



Article

Stalked crinoids (Echinodermata) collected by the R/V Polarstern and Meteor in the south Atlantic and in Antarctica

MARC ELÉAUME¹, JENS-MICHAEL BOHN², MICHEL ROUX¹ & NADIA AMÉZIANE¹

¹Muséum national d'Histoire naturelle, Département Milieux et Peuplements Aquatiques, UMR 7208-BOREA-MNHN/UMPC/IRD, CP 26, 57, rue Cuvier, 75231 Paris Cedex 05, France. E-mail: eleaume@mnhn.fr

²Zoologische Staatssammlung München, Münchhausenstraße 21, D-81247 Munich, Germany.

Abstract

During the last decades, R/V Meteor and R/V Polarstern deep-sea investigations in the south Atlantic and neighbouring Southern Ocean collected new samples of stalked crinoids belonging to the families Bathycrinidae, Phrynocrinidae and Hyocrinidae which are herein described. The species found are *Bathycrinus australis* A.H. Clark, 1907b (the most abundant), *Dumetocrinus* aff. *antarcticus* (Bather, 1908), *Hyocrinus bethellianus* Thomson, 1876, *Feracrinus heinzelleri* new species, and *Porphyrocrinus* cf. *incrassatus* (Gislén, 1933). As only stalk fragments of bathycrinids were frequently collected, a distinction between the two Atlantic species *B. australis* and *B. aldrichianus* is proposed using characters of columnal articulations. A few specimens attributed to *Porphyrocrinus* cf. *incrassatus*, *Hyocrinus bethellianus* and *Hyocrinus* sp. collected by the N/O Jean Charcot on the Walvis Ridge are also described, plus a new specimen of *Porphyrocrinus incrassatus* collected in the central mid-Atlantic. Biogeography and close affinities between species in the genera *Bathycrinus* and *Porphyrocrinus* suggest an Antarctic origin of some stalked crinoids among the north Atlantic deep-sea fauna. The presence of *B. australis* in both the Angola and Cape basins suggests that the Walvis Ridge is not a bio-geographical barrier for this relatively eurybathic species, which can attach to hard substrates as well as anchor in sediment. The genus *Dumetocrinus* seems to be an example of colonization of the west Antarctic platform from deeper environment where its ancestor lived.

Key words: Antarctica, south Atlantic, biogeography, deep-sea, stalked Crinoidea, Echinodermata, new species, *Bathycrinus*, *Feracrinus*, *Hyocrinus*, *Porphyrocrinus*

Résumé

Nous décrivons les crinoïdes pédonculés collectés au cours des dernières décennies par les R/V Meteor et R/V Polarstern dans l'Atlantique sud et la partie de l'océan Austral qui lui est proche. Les cinq espèces trouvées appartiennent aux familles Bathycrinidae, Phrynocrinidae et Hyocrinidae. Il s'agit de *Bathycrinus australis* A.H. Clark, 1907b (la plus abondante), *Dumetocrinus* aff. *antarcticus* (Bather, 1908), *Hyocrinus bethellianus* Thomson, 1876, une nouvelle espèce *Feracrinus heinzelleri* n.sp. et *Porphyrocrinus* cf. *incrassatus* (Gislén, 1933). Les spécimens de Bathycrinidae sont souvent très endommagés et seul le pédoncule est conservé. C'est pourquoi nous proposons de distinguer les deux espèces atlantiques *B. australis* et *B. aldrichianus* sur la base de caractères des articulations du pédoncule. Quelques spécimens collectés sur la ride de Walvis par le N/O Jean Charcot et attribués à *Porphyrocrinus* cf. *incrassatus*, *Hyocrinus bethellianus* and *Hyocrinus* sp. sont aussi décrits, ainsi qu'un nouveau spécimen de *Porphyrocrinus incrassatus* collecté dans l'Atlantique central. La distribution et les affinités étroites des espèces au sein des genres *Bathycrinus* et *Porphyrocrinus* suggèrent une origine antarctique de certains crinoïdes pédonculés abyssaux de l'Atlantique nord. La présence de *B. australis* à la fois dans les bassins de l'Angola et du Cap indique que la ride de Walvis n'est pas nécessairement une barrière biogéographique pour cette espèce eurybathe qui peut aussi se fixer sur des fonds rocheux. *Dumetocrinus* représenterait un genre ayant colonisé le plateau ouest-antarctique à partir d'un ancêtre vivant en milieux plus profonds.

Introduction

The first hyocrinid specimen, *Hyocrinus bethellianus* Thomson, 1876, was discovered in subantarctic waters off the Crozet Islands at a depth of 2926 m during the “Challenger” expedition, and described in detail by Carpenter (1884). A second specimen of the same species was collected at the foot of the slope of the Antarctic shelf off Enderby Land at a depth of 4636 m during the Deutschen Tiefsee Expedition (Döderlein 1912). In about the same depth range (3000–4500 m), two specimens of *Ptilocrinus brucei* Vaney, 1908 were dredged by the “Scotia” during the Scottish National Antarctic Expedition off the east coast of the tip of the Antarctic Peninsula (Vaney & John 1939). During the Expédition Antarctique Belge the “Belgica” collected *Dumetocrinus antarcticus* (Bather, 1908) at a shallower depth (480 m) on the western slope of the Antarctic Peninsula (John 1937). A. H. Clark (1915) summarized knowledge on all Antarctic crinoids to that date. Mironov & Sorokina (1998a–b) reported on new Antarctic specimens of hyocrinids collected by the recent Russian deep-sea investigations and described several new species from the vicinity of the type locality of *Ptilocrinus brucei* at depths exceeding 3000 m. They mentioned the presence of *H. bethellianus* in the northwestern Pacific, documenting a larger range of distribution of that Antarctic species than previously expected.

The “Challenger” dredged the first subantarctic bathyrcrinid at a depth of 2500–3000 m, west of the Crozet Islands. Carpenter (1884) attributed the specimen to *Bathyrcrinus aldrichianus* Thomson, 1876, but A.H. Clark (1907b) distinguished it as a new species, *Bathyrcrinus australis*. This species was later recorded from the southern Atlantic and southwestern Pacific at depths ranging from 1700 to 8300 m (Döderlein 1912, Gislén 1956, McKnight 1973, A.M. Clark 1977). Roux (1980a) mentioned *Porphyrocrinus* cf. *incrassatus* (Gislén, 1933) and *Hyocrinus* from the Walvis Ridge.

Here, we describe new specimens of stalked crinoids collected during R/V Meteor and R/V Polarstern cruises in the south Atlantic and Southern Ocean east of the Antarctic Peninsula with additional data on specimens collected in 1978 during the N/O Jean Charcot cruise on the Walvis Ridge. We also discuss their taxonomic affinities and the problems raised by their biogeography. The specimens collected during the cruises of R/V Meteor and R/V Polarstern are housed in the Bavarian State Museum Collection of Zoology in Munich. The zoological collections of the Muséum national d’Histoire naturelle in Paris house the material from French cruises. The author of the description of *Feracrinus heinzelleri* n. sp. is J.M. Bohn. For morphological terms, see Roux *et al.* (2002) and Roux & Lambert (2011).

Institutions are abbreviated as follows: Institut Royal des Sciences Naturelles de Belgique, Bruxelles = IRSNB; Natural History Museum, London = NHM; Muséum national d’Histoire naturelle, Paris = MNHN; Smithsonian Institution National Museum of Natural History, Washington = USNM; Bavarian State Museum Collection of Zoology, Munich = ZSM.

Taxonomy

Family Bathyrcrinidae Bather, 1899

Remark. The family Bathyrcrinidae is here accepted *sensu stricto* following Mironov (2008).

Genus *Bathyrcrinus* Thomson, 1872

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

Synonymy: *Bathyrcrinus* Thomson, 1872: 772; *Ilycrinus* Danielssen & Koren, 1877: 45; A.H. Clark, 1908a: 236; 1915: 153–154; 1917: 389–390; *Bathyrcrinus* Gislén, 1938: 14–15; Roux, 1977: 27–28; Rasmussen, 1978: T844; Roux *et al.*, 2002: 815, 818, 822; Mironov, 2008: 135–136; Hess, 2011a: T153.

Remarks. It is difficult to distinguish Atlantic species using only external morphological characters as proposed by A.H. Clark (1908a) in his key to species in the genus *Bathyrcrinus*. *B. aldrichianus* Thomson, 1876 and *B. gracilis* Thomson, 1872 have similarly very serrated crown profiles, and *B. gracilis* displays sharper median crests on the division series. However, A.M. Clark (1977: 160) suggested that “possibly further material may indicate that only

one species can be recognized". Both *B. carpenteri* Danielssen & Koren, 1877 from the Norwegian Sea and the Arctic Ocean and *B. australis* A.H. Clark, 1907b from the South Atlantic and Southern Ocean differ in having smooth rounded brachials. Characters other than external morphology are required to clearly distinguish among these different *Bathycrinus* species. As pointed out by Roux (1977), highly derived characters present in articulations of xenomorphic stalks allow a better distinction between taxa and can be used for taxonomic attribution of isolated stalks. The *Bathycrinus* stalk exhibits two divergent ontogenetic profiles of columnals: the first one develops rigidity in the mesistele, the second provides flexibility in the dististele (Duco & Roux 1981, Fig. 2). Below, we provide additional information on stalk synarthries and their ontogeny which can be used as discriminating characters in taxonomy.

For details on characters of external morphology used to distinguish *B. aldrichianus* and *B. australis*, see Gislén (1956) and A.M. Clark (1977). Moreover, new distinctive characters in bathycrinids such as pinnule architecture have been proposed by Mironov (2000, 2008).

***Bathycrinus aldrichianus* Thomson, 1876**

Figure 1; Table 1.

Synonymy: *Bathycrinus aldrichianus* Thomson, 1876: 47–51, fig. 1; *Bathycrinus campbellianus* P. H. Carpenter, 1884: 238–240, fig. 15; *Bathycrinus serratus* A.H. Clark, 1908b: 205–207, fig. 1; *Bathycrinus aldrichianus* Gislén, 1938: 15–16; 1951: 51–52, pl. (figs 1–2, 5); Macurda & Meyer, 1976: 647–667, figs. 1–5; pl. 1–5; A.M. Clark, 1977: 159–162, fig. 1g; Mironov, 2008: 143; Hess, 2011a: T153, fig. 75 (1m–n).

Material examined. Specimens from Pillsbury expedition, 1965, station P-292 (Table 1), housed in the collections of the Smithsonian Institution, Washington D.C., catalogue number USNM E17896.

TABLE 1. Sampling stations of *Bathycrinus aldrichianus* Thomson, 1876.

Cruise/Station	Location	Depth (m)	Reference	Remarks
Challenger Exped./106	01°47'N–24°26'W	3382	Thomson, 1876	Holotype (crown)
Albatross/2226	37°00'N–71°54'W	3739	A.H. Clark, 1908b	1 crown <i>B. serratus</i>
Albatross/2713	38°20'N–70°08.3'W	3398	A.H. Clark, 1908b	1 distal stalk
Atlantis/1948	34°53'N–46°24'W	4625	A.H. Clark, 1949	2 stalks
Swedish Deep-sea Exped./329	09°38'N–26°20'W	5600–5610	Gislén, 1951	1 small crown
Swedish Deep-sea Exped./371	24°12'N–63°23'W to 24°28'N–63°18'W	5850–5860	Gislén, 1951	1 stalk
Pillsbury, 1965	00°12'N–05°11'E	3595	Macurda & Meyer, 1976	12 specimens
Chain/50	37°59.2'N–69°26.2'W	3834	A.M. Clark, 1977	1 small armless
Atlantis II cruise 60/259A&D	37°13'S–52°45'W	3305–3317	A.M. Clark, 1977	2 crowns

Complementary description of stalk articulations. In *B. aldrichianus*, the transition from relatively rigid mesistele to flexible dististele is rapid and restricted to the distalmost stalk. The ratio of columnal height to maximum diameter is >2.8 (up to 3.6) in the mesistele and <1 in the dististele. The branched distal rootlike radix is adapted to anchoring into soft sediment. Macurda & Meyer (1976) were the first to describe the stalk articulations using SEM in a specimen from the Gulf of Guinea. From the same sample, we give additional information on their ontogeny (Fig. 1). In mesistele columnals of small juveniles, the proximal articular facet is flat and circular, whereas the distal facet has a ligamentary pit on each side of the wide rudimentary fulcral ridge (Fig. 1A). In middle-sized specimens, ligamentary depressions become deep and the fulcral ridge has concave lateral sides (Fig. 1B–D). In large stalks, synarthries are rounded oval in middle and distal mesistele with the longest diameter perpendicular to the fulcral ridge (Fig. 1E), which remains very wide (1/3 of diameter) and is covered by vermiculated syzygial stereom. A similarly wide fulcral ridge was observed in *B. gracilis* (Roux 1987: fig. 15E) confirming that the two species are very closely related. As usual in bathycrinids, dististele synarthries are strongly oval with the

longest diameter corresponding to a narrow fulcral ridge and wide ligamentary depressions (Fig. 1F). The axial canal separates the fulcral ridge into two segments with sharp inner ends, and with dense calcite and regular rows of small crenulae (up to 15–18 on each segment) along their axes.

Occurrence. *B. aldrichianus* is known from NW, central and SW Atlantic at depths ranging from 3317 to 5850 m, possibly from 3305 to 5860 m (Table 1).

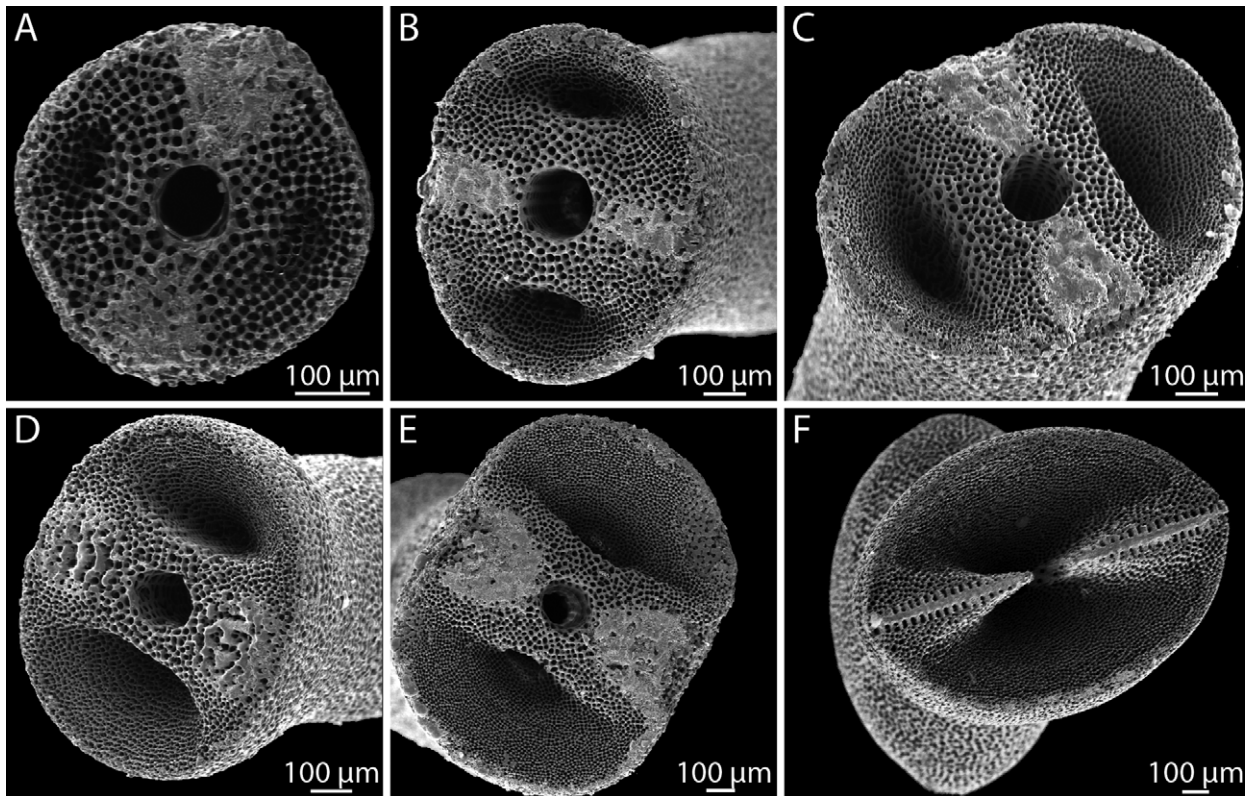


FIGURE 1. Stalk articulation in *Bathycrinus aldrichianus* (USNM E17896). A–B: proximal synarthries, C: mid mesistele synarthry, D–E: distal mesistele synarthries, F: dististele synarthry, A: small juvenile, B–D: medium-sized specimen, E–F: large specimen.

Bathycrinus australis A.H. Clark, 1907b

Figure 2; Tables 2–3.

Synonymy: *Bathycrinus aldrichianus* Carpenter, 1884: 241–243, pl. 7, pl. 7a (figs. 1–21), pl. 7b, pl. 8a (figs 4–5); *Bathycrinus australis* A.H. Clark, 1907b: 553–554; Döderlein, 1912: 9–10, pl. 5 (fig. 1), pl. 6 (fig. 7); *Ilycrinus australis* A.H. Clark, 1915: 154–155; Vaney & John, 1939: 661; *Bathycrinus australis* Gislén, 1938: 16; 1956: 61–62, pl. 1 (figs. 1–6); Mc Knight, 1973: 204–205; A.M. Clark, 1977: 162–164; *Bathycrinus* cf. *aldrichianus* Bohn, 2006: 7–9, fig. 2A; *Bathycrinus australis* Mironov, 2008: 141,143.

Material examined. External morphological features of specimens examined (Table 2) fall within the range of variation described by A.M. Clark (1977), especially with a flared radial ring and smooth flanged arms (Fig. 2A–B). Bohn (2006) reported only stalk fragments and a single incomplete juvenile crown from DIVA stations and attributed them to *B. cf. aldrichianus* mainly on biogeographical evidence. These specimens are attributed here to *B. australis* based the analysis of their stalk articulations.

Description of stalk articulations. The distal end of the stalk varies from several fused columnals bearing radicules that penetrate soft sediment (Fig. 2C) to robust ramification that encrust rocks or pebbles (Fig. 2E). Usually, the transition is gradual (Fig. 2D) between the mesistele which has columnals significantly higher than wide (ratio height to maximum diameter >3 in mid mesistele), and the dististele in which columnals are nearly as high as

wide (Fig. 2C, E). In the largest specimens, distal synarthries have a large extension of deep ligament fossae; each segment of the fulcral ridge is bottle-shaped and has two rows of 35–40 small crenulae underlining its axis (Fig. 2F–G). In the dististele of young specimens, synarthries resemble those of *B. aldrichianus* (Fig. 2H). Mesistele synarthries are well developed in juveniles and have larger and deeper ligamentary depressions (Fig. 2K–L), and medium-sized specimens have strongly rounded oval facets with the longest diameter perpendicular to the fulcral ridge. As growth increases, the fulcral ridge becomes relatively narrower around axial canal with convex lateral sides (Fig. 2I–J). Stalk articulations in *B. australis* and *B. aldrichianus* differ significantly, especially in their mesistele synarthries.

Occurrence. *B. australis* occurs in the South Atlantic with northern records from the deep Argentina plateau and Angola basin. It is also known from the Southern Ocean and the southern Indian Ocean from east of the Antarctic Peninsula to the Kermadec Trench and New Zealand (Tables 2–3). The depth range is large and extends from 1525 m to 8210 m, possibly from 1488 to 8300 m.

TABLE 2. Sampling stations of *B. australis* A.H. Clark, 1907b collected during R/V Polarstern (PS) and R/V Meteor (M) cruises. *: after Bohn (2006).

Cruise/Station	Location	Depth (m)	Catalogue n°	Remarks
EASIZ I/PS 39/18 AGT4b	73°16.70' S–21°25.50' W to 73°16.10' S–21°24.70' W	1538–1543	ZSM 20020004	10 specimens
DIVA I/M 48/1-327	19°59.2'S–3°00.9'E to 20°07.5'S–3°07.9'E	5439–5448	ZSM 20043082	1 stalk fragment *
DIVA I/M 48/1-334	19°12.5'S–3°49.0'E to 19°19.8'S–3°55.6'E	5425–5426	ZSM 20043081	3 stalk fragments *
DIVA I/M 48/1-337	18°18.9'S–4°42.7'E to 18°24.6'S–4°45.1'E	5392–5393	ZSM 20043085 ZSM 20020069	8 stalk fragments * 1 stalk fragment *
DIVA I/M 48/1-339	18°19.4'S–4°42.1'E to 18°25.3'S–4°44.0'E	5392–5395	ZSM 20043083	7 stalk fragments *
DIVA I/M 48/1-344	17°06.2'S–4°41.7'E to 17°07.5'S–4°42.3'E	5415	ZSM 20043084	1 stalk fragment *
DIVA II/M 63/2-42	28°0,206' S–7°16,905' E to 28°4,029' S–7°20,821' E	5082–5089	ZSM 20070048	1 stalk fragment
ANDEEP II/PS 61/131-4	65°19.47' S–51°32.55' W to 65°19.78' S–51°31.41' W	3049–3052	ZSM 20043097 ZSM 20043086	1 stalk fragment 1 broken crown
ANDEEP II/PS 61/132-3	65° 17.88' S–53°22.88' W to 65°17.35' S–53°22.89' W	2087–2084	ZSM 20043096	1 juvenile with proximal stalk
ANDEEP II/PS 61/134-3	65°19.54' S–48°05.47' W to 65°19.47' S–48°04.27' W	4060–4065	ZSM 20043098	1 large specimen
ANDEEP II/PS 61/138-4	62°57.80' S–27°52.14' W to 62°57.77' S–27°51.10' W	4543–4545	ZSM 20043095	1 specimen
ANDEEP III/ PS 67/057-2	69°24.50' S–5°19.27' W to 69°24.62' S–5°19.68' W	1819–1822	ZSM 20070049	1 specimen
ANDEEP III/PS 67/059-10	6730.37' S–03.74' E to 6730.27' S–04.34' E	4648–4648	ZSM 20070050	1 specimen
ANDEEP III/ PS 67/153-7	6319.31' S–6436.94' W to 6319.15' S–6437.18' W	2092–2118	ZSM 20070051	1 specimen
ANDEEP III/PS 67/153-8	63°19.21' S–64°37.07' W to 63°19.10' S–64°37.13' W	2108–2124	ZSM 20070052	235 specimens
ANT XXI/2/PS 65/109-1	70°47.88' S–11°21.56' W to 70°47.88' S–11°24.13' W	1488–1525	ZSM 20070047	~90 specimens

TABLE 3. Sampling stations of *Bathycrinus australis* A.H. Clark, 1907b previously published.

Cruise/Station	Location	Depth (m)	Reference	Remarks
Challenger Exped./147	46°16'S–48°27'E	2926	Carpenter, 1884	2 syntypes, see
Challenger Exped./146	46°46'S–45°31'E	2514	A.H. Clark, 1915	A.M. Clark, 1977
Tiefsee Exped./152	63°16'S–57°51'W	4636	Döderlein, 1912	1 specimen
Scotia	62°10'S–41°20'W	3246	Vaney & John, 1939	1 specimen
Galathea/649	35°16'S–178°40'W	8210–8300	Gislén, 1956	4 specimens
NZOI/G831	37°45'S–171°24.3'E	1730–1748	McKnight, 1973	1 specimen
Atlantis II cruise 60/245A&B	43°33'S–48°58.1'W	5208–5223	A.M. Clark, 1977	27 specimens
Atlantis II cruise 60/247A&B	36°55.7'S–53°01.4'W	2707	A.M. Clark, 1977	2 or 3 specimens

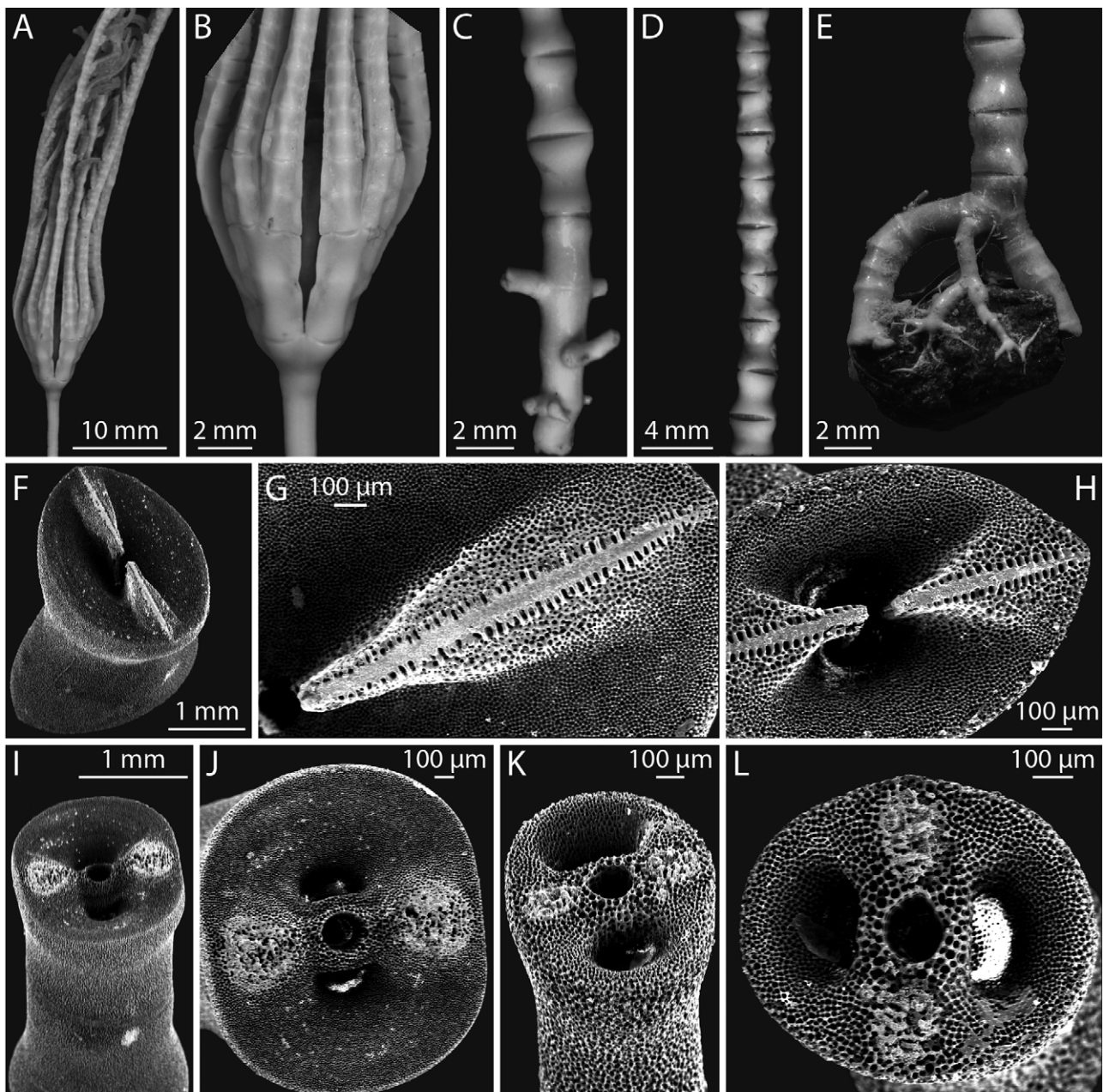


FIGURE 2. *Bathycrinus australis* (ZSM 20020004). A–G, I–J: large specimen; H, K–L: juvenile specimen; A–B: views of crown; C: distal stalk with bases of thin roots; D: progressive transition from dististele to mesistele; E: other distal stalk with large roots encrusting pebble; F–H: distal synarthries; I–L: mesistele synarthries.

Family Hyocrinidae Carpenter, 1884

Genus *Dumetocrinus* Mironov & Sorokina, 1998a

Type species of the genus by monotypy: *Ptilocrinus antarcticus* Bather, 1908.

Synonymy: *Dumetocrinus* Mironov & Sorokina, 1998a: 413; Mironov & Sorokina, 1998b: 19; *Ptilocrinus* sensu lato pars. Roux *et al.*, 2002: 822; *Dumetocrinus* Roux & Lambert, 2011: 45–48, fig. 33; Hess, 2011b: T174.

Dumetocrinus aff. *antarcticus* (Bather, 1908)

Figure 3.

Synonymy: *Dumetocrinus antarcticus* Gutt *et al.*, 2011: 6, fig. 4D.

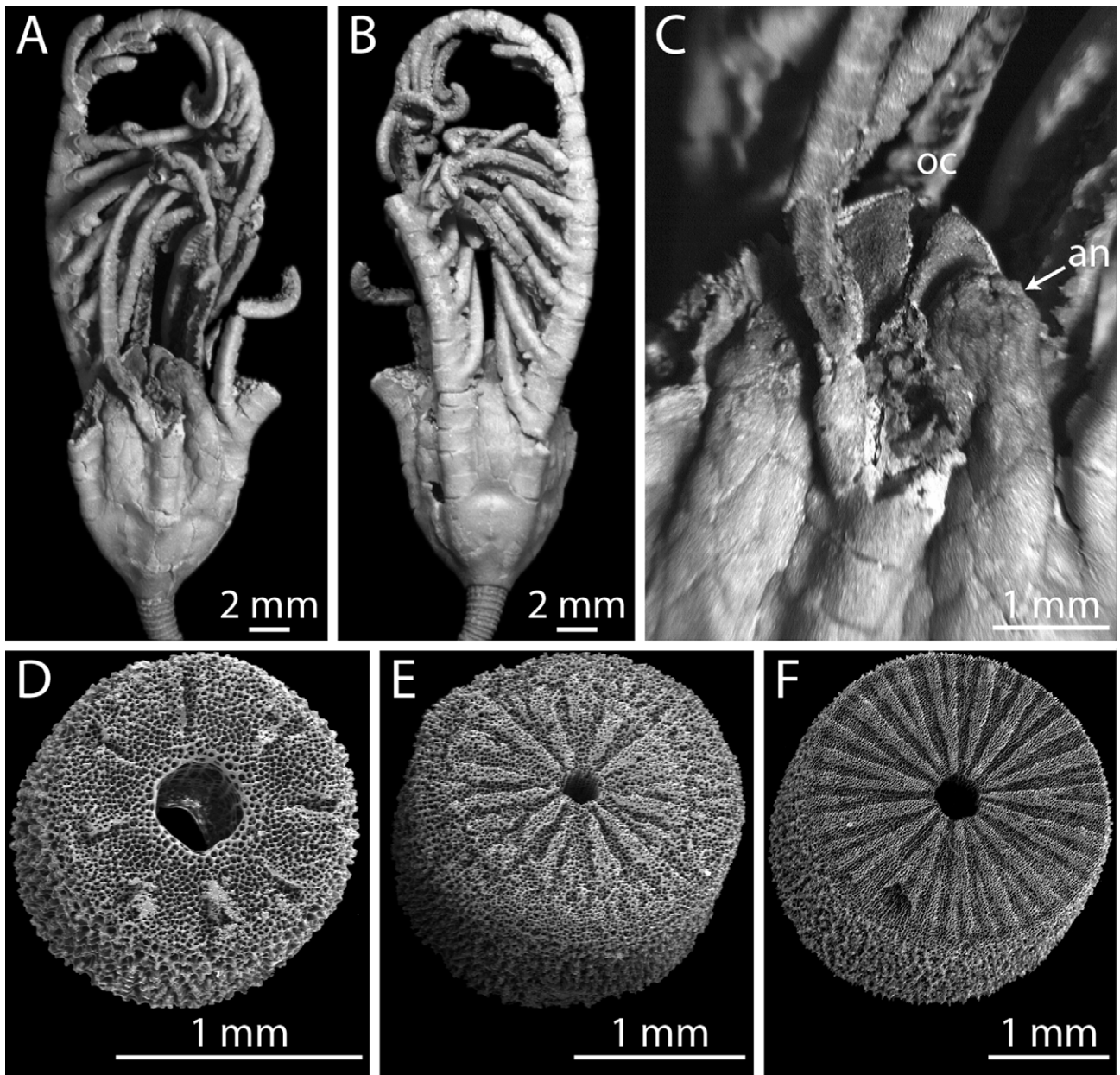


FIGURE 3. *Dumetocrinus* aff. *antarcticus*. A–E: specimen PS69/710-5; F: holotype of *Dumetocrinus antarcticus* (IRSNB 1897/1999-10131-589); D: symplexy of proximal mesistele; E–F: syzygies in distal stalk; an: anal sac; oc: oral cone.

Material examined. Holotype (spec. B) and two paratypes (spec. A, C), IRSNB 1897/1999-10131-589; paratype (spec. D) NHM 1937-4-29-1: Belgica Expedition, Faubert 11, sta. 589, W of Antarctic Peninsula, 70°23'S–82°47'W, 480 m, 1898. R/V Polarstern cruise ANT XXIII/8, station PS69/710-5 Larsen area, E of Antarctic Peninsula, 65° 32.94' S–61° 38.59' W, depth 242 m, 2007 (1 specimen with distalmost stalk missing).

Description. Specimen almost complete except for the distalmost stalk (Fig. 3A–B); length of preserved stalk 10.0 cm with proximalmost diameter 1.9 mm; height of aboral cup 6.3 mm with diameter at top of radial ring 6.9 mm; ratio of radial upper width to primibrachial width 2.0 to 2.2; arm length about 36 mm; maximum pinnule length 16 mm. Dorsal cup and tegmen smooth and brachials without lateral wings. Relatively gracile arms with up to 20 well-differentiated pinnules on each side; first pinnule always on Br4. Arm pattern 1+2 3 4 5+6 7 8+9 10 11 12 13 (3 cases), one arm broken at Br20 after 12 successive muscular articulations, the single complete arm with brachial pairs at 17+18 and 28+25. Tegmen moderately inflated with anal cone lower than oral cone and conspicuous concave orals (Fig. 3C). Pinnules without genital inflation and lateral plates, very sharp triangular cover plates as described by John (1937: fig. 2). Proximal columnals articulated by symplexies with 8 crenular units of 1 crenula (Fig. 3D), distal syzygies with radial crenularium of relatively wide crenulae (Fig. 3E).

Remarks. This specimen differs from specimens of the type-series of *D. antarcticus* mainly in lacking thecal ornamentation (see John 1937, fig.1), adoral inflation of arms and pinnules, H-shaped plates and lateral plates in pinnules (see Mironov & Sorokina 1998a, fig. 5), and by fewer number of crenular units in symplexies than described by Roux (1980b). However, the arm pattern, typically sharp cover plates, tegmen characters and general pattern of stalk articulation (see for comparison Fig. 3E and 3F) suggest very close affinities with *D. antarcticus*. In the genus *Ptilocrinus*, two closely related species also differ mainly in the presence versus absence of proximal inflation and lateral plates in pinnules (Roux & Lambert 2011). The absence of genital inflation in pinnules may also be a juvenile trait. However, both this specimen and those in the type series of *D. antarcticus* are of similar sizes. If this specimen without inflated genital pinnules is a juvenile, adults would be much larger than in *D. antarcticus*. It was also collected in shallower water than the latter species. Because a new species should not be described from a juvenile specimen, additional specimens are required to determine whether or not it is distinct from *D. antarcticus*.

Occurrence. East of the Antarctic Peninsula (Larsen area). Data from photographic survey (Gutt *et al.* 2011) document a depth ranging from 193 to 449 m (Julian Gutt and Stephanie Langner, personal communication), the shallowest record for any Hyocrinidae.

Genus *Feracrinus* Mironov & Sorokina, 1998a

Type species of the genus: *Feracrinus aculeatus* Mironov & Sorokina, 1998a.

Synonymy: *Ailsacrinus* Mironov & Sorokina, 1998a: 404–405; *Feracrinus* Mironov & Sorokina, 1998a: 410; *Camaecrinus* Mironov & Sorokina, 1998b: 21–22; *Feracrinus* Mironov & Sorokina, 1998b: 20; *Ptilocrinus* sensu lato pars. Roux *et al.*, 2002: 822; *Feracrinus* Amézière & Roux, 2011: 138–140; Roux & Lambert, 2011: 45–48, fig. 33; Hess, 2011b: T174.

Emended diagnosis. Proximal arm pattern usually 1+2 3 4 5+6 7+8 or 5+6 7 followed in middle arm by successive brachial pairs (a+b c+d ...) or by a+b c d+e f ...; distal arms with fewer than 5 successive muscular articulations in juvenile or small species and up to 22 in large specimens. First pinnule always on Br4. Proximal part of genital pinnules with one row of H-shaped plates. Anal cone lower or higher than oral cone. Basals fused, or basal ring with one to three sutures. Stalk symplexies and distal syzygies with well developed crenularium; symplexial crenular units 6–10 of 1–3 crenulae; distal stalk with syzygies of labyrinthic crenularium.

Feracrinus heinzelleri n. sp.

Figures 4–6.

Etymology. This new species is dedicated to Professor T. Heinzeller Ludwig-Maximilian-University, Munich (Germany), who has contributed substantially to our understanding of crinoid anatomy.

Material examined. Holotype (catalogue number ZSM 0000/1) and one paratype (catalogue number ZSM 0000/2) R/V Polarstern cruise ANT IX/3, station 18/192, 27.02.1991, off Queen Maud Land, 69°40.3' to 69°40.5' S–00°51.1' to 00°54.8' E, 1393–1398 m, housed in the Bavarian State Museum Collection of Zoology (ZSM) in Munich.

Diagnosis. A small species with robust arms of proximal pattern 1+2 3 4 5+6 7+8 or 5+6 7; beyond Br6 series of successive brachial pairs (a+b c+d e+f...) or brachial pairs alternating with free brachials (a+b c d+e f...); series of up to 4 successive muscular articulations. Pinnules relatively robust and rigid; insertion deep, carved on arm side and impacting the following brachial pair; synarthrial articulation on brachial with strong symmorphy; concave cover plates varying from lanceolate to rounded; genital pinnules with one row of additional H-shaped plates. Ratio of primibrachial width to upper radial height 0.73 to 0.85. Tegmen with oral cone higher than anal cone; orals large and erect around mouth; anal cone conspicuous in C–D inter-ray and bearing large bulging plates. Conical dorsal cup with ratio of cup height to upper diameter 1 to 1.3; basals fused; radials trapezoidal. Columnal symplexies with 8 crenular units; distal syzygies unknown.

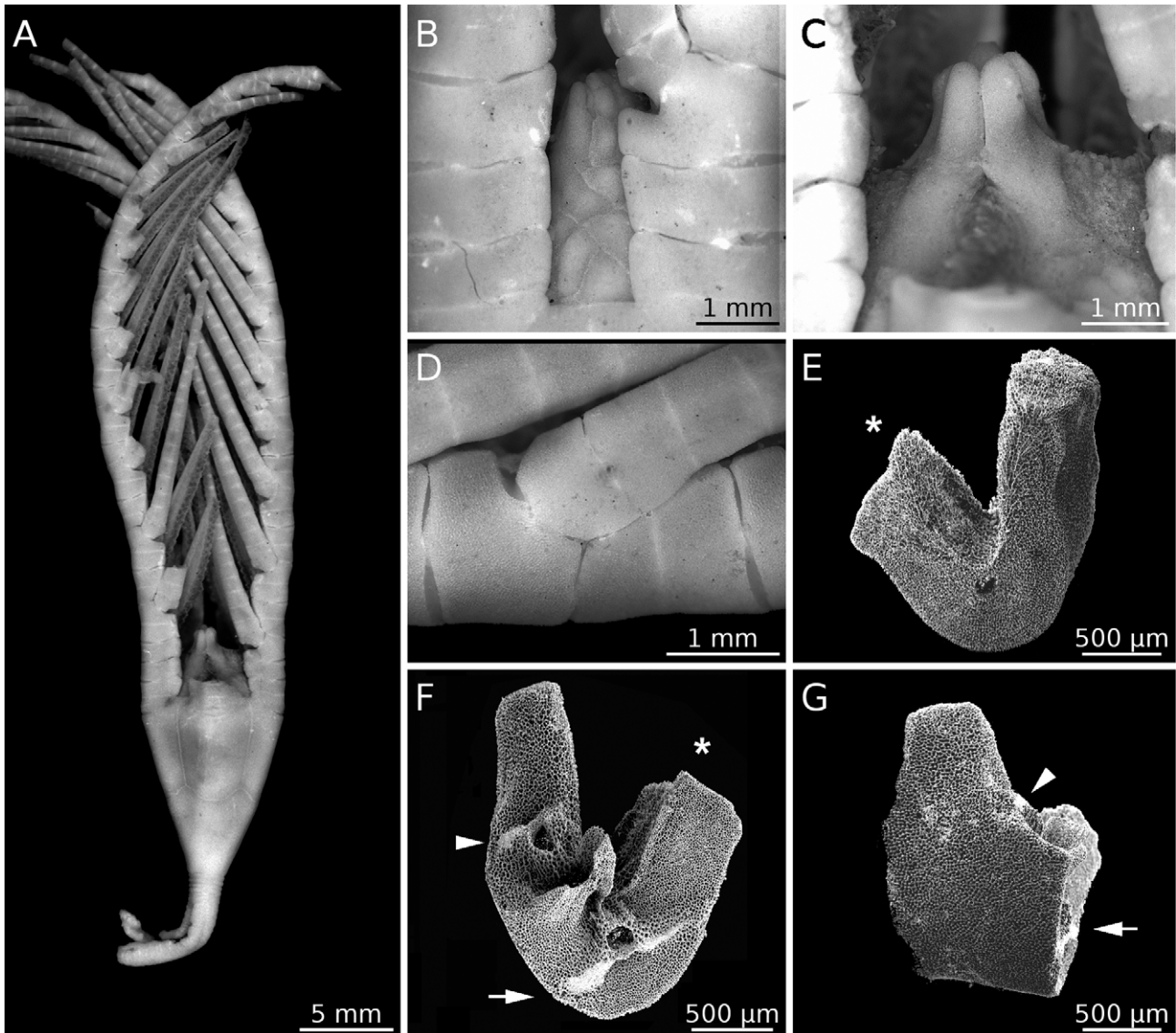


FIGURE 4. Holotype of *Feracrinus heinzelleri* n. sp. (ZSM 0000/1). A: general view with ray broken at Br2/3; B: anal sac in CD interray; C: oral cone, view from broken A ray; D: lateral view of pinnule insertion on arm; E: hyposynostosal brachial showing flat synostosal facet; F: episynostosal brachial, distal facet showing pinnule socket (arrow head) and interbrachial muscular synarthry (arrow); G: lateral view of same brachial (side of pinnule insertion). Star: muscular articulation.

Description of the holotype. Specimen consisting of proximalmost stalk, theca and partly broken crown (Fig.4A). Tegmen heavily plated and not inflated; tegminal plates of variable shape, some perforated by hydropores; anal cone height 2.8 mm, covered by relatively large bulging plates and conspicuous in C–D inter-ray (Fig. 4B); oral cone height 3.6 mm with conspicuous, convex and smooth orals surrounding beak-like mouth (Fig. 4C); ambulacral grooves merging into arms at height of Br4. Aboral cup tall conical with large ribs prolonging arm axes; cup height 9.3 mm, upper diameter 7.2 mm, lower diameter 2.0 mm, ratio of cup height to upper diameter 1.3.

Radials trapezoidal, height 5.3 mm, upper width 3.7 mm, lower width 2.7 mm. Ratio of primibrachial width to upper radial height 0.73 to 0.77. Basals fused, height of basal ring 3.7 mm. Remaining proximal stalk 6.6 mm long, proximalmost diameter 1.7 mm.

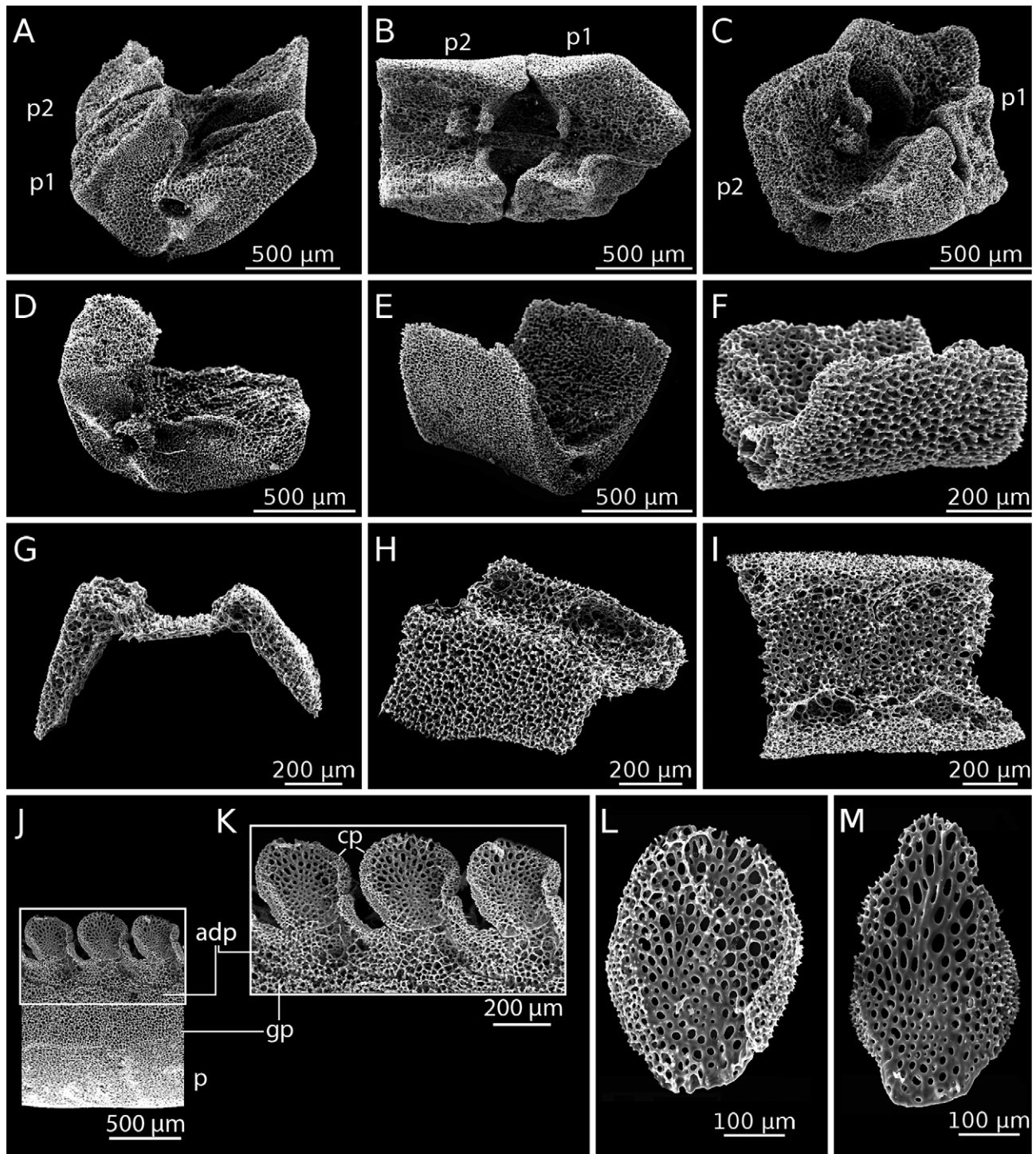


FIGURE 5. Holotype of *Feracrinus heinzelleri* n. sp. (ZSM 0000/1), pinnule ossicles. A–C: views of the two proximalmost pinnulars (p1 and p2); A: proximal adoral view showing facet of muscular transverse synarthry; B: adoral view, proximal transverse synarthry at right, distal synostosis at left, p1 articulated to p2 by muscular synarthry (see D); C: distal adoral view showing flat synostosomal facet; D: proximal synarthry of p2; E: pinnular in mid pinnule with synostosomal facets; F: distal pinnular with muscular articulations; G–I: H-shaped genital plate; G: front view; H: lateral external view, ambulacral side at top; I: lateral internal view; J: profile view of genital, H-shaped and covering plates on genital pinnule; K: detailed view of covering plates; L–M: dissociated proximal cover plate. adp: additional lateral plates; cp: cover plates; gp: genital H-shaped plates; p: pinnular.

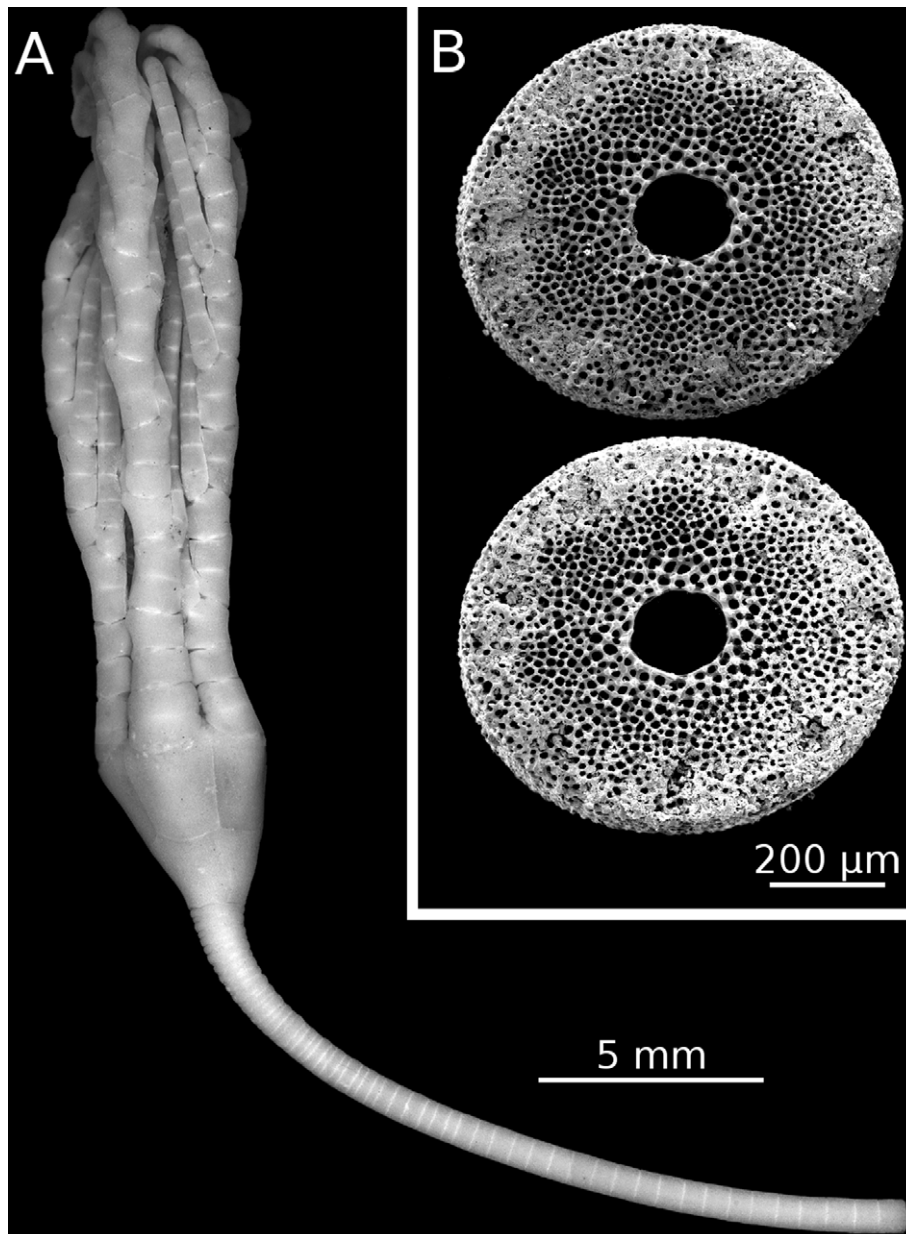


FIGURE 6. Paratype of *Feracrinus heinzelleri* n. sp. (ZSM 0000/2). A: general view; B–C: distal columnals of preserved stalk.

One arm broken at Br2–3, other arms with the same pattern: 1+2 3 4 5+6 7+8 9+10 11+12 13+14 15 16+17 18, with first pinnule on Br4. Series of successive muscular articulations up to 3. Primibrachial width 2.7 mm decreasing progressively to 2.0 mm at Br5+6. Most complete remaining arm 40 mm long and bearing 12 pinnules on each side. Pinnules relatively robust and rigid; width decreasing rapidly and progressively from proximal pinnular to distal end. Pinnule insertion deep, carved on arm side and impacting the following brachial pair (Fig. 4D). Most complete pinnule (24 pinnulars) in medial arm reaching a length of 16.0 mm. Brachial synostoses flat (Fig. 4E). Pinnule articulated on brachial by large transverse symmorphial synarthry with a deep ligament fossae (Fig. 4F–G). First pinnular (p1) with a sharply convex proximal facet (Fig. 5A–B); p1 and p2 articulated by well-developed muscular synarthry (Fig. 5B–D); other pinnulars articulated by synostoses (Fig. 5E–F). Proximal part (up to p12) of genital pinnules inflated, with H-shaped additional plates (Fig. 5 G–I) supporting a row of small upper lateral plates (Fig. 5J–K); cover plates concave varying from lanceolated to rounded (Fig. 5M–N).

Description of the paratype. Young immature specimen completely preserved except distal stalk and one arm broken at Br9+10 (Fig. 6A). Five relatively robust and smooth arms with 7–8 pinnules on each side; arm length about 19 mm with 27–28 brachials. Proximal pattern 1+2 3 4 5+6 7, with first pinnule on Br4; successive muscular

articulations up to 4. Primibrachial width 1.7 mm progressively decreasing to 1.0 mm beyond Br5+6; distance between arm base and synostosis Br5+6 3.9 mm. Pinnule length up to 8.9 mm for 17 pinnulars. Tegmen with large erect orals; oral cone height 1.8 mm, anal cone height 1.3 mm. Aboral cup with fused basals and trapezoidal radials, cup height 4.1 mm, upper diameter 4.0 mm, lower diameter 1.3 mm, ratio of cup height to upper diameter about 1. Basal height 1.6 mm, radial height 2.5 mm; lower radial width 1.6 mm, upper radial width 2.0 mm. Ratio of primibrachial width to upper radial width 0.85. Length of preserved stalk of 66 columnals 28.0 mm. Proximal most diameter 1.2 mm, decreasing to 0.8 mm at a distance of 2.8 mm from aboral cup and maintaining the same value to distal end. In distal half of preserved stalk, columnals barrel-shaped with height 0.6–0.7 mm. Columnal symplexes less developed, galleried stereom predominating with larger meshes around lumen; 8 small crenular units of 1 crenula near outer border (Fig. 6B–C).

Remarks. *F. heinzelleri* n. sp. is a species smaller than *F. aculeatus* and *F. koslowi*. It is distinguished by having a highly conical aboral cup, smooth convex orals, narrow inter-rays (ratio of primibrachial width to upper radial height >0.7), anal cone with relatively large bulging plates and pinnules deeply inserted on arm side impacting the following brachial pair. Stalk articulations are only known in the proximal part of a juvenile specimen, without data on distal syzygies which usually bear specific characters (Améziane & Roux 2011). *F. heinzelleri* n. sp. shares with *F. koslowi* the same pattern of proximal and mid-arm articulations with rare free brachials. These two species live at about the same depths, whereas *F. aculeatus* lives in deeper environments.

Occurrence. Antarctica slope, E of Weddell Sea, at a depth between 1393 and 1398 m.

Genus *Hyocrinus* Thomson, 1876

Type species of the genus: *Hyocrinus bethellianus* Wyville Thomson, 1876

Synonymy: *Hyocrinus* Thomson, 1876: 47; Carpenter, 1884: 217; A.H. Clark, 1915: 162; Mironov & Sorokina, 1998b: 30–31; Roux, 2002: 174; Roux & Lambert, 2011: 45–46, 48–52, fig. 33; Hess, 2011b: T173.

Hyocrinus bethellianus Thomson, 1876

Figures 7–8; Table 4.

Synonymy: *Hyocrinus bethellianus* Thomson, 1876: 51–54, figs 2–5; Carpenter, 1884: 218–224, pl. V (figs 4–10), pl. VI; Doderlein, 1912: 5–9, figs 1–2, pl. I (figs 1–5), pl. II (figs 1–6), pl. IX (fig. 1); Clark, 1915: 162–163; Rasmussen, 1978: T828, fig. 556-4; Roux, 1980b: 34, 36, 42–46, pl. II (figs 1–2); Mironov & Sorokina, 1998b: 31; *H. bethellianus bethellianus* Mironov & Sorokina, 1998b: 31; *H. bethellianus* subsp. n. Mironov & Sorokina, 1998b: 31–33, fig. 9, pl. 5 (Figs 1–4), pl. 10 (Fig. 5); *H. bethellianus* Roux & Pawson, 1999: 294; Roux *et al.*, 2002: 821; Roux & Lambert, 2011: 46, 48, 51, figs 33–34; Hess, 2011b: T173, fig. 85 (1a–b).

Material examined. R/V Polarstern cruise ANDEEP III/PS 67/142-6, 62°10'32"S, 48°29'41"W to 62°9'43"S, 48°30'43"W, depth 3403–3405 m (1 large specimen ZSM 20043128). Walvis I/ CP01, 33°53'6"S, 05°07'2"E to 33°53'6"S, 05°06'7"E, 5037–5040 m, 1978, (1 juvenile specimen, MNHN IE-2012-756).

Description. Specimen ZSM 20043128: Complete specimen except distal end of stalk (Fig. 7A). Tegmen not inflated, with a pyramidal oral cone of large concave orals (Fig. 7B–C); 15–20 tegminal plates of variable size and number per interray; C–D interray with small globular anal sac and oral with a conspicuous tubercle in center (Fig. 7B); food grooves with cover plates in a gathered arrangement forming a bridge between orals and Br6; tegmen height 4.5 mm at top of oral cone. Aboral cup slightly higher than broad, height 10.9 mm, upper radial diameter 9.9 mm; diameter at radial/basal sutures 8.1 mm, radial height 6.4 mm, radial width 6.3 mm; primibrachial width 1.5 mm, ratio of radial to primibrachial width 4.14. Inter-rays very wide and arms gracile (Fig. 7A). Maximum arm length about 80.0 mm; up to 11 pinnules per arm side; maximum pinnule length 16.5 mm, proximalmost arm pattern always 1+2 3+4 5+6 with the first pinnule on Br6 at left; usually (97%) brachial triplets (a+b+c) distally except two cases of brachial pair (a+b) on the same arm. Genital inflation in six or seven proximal pinnules of each arm, due to one row of H-shaped plates becoming irregular and smaller proximally with an additional row of lateral plates (Fig. 7D); cover plates regularly rounded with a radial ornamentation of small stereom meshes near the outer border (Fig. 7E). Length of proximal stalk attached to aboral cup 49.4 mm; proximalmost diameter 1.96 mm, distally decreasing to 1.65 mm at a distance of 3.4 mm from basal ring, to 1.55 mm at a distance of 6.4 mm

and up to 1.35 mm at distal broken end. Proximal columnal articulated by symplexes with 8 crenular units of 1–2 crenulae, areola of large stereom meshes and a large axial canal (ratio of lumen to columnal diameter 0.4) with a conspicuous claustrum (Fig. 7F–G); distalmost preserved columnals about as high as broad articulated by symplexes with smaller axial canal (ratio of lumen to columnal diameter 0.2) and predominating radial crenularium (Fig. 7H).

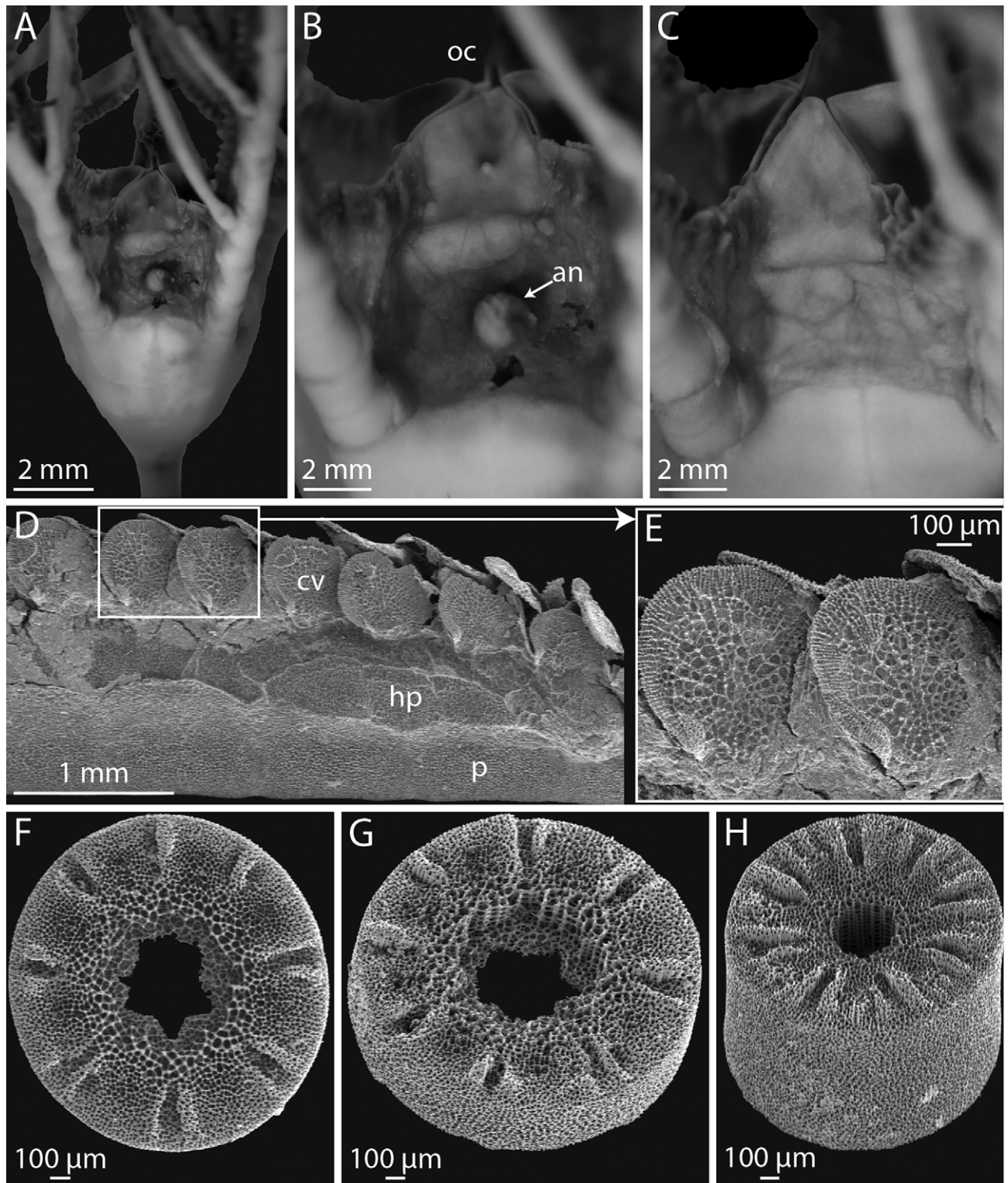


FIGURE 7. *Hyocrinus bethellianus* (ZSM 20043128). A: proximal arms and theca, view of anal (C–D) interarray; B: enlargement of A, showing tegmen with large oral cone (oc) and small anal cone (an); C: tegmen in A–B interarray; D: proximal inflation of genital pinnule (p: pinnular, hp: H-shaped plates, cv: cover plates); E: detail of cover plates; F–G: proximal columnal; H: distal columnal of the preserved stalk.

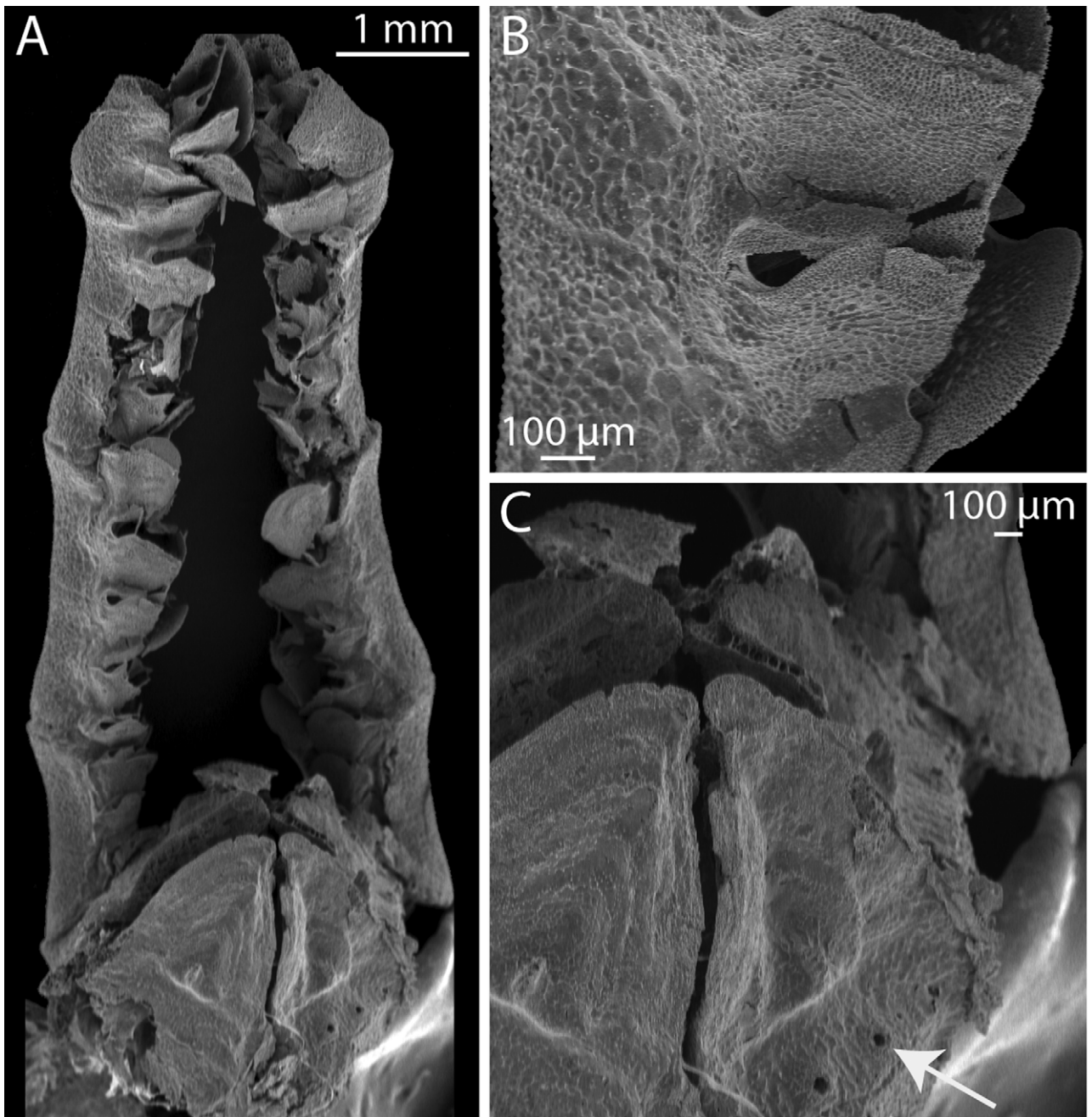


FIGURE 8. Juvenile of *Hyocrinus bethellianus* (MNHN IE-2012-756) from Walvis Ridge. A: oral cone with two proximal arms; B: lateral view of arm with cover plates; C: detail of orals with three hydropores at base of right oral (arrow).

Specimen MNHN IE-2012-756: Small juvenile (Fig. 8A). Arms broken at Br6 (length 6.2 mm), proximal pattern 1+2 3+4 5+6 with base of first pinnule on Br6; proximal pinnulars as wide as brachials; proximal arm cover plates rounded (Fig. 8B), resembling those on pinnules of ZSM 20043128 and becoming diamond-shaped distally. Tegmen restricted to oral cone (Fig. 8C); orals concave with hydropores at base, oral height 1.6 mm, diameter at tegmen base 3.1 mm, anal cone inconspicuous. Aboral cup broken. Length of preserved proximal stalk attached to broken basal ring 3.9 mm, proximalmost diameter 0.48 mm, diameter at broken end 0.39 mm.

Remarks. The holotype (Carpenter, 1884) and the Vityaz specimen (Mironov & Sorokina, 1998b) are relatively small. The specimen ZSM 20043128 is significantly larger. However, it is slightly smaller than the Tiefsee specimen (Döderlein, 1912). These four specimens share the main characters of the species despite the wide variations in their aboral cups. The mesistele symplexes of the holotype have 6 or 7 crenular units of 1 small crenula restricted to the facet border (Roux, 1980b), which correspond to an early stage of columnal ontogeny. The ZSM

specimen displays the derived characters (greater number of tegminal plates, well developed crenularium with 8 crenular units of up to 2 crenulae), which appear throughout ontogeny in larger specimens. The small juvenile from Walvis Ridge undoubtedly belongs to *H. bethellianus* because of its typical cover plates. The Vityaz specimen from the North Pacific documents a wider species distribution in the Indo-Pacific province than previously expected.

Occurrence. North Pacific, Antarctic slope off Enderby Land, W of Crozet Island and SW of Walvis Ridge, at depths of 2926 to 5037 m, possibly 2915 to 5040 m.

TABLE 4. Sampling stations of the five specimens of *Hyocrinus bethellianus* Thomson, 1876 currently known. N: number of specimens.

Cruise/Station	Location	Depth (m)	N	References
Challenger Exped./47	46°16' S–48°27' E	2926	1	Carpenter, 1884
Tiefsee Exped./152	63°16' S–57°51' E	4636	1	Döderlein, 1912
Vityaz, 1955/ 3364	48°21.2' N–168°54.1' E	2915–3015	1	Mironov & Sorokina, 1998b
Walvis I/ CP01	33°53'6 S–05°07'2 E to 33°53'6 S–05°06'7 E	5037–5040	1	juvenile this paper
ANDEEP III/PS 67/142-6	62°10'32"S–48°29'41"W to 62°9'43"S–48°30'43"W	3403–3405	1	this paper

Hyocrinus sp.

Figure 9.

Synonymy: « *Hyocrinus* proche de *H. (Gephyrocrinus) grimaldii* » Roux, 1980b: 903.

Material examined. Walvis I cruise, station DS01, 33°53'9 S–05°05'9 E to 33°53'9 S–05°06'4 E, 5205–5240 m, 1978 (1 juvenile, MNHN IE-2012-755).

Description. Complete specimen except distal stalk (Fig. 9A). Length of preserved stalk 5.1 mm, proximal-most diameter 0.7 mm, diameter at end of preserved stalk 0.5 mm. Aboral cup conical with basal fused, cup height 2.4 mm, upper radial diameter 3.3 mm, diameter at basal/radial suture 1.9 mm, lower basal ring diameter 0.9 mm, radial height 1.4 mm. Tegmen with small anal cone and moderately large orals (Fig. 9B); orals concave with a median knob in their lower part, tegmen height 1.1 mm. Arm length 12.8 mm, proximal arm pattern 1+2 3+4 5+6 with first pinnule on Br6; arm as wide as pinnule; cover plates triangular with sharp top (Fig. 9C).

Remarks. This juvenile specimen undoubtedly belongs to the genus *Hyocrinus* and to a different species than *H. bethellianus* based on its tegmen and cover plates. Cover plates with similarly sharp triangular ends have been described in *Hyocrinus cyanae* Bourseau *et al.*, 1991 (Roux 2004, Fig. 7b) collected off New Caledonia at a depth of 2536 m, suggesting that this specimen could belong to this latter species. Confirmation of its identity with new material, would give *Hyocrinus cyanae* a wide Indo-Pacific distribution similar to that of *H. bethellianus*.

Family Phrynocrinidae A.H. Clark, 1907a

Genus *Porphyrocrinus* Gislén, 1925

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

Synonymy: *Porphyrocrinus* Gislén, 1925: 91–92; ? *Monachocrinus* pars Gislén, 1933: 483–485; *Porphyrocrinus* A.M. Clark, 1973: 281–282; 1982: 123; Rasmussen, 1978: T847; Roux *et al.*, 2002: 815, 818, 824; Messing, 2007: 106–107; Hess, 2011a: T157.

Remarks. The species of the genus *Porphyrocrinus* have 5 arms or more with the first pinnule (or first branching) on Br8 or beyond and a basal ring with 5 conspicuous sutures. The xenomorphic stalk has proximal columnals with pentamerous symmetry and the same type of synarthry in the mesistele and dististele with a fulcral ridge of two separated segments always along the greater facet diameter.

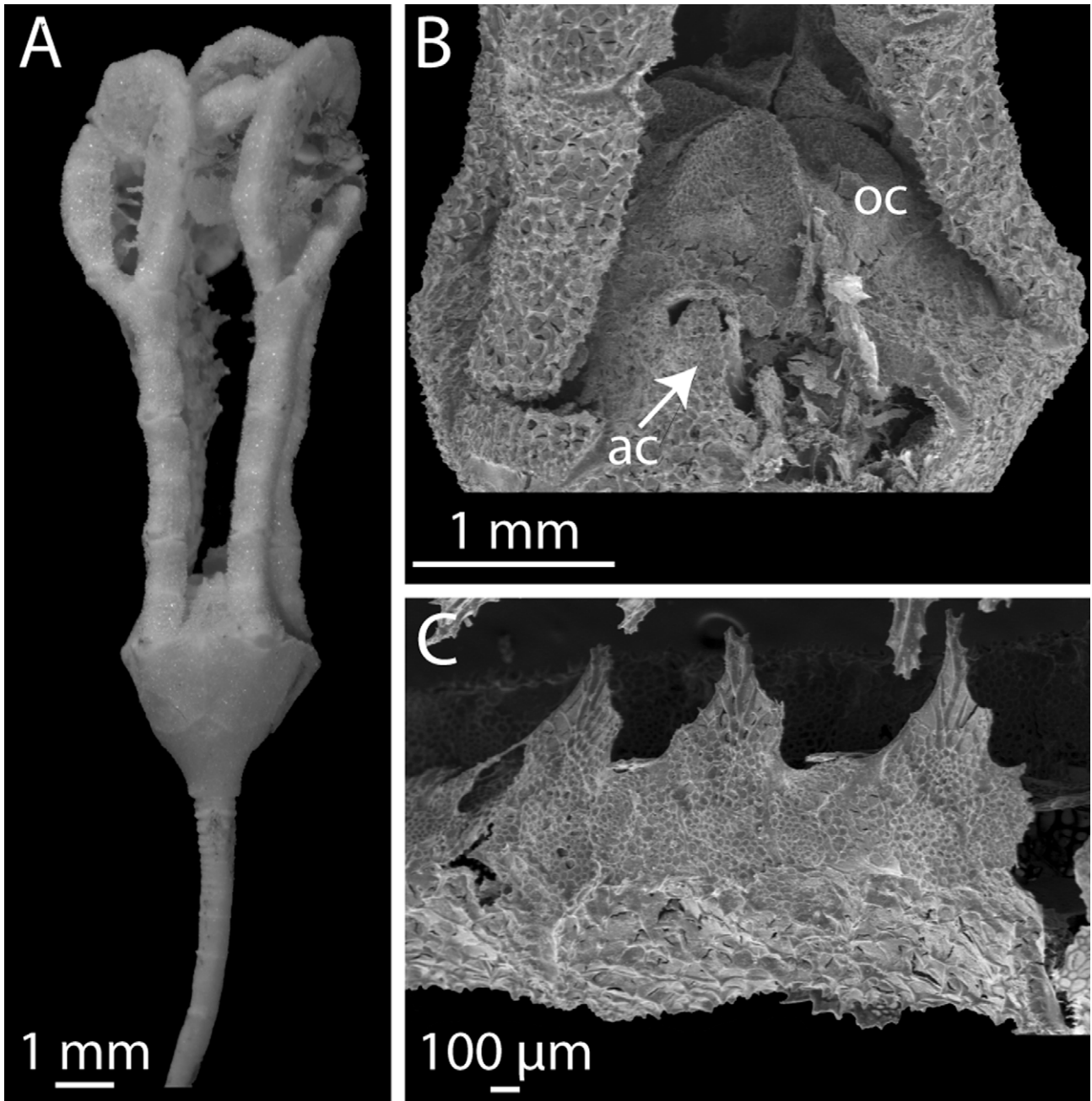


FIGURE 9. Juvenile of *Hyocrinus* sp. (MNHN IE-2012-755) from Walvis Ridge. A: general view; B: tegmen with oral cone (oc) and anal cone (ac), one arm removed; C: lateral view of arm with sharp cover plates.

***Porphyrocrinus incrassatus* (Gislén, 1933)**

Table 5.

Synonymy: *Monachocrinus incrassatus* Gislén, 1933: 483–485, text figs 6–9, pl. 23 (figs 5–7); 1938: 20; A.M. Clark, 1973: 281–282; *Porphyrocrinus incrassatus* Roux, 1977: 38, 55–56, text figs 1A, 15, pl. II (figs 4–5), pl. X (figs 1–7); 1985: 481; Roux *et al.*, 2002: 806, 824, fig. 2D.

Material examined (Table 5). Seven specimens collected from the Bay of Biscay (Roux 1977) are housed in the collections of the Muséum national d’Histoire naturelle, Paris (catalogue numbers MNHN IE-2012-758 and IE-2012-759). One additional specimen (catalogue number MNHN IE-2012-757) was collected during the French cruise “Hydrosnake” in Central Atlantic using the submersible “Nautilé” (dive HS18) on the western wall of the

axial valley of the Mid Atlantic Rise.

Description of Hydrosnake specimen. Complete stalk, aboral cup and first ring of brachials. Aboral cup height 1.63 mm, upper radial diameter 1.89 mm, basal ring low (ratio of radial to basal height 3.2) with conspicuous sutures. Stalk length 177 mm, proximalmost diameter 1.45 mm, decreasing to 1.02 mm at a distance of 17.9 mm from aboral cup, then progressively increasing with development in distalmost columnals of strongly elliptical synarthries up to 4.01 mm at fulcral ridge axis; proxistele of 10 thin columnals of equal height united by non-functional articulations; maximum columnal height 4.92 mm at a distance of 30 mm from distal end. Roux *et al.* (2002: fig. 2D) showed a well-developed distalmost elliptical synarthry with the same proximal mesistele with circular synarthries as in specimens from the Bay of Biscay (Roux, 1977: pl. X, figs 4–5).

Occurrence. North Atlantic (Mid-Atlantic Rise, Bay of Biscay) and South Atlantic (Saint Helena), at depths of 1300 to 2400 m, possibly 1300 to 2780 m.

TABLE 5. Sampling stations of the eleven specimens attributed to *Porphyrocrinus incrassatus* (Gislén, 1933) or with currently known close affinities (*). N: number of specimens..

Cruise/Station	Location	Depth (m)	N	References
Dana, 1930	Off Saint Helena ~15.5°S–5.4°W	2400–2780	1	Gislén, 1933 Holotype
Thalassa 1973/Z429	48°28'N–09°50'W	1300	1	Roux, 1977
Thalassa 1973/Z452	48°41'5 N–10°53'W to 48°39'N–10°55'2W	1420–1470	6	Roux, 1977
Walvis I, 1979/DS01	33°53'9S–05°05'9E to 33°53'9S–05°06'4E	5205–5240	1	Roux, 1980b* and this paper
Hydrosnake 1988/HS18	23°27'N–45°03'W	2068	1	This paper
DIVA II, 1994/M 63/2-42	28°0,206' S–7°16,905' E 28°4,029' S–7°20,821' E	5089–5082	1	This paper*

Porphyrocrinus cf. incrassatus (Gislén, 1933)

Figure 10; Table 5.

Synonymy: *Porphyrocrinus cf. incrassatus* Roux, 1980b: 904.

Material examined (Table 5). One distal stalk fragment (Bavarian State Museum Collection of Zoology in Munich, catalogue number ZSM 20070046) was dredged in the Cape Basin during R/V Meteor cruise DIVA II. One specimen which had been cited (Roux 1980b) but not described is housed in the collections of the Muséum national d'Histoire naturelle, Paris (catalogue number MNHN IE-2012-760). It was dredged by N/O Jean Charcot during the French cruise “Walvis I” (station DS01) at the south-eastern foot of the Walvis ridge.

Description. Walvis specimen: proximal stalk, aboral cup and proximal crown (Fig. 10A). Aboral cup of maximum height 1.9 mm with radial ring more flared than basal ring (Fig. 10B); diameter at basal/stalk junction 1.4 mm, at radial/basal sutures 1.6 mm, at upper radial border 2.3 mm, maximum basal height 0.9 mm, maximum radial height 1.1 mm; ratio of radial to basal height 1.2; five basals with conspicuous sutures. One arm preserved to Br9 (length 0.96 mm) with first pinnule on Br8, two arms to Br4, one to Br5, and fifth restricted to Br1+2; arm pattern with successive brachial pairs; all brachials constricted at mid height; muscular articulations larger than synostoses (Fig. 10C). Preserved stalk length 14.1 mm with 15 subcylindrical columnals and diameter at broken end 0.98 mm; proxistele of five columnals united by non-functional articulations; height of proximalmost columnal 0.4 mm, height of distalmost preserved columnal 1.16 mm (ratio of height to diameter 1.2); beyond proxistele, columnals articulated by synarthries with circular facet with 8-shaped deep ligamentary pit and short fulcral ridges of 6–7 small crenulae on each side (Fig. 10D–E).

Incomplete stalk from Cape Basin: length 57 mm, mesistele only, with proximal part of circular joints missing; diameter at fulcral ridge axis 0.8 mm proximally and 1.04 mm distally, columnal height respectively 3.5 mm and 4.3 mm with ratio of height to diameter 4.4 and 4.1. All articulations are synarthries with areolar depression and

fulcral ridge more developed at distal than at proximal end (Fig. 10F–G). This stalk fragment belongs to a specimen smaller than the Walvis one.

Remarks. The Walvis *P. cf. incrassatus* and Hydrosnake *P. incrassatus* are both about 1.75 larger than the holotype of *P. incrassatus* from Saint Helena (Gislén 1933) and the largest *Thalassa* specimens from the Bay of Biscay (Roux 1977). The Walvis specimen is the only one that retains the proximal crown. It differs from the Hydrosnake specimen in having shorter radials and fewer proximal columnals although these differences may be due to its larger size or to intraspecific variations. Such wide range of variation in external morphology was also observed (Messing 2007) in the Indo-Pacific species *P. verrucosus* Gislén, 1925 (= *P. polyarthra* A.M. Clark, 1973). This species is larger with short brachials not constricted at mid height, and lives at significantly shallower depths (218–400 m). Therefore, the Walvis and Cape Basin specimens are not interpreted as juvenile specimens of *P. verrucosus*. They lived at greater depth (more than 5000 m) than the other specimens of *P. incrassatus* (<3000 m). As a complete specimen of *P. incrassatus* has not yet been found, the attribution of specimens listed in Table 5 to a single species remains questionable.

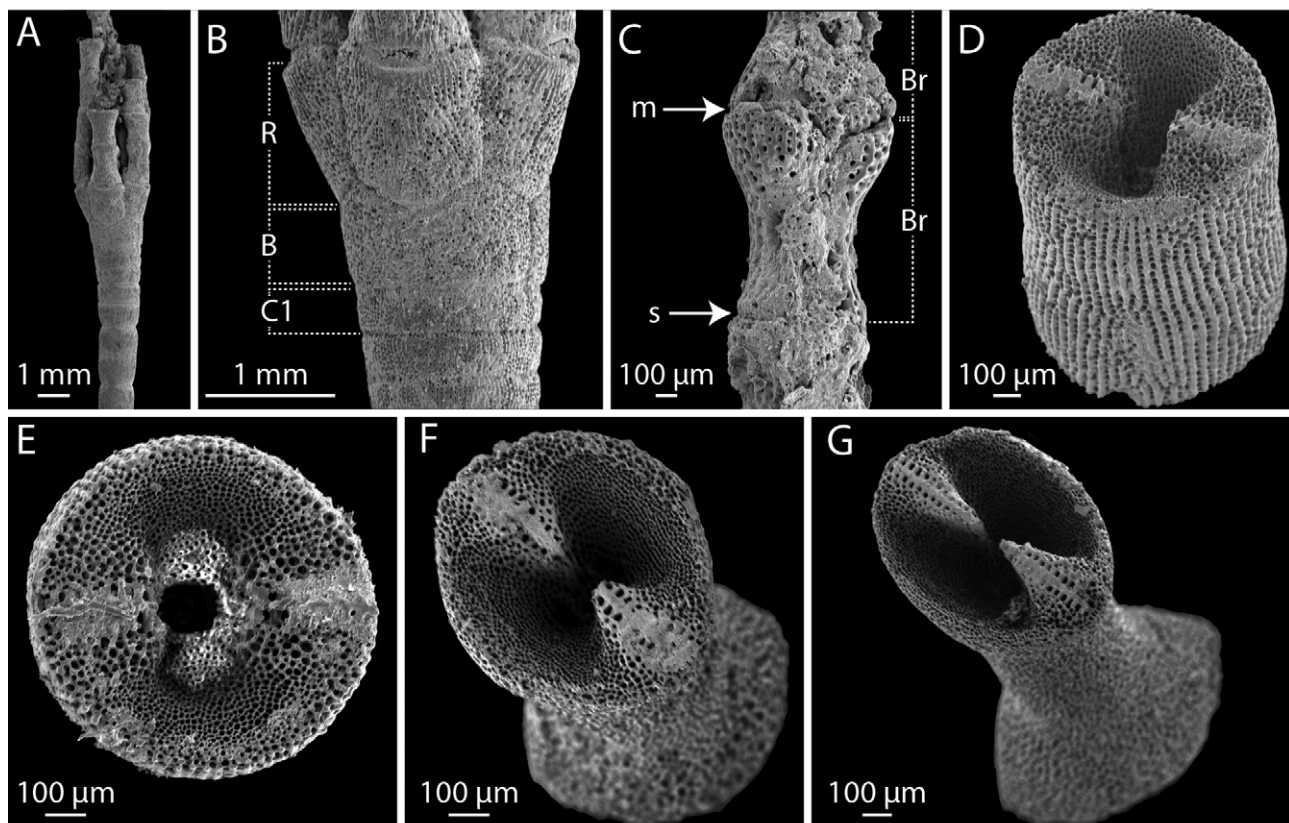


FIGURE 10. *Porphyrocrinus cf. incrassatus*. A–E: Walvis specimen (MNHN IE-2012-760); A: general view; B: aboral cup (B: basal ring, C1: proximalmost columnal, R: radial ring); C: detail of arm with muscular synarthry (m) and synostosis (s) Between brachial (Br) pairs; D–E: distal mesistele columnal of preserved stalk; F–G: Cape Basin stalk fragment (ZSM 20070046); F: proximal columnal (more distal position than D–E); G: distal columnal.

Biogeography

The recent records in the South Atlantic–Indian Ocean junction of *Feracrinus heinzelleri* n. sp. from the Antarctic slope east of the Weddell Sea, two species of *Hyocrinus* from south of the Walvis Ridge, and specimens of *Dumetocrinus* from the Larsen area, west of the Weddell Sea, confirm that many hyocrinid genera and species are more widely distributed in the Indo-Pacific province than previously expected. A new *Ptilocrinus* species was also found from the southern Indian Ocean (Kerguelen Plateau) and southern Pacific Ocean off the Ross Sea (Eléaume *et al.*, 2011). The genus *Feracrinus* was previously known from the North Pacific Ocean (Mironov & Sorokina, 1998b) and southern Tasmanian Seamounts (Amézière & Roux, 2011). *Hyocrinus bethellianus* is now known from the

North Pacific Ocean to the South Atlantic (Walvis Ridge). If the attribution of the Larsen specimen to *D. antarcticus* is confirmed, the species range would be extended to both the west and east of the Antarctic Peninsula. Larsen specimens live in an exceptionally shallow environment for hyocrinids. The ice shelf is thought to have provided a shelter against wave hydrodynamic stress and facilitated the emergence of bathyal fauna (see Gutt *et al.* 2011 for other examples).

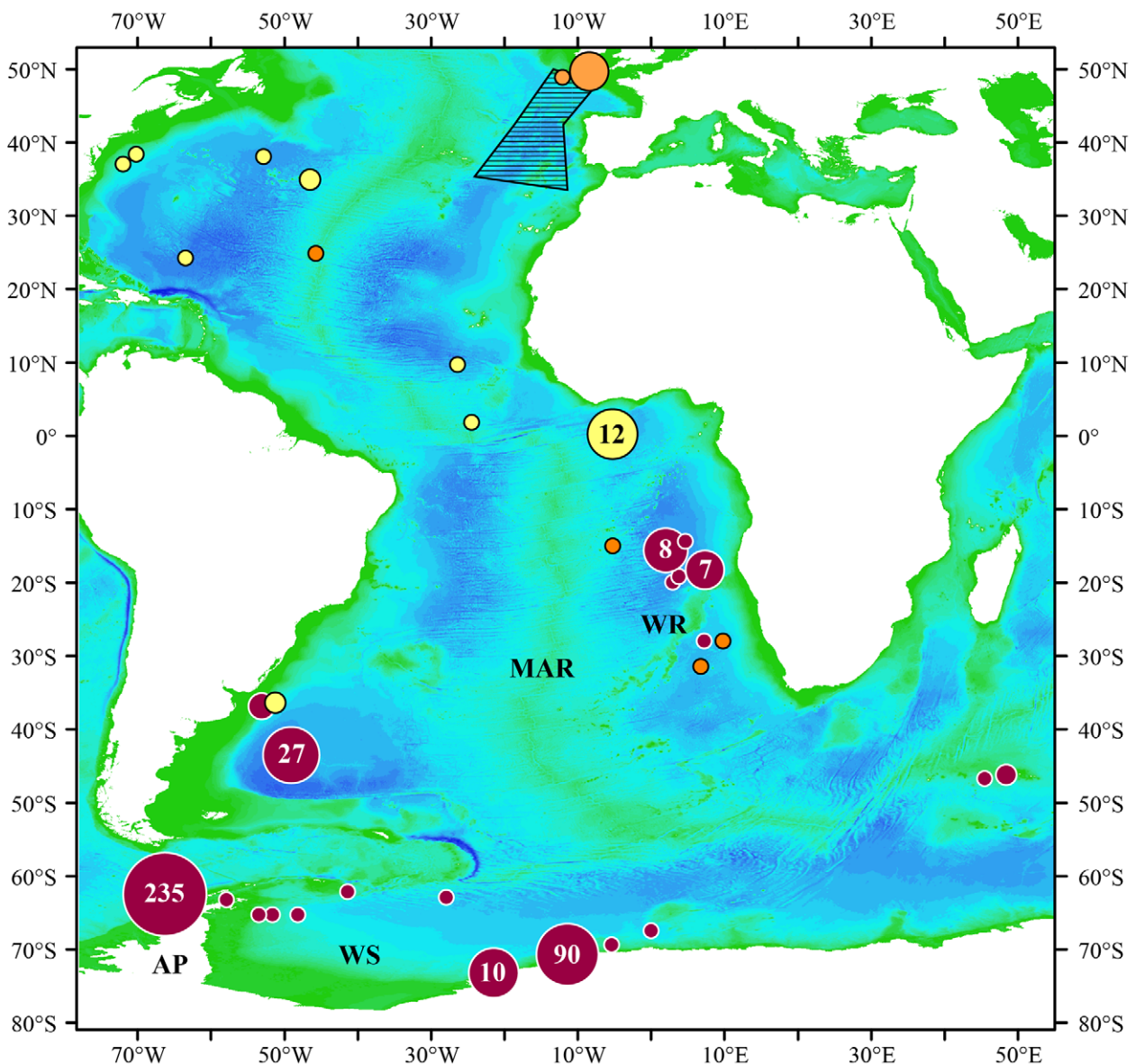


FIGURE 11. Records of species belonging to the genera *Bathycrinus* and *Porphyrocrinus* in the South Atlantic and neighbouring Southern Ocean waters. Hachured area: *Bathycrinus gracilis* record locations, orange dots: *Porphyrocrinus incrassatus* or closely related specimen record locations, red dots: *Bathycrinus australis* record locations, yellow dots: *Bathycrinus aldri-chianus* record locations, AP: Antarctic Peninsula, MAR: Mid Atlantic Ridge, WR: Walvis Ridge, WS: Weddell Sea. numbers indicate the number of specimens dredged at the given location.

Bathycrinus australis was found on both sides of the Walvis Ridge and also on both sides of the Antarctic Peninsula indicating that neither feature constitutes a barrier to its dispersal of *B. australis*. *B. australis* was collected in large numbers (Tab. 2, Fig. 11) mainly from the slope of the Antarctic Peninsula, at shallower depths (1500–2000 m) relative to the wide depth range of this species. These areas obviously constitute suitable habitats for this species where it certainly reproduces and recruits. Other deeper areas seem to shelter less successful populations as reflected by very low numbers of specimens. The Antarctic populations might thus be source populations that produce propagules that may be advected by the thermohaline expressway (Strugnell *et al.* 2008) and particularly the northward Weddell Sea Bottom Water (WSBW) flow. These conditions have existed since the Middle

Miocene (Maldonado *et al.*, 2003). It is therefore a possibility that the close affinity between *B. australis* and *B. aldrichianus*, their somewhat overlapping distribution areas (Fig. 11), and the depth range of *B. australis* are best explained by polar submergence of *Bathycrinus* and subsequent colonization of the deep Atlantic. The current lack of any robust morphological distinction between *B. aldrichianus* and *B. gracilis* (A.M. Clark 1977) suggests that these taxa have recently diverged and that the North Atlantic *B. gracilis* with its most derived characters represent a more recent and northern component of the *australis/aldrichianus* lineage.

B. australis is able to colonize both soft and hard substrata (Fig. 2E), whereas *B. aldrichianus* and *B. gracilis* with their thin roots are restricted to soft sediments. Madsen (1961) and Hansen (1975) first proposed that the abyssal fauna could have recently evolved from bathyal taxa. Such evolution related to the growth of the Antarctic ice cap since Oligocene times could explain the Atlantic biogeographical pattern of the genus *Bathycrinus* at the species level. Such a hypothesis might be strengthened by the distribution of *P. incrassatus*, but *Porphyrocrinus* is restricted by its encrusting terminal stalk disk to hard bottoms and might spread along the Mid Atlantic Rise and seamounts as suggested by Améziane and Roux (1997) for bathycrinids and hyocrinids.

Dumetocrinus species probably represent a case of polar emergence. As documented by Roux and Lambert (2011), the deep-sea *Ptilocrinus* species are basal to *Dumetocrinus*. This suggests that the common ancestor of *Ptilocrinus* and *Dumetocrinus* was a deep-sea species and that the upper slope to shelf distribution of the shallower *Dumetocrinus* results from the polar emergence of this lineage.

Conclusion

A clear demonstration of the importance of the analysis of the ontogeny of the stalk articulations in Bathycrinidae for species attribution is given. This criterion is successfully used to distinguish between three closely related *Bathycrinus* species presumably belonging to the same lineage: *B. australis*, *B. aldrichianus* and *B. gracilis*. The new species of Hyocrinidae *Feracrinus heinzelleri* n. sp. from Antarctic slope east of Weddell sea, and new records of *Dumetocrinus* and *Hyocrinus* from the west Weddell Sea and the Walvis ridge extend the known distributions of these three hyocrinid genera to the Southern Atlantic–Indian Ocean junction, indicating that they belong to the Indo-Pacific Province with a wider distribution than previously recognized. Reaching relatively shallow-water habitats on the Antarctic shelf and upper slope, perhaps associated with shelter from hydrodynamic wave stress by the ice cap, *Dumetocrinus* is a likely case of polar emergence whereas *B. australis*, *B. aldrichianus* and *B. gracilis* may represent a lineage that has undergone a polar submergence following the WSBW flow into the north Atlantic. These hypotheses need to be reassessed using independent datasets, e.g. molecular-based phylogenies.

Acknowledgements

We thank A. Cabrinovic for access to the specimens housed in the Natural History Museum (NHM) in London; D.L. Pawson for access to the specimens housed in the Smithsonian Institution (USNM) in Washington DC; C. Massin for access to the type series of *D. antarcticus* housed in the Institut Royal des Sciences Naturelles de Belgique (IRSNB); M. Segonzac who provided the specimen of *P. incrassatus* from the Hydrosnake cruise; M. Sibuet who provided specimens from the Walvis cruise; E. Lodde for granting access to the specimens in the Zoologische Staatssammlung München (ZSM). Special thanks are due to D. Meyer and CG Messing for their thorough reviews. Except for *Feracrinus heinzelleri* n. sp., the SEM pictures were done at the Plate-forme de Microscopie Electronique at the Muséum national d'Histoire naturelle, Paris. This work was funded by the Action Transversale du MNHN Biominéralisation.

References

- Améziane, N. & Roux, M. (1997) Biodiversity and historical biogeography of stalked crinoids (Echinodermata) in the deep sea. *Biodiversity and Conservation*, 6, 1557–1570.
- Améziane, N. & Roux, M. (2011) Stalked crinoids from Southern Tasmanian Seamounts. Part 1: Family Hyocrinidae. *Journal of Natural History*, 45 (3), 137–170.

- Bather, F.A. (1899) A phylogenic classification of the Pelmatozoa. British Association for the Advancement of Science, Report 1898, 916–923.
- Bather, F.A. (1908) *Ptilocrinus antarcticus* n. sp. a crinoid dredged by the Belgian Antarctic expedition. *Bulletin de l'Académie royale de Belgique*, 3, 296–299.
- Bohn, J.M. (2006) Crinoidea and Holothuroidea (Echinodermata) of the abyssal Angola Basin—Results of the DIVA-1 expedition of FS “Meteor” (Cruise M48/1). *Zootaxa*, 1276, 1–31.
- Bourseau, J.P., Améziame-Cominardi N., Avocat R. & Roux M. (1991) Echinodermata: Les crinoïdes pédonculés de Nouvelle-Calédonie, *Mémoires du Muséum national d'Histoire naturelle, Paris, A Zoologie*, 151, 229–333.
- Carpenter, P.H. (1884) Report upon the Crinoidea collected during the voyage of H.M.S. Challenger during the years 1874–1876. Part I - General morphology, with description of the stalked crinoids, 11, 1–442.
- Clark, A.H. (1907a) Two new crinoids from the North Pacific Ocean. *Proceedings of the United States national Museum*, 32, 507–512.
- Clark, A.H. (1907b) A new stalked crinoid (*Ptilocrinus pinnatus*) from the Pacific coast with a note on *Bathycrinus*. *Proceedings of the United States national Museum*, 32, 1547, 551–554.
- Clark, A.H. (1908a) Notice of some Crinoids in the collection of the Museum of Comparative Zoology. *Bulletin of the Museum of Comparative Zoology*, 51, 8, 233–248.
- Clark, A.H. (1908b) New stalked crinoids from the eastern coast of North America. *Proceedings of the United States national Museum*, 34, 205–208.
- Clark, A.H. (1915) Die crinoden der Antarktis. *Deutsche Südpolar-Expedition*, 16, Zoologie, 8, 101–209.
- Clark, A.H. (1917) A revision of the recent genera of the family Bourgueticrinidae with the description of a new genus. *Journal of the Washington Academy of Science*, 7, 388–392.
- Clark, A.H. (1949) Echinoderms from the mid-Atlantic dredged by the “Atlantis” in the summer of 1948. *Journal of the Washington Academy of Science*, 39, 371–377.
- Clark, A.M. (1973) Some new taxa of recent stalked Crinoidea. *Bulletin of the British Museum Natural History, Zoology*, 25, 7, 267–288.
- Clark, A.M. (1977) Notes on deep-water Atlantic Crinoidea. *Bulletin of the British Museum Natural History, Zoology*, 31, 4, 159–186.
- Clark, A.M. (1982) Inter-relationships of recent stalked non-isocrinid Crinoidea. *Australian Museum Memoir*, 16, 121–128.
- Danielssen, D.C. & Koren, J. (1877) Fra den norske Nordhavsexpedition: Echinodermer. *Nyt Magazin for Naturvidenskaberne*, 23, 3, 45–83.
- Döderlein, L. (1912) Die gestielten Crinoiden der deutschen Tiefsee-Expedition. *Wiss. Ergebnisse deutsche Tiefsee-Exped. "Valdivia" 1898–1899. Jena, G. Fischer*, 17, 1, 34.
- Duco, A. & Roux, M. (1981) Modalités particulières de croissance liées au milieu abyssal chez les Bathycrinidae (Echinodermes, Crinoïdes pédonculés), *Oceanologica Acta*, 4, 389–394.
- Eléaume, M., Hemery, L.G., Bowden, D.A., Roux, M. (2011) A large new species of the genus *Ptilocrinus* (Echinodermata, Crinoidea, Hyocrinidae) from Antarctic seamounts, *Polar Biology*, 34, 1385–1397.
- Gislén, T. (1925) Two stalked crinoids from the Kei Islands. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening*, 79, 85–95.
- Gislén, T. (1933) A small collection of crinoids from St. Helena. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening*, 93, 475–483.
- Gislén, T. (1938) A revision of the recent Bathycrinidae, with a study of their phylogeny and geographical distribution. *Lunds Universitets Arsskrift N.F.*, 34, 10, 1–30.
- Gislén, T. (1951) Crinoidea with a survey of bathymetric distribution of the deep-sea crinoids. *Reports of the Swedish Deep-sea Expedition*, 2, Zoology, 4, 49–59.
- Gislén, T. (1956) Crinoids from depths exceeding 6000 meters. *Galathea Report*, 2, 61–62.
- Gutt, J., Barratt, I., Domack, E., d'Udekem d'Acoz, C., Dimmler, W., Grémare, A., Heilmayer, O., Isla, E., Janussen, D., Jørgensen, E., Kock, K. -H., Lehnert, L. S., López-González, P., Langner, S., Linse, K., Manjón-Cabeza, M. E., Meißner, M., Montiel, A., Raes, M., Robert, H., Rose, A., Sañe Schepisi, E., Saucède, T., Scheidat, M., Schenke, H. -W., Seiler, J., Smith, C. (2011) Biodiversity change after climate-induced ice-shelf collapse in the Antarctic. *Deep-Sea Research II*, 58, 74–83.
- Hansen, B. (1975) Systematics and biology of the deep-sea holothurians. *Galathea Report*, 13, 1–262.
- Hess, H. (2011a) Bourgueticrinina. In: Seldon P. (ed), Ausich W.I. (coordinating author) *Treatise on Invertebrate Paleontology, Part T (Echinodermata 2, Revised)*, University of Kansas Press, Lawrence, Kansas 3: T146–158.
- Hess, H. (2011b) Hyocrinida. In: Seldon P. (ed), Ausich W.I. (coordinating author) *Treatise on Invertebrate Paleontology, Part T (Echinodermata 2, Revised)*, University of Kansas Press, Lawrence, Kansas 3: T172–177.
- John, D. (1937) Crinoidea. Résultats du voyage de S.Y. « Belgica », Expédition antarctique belge, Rapport scientifique, Zoologie, Anvers, 1–11.
- Mc Knight, D.G. (1973) Stalked crinoids from the New Zealand region. *New Zealand Oceanographic Institute Records*, 1, 14, 199–210.
- Macurda, D.B. & Meyer, D.L. (1976) The morphology and life habits of the abyssal crinoids *Bathycrinus aldrichianus* Wyville Thomson and its paleontological implications. *Journal of Paleontology*, 50, 4, 647–667.

- Madsen, F.J. (1961) On the zoogeography and origin of the abyssal fauna. *Galathea Report*, 4, 177–218.
- Maldonado, A., Barnolas, A., Bohoyo, F., Galindo-Zaldivar, J., Hernandez-Molina, J., Lobo, F., Rodriguez-Fernandez, J. Somoza, L. & Tomas Vazquez, J. (2003) Contourite deposits in the central Scotia Sea: the importance of the Antarctic Circumpolar Current and the Weddell Gyre flows. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 198, 187–221.
- Messing, C.G. (2007) The crinoid fauna (Echinodermata, Crinoidea) of Palau. *Pacific Science*, 61, 1, 91–111.
- Mironov, A. N. (2000) New taxa of stalked crinoids from the suborder Bourgueticrinina (Echinodermata, Crinoidea). *Zoologicheskii Zhurnal*, 79, 6, 712–728 (in Russian).
- Mironov, A. N. (2008) Stalked crinoids of the family Bathycrinidae (Echinodermata) from the eastern Pacific. *Invertebrate Zoology*, 5, 2: 133–153.
- Mironov, A. N. & Sorokina O.A. (1998a) Three genera of stalked crinoids of the family Hyocrinidae (Echinodermata, Crinoidea). *Zoologicheskii Zhurnal*, 77, 4, 404–416 (in Russian).
- Mironov, A. N. & Sorokina O.A. (1998b) Sea lilies of the order *Hyocrinida* (Echinodermata, Crinoidea). *Zoologicheskie Issledovaniya*, Moscow, 2, 1–117 (in Russian).
- Rasmussen, H.W. (1978) Crinoidea, Articulata, In: R.C. Moore & Teichert C., *Treatise on Invertebrate Palaeontology, Part T, Echinodermata 2, 1*, Geological Society of America (Ed.), Boulder, Colorado, and University of Kansas, Lawrence, T813–928.
- Roux, M. (1977) Les Bourgueticrinina (Crinoidea) recueillis par la "Thalassa" dans le golfe de Gascogne : anatomie comparée des pédonculés et systématique. *Bulletin du Muséum national d'Histoire Naturelle, Paris*, série 3, 426, 325–384.
- Roux, M. (1980a) Les Crinoïdes pédonculés (Echinodermes) photographiés sur les dorsales océaniques de l'Atlantique et du Pacifique. Implications biogéographiques. *Comptes Rendus de l'Académie des Sciences Paris*, 291, série D, 901–904.
- Roux, M. (1980b) Les articulations du pédoncule des Hyocrinidae. Intérêt systématique et conséquences. *Bulletin du Muséum national d'Histoire naturelle, Paris*, série 4, 2, sect. A(1), 31–57.
- Roux, M. (1987) Evolutionary ecology and biogeography of recent stalked crinoids as a model for the fossil record. In: Jangoux M. & Lawrence J.M. (Ed.) *Echinoderm Studies*. A.A. Balkema, Rotterdam, 2, 1–53.
- Roux, M. (2002) Two new species of the genus *Thalassocrinus* (Echinodermata: Crinoidea: Hyocrinidae) from the Pacific Ocean. *Species Diversity*, 7, 173–186.
- Roux, M. (2004) New hyocrinid crinoids (Echinodermata) from submersible investigations in the Pacific Ocean. *Pacific Science*, 58, 4, 597–613.
- Roux, M. & Lambert, P. (2011) Two new species of stalked crinoids from the north-eastern Pacific in the genera *Gephyrocrinus* and *Ptilocrinus* (Echinodermata, Crinoidea, Hyocrinidae). Effects of ontogeny and variability on hyocrinid taxonomy. *Zootaxa*, 2825, 1–54.
- Roux, M., Messing, C.G. & Améziane, N. (2002) An artificial key to the genera of living stalked crinoids (Echinodermata). *Bulletin of Marine Science*, 70, 3, 799–830.
- Roux, M. & Pawson, D.L. (1999) Two new Pacific Ocean species of hyocrinid crinoids (Echinodermata), with comments on presumed giant-dwarf gradient related to seamounts and abyssal plains, *Pacific Science*, 53, 3, 289–298.
- Strugnell, J.M., Rodgers, A.D., Prodöhl, P.A., Collins, M.A. & Allcock, A.L. (2008) The thermohaline expressway: the Southern Ocean as a centre of origin for deep-sea octopuses. *Cladistics*, 24, 853–860.
- Thomson, C.W. (1872) On the crinoids of the "Porcupine" deep-sea dredging expedition. *Proceedings of the Royal Society of Edinburgh*, 7, 764–773.
- Thomson, C.W. (1876) Notice on new living crinoids belonging to the Apiocrinidae. *Journal of the Linnean Society of London*, 13, 47–55.
- Vaney, C. (1908) *Ptilocrinus brucei*. In D.W. Wilton, Résultats de l'Expédition nationale Antarctique du S.Y. Scotia, 1902–1904, 4, *Zoologie*, 1, 1–133.
- Vaney, C. & John, D.D. (1939) Scientific results of the voyage of S.Y. Scotia, 1902–04: The Crinoidea. *Transactions of the Royal Society of Edinburgh*, 59, 661–672.