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# A TAXONOMIC REVIEW OF THE GENUS *ASTEROMORPHA* LÜTKEN (ECHINODERMATA: OPHIUROIDEA: EURYALIDAE)

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***ABSTRACT.*** — The genus *Asteromorpha* Lütken (Echinodermata: Ophiuroidea: Euryalidae: Euryalinae) is revised based on 52 specimens, including six syntypes of *Asteromorpha steenstrupi*, one syntype of *Asteromorpha perplexum* (Koehler), one syntype of *Asteromorpha koehleri* (Döderlein) and the holotype of *Astroschema capensis* Mortensen. We propose a new combination of *Asteroschema capense* (Euryalidae: Asteroschematinae) with the genus *Asteromorpha*. Consequently *Asteromorpha* includes four species: *A. capensis*, *A. koehleri*, *A. rousseaui*, and *A. tenax*. These four species are all redescribed. A taxonomic key to the species of the genus *Asteromorpha* is also provided.

***KEY WORDS.*** — Taxonomy, euryalid ophiuroid, *Asteromorpha*, *Asteroschema*, Indian Ocean, Pacific Ocean

## INTRODUCTION

The snake stars of the genus *Asteromorpha* (Ophiuroidea: Euryalida: Euryalidae: Euryalinae) are known from deep waters (75–382 m) of the south-western Indian Ocean, off Reunion Island (Michelin, 1862; Lütken, 1869; de Loriol, 1893), and from the south-western Pacific Ocean, eastern Indonesia and eastern Australia (Döderlein, 1898, 1911; Koehler, 1905, 1930; Mortensen, 1933; Baker, 1980). They have an oral bridge on the oral side of the vertebrae, arm spines with smooth lamina on the distal portion of the arms, and a body is covered by plate-shaped external ossicles.

This genus was erected by Lütken (1869) who designated *Asteromorpha steenstrupi* Lütken, 1869 as the genotype. Later, Lyman (1872) synonymised the genus *Asteromorpha* with the genus *Asteroschema* Örsted & Lütken, 1856 (in Lütken, 1856) (Euryalidae; Asteroschematinae) and synonymised *Asteromorpha steenstrupi* with *Asteroschema rousseaui* Michelin, 1862. For the next 60 years, *Asteromorpha* was considered to be a junior synonym of *Asteroschema* until Mortensen (1933) separated *Asteromorpha* from *Asteroschema* as a valid genus and synonymised the monotypic genus (*Ophiogelas* with *O. perplexum* Koehler, 1930 as type) with *Asteromorpha* (Mortensen, 1933). Mortensen (1933) included *Asteromorpha rousseaui* (Michelin, 1862) and *Asteromorpha perplexum* (Koehler, 1930) in *Asteromorpha*. Mortensen (1933) also suggested that *Astroschema koehleri* Döderlein, 1898 should be transferred to the genus *Asteromorpha* and *Asteromorpha perplexum* is a junior synonym of the *Asteromorpha koehleri* (Döderlein, 1898) in postscript (see Mortensen, 1933: 73). However, detailed justification for the synonymy of the two species has never been discussed. Baker (1980) included *A. rousseaui*, *A. koehleri* (Döderlein, 1898), and a new species *A. tenax* Baker, 1980 in *Asteromorpha* in his work of the euryalids from Australia and New Zealand. This genus is currently composed of three species: *A. rousseaui*, *A. koehleri*, and *A. tenax*.

External features of species in the genus *Asteromorpha* and some of the species of the *Asteroschema* are very similar and species can almost only be distinguished from each other by the differences in the internal vertebral ossicle morphology (Mortensen, 1933). However, the traditional taxonomic

descriptions of *Asteromorpha* and *Asteroschema* depended on external morphology. Some species of *Asteromorpha* were originally described as *Asteroschema* and vice versa, i.e., *A. rousseaui* and *A. koehleri* were originally described as species' of *Asteroschema*, while *Asteroschema laevis* (Lyman, 1872) was originally described as a species' of *Asteromorpha*. The genus *Asteroschema* now includes 35 valid species but the specific taxonomy has never been sufficiently investigated (Okanishi & Fujita, 2009; Okanishi et al., 2011b; Parameswaran & Jaleel, 2012). Therefore, some species of *Asteroschema* may in fact be *Asteromorpha*. *Asteroschema capense* Mortensen, 1925 has distinct external features, such as two arm spines on the basal portion of the arms (Mortensen, 1925) and Okanishi & Fujita, 2009 questioned its taxonomic position. *Asteroschema capense* has only been described once and the similarity to *Asteromorpha* has never been discussed.

In this study, specimens examined included eight type specimens and 43 additional specimens of *Asteromorpha* and the holotype of *Astroschema capensis* Mortensen, 1925, which has led to the conclusion that *A. perplexum* is certainly a junior synonym of *A. koehleri* as Mortensen (1933) suggested and *Asteroschema capense* is a species of the genus *Asteromorpha*.

## MATERIAL AND METHODS

The 52 specimens examined in this study are deposited in the Durban Natural Science Museum, South Africa (DNSM), the Zoologische Staatssammlung München, Germany (ZSM), The Muséum National d'Histoire Naturelle, France (MNHN), the National Museum of Natural History, Smithsonian Institution, USA (USNM), the Museum of Comparative Zoology, Harvard University, USA (MCZ), and Museum Victoria, Australia (MV).

The specimens of *Asteromorpha capensis* in MNHN and MV F111585 were fixed in 70% ethanol while the fixation methods of all other examined specimens are unknown.

Ossicles were isolated by immersion in domestic bleach (ca. 5% sodium hypochlorite solution), washed in deionised water, dried in air, and mounted on SEM stubs using double-sided conductive tape. The preparations were sputter-coated with gold-palladium and examined with a Jeol JSM 6380 LV SEM.

In recent descriptions, we used "epidermal ossicles" for superficial ossicles of euryalid ophiuroids (Okanishi et al., 2011b). However, we use here "external ossicles" for these ossicles because epidermis is frequently lost in echinoderms. The relative size and thickness of external ossicles is presented in terms of the length of the longest axis and the depth from external to internal side, respectively. The length and thickness are referred as "long" and "thick" in this study. The long of the ossicles was measured using an ocular micrometer on a binocular stereoscopic microscope without dissecting the ossicles. Some ossicles were dissected and separated, and the thick of each ossicle was measured. Other terms used to describe euryalid ophiuroids follow those of Okanishi & Fujita (2011), and terms for the structures of the ossicles are those of Martynov (2010). Family-level classification follows that of Okanishi et al. (2011a).

## TAXONOMY

### Family Euryalidae Gray, 1840, emend. Okanishi et al., 2011
### Subfamily Euryalinae Gray, 1840, emend. Okanishi et al., 2011
### *Asteromorpha* Lütken, 1869

*Asteromorpha* Lütken, 1869: 42–45; Mortensen, 1933: 57; Baker, 1980: 70–72
*Ophiogelas* Koehler, 1930: 42–43

***Type species.*** — *Asteromorpha steenstrupi* Lütken, 1869 (=*Asterochema rousseaui* Michelin, 1862)

***Diagnosis.*** — External ossicles on body either plate-shaped, in full contact with each other, or granule-shaped and only partly in contact. Teeth triangular or square. Oral papillae domed, granule-shaped, on lateral side of jaws. Tentacle pores with two arm spines from fourth (rarely fifth) arm segment. Radial shields may bear large domed tubercles. Oral side of vertebrae with an oral bridge. Lamina of distal arm spines smooth.

***Remarks.*** — Based on this study, *Asteromorpha* is currently composed of four species, *A. capensis* (Mortensen, 1925), *A. rousseaui* (Michelin, 1862), *A. koehleri* (Döderlein, 1898), and *A. tenax* Baker, 1980. A tabular key to the species of *Asteromorpha* is provided (Table 1).

Species of this genus are distributed in south-eastern Africa, south-western and eastern Australia, central Indonesia and south-eastern New Caledonia (Fig. 1).

### *Asteromorpha capensis* (Mortensen, 1925)
(Figs. 2–5)

*Astroschema capensis* Mortensen, 1925: 152–155, pl. VIII figs. 4–5, text-fig. 5; 1933: 221, 227 (new combination)
*Asteroschema capensis.* A. M. Clark & Courtman-Stock, 1976: 130; Sink et al., 2006: 469–470
*Asteroschema capense.* Okanishi & Fujita, 2009: 116, 119, 123, 125; 2011: 149

***Type material examined.*** — Dry holotype of *Astroschema capensis*, DNSM ECH1, ca. 29–32 km (18–20 miles) off Umvoti River Mouth, eastern South Africa, ca. 64–73 m (35–40 fathoms), Nov.1920 (Fig. 1).

***Other material examined.*** — Two dry specimens, USNM 1201805, Anton Bruun Ridge, northeast coast of Somalia, Madagascar, 11°37'S, 51°27'E, Anton Bruun Stn 465, 67–72 m, 18 Dec.1964; one ethanol preserved specimen, deposited in Echinoderm Collection at MNHN, south Madagascar.

***Diagnosis.*** — External ossicles on aboral surface of the body plate-shaped, polygonal, tessellated. No regular transverse rows of external ossicles on aboral and lateral surface of the arms. Body reddish purple with creamy white spots on aboral disc and white bands on aboral and lateral surface of the arms, or body light brown aborally and white orally. No tubercles on radial shields. Five arms, non-fissiparous.

***Description of USNM 1201805.*** — Disc diameter 6.3 mm, arm length ca. 34.5 mm (Fig. 2).

Disc five-lobed with notched interradial edges, no obvious fission plane. On aboral surface, radial shields and their surroundings tumid (Fig. 2A). Aboral surface of disc covered by slightly domed and polygonal plate-shaped external ossicles (Fig. 2A–C), ca. 100 µm long and 80 µm thick on periphery (Fig. 2B), and ca. 70 µm long and 80 µm thick on central area (Fig. 2C). Radial shields tumid, ca. 1.25 mm long and 0.60–1.25 mm wide (Fig. 2A) and completely covered by external ossicles.

Oral surface of disc entirely covered by flat and round plate-shaped external ossicles, ca. 70 µm long and 60 µm thick on periphery (Fig. 2D, E) and ca. 100 µm long and 100 µm thick on oral plates (Fig. 2D, F). Four square teeth forming a vertical row on dental plate (Fig. 2F). Six to seven domed oral papillae lying on each side of the jaw (Fig. 2D, E).

Lateral interradial surface of disc nearly vertical, covered by flat and round plate-shaped external ossicles similar to those on oral surface, ca. 50–80 µm long (Fig. 2G). Two genital slits in each interradius, 0.90 mm long and 0.30 mm wide. One oral interradial bulge present suggesting the presence of at least one madreporite plate.

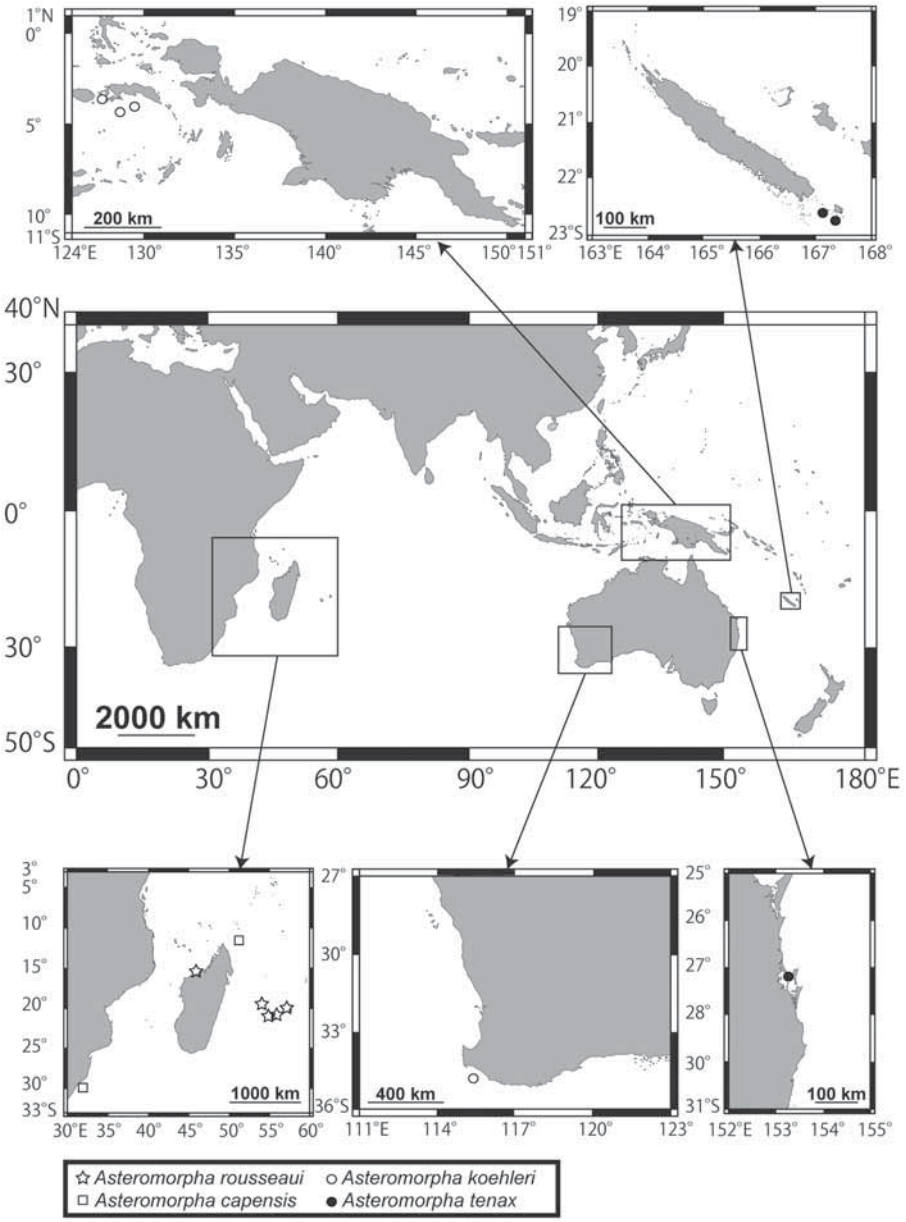


Fig. 1. Distribution of *Asteromorpha capensis*, *A. rousseaui*, *A. koehleri*, and *A. tenax*.

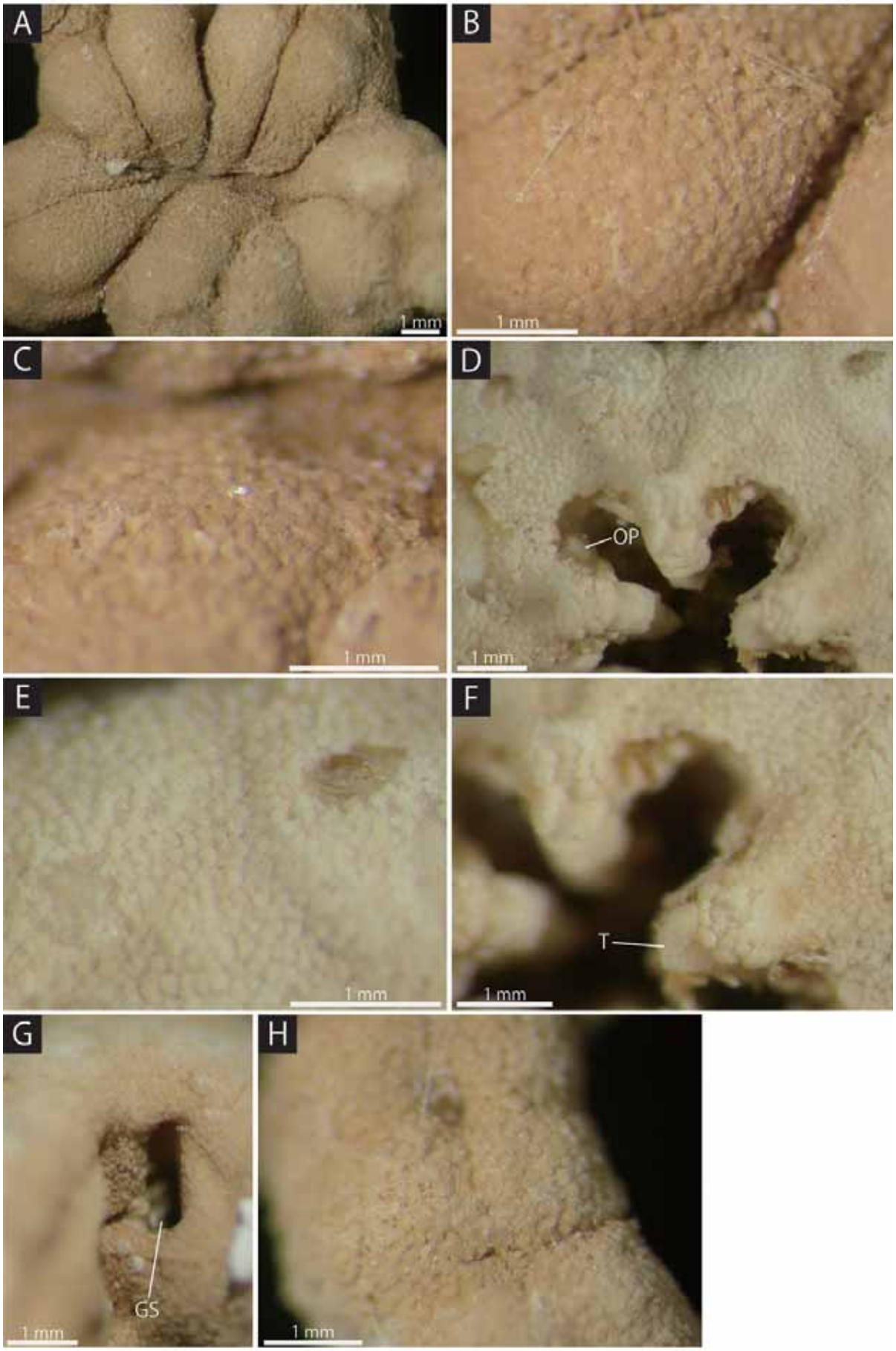


Fig. 2. *Asteromorpha capensis* (USNM 1201805): A, aboral disc; B, aboral periphery part of disc; C, aboral central part of disc; D, oral disc; E, oral periphery part of disc; F, jaws; G, lateral interradial part of disc; H, aboral basal portion of the arm. Abbreviations: GS, genital slit; OP, oral papillae; T, teeth.

Arms simple, five in number, no abrupt reduction in width of arms. Distal arms tapering gradually. Basal portion of arms 2.0 mm wide and 2.1 mm high, square in cross-section. Aboral surface arched and oral surface flattened from middle to distal portion of arms.

Basal portion of arms completely covered by slightly domed and polygonal plate-shaped external ossicles, ca. 100 µm long and 70 µm thick on aboral and lateral surface (Figs. 2H, 4A, B) and ca. 70–80 µm long and 50 µm thick on oral surface (Fig. 3A). These ossicles densely tessellated (Figs. 2H, 3A). In the middle portion of arms, aboral and lateral surface covered by plate-shaped external ossicles, similar to those on basal portion of arms (Fig. 3B), ca. 70–80 µm long and 70 µm thick. Oral surface covered by flat and round granule-shaped external ossicles, ca. 40–50 µm long and 50 µm thick (Fig. 3C). In distal portion of arms, aboral and lateral surface covered by flat and round granule-shaped external ossicles, ca. 50 µm long and 20 µm thick (Figs. 3D, 4C, D). External ossicles on oral surface gradually decreasing in size distally becoming absent near arm tips (Fig. 3E).

First to third tentacle pores lacking arm spines; fourth pores with one arm spine and from fifth pores, two arm spines (Fig. 3A). In first third of arms, arm spines ovoid and minute (Fig. 4H). Inner arm spines ca. one-third to half length of corresponding arm segment, while outer arm spines slightly shorter. In second third of arm, arm spines bear fine spinelets at tips (Fig. 4I). Inner arm spines ca. two-thirds length of corresponding arm segment, while outer arm spines almost same length as inner ones (Fig. 3C). In distal third of arms, arm spines hook-shaped with smooth lamina on distal side (Fig. 4J). Inner arm spines three quarters length of corresponding arm segment, while outer arm spines almost same length as inner ones.

Lateral arm plates concealed by external ossicles, with pairs of a muscle and nerve openings, associated with each arm spine articulation (Fig. 4E). Vertebrae with oral bridge from distal third on arms (Fig. 4F, G).

Colour: Uniformly light brown aborally and uniformly white orally (Fig. 3A, D).

***Ossicle morphology of DNSM ECH1.*** — Disc diameter 8 mm, arm length ca. 50 mm.

Vertebrae in distal portion of arms with oral bridge (Fig. 4K).

***Variation.*** — Some colour variations were observed across the four specimens. Holotype and one alcohol preserved MNHN specimen have white spots on aboral disc and bands on aboral and lateral surface of the arm (Fig. 5) but the two dry specimens (USNM 1201805) do not have such spots.

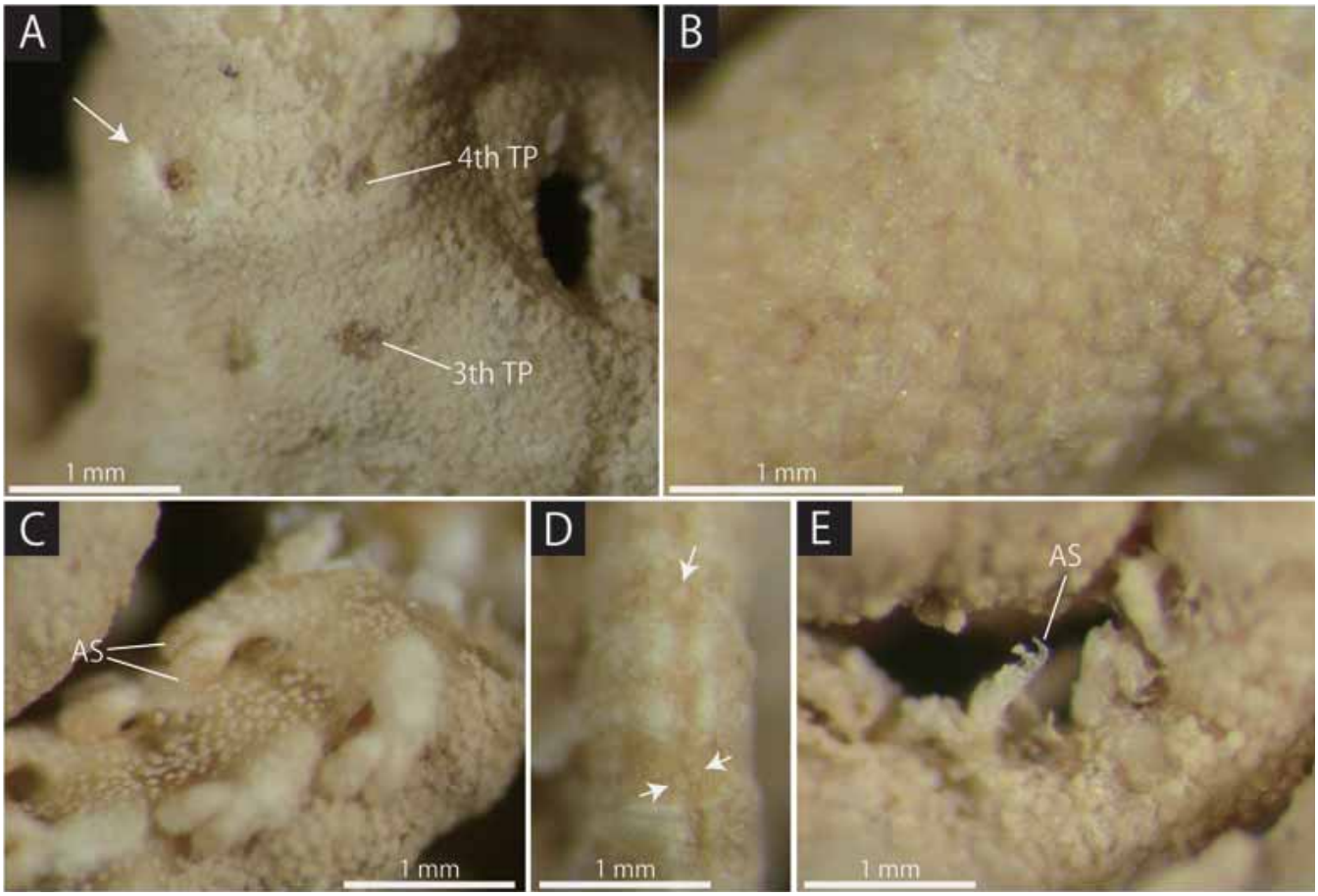


Fig. 3. *Asteromorpha capensis* (USNM 1201805): A, oral basal portion of the arm; B, aboral middle portion of the arm; C, oral middle portion of the arm; D, aboral distal portion of the arm, tiny and scattered external ossicles are indicated by arrows; E, lateral distal portion of the arm. Abbreviation: AS, arm spine; TP, tentacle pore.

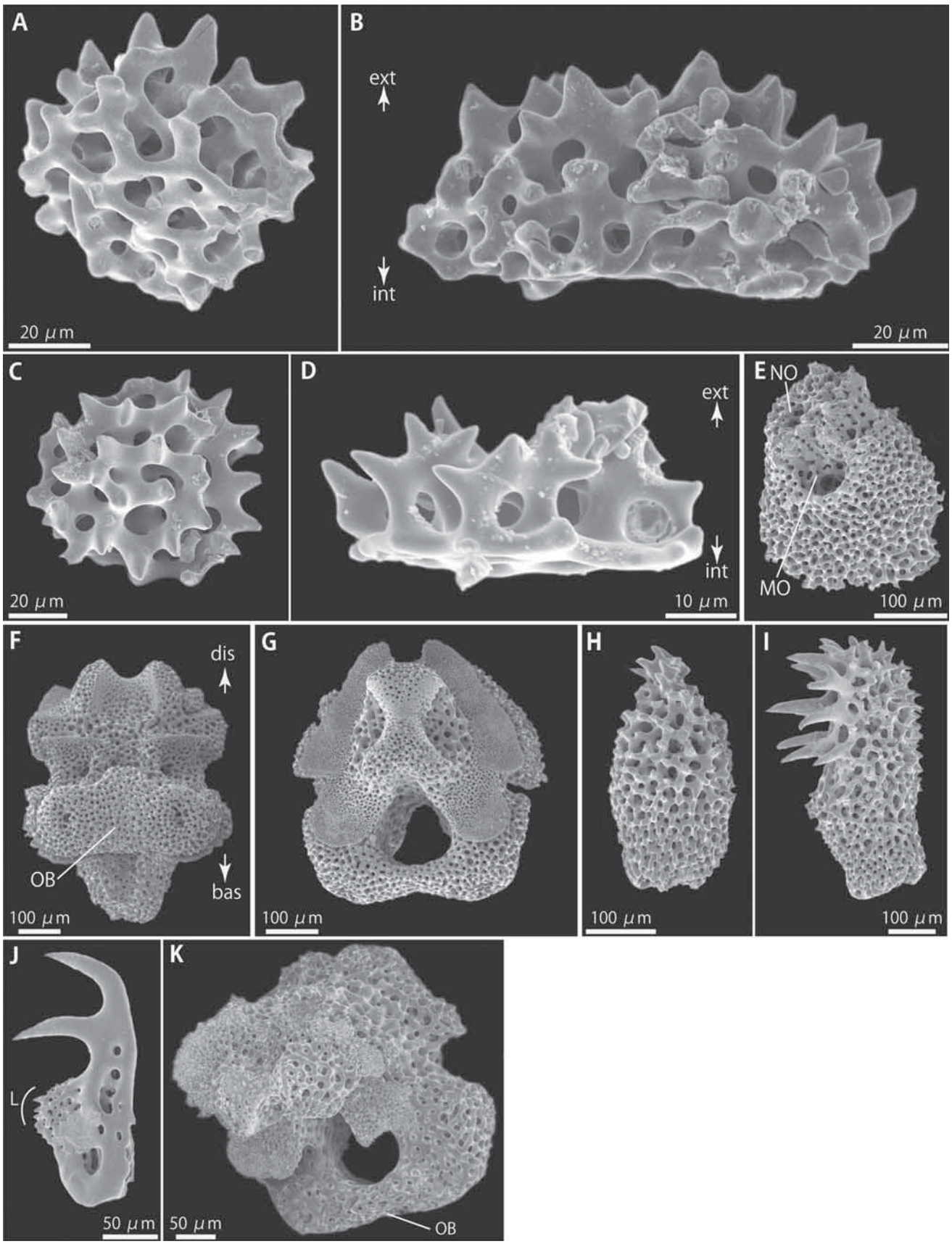


Fig. 4. *Asteromorpha capensis* (USNM 1201805) (A–J) and (DNSM ECHI1: holotype of *Astroschema capansis*) (K), SEM photographs of internal ossicles: A, B, plate-shaped external ossicles at aboral basal portion of the arm, external (A) and lateral (B) views; C, D, granule-shaped external ossicles at distal portion of the arm, external (C) and lateral (D) views; E, lateral arm plate at basal portion of the arm, external view; F, G, vertebrae at distal portion of the arm, oral view (F) and basal view (G); H–J, arm spines from basal portion of the arm (H), middle portion of the arm (I) and distal portion of the arm (J); (K), vertebrae at distal portion of the arm, distal view. Arrows indicate orientation (B, D, F): bas, basal side; dis, distal side; ext, external side; int, internal side. Abbreviation: L, lamina; MO, muscle opening; NO, nerve opening; OB, oral bridge.

***Distribution.*** — MADAGASCAR: south and northeast of Madagascar (present study); SOUTH AFRICA: off Umvoti River, 64–73 m (Mortensen, 1925).

***Remarks.*** — Mortensen (1925) described the present species as *Asteroschema* of present Asteroschematinae based on external observations. The holotype of *Astroschema capensis* deposited in the Durban Natural Science Museum has oral bridge on oral side of vertebrae of distal portion of arms (Fig. 4K) and two arm spines from fifth arm segment (Fig. 5C). These morphological features confirm an affiliation with the Euryalinae (Mortensen, 1933; Okanishi et al., 2011). Body being covered mostly by external ossicles and the distal arm spines having a smooth basal lamina support this species' placement in the the genus *Asteromorpha.* Thus, here we conclude that *Asteroschema capense* should be transferred to the genus *Asteromorpha* of Euryalinae.

*Asteromorpha capensis* (Mortensen, 1925) can be distinguished from the other species of *Asteromorpha* by its morphological characters: flat and polygonal plate-shaped external ossicles that are densely tessellated on aboral body; a body that is either reddish purple with creamy white spots on aboral disc and banded aboral and lateral surfaces of the arms, or light brown aborally and white orally; radial shields that lack tubercles; and five arms, showing no signs of fissiparity. See also remarks under *A. rousseaui* for a detailed account of these taxonomic characters (Table 1).

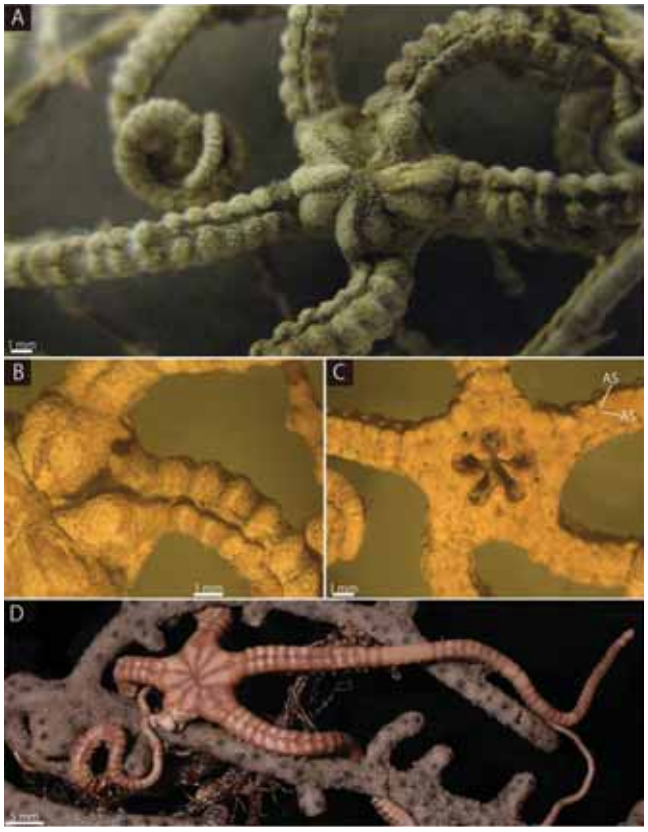


Fig. 5. *Asteromorpha capensis* (DNSM ECH1: holotype of *Astroschema capensis*) (A–C) and (MNHN specimen) (D): A, aboral view; B, aboral periphery of disc and basal portion of arms; C, oral disc and basal portion of arms, arrows indicate arm spines; D, aboral view. Abbreviation: AS, arm spine.

Table 1. Revised tabular characters key to the species of the genus *Asteromorpha*.

| Species | Colour, form and arrangements of epidermal ossicles | | Tubercles on radial shields | Body colour | Reproduction status |
|---|---|---|---|---|---|
| | Aboral surface of disc | Aboral and lateral surface of basal portion of arms | | | |
| *A. capensis* (Mortensen, 1925) | Flat plate-shaped, no regular arrangement | Flat plate-shaped, no regular arrangement | Absent | Two variations: 1) reddish purple with white spots on aboral disc and white bands on middle to distal arms; 2) aborally light brown and orally white | Non fissiparous |
| *A. rousseaui* (Michelin, 1862) | 1) Brown, round and domed, 2) white, polygonal and flat plate-shaped, regularly scattered | Three rows of brown ossicles appearing among tessellated white ossicles in each arm segment | Absent | White with brown spots on radial shields and/or brown interradial radiating lines from disc center, and brown bands on arms | Non fissiparous |
| *A. koehleri* (Döderlein, 1898) | 1) Brown, round and domed, 2) white, polygonal and flat plate-shaped, regularly scattered | Two pairs of alternating rows of brown and white ossicles in each arm segment | Absent | White with brown spots on aboral disc and brown bands on arms | Fissiparous |
| *A. tenax* Baker, 1980 | Flat plate-shaped, no regular arrangement | Flat plate-shaped, no regular arrangement | Present | Uniformly white | Fissiparous |

### *Asteromorpha rousseaui* (Michelin, 1862)
(Figs. 6–9)

*Asterochema rousseaui* Michelin, 1862: 6; Hoffman, 1874: 53
*Astroschema rousseaui* von Martens, 1869: 129; Lyman, 1880: 45; 1882: 278
*Asteroschema rousseaui* Lyman, 1872: 4; de Loriol, 1893: 55–56; –Döderlein, 1911: 111
*Asteromorpha perplexum*. A. M. Clark, 1976: 111, 112, 117, fig. 1. Non *Asteromorpha perplexum* (Koehler, 1930)
*Asteromorpha steenstrupi* Lütken, 1869: 60–63, one plate
*Asteromorpha rousseaui* Lütken, 1872: 96–98; Mortensen, 1933: 57–60, figs. 42–44, pl. VI figs. 6–9.
*Astroschema steenstrupi* Lyman, 1875: 26
*Asteroschema steenstrupi* Brock, 1888: 538

***Type material examined.*** — Six dry syntypes of *Asteromorpha steenstrupi*, ZMUC OPH-479, off Reunion Island.

***Other materials examined.*** — One dry specimen, USNM E5956, off Port Louis, Mauritius, 200 m, Dec.1929: three ethanol preserved specimens, MNHN IE-2013-4010, IE-2013-4002, IE-2013-4008, collected by R/V MARION DUFRESNE, MD32 CP172, north of Reunion Island, east of Madagascar, 20°52.S, 55°37.E 105–120 m, 8 Sep.1982: one ethanol preserved specimen, MNHN IE-2013-4011, collected by R/V MARION DUFRESNE, station MD 32 FA92, north of Reunion Island, east of Madagascar, 19°45.S, 54°07.E 75–125 m, 28 Aug.1982: one ethanol preserved specimen, respectively, MNHN IE-2013-4012, IE-2013-4006, collected by R/V MARION DUFRESNE, MD32 DC176, west of Reunion Island, east of Madagascar, 21°01.S, 55°10.E 165–195 m, 8 Sep.1982: one ethanol preserved specimen, MNHN IE-2013-8007, collected by MIRIKY, CP3260, between Majunga and Cape Saint-Andre, north-western Madagascar, 15°35.S, 45°45.E 179–193 m, 10 Jul.2009 (Fig. 1).

***Diagnosis.*** — Two types of external ossicles on aboral surface of body, one white, domed and round plate-shaped, while the other brown, flat and polygonal plate-shaped. Brown ossicles of disc forming radiating straight rows interradially and/or regularly arranged on radial shields, while the basal portion of arms (aborally and lateral surfaces), bears brown ossicles forming three transverse rows on each arm segment. White ossicles tessellated between these rows. No tubercles on radial shields. Five or six arms, non-fissiparous.

***Description of USNM E5956.*** — Disc diameter 6.1 mm, arm length ca. 52 mm (Fig. 6).

Disc circular with no fission plane (Fig. 6A). Aboral surface tumid, covered by both white, slightly domed and round plate-shaped external ossicles and brown, flat and polygonal plate-shaped external ossicles (Fig. 6B, C). Brown external ossicles forming five straight rows radiating from center of disc interradially, and patches of two or three brown external ossicles scattered at regular intervals among white external ossicles on radial shields (Fig. 6A). White external ossicles ca. 80–120 μm long and 70 μm thick and brown external ossicles ca. 70–100 μm long and 30 μm thick, respectively. Radial shields triangular, contiguous and completely covered by external ossicles, ca. 2.7 mm long and 1.3 mm wide, (Fig. 6A).

Oral surface of disc entirely covered by only white, flat and polygonal plate-shaped external ossicles (Fig. 6D), ca. 60–90 μm long and 30 μm thick on periphery (Fig. 6F) and ca. 100 μm long and 40 μm thick on oral plates (Fig. 6E). Four teeth forming vertical row on dental plate. Oralmost tooth triangular (Fig. 6E), remaining teeth square, domed oral papillae on each side of the jaws (Fig. 6E).

Lateral interradial surface of disc nearly vertical, covered by white, flat and polygonal plate-shaped external ossicles similar to those on oral surface (Fig. 6G). Two genital slits in each interradius, 1.0 mm long and 0.40 mm wide. Gonads visible inside each genital slit (Fig. 6G). No distinct ossicles suggesting presence of madreporites visible on oral interradius.

Arms five, simple, basal third and/or fourth arm segments thickened (2.0 mm wide and 2.0 mm in high), with flattened aboral and oral surfaces. Remaining segments 1.6 mm width and 1.45 mm height, with arched aboral surface and flattened oral surface. Arms tapering gradually from middle to distal extremities.

Aboral and lateral surface of basal portion of arms covered by white, slightly domed and round plate-shaped external ossicles, ca. 100–150 μm long and 80 μm thick, and brown, domed and round plate-shaped external ossicles, ca. 100–180 μm long and 40 μm thick (Fig. 6H), similar to those on aboral disc.

Basal arm segments (both aboral and lateral surface) covered entirely by white external ossicles interrupted by three transverse rows of brown ossicles. Basal-most row contains only brown ossicles while other two rows contain regularly scattered white ossicles (Fig. 6H). Oral surface of arms covered only by flat, polygonal plate-shaped external ossicles, ca. 50–80 μm long and 50 μm thick (Fig. 7A), similar to those on oral disc. In middle portion of arms, aboral and lateral surface also covered by white and brown external ossicles similar to those on basal portion of arms, ca. 100–130 μm long and 100 μm thick, and ca. 70–100 μm long and 50 μm thick, respectively (Fig. 7B). Similarly, on arm segments, brown external ossicles form two transverse rows, with basal rows being continuous and distal rows fragmented (Fig. 7B, D). Oral surface covered by white, flat and polygonal plate-shaped external ossicles, similar to those on basal portion of oral arms, ca. 50–80 μm long and 50 μm thick (Fig. 7C). Distal portion of arms entirely covered by uniform flat and round granule-shaped external ossicles, ca. 80 μm long and 30 μm thick (Fig. 7E, F). Each arm segment with row of brown external ossicles on aboral and lateral surface (Fig. 7F).

First to third tentacle pores lacking arm spines; from fourth pore, two arm spines (Fig. 7A). In first third of arms, arm spines ovoid and minute (Fig. 8F), with inner arm spines ca. one-third of length of corresponding arm segment and outer arm spines four-fifth of length of inner ones (Fig. 8F). In second third of arms, arm spines bearing fine spinelets at tips (Fig. 8G). Inner arm spines two-thirds of length of

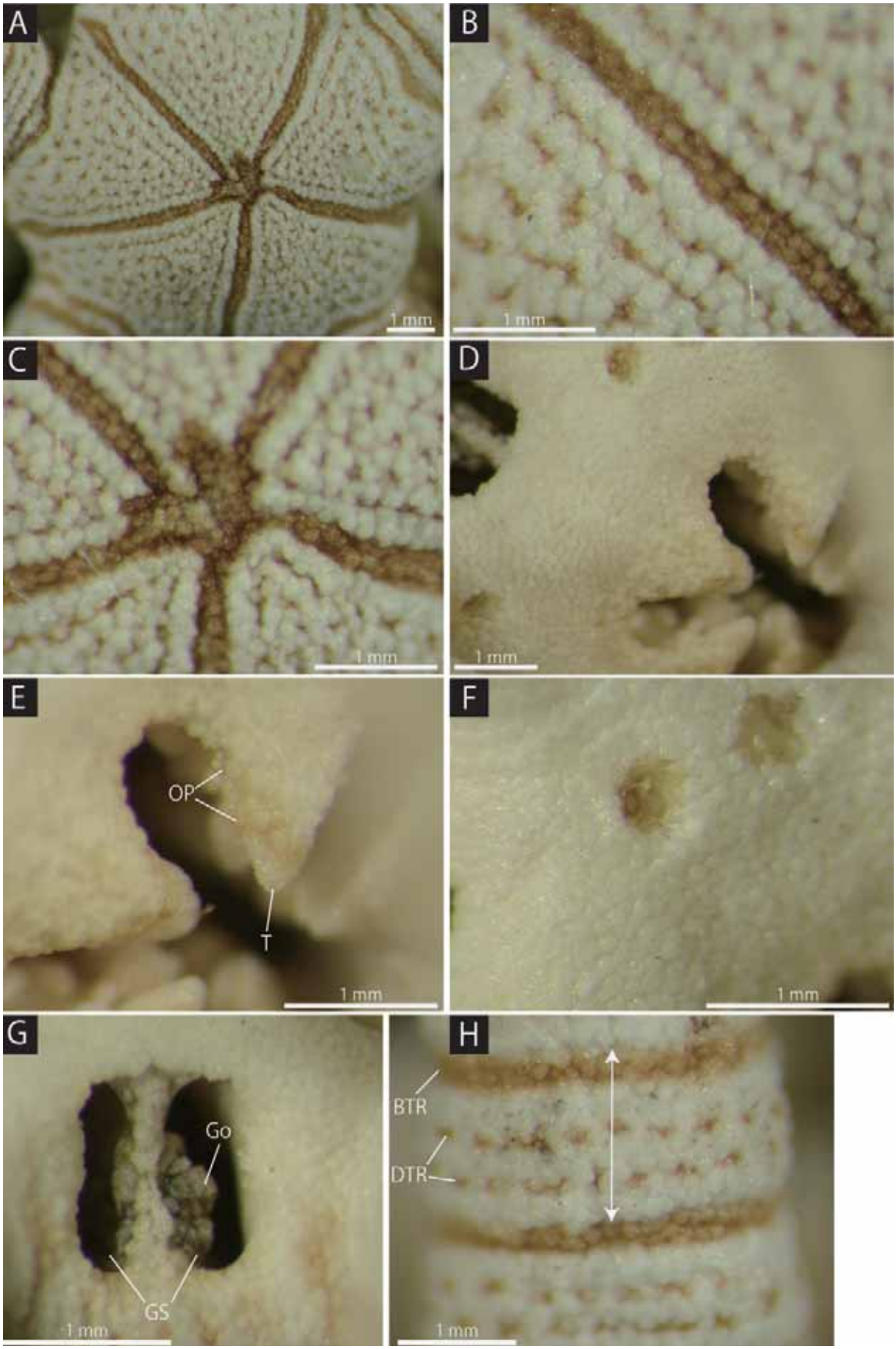


Fig. 6. *Asteromorpha rousseaui* (USNM E5956): A, aboral disc; B, aboral periphery part of disc; C, aboral central part of disc; D, oral disc; E, jaws; F, oral periphery of disc; G, lateral interradial part of disc; H, aboral basal portion of the arm. Double arrow indicates an arm segment. Abbreviations: BTR, basal transverse row; DTR, distal transverse row; Go. Gonad; GS, genital slit; OP, oral papillae; T, teeth.

corresponding arm segment and outer arm spines half length of inner ones (Figs. 7C, D, 8G). In distal third of arms, arm spines hook-shaped with smooth lamina on distal side (Fig. 8H). Inner arm spines half length of corresponding arm segment with outer arm spines almost same length as inner ones (Figs. 7E, 8H).Lateral arm plates concealed by external ossicles, with one or two pairs of a muscle and a nerve opening, and each of them associated with an arm spine articulation (Fig. 8E). Vertebrae in middle to distal portion of arms with oral bridge (Fig. 8I).

Colour: Aboral disc surface, five brown lines radiating interradially from disc center. Radial wedges are defined by scattered brown spots that form dashed concentric triangles

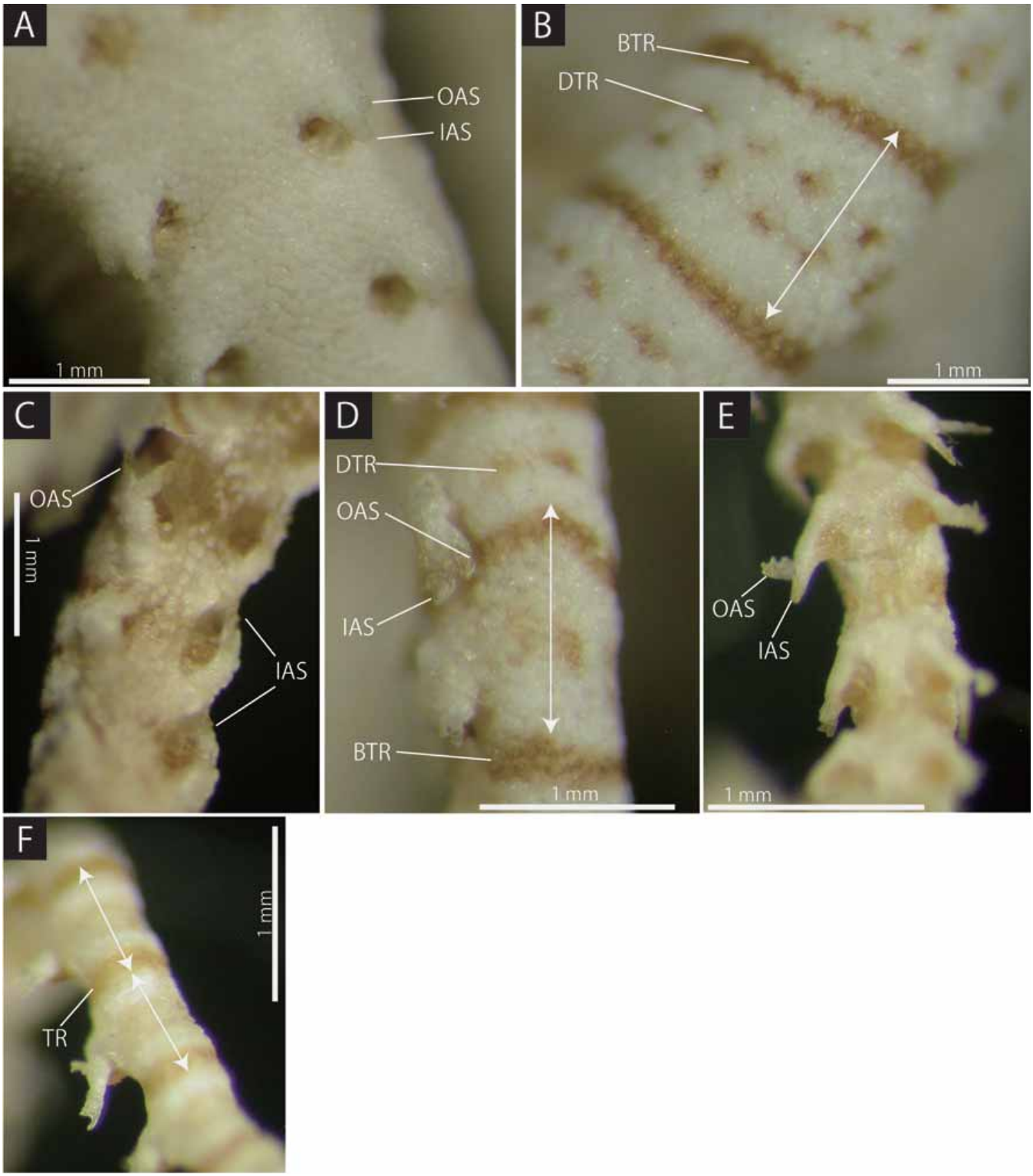


Fig. 7. *Asteromorpha rousseaui* (USNM E5956): A, oral basal portion of the arm; B, aboral middle portion of the arm, double arrow indicates an arm segment; C, oral middle portion of the arm; D, aboral distal portion of the arm, double arrow indicates an arm segment; E, oral distal portion of the arm; F, lateral distal portion of the arm. Double arrows indicate arm segments. Abbreviations: BTR, basal transverse row; DTR, distal transverse row; IAS, inner arm spine; OAS, outer arm spine; TR, transverse row.

(Fig. 6A–C). Aboral and lateral surface of arms white with brown transverse rows. Configuration of brown rows outlined above (Figs. 6H, 7B, D). Oral surface uniformly white.

***Variation*.** — Some colour variations were observed as Mortensen (1933) indicated. The specimens MNHN IE-2013-4006, IE-2013-4002, IE-2013-4008, IE-2013-8007 show similar colour to USNM E5956 described above and have radiating rows of brown plate-shaped external ossicles on aboral disc (Fig. 6A). However, syntypes of *A. steenstrupi* and specimens of MNHN IE-2013-4010, IE-2013-4011, IE-2013-4012 show no such rows or scattered brown ossicles on the aboral disc (Fig. 9A). Brown transverse rows appear on arms of all examined specimens (Fig. 9A, B).

***Distribution*.** — REUNION: around Reunion Island, 75–195 m (Lütken, 1869; present study). MAURITIUS: off Port Louis, 200 m (present study); northwest of Majunga, 179–193 m (present study).

***Remarks*.** — According to Mortensen (1933) and Baker (1980), *A. rousseaui* can be distinguished from other species by: 1) absence/presence of oral bridge of vertebrae in the basal portion of the arms, 2) fissiparous/non-fissiparous, 3) absence/presence of tubercles on radial shields, and 4) absence/presence of transverse rows of external ossicles on aboral and lateral surface of the arms.

Mortensen (1933) found that *A. rousseaui* possesses an oral bridge only in distal portion of the arms but the other species of *Asteromorpha* possess it throughout the arms (Mortensen, 1933). We refrain from using this character to distinguish the species because it might be variable depending on growth stage. Mortensen (1933) examined specimens of *A. rousseaui* that were much larger than those of *A. perplexum* (Mortensen, 1933). To determine the reliability of this character, examination of a series of smaller specimens of *A. rousseaui* is required.

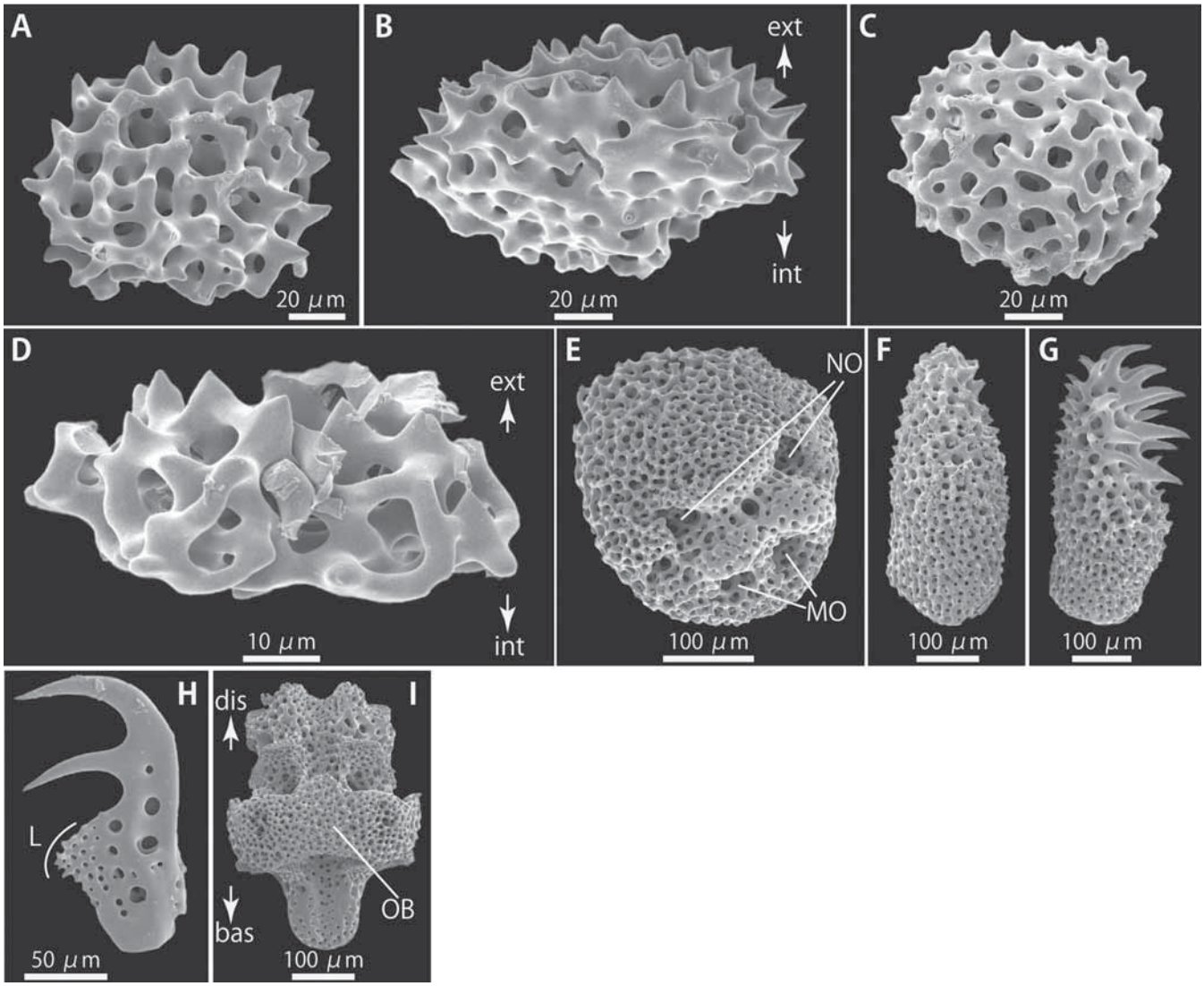


Fig. 8. *Asteromorpha rousseaui* (USNM E5956), SEM photographs of internal ossicles: A, B, white and domed plate-shaped external ossicles at aboral basal portion of the arm, external (A) and lateral (B) views; C, D, brown and flat plate-shaped external ossicles at oral basal portion of the arm, external (C) and lateral (D) views; E, lateral arm plate at basal portion of the arm, external view; F–H, arm spines from basal portion of the arm (F), middle portion of the arm (G) and distal portion of the arm (H); I, vertebrae at distal portion of the arm, oral view. Arrows indicate orientations (B, D, I): bas, basal side; dis, distal side; ext, external side; int, internal side. Abbreviations: L, lamina; MO, muscle opening; NO, nerve opening; OB, oral bridge.

Fissiparity and the absence/presence of tubercles on radial shields were useful taxonomic characters for distinguishing *A. rousseaui*. All examined specimens in this study of *Asteromorpha capensis* (N = 4) and *A. rousseaui* (N = 14) have five or six arms that are uniform in width and have no fission plane. On the other hand, 12 of 18 (67%) examined specimens of *A. koehleri* and 12 of 16 (75%) of *A. tenax* have fission planes and six arms with a different width (see Remarks of these two species). Twelve of 16 (75%) examined specimens of *A. tenax* (including specimens both with/without fission planes) have large tubercles on the radial shields, which are absent in *A. rousseaui* (see Remarks of each species; Table 1).

Presence/absence of transverse rows of brown external ossicles on the aboral and lateral surfaces of the arms also proved to be a useful taxonomic character but may require more rigorous investigation. Of the four *Asteromorpha* species, the transverse rows only occur in *A. rousseaui* and *A. koehleri*. In the basal portion of the arms, *A. koehleri* has two rows and *A. rousseaui* three (Table 1). In this study, the number of rows of external ossicles was also a useful diagnostic character that can distinguish *A. rousseaui* from *A. koehleri*.

Our study of 52 specimens of *Asteromorpha* revealed that body colour is also a useful diagnostic character. *Asteromorpha rousseaui* has brown spots at regular intervals and/or brown interradial radiating lines on aboral disc and brown bands on arms. *Asteromorpha koehleri* is similar to *A. rousseaui* in colour but lacks brown interradial radiating lines on aboral disc (Table 1).

Mortensen (1933) recognised two colour variations in *A. rousseaui* (see *Variation* above). These variations are distinct and could possibly be distinguished as different species or subspecies. However, we have not examined the type specimens of *A. rousseaui* and we refrain from describing these variations as different (sub)species here. If the type specimens of *A. rousseaui* have no radiating interradial lines like the syntypes of *A. steenstrupi*, then *A. steenstrupi* should be retained as a synonym of *A. rousseaui*, and specimens with the radiating lines should be described as a new species. However, if the type specimens of *A. rousseaui* have radiating lines, then *A. steenstrupi* could be revived. It is unfortunate that the colour pattern was not sufficiently detailed in the original description of *A. rousseaui* (Michelin, 1862). Therefore, examination of the type specimens of *A. rousseaui* is required for determining the taxonomic status of these two colour variations. Jangoux (1985) noted that the type specimen(s) were deposited in Museum d'histoire naturelle de Lyon. However, the whereabouts of the type specimens are unknown at present (Sabine Stöhr, pers. comm.).

### *Asteromorpha koehleri* (Döderlein, 1898)

(Figs. 10–12)

*Astroschema koehleri* Döderlein, 1898: 131–132, pl. 5, 5a
*Asteroschema koehleri* Döderlein, 1911: 111
*Astroschema rousseaui* Koehler, 1905: 123. Non *Asteromorpha rousseaui* (Michelin, 1862)
*Ophiogelas perplexum* Koehler, 1930: 43–45, pls. 2, 6; pls. 4, 9–12
*Asteromorpha perplexum* Mortensen, 1933: 60–62, 73, figs. 45, 46

***Materials examined.*** — One ethanol preserved syntype of *Astroschema koehleri*, ZSM 424/1, off Ambon, eastern Indonesia: dry holotype of *Ophiogelas perplexum,* MCZ E5864, off Ambon, eastern Indonesia, 125 m; 16 ethanol preserved specimens, MV F111585, collected by R/V SOUTHERN SURVEYOR, SS10/2005 18, off D'Entrecasteaux National Park, 34°53'10.S, 115°30'25.E–34°53'02.S, 115°29'56.E, 95–100 m, 21 Nov.2005.

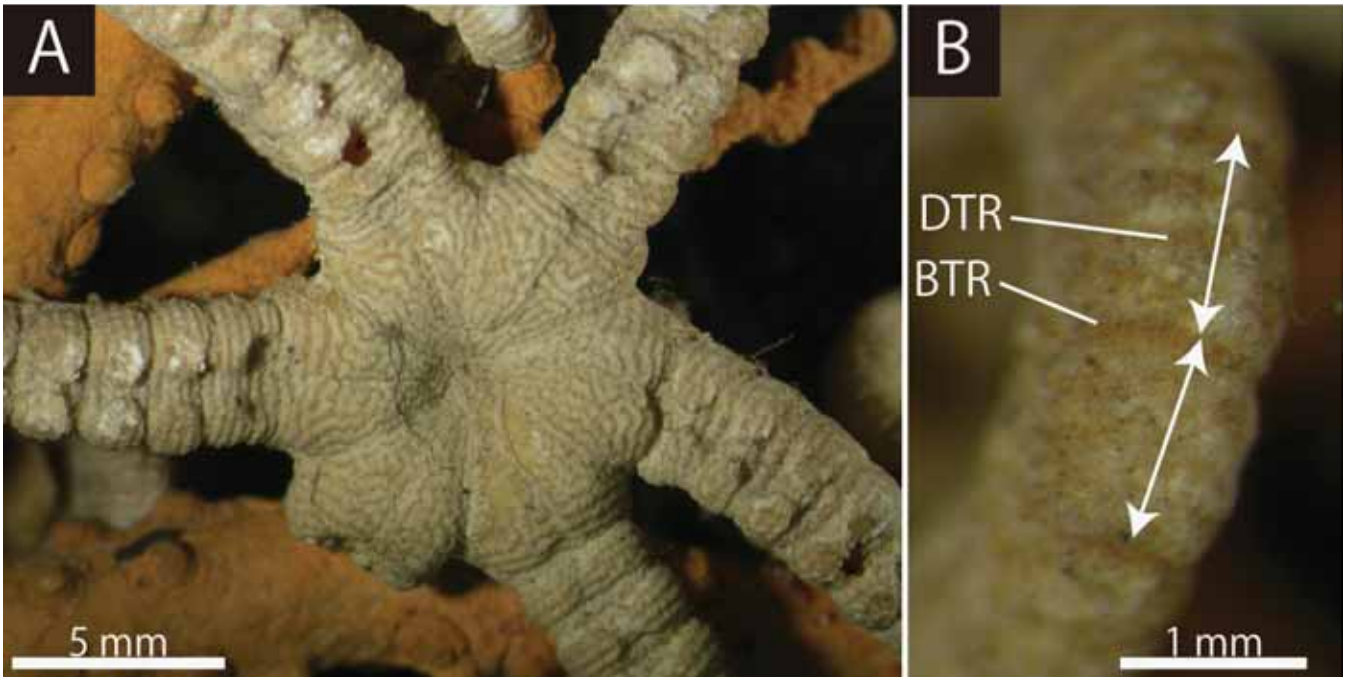


Fig. 9. *Asteromorpha steenstrupi* Lütken, 1869, one syntype (ZMUC OPH-479): A, aboral disc and basal portion of arms; B, aboral middle portion of arm. Double arrows indicate arm segments. Abbreviations: BTR, basal transverse row; DTR, distal transverse row.

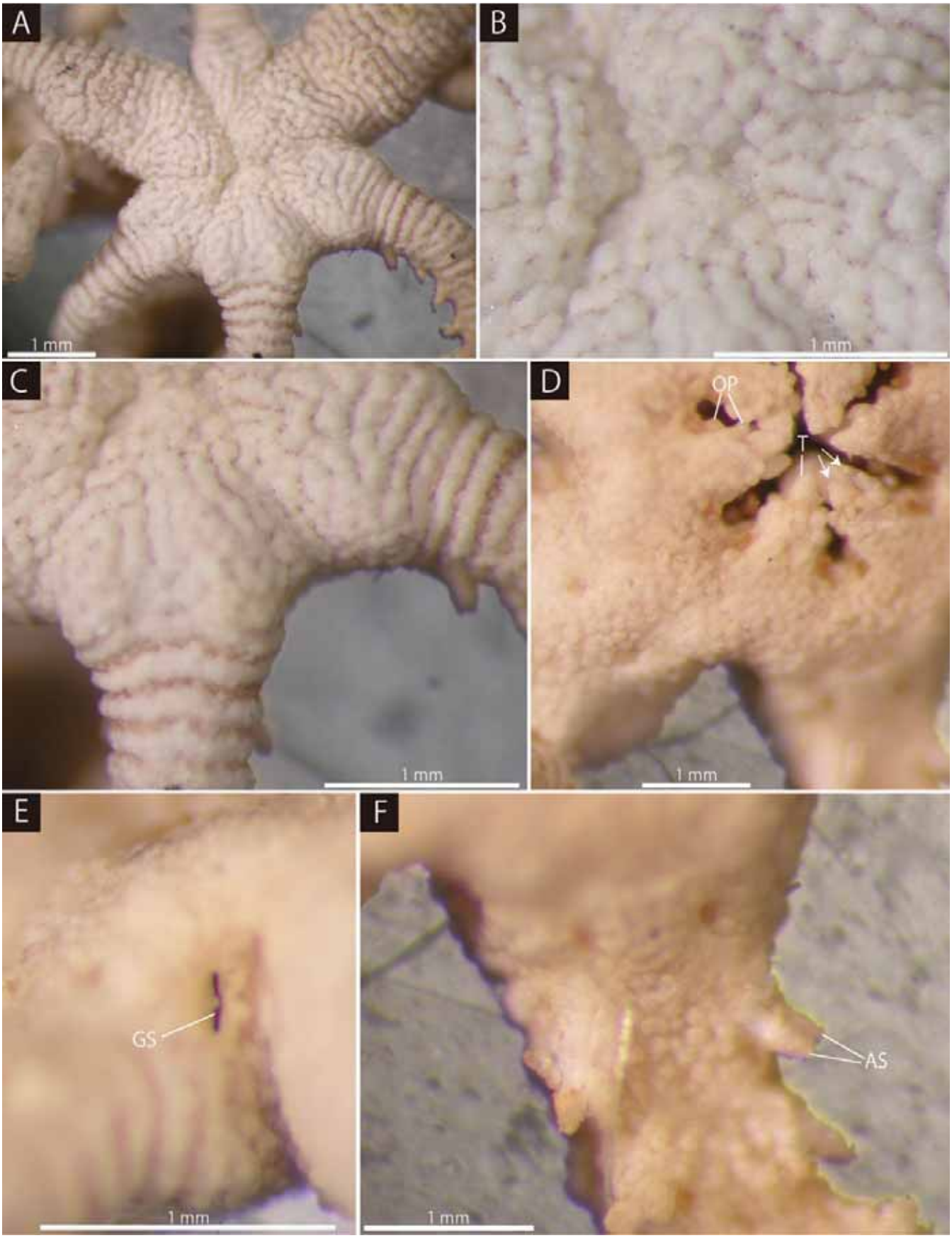


Fig. 10. *Asteromorpha koehleri* (MCZ E5864: holotype of *Ohphiogelas perplexum*): A, aboral disc and basal portion of arms; B, aboral central part of disc; C, aboral periphery part of disc and basal portion of arms; D, oral disc, two parallel oral-most teeth are indicated by arrows; E, lateral interradial part of disc; F, basal portion of oral arm. Abbreviations: AS, arm spine; GS, genital slit; T, teeth; OP, oral papillae.

***Diagnosis.*** — Two types of external ossicles on aboral surface of body, white, domed and round plate-shaped ossicles and brown, flat and polygonal plate-shaped ossicles. Brown ossicles regularly arranged on radial shields. External ossicles on aboral and lateral surface of arms forming alternative transverse rows of brown and white ossicles on each arm segment. Two rows of brown ossicles on each arm segment in basal portion of arms. No tubercles on radial shields. Usually six arms, fissiparous.

***Description of MCZ E5864.*** — Disc diameter 2.3 mm, arm length at least 12 mm (arms convoluted).

Disc six-lobed in shape with no fission plane. Aboral surface tumid in radial regions, covered by white, domed and round plate-shaped external ossicles as well as brown, flat and round plate-shaped external ossicles (Fig. 10A–C). Aboral surface of disc covered by white external ossicles with brown external ossicles scattered at regular intervals (Fig. 10B, C). White external ossicles and brown external ossicles ca. 70–110 µm long and 30–40 µm long, respectively (Fig. 10B, C). Radial shields oval, completely covered by external ossicles, ca. 1.1 mm long and 0.4 mm wide (Fig. 10A, C).

Oral surface of the disc entirely covered by only white, flat and polygonal plate-shaped external ossicles, ca. 80 µm long (Fig. 10D). Three to four teeth forming a vertical row on dental plate, except on two jaws that have two parallel teeth are in oral-most position (Fig. 10D). Four to five domed oral papillae lying on each side of the jaw (Fig. 10D).

Lateral interradial surface of disc nearly vertical, covered by white, flat and polygonal plate-shaped external ossicles similar to those on oral surface (Fig. 10E). Two narrow genital slits in each interradius, 50 µm long and 7.5 µm wide. No distinct ossicles suggesting existence of madreporites (Fig. 10E).

Arms simple, six. Two arms thickened (0.9 mm and 0.7 mm width, respectively) on basal third to fourth segments with flattened aboral and oral surfaces. Remaining segments, 0.3 mm in width, with arched aboral surface and flattened oral surface. Arms tapering gradually towards tip of arm from middle. Remaining four arms flattened on both aboral and oral surfaces, square in cross-section and tapering gradually towards arm tip.

In basal portion of arms, aboral and lateral surface completely covered by white, domed and round plate-shaped external ossicles, ca. 90–105 µm long, and brown, flat and round plate-shaped external ossicles, ca. 45–60 µm long (Fig. 10C), similar to those on aboral disc. Each arm segment entirely covered by two pairs of brown and white external ossicles forming alternately arranged transverse rows (Fig. 10C). Oral surface covered by white, flat and polygonal plate-shaped external ossicles ca. 45–60 µm long (Fig. 10F), similar to those on oral surface. In middle portion of arms, the aboral and lateral surface also covered by white and brown external ossicles similarly arranged to those on basal portion of arms, both ca. 60 µm long (Fig. 11A). Oral surface covered by white, flat and polygonal external ossicles, similar to those on basal portion of the arms, ca. 45 µm long. The distal aboral and lateral surfaces covered only with white granule-shaped external ossicles, ca. 45 µm long (Fig. 11B). No external ossicles on oral surface of distal portion of arms.

First to third tentacle pores lacking arm spines; from fourth pores, two arm spines present (Fig. 10F). In first third of arms, arm spines ovoid (Fig. 10F) with inner and outer arm spines almost same length, approximately half the length of corresponding arm segment (Fig. 10F). In second third of arms, inner arm spines half length of corresponding arm segment with outer arm spines four-fifths length of inner one (Fig. 11A) and from first third to midpoint of that, arm spines cylindrical (Fig. 11A) and from that midpoint to second third

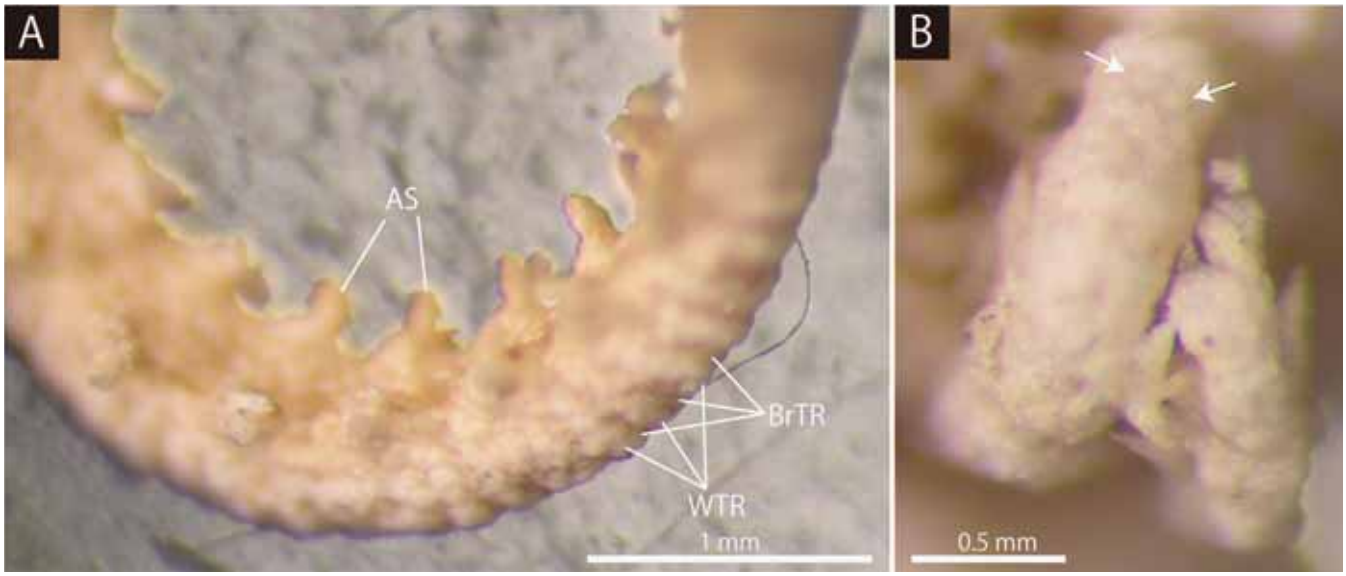


Fig. 11. *Asteromorpha koehleri* (MCZ E5864: holotype of *Ohphiogelas perplexum*): A, lateral middle portion of the arm; B, aboral distal portion of the arm, tiny and scattered external ossicles are indicated by arrows. Abbreviation: AS, arm spine; BrTR, brown transverse row; WTR, white transverse row.

of the arm, arm spines hook-shaped (Fig. 11A). In distal third of arms, all arm spines hook-shaped, inner arm spines half length of corresponding arm segment and outer arm spines almost same length as inner ones (Fig. 11B).

Colour: Aboral surface of disc white with brown spots scattered between white ones at regular intervals (Fig 10A). Arms banded from basal to middle portion of arms on aboral and lateral surfaces, (Figs. 10C, 11A). Distal portion of aboral arms (Fig. 11B) and whole oral surface uniformly white.

***Ossicle morphology of MV F111585.*** — Disc diameter 3.2 mm, arm length ca. 20 mm.

White and domed plate-shaped external ossicles on aboral surface of middle portion of arms, ca. 80 µm long and 40 µm thick (Fig. 12A, B) and white granule-shaped external ossicles on aboral surface of distal portion of arms, ca. 50 µm long and 20 µm thick (Fig. 12C, D). Lateral arm plates in middle portion of arms with one or two pairs of a muscle and a nerve opening, and each of them associated with arm spine articulation (Fig. 12E).

Vertebrae with oral bridge in distal portion of arm (Fig. 12F, G). Arm spines for first third of arms ovoid and minute (Fig. 12H) with remaining arm spines hook-shaped with inner teeth and smooth lamina on distal side gradually decreasing in size (Fig. 12I, J).

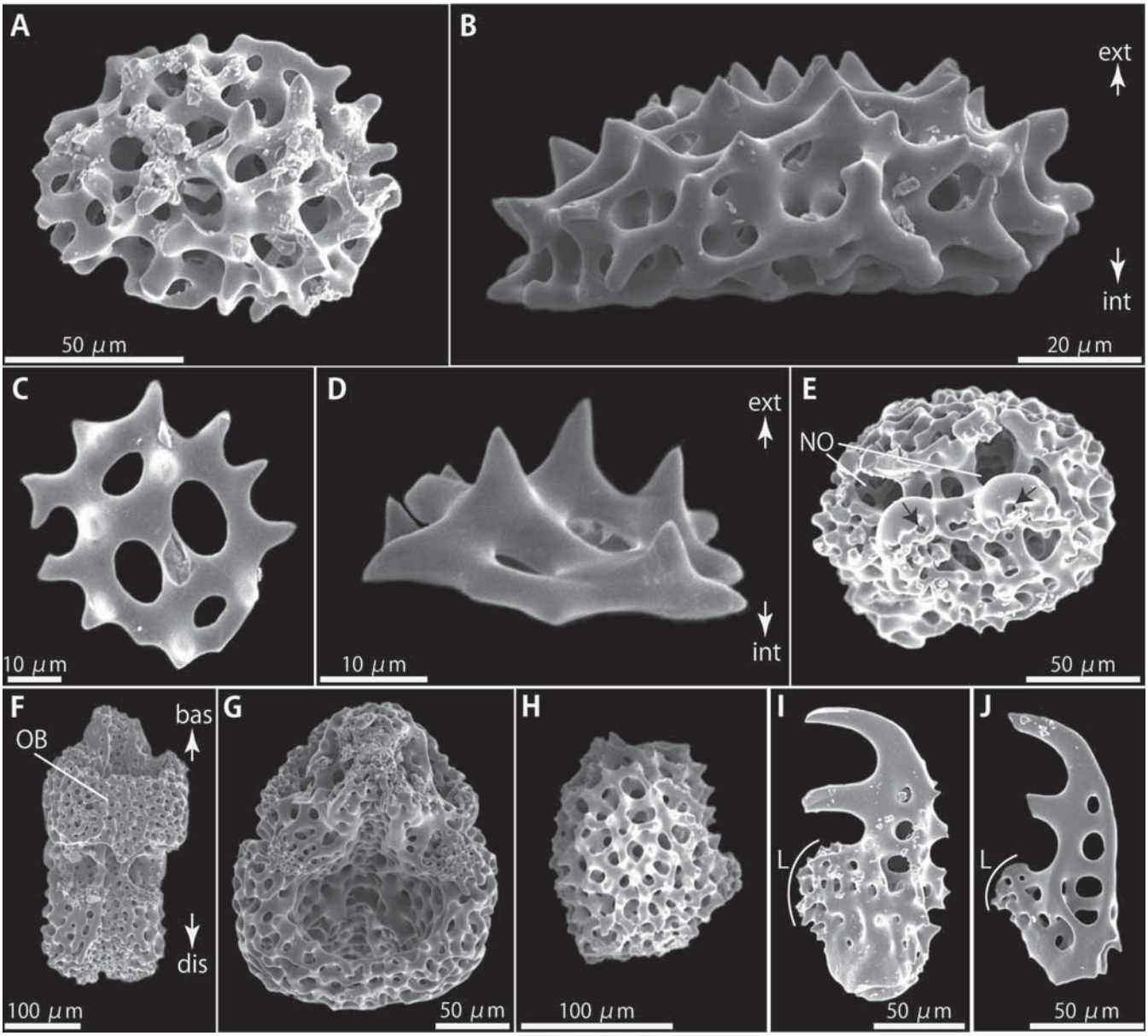


Fig. 12. *Asteromorpha koehleri* (MCZ E5864: holotype of *Ohphiogelas perplexum*), SEM photographs of internal ossicles: A, B, plate-shaped external ossicles at aboral basal portion of the arm, external (A) and lateral (B) views; C, D, granule-shaped external ossicles at distal portion of the arm, external (C) and lateral (D) views; E, lateral arm plate at middle portion of the arm, external view, muscle openings are indicted by arrows; F, G, vertebrae at distal portion of the arm, oral view (F) and basal view (G); H–J, arm spines from basal portion of the arm (H), middle portion of the arm (I) and distal portion of the arm (J). Arrows indicate orientations (B, D, F): bas, basal side; dis, distal side; ext, external side; int, internal side. Abbreviations: L, lamina; NO, nerve opening; OB, oral bridge.

***Variation.*** — This specimen and a syntype of *Astroschema koehleri* (Döderlein, 1898) show irregular brown bands on aboral and lateral surface of basal to middle portion of the arms, but 16 specimens from south-western Australia show thicker brown bands every three to five arm segments. This specimen shows an abrupt gap on basal portion of the arms in thickness, but this is not evident in any of the other specimens examined.

***Distribution.*** — INDONESIA: off Ambon Island and off Kei Island, eastern Indonesia, 90–125 m (Döderlein, 1898; Koehler, 1930); AUSTRALIA: off D'Entrecasteaux National Park, south-western Australia, 95–100 m (present study).

***Remarks.*** — *Asteromorpha koehleri* was originally described by Döderlein (1898) as a species of the genus *Asteroschema.* Koehler (1930) described *Ophiogelas perplexum* as a monotypic genus. Mortensen (1933) transferred *O. perplexum* to *Asteromorpha*, synonymising it with *A. koehleri* in a postscript. Baker (1980) also included *A. koehleri* in *Asteromorpha.*

Our comparison of a syntype of *Astroschema koehleri* with a syntype of *Ophiogelas perplexum* showed that these species both have alternating transverse rows of white, domed external ossicles and brown, flat external ossicles, both with two pairs of rows in basal portion of the arms. Based on this diagnostic character, we certainly conclude that the latter species (*O. perplexum*) is a junior subjective synonym of *A. koehleri* as Mortensen (1933) suggested.

*Asteromorpha koehleri* (Döderlein, 1898) can be distinguished from the other species of *Asteromorpha* by the following morphological characters: two types of external ossicles on the aboral body, first, white, domed and round plate-shaped ossicles, and second, brown, flat and polygonal plate-shaped ossicles; the radial shields covered in regularly arranged brown ossicles; on the aboral and lateral surface of the arms transverse rows of white ossicles and brown ossicles alternating; in the basal portion of the arms, two rows of brown ossicles on each arm segment; no tubercles on radial shields; usually six arms and fissiparous (Table 1).

Both *A. rousseaui* and *A. koehleri* have two types of external ossicles on their aboral body. In the basal portion of the arm of aboral and lateral surface, *A. koehleri* has two transverse rows of brown ossicles while *A. rousseaui* has three (see also Remarks of *A. rousseaui* above). *Asteromorpha capensis* and *A. tenax* possess only one type of external ossicles on their aboral body.

Of 18 examined specimens of *A. koehleri*, 17 have six arms and only one has five arms. Twelve of the 17 six-armed specimens show conspicuous fission planes in their discs which suggests that *A. koehleri* is fissiparous. *Asteromorpha tenax* is also fissiparous (see also Remarks of *A. tenax*), while *A. capensis* and *A. rousseaui* are non-fissiparous.

*A. koehleri* can be distinguished from the *A. tenax* by having no tubercles on their radial shields (see also Remarks of *A. tenax*).

### *Asteromorpha tenax* Baker, 1980
(Figs. 13–15)

*Asteromorpha tenax* Baker, 1980: 70–72, figs. 26a, 32

***Materials examined.*** — Twelve ethanol preserved specimens, MNHN IE-2013-4009, collected by the R/V VAUBAN, station DW205, southeast of New Caledonia, 22°38.S, 167°07.E 140–160 m, 27 Sep.1989: four ethanol preserved specimens, MNHN IE-2013-4003, collected by the R/V Le SUROIT, station PL18, southeast of New Caledonia, 22°46.S, 167°20.E 70–301 m, 3 Sep.1989.

***Diagnosis.*** — External ossicles on aboral surface of body polygonal plate-shaped, densely tessellated. No regular transverse rows of external ossicles on aboral and lateral surface of arms. Body uniformly white. Large tubercles on radial shields. Usually six arms, fissiparous.

***Description of MNHN IE-2013-4009.*** — Disc diameter 1.7 mm, arm length ca. 6.6 mm (Fig. 13)

Disc six-lobed with no fission plane (Fig. 13A). Radial shields and aboral interradial areas slightly tumid (Fig. 13A). Aboral surface of the disc covered by flat and polygonal plate-shaped external ossicles with three domed and round tubercles (Fig. 13A, B). On disc, external ossicles ca. 100 μm long and 50 μm thick on periphery and ca. 80 μm long and 40 μm thick in center (Fig. 13B). Tubercles ca. 4–6 mm in length, ca. 3–4 mm in height (Fig. 13B). Radial shields triangular, completely covered by external ossicles and tubercles, ca. 0.7 mm long and 0.2–0.4 mm wide (Fig. 13A, B).

Oral surface of disc entirely covered by domed and polygonal plate-shaped external ossicles, ca. 50 μm long and 50 μm thick (Fig. 13C, D). Three triangular teeth forming a vertical row on dental plate (Fig. 13D) with two or three domed oral papillae on either each side of jaw (Fig. 13D).

Lateral interradial surface of disc nearly vertical, covered by flat and polygonal plate-shaped external ossicles similar to those on oral surface (Fig. 13E). Two pore-like genital slits, 0.1 mm long and 0.06 mm wide in each interradius. No distinct ossicles suggesting existence of madreporites visible on oral interradius.

Arms simple, six, with no abrupt change in width of arms. Basal portion of arm 0.5 mm wide and 0.4 mm high, tapering gradually towards arm tip.

Basal portion of arms completely covered by flat and polygonal plate-shaped external ossicles, ca. 50–100 μm long and 50 μm thick on aboral and lateral surface (Fig. 13F), and ca. 50 μm long and 40 μm thick on oral surface (Fig. 13G). These ossicles densely tessellated (Fig. 13F, G). In middle portion of arms, aboral and lateral surface covered by flat and round granule-shaped external ossicles, ca. 50 μm long and 20 μm thick (Fig. 14A). Orally, external ossicles gradually decreasing in size disappearing from middle portion of arms. No external ossicles presenting on distal portion of arms (Fig. 14B).

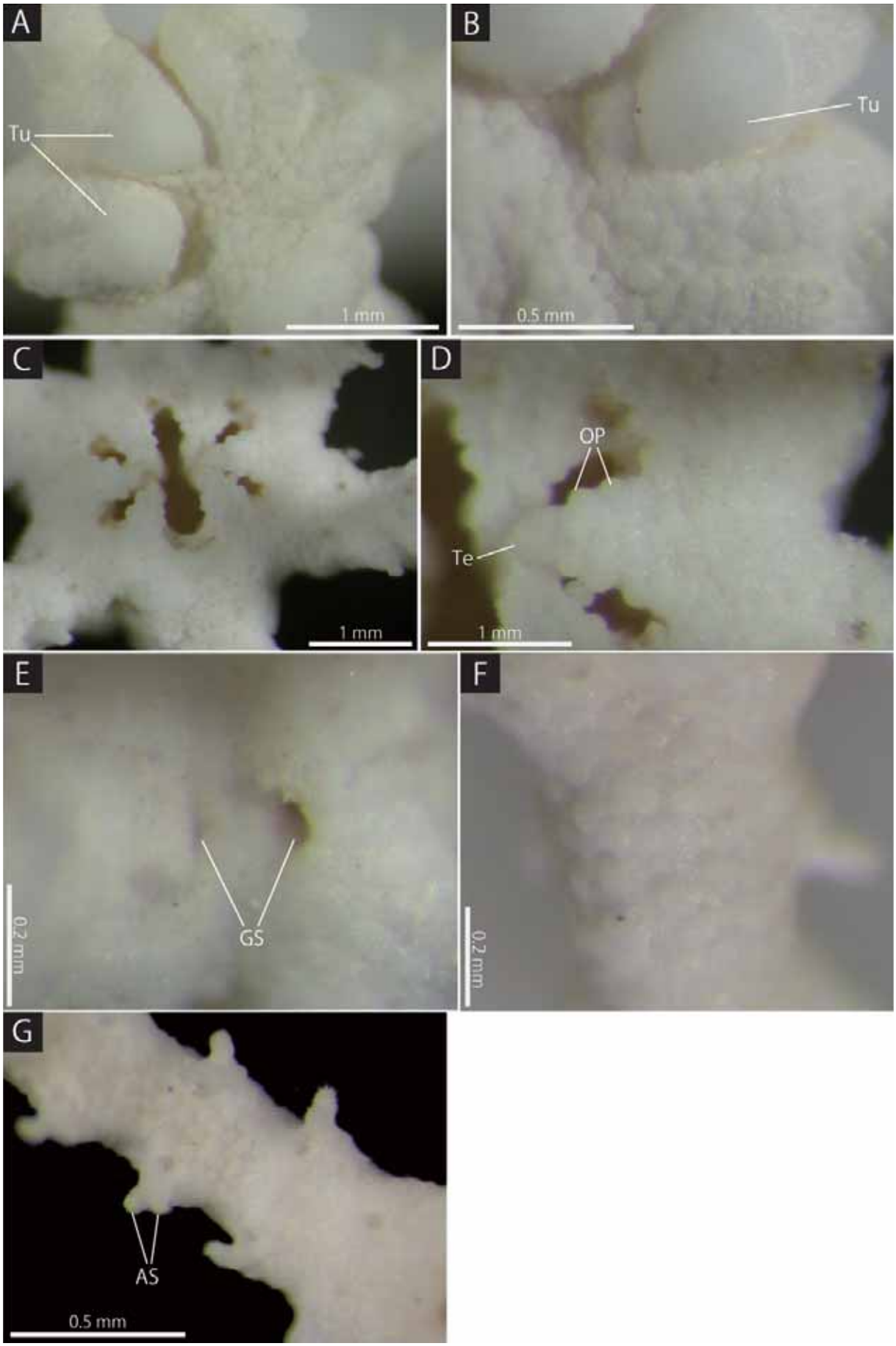


Fig. 13. *Asteromorpha tenax* (MNHN IE-2013-4003): A, aboral disc and oral basal portion of arms; B, aboral periphery part of disc; C, oral disc and basal portion of arm; D, oral periphery part of disc and jaws; E, lateral interradial part of disc; F, aboral basal portion of the arms; G, oral basal portion of the arm. Abbreviations: AS, arm spine; GS, genital slit; OP, oral papillae; Te, teeth; Tu, tubercle.

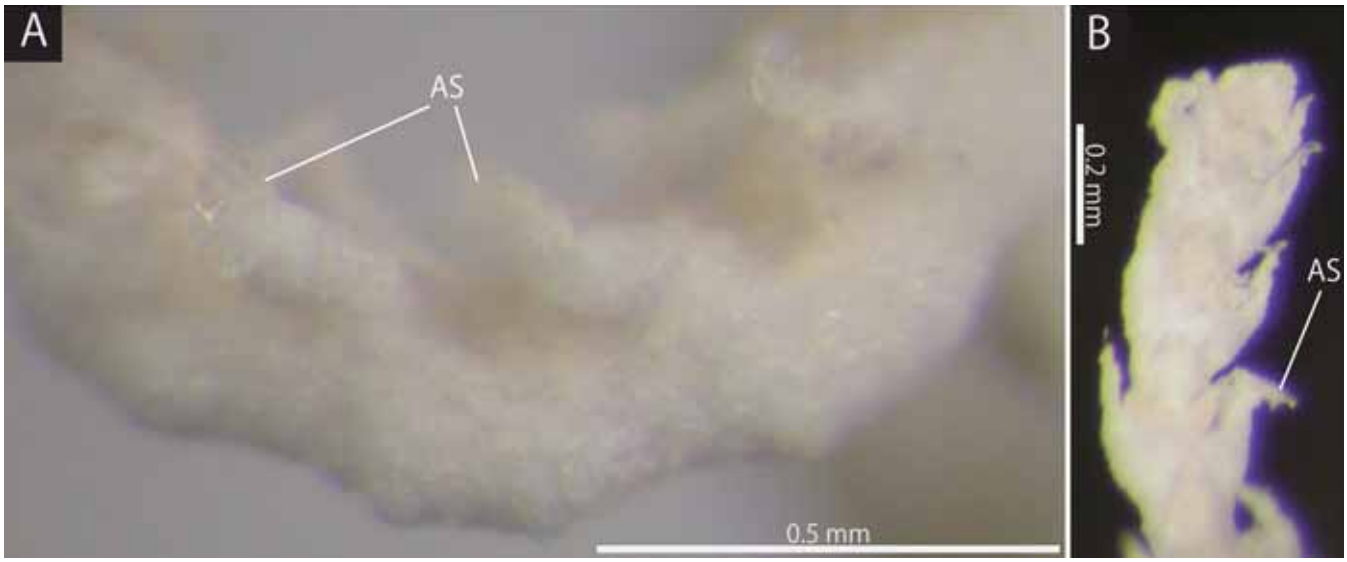


Fig. 14. *Asteromorpha tenax* (MNHN IE-2013-4003): A, lateral distal portion of the arm; B, oral tip of the arm. Abbreviation. AS, arm spine.

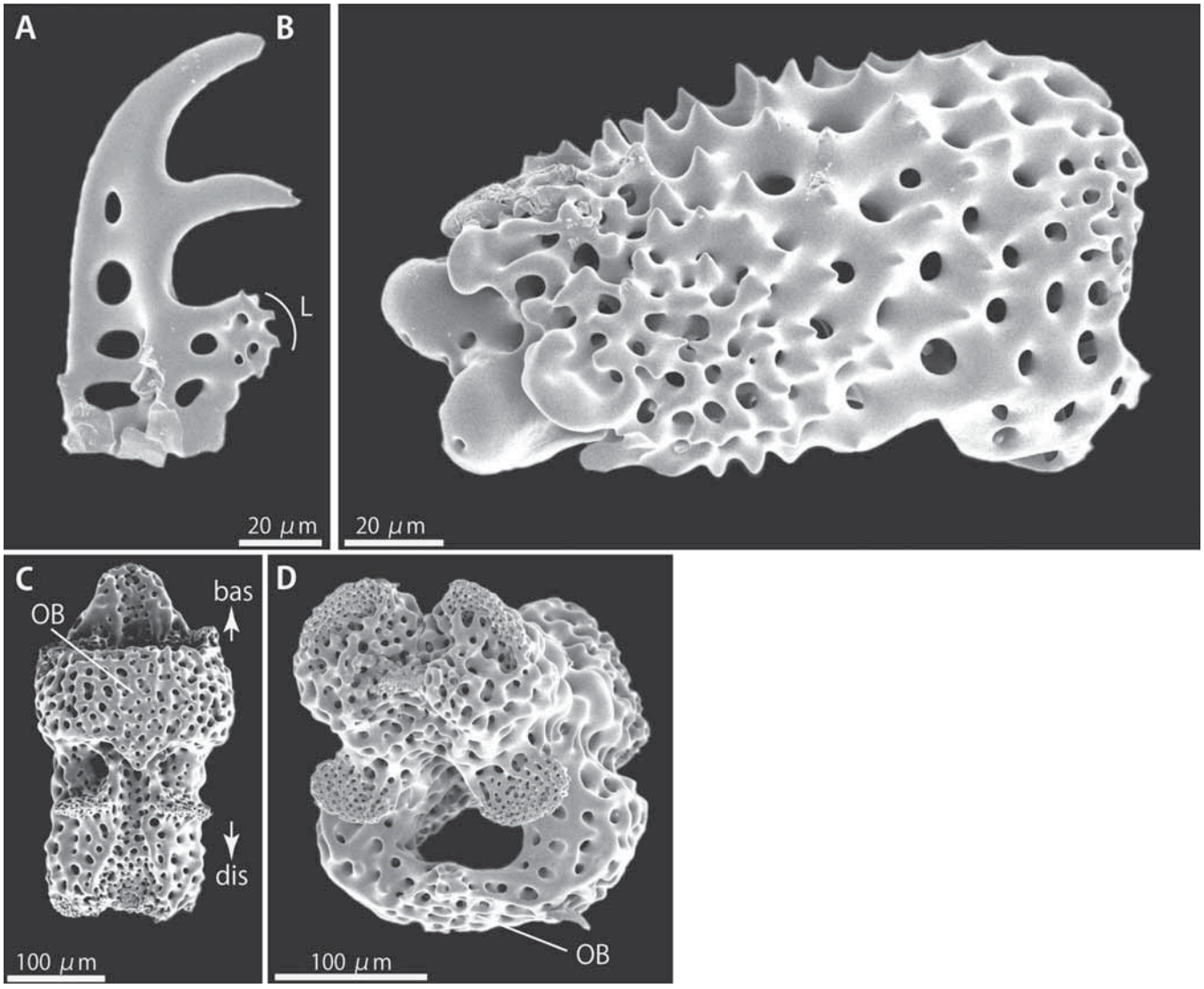


Fig. 15. *Asteromorpha tenax* (MNHN IE-2013-4003), SEM photographs of internal ossicles: A, arm spine from middle portion of the arm; B, lateral arm plate at middle portion of the arm, external view; C, D, vertebrae at distal portion of the arm, oral view (C), distal view (D). Arrows indicate orientations: bas, basal side; dis, distal side. Abbreviations: L, lamina; OB, oral bridge.

First to third tentacle pores lacking arm spines; from fourth pores with two arm spines (Fig. 13G). In first third of arms, arm spines ovoid and minute, both inner and outer arm spines one-third of the length of corresponding arm segment (Fig. 13G). In second and distal thirds of arms, arm spines hook-shaped, their number decreasing to one (Figs. 14B, 15A) which is half the length of corresponding arm segment (Fig. 14B).

Lateral arm plates concealed by external ossicles (Fig. 15B). Vertebrae with an oral bridge in distal portion of arms (Fig. 15C, D).

Colour: Uniformly white (Figs. 13, 14).

***Distribution.*** — AUSTRALIA: off Morton Bay, depth unknown (Baker, 1980); NEW CALEDONIA: south-eastern New Caledonia, 70–301 m (present study, new locality).

***Remarks.*** — *Asteromorpha tenax* is related to *A. capensis* in sharing polygonal plate-shaped external ossicles densely tessellated on aboral body while *A. rousseaui* and *A. koehleri* have two types of external ossicles on aboral body.

*Asteromorpha tenax* is also related to *A. koehleri* in sharing the same reproductive mode. Of the 16 examined specimens of *A. tenax*, 13 have six arms and the other three have three, four, and five arms. Eleven specimens with six arms and one specimen with four arms show conspicuous fission planes across their discs, suggesting fissiparous reproduction of this species. *A. rousseaui* and *A. capensis* are not fissiparous.

*Asteromorpha tenax* is distinguished from the other three species (*A. capensis*, *A. rousseaui*, and *A. koehleri*) in having large tubercles on the radial shields. One to four diagnostic large tubercles are present on the radial shields of 12 of the 16 examined specimens including specimens with/without fission planes. The other four specimens without the large tubercles have conspicuous fission planes and thus large tubercles may have been lost when their discs divided.

*Asteromorpha tenax* can also be distinguished from the other three species by having a uniformly white body colour (see Colour of *A. capensis*, *A. rousseaui* and *A. koehleri*).

## ACKNOWLEDGEMENTS

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