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Phylogenomics-guided revision of the genus *Rhytisma* Alderslade, 2000 (Octocorallia: Malacalcyonacea: Lemnaliidae), with descriptions of six new species

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ABSTRACT

The genus *Rhytisma* Alderslade, 2000 (Octocorallia: Malacalcyonacea: Lemnaliidae), formerly comprising four nominal species (*R. fulvum*, *R. fuscum*, *R. monticulum* and *R. rubiginosum*), is revised using an integrative approach. We combine morphological and phylogenomic data for newly collected and historical specimens. A neotype is designated for *R. fulvum* and a lectotype for *R. fuscum* to stabilise the application of these names. Six new species are described from the Indo-Pacific: *R. acoronatum* sp. nov., *R. calyaceum* sp. nov., *R. oblongum* sp. nov., *R. inaequale* sp. nov., *R. karibu* sp. nov. and *R. sperkolae* sp. nov. Species delimitation is supported by discrete combinations of morphological characters – particularly those of the tentacle and polyp sclerites – as well as multi-locus DNA barcoding and phylogenomic analyses of conserved elements (UCE and exon loci). Our findings highlight the diagnostic value of tentacle sclerites and reveal extensive species-level diversity that was previously obscured by insufficient morphological examination. The revised genus currently comprises 10 valid species, many of which display restricted geographic distributions, reflecting patterns of regional endemism in Indo-Pacific octocoral assemblages. These results underscore the importance of integrative taxonomy in uncovering hidden biodiversity.

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Introduction

Soft corals (Octocorallia: Malacalcyonacea) are abundant and often ecologically dominant sessile foundation species on shallow-water coral reefs across the Indo-Pacific and, in some regions, also in upper mesophotic habitats (e.g. Fabricius and Alderslade 2001; Benayahu *et al.* 2019). As climate change and other anthropogenic influences on the environment alter the species composition of coral reefs, the prevalence of octocoral-dominated reef communities is increasing (Lasker *et al.* 2020; Reverter *et al.* 2022; Lalas *et al.* 2024). Understanding the causes and consequences of these ecological shifts requires knowing which species are increasing or decreasing in abundance and which are shifting their geographic ranges, information that is lacking for the majority of shallow-water, zooxanthellate soft corals (McFadden *et al.* 2025). Many species of soft corals remain undescribed (Fabricius and Alderslade 2001), and the use of molecular evidence to interrogate species boundaries has revealed that some nominal species previously believed to have widespread geographic distributions are in fact cryptic species complexes of range-restricted endemics (van Ofwegen *et al.* 2013, 2016; McFadden *et al.* 2019, 2025). As a result of this taxonomic uncertainty and a lack of understanding of the morphological characters that reliably distinguish taxa (e.g. McFadden *et al.* 2017), discrimination and identification of even the most common soft coral species remain daunting challenges (Fabricius and Alderslade 2001).

Rhytisma Alderslade, 2000, is a geographically widespread, yet relatively uncommon genus of zooxanthellate soft coral with an encrusting growth form that can dominate hard reef substrate following ecological disturbances such as coral bleaching (Stobart *et al.* 2005). The genus includes four nominal species but the only one that is known in any detail is *Rhytisma fulvum* (Forskål, 1775). *Rhytisma fulvum* was described from the Red Sea where it occurs not only on shallow reefs but also at mesophotic depths (Liberman *et al.* 2018, 2022). It is commonly found growing on artificial as well as natural reef substrates (Benayahu and Loya 1977; Shoham and Benayahu 2017), and also thrives on reefs that have been degraded by anthropogenic influences (Tilot *et al.* 2008). The reproductive biology of *R. fulvum* has been well studied in the Red Sea; it was the first octocoral shown to exhibit surface brooding (Benayahu and Loya 1983) – a rare reproductive strategy among octocorals – and documentation of differences in reproductive success between shallow and mesophotic populations have suggested constraints on its ability to thrive at deeper depths (Liberman *et al.* 2018).

Although the genus *Rhytisma* includes three other species (two described from the southwestern Indian Ocean and one from the Great Barrier Reef), they have rarely been reported since their original description. By contrast, many recent studies have identified *R. fulvum* from locations throughout the Indo-Pacific (Benayahu 2002, 2013; Benayahu *et al.* 2003, 2004; Benayahu and van Ofwegen 2012; Schleyer *et al.* 2016, 2019; Schleyer and Benayahu 2018). Recent work documenting the geographic distribution of soft coral genotypes (i.e. DNA barcodes) across the Indo-Pacific has, however, suggested that *Rhytisma* comprises as many as 10 distinct operational taxonomic units (OTUs) (McFadden *et al.* 2025). The genus therefore requires taxonomic revision to determine if these OTUs represent distinct species, their correspondence to nominal species, and to identify morphological characters that can be used to discriminate them reliably.

The genus *Rhytisma* Alderslade, 2000 was established in response to taxonomic consequences of Groot and Weinberg's (1982) revision of *Parerythropodium* Kükenthal, 1916, which they treated as a subjective synonym of *Alcyonium* Linnaeus, 1758. *Parerythropodium* had originally been proposed by Kükenthal (1916) for species with membranous colony forms and retractile polyps, most of which possess small, radiate sclerites such as capstans and clubs. However, one species – *Litophyton fulvum* Forskål, 1775 – differed markedly, with much larger spindle sclerites forming a lattice-like surface network and distinctive granular scales in the tentacles. Groot and Weinberg's study of a large number of colonies of *Parerythropodium coralloides* (Pallas, 1766), the type species of *Parerythropodium*, led them to transfer it to *Alcyonium*, effectively invalidating *Parerythropodium* as a distinct genus as then defined. This left species such as *P. fulvum*, which was clearly distinct from both *Alcyonium* and other *Parerythropodium* species, without a suitable generic placement. Alderslade (2000) argued that the inclusion of morphologically divergent species like *P. fulvum* in *Alcyonium* would further expand an already taxonomically unstable and polyphyletic group. To resolve this, he erected *Rhytisma* to accommodate *P. fulvum* and morphologically similar taxa, based on their distinctive sclerite architecture, colony morphology, and polyp structure. However, Alderslade (2000) did not examine the type material or provide a species-level diagnosis for *R. fulvum* or for any other congener.

Compounding this issue, the taxonomic history of *R. fulvum* is complex. The species was originally described as *Litophyton fulvum* by Forskål (1775) – one of the first soft corals reported from the Red Sea – and subsequently transferred to *Sympodium* by Ehrenberg (1834), to *Alcyonium* by Kükenthal (1904), to *Parerythropodium* by Kükenthal (1916), back to *Alcyonium* again by Verseveldt (1965), and to *Parerythropodium fulvum fulvum* by Verseveldt (1969). Currently, four species are recognised within *Rhytisma*: *R. fulvum* (Forskål, 1775), *R. fuscum* (Thomson & Henderson, 1906), *R. rubiginosum* (Verseveldt, 1968) and *R. monticulum* (Verseveldt, 1982). The holotype of *L. fulvum* is considered lost (Verseveldt, 1969), and the types of the other species have not been re-examined since their original descriptions. As a result, morphological characters have remained poorly defined and inconsistently applied, contributing to persistent misidentifications. Numerous Indo-Pacific specimens have been assigned to *R. fulvum*, potentially concealing the true species-level diversity within the genus.

This study presents a comprehensive revision of the genus *Rhytisma*, based on integrative taxonomic methods. We re-examined type material of *Sympodium fuscum* Thomson & Henderson, 1906, *Parerythropodium rubiginosum* Verseveldt, 1968, and *Alcyonium monticulum* Verseveldt, 1982, along with additional material collected from across the Indo-Pacific. A neotype is designated for *R. fulvum* to stabilise its taxonomic identity, and a lectotype is designated for *R. fuscum*. Molecular analyses, including single-locus DNA barcoding (*mtMutS* and *28S rDNA*) and multi-locus target enrichment of conserved elements (UCEs and exons), were used to delineate species. Based on both morphological and molecular evidence, six new *Rhytisma* species are described, and the diagnosis of the genus is updated to reflect newly recognised interspecific variation. This revision highlights the critical diagnostic value of tentacle sclerite morphology and reveals previously unrecognised patterns of regional endemism within *Rhytisma*.

Material and methods

The study examined previously designated *Rhytisma* type specimens and other relevant material collected from a variety of Indo-Pacific coral reefs and preserved in >70% ethanol (Fig. 1, Supplementary Table S1). Photographs of live colonies taken *in situ* were available for some of the material collected since 2001. The material was provided by

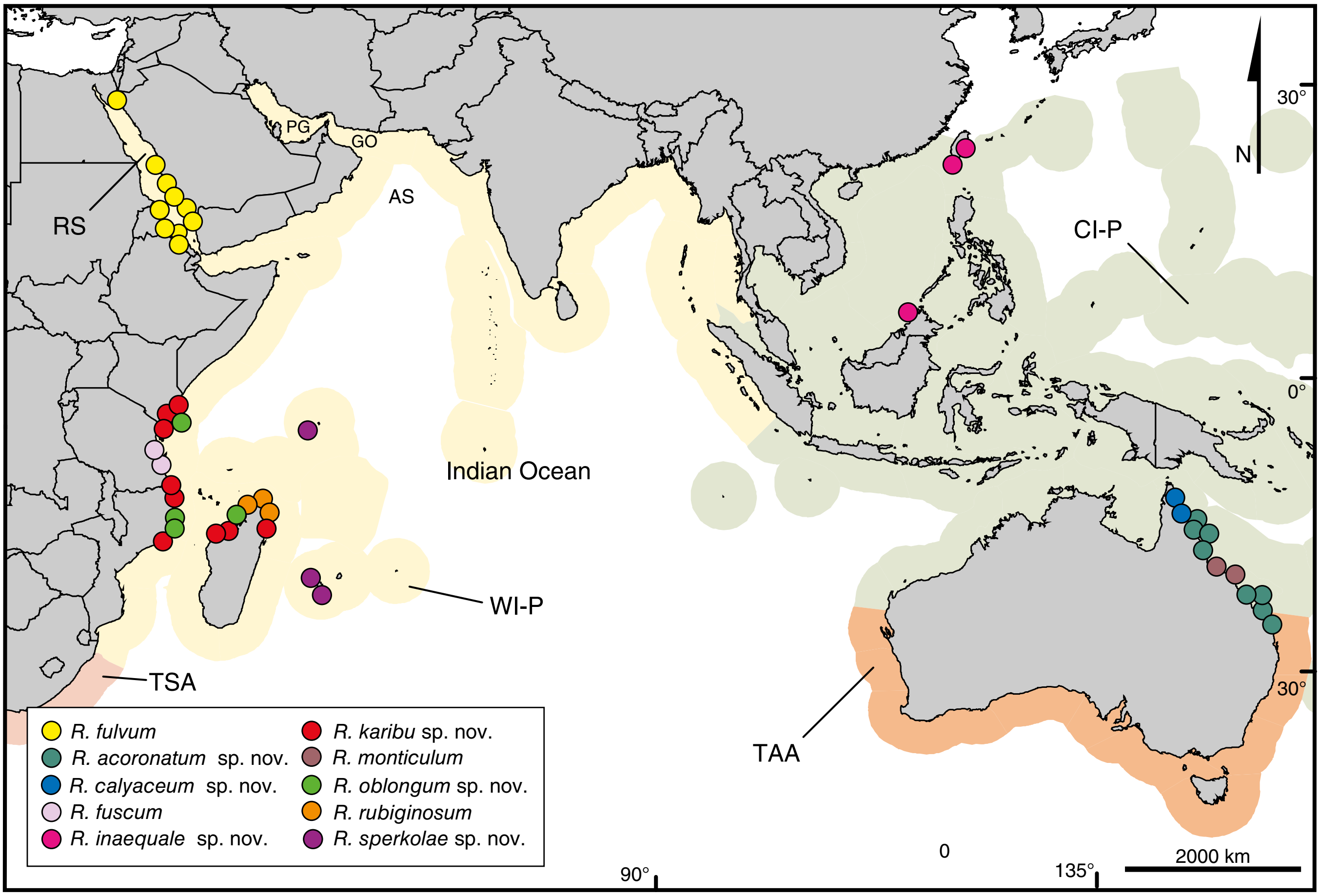

Fig. 1. Distribution of *Rhytisma* species reported and examined in this study. Distances between points are not to scale, and the number of points does not correspond to the number of samples. Background colour shades indicate marine realms as defined by Spalding *et al.* (2007). TSA, Temperate Southern Africa; WI-P, Western Indo-Pacific; CI-P, Central Indo-Pacific; TAA, Temperate Australasia; AS, Arabian Sea; PG, Persian Gulf; GO, Gulf of Oman; RS, Red Sea.

the Steinhardt Museum of Natural History at Tel Aviv University (SMNHTAU); the British Natural History Museum, London (BMNH); the Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie, Leiden, RMNH); the Queensland Museum (QM); the California Academy of Sciences (CAS); the Smithsonian National Museum of Natural History (USNM) and the Florida Museum of Natural History (UF).

Morphological studies

Colony morphology, including overall shape and colour, was examined to assist in distinguishing growth forms among species. For sclerite analysis, tissues were dissolved in 10% sodium hypochlorite and then repeatedly rinsed in distilled water to obtain clean sclerites. The arrangement of sclerites and their position within the polyp and in the mat were recorded separately under a light microscope by observing a few polyps and mat fragments as the tissue gradually dissolved in diluted sodium hypochlorite.

Scanning electron microscope (SEM) mounts were prepared, coated with Pd/Au, Pt/Pd or Au and examined mainly using a JEOL JSM-IT510 at Naturalis Biodiversity Center, or a JEOL JCM-6000 NeoScope at Tel Aviv University operated at 10 kV, and a Hitachi TM-1000 operated at 2 kV at Queensland Museum. SEM images were used to prepare plates illustrating the shape, surface tuberculation, other fine features, and the dimensions of the different sclerites in relation to their location in the tentacles, polyp body and mat. Because *Rhytisma* has sclerites with considerable variation in size and shape, the SEM plates were arranged so that species can be compared visually side by side. The lettering on the plates refers to sclerites from different parts of the polyp or colony; for example, (a) indicates tentacle platelets, (b) elongated platelets, and so on. The scale for each sclerite category is kept similar across species, except for the mat spindles in one species, which are markedly larger than in the others. Smaller sclerites are shown at higher magnification than larger ones to reveal surface details; consequently, several scale bars are provided on each plate. Separation of species based on light microscopy alone is not possible, as the fine details of the sclerites, particularly the tentacle platelets, cannot be seen satisfactorily, although it is sufficient for initial sorting of material.

Molecular phylogenetic and phylogenomic analyses

DNA barcoding

DNA was extracted from ethanol-preserved tissue using a Qiagen DNeasy Blood & Tissue kit following manufacturer's instructions. Two gene regions commonly used for barcoding of octocorals, one mitochondrial (*mtMutS*) and the other nuclear (*28S rDNA*), were amplified by polymerase chain reaction using published primers and protocols (*28S rDNA*: 28S-Far and 28S-Rar, McFadden and van Ofwegen 2012; *mtMutS*: ND4-2625F, McFadden *et al.* 2006, and mut3458R, Sánchez *et al.* 2003). Amplicons were purified by PEG-precipitation (Sánchez *et al.* 2003) prior to Sanger sequencing. Sequences were aligned using *MAFFT* (ver. 7.130b, see https://mafft.cbrc.jp/alignment/software/; Katoh *et al.* 2005), with published sequences from *Lemnalia* and *Paralemnalia* included as outgroups.

Preliminary phylogenetic analyses of *mtMutS* and *28S rDNA* using *PhyML* (ver. 3.0, see http://www.atgc-montpellier.fr/phyml/; Guindon and Gascuel 2003) indicated that the gene trees were congruent, so the two gene regions were combined and further analyses conducted on the concatenated alignment. Optimal models of evolution for each gene (*mtMutS*: HKY + F; *28S rDNA*: TNe + FQ + G4) were found using *ModelFinder* (see http://www.iqtree.org/ModelFinder/; Kalyaanamoorthy *et al.* 2017) and a maximum likelihood tree was constructed using *IQ-TREE* (ver. 2.1.2, see https://github.com/iqtree/iqtree2; Minh *et al.* 2020) with an edge-linked partition model (Chernomor *et al.* 2016) and 10,000 ultrafast bootstraps (Hoang *et al.* 2018). *MrBayes* (ver. 3.2, see https://github.com/NBISweden/MrBayes/; Ronquist *et al.* 2012) was used to infer a phylogeny using Bayesian inference with separate models of evolution applied independently to each gene partition (*mtMutS*: HKY + G; *28S rDNA*: GTR + G). *MrBayes* was run for 3 million generations (until standard deviation of split frequencies <0.01) with a burnin of 25% and default Metropolis coupling parameters.

Species delimitation analyses were run on the concatenated alignment using *mothur* (ver. 1.48, see https://github.com/mothur/mothur/; Schloss *et al.* 2009) and Assemble Species by Automatic Partitioning, *ASAP* (see https://bio.tools/asap-assemble; Puillandre *et al.* 2021). *mothur* separates operational taxonomic units (OTUs) based on application of an average pairwise genetic distance threshold between taxa. We applied thresholds of 0.003 and 0.005 (uncorrected *p*), which have been shown in previous studies of these octocoral barcodes to yield the highest concordance with morphospecies identifications (McFadden *et al.* 2014). *ASAP* applies a hierarchical clustering algorithm to pairwise genetic distances (uncorrected *p*) to identify barcode gaps from which multiple species partitions (i.e. primary species hypotheses) are proposed (Puillandre *et al.* 2021). Partitions are ranked using a scoring system that combines the width of the observed barcode gap with the probability of a cluster representing a species. Based on previous studies of the *mtMutS* and *28S rDNA* barcodes (McFadden *et al.* 2011, 2014) we only considered species partitions whose average genetic distance thresholds were <0.005.

Phylogenomic analyses and SNP-based species delimitation

Phylogenomic analyses were conducted on 24 individuals including two historical specimens (USNM 54020, USNM 54018), both collected from Madagascar in 1963–1964 and identified as *Parerythropodium rubiginosum* by J. Verseveldt. DNA was quantified using a Qubit 2.0 fluorometer and quality-checked using a NanoDrop spectrophotometer. In total, 600–1000 ng of DNA was sent to Arbor Biosystems (Ann Arbor, MI, USA) for library preparation, target enrichment and sequencing. Libraries were prepared using a Kapa Hyper Prep Kit (Kapa Biosystems) with dual-indexed iTru adapters. MYBAITS protocol (ver. 4, Arbor Biosystems) was used to target and enrich pools of eight libraries using the octocoral-v2 bait set of Erickson *et al.* (2021). Enriched libraries were sequenced on one lane of Illumina HiSeq 2500 (150-bp PE reads). The two historical samples were prepared with a Kapa library preparation kit and then target enriched as above, with modifications as in Quattrini *et al.* (2018). Sequencing was conducted on an Illumina NovaSeq 6000 (150-bp PE reads).

Read data were cleaned to remove adaptor sequences and low-quality bases using *illumiprocessor* (B. R. Faircloth, see https://github.com/faircloth-lab/illumiprocessor) and *Trimmomatic* (ver. 0.35, see https://github.com/usadellab/Trimmomatic; Bolger *et al.* 2014), then assembled into contigs using *SPAdes* (ver. 3.1, see https://github.com/ablab/spades; Bankevich *et al.* 2012). *PHYLUCE* (ver. 1.6.8, see https://github.com/faircloth-lab/phyluce; Faircloth 2016) was used to identify loci by matching probes to contigs (*phyluce_assembly_match_contigs_to_probes*) with a minimum coverage of 70% and minimum identity of 70%. Loci were extracted as fastas (*phyluce_assembly_get_fastas_from_match_counts*) and then aligned using *MAFFT* (Katoh and Standley 2013). Aligned loci were edge-trimmed (*phyluce_align_seqcap_align*) and concatenated into a data matrix with 75% of taxa present for each locus (*phyluce_align_get_only_loci_with_min_taxa*). A maximum likelihood tree was constructed using *IQ-TREE* (Minh *et al.* 2020) on a concatenated alignment of 24 individuals and 2 outgroups with ultrafast bootstrapping (-bb 1000, Hoang *et al.* 2018). A partitioned model was used (-p) with the best model of nucleotide substitution as determined with *ModelFinder* (-m MFP + MERGE, Kalyaanamoorthy *et al.* 2017).

To further explore species boundaries among clades, SNPs were obtained using modified scripts (Zarza *et al.*

2016, 2018) as outlined by Erickson *et al.* (2021). Trimmed reads for all samples, excluding the historical specimens from the USNM, were mapped to a reference conserved element (UCEs and exons) locus dataset. The sample with the greatest number of UCE/exon contigs (sample IPZ195) was used as the reference individual. SNPs were then filtered to one SNP per locus for loci ≤1000 bp, or to one per 1000 bp if loci were ≥2000 bp using *vcftools* (ver. 0.1.16, see https://vcftools.github.io/; Danecek *et al.* 2011; –min-alleles 2, –max-alleles 2, –thin 1000 –max-non-ref-af 0.99 –max-missing 1).

A species delimitation discovery approach was conducted to identify putative species boundaries using two different analyses. Discriminant Analysis of Principal Components (DAPC) (Jombart *et al.* 2010) and *STRUCTURE* (ver. 2.3.4, see https://web.stanford.edu/group/pritchardlab/structure.html; Pritchard *et al.* 2000) were used to identify clusters of genetically similar individuals using a SNP dataset (422 SNPs) with no missing data. DAPC was run using the *adegenet* package (ver. 2.1.7, see https://CRAN.R-project.org/package=adegenet; Jombart 2008) in *R* (ver. 3.6.3, R Foundation for Statistical Computing, Vienna, Austria, see https://www.r-project.org/). The optimal number of clusters necessary to minimise the Bayesian Information Criterion (BIC) was found using find.clusters. A best *K* result was displayed as a scatterplot. *STRUCTURE* (Pritchard *et al.* 2000) was run using *StRAuto* (ver. 1.0, see https://github.com/mountainpenguin/StRAuto; Chhatre and Emerson 2017) for 1 million generations with burnin = 10,000. Ten runs were completed at eight *K* groups. Results were then analysed using structureHarvester.py (Earl and von Holdt 2012) to determine the best *K* group using deltaK (Evanno *et al.* 2005), and a *K* indfile was created for *CLUMPP* (ver. 1.1.2, see https://rosenberglab.stanford.edu/clumpp.html) analysis (Jakobsson and Rosenberg 2007). *Distruct* (ver. 1.1, see https://github.com/KIT-MBS/distruct; (Rosenberg 2004) was used to visualise the best *K*. Based on the *STRUCTURE* results, a SNP subset (518 SNPs, no missing data) was created for a clade including populations from Taiwan, the Great Barrier Reef, and SW Indian Ocean. *STRUCTURE* analysis was conducted with 1 million generations (10,000 burnin), four *K* groups, and 10 iterations across each *K*.

Results

DNA barcoding

Sequences for both *mtMutS* (726 bp) and *28S rDNA* (776 bp) were obtained for 60 specimens of *Rhytisma*; only *mtMutS* was obtained for another 10 specimens and only *28S rDNA* for three specimens (Supplementary Table S1). All of the specimens for which *mtMutS* was obtained were included in the final concatenated alignment (1502 bp), with *28S rDNA* coded as missing data for the 10 specimens for which it was not obtained. Maximum likelihood and Bayesian phylogenies had identical topologies, with only some differences in levels of support for some clades (Fig. 2). Two major clades were observed with a deep genetic divergence between them. One of these clades comprised two distinct subclades, one (clade 7) with 10 specimens from eastern Australia (Lizard Is., Heron Is., and the Coral Sea Islands Territory) and the other (clade 6) consisting of a single specimen from Madagascar. Two of the specimens for which only *28S rDNA* was obtained that are not included in the concatenated analysis (SMNHTAU_Co_36061 from Madagascar and SMNHTAU_Co_32503 from Kenya) also belonged to clade 6.

The second major clade comprised four distinct subclades, two of which could be further subdivided by geography. All specimens from the Red Sea (Israel, Saudi Arabia) belonged to a well-supported and genetically distinct clade (clade 1), with no obvious genetic distinction between two different colour-morphs (grey, yellow) that occur at different depths (Liberman *et al.* 2018) (Fig. 2). Sister to clade 1 was a clade that included specimens from east Africa and Madagascar (clade 3) plus three specimens from the western Pacific (Taiwan, Malaysia) (clade 2). Although both ML and Bayesian analyses supported clade 2, support for clade 3 was weak (ultrafast bootstrap support = 84%; Bayesian posterior probability = 0.59). A third genetically distinct clade (clade 4) comprising specimens from eastern Australia (Lizard I., Townsville and the Coral Sea Islands) was sister to clades 1, 2 and 3. A fourth distinct and well-supported clade, sister to 1, 2, 3 and 4, included additional specimens from eastern Australia (Townsville and the Coral Sea Islands) as well as the Indian Ocean territory of Réunion. Both analyses separated Australia and Réunion into distinct subclades, but support for the Australian clade (clade 8) was weak in the ML tree (ultrafast bootstrap support = 87%) whereas the Réunion clade (clade 5) was not well supported in the Bayesian tree (pp = 0.72).

Single-locus species delimitation analyses

Application of a pairwise genetic distance threshold of 0.003 to the concatenated alignment delineated 14 operational taxonomic units (OTUs) (Fig. 2). Clades 2, 5, 6, and 7 each corresponded to a single OTU. Each of the other clades was divided into two or more OTUs. All of the Red Sea specimens (clade 1) belonged to a single OTU with the exception of three specimens (SMNHTAU_Co_37702, Co_37766 and SAU041) that were separated into two additional OTUs. Similarly, all specimens in clade 3 belonged to a single OTU with the exception of SMNHTAU_Co_36000 which was split as a separate OTU. Specimens in clade 4 were divided among three OTUs, and clade 8 was split into two OTUs (Fig. 2).

The highest scoring species partition identified by *ASAP* found six OTUs separated by an average genetic distance threshold of 0.0046 (Fig. 2). Clades 1, 4, 6 and 7 each comprised an OTU. Clades 2 and 3 were lumped together as a single OTU, as were clades 5 and 8. For comparison, applying a strict pairwise genetic distance threshold of

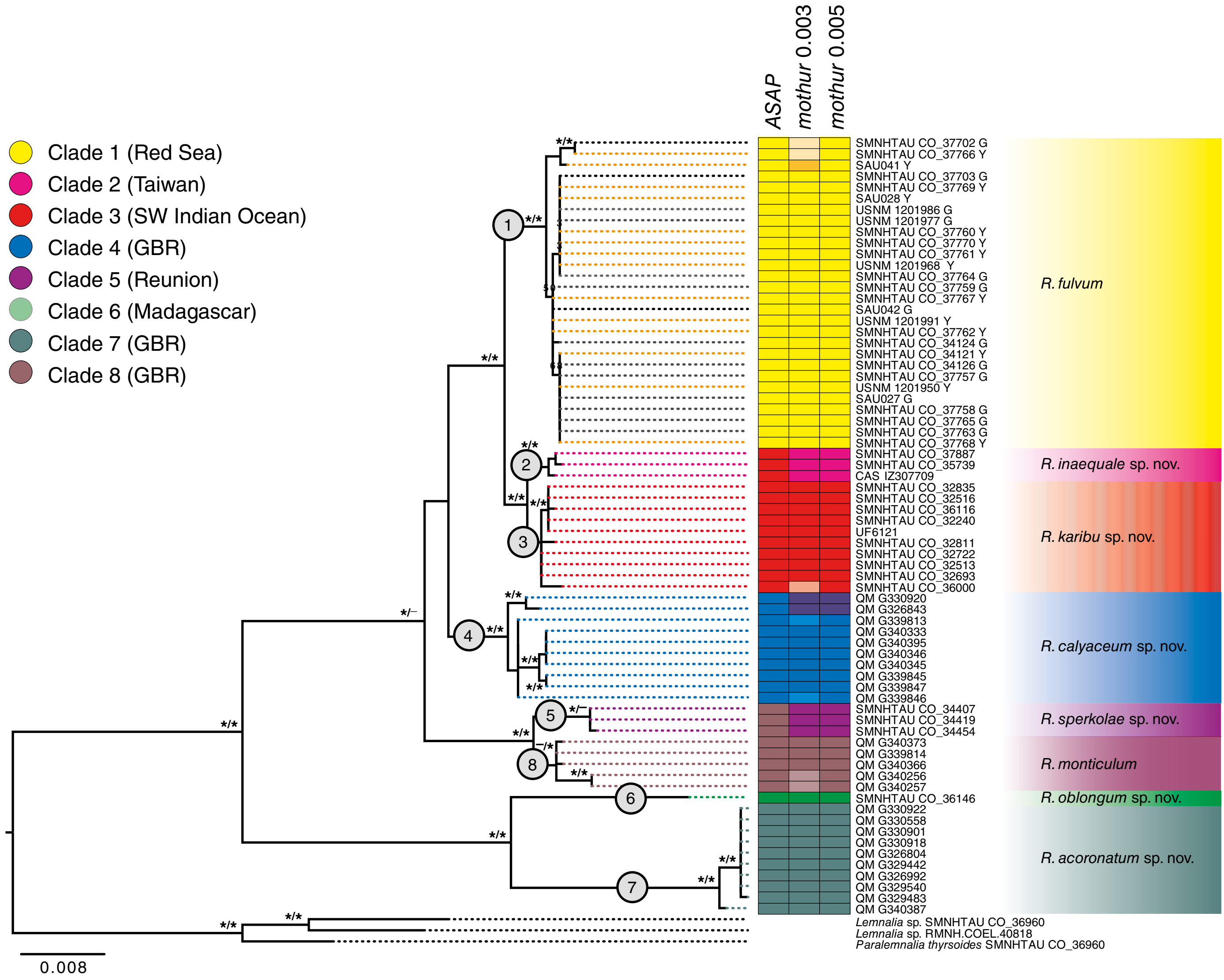

Fig. 2. Maximum likelihood phylogenetic reconstruction of *Rhytisma* based on a concatenated alignment of the single-locus barcoding markers *mtMutS* and *28S rDNA*. Clades corresponding to species are numbered (1–8) and colour-coded to correspond to other figures. Species delimitations determined using *ASAP*, *mothur* (0.003 threshold) and *mothur* (0.005 threshold) are indicated as bars with colours corresponding to OTUs. Y is *R. fulvum* yellow morph; G is *R. fulvum* grey morph. Symbols at nodes: */* = ultrafast bootstrap values > 90%, Bayesian pp > 0.95. */– = UF bootstrap > 90%, Bayesian pp < 0.90; –/* = UF bootstrap < 90%, Bayesian pp > 0.95. Nodes without symbols were not supported by either analysis (i.e. UF bootstrap < 90%, Bayesian pp < 0.90). GBR is the Great Barrier Reef, Australia.

0.005 with *mothur* identified nine OTUs (Fig. 2). Each of the eight clades comprised a single OTU with the exception of clade 4 in which two specimens from Lizard Is. (QM G330920, QM G326843) were separated as a ninth OTU.

Phylogenomic analyses and SNP-based species delimitation

Sequences for 1113 UCE/exon loci were obtained. No individuals belonging to clade 8 were included in the phylogenomic analysis. Numbers of loci recovered per sample ranged from 541 to 1995 for contemporary specimens; 34 loci were recovered from USNM 54020 and 1366 loci from USNM 54018. The 75% occupancy tree (1,355,818-bp alignment) recovered seven well-supported clades corresponding to clades 1–7 designated by single-locus barcodes (Fig. 3). The UCE/exon tree topology was slightly different from the single-locus tree (Fig. 2), with clade 4 sister to clades 2 and 3 rather than to clades 1, 2 and 3, and clade 1 sister to clades 2, 3 and 4 (Fig. 3). The two USNM specimens identified as *P. rubiginosum* fell into different clades, with USNM 54020 belonging to clade 3 and USNM 54018 in clade 6.

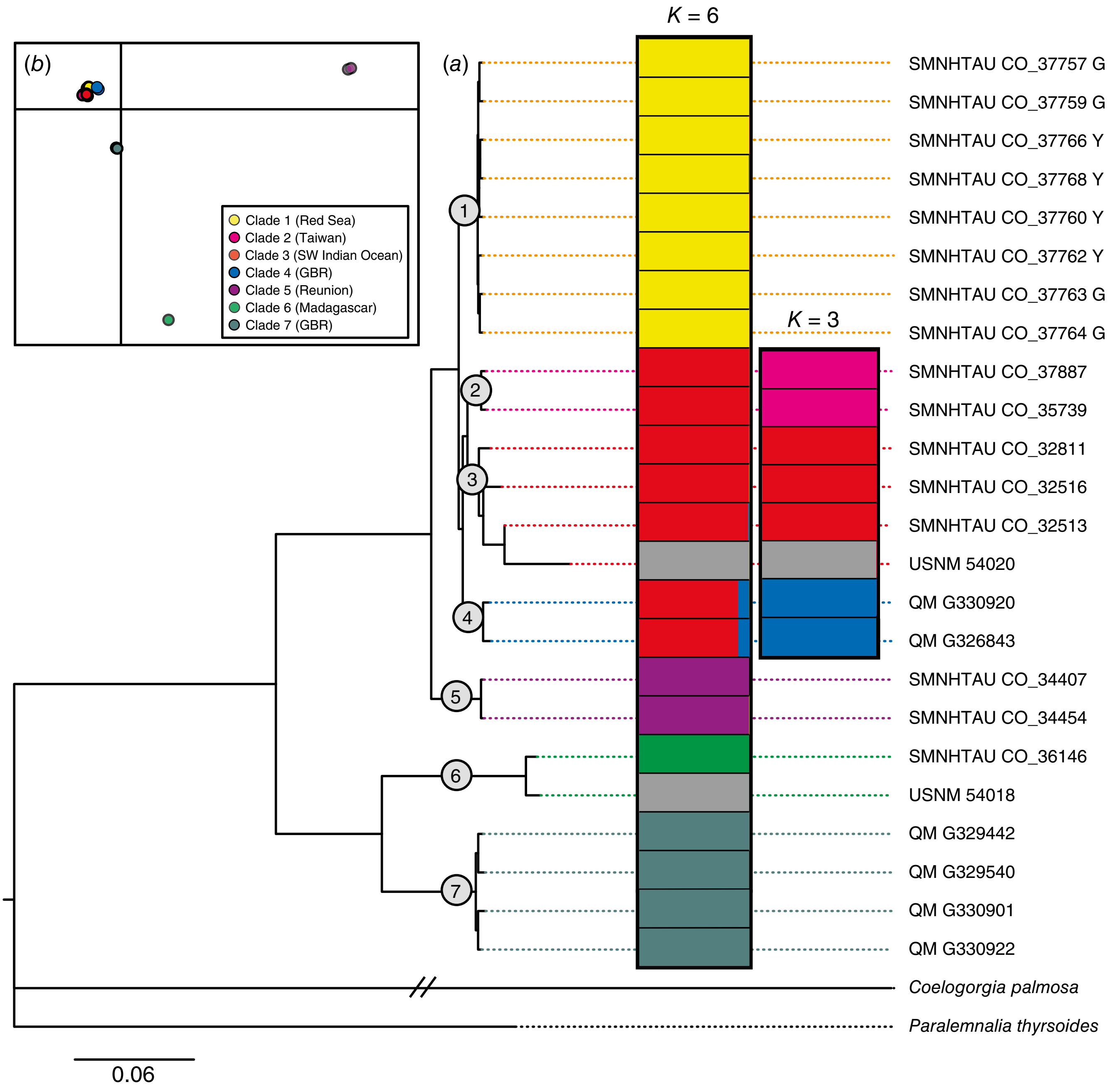

Fig. 3. (*a*) Maximum likelihood phylogenetic reconstruction of *Rhytisma* based on 1113 UCE and exon loci (75% occupancy matrix). All nodes have 100% ultrafast bootstrap support. Clades are numbered and coloured as in Fig. 2. Y is *R. fulvum* yellow morph; G is *R. fulvum* grey morph. Coloured bars indicate results of *STRUCTURE* analysis with *K* = 6 (422 SNPs) and *K* = 3 (518 SNPs). Grey bars indicate historical specimens not included in *STRUCTURE* or DAPC analyses; no UCE/exon sequences obtained for clade 8. Branch to outgroup taxon *Coelogorgia palmosa* has been shortened to enhance readability. (*b*) Discriminant Analysis of Principal Components (DAPC) plot, groups coloured to correspond to clusters identified by *STRUCTURE*.

DAPC supported seven clusters corresponding to the seven clades in the phylogeny (Fig. 3*b*). *STRUCTURE* ($K = 6$) suggested five clusters, with clades 1, 5, 6 and 7 distinct but clades 2, 3 and 4 belonging to a single cluster (Fig. 3*a*). A second *STRUCTURE* analysis of just clades 2, 3 and 4 with $K = 3$ separated them into three distinct clusters (Fig. 3*a*).

Systematics

Class **OCTOCORALLIA** Haeckel, 1866

Order **MALACALCYONACEA** McFadden, van Ofwegen & Quattrini, 2022

Family **LEMNALIIDAE** Gray, 1869

Rhytisma Alderslade, 2000

Type species: *Litophyton fulvum* Forskål, 1775 – by subsequent designation of Alderslade (2000, p. 238). [Neotype designated herein; see *Rhytisma fulvum*].

Type locality: Red Sea [exact locality not specified by Forskål; neotype herein designated from Eilat, Gulf of Aqaba].

Not included in current concept of *Rhytisma*

Litophyton (part) – Forskål (1775), p. 139.

Sympodium (part) – Ehrenberg (1834), p. 156; Klunzinger (1887), p. 42; May (1899), pp. 46–53; Wright and Studer (1889), pp. 270–271; Thomson and McQueen (1908), p. 49; Thomson and Henderson (1906), p. 409; Thomson and Dean (1931), p. 21.

Alcyonium – Kükenthal (1904), pp. 41–43; Verseveldt (1965), p. 29.

Alcyonium (part) – Kükenthal (1913), p. 2; Thomson and Mackinnon (1919), p. 173.

Alcyonium (*Erythropodium*) – Cohn (1908), pp. 237–238.

Parerythropodium (part) – Kükenthal (1916), pp. 461–464; Stiasny (1937), p. 739; Tixier-Durivault (1966), pp. 101–106; Tixier-Durivault (1972), p. 19; Verseveldt (1969), pp. 4–11; Groot and Weinberg (1982), p. 303.

Diagnosis (modified after Alderslade 2000)

Colonies are thin, encrusting mats of irregular shape, a few millimetres thick, occasionally with hillocks where the mat is considerably thickened, or with ribbon-like extensions. Polyps are monomorphic, fully retractile into surface apertures, often surrounded by raised calyx-like mounds. Coenenchymal mat sclerites consist of long spindles, up to several millimetres, typically curved or bent, with sparse low tubercles, sometimes forming a honeycomb-like network on the colony surface. Polyp sclerites arranged as collaret and points. The collaret sclerites are bent spindles arranged in multiple rows. Point sclerites are spindles or rods, often arranged *en chevron*. Tentacle sclerites consist of granular platelets, often with a central constriction or lateral notches, and may be symmetrical or asymmetrical. Elongated platelets may occur at the tentacle base. Colony colour variable in life (yellow, grey, purple, beige); preserved colonies are pale cream. All sclerites are colourless. Zooxanthellate.

Biogeographical distribution

Indo-Pacific reefs, including Red Sea, Tanzania, Kenya, Madagascar, Réunion, Taiwan, Malaysia and the Great Barrier Reef (Australia). There are additional records from Paternoster Islands and Papua New Guinea; Ryukyu Archipelago (Japan) (see Alderslade 2000); Mozambique and the Philippines (McFadden *et al.* 2025); and citizen science photographic records (iNaturalist) also indicate its occurrence in New Caledonia.

Depth distribution

Across its range, *Rhytisma* appears to be primarily a shallow-water genus. Most examined material and published records are from shallow reef habitats, with colonies occurring on reef slopes, patch reefs and other hard substrates (Alderslade 2000; Fabricius and Alderslade 2001; McFadden *et al.* 2025; present study). In the Red Sea, some populations extend into the upper mesophotic zone (present study; Shoham and Benayahu 2017; Benayahu *et al.* 2019), but comparable deep records have not yet been documented from other regions. At present, it is therefore unclear whether mesophotic occurrences reflect a general depth range of the genus or region-specific environmental conditions.

Remarks

Although the genus is uncommon, it can be locally abundant, typically overgrowing dead and occasionally live substrates (Stobart *et al.* 2005). Colonies may develop hillocks or ribbon-like extensions. Colony shape and colour are variable and currently do not serve as reliable taxonomic characters. Additional material and high-resolution underwater imagery may help reveal additional diagnostic features and provide insights into intraspecific variation.

Tentacle sclerites are particularly diagnostic at the species level. Previously referred to as ‘granular scales’ (Alderslade 2000; Fabricius and Alderslade 2001), these are herein redefined as granular platelets. They often exhibit central or lateral median constrictions or notches; symmetrical or asymmetrical. These sclerites possess a granular, microcrystalline surface texture distinct from other sclerite types (Fig. 4*a*).

The sclerites in the tentacles are arranged longitudinally and become smaller toward the tentacle base, where they resemble the shortest point sclerites. Elongated platelets may occur at the tentacle base, sharing the same granular surface texture of the tentacle platelets (Fig. 4*b*, *c*). By contrast, point sclerites show changes in surface texture: the shape of the microcrystals differs from that of the tentacle sclerites (Fig. 4*d*). Point sclerites are often arranged *en chevron* which may appear pronounced or weak in some species. The number of rows of sclerites in the collaret and points can be variable among polyps in the same colony.

Mat spindles are variable in size and shape, probably depending on colony age and location; older areas and larger polyps tend to have longer sclerites. The spindle surface has sparse simple tubercles (Fig. 4*e*, *f*).

Overall, for morphological species delimitation, sclerite size is of limited diagnostic value; the most informative

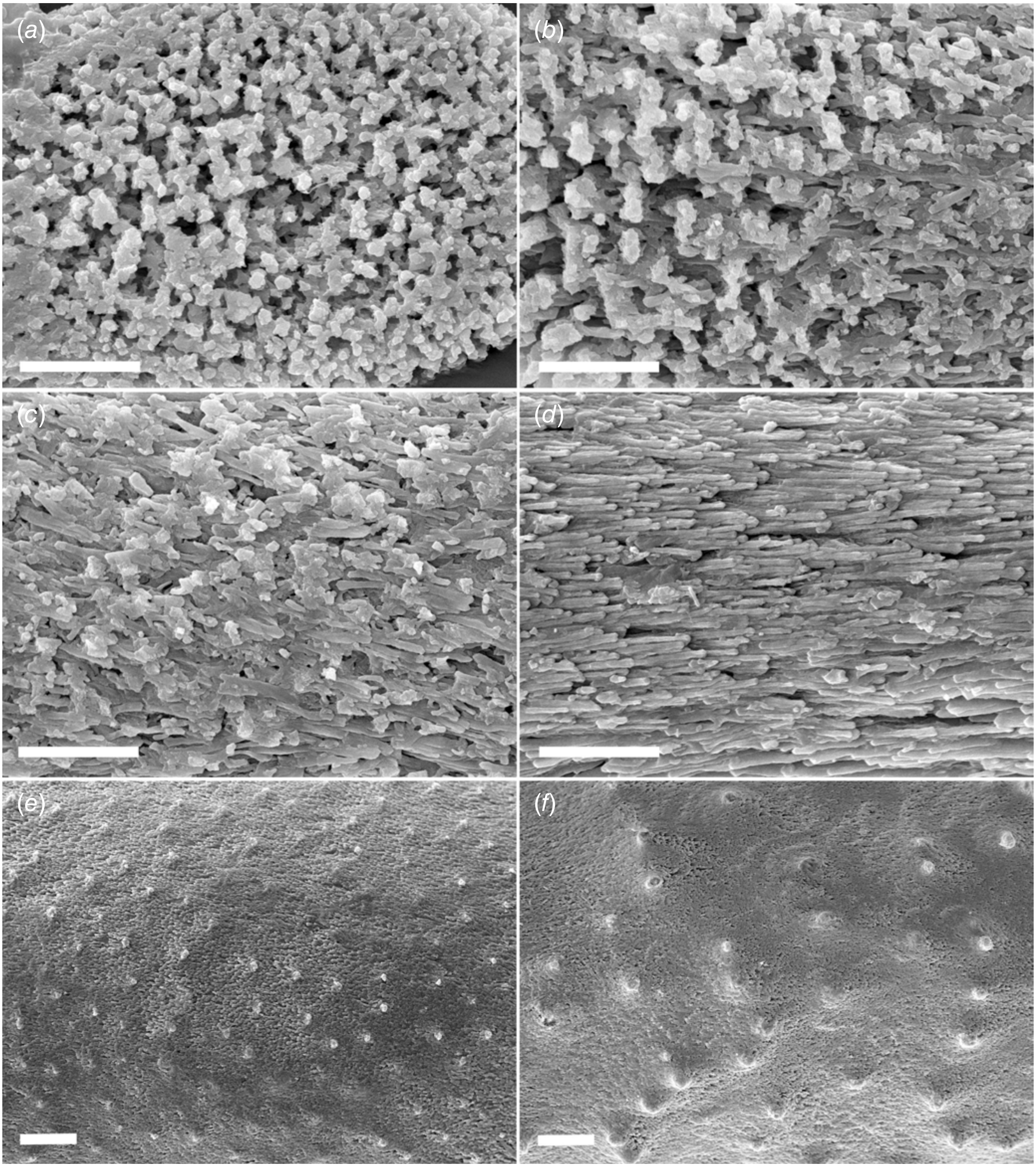

Fig. 4. Surface ornamentation and crystallisation patterns on different types of sclerites in *Rhytisma*. (*a*) Tentacle sclerites (*b*) Distal ends of tentacle-base sclerites (*c*) Central region of the tentacle-base sclerites (*d*) Collaret and point sclerites (*e*, *f*) Mat spindles with sparse low tubercles. Scale bars: *a*–*d*, 0.005 mm; *e*, *f*, 0.02 mm.

characters are the shape and surface sculpturing of the sclerites, especially those in the tentacles, followed by those in the collaret and points, and finally those in the mat. These features are best assessed from the SEM plates.

Key to species of the genus *Rhytisma*

1. Collaret sclerites are absent or rudimentary..*R. acoronatum* sp. nov.
   Collaret sclerites well developed..2

2. Tentacle sclerites exclusively elongated platelets; granular platelets absent..*R. sperkolae* sp. nov.
   Tentacle sclerites include granular platelets...................................3
3. Tentacle sclerites smooth, ellipsoid with faint or indistinct constriction; mat spindles up to 2.6 mm with bifurcated tips...*R. oblongum* sp. nov.
   Tentacle sclerites granular, with distinct constrictions or notches; mat spindles without bifurcate tips...4
4. Tentacle sclerites strongly asymmetrical, markedly irregular outline...*R. inaequale* sp. nov.
   Tentacle sclerites symmetrical or only slightly asymmetrical in outline...5
5. Tentacle sclerites with multiple constrictions or lateral notches, ends distinctly flared or bone-shaped........................*R. karibu* sp. nov.
   Tentacle sclerites with single median constriction..........................6
6. Tentacle sclerites with symmetrical median constriction, tips evenly tapered; point sclerites up to 0.33 mm...... *R. calyaceum* sp. nov.
   Tentacle sclerites with variable constriction, ends not tapered.......7
7. Tentacle sclerites with symmetrical median constriction, elongated platelets up to 0.1 mm...*R. rubiginosum*
   Tentacle sclerites with asymmetrical features; collaret sclerites longer than 0.50 mm...8
8. Colony commonly with prominent hillocks; tentacle sclerites elongated with faint constriction...................................*R. monticulum*
   Colony typically flat mat; tentacle sclerites with distinct asymmetrical features...9
9. Tentacle sclerites with asymmetrical lateral notches; point sclerites smooth with one end sharply pointed............................*R. fulvum*
   Tentacle sclerites with shallow median constriction, moderately asymmetrical up to 0.06 mm; point spindles with tuberculation..*R. fuscum*

Rhytisma fulvum (Forskål, 1775)

(Fig. 1, 5, 6, 32*a*, *b*.)

=*Litophyton fulvum* Forskål, 1775, p. 139 [original combination].

=*Sympodium fulvum* (Forskål, 1775) – Ehrenberg (1834), p. 156 [new combination]; Klunzinger (1887), p. 43; May (1899), pp. 52–53; Thomson and Dean (1931), p. 21.

=*Alcyonium fulvum* (Forskål, 1775) – Kükenthal (1904), pp. 41–43 [new combination]; Verseveldt (1965), pp. 29–30.

=*Alcyonium (Erythropodium) fulvum* var. *sclera* – Cohn (1908), pp. 237–238.

=*Parerythropodium fulvum* (Forskål, 1775) – Kükenthal (1916), p. 463 [new combination]; Tixier-Durivault (1966), pp. 101–103.

=*Rhytisma fulvum fulvum* (Forskål, 1775) – Benayahu *et al.* (2002), p. 278; Haverkort-Yeh *et al.* (2013), pp. 279–291.

=*Parerythropodium fulvum fulvum* (Forskål, 1775) – Verseveldt (1969), p. 7 [new subspecies].

Misidentifications

Sympodium fuscum – Thomson and Henderson (1906), pp. 408–409 (=*Parerythropodium fulvum fuscum*, Verseveldt, 1969, p. 8).

Not *Rhytisma fulvum fulvum* (Forskål, 1775) – Benayahu (2002), pp. 13, 16; Benayahu *et al.* (2003), p. 55; Benayahu *et al.* (2004), p. 550; Benayahu and van Ofwegen (2012), pp. 691–692; Benayahu (2013), p. 9; Schleyer *et al.* (2016), pp. 97–98; Schleyer and Benayahu (2018), p. 1645.

Not *Rhytisma fulvum* (Forskål, 1775) – Schleyer *et al.* (2019), p. 2487.

Material examined

NEOTYPE. ISRAEL: SMNHTAU_Co_34126, Gulf of Aqaba, Eilat, across from the Inter University Institute for Marine Sciences, 29.5040°N, 34.9179°E, 10–12 m, 24 July 2007, coll. Y. Benayahu.

Additional material

ERITREA: SMNHTAU_Co_30046, Red Sea, Dahlak Archipelago, Cundabilu, 15.7244°N, 39.8844°E, 9.5 m, 30 April 1997, coll. M. Schleyer.

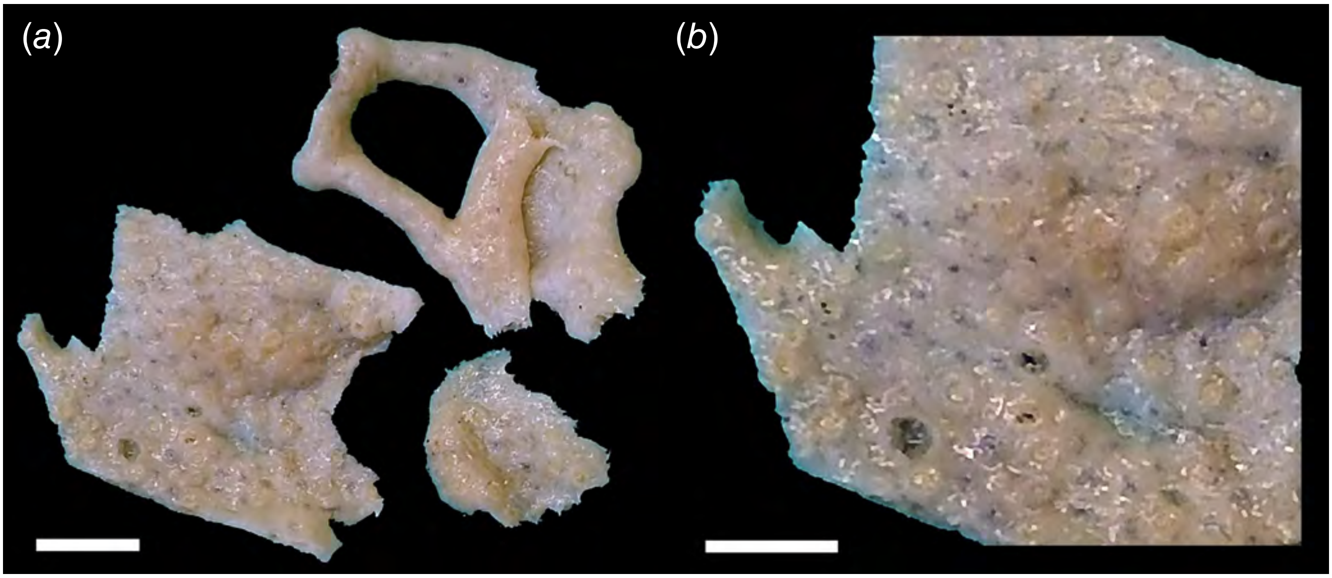

Fig. 5. *Rhytisma fulvum* (Forskål, 1775), neotype (SMNHTAU_Co_34126). (*a*) Fragments of colony with retracted polyps, one fragment shows stolon extensions (*b*) Fragment (enlarged) showing retracted polyps on the mat surface and thinner margins. Scale bars: 1 cm.

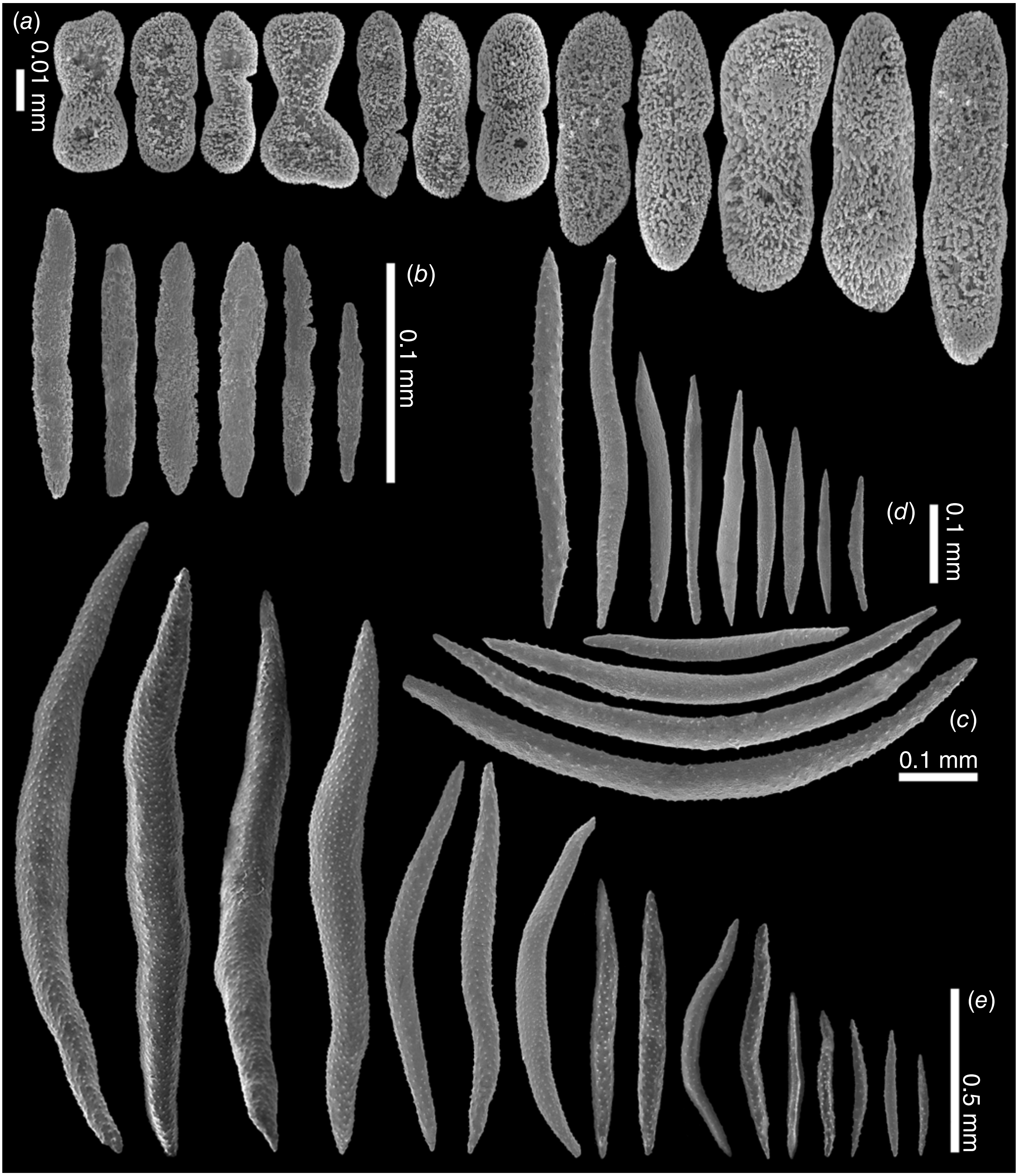

Fig. 6. *Rhytisma fulvum* (Forskål, 1775), neotype (SMNHTAU_Co_34126). (*a*) Tentacle sclerites (*b*) Elongated platelets at the base of the tentacles (*c*) Collaret sclerites (*d*) Point sclerites (*e*) Spindles of the mat.

ISRAEL: SMNHTAU_Co_34122–34124, Gulf of Aqaba, Eilat, Inter University Institute for Marine Sciences (IUI) Reef, 29.5023°N, 34.9179°E, 10–12 m, 24 July 2007, coll. Y. Benayahu; SMNHTAU_Co_34125, Gulf of Aqaba, Eilat, IUI Reef, 29.5023°N, 34.9179°E, 10–12 m, 24 July 2007, coll. Y. Benayahu; SMNHTAU_Co_37759, Gulf of Aqaba, Eilat, across from IUI, 29.5023°N, 34.9179°E, 43 m, 27 May 2019, coll. R. Liberman;

SMNHTAU_Co_37760, Gulf of Aqaba, Eilat, across from IUI Reef, 29.5023°N, 34.9179°E, 42 m, 20 August 2019, coll. R. Liberman; SMNHTAU_Co_37762, Gulf of Aqaba, Eilat, IUI Reef, 29.5023°N, 34.9179°E, 24 July 2019, coll. R. Liberman; SMNHTAU_Co_37763, Gulf of Aqaba, Eilat, IUI Reef, R43, 3–10 m, 6 April 2019, coll. R. Liberman; SMNHTAU_Co_37768, Gulf of Aqaba, Eilat, IUI Reef, 27 May 2019, coll. R. Liberman; SMNHTAU_Co_37766, Gulf of Aqaba, Eilat, IUI Reef, R46, 3–10 m, 27 May 2019, coll. R. Liberman; SMNHTAU_Co_37702, Gulf of Aqaba, Eilat, IUI Reef, 23 July 2018, coll. R. Liberman; SMNHTAU_Co_37703, Gulf of Aqaba, Eilat, Katzza North dock, 41 m, 25 July 2018, coll. R. Liberman; SMNHTAU_Co_37769, Gulf of Aqaba, Eilat, IUI Reef, R49, 8 m, 17 June 2019, coll. R. Liberman; SMNHTAU_Co_37770, Gulf of Aqaba, Eilat, IUI Reef, R50, 40 m, 17 June 2019, coll. R. Liberman; SMNHTAU_Co_37761, Gulf of Aqaba, Eilat, IUI Reef, R41, 43 m, 20 August 2019, coll. R. Liberman; SMNHTAU_Co_37764, Gulf of Aqaba, Eilat, IUI Reef, R44, 3–10 m, 6 April 2019, coll. R. Liberman; SMNHTAU_Co_37767, Gulf of Aqaba, Eilat, IUI Reef, R47, 3–10 m, 27 May 2019, coll. R. Liberman; SMNHTAU_Co_34121, Gulf of Aqaba, Eilat, IUI Reef, 71, 29.5023°N, 34.9179°E, depth 10.7–12.2 m, 24 July 2007, coll. Y. Benayahu; SMNHTAU_Co_37758, Gulf of Aqaba, Eilat, IUI Reef, R38, 44 m, 27 May 2019, coll. R. Liberman; SMNHTAU_Co_37765, Gulf of Aqaba, Eilat, IUI Reef, R45, 3–10 m, 6 April 2019, coll. R. Liberman.

SAUDI ARABIA: USNM1201950, Al Lith, South Brown Reef, 19.8167°N, 40.1167°E, 13 m, April 2011, coll. R.D. Haverkort-Yeh; USNM1201951, Al Lith, North Brown Reef, 19.8667°N, 40.1000°E; 9 m, April 2011, coll. R.D. Haverkort-Yeh; USNM1201968, Al Lith, Dora Reef 19.8167°N, 39.8833°E, 13 m, April 2011, coll. R.D. Haverkort-Yeh; USNM1201977, Al Lith, Marmar Reef, 19.8333°N, 39.9333°E, 5 m, April 2011, coll. R.D. Haverkort-Yeh; USNM1201986, Farasan Islands, Abulatt, 16.7833°N, 42.1833°E, 9 m, April 2011, coll. R.D. Haverkort-Yeh; USNM1201991, Farasan Islands, Abulatt, 16.7833°N, 42.1833°E, 9 m, April 2011, coll. R.D. Haverkort-Yeh; SAU027, SAU028, Red Sea, Saudi Arabia, Jeddah, 21.7127°N, 39.0803°E, 10 m, 25 Oct 2018, coll. C. McFadden (only DNA); SAU041, Red Sea, Saudi Arabia, Jeddah, 21.7127°N, 39.0803°E, 5 m, 25 Oct 2018, coll. C. McFadden (only DNA).

Description

The neotype consists of three fragments forming a mat-like colony, ~2 mm thick, thinning towards the edges (Fig. 5). Some low hillocks and irregular ribbon-like lateral extensions are present. Polyps are evenly distributed across the colony surface and are mostly fully retracted into small pit-like apertures (Fig. 5*b*).

Tentacle sclerites are mostly granular platelets, up to 0.08 mm long (Fig. 6*a*), with some showing a median constriction or asymmetrical lateral notches along their margins (Fig. 6*a*). Elongated platelets are present at the tentacle base and reach up to 0.10 mm long (Fig. 6*b*). These sclerites are arranged longitudinally in the tentacle, increasing in length toward the tentacle base, where they become similar in size to the shortest point sclerites.

Polyp sclerites form collaret and points. The collaret includes 5–6 rows of bent spindles up to 0.70 mm long (Fig. 6*c*). The point sclerites are up to 0.53 mm long (Fig. 6*d*), arranged *en chevron*. The smallest point sclerites are smooth with one end tapering to a sharp tip (Fig. 6*d*).

The mat spindles reach up to 1.72 mm in length (Fig. 6*e*), and are mostly curved or with a sinuous outline, ornamented with sparse, low tubercles. These sclerites can form a honeycomb pattern around the polyp.

Colour

The ethanol-preserved material is light cream to beige in colour.

Living features

Colonies grow on hard reef substrate and commonly on artificially deployed objects. They display a yellowish colour (Fig. 31*a*) which is the most abundant morph on the Red Sea reefs. The other colour-morph is grey, occasionally with a violet tint (Fig. 31*b*), and typically occurs in deeper waters, 20–55 m (Liberman *et al.* 2022). The fully expanded polyps give the colony a fleshy appearance, despite the underlying thin mat.

Morphological variation

The morphological features of the additional material examined varied in colony size with only minor differences in sclerites, such as longer spindles of the mat. SMNHTAU_Co_34123 has tentacle platelets resembling those of *R. karibu* sp. nov.

Remarks

The type material of *Litophyton fulvum* Forskål, 1775 is considered lost (Verseveldt 1969), a conclusion further supported by Y. Benayahu's visits to the Copenhagen Zoological Museum. The original description by Forskål lacked diagnostic detail, particularly regarding the polyp sclerites, which are now recognised as characteristic of the species (Verseveldt 1969, pp. 4–7). Verseveldt (1969) proposed that later records of *Sympodium fulvum* by Klunzinger (1887) and *Alcyonium fulvum* by Kükenthal (1904), both based on Red Sea material, likely matched Forskål's species, as they described polyp sclerites arranged in a chevron-like pattern. These two studies were among the first to recognise taxonomic significance of polyp sclerites. Verseveldt (1969) assigned two sub-species: *Parerythropodium fulvum fulvum* (Forskål, 1775) and *P. fulvum fuscum* (Thomson & Henderson, 1906), based primarily on differences in the robustness of the polyp sclerites. However, the present study finds no justification for retaining this subspecies distinction, as *R. fulvum* and *R. fuscum* are morphologically distinct enough to warrant recognition as separate species.

Since Forskål's original description, specimens identified as *Parerythropodium fulvum fulvum* or *Rhytisma fulvum* have been reported from across the Indo-Pacific, including the Ryukyu Archipelago (Benayahu 2002), Mozambique (Benayahu *et al.* 2003), Taiwan (Benayahu *et al.* 2004), Réunion (Benayahu and van Ofwegen 2012; Schleyer *et al.* 2016), Zanzibar (Benayahu 2013), Mayotte (Schleyer and Benayahu 2018) and Europa Island (Schleyer *et al.* 2019). However, detailed morphological analyses suggest that these records may not correspond to *R. fulvum sensu stricto*, which appears to be endemic to the Red Sea.

Given the uncertain identity of historical material and the absence of Forskål's original type specimen, it became necessary to stabilise the taxonomy of this species. Therefore, a neotype is designated here, fulfilling the provisions of ICZN Article 75.3. The neotype is deposited in the Steinhardt Museum of Natural History, Tel Aviv, under registration number SMNHTAU_Co_34126. It was collected from the Red Sea, the original type locality of *L. fulvum*, thereby satisfying Article 75.3.6. The neotype conforms to the original description as interpreted by subsequent authors and corresponds in all key diagnostic characters to additional material examined from the Gulf of Aqaba, central Red Sea, and southern Red Sea. It is therefore herein designated as the name-bearing type of *Rhytisma fulvum* (Forskål, 1775), in accordance with ICZN Article 75.3.

Rhytisma fulvum can be distinguished from its congeners by the shape and size of its tentacle sclerites, particularly the granular platelets with asymmetrically positioned lateral notches and a median constriction (Fig. 6*a*, Table 1). Additionally, the point spindles are smooth, with one end tapering to a sharp tip, and the elongated platelets at the base of the tentacle usually have tapered ends and a surface texture that differs from that of the tentacle platelets (Fig. 6). The species is genetically distinct from all other species described herein (Fig. 2, 3).

The current findings indicate that *R. fulvum* is endemic to the Red Sea; its presence at other localities in the western Indian Ocean awaits further validation.

Distribution

Red Sea (Fig. 1).

Rhytisma acoronatum Ekins, Benayahu, Samimi-Namin & McFadden, sp. nov.

(Fig. 1, 7, 8, 33*c*, *d*.)

ZooBank: urn:lsid:zoobank.org:act:6A90FF16-365B-4FA2-8C03-8A21E7982826

Material examined

HOLOTYPE. AUSTRALIA: QM G329540, four fragments, Sykes Reef, Heron Island, Capricorn Bunker Group, Great Barrier Reef, Queensland, 23.4107°S, 152.0399°E, 14–22 m, reef slope, 11 September 2008, SCUBA, CREEFS Expedition, coll. M. Ekins, M. Schlacher and P. Hendricks.

PARATYPES. AUSTRALIA: QM G329442, two fragments, Queensland, Masthead Island, Capricorn Bunker Group, Great Barrier Reef, 23.5330°S, 151.7469°E, 6–9 m, back reef, SCUBA, CREEFS Expedition, 2 September 2008, coll. M. Ekins, M. Schlacher, P. Hendricks; QM G330901, two fragments, Queensland, Great Barrier Reef, Lizard Island, 14.7021°S, 145.4503°E, 10–24 m, reef slope, SCUBA, CREEFS Expedition, 8 September 2010, coll. M. Ekins and M. Schlacher.

Other material

AUSTRALIA: QM G330922, Queensland, Lizard Island, Great Barrier Reef, 14.6615°S, 145.4717°E, 10–15 m, reef slope, 9 September 2010, SCUBA, CREEFS Expedition, coll. M. Ekins and M. Schlacher; QM G330918, Queensland, Lizard Island, Great Barrier Reef, 14.6615°S, 145.4717°E, 10–15 m, reef slope, 9 September 2010, SCUBA, CREEFS Expedition, coll. M. Ekins and M. Schlacher; QM G330558, Queensland, Heron Island, Great Barrier Reef, Sykes Reef, Capricorn Bunker Group, 23.4322°S, 152.0338°E, 5–9 m, back reef, 18 November 2009, SCUBA, coll. M. Schlacher; QM G329483, Queensland, Coral Cascades, Heron Island, Capricorn Bunker Group, Great Barrier Reef, 23.4352°S, 151.9195°E, 10–15 m, back reef, 6 September 2008, SCUBA, CREEFS Expedition, coll. M. Ekins, M. Schlacher and P. Hendricks; QM

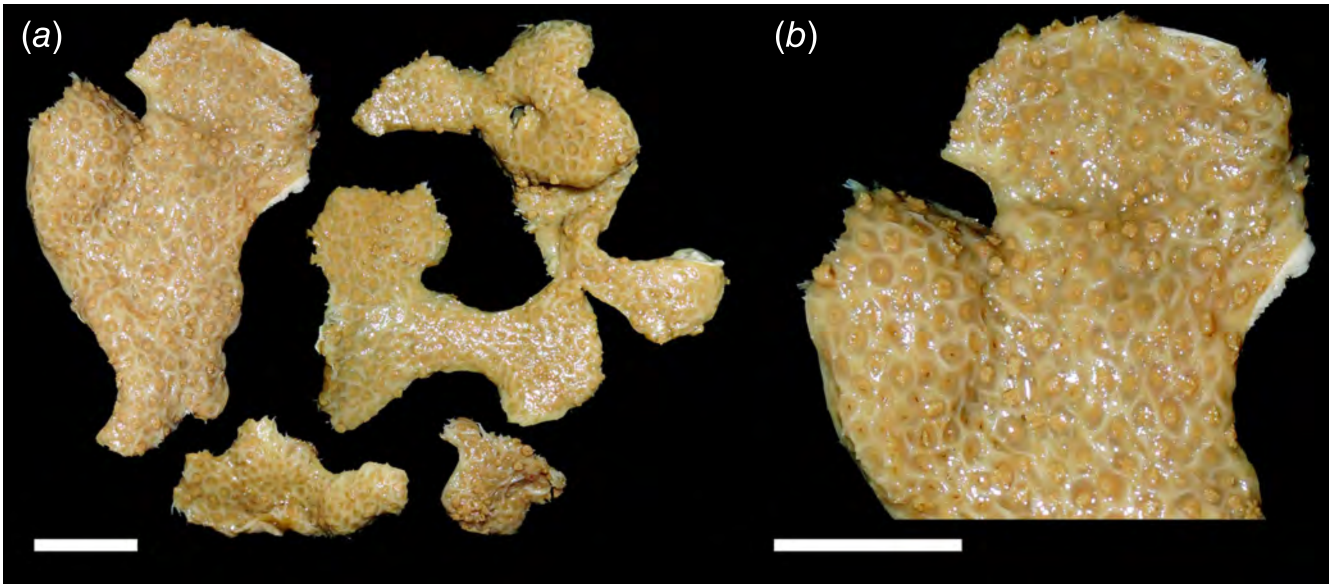

Fig. 7. *Rhytisma acoronatum* sp. nov., holotype (QM G329540). (*a*) Colony fragments (*b*) enlarged fragment with retracted polyps. Scale bars: 1 cm.

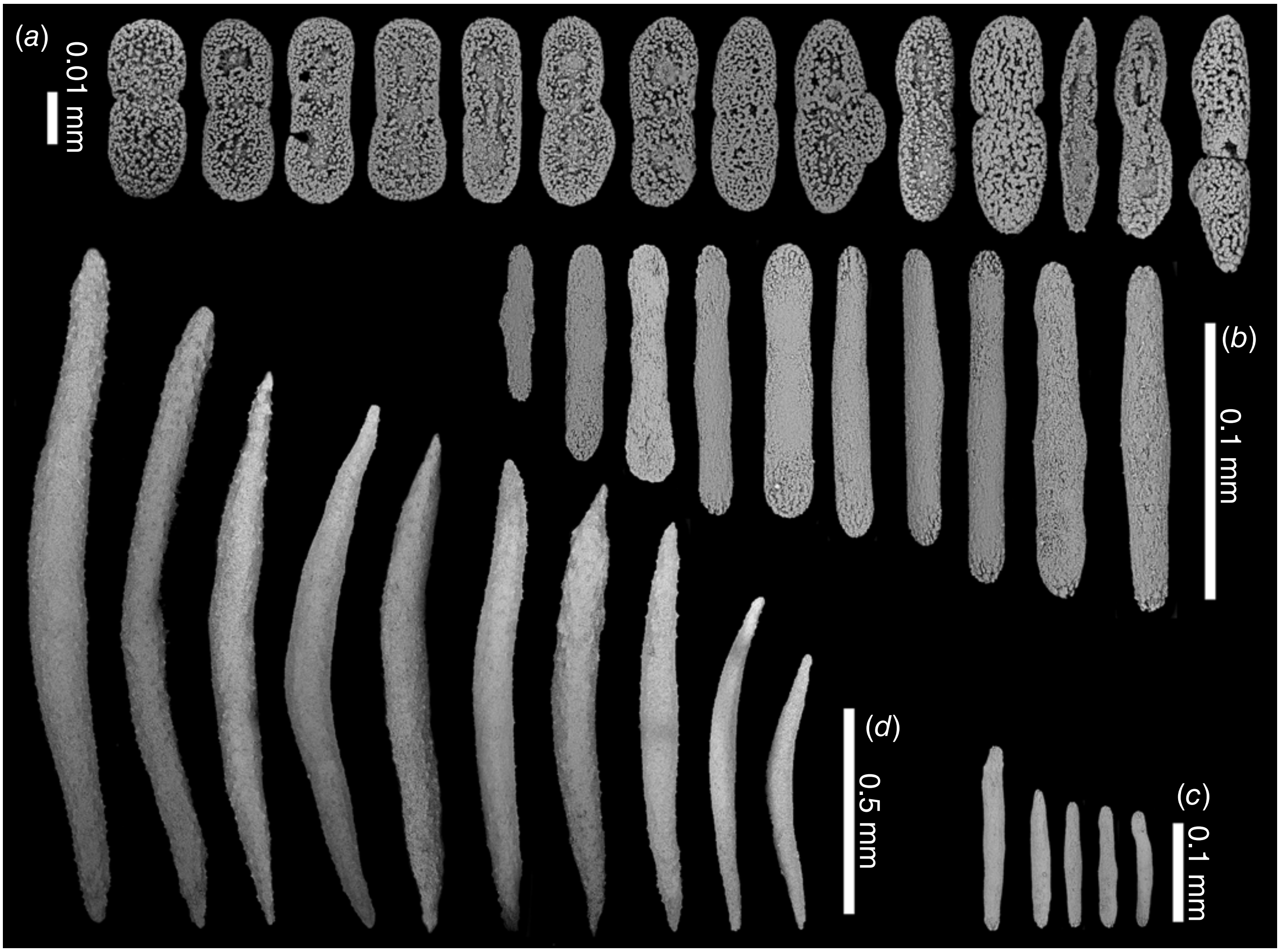

Fig. 8. *Rhytisma acoronatum* sp. nov., holotype (QM G329540). (*a*) Tentacle sclerites (*b*) elongated platelets at the base of the tentacles (*c*) point sclerites (*d*) spindles of the mat.

G326992, Queensland, Linnet Reef, Great Barrier Reef, 14.7917°S, 145.3367°E, 10–15 m, back reef, 13 April 2008, SCUBA, CREEFS Expedition, coll. M. Ekins, K. Fabricius, M. Schlacher and P. Hendricks; QM G326804, Queensland, Lizard Island, North Point, Great Barrier Reef, 14.6502°S, 145.4622°E, 12–15 m, reef slope, 9 April 2008, SCUBA, CREEFS Expedition, coll. M. Ekins, K. Fabricius, M. Schlacher and P. Hendricks; QM G340387, North Flinders Reef, Coral Sea, 17.43617°S, 148.3317°E, 7–12 m, eastern edge, 15 December 2022, SCUBA, coll. M. Ekins and S. Borghi. QM G306445, Queensland, Porpoise Cay, 22.1842°S, 155.3356°E, 20 m, coral bommies, 9 January 1996, SCUBA, coll. J. Kennedy and P.A. Tomkins; QM G306585, Queensland, Whale Bone Cay, Wreck Reef, 22.2014°S, 155.2339°E, 16 m, sandy bottom with isolated bommies, 14 January 1996, SCUBA, coll. J. Kennedy and P.A. Tomkins; QM G307545, Queensland, Polmaise Reef, 23.5508°S, 151.6525°E, 12 m, fringing coral reef, 12 August 1996, SCUBA, coll. J. Hooper, S. Cook, J. Kennedy and P. Tomkins; QM G307621, Queensland, Heron Island, Wistari Channel, 23.435°S, 151.885°E, 20 m, 13 August 1996, SCUBA, coll. J. Hooper, S. Cook, J. Kennedy and P. Tomkins; QM G309052, Queensland, NE Corner Little Broadhurst, 18.5677°S, 147.424°E, 8 m, channel, 31 January 1987, SCUBA, NCI Q66C0166-U, coll. Australian Institute of Marine Sciences and National Cancer Institute; QM G309159, Queensland, east side of Deloraine Island, 20.09°S, 149.043°E, 15 m, slope, 15 October 1987, SCUBA, NCI Q66C0821-I, coll. Australian Institute of Marine Sciences and National Cancer Institute; QM G314804, Queensland, Alcyonarian Point, Hook Island, Whitsunday Group, 20.0655°S, 149.9235°E, 15 m, coral bommies, caves and overhangs, 3 June 1999, SCUBA, coll. S. Cook, J. Kennedy, C. Adams, G. Woerheide and D. Edson; QM G314870, Queensland, Pinnacle Point, Hook Island, Whitsunday Group, 20.0606°S, 148.9611°E, 18 m, fringing reef and coral bommies, 3 June 1999, SCUBA, coll. S. Cook, J. Kennedy, C. Adams, G. Woerheide and D. Edson; QM G318049, Queensland, Prong Number 2 Reef, northern Swain Reefs, 21.7058°S, 151.7422°E, 10.4 m, small bommies and *Acropora* patches, 11 March 2000, SCUBA, coll. S. Cook, J. Kennedy, G. Woerheide and W. Delaney.

Description

The holotype is an encrusting mat-like colony, ~2 mm thick, comprising four fragments (Fig. 7). The colony forms a uniform honeycombed sheet with undulations and folds that reflect the underlying reef substrate. Polyps are evenly distributed across the colony surface and are partially expanded (Fig. 7*b*).

Tentacle sclerites are mostly granular platelets up to 0.04 mm long (Fig. 8*a*), some showing conspicuous symmetrical shallow median constrictions or lateral notches (Fig. 8*a*). Elongated platelets are present at the tentacle base, reaching up to 0.12 mm in length (Fig. 8*b*). These sclerites are arranged longitudinally in the tentacle, increasing in length toward the tentacle base, where they become similar in size to the shortest point sclerites.

Polyp sclerites are not arranged as collaret and points, as the collaret is absent or rudimentary. The point sclerites are up to 0.28 mm long (Fig. 8*c*), arranged *en chevron*.

Mat spindles in the holotype are up to 2.4 mm in length (Fig. 8*d*) and are mostly bent. The sub-surface spindles are visible in the ethanol-preserved material under a dissecting microscope.

Colour

The ethanol-preserved material is tan-coloured, with the polyps darker than the surrounding mat.

Living features

Live colonies are a translucent gold-yellow-greenish colour (Fig. 33*c*, *d*). Following collection, the colony is seen as yellow-greenish, and the exposed underside of the colony is yellow, or sometimes red due to the substrate. The tentacles are opaque yellow–white. The mat spindles are often visible *in vivo* when the tentacles are retracted, and they are easily visible after collection due to their large size.

Etymology

The specific epithet *acoronatum* is derived from the Latin adjective *acoronatus*, meaning 'without a crown', referring to the absence of collaret sclerites in the polyp body.

Morphological variation

The morphological features of the paratype fragments resemble those of the holotype, except for G330922, which displays a grey colour underwater. One of the paratypes (QM G340387) has mat spindles up to 3.2 mm in length.

Remarks

Rhytisma acoronatum sp. nov. is distinguished from all other congeners by the absence of collaret sclerites in the polyp body, a feature consistently present in other species of the genus. It is also genetically distinct from all other species described herein (Fig. 2, 3).

Distribution

Great Barrier Reef, Queensland (Fig. 1).

Rhytisma calyaceum Ekins, Benayahu, Samimi-Namin & McFadden, sp. nov.

(Fig. 1, 9, 10, 32*d*.)

ZooBank: urn:lsid:zoobank.org:act:15C457E8-6A6A-4D83-A0A6-7A2F14FD1E3C

Material examined

HOLOTYPE. AUSTRALIA: QM G330920, Queensland, Lizard Island, Great Barrier Reef, 14.6615°S, 145.4717°E, 10–15 m, reef slope, 9 September 2010, SCUBA, CREEFS Expedition, coll. M. Ekins and M. Schlacher.

PARATYPES. QM G326843, Queensland, Great Barrier Reef, Day Reef, 14.4766°S, 145.5441°E, 4–15 m, back reef, 10 April 2008, SCUBA, CREEFS Expedition, coll. M. Ekins, K. Fabricius, M. Schlacher

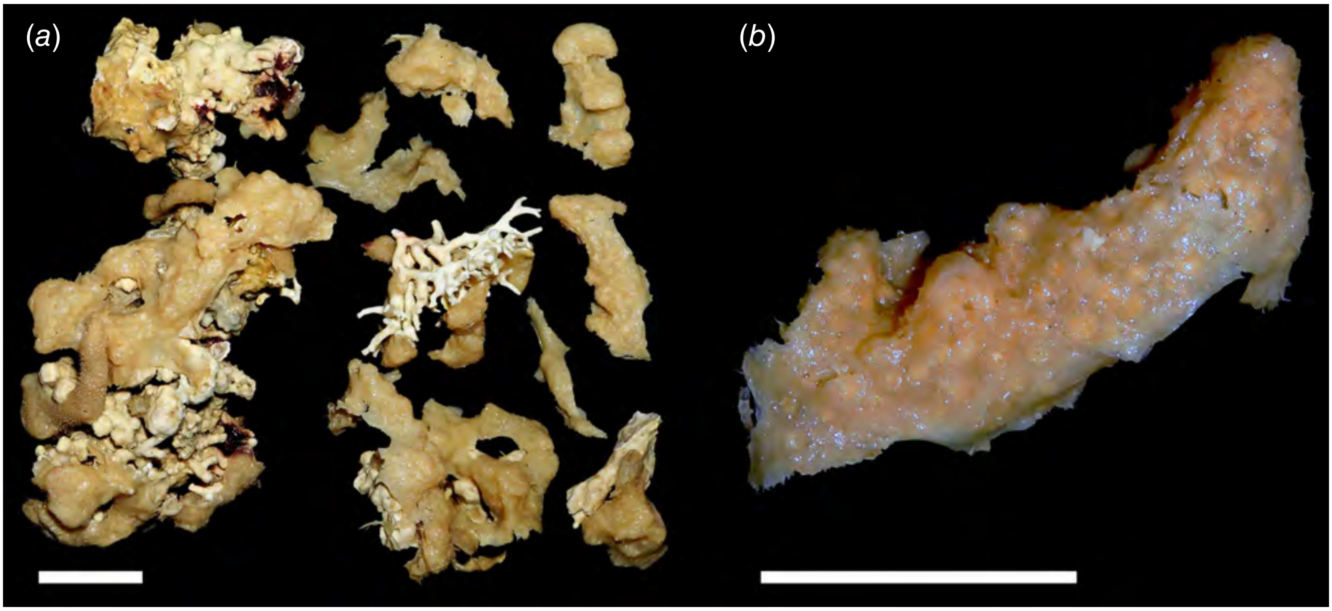

Fig. 9. *Rhytisma calyaceum* sp. nov., holotype (QM G330920). (*a*) Fragments of colony with retracted polyps (*b*) enlarged fragment. Scale bars: 1 cm.

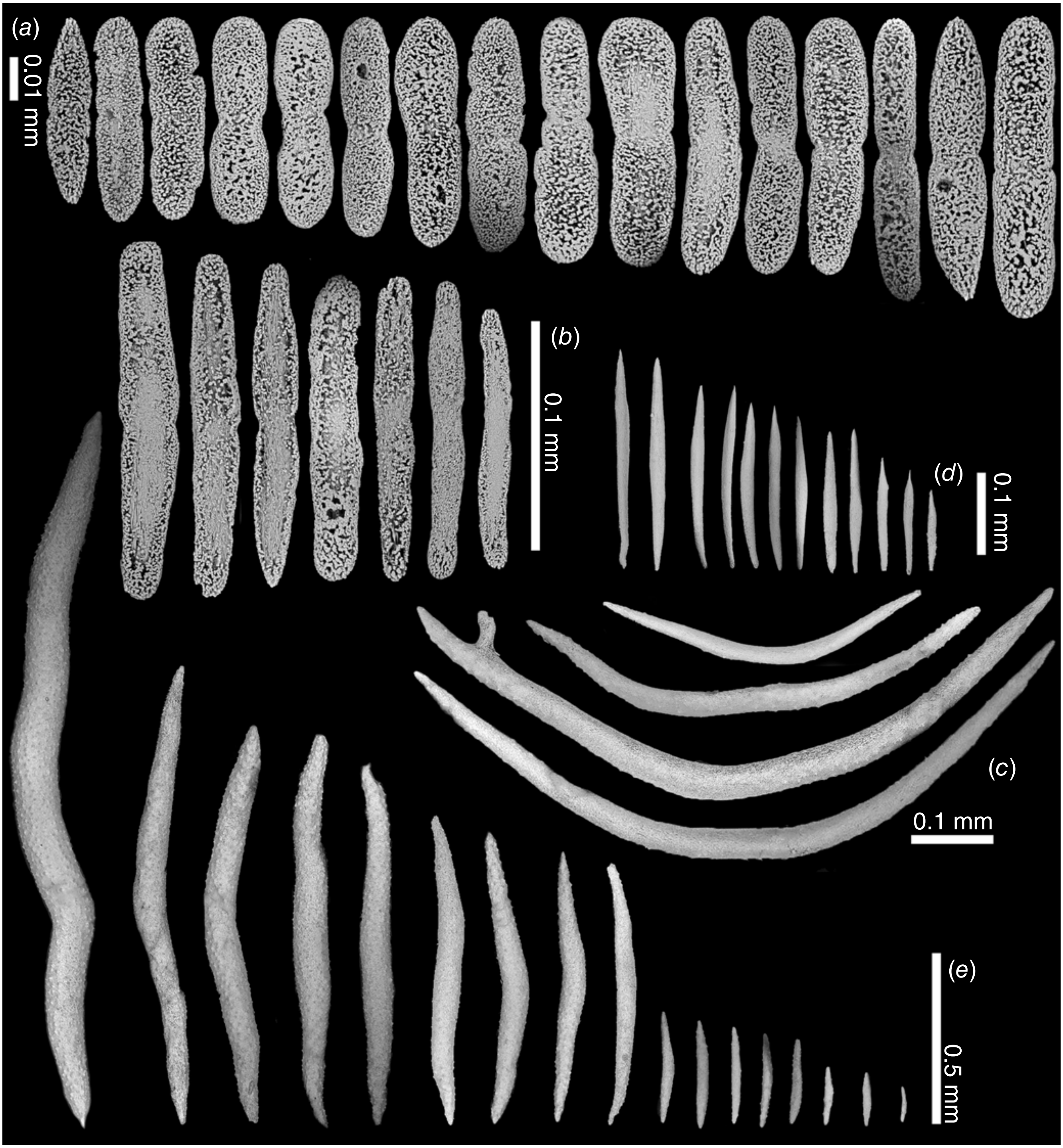

Fig. 10. *Rhytisma calyaceum* sp. nov., holotype (QM G330920). (*a*) Tentacle sclerites (*b*) elongated platelets at the base of the tentacles (*c*) collaret sclerites (*d*) point sclerites (*e*) spindles of the mat.

and P. Hendricks; QM G339813, Townsville, John Brewer Reef, Great Barrier Reef, 18.6308°S, 147.0811°E, 12 m, on SE outer slope, 22 November 2022, SCUBA, coll. M. Ekins and S. Borghi; QM G339845–47, Fantome Island, Palm Island Group, 18.66°S, 146.51°E, 1.5–3 m, north end of Fantome Island, 23 November 2022, SCUBA, coll. M. Ekins and S. Borghi; QM G340333, North Herald Cay, Coral Sea, 16.93°S, 149.19°E, 7–12 m, Bommie, 11 December 2022, SCUBA, coll. M. Ekins; QM G340345–46, South Herald Cay, Coral Sea, 17.019°S, 149.1397°E, 10–14 m, SE outside barrier wall, 12 December 2022, SCUBA, coll. M. Ekins and S. Borghi; QM G340395, North Flinders Reef, Coral Sea, 17.4362°S, 148.3317°E, 7–12 m, eastern edge of the reef, 15 December 2022, SCUBA, coll. M. Ekins and S. Borghi; QM G309093, Queensland, Fantome Island, 18.398°S, 146.305°E, 2 m, reef, 19 February 1987, NCIQ66C0445-X, coll. Australian Institute of Marine

Sciences and National Cancer Institute. QM G340334, Queensland, North Herald Cay, Coral Sea, 16.93°S, 149.19°E, 5–8 m, bommie, 11 December 2022, SCUBA, coll. M. Ekins: QM G340375, Queensland, leeward outside East Holmes Reef, Coral Sea, 16.5077°S, 147.9647°E, 8–12 m, wall, 14 December 2022, SCUBA, coll. M. Ekins and S. Borghi; QM G334595, Queensland, outside lagoon bommies, south side of South Western Herald Cay, 16.9879°S, 149.1289°E, 3–6 m, reef edge, 22 June 2016, snorkel, coll. M. Ekins.

Description

The holotype is encrusting, with mat ~2–4 mm thick, comprising several membrane-like extensions, overgrowing coralline algae (Fig. 9*a*). Polyps are evenly distributed across the colony surface. Most polyps are fully retracted and some are partially expanded (Fig. 9*b*).

Tentacle sclerites are mostly granular platelets up to 0.08 mm long (Fig. 10*a*), most with a symmetrical median constriction or lateral notches (Fig. 10*a*). Elongated platelets are present at the tentacle base, reaching up to 0.15 mm in length (Fig. 10*b*). These sclerites are arranged longitudinally in the tentacle, increasing in length toward the tentacle base, where they become similar in size to the shortest point sclerites.

Polyp sclerites are arranged as collaret and points. The collaret includes 4–6 rows of bent spindles up to 0.70 mm long (Fig. 10*c*). Point sclerites are up to 0.33 mm long (Fig. 10*d*), weakly arranged *en chevron*.

Coenenchymal sclerites (mat spindles) reach up to 2.6 mm in length (Fig. 10*e*) and are mostly bent or sinuous in outline (Fig. 10*e*). The sub-surface spindles are visible in the ethanol-preserved colony under a dissecting microscope.

Colour

The ethanol-preserved material is a uniform cream colour.

Living features

The colonies can overgrow large areas of coral rubble, with offshoot extensions. Underwater they are a beige or yellow colour (Fig. 32*d*). After collection, their colour is seen as a dull purple tint. The tentacles are white or yellow matching the colony colour (Fig. 32*d*). This species is common on the Great Barrier Reef, especially in shallow protected waters.

Etymology

The specific epithet *calyaceum* is derived from the Latin adjective *calyaceus*, meaning 'cup-like', from *calyx* (Latin). It refers to the calyx-like turrets into which the polyps retract.

Morphological variation

The morphological features of the paratypes resemble those of the holotype, except in dimensions. In QM G326843 the offshoot extensions are 5–10 mm in diameter.

Remarks

Rhytisma calyaceum sp. nov. differs from other congeners and sympatric species by its tentacle sclerites, which have a symmetrical median constriction and distinctly tapered ends. Additionally, the elongated platelets at the base of the tentacle are narrow, with some showing a symmetrical median constriction and tapered tips. Morphologically it is closest to *R. monticulum*, but it lacks the distinctive hillock-like formations with fully immersed polyps of *R. monticulum*. Conversely, the polyps are usually raised above the mat surface by turret-forming calyces. Additionally, *R. monticulum* has tentacle sclerites with asymmetrical and slightly irregular outlines that lack a distinct median constriction. The other sympatric species, *R. acoronatum* sp. nov., lacks a collaret. All three species are genetically distinct (Fig. 2, 3).

Distribution

Queensland, Great Barrier Reef (Fig. 1).

Rhytisma fuscum (Thomson & Henderson, 1906)

(Fig. 1, 11–13.)

Sympodium fuscum Thomson & Henderson, 1906, pp.408–409 [original description].

Parerythropodium fulvum fuscum (Thomson & Henderson, 1906) – Verseveldt (1969), p. 8 [new combination].

Rhytisma fuscum (Thomson & Henderson, 1906) – Alderslade (2000), p. 238.

Material examined

LECTOTYPE. TANZANIA: BMNH 1933.3.13.180, two fragments, Zanzibar, at ~6.1819°S, 39.1981°E, coll. J.A. Thomson [designated here]. **PARALECTOTYPE.** BMNH 1912.2.25.7, nine fragments; Zanzibar, approximate location (6.1819°S, 39.1981°E), coll. C. Crossland per Cambridge Museum [designated here].

Other material

TANZANIA: RMNH.COEL.46689 (e1); Mnemba Island, Prison, 6 January 1990.

SEYCHELLES: RMNH.COEL.45862, NIOP-E Seychelles Expedition 1992–1993, Sta. 735, La Digue Island, S coast, 4.3833°S, 55.8333°E, rocky shore, depth 8–16 m, scuba diving, 23 December 1992.

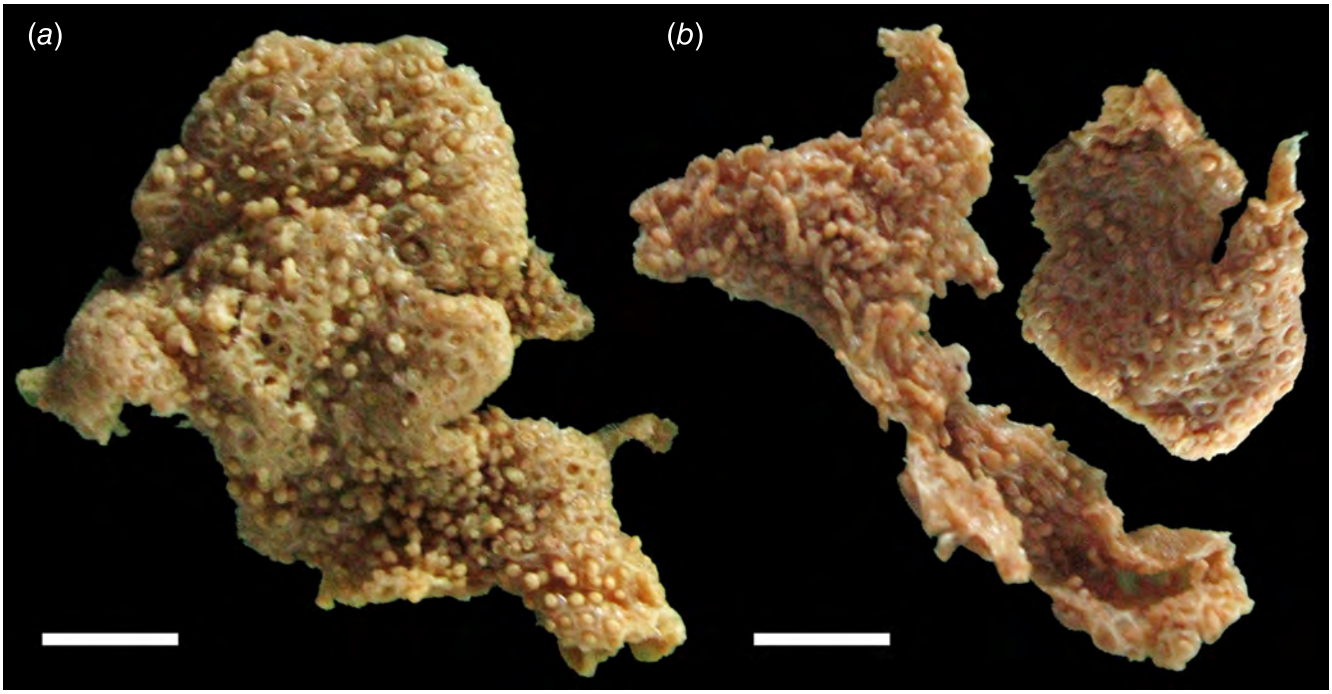

Fig. 11. *Rhytisma fuscum* (Thomson & Henderson, 1906). (*a*) Lectotype (BMNH 1933.3.13.180) with partly expanded polyps (*b*) paralectotype (BMNH 1912.2.25.7) with partly expanded polyps. Scale bars: 1 cm.

Re-description

The lectotype is a mat-like colony, ~1–2 mm thick, thinning towards the edge and exhibiting a honeycomb-like appearance (Fig. 11). Polyps are evenly distributed across the colony surface, some expanded and others retracted.

Tentacle sclerites are mostly granular platelets, up to 0.06 mm long, some featuring a shallow median constriction or asymmetrical lateral notches (Fig. 12*a*). Elongated platelets are present at the base of the tentacles, reaching up to 0.13 mm long (Fig. 12*b*). These sclerites are arranged longitudinally in the tentacle and become progressively shorter toward the tentacle base, approaching the size of the shortest point sclerites.

Polyp sclerites are arranged as collaret and points. The collaret comprises 5–6 rows of bent spindles up to 0.7 mm long (Fig. 12*c*). Point sclerites are up to 0.36 mm long (Fig. 12*d*), weakly arranged *en chevron*.

The mat spindles are up to 1.9 mm long (Fig. 12*e*). They are mostly bent or with a sinuous outline, and some are bifurcated at their tip.

Colour

The ethanol-preserved material is light yellow–beige.

Living features

According to Thomson and Henderson (1906, p. 408) the colonies were reddish-brown, with drab-brown tentacles.

Morphological variation

The morphological features of the paralectotype fragments (BMNH 1912.2.25.7) are consistent with those of the lectotype (Fig. 12, 13).

Remarks

The original description of *Sympodium fuscum* by Thomson and Henderson (1906) did not include a holotype designation and was based on more than one specimen, thus constituting a syntype series. Although the specimen BMNH 1912.2.25.7 has been referred to as 'type' at BMNH, it is not a formal holotype designation under the ICZN. In order to secure the objective application of the name, BMNH 1933.3.13.180 is here designated as lectotype of *Sympodium fuscum* Thomson & Henderson, 1906. The specimen BMNH 1912.2.25.7 is thus regarded as a paralectotype.

The current findings on the type material of *R. fuscum* correspond in general to the original description by Thomson and Henderson (1906), who reported the presence of sclerites in the colony, within the polyps, and a few small irregularly disposed sclerites in the tentacles. However, the original account did not include illustrations or measurements of the sclerite types. It was also noted that there is 'no transverse ring of spicules markedly different from the longitudinally disposed spicules', indicating the absence of collaret sclerites. Thomson and Henderson (1906, p. 409) also reported no tentacle sclerites in *Sympodium fulvum* (Forskål, 1775).

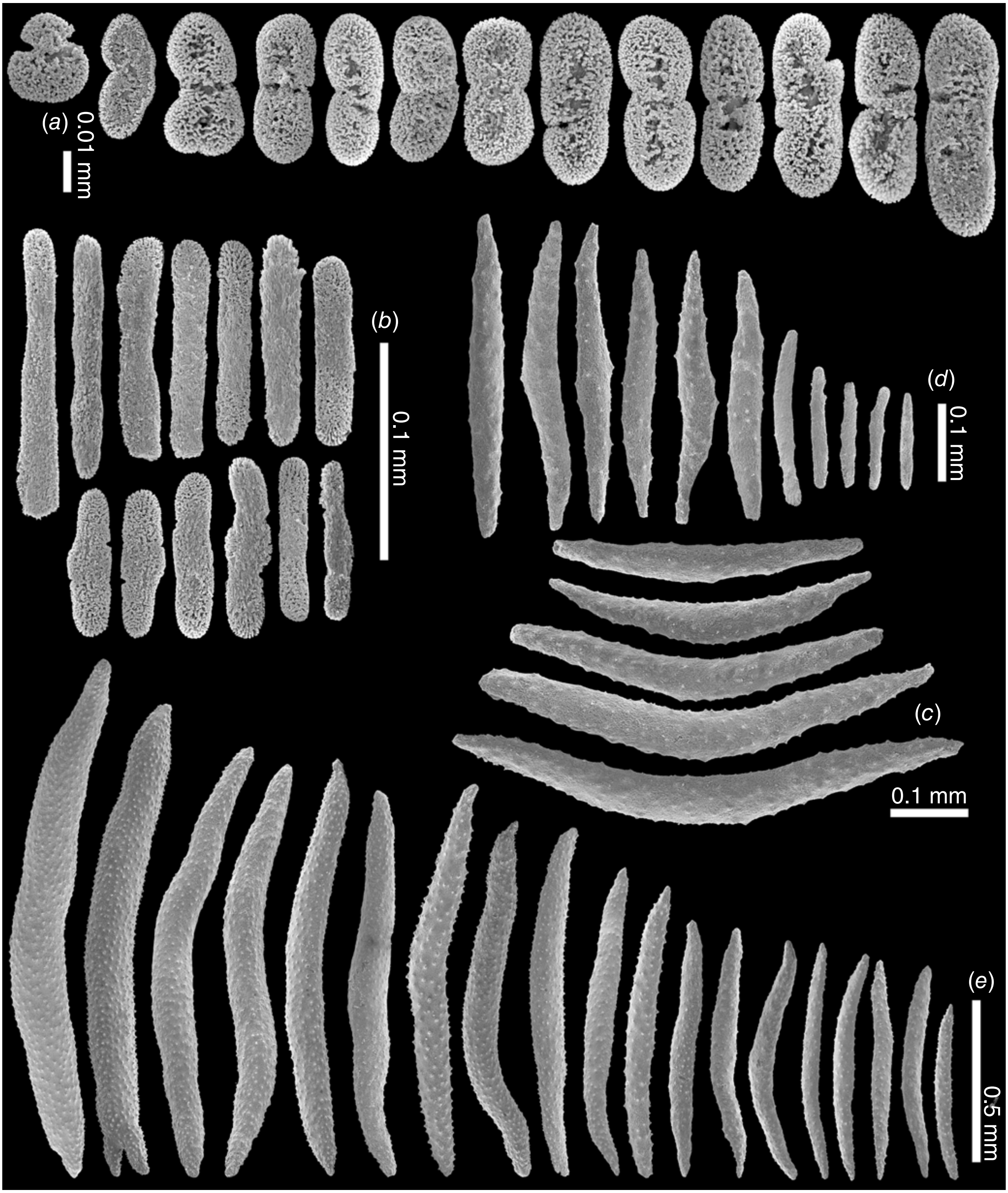

Fig. 12. *Rhytisma fuscum* (Thomson & Henderson, 1906), lectotype (1933.3.13.180). (*a*) Tentacle sclerites (*b*) elongated platelets at the base of the tentacles (*c*) collaret sclerites (*d*) point sclerites (*e*) spindles of the mat.

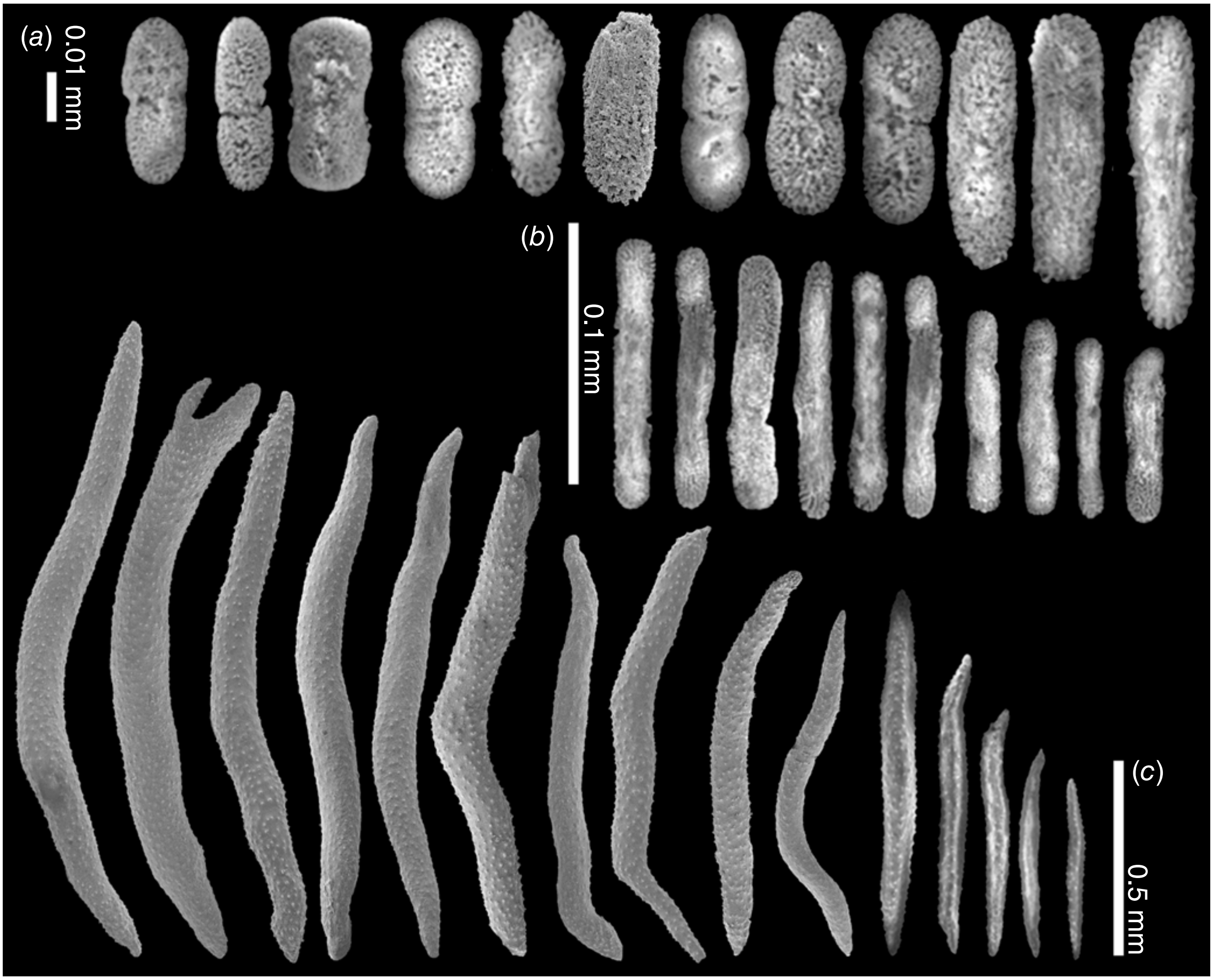

Fig. 13. *Rhytisma fuscum* (Thomson & Henderson, 1906), paralectotype (BMNH 1912.2.25.7). (*a*) Tentacle sclerites (*b*) elongated platelets at the base of the tentacles (*c*) spindles of the mat. Note that the collaret and point sclerites were not shown, they were too damaged and broken in the piece we examined.

Re-examination of both specimens confirms the presence of collaret sclerites in *R. fuscum*. However, BMNH 1912.2.25.7 exhibits only a weakly developed collaret. Verseveldt (1969) re-described the schizo-cotype (type fragment) under the name *Parerythropodium fulvum fuscum* (Thomson & Henderson, 1906), providing some details of the sclerites, although without figures except for a schematic drawing showing the arrangement of polyp sclerites and confirming the presence of a collaret (Verseveldt 1969, fig. 1b).

The diagnostic features of *R. fuscum* include the size and shape of the tentacle platelets, particularly those with median constrictions or lateral notches, and the presence of elongated platelets at the tentacle base (Fig. 12, 13, Table 1). The species is further distinguished by a weakly developed collaret and a faint chevron-like arrangement of the point sclerites.

Distribution

Thomson and Henderson (1906) reported this species from Tanzania and Kenya (Fig. 1).

Rhytisma inaequale Samimi-Namin, Benayahu, Ekins & McFadden, sp. nov.

(Fig. 14, 15, 32*c*.)

ZooBank: urn:lsid:zoobank.org:act:496F1D3C-A166-408A-B317-279751A7D641

Material examined

HOLOTYPE. TAIWAN: SMNHTAU_Co_35739, six fragments, Green Island, 22.6789°N, 121.4624°E, 11–15 m, 4 September 2012, coll. Y. Benayahu.

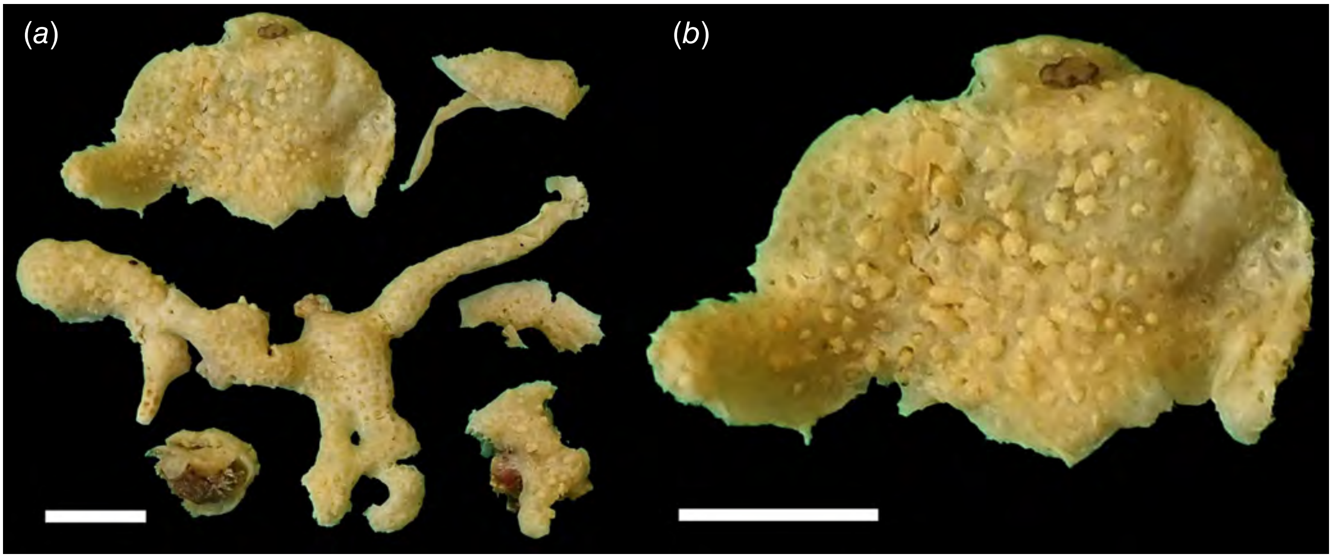

Fig. 14. *Rhytisma inaequale* sp. nov., holotype (SMNHTAU_Co_35739). (*a*) Fragments of colony, some with ribbon-like extensions, polyps mostly retracted (*b*) enlarged fragment. Scale bars: 1 cm.

PARATYPE. TAIWAN: SMNHTAU_Co_37887, five fragments, Green Island, Light House, 22.6756°N, 121.4624°E, 5.7–12.7 m, 4 October 2019, coll. Y. Benayahu.

Other material

MALAYSIA: CASIZ 307709, Sabah, Layang Layang Atoll, outer reef adjacent to L-L Resort and runway on S side of atoll. 7.37°N, 113.84°E, 17 October 2006, coll. Coral Reef Research Foundation.

Description

The holotype is an encrusting mat-like colony, ~1–3 mm thick, comprising six fragments, some with membrane-like extensions (Fig. 14). The colony surface exhibits a few hillocks where the mat reaches up to 2 mm in thickness, thinning toward the edges. Polyps are evenly distributed across the colony surface; some are fully retracted, whereas others are partially or fully expanded.

Tentacle sclerites are mostly granular platelets up to 0.08 mm long (Fig. 15*a*), with an asymmetrical lateral outline and conspicuous median constriction (Fig. 15*a*). Elongated platelets and rods are present at the tentacle base, reaching up to 0.06 mm in length (Fig. 15*b*). These sclerites are arranged longitudinally in the tentacle, increasing in length toward the tentacle base, where they become similar in size to the shortest point sclerites.

Polyp sclerites are arranged as collaret and points. The collaret includes 4–6 rows of spindles up to 0.60 mm long (Fig. 15*c*). Point sclerites are up to 0.40 mm long (Fig. 15*d*), arranged *en chevron*.

The mat spindles reach up to 1.30 mm in length (Fig. 15*e*) and are mostly straight, with some bent or curved in outline. The sub-surface spindles are visible in the ethanol-preserved colony under a dissecting microscope.

Colour

The ethanol-preserved material is light cream and the expanded polyps are whitish.

Living features

The colonies were found growing on hard reef substrate. The live specimen has a yellow colour and the polyps are yellowish when expanded (Fig. 32*c*).

Etymology

The specific epithet inaequale is derived from Latin, meaning ‘uneven, irregular’, and refers to the irregular lateral outline of the tentacle sclerites, which are strongly constricted and uneven in profile.

Morphological variation

The morphological features of the paratype fragments resemble those of the holotype, except in size.

Remarks

Rhytisma inaequale sp. nov. is characterised by its distinctive tentacle sclerites, which have a markedly asymmetrical, irregular outline and a conspicuous median constriction that is more pronounced than in any other congener (Fig. 15, Table 1). Genetically, the species is closely related to *R. karibu* sp. nov. (Fig. 2, 3), however their morphological features reliably distinguish them. In addition, the two species are geographically separated.

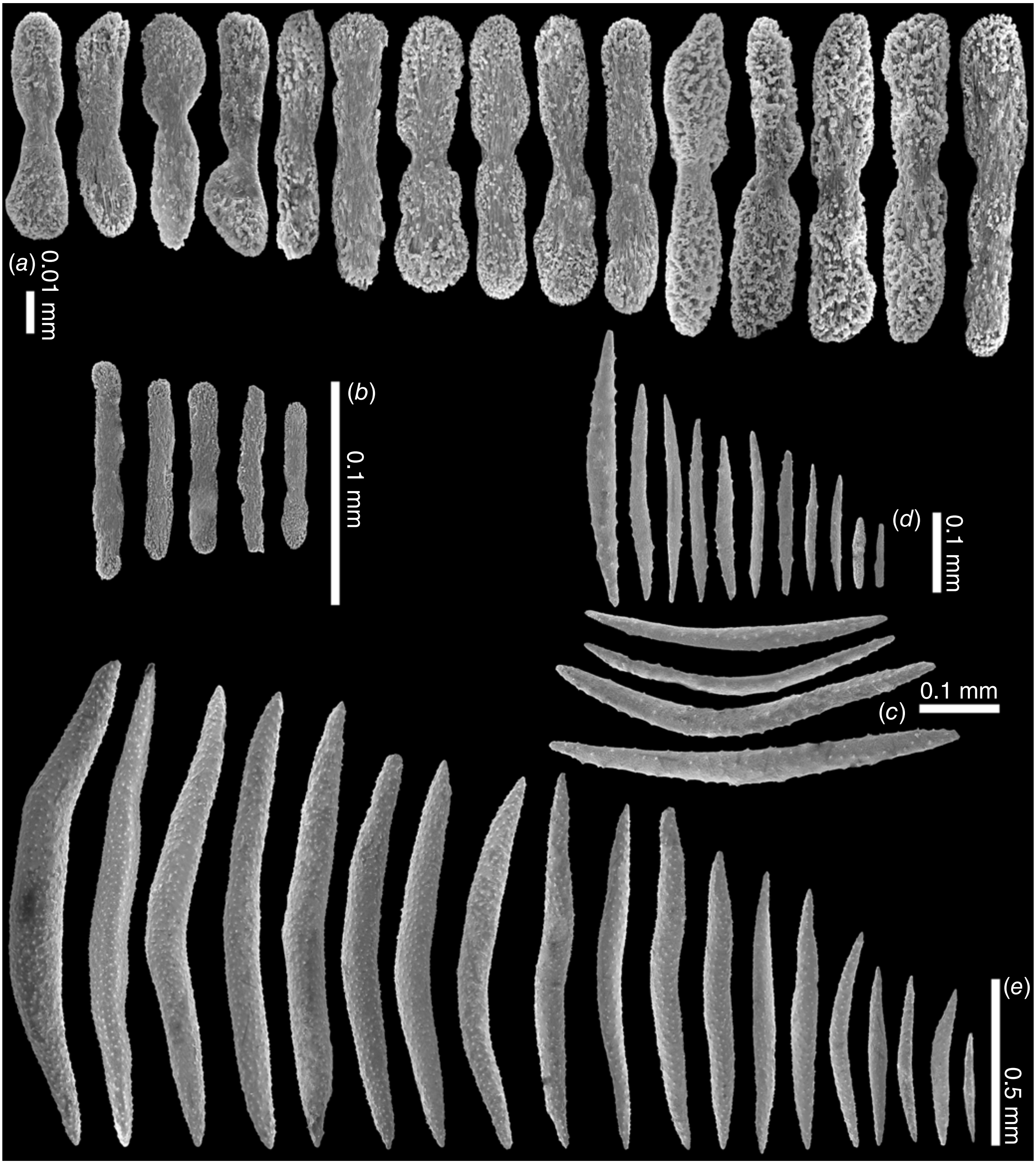

Fig. 15. *Rhytisma inaequale* sp. nov., holotype (SMNHTAU_Co_35739). (*a*) Tentacle sclerites (*b*) elongated platelets at the base of the tentacles (*c*) collaret sclerites (*d*) point sclerites (*e*) spindles of the mat.

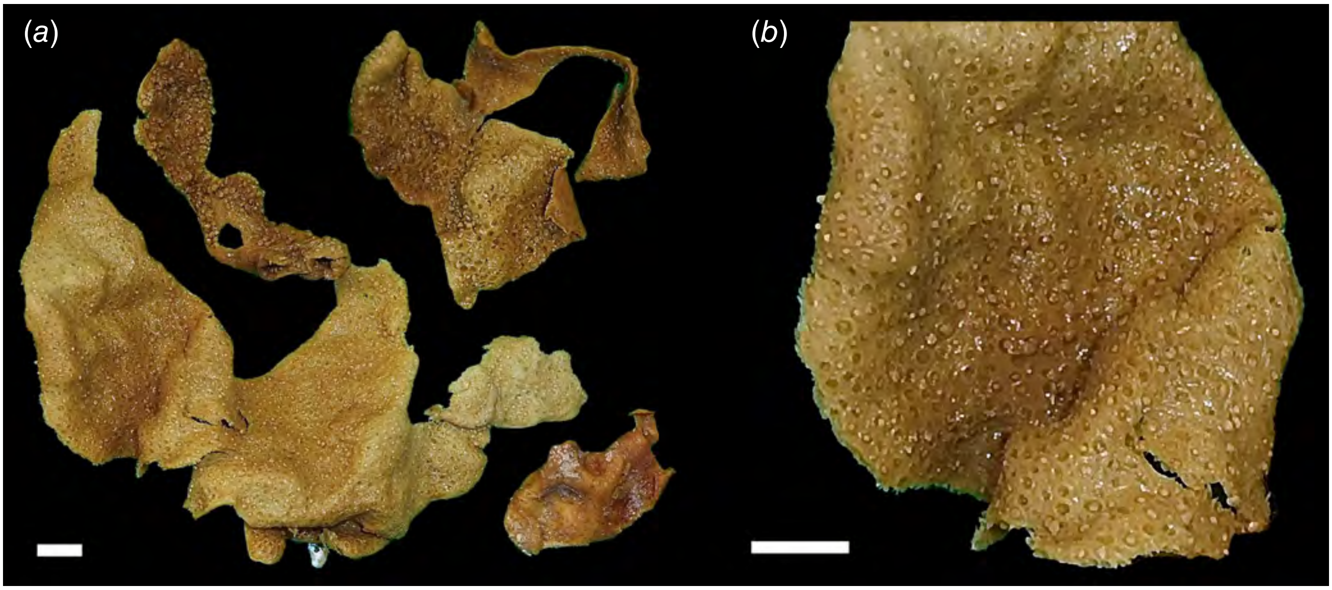

Fig. 16. *Rhytisma karibu* sp. nov., holotype (SMNHTAU_Co_32722). (*a*) Fragments of colony (*b*) enlarged fragment with partially retracted polyps. Scale bars: 1 cm.

Distribution

Green Island, Taiwan; Malaysia (Fig. 1). Molecular evidence suggests that this species also occurs in the Philippines (McFadden *et al.* 2025).

Rhytisma karibu Benayahu, Samimi-Namin, Ekins & McFadden, sp. nov.

(Fig. 1, 16–19, 33*a*, *b*.)

ZooBank: urn:lsid:zoobank.org:act:5BAD3DEF-2876-4033-812C-27B35CDAE46E

Material examined

HOLOTYPE. TANZANIA: SMNHTAU_Co_32722, three fragments of the same colony, Mwamba Wamba, on dead reef, 4.9261°S, 39.2506°E, 0–15 m, 9 December 2004, coll. Y. Benayahu.

PARATYPES. KENYA: SMNHTAU_Co_32513, three fragments of the same colony, Shimoni, 4.6564°S, 39.3592°E, 6 m, 5 February 2004, coll. Y. Benayahu; SMNHTAU_Co_32516, Shimoni, 4.6564°S, 39.3592°E, 6 m, 5 February 2004, coll. Y. Benayahu. SMNHTAU_Co_32518, Kitungamwe, 4.8137°S, 39.3667°E, 8 m, 7 February 2004, coll. Y. Benayahu. QM G322136, Nungwi, 5.22°S, 39.2593°E, 20 m, 4 September 2004, coll. S. Said.

TANZANIA: SMNHTAU_Co_32811, Pemba Is. Uvinje Gap, 5.1350°S, 39.6494°E, on deep wall, 0–30 m, 3 December 2004, coll. Y. Benayahu.

Other material

TANZANIA: SMNHTAU_Co_32693, Pemba Is. Uvinje Gap, 5.1350°S, 39.6494°E, on deep wall, 0–30 m, 3 December 2004, coll. Y. Benayahu; SMNHTAU_Co_32835, Shundo, 4.8814°S, 39.3028°E, 0–25 m, 10 December 2004, coll. Y. Benayahu. RMNH.COEL.49688, Mnemba Island.

MADAGASCAR: USNM54020, Nosy Be, Ambarionaombi Point, station JR–30, approximate location (13.4389°S, 48.3462°E), intertidal, 1 m, International Indian Ocean Expedition, 12 January 1964, coll. J.J. Rudloe; SMNHTAU_Co_36116, Nosy Be, Ronald Point, 3 December 2012, 13.3922°S, 48.0024°E, 19–27 m, coll. Y. Benayahu; SMNHTAU_Co_36000, Le Banc du Castor, 28 November 2012, 12.8518°S, 48.4181°E, depth 22–24 m, coll. Y. Benayahu; UF6121, off NW side of Nosy Tanikely, 13.4806°S, 48.2223°E, depth 4–6 m, 14 April 2008, coll. F. Michonneau, G. Paulay and T. Werner.

KENYA: SMNHTAU_Co_32240, Shundo, unknown, 11 February 2004, 4.8814°S, 39.3028°E, 12 m, coll. Y. Benayahu.

Description

The holotype is an encrusting mat-like colony, 1–3 mm thick, with some polyps expanded to varying degrees (Fig. 16).

Tentacle sclerites are mostly granular platelets, up to 0.06 mm long (Fig. 17*a*), exhibiting one or more symmetrical median and lateral constrictions or side notches (Fig. 17*a*). The sclerites have expanded or flared ends, giving them a flattened, bone-like appearance. Elongated platelets are present at the tentacle base and reach up to 0.12 mm in length (Fig. 17*b*). These sclerites are arranged longitudinally in the tentacle, increasing in length toward the tentacle base, where they become similar in size to the shortest point sclerites.

Polyp sclerites are arranged as collaret and points. The collaret includes 5–6 rows of bent spindles up to 0.60 mm long (Fig. 17*c*). Point sclerites are up to 0.36 mm long (Fig. 17*d*), weakly arranged *en chevron*.

The mat spindles reach up to 2.3 mm in length (Fig. 17*e*). They are mostly bent or with a sinuous outline and are sometimes bifurcated at the tips (Fig. 17*e*).

Colour

The ethanol-preserved holotype is dark yellowish-brown.

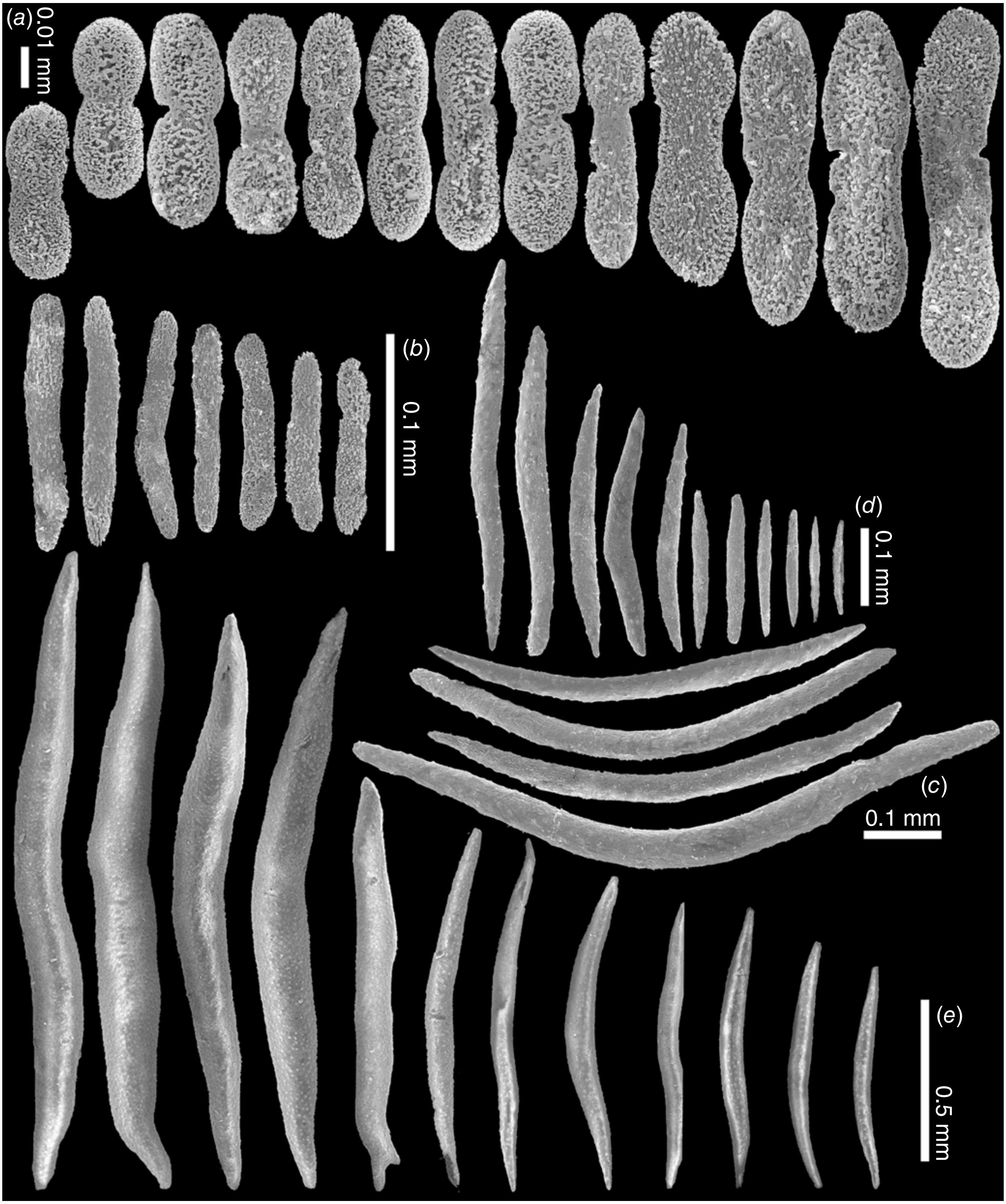

Fig. 17. *Rhytisma karibu* sp. nov., holotype (SMNHTAU_Co_32722). (*a*) Tentacle sclerites (*b*) elongated platelets at the base of the tentacles (*c*) collaret sclerites (*d*) point sclerites (*e*) spindles of the mat.

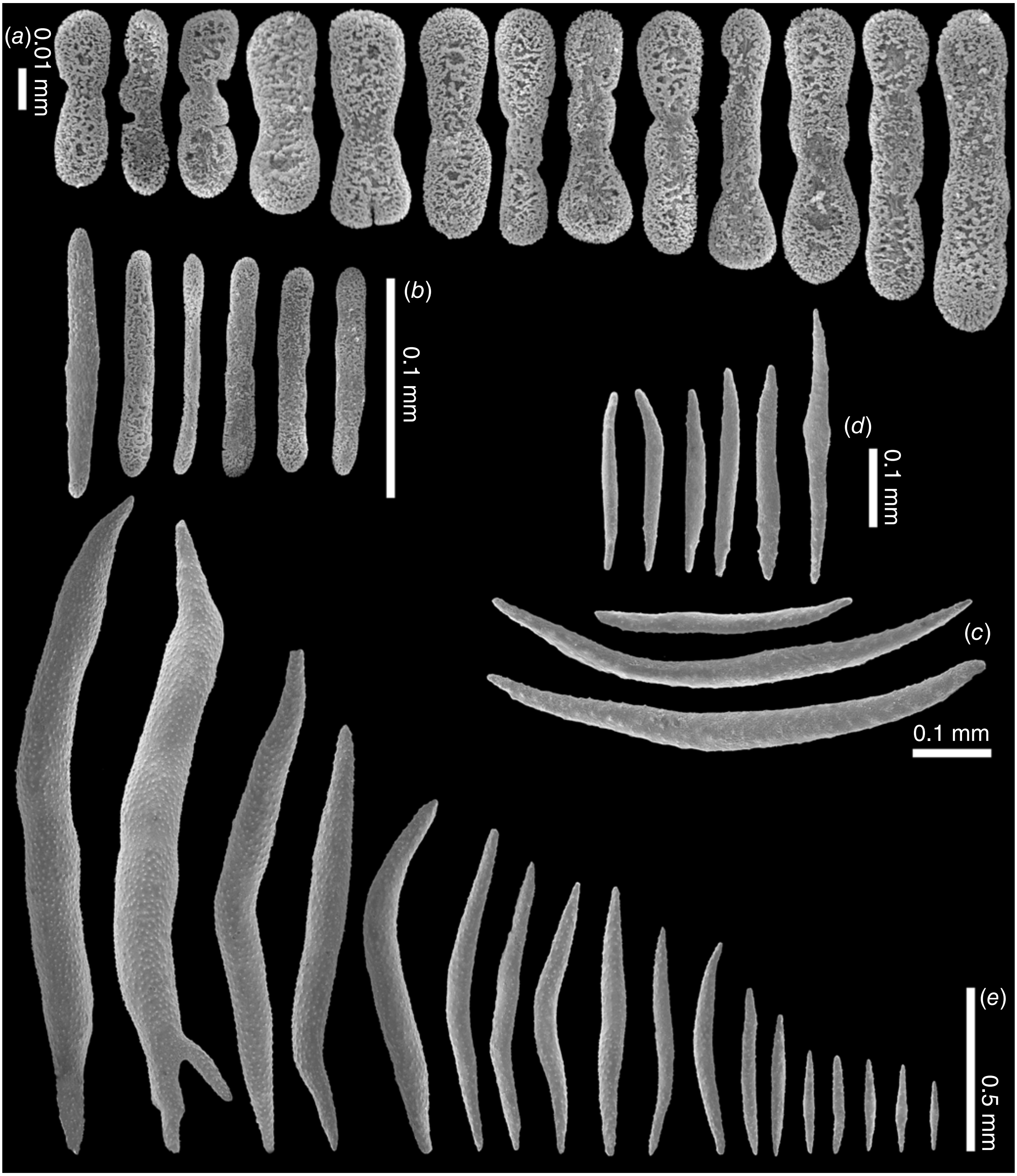

Fig. 18. *Rhytisma karibu* sp. nov., paratype (SMNHTAU_Co_32518). (*a*) Tentacle sclerites (*b*) elongated platelets at the base of the tentacles (*c*) collaret sclerites (*d*) point sclerites (*e*) spindles of the mat.

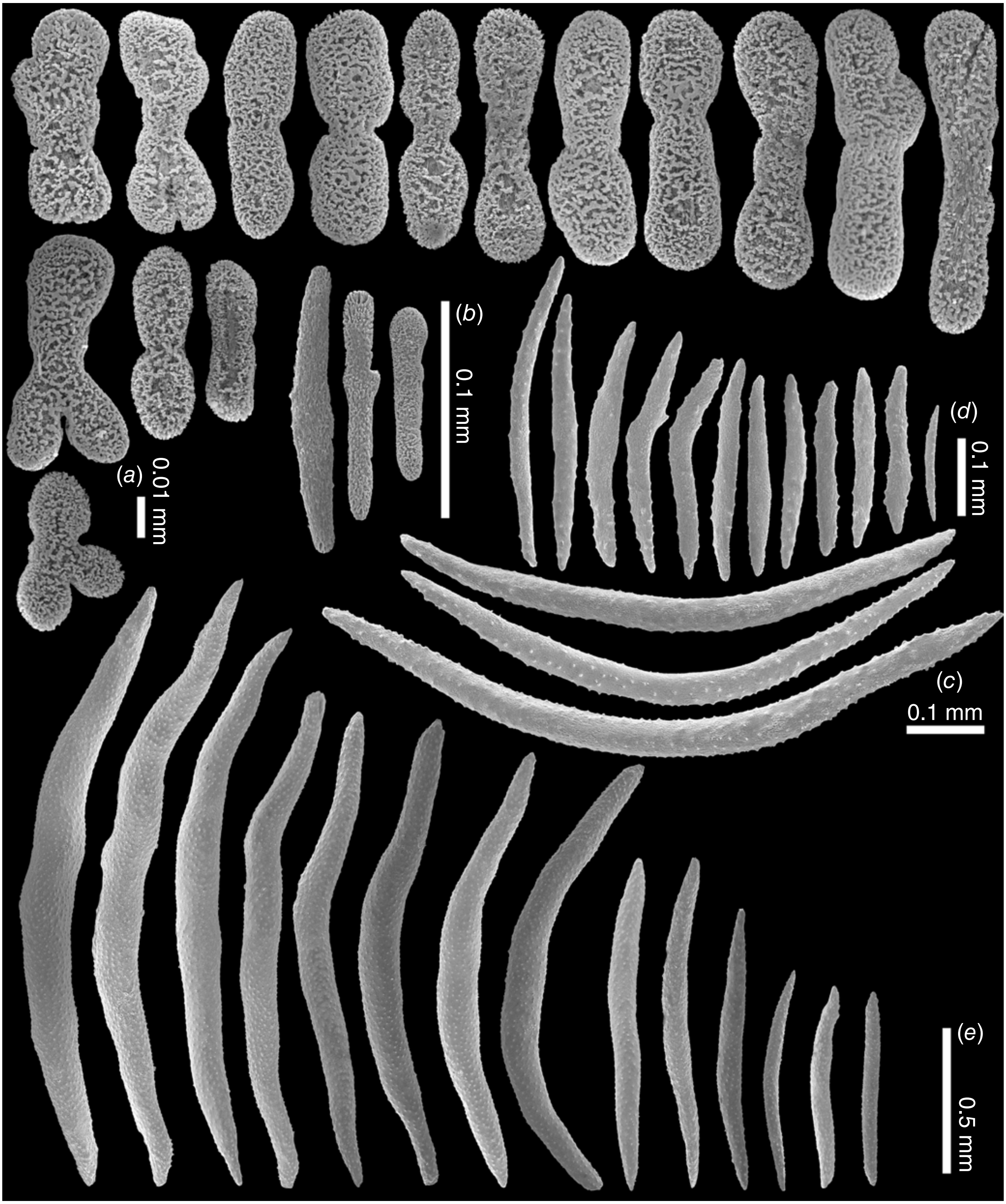

Fig. 19. *Rhytisma karibu* sp. nov., paratype (SMNHTAU_Co_32811). (*a*) Tentacle sclerites (*b*) elongated platelets at the base of the tentacles (*c*) collaret sclerites (*d*) point sclerites (*e*) spindles of the mat.

Living features

The colonies were found growing on seagrass blades or calcareous reef substrate, with visibly expanded yellow polyps (Fig. 33*a*, *b*). When the polyps are retracted, the mat surface reflects the contour of the underlying reef substrate. The live colony is yellow–grey in colour.

Etymology

The specific epithet *karibu* means 'welcome' in Swahili. It is designated to express gratitude for the warm hospitality extended to Y. Benayahu during fieldwork in Kenya and Tanzania.

Morphological variation

The paratypes (SMNHTAU_Co_32513, 32518) resemble the holotype in general (Fig. 17–19). They differ in colony size and colour, ranging from light cream to brown. Additionally, the holotype has more tuberculation on the collaret sclerites.

Remarks

Rhytisma karibu sp. nov. is distinguished from other species, especially the three sympatric species *R. rubiginosum*, *R. fuscum* and *R. oblongum* sp. nov., by a combination of the tentacle sclerites, including asymmetrical constrictions, an irregular lateral outline, notched margins, and flared ends that give the platelets a bone-like appearance (Fig. 17*a*–19*a*, Table 1). It is further characterised by its notably long and occasionally bifurcated mat spindles (Fig. 17*e*–19*e*).

Distribution

SW Indian Ocean (Kenya, Tanzania, Madagascar, Mozambique).

Rhytisma monticulum (Verseveldt, 1982)

(Fig. 1, 20–23, 32*f*.)

=*Alcyonium monticulum* Verseveldt, 1982, pp. 144–145.

Material examined

PARATYPE. AUSTRALIA: RMNH.COEL.13905, John Brewer Reef, near Townsville, Great Barrier Reef, on SE outer slope, at ~18.6305°S, 147.0808°E, 10 m, 2–6 November 1976, V602, coll. T. Done.

Other material

AUSTRALIA: QM G339814, Queensland, Townsville, Great Barrier Reef, John Brewer Reef, on SE outer slope, 18.6308°S, 147.0811°E, 12 m, 22 November 2022, SCUBA, coll. M. Ekins and S. Borghi; QM G340256, Queensland, Queen Christina Cay, Lihou Reef, Coral Sea, lagoon bommies, 17.3288°S, 152.0578°E, 12 m, 5 December 2022, SCUBA, coll. M. Ekins and S. Borghi; QM G340257, Queensland, Queen Christina Cay, Lihou Reef, Coral Sea, lagoon bommies, 17.3288°S, 152.0577°E, 10 m, 5 December 2022, SCUBA, coll. M. Ekins and S. Borghi; QM G340366, Queensland, West Holmes Reef, Coral Sea, leeward outside edge, 16.433°S, 147.852°E, 6–12 m, 13 December 2022, SCUBA, coll. M. Ekins and S. Borghi; QM G340373, Queensland, East Holmes Reef, Coral Sea, leeward outside edge, bommies, 16.5077°S, 147.9647°E, 8–12 m, 14 December 2022, SCUBA, coll. M. Ekins and S. Borghi; QM G12639, Queensland, Holbourne Island, 19.7333°S, 148.3667°E, 6 October 1979, coll. J. Coll; QM G307433, Queensland, Wistari Reef, Heron Island, 23.45°S, 151.85°E, 13 m, 10 August 1996, SCUBA, coll. P. Tomkins.

Re-description

The paratype RMNH.COEL.13905 is an encrusting mat-like colony, 2–10 mm thick, comprising nine fragments (Fig. 20). According to Verseveldt (1982), these fragments were originally connected by membrane-like offshoots. Some low hillocks or knob-like elevations are present where the mat is thickest, thinning toward the edges. Polyps are evenly

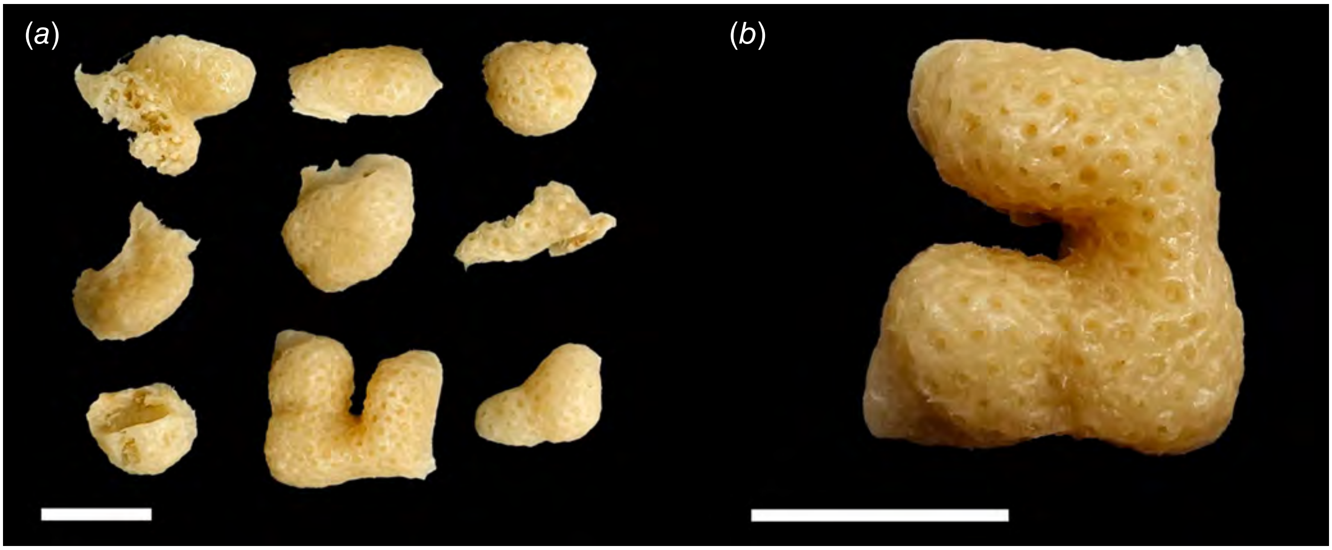

Fig. 20. *Rhytisma monticulum* (Verseveldt, 1982), paratype, RMNH.COEL.13905. (*a*) Paratype fragments (*b*) surface of the colonies at higher magnification. Scale bars: 1 cm.

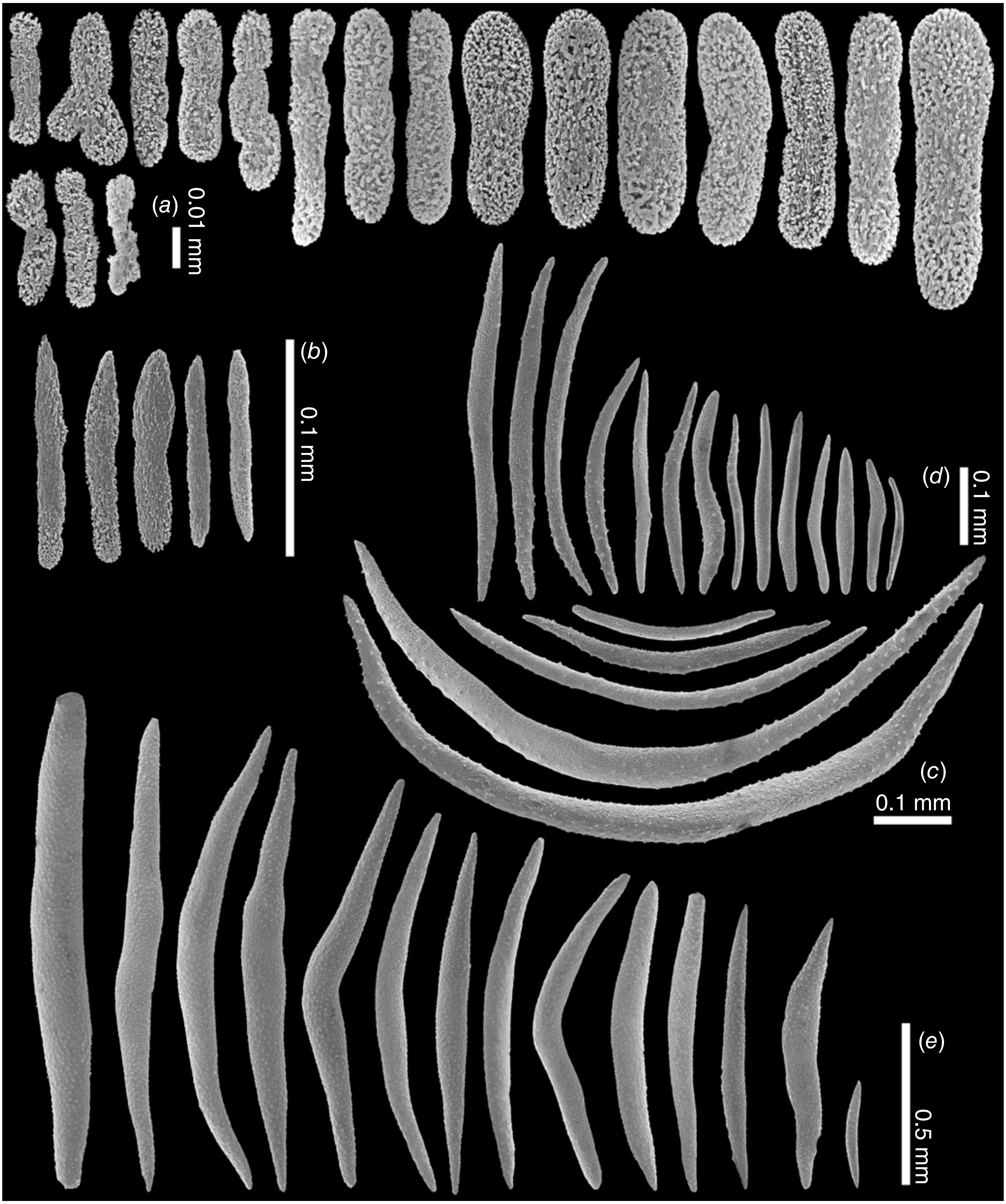

Fig. 21. *Rhytisma monticulum* (Verseveldt, 1982), paratype (RMNH.COEL.13905). (*a*) Tentacle sclerites (*b*) elongated platelets at the base of the tentacles (*c*) collaret sclerites (*d*) point sclerites (*e*) spindles of the mat.

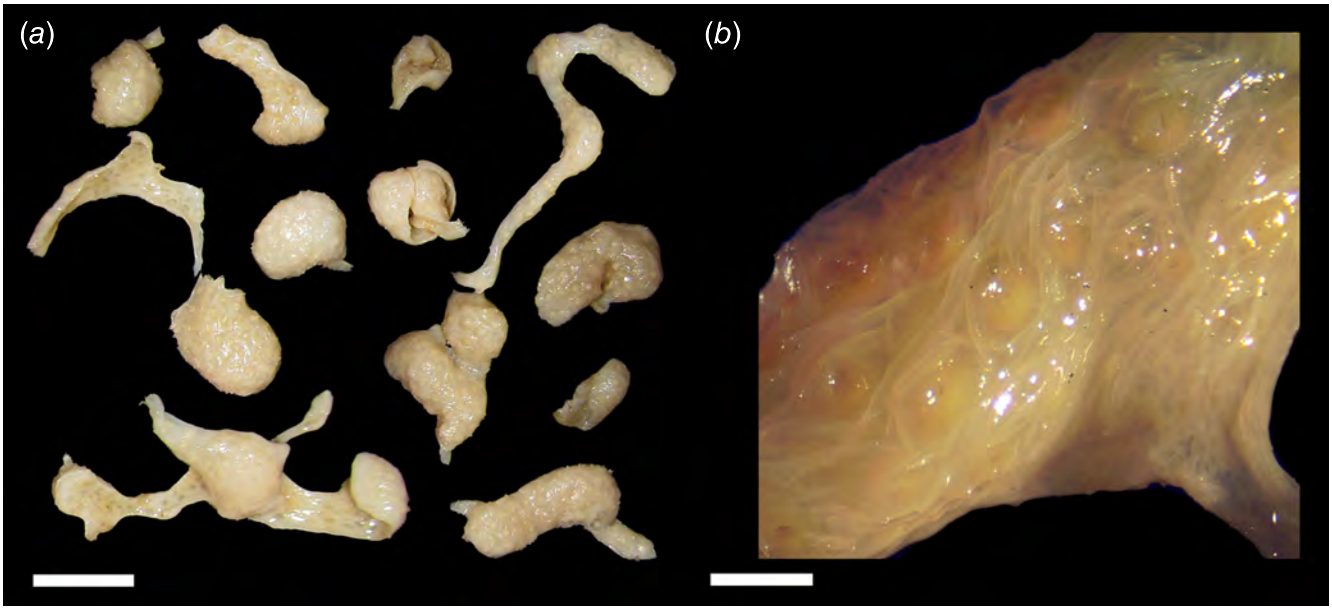

Fig. 22. *Rhytisma monticulum* (Verseveldt, 1982). (*a*) Topotype colony fragments (QM G339814) (*b*) surface of the colonies at higher magnification. Scale bars: *a*, 1 cm; *b*, 1 mm.

distributed across the colony surface and are fully retracted into small pit-like apertures (Fig. 20*b*).

Tentacle sclerites are mostly granular platelets up to 0.1 mm long (Fig. 21*a*), with some exhibiting asymmetrical shallow median constrictions or lateral notches (Fig. 21*a*). Elongated platelets and rods are present at the tentacle base and reach up to 0.10 mm in length (Fig. 21*b*). These sclerites are arranged longitudinally in the tentacle, increasing in length toward the tentacle base, where they become similar in size to the shortest point sclerites.

Polyp sclerites are arranged as collaret and points. The collaret includes 6–10 rows of spindles up to 0.80 mm long (Fig. 21*c*). Point sclerites are up to 0.58 mm long (Fig. 21*d*), arranged *en chevron*.

The mat spindles reach up to 1.6 mm in length (Fig. 21*e*), are mostly straight or curved in outline, and are visible in the ethanol-preserved colony under a dissecting microscope.

Colour

The ethanol-preserved material is light cream, and the expanded polyps are almost white.

Living features

Colony dark grey–blue with light grey–blue polyps (Verseveldt 1982).

Morphological variation

Fresh material from the type locality enabled comparative genetic analysis within the genus. The specimens collected from the type locality share the characteristic ribbon-like colony morphology (Fig. 20, 22) and exhibit sclerites similar to those of the paratype (Fig. 21, 23), with two specimens (QM G339814, QM G340366) having larger mat spindles up to 2 mm. All newly collected specimens are from the type locality (i.e. topotypes).

Remarks

The holotype (RMNH.COEL.13904) is too small for re-examination (Verseveldt 1982), and therefore the current study was based solely on paratype fragments. The original description erroneously placed the species in the genus *Alcyonium*, primarily due to the hillock-like colony form, although the sclerites and colony surface were noted to closely resemble those of *Parerythropodium fulvum* (Forskål, 1775). Colonies of *Rhytisma* species can occasionally exhibit thickened or fleshy hillocks (Fig. 32*f*), and the genus diagnosis has been amended accordingly.

The composition and size range of the sclerites of *A. monticulum* support its reassignment to the genus *Rhytisma*, as does the phylogenetic analysis of barcoding loci (Fig. 2). The paratype fragments examined here match the morphological features reported in the original holotype description, with some variation in size. The holotype displays slightly longer spindles (up to 2.6 mm) and longer tentacle sclerites (up to 0.10 mm).

Rhytisma monticulum is distinguished by its characteristic hillock- or knob-like colonies and by its tentacle sclerite morphology, which includes elongated tentacle platelets with indistinct median constrictions and irregular lateral notches (Fig. 21*a*, 23*a*, Table 1), as well as distinct collaret sclerites up to 1 mm long (Fig. 21*c*, 23*c*). It morphologically comes close to *Rhytisma calyaceum* sp. nov. from the Great

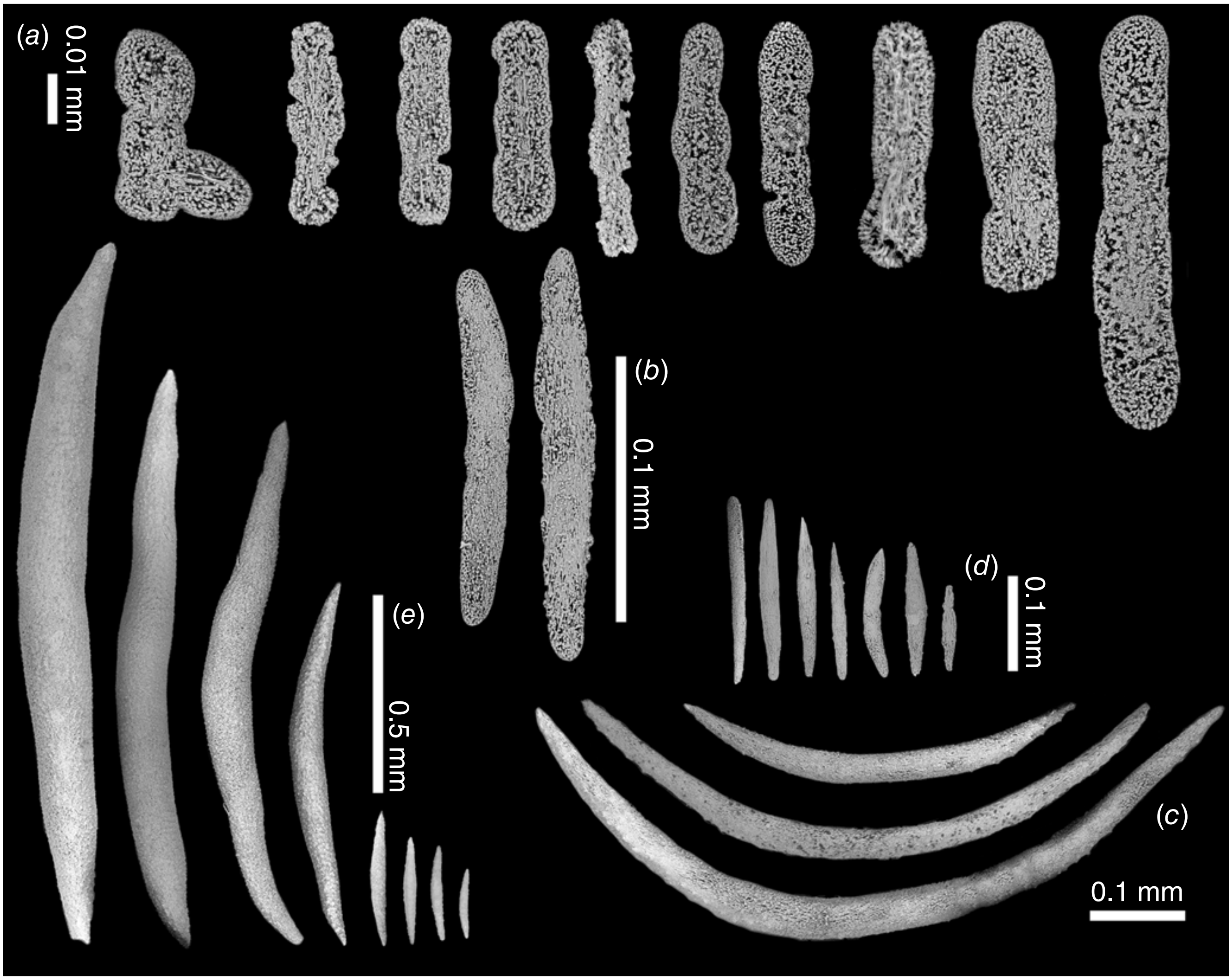

Fig. 23. *Rhytisma monticulum* (Verseveldt, 1982), QM G339814. (*a*) Tentacle sclerites (*b*) elongated platelets at the base of the tentacles (*c*) collaret sclerites (*d*) point sclerites (*e*) spindles of the mat.

Barrier Reef; however, *Rhytisma calyaceum* sp. nov. possesses tentacle sclerites with a pronounced median constriction (Fig. 8*a*). The availability of fresh material from the type locality has enabled genetic analyses, which suggest the two taxa are distinct species (Fig. 2).

Distribution

NE Australia, Great Barrier Reef.

Rhytisma oblongum Benayahu, Samimi-Namin, Ekins & McFadden, sp. nov.

(Fig. 1, 24–26, 33*e*, *f*.)

ZooBank: urn:lsid:zoobank.org:act:10014A07-52F6-4B76-B054-8770D7AAD4C2

Material examined

HOLOTYPE. MADAGASCAR: SMNHTAU_Co_36146, two fragments, Nosy Be, Ronald Point, Bai des Risses, 13.4834°S, 47.9787°E, 2–14 m, 3 December 2012, coll. Y. Benayahu.

Other material

MADAGASCAR: USNM54018, Nosy Be, Ambanoro Village, station JR–4, approximate location (13.403°S, 48.299°E), intertidal, 0.3 m, International Indian Ocean Expedition, 19 December 1963, coll. J.J. Rudloe; SMNHTAU_Co_36061, 12.9942°S, 48.4874°E, 4 m, 1 December 2012, coll. Y. Benayahu.

KENYA: SMNHTAU_Co_32503, five fragments of the same colony, Likoni, Shelly Beach, Mpwata Creek, opposite of Reef Hotel, ~4.0384°S, 39.7284°E, 9 m, 3 February 2003, coll. Y. Benayahu.

Description

The holotype is an encrusting mat-like colony, 1–2 mm thick, with thinner edges (Fig. 24). Polyps are retracted, and only the tentacle tips are visible on the colony surface (Fig. 24*b*).

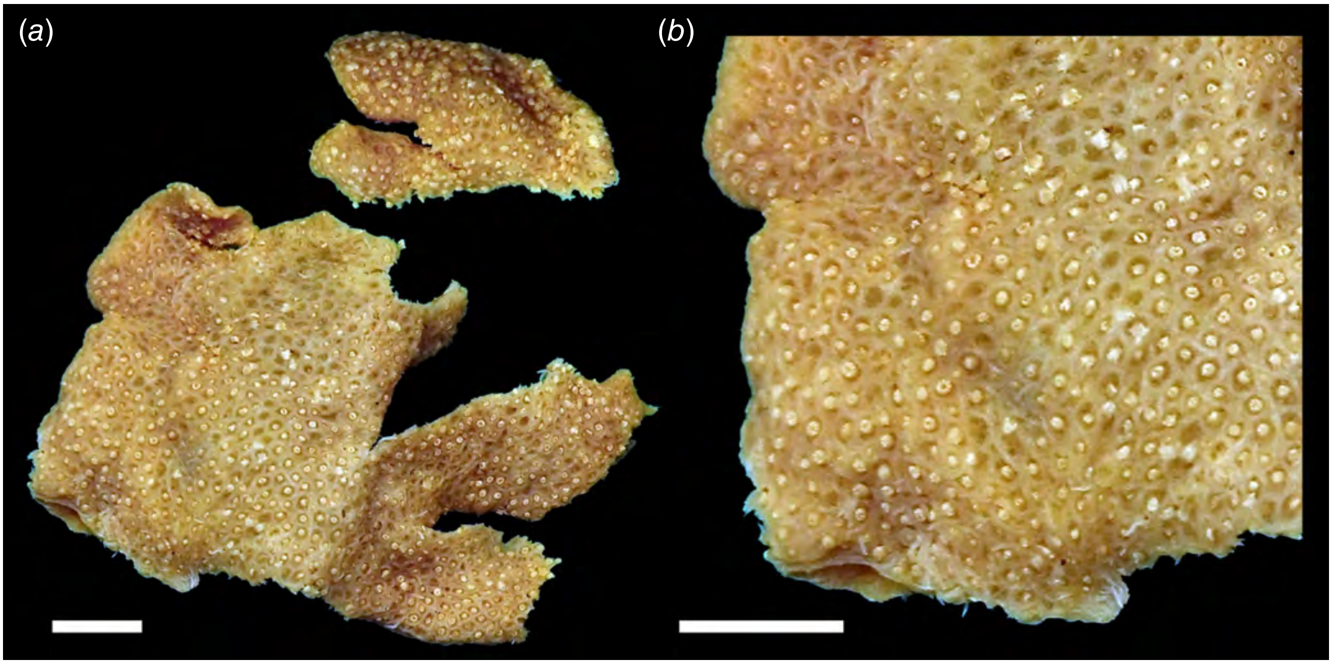

Fig. 24. *Rhytisma oblongum* sp. nov., holotype (SMNHTAU_Co_36146). (*a*) Fragments of colony (*b*) enlarged fragment with partly expanded polyps. Scale bars: 1 cm.

Tentacle sclerites are mostly granular platelets up to 0.09 mm long (Fig. 25*a*), with a nearly ellipsoidal outline, median constriction and faint lateral notches. Elongated platelets are present in the tentacle base, reaching up to 0.14 mm in length (Fig. 25*b*). These sclerites are arranged longitudinally in the tentacle, increasing in length toward the tentacle base, where they become similar in size to the shortest point sclerites.

Polyp sclerites are arranged as collaret and points. The collaret includes 5–6 rows of bent spindles up to 0.45 mm long (Fig. 25*c*). Point sclerites are up to 0.18 mm long (Fig. 25*d*), arranged *en chevron* and bearing conical tubercles (Fig. 25*d*).

The mat spindles reach up to 2.60 mm in length (Fig. 25*e*). They are mostly bent or sinuous in outline, occasionally divided at the tip (Fig. 25*e*). These sclerites have widely spaced tubercles (Fig. 25*e*).

Colour

The ethanol-preserved holotype is cream.

Living features

The live colony features expanded polyps displaying a greenish tinge (Fig. 33*e*, *f*). When the polyps are retracted, the surface reveals their openings.

Etymology

The specific epithet *oblongum* is derived from Latin, meaning 'elongated' or 'oblong', and refers to the shape of the platelets in the tentacles.

Morphological variation

One of the specimens (SMNHTAU_Co_32503) differs slightly from the holotype by having a greater number of tentacle sclerites with a median constriction, and more prominent yet more sparsely distributed tubercles on the collaret, point and mat sclerites (Fig. 26).

Remarks

Rhytisma oblongum sp. nov. is distinguished by its tentacle sclerites, which are granular platelets with a smooth, ellipsoidal to oblong outline and a faint or indistinct lateral constriction (Fig. 25*a*, 26*a*, Table 1). The mat spindles are notably long, reaching up to 2.6 mm (Fig. 25*e*, 26*e*). Additionally, the collaret, point and mat sclerites bear sparsely distributed but prominent tubercles that are more pronounced than in any other congener. This species is also genetically distinct from all other species described herein (Fig. 2, 3).

Distribution

SW Indian Ocean (Kenya, Madagascar, Mozambique) (Fig. 1).

Rhytisma rubiginosum (Verseveldt, 1968)

(Fig. 1, 27, 28.)

Parerythropodium rubiginosum Verseveldt, 1968, pp. 52–53 – Verseveldt (1969), pp. 8–11, fig. 2–4, pl. I fig. 1.

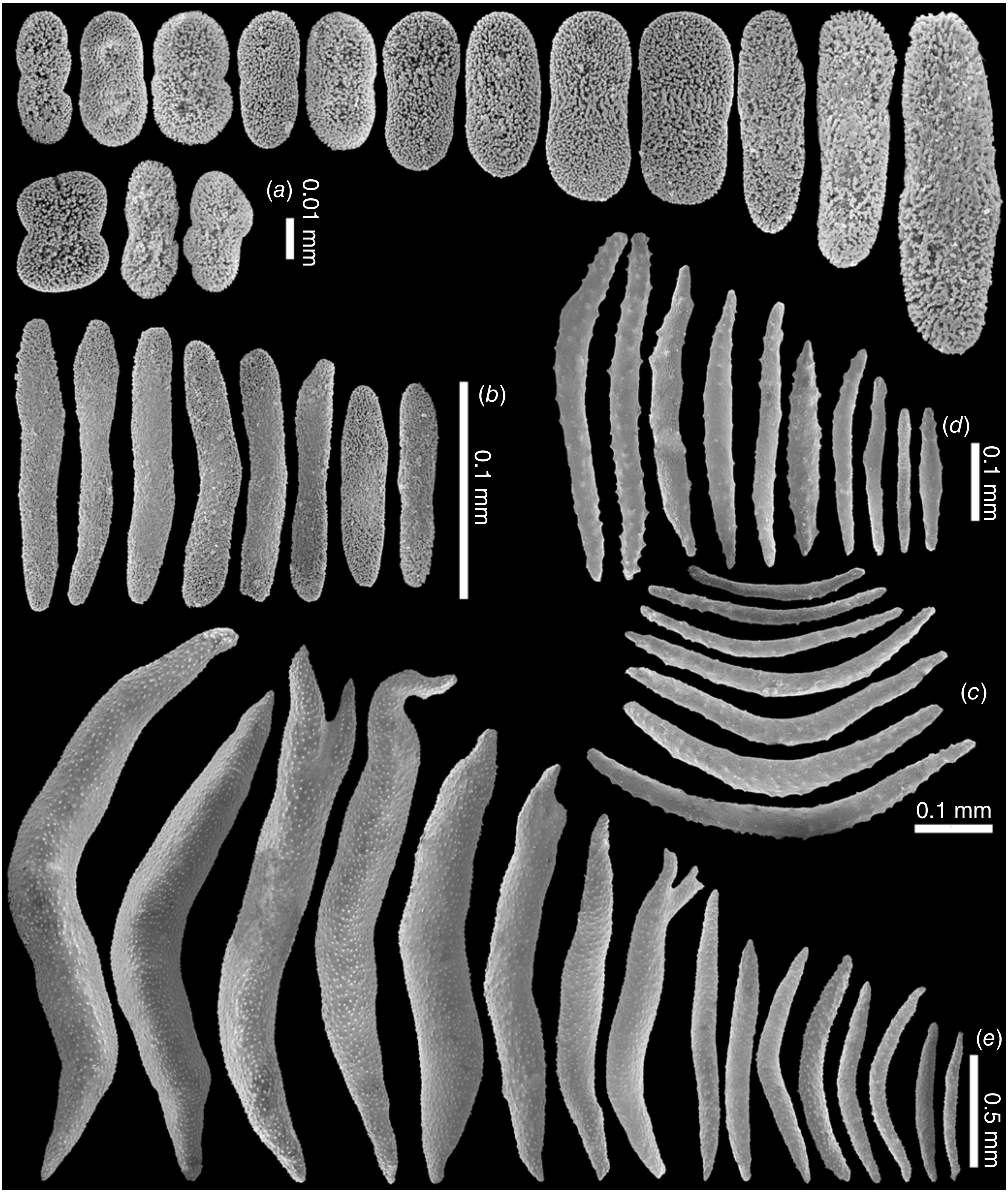

Fig. 25. *Rhytisma oblongum* sp. nov., holotype (SMNHTAU_Co_36146). (*a*) Tentacle sclerites (*b*) elongated platelets at the base of the tentacles (*c*) collaret sclerites (*d*) point sclerites (*e*) spindles of the mat.

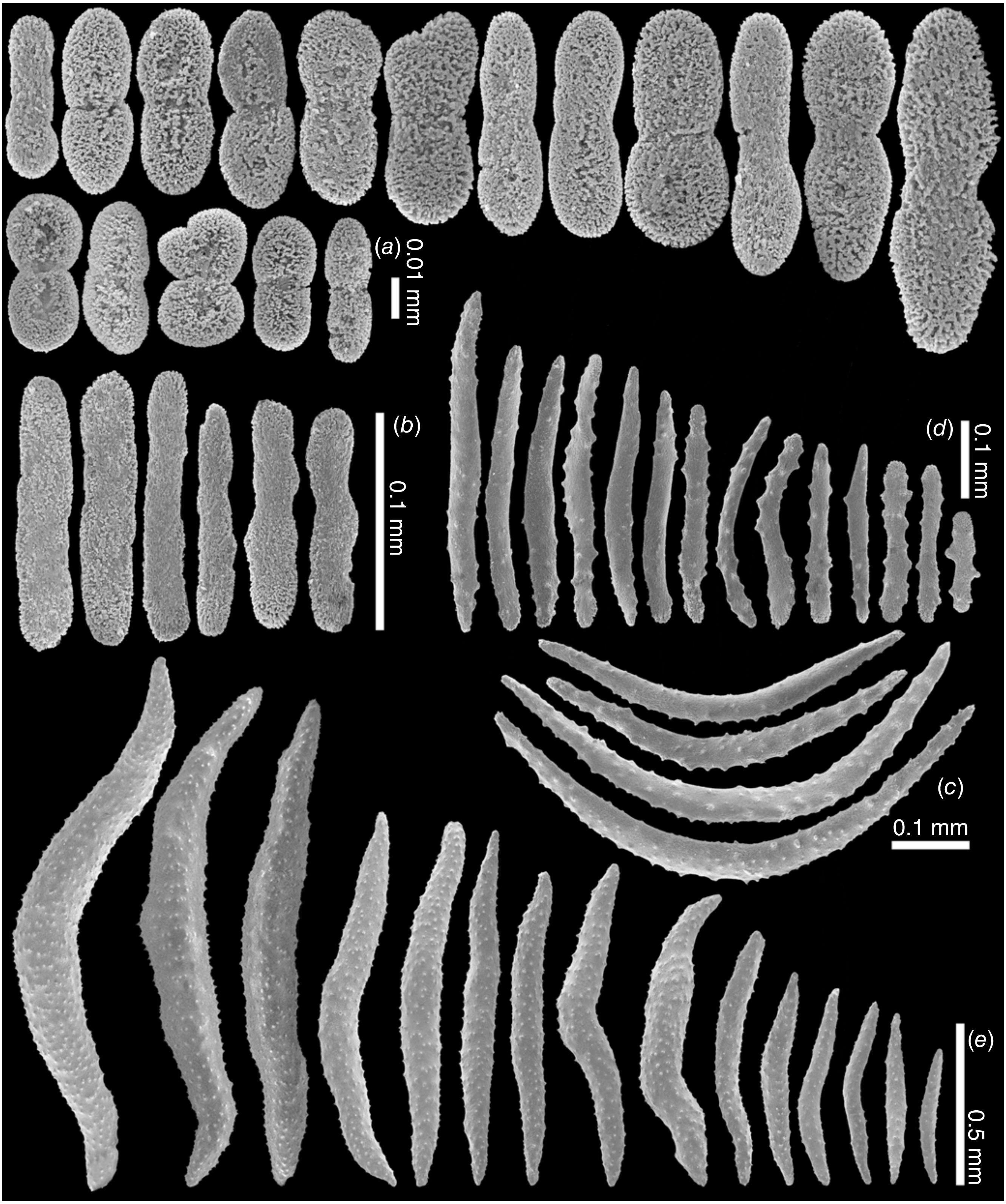

Fig. 26. *Rhytisma oblongum* sp. nov. (SMNHTAU_Co_32503). (*a*) Tentacle sclerites (*b*) elongated platelets at the base of the tentacles (*c*) collaret sclerites (*d*) point sclerites (*e*) spindles of the mat.

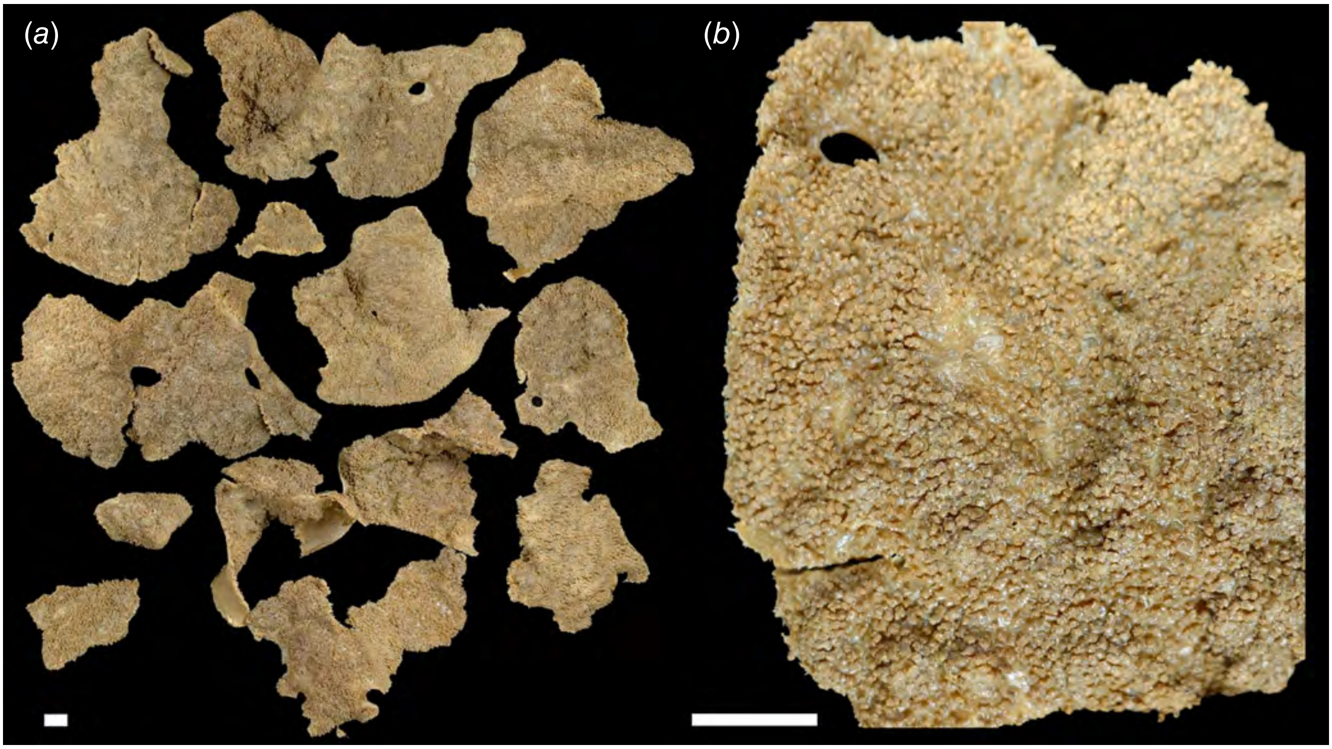

Fig. 27. *Rhytisma rubiginosum* (Verseveldt, 1968). (*a*) Paratype (RMNH.COEL.5009) (*b*) surface of the specimen with partly expanded polyps.

Material examined

PARATYPE. MADAGASCAR: RMNH.COEL.5009, East of Ambariobé, near Nosy Be, 2 m, collection number 959, 4 October 1964, coll. A. G. Humes.

Other material

MADAGASCAR: USNM54014, Nosy Be, Ambariobe Bay, station JR–33, approximate location (13.43°S, 48.368°E), International Indian Ocean Expedition, intertidal, 15 January 1964, coll. J. J. Rudloe.

Re-description

The paratype specimen (RMNH.COEL.5009) is an encrusting mat-like colony, 2–4 mm thick, composed of several fragments (Fig. 27). The colony surface displays occasional hillocks where the mat is thicker, gradually thinning toward the edges. Polyps are evenly distributed across the surface and are either partially or fully expanded (Fig. 27*b*).

Tentacle sclerites are mostly granular platelets up to 0.06 mm long (Fig. 28*a*), some of which exhibit a conspicuous symmetrical median constriction or lateral notches (Fig. 28*a*). Elongated platelets and rods are present at the tentacle base, reaching up to 0.10 mm in length (Fig. 28*b*). These sclerites are arranged longitudinally in the tentacle, increasing in length toward the tentacle base, where they become similar in size to the shortest point sclerites.

Polyp sclerites are arranged as a collaret and points. The collaret comprises 3–5 rows of bent spindles, up to 0.8 mm long (Fig. 28*c*). Point sclerites are up to 0.52 mm long (Fig. 28*d*), arranged *en chevron*.

The mat spindles reach up to 2.5 mm in length (Fig. 28*e*); they are generally bent or exhibit a sinuous outline.

Colour

The ethanol-preserved material is cream to brown, and the expanded polyps are cream in colour.

Living features

Colour of the live colony is yellow (Verseveldt 1968).

Morphological variation

The morphological features of the paratype (RMNH.COEL.5009) and additional material generally agree with the description of the holotype by Verseveldt (1969, pp. 8–11).

Remarks

Verseveldt (1968) did not designate any paratypes in the original description of the species, nor provide any illustration of the material (RMNH.COEL.3903) and its sclerites. In his subsequent study, Verseveldt (1969) designated one fragment as the holotype (RMNH.COEL.3909) and eight fragments as paratypes (RMNH.COEL.5009). He then listed additional material of *Rhytisma rubiginosum*, including RMNH.COEL.5008 from Pointe Mahatsinjo, Nosy Be, and RMNH.COEL.4997 from Banc des Frères, Isles Mitsio (Verseveldt 1969).

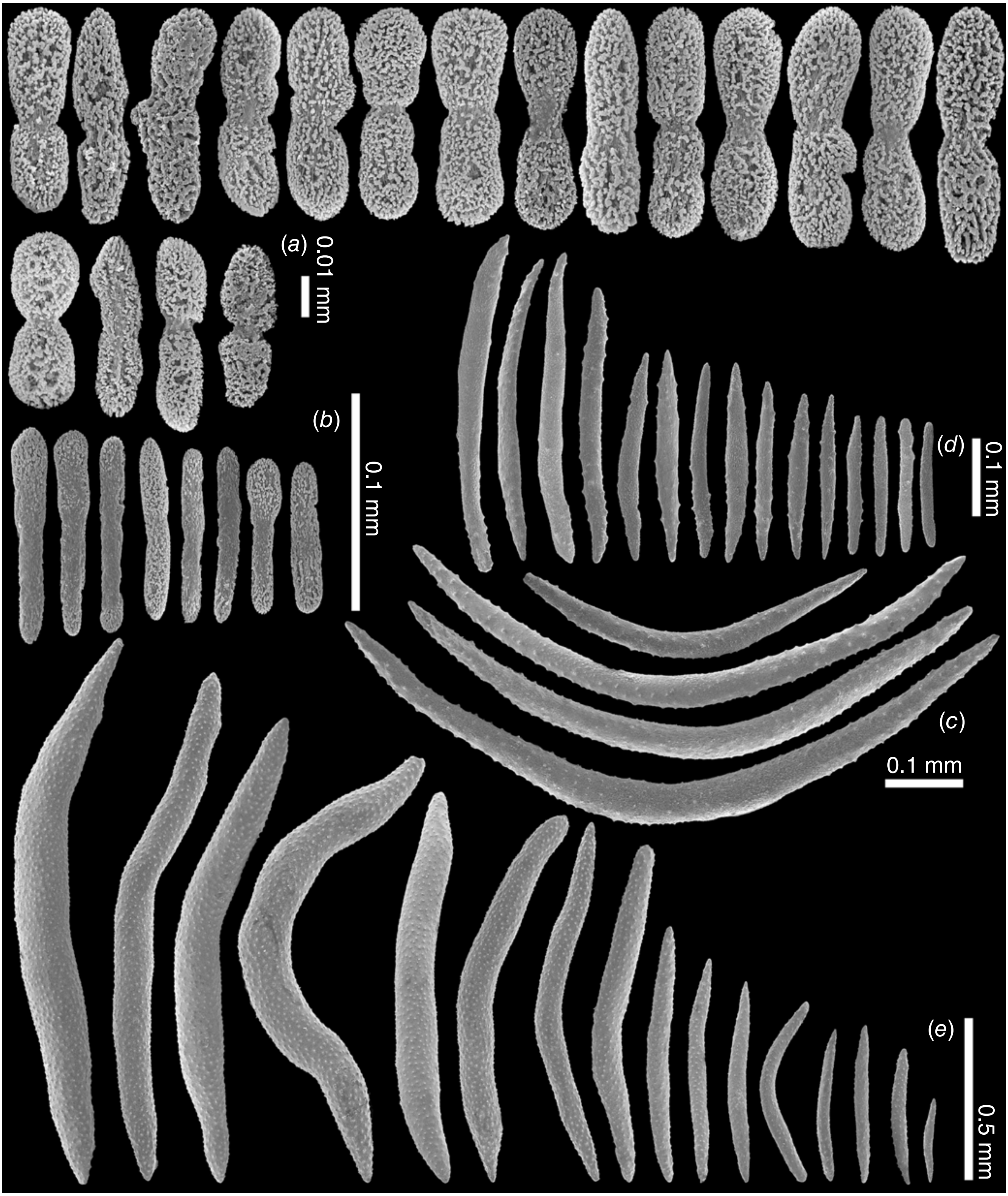

Fig. 28. *Rhytisma rubiginosum* (Verseveldt, 1968), paratype (RMNH.COEL.5009). (*a*) Tentacle sclerites (*b*) elongated platelets at the base of the tentacles (*c*) collaret sclerites (*d*) point sclerites (*e*) spindles of the mat.

Verseveldt distinguished *R. rubiginosum* from *R. fulvum* (Forskål, 1775) based on several features, including the absence of a honeycomb-like surface structure, differences in the number of rows of sclerites in the polyp collaret, and colony colour. The tentacle sclerites of these two species differ markedly in both shape and size of the platelets (Fig. 6*a*, 28*a*). Additionally, *R. rubiginosum* can be distinguished from other congeners, including the sympatric species *R. oblongum* sp. nov. and *R. karibu* sp. nov., by its tentacle sclerites, which have a symmetrical median constriction and distinctly tapered ends (Fig. 28*a*). Nonetheless, genetic data are still needed to confirm the phylogenetic placement of *R. rubiginosum* within the genus.

Distribution

Madagascar.

Rhytisma sperkolae Benayahu, Samimi-Namin, Ekins & McFadden, sp. nov.

(Fig. 1, 29–31, 32*e*.)

ZooBank: urn:lsid:zoobank.org:act:990DFC20-DC51-4ED6-B9EA-A79B56DDA67B

Material examined

HOLOTYPE. LA RÉUNION: SMNHTAU_Co_34407, two large fragments and two small ones of the same colony, Saint-Paul, Hermitage face au ponton au kiosque, 21.070°S, 55.216°E, reef slope, 14–19 m, 7 April 2008, coll. Y. Benayahu.

PARATYPE. LA RÉUNION: SMNHTAU_Co_34454, two fragments of the same colony. Saint-Leu, Pointe des Châteaux, 21.1512°S, 55.2701°E, 14–20 m, 10 April 2004, coll. Y. Benayahu. SMNHTAU_Co_34419, Saint-Paul, Cap la Houssaye, reef slope, 21.0175°S, 55.2376°E, 8 April 2008, coll. Y. Benayahu.

Other material

SEYCHELLES: RMNH.COEL.45904, NIOP-E Seychelles Expedition 1992–1993, Sta. 767, Poivre atoll, N rim, 5.7333°S, 53.3000°E, coral reef, scuba diving, 29–31 December 1992; RMNH.COEL.45855, NIOP-E Seychelles Expedition 1992–1993, Sta. 796, N of Platte Island atoll, 5.8167°S, 55.3667°E, N slope, scuba diving, 7 August 1993.

Description

The holotype comprises two fragments of an encrusting colony attached to a calcareous substrate (Fig. 29). The mat is 1–2 mm thick, thinner toward the colony edges, with some hillocks reflecting the uneven texture of the underlying substrate. Most polyps are fully or partly retracted (Fig. 29*b*).

Tentacle sclerites are mostly flattened rods up to 0.10 mm long (Fig. 30*a*), with an irregular lateral outline and notched appearance. Elongated platelets are present at the tentacle base and reach up to 0.19 mm in length (Fig. 30*b*). These sclerites are arranged longitudinally in the tentacle, increasing in length toward the tentacle base, where they become similar in size to the shortest point sclerites.

Polyp sclerites are arranged as collaret and points. The collaret includes 4–5 rows of spindles up to 0.75 mm long (Fig. 30*c*). The point sclerites are up to 0.40 mm long (Fig. 30*d*), arranged *en chevron*.

The mat spindles reach up to 1.90 mm in length (Fig. 30*e*), are mostly bent in outline, and form a honeycomb-like network on the upper colony surface surrounding the polyps.

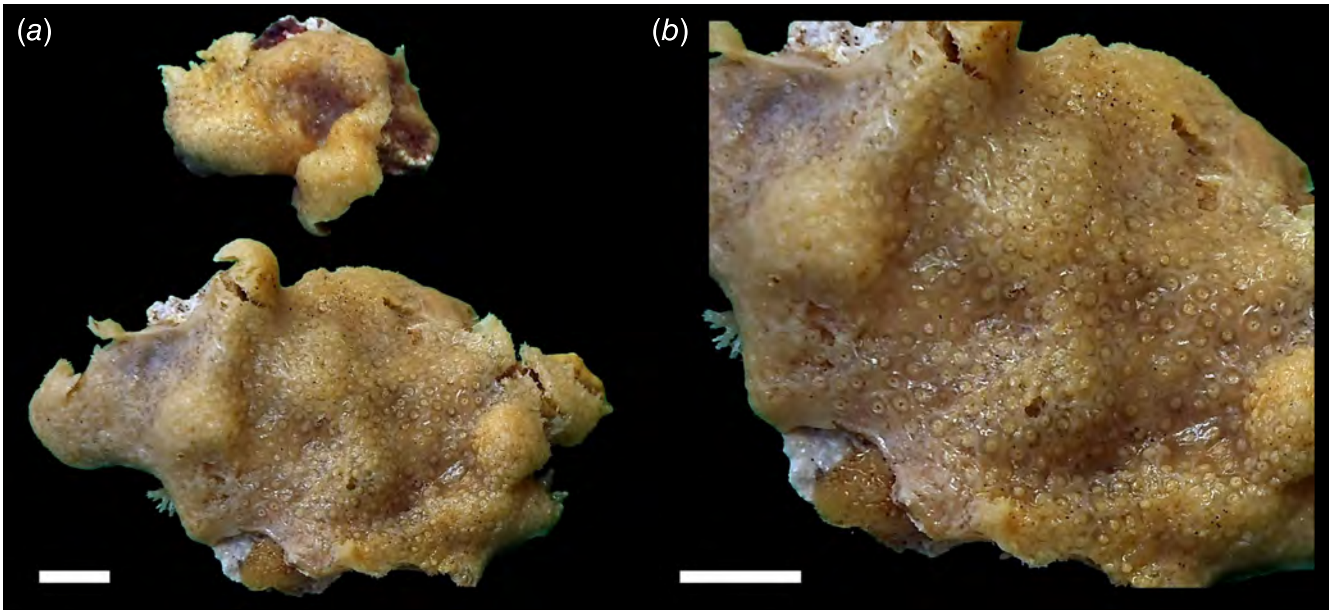

Fig. 29. *Rhytisma sperkolae* sp. nov., holotype (SMNHTAU_Co_34407). (*a*) Fragments of colony (*b*) enlarged fragment reflects underlying texture of substrate. Scale bars: 1 cm.

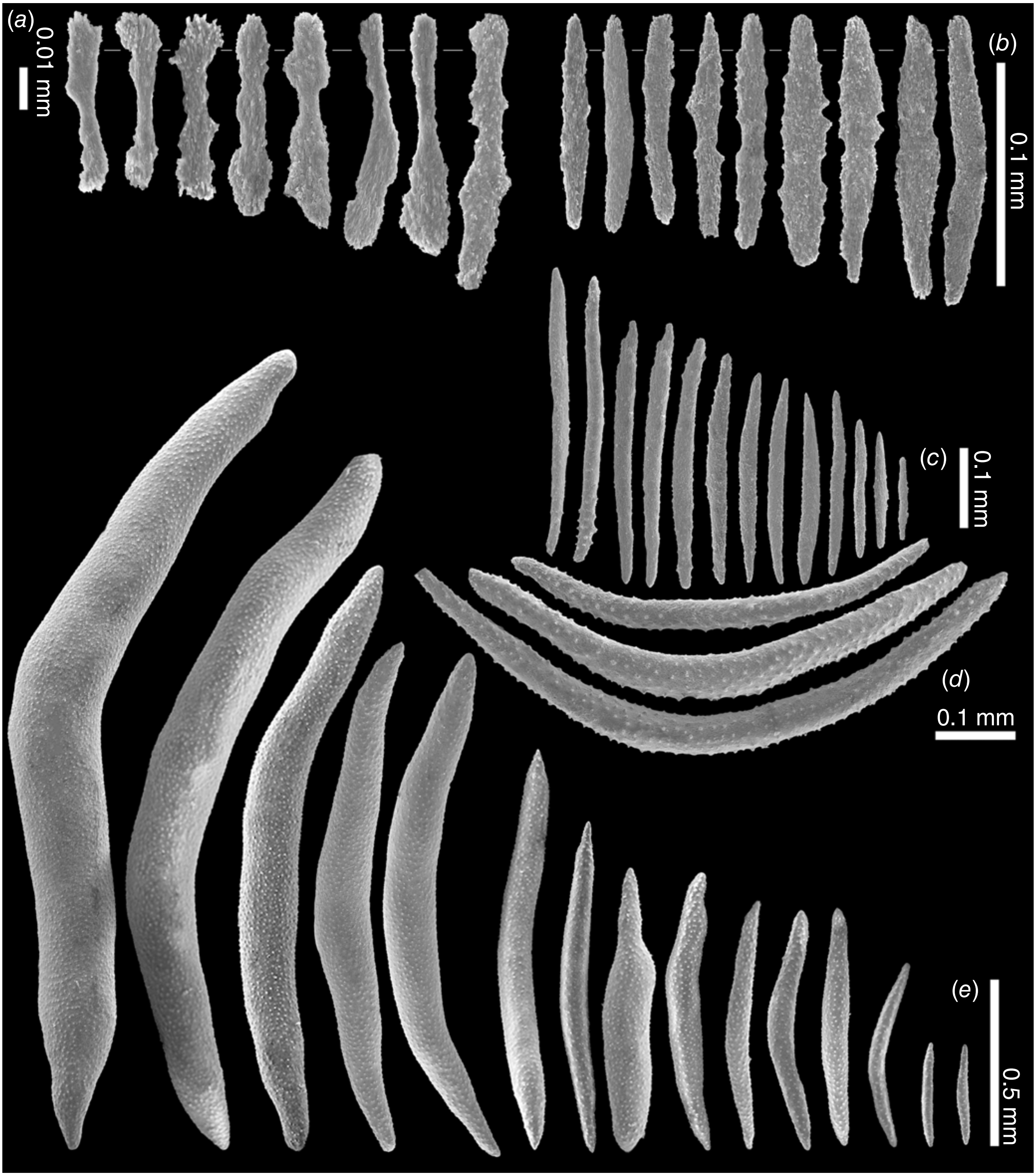

Fig. 30. *Rhytisma sperkolae* sp. nov., holotype (SMNHTAU_Co_34407). (*a*) Tentacle sclerites (*b*) elongated platelets at the base of the tentacles (*c*) collaret sclerites (*d*) point sclerites (*e*) spindles of the mat.

Colour

The ethanol-preserved material is light beige with a grey tint.

Living features

The yellow colonies were found growing on the reef substrate with expanded polyps (Fig. 32*e*).

Fig. 31. *Rhytisma sperkolae* sp. nov., paratype (SMNHTAU_Co_34454). (*a*) Tentacle sclerites (*b*) elongated platelets at the base of the tentacles (*c*) collaret sclerites (*d*) point sclerites (*e*) spindles of the mat.

Etymology

The specific epithet *sperkolae* honours the late Dr Shimrit Perkol-Finkel, a passionate and gifted marine biologist and former student of Y. Benayahu, who tragically lost her life at an early age in a road accident. The name is given in recognition of her enduring dedication to coral reef conservation and her lasting scientific legacy.

Morphological variation

The morphological features of the paratype fragments correspond to those of the holotype, including the shape and dimensions of the sclerites (Fig. 30, 31).

Remarks

This species is characterised by its unique tentacle sclerites, which are flattened rods with an irregular, jagged lateral

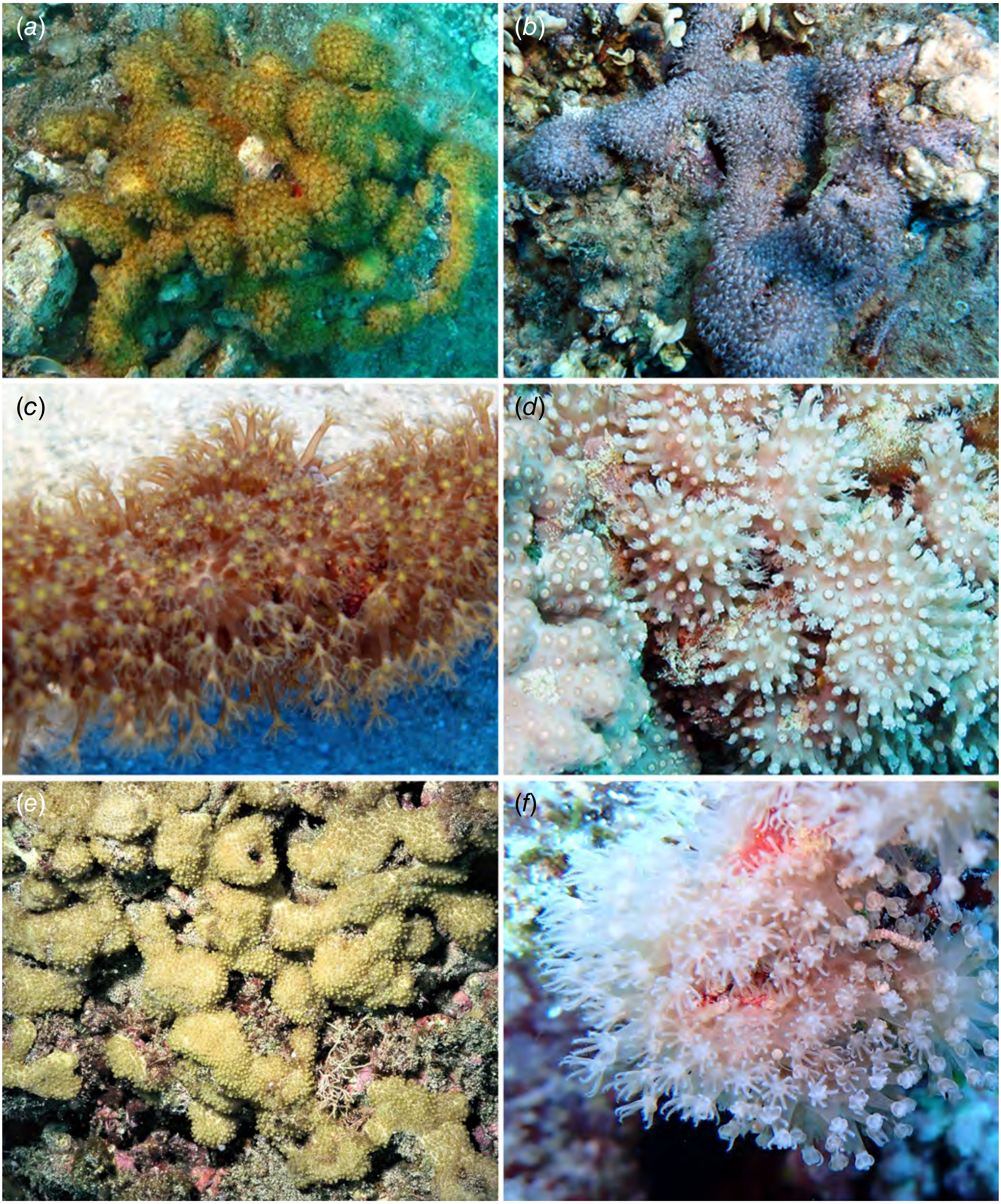

Fig. 32. Underwater images of *Rhytisma* species in their respective type localities. (*a*, *b*) *R. fulvum* yellow colour and grey colour morphs, polyps partly expanded (*c*) *R. inaequale* sp. nov., with expanded polyps (*d*) *R. calyaceum* sp. nov., with partially expanded polyps (*e*) *R. sperkolae* sp. nov., mat morphology reflects underlying irregular reef substrate, polyps partly expanded. (*f*) *R. monticulum* with expanded polyps. Photographs by (*a–c, e*) Y. Benayahu, (*d*, *f*) M. Ekins.

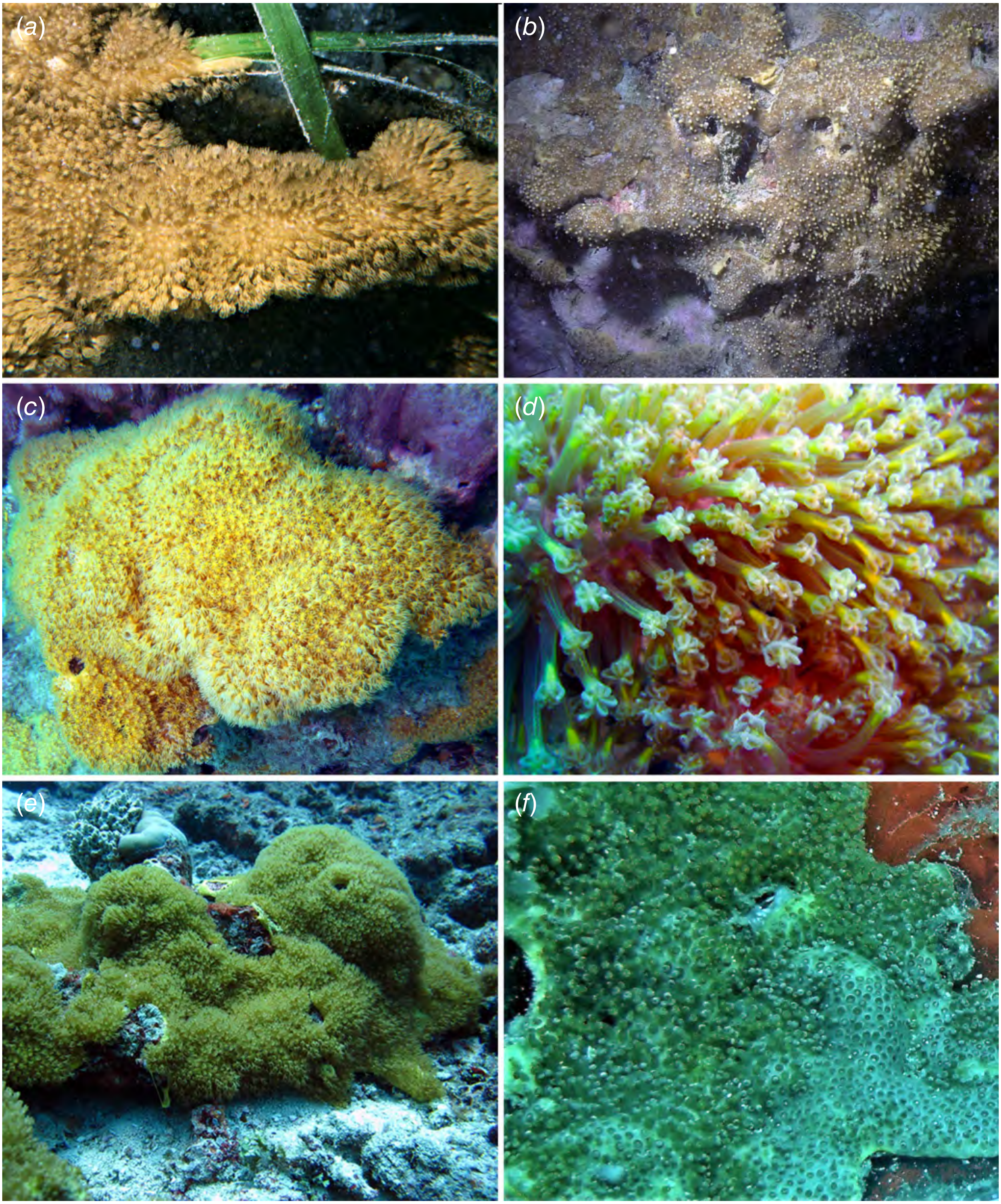

Fig. 33. Underwater images of *Rhytisma* species in their respective type localities. (*a*, *b*) *R. karibu* sp. nov., growing on seagrass blades and reef substrate (*c*, *d*) *R. acoronatum* sp. nov. (*e*, *f*) *R. oblongum* sp. nov. Photographs by (*a*, *b*, *e*, *f*) Y. Benayahu, and (*c*, *d*) M. Ekins.

outline (Fig. 30*a*, 31*a*, Table 1). It lacks granular platelets in the tentacles – a feature that distinguishes it from all known congeners, including the genetically similar *R. monticulum* (Fig. 21, 30, 31). Additionally, the elongated platelets of the tentacles are distinct, with narrow ends and sometimes a median constriction.

Distribution

La Réunion, Seychelles (Fig. 1).

Discussion

The morphological uniformity of *Rhytisma* colonies, a thin encrusting mat with occasional hillocks or ribbon-like projections, has historically led to misidentification and incorrect assignment of many specimens from various Indo-Pacific localities to *R. fulvum*. The current study indicates that, although colony morphology is fairly consistent among species, sclerite morphology provides far more informative characters for species delineation. All 10 valid species of *Rhytisma* (4 previously described and 6 newly introduced here) share a general sclerite composition: long spindles in the mat, shorter spindles and rods in the polyp body (usually arranged as collaret and points), and minute platelets plus elongated platelets in the tentacles (Table 1). These general patterns are taxonomically stable, but the species-level differences lie in the fine morphology of the tentacle sclerites. These sclerites, previously referred to as 'granular scales' (Alderslade 2000) or 'tiny spicules' (Verseveldt 1969), are shown here to exhibit a high degree of interspecific variability. The morphological analysis revealed significant differences in their shape (elliptical, elongated, platelets), surface ornamentation, outline (smooth, jagged, granular) and symmetry (symmetrical *v.* asymmetrical or irregular outlines with varying median constrictions or notches). This variability, especially when assessed together with the rest of the polyp sclerites, proved critical for distinguishing morphologically similar species that were nonetheless genetically distinct in the phylogenetic and phylogenomic analyses.

Our findings further highlight the diagnostic importance of polyp sclerites and are in line with previous studies demonstrating their taxonomic significance in octocorals (McFadden *et al.* 2009; Benayahu and van Ofwegen 2012; Samimi-Namin and van Ofwegen 2016; van Ofwegen 2020; McFadden *et al.* 2024; Lazar *et al.* 2025).

The species *R. fulvum* and *R. fuscum* have long been lumped together, with their distinguishing features obscured by their similar colony morphologies. Re-examination of type material led to the designation of a neotype for *R. fulvum* (Fig. 5, 6) and a lectotype for *R. fuscum* (Fig. 11, 12), clarifying their taxonomic identities. Notably, our findings refute the validity of the former subspecies status of *P. fulvum fuscum* and support treating *R. fuscum* as a distinct species based on its tentacle and polyp sclerites.

The six new species described in this study, i.e. *R. acoronatum* sp. nov., *R. calyaceum* sp. nov., *R. karibu* sp. nov., *R. oblongum* sp. nov., *R. inaequale* sp. nov. and *R. sperkolae* sp. nov., highlight previously overlooked species-level diversity within *Rhytisma*. Each species exhibits a distinct combination of tentacle sclerite morphologies. These findings are further supported by multilocus barcoding and phylogenomic analyses of UCEs, which corroborate the morphological boundaries proposed for each species. Molecular data revealed significant divergence and fine-scale endemism within *Rhytisma*, including several OTUs confined to limited geographic regions (McFadden *et al.* 2025). These results further support earlier suggestions that many soft coral taxa traditionally considered widespread may in fact represent species complexes of range-restricted endemics (Samimi-Namin and van Ofwegen 2016; McFadden *et al.* 2019, 2024, 2025; Benayahu *et al.* 2021, 2022).

In a biogeographic context, *Rhytisma* follows the broader pattern of Lemnaliidae: diversity peaks in the western Indian Ocean and on the north-east Australian shelf, whereas the family is absent or species-poor in many central and eastern Indo-Pacific provinces and on most oceanic islands, consistent with MOTU-based evidence for high regional endemism and strong faunal turnover compared with broadcast-spawning families such as Sarcophytidae and Cladiellidae (McFadden *et al.* 2025). Although *Rhytisma* is widespread in the Red Sea and much of the western Indian Ocean, it remains unrecorded from the Arabian Sea coasts of Oman and from the Persian Gulf despite intensive shallow-water surveys there (Samimi-Namin and van Ofwegen 2009, 2012). This apparent exclusion from marginal seas may reflect extreme temperature and salinity in the Gulf and turbid, upwelling-influenced waters along the Arabian Sea margin (Sheppard *et al.* 2010).

Across its range, *Rhytisma* appears to be primarily a shallow-water genus: most examined material and published records are from reef flats, patch reefs and upper reef slopes on hard substrates (Alderslade 2000; Fabricius and Alderslade 2001; McFadden *et al.* 2025; present study). In the Red Sea, some populations extend into the upper mesophotic zone (~40–60 m; Shoham and Benayahu 2017; Benayahu *et al.* 2019; present study), but comparable deep records have not yet been documented elsewhere. It therefore remains unclear whether these mesophotic occurrences reflect the general depth range of the genus or region-specific environmental conditions in the northern Red Sea. Within the genus, *R. fulvum* stands out as a depth generalist, occurring from shallow reef flats to the deepest margins of the upper mesophotic zone, whereas all other species are, as far as currently known, restricted to shallow reefs.

Overall, our results underscore the regional endemism of *Rhytisma* species. The discovery of several narrowly distributed species suggests limited dispersal of their sexual

Table 1. Summary of morphological characteristics of species of *Rhytisma* Alderslade, 2000.

Species	Tentacle sclerites	Mat sclerites	Collaret sclerites	Point sclerites
R. fulvum (Forskål, 1775)	Granular platelets, elongated platelets, **shallow to median constriction; asymmetrical notches**; up to 0.08 mm	Spindles up to 1.72 mm	Up to 0.70 mm	Spindles, some with conical tubercles: one end **sharply pointed**; up to 0.53 mm
R. acoronatum sp. nov.	Platelets, elongated platelets, **weak median constriction, often shallow or lateral notches**; up to 0.10 mm	Spindles up to 2.4 mm	**Absent or rudimentary**	Spindles up to 0.28 mm
R. calyaceum sp. nov.	Granular platelets, **symmetrical, median constriction, tips evenly tapered**; up to 0.08 mm	Spindles up to 2.6 mm	Up to 0.70 mm	Pointed spindles up to 0.33 mm
R. fuscum (Thomson & Henderson, 1906)	Granular platelets, **elongated platelets, shallow median constriction, moderately asymmetrical**; up to 0.06 mm	Spindles up to 1.9 mm	Up to 0.70 mm	Spindles up to 0.36 mm
R. inaequale sp. nov.	Granular platelets, elongated platelets, **strongly asymmetrical with irregular outline, median constriction**; up to 0.08 mm	Spindles up to 1.3 mm	Up to 0.60 mm	Pointed spindles up to 0.40 mm
R. karibu sp. nov.	Granular platelets**, multiple constrictions or lateral notches, bone-shaped or widened ends**; up to 0.06 mm	Spindles up to 2.3 mm	Up to 0.6 mm	Pointed spindles up to 0.36 mm
R. monticulum (Verseveldt, 1982)	**Elongate granular platelets, slightly asymmetrical, faint constriction**; up to 0.10 mm	Spindles up to 1.6 mm	Up to 0.80 mm	Spindles up to 0.58 mm
R. oblongum sp. nov.	**Ellipsoid platelets, smooth, faint or indistinct lateral constriction**; up to 0.10 mm	Spindles up to 2.6 mm, **bifurcate tips**	Up to 0.45 mm	Spindles up to 0.18 mm
R. rubiginosum (Verseveldt, 1968)	Platelets **with single, symmetrical median constriction; distinctly tapered ends**; up to 0.06 mm	Spindles up to 2.5 mm	Up to 0.80 mm	Spindles up to 0.52 mm
R. sperkolae sp. nov.	**Granular platelets absent, elongated platelets only; irregular jagged outline**; up to 0.10 mm	Spindles up to 1.9 mm	Up to 0.75 mm	Pointed spindles up to 0.32 mm

The more informative diagnostic features are in bold. For morphological species delimitation, sclerite size is of limited diagnostic value; the most informative characters are the shape and surface sculpturing of the sclerites, especially those in the tentacles, followed by those in the collaret and points, and finally those in the mat. These features are best assessed from the SEM plates and detailed descriptions provided in the main text.

progeny or even habitat specialisation, reinforcing the need for fine-scale biogeographical studies. The genus, once considered to contain only a few widespread taxa, is now shown to be more diverse, geographically structured and regionally differentiated than previously understood. The integrative approach adopted in the present study sets an important precedent for soft coral taxonomy by combining morphology, molecular data and re-evaluation of historical material. Advances in museomics (i.e. the study of genomic data obtained from museum specimens), such as genome skimming (Quattrini *et al.* 2024), now enable the recovery of extensive genomic data from historical type material including century-old specimens, ensuring that legacy collections can play a central role in resolving long-standing taxonomic questions.

Supplementary material

Supplementary material can be accessed from the article page online.

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Data availability. The data that support this study are available in the article and accompanying online supplementary material. All DNA sequences are available in GenBank, see Supplementary Table S1 and BioProjects PRJNA1171007 (*28S rDNA*), PRJNA1328774 (UCE sequences).

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