



Re-description of type material of *Xenia* Lamarck, 1816 (Octocorallia: Xeniidae)

ANNA HALÁSZ¹, CATHERINE S. MCFADDEN², ROBERT TOONEN³ & YEHUDA BENAYAHU^{1,4}

¹School of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, Ramat Aviv, Tel Aviv 69978, Israel.

E-mail: ann.halasz@gmail.com

²Department of Biology, Harvey Mudd College, 1250 N. Dartmouth Ave., Claremont, CA 91711, USA. E-mail: mcfadden@g.hmc.edu

³Hawaii Institute of Marine Biology, University of Hawaii at Manoa, 46-007 Lilipuna Road, Kane'ohe, HI 96744, USA.

E-mail: toonen@hawaii.edu

⁴Corresponding author. E-mail: yehudab@tauex.tau.ac.il

Table of content

Abstract	201
Introduction	202
Material and methods	203
Results	204
Systematic part	204
Order Alcyonacea Lamouroux, 1812	204
Family Xeniidae Ehrenberg, 1828	204
Genus <i>Xenia</i> Lamarck, 1816	204
Key to <i>Xenia</i> types examined during this study	204
<i>Xenia flexibilis</i> sp. n.	205
<i>Xenia bauiana</i> May, 1899	206
<i>Xenia blumi</i> Schenk, 1896.	207
<i>Xenia crassa</i> Schenk, 1896	209
<i>Xenia delicata</i> Roxas, 1933	211
<i>Xenia fusca</i> Schenk, 1896	211
<i>Xenia garciae</i> Bourne, 1894	213
<i>Xenia grasshoffi</i> Verseveldt, 1974.	214
<i>Xenia kuekenthali</i> Roxas, 1933.	215
<i>Xenia lepida</i> Verseveldt, 1971	216
<i>Xenia membranacea</i> Schenk, 1896.	217
<i>Xenia mucosa</i> Verseveldt & Tursch, 1979	218
<i>Xenia multispiculata</i> Kükenthal, 1909	219
<i>Xenia novaebritanniae</i> Ashworth, 1900	220
<i>Xenia rubens</i> Schenk, 1896	222
<i>Xenia sansibariana</i> May, 1899	222
<i>Xenia ternatana</i> Schenk, 1896	224
<i>Xenia viridis</i> Schenk, 1896	224
<i>Xenia umbellata</i> Lamarck, 1816	227
Discussion	234
Acknowledgements	236
References	236

Abstract

In this study we examined the original types of 21 of the 56 morphospecies of *Xenia* currently listed in WoRMS. Unfortunately, our attempts to locate additional type material failed, and we conclude that they have been lost. The type localities of the material examined include the Red Sea, West and Central Indian Ocean, the South Pacific, Indonesia, The Philippines, and the Bismarck Sea, reflecting the extensive biogeographical distribution of this genus throughout the Indo-Pacific Ocean. A neotype was designated from the northern Red Sea for *X. umbellata*, and sequencing established its position

in the phylogenetic tree in relation to other genera of the family Xeniidae. In addition, *X. flexibilis* n. sp. was described from The Philippines. The findings from the current study led to the synonymizing of *X. actiosa* with *X. sansibariana* and of *X. plicata* with *X. blumi*. Overall, the study has re-described the types of 17 species considered to be valid based on morphological characters. Validation of the morphological features of original type material along with species-diagnostic genetic characters are required in order to facilitate our ability to correctly employ Latin binomials, both in phylogenetic studies and in any other biological surveys.

Key words: Red Sea, sclerite microstructure, taxonomy, phylogeny, neotype, synonymy

Introduction

Members of the octocoral family Xeniidae contribute significantly to the living cover and diversity of shallow Indo-Pacific coral reefs (e.g., Fabricius 1998; Alderslade 2001; Janes 2013; Halász *et al.* 2014, 2015; McFadden *et al.* 2014a, 2017; Benayahu *et al.* 2018). They are also distributed in the upper mesophotic reef ecosystems, where they may occupy considerable space (Shoham & Benayahu 2017). Studies of xeniid life history have revealed that they reproduce both sexually and asexually (Kahng *et al.* 2011), contributing to high rates of colonization to the coral reef substrate (e.g., Tilot *et al.* 2008; Wood & Dipper, 2008; Wild & Naumann 2013) as well as invasive capabilities (Ruiz-Allais *et al.* 2014; Mantellato *et al.* 2018).

The long history of taxonomic studies on the family Xeniidae began following the historic collections conducted in the Red Sea during the course of Napoléon's voyage in the late 18th century (see Reinicke 1997). This collection led to the establishment of the genus *Xenia* Lamarck, 1816, along with *Anthelia* Lamarck, 1816. A later scientific expedition to the Red Sea established additional genera of this family, namely *Heteroxenia* (see Ehrenberg, 1834) and *Symphodium* Ehrenberg, 1834. Over the years, studies conducted in the Red Sea have revealed numerous xeniid species (e.g., Halász *et al.* 2014 and references therein) and laid the foundation for their taxonomic study throughout the Indo-Pacific (e.g., Great Barrier Reef, Australia: Hickson 1931a; Philippines: Roxas 1933; Madagascar: Verseveldt 1971; Japan: Utinomi 1977; Bismarck Sea: Verseveldt & Tursch 1979; Seychelles: Janes 2008; Andaman Sea: Janes *et al.* 2014).

A majority of the described species of Xeniidae feature a high density of minute sclerites (calcitic skeletal elements) in their tissues, although some have only a few or none (e.g., Halász *et al.* 2014; Benayahu *et al.* 2018). Xeniid sclerites have long been considered to be relatively simple, with low structural diversity compared to the sclerites of other octocoral families (Fabricius & Alderslade 2001). Accordingly, most of the older taxonomic publications do not depict xeniid sclerites, although they occasionally present their size-range (Halász *et al.* 2014 and references therein). The recent use of high-resolution scanning electron microscopy (SEM) to image xeniid sclerites has, however, revealed microstructural features not previously observed using light microscopy. In several cases these microstructural features have been found to be diagnostic of genera. For example, the discovery of a corpuscular sclerite-type among some of the originally described *Xenia* species led to the establishment of the genus *Ovabunda* Alderslade, 2001, while those species featuring a dendritic surface were retained in the original genus. Similarly, re-examination of species originally assigned to the xeniid genus *Cespitularia* Milne Edwards & Haime, 1850, led to the discovery of two novel sclerite morphologies that justified establishing the new genera *Conglomeratusclera* Benayahu, Ofwegen & McFadden, 2018 and *Caementabunda* Benayahu, Ofwegen & McFadden, 2018. Molecular phylogenetic studies support the distinctions among the genera *Caementabunda* and *Conglomeratusclera*, concordant with the microstructural characters of their sclerites (Benayahu *et al.* 2018).

Historically, diagnosis of xeniid species has been based on morphological characters associated with the soft tissue of the polyps, including the number of rows of pinnules (lateral projections) along the margin of the tentacles and the number of pinnules per row. Re-examination of museum type material of *Caementabunda*, *Conglomeratusclera* and *Ovabunda* has resulted in revisions of the old taxonomic descriptions and provided updated morphological data on those characters as well as on the microstructure of sclerites. In some cases, the original descriptions have been validated, while in others major taxonomic re-assignment at the generic and/or species level has been required (Halász *et al.* 2014; McFadden *et al.* 2017; Benayahu *et al.* 2018). These studies have also indicated that the number of rows of pinnules and the number of pinnules per row may vary within a species, and in some cases even between polyps of an individual colony. Therefore, it has been concluded that these soft tissue characters are not necessarily diagnostic for delineation of species in the genera *Caementabunda*, *Conglomeratusclera*, and *Ovabunda*.

The genus *Xenia* is the most speciose genus in the family Xeniidae, comprising 56 morphospecies (WoRMS Editorial Board 2018). Only a few studies to date have presented images of *Xenia* sclerites (*X. kusimotoensis*: Utinomi 1955: 264, fig. 1d; *X. macrospiculata* (= *O. macrospiculata*): Verseveldt 1971: 64, fig. 39c, see also Halász *et al.* 2014). SEM has revealed that *Xenia* sclerites are ellipsoids in form, composed of a latticework matrix of calcite rods, often dendritic and sinuous, and more or less radially arranged, at least in the peripheral region (Alderslade 2001: Fig. 35). The revision of the genus *Ovabunda* led to the reassignment of some of the type material originally described as *Xenia* to *Ovabunda* (Halász *et al.* 2014). Here we seek to validate the taxonomic status of the remaining *Xenia* species by examining original type material. Consequently, the current study re-describes 17 original *Xenia* types, using SEM to depict their sclerite microstructure. In addition, we describe a new *Xenia* species, and assign a neotype to *X. umbellata* Lamarck, 1816, the type of the family Xeniidae. Although the traditional characters of number of rows of pinnules and numbers of pinnules per row have been shown to be taxonomically uninformative in other xeniid genera (Halász *et al.* 2015, McFadden *et al.* 2017, Benayahu *et al.* 2018), while the taxonomic value of sclerite microstructure for species delimitation has yet to be confirmed, we nonetheless re-describe the type specimens using both character sets. As we use integrative taxonomic approaches to delimit species in recently collected material (e.g. McFadden *et al.* 2017), having a full understanding of the morphological characters of the type material is necessary in order to confirm species identifications and make further revisions to the genus.

Material and methods

We examined and re-described ethanol-preserved type specimens of *Xenia* obtained on loan from the British Museum of Natural History (BML); the Naturalis Biodiversity Center, formerly Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); Senckenberg Naturmuseum Frankfurt (SMF); Zoologisches Museum Berlin (ZMB); and the Steinhardt Museum of Natural History, Tel Aviv University (collection numbers preceded by ZMTAU). In addition, we examined freshly collected material from Eilat, northern tip of the Gulf of Aqaba—assigned here as a neo-type of *X. umbellata*—as well as relevant material deposited at the Smithsonian National Museum of Natural History, Washington DC (USNM). Morphological features of soft parts of the preserved colonies were recorded, including colony height, number of branches, stalk length, width at colony-base, and width at the uppermost part below the capitulum where the polyps arise. The number of rows of pinnules and number of pinnules on the outermost side of the tentacles were counted under a compound microscope. In addition, the length of the anthocodiae (consisting of the polyp body and extended tentacles), the dimensions of the pinnules (length and width at base), and the distance between adjacent pinnules were recorded (see also Halász *et al.* 2014). To examine the sclerites, the tissue was dissolved with 10% sodium hypochlorite followed by repeated rinses in distilled water. In this study only the polyp sclerites were examined under SEM and are presented here. SEM stubs for polyp sclerites of *Xenia* types were prepared following Aharonovich & Benayahu (2011), and examined with a Jeol 840Å electron microscope. Measurements of sclerite images were carried out using ImageJ 1.440 (National Institute of Health, USA). At least 20 randomly selected sclerites were measured for each colony in order to determine sclerite size variation. Number of sclerites measured is indicated in the text for each species. Since the sclerites are mostly ellipsoidal, their dimensions are presented as the range of their smallest diameters X the range of their largest diameters. The zoogeographical distribution of *Xenia* species is based on the type locality, as well as on previous publications whose findings correspond to the features of the re-described types.

Molecular phylogenetic analysis of *X. umbellata* neotype. DNA sequences from specimens of *X. umbellata* described in this study (including the neotype) have been published previously (McFadden *et al.* 2011; McFadden *et al.* 2017). To establish the phylogenetic position of *X. umbellata* within Xeniidae, sequences for two mitochondrial genes (*mtMutS* and *igr1+COI*) and the nuclear 28S rDNA were aligned with a recently published dataset that included representatives of all xeniid genera for which data are currently available (Benayahu *et al.* 2018). jModelTest2 (Darriba *et al.* 2012) was used to select appropriate models of evolution for analyses. Maximum likelihood analysis of the concatenated alignment used RaxML-ng (Kozlov 2018) with a GTR+G model of evolution and 1000 bootstrap replicates. Bayesian analyses of the concatenated alignment were run using MrBayes v. 3.2.1 (Ronquist *et al.* 2012) with separate data partitions and evolutionary models applied to each gene (*mtMutS*: HKY+G; *COI*: GTR+I+G; *28S*: GTR+I+G). MrBayes was run for 5,000,000 generations (until standard deviation of split partitions < 0.01) with a burn-in of 25% and default Metropolis coupling parameters.

Results

Systematic part

Order Alcyonacea Lamouroux, 1812

Family Xenidae Ehrenberg, 1828

Genus *Xenia* Lamarck, 1816

Type species: *Xenia umbellata* Lamarck, 1816

Diagnosis. Colonies are small and soft with cylindrical stalk, undivided or branched, terminating in one or more domed polyp-bearing regions. Polyps are not retractile and are always monomorphic. Sclerites are ellipsoid platelets, usually abundant in all parts of the colony. They are mostly up to 0.025 mm in maximal diameter, and are composed of calcite rods, often dendritic or sinuous, mostly radially arranged, at least at the periphery of the sclerites. Tips of rods can be observed on the surface of the platelet, commonly providing it with a granular appearance; in a few cases, distal parts of rods are arranged parallel to the sclerite surface. The rods are mostly uniform in width (0.1–0.2 μm), but in some species their distal ends are wider. The sclerites often tend to fracture during dehydration for SEM purposes, thus also enabling examination of their inner parts and the morphology and arrangement of rods.

Key to *Xenia* types examined during this study

1. No sclerites in any part of the colony

- One row of pinnules
8–10 pinnules in the outermost row *X. kuekenthali*
- Three rows of pinnules
18–23 pinnules in the outermost row *X. delicata**
28–34 pinnules in the outermost row *X. lepida*
- Four rows of pinnules
26–33 pinnules in the outermost row *X. sansibariana*
30–42 pinnules in the outermost row *X. mucosa*

2. Sclerites are ellipsoid platelets composed of calcite rods

2.2 No crests are present on the sclerite surface

2.2.1 Rods are mostly uniform in width throughout their length and radially arranged, at least at the sclerite periphery

- Two rows of pinnules
21–29 pinnules in the outermost row *X. multispiculata*
- Three rows of pinnules
10–14 pinnules in the outermost row *X. novaebritanniae**
18–20 pinnules in the outermost row *X. blumi*
- Four rows of pinnules
26–30 pinnules in the outermost row *X. bauiana*
14–32 pinnules in the outermost row *X. flexibilis* n. sp.

2.2.2 Rods more or less randomly arranged; sinuous, and with their distal ends aligned in parallel to the sclerite surface

- Two-three rows of pinnules
16–27 pinnules in the outermost row *X. umbellata*

2.3 Surface of sclerite appears uniformly granular

2.3.1 Sclerite internal structure: wide rods with a void in sclerite center

- Four rows of pinnules
12–19 pinnules in the outermost row *X. rubens*

2.3.2 Sclerites composed of calcite rods, arranged randomly within sclerite interior and thickening toward their distal ends

Four rows of pinnules

14–22 pinnules in the outermost row *X. fusca*

2.4 Crest on sclerite surface

Three rows of pinnules

13–18 pinnules in the outermost row *X. crassa**

15–22 pinnules in the outermost row *X. viridis*, *X. garciae*** , *X. ternatana*‡

Four rows of pinnules

15–24 pinnules in the outermost row *X. grasshoffi*

20–25 pinnules in the outermost row and presence of both ellipsoid platelets and irregular ones *X. membranacea*

* Occasionally 4th row present.

** Further examination of extent of presence of surface crests is needed.

‡ A full-size crest is also present.

Xenia flexibilis sp. n.

Fig. 1

Material. Type: ZMB 6105, Puerto Galera, Mindoro, Philippines, 1931, coll. A. Roxas

Description. The holotype is 20 mm high; its stalk is 10–12 mm long, 22–24 mm wide throughout its length. The base of the stalk has a shallow longitudinal furrow at about the median region on both sides. The polyp body is up to 10 mm long, and the tentacles are up to 4–6 mm long, featuring four rows of pinnules on each side. The pinnules are relatively short and slender, up to 0.50 mm long and 0.15 mm wide, 14–32 in the outermost row with no gap or up to one pinnule-wide space between adjacent pinnules.

Sclerites are ellipsoid platelets, 0.014–0.017 X 0.015–0.021 mm in diameter (Fig.1a, n=24), composed of calcite rods radially arranged at least at the sclerite periphery, thus providing a granular appearance to their fractured surface (Fig.1a, b). Under SEM the sclerites often appear in aggregates and the individual ones are cemented together in different orientations (Fig 1c). The ethanol-preserved type is white-beige in color.

Etymology. It was decided to retain the species name as it appears at the ZMB.

Remarks. ZMB 6105 was found labelled as *Xenia flexibilis* Tixier-Durivault, 1971. A thorough literature survey indicated that it has not previously been referred to elsewhere (<http://www.marinespecies.org/aphia.php?p=taxdetails&id=204396>). The current study carefully examined the type and concluded that it is a new *Xenia* species. The variation in the number of pinnules in the outermost row in the type is quite remarkable, 14–32 pinnules, greater than has been recorded in any other *Xenia* species. The variation in the number of pinnules is usually smaller, e.g. 26–33 in *X. sansibariana* May, 1899, 15–23 in *X. ternatana* Schenk, 1896 or as high as 16–27 in *X. umbellata* Lamarck, 1816 (see ahead).

Similar species and conclusion. Similar to *X. flexibilis* n. sp., both *X. grasshoffi* Verseveldt, 1974 and *X. bauiana* May, 1899 feature four rows of pinnules, and partly overlap in the number of pinnules in the outermost row, with *X. flexibilis* n. sp. featuring the largest range (15–24, 26–30 and 14–32, respectively). These species also share the same sclerite microstructures (Figs. 1, 2 and 8, respectively), although *X. grasshoffi* possesses crests on the sclerite surface (Fig. 8b), absent in the other two species. It is suggested that the presence of a crest on the sclerite surface might be diagnostic and important for xeniid species identification. Moreover, the range of variation in number of pinnules in the outermost row in *X. flexibilis* n. sp. is larger than in the other two species, and therefore it is concluded that the three species should be considered as separate.

Distribution. Philippines.

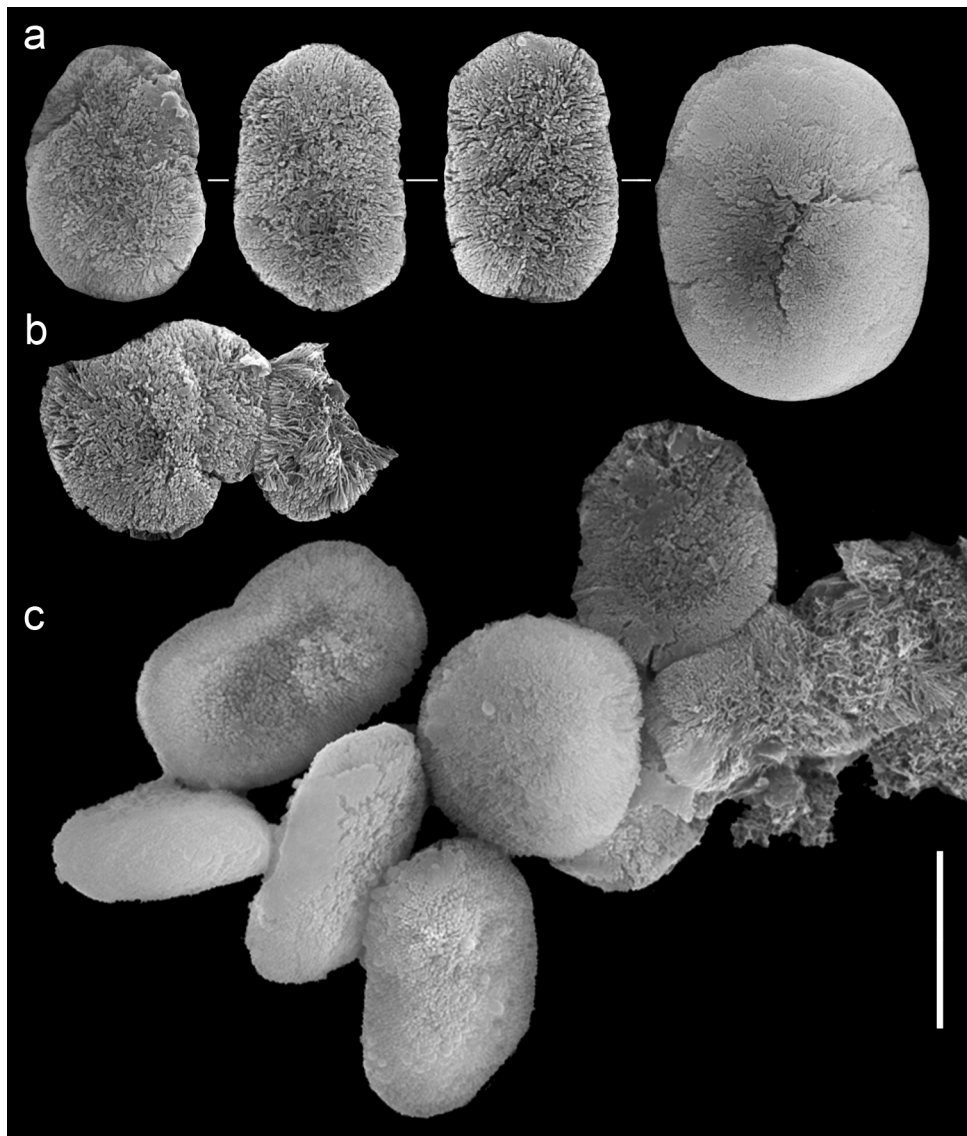


FIGURE 1. Scanning electron micrographs of polyp sclerites of *Xenia flexibilis* n. sp. holotype (ZMB 6105). a. Ellipsoid platelets, some fractured; b. Fractured sclerite revealing matrix of calcite rods, more or less radially arranged, at peripheral region; c. Overview of group of sclerites. Scale bar 0.010 mm.

***Xenia bauiana* May, 1899**

Fig. 2

Xenia bauiana May, 1899: 88

Xenia bauiana; Kükenthal 1902: 655–656

Material. Syntype: ZMB 3673, Zanzibar, 1885, coll. Sander.

Description. The syntype is 25 mm high; its stalk is 14–20 mm long and 12 mm wide at its base and 28 mm wide at the uppermost part. The polyp body is up to 9 mm long, and the tentacles are up to 4 mm long, featuring four rows of pinnules on each side. The pinnules are relatively short and slender, up to 0.50 mm long and 0.15 mm wide, 26–30 in the outermost row with no gap between adjacent pinnules.

Sclerites are ellipsoid platelets, occasionally slightly irregular 0.008–0.014 X 0.015–0.020 mm in diameter (Fig. 2a, n=25). They are composed of calcite rods (Fig. 2b) thus providing a granular appearance to the sclerite surface, which is mostly fractured (Fig. 1a). The ethanol-preserved holotype is brown-gray in color.

Remarks. In the original description of *X. bauiana*, May (1899) indicated three rows of pinnules, but not their

number on the margins of the tentacles. Later, Kükenthal (1902) noted that this species features six rows, probably referring to the total number – namely, three on each side of the tentacle. Both of these descriptions lack details regarding the number of pinnules and sclerite dimensions. The current findings further indicate that the number of rows of pinnules recorded in previous studies is erroneous (May 1899: 3 rows; Kükenthal 1902: 6 rows; and this study: 4 rows).

Similar species and conclusion. Both *X. bauiana* and *X. sansibariana* feature four rows of pinnules with 26–30 and 25–27 pinnules in the outermost row, respectively, and share the same type locality. Notably, *X. sansibariana* lacks sclerites and thus these two species should be considered as separate.

Distribution. Zanzibar.



FIGURE 2. Scanning electron micrographs of polyp sclerites of *Xenia bauiana* May, 1899 syntype (ZMB 3673). a. Ellipsoid platelets, mostly fractured; b. Fractured sclerite composed of dendritic rods, more or less radially arranged in the peripheral region; Scale bar at a 0.010 mm, at b 0.005 mm.

Xenia blumi Schenk, 1896

Figs. 3, 4

Xenia blumi Schenk, 1896: 65–66; May 1899: 81–82; Kükenthal 1902: 650; Roxas 1933: 83; Gohar 1940: 98–99; Verseveldt 1965: 45–46; Tixier-Durivault 1966: 365, fig 329; Utinomi 1977: 4; Benayahu 1990: 118, table 1, listed only.

Xenia plicata Schenk, 1896: 66–67—**new synonym**; Kükenthal 1902: 647; Tixier-Durivault 1966: 363, fig 327; Utinomi 1977: 6–7; Benayahu 1990: 118, table 1, listed only

Material. Holotype: SMF 44, Indonesia, Ternate Island, 1894, coll. W. Kükenthal; ***X. plicata* Holotype:** SMF 45, Indonesia, Ternate Island, January 1894, coll. W. Kükenthal.

Description. The holotype of *X. blumi* is 30 mm high; its stalk is 22 mm long and 20 mm wide at its base, 25 mm wide at the uppermost part. The polyp body is up to 5.5 mm long, and the tentacles up to 3 mm long. Tentacles bear three rows of pinnules, 18–20 in the outer row. The pinnules are up to 0.40 mm long and 0.15–0.20 mm wide, with no gap between adjacent pinnules.

Sclerites are mostly ellipsoid platelets, 0.008–0.012 X 0.014–0.018 mm in diameter (Fig. 3a, n=23). Under SEM they are mostly fractured thus enabling observation of the internal radially arranged calcite rods, occasionally branching towards the surface of the sclerite (Fig. 3b, c). Side view of the sclerites reveals their ellipsoidal platelet morphology (Fig. 3d). The ethanol-preserved holotype is gray in color. Unfortunately, the holotype is badly preserved and, therefore, the number of pinnule rows and the number of pinnules on the outermost row could not be clearly determined.

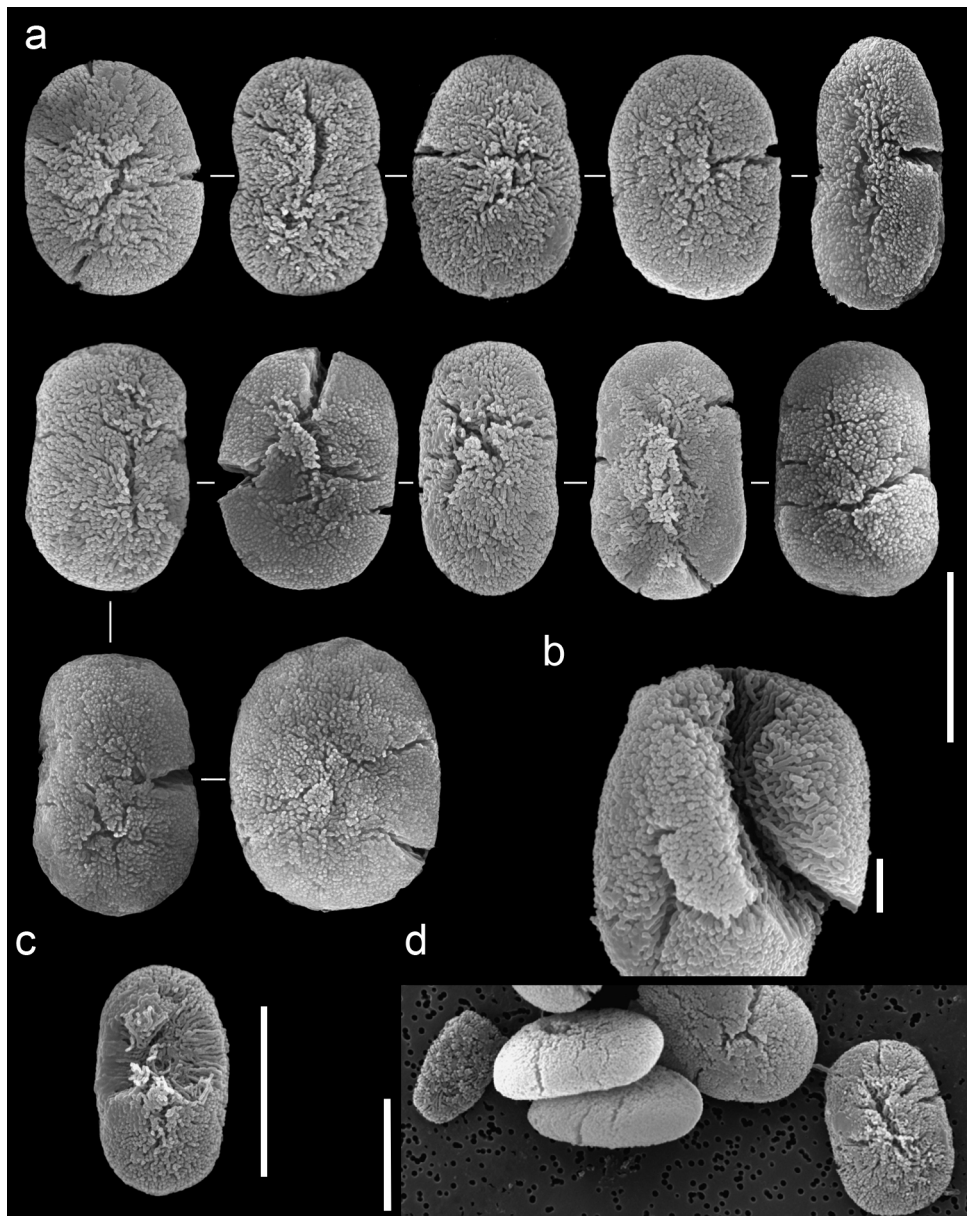


FIGURE 3. Scanning electron micrographs of polyp sclerites of *Xenia blumi* Schenk, 1896 holotype (SMF 44). a. Ellipsoid platelets, fractured; b. Fractured sclerite enlarged; c. Fractured sclerite composed of dendritic rods; d. Overview of sclerites. Scale bar at a, c and d 0.010 mm, at b 0.002 mm.

The holotype of *X. plicata* is 35 mm high; its stalk is 30 mm long, 12 mm wide at its base, and 15 mm wide at its uppermost part. The polyp body is up to 6 mm long, the tentacles up to 2–4 mm long, featuring three rows of pinnules on each side. The pinnules are relatively slender, 16–22 in the outermost row with no gap between adjacent pinnules. Sclerites are present in all parts of the colony; they are ellipsoid platelets, measuring 0.007–0.012 X 0.014–0.017 mm in diameter, some of which are fractured (Fig. 4a, n=22). They are composed of radially arranged calcite rods, uniform in width throughout their length and occasionally branched at their distal end (Fig. 4b, c). The surface of the sclerites is granular and often fractured. The ethanol-preserved holotype is gray in color.

Remarks. The original description of *X. blumi* indicated three rows of pinnules, 18–20 pinnules in the outermost row, and sclerites of 0.015–0.020 mm in diameter. Later, May (1900) described colonies of this species without examining the type. May's material was examined by Reinicke (1997), who compared it to the type and concluded that it did not belong to that species. The four specimens identified as *X. blumi* in Benayahu's study (1990) were re-examined during the present study and also found not to belong to that species, as suggested by Reinicke (1997). Gohar (1940: 98–99) described a colony of *X. blumi* from the Red Sea, indicating two to three

rows of pinnules and 10–16 pinnules in pulsatile polyps. These morphological characters do not correspond to the original description of that species (three rows of pinnules, 18–20 in the outermost row). Utinomi (1977) described *X. blumi* and *X. plicata* from Japan, and similarly neither of them correspond to the current description of the type.

Similar species and conclusion. *X. blumi* and *X. plicata* feature three rows of pinnules, with 16–22 and 18–20 pinnules in the outermost row, respectively. The present study confirms that these species share similar sclerite microstructure and therefore should be synonymized, giving a chronological priority to *X. blumi*, as suggested by Reinicke (1997: 18–22). The types of *X. viridis* Schenk, 1896 and *X. blumi* feature overlapping numbers of rows of pinnules and numbers of pinnules, but differ in sclerite microstructure. The sclerites of *X. viridis* occasionally reveal surface crests, which are lacking in *X. blumi*, thus the two species should be considered as separate.

Distribution. Indonesia: Ternate Island, Philippines, Madagascar.

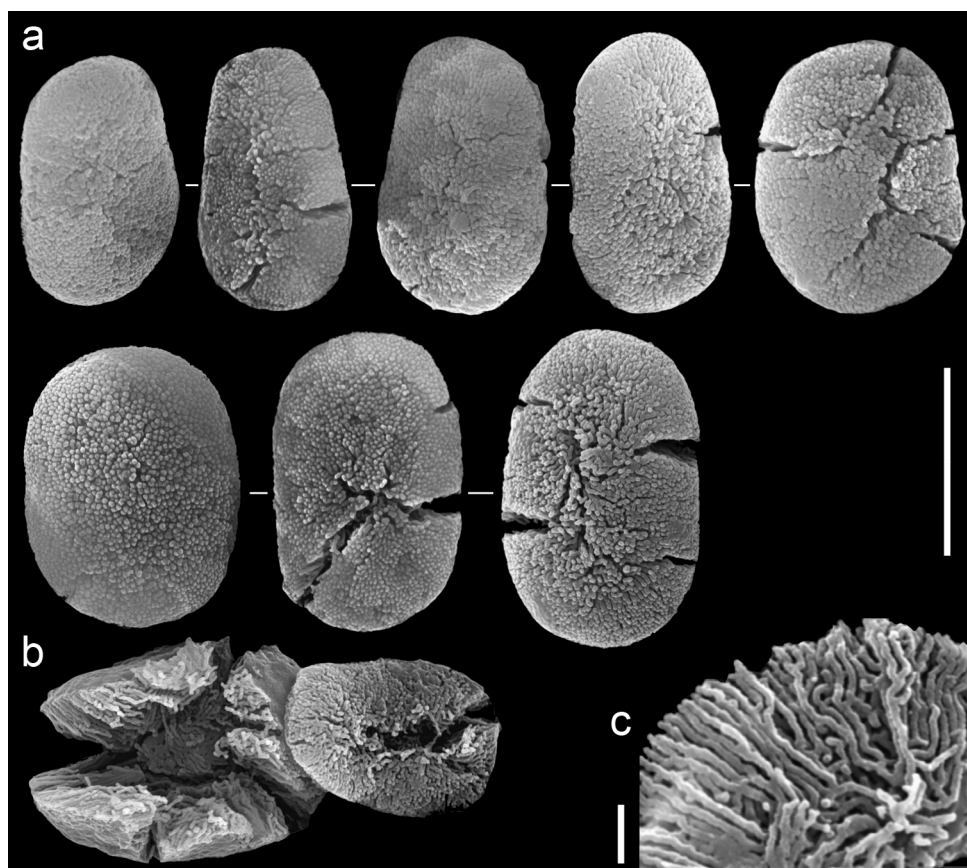


FIGURE 4. Scanning electron micrographs of polyp sclerites of *Xenia plicata* Schenk, 1896 holotype (SMF 45). a. Ellipsoid platelets, most fractured; b. Fractured sclerite; c. Fractured sclerite, enlarged, composed of calcite rods, often dendritic and sinuous, and more or less radially arranged in the peripheral region. Scale bar at a and b 0.010 mm, at c 0.001 mm.

Xenia crassa Schenk, 1896

Fig. 5

Xenia crassa Schenk, 1896: 58

Xenia crassa; Ashworth 1900: 510; Kükenthal 1902: 652; Hickson 1931a: 160; Thomson & Dean 1931: 28; Roxas 1933: 84; Tixier-Durivault 1966: 367; Utinomi 1977: 2–3; non *Xenia crassa*; Benayahu 1990: 18, listed only (identified by Reinicke, 1997 as *X. novaebritanniae* Ashworth, 1900); Benayahu 1990: 18 listed only.

Material. Holotype: SMF 39, Indonesia, Ternate Island, 1894, coll. W. Kükenthal.

Description. The holotype is 18 mm high; its stalk is 13 mm long, 11 mm wide at its base, and 14 mm wide at its uppermost part. The polyp body is 1.5–3 mm long, and the tentacles are up to 3–4 mm long, featuring three and sometimes four rows of pinnules on each side. The pinnules are up to 0.60 mm long and 0.20 mm wide, 13–18 in the outermost row with no gap between adjacent pinnules to a space of up to half a pinnule-width between adjacent pinnules.

Sclerites are present in all parts of the colony. They are ellipsoid platelets, and occasionally a crest is present on their surface (Fig. 5a, b). They occasionally feature a furrow on their apical narrow side. The sclerites measure 0.007–0.014 X 0.012–0.022 mm in diameter (n=26) and are composed of calcite rods which appear uniform in width (Fig. 5c). The sclerite surface is granular, including the crest, and often fractured. The ethanol-preserved holotype is gray and the tentacles are dark-gray in color.

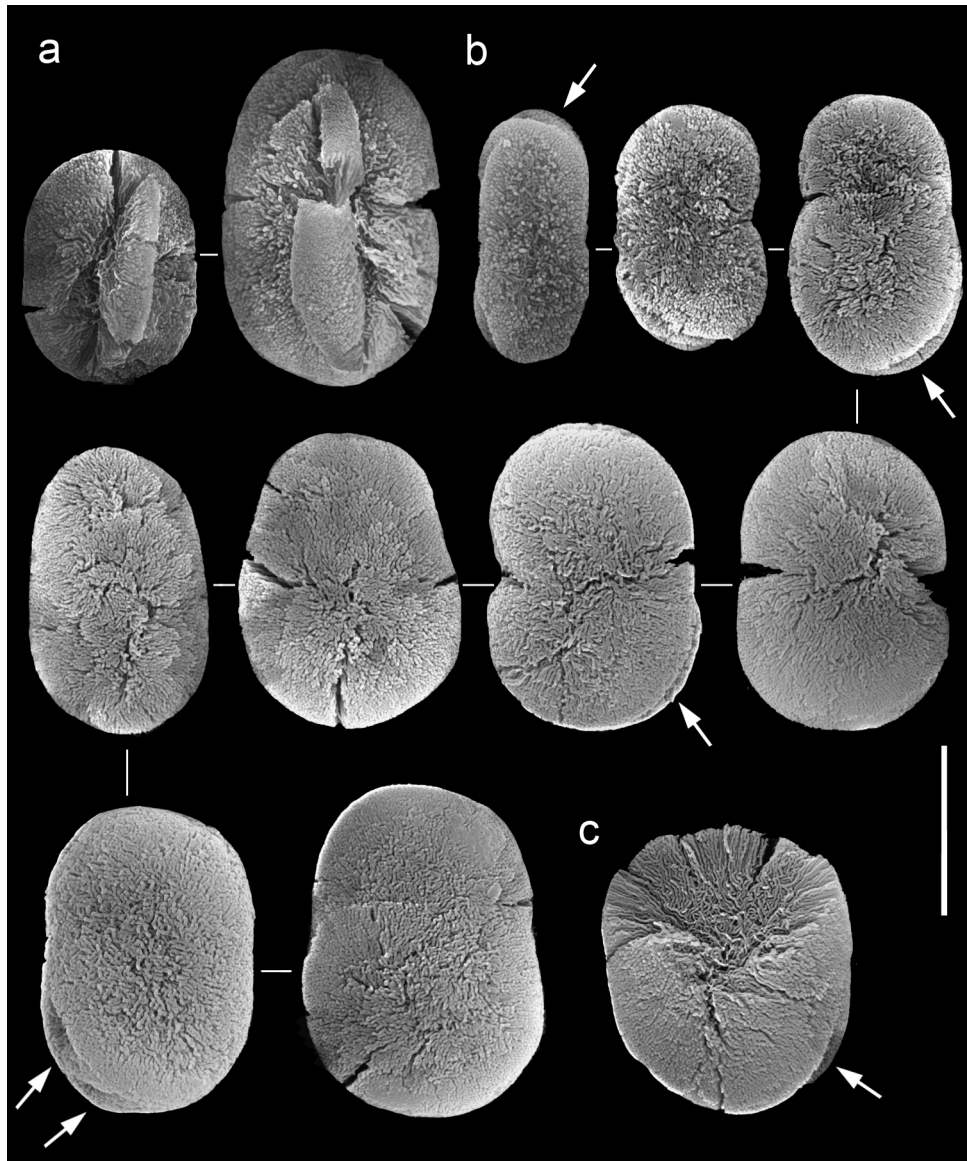


FIGURE 5. Scanning electron micrographs of polyp sclerites of *Xenia crassa* Schenk, 1896 holotype (SMF 39). a. Sclerites with a surface crest, fractured; b. Ellipsoid platelet, mostly fractured; c. Fractured sclerite composed of a latticework matrix of dendritic calcite rods and more or less radially arranged in the peripheral region. Arrows at b, c indicate surface furrow. Scale bar 0.010 mm.

Remarks. Schenk (1896) described *Xenia crassa* with three irregular rows of pinnules, 15–18 in the outermost one, thus corresponding to the current findings. The dimensions of the sclerites in that study differ from those in the current ones (0.02–0.030 mm vs. 0.007–0.014 X 0.012–0.022, respectively). Utinomi (1977: 3) described this species from Japan as featuring three rows of pinnules, 16–19 in the outermost row, and abundant “typical spicules”. That study reported the known distribution of *Xenia crassa* to include New Caledonia (Ashworth, 1900), Great Barrier Reef, Australia (Hickson 1931), Malay Archipelago (Schenk 1896; Thomson & Dean 1931), Philippines (Roxas 1933) and Madagascar (Tixier-Durivault 1966). Later, Reinicke (1997: 20) examined the type of *X. crassa*, compared it to Red Sea material identified by Benayahu (1990: 118), and concluded that the material identified as *X. crassa* by Benayahu belongs to *X. novaebritanniae* Ashworth, 1900.

Similar species and conclusion. *Xenia membranacea* Schenk, 1896 and *X. crassa* feature mostly three rows of pinnules and occasionally four. They differ in the number of pinnules in the outermost row (20–25 vs. 13–18, respectively) and in sclerite microstructure, and therefore they should be considered as separate species.

Distribution. Indonesia: Ternate Island, New Caledonia, Great Barrier Reef (Australia), Malay Archipelago, Philippines, Madagascar.

Xenia delicata Roxas, 1933

Xenia delicata Roxas, 1933: 89

Material. Holotype and 4 paratypes. ZMB 6908, Philippines, Puerto Galera Bay, Mindoro, 1912–1914, coll. members of the Zoology Department, University of the Philippines.

Description. The holotype is 21 mm high, its stalk is 8–9 mm wide, split into two branches, 4–5 mm long, and 4 mm wide. The polyp body is 4 mm long, tentacles up to 6 mm long, featuring three irregular rows of pinnules on each side and occasionally a fourth row. The pinnules are relatively short, up to 0.32 mm long and 0.10 mm wide, 18–23 in the outermost row with a space of 1–1.5 pinnule-widths between adjacent pinnules. There are no sclerites in any part of the colony. The ethanol-preserved holotype is light yellowish-beige.

The four paratypes resemble the holotype. The first paratype colony is 15 mm high; its stalk is 10 mm long and 3–4 mm wide, and does not split. The second is 15 mm high; its stalk is 10–12 mm long, divided into five branches, each 6–8 mm long and 3–4 mm wide. The third colony is 20 mm high, its stalk is 7–8 mm wide, splits into two branches, each 4–5 mm long and 3–4 mm wide. The fourth colony is 12–15 mm high; its stalk is 3–4 mm long and splits at the base into five branches, two of which split again into three, and another one into two branches, 2–3 mm above the colony base. They are 8–10 mm long, 4–5 mm wide at their base, and 3–4 mm at their uppermost part. Similar to the holotype, there are no sclerites in any part of the paratypes.

Remarks. Roxas (1933) described *X. delicata* as having four rows of pinnules and 18–20 pinnules in the outermost row, thus corresponding to the current findings. In contrast to the current findings, the original description indicated: “spicules present especially on external surface of tentacles and pinnules”; it also referred to only one colony although five were found under ZMB 6908. If the sclerites had dissolved due to the acidified preservative, *X. delicata* would in that case resemble *X. membranacea*.

Similar species and conclusion. *X. sansibariana*, *X. mucosa* Verseveldt & Tursch, 1979 and *X. delicata* lack sclerites in all parts of the colony, but differ in pinnule arrangement (*X. sansibariana*: 4 rows and 26–33, *X. mucosa*: 4 rows and 30–42, *X. delicata*: 3 and occasionally 4 rows and 18–23 pinnules) and thus should be considered as separate species.

Distribution. Philippines.

Xenia fusca Schenk, 1896

Fig. 6

Xenia fusca Schenk, 1896: 59

Material. Syntype: SMF 40, Indonesia, Ternate Island, 1894, coll. W. Kükenthal.

Description. The syntype is 38 mm high; its stalk is 32 mm long and 18 mm wide at its base, 25 mm wide at its uppermost part. The polyp body is up to 3 mm long, and the tentacles are up to 2.5–3 mm long, featuring mostly four rows of pinnules along each of the tentacle margins. Occasionally 3 and even 5 rows are present. The pinnules are relatively short and stout, up to 0.25 mm long and 0.10 mm wide, 14–22 in the outermost row, spacing ranging from no gap to up to a half pinnule-wide space between adjacent pinnules.

Sclerites are abundant in all parts of the colony; they are ellipsoid platelets, 0.006–0.014 X 0.013–0.019 mm in diameter (Fig. 6a, n=20). The sclerites are composed of dendritic rods assembled within the sclerite interior (Fig. 6b), providing a granular appearance to the sclerite surface. Few fractured sclerites were observed, and they remained intact after preparation (Fig. 6c). The ethanol-preserved holotype is dark gray in color.

Remarks. In the original description of *X. fusca*, Schenk (1896) indicated that the species has 6–7 irregular

rows of pinnules and 13–14 pinnules in each row, as opposed to the current findings that revealed mostly four rows and 14–22 pinnules in the outermost row. The dimensions of the sclerites obtained in the current study correspond to the original description. The sclerites of the type of *Xenia fusca* differ from those commonly occurring among other *Xenia* species (e.g., *X. bauiana*: Fig. 2, *X. blumi*: Fig. 3, *X. garciae* Bourne, 1894: Fig.7), feature a densely packed granular surface, and do not exhibit the typical radial cracks under SEM (e.g. *X. blumi*: Fig. 3, *X. plicata*: Fig. 4).

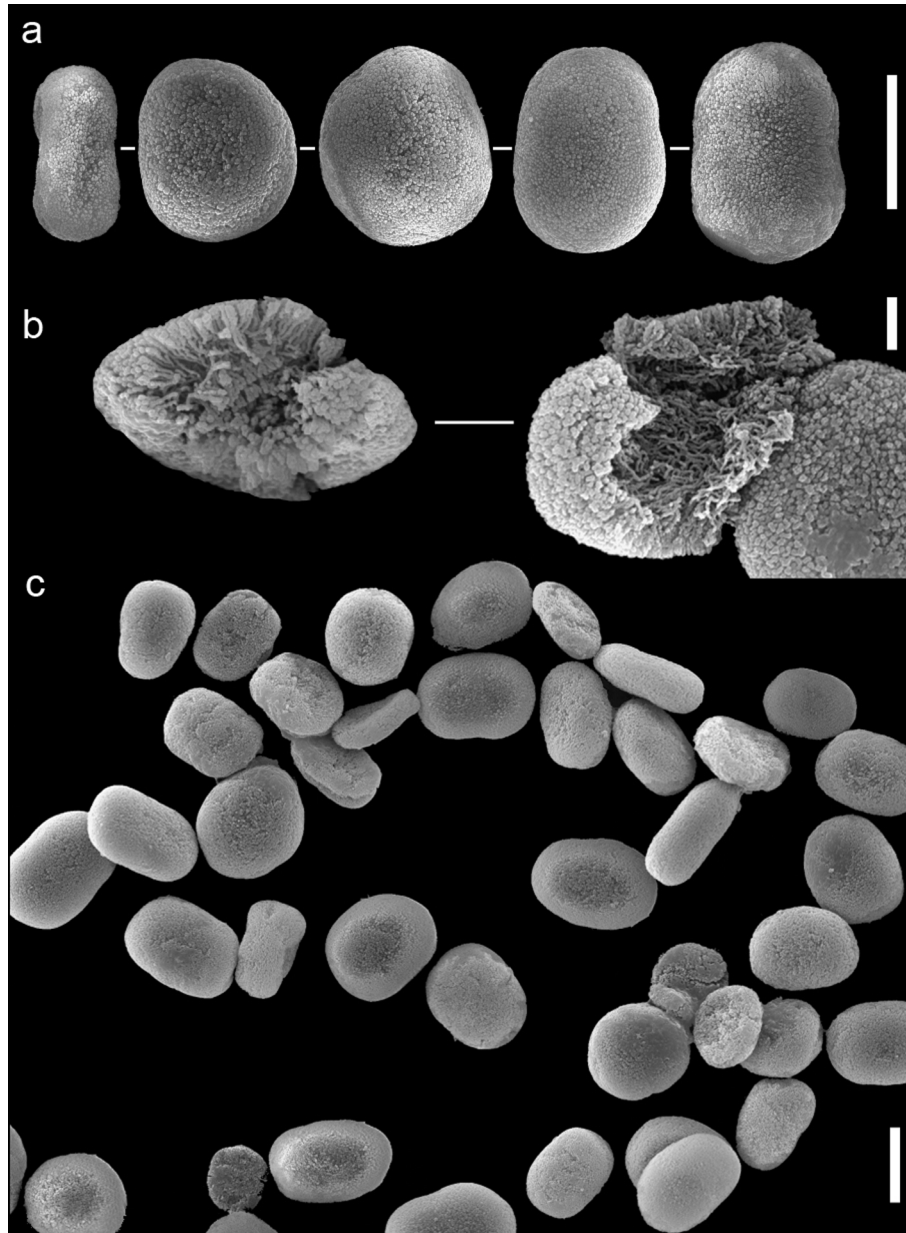


FIGURE 6. Scanning electron micrographs of polyp sclerites of *Xenia fusca* Schenk, 1896 syntype (SMF 40). a. Ellipsoid platelets; b. Fractured sclerites composed of a latticework matrix of dendritic calcite rods and more or less radially arranged in the peripheral region; c. Overview of sclerites. Scale at a and c 0.010 mm, at b 0.002 mm.

Similar species and conclusion. *X. fusca* and *Xenia rubens* Schenk, 1896 feature mostly four rows of pinnules and a similar number of pinnules in the outermost row. They also share the same type of sclerite surface but the internal structure of their sclerites differs: the latter with wide rods and a void in the interior and the former with randomly arranged calcite rods (Figs. 13 and 6, respectively). Therefore, it is concluded that the two species should be considered as separate until further data on freshly collected colonies and their sclerite microstructure become available.

Distribution. Indonesia: Ternate Island.

Xenia garciae Bourne, 1894

Fig. 7

Xenia garciae Bourne, 1894: 475, plate 12, Figs. 13–14; *Xenia garciae*; Ashworth 1900: 520; Kükenthal 1902: 652–653; Gohar 1940: 100–101; Tixier-Durivault 1966: 363; Verseveldt 1970: 210, listed only; Benayahu 1990: 118, listed only; Reinicke 1997: 38–39.

Material. Type: BML 1921.11.18.1, Indian Ocean, Chagos-Archipelago, Diego Garcia, 1886, coll. G. C. Bourne.

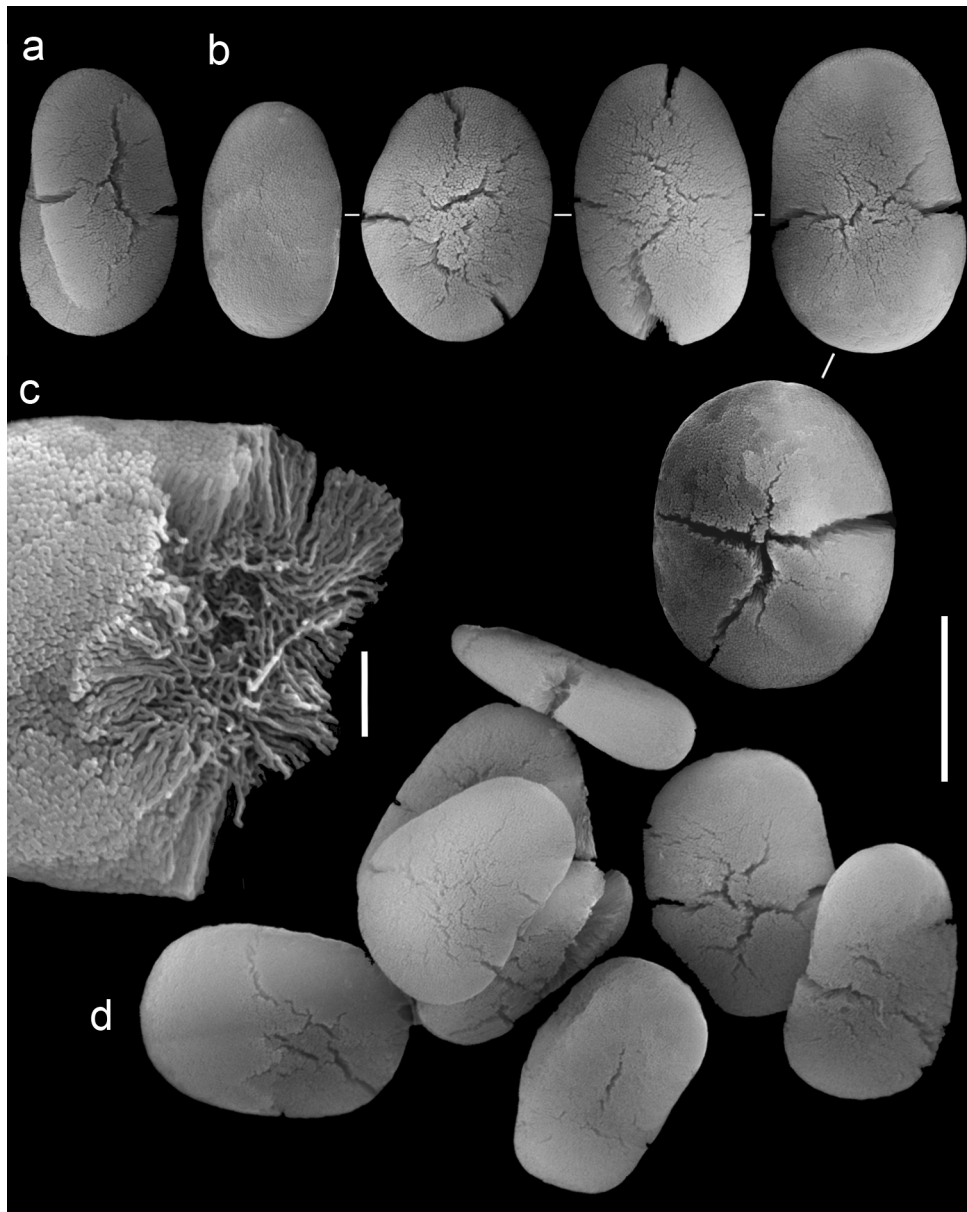


FIGURE 7. Scanning electron micrographs of polyp sclerites of *Xenia garciae* Bourne, 1894 type (BML 1921.11.18.1). a. Sclerite with a surface crest, fractured; b. Ellipsoid sclerites, fractured c. Fractured sclerite composed of a latticework matrix of calcite rods, dendritic and sinuous and radially arranged in the peripheral region; d. Overview of sclerites, fractured. Scale bar at a, b and d 0.010 mm, at c 0.002 mm.

Description. The colony is very small, its stalk is up to 5 mm high and undivided, with polyps tightly packed on the capitulum. Three rows of pinnules are aligned along each of the tentacle margins, 16–22 in the outermost row, separated by less than a pinnule-wide space.

Sclerites are ellipsoid platelets 0.009–0.016 X 0.016–0.021 mm in diameter (Fig. 7a–d, n=20). A surface crest can occasionally be observed (Fig. 7a). The sclerites are composed of calcite rods arranged radially and assembled

randomly within the sclerite interior (Fig. 7c). The rods are uniform in width throughout their length and provide a granular appearance to the sclerite's surface. Under SEM the sclerites are mostly fractured.

Remarks. The condition of the type of *Xenia garciae* is poor, probably due to inappropriate preservation; measurements of the colony and polyps could therefore not be made. According to Kükenthal (1902: 652–653), *X. garciae* features three rows of pinnules, 9–10 pinnules in the outermost row. Later, Gohar (1940) noted that *X. garciae* collected from the Red Sea, which was the first species to be reported from Hurgada, featured three rows of pinnules, 6–10 pinnules in the outermost row, and “spherical” sclerites, 0.018–0.025 mm in diameter. That study also noted that the colonies are non-pulsating and that the species is known from Diego Garcia (Bourne 1894: 475), Maldives (Hickson 1903: 479), Malay Archipelago (Thomson and Dean 1931), and at several Red Sea sites (Ghardaqa, Shadwan Island and Qoseir). The above two descriptions do not correspond to the current findings due to the much smaller number of pinnules described. Reinicke (1997) raised doubts concerning the species' presence in the Red Sea since Gohar's material could not be examined by him. Furthermore, colonies referred to by Reinicke (1995) as *X. garciae* were found in this study to belong to the genus *Ovabunda*: *Ovabunda gohari* (Reinicke, 1997) and *O. arabica* (Reinicke, 1995).

Similar species and conclusion. Both *Xenia blumi* and *X. garciae* feature three rows of pinnules, 18–20 pinnules in the outermost row and a similar sclerite microstructure. The current findings indicate that *X. garciae* occasionally features a small surface crest. Therefore, the two species should be considered as separate until further data on freshly collected colonies are available and the extent of these surface crests can be further investigated.

Distribution. Indian Ocean: Chagos-Archipelago.

Xenia grasshoffi Verseveldt, 1974

Fig. 8

Xenia grasshoffi; Verseveldt, 1974a: 34–35, Fig. 34

Material. Holotype: SMF 2616, northern Red Sea, Gulf of Aqaba, Eilat, 1968, coll. M. Grasshoff.

Description. The holotype is 28 mm high; its stalk is 23 mm long, 10 mm wide at its base and 25 mm wide at the uppermost part. The polyp body is up to 3 mm long, and the tentacles are up to 2 mm long, featuring four rows of pinnules on each side. The pinnules are relatively short and stout, up to 0.24 mm long and 0.20 mm wide, 15–24 in the outermost row with no gap between adjacent pinnules.

Sclerites are ellipsoid platelets, measuring 0.009–0.017 X 0.015–0.023 mm in diameter (Fig. 8a–d, n=27). Occasionally, a crest is present on the surface of the sclerite (Fig. 8b, d). Rarely, a median waist can be seen (Fig. 8a). They are composed of calcite rods arranged radially, and at the center of the sclerite they are randomly arranged (Fig. 8b, c). Many of the sclerites are fractured (Fig. 8a, b, d). The ethanol-preserved holotype is light cream in color and polyps are almost white.

Remarks. The current findings correspond to the original description of *X. grasshoffi* (Verseveldt 1974a: four rows and 15–24 pinnules vs. four and occasionally five rows and 16–20 pinnules, respectively). The sclerites were originally described as: "spicules of general xeniid type: round or oval corpuscle" and the current measurements reveal that their size corresponds to the original description (0.009–0.017 X 0.015–0.023 vs. 0.024 in the stalk and 0.021 in the tentacles, respectively).

Similar species. *Xenia flexibilis* n. sp. and *X. grasshoffi* feature four rows of pinnules and a certain overlap in the number of pinnules in the outermost row (14–32 vs. 15–24). However, the sclerites of *X. grasshoffi* feature surface crests which are absent in *X. flexibilis* and thus they should be considered as separate species.

Distribution. Red Sea.

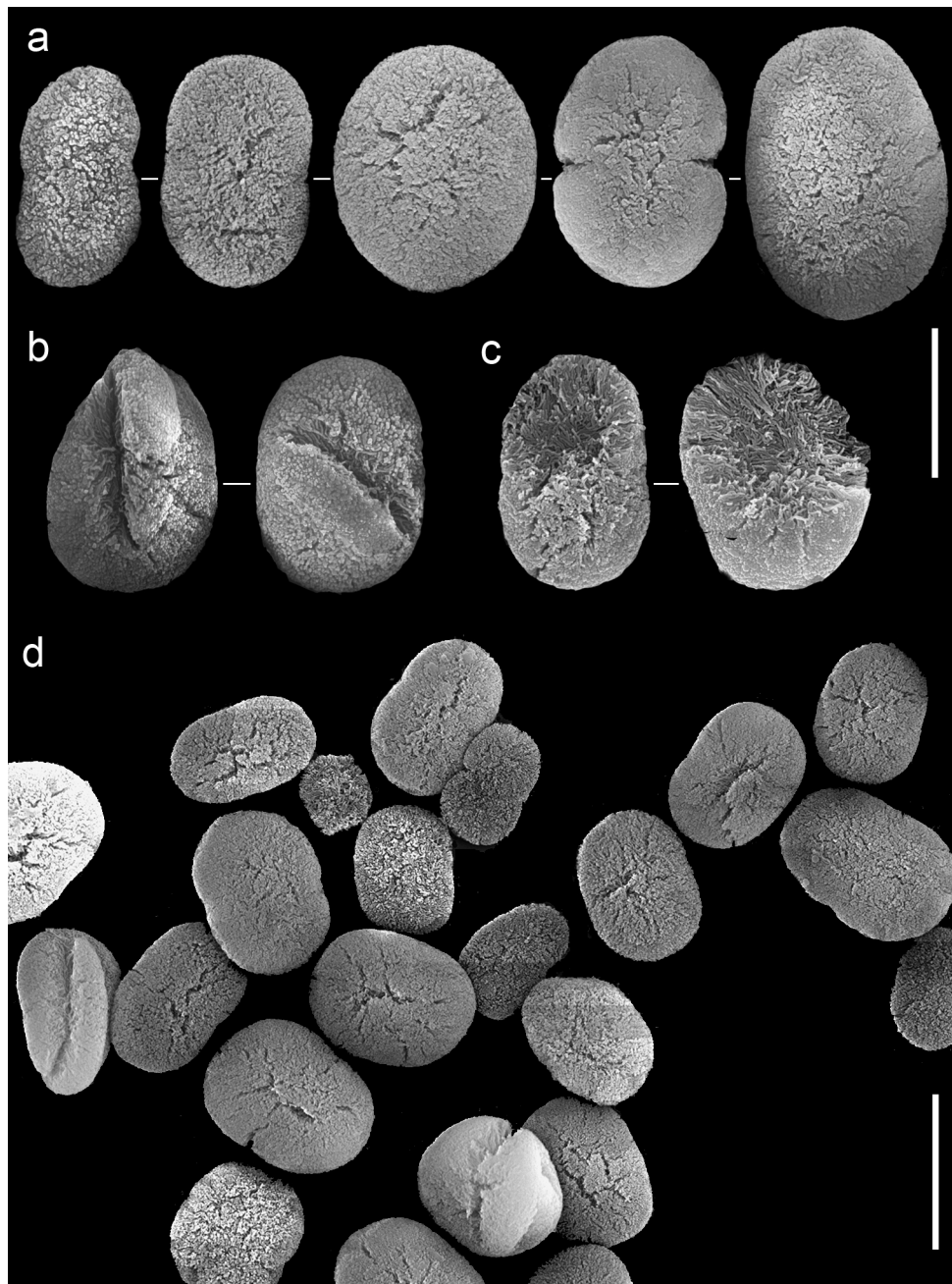


FIGURE 8. Scanning electron micrographs of polyp sclerites of *Xenia grasshoffi* Verveeldt, 1974 holotype (SMF 2616). a. Ellipsoid platelets, fractured; b. Sclerites with surface crest; c. Fractured sclerites composed of a latticework matrix of dendritic calcite rods radially arranged, at least in peripheral region; d. Overview of variety of sclerites. Scale bar at a, b and c 0.010 mm, at d 0.020 mm.

Xenia kuekenthali Roxas, 1933

Xenia kuekenthali Roxas, 1933: 79–80, plate 1, Fig. 1; *Xenia kuekenthali*; Utinomi 1950: 84, Fig. 2 d–g, 3a; Verveeldt & Cohen 1971: 61, table 1; Benayahu 1990: 114, table 1, listed only; Reinicke 1997: 31–32, plate 11.

Material. **Holotype** and two small fragments: ZMB 6917, Philippines, Mindoro, Puerto Galera, Sabang, 1912–1914, coll. members of the Zoology Department, University of the Philippines.

Description. The holotype is 45–50 mm high; its stalk is 13–15 mm long and splits at the base into five branches, four of which split again into two, 13–15 mm above the colony base; the latter branches are 10–14 mm

long, 7–8 mm wide at their base, 4–5 mm at their uppermost part. The colony stalk is 45 mm wide at its widest part. The holotype is extremely flabby. The polyp body is up to 4 mm long, and the tentacles up to 4 mm long, featuring one row of pinnules on each side, with 8–10 pinnules. The pinnules are extremely short, up to 0.10 mm long and 0.30 mm wide, with no gap between adjacent ones. No sclerites are found in any part of the colony. The ethanol-preserved colony is light beige. The two fragments have similar features to those of the holotype.

Remarks. The original description of *X. kuekenthali* by Roxas (1933) indicated two rows of pinnules with 8 pinnules in a row, thus not corresponding to the current findings of one row of pinnules. Utinomi (1950) referred to a specimen from Japan as having two rows with 10–12 pinnules in the outermost row. Later, Benayahu (1990) reported this species from the Red Sea based on the original description. Reinicke (1997) described a pulsating colony of the species from the Gulf of Aqaba, and indicated that the validation of its presence in the Red Sea should be based on the examination of additional material. The current examination of the type of *Xenia kuekenthali* revealed that the original description was inaccurate, and thus most probably led to the recurring errors in the subsequent studies.

Similar species and conclusion. *X. kuekenthali* is the only *Xenia* species among those examined in this study with one row of pinnules.

Distribution. Philippines.

Xenia lepida Verseveldt, 1971

Xenia lepida Verseveldt, 1971: 65–67

Xenia lepida; Janes 2013; Janes *et al.* 2014; McFadden *et al.* 2014b

Material. Holotype: RMNH Coel no. 6703, Indian Ocean, Madagascar, Nosy Bé, Pointe lokombe, 10 m, 18 July 1967, coll. A. G. Humes; **Paratype:** RMNH Coel. no. 6704, same collection data.

Description. The holotype is 40 mm high; its stalk splits three times, 15 mm above the colony attachment to the substratum. The first branch is 14 mm long, the second is 24 mm long and splits at its distal part, the third is 22 mm long and splits four times. They are all 5 mm wide at their base and at their uppermost part. The polyp body is up to 16 mm long, and the tentacles up to 12 mm long, featuring three rows of pinnules on each side, with approximately 28–34 pinnules in the outermost row. Most of the polyps are extended, and the arrangement of the pinnules is irregular, with the total number of pinnules reaching 40 and more. The pinnules are relatively slender, up to 0.24 mm long and 0.16 mm wide, with spacing of half a pinnule-width up to 2 pinnule-widths between adjacent pinnules. Sclerites are not present in any part of the colony. The ethanol-preserved holotype is light beige.

The paratype is 47 mm high; its stalk is 34 mm long, 5 mm wide at its base, and 5 mm wide at its uppermost part. The polyp body is up to 6 mm long, and the tentacles up to 7 mm long, featuring three rows of pinnules on each side. The pinnules are relatively slender, up to 0.50 mm long and 0.16 mm wide, 24–32 in the outermost row with spacing of no gap up to half a pinnule-width between adjacent pinnules. As in the holotype, no sclerites were found in the paratype. The ethanol-preserved paratype is light beige.

Remarks. The current findings correspond to the original description of *X. lepida*, except for the latter referring to sclerites 0.009 mm in diameter in the stalk and 0.015 mm long in the polyps, visible only under a polarizing microscope. The two measurements most probably refer to symbiotic algae (zooxanthellae), which confused the author, rather than to the sclerites. In the current study no sclerites were found in any part of the colony.

Similar species and conclusion. Both *X. sansibariana* and *X. lepida* feature a similar number of pinnules in the outermost row and lack sclerites in all parts of the colony. They differ in the number of pinnule rows (4 vs. 3, respectively) and thus should be considered as separate. The original description of *X. lepida* by Verseveldt (1971) mentioned its similarity to *X. distorta* Tixier-Durivault, 1966. For the purpose of the current study, inquiries made to the Muséum National d'Histoire Naturelle, Paris (MNHN) indicated that the type most probably got lost and therefore regrettably could not be compared to *X. lepida*.

Distribution. Indian Ocean: Madagascar, Indonesia: Lembah Strait.

Xenia membranacea Schenk, 1896

Fig. 9

Xenia membranacea Schenk, 1896: 60, plate 3, Fig 15

Xenia membranacea; Ashworth 1900: 512; Kükenthal 1902: 654–655; Ashworth 1900: 512; May 1899: 86; Thomson & Dean 1931: 31; Roxas 1933: 90, plate 2, Fig 7; Verseveldt 1960: 244–246; Utinomi 1977: 5–6; Benayahu 1990: 118, table 1, listed only; Reinicke 1997: 50–51; Janes 2013; McFadden *et al.* 2014a.

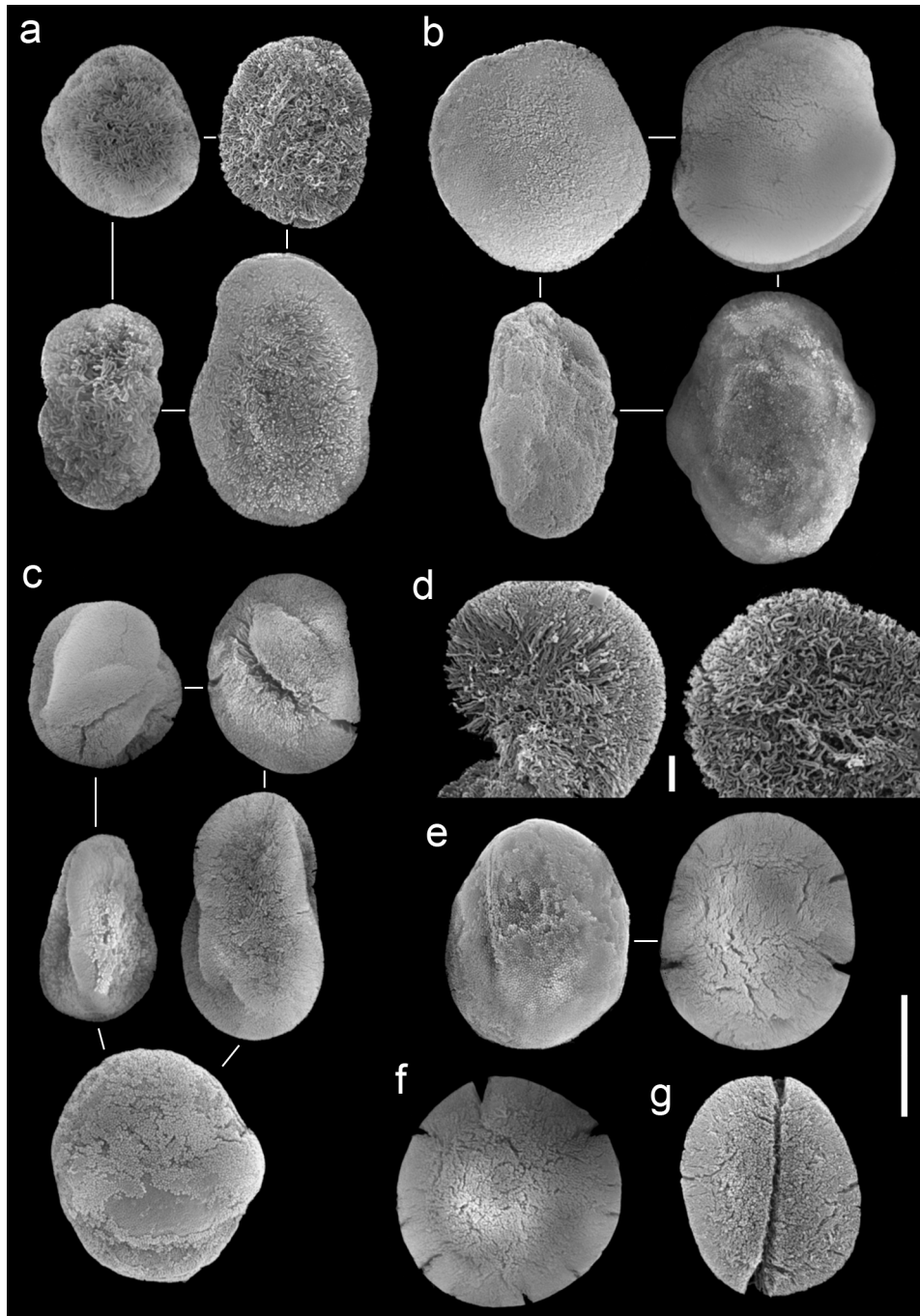


FIGURE 9. Scanning electron micrographs of polyp sclerites of *Xenia membranacea* Schenk, 1896 syntype (SMF 41). a. Irregular sclerites with rough surface texture ; b. Irregular sclerites with granular surface texture; c. Sclerites with surface crest, some fractured; d. Fractured sclerites composed of dendritic rods (enlarged). e. Ellipsoid platelets; f. Round sclerite; g. Fractured sclerite. Scale bar at a, b, c, e, f, g 0.010 mm, at d 0.002 mm.

Material. Syntype: SMF 41, Indonesia, Ternate Island, Moluccas, 1894, coll. W. Kükenthal.

Description. The syntype is 25 mm high; its stalk is 9 mm long and it splits 2–3 mm above its base into eight short branches, two of which split again into two; the length of each branch is 8–10 mm and their width is about 5 mm at the base and 5–6 mm at the uppermost part. The polyp body is up to 3 mm long, and the tentacles up to 4 mm long, featuring three and occasionally a partial fourth row of pinnules on each side. The pinnules are relatively slender, up to 0.75 mm long and 0.25 mm wide, 20–25 in the outermost row with no gap between adjacent pinnules.

Sclerites are present in all parts of the colony; most of them are ellipsoid platelets, 0.010–0.019 X 0.015–0.025 mm in diameter (Fig. 9, n=26). Their surface outline ranges from almost smooth to irregular (Fig. 9a, b). Some of the sclerites feature a crest, or surface depressions (Fig. 9c, e). Others are almost round (Fig. 9f) or feature a longitudinal furrow (Fig. 9g). The sclerites are composed of calcite rods arranged radially, at least on the surface of the sclerite (Fig. 9d), providing a granular appearance to all the various morphologies. The ethanol-preserved holotype is light gray in color.

Remarks. The original description of *Xenia membranacea* indicated 3–4 irregular rows of pinnules, 20–25 pinnules in each one. The sclerites were referred to as round discs, long ovals, or rod-like, 0.015–0.020 mm, 0.02–0.025 X 0.010–0.015 mm and 0.020–0.030 X 0.006–0.010 mm, respectively. Except for the latter, their measurements match our re-description of the type. Verseveldt (1960) identified material from Obi Latu (Indonesia) and from the Bay of Djakarta, Malay Archipelago. For the former he described four rows of pinnules, 20–24 in a row, and "numerous oval" sclerites measuring 0.018–0.022 X 0.013–0.015 mm; while for the one from the Malay Archipelago he described five rows of pinnules, referring to Thomson & Dean (1931: 31) who also described five rows for specimens from the same location. The material from Obi Latu corresponds to the *X. membranacea* type while the Malay material might belong to *X. fusca*. *X. membranacea* was reported from the Red Sea by Benayahu (1990) and Reinicke (1997).

Similar species and conclusion. Roxas (1933) identified two specimens from the Philippines as *Xenia membranacea* and noted that it had been synonymized by Hickson (1931a: 152) with *X. crassa*. *Xenia membranacea* and *X. crassa* feature three and sometimes four rows of pinnules, but differ in the number of pinnules. Their sclerite microstructure also differs (Figs. 9 and 5, respectively), and thus they should be considered as separate. Although features of *X. membranacea* also resemble those of *X. grasshoffi*, the former possesses sclerites with sinuous rods lacking in the latter, thus the two should be considered as separate species.

Distribution. Indonesia: Ternate Island, Moluccas, Philippines, Japan, Malay Archipelago, Red Sea.

Xenia mucosa Verseveldt & Tursch, 1979

Xenia mucosa Verseveldt & Tursch, 1979: 147–148

Material. Holotype: RMNH 12867, Bismarck Sea, Boëso I., South reef flat, 5 m, 1975–1977, King Leopold III Biological Station at Laing Island, coll. A. Tursch.

Description. The holotype is 50 mm high; its stalk splits 15 mm above its base into two branches, one of which splits again into two, 20 mm above the first; the latter branches are 14 and 13 mm long, 6 mm wide at their base, 15 and 10 mm wide at their uppermost part, respectively. The third branch does not split; it is 20 mm long, 5 mm wide at its base and 6 mm wide at the uppermost part. The polyp body is up to 8 mm long, the tentacles up to 13 mm long, featuring four rows of pinnules on each side. The pinnules are slender, up to 0.5 mm long and 0.2 mm wide, 30–42 in the outermost row with a space of 0.5–1.5 pinnule-widths between adjacent pinnules. No sclerites could be found in any part of the colony. The ethanol-preserved holotype is light beige in color.

Remarks. The re-description of *X. mucosa* corresponds to the original description.

Similar species and conclusion. Both *X. mucosa* and *X. sansibariana* feature four rows of pinnules and lack sclerites in all parts of the colony. The number of pinnules in their outermost row differs (*X. mucosa*: 30–42 and *X. sansibariana*: 26–33) and thus they should be considered as separate species.

Distribution. South-Western Pacific Ocean: Bismarck Sea.

Xenia multispiculata Kükenthal, 1909

Fig. 10

Xenia multispiculata Kükenthal, 1909: 47

Material. Syntype: ZMB 6920, South Pacific Ocean, Tonga Island, Viti, collected by Dr. H. Merton.

Description. The holotype is 28 mm high; its stalk is 16–20 mm long, 10 mm wide at its base and 15 mm wide at the uppermost part. The polyp body is up to 10 mm long, and the tentacles up to 9 mm long, featuring two irregular rows of pinnules on each side. The pinnules are short and stout, up to 0.8 mm long and 0.2 mm wide, 21–29 in the outermost row with a gap of one pinnule-width space between adjacent ones.

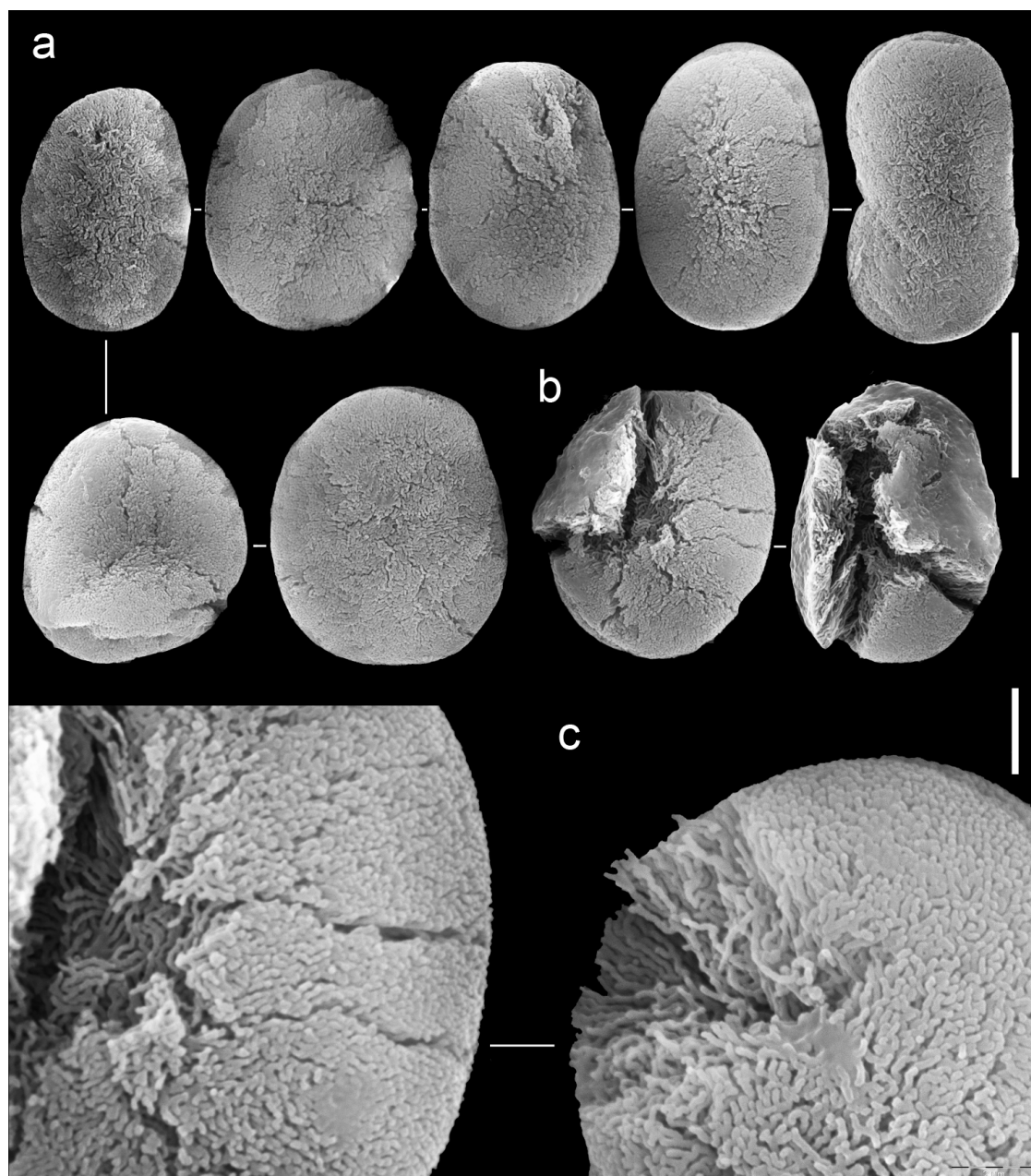


FIGURE 10. Scanning electron micrographs of polyp sclerites of *Xenia multispiculata* Schenk, 1896 Syntype (ZMB 6920). a. Ellipsoid platelets, some fractured; b. Fractured sclerites; c. Fractured sclerites composed of a latticework matrix of calcite rods, dendritic and sinuous, radially arranged in the peripheral region. Scale bar at a and b 0.010 mm, at c 0.002 mm.

Sclerites are ellipsoid platelets, measuring 0.011–0.018 X 0.019–0.025 mm in diameter (Fig. 10a, n=20). They are comprised of calcite rods, which are uniform in width and assembled randomly within the sclerite center (Fig.

10b, c). The sclerite surface is granular and occasionally fractured. The ethanol-preserved holotype is beige in color.

Remarks. The re-description of *X. multispiculata* corresponds to the original description.

Similar species and conclusion. *X. multispiculata* is the only *Xenia* species among those examined in this study to display two rows of pinnules. It shares sclerite microstructure with *X. novaebritanniae* Ashworth, 1900, *X. bauiana* and *X. blumi* but differs in pinnule arrangement and thus should be considered as a separate species.

Distribution. South Pacific Ocean: Tonga Island.

Xenia novaebritanniae Ashworth, 1900

Figs. 11, 12

Xenia novaebritanniae Ashworth, 1900: 521–522, plate 52–53, Figs. 1–3, 5–9

Xenia novaebritanniae; Benayahu 1990: 115, table 1, listed only; Reinicke 1997: 40–41

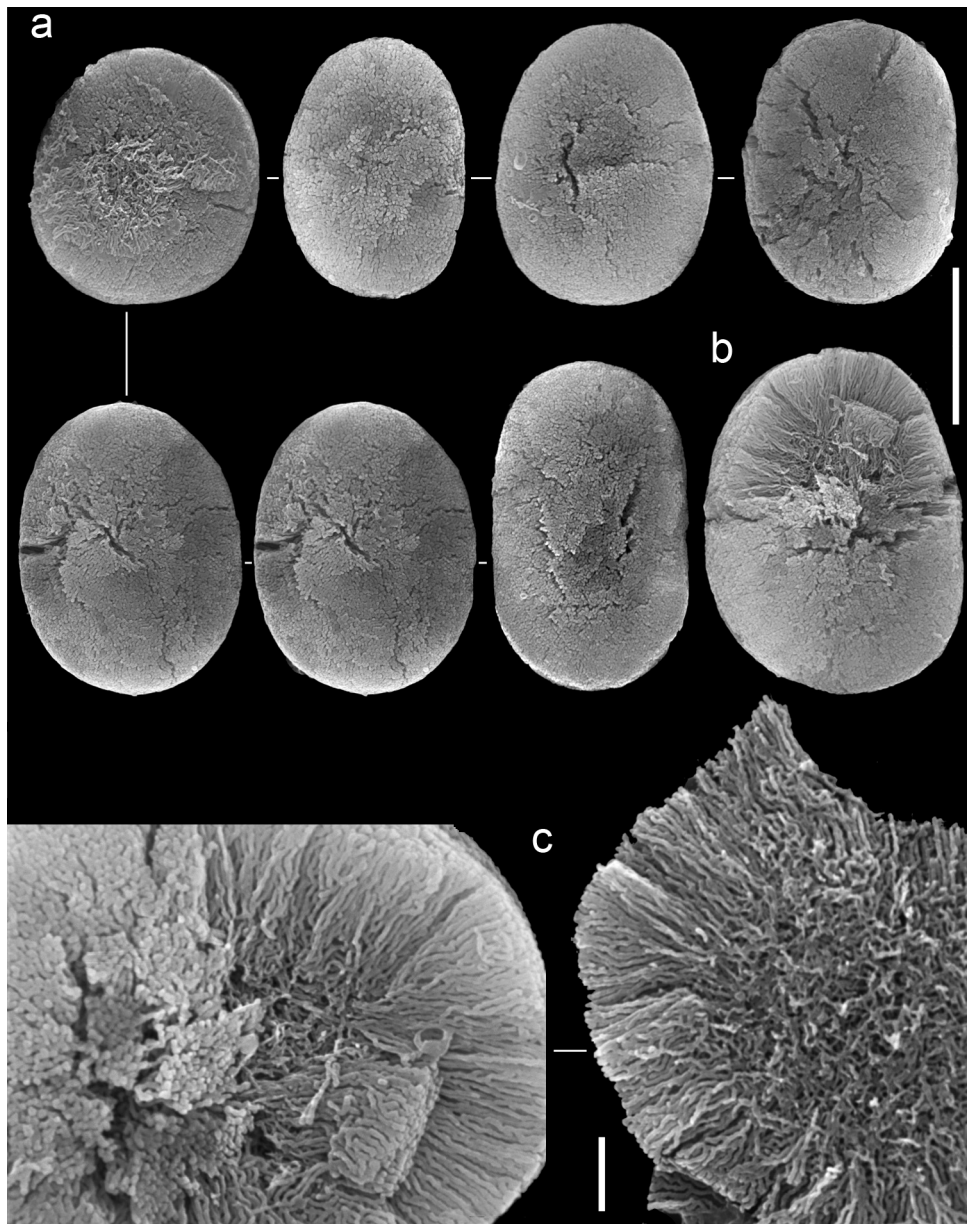


FIGURE 11. Scanning electron micrographs of polyp sclerites of *Xenia novaebritanniae* Schenk, 1896 syntype (BML 1962.7.20.148). a. Ellipsoid platelets, fractured; b. Fractured sclerite; c. Fractured sclerites enlarged composed of a latticework matrix of calcite rods, dendritic and sinuous, radially arranged in peripheral region. Scale bar at a and b 0.010 mm, at c 0.002 mm.

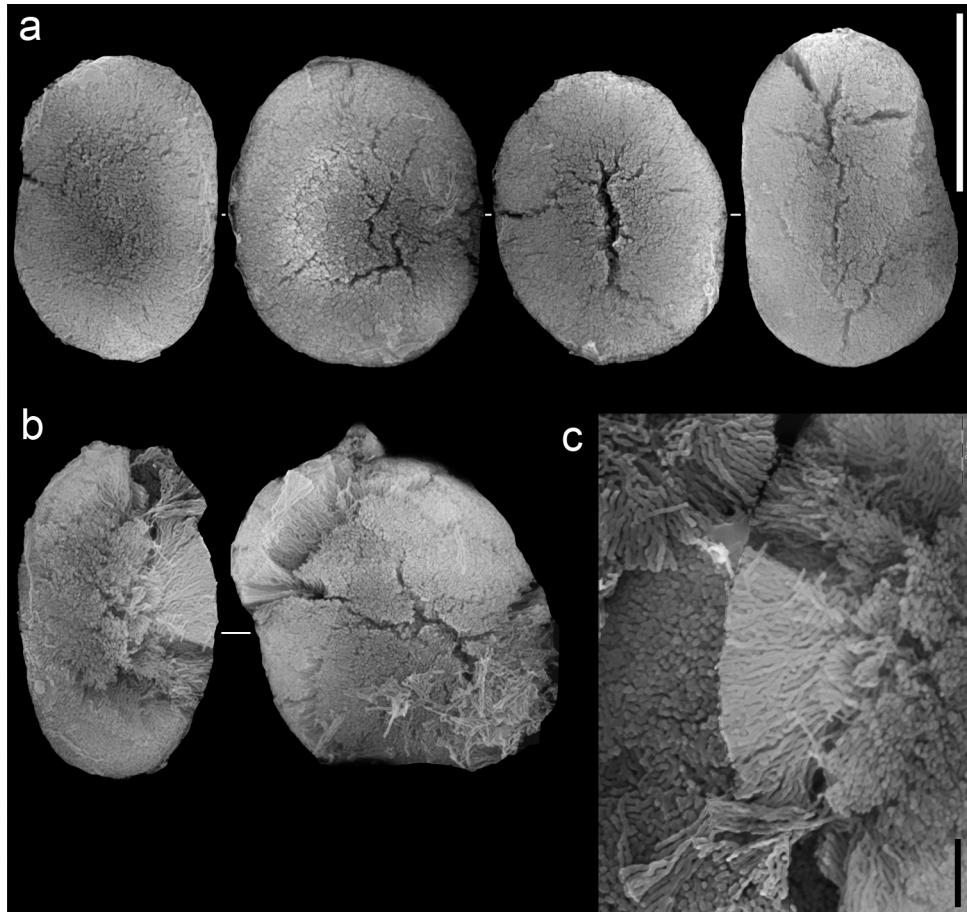


FIGURE 12. Scanning electron micrographs of polyp sclerites of *Xenia novaebritanniae* Schenck, 1896 syntype (BMNH 1962.7.20.149). a. Ellipsoid platelets, fractured; b. Fractured sclerites; c. Fractured sclerite enlarged, composed of calcite rods. Scale bar at a and b 0.010 mm, at c 0.002 mm.

Material. Syntype: *X. novaebritanniae* BML 1962.7.20.148, South Pacific Ocean, Lifu, Loyalty Island, November 1896, **Syntype:** BML 1962.7.20.149, Papua New Guinea, New Britain, Talili Bay, 1895.

Description. The syntype BML 1962.7.20.148 is 30 mm high; its stalk is 10 mm long and about 10 mm wide at its base and 20 mm wide at the uppermost part. The colony was cut into two more or less identical parts. There is a small fragment under the same collection number. The polyp body is up to 3 mm long, and the tentacles are up to 2 mm long, featuring two rows of pinnules on each side. The pinnules are short and stout, up to 0.2 mm long and 0.2 mm wide, 9–10 in the outermost row with no gap to occasionally a gap of one pinnule-width between adjacent pinnules.

Sclerites are ellipsoid platelets, 0.013–0.020 X 0.017–0.024 mm in diameter (Fig 11, n=20). They are composed of calcite rods, uniform in width throughout their length. A fractured sclerite revealed that the rods are arranged radially at the periphery, occasionally branched at their distal end, but oriented randomly at the sclerite center (Fig. 11c). The sclerite surface is granular and often fractured.

The dimensions of BML 1962.7.20.149 correspond to those of the other syntype (BML 1962.7.20.148). The polyp body is up to 2 mm long, and the tentacles are up to 3 mm long, featuring three and sometimes four rows of pinnules on each side. The pinnules are short and stout, up to 0.2 mm long and 0.2 mm wide, 10–14 in the outermost row with a gap of one pinnule-width between adjacent pinnules. Its sclerites are ellipsoid platelets, 0.012–0.017 X 0.018–0.022 mm in diameter (Fig. 12a, n=20). They are composed of calcite rods (Fig. 12c). The granular surface of the sclerites is fractured.

Remarks. Ashworth (1900) described *X. novaebritanniae* as featuring three rows of pinnules with 8–12 in each row. Examination of BML 1962.7.20.148 revealed that it has only two rows of pinnules and thus does not belong to the species and was probably mislabeled. However, the original description closely corresponds to the current findings for BML 1962.7.20.149. Benayahu (1990) listed this species for the Red Sea, based on the original

description. Reinicke (1997) examined the two syntypes and his description noted three and occasionally four rows of pinnules, 10–12 in the outermost row, similar to our description of BML 1962.7.20.149.

Similar species and conclusion. Both *X. novaebritanniae* and *X. crassa* feature three and occasionally four rows of pinnules and a similar number of pinnules in the outermost row (10–14 vs. 13–18); however, as *X. crassa* sclerites possess crests on their surface, the two species should be considered as separate.

Distribution. South Pacific Ocean: Loyalty Island, Papua New Guinea, New Britain, Red Sea.

Xenia rubens Schenk, 1896

Fig. 13

Xenia rubens Schenk, 1896: 67–68

Xenia rubens; Kükenthal 1902: 647–648

Material. Type: SMF 46, Indonesia, Ternate Island, 1894, coll. W. Kükenthal.

Description. The type is 60 mm high; its stalk is 45 mm long and splits 30 mm above the base into two branches; one branch is 20 mm long, 12 mm wide at its base and 18 mm wide at its uppermost part. The other branch is 18 mm long, 22 mm wide at its base and 35 mm wide at the uppermost part. The polyp body is up to 4 mm long, and the tentacles are up to 3 mm long. Mostly four rows of pinnules are aligned along each of the tentacle margins, occasionally 3 and even 5 rows, with 12–19 pinnules in the outermost row. The pinnules are relatively short and stout, up to 0.3 mm long and 0.15 mm wide, with spacing of no gap to up to a half pinnule-width between adjacent pinnules.

Sclerites are mainly ellipsoid platelets that appear in all parts of the colony, 0.009–0.013 X 0.011–0.023 mm in diameter (Fig. 13a, c, n=20). Some sclerites may feature a slightly rectangular outline and others are either round or elongated. Their surface appears uniformly granular with no fractures. Broken sclerites reveal the internal structure to consist of radial rods at the periphery and a centrally located void within their center (Fig. b). The ethanol-preserved type is light beige-yellow in color.

Remarks. In the original description Schenk (1896) indicates that *X. rubens* features 5–6 irregular rows of pinnules and 18–20 pinnules in the outermost row, which closely corresponds to the current findings.

Similar species and conclusions. Both *X. rubens* and *X. fusca* feature mostly four rows of pinnules and a similar number of pinnules in the outermost row (12–19 and 14–22, respectively). They share a similar type of granular sclerite surface but different internal microstructure (Figs. 13 and 6, respectively). Although the latter difference might be rather small, until further data based on freshly collected colonies become available the two species are considered as separate.

Distribution. Indonesia: Ternate Island.

Xenia sansibariana May, 1899

Xenia sansibariana May, 1899: 87

Xenia sansibariana; Kükenthal 1902: 655

Xenia actuosa Verseveldt & Tursch, 1979: 145–146—**new synonym**

Xenia actuosa Haverkort-Yeh *et al.* 2013

Material. Syntype: ZMB 3828, Indian Ocean, Zanzibar, 1885, coll. Sander. **Holotype of *X. actuosa*:** RMNH 12866, South-Western Pacific Ocean, Bismarck Sea, Boëso I., South reef flat, 5 m, 1975–1977, King Leopold III Biological Station at Laing Island, coll. A. Tursch.

Description. The syntype is 38 mm high; its stalk is 16–20 mm long, 15 mm wide at its base and 25–27 mm wide at the uppermost part. The polyp body is up to 10 mm long, and the tentacles are up to 6 mm long, featuring four rows of pinnules on each side. The pinnules are relatively short and slender, up to 0.7 mm long and 0.1 mm wide, 26–33 in the outermost row with a space of 0.5–1.5 pinnule-width between adjacent pinnules. No sclerites could be found in the syntype. Zooxanthellae can be seen in the stalk and also a few small gonads. The ethanol-preserved holotype is dark grey in color.

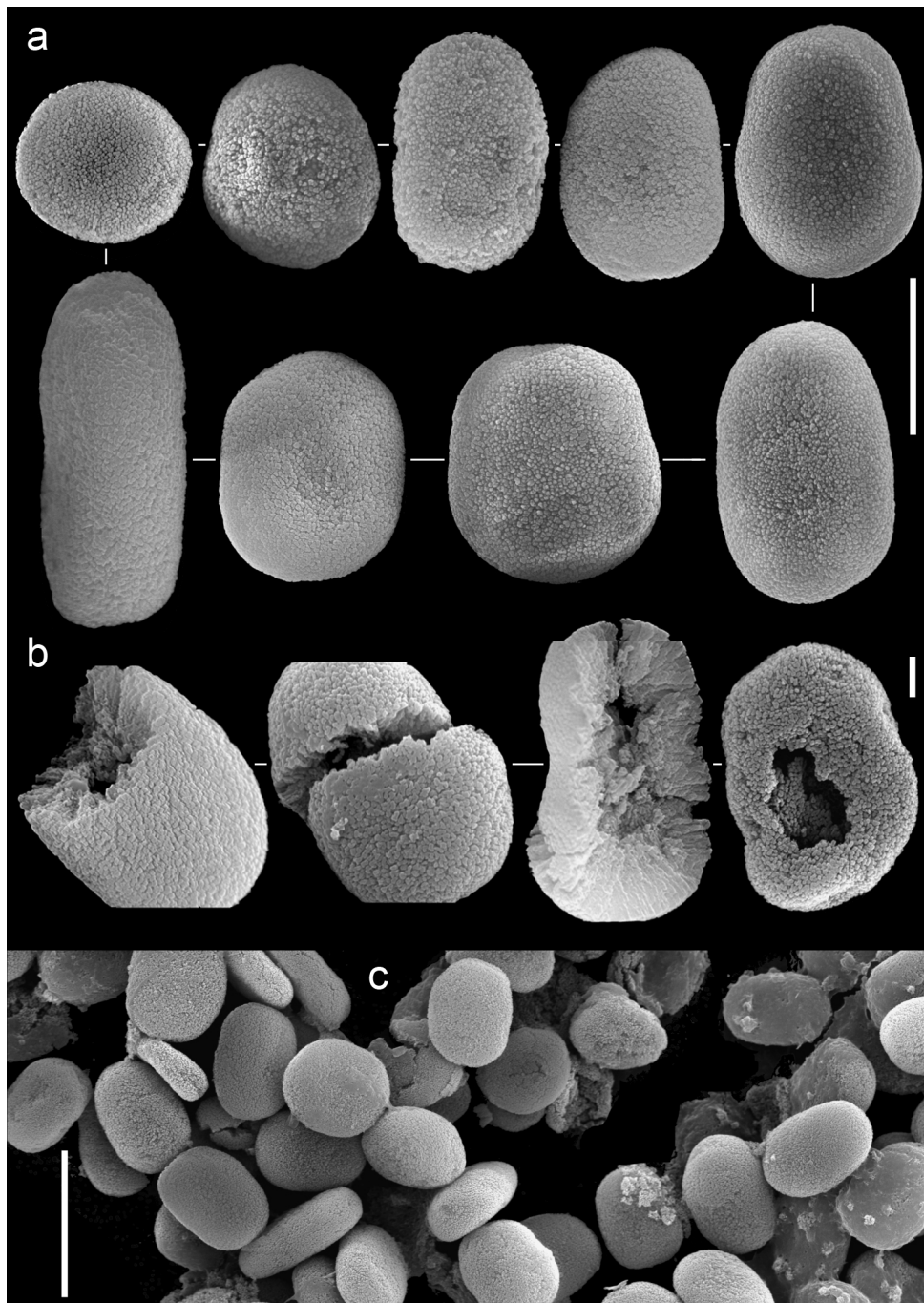


FIGURE 13. Scanning electron micrographs of polyp sclerites of *Xenia rubens* Schenk, 1896 type (SMF 46). a. Ellipsoid platelets; b. Fractured sclerites revealing internal void; c. Overview of sclerites. Scale bar at a 0.010 mm, at b 0.002 mm, at c 0.020 mm.

The holotype of *X. actuosa* is 40 mm high; its stalk splits at the base into three branches, two of which split again into two, the latter branches are 8 and 10 mm long, 15 and 20 mm wide at their base, 20 and 23 mm wide at their uppermost part, respectively. The third branch does not split; it is 30 mm long, 18 mm wide at its base and 40 mm at the uppermost part. The polyp body is up to 6 mm long, and the tentacles up to 11 mm long, featuring four rows of pinnules on each side. The pinnules are relatively short and stout, up to 0.80 mm long and 0.24 mm wide, 25–29 in the outermost row with a space of up to a half pinnule-width between adjacent pinnules. No sclerites could be found in any part of the colony. The original description indicated pulsating polyps for the live colonies. The ethanol-preserved holotype is yellow to dark beige in color.

Similar species and conclusion. The original description of *Xenia sansibariana* and Kükenthal's (1902)

revision referred to five rows of pinnules, in comparison to four rows recorded in the current study. Verseveldt & Tursch (1979) described *X. actiosa* with four rows of pinnules with 21–28 pinnules and no sclerites, in full correspondence to the current findings. The two species overlap in the number of pinnule rows, number of pinnules on the outermost row, and both lack sclerites. Therefore, based on their morphological features *X. actiosa* should be considered a junior synonym of *X. sansibariana*, given the priority of the earlier description. However, while considering the geographical distance between the type localities of *X. sansibariana* and *X. actiosa* (West Indian Ocean and South-Western Pacific Ocean, respectively), genetic data should be obtained to verify the synonymy.

Xenia mucosa and *X. sansibariana* both feature four rows of pinnules, but differ in the number of pinnules in the outermost row (25–29 and 30–42 respectively), and, therefore, the two species should be considered as separate.

Distribution. South-Western Pacific Ocean: Bismarck Sea, Indian Ocean: Zanzibar, Red Sea.

Xenia ternatana Schenk, 1896

Fig. 14

Xenia ternatana Schenk, 1896: 64, plate 3, Fig. 16

Xenia ternatana; Kükenthal 1902: 649; Tixier-Durivault 1966: 359; Verseveldt & Cohen 1971: 62; Benayahu 1990: 118, table 1, listed only; Reinicke 1997: 35–36; Janes 2013; Janes *et al.* 2014; McFadden *et al.* 2014a.

Material. Holotype and paratype: SMF 43, Indonesia, Ternate Island, 1894, coll. W. Kükenthal.

Description. The holotype is the larger colony under SMF 43, 25 mm high; its stalk is 18 mm long, 10 mm wide at its base and 15 mm at its uppermost part. The syntype is 23 mm high; its stalk is 12 mm long, 15 mm wide at its base, 22 mm wide at its uppermost part. The polyp body is up to 3.5–5 mm long, and the tentacles up to 3–3.5 mm long, featuring three rows of pinnules on each side. The pinnules are relatively slender, up to 0.5 mm long and 0.2 mm wide, 15–23 in the outermost row with no gap between adjacent ones.

Sclerites are present in all parts of the colony, more densely arranged on the aboral side of the tentacles and less so in the pinnules. They are ellipsoid platelets, measuring 0.008–0.015 X 0.017–0.021 mm in diameter (Fig. 14, n=20). Their surface is granular due to the dendritic rods that comprise the sclerite (Fig. 14c). Some sclerites feature a distinct longitudinal crest (Fig. 14c). The ethanol-preserved holotype is dark gray in color.

Remarks. The original description of *X. ternatana* by Schenk (1896) indicated two rows of pinnules and 18–22 pinnules in each row compared to the three rows and 15–23 pinnules in the outermost row as revealed in the present study. The current examination demonstrated that some of the sclerites possess a central crest, resembling those of *Yamazatum* Benayahu, 2010. As already indicated, it is suggested that the presence of a crest on the sclerite surface is diagnostic and important for xeniid species identification. Colonies of *X. ternatana* from various locations in the Red Sea (e.g., Kükenthal 1913; Verseveldt & Cohen 1971; Benayahu 1990) should be re-examined in order to verify the microstructure of their sclerites. Reinicke (1997) examined the type of *X. ternatana* and other material from the Red Sea, but repeated the original description and not his findings concerning the type; therefore, his material should also be re-examined. In McFadden *et al.* (2014a) a specimen collected from Indonesia bearing two rows of pinnules was identified as *X. ternatana*, which does not correspond to the current re-description of the type.

Similar species and conclusion. *X. viridis*, *X. blumi*, *X. umbellata* Lamarck, 1816 and *X. ternatana* share a similar pinnule arrangement, but differ in their sclerite microstructure (Figs 15, 3, 16 and 14, respectively), and therefore it is concluded that they should be considered as separate species.

Distribution. Indonesia: Ternate Island.

Xenia viridis Schenk, 1896

Fig. 15

Xenia viridis Schenk, 1896: 62–63, plate 2, Figs. 4–8

Xenia viridis; Ashworth 1900: 516–518 fig. 14; Kükenthal 1902: 649–650; Kükenthal 1911: 309; Thomson & Dean 1931: 26; Roxas 1933: 84 fig. 6; Verseveldt 1960: 246–247 fig. 4c; Tixier-Durivault 1966: 363–5, fig 328; Verseveldt 1971: 63–64; Benayahu 1990: 118, table 1, listed only; Janes 2013; Janes *et al.* 2014; McFadden *et al.* 2014a.

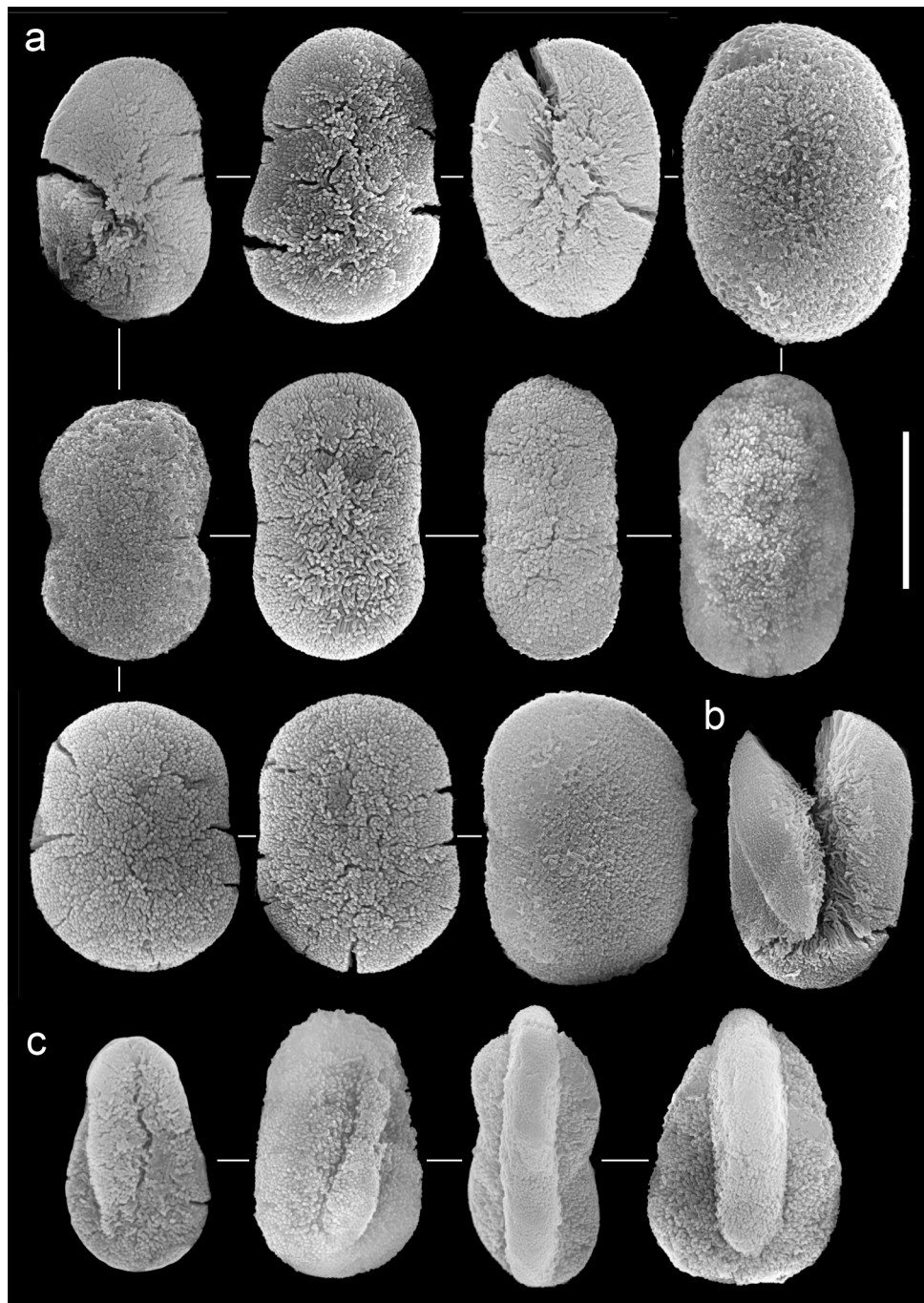


FIGURE 14. Scanning electron micrographs of polyp sclerites of *Xenia ternatana* Schenk, 1896 holotype (SMF 43). a. Ellipsoid platelets, most fractured; b. Fractured sclerite composed of dendritic calcite rods; c. Sclerites with surface crest. Scale bar 0.010 mm.

Material. Holotype: SMF 42, Indonesia, Ternate Island, 1894, coll. W. Kükenthal; **additional material:** SMF 77, Indonesia, Klein-kei Nuhu, 3–4 m, 1908, coll. Wertau, determined by: W. Kükenthal.

The holotype is 40 mm high; its stalk is 25 mm long, 17 mm wide at its base and 42 mm wide at its uppermost part. The polyp body is up to 3 mm long, and the tentacles up to 3.5–4 mm long, featuring three rows of pinnules on each side. The pinnules are slender, up to 0.50 mm long and 0.25 mm wide, 15–22 in the outermost row with spacing of no gap up to half a pinnule-width between adjacent pinnules.

Sclerites are present in all parts of the colony, less dense in the stalk than in the polyps and lacking in the distal parts of the pinnules. They are ellipsoid platelets, measuring 0.008–0.013 X 0.013–0.020 mm in diameter (Fig. 15, n=26). Some of the sclerites possess a longitudinal or diagonal-transverse crest (Fig. 15b) and some a furrow on

their narrow side (see arrow in Fig. 15a). They are composed of calcite rods arranged radially, but assembled randomly at the sclerite center (Fig. 15c). The sclerite surface is granular. The ethanol-preserved holotype is light beige in color, polyps are lighter.

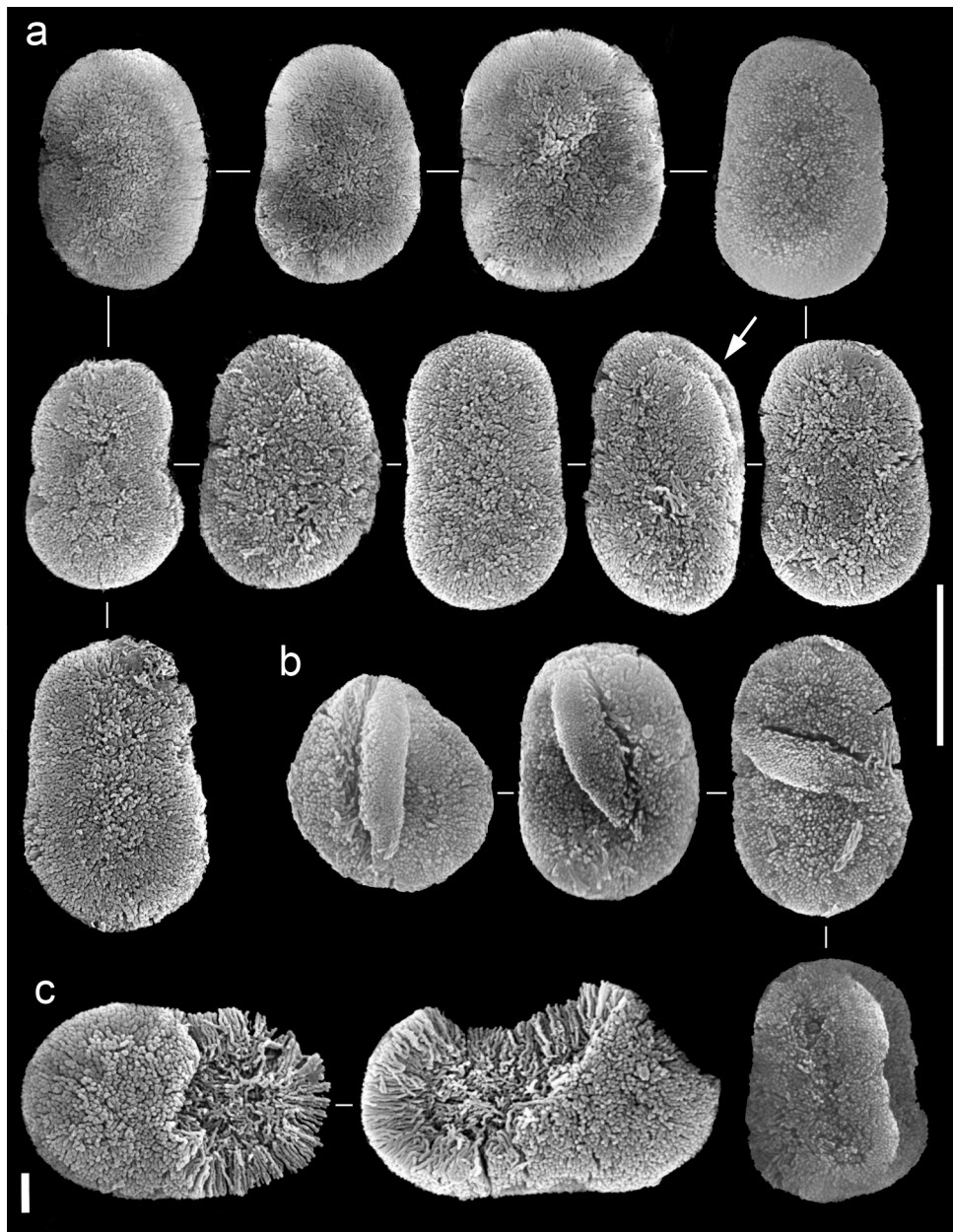


FIGURE 15. Scanning electron micrographs of polyp sclerites of *Xenia viridis* Schenk, 1896 holotype (SMF 42). a. Ellipsoid platelets featuring rough granulated surface, arrow indicates surface furrow; b. Sclerites with surface crest, fractured; c. Fractured sclerites composed of a latticework matrix of calcite rods, dendritic and sinuous, and radially arranged in peripheral region. Scale bar at a and b 0.010 mm, at c 0.002 mm.

The dimensions of the additional colony examined are similar to the holotype; its polyp body is up to 8 mm long, and the tentacles are up to 6 mm long, featuring three rows of pinnules on each side, 15–20 in the outermost row with a space of up to half a pinnule-width between adjacent pinnules. Sclerites are present in all parts of the colony, measuring 0.010–0.017 X 0.022–0.026 mm in maximal diameter (n=24). They are ellipsoid platelets, composed of calcite rods, arranged radially, at least on the sclerite surface. The ethanol-preserved colony is light beige in color.

Remarks. In the original description of *X. viridis*, Schenk (1896) indicated three rows of pinnules, with 14–15 pinnules in a row and sclerites of 0.010–0.015 mm in diameter. The number of rows corresponds to the current

findings, but the range in number of pinnules was found to be slightly larger, 15–22 in the holotype and 15–20 in the other material. The sclerite dimensions were found to be larger than in the original observation. In his revision of Xeniidae, Kükenthal (1902) indicated the presence of the species in New Caledonia. Verseveldt (1960) reported it in Indonesia, with three rows and 15–17 pinnules, and sclerites 0.017–0.020 X 0.015 mm in diameter, in full agreement with the type. Reinicke (1997) raised doubts concerning the presence of the species in the Red Sea, based on his examination of the material noted in Benayahu (1990), which he concluded should be assigned to *X. crenata* Reinicke, 1997 (= *O. crenata* in Halász *et al.* 2014). In McFadden *et al.* (2014) two specimens identified as *X. viridis* were described, bearing three rows and 14–18 pinnules in the outermost one, which partially overlaps with the current re-description of the type.

Similar species and conclusion. *Xenia blumi* and *X. viridis* feature three rows of pinnules and an overlapping number of pinnules in the outermost row. They also feature dendritic sclerite microstructures. Unlike *X. blumi*, *X. viridis* exhibits crests on the sclerite surface whose suggested taxonomic significance was noted above, and, therefore, it is concluded that these two species should be considered as separate.

Distribution. Indonesia: Ternate Island and Klein-kei Nuhu, Red Sea.

***Xenia umbellata* Lamarck, 1816**

Figs. 16–22

Xenia umbellata Lamarck, 1816: 403

Xenia umbellata;; Savigny 1817: 227 fig. 3; Ehrenberg 1834: 53–54; Klunzinger 1877: 39–40 fig. 3; Schenk 1896: 57; May 1899: 16–18; May 1899: 82–84; Ashworth 1900: 513–516 Figs. 10–13; Kükenthal 1902: 650–651; 1904: 34; Thomson and Henderson 1905: 273; 1906: 410–411; Thomson & McQueen 1907: 50; Gravier 1908: 206–207; Kükenthal 1913: 7; Thomson & Dean 1931: 26–27; Hickson 1931a: 156–157; Roxas 1933: 88–89 fig. 3; Gohar 1940: 93–95; Verseveldt 1965: 46–47; Tixier-Durivault 1966: 367, fig 330; Verseveldt 1971: 63; Utinomi 1977; Benayahu 1990: 118, table 1, listed only; Imahara 1996; Reinicke 1997; Benayahu *et al.* 2002: 279, table 1, listed only; Haverkort-Yeh *et al.* 2013; Janes *et al.* 2014.

Material. Neotype: ZMTAU CO 36788, northern Red Sea, Gulf of Aqaba, Eilat, reef across from the Interuniversity Institute for Marine Sciences in Eilat (IUI) (29°30'14.508"N, 34°55'9.84"E), 12 m, 19 March 2010. Additional material: ZMTAU CO 36780, northern Red Sea, Gulf of Aqaba, Eilat, IUI (29°30'6.54"N; 34°55'4.44"E), 5 m, 5 January 2010; ZMTAU CO 36792, northern Red Sea, Gulf of Aqaba, Eilat, the Pyramid site, on artificial reef (29°32'44.7"N, 34°57'26.3154"E), 22 m, 30 June 2010; ZMTAU CO 37034, northern Red Sea, Gulf of Aqaba, Eilat, Underwater restaurant, on artificial reef (29°32'49.43N; 34°57'14.51"E), 8 m, 22 June 2010. ZMTAU CO 36783, collection details as ZMTAU CO 36780; ZMTAU CO 36784, northern Red Sea, Gulf of Aqaba, Eilat, Dekel beach (29°32'26.1708"N, 34°56'52.731"E), 5 m, 26 January 2010; ZMTAU CO 36790, northern Red Sea, Gulf of Aqaba, Eilat, Tur Yam (29° 30' 56.4978"N, 34° 55' 36.1986"E), 5 m, 4 May 2010; ZMTAU CO 36791, northern Red Sea, Gulf of Aqaba, Eilat, Underwater restaurant (29°32'49.43N; 34°57'14.51"E), 11 m, 23 June 2010. All of the above collected by A. Halász; USNM 1202005, Saudi Arabia, Jeddah, 21°43'N, 39°06'E, 23 April 2011; USNM 1202010, same details; USNM 1202016, same details. All USNM material above collected by R. Haverkort-Yeh; ZMTAU CO 34073, northern Red Sea, Gulf of Aqaba, Eilat, Nature reserve, (29°30.6'N, 34° 55.35'E), 2.4–5.5 m, 24 July 2007, coll. Y. Benayahu; ZMTAU CO 34072, same collection details as above.

Description. The neotype, ZMTAU CO 36788, consists of one colony growing on a dead colony of a branched stony coral. Its maximal height is 20 mm; the stalk is unbranched, up to 5 mm long and 8 mm wide. The polyp body is up to 4 mm long, and the tentacles up to 3.5–5 mm long. The slender pinnules are up to 2.5 mm long and 0.2 mm wide, with a pinnule-wide space between them. The pinnules are arranged in three rows with 19–22 in the outermost one.

Sclerites are ellipsoid platelets, abundant in all parts of the colony, measuring 0.008–0.015 X 0.013–0.025 mm in diameter (Fig. 16, n=20). They are composed of calcite rods, uniform in width (0.1–0.2 μm). The rods are arranged more or less randomly and their distal tips are aligned in part parallel to the surface of the sclerite (Fig. 16b, c). Clusters of sclerites are densely packed in different spatial orientations (Fig. 16d). The ethanol-preserved neotype is white. Pulsation was observed in live colonies.

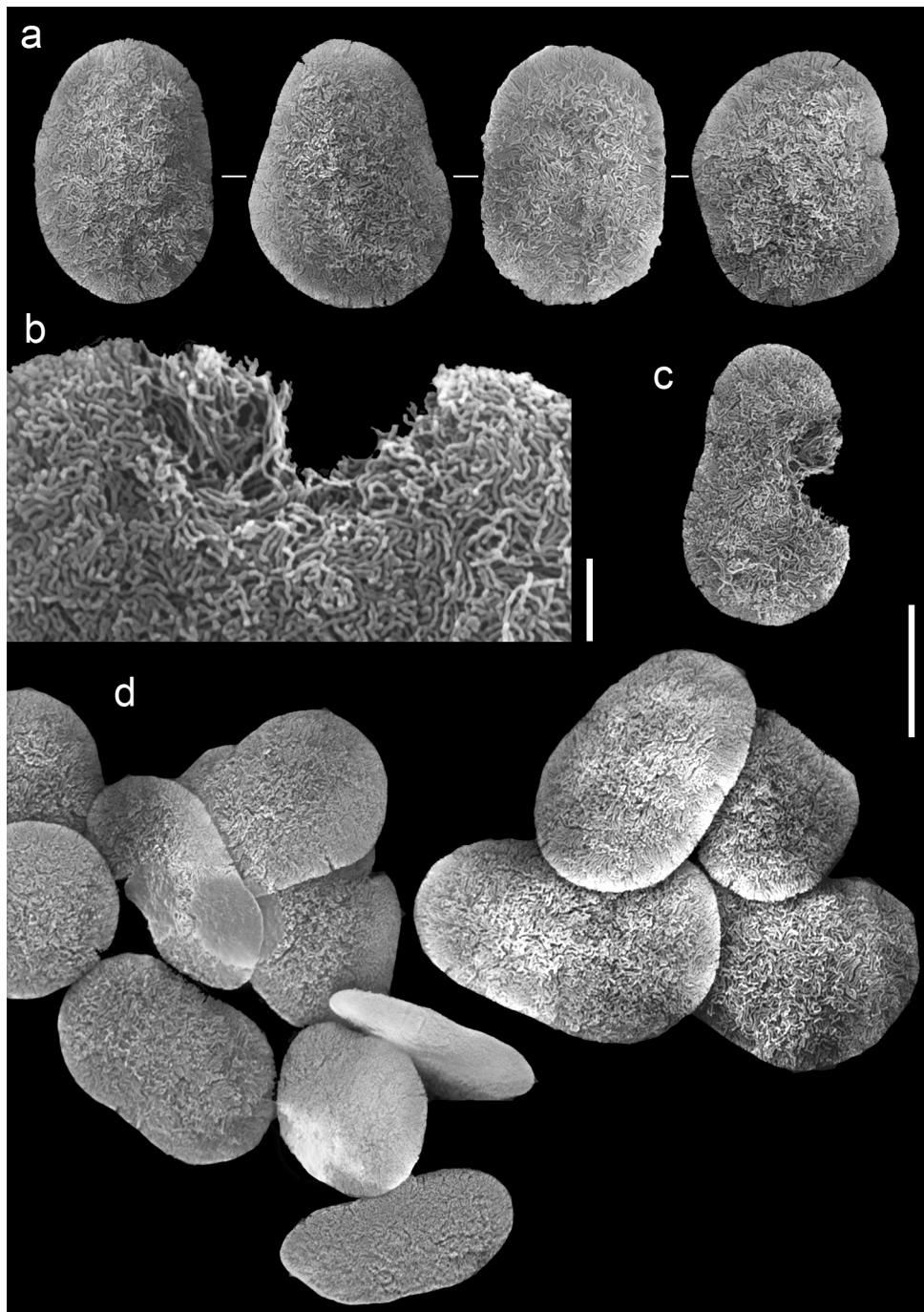


FIGURE 16. Scanning electron micrographs of polyp sclerites of *Xenia umbellata* Lamarck, 1816, neotype (ZMTAU CO 36788). a. Ellipsoid platelets; b. Fractured sclerite enlarged, composed of a latticework matrix of calcite rods, in part aligned horizontally on surface; c. Fractured sclerite; d. Overview of sclerites. Scale bar at a, c and d 0.010 mm, at b 0.002 mm.

The additional material, ZMTAU CO 36780, is 22 mm high. Its stalk splits into 3 branches 5 mm above its base, the branches are 9, 15 and 7 mm long; 5, 10, and 5 mm wide at their base; and 12, 13 and 7 mm wide at their uppermost part, respectively. The polyp body, tentacles and pinnules are similar in size to those of the neotype. The pinnules are arranged in three rows, 20–23 in the outermost row. Sclerites are abundant in all parts of the colony and are similar to those of the neotype, measuring 0.011–0.015 X 0.014–0.023 mm in diameter (Fig. 17, n=20). Their surface reveals a partially granular texture, but in addition the longitudinally aligned dendritic rods can be seen on the surface of the sclerites.

ZMTAU CO 36792 is similar in dimensions to the neotype. Pinnules are arranged in three rows, 22–27 in the outermost row. Sclerites are abundant in all parts of the colony, and their morphological features—including

surface texture (Fig. 18)—are similar to those of the neotype, measuring 0.011–0.015 X 0.017–0.022 mm in diameter (n=20).

ZMTAU CO 37034 consists of three small white-beige colonies. The first is a colony with multiple branches; its total height is 20 mm, and the stalk is up to 13 mm wide at its base and 25 mm wide at its uppermost part. The second colony is unbranched, similar in height to the first, 10 mm wide at its base, and 4 mm wide at its uppermost part. The third colony is 15 mm high; its stalk branches into three, and its base is 10 mm wide and 30 mm at the uppermost part at the branching point. The tentacle and pinnule dimensions are similar to ZMTAU CO 36780. The pinnules are arranged in three rows, 19–22 in the outermost row. Sclerites are scarce, ellipsoid platelets, round or egg-shaped and occasionally irregular, measuring 0.009–0.017 X 0.015–0.022 mm in diameter (Fig. 19, n=20). Their surface microstructure (Fig. 19a) is similar to that of the neotype (Fig. 19b). Sinuous dendritic rods are radially arranged, and can be seen in a fractured sclerite (Fig. 19c).

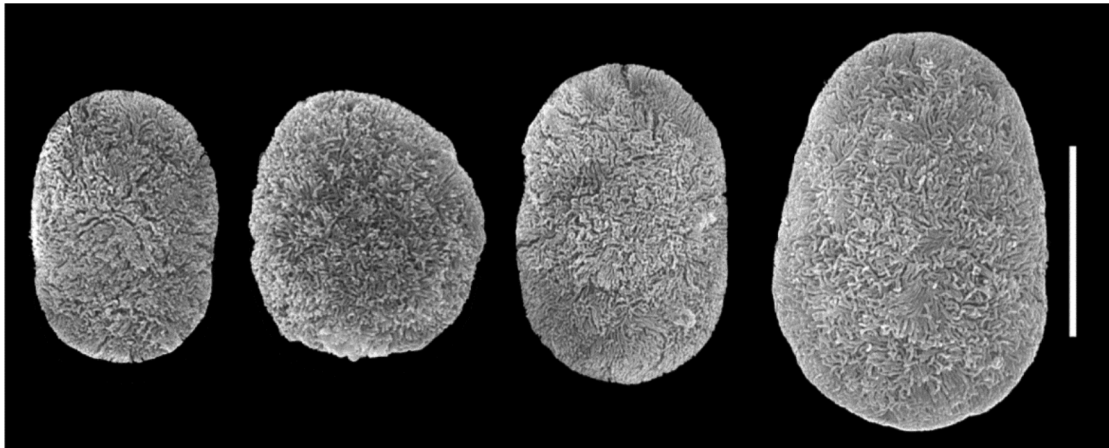


FIGURE 17. Scanning electron micrographs of polyp sclerites of *Xenia umbellata* Lamarck, 1816 (ZMTAU CO 36780). Ellipsoid sclerites. Scale bar 0.010 mm.

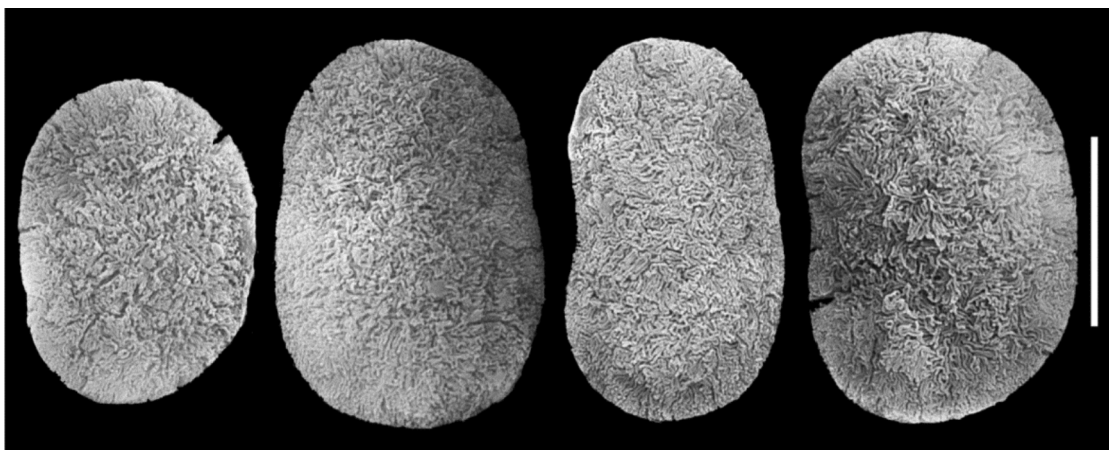


FIGURE 18. Scanning electron micrographs of polyp sclerites of *Xenia umbellata* Lamarck, 1816 (ZMTAU CO 36792). Ellipsoid sclerites. Scale bar 0.010 mm.

The size of all other colonies is rather similar to that of the neotype. ZMTAU CO 36783, 36790, 36791, USNM 1202005 and 1202016 feature three rows of pinnules with 21–24, 17–20, 18–20, 19–26 and 21–27 pinnules in the outermost row, respectively. ZMTAU CO 36784 and USNM 1202010 bear two rows of pinnules with 16–20 and 20–24 pinnules in the outermost row, respectively. Polyp sclerites of the three colonies collected in Saudi Arabia (USNM 122005, 1202010 and 1202016) all share a similar microstructure to that of the neotype and the Eilat colonies (Figs. 20, 21 and 22 respectively). Their sclerites typically maintain their intact shape following processing for SEM and only occasionally feature small marginal fractures (Fig. 22). Pulsation was observed in all live colonies.

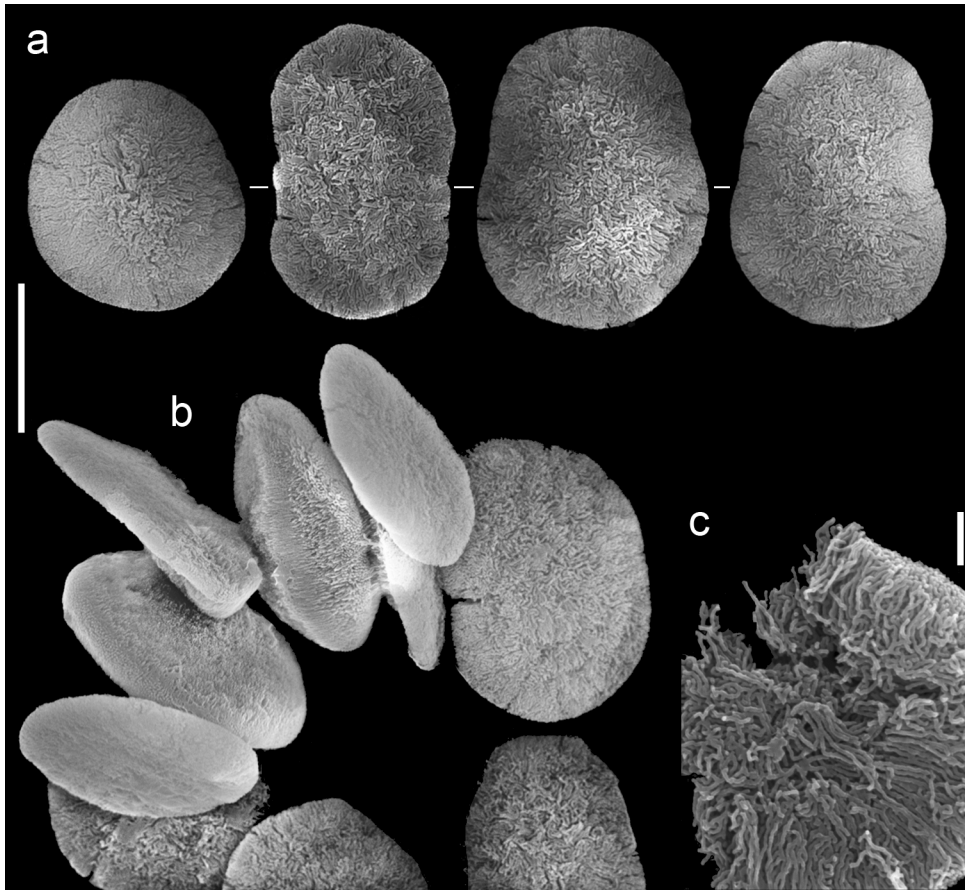


FIGURE 19. Scanning electron micrographs of polyp sclerites of *Xenia umbellata* Lamarck, 1816 (ZMTAU CO 37034). a. Ellipsoid platelets; b. Overview of sclerites. b. Fractured sclerite enlarged, revealing sinuous dendritic structure. Scale bar at a and c 0.010 mm, at b 0.002 mm.

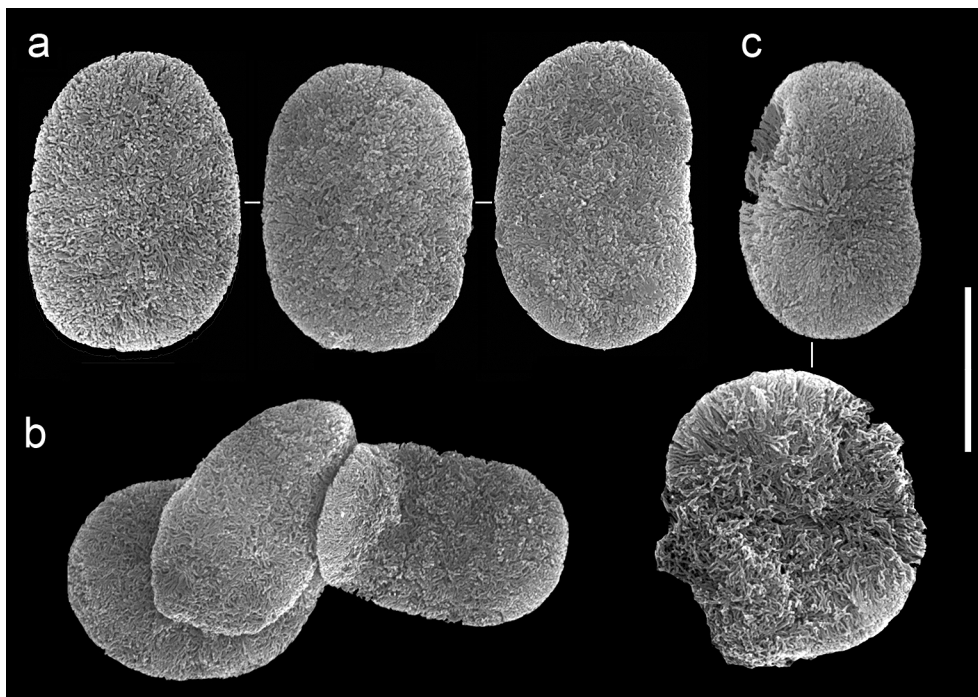


FIGURE 20. Scanning electron micrographs of polyp sclerites of *Xenia umbellata* Lamarck, 1816 (USNM 1202005). a. Ellipsoid platelets; b. Overview of sclerites; c. Fractured sclerites composed of a latticework matrix of calcite rods, dendritic and sinuous, and radially arranged in peripheral region. Scale bar 0.010 mm.

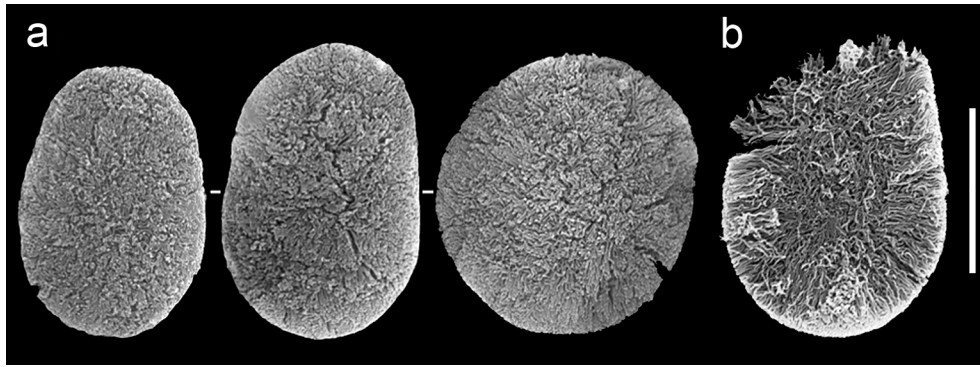


FIGURE 21. Scanning electron micrographs of polyp sclerites of *Xenia umbellata* Lamarck, 1816 (USNM 1202010). a. Ellipsoid platelets; b. Fractured sclerite composed of a latticework matrix of calcite rods, dendritic and sinuous, and radially arranged in peripheral region. Scale bar 0.010 mm.

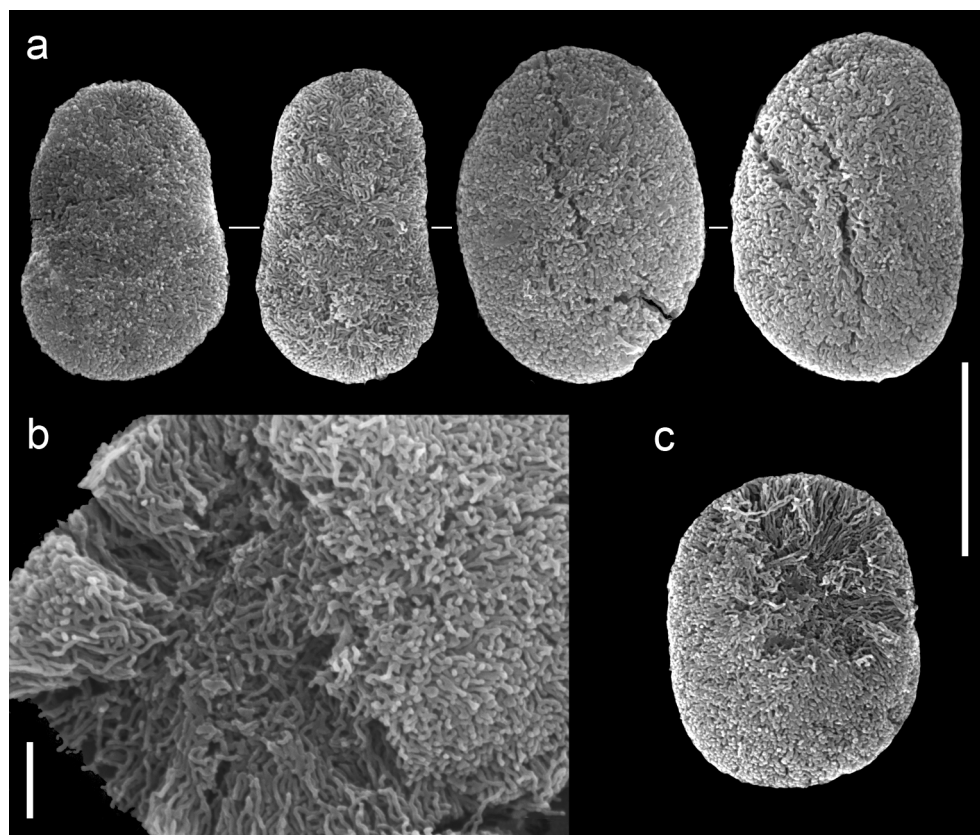


FIGURE 22. Scanning electron micrographs of polyp sclerites of *Xenia umbellata* Lamarck, 1816 (USNM 1202016). a. Ellipsoid platelets, some fractured; b. Fractured sclerite (enlarged) composed of a latticework matrix of calcite rods, dendritic and sinuous, and radially arranged in peripheral region. c. Fractured sclerite. Scale bar at a, c 0.010 mm, at b 0.002 mm.

Phylogenetic affiliation. All of the *X. umbellata* colonies described above shared identical DNA sequences at *mtMutS*, *igr1+COI*, and 28S rDNA (Fig. 23); species delimitation analyses that included those loci plus four additional genes further supported the conclusion that all of the *X. umbellata* specimens examined here belong to one species (McFadden *et al.* 2017). Two specimens previously identified as *X. hicksoni* (ZMTAU Co34072, 34073; McFadden *et al.* 2011) were also genetically identical to *X. umbellata* (Fig. 23). *X. umbellata* belonged to a strongly supported clade that included members of the genus *Ovabunda* from the Red Sea and Thailand (Fig. 23). This [*Ovabunda* + *X. umbellata*] clade was nested within a larger clade of *Xenia* that included specimens previously identified as *X. lepida*, *X. ternatana* and *X. viridis* (clade X1 of McFadden *et al.* 2014a). Additional species of *Xenia*, including material identified as *X. sansibariana* (= *X. actiosa*; Haverkort-Yeh *et al.* 2013) belonged to a second distinct clade that also included species of *Heteroxenia* (clade X2 of McFadden *et al.* 2014a).

Finally, specimens identified previously as *X. kusimotoensis* and *X. membranacea* belonged to a clade with species of *Sansibia*, *Sarcothelia* and *Yamazatum* (clade X3; McFadden *et al.* 2014a).

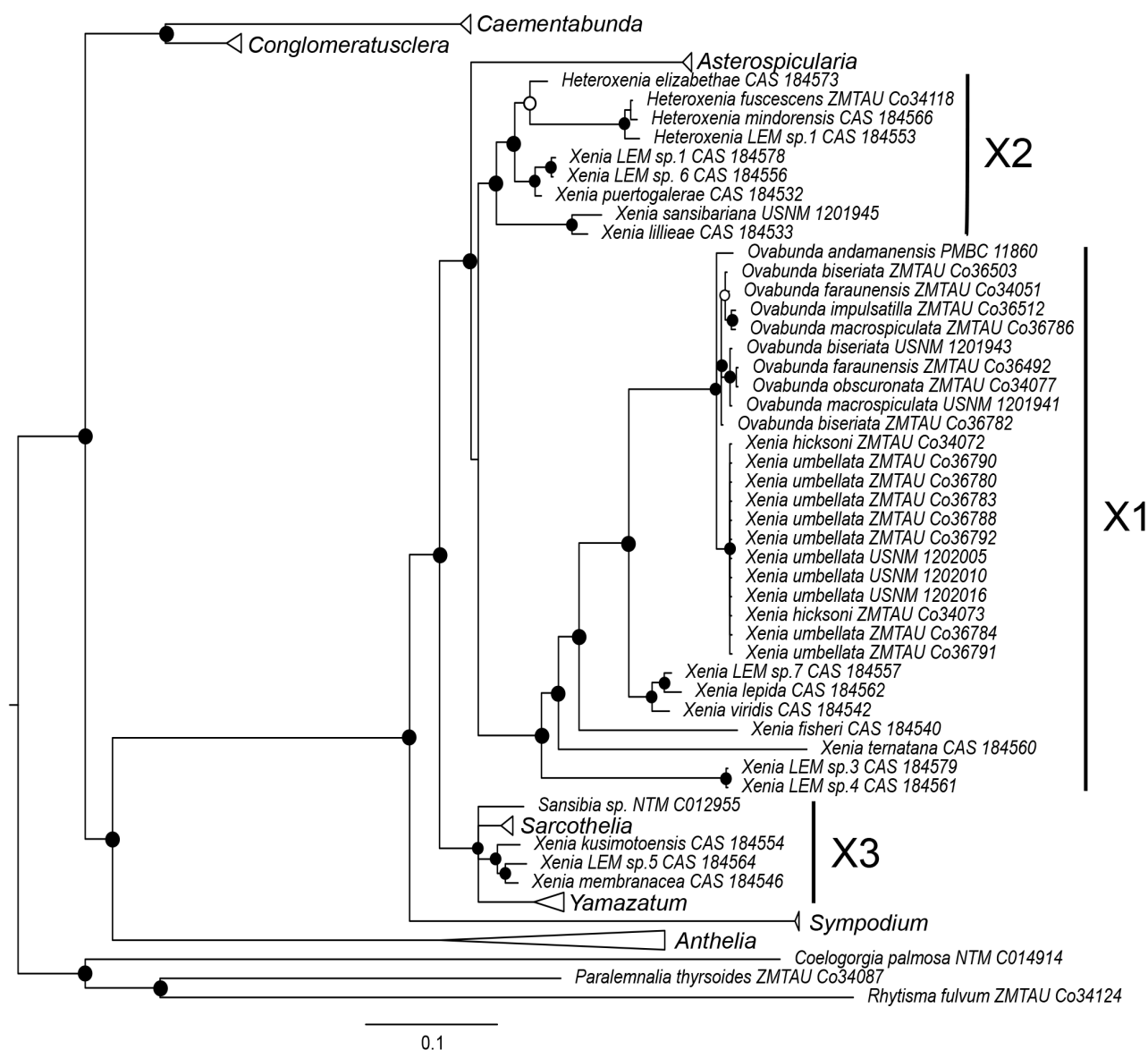


FIGURE 23. Bayesian tree of family Xenidiidae based on partitioned analysis of *mtMutS*, *igr1+COI* and 28S rDNA. Solid circles: posterior probability > 0.9, ML bootstrap value >70%; open circles: pp > 0.9, bs <70%. Genera other than *Xenia*, *Heteroxenia* and *Ovabunda* have been collapsed to facilitate readability. X1, X2 and X3 denote clades defined by McFadden *et al.* 2014.

Remarks. In the original description of *X. umbellata*, the type species of this genus, Lamarck (1816: 410) referred to dark-blue colonies from the Red Sea, bearing slender, tightly packed pinnules, arranged in two rows. Lamarck referred to drawings of colonies collected from the Red Sea that were published by Savigny (1817). Based on these drawings it is evident that the tentacles feature two rows of pinnules with 27–32/22–25 and 30–35/29–31 pinnules in the outer/inner row (Reinicke 1997: Fig. 18). No additional data were presented regarding the sclerite shape and dimensions or the exact type locality. Inquiries to various collections, including MNHN, led to the conclusion that the type should be considered lost (see also Reinicke 1997).

Since the original description of *X. umbellata* by Lamarck (1816), specimens collected from many Indo-Pacific reefs were referred to this species (see ahead), also attributing to it rather variable morphological features. Undoubtedly, the extensive literature has made it the most common *Xenia* species reported in the entire Indo-Pacific region, giving the impression that it is the commonest species of its genus. In contrast to the two rows of

pinnules indicated in the original description by Lamarck (1816: 410), Ehrenberg (1834: 53–54) described this species from the Red Sea as having three rows. That study established the notion that three rows of pinnules should be attributed to *X. umbellata*. Subsequently, other studies referred to *X. umbellata* as featuring a different number of rows and also with a wide range of pinnule numbers in the outermost row compared to Lamarck's (1816) description. For example, Schenk (1896: 57) indicated three rows and 12–15 pinnules (Ternate, Indonesia); Ashworth (1900) 3–4 rows and 12–15 pinnules (Red Sea); and three rows, 22–29 pinnules (Papua New Guinea: New Britain). Subsequently, Kükenthal (1902: 561) indicated three rows, 12–29 pinnules in the outermost row (Red Sea, Indian Ocean, East Africa and Papua New Guinea: New Britain). Hickson's (1931a) revision of the Xeniididae described material collected in the Great Barrier Reef with three rows of pinnules and about 25 pinnules in the outermost row, and sclerites “round in outline”, 0.020 mm in diameter. That study also noted the resemblance to *X. plicata*. Roxas (1933) described *X. umbellata* as having three rows of pinnules, 17–20 in a row, and sclerites 0.014–0.018 X 0.010–0.018 mm in diameter (Puerto Galera Bay, Philippines). Gohar (1940) referred to pulsating colonies of *X. umbellata* from Hurgada, Red Sea, featuring 2–3 rows of pinnules and 16–22 pinnules in the outermost row (14–18 and 10–12 in the inner rows), and sclerites with a maximal diameter of 0.016–0.022 mm. He further described the sclerites as: “general xeniid structure, minute, roughly circular, oval or slightly oblong corpuscles”. Later, Verseveldt (1971) reported the species from Madagascar, referring to Gohar's description. Utinomi (1977) reported it from Okinawa, Japan, with 2–3 rows of pinnules, 15–17 in the outer row. Imahara (1996) noted the presence of the species from the same location and referred to the description by Utinomi (1977). Reinicke (1997: 19; Fig. 8a) depicted sclerites of *X. umbellata* collected in the Red Sea, and presented its sclerite surface microstructure for the first time using SEM. Undoubtedly, these studies may have raised confusion concerning the real identity of the species and its taxonomic features.

The Red Sea material examined in the current study, including the neotype and the additional material, encompasses 2–3 rows. The recorded number of pinnules in the outermost rows is mostly 19–22, but occasionally up to 27 or as few as 16, but not lower than that. These findings correspond to those of some of the previous taxonomic studies on this species (see above). Despite the variation attributed to the Red Sea colonies, they share a similar sclerite microstructure (Figs. 16–19) and identical DNA sequences at the molecular markers analyzed here (Fig. 23). It should also be noted that there is variation in the abundance of sclerites in the colonies: while they are usually abundant in all parts of the colony, they can also be scarce, but then confined mainly to the colony base.

The purpose of the designation of the neotype is to clarify the species' taxonomic status, and to provide an account of its soft tissue morphological features, its sclerite microstructure and its genetic affiliation. The designation of the neotype is conducted here not within the framework of a full taxonomic revision of the genus *Xenia*, but rather is based on a comprehensive examination and re-description of 21 original *Xenia* types, including some from the Red Sea. It should also be noted that attempts to obtain additional types of the genus failed. This approach allows us to designate a neotype despite the convention that designation of neotypes is made only within the framework of a full revision of a genus (<http://iczn.org/nontaxonomy/term/540>). The original description of *X. umbellata* indicated that the species had been collected in the Red Sea, but without providing an exact location. Therefore, it is fully justified that the currently designated neotype as well as the additional material used for comparison, have been collected in Red Sea sites: Eilat and Saudi Arabia.

The geographical distribution of *X. umbellata* based on the literature encompasses regions and sites across the Indo-Pacific reef systems. It includes the Pacific Ocean: Japan (e.g. Utinomi 1977; Imahara 1996), Indonesia (Schenk 1896), the Philippines (Roxas 1933), Papua New Guinea: New Britain (Ashworth 1900) and the Great Barrier Reef, Australia (Hickson 1931a); Indian Ocean: Zanzibar and Madagascar (e.g. Tixier-Durivault 1966; Verseveldt 1971), and the Red Sea (e.g. Ehrenberg 1834; Gohar 1940, Benayahu 1990, Benayahu *et al.* 2002). In agreement with the note published by Reinicke (1997), as well as recent genetic insights into xeniid biogeography (McFadden *et al.* 2019), records from locations outside the Red Sea should be re-evaluated to determine if those specimens indeed share features of the neotype that had not been indicated previously, specifically its sclerite microstructure and genetic affiliation.

Similar species and conclusions. *X. umbellata*, *X. blumi*, *X. ternatana* and *X. viridis* all possess three rows of pinnules and have overlapping numbers of pinnules in the outermost row (16–27, 16–22, 15–23 and 15–22, respectively). All have sclerites that are composed of calcite rods, uniform in width, although *X. ternatana* and *X. viridis* also feature surface crests (Figs. 14 and 15, respectively). The sclerites of *X. umbellata* differ from those of the other three species, as the tips of the rods are aligned parallel to the sclerite surface and are sinuous (Figs. 16–

22), unlike those of other *Xenia* species, which are radially arranged and terminate vertically towards the sclerite surface (Figs. 1–15). Therefore, it is concluded that such differences in sclerite microstructure along with the distinct phylogenetic position of *X. umbellata* from the Red Sea compared to other *Xenia* species make *X. umbellata* unique and justify its designation as a separate species (see also Fig. 23).

X. hicksoni Ashworth, 1899 also resembles *X. umbellata*. It was described from Indonesia (Talisie, north Celebes) as bearing three rows of pinnules, 12–20 pinnules per row, with no sclerites in the tentacles and pinnules. Later, Roxas (1933) described it from the Philippines with three rows of pinnules, 16–18 pinnules in the outermost row, and numerous sclerites. Gohar (1940) examined the type and concluded that it is a good species, adding some notes on specimens he had collected in the Red Sea (Hurgada). That study also noted pulsating colonies of *X. hicksoni*, smaller than *X. umbellata*, bearing 2–3 rows of pinnules, 18–26 in the outermost row, with the sclerites appearing in patches throughout the colony, “unevenly scattered on the surface” (Gohar, 1940: 96). Accordingly, *X. umbellata* and *X. hicksoni* seem to share some similar morphological features of their soft tissue. Both species have 2–3 rows of pinnules and an overlapping number of pinnules in the outermost row, but differ in the presence of sclerites, with *X. hicksoni* having only a few or none (see also Reinicke 1997). The current study has shown that *X. umbellata*, too, may occasionally have a low abundance of sclerites. Two colonies collected in Eilat and identified as *X. hicksoni* (McFadden *et al.*, 2011: ZMTAU CO 34072, 34073) share identical sequences with the *Xenia umbellata* examined during this study (Fig. 23). Both were re-examined here, and the former was found to have sclerites only in the colony base, while the latter lacks sclerites entirely. Colonies collected in Eilat during the current study and identified as *X. hicksoni* unfortunately could not be sequenced. Two of them lack sclerites in all parts of the colony (ZMTAU CO 36874 and 36892), and one has sclerites only in the colony base (ZMTAU CO 36853). Therefore, based on Red Sea material, *X. hicksoni* and *X. umbellata* might be considered synonyms. However, *X. hicksoni* from its type locality (Indonesia) might still represent a valid and different species, and should be compared genetically and morphologically with the Red Sea material.

Distribution. Red Sea, Japan, Philippines, Indonesia, Papua New Guinea: New Britain, Great Barrier Reef (Australia), Zanzibar and Madagascar.

Discussion

Soft tissue morphological features. The morphological distinctions and key to species of *Xenia* presented here apply only to the type material that has been re-described in this study, encompassing 21 of the 56 morphospecies currently listed in WoRMS (WoRMS Editorial Board, 2018). For most of these species only a single colony representing the type specimen exists. Consequently, intraspecific variation of their morphological characters is not known. Recognizing such variation is highly significant as demonstrated in the current study for *X. umbellata* colonies. They feature variation in number of rows of pinnules (2 vs. 3) and pinnules (e.g., ZMTAU Co36784: 16–20 vs. Co36792: 22–27), as well as sclerite density, which ranged from abundant in all parts of the colony to absent entirely, yet all were confirmed to be genetically identical. Considerable intraspecific variation in pinnules has also been reported in other xeniid genera, suggesting that these characters are not reliable for drawing species boundaries (*Ovabunda*: Halász *et al.* 2015, McFadden *et al.* 2017; *Caementabunda* and *Conglomeratusclera*: Benayahu *et al.* 2018). Nonetheless, before concluding that those morphological features lack taxonomic importance among Xeniidae in general, additional cases need to be verified.

In the related xeniid genus *Ovabunda*, polyp pulsation has been shown to be species-specific and therefore an important diagnostic taxonomic character (Halász *et al.* 2015, McFadden *et al.* 2017). Unlike most *Ovabunda* morphospecies, however, the original descriptions of *Xenia* types mostly lack information on their ability to pulsate, except for *X. actuosa* (Verseveldt & Tursch 1979) and *X. umbellata* (Gohar 1940, this study). The taxonomic importance of behavioral traits such as polyp pulsation should be carefully explored in *Xenia* and also *Heteroxenia* Kölliker, 1874 (Kremien *et al.* 2013). While such traits cannot be observed in preserved material, they may provide an important means to identify and discriminate xeniid species in the field, being important for example in ecological surveys.

***Xenia* sclerite microstructure.** The dendritic sclerite microstructure is not unique to the genus *Xenia* as it also occurs in other xeniid genera, including *Heteroxenia* (Reinicke 1997: 19, fig. 10), *Ingotia* (Alderslade 2001: 23–40, figs. 7–12, 14, 15, 18–20), *Ezziona* (Alderslade 2001: 16–22, figs. 1, 3 and 4, as *Ixion*), *Sansibia* (Benayahu 1993:

14, fig. 7, but erroneously assigned to *Anthelia*), *Sympodium* (Reinicke 1997: 19, fig 7), and *Yamazatum* (Benayahu 2010: figs. 5, 6, 8, 9, 11, 12). Interestingly, this dendritic microstructure is not confined to the Xenidiidae as it has also been recorded in polyp sclerites of the octocoral genera *Clavularia*, *Knopia* and *Moolabalia* (Clavulariidae), *Tubipora* (Tubiporidae) and *Klyxum* (Alcyoniidae) (Alderslade 2001; Alderslade & McFadden 2007). Evidently, the dendritic microstructure of sclerites appears to have evolved in several octocoral families, constituting part of the array of their sclerite morphology. Among xeniids, especially the speciose genus *Xenia*, this microstructure is undoubtedly the prevalent one.

In general, the SEM images of the polyp sclerites of the *Xenia* types (Figs. 1–16) support Alderslade's (2001) finding on the dendritic structure of these sclerites, and document for the first time the range of microstructural variation within this genus. This variation cannot be attributed to differences in the preservation method or to the time elapsed since collection and subsequent preservation, as variation was observed among specimens collected at the same time and location, and most probably preserved and kept in the same manner throughout the years. For example, the types of *X. blumi*, *X. fusca*, *X. membranacea*, *X. rubens*, and *X. ternatana* were all described by Schenk (1896) from Ternate (Indonesia) and deposited in the same museum (SMF). The sclerites of *X. blumi* are ellipsoid platelets, composed of calcite rods, uniform in width, arranged radially at the surface of the sclerite and thus presenting a granular surface texture (Figs. 3, 4). In *X. ternatana* they are also ellipsoid platelets, but their surface morphology is variable: some feature an obvious dendritic structure and tend to fracture (Fig. 14a, b), similar to other *Xenia* species (e.g. *X. blumi*: Fig. 3 and *X. garciae*: Fig. 7), while others possess a granular surface with a partial or complete distinct crest along the sclerite surface (Fig. 14c). In this respect their sclerites resemble *Yamazatum* Benayahu, 2010, although that genus features a different suite of sclerite types. Recently, molecular phylogenetic studies have confirmed the status of *Yamazatum* as a separate genus (Benayahu *et al.* 2018). Most of the sclerites in *X. membranacea* are ellipsoid platelets along with some that are irregular (Fig. 9a–d); some feature a single or multiple crests on their surface (Fig. 9c). The sclerites in *X. fusca* are composed of dendritic rods distributed randomly within the sclerite interior, thickening toward their periphery and presenting a granular surface (Fig. 6b). These sclerites do not tend to fracture under SEM, as commonly occurs in most of the other type material examined in the current study. Finally, in *X. rubens* fractured sclerites expose the internal structure, which features radial dendritic rods at the periphery and a void in the center (Fig. 13b). The taxonomic significance of this variation in sclerite microstructure among *Xenia* species needs to be further explored and substantiated by both morphological and genetic examination of additional material, preferentially from the type locality. Such studies are needed in order to separate intra- from interspecific variation, and to understand the implications of variation in sclerite microstructure for inferring species boundaries.

The SEM images obtained for multiple, genetically homogeneous specimens of *X. umbellata* suggest that in that species sclerite microstructure does not vary intraspecifically (Figs. 16–22). In the absence of similar data for multiple individuals of any of the other *Xenia* species, however, it still remains to be confirmed if the observed differences in microstructural characters—such as the presence of a crest or the arrangement and dimensions of rods—are similarly invariant within a species and therefore taxonomically informative for drawing its boundaries. It should be noted that the validity of the key presented above for discriminating *Xenia* species rather than just type specimens, therefore, remains to be tested. Similarly, the status of many of the species themselves await future genetic validation.

The scope of the current study, while not constituting a complete revision of the genus *Xenia*, has nonetheless enabled the designation of a neotype for *X. umbellata*, collected in the type region (northern Red Sea). Sclerites from colonies obtained in Eilat and Saudi Arabia share a similar characteristic microstructure (Figs. 16–22). They are composed of a latticework matrix of sinuous calcite rods, uniform in width and arranged more or less randomly, with their distal tips generally oriented parallel to the surface of the sclerite (Fig. 16). This arrangement differs from that of other *Xenia* species in which the distal tips are oriented vertically relative to the sclerite surface (e.g., *X. bauiana*, *X. viridis* figs. 2, 15, respectively). The designation of a neotype for *X. umbellata* is considered significant, not only in light of its distinctive sclerites, but also due to the molecular data for this species—the type for both *Xenia* and Xenidiidae—constituting a reference point for future phylogenetic analyses.

***Xenia* phylogenetic relationships.** As noted in previous molecular phylogenetic analyses, the genus *Xenia* appears to be paraphyletic (McFadden *et al.* 2014a; Janes *et al.* 2014; Benayahu *et al.* 2018). Three distinct molecular clades have been identified: one (X1) paraphyletic with *Ovabunda*, another (X2) paraphyletic with *Heteroxenia*, and a third (X3) in an unresolved clade with *Sansibia*, *Sarcothelia* and *Yamazatum* (Fig. 23). *X.*

umbellata belongs to clade X1, where it is united with species of *Ovabunda* within a strongly supported subclade. Despite the genetic similarity between *X. umbellata* and *Ovabunda*, the latter genus is morphologically distinct due to the unique corpuscular microstructure of its sclerites (Alderslade 2001; Aharonovich & Benayahu 2011; Halász *et al.* 2014), a character not shared by *X. umbellata*. Although it appears clear from the molecular phylogeny that Xeniidae is in need of revision and that *Xenia* should perhaps be divided among several genera, morphological characters congruent with the molecular clades have not yet been identified. Moreover, most of the material that has been sequenced so far has been identified from the literature rather than by direct comparison to type material, and the species identifications should therefore be considered unverified. As shown here, the original species descriptions often include incomplete, inaccurate or erroneous descriptions of the type specimens, deficiencies the present study has hopefully corrected.

Conclusions. The re-examination of octocoral type material has already proven to be highly important in revealing previously overlooked, taxonomically significant morphological traits in other xeniid genera (e.g. Halász *et al.* 2014; Benayahu *et al.* 2018). Because of the variation observed in traits such as pinnule number and sclerite density that were formerly considered to be species-diagnostic, however, assigning binomials to living or recently collected material remains challenging. Obtaining sequence data from types will enable the use of species-diagnostic genetic characters to confirm the identity of newly collected specimens as well as historical material housed in museums (McCormack *et al.* 2016). Along with advances in molecular tools aimed at delimiting species and elucidating relationships among different taxa, validation of the morphology of original type material should be taken into account. The latter will facilitate our ability to correctly employ Latin binomials, both in phylogenetic studies and in any other biological or ecological surveys.

Acknowledgements

Support for this project came from the U.S.-Israeli Binational Science Foundation grant #2008186 to Y.B., C.S.M. & R.J.T. and from the Israel Taxonomy Initiative (ITI). This research (Applications DE-TAF-662, AT TAF 2064, and GB TAF 3027) received support from the SYNTHESYS Project <http://www.synthesys.info/> which is financed by European Community Research Infrastructure Action under the FP7 "Capacities" Program. It also was in part supported by a Temminck Fellowship, the Naturalis Biodiversity Centre, and The Israel Cohen Chair in Environmental Zoology to Y.B. We thank curators of the following museums for loan of material: A. Cabrinovic, The Natural History Museum London (BML); L.P. van Ofwegen, the Naturalis Biodiversity Center, formerly Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); M. Grasshoff, Senckenberg Naturmuseum Frankfurt (SMF); C. Lüter, Zoologisches Museum Berlin (ZMB); S. D. Cairns, Smithsonian National Museum of Natural History, Washington DC (USNM); and A. Andouche, Musée National d'Histoire Naturelle, Paris (MNHN). We thank The Interuniversity Institute for Marine Sciences (IUI) for assistance and use of facilities. We acknowledge Alex Shlagman for professional curatorial skills, Y. Delaria and V. Holdengreber for SEM work, V. Vexler for digital editing, and N. Paz for editorial assistance. We also acknowledge the reviewers whose comments much contributed to the quality of the manuscript. This work was completed by A.H. as partial fulfilment of the requirements for a PhD at Tel Aviv University.

References

- Aharonovich, D. & Benayahu, Y. (2011) Microstructure of octocoral sclerites for diagnosis of taxonomic features. *Marine Biodiversity*, 42, 173–177.
<https://doi.org/10.1007/s12526-011-0102-3>
- Alderslade, P. (2001) Six new genera and six new species of soft corals, and some proposed familial and subfamilial changes within the Alcyonacea (Coelenterata: Octocorallia). *Bulletin of the Biological Society of Washington*, 10, 15–65.
- Alderslade, P. & McFadden, C.S. (2007) Pinnule-less polyps: a new genus and new species of Indo-Pacific Clavulariidae and validation of the soft coral genus *Acrossota* and the family Acrossotidae (Coelenterata: Octocorallia). *Zootaxa*, 1400 (1), 27–44.
<https://doi.org/10.11646/zootaxa.1400.1.2>
- Ashworth, J.H. (1899) The structure of *Xenia hicksoni* nov. sp. with some observations on *Heteroxenia elizabethae* Kölliker. *Quarterly Journal of Microscopical Sciences*, New Series, 42, 245–304.

- Ashworth, J.H. (1900) Report on the Xeniiidae collected by Dr. Willey. In: *Zoological results based on material from New Britain, New Guinea, Loyalty Islands and elsewhere, collected by Dr. A. Willey during the years 1895–1897*. Cambridge University Press, Cambridge, pp. 509–530.
- Benayahu, Y. (1990) Xeniiidae (Cnidaria: Octocorallia) from the Red Sea with description of a new species. *Zoologische Mededelingen Leiden*, 64, 113–120.
- Benayahu, Y. (1993) Corals of the south-west Indian Ocean, 1. Alcyonacea from Sodwana Bay, South Africa. *Oceanographic Research Institute, Durban (ORI) Investigational Report*, 69, 1–15.
- Benayahu, Y. (2002) Soft corals (Octocorallia: Alcyonacea) of the southern Ryukyu Archipelago: The families Tubiporidae, Clavulariidae, Alcyoniidae and Briareidae. *Galaxea JSRS*, 4, 1–21.
<https://doi.org/10.3755/jcrs.2002.11>
- Benayahu, Y. (2010) A new genus of a soft coral of the family Xeniiidae (Cnidaria: Octocorallia) from Japan. *Galaxea JSRS*, 12, 53–64.
<https://doi.org/10.3755/galaxea.12.53>
- Benayahu, Y., Tesfamariam, Y. & Schleyer, M.H. (2002) Soft corals (Octocorallia, Alcyonacea) of the southern Red Sea. *Israel Journal of Zoology*, 48, 273–283.
<https://doi.org/10.1560/HYC7-TUTH-EV77-BEUQ>
- Benayahu, Y., van Ofwegen, L.P. & McFadden, C.S. (2018) Evaluating the genus *Cespitularia* Milne Edwards & Haime, 1850, with descriptions of new genera of the family Xeniiidae (Octocorallia, Alcyonacea). *ZooKeys*, 754, 63–101.
<https://doi.org/10.3897/zookeys.754.23368>
- Bourne, G.C. (1894) On the structure and affinities of *Heliopora coerulea*, Pallas. With some observations on the structure of *Xenia* and *Heteroxenia*. *Philosophical Transactions of Royal Society (B)*, 186, 455–483.
- Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods*, 9, 772.
<https://doi.org/10.1038/nmeth.2109>
- Ehrenberg, C. (1828) Pars zoological II. Animalia evertibrata exclusis insectis. In: Hemprich, F. & Ehrenberg, C.G. (Eds.), *Symbolae physicae, seu icones et descriptiones corporum naturalium novorum aut minus cognitorum quae ex itineribus per Libyam, Aegyptium, Nubiam, Dongalam, Syriam, Arabiam et Habessiniam*. Ex Officina Academica, venditur a Mittler, Berolini, 152 pp.
- Ehrenberg, G.C. (1834) Beitrage zur physiologischen Kenntniss der Corallenthiere im allgemeinen, und besonders des Rothen Meeres, Nebst einem Versuche zur physiologischen Systematik derselben. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin*, 1, 225–380.
- Fabricius, K.E. (1998) Reef invasions by soft corals: which taxa and which habitats? *Proceedings of the Australian Coral Reef Society 75th Anniversary Conference, Heron Island, Great Barrier Reef, October 1997*. School of Marine Science, The University of Queensland, Brisbane, pp. 77–90.
- Fabricius, K.E. & Alderslade, P. (2001) *Soft Corals and Sea Fans: A Comprehensive Guide to the Tropical Shallow-Water Genera of the Central-West Pacific, the Indian Ocean and the Red Sea*. Townsville, Australian Institute of Marine Science, pp. 264.
- Gohar, H.A.F. (1940) Studies on the Xeniiidae of the Red Sea. Their ecology, physiology, taxonomy and phylogeny. *Publications of the Marine Biological Station, Ghardaqa, Red Sea*, 2, 27–118.
- Gravier, C. (1908) Recherches sur quelques Alcyonaires du Golfe de Tadjourah. *Archives de zoologie expérimentale et générale*, Series 4, 8 (2), 179–266, pls. 5–11.
- Halász, A., McFadden, C.S., Aharonovich, D., Toonen, R.J. & Benayahu, Y. (2014) A revision of the octocoral genus *Ovabunda* Alderslade, 2001 (Anthozoa, Octocorallia, Xeniiidae). *ZooKeys*, 373, 1–41.
<https://doi.org/10.3897/zookeys.373.6511>
- Halász, A., Reynolds, A.M., McFadden, C.S., Toonen, R.J. & Benayahu, Y. (2015) Could polyp pulsation be the key to species boundaries in the genus *Ovabunda* (Octocorallia: Alcyonacea: Xeniiidae)? *Hydrobiologia*, 759, 95–107.
<https://doi.org/10.1007/s10750-014-2106-z>
- Haverkort-Yeh, R.D., McFadden, C.S., Benayahu, Y., Berumen, M., Halász, A. & Toonen, R.J. (2013) A taxonomic survey of Saudi Arabian Red Sea octocorals (Cnidaria: Alcyonacea). *Marine Biodiversity*, 43, 279–291.
<https://doi.org/10.1007/s12526-013-0157-4>
- Hickson, S.J. (1903) The Alcyonaria of the Maldives. The genera *Xenia*, *Telesto*, *Spongodes*, *Nephthya*, *Paraspongodes*, *Chironephthya*, *Siphonogorgia*, *Solenocaulon*, and *Melithodes*. In: *The Fauna and Geography of the Maldives and Lacadive Archipelago*, II (Part 1). pp. 473–502, pls. XXI and XXVII.
- Hickson, S.J. (1931a) The alcyonarian family Xeniiidae, with a revision of the genera and species. *Great Barrier Reef Expedition*, 1931, 137–179.
- Hickson, S.J. (1931b) Three species of *Alcyonaria* from the Gulf of Manaar. *Bulletin of the Madras Government Museum. Natural History*, 1, 79–89.
- Imahara, Y. (1996). Previously recorded octocorals from Japan and adjacent seas. *Precious Corals & Octocoral Research*, 4, 17–44.
- Janes, M.P. (2008) A study of the Xeniiidae (Octocorallia, Alcyonacea) collected on the "Tyro" expedition to the Seychelles with a description of a new genus and species. *Zoologische Mededelingen Leiden*, 82, 599–626.

- Janes, M.P. (2013) Distribution and diversity of the soft coral family Xenidiidae (Coelenterata: Octocorallia) in Lembeh Strait, Indonesia. *Galaxea JCRS*, 15 (Supplement), 195–200.
<https://doi.org/10.3755/galaxea.15.195>
- Janes, M.P., McFadden, C.S. & Chanmethakul, T. (2014) A new species of *Ovabunda* (Octocorallia, Xenidiidae) from the Andaman Sea, Thailand with notes on the biogeography of this genus. *Zookeys*, 431, 1–17.
<https://doi.org/10.3897/zookeys.431.7751>
- Kahng, S.E., Benayahu, Y. & Lasker H.R. (2011) Sexual reproduction in octocorals. *Marine Ecology Progress Series*, 443, 265–283.
<https://doi.org/10.3354/meps09414>
- Klunzinger, C.B. (1877) *Die Korallthiere des Rothen Meeres. I: Die Alcyonarien und Malacodermen*. Gutmann, Berlin, 98 pp.
- Kölliker, A. (1874) *Die Pennatulide Umbellula und zwei neue Typen der Alcyonarien. Festschrift zur Feier des 25-Jährigen Bestehens der Physikalisch-Medicinischen Gesellschaft*. Stahl, Würzburg, 23 pp. [pp. 5–23]
- Kozlov, A. (2018) *amkozlov/raxml-ng: RAxML-NG v0.6.0 BETA (Version 0.6.0)*. Zenodo, Genève. [program]
<https://doi.org/10.5281/zenodo.1291478>
- Kremien, M., Shavit, U., Mass, T., Genin, A. (2013) Benefit of pulsation in soft corals. *Proceedings of the National Academy of Sciences*, 110, 8978–8983.
<https://doi.org/10.1073/pnas.1301826110>
- Kükenthal, W. (1902) Versuch einer Revision der Alcyonarien: I. Die Familie der Xeniden. *Zoologisches Jahrbuch, Abteilung für systematic, Geographie und Biologie der Tiere*, 15, 635–662.
<https://doi.org/10.5962/bhl.part.19040>
- Kükenthal, W. (1909) Diagnosen neuer Alcyonarien. *Zoologischen Anzeiger*, Bd XXXV, 1–816.
- Kükenthal, W. (1911) Alcyonarien von den Aru- und Kei-Inseln nach den sammlungen von Dr H. Merton.—*Abhandlungen Senckenbergische Naturforschende Gesellschaft. Senckenb. Frankfurt*, 33, 307–346, figs. 1–83, pls. 19–23.
- Kükenthal, W. (1913) Alcyonaria des Roten Meeres. In: Expeditionen S.M. Schiff “pola” in das Rote Meer. *Zoologische Ergebnisse*, 29, pp. 1–33.
- Lamarck, M.C. (1816) Les Caracteres Generaux et Particuliers de ces Animaux, leur Distribution, leur Classes, leurs Familles, leurs Genres, et la Citation des Principales Especies qui s'y Rapportent." *Histoire Naturelle des Animaux sans Vertebres*, 2, 388–421.
- Lamouroux, J.V.F. (1812) Memoires sur la montee et sur une nouvelle classification des polypiens coralligenes non entierement pierreux. *Nouveau Bulletin Society Philomath, Paris*, 1812, 181–188.
- Mantellato, M.C., Silva, A.G., Louzada, T.S., McFadden, C.S. & Creed, J.C. (2018) Invasion of aquarium origin soft corals on a tropical rocky reef in the southwest Atlantic, Brazil. *Marine Pollution Bulletin*, 130, 84–94.
<https://doi.org/10.1016/j.marpolbul.2018.03.014>
- May, W. (1898) Osafrikanischen Alcyoneen des Hamburger Museum. *Mittheilungen aus dem Naturhistorischen Museum*, 15, 1–38.
- May, W. (1899) Beiträge zur Systematik und Chorologie der Alcyonaceen. *Jenaische Zeitsch. Naturwiss*, 33 (Neue Folge 26), 1–180.
- McCormack, J.E., Tsai, W.L.E. & Faircloth, B.C. (2016) Sequence capture of ultraconserved elements from bird museum specimens. *Molecular Ecology Resources*, 16, 1189–1203.
<https://doi.org/10.1111/1755-0998.12466>
- McFadden, C.S., Benayahu, Y., Pante, E., Thoma, J.N., Nevarez, P.A. & France, S.C. (2011) Limitations of mitochondrial gene barcoding in Octocorallia. *Molecular Ecology Resources*, 11, 19–31.
<https://doi.org/10.1111/j.1755-0998.2010.02875.x>
- McFadden, C.S., Reynolds, A.M. & Janes, M.P. (2014a) DNA barcoding of xeniid soft corals (Octocorallia: Alcyonacea: Xenidiidae) from Indonesia: species richness and phylogenetic relationships. *Systematics and Biodiversity*, 12, 247–257.
<https://doi.org/10.1080/14772000.2014.902866>
- McFadden, C.S., Brown, A.S., Brayton, C., Hunt, C.B. & van Ofwegen, L.P. (2014b) Application of DNA barcoding in biodiversity studies of shallow-water octocorals: molecular proxies agree with morphological estimates of species richness in Palau. *Coral Reefs*, 33, 275–286.
<https://doi.org/10.1007/s00338-013-1123-0>
- McFadden, C.S., Haverkort-Yeh, R., Reynolds, A.M., Halász, A., Quattrini, A.M., Forsman, Z.H., Benayahu, Y. & Toonen, R.J. (2017) Species boundaries in the absence of morphological, ecological or geographical differentiation in the Red Sea octocoral genus *Ovabunda* (Alcyonacea: Xenidiidae). *Molecular Phylogenetics and Evolution*, 112, 174–184.
<https://doi.org/10.1016/j.ympev.2017.04.025>
- McFadden, C.S., Gonzalez, A., Imada, R., Shi, S.S., Hong, P., Ekins, M. & Benayahu, Y. (2019) Molecular operational taxonomic units reveal restricted geographic ranges and regional endemism in the Indo-Pacific soft coral family Xenidiidae. *Journal of Biogeography*, 46, 992–1006.
<https://doi.org/10.1111/jbi.13543>
- Milne Edwards, H. & Haime, J. (1850) A monograph of the British fossil corals – Part I: Introduction, corals from the Tertiary and Cretaceous formation. Palaeontographical Society, London, 71 pp.
- Reinicke, G.B. (1995) Xenidiidae des Roten Meeres (Octocorallia, Alcyonacea). *Beiträge zur Systematik und Ökologie. Essener*

Ökologische Schriften, 6, 1–168.

- Reinicke, G.B. (1997) Xeniiidae (Coelenterata: Octocorallia) of the Red Sea, with descriptions of six new species of *Xenia*. *Fauna of Saudi Arabia*, 16, 5–62.
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542.
<https://doi.org/10.1093/sysbio/sys029>
- Roxas, H.A. (1933) Philippine Alcyonaria, the Families Cornulariidae and Xeniiidae. *The Philippine Journal of Science*, 50, 49–108.
- Ruiz Allais, J.P., Halász, A., McFadden, C.S., Amaro, M.E. & Benayahu, Y. (2014) The first incidence of an alien soft coral of the family Xeniiidae in the Caribbean, an invasion in eastern Venezuelan coral communities. *Coral Reefs*, 33, 287.
<https://doi.org/10.1007/s00338-013-1122-1>
- Savigny, J.C. (1817) *Description de l'Égypte ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'expédition de l'Armée Française. Atlas. Histoire naturelle*, Paris, 244 pls.
- Schenk, A. (1896) Clavulariiden, Xeniiiden und Alcyoniiden von Ternate. *Abhandlungen der Senkenbergischen Naturforschenden Gesellschaft*, 23, 40–80.
- Shoham, E & Benayahu, Y. (2017) Higher species richness of octocorals in the upper mesophotic zone in Eilat (Gulf of Aqaba) compared to shallower reef zones. *Coral Reefs*, 36, 71–81.
<https://doi.org/10.1007/s00338-016-1528-7>
- Tilot, V., Leujak, W., Ormond, R.F.G., Ashworth, J.A. & Mab-Rouk, A. (2008) Monitoring of South Sinai coral reefs: influence of natural and anthropogenic factors. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 18, 1109–1126.
<https://doi.org/10.1002/aqc.942>
- Tixier-Durivault, A. (1966) Octocoralliaires. *Faune de Madagascar*, 21, 1–456.
- Thomson, J.A. & Henderson, W.D. (1905) Report on the Alcyonaria collected by Professor Herdman at Ceylon, in 1902. *Ceylon Pearl Oyster Fisheries supplementary reports*, 20, 269–328.
- Thomson, J.A. & Henderson, W.D. (1906) Alcyonacean from Zanzibar, the Marine Fauna of Zanzibar and British East Africa from Collections made by Cyril Crossland in the years 1901–1902. Alcyonaria. *Proceedings of the Zoological Society of London*, 393–44.
- Thomson, M.A. & McQueen, J.M. (1907) Report on the Marine Biology of the Sudanese Red Sea.—VIII. The Alcyonarians. *Journal of The Linnaean Society of London*, 35, 48–74.
- Thomson, J.A. & Dean, L.M.I. (1931) The Alcyonacea of the Siboga expedition: with an addendum to the Gorgonacea. *Siboga Expedition Monograph*, 13d, 1–227, 28 pls.
- Utinomi, H. (1950) Some Xeniid Alcyonarians from Japan and Adjacent Localities. *Publications of the Seto Marine Biological Laboratory*, 1, 7–17.
<https://doi.org/10.5134/174440>
- Utinomi, H. (1955) Two new species of *Xenia* from Kusimoto (Coelenterata, Alcyonaria). *Publications of the Seto Marine Biological Laboratory*, 4, 263–267.
<https://doi.org/10.5134/174522>
- Utinomi, H. (1977) Shallow-water octocorals of the Ryukyu Archipelago (Part II). *Sesoko Marine Science Laboratory Technical Report*, 5, 1–11.
- Verseveldt, J. (1971) Octocorallia from North-Western Madagascar (Part II). *Zoologische Verhandelingen, Leiden*, 117, 1–73.
- Verseveldt, J. & Tursch, A. (1979) Octocorallia from the Bismarck Sea, Part 1. *Zoologische Mededelingen Leiden*, 11, 1–25.
- Verseveldt, J. & Cohen, J. (1971) Some new species of Octocorallia from the Gulf of Eilat (Red Sea). *Israel Journal of Zoology*, 20, 53–67.
- Verseveldt, J. & Tursch, A. (1979) Octocorallia from the Bismarck Sea, Part 1. *Zoologische Mededelingen Leiden*, 11, 1–25.
- Verseveldt, J. (1960) Biological results of the Snellius-Expedition XX. Octocorallia from the Malay Archipelago (Part 1). *Temminckia*, 10, 209–251.
- Verseveldt, J. (1965) Report on the Octocorallia (Stolonifera and Alcyonacea) of the Israel South Red Sea Expedition 1962, with notes on other collections from the Red Sea. *Fishery Research Station Haifa Bulletin*, 40, 28–48.
- Verseveldt, J. (1970) Reports of some Octocorallia (Alcyonacea) from the northern Red Sea. *Israel Journal of Zoology*, 19, 209–229.
- Verseveldt, J. (1971) Octocorallia from North-Western Madagascar (Part II). *Zoologische Verhandelingen Leiden*, 11, 1–73.
- Verseveldt, J. (1974a) Alcyonacea (Octocorallia) from the Red Sea, with a discussion of a new *Simularia* species from Ceylon. *Israel Journal of Zoology*, 23, 1–37.
- Verseveldt, J. (1974b) Octocorallia from New Caledonia. *Zoologische Mededelingen Leiden*, 48, 96–122.
- Wild, C. & Naumann, M.S. (2013) Effect of active water movement on energy and nutrient acquisition in coral reef-associated benthic organisms. *Proceedings of the National Academy of Sciences*, 110, 8767–8768.
<https://doi.org/10.1073/pnas.1306839110>
- Wood, E. & Dipper, F. (2008) What is the future for extensive areas of reefs impacted by fish blasting and coral bleaching and now dominated by soft corals: a case study from Malaysia. *Proceeding of the 11th International Coral Reef Symposium, Fort Lauderdale, Florida*, 7–11 July 2008 (Session number 12.24), 403–407.