

# A taxonomic review of the genus *Astrodia* (Echinodermata: Ophiuroidea: Asteronychidae)

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*The genus Astrodia (Echinodermata: Ophiuroidea: Asteronychidae) was revised based on 34 specimens including two syntypes of Asteronyx excavata, two syntypes of Asteronyx plana and two syntypes of Ophiocreas abyssicola. We proposed a transfer of Ophiocreas abyssicola (Euryalidae) to the genus Astrodia. Consequently, Astrodia now includes four species, Astrodia abyssicola, A. excavata, A. plana and A. tenuispina. These four species are all redescribed. A taxonomic key to the species of the genus Astrodia is also provided.*

**Keywords:** brittle star, deep sea, *Ophiocreas*, new combination, taxonomy, redescription

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## INTRODUCTION

The genus *Astrodia* (Ophiuroidea: Euryalida: Asteronychidae) was erected by Verrill (1899) for *Asteronyx tenuispina* Verrill, 1884 and *Asteronyx plana* Lütken & Mortensen, 1899, the former being the genotype. Koehler (1922) described a third species *Astrodia bispinosa* from Southern Australia (Figure 1). Döderlein (1927) transferred *Asteronyx excavata* Lütken and Mortensen, 1899 to this genus. Later, Baker synonymized *Astrodia bispinosa* with *A. tenuispina* in his work on the euryalids from Australia and New Zealand. Consequently, this genus is currently composed of three species, *A. tenuispina* (Verrill, 1884), *A. plana* (Lütken & Mortensen, 1899) and *A. excavata* (Lütken & Mortensen, 1899).

Taxonomic works on *Astrodia* are few. Although *A. tenuispina* was redescribed relatively recently by Baker (1980), the most recent descriptions of the other two species were the original description of Lütken & Mortensen (1899) for *A. excavata* and Döderlein (1927) for *A. plana*. However, these descriptions lacked detailed quantitative accounts of diagnostic characters. Thus, to revise the taxonomy of species within *Astrodia*, detailed redescriptions of the three species, including as many type specimens as possible, were required.

The genus *Astrodia* can be distinguished from the other euryalid genera in lacking hooked arm spines even on the distal part of the arms, but other external features are similar to species of the genus *Ophiocreas* of the Asteroschematinae (Euryalidae) (Fell, 1960; Downey, 1967; Baker, 1980; McKnight, 2000). Arm spines on the distal portion of the arms of *Ophiocreas* are hook-shaped, except for *O. abyssicola* Lyman, 1879 and *O. carnosus* Lyman,

1879. These two species were described without notes on the arm spines on the distal portion of the arms (Lyman, 1879, 1882), and whether they have hooks or not is unknown. *Ophiocreas abyssicola* also has distinct short genital slits which have never been found in other *Ophiocreas* species. The short genital slits are also present in the species of *Astrodia*. However, that this species probably belongs in *Astrodia* has never been discussed.

In this study, we investigate four type specimens and 29 other specimens of *Astrodia* and two type specimens of *Ophiocreas abyssicola*. We conclude that *O. abyssicola* is a species of the genus *Astrodia*. We have designated lectotypes and paralectotypes of *A. excavata* and *A. plana*.

## MATERIALS AND METHODS

The 34 examined specimens in this study are deposited at the Museum of Comparative Zoology at Harvard University, USA (MCZ), the National Museum of Natural History, Smithsonian Institution, USA (USNM), and the National Museum of Nature and Science, Japan (NSMT).

The specimens at NSMT were fixed in 70% ethanol while the fixation methods of all other specimens are unknown.

Arm tips of a specimen of *Ophiocreas abyssicola* (NSMT E-6283) were dissected for examination by scanning electron microscopy (SEM). Ossicles were isolated by immersion in domestic bleach (approximately 5% sodium hypochlorite solution), washed in deionized water, dried in air, and mounted on SEM stubs using double-handed conductive tape. The preparations were sputter-coated with gold-palladium and examined with a HITACHI S-4300 SEM at the Seto Marine Biological Laboratory (Kyoto University).

We followed Kroh (2004), Martynov (2010), Okanishi *et al.* (2011a) and Stöhr *et al.* (2012) on morphological terms and Okanishi *et al.* (2011b) for family-level systematics.

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Length of genital slits against the height of the disc is an important character for the classification of *Astrodia*. In this study, this 'height of the disc' is defined as the length between the distal edge of an oral shield and an aboral disc edge (see Figure 3A).

## SYSTEMATICS

Order EURYALIDA Lamarck, 1816  
 Family ASTERONYCHIDAE Müller & Troschel, 1842  
 Genus *Astrodia* Verrill, 1899  
 (New Japanese name: Hari-kinugasa-moduru Zoku)

*Astrodia* Verrill, 1899: 371; Downey, 1967: 45; Baker, 1980: 15; Paterson, 1985: 13; McKnight, 2000: 15.

### TYPE SPECIES

*Asteronyx tenuispina* Verrill, 1884, by original designation.

### DIAGNOSIS

Maximum of two to four arm spines near each tentacle pore. Arm spines never hooked, cylindrical throughout the arms. Two short genital slits in each interradius. Disc sometimes covered by external ossicles. Lateral furrow of vertebrate declining from aboral distal side to oral proximal side (Fell, 1960; Downey, 1967; Jagt, 2000).

### REMARKS

Based on this study, *Astrodia* is currently composed of four species, *A. abyssicola* (Lyman, 1879), *A. excavata* (Lütken & Mortensen, 1899), *A. plana* (Lütken & Mortensen, 1899) and *A. tenuispina* (Verrill, 1884). A tabular key to the species of *Astrodia* is provided (Table 1).

*Astrodia abyssicola* (Lyman, 1879) comb. nov.  
 (New Japanese name: Hari-kinugasa-moduru)  
 (Figures 2–4)

*Ophiocreas abyssicola* Lyman, 1879: 64–65, pl. 17 figures 470–473; 1880: 45; 1882: 282–283, pl. 32 figures 1–4.

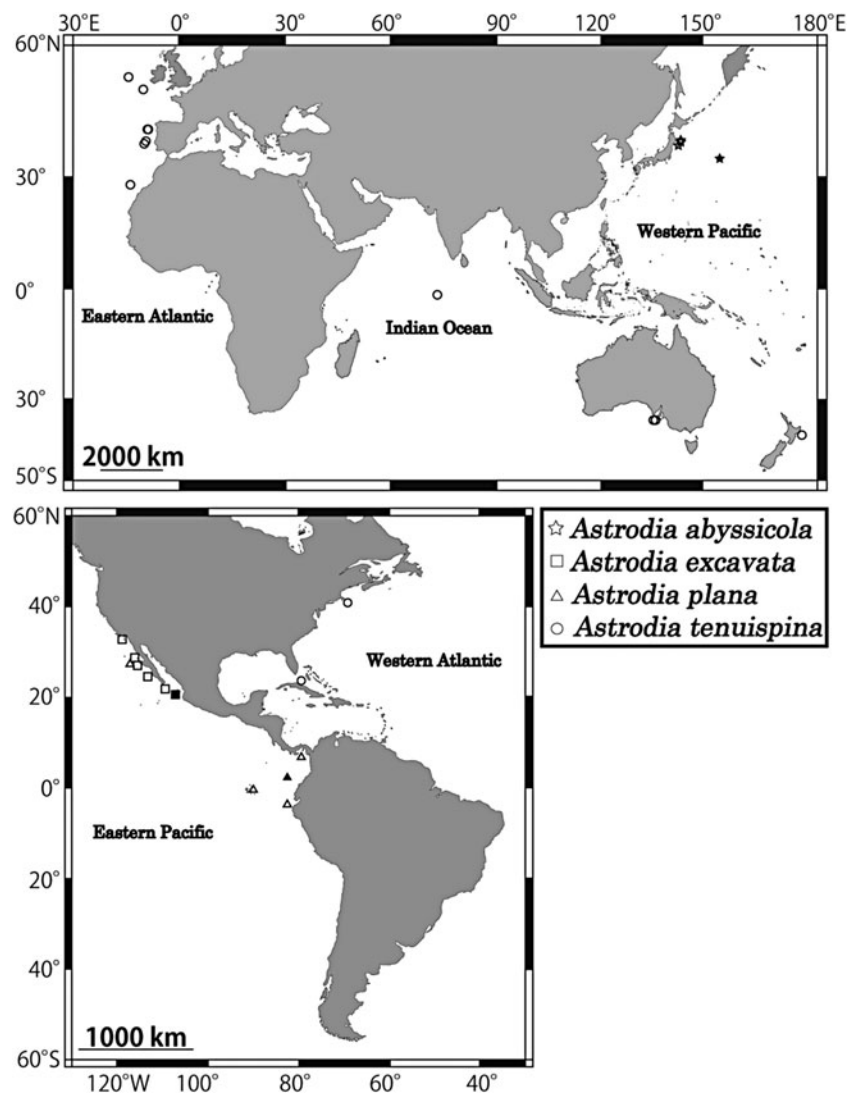


Fig. 1. Known distribution of *Astrodia abyssicola* comb. nov., *A. excavata*, *A. plana* and *A. tenuispina*. Solid marks indicate type localities of each species.

**Table 1.** Tabular key to the species of *Astrodia*.

Species	External ossicles on aboral surface of the disc	Length of genital slits related to the height of the disc	Lateral arm plates on middle to distal portion of arms	
			Shapes	Projections
<i>A. abyssicola</i> (Lyman, 1879)	Plate-shaped on periphery	Short, ~1/5	Oblong	Absent
<i>A. excavata</i> (Lütken & Mortensen, 1899)	Granule-shaped near radial shields and genital slits	Large, ~2/3	Bar like	Present
<i>A. plana</i> (Lütken & Mortensen, 1899)	Absent	Short, ~1/4	Oblong	Absent
<i>A. tenuispina</i> (Verrill, 1884), Type species	Plate shaped on periphery, granule-shaped on centre	Short, ~1/2	Unknown	Absent

*Ophiocreas abyssicolum*. H.L. Clark, 1908: 299; 1915: 177; Downey, 1969: 108.

*Asteroschema (Ophiocreas) abyssicola*. Döderlein, 1911: 113; Matsumoto, 1917: 53.

#### TYPE MATERIAL

*Ophiocreas abyssicola* Lyman, 1879. Two paratypes: dry specimens (HMS 'Challenger', Station 241, North Pacific, east of Japan; 35°41'N 157°42'E water depth: ~4209 m) (MCZ 2826) 23 July 1875. Bottom temperature 1.1°C, red clay.

#### COMPARATIVE MATERIAL EXAMINED

*Ophiocreas abyssicola* Lyman, 1879. Five ethanol specimens: 1 (NSMT E-6257), 4 (NSMT E-6285) specimens; RV 'Soyo-maru', Station Onahama-oki 3 (off Onahama, Japan, 36°57.1'N 142°39.9'E–36°53.6'N 142°36.9'E) collected on 7 August 2007, 4123–4094 m. Twenty-one specimens: 1 (NSMT E-6284), 14 (NSMT E-6286), 2 (NSMT E-6287), 3 (NSMT E-6288), 1 (NSMT E-6289) specimens; RV 'Soyo-maru', Station Kinkasan-oki 3 (off Kinkasan, Japan, 38°29.0'N 143°40.1'E–38°33.2'N 143°41.5'E) collected on 7 August, 2007, 3990–4181 m. One ethanol specimen (NSMT E-6944); RV 'Soyo-maru', Station Taiheiyo 3 (off Miyako, Japan, 39°56.4'N 143°53.0'E) collected on 8 August 2009, 3732–3728 m. One dry specimen (NSMT E-6283); the same locality as NSMT E-6257 and E-6285 mentioned above.

#### DIAGNOSIS

External ossicles separate, granule-shaped, scattered on periphery of disc. Short genital slits on lateral disc, approximately one-fifth of the height of the disc. Lateral arm plates oblong and not projected from the arm surface on middle to distal portion of arms.

#### DISTRIBUTION

North-western Pacific (Type locality: Lyman, 1879); off Pacific coast of north-eastern Japan (present study). Bathymetric range is 3732–4209 m (Figure 1).

#### DESCRIPTION OF PARATYPE (MCZ 2826)

Disc diameter 8 mm, arm length approximately 60 mm (Figure 2A).

*Disc*. Disc pentagonal with slightly notched interradial edges (Figure 2A, C). Aboral surface almost flat, but radial shields and the area around them tumid (Figure 2C). Entirely covered by a thin skin with embedded flat and granule-shaped external ossicles not in contact, 170–220 µm

on periphery of disc (Figure 2D). Radial shields completely covered by skin, oblong, approximately 5.2 mm long and 1 mm wide, not reaching the centre of the disc (Figure 2D).

Oral surface of disc entirely covered by skin (Figure 2E). Jaws cannot be observed because of a gorgonian colony gripped by the paratype (Figure 2E).

Lateral interradial surface of disc entirely covered by skin (Figure 2E). Two genital slits (0.4 mm long and 0.2 mm wide) present on oral side of each interradius. No distinct ossicles suggesting existence of madreporites observed on any oral interradius (Figure 2E).

*Arms*. Arms simple, five in number, no abrupt change in width near the proximal arm (Figure 2A, B). Proximal portion of the arm 1.4 mm wide and 1.5 mm high, with an arched aboral surface and flattened oral surface. Arms tapering gradually toward the arm tip (Figure 2A, F–I).

Arms entirely covered by naked skin (Figures 2F–I, 3A–C). First to third tentacle pores lacking arm spines; fourth to sixth pores with one arm spine (Figure 3A) and following tentacle pores with two arm spines. Arm spines on proximal third of arm ovoid, minute, gradually increasing the length from approximately one-fifth to half length of corresponding arm segment (Figure 3A). On middle third of arm, inner arm spines as long as corresponding arm segment (Figure 2H, I). Outer arm spines half as long as inner arm spines (Figures 2H, I, 3B). On distal third of arm, inner arm spines gradually decreasing to two-thirds the length of the corresponding arm segment (Figures 2I, 3C). Outer arm spines as long as corresponding arm segment (Figure 3C). Except the ovoid arm spines on proximal third of arms within disc, all arm spines cylindrical and bearing fine thorns at their apex. All tentacle pores lacking a sheath around the cylindrical, narrow tube feet (Figures 2E, 3A–C).

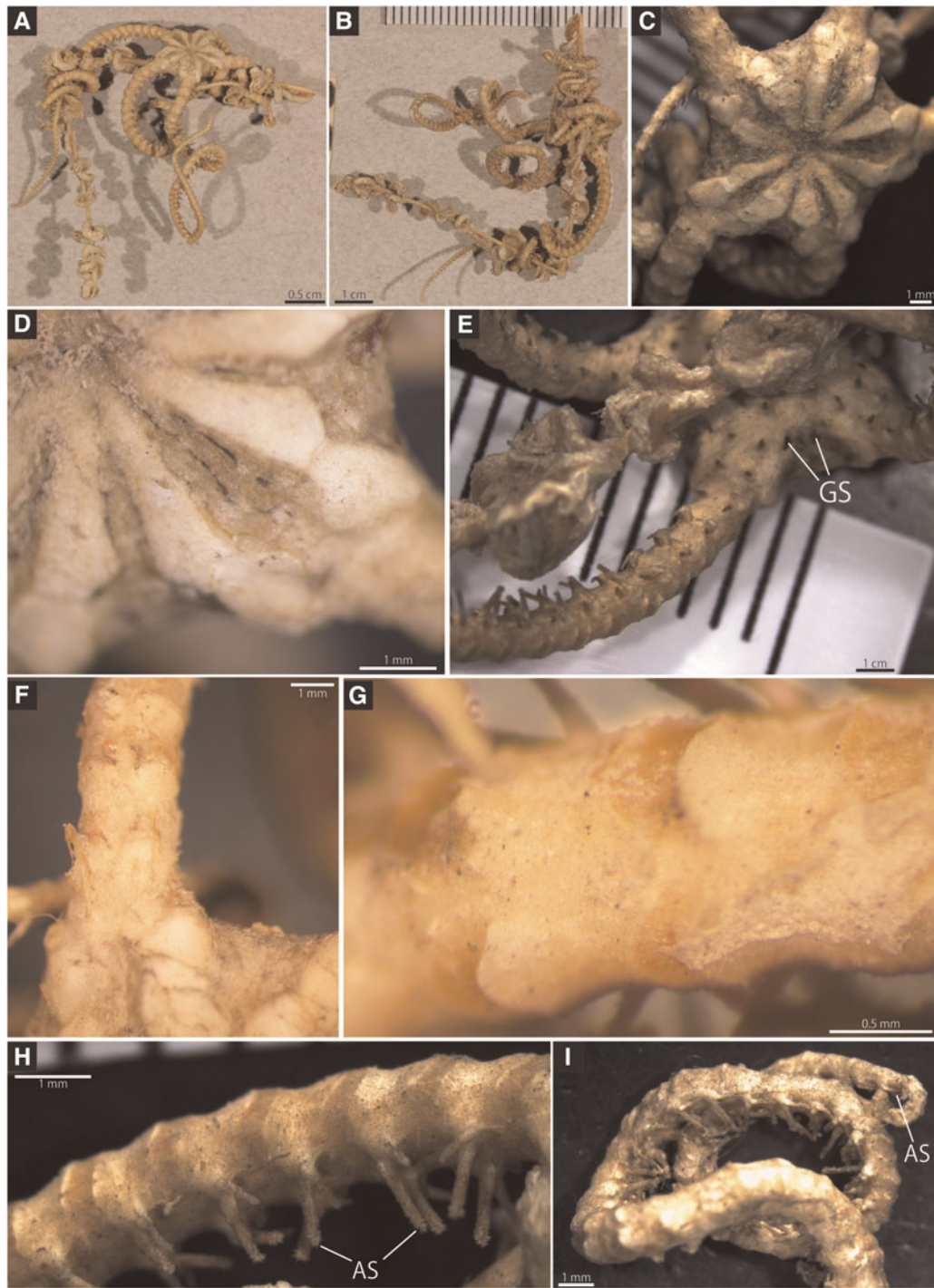
Lateral and ventral arm plates completely concealed by thick skin on proximal to middle portion of arms, but distally skin becoming thinner and lateral arm plates visible (Figure 3C).

*Colour*. Colour on disc, radial shields and oral side white and the other parts brown. Other body parts entirely white (Figure 3).

#### DESCRIPTION OF ANOTHER PARATYPE

MCZ 2826: disc diameter 6.7 mm, arms broken.

Four to five triangular teeth forming a vertical row on a dental plate. Each side of jaw covered by domed granule-shaped oral papillae (Figure 3D, E). Oral shields elliptical and one of them enlarged, as the madreporite (Figure 3D).



**Fig. 2.** *Astrodia abyssicola* (Lyman, 1879) comb. nov., a paratype, disc diameter 8 mm (MCZ 2826). (A) aboral view; (B) oral view; (C) aboral disc and proximal portions of the arms; (D) aboral periphery of the disc; (E) oral and lateral disc and proximal portion of the arms; (F) aboral proximal portion of an arm; (G) aboral middle portion of an arm; (H) lateral middle portion of an arm; (I) middle to distal portion of an arm, lateral view. Abbreviations: AS, arm spine; GS, genital slit.

**OSSICLE MORPHOLOGY OF NSMT E-6283**

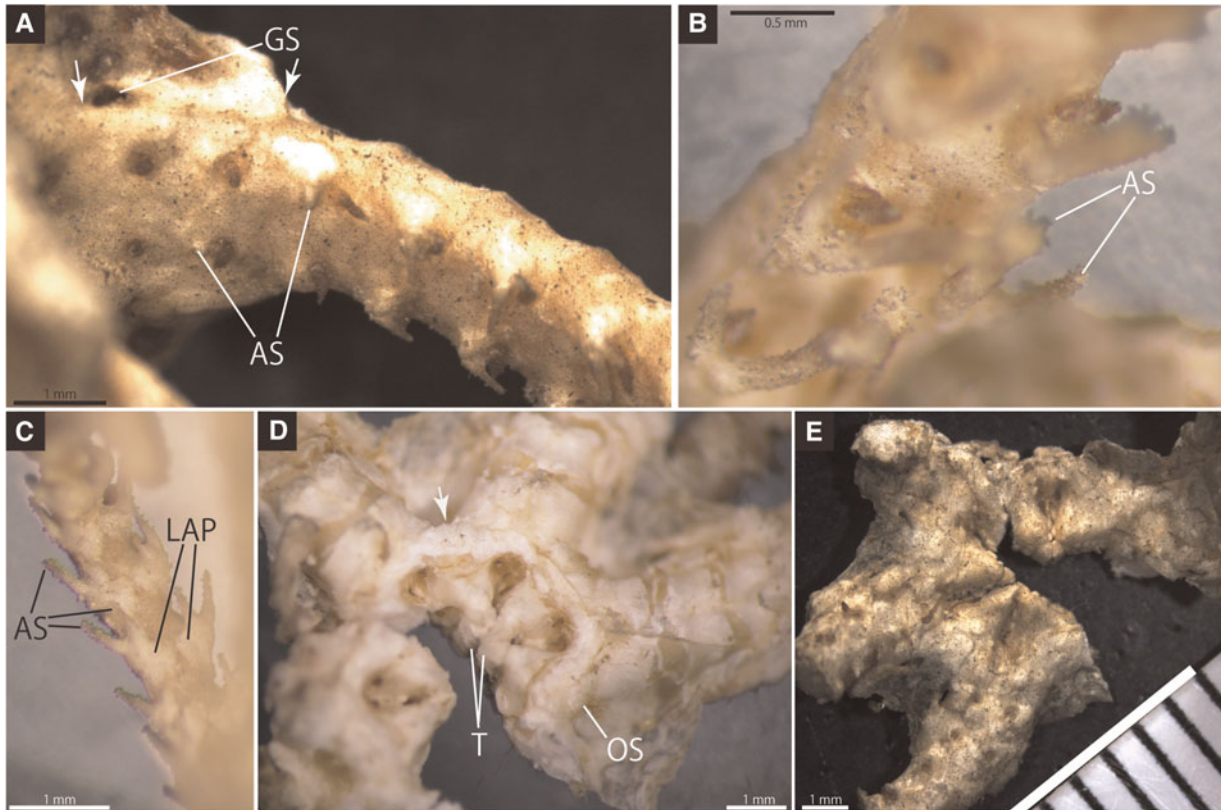
Lateral furrow of vertebrae declining from aboral distal side to oral proximal side (Figure 4A) indicating its affiliation to the family Asteronychidae (Jagt, 2000). Throughout the arms, oral side of each arm vertebra with a longitudinal groove along midline, no oral bridge formed to surround the radial water vessel and nerve (Figure 4B–E).

Arm spines cylindrical, never hooked and bearing fine thorns at tip throughout the arms (Figure 4F–H).

Lateral arm plates associated with two arm spines, each articulation with separate muscle and nerve openings (Figure 4I, J).

**REMARKS**

The families Asteronychidae and Euryalidae (the parent taxon of the subfamily Asteroschematinae) have been distinguished mainly by internal morphological characters, such as arrangements of articulations for teeth on dental plates, positions of



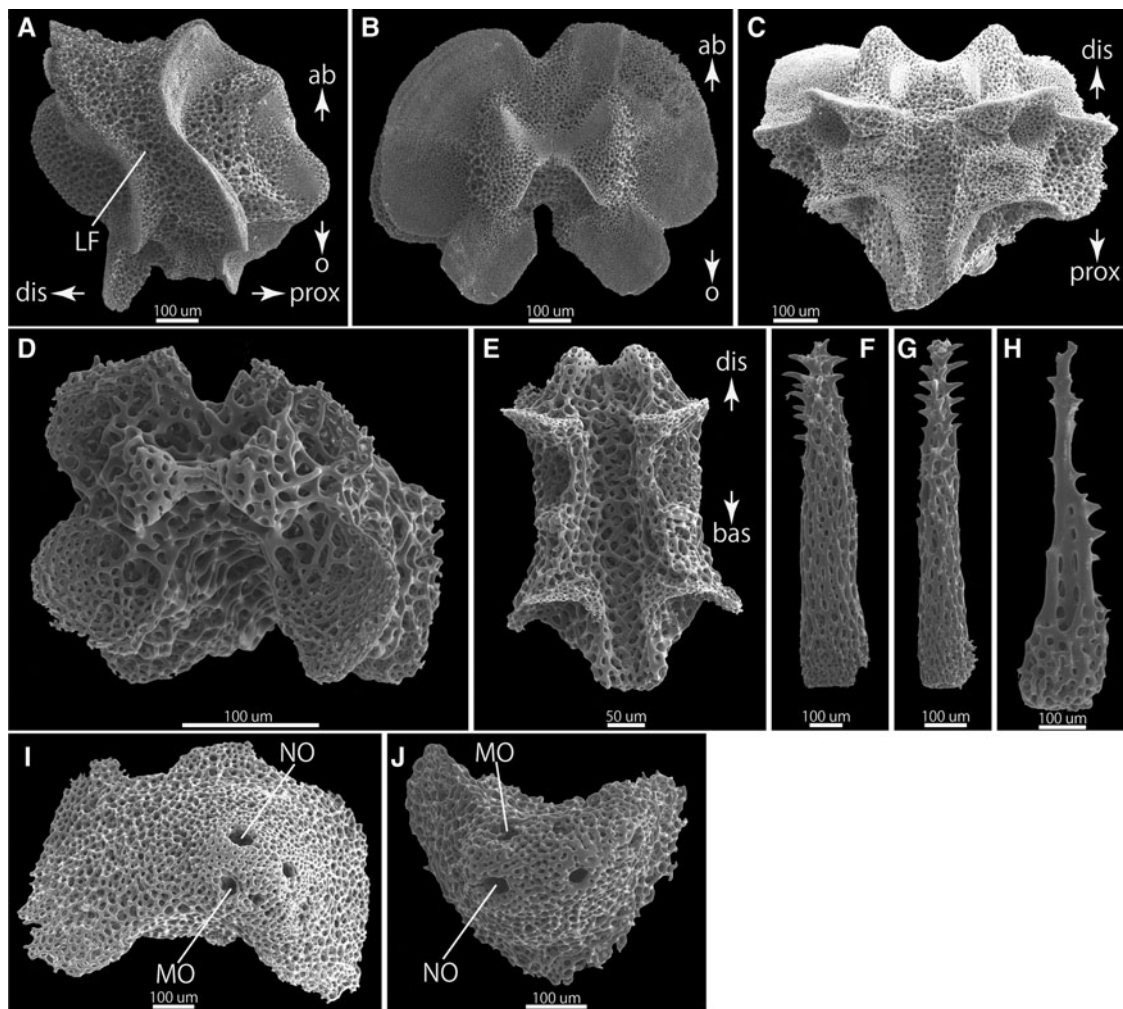
**Fig. 3.** *Astrodia abyssicola* (Lyman, 1879) comb. nov., a paratype, disc diameter 8 mm (A–C) and a paratype, disc diameter 6.7 mm (D, E) (MCZ 2826). (A) oral proximal portion of an arm, arrows indicate a side of oral shield and an aboral disc edge, respectively; (B) oral middle portion of an arm; (C) oral distal portion of an arm; (D) oral disc and proximal portion of the arms, skin removed to show internal ossicles, arrow indicates a madreporite; (E) oral disc and proximal portion of the arms. Abbreviations: AS, arm spine; GS, genital slit; LAP, lateral arm plate; OS, oral shield; T, teeth.

genital plates with respect to the proximal vertebrae, and the presence/absence of extension of gonads into the proximal arms (Fell, 1960; Smith *et al.*, 1995; Okanishi *et al.*, 2011b). Out of the four genera of Asteronychidae, *Asteronyx*, *Astronebris* and *Ophioschiza* can be distinguished from all species of Asteroschematinae by three external characters as well as the internal characters mentioned above: presence/absence of external ossicles of granules, cone or plate-shaped; the maximum number of arm spines near each tentacle pore; and the number of genital slits (Fell, 1960; Downey, 1967; Okanishi *et al.*, 2011a). However, external characters of the genera *Astrodia* and *Ophiocreas* (Asteroschematinae) are very similar and they have not been distinguished from each other by the three external characters. Verrill (1899) found that species of *Astrodia* possess cylindrical arm spines even on the distal portion of the arms and that this was the key diagnostic character of the genus. In contrast, *Ophiocreas* species possess hook-shaped arm spines on the distal portion of the arms. However, before 1899, all descriptions of *Ophiocreas abyssicola* lacked information on the shape of the distal arm spines and therefore it has been difficult to assign this species correctly (Lyman, 1879, 1882). In this study, our morphological observation of two paratypes of *O. abyssicola* (MCZ 2826) showed that they do have cylindrical not hooked arm spines throughout the arms (Figures 2H, I, 3B, C). The lateral furrow in the vertebrae of the Asteronychidae is declined from the aboral distal side to the oral proximal side but those of the Asteroschematinae are not declined (Jagt, 2000). We did not examine the vertebrae of type specimens of *O.*

*abyssicola*, but found that a specimen of *O. abyssicola* collected from Japan (NSMT E-6283) did have declined vertebrae (Figure 4A). We also found an additional diagnostic character to distinguish these genera. The genital slits of *Ophiocreas* are wide and long, almost the same length as the height of the disc, whereas those of *Astrodia* are relatively short, not exceeding two-thirds of the height of the disc. In this study, we recognized that the genital slits of the two paratypes of *O. abyssicola* are short. Therefore, we here propose that *O. abyssicola* should be transferred from Asteroschematinae (Euryalidae) to the genus *Astrodia* of the Asteronychidae. With this transfer, the length of genital slits can be added as a diagnostic character to distinguish Asteronychidae and Asteroschematinae.

*Astrodia abyssicola* comb. nov. resembles *A. excavata* and *A. tenuispina* in having external ossicles on the aboral disc. *Astrodia abyssicola* has scattered flat and round granule-shaped external ossicles on the aboral periphery of the disc while the aboral disc of *Astrodia tenuispina* is covered by granule-shaped external ossicles on its central part and plate-shaped ossicles on its periphery. *Astrodia excavata* is also covered by granule-shaped external ossicles, but they are located only near the radial shields and genital slits. *Astrodia plana* has no external ossicles on the disc (see descriptions of the three species below).

*Astrodia abyssicola* can be distinguished from the other three species also by previously known characters, genital slits and the shape and projection of the lateral arm plates on the middle to distal portion of the arms (Lütken & Mortensen, 1899). The length of the genital slits of *A. abyssicola* is approximately



**Fig. 4.** *Astrodia abyssicola* (Lyman, 1879) comb. nov., (NSMT E-6283), SEM photographs. (A–C) vertebrae from proximal arms, lateral view (A), distal view (B) and oral view (C); (D, E) vertebrae from distal arms, distal view (D) and oral view (E); (F–H) arm spines from proximal (F), middle (G) and distal (H) portions of arms; (I, J) lateral arm plates from proximal (I) and middle (J) arms. Abbreviations. LF, lateral furrow; MO, muscle opening; NO, nerve opening. Arrows indicate the orientation (A, B, C, E). ab, aboral side; prox, proximal side; dis, distal side; o, oral side.

one-fifth of the height of the disc (Figure 3A). In contrast, the length is approximately two-thirds for *A. excavata*, a quarter for *A. plana* and half for *A. tenuispina* (see descriptions of these species below). The lateral arm plates of *A. abyssicola* are oblong and do not project from the oral surface of the arms on the middle to distal portion of the arms, whereas those of *A. excavata* are long, bar-like and distinctly projecting from the oral surface of the arms. The oblong and unprojected lateral arm plates are also present in *A. plana* and *A. tenuispina* (see Remarks on *A. excavata* and Table 1).

*Astrodia* species were known from Australia, New Zealand, Indian Ocean, northern Atlantic and north-eastern Pacific (see Distributions of all four species). The present study revealed that *Astrodia* also occurs in eastern Japan. The geographical distribution of this genus is thus extended to the north-western Pacific.

*Astrodia excavata* (Lütken & Mortensen, 1899)  
(Figures 5–7)

*Asteronyx excavata* Lütken & Mortensen, 1899: 185–186, pl. 22 figures 2–6; H.L. Clark, 1913: 219; 1915: 180; 1923: 157; Campbell, 1921: 49; Downey, 1969: 41.

*Astrodia excavata*. Döderlein, 1927: 59, 98; Caso, 1961: 214; Luke, 1982: 25; Yvonne, 1987: 194, 245.

#### TYPE MATERIAL EXAMINED

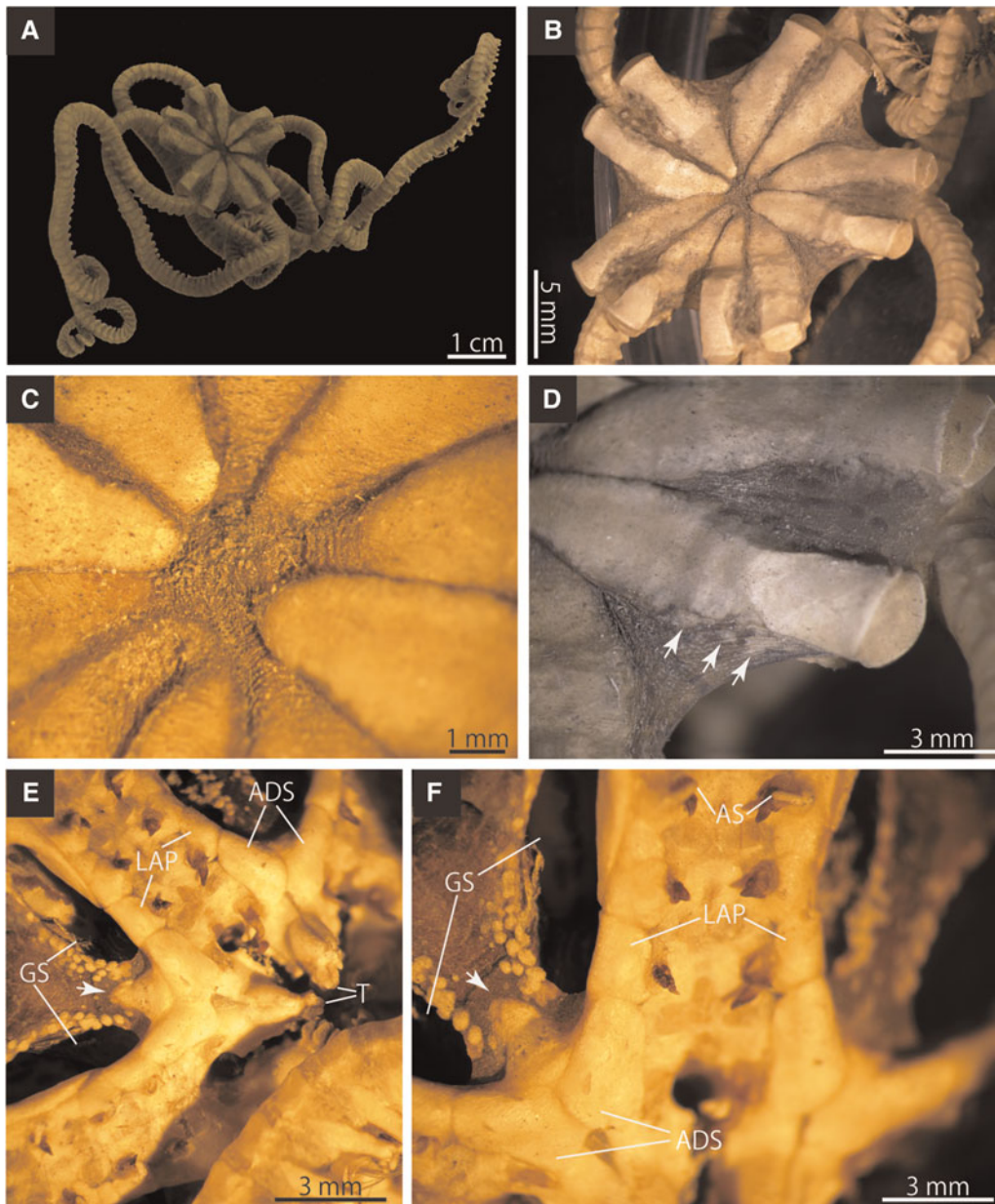
One syntype of *Asteronyx excavata* Lütken & Mortensen, 1899: dry specimen (RV ‘Albatross’, Station 3424, near Tres Marias Islands; water depth: ~1237 m) (MCZ 2817) 1891. One syntype of *Asteronyx excavata* Lütken & Mortensen, 1899: ethanol specimen (RV ‘Albatross’, Station 3426, off Marias Islands, Maria Magdalena Island, 21°21’N 106°25’W; water depth: ~267 m) (USNM 19598) 18 April 1891.

#### DIAGNOSIS

Granule-shaped external ossicles present near radial shields and genital slits. Genital slits long, approximately two-thirds of the height of the disc. Lateral arm plates long, bar-like and projecting from oral surface on middle to distal portion of arms.

#### DISTRIBUTION

Mexico: near Tres Marias Island (Type locality: Lütken & Mortensen, 1899). USA: off California (H.L. Clark, 1923;



**Fig. 5.** *Astrodia excavata* (Lütken & Mortensen, 1899), the lectotype (MCZ 2817). (A) aboral view; (B) aboral disc and proximal portions of the arms; (C) aboral central part of disc; (D) aboral periphery of the disc; (E) jaws; (F) oral and lateral disc and proximal portion of the arms. Abbreviations. AS, arm spine; ADS, adoral shield; GS, genital slit; LAP, lateral arm plate; T, teeth. Arrows indicate external ossicles (D) and madreporites (E, F).

Luke, 1982; Yvonne, 1987). Peru: off Mancora Bank (Yvonne, 1987). Bathymetric range is 267–1273 m (Figure 1).

#### DESIGNATION OF LECTOTYPE AND A PARALECTOTYPE

We designate MCZ 2817 as the lectotype and USNM 19598 as a paralectotype of *Asteronyx excavata* Lütken & Mortensen, 1899. They were collected by a voyage of RV 'Albatross' from Stations 3424 and 3426, respectively. Morphological traits of the lectotype concur with the original description by Lütken & Mortensen (1899).

#### DESCRIPTION OF THE LECTOTYPE (MCZ 2817)

Disc diameter 18 mm, arm length approximately 210 mm (Figure 5A).

**Disc.** Disc five-lobed with notched interradial edges (Figure 5A, B). Aboral surface almost flat, but radial shields and the area around them tumid and depressed centrally (Figure 5B). Entirely covered by a thin skin with some granule-shaped external ossicles, approximately 500–700  $\mu\text{m}$  long, at the lateral edge of each radial shield (Figure 5C, D). Radial shields completely covered by skin, oblong, approximately 6.3 mm long and 2.1 mm wide, almost reaching the centre of the disc (Figure 5B).

Oral surface of disc entirely covered by skin (Figure 5A, B). Spear-head-shaped teeth scattered on dental plate. Each side of jaw covered by domed granule-shaped oral papillae (Figure 5E, F). Oral shields on oral interradius triangular, one of them enlarged as madreporite; adoral shields pentagonal (Figure 5E, F).

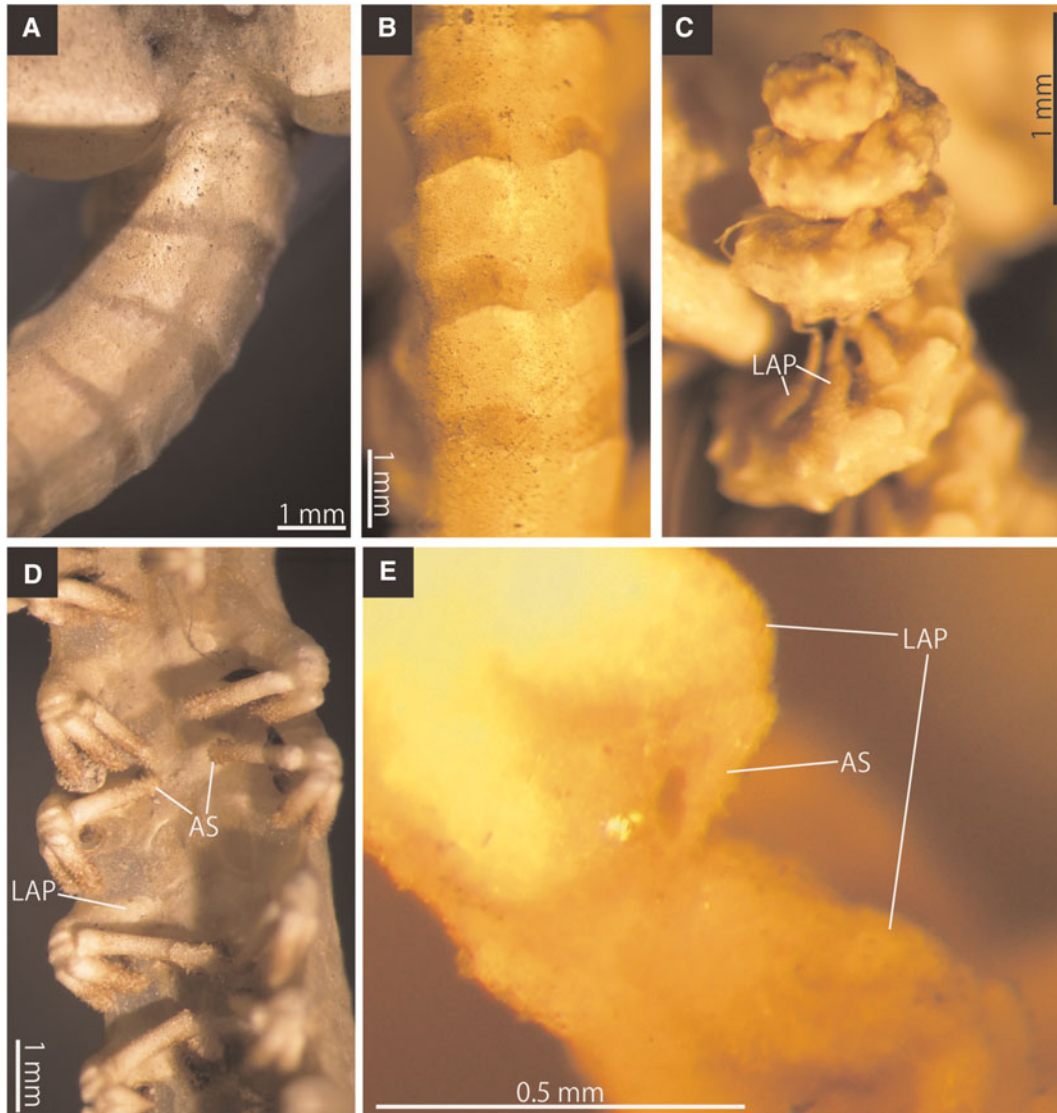


Fig. 6. *Astrodia excavata* (Lütken & Mortensen, 1899), the lectotype (MCZ 2817). (A) aboral proximal portion of an arm; (B) aboral middle portion of an arm; (C) aboral and lateral distal portion of an arm (D) oral middle portion of an arm; (E) lateral distal portion of an arm. Abbreviations: AS, arm spine; LAP, lateral arm plate.

Lateral interradial surface of disc covered by skin (Figure 5E), with several granule-shaped external ossicles, approximately 300–600  $\mu\text{m}$  long, on inner edge of each genital slit (Figure 5E, F). Two genital slits (7.2 mm long and 1.6 mm wide) present on oral side of each interradius (Figure 5E, F).

**Arms.** Arms simple, five in number, no abrupt change in width near the proximal arm (Figure 6A). Proximal arm nearest the disc edge 2.0 mm wide and high, with an arched aboral surface and flattened oral surface. Arms tapering gradually toward the tip (Figure 6A–C).

Arms entirely covered by naked skin (Figure 6). All arm spines cylindrical. First to fourth tentacle pores lacking arm spines; fifth to ninth pores with one arm spine (Figure 5F). On middle third of arm each tentacle pore with three spines. Inner-most arm spines as long as corresponding arm segment and outer two arm spines two-thirds as long as inner spines (Figure 6D). On distal third of arm the number of arm spines at each tentacle pore decreases to two, both

inner and outer arm spines of equal length, half as long as the corresponding arm segment (Figure 6E). All tentacle pores lacking a sheath around the cylindrical, narrow tube feet (Figures 5E, 6D, E).

Lateral arm plates visible throughout the arms. On middle to distal portion of arms, lateral arm plates distinctly projecting from oral surface of arms (Figures 5E, F, 6).

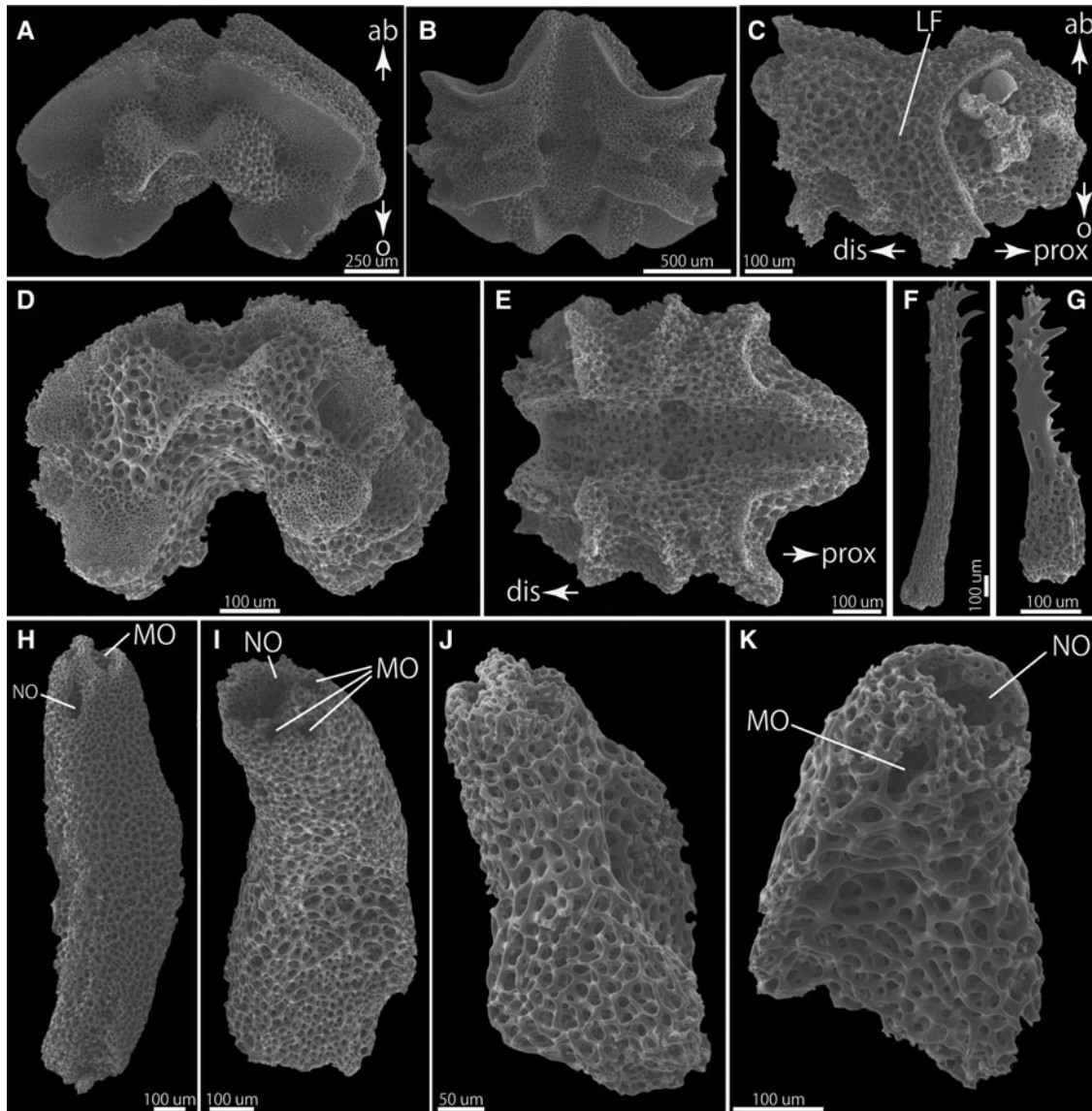
**Colour.** On disc, other than radial shields and lateral side dark brown (Figure 5B, F). The rest of the body white (Figures 5, 6).

#### OSSICLE MORPHOLOGY OF A PARALECTOTYPE (USNM 19598)

Lateral furrow of vertebrae declining obliquely from aboral distal side to oral proximal side (Figure 7C). Throughout the arms, oral side of each vertebra with a longitudinal groove along midline, no oral bridge covering the radial water vessel and nerve (Figure 7A, B, D, E).

Arm spines cylindrical, never hooked and bearing fine thorns at tip throughout the arms (Figure 7F, G).





**Fig. 7.** *Astrodia excavata* (Lütken & Mortensen, 1899), a paralectotype (USNM 19598), SEM photographs. (A, B) vertebrae from proximal arms, distal view (A), oral view (B); (C–E) vertebrae from distal arms, lateral view (C), distal view (D) and oral view (E); (F, G) arm spines from middle portions of arm, inner (F) and outer (G) spines; (H–K) lateral arm plates from proximal (H, I) and middle (J, K) arms. Abbreviations. LF, lateral furrow; MO, muscle opening; NO, nerve opening. Arrows indicate the orientation (A, C, E). ab, aboral side; prox, proximal side; dis, distal side; o, oral side.

Lateral arm plates long (Figure 7F–K), each associated with two or three arm spines and articulations with separate muscle and nerve openings (Figure 7H–K).

#### REMARKS

*Astrodia excavata* can be distinguished from the other species in having granule-shaped external ossicles near the radial shields and genital slits (Figure 5C, D; see descriptions of the three species), distinctly long genital slits, approximately two-thirds of the height of the disc (Figure 5F).

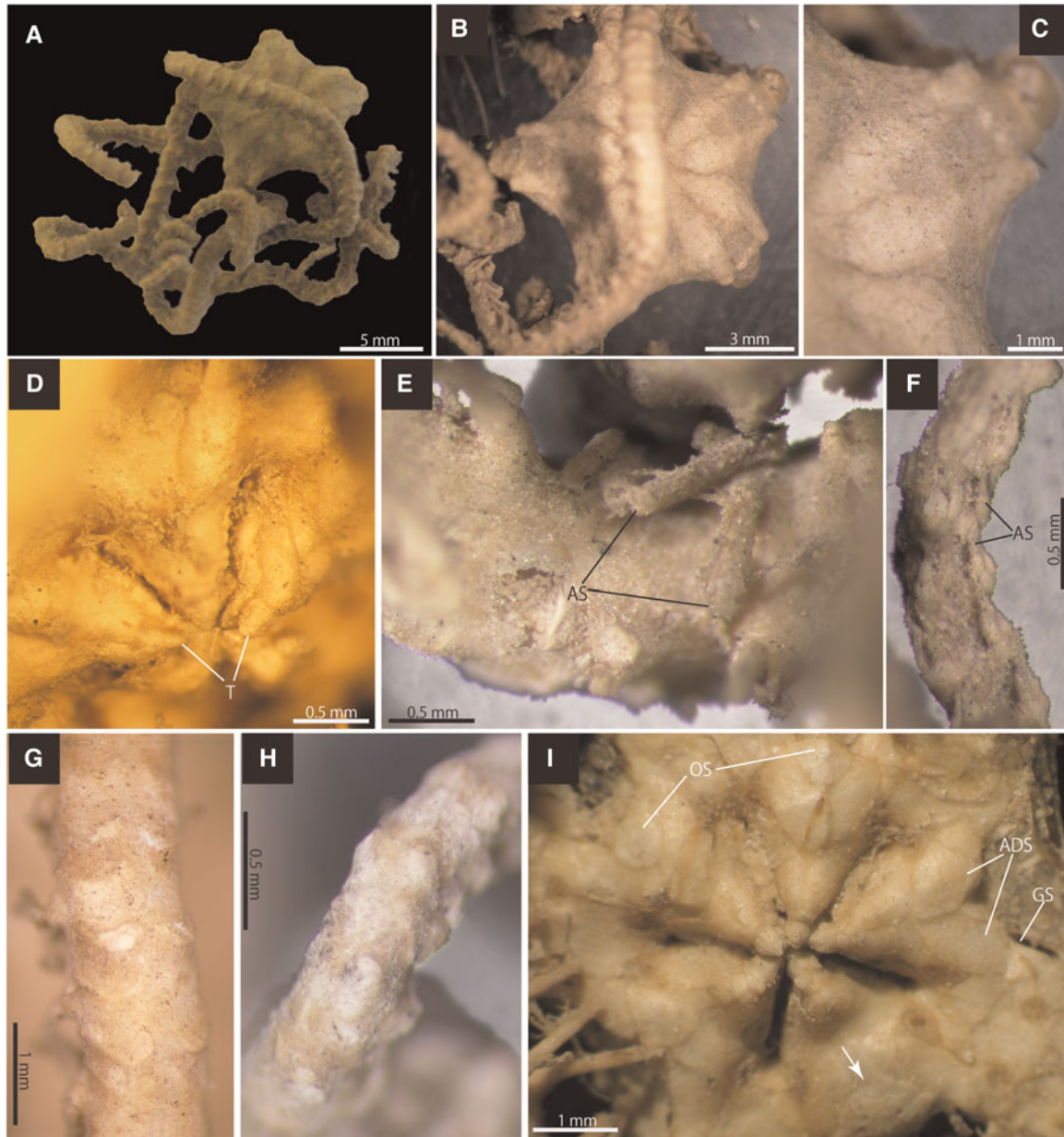
In addition to the two characters above, the shape of the lateral arm plates of *A. excavata* is also characteristic. They are bar-like and the ratio of width to length is approximately 4:4.5 on the middle section (Figure 7H, I), 2.5:3 on the distal section (Figure 7J, K) of the arms, whereas the other species possess shorter lateral arm plates. The ratios for the middle and distal plates are, respectively, approximately 1.5 and 1.2 for *A. abyssicola* (Figure 4I, J) and 1.5 for both for *A. plana*

(Figure 9J, K). Those of *A. tenuispina* were unavailable because the examined specimen (USNM 3730) was not dissected. However, the external appearance of the lateral arm plates on the middle to distal sections of the arms are similar to those of *A. abyssicola* and *A. plana*, rather than *A. excavata* (Figures 3B, C, 6D, E, 8F, 11D, E).

The bar-like lateral arm plates of *A. excavata* project from the oral surface of the arms (Figure 6C–E). The lateral arm plates of the other three species do not project (Figures 3B, C, 8F, 11E) (Table 1).

*Astrodia plana* (Lütken & Mortensen, 1899)  
(Figures 8, 9)

*Asteronyx plana* Lütken & Mortensen, 1899: 186–187, pl. 21 figures 3–4, pl. 22 figures 7–9; H.L. Clark, 1915: 180; Döderlein, 1911: 116.



**Fig. 8.** *Astrodia plana* (Lütken & Mortensen, 1899), the lectotype (MCZ 2824) (A–H) and a paralectotype (USNM 19601) (I). (A) aboral view; (B) aboral disc; (C) aboral periphery of the disc; (D) jaws; (E) oral middle portion of an arm; (F) oral distal portion of an arm; (G) aboral middle portion of an arm; (H) distal middle portion of an arm; (I) oral disc, an arrow indicates a madreporite. Abbreviations: ADS, adoral shield; AS, arm spine; GS, genital slit; OS, oral shield; T, teeth.

*Astrodia plana*. Döderlein, 1927: 69–70, 98 pl. 8 figures 1–2d; Downey, 1969: 43; Bayer *et al.*, 1970: A107, A235; Yvonne, 1987: 194, 245.

#### TYPE MATERIAL EXAMINED

One syntype of *Asteronyx plana* Lütken & Mortensen, 1899: dry specimen (RV 'Albatross', Station 3376, off south-west of Malpelo Island, 3°9'N 82°8'W; water depth: ~2071 m) (MCZ 2824) 1891. One syntype of *Asteronyx plana* Lütken & Mortensen, 1899: dry specimen (RV 'Albatross', Station 3375, off south of Malpelo Island, Colombia, 2°34'N 82°29'W; water depth: ~2197 m) (USNM 19601) 4 March 1891.

#### DIAGNOSIS

No external ossicles on body. Genital slits short, approximately a quarter of the height of the disc. Lateral arm

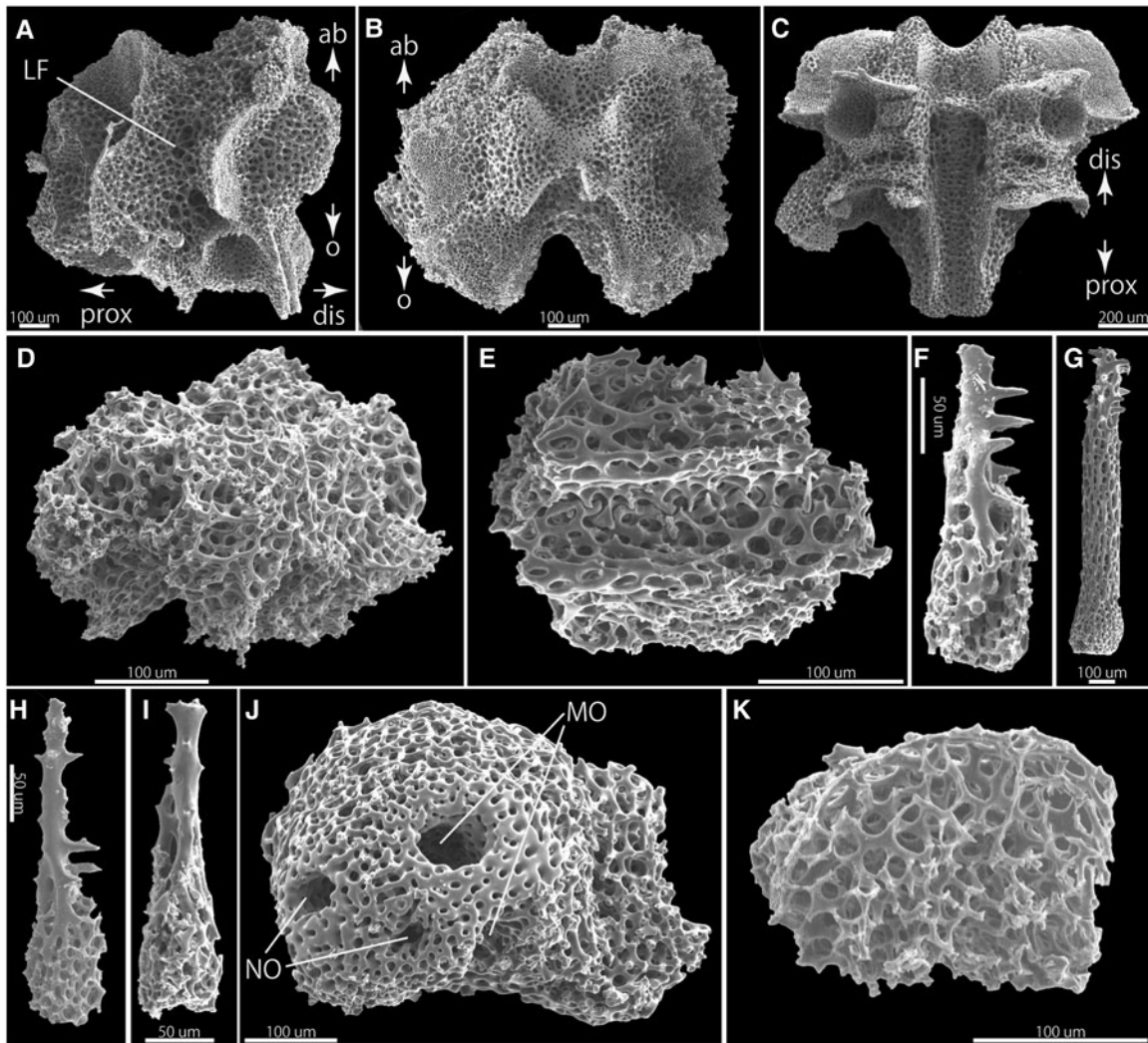
plates oblong and not projecting on middle to distal portion of arms.

#### DISTRIBUTION

Colombia: off Malpelo Island (Lütken & Mortensen, 1899). Panama Bay: (Lütken & Mortensen, 1899; Bayer *et al.*, 1970; Yvonne, 1987). Ecuador: off Galapagos Island (Yvonne, 1987). Bathymetric range is 716–3200 m (Figure 1).

#### DESIGNATION OF THE LECTOTYPE AND A PARALECTOTYPE

We designate MCZ 2824 as the lectotype and USNM 19601 as a paralectotype of *Asteronyx plana* Lütken & Mortensen, 1899. They were collected by a voyage of RV 'Albatross' from Stations 3375 and 3276, respectively. Morphological traits of



**Fig. 9.** *Astrodia plana* (Lütken & Mortensen, 1899), a paralectotype (USNM 19601), SEM photographs. (A–C) vertebrae from middle arms, lateral view (A), distal view (B) and oral view (C); (D, E) vertebrae from distal arms, distal view (D) and oral view (E); (F–I) arm spines from middle portions of arm, inner (F) and outer (G) spines, from distal arm, inner (H) and outer (I) spines; (J, K) lateral arm plates from middle (J) and distal (K) arms. Abbreviations. LF, lateral furrow; MO, muscle opening; NO, nerve opening. Arrows indicate the orientation (A, B, C). ab, aboral side; prox, proximal side; dis, distal side; o, oral side.

the lectotype concur with the original description by Lütken & Mortensen (1899).

#### DESCRIPTION OF THE LECTOTYPE (MCZ 2824)

Disc diameter 9.7 mm, arm length approximately 100 mm (Figure 8A).

**Disc.** Disc pentagonal with slightly notched interradiar edges (Figure 8A). Aboral surface hemisphaeroid, but radial shields and the area around them tumid (Figure 8A–C). Entirely covered by a thin skin and lacking external ossicles. Radial shields completely covered by skin, oblong, approximately 4.2 mm long and 1.4 mm wide in centre and 0.4 mm wide at periphery, almost reaching the disc centre (Figure 8A, B).

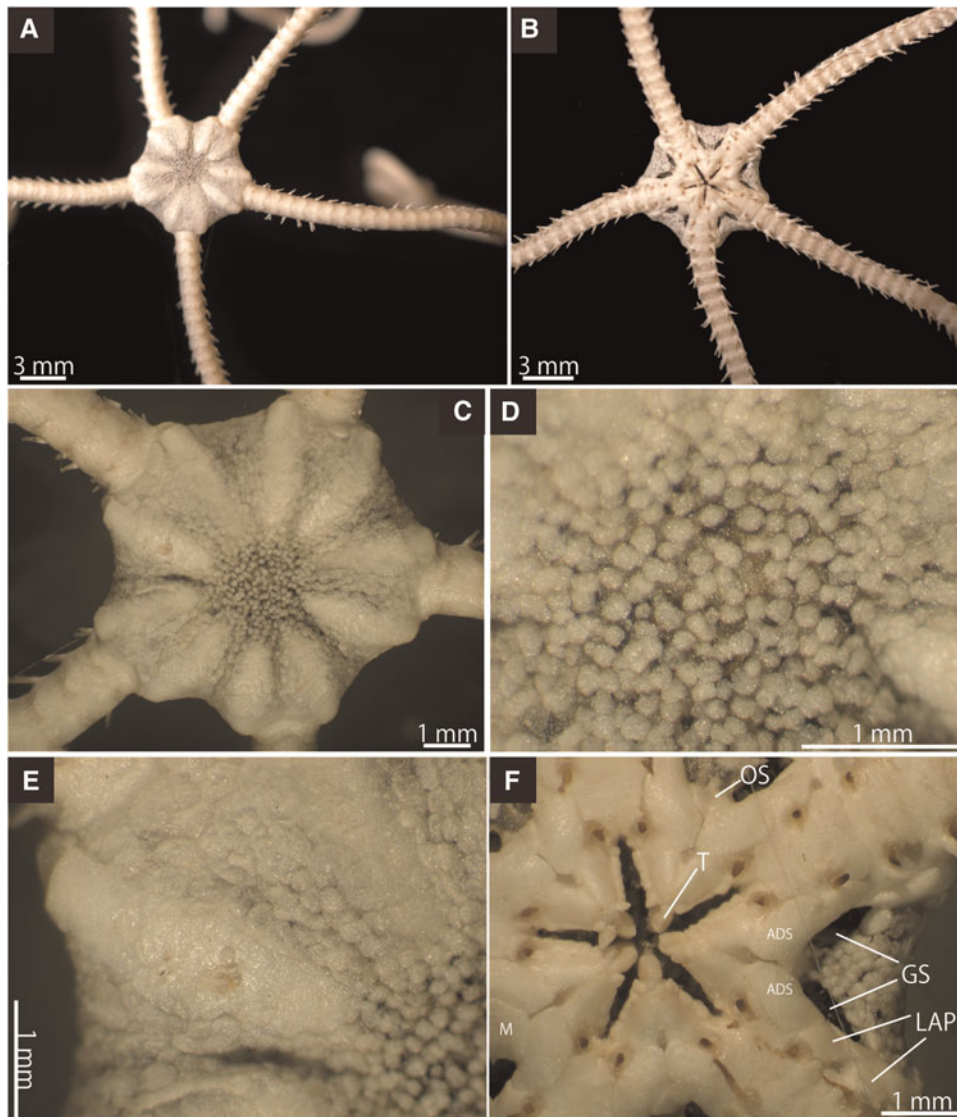
Oral surface of disc entirely covered by skin (Figure 8D). Triangular teeth vertically on dental plate and each side of jaw covered by domed granule-shaped oral papillae (Figure 9D).

Lateral interradiar surface of disc covered by skin, two genital slits present on each oral interradius.

**Arms.** Arms simple, five in number, no abrupt change in width near the proximal arm (Figure 9A). The proximal portion of the arm 1.4 mm wide and 1.0 mm high, with an arched aboral surface and flattened oral surface. Arms tapering gradually toward their tip (Figure 9A, E–H).

Arms entirely covered by naked skin (Figure 9E–H). First to fourth tentacle pores lacking arm spines; following pores with one to three arm spines (Figure 9E, F). All arm spines cylindrical. On proximal third of arm, inner-most spines approximately two-thirds as long or equal to corresponding arm segment. On middle third of arm, each tentacle pore with three arm spines. Inner-most arm spines to 1.5 times as long as corresponding arm segment and outer two arm spines two-thirds as long as inner spines (Figure 8E). On distal third of arm, the number of arm spines on each tentacle pore decreasing to two (Figure 8F). Inner arm spines as long as corresponding arm segments, outer spines two-thirds as long as inner spines (Figure 8F). All tentacle pores lacking a sheath around the cylindrical, narrow tube feet (Figure 8D, E).

Lateral arm plate visible on distal arms, not distinctly projecting from oral surface of arms (Figure 8E, F).



**Fig. 10.** *Astrodia tenuispina* (Verrill, 1884) (USNM 3730). (A) aboral view; (B) oral view; (C) aboral disc and proximal portions of the arms; (D) aboral central part of the disc; (E) aboral periphery of the disc; (F) oral and lateral disc and proximal portion of the arms. Abbreviations: ADS, adoral shield; GS, genital slit; LAP, lateral arm plate; M, madreporite; OS, oral shield; T, teeth.

**Colour.** Whole body greyish-white (Figure 8A–H).

**DESCRIPTION OF PARALECTOTYPE (USNM 19601)**

Disc diameter 5.0 mm (Figure 8I).

Oral shields triangular and one of them enlarged, as madreporite. Adoral shields oblong. Two genital slits (0.7 mm long and 0.07 mm wide) present on each oral interradius (Figure 9I).

Lateral furrow of vertebrae declining aboral–proximally (Figure 9A). Throughout the arms, oral side of each arm vertebra with a longitudinal groove along midline, no oral bridge (Figure 9B–E).

Arm spine cylindrical, never hooked and bearing fine thorns at tip throughout the arms (Figure 9F–I).

Each lateral arm plate spine articulation with separate muscle and nerve openings (Figure 9J, K).

**REMARKS**

*Astrodia plana* can be distinguished from the other species in having no external ossicles (Figure 8), short genital slits,

approximately a quarter of the height of the disc (Figure 8I), oblong and unprojected lateral arm plates on the middle to distal sections of the arms (Figures 8F, 9J, K) (Table 1).

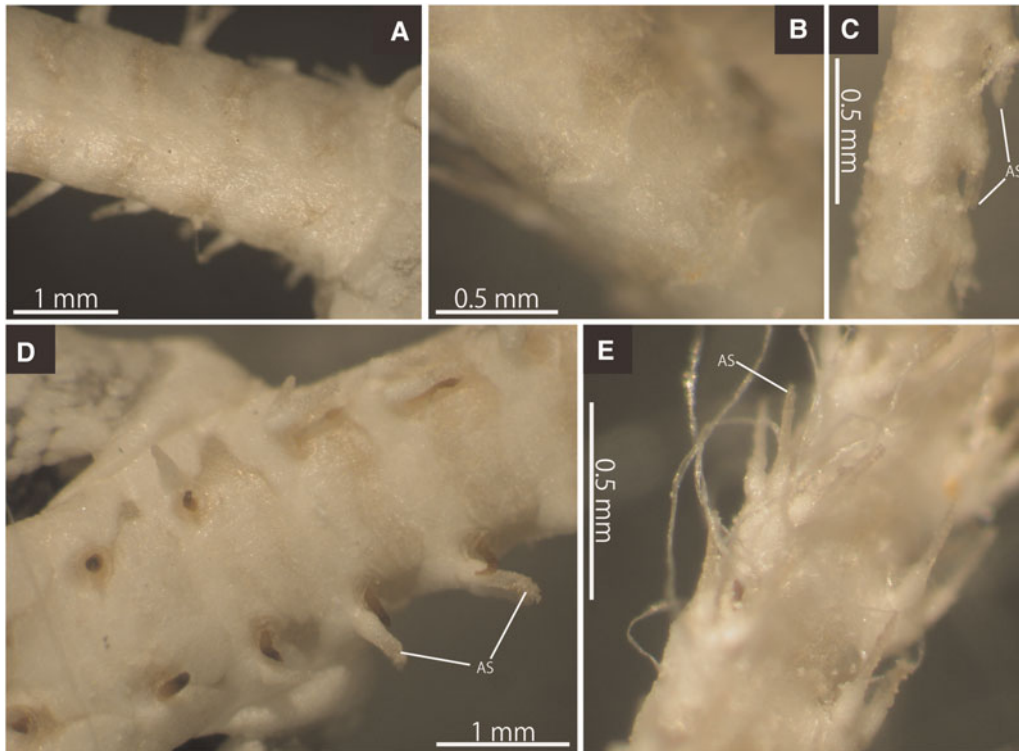
*Astrodia tenuispina* (Verrill, 1884)  
(Figures 10, 11)

*Astronyx tenuispina*. Verrill, 1884: 219.

*Hemieuryale tenuispina*. Verrill, 1885: 550.

*Astrodia tenuispina*. Verrill, 1899: 371, pl. 21 figures 48–50; Koehler, 1906: 6, 33, 34, pl. 3 figures 48–50; 1907: 304, pl. 21 figures 48–50; Döderlein, 1911: 116; 1927: 59, 97; 1930: 385–387, pl. 3 figures 2, 3, 3a, 4; H.L. Clark, 1941: 75; Madsen, 1967: 141; Downey, 1969: 50; Baker, 1980: 18–20, figure 3, 29; Gage *et al.*, 1983: 287; Paterson, 1985: 15, 16, figure 9a–d; Rowe & Gates, 1995: 356; McKnight, 2000: 15, pl. 2.

*Astrodia bispinosa* Koehler, 1922: 11, 12 pl. 76 figures 12–15; Döderlein, 1927: 98; 1930: 387; Madsen, 1967: 141; Baker, 1980: 18; Rowe & Gates, 1995: 356.



**Fig. 11.** *Astrodia tenuispina* (Verrill, 1884) (USNM 3730). (A) aboral proximal portion of an arm; (B) aboral middle portion of an arm; (C) aboral distal portion of an arm; (D) oral proximal portion of an arm; (E) oral middle portion of an arm. Abbreviation: AS, arm spine.

#### MATERIAL EXAMINED

*Astrodia tenuispina* (Verrill, 1884). One dry specimen (USNM 3730); RV 'Caroline', Johnson–Smithsonian Expedition Puerto Rico Caribbean Sea, collected in 1933.

#### DIAGNOSIS

External ossicles on aboral disc in contact, plate-shaped on periphery and separate, granule-shaped on central part of disc. Genital slits short, approximately half of the height of the disc. Lateral arm plates not projecting on middle to distal portion of arms.

#### DISTRIBUTION

North America; off Nantucket Islands (Verrill, 1884; Downey, 1969). Caribbean Sea; off Puerto Rico (this study); Iberia Peninsula; western Portuguese; western Spain (Koehler, 1907; Paterson, 1995); Ireland: western Ireland (Gage *et al.*, 1983; Paterson, 1995). Gulf of Mexico: southern Cay Sal Bank, Nicholas Channel (Clark, 1941). Australia; western Kangaroo Island (Koehler, 1922; Baker, 1980). New Zealand; east coast of North Island (McKnight, 2000). Maldive Islands (Döderlein, 1927). The Canary Islands; southern Canary Islands (Döderlein, 1930). Bathymetric range is 512–3548 m (Figure 1).

#### DESCRIPTION OF A USNM SPECIMEN (USNM 3730)

Disc diameter 7.2 mm, arm length approximately 60 mm (Figure 10A).

**Disc.** Disc pentagonal with slightly notched interradial edges (Figure 10A, B). Aboral surface almost flat, but radial

shields and the area around them tumid (Figure 10C). Central disc covered by granule-shaped external ossicles, approximately 120–140  $\mu\text{m}$  (Figure 10D). Peripheral disc covered by plate-shaped external ossicles, approximately 200  $\mu\text{m}$  (Figure 10E). External ossicles covered by a thin skin. Radial shields completely covered by external ossicles, oblong, approximately 3.0 mm long and 1.0 mm wide, not reaching the centre of the disc (Figure 10E).

Oral surface of disc entirely covered by skin (Figure 10F). Spear-head shaped teeth vertically on dental plate. Each side of jaw covered by domed granule-shaped oral papillae (Figure 10F). Oral shields triangular on an oral interradius, one of them enlarged as madreporite (Figure 10F). Adoral shields pentagonal and oblong (Figure 10F).

Lateral interradial surface of disc covered by plate-shaped external ossicles, approximately 200  $\mu\text{m}$  (Figure 10F). Two genital slits (1.0 mm long and 0.2 mm wide) present on oral side of each interradius (Figure 10F).

**Arms.** Arms simple, five in number, no abrupt change in width near the proximal arm (Figures 10A, 11A). Proximal portion of the arm 1.7 mm wide and high, with an arched aboral surface and flattened oral surface. Arms tapering gradually toward their tip (Figure 11).

On the aboral surface, proximal arms covered by plate-shaped external ossicles, approximately 250  $\mu\text{m}$  (Figure 11A). Oral surface from the proximal arms to the tip covered by naked skin (Figure 11B–E). First to fourth tentacle pores lacking arm spines; fifth and sixth pores with one arm spine (Figure 11D). All arm spines cylindrical. Two arm spines with each tentacle pore, of equal length, approximately two-thirds as long as corresponding arm segment (Figure 11D). On middle third of arms each tentacle pore

with three arm spines, of equal length, two-thirds as long as corresponding arm segment (Figure 11E). On distal third of arms, the number of arm spines on each tentacle pore decreasing to two, both arm spines half as long as the corresponding arm segment (Figure 11C). Each tentacle pore with a low sheath and a tube foot extruding through the sheath (Figure 11D, E).

Lateral arm plates visible throughout the arms, not projecting from oral surface of arms (Figure 11D, E).

**Colour.** Basically externally white except in disc centre, where dark brown skin is visible between granule-shaped external ossicles (Figure 10A, B).

#### REMARKS

*Astrodia tenuispina* can be distinguished from the other species in having external ossicles on the aboral and lateral surface of disc and aboral proximal portion of arms (Figure 10D, E), short genital slits, approximately half of the height of the disc (Figure 10F), not projecting lateral arm plates on middle to distal portion of arms (Figure 10D, E) (Table 1).

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