under a Nikon Eclipse 80i light microscope at X200-400 magnification (see also Aharonovich & Benayahu 2011). As this examination revealed no differences between sclerites of the two colony regions, SEM mounts were prepared from the polyp sclerites. Each stub contained numerous sclerites, and the samples were coated with Pd/Au and viewed under a Quanta 200 FEG (Field Emission Gun) ESEM operated at 5-20 kV and Jeol 6480LV SEM at 10 kV. The material used for the molecular and morphological studies was collected by JPRA in Valle Seco, Bahia Conoma, Estado Sucre, Venezuela (November 2012) and preserved in 95% ethanol; by CSM in Ushibuka, Kumamoto Prefecture, Japan (September 2018) and by YB in Green Is (Lüdao), Taiwan (October 2019) (Table 1).

Molecular phylogenetic analyses. DNA was extracted from EtOH-preserved tissue using a Qiagen DNEasy Blood & Tissue Kit. The *mtMutS* mitochondrial gene and nuclear 28S rDNA were amplified by PCR, and Sanger-sequenced using published primers and protocols (McFadden *et al*. 2014a). A multilocus DNA barcode that includes these two genes has been shown to discriminate most species of xeniids (McFadden *et al*. 2017, 2019). The L-INS-i method in MAFFT (Katoh *et al*. 2005) was used to align new sequences to a reference set of xeniid taxa used in a previous study (McFadden *et al*. 2019). Genetic distances (uncorrected p) between sequences were calculated using MEGA 5.05 (Tamura *et al*. 2011). Maximum likelihood analyses were run using PhyML (Guindon & Gascuel 2003) with a GTR+I+G model applied to the concatenated alignment of both genes. In addition, a partitioned analysis was run using MrBayes v. 3.2.1 (Ronquist *et al*. 2012), applying a GTR+I+G model separately to each gene. MrBayes was run for 2,000,000 generations (until standard deviation of split partitions < 0.01) with a burn-in of 25% and default Metropolis coupling parameters.

TABLE 1. Specimens included in the molecular phylogenetic analysis of *Unomia* n. gen. ZMTAU: Steinhardt Museum of Natural History, Tel Aviv University; CASIZ: California Academy of Science; QM: Queensland Museum.

		Collection	GenBank Acc. No.	
Species	**Museum Acc No**	**Location**	**mtMutS**	**28S rDNA**
Unomia stolonifera	ZMTAU CO 39081	Venezuela	MT482554	MT489336
Unomia complanatis	ZMTAU CO 38120	Kumamoto	MW118279	NA
Unomia complanatis	ZMTAU CO 38125	Kumamoto	MW118280	MW127882
Unomia complanatis	ZMTAU CO 38126	Kumamoto	MW118281	MW127883
Unomia complanatis[2]	ZMTAU CO 35154	Yonaguni I.	MK030436	MK030546
Unomia complanatis	ZMTAU CO 37846	Green I.	MW118283	MW127885
Unomia complanatis	ZMTAU CO 37813	Green I.	MW118282	MW127884
Xenia membranacea[1]	CASIZ 184546	Sulawesi	KJ511346	KJ511309
Xenia membranacea[1]	CASIZ 184549	Sulawesi	KJ511358	KJ511320
Xenia sp. 5[1]	CASIZ 184564	Sulawesi	KJ511348	KJ511310
Xenia sp. MOTU17[2]	QM G334128	W. Australia	MK030406	MK030517
Xenia sp. MOTU17[2]	QM G334055	W. Australia	MK030405	MK030515

[1]data published previously in McFadden *et al*. 2014a
[2]data published previously in McFadden *et al*. 2019

Results

Systematics part

Order Alcyonacea Lamouroux, 1812

Family Xeniidae Ehrenberg, 1828

Unomia gen. n.

Type species *Cespitularia stolonifera* Gohar, 1938: 483-485, plate I, here designated.

Diagnosis. Colonies soft with a stalk, commonly divided into branches. Polyps monomorphic and non-retractile, mostly clustering on a polyp-bearing region (polypary). Noticeably, individual polyps are also found on the stalk, branches or the membranous base of the colonies thus indicating the diffuse nature of the distribution of the more proximal polyps. Sclerites present as ellipsoid platelets, abundant in all parts of the colony. They reach up to 0.025 mm in maximal diameter, and are composed of densely placed calcite rods whose tips are distinct on the surface of the platelets, commonly providing them with a granular appearance. The rods are mostly uniform in width (0.001-0.002 mm). During dehydration for SEM purposes some sclerites may fracture. Zooxanthellate.

Etymology. The generic name is derived from the Latin: *unum,* which refers to solitary. Here it denotes the individual polyps randomly found on the divided stalk or on branches below the polypary level. Gender: feminine.

Type species

***Unomia stolonifera* (Gohar, 1938)**
Figs. 1–5

Cespitularia stolonifera Gohar, 1938: 483–485, plate I, fig. 1; Utinomi 1950: 16; Utinomi 1959: 305.

Material. Type. Indonesia: BMNH 1889.5.27, Amboina, st. 233, shallow water, coll. H.M.S. Challenger, 1889. **Additional material. Indonesia**: RMNH.COEL. 42436, SW Sulawesi, Spermonde Archipelago, west of Lumu-Lumu Isl. (=28 km NW of Ujungpandang), 4°58'S 119°12'E, coral reef, scuba diving, 27 May 1994, Bug. Prog. UNHAS-NNM. coll. B.W. Hoeksema & L.P. van Ofwegen; RMNH.COEL. 42437 details as above; **Venezuela:** ZMTAU Co. 38081, Valle Seco, Bahia Conoma, Estado Sucre, 4–6 m, 28 November 2012, coll. Juan P. Ruiz Allais, four specimens; ZMTAU Co. 38082 details as above, two specimens.

Description. The type, BMNH 1889.5.27, consists of four soft colonies attached by a spreading membrane to a skeleton fragment of branched *Acropora* stony coral and an additional colony similarly attached to a smaller fragment (Fig. 1A), each measuring approximately 3 X 4 cm. The spreading membrane overgrowing the calcareous substrate is clearly presented in Fig. 1B, in which the type colonies are viewed from the opposite side. The colonies ramify into a number of short branches up to 12–25 mm long, each with a polyp-bearing region on their upper part. Individual polyps are also found on the branches or on the stalk thus indicating the diffuse nature of the polypiferous part of the colony. Some of the polyps are damaged, mostly having lost their tentacles. The polyp body is up to 10–14 mm long and the tentacles up to 5–7 mm long. The pinnules are arranged in 3 rows and occasionally 2 rows, with 18–25 in the outermost row. The pinnules are almost completely contracted, 0.5 mm wide, with an approximately one pinnule-wide space between adjacent ones.

The sclerites are ellipsoid platelets, highly abundant in all parts of the colony, measuring 0.012–0.015 X 0.018–0.021 mm in diameter (Fig. 2A). They are composed of calcite rods, uniform in diameter of about 0.001–0.002 mm, and the tips of the rods are perpendicular to the surface of the sclerite (Fig. 2B). The ethanol-preserved type material is cream-white.

RMNH.COEL. 42436, is a flattened, very soft colony, 9 cm high and 6 cm wide, and attached to calcareous fragments by a spreading membrane (Fig. 1C). Its stalk is split into 5–6 short branches, each featuring a cluster of polyps; individual polyps are also found on the branches below these clusters. The polyp body is up to 10 mm long and the tentacles are up to 15 mm long. The pinnules are arranged mostly in 3 rows, or rarely in 2 rows, with 18–24 pinnules in the outermost row, exhibiting a gap of up to a pinnule-width between adjacent ones. Some pinnules are contracted and the fully extended ones are up to 2 mm long. The sclerites resemble those of the type, measuring 0.010–0.015 X 0.015–0.021 mm in diameter (Fig. 3). RMNH.COEL.42437 differs from RMNH.COEL.42436 only in size (Fig. 1D). Both ethanol-preserved colonies are light beige-white in color.

ZMTAU CO 38081 consists of four Venezuelan colonies (Fig. 1E). Their morphology resembles the type material, featuring a diffused polypiferous part of the colonies. The polyp body is up to 25 mm long and the tentacles up to 10 mm long, bearing pinnules arranged in 3 rows with 20–25 pinnules in the outermost row and a gap of up to a pinnule-width between adjacent ones. The sclerites also resembles those of the type, measuring 0.014–0.017 X 0.018–0.025 mm in diameter (Fig. 4). ZMTAU CO 38082 (not depicted) resembles ZMTAU CO 38081.

Underwater photographs of live colonies taken at Valle Seco, Bahia Conoma, Estado Sucre, Venezuela, reveal the diffuse nature of the polypiferous part of the colonies (Fig. 5A). The live polyps feature elongate dark brown tentacles due to the symbiotic zooxanthellae as well numerous sclerites as presented in Fig. 5B. Individual polyps are found on the stalk, below the level of the polypary (Fig. 5C, D).

Remarks. The material from Sulawesi (RMNH.COEL. 42436, 42437) resembles the type of *Unomia* **gen. n.** (BMNH 1889.5.27). Notably, the invasive xeniid from Venezuela, which was originally identified as a "xeniid with close genetic affinities to *Xenia membranacea* Schenk, 1896" (Ruiz Allais *et al*. 2014), matches well the above material. The freshly collected and ethanol-preserved specimens from that site enabled the molecular analysis and placement of the species in the phylogenetic tree. Consequently, the taxonomic status of this peculiar invasive soft coral is now confirmed to be *U. stolonifera* (Gohar, 1938).

Distribution. Indonesia (Ambon, Sulawesi), Venezuela.

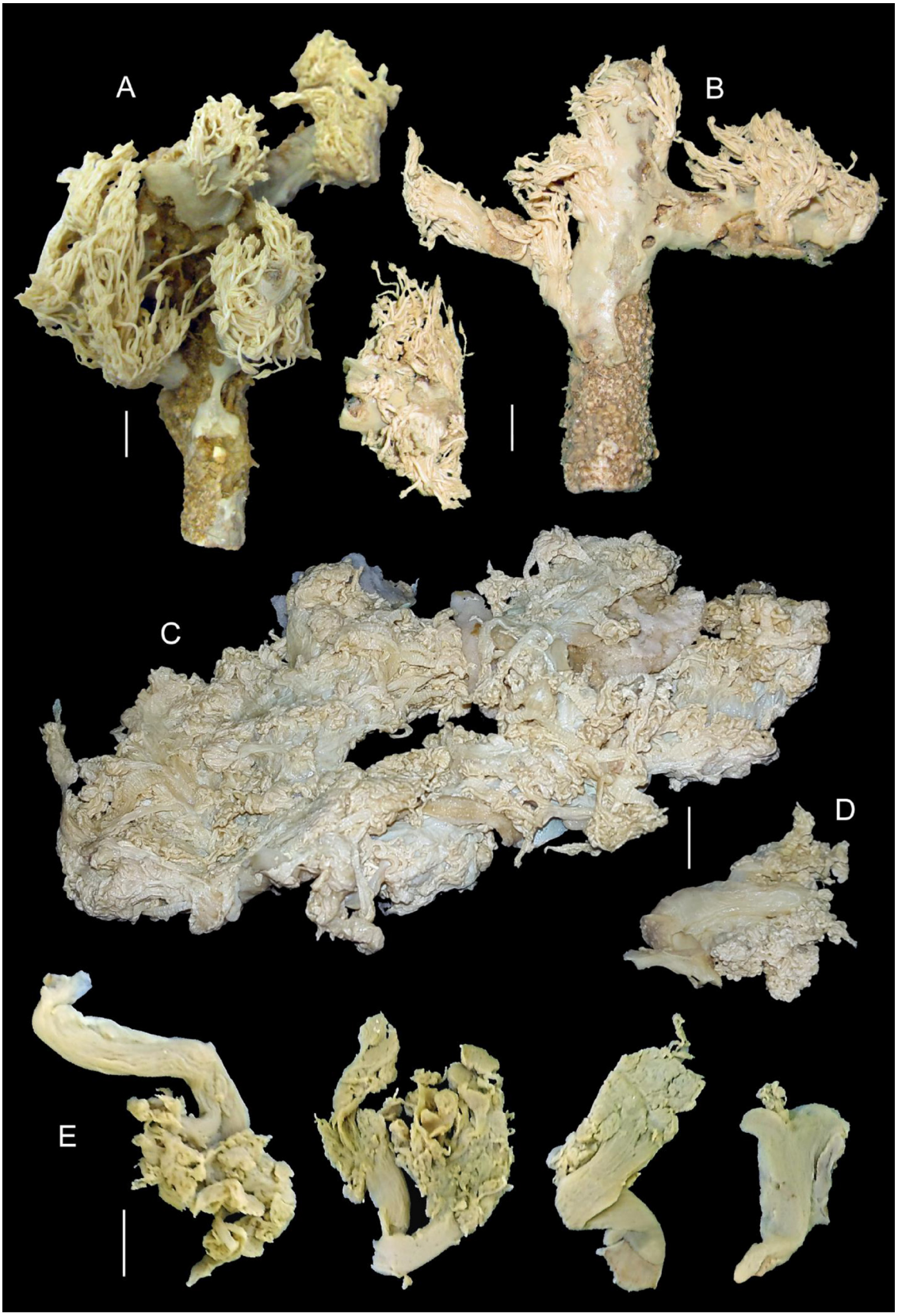

FIGURE 1. *Unomia stolonifera* (Gohar, 1938) (A) Type BMNH 1889.5.27 consists of five colonies attached by a spreading membrane to skeleton fragments of branched *Acropora* stony coral; (B) Same type colonies viewed from the opposite side showing the spreading membrane. The colonies ramify into short branches, each with a polyp-bearing region. Individual polyps are also found on the branches below the polypary; (C) RMNH.COEL. 42436 and (D). RMNH.COEL. 42437 from Sulawesi, Indonesia; (E) ZMTAU Co. 38081 from Valle Seco, Bahia Conoma, Estado Sucre, Venezuela. All scale bars 1 cm.

FIGURE 2. Scanning electron micrographs of sclerites of *Unomia stolonifera* (Gohar, 1938) type BMNH 1889.5.27. (A) Ellipsoid platelets, some fractured; (B) Tips of dendritic rods on the surface of the platelet.

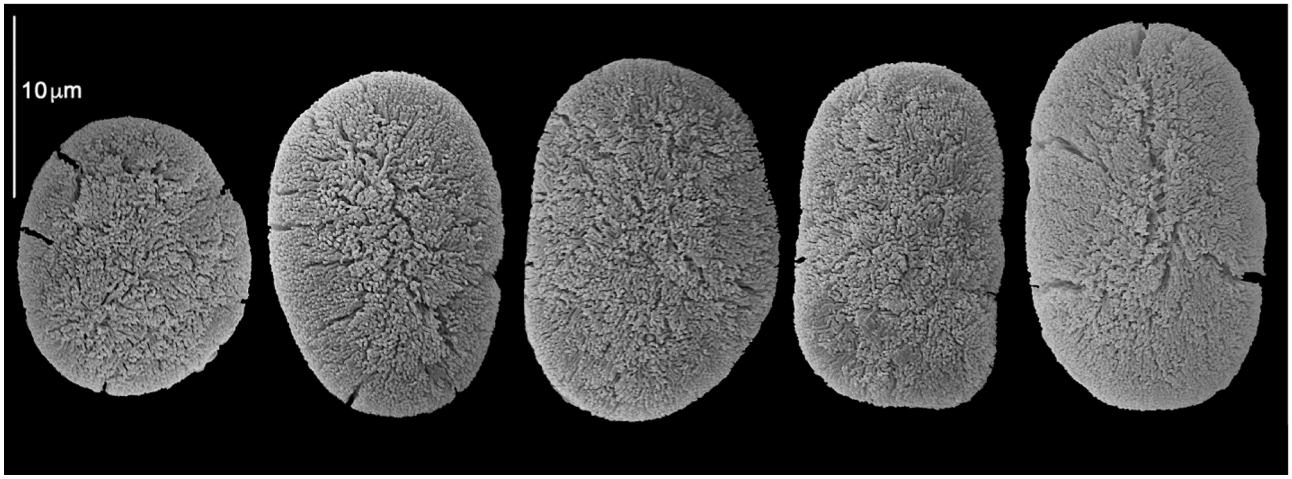

FIGURE 3. Scanning electron micrographs of sclerites of *Unomia stolonifera* (Gohar, 1938) (RMNH.COEL. 42436). Ellipsoid platelets, some fractured composed of dendritic calcite rods.

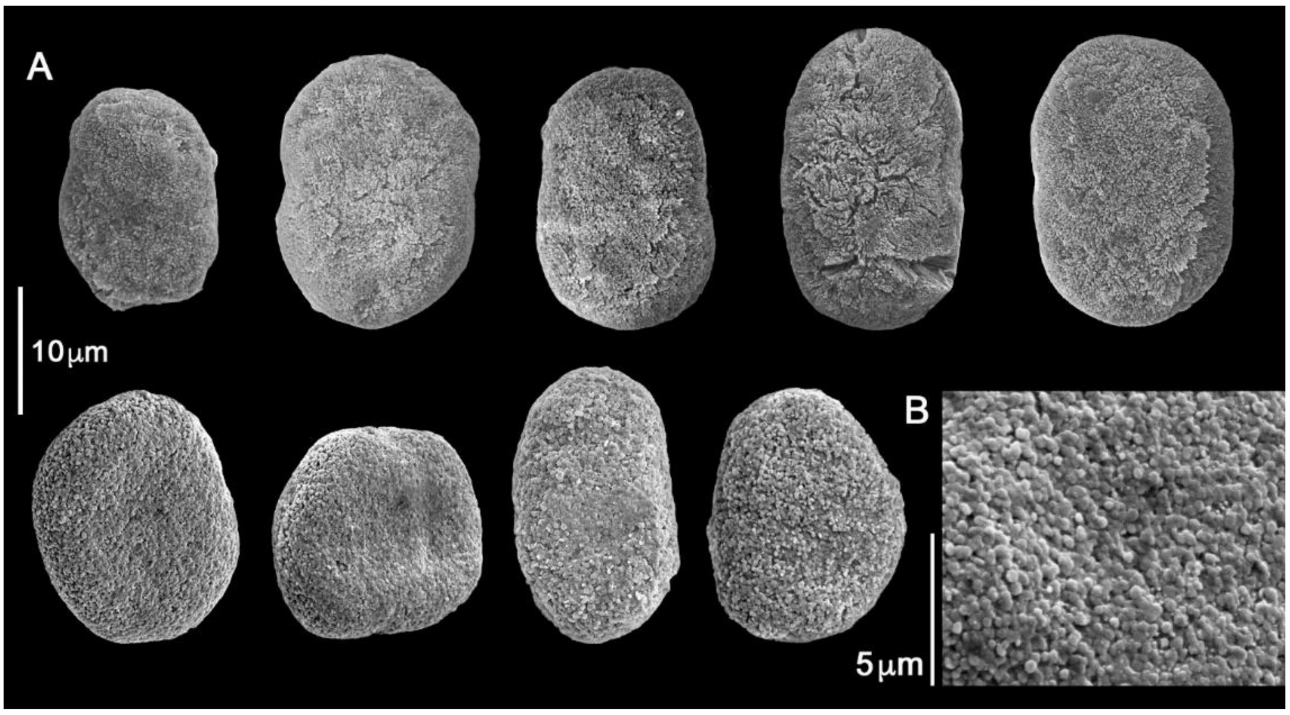

FIGURE 4. Scanning electron micrographs of sclerites of *Unomia stolonifera* (Gohar, 1938) (ZMTAU Co. 38081). (A) Ellipsoid platelets, some fractured; (B) Tips of dendritic rods on the surface of the platelet.

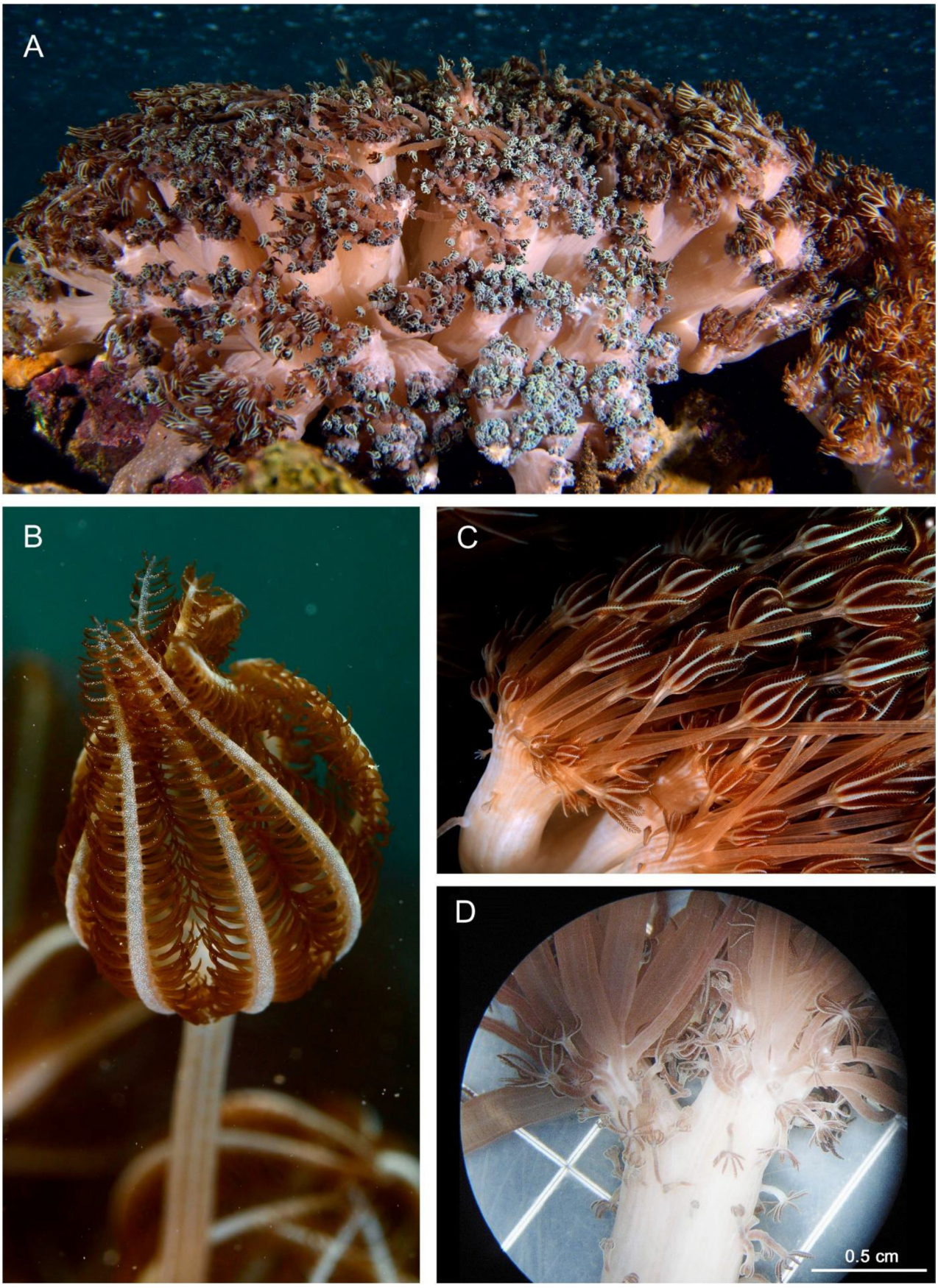

FIGURE 5. Live colonies of *Unomia stolonifera* (Gohar, 1938) on the reef of Vale Seco, Cunamá Bay, Estado Sucre, Venezuela. (A) Colonies with distinct polyp-bearing region; (B) Polyp featuring elongate dark brown tentacles due to the symbiotic zooxanthellae; (C–D) Individual polyps found below the level of the polyp-bearing region.

***Unomia complanatis* gen. n. sp. n.**
Figs. 6–11

Material. Holotype. Japan, ZMTAU CO 38120, Kumamoto Prefecture, Ushibuka, 32.1552°N,130.0444ºE, 8 m, 18 September 2018, coll. C.S. McFadden. **Paratypes:** ZMTAU CO 38124, ZMTAU CO 38125, ZMTAU CO 38126, details as above. **Additional material**. **Japan**: ZMTAU CO 35154, Ryukyu Archipelago, Yonaguni Island, west Point, 16–22 m, 5 July 2010; **Taiwan:** ZMTAU CO 37813 (4 colonies), Green Island, Gong-Guan-Bi reef, 22°40’47.46” N, 121°29’24.42” E, 6.6–18 m, 2 October 2019, coll. Y. Benayahu; ZMTAU CO 37846 (4 colonies), Light House reef, Green Island, 22°40’31.38” N, 121° 27’42.90” E, 7.7–11.9 m, 3 October 2019, coll. Y. Benayahu.

Description. The holotype from Japan (ZMTAU CO 38120) is an encrusting flattened colony, 12–14 mm high and 20 X 25 mm in diameter (Fig. 6A). The stalk is not distinct as the polyps actually arise from the membranous base and leave almost no bare space down to the colony base. The polyp body is up to 4–5 mm long, and the tentacles are up to 2 mm long. The pinnules are fully contracted and seem to be arranged in 1–2 rows on each side also noted by tiny pits on the tentacles.

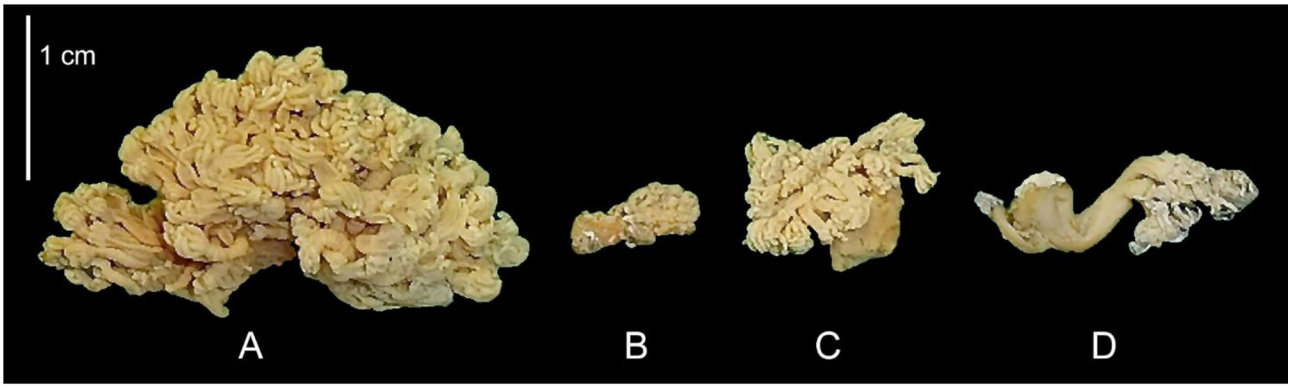

FIGURE 6. *Unomia complanatis* **gen. n. sp. n.** The variable morphology of colonies from Ushibuka, Kumamoto Prefecture, Japan is visible. (A) Holotype (ZMTAU CO 38120); (B-D**)** Paratypes (ZMTAU CO 38124, ZMTAU CO 38125 and ZMTAU CO 38126).

The sclerites are ellipsoid platelets 0.012–0.017 X 0.018–0.024 mm in diameter (Fig. 7A). They are composed of dendritic calcite rods, uniform in diameter of about 0.001–0.002 mm, and their tips are either perpendicular or more or less parallel to the surface of the sclerite (Fig. 7B). The ethanol-preserved holotype is cream.

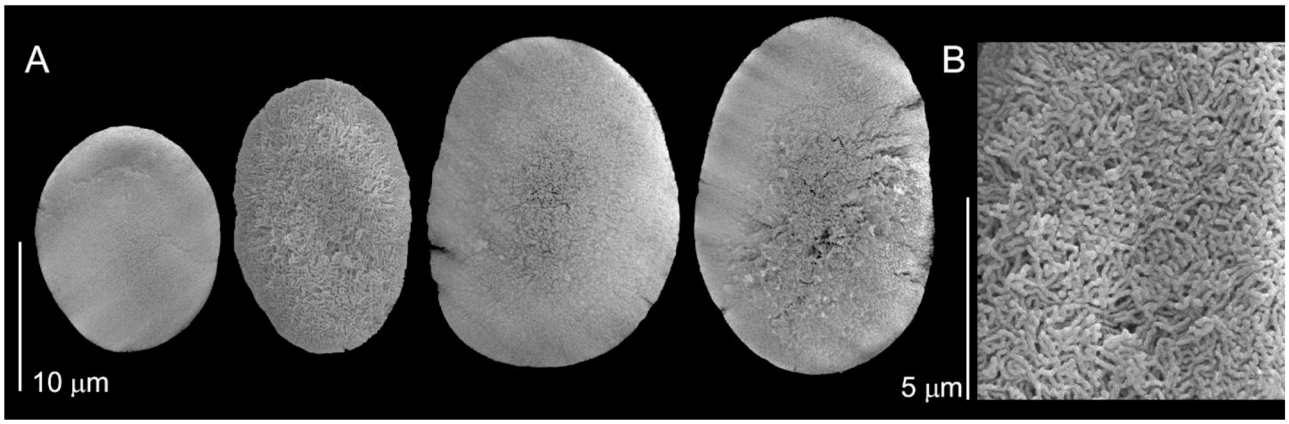

FIGURE 7. Scanning electron micrographs of sclerites of *Unomia complanatis* **gen. n. sp. n.** Holotype (ZMTAU CO 38120). (A) Ellipsoid platelets; (B) Terminal parts of dendritic rods on the surface of the platelet.

Variation. The preserved paratypes are smaller than the holotype. ZMTAU CO 38124 is an encrusting colony with almost no recognizable stalk (Fig. 6B). ZMTAU CO 38125 and ZMTAU CO 38126 (Fig. 6C, D), both have a distinct stalk bearing a polypary, the latter with a polyp emerging from its base. These characters are similarly con-

firmed by the underwater images (Fig. 10A). Sclerite forms and size ranges are consistent throughout all paratypes (Fig. 8A, B: ZMTAU CO 38124, not shown for ZMTAU Co 38125 and ZMTAU CO 38126).

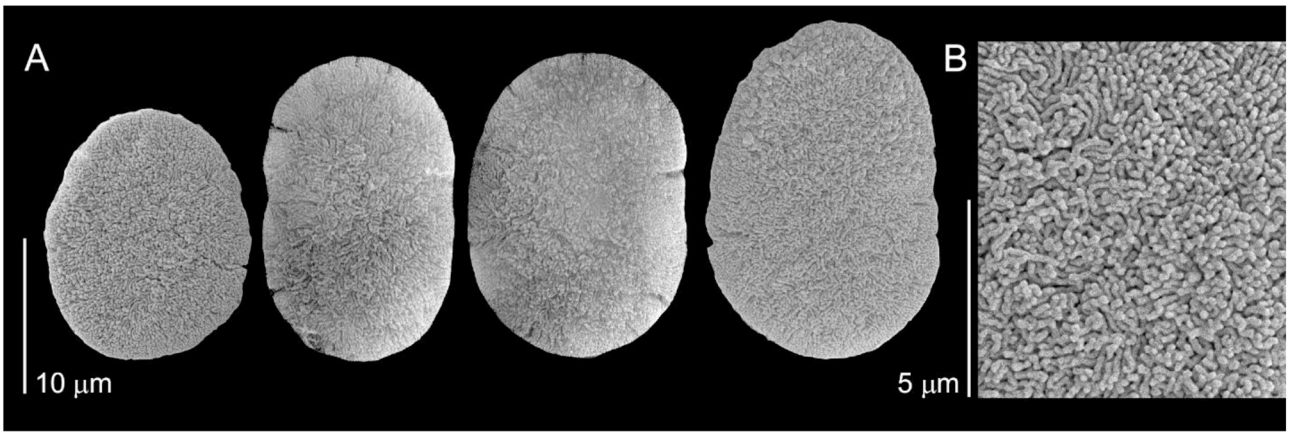

FIGURE 8. Scanning electron micrographs of sclerites of *Unomia complanatis* **gen. n. sp. n.** Paratype (ZMTAU CO 38124). (A) Ellipsoid platelets; (B) Terminal parts of dendritic rods on the surface of the platelet.

The Yonaguni Island, Ryukyu Archipelago material (ZMTAU CO 35154) are small encrusting colonies, much resembling the holotype (ZMTAU CO 38120). The Green Island (Taiwan) material (ZMTAU CO 37813 and ZMTAU CO 37846) are all encrusting colonies as demonstrated both by the preserved (Fig. 9) and living colonies (Fig. 10B). The polyps of these colonies are arranged in several distinct groups corresponding to polyparies, whose number depends on the colony size. Their stalk is narrow, being only a few mm high. The sclerites of ZMTAU CO 37813 (Fig. 11) resemble those of the holotype (not shown for ZMTAU CO 37846).

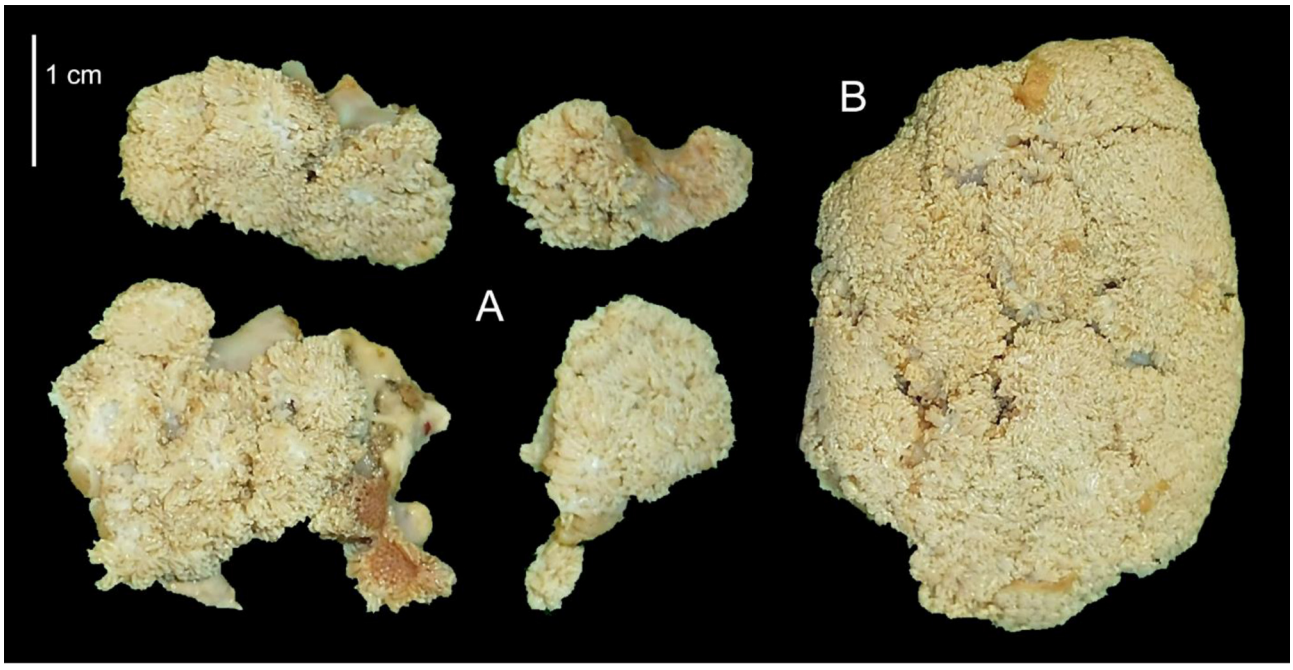

FIGURE 9. *Unomia complanatis* **gen.n. sp. n.** from Taiwan (Green Island). (A) ZMTAU CO 37813 and (B**)** ZMTAU CO 37846.

Etymology. The species name is derived from the Latin: "complanatis", flattened, and denotes morphology of the colonies. Gender: neuter.

Distribution. Japan, Taiwan.

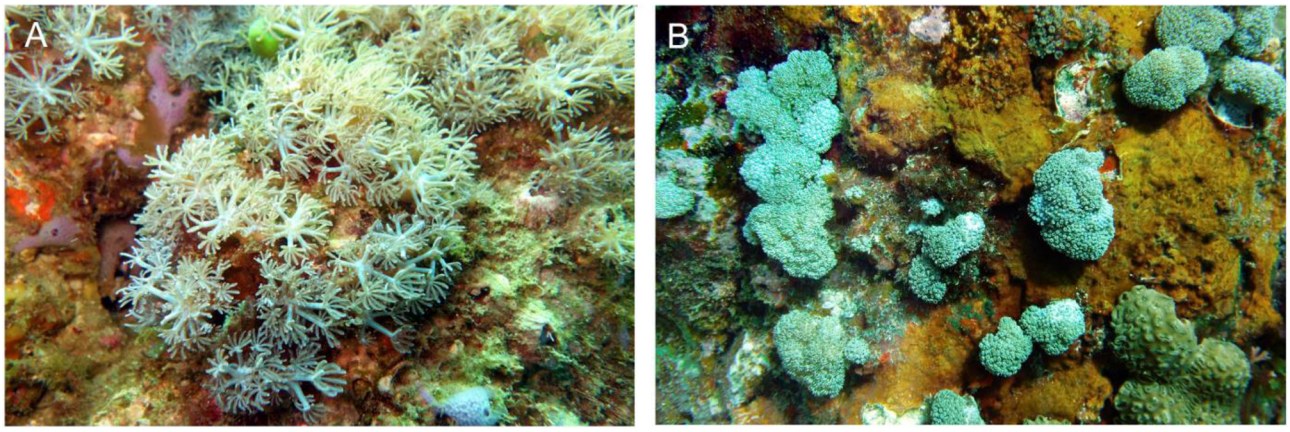

FIGURE 10. *Unomia complanatis* **gen n. sp. n.** live colonies. (A) Colonies from Japan (Kumamoto Prefecture) and (B) Colonies from Taiwan (Green Island).

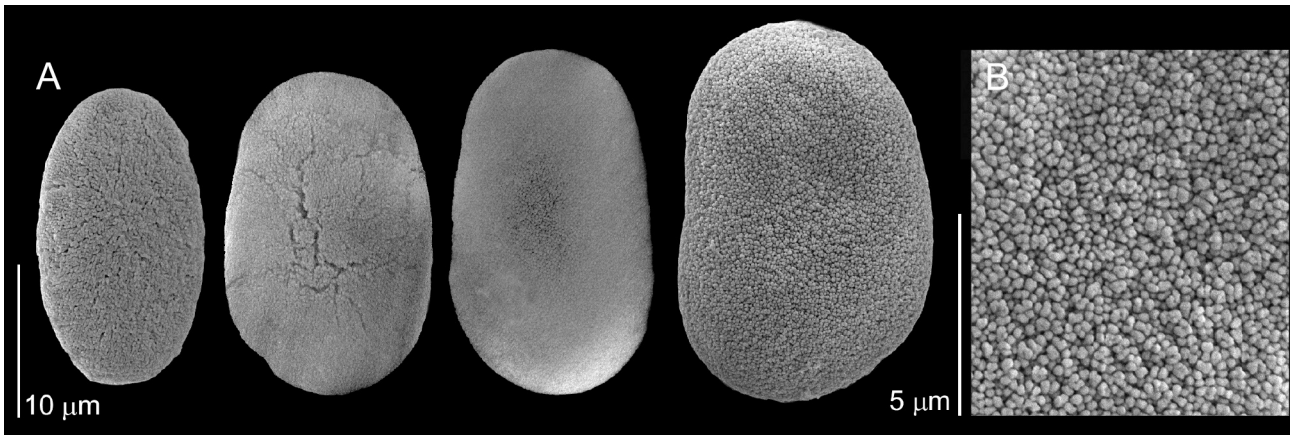

FIGURE 11. Scanning electron micrographs of sclerites of *Unomia complanatis* **gen. n. sp. n.** from Taiwan (Green Island) (ZMTAU CO 37813). (A) Ellipsoid platelets; (B) Tips of dendritic rods on the surface of the platelet.

Molecular Phylogenetic Results

Maximum likelihood and Bayesian analyses both supported the placement of *Unomia* **n. gen.** in a clade that includes the xeniid genera *Sansibia* Alderslade, 2000*; Sarcothelia* Verrill, 1928; *Yamazatum* Benayahu, 2010 and *Ezziona* Alderslade & Janes, 2017 as well as several species identified previously as *Xenia* Lamarck, 1816 (Fig. 12). This clade is far removed phylogenetically from *Caementabunda* and *Conglomeratusclera*, two genera that have recently been established for other former members of *Cespitularia* (see Benayahu *et al*. 2018). Within this clade, *Unomia stolonifera* **n. comb.** and *U. complanatis* **n. gen. n. sp.** each belong to separate, well-supported sub-clades. *U. stolonifera* ZMTAU CO 38081 shares an identical multilocus barcode sequence with a colony collected from Lembeh, Sulawesi, Indonesia that was identified as *X. membranacea* Schenk, 1896 by McFadden *et al*. (2014a). It differed from *U. complanatis* by a genetic distance (uncorrected p) of 0.4–0.8% at *mtMutS* and 0.5–1.0% at 28S rDNA. The six specimens of *U. complanatis* that were sequenced grouped together in a well-supported clade in the maximum likelihood analysis (Fig. 12). All shared identical *mtMutS* sequences; two specimens from Green Island, Taiwan, differed from the others by 0.3–0.4% in 28S rDNA. In the Bayesian tree only (not shown), *X. kusimotoensis* was also included in this clade as sister to the Green Island specimens, but with relatively low support (pp = 0.83); it differed from *U. complanatis* by 0.8–1.5% at 28S rDNA and 0.2–0.3% at *mtMutS*.

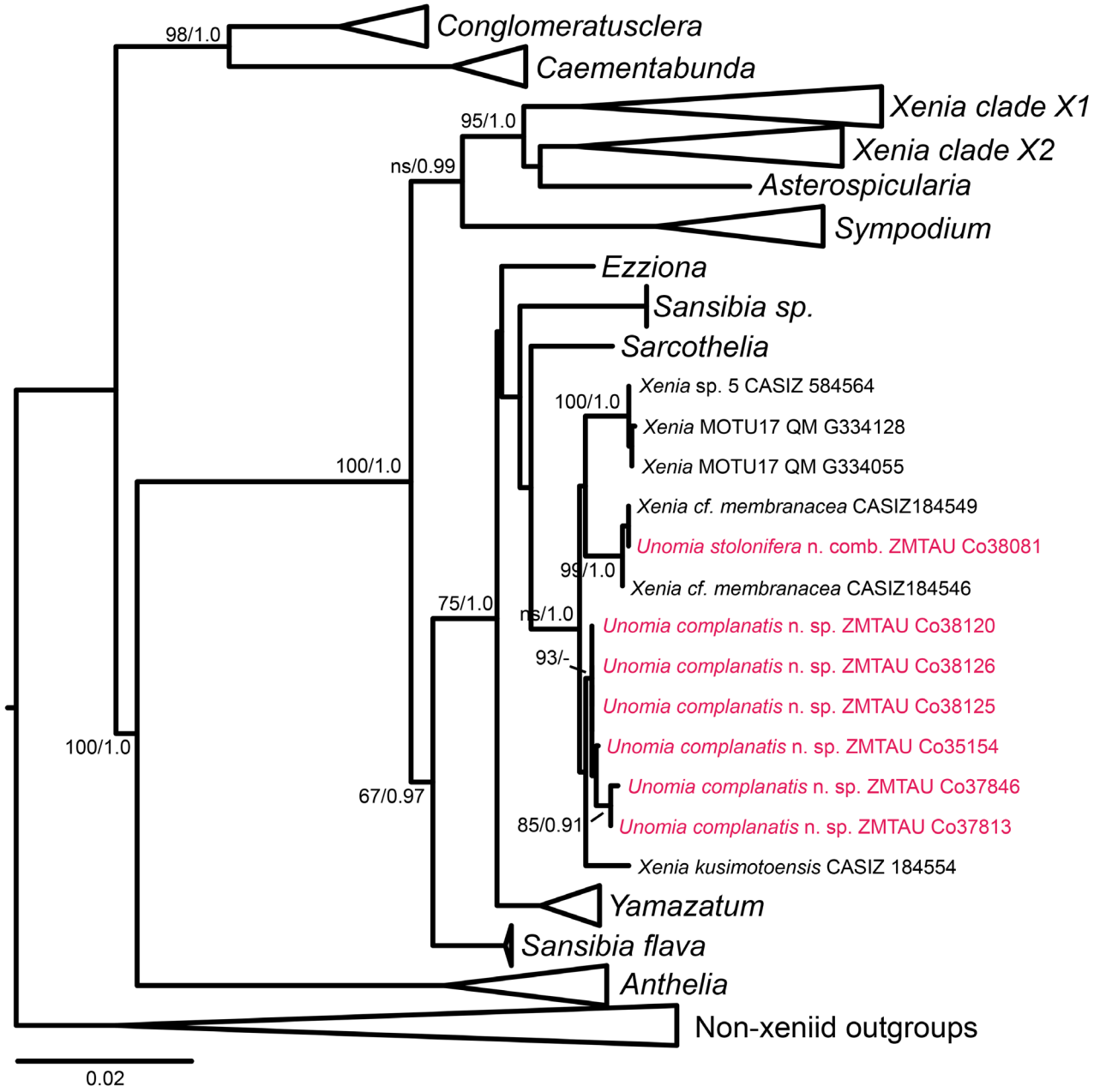

FIGURE 12. Maximum likelihood phylogeny of family Xeniidae using concatenated *mtMutS* and 28S rDNA fragments (1486 bp). New sequence data for *U. stolonifera* **n. comb.** and *U. complanatis* **n. sp.** (Table 1) were added to the alignment of 165 taxa analyzed by McFadden *et al*. (2019). ML bootstrap values/Bayesian posterior probabilities are indicated only for nodes that were well supported by one or both analyses. Some clades with strong support have been collapsed to facilitate readability. *Xenia* clade X1 includes *Ovabunda*, and *Xenia* clade X2 includes *Heteroxenia*. See Appendix 1 in McFadden *et al*. (2019) for complete list of all material included in the phylogenetic analysis.

Discussion

The original description of the type of *Cespitularia stolonifera* by Gohar (1938) referred to five colonies collected by the Challenger Expedition and deposited at the BMNH. The current examination of this material (Fig. 1) largely agrees with this earlier description and therefore validates BMNH 1889.5.27 as that type. Notably, these colonies were initially assigned by Wright & Studer (1889: 252) to *Xenia elongata* Dana, 1846. However, based on their branched morphology and the presence of polyps along the entire length of the branches, Gohar (1938) concluded

that the colonies should be assigned to the genus *Cespitularia* Milne Edwards & Haime, 1850. Although the original description of *C. stolonifera* indicates 2–3 rows of pinnules, no information is provided regarding the number of pinnules in each row. The sclerites are referred to as disks, ovals, and oblongs, 0.012 x 0.020 mm in size, but are not depicted. Undoubtedly, the morphological features of the colonies, including their polyps and sclerites, justify their assignment to the Xeniidae (Fabricius & Alderslade 2001). However, the generic assignment by Gohar (1938) to *Cespitularia* cannot be confirmed, as the taxonomic status of *Cespitularia sensu stricto* Quoy & Gaimard (1833) cannot be clearly determined until new xeniid material can be obtained from the original type locality (see details in Benayahu *et al*. 2018a).

When considering colony morphology, it should be noted that the location and arrangement of polyps among branched xeniids exhibit certain variations. For example, the polyps of branched colonies of *Xenia* Lamarck, 1816 and *Ovabunda* Alderslade, 2001 are typically arranged in one or more distinct, domed polyp-bearing regions (polyparies). The lower border of the polypary in both genera is well-defined, appearing as a sharp line below which no polyps are found on the stalks. Furthermore, all species assigned so far to those two genera exhibit a similar colony morphology (Halász *et al*. 2014, 2019). In *Conglomeratusclera*, polyps are found along the branches, and sometimes also on the stalk, whereas in *Caementabunda* they appear on the lobes and occasionally also on some parts of the colony base. The current examination of the type of *C. stolonifera* indicates that most of the polyps arise from the upper part of the branches where they are crowded together to form polyp-bearing regions, while those polyps on the lower parts of the branches are sparse individuals (Fig. 1). It is therefore concluded that among the branched xeniid taxa polyps can be: (1) exclusively grouped together in a terminal polypary in the shape of domed polyp-bearing regions; or (2) scattered along the branches, or (3) feature both a polypary and individual polyps below it that may merge together leading to an encrusting and flattened colony morphology. The latter case is noted here for *Unomia* **gen. n.**, making it unique among all the previously described xeniid genera. Notably, *U. stolonifera* features a distinct polypary on the upper part of the stalk (Fig. 1) whereas in *U. complanatis* colony morphology is variable, ranging from stalked to flattened and encrusting (Figs. 6, 9). Such variation seems to be unique among the xeniid genera studied so far, although preliminary studies of *Sympodium* suggest that it may exhibit similar variation in colony morphology (Benayahu, unpubl. data).

Similar to most of the earlier xeniid literature (see also Aharonovich and Benayahu 2011), Gohar (1938) did not depict any *C. stolonifera* sclerites. The only previous hand-drawings of sclerites of this species are of a colony from Formosa (Utinomi, 1950: 15, Fig. 3f). The present study is the first to present SEM sclerite images of the type, featuring ellipsoid platelets composed of dendritic calcite rods (Fig. 2). The tips of the rods can be observed on the surface of the platelet, commonly providing it with a granular appearance. This dendritic sclerite microstructure is not unique to *Unomia* **gen. n.**, however, as it also occurs in several other xeniid genera, including *Heteroxenia* (Reinicke 1997: 19, fig. 10), *Ingotia* (Alderslade 2001), *Ezziona* (Alderslade 2001), *Sansibia* (Benayahu 1993, but erroneously assigned to *Anthelia)*, *Sympodium* (Reinicke 1997), *Xenia* (Halász *et al*. 2019) and *Yamazatum* (Benayahu 2010). Moreover, this dendritic microstructure is not confined solely to the Xeniidae, as discussed by Halász *et al*. (2019). It is thus evident that the sclerite microstructure alone cannot be considered exclusively diagnostic of *Unomia* **gen. n.** Nonetheless, the combined features of polyp arrangement in the colony (i.e. a polyp-bearing region, additional individual polyps on the branches below or a flattened, encrusting morphology) along with the dendritic sclerite microstructure, characterize the genus and differentiate it from other genera.

The material from Sulawesi identified by McFadden *et al*. (2014a) as *X. membranacea* is currently unavailable for study, but the genetic analyses suggest it is likely the same as *U. stolonifera*. McFadden *et al*. (2014a) described these colonies as having three (with occasionally a partial fourth) rows of pinnules with 23–27 pinnules in the outer row; several colonies (including CASIZ 184546) were also observed to have a loosely defined polypary with some isolated polyps occurring below it on the stalk (M. Janes, unpubl. data). They were identified as *X. membranacea* based on the original description of that species in the literature rather than on direct comparison to existing type material. McFadden *et al*. (2014a) also noted that *X. membranacea* and two other species they identified as *Xenia* (*X. kusimotoensis* Utinomi, 1955 and *Xenia* sp. 5) belonged to a distinct clade (*Xenia* clade X3) that was well separated from all other *Xenia* species (*Xenia* clades X1 and X2, Fig. 12). Access to and further examination of these specimens will be necessary to confirm if they may also belong to *Unomia* n. gen. as the phylogenetic reconstruction suggests (Fig. 12).

Examination of recently collected material from Japan and Taiwan justified the establishment of *U. complanatis* **sp. n.**, demonstrating the morphological variation of the colonies assigned to *Unomia*. Although the two colonies

from Green I. differ slightly from the others in both colony form and at 28S rDNA, for now we consider that variation to be intraspecific; genetic distances of <0.5% are within the range typical of intraspecific variation in octocoral 28S rDNA (McFadden *et al*. 2014b). The results also indicate that the biogeographic distribution of *Unomia* **gen. n.** includes several Pacific regions as well as the invaded Venezuelan reefs.

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