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Two New Pacific Ocean Species of Hyocrinid Crinoids (Echinodermata), with Comments on Presumed Giant-Dwarf Gradients Related to Seamounts and Abyssal Plains[1]

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ABSTRACT: *Hyocrinus foelli,* n. sp. is a small hyocrinid sea lily from the abyssal ferromanganese nodule fields of the North Pacific Ocean. *Hyocrinus giganteus,* n. sp. is a very large hyocrinid from Horizon Seamount in the eastern Pacific that shows close affinities to *H. cyanae* from the western Pacific, off New Caledonia. A possible giant-dwarf heterochronic gradient, related to scarcity of food supply in abyssal plains and its abundance in seamount environments, is discussed.

THE FIRST HYOCRINID to be described was the small form *Hyocrinus bethellianus* (Wyville-Thomson 1876, Carpenter 1884), collected in the southern Indian Ocean by the RMS *Challenger.* Recognizing the uniqueness of this genus, Carpenter placed it in a new family, Hyocrinidae. Then A. Agassiz (1892) described the very large species *Calamocrinus diomedeae,* collected off the Galápagos Islands. Initially, Agassiz referred his new genus and species to the Family Millericrinidae, but A. H. Clark (1912) recognized the fact that, despite the size discrepancy, these two taxa belonged within the same family, Hyocrinidae. Gislen (1939) discussed affinities with Cyrtocrinina, especially Eugeniacrinidae, Holopodidae, and Plicatocrinidae. A. M. Clark (1973) erected two subfamilies, the Calamocrininae (containing the single genus *Calamocrinus*) and Hyocrininae (containing all other genera). After a study of stalk joints and a review of arm and basal ring patterns, Roux (1980*a*) confirmed the affinities with Cyrtocrinina and proposed that all of the large-sized genera with the first pinnule at Br4 be referred to Calamocrininae and that smaller genera remain in Hyocrininae, with *Anachalypsicrinus* having an intermediate taxonomic position. Rasmussen's (1978) classification, a cladistic analysis of articulate crinoids, unfortunately did not cite all studies on modern fauna and placed Hyocrinidae in the millericrinid crinoids (Simms 1988). Ontogenetic analysis shows a mosaic pattern of heterochronicities and does not confirm the validity of characters used in Simms' cladogram (Améziane-Cominardi and Roux 1994). In this paper we retain Gislen's (1939) interpretation of cyrtocrinid-hyocrinid affinities, and we find no evidence of a direct affiliation between millericrinids and hyocrinids.

Hyocrinus bethellianus, the type species of *Hyocrinus,* is known from just two specimens collected in the Indian Ocean (Carpenter 1884, Doderlein 1912). During a Calsub cruise off New Caledonia, the first species of *Hyocrinus* of medium size was collected (Bourseau et al. 1991). Here, we describe a very large species based on a single specimen from Horizon Seamount, and a small species based on about 20 specimens from Pacific Ocean abyssal plains.

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Family HYOCRINIDAE Carpenter, 1884

Subfamily HYOCRININAE A. M. Clark, 1973

Genus *Hyocrinus* Wyville-Thomson, 1876

Hyocrinus foelli Roux & Pawson, n. sp.
Plate I; Plate II, Figures 1–8; Plate IV

ETYMOLOGY: This new species is dedicated to Eric J. Foell of Gloucester, Virginia, who was instrumental in preserving the type series for science.

MATERIAL: All specimens are catalogued in the collections of the National Museum of Natural History (USNM) in Washington, D.C. They were collected in the northeastern equatorial Pacific Ocean between Clarion and Clipperton Fracture Zones during a survey of ferromanganese nodule fields by Deepsea Ventures, Inc. (DVI) and Ocean Minerals Company (OMCO).

TYPE MATERIAL: HOLOTYPE: USNM E47374. PARATYPES: USNM E47375, 1 specimen; E47376, 1 specimen; E47377, 2 specimens; E47378, 1 specimen; E47379, 1 specimen. The seven specimens of the type series were collected by DVI near and within DOMES Site C (14° 40′ N, 125° 25′ W) at a depth range of 4300–4700 m (see Foell and Pawson 1986, Foell et al. 1991).

OTHER MATERIAL EXAMINED: Other specimens (Table 1) were collected by OMCO at a depth of 4750–4880 m in the same general area as the type series (13° 13–14′ N, 129° 52–55′ W). We also used additional data provided by seafloor photographs taken during U.S. and French cruises on the manganese nodule fields.

DIAGNOSIS: Small species with stalk length of up to 120 mm. Dorsal cup with ribbed ornamentation usually present. Arm with series of two or frequently three brachials united by synostosis. First pinnule at Br4 to Br7 with a high frequency at Br5. Tegmen with conical oral ring. Columnals of proximal and middle part of stalk with seven irregular small crenellae and angular stereom meshwork around axial canal.

DESCRIPTION: Holotype (USNM E47374): Illustrated in Plate I, Figures 1(*a–c*) and 2. Dorsal cup conical, with fused basals and radial sutures only slightly perceptible. Cup height 4.3 mm along arm axis. Diameter at base of basal ring 1.5 mm. Radial with axial rib as wide as arm and in line with it; near radial-basal suture, rib can be divided into two smaller ribs. Sides of radials become higher between arms, where they develop ornamentation of transverse ribs or triangular thickened pimples and have a concave rim inclined toward tegmen. Maximum diameter at top of radial ring 5.5 mm. Width of first brachials 1.1 mm. Five large oral plates occupy conical surface of tegmen, restricting to outer border 4–6 granulated tegminal plates and anal cone. Radial edges of orals festooned. At center of each oral junction ambulacral groove and plates disappear inside oral ring toward mouth.

TABLE 1

SPECIMENS OTHER THAN TYPE MATERIAL OF *Hyocrinus foelli*

USNM NO.	OMCO CRUISE	LOCATION	DEPTH (m)	MATERIAL
E47360	80-04	13°13′00″ N–129°52′ W	4,850	1 specimen
E47361	80-02	13°13′48″ N–129°52′ W	4,820	Broken stem
E47362	80-02	13°13′48″ N–129°52′ W	4,820	2 specimens
E47363	80-04	13°13′00″ N–129°52′ W	4,850	2 specimens
E47364	80-01	13°13′00″ N–129°52′ W	4,850	1 specimen
E47365	80-02	13°13′48″ N–129°52′ W	4,880	1 specimen
E47366	80-02	13°13′48″ N–129°52′ W	?	1 specimen
E47367	80-01	13°13′00″ N–129°52′ W	4,865	Broken specimen
E47368	80-01	13°13′00″ N–129°52′ W	4,865	2 specimens
E47369	80-02	13°13′48″ N–129°52′ W	4,880	Broken specimen
E47370	80-02	13°13′48″ N–129°52′ W	?	Broken arms
E47371	80-02	13°13′48″ N–129°52′ W	4,758	Broken specimen
E47372	80-01	13°13′00″ N–129°52′ W	4,850	1 specimen

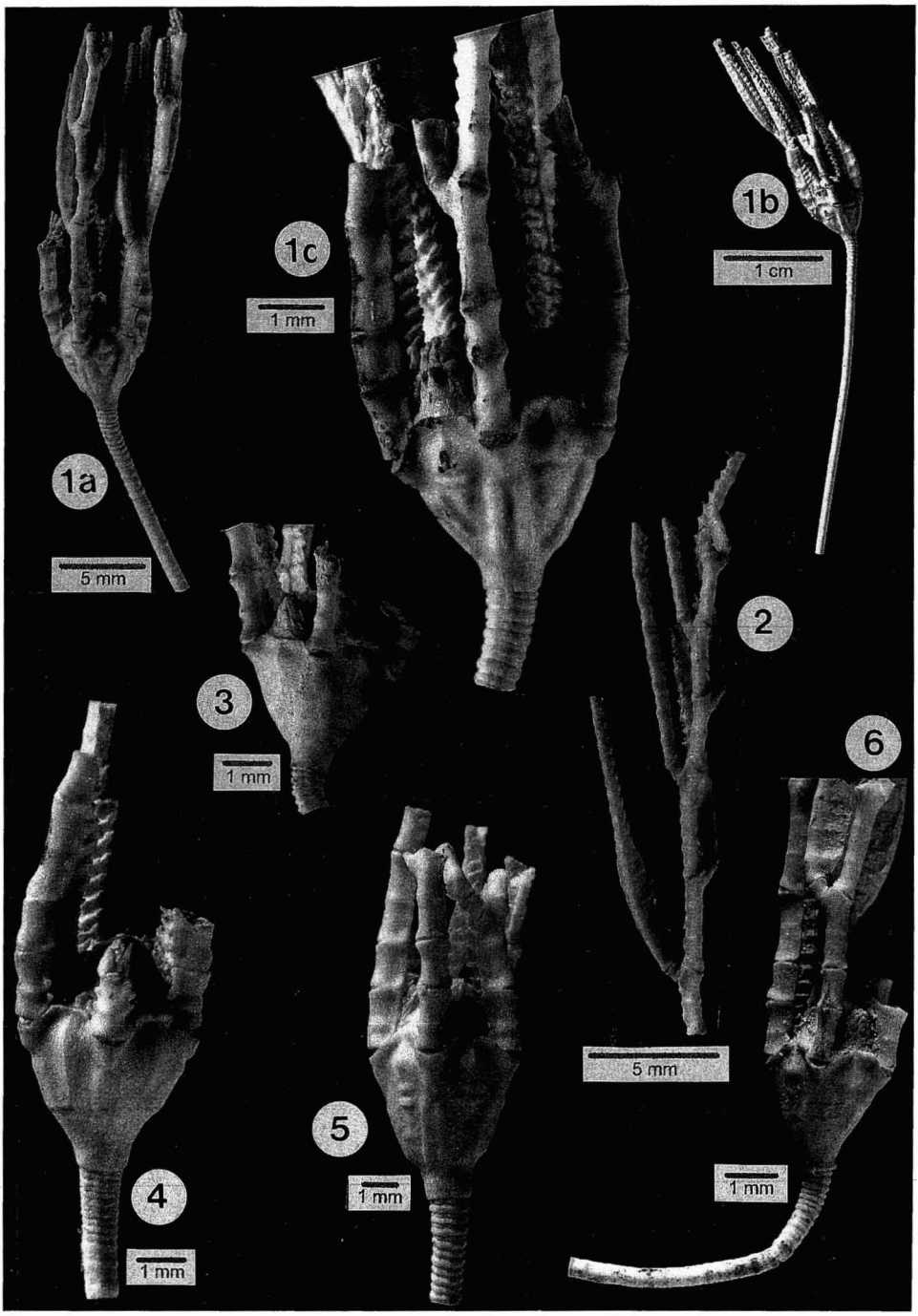

PLATE I. Figure 1. *Hyocrinus foelli,* n. sp., holotype. 1*a*, general view; 1*b*, 1*c*, general views, showing interradius CD with anal cone. Figure 2. Holotype, proximal fragment of arm showing genital pinnule at lower left. Figure 3. Paratype (E47377), general view. Figure 4. Paratype (E47375), general view. Figure 5. Paratype (E47379), general view. Figure 6. Paratype (E47376), general view, with arm of D radius carrying genital pinnule.

First pinnule appears on four arms at Br5 with following arm pattern: 1 + 2 3 4 + 5. On fifth arm pattern is 1 + 2 3 4 + 5 + 6 with first pinnule at Br6. Distal to brachial bearing first pinnule, two arm patterns observed: 6 + 7 + 8 9 + 10 + 11 12 + 13 + 14 or 7 + 8 9 + 10 11 + 12 + 13. The nonmuscular articulations are flat synostosial articulations. Proximal parts of arms bear two or three typical genital pinnules, looking like small rigid arms, with well-developed ambulacral plates.

Proximal part of stalk is preserved; total length 33 mm. External surface of stalk smooth, without ornamentation. Uppermost proximal columnals heterometric in diameter and height, permitting flexibility of stalk. Columnals circular in section, diameter 1.3 mm, rapidly decreasing to 1 mm or less. Height of proximal columnals 0.25 mm, increasing to 0.4 mm at a distance of 10 mm from basal ring and to 0.7 mm at 35 mm distance. At greater distances from basal ring, the columnal height may reach twice the diameter.

Paratypes: Type series shows important variation in characters. On dorsal cup axial ribs, ornamentation, and radial sutures are variable; they may be more or less conspicuous. In contrast, concave rims of radials inclined toward tegmen is a consistent character (Plate I). Ratio D/H (diameter of radial ring/calyx height) provides an index of shape of conical dorsal cup; D/H ranges from 0.94 to 1.29. Specimen USNM E47378 has inflated basal ring and more complete arm of 27 mm length, and proximal stem diameter of 0.9 mm.

In paratypes plus holotype, first pinnule appears at Br4 (1 case), Br5 (21 cases), or Br6 (4 cases). Pinnules separated by series of two or three brachials joined by flat synostosial articulations (Plate II, Figure 6). Three brachials between two pinnules is most frequent pattern (59.4%). Proximal to first pinnule, four cases of three brachials series occur. Muscular articulations are synarthries where boundary between muscle area and ligament area is not conspicuous as in other hyocrinids (Roux 1990, Holland et al. 1991). In absence of galleried stereom, dorsal ligament area is large and deep (Plate II, Figures 7–8).

Deep-sea photographs show generally 13 pinnules or fewer per arm, exceptionally up to 17 pinnules. Arm patterns known behind first pinnule are as follows:

USNM E47379 1 + 2 3 4 + 5+, 1 + 2 3 4 + 5, 1 + 2 3 4 + 5 6+ (2 cases),
USNM E47378 1 + 2 3 4 + 5, 1 + 2 3 4 + 5 6 + 7 + 8 9 + 10 11 + 12 13 + 14 15 + 16, 1 + 2 3 4 + 5 6 + 7 + 8,
USNM E47375 1 + 2 3 4 + 5 6 + 7, 1 + 2 3 4 + 5 6,
USNM E47377 (less complete specimen) 1 + 2 3 4 + 5, 1 + 2 3 4 + 5 6 + 7 + 8,
USNM E47377 (more complete specimen) 1 + 2 3 4 + 5 6 + 7 + 8 9 + 10 + 11 12+, 1 + 2 3 4 + 5 + 6, 1 + 2 3 4 + 5 + 6 7 + 8, 1 + 2 3 4 + 5 6 + 7 + 8 9+, 1 + 2 3 4 + 5 6 + 7 + 8 9 + 10 + 11 12 + 13 14 + 15 16 + 17,
USNM E47376 1 + 2 3 4 + 5 6 + 7 + 8 9 + 10 + 11 12 + 13 + 14, 1 + 2 3 4 + 5 6 + 7 + 8 9 + 10 + 11 12 + 13, 1 + 2 3 4 + 5 6 + 7 + 8, 1 + 2 3 4 + 5 6 + 7 8 + 9 10 + 11 12.

Stalk of specimen USNM E47379 almost complete, of total length 126 mm, diameter up to 1.2 mm immediately distal to the basal ring, 0.8 mm along main part, and distalmost columnals 1.1 mm in diameter. Columnal height is up to 0.3 mm immediately distal to the dorsal cup, 1.5 to 1.6 mm at a distance of 8 mm from the cup, about 2 mm in the middle part, and from 2.1 to 1.5 mm in the distal part. Stalk generally circular in cross section, except for specimen USNM E47375, where proximal columnals are slightly hexagonal. External surface of columnals always smooth, without ornamentation.

Articular facet of first order proximal columnals (Plate II, Figure 1) with pentalobate axial canal at center of a claustrum depression. Areola divided into seven areas by coarse synostosial stereom, which sketches a very irregular crenularium. During growth, as column height increases, claustrum disappears, resulting in enlargement of axial canal, which becomes subcircular (Plate II, Figure 2) as described for *Calamocrinus* by Holland et al. (1991). In middle part of stalk, facets present typical symplexial features (Plate II, Figures 3,5) with seven small cren-

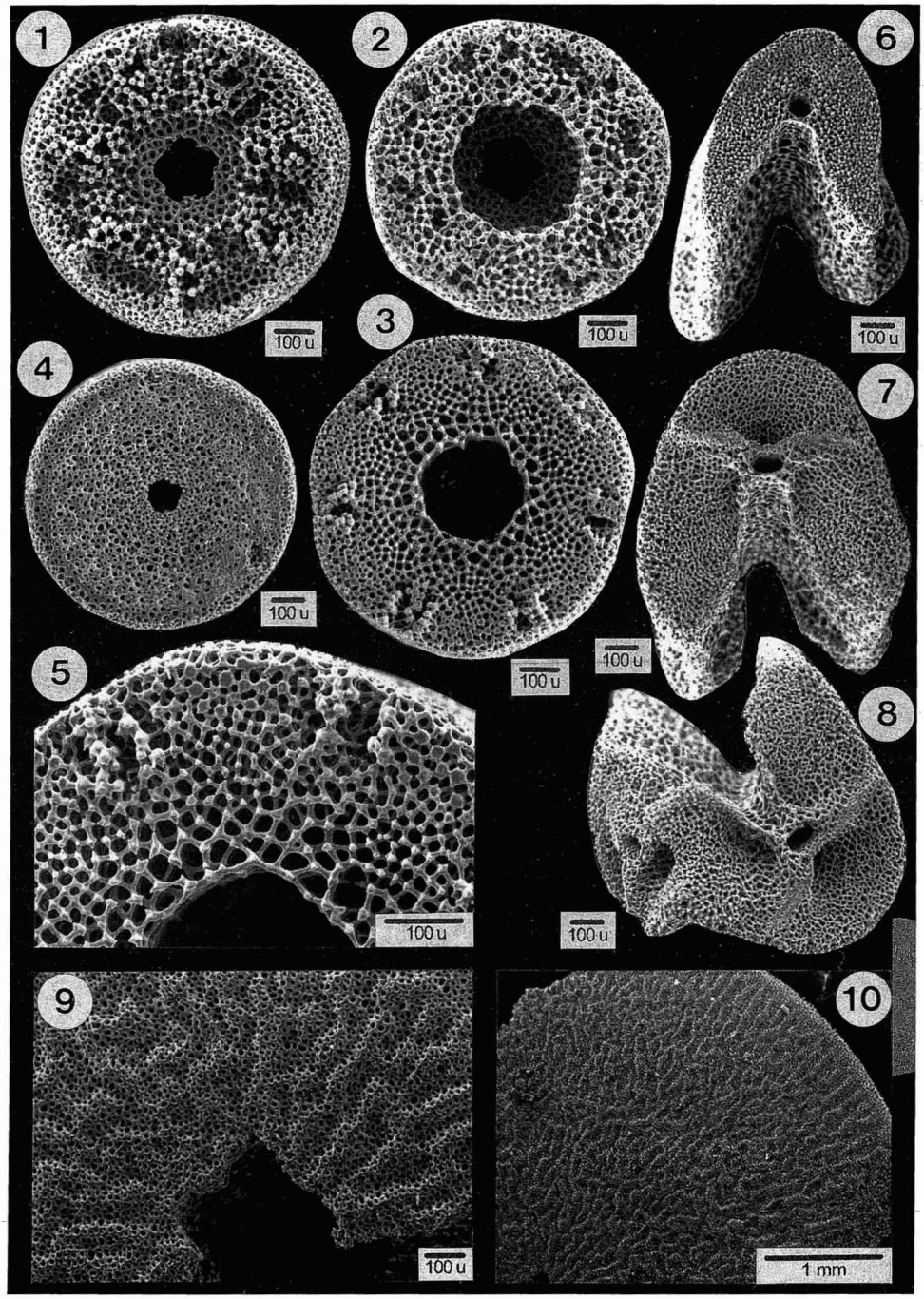

PLATE II. Figures 1–8. *Hyocrinus foelli,* n. sp. Figure 1. Articular facet of proximalmost columnal. Figure 2. Articular facet of second columnal. Figure 3. Articular facet from middle part of stalk. Figure 4. Syzygial facet of distalmost columnal. Figure 5. Articular facet from middle part of stalk. Figure 6. Nonmuscular arm articulation with a flat synostosial facet. Figure 7. Synarthrial facet of muscular articulation (brachial without pinnule). Figure 8. Synarthrial facets of arm and pinnule muscular articulations (brachial bearing a pinnule to the left). Figures 9–10. *Hyocrinus giganteus,* n. sp., holotype, syzygial facet of distalmost columnal. Figure 9. Center of syzygial facet, showing pentalobate lumen. Figure 10. General view of facet.

ellae and synostosial stereom on outer ring, the areola with galleried stereom with large angular meshes around axial canal. Facets of distal columnals are flat syzygies (Plate II, Figure 4) with synostosial stereom around axial canal.

Other specimens (Table 1) offer additional information on character variation. Dorsal cup ornamentation is more frequently absent than in type series. Shape variation of dorsal cup is independent of specimen age (D/H from 0.98 to 1.75). The larger specimen (E47367) has the following values: D = 11.2 mm, H = 6.4 mm for dorsal cup, proximal stalk diameter 2.1 mm. Tegmen with relatively smaller orals, allowing development of tegminal and ambulacral plates, evidence of peramorphic ontogenetic tendencies. Maximum preserved stalk length is 56 mm for a stalk diameter of 1.3 mm (specimen E47630). Brachial bearing first pinnule is Br4 (3 cases), Br5 (13), Br6 (2), and Br7 (1). In three cases, there is a series of three brachials joined by synostosis before the first pinnule. Distal to first pinnule, three brachial units are most frequent cases observed (63.6%).

DISCUSSION: *Hyocrinus foelli* has close affinities with *H. bethellianus.* General features and main aspects of arm patterns are similar. *Hyocrinus foelli* is distinctive in having variable external morphology of the dorsal cup, conical oral ring, smooth exterior surface on the proximal stalk, location of the first pinnule from Br4 to Br7, most frequently at Br5, and the occasional presence of a series of three brachials united by synostosis before the first pinnule. In *H. bethellianus* the dorsal cup is always smooth, with a sharp and narrow rib extending along the arm axis; the oral edges support ambulacral plates; thin columnal epifacets give a rough surface to the proximal stalk; the arms are longer and more gracile; and the most frequent location of the first pinnule is at Br6 (Carpenter 1884, Doderlein 1912, Roux 1980*a*). There are also differences in columnal facets from the proximal and middle parts of the stalk: *H. bethellianus* has a more regular crenularium, and large stereom meshes around the axial canal are rare or absent (Roux 1980*a* and unpubl. obs.). More material of *H. bethellianus* is needed to further document these differences. Both species seem to be adapted to an abyssal plain environment, where hard substrates (manganese nodules or rocky outcrops) occur (Plate IV). The photograph taken on a CYAMEX cruise on the East Pacific Rise (Roux 1980*b*) shows what is probably a young specimen of *H. foelli.*

Hyocrinus giganteus Roux & Pawson, n. sp.
Plate II, Figures 9–10; Plate III

ETYMOLOGY: The species name refers to the unusually large size of the single specimen.

MATERIAL: HOLOTYPE: USNM E35280, North Pacific, Cruise of *Posse,* DSRV *Alvin* dive 1814 (Observer B. Schwab), March 1987, from edge of Horizon Seamount, depth approximately 1830 m.

DIAGNOSIS: Very large species, stalk approximately 1 m long. Tegmen well developed and inflated. Dorsal cup with broad radially placed ribs in line with arm axes. More than 45 pinnules on each arm; first pinnule at IBr6. Arm pattern with sequences of two brachials united by synostosis.

DESCRIPTION: Single specimen consists of calyx and tegmen with one broken arm 16 cm long bearing pinnules, the other arms broken off, only the first few cm present (Plate III, Figures 1–4). Height of basal ring 6 mm; diameter at base of basal ring 6 mm; diameter at base of radial ring 11.7 mm; height of radials 10 mm; width of radials 9.5 mm; diameter at top of radial ring 18 mm; height of tegmen 8.5 mm; width of first brachials 4.5 mm; length of pinnules more than 42 mm.

On all arms first pinnule appears at Br6. Pattern of arm organization (data from two arms) appears to be very regular: 1 + 2 3 + 4 5 + 6 7 + 8 9 + 10, etc. External morphology of pinnules is distinctive. Articular facets of brachials and pinnulars are very similar. Nonmuscular joints are flat synostosial articulations (Plate III, Figure 7) and synarthries show large and deep dorsal ligament areolae,

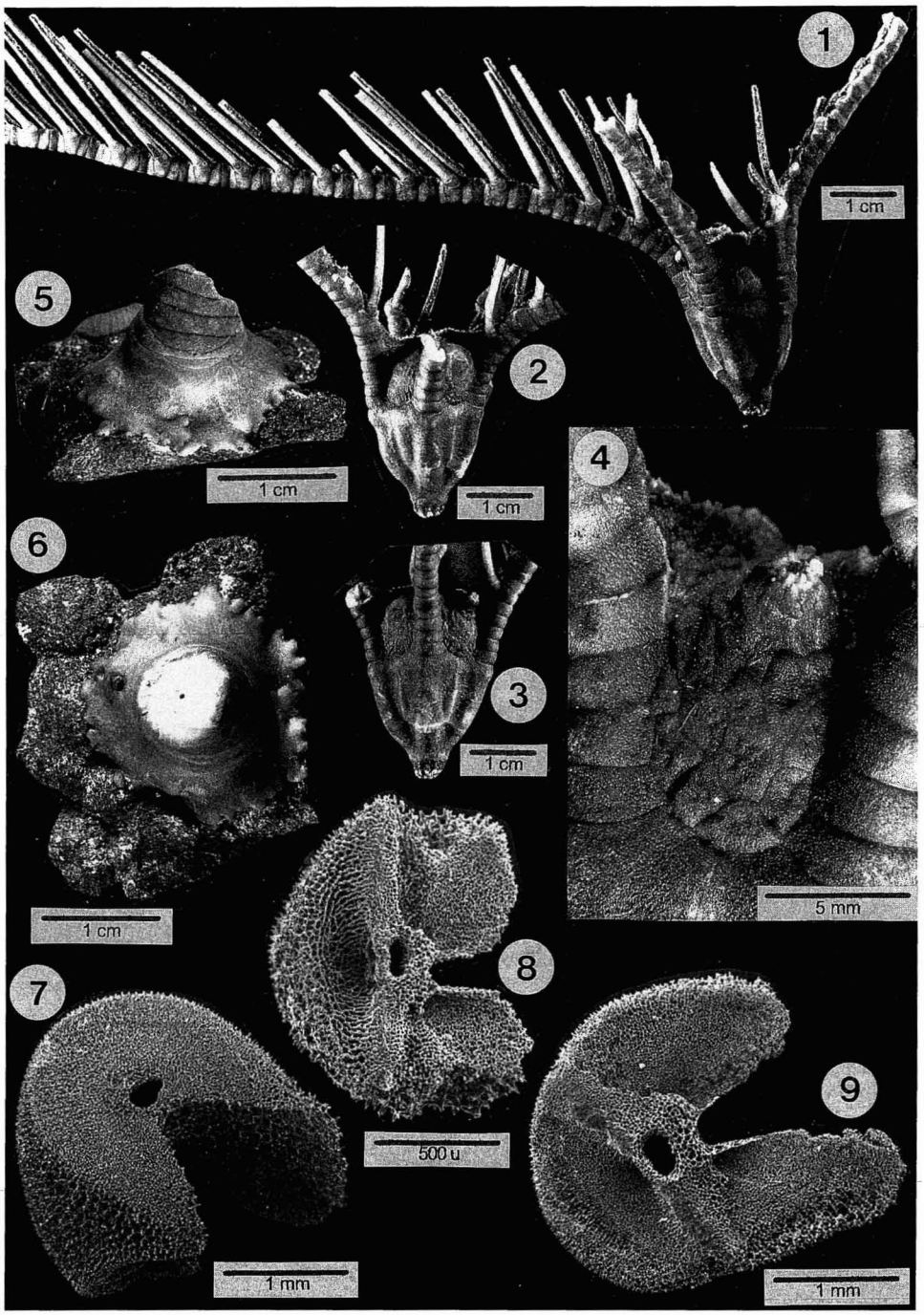

PLATE III. *Hyocrinus giganteus,* n. sp., holotype. Figure 1. General view of calyx and arms. Figure 2. Calyx with E radius at center. Figure 3. Calyx, with D radius at center. Figure 4. Calyx, CD interradius with anal cone. Figures 5, 6. Attachment disk of stalk on a ferromanganese crust. Figure 7. Nonmuscular arm articulation with a flat synostosial facet. Figure 8. Synarthrial facet of muscular articulation of proximal pinnular. Figure 9. Synarthrial facet of muscular brachial articulation.

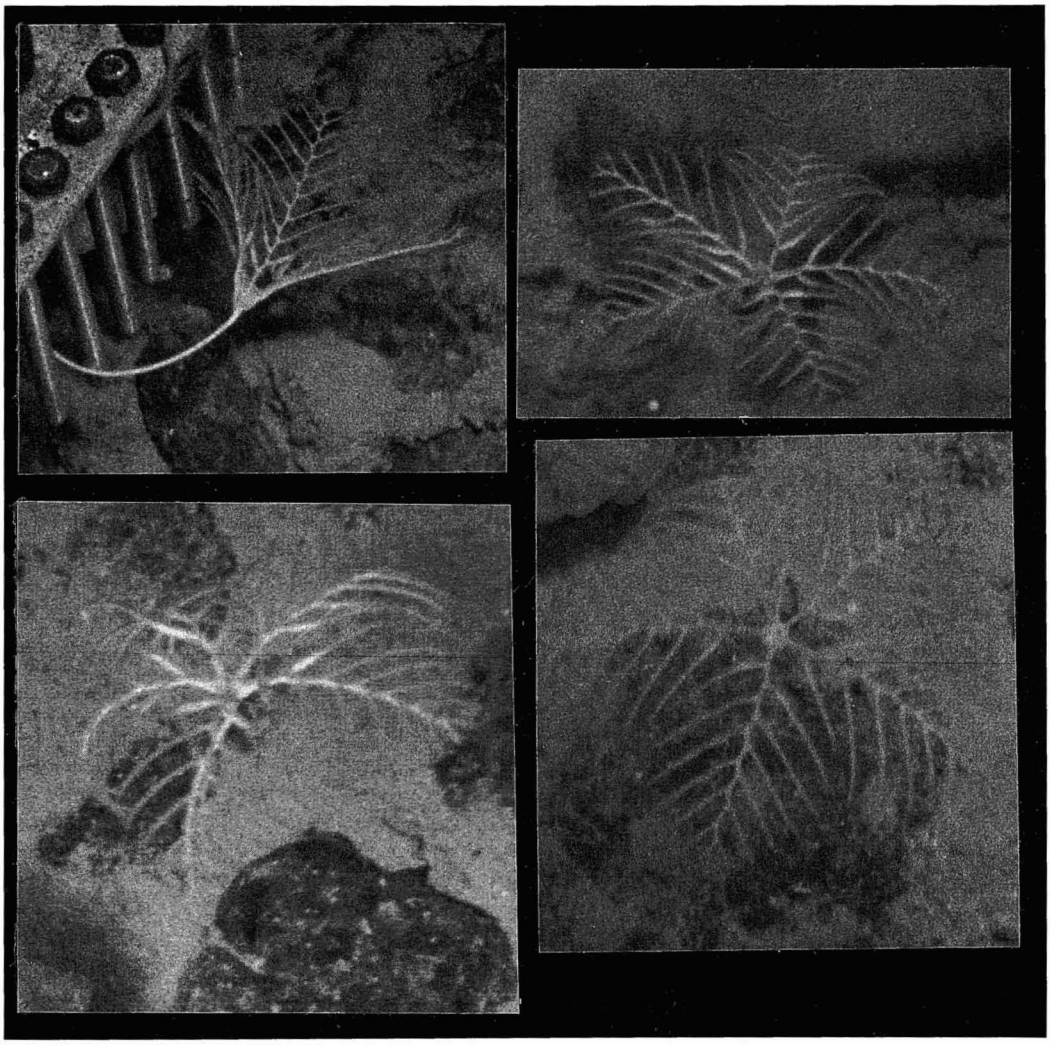

PLATE IV. *Hyocrinus foelli,* n. sp., in situ photographs taken in the Clarion-Clipperton Fracture Zone. All photographs were taken by Deepsea Ventures, Inc., in September 1978, in the vicinity of 14° 40′ N, 125° 25′ W, at depths of 4300–4700 m.

the boundary between inner ligament area and muscle area being more distinct on pinnular (Plate III, Figures 8, 9). The well-preserved arm bears 22 pairs of pinnules.

Tegmen inflated, with heightened ambulacral grooves supported by five orals covering mouth at center of upper surface. Prominent anal cone emerges laterally through pavement of tegminal plates (Plate III, Figure 4). Conical dorsal cup has five broad, conspicuous ribs that are aligned with arms. Basals fused, radial sutures conspicuous (Plate III, Figures 2–3).

Stem originally approximately 1 m long, not preserved (B. Schwab, pers. comm.). Attachment disk preserved, with few distalmost columnals (Plate III, Figures 5–6); diameter of these columnals 7.8 mm. Proximal columnals attached to calyx up to 5 mm in diameter. Distal joints are multiradiate syzygies

with pentalobate axial canal (Plate II, Figures 9, 10).

DISCUSSION: *Hyocrinus giganteus* is very similar to *H. cyanae* from the New Caledonia slope, collected at a depth of 2536 m (Bourseau et al. 1991). In both species the regular arm pattern is the same, with the first pinnule at Br6, and pinnules are more numerous and gracile than in other species of the genus. *Hyocrinus cyanae* is smaller than *H. giganteus* (total arm length 7.5 cm, stalk diameter less than 2 mm), the radial ribs on the dorsal cup are much less prominent, and the interadial space between arms at the level of the joint R-Br1 is narrower. Columnal articular facets of the proximal and medial parts of the stem are unknown in both species. It is possible that these species are synonymous, but until more material becomes available from both sides of the Pacific Ocean, we consider that the characters of the new material warrant erection of a new species.

Giant-Dwarf Gradients, and Distribution Patterns of Hyocrinids

The family Hyocrinidae is apparently restricted to the deep ocean, generally at depths in excess of 700 m. The hyocrinids are stalked crinoids in which differences in size are the most marked. The two new species described here show the maximum size gradient. The largest known species are the slope and seamount forms *Hyocrinus giganteus* and *Calamocrinus diomedeae,* and the smallest are *H. bethellianus* and *H. foelli,* which live on abyssal plains. As in other stalked crinoids, hyocrinid size decreases as depth increases and as the food supply becomes more tenuous (Roux 1987). This apparent giant-dwarf gradient in hyocrinids requires further investigation.

In the Pacific Ocean hyocrinids it can be seen that stalk diameter and arm length are a function of general body size, but the number of pinnules per arm is not a function of body size. *Hyocrinus giganteus* follows the general trend as far as pinnule numbers are concerned, but this species is clearly distinctive in terms of its size. The unusually large size of this species must be related to currents and food concentrations in the seamount environment (Rodgers 1994). Conversely, the small size of *H. foelli* can be related to limited food resources on abyssal plains of the central Pacific.

Hyocrinids attach to hard substrata by means of a calcareous disk. Thus, they do not occur where soft sediments predominate, unless such structures as rocky outcrops or manganese nodules are also present. According to the model proposed by Roux (1987), passive separation of populations living in mesobathyal depths during seafloor spreading is possible, resulting in progressive isolation of seamount faunas through geological time. The affinities between *H. cyanae* and *H. giganteus* lend some support to the model of Roux (1987). The ancestor(s) of these two species would not seem to be from abyssal species such as *H. bethellianus* or *H. foelli.* We suggest an evolution in the Pacific Ocean from a bathyal slope ancestor of medium size (like *H. cyanae*) toward giant species in seamount environments (like *H. giganteus*) or toward dwarf species on deep abyssal plains (like *H. foelli*).

Our knowledge of larval dispersal in stalked crinoids remains very poor. The cosmopolitan distribution of the family Hyocrinidae may have been achieved by larval dispersal with the aid of deep-sea currents or by passive processes related to plate tectonics through geological time. The fossil history of the family (Lower Tertiary to Recent) is sketchy and contributes little to these speculations.

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