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Studies on Ophiocomid Brittlestars. I. A New Genus (Clarkcoma) of Ophiocominae with a Reevaluation of the Genus Ophiocoma

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ABSTRACT

Devaney, Dennis M. Studies on Ophiocomid Brittlestars. I. A New Genus (*Clarkcoma*) of Ophiocominae with a Reevaluation of the Genus *Ophiocoma*. *Smithsonian Contributions to Zoology,* 51:1–41, 1970.—Internal as well as external skeletal features support the decision to divide the shallow water tropical genus *Ophiocoma* into species groups. Differences in embryological and larval morphology also suggest partition of the genus. Two species formerly in *Ophiocoma* are now placed in the new genus *Clarkcoma* (type-species, *Ophiocoma canaliculata* Lütken). The relationship of the oral papillae and buccal tentacle scale, sequence of arm spines, and nature of oral and dental plates have been analyzed in order to reach conclusions regarding the taxonomic position of the taxa. These characters also suggest intergeneric relations within the subfamily. Descriptions and keys are given for the two genera as well as for the intrageneric groups and species of *Ophiocoma;* also, the specific limits of many species are reviewed.

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Studies on Ophiocomid Brittlestars. I. A New Genus (Clarkcoma) of Ophiocominae with a Reevaluation of the Genus Ophiocoma

Stimulated in part by H. L. Clark's (1921) revision of the Ophiocominae and by Murakami's (1963) report on the oral and dental plates of ophiuroids, recent examination of many species of ophiocomid brittlestars has made it possible to reach some substantial conclusions regarding the relationships among this largest subfamily of Ophiocomidae in the order Chilophiurida (Matsumoto, 1917). Of particular interest has been the genus *Ophiocoma,* whose species not only show affinity with other genera in the subfamily but indicate a polyphyletic assemblage of related taxa. At the same time, conventional external characters have been found inadequate to define the genus, and careful examination of internal skeletal plates has necessitated the removal of two species (*bollonsi* and *canaliculata*) from *Ophiocoma* and the formation of four separate groups.

This study has resulted to a large extent from research on the systematics and postlarval growth changes of ophiocomid brittlestars.[1] Part of the work was completed while the author held a visiting postdoctoral research associateship through the National Research Council at the Smithsonian Institution in 1968–1969. Essential to this study has been the availability of the collections at the United States National Museum (USNM) which contain specimens collected by the *Albatross* and other important specimens. I thank Dr. David L. Pawson and Miss Maureen Downey in the Division of Echinoderms at the Smithsonian Institution for their encouragement during this project. My sincere appreciation is also extended to Dr. H. B. Fell at the Museum of Comparative Zoology (MCZ), Captain Fred Ziesenhenne at the Allan Hancock Foundation (AHF), Dr. H.-E. Gruner at the Zoologisches Museum Berlin (ZMB), and Miss Ailsa M. Clark at the British Museum (Natural History) for making collections at their institutions available or for contributing valuable suggestions during this study. I am deeply grateful to Dr. Roland W. Force, director of the Bernice P. Bishop Museum (BPBM), Honolulu, for permitting me to participate in the 1967 Smithsonian-Bishop Museum-National Geographic Mollusk Expedition to southeastern Polynesia, from which specimens essential to this work were collected and now are deposited in the Bishop Museum.

This publication is the first in an anticipated series of reports dealing with the species and genera of the Ophiocomidae.

Clarkcoma, new genus

TYPE-SPECIES.—*Ophiocoma canaliculata* Lütken, 1869.

DIAGNOSIS.—Ophiocominae with thin, compressed, minutely serrated arm spines; five to eight arm spines

[1] In partial fulfillment of requirements for the PhD degree, Department of Zoology, University of Hawaii, 1968.

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along each side of arm segments just beyond disc edge and fewer distally; second or third spine in row longest (Figure 9). Disc granules low, rounded and evenly distributed over aboral surface; ambital granules sometimes slightly larger or more elongate; granules absent or reduced and scales exposed interradially near oral shields and genital slits. Oral plates (jaws) with abradial muscle area auriculate, having a deep central region with median ridge and short branching processes (Figure 4); adradial muscle area less than one-third total length of plate and confined to lower (oral) portion (Figure 5). Adoral shields with proximal edges well in front of oral shield and nearly or actually meeting (Figures 1, 2). Four or five oral papillae along each jaw margin; outer papilla broadest, but one or more small granules usually present between outer papilla and buccal tentacle scale; buccal tentacle scale separated from outer oral papilla and not abutting against adoral shield (Figures 1, 2); an integumentary area separates these two ossicles. Upper (aboral) arm plates rhomboidal, with narrowly tapering lateral borders; less than one-half of maximum breadth contiguous with adjacent plates along distal and proximal edges (Figures 10, 11). Lower (oral) arm plates approximately two times broader than long (Figures 12, 13). Dental plate from 1.9 to 3.2 times longer than broad; septum of upper tooth foramen equal to or narrower than lower septum (Figures 8, 14).

REMARKS.—When H. L. Clark (1921) reviewed the genus *Ophiocoma* he was unable to relate either *O. bollonsi* or *O. canaliculata* within his species-group framework. Discussing *canaliculata* he stated (p. 128): "The species is a very distinct one, quite different from any other member of the genus, particularly in the form of the arm-spines and the large adoral plates." He noted that *bollonsi* (known at the time only from the type-specimen) was "apparently most nearly related to *canaliculata,* with which species it has several important characters in common, notably the large adoral plates" (Clark, 1921, p. 132). Several characters of each species in new material at hand indicate the necessity to remove these species from *Ophiocoma* and place them in a new genus, *Clarkcoma.*

The following features characterize *Clarkcoma,* new genus, and serve to separate it from *Ophiocoma*: (1) The arm spines are quite thin and compressed, in contrast to the more rounded, thicker spines of *Ophiocoma* (with the exception of *O. pusilla*); (2) the adoral shields converge in front of the oral shield and often come in contact (Figures 1, 2), whereas in *Ophiocoma*

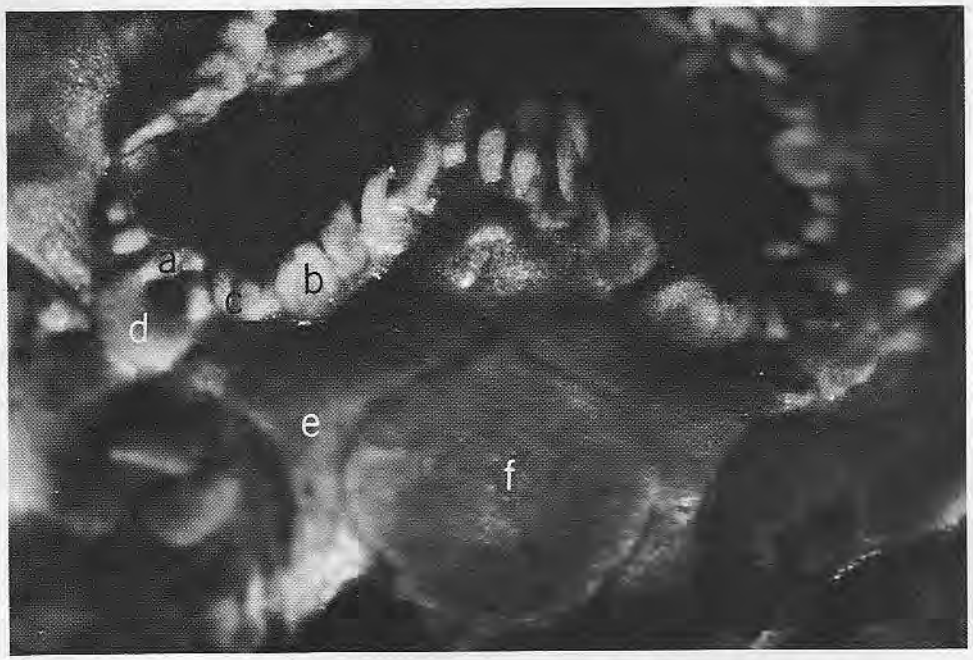


FIGURE 1.—*Clarkcoma canaliculata;* oral mouth sectors (d.d. 15 mm): *a,* buccal tentacle scale; *b,* outer oral papilla; *c,* accessory oral papillae; *d,* ventral shield; *e,* adoral shield; *f,* oral shield.

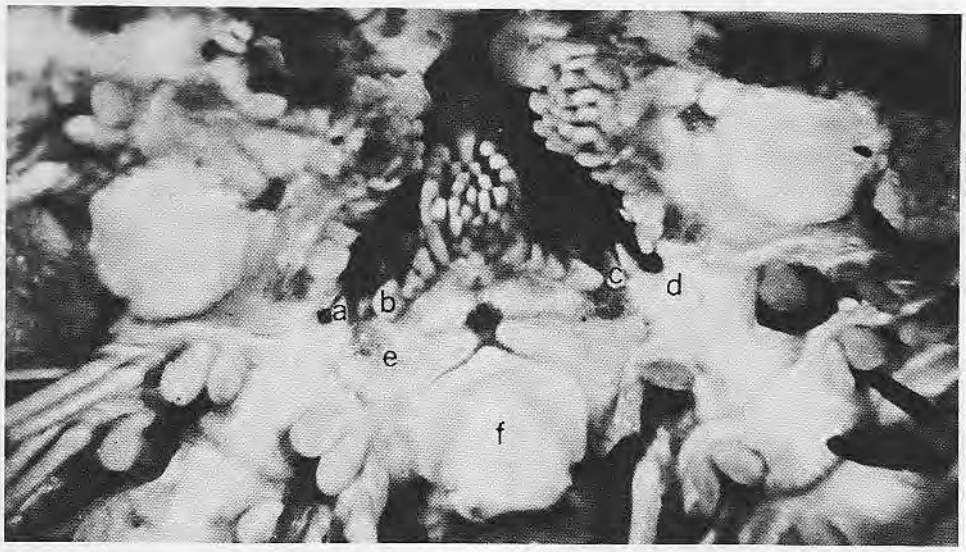


FIGURE 2.—*Clarkcoma canaliculata;* oral mouth sectors (d.d. 20 mm). (Abbreviations as in Figure 1.)

the adorals are confined to the sides of the oral shield (Figure 3); (3) the buccal tentacle scale is small, vertically directed, and separated from the adoral shield, and one or more small rounded granular papillae intrude between the broad outer oral papilla and the buccal tentacle scale (Figures 1, 2), whereas in *Ophiocoma* the buccal tentacle scale is relatively large, more horizontally directed, adjacent to the outer oral papilla, in contact with the adoral shield, and no small papillae occur between the outer oral papilla and buccal tentacle scale (Figure 3); (4) the oral plate shows an abradial muscle surface with a deep convexity, a narrow median ridge, and several short processes (Figure 4); the adradial muscle is restricted to only a small part of the adradial side of the plate (Figure 5). In *Ophiocoma* however, the abradial muscle surface is broken into a series of shallow somewhat parallel ridges and grooves (except *O. pusilla*) and the adradial muscle surface extends the whole length of the plate (Figure 44).

Both species of *Clarkcoma* are limited to southern temperate waters, whereas species of *Ophiocoma,* as now restricted, appear in tropical and subtropical waters. The two genera have been reported together only at one Western Australian locality (Rottnest Island, where *Ophiocoma occidentalis* and *Clarkcoma canaliculata* were collected (H. L. Clark, 1938, 1946).

The new genus is named in honor of Hubert Lyman Clark, Austin H. Clark, and Ailsa M. Clark, all of whom have made many significant contributions in echinoderm systematics.

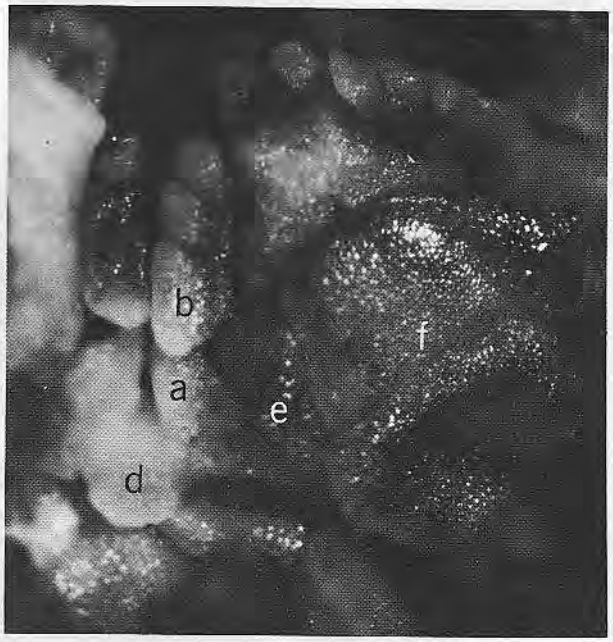


FIGURE 3.—*Ophiocoma erinaceus;* oral mouth sector (d.d. 11 mm), oral shield aberrantly split. (Abbreviations as in Figure 1.)

RELATIONSHIPS.—In the separation of the outer oral papilla from the buccal tentacle scale, *Clarkcoma* approaches the more evident separation of these ossicles

found in *Ophiocomina* (Figure 6) and in *Ophiopteris* (Figure 7) within the subfamily Ophiocominae. In all three genera the buccal tentacle scale is not in contact with the adoral shield, in contrast to the condition in the other genera—*Ophiocoma* (Figure 3), *Ophiomastix*, *Ophiarthrum*, and *Ophiocomella*—in the subfamily. Likewise, *Clarkcoma*, *Ophiocomina*, and *Ophiopteris* are similar in having the adoral shields located along the interior angle of a broad oral shield and usually meeting within. In this respect they also differ from the four other genera in the subfamily.

FIGURE 4.—*Clarkcoma bollonsi;* abradial surface of oral plate. *g*, Abradial muscle scar.

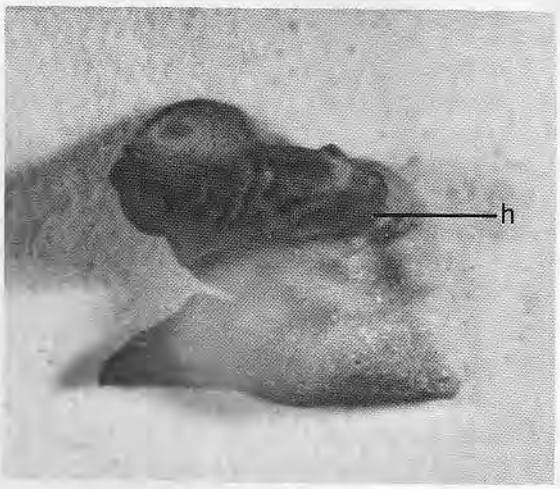


FIGURE 5.—*Clarkcoma bollonsi;* adradial surface of oral plate. *h*, Adradial muscle scar.

FIGURE 6.—*Ophiocomina nigra;* oral mouth sectors (d.d. 10 mm). (Abbreviations as in Figure 1.)

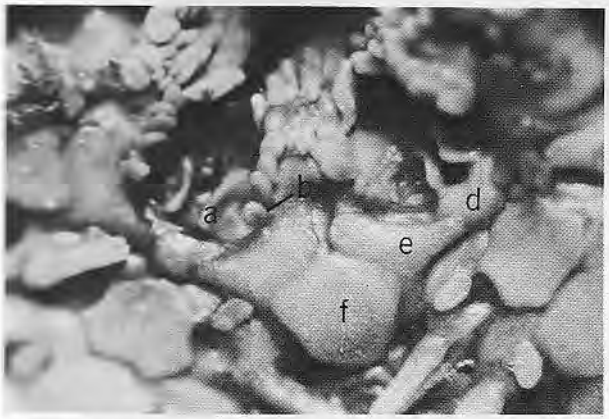


FIGURE 7.—*Ophiopteris papillosa,* oral mouth sectors (d.d. 12 mm). (Abbreviations as in Figure 1.)

In the nature of the thin, compressed arm spines *Clarkcoma* also shows greater similarity to *Ophiopteris* and to *Ophiocomina* than to the other genera.

Clarkcoma, however, is easily distinguished from *Ophiocomina* and *Ophiopteris* by the presence of hylinated tips of the teeth, a character which it shares with the other genera of Ophiocominae. *Clarkcoma* has well-developed teeth foramina in the dental plate (Figure 8), whereas these are reduced in *Ophiopteris* and absent in *Ophiocomina.* The jaw plate of *Ophiocomina* has a smooth and relatively smaller abradial muscle surface, unlike the condition noted for *Clarkcoma.* The adradial muscle surface of the jaw plate, however, is approximately the same size and shape in *Clarkcoma, Ophiocomina,* and *Ophiopteris,* being short and restricted to the oral portion of the plate, whereas in other genera of Ophiocominae it is elongate and often crosses most of the plate.

Clarkcoma, Ophiocomina, and *Ophiopteris* each has two species restricted to temperate waters, in contrast to the more tropical distribution of the other Ophiocominae genera.

Clarkcoma appears to be more closely related to the *Ophiocomina-Ophiopteris* branch of the Ophiocominae than to other genera in the subfamily.

SPECIES EVALUATION. *Clarkcoma bollonsi* is known from temperate waters around New Zealand, while *C. canaliculata* has been reported from temperate waters of Australia. The species show many similarities, and in the following evaluation the two taxa are considered together for purposes of comparison.

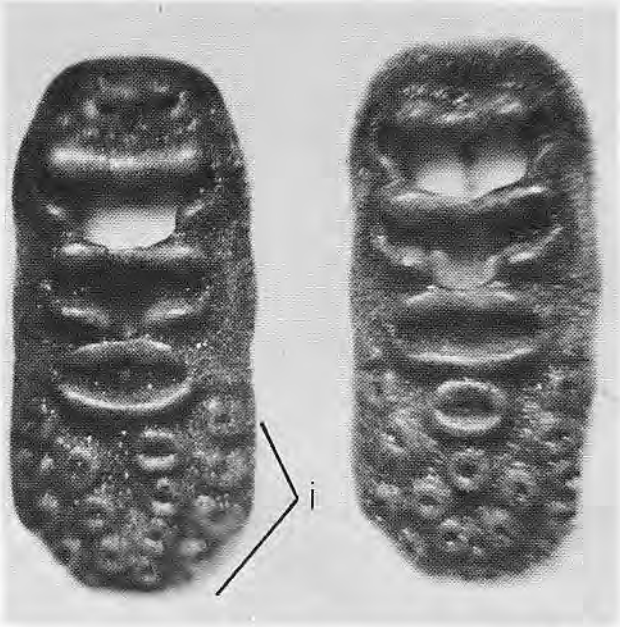


FIGURE 8.—*Clarkcoma canaliculata;* proximal surface of dental plates (d.d. 18 mm). *i,* Dental papillae area.

Clarkcoma bollonsi (Farquhar)

Ophiocoma bollonsi Farquhar, 1908, p. 108.—H. L. Clark, 1921, p. 132.—Koehler, 1922, p. 314.—Mortensen, 1924, p. 120, fig. 9; 1936, p. 260.—Fell, 1949a, p. 123, fig. 10; 1952, p. 24; 1958, pp. 2, 29; 1962, pp. 58 (fig. b), 59.—Hurley, 1959, pp. 144–145, figs. 2–4.—Graham, 1962, p. 200.—Pawson, 1965, p. 255.—McKnight, 1967, pp. 305–306.

MATERIAL EXAMINED.—New Zealand: Cook Strait, BPBM, no number (4); Foveaux Strait, USNM E10,137 (2); no definite locality, BPBM W1611 (1).

DIAGNOSIS.—See under *Clarkcoma canaliculata* (Lütken).

Clarkcoma canaliculata (Lütken)

Ophiocoma canaliculata Lütken, 1869, p. 46; Lyman, 1882, pp. 168, 177; Koehler, 1904, p. 75, figs. 30–32; 1922, p. 314; H. L. Clark, 1921, pp. 123, 128; 1928, p. 437, figs. 130a,b; 1938, p. 332; 1946, p. 244; A. M. Clark, 1966, pp. 291, 294, 327.

Ophiocoma canaliculata var. *pulchra* H. L. Clark, 1928, p. 439, figs. 131a,b.

Ophiocoma punctata Koehler, 1931, p. 205, pl. 14, figs. 2–5.

Ophiocoma pulchra H. L. Clark, 1938, p. 333; 1946, p. 244.—Dakin, Bennett, and Pope, 1960, p. 324, pl. 85 (bottom).—A. M. Clark, 1966, pp. 291, 327.

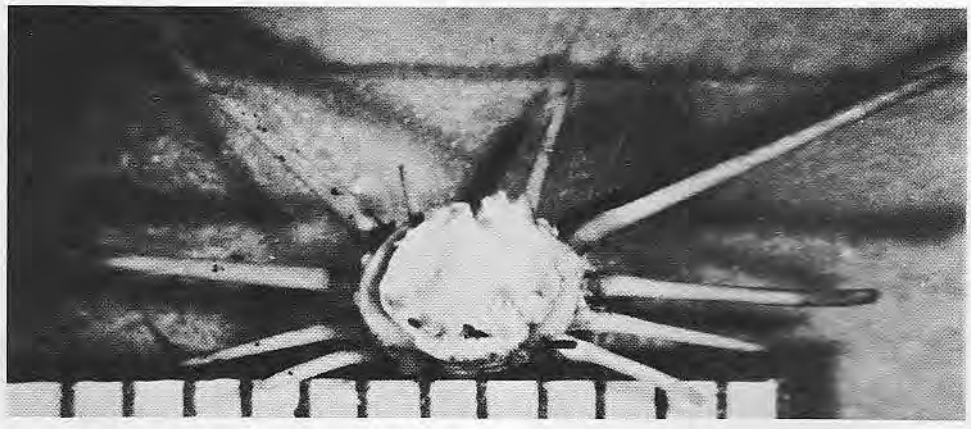


FIGURE 9.—*Clarkcoma canaliculata;* proximal view of arm segment and spines (segment 15).

FIGURE 10.—*Clarkcoma bollonsi;* upper and part of lateral arm plates with arm spines removed (d.d. 20 mm).

MATERIAL EXAMINED.—New South Wales: Newport, MCZ 6726 (1); Port Jackson, MCZ 5905 (paratype, *Ophiocoma punctata* Koehler); USNM 38638 (1); Shell Harbor, MCZ 5237 (1). South Australia: St. Vincent Gulf, MCZ 3462 (3), 5905 (1); Spencer Gulf, MCZ 4664 (2 paratypes, *Ophiocoma pulchra* H. L. Clark). Western Australia: Bunkers Bay, MCZ 5218 (2); Cape Naturaliste, BPBM, no number (5); Cheyne Beach, BPBM, no number (2).

DIAGNOSIS (for *Clarkcoma bollonsi* and *C. canaliculata*).—Disc diameter (d.d.) of both species to 24 mm; arms between three and four times as long as disc diameter. Granules in both species covering aboral surface of disc and extending into oral interradial area to variable extent. Specimens of *C. canaliculata* from New South Wales having more extensive granulation interradially than those from South and Western Australia. Aboral surface of longest arm spines of both species often showing evidence of a slight central depression ("canaliculate"); more evident for specimens of *C. canaliculata* examined. Longest spines frequently widened at tip (Figure 11). Mortensen (1924, p. 121) noted the outer part of a few of the arm spines in *C. bollonsi* was swollen. He suggested that a "parasitic organism" might be the cause of this condition, and in sectioning these spines, he found a "peculiar radiating structure." No evidence of a foreign organism could be detected, however, but Fell (1952, p. 24) noted "the presence of three kinds of spines on otherwise similar material" and concluded that "this would confirm Mortensen's opinion that club-shaped spines are pathological."

Sequence of spines on each side of first ten proximal arm segments for an 11-mm (d.d.) specimen of *C. bollonsi:* 3-4-4(or 5)-5-6-6(or 7)-6(or 7)-6-6-5(or 6); number of spines decreasing distally, with four and five spines beyond 25th segment. Farther out on the arm, four, and finally three spines.

Three specimens of *C. canaliculata* (d.d. 7–18 mm) with following spine sequence: each side of first four proximal segments with 3-3(or 4)-3(or 4)-4(or 5) spines; beyond segment 3, an increase in number of spines on each segment with increasing size of speci-

men determined by comparing spine sequence of small and large specimens (see Table 1).

An evident specific difference between *C. bollonsi* and *C. canaliculata* appears in the shape of the dental plates, and this is reflected externally by the extent of the dental papillae. In *C. bollonsi* a greater proportion of the plate is occupied by dental papillae tubercles, and the overall length to breadth ratio of the plate is greater than for *C. canaliculata* (compare Figure 8, 14). This difference appears in similar-sized specimens of each species.

Clarkcoma bollonsi has dental papillae arranged regularly in several transverse rows, their number reduced toward the teeth; papillae in the lateral columns are larger than those of center. *Clarkcoma canaliculata* has papillae occurring in nearly the same

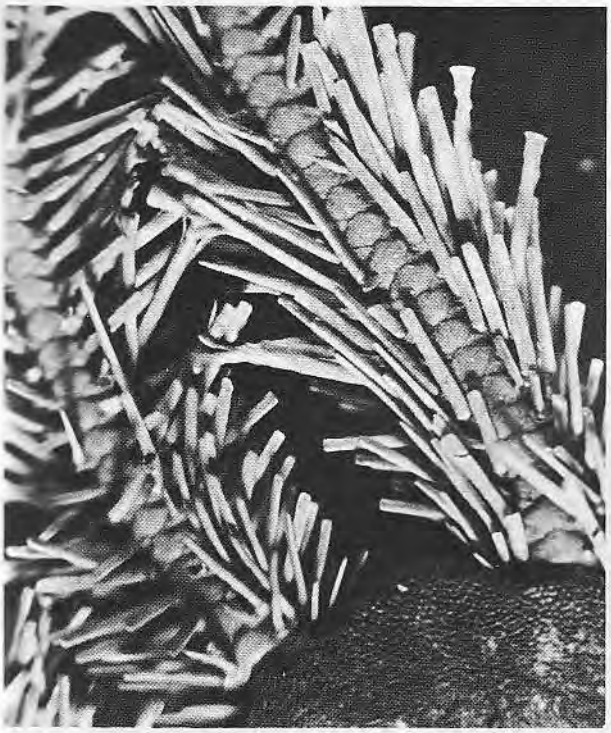


FIGURE 11.—*Clarkcoma canaliculata;* aboral side of disc, upper arm plates and arm spines (d.d. 20 mm).

TABLE 1.—*Number of arm spines on arm segments of* Clarkcoma canaliculata

Disc diameter	*Number of spines*	*Segments*
7 mm	6	segment 6
18 mm	6	segments 5–15
7 mm	7	none
18 mm	7	segments 6–10
7 mm	5	out to segment 12
18 mm	5	out to segment 35
7 mm	3	segments 21 to end
18 mm	3	segments 47 to end

FIGURE 12.—*Clarkcoma bollonsi;* lower arm plates and tentacle scales, some removed or broken (d.d. 20 mm.)

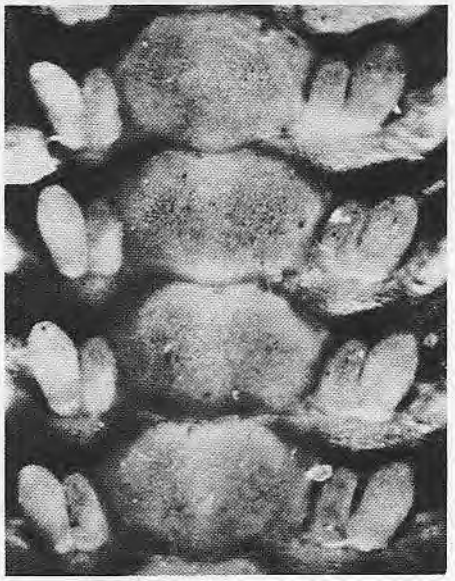


FIGURE 13.—*Clarkcoma canaliculata;* lower arm plates and tentacle scales, including segment 15 (d.d. 24 mm).

number above and below (near teeth); irregularly placed in three or four columns; relatively larger and less extensive than for *bollonsi* of similar size. Number of papillae varying according to size of specimens. *C. bollonsi* with dental papillae area slightly wider than area occupied by teeth (Figure 14); length-to-breadth ratio of plate, 2.9–3.1 : 1. For *C. canaliculata* dental papillae area about same width as tooth area (Figure 8); length-to-breadth ratio, 2.0–2.7 : 1.

FIGURE 14.—*Clarkcoma bollonsi;* proximal surface of dental plate (d.d. 20 mm).

There is greater evidence of the canaliculate shape of the upper surface of the longer arm spines in *C. canaliculata* than in *C. bollonsi,* but the presence of these spines on *C. bollonsi* makes the character difficult to use as a means for species differentiation.

In his key to the species of *Ophiocoma,* H. L. Clark (1921, p. 123) distinguished *canaliculata* and *bollonsi* by differences in disc granules: those of *bollonsi* "at least near the disc-margin, higher than thick, becoming more or less markedly spiniform"; those of *canaliculata* "nearly or quite spherical and of more or less uniform size." The spiniform nature of the granules at the disc margin as originally reported by Farquhar (1908) for the type of *bollonsi* has not been apparent, however, in the specimens I have examined. In these specimens the marginal disc granules do not appear to differ from those on either the oral or aboral surface of the disc. It must be assumed that there is a certain amount of individual variation in this character and that such variation does not reflect a constant specific distinction between the two species.

HABITAT AND DISTRIBUTION.—*Clarkcoma bollonsi* was first taken from a depth of 16 meters in Cook Strait, New Zealand (Farquhar, 1908). Mortensen (1924) recorded specimens collected from a "hard bottom" in depths ranging from 5 to 120 fathoms at several New Zealand localities and, later (1936), a single specimen from 128 meters in Cook Strait. Hurley (1959) gave an interesting report on the habitat and apparent density of *C. bollonsi* through the use of underwater photography. He noted the ophiuroids occurring in gregarious masses, and related this to their manner of feeding, suggesting that this species formed part of "a typical filter or detritus feeding community in an outer sublittoral cobble bottom where there is considerable seafloor current" (Hurley, 1959, p. 145). Fell (1958) reported this species from a number of New Zealand stations ranging in depth from 3 to 350 fathoms. Pawson (1965) reported specimens from the holdfasts of the algae *Lessonia* and *Durvillea* apparently collected intertidally at the Snares Islands. McKnight (1967) listed *C. bollonsi* from the Chatham Rise off eastern New Zealand collected in 210 meters.

Clarkcoma bollonsi, therefore, apparently is restricted to waters along the coast of New Zealand and on the Chatham Rise. The southern limit of this species appears to be the Snares Islands at latitude 48° South (Pawson, 1965).

Dakin, Bennett, and Pope (1960, p. 324) mention the occurence of *C. canaliculata* (as *Ophiocoma pulchra*) from Australian low water level on rocky coasts, "especially where there are rockpools and large stones resting upon pockets of sand or gravel. The ophiuroids lie under the stones and keep strictly in the shade under such conditions." Koehler (1931) obtained his specimens (as *Ophiocoma punctata*) in depths of 5 to 8

meters off Port Jackson, Australia, and A. M. Clark (1966) reported specimens (as *Ophiocoma canaliculata*) from two stations at depths of 1.5 and 4.5 fathoms at Port Phillip, Victoria.

Clarkcoma canaliculata is known from temperate Australian waters. Its range extends from the vicinity of Shell Harbor, New South Wales (lat. 34° S), along the South Australian coast to Rottnest Island, Western Australia (lat. 33° S); it has not yet been reported from Tasmania.

DISCUSSION.—H. L. Clark (1928) considered *Ophiocoma canaliculata* to have two color forms, and he designated one form by the variety name *pulchra*. The basic difference was in pigmentation of the arm spines and oral arm plates. In 1931 Koehler described a species from Port Jackson, New South Wales, under the name *Ophiocoma punctata*. Although resembling *O. canaliculata* quite closely, Koehler listed several characters which he regarded as sufficient to distinguish the two species. These included the form of the upper arm plates, less-pronounced grooves on the spines, a difference in the shape of the oral shields, disc-granule size, and pigmentation (Figure 15). H. L. Clark (1938) regarded Koehler's species to be identical with *O. canaliculata* var. *pulchra*, and considered *pulchra* a distinct species because no intermediate specimens of *O. canaliculata* and *O. pulchra* had been seen. He noted, however, that the distributional range of the two species coincided and their morphological features were remarkably similar. Later, a similar diagnosis was made, and he noted that "the actual relationship of the two forms still is an open question" (H. L. Clark, 1946, p. 245).

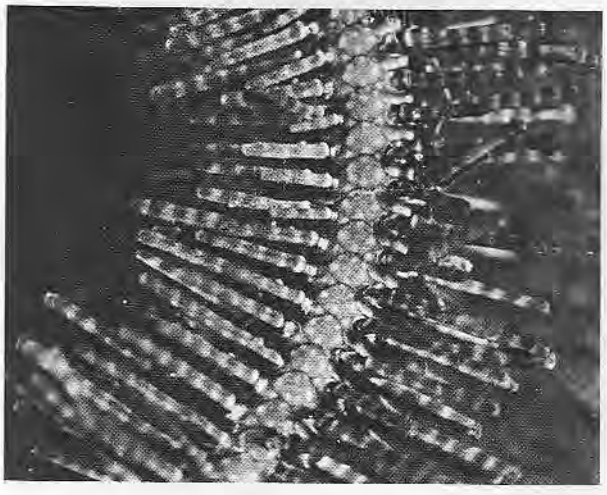


FIGURE 15.—*Clarkcoma canaliculata* (MCZ 5237, labeled "Ophiocoma pulchra, Shell Harbor, Australia"); upper side of arm.

Two of H. L. Clark's paratypes labeled *Ophiocoma pulchra* (MCZ 4664) and one of Koehler's paratypes described as *O. punctata* (MCZ 5901) have been examined. Comparison with specimens identified as *O. canaliculata* reveals several of the differences mentioned by Koehler (1931) which distinguished *punctata* from *canaliculata*, basically in the pigmentation. I am not convinced, however, that the differences are specific; they may only reflect variation in a single species. Until more specimens are available for comparison, *Ophiocoma pulchra* is considered conspecific with *Clarkcoma canaliculata*.

Genus *Ophiocoma* Agassiz

Ophiocoma Agassiz, 1836, p. 192.—Müller and Troschel, 1842, p. 98.—Lütken, 1869, p. 94.—Lyman, 1882, pp. 167–168.—H. L. Clark, 1921, pp. 120–121.

TYPE-SPECIES.—*Ophiura echinata* Lamarck, 1816 (see H. L. Clark, 1915, p. 290).

DIAGNOSIS.—Ophiocominae with three to seven solid (except *O. pusilla*), generally smooth arm spines. Disc with granules, uniform or variable in size and shape, sometimes extending into oral interradial region. Oral plates (jaws) with well-developed abradial muscle surface having a series of indentations or shallow ridges and grooves (except *O. pusilla*). Adoral shields confined to sides of oral shield and not meeting in front of oral shield. Oral papillae, 3, 4, rarely 5, contiguous; outer usually widest. Buccal tentacle scale in contact with both ventral and adoral shields.

REMARKS.—Louis Agassiz (1836) first proposed the generic name *Ophiocoma* for a large number of species described by Lamarck in 1816. Agassiz simply included all the species in Lamarck's genus *Ophiura* which had been designated and listed as section B by Blainville (1834, p. 244) for that group of species characterized by long arm spines that were not appressed against the arm segments. As Loriol (1894, p. 25) pointed out, this brief diagnosis was applicable to many species which subsequently became separated into several other genera.

Only three species considered by Agassiz as *Ophiocoma* belong to this genus under its present definition, and two of these, *O. squamata* and *O. echinata*, were nominally designated by Agassiz in his original work.

A third Lamarckian species, *scolopendrina,* was included along with the other species merely by "etc." H. L. Clark (1915, p. 290) designated the type-species of the genus correctly as *Ophiura echinata,* even though Lyman (1865, p. 70) had erroneously designated *O. scolopendrina* Agassiz.

Müller and Troschel (1842) focused attention on fundamental characters by which the genus could be more accurately defined. They indicated the importance of both oral and dental papillae (which were to become the key family characters) as well as the granulation of the disc. Greater elaboration of the generic characters was presented by Lyman (1882), but his intrageneric characters (internal disc scaling and nature of the radial shields) have not lead to definitive conclusions regarding species interrelationships.

Lütken (1869) first pointed out that certain species of *Ophiocoma* shared characters that linked them more closely to each other than to other species in the genus. The possible relationships of the species were discussed in more comprehensive terms by H. L. Clark (1921) who noted that differences in disc granulation, number of tentacle scales, pigmentation, and limits of geographic distribution could be used to divide the genus into three groups—designated BREVIPES, PUMILA, and SCOLOPENDRINA after nominal species in each group. All but four of the species of *Ophiocoma* recognized by Clark were placed in these groups. Two of the four not grouped by Clark (*bollonsi* and *canaliculata*) have been removed and form the new genus *Clarkcoma,* while the other two (*pica* and *pusilla*), together with *O. longispina,* form a separate group in the genus *Ophiocoma.*

Through the work of Grave (1898) and Mortensen (1921, 1931, 1937) we know that three species of *Ophiocoma* in the SCOLOPENDRINA group (*echinata, erinaceus,* and *scolopendrina*) have a unique "thorny" fertilization membrane as well as larvae with very similar skeletons. In contrast, Mortensen (1937) found *Ophiocoma pica* to have a smooth fertilization membrane and a markedly different larval skeleton. Recently *Ophiocoma pumila,* collected in British Honduras (7 March 1969), was fertilized, and stages in its larval development were followed. In contrast to members of the SCOLOPENDRINA group, but similar to *O. pica,* the fertilization membrane of *pumila* is smooth, yet the skeleton shows the well-developed body rods with transverse and end rods in contact (Figure 16). In this respect the larval skeleton is more like that found in the SCOLOPENDRINA group. Thus, although the evidence is not complete, there are differences in embryological and larval characters between several species of *Ophiocoma,* which, on the basis of adult characters, are considered in separate groups. Extension of this study may further show that premetamorphosis stages provide morphological characters that support the separation of the species in these and other ophiuroid taxa.

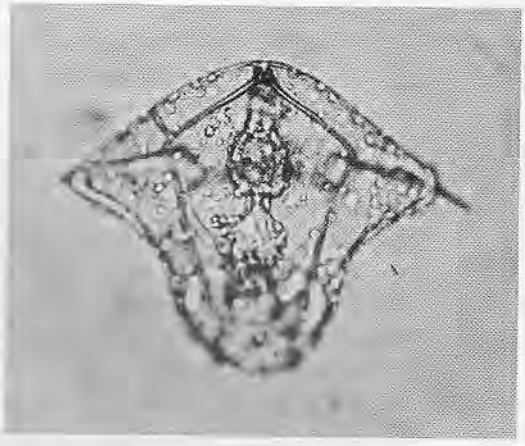


FIGURE 16.—*Ophiocoma pumila;* 13-day-old larva.

RELATIONSHIPS.—H. L. Clark (1921) briefly discussed the relationships of other genera in the subfamily to *Ophiocoma.* Although distinguishing *Ophiomastix* from *Ophiocoma,* he felt that the line separating the two genera was not clear. For example, three species of *Ophiomastix* (*asperula, elegans,* and *mixta*) were considered to be difficult to separate from species of *Ophiocoma* in the PUMILA group on the basis of the disc granulation alone. Further, he recognized *Ophiocoma pusilla,* which was considered to have "club-shaped" arm spines, a primary diagnostic feature of *Ophiomastix,* while other species of *Ophiocoma* also shared this character with *Ophiomastix* even though lacking distinct disc spinules. With the exception of Lütken (1869, p. 95), Clark and others, however, failed to note that species of *Ophiomastix* have an alternating number of arm spines beyond the disc edge occurring on opposite sides of the same segment or on adjacent segments, in addition to having the upper spine usually greatly enlarged or swollen (Figure 50). The important consideration here is that the alternating sequence and enlargement of the upper arm spines also are charac-

teristic of species in the SCOLOPENDRINA group of *Ophiocoma* (although these species do not have the arm spines as strongly modified into "clubs" as do some of the species in *Ophiomastix*).

The alternation and enlargement of the upper arm spines is also evident in the genus *Ophiarthrum,* whose three species H. L. Clark regarded simply as specialized offshoots of *Ophiocoma* in which the disc granules were lost. The relationship of *Ophiomastix* and *Ophiarthrum* to the SCOLOPENDINA group of *Ophiocoma* is further indicated by the similarity in the shape of the oral and dental plates.

The genus *Ophiopteris,* with two species showing an interesting and puzzling discontinuous distribution on opposite sides of the Pacific, was suggested by H. L. Clark to have been derived independently from two species of *Ophiocoma* (*aethiops* and *erinaceus*) in the SCOLOPENDRINA group. There is no evidence, however, to support this suggestion, and there are striking differences in the relationships of the oral papillae and buccal tentacle scale as well as in characteristics of the oral and dental plates between the two genera. Furthermore, the arm spines are of an entirely different nature and do not alternate in *Ophiopteris* as in the SCOLOPENDRINA group. In fact, there is no evidence of *Ophiopteris* having evolved from any extant species of *Ophiocoma,* and *Ophiopteris* shows closer morphological affinity to *Ophiocomina* and *Clarkcoma* as indicated earlier.

Another genus, *Ophiocomella,* made up of small, primarily hexamerous species, had not been established at the time of Clark's 1921 review of the subfamily; however, one species, *parva,* considered (as *O. sexradia*) in this genus was placed in the PUMILA group of *Ophiocoma.* Arguments supporting the validity of *Ophiocomella* have been presented by A. H. Clark (1939) and Ailsa M. Clark (in Parslow and Clark, 1963). Further evidence (given in the present paper) is based on differences in the arm spine sequence and oral (jaw) plate that indicate separation of *Ophiocomella* from species in the PUMILA group of *Ophiocoma.*

Ophiocomina, the sixth genus in the subfamily, was considered by H. L. Clark (1915, 1921) to belong in another family (Ophiacanthidae). Mortensen (1920) and Koehler (1922) nonetheless gave strong evidence to support the inclusion of *Ophiocomina* in the Ophiocomidae. The very small and smooth surface of the abradial muscle area of the oral plate and the lack of hylinated teeth separate *Ophiocomina* from any species of *Ophiocoma;* yet, these and other features suggest closer affinity to *Ophiopteris* and *Clarkcoma.*

SPECIES EVALUATION.—By the time H. L. Clark (1921) reviewed the genus *Ophiocoma* 32 specific names had been assigned to it. Of these, Clark removed 22 names as synonyms in other genera. In addition, species correctly assigned to *Ophiocoma* which are considered merely synonyms for other species in the genus also were listed by Clark. Several corrections (based on the present study) to this evaluation are as follows:

(1) *Ophiocoma dentata* Müller and Troschel, 1842, is the senior synonym for *O. insularia* Lyman, 1861, *O. variegata* Smith, 1876, and H. L. Clark's (1921) two varieties of *O. brevipes* (*dentata* and *doederleini*).

(2) *O. doederleini* Loriol, 1899, is considered a valid species.

(3) *O. insularia* var. *longispina* H. L. Clark, 1917, is considered a valid species.

(4) *O. tumida* Müller and Troschel is a junior synonym of *Ophioderma longicauda* (according to Koehler, 1924, p. 342).

(5) *O. wendti* Müller and Troschel, 1842, is the senior synonym for *O. riisei* Lütken, 1859.

(6) *O. punctata* Duchassaing, 1850, is a junior homonym for *O. punctata* Forbes, 1841, and apparently is a synonym of *O. pumila* (according to Lyman, 1872, p. 7) or *O. brevipes* (according to Koehler, 1907a, p. 327).

Since 1915, several new species have been proposed, and their taxonomic position in the genus *Ophiocoma* is as follows:

(1) *Ophiacantha macroplaca* H. L. Clark, 1915, is a valid species of *Ophiocoma.*

(2) *Ophiocoma pulchra* H. L. Clark, 1928, appears to be merely a color form of *O. canaliculata* Lütken, 1869 (now considered in the genus *Clarkcoma*).

(3) *Ophiocoma punctata* Koehler, 1931, is a junior primary homonym for *O. punctata* Forbes, 1841, and a junior synonym for *O. canaliculata* Lütken, 1869.

(4) *Ophiocoma delicata* H. L. Clark, 1932, is a species of *Ophiarachna* (family Ophiodermatidae).

(5) *Ophiocoma anaglyptica* Ely, 1944, is retained as a valid species.

(6) *Ophiocoma latilanxa* Murakami, 1943, is considered a junior synonym for *O. pusilla* (Brock, 1888).

(7) *Ophiocoma alternans* Endean, 1963, is a junior homonym for *O. alternans* Martens, 1870.

O. scolopendrina - H.L. Clark, 1921

Key to Species-Groups of *Ophiocoma*

1. Similar number of arm spines on each side of arm segments beyond disc; upper arm spines not noticeably thickened 2
   Alternating number of arm spines, usually 3 and 4 on each side of same or adjacent segments beyond disc; upper arm spine thicker and often markedly longer than lower spines. **Scolopendrina** group
2. Disc granules uniform in size, rarely elongate or spiniform; two tentacle scales on more than first five proximal segments 3
   Disc granules variable in size, some elongate or spiniform; one tentacle scale on all but the first five proximal segments ..... **Pumila** group
3. Upper arm plates with angular lateral margins and much broader along distal than proximal border (Figure 27); disc granules not closely packed around oral shield ..... **Pica** group
   Upper arm plates with broadly rounded margins and not much broader along distal than proximal border (Figure 17); disc granules closely packed up to oral shield. **Brevipes** group

1. Brevipes Group

Three species in the BREVIPES group of *Ophiocoma* are recognized in this paper: *O. brevipes* Peters, 1851; *O. dentata* Müller and Troschel, 1842; and *O. doederleini* Loriol, 1899. All three species have Indo-Pacific distribution, and have been found primarily in shallow sublittoral waters, usually under boulders or attached coral on a sand or sand-and-rubble substratum.

DIAGNOSIS.—Four to six arm spines on each side of proximal arm segments beyond disc edge; upper arm spine seldom equal to and usually shorter than other spines in the same row (Figure 18). Dental plate between 1.8 and 2.3 times longer than broad, with a wide vertical septum dividing each tooth foramen, and dental papillae region limited to approximately 25 percent of the total plate length (Figure 19). Upper arm plates broadly oval, with outer edges only slightly curved and contiguous along distal edge of following plate for about 45 percent of maximum breadth (Figure 17). Disc granules closely packed, small and spherical, covering oral interradial region entirely to mouth shields and nearly to genital slits. Two tentacle scales on each side of oral arm plate on many segments from beginning of arm.

In contrast to other members of the genus, the BREVIPES group is characterized by having a dental plate that is relatively much shorter, and broader than long (Figure 19). It shows a very small semicircular region for the tooth papillae and wide flat septa which divide the teeth foramina. The nature of this skeletal ossicle together with other morphological features listed above serve to separate the species in this group from others in the genus.

FIGURE 17.—*Ophiocoma dentata;* upper arm plates and arm spines, about segment 15 (d.d. 19 mm).

Key to Species

1. Similar number of arm spines on each side of arm segments beyond disc; upper arm spines surface white or yellow-white ..... ***O. brevipes***
   Length of second and third arm spines equal to or more than breadth of proximal upper arm plate; oral surface gray, brown or variegated 2
2. Arm spines conspicuously annulated in color (Figures 18, 20); 5 (seldom 4) arm spines on segment 6 ..... ***O. doederleini***
   Arm spines not annulated in color; 4 (seldom 5) arm spines on segment 6 ..... ***O. dentata***

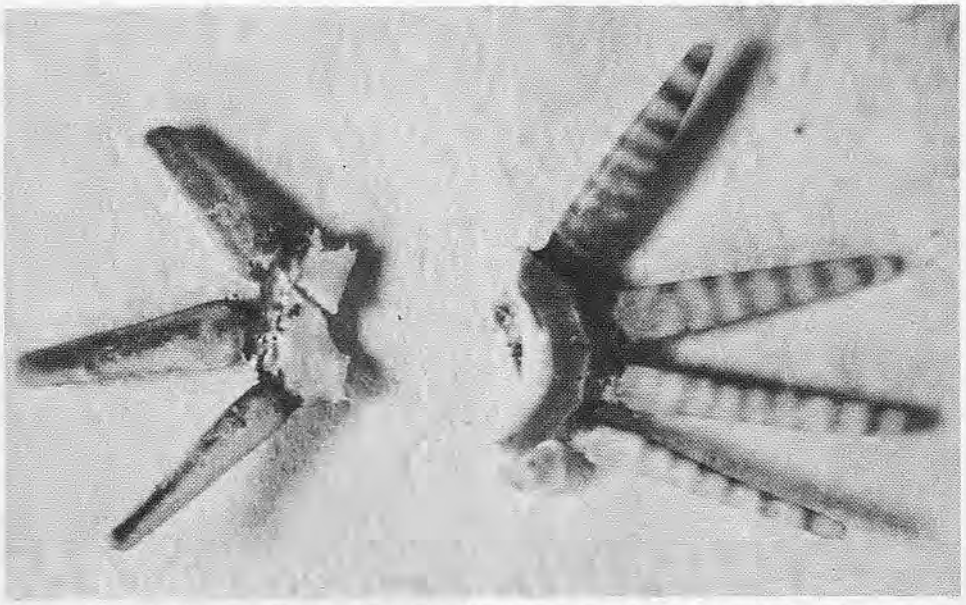


FIGURE 18.—*Ophiocoma dentata* (left) and *Ophiocoma doederleini;* lateral view of arm spines. Both views from about segment 15; specimens from Eniwetok (d.d. 21 mm).

FIGURE 19.—*Ophiocoma dentata;* proximal (left) and distal sides of dental plates (d.d. 21 mm).

DISCUSSION.—According to H. L. Clark (1921), the BREVIPES group was the ancestral stock from which both the SCOLOPENDRINA and PUMILA groups evolved. Clark followed Matsumoto's (1917) speculation that *Ophiocoma brevipes* was the most primitive species in the genus, based on its limited number of dental papillae. There is no reason, however, to consider this character as necessarily primitive; just as likely it could be a particular specialization related to the feeding habits of the species. Likewise, there is no paleontological evidence to support H. L. Clark's suggestions that the SCOLOPENDRINA and PUMILA groups evolved from *brevipes* through (a) changes in pigmentation, (b) changes in disc granulation size, (c) increase in the number of dental papillae. Without better support, it seems advisable to consider the BREVIPES group as a relatively homogeneous species complex in the genus.

SPECIES EVALUATION.—As an aid in following the somewhat complicated taxonomic revision of the species in the BREVIPES group, synonymies are given below with the major references included for each species.

Ophiocoma brevipes Peters

Ophiocoma brevipes Peters, 1851, p. 466.—Lyman, 1865, p. 92; 1874, p. 225; 1882, p. 172 (part).—Martens, 1870, p. 252.—H. L. Clark, 1921, p. 129, pl. 13, fig. 7, pl. 34, figs. 3, 4; 1938, p. 333; 1946, p. 342.—Ely, 1942, p. 56, figs. 16a, b, pl. 13c.—A. H. Clark, 1949, p. 53.

Ophiocoma brevispinosa Smith, 1876, p. 40.

Ophiocoma dentata Müller and Troschel

Ophiocoma dentata Müller and Troschel, 1842, p. 99, pl. 7, figs. 3,3a.—Lütken, 1859, p. 267.—Lyman, 1865, p. 70.—H. L. Clark, 1921, p. 121.—Koehler, 1922, p. 314.

(?) *Ophiocoma squamata* (Lamarck).—Müller and Troschel, 1842, p. 102.

Ophiocoma insularia Lyman, 1861, p. 80; 1865, p. 89; 1874, p. 225.—H. L. Clark, 1915, p. 291, pl. 15, figs. 3, 4.—Ely, 1942, p. 57, fig. 17, pl. 13a.

Ophiocoma ternispina Martens, 1870, p. 252.—Lyman, 1874, p. 225.

Ophiocoma brevipes Peters.—Lyman, 1874, p. 225; 1882, p. 172 (part).—Loriol, 1894, p. 25, pl. 23, figs. 4, 4a.—Koehler, 1922, p. 319, pl. 72, figs. 6–9; Matsumoto, 1917, p. 343 (part), figs. 3a–c.

Ophiocoma variegata Smith, 1876, p. 39; 1879, p. 565, pl. 51, figs. 1–1c.

Ophiocoma marmorata Marktanner-Turneretscher, 1887, p. 303, pl. 12, figs. 16, 17.—H. L. Clark, 1915, p. 294.

Ophiocoma brevipes var. *variegata* Smith.—H. L. Clark, 1921, p. 130 (forma *dentata* and *doederleini*).

Ophiocoma brevipes var. *insularia* Lyman.—H. L. Clark, 1921, p. 130.

Ophiocoma scolopendrina (Lamarck).—H. L. Clark, 1909, p. 524 (according to H. L. Clark, 1938, p. 559).

Ophiocoma insularia var. *variegata* Smith.—H. L. Clark, 1938, p. 330 (forma *dentata* and *doederleini*); 1939, p. 94; 1946, p. 246 (forma *dentata* and *doederleini*).—Ely, 1942, p. 60, pl. 13b.—Endean, 1957, p. 244.—Domantay and Domantay, 1966, p. 53.

Ophiocoma doederleini Loriol

Ophiocoma doederleini Loriol, 1899, p. 30, pl. 3, fig. 2.—Koehler, 1905, p. 60; 1922, p. 312, 321–322, pl. 72, figs. 1–3.

REMARKS.—In 1938, H. L. Clark considered the problem relating to various species which had been designated as *Ophiocoma brevipes* and *O. insularia*. On the basis of adult specimens from Lord Howe Island, he described two color forms of *Ophiocoma insularia* var. *variegata*. One form was characterized by a reticulated disc pattern and was considered identical to *Ophiocoma dentata* described by Lütken (1859); the other, with a spotted disc, was considered similar to *O. doederleini* described by Loriol (1899).

For H. L. Clark, this appearance of two apparently sympatric color forms confirmed the relationship between Lütken's and Loriol's species. He stated that they were "easily recognized but seem to be unquestionably mere color forms of *variegata*" (H. L. Clark, 1946, p. 246). Recent examination of specimens from several other Indo-Pacific localities has revealed, however, that H. L. Clark's interpretation requires modification.

At Eniwetok, specimens with a gray, reticulated disc pattern and very definite annulated arm spines were collected together with specimens having a brownish disc covered with blackish spots but lacking annulated arm spines (Figures 20, 21). The pigmentation of the

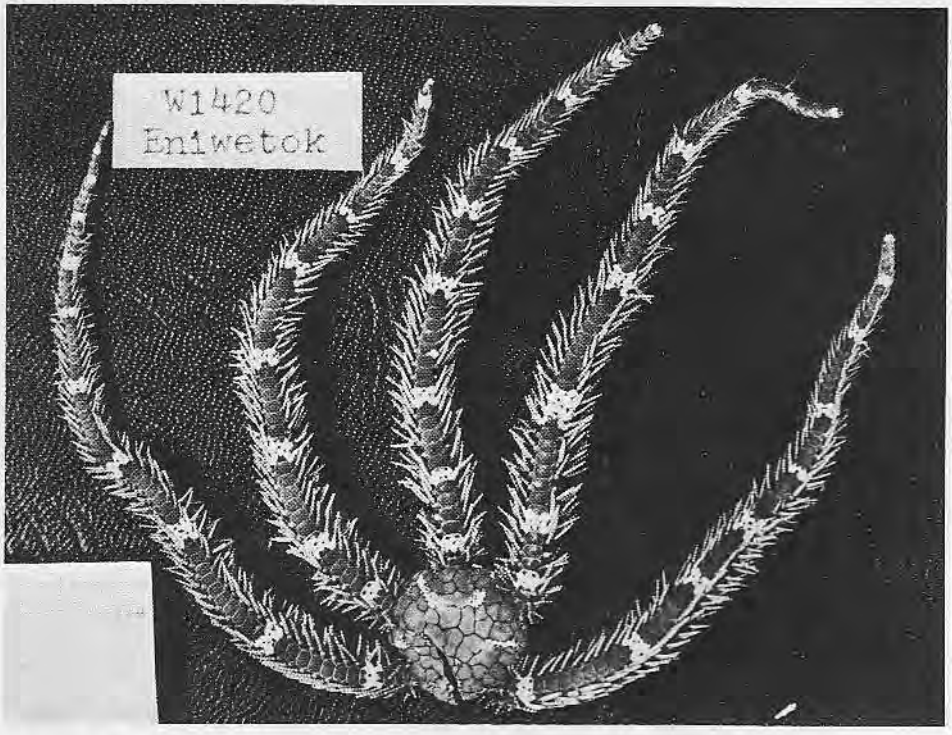


FIGURE 20.—*Ophiocoma doederleini;* upper side of specimen with reticulated disc pattern (d.d. 23 mm).

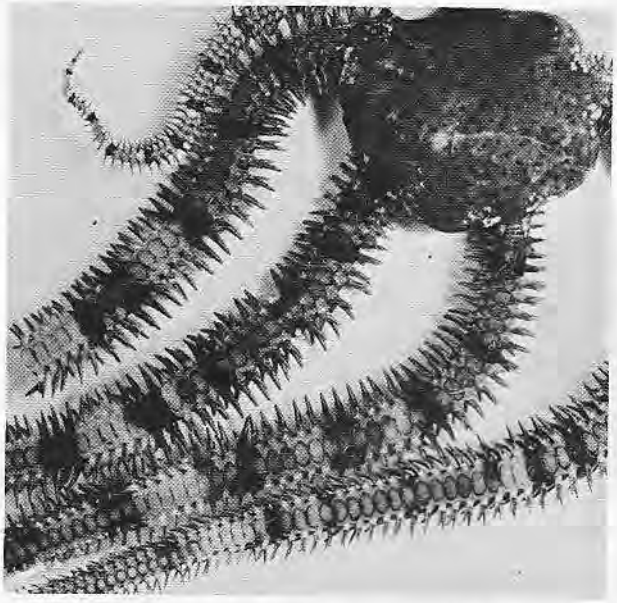


FIGURE 21.—*Ophiocoma dentata;* upper side of specimen with spotted disc pattern (d.d. 26 mm).

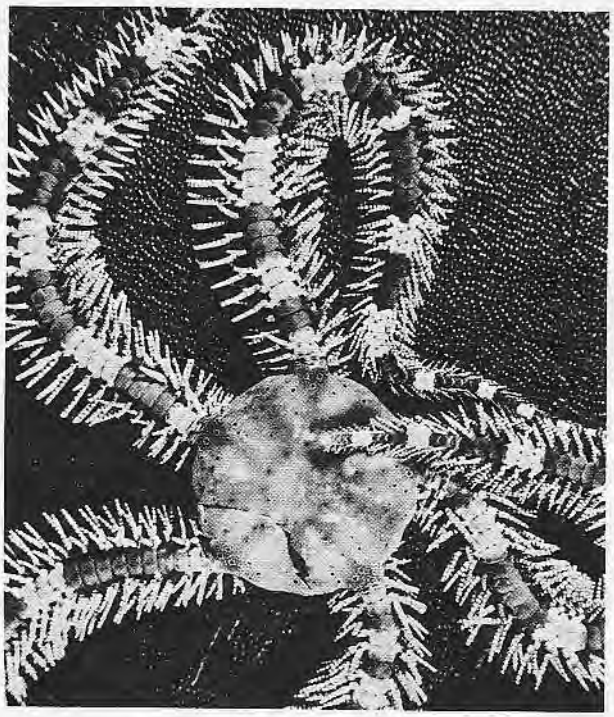


FIGURE 22.—*Ophiocoma doederleini;* upper side of specimen with spotted disc pattern (d.d. 19 mm).

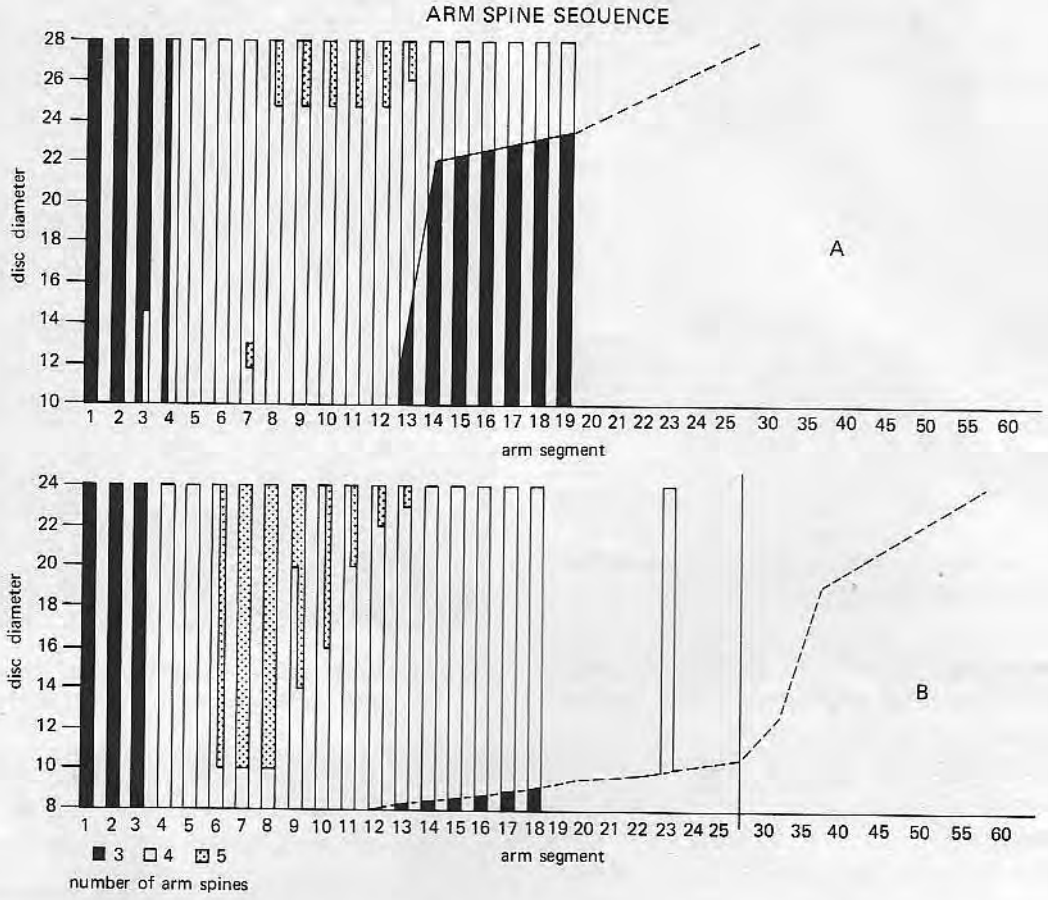
disc at first recalled H. L. Clark's (1938) color forms, *dentata* and *doederleini,* respectively. Clark, however, had not mentioned the appearance of annulated arm spines on either of his Lord Howe Island forms, although Loriol (1899) reported this feature in his original description of *O. doederleini.* Moreover, the occurrence of another color variety from Eniwetok (Figure 22) corresponded closely with Koehler's (1922) redescription and figures of the type-specimen of *O. doederleini.* Koehler had compared the type with specimens of *O. dentata* (as *O. brevipes*) and noted that there were small black spots irregularly arranged on the disc of *O. doederleini* and that "each of them is surrounded by a lighter circle, a feature which Loriol did not notice" (Koehler, 1922, p. 321).

When the Eniwetok specimens having the reticulated disc and annulated arm spines were compared with the specimen having spots encircled with a lighter outline and also having annulated arm spines, close morphological similarity was revealed. In contrast, several differences aside from pigmentation were noted between these specimens and those which lacked the annulated arm spines. First, a difference in the arm spine sequence was noted (see Table 2). Seven specimens with annulated arm spines (*Ophiocoma doederleini*) were compared with five specimens without annulated arm spines (*Ophiocoma dentata*). Differences between the two species on the basis of the sequence of arm spines are given below:

Ophiocoma doederleini	*Ophiocoma dentata*
Four arm spines on segment 4.	Three and four arm spines on segment 4.
Four or five arm spines on segment 6.	Four spines on segment 6.
Five spines on segments 7 and 8 (d.d. more than 12 mm); five out to segment 14 with increase in size.	Five spines on segments 7 and 8 (rarely five, when d.d. more than 20 mm); five out to segment 13 (d.d. more than 23 mm).
Four arm spines as far as segments 32 to 38 (d.d. 13–14 mm) and out to approximately segment 55 in a 24-mm specimen.	Four arm spines as far as segment 17 (d.d. 13–14 mm) and out to approximately segment 25 in a 24-mm specimen.

The above data support Koehler's (1922) findings. His examination of the type of *doederleini* revealed the presence of five arm spines on each side of the arm segments at the base of the arm, dropping to four spines some distance from the arm base. For *dentata* (as *brevipes*) he noted, however, that five arm spines were quite unusual and four spines did not occur far from the arm base.

TABLE 2.—*Arm spine sequence of* (*a*) Ophiocoma dentata *and* (*b*) O. doederleini



In addition, Koehler reported that the breadth of the arms of *doederleini* was greater than that of *dentata* (as *brevipes*) due to a greater length of arm spines as well as a greater breadth without arm spines. To verify this, the arm span (composed of the length of longest arm spines on each side of segment, the breadth of the aboral arm plate, and the breadth of the lateral plates) was analyzed, taking the tenth segment beyond the disc edge for comparison and using the specimens determined as *dentata* and *doederleini* from Eniwetok (see Table 3). The percentage of the total arm span occupied by the longest arm spines, aboral plate breadth, and lateral arm plates is given for each specimen examined.

The percentage means of the total arm span occupied by the arm spines differed significantly between the two species ($t=4.4$, 11 degrees of freedom), with specimens of *dentata* having a range from 54 to 61 percent and *doederleini* having a range from 61 to 65 percent. The difference in the percentage means of the arm span taken up by the breadth of the aboral arm plate showed an opposite trend: the aboral arm plate of *dentata* occupied a significantly greater part of the arm span than that of *doederleini* ($t=6.3$, 11 degrees of freedom), and no overlap between the two samples was noted. Comparison of the total arm span for the two species supports Koehler's contention that *doederleini* has a relatively greater arm span than *dentata* for specimens of comparable size. For example, the arm span of a 26–28-mm (d.d.) specimen of *dentata* was 13.1 mm, while for a smaller specimen of *doederleini* (d.d. 24 mm), the arm span was 15.2 mm.

Further evidence for the separation of the two species resulted when the Eniwetok specimens were compared with several specimens identified as *Ophiocoma brevipes* from Cocos-Keeling (USNM E7450) and those identified as *O. insularia* var. *variegata* forma *dentata* and *doederleini* by H. L. Clark

TABLE 3.—*Arm span (10th free segment) of* Ophiocoma dentata *and* O. doederleini *from Eniwetok*

Disc diameter (mm)	Percent spine length	Percent aboral plate	Percent lateral plates	Total arm span (mm)
Ophiocoma dentata (N=5)				
12–15	56	26	18	7.4
22	61	28	11	11.9
23.5	60	27	13	12.0
25–27	55	32	13	11.4
26–28	54	28	18	13.1
Range: 12–28	54–61%	26.32%		
$\bar{X}$	57.2%	28.2%		
$s_{\bar{x}}$	3.12	2.26		
Ophiocoma doederleini (N=7)				
9	64	20	16	7.0
11–12.5	61	22	17	8.3
14	62	22	16	10.7
19.5	62	24	14	11.7
21.5	63	21	16	13.7
23	63	22	15	14.4
24	65	21	14	15.2
Range: 9–24	61–65%	20–24%		
$\bar{X}$	62.9%	21.8%		
$s_{\bar{x}}$	1.39	1.30		

(1938, 1946) from Lord Howe Island (MCZ 5228, 5227). In both cases there are specimens with reticulated or spotted discs but lacking annulated arm spines. The arm spine sequence for these specimens was similar to that noted in the specimens determined as *dentata* from Eniwetok and additional specimens from the Hawaiian Islands.

It is apparent now that both *dentata* and *doederleini* have at least two color forms. The reticulated-disc color variety of *doederleini* (Figure 20) is reported here from Eniwetok for the first time. Additional specimens of this color form of *doederleini* also have been collected by the author from the Marquesas Islands (where *dentata* was not found and not previously reported); also, examples of this color form from the Indian Ocean (Mauritius and Amirantes Islands) and Tahiti are deposited in the United States National Museum.

The spotted-disc color variety of *doederleini* can be distinguished from that of *dentata* by the presence of white rings around the disc spots as well as by the presence of annulated arm spines. It is quite evident after reexamination that the specimens which H. L. Clark (1938, 1946) considered as *doederleini* represent merely a spotted variety of *dentata* and are not conspecific with Loriol's species. Furthermore, it is evident that the reticulated specimens (with annulated arm spines) from Eniwetok, the Marquesas, and other Indo-Pacific localities differ from those reported by H. L. Clark (1938, 1946) as *O. insularia* var. *variegata* forma *dentata*. The same is probably true in the case of Lütken's (1859) specimens of *O. dentata* from the Nicobar Islands, and Marktanner-Turneretscher's (1887) reticulated form described as *Ophiocoma marmorata*. With the exception of the reticulated disc pattern, neither of these specimens was reported as having annulated arm spines or more than four arm spines. In these and other respects they agree with the external features noted for *Ophiocoma dentata* as originally described by Müller and Troschel.

The status of Müller and Troschel's species, *Ophiocoma dentata*, has been determined after examination of the type-specimen deposited in the Zoologisches Museum Berlin (No. 931). The following is a clarification of the taxonomy of this species. Lyman (1865, p. 70) stated that Müller and Troschel's *Ophiocoma dentata* was invalid, appearing to be "only a middling sized *Ophiocoma echinata*." Lütken (1859) described

additional specimens from the Nicobar Islands (see above) which he considered *O. dentata.* Subsequent reports, especially by Lyman (1882) and H. L. Clark (1921), considered Lütken's specimens to represent a species different from that of Müller and Troschel.

The type-specimen of *dentata,* however, reveals characters which not only indicate that Lyman was mistaken in considering it as *O. echinata* but confirms the fact that it belongs in the BREVIPES group of *Ophiocoma* and also supports the conclusion that Müller and Troschel's *dentata* is conspecific with Lyman's (1861) *Ophiocoma insularia* and Smith's (1876) *Ophiocoma variegata.* Of primary importance is the similarity in the nature of the arm spines and their nonalternating sequence. Examination of several of Lyman's syntypes of *insularia* at the Museum of Comparative Zoology, Harvard, and data sent by Ailsa M. Clark on Smith's type of *variegata* substantiate the conspecificity of these species with *dentata.* Furthermore, the species identified as *Ophiocoma ternispina* by Martens (1870) from the Philippines (Flores) cannot, on the basis of its description, be separated from *dentata,* and examination of comparative material from that locality suggests that *ternispina* is synonymous with *dentata.*

The description of *Ophiocoma squamata* (Lamarck) by Müller and Troschel (1842) certainly suggests *dentata.* As Lyman (1874, p. 225) mentioned, however, the type-specimen of *squamata* was lost, so the brief description could be of either *brevipes* or *dentata.*

The variability in the color of the aboral surface occurring in *O. dentata* has, as I have pointed out, resulted in the previous establishment of new species and color varieties. The aboral surface of the disc and arms may be either variegated, with brown and white or dark gray and white, or they may be uniformly brown or gray. Orally, the color is generally lighter brown or gray, seldom white. The very uniformly dark gray variety is typical of the specimens described as *O. insularia* by Lyman. In the Hawaiian Islands and eastern part of the Indo-Pacific many specimens show a uniformly dark gray color as adults, although younger specimens are often variegated aborally. The color forms in which the arms are variegated or marbled brown with gray and white, the disc pattern reticulated and the arm spines, while not annulated, but broadly banded, appear to be more common in the west-central Pacific and in the Indian Ocean.

Specimens identified by Balinsky (1957) as *Ophiocoma insularia* from Inhaca Island, Mozambique, and reexamined by the author are considered to be *O. pusilla* (Brock), as has been proved to be the case in several other instances based on published reports and in museum collection records (see pages 27–28).

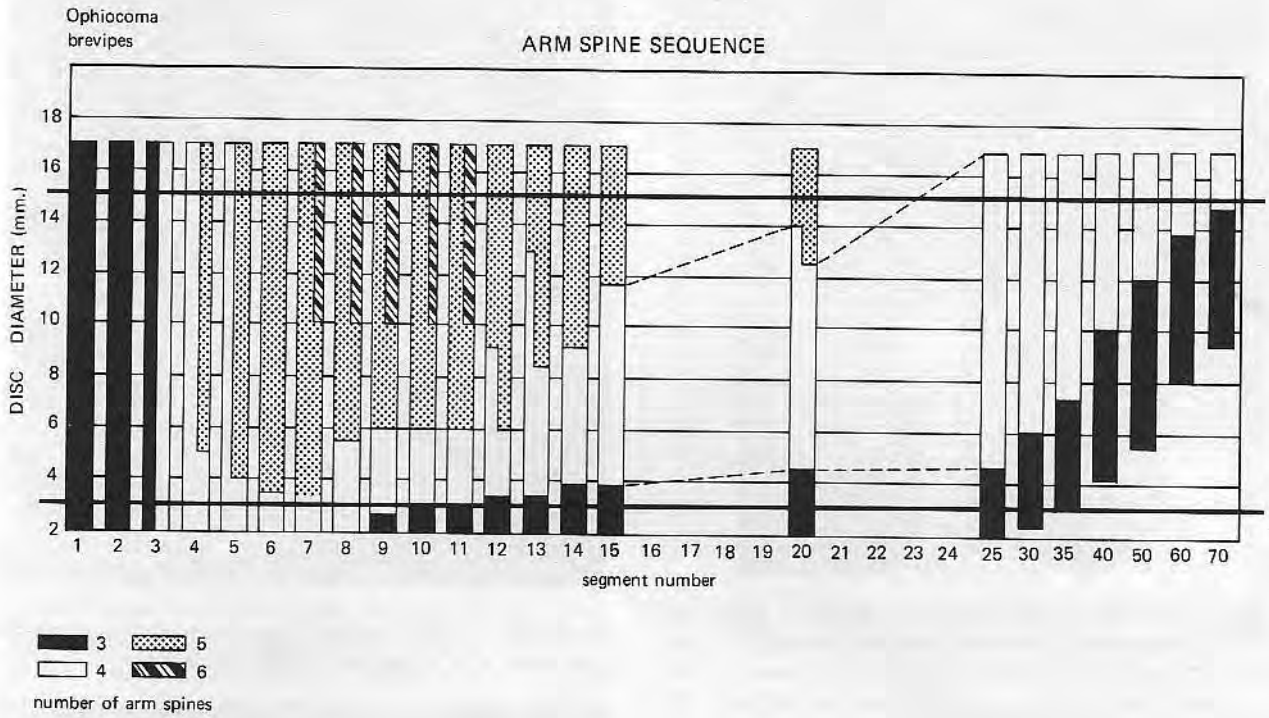
A species syntopic with *O. dentata* and often confused with the latter is *O. brevipes* Peters. H. L. Clark (1938, 1946) was able to distinguish the two species after his earlier (1921) attempts at separation were inconclusive. Ely (1942) also correctly distinguished the two species based on Hawaiian specimens. Lyman (1874) unfortunately had confused the issue when he commented on the type-specimens of *O. brevipes, O. ternispina,* and *O. insularia* (the last two species are now considered *O. dentata*). In reference to *brevipes* he stated, with regard to the number and length of the arm spines, "five spines occur on the first eight joints, and then four, and . . . the upper . . . the longest" (Lyman, 1874, p. 225). My own examination of five of Peter's (1851) syntypes (ZMB 961, 962, 4660) having disc diameters of from 12 to 18 mm showed (a) an arm spine-sequence of 3-3-3-4 for the first four segments with five and/or six spines to segment 10 and then four spines continuing distally well beyond segment 30, and (b) in no case the upper arm spine longest, rather the third spine often the longest in the row. The arm spine sequence for these type-specimens closely parallels that found on specimens from a number of Indo-Pacific localities (see Table 4).

Separation of *brevipes* from *dentata* and *doederleini* can be made by comparing the arm spine sequences for specimens of similar size (see Tables 2 and 4). Equally good as a distinguishing character is the relationship between the maximum arm spine length and the breadth of the upper (aboral) arm plate: in *O. brevipes* the longest arm spine rarely exceeds, and usually is less than, the breadth of the arm plate; in comparison, *O. dentata* and *O. doederleini* have the longest arm spine greatly exceeding the breadth of the upper plate. A third means of separating *O. brevipes* from the other two species is by differences in the pigmentation: *O. brevipes* is nearly all white or light cream colored on the oral surface of arms and mouth plates, whereas the other two species show gray, brown, or variegated coloration on the oral surface.

2. PICA Group

Three species are considered in the PICA group of *Ophiocoma: O. longispina* H. L. Clark, 1917, in south-

TABLE 4.—*Arm spine sequence of* Ophiocoma brevipes



eastern Polynesia (Easter and Pitcairn Islands), and *O. pica* Müller and Troschel, 1842, and *O. pusilla* (Brock, 1888), both in the Indo-Pacific. These three species are known to occur together only at Pitcairn Island.

DIAGNOSIS.—Four to seven arm spines on each side of proximal arm segments beyond disc margin; second or third spine in row longest (Figure 23); spines tapering and elongate. Dental plate 2.3 to 3.0 times longer than broad; dental papillae region occupying one third of total plate length; septa dividing tooth foramina flat and widened in *O. pica* and *O. longispina* but narrow in *O. pusilla* (Figures 24–26). Upper arm

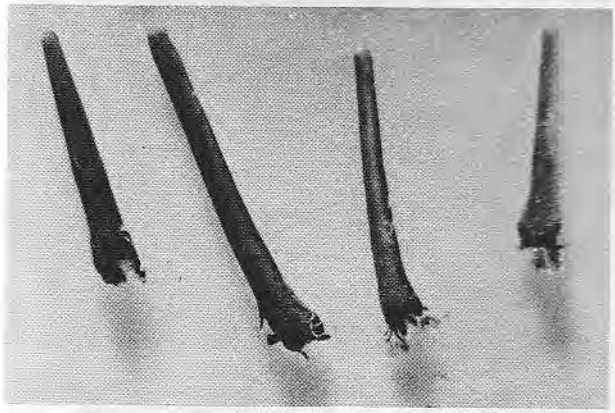


FIGURE 23.—*Ophicoma pica;* arm spines from segment 15 (upper spines at left, lower spines at right).

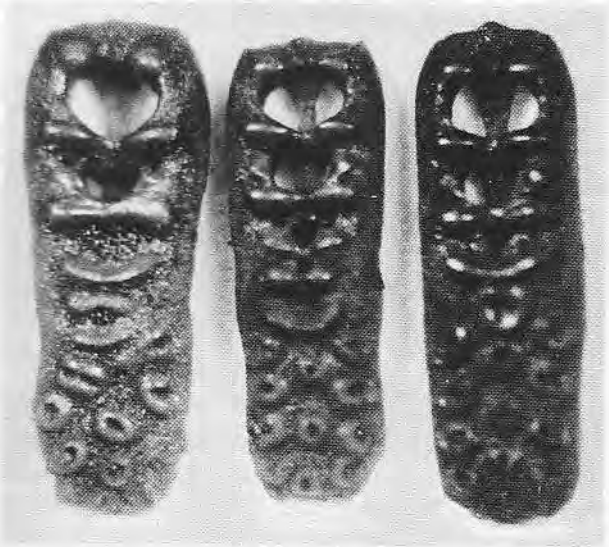


FIGURE 24.—*Ophiocoma pica;* proximal side of three dental plates from different specimens (d.d. 15–19 mm).

plates with convex or median truncated distal edge, narrowing proximally, with even, tapering lateral margins (Figures 27–29). Disc granules small, rounded, uniform in size, closely packed, and extending over part of oral interbrachial region. Two tentacle scales, the outer larger and tapering toward tip.

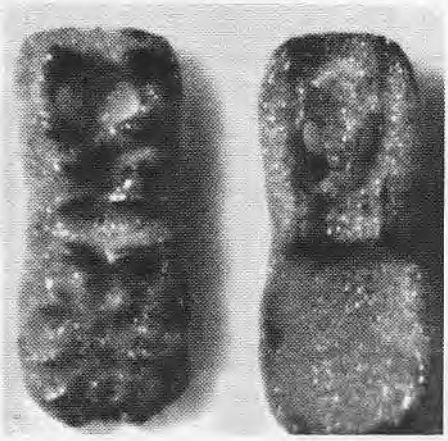


FIGURE 25.—*Ophiocoma longispina;* proximal (left) and distal views of dental plates (d.d. 10 mm).

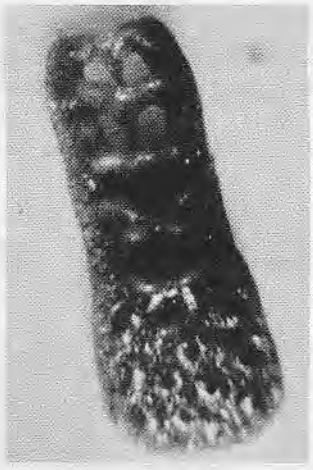


FIGURE 26.—*Ophiocoma pusilla;* proximal side of dental plate (d.d. 7.5 mm).

DISCUSSION.—Similarity in the size and shape of the disc granules, regularity and sequence of the arm spines, number of tentacle scales, length-to-breadth ratio of the oral shields, and shape of the upper and lower arm plates suggest inclusion of the three species in the PICA group of *Ophiocoma.*

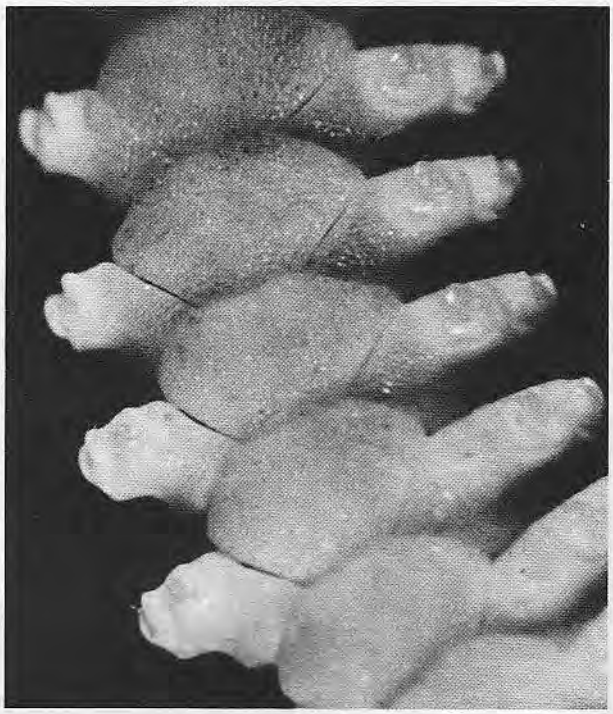


FIGURE 27.—*Ophiocoma pica;* upper arm plates and lateral arm plates with spines removed, including segment 15 (d.d. 19 mm).

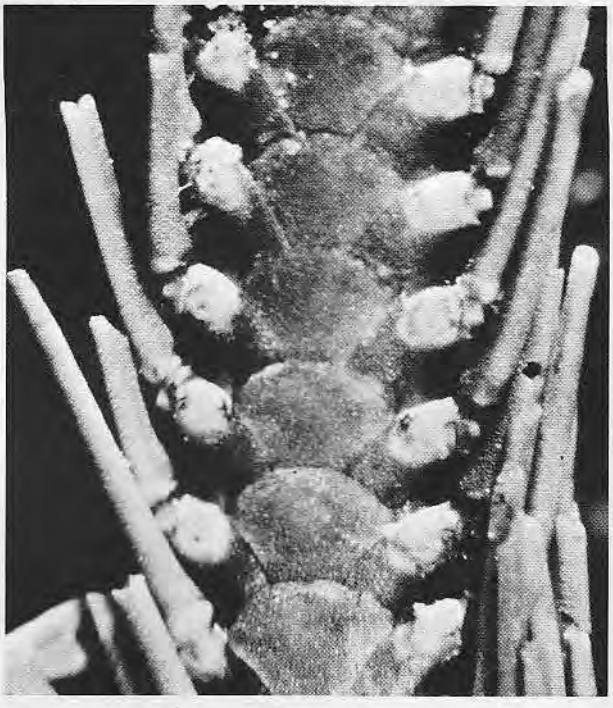


FIGURE 28.—*Ophiocoma longispina;* upper arm plates with some spines attached. Easter Island specimen (d.d. 10 mm).

FIGURE 29.—*Ophiocoma pusilla;* upper arm plates, segments 9–14 (d.d. 6 mm).

Variation in the thickness and length of the arm spines, pigmentation, number of oral papillae, and certain features of the oral and dental plates serve to distinguish the three species.

In contrast to species in the other groups of *Ophiocoma,* those in the PICA group show some differences in the morphological features of the oral and dental plates. The oral and dental plates of *O. longispina* are intermediate between those of *O. pica* and *O. pusilla.* It is evident that *pusilla* shows the greatest divergence from the typical *Ophiocoma* condition in the nature of the oral plate. A comparison of the oral and dental plates of the three species will now be considered.

Oral plate. Murakami (1963, p. 28, pl. VII, figs. 11, 12, 15, 16) described and illustrated this plate for *pica* and *pusilla* (as *latilanxa*). In *pica* the abradial muscle area has well-defined ridges and grooves, and these interrupt or break into the midproximal edge of the muscle surface. In *longispina* these ridges and grooves are reduced, and there is a less-marked interruption of the midproximal edge of the muscle surface (Figure 30). In *pusilla,* unlike any other species of *Ophiocoma,* the ridges and grooves are absent, and the proximal edge of the muscle area curves inward but is uninterrupted.

FIGURE 30.—*Ophiocoma longispina;* abradial surface of oral plate (d.d. 9 mm).

In addition to the abradial surface, Murakami also noted that the oral plate of *pica* was "higher than long" while that of *pusilla* (as *latilanxa*) was "rather low and about as long as high." Murakami's "length" was measured along the oral-aboral axis of the plate, and his "height" was measured along the distal-proximal axis. The oral plate of *longispina* is about as high as long (Figure 30). The adradial muscle scar was described by Murakami (1963) for *pica* as "very narrow and somewhat J-shaped," while that of *pusilla* (as *latilanxa*) was "narrow and elongate S-shaped." The adradial muscle of *longispina* resembles *pica* in having the oral part curved to almost form a J-shape (Figure 31).

Dental plate. Murakami (1963, pp. 26–27, pl. III, figs. 2, 3) described and illustrated this plate for *pica* and *pusilla* (as *latilanxa*). The dental plate of *pica* was said to be "two and a half times as long as broad somewhat slipper-shaped as that of *O. latilanxa.*" Further examination of the dental plate for both

Key to Species

1. Arm spines very fragile, hollow; 3 (seldom 4) oral papillae on each jaw angle..... ***O. pusilla***
   Arm spines not fragile, solid; 4 (sometimes 5) oral papillae on each jaw angle.....2
2. Disc variegated with yellowish lines and yellow spot on each side of arm base of disc; lower arm plates lighter along distal edge..... ***O. pica***
   Disc uniformly blackish; lower arm plates near disc uniformly dark..... ***O. longispina***

species shows that the expanded oral portion of the dental plate of *pica* is not characteristic as Murakami indicated; rather, this portion of the plate is usually straight or tapering inward (Figure 24). Further, there is a difference in the nature of the septa dividing the teeth foramina: in *pica*, the septa are flattened and wide, while in *pusilla* they are narrow and compressed (Figures 24, 26). The dental plate of *longispina* has the same septal characteristics as that of *pica* but shows the evident expanded oral portion (Figure 25) similar to *pusilla*.

In thickness, the arm spines of *longispina* appear to be intermediate between those of *pica* and *pusilla*. They are not nearly as robust as those of *pica*, and they show a small lumen, in contrast to the nearly solid spines of *pica* and the very hollow spines of *pusilla*.

With the exception of *pica* we know nothing about the larvae of this group. Mortensen (1937) did show that the larval skeleton of *pica* (as *lineolata*) differs significantly from other members of the Ophiocominae (*Ophiocomina nigra, Ophiocoma echinata, O. erinaceus,* and *O. scolopendrina*). More recently, it has been found to differ from that of *Ophiocoma pumila* as well.

SPECIES EVALUATION.—Because of the taxonomic changes necessitated in review of the PICA group, rather detailed species evaluations are presented for *Ophiocoma longispina* and *O. pusilla*. A clarification of the taxonomy of these two species is presented below.

Ophiocoma longispina H. L. Clark

Ophiocoma insularia var. *longispina* H. L. Clark, 1917, p. 441.

Ophiocoma brevipes var. *longispina* H. L. Clark, 1921, p. 131.

Ophiocoma insularia longispina H. L. Clark: Downey, 1969, p. 104.

MATERIAL EXAMINED.—Easter Island: USNM E647 (type, Shore, 21 December 1904, *Albatross* collection); BPBM, no numbers (3: two specimens from west coast, between Hanga Roa and Hanga Piko, tidepool, 0–2 feet, 25 January 1969, and a specimen having no specified locality, both collected by J. E. Randall). Pitcairn Island: BPBM, no number (1, Sta. PIT VIII, off south coast, coral bottom, 20–25 fathoms, dredge haul 4, 20 October 1967, collected by D. M. Devaney).

DIAGNOSIS (based on specimens having disc diameters of 9–12 mm).—Arm spines long, tapering; sequence: 3-3-4-4(or 5)-4(or 5)-5-5-5-5-5, and four spines as far as segments 29 or 32, decreasing to three spines on distal segments. Upper arm spines longest, 4 to 6 mm, equal to length of four segments (Figure 32). Arm four to five times disc diameter in length. Disc granules small, rounded, closely packed, covering radial shields and extending some distance into interradial region. Upper arm plates broadly rounded and widest distally, inwardly tapering proximally, fan-shaped, slightly broader than long in proximal part of arm, becoming longer than broad on distal segments (Figure 28). Lower arm plates in proximal part of arm broader than long, distal border rounded medially (although sometimes with slight central concavity) with moderately acute lateral edges and incurved sides directed toward proximal edge (Figure 35). Tentacle scales two, of about equal length, outer widest, both tapering toward tip (Figure 35). Oral shields longer than broad, ovate. Adoral shields triangular, with widest angle proximally directed (Figure 33). Usually four oral papillae, outer broadest, overlying part of buccal tentacle scale (Figure 33). One to four additional papillae above (oral to) jaw apex. Five to ten dental papillae. Teeth, three or four each jaw, narrow with hylinated tips. Dental plate 2.4 to 2.9 times longer than broad; septa dividing teeth foramina wide and flat; dental papillae region widened, occupying about one third of total length (Figures 25, 34). Oral plates (jaws): abradial muscle surface with evidence of shallow ridges and grooves, outer margin interrupted (Figure 30); adradial muscle surface J-shaped (Figure 31). Pigmentation: blackish-brown in alcohol, only slightly darker above than below; borders of oral shields and dental and oral papillae whitish.

Size range examined: disc diameter, 9 to 14 mm; arm length, 45 to 60 mm.

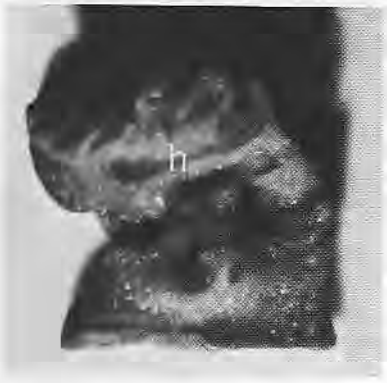


FIGURE 31.—*Ophiocoma longispina;* adradial surface of oral plate (d.d. 9 mm). *h,* Adradial muscle scar.

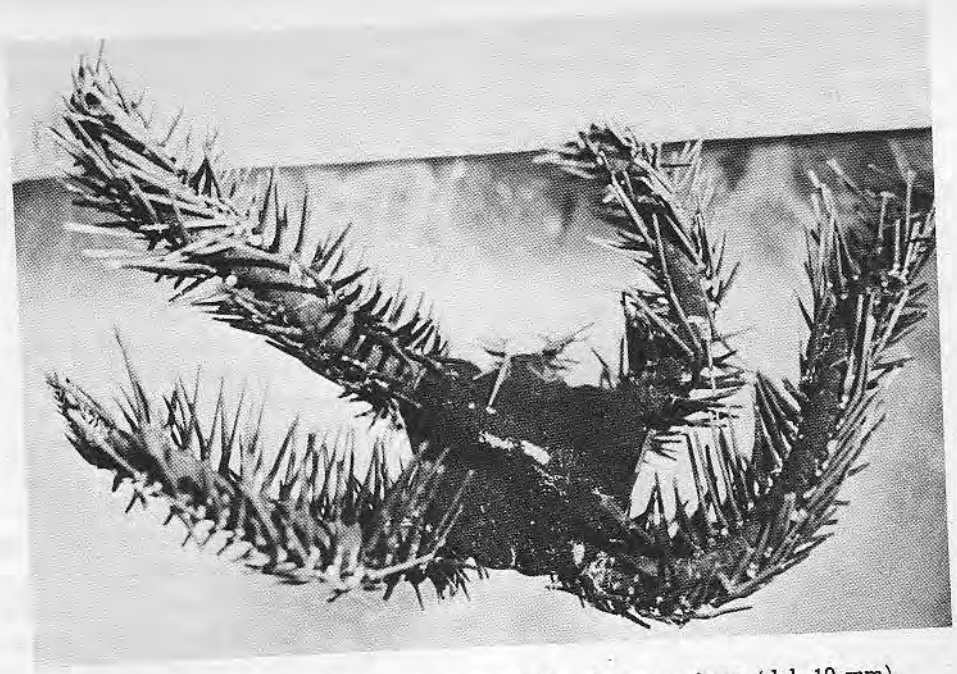


FIGURE 32.—*Ophiocoma longispina;* aboral side of type-specimen (d.d. 10 mm).

FIGURE 33.—*Ophiocoma longispina;* oral mouth sectors of type-specimen (d.d. 10 mm).

DISCUSSION.—The original description of this species by H. L. Clark (1917) was based on a single specimen collected at Easter Island. Clark was unsure of the status of this ophiuroid. He correctly noted several differences from specimens of *O. insularia* (=*dentata*) also collected at Easter Island but he provisionally left the specimen as a variety (*longispina*) of that species. Later, Clark (1921) again mentioned this form, but he added no further information, having only transferred *O. insularia* to *O. brevipes* and making *longispina* a variety of the latter. Recently, Downey (1969) listed *Ophiocoma insularia longispina* H. L. Clark in her type catalog.

Failure to recognize the specific taxonomic position of *longispina* was corrected when additional specimens were made available to the author by Dr. J. E. Randall, who visited Easter Island in January and February 1969. Three specimens of *longispina* collected syntopically with six specimens of *O. dentata* allowed further comparison of the two species and, most importantly, made examination of internal characters possible. This provided convincing evidence for the recognition of *longispina* as a separate species and led to its recognition from Pitcairn Island.

The additional specimens show that *longispina* can be distinguished from *dentata* (with which it was originally allied) in the following ways:

(1) Greater length of the arm spines (suggested by H. L. Clark, 1917).

(2) Different sequence of arm spines: *longispina* has four spines on segment 3 and five or four spines on segment 4; *dentata* has only three spines on segment 3 and four spines on segment 4. Also, *longispina* has a greater number of segments with four spines than *dentata,* even when specimens of the latter species are larger. For example, four specimens of *longispina* from Easter Island (including the type), with disc diameters of from 9 to 14 mm, had four spines as far as segments 29 to 35. Four specimens of *dentata* from the same locality, with disc diameters 13 to 23 mm, had four arm spines only as far as segments 18 to 24.

FIGURE 34.—*Ophiocoma longispina* (left) and *O. dentata;* proximal side of dental plates, both from specimens collected at Easter Island (d.d. 10 mm).

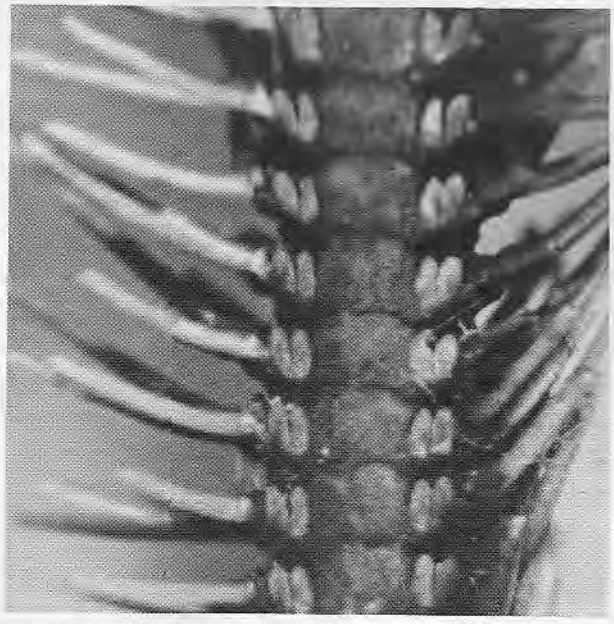


FIGURE 35.—*Ophiocoma longispina;* oral arm plates, tentacle scales, and arm spines (d.d. 12 mm).

(3) Difference in shape of the arm spines: *longispina* with more-elongate, tapering spines (Figure 32), in contrast to the broader, stubby, more truncated spines of *dentata* (Figures 17, 18).

(4) Disc granulation: *longispina* with portions of the oral interradial region free of granules, whereas there is nearly complete granulation of this region in *dentata* (and in all species in the BREVIPES group). In both species the granules are approximately the same size but they appear less closely packed in *longispina.*

(5) Differences in the size and shape of the dental plates (Figure 34): length-to-breadth ratio and area occupied by the dental papillae are greater for *longispina* than for *dentata.*

(6) Differences in shape of upper arm plate: *longispina* with more angular lateral margins (Figure 28), compared to the broadly rounded lateral margins of *dentata* (Figure 17).

(7) Difference in shape of the oral shields: in *longispina* the oral shields are relatively longer than broad, compared to the more rounded ones of *dentata.*

Several characters separate *longispina* from its apparently closest relative, *O. pica.* Pigmentation provides a convenient way to distinguish the two species. For *pica* there is a yellowish spot at either side of the arm base on the disc. Usually there are also radiating lines of yellow on the dark-brown background of the disc, normally there is a considerable amount of yellow on the proximal parts of the lower arm plates near the disc, and there also is yellow on the peripheral sides of the oral and adoral shields. In contrast, *O. longispina* is uniformly dark blackish brown. Morphologically, *longispina* has a greater portion of the oral interradial region of the disc granulated, and the relative length of the arm spines is greater than for *pica.* Furthermore, on *longispina* the two tentacle scales are the same length (Figure 35), whereas on *pica* the inner scale is narrower and longer than the outer one. Differences in the oral and dental plates of the two species have been discussed above.

Ophiocoma pica Müller and Troschel

Ophiocoma pica Müller and Troschel, 1842, p. 101.—Loriol, 1894, p. 28 (with a complete bibliography to that date).—H. L. Clark, 1915, p. 293; 1921, p. 127, pl. 13, fig. 8 (color); *1938, p. 333; 1946, p. 244.—Ely, 1942,* p. *54,* figs. 15a,b, pl. 12b.—A. H. Clark, 1949, p. 51.—A. M. Clark, 1952, p. 207; 1967, pp. 47, 55.—Balinsky, 1957, pp. 26, 31.

Ophiocoma lineolata Müller and Troschel, 1842, p. 102.—Loriol, 1894, p. 28 (with a complete bibliography to that date).—Koehler, 1922, p. 324, pl. 73, figs. 1–4.—Mortensen, 1937, pp. 51–52, fig. 41 (larval skeleton), pl. 8, figs. 1–3 (larva).—Boone, 1938, p. 148, pl. 52.—Tortonese, 1953, p. 33.

Ophiocoma sannio Lyman, 1861, p. 81; 1865, p. 91.

DIAGNOSIS.—The external features of *O. pica* have been adequately described by several authors. Two works which may be consulted are those of Lyman (1865) and Ely (1942). Additional comments referring to the internal morphology of this species have been presented in this paper in the discussion of the PICA group, and characters separating *pica* from *longispina* have been given.

DISCUSSION.—This species, which is widely distributed throughout the Indo-Pacific (H. L. Clark, 1921), appears to be primarily a coral dwelling form. In the Hawaiian Islands, Johnston Island, the Tuamotus, and Pitcairn Island, I found it most commonly between the branches of the scleractinian coral *Pocillipora meandrina* var. *nobilis.* I did not find *Ophiocoma pica* at the Marquesan Islands in 1967, and found no evidence of *Pocillopora meandrina* there; however, at the northern Tuamotu Islands of Takaroa and Manihi, near the Marquesas, I found *O. pica* within the branches of *P. meandrina.* Additional specimens were collected from this same coral species at Pitcairn Island. A. H. Clark (1952) reported the species from the coral *Stylophora mardax* at Rongerik Atoll, Marshall Islands. My own collecting of *O. pica* indicates that small specimens, especially, are most common in the coral habitat. Specimens less than 15 mm (d.d.) were found in *Pocillopora,* but larger specimens occasionally were found under rock or dead coral rubble as well as in living coral.

One still finds modern descriptions of *Ophiocoma pica* under the name *O. lineolata* Desjardins, even though the conspecific nature of the two species was recognized by Lyman (1865) after examination of the two type specimens and after unanimous agreement that the two species were synonymous. The continued use of the name *O. lineolata* (although appropriately descriptive) is unacceptable since Müller and Troschel were the first to publish and describe both species in 1842, and Lyman clearly established *pica* as the nominal species.

Ophiocoma pusilla (Brock)

Ophiomastix pusilla Brock, 1888, p. 499 (Amboina).—Pfeffer, 1900, p. 85 (Ternate, no other data).—Koehler, 1905, p. 65, pl. 6, figs. 9, 10, pl. 13, fig. 3 (Moluccas).—Ailsa M. Clark, 1967, p. 45, fig. 5 (Red Sea, Aqaba).

Ophiocoma pusilla (Brock).—H. L. Clark, 1921, p. 131.

Ophiocoma latilanxa Murakami, 1943a, p. 194, fig. 13 (Palao); 1943b, p. 217 (Ryukyu).

Ophiocoma sp.—Ailsa M. Clark, 1952, p. 208 (Red Sea).

Ophiocoma insularia Lyman.—Balinsky, 1957, p. 26 (Mozambique).

Ophiocoma insularia var. *variegata* Smith.—H. L. Clark, 1938, p. 330 (part, Lord Howe Island).

Ophiocoma scolopendrina (Lamarck).—H. L. Clark, 1921, pl. 13, fig. 9 (color) (Torres Strait).

STATUS OF TYPE MATERIAL.—In the original description of *Ophiomastix pusilla,* Brock gave the size of his largest individual as 8 mm (d.d.), with a disc-diameter-to-arm-length ratio of 1:5. Aside from this, there was no indication that a specific individual was being described nor was there any type designation. Brock mentioned only, "wurde von mir in zahlreichen Exemplaren in Amboina erbeutet" (Brock, 1888, p. 500).

Dr. P. Kuenzer at the Göttingen Museum informed me that Brock's original specimens deposited there were destroyed in World War II. Apparently, however, two specimens from Brock's original series were transferred to the Zoologisches Museum Berlin prior to that time. These specimens have been examined and, although smaller than Brock's largest specimen, they are considered part of the syntypic series. The fact that the two specimens differ slightly in certain external characters (with one showing more evidently the characters originally presented by Brock) leads me to designate a lectotype in this paper. Some of the more important features and variations of the two specimens are given below in the description of the species.

LECTOTYPE.—ZMB 5429 (Marine Tiergruppen); disc diameter, 4 mm. Label with specimen: "*Ophiomastix pusilla,* Amboina 5429 Brock. Type."

PARALECTOTYPE: ZMB 4777 (Marine Tiergruppen); disc diameter, 3.5 mm.

DIAGNOSIS—Disc diameter up to 10 mm; sexually mature specimens from 6 mm (Eniwetok, September

1966). Small, uniformly distributed granules entering oral interradial area but not reaching oral shields and leaving an area near genital openings with exposed scales (paralectotype with several widely spaced spiniform granules among normal granules near edge of disc aborally). Two tentacle scales each side of proximal arm segments (lectotype with two scales to segment 22; larger specimen, d.d. 7.5 mm, with two scales to segment 40); outer scale largest. Arm spines typically long, tapering, fragile, and *hollow* (lumen of spine greater than thickness of spine wall) also not smooth; occasional thickening of one to three adjacent, next to uppermost arm spines occurring from segments 8 to 12; enlargement of outer part of these spines also combined with increased length of these modified spines, in alcohol appearing as a gelatinous epithelial envelope around spine (lectotype with enlarged spines only on one side of 10th segment of three arms; paralectotype without enlarged spines). Arm spine sequence for 7-mm specimen: 3-3-4-4(or 5)-5(or 4)-5(or 6)-5(rarely 6)-5-5-5 for the proximal ten segments; beyond segment 6, development of fifth arm spine on more segments with size increase to segment 20 (lectotype with five spines to segment 8); distally, number of spines 4 then, near arm tip, 3. Oral papillae 3, less often 4, outer papilla broadest, its outer margin overlapping inner edge of buccal tentacle scale. Dental papillae in two and three rows, marginal papillae slightly larger than medial ones; from 6 to 15 papillae depending on size (lectotype with 6–8 in two rows). One to four granular papillae above (oral to) apex of each jaw. Dental plate (Figure 26) with widened lower portion, narrow septa dividing teeth foramina; length-to-width ratio, 2.3–2.7 : 1. Teeth 3 or 4; oralmost shortest and narrow, second and third longer and narrow; tips of teeth hylinated. Oral shields longer than wide; length-to-width ratio, 1.2 to 1.7 : 1 (lectotype, 1.3 : 1; in no case were these plates noted to be twice as long as broad, as originally indicated by Brock). Adoral shields widely separated, triangular, outer edge in contact with ventral shield; limited to sides of mouth shields. Oral plate (jaw) lacking ridges and grooves on abradial muscle surface (see Murakami, 1963, pl. VII, fig. 11). Upper arm plates with margin broadly arched distally and tapering sharply proximally (Figure 29). Lower arm plates with convex distal margin, tapering proximally. Arms banded in most cases, dark brown and lighter yellowish or white; dark aboral arm plates often with various mottled pattern, or uniform tan to black; oral surface of arms lighter than aboral surface. Disc spotted, reticulated, or solid color (brown or gray), usually with white spot on either side of each arm base; periphery of disc sometimes gray with median white area and a dark gray spot centrally located (lectotype with tan disc and lighter ambital area).

DISCUSSION.—Brock (1888) originally characterized *pusilla* as having club-shaped or claviform arm spines. Unlike any other species of *Ophiomastix,* however, these arm spines occurred on the second rather than the uppermost spine and only on a few adjacent segments in the proximal region of the arm. *Ophiomastix pusilla* was considered different from other species in the genus not only by the number, position, and shape of its club-shaped spines but by its color, small size, and presence of fine disc granules without disc spinules. The combination of the fine, even covering of granules and the transformed second row of arm spines into clubs led Brock (1888) to consider *Ophiomastix pusilla* as an aberrant species, possibly to be placed in a separate genus.

Koehler (1905) reported two specimens from the Siboga Expedition in the Dutch East Indies (Indonesia) which he compared with one of Brock's original specimens. Koehler's largest specimen, with a disc diameter of only 5 mm (compared with Brock's largest, 8 mm), showed only a partial development of the club-shaped arm spines from the second row. It was concluded that this characteristic was perhaps a reflection of the smaller size of the specimen, especially since Koehler's smallest specimen revealed no trace of claviform spines. In other respects the specimens were essentially the same as those described by Brock.

H. L. Clark (1921) transferred the species to *Ophiocoma* on the basis that granules rather than spinules on the disc outweighed the presence of clavate arm spines as a generic character. He was inclined to believe the species might be the young of some larger and as yet unknown *Ophiocoma.* Unknowingly, he gave a color figure of *pusilla*—which was called *Ophiocoma scolopendrina* juv. (H. L. Clark, 1921, pl. 13, fig. 9)—wherein the limited presence and position of the swollen arm spines are clearly indicated.[2] This dry speci-

[2] A reexamination of one of the specimens (MCZ 3766; d.d. 6.5 mm) confirmed the identity as *O. pusilla.* According to one label, this specimen, collected at Mer Island, Torres Strait, was drawn by a Mr. Gross. Other labels read: "Ophiocoma scolopendrina? juv." and "May be young erinaceus."

men shows the enlarged, next to uppermost arm spines on the tenth segment of only two rays in contrast to Clark's figure, which shows these spines on each side of one segment of each ray.

The known distributional range of *Ophiocoma pusilla* was expanded when A. M. Clark (1967) reported several specimens from the Red Sea and Gulf of Aqaba. She continued to use the generic name *Ophiomastix,* noting that several other species of *Ophiomastix* had a continuous coat of granules with spinelets intermingled. The typical absence of spinelets, however, is unknown in any species of *Ophiomastix. Ophiocoma pusilla* also was compared with *O. brevipes,* and similarity was noted in color pattern and extension of the fine disc granules to the oral side of the disc. Considerable variation was found in the number and, to a lesser degree, in the position of the club-shaped spines. These modified spines were observed from the eighth to twelfth segments, usually on two or three consecutive segments. In contrast to Koehler's (1905) conclusion noted above, Miss Clark found the clavate spines less conspicuous in the larger (d.d. 7 mm) than in the smaller specimens at her disposal.

Murakami (1943a) erected the species *Ophiocoma latilanxa* from Palau Islands in the western Pacific; and he reported additional specimens from Yaeyama Island in the Ryukyu Group (Murakami, 1943b). The type was described as small (d.d. 6.5 mm) and covered with fine, dense granules which did not reach the oral shield ventrally. The arm spines were slender with the upper one or two quite long. No mention was made concerning a thickening of the spines. *Ophiocoma latilanxa* was considered most closely related to *O. lubrica* Koehler, 1898. It was distinguished from *O. lubrica,* however, by having broad pentagonal lower arm plates, more numerous dental papillae, and a differently shaped oral shield. It should also be noted that in Koehler's (1898) description of *O. lubrica,* the arm spines were four in number, cylindrical, thick, and blunt at the tip; in these respects they differed from the spines of *O. latilanxa* as Murakami described them. Although H. L. Clark (1921) considered *O. lubrica* as a synonym for *O. scolopendrina,* the status of *O. lubrica* awaits clarification by examination of the type-specimens, deposited in Calcutta.

The description of *Ophiocoma latilanxa* did not suggest relationship to *Ophiocoma pusilla,* primarily because of the emphasis on the modified club-shaped spines attributed to the latter species and of their absence in the former. Several new lines of evidence, however, have suggested reconsideration, and the likelihood that the two species are conspecific.

First, several brittlestars described (by Balinsky, 1957) as *Ophiocoma insularia* from Inhaca Island, Mozambique, were made available to me. On examination, however, the specimens proved not to be *O. insularia.* Differences in the shape, size, and sequence of arm spines, the nature of the dental and oral plates, and the number of dental papillae indicated that the specimens were quite distinct from any species in the BREVIPES group of *Ophiocoma.* The specimens were small, with a disc diameter less than 10 mm. One specimen had peculiar dark circles, each of which was surrounded by a lighter ring. This color pattern was noted by Balinsky, and it led him to compare his specimens with *Ophiocoma delicata* described by H. L. Clark (1932). At my request, Ailsa M. Clark kindly examined the type specimen of *O. delicata,* deposited in the British Museum, and reported that the specimen represented a species of *Ophiarachna* near *mauritiensis* (family Ophiodermatidae). My own examination of a paratype of *Ophiocoma delicata* deposited in the Museum of Comparative Zoology, Harvard, agreed with her determination. She suggested that Balinsky's specimens (as *Ophiocoma insularia*) might be the same species as a small specimen which she described as *Ophiocoma* sp. from the Red Sea (A. M. Clark, 1952) and which she later united with additional material from the Gulf of Aqaba as *Ophiomastix pusilla* (A. M. Clark, 1967).

Second, in another collection of small ophiuroids from Eniwetok atoll, Marshall Islands, I found specimens similar to those from Inhaca Island. The fact that the Eniwetok specimens were sexually mature removed doubts that they were juvenile forms of some larger species.

The relationship between both the Eniwetok and Inhaca Island specimens and Murakami's *Ophiocoma latilanxa* finally became apparent after a comparison of the dental and oral plates. Murakami's (1963) description and figures of these plates for *O. latilanxa* coincided remarkably well with those dissected from the Eniwetok and Inhaca Island specimens.

A careful examination of the Inhaca Island specimens revealed the presence of several thickened arm spines in one specimen. Instead of the presence of the swollen clavate spines on the next to uppermost arm

spine, the enlarged spines were located on the third or even fourth spine in a row. The thickened arm spines appeared irregularly on one or both sides of two or three segments on three arms only. The other three larger and smaller specimens from Inhaca Island lacked the swollen spines. Eniwetok specimens (four) also had no modified arm spines. Examination of three specimens (USNM E8620) labeled *Ophiocoma brevipes* var. *variegata,* from Yap Island (Caroline Islands), and identical with Eniwetok material of *O. pusilla* showed the modified arm spines on only two arms of one specimen.

Additional specimens (in MCZ) identified as *Ophiocoma insularia* var. *variegata* by H. L. Clark proved, on examination, to be *O. pusilla*. These specimens are from Green Island on the Great Barrier Reef (MCZ 3754, 1 specimen), Lord Howe Island (MCZ 5227, 1 specimen; 5229, 4 specimens),[3] and Port Galera, Mindoro, in the Philippine Islands (MCZ 4002, 1 specimen).

Final verification of the taxonomy of *O. pusilla* came when two of Brock's original specimens of *Ophiomastix pusilla* from Amboina and deposited in the Zoologisches Museum Berlin were made available through the kindness of Dr. Gruner. These specimens left no doubt that the specimens from Inhaca Island, Eniwetok, and other localities mentioned above were conspecific with Brock's species. Unfortunately, attempts to examine Murakami's type specimens of *Ophiocoma latilanxa* have been unsuccessful and correspondence with Dr. Kikuchi of the Amakusa Marine Biological Laboratory in Japan indicated that the type specimens are lost.

Recent collections by the author reveal the presence of *Ophiocoma pusilla* in several southeastern Polynesian localities, including Anaa, Manihi, and Puka Puka Atolls in the Tuamotu group, and Pitcairn Island. A specimen also was collected by Dr. John E. Randall at Marcus Island in the north-central Pacific Ocean. These specimens as well as those from Inhaca Island and Eniwetok are, for the most part, deposited in the collections of the Bernice P. Bishop Museum, Honolulu.

The retention of *pusilla* in the genus *Ophiomastix* on the basis of the peculiar thickening of a few arm spines is considered unwarranted in view of the differences in the sequence of the arm spines (in *Ophiomastix,* but not in *pusilla,* there is an irregular alternation of arm spines similar to that noted for the SCOLOPENDRINA group of *Ophiocoma*) and typical lack of disc spinules in *pusilla*. This species, while showing several peculiar features, is best considered as a member of the PICA group of *Ophiocoma*. The relationship of *O. pusilla* with other species in the PICA group has been discussed above.

HABITAT.—Brock (1888) gave no particular information on the habitat or depth at which his specimens of *pusilla* were collected at Amboina. In his ecological notes, Balinsky (1957, pp. 30–31) recorded some of the major biotopes in which ophiuroids were found at Inhaca Island, Mozambique. He reported *Ophiocoma pusilla* (as *O. insularia*) from a coral reef environment "in the infralittoral fringe," where it was listed among the less-common and rare species. Further on, this species also was reported as common in another "more tropical" reef area (Ponta Torres Reef) where the base of the reef was very shallow. Dr. Balinsky has informed me that this species favored dead coral heads. The fragile nature of the arm spines and the fact that a barnacle was found on one of the oral arm plates suggest that the species avoids contact with a coarse particulate substratum where repeated abrasion might occur. Specimens from Eniwetok were collected from relatively quiet water and were extracted from broken pieces of coral at depths of from five to ten feet. Tuamotu specimens were collected from live and dead coral heads, usually at the base of the broken coral. Specimens from Pitcairn Island were dredged, with broken coral, from 20 to 58 fathoms. As Koehler (1905) suggested, a Siboga station depth record of 701 meters for this species probably is a mistake. It appears that *Ophiocoma pusilla* is confined to the shallow sublittoral zone within a coral substratum.

3. PUMILA Group

The PUMILA group of *Ophiocoma* is represented by three species: *O. alexandri* Lyman, 1860, in the tropical eastern Pacific; *O. pumila* Lütken, 1856, in the tropical West Indies and tropical West Africa; and *O. valenciae* Müller and Troschel, 1842, in tropical East Africa and the western Indian Ocean.[4]

[3] These specimens are among those designated by H. L. Clark (1938, 1946) as *Ophiocoma insularia* var. *variegata* forma *dentata*).

[4] Martens (1870, p. 250) listed *O. valenciae* from collections made at Fiji and Samoa in the Indo-Pacific, but this listing is assumed to be based on erroneous data or species identification. Pacific records require verification.

Ophiocoma alexandri has been reported from Baja California (Santa Maria Bay) and the Revillagidedo Islands to Ecuador and the Galapagos Islands. *O. pumila* shows a wide distribution from insular and mainland regions of the Caribbean, north to Bermuda and south to Brazil, and off the west African coast (Azores, Gulf of Guinea, Cape Verde Islands). *O. valenciae* is known from the east coast of Africa to Durban in the south, up into the Red Sea, and from several localities in the Indian Ocean. With few exceptions, none of the species has been reported from depths exceeding 25 meters.

DIAGNOSIS.—Four to seven arm spines on each side of proximal arm segments beyond disc margin; second or third arm spine longer than uppermost (Figure 36). Dental plate 2.4 to 2.8 times as long as broad, with a narrow vertical septum dividing each tooth foramen and dental papillae region occupying approximately 30 percent of the total plate length (Figures 37–39). Upper (aboral) arm plates oval, contiguous along distal edge of following plate from 25 percent to (rarely) 50 percent of maximum breadth of plate (Figures 40, 41). Disc with rounded granules and more-elongate, squat, spiniform granules interspersed and not tightly packed (Figure 42), fewer extending orally nearly to mouth shield and genital apertures. Two tentacle scales on only a few proximal segments, followed by a single scale on more distal segments.

Key to Species

1. Five arm spines seldom beyond segment 10 (d.d. over 6 mm) ..... ***O. pumila***
   Five arm spines continuing beyond segment 10 (d.d. over 6 mm) 2
2. Light-colored stripe along middle of oral arm plates ..... ***O. alexandri***
   No light-colored stripe along middle of oral arm plates ..... ***O. valenciae***

DISCUSSION.—The three species in the PUMILA group are typically pentamerous. According to H. L. Clark (1921, 1946) the young of *Ophiocoma alexandri* and *O. pumila* were thought to exist as both five- and six-armed individuals in their smaller sizes. Morphological criteria established by A. H. Clark (1939), Ailsa M. Clark (in Parslow and Clark, 1963), and the present investigator strongly suggest, however, that the small hexamerous ophiocomids should be separated and placed in the genus *Ophiocomella*. A significant point to be made here is that recent study indicates that *Ophiocomella* exists in the hexamerous or pentamerous (rarely seven arms) form with the six-armed form most common. Owing to the small size of ophiocomellids, external features relatively similar to small specimens of the PUMILA group of *Ophiocoma*, and the failure to recognize the existence of pentamerous individuals of *Ophiocomella*, there has been some confusion as to their taxonomic position.

Although a more complete discussion of the systematics and re-evaluation of the genus *Ophiocomella* will be forthcoming, several morphological features

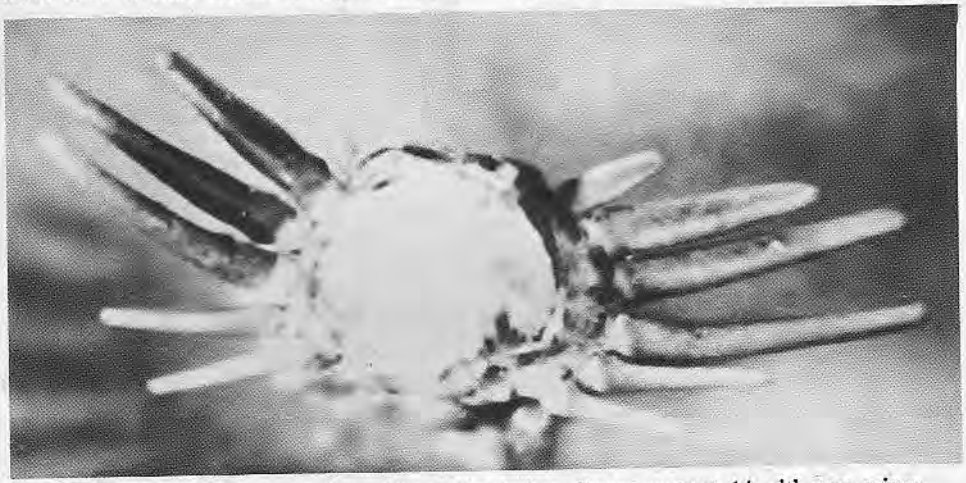


FIGURE 36.—*Ophiocoma alexandri;* proximal view of arm segment 14 with arm spines (d.d. 18 mm).

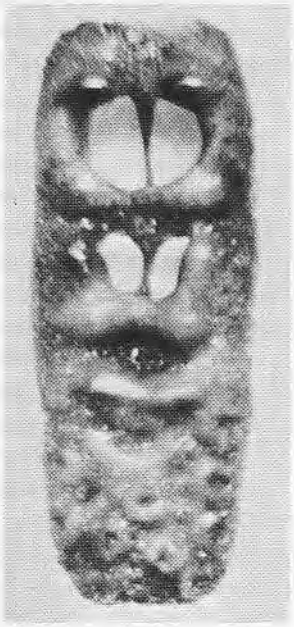


FIGURE 37.—*Ophiocoma pumila;* proximal side of dental plate (d.d. 12 mm).

FIGURE 39.—*Ophiocoma valenciae;* proximal side of dental plate, broken (d.d. 13 mm).

FIGURE 38.—*Ophiocoma alexandri;* proximal side of dental plate (d.d. 13 mm).

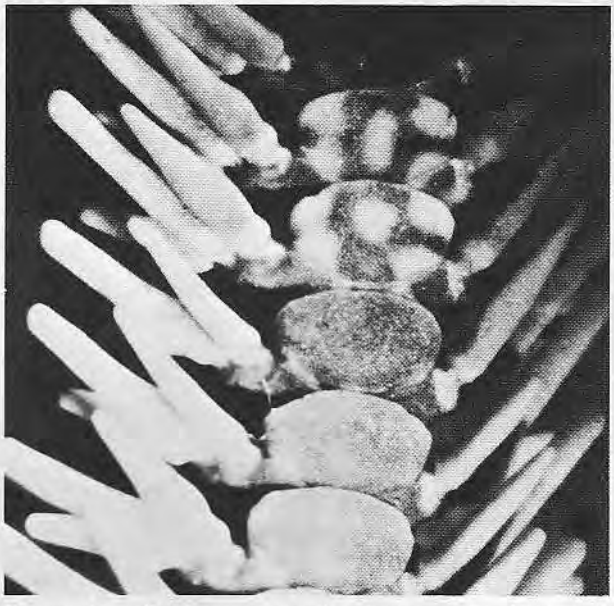


FIGURE 40.—*Ophiocoma pumila;* upper arm plates and spines, from segments 12–17 (d.d. 13 mm).

have been found which serve to differentiate that genus from those species in the PUMILA group of *Ophiocoma.*

First, with few exceptions, *Ophiocomella* is characterized by an arm spine sequence of 2 or 2 and 3-3-3 or 3 and 4 for the proximal three segments. In a few cases the pattern 3-3-3 and 4 or 2 and 3-3-4 has been observed. In contrast, the three species of *Ophiocoma* in the PUMILA group quite consistently show a sequence of 3-3-4 regardless of the size of the specimen.

Second, the oral plate (jaw) reveals a significant difference in the two genera: for *Ophiocomella* there

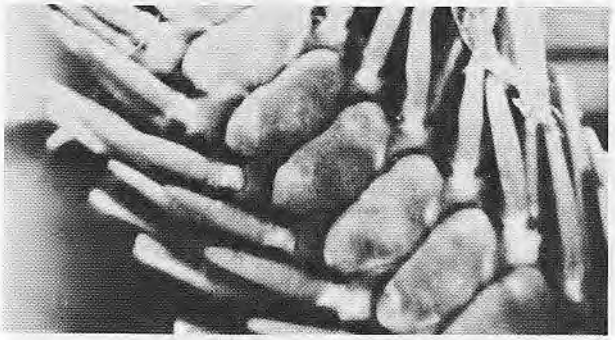


FIGURE 41.—*Ophiocoma alexandri;* upper arm plates and spines, from segments 15–20 (d.d. 17 mm).

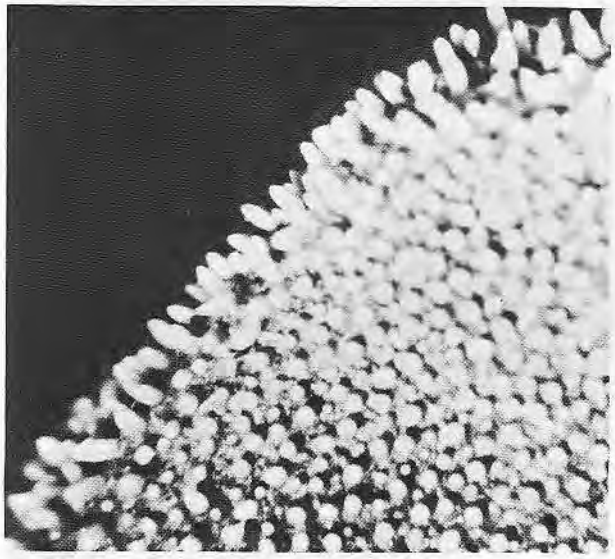


FIGURE 42.—*Ophiocoma alexandri;* edge of disc showing granules (d.d. 17 mm).

is characteristically an opening near the center of the adradial muscle scar (Figure 43*a,b*); no specimens of *Ophiocoma,* including all three species in the PUMILA group have revealed this opening on the adradial surface of the oral plate (Figure 44*a*). The functional significance of this aperature remains to be defined. Its presence in the commonly self-dividing (fissiparous) genus *Ophiocomella* and a similar feature in the fissiparous *Ophiactis savignyi* may suggest, however, a relationship to the phenomenon of fissiparity. The opening is thought to lead to the water vascular system.

In addition to morphological characters, species in the PUMILA group of *Ophiocoma* show differences in distribution from *Ophiocomella.* In the Indo-Pacific, *Ophiocomella sexradia* (synonyms: *Ophiocoma parva, Ophiocomella clippertoni, O. schultzi,* and *Ophiomastix sexradiata*) is widely distributed, however, there is no representative of the PUMILA group in the Indo-Pacific except in the western Indian Ocean, where the range of *Ophiocoma valenciae* and *Ophiocomella sexradia* overlap (Balinsky, 1957). In the eastern tropical Pacific, *Ophiocomella* has been reported from Clipperton Island (as *O. clippertoni*) and the Galapagos Islands (as *O. schmitti*) by A. H. Clark (1939). Geographic overlap of *Ophiocomella* and *Ophiocoma alexandri* (based on examination of specimens in AHF, USNM, and MCZ) has been noted at the Galapagos, Revillagidedo Islands (Clarion Island), western Panama (Secas Island), and Costa Rica (Port Culebra and Parker Bay). Further north along the Central American coast up to Baja California, however, there is no evidence of *Ophiocomella* occur-

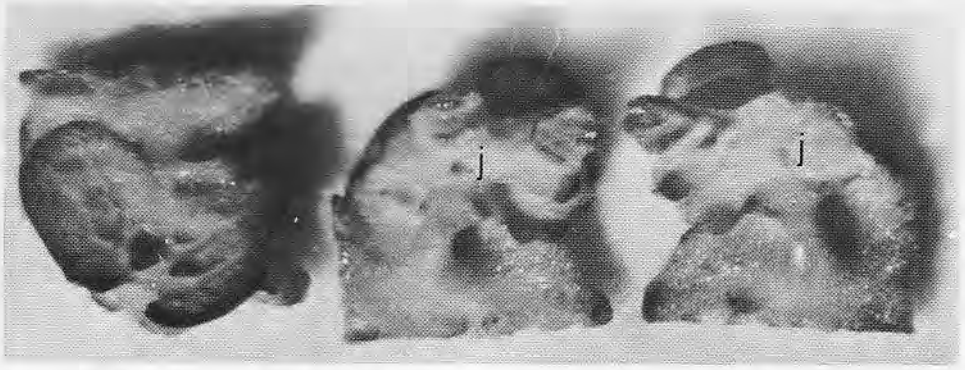


FIGURE 43.—*Ophiocomella;* abradial surface of oral plate (left) and adradial surfaces of oral plates (middle and right) from specimens collected at Bermuda (dd. 7 mm). *j,* Aperture through adradial muscle scar.

ring, although *Ophiocoma alexandri* is well known. In the Caribbean and throughout the West Indian report of any small hexamerous ophiocomids from the appear to be widely distributed, however, there is no report of any small hexamerous ophiocomids from the West African localities where *Ophiocoma pumila* has been collected. There is some evidence that *Ophiocomella* and the young of *Ophiocoma pumila* and *O. alexandri* share a similar habitat. Their syntopic association does not preclude different ecological niches, but presently little is known concerning aspects of their life histories.

The suggestion by H. L. Clark (1921, p. 124) that species in the PUMILA group evolved "directly from *brevipes*," based on a similarity in pigmentation, is doubtful. Very marked differences in the dental plates, the presence of only a single tentacle scale on all but a few of the most proximal arm segments in species in the PUMILA group, and differences in the size and extent of disc granules clearly separate representatives of the two groups.

FIGURE 44.—*Ophiocoma pumila;* abradial (above) and adradial surfaces of oral plates (d.d. 13 mm).

Within the group, *valenciae* and *alexandri* are more alike in their arm spine sequences. Both species show the development of six (up to seven in *alexandri*) arm spines on segments near the disc and have a large number of segments with five arm spines, and in both respects differ from *pumila*. Furthermore, Ailsa M. Clark (1966, p. 44) found that the ratio of arm length to disc diameter for *valenciae* can range from 5.25 to 8.5 : 1. This range is well within that indicated by H. L. Clark (1921, p. 123) for *alexandri* and *pumila* and thus does not offer a character by which *valenciae* can be separated from these species as he indicated in his key.

In the PUMILA group, the third arm spine in the row (counting from the bottom) is generally the longest, being distinctly longer than the lower two spines on those segments beyond the disc. This means that on the tenth free segment (beginning with the first segment with a well-developed upper arm plate) the longest spine for *pumila* is the next to uppermost in the row, since in this species only four spines occur that far out on the arm. For *alexandri* and *valenciae*, however, with as many as five or six arm spines on the tenth free segment, the longest arm spine is the third or fourth spine from the top, respectively. Although this relationship is generally true, I have found some specimens of *valenciae* having the fourth from the lowest arm spine equaling or slightly exceeding the length of the third lowest spine.

Development and larval rearing of *O. pumila* were carried out by the author. It is significant that the fertilized egg has a smooth membrane in contrast to that of species in the SCOLOPENDRINA group and that the larval skeleton shows body rods coming together with the formation of small terminal and end rods (Figure 16) in contrast to the condition noted by Mortensen (1937) for the larval skeleton of *O. pica*.

4. SCOLOPENDRINA Group

The SCOLOPENDRINA group of *Ophiocoma* has the greatest number of species in the genus and shows a pan-tropical distribution: *O. aethiops* Lütken, 1859,

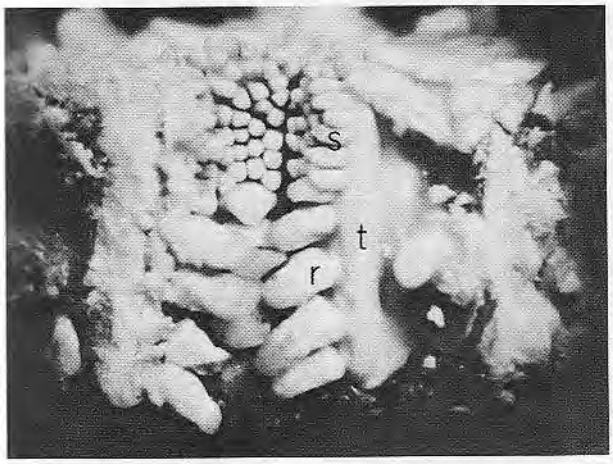


FIGURE 45.—*Ophiocoma erinaceus;* internal view, three sectors of jaw (d.d. 28 m): *r*, teeth; *s*, dental papillae; *t*, dental plate.

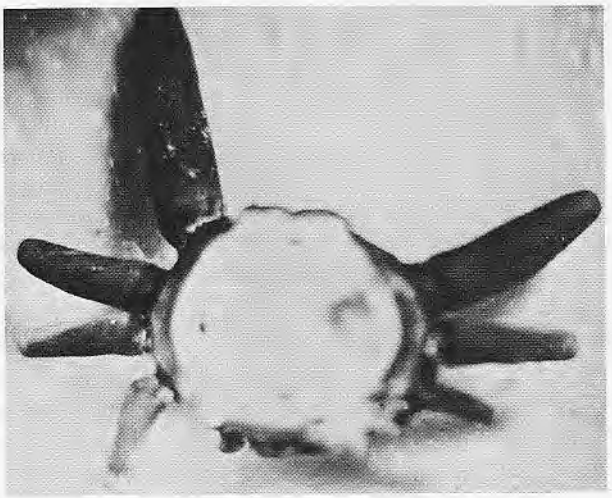


FIGURE 46.—*Ophiocoma erinaceus;* distal view of 10th arm segment (d.d. 20 mm).

tropical eastern Pacific; *O. "alternans"* Endean, 1963, subtropical southeast Australia; *O. anaglyptica* Ely, 1944, tropical central Pacific; *O. echinata* (Lamarck, 1816), tropical West Indies;[5] *O. erinaceus* Müller and Troschel, 1842, tropical Indo-Pacific; *O. macroplaca* (H. L. Clark, 1915), eastern Indo-Pacific; *O. occidentalis* H. L. Clark, 1938, subtropical Western Australia; *O. scolopendrina* (Lamarck, 1816), tropical Indo-Pacific; *O. wendti* Müller and Troschel, 1842, tropical West Indies.

DIAGNOSIS.—Three to five (rarely six) arm spines on each side of proximal arm segments beyond disc edge, with upper spine longest and often thickened; a short distance beyond disc, arm spines alternate (typically three and four) either on opposite sides of the same arm segment or on adjacent segments (Figure 46). Dental plate between 2.4 and 2.6 times as long as broad, with very narrow vertical septa dividing the teeth foramina, and dental papillae region occupying one third of the total plate length (Figures 45, 47). Upper (aboral) arm plates with uneven lateral borders where arm spines alternate on each side of same segment (Figure 48). Disc granules coarse and spherical, except in *O. anaglyptica* where they may be more flattened. One or two tentacle scales on each side of oral arm plates.

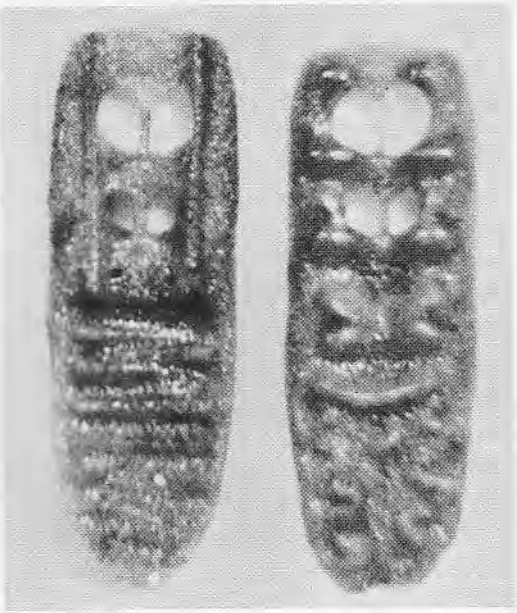


FIGURE 47.—*Ophiocoma anaglyptica;* proximal (left) and distal surfaces of dental plate (d.d. 11 mm).

FIGURE 48.—*Ophiocoma erinaceus;* aboral view of 10th arm segment with upper arm plate and arm spines (d.d. 15 mm).

[5] *Ophiocoma echinata* has been reported from Liberia (H. L. Clark, 1921) but that record requires further verification.

Key to Species

1. A group of exposed and enlarged scales in oral interbrachial disc region; disc granules often flattened, pavement-like; fourth (upper) arm spine flask-shaped (Figure 49). ***O. anaglyptica***
   No enlarged scales in oral interbrachial disc region; disc granules rounded; upper arm spines not flask-shaped 2
2. Four spines on each side of third arm segment ..... ***O. macroplaca***
   Three spines on each side of third arm segment 3
3. Oral surface of arms, especially proximally, white or yellow-white, sometimes variegated but never all black; Indo-Pacific ..... ***O. scolopendrina***
   Oral surface of arm, including proximal area, partly or all black, reddish, or dark brown to tan 4
4. Two spines on each side of first arm segment; Caribbean ..... ***O. wendti***
   Three spines on each side of first arm segment 5
5. Upper arm spine, on side with 3 spines, as long as or longer than upper arm spine on opposite or adjacent side of segment with 4 arm spines; eastern tropical Pacific ..... ***O. aethiops***
   Upper arm spine on side with 4 spines longer than upper arm spine on opposite or adjacent side of segment with 3 arm spines 6
6. Twenty to 36 disc granules per square mm 7
   Nine to 16 granules per square mm; Indo-Pacific 8
7. Disc granules entering as V-shaped group into oral interradial region, leaving scales usually exposed between disc and oral shield; West Indies ..... ***O. echinata***
   Disc granules covering all but small portion of oral interradial region, not leaving scales exposed between disc and oral shield; Australia ..... ***O. "alternans"***
8. Oral surface of arms and spines reddish brown; Western Australia ..... ***O. occidentalis***
   Oral surface of arm and spines black or dark gray; Indo-Pacific ..... ***O. erinaceus***

DISCUSSION.—The sequence of arm spines on particular segments has been of considerable help in distinguishing several species of *Ophiocoma* in the SCOLOPENDRINA group. Arm spines on the first several proximal segments characteristically remain constant throughout the growth of an individual for all species of *Ophiocoma* examined. The arm spines on more distal segments increase in number in a relatively consistent manner for each species.

The identity of *Ophiocoma macroplaca* and its separation from the sympatric *O. erinaceus* in the Hawaiian Islands were determined in part by the use of the arm spine sequence. *O. macroplaca* was originally described in the genus *Ophiacantha* by H. L. Clark (1915) on the basis of a single, small (d.d. 2 mm) specimen. In 1949, A. H. Clark transferred the species to *Ophiomastix asperula* on the basis of the few scattered elongate granules noted on the disc of the original specimen. My own examination of the type-specimen (MCZ 3700) and comparison with additional specimens of *Ophiocoma* collected in the Hawaiian Islands indicated that disc granules *alone* are typical of *macroplaca* and that it is a member of the genus *Ophiocoma* in the SCOLOPENDRINA group. A comparison of the arm spine sequences over the size ranges of *erinaceus* and *macroplaca* illustrates one method for distinguishing the two species (see Table 5). The regular presence of four spines on the third segment for *macroplaca* and three spines on the third segment for *erinaceus* is characteristic. The alternation of the arm spines for both species as characteristic of the group is indicated by the diagonal lines in Table 5.

The arm spine sequence was instrumental in proving that records of *Ophiocoma scolopendrina* from the Hawaiian Islands are erroneous. Examination of the specimens recorded as *scolopendrina* by A. H. Clark (1949, pp. 52–53) from the 1902 *Albatross* stations around the Hawaiian Islands shows that all but two (USNM E7089 and E7088 are close to *Ophiacantha bisquamata* Matsumoto) should be referred to *macroplaca*. Moreover, the specimen listed by Ely (1942, p. 52) and described by H. L. Clark as *scolopendrina* from Maui (MCZ 4515) has been reexamined and also found to be *macroplaca*. The following characteristics separate the two taxa:

1. *macroplaca:* 4 arm spines on each side of segment 3.
   scolopendrina: 3 spines on each side of segment 3.
2. *macroplaca:* ratio of upper arm spine length to aboral arm plate length (for segment 10) 3.5–4.1 : 1 (X=3.4 : 1) (N=28).
   scolopendrina: ratio, 2.2–2.5 : 1 (X=2.4 : 1) (N=23).
3. *macroplaca:* oral arm plate with distal margin broadly rounded, not concave, and lateral margins flared distally at outer edges.
   scolopendrina: oral arm plate with distal margin broadly truncated, sometimes concave; lateral margins not flared distally at outer edges.
4. *macroplaca:* Two tentacle scales present on specimens larger than 2 mm (d.d.) and increasing regularly on more segments with growth.
   scolopendrina: One or two tentacle scales, only a few proximal segments with two scales on specimens less than 10 mm (d.d.); frequently irregular number on distal segments with growth.

In addition to morphological criteria, *macroplaca* and *scolopendrina* are differentiated ecologically. Several workers (H. L. Clark, 1921; Murakami, 1938; Balinsky, 1957; Ailsa M. Clark, 1952; Magnus, 1962, 1964; Shiino, 1964) have given accounts of the restricted littoral habitat of *scolopendrina.* In contrast, *O. macroplaca* has only once been collected in the littoral zone (H. L. Clark, 1915) and is much more common in depths between 5 and 100 meters.

FIGURE 49.—*Ophiocoma anaglyptica;* upper arm spines.

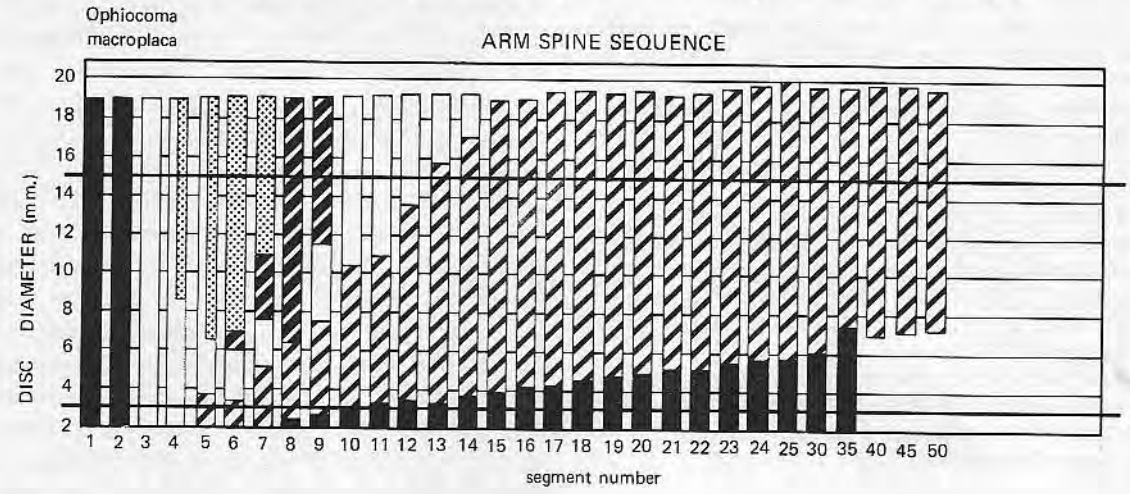
The specimens listed by Koehler (1907a) as *Ophiocoma scolopendrina* from "iles Sandwich" are deposited in the Muséum d'Histoire Naturelle de Paris but cannot be located (Dr. Cherbonnier, personal communication), and their determination remains suspect until verification can be made. Likewise, the species described as *Ophiocoma variabilis* by Grube (1857) from Hawaii (Insel Woahu=Oahu) suggests that this species is probably conspecific with *scolopendrina* and that there must have been a mistake in the locality record. With reference to the arm spines, Grube later stated: "mit Ausnahme der ersten 3, im Bereich der Scheibe befindlichen Facher meist ze je 4, dort nur zu je 3" (Grube, 1860, p. 32), which implies that the first three segments have only three arm spines. It has been shown above that Hawaiian specimens of *macroplaca* carry four spines on the third segment. In addition, Grube's description of the relative length of the upper arm spine comes closer to that noted for *scolopendrina,* and the pigmentation also is similar to that known for this species. Unfortunately, no examination of Grube's specimens has been possible because the whereabouts of the types originally deposited in the Tartu Museum cannot be confirmed.

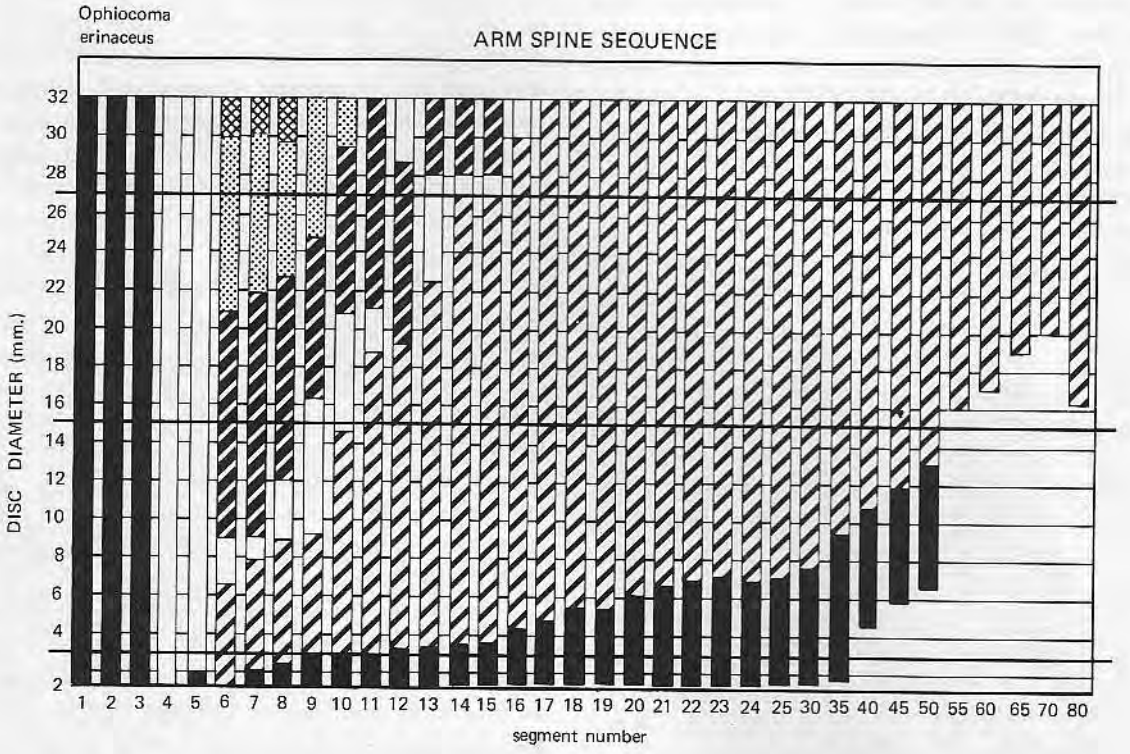
The arm spine sequence was also instrumental in confirming Lütken's (1856, p. 2; 1859, p. 245) and Martens' (1870, p. 251) suspicions that *Ophiocoma riisei* is indeed a junior synonym for *O. wendti* described by Müller and Troschel in 1842.[6] An examination of the type of *O. wendti* (ZMB 929) showed the presence of only two arm spines on each side of the first arm segment, a characteristic of this West Indian species *alone* among other species in the SCOLOPENDRINA group. Indo-Pacific records of *O. wendti* refer to several different taxa and are considered in more detail below.

The erroneous records of *O. wendti* from the Indo-Pacific have been shown in part by an examination of specimens Koehler (1922) described as this species: six specimens from Samoa (USNM E4890) and one specimen from the Philippines (USNM 40948) represent *O. erinaceus* (*schoenleini* form) and *O. scolopendrina,* respectively. Koehler's (1905, 1927) records of this species from Indonesia and the Fiji Islands appear to represent the same polymorphic form of *O. erinaceus,* based on the descriptions and my compari-

[6] Ljungman (1872, p. 615) correctly considered some West Indian material as *Ophiocoma wendti,* following Martens' suggestion.

TABLE 5.—*Arm spine sequence of* Ophiocoma macroplaca *and* O. erinaceus





son of similar specimens from those localities. H. L. Clark (1938, p. 336) probably was correct in his assumption that Koehler's (1907b) record of *O. wendti* from Shark Bay, Western Australia, is conspecific with *O. occidentalis*. I have examined a specimen (ZMB 4559) labeled *O. wendti* from the same locality and it conforms closely with *O. occidentalis*. Boone's (1938) record of *wendti* from the Hawaiian Islands is certainly in error, as her description and photographs strongly indicate *O. erinaceus*. The color, large number of arm segments with two tentacle scales, and arm spine sequence point to this. In addition, the specimens (ZMB 7076) reported by Hertz (1927, p. 118) as *wendti* from the Seychelles have been reexamined. The presence of three arm spines on the first segment together with other differences show that these specimens are not *wendti* but are examples of *scolopendrina*.

Several lines of evidence, however, suggest that another species from the Indo-Pacific (perhaps in the genus *Ophiomastix*) also has been mistakenly named *Ophiocoma wendti*. Koehler (1907a, pl. 13, fig. 38) described and illustrated a specimen with enlarged claviform arm spines that were distinctly annulated. The disc cover revealed coarse granules. H. L. Clark (1921, pp. 129, 134) reported a similar specimen under the name *wendti* from Zanzibar. That specimen (MCZ 1795), with a disc diameter of 25 mm, combines the characters of *Ophiocoma* in the nature of the disc granules with those of *Ophiomastix* in the nature of the arm spines. Ailsa M. Clark reports (personal communication) that the British Museum has two specimens from Zanzibar that also fit this description. Since Koehler's (1907a) material with the claviform arm spines could be from the same locality, it is possible that it does repesent a new taxon. It remains for more specimens, especially smaller individuals, to be examined before a satisfactory taxonomic decision can be reached.

Each of the species in the SCOLOPENDRINA group appears to develop the disc granules at a characteristic size. Those species and the mimimum disc diameters at which granules have been observed are as follows:

O. aethiops:	5.5 mm	*O. macroplaca:*	2.0 mm
O. anaglyptica:	4.5 mm	*O. scolopendrina:*	2.5 mm
O. echinata:	2.3 mm	*O. wendti:*	7.5 mm
O. erinaceus:	7.5 mm		

This feature offers one method by which young specimens in the group can be identified, and it is especially helpful where closely related species may be collected

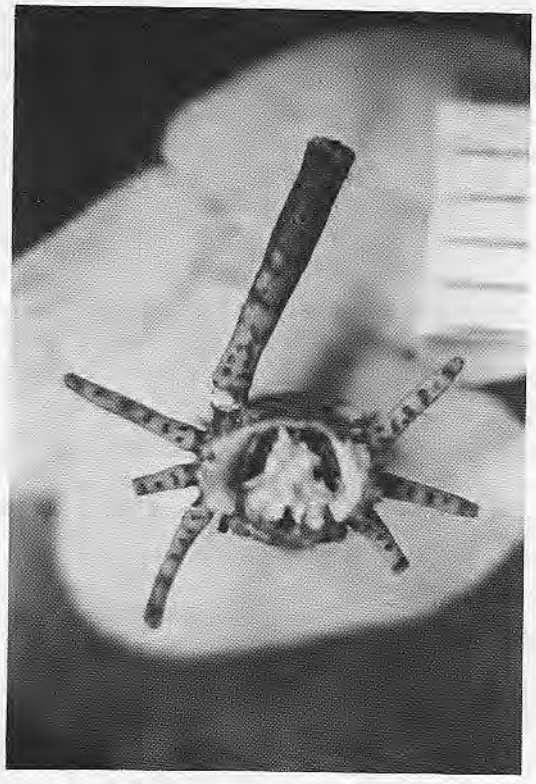


FIGURE 50.—*Ophiomastix annulosa;* proximal view of arm segment (d.d. 19 mm).

together (for example, *O. echinata* and *O. wendti;* and *O. erinaceus* and *O. scolopendrina* or *O. macroplaca*).

Martens (1870) described *Ophiocoma alternans* from the Philippines, based on a small specimen which subsequently has been considered a synonym of *O. scolopendrina* (H. L. Clark, 1921, p. 121). The species described by Endean (1963) as *Ophiocoma alternans* becomes a junior homonym, and a new name will have to be given for this Australian species. An apparently well-defined geographic boundary seems to separate Endean's species from northern relatives at the Great Barrier Reef. It is difficult to judge the merit of several qualitative differences used by Endean to separate his species from *O. erinaceus* or *O. occidentalis,* but the extension of the disc granules to the oral shield apparently is the best character for separating *O. "alternans"* from those two species. Examination of three paratypes of *"alternans"* deposited in the Allan Hancock Foundation (AHF 797.1) also indicates that the pigmentation as reported by Endean differs from *erinaceus.*

Variation in several morphological characters has led some workers to consider some examples of *Ophiocoma erinaceus* as representing more than a single species. For example, *Ophiocoma schoenleini* Müller and Troschel, 1842, has been distinguished from *O. erinaceus* primarily by having only one tentacle scale, relatively shorter upper arm spines, and a different pattern of disc granulation. Over a limited range in the Indo-Pacific, both this form and that with two tentacle scales (typical *erinaceus*) have been collected together. Both forms have been reported by Matsumoto (1917) from the Ryukyu Islands and Formosa, by H. L. Clark (1921) from Amboina and Torres Strait, by A. H. Clark (1954) from Fiji, Samoa, and the Gilbert Islands,[7] by H. L. Clark (1921, 1946) and Endean (1957) from several localities along the Great Barrier Reef, and by Domantay and Domantay (1966) from the Philippines.

Specimens of both forms, from syntopic collecting sites, have been examined from the Philippines, Torres Strait, Fiji, and Samoa. These have been compared with the type-specimen of *O. schoenleini* (ZMB 930). In addition to the difference in the number of tentacle scales, the two forms show several contrasting characters, but these overlap to a variable extent in some specimens from the same locality. A comparison of contrasting characters usually associated with each of the two forms is presented below. Data are based on specimens from 8 to 20 mm (d.d.).

Specimens with two tentacle scales (N=22)	*Specimens with one tentacle scale (N=39)*
1. Four arm spines most often on fourth segment.	1. Three arm spines most often on fourth segment.
2. Maximum arm spine length to breadth of oral plate (tenth free arm segment), X=2.2:1; range, 1.9 to 2.6:1.	2. Maximum arm spine length to breadth of oral plate (tenth free arm segment), X=2.8:1; range, 2.3 to 3.2:1.
3. Disc granules less often extending into oral interradius of disc.	3. Disc granules more often extending into oral interradius of disc.

There appeared to be no difference in the pigmentation of the two forms examined, and on both forms the disc granules were not noted in specimens of less than 7.5 mm (d.d.).

[7] The specimens reported from the Gilbert Islands (USNM E8061) have been reexamined and found to be *O. scolopendrina*.

The syntopic occurrence of both the one-scale and two-scale forms in certain parts of the central Indo-Pacific and the presence of some specimens with characters (listed above) which were intermediate or mixed between the two forms suggest that we are dealing with polymorphs of the same species having phenotypically linked morphological characters. In the Indian Ocean and eastern part of the Pacific only the form of *O. erinaceus* having two tentacle scales is known.

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