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A new species of the sessile crinoid *Holopus* d'Orbigny from the tropical western Atlantic, with comments on holopodid ecology (Echinodermata: Crinoidea: Holopodidae)

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Abstract

Holopus mikihe new species is only the sixth extant holopodid crinoid to be described. It differs from all other extant holopodids in having large and distinct raised tubercles in the center line of the aboral surface of proximal secundibrachials, giving it the appearance of a mailed fist. The holotype, from 758 m, also comes from outside the known depth range of the other tropical western Atlantic species, *H. rangii* d'Orbigny. Some comments are provided on the ecology of Caribbean holopodids, based upon data obtained during dives of the *Johnson-Sea-Link* manned submersibles.

Key words: *Holopus,* Crinoidea, systematics, ecology

Introduction

Apart from the widely distributed, vagile comatulids, extant crinoids, mainly stalked taxa, are usually confined to depths greater than 100m, although *Gymnocrinus richeri* Bourseau *et al.* (1987) was collected recently near Vanuatu in the Pacific Ocean from a depth of only 80–90m (Richer de Forges, personal communication). Stalked crinoids are sessile under normal conditions (but see Messing *et al.*, 1988; Baumiller & Messing, 2007). The holopodids (Early Jurassic to Recent; Simms *et al.*, 1993, p. 505) are morphologically distinct from the comatulids and most stalked taxa. Holopodids have lost the stalk, but, unlike comatulids, they are not vagile and they cement directly to the substrate. The dorsal (=aboral) cup is a fused tube in which plate sutures are not apparent (Grimmer & Holland, 1990; Donovan, 1992). The short arms form a watertight seal when closed over the tegmen (J.C. Grimmer pers. comm. in Donovan, 1992, p. 667). This peculiar morphology has led to them being compared with barnacles (Bather, 1928, p. lxxv; Donovan & Jakobsen, 2004).

Five extant holopodid taxa have been described (Table 1). Herein we describe a sixth species, based on a specimen (USNM E41507) originally treated as *Holopus rangii* d'Orbigny by Donovan (1992, figure 1.2; Figure 1 herein). At the time that Donovan (1992) was being written, only one living species of *Holopus* had been described. However, a second species, *Holopus alidis*, was published by Bourseau *et al.* (1991) while Donovan's contribution was 'in press'. Although known from different oceans separated by physical barriers and large distances, these two taxa are closer in many aspects of gross morphology than our new species is to *H. rangii*. We now describe this specimen as the holotype of a new species of these enigmatic crinoids. The only fossil species, *Holopus spileccense* (Schlüter, 1878) (Eocene, Italy), is too poorly known for comparison (Manni, 2005).

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TABLE 1. Ecology of extant holopodid crinoids (revised after Donovan & Jakobsen, 2004, table 1). Key: [1] see Cherbonnier & Guille (1972), Fechter (1973) and Améziane *et al.* (1999, table 1); [2] see Heinzeller *et al.* (1996) and Améziane *et al.* (1999, table 4); [3] see Améziane *et al.* (1999, table 6); [4] see Bourseau *et al.* (1991) and Améziane *et al.* (1999, table 9); [5] see Meyer *et al.* (1978), Donovan (1992) and references therein, Améziane *et al.* (1999, table 8), and USNM collections; [6] see herein (quoted as 727m depth in Améziane *et al.*, 1999, table 8).

Species	Depth range (m)	Substrate
[1] *Cyathidium foresti* Cherbonnier & Guille, 1972	380–900 m	boulders
[2] *Cyathidium plantei* Heinzeller *et al.*, 1996	circa 200 m	cave ceilings
[3] *Cyathidium pourtalesi* Améziane *et al.*, 1999	171–249 m	rocks
[4] *Holopus alidis* Bourseau *et al.*, 1991	355–470 m	rocks
[5] *Holopus rangii* d'Orbigny, 1837	100–654m	rocks
[6] *Holopus mikihe* new species	758 m	rocks

This new species, and numerous specimens of *H. rangii* were observed live, and collected, in the vicinity of the Bahama Islands during a series of *Johnson-Sea-Link I* and *II* submersible dives between 1983 and 1989. This research project, jointly sponsored by the Smithsonian Institution (SI) and by Harbor Branch Oceanographic Institution, Inc. (HBOI), was led by John E. Miller (HBOI); other participants included Porter M. Kier (SI), Gordon Hendler (SI and Los Angeles County Museum of Natural History) and David L. Pawson (SI). Detailed taxonomic information on these specimens will be presented elsewhere; below, we provide some brief notes on the ecology of *H. mikihe* and *H. rangii*.

Terminology of the crinoid endoskeleton follows Ubaghs (1978) and Moore *et al.* (1978). Classification of the articulate crinoids follows Simms & Sevastopulo (1993) and Simms *et al.* (1993). The specimens illustrated and described herein are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Class Crinoidea J.S. Miller, 1821

Subclass Articulata von Zittel, 1879

Order Millericrinida Sieverts-Doreck, 1952

Suborder Cyrtocrinina Sieverts-Doreck, 1952

Infraorder Holopodinidia Arendt, 1974

Family Holopodidae von Zittel, 1879

Genus *Holopus* d'Orbigny, 1837

Type species: *Holopus rangii* d'Orbigny, 1837, pp. 6–8, pl. 1, by monotypy.

Other species: *Holopus alidis* Bourseau *et al.*, 1991; *H. mikihe* new species; *H. spileccense* (Schlüter, 1878).

Diagnosis: (After Rasmussen, 1978, p. T838.) "Cup tubular, more or less irregular, commonly with radial ridges or rows of tubercles. Wall of cup very thick, radial cavity moderate. Upper edge more or less five-sided. Radial articular face[t] for arms rather large, sloping slightly outward. Interarticular ligament fossae large. Radials and arms different in size, more or less distinctly arranged as group of 3 larger arms and group of 2 smaller arms. Arms stout, strongly curved, each branch with up to 25 to 30 brachials forming spiral and meeting laterally as cover over ventral side of theca when retracted. Proximal 3 to 10 large secundibrachials are succeeded by distinctly smaller brachials. Some brachials may be irregular, often smaller and triangular to fit within cover. Orals large, triangular."

Remarks: The Holopodidae includes only two genera, *Holopus* and *Cyathidium* Steenstrup, 1847. In *Cyathidium*, the more cap-like crown includes arms that are greatly reduced in comparison with those of *Holopus*, and are not visible when enrolled (Roux *et al.*, 2002, pp. 808, 819). The reported divergent molecular signatures of *Holopus* and *Cyathidium* are considered to be an artifact, as was also suggested by Cohen *et al.* (2004). We recognize the close relationship of the two genera, as demonstrated by their numerous morphological similarities and distinctness from all other crinoid taxa (Heinzeller *et al.*, 1996).

Holopus mikihe **new species**

Figures 1, 2, 3E

Holopus rangii d'Orbigny.- Donovan, 1992, fig. 1.2; Améziane *et al.*, 1999, table 8, USNM 41507.
Non: *Holopus rangii* d'Orbigny, 1837.

Diagnosis: *Holopus* with dorsal cup unsculptured apart from faint radial ridges and with proximal secundibrachials bearing strong midaboral tubercles on the external surface.

Material examined: Holotype: USNM E41507, in alcohol. The only specimen known.

Locality: Off Gouldings Key, New Providence, Bahamas, 24º 59' 59" N, 77º 34' 34" W. Dive #JSL-II-1501, 758 m, 20 Oct 1987.

Description: Stemless crinoid cemented at base to hard substrate (Figure 3E), although holotype, about 33 mm high, broken off above attachment area. Walls of dorsal cup thick; broken section 8.6 mm in maximum diameter, but maximum diameter of body cavity only 3.2 mm. Dorsal cup tall (slightly less than 50 % total height of crinoid), pentagonal in cross-section with angles in mid-radius, narrowest just above attachment and widest at oral surface, not perfectly pentagonal conical, but skewed slightly to one side (Figures 1, 2A, B). No plate sutures apparent within cup. Radial facets wide, in contact, scalloped; scalloping apparent on surface of cup as faint stacked growth (?) lines. External coloration purple.

Arms branch once at IBr_1. Ten arms, uniserial, consisting of circa 30 brachials (Figure 2C–F). Arms divided into a bivium of two shorter arms and trivium of three longer arms. Arms enrolled and in close contact; sutures between arms crenulated, giving the crown the appearance of a clenched, ten-fingered fist. Arms strongly tapered towards the distal end and geniculated at about $IIBr_{8\text{-}9}$, after which arms become much narrower (Figure 2C, F). The primaxillary (IBr_1) is large, broad, pentagonal in external view, swollen on aboral surface and with two low tubercles towards the center corresponding to the base of faint, low ridges that continue distally. Proximal facet broad with a central, oval axial canal and a broad, V-shaped adoral groove; distal facets equal in size. Proximal secundibrachials wedge-shaped and with large raised midaboral tubercles on each. Adoral groove central, parallel to long axis of arm and with lateral branches extending to pinnule facets. Cover plates small, polygonal.

All brachials except IBr_1 pinnulate. Pinnules situated on alternate sides of arms on adjacent brachials, curling adorally when enrolled (Figure 2C, F), and composed of broad, low ossicles.

Mouth bordered by five triangular oral plates. Anal pyramid located to left of removed arm, that is, this arm represents the C ray. Thus, B-C-D is the trivium and E-A the bivium.

Ecology: Like its congener *H. rangii*, *H. mikihe* lives attached to a hard rock substratum (Figure 3E), in this case an almost vertical rock face a few meters above the sediment-covered seabed. Apparently, the single specimen was not observed in the open position.

FIGURE 1. *Holopus mikihe* new species, holotype, USNM E41507, A-ray central (after Donovan, 1992, figure 1.2). Crown about 33 mm high.

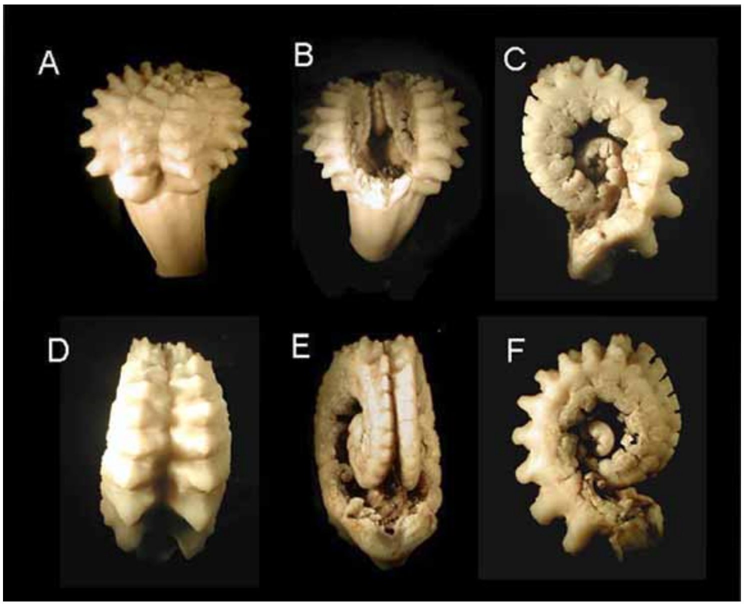

FIGURE 2. *Holopus mikihe* new species, holotype, USNM E41507. A, B, crown, about 33 mm high. A, note the 'mailed fist' appearance produced by the tuberculate, near-spinose proximal secundibrachials. B, reverse side of crown with C ray arm removed. C–F, C ray arm. C, F, lateral views; note pinnulation and profiles of large, aboral tubercles of proximal secundibrachs. D, aboral view. E, adoral view. Note that the specimen had an arm removed after it was examined by S.K.D. in 1989 (see Figure 1).

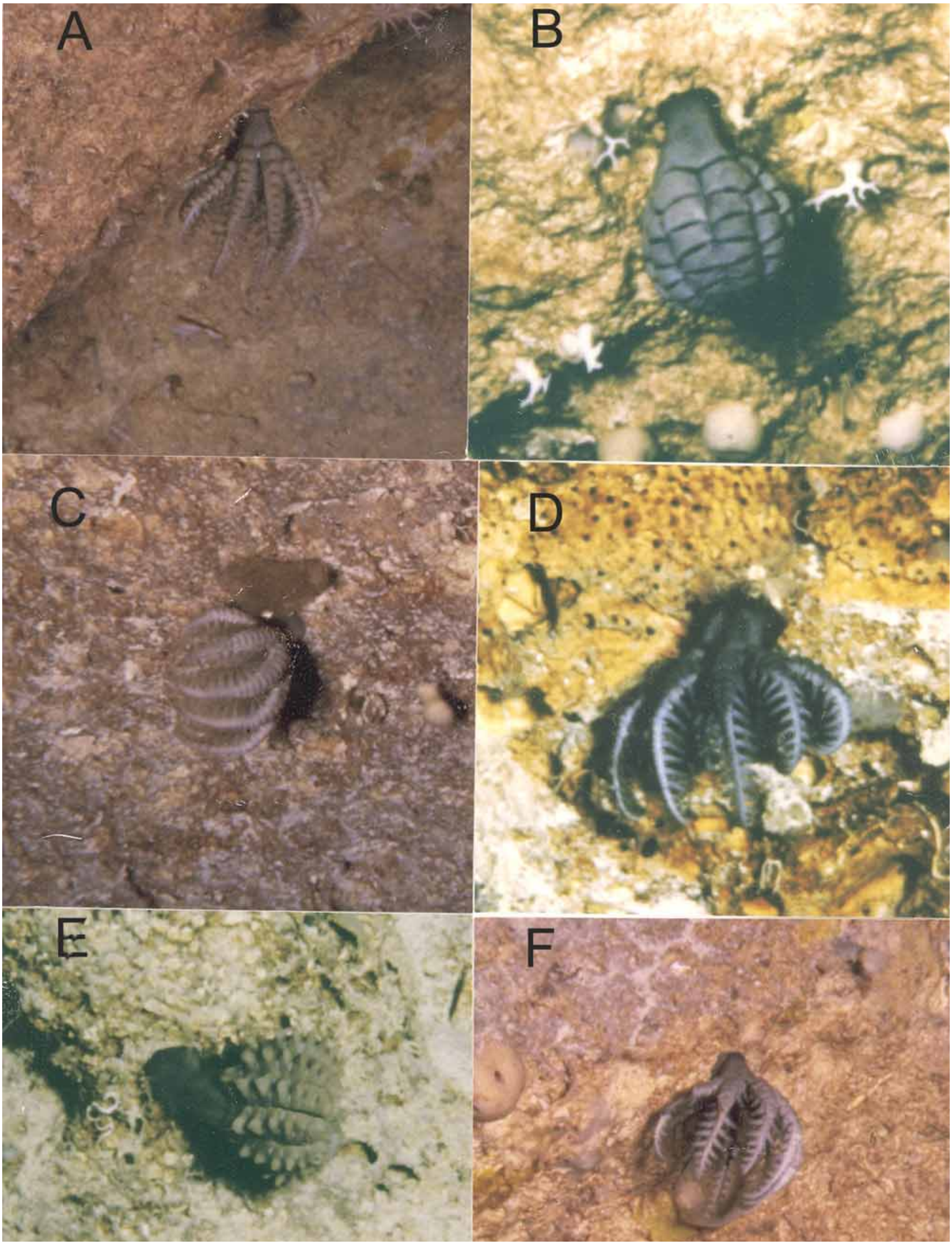

FIGURE 3. *Holopus* from the tropical western Atlantic Ocean, Bahamas, in life position. A–D, F, *Holopus rangii* d'Orbigny, 1837. A, Johnson-Sea-Link I Dive 2276, 369m. Attached to overhang with arms opened for feeding, near-straight to curved. B, Johnson-Sea-Link I Dive 2051, 654–488m. Arms closed. C, Johnson-Sea-Link I Dive 2260, 619m. Arms open and forming an open 'cage'. D, Johnson-Sea-Link II Dive 1497, 591m. Arms widely open, with tips of some arms recurved. F, Johnson-Sea-Link I Dive 2276, 396 m. Oblique view into a feeding 'cage'. Note that some arms appear to be in contact with the substrate. E, *Holopus mikihe* new species, holotype, USNM E41507. Johnson-Sea-Link II Dive 1501, 758 m. Arms closed.

Etymology: The trivial name of this species, *mikihe*, is derived from the first two letters of the surnames of colleagues who were involved in the 1983–1989 echinoderm research on the Johnson-Sea-Link I and II. The first syllable, "mi-", is from John E. Miller. The second syllable, "-ki-", is from Porter M. Kier. The third syllable, "-he", is from Gordon Hendler.

Remarks: Although based on a single specimen, the distinctive morphology is sufficient to warrant recognition of a new species. Of the three known species of *Holopus*, *H. rangii* (tropical western Atlantic; see, for example, Springer, 1924, pls 1–3; Rasmussen, 1978, fig. 562.1a, d; Grimmer & Holland, 1990, fig. 1; Donovan, 1992, fig. 1.1) and *H. alidis* (southwest tropical Pacific; see Bourseau *et al.*, 1991, pl. 12, figs 1–5) are much closer to each other in gross morphology than either is to *H. mikihe*, despite their wide geographic separation. Indeed, the strongly spinose arms of *H. mikihe* are distinct from those of all known holopodids (Heinzeller *et al.*, 1996, pp. 82–83). Such a strongly spinose crown is more reminiscent of some Paleozoic crinoids, although there are other post-Paleozoic exceptions (such as Simms, 1989, pl. 13, fig. 1).

As noted above, we regard previous instances where *H. rangii* and *H. mikihe* were 'lumped' together to be no more than that. In addition to the obvious morphological differences, *H. mikihe* comes from a greater water depth than any other *Holopus*. David *et al.* (2006) distinguished three western Atlantic subspecies of the sea lily genus *Endoxocrinus*, partly on the basis of their bathymetric separation. *Holopus mikihe* is considered to be most closely related to *H. rangii*, as both species lack an abrupt bend of the arms, a feature of *H. alidis* and *Cyathidium* spp. (Heinzeller *et al.*, 1996, fig. 4).

Notes on ecology of Caribbean holopodids

During submersible diving operations in the Bahamas in 1983–1989, *Holopus rangii* was encountered many times and, without exception, it was attached to hard rock, usually under overhangs (Figure 3A–D, F), so that the animal lives "upside down." The single specimen of *H. mikihe* extended almost laterally from a vertical rock face. For the most part, *Holopus* individuals were tightly closed (Figure 3B, E), and individuals with open arms were rarely encountered. (Figure 3A, C, D, F). Unlike comatulids and stalked crinoids, *H. rangii* does not form a filtration fan *per se*, but instead orients its arms in a funnel-like array (Macurda & Meyer, 1974; Figure 3A, C, D, F herein). As the submersible approached an open specimen, the animal would invariably and rapidly close, a process that took 0.8 to 1.0 seconds. The closure occurred in response either to the approaching submersible light or to the gentle bow wave created by the slow-moving submersible. Grimmer & Holland (1990) and Heinzeller *et al.* (1996) proposed that this may be an adaptation for actively capturing prey. No active capture of prey organisms, large or small, was observed from the submersible. It is also significant to note that *H. rangii* and *H. mikihe* live in areas of low current velocity, making them near-rheophobic, and thus more likely to capture active prey than most living crinoids, which are obligate rheophiles.

As discussed by Grimmer & Holland (1990) and Donovan (1992), the bivium (two short arms) and trivium (three long arms) of *H. rangii* were previously considered to define the C and D, and E, A and B rays, respectively. Actually, their position differs with respect to the CD interray (=posterior) from specimen to specimen, as defined by the position of the anus. Thus, the bivium and trivium do not correspond to particular groups of rays. Presumably, this is also true of *H. mikihe*. It has been suggested that the asymmetry of the crown in adults of the closely related cyrtocrinids was a response to unidirectional current flow by sessile rheophiles (Žítt, 1983, pp. 76–79; Grimmer & Holland, 1990, p. 66).

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