

# ZOOTAXA

3951

## Calcareous sponges of Indonesia

ROB W.M. VAN SOEST\* & NICOLE J. DE VOOGD

*Naturalis Biodiversity Center, P.O. Box 9617, 2300 RA Leiden, The Netherlands,*  
*E-mail: rob.vensoest@naturalis.nl; nicole.devoogd@naturalis.nl*  
*\*Corresponding author*



Magnolia Press  
Auckland, New Zealand

ROB W.M. VAN SOEST & NICOLE J. DE VOOGD

**Calcareous sponges of Indonesia**

(*Zootaxa* 3951)

105 pp.; 30 cm.

30 Apr. 2015

ISBN 978-1-77557-683-9 (paperback)

ISBN 978-1-77557-684-6 (Online edition)

FIRST PUBLISHED IN 2015 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: [zootaxa@mapress.com](mailto:zootaxa@mapress.com)

<http://www.mapress.com/zootaxa/>

© 2015 Magnolia Press

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

## Table of contents

Abstract .....	4
Introduction .....	4
Materials and methods .....	5
Results .....	6
Systematic descriptions .....	6
Phylum Porifera Grant, 1836 .....	6
Class Calcarea Bowerbank, 1864 .....	6
Subclass Calcinea Bidder, 1898 .....	6
Order Clathrinida Hartman, 1958 .....	6
Family Clathrinidae Minchin, 1900 .....	7
Genus <i>Clathrina</i> Gray, 1867 .....	7
<i>Clathrina purpurea</i> sp.nov.....	7
<i>Clathrina chrysea</i> Borojevic & Klautau, 2000 .....	9
<i>Clathrina heronensis</i> Wörheide & Hooper, 1999 .....	10
<i>Clathrina beckingae</i> sp. nov. ....	10
<i>Clathrina aff. luteoculicella</i> Wörheide & Hooper, 1999 .....	13
<i>Clathrina sororecula</i> sp. nov.....	14
<i>Clathrina stipitata</i> (Dendy, 1891) comb. nov. ....	16
Genus <i>Arthuria</i> Klautau, Azevedo, Cónedor-Luján, Rapp, Collins & Russo, 2013 .....	17
<i>Arthuria tenuipilosa</i> (Dendy, 1905) .....	17
<i>Arthuria tubuloreticulosa</i> sp. nov. ....	20
Genus <i>Ernstia</i> Klautau, Azevedo, Cónedor-Luján, Rapp, Collins & Russo, 2013 .....	21
<i>Ernstia indonesiae</i> sp. nov.....	21
<i>Ernstia chrysops</i> sp. nov. ....	23
<i>Ernstia klautauae</i> sp. nov. ....	27
<i>Ernstia naturalis</i> sp. nov. ....	28
Family Levinellidae Borojevic & Boury-Esnault, 1986 .....	30
Genus <i>Burtonulla</i> Borojevic & Boury-Esnault, 1986 .....	30
<i>Burtonulla sibogae</i> Borojevic & Boury-Esnault, 1986 .....	31
Family Leucaltidae Dendy & Row, 1913 .....	33
Genus <i>Ascandra</i> Haeckel, 1872 .....	33
<i>Ascandra kakaban</i> sp. nov. ....	36
<i>Ascandra crewsi</i> sp. nov. ....	36
Genus <i>Leucaltis</i> Haeckel, 1872 .....	39
<i>Leucaltis nodusgordii</i> (Poléjaeff, 1883) comb. nov. ....	39
Family Leucascidae Dendy, 1893 .....	44
Genus <i>Ascaltis</i> Haeckel, 1872 .....	44
<i>Ascaltis angusta</i> sp. nov. ....	44
Genus <i>Leucascus</i> Dendy, 1893 .....	47
<i>Leucascus flavus</i> Cavalcanti, Rapp & Klautau, 2013 .....	47
Genus <i>Ascoleucetta</i> Dendy & Frederick, 1924 .....	49
<i>Ascoleucetta sagittata</i> Cavalcanti, Rapp & Klautau, 2013 .....	49
Family Leucettidae De Laubenfels, 1936 .....	51
Genus <i>Leucetta</i> Haeckel, 1872 .....	51
<i>Leucetta chagosensis</i> Dendy, 1913 .....	51
<i>Leucetta microraphis</i> Haeckel, 1872 .....	54
Genus <i>Pericharax</i> Poléjaeff, 1883 .....	57
<i>Pericharax orientalis</i> sp. nov. ....	57
Order Murrayonida Vacelet, 1981 .....	61
Family Lelapiellidae Vacelet, 1977 .....	61
Genus <i>Lelapiella</i> Vacelet, 1977 .....	61
<i>Lelapiella sphaerulifera</i> Vacelet, 1977 .....	61
Subclass Calcaronea Bidder, 1898 .....	61
Order Leucosolenida Hartman, 1958 .....	61
Family Sycettidae Dendy, 1893 .....	61
Genus <i>Sycetta</i> Haeckel, 1872 .....	61
<i>Sycetta vinitincta</i> sp. nov. ....	62
Genus <i>Sycon</i> Risso, 1827 .....	66
<i>Sycon</i> spec. ....	66
Family Grantiidae Dendy, 1893 .....	69
Genus <i>Leucandra</i> Haeckel, 1872 .....	69
<i>Leucandra irregularis</i> (Burton, 1930) comb. nov. ....	69

Family Jenkinidae Borojevic, Boury-Esnault & Vacelet, 2000.....	72
Genus <i>Anamixilla</i> Poléjaeff, 1883 .....	72
<i>Anamixilla torresi</i> Poléjaeff, 1883 .....	72
<i>Anamixilla singaporensis</i> sp. nov. ....	74
Genus <i>Uteopsis</i> Dendy & Row, 1913 .....	76
<i>Uteopsis argentea</i> (Poléjaeff, 1883) .....	76
Family Heteropidae Dendy, 1893.....	80
Genus <i>Sycettusa</i> Haeckel, 1872.....	80
<i>Sycettusa sibogae</i> (Burton, 1930) .....	80
Genus <i>Grantessa</i> Von Lendenfeld, 1885.....	82
<i>Grantessa borojevici</i> sp. nov. ....	82
<i>Grantessa tenhoveni</i> sp. nov. ....	84
Genus <i>Heteropia</i> Carter, 1886.....	87
<i>Heteropia minor</i> Burton, 1930 .....	87
Genus <i>Vosmaeropsis</i> Dendy, 1893.....	91
<i>Vosmaeropsis grisea</i> Tanita, 1939 .....	91
Family Amorphiscidae Dendy, 1893.....	93
Genus <i>Amphoriscus</i> Haeckel, 1872.....	93
<i>Amphoriscus semoni</i> Breitfuss, 1896 .....	93
Genus <i>Leucilla</i> Haeckel, 1872.....	95
<i>Leucilla australiensis</i> (Carter, 1886).....	95
Additional Indonesian Calcarea not represented in the present collections .....	97
<i>Arthuria darwinii</i> (Haeckel, 1870) comb. nov. ....	98
<i>Leucosolenia sertularia</i> (Haeckel, 1872) .....	98
<i>Clathrina flexilis</i> (Haeckel, 1872) comb. nov. ....	98
<i>Grantia capillosa</i> var. <i>longipilis</i> sensu Breitfuss, 1896 .....	98
<i>Aphroceras caespitosa</i> (Haeckel, 1872) .....	99
<i>Eilhardia schulzei</i> Poléjaeff, 1883 .....	99
Discussion .....	99
Acknowledgements .....	101
References .....	102

## Abstract

The calcareous sponges collected during Indonesian-Dutch research projects, incorporated in the collections of the Naturalis Biodiversity Center (formerly the Rijksmuseum van Natuurlijke Historie and the Zoölogisch Museum of the University of Amsterdam), are described and discussed. A total of 37 species were distinguished, of which 16 are new to science, while several others are very poorly known. The new species are *Clathrina purpurea* sp.nov., *Clathrina beckingae* sp.nov., *Clathrina sororcula* sp.nov., *Arthuria tubuloreticulosa* sp.nov., *Ernstia indonesiae* sp.nov., *Ernstia chrysops* sp.nov., *Ernstia klautauae* sp.nov., *Ernstia naturalis* sp.nov., *Ascandra kakaban* sp.nov., *Ascandra crewsii* sp.nov., *Ascalcis angusta* sp.nov., *Pericharax orientalis* sp.nov., *Sycetta vinitincta* sp.nov., *Anamixilla singaporensis* sp.nov., *Grantessa borojevici* sp.nov. and *Grantessa tenhoveni* sp.nov. An additional six species reported from Indonesia, but not represented in our material, are briefly characterized.

**Keywords:** Porifera, Calcarea, new species, South East Asia, Indonesia

## Introduction

Indonesia and surrounding region, often named the Coral Triangle (e.g. Hoeksema 2007; 2013), comprises a generally recognized biodiversity hotspot. For most marine animal groups, the region shows enhanced numbers of higher and lower taxa, and especially for sessile biota the area is the richest of all oceans (Briggs 1974). Sponges are probably no exception, although this is obscured by a distinct research effort bias (Van Soest *et al.* 2013). Whereas quite a lot of data has been published for the region on the largest sponge class, the Demospongiae Sollas (1885) (cf. Van Soest 1989; Van Soest 1997; Hooper *et al.* 2002), the information on diversity in the Coral Triangle of one of the smaller classes, the rather enigmatic Calcarea Bowerbank, 1864 is largely lacking. In fact, the World Porifera Database (Van Soest *et al.* 2015) lists only 12 ‘accepted’ species from Indonesia, which comprise the species originally described (‘endemics’) from Indonesia. Earlier, Haeckel (1872) described three species from

Indonesia, Topsent (1897) reported one ‘European’ species, Breitfuss (1896a; 1896b; 1898) listed ten species, five of which were ‘European’, and finally Burton (1930) listed twenty species, nine of which were ‘European’ names. These low numbers would indicate that Calcarea are indeed rare and/or inconspicuous in Indonesian waters, as Breitfuss (1898) concluded. However, from the many images of beautiful and intriguing calcareous sponges appearing in regional underwater color guides (e.g. Colin & Arneson 1995; Gosliner *et al.* 1996; Erhardt & Baensch 1998; Weinberg 2004) and on diver websites, we suspect that the diversity of Calcarea is not poor but probably comparable to the other marine groups. So far, the identity of many of those beautiful species remains largely undetermined until now, justifying a study focused on the Calcarea of Indonesia and adjacent countries. Added inducements for us to attempt this enterprise are the absence of virtually any scientific studies on Indonesian Calcarea since 1930 and the presence of large numbers of specimens in the collections of the Naturalis Biodiversity Center.

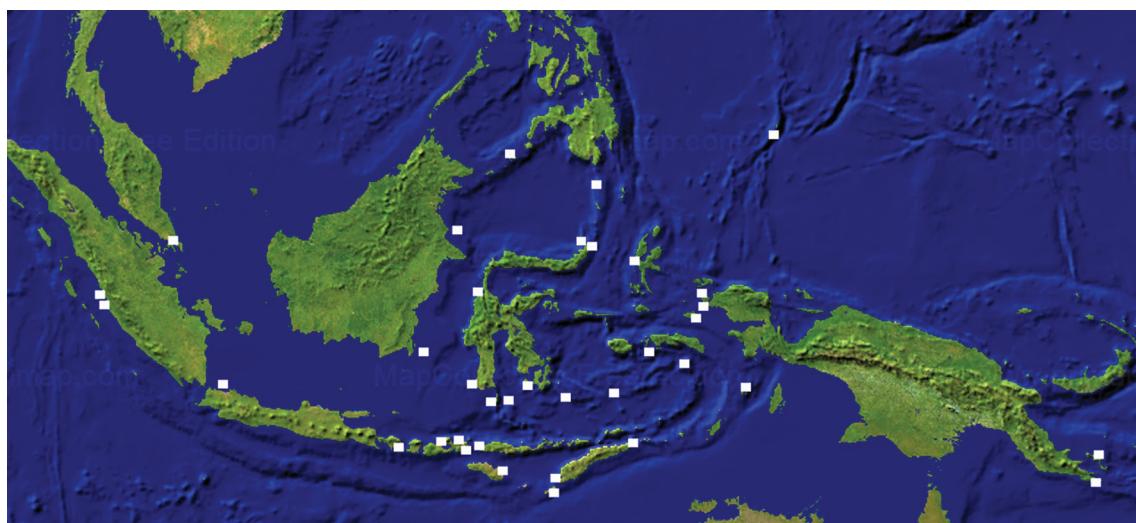
The taxonomy of calcareous sponges (class Calcarea) has long suffered from inaccessibility to any but a handful of informed specialists. With the advent of the Calcarea chapters of the *Systema Porifera* (Borojevic and colleagues in Hooper & Van Soest 2002), the situation improved greatly by the establishment of a single ‘accepted’ classification down to the level of genera, in particular for subclass Calcinea/Order Clathrinida (Borojevic *et al.* 2002a) and subclass Calcaronea/Order Leucosolenida (Borojevic *et al.* 2002b). While recognizing that these Calcarea chapters are a masterful and admirable effort by Radovan Borojevic and co-authors to bring Calcarea systematics within reach of the wider sponge community, we also have to conclude that several problems still remain. Due to the rather concise definitions, limited illustrations, and limited review of species assigned to or recognized as belonging to the genera and families distinguished in the various groups, the Calcarea chapters do not function as well as was hoped for. Still, the publication of the *Systema Porifera* resulted in an enhanced effort on the taxonomy of calcareous sponges by taxonomists from Brazil-France, Germany-Australia, and Norway, combining morphological and molecular tools to further disclose the biodiversity of this group (see e.g. Klautau & Valentine 2003; Manuel *et al.* 2004; Dohrmann *et al.* 2008; Voigt *et al.* 2012; Klautau *et al.* 2013). In view of these developments, we judged it timely to present here descriptions of all Indonesian calcareous sponges incorporated in the collections of the Naturalis Biodiversity Center and to attempt to assign them to their proper affiliation.

## Materials and methods

Our material consisted of a mix of old collection specimens, e.g. those of the Siboga Expedition (1899–1900) described by Burton (1930), specimens collected by the first author during the Indonesian-Dutch Snellius II Expedition (1984–85), and relatively recent (two-)yearly collections made by the second author (1997–2013). During these recent fieldwork episodes, our own collecting activities were augmented by incidental samples collected by our colleagues specialized in other sessile groups. Additionally, several voucher specimens or fragments sent to us for identification by various natural products research groups were included in our material. Specimens and fragments are all registered in the sponge collection of the Naturalis Biodiversity Center, either as RMNH’s Por. four-digit registration number or ZMA’s Por. five-digit registration number. The latter concern specimens previously belonging to the Zoological Museum of Amsterdam. We also borrowed several slides from the Natural History Museum in London (indicated as BMNH) to assist in our identifications. The combined collections numbered 155 samples identified as belonging to the class Calcarea, predominantly from localities within the EEZ of the Republic of Indonesia, but occasionally samples originated from adjacent states Timor Leste, Singapore, Papua New Guinea, Philippines and Palau. Approximate locations from where the samples were collected are presented in Fig. 1, demonstrating that the combined samples are representative of most geographic parts of the Coral Triangle. Precise localities and further details of each specimen are provided in the Material Examined section given with each species description. Geographic coordinates are in decimal degrees rounded off to four decimals or less.

Depending of the taxonomic group and the state and size of the specimens, we made thick sections perpendicularly and/or tangentially, either by hand directly from the alcohol preserved material, or we made histological sections from a fragment that was first stained, using haemalum-eosin or fuchsin stains, then was transferred into paraffin, and subsequently sectioned by hand. Spicule suspensions were made by keeping a fragment of the material in household bleach for a variable period depending of the thickness and state of

preservation. The residual suspensions were washed five times in distilled water using a table centrifuge to precipitate the spicules. Spicules were plated on microscope glass for light microscopy and on SEM stubs for imaging, using a wide mouthed pipette to make sure all spicule types were included. Illustrations of sections were made by a Leica DM5500 stacking microscope and of spicules by a JEOL Scanning Electron Microscope. In all our preparations we made sure that parts of the sponge with different spicule types (cortical, choanosomal, atrial and fringe skeletons) were represented, in order not to miss any spicule types. Measurements of the spicules were made under light microscopy. Measurements included smallest—*average*—largest dimensions of each spicule type of each specimen, based on 25 randomly selected spicules, unless otherwise indicated. In the case of equiaxial spicules, measurements are provided of length and thickness of the actines of the triactines and the basal radiate system of the tetractines, and additionally of the apical actines of the latter. In the case of sagittal spicules, unpaired and one of the paired actines were measured separately. In the case of pseudosagittal or parasagittal spicules all actines were measured separately. Apical actines of tetractines were sometimes less easy to measure in the preparations, so occasionally we provide only the observed range of length and thickness. Terminology for the skeletal structures and the spicules was taken from the Thesaurus of Sponge Morphology (Boury-Esnault & Rützler 1997), occasionally expanded with adjectives to draw attention to special spicule features.



**FIGURE 1.** Map of Indonesia and adjacent countries showing approximate distribution of the sample location. Each white square represents one or more localities, and one or more specimens. Detailed locality positions are provided in the material examined data with each species (Free Edition map courtesy [www.primap.com](http://www.primap.com))

## Results

The specimens available to us in the present study were assigned to a total of 37 species, 24 of which belonged to the subclass Calcinea, 13 to the subclass Calcaronea. For the classification and the order in which higher taxa are treated we follow the Systema Porifera chapters of Borojevic *et al.* (2002a; 2002b; 2002b).

### Systematic Descriptions

#### Phylum Porifera Grant, 1836

#### Class Calcarea Bowerbank, 1864

#### Subclass Calcinea Bidder, 1898

#### Order Clathrinida Hartman, 1958

## Family Clathrinidae Minchin, 1900

**Remarks.** This family unites the Clathrinida species with an asconoid aquiferous system with simple unfolded choanoderm. Most species have a cormus consisting of a network of thin-walled tubes lined by an unstructured layer of mostly small triactines and/or tetractines, with occasional presence of diactines. The family was recently revised using molecular sequence data (Klautau *et al.* 2013). This resulted in the erection of new genera subdividing the former genus *Clathrina* Gray, 1867 *s.l.*, some of which appeared to be affiliated to other families of the Clathrinida. The present classification into genera *Clathrina* *s.s.*, *Ernstia* Klautau *et al.*, 2013, *Arthuria* Klautau *et al.*, 2013, *Borojevia* Klautau *et al.*, 2013, *Brattegardia* Klautau *et al.*, 2013, and a restricted *Guancha* Miklucho-Maclay, 1868, appears not yet fully operational for classifying former *Clathrina* *s.l.* specimens because it is based primarily on molecular analysis. Some former *Clathrina* species, are now assigned to *Ascalitis* Haeckel, 1872 (family Leucascidae). These changes mean in practice that *Clathrina*-like new species in this group cannot be easily assigned to their proper genus unless sequence data are available, excepting *Clathrina* *s.s.*, which remain morphologically recognizable. Morphological differences of the various genera, such as proportion of triactines and tetractines, or clathroid versus loosely anastomosed tubules, appear to be rather overlapping and not precise. We will give informal diagnoses of the genera based on our perception of their variability. These diagnoses should not be considered as formal definitions. For the classification of the known species we follow here the World Porifera Database (Klautau in Van Soest *et al.* 2014), but for the new species the assignment to genera is tentative.

According to the molecular analysis of Klautau *et al.* (2013), *Ascandra* Haeckel, 1872 - in the Systema Porifera assigned to family Leucaltidae Dendy & Row, 1913 - is very probably also a member of Clathrinidae. Nevertheless, we here continue to assign it to Leucaltidae.

## Genus *Clathrina* Gray, 1867 sensu Klautau, Azevedo, Cónedor-Luján, Rapp, Collins & Russo, 2013

Clathrinidae with a cormus of anastomosed tubes, asconoid aquiferous system, and lacking tetractine spicules (after Klautau *et al.* 2013).

### *Clathrina purpurea* sp. nov.

Figures 2a–e

*Clathrina* sp. Erhardt & Baensch 1998: 22.

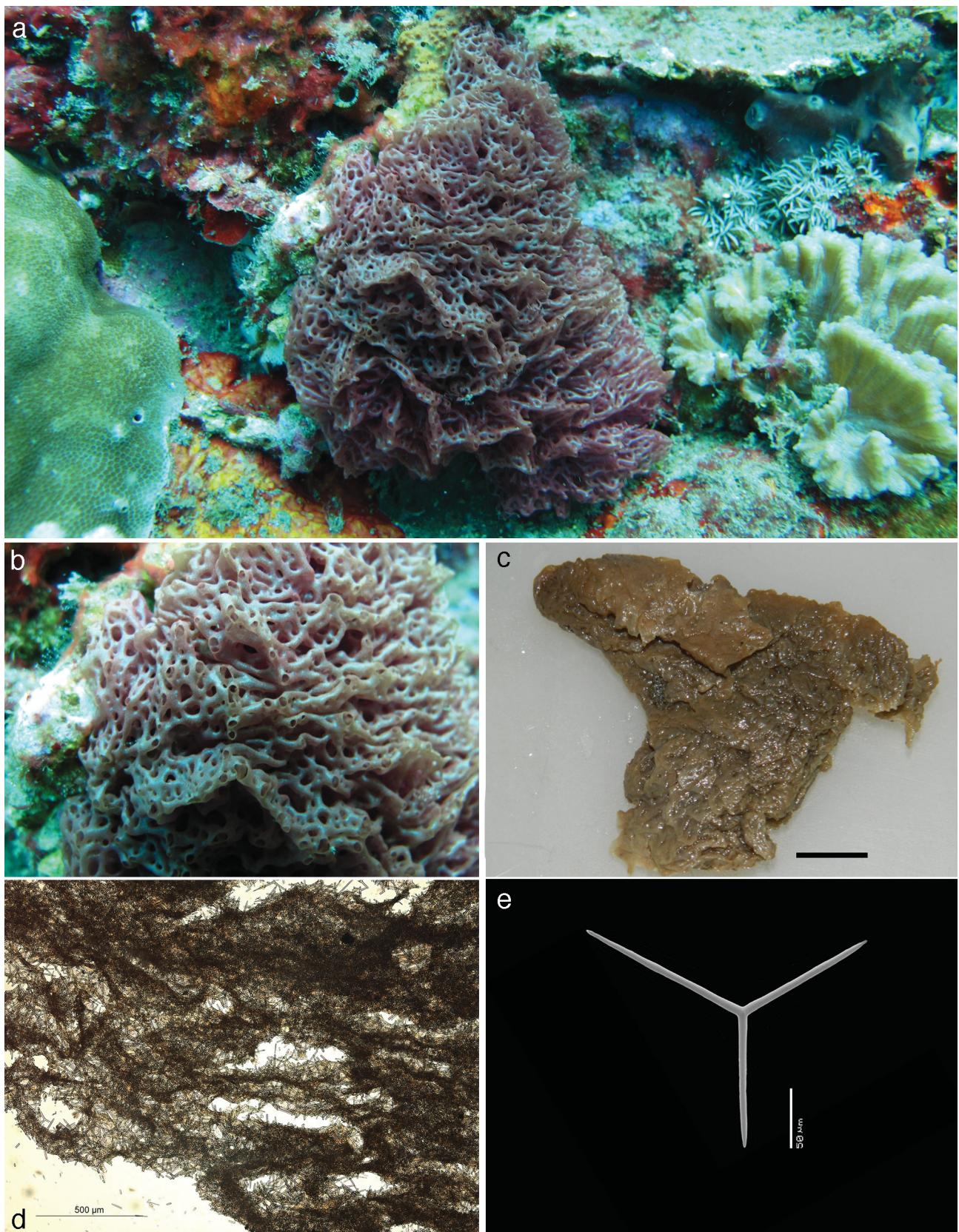
**Material examined.** Holotype RMNH Por. 6625, Indonesia, N Sulawesi, Lembeh Strait, Teluk Makawide, 1.4847°N 125.2406°E, depth 15 m, SCUBA, coll. N.J. de Voogd, #LEM19/090202/064, 9 February 2012.

**Description.** A thick, seemingly conical (Fig. 2a) mass of thin, loosely anastomosed tubes of 2–3 mm in diameter, forming an undulated uneven surface. There are frequent oscules (Fig. 2b), several of which are raised, but water-collecting tubes with terminal oscules are lacking. Total size in life 15 x 10 cm; the preserved specimen has shrunk to 5 x 5 x 0.5 cm (Fig. 2c). Color a distinctive reddish purple in life, dark red-brown and quite limp in preserved condition. Consistency soft, easily torn.

**Skeleton.** The walls of the tubes (Fig. 2d) consist of a thin layer of triactines.

**Spicules.** Regular triactines only. Triactines (Fig. 2e) equiangular equiaxial, with thin cylindrical actines, 78–120.3–153 x 5.5–6.1–7 µm.

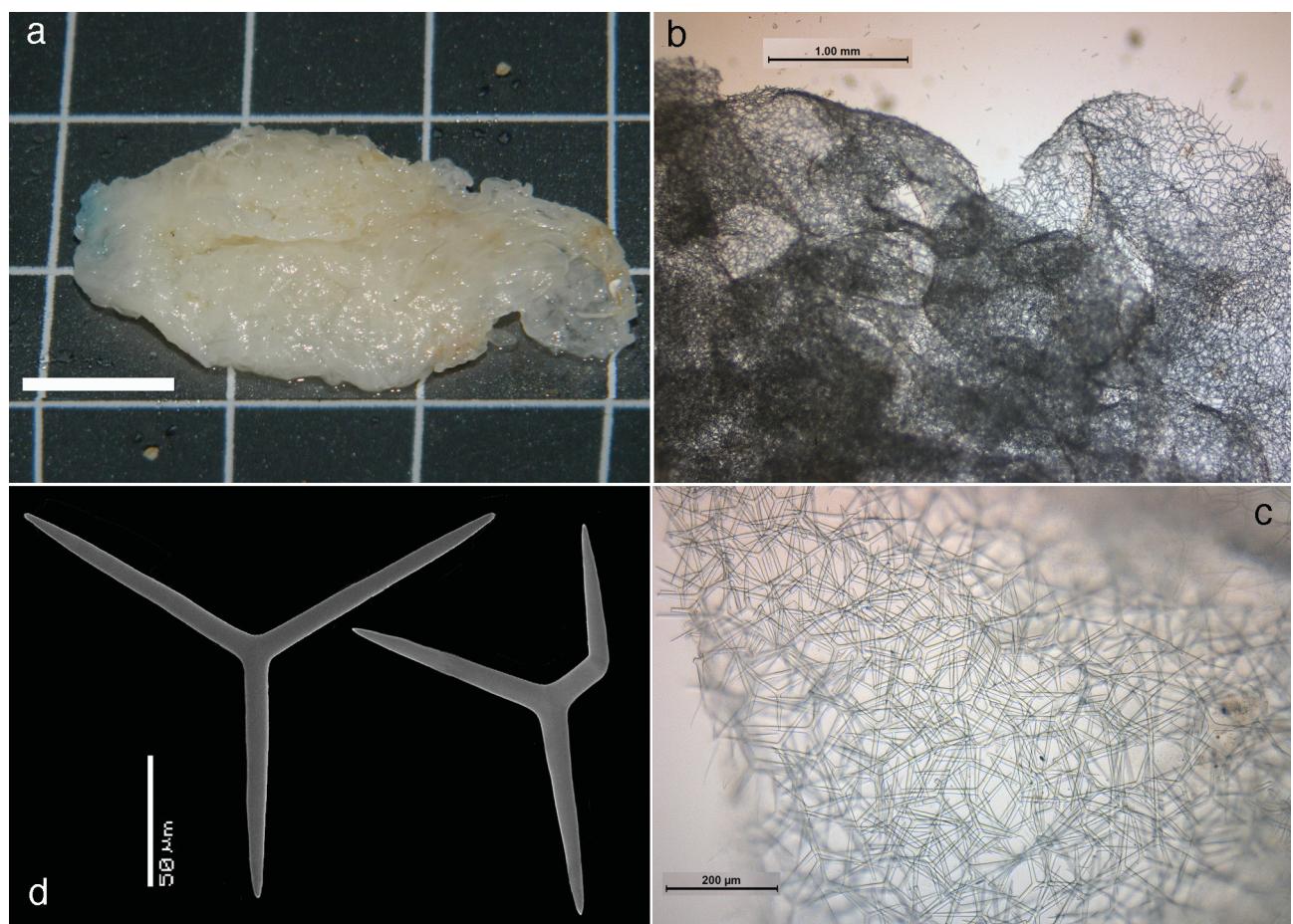
**Ecology.** On reefs, at shallow depth.



**FIGURE 2.** *Clathrina purpurea* sp. nov., holotype RMNH Por. 6625, a, habitus *in situ* at N Sulawesi (photo N.J. de Voogd), b, detail of surface *in situ* showing distribution of oscules (photo N.J. de Voogd), c, preserved holotype (scale bar = 1 cm), d, overview of skeleton (scale bar = 500  $\mu$ m), e, SEM image of triactine.

**Remarks.** This specimen is assigned to *Clathrina* in the restricted sense of Klautau *et al.* (2013) on account of its habitus of anastomosed tubes and continuous choanoderm in combination with its lack of tetractines. Although there are already numerous *Clathrina* species described, the present species stands out by its distinctive color and large size, combined with numerous oscules and cylindrical triactines of intermediate size. Using the key of Klautau & Valentine (2003) we were unable to find a matching species and assume here that it is undescribed. There is some resemblance in habitus to *Clathrina ceylonensis* (Dendy, 1905), as redescribed by Klautau & Valentine (2003: 16, fig. 10) but shape of the spicules of that species (conical actines) and length of the actines (67–96 µm) are sufficiently distinct from our specimen to belong to a different species.

The photo on p. 22 of the Meeres Atlas 5 of Erhardt & Baensch is obviously this species; like our holotype it was photographed in Lembeh Strait.



**FIGURE 3.** *Clathrina chrysea* Borojevic & Klautau (2000), ZMA Por. 16165 from SW Sulawesi, a, preserved habitus (scale bar = 1 cm), b, overview of skeleton (scale bar = 1 mm), c, detail of surface skeleton (scale bar = 200 µm), d, SEM images of spicules.

### *Clathrina chrysea* Borojevic & Klautau, 2000

Figures 3a–d

*Clathrina* spec. Lévi, Laboute, Bargibant & Menou, 1998: 74.  
*Clathrina chrysea* Borojevic & Klautau, 2000: 189, fig. 1.

**Material examined.** ZMA Por. 16165, Indonesia, SW Sulawesi, Spermonde Archipelago, Samalona, 4.8747°S 119.3419°E, depth 6 m, SCUBA, coll. N.J. de Voogd, 20 April 1997.

**Description.** Cushion-shaped (Fig. 3a), slightly lobate, cormus of loosely anastomosed tubes. Water-collecting tubes are lacking. Overall size 4.5 x 3 cm, height 0.5 cm, tubes 2–3 mm in diameter. Consistency soft, limp. Color in life not noted (presumably yellow), in alcohol pale transparent white.

**Skeleton.** (Fig. 3b–c) Wall of tubes thin, at most two or three layers of triactines (Fig. 3c).

**Spicules.** Triactines only.

Triactines (Fig. 3d), regular equiangular, with conical actines,  $75\text{--}117.2\text{--}144 \times 7.5\text{--}9.1\text{--}11$ ; a minority of the spicules have one actine crooked, either upwards or downwards, and these are usually smaller than the regular spicules (average actine length 82  $\mu\text{m}$ ).

**Ecology.** In reefs and reef lagoons, 6–28 m.

**Distribution.** Indonesia, New Caledonia.

**Remarks.** The identification of this material with *Clathrina chrysea* is based on shape of the specimen and size and shape of the triactines. A similar species appears to be *Clathrina heronensis* Wörheide & Hooper, 1999 from the Great Barrier Reef, Australia, but its habitus is dissimilar in being flat, tubes are thinner (1 mm), and in alcohol the color turns brown. Below, we assign a distinctly different specimen of our collection to *C. heronensis*.

### ***Clathrina heronensis* Wörheide & Hooper, 1999**

Figures 4–e

*Clathrina heronensis* Wörheide & Hooper, 1999: 863, figs 3A–F; Klautau & Valentine, 2003: 28, fig. 21.

**Material examined.** RMNH 4499, Indonesia. Kalimantan, Berau region, Derawan Islands, Maratua Island, Haji Buang Marine Lake,  $2.2044^\circ\text{N}$   $118.5987^\circ\text{E}$ , depth 1–2 m, snorkeling, coll. L.E. Becking, # LE156, 11 September 2008.

**Description.** (Fig. 4a) Small, flatly encrusting loosely open network of thin tubes. Water collecting tubes or oscules not apparent. *In situ* color is transparent white, discoloring to brown in preserved condition (Fig. 4b). Size of cormus  $1.5 \times 2$  cm, tubes thin, at most up to 2 mm in diameter, usually less than 1 mm. Consistency in preserved state stiff, fragile.

**Skeleton.** (Figs 4c–d) Several layers of irregularly arranged triactines.

**Spicules.** Triactines only.

Triactines (Fig. 4e), mostly equiangular equiaxial, but some are faintly parasagittal, size of conico-cylindrical actines  $93\text{--}125.9\text{--}162 \times 8\text{--}9.3\text{--}11.5 \mu\text{m}$ .

**Ecology.** Shallow-water, in marine lake on mangrove roots. Elsewhere in caves.

**Distribution.** Indonesia, NE Australia.

**Remarks.** The specimen, which is now broken into two fragments, is closely similar to Australian material according to descriptions of it in Wörheide & Hooper (1999) and Klautau & Valentine (2003). White color, brown discoloration in alcohol, cormus shape and spicule size and form of our material fit well with the type.

### ***Clathrina beckingae* sp. nov.**

Figures 5a–e

?*Leucosolenia clathrus*; Breitfuss, 1896a: 434; Breitfuss, 1898: 171 (not: Schmidt, 1864).

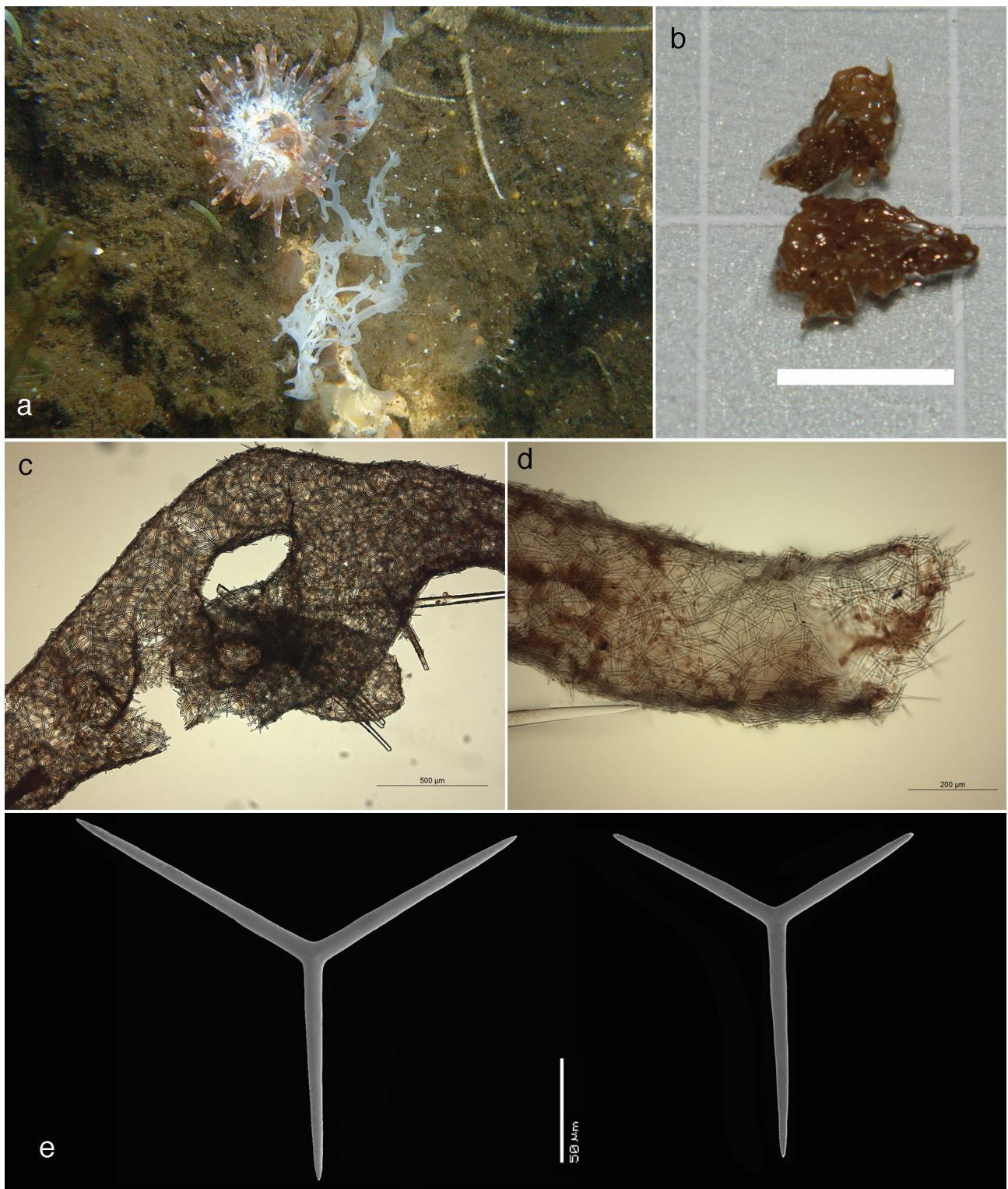
**Material examined.** Holotype RMNH Por. 1437, Indonesia, NE Kalimantan, Berau region, Derawan Islands, Maratua Island, depth 1 m, snorkeling, coll. L. Colin, Kalimantan-Berau Expedition 2003, 23 October 2003.

Paratype RMNH Por. 4482, Indonesia, East Kalimantan Province, Berau Region, Maratua Island, Haji Buang marine lake,  $2.2044^\circ\text{N}$   $118.5987^\circ\text{E}$ , depth 1–2 m, snorkeling, coll. L.E. Becking, #LE 177, 11 September 2008.

**Description.** (Figs 5a, holotype, and 5b, paratypes). Cormus forming a conical mass of loosely anastomosing tubes with several water collecting tubes ending in oscules elevated above the surface of the body. Color transparent white *in situ* (verging to pale cream in the holotype specimen), becoming pale greyish yellow in preserved condition (Fig. 5c). Size up to  $2.5 \times 2 \times 2$  cm, individual tubes 0.5–1 mm in diameter. Consistency soft, limp.

**Skeleton.** (Fig. 5d) Walls of tubes having only two or three layers of partly overlapping triactines, not densely arranged.

**Spicules.** Triactines only.

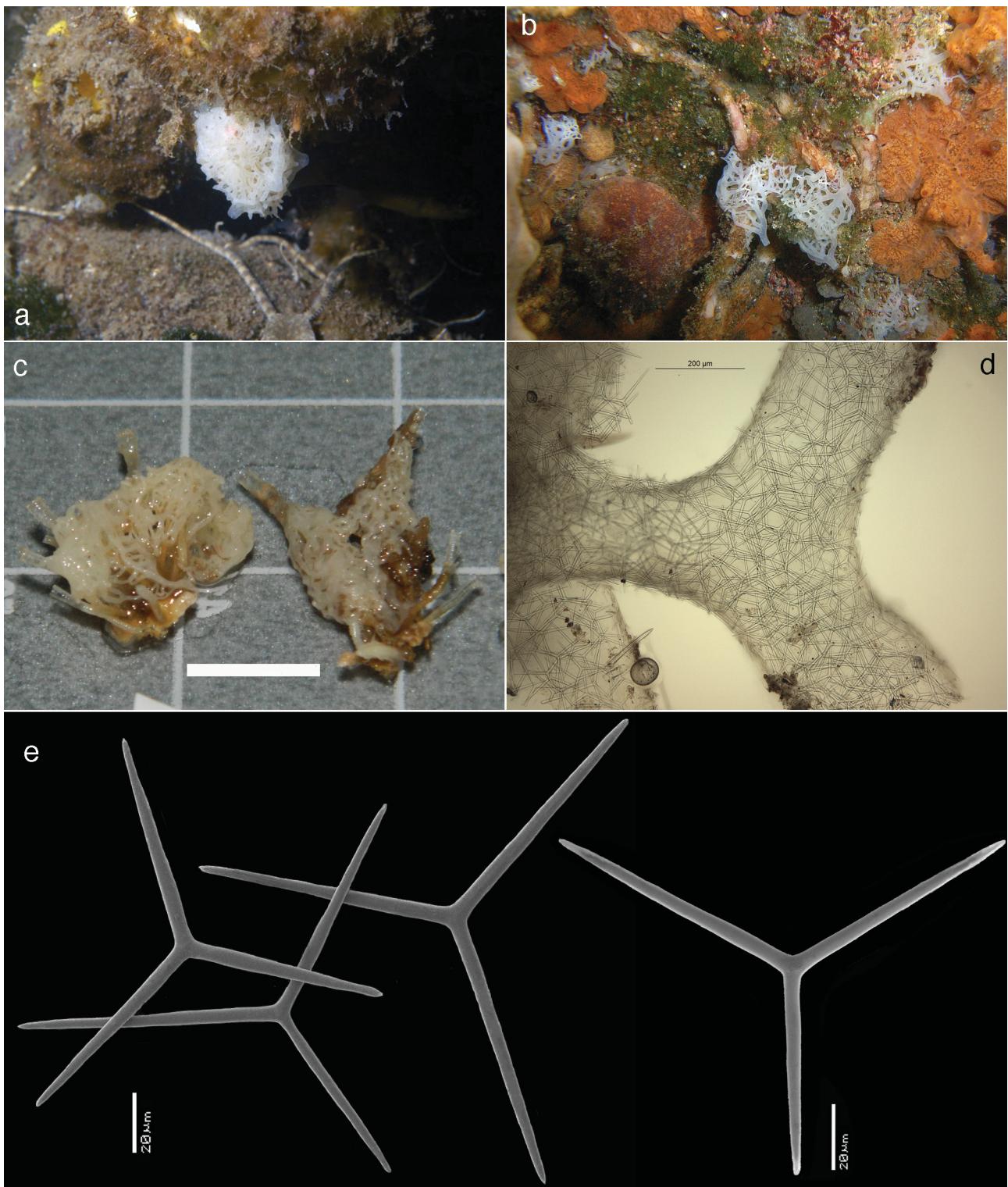


**FIGURE 4.** *Clathrina heronensis* Wörheide & Hooper (1999), RMNH Por. 4499 from Maratua, a, habitus *in situ* (photo L.E. Becking), b, habitus in preserved state (scale bar = 1 cm), c, overview of tubar skeleton (scale bar = 500 µm), d, detail of tube (scale bar = 200 µm), e, SEM images of spicules.

Triactines (Fig. 5e), equiangular equiaxial, with thin cylindrical actines, size of actines 48–84.9–106 x 4–4.7–6 µm.

**Ecology.** Marine lake inhabitant.

**Distribution.** Indonesia.



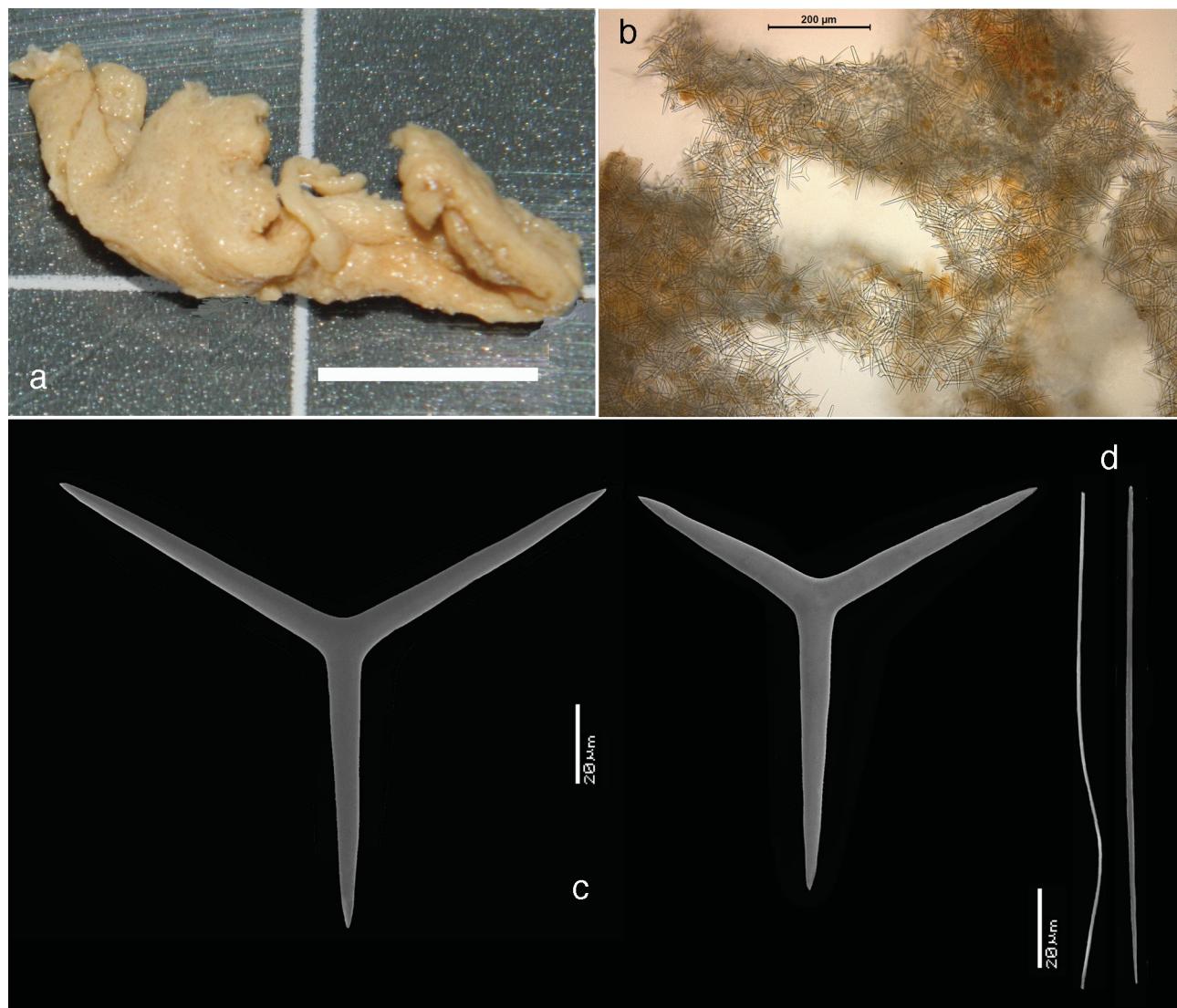
**FIGURE 5.** *Clathrina beckingae* sp. nov., a, holotype RMNH Por. 1437, photographed *in situ* in Maratua marine lake (photo L. Colin), b, paratypes RMNH Por. 4482, ditto (photo L.E. Becking), c, preserved type material (scale bar = 1 cm), d, skeleton of tubes (scale bar = 200 µm), e, SEM images of spicules of holotype (three on the left) and paratype (right).

**Etymology.** Named after our colleague Leontine E. Becking, expert on marine lake biota, to acknowledge her assistance in the field and for collecting material of several of the species described in this paper, including the paratype of the present species.

**Remarks.** By being white and having thin semitransparent tubes the new species resembles *Clathrina heronensis* described above, and also occurring in the same habitat. However, there are several important and

significant differences: (1) the actine length and thickness of the triactines is considerably smaller and the shape is cylindrical, not conico-cylindrical, (2) distinct water-collecting tubes are present, elevated above the cormus, and (3) the cormus is forming a conical mass elevated above the substratum, not flattened.

Although Breitfuss (1896a, 1898) did not provide adequate descriptive information or illustrations, the spicule size data make it possible that his report of *Clathrina* (as *Leucosolenia*) *clathrus* from Ternate concerns the present species. *C. clathrus* is restricted to European waters and it is highly unlikely that it would occur in Indonesia.



**FIGURE 6.** *Clathrina* aff. *luteoculcitella* Wörheide & Hooper, 1999, ZMA Por. 08567 from SW Salayar, a, preserved habitus (scale bar = 1 cm), b, detail of surface skeleton (scale bar = 200 µm), c–d, SEM images of spicules, c, triactines, d, (pieces of rare) diactines.

#### *Clathrina* aff. *luteoculcitella* Wörheide & Hooper, 1999

Figures 6a–d

? *Clathrina luteoculcitella* Wörheide & Hooper, 1999: 868, fig. 5; Klautau & Valentine, 2003: 30, fig. 23.  
*Clathrina luteoculcitella* 'Indonesia'; Klautau *et al.* 2013: 12.

**Material examined.** ZMA Por. 08657, Indonesia, SE Sulawesi, SW Salayar, NW coast of Pulau Guang, 6.35°S 120.45°E, depth 4–12 m, SCUBA, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition stat. 152/III/40, 29 September 1984.

**Description.** Dense, partially digitate mass of tightly anastomosed thin tubes (Fig. 6a). Water-collecting tubes

are lacking. Overall size 2.5 cm long, 1 cm wide, digitations 0.5–1 cm high. Live color noted as pale yellowish, in alcohol it is beige-yellow.

**Skeleton.** (Fig. 6b) A dense layer of small triactines, with occasional diactines, but these are invariably broken off.

**Spicules.** Triactines, possibly diactines.

Triactines, (Fig. 6c) equiangular equiaxial, with conical actines, 67–87.3–98 x 6–8.1–10 µm; rarely one of the actines is crooked.

Diactines, (Fig. 6d) not certainly proper, few are present and these consist mostly of short broken pieces, 80–120 x 6 µm.

**Ecology.** Caves and overhangs in reef environment, 4–25 m.

**Distribution.** Indonesia, NE Australia.

**Remarks.** Klautau *et al.* (2013) listed this material as *Clathrina luteoculcitella* Wörheide & Hooper, 1999 on account of the tightly anastomosed mass of fine tubes in combination with the small triactines with relatively robust conical actines and a presence of diactines. The presence of diactines is a less convincing similarity with the Australian material as these were only few and mostly broken in our specimen, whereas Wörheide & Hooper pictured a specimen with lots of diactines sticking from its surface (their fig. 5B). Dr Michelle Klautau (personal communication) used the present material in her phylogenetic analysis (see Klautau *et al.* 2013: fig. 1) and it appeared in the same clade - but at some distance - as the Australian holotype of *C. luteoculcitella*. We assume here that it is close to *C. luteoculcitella* but possibly distinct.

We note here that the specimen is also close to the Sri Lankan *Clathrina ceylonensis* (Dendy, 1905) (as *Leucosolenia coriacea* var. *ceylonensis* Dendy, 1905: 226, pl. XIII fig. 8). This also has a cormus of tightly anastomosed tubes and triactines in exactly the same size and shape. Dendy (1905: 227) noticed diactines in some of the specimens.

### *Clathrina sororcula* sp. nov.

Figures 7a–c, 8a–e

*Leucosolenia coriacea*; Burton, 1930: 2, in part (not: Montagu, 1814)

? *Clathrina* sp. Colin & Arneson, 1996: 59, photo 227; Lim, De Voogd & Tan, 2008: 162.

**Material examined.** Holotype RMNH Por. 2576, Singapore, Pulau Subar Darat (Little Sister), NW side, 2.2149°N 103.8318°E, depth 10 m, SCUBA, coll. N.J. de Voogd, #SIN16/010406/138, 1 April 2006,

Paratypes ZMA Por. 00135, Indonesia, Sulawesi, Salayar anchorage, 6.0963°S 120.4481°E, depth 0–36 m, trawl, coll. Siboga Expedition stat. 213, 26 September 1899; ZMA Por. 00183a, Indonesia, Kalimantan, Karang Lintang, Pulau Palabangan, Moearas Reef, 1.7714°N 118.9615°E, depth 0–54 m, trawl, hard coral sand, coll. Siboga Expedition stat. 091, 22 June 1899; RMNH 2065, Indonesia, Java Sea, Kepulauan Seribu (Thousand Islands), 5.7606°S 106.7546°E, depth 12 m, SCUBA, coll. N.J. de Voogd, #SER.27, Kepulauan Seribu Expedition 2005, 17 September 2005.

**Description.** Rather loosely anastomosed cushion of white, semi-transparent tubes (Figs 7a, 8e), encrusting rocks and mussels. Size up to 4 x 3 cm in lateral expansion, at least 1–3 cm in height in preserved condition. Several oscules are visible in the *in situ* photo, but they are solitary and flush with the surface and do not appear to be distinct endings of water-collecting tubes. Pale greyish brown to dirty white in preserved condition (Figs 7b, 8a). The preserved holotype is broken into two equally sized fragments (Fig. 7b).

**Skeleton.** (Figs 8b–c) Walls made up of three or more layers of robust triactines.

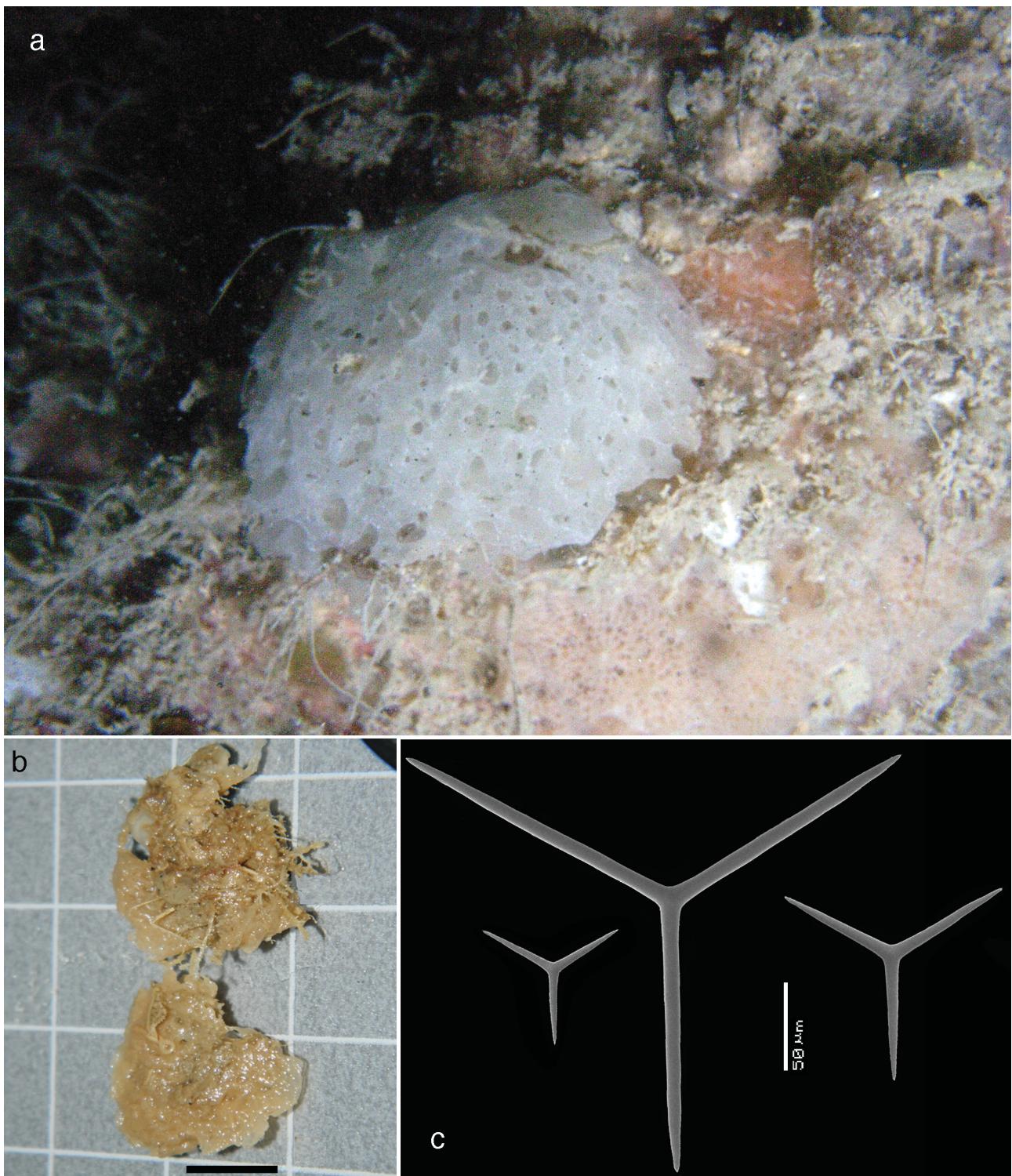
**Spicules.** Triactines only.

Triactines (Figs 7c, 8d), equiangular equiaxial, cylindro-conical actines with rather abruptly sharp-pointed ends, a small proportion are parasagittal, actines in a large size range, possibly divisible in two sizes, overall size 97–151.6–201 x 9–12.6–21 µm.

**Ecology.** Shallow-water.

**Distribution.** Singapore, Indonesia.

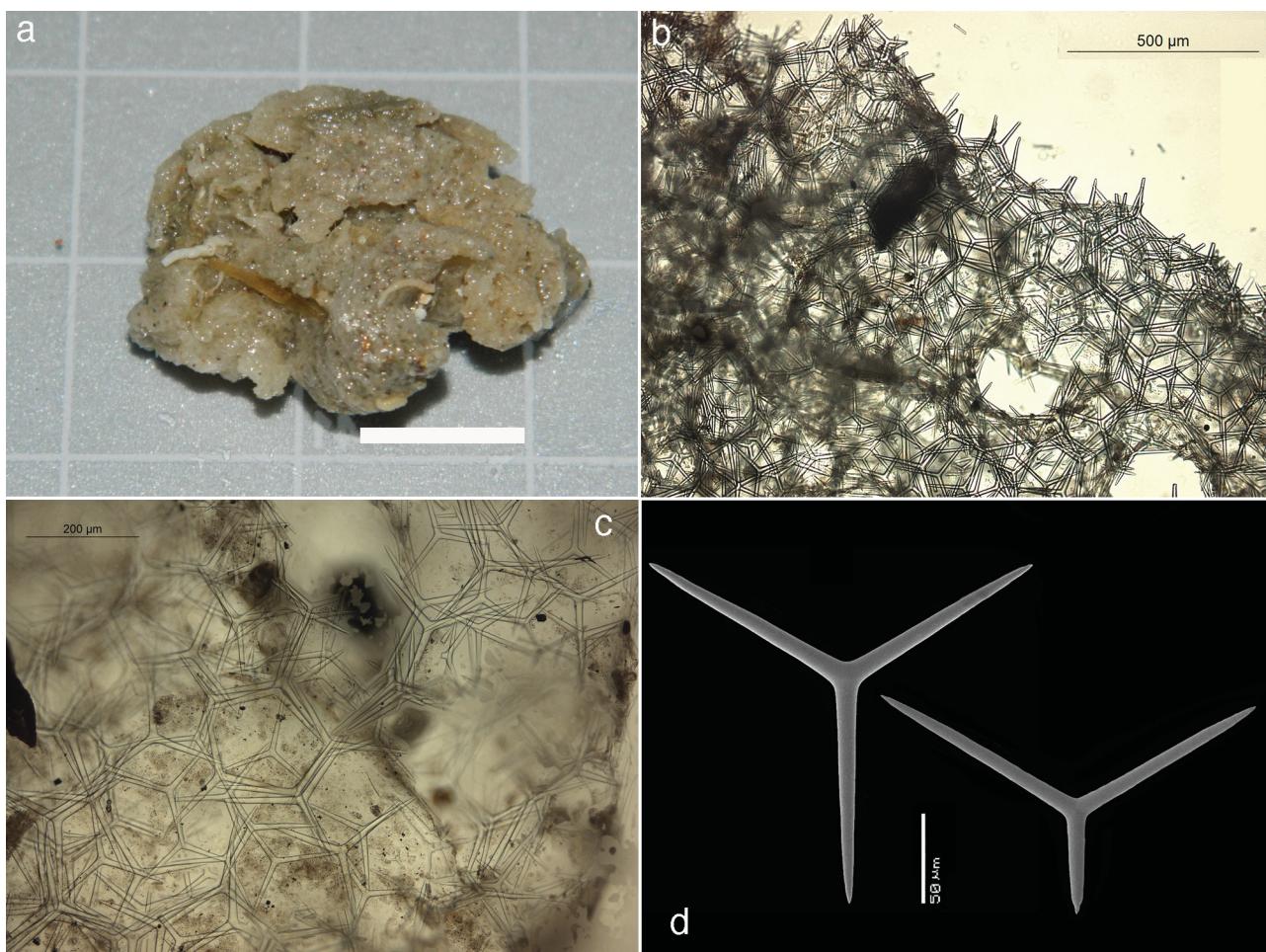
**Etymology.** The word *sororcula* (L.) means ‘little sister’, referring to the locality Pulau Subar Darat, Little Sister Island.



**FIGURE 7.** *Clathrina sororcula* sp.nov., holotype RMNH Por. 2576, a, photo *in situ*, from Singapore (photo N.J. de Voogd), b, preserved fragments (scale bar = 1 cm), c, SEM images of the spicules.

**Remarks.** The new species differs from the *Clathrina* species reported here from Indonesian waters by the combination of white semitransparent color and robust spicules. Using the key of Klautau & Valentine (2003) this species keys out as the Northeast Australian *Clathrina parva* Wörheide & Hooper, 1999. The skeleton and the spicules are indeed similar to the description of the type of that species, but the habitus and the size of the cormus are quite different: cormus may reach 4 cm in lateral dimension (1 cm in *C. parva*), oscules are singly and flush (on the top of fused tubes in *C. parva*), spicules are conico-cylindrical and sharply pointed (cylindrical and bluntly

pointed in *C. parva*). Furthermore, we assume that photo's in Colin & Arneson (1996: *Clathrina* sp. 227, Papua New Guinea) and Lim *et al.* (2008, Singapore) are also referable to the present species.



**FIGURE 8.** *Clathrina sororcula* sp. nov., paratype ZMA Por. 00183a, a, preserved material collected by the Siboga Expedition (scale bar = 1 cm), b, skeleton of tubes (scale bar = 500 µm), c, detail of the same (scale bar = 200 µm), d, SEM images of the spicules.

Burton (1930) referred this (and other specimens of the Siboga Expedition) to the European species *Clathrina* (as *Leucosolenia*) *coriacea* (Montagu, 1814), which is erroneous because that species has much more densely anastomosed tubes and smaller spicules. Siboga specimens ZMA Por. 00136 and 00183b, identified by Burton also as *Clathrina* (as *Leucosolenia*) *coriacea* possess tetractines, and are here assigned to *Ernstia naturalis* sp.nov. (see below).

#### *Clathrina stipitata* (Dendy, 1891) comb. nov.

Figures 9a–b

*Leucosolenia stipitata* Dendy, 1891: 51, pl. I figs 4–6, pl. IV fig. 2, pl. IX fig. 5  
*Leucosolenia macleayi*; Burton, 1930: 2 (not: *Ascertta macleayi* Von Lendenfeld, 1885)

**Material examined.** ZMA Por. 00134, Indonesia, Sulawesi, Karkaralong Islands, anchorage off Kawio and Kamboling Islands, 4.67°N 125.4015°E, depth 23–31 m, dredged, coll. Siboga Expedition stat. 129, 22 July 1889.

**Description.** Stalked small sponge, dirty white in alcohol (Fig. 9a). Upper part consists of a tight mass of thin tubes. Stalk approximately 6 mm long, body 8 x 6 mm. Consistency soft, easily damaged.

**Skeleton.** The wall of the tubes consist of several layers of triactines (Fig. 9b).

**Spicules.** (Fig. 9b) Triactines only, in two categories.

Small equiangular equiaxial triactines, actines 69–76.5–84 x 5–5.9–7 µm.

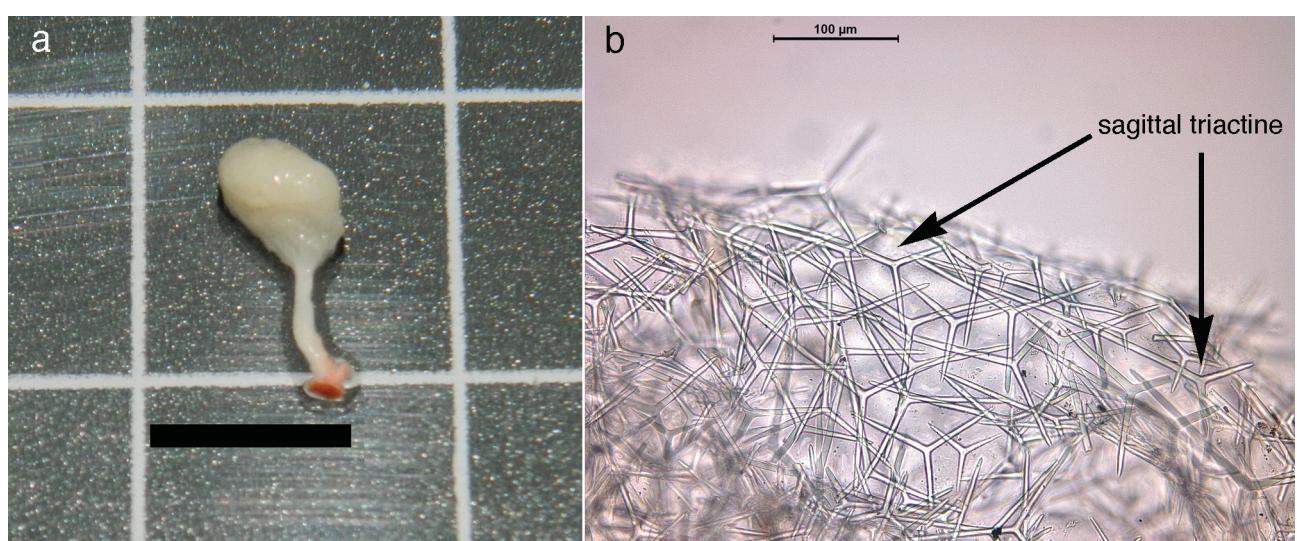
Small parasagittal triactines (arrows in Fig. 9b), unpaired actines 123–135.8–151 x 6–6.6–7 µm, paired actines 66–73.8–85 x 5–5.4–6 µm.

**Ecology.** Deeper water down to 32 m.

**Distribution.** Indonesia, South East Australia.

**Remarks.** The identification is not entirely certain as Dendy cites slightly shorter unpaired actines for the type. *Clathrina macleayi* (Von Lendenfeld, 1885) has much smaller spicules and is unlikely to be conspecific. Remarkably, Burton (1963) in his list of specimens/slides in the collection of the Natural History Museum lists a slide of the Siboga collection (BMNH 1928.6.18.3) as *Leucosolenia stipitata*, whereas he used the name *L. macleayi* in the 1930 description.

Because of the stalked habitus of the present species, it would have been assigned to the genus *Guancha* in the Systema Porifera classification (Borojevic *et al.* 2002a). However, in the recent revision of Klautau *et al.* (2013) they demonstrated that the genus is polyphyletic and its type species falls in the same clade as *Clathrina*.



**FIGURE 9.** *Clathrina stipitata* (Dendy, 1891), ZMA Por. 00134, from N Sulawesi, a, preserved habitus (scale bar = 1 cm), b, detail of surface skeleton showing regular and sagittal triactines (arrows) (scale bar = 100 µm).

### Genus *Arthururia* Klautau, Azevedo, Cónodor-Luján, Rapp, Collins & Russo, 2013

Clathrinidae with asconoid aquiferous system possessing both triactines and tetractines, the latter in low proportion (after Klautau *et al.* 2013).

#### *Arthururia tenuipilosa* (Dendy, 1905)

Figures 10a–f

*Leucosolenia (Clathrina) tenuipilosa* Dendy, 1905: 227, pl. XIII fig. 9.

*Clathrina tenuipilosa*; Klautau & Valentine, 2003: 40, fig. 32.

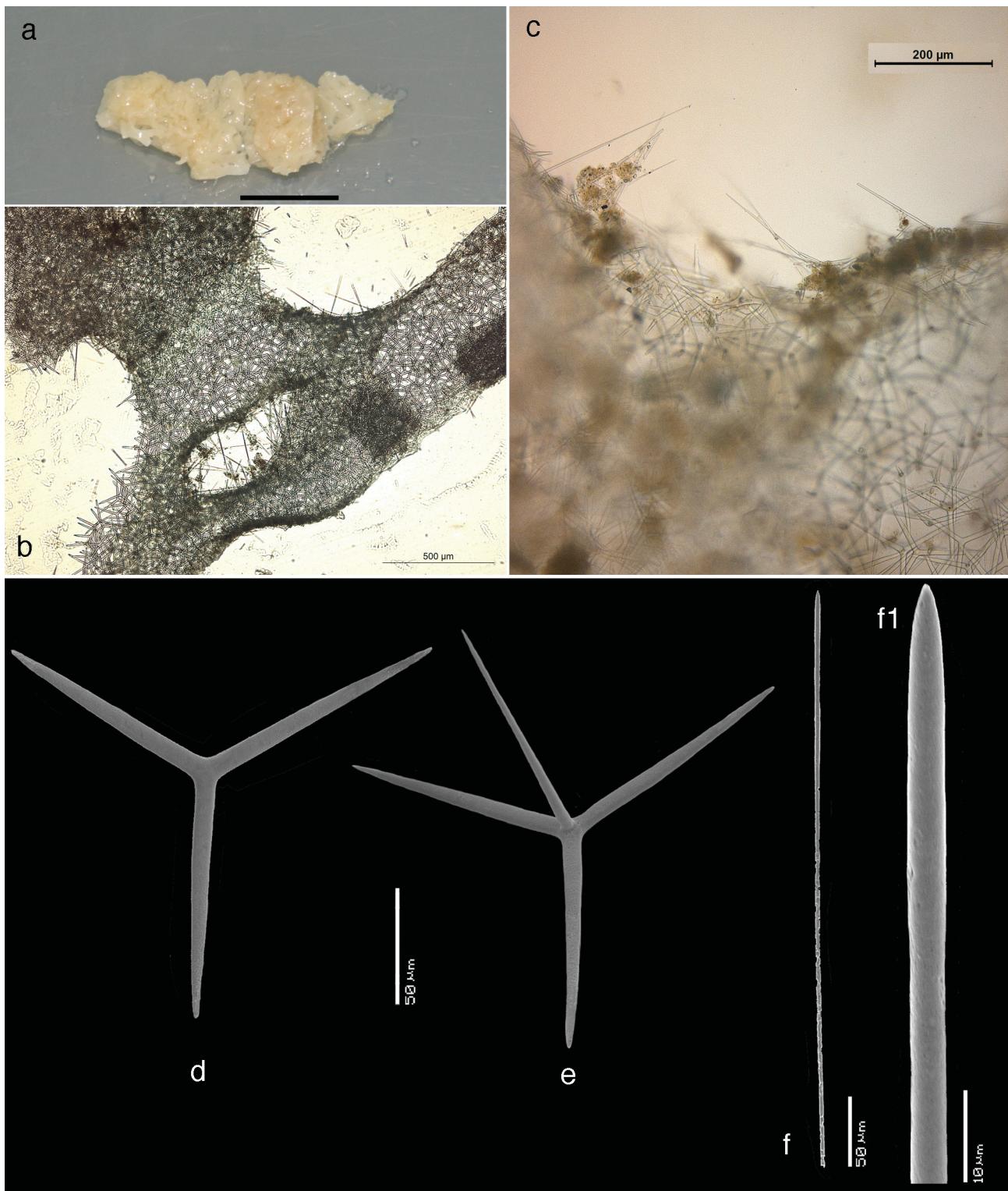
*Arthururia tenuipilosa*; Klautau *et al.* 2013: 12.

**Material examined.** ZMA Por. 15509b, Indonesia, Indonesia, SE Sulawesi, SW Salayar, NW coast of Pulau Guang, 6.35°S 120.45°E, depth 3–4 m, SCUBA, coll. H.A. ten Hove, Indonesian-Dutch Snellius II Expedition stat. 152/II/Cave 1/A3, 28 September 1984.

**Description.** White mass of loosely anastomosed tubes (Fig. 10a), size 3 x 1.5 x 0.5 cm. Water-collecting tubes are absent. Wall of tubes microscopically echininated by hairy-thin diactines (Figs 10b–c).

**Skeleton.** (Fig. 10b) The tube walls consist of a thin layer of triactines and tetractines.

**Spicules.** (Figs 10d–f) Triactines, tetractines, diactines.



**FIGURE 10.** *Arthuria tenuipilosa* (Dendy, 1905), ZMA Por. 15509b.a, preserved habitus (scale bar 1 cm), b, overview of cormus (scale bar = 500 µm). c, detail of surface with protruding diactines (scale bar = 200 µm), d–f, SEM images of the spicules, d, triactine, e, tetractine, f, broken diactine, f1, detail of apex of diactine.

Triactines (Fig. 10d) equiangular equiaxial, 81–107.1–119 x 8–8.9–10.5 µm.

Tetractines (Fig. 10e), with equiangular equiaxial basal radiate system, actines 89–103.6–121 x 8–8.7–10 µm, apical actines 62–100 x 6–6.5 µm.

Diactines (Fig. 10f), with slightly swollen endings (Fig. 10f1) on one side and thinly pointed endings on the opposite side, usually broken, 350–422 x 2.5–3 µm.

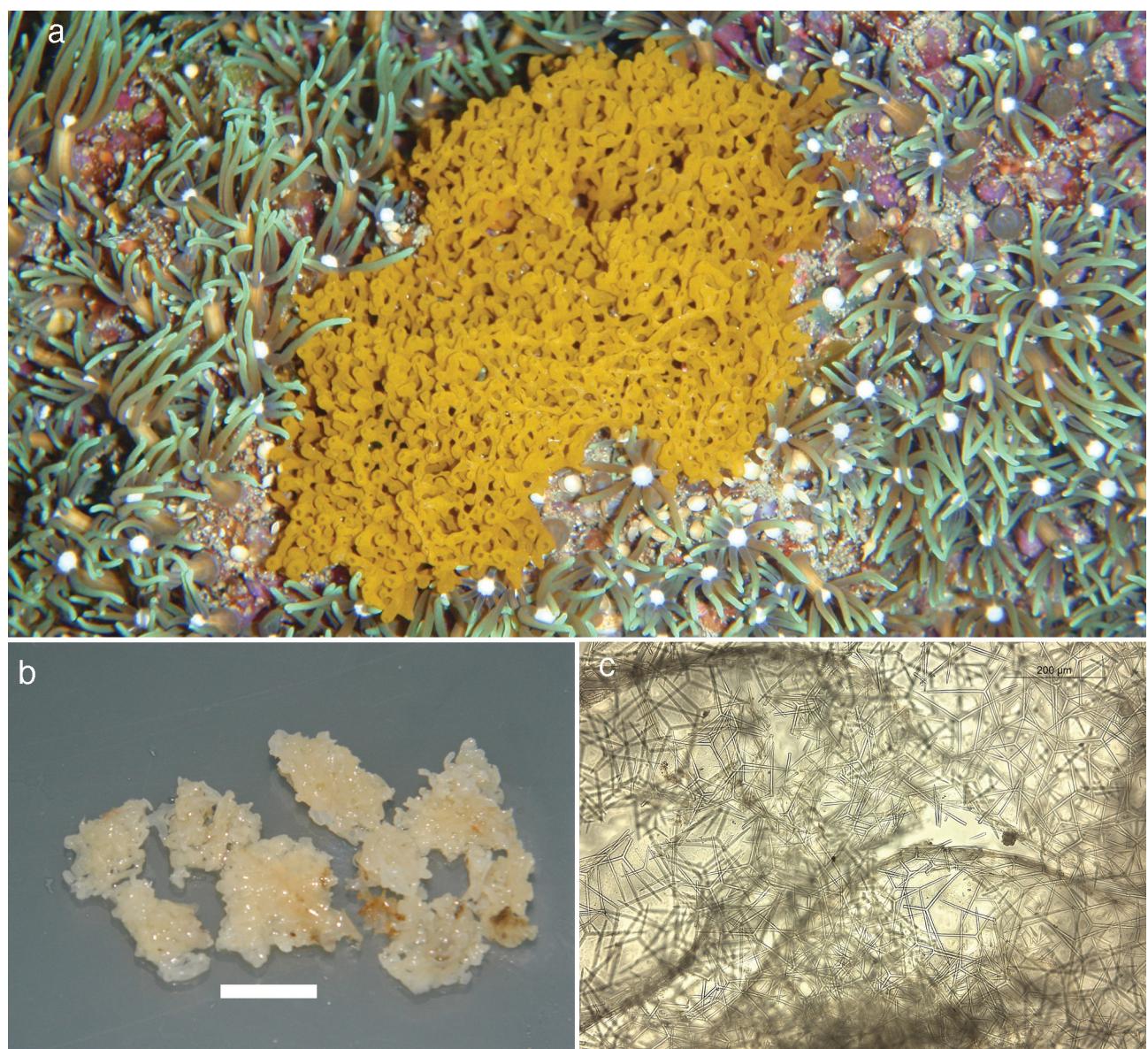
**Ecology.** On the upper wall of a shallow-water cave.

**Distribution.** Indonesia, Sri Lanka.

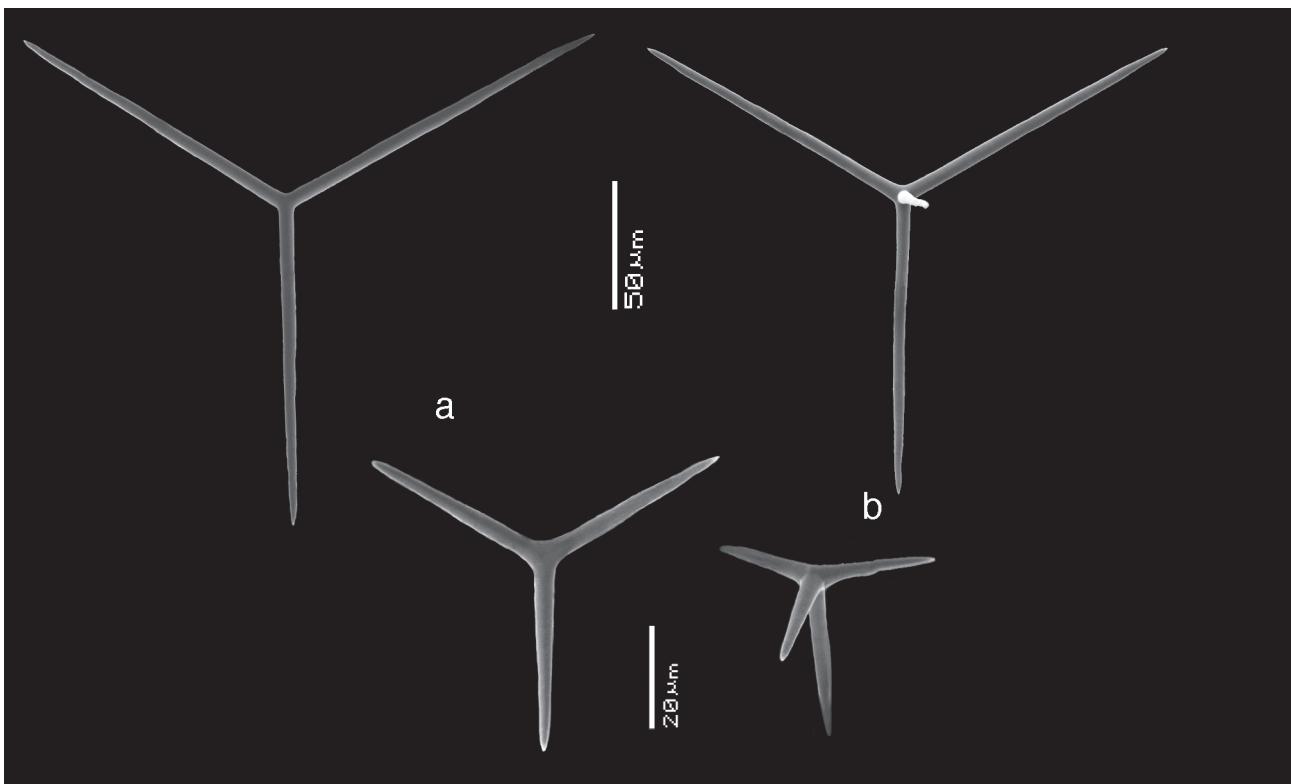
**Remarks.** The spicule size data of our specimen conform closely to those given by Dendy (1905: 227) for the type material, but differ from the measurements of Klautau & Valentine (2003: 41) taken from a paratype in having on average longer and slightly thinner actines. Trichoxeas described by Klautau & Valentine (2003: 41) are thinner (only 0.3  $\mu\text{m}$ ) than the diactines we measured in our material.

*Clathrina luteoculcitella* Wörheide & Hooper, 1999 also has a fringe of diactines sticking out of the tubewalls, but that species has no tetractines and the live color is yellow.

*Ernstia indonesiae* sp.nov. described below has similar habitus and general spiculation, but the actines of both triactines and tetractines are twice as long and thick, there is a complement of sagittal tri-and tetractines. The diactines are also longer and thicker and do not stick out.



**FIGURE 11.** *Arthuria tubuloreticulosa* sp. nov., holotype RMNH Por. 5547, a, habitus *in situ* at Ternate (photo N.J. de Voogd), b, preserved habitus (scale bar = 1 cm), c, surface view of skeleton (scale bar = 200  $\mu\text{m}$ ).



**FIGURE 12.** *Arthuria tubuloreticulosa* sp. nov., holotype RMNH Por. 5547, SEM images of spicules, a, triactines, b, tetractines.

#### *Arthuria tubuloreticulosa* sp. nov.

Figures 11a–c, 12a–b

**Material examined.** Holotype RMNH Por. 5547, Indonesia, Halmahera, Ternate, Sulamadaha Bay, 0.8661°N 127.3316°E, depth 5–15 m, SCUBA, coll. N.J. de Voogd, #TER.05/261009/1, Ternate-Halmahera Expedition, 26 October 2009.

**Description.** An orange flattened mass of short oscular tubes (Fig. 11a), connected at the substratum by a basal tubular network, growing on an encrusting octocoral (*Briareum*). The erect tubes maybe divided into one or two side tubes. The preserved specimen (Fig. 11b) is fragmented, but there are several larger pieces that show the short erect tubes forming the main basis of the specimen. Overall size estimated to be 5 x 3 cm, with small tubes about 2–4 mm in diameter. Color beige in preserved condition.

**Skeleton.** (Fig. 11c) The walls of the tubes are thin, approximately 15  $\mu\text{m}$  in thickness. The spicules are dominated by triactines. The choanoderm lines all internal surfaces.

**Spicules.** (Figs 12a–b) Triactines, tetractines.

Triactines (Fig. 12a), equiangular, predominantly equiaxial, but a fair number are slightly parasagittal, with the longer actines often slightly wobbled; most actines are cylindrical with abruptly pointed ends, but small triactines may have their actines conical, size of actines 63–112.1–138 x 4–5.3–6.5  $\mu\text{m}$ .

Tetractines (Fig. 12b), similar to triactines in size and shape, actines of basal triadiate system, 62–119.5–156 x 4–5.4–6  $\mu\text{m}$ ; apical actines 39–132 x 3.5–6.5  $\mu\text{m}$ .

**Ecology.** Shallow-water reef.

**Distribution.** Known only from the type locality, Ternate.

**Etymology.** The name reflects the combination of a network of tubes on the substratum and erect tubes protruding from it.

**Remarks.** The dominance of triactines over tetractines, and the normal-shaped apical actines of the tetractines makes this *Clathrina*-like species a likely member of the recently erected genus *Arthuria*. The genus has a few

Indo-Pacific species, but none of them seem to be close to our new species: South Australian *A. dubia* (Dendy, 1891) (as *Leucosolenia*) has much thicker actines (averaging 15–16 µm) and the tetractines are very rare (they were not mentioned by Dendy, but subsequently reported by Klautau & Valentine, 2003: 26). Red Sea *A. sueziana* Klautau & Valentine, 2003 has a different habitus and also much thicker actines. The above-described *A. tenuipilosa* possesses diactines.

Haeckel's (1872) description and figures of *Ascalitis darwinii* reminds rather strongly of the present species and at first we assumed that it could be conspecific. However, shapes and sizes of the tri- and tetractines presented by Haeckel consistently differ: actines are equiangular equiaxial, shorter (80–100 µm) but more robust and conical (10–12 µm thick) than those of our new species. *Clathrina darwinii* should be transferred to *Arthuria* (see below).

### Genus *Ernstia* Klautau, Azevedo, Cónedor-Luján, Rapp, Collins & Russo, 2013

Clathrinidae with asconoid aquiferous system possessing both triactines and tetractines in approximately equal proportions or tetractines more frequently. The apical actine of the tetractines is long and thin (after Klautau *et al.* 2013).

#### *Ernstia indonesiae* sp. nov.

Figures 13a–c, 14a–d, 15a–e

? *Clathrina* sp. Colin & Anderson, 1995: 59, photo 228.

**Material examined.** Holotype ZMA Por. 16659, Indonesia, SW Sulawesi, Spermonde Archipelago, Langkai, 5.019°S 119.063°E, depth 6 m, SCUBA, coll. B.W. Hoeksema, #LK-186, 14 June 1997.

Paratypes ZMA Por. 07934, Indonesia, SE Sulawesi, Tukang Besi Islands, southern reef of Karang Kaledupa, 5.9333°S 123.8°E, depth 2–6 m, snorkeling, coll. J.C. den Hartog, Indonesian-Dutch Snellius II Expedition stat. 016/II/26, 8 September 1984; ZMA Por. 09107, Indonesia, SE Sulawesi, SW Salayar, NW coast of Pulau Guang, 6.35°S 120.45°E, depth 0–2 m, snorkeling, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition stat. 152/Cave 2/02, 28 September 1984; ZMA Por. 09486, Indonesia, SE Sulawesi, SW Salayar, NW coast of Pulau Guang, 6.35°S, 120.45°E, depth 2–4 m, SCUBA, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition stat. 152/Cave 1/06A, 28 September 1984; ZMA Por. 15509c, Indonesia, SE Sulawesi, SW Salayar, NW coast of Pulau Guang, 6.35°S 120.45°E, depth 3–4 m, SCUBA, H.A. ten Hove, Indonesian-Dutch Snellius II Expedition stat. 152/Cave 1/A3, 28 September 1984.

**Description.** Rounded mass of interwoven tubes (Fig. 13a), individual tubes 1–3 mm in diameter. In the one *in situ* photo several oscules at the end of water-collecting tubes are apparent but these are not visible in the preserved material (Figs 13b, 15a). Live color pinkish white, in alcohol pale orange. Overall size of specimens up to 5 x 4.5 x 2 cm.

**Skeleton.** (Figs 13c, 15b) Walls of tubes formed by a one or two layers of triactines and tetractines arranged without apparent order.

**Spicules.** (Figs 14a–d, 15c–e) Triactines, tetractines, diactines.

Triactines (Figs 14a, 15d), equiangular equiaxial, in a large size range, but no clear division in larger and smaller categories, 90–206.7–269 x 10–17.3–22 µm

Tetractines (Figs 14b–d, 15c), less diverse in size, but divisible into those with regular equiangular equiaxial basal radiate systems, actines 85–214.2–249 x 12–17.8–22 µm, apical actines long and sometimes wavy, 57–124.1–204 x 6–10.7–14 µm; and parasagittal tetractines with unpaired actines, straight, 198–210 x 12–14 µm, paired actines usually curved or wavy, 137–159 x 12–14 µm, apical actines 50–60 x 10 µm.

Diactines (Fig. 15e), uncommon, curved, usually with one end thicker and mucronate, (Fig. 15e1) the other end tapering gradually into a thin straight or curved ending, usually broken into fragments, 200–345–600 x 2–4.6–9 µm.

**Ecology.** Reefs, shallow depth.

**Distribution.** Indonesia.

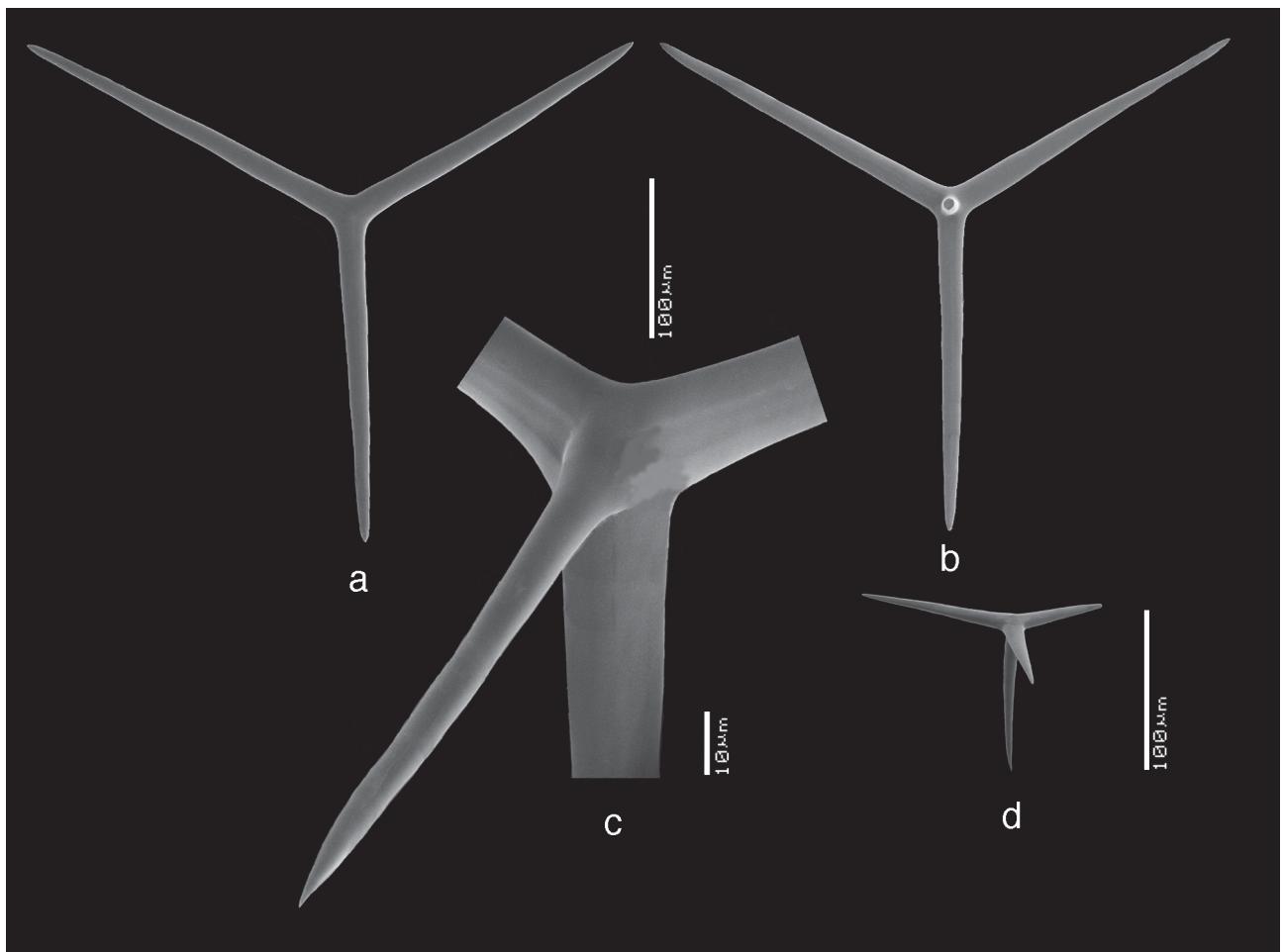
**Etymology.** Named after the country Indonesia.



**FIGURE 13.** *Ernstia indonesiae* sp. nov., holotype ZMA Por. 16659 from Langkai, SW Sulawesi, a, habitus *in situ* (photo B.W. Hoeksema), b, preserved holotype (scale bar = 1 cm), c, overview of skeleton (scale bar = 500 µm).

**Remarks.** In the key of Klautau & Valentine (2003), this material keys out as the Japanese *Clathrina sagamiana* (Hôzawa, 1929) (p. 281, pl. XIII figs 1–2, textfig. 1), assigned to *Ernstia* in Klautau *et al.* 2013. There are considerable differences between *E. sagamiana* and our specimens: the triactines of the former are smaller, the apical actines of the tetractines are longer, and the diactines are also longer. Parasagittal tetractines were not mentioned by Hôzawa. A further problem is that our material is all from shallow-water reefs and reef caves, whereas the Japanese material was collected at 171 m depth.

It is likely that our specimens are conspecific with *Clathrina* sp. sensu Colin & Arneson (1996: photo 228) from Papua New Guinea.



**FIGURE 14.** *Ernstia indonesiae* sp. nov., holotype ZMA Por. 16659, SEM images of the spicules, a, triactine, b, tetractine, c, detail of apical actine of tetractine, d, small tetractine.

***Ernstia chrysops* sp. nov.**

Figures 16a–c, 17a–e

?*Clathrina* sp. Gosliner et al. 1996: 15, photo 1.

**Material examined.** Holotype RMNH Por. 1773, Indonesia, North Sulawesi, Manddin, between Bunaken and Manado Tua, 1.612°N 124.7322°E, depth 20 m, SCUBA, coll. N.J. de Voogd, #MD04/180502/092, 18 May 2002.

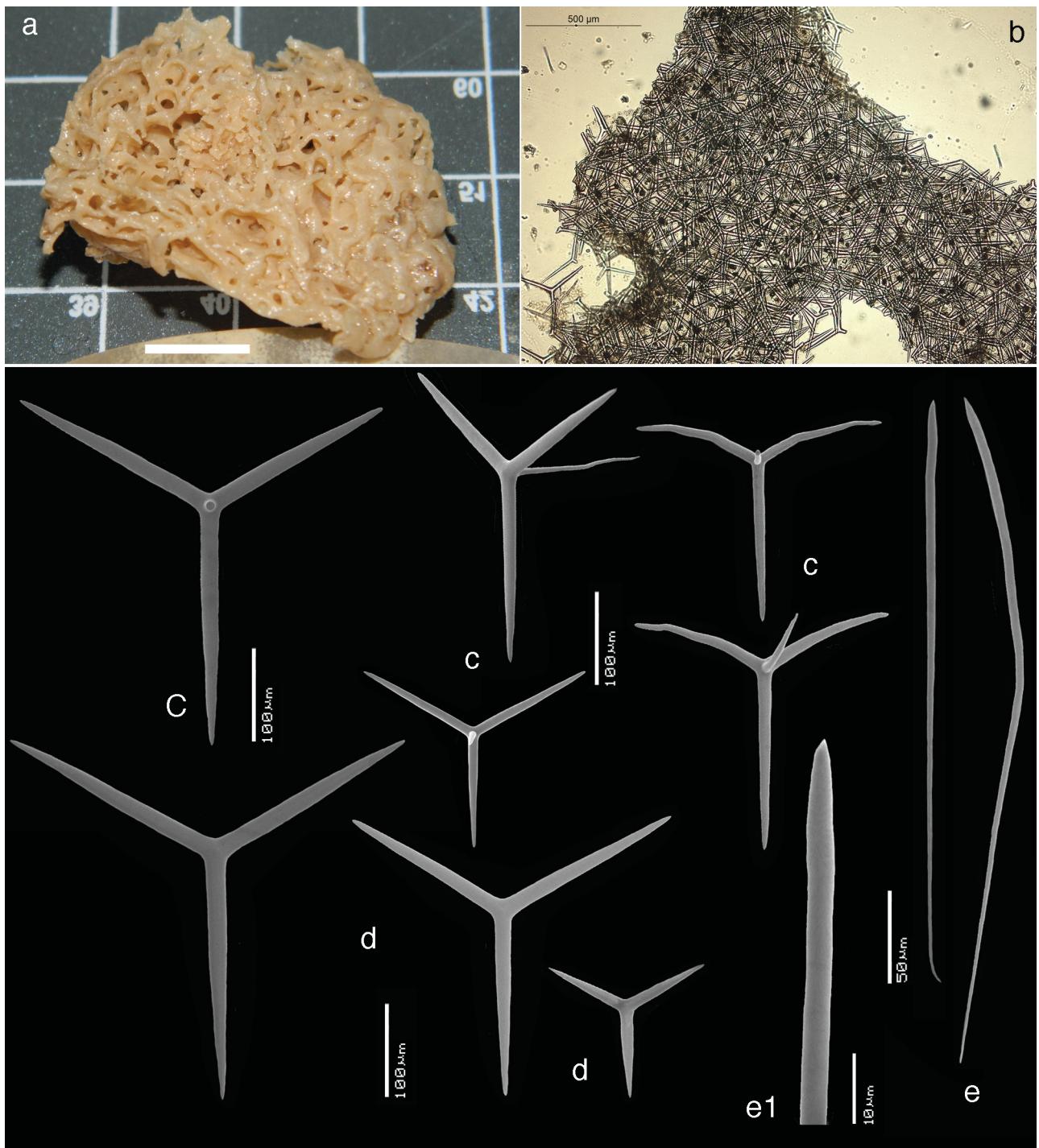
**Description.** Mass of loosely anastomosed golden yellow tubes (Figs 16a–c) with few but prominent water-collecting tubes (Figs 16a–b) some of which protrude 1 cm or more above the cormus. Size of cormus up to 5 x 6 x 1 cm. Individual tubes up to 5 mm in diameter. Oscules about as wide as the tubes (Fig. 16c), not flaring. In preserved condition (Fig. 17a) oscules are not clearly visible and the specimens get a pale yellowish orange color and have a ‘glassy’ outlook. Consistency soft.

**Skeleton.** (Fig. 17b) The walls of the tubes have a thin layer of triactines and tetractines, in equal proportion, with apical actines of the larger tetractines projecting into the lumen of the tubes.

**Spicules.** (Figs 17c–e) Triactines, tetractines; a few small diactines were found.

Triactines (Fig. 17c) equiangular equiaxial, in a large size range, possibly divisible in smaller and larger, overall actine sizes 75–210.3–330 x 9–13.8–18 μm (smaller (Fig. 17c1): 75–213 μm, larger (Fig. 17c): 255–330 μm); occasionally a triactine occurs with one of the actines angularly bent.

Tetractines (Fig. 17d), regular, on average larger than the triactines, likewise possibly divisible in smaller and larger spicules, overall the upper sizes somewhat larger than the triactines, with actines of the basal triradiate system 186–362.4–661 x 14–25.5–48 μm (smaller: Fig. 17d1): 186–276 μm, larger (Fig. 17d): 300–661 μm), apical actines straight or more often curved (Fig. 17e), 18–45.9–122 x 4–10.1–18 μm.



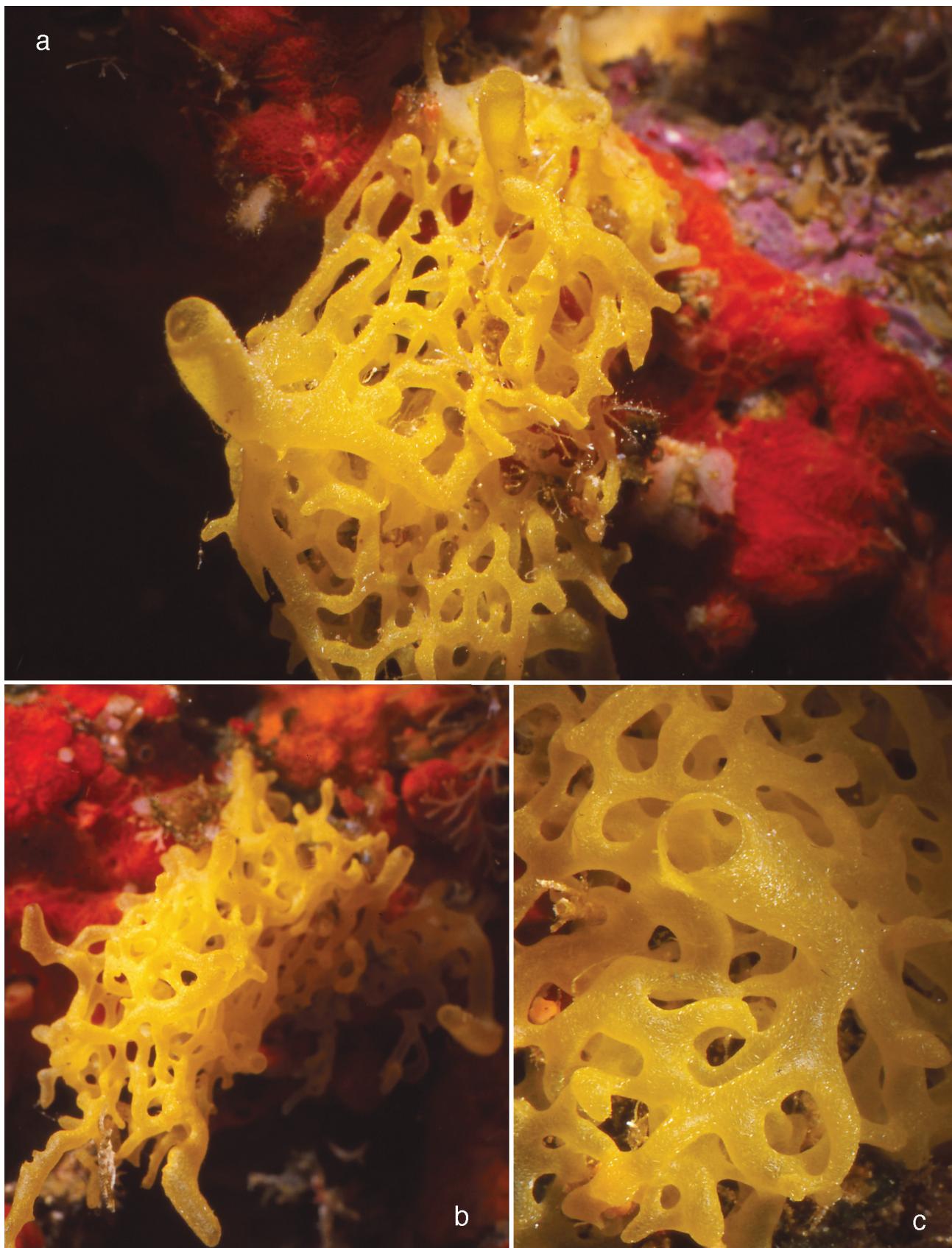
**FIGURE 15.** *Ernstia indonesiae* sp.nov., paratype ZMA Por. 07934 from Karang Kaledupa, SE Sulawesi, a, preserved habitus (scale bar = 1 cm), b, overview of skeleton (scale bar = 1 mm), c–e, SEM images of the spicules, c, various tetractines, d, various triactines, e, diactines, e1, detail of apex.

**Ecology.** Deeper part of the reef.

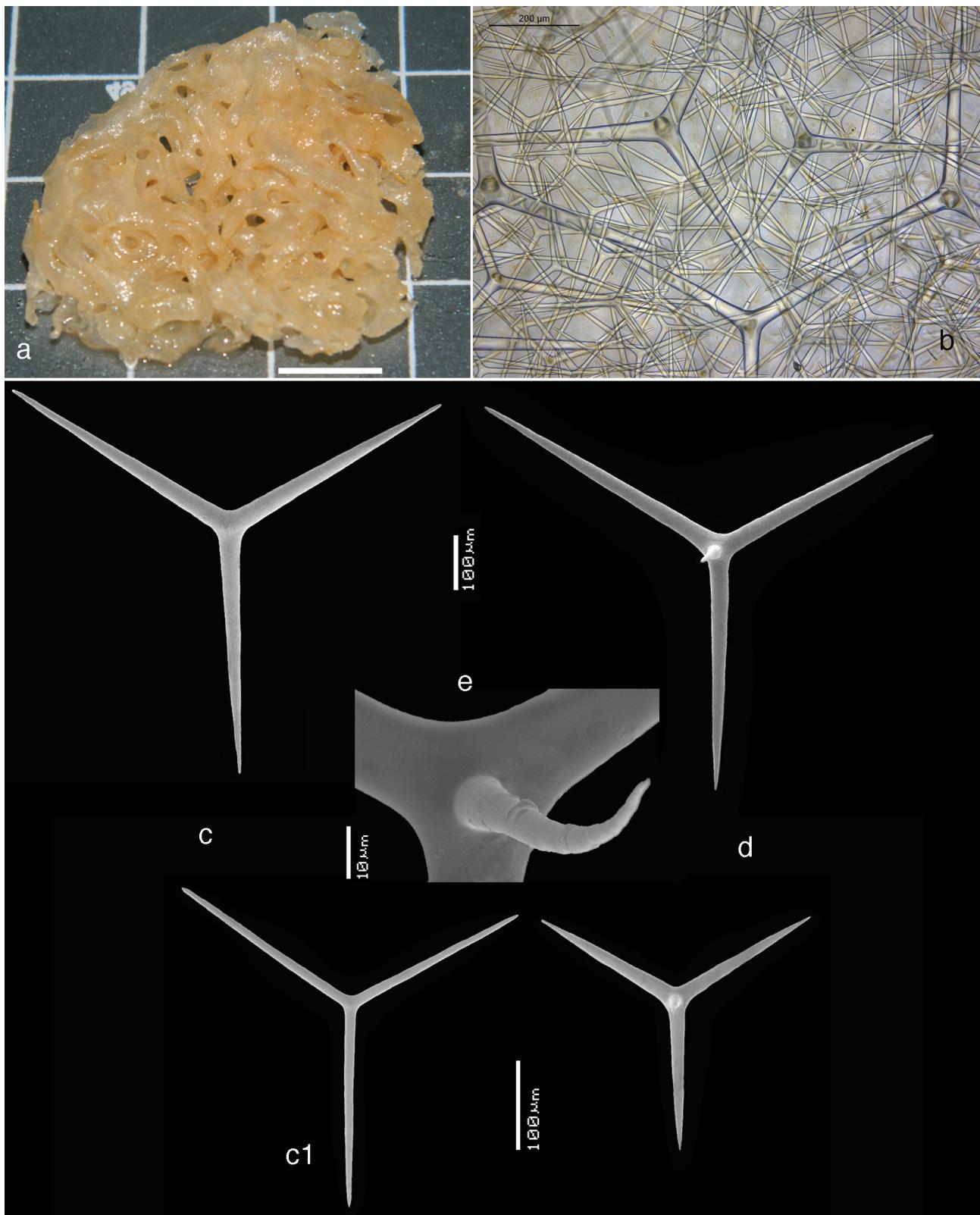
**Distribution.** Indonesia; probably Philippines.

**Etymology.** The word chrysops (Gr.) means shining like gold, referring to the color.

**Remarks.** This species is close to *Ernstia indonesiae* sp.nov. in shape, but the color and the large size range in smaller and larger spicules with upper size of the tetractines to reach 660 µm, the relatively wider tubes, which have a ‘glassy’ outlook (preserved material), and the absence of diactines together appear solid indications of distinctness. It is likely that the Philippine *Clathrina* sp. (photo 1) of Gosliner *et al.* 1996 belongs to the present species.



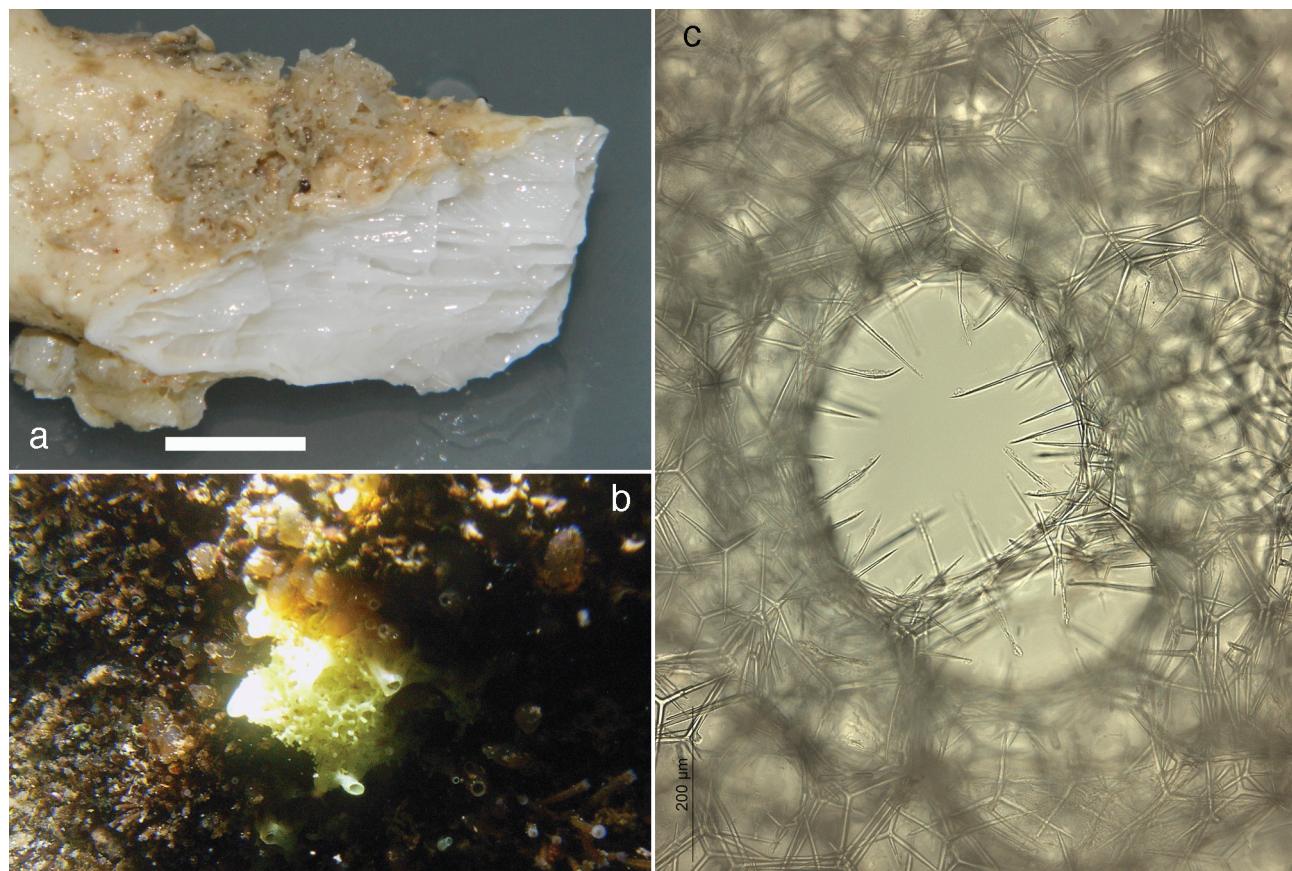
**FIGURE 16.** *Ernstia chrysops* sp. nov., holotype RMNH 1773 (photos N.J. de Voogd), a, *in situ* at N Sulawesi, b, ditto, c, detail of cormus and oscule.



**FIGURE 17.** *Ernstia chrysops* sp. nov., holotype RMNH Por. 1773, a, preserved holotype from N Sulawesi (scale bar = 1 cm), b, surface skeleton showing large diversity in size of tetractines (scale bar = 200 µm), c–e, SEM images of spicules, c, large triactine, c1, small triactine, d, large tetractine, e, detail of large tetractine,.

Our collection also contained a flimsy fragment from deep water (240 m) off the coast of Sumba (ZMA Por. 09219, coll. Indonesian-Dutch Snellius II Expedition stat. 60), resembling in skeletal and spicular characters the present new species: tetractines with basal triradiate system having actines up to 350 x 12 µm and strongly

upcurved apical actines of approximately 100 µm, triactines on average smaller than the tetractines. In view of the depth and the tiny size we hesitatingly assign this specimen to the present species.



**FIGURE 18.** *Ernstia klautauae* sp.nov., holotype ZMA Por. 08390 from Komodo, a, preserved habitus encrusting a dead coral (scale bar = 1 cm), b, paratype RMNH Por. 9341, habitus *in situ* (Photo L. E. Becking), c, detail of cormus of holotype showing apical actines of tetractines protruding in the atrial lumen (scale bar = 200 µm).

#### *Ernstia klautauae* sp. nov.

Figs 18a–c, 19a–c

*Clathrina* sp.nov. 13 ‘Indonesia’; Klautau *et al.* 2013: 5, table 2.

**Material examined.** Holotype ZMA Por. 08390, Indonesia, Nusa Tenggara, E of Komodo, Selat Linta, 8.5833°S 119.57°E, depth 4–11 m, SCUBA, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition stat. 079/III/15, 18 September 1984.

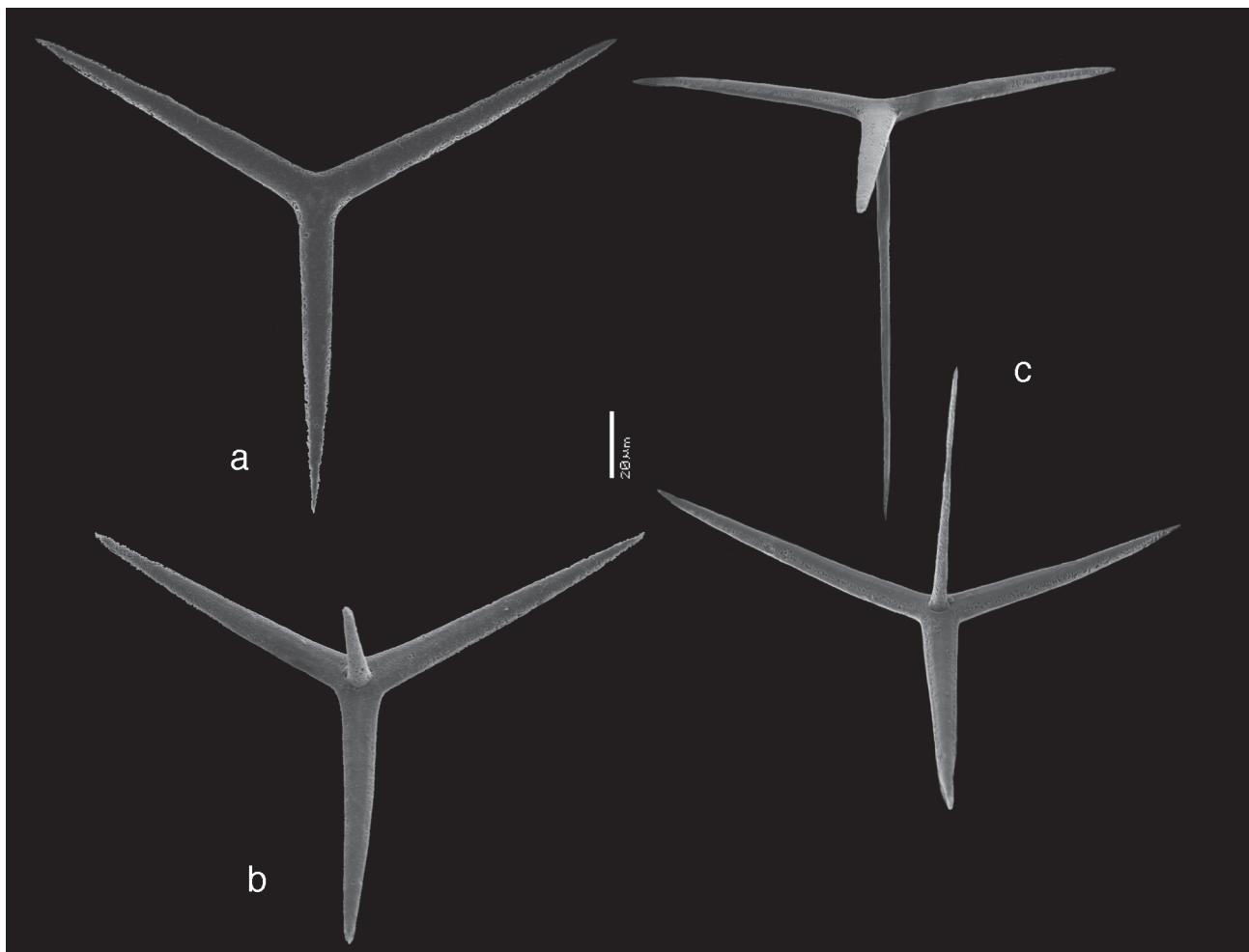
Paratype RMNH Por. 9341, Indonesia, Papua, Misool, Raja Ampat, 1.984°S 130.5164°E, depth 0–2 m, snorkeling, coll. L.E. Becking, # LE 652/MIS01/RIMG0679, 20 May 2011.

**Description.** Tightly anastomosed mass of thin tubes (Figs 18a–b). Tubes 1–2 mm in diameter. The *in situ* photo (Fig. 18b) shows two water-collecting tubes with terminal oscules elevated above the cormus. Overall size 2 x 1 cm. Color (pale) yellow. Consistency soft.

**Skeleton.** Tetractines are dominating in the holotype, while tri- and tetractines are about equally present in the paratype. Apical actines of tetractines protrude far and characteristically into the lumen between the tubes (Fig. 18c).

**Spicules.** (Figs 19a–c) Triactines, tetractines.

Triactines (Fig. 19a), with conical actines, in a wide range of thicknesses, overall size 93–108.4–125 x 6–8.8–11 µm.



**FIGURE 19.** *Ernstia klautauae* sp.nov., holotype ZMA Por. 08390, SEM images of spicules, a, triactine, b, normal tetractine, c, tetractines with long thin apical actines.

Tetractines, with conical actines of basal triadiate system  $60\text{--}106.4\text{--}126 \times 6\text{--}7.9\text{--}10 \mu\text{m}$ , apical actines variable,  $32\text{--}90.4\text{--}165 \times 4\text{--}5.4\text{--}7 \mu\text{m}$ . On the basis of the apical actines these spicules are possibly divisible in two types, with relatively thick straight apical actines (Fig. 19b), and with thin sharply pointed apical actines (Fig. 19c), straight or slightly curved.

**Ecology.** Shallow coral reefs, marine lakes.

**Distribution.** Indonesia (Komodo, Papua).

**Etymology.** Named after Dr Michelle Klautau (Universidade Federal do Rio de Janeiro, Brazil) for her pioneering efforts in calcarean taxonomy and phylogeny.

**Remarks.** The new species is assigned to *Ernstia*, because of proportion of tri- and tetractines (equal or more tetractines) and the sharp thin apical actines of the tetractines. DNA of the present holotype material was extracted by Klautau *et al.* (2013: table 2) and its sequence classified closely with *Ernstia tetractina* (Klautau & Borojevic, 2001) (Klautau *et al.* 2013: Fig. 1).

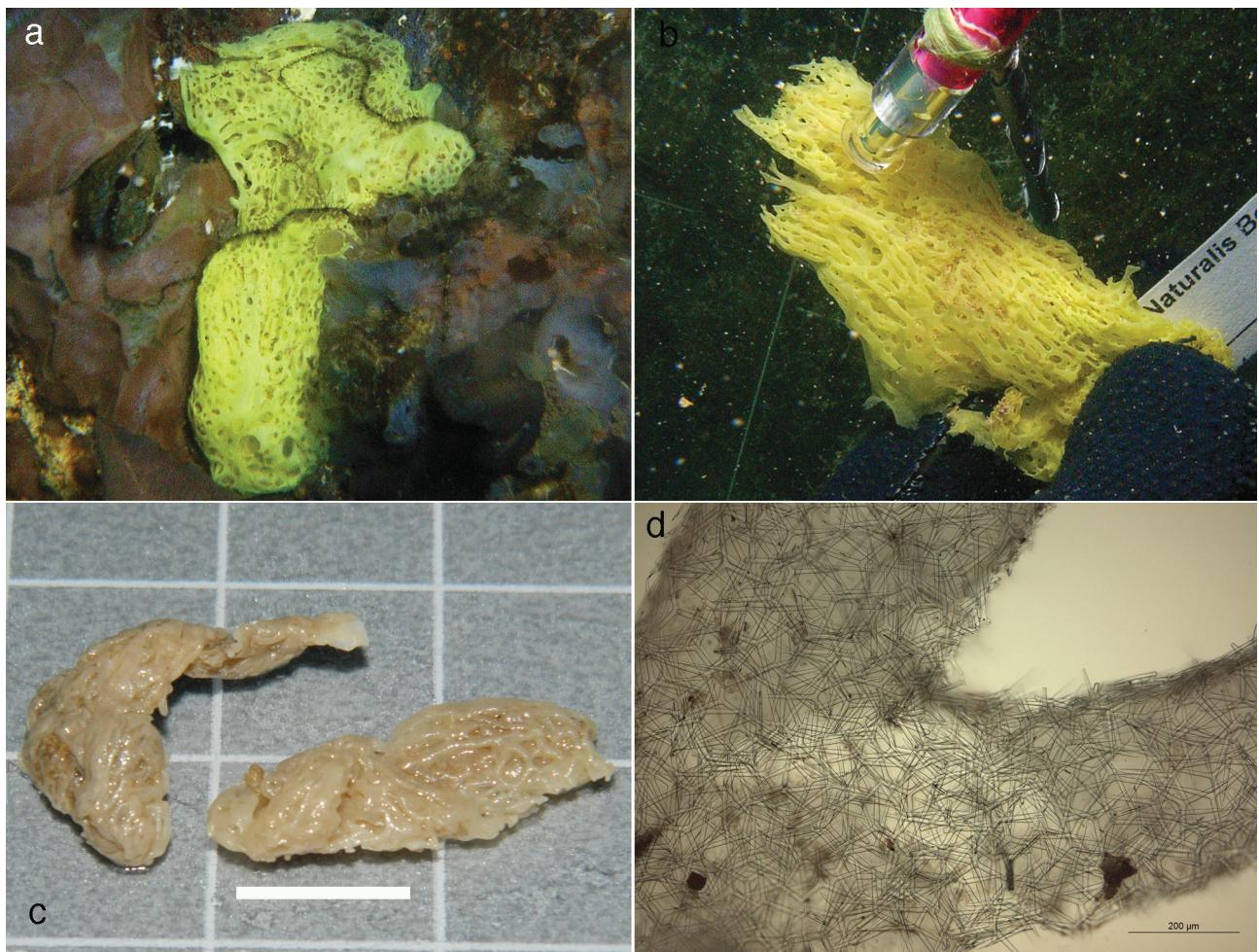
The habitus reminds of Norwegian *Clathrina cibrata* Rapp, Valentine & Klautau, 2001 but that species has triactines only.

#### *Ernstia naturalis* sp. nov.

Figures 20a–d, 21a–d

*Leucosolenia coriacea*; Burton, 1930: 2, in part (not Montagu, 1814).

?*Clathrina* sp.; Erhardt & Baensch, 1998: 20.



**FIGURE 20.** *Ernstia naturalis* sp. nov., a, holotype RMNH Por. 9342 *in situ* (photo L.E Becking), b, paratype RMNH Por. 5001 just after collecting (still under water) (photo L. E Becking, c, paratype RMNH Por. 5001, preserved fragments (scale bar = 1 cm), d, paratype RMNH Por. 5001, overview of tubar skeleton (scale bar = 200 µm).

**Material examined.** Holotype RMNH Por. 9342, Indonesia, Papua, Misool, Raja Ampat, Panah Panah, marine lake, 1.9386°S 130.3744°E, depth 0–2 m, snorkeling, coll. LE Becking, # LE745/MIS1/RIMG0679, 28 May 2011.

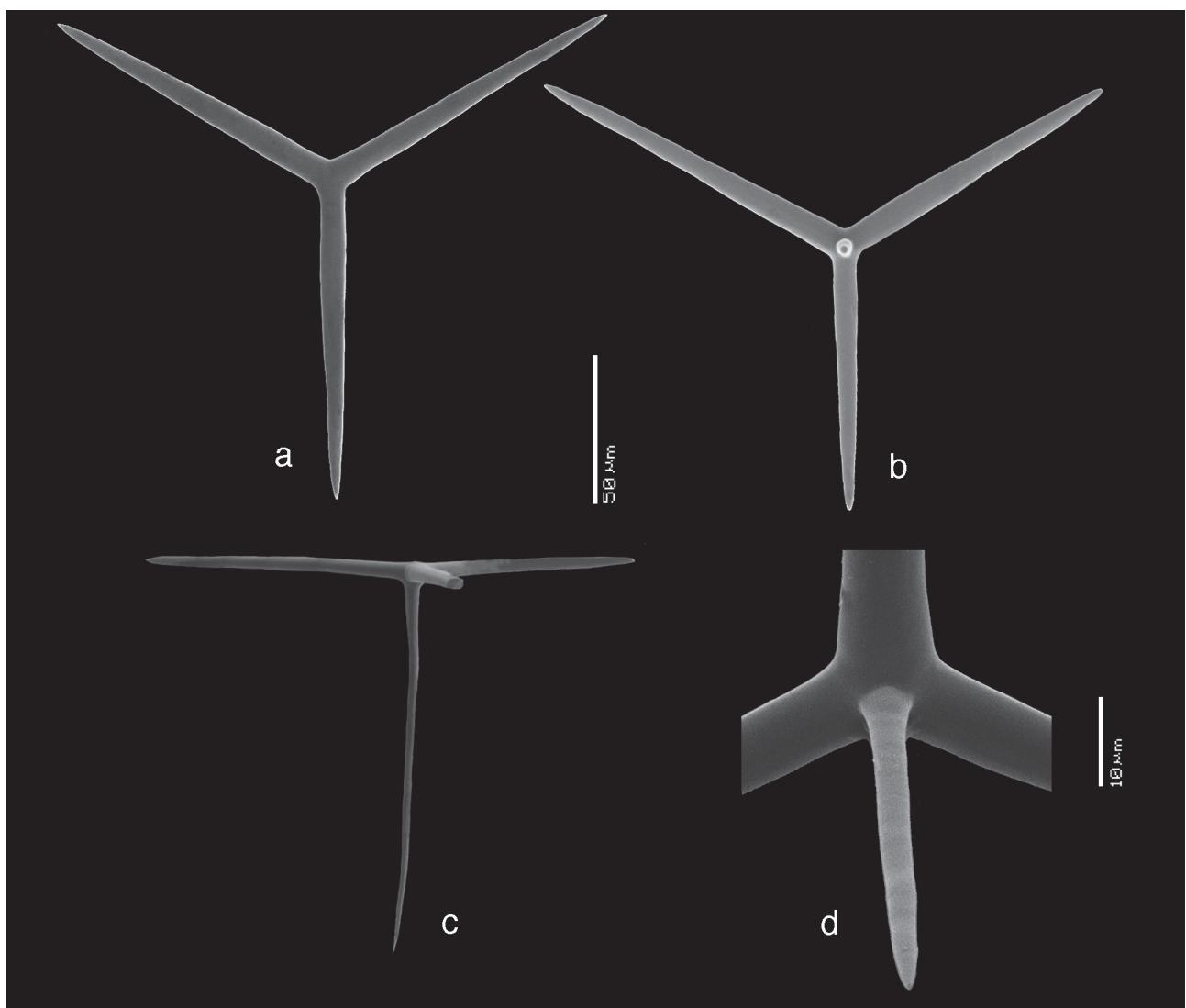
Paratypes ZMA Por. 00136, Indonesia, Nusa Tenggara, Sumbawa, Saleh Bay, anchorage E of Dangar Besar, 8.4254°S 117.7296°E, depth 0–36 m, trawl, coll. Siboga Expedition stat. 313, 14 February 1900; ZMA Por. 00183b, Indonesia, Papua, 1.7083°S 130.7916°E, depth 23 m, trawl, coll. Siboga Expedition stat. 164, 20 August 1899; RMNH 5000 Indonesia, East Kalimantan Province, Berau Region, Kakaban island, Kakaban marine lake, 2.4133°N 118.5078°E, depth 0–2 m, snorkeling, coll. L.E. Becking #KKB/LE 536, 21/05/2009; RMNH 5001, Indonesia, East Kalimantan Province, Berau Region, Kakaban island, Kakaban marine lake, 2.4133°N 118.5078°E, depth 0–2 m, snorkeling, coll. L.E. Becking, #KKB/LE 537, 21 May 2009; RMNH Por. 9343, Papua New Guinea, E of Wongat Island, Stat. PR53, 5.1353°S, 145.8228°E, depth 20 m, SCUBA, coll. L.E. Becking , #LE305/PB174146, 17 November 2012.

**Description.** (Figs 20a–c) Large, massive cormi made up of closely anastomosed but individually distinct tubes. Overall size up to 4–5 cm, tubes 0.3–1.5 mm in diameter. No distinct water collecting tubes, but several large flush oscula are visible in the *in situ* photo of the holotype (Fig. 20a). Color in life, bright yellow (Fig. 20b), orange-yellow or brownish yellow. Beige in preserved condition (Fig. 20c). Consistency soft.

**Skeleton.** (Fig. 20d) Layers of tri- and tetractines rather dense and thick. Triactines and tetractines in approximately similar proportion (most specimens) or with more triactines (ZMA 00183b).

**Spicules.** (Figs 21a–d) Triactines and tetractines.

Triactines (Fig. 21a), with conical actines, 76–107.5–168 x 7.5–9.1–18 µm.



**FIGURE 21.** *Ernstia naturalis* sp. nov., a, holotype RMNH Por. 9342, images of the spicules, a, triactine, b–c, tetractines, d, detail of apical actine of tetractine.

Tetractines (Figs 21b–d), with actines of basal triaradiate system, 84–109.6–153 x 6–8.7–16 µm, apical actines, thin and sharp (Figs 21c–d), 29–82.4–147 x 3–5.3–8 µm.

**Ecology.** In marine lakes and on reefs, from the surface down to 36 m.

**Distribution.** Indonesia, Papua New Guinea; possibly Palau (Erhardt & Baensch, 1998).

**Etymology.** Named after our host institute, Naturalis Biodiversity Center, Leiden.

**Remarks.** Among the *Ernstia* species reported from the Indo-West Pacific, *Ernstia adusta* (Wörheide & Hooper, 1999 as *Clathrina*) is the most similar in shape and spicule sizes. However, that species is white, whereas all our specimens of which color information was noted are yellow or yellow-brown in life.

Several specimens were found to contain isolated broken pieces of diactines, but these were insufficiently common to consider them proper to the sponge.

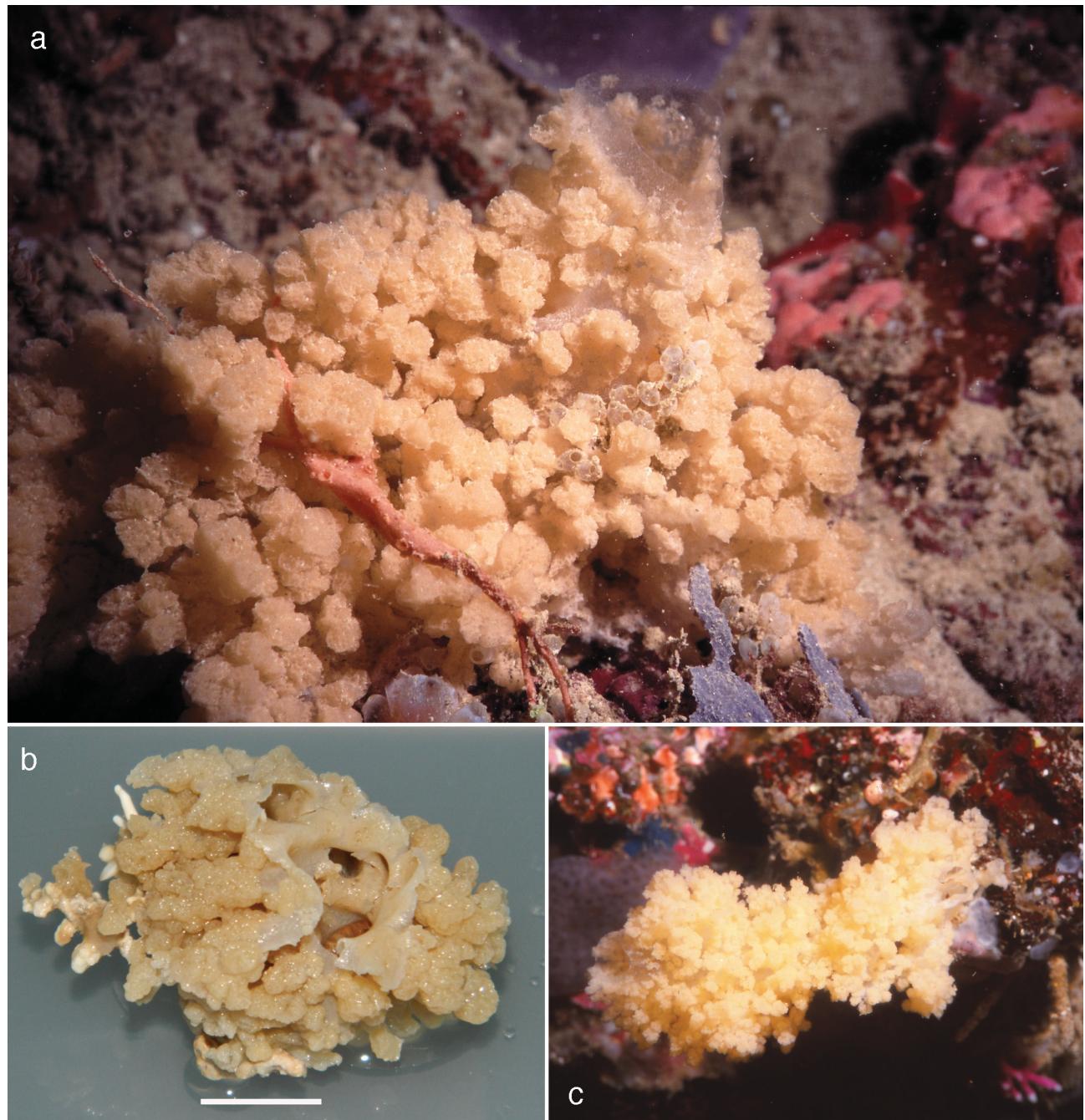
#### Family Levinellidae Borojevic & Boury-Esnault, 1986

#### Genus *Burtonulla* Borojevic & Boury-Esnault, 1986

**Burtonulla sibogae Borojevic & Boury-Esnault, 1986**

Figures 22a–c, 23a–f

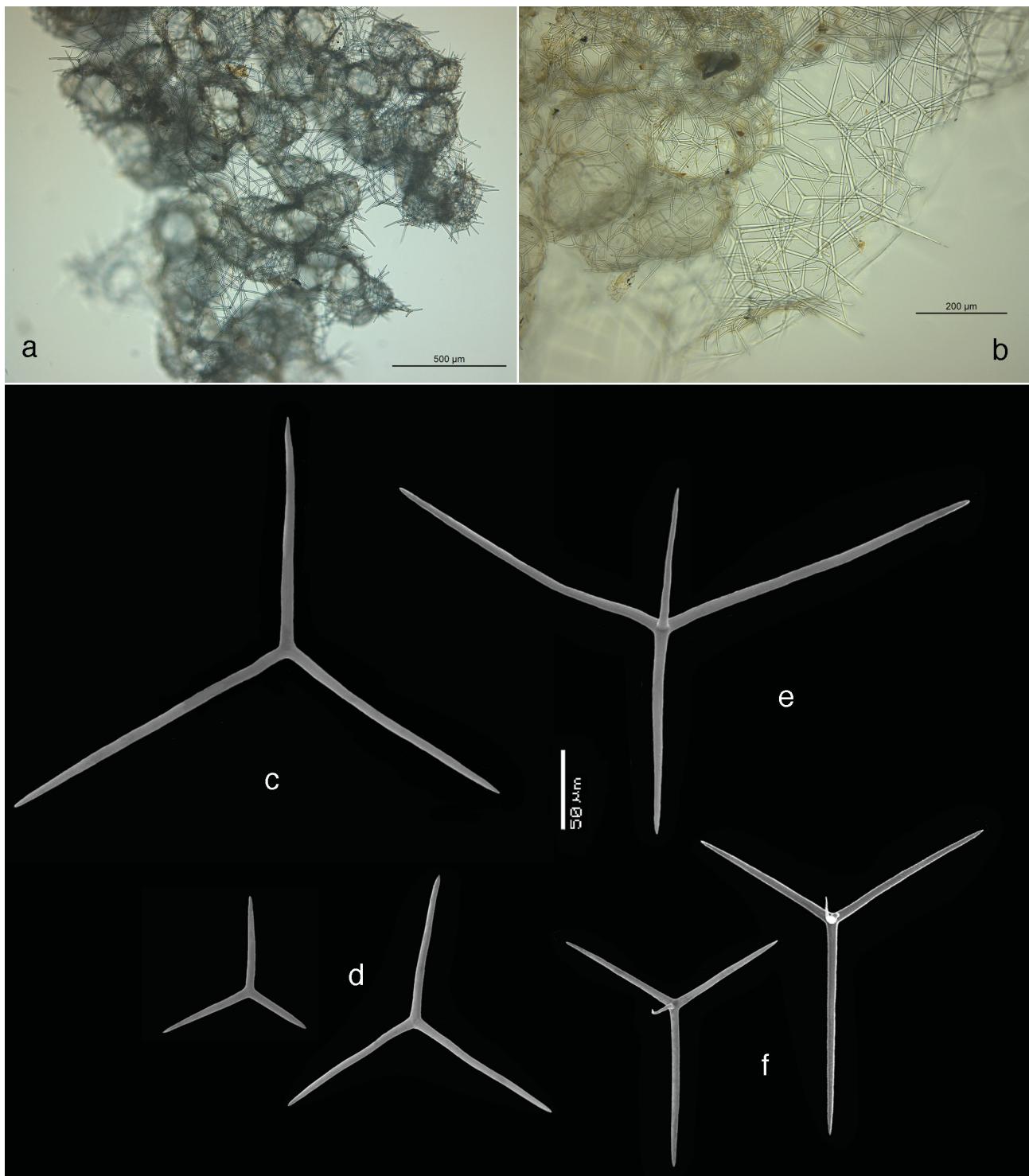
*Dendya prolifera*; Burton, 1930: 2, figs 1–2; Colin & Arneson, 1995: 61, photo 234 (not: Dendya, 1913: 6)  
*Burtonulla sibogae* Borojevic & Boury-Esnault, 1986: 447, text-fig. 2, pl. 2 figs A–D.



**FIGURE 22.** *Burtonulla sibogae* Borojevic & Boury-Esnault (1986), a, *in situ* image of RMNH Por. 1653 from the Palau Islands (photo N.J. de Voogd), b, preserved holotype ZMA Por. 00146 (scale bar = 1 cm), c, *in situ* image of RMNH 1821 from Maratua Island (photo B.W. Hoeksema).

**Material examined.** Holotype ZMA Por. 00146 (Fig. 22b), Indonesia, Lesser Sunda Islands, E coast of Roti Island, Papela Bay, 10.63°S 123.42°E, depth 22 m, trawl, Siboga Expedition stat. 301, 30 January 1900.

Paratype ZMA Por. 00145, Indonesia, Irian Jaya, 1.71°S 130.79°E, depth 32 m, dredge, coll. Siboga Expedition stat. 164, 20 August 1899.



**FIGURE 23.** *Burtonella sibogae* Borojevic & Boury-Esnault (1986), a, holotype ZMA Por. 00146, overview of skeleton (scale bar= 500  $\mu\text{m}$ ), b, detail of skeleton of diverticula and tube wall (scale bar = 200  $\mu\text{m}$ ), c–f , SEM images of spicules, c, large triactine of the tube wall, d, small triactines of the diverticula, e, large tetractine of the tube wall, f, small tetractines of the diverticula.

Additional specimens. RMNH Por. 1653, Palao Islands, channel between Koror and Babedaob, SW side near Telblong Island, 7.34°N 134.517°E, depth 12 m, SCUBA, coll. N.J. de Voogd, #KOR04/130505/029, 13 May 2005; RMNH Por. 1821, Indonesia, Kalimantan, Berau region, Maratua, depth not recorded, barrier reef, coll. L. De Senerpont Domis, #BER28/171003/206; RMNH Por. 1824, Indonesia, Bali, Tulamben area, Temple Bay E, 8.27°S 115.6°E, depth 20 m, SCUBA, coll. N.J. de Voogd, #BAL24/140401/192, 14 April 2001; RMNH 1922,

Indonesia, Nusa Tenggara, Bali, N side of Nusa Pandida, off Desa Byuk, 8.6736°S 115.5436°E, depth 15–20 m, deep reef slope with patches of sand, SCUBA, coll. N.J. de Voogd, #BAL34/NV/210401/263, 21 April 2001; RMNH Por. 1924, Indonesia, North Sulawesi, Manddin, between Bunaken and Manado Tua, depth 18 m, SCUBA, coll. N.J. de Voogd, #MD04/190502/117, 19 May 2002; RMNH 2158, Indonesia, Sulawesi, Spermonde Archipelago, Kundingareng Keke, 5.642°S 119.74°E, depth 10–15 m, SCUBA, coll. N.J. de Voogd, #UP/KK/180500/054, 18 May 2000; RMNH 9195, Indonesia, Halmahera, Tidore Dea Taha, 0.7528°N 127.392°E, depth 10–15 m, SCUBA, coll. N.J. de Voogd, #TER07/281009/, Ternate-Halmahera Expedition 2009, 28 October 2009; RMNH Por. 9344 Indonesia, Papua, Raja Ampat, Pulu Wai East, reef, 0.6999°S 130.6666, depth 10–20 m, SCUBA, coll. L.E. Becking, #RAJ61/LE222/245, Naturalis-LIPI 2007 Expedition, 11 December 2007; RMNH Por. 9345, Indonesia, Papua, Raja Ampat, Pulu Wai East, reef, 0.6999°S 130.6666, depth 10–20 m, SCUBA, coll. L.E. Becking, #RAJ61/LE233, Naturalis-LIPI 2007 Expedition, 11 December 2007.

**Description** (Figs 22a–c) Very characteristic yellow or pale light brown masses of small rounded globules hiding for the most part a central tube, which usually protrudes slightly at the top. Basically, the cormus consist of a single tube, ending in a small oscule with slightly raised rims, with side outgrowths (diverticulae or side-canals) taking the form of clusters of globules reminding of the alveolae of human lungs. We propose ‘alveolae’ as the term for these globules. Inbetween the clusters of these alveolae the walls of the tube and its diverticulae are here and there visible as a smooth membrane. Size of individuals may be up to 8 x 5 x 5 cm. Consistency soft.

**Histology.** Choanocytes are confined to the inner surfaces of the alveolar outgrowths, absent from the walls of the tube (see extensive description of Borojevic & Boury-Enault, 1986).

**Skeleton.** (Figs 23a–b) The alveolae possess a skeleton consisting of a single layer of *small* equiangular and equiaxial triactines and tetractines. The atrial wall possesses a single layer of *large* equiangular and sagittal triactines and tetractines, the latter dominating.

**Spicules.** (Figs 23c–f) Large and small triactines and tetractines.

Large triactines (Fig. 23c), thin, cylindrical, slightly inequiaxial, but not truly sagittal, actines 186–226.4–306 x 7–7.8–9 µm

Large tetractines (Figs. 23e), thin, cylindrical, similarly equiaxial, except for apical actines, actines of the basal triradiate system 192–270.3–390 x 6–7.4–10 µm, apical actines 84–330 µm x 4–6 µm.

Small triactines (Figs. 23d), usually slightly inequiaxial, 30–82.6–138 x 3.5–5.4–6.5 µm.

Small tetractines (Figs 23f), actines of the basal triradiate system 81–103.2–148 x 4–5.6–7 µm, apical actines 27–51.9–84 x 3–3.7–5 µm.

**Ecology.** Deeper parts of the reef.

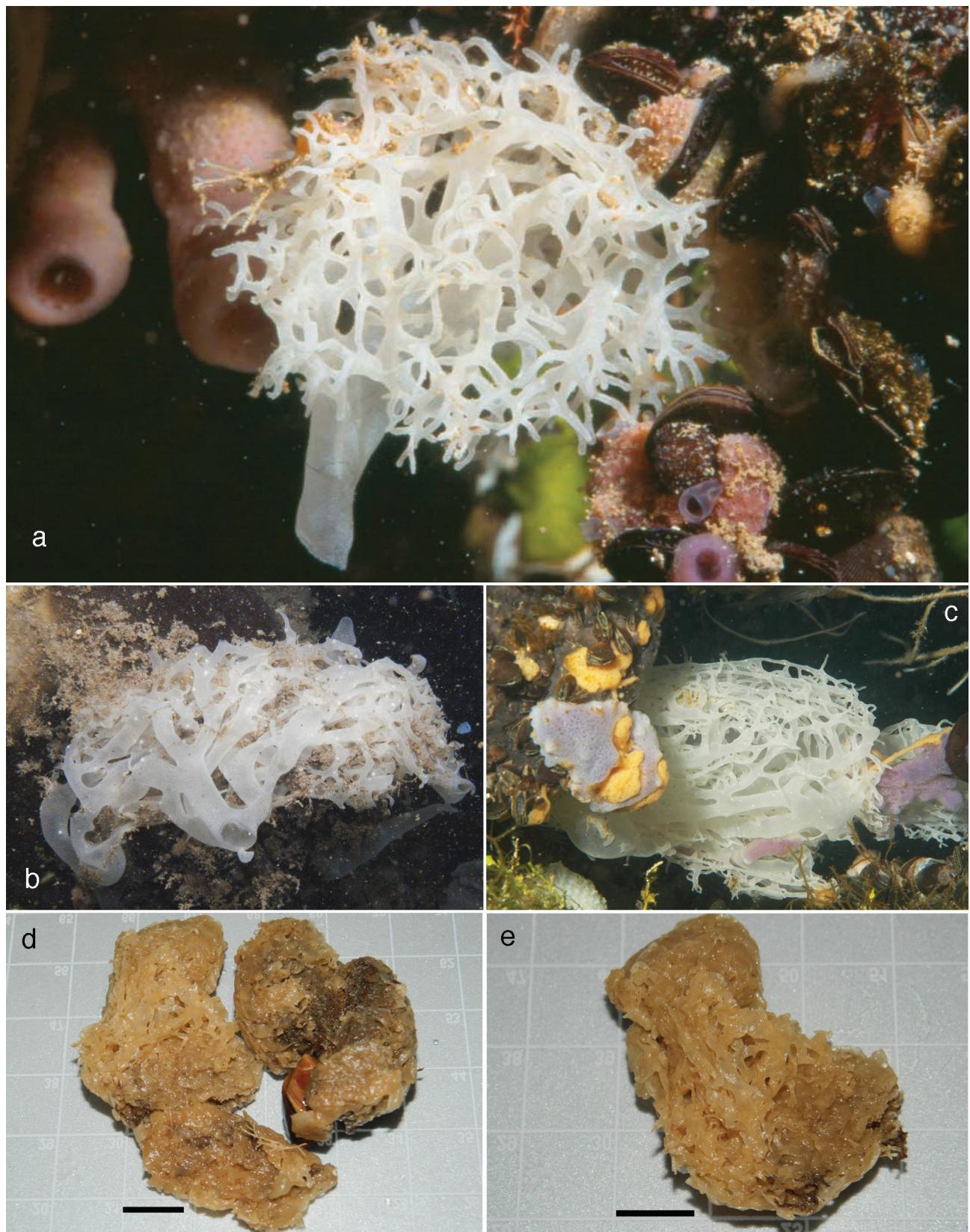
**Distribution.** Indonesia, Palau.

**Remarks.** Burton (1930) in his work on the Calcarea of the Siboga Expedition assigned this species to *Dendya prolifera* Dendy, 1913 (now *Levinella prolifera*), but this is clearly a different species with less prominent alveolar diverticulae, and the choanocytes distributed all over the inner atrial surface. The present species was described by Borojevic & Boury-Esnault (1986) on the basis of the misidentified Siboga specimens. It appears to be rather common in Indonesia and surrounding regions, as it is pictured in several underwater guides.

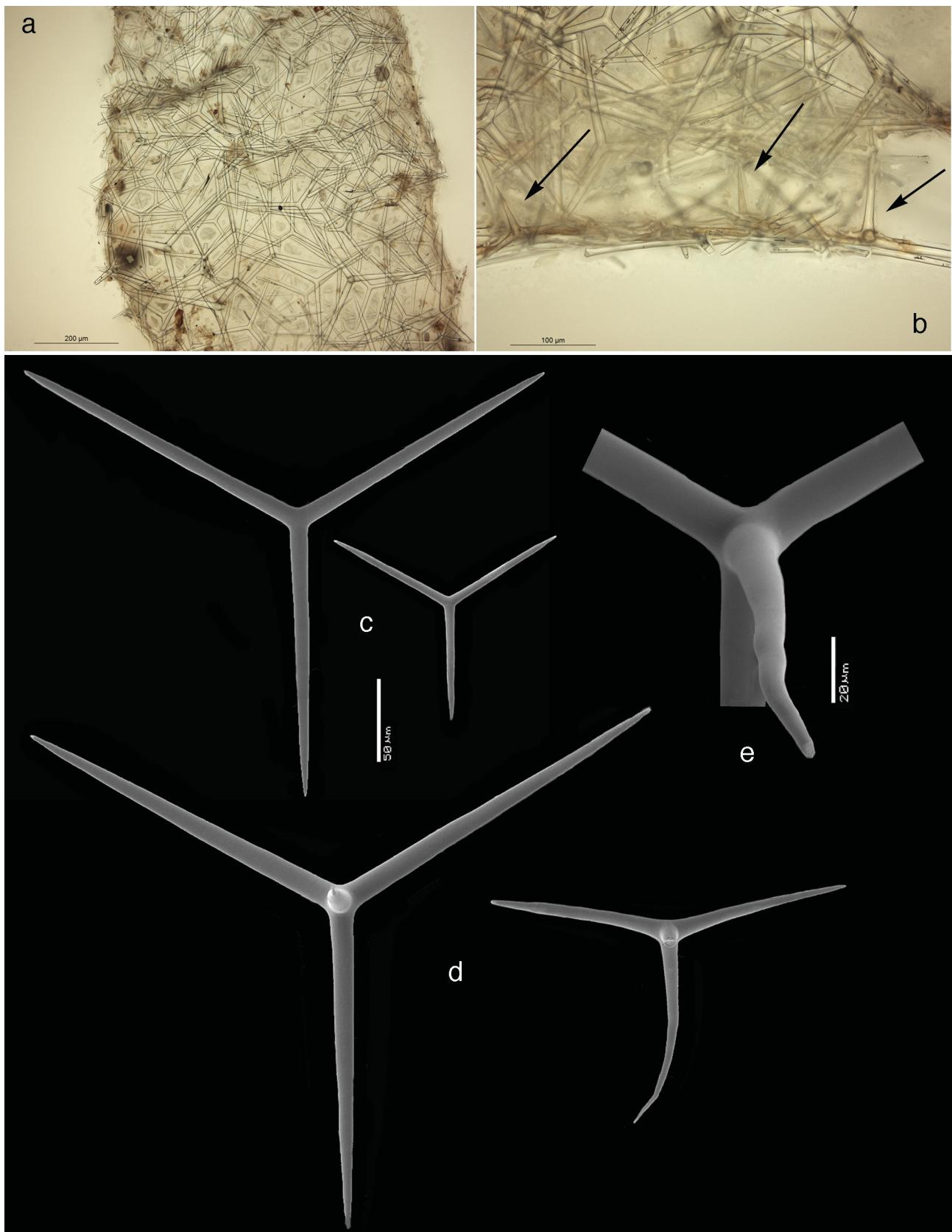
## Family Leucaltidae Dendy & Row, 1913

### Genus *Ascandra* Haeckel, 1872

**Remarks.** The genus is assigned to Leucaltidae in the Systema Porifera, but it resembles loosely built Clathrinidae, with the added peculiarity that the continuous choanoderm is folded over the long apical actines of the tetractines. The latter occur usually in larger proportions than the triactines. Skeleton not differentiated in cortical and atrial skeleton. In the molecular sequence analysis of Klautau *et al.* (2013) members of the genus appeared to end up with the Clathrinidae clade.



**FIGURE 24.** *Ascandra kakaban* sp. nov., a, holotype RMNH Por. 1696, *in situ* photo from Kakaban Island (photo N.J. de Voogd), paratype RMNH Por. 4625, *in situ* photo from Kakaban Island (photo L.E. Becking), c, specimen not collected, *in situ* photo from Kakaban Island (photo Lori Colin), d, holotype RMNH Por. 1696, reserved fragments (scale bar = 1 cm), e, largest preserved fragment of holotype (scale bar = 1 cm).



**FIGURE 25.** *Ascandra kakaban* sp. nov., a–b, paratype RMNH Por. 4625, a, light microscopy overview of skeleton of tube (scale bar = 200  $\mu\text{m}$ ), b, detail of atrial surface showing apical actines of the tetractines (arrows) protruding in the atrial lumen (scale bar = 100  $\mu\text{m}$ ), c–e, holotype RMNH Por. 1696, SEM images of the spicules, c, triactines, d, tetractines, e, detail of apical actine of larger tetractine.

***Ascandra kakaban* sp.nov.**

Figures 24a–e, 25a–e

**Material examined.** Holotype RMNH Por. 1696, Indonesia, Kalimantan, Berau Islands, Kakaban island, 2.1409°N 118.5112°E, depth 0.5 m, snorkeling, coll. N.J. de Voogd, #BER08/121003/123, 12 October 2003.

Paratype RMNH 4625, Indonesia, East Kalimantan Province, Berau Region, kakaban island, Kakaban marine lake, 2.4133°N 118.5078°E, depth 0–2 m, snorkeling, coll. L.E. Becking, #LE043, 31 August 2008.

**Description.** The cormus (Figs 24a–c) consists of a single (holotype, Fig. 24a) or several (paratype, Fig. 24b) wide semi-transparent tubes, which are probably water collecting tubes, issuing from a network of relatively few thinner tubes. In some, possibly ageing, individuals, like the holotype, these tubes at their base proliferate into a cluster of intertwined ‘blind’ tubules, more brightly white colored, but in other individuals (paratype) this is less developed. Size of the cormus in preserved condition (Figs 24d–e) up to 7.5 x 7 x 3 cm, largest fragment 4 x 3.5 x 3 cm (Fig. 24e).

**Skeleton.** (Figs 25a–b) The wall of the tubes is built of a thin layer of triactines and tetractines (Fig. 25a), with the apical actines of the tetractines directed into the tubar lumen (Fig. 25b, arrows).

**Spicules.** (Figs 25c–e) Triactines, tetractines.

Triactines (Figs 25c), equiangular equiaxial, in a large size range, possibly divisible in two overlapping size classes, actines thinly conical, tapering to sharp apices, overall length of actines, 57–154.0–220 x 4–9.4–12 µm.

Tetractines (Figs 25d), similar in shape to triactines but distinctly larger, actines of the basal triradiate system, 74–197.4–267 x 8.5–12.4–16 µm, apical actines curved, often wobbly (Fig. 25e), 35–110.3–237 x 4.5–10.3–16 µm.

**Ecology.** So far known only from a marine lake, at shallow depth on mangrove roots.

**Distribution.** So far known only from Kakaban.

**Etymology.** Named after the type locality, the island of Kakaban, one of the famous marine lakes of Indonesia.

**Remarks.** The new species is assigned to the genus *Ascandra* on account of the combination of independent central tubes with proliferated ‘blind’ side tubes, and tetractines lining and echinating the inner tube surfaces with their long curved apical actines. We were unable to demonstrate the presence of a folded choanoderm, but assume the prominent apical actines protruding far into the tube lumen to be sufficient circumstantial evidence for membership of *Ascandra*. We were able to compare the present species with a specimen of the type species of *Ascandra*, *A. falcata* Haeckel, 1870 from NE Spain (ZMA Por. 14591). Shape, color and spiculation are different: *A. falcata* forms more definitely a group of (yellow) tubes and possesses strongly curved diactines in addition to the triactines and tetractines. It is similar to the present new species in being semitransparent and having the tri- and tetractines approximately similar in size - although more robust - and likewise it has the tetractines larger than the triactines.

The Indonesian species originally described by Haeckel (1872) as *Ascandra sertularia*, subsequently reassigned to *Leucosolenia* by Dendy & Row (1913), on paper appears somewhat similar in habitus to our new species. However, Haeckel clearly describes large, peculiarly ornamented diactines arranged perpendicular to the surface, which are not present in our material.

The habitus of our new species is quite striking and distinct, but there is a strong resemblance to *Ascandra crewsi* sp.nov. described below. The difference between the two is found mostly in the rarity or virtual absence of triactines in *A. crewsi* sp.nov., whereas the two spicule types are in equal proportions in the present species.

***Ascandra crewsi* sp. nov.**

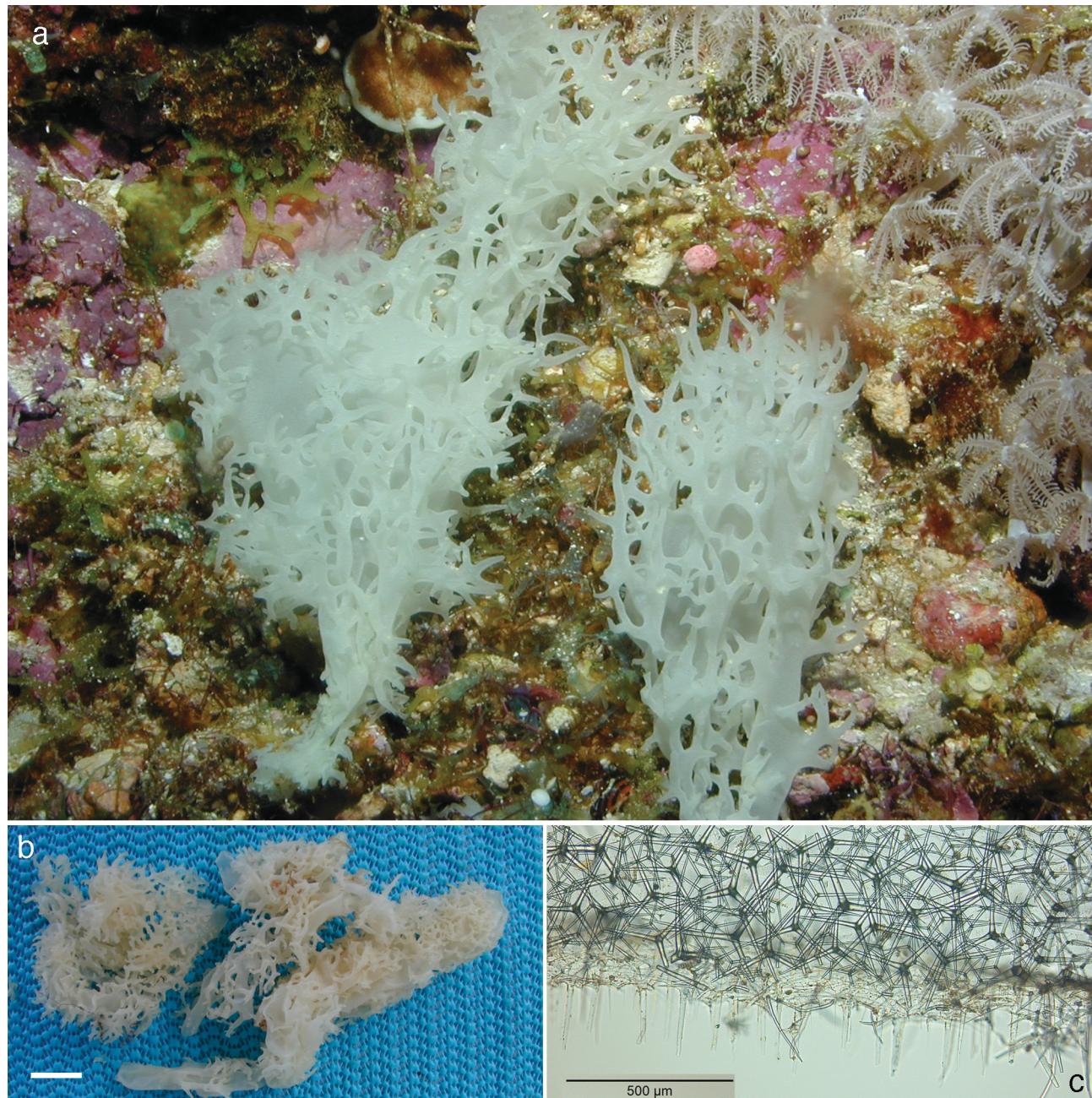
Figures 26a–c, 27a–e

*Leucosolenia* sp.; Ralifo, et al., 2007: 7.

**Material examined.** Holotype ZMA Por. 17556, Papua New Guinea, Wahoo, 10.2518°S 150.758°E, depth 21 m, in cave, SCUBA, coll. R. Sonnenschein #02130, 29 May 2002.

**Description.** (Figs 26a–b) The material consists of two samples showing thin-walled tubes with extensive system of thin side branches forming a reticulation around the central tube. Size of the whole specimens in preserved condition (Fig. 26b) up to 10 x 4 x 3 cm, central tubes less than 1 cm in diameter and branches of the

network 1–2 mm in diameter. The network of side branches is frequently dead-ended, and these ends taper to a fine point. The central tube ends in a wide oscule. Color snow-white, but the central tubes are semi-transparent. Consistency soft, becoming limp out of the water, easily damaged.



**FIGURE 26.** *Ascandra crewsi* sp. nov., holotype ZMA Por. 17556 from Papua New Guinea, a, habitus *in situ* (photo L. E. Becking), b, preserved holotype (scale bar = 1 cm), c, oblique tangential view of skeleton of atrial surface showing the protruding apical actines of the tetractine spicules (scale bar = 500 µm).

**Skeleton.** The wall of the central tube and the side branches is formed by a single layer of tetractines, with the long thin apical actines protruding far out into the tubar lumen (Fig. 26c).

**Spicules.** (Figs 27a–e) Predominantly tetractines, a few triactines.

Large tetractines (Figs. 27a) equiangular equiaxial, with actines of the basal triradiate system 159–206.4–246 x 15–18.8–21 µm, apical actines usually curved at the end (Fig. 27d), 181–226.3–279 x 13–15.3–17 µm.

Small tetractines (Figs 27c), likewise equiangular equiaxial, with actines of the basal triradiate system 54–90.2–117 x 7–7.3–8 µm, apical actines straight and needle-sharp (Fig. 27e), 62–95.8–114 x 2.5–3.1–3.5 µm.



**FIGURE 27.** *Ascandra crewsi* sp.nov., holotype ZMA Por. 17556, SEM images of the spicules, a, large tetractine, b, rare triactine, c, small tetractine, d, apical actine of large tetractine, e, apical actine of small tetractine.

Small triactines (Fig. 29b), equiangular equiaxial, relatively robust, only a few were observed, actines 140–150 x 10–12  $\mu\text{m}$ .

**Ecology.** Deeper part of the reef.

**Distribution.** So far known only from Papua New Guinea.

**Etymology.** Named after Dr. Phil Crews of the University of California at Santa Cruz, who leads the research group that was responsible for collecting the present specimens, and to acknowledge his great contributions to sponge natural products detection and elucidation.

**Remarks.** The specimens from Papua New Guinea are considered to be a distinct species despite the overall similarity to *Ascandra kakaban* sp.nov. described above. The present material has a larger cormus and there are distinct differences in the spicules: triactines are virtually missing (only a few could be found and these were only small ones), while the tetractines were more definitely in two size classes with the large tetractines having much longer apical actines than those of *A. kakaban* sp.nov. Like in the Kakaban species, the present specimens look

deceptively like Clathrinidae, but the central tube and reticulated side branches, the dominance of tetractines with their long apical actines protruding far into the atrial lumen, and the paucity of triactines, are indicative of *Ascandra*. There is also a resemblance with regional species of the genus *Soleneiscus* Borojevic, Boury-Esnault & Vacelet, 1990 like *S. radovani* Wörheide & Hooper, 1999 and *S. stolonifer* (Dendy, 1891), from which the new species differs in the lack of diactines and the reticulated habitus.

As discussed above, *Ascandra sertularia* Haeckel (1872) is distinct by having large diactines.

The present material was preliminarily identified as *Leucosolenia* sp. by one of us (RVS), under which name the presence of novel secondary metabolites - leucosolenamides - were reported (Ralifo *et al.* 2007).

## Genus *Leucaltis* Haeckel, 1872

### *Leucaltis nodusgordii* (Poléjaeff, 1883) comb. nov.

Figures 28a–c, 29a–d, 30a–e

*Heteropogema nodusgordii* Poléjaeff, 1883 (in part, only the Torres Strait material): 45, pl. I fig. 7, pl. IV figs 1a–d; Dendy, 1905: 230; Jenkin, 1908: 453, fig. 103.

?*Leucaltis bathybria* var. *mascarenica* Ridley, 1884: 628, pl. LIV figs a, a'.

*Leucaltis clathria* sensu Dendy, 1913: 16, pl. 2 figs 1–2; Hôzawa, 1940: 136, pl. VI fig. 3; Tanita, 1943: 394, pl. XIII fig. 27; Borojevic & Klautau, 2000: 190, figs 2–3.

(not: Haeckel, 1872: 159, pl. 29 figs 3a–3c).

*Leuconia paloensis*; Colin & Arneson, 1995: 61, photo 235; Gosliner *et al.* 1996: 17, photo 8; Erhardt & Baensch, 1998 Atlas 4: 21, 24–25 (not: Tanita, 1943).

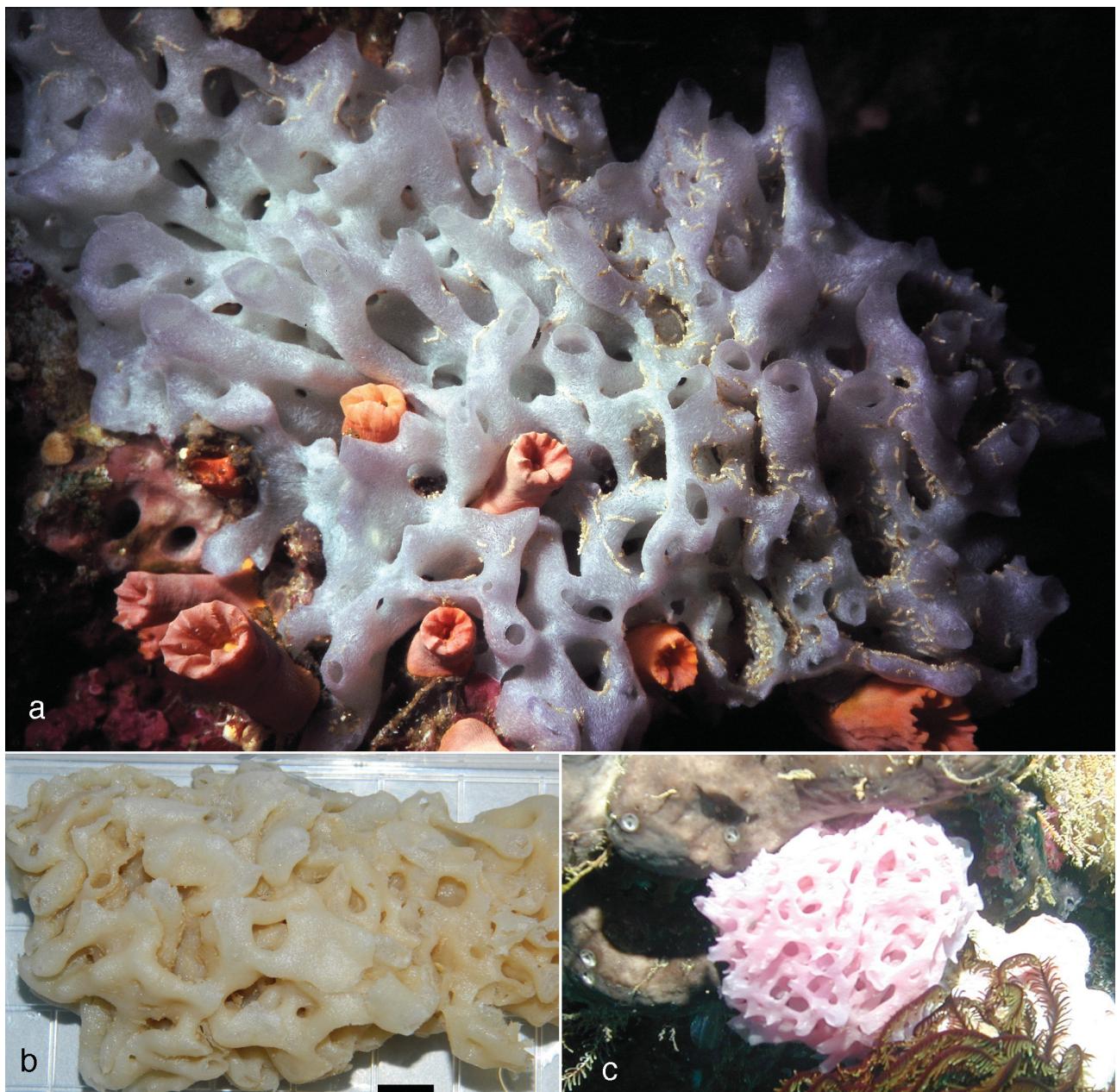
**Material examined.** RMNH Por. 1772, Indonesia, North Sulawesi, Negeri, Manado Tua South, depth 20 m, SCUBA, coll. N.J. de Voogd, #MD08/160502/043, 16 May 2002 (several individuals); ZMA Por. 17557, Papua New Guinea, Normanby Island, N point, 9.7328°S 150.7402°E, depth 21 m, SCUBA, coll. R. Schonnenschein, #02136, 30 May 2002.

Examined for comparison. BMNH 1884.4.22.23a, two slides labeled ‘Type’ and ‘from type’, ‘Challenger Torres Straits, coll. Brit.Mus. 27’ (subsequently labeled as *Leucaltis clathria*); ZMA Por. 12443, Seychelles, Amirante Islands, Poivre Atoll, N rim, 5.7333°S 53.3167°E, depth 7–8 m, SCUBA, coll. R.W.M. van Soest, Netherlands Indian Ocean Program E stat. 768/08, 31 December 1992; ZMA Por. 16248, Seychelles, Mahé, SE coast, Anse Royale Bay, 4.7333°S 55.5167°E, depth 2–13 m, SCUBA, coll. R.W.M. van Soest, Netherlands Indian Ocean Program E stat. 740/04, 24 December 1992; RMNH Por. 9314, off Guyana, 7.7°N 57.5°W, depth 65 m, dredged, bottom muddy sand and shells, coll. ‘Luymes’ Guyana Shelf Expedition stat. 107, 5 September 1970.

**Description.** A clathrate mass of anastomosing tubes (Figs 28a, c), largest individual 12 x 6 x 6 cm, individual tubes quite variable in length and diameter, undivided tube lengths up to 2.5 cm, diameter 2–8 mm. Tubes ending in oscules, as wide as the tube (upright) or more often smaller (flush with the surface); oscules naked. Surface smooth, consistency brittle but somewhat compressible. Color white or pinkish white, lavender-colored, becoming yellowish white in preserved condition (Fig. 28b).

**Histology.** The choanocyte chambers (Figs 29b–d) are long, broad and branching, somewhat inbetween syconoid and sylleibid.

**Skeleton.** (Figs 29a–d) Cortical skeleton formed by the basal triradiate system of giant tetractines mixed with giant triactines (Figs 29a, c–d). Actines of the giant tetractines and triactines protrude into the choanomal skeleton. Next to the actines of the giant tri- and tetractines, the choanosomal skeleton (Figs 29a–c) contains scattered intermediate to small-sized regular triactines and tetractines, lining the choanocyte chambers, with free actines of these spicules protruding into the lumen of the choanocyte chambers. The atrial skeleton (Figs 29a–b) consists of a single layer of sagittal triactines, and less common tetractines, provided with characteristic abruptly curved paired actines, the paired actines lined up in a single plane. There is a distinct complement of diactinal, triactine-derived, spicules which may be the product of broken-off third actines, but the common occurrence indicates it may be a reduced spicule form. Likewise, there are club-shaped irregular diactinal spicules, probably derived from the abruptly curved sagittal triactines, scattered in the atrial region; occasional forms of these spicules occur with reduced or absent unpaired actines.



**FIGURE 28.** *Leucaltis nodusgordii* (Poléjaeff, 1883), a, habitus *in situ* of RMNH 1772 from Manado (photo N.J. de Voogd), b, preserved specimen RMNH Por. 1772 (scale bar = 1 cm), c, habitus *in situ* of ZMA Por. 17557 from Papua New Guinea (photo R. Sonnenschein).

**Spicules.** (Figs 30a–e) Giant triactines and tetractines, small regular triactines and tetractines, sagittal ‘abruptly curved’ triactines and tetractines, reduced forms of the latter.

Giant triactines (Fig. 30a), equiangular, actines more or less equiaxial, 252–458.1–792 x 19–47.3–108 µm.

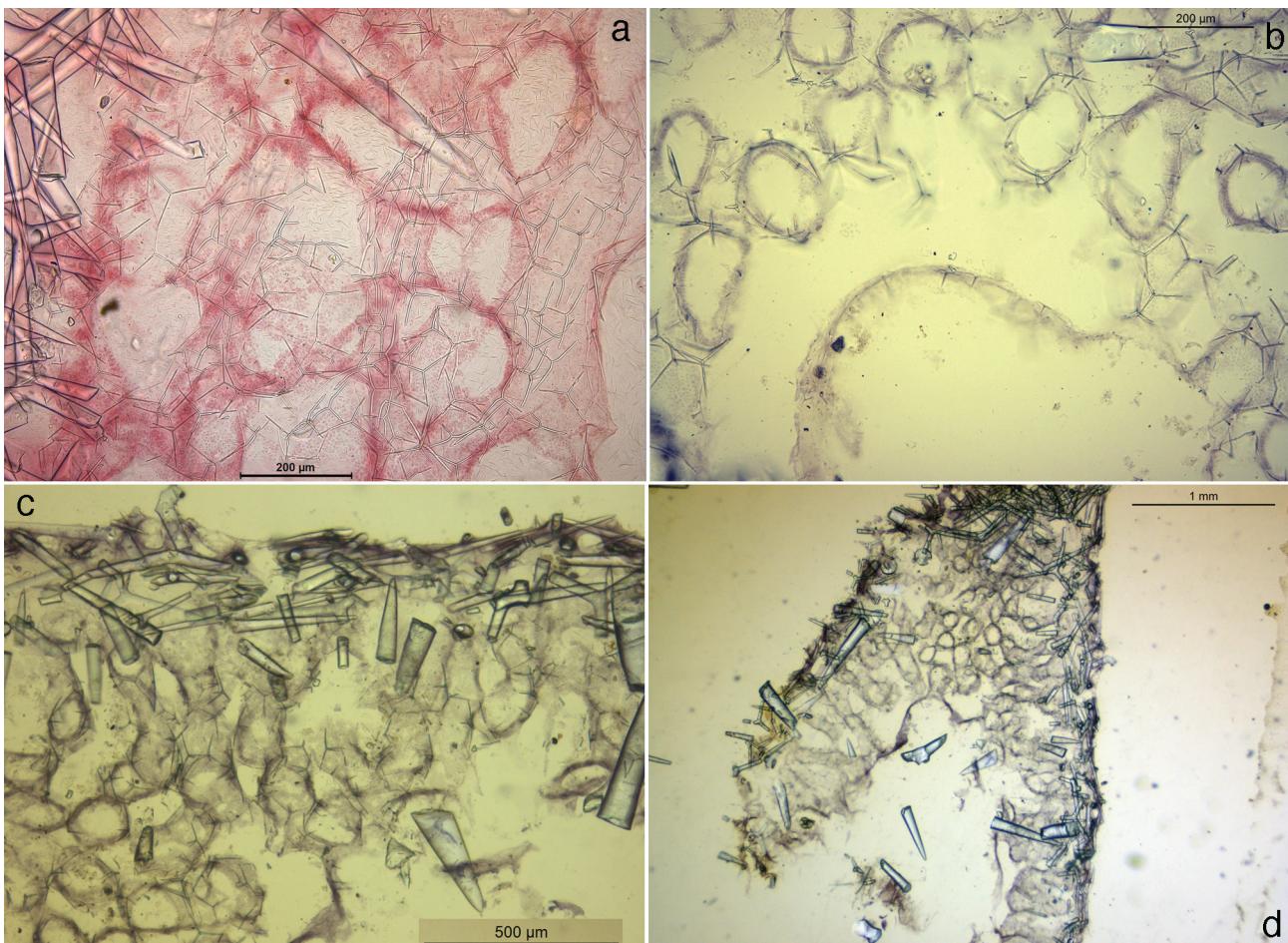
Giant tetractines (Fig. 30b), equiangular, actines more or less equiaxial, or occasionally with slightly longer basal actine, 624–820.1–1110 x 66–85.2–97 µm.

Additionally, a single giant diactine, 846 x 36 µm, was observed. Possibly, it represented a reduced triactine.

Regular equiaxial triactines (Fig. 30d), occasionally tripod-shaped, 30–79.1–193 x 1.5–4.7–13 µm.

Regular tetractines (Fig. 30d), actines of the basal radiate system and apical actines more or less similar, 21–83.9–138 x 2–4.4–7.5 µm.

Sagittal, abruptly angled triactines (Fig. 30e), unpaired actine 42–47.3–60 x 2.5–2.9–3.5 µm, paired actines, 42–62.1–72 x 3–3.8–4.5 µm.



**FIGURE 29.** *Leucaltis nodusgordii* (Poléjaeff, 1883), a, histological cross section of tube wall of RMNH Por. 1772 showing from left to right cortical skeleton of giant tri- and tetractines, equiangular triactines of the choanocyte chamber region, and abruptly angled tri- and tetractines of the atrial skeleton (scale bar = 200 µm), b–d, cross sections of holotype BMNH 1884.4.22.23a, b, detail of atrial skeleton and subatrial chamber region (scale bar = 200 µm), c, cross section of chamber region and cortex (scale bar = 500 µm), d, overview of cross section of tube wall (scale bar = 1 mm).

Sagittal, abruptly angled tetractines (Fig. 30f), unpaired actine 60–64.2–66 x 4–4.2–5 µm, paired actines 78–79.3–87 x 6.5–6.8–7 µm, apical actine short, difficult to measure, approximately 10 x 3 µm.

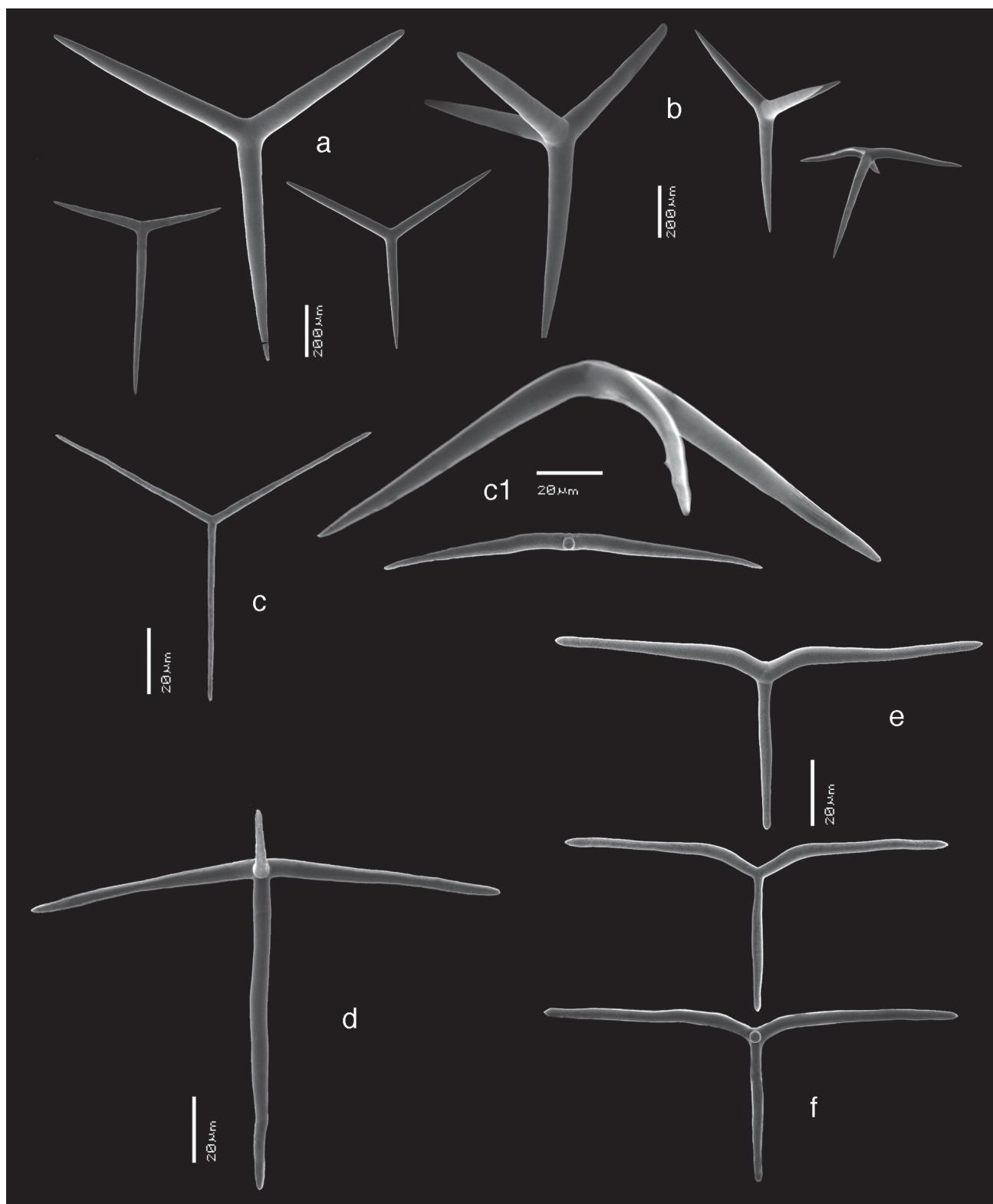
Reduced diactinal modifications of sagittal triactines, size of actines 60–64.4–69 x 2.5–3.1–4 µm (not shown).

**Ecology.** Coral reefs, among living corals, 15–25 m.

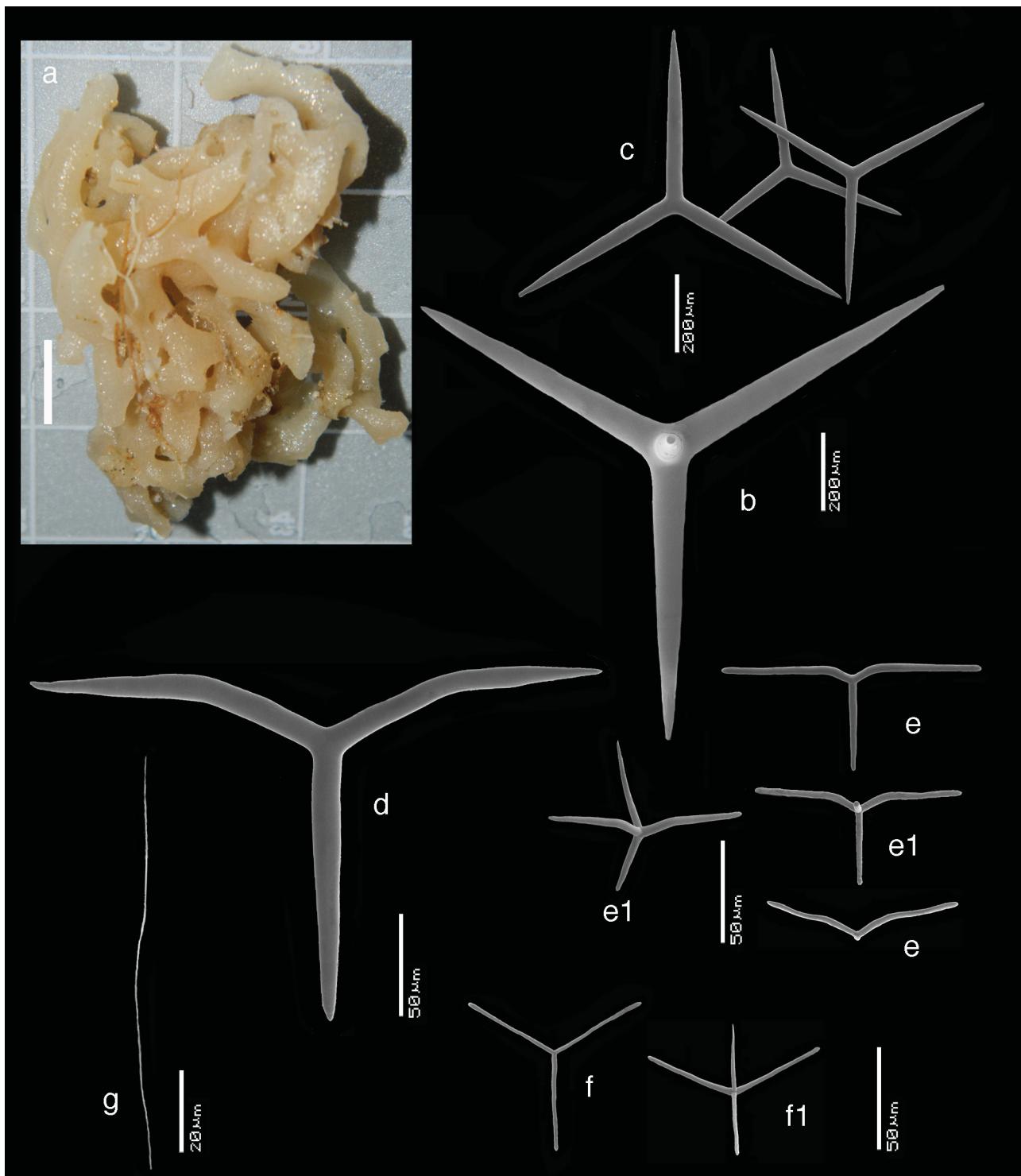
**Distribution.** At least North Australia, New Caledonia, Indonesia, Papua New Guinea, Seychelles, Zanzibar; possibly South Australia, Japan, Sri Lanka.

**Remarks.** The Papua New Guinea material (ZMA Por. 17757) included in the above given spicule data, had somewhat smaller spicules: giant triactines 228–602 x 20–47 µm, giant tetractines 570–998 x 65–104 µm, small triactines 54–66 x 2–3 µm, small tetractines paired & unpaired actines 54–66 x 1.5–2.5 µm and apical actines 8–12 x 2 µm, atrial triactines & tetractines with paired & unpaired actines 33–74 x 3–6 µm, apical actines 8–12 x 6 µm, and diactines 50–60 x 4 µm.

We report here also two specimens belonging to this species from outside Indonesia, viz. the Seychelles (ZMA Por. 12443 and 16248), with essentially similar habitus and spicule size data: giant triactines 111–610 x 18–54 µm, giant tetractines 552–1230 x 90–156 µm, small triactines 48–126 x 2–7 µm, small tetractines with actines of the basal triradiate system 66–115 x 2–5 and apical actines 10–35 x 2–5 µm, atrial triactines and tetractines with paired and unpaired actines 45–60 x 2.5–6 µm and apical actines 10–15 x 6 µm, diactines 67–72 x 3–4 µm.



**FIGURE 30.** *Leucaltis nodusgordii* (Poléjaeff, 1883), SEM images of the spicules of RMNH Por. 1772, a, giant and intermediate sized triactines of the cortical region, b, giant and intermediate sized tetractines of the cortical region, c, small regular-shaped triactines of the chamber layer, c1, small triactines seen from the side, d, regular equiangular tetractine of the chamber layer, e, ‘abruptly angled’ triactines, f, ‘abruptly angled’ tetractines, both from the atrial region.



**FIGURE 31.** *Leucaltis clathria* (Haeckel, 1872), RMNH Por. 9314, from the Guayana shelf, Atlantic Ocean, a, habitus of preserved specimen (scale bar = 1 cm), b–g, SEM figures of the spicules, b, giant tetractine, c, giant triactines, d, large abruptly angled triactines, e–e1, small abruptly angled tri- and tetractines, f–f1, regular tri- and tetractines, g, trichoxea.

We name this material *Leucaltis nodusgordii*, against the consensus in the literature that it should be named *Leucaltis clathria* (Haeckel, 1872) (e.g. Dendy 1913; Lévi *et al.* 1998; Wörheide & Hooper 1999; Borojevic & Klautau 2000). The treatment by previous authors of this and related specimens is rather frustrating. The subsequent authors all refer to Poléjaeff's admittedly excellent description, but fail to compare it in detail with Haeckel's type of *L. clathria*. This should have been done, e.g. by Dendy (1913), who saw fragments of Haeckel's type brought to the Natural History Museum in London by Mr. R.W.H. Row. Dendy (1913: 17) stated that he

examined the fragments carefully, and he gives some comments indicating that Haeckel's description was incomplete, but failed to provide measurements of the spicules. Unfortunately, we were not able to lay our hands on a slide of Haeckel's type still remaining in the collections in London, cited by Burton (1963: 598) and Wörheide & Hooper (1999: 877). Both these sources, like Dendy (1913), did not describe the contents of the slide. The external form is apparently so characteristic and convincing that proper description of the spicules and their variation is largely neglected by most authors.

Haeckel (1872: 159, pl. 29 figs 3a–c) described a brownish (alcohol) clathrate mass of tubes, size 3–6 cm, from a depth of 63 m off the coast of Florida, collected by A. Agassiz, as *Leucaltis* (or alternatively *Artynas*) *clathria*, with the spicules described and measured as:

Triactines ('mittelgross' = middlesized) 400–600 x 30–50 µm. Tetractines ('colossal') 800–1200 x 100–150 µm, occasionally as long as 2000 µm. Sagittal tri- and tetractines (drawn with paired actines in 180° degree angle and with bluntly rounded ends), paired actines 50–70 x 2–3 µm, unpaired actines 30–40 µm. Triactines more common than tetractines. Occasional subregular triactines 400–700 x 1–2 µm. Although in his description he mentions small choanosomal tri- and tetractines supporting the choanocyte chambers he does not provide measurements. Dendy (1913) stated that these were amply present in the London fragments of the type.

We report here a specimen in the collections of the Naturalis Biodiversity Center, RMNH Por. 9314, from the Guyana shelf (7.7°N 57.5°W, depth 65 m), which may be considered representative for the Western Atlantic population to which Haeckel's type is assumed to belong. The habitus (Fig. 31a) and the spiculation (Figs 31b–g) (actines of giant tri- and tetractines: 210–530 x 15–63 µm, actines of small equiangular tri- and tetractines: 40–55 x 2–3 µm, abruptly angled tri- and tetractines with unpaired angles 40–45 x 3–4 µm, paired actines 50–65 x 3–4 µm) of this specimen are indeed strikingly similar to the Indo-West Pacific specimens listed and described above. However, there is one obvious difference in the spicule complement (see Fig. 31d), namely the presence in the Guyana specimen of a second category of large 'abruptly angled' triactines with paired actines 122–141 x 8.5–10 µm and unpaired actines 111–126 x 6–10 µm, clearly twice as long and thick as the usual spicules reported by us above. These spicules are not very common, so they might have been overlooked by Haeckel and Dendy. It appears to us that this difference supports the specific distinctness of specimens from West Pacific and West Atlantic localities. Klautau et al. (2013) found considerable DNA sequence distance between *Leucaltis clathria* from the Caribbean and individuals assigned to *L. clathria* from Australia, and on that basis pleaded for making a specific distinction. This confirms that both morphologically and genetically a separate species *Leucaltis nodusgordii* is valid.

## Family Leucascidae Dendy, 1893a

### Genus *Ascalitis* Haeckel, 1872

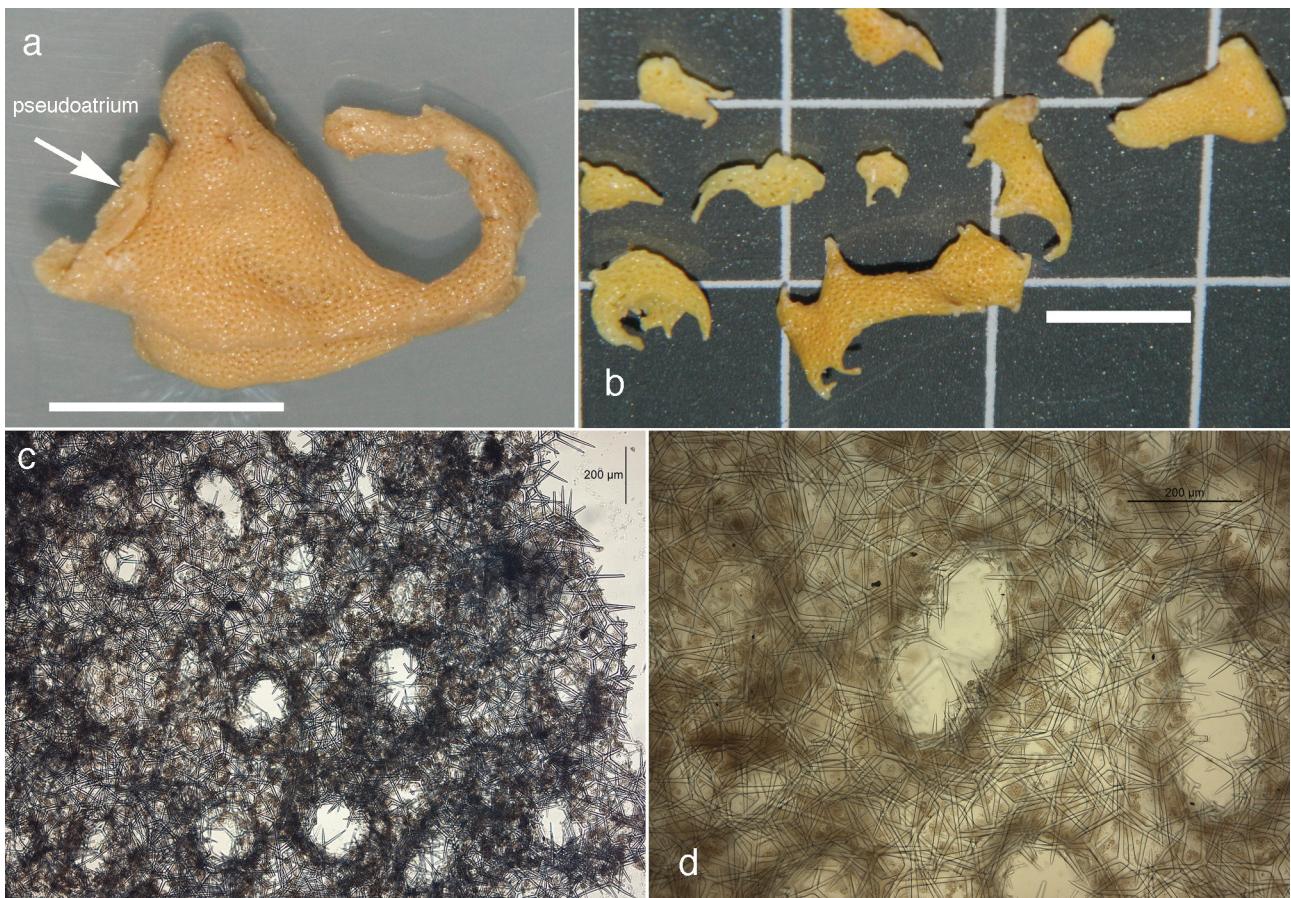
*Clathrina*-like Leucascidae with pseudoatrium and tightly anastomosed asconoid aquiferous system covered by a thin 'skin'-like single layer of spicules. The anastomosed tubes form a cortex-like structure, obscuring individual tubes. Spicules are small triactines and tetractines, and may occasionally include diactines. (after Klautau, et al. 2013).

#### *Ascalitis angusta* sp.nov.

Figures 32a–d, 33a–d

**Material examined.** Holotype ZMA Por. 09097, Indonesia, SE Sulawesi, Salayar, NW coast of Pulau Guang, 6.35°S 120.45°E, depth 2–4 m, SCUBA, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition stat. 152/II/Cave 1/06.

Paratypes ZMA Por. 08221a (ten individual cormi), Indonesia, SE Sulawesi, Tukang Besi Islands, southern reef of Karang Kaledupa, 5.9333°S 123.8°E, depth 4–11 m, SCUBA, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition stat. 016/III/10, 8 September 1984.



**FIGURE 32.** *Ascalcis angusta* sp. nov., a, preserved holotype ZMA Por. 09097 (arrow indicates slit-like pseudoatrium) (scale bar = 1 cm), b, preserved paratypes ZMA Por. 08221 (scale bar = 1 cm), c, overview of skeleton of one of the paratypes (scale bar = 200  $\mu$ m), d, detail of surface skeleton (scale bar = 200  $\mu$ m).

**Description.** (Figs 32a–b) Tight masses of thin tubes, surrounding a thin slit-like pseudoatrium (arrow in Fig. 32a). Individual specimens often occurring in small patches of a few  $\text{cm}^2$ , connected by single tubes to form a cormus-network. Size variable, the holotype (Fig. 32a) is 2 cm long and maximally 1.2 cm wide. Live color white, but in alcohol this turns into yellow or beige. Oscules few, at the apices of single water-collecting tubes.

**Skeleton.** (Figs 32c–d) Tube system on the outside covered with a thin, often damaged membrane consisting of a single spicule layer (Fig. 32c). Granular cells abound in the surface (Fig. 32d). Underneath, the tubes have thin walls of usual two layers of spicules (Fig. 32d).

**Spicules.** (Figs 33a–d) Small triactines and tetractines of variable but similar shape, partially slightly or more distinctly parasagittal.

Triactines, equiaxial, (Fig. 33a) length of actines 72–101.8–196 x 6–9.1–13  $\mu$ m; parasagittal triactines (Figs 33c) with unpaired actines 180–198  $\mu$ m, and shorter paired actines.

Tetractines, equiaxial (Fig. 33b) with actines of basal radiate system 80–103.4–126 x 6–8.6–11  $\mu$ m, smooth apical actines 45–105 x 4–6  $\mu$ m; parasagittal tetractines (Fig. 33d) with unpaired actines 120–186  $\mu$ m, paired actines shorter.

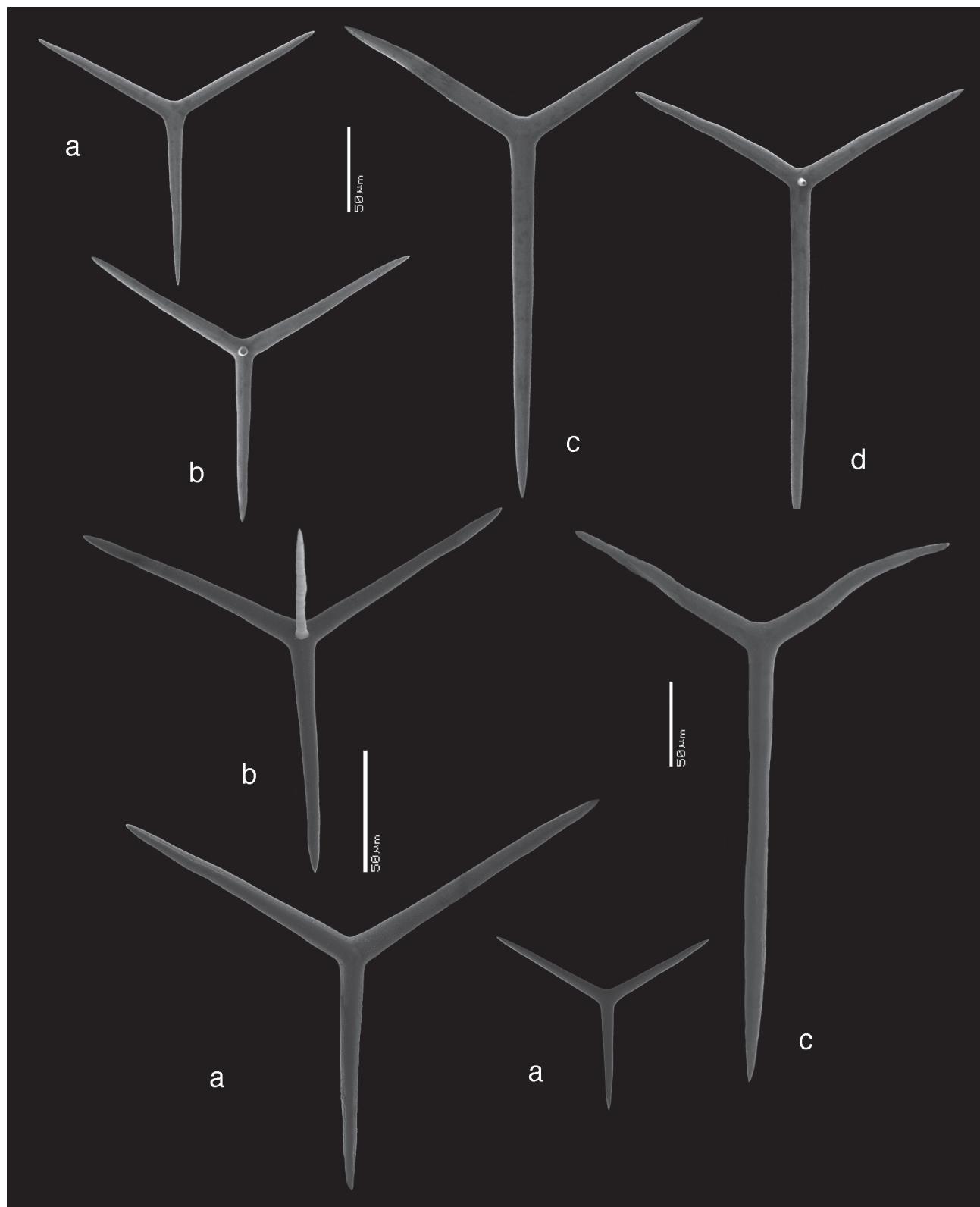
**Ecology.** Shallow water reefs, often in caves.

**Distribution.** Indonesia.

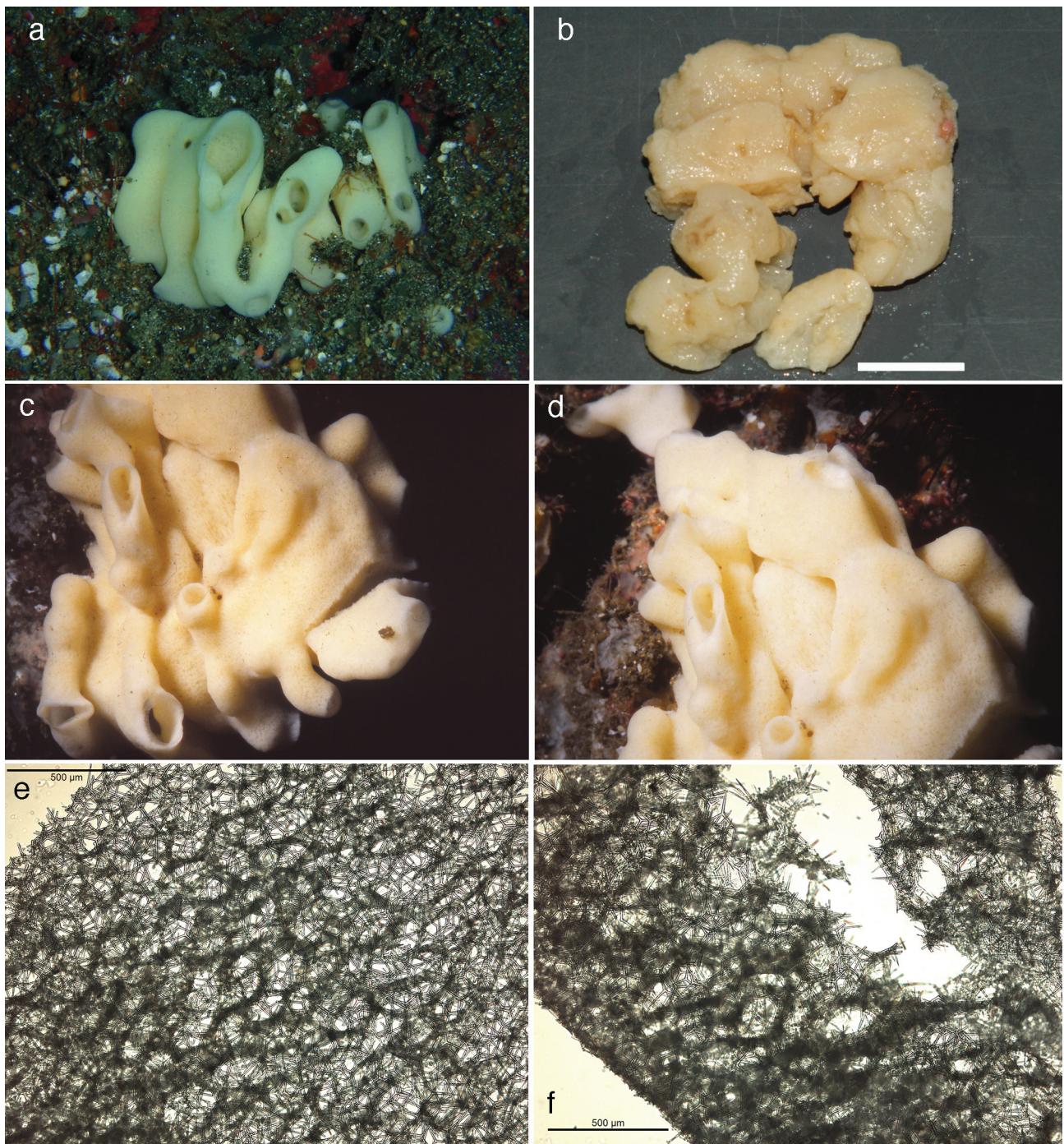
**Etymology.** The word *angustus* (L.) means narrow, tight, referring to the tight anastomosis of the tubes of the cormus in this species.

**Remarks.** Because the habitus of our new species with its pseudoatrium and its tight-meshed cormus matches the definition of the genus *Ascalcis*, we believe it is a likely member of that genus. The thin membrane enclosing the whole cormus is not always clearly visible and appears present only in places (preserved material). The new species shows considerable resemblance to *Ascalcis gardineri* (Dendy, 1913) (as *Leucosolenia*), previously

considered a member of *Clathrina* (cf. Klautau & Valentine 2003), but subsequently assigned to *Ascalcis* by Klautau *et al.* 2013). However, there are distinct differences in the spicules. Klautau & Valentine (2013: 26) in their redescription of the type material noticed the occurrence of two distinct size categories with differently shaped apical actines of the tetractines. No parasagittal spicules occur in *A. gardineri*.



**FIGURE 33.** *Ascalcis angusta* sp. nov., holotype ZMA Por. 09097, SEM images of spicules a, regular equiangular equiaxial triactine, b, regular equiangular equiaxial tetractines, c, sagittal triactines, d, sagittal tetractine.



**FIGURE 34.** *Leucascus flavus* Cavalcanti et al. (2013), a, habitus *in situ* of RMNH Por. 2279 from Bali (photo N.J. de Voogd), b, preserved habitus of holotype ZMA Por. 13145 from SW Sulawesi (scale bar = 1 cm), c+d, *in situ* images of RMNH Por. 9346, from Ternate (photo N.J. de Voogd), e, tangential view of surface skeleton (scale bar = 500 µm), f, cross section (scale bar = 500 µm).

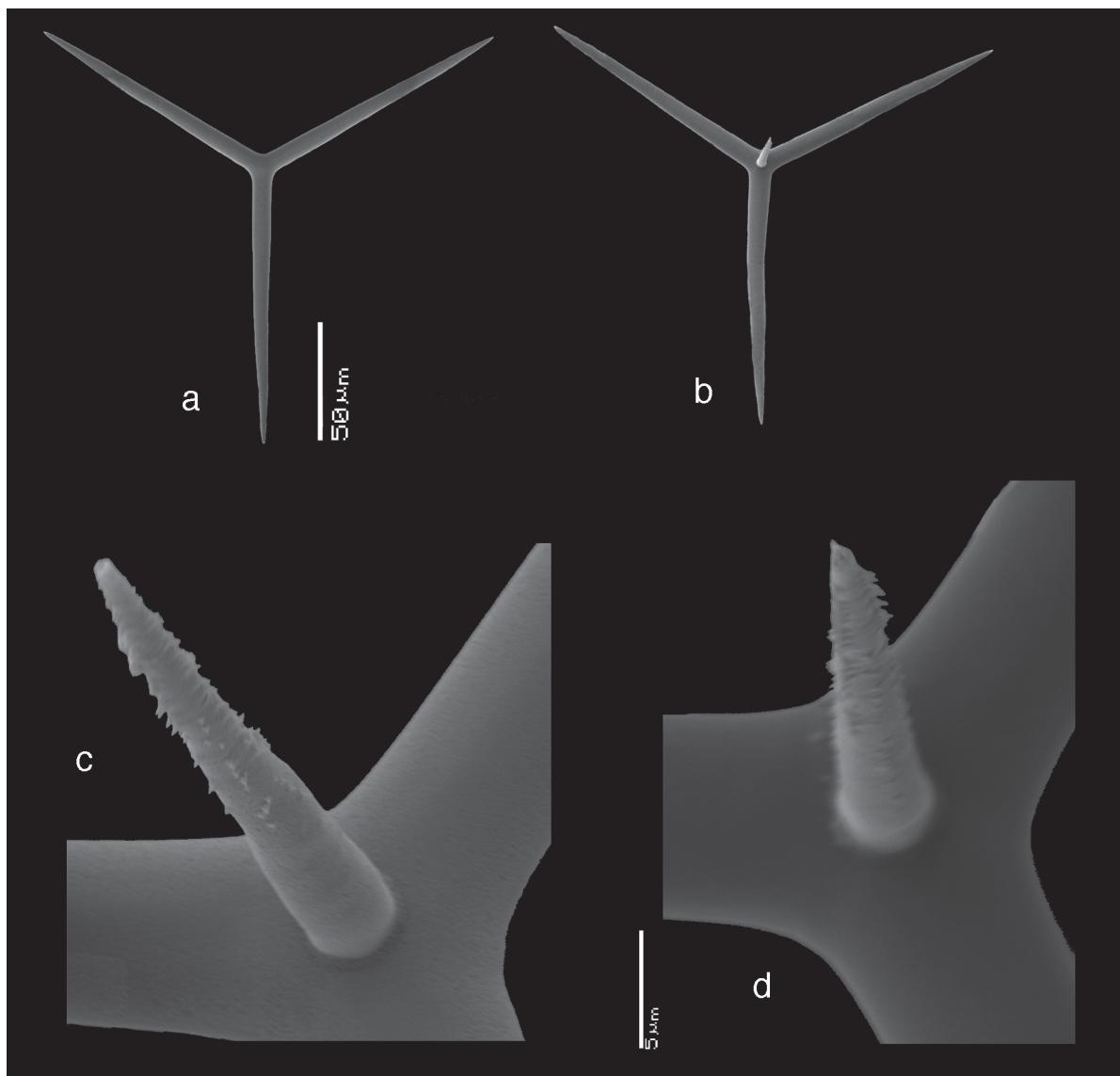
### Genus *Leucascus* Dendy, 1893a

#### *Leucascus flavus* Cavalcanti, Rapp & Klautau, 2013

Figures 34a–f, 35a–d

? *Leucosolenia cerebrum*; Breitfuss, 1896a: 434; Breitfuss, 1898: 172 (not Haeckel, 1872)

*Leucascus flavus* Calvalcanti et al., 2013: 297, Figs 14–15.



**FIGURE 35.** *Leucascus flavus* Cavalcanti *et al.* (2013), SEM images of the spicules, a–c, holotype ZMA Por. 13145, a, triactine, b, tetractine, c, detail of apical actine of tetractine showing the characteristic spinulation, d, ditto of RMNH Por. 9347 from Ternate.

**Material examined.** Holotype ZMA Por. 13145 ((Fig. 34b), Indonesia, SW Sulawesi, Spermonde Archipelago, Bone Baku, 5.132°S 119.361°E, depth 12 m, SCUBA, coll. N.J. de Voogd #BB/NV/160597/27, 16 May 1997.

Additional specimens. RMNH 2279, Indonesia, Bali, Tulamben area, bay S of ‘Emerald Hotel’, 8.2847°S 115.6031°E, depth 20 m, SCUBA, coll. N.J. de Voogd, #BAL 23/120401/151, 12 April 2001 (Figs 34a, c–d); RMNH 9346, Indonesia, Ternate, Halmahera, Sulamadaha Beach, 0.8632°N 127.3345°E, depth 15 m, SCUBA, coll. N.J. de Voogd, #TER.04/2661009/NV017, Ternate-Halmahera Expedition 2009, 26 October 2009; RMNH 9347, Indonesia, Halmahera, Tidore Cobo, 0.7552°N 127.4066°E, depth 15 m, SCUBA, coll. N.J. de Voogd, #TER.15/0111009/, Ternate-Halmahera Expedition 2009, 1 November 2009.

**Description.** The description of the holotype (Fig. 34b) is here summarized from Cavalcanti *et al.* 2013: Yellow massive sponge, with a thin skin (Fig. 34e) covering a tight mass of anastomosed tubes (Fig. 34f). Large oscules, without membrane or spicule fringe. Spicules triactines 70–120 x 7.5–11 µm, tetractines with actines of the basal triradiate system 75–115 x 7.5–10 µm, apical actines 41–61 x 4–5 µm. The apical actines are rugose-spined (Fig. 35c) and protrude into the choanocyte tubes.

Description of additional specimens, also from *in situ* photos: lobate-folded massive sponges (Figs 34a–c) with a pale-yellow or whitish yellow color *in situ*. Oscules wide, rounded or elongate, at the top of lobes.

**Spicules.** (Figs 35a–d) Triactines and tetractines.

Triactines (Fig. 35a), equiangular equiaxial, occasionally parasagittal, 96–118.1–141 x 7.5–8.5–11 µm.

Tetractines (Fig. 35b), triradiate system equiangular and equiaxial, 90–114.3–127 x 7–9.2–10 µm, apical actines spined (Figs 35c–d), 45–54.7–68 µm.

**Ecology.** Shallow-water reefs.

**Distribution.** So far known only from Indonesia, but widely distributed there (Sulawesi, Bali, Ternate).

**Remarks.** This species was recently described by Cavalcanti *et al.* (2013) on the basis of an Indonesian specimen collected by one of us (NDV). Since then, the species was found several times in localities all over the Indonesian archipelago. It may be mistaken for other yellowish massive calcineans, such as *Ascoleucetta sagittata* Cavalcanti *et al.*, 2013 and *Leucetta chagosensis* Dendy, 1913 (cf. below), but these differ in color (more definitely brightly yellow), shape not so lobate but more massive and rounded, presence of large triactines and the lack of spined apical actines of the tetractines. The latter is not easily seen with light microscopy but it is very obvious under SEM.

There is a possibility that this species was previously reported by Breitfuss (1896a, 1898) from Ternate as *Leucosolenia cerebrum*, a Mediterranean species now assigned to the genus *Borojevia*. Although his description is quite concise and generally inadequate, he specifically mentions spined apical actines of the tetractines. It is also possible that this concerns a so far undescribed species of *Borojevia*.

## Genus *Ascoleucetta* Dendy & Frederick, 1924

### *Ascoleucetta sagittata* Cavalcanti, Rapp & Klautau, 2013

Figures 36a–f

*Ascoleucetta sagittata* Cavalcanti *et al.*, 2013: 308, Figs 21–22.

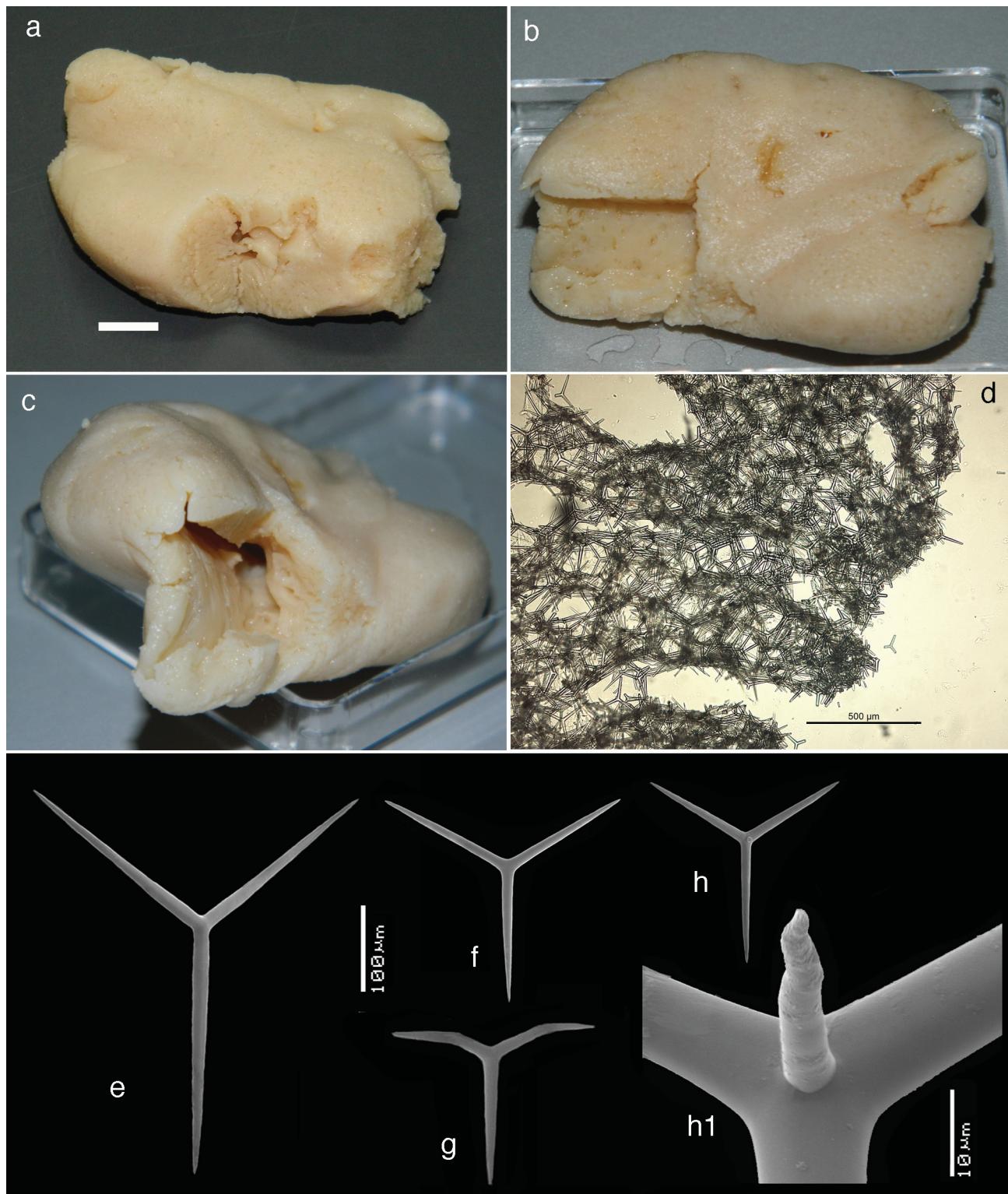
**Material examined.** Holotype ZMA Por. 13283, Indonesia, SW Sulawesi, Spermonde Archipelago, Kudingareng Keke, depth 15 m, SCUBA, coll. N.J. de Voogd, #KK/NV/130497/32, 13 April 1997.

**Description.** The holotype description is here summarized from Cavalcanti *et al.* 2013: Yellow massive sponge (Figs 36a–c) presumably consisting of a tight mass of tubes, but this is largely obscured. Instead there are some folded portions and lacunae in the interior (Fig. 36d), which indicate the tubes. Presumably the aquiferous system is solenoid, but this is not elaborated. The skeleton contains three categories of triactines, one large regular (Fig. 36e), 300–550 x 20–55 µm, one small sagittal (Fig. 36g) with unpaired actines 85–144 x 5–10 µm and paired actines 80–150 x 5–10 µm, one small regular (Fig. 36f), 110–160 x 12–15 µm, and small regular tetractines (Fig. 36h) with actines of the basal radiate system 110–150 x 10–12.5 µm and apical actines (Fig. 36h1) 37–65 x 5–7.5 µm. The latter are protruding into the lumen of the internal tubes.

**Ecology.** Shallow-water reefs.

**Distribution.** Indonesia.

**Remarks.** This species was recently described from a fragment, and we provide here images of the whole specimen. The presence of sagittal triactines is not observed very frequently, and they are not associated with the oscules, since there are no proper oscules in the holotype specimen. This species was earlier confused with specimens assigned to *Leucetta chagosensis* because of similarity in spiculation with it (see below). By careful comparison, we have become convinced that *Ascoleucetta sagittata* and the yellow globular-massive *Leucetta*-like specimens, which are so commonly encountered in the shallow reefs of Indonesia and the adjacent regions, are virtually indistinguishable and may very well be the same species. From molecular sequence results of Voigt *et al.* (2012) there are indications that *L. chagosensis* is not closely related to other *Leucetta* species like *Leucetta microraphis* Haeckel, 1872, which might support the idea that *L. chagosensis* is an *Ascoleucetta*, not a genuine *Leucetta*, conspecific or very closely related to *A. sagittata*. This would require careful histological sections. We refrain from making a definite conclusion on this species because of a forthcoming revision of Klautau *et al.* on *Leucetta*.



**FIGURE 36.** *Ascoleucetta sagittata* Cavalcanti et al. (2013), holotype ZMA Por. 13283, a–c, various images of preserved holotype, showing surface and atrium (scale in a = 1 cm), d cross section of skeleton, showing layered structure (scale bar = 500 µm), e–f, SEM images of the spicules, e, large triactines of the surface, f, small triactine, e, sagittal triactine, f, tetractine, f1, detail of tetractine.

## Family Leucettidae De Laubenfels, 1936

### Genus *Leucetta* Haeckel, 1872

**Remarks.** The present collections contained two distinct species, (1) yellow or bright yellow, globular or with rounded lobes, with large oscules often provided with a thin low rim, and (2) pink, massive with one or more, frequently several, tubiform, smooth or grooved, elevations. Both species have a predominance of triactine spicules in two distinct size categories, and rare small tetractine spicules. The spiculation of the two differs mostly in the length and thickness of the large ('giant') triactines, with the yellow lobes having the dimensions approximately 300–700 x 20–40 µm, and the pink tubes having these giant triactines with actine size 1000–1800 x 80–250 µm.

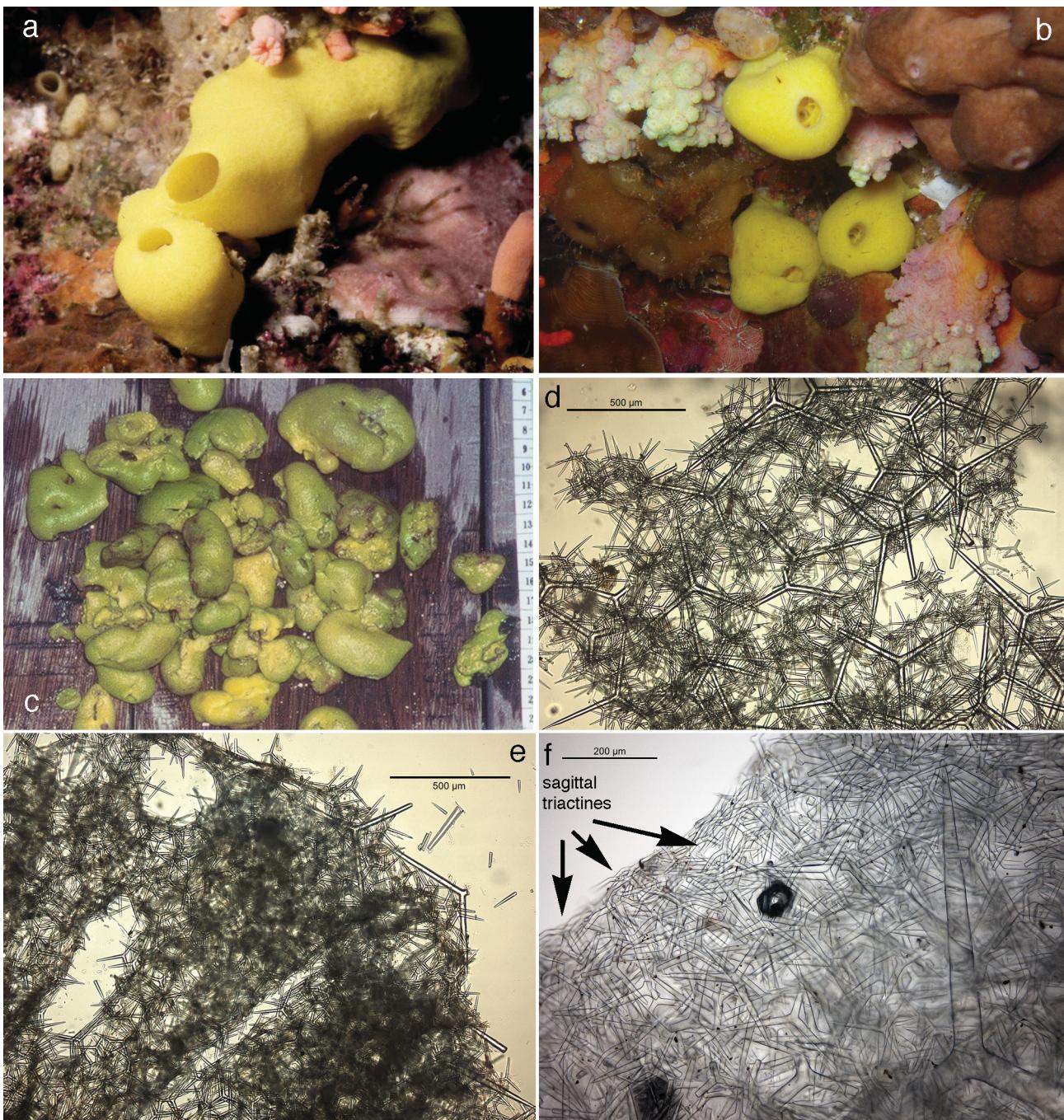
It is customary in the scientific literature to use the name *Leucetta chagosensis* Dendy, 1913 for the yellow species (see e.g. Wörheide & Hooper 1999), but the pink species is only recently again named *Leucetta microraphis* Haeckel, 1872, originally as *L. primigenia* var. *microrraphis*), after periods in which the name *L. primigenia* Haeckel, 1872 was used. These assignments are debatable and await proper revision of type material, but for the time being we keep here the customary names. The status of *L. chagosensis* is also discussed above under *Ascoleucetta sagittata*.

#### *Leucetta chagosensis* Dendy, 1913

Figures 37a–f, 38a–d

*Leucetta chagosensis* Dendy, 1913: 10, Pl. 1 fig. 6, Pl. 4 fig. 2; Gosliner *et al.*, 1996: 16, photos 3 and 5; Lévi *et al.*, 1998: 77; Wörheide & Hooper, 1999: 882, figs 8H–M (with additional synonyms); Borojevic & Klautau, 2000: 194, fig. 6; Wörheide *et al.*, 2002: 1753; Baine & Harasti, 2007: 15.  
*Leucetta* 'lemon' Colin & Arneson, 1995: 60, photo 230.

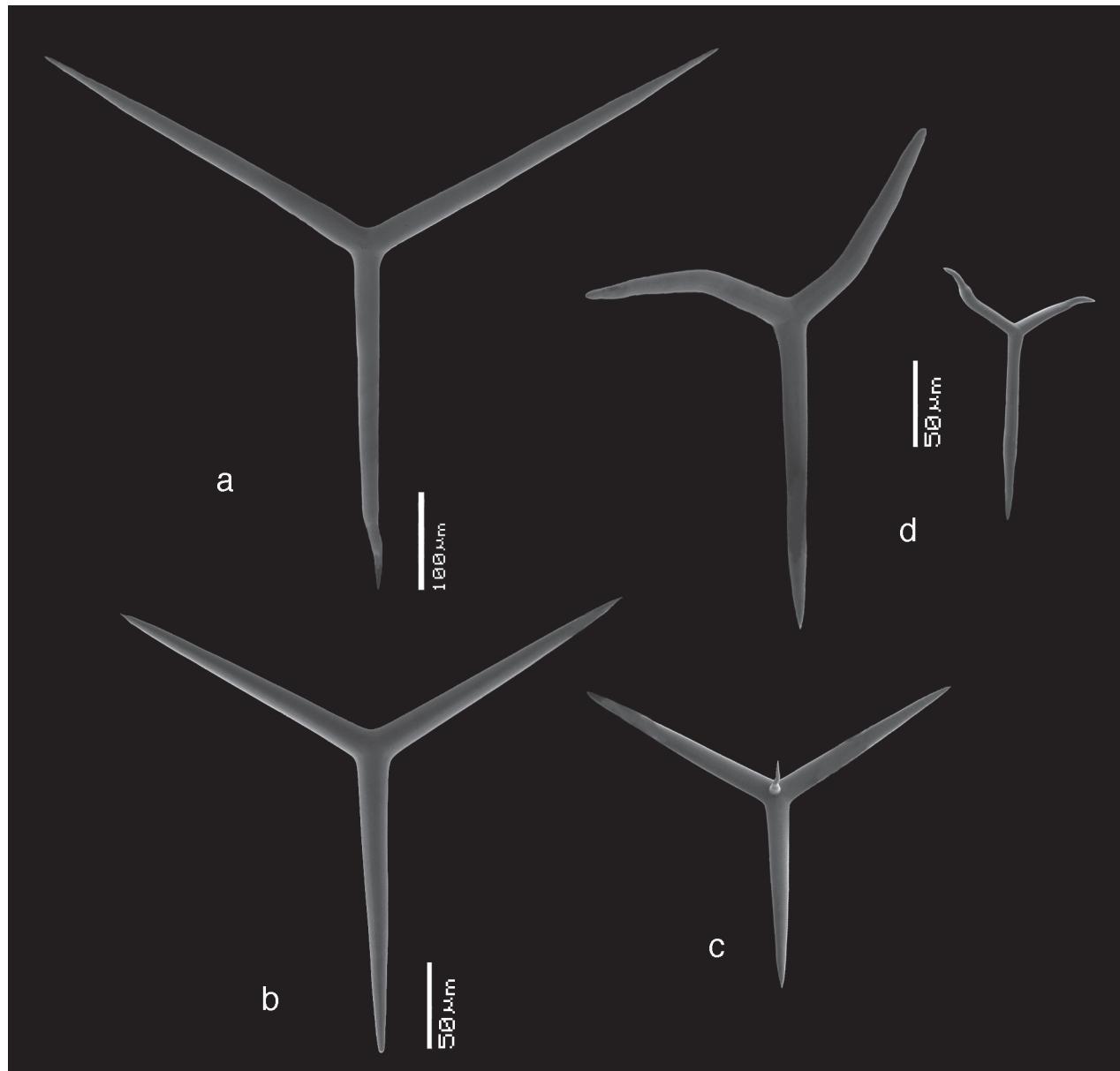
**Material examined.** ZMA Por. 08048, Indonesia, Nusa Tenggara, N of Sumbawa, Bay of Sanggar, 8.32°S 118.24°E, depth 2–4 m, SCUBA, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition stat. 114/II/05, 22 September 1984; ZMA Por. 08513, Indonesia, Nusa Tenggara, N of Sumbawa, Bay of Sanggar, 8.32°S 118.24°E, depth 5–7 m, SCUBA, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition stat. 114/III/16, 21 September 1984; ZMA Por. 08694, Indonesia, Maluku, Pulau Pulau Maisel, reef edge N of Mai, 5.4667°S 125.5167°E, depth 6–13 m, SCUBA, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition stat. 013/IV/22, 4 September 1984; ZMA Por. 08923, Indonesia, SE Sulawesi, NE Take Bone Rate, S of Tarupa Kecil, 6.5°S 121.1333°E, depth 10–15 m, SCUBA, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition stat. 133/IV/42, 25 September 1984; ZMA Por. 10846, Indonesia, Nusa Tenggara, Bali, Pulau Menjangan, 8.1167°S 114.5167°E, depth 4 m, coll. C.C. Hofman, #11, 30 July 1991; ZMA Por. 15947, Indonesia, Sumatera, Padang, Pandan Island, 0.3833°S 100.2167°E, depth 10 m, coll. M. Pampus, 7 November 1995; ZMA Por. 16012, Indonesia, Sulawesi, Spermonde Archipelago, Bone Baku, 5.132°S 119.361°E, depth 6 m, SCUBA, coll. B.W. Hoeksema, 14 May 1997; ZMA Por. 17167, Indonesia, SW Sulawesi, Spermonde Archipelago, Kapoposang Island, 4.6885°S 118.9367°E, depth 12.3 m, coll. R.A. Edrada, #TM84, 7 August 1997; ZMA Por. 17364, Indonesia, SW Sulawesi, Spermonde Archipelago, Barong Lombo, depth 14.4 m, coll. R.A. Edrada, #TM14, 8 August 1997; ZMA Por. 17555, Papua New Guinea, 10.9561°S 150.4188°E, depth 12–18 m, SCUBA, coll. Rachel Sonnenschein, #02126, 28 May 2002; ZMA Por. 17709, Papua New Guinea, Milne Bay, 9.1695°S 150.3012°E, depth 9 m, SCUBA, coll. Karen Tenney, #03554, 17 December 2003; ZMA Por. 19879, Indonesia, North Sulawesi, Siladen Island, 1.63°N 124.8°E, depth 10 m, coll. S. Tsukamoto, June 2006; RMNH Por. 1627, Palau, Koror, Siaes Reef, western barrier, 7.3116°N 134.2268°E, depth 25 m, SCUBA, coll. N.J. de Voogd, #KOR07/170505/045, 17 May 2005; RMNH Por. 1628, Palau, Koror, Mutremdiu, W side Uchelbeluu Reef, 7.2737°N 134.5241°E, depth 20 m, SCUBA, coll. N.J. de Voogd, #KOR.03/210505/087, 21 May 2005; RMNH Por. 1652, Palau, Koror, Toagel Mlungi Channel, western barrier reef off Babeldaob, 7.5425°N 134.4685°E, depth 27 m, SCUBA, coll. N.J. de Voogd, #KOR09/180505/53B, 18 May 2005; RMNH 1792, Indonesia, NE Kalimantan, Berau Islands, NE-side Maratua Island, 2.2802°N 118.6029°E, depth 0–30 m, SCUBA, coll. C. Fransen, #BER17/101003/092, East Kalimantan Expedition 2003, 10 October 2003; RMNH Por. 1880, Indonesia, NE Kalimantan Islands, off Tanjung Batu, 2.2396°N 118.0934°E, depth 0–30 m, SCUBA, coll. B.W. Hoeksema, #BER19/131002/151, East Kalimantan



**FIGURE 37.** *Leucetta chagosensis* Dendy (1913), a, habitus *in situ* of ZMA Por. 16012 from SW Sulawesi (photo B.W. Hoeksema), b, habitus *in situ* of ZMA Por. 17709 from Papua New Guinea (photo K. Tenney), c, habitus ‘on deck’ of samples ZMA Por. 17167 from SW Sulawesi, d, tangential view of surface skeleton (scale bar = 500  $\mu\text{m}$ ), e, cross section of peripheral region (scale bar = 500  $\mu\text{m}$ ), f, oscular rim of ZMA Por. 17167 showing concentration of sagittal triactines (arrows) (scale bar = 200  $\mu\text{m}$ ).

Expedition 2003, 13 October 2003; RMNH Por. 1923, Indonesia, Nusa Tenggara, Bali, SE-end of Tulamben beach, 8.2778°S 115.5959°E, depth 18 m, SCUBA, coll. N.J. de Voogd, #BAL22/NV/130401/183, Bali Lombok Strait Expedition 2001, 13 April 2001; RMNH Por. 2910, Indonesia, Nusa Tenggara, Bali, NE side of Pulau Serangan, off lighthouse, 8.7214°S 115.2586°E, depth 0–17 m, SCUBA, coll. N.J. de Voogd, #BAL14/050401/073, Bali Lombok Strait Expedition 2001, 5 April 2001; RMNH Por. 9196 Indonesia, Halmahera, Maitara Maitara W, 0.7299°N 127.3624°E, depth 0–30 m, SCUBA, coll. N.J. de Voogd, #TER09/291009/, Ternate-Halmahera Expedition 2009, 29 October 2009; RMNH Por. 9197, Indonesia, Halmahera, off Hiri Pulau Maka, 0.9119°N 127.3091°E, depth 0–30 m, SCUBA, coll. N.J. de Voogd, #TER13/311009/, Ternate-Halmahera Expedition 2009,

31 October 2009; RMNH Por. 9348, Indonesia, off Halmahera mainland, Teluk Dodinga, Karang Galiasa Kecil W, 0.8525°N 127.5888°E, depth 0–30 m, SCUBA, coll. N.J. de Voogd, #TER39/141109/, Ternate-Halmahera Expedition 2009, 14 November 2009.



**FIGURE 38.** *Leucetta chagosensis* Dendy (1913), SEM images of the spicules of ZMA Por. 08694 from the Maisel Archipelago (Banda Sea), a, large triactine from the surface skeleton, b, small triactine, c, tetractine, d, sagittal triactines.

**Description.** (Figs 37a–c) Yellow globular, semiglobular or massively lobate sponge with one or more prominent oscules with slightly raised rim. There is usually an ‘atrium’ or large internal cavity, while the choanosome is provided with irregularly elongate radiate canals. Size up to 12 x 8 x 8 cm. Surface optically smooth, but harsh to the touch. Consistency toughly compressible.

**Histology.** Leuconoid aquiferous system.

**Skeleton.** Ectosomal skeleton (Fig. 37d) a thin layer of small triactines forming small rounded (‘alveolar’) meshes, carried by subectosomal large triactines. Choanosomal skeleton lacunose (Fig. 37e), in places similar to ectosomal arrangement of small alveolae, with large lacunae. These lacunae are bordered by rare tetractines, sticking into the lumen with their apical actines. Oscular rims have a layer of sagittal triactines (Fig. 37f arrows).

**Spicules.** (Figs 38a–d) Large triactines, small triactines, tetractines.

Large triactines (Fig. 38a), equiangular equiaxial, 274–480.1–720 x 20–32.3–60 µm.

Small triactines (Fig. 38b), equiangular equiaxial, 102–138.9–186 x 8–10.9–17 µm, rarely some triactines have crooked ‘paired’ or single actines and these may then appear sagittal (Fig. 38d); these are particularly concentrated in the rims of the oscules (see arrows in Fig. 37f) and are of the same general size as the regular small triactines.

Small tetractines (Fig. 38c), rare, with equiangular equiaxial basal radiate system, actines 104–126.2–135 x 9–11.5–13 µm, with small apical actines, 12–15 x 6–8 µm.

**Ecology.** Shallow-water reefs.

**Distribution.** Indonesia, Papua New Guinea, Palau Islands. Elsewhere reported from a.o. Northeast Australia, New Caledonia, Vanuatu, French Polynesia, the Western Indian Ocean, and the Red Sea (Wörheide *et al.* 2008).

**Remarks.** By the bright yellow color our specimens differ clearly from the pink or whitish *Leucetta microraphis* (cf. below), and also by the much larger size of the triactines of that species.

*L. chagosensis* may be confused with small light-colored *Pericharax orientalis* sp.nov., but the surface of that species is supported by a layer of special cortical sagittal triactines, lacking in the present species. The oscular sagittal triactines of *L. chagosensis* bear a resemblance to these cortical triactines of *P. heteroraphis*.

Furthermore, there is considerable resemblance to *Ascoleucetta sagittata* (cf. above), a yellow massive-globular species with a central atrium and strongly folded choanosome. If this species is genuinely different from *L. chagosensis* then they can be kept apart by the lack of oscules and oscular rims with concentrations of sagittal triactines in *A. sagittata*. We will await further research before it can be decided that the two must be merged.

Over its large distribution, this species was demonstrated to have considerable genetic structure with recognizable discrete geographic populations (see Wörheide *et al.*, 2002).

### ***Leucetta microraphis* Haeckel, 1872**

Figures 39a–d, 40a–d

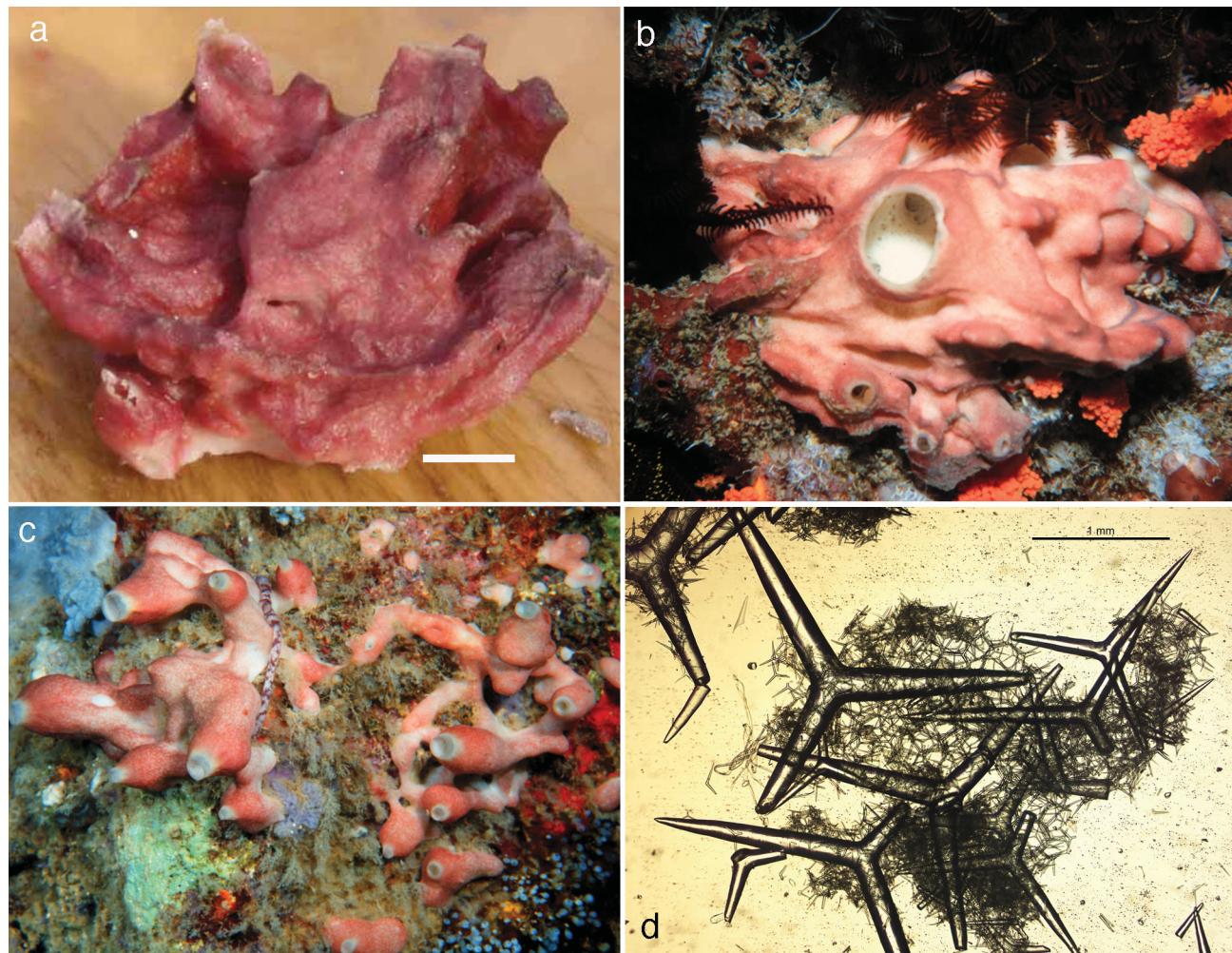
*Leucetta primigenia* var. *microraphis* Haeckel, 1872: 119, pl. 21 Figs 10–17.

*Leucetta primigenia*; Lendenfeld, 1885: 1117; De Laubenfels, 1954: 253, fig. 179; Borojevic, 1967b: 3, fig. 2; Borojevic & Klautau, 2000: 193, fig. 5; Colin & Arneson, 1995: 60, photo 229; Gosliner *et al.*, 1996: 16, photo 4; Erhardt & Baensch, 1998: 22.

?*Leucetta solida*; Breitfuss, 1896: 434; 1898: 169 (not: Schmidt, 1862).

**Material examined.** ZMA Por. 00152, Indonesia, Nusa Tenggara, E coast of Sumbawa, Sapeh Bay, 8.5839°S 119.0324°E, depth 0–38 m, dredge and reef exploration, Siboga Expedition stat. 311, 12 February 1900; ZMA Por. 08108, Indonesia, Nusa Tenggara, N of Sumbawa, Bay of Sanggar, 8.3417°S 118.262°E, depth 1–4 m, coastal reef with sea grass, snorkeling, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition stat. 120/II/06, 21 September 1984; ZMA Por. 08510, Indonesia, Nusa Tenggara, N of Sumbawa, Bay of Sanggar, 8.32°S, 118.24°E, depth 5–7 m, SCUBA, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition 1984 stat. 114/III/13, 21 September 1984; ZMA Por. 08649, Indonesia, SE Sulawesi, SW Salayar, NW coast of Pulau Guang, 6.35°S, 120.45°E, depth 4–12 m, SCUBA, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition 1984 stat. 152/III/32, 28 September 1984; ZMA Por. 09051, Indonesia, Nusa Tenggara, NE coast of Sumba, 9.95°S 120.8°E, depth 50 m, dredge, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition 1984 stat. 68/V/17, 16 September 1984; ZMA Por. 14536, Indonesia, North Sulawesi, Bunaken, SW Nain Island, 1.7681°N 124.7671°E, depth 18 m, SCUBA, coll. B.W. Hoeksema, #SYMBIOSPONGE 98/NS/MAY08/BH090, 8 May 1998; ZMA Por. 15917, Indonesia, Sumatera, W, Padang, Pandan Island, W, 0.3833°S 100.2167°E, depth 5 m, SCUBA, coll. M. Pampus, #PA B13, 7 November 1995; ZMA Por. 15936, Indonesia, Sumatera, Padang, Pisang Island, 0.95°S 100.1667°E, depth 5 m, SCUBA, coll. M. Pampus, # PP1, 1 December 1995; ZMA Por. 16011, Indonesia, SW Sulawesi, Spermonde Archipelago, Samalona W, 5.125°S 119.342°E, depth 5–10 m, SCUBA, coll. B.W. Hoeksema, #2, 8 May 1997; ZMA Por. 16682, Indonesia, SW Sulawesi, Spermonde Archipelago, Lae-lae, 5.1336°S 119.3381°E, depth 5–10 m, SCUBA, coll. N.J. de Voogd, #LL/NV/240597/D, 24 May 1997; ZMA Por. 17740, Indonesia, Kalimantan, Berau Islands, SE-side Kakaban Island, 2.1261°N 118.5517°E, depth 0–30 m, SCUBA, coll. R.G. Moolenbeek, #BER03/36; ZMA Por. 20126, Indonesia, North Sulawesi, S of Siladen Island, 1.63°N 124.8°E, depth 10 m, coll. S. Tsukamoto, #06M039, 6 June 2006; RMNH Por. 1777, Indonesia, NE Kalimantan, Berau Islands, NE-side Maratua Island, 2.2802°N 118.6029°E, depth 5 m, SCUBA, coll. K. van

Egmond, #BER17/101003/093, East Kalimantan Expedition 2003, 10 October 2003; RMNH Por.1809, Indonesia, Nusa Tenggara, Bali, Tulamben area, bay S of ‘Emerald’ Hotel, 8.2847°S 115.6031°E, depth 30 m, SCUBA, coll. N.J. de Voogd, #BAL23/NV/140401/205, Bali Lombok Strait Expedition 2001, 14 April 2001; RMNH Por. 1883, Indonesia, Sulawesi, Spermonde Archipelago, Bone Lola, 5.0°S 119.35°E, depth 6 m, SCUBA, coll. N.J. de Voogd, 29 October 2002; RMNH Por. 2129, Indonesia, Java Sea, off Jakarta, Kepulauan Seribu, Payung Besar Island, E side, 5.8219°S 106.5631°E, depth 10–15 m, SCUBA, coll. N.J. de Voogd, #SER43/260905/167, Kepulauan Seribu Expedition 2005, 26 September 2005; RMNH Por. 6610, Indonesia, North Sulawesi, Lembeh Strait, SW Sarena Kecil, 1.4555°N 125.2236°E, depth 25 m, SCUBA, coll. K. van Egmond, #LEM15/070212, 7 February 2012.



**FIGURE 39.** *Leucetta micrraphis* Haeckel (1872), a, habitus ‘on deck’ of ZMA Por. 20126 from N Sulawesi (scale bar = 1 cm) b, habitus *in situ* of ZMA Por. 16011 from SW Sulawesi (photo B.W. Hoeksema), c, habitus *in situ* (not collected), photo B.W. Hoeksema, d, overview of spicules of ZMA Por. 08649 from Salayar (scale bar = 1 mm).

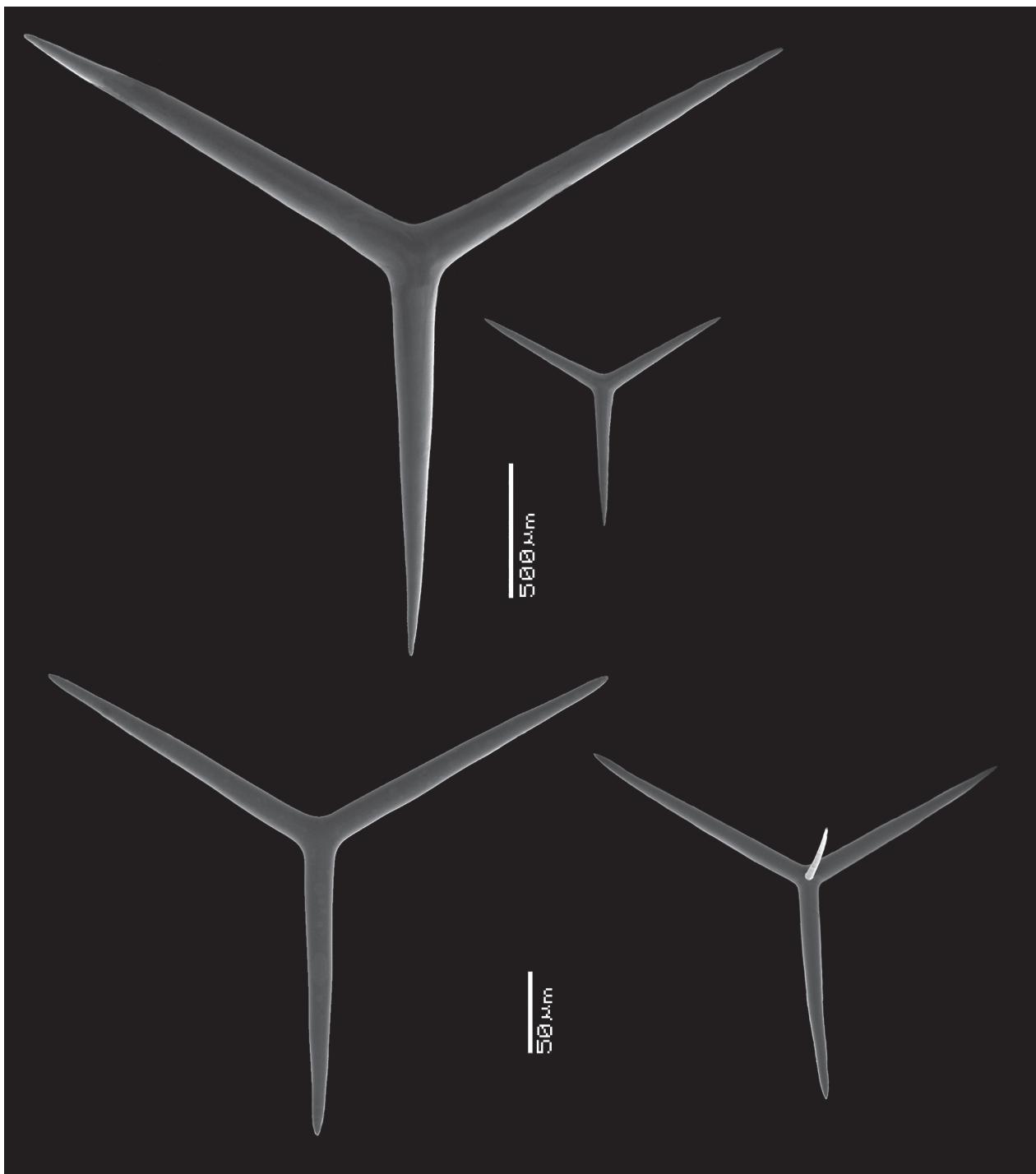
**Description.** (Figs 39a–c) Dark pink, brownish pink or pinkish-white sponges with variable shape, lobate, flabellate or massive, with raised or terminal oscules of 0.5–2 cm diameter, atrial lumen up to 2 cm in diameter. Size up to 11 x 10 x 6 cm.

**Histology.** Leuconoid aquiferous system.

**Skeleton.** Essentially ‘alveolar’, small rounded meshes encircling the choanocyte chambers. Just below the surface there are giant triactines (Fig. 39d).

**Spicules.** (Figs 40a–d) Giant triactines, small triactines, tripods, small tetractines.

Giant triactines (Fig. 40a), equiangular equiaxial, with conical actines, 1175–1536.3–1980 x 132–169.3–216  $\mu\text{m}$ .



**FIGURE 40.** *Leucetta microraphis* Haeckel (1872), SEM images of the spicules of ZMA Por. 16682 from SW Sulawesi, a, giant triactine, b, intermediate-sized triactine, c, small triactine, d, tetractine.

Intermediate (Fig. 40b) and small (Fig. 40c) triactines, equiangular equiaxial, 99–175.7–270 x 8–15.8–33  $\mu\text{m}$ ; rare tripods with undulating paired actines 150–200  $\mu\text{m}$ .

Small tetractines (Fig. 40d), rare, actines of basal radiate system 135–150 x 9–12  $\mu\text{m}$ , apical actines 50–70  $\mu\text{m}$ .

**Ecology.** Shallow-water reefs down to 30 m.

**Distribution.** Indonesia, Papua New Guinea, New Caledonia, tropical Australia.

**Remarks.** This species is in urgent need of revision. Haeckel's treatment of the name *L. microraphis* makes the species unrecognizable and its type locality unknown. No original specimens have ever been redescribed. The use of the name is entirely based on 'tradition'. Pinkish brown specimens identified by us under this name can be

confused with smaller brownish specimens of *Pericharax orientalis* sp.nov., but the sharp ridges and yellow interior color of that species do not occur in *L. microraphis*.

Breitfuss' (1896, 1898) record of the Mediterranean *Leucetta solida* (Schmidt, 1862 as *Grantia*) from Ternate quite possibly concerns the present species as large and small triactines were mentioned. No detailed spicule size data were provided by Breitfuss.

### Genus *Pericharax* Poléjaeff, 1883

**Remark.** The commonly reported tropical shallow-water *Pericharax heteroraphis* of authors is here given a new name for reasons presented below.

#### *Pericharax orientalis* sp. nov.

Figures 41a–e, 42a–e

*Pericharax heteroraphis*; Dendy, 1913: 13; Colin & Arneson, 1995: 60, photo 232, (?also photo 231); Gosliner *et al.*, 1996: 16, photo 6; Allen & Steene, 1996: 30–31; Wörheide & Hooper, 1999: 886, figs 9G–M; Borojevic & Klautau, 2000: 195; Baine & Harasti, 2007: 15 (not: *Pericharax carteri* var. *heteroraphis* Poléjaeff, 1883: 66, pl. II fig. 5, pl. VII fig. 8 = *P. carteri*)

**Material examined.** Holotype RMNH Por. 5259, Indonesia, Halmahera, restaurant Floridas, 0.7599°N 127.3571°E, depth 12 m, SCUBA, coll. N.J. de Voogd, #TER03/251009/010, Ternate Halmahera Expedition 2009, 25 October 2009.

Paratypes ZMA Por. 08220, Indonesia, SE Sulawesi, Tukang Besi Islands, southern reef of Karang Kaledupa, east entrance, 5.9333° S 123.8° E, depth 4–11 m, SCUBA, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition stat. 016/III/08, 6 September 1984; ZMA Por. 17280, Indonesia, Sumatera, Painan coast, Aua Island, 60 km from Padang, 1.3667°S 100.5667°E, depth 5–10 m, SCUBA, coll. R.A. Edrada, #DH77, 13 July 2002; RMNH Por. 8551, Indonesia, Nusa Tenggara, Bali, Tulamben area, bay S of Emerald Hotel, 8.2847°S 115.6031°E, depth 20 m, SCUBA, coll. N.J. de Voogd, #BAL23/NV/150401/207, Bali Lombok Strait Expedition 2001, 15 April 2001.

Additional specimens. ZMA Por. 00149, Indonesia, Irian Jaya, 1.7083° S 130.7916° E, depth 32 m, trawled, coll. Siboga Expedition stat. 164, 20 August 1899; ZMA Por. 00150, Indonesia, Irian Jaya, 1.7083° S 130.7916° E, depth 32 m, trawled, coll. Siboga Expedition stat. 164, 20 August 1899; ZMA Por. 00151, Indonesia, Irian Jaya, 1.7083° S 130.7916° E, depth 32 m, trawled, coll. Siboga Expedition stat. 164, 20 August 1899; ZMA Por. 00181a, Indonesia, S Sulawesi, anchorage off S point Kabaena Island, 5.5165° S 121.9502° E, depth 22 m, trawled, coll. Siboga Expedition stat. 209, 23 September 1899; ZMA Por. 00181b, Philippines, Sulu Islands, anchorage off N Ubian, 6.126° N 120.4333° E, depth 16–23 m, trawled, coll. Siboga Expedition stat. 099, 28 June 1899; ZMA Por. 06526, Indonesia, Nusa Tenggara, N of Sumbawa, Bay of Sanggar, 8.3417°S 118.2617°E, depth 0–1 m, snorkeling, coll. J. Brouns, Indonesian-Dutch Snellius II Expedition 1984 stat. 120/A2, 21 September 1984; ZMA Por. 08561, Indonesia, Sulawesi, SE, Take Bone Rate, NE, western edge of reef Taka Garlarang, 6.45°S 121.2083°E, depth 6–8 m, SCUBA, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition 1984 stat. 147/III/08, 27 September 1984; ZMA Por. 08627, Indonesia, Sulawesi, SW, Salayar, SW, Pulau Guang, NW coast, 6.35°S 120.45°E, depth 4–12 m, SCUBA, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition 1984 stat. 152/III/09, 28 September 1984; ZMA Por. 08628, Indonesia, SE Sulawesi, Salayar SW, Pulau Guang, NW coast, 6.35°S 120.45°E, depth 4–12 m, SCUBA, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition stat. 152/III/10, 28 September 1984; ZMA Por. 08786, Palau Islands, Argulpelu Reef, depth 15 m, SCUBA, coll. M.K. Harper, #DJF 81–133, 1981; ZMA Por. 16010, Indonesia, SW Sulawesi, Spermonde Archipelago, Kudinggaeng Keke, 5.102°S 119.286°E, depth 10–15 m, SCUBA, coll. B.W. Hoeksema, #4, 24 April 1997; ZMA Por. 17168, Indonesia, SW Sulawesi, Spermonde Archipelago, Kapoposang, 4.6885°S 118.9367°E, depth 13.2 m, SCUBA, coll. R.A. Edrada, #TM87, 8 August 1997; ZMA Por. 17364, Indonesia, Sulawesi, Spermonde Archipelago, Barang Lombo, 5.05°S 119.3°E, depth 14.4 m, SCUBA, coll. R.A. Edrada, 25 July 1997; ZMA Por. 17412, Indonesia, SW Sulawesi, Spermonde Archipelago, Bone Lola, 5.0°S 119.35°E, depth 6 m, SCUBA, coll. N.J. de Voogd, #NV/BL/291002/349, 29 October 2002; ZMA Por. 17558, Papua New Guinea, Solomon Sea, 10.22°S

150.87°E, depth 18–24 m, SCUBA, coll. R. Sonnenschein, #02160, 2 June 2002; ZMA Por. 17708, Papua New Guinea, Milne Bay, 9.62°S 150.9556°E, depth 6–21 m, SCUBA, coll. R. Sonnenschein, #03513, 12 December 2003; ZMA Por. 17740, Indonesia, Kalimantan, Berau Islands, SE side Kakaban Island, 2.1261°N 118.5517°E, depth 25–30 m, SCUBA, coll. R.G. Moolenbeek, #BER03/36, 2003; RMNH Por. 1633, Palau, Koror, W of Ulong Island, Ngerumekaul Channel, 7.2819°N 134.2454°E, depth 27 m, SCUBA, coll. N.J. de Voogd, #KOR08/170505/053A, 17 May 2005; RMNH Por. 1935, Indonesia, Manddin, between Bunaken and Manado Tua, depth 17 m, SCUBA, coll. N.J. de Voogd, #MD4/180502/093, 18 May 2002; RMNH Por. 9351, Indonesia, Sulawesi, Kabaena Island, anchorage off S point, 5.5165°S 121.9502°E, depth 22 m, dredge, hard bottom, coll. Siboga Expedition stat. 209, 23 September 1899; RMNH Por. 9352 Philippines, Sulu Islands, anchorage off North Ubian, 6.125°N 120.4333°E, depth 16–23 m, dredge, hard bottom, coll. Siboga Expedition stat. 099, 30 June 1899.

**Description.** (Figs 41a–c) Upright thick-walled tubular individuals with central vent, occasionally several individuals are grouped together (Fig. 41a). In mature condition the sides of the tubes are sharply ridged (Fig. 41a, c), and colors are a mottled reddish brown, green-brown, grey-green and greyish yellow (Fig. 41a). In young specimens, which are usually lighter colored, the walls often lack ridges and at most show rounded folds (Fig. 41b). Color of the atrial wall (inside the vent) is yellow or limegreen. Size in mature condition may be considerable. The preserved holotype is 11 cm high and 15 cm wide (the preserved part is one half of the *in situ* specimen), with vents approximately 4 x 1.5 cm; one of the paratypes is even 15 cm high. Overall, specimens may reach 15–30 cm in height, and 8–20 cm in widest expansion. Surface smooth, but harsh to the touch, prickly because of large triactines. Consistency firm to hard, usually somewhat compressible.

**Histology.** Leuconoid aquiferous system.

**Skeleton.** At the surface (Fig. 41e) there is a cortex of small, predominantly slightly sagittal triactines, overlying a layer of subdermal rounded lacunae supported by subcortical giant triactines (Fig. 41d). The choanosomal skeleton is basically alveolar but this is often obscured (Fig. 41d), consisting of small regular triactines surrounding the choanocyte chambers. The atrial wall (Fig. 41f) shows a predominance of small tetractines, with their apical actines protruding in the atrium.

**Spicules.** (Figs 42a–e) Giant triactines, small regular triactines, small sagittal triactines, small tetractines.

Giant triactines (Fig. 42a), equiangular equiaxial, tapering to conical ends, 360–834.2–1560 x 25–67.9–132 µm.

Small regular triactines (Fig. 42c), 60–159.3–228 x 7–12.2–18 µm.

Ectosomal sagittal triactines (Fig. 42b), unpaired actines 61–95.1–132 x 6–8.6–13 µm, paired actines 60–83.2–138 x 5–8.1–12 µm; rarely the sagittal triactines develop a fourth actine (Fig. 42d).

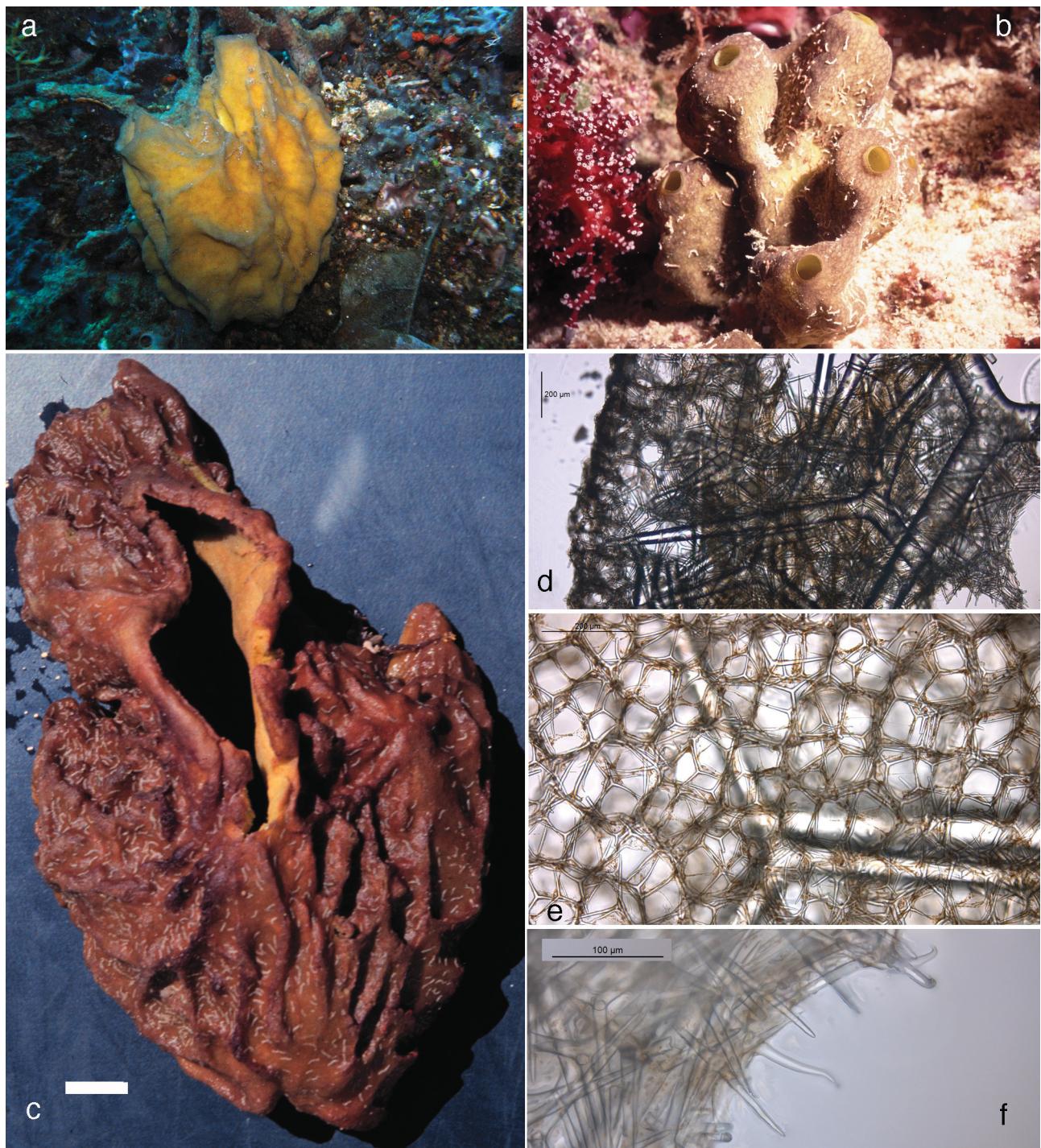
Atrial small regular tetractines (Fig. 42e), actines of basal triradiate system 126–177.8–228 x 7–9.9–14 µm, apical actines curved, 57–87.4–111 x 6–7.4–9 µm.

**Ecology.** Coral reefs, 4–36 m.

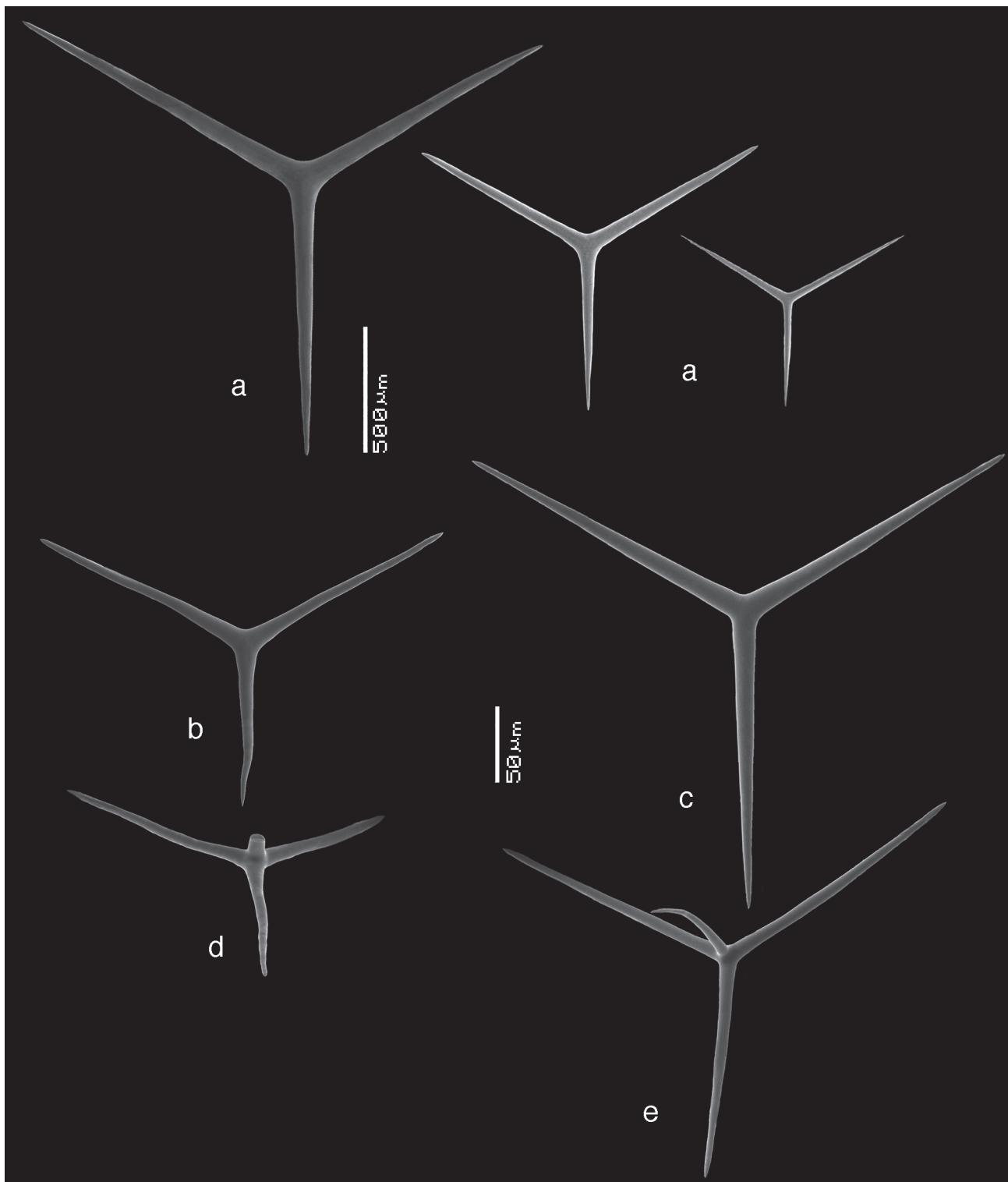
**Distribution.** Indonesia, Papua New Guinea, NE Australia, New Caledonia, Philippines, Seychelles, Southern Japan (not: Tristan da Cunha).

**Remarks.** This is a very common species, as is evident from the frequency with which it appears in underwater color guides. In many ways it can be called iconic: it is almost certainly one of the largest calcareous sponges, and has a distinctive mottled brown-yellow appearance and hard consistency, quite the opposite of mainstream calcareous sponges which tend to be small, whitish and soft. Despite its common occurrence its usually employed name, *Pericharax heteroraphis* turned out to be problematic and we were forced to replace it for reasons given below.

Our extensive material generally fits the description of a specimen from the Chagos Archipelago, Western Indian Ocean, named as *Pericharax heteroraphis* Poléjaeff, 1883 by Dendy (1913). Spicule sizes and shapes given by him match closely with ours. Dendy compared the Tristan da Cunha deep-water type material of Poléjaeff's *Pericharax carteri* var. *homoraphis* and *P. carteri* var. *heteroraphis* with his specimen. Unfortunately, he did not emphasize several observed differences with his own specimen (e.g. size of the giant triactines and shape of the apical actines of the tetractines) and failed to erect a new species for his shallow-water tropical material. It is highly unlikely that specimens from shallow-water coral reefs (4–36 m) as treated here and by Dendy (Salomon Reef, 25 m) are conspecific with the type material from 108 m deep in the cold South Atlantic waters off Tristan da Cunha. We derive this hypothesis from research into the allegedly cosmopolitan distribution of two sponge species in Calcarea (see Solé-Cava *et al.* 1991), which demonstrated that such species consist of several genetically different cryptic species with limited geographic distributions.



**FIGURE 41.** *Pericharax orientalis* sp. nov., a, habitus *in situ* of holotype RMNH Por. 5259 from Ternate (photo N.J. de Voogd), b, habitus *in situ* of RMNH 1633 from Palau (photo N.J. de Voogd), c, habitus of paratype ZMA Por. 08220 ‘on deck’ (scale bar = 1 cm), d, cross section of wall just below the oscules of holotype ZMA Por. 5259 showing cortical skeleton (left) choanosomal skeleton with giant, inytermediate and small regular triactines, and atrial skeleton (scale bar = 200 µm), e, tangential view of surface skeleton of holotype showing cortical skeleton of sagittal triactines (scale bar = 200 µm), e, detail of atrial skeleton of holotype with curved apical actines of tetractines protruding in the atrial lumen (scale bar = 100 µm).



**FIGURE 42.** *Pericharax orientalis* sp. nov., SEM figures of paratype ZMA Por. 08220, a, giant triactines, b, small sagittal triactine, c, small regular triactine, d, rare sagittal tetractine, e, regular tetractine.

A further problem is that Dendy (1913) as a first reviser failed to choose one of the two varieties described by Poléjaeff as the typical variety, which - as the nominotypical taxon in the sense of the Code - has to be called *Pericharax carteri carteri*, leaving one of the two other names as name for the second variety. According to Dendy (1913) and Dendy & Row (1913), the variety *homoraphis* is not a proper *Pericharax*, but a *Leucetta*. If we wish to save the genus name *Pericharax* from becoming a synonym of *Leucetta*, it is imperative that the variety *heteroraphis* is chosen as the typical variety, because from Poléjaeff's text and his Plate II fig. 5, and from Dendy's

(1913) comparisons, it is clear that it is the variety that has the characters of the genus *Pericharax* (e.g. the cortical skeleton). This means without any doubt (see ICBN articles 45.6.4 and 47) that the name *heteroraphis* has to be replaced by *carteri*. Hence, from now onwards the Tristan da Cunha *Pericharax* material is to be called *Pericharax carteri* Poléjaeff, 1883 with *P. heteroraphis* as an objective junior synonym. The species to which Dendy's and our specimens belong obviously needs a different name.

A candidate for it is *Pericharax peziza* Dendy, 1913 from 23 m depth off Cargados Carajos. Its skeleton is generally similar to our specimens and also the spicules do not differ significantly. However, the shape is a wide shallow cup, unlike our specimens and unlike all the specimens depicted in many color guides. Also, Dendy himself considered it a different species from his *P. 'heteroraphis'*.

*Pericharax canaliculata* Burton & Rao, 1932 from the Birmese Mergui Archipelago differs strongly in shape and spicule sizes, and might not even be a proper *Pericharax*.

For these reasons, we decided to propose the new name *Pericharax orientalis* sp.nov.

## Order Murrayonida Vacelet, 1981

### Family Lelapiellidae Vacelet, 1977

#### Genus *Lelapiella* Vacelet, 1977

##### *Lelapiella sphaerulifera* Vacelet, 1977

Figures 43a–g

*Lelapiella incrassans* subsp. *sphaerulifera* Vacelet, 1977: 362, fig. 7.

**Material examined.** ZMA Por. 09087, Indonesia, SE Sulawesi, NE Take Bone Rate, western edge of reef Taka Garlarang, 6.45°S 121.2083°E, depth 35 m, SCUBA, coll. H.A. ten Hove, Indonesian-Dutch Snellius II Expedition stat. 114/V/05, 27 September 1984.

**Description.** White encrusting sponge (Fig. 43a) on dead coral, size 1.5 x 0.5 x 0.3 cm. Surface irregular, with thin grooves and small pits; harsh to the touch.

**Skeleton.** (Fig. 43b) The cortex consists of a dense mass of spherules and tripods, carried over a large subcortical space by tracts of diactines. The basal skeleton is a mass of 'hockey-stick' diactine spicules and spherules.

**Spicules.** (Figs 43c–g) Tripods, tetractines, diactines, 'hockey-stick' diactines, spherules.

Tripods (Fig. 43c), usually inequiaxial, 171–226.2–285 x 36–46.0–57 µm.

Tetractines (Fig. 43d), rare, actines of the basal radiate system 78–100 x 9, short apical actine, 10–20 µm.

Diactines (Fig. 43g) slightly crooked in the middle, tapering to bluntly rounded endings, 126–193.2–297 x 13–17.2–27 µm

'Hockey-stick' diactines (Fig. 43f), club-shaped, 84–95.8–106 x 18–19.1–21 µm (shaft), thickened part 30–33 µm in diameter.

Spherules (Fig. 43e), bean-shaped, often asymmetrical, 26–30.2–36 x 17–18.2–20 µm.

**Ecology.** Deeper water under overhangs, in reefs.

**Distribution.** Indonesia, New Caledonia.

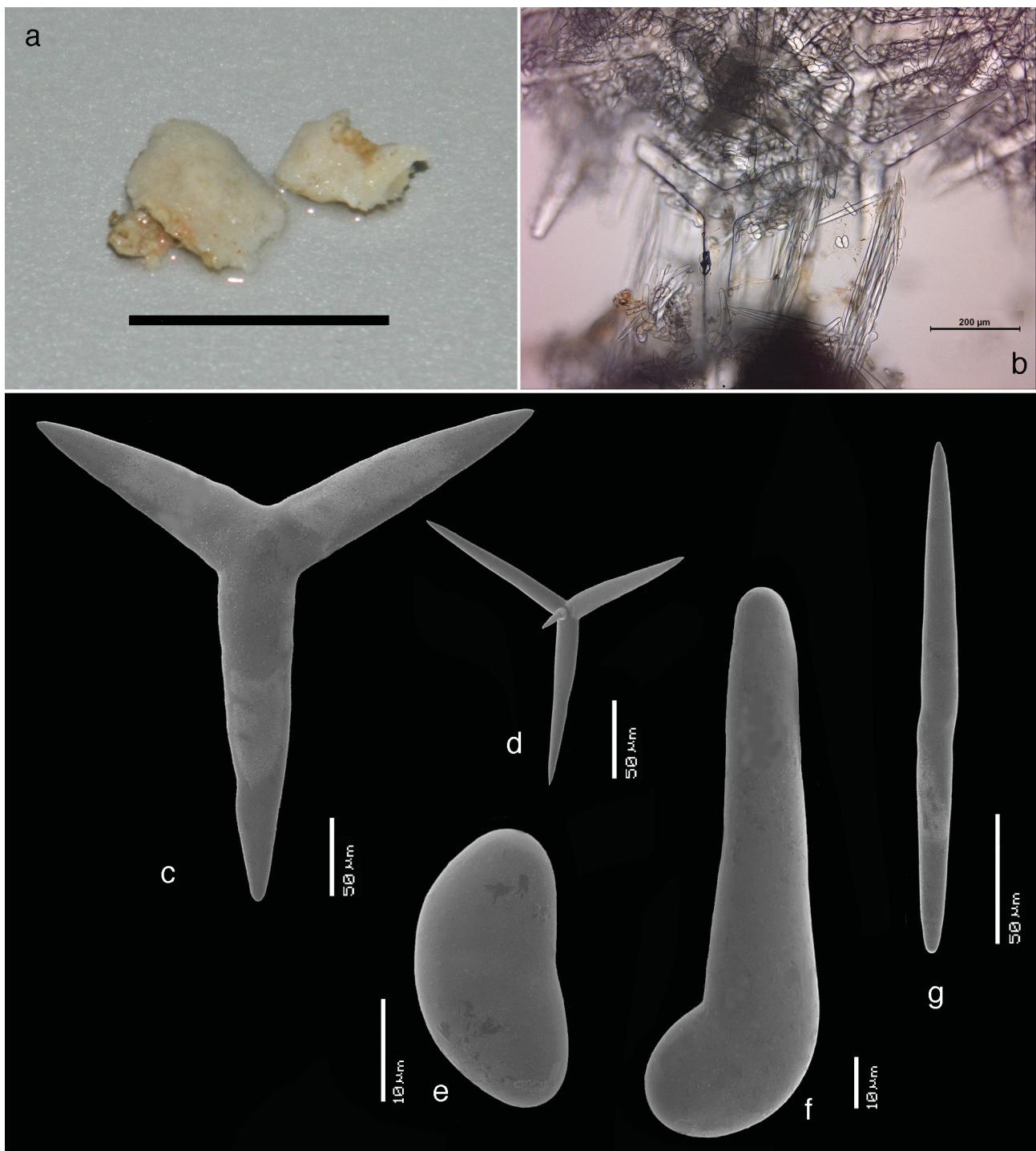
**Remark.** The present material matches the type in great detail.

## Subclass Calcaronea Bidder, 1898

### Order Leucosolenida Hartman, 1858

#### Family Sycettidae Dendy, 1893a

#### Genus *Sycetta* Haeckel, 1872

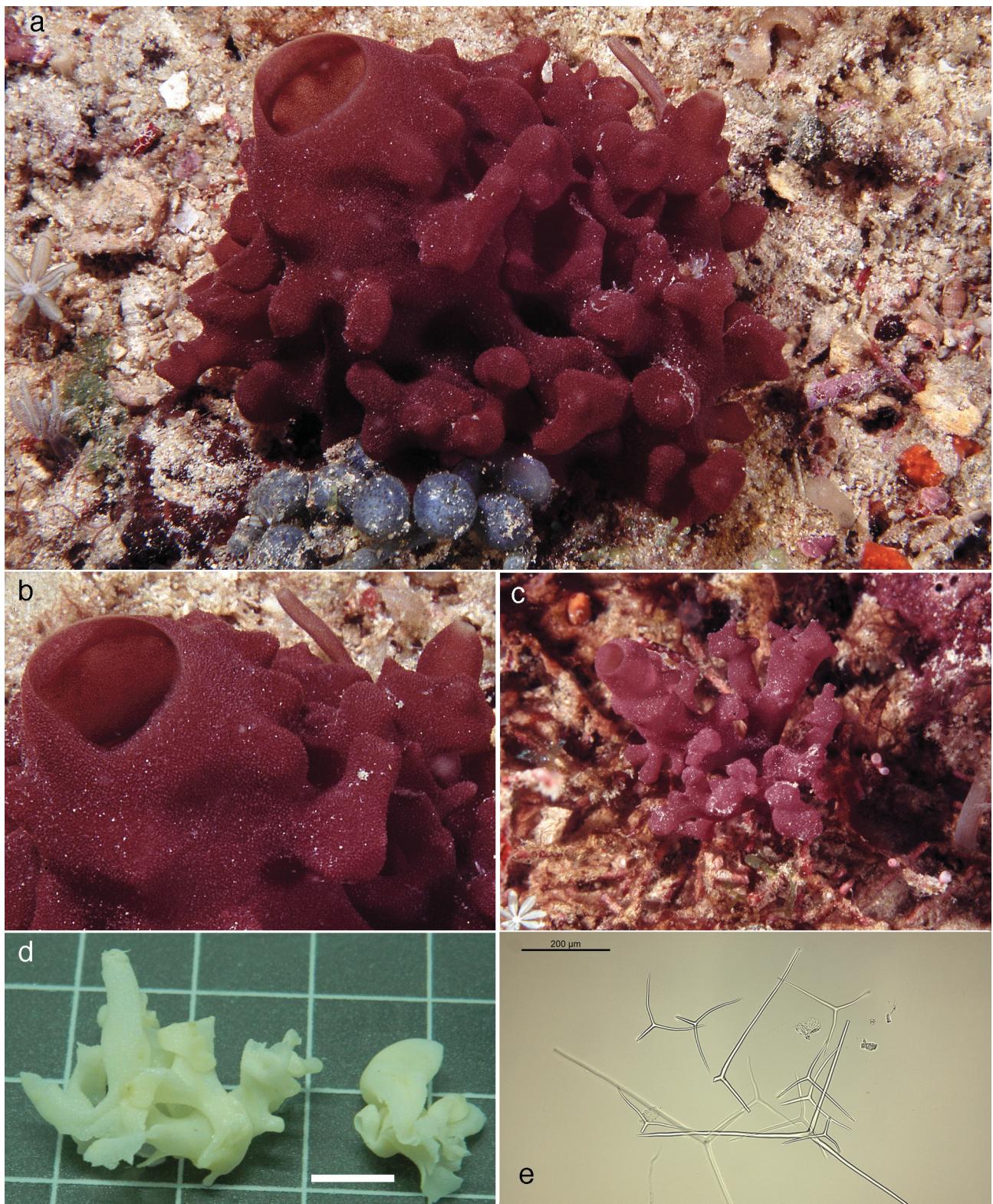


**FIGURE 43.** *Lelapiella sphaerulifera* Vacelet (1977), ZMA Por. 09087, a, preserved fragments (scale bar = 1 cm), b, cross section of cortex and subcortical space showing cortical tripods, spherules and tracts of diactines (scale bar = 200  $\mu\text{m}$ ), c–g, SEM images of the spicules, c, tripod, d, tetractine, e, spherule, f, hockeystick spicule, g, diactine.

***Sycetta vinitincta* sp. nov.**

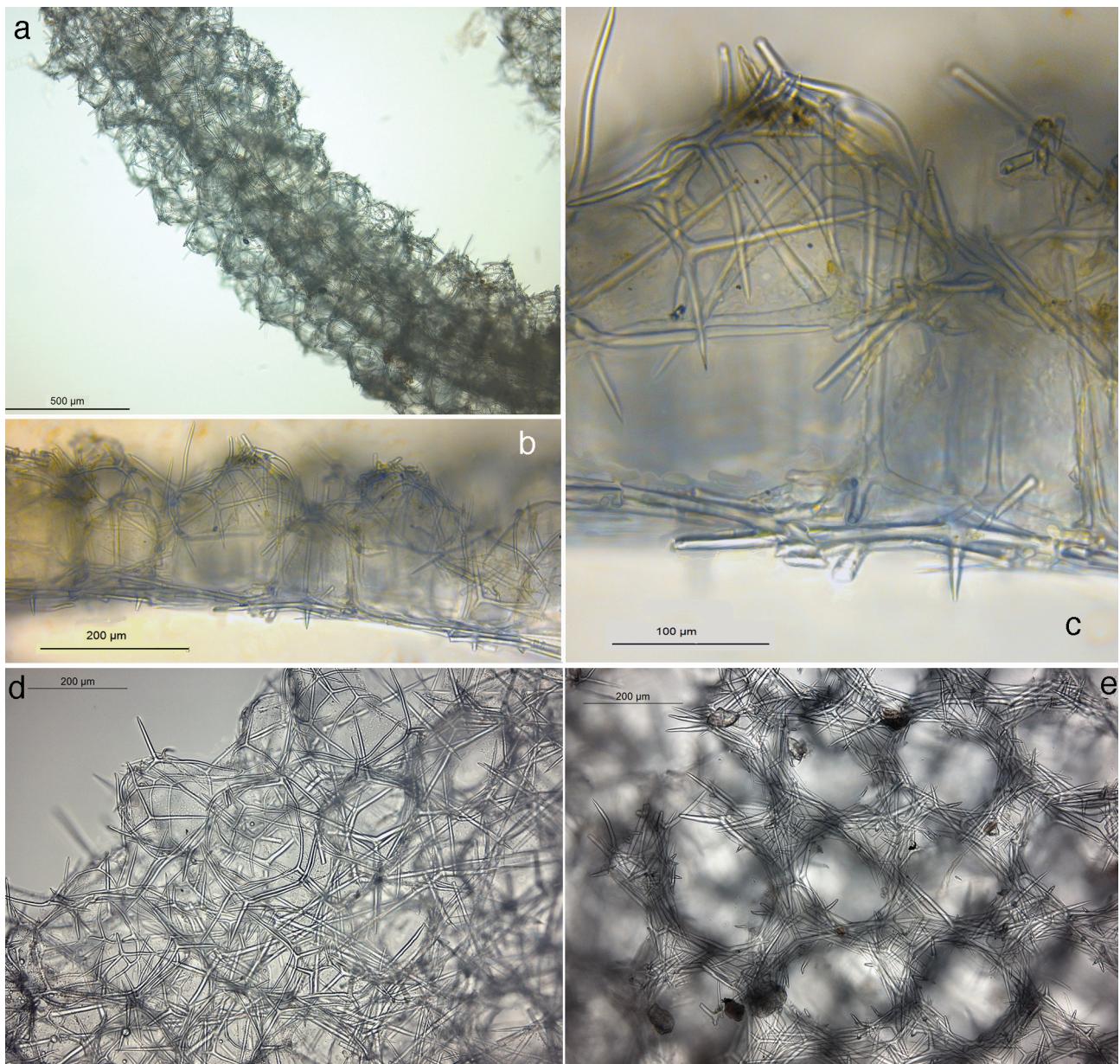
Figures 44a–e, 45a–e, 46a–h

**Material examined.** Holotype RMNH Por. 1873, Indonsesia, NE Kalimantan, Berau Islands, Samama Island, 2.1254°N 118.336°E, depth 2 m, SCUBA, coll. B.W. Hoeksema, #BER10/071003/053, Berau 2003 Expedition, 7 October 2003.



**FIGURE 44.** *Sycetta vinitincta* sp. nov., a, habitus *in situ* of the holotype RMNH Por. 1873 from the Berau region (photo B.W. Hoeksema), b, detail of holotype to show papillar surface, c, a second specimen from the same locality (not collected), d, preserved paratype ZMA Por. 08633 from Salayar (scale bar = 1 cm), e, overview of spicules (scale bar = 200  $\mu$ m).

Paratype ZMA Por. 08633, Indonesia, SE Sulawesi, Salayar, SW coast, off the NW coast of Pulau Guang, 6.35°S 120.45°E, depth 4–12 m, SCUBA, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition stat. 152/III/15, 29 September 1984.

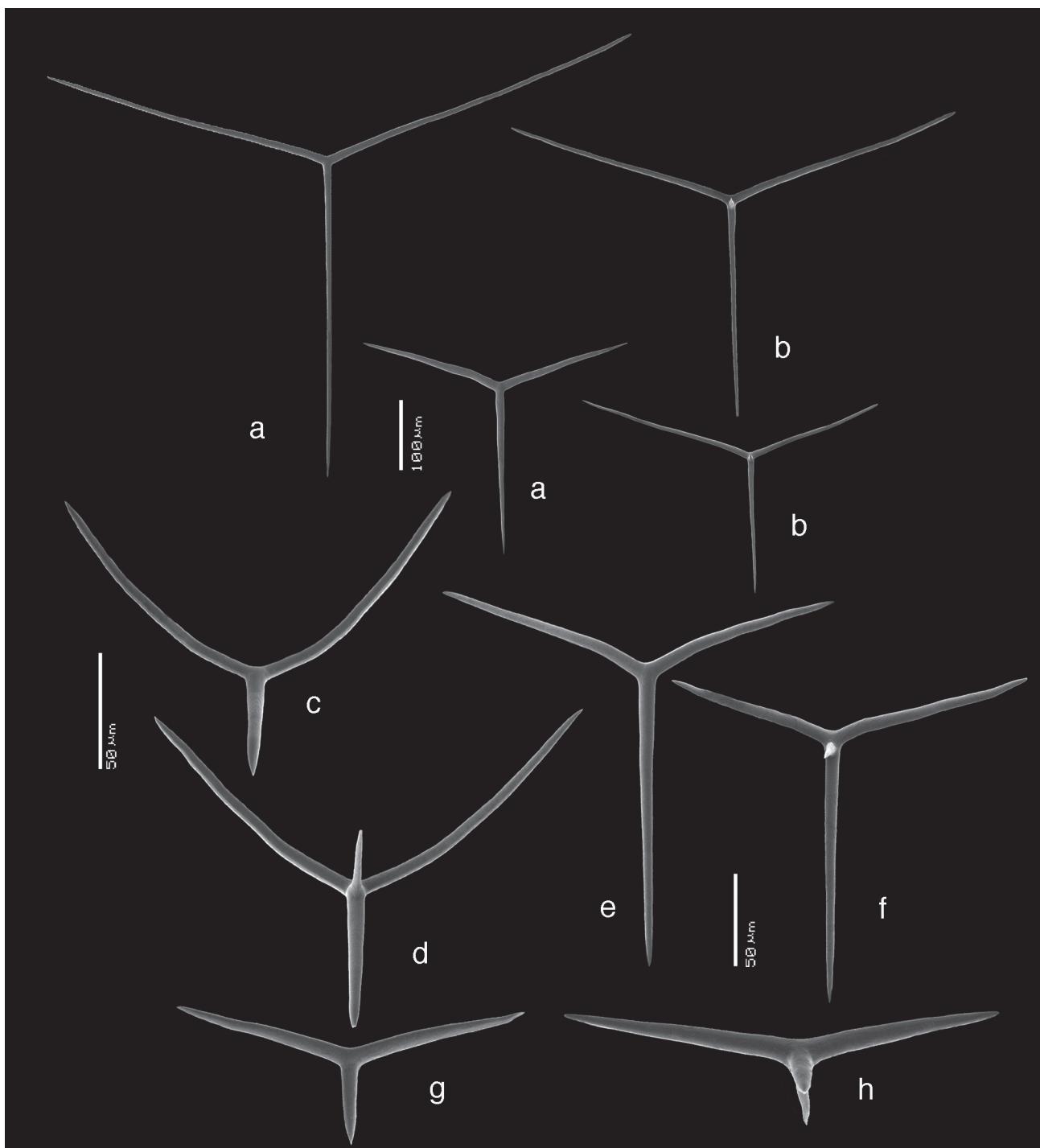


**FIGURE 45.** *Sycetta vinitincta* sp. nov., holotype RMNH Por. 1873, light microscopic images, a, overview of peripheral protrusion showing the papillary surface (scale bar = 500  $\mu\text{m}$ ), b, cross section of the tubar wall to show atrial and papillary skeleton (scale bar = 100  $\mu\text{m}$ ), c, detail of a single papilla showing ‘inarticulated’ tubar skeleton, d, tangential view of outer surface skeleton (scale bar = 200  $\mu\text{m}$ ), e, tangential view of atrial surface (scale bar = 200  $\mu\text{m}$ ).

Additional material. ZMA Por. 08221b, Indonesia, SE Sulawesi, Tukang Besi Islands, southern reef of Karang Kaledupa, 5.9333°S 123.8°E, depth 4–11 m, SCUBA, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition stat. 016/III/10, 8 September 1984.

**Description.** Wine-red irregular broadly sac-shaped thin-walled tubes (Figs 44a–c), with irregular-shaped knob-like side-tubes (diverticula ?). In alcohol the specimens become white (Fig. 44d). Surface of tube and side projections is covered in tiny rounded papillae of up to 0.5 mm in height and width (Fig. 44b). Size of entire specimens up to 4 cm high, individual side-tubes, up to 3 cm long and 8 mm in diameter, overall the sponge may be 4–5 cm wide, atrial lumen up to approximately 2 cm in diameter. Consistency soft and easily damaged.

**Histology.** No histological section was made, but thin hand sections of the skeleton indicate that it has a probable syconoid aquiferous system (Fig. 45a–c), but with choanocyte chambers shallow and closely adjacent to each other in the papillae. See also the Remarks below.



**FIGURE 46.** *Sycetta vinitincta* sp. nov., SEM images of the spicules of holotype RMNH Por. 1873, a, large slightly sagittal triactines of the atrial skeleton, b, large slightly sagittal tetractines of the atrial skeleton, c, oxhorn triactine spicules of the papillary surface, d, oxhorn tetractine spicules of the papillary surface, e, subatrial sagittal triactine, f, subatrial sagittal tetractine, g, atrial triactine with short unpaired actine, h, atrial tetractine with short unpaired actine.

**Skeleton.** (Figs 45a–e) The walls of the atrial tube and the side-tubes bear continuous close-set semi-globular ('alveolar') papillae (Figs 45a–b, d). Spicules of these alveolar papillae are predominantly characteristic 'oxhorn-shaped' small triactines and tetractines (with upturned paired actines) in a single layer, but near the atrial lumen there is an additional subatrial smaller sagittal triactine spicule located (Fig. 45b–c), differing from the alveolar oxhorn-shaped spicules in having the paired actines recurved. The atrial wall (Fig. 45c, e) is supported by regular larger tri- and tetractines, predominantly tetractines and smaller sagittal tri- and tetractines with paired actines

almost in one plane and characteristic short unpaired actines. The skeletal structure of this species might be interpreted as inarticulate.

**Spicules.** (Figs 44e, 46a–h) Regular equiangular equiaxial triactines and tetractines in two size categories, oxhorn-shaped sagittal triactines and tetractines, small sagittal tri- and tetractines in two categories.

Atrial triactines (Fig. 46a) with unpaired actine up to 330–444.3–530 x 8–10.3–13 µm, paired actines up to 190–378.8–489 x 9–10.5–13 µm.

Atrial tetractines (Figs 46b, f) often with shorter unpaired actine, up to 210–359.2–479 x 9–11.8–14 µm, paired actines up to 240–396.6–426 x 9–10.7–12 µm, and apical actines 18–21.8–34 x 4–6.6–10 µm.

Triactines with recurved actines (Fig. 46e), unpaired actines 149–176.8–242 x 7.5–8.3–9 µm, paired actines 108–126.4–135 x 6.5–7.6–9 mm.

Triactines of the alveolar papillae, oxhorn-shaped (Fig. 46c), with unpaired actines 28–68.0–123 x 5–6.2–8 µm, paired actines 91–110.2–129 x 5–5.9–8 µm.

Tetractines of the alveolar papillae, oxhorn-shaped (Fig. 46d), with unpaired actine up to 48–106.1–180 x 8 µm, paired actines up to 93–120.8–135 x 6–6.8–8 µm and apical actine approximately 20–36.5–61 x 4.5–5.6–7 µm.

Atrial triactines, sagittal, with short unpaired actines (Fig. 46g), and paired actines almost in one plane, unpaired actines 68–89.3–112 x 7–8.3–10 mm, paired actines 153–174.3–193 x 8–9.2–11 mm.

Atrial tetractines, sagittal, with short unpaired actines (Fig. 46h) and paired actines almost in one plane, unpaired actines 18–33.2–53 x 8–8.6–11 mm, paired actines 88–172.0–361 x 8–8.8–10 mm, apical actines 25–47.4–95 x 7–8.1–9 mm.

**Ecology.** Shallow-reefs.

**Distribution.** So far known only from Indonesia, at Salayar and the Berau region.

**Etymology.** The word *vinum* (L.) means wine, *tinctus* (L.) means colored, referring to the wine-red color of the species.

**Remarks.** The genus assignment is tentative. Among Calcaronea, the papillate surface and a wall of alveolar choanocyte chambers only occur in the poorly known genus *Sycetta*, with type species the Indian Ocean *S. sagittifera* (Haeckel, 1872), and other species the Mediterranean *S. conifera* (Haeckel, 1872), and two Antarctic species, *S. antarctica* Brøndsted, 1931 and *S. primitiva* (Brøndsted, 1931) (originally as *Tenthrenodes*). The spicule shapes and sizes of these species are clearly different from those of the present species, especially the Indian Ocean *S. sagittifera*, which lacks tetractines. Oliver Voigt (personal communication) made histological sections of the paratype, ZMA Por. 08633, and this confirmed that the alveolar structures are indeed syconoid choanocyte chambers, with choanocytes lining the entire internal walls. He pointed out that there is a great similarity in skeletal structure and histology with the South Australian '*Sycon*' *carteri* Dendy, 1893. The two are probably closely related, differing in habitus ('*S.*' *carteri* is a strongly divided bush of thin orange colored tubes) and spiculation ('*S.*' *carteri* has brushes of short diactines on the papillae). Molecular work (Voigt *et al.* 2012) also demonstrated that '*S.*' *carteri* is in its turn closely related to *Leucascandra caveolata* Borojevic & Klautau, 2000 (described also in Lévi *et al.* (1998: 79). This species is rather more distinct in habitus and skeletal features: it is a dense mass of orange-brown, smooth, delicate tubes provided with thinner side tubes, the walls of the tubes are 'caveolate', i.e. rounded-syconoid (our interpretation), and there is a distinct cortex. There is no papillate surface as in *Sycetta vinitincta* sp.nov. and '*Sycon*' *carteri*, but the three species share similar oval syconoid choanocyte chambers and the inarticulate skeleton. *Leucascandra* is at present assigned to the family Jenkinidae, which is, however, postulated to be polyphyletic (Voigt *et al.* 2012; Dohrmann *et al.* 2006).

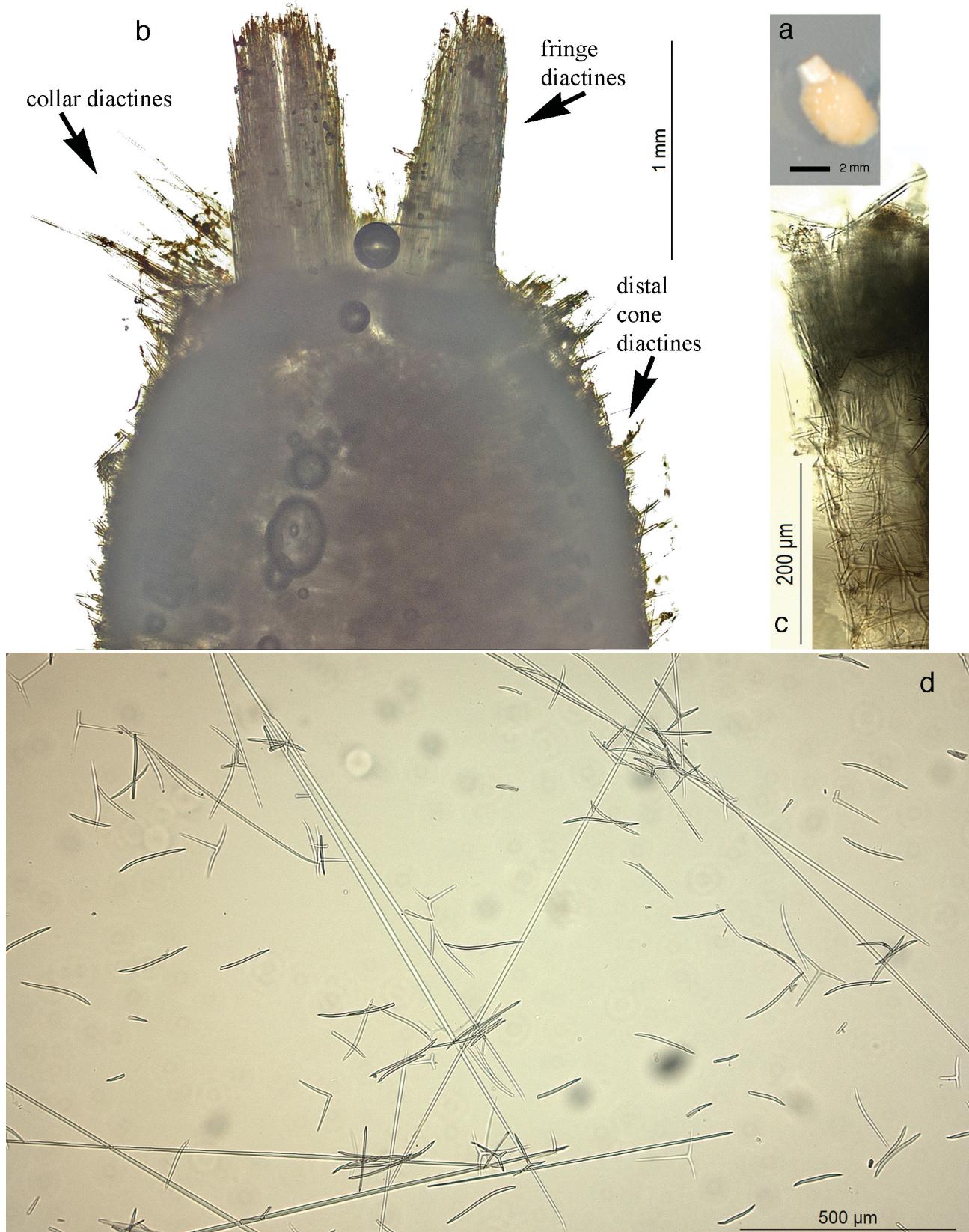
## Genus *Sycon* Risso, 1827

### *Sycon* spec.

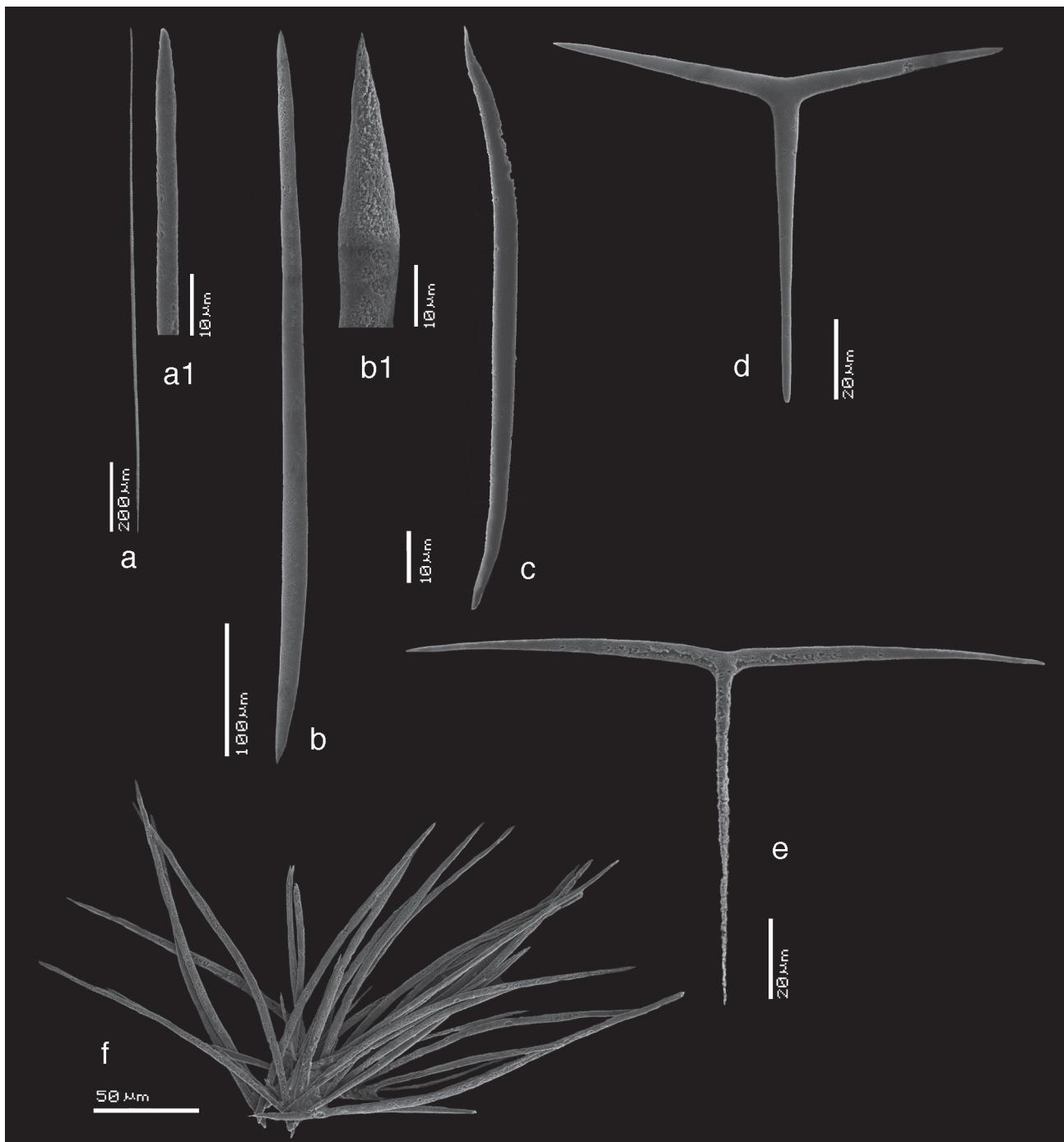
Figures 47a–d, 48a–e

?*Sycon raphanus* var. *tergestinum*; Breitfuss, 1896: 434; Breitfuss, 1898: 173 (not: Haeckel, 1872)

**Material examined.** ZMA Por. 15509d, Indonesia, SE Sulawesi, SW Salayar, NW coast of Pulau Guang, 6.35°S 120.45°E, depth 3–4 m, SCUBA, H.A. ten Hove, Indonesian-Dutch Snellius II Expedition stat. 152/Cave 1/A3, 28 September 1984.



**FIGURE 47.** *Sycon* spec., ZMA Por. 15509d, from Salayar, a, preserved habitus (scale bar = 2 mm), b, microscopic overview of upper part and fringe (scale bar = 1 mm), c, cross section of tube wall showing palisade of small diactines at the distal cones, and tubar skeleton of T-shape triactines (scale bar = 200  $\mu\text{m}$ ), d, overview of spicules (scale bar = 500  $\mu\text{m}$ ).



**FIGURE 48.** *Sycon* spec., ZMA Por. 15509d, from Salayar, SEM images of spicules, a, thin diactine from the oscular fringe, a1, detail of apex, b, large diactine, b1, detail of apex, c, small diactine of distal cone, d, T-shaped triactine from the tubar skeleton, e, T-shaped triactine of the atrial skeleton, f, bouquets of diactines of the distal cones.

**Description.** Tiny sponge (Fig. 47a), 4 mm high, 3 mm in diameter. Color cream in alcohol. Oscules provided with silvery white-opaque stiff dense fringe, underneath which there is a loose collar of widespread diactinal spicules (Fig. 47b, arrows). Surface of main body microconulose-spinose.

**Skeleton.** Typical radial arrangement (Fig. 47c) of tubar spicules lining the syconoid chambers, with distal cones crowned by bouquets of diactines (Fig. 48f); atrial skeleton with several layers of triactines; central tube crowned by peripheral fringe of long thin diactines (Fig. 47b), at the base of which there is a circle of thick diactines forming a collar. These diactines are also found spread over the body.

**Spicules.** (Figs 47d, 48a–f) Tubar triactines, atrial triactines, fringe diactines, large collar diactines, small diactines of the distal cones.

Diaactines of the oscular fringe (Figs 48a, a1), thin, but elongately fusiform, 1000–1500 x 6–10 µm.  
Diaactines of the collar (Figs 48b, b1), thick, fusiform, 500–650 x 15–22 µm.  
Diaactines of the distal cones curved (Figs 48c, f), at both ends tapering to sharp points, 120–220 x 5–6 µm.  
Tubar triactines (Fig. 48d), sagittal, T-shaped, with unpaired actines longer than paired actines, unpaired actines sharply pointed; unpaired actines 90–110 x 5–6 µm, paired actines 45–60 x 4–6 µm.  
Triactines of the atrium (Fig. 48e), sagittal, T-shaped, with unpaired actines shorter than paired actines, unpaired actines sharply pointed, 45–80 x 6 µm, paired actines 90–100 x 6 µm.

**Ecology.** Shallow-water reef cave.

**Distribution.** Indonesia.

**Remarks.** We consider this description as preliminary and refrain from naming the present species, because the single specimen was tiny and most of the material was used up in making a few inadequate preparations. The habitus reminds of the Mediterranean *Sycon humboldti* (Risso, 1827), type species of the genus, but that has tetractines. Only few *Sycon* species lacking tetractines have been described, e.g. *Grantia cupola* (Haeckel, 1872) from Japan (it has no diaactines), and *Sycon grantioides* Dendy, 1916 from the Indian Ocean (tubar triactines with unpaired actines twice as long).

Breitfuss' (1896, 1898) report of the Mediterranean (sub)species *Sycon raphanus tergestinum* from Ternate may possibly concern our present species. No spicule data were provided by Breitfuss, and, of course, the occurrence of a Mediterranean *Sycon* species in Indonesian waters is highly unlikely.

New Caledonian *Sycon gelatinosum* (Blainville, 1834), as redescribed by Borojevic & Klautau (2000) and Northeast Australian *Sycon capricorn* Wörheide & Hooper, 2003 differ strongly from the present material by having a branched tubular habitus, relatively smooth surface, possessing atrial tetractines, and differently shaped spicules.

## Family Grantiidae Dendy, 1893b

### Genus *Leucandra* Haeckel, 1872

#### *Leucandra irregularis* (Burton, 1930) comb. nov.

Figures 49a–b, 50a–e

*Anamixilla irregularis* Burton, 1930: 6, fig. 5.

Not: Hôzawa, 1940: 155, pl. VII fig. 12.

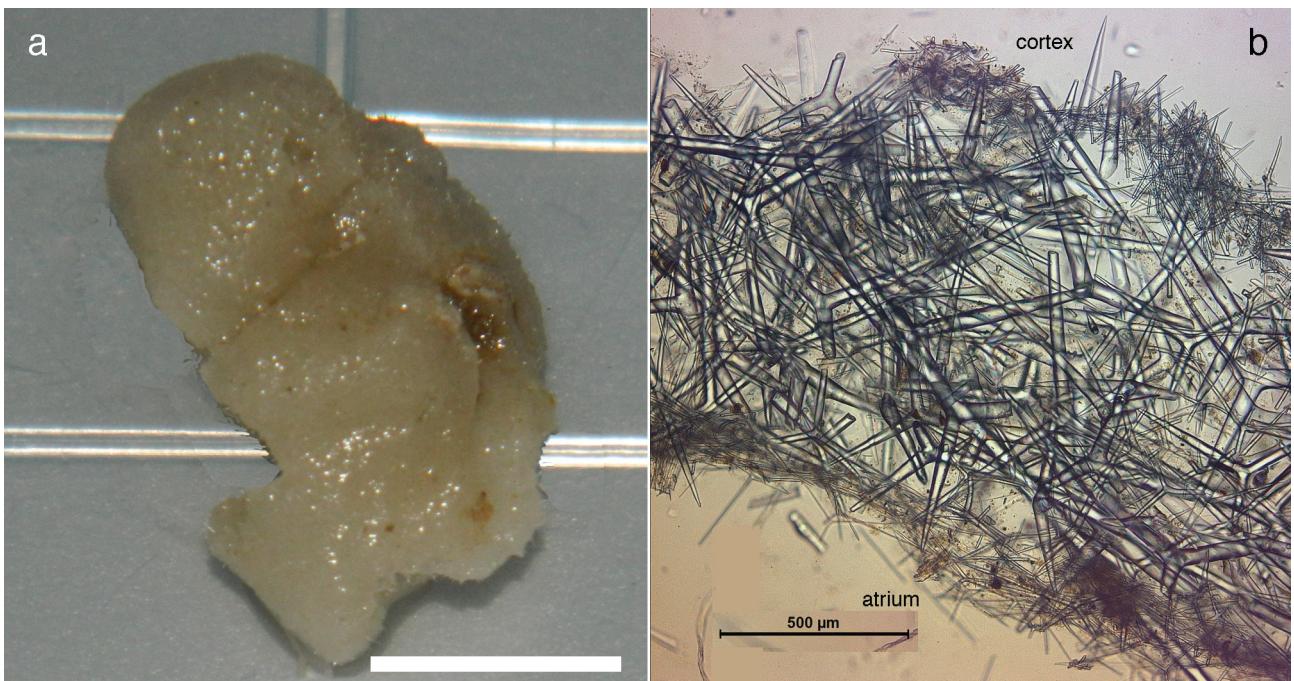
**Material examined.** Holotype ZMA Por. 00144, Indonesia, Nusa Tenggara, Sumbawa, Bay of Bima near South Fort, 8.505°S 118.695°E, depth 55 m, trawled, bottom mud with patches of coral sand, coll. Siboga Expedition stat. 047, 8 April 1899; BMNH 1929.8.30.6, five slides made from the holotype.

**Description.** Hispid thick-walled pear-shaped tube (Fig. 49a), size approximately 2.5 cm high, 1 cm in widest diameter, dirty white in color (alcohol), with rather soft consistency. The original specimen had a narrow apical opening with naked rim, but this has been cut off and mounted in one of the slides, kept in the Natural History Museum.

**Skeleton.** (Fig. 49b) Due to the poor preservation, histological sections show a jumbled skeleton, but here and there rounded choanocyte chambers are apparent indicating a leuconoid aquiferous system. There is a cortex of smaller triactines (Fig. 49b top) overlying a choanosomal skeleton of confusedly arranged giant triactines, with occasional giant diaactines at sharp angles to the surface. The atrial skeleton (Fig. 49b bottom) is predominantly formed by tetractines. The specimen originally was in the possession of a naked osculum, supported by tangential lengthwise arranged diaactines, but this has not survived in the present remains. One of the slides made by Burton and kept in the Natural History Museum collection shows the oscular skeleton to be formed by a dense mass of tetractines similar to those of the atrial skeleton.

**Spicules.** (Figs 50a–e) Giant triactines, intermediate and smaller triactines, smaller tetractines, giant diaactines.

Cortical triactines (Fig. 50d), actines relatively thin, usually sagittal or parasagittal, rarely regular equiangular and equiaxial, paired actines not infrequently somewhat wobbly, unpaired actines 84–221.2–311 x 7–10.7–15 µm, paired actines, 123–263.2–510 x 6–10.4–15 µm.



**FIGURE 49.** *Leucandra irregularis* (Burton, 1930), holotype ZMA Por. 00144 from Sumbawa, a, preserved holotype (scale bar = 1 cm), b, cross section of the holotype BMNH 1929.8.30.6, showing an upper cortical skeleton of small triactines, a choanosomal skeleton of giant triactines and a few oscular diactines, and an atrial skeleton of tetractines (scale bar = 500  $\mu$ m).

Choanosomal giant or large triactines (Figs 50a–b), usually slightly sagittal, but with actines almost invariably strongly different in length, even when equiangular. The shape somewhat resembles pseudosagittal triactines. Size quite variable but recognizable by relatively thick actines, 270–597.1–1080 x 23–38.4–52  $\mu$ m.

Atrial tetractines (Figs 50c), rather irregular in shape, apical actine prominent, unpaired actines, 174–293.3–420 x 5–10.3–13  $\mu$ m, paired actines 120–287.2–438 x 4–10.8–17  $\mu$ m, apical actines 20–60.8–120 x 4–6.8–10  $\mu$ m.

Oscular diactines (Fig. 50e), occasionally also in the tubar skeleton, 820–1242.9–2100 x 45–55.5–63  $\mu$ m.

**Ecology.** On soft bottom at 55 m.

**Distribution.** Indonesia, known only from the type locality off the island of Sumbawa.

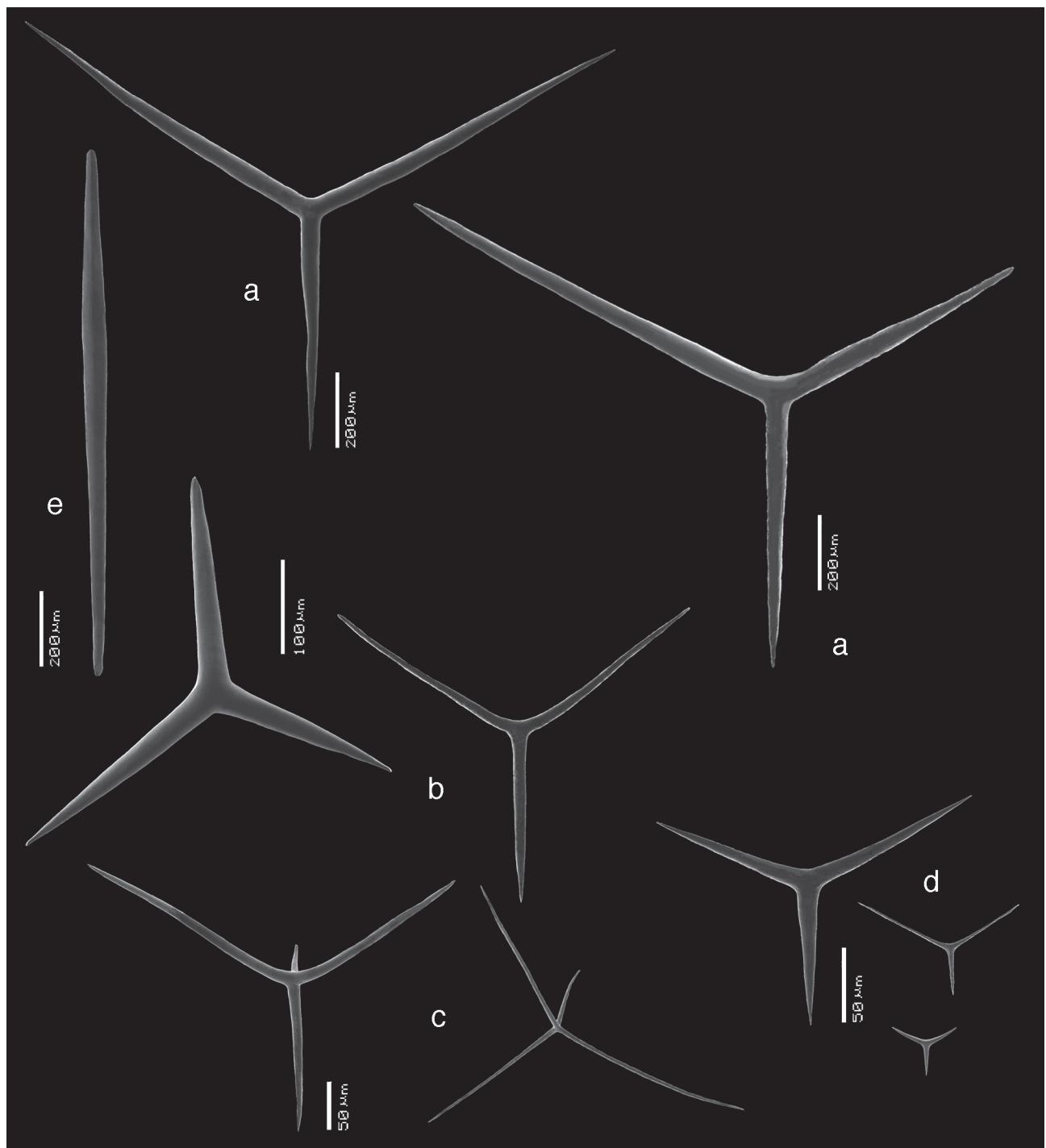
**Remarks.** Burton assigned this species to *Anamixilla* probably because of the similarity of the complement of giant triactines, which also often show a parasagittal shape with unequal actine lengths. However, the structure of the skeleton and the aquiferous system differ clearly from *Anamixilla torresi* Poléjaeff, 1883 (see below). Remarkably, at a later date (1963) Burton omitted to report the presence of giant diactines in this species, which is one of the distinguishing features.

There is a compelling general similarity with Sri Lankan *Leucandra donnani* Dendy, 1905, which shares the shape, skeletal organization and spiculation. Differences are found in the sizes of the various spicule types, with overall smaller lengths and widths.

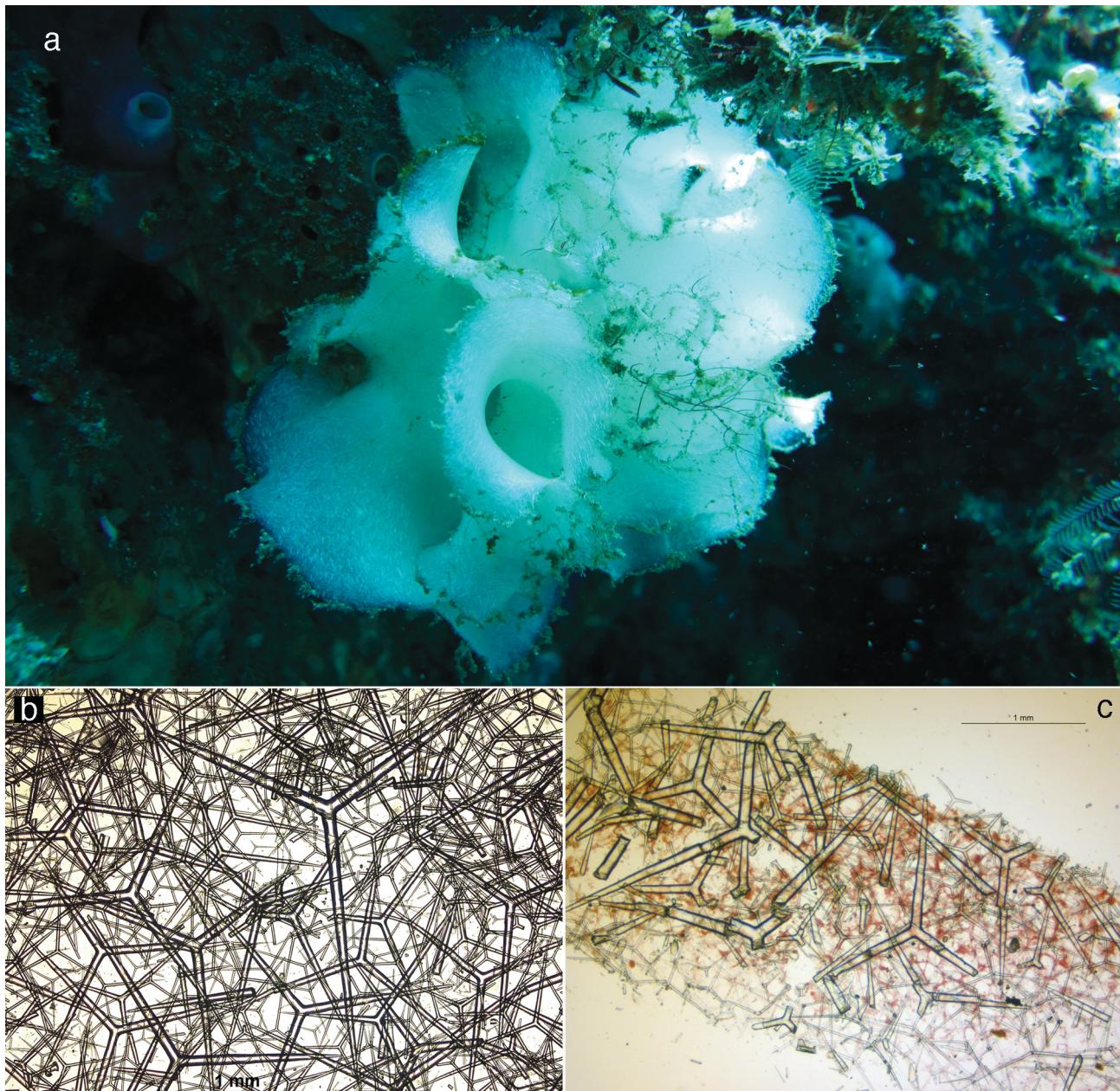
It also shows similarity with Japanese *Leucandra rigida* Hôzawa, 1940, which shares the giant triactines and diactines, differing in the presence of small choanosomal diactines. Northeast Australian *Leucandra sphaeracella* Wörheide & Hooper, 2003 has giant triactines and diactines, differing likewise from *L. irregularis* by having small diactines, but these are found in the ectosomal cortex. Both species have the spicule sizes in the same range as those of *L. irregularis*, so they are to be regarded as members of a regional complex of closely similar species. *Leucandra nicolae* Wörheide & Hooper, 2003 is also similar in spicule sizes, but it lacks the giant diactines, and has two types of microdiactines. A further close form probably is *Leucandra tropica* Tanita, 1943 from Palau (also reported by De Laubenfels, 1954). It differs by the presence of cortical tetractines, in addition to atrial tetractines.

Hôzawa (1940) recorded this species from Haiti (Caribbean), but provided no description of the spicules. The habitus figure he provided differs in shape from the holotype. Its identity is unclear, but in view of the localities at opposite parts of the globe it is not likely conspecific with the Indonesian specimen.

The resemblance of the choanosomal triactines to pseudosagittal spicules is perhaps attributable to the possible polyphyletic nature of these spicules, occurring in Grantiidae and Heteropiididae as discussed in Voigt *et al.* (2012).



**FIGURE 50.** *Leucandra irregularis* (Burton, 1930), holotype ZMA Por. 00144, SEM images of the spicules, a, giant triactines, b, intermediate-sized triactines of the choanosome, c, atrial tetractines, d, cortical triactines, e, oscular diactine.



**FIGURE 51.** *Anamixilla torresi* Poléjaeff (1883), RMNH Por. 6572, a, habitus *in situ* in North Sulawesi (scale bar = 1 cm, photo N.J. de Voogd). b, tangential view of surface skeleton (scale bar = 1 mm), c, histological cross section showing cortical and choanosomal giant and smaller triactines, subatrial triactines and atrial tetractines (scale bar = 1 mm).

### Family Jenkinidae Borojevic, Boury-Esnault & Vacelet, 2000

#### Genus *Anamixilla* Poléjaeff, 1883

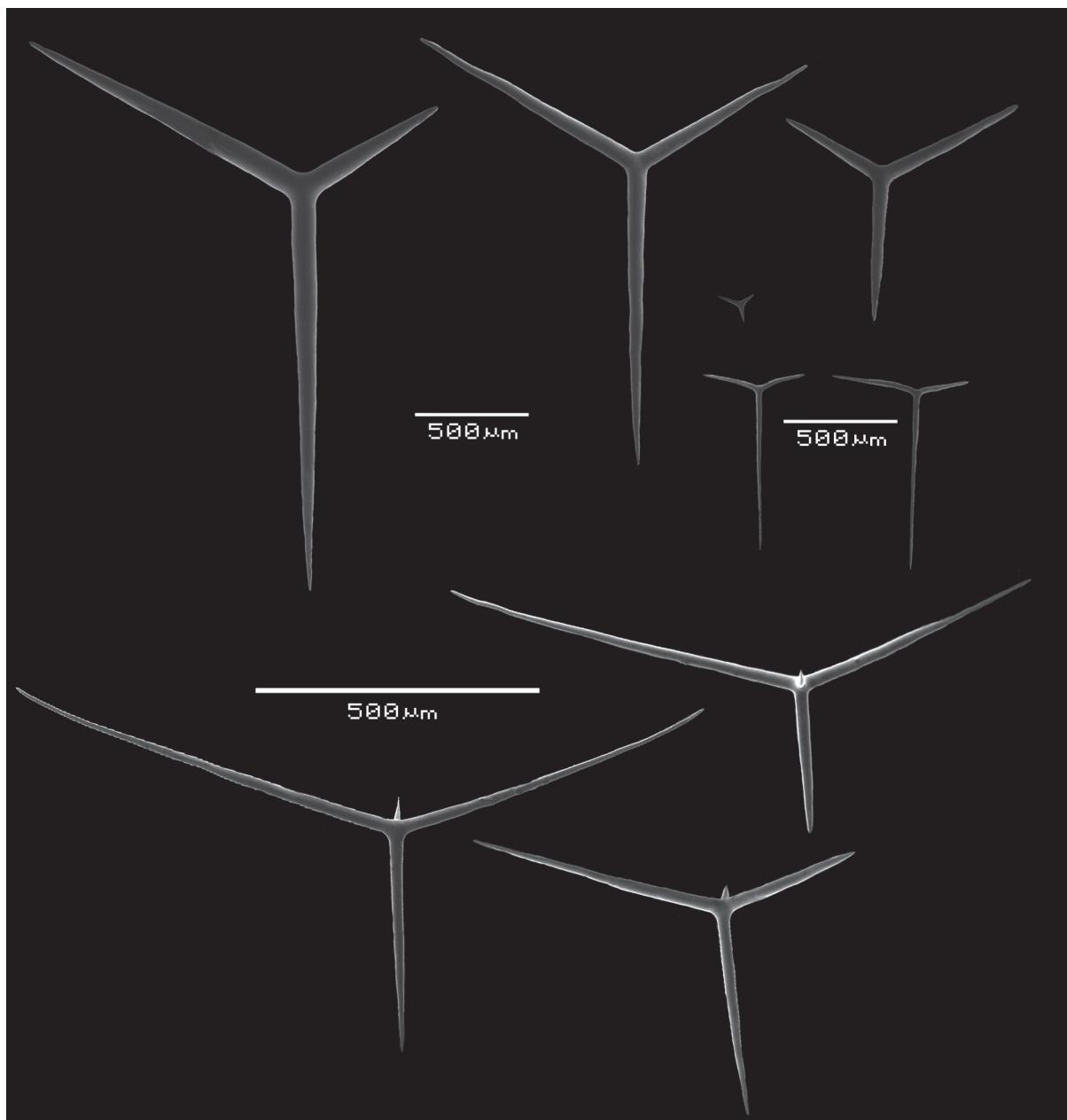
##### *Anamixilla torresi* Poléjaeff, 1883

Figures 51a–c, 52a–c

*Anamixilla torresi* Poléjaeff, 1883: 50, pl. IV figs 2a–c; Dendy, 1893a: 97; Burton, 1930: 5, fig. 4; Borojevic, 1967b: 9; Erhardt & Baensch, 1998: 73.

**Material examined.** ZMA Por. 00139, Indonesia, Irian Jaya, 1.71°S 130.79°E, depth 32 m, trawled, coll. Siboga Expedition stat. 164, 20 August 1899; ZMA Por. 00140, Indonesia, Nusa Tenggara, Timor, Samau Island,

Haingsisi, 10.1358°S 123.6297°E, depth 0–38 m, trawled, coll. Siboga Expedition stat. 303, 2 February 1900; ZMA Por. 00141, Indonesia, Maluku, Banda anchorage, 4.5398°S 129.9084°E, depth 9–45 m, trawled, coll. Siboga Expedition stat. 240, 22 November 1899; ZMA Por. 00142, Indonesia, Ambon anchorage, 3.7°S 128.15°E, depth 40 m, trawled, coll. Siboga Expedition stat. 231, 14 November 1899; ZMA Por. 08006, Indonesia, Nusa Tenggara, E of Komodo, Teluk Slawi, 8.8°S 119.52°E, underneath coral head, depth 1–4 m, snorkeling, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition stat. 069/II/13, 17 September 1984; ZMA Por. 16351, Indonesia, North Sulawesi, Bunaken Island, in cave, 1.6132°N 124.7797°E, depth 32 m, SCUBA, coll. H. Erhardt, 17 September 1996; RMNH Por. 6572, Indonesia, North Sulawesi, Lembeh Strait, Teluk Makawide, 1.48°N 125.24°E, depth 12 m, SCUBA, coll. N.J. de Voogd, #LEM19/090212/062, 9 February 2012; RMNH Por. 6612, Indonesia, North Sulawesi, Lembeh Strait, Tanjung Pandea, 1.4°N 125.17°E, depth 14 m, SCUBA, coll. N.J. de Voogd, #LEM24/110212/126, 11 February 2012.



**FIGURE 52.** *Anamixilla torresi* Poléjaeff (1883), RMNH Por. 6572, SEM images of spicules, a, equiangular parasagittal giant, intermediate and small triactines, b, subatrial sagittal triactines, c, atrial tetractines (trichoxeas from the fringe not shown).

**Description.** Wide irregular-shaped tubes (Fig. 51a) of up to 2.5 cm diameter and with short fringe at the rim of flaring, trumpet-like tube-endings. Overall size of cormus up to 10 cm or more in length. Color white, with blueish fringe in larger tubes. Consistency brittle, but limp when taken out of the water.

**Histology.** Syconoid aquiferous system.

**Skeleton.** Inarticulate, with a cortex formed by tangential giant and medium sized triactines (Fig. 51b), a choanosomal skeleton (Fig. 51c) formed by similar giant triactines and the unpaired actines of subatrial triactines. Atrial skeleton (Fig. 51c) consists of tetractines.

**Spicules.** (Figs 52a–c) Giant triactines, medium sized triactines, small triactines, medium sized and small tetractines; these spicules are all parasagittal. There are also - mostly broken - trichoxeas, uncommon, which likely represent spicules from the tubar fringe.

Giant triactines (Fig. 52a), equiangular with unequal length actines (parasagittal), 990–1640–2010 x 66–84.2–120  $\mu\text{m}$ .

Medium-sized triactines (Fig. 52b) with unequal length actines (parasagittal), usually with an unpaired actine longer than both unequal length paired actines, 330–471.3–602 x 13–24.7–35  $\mu\text{m}$ .

Tetractines (Fig. 52c), with unpaired actines usually shorter than the paired actines, in a large size range from giant-sized to small, 30–394.1–690 x 2–16.6–24  $\mu\text{m}$ , paired actines 50–590.6–900 x 2–16.1–20  $\mu\text{m}$ , apical actines approximately 31–53.8–90 x 7–11.3–19  $\mu\text{m}$ .

Trichoxeas, in bundles or loose, mostly broken, up to at least 300 x 2.5  $\mu\text{m}$  (only observed in RMNH Por. 6572).

**Ecology.** Mostly in the deeper reef environment, 20–40 m.

**Distribution.** Indonesia, elsewhere North Australia and New Caledonia.

**Remarks.** This material generally conforms closely to Poléjaeff's description, and to brief characterizations of Burton and Borojevic. The species is apparently not uncommon.

### *Anamixilla singaporenensis* sp. nov.

Figures 53a–c, 54a–d

?*Leucosolenia* sp. Lim et al. 2008: 163.

**Material examined.** Holotype RMNH Por. 9350, Singapore, Pulau Subar Laut, NW, 1.2°N 103.83°E, depth 6 m, SCUBA, coll. N.J. de Voogd, #SIN22/040406/160, 4 April 2006.

**Description.** Small group of whitish or pale beige tubes; a single basal tube may divide into two or three (Fig. 53a), ending in wide oscules, with frayed rim or coarse fringe. Diameter of tubes less than 1 cm, length up to 3 cm, usually slightly constricted at the open end. Consistency brittle, easily damaged.

**Skeleton.** (Figs 53b–c) Inarticulate, with a cortical thick layer of giant and intermediate-sized triactines. Choanosomal skeleton (Fig. 53b) formed by the unpaired actines of subatrial sagittal triactines. Atrial skeleton (Fig. 53c) thin, built by tetractines, with their apical actines protruding into the atrial lumen. The oscular rim has a thin spread of perpendicular trichoxeas.

**Spicules.** (Figs 54a–d) Giant and intermediate triactines, sagittal triactines, tetractines, thin diactines.

Equiangular equiaxial triactines (Fig. 54a) of the cortical region, in a wide size range from giant to intermediate sizes, 165–331.1–905 x 7–26.2–78  $\mu\text{m}$ .

Sagittal triactines (Fig. 54b), usually with long unpaired actine and wide-angled to almost straight paired actines, unpaired actines 88–288.3–434 x 5–8.1–10  $\mu\text{m}$ , paired actines 72–129.2–172 x 6–7.6–9  $\mu\text{m}$ .

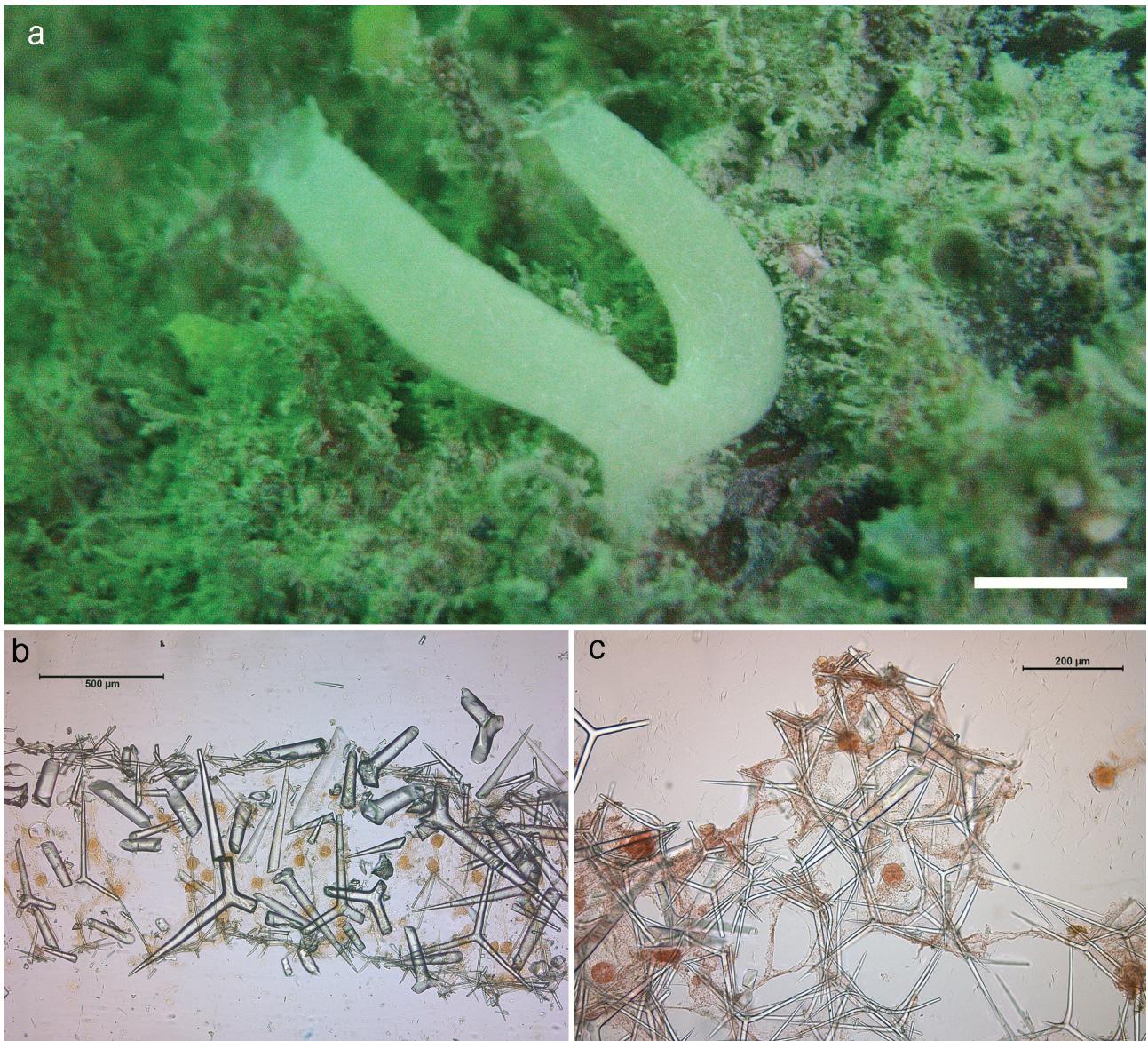
Tetractines (Fig. 54c), predominantly regular, but with apical actine often curved, unpaired actines 180–277.3–342 x 8–10.7–12  $\mu\text{m}$ , paired actines 182–204.2–222 x 8–8.8–10  $\mu\text{m}$ , apical actines 42–58.3–90 x 6–7.4–8  $\mu\text{m}$ .

Thin diactines (Fig. 54d), usually broken, approximately 75–210 x 2–3  $\mu\text{m}$ .

**Ecology.** Shallow water amongst filamentous algae.

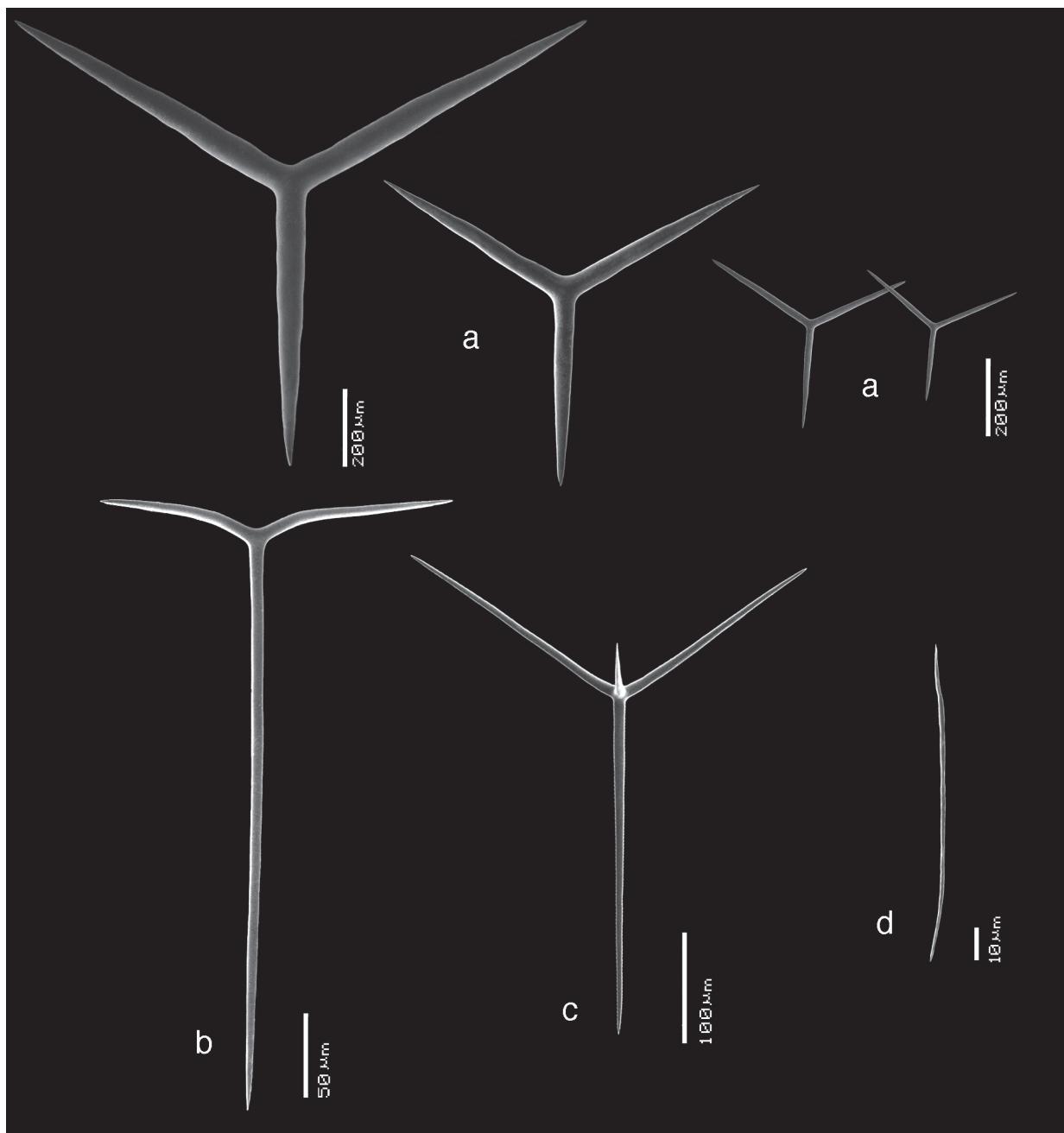
**Distribution.** Known only from the type locality off the coast of Singapore.

**Etymology.** The name refers to the type locality.



**FIGURE 53.** *Anamixilla singaporensis* sp. nov., holotype RMNH 9350 from Singapore, a, habitus *in situ* at 6 m depth (scale bar = 1 cm, photo N.J. de Voogd), b, histological cross section showing sconoid aquiferous system and inarticulate skeleton of giant triactines (scale bar = 500 µm); upper part: cortical skeleton of giant and intermediate-sized triactines, lower part: atrial skeleton of tetractines, c, tangential view of atrial surface (scale bar = 200 µm), showing atrial tetractines and subatrial triactines.

**Remarks.** The species is close to *Anamixilla torresi* in skeletal structure and spicular composition, but the habitus of the new species is simply tubular without the flaring trumpet ending of *A. torresi*, and two spicule types are distinctly different in shape and size. The actines of the giant triactines are only up to 905 µm in the present species, against up to 2000 µ or more in *A. torresi*. The sagittal triactines of the choanosomal skeleton in our new species have short straight paired actines; the unpaired actines are only up to 434 x 10 µm against up to 602 x 35 µm in *A. torresi*, which also has the angle of the paired actines more equiangular. Especially the atrial tetractines show a striking difference in that in *A. torresi* the paired actines of these spicules are very often much longer than the unpaired actines, whereas those of the new species are almost equal in length. Also, the unpaired actines of the new species are only half the length of those of *A. torresi* (up to 342 x 12 against 690 x 24 µm in *A. torresi*), and the paired actines only a third in length (up to 222 x 10 vs. up to 900 x 23 µm in *A. torresi*).



**FIGURE 54.** *Anamixilla singaporensis* sp. nov., holotype RMNH 9350, SEM images of spicules, a, cortical and choanosomal equiaangular equiaxial triactines, b, subatrial sagittal triactine, c, atrial sagittal tetractine, d, trichoxea.

### Genus *Uteopsis* Dendy & Row, 1913

#### *Uteopsis argentea* (Poléjaeff, 1883)

Figures 55a–b, 56a–c, 57a–g

*Ute argentea* Poléjaeff, 1983: 43, pl. I fig.3, pl. IV fig.3, pl. V figs 1a–p; Dendy, 1893a: 92.

*Uteopsis argentea*; Dendy & Row, 1913: 769; Burton, 1930: 5, fig. 3; Burton, 1963: 530.

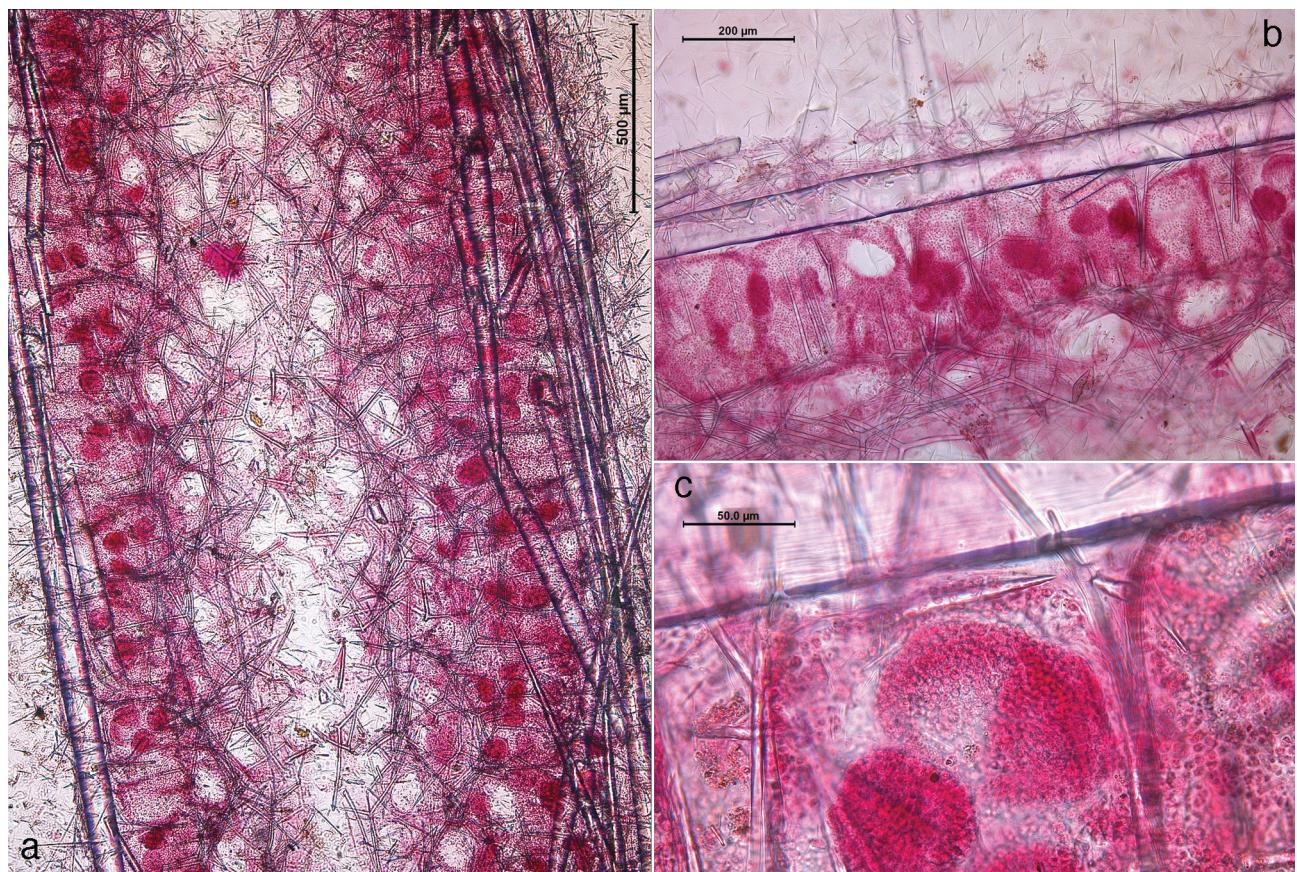
*Sycon* sp.; Colin & Arneson, 1995: 61, photo 238.



**FIGURE 55.** *Uteopsis argentea* (Poléjaeff, 1883), RMNH Por. 6593 from N Sulawesi, a, habitus *in situ* (photo B.W. Hoeksema), b, preserved specimen (scale bar = 1 cm).

**Material examined.** ZMA Por. 00155, Indonesia, Lesser Sunda Islands, West Timor, Samau Island, Haingsisi, 10.205°S 123.4591°E, depth 23 m, trawled, coll. Siboga Expedition stat. 060, 27 April 1899; ZMA Por. 00182, Indonesia, Irian Jaya, 1.7083°S 130.7916°E, depth 32 m, trawled, coll. Siboga Expedition stat. 164, 20 August 1899; RMNH Por. 1871, Indonesia, NE Kalimantan, Berau Islands, off Tanjung Batu, 2.2396°N 118.0934°E, 10–

15 m, SCUBA, coll. B.W. Hoeksema, #BER.19/091003/158, East Kalimantan-Berau Expedition 2003, 9 October 2003; RMNH Por. 2598, Singapore, Pulau Subar Laut, NW, 1.2°N 103.83°E, depth 6 m, SCUBA, coll. N.J. de Voogd, #SIN22/040406/160, 4 April 2006; RMNH Por. 6593, Indonesia, North Sulawesi, Lembeh Strait, Pulau Abadi, 1.4336°N 125.2062°E, depth 30 m, SCUBA, coll. B.W.Hoeksema, #LEM22/100212/104, 10 February 2012.



**FIGURE 56.** *Uteopsis argentea* (Poléjaeff, 1883), RMNH Por. 6593, histological sections, a, lengthwise section through entire tube showing cortical oxeas, inarticulate choanosomal skeleton formed by the unpaired actines of subatrial triactines, and atrial skeleton of tetractines (scale bar = 500  $\mu$ m), b, detail of cross section, showing from top downwards cortical triactines, giant diactine, syconoid choanocyte chambers supported by subatrial sagittal triactines and containing numerous embryos, and atrial skeleton of tetractines and triactines (scale bar = 200  $\mu$ m), c, detail of choanosome showing amphibiaula embryos (scale bar = 50  $\mu$ m).

**Description.** Bush of thin tubes (Figs 55a–b). Individual tubes up to 8 cm high, 3–4 mm in diameter, maintaining this diameter over most or all their length. Tubes may divide into two at a short distance above the substratum, but are unbranched for most of their length. Terminal oscules provided with a very short lighter colored fringe. Smooth surface, tough-hard consistency. Color pale brown.

**Histology.** Syconoid aquiferous system (Fig. 56b), with oval-rounded choanocyte chambers.

**Skeleton.** (Figs 56a–c) Strong, dense cortex of aligned tangential giant diactines (Fig. 56a), covered by a thin layer of small equiangular or sagittal triactines and scattered small diactines. Choanosomal skeleton inarticulate (Fig. 56b), thin and predominantly formed by the unpaired actines of subatrial sagittal triactines, with a minority of similar tetractines. Atrial skeleton of small sagittal tetractines and triactines, with scattered small diactines.

**Spicules.** (Figs 57a–g) Giant diactines, small diactines, triactines, tetractines.

Giant diactines (Fig. 57a) from the cortex, 1200–2170.0–3600 x 36–60.6–78  $\mu$ m.

Small diactines (Fig. 57b), 105–211.0–360 x 1.5–3.4–8  $\mu$ m.

Triactines from the cortical skeleton (Fig. 57c), unpaired actines 96–104.7–126 x 6–6.1–6.5  $\mu$ m, paired actines 60–75.2–93 x 6–6.7–7  $\mu$ m.



**FIGURE 57.** *Uteopsis argentea* (Poléjaeff, 1883), RMNH Por. 6593, SEM images of the spicules, a, giant diactines, b, small diactines, c, cortical triactine, d, choanosomal triactine, e, subatrial triactines, f, subatrial tetractine, g, atrial tetractines.

Triactines from the choanosome (Fig. 57d), unpaired actines 252–430.4–576 x 5–7.8–11  $\mu\text{m}$ , paired actines 96–180.6–258 x 5–8.6–9  $\mu\text{m}$ .

Triactines from the atrial skeleton (Fig. 57e), unpaired actines 99–121.2–135 x 4–5.1–7  $\mu\text{m}$ , paired actines 142–155.3–165 x 6–7.0–9  $\mu\text{m}$ .

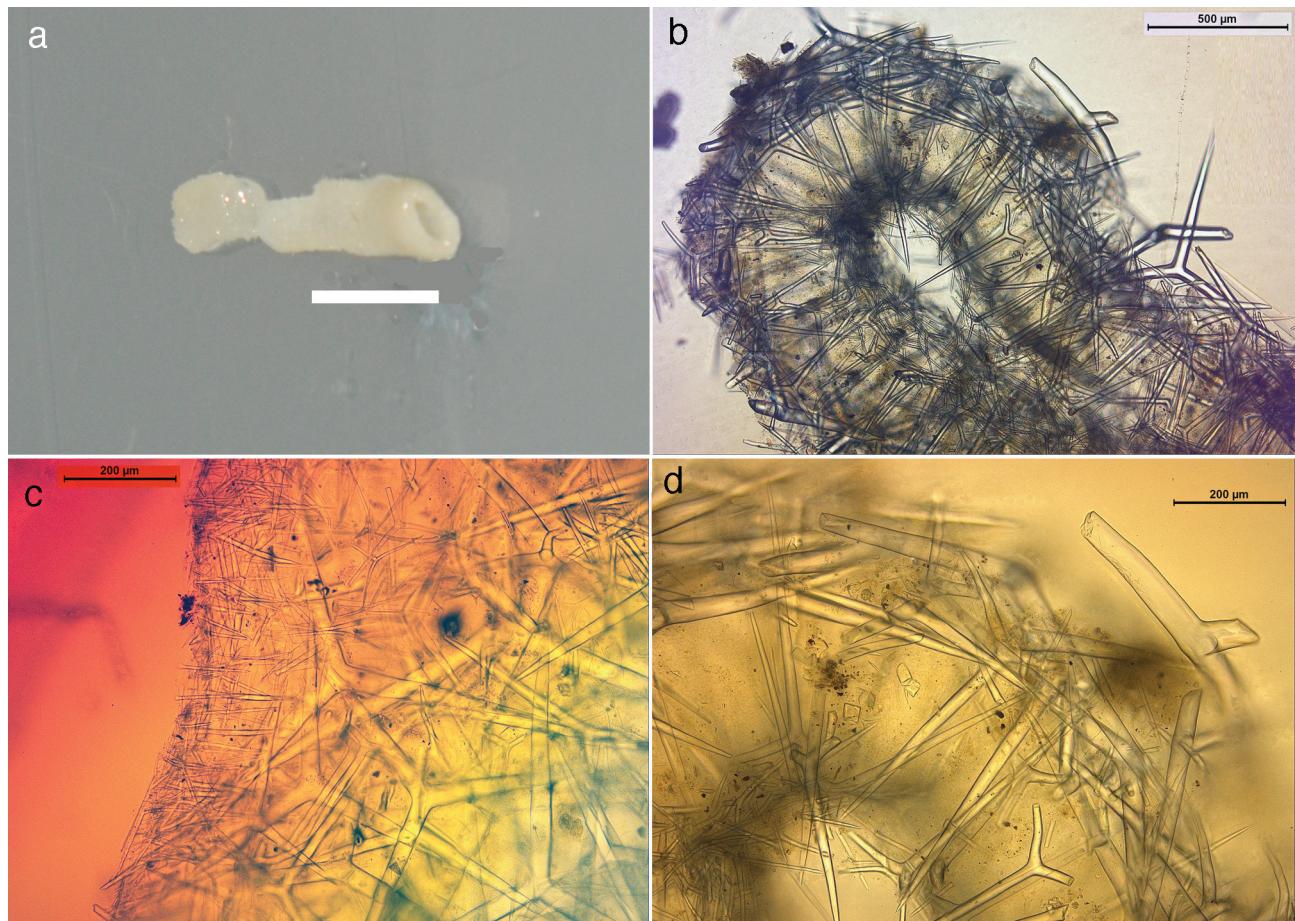
Tetractines from the choanosome (Fig. 57f), unpaired actines 250–301.7–384 x 8–8.1–8.5  $\mu\text{m}$ , paired actines 126–159.0–181 x 6–8.3–11  $\mu\text{m}$ , apical actines 45–58 x 6  $\mu\text{m}$ .

Tetractines from the atrial skeleton (Fig. 57g), unpaired actines 96–185.3–312 x 5–5.7–6  $\mu\text{m}$ , paired actines 96–114.0–129 x 5–6.7–8  $\mu\text{m}$ , apical actines 20–24 x 4  $\mu\text{m}$ .

**Ecology.** Deeper parts of the reefs.

**Distribution.** Indonesia, elsewhere South Australia.

**Remarks.** The type of *Uteopsis argentea* from the SE coast of Australia is similar in shape and overall spiculation, but there are a few discrepancies. Atrial tetractines of the type have much shorter unpaired actines, and the unpaired actine of the choanosomal triactines may be up to 750 µm in length. These differences are considered too small for specific separation. Future records of the species may find consistent differences among the widely separated populations.



**FIGURE 58.** *Sycettusa sibogae* (Burton, 1930), holotype ZMA Por. 00148 from Kalimantan, a, habitus of preserved holotype (scale bar = 1 cm), b–d, BMNH 1929.8.30.2a slides of holotype, b, cross section showing inarticulate skeleton made up of the paired actines of pseudosagittal triactines on the outside covered by the paired actines of regular giant triactines, on the atrial side with a cover of atrial sagittal triactines (scale bar = 500 µm), c, tangential view of the skeleton of the oscule showing a short fringe of trichoxeas (scale bar = 200 µm), d, detail of the peripheral skeleton showing giant cortical triactines and subcortical pseudosagittal triactines (scale bar = 200 µm).

## Family Heteropiidae Dendy, 1893a

### Genus *Sycettusa* Haeckel, 1872

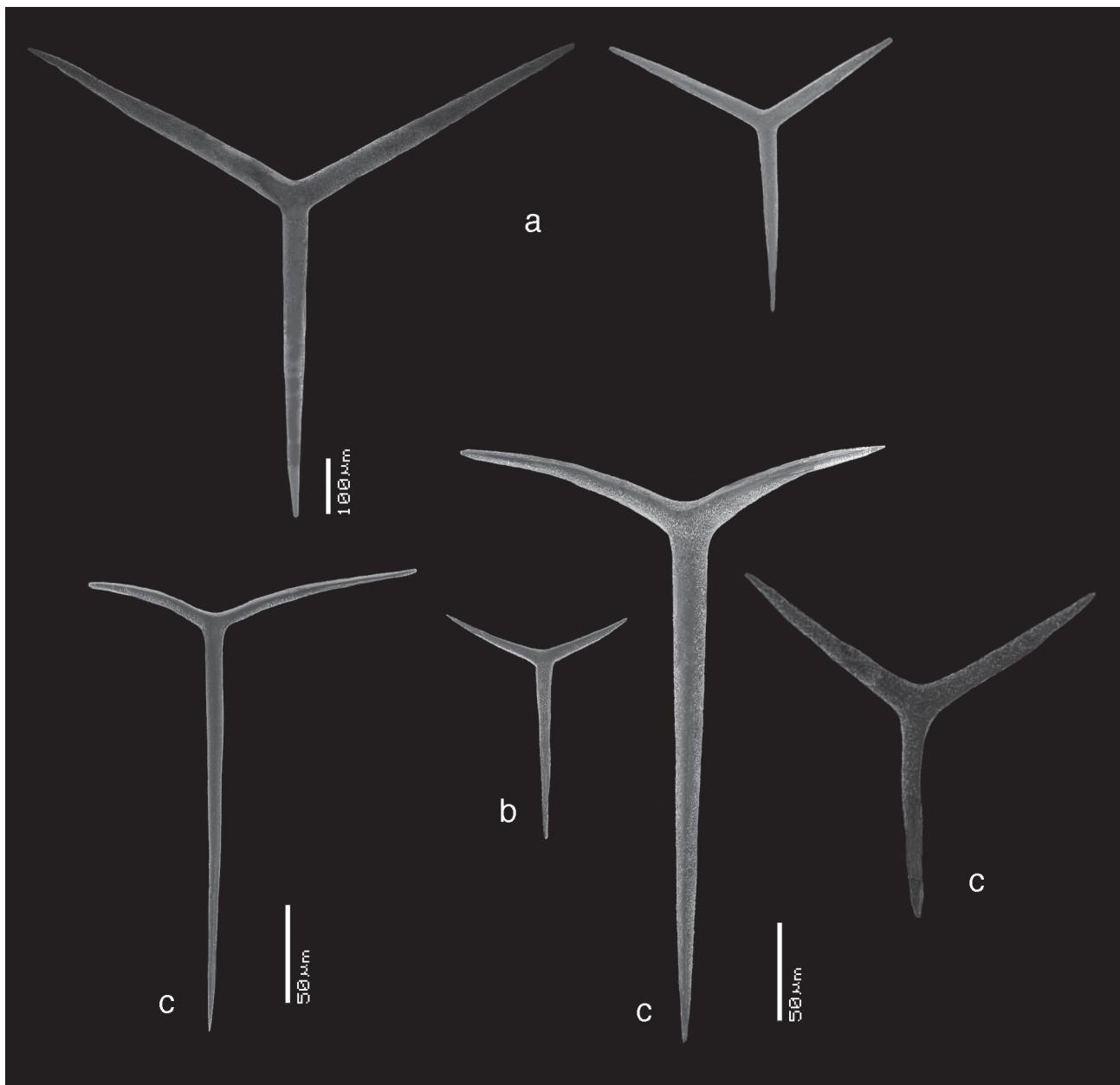
#### *Sycettusa sibogae* (Burton, 1930)

Figures 58a–d, 59a–c

*Grantessa sibogae* Burton, 1930: 4.

? *Sycettusa sibogae*; Van Soest et al., 2011: 40, fig. 19.

**Material examined.** Holotype ZMA Por. 00148, Indonesia, Borneo Bank, E of Kalimantan, 3.45°S 117.6°E, depth 59 m, dredge, bottom fine grey sand, coll. Siboga Expedition stat. 077, 10 June 1899; BMNH 1929.8.30.2a, 2 slides from holotype, same data.



**FIGURE 59.** *Sycettusa sibogae* (Burton, 1930), holotype ZMA Por. 00148 from Kalimantan, SEM images of the spicules, a, giant and intermediate regular triactines, b, sagittal triactines, c, pseudosagittal triactines (diactines of the oscular fringe were not available for SEM study).

**Description.** A single thin-walled elongated tube (Fig. 58a), with terminal naked oscule (but examined microscopically, there is evidence of a very short fringe, Fig. 58c), size 2 cm high, 0.5 cm diameter, whitish in alcohol, surface rough to the touch, consistency firm, brittle.

**Histology.** Syconoid arrangement (assumed on the basis of genus assignment).

**Skeleton.** Inarticulate (Figs 58b, d), with a thick cortex of giant triactines, supported by the unpaired and the smaller paired actines of subcortical pseudosagittal triactines. Trichoxeas are found in a very short oscular fringe (Fig. 58c) and are scattered in low abundance in the cortical region. The choanosomal skeleton is formed by the longer unpaired actines of the pseudosagittal spicules (Figs 58b, d). Atrial skeleton formed by multiple layers of smaller sagittal triactines (Fig. 58d).

**Spicules.** (Figs 59a–c) Giant triactines, pseudosagittal triactines, sagittal triactines, trichoxeas.

Giant triactines (Fig. 59a), equiangular, equiaxial, actines variable in size,  $282\text{--}475.5\text{--}660 \times 32\text{--}36.8\text{--}44 \mu\text{m}$  (Burton gives  $400 \times 36 \mu\text{m}$ ).

Atrial sagittal triactines (Fig. 59b), equiangular, unpaired actines 100–128.3–165 x 7–7.8–10 µm, paired actines up to 50–57.1–66 x 6.5–6.6–7 µm.

Pseudosagittal triactines (Fig. 59c), variable in size, unpaired actines 66–166.7–240 x 14–17.3–22 µm, longer paired actines 129–294.8–486 x 12–18.8–22 µm, and shorter paired actines 51–123.7–220 x 12–17.3–19 µm.

Trichoxeas, straight, invariably broken, pieces varying between 50 and 500 x 1 µm (discovered only in the sections; probably because of their thinness these were not found in the SEM preparation).

**Ecology.** Sandy bottom at 59 m depth beyond the reefs.

**Distribution.** Indonesia; ?Clipperton Island.

**Remarks.** Among the species of *Sycettusa*, the present species is unusual in possessing a cortical skeleton of giant triactines, with actines up to 600 µm. Burton (1963) synonymized this species with Mauritian *Sycettusa sycilloides* (Schuffner, 1877) (originally as *Sycortis*), without further comment. There are large differences in spicule sizes with this species, e.g. the subectosomal pseudosagittal triactines have the longer actine twice as large as in *S. sibogae*, the triactines of the ectosomal cortex in contrast are much smaller than in *S. sibogae*. Together these differences are sufficient to keep the two species separate.

Van Soest *et al.* (2011) reported this species from Clipperton Island, East Pacific, depths 17–32 m, with hesitation (indicated as ‘aff.’ *sibogae*). This specimen consisted of a cluster of yellow-brown tubes (in alcohol), which have similar spiculation as *S. sibogae*. The cluster of tubes, the color (in alcohol) and the geographic distance make conspecificity not very likely.

## Genus *Grantessa* Lendenfeld, 1885

### *Grantessa borojevici* sp. nov.

Figures 60a–g

**Material examined.** Holotype ZMA Por. 09164, Indonesia, Nusa Tenggara, Komodo, E side, Selat Linta, 8.5433°S 119.6133°E, depth 150 m, Van Veen grab, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition stat. 081/VI/01, 18 September 1984.

**Description.** Group of small hairy tubes (Fig. 60a) rising from a common base. Life color white, in alcohol dirty white. Individual tubes with hispid surface, *Sycon*-like in appearance, but without oscular fringe, approximately 1 cm in height 3–4 mm in diameter. Overall size of specimen 2 x 2 x 1 cm. Consistency soft.

**Histology.** Syconoid aquiferous system (Fig. 60b).

**Skeleton.** Articulate (Fig. 60b). Ectosomal cortex consisting of a single layer of equiangular triactines and bouquets of diactines marking the distal cones of the choanosomal tubes. The choanosomal skeleton is formed by the longer paired actine of the pseudosagittal subectosomal triactines and the centrifugal unpaired actines of sagittal tubar triactines. As the wall of the individual ‘person’ is thin, only few tubar triactines are present, 2–3 on average, in places only a single tubar spicule is found. Tubar triactines often have slightly wavy paired actines. Near the atrial surface there are layers of subatrial triactines similar in shape to the tubar triactines, but with straight paired actines, not wavy. Atrial skeleton a single layer of predominantly tetractines (with a minority of triactines), with the apical actine protruding slightly into the atrial cavity.

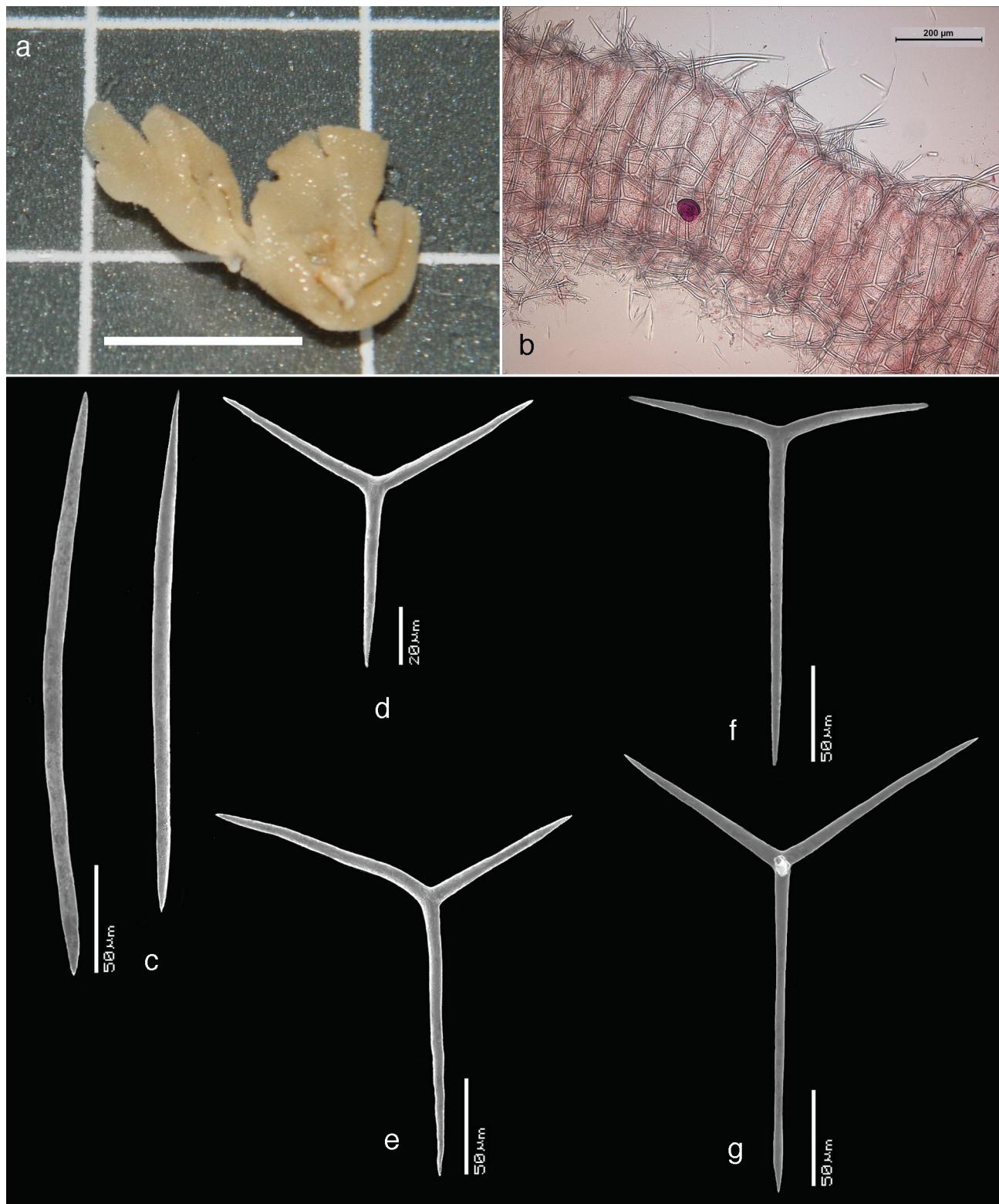
**Spicules.** (Figs 60c–g) Equiaxial triactines, pseudosagittal triactines, sagittal triactines, sagittal tetractines, diactines.

Diactines from the distal cones (Fig. 60c), lance-shaped, 258–295.3–342 x 7–9.6–12 µm.

Cortical equiaxial triactines (Fig. 60d), small, frequently with differences in actine lengths between the three actines of a single spicule, and also the angle of the actines may vary, 57–97.7–121 x 5.5–6.5–9 µm.

Pseudosagittal triactines (Fig. 60e), unpaired actines tending to be elongated-conical, 63–92.2–126 x 6–7.8–9 µm, longest paired actine 91–159.3–204 x 6.5–7.4–8.5 µm, shortest 84–110.1–135 x 6–7.2–8 µm.

Sagittal tubar and subatrial triactines (Fig. 60f), with relatively long tapering unpaired actines and short abruptly curved paired actines, unpaired actines 116–194.7–241 x 6–7.6–10 µm, paired actines 59–82.6–129 x 6–6.8–8 µm.



**FIGURE 60.** *Grantessa borojevici* sp. nov., holotype ZMA Por. 09164, from Komodo, a, preserved specimen (scale bar = 1 cm), b, histological cross section of tube wall, showing syconoid structure, articulate skeleton with cortical brushes of diactines and layer of triactines, with subcortical pseudosagittal triactines and subatrial sagittal triactines together forming the choanosomal skeleton, and with atrial skeleton of sagittal tetractines (scale bar = 200  $\mu$ m), c–g, SEM images of the spicules, c, cortical diactines, d, cortical equiangular triactine, e, subcortical pseudosagittal triactine, f, subatrial sagittal triactine, g, atrial sagittal tetractine.

Sagittal tetractines (Fig. 60g), usually with an elongated unpaired actine and short apical actines, but occasionally small tetractines may be more or less equiaxial, unpaired actines 63–201.4–315 x 6–6.8–8.5 µm, paired actines 81–129.6–165 x 6–7.0–8.5 µm, apical actines 9–17.6–45 x 5–6.1–7 µm.

**Ecology.** The material is from upper bathyal depth, 150 m.

**Distribution.** Indonesia.

**Etymology.** Named after Professor Radovan Borojevic, to honour him for his life long contribution to Calcarea systematics.

**Remarks.** The genus *Grantessa* is large, with 26 accepted species listed by Van Soest *et al.* (2015), the majority of which were described from Australia and Japan. We compare here our new species with representatives of the genus that show similarities with it and for completeness sake we also point out differences with other Indo-Pacific species.

Four species show general similarity in spiculation with our new species: Australian *Grantessa intusarticulata* (Carter, 1886) (p. 45, as *Hypogrammia*) has a characteristic ectosomal palisade of microdiactines (75–90 µm), unlike the bouquets of larger diactines in our new species, and it has robust atrial tetractines dissimilar to those of *G. borojevici* sp.nov. *Grantessa boomerang* (Dendy, 1893) (p. 82, as *Sycon*) also has small diactines (80 µm) and the apical rays of the tetractines are boomerang-shaped. Japanese *Grantessa nemurensis* Hôzawa, 1929 (p. 315) is a large mass of stiff tubes, rather different from our new species in habitus, and the apical actines of the atrial tetractines may grow as long as 480 µm. The species occurs in northern Japan (Hokkaido), well away from tropical waters. South African shallow-water *Grantessa ramosa* (Haeckel, 1872) as redescribed by Borojevic (1967b: 204) has the unpaired actines of tubar triactines and tetractines distally swollen and the paired and apical actines very short, unlike those of our new species.

The new species shows some resemblance with the Australian *Grantessa hirsuta* (Carter, 1886) (p. 41, as *Hypogrammia*), *Grantessa hispida* Dendy, 1893 (p. 107), *Grantessa sacca* Von Lendenfeld, 1885 (p. 1098), *Grantessa gracilis* (Von Lendenfeld, 1885) (p. 1111, as *Vosmaeria*), the Palau shallow-water *Grantessa plumosa* (Tanita, 1943) (p. 404 as *Sycon*), the Japanese shallow-water *Grantessa shimoda* Tanita, 1942 (p. 40), and the Japanese bathyal species *Grantessa sagamiana* Hôzawa, 1916 (p. 8), but all these differ in shape as they are a single ‘person’, and the sizes of their diactines clearly exceed that of our species as they reach 700–3000 x 16–80 µm. South Australian *Grantessa spissa* (Carter, 1886) (p. 54, as *Heteropia*), *Grantessa pluriosculifera* (Carter, 1886) (p. 52, as *Heteropia*), *Grantessa polyperistomia* (Carter, 1886) (p. 47, as *Heteropia*), *Grantessa erinaceus* (Carter, 1886) (p. 130, as *Leuconia*), and Japanese *Grantessa mitsukurii* Hôzawa, 1916 (p. 23) have no tetractines and spicule sizes are much larger, while South African *Grantessa rarispinosa* Borojevic, 1967 (p. 207) likewise has no tetractines while its spicules are smaller than those of our new species. Japanese *Grantessa parva* Tanita, 1942 (p. 38), lacks diactines and overall spicule sizes are smaller, whereas Japanese *Grantessa basipapillata* Hôzawa, 1916 (p. 19), likewise lacking diactines, has overall slightly larger spicules. Australian *Grantessa erecta* (Carter, 1886) (p. 53, as *Heteropia*), *Grantessa compressa* (Carter, 1886) (p. 51, as *Heteropia*) and Japanese *Grantessa ampullae* Hôzawa, 1940 (p. 38), have neither diactines nor tetractines.

### *Grantessa tenhoveni* sp. nov.

Figures 61a–d, 62a–h

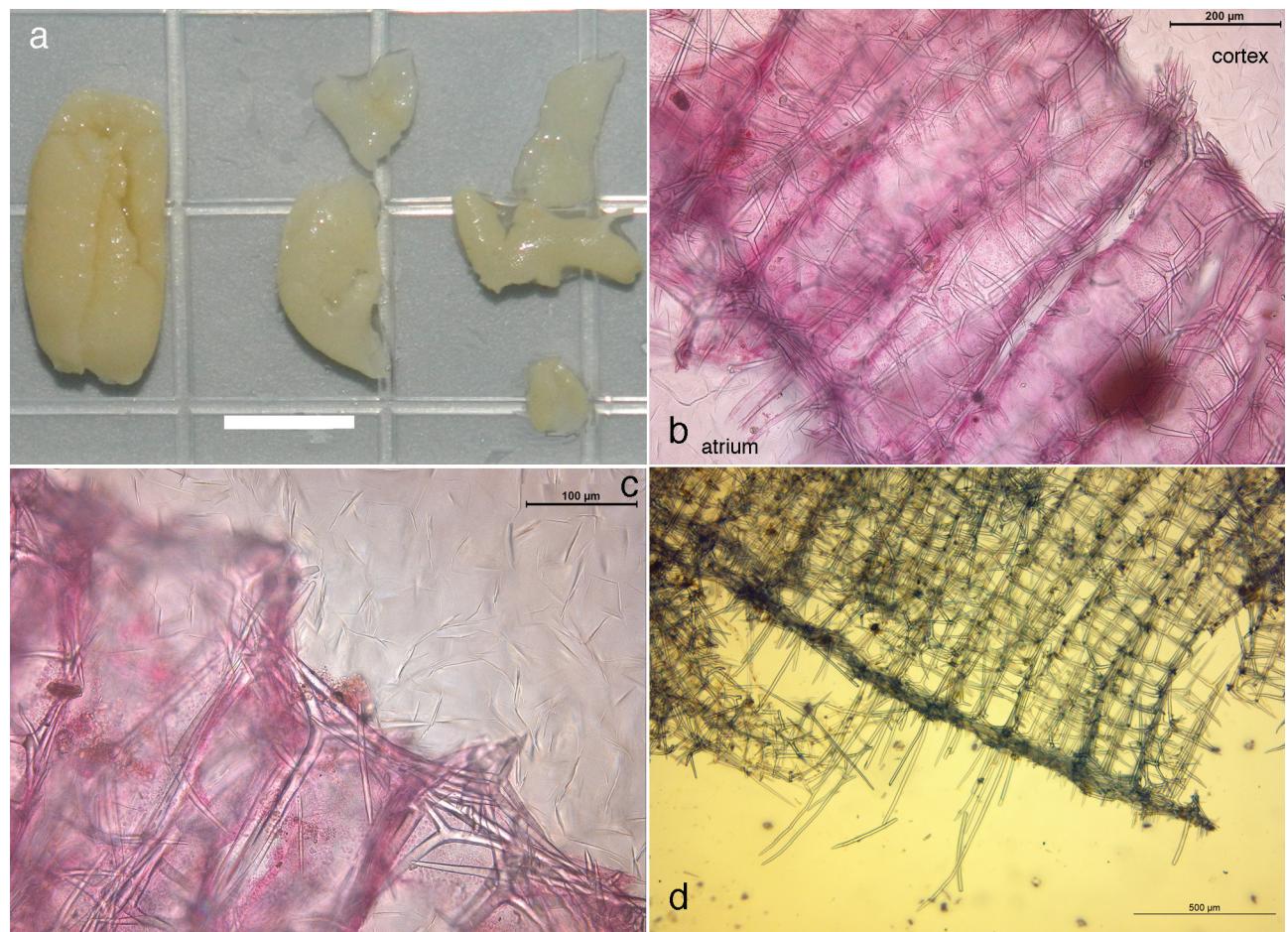
**Material examined.** Holotype ZMA Por. 15509a, Indonesia, Salayar, Guang, in cave, 6.35°N 120.45°E, depth 3–4 m, SCUBA, coll. H.A. Ten Hove, Indonesian-Dutch Snellius II Expedition stat. 152/A3, 28 September 1984.

**Description.** A group of anastomosed thick-walled small tubes (Fig. 61a), now fragmented. Color white in life and cream in alcohol. Largest tube fragment up to 2 cm high, 1 cm in diameter. No oscular fringe is apparent. Consistency soft, easily damaged.

**Histology.** Syconoid aquiferous system.

**Skeleton.** Articulate (Fig. 61b). In cross section the skeleton shows a cortical layer of small sagittal triactines with the ends of radial tubes ornamented by a tuft of microxeas. Subcortical skeleton a layer of pseudosagittal triactines (Fig. 61c). Choanosomal skeleton (Fig. 61b) consists of a neatly organized tubar skeleton of predominantly sagittal tetractines, basal unpaired actines centripetally arranged, with a minority of similar-shaped triactines. Atrial skeleton (Fig. 61d) multilayered, consisting of three morphologically distinct types of sagittal tri-

and tetractines, (1) sagittal tetractines similar in shape to the tubar tetractines, with unpaired actines protruding into the atrial lumen, (2) tangentially arranged tri- and tetractines with an elongated unpaired actine that is characteristically swollen in the distal part, lying tangentially in the atrial cortex, and (3) perpendicularly arranged tetractines with very long apical actines protruding far into the atrial lumen, with the basal triradiate system forming the atrial cortex along with (1 and 2). The atrial surface thus appears characteristically bristly.



**FIGURE 61.** *Grantessa tenhoveni* sp. nov., holotype ZMA Por. 15509a, a, preserved parts of group of tubes (scale bar = 1 cm), b, histological cross section of tube wall showing syconoid structure (scale bar = 200 µm), c, detail of histological cross section showing cortical skeleton of regular triactines, diactines and subcortical pseudosagittal triactines (scale bar = 100 µm), d, cross section of atrial skeleton of tetractines with protruding apical actines, and subatrial tubar triactines (scale bar = 500 µm).

**Spicules.** (Figs 62a–h) Sagittal triactines, pseudosagittal triactines, sagittal tetractines, diactines.

Cortical diactines of the distal cones (Fig. 62h), 63–77.3–91 x 3–4.8–6 µm.

Cortical triactines (Fig. 62a), usual slightly sagittal, actines 51–67.8–100 x 5–6.2–9 µm, (unpaired actines 72–100 x 6–7 µm, paired actines up to 51–65 x 5 µm).

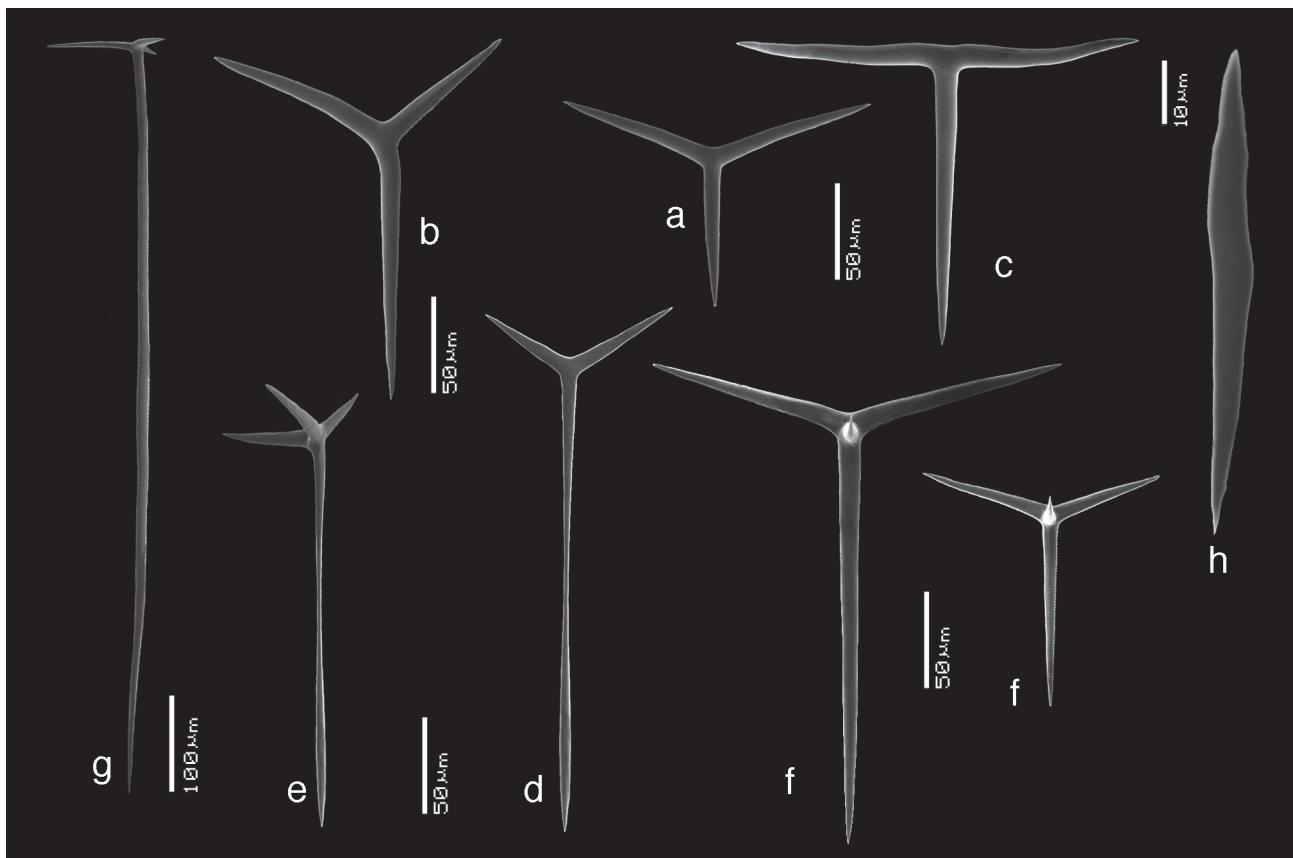
Pseudosagittal triactines (Fig. 62b), longest paired actines up to 90–155.6–239 x 8–9.6–14 µm, shortest paired actines 84–100.8–141 x 8–9.3–12 µm, unpaired actines 69–90.2–108 x 7–8.9–11 µm.

Sagittal triactines (Fig. 62c) of the radial tubes, unpaired actines up to 66–177.4–288 x 6–9.7–14 µm, paired actines up to 39–88.0–123 x 5–9.1–12 µm.

Subatrial sagittal tetractines (Fig. 62f), variable in shape, unpaired actines 156–220.1–301 x 7–11.6–13 µm, paired actines 96–113.5–123 µm, apical actines 18–33.3–48 x 7–8.5–10 µm.

Atrial sagittal triactines (Fig. 62d) with distally swollen unpaired actines with sizes 165–215.3–270 x 5.5–7.3–9 µm, paired actines 29–88.5–129 x 6–9.6–12 µm.

Atrial sagittal tetractines (Fig. 62e) with distally swollen unpaired actines with sizes 174–230.2–291 x 7–8.2–10 µm, paired actines 42–55.2–63 x 8–9.8–12 µm, apical actines 24–39.6–54 x 7–8.1–10 µm.



**FIGURE 62.** *Grantessa tenhoveni* sp. nov., holotype ZMA Por. 15509a, SEM images of the spicules, a, cortical triactine, b, subcortical pseudosagittal triactine, c, sagittal tubar triactine, d, atrial tangential triactine, e, atrial tangential tetractine, f, subatrial sagittal tetractines, g, specialized atrial tetractines with giant apical actines, h, cortical diactine.

Atrial sagittal tetractines (Fig. 62g) with very long apical actines up to 660–840–960 x 12 µm, actines of the basal triadiate system 60–96.0–135 x 5–7.1–10 µm.

**Ecology.** In shallow-water reef caves.

**Distribution.** Known only from the type locality, the island of Guang, W of Salayar, Indonesia.

**Etymology.** Named after our colleague, serpulid specialist Dr Harry A. Ten Hove, who collected the present material, and to acknowledge his friendship exhibited during many biodiscovery expeditions.

**Remarks.** The species differs from most *Grantessa* species in having tetractines supporting the walls of the choanosomal tubes, and the long apical actines of the atrial tetractines are also characteristic. Our new species is close to *Grantessa intusarticulata* (Carter, 1886), originally from SE Australia, but subsequently reported from several wideranging localities (Western Australia, New Zealand, Japan, see Burton, 1963). The habitus and general spiculation matches that species. The differences appear to be mostly in the sizes and shapes of the spicules, with the extreme length of the apical actines of the atrial sagittal tetractines as the most salient. Moreover, cortical diactines in our specimens are longer than those cited by Carter. South African *Grantessa ramosa* (Haeckel, 1872) as described by Borojevic (1967a) is also closely similar but likewise differs in lacking the very long protruding apical actines of the atrial tetractines, and the cortical diactines are longer.

From *Grantessa borojevici* sp.nov. described above, the new species differs in shape, surface characteristics, size of diactines of the distal cones, presence of tubar tetractines, shape and size of the atrial tetractines, and the prolonged apical actines of many atrial tetractines. The present material originated from shallow caves, whereas *G. borojevici* sp.nov. is bathyal.

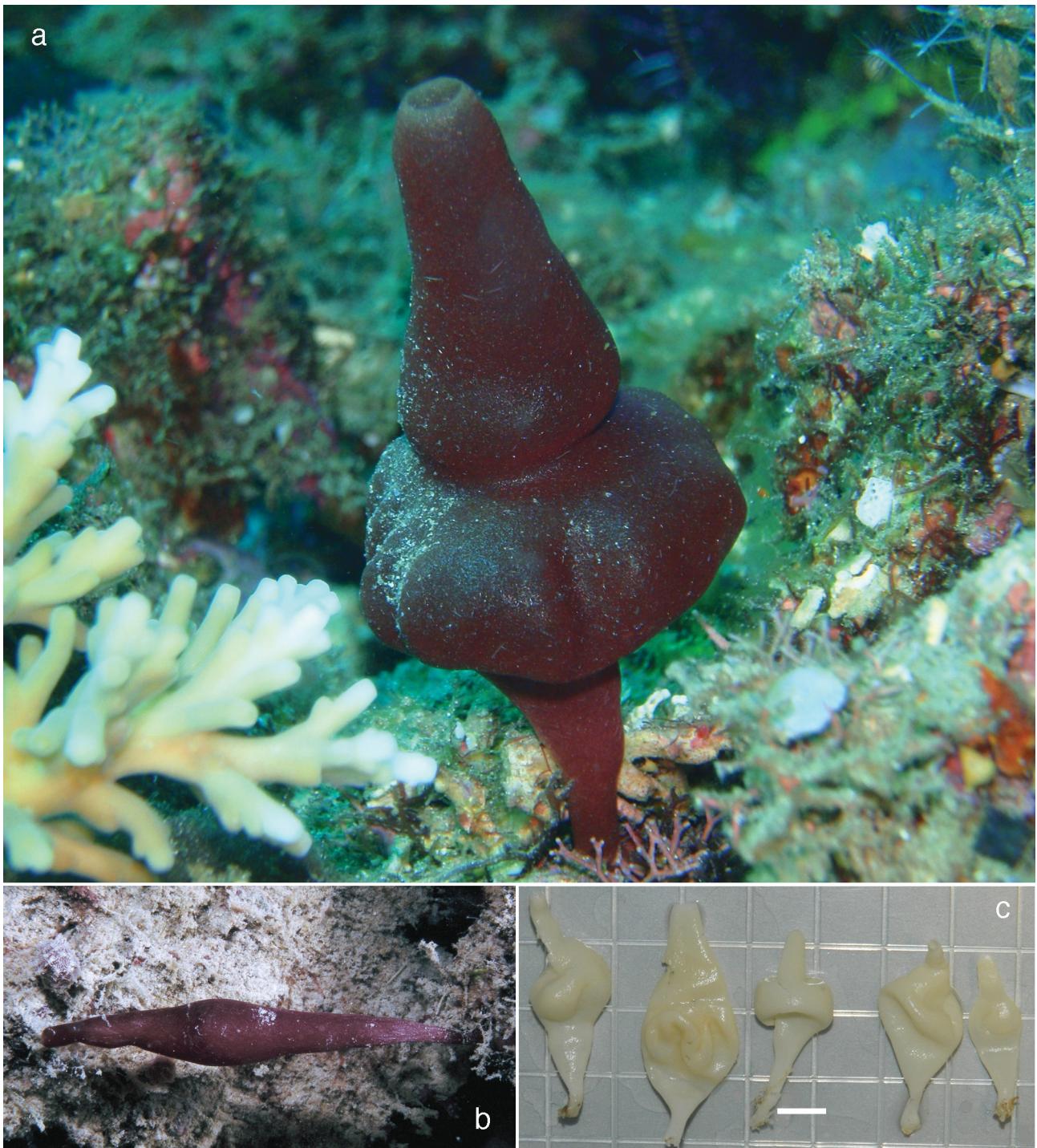
**Genus *Heteropia* Carter, 1886**

***Heteropia minor* Burton, 1930**

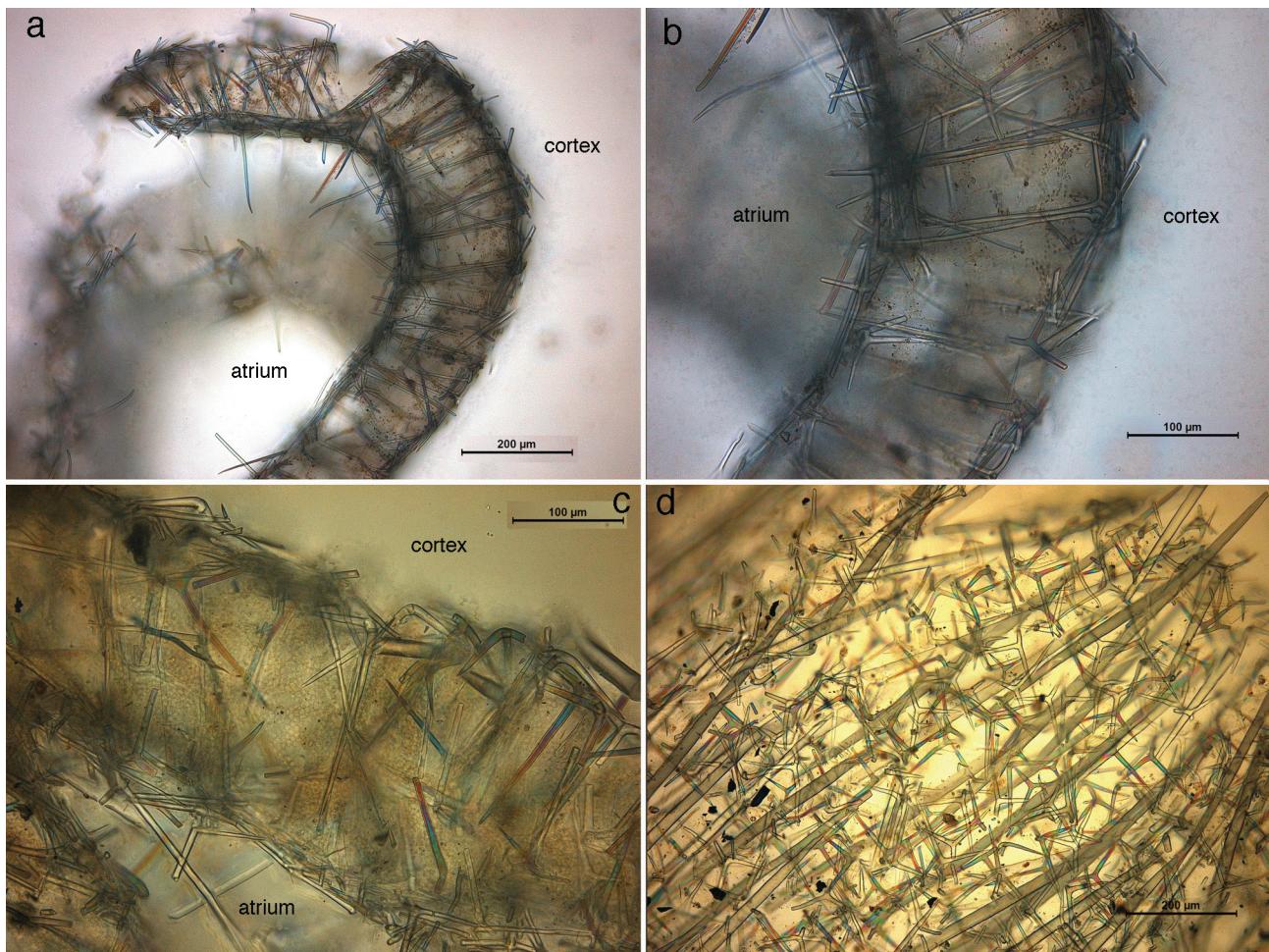
Figures 63a–c, 64a–d, 65a–f

*Heteropia striata* var. *minor* Burton, 1930: 4.

*Pericharax* sp.; Colin & Arneson, 1995: 61 photo 233; Gosliner *et al.*, 1996: 17, photo 7; Erhardt & Baensch, 1998: 23.



**FIGURE 63.** *Heteropia minor* Burton (1930), a, habitus *in situ* of RMNH Por. 9194 from Ternate (photo N.J. de Voogd), b, habitus *in situ* of RMNH Por. 1872 from the Berau region (photo B.W. Hoeksema), c, preserved specimens of sample RMNH Por. 9194 from Ternate (scale bar = 1 cm).



**FIGURE 64.** *Heteropia minor* Burton (1930), light microscopic sections, a, cross section of tube wall of ZMA Por. 08955 from Komodo showing inarticulate skeleton (scale bar = 200  $\mu\text{m}$ ), b, detail of cross section of ZMA Por. 08955 showing cortical triactines, pseudosagittal triactines, subatrial triactines and atrial tetractines (scale bar = 100  $\mu\text{m}$ ), c, BMNH 1929.8.30.3 cross section of holotype (ZMA Por. 00143) from Timor Leste showing essentially the same structure and spicules as in (b) (scale bar = 100  $\mu\text{m}$ ), d, BMNH 1929.8.30.3 tangential surface section of holotype (ZMA Por. 00143) showing cortical triactines and diactines (scale bar = 200  $\mu\text{m}$ ).

**Material examined.** Holotype ZMA Por. 00143, Siboga Expedition Stat. 282, Timor-Leste, Timor, anchorage between Nusa Besi and the NE point of Timor, 8.42°S 127.3066°E, depth 27–54 m, trawl, bottom sand with corals and coralline algae, coll. Siboga Expedition stat. 282, 15–17 January 1901; three slides of the holotype: BMNH 1929.8.30.3a.

Additional specimens. ZMA Por. 06536, Indonesia, Komodo, N Cape, 8.4833°S 119.5683°E, depth 30 m, SCUBA, coll. H.A. ten Hove, Indonesian-Dutch Snellius II Expedition stat. 096/04, 19 September 1984; ZMA Por. 08391, Indonesia, Komodo lagoon, 8.5833°S 119.57°E, depth 4–11 m, SCUBA, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition stat. 79/III/16, 18 September 1984; ZMA Por. 08955, Indonesia, Saleyar, Bahuluang, 6.45°S 120.43°E, depth 10–15 m, SCUBA, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition stat. 169/IV/36, 30 September 1984; ZMA Por. 16835, Indonesia, North Sulawesi, Donggala, 0.6981°S 119.7713°E, depth 15 m, SCUBA, coll. S. Weinberg, 30 August 1995; RMNH Por. 1872, Indonesia, NE Kalimantan, Berau Islands, lighthouse Panjang, Island, NE side, 2.3873°N 118.2094°E, depth 10–15 m, SCUBA, coll. B.W. Hoeksema, #BER14/091003/082, 9 October 2003; RMNH Por. 2164, Indonesia, Central Sulawesi, Donggala, South Atoll, 0.69°S 119.7°E, depth 15–20 m, SCUBA, coll. N.J. de Voogd, #DG/240601/266, 24 June 2001; RMNH Por. 3603, Indonesia, N Sulawesi, off Manado, Nain Islands, Jelan Masak, 1.7567°N 124.7857°E, depth 5 m, SCUBA, coll. N.J. de Voogd, #MD13/190502/114, 19 May 2002; RMNH Por. 5268, Indonesia, Ternate, Sulamadaha Beach, 0.8632°N 127.3345°E, depth 5–10 m, SCUBA, coll. N.J. de Voogd, #TER.04/261009/NV019, Ternate-Halmahera Expedition 2009, 26 October 2009; RMNH 9193, Indonesia, Ternate, off Danau Laguna,

0.7583°N 127.3498°E, depth 12 m, SCUBA, coll. N.J. de Voogd, # TER.02/251009/, Ternate-Halmahera Expedition 2009, 25 October 2009; RMNH 9194, Ternate, Kampung Cina, Tapak 2, 0.7875°N 127.3435°E, depth 10–15 m, SCUBA, coll. N.J. de Voogd, #TER.06/271009/, Ternate-Halmahera Expedition 2009, 27 October 2009; RMNH 9349, Indonesia, Papua, Raja Ampat, 0.5695°S 130.2739°E, depth 10–20 m, SCUBA, coll. L.E. Becking, #RAJ67/LE243, 7 December 2007.

**Description.** Short-stalked, thin-walled, sac-shaped or balloon-shaped sponge (Figs 63a–b), in life limp. When taken out of the water, the interior ‘empties’ and the opposite walls may stick together to form a double-walled envelope (Fig. 63c). In alcohol the walls become rigid and very easily damaged, or torn. Color red, dark red, wine red, brown red in life, whitish, cream or yellowish in preserved condition. What is left of the holotype is a tiny tube, of which most spicules are ‘corroded’. Sections and dissociated spicule preparations in the collection of the Natural History Museum, London, are an important part of the type material.

**Histology.** Sylleibid aquiferous system, possibly syconoid in some parts.

**Skeleton.** (Figs 64a–d) In cross section from exterior to atrial cavity, there is an ectosomal cortex built from tangential triactines, a variable amount of tangential long diactines (Fig. 64d), and parasagittal triactines with the unpaired actine directed proximally (inwards), and the paired actines carrying the diactines. The choanosomal skeleton is inarticulate (Figs 64b–c) and consists of the longest of the paired actines of the cortical para/pseudosagittal triactines and the unpaired actines of subatrial sagittal tetractines and triactines.

The atrial skeleton is composed of the paired actines and tangentially arranged unpaired actines of predominantly tetractinal sagittal atrial spicules, strengthened by the paired actines of smaller atrial tetractines whose apical actines protrude into the atrial cavity (Fig. 64b).

**Spicules.** (Fig. 65a–f) Equiaxial triactines, pseudosagittal triactines, sagittal triactines, sagittal tetractines, diactines.

Ectosomal diactines (Fig. 65a) up to 264–724.7–1420 x 4–14.2–22 µm. Holotype: 340–110 x 11–22 µm; additional specimens 264–1420 x 4–20 µm.

Ectosomal cortical triactines (Fig. 65b), usually characteristic equiaxial or slightly sagittal tripods, unpaired actines 99–140.3–252 x 4–5.4–7 µm, paired actines 75–99.7–150 x 4–4.8–6 µm. Holotype: unpaired actines 135–177 x 5–7 µm, paired actines 55–138 x 3–6 µm; additional specimens, unpaired actines 99–252 x 4–7 µm, paired actines 55–150 x 4–6. Overall actines (paired and unpaired) 55–252 x 3–7 µm.

Subcortical para/pseudosagittal triactines (Fig. 65c), with the paired actines at different planes with regard to the unpaired actines, and occasionally abruptly curved in the middle, or one of the paired actines may be ‘wavy’; unpaired actines 66–159.1–242 x 5–6.6–8 µm, paired actines, unequal in length but only barely so, 48–101.8–135 x 4–5.5–7 mm. Holotype: unpaired actines 123–242 x 5–8 µm, paired actines 75–133 x 5–7 µm. Additional specimens: unpaired actines 66–222 x 5–8 µm, paired actines 72–132 x 4–6 µm.

Subatrial sagittal triactines (Fig. 65d), relatively rare, unpaired actines 96–226.2–450 x 5–6.3–9 µm, paired actines 81–152.4–300 x 5–5.9–6.5 µm. Holotype: unpaired actines 96–222 x 6–7 µm, paired actines 102–240 x 5–6.5 µm. Additional specimens: unpaired actines 153–420 x 5–9 µm, paired actines 81–300 x 5–6 µm.

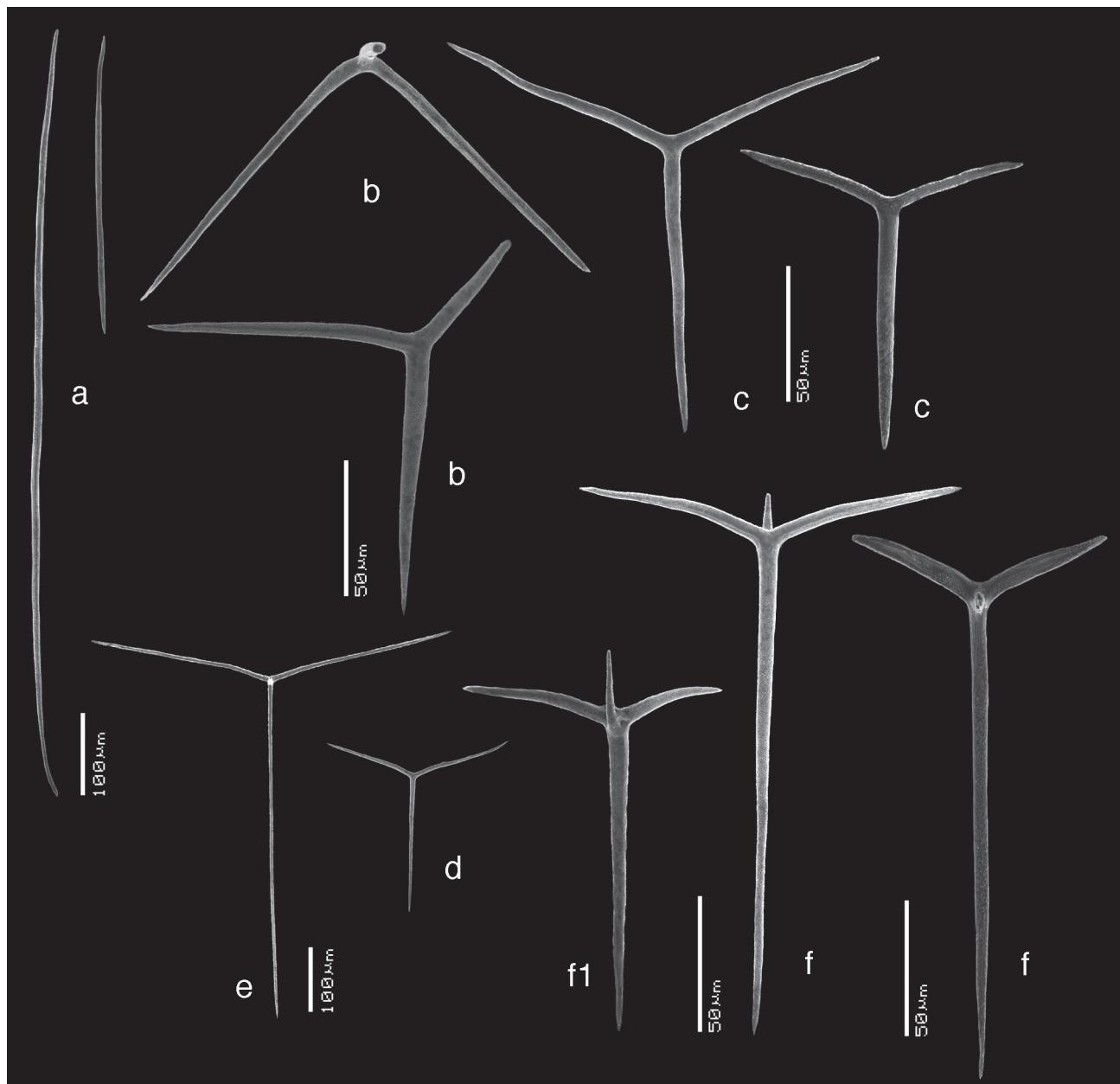
Subatrial sagittal tetractines (Fig. 65e), unpaired actines 186–330.6–570 x 5–6.4–9 µm, paired actines 90–180.3–324 x 6–6.7–9 µm, apical actines 10–19.8–57 x 4–4.8–6 µm. Holotype: unpaired actines 186–390 x 5–7 µm, paired actines 90–186 x 4–7 µm, apical actines 15–57 x 4–6 µm. Additional specimens: unpaired actines 216–570 x 6–9 µm, paired actines 120–324 x 6–9 µm, apical actines 10–21 x 4–6 µm.

Atrial sagittal tetractines (Figs 65f, f1), unpaired actines 122–182.6–228 x 5–6.5–8 µm, paired actines 63–129.0–180 x 4.5–5.3–7 µm, apical actines 27–51.5–78 x 3–4.3–5 µm. Holotype: unpaired actines 186–216 x 5–6.5 µm, paired actines 96–180 x 4.5–6 µm, apical actines 30–66 x 3–6 µm. Additional specimens: unpaired actines 122–228 x 6–8, paired actines 63–120 x 5–7 µm, apical actines 27–78 x 4–5 µm.

**Ecology.** In coral reef localities, at depths between 4 and 54 m.

**Distribution.** Indonesia, Papua New Guinea.

**Remarks.** Burton (1930) assigned this species to the genus *Heteropia*, but according to the Systema Porifera (Borojevic *et al.* 2002b) that genus has an articulate skeleton unlike the present Indonesian material, and the subcortical triactines should be genuine pseudosagittal spicules, whereas our specimens including the holotype in that position show predominantly pseudosagittal spicules appearing almost parasagittal. We propose to extend the content of *Heteropia* to accommodate the present species.



**FIGURE 65.** *Heteroplia minor* Burton (1930), SEM images of the spicules of RMNH Por. 9194, a, cortical diactines, b, cortical (tripod-like) triactines, c, subcortical pseudosagittal / parasagittal triactine, d, subatrial triactine, e, subatrial tetractine, f, f1, atrial tetractines.

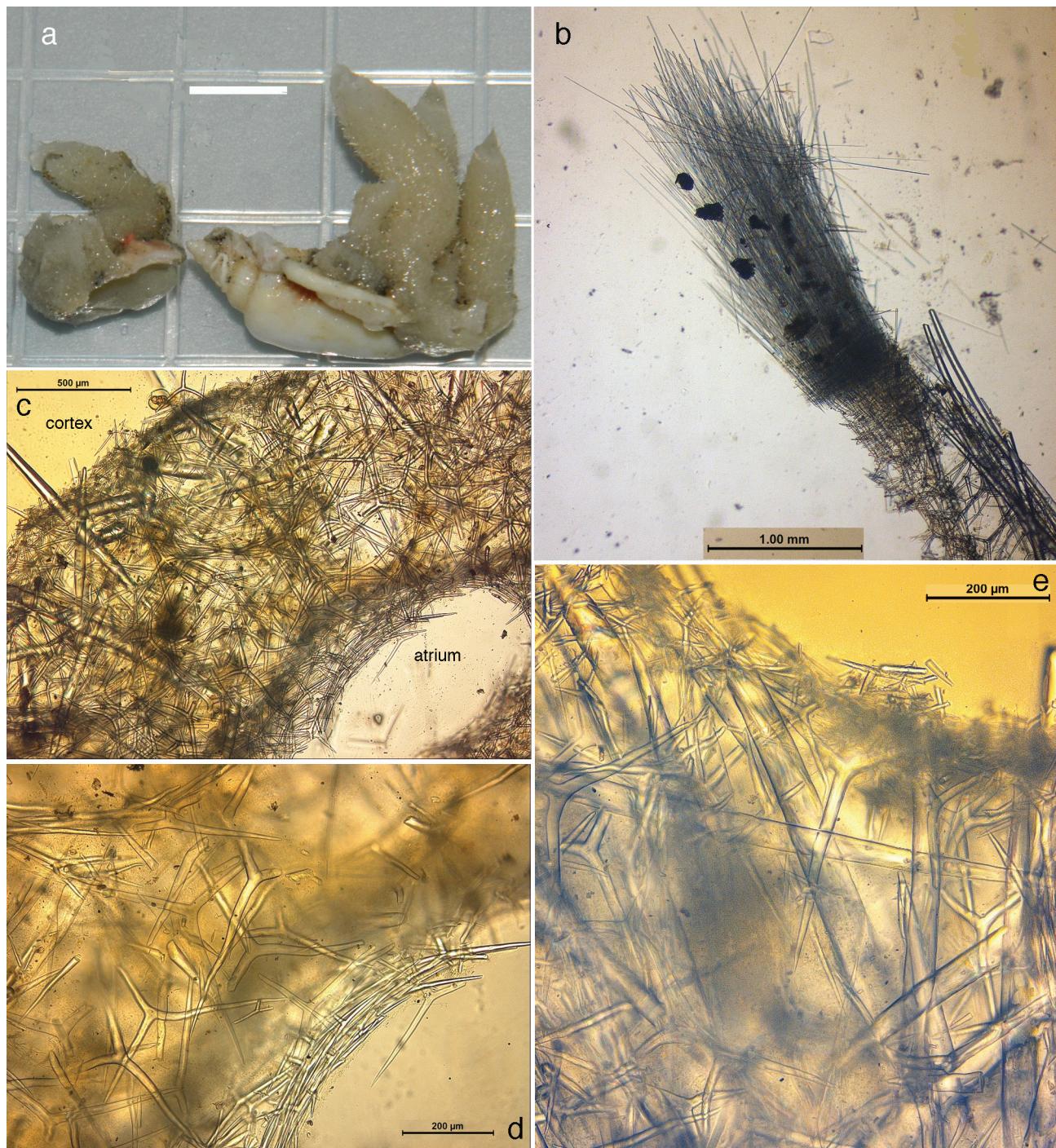
*Heteroplia striata* Hôzawa, 1916, of which the present species was deemed a ‘variety’ by Burton, has indeed a certain similarity with our specimens in skeletal and spicule characters, and like our species it has an inarticulate skeleton. However, the shape is more definitely simply tubular, without the distended middle part, there may be an oscular fringe, lacking in our specimens, the aquiferous system is more elaborately sylleibid, with extensively branched chambers, it has larger and much thicker ectosomal oxeas (up to 2000 x 90 µm), the tangentially arranged atrial spicules are predominantly triactinal (not tetractinal as in our specimens), and most spicule measurements of all categories differ from those of the present material. There can be little doubt that this is a different species.

**Genus *Vosmaeropsis* Dendy, 1893a**

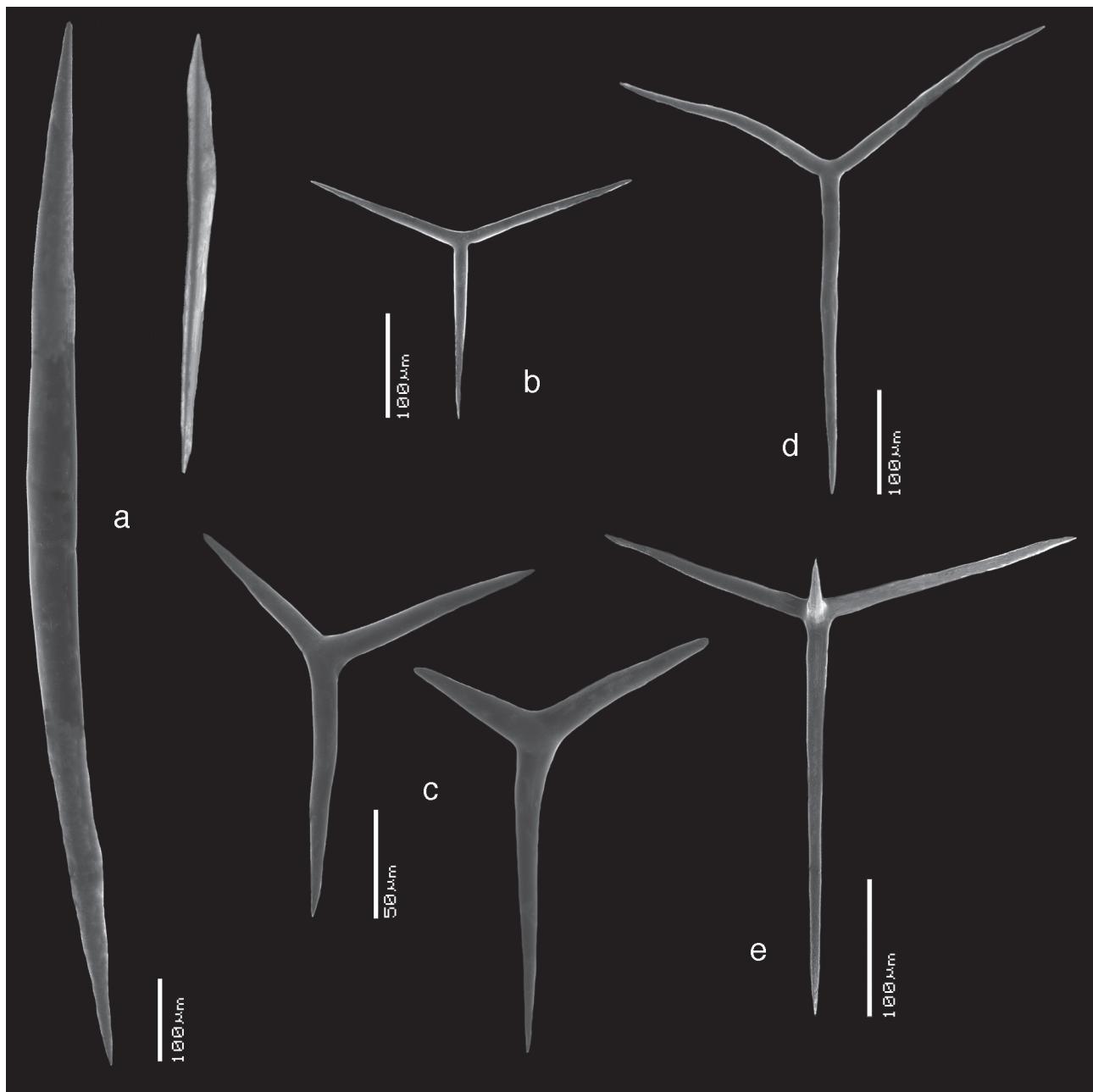
***Vosmaeropsis grisea* Tanita, 1939**

Figures 66a–e, 67a–e

*Leuconia capillata* sensu Burton, 1930: 5 (not: Poléjaeff, 1883: 55, pl. II fig. 1 as *Leuconia multiformis* var. *capillata*)  
*Vosmaeropsis grisea* Tanita, 1939: 319, figs 1–2 (mandatory correction to *V. grisea*, cf. ICBN article 31.2).



**FIGURE 66.** *Vosmaeropsis grisea* Tanita (1939), ZMA Por. 00147, from Banda, erroneously assigned to *Leuconia capillata* by Burton (1930), a, habitus of preserved specimens (scale bar = 1 cm), b–e, Burton's slides, BMNH 1928.6.18.19a, b, oscular fringe (scale bar = 1 mm), c, cross section of tube wall showing confused choanosomal skeleton and protruding giant diactines (scale bar 500  $\mu$ m), d, detail of atrial region with confused mass of pseudosagittal triactines and multilayered atrial skeleton consisting of sagittal triactines and regular tetractines (scale bar = 200  $\mu$ m), e, detail of cortical skeleton of small triactines and subcortical pseudosagittal triactines (scale bar = 200  $\mu$ m).



**FIGURE 67.** *Vosmaeropsis grisea* Tanita (1939), ZMA Por. 00147, from Banda, erroneously assigned to *Leuconia capillata* by Burton (1930), SEM images of the spicules, a, diactines, b, cortical triactine, c, pseudosagittal triactines, d, sagittal triactine, e, sagittal tetractine (trichoxeas and diacrinies of the fringe not shown).

**Material examined.** ZMA Por. 00147, Indonesia, Maluku, Banda anchorage, 4.5398°S 129.9084°E, depth 9–45 m, trawled, coll. Siboga Expedition stat. 240; BMNH 1928.6.18.19a, two slides from Siboga material.

Examined for comparison: *Vosmaeropsis macera*, slides from the Dendy collection from South Australia, BMNH 1897.7.12.62a.

**Description.** A group of five *Sycon*-like individuals (Fig. 66a) attached to a dead gastropod shell. Surface shaggy with prominent oscular fringe (Fig. 66b). Size up to 2.5 cm high, 1 cm in diameter. Consistency firm. Color pale greyish brown (alcohol).

**Histology.** Due to bad preservation, choanocyte chambers could not be made visible, but the overall skeletal structure leaves little doubt that it is certainly not syconoid, very likely leuconoid, although a sylleibid arrangement cannot be excluded.

**Skeleton.** (Figs 66c–e) The cortex (Fig. 66e) consists of regular triactines (although tending to be slightly sagittal), scattered trichoxeas, and the shorter paired actines of pseudosagittal triactines, pierced by giant diactines

at sharp angles (Fig. 66c). The choanosomal skeleton is dominated by perpendicular or more often sharp-angled giant diactines and scattered pseudosagittal triactines (Fig. 66c). Atrial skeleton (Fig. 66d) consisting of several layers of sagittal triactines and regular tetractines. The oscular fringe (Fig. 66b) is long and consists of a thick mass of long thin diactines.

**Spicules.** (Figs 67a–e) Giant diactines, equiangular triactines, pseudosagittal triactines, sagittal triactines, equiangular tetractines, trichoxeas.

Giant diactines (Fig. 67a), fusiform, 500–1316.6–1760 x 20–44.3–54 µm (predominantly in the size range of 1000–1500 µm).

Cortical equiangular triactines (Fig. 67b), 141–176.0–219 x 8–10.1–12 µm.

Pseudosagittal triactines (Fig. 67c), all actines of different length, and at variable angles, longest paired actines 168–275.6–361 x 9–15.6–21 µm, shortest paired actines 96–194.1–329 x 9–15.5–21 µm, unpaired actines 155–233.5–390 x 8–15.8–21 µm.

Sagittal triactines (Fig. 67d), with unpaired actines 111–174.0–249 x 4–8.6–12 µm, paired actines 78–130.8–204 x 4–8.3–12 µm.

Equiangular tetractines (Fig. 67e), with unpaired actines 126–166.3–192 x 9–11.5–15 µm, paired actines 117–164.2–261 x 11–13.2–16 µm, and apical actines 18–36.2–54 x 4–6.5–11 µm.

Trichoxeas, invariably broken, pieces vary in size, 150–242.6–390 x 1–3 µm.

Diactines of the oscular fringe 1170–1980 x 2–4 µm.

**Ecology.** Deeper water in sandy reef environment.

**Distribution.** Indonesia, Japan.

**Remarks.** Burton assigned this material to the Philippine species *Leuconia capillata* Poléjaeff, 1883 (as *Leuconia multiformis* var. *capillata*), but there are large differences with Poléjaeff's description. The most important difference is that the subcortical triactines in the present specimen are distinctly pseudosagittal, not regular or subregular as in *L. capillata*. Measurements of all the spicules differ significantly from Poléjaeff's description, e.g. the giant diactines in *L. capillata* are up to 6 mm against a maximum of 1.76 mm in the present material.

Assignment of this material to *Vosmaeropsis* is based on the combination of pseudosagittal triactines, a rather confused choanosomal skeleton, and presumed leuconoid aquiferous system. Recent descriptions of two *Vosmaeropsis* species from Brazil (Cavalcanti *et al.* 2015) appear to be similar in most aspects to our specimens, so we are confident that they are congeneric. Some doubts about the present classification was raised by a comparison with the type species of *Vosmaeropsis*, *V. macera* (Carter, 1886) (as *Heteropia*). That species has a sylleibid aquiferous system and, more importantly, an inarticulate skeleton (cf. Dendy, 1893: fig. 19), unlike our specimens. We were able to confirm this by examination of two slides of the type made by Dendy (1893), BMNH 1897.7.12.62a, borrowed from the Natural History Museum, London.

Of the described species of *Vosmaeropsis*, *V. grisea* Tanita, 1939 appears the most similar, in shape as well as spicular measurements. The only difference of possible significance is the shape of the subgastral sagittal triadiates, the majority of which have their unpaired actines shorter than their paired actines in Tanita's description.

*Vosmaeropsis dendyi* Row & Hôzawa, 1931 from Western Australia has the pseudosagittal triactines distinctly smaller than our species, and there are cortical tetractines in addition to several spicule categories distinguished by Row & Hôzawa (1931), which have not been found in our specimen. Burton (1963) assigned *V. dendyi* to the synonymy of *V. macera*, but this differs strongly in habitus from *V. dendyi* and from our species. A similar species is *Vosmaeropsis mackinnoni* Dendy & Frederick, 1924, which was also synonymized with *V. macera* by Burton (1963). It has much larger cortical triactines than our species.

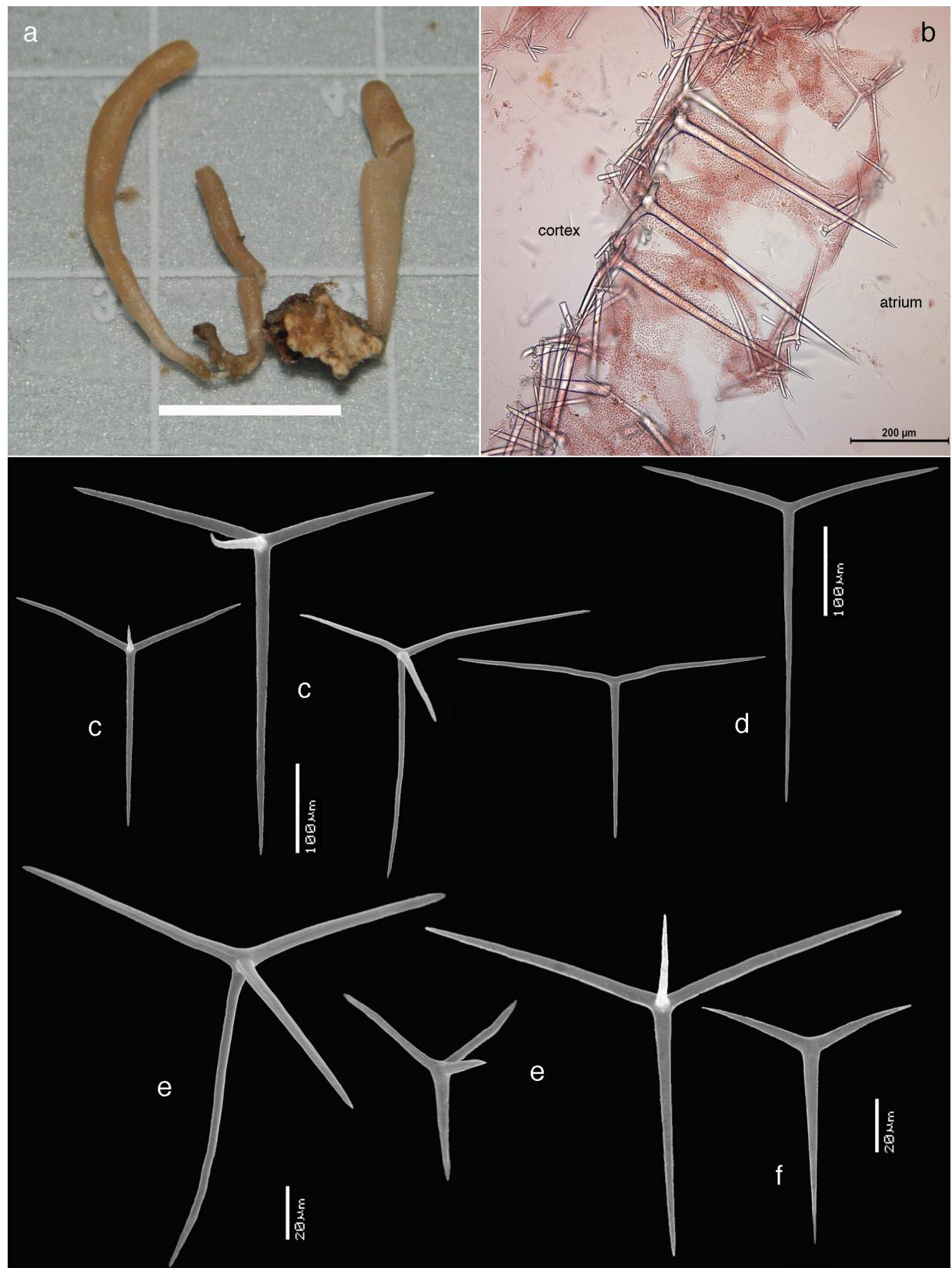
## Family Amorphiscidae Dendy, 1893a

### Genus *Amphoriscus* Haeckel, 1870

#### *Amphoriscus semoni* Breitfuss, 1896

Figures 68a–f

*Amphoriscus semoni* Breitfuss, 1896b: 435; Breitfuss, 1898: 221.



**FIGURE 68.** *Amorphiscus semoni* Breitfuss (1896), ZMA Por. 08073, a, habitus (scale bar = 1 cm), b, histological cross section showing syconoid aquiferous system and inarticulate skeleton (scale bar = 200 µm); left side: ectosomal skeleton formed by the paired and unpaired actines of giant tetractines, right side: atrial skeleton of triactines and tetractines, c–f, SEM images of spicules, c, giant tetractines, d, large sagittal triactines of the choanosomal / subatrial skeleton, e, atrial tetractines, f, small subatrial sagittal triactine.

**Material examined.** ZMA Por. 08073, Indonesia, Nusa Tenggara, Sumbawa, Bay of Sanggar, 8.32°S 118.24°E, depth 1 m, sea grass meadow, snorkeling, coll. F. Leys, Indonesian-Dutch Snellius II Expedition stat. 114/01, 21 September 1984.

**Description.** A small group of elongated thin-walled curved tubes (Fig. 68a), with smooth surface, live color green. The three are basally connected on the surface of a small limestone fragment, but are otherwise free. Length of longest tube 2.5 cm, diameter 0.4 cm. Consistency fragile, easily damaged.

**Histology.** Syconoid aquiferous system (Fig. 68b).

**Skeleton.** Inarticulate (Fig. 68b). Very organized. The ectosomal skeleton is formed by the paired and unpaired actines of giant tetractines. The apical actines of these form the choanosomal skeleton, together with the unpaired actines of the subatrial triactines. Atrial skeleton is formed by the paired actines of the subatrial triactines and a thin layer of atrial tetractines. The wall of the tubes is thin, often thinner than the length of the apical actines of the giant tetractines (less than 600–800 µm in length), which may protrude into the atrial lumen along with the apical actines of the small atrial tetractines.

**Spicules.** (Figs 68c–f) Large sagittal tetractines, small more or less equiaxial tetractines, large and small sagittal triactines.

Large tetractines (Fig. 68c), with long apical actine and almost equiangular equiaxial paired and unpaired actines. Unpaired actines 122–203.8–271 x 13–15.6–18 µm, paired actines, 210–432.9–602 x 15–18.4–23 µm, apical actines 378–517.1–600 x 18–21.5–35 µm.

Small tetractines (Fig. 68e), basal system approximately equiangular equiaxial, smaller apical actines, unpaired actines 54–113.6–174 x 6–8.7–11 µm, paired actines 48–106.6–175 x 5–7.0–11 µm, apical actines 9–44.6–84 x 5–5.9–8 µm.

Triactines (Figs 68d, f), sagittal, in a wide size range, possibly divisible in two size classes, unpaired actines overall 72–241.5–372 x 5–11.6–16 µm, paired actines overall 48–158.5–222 x 5–8.6–11 µm.

**Ecology.** Shallow water.

**Distribution.** Indonesia (Amboin, Sumbawa).

**Remarks.** The specimens conform closely with the Amboin material of Breitfuss (1896b). He described the holotype as shiny white, but his material was preserved without field data (received from W. Weltner who passed it on from the collector R. Semon). The length of the choanosomal (apical) actine of the giant tetractines is given as 520–790 µm, whereas in our material this did not exceed 600 µm.

## Genus *Leucilla* Haeckel, 1872

### *Leucilla australiensis* (Carter, 1886)

Figures 69a–i

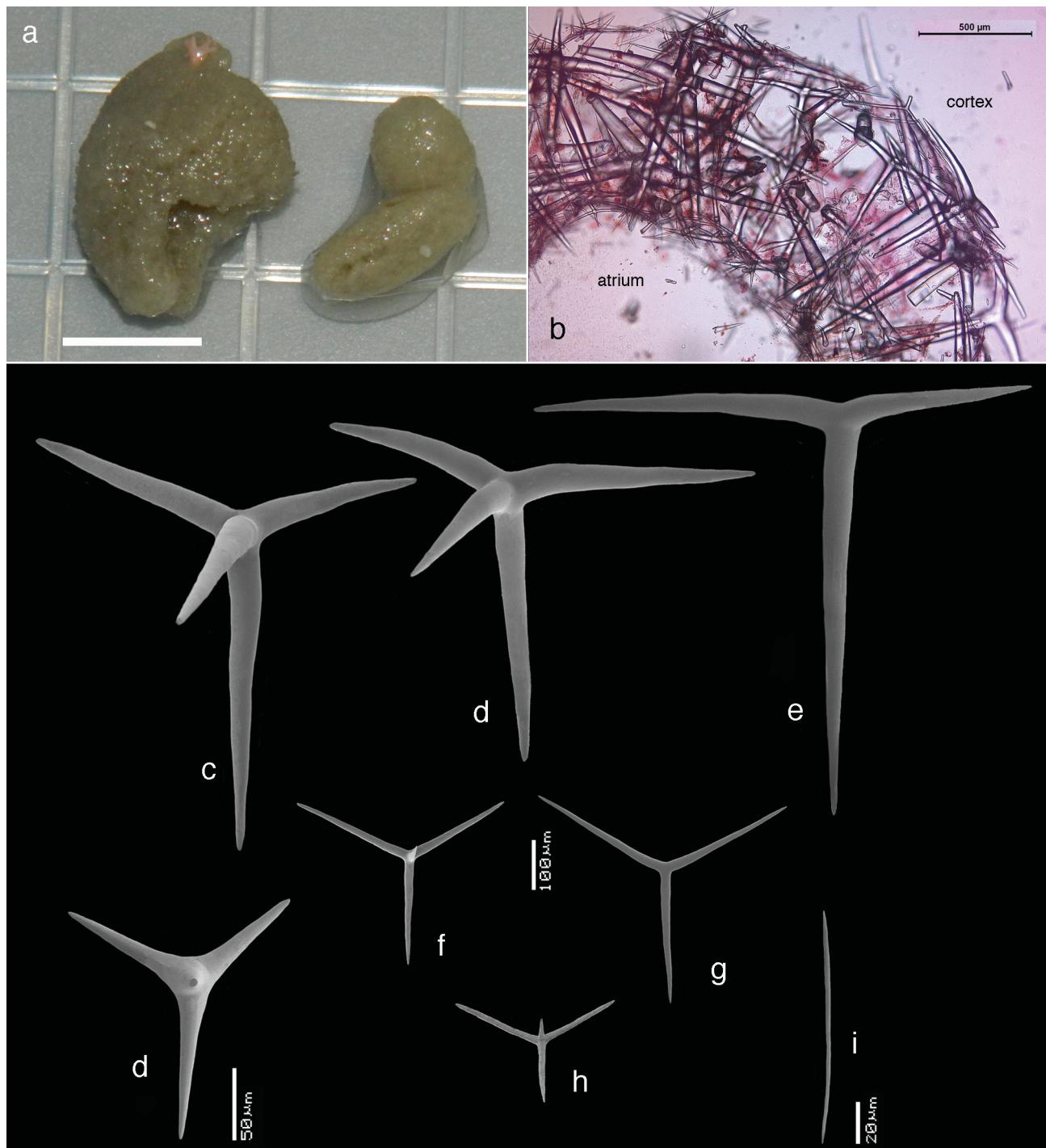
*Leucilla uter* Poléjaeff, 1883: 53 (in part, only the Philippine specimen, which is not conspecific with the type from Bermuda). *Leuconia johnstonii* var. *australiensis* Carter, 1886: 133.

*Leucilla australiensis*; Dendy & Row, 1913: 783; Burton, 1930: 7, fig. 6; Borojevic, 1967a: 221, fig. 25.

(Not: *Leucilla australiensis*; Borojevic & Peixinho, 1976: 1031, fig. 27; nec: *Leucilla uter* sensu Borojevic & Boury-Esnault, 1987: 35 (both = *Leucilla sacculata* (Carter, 1890) fide: Muricy *et al.* 2011: 25)).

**Material examined.** ZMA Por. 00137, Indonesia, Maluku, Kai Islands, off Nuhu Jaan, 5.6083°S 132.92°E, depth 90 m, dredge, sandy bottom, coll. Siboga Expedition stat. 260, 16 December 1899; ZMA Por. 00138, Indonesia, Maluku, Banda anchorage, 4.5398°S 129.9084°E, depth 9–45 m, trawled, coll. Siboga Expedition stat. 240, 22 November 1899; ZMA Por. 16165b, Indonesia, SW Sulawesi, Samalona, 4.8747°S 119.3419°E, depth 6 m, SCUBA, coll. N.J. de Voogd, #SA/200497/06, 20 April 1997 (incorporated in a mass of *Clathrina chrysea* tubes); ZMA Por. 20719, Indonesia, Nusa Tenggara, Sumba, NE coast off Melolo, 9.9°S 120.7083°E, depth 6 m, SCUBA, coll. R.W.M. van Soest, Indonesian-Dutch Snellius II Expedition stat. 048, 13 September 1984.

**Description.** Thick-walled semiglobular or tubular individuals (Fig. 69a), up to 2 cm in height and width. There is an atrial chamber with a naked osculum with small fringe. Surface irregular. Consistency soft. Color dirty white, in alcohol it is greyish.



**FIGURE 69.** *Leucilla australiensis* (Carter, 1886), a, habitus of preserved specimens of ZMA Por. 00137 from the Kai Islands (scale bar = 1 cm), b, cross section of tube wall showing inarticulate skeleton of giant tetractines and triactines covered by a thin cortex of small triactines and with an atrial skeleton of small sagittal tetractines (scale bar = 500 µm), c–h, SEM images of the spicules of ZMA Por. 00137, c, giant tetractine of the cortex, d, giant tetractines of the choanosome (including tetrapod-like smaller spicule), e, giant triactine, f, regular small tetractine, g, cortical regular triactine, h, sagittal atrial tetractine, i, trichoxea .

**Histology.** Leuconoid aquiferous system (Fig. 69b).

**Skeleton.** Inarticulate (Fig. 69b). In cross section the dermal cortex, where present, is formed by small equiangular triactines, and these are carried by subcortical giant tetractines with very long unpaired actines. The choanosomal skeleton (Fig. 69b) is formed primarily by the long unpaired actines of the cortical tetractines and supported by confusedly arranged giant and smaller tetractines with almost equal actines and the unpaired actines of slightly sagittal subatrial giant triactines. The atrial skeleton consists of a layer of small sagittal triactines. The

thin oscular rim contains bundles of thin diactines and thinner forms of the small cortical triactines and atrial tetractines.

**Spicules.** (Figs 69c–i) Giant tetractines and triactines, small regular triactines, small regular tetractines, sagittal tetractines, trichoxeas of the oscular rim.

Giant tetractines of the cortical skeleton (Fig. 69c), strongly sagittal, unpaired actines 330–650.4–1300 x 18–40.5–54 µm, paired actines 320–45.9–660 x 19–38.3–55 µm, apical actines 42–151.9–330 x 20–36.9–55 µm.

Giant tetractines of the choanosome (Fig. 69d), slightly smaller, basal triradiate system equiaxial, paired and unpaired actines 330–528 x 19–38 µm, apical actines 42–252 x 20–36 µm.

Giant triactines (Fig. 69e), equiaxial, actines 384–491.3–690 x 18–30.8–42 µm

Regular equiangular tetractines (Fig. 69f), actines of basal triradiate system 60–82.2–111 x 4–5.8–8 µm, apical actines small, approximately 10 µm.

Cortical small triactines (Fig. 69g), equiangular or occasionally tripod-like, 78–185.1–298 x 4–10.9–19 µm.

Sagittal tetractines (Fig. 69h), unpaired actines 78–113.3–127 x 5–7.2–9 µm, paired actines 57–93.2–132 x 4–5.8–8 µm, apical actines 20–30.5–39 x 3–4.3–6 µm.

Trichoxeas (Fig. 69i) of the oscular rim, mostly broken in the slides, 60–500 x 1–2 µm.

**Ecology.** Occurring in a wide depth range: 6 m down to 90 m, on reefs and on sandy bottom.

**Distribution.** Indonesia, Philippines, South Australia, South Africa.

**Remarks.** Poléjaeff assigned specimens from widely divergent areas to the type series for his *Leucilla uter*. Burton (1963: 636) assigned lectotype status to Poléjaeff's Bermuda specimen, whereas the Philippine specimen is the paralectotype (named 'co-type' by Burton). This assignment makes it clear that the name *L. uter* cannot be employed for our specimens. *Leucilla australiensis* is the next eldest name and its type locality is sufficiently close to justify us to name our material *L. australiensis*.

The present material conforms to Poléjaeff's description of *Leucilla uter* in most aspects (skeleton and spicule dimensions), although Poléjaeff only provides upper values of the spicule sizes. Our smaller atrial tetractines are on average considerably smaller than Poléjaeff's data, but the upper values match. Poléjaeff fails to mention or illustrate the cortical small triactines, but these are also rare or absent in many parts of our specimens.

Burton (1930) also assigned the present specimen to *L. australiensis* and compared them with slides of Carter's holotype. Although the general structure and the spicule categories appear to conform to Carter's holotype from Port Philip Bay, South Australia, there are some compelling differences with the Indonesian specimens, such as the larger sizes of the giant tetractines and triactines, and the smaller sizes of the cortical and atrial triactines and the choanosomal tetractines. However, Carter's description is deficient and both Dendy (1913) and Borojevic (1967a) maintain that these aspects are variable among specimens of a widely distributed *L. australiensis*. Burton (1963) reverted his decision to associate the present material to *L. australiensis* and considered it to belong to the Southeast Australian *Paraleucilla saccharata* (Haeckel, 1872) (originally as *Leucandra*). We will not follow this controversial decision.

## Additional Indonesian Calcarea not represented in the present collections

Species reported from Indonesia by other authors, which do not appear to be represented in our collections, are listed here for completeness sake. Most of these records are insufficiently characterized or described.

### *Arthuria darwinii* (Haeckel, 1870) comb. nov.

*Leucosolenia darwinii* Haeckel, 1870: 243;

*Ascalitis darwinii* (Haeckel, 1872) (II): 57, (III) pl. 9 fig. 4, pl. 10 figs 3a–c

(*Olynthus*, *Cistolynthus*, *Soleniscus*, *Nardorus*, *Tarrus*, *Auloplegma*, *Ascometra*, *Ascertta*, *Ascilla darwinii* (Haeckel, 1872) (II): 57–58.

*Ascalitis erasmi* Haeckel, 1872 (II): 58.

*Ascalitis caroli* Haeckel, 1872 (II): 58.

*Ascalitis darwinii* var. *erasmi* Haeckel, 1872 (II): 58.

*Ascalitis darwinii* var. *caroli* Haeckel, 1872 (II): 58.

Description (summarized from Haeckel, 1972 (II): 57): Apparently a variable network of partially upright tubes ending in small oscules, together forming an encrustation on algal fronds. Size of cormus up to 30 mm in lateral expansion. Skeleton and spicules: the walls of the tubes consist of a single layer of spicules. Tri- and tetractines are similar in shape, equiangular equiaxial, 80–100 x 10–12 µm, with apical actines of the tetractines often curved upwards.

Type locality: Java (collected by Mulder); also reported by Haeckel from Sri Lanka (collected by Wright) and the Red Sea (collected by Frauenfeld).

### ***Ascandra(?) sertularia* (Haeckel, 1872)**

*Ascandra sertularia* Haeckel, 1872 (II): 100, (III) pl. 15 figs 4a–f, pl. 17 fig. 5

*Soleniscus sertularia* Haeckel, 1872 (II): 100.

*Leucosolenia sertularia*; Dendy & Row, 1913: 723.

Description (summarized from Haeckel, 1872 (II): 100–101): Hydroid-shaped, with a thin central tube from which branch off two-dimensionally numerous side tubes, which in turn have side branches themselves. The drawing of Haeckel is rather stylized, but apparently the sponge was bilaterally symmetrical. Length of cormus 28 mm, width 14 mm. The central tube is 2 mm in diameter, the side tubes 1 mm. The sponge has a small holdfast with which it is attached to a red alga. The central tube is open distally. The surface is hidrid from protruding large diactines. Skeleton and spicules: the walls of the tubes are formed by aligned tri- and tetractines, similar in size and shape, together forming regular rectangular meshes. Sizes of the paired actines 120 x 10 µm, unpaired actines 60 x 5 µm. Diactines of 500–600 x 30–40 µm, with a lancet-shaped protruding end set off by a thickened ring, are arranged perpendicular to the wall of the tubes.

Type locality: Java (collected by Mulder).

### ***Clathrina flexilis* (Haeckel, 1872) comb. nov.**

*Ascetta flexilis* Haeckel, 1872 (II): 43, (III): pl. 5 fig. 8

*Leucosolenia flexilis*; Dendy & Row, 1913: 725.

Description (summarized from Haeckel, 1872 (II): 43): Barely recognizable. It is described as forming an anastomosing network of thin tubes similar to *Clathrina coriacea*. Walls of the tubes with unorganized layer of triactines, shaped irregularly: unequiangular and unequiaxial. No further information.

Type locality: Singapore (collected by Putnam).

### ***Grantia capillosa* var. *longipilis* sensu Breitfuss, 1896**

*Grantia capillosa* var. *longipilis*; Breitfuss, 1896a: 434; Breitfuss, 1898: 174 (not: Haeckel, 1872).

Description: The specimens are cylindrical – conical with terminal oval oscules. The surface is shaggy. The specimens are considerably larger than the Adriatic Sea type specimen, as they had a length of 40–57 mm. The spicules consist of diactines, triactines and tetractines. It is unclear to which actual species this material belongs. *Grantia capillosa* has had a chequered history and its present status is uncertain.

### ***Leucandra pumila* sensu Topsent, 1897**

*Leucandra pumila*; Topsent, 1897: 432 (not: Bowerbank, 1866 as *Leuconia*); Breitfuss, 1898: 178.

Two specimens reported from Ambon. No description given.

## *Aphroceras caespitosa* (Haeckel, 1872)

*Leucandra alcicornis* var. *caespitosa* Haeckel, 1872: 185.

Comment: Haeckel (1872: 185 and 186) described this species as a variety of Gray's (1858) *Aphroceras alcicornis*. Haeckel's Indonesian material from Java was collected by Mulder. It is not certain that the present variety was described from Indonesia as Haeckel did not clearly distinguish this variety from *Leucandra alcicornis* var. *cladocora*, mentioned on the same page, and later considered as the typical variety of *A. alcicornis* from Hong Kong by Burton (1963: 491). The descriptions of both varieties are insufficiently detailed to recognize *A. caespitosa* as a distinct species. No material resembling *A. alcicornis* was found among our specimens. The identity of this species is unclear. Ferrer Hernandez (1912) reported a sponge under the name *Leucandra caespitosa* from the Mediterranean, but Haeckel's specimens were all from the Indo-Pacific. According to Burton (1963: 573) this is a *species inquirenda*.

## *Eilhardia schulzei* Poléjaeff, 1883

*Eilhardia schulzei* Poléjaeff, 1883: 70, pl. II fig. 7, pl. X figs 1–10; ?Breitfuss, 1896a: 434; ?Breitfuss, 1898: 177.

Description: Poléjaeff's specimens were cup-shaped sponges with giant triactines, sagittal triactines, giant diactines, small diactines and microdiactines. Locality South East Australia. The Indonesian record is based on a small fragment from Ternate reported by Breitfuss (1896a, 1898). The description is inadequate and the only spicule measurements concern the microdiactines of 25–31 x 1–2 µm. The occurrence in Indonesia of this remarkable species, which belongs to the order Baerida Borojevic *et al.* 2002c, needs further substantiation.

## Discussion

### The Indonesian Calcarea

The famous proponent of recent Calcarea taxonomy, Radovan Borojevic, wrote in 1967b "Les Éponges Calcaires de la région Indo-Pacifique sont relativement bien connues...". This statement is not supported by us, as we managed to almost double the number of species known from Indonesian waters at the time that Borojevic made the statement. Burton (1930) listed 20 species for the region (including 9 species not studied by him), while we present 37 species (and 6 dubious species). The 'known' species were in majority also found to be quite insufficiently characterized, which is now partially improved, but still species remain unknown in the 'fresh' state, and more work is needed.

How comprehensive can we consider the present attempt to describe the calcareous sponge fauna of Indonesia? We suspect that many more species are to be discovered. We have several arguments to support this:

- only about half the species reported by Burton (1930) were also collected by us
- many species described above were found only once (17 out of 37)
- many species reported from adjacent regions (Philippines, Japan, New Caledonia, Northeast Australia, West Australia, Indian Ocean) have not been found by us so far
- several genera apparently common in adjacent regions are not represented in our collection
- efforts of ourselves and our colleagues were not focused on collecting Calcarea
- cryptic habitats (caves, coral rubble), man-made objects (pontoons), and deep-water habitats were only rarely included in the collecting activities

## Classification

We employed here the classification as presented in the Systema Porifera (Borojevic *et al.* 2002a; 2002b; 2002c),

but from several recent attempts to evaluate this classification with ‘independent’ molecular characters it appears likely that major changes of the classification are imminent. Only the two subclasses Calcinea and Calcaronea appear to be well established, both morphologically and molecularly, but ordinal, family and genus classifications as presented in the Systema Porifera are so far not or only partially supported by morphological (Manuel *et al.* 2003) and molecular markers ([Manuel *et al.* (2004); Dohrmann *et al.* (2008); Voigt *et al.* (2012), Klautau *et al.* (2013)]. The relatively simple evolutionary schemes that form the basis of the present classification, usually hypothesized as grading from an asconoid basis into complex skeletal structures, thus appear largely unsupported by molecular analysis. It is clear that for the development of a phylogenetic classification more comprehensive studies are necessary, combining morphology (soft tissues, skeletal structures, spicule geometry and sizes) with molecular data. A simple representation of the various groups by a few seemingly randomly chosen species cannot serve as an adequate taxon spread to test present classifications and develop new ones. In a higher taxa revision using a comprehensive dataset (morphology and molecules), the genera and families need to be represented by their type species and type genera, in order to guard continued stability of nomenclature. If types are not included, the new classifications will be potentially corrupted and unstable. Locating, revising and sequencing type material should get a high priority for attempts to improve the classification. If type specimens fail to yield sufficiently quality DNA, they should be replaced by reliably identified members of the same species. Until such revisions have been made using proper standards it seems unwise to adopt new classifications.

In the meantime, the current classification shows some user problems, which we encountered during this study. We feel it is useful to point out some of these problems, also because it will indicate the strength of our decisions for the use of combinations in particular cases. A general problem is that the Systema Porifera Calcarea classification does not present comprehensive descriptions of the type species of the genera, like it was done for the other sponge groups. The type species for a given genus is mentioned in most cases, but no formal redescriptions with type specimen registration numbers and museum allocations can be found in the various chapters. Furthermore, species other than the type species belonging to a genus are only occasionally mentioned. These problems aggravate the generally poor accessibility of the classification and make it more difficult to attempt identification of species and genera. Specifically, we had problems using the classification in the following cases:

(1) The recent Clathrinidae revision of Klautau *et al.* (2013) subdivided the genus *Clathrina* into five genera, each of which was loosely defined, a type species indicated, a photo of the habitus and spicules provided, and some additional species mentioned. Unfortunately for us, few species from the Indo-West Pacific were reallocated to these new genera, and several of the genera had overlapping morphological definitions. This meant that allocation of Indonesian *Clathrina*-like sponges to their proper genus remained rather uncertain. We believe that species, genera and families should be recognizable by unambiguous morphological traits in order not to hamper the biodiscovery of calcareous sponges.

(2) *Leucascus*, *Ascoleucetta* and *Leucetta (chagosensis)*: on the basis of the Indonesian material we assigned to these taxa, we had difficulties understanding and recognizing the traits by which to separate these genera. All three appear to be massive Calcinea, with some internal cavities and lumina in various states of folding. Apparently, *Leucascus* can be with certainty recognized using SEM by the spined apical actines of the tetractines, but the other two appear to overlap in spicular characters. A recent revision of the two leucascid genera (Cavalcanti *et al.* 2015) including the species *Leucascus flavus* and *Ascoleucetta sagittata* did not discuss the macroscopic similarity with some *Leucetta*'s and this makes assignment of undetermined material ambiguous. Proper fixation for histology, in the field or shortly after collection, is necessary to assign these yellow sponges to their correct genus.

(3) *Sycetta* is an ill-known genus, defined in Borojevic *et al.* (2002b: 1162), as Sycettidae with ‘short completely separate radial tubes’, and ‘no defined inhalant aquiferous system’. In the key to all genera of Leucosolenida in the Systema Porifera (Borojevic *et al.* 2002b: 1158) the sycettid genus *Sycetta* is keyed out by ‘elongate radial tubes’ and the ‘incurrent water enters directly through pores into the radial choanocyte chambers’. These statements are rather contrasting, possibly because the genus remains imperfectly known. The emphasis on ‘completely separate’ radial tubes which would be ‘short’ or ‘elongate’ appears to be unnecessarily restrictive and not operational. Descriptions by us and by Brøndsted (1931: 23–27) indicate that the surface bearing ‘papilla-like’ (our term) or ‘pyramide-like’ (Brøndsted’s term) choanocyte chambers are more characteristic of most species. The apparent close relationship with the jenkinid *Leucascandra* (cf. Voigt *et al.* 2012) is not readily understood from a morphological point of view.

(4) *Anamixilla* and *Uteopsis* are assigned to the same family Jenkinidae, but this is hard to understand in view

of the extremely disparate skeletal characters of these two genera, with giant triactines in the former, and giant diactines in the latter. *Anamixilla* has no special category of smaller cortical triactines (in stead of which the giant and intermediate-sized triactines are considered to form the cortex, but they grade into the choanosomal spicules). Likewise the tetractines grade from the choanosome into the atrial region. In contrast, *Uteopsis* is highly organized and zoned with special cortical triactines (overlying the layer of giant diactines), subcortical sagittal triactines, tubar tri- and tetractines, and atrial tetractines. The definition of the family Jenkinidae is also quite expansive and it is difficult to decide whether newly discovered sponges fit the family or not.

(5) *Syconessa*, *Sycettusa* and *Grantessa*, clearly demarcated on paper as syconoid heteropiidae with articulate (*Grantessa*) or inarticulate (*Sycettusa* and *Syconessa*) skeletons, possessing cortical triactines (*Grantessa* and *Sycettusa*) or lacking them (*Syconessa*). In the two species that we eventually assigned above to *Grantessa*, we observed that the articulate skeleton becomes almost inarticulate in thinner parts of the tubes, and also the presence of a continuous layer of cortical triactines is often found to be variable depending on the thickness of the walls. These variations were present in our material to the extent that we at first assigned one of the two of species to *Syconessa*, and only arrived at the proper assignment of the genus by looking at different ‘persons’ and different parts along the walls. One wonders how strictly these characters should be interpreted.

(6) *Heteropia* is defined (Borojevic *et al.* 2002b) as Heteropiidae with an articulate skeleton and a cortex of small triactines and parallel (giant) diactines, but the common species *Heteropia minor* has an inarticulate skeleton. Moreover, the subcortical pseudosagittal spicules, which should occur in Heteropiidae are not clearly pseudosagittal in shape, but look merely irregular parasagittal. The species is not obviously assignable to a different existing genus, and the presence of the large parallel diactines at the outer surface fits with *Heteropia*. Again the articulate vs. inarticulate status of the tubar skeleton appears to be at odds with other morphological characteristics.

(7) *Vosmaeropsis* is (vaguely) defined (Borojevic *et al.* 2002b) as Heteropiidae with a sylleibid or leuconoid aquiferous system and a skeleton of ‘proximal subatrial triactines and an irregular layer of scattered triactines and tetractines’. In the ‘Scope’ paragraph following the definition Borojevic *et al.* explain the vagueness by admitting that thin-walled and thick-walled specimens may show considerable differences in the ‘radial organization’. The type species *V. macera* is apparently a thin-walled species, showing an inarticulate organization, while in other species, including the Indonesian species described above, the organization becomes considerably confused. It is not entirely clear to us, why the two ‘types’ of *Vosmaeropsis* should be united in a single genus (and indeed the above discussed genus *Heteropia*), while *Sycettusa* and *Grantessa* remain separated.

## Acknowledgements

Elly Beglinger (Naturalis Biodiversity Center, Leiden) assisted with the SEM and the registration of specimens. Rob Langelaan (Naturalis Biodiversity Center, Leiden) made the histological sections. Michelle Klautau (UFRJ, Brazil) gave valuable coaching and advice. Emma Sherlock (Natural History Museum, London) kindly sent us slides of the BMNH collection on loan. Colleagues participating during the Indonesian-Dutch Snellius II Expedition (notably Harry Ten Hove, Francien Heys, and Joop Brouns) contributed by collecting several of the Indonesian Calcarea specimens. Many thanks to Dr. Bert W. Hoeksema who organized the Ternate and Lembeh Strait expedition together with Ir. M.I. Yosephine Tuti Hermanlimianto under the umbrella of E-Win (Ekspedisi Widya Nusantara). LIPI Ternate and LIPI Bitung are acknowledged for accommodating the research at their field stations. LIPI and RISTEK granted research permits. Bert Hoeksema also contributed many specimens and *in situ* photographs. Charles Fransen and Koos van Egmond (Naturalis Biodiversity Center, Leiden), Lori Colin (Coral Reef Research Foundation, Palau), and Lisa Becking (IMARES, Netherlands) collected specimens and also provided *in situ* photographs. Natural products chemistry groups (notably Phil Crews, Rachel Sonnenschein and Karen Tenney, Santa Cruz, California) sent us important specimens for identification. Participation of NDV at the 14<sup>th</sup> International Marine Biology workshop held in Singapore was made possible by a grant of the Schure-Beijeringk-Popping Fund (SBP 2006-49).

## References

- Allen, G.R. & Steene, R. (1996). *Indo-Pacific coral reef field guide*. Tropical Reef Research, Singapore, pp. 1–378.
- Arndt, W. (1941) Eine neuere Ausbeute von Meeresschwämmen der West- und Südküsten Portugals. Mit einer Übersicht über die bisher an und vor den Küsten Portugals nachgewiesenen rezenten Spongiarten überhaupt und Bemerkungen über nutzbare Schwämme in portugesischen Gewässern. Coimbra Editoria, Lda. Coimbra, pp. 1–75.
- Baine, M. & Harasti, D. (2007) *The marine life of Bootless Bay, Papua New Guinea*. Motupore Island Research Centre, Papua New Guinea, pp. 1–144.
- Bidder, G.P. (1898) The Skeleton and Classification of Calcareous Sponges. *Proceedings of the Royal Society*, 64, 61–76.
- Blainville, H.M.D. De (1834) *Manuel d'Actinologie ou de Zoophytologie*. F.G. Levrault, Paris, Strasbourg, Volume 1, pp. i–viii, 1–644; Volume 2, pls I–C.
- Borojevic, R. (1967a) Spongiaires d'Afrique du Sud. (2) Calcarea. *Transactions of the Royal Society of South Africa*, 37 (3), 183–226.
- Borojevic, R. (1967b) Éponges calcaires recueillies en Nouvelle-Calédonie par la Mission Singer-Polignac. *Expédition Française sur les récifs coralliens de Nouvelle-Calédonie*, Paris, 2, 1–10.
- Borojevic, R. & Boury-Esnault, N. (1986) Une nouvelle voie d'évolution chez les éponges Calcinea: description des genres *Burtonulla* n. g. et *Levinella* n. g. *Bulletin du Muséum national d'Histoire naturelle*, (4, A) 8 (3), 443–455.
- Borojevic, R. & Boury-Esnault, N. (1987) Revision of the genus *Leucilla* Haeckel, 1872, with a re-description of the type species *Leucilla amphora* Haeckel, 1872. In: Jones, W.C. (Ed.), *European Contributions to the Taxonomy of Sponges*. Sherkin Island Marine Station, Sherkin Island, County Cork, pp. 29–40.
- Borojevic, R. & Klautau, M. (2000) Calcareous sponges from New Caledonia. *Zoosystema*, 22 (2), 187–201.
- Borojevic, R. & Peixinho, S. (1976) Éponges calcaires du Nord-Nord-Est du Brésil. *Bulletin du Muséum national d'Histoire naturelle*, (3, A) 402, 987–1036.
- Borojevic, R., Boury-Esnault, N. & Vacelet, J. (2000) A revision of the supraspecific classification of the subclass Calcaronea (Porifera, class Calcarea). *Zoosystema*, 22 (2), 203–263.
- Borojevic, R., Boury-Esnault, N., Manuel, M. & Vacelet, J. (2002a) Order Clathrinida Hartman, 1958. In: Hooper, J.N.A. & Van Soest, R.W.M. (Eds.) *Systema Porifera. A guide to the classification of sponges*. 2. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 1141–1152.
- Borojevic, R., Boury-Esnault, N., Manuel, M. & Vacelet, J. (2002b) Order Leucosolenida Hartman, 1958. In: Hooper, J.N.A. & Van Soest, R.W.M. (Eds.) *Systema Porifera. A guide to the classification of sponges*. 2. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 1157–1184.
- Borojevic, R., Boury-Esnault, N., Manuel, M. & Vacelet, J. (2002c) Order Baerida Borojevic, Boury-Esnault & Vacelet, 2000. In: Hooper, J.N.A. & Van Soest, R.W.M. (Eds.) *Systema Porifera. A guide to the classification of sponges*. 2. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 1193–1200.
- Boury-Esnault, N. & Rützler, K. (eds) (1997) Thesaurus of sponge morphology. *Smithsonian Contributions to Zoology*, 596, 1–55.
- Bowerbank, J.S. (1864) *A Monograph of the British Spongiidae*. Volume 1. Ray Society, London, pp. i–xx, 1–290.
- Bowerbank, J.S. (1866) *A Monograph of the British Spongiidae*. Volume 2. Ray Society: London, pp. i–xx, 1–388.
- Breitfuss, L.L. (1896a) Kalkschwämme von Ternate Molukken), nach den Sammlungen Prf. W. Kükenthal's (Vorläufige Mittheilung). *Zoologischer Anzeiger*, 19, 433–435.
- Breitfuss, L.L. (1896b) *Amphoriscus semoni*, eine neue Art heterocoeler Kalkschwämme. *Zoologischer Anzeiger*, 19, 435–436.
- Breitfuss, L.L. (1898) Kalkschwämme von Ternate. *Abhandlungen der Senckenbergischen Naturforschender Gesellschaft*, 24, 169–178.
- Briggs, J.C. (1974) *Marine Zoogeography*. McGraw-Hill, New York, pp. 1–475.
- Brøndsted, H.V. (1931) Die Kalkschwämme der Deutschen Südpolar-Expedition 1901–1903. *Deutsche Südpolar-Expedition, 1901–03*, 20, 1–47.
- Burton, M. (1930) The Porifera of the Siboga Expedition. III. Calcarea. In: Weber, M. (Ed.), *Siboga-Expeditie. Uitkomsten op zoölogisch, botanisch, oceanographisch en geologisch gebied verzameld in Nederlandsch Oost-Indië 1899–1900 aan boord H.M. Siboga onder commando van Luitenant ter zee Ie kl. G. F. Tydeman. III (Monographie VIa2)*. E.J. Brill, Leiden, pp. 1–18.
- Burton, M. (1963) Revision of the classification of the calcareous sponges. London. British Museum (Natural History), London, pp. 1–693.
- Carter, H.J. (1886) Descriptions of Sponges from the Neighbourhood of Port Phillip Heads, South Australia, continued. *Annals and Magazine of Natural History*, (5) 17 (97, 98, 101, 102), 40–53, 112–127, 431–441, 502–516.
- Carter, H.J. (1890) Porifera. In: Ridley, H.N. (Ed.) *Notes on the Zoology of Fernando do Noronha. Journal of the Linnean Society 1890 (The Natural History of the island of Fernando de Noronha based on the collections made by the British Museum Expedition in 1887)*. British Museum (Natural History), London, pp. 564–569.
- Cavalcanti, F.F., Rapp, H.T. & Klautau, M. (2013) Taxonomic revision of *Leucascus* Dendy, 1892 (Porifera: Calcarea) with revalidation of *Ascoleucetta* Dendy & Frederick, 1924 and description of three new species. *Zootaxa*, 3619 (3), 275–314. <http://dx.doi.org/10.11646/zootaxa.3619.3.3>
- Cavalcanti, F.F., Bastos, N. & Lanna, E. (2015) Two new species of the genus *Vosmaeropsis* Dendy, 1893 (Porifera, Calcarea),

- with comments on the distribution of *V. sericata* (Ridley, 1881) along the Southwestern Atlantic Ocean. *Zootaxa*, in press.
- Colin, P.L. & Arneson, C. (1995) *Tropical Pacific Invertebrates. A field guide to the Marine Invertebrates occurring on Tropical Pacific Coral Reefs, Seagrass Beds and Mangroves*. Coral Reef Press: Irvine, USA, pp. 1–296.
- De Laubenfels, M.W. (1936) A Discussion of the Sponge Fauna of the Dry Tortugas in Particular and the West Indies in General, with Material for a Revision of the Families and Orders of the Porifera. *Carnegie Institute of Washington Publication 467 (Tortugas Laboratory Paper 30)*, 1–225.
- De Laubenfels, M.W. De (1954) The Sponges of the West-Central Pacific. *Oregon State Monographs, Studies in Zoology*, 7, 1–x, 1–306.
- Dendy, A. (1891) A monograph of the Victorian sponges, I. The organisation and classification of the Calcarea Homocoela, with descriptions of the Victorian Species. *Transactions of the Royal Society of Victoria*, 3, 1–81.
- Dendy, A. (1893a) Synopsis of the Australian Calcarea Heterocoela; with a proposed Classification of the Group and Descriptions of some New Genera and Species. *Proceedings of the Royal Society of Victoria (New Series)*, 5, 69–116.
- Dendy, A. (1893b) Studies on the Comparative Anatomy of Sponges. V. Observations on the Structure and Classification of the Calcarea Heterocoela. *Quarterly Journal of Microscopical Science*, 35, 159–257.
- Dendy, A. (1905) Report on the sponges collected by Professor Herdman, at Ceylon, in 1902. In: Herdman, W.A. (Ed.) *Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar* 3 (Supplement 18). Royal Society, London, pp. 57–246.
- Dendy, A. (1913) The Percy Sladen trust expedition to the Indian Ocean in 1905 (V). I. Report on the Calcareous Sponges collected by HMS ‘Sealark’ in the Indian Ocean. *Transactions of the Linnean Society of London*, (2) 16 (1), 1–29.
- Dendy, A. (1916) Report on the Calcareous Sponges collected by Mr. James Hornell at Okhamandal in Kattiawar in 1905–6. *Report to the Government of Baroda on the Marine Zoology of Okhamandal in Kattiawar*, 2, 79–91.
- Dendy, A. & Frederick, L.M. (1924) On a Collection of Sponges from the Abrolhos Islands, Western Australia. *Journal of the Linnean Society, Zoology*, 35, 477–519.
- Dendy, A. & Row, R.W.H. (1913) The Classification and Phylogeny of the Calcareous Sponges, with a Reference List of all the described Species, systematically arranged. *Proceedings of the Zoological Society of London*, 1913 (3), 704–813.
- Dohrmann, M., Voigt, O., Erpenbeck, D. & Wörheide, G. (2006) Non-monophyly of most supraspecific taxa of calcareous sponges (Porifera, Calcarea) revealed by increased taxon sampling and partitioned Bayesian analysis of ribosomal DNA. *Molecular Phylogenetics and Evolution*, 40, 830–843.
- Erhardt, H. & Baensch, H.A. (1998) *Meerwasser Atlas 4. Wirbellose*. Mergus Verlag, Melle, Germany, pp. 1–1214.
- Ferrer Hernández, F. (1912) Notas sobre algunas esponjas de Santander. *Boletín de la Real Sociedad Española de Historia natural*, 12, 573–588.
- Gosliner, T.M., Behrens, D.W & Williams, G.C. (1996) *Coral reef animals of the Indo-Pacific: animal life from Africa to Hawaii exclusive of the vertebrates*. Sea Challengers, Monterey, pp. 1–314.
- Grant, R.E. (1836) Animal Kingdom. In: Todd, R.B. (Ed.), *The Cyclopaedia of Anatomy and Physiology*. Volume 1. Sherwood, Gilbert and Piper, London, pp. 107–118.
- Gray, J.E. (1858) Description of *Aphroceras*, a new genus of calcareous Spongiidae brought from Hong-Kong by Dr. Harland. *Proceedings of the Zoological Society of London*, 26, 113–114.
- Gray, J.E. (1867) Notes on the Arrangement of Sponges, with the Descriptions of some New Genera. *Proceedings of the Zoological Society of London*, 1867 (2), 492–558.
- Haeckel, E. (1870) Prodromus eines Systems der Kalkschwämme. *Jenaische Zeitschrift für Medicin und Naturwissenschaft*, 5, 236–254 (also appeared in English as: Haeckel, E. 1870. Prodromus of a system of the Calcareous sponges. *Annals and Magazine of Natural History*, (4) 5, 176–191).
- Haeckel, E. (1872) *Die Kalkschwämme. Eine Monographie in zwei Bänden Text und einem Atlas mit 60 Tafeln Abbildungen*. G. Reimer, Berlin, 1, 1–484; 2, 1–418; 3, pls 1–60.
- Hanitsch, R. (1895) Notes on a Collection of Sponges from the West Coast of Portugal. *Transactions of the Liverpool Biological Society*, 9, 205–219.
- Hartman, W.D. (1958) Re-examination of Bidder’s classification of the Calcarea. *Systematic Zoology*, 7 (3), 55–110.
- Hoeksema, B.W. (2007) Delineation of the Indon-Malayan Centre of Maximum Marine Biodiversity: the Coral Triangle. In: W. Renema (ed.) *Biogeography, Time, and Place: Distributions, Barriers, and Islands*. Springer Verlag, Heidelberg, pp. 117–178.
- Hoeksema, B.W. (2013) In search of the Asian-Pacific centre of maximum marine biodiversity: explanations from the past and present. *Galaxea: Journal of Coral Reef Studies*, 15, 1–8.
- Hooper, J.N.A., Kennedy, J.A. & Van Soest, R.W.M. (2000) Annotated checklist of sponges (Porifera) of the South China Sea region. *The Raffles Bulletin of Zoology*, 2000 (supplement 8), 125–207.
- Hooper, J. N. A. & Van Soest, R. W. M. (Eds.) (2000) *Systema Porifera. A guide to the classification of sponges*. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, Volume 1, pp. i–xix, 1–1101, Volume 2, 1103–1706.
- Hôzawa, S. (1916) On some Japanese Calcareous Sponges belonging to the family Heteropidae. *Journal of the College of Sciences Imperial University of Tokyo*, 38 (5), 1–41.
- Hôzawa, S. (1929) Studies on the calcareous sponges of Japan. *Journal of the Faculty of Sciences Imperial University of Tokyo*, 1, 277–389.

- Hôzawa, S. (1940) Reports on the calcareous sponges obtained by the Zoological Institute and Museum of Hamburg. *Science Reports of the Tôhoku Imperial University*, 15, 131–163.
- Jenkin, C.F. (1908) The Marine Fauna of Zanzibar and British East Africa, from Collections made by Cyril Crossland, M.A., in the Years 1901 & 1902. The Calcareous Sponges. *Proceedings of the Zoological Society of London*, 1908, 434–456.
- Klautau, M. & Borojevic, R. (2001) Calcareous sponges from Arraial do Cabo-Brazil, 1: the genus *Clathrina*. *Zoosystema*, 23, 395–410.
- Klautau, M. & Valentine, C. (2003). Revision of the genus *Clathrina* (Porifera, Calcarea). *Zoological Journal of the Linnaean Society*, 139 (1), 1–62.
- Klautau, M., Azevedo, F., Cóndor-Luján, B., Rapp, H.T., Collins, A. & Russo, C.A.M. (2013) A Molecular Phylogeny for the Order Clathrinida Rekindles and Refines Haeckel's Taxonomic Proposal for Calcareous Sponges. *Integrative and Comparative Biology*, 53 (3), 447–461.  
<http://dx.doi.org/10.1093/icb/ict039>
- Lévi, C., Laboute, P., Bargibant, G. & Menou, J.L. (Eds.) (1998) *Sponges of the New Caledonian Lagoon*. Éditions ORSTOM, pp. 1–211.
- Lim, S.C., De Voogd, N.J. & Tan, K.S. (2008) *A guide to sponges of Singapore*. Science Centre, Singapore, pp. 1–173.
- Manuel, M., Borchiellini, C., Alivon, E., Le Parco, Y., Vacelet, J. & Boury-Esnault, N. (2003) Phylogeny and evolution of calcareous sponges: monophyly of Calcinea and Calcaronea, high level of morphological homoplasy, and the primitive nature of axial symmetry. *Systematic Biology*, 52, 311–333.
- Manuel, M., Borchiellini, C., Alivon, E. & Boury-Esnault, N. (2004) Molecular phylogeny of calcareous sponges using 18S rRNA and 28S rRNA sequences. *Bollettino dei Musei e degli Istituti Biologici della Università di Genova*, 68, 449–461.
- Miklucho-Maclay, N. (1868) Beiträge zur Kenntniss der Spongiens I. *Jenaische Zeitschrift für Medicin und Naturwissenschaft*, 4, 221–240.
- Minchin, E.A. (1900) Chapter III. Sponges. In: Lankester, E.R.(Ed.), *A Treatise on Zoology. Part II. The Porifera and Coelenterata*. 2. Adam & Charles Black, London, pp. 1–178.
- Muricy, G., Lopes, D.A., Hajdu, E., Carvalho, M.S., Moraes, F.C., Klautau, M., Menegola, C. & Pinheiro, U. (2011) *Catalogue of Brazilian Porifera*. Museu Nacional, Série Livros, pp. 1–300.
- Montagu, G. (1814) An Essay on Sponges, with Descriptions of all the Species that have been discovered on the Coast of Great Britain. *Memoirs of the Wernerian Natural History Society*, 2 (1), 67–122.
- Poléjaeff, N. (1883) Report on the Calcarea dredged by H.M.S.'Challenger', during the years 1873–1876. *Report on the Scientific Results of the Voyage of H.M.S. 'Challenger', 1873–1876, Zoology*, 8 (2), 1–76,
- Ralifo, P., Tenney, K., Valeriote, F.A. & Crews, P. (2007) A distinctive structural twist in the aminoimidazole alkaloids from a calcareous marine sponge: isolation and characterization of leucomenamines A and B. *Journal of Natural Products*, 70 (1), 33–38.
- Rapp, H.T., Klautau, M. & Valentine, C. (2001) Two new species of *Clathrina* (Porifera, Calcarea) from the Norwegian coast. *Sarsia*, 86, 69–74.
- Ridley, S.O. (1884) Spongiida. In: *Report on the Zoological Collections made in the Indo-Pacific Ocean during the Voyage of H.M.S. 'Alert'*, 1881-2. British Museum (Natural History), London, pp. 366–482, 582–630.
- Risso, A. (1827) *Histoire naturelle des principales productions de l'Europe Méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes*, Volume 5 [imprint 1826]. F.-G. Levraud, Paris, pp. i–vii, 1–403.
- Row, R.W.H. & Hôzawa, S. (1931) Report on the Calcarea obtained by the Hamburg South-West Australian Expedition of 1905. *Science Reports of the Tôhoku University*, (4) 6 (1), 727–809.
- Schmidt, O. (1862) *Die Spongiens des adriatischen Meeres*. Wilhelm Engelmann: Leipzig, pp. i–viii, 1–88.
- Schmidt, O. (1864) *Supplement der Spongiens des adriatischen Meeres. Enthal tend die Histologie und systematische Ergänzungen*. Wilhelm Engelmann, Leipzig, pp. i–vi, 1–48.
- Schuffner, O. (1877) Beschreibung einiger neuer Kalkschwämme. *Jenaische Zeitschrift für Naturwissenschaft*, 11, 403–433.
- Solé-Cava, A.M., Klautau, M., Boury-Esnault, N., Borojevic, R. & Thorpe, J.P. (1991) Genetic evidence for cryptic speciation in allopatric populations of 2 cosmopolitan species of the calcareous sponge genus *Clathrina*. *Marine Biology*, 111 (3), 381–386.
- Sollas, W.J. (1885) A Classification of the Sponges. *Annals and Magazine of Natural History*, (5) 16 (95), 395.
- Tanita, S. (1939) Two new Calcarea from Saseho, Japan. *Science Reports of the Tôhoku Imperial University*, (4) 14, 319–326.
- Tanita, S. (1942) Report on the Calcareous sponges obtained by the Zoological Institute and Museum of Hamburg. Part II. *Science Reports of the Tôhoku University*, (4) 17 (2), 105–135.
- Tanita, S. (1943) Studies on the Calcarea of Japan. *Science Reports of the Tôhoku Imperial University*, 17, 353–490.
- Topsent, E. (1897) Spongaires de la Baie d'Amboine. (Voyage de MM. M. Bedot et C. Pictet dans l'Archipel Malais). *Revue suisse de Zoologie*, 4, 421–487.
- Vacelet, J. (1977) Éponges pharétronides actuelles et sclérosponges de Polynésie française, de Madagascar et de la Réunion. *Bulletin du Muséum national d'Histoire naturelle*, (3, Zoologie) 444 (307), 345–368.
- Vacelet, J. (1981) Éponges hypercalcifiées ('Pharétronides' 'Sclérosponges') des cavités des récifs coralliens de Nouvelle-Calédonie. *Bulletin du Muséum national d'Histoire naturelle*, (4, A) 3 (2), 313–351.
- Van Soest, R.W.M. (1989) The Indonesian sponge fauna: a status report. *Netherlands Journal of Sea Research*, 23 (2), 223–230.

- [http://dx.doi.org/10.1016/0077-7579\(89\)90016-1](http://dx.doi.org/10.1016/0077-7579(89)90016-1)
- Van Soest, R.W.M. (1997) Indonesian sponges: ecology and biogeography. In: Tomascik, T., Mah, A.J., Nontji, A. & Kasim Moosa, M. (eds) *The ecology of the Indonesian seas, Part Two*. Periplus Editions (HK) Ltd., Singapore, pp. 1060–1063.
- Van Soest, R.W.M., Boury-Esnault, N., Vacelet, J., Dohrmann, M., Erpenbeck, D., De Voogd, N.J., Santodomingo, N., Vanhoorne, B., Kelly, M. & Hooper, J.N.A. (2012) Global Diversity of Sponges (Porifera). *PLoS ONE*, 7 (4), e35105.  
<http://dx.doi.org/10.1371/journal.pone.0035105>
- Van Soest, R.W.M., Boury-Esnault, N., Hooper, J.N.A., Rützler, K., de Voogd, N.J., Alvarez de Glasby, B., Hajdu, E., Pisera, A.B., Manconi, R., Schoenberg, C., Janussen, D., Tabachnick, K.R., Klautau, M., Picton, B., Kelly, M., Vacelet, J., Dohrmann, M., Díaz, M.C. & Cárdenas, P. (2015) *World Porifera database*. Available from: <http://www.marinespecies.org/porifera> (Accessed 30 Apr. 2015)
- Van Soest, R.W.M., Kaiser, K. & Van Syoc, R. (2011) Sponges from Clipperton Island, East Pacific. *Zootaxa*, 2839, 1–46.
- Voigt, O., Wülfing, E. & Wörheide, G. (2012) Molecular phylogenetic evaluation of classification and scenarios of character evolution in calcareous sponges (Porifera, Class Calcarea). *PLOS One*, 7 (3), e33417.  
<http://dx.doi.org/10.1371/journal.pone.0033417>
- Von Lendenfeld, R. (1885) A Monograph of the Australian Sponges (Continued). Part III. Preliminary description and classification of the Australian Calcispongiae. *Proceedings of the Linnean Society of New South Wales*, 9, 1083–1150.
- Weinberg, S. (2004) *Découvrir l'océan Pacifique tropical*. Éd. Nathan, Paris. 450 pp.
- Wörheide, G., Epp, L.S. & Macis, L. (2008) Deep genetic divergences among Indo-Pacific populations of the coral reef sponge *Leucetta chagosensis* (Leucettidae): founder effects, vicariance, or both? *BMC Evolutionary Biology*, 8, 24 (18 pp).  
<http://dx.doi.org/10.1186/1471-2148-8-24>
- Wörheide, G. & Hooper, J.N.A. (1999) Calcarea from the Great Barrier Reef 1: Cryptic Calcinea from Heron Island and Wistari Reef (Capricorn-Bunker Group). *Memoirs of the Queensland Museum*, 43 (2), 859–891.
- Wörheide, G. & Hooper, J.N.A. (2003) New species of Calcaronea (Porifera: Calcarea) from cryptic habitats of the southern Great Barrier Reef (Heron Island and Wistari Reef, Capricorn-Bunker Group, Australia). *Journal of Natural History*, 37, 1–47.
- Wörheide, G., Hooper, J.N.A. & Degnan, B.M. (2002) Phylogeography of Western Pacific *Leucetta 'chagosensis'* (Porifera: Calcarea) from ribosomal DNA sequences: implications for population history and conservation of the Great Barrier Reef World Heritage Area (Australia). *Molecular Ecology*, 11, 1753–1768.  
<http://dx.doi.org/10.1046/j.1365-294X.2002.01570.x>