New Hyocrinid Crinoids (Echinodermata) from Submersible Investigations in the Pacific Ocean[1]

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Abstract: A few specimens belonging to the deep-sea family Hyocrinidae (stalked Crinoidea, Echinodermata) collected by submersible in the eastern and western Pacific Ocean are described. *Laubiericrinus pentagonalis*, n. genus, n. sp., from the North Fiji Rise is the first discovery of a hyocrinid crinoid with a pentaradially symmetrical stalk. *Hyocrinus biscoitoi*, n. sp., from the East Pacific Rise attains large size and has close affinities with *H. giganteus* from Horizon Seamount. Additional information is given concerning *H. foelli* found near cold seeps on the Mexican continental margin; *H. cyanae*, previously collected on New Caledonian slopes; and *Calamocrinus diomedae* from the Cocos Ridge and Galápagos slopes. For the latter, the first young specimens known document ontogenetic trends in this famous species.

HYOCRINIDS ARE stalked crinoids that attach to rocky substrates by their encrusting disk. They live in cold, deep water on continental margins, rises, seamounts, and ferromanganese nodule fields in abyssal plains. *Ptilocrinus antarcticus* excepted (depth range 450–500 m), hyocrinid crinoids inhabit depths in excess of 700 m. Specimen are scarce in dredge and trawl samples, but deep-sea photographs taken via submersible have revealed several cases of abundant stalked crinoid populations including hyocrinids on rocky current-swept substrates (Roux 1980*a*, 1985). During the last decade our knowledge of hyocrinids has progressed rapidly. In 2002, Roux et al. listed 20 species of living Hyocrinidae, eight of which were known in 1973 (Roux 1980*b*) and 10 described since 1998 mostly by Mironov and Sorokina (1998). Here, I describe a few specimens including two new species and a new genus from material collected by submersibles in the Pacific Ocean over the last two decades.

In the family Hyocrinidae, Mironov and Sorokina (1998) erected four subfamilies using the architecture of genital pinnules as one of the most important characters. Two of these subfamilies (Calamocrininae and Hyocrininae) had been proposed previously by A. M. Clark (1973), and the others (Dumetrocrininae and Ptilocrininae) issued from changes and restrictions in the diagnosis of the genus *Ptilocrinus*. However, as with other stalked crinoids, the most important taxonomic character lies in the pattern of branching and arrangement of articulations in the arms (Roux 2002), especially in their proximal part. Stalked crinoid ontogeny shows a complex mosaic of heterochronic development (Améziane-Cominardi and Roux 1994), providing a wide field of phenotypic variations at different taxonomic levels. Among hyocrinids, heterochronic gradients have been documented in *Hyocrinus foelli*, with wide intraspecific variations (Roux and Pawson 1999), and in *Thalassocrinus* at the generic level (Roux 2002). A statistical approach to morphological variations is desirable, but is currently not possible, because numerous hyocrinid taxa are known from single specimens only. That is why intermediate taxonomic levels (subfamily, subgenus, and subspecies) are not used in this paper. Their validity will be discussed in a forth-

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coming paper that will include additional information on *Ptilocrinus* ontogeny. Here, both *Hyocrinus* and *Ptilocrinus* are treated sensu lato as in Roux et al. (2002).

Evidence for a cyrtocrinid origin of Hyocrinidae has accumulated through time (A. H. Clark 1915, Gislèn 1939, Améziane et al. 1998, Mironov and Sorokina 1998), and the affinity of this family with the Guillecrinidae was suggested recently (Mironov and Sorokina 1998, Améziane and Roux 2003).

For an explanation of terms, see Roux et al. (2002).

Family HYOCRINIDAE Carpenter, 1884

Genus *Laubiericrinus* Roux, n. genus

ETYMOLOGY: This new genus is dedicated to Lucien Laubier, who developed modern deep-sea biology in France and collected the first specimen described here.

DIAGNOSIS: Genus of Hyocrinidae with first pinnule at Br5. Arm pattern mostly 1+2 3 4+5 or 1+2 3+4 5 6+7 and, beyond Br5, a+b c+d e+f (that is, with synostoses [+] alternating with muscular articulations). Well-developed cylindrical anal tube. Basal ring with 3 sutures. Columnal symplexies with 5 crenular units.

Laubiericrinus pentagonalis Roux, n. sp.

Figures 1–3

ETYMOLOGY: The species name refers to the pentaradial pattern of proximal columnal symplexies.

TYPE MATERIAL: Holotype: collected in July 1989 by the French submersible *Nautile* during *Starmer II* cruise in the southwestern Pacific, North Fiji Rise (18° 50′ S, 173° 29′ W), dive 19, depth 2,765 m; catalogued in the zoological collections of the Museum national d'Histoire naturelle (MNHN) in Paris, no. EcPs10269.

DIAGNOSIS: Variable proximal arm pattern, mostly of 1+2 3 4+5; beyond Br5, pattern mostly a+b c+d; brachials and 2 proximal ossicles of pinnules with lateral projections having a maximum development at Br4. First pinnule on Br5; genital pinnules with a rigid proximal part of about 8 ossicles and 1 row of rectangular lateral plates; cover plates wide and rounded. Aboral cup with a ratio of radial upper width to primibrachial width of 1.3 to 1.4; basal ring with 3 sutures. Tegmen with a well-developed cylindrical anal tube shorter than oral cone; top of each oral with 1 fingerlike projection. Columnal symplexies with 5 crenular units of 1 (in juvenile) to 3 crenulae between areolar lobes.

DESCRIPTION: Complete single specimen (Figure 1*a–b*). Height of basal ring 4.2 mm; diameter at base of basal ring 2 mm; diameter at base of radial ring 5.9 mm; height of radials 6.7 mm; width of radials 5.2 mm; ratio of radial upper width to primibrachial width 1.3 to 1.4; diameter at top of radial ring 8.5 mm; height of tegmen 4.3 mm; height of well-developed anal tube 3.4 mm. Radials subrectangular with axial rib sometimes divided into 2 small ribs toward basal ring; sutures between radials slightly raised (Figure 1*c*). Conical basal ring showing 3 irregular sutures. Oral cone well developed; top of each large oral forming 1 fingerlike projection (Figure 1*i–j*). Bases of orals and tegminal plates with a hillocky surface obscuring plate sutures; about 6 (may be more) tegminal plates per interadius. Cylindrical anal tube shorter than oral cone, with its apex covered by small, fingerlike projections (Figure 1*i*); apparently cone-shaped when arms closed (Figure 1*d*). Food grooves passing directly from arms to base of oral cone.

Length of arms 10.5 cm; length of proximal arms bearing genital pinnules 5.8 cm; width of arm at articulation Br1+2 1.6 mm; width of arm at articulation Br19+20 1 mm; height of Br1+2 2.6 mm; height of Br6+7 2.7 mm; length of genital pinnules up to 37 mm, each with a proximal inflated part up to 9.7 mm long. Genital pinnules (Figure 2) with a rigid proximal part of about 8 pinnulars and 1 row of rectangular lateral plates; cover plates wide and rounded. Only the end of gracile and flexible part of pinnules tending to be rolled up. First pinnule always on Br5. Proximal arm pattern of 1+2 3 4+5 6+7 (3 cases), 1+2 3+4 5 6+7 (1 case), or 1+2 3 4+5 6 7+8 (1 case). Middle and distal arm pattern consisting of successive brachial pairs

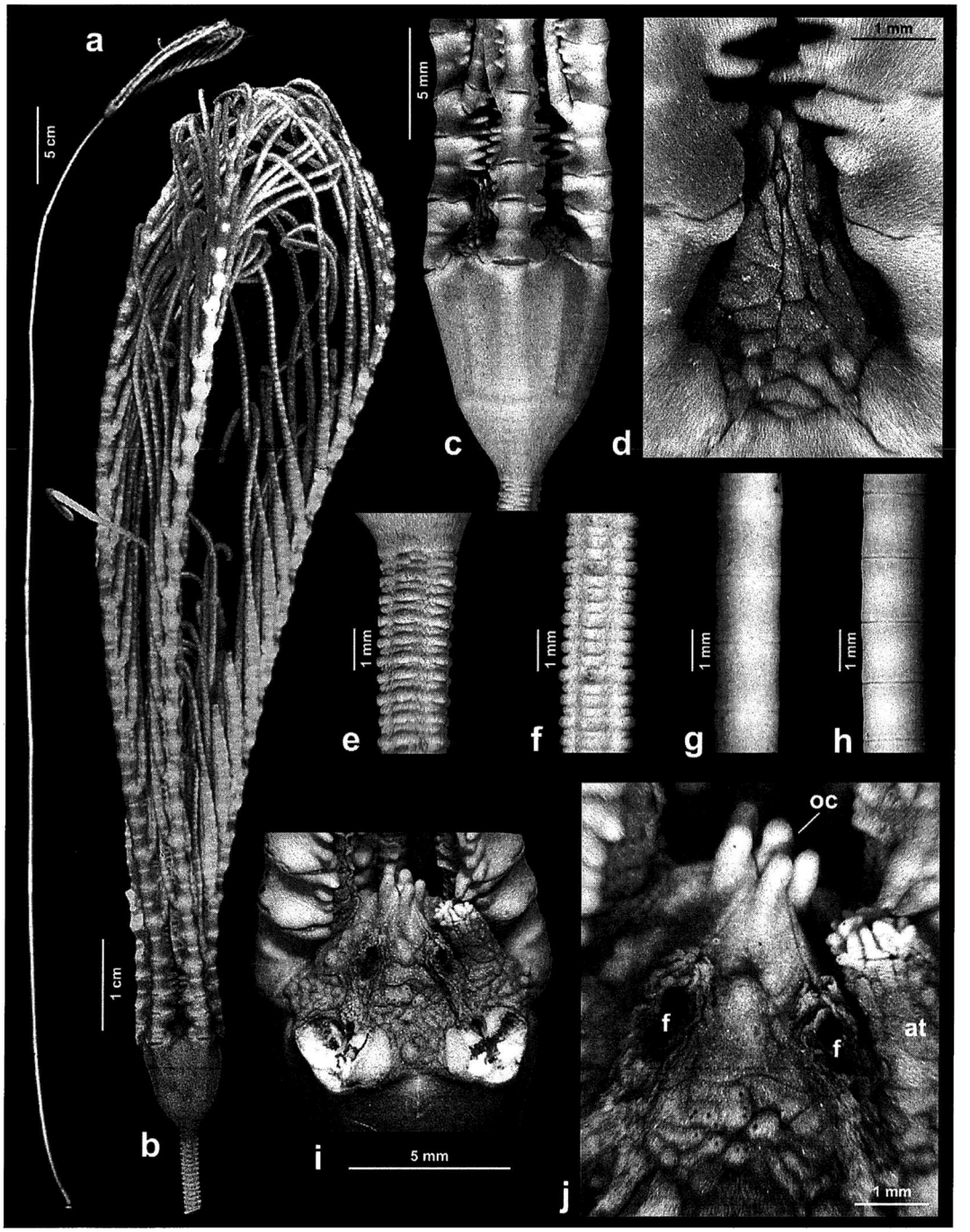

FIGURE 1. *Laubiericrinus pentagonalis*, n. sp. *a–b:* lateral views; *c:* aboral cup and proximal arms; *d:* anal interradius with arms closed; *e–h:* changes in stalk morphology from proximal (*e*) to distal (*h*); *i–j:* views of tegmen with two arms removed (at, anal tube; f, food groove; oc, oral cone).

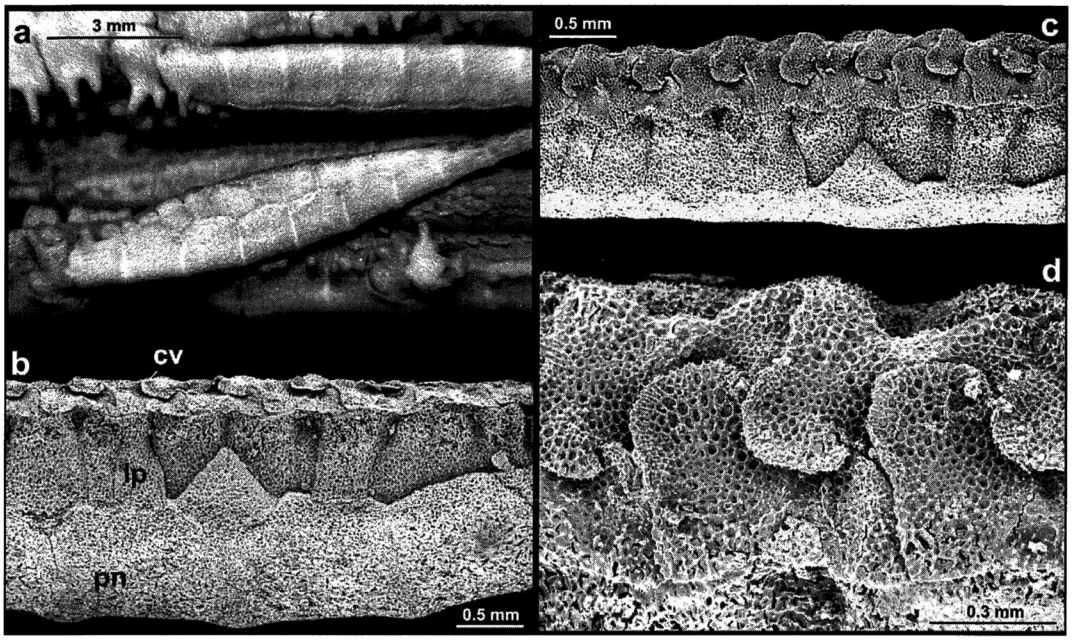

FIGURE 2. *Laubiericrinus pentagonalis*, n. sp., genital pinnule. *a:* ambulacral view of proximal arm bearing genital pinnules; *b:* lateral view of proximal inflated part of a genital pinnule (cv, cover plate; lp, lateral plate; pn, aboral pinnular ossicle); *c:* oblique view of the same; *d:* imbricated cover plates (*b–d*, SEM views).

united by synostosis (a+b c+d e+f, etc.), except a few cases in which 3 successive brachials are joined by 2 muscular articulations (a+b c d+e). Brachial pairs and isolated brachials constricted midway between their 2 muscular articulations; brachials and the 2 proximal ossicles of pinnules with lateral projections best developed on Br4 (Figure 1*c*).

Total length of stalk 70 cm. Proximalmost diameter of stalk 1.8 mm, decreasing to 1.5 mm at a distance of 33 mm from basal ring, increasing to 2.8 mm at a distance of 6 mm from attachment disk; height of columnal 1.3 mm at a distance of 62 mm from basal ring, increasing up to 2.2 mm at a distance of 20 mm from attachment disk (Figure 3*j*). Proximal stalk very heteromorphic for first 19 mm from crown, with pentolobate to pentagonal cross section; columnals becoming cylindrical at a distance of 11.5 cm from basal ring (Figure 1*e–h*). Columnal symplexies (Figure 3*a–g*) with 5 crenular units of 2 to 3 crenulae and pentalobate areola. Tallest columnals with deep irregular pits in areolar lobes (Figure 3*d–f*). Large-meshed, galleried stereom of perilumen contrasting with finer-meshed stereom of areolar lobes and claustrum. Distal syzygies with low, multiradiate crenularium (Figure 3*h–i*). Distalmost joints are flat synostoses (Figure 3*k*) with the juvenile symplexial pattern of 5 crenular units of 1 crenula each visible at center (Figure 3*k–l*).

DISCUSSION: The other hyocrinid genera with the first pinnule usually at Br5 are *Thalassocrinus* and *Anachalypsicrinus*. The tegmen and arms of *Laubiericrinus* have close affinities with those of *Thalassocrinus*. However, *Thalassocrinus* differs in having columnal joints always with 6 crenular units and the proximal arm pattern uniformly 1+2 3 4+5 6+7 or tending to 1+2 3 4 5+6 with the first pinnule at Br4 in older specimens (Roux 2002). In *Anachalypsicrinus*, the anal cone is very low and columnal symplexies have 9 to 12 crenular units (A. M. Clark 1973, Roux 1980*b*,

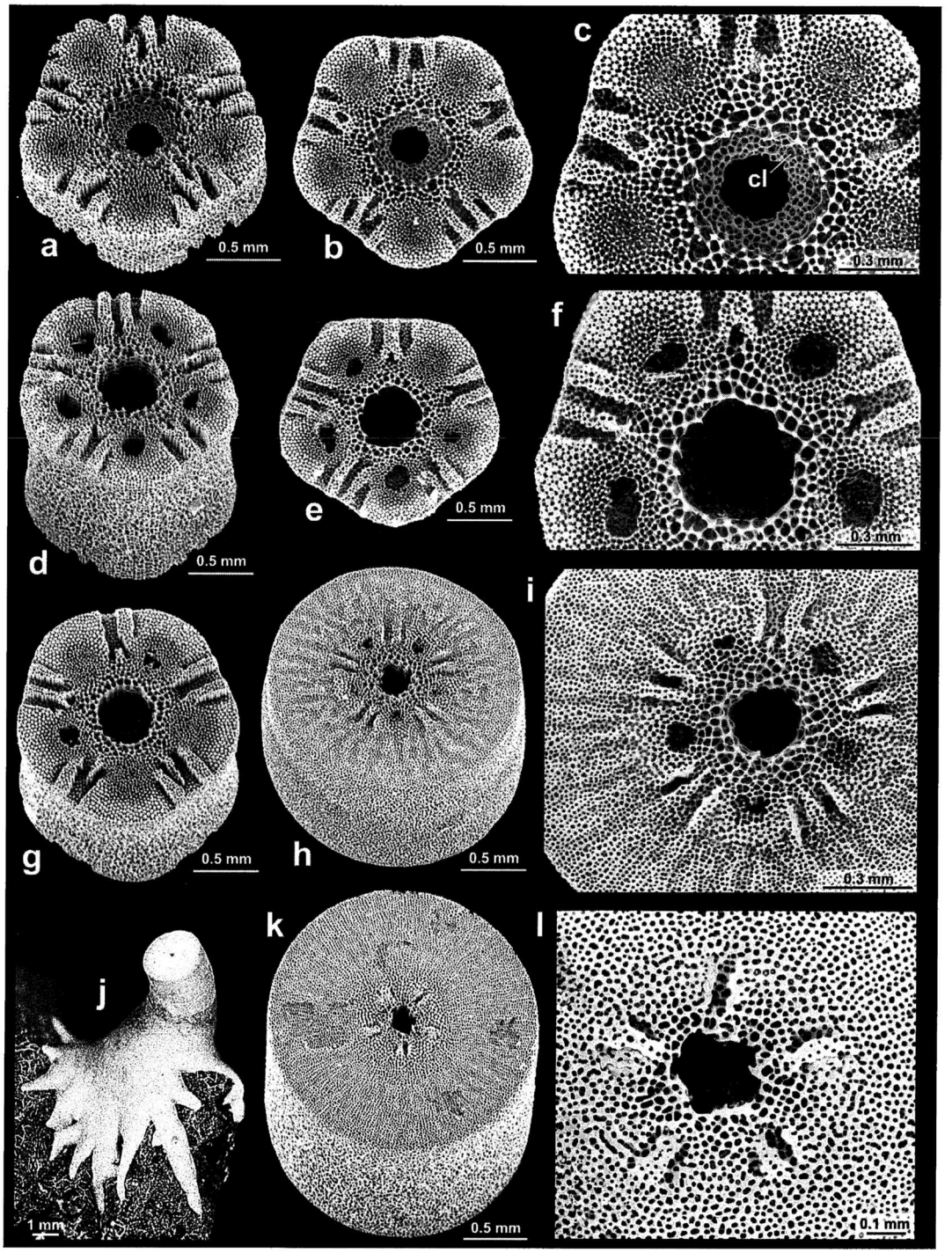

FIGURE 3. Columnals of *Laubiericrinus pentagonalis*, n. sp. *a–c:* proximal columnal (cl, claustrum); *d–f:* columnal of maximum height; *g:* distal symplexy before increase in diameter; *h–i* and *k–l:* distal syzygies with juvenile symplexial pattern at center; *j:* holdfast with distalmost syzygy observed in *k–l* (*a–i*, and *k–l*, SEM views).

Mironov and Sorokina 1998). The presence of a single 1+2+3+4 variant in the proximal arm of *Laubiericrinus pentagonalis* suggests some affinities with *Hyocrinus*. *Laubiericrinus pentagonalis* is the first known hyocrinid crinoid with a fivefold symmetry in the stalk with symplexies closely resembling the proximal joints of young *Guillecrinus*. So, affinities between Guillecrinidae and Hyocrinidae (Mironov and Sorokina 1998, Améziane and Roux 2003) seem to be confirmed.

Genus *Hyocrinus* Wyville-Thomson, 1876

Hyocrinus foelli Roux & Pawson, 1999
Figure 4*j*

MATERIAL EXAMINED: One specimen collected in January 1994 by the French submersible *Nautile* during *Nautimate* cruise in the eastern Pacific off Mexico, site 3 near cold seeps, 18° 23′ N, 104° 23′ W, depth 3,030 m, dive NM 10; catalogued in the zoological collections of the Museum national d'Histoire naturelle (MNHN) in Paris, no. EcPs10270.

DESCRIPTION: Complete specimen with crown length 20.2 mm; aboral cup height 4.3 mm; maximum diameter at top of radial ring 3.9 mm; diameter at base of basal ring 1.35 mm. Stalk length 43 mm; stalk diameter 0.8 mm at 4 mm under aboral cup and 0.7 mm at 12.5 mm; columnal diameter 0.75 mm near distal attachment disk. Aboral cup ornamentation is the most developed known in the species, with a pair of conspicuous ribs in line with each arm and 3 to 5 transverse ribs. Tegmen granulated, with anal tube higher than oral cone; base of orals with 1 fingerlike projection. Arm articulation on radial relatively wide and proximal brachials with lateral extensions tending to cover the tegmen when crown closed. Ratio of radial upper width to primibrachial width 1.2 to 1.3. Proximal arm pattern 1+2 3 4+5; beyond Br5 mostly a+b c+d, etc., with one case of 6+7+8; first pinnule always at Br5. Arm without genital pinnules. Distal part of arms and pinnules tending to roll up.

DISCUSSION: As observed by Roux and Pawson (1999), *H. foelli* presents wide intraspecific variations. The specimen collected off Mexico illustrates an extreme phenotype with strongly ornamentated aboral cup and tegmen, and with relatively wide proximal brachials. The absence of genital pinnules could be related to cyclic reproduction in a marginal environment depending on seasonal food supply, as opposed to continuous reproduction in the abyssal plain environment of the central Pacific where food supply is lower but more regular (Gage and Tyler 1991).

Mironov and Sorokina (1998) described one specimen attributed to *H. bethellianus*, n. ssp., from the North Pacific Ocean at a depth of 2,915–3,015 m. According to A. Mironov (pers. comm.), this specimen belongs to the morphotype of *H. foelli* with narrow arms and without ornamentation.

These data extend the depth range of *H. foelli* from 4,300–4,880 m to 3,015 m (possibly 2,915 m) and its occurrence from ferromanganese nodule fields of the northeastern equatorial Pacific Ocean to its northern and northeastern margins and rises.

Hyocrinus biscoitoi Roux, n. sp.
Figures 4*a–i*, 5, 7*c*

ETYMOLOGY: This new species is dedicated to Manuel Jose Biscoito, Station of Marine Biology of Funchal, Madeira, who collected and took deep-sea photographs of the holotype.

TYPE MATERIAL: Holotype: single specimen collected by the French submersible *Nautile* during *Hope* 99 cruise on the East Pacific Rise, Southeastern Seamount, 12° 42.50′ N, 103° 52.80′ W, depth 2,410 m, dive 1365 (21 April 1999); catalogued in the zoological collections of the Museum national d'Histoire naturelle (MNHN) in Paris, no. EcPh90.

DIAGNOSIS: Very large species reaching stalk length of 1 m; diameter at top of aboral cup up to 27 mm. Tegmen well developed and moderately inflated, with additional small plates between small oral cone and 3 to 5 large, polygonal marginal tegminal plates. Proximal food grooves not elevated above the tegmen surface. Ratio of radial upper width to primibrachial width 1.6 to 2. First pinnule at IBr6. Proximal arm pattern of

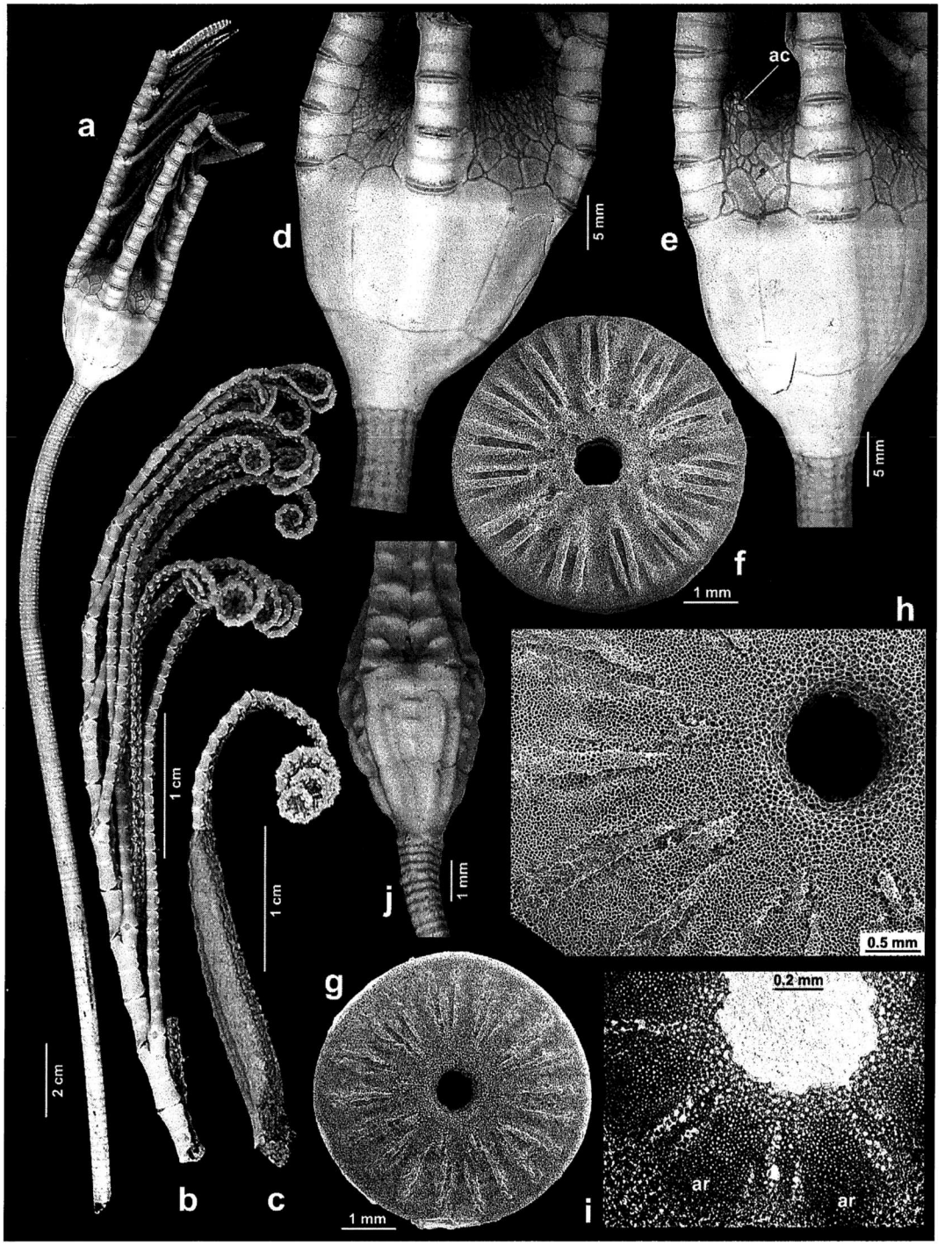

FIGURE 4. *Hyocrinus biscoitoi*, n. sp. (*a–i*) and *Hyocrinus foelli* (*j*). *a:* lateral view of stalk, theca, and remaining attached proximal arms; *b:* distal part of an arm; *c:* genital pinnule; *d–e* and *j:* lateral view of theca (ac, anal cone); *f:* proximal stalk symplexy; *g–h:* columnal near distal broken end of stalk; *i:* thin cross section under a facet of the same columnal (ar, areolar lobe) (*f–h*, SEM views; *i*, light microscopy).

1+2 3+4 5+6; variable pattern after Br6 with either series of a+b+c or only a+b c+d, etc.; distally only a+b c+d. Columnal facet with 10–11 crenular units of 1 (in juvenile) to 4 crenulae well developed in the proximal stalk.

DESCRIPTION: Preserved part of holotype consisting of crown, calyx, and proximal stem (Figure 4*a*). Height of basal ring 9.4 mm; diameter at base of basal ring 7.1 mm; diameter at base of radial ring 17 mm; height of radials 14.7 mm; width of radials 14 mm; ratio of radial upper width to primibrachial width about 1.6 to 2; diameter at top of radial ring 27 mm; height of tegmen 13.4 mm; height of anal tube 5 mm. Tegmen moderately inflated, with numerous, frequently elongated plates lying between 3 to 5 large, polygonal marginal interradial plates and small oral cone; food grooves not clearly elevated above tegmen surface and passing from arm to tegmen at level of Br4 or 5. Anal cone relatively low, in external position. Basals fused.

Length of crown 25 cm; each arm bearing about 35 pinnules on each side (Figure 5); length of proximal arm with genital pinnules 10.5 cm; width of Br1 8.1 mm; width of Br6 4.7 mm; width of Br16 4.0 mm; height of Br1+2 5.4 mm; height of Br5+6 4.8 mm; length of genital pinnules up to 45 mm, with a proximal inflated part up to 23 mm long and 3.5 mm wide; length of distal, nongenital pinnules about 30 mm. Genital pinnules with 2 parts strongly differentiated: a rigid proximal part of about 14 ossicles bearing 1 row of trapezoidal to rectangular lateral plates, and a gracile distal part tending to be rolled up as in the very flexible nongenital pinnules (Figure 4*b–c*). Cover plates with long triangular end, covering just a part of the food groove (Figure 7*c*). First pinnule always on Br6, with proximal arm pattern of 1+2 3+4 5+6. Between Br6 and Br18, 2 or 3 series of three brachials united by synostoses. Middle and distal arm pattern a+b c+d e+f, etc.

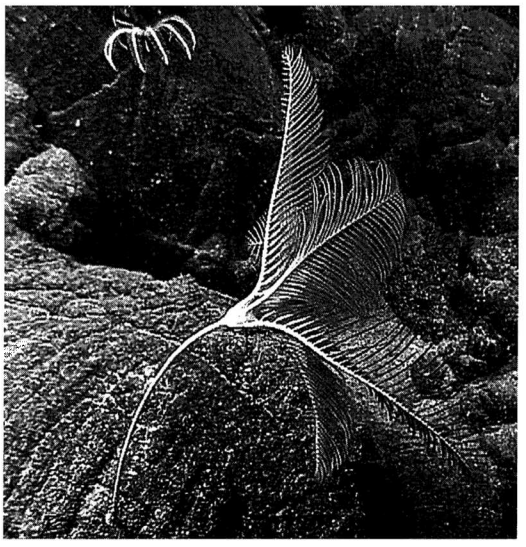

FIGURE 5. *Hyocrinus biscoitoi*, n. sp., in situ photograph of the holotype taken from the submersible *Nautile* (courtesy of Daniel Desbruyères).

Total length of preserved stalk 22.5 cm; distal part and attachment disk missing. Proximalmost diameter of stalk 6.2 mm, decreasing to 5.2 mm at a distance of 23 mm from basal ring, increasing to 5.5 mm at 68 mm (transition from polygonal to circular in cross section) and decreasing again to 5.1 mm at broken end; columnal height 1 mm at a distance of 68 mm from basal ring, increasing to 2.5 mm at broken end. Columnal articulations are multiradiate symplexies. Facets of proximal columnals with 10–11 variable crenular units of 3 to 4 crenulae; crenulae either long, regular, and parallel or shorter and more irregular (Figure 4*f*). Crenular unit frequently with 2 median crenulae united in a tuning fork shape and 1 or 2 short external crenulae (Figure 4*h*). Distal symplexies with a multiradiate crenularium of low relief; perilumen forming a conical depression toward the axial canal (Figure 4*g*); cross section 1.5 mm under articular facet shows its juvenile pattern (i.e., 10 crenular units of 1 or 2 crenulae isolating 10 areolar lobes) (Figure 4*i*).

DISCUSSION: *Hyocrinus biscoitoi* is larger than the holotype of *H. giganteus*, which was the first giant species of the genus *Hyocrinus* found, at Horizon Seamount in the eastern Pacific (Roux and Pawson 1999), and its aboral cup is more bowl-shaped with less conspicuous broad radial ribs. *Hyocrinus biscoitoi* differs mainly in having series of three brachials united by synostoses between Br6 and

Br18 and by narrow triangular cover plates. *Hyocrinus giganteus* has series of two brachials united by synostoses and large, rounded cover plates (Figure 7*d*). Proximal parts of food grooves are elevated above the tegmen in *H. giganteus* and incorporated in the tegmen surface in *H. biscoitoi*. In *H. giganteus*, the ratio of radial upper width to primibrachial width is greater (2.1) than in *H. biscoitoi*. Unfortunately, the stalk of *H. giganteus* and its columnal articulations are unknown except for the distalmost syzygy.

Roux and Pawson (1999) suggested that *H. giganteus* and *H. cyanae* might have close affinities. *Hyocrinus cyanae* was described from external morphology only (Bourseau et al. 1991), so additional information on its pinnules, tegmen, and stalk articulations is required for a detailed comparison with *H. giganteus* and *H. biscoitoi*, as follows.

Hyocrinus cyanae Bourseau, Améziane-Cominardi, Avocat & Roux, 1991
Figures 6, 7*a–b*

MATERIAL EXAMINED: Holotype, collected by the french submersible *Cyana*, off Lifou Island, New Caledonia (20° 35.4′ S, 167° 12.0′ E), depth 2,536 m, catalogued in the zoological collections of the Museum national d'Histoire naturelle (MNHN) in Paris, no. EcPs244.

AMENDED DIAGNOSIS: Medium-sized species. Tegmen with moderately developed oral cone and small anal cone; 4 to 6 large, rectangular tegminal plates per interadius; ambulacral axes mainly in relief. Narrow proximal brachials, ratio of radial upper width to primibrachial width 2.5 or more. Basals fused. First pinnule on Br6. Genital pinnules with lateral plates having coarsely meshed stereom; cover plates lozenge-shaped with a sharp end. Arm pattern of 1+2 3+4 5+6 7+8, etc. Stalk symplexies with 9 crenular units of 1 crenula each; external surface of primicolumnals bearing long tubercules.

DESCRIPTION: Arm length 75 mm; maximum length of pinnules 28 mm. Aboral cup diameter at top of radial ring 8.2 mm; height of aboral cup 8.5 mm; ratio of radial upper width to primibrachial width about 2.5 or more. Length of stalk 21 cm, broken near distal end. Diameter of stalk 2 mm at proximal end, 1.2 mm at a distance of 5 cm under aboral cup, 1.8 mm at distal end.

Tegmen with 4 to 6 large, rectangular plates per interadius; orals moderately developed; low anal cone; small elongated lateral plates supporting food grooves above surrounding tegmen (Figure 6*a*). Dorsal cup with wide, radially placed ribs in line with arm axes. Regular arm pattern of 1+2 3+4 5+6 7+8, etc., with first pinnule always on Br6. Proximal part of genital pinnules showing 1 row of trapezoidal lateral plates bearing cover plates; labyrinthic stereom of lateral plates with large meshes; lozenge-shaped cover plates with needlelike projections at top (Figure 7*a*). Distal part of genital pinnule bearing cover plates larger than pinnulars (Figure 7*b*).

Outer surface of primicolumnals with long tubercules, giving the entire stalk a roughened appearance. Columnals articulated by symplexies with 9 crenular units of 1 well-developed crenula each. Proximal columnals with claustrum and small subpentagonal lumen (Figure 6*b–d*). Taller, proximal columnals with a large axial canal surrounded by galleried stereom with large meshes (Figure 6*e–f*). Articular facets very similar in proximal and distal stalk. Distalmost articulations unknown.

DISCUSSION: Affinities between *H. cyanae*, *H. giganteus*, and *H. biscoitoi* are confirmed. In the three species, the first pinnule is always on Br6, but they differ in heterochronic development of other characters. In *H. cyanae*, oral plates directly adjacent to a few main tegminal plates and food grooves in relief above the tegmen surface indicate affinities with *H. bethellianus* and *H. foelli*. In *H. foelli*, substantial intraspecific variations suggest ontogenetic trends and possible relationships between differents species of the genus *Hyocrinus* as follows.

When the oral cone decreases in size relative to the tegmen during ontogeny, development of the tegmen requires either growth of a few primary interradial tegminal plates as in *H. cyanae* or multiplication of new small tegminal plates as in *H. biscoitoi*,

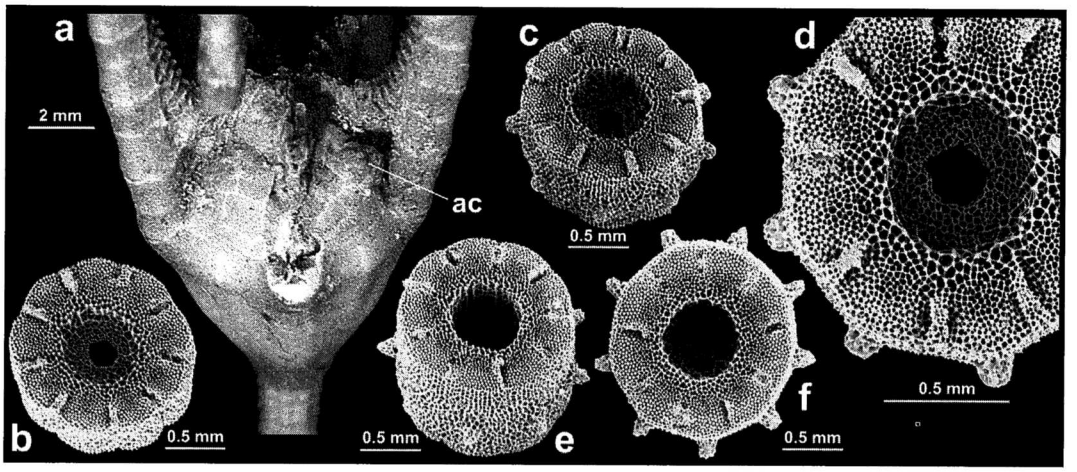

FIGURE 6. *Hyocrinus cyanae. a:* oblique lateral view of theca with one arm removed (ac, anal cone); *b–d:* proximal columnals, *c–d:* primicolumnal; *e–f:* distal primicolumnal (*b–f,* SEM views).

allowing inflation of the tegmen as in peramorphic specimens of *H. foelli.* The new tegminal plates seem to originate from the development of elongated lateral plates between proximal brachials and their cover plates when food grooves stand above the tegmen surface. In *H. biscoitoi,* these elongated lateral plates clearly become incorporated onto the inflated tegmen architecture, and the elevation of food grooves above the tegmen surface becomes reduced or disappears. In *H. giganteus,* the inflated tegmen is built mainly by growth of primary tegminal plates with just a few additional small plates of lateral arm origin, and the food grooves remain in relief above the tegmen surface.

During ontogeny, the difference between the radial upper width and primibrachial width increases with the allometric differentiation between the two ossicles. The narrow proximal brachials of *H. cyanae* represent a peramorphic morphology, whereas the relatively wide proximal brachials of *H. biscoitoi* and of the *H. foelli* specimen described here are paedomorphic. The development of wide crenular units of numerous crenulae in the stalk symplexies of *H. biscoitoi* depends mainly on the large size of specimens and is attributed to a hypermorphic process.

Genus *Calamocrinus* Agassiz, 1890

AMENDED DIAGNOSIS: Genus of Hyocrinidae with arms irregularly branched, first pinnule on Br4, and proximal arm pattern 1+2 3 4 5+6. One branch of a pair wider than the other; place of first branching varies from IBr8 to IBr15. Basals fused or with a few inconspicuous sutures. Tegmen inflated, with well-developed anal cone. Columnal articulation with 7 to 16 crenular units.

Calamocrinus diomedae Agassiz, 1890

Figures 7*e–f,* 8

MATERIAL EXAMINED: Five specimens are catalogued in the collections of the National Museum of Natural History (USNM) in Washington, D.C. Two specimens were collected during *Albatross* expeditions: the holotype, USNM 18144 from the Galápagos, Indefatigable Island (00° 29.0′ S, 89° 54.3′ W), depth 717 m, 1888; 1 specimen, USNM 18145 from Mariato Point off Coiba Island (06° 35.0′ N, 81° 44.0′ W), depth 1,430 m, 1891. Three specimens forming the ontogenetic sequence no. 1 were collected in 1986 by the submersible *Johnson Sea-Link* on Cocos Ridge off the Costa Rican island of

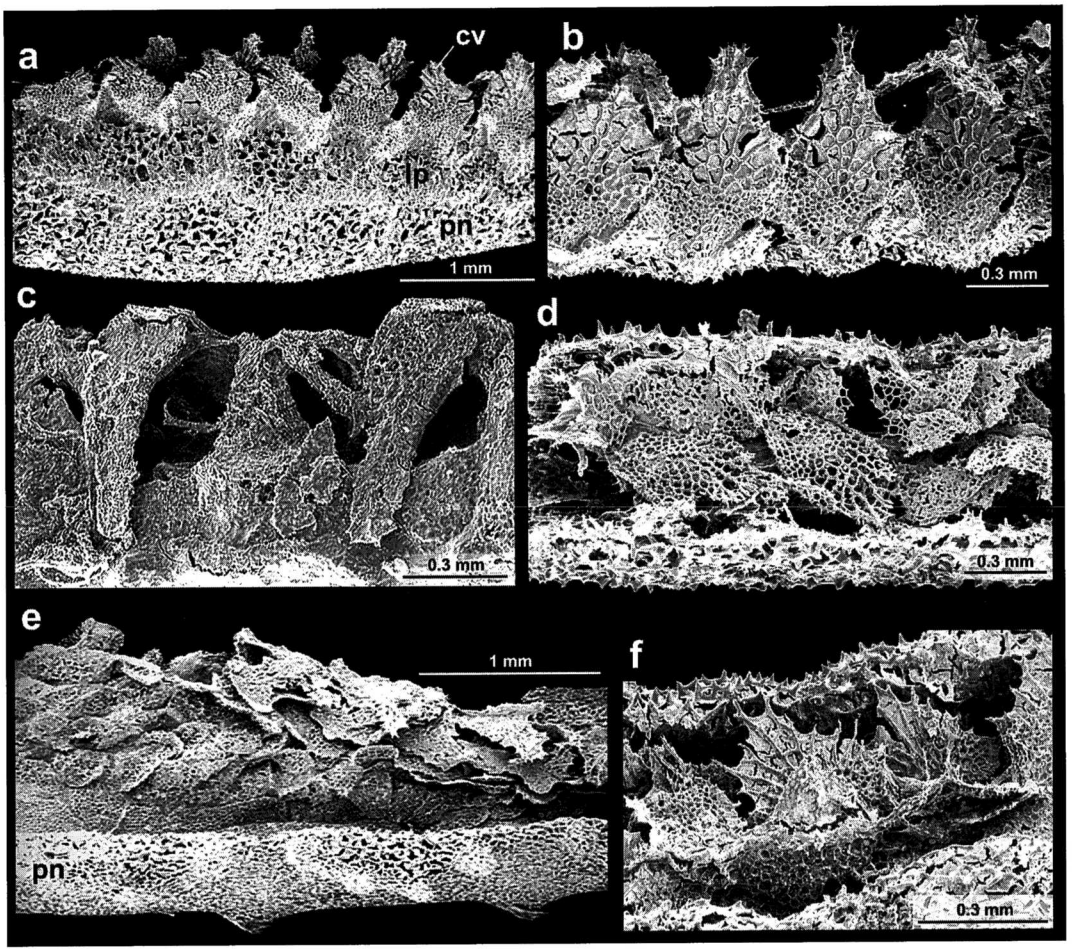

FIGURE 7. Genital pinnules (SEM views). *a–b: Hyocrinus cyanae*, *a:* lateral view of inflated proximal part (cv, cover plate; lp, lateral plate; pn, aboral pinnular ossicle); *b:* lateral view of distal part and cover plates; *c–d* and *f:* oblique ambulacral view of cover plates, *c: Hyocrinus biscoitoi; d: Hyocrinus giganteus; e–f: Calamocrinus diomedae*, *e:* lateral view of inflated proximal part.

Cocos (05° 24.0′ N, 87° 10.0′ W), depth 714 m. They are catalogued in the collections of the Harbor Branch Oceanographic Institute, Fort Pierce, Florida: 14-XI-86-1-12V (small specimen), 14-XI-86-1-23V (medium-sized specimen), 30-XI-86-1-21V (large specimen). Three other specimens forming the ontogenetic sequence no. 2 were collected during *Johnson Sea-Link* dives off the Galápagos Islands in 1998 (Pawson and Ahearn 2001): 1 very small specimen, USNM E47882, from Fernandina Island, dive 3100 (00° 17.24″ S, 09° 39.0′ W), depth 625 m; 1 medium-sized specimen, USNM E47881, from Seymour Island (00° 21.42′ S, 09° 15.0′ W), depth 619 m; 1 large specimen, USNM E47880, same dive, depth 525 m.

AMENDED DIAGNOSIS: Large species with variable arm branching usually from IBr8 to IBr15 (most frequent at IBr10–12), from IIBr6 to IIBr20, from IIIBr6 to IIIBr17, from IVBr6 to IVBr24. Basals fused or with very

inconspicuous sutures; aboral side of basal ring flanged in small and medium-sized specimens. Tegmen inflated, with 15 to 30 polygonal and unperforated interradial plates; numerous hydropores localized in upper part of tegmen; anal cone very tall and oral cone inconspicuous except in juvenile specimens, in which orals are strongly concave. Oral side of arms with tack-shaped lateral plates; pinnulars with oral lateral wings and dorsal needlelike stereom projections; genital pinnules with numerous imbricated small lateral plates, and subtriangular cover plates tipped with sharp stereomic projections. Columnals flanged in small and medium-sized specimens; symplexies with 7 (in juveniles) to 16 (most frequently about 14) crenular units of 1 to 4 (largest specimens) crenulae; distal syzygies with multiradial crenularium.

DESCRIPTION: The 6 new specimens collected in 1986 and 1998 document the ontogenetic development of the species and its range of morphological variation.

Ontogenetic sequence no. 1: First pinnule always at IBr4, with the arm pattern IBr 1+2 3 4 5+6; most frequent pattern beyond Br6 a+b c d+e. Arm branching always with one branch wider than the other; first pinnule of the wide branch at Br1, exceptionally at Br2; first pinnule of the small branch at Br2, 3, or 4.

Small specimen (Figure 8*a*) with a conical aboral cup with 1 broad rib in line with each arm; theca height 10 mm; height of dorsal cup 3.7 mm; radial ring diameter 4 mm; ratio of radial ring diameter to height of aboral cup about 1.1; ratio of radial upper width to primibrachial width 1.2 to 1.3; basal fused and bearing a distal flange; tegmen moderately developed, with concave interradial surface of 15–20 polygonal tegminal plates and relatively small orals. Maximum arm length 30 mm; arm base width 2.1 to 2.3 mm; adjacent IBr1 nearly touching when crown closed; arms branching at IBr10ax (1 case) and IBr11ax (3 cases); 2 arms broken at IBr6 and IBr8; first pinnule length about 14 mm (tip broken); pinnule length at midarm 8.5 mm; distal pinnules like small arms. Preserved stalk length 10 mm, rough, with flanged columnals; proximalmost stalk diameter 2.1 mm; stalk diameter at broken end 1.5 mm; columnal height up to 0.23 mm; young columnals with 13 short crenular units of 1 crenula each and with a well-developed claustrum (Figure 8*f*).

Medium-sized specimen (Figure 8*b*) with a conical aboral cup with proximal arms clearly separated when crown closed; theca height 22.5 mm; upper radial ring diameter 12.1 mm; diameter at radial-basal suture 7.5 mm; ratio of maximum radial ring diameter to height of dorsal cup 1.2 to 1.3; ratio of radial upper width to primibrachial width about 1.4; basal ring with 1 or 2 inconspicuous sutures and without ribs. Tegmen with convex interradial surface of about 20 subequal tegminal plates reaching Br4 to Br6; long anal cone inflated at its base. Maximum length of arms 87 mm; arm base width 4.1 to 5.0 mm; arms branching at IBr8, 10, 12 (1 case each), or 13 (2 cases), at IIBr7, 10, or 16 (each 1 case), at IIIBr10 (1 case); 1 case of 4 successive muscular articulations before IBr10. Pinnule length (tip broken) about 26 mm; genital pinnules with numerous imbricated, small lateral plates, and subtriangular cover plates tipped with sharp stereomic projections (Figure 7*e–f*). Preserved stalk length 118.5 mm; proximalmost diameter 5.1 mm; diameter at distal broken end 2.8 mm; columnal height up to 1.7 mm; primicolumnals flanged; distalmost preserved symplexies with 12–13 regular crenular units of 1 crenula each (Figure 8*g*).

Large specimen (Figure 8*c*) with a bowl-shaped aboral cup; theca height 32 mm; upper radial ring diameter 25.2 mm; diameter at radial-basal suture 18.5 mm; ratio of maximum radial ring diameter to height of dorsal cup 1.3; ratio of radial upper width to primibrachial width 1.5; basal ring with 2 small ribs in line with each arm (Figure 8*d*), very conspicuous on 2 rays, and sometimes 1 or 2 inconspicuous sutures. Tegmen inflated and including proximal part of first and second pinnules; about 20 relatively large and polygonal tegminal plates per interradius. Four arm trunks preserved; maximum arm length about 110 mm (end regenerating); diameter at arm base 24 to 25 mm; arms branching at IBr9 (1 case) or IBr10 (3 cases), at IIBr6 (3 cases) and

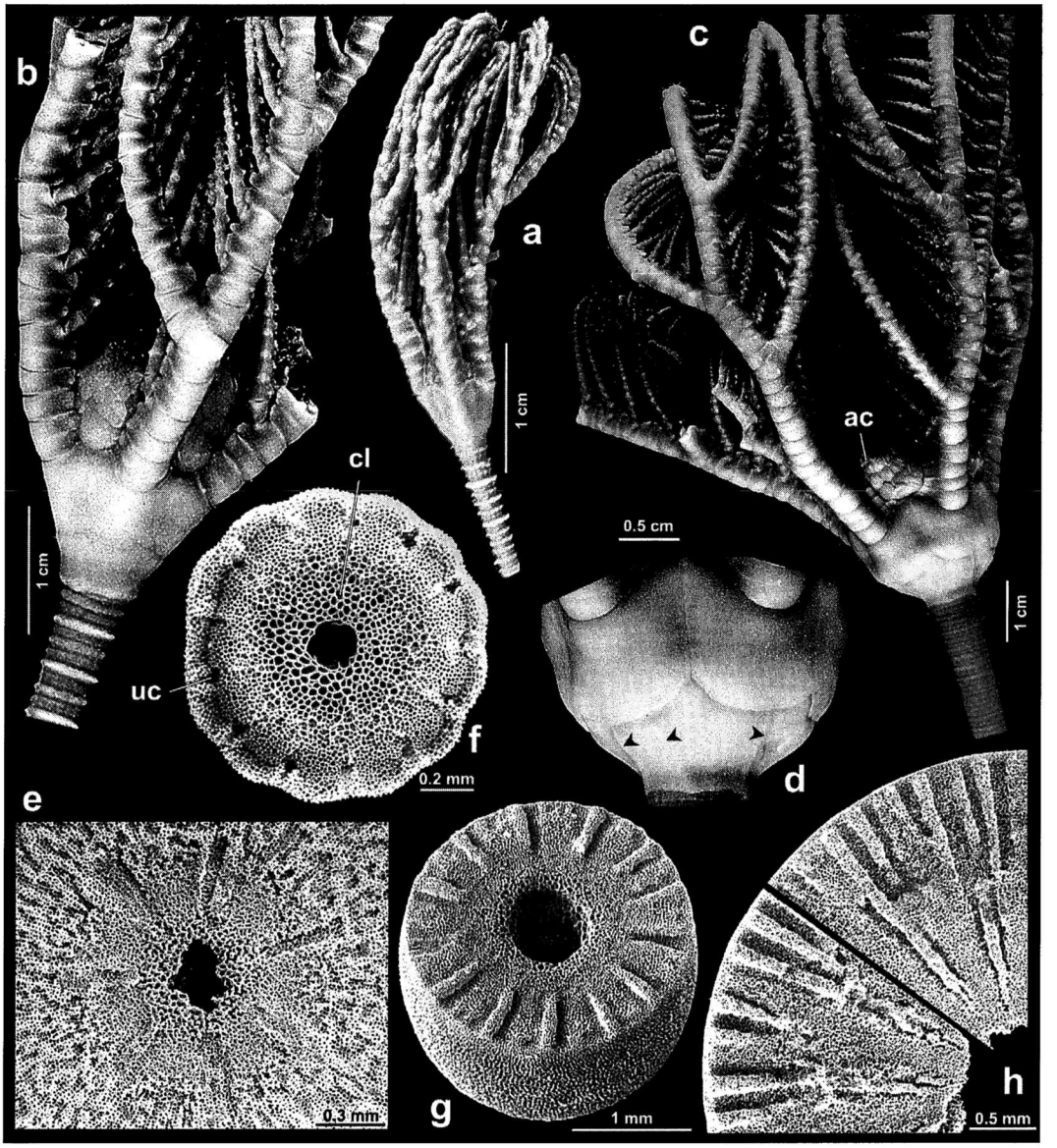

FIGURE 8. *Calamocrinus diomedae*. *a–d:* ontogenetic sequence no. 1 (courtesy of C. G. Messing) from juvenile (*a*) to large adult (*c–d*) with lateral view of aboral cup of large adult (*d*) (ac, anal cone; arrowheads, ribs in line with arms); *e–h:* ontogenetic sequence of stalk symplexies, *e:* juvenile pattern preserved at center of distal syzygy (specimen USNM 18145); *f:* young proximal columnal of the juvenile specimen (*a*) (cl, claustrum; uc, crenular unit); *g:* mature columnal of the medium-sized specimen (*b*); *h:* columnal facet near stalk end of the large specimen (*c*).

IIBr8 (1 case), at IIIBr6, 7, or 8 (1 case each), and at IVBr6, 8, or 20 (1 case each). Following a branch, ratio of wider arm to narrower arm width 1.26 for IIBr, 1.15 for IIIBr, 1.1 for IVBr, and 1.07 for VBr. First pinnule length 44 mm; pinnule length in middle of arm 23.5 mm. Preserved stalk 44 mm; proximalmost diameter 8.3 mm; diameter at

distal broken end 5.2 mm; columnals without flanges; columnal height up to 1.1 mm; distalmost preserved symplexies with 13 crenular units of 1 crenula each divided into 3–4 crenulae in inner facet and with additional crenulae between units in outer facet (Figure 8*b*).

Ontogenetic sequence no. 2: First pinnule at IBr4 with proximal arm pattern IBr 1+2 3 4 5+6, except for the large specimen, in which 1 ray has IBr 1+2 3 4+5 and first pinnule on Br5, and 2 other rays with first pinnule at Br6. Beyond Br6 most frequent pattern is a+b c d+e; never more than 3 successive muscular joints before first branching. Arm branching always with one branch wider than the other; first pinnule of the wide branch at Br1, exceptionally at Br2; first pinnule of the small branch at Br2, 3, or 4.

Small, immature specimen with a conical aboral cup; height of aboral cup 2.7 mm; radial ring diameter up to 3.8 mm; ratio of radial ring diameter to height of aboral cup about 1.4; ratio of radial upper width to primibrachial width 1.2 to 1.3; basals fused and bearing a distal flange. Tegmen relatively low, with strongly concave conspicuous orals, each bearing 1 or 2 tubercules at the base; anal cone much taller than oral cone, with long, fingerlike apical projections; interradius bearing about 10 tuberculate tegminal plates. Crown length 14.4 mm; arms and pinnules undifferentiated. Stalk length 13.5 mm, rough, with flanged columnals except for the 8 distalmost columnals; proximalmost stalk diameter 1.1 mm, decreasing to 0.95 at a distance of 30 mm from dorsal cup; stalk diameter at broken distal end 1.2 mm.

Medium-sized specimen ressembling the medium-sized specimen of ontogenetic sequence no. 1. It was illustrated by C. G. Messing in Roux et al. (2002). Theca height 13.8 mm; height of aboral cup 8.9 mm; radial ring diameter up to 10.2 mm; ratio of maximum radial ring diameter to height of aboral cup 1.1 to 1.2; ratio of radial upper width to primibrachial width 1.5 to 1.6; diameter at radial-basal suture 7.5 mm; basal ring without suture or rib; diameter at flanged base 4.1 mm. Tegmen moderately inflated with a conspicuous oral cone; interradial surface bearing 20–25 unperforated tegminal plates. Crown length 63.5 mm; arm base width 3.8 to 4 mm; length of first pinnule 25 mm; arms branching at IBr10 (2 cases), 12, 13, or 18 (1 case each), at IIBr6 (2 cases), 7, 9, or 10 (1 case each), and at IIIBr8, 9, or 11 (1 case each). Stalk length 326 mm; stalk diameter 3.0 mm at a distance of 3 cm from dorsal cup, 2.3 mm at 10 cm, 2.5 mm at 15.5 cm, and 2.6 mm at distal end; proximal columnals flanged.

Large specimen with 23 arms and inflated tegmen including proximal part of first and second pinnules. More than 35 unperforated tegminal plates per interradius. Height of aboral cup up to 15.1 mm; height of rectangular radials 8.9 mm; diameter of radial ring up to 19.8 mm; ratio of maximum radial ring diameter to height of aboral cup 1.3; ratio of radial upper width to primibrachial width 1.4 to 1.5; diameter at radial-basal suture 3.6 mm; basal ring with 2 more-or-less conspicuous small ribs in line with each arm, but without clear sutures. Maximum length of arms 165 mm; length of first pinnule 35 mm; arms branching at IBr12 (1 case), 13 (3 cases), or 15 (1 case), at IIBr6, 10, 11, 12, 16, or 50 (1 case each), at IIIBr11, 15, 17, or 28 (1 case each), at IVBr12, 15, or 24 (1 case each), and at VBr1 (1 case); 1 pinnule regenerating into a small arm in a brachitaxis IV. Stalk length 483 mm; stalk diameter 4.1 mm at a distance of 14.8 cm from dorsal cup, 3.6 mm at 23 cm, 2.5 mm at 15.5 cm; all columnals without flange.

DISCUSSION: In his famous book on *Calamocrinus diomedae*, which included fine-detailed illustrations, Agassiz (1892) described three broken specimens (the type series) from Indefatigable Island and illustrated one complete specimen from Mariato Point. Holland et al. (1991) described in detail (scanning electron microscope, transmission electron microscope, and light microscope histology) the medium-sized specimen from Cocos, with additional information on distalmost stalk articulations using the specimen from Mariato Point. With the additional specimens described here, we now have a much better knowledge of morphological variation and the main ontogenetic trends in this species. *Calamocrinus diomedae* is now known from the Galápagos to Central America over a depth

range of 525 to 1,430 m; it attains relatively shallow depths for a hyocrinid crinoid.

Among the Hyocrinidae, *C. diomedae* is singular in having arm divisions. Arms and pinnules are homologous in crinoids (Gislèn 1924, Améziane-Cominardi and Roux 1994). In the crown of the youngest specimen, arms and pinnules are undifferentiated. Arm division is a paedomorphic process without pinnule differentiation. It can be secondarily brought about by regeneration after pinnule breakage as in specimen E47880. In *C. diomedae*, one branch always grows larger than the other, and the difference increases during ontogeny (i.e., a larger-to-smaller arm-width ratio of 1 in the youngest specimen reaches 1.26 in the proximal arm of the largest specimen). The place of arm division is strongly variable in *C. diomedae*, from IBr8 to IBr18 (most frequent at IBr10–12), from IIBr6 to IIBr50, from IIIBr6 to IIIBr28, and from IVBr6 to IVBr24. In contrast, the proximal arm pattern is always 1+2 3 4 5+6, usually with the first pinnule on Br4, the second on Br6, and the third on Br7 or Br8, though more frequently on Br8. Agassiz (1892) considered *C. diomedae* to be a living representative of the Jurassic genus *Apiocrinus*. At that time, following de Loriol (1883–1884), he included in *Apiocrinus* the largest species of *Millericrinus*, which had five large basals (such as *M. magnificus* or *M. crassus*), and, in general, appeared similar to *Calamocrinus*. Agassiz' figures (1892, plates 2–3) of the four *Albatross* specimens show a basal ring with five conspicuous and regular sutures as in Jurassic *Millericrinus*. However, these figures are inconsistent with the text, because he wrote (p. 14): "the basal ring ... is completely anchylosed ... on the outer surface ... no actual line of suture is visible." As a matter of fact, I never found five clear basal sutures either in the type series (Améziane et al. 1998) or in the specimens described here. As in the other hyocrinids, basals are fused or with one to three sutures, never more, and they are clearly fused in the two young specimens of *Calamocrinus* described here. Agassiz probably confused the fine ribs that lie in line with the arms with basal sutures, which are usually inconspicuous or absent in *Calamocrinus*. The importance of careful, detailed description must be emphasized, because some paleontologists used Agassiz' interpretation of basal sutures to propose a phyletic relationship between *Calamocrinus* and millericrinids (Rasmussen 1978, Simms 1988).

The different stages of columnal ontogeny during stalk development in *Calamocrinus* are now well documented. The youngest stage, preserved in the center of distal syzygies, is a symplexy with 7 crenular units of 1 crenula (Holland et al. 1991) (Figure 8*e*). The number of crenular units rapidly increases to 13 during juvenile growth (Figure 8*f*). Proximal columnals of a large specimen of the type series have as many as 16 crenular units (Agassiz 1892). More distally, in the largest specimen described here, crenular units develop up to 4 external crenulae as columnal diameter increases (Figure 8*h*). Distal articulations become syzygies with a multiradial crenularium (Agassiz 1892). The change from symplexy to syzygy is progressive, with an irregular crenularium, sometimes with a labyrinthic pattern (Holland et al. 1991), appearing during intermediate stages. The major ontogenetic processes in *Calamocrinus* symplexies are acceleration in juveniles (from 7 to 13 crenular units) followed by hypermorphosis (multiplication of radial crenulae during diameter growth). As in *Hyocrinus*, multiplication and development of radial crenulae through ontogeny is associated with an increase in stalk diameter.

In *Calamocrinus*, the regular arm pattern 1+2 3 4 5+6 and the first pinnule usually at Br4 suggest affinities with *Ptilocrinus*. Numerous lateral plates without regular rows in the proximal part of genital pinnules were also described in *P. brucei* by Mironov and Sorokina (1998). According to John (1937), Gislèn (1939), and Roux (1980*b*), tendencies to arm division are also present in *P. antarcticus* and *Gephyrocrinus grimaldii*. In fact, arm branching cannot justify keeping a distinct subfamily Calamocrininae only for *Calamocrinus* as proposed by A. M. Clark (1973) and Mironov and Sorokina (1998). The arm pattern and first pinnule at Br4 suggest close affinities among *Calamocrinus*, *Ptilocrinus*, and *Gephyrocrinus*.

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