**Hirsutocrinus duplex**, a New Genus and Species of Sea Lilies (Crinoidea, Comatulida, Bathycrinidae) from the Western North Pacific

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**Hirsutocrinus duplex**, a new genus and new species of the Bathycrinidae, collected from Okinawa, Japan at a depth of 596–606 m, is described. The main diagnostic characters of the new genus are the presence of side plates in pinnules and of knobby processes on Brs 1–2. Knobby processes on secundibrachials are found for the first time. *Monachocrinus* A. H. Clark, 1913 shares side plates with *Hirsutocrinus*. It differs from the new genus in having knobby processes on IBrs 1, parallel ridges on the articular surface of knobby processes, proximal and distal arm pattern a b c d e f, saccules, in lacking knobby processes on IBrs 2 and Brs 1–2, pinnule on every second Br, x-shaped tube-feet plates, needle-like spines on external surface of IBrs and Brs. The cover and side plates are similar to each other in *Monachocrinus*, and quite different in *Hirsutocrinus*. *Hirsutocrinus duplex* is the shallowest species in the abyssal family Bathycrinidae usually known from 1100 to 9735 m. Other than *H. duplex*, only three among 25 nominal bathycrinid species are known from depths less than 1000 m.

**Key Words:** crinoids, deep-sea, knobby processes, side plates, combinations of morphological features.

**Introduction**

The classification of crinoids with a xenomorphic stalk remained very confused for a long time. Complicated history of the bathycrinid classification has already been traced in several recent publications including Mironov and Pawson (2014) and Roux et al. (2019). The family Bathycrinidae traditionally included both five-armed and ten-armed crinoids with xenomorphic stalks (Gislén 1938; A. M. Clark 1973; Roux 1977; Rasmussen 1978). Over the past two decades, the composition of the family has changed markedly due to the study of new materials, the use of new diagnostic characters, as well as molecular analyses (Roux et al. 2002, 2013, 2019; Cohen et al. 2004; Mironov 2008; Hess 2011; Éléaume et al. 2012; Rouse et al. 2013; Hemery et al. 2013; Mironov and Pawson 2014). As results of these studies, Bathycrinidae currently consists of only ten-armed crinoids with xenomorphic stalks and knobby processes on primibrachials (Roux et al. 2019; Messing 2020), previously defined as a subfamily Bathycrininae of the family (Hess 2011). It includes five extant genera, *Bathycrinus* Thomson, 1872, *Naumachocrinus* A. H. Clark, 1912, *Monachocrinus* A. H. Clark, 1913, *Cingocrinus* Mironov, 2000, and *Discolocrinus* Mironov, 2008.

The molecular studies indicate a close relationship between Bathycrinidae, Rhizocrinidae, and Atelecrinidae although these families differ in external morphology: Bathycrinidae is xenomorphically stalked and ten-armed, Rhizocrinidae is xenomorphically stalked and five- or ten-armed, and Atelecrinidae is unstalked and ten-armed. Meanwhile *Caledonicrinus* Avocat and Roux, 1990 of family Caledonicrinidae and *Rouxicrinus* Mironov and Pawson, 2010 of Septocrinidae share a xenomorphic stalk and ten arms with Bathycrinidae, but the two genera belong to clades distantly separated from the clade of Bathycrinidae, Rhizocrinidae, and Atelecrinidae (Rouse et al. 2013; Hemery et al. 2013). Xenomorphic stalk with synarthries and arm number, which had previously been considered having great taxonomic or phylogenetic value, are thought to result from convergences or iterations (Roux et al. 2013). On the contrary, molecular studies suggested taxonomic value of some other characters. Closely related Bathycrinidae, Rhizocrinidae, and Atelecrinidae share knobby processes described as “prolobus adapis” in Atelecrinidae by Messing (2003, 2013), while distantly related *Caledonicrinus* and *Rouxicrinus* lack them (Mironov and Pawson 2014; Roux et al. 2019). *Bathycrinus* with only cover plates and *Monachocrinus* with both cover and side plates are supported as distinct genera by molecular study (Hemery et al. 2013). Pinnule architecture is quite different in Bathycrinidae and Septocrinidae (including *Rouxicrinus*) (Mironov and Pawson 2010). The pinnules in Septocrinidae are without both cover and side plates, but with rows of large rod-like spicules. The separation of Septocrinidae from Bathycrinidae was also supported by a molecular study (see Mironov and
A. N. Mironov and T. Fujita

In the molecular study by Rouse et al. (2013), the septocrinid Rouxicrinus vestitus Mironov and Pawson, 2010 was misidentified as Monachocrinus caribbeus (A. H. Clark, 1908) and this species was placed outside of the family Bathycrinidae in their tree. These results suggested the presence/absence of knobby processes in primibrachials, and the arrangement of cover and side plates in pinnules are significant taxonomical characteristics reflecting the molecular phylogeny.

In the family Bathycrinidae, four genera differ from each other basically by the pinnule architecture (Mironov 2008; Mironov and Pawson 2014). Pinnule architecture is unknown in Naumachocrinus, and the placement of this genus in Bathycrinidae is questionable. The presence of knobby processes (Roux et al. 2019; fig. 3A), a mesistele with "Bourgueticrinus-type" synarthries (Bourseau et al. 1991), and arm branching at IBr2 (IBr2ax) definitely makes it a Bourgueticrinina. Provisionally, Naumachocrinus was maintained by Roux et al. (2019) within the Bathycrinidae, awaiting additional data on distal stalk synarthries, pinnule architecture and DNA sequencing. This paper describes a new genus and species Hirsutocrinus duplex in the family Bathycrinidae based on a specimen collected in Japan at a depth of 596–606 m. The new genus differs from other bathycrinid genera in having both unique morphological features and a unique combination of characters previously used in generic diagnoses.

**Materials and Methods**

The description was based on a fragile specimen collected by the RV Toyoshio-maru of Hiroshima University in 2003. It was collected by a beam trawl and preserved in 96% ethanol. The specimen was in poor condition. It is characterized by an RR-ring with incomplete arms, two fragments of arms and two fragments of stalk; basal plates were absent. The arms and radix were covered with mucous fouling. Tegmen, two basal arms and some fragments of the stalk were dissociated (using 12% sodium hypochlorite solution) to prepare separate ossicles for examination by scanning electron microscopy (SEM). The fragments of the specimen and the ossicles examined using SEM are stored at the National Museum of Nature and Science (NSMT).

Terminology of morphological characters of aboral cup, arms and stalk, as well as their abbreviations, follows Roux et al. (2002) and Hess (2011). Abbreviations: ax, arm branching, e.g., IBr2ax, arm branching at IBr2; BB, basal plates; Br(s), brachial(s) of free arms; Br1, Br2, and Brs 1–2, first, second, and first and second secundibrachials of free arms; IBr1, IBr2, and IBrs 1–2, first, second, and first and second primibrachials; C, aboral cup; D, maximum diameter of radial ring or columnal facet; d, minimum diameter of columnal facet; H, height; P(s), pinnule(s), e.g., P1 and P2, first, and second pinnules, Ps 5–8, fifth to eighth pinnules; Pn(s), pinnularia(-ies), e.g., Pns 3–5, third to fifth pinnules; RR, radial plates; W, width. A sign (+) indicates a nonmuscular (ligamentary) articulation uniting a brachial pair. The arm pattern is simplified by indication of brachial pairs only: e.g., 1+24+57+8 means nonmuscular articulations between Br1 and Br2, between Br4 and Br5, and between Br7 and Br8.

**Taxonomy**

**Suborder Bourgueticrinina Sieverts-Doreck, 1953**

**Family Bathycrinidae Bather, 1899**

**Type genus.** Bathycrinus Thomson, 1872.

**Included extant genera.** Bathycrinus Thomson, 1872, Cingocrinus Mironov, 2000, Discolorocrinus Mironov, 2008, Monachocrinus A. H. Clark, 1913, Naumachocrinus A. H. Clark, 1912, and Hirsutocrinus n. gen.

**Remarks.** Emended diagnosis of Bourgueticrinina was given in Roux et al. (2019). The family includes the same genera as the subfamily Bathycrininae in Hess (2011). Following Roux et al. (2019), Naumachocrinus is provisionally maintained here within the Bathycrinidae.

**Genus Hirsutocrinus n. gen**

**Type species.** Hirsutocrinus duplex n. sp.

**Included species.** Hirsutocrinus duplex n. sp.

**Etymology.** The generic name is derived from the Latin word hirsuta (spinulated) in reference to the secundibrachials covered in small spines.

**Differential diagnosis.** New genus differing from other genera in the family Bathycrinidae in having knobby processes both on IBr2 and Br1+2, and distinct side plates in pinnules.

**Remarks.** In addition to Hirsutocrinus, the genus Monachocrinus is characterised by presence both cover and side plates. The side and cover plates in pinnules are strictly different from each other in their shape in Hirsutocrinus, and they are similar in Monachocrinus. See Table 1 and discussion below for comparison between Hirsutocrinus n. gen. and other bathycrinid genera.

**Hirsutocrinus duplex n. sp.**

(Figs 1–5)

*Bathycrinus pacificus* non A. H. Clark, 1907: Kogo and Fujita 2005: 234 (in part).

**Etymology.** The specific epithet is derived from the Latin word *duplex* in reference to the presence of the knobby processes at two levels: on IBr2 and Brs 1–2.

**Diagnosis.** Radials and primibrachials rather short; ratios RRH/RRD and IBr2H/Br2W < 1.0. Number of knobby processes on primibrachials 4. External surface of IBr1s and Brs covered by dense needle-like spines. Brachial pattern the same in proximal and distal free arm: 1 + 2 + 4 + 5 + 7 + 8 + 10 + 11 + 13 + 14 and so on. P1 on Brs 8–10. Starting with the brachial bearing P1, every third brachial lack pinnule. Strong distinction between the cover and side plates in pinnules. Tube feet
**Hirsutocrinus duplex** new genus and species

Table 1. Comparison of the main morphological features of *Hirsutocrinus* n. gen. with other bathycrinid genera (Bourseau et al. 1991; Mironov 2000, 2008, 2019; Mironov and Pawson 2014; Roux et al. 2002, 2019). +: yes, -: no, ?: unknown. Abbreviations of generic names: Hir, *Hirsutocrinus*; Bat, *Bathyocrinus*; Cin, *Cingocrinus*; Dis, *Discolocrinus*; Mon, *Monachocrinus*; Nau, *Naumachocrinus*.

| Features | Hir | Bat | Cin | Dis | Mon | Nau |
|----------|-----|-----|-----|-----|-----|-----|
| Ratio height/width of RR-ring < 1.7 | + | - | + | + | + | - |
| Ratio height/width of IBrs 2 < 1.4 | + | + | + | + | + | - |
| Brs bearing P1 | 8–10 | 5–15 | 5–10 | 10–14 | 10–16 | 4 |
| Number of knobby processes on IBrs 1 | 0 | 0–9 | 0 | 10–9 | 9 | ? |
| Number of knobby processes on IBrs 2 | 4 | 4–10 | 9 | 10–9 | 0 | ? |
| Knobby processes on Brs 1–2 present | + | + | + | - | + | - |
| Cover plates | + | + | + | - | + | + |
| Most frequent arm pattern a b c + d e f + g h i | + | -/+ | - | - | - | -/+
| Numerous needle-like spines on external surface of IBrs and Brs | + | - | - | - | - | - |
| Pinnule absent in every third Br (distal arm) | + | -/+ | - | - | - | - |
| Side plates in pinnules | + | + | + | - | + | - |
| X-shaped tube feet plates present | + | + | + | - | + | - |
| Saccules present | - | - | - | - | + | - |
| Deep ligament depression in mesistele synarthries | - | + | + | + | + | - |
| Attachment by root-like radix | + | + | + | - | + | - |

1 knobby processes absent in B. kirilli and B. volubilis.
2 only in B. rozhnovi; in other *Bathycrinus* species distal pattern of arm a b c d + e f.
3 only in B. rozhnovi and possibly B. australocrinus; in other *Bathycrinus* species pinnule absent in every second brachial.
4 except B. aquatorialis, attached by incrustated disk.
5 unknown for *D. tselini* Mironov and Pawson, 2014.

with x-shaped plates. Sacculi absent. Mesistele synarthries with moderate ligament depression. Dististele synarthries strongly oval with regular secondary crenularium on fulcral ridge axis. Distal end of stalk with rootlike radix.

**Holotype.** NSMT E-5200.

**Type locality.** North of Kuroshima Island, Okinawa Prefecture, Japan. RV *Toyoshio-maru*, St. 11, 24 May 2003, 26°19.18’N, 127°25.56’E, depth 596–606 m.

**Material examined.** Only holotype restricted to RR-ring with incomplete arms, two fragments of arms, and two fragments of stalk.

**Description.** Radial ring inverted conical, broader than high (Figs 1A, 2A). RRD = 1.97 mm; RRH/RRD = 0.66. RR external surface with numerous fine longitudinal ridges. Tegmen raised up to distal part of Br2. Ambulacral grooves not reaching oral opening, extending out to circumoral elevation of soft tissue. Two oral tentacles located in each interradius at aboral margin of circumoral elevation; two flat rounded plates located aborally of these oral tentacles. Oral tentacles differing from neighbouring ambulacral tube feet in having much larger size and non-transparent soft tissue. Plates at the top of tegmen various in shape and size (Fig. 3C). The rounded plates on the sides of tegmen (Fig. 3A) and low anal sac (Fig. 3B) less diverse in shape; the latter somewhat thicker than the former.

Length of IBrs 1 + 2 2.45 mm; ratio IBrs 1/RRH approximately 1.0; IBrs 1/Br2L 1.12; IBrs 1/Br1W 1.04; Br2H/Br2W 0.82. First and second primibrachials slightly broader distally than proximally (Figs 1A, 2A); their sides flattened into wide lateral flanges (Fig. 1A). Broad rounded keel with fine ribs. All IBrs 1 without knobby processes (Fig. 2C). IBrs 2-circle with 4 knobby processes: one of IBrs 2 with two knobby processes, two IBrs 2 with one knobby process confined to the upper part of IBrs 2, and two IBrs 2 without knobby processes. Articular surface of knobby processes covered by small sharp spines not arranged in parallel pattern (Fig. 2D, E).

Lateral compression of corona indistinct. All free arms incomplete: 5 with 9 Brs, others with 6, 11, 13, 30, 43 respectively, the best-preserved (43 Brs) approximately 25.5 mm long, with 13 Ps on a side. Arm fragment 13.7 mm long with 21 Brs. Lateral flanges wide in proximal Brs (Figs 2F, G, I, J, 4A), becoming progressively narrower distally; distal to Br28 continues as low longitudinal rib (Fig. 1E). Brs 1–12 with broad rounded keel; profile of this part smooth viewed from side (Fig. 1F). Brs 13–24 with narrower and sharper median keel including a small tooth in every hyposynostosial Br. Distal to Br24 arm profile serrated (Fig. 1E). External surface of Brs covered by dense needle-like spines (Figs 2G, 4B, C). Brachial side surface with fine ribs near the pinnule socket (Fig. 1F). Each Br2 and some Brs 1 bearing a single knobby process. Process developed along the entire length of the Br2 (Fig. 2H, I) and restricted to the distal part of Br1 (Fig. 2J). The knobby processes of adjacent free arms (attached to the same IBrs 2) in contact with each other by spiny articular surface.

P1 on outer side of Br8 in three arms, on inner side of Br9 in four arms, position unknown in three arms. Among three arms without P1, two with 9 Brs, suggesting P1 located on Br10 or more distally. Proximal and distal free arm pattern alternating brachial pairs and free brachials (1+2 4+5 7+8 and so on), with the single exception in the best-preserved arm (+17 20+). Starting with the brachial bearing P1, every third brachial lack pinnule. As viewed from side, every third...
Fig. 1. *Hirsutocrinus duplex* n. gen. and sp., holotype. A, Radial ring with proximal arms; B, fragment of stalk with distal proxistele and upper mesistele; C, mesistele; D, dististele; E, Brs 26–33 with P7 and P8; F, Brs 8–11 with P1.
Fig. 2. *Hirsutocrinus duplex* n. gen. and sp., holotype. A, Radial ring with arms; B, dististele and radix with fouling; C, IBr1, view from inside; D, IBr2 with knobby process, view from inside; E, detail of knobby process articular surface; F, distal facet of Br6 (muscular synarthry); G, proximal facet of Br3 (muscular synarthry); H, Br2 with knobby process, view from inside; I, Br2 with knobby process, distal view (muscular synarthry); J, Br1 with knobby process, proximal view (asymmetrical muscular synarthry).
Fig. 3. *Hirsutocrinus duplex* n. gen. and sp., holotype. A, Isolated plates from the sides of tegmen; B, plates from anal sac; C, plates from tegmen top; D, plates from Brs 2–4; E, plates from Brs 5–8; F, typical (well developed) cover plates from pinnule; G, typical side plates from pinnule.
Hirsutocrinus duplex new genus and species

Fig. 4. *Hirsutocrinus duplex* n. gen. and sp., holotype. A, Distal facet of hyposynostosial II\(\mathrm{Br}\)7 (ligamentary synarthry); B, II\(\mathrm{Br}\)4, aboral external view; C, detail of B showing numerous needle-like spines; D, synarthrial facet of columnal 38 (mesistele); E, synarthrial facet of columnal 59 (dististele); F, detail of E showing fulclar ridge axis of columnal 59.
A. N. Mironov and T. Fujita

94.7 mm long (excluding radix), with 62 columnals. Diameter of columnals decreasing from 0.76 in proximal column to 0.65 mm in column 19, then increasing slowly up to 1.60 mm in column 62. Maximum H/D 2.8 at column 31. Synarthries articulating mesistele columnals of moderately ovoid facets with only discrete ligament depressions; fulcral ridge axis always corresponding to the greatest facet diameter and forming two main segments connected by perilumen stereom (Fig. 4D). Synarthries articulating dististele columnals strongly ovoid, with deep ligament depressions; maximum D/d ratio in distalmost columnals 1.75; fulcral ridge separated in two segments by axial canal, with regular relief on secondary crenulanium (Fig. 4E, F). Only proximal part of root-like radix preserved (Fig. 2B).

Discussion

The following features of the new genus are unique to the family Bathycrinidae (Table 1): dense needle-like spines covering Brs external surface (Fig. 4B, C), small number (4) of knobby processes on the primibrachials restricted to IBBr2 (Fig. 2C, D), presence of knobby processes on Brs 1–2 (Fig. 2H–J), and strong distinction between the cover and side plates in the pinnules (Fig. 3F, G). Two latter features are considered here as the main diagnostic characters of Hirsutocrinus. Knobby processes are found on Brs 1–2 for the first time. The circle of Brs 2 is a complex and massive structure with developed knobby processes on the inner side of adjacent free arms (attached to the same IBr2). Knobby processes on secundibrachials appear to be the result of significant evolutionary transformations. The separation of Hirsutocrinus from other genera is also based on the presence of unique combinations of characters, side plates and x-shaped tube feet plates, or side plates and most frequent distal arm pattern a b c + d e f + g h i.

The number of knobby processes on primibrachials ranges from 8 to 20 in other bathycrinids (Mironov and Pawson 2014). The exceptions are two lower hadal species, Bathycrinus kirilli Mironov, 2019 and B. volubilis Mironov, 2000, in which the knobby processes are absent. Mironov (2019) interpreted the absence of knobby processes as the result of their reduction during the late colonization of the lower hadal environment. Apparently the small number of knobby processes on primibrachials in the upper bathyal species Hirsutocrinus duplex contradicts this interpretation. However, here, the presence of knobby processes on Brs 1–2 provide an additional reinforcement for the arm bases compensating for the restricted number of knobby processes on IBrs. It is likely that B. kirilli and B. volubilis are also phylogenetically different from the other Bathycrinus species like the present new species, but molecular data is required to show the phylogeny of the species with small number of knobby processes.

Monachocrinus shares side plates with Hirsutocrinus. It differs, however, from the new genus in having knobby processes on IBrs 1, parallel ridges on the articular surface of knobby processes, distal arm pattern a b + c d ± e f, sacculae, and in lacking knobby processes on IBrs 2 and Brs 1–2, pin-

![Diagram](image-url)
nule on every second Br, x-shaped tube-feet plates, needle-like spines on Brs external surface (Table 1). The cover and side plates in *Monachocrinus* are similar to each other.

A. H. Clark (1917) and Gislén (1938) considered the pattern of proximal free arms as the main character distinguishing *Bathyocrinus* from *Monachocrinus*. Mironov (2008) distinguished these two genera using pinnule architecture: only cover plates in *Bathyocrinus*, both cover and side plates in *Monachocrinus*. According to Roux and Messing (2017), the absence of side plates in *Bathyocrinus equatorialis* is a more significant diagnostic character than the absence of side plates in *Bathycrinus* both cover and side plates distinguished these two genera using pinnule architecture: distinguishing pattern of proximal free arms as the main character distinguishing *Monachocrinus* from *Bathyocrinus* side plates in *Bathycrinus* are similar to each other. According to this criterion, they confirmed that *B. equatorialis*, which lacks side plates, belongs to the genus *Bathycrinus*. In agreement with the same criterion as theirs, *Hirsutocrinus duplex* (having side plates) should not be classified as *Bathycrinus* (without side plates).

*Hirsutocrinus* shares the same distal arm pattern with *Bathyocrinus rozhnovi* Mironov, 2019 and possibly with *B. australocruces* McIntosh, 1973. If the *rozhnovi* is a typical *Bathyocrinus* species then the assignment of *B. australocruces* to *Bathyocrinus* requires confirmation, because diagnostic characters of the genus, such as the form and position of knobby processes, presence of x-shaped tube feet plates, and absence of side plates, are unknown for this species. According to McIntosh (1973), *B. australocruces* has free arms with sxzyggyes at 1 + 2 + 5 + 7 + 8 and so on, succeeding pinnules at about every fourth articulations, and side plates large and prominent. McIntosh probably designates cover plates as side. *Hirsutocrinus duplex* differs from *B. australocruces* at least by the location of the pinnules: as viewed from side, every third Br with P in the former and every fourth Br with P in the latter.

*Hirsutocrinus duplex* with a depth range of 596–606 m is the shallowest species in the abyssal family of Bathyocrinidae, which is usually known from 1100 to 9735 m. In addition to *H. duplex*, only three among 25 bathyocrinid species are also known from depths less than 1000 m. *Bathycrinus carpenteri* (Danielsen and Koren, 1877) occurs in the Arctic Ocean at depths of 460–3800 m, however the few specimens from 460 to 950 m were only known from stalk fragments and attribution to this species must be confirmed. Rogacheva et al. (2013) and Mironov et al. (2013) suggested that *B. carpenteri* originally emerged from the deep-sea Arctic. *Bathyocrinus australocruces* was described at depths from 693 to 838 m off New Zealand. *Naumachocrinus hawaiensis* A. H. Clark, 1912 also occurs in the western Pacific, from Japan to Kermadec and from Indonesia to Hawaiian Islands at depths from 516–1440 m (Bourseau et al. 1991; Oji and Kitazawa 2008; Tunnincliffe et al. 2015). Similar bathymetrical and geographical distribution patterns of the monotypic genera *Hirsutocrinus* and *Naumachocrinus*, each with a unique combination of features of taxonomic significance suggest that the western Pacific is an area with a deep history of bathycrinid penetration into the deep-sea.

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