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On some encrusting Xeniidae (Octocorallia): Re-examination of the type material of *Sansibia flava* (May, 1898) and a description of new taxa

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Abstract

The type of the xeniid soft coral *Sansibia flava* (May, 1898) is re-described for the first time and its morphological diagnosis is presented. A subsequent integrated analysis of molecular and morphological characters of related Xeniidae, including species indigenous to the Indo-Pacific Ocean and invasive in the Atlantic (Brazil), led to the description of a new *Sansibia* species, as well as two new genera comprising an additional three new species. All of these taxa are encrusting, with polyps arising directly from a spreading basal membrane. Molecular phylogenetic analyses show that these genera are not sister taxa, thus further emphasizing the remarkable phylogenetic diversity of xeniids with such a growth form. The sclerites of all species are uniformly ellipsoid platelets, abundant throughout the colony. The species exhibit restricted, non-overlapping geographic ranges, with distinct genotypes (molecular operational taxonomic units) found in different marine realms. The results emphasize the importance of re-examination of original old type material while applying molecular phylogenetic analyses in order to delineate species boundaries and to recognize biodiversity patterns.

Key words: Indo-Pacific region, taxonomy, new taxa, molecular phylogeny, MOTUs, sclerite microstructure

Introduction

The soft-coral genus *Sansibia* of the family Xeniidae was established by Alderslade (2000), who designated *Clavularia flava* May, 1899 (family Clavulariidae), collected in Zanzibar, as the type species of the genus. Alderslade also discussed the generic boundaries between this newly-established genus and other morphologically similar xeniids of the genera *Anthelia* Lamarck, 1816 and *Sarcothelia* Verrill, 1928. In the same study he further presented a detailed history of the taxonomic status of *C. flava* justifying the new genus, while reviewing changes in the taxonomic position of *C. flava* since its original description. *C. flava* was alternately placed in the genera *Clavularia* and *Anthelia,* which also resulted in alterations of its family-level assignment. Notably, the indication of the year of authority of this species was not consistent in the subsequent literature: Cohn (1908: 243) adopted *C. flava* May, 1898; Thomson & Mackinnon (1910: 171) adopted *A. flava* (May, 1899), while Molander (1921: 2–4) adopted *A. flava* (May, 1898), and all of those combinations were assigned to the family Cornulariidae. Later, Hickson (1931: 175) proposed the inclusion of *C. flava* May, 1900 in the family Xeniidae; but Roxas (1933: 63) who referred to this species as *A. flava* (May, 1899) included it in Clavulariidae. Later still, Tixier-Durivault (1966) assigned *A. flava*

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(May, 1899) to Xeniidae. Benayahu (1993: 14–15) erroneously referred to material collected by him in Sodwana Bay (South Africa) as the type of *A. flava* (May, 1899) and similarly placed it in the Xeniidae. The latter study presented SEM images of some sclerites, featuring oval platelets described by Alderslade (2000) as having a "cat's tongue" surface.

The literature indicates that throughout the years *C. flava* has been recorded from Tamatave, Madagascar (Cohn 1908); Cagados Carajos, Egmont and Salmon, Mauritius (Thomson & Mackinnon 1910); and *A. flava* from Palawan, Philippines (Roxas 1933); Mauritius (Tixier Durivault 1966) and South Africa (Benayahu 1993). Since its assignment to the genus *Sansibia*, its distribution has been noted as the tropical and subtropical waters of the Indian and Pacific Oceans (Fabricius & Alderslade 2001). *S. flava* was recorded in southern Taiwan (Benayahu *et al.* 2004), Hong Kong (Benayahu & Fabricius 2010), and Singapore (Benayahu & Chou 2010); and *Sansibia* sp. in Hong Kong (Fabricius & McCorry 2006, Yeung *et al.* 2014), Palau (Fabricius *et al.* 2007), Mozambique (Schleyer & Benayahu 2008), Thailand (Andaman Sea, Chanmethakul *et al.* 2010), western Australia (Richards *et al.* 2013, Bryce *et al.* 2018), Lembeh, Indonesia (Janes 2013, McFadden *et al.* 2014a), and Moreton Bay (Australia, Alderslade 2011, Olds *et al.* 2014). In addition, *Sansibia* sp. was reported as an invasive species of reef-aquaria origin in the southern Atlantic, Brazil (Mantelatto *et al.* 2018).

To date, our revisionary studies on the family Xeniidae have covered the genera *Ovabunda* (Hálasz *et al.* 2014, McFadden *et al.* 2017), *Conglomeratusclera* and *Caementabunda* (Benayahu *et al.* 2018), *Xenia* (Hálasz *et al.* 2019), *Unomia* (Benayahu *et al.* 2021), and *Sympodium* (Benayahu *et al.* 2021). All of these studies have demonstrated the importance of examining both old type material and corresponding freshly collected material, while integrating both classical taxonomy and novel genetic data for delineation of taxa and assignment of Latin binomials. That said, the current study re-examines the original type of *S. flava* (May, 1898) for the first time since its initial description. In addition, we examine morphologically related soft coral material collected in various Indo-Pacific regions as well as an invasive soft coral from Brazil (Mantelatto *et al.* 2018). The results of the genetic analyses have enabled assignment of the samples to distinct molecular operational taxonomic units (MOTUs), including some that had already been previously recognized (McFadden *et al.* 2019) as well as several new ones. A distribution map of the examined material according to the different marine realms is also provided (Fig. 1). The genetic results in congruence with the morphological findings yielded two new genera and four new species. The study demonstrates that xeniid taxa have remarkably restricted geographic distributions. Moreover, it further highlights the importance of integrating classical taxonomy with molecular phylogenetic analyses in order to elucidate the species inventory of the Indo-Pacific soft corals (e. g. McFadden *et al.* 2019, Benayahu *et al.* 2021).

Materials and methods

The study examined the original type specimen of *C. flava* May, 1898 deposited at the Zoologisches Museum Hamburg (ZMH), along with material from the Steinhardt Museum of Natural History at Tel Aviv University (SNHMTAU), Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie, Leiden, RMNH), Queensland Museum (QM), Western Australian Museum (WAM), Museum and Art Gallery of the Northern Territory (MAGNT), and the British Museum of Natural History (BMNH).

Morphological studies. Morphological features (shape and dimensions) of the preserved colonies were recorded. The retractility 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 dimensions 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 light microscope at X200–400 magnification (see also Aharonovich & Benayahu 2011). SEM mounts were prepared from the sclerites, 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; Au coated and viewed under a Hitachi TM–1000 ESEM, and Jeol 6480LV SEM operated at 10 kV.

Molecular phylogenetic analyses. DNA was isolated from ethanol-preserved tissue using the Qiagen DNEasy Blood & Tissue kit following manufacturer's instructions. Two mitochondrial gene fragments (*mtMutS*, *COI*) and a fragment of the nuclear *28S rDNA* gene were amplified by polymerase chain reaction, and Sanger-sequenced using

TABLE 1: Focal specimens included in molecular phylogenetic analysis. Sequences were added to the alignment analyzed in McFadden *et al.* (2019). M# = molecular operational taxonomic unit (MOTU) as per McFadden *et al.* (2019).

Species	M#	Museum Acc. No.	Collection Location	GenBank Acc. No.		
				mutS	COI	28S
Sansibia flava	23	SMNHTAU Co_36007	Madagascar	OK670710	OK670736	OK746234
Sansibia flava	23	SMNHTAU Co_36006	Madagascar	MK030380	MK0329204	MK030486
Sansibia flava	23	SMNHTAU Co_36001	Madagascar	OK670711	OK670737	NA
Sansibia flava	23	SMNHTAU Co_36003	Madagascar	OK670712	OK670727	OK746235
Sansibia flava	23	SMNHTAU Co_36004	Madagascar	MK396681	MK396728	MK400137
Sansibia flava	23	SMNHTAU Co_36073	Madagascar	MK030381	MK0329205	MK030487
Sansibia flava	23	SMNHTAU Co_33276	Kenya	OK670714	NA	OK746236
Sansibia flava	23	SMNHTAU Co_32573	Kenya	OK670713	OK670728	NA
Sansibia claereboudti **sp. nov.**	74	RMNH Coel. 42195	Oman	OK670715	NA	OK746237
Sansibia claereboudti **sp. nov.**	74	RMNH Coel. 42196	Oman	NA	NA	OK746238
Latissimia ningalooensis **gen. nov. sp. nov.**	8	NTM C012955	NT, Australia	DQ302840	OK670740	NA
Latissimia ningalooensis **gen. nov. sp. nov.**	8	QM G330077	WA, Australia	MK030385	MK0329208	MK030491
Latissimia ningalooensis **gen. nov. sp. nov.**	8	QM G330711	WA, Australia	MK030387	MK0329209	MK030492
Latissimia ningalooensis **gen. nov. sp. nov.**	8	QM G334196	WA, Australia	MK030382	MK0329206	MK030488
Latissimia ningalooensis **gen. nov. sp. nov.**	8	QM G334151	WA, Australia	MK030383	MK0329207	MK030489
Latissimia ningalooensis **gen. nov. sp. nov.**	8	QM G334150	WA, Australia	MK030384	NA	MK030490
Latissimia ningalooensis **gen. nov. sp. nov.**	8	QM G330421	WA, Australia	OK670716	NA	NA
Latissimia ningalooensis **gen. nov. sp. nov.**	8	SMNHTAU Co_38205	Brazil	OK670717	OK670729	OK746239
Latissimia ningalooensis **gen. nov. sp. nov.**	8	SMNHTAU Co_38206	Brazil	MG677564	MG677569	MG677558
Latissimia opalia **gen. nov. sp. nov.**	72	QM G317204	QLD, Australia	OK670718	OK670730	OK746240
Latissimia opalia **gen. nov. sp. nov.**	72	QM G339447	QLD, Australia	OK670719	OK670731	OK746241
Latissimia opalia **gen. nov. sp. nov.**	72	QM G339448	QLD, Australia	OK670720	OK670732	OK746242
Latissimia opalia **gen. nov. sp. nov.**	72	QM G339449	QLD, Australia	OK670721	OK670733	OK746243
Latissimia opalia **gen. nov. sp. nov.**	72	QM G339459	QLD, Australia	OK670722	OK670734	OK746243
Latissimia opalia **gen. nov. sp. nov.**	72	QM G333523	QLD, Australia	OK670723	OK670735	OK746245
Latissimia sp.	42	CAS IZ 184572	Sulawesi	OK670724	KJ511384	OK746246
Latissimia sp.	70	SMNHTAU Co_30386	Kenya	OK670725	OK670738	OK746247
Quattuoria pallida **gen. nov. sp. nov.**	71	SMNHTAU Co_36071	Madagascar	OK670726	OK670739	OK746248
Sarcothelia cf. *edmondsoni*	73	SMNHTAU Co_38212	Oahu, Hawaii	JX203814	JX203868	JX203757
Sarcothelia sp.	73	SMNHTAU Co_38213	aquarium trade, US	KM201456	KM201462	KM201434

previously published primers and protocols (McFadden *et al.* 2014a, b). A DNA barcode consisting of these three genes concatenated has been shown to discriminate 75–90% of octocoral species (McFadden *et al.* 2014b), and has contributed to species discovery in other genera of xeniids (Benayahu *et al.* 2018, 2021). New sequences were added to an alignment of ~190 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). In addition to the material newly described here, we also included sequence data for specimens that had been identified as *Sansibia* in previous molecular phylogenetic studies (McFadden *et al.* 2006; McFadden *et al.* 2014a).

Phylogenetic trees were constructed for each locus using PhyML (Guindon and Gascuel 2003), and after checking for congruence of trees the three genes were concatenated. Optimal models of evolution for each gene were found using ModelFinder (Kalyaanamoorthy *et al.* 2017) and a maximum likelihood tree was constructed using an edge-linked partition model (Chernomor *et al.* 2016) with 10,000 ultrafast bootstraps (Hoang *et al.* 2018) in IQTree v. 2.1.2 (Nguyen *et al.* 2015). MrBayes v. 3.2 (Ronquist *et al.* 2012) was used to infer a phylogeny using Bayesian inference with the GTR+I+G model of evolution applied independently to each gene partition. MrBayes was run for 4 million generations (until standard deviation of split frequencies <0.01) with default MCMC settings.

Mothur v. 1.42 (Schloss *et al.* 2009) was used to separate specimens into molecular operational taxonomic units (MOTUs) using an average genetic distance (uncorrected p) threshold of 0.3% applied to the concatenated alignment. This value has been shown in previous studies to yield the highest concordance between MOTUs and morphospecies concepts (McFadden *et al.* 2014b). Pairwise genetic distances (uncorrected p) were calculated separately for each gene region using MEGA v. 7 (Kumar *et al.* 2016).

Results

Systematics

Order Alcyonacea Lamouroux, 1812

Family Xeniidae Ehrenberg, 1828

Sansibia Alderslade, 2000

Diagnosis. Xeniidae with non-retractile polyps arising directly from a spreading membrane or ribbon-like stolons. Polyps monomorphic. Sclerites are abundant and present as ellipsoid platelets, some with a waist-like median narrowing. The sclerites reveal a dendritic surface microstructure. Colonies harbor symbiotic unicellular algae.

Type species: *Sansibia flava* (May, 1898).

Sansibia flava (May, 1898)

Figures 1–4, 5A–B

Clavularia flava May 1898: 8; May 1899: 43–44, Plate I, Fig. 3.
?*Clavularia flava* Thomson & Henderson 1906: 402, Plate XXX, Fig. 4; Cohn 1908: 243; Hickson 1931: 175 (listed only).
?Anthelia flava Molander 1921: 3 (listed only); Thomson & Mackinnon 1910: 171; Roxas 1933: 63; Tixier-Durivault 1966: 348–349, Fig. 317.
Anthelia flava Benayahu 1993: 14–15, Fig. 7.

Material examined. Holotype: Sansibar. ZMH C 2570, three fragments, Kokotoni, coll. Stuhlmann. **Additional material.** Kenya. SMNHTAU_Co_32573, Kitungamwe, on Tanzanian border, 20 m, 5 February 2003, coll. Y. Benayahu; SMNHTAU_Co_36076, Shelly Beach, Mtwapa Creek, Likoni, 9 m, 8 February 2003, coll. Y Benayahu; Madagascar. SMNHTAU_Co_36001, Le Banc du Castor (12.851833° S, 48.426050° E), 22–24 m, 28 November 2012, coll. Y. Benayahu; SMNHTAU_Co_36003, same details; SMNHTAU_Co_36004, same details; SMNHTAU_Co_36006, Le Banc du Castor, same details, 14–16 m, 28 November 2012, coll. Y. Benayahu; SMNHTAU_Co_36007, same details; SMNHTAU_Co_36073, 4 Frére (12.994250° S, 48.487467° E), 4–15 m, 1 December 2012, coll. Y. Benayahu; Zanzibar. BMNH 1912.2.25.5; Zanzibar shore, coll. J. A. Thomson; 1933.3.13.194, same details; BMNH, 1933.3.13.195, same details.

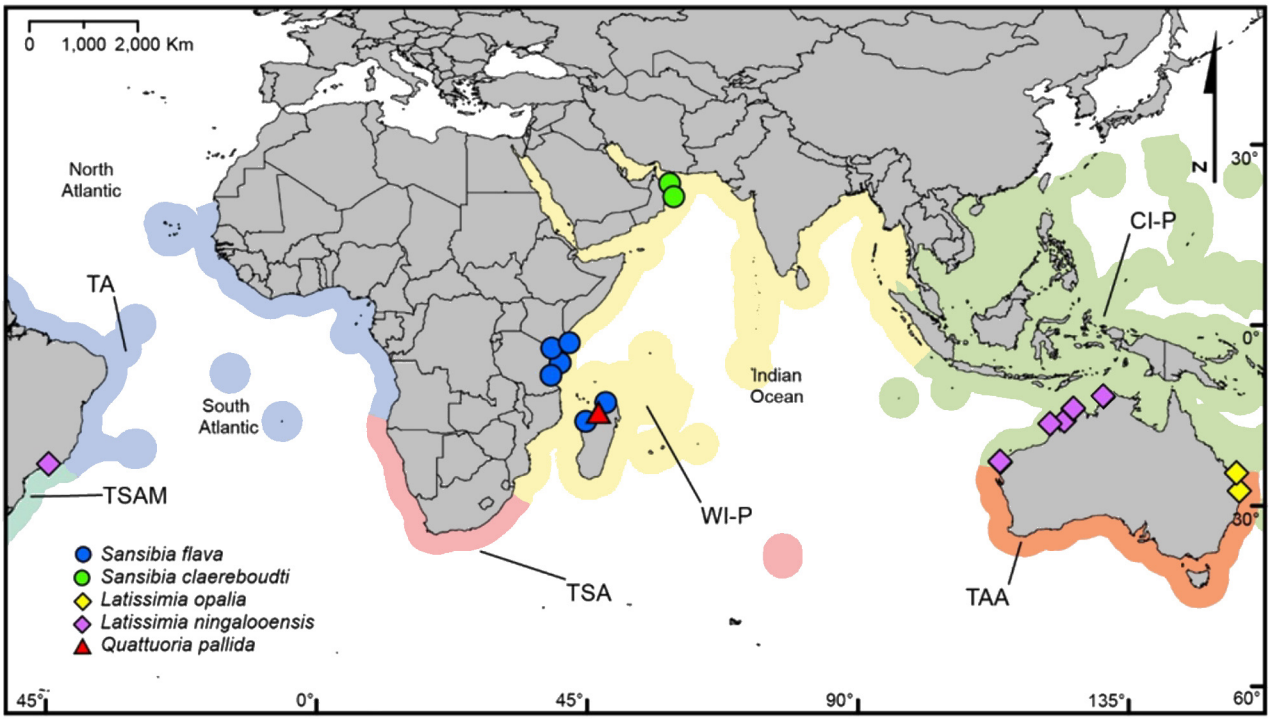

FIGURE 1. Distribution map of the material examined in the current study. Color shades on the background represent different marine realms. TA = Tropical Atlantic, TSAM = Temperate Southern America, TSA = Temperate Southern Africa, WI-P = Western Indo-Pacific, CI-P = Central Indo-Pacific, and TAA = Temperate Australasia.

Diagnosis. The holotype, ZMH C 2570, consists of three fragments, probably of the same colony, each with a basal spreading membrane from which polyps emerge. One of the fragments (Fig. 2A) measures 20 x 10 mm and was closely examined. Its soft spreading membrane is approximately 1 mm thick and the polyps are flaccid. The polyp body is 6–10 mm long, depending on the degree of contraction, and the tentacles are 4–5 mm long. The pinnules are arranged in 3–4 rows, with up to 25 pinnules in the outermost row. They are short and pointed, approximately 1 mm long and 0.5 mm wide, with almost no space between adjacent ones.

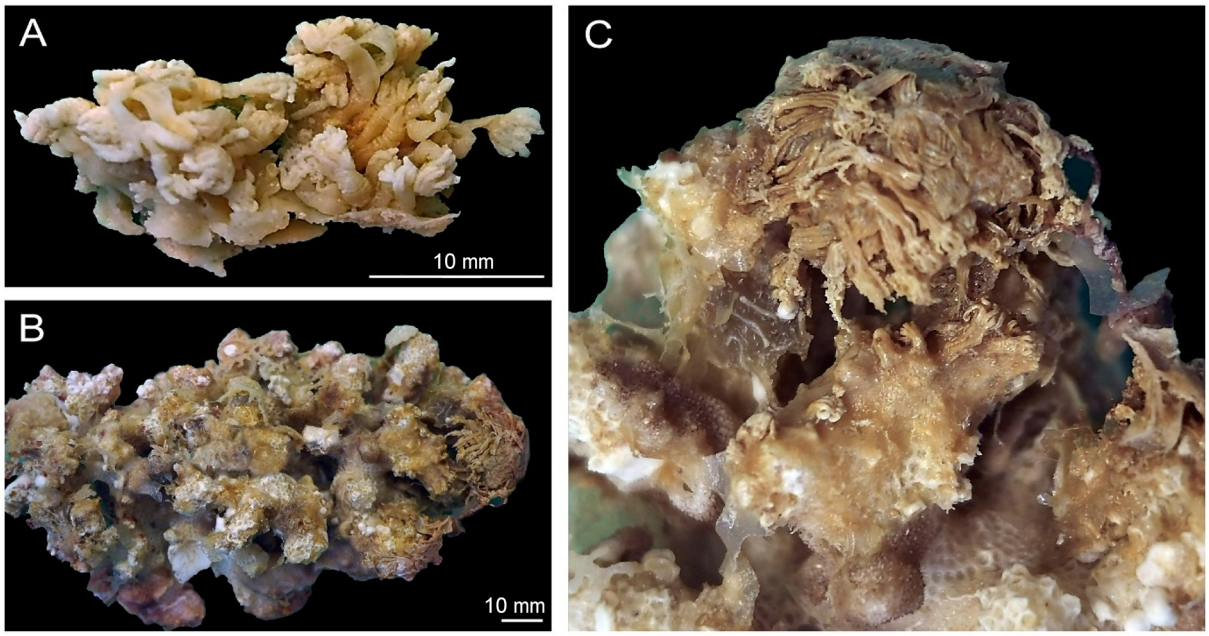

FIGURE 2. *Sansibia flava* (May, 1898): morphology of colonies. (A) Holotype (ZMH C 2570) comprises three fragments, one shown here. SMNHTAU_Co_36007: (B) Colony attached to calcareous substrate. (C) Magnified part of colony.

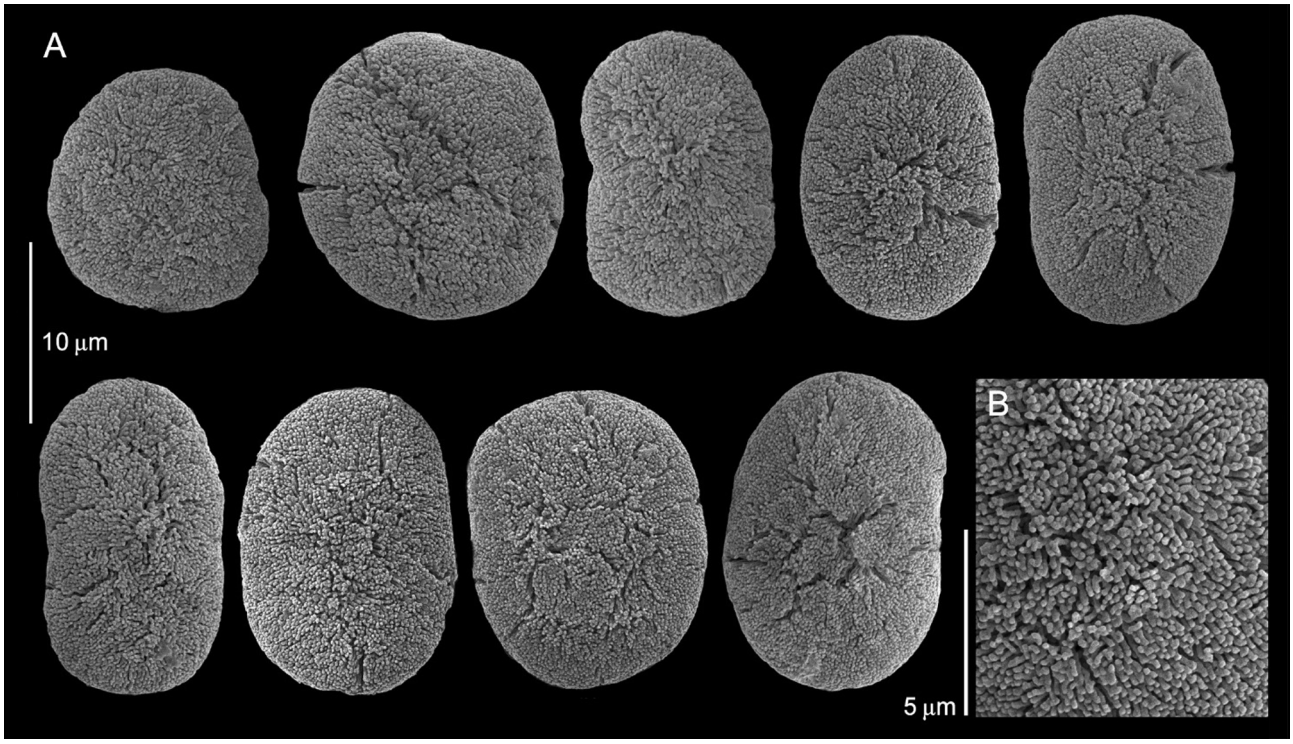

FIGURE 3. Scanning electron micrographs of sclerites of *Sansibia flava* (May, 1898). Holotype (ZMH C 2570): (A) Ellipsoid platelets. (B) Tips of calcite rods more or less perpendicular to the surface of the sclerite, giving it a granular appearance.

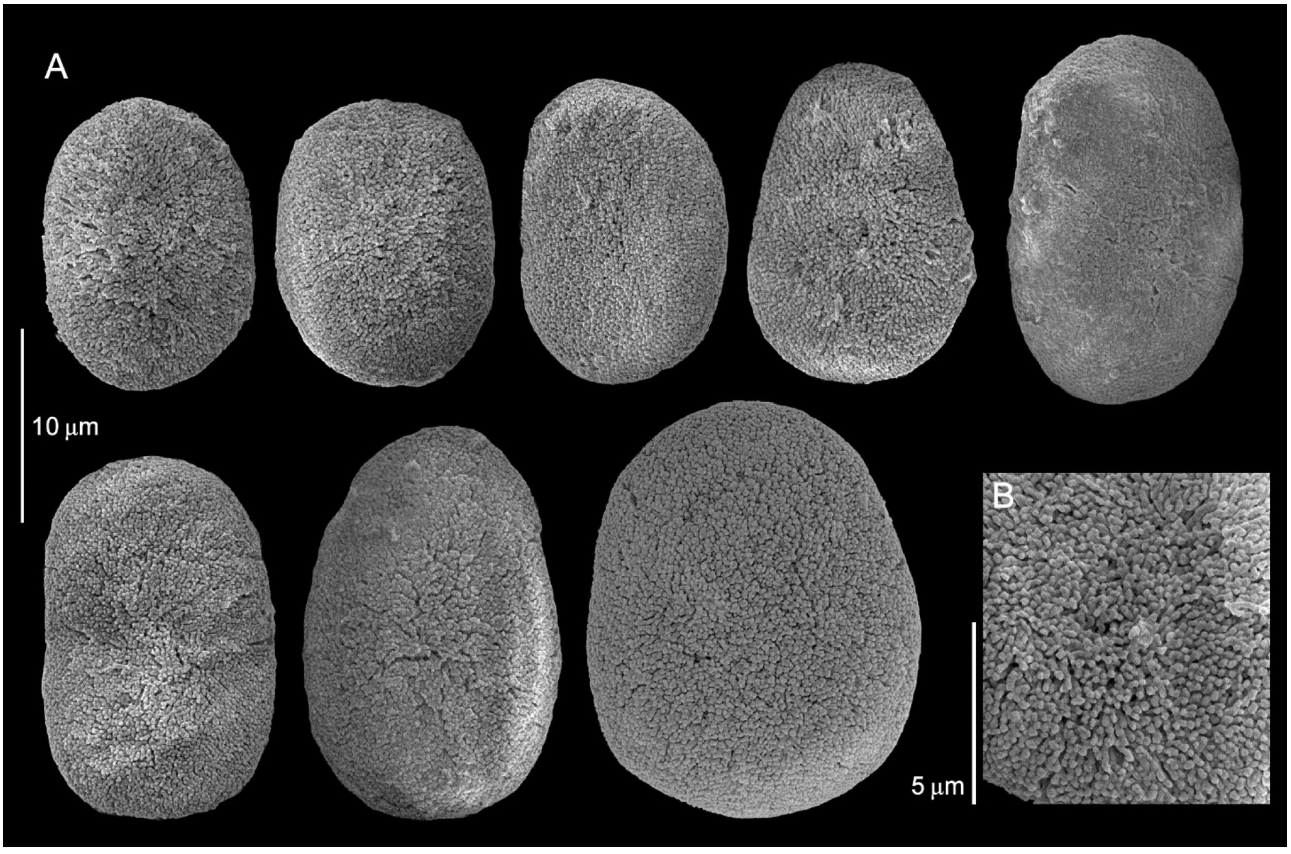

FIGURE 4. *Sansibia flava* (May, 1898) (SMNHTAU_Co_36007): (A) Ellipsoid platelets. (B) Tips of calcite rods providing a granular appearance to the sclerite surface.

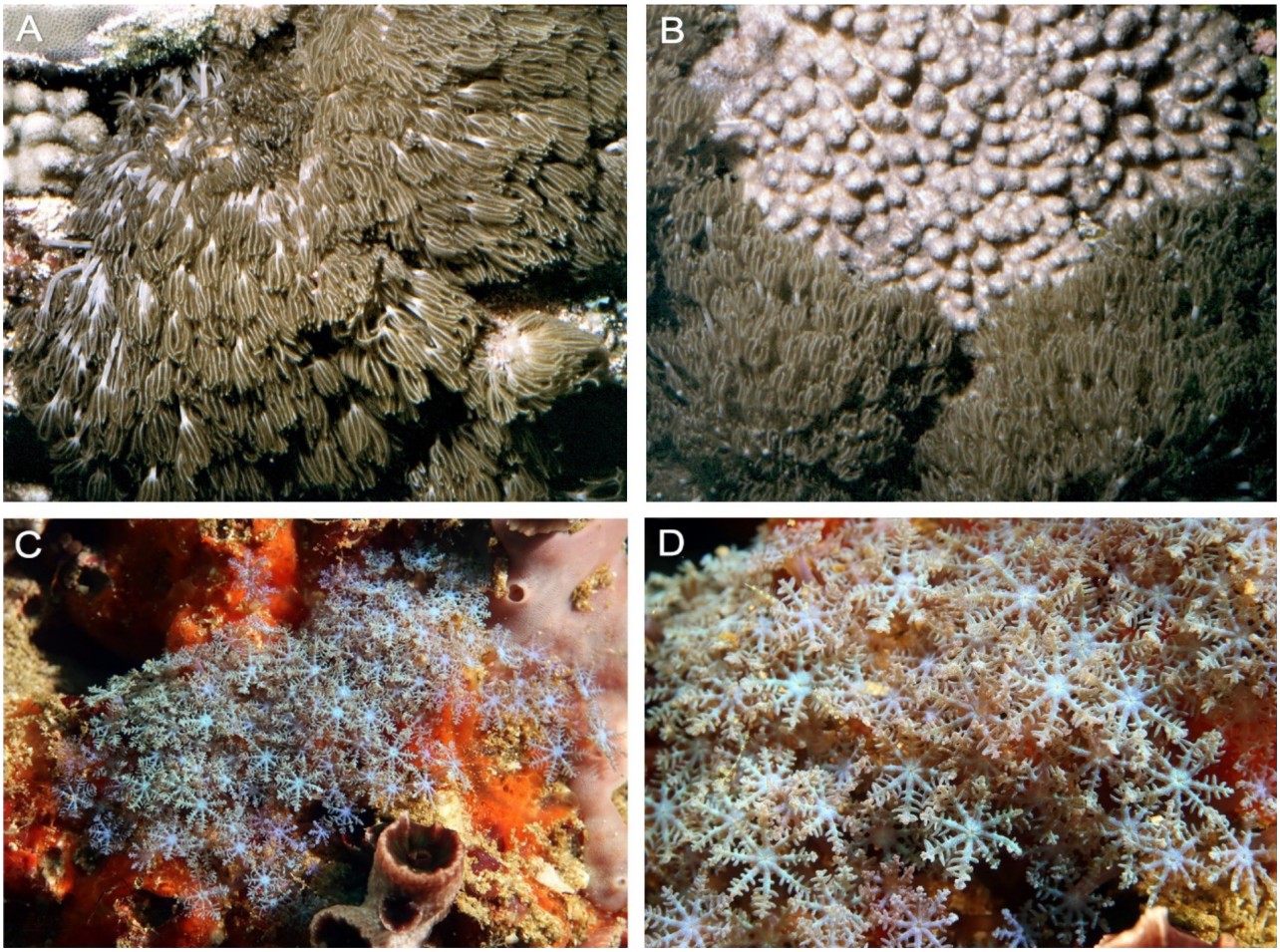

FIGURE 5. Live colonies of *Sansibia* species. *S. flava* (May, 1898) on the reef: (A) Colony with expanded brown polyps and bright, almost white polyp body. (B) Colony with expanded polyps. *S. claereboudti* **sp. nov.**: (C, D) Encrusting colonies with expanded polyps and distinct pinnules along the margins of the tentacles (photos C, D: courtesy of M. Claereboudt).

The sclerites are highly abundant throughout the holotype. They are ellipsoid platelets mostly with a smooth margin, measuring 0.008–0.013 x 0.013–0.018 mm in diameter, and under SEM they are mostly fractured (Fig. 3A). The sclerites are composed of calcite rods, uniform in diameter of ca. 0.001 mm; the tips of the rods are more or less perpendicular to the surface of the sclerite, giving it a granular appearance (Fig. 3B).

Color. The ethanol–preserved holotype colonies are light cream.

Variation. The morphological features of the sequenced SMNHTAU colonies (see additional material above) resemble the holotype, except in size. They similarly feature a thin spreading membrane attached to a hard calcareous substrate or sand grains. The polyps can be up to 20 mm long (e. g. Fig. 2B, C: SMNHTAU_Co_36007) with their pinnules arranged in 2–4 rows with a variable number of pinnules on the outermost one (14–25). In all examined colonies the polyps and all the pinnules are expanded. The sclerites of SMNHTAU_Co_36007 are slightly larger compared to those of the holotype, up to 0.016 x 0.021 mm in diameter (Fig. 4A). Their smooth margin and granular surface microstructure (Fig. 4B) agree with the holotype. Our morphological examination of material from the BMNH (see additional material above), originally labeled as *A. flava*, confirms it to be *S. flava* (data not shown).

Color. The ethanol-preserved samples are cream or light brown.

Remarks. The current study is the first to re-describe the holotype of *S. flava* since its establishment by May (1898). The original description of the holotype material by May corresponds well to the current findings. The current SEM images of the holotype sclerites are the first to reveal their surface microstructure (Fig. 3), which is also considered to be diagnostic for several other xeniid genera (see Discussion below). It should be noted that the correct authority year of the species should be 1898 and not 1899, as erroneously appears in several publications (Thomson & Mackinnon 1910, Roxas 1933, Tixier-Durivault 1966, Benayahu 1993, Alderslade 2000). Indeed, both of May's publications (of 1898 and 1899) provide a similar taxonomic description of *C. flava*, but the former

unquestionably should be prioritized. In addition, Hickson (1931) incorrectly referred to 1900 as the authority year of the species.

The other material examined in the current study exhibits some morphological variation with respect to the number of rows of pinnules and the number of pinnules in the outermost row. These findings further demonstrate the intraspecific variation of these characters, which are commonly used in the taxonomic literature for xeniid species delineation (e.g. Benayahu *et al.* 2021). It should be noted that the morphological features of SMNHTAU_Co_27901 collected from Sodwana Bay (South Africa) and identified as *A. flava* (see Benayahu 1993, Alderslade 2000) agree with the holotype of *S. flava*, and therefore its identification has been changed accordingly.

All of the sequenced samples (see other SMNHTAU material above) have been assigned to MOTU23 (McFadden *et al.* 2019), thus indicating that the geographic distribution of *S. flava* includes the western Indian Ocean coral reefs (Fig. 1). It is still questionable whether its distribution includes the Pacific Ocean, as suggested in several past studies based only on morphological identification (e. g. Taiwan: Benayahu *et al.* 2004, Hong Kong: Benayahu & Fabricius 2010 and Singapore: Benayahu & Chou 2010). Unfortunately, the latter samples are not appropriate for genetic analysis and, therefore, a conclusive taxonomic assignment of these samples still awaits future studies.

Living features. The encrusting live colonies feature a basal spreading membrane attached to the reef substrate, an expanded, relatively long, almost white, polyp body (Fig. 5A), and dark brown tentacles (Fig. 5A, B). The latter coloration is provided by the presence of numerous symbiotic algal cells.

Distribution. Zanzibar, Tanzania, Kenya, Madagascar, South Africa (Fig. 1).

Sansibia claereboudti Samimi-Namin, Benayahu & McFadden sp. nov.

Figures 1, 5C–D, 6, 7

http://zoobank/urn:lsid:zoobank.org:act:E8115341-B5FE-40A7-A1D8-3B7D7B1DB628

Material. Oman, **Holotype**: RMNH Coel. 42915, Oman Sea, Bandar Al-Khiran (23.501662° N, 58.763671° E), 8–10 m, 2013, coll. K. Samimi-Namin & M. Claereboudt; **Paratypes:** RMNH Coel. 42916, same details; SMNHTAU_Co_38229, same details.

Description. The holotype has a stoloniferous growth form and encrusts a limestone fragment (Fig. 5 C–D, 6A). Polyps are monomorphic, and their distribution varies from well-spaced to dense clumps. They arise from anastomosing stolons that criss-cross the substrate Fig. (6 A–B). The polyps are flabby and lie horizontally on the colony surface. The polyp body is up to 2 mm long and the tentacles are >1 mm long. There is a single row of 5–7 plump pinnules along each side of a tentacle. The smaller polyps may have fewer pinnules or even none, probably representing young ones. The stolons are rather thin and delicate, up to 1 mm thick.

The sclerites of the holotype are ellipsoid platelets, highly abundant throughout the colony, measuring 0.010–0.016 x 0.014–0.020 mm (Fig. 7A). Some sclerites tend to fracture due to the SEM preparation. They are composed of calcite rods whose tips provide a granular appearance to the sclerite surface (Fig. 7B).

Color. The ethanol-preserved samples are cream or light brown.

Etymology The species is named after Michel Claereboudt, Sultan Qaboos University, Oman, for his contributions to knowledge of the marine biodiversity of the Middle East.

Variation. The morphological features of the paratype colonies (Fig. 6C) resemble the holotype, except in size.

Remarks. *S. claereboudti* **sp. nov.** is the second confirmed species of this genus. Although Alderslade (2000) included *Anthelia boquetei* Roxas, 1933, *Anthelia formosana* Utinomi, 1950, and *?Anthelia lineata* Stimpson, 1855 in the genus *Sansibia*, all three of those species need re-examination prior to a concrete decision on their taxonomic status. The morphology of *S. claereboudti* **sp. nov.** differs markedly from that of *S. flava* whose polyps are not contractile, while those of *S. claereboudti* **sp. nov.** can completely contract. *S. flava* has a spreading membrane, while *S. claereboudti* **sp. nov.** has stolons growing over the reef substrate. *S. claereboudti* **sp. nov.** features tentacles with a single row of 5–7 pinnules compared to *S. flava* which has 3–4 rows and up to 25 pinnules in the outermost row. The sclerites of both species are ellipsoid platelets, highly abundant throughout the colony, and those of *S. claereboudti* **sp. nov.** are a bit smaller in diameter compared to *S. flava* (0.008–0.013 x 0.013–0.018 and 0.010–0.016 x 0.014–0.020 mm, respectively). *S. flava* has sclerites with a rather smooth and roundish margin except for some cracks, while *S. claereboudti* **sp. nov.** has some sclerites with a waist. Despite these morphological differences between the

two congeners, the molecular data suggest a close genetic relationship between *S. flava* and *S. claereboudti* **sp. nov.** Based on the description of the latter two species an updated diagnosis of *Sansibia* is presented. So far, these two species exhibit restricted, non-overlapping geographic ranges: Oman Sea vs. SW Indian Ocean.

Living features. The live colonies are iridescent blue-purple or green due to the light-refraction properties of the sclerites (Fig. 5C, D). *In situ* photographs show the polyps in various states, from moderately expanded to completely contracted. Expanded polyps are 2–6 mm in width when alive and the tentacles are up to 4 mm long and 2 mm wide. Polyps contract when stimulated physically.

Distribution. Oman Sea, Arabian Sea (Fig. 1).

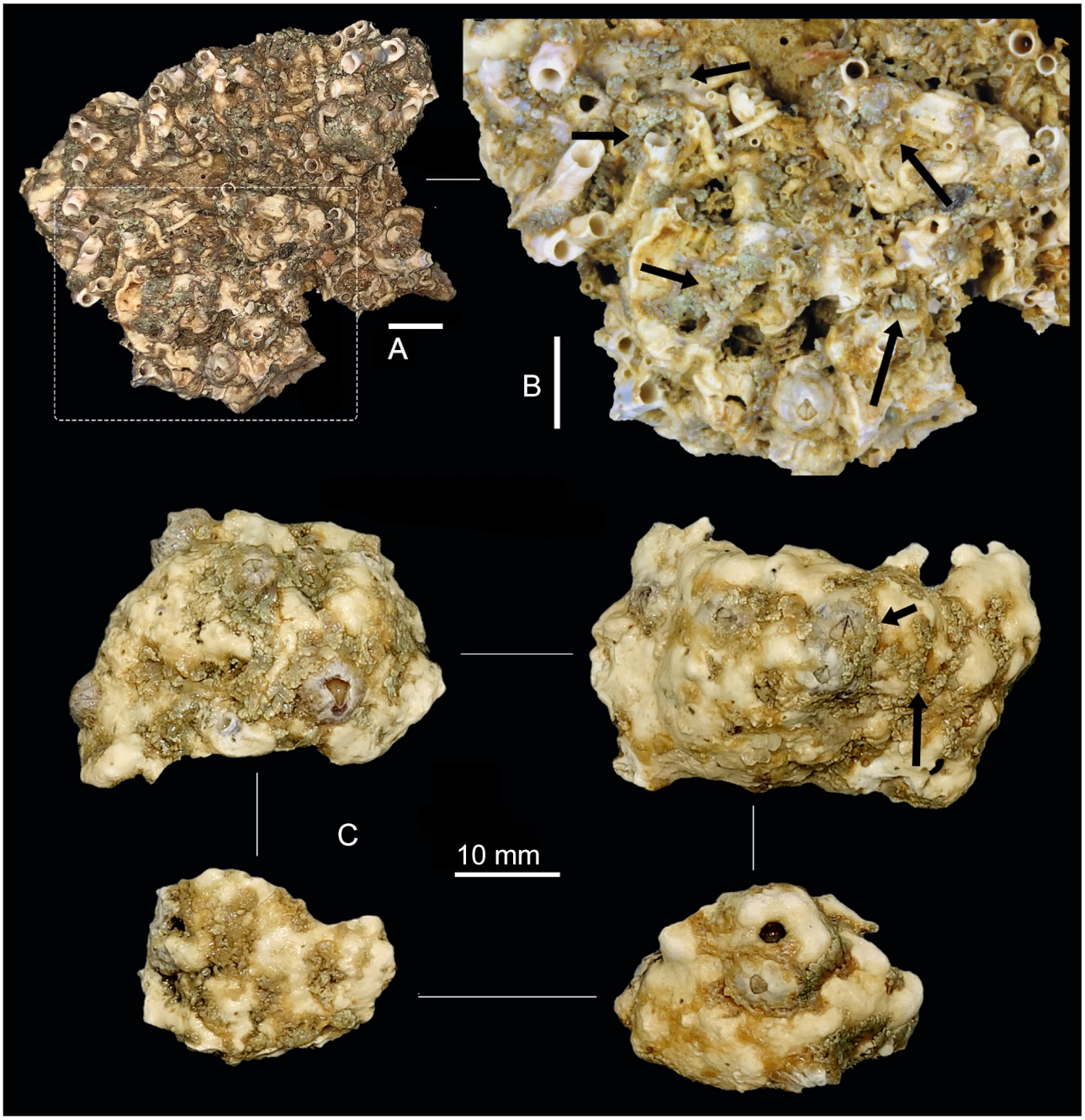

FIGURE 6. *Sansibia claereboudti* **sp. nov.**: (A) Holotype (RMNH Coel. 42915). (B) Enlarged portion of (A) marked by dashed rectangle, arrows indicate clusters of polyps. (C) Paratype colonies (RMNH Coel. 42916) attached to calcareous substrate.

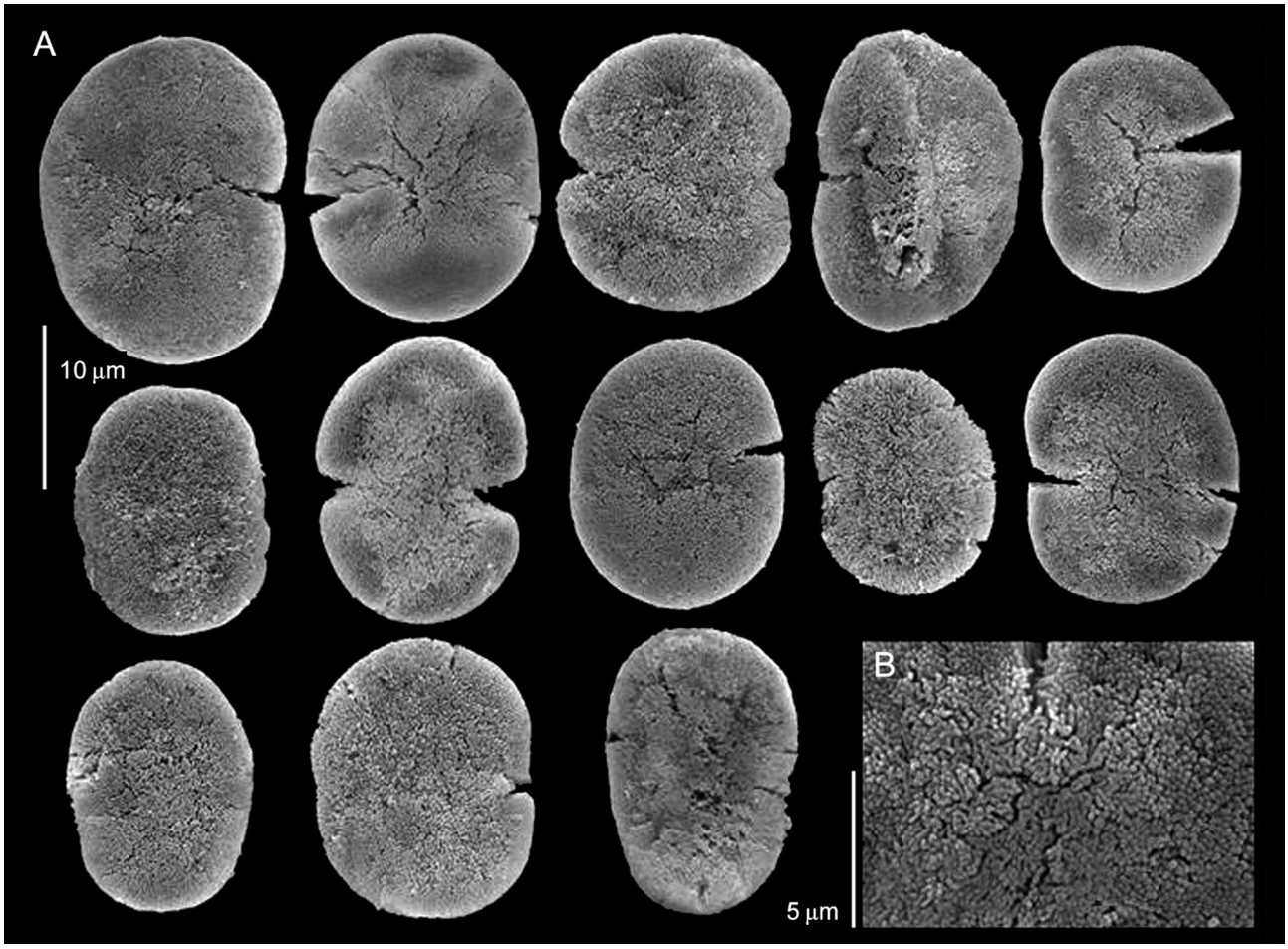

FIGURE 7. Scanning electron micrographs of sclerites of *Sansibia claereboudti* **sp. nov.** Holotype (RMNH Coel. 42915): (A) Ellipsoid platelets. (B) Tips of calcite rods provide uniform granular appearance to the sclerite surface.

Latissimia **Benayahu, Ekins & McFadden, gen. nov.**
http://zoobank/urn:lsid:zoobank.org:act:363FCB88-4355-4D49-A41C-12FAD9F66A0E

Diagnosis. Xeniidae with polyps arising directly from a relatively thick spreading membrane which provides the colony with a fleshy texture. Polyps monomorphic and non-retractile. Sclerites present as ellipsoid platelets, some with a waist-like median narrowing, abundant in all parts of the colony. The sclerites reach up to 0.023 mm in diameter, and reveal a dendritic surface microstructure. The live colonies feature a characteristic blue tint due to the sclerite light-refraction properties, commonly providing a blue appearance to the tissue. Zooxanthellate.

Type species: *Latissimia opalia* Ekins, Benayahu & McFadden, **sp. nov.** by original designation.

Etymology. The generic name *Latissimia* (gender: feminine) is derived from the Latin: *latissime*, which refers to widespread. Here, it denotes the wide distribution of this genus on various eastern and western Australian reefs, while also being an invasive in the western Atlantic Ocean (Brazil).

Latissimia opalia **Ekins, Benayahu & McFadden, sp. nov.**
Figures 1, 8–10
http://zoobank/urn:lsid:zoobank.org:act:7CA36992-98F8-478D-BE5A-A2318722193D

Material. Australia. **Holotype:** QM G339447, Shelly Beach, Caloundra, Queensland (26.79972° S, 153.150278° E), Intertidal pools of beach rock, 0.1–1 m, 23 February 2021, coll. M. Ekins; **Paratypes**: QM G339756-QM G339762 and QM G339448-QM G339450, all same details; QM G333523, same location as the holotype, 4 June 2013, coll. M. Ekins & J. Johnson; QM G317135, same location as the holotype, 30 June 2000, coll. S. Cook, & D.

Edson; QM G317204, Dunwich, North Stradbroke Island, Queensland, Australia (27.494167° S, 153.400000° E), 0.1–1 m, 23 September 2000, coll. J. Hooper, S. Cook, J. Kennedy, S. List-Armitage, D. Edson and G. Wörheide.

FIGURE 8. *Latissimia opalia* **gen. nov. sp. nov.** (A) Holotype (QM G339447) with expanded polyps emerging from the encrusting spreading membrane. (B–H) Paratype colonies.

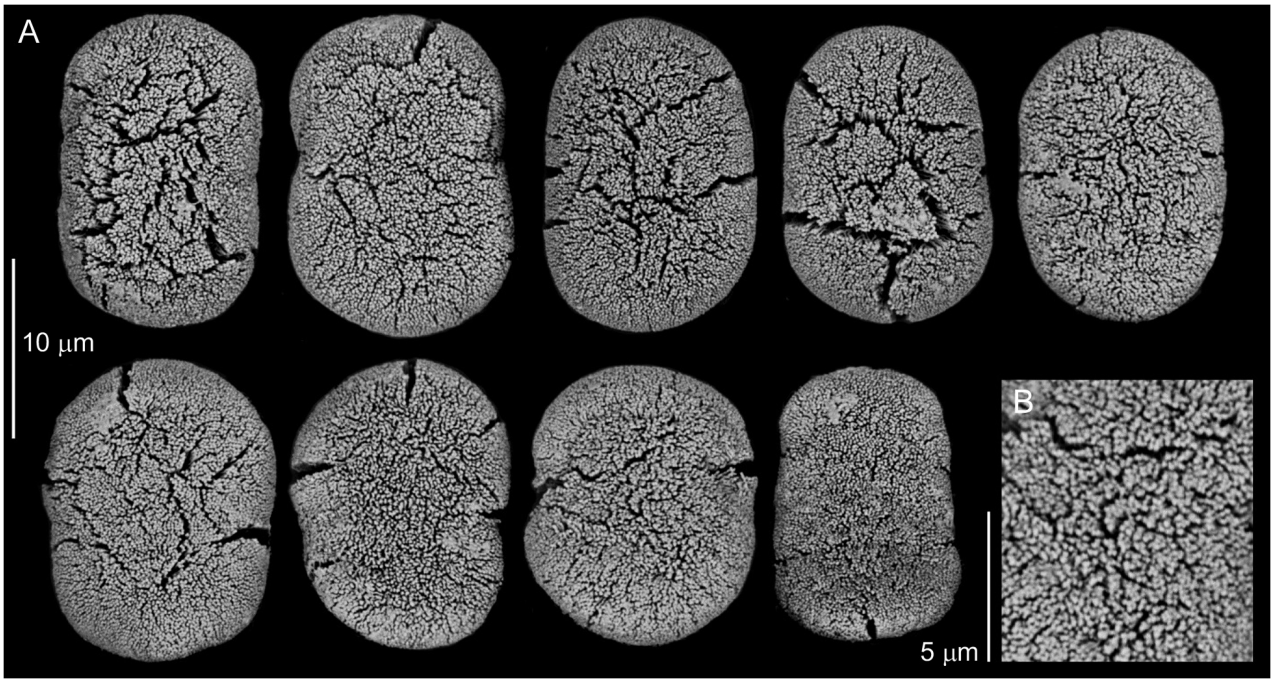

FIGURE 9. Scanning electron micrographs of sclerites of *Latissimia opalia* **gen. nov. sp. nov.** Holotype (QM G339447): (A) Ellipsoid platelets. (B) Tips of calcite rods provide a uniform granular appearance to the sclerite surface.

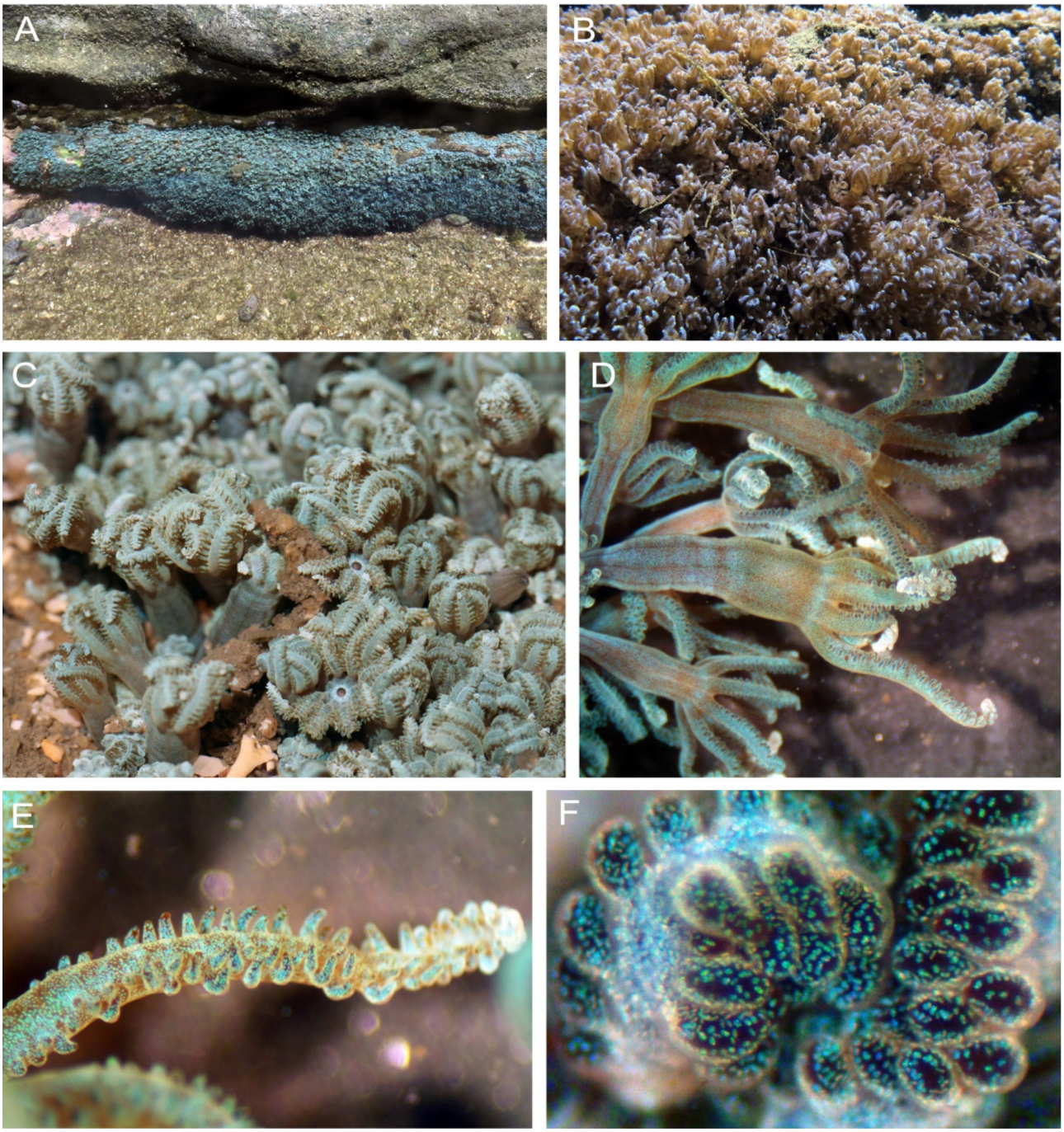

FIGURE 10. Live colonies of *Latissimia opalia* **gen. nov. sp. nov.**: (A, B) View of encrusting colonies. (C, D) Polyps exhibiting characteristic blue coloration of sclerites with creamy brown color of underlying tissue containing symbiotic algal cells. (E, F) Magnified tentacles with pinnules exhibiting the above coloration features.

Description. The holotype measures 30 x 23 mm and is 8 mm in height (Fig. 8A), featuring polyps attached to an encrusting 3 mm thick spreading membrane. The polyps are up to 11 mm in length with the majority being around this size, and a few contracted ones of only 2 mm in length. The lower part of the polyps below the tentacles is 1–1.5 mm in width. The expanded tentacles are approximately 1.5 mm long with two rows of 24–30 pinnules on either side of the tentacle.

The sclerites of the holotype are ellipsoid platelets, a few with a waist-like median narrowing, either on one or both sides of the sclerite (Fig. 9A). Under an incident light microscope they are opalescent blue and abundant throughout the colony, measuring 0.008–0.013 x 0.016–0.019 mm in diameter. The sclerites are composed of calcite

rods whose tips provide a uniform granular appearance to the sclerite surface (Fig. 9B). Some sclerites tend to fracture during the dehydration process necessary for SEM.

Color. The ethanol-preserved holotype is cream/light orange.

Etymology. The species name, *opalia*, is derived from the Latin *opalus*, referring to the opal-blue color of the live colonies.

Variation. The morphological features of the paratype colonies resemble the holotype, except in size (Fig. 8 B–H).

Remarks. *L. opalia* is characterized by large non-retractile blue polyps when alive (Fig. 10) and a relatively thick spreading membrane providing a fleshy appearance. Another xeniid, *Sympodium caeruleum* Ehrenberg, 1834, similarly has encrusting colonies with a bluish tinge when alive (Benayahu *et al.* 2021). However, it differs from *L. opalia* by having a much thinner and more delicate spreading membrane and fully retractile polyps. All of the sequenced samples of *L. opalia* were assigned to MOTU72, thus indicating that the geographic distribution of *L. opalia* includes the Queensland (eastern Australia) intertidal rock platforms and mudflats (Fig. 1).

Living features. The live colonies are blue/brown in color (Fig. 10 A–B**).** Higher magnification of the polyps and tentacles clearly demonstrates the characteristic blue coloration of the sclerites (Fig. 10 C–F). At low tide the polyps in direct sunlight contract such that their sclerites form an almost complete barrier blocking out the sunlight and giving the colonies their blue color, with the creamy-brown color of the underlying tissue apparent between the sclerites.

Distribution. South-eastern Queensland and northern New South Wales, Australia (Fig. 1).

Latissimia ningalooensis Ekins, Benayahu & McFadden, sp. nov.

Figures 1, 11–14

http://zoobank/urn:lsid:zoobank.org:act:33E744E2-542B-4CF6-85D1-DD020E4FD10B

Material. Australia. **Holotype:** QM G330711, Ningaloo Reef, Western Australia, Australia (22.77661° S, 113.696432° E), patch reef, lagoon, 5–7 m, 20 May 2010, coll. M. Ekins & M. Bryce, NR10–030; **Paratypes**: QM G339754, QM G339755 and WAM Z29359 same details as QM G330711; QM G330077, Ningaloo Reef, inside Norwegian Bommies, Western Australia, Australia (22.62157° S, 113.6424° E), patch reef, lagoon, 5–6 m, 19 May 2010, coll. M. Ekins & M. Bryce, NR09–035; QM G334151, Long Reef, Kimberley, Western Australia, Australia (13.83015° S, 125.83257° E), mid-littoral reef terrace, 0–1 m, 21 October 2010, coll. M. Ekins & M. Bryce, K-48; WAM Z59816 same details as QM G334151; QM G334150, Long Reef, Kimberley, Western Australia, Australia (13.9018° S, 125.79108° E), sub-littoral reef platform, 2–5 m, 22 October 2010, coll. M. Ekins & M. Bryce, K–49; WAM Z59815 same details as QM G334150; QM G334196, Champagney Islands, Kimberley, Western Australia, Australia (15.33074° S, 124.21692° E), intertidal, mid-littoral reef platform, Champagney Islands, Kimberley 1 m, 15 October 2011, coll. M. Ekins & M. Bryce, K-63; WAM Z54716 same details as QM G334196; QM G330421, Montgomery Reef, Kimberley, Western Australia, Australia (15.897183° S, 124.323967° E), intertidal, mid-littoral reef terrace, 0–1 m, 19 October 2009, coll. M. Bryce, K-15; WAM Z54909 same details as QM G330421. **Other material:** Brazil. SMNHTAU_Co_38205 Rio de Janeiro, Ilha Grande Bay (23.026° S, 44.501° W), September 2017, coll. J. Creed: SMNHTAU_Co_38206 same details.

Description. The holotype growing on a dead stony coral measures 11 x 9 mm (Fig. 11A), with a 1 mm thick spreading membrane with polyps. The polyps are usually 3.5 mm in height, and their body is 0.9 mm in width. The majority of the polyps are fully expanded, with only a small number partly contracted. They have two rows of 18–22 pinnules on either side of the tentacle. The relatively long and expanded polyps give the colonies a fleshy appearance.

The sclerites of the holotype are ellipsoid platelets, some with a median narrowing (Fig. 12A). Under a light microscope they are opalescent and abundant throughout the colony, measuring 0.010–0.017 x 0.013–0.023 mm in diameter. The sclerites are composed of calcite rods whose tips provide a granular microstructure to their surface, often forming a labyrinthic appearance and arranged in dense patches with some space in between (Fig. 12B). The sclerites often tend to fracture during the dehydration process necessary for SEM.

Color. The ethanol-preserved holotype has a pale brown membrane and polyp bodies and cream tentacles.

Etymology. The species name, *ningalooensis*, refers to Ningaloo, the type locality of the species.

Variation. The morphological features of the paratype colonies resemble the holotype, except in size (Fig. 11 B–C).

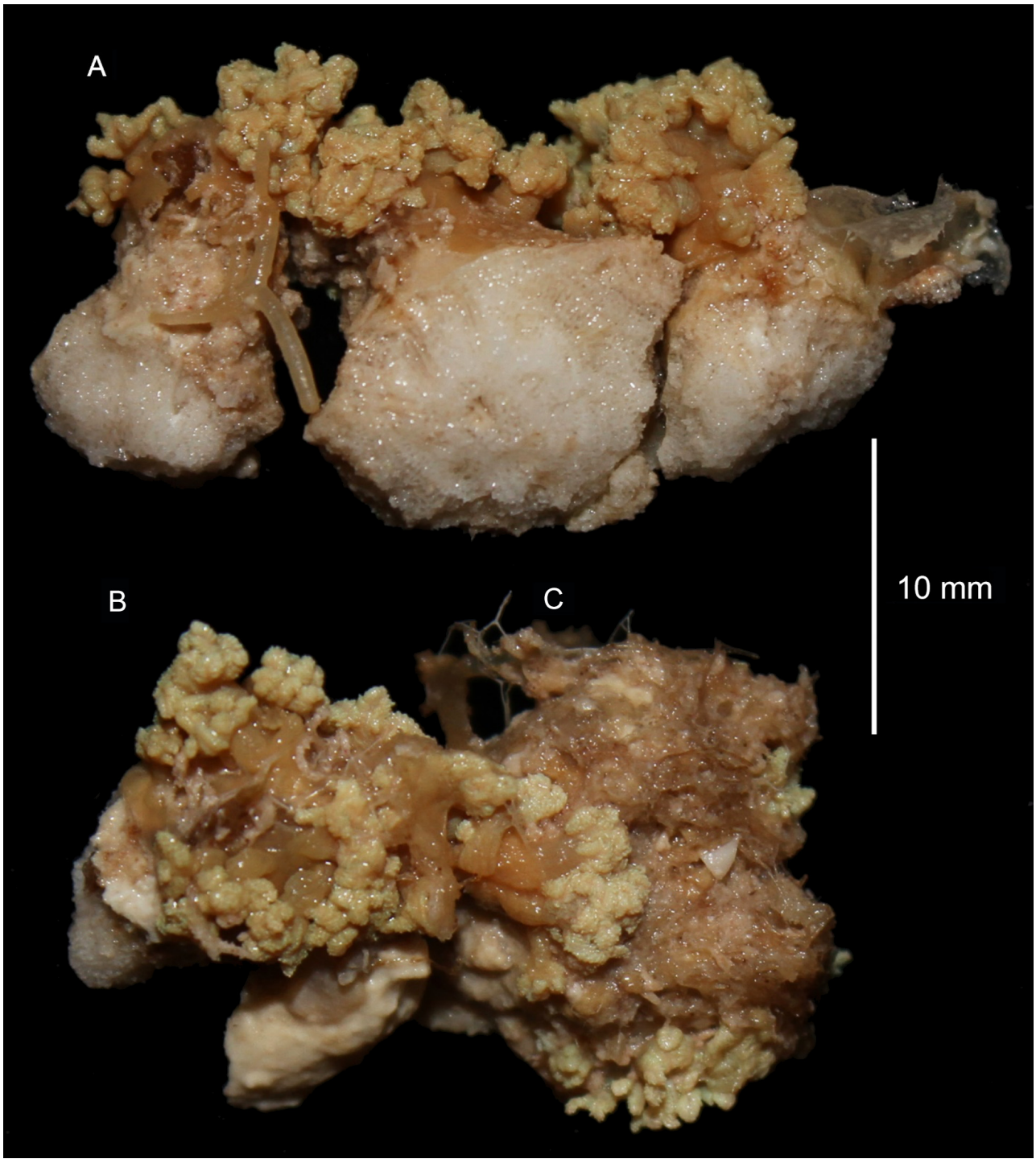

FIGURE 11. *Latissimia ningalooensis* **gen. nov. sp. nov.**: (A) Holotype (QM G330711) top and side view showing expanded polyps emerging from the encrusting spreading membrane. (B, C) Paratype colonies (QM G339754, and QM G339755).

Remarks. The paratypes of *L. ningalooensis* **sp. nov.** differ from the holotype by their size. This species is distinguished from *L. opalia* **sp. nov.** by its smaller polyps and sclerites, whose granular surface microstructure features a labyrinthic appearance. In addition, the species has fewer pinnules on the tentacles compared to its congener (18–22 *vs*. 24–30 pinnules). The ethanol-preserved holotype and paratypes of *L. ningalooensis* were sequenced and subsequently assigned to MOTU8 (McFadden *et al.* 2019), unlike *L. opalia* which was assigned to MOTU72. The mean genetic distance (uncorrected p) between the two species was 0.2% at *mtMutS* and *COI*, and 1.1% at *28S rDNA*.

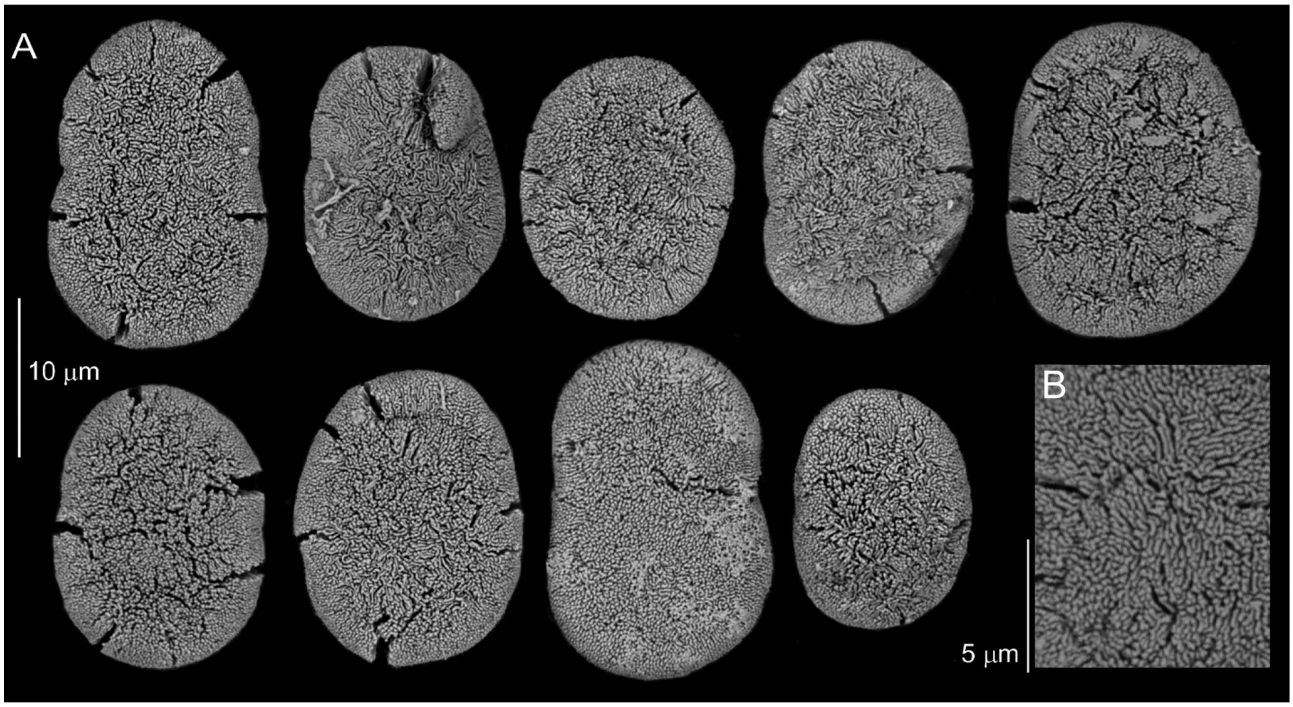

FIGURE 12. Scanning electron micrographs of sclerites of *Latissimia ningalooensis* **gen. nov. sp. nov.** Holotype (QM G330711): (A) Ellipsoid platelets. (B) Tips of calcite rods provide a uniform granular appearance to the sclerite surface.

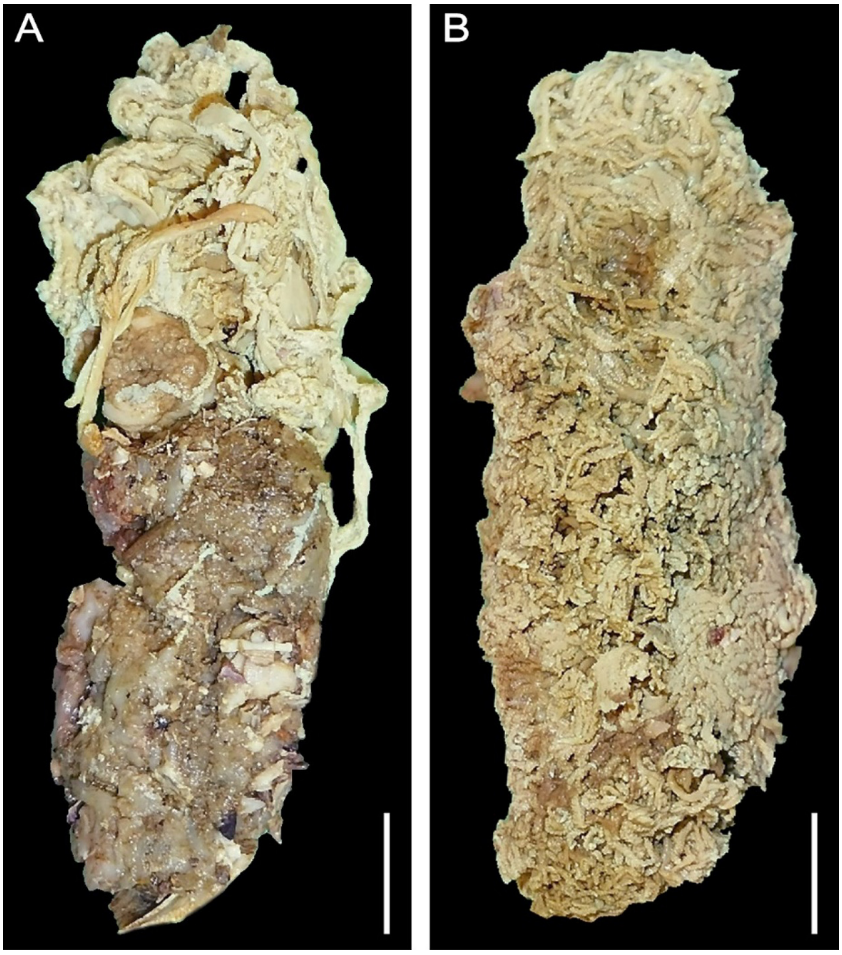

FIGURE 13. Colonies of *Latissimia ningalooensis* **gen. nov. sp. nov.**, invasive to Brazil, featuring a spreading membrane and non-retractile polyps: (A) SMNHTAU_Co_38205. (B) SMNHTAU_Co_38206.

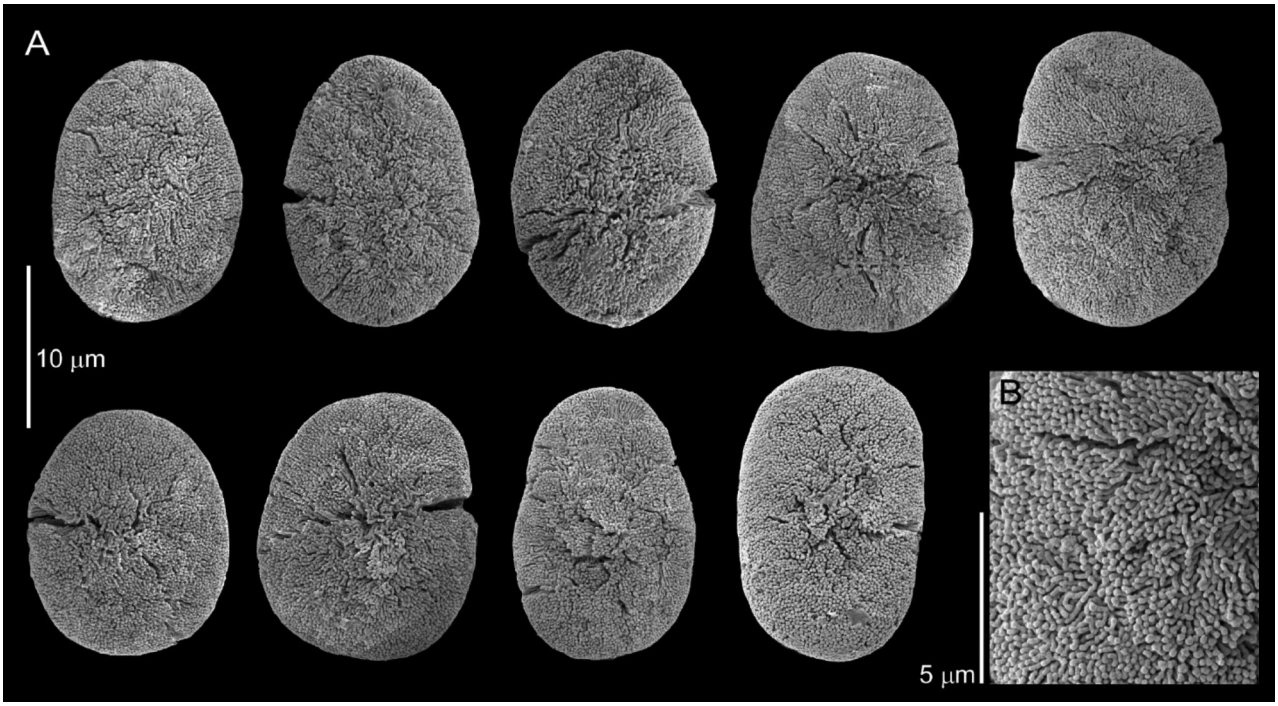

FIGURE 14. Scanning electron micrographs of sclerites of *Latissimia ningalooensis* **gen. nov. sp. nov.** invasive to Brazil (SMNHTAU_Co_38205): (A) Ellipsoid platelets with hexagonal outline. (B) Tips of calcite rods provide a granular appearance to the sclerite surface, organized in patches with space in between.

The examined colonies of the xeniid that is invasive in Brazil (SMNHTAU_Co_38205 and SMNHTAU_Co_38206) are encrusting, featuring a spreading membrane and non-retractile polyps (Fig. 13). The polyps feature two rows of 35–50 pinnules on either side of the tentacle, a higher number compared to the two rows of only 18–22 pinnules in the holotype. Their sclerites are ellipsoids, measuring 0.011–0.013 x 0.016–0.018 mm, and some have a median narrow waist (Fig. 14A). The sclerites are composed of calcite rods whose tips provide a granular appearance to the sclerite surface (Fig. 14B). The sclerites often tend to fracture during the dehydration necessary for SEM purposes. These two samples were sequenced and subsequently assigned to MOTU8, and therefore it is concluded that this invasive xeniid should be assigned to *L. ningalooensis* **sp. nov.** The morphological differences in pinnule number between the Brazilian and the West Australian material (see above) do not justify establishing a separate species and further indicate the problematic nature of pinnule count for species delineation among xeniid soft corals. In addition, the length of the polyp body varies greatly among the colonies of *L. ningalooensis* **sp. nov.** found in Brazil, from 3.5 mm to 3.75 cm (Mantellato *et al.* 2018), perhaps as a result of differing degrees of contraction.

Living features. The live colonies of *L. ningalooensis* from western Australia are light brown with a blue tinge that varies in strength (Figs. 15A, B). The colonies invasive to Brazil are encrusting (Figs. 15C, D) and exhibit a similar coloration, but their symbiotic algae may significantly mask the blue tinge. The colonies can extensively cover the hard substrate while displaying a mixed blue-brown coloration.

Distribution. North-western Australia, Northern Territory (Darwin), Brazil (introduced) (Fig. 1).

Quattuoria Benayahu & McFadden, gen. nov.

http://zoobank/urn:lsid:zoobank.org:act:122B9756-61C9-495E-A878-15F242F816B5

Diagnosis. Xeniidae with polyps arising directly from a spreading basal membrane. Polyps monomorphic and non-retractile. The numerous pinnules are scattered randomly on the oral surface of the tentacles and no distinct pinnule-rows can be recognized. Sclerites are ellipsoid platelets with a dendritic surface microstructure, abundant in the colony. Zooxanthellate. Type species: *Quattuoria pallida* **sp. nov.** by original designation and monotypy.

Etymology. The generic name *Quattuoria* (Gender: feminine) is derived from the Latin *quattuor,* referring to four. Here, it denotes the type locality of this genus, Les Quatre Frères (The Four Brothers), Madagascar.

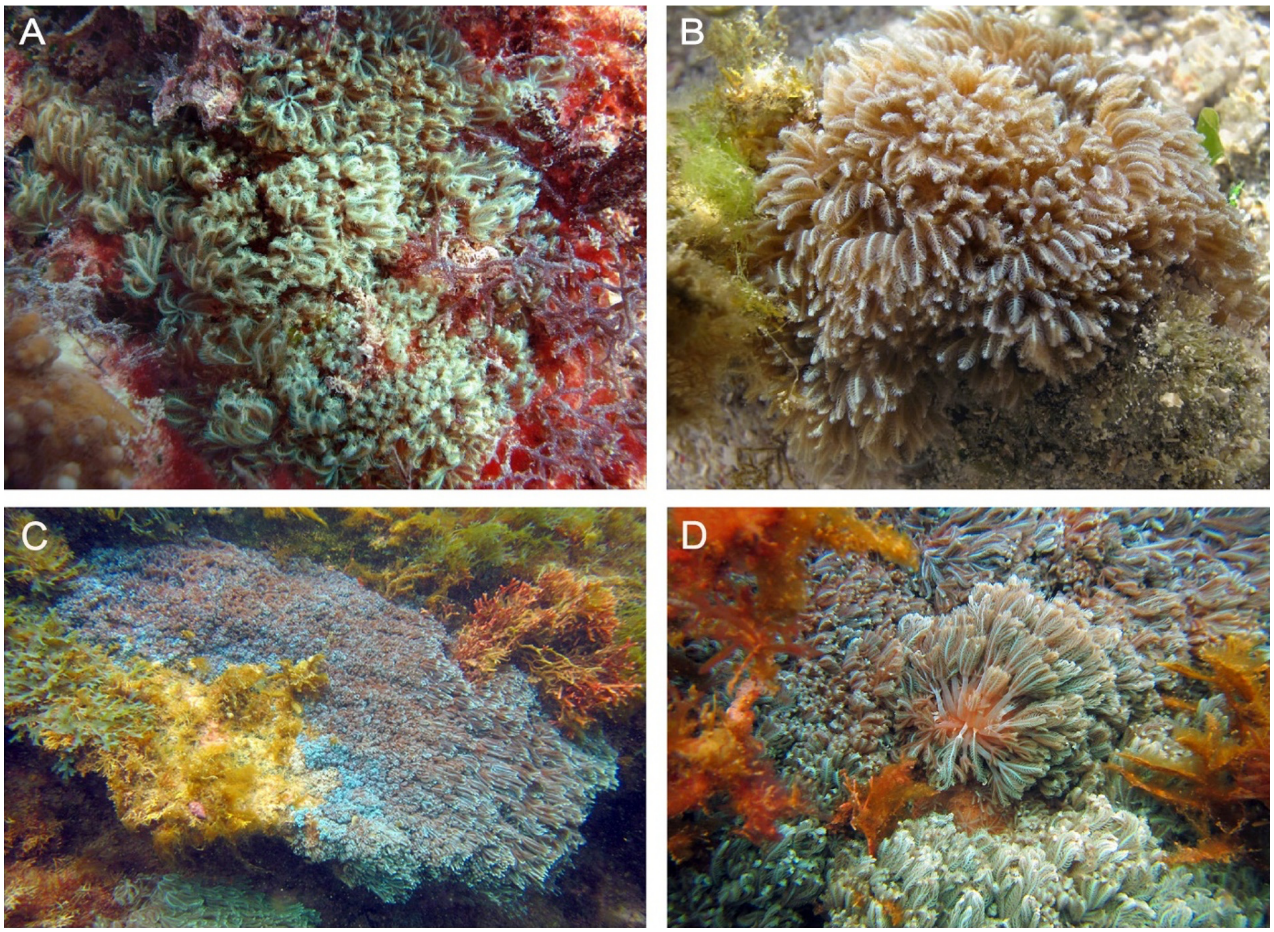

FIGURE 15. Live colonies of *Latissimia ningalooensis* **gen. nov. sp. nov.**: (A–B) Colonies from western Australia exhibiting mixed blue-brown coloration. (C–D) Encrusting colonies invasive to Brazil with their expanded polyps displaying mixed blue-brown color. Photos C–D courtesy of Joel C. Creed (Universidade do Estado do Rio de Janeiro).

Quattuoria pallida Benayahu & McFadden gen. nov. sp. nov.

Figures 1, 16–17

http://zoobank/urn:lsid:zoobank.org:act:434D2C4A-B44C-4B17-9B7A-60778ECEB808

Material examined. Madagascar**. Holotype**. SMNHTAU_Co_36071 (MAD95), 4 Frére (12.994250° S, 48.487467° E), 4–15 m, 1 December 2012, coll. Y. Benayahu.

Description. The holotype is an encrusting colony featuring a thin, irregular spreading membrane (< 1 mm) growing on dead coral skeleton and measuring approximately 10 x 18 mm (Fig. 16A). Some smaller detached fragments of a few polyps each are also included in the holotype. All polyps are fully expanded (Fig. 16B): the polyp body is 4–5 mm long and the tentacles up to 3–4 mm. When the tentacles are viewed from the aboral side 18–25 pinnules can be counted on either margin of the tentacle, with almost no space between adjacent ones. When viewed from the oral side, numerous densely placed pinnules occupy almost the entire oral side of the tentacle, notably not arranged in rows.

The sclerites are spheroid or ellipsoid platelets (Fig. 17A) measuring 0.012–0.018 x 0.015–0.020 mm in diameter, abundant throughout the colony. A few sclerites feature surface irregularity. They are composed of calcite rods whose tips provide a granular appearance to the sclerite surface (Fig. 17B). The sclerites often tend to fracture during the dehydration necessary for SEM.

Color. The ethanol-preserved holotype is light cream, almost white.

Etymology. The species name is derived from the Latin *pallida,* referring to the pale color of the holotype.

Remarks. *Q. pallida* is characterized by its pinnule arrangement which lacks the organization in rows that is typical of other xeniid taxa. The ethanol-preserved holotype was sequenced and subsequently assigned to MOTU71. Unfortunately, no image of a live colony is available.

Distribution. Madagascar (Fig. 1).

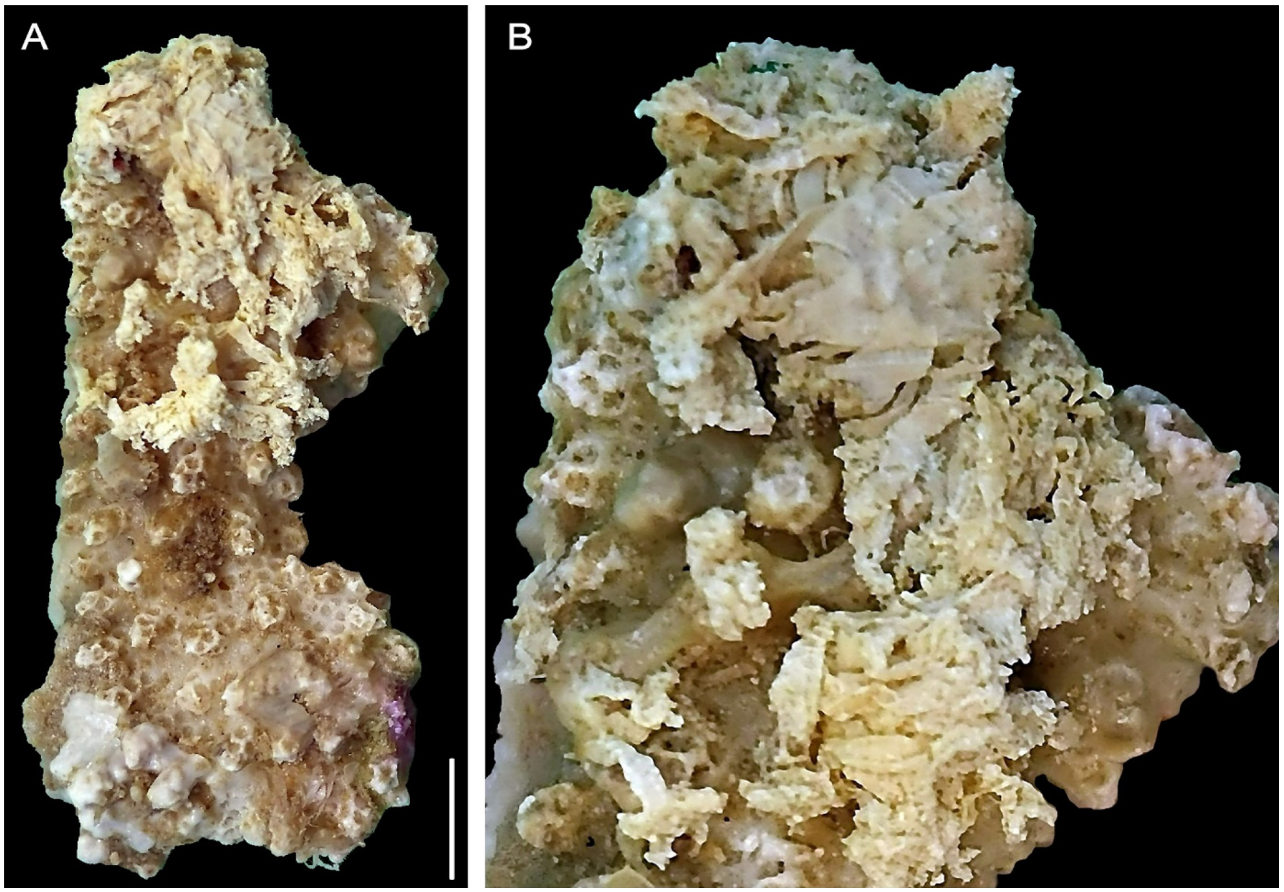

FIGURE 16. *Quattuoria pallida* **gen. nov. sp. nov.** Holotype (SMNHTAU_Co_36071): (A) Encrusting colony attached to a calcareous fragment. (B) Magnified portion of holotype showing expanded polyps.

Molecular results

Both maximum likelihood and Bayesian analyses recovered identical tree topologies in which *Sansibia*, *Latissimia* **gen. nov.** and *Quattuoria* **gen. nov.** all belonged to a well-supported clade that also included the xeniid genera *Sarcothelia*, *Ezziona* Alderslade & Janes, 2017, *Unomia* Benayahu, Ofwegen, Allais & McFadden, 2021, and *Yamazatum* Benayahu 2010 (Fig. 18). *Sansibia flava* and *S. claereboudti* **sp. nov.** formed a clade that was well separated from and sister to the remaining genera. *Quattuoria pallida* **gen. nov.**, **sp. nov.** was sister to *Sarcothelia*, from which it differed by genetic distance values (uncorrected p) ranging from 0.4% at *COI* to 1.3% at *mtMutS* and 1.9–2.0% at *28S rDNA*. The two *Latissimia* species grouped together in a well-supported clade that was sister to [*Sarcothelia* + *Unomia* + *Quattuoria* **gen. nov.**]. Two additional specimens previously identified as *Sansibia* sp. also belonged to the *Latissimia* clade. At the 0.3% average genetic distance threshold, each species (*S. flava*, *S. claereboudti* **sp. nov.**, *Q. pallida* **sp. nov.**, *L. opalia* **sp. nov.** and *L. ningalooensis* **sp. nov.**) was assigned to a different MOTU, with all individuals of each species belonging to the same MOTU. Within *Latissimia* **gen. nov.**, specimens CASIZ 184572 from Sulawesi (McFadden *et al.* 2014a) and SMNHTAU_Co_30386 from Kenya each belonged to unique MOTUs separate from *L. opalia* **sp. nov.** and *L. ningalooensis* **sp. nov.**, suggesting that they represent additional undescribed species of that genus.

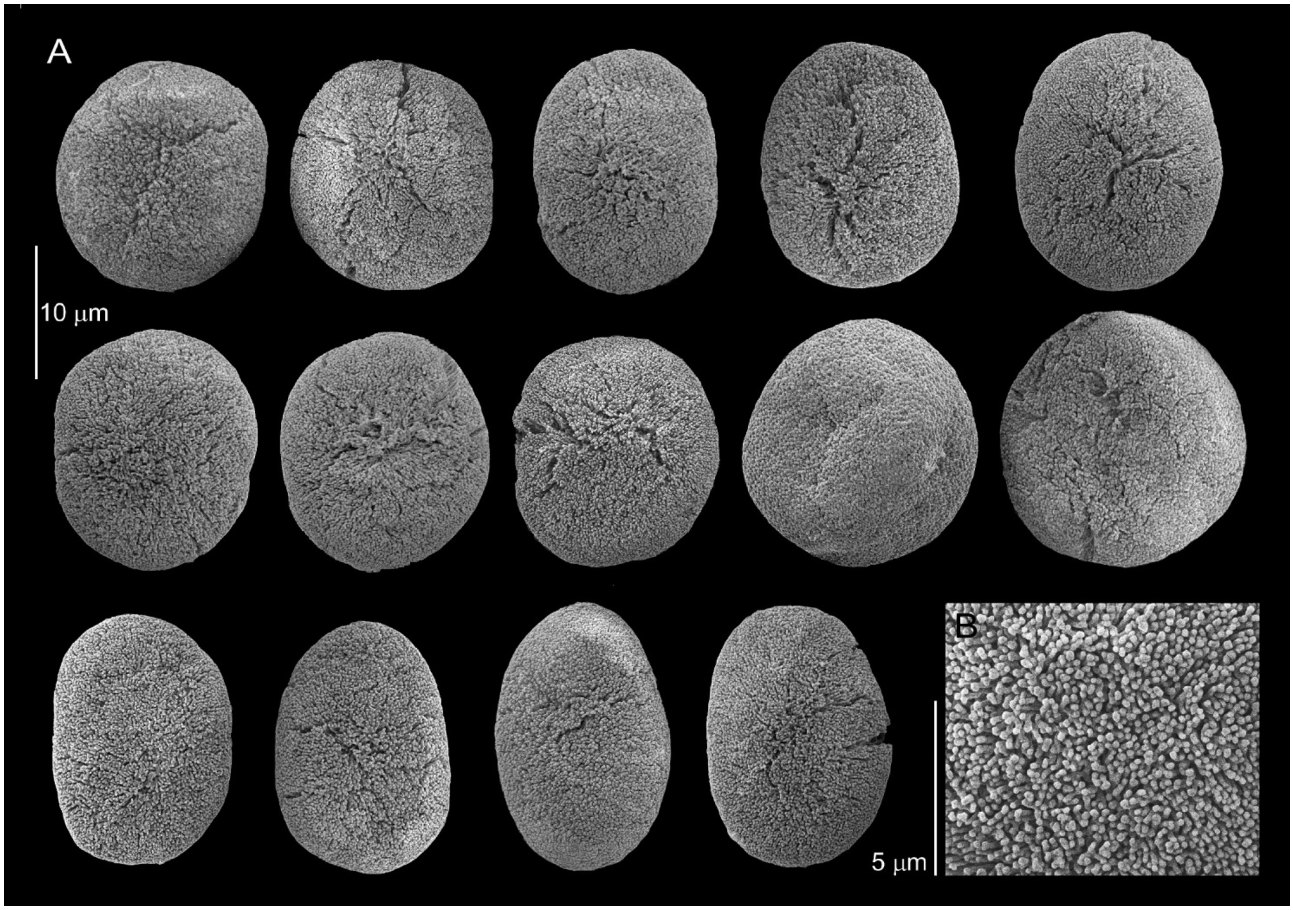

FIGURE 17. Scanning electron micrographs of sclerites of *Quattuoria pallida* **gen. nov. sp. nov.** Holotype (SMNHTAU_Co_36071): (A) Ellipsoid platelets, a few with surface irregularity. (B) Tips of calcite rods provide a uniform grainy appearance to the sclerite surface.

Discussion

Members of the soft-coral family Xeniidae exhibit several distinct colony morphologies (Fabricius & Alderslade 2001). They include capitate genera (e.g. *Heteroxenia* Kölliker, 1874; *Ovabunda* Alderslade, 2001; *Unomia* and *Xenia* Lamarck, 1816); branched (e.g., *Caementabunda* Benayahu *et al.*, 2018 and C*onglomeratusclera* Benayahu *et al.*, 2018) and encrusting ones (*Anthelia* Lamarck, 1816*; Sarcothelia* Verrill, 1928; *Sansibia*; *Ingotia* Alderslade 2001; *Ezziona* Alderslade & Janes, 2017; *Orangaslia* Alderslade, 2001 and *Sympodium* Ehrenberg, 1834). The current study assigns an additional two new encrusting genera to this family: *Latissimia* **gen. nov.** and *Quattuoria* **gen. nov.**, thus further indicating the high genus-level diversity of this morphology, currently totaling nine genera. Among these encrusting forms, the two newly described genera are most similar both morphologically and genetically to *Sarcothelia*. *Sarcothelia* is a monotypic genus, with *S. edmondsoni* Verrill, 1928 the only known species. It has not been revised since Verrill's original description which contends that it lacks sclerites (see also Alderslade 2000). Hawaii is the type locality of this species, where it is considered to be the only xeniid ever recorded there. For the purpose of the current study, two colonies from Hawaii corresponding to *S. edmondsoni* were examined (SMNHTAU_Co_38211, Oahu, Lanikai Beach, 6 feet, 14 August 2008 and SMNHTAU_Co_38212, Oahu, Shark's Cove, 20 feet, 23 August 2008, for both coll. S. Kahng). Both colonies feature numerous ellipsoid or spheroid platelets in their tissues (Fig. 19: SMNHTAU_Co_38211). Consequently, the confusion concerning the morphological characters of this encrusting xeniid should be clarified by future examination of the original type material of *S. edmondsoni*.

Anthelia Lamarck, 1816 was the first encrusting xeniid genus ever described. Its sclerites are short flattened rods (Fabricius & Alderslade 2001), and their shape stands in contrast to the eight other encrusting xeniid genera listed

above which share sclerites that are ellipsoid or spheroid platelets. These are the only recognized type of sclerites in some of the genera (*Sansibia*: Fig. 3; *Sarcothelia*: Fig. 19; *Sympodium*: Benayahu *et al.* 2021: Fig. 5; *Latissimia* **gen. nov.**: Figs. 9, 12. and *Quattuoria* **gen. nov.**: Fig. 17), whereas in other genera they are part of a more diverse suite of sclerites (*Ingotia*, *Ezziona* and *Orangaslia*: Alderslade 2001). The same types of ellipsoid or spheroid platelets exist in the capitate xeniid genera (*Heteroxenia*: Reinicke 1997, *Xenia*: Halász *et al.* 2019, and *Unomia*: Benayahu *et al.* 2021). Clearly, sclerite microstructure alone cannot be considered as an ultimate diagnostic character for genus- or species-level identification, either among encrusting xeniids or among some other members of the family. Consequently, a thorough genus and species level validation of the xeniid taxa, in particular of those established centuries or decades ago, needs to be substantiated by an examination of original type material when available.

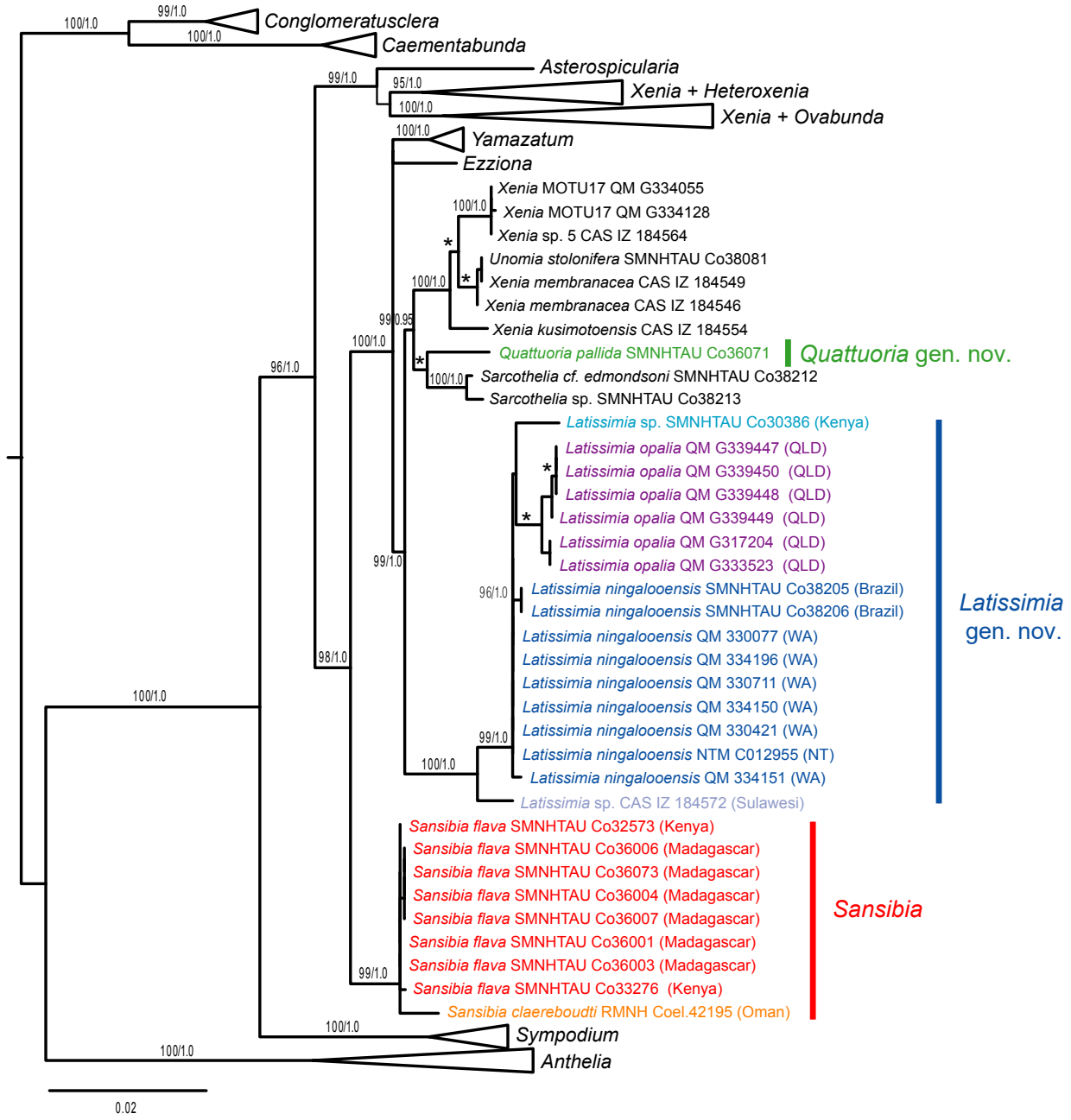

FIGURE 18. Maximum likelihood reconstruction of Xeniidae based on concatenated *mtMutS*, *COI* and *28S rDNA* (total = 1981 bp). To facilitate readability, clades without focal genera have been collapsed to triangles and outgroup taxa are not shown. Numbers on branches: ML bootstrap percentages (10,000 ultrafast bootstraps) / Bayesian posterior probabilities (pp). Asterisk indicates bootstrap = 100%, pp > 0.98.

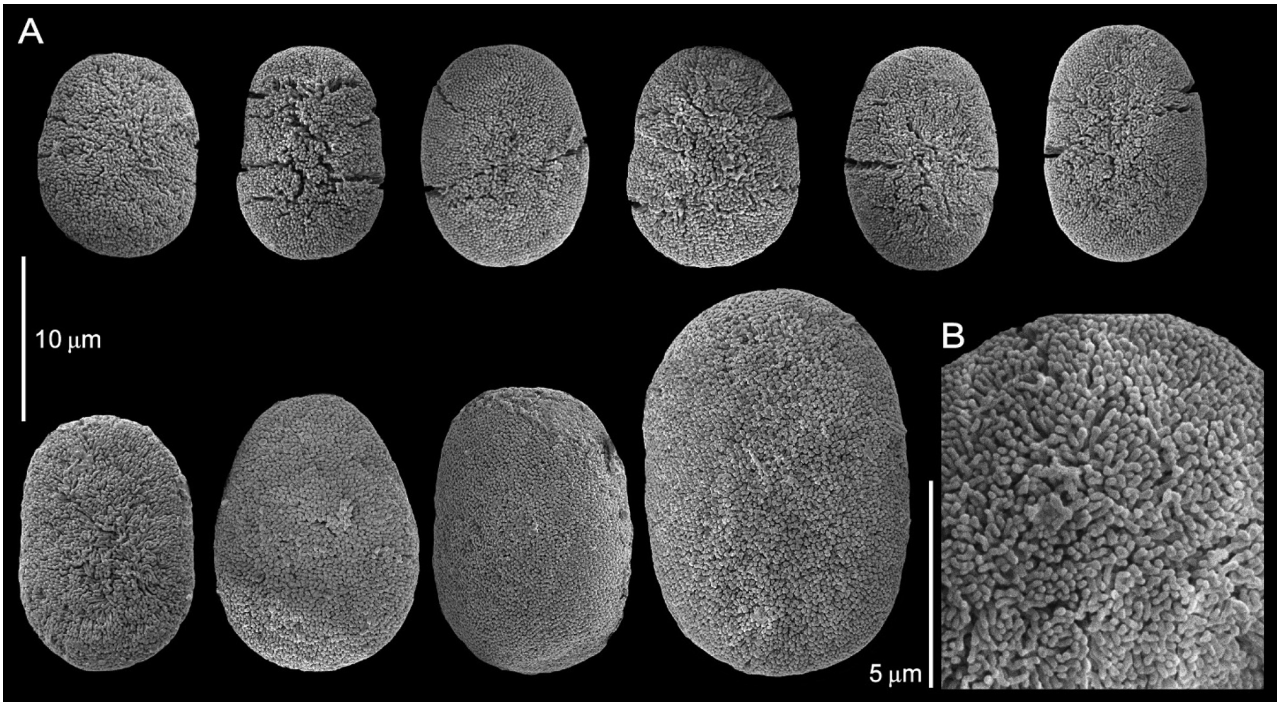

FIGURE 19. Scanning electron micrographs of sclerites of *Sarcothelia edmondsoni* Verrill, 1928. (SMNHTAU_Co_38211): (A) Ellipsoid platelets. (B) Tips of calcite rods provide a uniform grainy appearance to the sclerite surface.

Similar to the recent study on *Sympodium* (Benayahu *et al.* 2021), the initial taxonomic examination of the material in the current study erroneously assigned several samples to the wrong genera, with some specimens remaining unidentified. A subsequent taxonomic identification was facilitated by a molecular analysis of the material, which demonstrated some distinct MOTUs, each mostly confined to a particular Indo-Pacific location (McFadden *et al.* 2019). The genetic analyses also contributed to the correct taxonomic assignment of the material in congruence with the morphological characters required for species delineation and determination of their non-overlapping geographic distributions in different marine realms (Fig. 1). The current study has confirmed several already recognized MOTUs as distinct species as well as yielding new ones, in total corresponding to five encrusting xeniid species belonging to three genera. In addition to the taxonomic descriptions, phylogenetic analyses of existing sequence data suggest that one additional species of *Latissimia* occurs in Kenya (SMNHTAU_ Co_30386, MOTU70), and another in Lembeh (Sulawesi, Indonesia) (CAS 184572, MOTU42). Neither of these specimens could be obtained for taxonomic examination at the present time. The identity of the species released from the aquarium trade and invasive in Rio de Janeiro, Brazil (Mantellato *et al.* 2018) is updated by us from *Sansibia* sp. to *Latissimia ningalooensis* **gen. nov.**, **sp. nov.**; it is the second xeniid invasive to the Atlantic following *U. stolonifera* (see Benayahu *et al.* 2021). This result further emphasizes the potential of certain soft corals, in particular members of the family Xeniidae, to spread beyond their indigenous region. Moreover, the current study highlights the need to review the biogeographic distribution and species diversity of zooxanthellate octocorals throughout the entire Indo-Pacific region.

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