



## Plio-Pleistocene deep-sea crinoid (Echinodermata) diversity from the western Rodrigues Ridge, Indian Ocean, revealed by microfossil evidence

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### Abstract

The deep-sea crinoid fauna of the Indian Ocean is still only partially known and its relationships with the Atlantic and W Pacific faunas remain questionable. Isolated ossicles, more or less biocorroded, of six species belonging to five families of stalked crinoids and one of comatulids were found in a sediment of late Pliocene to early Pleistocene age collected at a depth of 1460 m on the western Rodrigues Ridge. The material described contains three species of stalked crinoids including two new species of Rhizocrinidae. *Paraconocrinus*, a common genus in the Eocene, was previously unknown beyond the early Miocene. *Cherbonniericrinus* and *Porphycrinus* have representatives in the present-day oceans, the former only in the NE Atlantic, the latter in the Atlantic and Indo-western Pacific. The ossicles of *Porphycrinus* have been attributed to the extant species *P. polyarthra* known from the southwestern Indian Ocean, and have allowed us to improve the species diagnosis. *P. polyarthra* presents close affinities with two Atlantic species. The apparently high diversity of this Plio-Pleistocene fauna is due to a mixture of ossicles from autochthonous mesobathyal species and allochthonous epibathyal ones that lived at shallower depths.

**Key words:** bathyocrinid, *Cherbonniericrinus*, comatulid, Crinoidea, hyocrinid, *Paraconocrinus*, Pleistocene, Pliocene, *Porphycrinus*

### Introduction

The extant deep-sea crinoid fauna from the Indian Ocean is relatively poorly documented, particularly for stalked crinoids (A.H. Clark 1912; Messing 2017; Roux *et al.* 2002; Eléaume *et al.* 2012). Its relationships with the fauna of the adjacent oceans (Atlantic and Pacific) assumedly depend on exchanges favored by the circulation of deep bottom waters and the continuity of mid-ocean ridges (Améziane & Roux 1997). Isolated ossicles preserved in deep-sea sediments represent a highly promising but largely unexplored source of evidence to reconstruct present-day and ancient crinoid diversity.

In 1987, a NERC (UK) funded expedition to the Indian Ocean, on board the RRS “Charles Darwin”, dredged the area around the Rodrigues Ridge, on the Mascarene Plateau, to the east and west of the island of Rodrigues. Although the primary purpose of this research was to obtain igneous rock samples with which to date the ridge, a significant number of bathyal sediment samples was also recovered, using piston coring and pipe-dredges, and an Agassiz Trawl was used to obtain material of living deep-sea faunas.

Here, we describe the crinoid ossicles retrieved from the Plio-Pleistocene sediments sampled off Rodrigues Island, on the western Rodrigues Ridge, at a depth of 1460 m. Most of the taxa identified based on the ossicles are closely related to extant species. Some are known since the Eocene but have not yet been identified in Pliocene and younger records.

## Material and methods

**TABLE 1.** Plio-Pleistocene material examined from the site RR13A on the western Rodrigues Ridge, Indian Ocean, and housed in the collections of the National Museum of Natural History Luxembourg (acronym MNHNL). Abbreviations: AC: aboral cup, BB: basal circlet, Br: brachial, Brax: axillary brachial, Brfree: free brachial, Brsyz: brachial with one syzygial facet, Ci: cirral, Col: columnal, dist: distal, mes: mesistele, mes+dist: mesistele + dististele.

taxa	Catalogue n°	ossicles	figures	remarks
<i>Porphyrocr. polyarthra</i>	OPH199	1 Col.	Fig. 3A	mid mes
<i>Porphyrocr. polyarthra</i>	OPH200	1 Col.	Fig. 3B	mes dist
<i>Porphyrocr. polyarthra</i>	OPH201	1 Col.	Fig. 3C–D	mes dist
<i>Porphyrocr. polyarthra</i>	OPH202	1 Col.	Fig. 3E	dist most
<i>Porphyrocr. polyarthra</i>	OPH203	6 Col.	not figured	mes+dist
<i>Porphyrocr. polyarthra</i>	OPH204	3 Br	Fig. 4A–B,D–E,G–H	
<i>Porphyrocr. polyarthra</i>	OPH205	15 Br	not figured	
<i>Cherbonn. pliocenicus</i>	OPH206	1 AC	Fig. 5F–G	holotype
<i>Paracon. rodriguesensis</i>	OPH207	1 AC	Fig. 5C–E	holotype
<i>Paracon. rodriguesensis</i>	OPH208	1 AC	Fig. 5A–B	paratype
<i>Paracon. rodriguesensis</i>	OPH209	4 AC	not figured	paratypes
<i>Bathycrinus</i> sp	OPH210	1 BB	Fig. 6A–B	
<i>Bathycrinus</i> sp	OPH211	2 Brax	Fig. 6D (1 figured)	1 broken
Hyocrinidae gen.	OPH212	1 Col	Fig. 6F	
Unstalked crinoid sp	OPH213	4 Br	Fig. 7A (1 figured)	2 broken
Unstalked crinoid sp	OPH214	1 Brax	Fig. 7B	broken
Unstalked crinoid sp	OPH215	3 Br	Fig. 7C–E	
Unstalked crinoid sp	OPH216	2 Brfree	Fig. 7F (1 figured)	
Unstalked crinoid sp	OPH217	18 Brsyz	not figured	
Unstalked crinoid sp	OPH218	34 Brfree	not figured	
Unstalked crinoid sp	OPH219	72 Pin	not figured	
Unstalked crinoid sp	OPH220	70 Ci	not figured	

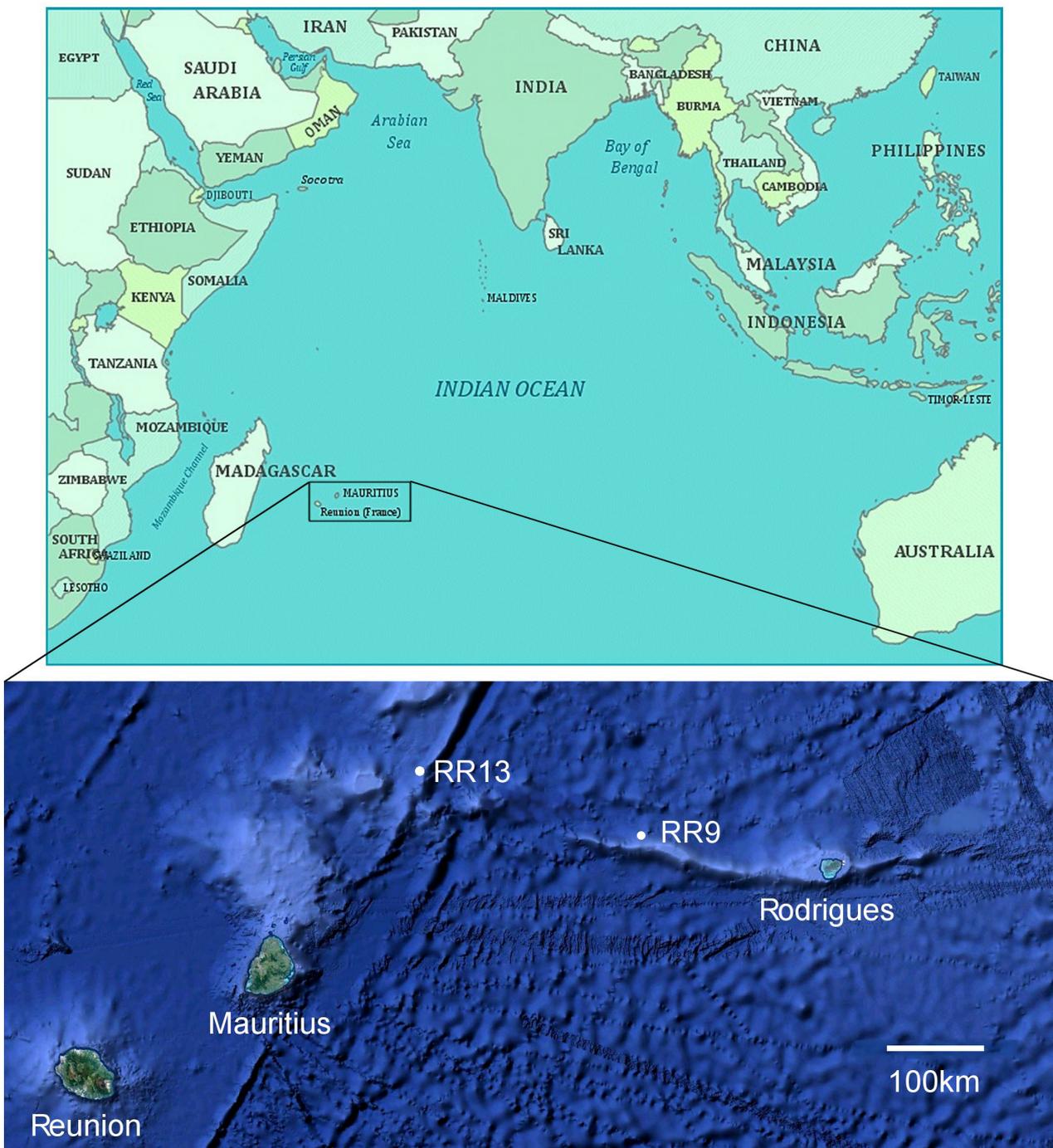
Despite frequent biocorrosion of the stereom (Fig. 2) and occasional abrasion marks (e.g. Figs. 3–4), the Plio-Pleistocene crinoid ossicles (Supplementary Table) are usually well-preserved. They were retrieved from the sieving residues of sediments from a pipe-dredge sample at site RR13A taken at the western end of the Rodrigues Ridge (Fig. 1) (Gale 2020) at 1460 m water depth; 18° 28' N 59° 18' W. They are listed in Table 1. The sediments consisted of carbonate sands containing basalt fragments and manganese-coated bioclasts and yielded an abundant fauna of fossil gastropods, bivalves, corals, echinoderm ossicles, fish otoliths and cirripede plates. The fossil cirripede faunas obtained from the region were described by Gale (2020a, b). The dating provided in Gale (2020a, b) was based on one sample (RR9), which yielded abundant planktonic foraminiferans, indicating a Pliocene age (PI3–PI6; 3.59–1.95 Mya), but calcareous nannofossils suggested that an early Pleistocene element was also present in the assemblage. Therefore, the material is dated to late Pliocene–early Pleistocene.

For comparison and identification of Plio-Pleistocene material, a few extant specimens housed in the zoological collection of the Muséum national d'Histoire naturelle (MNHN) in Paris (Table 2) were dissociated in household bleach (12% sodium hypochlorite solution) overnight (~10 h), rinsed in distilled water, and air dried. For scanning electron microscopy (SEM), fossil and extant ossicles were mounted on stubs and coated with colloidal gold. SEM images were taken at the Plate-forme de Microscopie Electronique, MNHN using a JEOL-840A operated at 15kV.

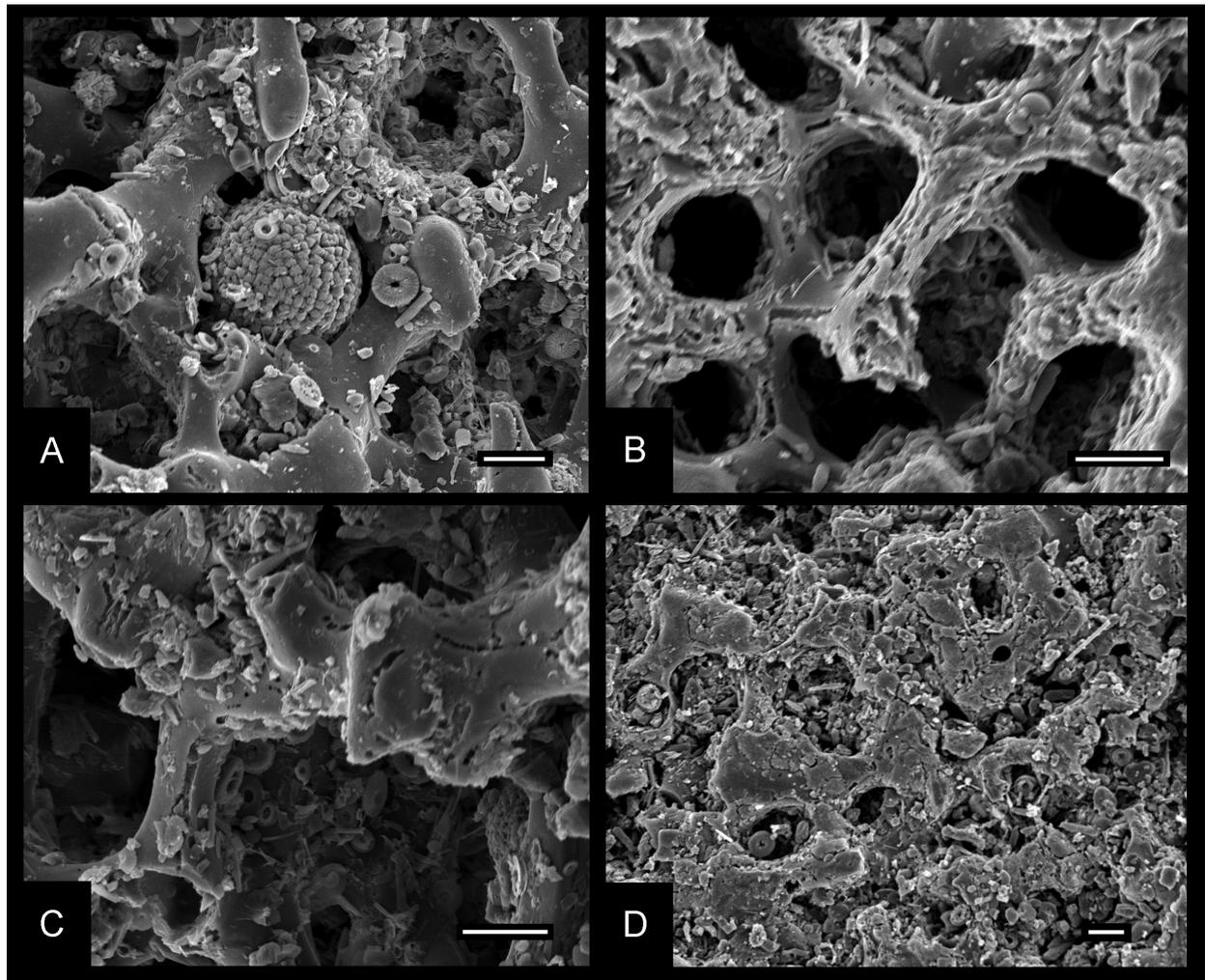
For crinoid morphological terminology, we refer to Roux *et al.* (2002) and Hess & Messing (2011), and specifically for microstructure and terminology of crinoid skeleton articulations to Macurda *et al.* (1978) and Améziane *et al.* (2021).

**TABLE 2.** Extant crinoid species from MNHN zoological collection examined for comparison with Plio-Pleistocene material from the site RR13A on the western Rodrigues Ridge.

Genus and species	Occurrence	Catalogue number	Figures
<i>Porphyrocrinus thalassae</i>	NE Atlantic	MNHN CE13008	Fig. 3C,F,I
<i>Porphyrocrinus verrucosus</i>	S Indian Ocean	MNHN IE-2018.2	Not figured
<i>Cherbonn. cherbonnieri</i>	NE Atlantic	MNHN IE-2016-748	Fig. 5H
<i>Bathycrinus carpentieri</i>	Norwegian Sea	MNHN NORBI	Fig. 6C



**FIGURE 1.** Location of the sites RR13A and RR9 on the western Rodrigues Ridge, Indian Ocean.



**FIGURE 2.** Ossicle biocorrosion at site RR13A on the western Rodrigues Ridge. A: moderate biocorrosion with large part of stereom remaining of smooth surface, see framboid spherule of pyrite at center, B–C: development of microperforations, B: dense rectilinear perforations, C: meshworked perforations, D: high biocorrosion providing dislocation of stereom and micrite filling in porosity. A, C–D: *Porphyrocrinus polyarthra*; A, C: brachials, D: distal columnal; B: Basal ring of *Bathycrinus* sp. Scale bars equal 10  $\mu\text{m}$ .

## Results

### Taxonomical descriptions

#### Family Phrynocrinidae A.H. Clark, 1907

Remarks: See emended diagnosis in Messing (2016).

Stratigraphical distribution: Eocene–Recent (see Merle & Roux 2018).

#### Genus *Porphyrocrinus* Gislén, 1925

Type species of the genus: *Porphyrocrinus verrucosus* Gislén, 1925.

Stratigraphical distribution: late Miocene–Recent.

Emended diagnosis: Crown usually of five rays, exceptionally up to 17 rays; arms usually undivided or with axillaries beyond IBr7, arm pattern of consecutive brachial pairs (rarely triplets) or alternating brachial pairs and free brachials, trifascial ligamentary articulation uniting two brachials of a pair, usually Br7 to 9 bearing first pinnule;

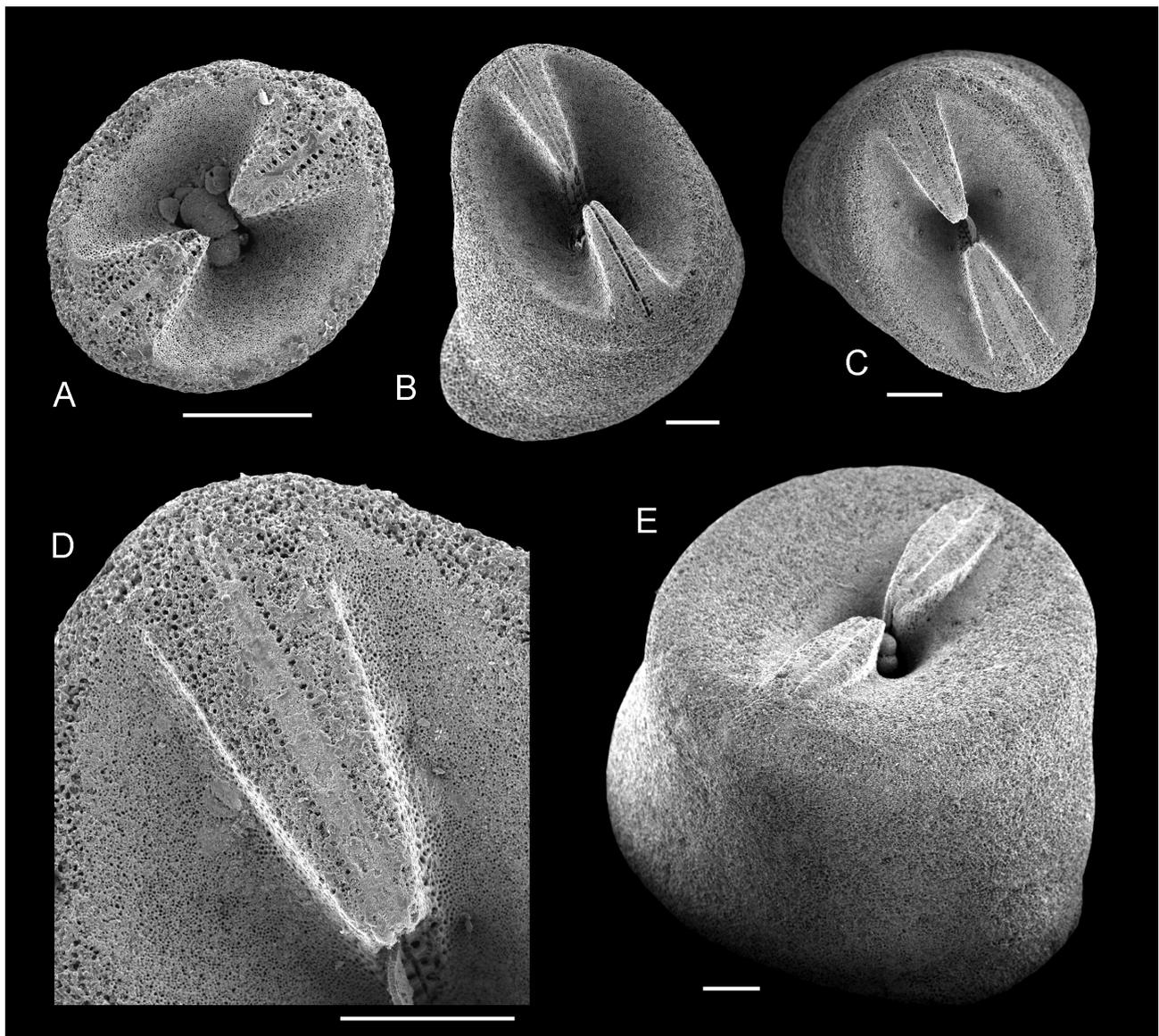
aboral cup at least slightly conical, usually taller than wide, basals conspicuous never fused, usually pentagonal; proxistele well-differentiated with very variable number of discoidal columnals frequently united by syzygies of pentalobate facets; mesistele columnals of synarthries moderately oval, variable number of cryptosynarthries or ankylosed synarthries in distal mesistele or dististele.

***Porphyrocrinus polyarthra* A.M. Clark, 1973**

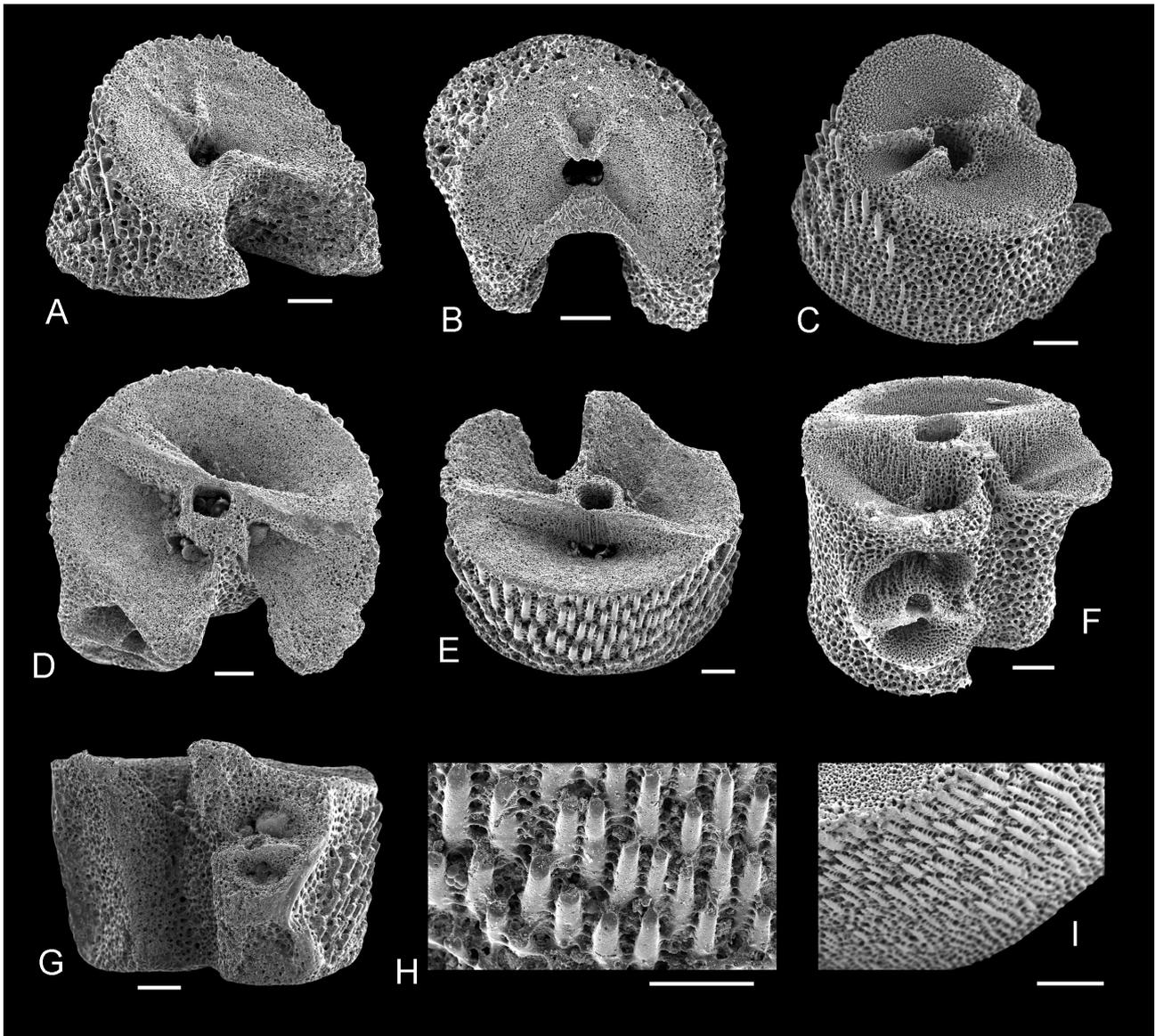
Figs. 3 and 4 A–B, D–E, G–H, Tabs. 3–4

Synonymy: *Porphyrocrinus polyarthra* A.M. Clark, 1973: 282–285, fig. 6a–g; Roux 1977: 32, 38; Roux *et al.* 2002: 824; *Porphyrocrinus verrucosus* Messing 2007: 107; 2016: 3; Eléaume *et al.* 2012: 18; Tunnichliffe *et al.* 2016: 373; *Porphyrocrinus polyarthra* Roux *et al.* 2019: 60, fig. 4E

Not *Porphyrocrinus polyarthra* Eléaume *et al.* 2014: fig. 1c.



**FIGURE 3.** *Porphyrocrinus polyarthra*, columnal synarthries from site RR13A on the western Rodrigues Ridge. A: OPH199, in mid mesistele, B: OPH200, in mid distal mesistele, C–D: OPH201, in distal mesistele, D: detail of fulcral ridge, E: in dististele. Scale bars equal 0.5 mm.



**FIGURE 4.** Brachials of *Porphyrocrinus*. A–B, D–E, G–H: OPH204, *P. polyarthra* from site RR13A, A–B: same proximal brachial of a pair, D,E,H: same distal brachial of a pair, G: distal brachial of another pair; C, F, I: *P. thalassae* from Bay of Biscay (NE Atlantic), A–C: trifascial facets of ligamentary articulations; D–F: distal brachials of a pair with muscular synarthry; H–I: spines on aboral side surface; A–F: more or less oblique distal views; G: adoral side view; H–I: aboral side views. Scale bars equal 0.2 mm.

Material examined: 10 columnals (included 4 figured), 18 brachials (included 3 figured).

Emended diagnosis: distal stalk with smooth columnals, synarthries with stout fulcral ridge of wide dense calcite axis and up to seven consecutive cryptosynarthries of radiating syzygial outer crenularium; aboral cup approximately cylindrical, but slightly constricted medially

Description: Quantitative columnal characters given in Table 3. Three columnals 1.5 times taller (H) than wide (D) belonging to mid mesistele (Fig. 3A), with diameter at mid-height (1.12 mm) smaller than that of articular facets perpendicular to fulcral ridge ( $d$  1.15 mm), synarthries slightly oval ( $D/d$  101) with massive triangular fulcral ridge segments allowing only a very small range of movement. Three other columnals attributable to the dististele-mesistele transition, almost as high as wide with marked ellipticity of synarthries (Fig. 3B–D) allowing stalk flexibility, robust fulcral ridge with more elongated segments and a broad axis of dense calcite (Fig. 3D). Other columnals of variable shape with distinctly less elliptical synarthries ( $D/d < 1.15$ ) belonging to the dististele; including a largest one wider than high, widening towards distal facet, with proximal facet having a marked ligament

pit restricted to center and evoking an articulation in the process of ankylosis (Fig. 3–E) probably corresponding to a columnal preceding attachment disc. Arms mainly made up of brachial pairs, each composed of two brachials joined by trifascial ligamentary articulation (Fig. 4A–B), distal brachial bearing one pinnule, except for a few free brachials (2%) with only muscular synarthries; no axillary observed. Quantitative characters of brachials examined here are given in Table 4. Diameter varying from >1 up to 1.70 mm; thickness (H/D) varying according to brachial type and its position along arm; free brachials the thickest (>0.72) and proximal brachial of a pair the least thick (<0.56), thickness tending to decrease from distal to proximal arm in *Porphyrocrinus*. Ligamentary articulation uniting two brachials of a pair with a fulcral ridge separating two lateral ligament depressions and forming a more or less open V framing deep aboral fossa (Fig. 4A–B). Muscular synarthries having a straight-line fulcral ridge, aboral ligament areas wide and deep, boundary between internal ligament and muscle areas indistinct (Fig. 4D–E). Pinnule socket subcircular and relatively wide (0.4 times brachial diameter) (Fig. 4D–G). External surface covered by broken spines (Fig. 4E, H).

**TABLE 3.** Quantitative characters of *Porphyrocrinus polyarthra* columnals from the site RR13A on the western Rodrigues Ridge. Listed from distal (above) to proximal (below), Ap: proximal facet. H: columnal height, D: maximum facet diameter, d: minimum facet diameter, dist: distal facet, dist mes: dististele-mesistele transition, distmost: near distal stalk end, prox: proximal facet. Values in mm, except ratios.

Catalogue n°	H	D	d	H/D	D/d	place	remark
OPH202 dist	3.23	4.55	4.15	0.71	1.10	distmost	not figured
OPH202 prox	3.23	4.25	3.80	0.76	1.12	distmost	Fig. 3E
OPH203 a	2.15	1.60	1.43	1.34	1.12	distal	not figured
OPH203 b	1.80	1.40	1.25	1.29	1.12	distal	not figured
OPH203 c	2.19	1.95	1.75	1.12	1.14	distal	not figured
OPH201	2.95	2.90	2.40	1.02	1.21	dist mes	Fig. 3C–D
OPH203 d	2.40	2.12	1.75	1.13	1.21	dist mes	not figured
OPH200	3.15	2.95	2.35	1.07	1.25	dist mes	Fig. 3B
OPH203 e	2.50	1.70	1.50	1.47	1.13	mid mes	not figured
OPH199	2.06	1.35	1.20	1.53	1.12	mid mes	Fig. 3A
OPH203 f	broken	1.30	1.15	-	1.13	mid mes	not figured

**TABLE 4.** Quantitative characters of *Porphyrocrinus polyarthra* brachials from the site RR13A on the western Rodrigues Ridge. H: height, D: diameter, H/D: thickness, hypo: proximal brachial of a brachial pair, epi: distal brachial with pinnule socket of a brachial pair. Values in mm except ratio.

Catalogue n°	H	D	H/D	type	Figure
OPH204 a	0.62	1.12	0.55	hypo	Fig. 4A–B
OPH204 b	0.90	1.53	0.59	epi	Fig. 4D–E, H
OPH204 c	0.95	1.35	0.70	epi	Fig. 4G
OPH205 a	0.80	1.59	0.50	hypo	not figured
OPH205 b	1.05	1.57	0.67	epi	not figured
OPH205 c	1.06	1.65	0.64	epi	not figured
OPH205 d	0.85	1.55	0.55	hypo	not figured
OPH205 e	1.25	1.70	0.73	free	not figured
OPH205 f	1.05	1.35	0.78	free	not figured

Remarks: The genus *Porphyrocrinus* is known from all oceans except the eastern Pacific (Roux *et al.* 2002; Eléaume *et al.* 2012; Messing 2007, 2016). *P. polyarthra* is the single phrynocrinid species described from the Indian Ocean. Two specimens without arms and a few arm fragments were collected at a depth of 400 m on the South-west Indian Ocean submarine ridge about half-way between South Africa and Amsterdam Island. The species

name corresponds to the presence of successive cryptosynarthries in the distal stalk (A.M. Clark, 1973, fig. 6a, g). Very similar cryptosynarthries with conspicuous radial syzygial crenularium were also observed in the two Atlantic species *P. thalassae* and *P. daniellalevyae* (Roux 1977; Messing 2016). Messing (2007) considered that *P. polyarthra* was a junior synonym the western tropical Pacific *P. verrucosus*. However, such cryptosynarthry with radiating syzygial crenularium is absent in the distal stalk of western Pacific *Porphyrocrinus* specimens and the synonymy *verrucosus/polyarthra* remains questionable. Our Plio-Pleistocene brachials and columnals share with the extant Atlantic species *P. thalassae* and *P. daniellalevyae* the same trifascial brachial articulations (Fig. 2C), large pinnule socket (Fig. 2F), spiny external ornamentation (Fig. 2I), and distal columnal of smooth external surface with robust fulcral ridges. Unfortunately, stalk cryptosynarthries were not observed because the Rodrigues material includes only a few distal columnals. Eléaume *et al.* (2014, fig. 1c) published a view of a distal columnal synarthry belonging to a specimen from the southern Indian Ocean attributed to *P. polyarthra*. This specimen differs from the Rodrigues specimens in having (1) brachials with a smooth outer surface without spines, (2) distal columnals with their outer surface punctuated by irregular depressions, and more elliptical synarthries showing a thinner fulcral ridge whose axis is marked by a distinctly narrower axe of dense calcite, and (3) synarthries of the mesistele with larger and deeper ligament fossae. It could therefore belong to *P. verrucosus* rather than *P. polyarthra*. In the present state of knowledge, it seems that two species of *Porphyrocrinus* occur in the Indian Ocean, one attributable to *P. verrucosus* in agreement with Roux *et al.* (2019, fig. 4E), the other corresponding to *P. polyarthra* to which the ossicles collected off Rodrigues Island belong.

Occurrence: Indian Ocean, about half-way between South Africa and Amsterdam Island to the east at a depth of 400 m (extant specimens) and off Rodrigues Island, on the western Rodrigues Ridge, with the biotope not clearly determined but at a depth shallower than 1460 m (Plio-Pleistocene).

#### Family Rhizocrinidae Jaekel, 1894

Remarks: see emended diagnosis in Roux *et al.* 2019.

Stratigraphical distribution: late Cretaceous (Campanian)–Recent.

#### Genus *Cherbonniericrinus* Roux *et al.*, 2019

Type species of the genus: *Conocrinus cherbonnieri* Roux, 1976.

Stratigraphical distribution: Paleocene–Recent.

#### *Cherbonniericrinus pliogenicus* sp. nov.

Fig. 5F–G

Type material: a single aboral cup (holotype OPH206).

Etymology: from sediment dated to the Pliocene.

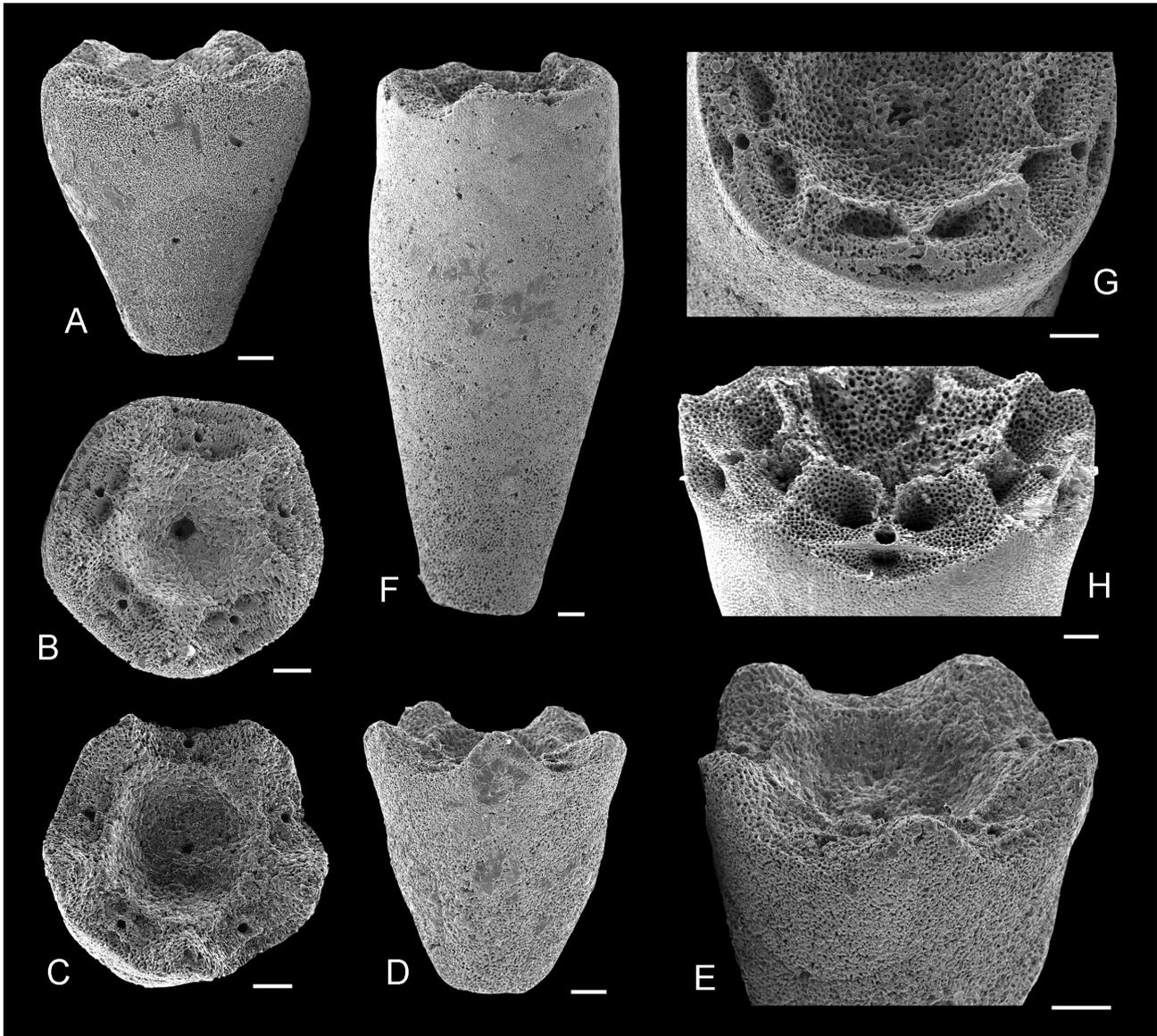
Diagnosis: as the description of the holotype. Arms and stalk unknown.

Type locality: Mascarene Plateau, to the east and west of the island of Rodrigues, Indian Ocean.

Description of the holotype: Elongate aboral cup with lower half inverted conical and upper half subcylindrical (Fig. 5F), basals fused, discrete suture between radials, height (H) 1.90 mm, (D) maximum diameter 0.85 mm, H/D 2.23, diameter of radial ring 0.81 mm, aboral diameter (Dp) 0.40 mm, Dp/D 0.47; adoral face with moderate central depression at bottom of which lumen of axial canal obscured by stereomic plug, discrete adoral radial grooves, ratio central depression to radial ring diameter 0.59; distal synarthry of radials with deep muscular areas, aboral ligament area restricted to outer margin and very prominent interrarial ridges on inner side (Fig. 5G).

Remarks: The good preservation of the adoral face morphology allows us to see that *Cherbonniericrinus pliogenicus* n. sp. displays characters identical to those of the type species of the genus (Fig. 3H) as described by Roux *et al.* (2019). *C. cherbonnieri* differs in having a slightly greater cup size (H 2.2 mm, D 1.50 mm) a regular inverted conical shape moderately elongated (H/D 1.47) with sides slightly convex, and a smaller adoral diameter (Dp/D 0.40) (Roux 1976).

Occurrence: Indian Ocean, western Rodrigues Ridge at a depth of 1460 m (biotope possibly shallower). Plio-Pleistocene.



**FIGURE 5.** Rhizocrinid aboral cups from site RR13A on the western Rodrigues Ridge (A–G) and from Bay of Biscay (H). A–E: *Paraconocrinus rodriguesensis* n. sp., A–B: OPH208, paratype 1, C–E: OPH207, holotype; F–G: *Cherbonnierocrinus pliogenicus* n. sp., OPH206, holotype; H: extant specimen of *Cherbonnierocrinus cherbonnieri* from Bay of Biscay. A, D, F: side view, B–C adoral view of radial ring, E, G, H: oblique distal view of radial ring. Scale bars equal 0.1 mm.

### Genus *Paraconocrinus* Roux *et al.*, 2019

Type species of the genus: *Eugeniocrinus pyriformis* Münster in Goldfuss, 1826.

Stratigraphical distribution: early Eocene–Plio-Pleistocene.

#### *Paraconocrinus rodriguesensis* n. sp.

Fig. 5A–E

Type material: 6 aboral cups (holotype OPH207, 1 figured paratype OPH208, 4 paratypes OPH209 not figured).

Etymology: from sediment off the island of Rodrigues, western Rodrigues Ridge.

Diagnosis: species with aboral cup regularly inverted conical of height usually slightly greater than diameter (Hc/Dc 1.03 to 1.31), diameter lesser than 0.75 mm, basals slightly higher than radials and ratio central adoral depression to radial ring diameter 0.47 to 0.55. Arm and stalk unknown.

Type locality: Mascarene Plateau, western Rodrigues Ridge, Indian Ocean.

Description of the type series: Aboral cup height (Hc) up to 0.80 mm and diameter (Dc) up to 0.72 mm, ratio Hc/Dc varying from 1.03 to 1.31 independently to growth (Table 5), ratio adoral to maximum diameter (Dp/Dc) 0.30–0.35. Like the holotype, all cups inverted conical, basals indistinct (Fig. 5D) sometimes underlined by discreet sutures (Fig. 5A), basals slightly higher than radials, coarse interradial adoral ribs separating oval muscular synarthries (Fig. 5E). Central depression of adoral face without basal plug, hemispherical in holotype (Fig. 5C) to more flared like in paratype 1 (Fig. 5B); ratio central depression to radial ring diameter 0.47 in holotype and 0.55 in paratype 1.

**TABLE 5.** Quantitative characters of aboral cups in the type series of *Paraconocrinus rodriguesensis* n. sp. from the site RR13A on the western Rodrigues Ridge. Hc: height, Dc: maximum diameter. Dc used as growth index. Values in mm except ratio.

Catalogue n°	Hc	Dc	Hc/Dc	Figure	Remark
OPH209 a	0.80	0.72	1.11	not figured	paratype 2
OPH209 b	0.70	0.68	1.03	not figured	paratype 3
OPH208	0.85	0.65	1.31	Fig. A–B	paratype 1
OPH207	0.75	0.62	1.21	Fig. 5C–E	holotype
OPH209 c	0.75	0.60	1.25	not figured	paratype 4
OPH209 d	0.65	0.60	1.08	not figured	paratype 5

Remarks: According to Roux *et al.* (2019), the presence of coarse interradial ribs developed up to the outer edge of adoral face excludes that these small cups are juveniles of *Cherbonnierocrinus pliocenicus* n. sp. described above. *Paraconocrinus* was identified from the Eocene and the Early Miocene of southern France and northeastern Italy (Merle & Roux 2018; Roux *et al.* 2019; Roux & Philippe 2021). The material described herein extends its stratigraphical distribution to the Pliocene. The genus remains unknown in extant fauna.

Occurrence: Indian Ocean, western Rodrigues Ridge at a depth of 1460 m (biotope possibly shallower).

### Family Bathycrinidae Bather, 1899

Remarks: Roux *et al.*, (2019) restricted the family Bathycrinidae to Bourgueticrinina with IBr2ax other than Atelecrinidae.

Stratigraphical distribution: Paleocene–Recent.

### Genus *Bathycrinus* Thomson, 1872

Type species of the genus: *Bathycrinus gracilis* Thomson, 1872.

#### ?*Bathycrinus* sp.

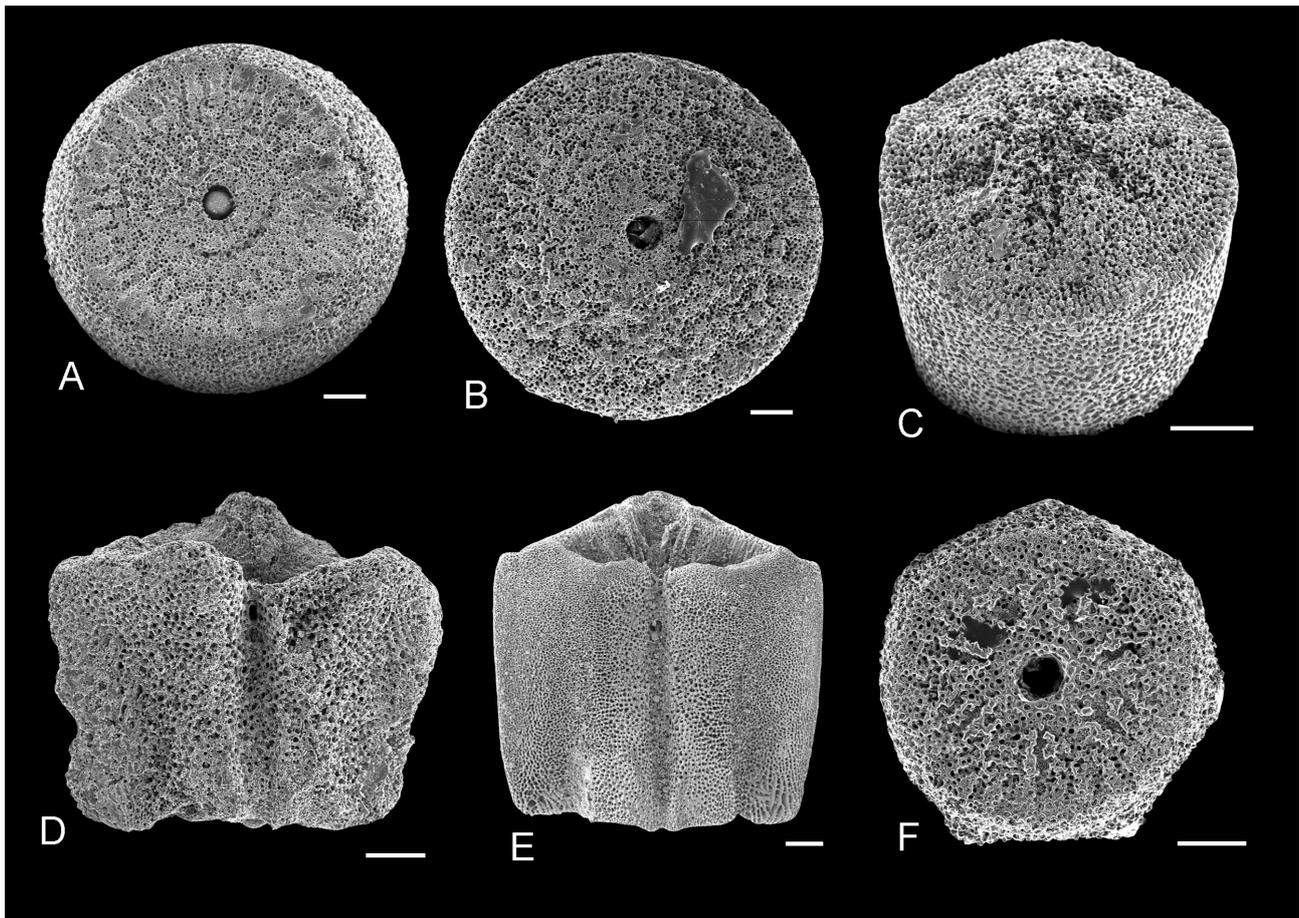
Fig. 6A–B

Material examined: one basal cirlet (OPH210), two axillary brachial (IBr2ax) (OPH211).

Description: Basals fused, aboral face slightly concave with an irregular radiate crenularium (Fig. 6A), adoral face convex slightly granulose without trace of pentagonal symmetry or nervous canal lumen and wide perilumen flat without granulation (Fig. 6B); adoral diameter 1.47 mm, aboral diameter 1.02 mm, height 1.91 mm. Axillary brachial (IBr2ax) with aboral surface smooth, adoral face poorly preserved having a marked axial groove (Fig. 6D),

height 1.91 mm, maximum width 1.85 mm and proximal width 1.00 mm. Another similar but smaller IBr2ax with maximum width 1.30 mm.

Remarks: The shape of the basal ring and the absence of a conspicuous lumen of interradial nervous canals on the adoral face is usual in *Bathycrinus*, which sometimes shows a discrete pentalobate figure like in *B. carpenteri* (Danielssen & Koren 1877) (Fig. 4C). The radiate crenularium on the basal ring adoral face or on the proximal columnal facets has never been observed in bathycrinids and rhizocrinids. *Monachocrinus* differs in having free basals with conspicuous interradial nervous canal open on adoral face (Roux, in preparation). The adoral face of IBr2ax resembles those of *Monachocrinus* (Fig. 6E), but unfortunately the material is too poorly preserved for a more conclusive comparison. Pending additional material, the two ossicles described above are attributed to ?*Bathycrinus* sp.



**FIGURE 6.** Bathycrinid and hyocrinid ossicles. A–B, D, F: from site RR13A on the western Rodrigues Ridge; A–C: basal circlets, A–B: *Bathycrinus* sp., OPH210, A: aboral facet, B: adoral facet, C: oblique proximal view, extant *B. carpenteri* from Norwegian sea; D–E: axillary primibrachial (IBr2ax), D: *Bathycrinus* sp., OPH211, E: *Monachocrinus recuperatus*, from NE Atlantic; F: hyocrinid columnal, OPH212. Scale bars equal 0.2 mm.

### Family Hyocrinidae Carpenter, 1884

Fig. 6F

#### Undetermined genus and species

Material examined: a single small columnal (OPH212).

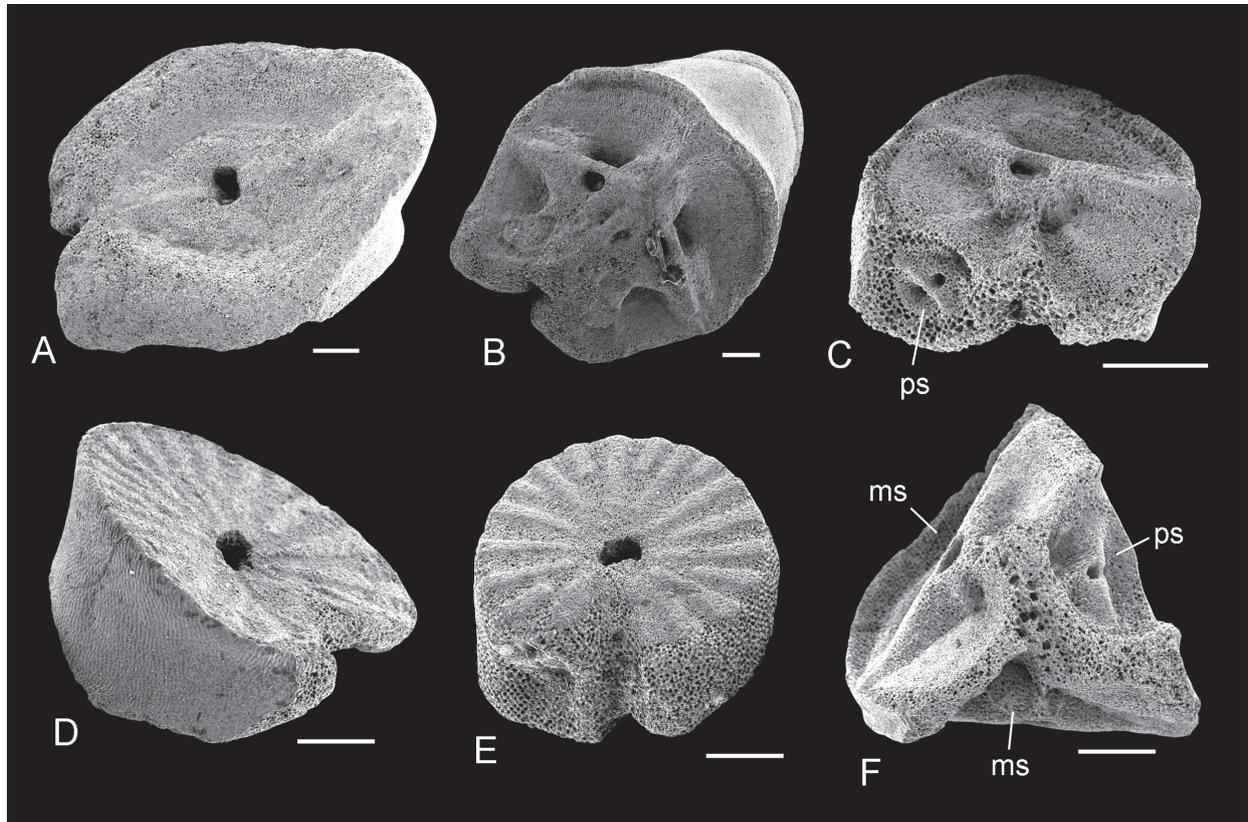
Description: columnal of heptagonal facet with radiate crenulae poorly preserved (Fig. 6F), diameter 0.75 mm, height 0.50 mm.

Remarks: Heptagonal shape, or 7 crenular units on articular facets, is a frequent condition in hyocrinid columnals (Mironov & Sorokina, 1998; Roux & Lambert, 2011) but unknown in other extant stalked crinoid families. Moreover, symmetry 6–7 is more common in juvenile stalks and tends to disappear during growth by adjunction of new

crenular units and generalization of circular articular facets. The small size of this columnal suggests that it belongs to a juvenile specimen which cannot be attributed at the genus rank.

### Comatulids, undetermined family and genus

Figs. 7–8, Tabl. 6



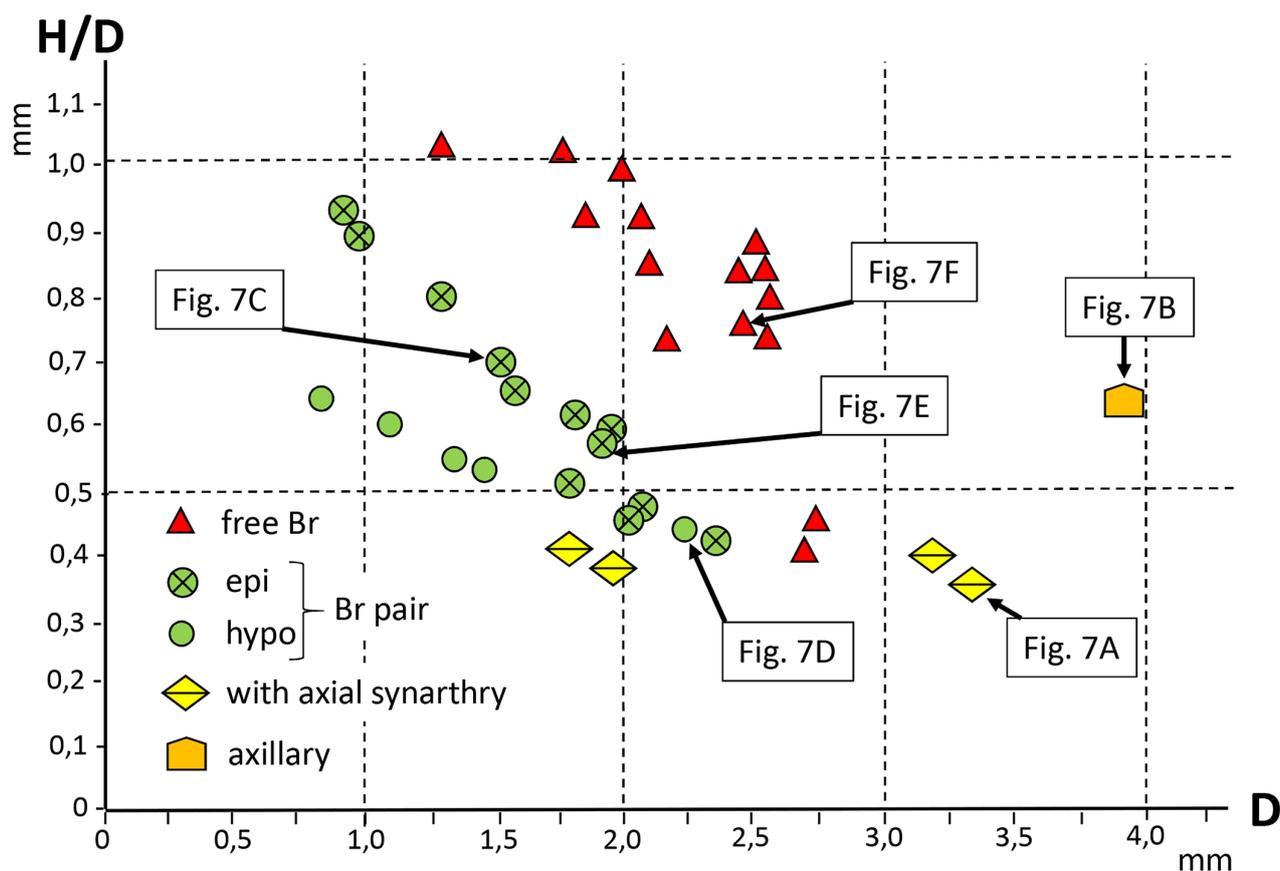
**FIGURE 7.** Comatulid brachials from site RR13A on the western Rodrigues Ridge. A: OPH213, IIBr1 distal ligamentary synarthry, B: OPH214, IBr2ax distal muscular synarthries, C: OPH215, episzygial brachial, distal facet with muscular synarthry and pinnule socket, D–E: OPH215, multiradial syzygies, distal facet of hyposzygial brachial, F: OPH216, free Br with highly oblique muscular synarthries (ms: muscular synarthry, ps: pinnule socket). Scale bars equal 0.5 mm.

Material examined: 62 brachials (included 6 figured), 70 cirrals, and 72 pinnulars.

Description: Quantitative characters of brachials not belonging to the taxa described above are given in Tabl. 6 (see also supplement Table) and Fig. 8. Four kinds of brachials were identified: 5 brachials with one ligament articulation of axial synarthry type (Fig. 7A) including 1 axillary (Fig. 7B), 21 brachials (34%) corresponding to brachial pairs (two brachials united by ligament articulation) with one radial syzygial facet (Fig. 7D–E) and the other of muscular synarthry (Fig. 7C), 36 free brachials (58%) only articulated by muscular synarthries (Fig. 7F), free brachials being 3 times more numerous than brachial pairs. The different types of brachials can be clearly distinguished by their quantitative characters, with IIBr showing a regular decrease in thickness (H/D) correlated to the growth in diameter (Fig. 8). Muscular synarthries articulating brachial pairs to adjacent brachials have a pattern usually observed in various crinoid taxa with a well-developed and deep adoral ligament area (Fig. 7B–C). Largest axial synarthries slightly oval (ratio maximum to minimum diameter 1.14), poorly preserved nevertheless allowing to distinguish a continuous robust fulcral ridge encompassing the axial canal and crescent ligament areas on both sides (Fig. 7A); smallest ones trapezoidal in shape with the same type of fulcral ridge. Syzygies with radiate crenularium, usually 15 to 18 crenulae alternating long and short (Fig. 7D–E), <12 crenulae often just outlined in smallest brachials, hyposzygials distinctly thinner than episzygials bearing pinnule when brachial diameter <1.7 mm (Fig. 8). Free brachials with strongly oblique muscular synarthries and large pinnule socket giving them a nearly tetrahedral shape (Fig. 7F).

**TABLE 6.** Selected measured comatulid brachials from the site RR13A on the western Rodrigues Ridge with main quantitative data. The smallest brachials were not measured. List restricted to figured brachials and brachials with minimum or maximum values of diameter in each type; diameter used as brachial growth index. D: maximum diameter, H: height, epi: episyzygial Br, hypo: hyposyzygial Br, musc: muscular synarthry (mu/musc: on both proximal and distal facets), pin: pinnule socket, sax: axial synarthry, syz: syzygy with radiate crenularium. Values in mm except ratio. See supplementary table for complete list and data of all measured brachials. Values in mm except ratio.

Catalogue n°	H	D	H/D	Figure	Articulations	Type	Remark
OPH213	2.65	3.95	0.67	Fig. 7B	sax/musc	axillary	I Br2ax?
OPH214 a	1.16	3.31	0.35	Fig. 7A	sax/musc/pin	epi	IIBr2?
OPH214 b	1.23	3.18	0.39	not figured	sax/musc/pin	epi	IIBr2?
OPH214 d	0.71	1.78	0.40	not figured	sax/musc	hypo	IIIBr?
OPH217 a	1.02	2.37	0.43	not figured	syz/musc/pin	epi	Maximum
OPH215 a	0.98	2.25	0.44	Fig. 7D	syz/musc	hypo	Maximum
OPH215 b	1.12	1.92	0.58	Fig. 7E	syz/musc/pin	epi	
OPH215 c	1.03	1.50	0.69	Fig. 7C	syz/musc/pin	epi	
OPH217 m	0.87	0.93	0.93	not figured	syz/musc/pin	epi	Minimum
OPH217 n	0.51	0.80	0.64	not figured	syz/musc	hypo	Minimum
OPH218 a	1.08	2.73	0.40	not figured	mu/musc/pin	free	Maximum
OPH216	1.73	2.32	0.75	Fig. 7F	mu/musc/pin	free	
OPH218 n	1.30	1.26	1.03	not figured	mu/musc/pin	free	Minimum



**FIGURE 8.** Variation in size and morphology of comatulid brachials from the site RR13A on the western Rodrigues Ridge. D: maxi diameter, H: height, H/D: thickness, hypo: proximal brachial of a brachial pair, epi: distal brachial with pinnule socket of a brachial pair. See supplement table for all values of quantitative characters.

Remarks: Most of the variation in quantitative characters of brachials is related to growth and thus position along the arms, the youngest brachials being the most distal and the oldest the most proximal (Fig. 8). The size of the cirrals and pinnulars is compatible with that of the brachials and the pinnule sockets. All of these ossicles can be considered to belong to a single species. Well-developed muscular synarthries with a strongly oblique orientation of free brachials indicate highly flexible arms and can suggest the ability to swim.

In the absence of hydrodynamic segregation, with the frequency and size of brachials the crown organization can be approximately assumed. The axillary with its proximal axial synarthry would belong to the primibrachitaxis (IBr2ax). Episzygial brachials bearing pinnule of diameter >3.0 mm can only belong to secundibrachitaxes of more than 2 brachials. The free brachials of H/D < 0.5 could also be IIBr. The absence of another axillary besides the single IBr2ax indicates that third branching (IIBrax) is infrequent. Their existence is suggested by the two trapezoidal brachials with axial synarthry of diameter < 2 mm that could be located in the proximal part of tertibrachitaxes. The sublinear increase in H/D correlated with the decrease in diameter distally (Fig. 8) suggests a fairly regular distribution of brachial pairs united by syzygy along uniramous arms.

Pending additional material including centrodorsals and a sufficient quantity of proximal brachials, precise assignment to a family of comatulids is not possible. In the present state of knowledge, the main characters observed on the brachial articulations are not discriminating given the frequent convergences between families (Hemery *et al.* 2013) and the lack of extensive precise SEM data available on the extant comatulid genera (Eléaume 2006).

## Discussion

### Biocorrosion and taphonomy

All ossicles are biocorroded but to varying degrees. None are recrystallised and the pores of the calcite network (stereom) are filled with micrite, albeit incompletely in most cases (Fig. 2). Microperforations on the stereom framework makes most ossicles very brittle and susceptible to attrition and abrasion. Biocorrosion of *Porphyrocrinus* columnals is the most pronounced and accompanied by marked attrition of the synarthry borders (Figs. 2D and 3), which formed sharp edges originally (Roux 1977; Messing 2016). Brachials are generally better preserved and often without evidence of attrition (Fig. 4), nevertheless the spines covering their external surface are generally broken near their base (Fig. 4E–H). Most pinnulars and cirri of the unstalked crinoid species are well preserved, while brachials show variable degrees of biocorrosion, either limited to the surface or deeply marked and accompanied by wear in the larger ones (Fig. 7A). Different stages of stereom biocorrosion were described in previous works (Gaspard & Roux 1975; Améziane-Cominardi & Roux 1987; Merle & Roux 2018) and observed here: (1) well-preserved smooth stereom, poorly perforated, with locally developed framboid spherules of pyrite, and partial filling of micrite formed only by non-echinodermal nannobioclasts (Fig. 2A), (2) development of rectilinear (Fig. 2B) or networked (Fig. 2C) microperforations leading to fractionation into calcitic nanoparticles, (3) strong dislocation of the stereom of which only a few isolated patches remain, filling of the stereom meshes by a micrite largely resulting from fractionation of crinoid calcite (Fig. 2D).

Two stalked crinoids identified here are known to live attached on hard substrate by an encrusting disc (*Porphyrocrinus polyarthra* and Hyocrinidae), while others develop rhizoids to anchor themselves in soft substrates (Rhizocrinidae, Bathycrinidae). The comatulid species anchor themselves on various substrates with their cirri. The ossicles of the species fixed on hard substrate were probably displaced before their final burial in fine-grained sediment. However, since the ossicles of *P. polyarthra* include brachials and columnals of different size and shape thus precluding hydrodynamic selection of ossicles depending on their shape and size, transportation by current action must have been very limited, if present at all. However, the absence of significant hydrodynamic sorting does not rule out displacement due to gravitational sedimentation (mass sliding, debris flow, mud flow). Current-related dislocation can be excluded altogether for the unstalked species whose abundant (nearly 200), usually well-preserved and diversified ossicles (all sizes of cirrals, brachials and pinnulars) were buried in the original sedimentary biotope. Therefore, the fossil assemblage studied here may correspond to a mixture of ossicles from different biotopes staggered along a slope.

## Diversity and biogeography

The extant Indo-Pacific species of Bathycrinidae and Hyocrinidae appear around at depth of 500–600 m but become more abundant from depths >1000 m, while *Porphyrocrinus verrucosus* and closely related species including *P. polyarthra* live at depths of 200–600 m (Tunnicliffe *et al.* 2016). *Cherbonnierocrinus* was collected in the Bay of Biscay at a depth range of 330–627 m (Roux 1976; Roux *et al.* 2019). In accordance with our comments on taphonomy, we can assume that the Pliocene sediment collected at 1460 m depth off Rodrigues thus contains a mixture of ossicles from autochthonous or sub-autochthonous species that lived at a depth at least 600–1000 m. The presence of bathycrinids and hyocrinids suggests that the depth of the depositional environment was most likely greater than 1000 m. In addition, the seabed may have subsided since the Pliocene.

The inventory of crinoid ossicles observed in the Plio-Pleistocene sediment off Rodrigues shows a relatively high taxonomic diversity for a deep environment (Table 1). Six species, each belonging to a different genus, fall into five families, four of which are stalked crinoids (Phrynocrinidae, Rhizocrinidae, Bathycrinidae, Hyocrinidae) and one an indeterminable comatulid. However, this apparent diversity is biased by the mixing of species from different biotopes and bathymetric levels. The rhizocrinid genus *Paraconocrinus* was known from late Ypresian to early Miocene in Pyrenean and Alpine foreland basins of Western Europe (Merle & Roux 2018; Roux & Philippe 2021) and remains unknown in the extant fauna. Its Plio-Pleistocene occurrence off Rodrigues is new and suggests that the genus may still live in the present-day Indian Ocean. The other identified genera have extant representatives. *Cherbonnierocrinus* was previously known only from a few specimens collected in the Danian of the Denmark, the lower Ypresian of north Pyrenean foreland basin and one extant species of the Bay of Biscay (Roux 1976; Roux *et al.* 2019, 2021). Its presence in the Indian Ocean considerably extends its geographical and paleogeographical distribution. Eléaume *et al.* (2012), analyzing the close relationships between Antarctic and Atlantic species in the genera *Bathycrinus* and *Porphyrocrinus*, suggested that deep-sea crinoid species from the Indian Ocean migrated to the central Atlantic driven by Antarctic deep bottom water currents via the South Atlantic. Moreover, taxa fixed on rocky substrate could disperse through the relative continuity of mid ocean ridges and seamount chains (Améziane & Roux 1997). The close affinities of *Porphyrocrinus polyarthra* with *P. daniellaleyae* and *P. thalassae* tend to support this hypothesis.

## Authors' contributions

M.R., B.T. and A.S.G. designed the study and wrote the manuscript; A.S.G. and B.T. collected the material; M.R. took the scanning electron microscope images; M.R., B.T. and A.S.G. compiled the figures; M.R. and B.T. analyzed and interpreted the data. All authors reviewed the final manuscript.

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## Conflict of interest

The authors declare no conflict of interest.

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**Supplementary Materials.** The following supporting information can be downloaded at the DOI landing page of this paper:

**Supplementary Table.** Measured comatulid brachials from the site RR13A on the western Rodrigues Ridge with main quantitative data. The smallest brachials (D<0.80 mm) were not measured. D: maximum diameter, H: height, epi: episyzygial brachial, hypo: hyposyzygial brachial, musc: muscular synarthry (mu/musc: on both proximal and distal facets), pin: pinnule socket, sax: axial synarthry, syz: syzygy with radiate crenularium. Values in mm except ratio.