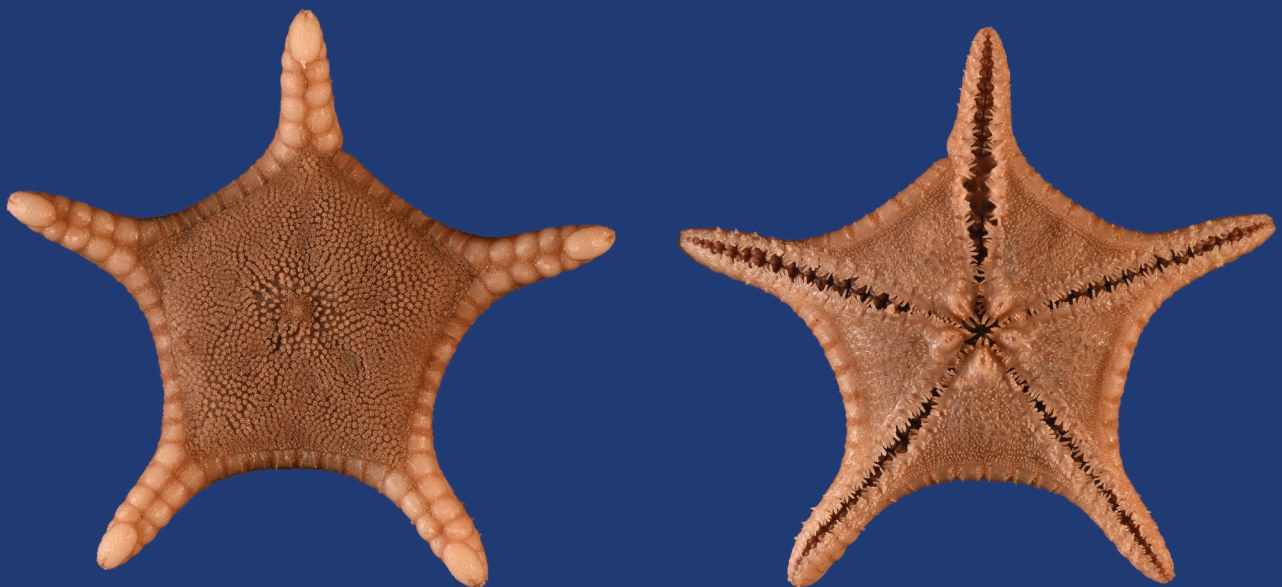


Revision of the genus *Benthogenia* Fisher, 1911
(Asteroidea, Echinodermata), with description
of a new species and ossicle anatomy

Marine FAU



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Benthogenia mahi n. sp. in abactinal and actinal view.

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Revision of the genus *Benthenia* Fisher, 1911 (Asteroidea, Echinodermata), with description of a new species and ossicle anatomy

Marine FAU

Department of Paleobiology,
National Museum of Natural History, Smithsonian Institution,
10th Street and Constitution Avenue, NW
Washington, DC 20560 (United States of America)
faum@si.edu (corresponding author)

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ABSTRACT

Porcellanasteridae Sladen, 1883 is a family of mud-dwelling sea stars, living in bathyal and abyssal environments. Among the twelve currently recognized genera of this family, *Benthenia* Fisher, 1911 is the only one known occurring at depth shallower than 1000 m. *Benthenia* differs from all other porcellanasterids by having cribriform organs between all its marginals, from the disc to the tip of the arms. *Benthenia cribellosa* Fisher, 1911 is reported from a locality as shallow as 111 m, and a new species, *Benthenia mahi* n. sp., is described from material housed in the Muséum national d'Histoire naturelle, Paris (MNHN). *Benthenia mahi* n. sp. is represented by twelve specimens, collected at depth ranging from 400 to 1200 m during four different expeditions. *Benthenia cribellosa* is represented by two specimens from the MNHN, plus the holotype and two specimens from the National Museum of Natural History (Smithsonian Institution), Washington D.C. *Benthenia mahi* n. sp. differs from *B. cribellosa* mostly by having more robust arms, fewer oral and adambulacral spines, and by the cribriform organs not covering the entire surface of the supermarginals of the disc. Molecular data (16S rDNA) were also used as an independent dataset to test for divergence between the two species. *Benthenia mahi* n. sp. occurs in New Caledonia, Solomon Islands and Vanuatu, whereas *B. cribellosa* is only known from the Philippines. Detailed descriptions of both species are provided, as well as a detailed description of the skeleton of the new species.

KEY WORDS

Porcellanasteridae,
deep-sea fauna,
systematics,
anatomy,
new species.

RÉSUMÉ

Révision du genre *Benthogenia* Fisher, 1911 (Asteroidea, Echinodermata), avec la description d'une nouvelle espèce et de l'anatomie des ossicules.

Porcellanasteridae Sladen, 1883 est une famille d'étoiles de mer vivant ensevelie dans le sédiment dans des environnements bathyaux et abyssaux. Parmi les douze genres actuellement reconnus au sein de cette famille, *Benthogenia* Fisher, 1911 est le seul à avoir été signalé à des profondeurs inférieures à 1000 m. *Benthogenia* diffère de tous les autres porcellanastéridés par la présence d'organes cribriiformes entre toutes ses plaques marginales, du disque à l'extrémité des bras. *Benthogenia cribellosa* Fischer, 1911 est signalée dans une localité aussi peu profonde que 111 m, et une nouvelle espèce, *Benthogenia mabi* n. sp., est décrite à partir de matériel conservé au Muséum national d'Histoire naturelle, Paris (MNHN). *Benthogenia mabi* n. sp. est représenté par douze spécimens, collectés au cours de quatre expéditions différentes à des profondeurs allant de 400 à 1200 m. *Benthogenia cribellosa* est représentée par deux spécimens du MNHN, plus l'holotype et deux autres spécimens conservés au National Museum of Natural History (Smithsonian Institution), Washington D.C. *Benthogenia mabi* n. sp. diffère de *B. cribellosa* principalement par ses bras plus robustes, moins de piquants oraux et adambulacraires, et par les organes cribriiformes ne couvrant pas toute la surface des plaques supéromarginales du disque. Des données moléculaires (ADNR 16S) ont également été collectées pour tester la divergence entre les deux espèces. *Benthogenia mabi* n. sp. est présent en Nouvelle-Calédonie, aux Îles Salomon et au Vanuatu, alors que *B. cribellosa* n'est connue qu'aux Philippines. Des descriptions détaillées des deux espèces sont fournies, ainsi qu'une description détaillée du squelette de la nouvelle espèce.

MOTS CLÉS
Porcellanasteridae,
faune des grands fonds,
systématique,
anatomie,
espèce nouvelle.

INTRODUCTION

The Porcellanasteridae Sladen, 1883 is a family of deep-sea infaunal sea stars, belonging to the order Paxillosida Perrier, 1884. The family currently comprises 12 genera and 31 extant species (Mah & Blake 2012; Mah 2023). The monotypic genus *Benthogenia* Fisher, 1911 was first described by Fisher (1911) from one specimen, the holotype of *Benthogenia cribellosa* Fisher, 1911, collected in the Philippines by the U. S. Fisheries steamer *Albatross* in 1909. Porcellanasterids occur at depths ranging between 1000 to 7000 m (Mironov *et al.* 2016), *Benthogenia* is unusual because it is the only porcellanasterid that occurs at depths shallower than 1000 m (Fisher 1911, 1919; Madsen 1961; Clark & Downey 1992; Mironov *et al.* 2016). In the present study are reported new occurrences of *B. cribellosa* at depth as shallow as 111 m (Table 1), and a new species from the Solomon Islands. The geographic distribution of the genus is also discussed.

The phylogenetic affinities of *Benthogenia* are still unclear. Madsen (1961) suggested that the Porcellanasteridae could have evolved through pedomorphosis, implying that the species with the simplest morphology was the most derived. This hypothesis would support *Benthogenia*, the only porcellanasterids to have cribriform organs on all its marginals, as the most plesiomorphic genus. Madsen (1961) also hypothesized that the ancestor of the Porcellanasteridae most likely had cribriform organs on all its marginals similar to the Gonioplectinidae Verrill, 1889 and the fascioles of the Astropectinidae Gray, 1840. However, Madsen (1961) did not observe any *Benthogenia* specimens. On the other hand, Belyaev (1969, 1985) suggested that porcellanasterids with the most complex morphology were the most derived. More recently, Mironov *et al.* (2016) concluded that porcellanasterids evolved through morphological simplification, among

which are the reduction of papulae and paxillae, decrease in the number of cribriform organs, reduction of body size, and retention of juvenile characters by adults. However, this conclusion was challenged by Petrov *et al.* (2016)'s phylogenetic analysis. Here is provided new insight into the anatomy of the genus *Benthogenia*, with the first detailed description of internal ossicles for the family Porcellanasteridae.

MATERIAL AND METHODS

TAXON SAMPLING

The specimens were collected during six different surveys MUSORSTOM 3 (Philippines), PANGLAO 2005 (Philippines), MUSORSTOM 8 (Vanuatu), CONCALIS (New Caledonia), BATHUS (New Caledonia), SALOMONBOA 3 (Solomon Island), and are housed in the Muséum national d'Histoire naturelle (MNHN), Paris, France. In total, 17 individuals represented by 14 lots were studied. Complete specimens information is presented in Table 1. DNA data were extracted from the only six specimens preserved in alcohol. The holotype of *Benthogenia cribellosa*, and two additional specimens housed at the National Museum of Natural History (USNM), Washington DC, United States were studied for comparison.

DISSECTION AND TERMINOLOGY

One arm from MNHN-IE-2013-2199 was dissected to study ossicle anatomy following protocols described in Fau & Villier (2018, 2020). The arm was immersed in a dilute solution of sodium hypochlorite (bleach), rinsed, dried, and the isolated ossicles were then mounted on scanning electron microscope (SEM) stubs. Samples were SEM imaged using a Hitachi TM3000 (Centre de Recherche en Paléontologie de Paris, France (CR2P)).

TABLE 1. — List of specimens investigated.

Collection number	ID	Country	GPS coordinate	Depth (m)	Dry/ wet	Measurements R/r (mm)	Remarks/ GenBank
							accession no.
USNM 28655	<i>Benthogenia cribellosa</i> Fisher, 1911	Philippines	8°16'45"N, 124°02'48"E	924	alcohol	R = 75/r = 33	holotype
USNM 40412	<i>Benthogenia cribellosa</i>	Philippines	9°37'45.1"N, 121°10'58.8"E	905	alcohol	R = 12	–
USNM 40417	<i>Benthogenia cribellosa</i>	Philippines	9°37'45.1"N, 121°10'58.8"E	905	alcohol	R = 5.5	2 individuals, gut content of <i>Prionaster gracilis</i>
MNHN-IE-2019-3848	<i>Benthogenia cribellosa</i>	Philippines	14°01'12.0"N, 120°16'48.0"E	111-115	dry	R = 60/r = 31	–
MNHN-IE-2007-1828	<i>Benthogenia cribellosa</i>	Philippines	9°16'48.0"N, 123°22'48.0"E	784-786	alcohol	R = 72/r = 27	OR802153
MNHN-IE-2019-3811	<i>Benthogenia mahi</i> n. sp.	Vanuatu	17°49'54.0"S, 168°11'31.2"E	547-585	dry	R = 16/r = 9	–
MNHN-IE-2019-3879	<i>Benthogenia mahi</i> n. sp.	Vanuatu	16°53'37.2"S, 168°10'29.4"E	486-494	dry	R = 65/r = 27	–
MNHN-IE-2007-1580	<i>Benthogenia mahi</i> n. sp.	New Caledonia	20°16'58.8"S, 163°49'20.4"E	650-1200	alcohol	R = 27/r = 13	OR802151
MNHN-IE-2009-2066	<i>Benthogenia mahi</i> n. sp.	New Caledonia	20°34'00.6"S, 164°57'10.8"E	497-520	dry	R = 18/r = 8	–
MNHN-IE-2007-1335	<i>Benthogenia mahi</i> n. sp.	Solomon Islands	10°44'32.4"S, 162°19'39.0"E	410-430	alcohol	R = 70.5/r = 30	OR802152
MNHN-IE-2013-2199	<i>Benthogenia mahi</i> n. sp.	Solomon Islands	9°34'53.4"S, 160°47'09.0"E	414-456	alcohol	R = 67/r = 31	OR802149/ dissected
MNHN-IE-2013-2216	<i>Benthogenia mahi</i> n. sp.	Solomon Islands	10°25'45.0"S, 161°21'57.6"E	381-422	alcohol	R = 69/r = 27	holotype OR802154
MNHN-IE-2013-2233	<i>Benthogenia mahi</i> n. sp.	Solomon Islands	9°34'53.4"S, 160°47'09.0"E	414-456	alcohol	R = 25/r = 14.3	OR802150
MNHN-IE-2019-4320	<i>Benthogenia mahi</i> n. sp.	?	?	?	dry	R = 50 to 67/ r = 23 to 32	4 individuals

The following conventions are used to describe ossicle orientation: 1) the actinal surface (adoral) vs the abactinal surface (aboral); 2) the adradial direction that points toward the radial plane of symmetry vs the abradial direction, that points away from the radial plane of symmetry; and 3) the proximal direction toward the centre of the disc vs the distal direction toward the tip of the arm. Measurements of the specimens are expressed as followed: R is the radius from the center of the disc to the end of the arms, r is radius of the disc from the center of the disc to the edge of the disc.

The anatomy of asteroid ossicles has been described previously (Turner & Dearborn 1972; Blake 1973; Gale 2011). The nomenclature used here is adapted from Fau & Villier (2018, 2020), Gale (2011) and Turner & Dearborn (1972). Anatomical terms and abbreviations present in Table 2 are provided in italics in the text. Clark & Downey (1992) gave the following definition of cribriform organs “vertical indentation between marginal plates of both series containing ciliated epithelium supported by vertical rows of platelets or papillae” (see the glossary). Mironov *et al.* (2016) added that “[cribriform organs] consist of parallel rows of small spines, the shape of which varies from papilla-like (i.e., circular in cross section) to lamella-like (flat lamellae)”. Cribriform organs of *Benthogenia* are indentations on the marginals filled by small specialized spines that are aligned vertically. These spines are flattened and possess a broader flat base.

MOLECULAR ANALYSES

Genomic DNA was extracted from tube feet tissue using NucleoSpin 96 tissue core kit (Macherey-Nagel) following the manufacturers' protocols. Fragment of 16S rRNA were amplified with standard polymerase chain reaction (PCR), using primers from Smith *et al.* (1993) 16Sar (CGCCT-GTTTATCAAAAACAT) and 16Sbr (CCGGTCTGAACT-CAGATCACGT). DNA amplifications were performed in 20 µl PCR reaction mixtures, containing 0.12 µl Taq DNA polymerase (Qiagen), 15.44 µl ddH₂O, 2 µl 10X Standard Taq Reaction Buffer, 0.8 µl dNTPs, 1 µl DMSO, 0.32 µl of each forward and reverse primer, and 1 µl template DNA. Amplification products were generated by an initial pre-denaturation step of 4 min at 95°C followed by 45 cycles of denaturation at 95°C for 30s, annealing at 52°C for 40s, extension at 72°C for 1 min and a final extension step at 72°C for 10 min.

PCR products were sequenced using the same primers, and in both directions, to ensure the accuracy of base calls. Chromatograms were edited and aligned using Geneious Prime software (<https://www.geneious.com>; Kears *et al.* 2012). Genetic distances were calculated using Kimura 2-parameter distance (K2P; Kimura 1980) in the software MEGA X (Kumar *et al.* 2018) for MacOS (Stecher *et al.* 2020), aligned using the Muscle algorithm. All sequences were deposited in GenBank (see Table 1 for vouchers).

TABLE 2. — List of the terms and abbreviations used in this paper, updated from Fau & Villier (2018, 2020). In the second column, abbreviations used by Gale (2011) when they differ, or when the structures were not named (–).

Terms/abbreviation	Gale (2011)	Definition
1st tf	–	On the oral ossicle, area between the proximal and the distal process where the first tube feet lie. Generally associated with denser and flatter stereom
abiiim	–	Interoral abactinal muscle
ab.r	abr	Abactinal ridge on ambulacral
abtam	–	Transverse abactinal interambulacral muscle
aciim	–	Interoral actinal muscle
actam	–	Transverse actinal interambulacral muscle
act.r	actr	Actinal ridge on ambulacral; keel in Turner & Dearborn (1972)
dada	ada 2, ada 3	Ambulacral/adambulacral articulation (distal on the ambulacral, proximal on the adambulacrals)
dadam	–	Distal ambulacral/adambulacral muscle, on the ambulacrals
dis.p	dcp	Distal process of the orals and first ambulacrals
doda	–	Distal oral/odontophore articulation on the oral
f.spa	–	Furrow spine attachment structure
iioa	–	Interoral articulation
interada	adada	Interadambulacral articulation
interadam	adadam	Interadambulacral muscle
keel	–	On the odontophore
lia	–	Longitudinal interambulacral articulation
lim	–	Longitudinal interambulacral muscle
odom	–	Odontophore-oral muscle
orada	–	Oral-adambulacral articulation, on the oral
oradam	oradm	Oral-adambulacral muscle, on the oral
pada	ada1, ada1a, ada1b	Ambulacral-adambulacral articulation, (proximal on the ambulacral, distal on the adambulacral)
padam	–	Proximal ambulacral-adambulacral muscle, on the ambulacral
poda	–	Proximal odontophore-oral articulation
prox.p	pcp	Proximal process of the orals and first ambulacrals
riom	–	Interoral muscle
rng	–	Passageway of the nervous oral ring
rvg	–	Groove along the oral ossicles in which lies the ring canal of the ambulacral system
spa	sos	Spine attachment structure
teeth	de	Imbricating teeth and socket structures, on the ambulacral head (<i>dentition</i> in Turner & Dearborn 1972)
wings	–	Proximal and distal extensions at the base of the ambulacral for attachment of the ambulacral/adambulacral muscles (Turner & Dearborn 1972)

TABLE 3. — Genetic divergence (16S) of *Benthogenia* Fisher, 1911 species using kimura 2-parameters.

Species (MNHN)	IE-2013-2199	IE-2013-2233	IE-2007-1580	IE-2007-1335	IE-2013-2216	IE-2007-1828
<i>B. mahi</i> MNHN-IE-2013-2199	/	–	–	–	–	–
<i>B. mahi</i> MNHN-IE-2013-2233	0.000	/	–	–	–	–
<i>B. mahi</i> MNHN-IE-2007-1580	0.000	0.000	/	–	–	–
<i>B. mahi</i> MNHN-IE-2007-1335	0.000	0.000	0.000	/	–	–
<i>B. mahi</i> MNHN-IE-2013-2216	0.000	0.000	0.000	0.000	/	–
<i>B. cribellosa</i> MNHN-IE-2007-1828	0.024	0.024	0.024	0.022	0.024	/

ABBREVIATIONS

MNHN Muséum national d’Histoire naturelle, Paris;
 USNM National Museum of Natural History, Smithsonian Institution, Washington D.C.

RESULTS

Genetic divergence from mitochondrial marker 16S were calculated using Kimura 2-parameter distance (Kimura 1980; Table 3). Genetic divergence was absent between the five specimens of *Benthogenia mahi* n. sp., which is

consistent with the morphology. The specimen MNHN-IE-2007-1828 (Fig. 1C, D), *Benthogenia cribellosa*, differed from *Benthogenia mahi* n. sp. by 2.4% for four specimens, and by 2.2% for the specimen MNHN-IE-2007-1335. *Benthogenia mahi* n. sp. and *Benthogenia cribellosa* also occur in different region. *Benthogenia cribellosa* has only been collected from the Philippines, while the geographical range of *Benthogenia mahi* n. sp. includes the Solomon Islands, New Caledonia, and the Vanuatu (Table 1). These results are consistent with the morphological results presented herein.

SYSTEMATICS

Superorder VALVATACEA Blake, 1987
 Order PAXILLOSIDA Perrier, 1884
 Family PORCELLANASTERIDAE Sladen, 1883

Genus *Benthogenia* Fisher, 1911

Benthogenia Fisher, 1911: 415.

TYPE SPECIES. — *Benthogenia cribellosa* Fisher, 1911.

DIAGNOSIS. — Emended from Fisher (1911). Cribriform organs present between all marginals from the disc to the tip of the arms. Dorsal distal half part of the arms covered by cribriform organs. Presence of a large oval terminal ossicle bearing up to five or six spines. Terminal ossicle resting on the two to three distalmost superomarginals. No odd interradial marginal. Some superomarginals with large spines. From half length of the arms to the tip, superomarginals in contact dorsally. Inferomarginals and superomarginals corresponding one to one proximally, offset distally. Adambulacral ossicles with numerous furrow spines (four to eight). Subambulacral smaller spines or spinelets, usually more than 10. Actinal ossicles scale like plates covered with small spinelets, extending almost to the end of the arms. Abactinal paxillae large, bearing up to 35–50 spinelets.

Benthogenia cribellosa Fisher, 1911
 (Figs 1; 2A, C; 3A, C, E; 4A, C, E; 5A, C)

Benthogenia cribellosa Fisher, 1911: 415–417; 1919: 39–443, pl.1 fig. 1, 2 fig. 1, 8 fig. 2. — Madsen 1961: 81–82. — Clark & Downey 1992: 92. — Gale 2005: 393–395. — Blake & Mah 2014: 182–188. — Mironov *et al.* 2016: 503–516.

TYPE LOCALITY. — Republic of the Philippines, Mindanao Island, Iligan Bay, Tabu Point, 8°16'45"N, 124°02'48"E.

TYPE MATERIAL. — **Holotype.** Republic of the Philippines • Mindanao Island, Iligan Bay, Tabu Point; station 5513; 8°16'45"N, 124°02'48"E; depth 924 m; 7.VIII.1909; United States Fish Commission; USNM 28655.

MATERIAL EXAMINED. — **Republic of the Philippines** • 1 individual; South East of Cagayan Island; station 5425; 9°37'45.1"N, 121°10'58.8"E; depth 905 m; 31.III.1909; United States Fish Commission; USNM 40412 • 1 individual; South East of Cagayan Island; station 5425; 9°37'45.1"N, 121°10'58.8"E; depth 905 m; 31.III.1909; United States Fish Commission; USNM 40417 • 1 individual; West of Luzon Island; station CP107; 14°01'12.0"N, 120°16'48.0"E; depth 111–115 m; 2.VI.1985; Bouchet & Triclot leg.; MUSORSTOM 3, dry; MNHN-IE-2019-3848 • 1 individual, Bohol Sea; station CP2389; 9°16'48.0"N, 123°22'48.0"E; depth 784–786 m; 30.V.2005; coll. PANGLAO 2005 Deep Sea Cruise, GenBank: OR802153; MNHN-IE-2007-1828.

DIAGNOSIS. — Emended from Fisher (1911). Sea star with pentagonal disc, arms tapering significantly, cribriform organs well developed, present between all the marginals as well as the dorsal part of the superomarginals, from the disc to the tip of the arms. Cribriform organs covering entirely the six most proximal superomarginals of each interbrachium (arm tip to arm tip). From half way of the arm to the tip, superomarginals abutted dorsally along midline. Superomarginals 30 to 34 per interbrachium in large individuals, inferomarginals 32 to 34 per interbrachium. Adambulacral ossicles with five to eight furrow spines, most often seven or eight, and numerous subambulacral smaller spines or spinelets (usually 10

to 15). Oral ossicles large, with nine to 12 furrow spines, the most proximal spine, enlarged (two or three times the width of other oral furrow spines), pointed toward the mouth. Abactinal paxillae large, bearing up to 35 spinelets.

DESCRIPTION

Description based on the specimens MNHN-IE-2019-3848 (Fig. 1E, F), MNHN-IE-2007-1828 (Fig. 1C, D), and the original description of the holotype USNM 28655 (Fig. 1A, B) in Fisher (1911).

Body pentagonal (R/r between 1.9 and 2.6), arms tapering. Superomarginals form distinct border when viewed abactinally, interbrachium (from arm tip to arm tip) composed of 30 superomarginals and 34 inferomarginals (34 superomarginals in MNHN-IE-2007-1828), the 10 proximalmost superomarginals forming the disc, the remainder abutting abactinally on the arms. Abutted superomarginals variably aligned regularly or offset in a same individual depending on the arm. Superomarginal plates decreasing in size along the arms, with the largest plates being the one proximal to the superomarginals abutted dorsally along the arms.

Paxillae densely packed on the abactinal surface, the largest paxillae on the distal part of the disc directly above the ambulacral groove with 28 or 30 spinelets par paxillae, in some up to 35. Smaller paxillae at the center of the disc with 15 to 25 spinelets each and smallest paxillae next to the marginal edges with four to five spinelets.

Madreporite close to the edge of the disc, 1 to 2 mm away from closest superomarginals, largest diameter 4 mm in MNHN-IE-2019-3848 and 6.5 mm in MNHN-IE-2007-1828. Terminal ossicles oval, relatively large (4 mm in MNHN-IE-2019-3848; 5 mm in MNHN-IE-2007-1828), overlapping the two distalmost superomarginals on each side of the arms, each terminal resting over four superomarginals in total. Terminal ossicles bearing spines up to five or six small spines.

Cribriform organs well developed on the disc and on the arms (Fig. 2A, B), covering all or almost all the surface of the ten proximalmost superomarginals (Figs 2A, B; 3A, C), forming one continuous surface. Cribriform organs never covering the entire surface of the inferomarginals (Fig. 2A, B), but rather three quarters in the 10 proximalmost inferomarginals, with a bare area left in the center of the ossicles (Fig. 2B). Cribriform organs less developed on the arms, present between the abutted superomarginals on the abactinal side of the arms up to the terminal ossicle, and reduced to two rows of spinelets per fasciolar band on the distal part of the arms. Superomarginals with small spines directed abactinally, one per ossicle (Fig. 3E), no spines observed on inferomarginals (except for the cribriform organs). Inferomarginals aligned with superomarginals on disc, but offset distally due to their sizes decreasing more drastically than the superomarginals (Fig. 4E).

Actinals are scale like, covered in small spines (Fig. 4A, C). Adambulacral with five to seven furrow spines, mostly six to seven (Fig. 4A, C). Subambulacral spines organized around the edges of the adambulacral mostly, a few additional ones at the

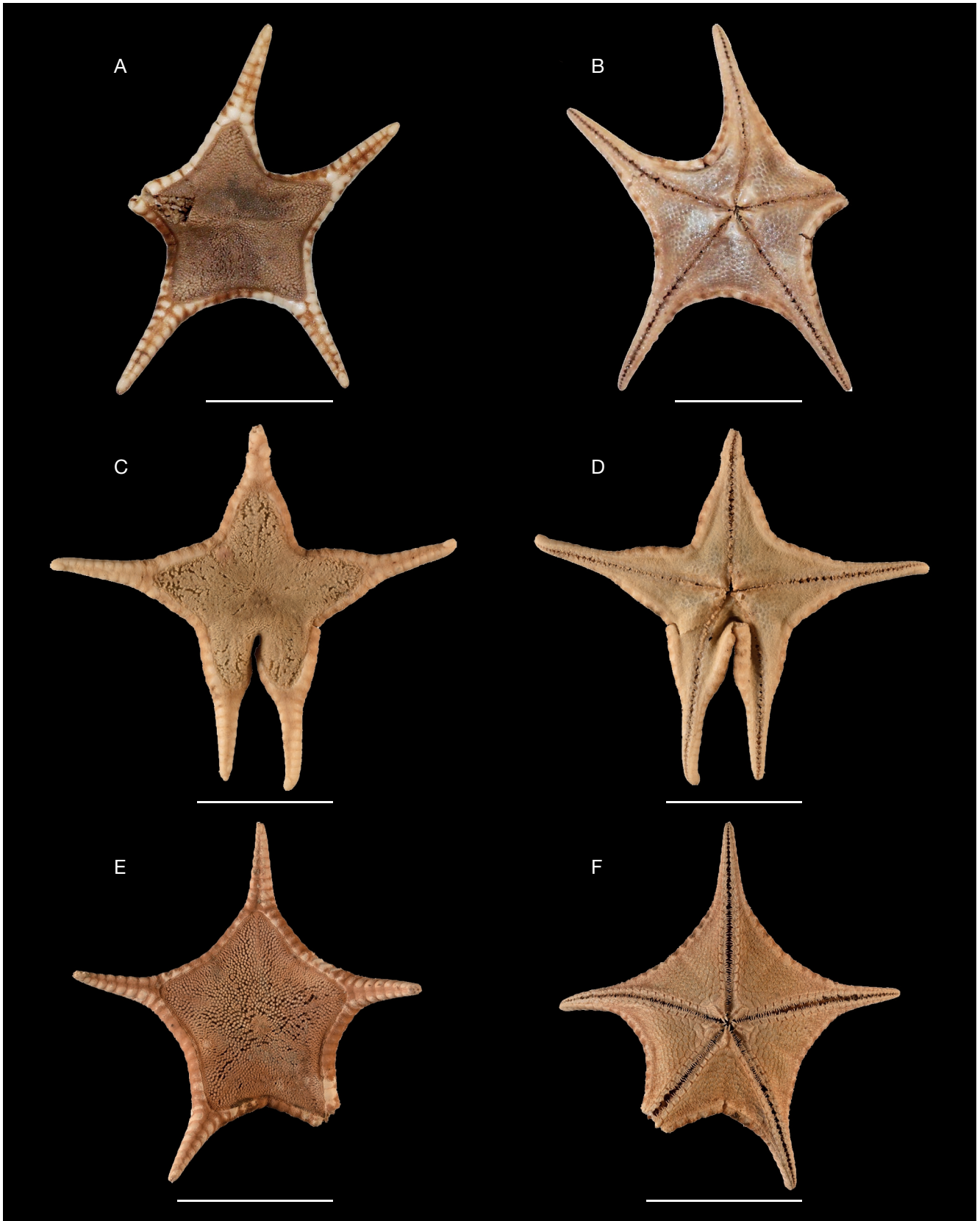


FIG. 1. — *Benthogenia cribellosa* Fisher, 1911 in abactinal (A, C, E) and actinal view (B, D, F): A, B, holotype USNM 28655; C, D, MNHN-IE-2007-1828; E, F, MNHN-IE-2019-3848. Scale bars: 5 cm.

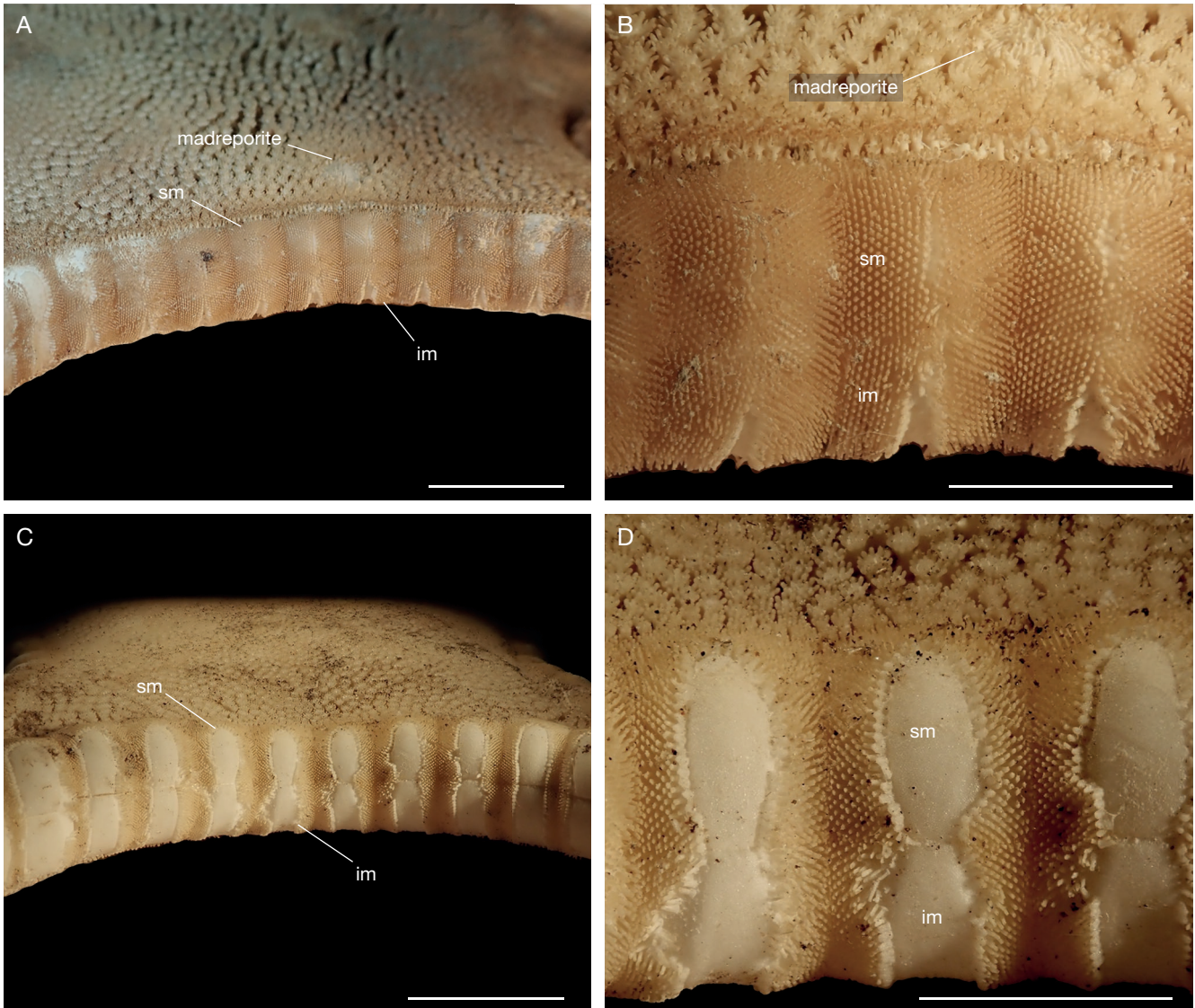


FIG. 2. — Cribriform organs on the marginals of the disc: **A, B**, *Benthogenia cribellosa* Fisher, 1911 MNHN-IE-2019-3848; **C, D**, *Benthogenia mahi* n. sp. MNHN-IE-2019-3879. Abbreviations: **im**, inferomarginals; **sm**, superomarginals. Scale bars: A, C, 1 cm; B, D, 5 mm.

center of the ossicles (Fig. 4A). Very few small subambulacral spines on proximal adambulacral, less than 10 per ossicle, increasingly distally to up to 12/16 spines on mid-arm ossicles.

Oral ossicles big, with a single tooth-like-spine per ossicle directed into the mouth, and eight to nine spines bordering the ambulacral groove (furrow spines), same shape as the ambulacral spines, nine to 10 furrow spines in total (Fig. 5A, C). More than 20 furrow spines, aligned along the edges of the orals. Proximal spines the biggest.

REMARKS

Three specimens, included in USNM 40412 and USNM 40417, were described by Fisher (1919), with the latter specimen containing two individuals collected from gut contents of a gonioplectinid, *Prionaster gracilis* Fisher, 1913. Fisher (1919) provided a detailed description of the largest speci-

men USNM 40412, $R = 12$ mm, but expressed doubt on its taxonomic identification, stating its resemblance with the genus *Hyphalaster* Sladen, 1883 and especially *Hyphalaster hyalinus* Sladen, 1883. Examination of both specimens confirms Fisher's observations that the specimens are *B. cribellosa* but due to their small size, lack characters present only in adults. USNM 40412 shows juvenile cribriform organs between all its marginals (i.e., the cribriform organs do not cover the entire surface of the marginals unlike larger specimens), possessed thick and round marginals, and a relatively large terminal ossicle covering the arm tip. This terminal ossicle morphology is typical of juvenile asteroids. Specimen USNM 40417 was not as well-preserved and included only a fragment of the arm, which also included part of the oral frame. Fisher (1919) described this specimens as the smallest, measuring $R = 5.5$ mm.

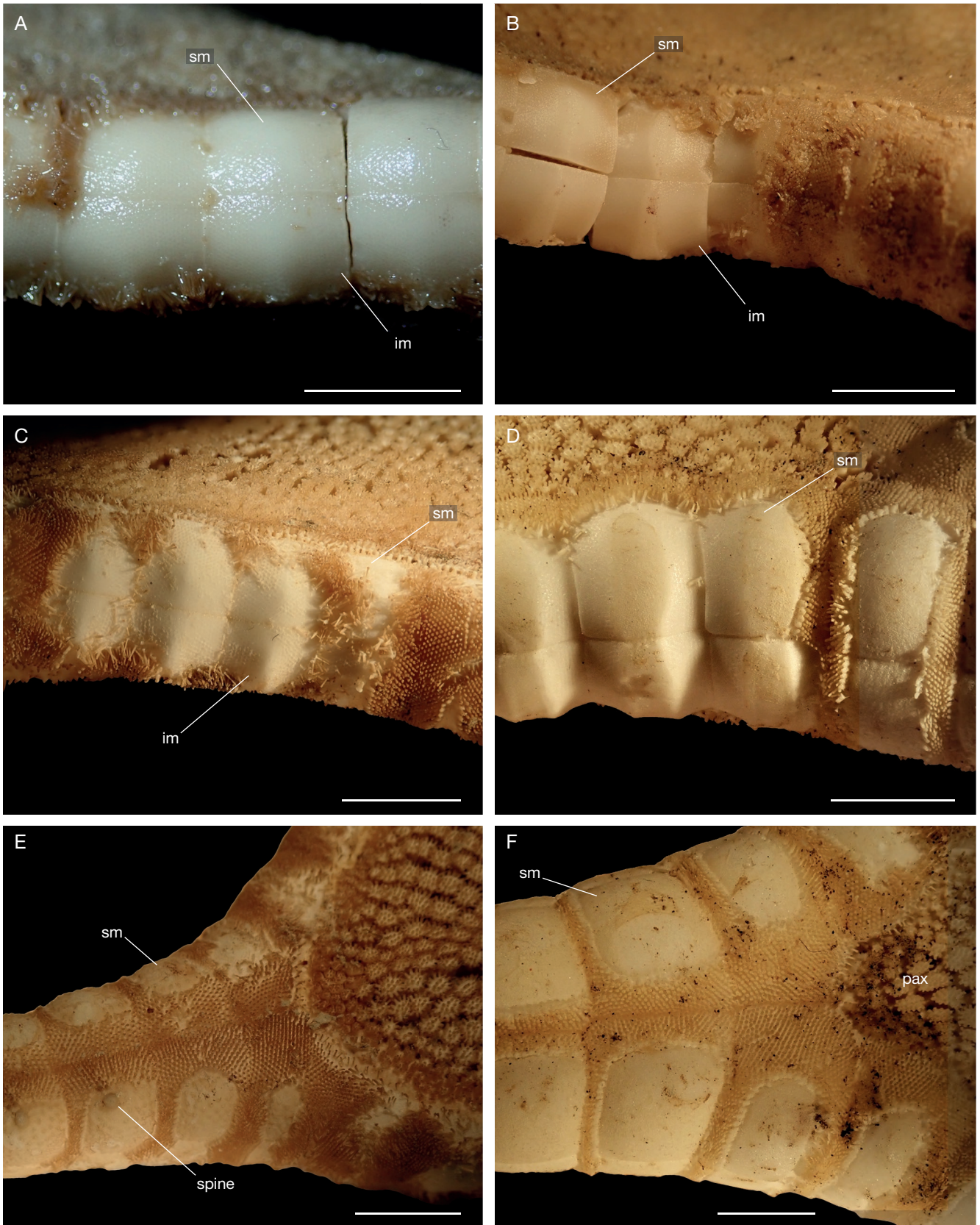


FIG. 3. — Marginals and arms in abactinal view of *Benthogenia cribellosa* Fisher, 1911 (A, C, E) and *Benthogenia mahi* n. sp. (B, D, F): A, holotype USNM 28655; B, holotype MNHN-IE-2013-2216; C, E, MNHN-IE-2019-3848; D, F, MNHN-IE-2019-3879. Abbreviations: im, inferomarginals; pax, paxillae; sm, superomarginals. Scale bars: 5 mm.

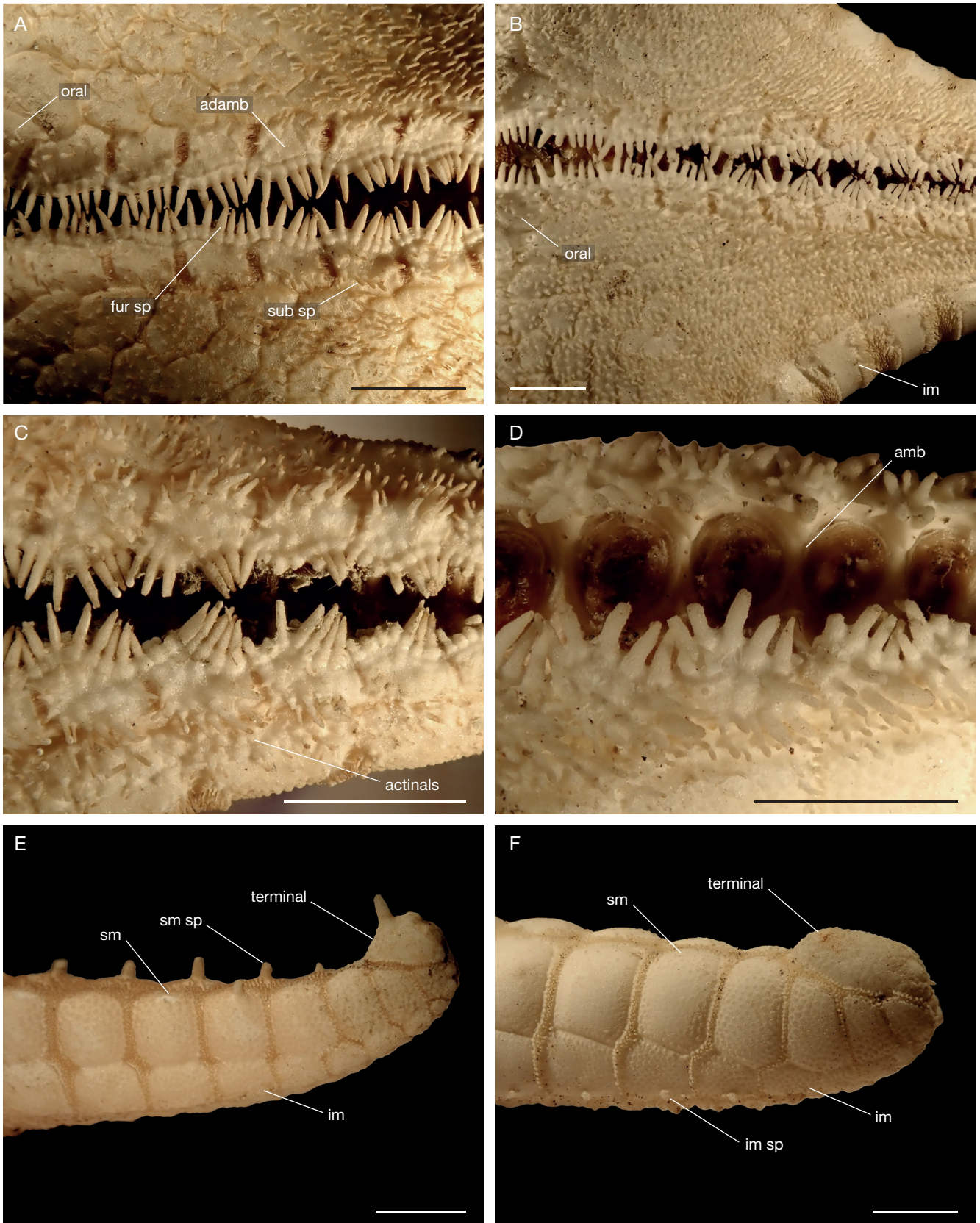


FIG. 4. — Ambulacral furrow and distal part of the arm of *Benthogenia cribellosa* Fisher, 1911 MNHN-IE-2019-3848 (A, C, E) and *Benthogenia mahi* n. sp. MNHN-IE-2019-3879 (B, D, F): A, B, proximal part of the ambulacral furrow; C, D, distal part of the ambulacral furrow; E, F, distal view of the arm showing terminal ossicle. Abbreviations: **adamb**, adambulacral; **amb**, ambulacral; **fur sp**, furrow spines; **im**, inferomarginals; **im sp**, inferomarginal spines; **sm**, superomarginals; **sm sp**, superomarginal spines. Scale bars: 5 mm.

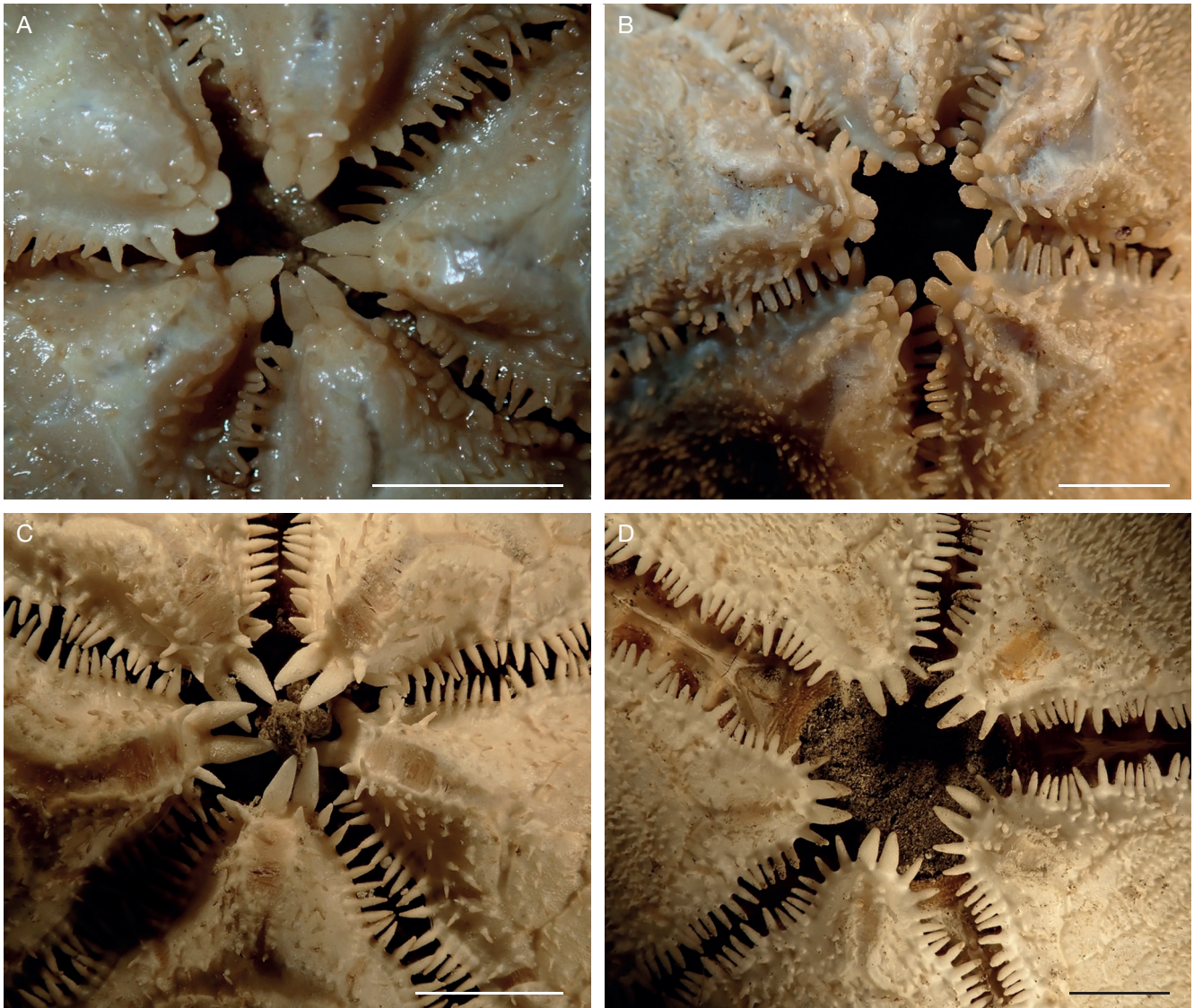


Fig. 5. — Oral frame of *Benthogenia cribellosa* Fisher, 1911 (A, C) and *Benthogenia mahi* n. sp. (B, D): A, holotype of *Benthogenia cribellosa* USNM 28655; B, holotype and *Benthogenia mahi* n. sp. MNHN-IE-2013-2216; C, MNHN-IE-2019-3848; D, MNHN-IE-2019-3879. Scale bars: 5 mm.

Benthogenia mahi n. sp.
(Figs 2B, D; 3B, D, F; 4B, D, F; 5B, D; 6; 7)

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Benthogenia aff. *cribellosa* – Mironov *et al.* 2016: 503-516.

Benthogenia aff. *gribellosa* (typographic error) – Mironov *et al.* 2016: figs 1A; 2A; 3A.

TYPE MATERIAL. — **Holotype.** Solomon Islands • West of San Cristobal Island; station CP2837; 10°25'45.0"S, 161°21'57.6"E; depth 381-422 m; 22.IX.2007; Richer & Boisselier leg.; SALOMONBOA 3, GenBank: OR802154; MNHN-IE-2013-2216.

Paratypes. Solomon Islands • 1 individual; East of San Cristobal Island; station CP2832; 10°44'32.4"S, 162°19'39"E; depth 410-430 m; 1.X.2007; Richer & Boisselier leg.; SALOMONBOA 3; GenBank: OR802152; MNHN-IE-2007-1335 • 1 individual; East of Guadalcanal Island; station CP2848; 9°34'53.4"S, 160°47'09.0"E;

depth 414-445 m; 2.X.2007; Richer & Boisselier leg.; SALOMONBOA 3; GenBank: OR802150; MNHN-IE-2013-2233 • 1 individual; East of Guadalcanal Island; station CP2848; 9°34'53.4"S, 160°47'09.0"E; depth 414-445 m; 2.X.2007; Richer & Boisselier leg.; SALOMONBOA 3; partially dissected for ossicle anatomy, GenBank: OR802149; MNHN-IE-2013-2199.

OTHER MATERIAL. — **Republic of Vanuatu** • 1 dry individual; Southwest of Efate Island, Mele Bay; station DW1011; 17°49'54.0"S, 168°11'31.2"E; depth 547-585 m; 27.IX.1994; Bouchet & Richer de Forges IRD leg.; MUSORSTOM 8; MNHN-IE-2019-3811 • 1 dry individual; South of Epi Island; station CP1047; 16°53'37.2"S, 168°10'29.4"E; depth 486-494 m; 30.IX.1994; Bouchet & Richer de Forges IRD leg.; MUSORSTOM 8; MNHN-IE-2019-3879.

New Caledonia • 1 wet individual; North of New Caledonia, Grand Passage; station CP3028; 20°16'58.8"S, 163°49'20.4"E; depth 650-1200 m; 10.V.2008; Bouchet leg.; CONCALIS; GenBank: OR802151; MNHN-IE-2007-1580 • 1 dry individual; East cost

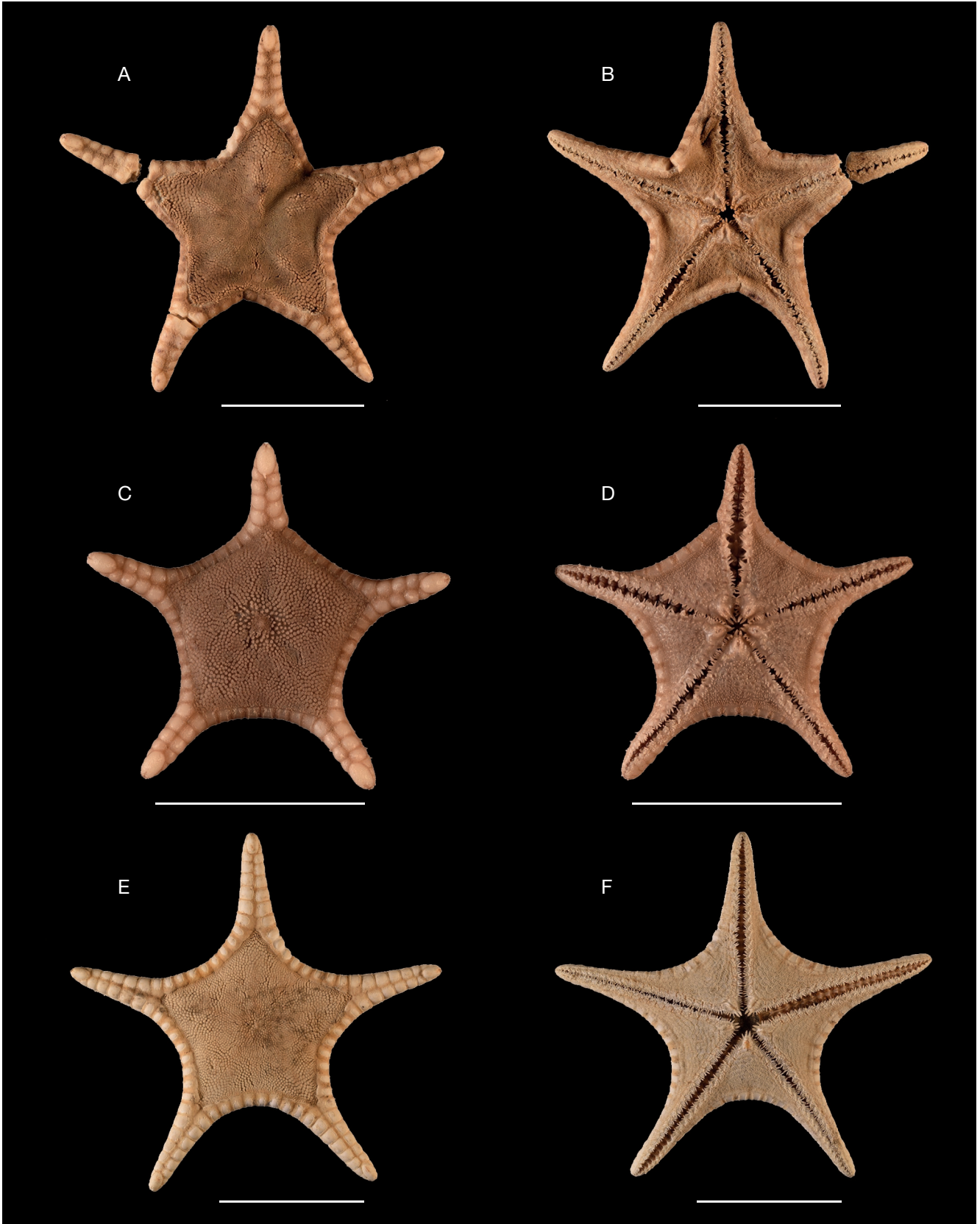


FIG. 6. — *Benthogenia mahi* n. sp. in abactinal (A, C, E) and actinal view (B, D, F): A, B, holotype MNHN-IE-2013-2216; C, D, MNHN-IE-2007-1580; E, F, MNHN-IE-2019-3879. Scale bars: 5 cm.

of New Caledonia; station DE696; 20°34'0.6"S, 164°57'10.8"E; depth 497–520 m; 17.III.1993; Bouchet & Richer de Forges leg.; BATHUS 1; MNHN-IE-2009-2066.

No data • 4 dry individuals; MNHN-IE-2019-4320.

DIAGNOSIS. — Disc pentagonal (R/r between 2.1 and 2.5 for specimen R > 60 mm), arms only tapering. Cribriform organs present between all the marginals from the disc to the tip of the arms. Dorsal/abactinal surface of supermarginals covered by cribriform organs, save for large, quadrate bare regions with rounded edges present on dorsolateral surface of each plate. These bare regions smooth, strongly convex. Cribriform organs larger and more developed on the proximal supermarginals of the disc, getting thinner, rudimentary distally. From half length of the arms to the tip, supermarginals in contact abactinally, abutted. Supermarginals 24 to 26 per interbrachium (from arm tip to arm tip) in large individuals (R > 50 mm), 20 to 22 supermarginals for specimens smaller than R > 20 mm, inferomarginals 26 to 32 per interbrachium. Adambulacral ossicles with four to six furrow spines, and numerous subambulacral smaller spines or spinelets (more than 10). Abactinal paxillae large, bearing up to 50 spinelets.

ETYMOLOGY. — For Dr Christopher L. Mah, an echinoderm zoologist at the National Museum of Natural History, Smithsonian Institution, specialized in Asteroidea.

TYPE LOCALITY. — Solomon Island.

DESCRIPTION

Arms five, body pentagonal, R/r between 2.1 and 2.5 for specimen R > 60 mm (holotype: R = 69 mm, r = 27 mm), interradial arc weakly curved to straight (Fig. 6). Marginals forming distinct periphery. Arms robust, slightly larger than high in mid-section (MNHN-IE-2019-3879: height = 8.4 mm; width: 9 mm).

Abactinal surface covered by densely packed paxillae. Paxillae at arm base, each with 30 to 50 spinelets, those at disc center, each with fewer than 20, usually five to 15. Paxillae closest to the supermarginal contact, displaying fewer than 10 spinelets. Madreporite big, close to the marginal edge of the disc, about 2 mm away from the supermarginals. Partially covered by spinelets, deep ridges of the madreporite visible.

Supermarginals 24 to 26 per interbrachium of which eight are along the disc in large individuals (R > 50 mm), less in smaller individuals, inferomarginals 26 to 32 per interbrachium (MNHN-IE-2019-3811, R = 16 mm: 20 supermarginals and 20 inferomarginals; MNHN-IE-2009-2066, R = 18 mm: 22 supermarginals and 24 inferomarginals). Supermarginals abutted along the distal half part of the arms. Supermarginals higher than long, more so proximally, supermarginals in the middle of the arms larger with cubic or quadrate shape. Inferomarginals and supermarginals aligned around the disc up to mid-arms, inferomarginals smaller and offset compared to the supermarginals distally. Cribriform organs well developed, extending from the lateral sides of the inferomarginals to the lateral sides and abactinal edge of the supermarginals (Figs 2C, D; 3B, D). Cribriform organs covering the middle of the arms between the abutted supermarginals, until the terminals (Figs 3F; 4F). The marginals of the disc with the most extensive cribriform organs, covering up to half of the ossicle surfaces (abactinal and lateral sides of the supermarginals), with a bare central area left (Figs 2C, D; 3B). Inferomarginals with extensive cribriform organs on the

sides and bare central area. Extension of the cribriform organs diminishing along the arms, rudimentary distally (Fig. 4F). Rest of the marginal ossicles mostly bare, with a slight granular texture (Fig. 4F). Some supermarginals with small spines directed abactinally, not present in all specimens. Small spines on inferomarginals directed actinally (Fig. 4F; present in only MNHN-IE-2013-2233, MNHN-IE-2019-3879 and one of the four individuals of MNHN-IE-2019-4320).

Terminal ossicles big (7 to 9 mm total length for specimens R > 50 mm), oval shaped, resting on the three or four distalmost supermarginals on each side of the arm, resting on six to eight supermarginals in total. Terminals with granular texture similar to the marginals, most often bearing spines (Fig. 4F).

Actinal plates scalar, imbricate, extending up to 90% of the arms. Actinals covered in small spinelets, up to 15–17 spinelets on bigger actinals around the mouth. Ambulacral with four to seven diamond-shaped furrow spines, most often four to six (Fig. 4B, D) and 10 to 15 smaller blunt subambulacral spines. Oral ossicles big, with seven to nine spines bordering the ambulacral groove (furrow spines), among which the proximalmost spines bigger, tooth-like and directed toward the mouth (Fig. 5B, D). Rest of the furrow spines similar in shape to ambulacral furrow spines. Remainder of the orals surface covered by small spinelets similar to the one on the actinals, up to 20 spinelets (subambulacral spines).

Description of internal ossicles

Mouth frame. Oral ossicles (Fig. 7A, B) with a blade like shaped body directed proximally and two processes (proximal *prox.p* and distal *dist.p*), with a straight line of denser stereom where the furrow spines are attached (*f.spa*, Fig. 7A) on the actinal surface. Additional spine attachment structure on the blade (*spa*, Fig. 7A). In distal position, approximately 25 percents of the length of the ossicle, muscle insertion *oradam* and articulation *orada* with the adambulacral. Muscle insertion *odom* (with the odontophore) large, in the middle of the blade, between two distinct articulation areas *ioa*. Muscle insertion area *aciim* narrow, on the proximal end of the blade (Fig. 7B).

Odontophore bilaterally symmetrical, with proximal and distal processes (Fig. 7E, F). The actinal median process, called the *keel* (Fig. 7E), relatively shallow, not very pronounced. Abactinal surface of the odontophore flat (Fig. 7F). Proximal processes well pronounced and projected actinally, ending with the articulation area *pada*. Distal processes slightly less developed, each with an articulation area *doda*.

First ambulacral (Fig. 7C, D), also called circumoral ossicles, strongly differentiated from all the other ambulacral, “inversed Y”-shaped, with a long shaft and a pointed head. The base of the first ambulacral with two processes, proximal and distal, each articulated with the corresponding processes of the oral ossicles. Proximal process slightly shorter, distal process slightly longer and larger due to abactinal extension.

Ambulacral skeleton. The most proximal ambulacral (second and third ambulacral; Fig. 7G, H) compressed because of the first ambulacral leaning on distally. Second ambulacral

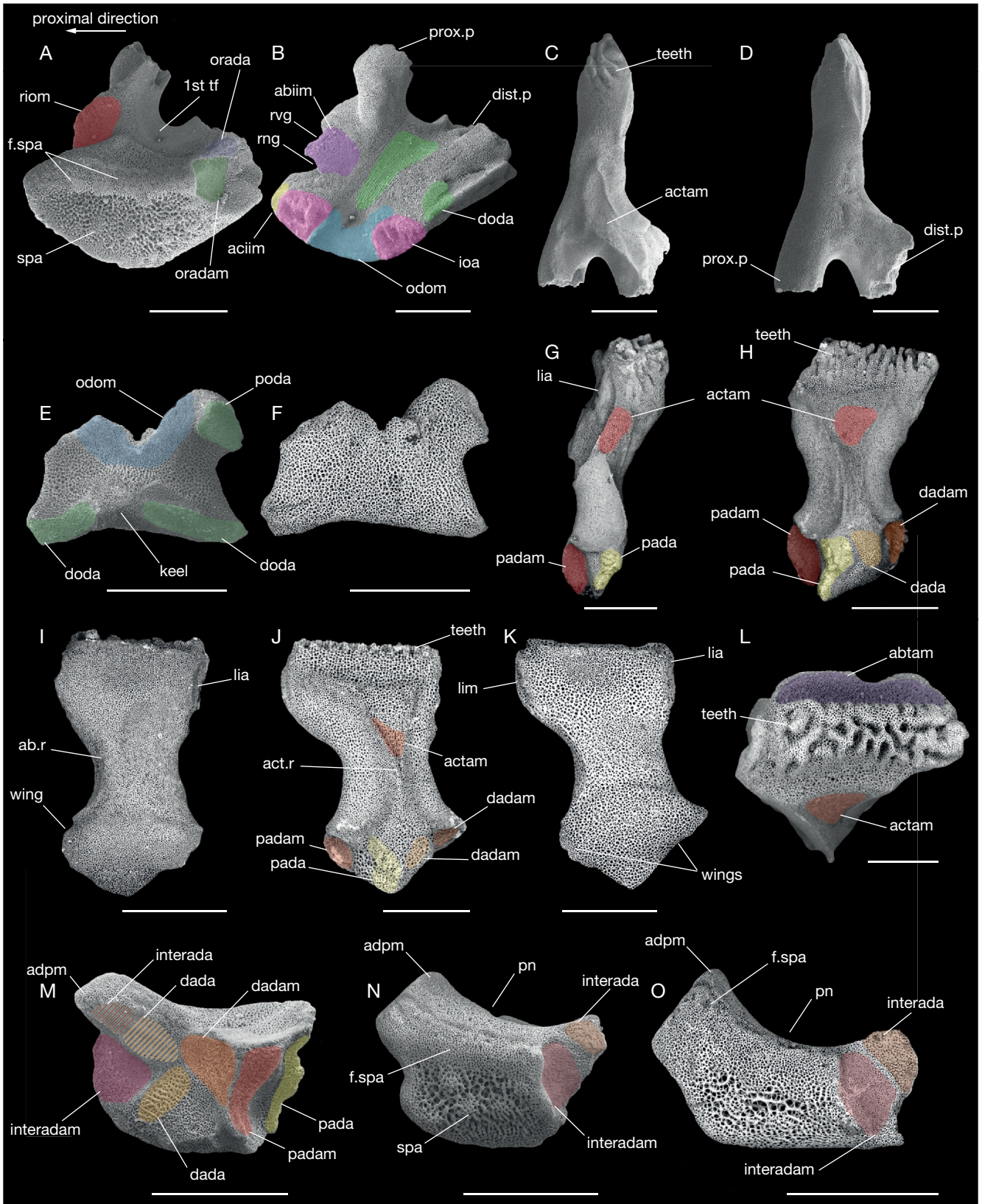


FIG. 7. — Scanning electron microscopy (SEM) images of the orals (A, B), 1st ambulacrals (C, D), odontophores (E-F), ambulacrals (G-L), and adambulacrals (M-O) of *Benthogenia mahi* n. sp., specimen MNHN-IE-2013-2199: A, oral in adradial view; B, oral in abradial view; C, 1st ambulacral in adradial view; D, 1st ambulacral in abradial view; E, odontophore in actinal view; F, odontophore in abactinal view; G, second ambulacral in adradial view; H, third ambulacral in abradial view; I, K, ambulacrals in abradial view; J, ambulacral in abradial view; L, ambulacral in abactinal view; M, adambulacral in abactinal view; N, O, adambulacrals in actinal view. Colored areas indicate the presence of a differentiated stereom. See Table 2 for abbreviations. Proximal direction to the left, actinal direction to the bottom except for M-O, adradial direction to the top. Scale bars: A-I, M-O, 2 mm; J-L, 1 mm.

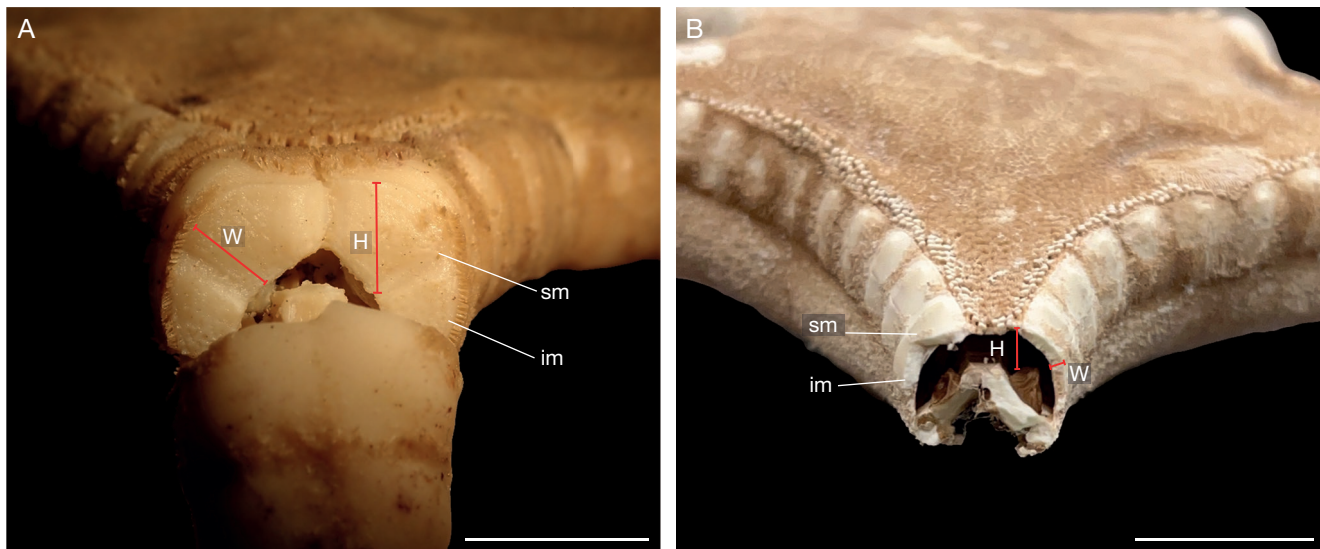


FIG. 8. — Arm sections of *Benthogenia mahi* n. sp. holotype MNHN-IE-2013-2216 (A) and *Hyphalaster inermis* Sladen, 1883 USNM 1018661 (B). Red bars show the width (W) of and the height (H) of the superomarginals. Scale bars: 1 cm.

with an “s”-shaped body, head severely compressed (Fig. 7G), leaning in distal direction, with elongated articulation with the first ambulacral. Third ambulacral also with its head leaning distally, but not compressed. Rest of the ambulacrals (Fig. 7I-L) more robust, hourglass-shaped with large shaft, head slightly leaning in the proximal direction. *Teeth* and abactinal muscle insertion *abtam* present on the entire length of the head (Fig. 7L). Actinal ridge *act.r* well pronounced, forming an “Y” shape from the muscle insertion *actam* to the base of the ambulacrals (Fig. 7H, J). Proximal and distal wings well developed.

Adambulacrals longer than wide, podial notch (*pn*) forming a regular curve adradially, delimited proximally by a proximal extension *adpm* (Fig. 7M-O). Actinal surface with spine attachment structure for subambulacral spines (*spa*) and furrow spines (*f.spa*; Fig. 7N, O). Interambulacral articulation *interada* and muscle insertion *interadam* at the distal end of the adambulacrals on the actinal surface (Fig. 7N, O), on the proximal end of the abactinal surface (Fig. 7M). Proximal articulation *pada* and muscle insertion *padam* with ambulacrals on the distal end of the adambulacrals due to the structure being named for their position on ambulacrals. Distal articulation *dada* generally present in two distinct areas (*ada2* and *ada3* in Gale 2011), here only one area distinguishable in abradial position. No difference in the texture of stereom permitting to distinguish the two articulations. Superambulacrals absent (always absent in the Porcellanasteridae).

REMARKS

Benthogenia mahi n. sp. is distinguished from *Benthogenia cribellosa* mainly by its bare patches on the surface of the most proximal superomarginals, its more robust arms, larger paxillae covered by greater number of spinelets (from 25 to *c.* 50 whereas *B. cribellosa* largest paxillae are covered by 20 to 35 spinelets), less numerous marginals (for specimen

of comparable size) and less numerous oral and adambulacral furrow spines. Some specimens of *B. mahi* n. sp. do not have spines on superomarginals, whereas all specimens of *B. cribellosa* examined have superomarginal spines. Three specimens of *B. mahi* n. sp. possess relatively small conical inferomarginal spines, no inferomarginal spines were observed in *B. cribellosa*.

DISCUSSION

The study of the ossicles of *Benthogenia mahi* n. sp. showed many characters shared with another porcellanasterid, *Styracaster chuni* Ludwig, 1907 (Gale 2011). Indeed, *B. mahi* n. sp. possesses similar elongated and distally-leaning first ambulacrals (Fig. 7C, D) to *Styracaster chuni*, which give the oral frame a stellate look when seen in abactinal view (see Gale 2011: pl. 12; fig. 4). This very special organisation of the oral frame impacts the rest of the ambulacral skeleton with the second and third ambulacrals being compressed (Fig. 7G), character also noted by Gale (2011: 54). On the odontophore, the *keel* (Fig. 7E) of *B. mahi* n. sp. is relatively shallow and less developed compared to other paxillosids like the *Luidia superba* A.H.Clark, 1917 (De los Palos-Peña *et al.* 2021) and *Ctenodiscus crispatus* (Bruzelius, 1805) (Turner & Dearborn 1972; Gale 2011). *Styracaster chuni* (Gale 2011: pl. 15; fig. 8) possesses a similar very shallow keel, but with shallower proximal processes.

On the adambulacrals, observation of *B. mahi* n. sp. is congruent with the confluence of the most adradial part of the ambulacral-adambulacral articulation (*dada* in Figure 7M, or *ada2* in Gale 2011) with the interambulacral articulation *interada*. This character was described by Gale (2011) on *Styracaster chuni* and *Ctenodiscus crispatus*, and proposed as a synapomorphy of the clade Cribellina Fisher, 1911.

In the literature *Benthogenia* has been compared to *Thoracaster* Sladen, 1883, *Hyphalaster* Sladen, 1883 and *Lysaster* Bell, 1909. Comparisons were made based on their general appearances, the presence of true paxillae, and the cribriform organs, which are present between all the marginals of the disc in *Benthogenia*, whereas other Porcellanasteridae possess fewer cribriform organs, sometimes as few as only one per interradius. *Benthogenia* also possesses paxillae, which are absent in other genera (Fisher 1911, 1919; Madsen 1961; Mironov *et al.* 2016). *Benthogenia* is the only genus that possesses cribriform organs between all its marginals, with extension of the cribriform organs on the abactinal surface of the arms (Fig. 3). In addition, *Benthogenia* possesses wider, more robust marginals than any other Porcellanasteridae (Fig. 8). *Benthogenia*'s marginals are similar in shape to the marginals of *Goniopecten demonstrans* Perrier, 1881 (illustrated in Gale 1987; Gale 2011). They are as wide as high, with a triangular profile in proximal and distal view whereas in contrast, *Thoracaster* and *Hyphalaster* have narrow marginals (Fig. 8B). This is the case for both superomarginals and inferomarginals, regardless of their position on the disc or the arms. *Lysaster lorioli* Bell, 1909 (MNHN-IE-2013-9106) was studied from photographs (courtesy of Dr C. Mah): it shows straight not tapering arms, suggesting marginals of evenly thickness along the entire length of the arm, and a slight abactinally bulging of the superomarginals (as illustrated in Clark 1952: fig. 1) similar to *Benthogenia*'s bulged superomarginals. This suggests that the marginals of *Lysaster* could be of intermediate thickness compared to *Benthogenia* and other porcellanasterids. However as the specimen of *Lysaster lorioli* MNHN-IE-2013-9106 is complete and do not present a clear cross section of one of its arm, the thickness of its marginals cannot be verified here. The phylogenetic analysis of Petrov *et al.* (2016) supports the Gonioplectinidae as sister taxa to the Porcellanasteridae. In this case, the thickness of the marginals would support the interpretation of *Benthogenia* as plesiomorphic within the Porcellanasteridae, as previously formulated by Madsen (1961) and Mironov *et al.* (2016). However, the phylogenetic hypothesis of Petrov *et al.* (2016) did not include any *Benthogenia* specimens, and support *Hyphalaster* and *Thoracaster* as derived within the Porcellanasteridae. This highlights the need for future comprehensive morphological and molecular studies of the Porcellanasteridae to understand the phylogenetic relationships within the family.

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