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THE SYSTEMATICS AND POST-LARVAL GROWTH CHANGES IN OPHIOCOMID BRITTLESTARS

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ABSTRACT

THE SYSTEMATICS AND POST-LARVAL SKELETAL CHANGES IN OPHIOCOMID BRITTLESTARS

Brittlestars in the family Ophiocomidae, particularly in the subfamily Ophiocominae, are studied in reference to their systematic relationships. The comparative morphology of the skeleton, especially concerned with changes during post-larval growth, is analyzed quantitatively for species in the Hawaiian Islands. Morphological evaluation of taxonomic characters has been made in order to determine the extent of variation and degree of change occurring with increase in size. The bases for generic and specific designation are reviewed. In some cases, conventional criteria are found inadequate for specific determination, especially during early stages of post-larval development. Several new characters are found which differentiate species during all stages of growth. The form of the dental plate and proximal arm vertebrae, sequence of arm spines, and shape of the aboral arm plates are among the most important new features used to define both genera and species.

Division of the genus <u>Ophiocoma</u> into at least four groups is proposed. The circum-tropical Scolopendrina group shows obvious relationships to the Indo-Pacific genera <u>Ophiomastix</u> and <u>Ophiarthrum</u>. The Pumila group is considered polymorphic

with species having pentamerous and hexamerous forms. An exception is noted in the Indo-Pacific where only hexamerous specimens of _Ophiocoma sexradia_ are known, the result of asexual reproduction. The Brevipes group is well defined and occurs throughout the Indo-Pacific. The Canaliculata group is restricted to temperate waters around New Zealand and southern Australia.

The genus _Ophiocomina_ shows a peculiar north and south temperate water distribution with two species represented. A similar distribution, but on either side of the Pacific Ocean, is noted for _Ophiopteris_. The morphological features of this genus suggest relationship to the Canaliculata group of _Ophiocoma_. _Ophiocomella_ is considered to be made up of hexamerous forms of the Pumila group of _Ophiocoma_.

An emended subfamily diagnosis is presented together with keys to the genera and species, and the phylogenetic relationships of the group are discussed. In addition to line drawings, photomicrographs are incorporated to show the detailed morphology of the ophiocomid skeleton.

Biological notes, including ecological and behavioral information, are given for a number of species, and the use of larval morphology is considered an aid in the systematics of the group.

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INTRODUCTION

The family Ophiocomidae, partucularly members of the subfamily Ophiocominae, includes shallow water species of brittlestars many of which are found in tropical and subtropical regions. Because of the common occurrence of several species, the subfamily is considered in many publications dealing with the shallow water benthic fauna.

During the course of this work, it became apparent that certain problems and misconceptions were present in the systematic evaluation of the Ophiocominae. Most of the difficulty appeared to be the result of earlier workers failing to take into account the growth changes in skeletal parts as well as the relative variability in key taxonomic characters. In this study it was found, both by a careful comparison of many of the species involved and by examination of a series of specimens covering the size range for several of the species, that it would be possible to alleviate many of the problems formerly connected with the taxonomy of the subfamily.

An understanding of the classification and phylogeny of the Ophiuroidea was advanced to a considerable extent by Matsumoto (1915, 1917) and Murakami (1963). Their works emphasize the importance of internal as well as external morphology, exclusively skeletal parts, and lead to a compatible classification which is followed in this paper. Although these works did much to show the relationships between the higher taxonomic categories, they did little to unravel the relationships between subfamilies, genera, and species.

Unfortunately, few workers have attempted to utilize the internal skeletal characters in establishing the genera and species of ophiuroids, being content for the most part to depend on external morphology and pigmentation. This has resulted in a limited ability to discern the relationships of both genera and species. In the present study an attempt is made to clarify these relationships in the subfamily Ophiocominae.

This study then is a critical essay which is directed towards a comprehensive review of the subfamily Ophiocominae in terms of its systematic structure by: a) determining the extent and limitations of genera and species; b) analyzing the phylogenetic relationships more thoroughly. These two points are realized through new interpretation of taxonomic criteria, some presented for the first time.

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My deepest appreciation is to Dr. H. B. Fell at the Museum of Comparative Zoology, Dr. David Pawson and

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A special thanks to my wife, Gail, whose patience, hard work, and understanding made this endeavor a reality.

METHODS AND MATERIALS

Methods

Prior to preservation, it was necessary to relax living specimens to prevent autotomy. Immersion in fresh water or preferably a 10% magnesium sulfate solution in sea water was effective for all species. The ophiuroids were then fixed in 10% sea water formalin from one to three days. After rinsing in fresh water, they could either be preserved in 70% ethyl alcohol or dried.

In order to prepare the brittlestars for examination of separate skeletal elements, especially the internal ossicles, it was found effective to use a weak solution of sodium hypochlorite (Chlorox). This reagent removed the organic material and left the skeleton quite clean. By varying the strength of the Chlorox solution, different rates of disarticulation were obtained. Prior to immersion in the Chlorox solution, the animal or portion of the specimen was first placed in a water bath to remove the alcohol or, in the case of dried specimens, to soften the tissue. After the skeleton had reached the stage of disarticulation desired, the Chlorox was gently removed with a syringe and water replaced in the same way. Small pieces of an absorbent paper or blotter were then placed in with the ossicles.

Selected skeletal elements were transferred onto the blotter, the water carefully removed, and the ossicles allowed to dry. For illustration purposes, a greater degree of contrast was obtained by staining the ossicles with a drop of 10% Harris Haemotoxylin. Very small ossicles which were difficult to handle were kept in glycerin where they could be used without being lost.

Photomicrographs were made using the lenses of a dissecting microscope to which a 35 mm single lens reflex camera was mounted on the ocular. Kodak Tri-X (ASA 400) and Plus-X (ASA 120) panatomic film were found satisfactory for the photographs.

Materials

Species of *Ophiocoma* collected in the Hawaiian Islands were used extensively for examination of growth change analyses of selected skeletal characters. Specimens from other Indo-Pacific localities supplemented the Hawaiian collections. Comparative studies were made, using other species of *Ophiocoma* and species in other genera in the subfamily Ophiocominae.

Whenever possible, type specimens were obtained and examined. Material deposited in the U. S. National Museum, Museum of Comparative Zoology (Harvard), and Allan Hancock

Foundation was examined during December and January, 1966-67. Additional specimens were supplied to the author from these institutions during the period of investigation in Hawaii. Types of several species were received from the Zoologisches Museum in Berlin. In addition, an extensive collection of ophiocomid material was utilized at the B. P. Bishop Museum.

The author's collection is being deposited in the B. P. Bishop Museum and a representative series of specimens is being given to the Hawaii Institute of Marine Biology.

As part of the systematic evaluation for many of the species considered in this paper, I have included one section designated, MATERIAL EXAMINED, which gives the locality where the specimens were collected, their place of deposition, the catalog or registration number, and number of specimens (in parentheses).

Throughout the paper several abbreviations are used, the full contex of these follows.

Abbreviations

AHF - Allan Hancock Foundation, Los Angeles, California

BMNH - British Museum (Natural History), London, England

BPBM - Bernice P. Bishop Museum, Honolulu, Hawaii

MCZ - Museum of Comparative Zoology, Cambridge, Mass.

Pers. Coll. - Author's Collection

USNM - United States National Museum, Washington, D. C.

ZMB - Zoologisches Museum, (East) Berlin, Germany

d.d. - Disc diameter

t.s. - tentacle scale

SYSTEMATIC BASIS FOR THE SUBFAMILY OPHIOCOMINAE

The family Ophiocomidae was originally established by Ljungman (1866) and included four genera: *Ophiocoma*, *Ophiomastix*, *Ophiarthrum*, and *Ophiopsila*. The morphological characters used to define the family were external, for the most part based on skeletal elements. The presence of both oral and dental papillae was most characteristic, although the position and length of the arm spines together with the usually granular disc covering were good supporting characters.

Since the original diagnosis several attempts have been made to classify the Ophiocomidae with the rest of the Ophiuroidea. Perrier (1891) included the Ophiocomidae among those brittlestars in his suborder Nectophiura in which the arm spines projected at right angles to the arms. Apart from this character, the family was separated from others in the suborder by having numerous dental papillae. Unfortunately, Perrier failed to note the importance of *both* dental and oral papillae as originally established by Ljungman (*op. cit.*) and confirmed by Lütken (1869) for the family. Thus eight additional genera were included, only one of which (*Ophiopteris*) is currently recognized in the family. Furthermore, *Ophiopsila* was removed, probably on the basis of the nature of the arm spines.

A year later, Bell (1892) proposed a new classification of the Ophiuroidea based on the type of articulation of the arm vertebrae. In the family Ophiocomidae he retained Ophiopsila, deleted Perrier's additional genera except for Ophiopteris, and included the rest of the original genera. No additional characterization of the family was made.

Meissner (In, Ludwig and Hamann, 1901, p. 939) favored a classification of the Ophiuroidea which combined the hierarchial arrangement of both Perrier and Bell. His characterization of the Ophiocomidae was based on Ljungman's original diagnosis and he included the original genera with the exception of Ophiopsila which, in the style of Perrier, was placed in the family Amphiuridae, while Ophiocymbium and Ophiarachna were added.

No further elaboration on the systematic evaluation of the Ophiocomidae occurred until Matsumoto (1915, 1917) published a revised classification of the Ophiuroidea. He established a new system based on internal skeletal features. The structure of the radial shields, genital plates, genital scales, and their relationships to one another were of primary importance in setting up his higher levels of classification. The Ophiocomidae was placed in the order Chilophiurida, a group characterized by having both the radial shield and genital plate articulate with each other by means of two articular processes and a single depression on both the plates. Matsumoto distinguished the Ophiocomidae from other families in the order by their long and erect arm spines, well developed dental papillae which formed a vertical clump at the apex of each jaw, and stout arms, having their greatest width some distance from the edge of the disc (1917, p. 233). His diagnosis of the Ophiocomidae was considerably more detailed than Ljungman's (op. cit.) and nearly twice as many characters were used in defining the family.

Matsumoto went further by dividing the family into two subfamilies, Ophiocominae and Ophiopsilinae. Ophiopsilinae contained only the genus Ophiopsila whereas Ophiocominae included four genera: Ophiocoma, Ophiomastix, Ophiarthrum, and Ophiopteris. This separation was warranted by differences in the shape of the radial shield, the number and shape of the arm spines, and in the shape of the tentacle scales. Matsumoto examined two species of Ophiocoma (brevipes, and erinaceus), three species of Ophiomastix (annulosa, luetkeni, and mixta), and Ophiarthrum elegans. Characters common to these species were used for the subfamily diagnosis. These characters together with the implied relationships to other ophiuroid groups follow:

1. Radial shields: Very stout and boot-shaped, each with a radially directed bar and transverse projection from the outer edge of the bar (Pl. VIII, fig. 3). This differed in shape from that of Ophiopsilinae.
2. Genital plate (Pl. VII, fig. 1,a): Bar-like, slightly curved laterally and articulating with the genital scale at some distance inside the proximal end. This was considered a common character of other Chilophiuroid groups such as the Ophiomastinae, Ophiolepidinae, Ophiodermatidae, Ophiochitonidae, and Ophiopsilinae.
3. Genital scales (Pl. VII, fig. 1,c): Bar-like, more or less flattened.
4. Peristomial plates: Double and rather small, the two being firmly united; in this respect considered similar to <u>Ophiodoris</u> (Fam. Ophiochitonidae) and <u>Ophionereis</u> (Fam. Ophionereididae).
5. Oral plates: Very stout with an extremely well developed adoral muscular surface for the attachment of very large masticatory muscles (Pl. XI, fig. 5,d); a similar development noted in the Amphiuridae, Ophiothricidae, <u>Ophioceramis</u> (Fam. Ophiuridae), and Ophionereidinae.
6. Dental plate (Pl. XI, fig. 2,b): This plate completely overlapping the oral plates; in dorsal (aboral) view the

oral and dental plates were π shaped, characteristic of the Ophionereidinae.

7. Arm vertebrae: The dorsal surface of the vertebrae was rhomboidal and not strongly notched at its inner aboral end (Pl. VI, fig. 4), thus differing from the Ophionereididae.

Based on comparative studies, the Ophiocomidae was considered slightly more advanced than the Ophionereidinae as far as the oral skeleton (oral plates and dental plates).

However Matsumoto was reluctant to consider the Ophionereididae directly ancestral to the Ophiocomidae because of the difference in shape of the proximal end of the arm vertebrae.

The next important consideration of the Ophiocominae came when H. L. Clark (1921) presented a taxonomic review of the subfamily, including keys to the genera and species. Clark went further than preceding workers in attempting to show phylogenetic relationships between the genera and species. Details of Clark's evaluation are discussed in sections of this paper dealing with each genus.

More than forty years passed before Murakami (1963) made his important contribution to ophiuroid systematics in a detailed study of the oral and dental plates. Five species of *Ophiocoma*, seven species of *Ophiomastix*, two species of

Ophiarthrum and one species of Ophiopsila were considered as a part of this work. Further evidence for the subdivision of the Ophiocomidae into the Ophiocominae and Ophiopsilinae was presented on the basis of differences in the oral and dental plates. Furthermore, Murakami considered the family related to the Ophionereididae but more advanced because of greater elaboration of ridges and projections on the distal surface of the dental plate and greater development of the abradial surface of the oral plate.

In addition to the characters used by Matsumoto and Murakami to define the subfamily Ophiocominae, my studies indicate several other features equally characteristic of the group. These are based on examination of more species, including representatives of the genera Ophiocomina and Ophiopteris, neither of which were examined before. My findings are indicated below.

First, there is a pair of interradial attachment plates present on the abradial border of the disc at the proximal edge of each genital slit. These plates are short, thin, and firmly fixed to the distal end of the oral shield. Although these plates are not unique to the Ophiocomidae--Matsumoto (1917, p. 143) indicated their presence in the order Gnathophiurida--their presence in the order Chilophiurida has not been reported before.

Second, the first arm vertebra has a calcareous septum which separates the radial nerve from the radial water vessel (Pl. I, fig. 1,d). I have noted its presence in many species of Ophiocoma and Ophiomastix, as well as in Ophiopteris papillosa (Pl. XVII, fig. 9) and two species of Ophiopsila (riisei and californica) (subfamily Ophiopsilinae).

Third, the teeth are characterized by having a hyalinated tip found in all genera except Ophiocomina and Ophiopteris. This same feature has been noted in species of Ophionereis and Ophiopsila also.

Emended diagnosis of the subfamily Ophiocominae

1. Disc covered with granules and/or spinules or spines except for Ophiarthrum which has the disc bare.
2. Four to six oral papillae on either side of a jaw angle; outer-most (Pl. XII, fig. 6,o) pointed inwards and aboral to the next one, usually abutting on adradial shield.
3. Dental papillae present sometimes forming a cluster at the apex of each jaw (Pl. XII, figs. 2,4,p).
4. Teeth with hyalinated tip (except Ophiopteris, Ophiocomina); from 3 to 5 teeth on each dental plate in adult condition.
5. Dental plate entire, bearing a series of elevations or bosses for attachment of dental papillae; foramina for

teeth divided by vertical septa and distal margins with elevated ridges (Pl. XII, fig. 1).

6. Oral plate with well developed abradial muscle surface, which may or may not have shallow elongate grooves (scars) on its surface (Pl. XVIII, fig. 6).
7. First arm vertebra with oral septum separating radial water canal from radial nerve (except Ophiarthrum elegans) (Pl. I, figs. 1, 2).
8. Peristomial plates double.
9. A pair of interradial attachment plates at distal end of oral shield connected to proximal edge of genital openings.
10. Adoral mouth shields either at sides of oral shields (Pl. XII, fig. 6,m,n) or meeting in front of oral shields (Pl. XIX, fig. 1,m,n).
11. Arms widest outside base of disc.
12. One or two tentacle scales (except Ophiomastix janualis with none).
13. Arm spines generally solid (hollow in Ophiocomina, and Ophiocoma pusilla); always two or three on first arm segments, and three distally; considerable variation in their size, regularity, and position.
14. Bathymetric range: littoral to 200 meters.

Synoptic key to genera in the subfamily Ophiocominae

1 Disc covered with scales which are sometimes imbedded in a thick integument; few to many granules, spinules, or both covering disc and often concealing scales...................... 2

Disc covered with a smooth, naked skin; bearing neither granules nor spinules...........OPHIARTHRUM

2 (1) Teeth with hyalinated grinding surface at tip......3

Teeth without hyalinated grinding surface at tip..4

3 (2) Disc bearing only granules.................OPHIOCOMA

Disc bearing spinules, or spinules and granules..... ....OPHIOMASTIX

4 (2) Modified scale-like upper arm spines (Pl. XIX, fig. 2)................................OPHIOPTERIS

No modified upper arm spines.............OPHIOCOMINA

SYSTEMATIC DIVISION OF THE SUBFAMILY OPHIOCOMINAE

PHYLUM Echinodermata

CLASS Asterozoa

SUBCLASS Ophiuroidea

ORDER Chilophiurida Matsumoto, 1915

FAMILY Ophiocomidae Ljungman, 1866

SUBFAMILY Ophiocominae Matsumoto, 1915

GENUS _Ophiarthrum_ Peters, 1851

O. elegans Peters, 1851

O. lymani Loriol, 1893

O. pictum (Müller and Troschel), 1842

GENUS _Ophiocoma_ Agassiz, 1835

O. aethiops Lütken, 1859

O. alexandri Lyman, 1860

O. anaglyptica Ely, 1944

O. "alternans" Endean, 1963

O. bollonsi Farquhar, 1908

O. canaliculata Lütken, 1869

O. dentata Müller and Troschel, 1842

O. doederleini Loriol, 1899

O. echinata (Lamarck), 1816

O. erinaceus Müller and Troschel, 1842

O. macroplaca (H. L. Clark), 1915

O. occidentalis H. L. Clark, 1938

O. pica Müller and Troschel, 1842

O. pumila Lütken, 1856

O. sexradia (Duncan), 1886

O. scolopendrina (Lamarck), 1816

O. wendtii Müller and Troschel, 1842

GENUS Ophiocomina Koehler, 1921

O. australis H. L. Clark, 1928

O. nigra (Abildgaard), 1789

GENUS Ophiomastix Müller and Troschel

O. annulosa (Lamarck), 1816

O. asperula Lütken, 1869

O. bispinosa H. L. Clark, 1917

O. caryophyllata Lütken, 1869

O. corallicola H. L. Clark, 1915

O. elegans Brock, 1888

O. flaccida Lyman, 1874

O. janualis Lyman, 1871

O. luetkeni Pfeffer, 1900

O. mixta Lütken, 1869

O. notabilis H. L. Clark, 1938

O. ornata Koehler, 1905

O. palaoensis Murakami, 1943

O. variabilis Koehler, 1905

O. venosa Peters, 1851

GENUS *Ophiopteris* Smith, 1877

O. antipodum Smith, 1877

O. papillosa (Lyman), 1875

GENUS OPHIARTHRUM

The genus *Ophiarthrum* was established by Peters (1851) for *O. elegans* to account for a peculiar ophiocomid-like specimen which showed well developed oral and dental papillae but had a completely naked disc composed of a smooth, slimy integument bearing neither granules, spinules, nor well developed scales.

In 1842, Müller and Troschel described *Ophiocoma picta*. These workers made no attempt to separate this species from other *Ophiocoma* species even though the disc lacked granules, a fact which they failed to mention. Lyman (1874), who examined the type specimen of *O. pictum*, realized at once the similarity to *Ophiarthrum elegans* and placed the species in this genus as *Ophiarthrum pictum*.

One more species, known only from the original description was reported from Mauritius by Loriol (1893b). This species was named *Ophiarthrum lymani*.

The deficiently calcified disc, lacking either granules or spinules, is the most characteristic feature of the genus *Ophiarthrum*. The arm spines show an alternating pattern on either side of the same arm segment or adjacent segments beyond the radius of the disc. The maximum number of arm spines is four, but two and three are quite common well beyond the disc. Lyman (1882, p. 173) stated that species in this genus had "from four to six" arm spines. This has not been confirmed in my studies nor in other reports. The upper arm spine is longest, and may be thickened, but is not claviform. Only one tentacle scale is present on all segments except the first which may have two scales.

Ophiarthrum shows its most obvious relations with *Ophiomastix*. This is especially true in the case of *Ophiarthrum pictum* and *Ophiomastix venosa*. In the latter, the disc is without scales, granules, and may or may not have widely scattered spinules. Only the typical presence of very enlarged club-shaped upper arm spines in specimens without disc spinules serves to distinguish this species from *Ophiarthrum pictum*.

The three species of *Ophiarthrum* are most easily distinguished on the basis of differences in pigmentation (see following key). The first arm vertebra of *O. elegans* is unique among the ophiocomids I have examined in lacking the calcareous septum separating the radial water canal from the radial nerve (Pl. XIII, fig. 9). This septum is well developed in the vertebra of *O. pictum* but nothing is known about it in *O. lymani*.

For the present, it seems best to consider *Ophiarthrum* most closely allied to that branch of *Ophiomastix* which shows a deficiently calcified disc, with scattered spinules, and having an arm spine sequence of two spines on the proximal segments and two or three spines irregularly alternating beyond the disc. The complete lack of disc spinules and claviform arm spines are still the best characters which serve to separate species in this genus from other ophiocomids.

Synoptic key to species in the genus Ophiarthrum

1 Arm spines light, spotted or ringed with dark color; disc with dark lines or central area dark aborally, but lighter orally 2

Arm spines uniformally grey or brown; disc black aborally and orally .... *O. lymani* Loriol

2 (1) Disc very dark centrally; no median dark line on the upper side of arms .... *O. elegans* Peters

Disc with thin wavy dark lines; very distinct median dark line on upper side .... *O. pictum* Müller and Troschel

Ophiarthrum elegans Peters

(Plate XVIII, figs. 6-9)

SYNONYMY

Ophiarthrum elegans Peters, 1851, p. 463; 1852, p. 82;

Koehler, 1905a, p. 73 (a complete bibliography up to this date); 1907, p. 329; 1922, p. 331; 1930, p. 208; H. L. Clark, 1908, p. 297; 1915, p. 296; 1921, p. 139, Pl. 13, fig. 1 (color); 1938, p. 339; 1946, p. 252; Matsumoto, 1917, p. 351, fig. 100, 2-c; Murakami, 1943, p. 201; A. H. Clark, 1954, p. 261; Endean, 1957, p. 245.

Ophiarthrum elegans var. *unicolor* H. L. Clark, 1932, p. 208; 1946, p. 252; Murakami, 1943, p. 201.

MATERIAL EXAMINED

Caroline Islands (Yap) - USNM: E8631 (8)

Marshall Islands (Eniwetok) - BPBM: W1465 (1), W1510 (1), W1511 (1)

Fiji - BPBM: W853a-d (4)

Mossambique - BPBM: W1581 (1)

Ryukyu Islands - BPBM: W1403b (1)

Samoa - BPBM: W1413a-c (3), W1414a-c (3), W1668 (1)

DIAGNOSIS AND DISCUSSION

A great deal of attention has been paid to the pigmentation of this species by H. L. Clark (1921, 1932, 1946) in which variation has been noticed. This resulted in his designation of a variety name, *unicolor*, for one of the color phases. The normal color pattern is for the disc to be dark centrally with lighter color interradially; there is apparently great individual diversity in the amount of the disc that is dark. The arm spines are light with dark rings or spots. In the variety unicolor the entire disc is dull brown above and below, and Murakami (1943) pointed out that in the living animal red speckles present on the dorsal side of the arm were lost in preservation. The oral side of the arms and mouth plates in the typical and variety forms is very light; aborally the arms are banded.

A good description of the oral armature of the disc, and general shape of the external skeletal plates with figures was given by Koehler (1898).

An analysis of the arm spine sequence was made for several specimens. On each side of the first three arm segments there are only 2 spines. The fourth and fifth segments have 3 spines. Beginning on the sixth segment and extending some distance out on the arm, 3 and 4 arm spines alternate irregularly. Often 2 spines also alternate with 3 spines but not nearly as often as seen in O. pictum. My observations indicate that the sequences for these two species differ significantly.

The first arm vertebra of Ophiarthrum elegans has already been described (p. 21) and a figure of this is given (Pl. XVIII, fig. 9).

Murakami (1963) described the oral and dental plates for this species. I have added photographs of these (Pl. XVIII, figs. 6, 7,b). The dental plate is two-and-one-half times as long as broad, the dental papillae area makes up less than twenty percent of the total length. The teeth foramina are divided by very narrow septa. The oral plate shows a very noticeable spine present in the incised border of the abradial muscle scar; this was not noted in Murakami's figure of this plate.

Additional skeletal plates are shown in Pl. XVIII, fig. 7; very characteristic is the elongated genital plate (a) and genital scale (c); the hyalinated tip of a tooth (t) is shown, and the small radial shield (e).

HABITAT

Little is known concerning the habitat of this species. H. L. Clark (1921, p. 139) reported O. elegans occurring under rocks and coral fragments on the reef-flats at Mer Island (Torres Strait).

DISTRIBUTION

The known distributional range of this species extends from Mossambique and Zanzibar eastward to the Society Islands and from the Great Barrier Reef, northward to the Ryukyu Islands. Specimens have also been reported from several localities in Micronesia (H. L. Clark, 1921; A. H. Clark, 1954). Bathymetric records indicate the presence of this species from the littoral zone (Murakami, 1943) or shallow sublittoral zones, although Koehler (1905) reported specimens to 83 meters.

Ophiarthrum Lymani Loriol

SYNONYMY

Ophiarthrum lymani Loriol, 1894, p. 34, Pl. XXIV, figs. 2a-d; H. L. Clark, 1921, p. 140.

DIAGNOSIS AND DISCUSSION

The type and only known specimen from Mauritius had a disc diameter of 21 mm and an arm length of 110 mm. Without having seen this species it seems best to indicate those features which Loriol felt separated *O. lymani* from the other known species in the genus. Loriol considered his new species resembled *O. pictum* but that it could be distinguished from the latter by having:

a) the oral plates more elongated and regularly pentagonal (Lyman, in 1874, described the oral plates of *O. pictum* as nearly round slightly tapering on the inside border, and having a length to breadth ratio of 1:1).

b) oral arm plates excavated on the sides and narrow on the proximal border, with the result that they are hexagonal or slightly quadrangular (in O. pictum these plates are about as broad as long, with the outer side only slightly curved); a length to breadth ratio of 1:1).

c) aboral arm plates regularly transversely oval, and more imbricating (Lyman's 1874 description of O. pictum indicated that these plates are hexagonal, not broadly oval but still broader than long, with a ratio of 1.4:2).

d) the arm spines always four except distally; arm spines thicker, less pointed, more unequal in length, and not annulated in color. I have already pointed out that the number of arm spines in O. pictum alternate irregularly. This point was not reported by other workers in the past (Lyman, in 1874 stated that there were only three spines; Müller and Troschel (1842) stated there were four in the type). Owing to Loriol's indication of the unequal size of the spines in O. lymani, it seems likely that there is alternation of arm spines in

O. lymani and four may alternate with three spines. However, only examination of the type or further material from the type locality will resolve this problem.

e) the arms much shorter, only about five times the disc diameter instead of nine times (however, H. L. Clark (1921) points out that for O. pictum the arm length: disc diameter ratio can vary from 5.5 to 8 : 1).

Loriol went on to indicate that O. elegans differed from O. lymani in having:

a) different shaped oral shields, oral arm plates, and oral papillae (in O. lymani the outer oral papilla was described as the largest whereas in O. elegans the papillae are about the same size).

b) fewer dental papillae (I have already pointed out the small portion of the dental plate of O. elegans which is occupied by dental papillae).

c) more slender and longer arms.

d) shorter, more slender and pointed arm spines which number only three and which are annulated and less irregular in size; the upper arm spine not reaching the same size. (Loriol described the upper arm spine of O. lymani as one-and-a-half to two times as long as the other spines, more swollen and up to 8 mm in length in the middle of the arm).

HABITAT AND DISTRIBUTION

No details as to the depth or habitat were given in the original description of _Ophiarthrum lymani_. The only known record of this species is from Mauritius Island in the Indian Ocean.

The type specimen is deposited in the Museum d'Histoire Naturelle, Geneva, Switzerland.

Ophiarthrum pictum (Müller and Troschel)

SYNONYMY

Ophiarthrum picta Müller and Troschel, 1842, p. 102; Herklots, 1869, p. 12, Pl. 5, fig 2 (color figure of type).

Ophiarthrum pictum (Müller and Troschel): Lyman, 1874, p. 225, Pl. VII, figs. 204; Koehler, 1905a, p. 72 (complete bibliography up to this date); 1930, p. 208; H. L. Clark, 1921, p. 140, Pl. 12, fig. 1; 1938, p. 339; 1946, p. 252; Ohshima, 1935, p. 62, fig. 28b-c; Boone, 1938, p. 161, Pls. 59-60; A. H. Clark, 1954, p. 261, Endean, 1957, p. 245.

MATERIAL EXAMINED

Caroline Islands (Yap) - USNM: E8632 (2), E8590 (1)

DIAGNOSIS AND DISCUSSION

Very complete descriptions of this species have been given by Lyman (1874) and Boone (1938). O. pictum differs from other species in the genus in pigmentation. H. L. Clark (1921) gave a good account of the color. The disc is ornamented with meandering dark lines on a lighter background. A dark line also runs along the upper arm, and the arm spines are annulated with dark rings.

Murakami (1963) gave figures and descriptions of the dental and oral plates for O. pictum. The dental plate differs significantly from that of O. elegans in having a tapering oral region; in contrast, the dental plate of O. elegans has a broad oral region (Pl. XVIII, fig. 7,b).

I examined the arm spine sequence of several specimens of O. pictum (disc diameters between 18 and 23 mm). The first three arm segments have 2 spines on each side, in this respect, similar to O. elegans. The fourth segment may have 2 to 3 spines and the fifth segment has 3 spines. With increase in size above 10 mm, 3 and 4 spines alternate from the seventh to twentieth segment with 2 and 3 alternating on more distal segments.

Ophiarthrum pictum shows a close relationship to Ophiomastix venosa especially in the nature of the dental plate and arm spine sequence.

HABITAT

This species has been most commonly collected from the shallow sublittoral zone and Koehler (1905) reported it from a depth of 37 meters. Clark (1921) collected specimens from under large coral pieces at Mer Island (Torres Strait).

DISTRIBUTION

O. pictum is reported to have a more restricted distribution than *O. elegans*, not being found west of Java, the type locality. H. L. Clark reported it being common in Indonesia, the Phillipines, and throughout the Caroline Islands. The southern record appears to be about 21° S at Lindeman Island off Australia.

The type specimen is deposited in the Museum zu Leyden, Leyden, Germany.

GENUS OPHIOCOMA

Louis Agassiz (1836, p. 192) first proposed the generic name _Ophiocoma_ for a large number of species described by Lamarck in 1816. Agassiz simply included all the species of 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 species, _O. scolopendrina_, was included along with the other species merely by "etc". It remained for H. L. Clark (1915, p. 290) to designate the type species of the genus _O. echinata_, even though Lyman (1865) 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 as well as the granulation of the disc. In doing so, they added fourteen new species. However, seven of these have since been removed from the genus.

In addition to Müller and Troschel's seven erroneous species, an additional fifteen species, referred to the genus, were found to belong to other genera according to H. L. Clark (1921, p. 121) who lists these and gives their synonymy.

Species correctly assigned to the genus which were considered synonyms for other species of _Ophiocoma_ were also listed. My own study however, indicates several corrections to his evaluation 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) several varieties of _O._ _brevipes_.
2. _O._ _doederleini_ Loriol (1899) is considered a valid species.
3. _O._ _wendtii_ Müller and Troschel (1842) is the senior synonym for _O._ _riisei_ Lütken (1859).
4. _O._ _brevipes_ var. _longispina_ H. L. Clark (1921) is a synonym for _O._ _pusilla_ (Brock).
5. _O._ _lubrica_ Koehler (1898) is probably a synonym for

O. pusilla (Brock, 1888), not O. scolopendrina.

Since 1921, several new species of Ophiocoma have been proposed and their taxonomic position is considered in this study as follows:

1. Ophiocoma punctata Koehler (1930) is a junior homonym for O. punctata Forbes (1841), and is considered a junior synonym for O. canaliculata Lütken (1869).
2. O. pulchra H. L. Clark (1928) appears to be merely a color form of O. canaliculata Lütken.
3. O. latilanxa Murakami (1943) is a junior synonym for O. pusilla (Brock).
4. O. anaglyptica Ely (1941) is retained as a valid species.
5. Ophiacantha macroplaca H. L. Clark (1915) has been found to be a valid species of Ophiocoma.
6. Ophiocoma delicata H. L. Clark (1932) has been found to be a species of Ophiarachna based on examination of the holotype by Ailsa M. Clark (pers. comm.) and my own examination of a paratype deposited in the Museum of Comparative Zoology, Harvard.
7. O. alternans Endean (1963) is a junior homonym for O. alternans Martens (1870).

Species interrelationships in the genus Ophiocoma are based on interpretations of the skeletal parts.

Fundamental relationships appear to depend upon both internal and external characters.

It has been known for some time that certain species in the genus share characters which link them more closely together than to other species. Lütken (1869, p. 23 and 87) noted a similarity in the well developed and irregular arrangement of the upper arm spines in several species of Ophiocoma including echinata (as crassispina), erinaceus, scolopendrina, and wendtii (as riisei). However, it remained for H. L. Clark, (1921) to first discuss the possible relationships of the species in more comprehensive terms. He noted that differences in the disc granulation, number of tentacle scales and pigmentation, as well as limits of geographic distribution could be used to divide the genus Ophiocoma into three sections or groups. These he designated as Brevipes, Pumila, and Scolopendrina after nominal species in each group. Clark agreed to Matsumoto's (1917) suggestion that Ophiocoma brevipes was the most primitive species in the genus. Although it is not clear how Matsumoto arrived at this conclusion, Clark assumed that the limited number of dental papillae, close, fine disc granules, and greenish pigmentation represented primitive characters. Unfortunately, there is no evidence which supports these considerations. Clark indicated that species in the Scolopendrina group were derived from O. brevipes by a reduction in the number, but an increase in the size, of the disc granules, and by an increase in the number of dental papillae and their more defined arrangement. The evolution of the Pumila group from O. brevipes was also proposed. Clark (op. cit.) stated, "...the color has tended to become lighter, and green is an evident feature of young individuals and of recently regenerated arms. Now the color green is known in the genus otherwise only in brevipes, a fact which suggests that the pumila group has originated directly from brevipes" (p. 123).

Intraspecific evolution within each group was also proposed on the basis of differences in pigmentation and number of tentacle scales. However, the present study shows that these characters are considerably more variable than Clark realized. Yet more substantive criteria support the decision to divide the genus into several complexes. Differences in the oral and dental plates, the type of disc granulation, and the sequence of arm spines are among the most important characters indicating partition of the genus. Four species of Ophiocoma not included by Dr. Clark can be shown to divide the genus even further. Ophiocoma bollonsi and O. canaliculata are now included as the Canaliculata group. Two other species, O. pica and O. pusilla, while showing characters common to several of the groups (and other genera), cannot be placed with these and are considered separately.

It seems premature to suggest that direct evolution of any of the species groups from one another as Clark suggested. It appears more likely that each of the species' complexes, although allied, represents several derivations from one or more ancestral stocks.

Unfortunately, there is very little palaentological evidence available which supports phylogentic considerations.

Hess (1960, p. 754) indicated that up to this time no species in the genus Ophiocoma had been positively determined from the fossil record. Lütken (1869) had already given good reasons for the exclusion of previously described fossil species in this genus, primarily because the specimens had lacked the distinguishing disc and mouth parts. However, Wolburg (1939, p. 35) reported the fossil remains of Ophiocoma scolopendrina var. erinaceus as well as Ophiarthrum elegans from Liassic strata (lower Mesozoic, about 180 million years ago) in Europe.

Hess (loc. cit.) named Ophiocoma ? rasmusseni from a fossil ophiuroid arm section. He considered the arm vertebrae similar to the condition noted in O. aethiops (by Lyman, 1882, Pl. LXII, figs. 10-11). From the figures given by Hess for O. ? rasmusseni, one sees that the upper arm plates are very regular along their lateral edges without any obvious truncation. Furthermore, there is no evidence of an alternation in the number of arm spines which can be observed in his figure of the side of the arm. These two characters would exclude any of the species of Ophiocoma in the Scolopendrina group, including O. aethiops.

In 1964, Hess identified another species, again based on a partial arm sector, as Ophiocoma ? nereida (Wright). The grounds for this inclusion are difficult to interpret. In this case, as well as for O. ? rasmusseni, I would hesitate in considering either of Hess' species as ophiocomids without the supporting evidence based on structures of the disc or mouth skeleton.

Synoptic key to species in the genus Ophiocoma

1 Similar number of arm spines on each side of arm segment or adjacent segments; upper arm spine not noticeably thickened nor markedly longer than lower spines........................ 2

Irregular number of arm spines, alternating three and four, on each side of same segment or adjacent segments; upper arm spine thicker and markedly longer than lower spines ....................SCOLOPENDRINA GROUP 11

2 (1) Upper arm spines delicate, thin, minutely serrated, and compressed; lateral borders of upper arm plates extended, forming acute angle 3

Upper arm spines not delicate, thin, serrated nor compressed; lateral borders of upper arm plates not extended but rounded............. 5

3 (2) Adoral shields nearly or actually meeting in front of oral shields; oral shields broader than long .... CANALICULATA GROUP 4

Adoral shields confined to sides of oral shields; oral shields longer than broad; Indo-Pacific .... _O. pusilla_ (Brock)

4 (3) Disc granules near margin higher than thick; dental plate spatulate; New Zealand .... _O. bollonsi_ Farquhar

Disc granules no where higher than thick; dental plate not spatulate; southern

Australia.................. *O. canaliculata* Lütken

5 (2) Disc granules uniform in size, never elongate; with two tentacle scales on all proximal segments............................ 6

Disc granules variable in size, some elongate; with one tentacle scale on all except first few segments..... PUMILA GROUP [1] 9

6 (5) Upper arm spine shorter than lower, not tapering; disc granules very fine, 8 to 11 per millimeter........... BREVIPES GROUP 7

Upper arm spine longer than lower, tapering; disc granules coarser, 5 to 7 per millimeter...... *O. pica* Müller & Troschel

7 (6) Length of second and third arm spines less than breadth of aboral arm plate; oral surface white to yellow-white; maximum disc diameter 20 mm..... *O. brevipes* Peters

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[1] Small (d.d. to 7 mm) six armed forms of *Ophiocoma* are considered polymorphic forms of five armed species included in this key in the Pumila group; an exception is *O. sexradia* in which the pentamerous morph is unknown.

Length of second or third arm spine equal to or more than breadth of aboral arm plate; oral surface grey, brown or variegated; maximum disc diameter exceeding 20 mm 8

8 (7) Arm spines conspicuously annulated in color; 5 arm spines common on segment six .... O. doederleini Loriol

Arm spines not annulated in color; 4 arm spines on segment six .... O. dentata Müller & Troschel

9 (5) 5 arm spines continuing well beyond segment 10; third from upper arm spine longest;.................................. 10

5 arm spines seldom beyond segment 10; second from upper arm spine longest;............... .... O. pumila Lütken

10 (9) A light stripe down middle of oral arm surface;....................... O. alexandri Lyman

No light stripe down middle of oral arm surface;............ O. valenciae Müller & Troschel

11 (1) A series of enlarged scales in oral interbrachial disc region; disc granules

flattened, pavement-like; fourth upper
arm spine flask-shaped.......... O. anaglyptica Ely

No enlarged scales in oral interbrachial
disc region; disc granules rounded;
upper arm spines not flask-shaped.............. 12

12 (11) Four arm spines on each side of third
arm segment;............ O. macroplaca (H. L. Clark)

Three arm spines on each side of third
arm segment.................................... 13

13 (12) Oral surface of arms, especially proximal,
white or yellow-white; Indo-Pacific................
.... O. scolopendrina (Lamarck

Oral surface of arm, including proximal
area, black, dark brown, or tan................. 14

14 (13) Two arm spines on each side of first arm
segment; Caribbean.. O. wendtii Müller and Troschel

Three arm spines on each side of first
arm segment.................................... 15

15 (14) Third upper arm spine longer than fourth
upper arm spine of opposite side or adja-
cent segment; Baja, California to Equador
and Galapagos.................. O. aethiops Lütken

Fourth upper arm spine longer than third upper arm spine of opposite side or adjacent segment;............................ 16

16 (15) Disc granulation 25 to 36 granules per square millimeter; Caribbean. *O. echinata* (Lamarck)

Disc granulation 9 to 16 granules per square millimeter; Indo-Pacific................ 17

17 (16) Oral surface of arms and spines reddish brown; Western Australia...................... .... *O. occidentalis* H. L. Clark

Oral surface of arms and spines black or dark grey; Indo-Pacific and Clipperton Island.......... *O. erinaceus* Müller and Troschel

Brevipes Group

Species in the Brevipes group of *Ophiocoma* are limited to the Indo-Pacific region. Three species are recognized in this paper. The group can be separated from others in the genus on the basis of several distinctive characteristics.

1) There are four to five arm spines on each side of the arm segments proximally occurring on a greater number of segments the larger the individuals become.

2) The upper arm spine is seldom equal to, and usually

shorter than other arm spines in the same row.

3) The dental plate is characterized by: a) being between 1.8 and 2.3 times as long as broad; b) having wide flattened vertical septa dividing each tooth foramina; c) having the dental papillae region limited to less than twenty percent of the total length.

4) There are five oral papillae confined to each side of the oral angle of the jaw; in rare cases two of the oral papillae coalesce giving only four.

5) The disc granules are small, closely packed, and spherical, covering the aboral and interbrachial regions of the disc entirely to the mouth shields and almost to the genital apertures.

6) Two tentacle scales are present on each side of the oral arm plates for some distance from the base of the arm; the number of segments with two scales is a function of size.

Species of Ophiocoma in the Brevipes group include:

Species	Distribution
O. brevipes Peters	Tropical Indo-Pacific
O. dentata Müller and Troschel	Tropical Indo-Pacific
O. doederleini Loriol	Tropical Indo-Pacific

Ophiocoma brevipes Peters

(Plate VII, figs. 1-11)

SYNONYMY

Ophiocoma brevipes Peters, 1851, p. 466; 1852, p. 85; von Martens, 1870, p. 252; Lyman, 1865, p. 92; 1874, p. 225; 1882, p. 172 (pt.); Walter, 1887, p. 371; Whitelegge, 1903, p. 12; H. L. Clark, 1909, p. 542 (pt.); 1915, p. 291; 1917, p. 440; 1921, p. 129, Pl. 13, fig. 7, Pl. 34, figs. 3-4; 1925, p. 91, 1938, p. 333; 1946, p. 342; Matsumoto, 1917, p. 343 (pt.); Ely, 1942, p. 56, fig. 16a-b, Pl. 13c; Murakami, 1942, p. 34; 1943a, p. 193; 1943b, p. 217; Edmondson, 1946, p. 84, fig. 40a; A. H. Clark, 1949, p. 53; 1952, p. 296; 1954, p. 260; Endean, 1953, p. 55; 1956, p. 126; 1957, p. 244; Domantay and Domantay, 1966, p. 51.

Ophiocoma brevispinosa Smith, 1876, p. 40; 1879, Pl. LI, fig. 1.

Ophiocoma breviceps [sic] Peters: Etheridge, 1887, p. 39.

MATERIAL EXAMINED

Christmas Island (Pacific Ocean) - BPBM: W565a (1)

Gilbert Islands (Onotoa Atoll) - USNM: E8068 (1)

Hawaiian Islands

Hawaii - USNM: E6757 (1), E7099 (1); Pers. Coll. (15)

Kauai - BPBM: W1552a-b (2)

Kure - BPBM: W336 (1)

Laysan - BPBM: W285 (1)

Midway - BPBM: W284 (1)

Oahu - BPBM: W862 (1), W1099 (1), W1387 (2); Pers. Coll. (39)

Pearl and Hermes Reef - BPBM: W337 (1)

Marshall Islands

Eniwetok Atoll - BPBM: W1445 to W1451 (6)

Rongerik Atoll (Bigonattan Islet) - USNM: E7330 (1)

Mossambique - BPBM: W1571 (1); ZMB: No. 961 (1), No. 962 (1), (SYNTYPES)

Querimba Islands (Mossambique Channel, Indian Ocean) - ZMB: No. 4660 (3) (SYNTYPES)

DIAGNOSIS

Size. Largest specimen examined with d.d. 19 mm and arm length 80 mm. Sexually mature specimens from 7 mm (d.d.).

Disc cover. Beset with fine, closely grouped granules extending completely into oral interradial region.

Tentacle scales. Two on each pore proximally and occurring on more distal segments with increase in size. Very strong positive correlation ($r = 0.88$) between number of segments with two scales and size of specimen (based on breadth of tenth oral arm plate) (TABLE I). Student's t test for 19 degrees of freedom, 7**, highly significant. Regression formula, Y = 88.90X - 21.90.

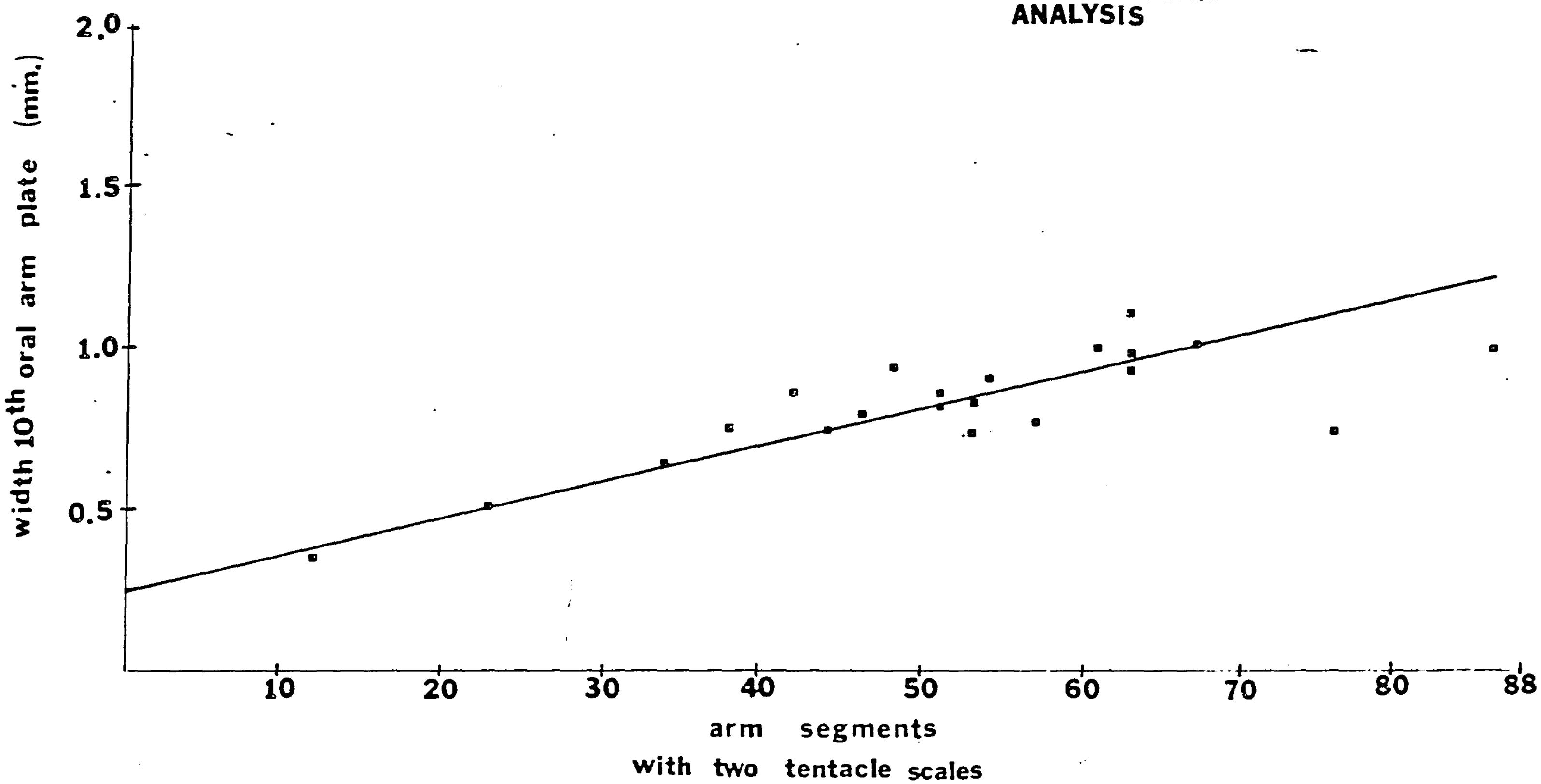
Arm spines. Number of spines on all but most proximal segments increasing with size. Upper two spines in row shorter and more compressed than lower spines, especially in proximal half of arm. Maximum arm spine length seldom greater than breadth of aboral arm plate.

Sequence of arm spines (TABLE II) based on forty-eight specimens from Hawaiian Islands. At least three arms on each animal counted from specimens ranging in size between 2.0 to 17 mm (d.d.). Results show: a) proximal three segments with 3-3-4 spines; b) presence of fifth spine beginning on segment four at size approximately 5 mm (d.d.), and occurring to segments six and seven by 5 mm (d.d.); c) 6 spines on segments seven through eleven in specimens from 10 mm (d.d.); d) number of segments bearing 4 spines increasing as individuals becoming larger, as far as segment seventy in specimens 15 mm or larger.

Dental papillae. One or two semicircular rows around base of lower (oral) tooth, in specimens larger than 10 mm (d.d.); from three to six papillae at apex of jaw

TABLE I

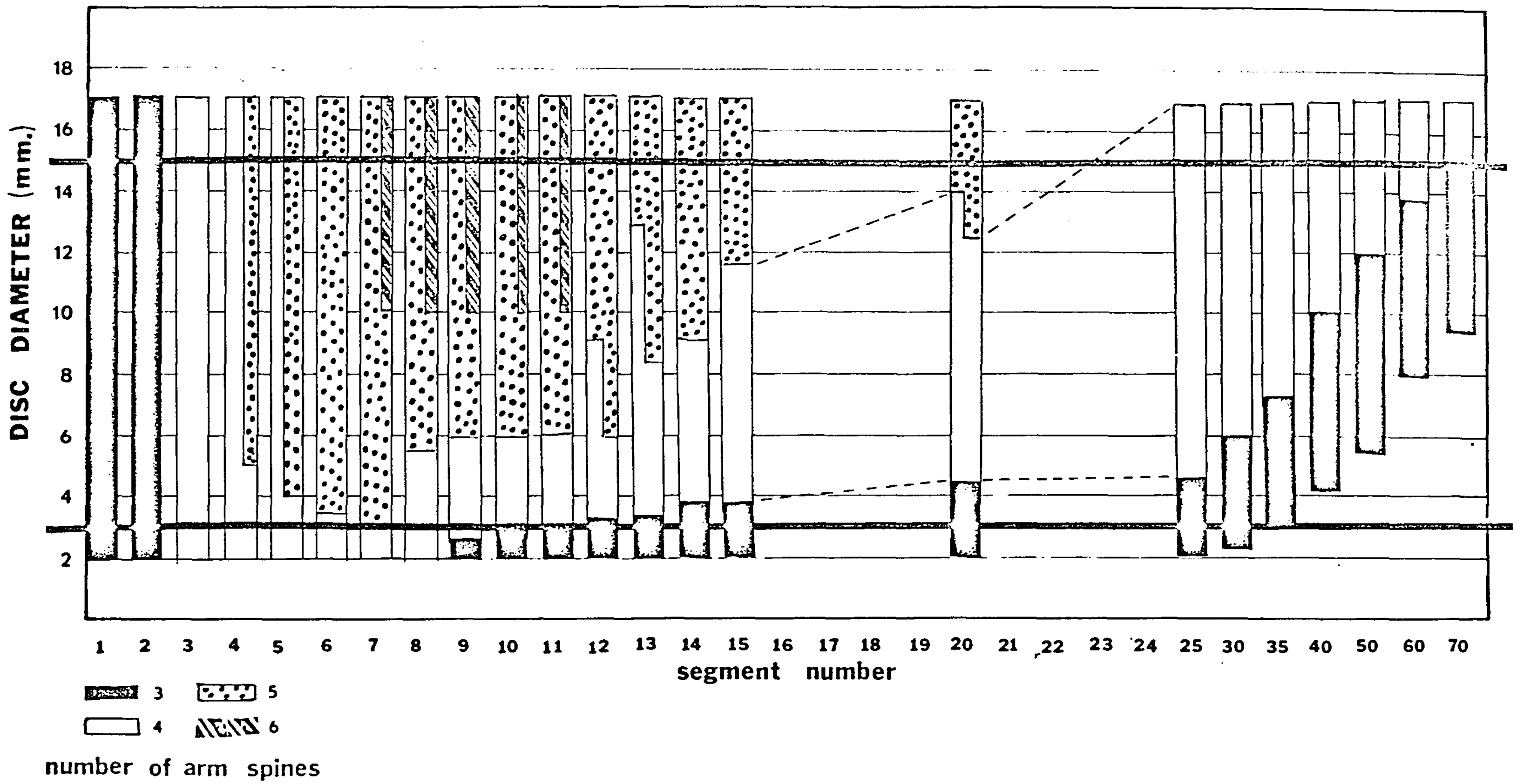
OPHIOCOMA BREVIPES — TENTACLE SCALE ANALYSIS



Ophiocoma brevipes

TABLE II

ARM SPINE SEQUENCE



and occurring above, not on, dental plate.

Dental plate (Pl. VII, figs. 6,9,11,b). Length to breadth ratio, less than 2.4 : 1; shape of vertical septa between tooth foramina as well as restriction of dental papillae to base of the plate similar to condition for other species in Brevipes group (i.e. dentata and doederleini). Ely's (1942, p. 57) statement that the dental plate was "twice as broad as long" is erroneous.

Oral papillae. Five on each jaw angle; fourth distal papilla widest.

Oral plate (Pl. VII, fig. 11,d). Similar to condition noted for O. dentata and O. doederleini.

Oral shields. Generally oval, slightly longer than broad, but varying to broader than long.

Adoral shields. Triangular, widely separated; sometimes with several granules along distal angle (Ely, 1942).

Pigmentation. Presence of pair of grey spots on edge of disc where arm emerges (in specimens preserved in alcohol these may fade out); oral surface uniformly white, except toward tips of arms. Additional color notes in Ely (1942).

HABITAT AND BEHAVIOR

Based on my observation in Hawaii, specimens of *O. brevipes* have been found under or within lava or dead coral which covers a sandy substratum. In several instances this species was observed partially buried in the sand, and because of the light, variegated pigmentation of the aboral surface of the disc and arms, specimens were difficult to see. Ely (1942) found only one or two specimens at a time occurring together. I have also observed few specimens in any one place together. In contrast to *Ophiocoma dentata*, I have not observed *O. brevipes* exhibiting a posture in which the arms extend vertically above the disc when a specimen was released in water above the substratum. Instead, the arms of *O. brevipes* coil horizontally. H. L. Clark (1938, 1946) reported that this species had the habit of bringing in and folding the arms closely around the disc as individuals were observed in holes or depressions among coral or coralline algae.

ASSOCIATES

The ectocommensal plynoid worm, *Hololepidella nigropunctata* (Horst) has been found on *O. brevipes* and other echinoderm hosts in Hawaii (Devaney, 1967). The worm appears to be less commonly associated with *O. brevipes* than *O. dentata*.

DISTRIBUTION

The species has a broad Indo-Pacific range, but the exact limits are not clearly defined owing to a number of workers confusing this species with *O. dentata*. The original specimens came from the East African coast (Peters, 1851). Indian Ocean records were made by Smith (1876), von Martens (1870), and Walter (1885). Domantay and Domantay (1966) record the species from the Philippines, and Endean (1957) gives Australian records. A specimen from the Gilbert Islands was reported by Whitelegge (1903) and others by Lyman (1865). Specimens I have examined indicate the dispersal of *O. brevipes* to many Pacific localities. In southeastern Polynesia, H. L. Clark (1917) reported this species from the Tuamotus. Records from the Ryukyu Islands and southern Japan (Matsumoto, 1917; Murakami, 1942) may be valid, but there is a chance that these are based on specimens of *O. dentata*.

The bathymetric range of this species is not clearly defined; most specimens are taken in the shallow sublittoral to a depth of about five meters. Specimens from deeper waters have been recorded (A. H. Clark, 1949) and in my own collection there are specimens from 50 meters off Hawaii.

DISCUSSION

A number of reports of Ophiocoma brevipes is probably based on specimens which should be designated as O. dentata. Lyman (1874) confused the issue when he had the opportunity to comment on the type specimens of O. brevipes, O. ternispina and O. insularia (the last two considered synonyms for O. dentata). In reference to O. 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" (p.225). My own examination of five of Peter's syntypes (d.d. 12 to 18 mm) reveals: a) an arm spine sequence of 3-3-3-4 for the first four segments with 5 and/or 6 spines to segment ten; 4 arm spines continued distally well beyond segment thirty; 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 specimens of O. brevipes closely parellels what I have already shown for specimens from Hawaii (see TABLE II). It will be noted however that there is one significant difference; in the Hawaiian specimens, 4 spines occur on the third segment, whereas only 3 occur on this segment in the types. I interpret this to be a subspecific difference, indicative of the isolated, peripheral position of Hawaii in the Indo-Pacific. Specimens from Christmas Island (Pacific Ocean) and Eniwetok Atoll, showed both 3 and 4 spines on the third segment, suggesting the genetic potential for either condition.

Those records of *O. brevipes* which appear to be for *O. dentata* have been listed in the synonymy section of the latter species. In some cases I have made these determinations on the basis of the size of the specimen(s) recorded; if a disc diameter of over 20 mm was given it can be fairly certain that the worker dealt with a species other than *O. brevipes*. In other cases, where possible, pigmentation and additional morphological characters have been used as well.

Separation of *Ophiocoma brevipes* from *O. dentata* and *O. doederleini* can be made on the basis of the arm spine sequence for specimens of similar size. Equally as good a character is the relationship between the maximum arm spine length and the breadth of the aboral arm plate. In *O. brevipes* the longest arm spine rarely exceeds the breadth of the arm plate and is usually less; in *O. dentata* and *O. doederleini* particularly, the longest arm spine greatly exceeds the breadth. In the field, pigmentation differences make the species easy to distinguish. *O. brevipes* is nearly all white or light cream colored on the oral surface whereas the other two species show grey, brown, or variegated coloration.

In addition to the five syntypes listed in the material examined section of this paper, there is at least one additional specimen deposited in the Berlin Museum from Mossambique (ZMB: No. 963). Designation of a lectotype will be made in subsequent publication.

The holotype of *Ophiocoma brevispinosa* (Smith, 1876) is deposited in the British Museum (Natural History) under registrar No. 76.5.5.25.

Ophiocoma dentata Müller and Troschel
(Plates I-VI; VIII, figs. 1, 3-9; IX, figs. 4-7; X, figs. 3-4)

SYNONYMY

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

Devaney, 1967, p. 296, fig. 5,a.

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

Ophiocoma insularia Lyman, 1861, p. 80; 1865, p. 89; 1874, p. 225; Ljungmann, 1866, p. 329; H. L. Clark, 1915, p. 291, Pl. 15, figs. 3,4; Koehler, 1922, p. 314; Galtsoff, 1933, p. 19; Ely, 1942, p. 57, fig. 17, Pl. 13,A; A. H. Clark, 1949, p. 50; Edmondson, 1946, p. 84, figs. 40b, 41i,j; Domantay and Domantay, 1966, p. 52.

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

Ophiocoma brevipes Peters: Lyman, 1874, p. 225; 1880, p. 27 (pt.); 1882, p. 172 (pt.); Walter, 1884, p. 371; Bell, 1887, p. 648; Marktanner-Turneretscher, 1887, p. 303; Loriol, 1893b, p. 25, Pl. XXIII, figs. 4-4a; Koehler, 1905, p. 61; 1922, p. 319, Pl. 72, figs. 6-9; H. L. Clark, 1908, p. 296; Benham, 1911, p. 153; Matsumoto, 1917, p. 343 (pt.), fig. 3, a-c.

Ophiocoma variegata Smith, 1876, p. 39; 1879, p. 565, Pl. LI, 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*); 1923a, p. 247 (forma *dentata* and *doederleini*); 1926, p. 186 (forma *dentata* and *doederleini*); Edmondson, 1933, p. 71, fig. 32c.

Ophiocoma brevipes var. *insularia* Lyman: H. L. Clark, 1921, p. 130; 1925, p. 92.

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; Edmondson, 1946, p. 84; Endean, 1953, p. 55; 1957, p. 244; Domantay and Domantay, 1966; p. 53.

MATERIAL EXAMINED

Australia (Green Island, Queensland) - MCZ: No. 3754 (1)

Easter Island - USNM: E.648 (2), E9797 (6)

Eniwetok Atoll - BPBM: W1512, W1513 (2), W1498 (1), W1657 (1)

Fiji Islands - BPBM: W852c (1)

Hawaiian Islands

Kure - BPBM: W286 (2)

Kahoolawe - BPBM: W510 (1)

Laysan - BPBM: W287 (13)

Maui - BPBM: W870 (1)

Oahu - BPBM: W288 (2) W327 (1), W328 (12), W331 (2), W755 (2), W970 (11), W1347 (1), W1390 (1); MCZ: No. 319 (12)
(SYNTYPES, Ophiocoma insularia); Pers. Coll. (47)

Indian Ocean

Cocos-Keeling Island - USNM: E7450 (7)

Mauritius - MCZ: No. 5337 (4)

Japan (Tanegashima) - USNM: No. 25833 (4)

Raratonga - BPBM: W772 (1)

Tahiti - MCZ: No. 4510 (1), USNM: E8899 (2)

Unknown locality - ZMB: No. 931 (HOLOTYPE, Ophiocoma dentata)

DIAGNOSIS

Size. Specimens examined from 0.7 mm to 34 mm (d.d.); arm length largest specimen, 153 mm. Sexually mature individuals from 12 mm (d.d.).

Disc cover. Granules, small, closely packed covering aboral and oral interbrachial areas completely.

Tentacle scales. Two on each pore starting proximally and occurring on more distal segments with increase in size.

For specimens from 1.8 to 30 mm (d.d.), a very strong correlation between size (based on the breadth of the tenth oral arm plate) and the number of segments with two tentacle scales (TABLE III). Results showing: a) a positive rectilinear regression of size on the number of segments with two scales; b) regression equation, $Y = 37.55X - 3.55$; c) correlation coefficient ($r = 0.91$) and Student's t test for 31 degrees of freedom giving value of 15**, indicating a highly significant relationship between size and number of segments with two scales.

Arm spines. Analysis of the arm spine sequence for a series of eighty-two specimens from the Hawaiian Islands ranging from 2 mm to 30 mm (d.d.) (TABLE IV). Results showing: a) proximal four segments each retain same number of spines regardless of size of specimen; b) beyond first four proximal segments, number of spines increasing with size; c) maximum number of spines 5, occurring on segments seven to ten (comparison with TABLE V, p. 71 where specimens larger than 24 mm (d.d.) from Eniwetok which shows 5 arm spines occasionally out to segment thirteen); d) 4 arm spines occurring on more segments distally with size increase, seldom found

TABLE III

OPHIOCOMA DENTATA – TENTACLE SCALE ANALYSIS

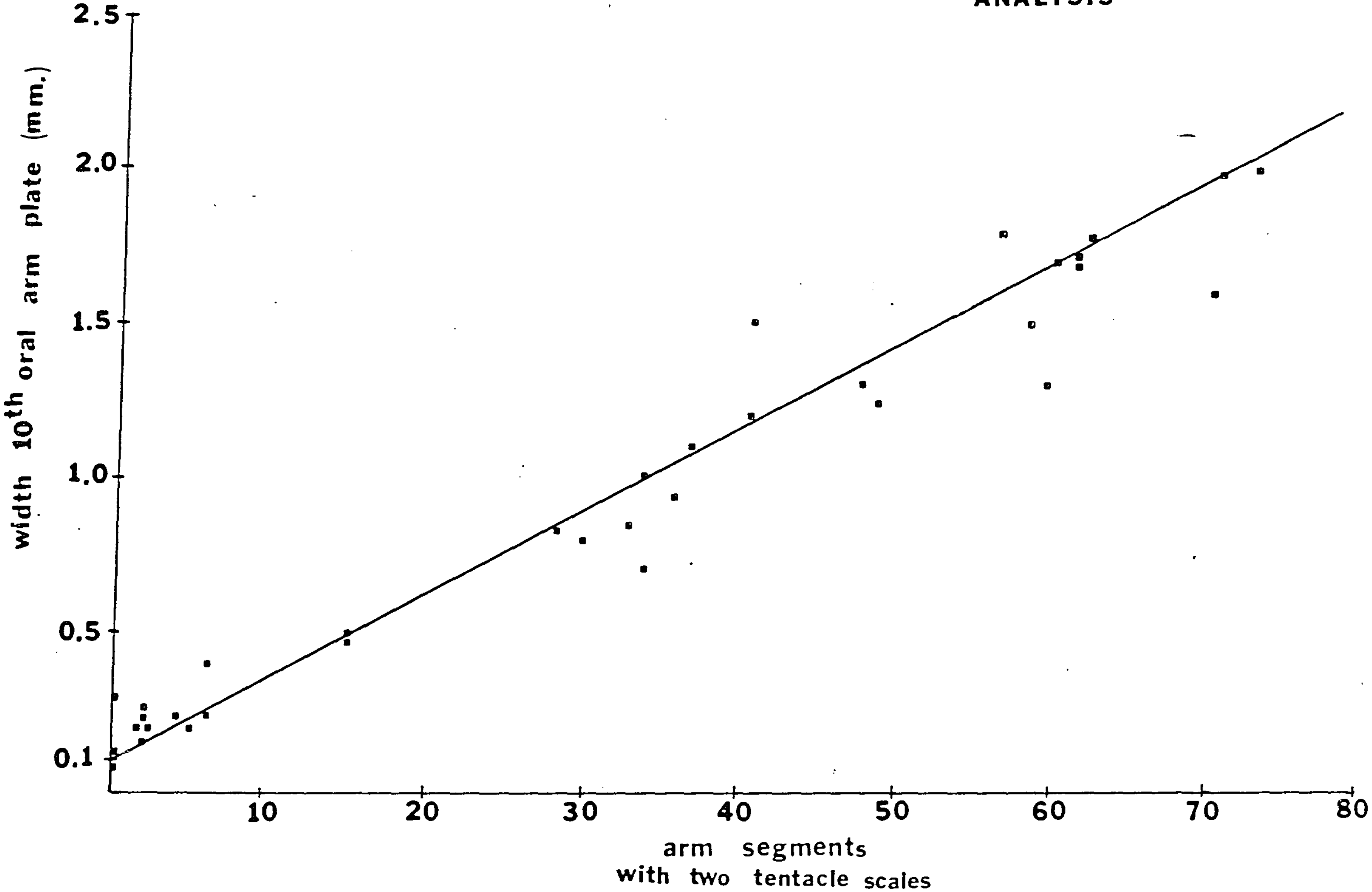
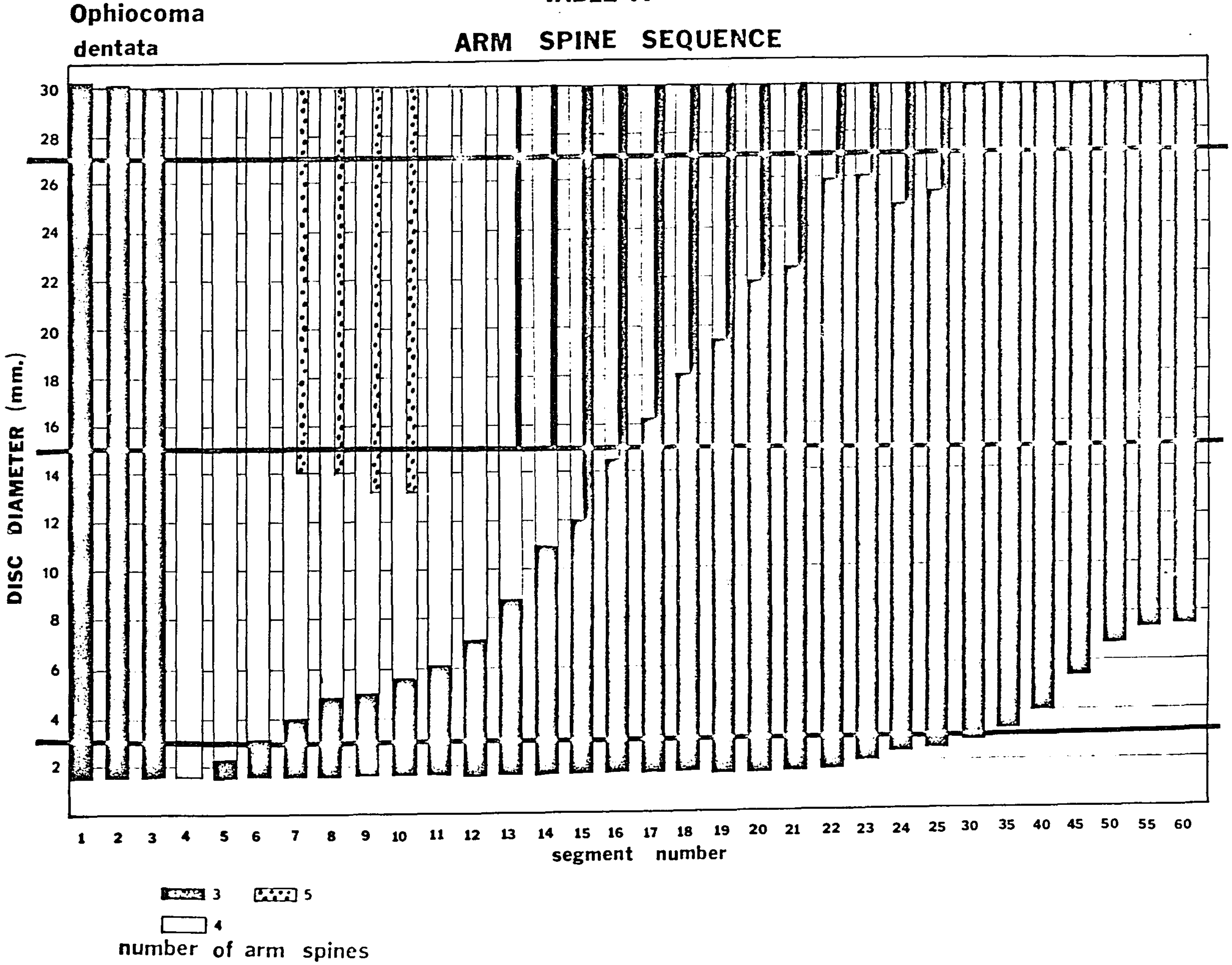


TABLE IV



Ophiocoma
dentata
ARM SPINE SEQUENCE
DISC DIAMETER (mm.)
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 30 35 40 45 50 55 60
segment number
3
5
4
number of arm spines

beyond segment twenty-five (to segment thirty in Eniwetok specimens, TABLE V, p. 71); e) distally, number of arm spines 3. Sequence for type specimen (d.d. 17.5 mm) 3-3-3-4, with 4 spines continuing to segment eighteen and, on one sector, irregularly to segment twenty-eight; 5 spines only on one side of one arm (segment eight); 3 spines on distal segments. Upper arm spine in most specimens distinctly shorter and broader than lower spines; second or third spine longest (Pl. X, fig. 3).

Dental papillae. Limited to two semicircular rows on oral part of dental plate. Also group of papillae often above apex of jaw, not attached to dental plate in specimens above 10 mm (d.d.).

Dental plate. (Pl. VIII, fig. 1, lower; fig. 2). Typical Brevipes group characters; a) length to breadth ratio 1.8 - 2.3 : 1; b) vertical septa between teeth foramina wide and thin; c) less than one-third of total length occupied by dental papillae area.

Teeth. Quite stout and broad, with well defined hyalinated tips.

Oral papillae. Typical for Brevipes group with five along each jaw margin, having outer papilla slanted inward.

Oral plate. Characters in common with O. brevipes and O. doederleini; i. e. abradial muscle surface well developed with distinct muscle scars. In other respects, conforming well with Murakami's (1963, p. 28) description of this plate for O. brevipes.

Pigmentation. See DISCUSSION (p. 67).

HABITAT

Ophiocoma dentata has been frequently collected in the shallow sublittoral waters of Hawaii where it ranks as one of the most common ophiuroids. It is usually found where lava or coral boulders cover a sandy or pebbly substratum. This species, like other Hawaiian ophiocomids is uncommon or absent where silt and mud accumulate and form the predominant bottom deposit.

ASSOCIATES

A small ectocommensal polynoid identified as Hololepidella nigropunctata (Devaney, 1967) has frequently been observed on Ophiocoma dentata collected in the Hawaiian Islands. Although the commensal is not restricted to this host alone, it appears, in Hawaii, most commonly associated with O. dentata.

DISTRIBUTION

The locality of the type specimen is unknown. Lütken's (1859) specimens of *Ophiocoma dentata* were taken from the Nicobar Islands, Indian Ocean. Smith (1876) collected his specimen (as *O. variegata*) from Mauritius Island, Indian Ocean. H. L. Clark (1921) lists specimens from Lord Howe Island, Zanzibar, and Torres Strait and in 1923 (as *O. brevipes* var. *variegata*) from the West Australian coast (Abrolhos Islands). I have examined H. L. Clark's (1911) specimens (identified as *O. brevipes*) from southern Japan which verified the existence of *O. dentata* there. The colored illustration of *O. dentata* (as *O. brevipes*) by Utinomi (1961) also indicates the presence of this species in Japanese waters, as Matsumoto's (1917) record (as *O. brevipes*) suggested.

Pacific records include a large number of island groups. Lyman's (1861) specimens of *O. insularia* were collected in Hawaii and the Gilbert Islands. Additional records include Easter Island (H. L. Clark, 1917), and the Society Islands, Fiji, and the Marshall Islands based on material I have examined. The species has also been reported (Endean, 1965) from Australian Great Barrier Reef localities.

Bathymetrically, *O. dentata* is not known below approximately 20 meters, and is much more common between 1 and 5 meters. H. L. Clark's (1939) small specimen (d.d. 3.5 mm) from 73-165 meters off Zanzibar is suspect and will require verification.

DISCUSSION

Lyman (1865, p. 70) stated that Müller and Troschel's name, *Ophiocoma dentata* was invalid, appearing to be "...only a middling sized *Ophiocoma exhinata*." Lütken (1859) described additional specimens which he considered *O. dentata*. Subsequent reports, especially by Lyman (1882) and H. L. Clark (1921) considered Lütken's specimens to be different from Müller and Troschel's. An examination of Müller and Troschel's type specimen deposited in the Berlin Zoologisches Museum shows that Lyman was mistaken in considering the specimen *Ophiocoma echinata*, and there is no doubt that it belongs in the Brevipes group of *Ophiocoma*.

Several important features support the conclusion that the specimens named by Lyman as *O. insularia* and by Smith as *O. variegata* are synonymous with *O. dentata*. Several characters which were not listed by Müller and Troschel in their very brief original description are essential in showing the taxonomic position of this species based on the type:

a) the disc diameter is 17.5 mm; the arms are all broken, and the maximum number of arm segments remaining is thirty-seven.

b) the disc granules are very fine, closely packed and approximately 0.07 mm in diameter; the granules extend to the mouth shields orally and to the edge of the genital slits.

c) the teeth are broad and hyalinated at the tip.

d) the oral papillae are five on each jaw edge.

e) the arm spine sequence has already been considered (p.59).

In the above respects, the type of O. dentata resembles Lyman's (1865) description of O. insularia very closely. Examination of several of the type specimens of O. insularia indicates that this species should certainly be considered a synonym of O. dentata.

Ailsa M. Clark kindly sent me information on the arm spine sequence for Smith's type of O. variegata. This specimen, with a disc diameter of 28 mm has 3 spines on segments one to three followed by 4 spines, with few exceptions, as far as segment twenty-one. Then, 3 or 4 spines (generally 3) to segment twenty-eight, and 3 spines on the distal segments. None of the segments apparently carries 5 spines. A comparison of other morphological characters described by Smith indicates that *O. variegata* should also be considered a synonym of *O. dentata*.

Considerable variability in the color of the aboral surface occurs in *O. dentata* and has resulted in the establishment of new species and color varieties. Details concerning the various color patterns of the disc and several morphological features distinguishing *O. dentata* from closely related species are presented in my diagnosis of *Ophiocoma doederleini* (p.81). The major points which have been noted show that the aboral surface of the disc and arms may be either variegated with brown and white or dark gray and white or uniformly brown or gray. Orally, the color is generally light brown or grey, seldom white. The very uniformly dark grey 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, and the disc pattern reticulated or spotted (Pl. IX, figs. 4-5, 7-9) appear to be more common in the western Central Pacific and Indian Ocean.

The species identified as Ophiocoma ternispina by Martens from the Philippines (Flores) and O. marmorata by Marktanner-Turneretscher cannot, on the basis of their descriptions, be separated from O. dentata and are considered synonymous.

The description of Ophiocoma squamata (Lamarck) by Müller and Troschel certainly suggests O. dentata. However, as Lyman pointed out the type specimen of O. squamata (1874, p. 225) was lost, and the brief description could equally be of O. brevipes. With this in mind, it seems advisable to suggest a rejection of the name Ophiocoma squamata from zoological nomenclature.

One further note should be made. Specimens identified by Balinsky (1957) as Ophiocoma insularia from Inhaca Island, Mossambique have been re-examined by me. They represent the species Ophiocoma pusilla (Brock) (see p. 154).

Type specimens synonymous with O. dentata not listed above in MATERIAL EXAMINED are located in the following places:

Ophiocoma variegata Smith - British Museum (Natural History); Registrar No. 76.5.5.21

Ophiocoma ternispina Martens - Zoologisches Museum, Berlin; No. 1815

Ophiocoma marmorata Marktanner-Turneretscher - K. K. Naturhistorischen Hofmuseums, Wien, Austria

Ophiocoma doederleini Loriol

(Plates VIII, figs. 1-2; IX, figs. 1-6; X, figs. 1-2, 4-5, 7)

SYNONYMY

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

NOT *Ophiocoma brevipes* var. *variegata* forma *doederleini*: H. L. Clark, 1921, p. 130.

NOT *Ophiocoma insularia* var. *variegata* forma *doederleini*: H. L. Clark, 1938, p. 330; 1946, p. 246.

MATERIAL EXAMINED

Marshall Islands (Eniwetok Atoll) - BPBM: W1419a-b (2), W1420 (1), W1421 (1), W1422a-b (2), W1509 (1), W1532 (1), W1659a-b (2), W1660a-b (2), W1662 (1)

Society Islands (Moorea) - USNM: E8903 (1)

DIAGNOSIS

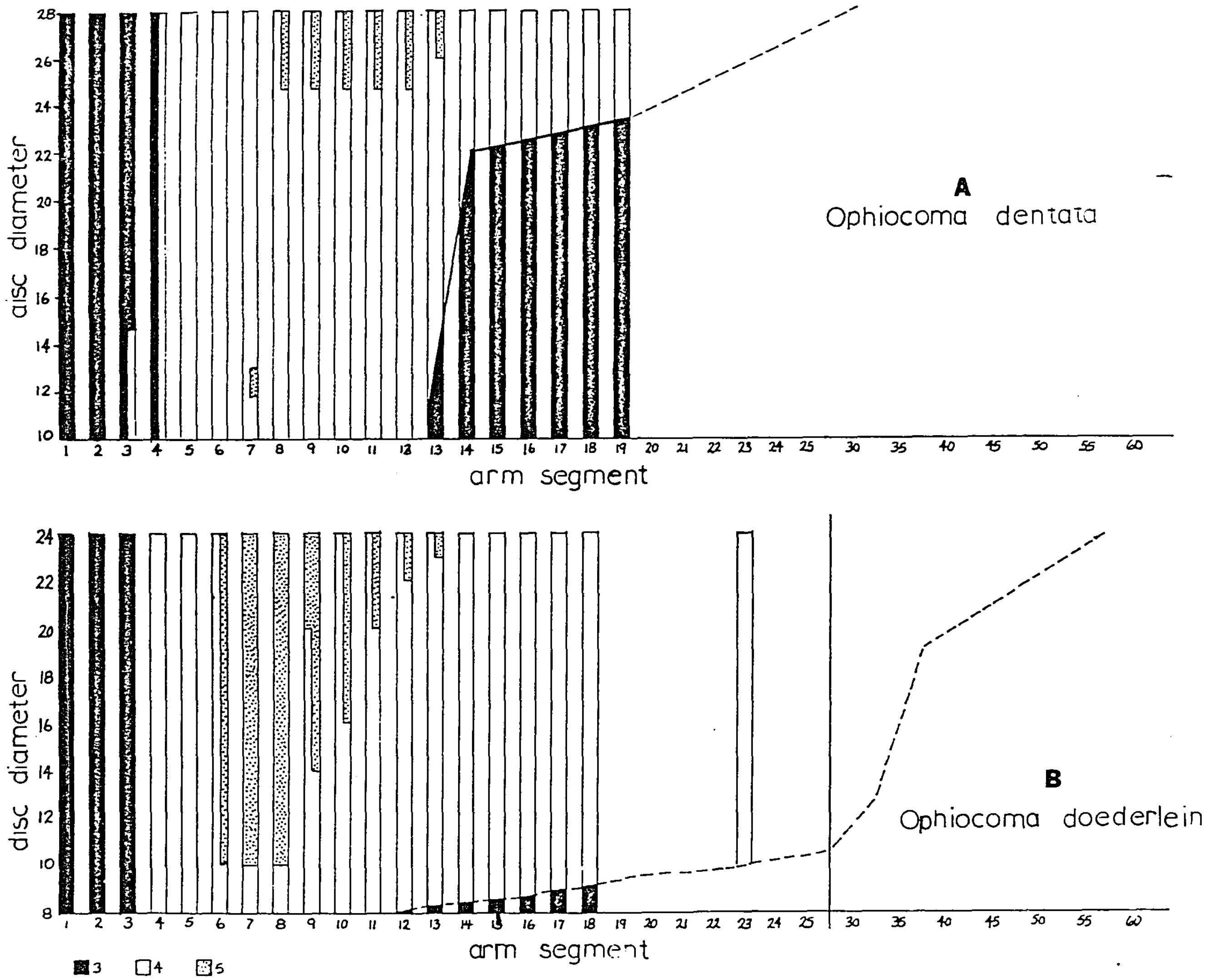
The basic external features of *Ophiocoma doederleini* were considered by both Loriol in his original description, and Koehler in 1922. Because a great amount of confusion has arisen concerning the taxonomic position of this species, especially in relation to *O. dentata*, several features are considered which support the taxonomic integrity of *O. doederleini*. The characters discussed also further clarify the specific characters of both *O. dentata* and *O. brevipes*.

Arm spines. Arm spine sequence of seven specimens of *O. doederleini* (d.d. 9 to 24 mm) and five specimens of *O. dentata* compared (TABLE V). All specimens from Eniwetok. The following differences between the two species noted:

O. doederleini	*O. dentata*
1. Only 4 arm spines on segment four	1. 3 and 4 arm spines on segment four
2. 4 or 5 spines on segment six	2. Only 4 spines on segment six
3. 5 spines occurring on segments seven and eight (d.d. from 12 mm),	3. 5 arm spines rare on segments seven and eight (d.d. exceeding 20 mm);

TABLE V

ARM SPINE SEQUENCE



number of arm spines

O. doederleini cont.	*O. dentata* cont.
and out to segment four-teen with increase in size	out to segment thir-teen (above 23 mm d.d.)

4. For specimens of comparable size, a greater number of arm segments bearing 4 arm spines in *O. doederleini* than in *O. dentata*. Specimens of *O. doederleini* between 13 and 14 mm (d.d.) with four spines to segments thirty-two to thirty-eight; specimens of *O. dentata* of the same size with 4 spines to only segment seventeen. The sharp rise (indicated by the broken line in TABLE V) in the development of the fourth arm spine for *O. dentata* from segment thirteen to fourteen suggests that some factor suppresses the development of the fourth arm spine or at least retards this process after a certain size is reached. This is not the case for *O. doederleini* where the fourth spine appears consistently on more segments with increase in size (the same holds true for *O. brevipes*, see TABLE II).

In order to test the validity of Koehler's (1922, p. 321) statement that the width of the arm of *O. doederleini* was greater than for *O. dentata* (as *O. brevipes*), an analysis of the breadth of the arm has been made. The tenth free arm segment was used for each specimen. This segment corresponds to segments fifteen to seventeen counting those segments beneath the disc in specimens larger than 8 mm (d.d.).

The total breadth of the arm segment is herein designated as the arm span consisting of three components: a) the combined length of the longest arm spine from each side of the segment (spine length); b) the breadth of the aboral arm plate (ab. plate); c) the extension of the lateral arm plates (lat. plate). The arm spines were first removed from the arm segment and measured separately. To their length was added the measurement of the above two components combined. Each of the components was converted to a percentage of the total arm span. The data obtained for *O. doederleini* and *O. dentata* are presented below (TABLES VI and VII).

TABLE VI. ARM SPAN (10TH FREE SEGMENT) - OPHIOCOMA DOEDERLEINI LORIOL

Locality	Disc Diameter (mm)	% Spine Length	% Ab. Plate	% Lat. Plate	Total Arm Span (mm)
Eniwetok	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
Society Islands (USNM E8903)	18.5	62	22	16	12.6
Zanzibar* (Brit. Mus.)	22		23		16
	23		26		15
Mauritius† TYPE	31				17

	Range	61-65%	20-24%
Eniwetok &	X	62.8 %	21.8 %
Society	s	1.32	1.18
Islands			
N=8			

* Data from Ailsa M. Clark (pers. comm.)

† After Koehler (1922, p. 321)

TABLE VII. ARM SPAN (10th FREE SEGMENT) - OPHIOCOMA DENTATA MULLER AND TROSCHEL

Locality	Disc Diam. (mm)	% Spine Length	% Ab. Plate	% Lat. Plate	Total Arm Span (mm)
Hawaii	9.5	60	24	16	6.50
	15.5	58	28	14	10.00
	18.0	64	24	12	11.40
	20	62	25	13	12.25
	25	63	25	12	15.35
	25	58	29	13	14.20
	28	63	26	11	17.20
	31	61	30	8	17.10
Unknown-TYPE *O. dentata*	17.5	54	28	18	11.00
Rodriguez Is. TYPE - *O. variegata*	28	58	29	13	13.5
Cocos-Keeling Is. (USNM E7450)	15	58	32	10	10.0
	16.5	61	26	13	9.7
	19	56	33	10	11.2
	21	61	30	9	11.5
	22.5	58	34	9	11.7
Easter Is. (USNM E648)	12.5	59	28	13	7.3
	22.5	59	24	17	12.3
Fiji Is.	16	62	27	14	8.2
	16	62	29	9	9.9
Barrier Reef	24	58	29	13	12.0
Mauritius	23	62	29	8	11.0
East Indies	19	66	25	9	13.0
Maldives	19	59	26	15	11.0

TABLE VII. (Continued)

Locality	Disc Diameter (mm)	% Spine Length	% Ab. Plate	% Lat. Plate	Total Arm Span (mm)
Eniwetok (Marshall Islands)	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
Total Sample N=28	Range 9.5-31	54-66%	24-34%	8-18	6.5-17.2
	X	59.5%	27.9 %		
	s	3.00	2.73		
Hawaii N=28	Range 9.5-31	58-64%	24-30%		
	X	61.6 %	26.4 %		
Eniwetok N=5	Range 12-28	54-61%	26-32%		
	X	57.2%	28.2 %		
	s	1.82	2.23		

The comparison of the arm span between the two species from the same locality, Eniwetok (and one specimen of _O._ _doederleini_ from the Society Islands), for specimens 9 to 28 mm (d.d.), gave the following results:

First, the difference in mean percentage of the total arm span occupied by the arm spines in the two species was highly significant (for 11 degrees of freedom, a Student's t test gave a value of 9.2**). The five specimens of _O._ _dentata_ from Eniwetok had a percentage range between 54 and 61; specimens of _O._ _doederleini_ a percentage range between 61 and 65.

Second, examination of the difference in the mean percentage of the arm span taken up by the breadth of the aboral arm plate showed an opposite trend. In this case, the aboral arm plates of _O._ _dentata_ occupied a significantly greater part of the arm span (for 11 degrees of freedom, t= 2.97**). No overlap between the two samples was noted.

Third, comparison of the total arm span for the two species supports Koehler's (1922) contention that _O._ _doederleini_ has a greater arm span than _O._ _dentata_ for specimens of comparable size. For example, the total arm span of a 26-28 mm (d.d.) specimen of _O._ _dentata_ was 13.1

mm; for a specimen of O. doederleini with a disc diameter of only 24 mm, the arm span was 15.2 mm.

It should be noted however, that where specimens of O. dentata from localities other than eniwetok were compared with O. doederleini there was less contrast in the arm span for specimens of comparable size. This was especially true for Hawaiian specimens of O. dentata which showed a relatively greater arm span than specimens from other localities examined.

In addition to the arm spine sequence and the arm span, the length of arm spines from two different segments on an arm of the same individual were compared. The same five specimens of O. doederleini from Eniwetok and a single specimen from the Society Islands used in the arm span analysis were again examined. In these specimens, ranging in size from 9 to 24 mm (d.d.), it was found that the penultimate or antepenultimate upper spine was the longest on the tenth true arm segment. The length of the longest arm spine ranged from 2.2 mm in the 9 mm (d.d.) specimen to 3.9 mm in the 24 mm (d.d.) specimen. The upper and lower arm spines were approximately the same length, but either could be slightly longer than the other. From the tenth free segment (approximately the fifteenth to seventeenth true segment) the middle spines were also the longest; these however showed an increase in length of 2.5 mm to 4.9 mm in specimens the same size as above. In contrast to the tenth true segment, the lower spine was longer than the upper spine in all cases.

The relative length of the arm spines from the tenth free segment are shown in Plate X, fig. 4, for specimens of O. doederleini and O. dentata the same size from Eniwetok. The spines of the former species were found to be relatively longer than wide compared with those of the latter.

Dental plate. These plates, from similar sized specimens of O. doederleini and O. dentata (d.d. 21 mm) revealing a difference in shape (Pl. VIII, fig. 1). In O. doederleini a distinct widening of the lower (oral) region at the level where tooth papilla indentations terminate (arrow). In a smaller specimen of O. doederleini (d.d. 9 mm) only the beginning trace of the widening was noted (Pl. VIII, fig. 2). No widening noted for the dental plate of O. dentata nor O. brevipes of any size. In other respects the dental plate of O. doederleini with characteristics of the Brevipes group of Ophiocoma, i.e. length to breadth ratio (1.9 to 2.1 : 1); tooth papillae region about one-third or less of the length of the plate; and very thin, wide septa between the teeth fossae.

Pigmentation. Disc orally and aborally grey, either with darker spots of varying size encircled with white (Pl. IX, figs. 5,6), or reticulated, in which darker color making distinct mesh pattern (Pl. IX, figs. 1-3). Arm aborally alternating with dark grey and lighter white segments; lighter segments (2-4 in series) with dark central spots or blotches; similar marking of arm orally, except lighter shade of grey. Mouth shields mostly white with various amounts of grey centrally. Arm spines conspicuously annulated, gray and white (Pl. X, figs. 5,7). In specimens less than 10 mm (d.d.) the disc pattern (spotted or reticulated) may not be assumed, and the disc more or less all gray (Pl. X, figs. 1-2).

DISTRIBUTION

Loriol (1899) recorded the type specimen from Mauritius Island. Other Indian Ocean records are from Zanzibar (Ailsa M. Clark, pers. comm.). Koehler's (1905) specimen was collected in the vicinity of Borneo. In the Pacific I have specimens from Eniwetok Atoll and single specimen from the Society Islands.

Specimens collected at Eniwetok were taken in one to two meters depth while the Society Island specimen was collected at a depth of seventy feet, two hundred yards east of a pass into Papetoa Bay, Moorea.

DISCUSSION

In 1938, H. L. Clark took up the problem concerning the various species which had been designated as Ophiocoma brevipes and O. insularia. On the basis of adult specimens from Lord Howe Island off the east coast of Australia, he described two color forms of Ophiocoma insularia var. variegata. He stated; "The more common of these...is dentata Ltk. in which the disk is handsomely reticulated with dark brown lines on a lighter background...the size of the meshes in the network shows some diversity, but as a rule the larger the disk, the smaller the meshes. The other form, named doederleini by Loriol, has the disk spotted with black...in large individuals the ground color is so dark the spots do not stand out well in dried specimens; they are more evident in life" (p. 330). In addition to the disc, Clark described the pigmentation of the arms of both forms to be, "...more or less conspicuously banded with shades both lighter and darker than the ground color". On smaller individuals (d.d. 4 to 8 mm), he did not notice the characteristic color pattern on the disc, but found the banding of the arms more evident than on the larger specimens. However, there was no mention of the arm spines being annulated, as originally described by Loriol for doederleini.

For H. L. Clark, this description of the two apparently sympatric color forms confirmed the relationship between Lütken's O. dentata and Loriol's doederleini and in 1946, he stated, "...Lütken's dentata and Loriol's doederleini are easily recognized but seem to be unquestionably mere color forms of variegata" (p. 246).

Recent examination of specimens from several Indo-Pacific localities, especially Eniwetok in the Marshall Islands, has revealed that H. L. Clark's interpretation requires modification and re-evaluation.

At Eniwetok, specimens with a grey reticulated disc pattern and very definite annulated arm spines were found together with specimens having a brownish disc covered with black spots but lacking annulated arm spines (Pl. IX, figs. 1-4). These two forms at first recall H. L. Clark's (1938) color forms of O. insularia, as dentata and doederleini, respectively. Yet, as we shall see, the two differ in a number of other characters. Furthermore, the remarkable occurrence of still another color variety (Pl. IX, figs. 5-6) compared favorably with Koehler's (1922) redescription of the type specimen of O. doederleini.

It now appeared that perhaps the specimens which H. L. Clark (1938) had considered as O. doederleini represented merely a spotted variety of O. dentata (as insularia var. variegata) and was not conspecific with O. doederleini. There appeared to be some differences between the reticulated specimens from Eniwetok and those reported by H. L. Clark (op. cit.) as O. insularia var. variegata forma dentata, as well as Lütken's (1869) description of O. dentata, and Marktanner-Turneretscher's (1887) reticulated form described as O. marmorata. First, with the exception of the disc pattern, none of these forms were reported having annulated arm spines nor more than four arm spines. Second, not only do the reticulated specimens from Eniwetok have annulated spines, but five arm spines are common on segments beyond the disc edge (TABLE V).

Finally, comparison of the Eniwetok specimens with specimens from Cocos-Keeling Island having both reticulated and spotted discs (Pl. IX, figs. 7-9), but otherwise quite similar to O. dentata, strongly suggested that there are two species, each having two color forms. The reticulated color variety of O. doederleini is reported here for the first time, on the basis of the Eniwetok specimens. The spotted color variety of *O. doederleini*, in contrast to that of *O. dentata*, can be distinguished by the added characters of white rings around the disc spots plus annulated arm spines.

Examination of the smallest specimen of *O. doederleini* available (d.d. 9 mm) showed annulated arm spines (Pl. X, figs. 10-11). The appearance of these arm spines toward the tip of the arm in this and larger specimens indicates that this character is probably present in even smaller specimens. In contrast however, the 9 mm specimen showed no evidence of a reticulated or spotted disc pattern, and it is assumed that the disc pattern develops only with growth. H. L. Clark (1938) noted the same thing for the spotted and reticulated forms of *O. dentata*.

Koehler had previously (1922) published a redescription of Loriol's type specimen of *O. doederleini*, comparing it with specimens of *O. dentata* (as *O. brevipes*). He pointed out several characters of *O. doederleini* which served to differentiate it from *O. dentata*. First, he noted the pigmentation of the disc, with small black spots irregularly arranged as Loriol had described, adding that "... each of them [is] surrounded by a lighter circle, a feature which Loriol did not notice" (p. 321). Second, he mentioned the greater development of the breadth of the arms, due to both the greater length of the arm spines as well as to the arm breadth (without spines). Third, he noticed the appearance of five arm spines at the base of the arm, dropping to four some distance from the base, whereas in *O. dentata* five arm spines were quite abnormal.

Each of these characters described by Koehler for the type of *O. doederleini* has been verified in the present paper for additional specimens. In addition to these features, the dental plate has features which separate *O. doederleini* from both *O. dentata* and *O. brevipes* (see p. 79). Together these characters serve to substantiate the taxonomic position of *O. doederleini* as a valid species in the Brevipes group of *Ophiocoma*.

Canaliculata Group

Only two species are considered comprising the Canaliculata group of Ophiocoma. One species is confined to the temperate waters of New Zealand and the other to those of Australia. H. L. Clark (1921, p. 124) considered the Australian form, Ophiocoma canaliculata "...an isolated and well-marked species", while O. bollonsi from New Zealand although known, was unavailable to Dr. Clark for comparison. My own study indicates a very close morphological similarity between the two species and several morphological characters separate the two from other members in the genus. The most distinctive characters include the following:

1) The arm spines are quite thin, compressed and minutely serrated (Pl. XIX, figs. 5, 7,s, 9).
2) Between 6 and 8 arm spines occur along each side of the arm segments just beyond the disc edge; a greater number of segments with 6 to 8 spines is a function of increase in size.
3) The oral plate is nearly devoid of any well defined grooves (muscle scars) on the abradial surface (Pl. XIV, figs. 3d, 4d).
4) The oral papillae resemble the condition found in Ophiopteris: the outer papilla is quite small and

appears attached to the ventral shield; and there is a separation between this outer papilla and those attached to the jaw edge.

5) In contrast to other species in the genus the adoral shields meet in front of a very broad oral shield.

Species of Ophiocoma in the Canaliculata group include:

Species	Distribution
O. bollonsi Farquhar	Temperate New Zealand
O. canaliculata Lütken	Temperal Southern Australia

It has appeared advisable to consider the two species in the Canaliculata group together in the diagnosis and discussion where comparative features can be consolidated.

Ophiocoma canaliculata Lütken

(Plates XIV, figs. 1-2, 6-8; XIX, figs. 5, 7-9)

SYNONYMY

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, p. 128; 1928, p. 437, fig. 130a-b; 1938, p. 332; 1946, p. 244.

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

Ophiocoma punctata Koehler, 1930, p. 205, Pl. XIV, figs. 2-5.

Ophiocoma pulchra H. L. Clark, 1938, p. 333; 1946; p. 244.

MATERIAL EXAMINED

New South Wales

Newport - MCZ: No. 6726 (1)

Port Jackson - MCZ: No. 5905 (1) PARATYPE, *Ophiocoma punctata*

Shell Harbor - MCZ: No. 5237 (1)

South Australia

St. Vincent Gulf - MCZ: No. 3462 (3); No. 5905 (1)

Spencer Gulf - MCZ: No. 4664 (2) PARATYPES, *Ophiocoma, pulchra*

West Australia

Bunkers Bay - MCZ: No. 5218 (2)

New Zealand (Wellington) - BPBM: W1611 (1)

Ophiocoma bollonsi Farquhar

(Pl. XIV, figs. 3-5)

SYNONYMY

Ophiocoma bollonsi Farquhar, 1908, p. 108; H. L. Clark, 1921, p. 132; Koehler, 1922, p. 314; Mortensen, 1924,

p. 120, fig. 9; fell, 1949, p. 123, fig. 10; 1958, pp. 2, 29; Hurley, 1959, pp. 144-145, figs. 2-4.

DIAGNOSIS (Both Species)

Size. Largest specimen of O. canaliculata reported, 21 mm (d.d.) with arm length about three times disc diameter (H. L. Clark, 1928); O. bollonsi recorded to 20 mm (d.d.) with arms three to four times as long.

Disc cover. Granules covering the aboral surface of disc in both species and extending into oral interradial area to variable extent.

Arm spines. (Pl. XIX, figs. 5, 7,s, 9) Very characteristic of both species is the shape and thickness of the arm spines: in addition to being very thin, spines flattened in the oral aboral plane and with very narrow and shallow grooves running length of spine (noted by Lütken in his original diagnosis of O. canaliculata and also quite evident in the spines of O. bollonsi). In the aboral surface of longer arm spines in both species generally with evidence of slight central depression; the tips of the longest arm spines in O. bollonsi not widened at the tip, but this condition characteristic in O.

canaliculata. Mortensen (1924, p. 121) noticed that a few of the arm spines in *O. bollonsi* were swollen in the outer part. He suggested that a "parasitic organism" might be the cause of this feature and, in sectioning these spines, he found a "peculiar radiated structure". However, no evidence of a foreign organism could be detected. The description of this condition of the spines recalls what was described by Brock (1888) and Ailsa M. Clark (1963) as the "claviform" spines of *Ophiocoma* (as *Ophiomastix*) *pusilla*.

Sequence of spines for proximal arm segments for single specimen of *O. bollonsi* (d.d. 11 mm), on each side of the arm segments gave: 3-4-5-5-6-(6 or 7)-(6 or 7)-6-6-(5 or 6) for the first ten segments. The number of spines decreased distally with 4 and 5 spines observed beyond the twenty-fifth segment. Farther out on the arm, 3 and 4 spines occurred. Toward the very tip of the arm only 3 spines were noted. For three specimens of *O. canaliculata*, two from So. Australia (d.d. 7 mm and 18 mm) and one from New South Wales (d.d. 9 mm) the following arm spine sequence noted: for the first three proximal segments each side with 3, 3 or 4, 3 spines; beyond segment three an increase in number of spines occurring with increasing size of the specimens. This was determined by comparing the smallest specimen with the largest (TABLE VIII).

TABLE VIII. NUMBER OF ARM SPINES ON ARM SEGMENTS, OPHIOCOMA CANALICULATA

d.d.	Number of Spines	Segments
7 mm	6	6
18 mm		5-15
7 mm	7	none
18 mm		6-10
7 mm	5	out to 12
18 mm		out to 35
7 mm	3	from 21
18 mm		from 47

Dental papillae. For *O. bollonsi*, papillae arranged regularly in several transverse rows, number of papillae diminish toward the teeth; the outer row of papillae slightly larger than those of center. For *O. canaliculata*, dental papillae not so arranged, but occur in nearly same number above and below (near teeth); relatively larger than for *O. bollonsi* and irregularly placed in three or four rows.

Teeth (Pl. XIX, fig. 7,t). Both species with hyalinated tip.

Dental plate. Dental papillae area of O. bollonsi, for a specimen 11 mm (d.d.), expanded, wider than area occupied by teeth (Pl. XIV, figs. 3, 5,b). Dental plate of O. canaliculata (Pl. XIV, figs. 1, 2,b; Pl. XIX, fig. 8) only slightly expanded in the area of the dental papillae in young specimen (d.d. 7 mm) (P. XIV, fig. 2) and not at all in larger specimen (d.d. 18 mm) (Pl. XIV, fig. 1).

Oral plates. In both species, oral plates lacking grooves on the abradial muscle scar (Pl. XIV, figs. 1-3,d). Adradial muscle area less than one-third the length of the plate.

Adoral shields. Characteristicly meet in front of oral shields.

Arm vertebrae. O. canaliculata differing from other known species in subfamily by having radial nerve and radial water canal separated in both first and second vertebrae (Pl. XIV, fig. 6-8). In O. bollonsi, only first vertebrae with separation.

HABITAT

To my knowledge there has been no record of the habitat or ecology of O. canaliculata. Bathymetrically it appears to be found in the sublittoral. Koehler (1930) obtained his specimens (as O. punctata) from 5 to 8 meters off Port Jackson, Australia.

O. bollonsi was taken at a depth of 16 meters in Cook Strait, New Zealand (Farquhar, 1908) and Mortensen (1924) records specimens taken from a "hard bottom" in depths ranging from 5 to 125 fathoms. Hurley (1959) gives a very interesting report on the habitat and apparent density of O. bollonsi, through the use of underwater photography. He considered this ophiuroid as occurring in gregareous 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" (p. 145).

DISTRIBUTION

O. canaliculata appears to be endemic to temperate waters of Australia. Its range extends from the vicinity of Shell Harbor, New South Wales (lat. 34° S) along the South Australian coast to Rottsnest Island, Western Australia (lat. 33° S); it has not been reported from Tasmania. O. bollonsi shows a more restricted distribution in Cook Strait region between the North and South Islands of New Zealand.

DISCUSSION

H. L. Clark (1928) considered *Ophiocoma canaliculata* to have two color forms and designated one form by the variety name *pulchra*. The basic differences were in pigmentation of the arm spines and oral arm plates. In 1930, Koehler described a species from Port Jackson, New South Wales, Australia under the name *Ophiocoma punctata*. This binomial had already been used by Forbes in 1841 and thus was unavailable. 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 and disc granule size, as well as pigmentation. H. L. Clark (1938) regarded Koehler's species to be identical with the form he earlier named *O. canaliculata* var. *pulchra*. He considered this form as a distinct species on the basis that "...no intermediate specimens of *O. canaliculata* and *O. pulchra* had been seen" (p. 322). However, he noted that the distributional range of the two coincided and their morphological features were remarkably similar. He made a similar diagnosis in 1946 but noted that "...the actual relationship of the two forms still is an open question".

I have examined two of H. L. Clark's paratypes labeled O. pulchra (MCZ: No. 4664). Comparison with specimens identified as O. canaliculata showed several of the differences mentioned by Koehler for O. punctata. However, I am not convinced the differences are specific, but may reflect variation in a single species. Until more specimens are available for comparison, I would consider O. pulchra and O. canaliculata synonymous.

Pumila Group

The Pumila group is represented by four tropical species. At least one species in the group is unique among the ophiocomid brittlestars in having hexamerous and pentamerous forms. Morphological and distributional evidence presented in this paper suggests that the hexamerous forms probably include those species defined and included by A. H. Clark (1939) as constituting the genus Ophiocomella. It appears that these species are only the asexually reproducing progeny of existing or formerly existing pentamerous adults. Characters of the six-rayed forms are different from those of the adults and are discussed in the body of the paper (pp. 107-109). The most distinctive taxonomic characters of the five armed form are as follows:

1) The number of arm spines are the same on each side of an arm segment. Five spines occur on a greater number of segments the larger the specimen becomes.
2) The second or third spine in a row is longer than the uppermost.
3) The aboral arm plates are broadly oval with rounded lateral edges.
4) Two tentacle scales are restricted to only a few proximal arm segments.

5) Disc granules are of several sizes, generally spherical not tightly packed, and seldom spiniform (except in juveniles).

Species of Ophiocoma in the Pumila group include:

Species	Distribution
O. alexandri Lyman	Eastern Tropical Pacific
O. pumila Lütken	Tropical Caribbean
O. sexradia (Duncan)	Tropical Indo-Pacific
O. valenciae Müller & Troschel	Western Tropical and Subtropical Indian Ocean

Ophiocoma alexandri Lyman

SYNONYMY

Ophiocoma alexandri Lyman, 1860, p. 256; 1865, p. 74; 1882, p. 171; Verrill, 1867a, p. 259; 1867b, pp. 327, 329, 330, 341; 1871, p. 594; Ljungman, 1866, p. 328; H. L. Clark, 1915, p. 291, Pl. 16, figs. 5-6; 1917, p. 440; 1921, p. 131; 1923, p. 157; 1940, p. 341; Koehler, 1914, p. 116; 1922, p. 313; Boone, 1928, p. 7; Nielsen, 1932, pp. 243, 248-249, fig. 1; Ziesenhenne, 1937, p. 226; Steinbeck and Ricketts, 1941, p. 387, Pl. 9, fig. 1; Caso, 1951, p. 235, figs. 7-10; 1961, pp. 143-149, figs. 53-56.

? Ophiocomella schmitti A. H. Clark, 1939b, p. 8, Pl. I, figs. 3-4; Parslow and Clark, 1963, pp. 42-43.

MATERIAL EXAMINED

Baja California (Cape San Lucas) - MCZ: No. 1663 (2) PARATYPES; USNM: E1171 (1) PARATYPE

Costa Rica - BPBM: W1678a-3 (5)

Galapagos Islands - BPBM: W1646a-j (10); MCZ: No. 5649 940, 5650 (5)

Gulf of California - BPBM: W1645a-j (10); USNM: E6230 (2)

Panama

Bahia Honda - AHF: Velaro Sta. 863-38 (20)

Secas Islands - AHF: Velaro Sta, 447-35 (2)

Taboga Island - BPBM: W1637a-i (9); USNM: E4949 (1)

Mexico - BPBM: W1643a-f (6)

DIAGNOSIS

Ophiocoma alexandri has received careful attention with regard to its external morphology primarily after the work of Lyman (1860), Verrill (1867a), and Nielsen (1932), with some of the variations encountered being discussed.

HABITAT

Ophiocoma alexandri has been reported primarily from specimens taken in shallow sublittoral waters, in sand under large rocks, or in holes of rocks and coral (Steinbeck and Ricketts, 1941). This species has also been found in coral in deeper water, but not commonly.

DISTRIBUTION

Ziesenhenne (1937) indicated the range of this species was from Lower California to the Galapagos Islands. A specimen was also reported from Clarion Island by the same worker. H. L. Clark (1940) gave a bathymetric range from 1 to 10 meters.

DISCUSSION

Most reports have indicated only five armed specimens of O. alexandri exist (Lyman, 1865; Nielsen, 1929; A. H. Clark, 1939a; 1939b). However, H. L. Clark (1921; and, in, A. H. Clark, 1939b, p. 6) was of the opinion that this species had a six armed young stage. Specimens in the Allan Hancock Foundation, identified by Fred Ziesenhenne as O. alexandri from several tropical American localities including Clarion Island and the Galapagos Islands have six arms. These specimens are of small size with a disc diameter not greater than 6 mm and are mixed with additional large five armed specimens. The morphological criteria listed by A. H. Clark (1939b, p. 6) to separate small (d.d. about 5 mm) specimens of Ophiocomella parva and even smaller paratypes of Ophiocoma alexandri serve to distinguish the two forms. However, the amount of variation in the characters used by A. H. Clark for O. parva is considerable (see pp. 108-110).

Further examination of specimens not possible in this report will be necessary before it can be concluded that the six armed specimens from Clarion Island and the Galapagos Islands are conspecific or different from O. alexandri. The specimen described as Ophiocomella schmitti by A. H. Clark (1939b) from the Galapagos Islands could be the pentamerous form of O. alexandri from that locality. There seems to be no reason why both five and six armed individuals could not, like the condition noted for O. pumila, be conspecific, where some populations have only pentamerous forms (Baja California), while others have both pentamerous and hexamerous forms. It is anticipated that breeding experiments can clarify this problem.

Another alternative, suggested by the close morphological similarity between Ophiocoma sexradia from Clipperton Island and several Indo-Pacific localities (Hawaii, Marshall Islands) and Ophiocomella schmitti from the Galapagos Islands, is that these two species should be united, and actually belong to a single widely distributed species as suggested by Ailsa M.

Clark (in, Parslow and Clark, 1963, p. 43).

The type specimen of Ophiocoma alexandri, is deposited in MCZ as No. 1825. The type specimen of Ophiocomella schmitti, is deposited in USNM as E5638.

Ophiocoma pumila Lütken

SYNONYMY

Ophiocoma pumila Lütken, 1856, p. 13; 1859, p. 248, Pl. IV, figs. 5a-d; Lyman, 1865, pp. 71-73; 1882, p. 171; 1883, p. 255; Verrill, 1867b, p. 341; 1899a, p. 23; 1899b, p. 375; 1907, p. 328, Pl. 34E, fig. 1 (3 specimens with 5 rays, 3 specimens with 6 rays); Greeff, 1882, p. 156; H. L. Clark, 1899, pp. 118, 131; 1901, p. 340; 1902, p. 245; 1915, p. 293; 1919, p. 58; 1921, p. 131; 1933, pp. 67, 125, 126, 127, 128, 129, 130 (distribution); 1942, p. 378; Koehler, 1913, p. 375; 1914, pp. 117, 160; A. H. Clark, 1922, p. 212; 1939b, p. 451, Pl. 54, fig. 3; Tortonese, 1934, p. 40, Pl. V, fig. 22; Engel, 1939, p. 9; Fontaine, 1953, p. 203, fig. 6; Ailsa M. Clark, 1955, p. 51; Parslow and Clark, 1963, pp. 27, 47.

Ophiocoma placentigera Lütken, 1859, p. 147.

Ophiacantha ophiactoides H. L. Clark, 1902, p. 249, Pl. XV, figs. 5-8; Parslow and Clark, 1963, p. 37.

Ophiacantha oligacantha H. L. Clark, 1918, p. 265-267, Pl. VII, fig. 5; Parslow and Clark, 1963, p. 37.

Ophiocomella caribbaea A. H. Clark, 1939a, pp. 7-8; Parslow and Clark, pp. 37, 42, 43, fig. 11c-d.

Ophiocomella ophiactoides (H. L. Clark): Parslow and Clark, 1963, pp. 37-42, Pl. 112-f.

MATERIAL EXAMINED

British West Indies

Barbados (Pelican Island) - USNM: E4408 (3)

Tobago - BPBM: W1637 (12)

Panama - BPBM: W1639a-c (3); W1640a-c (3); W1641a-c (3)

Puerto Rico - Pers. Coll. (8)

DIAGNOSIS

Formal diagnosis of Ophiocoma pumila have been given by Lütken (1859), Lyman (1865), and Verrill (1907), dealing for the most part with the external morphology. Hexamerous specimens were dealt with by A. H. Clark (1939a, 1939b) and by Ailsa M. Clark (In, Parslow and Clark, 1963). A detailed analysis of the relationship between the pentamerous and hexamerous forms of this species is given in this paper (see DISCUSSION).

HABITAT

H. L. Clark (1933) records the common habitat of this species as being, "...in nooks and crannies of coral rock or among coralline algae close to the low water mark. It is particularly partial to algae, amongst which its greenish and brownish coloration renders it very inconspicuous".

DISTRIBUTION

According to H. L. Clark (1933, p. 67), *O. pumila* shares a nearly similar geographical range as *O. echinata* and *O. wendtii* (as *O. riisei*) from Bermuda to Florida and throughout the West Indies south to Brazil. The West Indian localities are summarized in Parslow and Clark (1963). In 1921, H. L. Clark mentions the distribution of *O. pumila* on the west coast of Africa and the Cape Verde Islands. The first west African record was by Greeff (1882) from the Gulf of Guinea (Sao Thomas Island), and more recently by Ailsa M. Clark (1955) from the Gold Coast. Koehler (1914, p. 160) recorded this species from *Albatross* stations ranging in depth from 23 to 201 fathoms. However, most records have been in much shallower waters.

DISCUSSION

The status of hexamerous ophiocomids will be reviewed in this discussion. Many of the points to be made result from an analysis of specimens of *Ophiocoma pumila*.

Small six armed ophiocomid brittlestars have been considered as: 1) the young of larger five armed adults in the genus _Ophiocoma_; or 2) a group of closely related species making up a separate genus, _Ophiocomella_. The first of these considerations is based on three lines of evidence. First, both five and six armed specimens have been collected together, and their morphological characters are quite similar. Second, large specimens, with a disc diameter more than 8 mm, have only been noted in the pentamerous condition. Third, it is generally conceded that the six armed forms undergo asexual reproduction by means of dividing based on finding specimens which have three well developed arms (rays) and the other arms in various stages of development. It has been assumed that the six armed form, during its terminal division, regenerates only two rays to form a five armed individual which thereafter grows in size to the adult condition. Unfortunately, there are very few authentic records of this occurrence and the regeneration of three new arms is far more common.

Lütken (1859) reported that eight of the type specimens of _Ophiocoma pumila_ had six arms. In addition, H. L. Clark (in A. H. Clark, 1939, p. 8) considered the type of _Ophiocomella caribbaea_ with six arms to be a young specimen of _Ophiocoma alexandri_. Hyman (1955, p. 643) reported that

Ophiocoma valenciae as well as O. pumila could reproduce asexually. All of these species of Ophiocoma are closely related, and are considered in the Pumila group of Ophiocoma. There are thus at least three well recognized, typically pentamerous species of Ophiocoma, morphologically quite similar, which have been reported to have a hexamerous stage and which are assumed to reproduce asexually, by a method of fission (fissiparity).

The other consideration, that the six armed form represents another separate genus, Ophiocomella, was formally proposed by A. H. Clark (1939b). His evidence was based on the following: a) several six armed specimens from Clipperton Island appeared to be nearly identical with a species described by H. L. Clark (1915) as Ophiocoma parva from Torres Strait. H. L. Clark in subsequent publications (1921, 1938, 1946), considered O. parva to be the young of some larger, undetermined, five armed ophiocomid, especially after his recognition of the close similarity between parva and the six armed specimens which he considered were the young of Ophiocoma pumila in the Caribbean. However, A. H. Clark (op. cit.) pointed out that comparison of six armed and five armed forms (as Ophiocoma pumila) of the same size from the Caribbean, indicated "...such marked differences...that they certainly cannot represent the same species" (p.1); b) In addition

A. H. Clark noted that no five armed specimens related to *O. pumila* had been found either at Clipperton Island or at Torres Strait. On the basis of these two points, he considered the six armed ophiocomids distinct, forming the genus *Ophiocomella*. An evaluation of this genus is important.

Three species were recognized initially; 1) *Ophiocomella parva* (H. L. Clark), described as the type species (however, A. H. Clark was uncertain at this time whether the specimens from Clipperton Island and those described from Torres Strait were conspecific, and he published the name *Ophiocomella clippertoni* conditionally for the eastern Pacific specimens should they prove distinct). In 1949, 1952, and 1954, he firmly established the name *O. clippertoni* for specimens from the Hawaiian, Marshall, and Marianas Islands, respectively; 2) *O. caribbaea*, described for hexamerous specimens from Caribbean localities and Bermuda, including those specimens previously considered to be the young of *Ophiocoma pumila* with six arms; 3) *O. schmitti* described for a specimen taken from the Galapagos Islands.

A. H. Clark's diagnosis of the genus was based on the small size of the specimens, the number of arms, the type of disc cover, and the number and length of arm spines. Each of these characters, however, has been found to apply equally well to five armed specimens in the Pumila group of *Ophiocoma*, especially *O. pumila*. These characters are discussed in greater detail later on in this paper when a comparison of the hexamerous and pentamerous forms is made. Other characters, including the number of arm segments with two scales, shape of the oral shields, and shape of the disc spinules were used by A. H. Clark to distinguish *Ophiocomella* from the closely related species of *Ophiocoma* in the Pumila group. These characters have been found, both in my study and that by Ailsa M. Clark (In, Parslow and Clark, 1963), to be subject to change with an increase in size of the individual.

In order to verify the differentiation between the five and six armed forms, both A. H. Clark (1939) and Ailsa M. Clark (*op. cit.*) compared several morphological characters. The characters used by these workers were quite similar and are tabulated below (TABLE IX).

TABLE IX. COMPARISON BETWEEN OPHIOCOMELLA CARIBBAEA AND OPHIOCOMA PUMILA (after A. H. Clark, 1939b)

1. Six arms.	1. Five arms.
2. Arm length, 13 mm; disc diam, 4 mm; Ratio - 3:1.	2. Arm length, 28 mm; disc diam, 5 mm; Ratio - 6:1.
3. 50-60 spinules/mm 2 on disc mostly about 2x as high as thick or higher; swollen, conical, usually with rounded tips; separated by several times their basal diam; central portion of interbrachial areas bearing a few widely scattered spiniform granules.	3. Rather close granules, somewhat irregularly placed about their thickness apart, with much diversity in size and shape; largest about 1/2 again as long as greatest thickness; tip more or less broadly rounded; central portion of interbrachial areas below, thickly covered with granules.
4. First tentacle pore with two tentacle scales, those following with one.	4. First and sometimes second tentacle pore with two scales.
5. Four arm spines until near the end of the arm, when the number falls to three.	5. Five arm spines on first side arm plates beyond disc, upper longest, lowest shortest; number then falls to four, then three in terminal part of arm.
*6. No pronounced color banding of the arms.	6. Conspicuous brown bands at intervals on the arms.

*Considered only by Ailsa M. Clark (In, Parslow and Clark, 1963).

My own evaluation of these features based on examination of two samples from Puerto Rico and Tobago Island in the British West Indies will now be discussed.

Seven specimens from Puerto Rico and twelve from Tobago Island were analyzed, using the characters established by A. H. and A. M. Clark to distinguish between *Ophiocomella* and *Ophiocoma pumila*. In TABLE X, a summary of these findings is listed. Specimens from Puerto Rico with six arms ranging in size from 2 to 5 mm (d.d.) are listed (a to f) in the table, the other two specimens (g, h) with disc diameters 3.5 and 4.5 mm have only five arms.

The results of this comparison showed that five arm spines are not limited to pentamerous specimens, also the pigmentation of both forms is often very nearly identical, whereas hexamerous specimens could show very different color patterns (tan and cream or green and white). Furthermore, in none of the specimens did the disc granulation or number of tentacle scales suggest *O. pumila*, which would have been expected in the two five armed specimens. Three of the six armed specimens, but none of the five armed specimens, show evidence of fission. Considerable variation in the "key characters" established by both A. H. Clark and Ailsa M. Clark to separate the two forms was evident but, because of the small sample, there was still doubt whether the specimens represented one or two species.

From Tobago Island in the British West Indies (Lesser Antilles) another series of small five and six armed ophiocomids provided added evidence to show that the characters used to distinguish the two forms were quite variable. Twelve specimens with a disc diameter 6 mm or less were examined. Of these, five were pentamerous, and seven hexamerous. The smallest pentamerous specimen was slightly less than 4 mm (d.d.). An analysis of the characters is presented in TABLE X. Specimens i through m are pentamerous forms, specimens n through t, hexamerous. The results of this examination showed that <u>both</u> five and six armed individuals can have the characters assigned for <u>either</u> species. For example, at least one of the six armed forms (p) showed clear transitional features between the typical five armed <u>Ophiocoma pumila</u> and the hexamerous form in the nature of the disc granulations, arm spine number, and number of tentacle scales. There was some indication that several of the morphological features could be found together more frequently in one form than another, but in no case were these significantly correlated on the basis of my sample.

It should be pointed out that Ailsa M. Clark (In, Parslow

TABLE X. COMPARISON OF FIVE AND SIX ARMED OPHIOCOMIDS FROM TWO CARIBBEAN LOCALITIES (Based on Characters Established by A. H. Clark, 1939)[1]

CHARACTER	PUERTO RICO specimens								TOBAGO ISLAND specimens											
	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q	r	s	t
1. Number of arms	O	O	O	O	O	O	P	P	P	P	P	P	P	O	O	O	O	O	O	O
2. Ratio, arm length: disc diameter	O	O	O	O	O	O	O	P	O	O	O	O		O	O	O	-	O	O	-
3. Disc cover (density and shape-length of granules or spinules)	O	O	O	O	O	O	O	O	OP	OP	OP	OP	P	P	O	OP	P	O	O	O
4. Tentacle scales; presence or absence of 2 on segments 1-2	O	-	O	O	O	O	O	O	O	O	O	O	P	O	O	P	O	O	O	-
5. Maximum number of arm spines	O	P	O	O	O	O	O	O	P	P	P	P	P	P	P	P	P	O	O	O
5'. Relative length of arm spines	O	O	O	O	O	O	O	O											OP	
6. Pigmentation of arms		P (others with tan arm bands)							O	O	P	P	P	P	P	P	P	P	P	-

[1]Characters 5' and 6 have been adapted from A. M. Clark (In, Parslow & Clark, 1963)
P - Character ascribed to Ophiocoma pumila (with five arms)
O - Character ascribed to Ophiocomella ophiactoides (= caribbaea)

and Clark, 1963, pp. 40-41) even though noting the differences between the five and six armed hexamerous specimens, admitted that there were many points of similarity between the two forms in the form and structure of the jaw. In addition she noted that several of her key characters showed some variations. For example, one of her smaller (3 mm) five armed specimens from St. Barts in the Lesser Antilles showed only four arm spines on the free arm segments, whereas a second specimen had the typical five arm spines; another five armed specimen lacked the two tentacle scales on the second segment. In another individual variation was also noted in the concentration of the disc spinules or granules. She concluded that additional small five armed specimens and breeding experiments would be necessary before one could be sure whether or not the five and six armed specimens were conspecific.

In addition to the characters listed above, I have analyzed the arm spine sequence for the Puerto Rico and Tobago Island specimens. Twenty-eight different sequences were observed, counting spines out to the tenth arm segment. Assuming that the proximal three segments retain their initial pattern without increase or loss of arm spines with growth, the sequences can be divided into seven categories based on the different number of spines on the first three arm segments. The results of these analyses are presented in TABLE XI. Several points can readily be observed:

a) Nearly 50% of the specimens examined have a spine sequence of 2-3-3 - - for the first five segments. It is assumed that variation beyond the third segment is due to the size of the arm ray; i.e. an addition of more spines occurring with size increase. Although, approximately 65% of the sides examined with this sequence were from hexamerous specimens, no significance is considered since in the Tobago Island sample (n = 12), the hexamerous and pentamerous specimens showed this sequence in nearly a 1:1 ration.

b) The occurrence of the fifth arm spine appears rarely by the fifth arm segment but more commonly on the sixth segment; the fifth spine was observed to the eighth segment but not beyond, in both five and six armed specimens.

c) Examination of specimens larger than 6 mm in disc diameter (from Tobago Island) all with five arms, generally reveals a 3-3-4-4-4 sequence. Unfortunately, no large specimens of _O._ _pumila_ were available from Puerto Rico. In addition, an examination of ten specimens identified

TABLE XI. ARM SPINE SEQUENCES FOR FIVE AND SIX ARMED SPECIMENS OF OPHIOCOMA PUMILA (d.d. 6 mm maximum)

Arm Spine Sequences: Segment Number 1	2	3	4	5	6	7	Puerto Rico 6 arms (Number of Sides)	Puerto Rico 5 arms (Number of Sides)	Tobago Island 6 arms (Number of Sides)	Tobago Island 5 arms (Number of Sides)	% of Total No. Sides
1	3	3	4	4	4	4			3		3
1	3	3	4	4	4	5	1				
2	2	3	2	4	4	4	1				
2	2	3	3	4	4/5	4/5	3			1	
2	2	3	4	4	4	4	3	1			6
2	2	4	4	4	4	4	2				
2	3	3	3	4	4	4	1	1	1		
2	3	3	4	4	4/5	4/5	25	2	27	24	49
2	3	3	4	5	5	5			1	2	
2	3	4	4	4	4/5	4/5	3	8	2	1	8
3	2	3	3/4	4	4	4		3			3
3	3	3	4	4	4/5	4/5	3	2	14	8	16
3	3	4	4	4/5	4/5	4/5	8	1	5	12	15
3	4	4	4	4	4	4		1			1
							50	19	53	48	

Total number of sides examined = 171

as *O. pumila* from Caledonia Bay, Panama, and three from Pelican Island in the Lesser Antilles (USNM: E4408) with disc diameters ranging from 3 mm to 16 mm and all pentamerous, had an arm spine sequence of 3-3-4-4-4. On only two sides of one specimen did two spines occur on the first segment and only rarely was a fifth spine noted on segment four or five. Hexamerous specimens were not among material from this locality. The very regular occurrence of three arm spines on the first arm segment in larger well defined five armed specimens of *O. pumila* leads to the assumption that the young five armed specimens are the progeny of larger specimens, and that another arm spine is added to the first segment during development. This is unlike the condition noted for other species in the Ophiocominae however, where the proximal three to five arm spines normally retain their initial arm spine sequence throughout the post-larval development.

With regard to the fate of the pentamerous and hexamerous individuals several alternatives appear possible. A. M. Clark (In, Parslow and Clark, 1963) stated: "Even if the six armed forms prove to be the progeny of five armed adults, I doubt whether the form can then be reversed by three armed halves regenerating only two arms to produce five. There seems to be no reason why the six armed form should not be perpetuated indefinitely" (p. 42).

As a result of my study, there appears every reason to believe that both the pentamerous and the hexamerous are conspecific forms. In some non-ophiocomid species however, there is evidence that five, six, and seven armed specimens may result from fission. Several workers have commented on the strong fission activity in *Ophiactis savignyi*, especially when the individuals are young (Simroth, 1877; Hyman, 1955, p. 669; Delavault, 1966, p. 633). Hyman (*loc. cit.*) mentioned that in this species, reproduction apparently ceases with maturity and that at the last fission the three armed segment regenerated only two jaws and arms. However, this does not appear to always be the case, as I have found mature six armed individuals in Hawaiian waters. However pentamerous specimens of *O. savignyi* have been found much less frequently than hexamerous specimens (A. M. Clark, *op. cit.*). In summary, evidence based on the examination of small pentamerous and hexamerous specimens of *Ophiocoma* from two Caribbean localities, Puerto Rico and Tobago Island, supports the hypothesis that these animals represent different forms of the same variable species. Because of priority, the name Ophiocoma pumila should be applied and the name Ophiocomella ophiactoides (= caribbaea) reduced to synonymy. Comparison of the six morphological characters used by A. H. Clark (1939) and A. M. Clark (In, Parslow and Clark, 1963) to distinguish between the six armed form (as Ophiocomella caribbaea) and the five armed form (Ophiocoma pumila) shows that considerable variation occurs for each of the characters.

In conclusion, the presence of small pentamerous and hexamerous sympatric specimens which cannot otherwise be distinguished morphologically, strongly suggests that these are two polymorphs of the same species. Furthermore, the evidence indicates that the six armed specimens rarely, if ever, divide (or reproduce sexually) to form five armed individuals. Rather, they perpetuate only six armed individuals by fissiparity and attain limited size (d.d. less than 8 mm). Only the small five armed forms are presumed to be able to lead to the adult form, and these then reproduce asexually to produce five and six armed individuals.

In some localities it is not inconceivable that only five armed progeny might be produced, accounting for the apparent absence of the hexamerous form. This would account for not only pentamerous specimens of O. pumila in several

Caribbean localities but also *Ophiocoma alexandri* along the west tropical American coast, and *O. valenciae* along the east African coast.

Lütken (1859) used the name *Ophiocoma placentigera* as a manuscript name for specimens which he described as *O. pumila*.

The synonymy of *Ophiacantha ophiactoides*, *O. oligacantha*, *Ophiocomella caribbaea*, and *O. ophiactoides* with *Ophiocoma pumila* is based principally on the diagnosis of these six armed West Indies species by Ailsa M. Clark (In, Parslow and Clark, 1963).

Koehler (1914, p. 117) pointed out that the species reported by Duchassaing (1850) in the West Indies as *Ophiocoma scolopendrina* and *Ophiura hexactis* were actually *Ophiocoma pumila*.

No holotype was designated by Lütken (1859) for *O. pumila*; the syntypes are deposited in the Copenhagen Museum.

The type specimens of *Ophiacantha ophiactoides* and *Ophiocomella caribbaea* are deposited in the U. S. National Museum.

Ophiacantha oligacantha is deposited in the Museum of Comparative Zoology, Harvard University.

Ophiocoma sexradia (Duncan) New Combination

(Plate XVII, figs. 1-9)

SYNONYMY

Ophiocnida sexradia Duncan, 1887a, p. 92, Pl. VIII, figs. 10-11.

Amphiacantha sexradia (Duncan): Matsumoto, 1917, p. 178; Koehler, 1905, p. 33; 1930, p. 113; Parslow and Clark, 1963, p. 42.

Ophiocoma parva H. L. Clark, 1915; p. 292, Pl. 14, figs. 8-9; 1917, p. 442; 1921, p. 132, Pl. 13, fig. 4; 1925, p. 92; 1938, pp. 331-332; 1946, p. 247; Ely, 1942, p. 60, fig. 18a-b; Edmondson, 1946; pp. 81, 84, fig. 40c; Balinsky, 1957, p. 27; Endean, 1957, p. 245; Domantay and Domantay, 1966, pp. 53-54

Ophiocomella parva (H. L. Clark): A. H. Clark, 1939b, pp. 5-7, Pl. I, figs. 1, 2; Parslow and Clark, 1963, pp. 42-43.

Ophiocomella clippertoni A. H. Clark, 1939b, p. 7, Pl. I, figs. 1-2; 1949, pp. 54, 71; 1952, pp. 296, 299; 1954, p. 260.

Ophiocomella schultzi A. H. Clark, 1941, pp. 481-483; Parslow and Clark, 1963, pp. 42-43.

Ophiomastix sexradiata A. H. Clark, 1952, p. 296.

? _Ophiocoma parva compacta_ Domantay and Domantay, 1966, p. 54.

MATERIAL EXAMINED

Hawaiian Islands

Oahu - BPBM: W1034 (2), W1100 (1); Pers. Coll. (6); USNM: E6605 (6), E6759 (3)

Laysan Island - BPBM: W342 (5)

Lisiansky Island - BPBM: W343 (2)

Pearl and Hermes Reef - BPBM: W344 (1)

Howland Island - BPBM: W590 (200 +)

Jarvis Island - BPBM: W581 (3), W1054 (3)

Johnston Island - Pers. Coll. (1)

Line Islands

Palmyra - BPBM: W346 (1), W864 (1)

Washington - BPBM: W580 (1)

Mossambique (Inhaca Island) -- Pers. Coll. (12)

Marshall Islands (Eniwetok Atoll) -- Pers. Coll. (15)

Samoa - BPBM: W1053 (33), W1072 (1), W1073 (1), W1074 (1), W1082 (1)

DIAGNOSIS

Size. Specimens examined with disc diameter to 6 mm; H. L. Clark (1938) records specimens to maximum of 7 mm (d.d.).

Disc cover. Spiniform granules scattered over disc aborally; not smooth, rather minutely serrated, forming a blunt crown at tip; height of granules exceeding diameter, slightly to two-and-one-half times; density of granules variable; none contiguous; few often entering oral interradial space.

Tentacle scales. One and/or two on each side of first segment; sometimes second scale also on segment two or three but not typical; single scale on more distal segments.

Arm spines.

1. Growth changes in number of spines (based on regenerating arms and terminal segments) as follows:
   a. Oral spine develops first; additional spines in row develop subsequently, although next spine may form simultaneously with first.
   b. When eight segments have formed, third spine evident on segments two, three, or four.
   c. First spine longer than second until third spine formed, then second spine length equals that of first;
   d. Three spines present on segments one through twelve or thirteen by time arm has fifteen

segments (often first segment only has two spines).

e. Fourth arm spine appears first on segment four (rarely on segment five), and appearing when arm has between sixteen and twenty-four segments.

f. Fourth spine to segment thirty in specimen with seventy segments.

2. Arm spine sequences noted, counting the spines from the first seven segments:

A	2-3-3-4-4-4-4	E	2-3-4-4-4-4-4
B	2-3-3-3-4-4-4	F	2-3-3-4-4-5-5
C	2-2-3-3-4-4-4	G	2-3-3-4-5-5-4
D	3-3-4-4-4-4-4	H	3-3-3-4-4-4-4

Sequence A was the most common noted, occurring in over 50% of the counts made.

Dental plate (Pl. XVII, fig. 5,b). Two foramina with narrow vertical septa between; distinctly expanded in oral portion below foramina; length to breadth ration, 2.1 to 2.5 : 1 (specimens 3 mm (d.d.) and larger).

Oral plate (Pl. XVII, figs. 1, 2). Abradial surface (fig. 1) with ear-shaped muscle scar, without grooves; adradial surface (fig. 2) with narrow, curved muscle scar.

HABITAT

Ophiocoma sexradia appears to occupy a wide range of habitats within the coral reef environment. The original specimens of *O. parva* (H. L. Clark, 1915b) were found "... on the under surface of rock fragments or in the crevices of sponges and coral" (p. 292). A. H. Clark (1941) reported the occurrence of *Ophiocomella schultzi* from the lagoon at Canton Island. Hawaiian records (A. H. Clark, 1949) report *O. sexradia* (as *Ophiocomella clippertoni*) from coral on the reef at Waikiki (Oahu). I have collected specimens from the base of the alga, *Sargassum polyphyllum*, in a tide pool on a reef platform at Makua, Oahu (Oct. 1964).

DISTRIBUTION

If this is truly a single Indo-Pacific species, as I am inclined to believe, then the zoogeographic range is extensive. The following distributional records are noted: Balinsky (1957), Mossambique; Duncan (1887a), Mergui Archipelago; H. L. Clark (1921), Torres Strait; Koehler (1905), Banda; A. H. Clark, (1952), Marshall Islands; A. H. Clark (1941), Canton Island; H. L. Clark (1925), Ely (1942), and A. H. Clark (1949), Hawaiian Islands and Palmyra; H. L. Clark (1917), Tuamoto group.

DISCUSSION

In the eastern Indo-Pacific, outside the range of Ophiocoma valenciae there is only one record of any pentamerous species of Ophiocoma in the Pumila group. However, hexamerous ophiocomids (listed in the synonymy) have been recorded throughout the region. This form is considered Ophiocoma sexradia in this paper, and very often shows evidence of fissiparous asexual reproduction (Pl. XVII, figs. 8-9). In the majority of cases self division results in two three armed individuals, one or both of which regenerate three additional rays. H. L. Clark (1938, p. 332) found at least three pentamerous specimens which appeared to be regenerating one or two new rays, and two seven armed specimens also showing regeneration.

Ailsa M. Clark (In, Parslow and Clark, 1963, p. 42) established the taxonomic position of Ophiocoma sexradia which I am using in this paper. The morphological characters used to separate the species, considered here as synonyms of Ophiocoma sexradia, are variable and subject to growth change. It is too early to tell whether specimens from different geographical areas constitute sub-specific designation, but as Miss Clark pointed out, on the basis of morphological criteria, specific separation is not warranted.

A. H. Clark (1952) distinguished his new species, *Ophiomastix sexradiata*, from *Ophiocoma sexradia* (as *Ophiocomella clippertoni*) on the basis of the number of arm segments with four spines and the shape of the spines. My own examination of specimens from the same general locality - which I consider *O. sexradia* - shows considerable variation in these characters and I see no reason to maintain A. H. Clark's species.

It is not known if *Ophiocoma sexradia* reproduces sexually. My examination of specimens has failed to show any specimens with well defined gonads. For now, I would suggest that this Indo-Pacific species, without any known pentamerous parental stock, is an asexually reproducing polymorph of either an extant or extinct pentamerous form.

Recently, Domantay and Domantay (1966) proposed the subspecific name, *compacta*, for *Ophiocoma parva* based on a single specimen from Jolo, in the Philippines. The size (d.d. 8 mm) exceeds that known for *O. sexradia*, and the presence of two tentacle scales and five arms makes the determination suspect. Examination of the specimen should clarify this matter; the description suggests *Ophiocoma pusilla* to some extent.

Duncan's type specimen of *Ophiocnida sexradia* is deposited in the Indian Museum, Calcutta, India. The deposition of the other synonomyous type specimens (syntypes in several cases) is given in the original sources for each species.

Ophiocoma valenciae Müller and Troschel

SYNONYMY

Ophiocoma valenciae Müller and Troschel, 1842, p. 102; Peters, 1851, p. 466; 1852, p. 86; Lütken, 1859, p. 141; Dujardin and Hupé, 1861, p. 266; Lyman, 1865, p. 71; 1882, p. 172; Ljungmann, 1866, p. 329; Martens, 1869, p. 129; 1870, p. 250; Möbius, p. 50; Marktanner-Turneretscher, 1887, p. 303; Ludwig, 1899, p. 547; Bell, 1902, p. 228; McIntosh, 1911, p. 160 (?); Koehler, 1907b, p. 327; 1922, p. 313; H. L. Clark, 1915, p. 293, Pl. 16, figs. 7-8; 1921, p. 131; Mortensen, 1933, p. 375; 1940, p. 73; Tortonese, 1936, p. 223; 1951, p. 39; Balinsky, 1957, p. 27; Ailsa M. Clark and Davies, 1965, pp. 599, 601; Ailsa M. Clark 1966, pp. 44-45.

Ophiocoma valentiae (sic) Müller and Troschel: Loriol, 1894, pp. 29-31.

MATERIAL EXAMINED

Mossambique (Inhaca Island) - BPBM: W1600 (1)

DIAGNOSIS

An examination of a specimen collected at Inhaca Island, Mossambique gave the following characters:

Size. Disc diameter, 12.5 mm; Balinsky (1957) records specimens to 17 mm.

Disc cover. Granules of two types; a small cylindrical form and a larger more elongate nearly spiniform type; fairly widely spaced, almost reaching the mouth shields in a reduced fashion down center of oral interradial area.

Tentacle scales. Two over each pore of segments one and two, sometimes on segment three; one on each pore of distal segments.

Arm spines. Sequence (based on examination of three sectors); 3 on segments one to three; 4 on segments four and five; 5 on segments six and seven; 6 on one side of segment eight, usually 5; 5 spines regularly on segments nine to twenty, irregularly as far as segment twenty-three; 4 spines farther distally, then 3 most distally to tip.

In each row, beyond disc margin, uppermost and second spine approximately same length; third very slightly longer and thicker than others; lower two spines shortest.

Dental papillae. In three rows, with 3 in each row.

Dental plate. Twice as long as broad with septa between tooth foramina narrow and thin.

Aboral arm plate. Much broader than long, with even, rounded lateral borders.

Oral papillae. 4 on each jaw margin.

HABITAT

Balinsky (1957, p. 27) reported the occurrence of *O. valenciae* from beneath rocks on Ponta Torres reef at Inhaca Island, Mossambique, as well as from beneath algae (*Cymodocea ciliata*) together with *O. scolopendrina* (p. 30). Mortensen (1933) recorded a specimen from rock pools near Durban, South Africa.

DISTRIBUTION

H. L. Clark (1921) reported this species to be probably "confined to the east Coast of Africa, from Mossambique to the Red Sea and the Mascarene Islands" (p. 131). Koehler (1922) extended the limits of *O. valenciae* by including the Laccadive Islands, Mergui Archipelago, Fiji Islands and Samoa. The last two localities require verification. Mortensen (1933) extended the distribution much farther south on the African coast to Durban, South Africa (lat. 29° S), and in 1940 reported a specimen from the Persian Gulf. Bell (1902) reported the species as common in the

Maldive Islands, but this record could not be verified by Ailsa M. Clark (In, Ailsa M. Clark and Davies, 1965, p. 601).

DISCUSSION

Morphologically, H. L. Clark (1921, p. 123) separated O. valenciae from the closely related O. pumila and O. alexandri on the basis of the ratio of arm length to disc diameter (for O. valenciae 4.0 to 5.5 : 1; for O. pumila and O. alexandri, 6 to 10 : 1). Ailsa M. Clark (1966) noted considerable variation in this character for specimens from the Red Sea; for seven specimens she obtained a range of 5.25 to 8.4 : 1 ($\bar{x}$ = 7.0), and one specimen had a ratio of 8.5 : 1.

I have considered relative lengths of the arm spines and color of the arms to distinguish this species (p. 44). In this respect, O. valenciae can be separated from O. alexandri. The pigmentation of O. valenciae was described by Balinsky (1957) for living specimens.

As H. L. Clark (1921, p. 132) pointed out, nothing is known of the growth changes of O. valenciae. Hyman (1955, p. 643) stated that this species reproduces asexually. Mortensen (1940) had earlier reported a hexamerous specimen which he identified as O. valenciae. However, he failed to note any morphological differences between this specimen and *O. sexradia* (as *O. parva*) described by H. L. Clark in 1915.

If Mortensen was correct, it could mean that six armed ophiocomids which occur throughout the range of *O. valenciae* might be only polymorphs of this species. Consequently, records of *Ophiocoma parva* (for *O. sexradia*) in this area (Balinsky, 1957) might refer to the polymorphic form of *O. valenciae*. However, until breeding experiments or conclusive morphological criteria are found which substantiate this hypothesis, there is still the possibility that the six armed east African form should be considered *Ophiocoma sexradia*. My own examination of hexamerous individuals from Inhaca Island, Mossambique fails to show morphological characters significantly different from Pacific specimens determined as *O. sexradia*.

Ophiocoma pica Müller and Troschel

(Plates XV, figs. 1-11; XVI, figs. 1-10)

SYNONYMY

Ophiocoma pica Müller and Troschel, 1842, p. 101; Loriol, 1893a, p. 28 (a complete bibliography up to this date); H. L. Clark, 1915, p. 293; 1921, p. 127, Pl. 13, fig. 8 (color); 1925, p. 92; 1938, p. 333; 1946, p. 244; Edmondson, 1933, p. 70, fig. 32d; 1946, p. 81, fig. 39d; Ely, 1942, p. 54, fig. 15a-b, Pl. 12, fig. B; A. H. Clark, 1949, p. 51, 104; 1952, p. 295; 1954, p. 260; Ailsa M. Clark, 1952, p. 207; 1965, p. 599; 1966, p. 47, 55; Endean, 1965, p. 231.

Ophiocoma lineolata Müller and Troschel, 1842, p. 102; Loriol, 1893a, p. 28 (a complete bibliography up to this date); Koehler, 1905, p. 62; 1907, p. 326; 1922, p. 324, Pl. 73, figs. 1-4; 1930, p. 204; Mortensen, 1937, pp. 51, 52, fig. 41 (larval skeleton), Pl. Viii, figs. 1-3 (larva); Boone, 1938, p. 148, Pl. 52; Tortonese, 1953, p. 33.

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

MATERIAL EXAMINED

Hawaiian Islands

Kure - BPBM: W281 (3)

Laysan - BPBM: W360a-b (2)

Midway - BPBM: W842 (3), W1011 (1)

Oahu - BPBM: W357 (2), W1102 (1), W1109 (5), W1119 (2), W1213 (1), W1222 (2), W1233 (2); Pers. Coll. (29)

Johnston Island - W283 (1); Pers. Coll. (3)

Marshall Islands (Eniwetok Atoll) - BPBM: W1418a-f (6)

Mossambique - BPBM: W1580 (1)

DIAGNOSIS

Size. Maximum disc diameter recorded, 27 mm (d.d.) (Lyman, 1861); mature specimens (gonads developed) from 10 mm (d.d.).

The ratio of the arm length to disc diameter has been used as a character for this species. *O. pica* is characterized by having shorter arms than most of the other species of *Ophiocoma* with the exception of *O. canaliculata* and *O. bollonsi*. In *O. pica* and these species the arms seldom exceed four times the disc diameter. However, the lower limit of the ratio is variable. My own estimations for *O. pica* were based on the measurement of the longest arm (from the edge of the disc), divided by the diameter of the disc. Several estimates of the arm length to disc diameter ratio are given in TABLE XII.

TABLE XII. ARM LENGTH : DISC DIAMETER RATIO, OPHIOCOMA PICA

Source	N*	Ratio	Range
Lyman (1865)	1	3.33 : 1	---
	(2)	3.14 : 1	2.50 to 3.78 : 1
Dujardin &	1	4.00 : 1	---
Hupé (1861)	(1)	4.00 : 1	---
Loriol (1893)	-	3 to 4 : 1	---
H. L. Clark (1921)	-	seldom over 4 : 1	---
H. L. Clark (1938)	1	2.96 : 1	---
Boone (1938)	13	1.93 : 1	1.50 to 2.40 : 1
Kaneohe Bay	(5)	2.37 : 1	2.00 to 2.50 : 1
Ely (1942)	2	2.18 : 1	1.95 to 2.40 : 1
present study	46	3.42 : 1	2.48 to 4.10 : 1
all Hawaiian	(15)	3.32 : 1	2.35 to 3.60 : 1
present study	20	3.28 : 1	2.46 to 3.91 : 1
Kaneohe Bay	(6)	3.58 : 1	2.59 to 3.74 : 1

*Number of specimens in parentheses are less than 10 mm (d.d.) disc diameter

From the above table one notes the considerable variability which has been reported for this character. The very low figures obtained by Ely and Boone for Hawaiian specimens at first suggested that this population might have relatively shorter arms than specimens from other localities. However, my own examination of additional Hawaiian specimens revealed a higher ratio than obtained by either Ely or Boone, and indicates that the Hawaiian specimens are closer to the ratio estimated by earlier workers for specimens from various parts of the distributional range of the species.

Disc cover. Granules low (their height less than their diameter), not closely packed, but evenly distributed over aboral surface of disc. Interradial areas free of granules and with large imbricating scales.

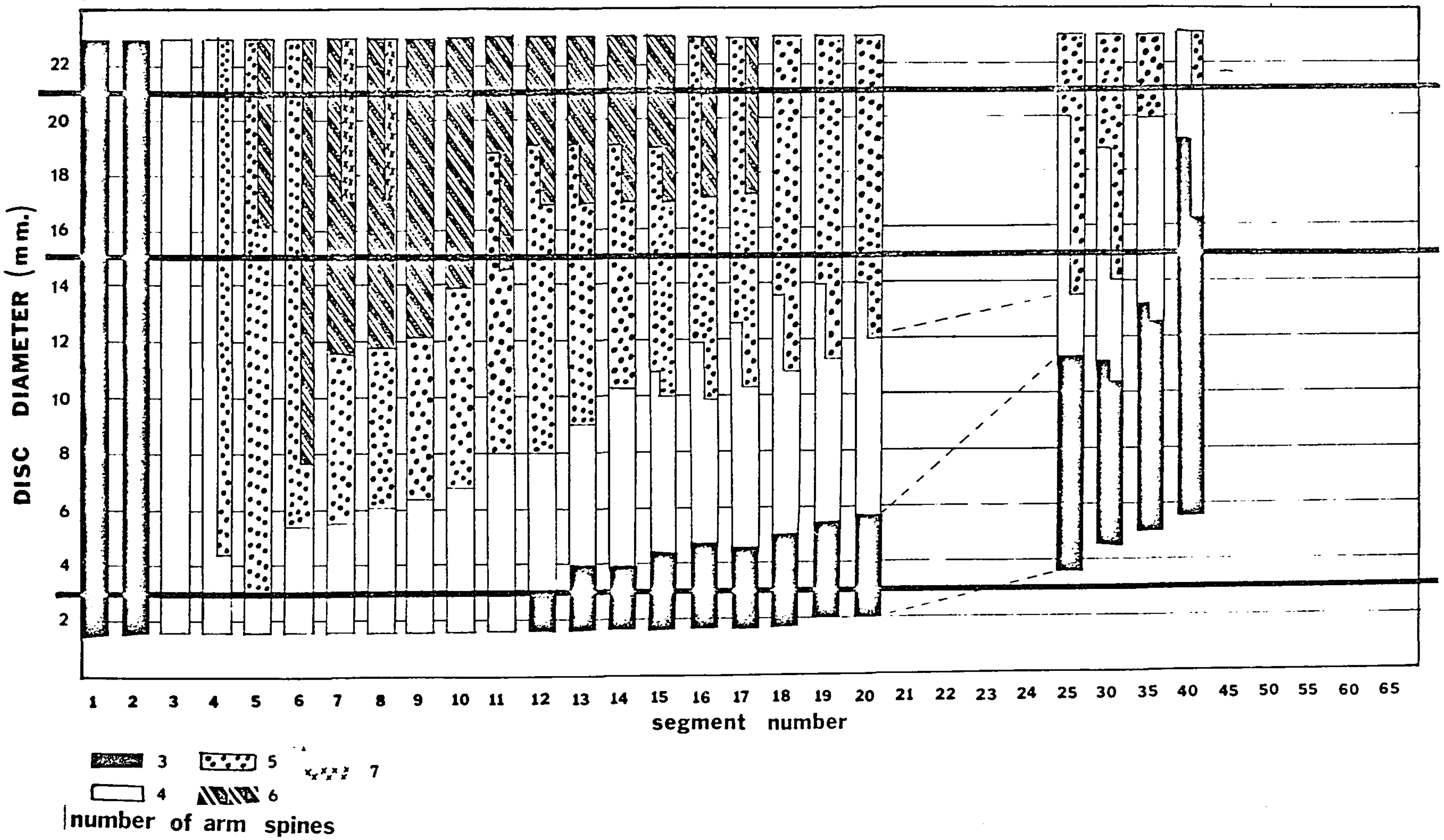
Arm spines. The number of arm spines on each side of the arm segments has been counted for sixty-two specimens of sizes ranging from 1.8 to 23 mm (d.d.). Specimens were primarily from the Hawaiian Islands, with a few from Eniwetok Atoll, Marshall Islands. The results of this analysis are given in TABLE XIII. The arm spine sequence shows several characteristics:

a) Each of the first three arm segments retain the same number of arm spines over the size range examined.

Ophiocoma pica

TABLE XIII

ARM SPINE SEQUENCE



b) Beyond the first three segments, there is an increase in the number of arm spines with increase in the size of the specimen.

c) Six arm spines are often evident on one or more segments when the disc diameter reaches 12 mm and are present out to segment seventeen in larger specimens.

d) Seven spines are the maximum noted, and only on segments seven and eight in specimens 17 mm (d.d.) or larger.

e) The distal, newly formed, segments have only three spines.

The upper arm spines are typically the longest in a row, sometimes the uppermost but often the penultimate. The next to lowermost spine is normally curved. The spines are usually tapered, and not swollen along their length; the tip is more or less acute, especially on distal segments. However, Koehler (1922, p. 325) described variation in the shape of the upper arm spines with considerable thickening and shortening indicated in some specimens.

Dental papillae. Dental papillae well developed and, in specimens larger than 10 mm (d.d.), occurring in three or four columns with two to four in each column (Pl. XVI, fig. 7).

Teeth. Wide and stout with hyalinated tip; either three or four teeth on each dental plate (Pl. XVI, fig. 7).

Dental plate. Dental plate of *O. pica* described and figured by Murakami (1963, p. 26). He noted that it was about two-and-one-half times as long as broad, "somewhat slipper-shaped" and in this respect resembled *O. pusilla* (as *O. latilanxa*). I examined the dental plate of several different sized specimens from Hawaii. These failed to reveal any widening of the lower portion of the plate in the region of the dental papillae (Pl. XVI, figs. 1-6), and thus differed from the condition in *O. pusilla* (see Pl. XIX, fig. 6). The vertical septa dividing the teeth foramina are of the wide, thin type, with the upper septum narrower than the lower. One-third or more of the length is occupied by the tooth papillae area, and the length is between 2.6 and 3.0 times the maximum breadth.

Oral papillae. Four or five oral papillae, of which outer two broader than inner papillae (Pl. XVI, fig. 9).

Tentacle scales. The number of tentacle scales is consistently two on each side of the arm segments. The number of segments with two scales increase with size of the specimens.

In order to show this, the width of the tenth oral arm segment was taken as a size perimeter and compared with the number of segments having two scales. The results of this analysis on twenty-four specimens of O. pica are given in TABLE XIV. A positive rectilinear regression of size of the oral arm plate on the number of segments with two tentacle scales was observed. The regression formula is $Y = 26.58X - 0.41$. The correlation coefficient (r) is 0.97. A Student's t test for 24 degrees of freedom gives a t value of 19**, highly significant.

Pigmentation. One of the most characteristic features of O. pica is color pattern. The disc, aborally, is lineolated with narrow bands of yellow radiating out from the center to the edge of the disc. The yellow bands are in sharp contrast to the background of dark brown. The bands often continue to the interradial surface or may loop around back to the aboral side of the disc. The distal sides of the mouth shields and portions of the adoral shields are yellow. The lateral borders of approximately every other dorsal arm plate and the lateral arm plates are yellow.

HABITAT

Collection in the Hawaiian Islands, and Johnston Island of O. pica has shown this species commonly associated in the coral Pocillipora meandrina var. nobilis. I have

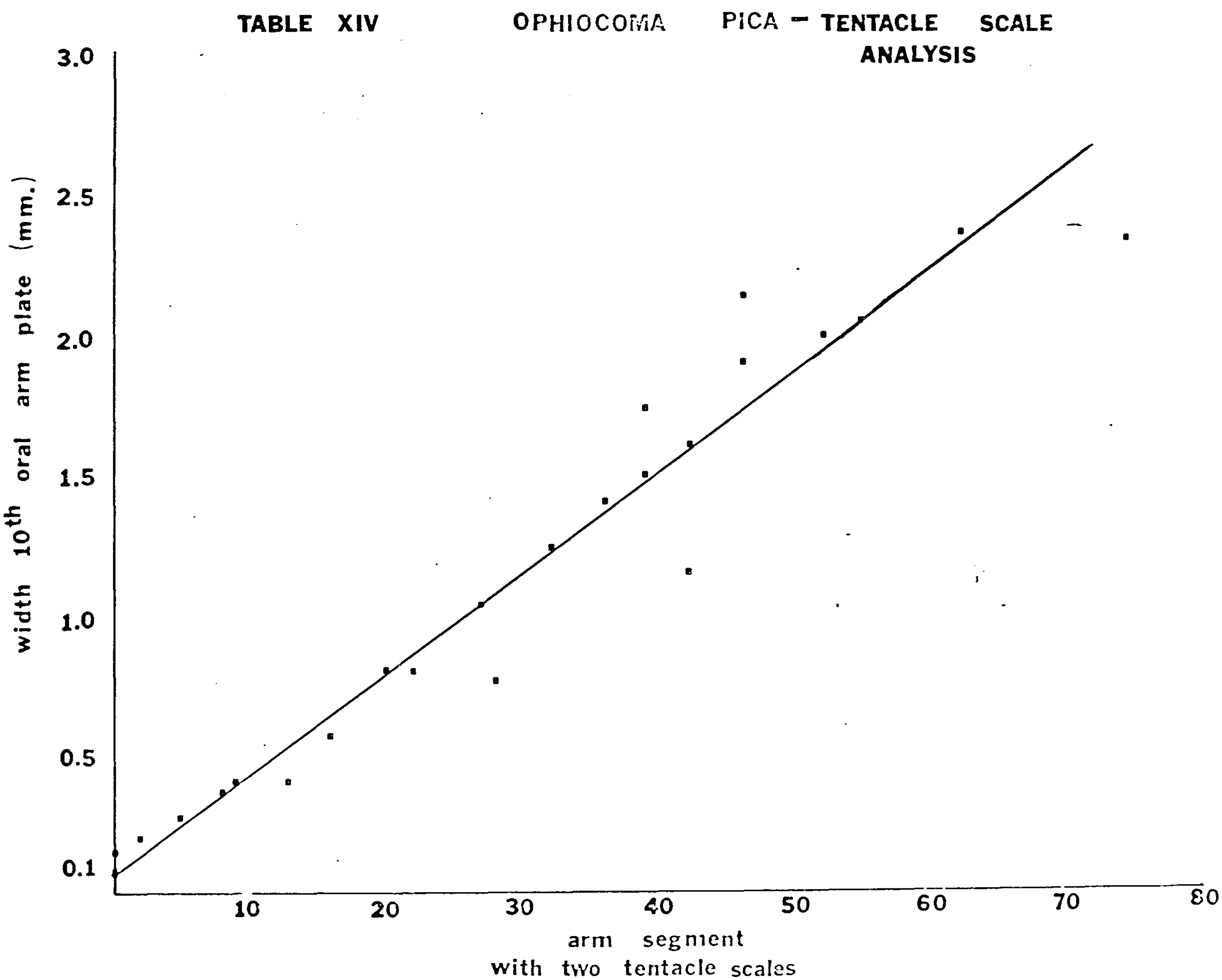


TABLE XIV OPHIOCOMA PICA — TENTACLE SCALE ANALYSIS
3.0
2.5
2.0
1.5
1.0
0.5
0.1
width 10th oral arm plate (mm.)
10
20
30
40
50
60
70
80
arm segment
with two tentacle scales

removed as many as fifteen specimens, ranging in size from 3 to 21 mm in disc diameter, from a single colony of this coral. The coral dwelling habitat of this species was reported by H. L. Clark (1921, p. 128) during his collecting at Mer Island, Torres Strait, "...far out on the reef-flat, among the living corals". A. H. Clark (1952, p. 295) also reported a specimen of _O. pica_ from "a clump of _Stylophora mardax_" at Rongerik Atoll, Marshall Islands. H. L. Clark (1946, p. 244) regarded the scarcity of _O. pica_ from most collections to be the result of "its very secretive habits, living ... in the crannies of large coral heads and colonies where it is difficult to reach". In support of this, Ely (1942, p. 56) reported _O. pica_ as "closely associated with _O. erinaceus_, but ... much less common".

My own collecting of _O. pica_, indicates that the young specimens especially appear to be restricted to the coral habitat; I was unable to find specimens less than 15 mm (d.d.) except in _Pocillopora_ colonies. Larger specimens were found occasionally under rocks or dead coral, but these also were more common in the living coral.

DISTRIBUTION

The type locality of _O. pica_ is unknown; _O. lineolata_ was based on a specimen from Mauritius. This species has a very wide distribution throughout the Indo-Pacific, the geographical range extending from East Africa (lat. 25° S) through the Red Sea to the Tuamotu Archipelago and Hawaiian Islands. It occurs as far north as the Ryukyu Islands but has not been reported from Southern Japan. Endean (1965) reported _O. pica_ from Heron Island in the Capricorn Group (lat. 26-27° S) off the Australian coast, and it was found at Lord Howe Island (lat. 31° S) by H. L. Clark (1938). Boone (1938, p. 149) gave a good account of additional distributional records and their references up to 1938. Additional Central Pacific records were given by A. H. Clark (1952; 1954).

DISCUSSION

One still finds descriptions of _Ophiocoma pica_ under the name _O. lineolata_, 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_ is derived from the fact that Müller and Troschel accepted this name based on an unpublished proposal by J. Desjardins; but they were the first to publish the name as _Ophiocoma lineolata_. However, because of page priority, *Ophiocoma pica* must be recognized as the nominal species, and *O. lineolata* as a synonym.

Ophiocoma pica, although consistent in its morphological characters, cannot be placed in any of the larger groups of *Ophiocoma*. On the basis of morphological grounds established for the different species complexes in this genus, *O. pica* appears to share characters in common to species in several of the groups, while at the same time has characters which separate it from these species. For example, the dental plate resembles that of the Scolopendrina group in its length to breadth ratio and area occupied by the dental papillae, but the septa dividing the teeth foramina are similar to the condition found in the Brevipes group.

In the number and arrangement of the arm spines *O. pica* resembles the Canaliculata group, but, in the former, the spines are much more robust. Also the oral plate of *O. pica* shows striking differences: on the abradial surface of this plate there are well defined muscle scars (see Murakami's figure (1963, p. 33, Pl. Vii, figs. 15-16) whereas these are characteristically absent in Canaliculata species; the adradial muscle scar is also much more developed in *O. pica* than in these species. In both respects, the oral plate resembles that of Scolopendrina species more closely.

However, in _O. pica_ there is no indication of the alternating arm spines so characteristic of the Scolopendrina group.

None of the Pumila species help in clarifying the relationship of _O. pica_. The presence of two tentacle scales characteristic of _O. pica_ is not evident in species in this group. Furthermore, there is a noticeable difference in the shape of the upper arm plates and arm spines between _O. pica_ and these species.

The disc granules of _O. pica_ have been considered intermediate in coarseness between Scolopendrina and Brevipes species (H. L. Clark, 1921). The fact that the granules stop at the edge of the disc separates _O. pica_ from the Brevipes group immediately.

In light of the foregoing discussion I propose considering _O. pica_ as a distinct branch of the genus _Ophiocoma_, showing mixed relations to the other groups in this genus. In none of its characters does _O. pica_ resemble other genera in the subfamily Ophiocominae as closely as it does to congeneric species.

Ophiocoma pusilla (Brock)

(Plate XIX, fig. 6)

SYNONYMY

Ophiomastix pusilla Brock, 1888, p. 499; Koehler, 1905, p. 65, Pl. VI, figs. 9-10, Pl. XIII, fig. 3; Ailsa M. Clark, 1965, p. 45, fig. 5.

? Ophiocoma lubrica Koehler, 1898

Ophiocoma insularia var. longispina H. L. Clark, 1917, p. 441; 1921, p. 131.

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

Ophiocoma latilanxa Murakami, 1943a, p. 194, fig. 13; 1943b, p. 217.

Ophiocoma sp. Ailsa M. Clark, 1952, p. 208.

Ophiocoma insularia Lyman: Balinsky, 1957, p. 26.

MATERIAL EXAMINED

Australia (Green Island) - MCZ: No. 3754 (1)

Lord Howe Island - MCZ: No. 5229 (1)

Caroline Islands (Yap Island) - USNM: E8620 (3)

Easter Island - USNM: E647 (1)

Marshall Islands (Eniwetok Atoll) - BPBM: W1504-W1507 (4)

Mossambique (Inhaca Island) - BPBM: W1578 to W1579 (2), W1584 to W1585 (2)

Philippines (Port Galera, Mindoro) - MCZ: No. 4002 (1)

DIAGNOSIS

Size. Disc diameter not exceeding 10 mm. Sexually mature individuals with disc diameter from 6 mm (Eniwetok, September 1966).

Disc cover. With very small, fine closely packed granules, not often reaching oral shields interradially, and leaving an area near genital slits bare.

Tentacle scales. Two, on each side of arm segments; extent to which two scales developed depending upon size of specimen with more segments having two scales as size increases: smallest specimens (d.d. 5.5 mm) with two scales out to segment twenty-six; largest (d.d. 7.5 mm) with two scales to segment forty. In specimens less than 6 mm (d.d.) two tentacle scales out to segments in middle part of arm. Outer scale on each side largest, inner scale developing last.

Arm spines. Thickening and enlargement of a few dorsal pentultimate arm spines have been reported as characteristic of Ophiocoma pusilla (see Ailsa M. Clark, 1966, fig. 5). However, variation in the number, position and extent of these modified arm spines has also been reported and verified in my own examination of specimens (see p. 155). The complete absence of these modified spines in many specimens suggests that this feature should not be considered as a primary diagnostic character, but presence of these enlarged spines, however, does offer corroborative specific identification. More consistent, and of more importance, is the fact that the arm spines are very fragile and hollow (the lumen of the spine being greater than the thickness of the wall of the spine). In this respect the arm spines recall the condition found in *Ophiocomina nigra*. Hollow spines are unknown in any other species of *Ophiocoma*.

Arm spine sequence: First three arm segments carry 3, 3, and 4 arm spines on each side, respectively; segment four with 4 or 5 spines, usually 4; segment five, usually with 5 spines (although occasionally 4); segment six with 5 spines, occasionally 6 in larger specimens; 6 spines also noted on segment seven in one example. Beyond segment seven, development of fifth arm spine appears to be a function of age and growth, seldom occurring beyond segment twenty: Largest specimen examined (d.d. 9.5 mm) with 5 arm spines as far as segment 22, while in smaller specimens fewer segments with five spines. Distally, number of arm spines 4, and then 3 near tip.

Oral papillae. Generally four, but sometimes five; distinction between terminal oral papilla and upper dental papillae sometimes difficult to determine. Second oral papilla broadest, its outer margin overlapping the inner edge of outer (distal) oral papilla typically directed downward into mouth. Murakami's (1943a, p. 194) description is very accurate and his figure is consistent with my observations.

Dental papillae. Brock (1888) in his original description of *Ophiomastix pusilla*, merely stated that these were as found in *Ophiocoma*. Murakami (*op. cit.*) described them as occurring in three series and numbering about fifteen and this is consistent with my observations. In number, size, and arrangement, the papillae differ from those found in the Brevipes complex of *Ophiocoma*. The marginal papillae are slightly larger than those in the middle, more like the condition found in *Ophiocoma bollonsi*.

Dental plate (Pl. XIX, fig. 6,b). Eniwetok and Inhaca Island specimens agree with Murakami's (1963) description and figure of this plate for *Ophiocoma latilanxa*. In shape it bears a very close similarity to the dental plate of *Ophiocoma bollonsi* with a widened, spatulate lower portion. The dental plate is also similar to *O. bollonsi* in the shape of the very thin septa dividing the teeth foramina.

Teeth. Three or four; first (oralmost) shortest and narrow; second, longer and slightly broader; third, longest and broadest; and fourth, narrow and shorter than third. All teeth with distal end hyalinated (Pl. XIX, fig. 6,t).

Oral shields. Noticeably longer than wide; e.g. specimens from Eniwetok and Inhaca Island with length to width ratio from 1.2 to 1.7 : 1.

Adoral shields. Widely separated, triangular, outer edge in contact with ventral shield.

Oral angle plate. Lack of well defined indentations for attachment of the abradial muscles evident.

Pigmentation. The descriptions of the color of this species are nearly as numerous as the different names which have been applied to the species. Several features are more consistent than others; the arms appear to be banded in nearly all cases, dark brown and lighter yellowish; the dark aboral arm plates can have various patterns or be uniformly colored. The oral surface of the arms is lighter than the aboral surface. The disc can be spotted, reticulate, or a solid color, usually brown or grey. I have ever seen the periphery of the disc grey with median white area and a dark grey spot centrally located.

HABITAT

In his ecological notes, Balinsky (1957, pp. 30-31) recorded some of the major biotopes in which ophiuroids were found at Inhaca Island, Mossambique. 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 was also reported as common in another "more tropical" reef area (Ponta Torres reef), where the base of the reef was very shallow. Dr. Balinsky also informed me (pers. comm.) that this species favored dead coral heads. The fragile nature of the arm spines, and the fact that I found a barnacle growing on one of the oral arm plates, suggests 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 dead coral.

DISTRIBUTION

The following records establish *Ophiocoma pusilla* as widely distributed throughout the Indo-Pacific:

Eastern Coast of Africa - Balinsky (1957)

Red Sea (Gulf of Aqaba) - Ailsa M. Clark (1952, 1965)

Laccadive Islands - Koehler (1898)

Indonesia - Koehler (1905)

Amboina (Indonesia) - Brock (1888)

Barrier Reef, Australia

Lord Howe Island

Philippines, Mindoro

Ryukyu Islands - Murakami (1943b)

Western Pacific Islands - Murakami (1943a)

Eniwetok, Marshall Islands

Easter Island - H. L. Clark (1917)

The bathymetric range is inconclusive. Koehler (1898) records *O. pusilla* (as *O. lubrica*) from a depth of 30 to 50 fathoms. In 1905 the same worker questions a Siboga Station record from a depth of 701 meters. It appears from the other records that this species is most common in the shallow sublittoral.

DISCUSSION

This species, first described by Brock (1888) as *Ophiomastix pusilla*, was said to be characterized by the presence of club-shaped, or claviform, arm spines. Unlike any other species in the genus, these arm spines occurred as the second rather than the uppermost spine and only on a few adjacent segments in the proximal region of the arm. It was considered different from other species in the genus not only by the number, position, and shape of the club-shaped spines, but by its color, small size, and presence of fine disc granules. The combination of a fine, even covering of granules and the transformation of the second row of arm spines into clubs led Brock (op. cit.) to consider Ophiomastix pusilla as an aberrant species, possibly to be placed in a separate genus.

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

H. L. Clark (1921), without having seen a specimen, 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 only be the young of some larger as yet unknown Ophiocoma.

Ailsa M. Clark (1966) expanded the distributional record for Ophiomastix pusilla by describing several specimens from the Red Sea and Gulf of Aqaba. She continued to use the generic name Ophiomastix, noting that several species of Ophiomastix also had a continuous coat of granules on the disc with spinelets intermingled with the granules. O. pusilla was also compared with Ophiocoma brevipes, showing similarity in color pattern and in the 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 the position of the club-shaped spines. These modified spines were observed from the eighth to the twelfth segments, usually on two or three consecutive segments. In contrast to Koehler's (op. cit.) conclusion, Miss Clark found the clavate spines less conspicuous in the larger (d.d. 7 mm) than in smaller specimens.

Murakami (1943a) reported a new species of ophiocomid which he called Ophiocoma latilanxa from Palao Island in the western Pacific; additional specimens were reported from Yaeyama Island and the Riukiu Islands in the Ruuku 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 the thickening of the spines. O. latilanxa was considered related most closely to Ophiocoma Lubrica Koehler. However, it was distinguished from O. lubrica by having broad pentagonal ventral arm plates, more numerous dental papillae, and a different shape of the oral shield. In Koehler's (1898) description of O. lubrica, the arm spines were described as being four, cylindrical, thick, and blunt at the tip, and in this respect they also differed from O. latilanxa. H. L. Clark (1921) considered O. lubrica as a synonym for O. scolopendrina. A review of the original description especially the bathymetric records makes this doubtful, and the characters suggest O. pusilla most closely.

The discovery of O. latilanxa did not suggest any relationship to Ophiomastix pusilla, primarily because of the emphasis on the modified club-shaped spines attributed to the latter species, and their absence in the former. However, several new lines of evidence have suggested reconsideration of the close relationship of the two species.

Several brittlestars described as *Ophiocoma insularia* by Balinsky (1957) from Inhaca Island, Mossambique, were made available to me. The specimens proved on examination not to be *O. insularia*. Differences in the shape and size of the arm spines, nature of the dental plate, and number of dental papillae indicated that the specimens were quite distinct from any species in the Brevipes complex of *Ophiocoma*. The specimens I have examined were small with a disc diameter less than 10 mm. One specimen had peculiar dark circles surrounded by a lighter ring. This was one of several color patterns noted by Balinsky. Balinsky had compared his specimens to H. L. Clark's *Ophiocoma delicata* on the basis of size and color pattern. Ailsa M. Clark (pers. comm.) at my request examined the type specimen of *O. delicata*, deposited in the British Museum, and reported that the specimen represented a species of *Ophiarachna* near *mauritiensis* (fam. Ophiodermatidae). My own examination of a paratype of *Ophiocoma delicata* deposited at the Museum of Comparative Zoology, Harvard, agreed with Miss Clark's determination. She suggested that Balinsky's specimens (as *Ophiocoma insularis*) might be the same as a small specimen which she described as *Ophiocoma* sp. from the Red Sea in 1952, and which she later united with additional material from the Gulf of Aqaba as Ophiomastix pusilla (1966).

In another collection of small ophiuroids from Eniwetok Atoll, Marshall Islands, I found specimens similar to those from Inhaca Island. Since the Eniwetok specimens were sexually mature, they removed doubts that O. pusilla was made up of juvenile forms of some other species.

The relationship between both the Eniwetok and Inhaca Island specimens and Murakami's Ophiocoma latilanxa finally became apparent after an examination of the dental plate. Murakami's (1963) description and figure of the dental plate of O. latilanxa coincided remarkably well with the shape of this plate in the Eniwetok and Inhaca Island specimens (Pl. XIX, fig. 6,b). The unique shape of this dental plate, conspicuously broadened in the oral region, is very characteristic.

Finally a careful examination of the Inhaca Island material revealed the presence of several thickened arm spines in one of the specimens. Instead of the usual arrangement, with club-shaped spines occurring on the next to uppermost arm spine on each side, the enlarged spines were located on the third or even fourth spine in a row. The thickened arm spines appeared irregularly and several larger and smaller specimens from Inhaca Island showed the complete absence of the modified arm spines. Eniwetok specimens also revealed no modification of arm spines. Recent examination of three specimens labeled *Ophiocoma brevipes* var. *variegata*, deposited at the U. S. National Museum, from Yap Island, (Caroline Islands) showed the modified arm spines on only two arms of one of the specimens. In other respects these specimens conformed to the characteristics of *Ophiocoma pusilla*.

Additional specimens identified as *Ophiocoma insularia* var. *variegata* from Green Island on the Great Barrier Reef, Lord Howe Island off north eastern Australia, and Port Galera, Mindoro, in the Philippine Islands, proved on examination to be *O. pusilla*. My examination of the specimen, identified by H. L. Clark (1917) as *Ophiocoma insularia* var. *longispina* from Easter Island, also indicated that this specimen should be considered *O. pusilla*.

Finally, it has been found that *Ophiocoma pusilla* has morphological characters which more strongly relate it to the genus *Ophiocoma*, especially to the Canaliculata group. The dental papillae and dental plate resemble *Ophiocoma bollonsi* and the shape of the oral arm plates and presence of two tentacle scales are common to the members of the Canaliculata group. However, the nature of the arm spines, by being hollow, indicates possible relationship with *Ophiocomina*.

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 differences in the sequence of the arm spines and the very different form of the spines. For the present, it seems best to consider this species as a possible link between the genus *Ophiocoma* and *Ophiocomina*.

Scolopendrina Group

The Scolopendrina group of Ophiocoma is the most successful in terms of the number of species and overall distribution. Nine species are known and representatives are found circumtropically with the possible exception of West Africa.[1] There are several characters which distinguish this group from other species in the genus. Among these characters:

1) there is an alternation of the arm spines (typically three and four) occurring either on opposite sides of the same arm segment or adjacent segments (Pl. XI, fig. 3).

2) as a consequence of the alternation of arm spines, the aboral arm plates often show uneven lateral borders. That is, on the side where four spines occur, there is a greater development of the lateral arm plate and this encroaches on the aboral arm plate leaving it truncated on its lateral edge (Pl. XIII, figs. 2-3). In contrast, the opposite side (when only three spines occur) shows the border of the aboral arm plate tapering.

3) the dental plate is also characteristic (Pl. XVIII, fig.

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[1] See O. echinata, p.171

5). The length : breadth ratio is between 2.4 and 2.6 : 1. The area occupied by the dental papillae is approximately one-third the total length. Very narrow vertical septa divide the teeth foramina.

4) the number of oral papillae is usually four, although one or more may occasionally split or coalesce to give five or three, respectively.

5) the disc granules are coarse and spherical except in Ophiocoma anaglyptica where they are flattened at the top.

6) the arm spines are generally thick especially the fourth spine, when present, which is also usually much longer than the other spines.

Species of Ophiocoma in the Scolopendrina group include:

Species	Distribution
O. aethiops Lütken	Eastern Tropical Pacific
O. 'alternans' Endean	Southeast Sub-Tropical Australia
O. anaglyptica Ely	Central Tropical Pacific
O. echinata (Lamarck)	Tropical Caribbean
O. erinaceus Müller & Troschel	Tropical Indo-Pacific
O. macroplaca (H. L. Clark)	Eastern Indo-Pacific (Hawaii)
O. occidentalis H. L. Clark	Western Sub-Tropical Australia
O. scolopendrina (Lamarck)	Tropical Indo-Pacific
O. wendtii Müller & Troschel	Tropical Caribbean

Ophiocoma aethiops Lütken

SYNONYMY

Ophiocoma aethiops Lütken, 1859, pp. 141, 145; Lyman, 1865, pp. 78-80; 1875, p. 4; 1882, p. 171, Pl. XLII, figs. 9-11; Verrill, 1867a, p. 258; 1867b, pp. 327, 329, 330, 341; 1871, p. 594; Ljungman, 1866, p. 329; H.L. Clark, 1902, p. 525; 1913, p. 217; 1915, p. 291, Pl. 13, figs. 6-7; 1917, p. 440; 1921, p. 128; 1923b, p. 156; 1940, p. 341; Campbell, 1921b, p. 48; Koehler, 1907b, p. 325; 1922, p. 312; Nielsen, 1932, pp. 246-248; Boone, 1933, pp. 112-113, Pl. 65A-D; Ziesenhenne, 1937, p. 226; Steinbeck and Ricketts, 1941, p. 387, Pl. 13, fig. 1; Caso, 1951, pp. 227, Figs. 3-6; 1961, pp. 149-150, Figs. 57-60.

NOT Ophiocoma aethiops Lütken: Andrews, 1900, p. 117, Bell, 1887a, p. 140; 1887b, p. 523.

MATERIAL EXAMINED

Baja California - BPBM: W1626a-b (2)

Columbia - BPBM: W1628a-3 (5)

Costa Rica - BPBM: W168a-d (4)

Equator - BPBM: W1630a-d (4)

Galapagos Islands - BPBM: 1627a-d (4)

Gulf of California - BPBM: 1629a-e (5)

Panama - BPBM: W507 (1)

DIAGNOSIS

Ophiocoma aethiops is well differentiated from other members of the Scolopendrina group by extremely broad aboral arm plates often more than three times broader than the length of the oral arm plates. In addition, in specimens larger than 10 mm (d.d.), the next to uppermost arm spine is the longest, especially where four arm spines are present on segments beyond the disc margin. At the same time, as Koehler (1922) pointed out, the upper spine is thicker than the others although not swollen, rather broadened, with a distinctly truncated tip. This relative size and shape of the upper arm spines appears to be unique among species in the Scolopendrina group of *Ophiocoma*.

My own examination of specimens of *O. aethiops* shows that disc-granules are present on specimens as small as 3 mm (d.d.).

Additional comments on the external morphology of *O. aethiops* have been given by Lyman (1865) and Nielsen (1932). The latter described the variation in the number and position of the dental papillae for specimens of different sizes as well as the number of oral papillae.

Together with Lyman (*op. cit.*) and Koehler (1922), Nielsen considered the considerable variation in the number of tentacle scales. The presence of three scales on some of the proximal pores is evident in some of the specimens I have examined, but as Nielsen suggested, the frequency of this condition is not constant nor completely dependent upon size. In general two scales are found on the proximal ten to twenty segments, but even fewer segments may have two tentacle scales.

H.L. Clark (1902) mentioned three characters by which *O. aethiops* could be distinguished from the Caribbean species, *O. echinata*. These included the width of the upper arm plates, the shape of the arm spines and the shape of the oral shields. A specimen of 40 mm (d.d.) was recorded, making this the largest individual known in the subfamily.

Lyman (1882) presented illustrations of the internal disc scalation as well as the distal and proximal surfaces of the arm vertebra.

Nielsen's (1932) description of *O. aethiops* is especially valuable in presenting added information about Lütken's type specimen in the Copenhagen museum.

HABITAT AND DISTRIBUTION

H.L. Clark (1940) reports that the bathymetric range of this species is 0 to 10 fathoms. Most specimens have been taken from beneath rock boulders or in the interstices thereof. In several places it has been taken in large numbers (Steinbeck and Ricketts, 1940) and it appears to be gregarious.

This species is the only member of *Ophiocoma* in the Scolopendrina group occurring along the tropical and subtropical Eastern Pacific Coast. Specimens range from central Baja California in the north to Equador in the south. Specimens have been recorded from the Galapagos Islands (H.L. Clark, 1902; Boone, 1933) and Clarion Island (Zeisenhenne, 1937).

Records of *O. aethiops* from Indian Ocean localities by Bell, (1887a, 1887b) and Andrews, et al (1900) are probably based on specimens of *O. erinaceus*.

Ophiocoma "alternans" Endean

SYNONYMY

Ophiocoma alternans Endean, 1963, p. 265, Text Fig. 1, Pl. XVII, figs. 1-2; 1965, p. 231.

Ophiocoma erinaceus Müller and Troschel: Endean, 1961, p. 292.

NOT *Ophiocoma alternans* Martens, 1870, p. 251.

DISCUSSION

In 1870, Martens described *Ophiocoma alternans* from the Philippines based on a small specimen which has subsequently been considered a synonym of *O. scolopendrina* (H. L. Clark, 1921, p. 121). Therefore, *Ophiocoma alternans* Endean, 1963, becomes a junior homonym and a new name will have to be given for this Australian species.

Endean's species was described from specimens collected at Hastings Point, northern New South Wales, Australia under boulders in rock pools near the littoral fringe. Additional specimens have been taken on the southern Queensland coast at Caloundra, latitude 27° S (Endean, 1965). The most closely related species of *Ophiocoma*, *erinaceus* and *scolopendrina*, have not been found south of the Great Barrier Reef nor on the Queensland mainland coast where *O.* "*alternans*" has been reported (Endean, pers. comm.). Thus a well defined boundary appears to separate this species from its northern, Barrier Reef, relatives.

In addition to zoogeographical separation, Endean (1963) presented several qualitative morphological features to separate *O.* "*alternans*" from *O.* *erinaceus* and *O.* *scolopendrina*. Among these are: a) the coarseness of the disc granules and their extent into the interradial part of the disc; b) the size, shape, and arrangement of the arm spines; c) pigmentation; d) relative length of the arms to disc diameter.

Without having had the opportunity to examine specimens of *O.* "*alternans*" it is difficult to judge the merit of these qualitative differences separating this species from *O.* *erinaceus* especially. However, the characters listed above by Endean present a great deal of intraspecific variation in *O.* *erinaceus* and it would be more satisfying if meristic or morphometric characters could be found to differentiate the two species. An examination of the arm-spine sequence of *O.* "*alternans*" might prove revealing. Type specimens of *O.* "*alternans*" are deposited in the Australian Museum, Sydney, Australia.

Ophiocoma anaglyptica Ely
(Plate XI, figs. 1, 3, 5-7)

SYNONYMY

Ophiocoma anaglyptica Ely, 1955, p. 373, fig. 1; A.H. Clark, 1952, p. 294; 1954, p. 260.

MATERIAL EXAMINED

Canton Island - USNM: (TYPE SPECIMEN) E.6847.

Christmas Island (Pacific Ocean) - BPBM: W562a-u (21)

Howland Island - BPBM: W588c (1)

Jarvis Island - BPBM: W1005 (1)

Washington Island - BPBM: W578a (1)

Samoa - BPBM: W1090a-f (6); W1091a-d (4); W1092a-c (3); W1669a-j (10); W167a-e (5).

DIAGNOSIS

The maximum disc diameter of specimens I have examined is 20 mm . In specimens this size the arm length is approximately 5 times greater than the diameter of the disc. Specimens with mature gonads have been observed from 6 mm (d.d.).

The disc granules are unique in being flattened on the top or pavement-like. They enter the interbrachial area of the disc to a variable extent but leave a large area toward the oral shield bare. In this part of the disc a series of enlarged scales are evident, characteristic of the species.

Two tentacle scales usually occur on the proximal segments quite regularly, occurring on more segments distally with increase in size. Ely reported two or three scales on the first three segments, but this condition is not common.

The arm spines alternate very regularly on opposite sides of the same segment with 3 and 4 spines. This is characteristic beyond the disc edge. Some segments near the disc edge carry five spines. The upper (fourth) arm spine is quite swollen in the middle or flask-shaped (Pl. XI, figs. 1,s, 3). Distally there are only three spines.

The dental papillae are arranged in two outer columns, three or four deep, with one or two located between. Several papillae sometimes occur above the jaw level at the apex. Ely mentioned only "5 or 6" dental papillae in the type specimen. I noted 10 papillae in an 11 mm (d.d.) specimen and up to 15 in a 20 mm (d.d.) specimen.

The teeth number three and four and have a hyalinated tip.

The dental plate shows characteristics common to other members of the Scolopendrina group of Ophiocoma (Pl. XI, fig. 1,b).

Specimens are dark-brown, nearly black in color aborally, with little contrast between disc and arms. The arm spines are also dark. Ely reported the presence of linear white bands or sometimes spotting at the base of the uppermost arm spines on the type specimen. This is not consistent however, at least in alcoholic or dried specimens at my disposal. The oral surface is usually slightly lighter than the upper surface; I have been unable to verify Ely's description of the oral surface being "variously spotted or mottled with white, yellow, and light brown" at least in preserved specimens. The mouth region however can be nearly white or brown or mottled with white and brown. Ely gave a few additional variations of this basic color pattern.

HABITAT

The type specimens were collected at Canton Island, from the reef near shore, beneath loose coral blocks on November 18, 1941. A.H. Clark (1952) reported specimens from Bikini Atoll and Eniwetok Atoll which were collected from under loose, flat coral heads on a rocky shore. Specimens in the Bishop Museum from Samoa and Christmas Island were collected on shallow reef flat areas.

ASSOCIATES

Devaney (1967, p. 297) reported the association of *Ophiocoma anaglyptica* and the ectocommensal polynoid worm, *Hololepidella nigropunctata* from Eniwetok Atoll.

DISTRIBUTION

In addition to the localities listed in material examined (above) *Ophiocoma anaglyptica* has been reported from the Gilbert Islands (A. H. Clark, 1954) and the Marshall Islands (A. H. Clark, 1952). The records indicate a limited Central Pacific distribution which may be due in part to the inability of previous workers to distinguish this species from other closely related forms, i.e. *O. erinaceus*. The zoogeographical limits of *O. anaglyptica* are by no means complete yet, and it may eventually be found more widely dispersed in the Pacific.

DISCUSSION

Ophiocoma anaglyptica shows characters in common with other species of *Ophiocoma* in the Scolopendrina group in the arrangement of the arm spines (sequence) and shape and number of oral and dental papillae. Distinctive features include the nature of the disc granulation, shape of the upper arm spines and the enlargement of the interradial disc scales.

Ophiocoma echinata (Lamarck)

SYNONYMY

Ophiura echinata Lamarck, 1816, p. 543.

Ophiocoma crassispina Say, 1825, p. 147; Lütken, 1859, p.

142, Pl. iv. , figs. 7a-d; Müller and Troschel, 1842, p. 103; Lyman, 1865, p. 84.

Ophiocoma echinata (Lamarck): Agassiz, 1836, p. 192; Lyman, 1865, p. 81, Fig. 5; 1882, p. 171, Pl. XLII, figs. 12-13; Verrill, 1867a, pp. 258, 341; 1899, p. 22; 1899 b, p. 375; 1900, p. 586; 1907, p. 327, Pl. 34D, figs. 2 (1,2); Rathbun, 1879, p. 152; Grave, 1898, p. 7, Figs. 1-2 (fertilized egg); H.L. Clark, 1899, pp. 118, 131; 1901, p. 340; 1902, p. 245; 1915, p. 291; 1919, p. 57; 1921, p. 125; 1933, pp. 65, 125, 126, 127, 128, 129, 130 (distribution); 1942, p. 378; Koehler, 1913, p. 374; 1914, pp. 117, 159; A.H. Clark, 1922, p. 211; 1939a, p. 450, Pl. 54, fig. 4; Mortensen, 1921, pp. 131-132, Fig. 57, (larva); 1931, pp. 4, 26-28, Fig. 11a-c (larval stages); Tortonese, 1934, p. 39, Pl. V, figs. 26-27; Engel, 1939, p. 8; Fontaine, 1953, p. 203, Fig. 7; Brito, 1962, p. 2, Pl. i. fig. 3; Parslow and A.M. Clark, 1963, pp. 27, 46.

Ophiocoma serpentaria Müller and Troschel, 1842, p. 98; Lyman, 1865, p. 84.

? Ophiocoma tumida Müller and Troschel, 1842, p. 100; Lyman, 1865, p. 70; Koehler, 1922, pp. 317, 319.

MATERIAL EXAMINED

Panama - BPBM: W1642a-f (6)

Puerto Rico - BPBM: W1673a-d (4)

DIAGNOSIS

A very complete description of Ophiocoma echinata has been given by Lyman (1865) for the adult condition. Juvenile characters were discussed by both H. L. Clark (1933) and A. H. Clark (1939a).

HABITAT

O. echinata is a common faunal element in boulder strewn areas, or in reefs among deal coral rubble. The bathymetric range for this species is in the shallow sub-littoral to 13 fathoms (Verrill, 1900). The species has been collected together with O. wendtii (as O. riisei) both as adults and juvenile stages (A. H. Clark, 1939a) and the ecological distinction between the two species has yet to be elucidated.

DISTRIBUTION

According to H. L. Clark (1919; 1933) and others, O. echinata has been taken at Bermuda, the Bahamas, Florida, the Tortugas, the eastern Panama coast, and along the South American coast to northern Brazil (Rathbun, 1879). H. L. Clark (1921) also reported a specimen in the Paris Museum which is supposed to be from Liberia. This latter record would make O. echinata together with O. pumila (Ailsa M.

Clark, 1955) the only ophiocomids known from the West African coast.

DISCUSSION

In many respects *Ophiocoma echinata* appears to be a West Indian counterpart of *O. erinaceus* and *O. scolopendrina*. H. L. Clark (1921) noted the similarity between *echinata* and *scolopendrina* and "...that it is only with great care that they can be distinguished". Furthermore, "Many specimens would be almost indistinguishable were the locality whence they came not known" (p. 125). However, in his key to the species of *Ophiocoma*, the same worker (pp. 122-123) differentiated *O. echinata* from both *O. erinaceus* and *O. scolopendrina* on the basis of the shape of the oral shields, the number (coarseness) of the disc granules, and the shape of the uppermost arm spine.

The presence of disc granules in specimens as small as 3 mm (d.d.) (H. L. Clark, 1933) would immediately serve to separate the young of *O. echinata* from *O. erinaceus*. In the latter species, granules are seldom found in specimens less than 10 mm (d.d.).

Ecologically, *O. echinata* and *O. erinaceus* are more similar than *O. echinata* and *O. scolopendrina*. The restricted littoral habitat and unique feeding behavior noted for the latter (Magnus, 1962, 1964) has not been recorded for O. echinata.

The type specimen of Ophiura echinata is said to be deposited in the Paris Museum of Natural History (Lyman, 1865, p. 84). The type of Ophiocoma crassispina is deposited in the Philadelphia Academy of Natural Sciences. The type specimen of Ophiocoma tumida is in the Leyden Museum. According to Koehler (1922, p. 319) the description of O. tumida suggests O. echinata, but the locality (Gulf of Genoa) is difficult to explain and may be erroneous as Lyman (1865, p. 70) suggested. Re-examination of the type specimen should clear up the matter. The specimen designated as Ophiocoma serpentaria by Müller and Troschel is in the Paris Museum.

Ophiocoma erinaceus Müller and Troschel

(Plates XII, figs. 2, 4, 6; XIII, 1-9)

SYNONYMY

Ophiocoma erinaceus Müller and Troschel, 1842, p. 98; Loriol, 1894, p. 21 (with complete bibliography up to 1893); Koehler, 1907b, p. 327; 1922, pp. 311-313, 322-324, Pl. 73, fig. 7; 1927, p. 4; 1930, p. 204;

H. L. Clark, 1908, p. 296; 1915, p. 291, Pl. XV, figs. 5-6; 1917, p. 441; 1921, p. 127; 1923, p. 348; 1925, p. 92; 1932, p. 209; 1938, p. 329; 1946, p. 244; Domantay, 1936, p. 396, Pl. vi, fig. 53; Mortensen, 1937, pp. 48-49, Fig. 37 (larval skeleton), Pl. VIII, fig. 4 (larva); Ely, 1942, pp. 30-31, 51-54, text-figs. 4, 14, Pl. 12a; Murakami, 1943a, p. 196; 1943b, p. 217; Edmondson, 1946, p. 81, Figs. 39c, 41g-h; A. H. Clark, 1952, p. 295; 1954, p. 260; Ailsa M. Clark, 1952, pp. 302, 208; 1965, pp. 599, 603; 1966, pp. 47, 55; Endean, 1953, p. 55; 1956, p. 126; 1957, p. 244; 1961, 292; Balinsky, 1957, pp. 25-26, 30; Domantay and Domantay, 1966, p. 50.

Ophiocoma schoenleinii Müller and Troschel, 1842, p. 99; Lyman, 1865, p. 70; 1882, p. 171; H. L. Clark, 1908, p. 296; 1915, p. 293, Pl. XV, figs. 1-2; 1921, p. 128; 1923c, p. 349; Koehler, 1922, p. 323, Pl. 73, fig. 7; A. H. Clark, 1954, p. 260; Domantay and Domantay, 1966, p. 50.

Ophiocoma tartarea Lyman, 1861; p. 78.

Ophiocoma nigra (Abildgaard): Michelin, 1862, p. 2.

Ophiocoma scolopendrina (Lamarck): Walter, 1885, p. 369 (pt.); Marktanner-Turneretscher, 1887, p. 302 (pt.);

Brock, 1888, p. 495 (pt.); Ludwig, 1899, p. 546 (pt.); H. L. Clark, 1909, p. 542 (pt.); Boone, 1938; A. H. Clark, 1939a, p. 4.

Ophiocoma crenacea [sic] Müller and Troschel: Etheridge, 1887, p. 39.

Ophiocoma erinacea Müller and Troschel: Doederleini, 1896, p. 291; H. L. Clark, 1911, p. 257.

Ophiocoma scolopendrina var. erinaceus Müller and Troschel: Doederleini, 1896, p. 289; Whitelegge, 1897, p. 160; Koehler, 1905, p. 60; 1907b, p. 326; Matsumoto, 1917, p. 345, Figs. 96a-d; Djakonov, 1930, p. 345.

Ophiocoma wendtii Müller and Troschel: Koehler, 1905, p. 63, Pl. XIV, figs. 5-7; 1907a, p. 246; 1907b, p. 327 (pt.); 1922, p. 328, Pl. 75, figs. 7-8; H. L. Clark, 1908, p. 297; Boone, 1938, p. 155, Pls. 55-56.

Ophiocoma scolopendrina var. schoenleinii Müller and Troschel: Matsumoto, 1917, p. 345; Djakonov, 1930, p. 245.

MATERIAL EXAMINED

Australia (Queensland)

Green Island - MCZ: No. 3762 (1)

Frankland Islands - MCZ: No. 4592 (1)

Celebes - ZMB: 929 TYPE, Ophiocoma schoenleinii Müller and Troschel

Marshall Islands

Eniwetok Atoll - Pers. Coll. (3)

Fiji Islands - BPBM: W852c (1), W1664 (1); MCA: No. 4440 (1)

Guam - BPBM: W487a-b (2)

Hawaiian Islands

Hawaii - USNM: E7066 (1); Pers. Coll. (15)

Kauai - BPBM: W1549 (1), W1561 (1); Pers. Coll. (5)

Laysan - BPBM: W280 (1); USNM: E7067 (5)

Necker - BPBM: W279 (1)

Oahu - BPBM: W353 (2), WW756 (5), W791 (2), W1216 (15), W1549 (1), W1554a-b (2), W1671 (1); Pers. Coll. (53)

Unspecified - USNM: E7060 (3), E7062 (1), E7064 (3), E7069 (3), E7095 (1)

Howland Island - BPBM: W587 (1)

Johnston Island - BPBM: W372 (6); Pers. Coll. (10)

Line Islands

Christmas Island - BPBM: W560 (8)

Palmyra Island - BPBM: W340 (4), W877 (1), W942 (1), W1632 (1)

Washington Island - BPBM: W579 (2)

Mossambique - BPBM: W1582, W1583 (2)

Philippine Islands - BPBM: W1633a-b (2); USNM: No. 40948 (1) (as _O. wendtii_)

Raratonga Island - BPBM: W341 (1)

Samoa Islands - BPBM: W926 (1), W1060 (1), W1061 (1), W1075 (1), W1415 (1), W1650a-f (6), W1651a-c (3), W1667 (1); MCA: No. 4362 (1), No. 4412 (3), No. 6782 (1), No. 6783 (2); USNM: E4890 (6) (as _O. Wendtii_)

Torres Starit (Mer Island) - MCZ: No. 3757 (12), No. 3762 (4 ≠)

DIAGNOSIS

Size. Specimens examined with disc diameter 1.3 to 32 mm.

Disc cover. Granules, coarse, rounded, usually limited to aboral side, not formed in specimens less than 10 mm disc diameter.

Tentacle scales. Two, each side, on first arm segment in specimens larger than 5 mm (d.d.); one or two scales follow on distal segments depending on geographical population; this character polymorphic (see pp. 188-189).

Arm spines (Pl. XIII, fig. 1, 3). Irregular pattern, on each side 3 and 4 spines; upper (fourth) spine thickened, nearly always longer than third of opposite side. 3 spines on each side of the first three segments.

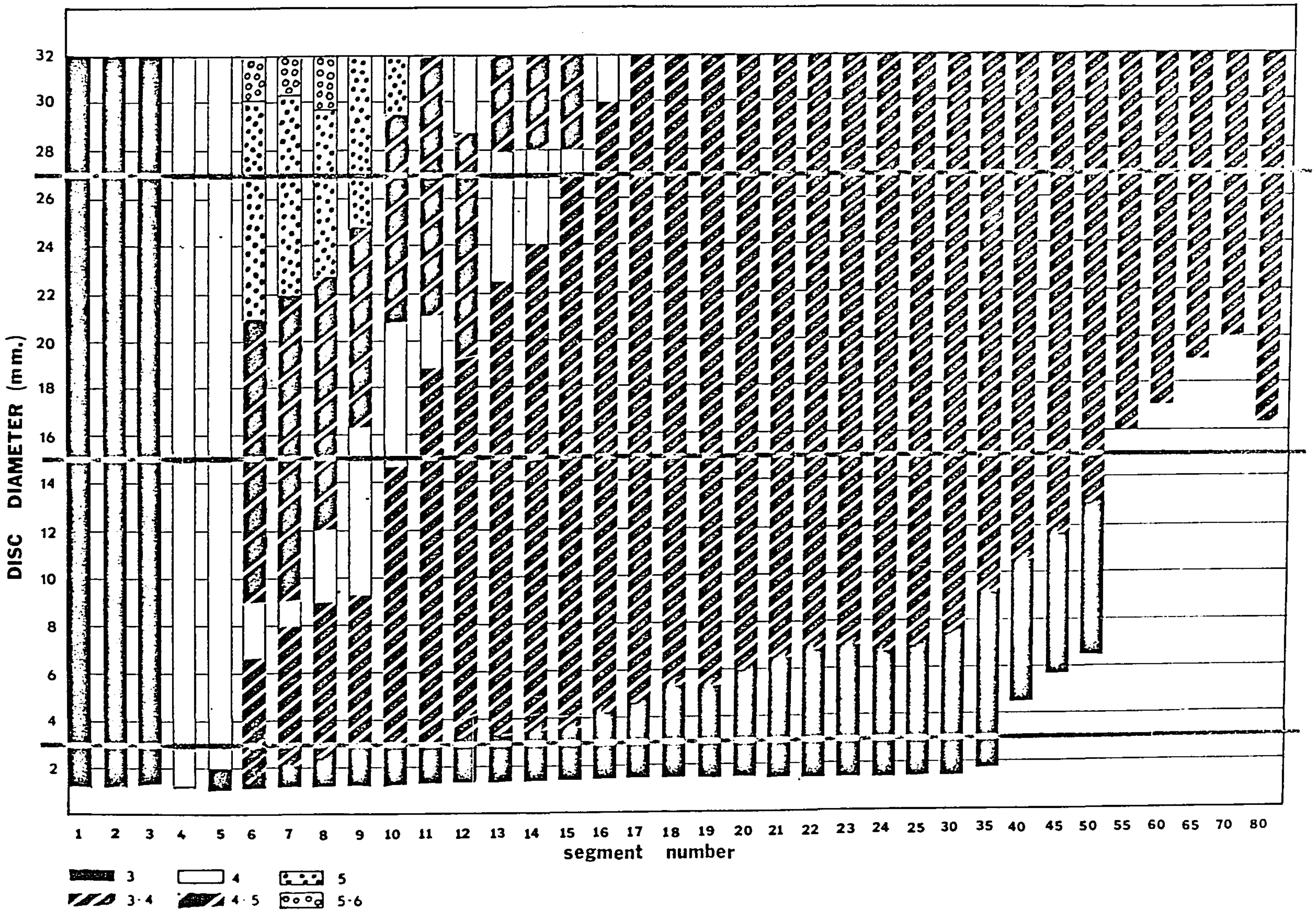
The arm spine sequence was analyzed (TABLE XV). For each specimen at least three arms were examined on both sides out to segment fifteen and every fifth segment thereafter. In most specimens the spines on all arms were counted, expecially on the proximal ten segments. Specimens of Ophiocoma erinaceus from the Hawaiian Islands show a very definite pattern of growth and development of arm spines. Beginning with an initial three spines on each side of the arm segment developing at the sides of the lateral arm plate, I found an increase in the number of spines with increase in size. This increase follows a definite pattern. Several other features of the external morphology also undergo definite growth changes simultaneously with the arm spine changes. A composite arm spine sequence for O. erinaceus is given in Table XV. In order to follow the changes sequentially, specimens were divided into class intervals, using the diameter of the disc as a basic criterion of size.

a) 0.1 - 2.0 mm: 3 arm spines on each side of all segments; the early development of the fourth arm spine appearing above (aboral to) the existing spines and usually on the fourth segment, or fourth and fifth segments simultaneously. A fourth spine has not been observed on specimens smaller than 1.6 mm (d.d.). None of the arm

Ophiocoma erinaceus

TABLE XV

ARM SPINE SEQUENCE



number of arm spines

segments has yet formed two tentacle scales. Twenty arm segments being the maximum number in a 2 mm specimen.

b) 2.1 - 4.0 mm: fourth spine occurring as far as segment eighteen; a typical somewhat irregular pattern of 3 and 4 arm spines evident beyond segment eight. Fourth spine beginning to thicken and larger than the third (upper) spine on opposite side of segment. Two tentacle scales also as far as segment ten and number of arm segments thirty five to forty by a size of 4 mm (d.d.).

c) 4.1 - 8.0 mm: continued development of fourth arm spine on distal segments but two tentacle scales do not occur as far distally as development of fourth spine. Up to seventy arm segments may be found on specimens of 8 mm (d.d.).

d) 8.1 - 10.0 mm: fourth spine occurring as far as segment thirty five; arm segments from four to ten not having alternating 3/4 arm spine pattern, but with 4 spines regularly. No increase in number of arm spines on first proximal five segments. Later, with increase in size however, fifth or even sixth spine can develop on segments seven to ten. Two tentacle scales extending as far as segment twenty-five by 10 mm (d.d.) and as many as 80 arm segments. Disc granules beginning to appear also at this size.

e) 10.1 - 12.0 mm: fourth spine extends as far as segment 50; two tentacle scales develop this far also. Number of arm segments increasing to ninety and disc granules usually covering aboral surface of disc.

f) 12.1 - 20.0 mm: distal development of 3/4 irregular pattern of arm spines continuing as well as similar regular development of second tentacle scale. Maximum number of arm segments increases, but considerable variation noted, possibly due to regeneration. Presence of fifth arm spine on segments seven to twelve variable; it may be absent altogether on all sectors of one individual or may occur on one or both sides of one or more sectors of another.

g) 20.1 - 25.0 mm: with exception of increase in size similar pattern occurring; however greater number of segments with fifth spine, occasionally alternating with four spines. Presence of a sixth spine observed on segments eight to ten. New spines added above existing spines.

h) 25.1 - 32.0 mm: maximum size range for species. Maximum number of arm segments noted, one hundred and thirty-four. Two tentacle scales out to segment one hundred and twelve and 3/4 alternation of arm spines also this far; fifth arm spine may occur as far as segment twenty-five, alternating with four spines on opposite side. A comparison of the arm spine sequence of *Ophiocoma erinaceus* with that of *Ophiocoma macroplaca* shows very close similarities (TABLE XV and TABLE XVIII). The alternation of three and four arm spines is shared by all species of *Ophiocoma* in the Scolopendrina group as well as *Ophiomastix* and *Ophiarthrum*. However, there are often some very constant differences in the arm spine sequences. For *O. erinaceus* and *O. macroplaca*, the difference is clearly seen in the number of arm spines on the third segment, the latter species having 4 rather than 3. Other changes can be recognized for similar sized specimens of each species.

Dental papillae (Pl. XII, figs. 2, 4). Well developed into three or four columns in specimens larger than 10 mm (d.d.); smaller specimens with fewer papillae.

Teeth. Three and four on adjacent dental plates (Pl. XII, figs. 2, 4).

Dental plate (Pl. XII, fig. 4,b). Adult condition: between 2.6 and 2.9 times as long as broad; very narrow septa between tooth foramina; dental papillae extend approximately thirty per cent of total length.

Oral arm plate. Above 4.0 mm (d.d.) oral arm plate of tenth segment becoming broader than long: change from longer than broad to broader than long indicating growth increase. Arm plates becoming longer than broad farther out (distally) on arm where juvenile characters still evident.

Tentacle scales. Based on examination of specimens collected from the Hawaiian Islands the following results have been noted:

a) The first tentacle scale does not form until the disc diameter reaches a size between 1.5 and 2.0 mm.

b) There is a good correlation between the development of the first tentacle scale on the first arm segment and the formation of the outer and papilla. This would appear to substantiate, at least indirectly, the claim by Ludwig (1878) that the adoral shield is homologous with the lateral arm plates and that the outer oral papilla corresponds to a tentacle scale.

c) Tentacle scales have formed on distal segments prior to appearance of the first tentacle scale on the first arm segment.

d) The development of the second tentacle scale on each side of the arm segment is a function of increasing size. The second tentacle scale begins on the inner edge of the first scale, and appears initially on the first arm segment at a size of 3 to 4 mm disc diameter (in some cases the second scale forms initially on the second segment). There is a rapid development of the second scale as far as segment seven by the time the disc diameter reaches 5 mm. A correlation between the number of segments with two scales and size (using the width of the tenth oral arm plate) has been made and recorded in TABLE XVI.

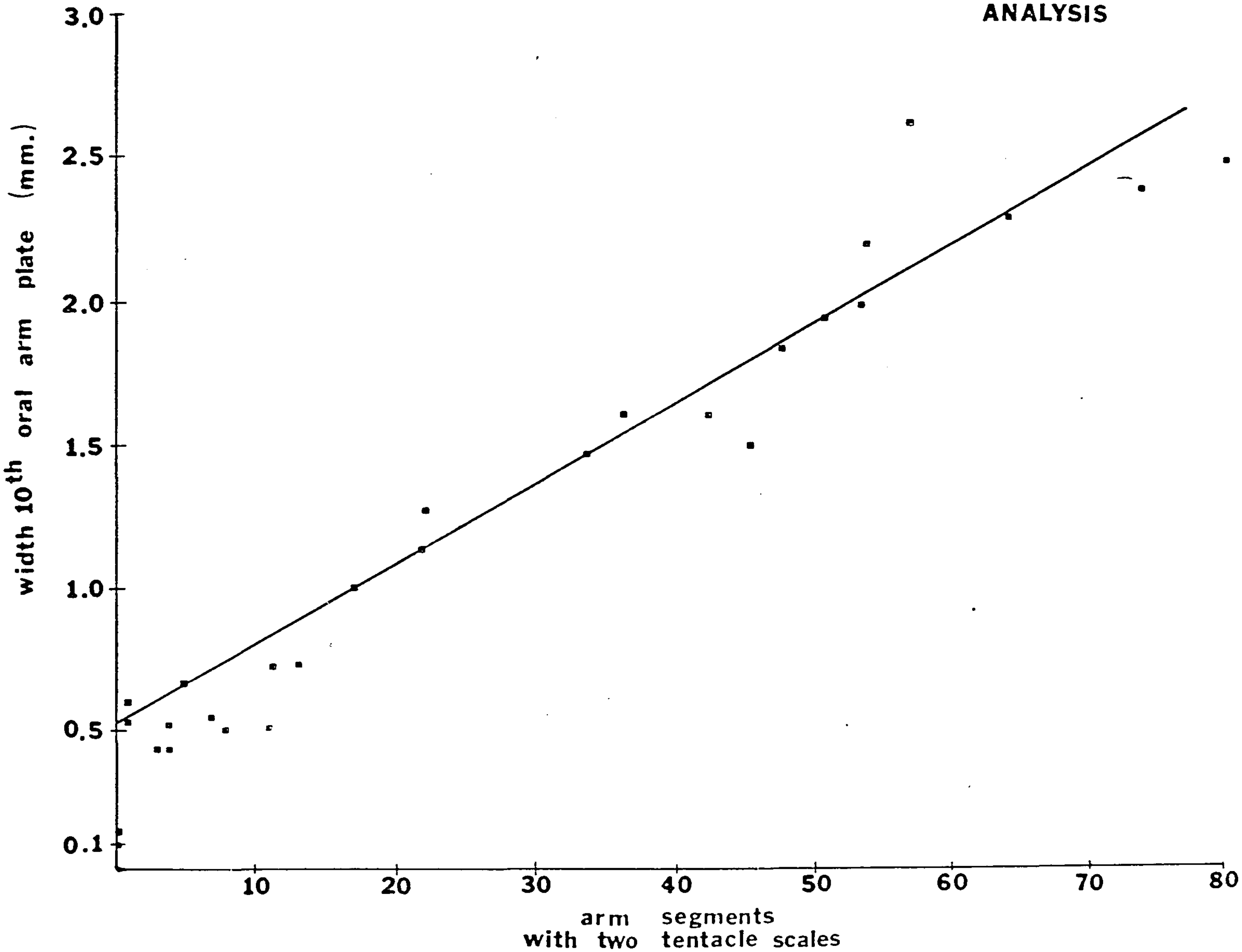
Pigmentation. Dense black or dark brown color in adults seldom mottling or variation in color; young (Pl. XIII, fig. 5) with white and black banding of arms and mouth plates and some white on the disc, aborally.

HABITAT

Ophiocoma erinaceus is commonly found in branches of live or dead coral or in rubble. It appears able to occupy many areas where a solid substratum is available and is less common on sandy bottoms. H. L. Clark (1921) characterized the habitat of *O. erinaceus* and *O. scolopendrina* and used this as an important reason for maintaining them as separate species: the latter occupies a higher level on the shore

TABLE XVI

OPHIOCOMA ERINACEUS — TENTACLE SCALE ANALYSIS



commonly uncovered at ordinary low tides; the former occurs farther out on the reef flat.

I have collected very young specimens (disc diameter, 1.3 - 2.8 mm) of O. erinaceus from the base of the alga, Sargassum polyphyllum at Makua, Oahu (Nov. 1964). On a few occasions, slightly larger specimens (d.d. to 5 mm) have been found clinging to adult brittlestars.

Bathymetrically, this species appears most common in the shallow sub-littoral region, although specimens have been collected to a depth of 100 meters.

ASSOCIATES

An ectocommensal polynoid, Hololepidella nigropunctata (Horst) has been found on O. erinaceus both at Hawaii and at Johnston Island (Devaney, 1967). In Hawaii however, another ophiocomid, O. dentata, is the more common host where both brittlestars species occur together.

The small amphiurid brittlestar, Amphipholis squamata has been reported clinging to the arms of ophiocomid brittlestars; H. L. Clark (1921, p. 107) noted this association with an undetermined species of Ophiocoma at Mer Island (Torres Strait) but considered this a chance occurrence. Ely (1942, p. 38), in Hawaii, observed a similar association, frequently with other individuals of Ophiocoma, located under stones and he considered this to be more than a chance occurrence. My own observations in Hawaii support Ely's, as I have found on many occasions *A. squamata* among the arm spines of both *O. erinaceus* and *O. dentata*.

DISTRIBUTION

O. erinaceus is widespread throughout the Indo-Pacific area. H. L. Clark (1921, p. 127) gave the broad geographical limits of this species. Recently Sachet (1962) listed this species from Clipperton Island in the Eastern Pacific, based on a redetermination of the specimen identified as *O. scolopendrina* by A. H. Clark (1939a).

DISCUSSION

Variation in several morphological characters has led some workers to consider *Ophiocoma erinaceus* as more than a single species. One species, *Ophiocoma schoenleinii*, has long been distinguished from *O. erinaceus* primarily by having only one tentacle scale, relatively shorter upper arm spines, and a different pattern of disc granulation. In many geographical areas both forms occur and a record of these from Amboina and Torres Strait (H. L. Clark, 1921), Fiji, Samoa, and the Marshall Islands (A. H. Clark, 1954), several places along the Great Barrier Reef (H. L. Clark, 1921; 1946; Endean, 1957), and the Philippines (Domantay and Domantay, 1966) have been reported.

I have examined specimens with one or two tentacle scales from the Philippines, Torres Strait, Fiji, and Samoa as well as the type specimen of *O. schoenleinii* from the Celebes. In addition to the difference in the number of tentacle scales, and two forms showed several other contrasting characters which however, overlapped to a variable extent in specimens from the same population. A comparison of several of the morphological features is presented below. Data are based on specimens between 12 and 20 mm (d.d.).

Specimens with two tentacle scales (N=7)	Specimens with one tentacle scale (N=9)
1. 4 arm spines most often on fourth segment.	1. 3 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, 1.9-2.6:1	2. maximum arm-spine length to breadth of oral plate (tenth free arm segment) X=2.8:1 range, 2.3 - 3.2:1
3. disc granules not usually extending into interradial part of disc.	3. disc granules extending some distance into interradial part of disc.

In addition to close morphological similarity, both forms occur in the same macrohabitat and are found in close proximity. H. L. Clark (1921) collected both from similar habitats among living coral heads between six hundred and twelve hundred feet from the high-tide mark at Mer Island (Torres Strait). I have examined specimens which were collected together at Samoa also from a similar habitat, and there is no evidence to support ecological nor behavioral differences.

Although the several characters above appear linked in each of the two forms, there is a possibility that the two forms represent polymorphs of the same species. I could find no evidence to suggest sex-linked polymorphism however, having observed ovaries and testes in individuals of both forms. The specific taxonomic position of the form with only one tentacle scale and considered as Ophiocoma schoenleinii awaits more critical evidence, perhaps that based on breeding experiments. However, the syntopic occurrence of both the one and two scale forms and their overlap in morphological characters suggests that they are polymorphs of the same species, but having phenotypically linked morphological characters.

The consideration that Ophiocoma erinaceus represents merely a varietal form of O. scolopendrina (see Matsumoto, 1917, for review) has generally been refuted. Evidence based on morphology and pigmentation (Koehler, 1922; Ailsa M. Clark,

1965) behavior (H. L. Clark, 1921; Ailsa M. Clark, 1965), and ecology (H. L. Clark, 1921) supports the differentiation of the two species. Details of these differences are discussed more fully in the section of this work dealing with _O. scolopendrina_ (see p. 207).

Type specimens of _O. erinaceus_ and others considered as synonyms of this species are located in the following places:

Zoologisches Museum, (East) Berlin, Germany (No. 921) - _Ophiocoma erinaceus_

Zoologisches Museum, (East) Berlin, Germany (No. 930) - _Ophiocoma schoenleinii_

Museum of Science, Boston, Massachusetts - _Ophiocoma tartarea_

Ophiocoma macroplaca (H. L. Clark) New Combination

(Plates XI, figs. 2, 4; XVII, fig. 5)

SYNONYMY

Ophiacantha macroplaca H. L. Clark, 1915, p. 200, Pl. I, figs. 6-7.

Ophiocoma erinaceus Müller and Troschel: H. L. Clark, 1921, p. 127 (Hilo, Hawaii); A. H. Clark, 1949, p. 49 (USNM: E7064).

Ophiocoma scolopendrina (Lamarck): Koehler, 1907b, p. 326; Ely, 1942, p. 52 (Maui, Lahaina, MCZ: No. 4515); A. H.

Clark, 1949, pp. 52-53 (all specimens except USNM: E7088 and E7089 which are Ophiacantha bisquamata Matsumoto).

Ophiomastix asperula Lütken: A. H. Clark, 1949, p. 48.

MATERIAL EXAMINED

Hawaii (Hilo) - MCZ: No. 3700 TYPE, Ophiacantha macroplaca

Hawaiian Islands[1] - USNM: E7081 (1), E7082 (4), E7084 (1), E7085 (2), E7086 (1), E7091 (2) E7092 (2), E7094 (4)

Kauai - BPBM: W1550 (1), W1551 (1)

Laysan Island - BPBM: W360a-b (2), W338 (2); USNM: E7093 (1)

Maui - MCZ: No. 4515 (1)

Molokai - BPBM: W1558 (1)

Oahu - BPBM: W1553 (1), W1555a-b (2), W1556 (1), W1557 (1), W1559a-c (3), W1562a-b (2), W1616a-d (4), W1623 (1), W1624 (1), W1625 (1); Pers. Coll. (32)

DIAGNOSIS

Size. Disc diameter of specimens examined from 1.7 mm to 19.5 mm.

Disc cover. Moderately coarse granules in specimens from

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[1]Specimens collected by Albatross, 1902; for precise locality see A. H. Clark, 1949, pp. 52-53.

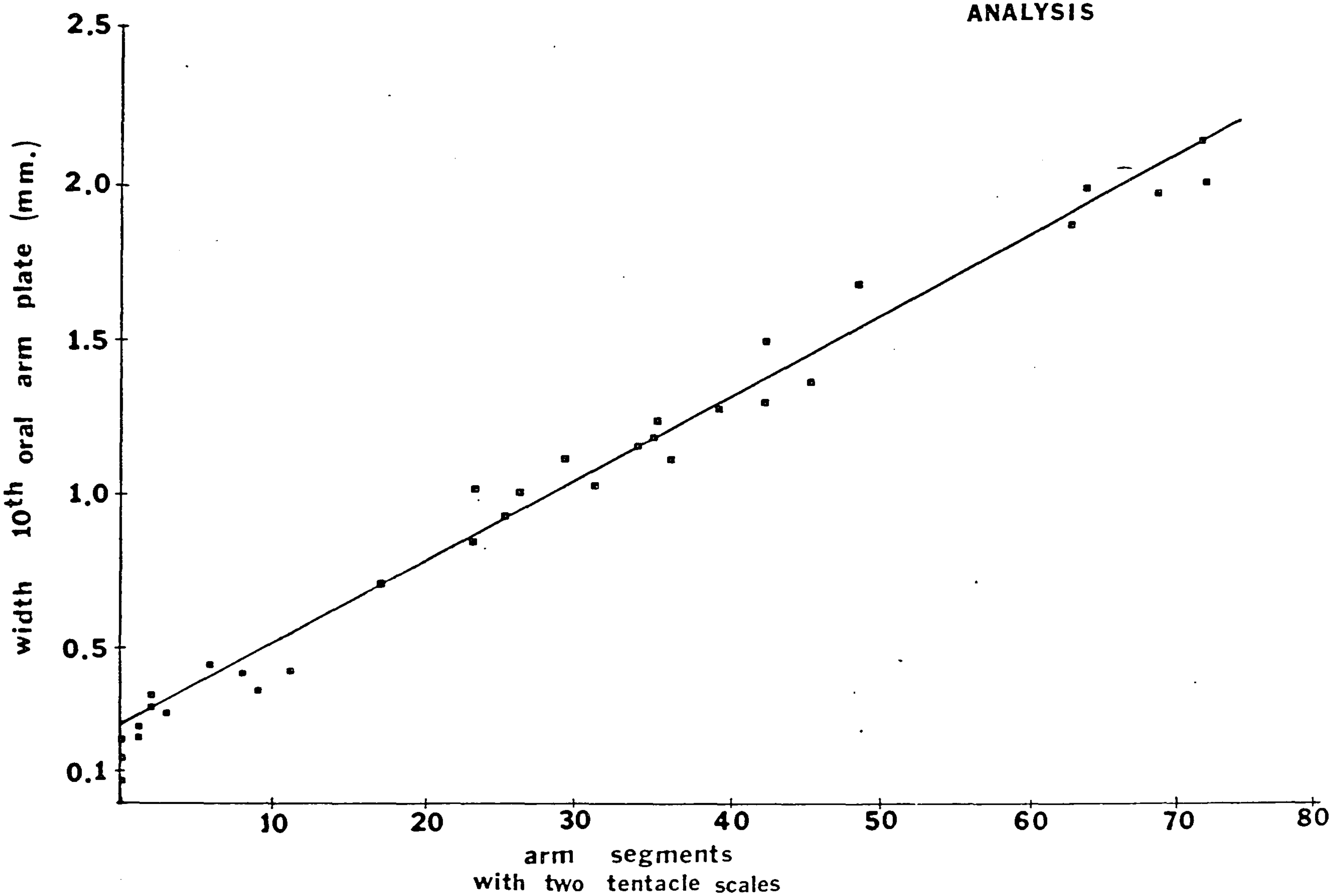
approximately 2 mm (d.d.), on aboral side; in rare cases occasional spiniform granules. Extent of granulation orally, into interradial spaces, increasing with size; by 10 mm (d.d.) a few granules to distal end of oral shields; lateral region near genital openings without granules except single row of small granules usually along edge of openings.

Tentacle scales (TABLE XVII). Two on each pore in specimens exceeding 2 mm (d.d.); number of segments with two scales increasing with growth. Second scale first forming on proximal segments, appearing on more distal segments as size increases, e.g. specimen 2.5 mm (d.d.) with two scales on segments one through eight; larger specimen (d.d. 19 mm) with two scales out to segment sixty-seven.

Arm spines. Upper arm spines tapering to blunt point, not thickened along their length. Arm spine sequence (TABLE XVIII) with growth: a) regardless of size (d.d.), number of spines on each side of first three segments constant 3-3-4; b) regular increase in number of spines from segment four with size increase of specimen; c) irregular alternation of spines on either side of same segment or adjacent segments, starting from segment six, continuing distally as size increases; d) maximum number of spines rarely exceeds five; three and four typical beyond disc edge; e) 3 spines on most recently

TABLE XVII

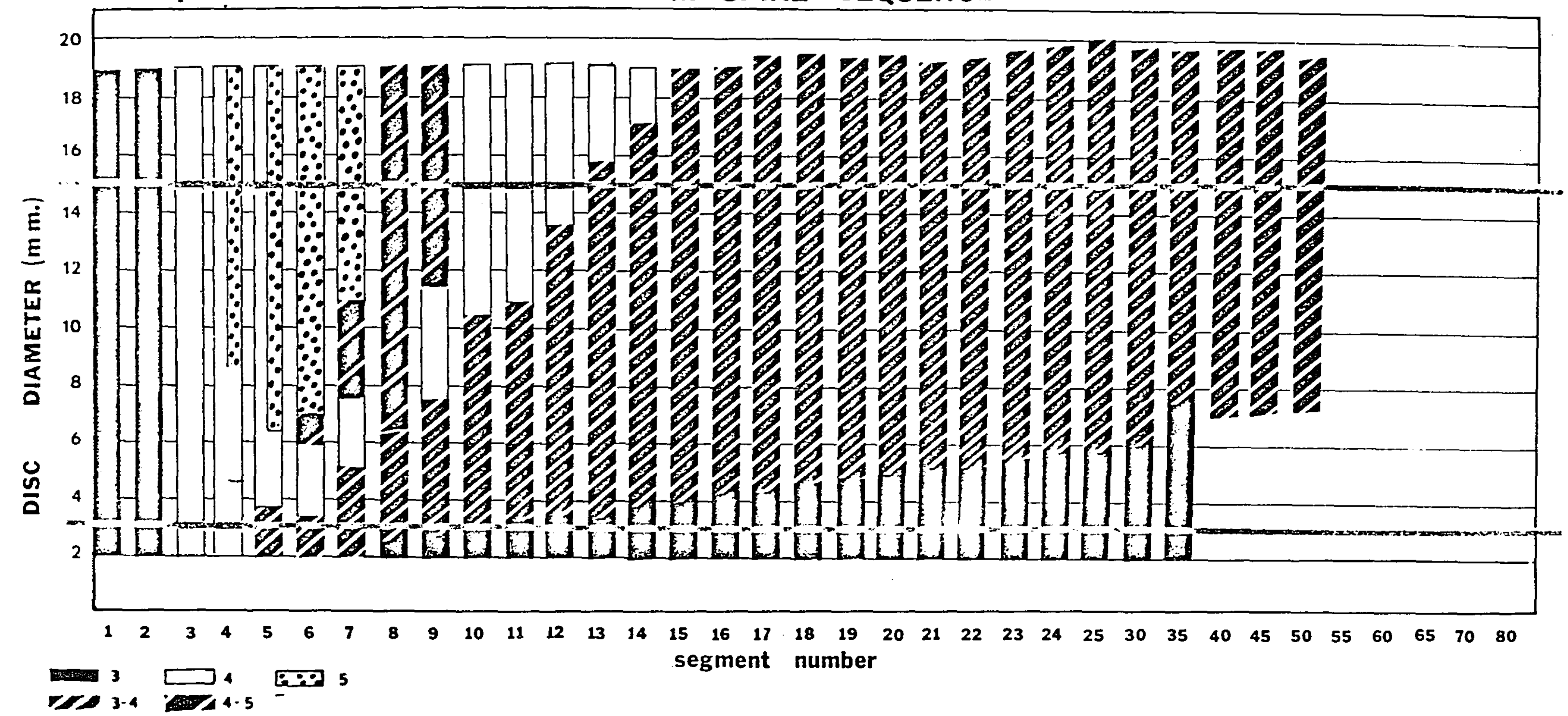
OPHIOCOMA MACROPLACA – TENTACLE SCALE ANALYSIS



Ophiocoma
macroplaca

TABLE XVIII

ARM SPINE SEQUENCE



number of arm spines

formed segments and most of segments in smaller specimens (suggests early ontogenetic spine number).

Dental papillae. In adult condition (d.d. greater than 7 mm) papillae in two or three columns in three rows deep; in juvenile condition, only apical pair initially; number increasing with size. One to three papillae common above level of jaw at apex.

Teeth. By 5 mm (d.d.) three and four teeth on adjacent dental plates. Teeth with hyaline tip.

Dental plate (Pl. XVii, fig. 5). Typical of Scolopendrina group of Ophiocoma.

Oral papillae. Typically four; outer (distal) one entering inward and aboral to next proximal papilla; outer papilla last to form and concavely notched on outer edge; next innermost papilla largest, wider on outer margin; inner two papillae smaller, conical.

Aboral arm plates. In juvenile condition or on distal segments of adults, longer than broad; with increase in size of specimen, becoming broader than long. Lateral margin truncated on side bearing fourth (upper) arm spine; opposite side, with only three spines, tapering to blunt tip.

Oral arm plates. In juvenile condition or on distal segments of adults, longer than broad; mature plates in larger specimens becoming broader than long. Ration, length to breadth for 18 mm (d.d.) specimen for several segments along length of arm as follows: segments 19, 32, 40 and 51 with ratio 0.79 to 0.89 : 1; for distal segments 61, 72, 81, 87, and 92 with ratio 1.41 to 1.54 : 1. Proximal lateral border notched where tentacle scales cover podium.

Pigmentation. Arms dark-brown to tan aborally, generally with banded appearance due to alternation of light and dark-brown; one to three white spots on distal part of lighter plates. Orally arms light tan or less commonly white. Arm spines uniformly brown. Disc generally dark-brown, not black; granules brown, spinules (rare), white.

HABITAT

With the exception of the type specimen, which was collected beneath a stone on a shore reef, *Ophiocoma macroplaca* has been taken from depths exceeding five meters. Specimens taken by the albatross in 1902 (A. H. Clark, 1949, as *O. scolopendrina*) were from stations ranging from 26 to 95 meters. Additional material finds the maximum depth not exceeding 100 meters.

Bottom samples from the *Albatross* collections containing *O. macroplaca* showed coral, shell, gravel, and sand predominating substratum. My own collection of this species has been from the base of corals, primarily *Pocillipora* spp. and less commonly from coral rubble. In depths from five meters *O. macroplaca* and *O. erinaceus* appear sympatric, except the latter apparently is able to occupy more habitats.

DISTRIBUTION

Ophiocoma macroplaca shows a restricted distribution confined to the Hawaiian Island chain from Laysan Island to the Island of Hawaii.

DISCUSSION

The danger in determining a new species on the basis of a single specimen, especially one which is small and may represent a juvenile condition, is apparent when we deal with *Ophiocoma macroplaca*. The taxonomic position of this species has been determined in a large part by a careful analysis of the growth changes which were found to accompany increase in size.

H. L. Clark (1915) described the species first as *Ophiacantha macroplaca* (Fam. Ophiacanthidae). Two characters, based on my re-examination of the type specimen, immediately show that it does not belong to the genus *Ophiacantha*:
a) the arm spines are not hollow but solid; b) the adoral shields do not meet in front of the oral shields (in contrast to the original description).

In 1949, A. H. Clark considered the presence of both disc granules and the few scattered spinules as well as the "... very small and widely separated" adoral shields reasons to place the species in the genus _Ophiomastix_ (Fam. Ophiocomidae). The presence of a single tentacle scale indicated _O. asperula_ according to H. L. Clark's key (1921, p. 134). However, the presence of both disc granules and a few spinules is not typical for the species as my examination of over seventy specimens has revealed. In only two cases other than the type specimen have spinules been observed and the typical condition is for only granules to be present. Furthermore, the presence of a single tentacle scale, characteristic of the type, is strictly a juvenile characters. I have already indicated (TABLE XVII) that two scales develop on more pores distally as the specimens become larger. And finally, there is absolutely no evidence to show that the upper arm spine is swollen, enlarged, or in any way claviform. In these respects, the inclusion of this species in the genus _Ophiomastix_ is not tenable. It is much more apparent that the species belongs in the genus _Ophiocoma_.

On the basis of the arm spine sequence, shape of the aboral arm plates, and shape of the dental plate, _Ophiocoma macroplaca_ shows characters typical of the Scolopendrina group of *Ophiocoma*. The only Hawaiian member of this group, *O. erinaceus*, is easily distinguished from *O. macroplaca* in several ways. These are given below.

Ophiocoma macroplaca	*Ophiocoma erinaceus*
1. Arm spines 3-3-4 on each side segments one through three; aboral arm spine not thickened.	1. Arm spines 3-3-3 each side segments one through three; aboral arm spine often thickened.
2. Disc granules by size of 2 mm (d.d.); encroaching into interradial space in larger specimens.	2. Disc granules by about 10 mm (d.d.); usually restricted to aboral side, larger specimens.
3. Color, tan to dark-brown, not black; arms often variegated light and dark aborally, light orally.	3. Color black or dark-grey; arms usually black not variegated.
4. Seldom in depths above 5 meters.	4. Quite common in depths above 5 meters.

H. L. Clark (1921, p. 127) recorded from Hilo, Hawaii what he considered to be a color form of *Ophiocoma erinaceus*, having red tentacles and a general color of reddish brown instead of the usual black. The arms of the specimen were also distally banded with light and dark red-brown. The description fits that known for O. macroplaca more closely than for O. erinaceus.

The present study has revealed that records of Ophiocoma scolopendrina from the Hawaiian Islands are erroneous. Examination of specimens recorded as O. scolopendrina by A. H. Clark (1949, pp. 52-53) from the 1902 Albatross stations around the Hawaiian Islands shows that all but two should be referred to O. macroplaca (the other two specimens appear to be Ophiacantha bisquamata Matsumoto). Moreover, a specimen listed by Ely (1942, p. 52) and described by H. L. Clark as O. scolopendrina from Maui, also has been examined and is O. macroplaca.

The specimens listed by Koehler (1907b, p. 326) as O. scolopendrina from the Hawaiian Islands, deposited in the Museum of Natural History in Paris have not been located (Cherbonnier, pers. comm.) and their determination remains suspect until verified.

Specimens of Ophiocoma scolopendrina from several Indo-Pacific localities have been compared with O. macroplaca. The results of this comparison strongly indicate that O. scolopendrina is not found in the Hawaiian Islands and that this species has been confused in all cases with O. macroplaca when it is based on Hawaiian records. The following criteria suggest the well-defined separation of the two species.

Ecologically the two species appear to be different. A number of workers (H. L. Clark, 1921; Murakami, 1938; Balinsky, 1957; Ailsa M. Clark, 1952; Magnus, 1962, 1964; and Shiino, 1964) give accounts of the peculiar restricted habitat of *O. scolopendrina* in the intertidal areas of the coral reefs. In addition the feeding behavior is unique as described (p. 210). *O. macroplaca*, in contrast, has only once been collected in the littoral zone (H. L. Clark, 1915b) and is much more common between 5 and 100 meters.

Several morphological characters serve to distinguish *O. macroplaca* from *O. scolopendrina*. These are listed below.

O. macroplaca	*O. scolopendrina*
1. 4 arm spines on each side of segment three.	1. 3 and 4 arm spines on the sides of segment three.
2. Ratio, aboral arm-spine length : aboral arm plate length (for segment 10) - 3.5 - 4.1 : 1 ($\bar{x}$=3.4 : 1) n=28.	2. Ratio, aboral arm-spine length : aboral arm plate length (for segment 10) - 2.2 - 2.5 : 1 ($\bar{x}$=2.4 : 1) n=28.
3. Oral arm plate with distal edge usually broadly rounded	3. Oral arm plate with distal edge broadly truncated,

not concave; lateral margins flared distally at greatest lateral border.	sometimes concave; lateral margins distally not flared laterally.
4. Tentacle scales 2, present on specimens larger than 2 mm; increasing regularly on distal segments with growth.	4. Tentacle scales 1 or 2, few segments with 2 scales on specimens less than 10 mm; often irregular on distal segments with growth.

In addition to the above species, *Ophiocoma macroplaca* can be distinguished from *O. variabilis* described by Grube (1857b) from Hawaii. Careful review of his original description suggests that *O. variabilis* is synonymous with *O. scolopendrina*. In the first place, Grube stated with reference to the arm spines, "...mit Ausnahme der ersten 3, im Bereich der Schiebe befindlichen Facher meist zu je 4, dort nur zu je 3," (p. 32) which implies that the first three segments have only three arm spines. The condition noted in *O. macroplaca* is for the third segment to carry four arm spines. In addition, Grube's description of the relative length of the upper arm spine comes closer to that noted for *O. scolopendrina*. And finally, the pigmentation is more like that for *O. scolopendrina*. With these considerations in mind it would appear that *O. variabilis* is most likely a synonym for _O_. _scolopendrina_ and could not have been collected in the Hawaiian Islands since _O_. _scolopendrina_ is not considered to occur in this Island group.

In conclusion, the use of post-larval growth changes in several skeletal features appears to be of specific value in determining the correct taxonomic position of a poorly known Hawaiian ophiocomid, _Ophiocoma macroplaca_. Morphological, ecological, and behavioral differences serve to separate this species from closely related forms.

Ophiocoma scolopendrina (Lamarck)

SYNONYMY

Ophiura scolopendrina Lamarck, 1816, p. 544; Blainville, 1834, p. 244.

Ophiocoma scolopendrina (Lamarck): Agassiz, 1836, p. 192; Loriol, 1894, p. 23 (a complete bibliography up to 1893); Koehler, 1905, p. 60 (a complete bibliography between 1894 and 1905); 1907a, p. 246; 1907b, p. 326; 1922, p. 325, Pl. 73, fig. 5, Pl. 74, figs. 1-7; 1927, p. 4; 1930, p. 204; H. L. Clark, 1908, p. 297; 1909, p. 542 (pt.); 1915, p. 293, Pl. 14, figs. 10-11; 1917, p. 442; 1921, p. 125, Pl. 13, fig. 9; 1923c, p. 348; 1925, p. 92; 1932, p. 208; 1946, p. 243; Matsumoto, 1917, p. 345 (pt.); Mortensen, 1932, p. 21; 1937, pp. 49-50, figs. 38-40 (egg and larval skeleton), Pl. VIII, fig. 5 (larva); 1940, p. 73; Hertz, 1927, p. 117; Domantay, 1936, p. 396; Pl. vi, fig. 54; Murakami, 1938, p. 40; 1939, p. 37; 1943a, p. 196; 1943b, p. 218; Tortonese, 1936, p. 222; 1951, p. 38; Ely, 1942, p. 52 (pt.); A. H. Clark, 1952, p. 295; 1954, p. 260; Ailsa M. Clark, 1952, pp. 203, 207; 1965, pp. 599, 610; 1966, p. 47; Endean, 1953, p. 55; 1956, p. 126; 1957, p. 245; Balinsky, 1957, p. 25, 29; Magnus, 1962, p. 471; 1964, p. 110; Ooishi, 1964, p. 213; Domantay and Domantay, 1966, p. 48.

Ophiocoma variabilis Grube, 1857a, p. 342; 1857b, p. 31, Pl. 1, figs. 4, 4a.

Ophiocoma molaris Lyman, 1861, p. 79; 1865, p. 87.

Ophiocoma alternans Martens, 1870, p. 251; Lyman, p. 225.

Ophiocoma scolopendrina scolopendrina (Lamarck): Djakonov, 1930, p. 245.

Ophiocoma scolopendrina var. *alternans* Martens: Loriol, 1893, p. 407; Studer, 1889, pp. 235, 248.

Ophiocoma scolopendrina "forma *monolepis*" H. L. Clark, 1926, p. 187.

MATERIAL EXAMINED

Baker Island - BPBM: W591 (1)

Eniwetok Atoll - BPBM: W1478-W1485 (8); W1499-W1501 (3); W1631a-d (4); W1846 (1).

Fiji Islands - BPBM: W851a-d (4); W1238 (1)

Howland Island - BPBM: W588a-b (2); W891; (1); W899a-b (2)

Mossambique - BPBM: W1572-W1577 (6)

Okinawa - BPBM: W1097-W1098 (2)

Palmyra Atoll - BPBM: W329a-b (2); W355 (1); W356a-b (2); W509a-h (8); W774a-b (2).

Samoa - BPBM: W927 (1); W1112 (7); W1407-W1412 (75)

Swain's Island - BPBM: W896 (1)

Tuamotu Islands (Manihi Atoll) - Pers. coll. (10)

Washington Island - BPBM: W578b (1)

DIAGNOSIS

Good descriptions of the external characters of this species have been given by Loriol (1893), Lyman (1865), Duncan (1886), and Lütken (1859). A few of the most diagnostic characters are given below.

Size. Disc diameter up to 32 mm; arm length between 5 and 7.5 times disc diameter.

Disc cover. Granules, coarse, rounded, usually extending some distance into interradial oral region; present on specimens 3 mm (d.d.) and larger.

Arm spines. Proximal five segments typically with sequence of 3-3-3-4-4 on each side; fifth spine rarely on segment six or out to segment ten. An alternation of 3 and 4 spines on same or adjacent segments beyond segment ten, extending distally with increase in size. Ratio, maximum length upper arm spine to width of upper arm plate (for tenth segment counted beyond margin of disc), 2.5: 1 with range 2.0-3.3 : 1 (based on data from Ailsa M. Clark, 1965, p. 599).

Tentacle scales. One or two on each pore; usually two scales on first segment.

Pigmentation. Upper surface of disc and arms often variegated; sometimes black and white, dark grey or brown and off white, faded yellowish or light brown; specimens less than 15 mm (d.d.) seldom without variegation of upper arm plates, commonly with light spots at distal end of plates; larger specimens sometimes with uniformly dark grey discs and arms, arms variegated only near ends. Oral surface with proximal arm plates much lighter, almost white, often on most of arm. Arm spines frequently annulated dark and light.

HABITAT

Ophiocoma scolopendrina has been shown to occupy a restricted environment among dead coral rubble and coarse sand in the intertidal zone (H. L. Clark, 1921; Magnus, 1962), especially in reef flat areas. The species is often found in large aggregates and as many as fifty specimens per square meter have been recorded (Macnae and Kalk, 1962, p. 100). Magnus (1962, 1964) provided evidence which indicated that *O. scolopendrina* depends upon the ebb and flow of the tide for its food. It has not been established whether the young of this species is also restricted to the littoral zone. Koehler's (1905) sublittoral records of this species require verification.

DISTRIBUTION

Ophiocoma scolopendrina has a wide Indo-Pacific range from the East coast of Africa, south of Mossambique (lat. 26° S), to the Red Sea. It occurs throughout the tropical and sub-tropical Indian Ocean to northwestern Australia, to Torres Strait, the Philippines, into the Pacific, and north to Japan (lat. 34° N). It has been taken at many Pacific localities, including major central Pacific Islands, i.e. the Marshall Islands, Fiji, Gilbert, and south to the Society and

Tuamotu Groups. Although previously recorded from the Hawaiian Islands (see A. H. Clark, 1949), there is little doubt that these records are based on other species (see p. 200).

DISCUSSION

My own examination of a number of specimens of _Ophiocoma scolopendrina_ provides more information concerning the variability of certain taxonomic characters. A few of these will be mentioned in order to clear up misconceptions and reduce misidentification of this and other closely related _Ophiocoma_ species.

The two species of Indo-Pacific ophiocomids which have been or are most likely to be confused with _Ophiocoma scolopendrina_ are _O._ _erinaceus_ and _O._ _macroplaca_. This latter species can be distinguished from _O._ _scolopendrina_ (and other members of the Scolopendrina group of _Ophiocoma_) by the presence of 4 arm spines on both sides of the third segment. In rare cases four arm spines occur on the third segment of _O._ _scolopendrina_ but never on more than one or two rays in a single individual.

Pigmentation has been found to be quite variable in _O._ _scolopendrina_ and has been used as an argument by some workers

(Ludwig, 1880, 1899; Koehler, 1989, 1905, 1907; Walter, 1885; Matsumoto, 1917) to unite this species with *O. erinaceus*. However, H. L. Clark (1921, 1938), Koehler (1922), and Ailsa M. Clark (1965) have indicated that pigmentation can be used as a specific character to separate the two species. I concur with the last three authors, having found that the oral surface of the arm plates of *O. scolopendrina*, especially in the proximal region, is white or yellow white, whereas in *O. erinaceus* the plates are dark black or brown.

Because the number of tentacle scales is variable in both *O. scolopendrina* and *O. erinaceus* it is not considered a reliable character separating the two species.

Likewise, the shape of the oral (mouth) shield, as pointed out by Koehler (1922), and ratio of arm length to disc diameter, are so variable in the above two species that on an individual basis these characters cannot be relied upon.

The extent to which granules enter into the interradial area of the disc is quite variable in *O. erinaceus*, but typically they stop at the margin of the disc. In contrast, granules enter into the interradial disc region in *O. scolopendrina*. More importantly, it is possible to distinguish small specimens of the two species by the presence or absence of granules on the disc. In *O. scolopendrina* granules have appeared by the time the specimen reaches a disc diameter of 3 mm, whereas in O. erinaceus granules seldom appear before a size of 10 mm (d.d.) is attained.

In addition to the criteria already described, behavioral differences separate O. scolopendrina from other Indo-Pacific species in the Scolopendrina group. Magnus (1962, 1964) was able to report that this species exhibits an extension of the arms during tidal movements and that this is correlated with a cilliary-mucoid type of feeding. The arm podia transport suspended food material toward the mouth. Although this type of feeding has been reported in Ophiocoma nigra (Fontaine, 1961) the actual sampling of the air-water interface is apparently unique to O. scolopendrina among ophiocomids. This behavior may account for the abundance, if not the restriction, of O. scolopendrina in the littoral zone.

The type specimens of species considered as Ophiocoma scolopendrina and their location are as follows:

Ophiura scolopendrina Lamarack: Museum de l'Histoire Naturelle, Paris, France

Ophiocoma variabilis Grube: Dorpat Museum, Tartu, Estonia, U.S.S.R.

Ophiocoma molaris Lyman: Museum of Comparative Zoology, Cambridge, Massachusetts

Ophiocoma alternans Martens: Zoologisches Museum, (East) Berlin, Germany

Ophiocoma occidentalis H. L. Clark

SYNONYMY

Ophiocoma occidentalis H. L. Clark, 1938, p. 334, Pl. 25, fig. 1; 1946, p. 245.

MATERIAL EXAMINED

Western Australia - MCZ: No. 5239 (TYPE specimen)

DISTRIBUTION AND DISCUSSION

Ophiocoma occidentalis is based on H. L. Clark's (1938) record from the south western coast of Australia in the vicinity of Fremantle, specifically Rottnest Island and Point Peron. As H. L. Clark (1946, p. 245) mentions, there is a chance that Koehler's (1907b) description of Ophiocoma wendtii also refers to this species, collected at Shark's Bay further north.

The species is separable from Ophiocoma erinaceus primarily by color differences. Moreover, H. L. Clark in his original description of O. occidentalis suggested that this species was closely related to Ophiocoma aethiops and O. schoenleinii, but differed from these in having shorter arms, a different shape of the oral arm plates, and could be distinguished from the former species in having "...larger, more generally single tentacle scales" (p. 336), and from the latter, in having smooth lateral arm plates.

There is some evidence that we are dealing in this case with a geographically separated species of Ophiocoma, but the specific limits, especially the characters differentiating this species from other species in the Scolopendrina group must await additional material before its taxonomic position is clearly verified.

Ophiocoma wendtii Müller and Troschel
(Plate XII, figs. 1,3,5,7)

SYNONYMY

Ophiocoma wendtii Müller and Troschel, 1842, p. 99; Lyman, 1865, p. 70; 1882, p. 171.

Ophiocoma riisei Lütken, 1856, p. 14; 1859, p. 245, Pl. 4, figs. 6a-b; Verrill, 1868, p. 341; 1899a, p. 22; 1899b, p. 375; 1900, p. 586; 1907, p. 328, Pl. 34D, fig. 2 (3); Lyman, 1865, p. 76; 1882, p. 171; Rathbun, 1879, p. 152; H. L. Clark, 1901, p. 245; 1915, p. 293; 1919, p. 54; 1921, pp. 123, 128; 1933, p. 66; 1942, p. 377; Koehler, 1913, p. 375; 1914, pp. 118, 159; Tortonese, 1934, p. 40, Pl. V, fig. 25; Engel, 1939, p. 9; A. H. Clark, 1939b, p. 450, Pl. 54, fig. 5; Fontaine, 1953, p. 203, fig. 6;

Parslow and Clark, 1963, p. 27, 47.

NOT Ophiocoma wendtii: Koehler, 1905, p. 63, Pl. 14, figs. 5-7; 1907a, p. 246; 1907b, p. 327, Pl. 3, fig. 38; 1922, p. 328, Pl. 75, figs. 7-8; 1927, p. 5; H. L. Clark, 1908, p. 297; 1921, p. 129; 1938, p. 336; Hertz, 1927, p. 118, Pl. IX, fig. 15; Boone, 1938, p. 155, Pls. 55-56.

MATERIAL EXAMINED

British West Indies (Tobago Island) - AHF: A-41-39 (6); BPBM: W1636a-b (2)

Panama (Caledonia Bay) - AHF: A-50-39 (2), A-57-39 (2); BPBM: W1634 (1), W1635a-b (2)

Puerto Rico - BPBM: W1674a-c (3)

Unknown locality - (Ophiocoma wendtii) - ZMB: No. 929 (TYPE specimen)

DIAGNOSIS

Size. Disc diameter to 32 mm (H. L. Clark, 1921); of type specimen, 25 mm.

Disc cover. Granules coarse, rounded; diameter and height of these equal (1.7 mm from type specimen); granules forming late in development, present in specimens more than 8 mm (d.d.). Radial shields progressively covered as size increases.

Reaching nearly to oral shields interradially; granules absent in lateral part of interradial space.

<u>Tentacle scales</u>. Two scales each pore developed on proximal segments (type specimen with two scales on first seven proximal segments, except two sides of segment one having three scales); variation in number of segments with two scales: two scales from first segment as far as segment nine; rarely, and irregularly, on more distal segments.

<u>Arm spines</u>. For type specimen and additional specimens, sequence of spines on each side of first six proximal arm segments, 2-3-3-4-4-4: 4 and/or 5 spines on segments seven and eight (specimens larger than 10 mm (d.d.)); 3 and 4 spines alternate irregularly on distal segments. Upper arm spine, on segments beyond disc, much longer than lower spines (nearly 10 mm in type specimen) where four spines occur in row; upper (third) spine on opposite side much shorter (3-5 in type specimen); no indication of swelling or enlargement of spines at tip, rather spines taper to blunt point except toward distal part of arm where acute.

<u>Dental papillae and teeth</u>. Dental papillae increasing in number with size; type specimen with papillae present in three columns, five rows deep; papillae in outer columns wider than in center. Teeth with hyalinated tip; alternating three

and four.

Oral papillae. Typically four oral papillae each side of jaw (type specimen with three or four, where three, it appears that second and third have coalesced, a feature not uncommon in larger specimens of ophiocomids); second papilla largest; first (outermost) directed downwards into jaw angle below second which partially covers it.

Aboral arm plate. Lateral border truncated on side where fourth (upper) arm spine encroaches; opposite lateral border, where three spines occur, tapered (Pl. XII, fig. 5). An accurate description of the change in shape of this plate in different parts of the arm was given by Lyman (1865).

Pigmentation. Disc, brown orally and aborally. Often, three to four aboral arm plates together each with two transverse white lines crossing near distal and proximal borders (Pl. XII, figs. 1, 3, 5); these plates followed by three or four uniformly dark brown plates before repeat of pattern (observed on type and several other specimens). Oral arm plates uniformly brown except for small white area along proximal edge. Arm spines and tentacle scales also brown.

DISTRIBUTION

Ophiocoma wendtii (more commonly, but incorrectly, known as *O. riisei*) is widely distributed throughout the West

Indies and Caribbean from Southern Florida to the coast of Venezuela (Parslow and Clark, 1963). This species has also been reported from Bermuda (Verrill, 1900) as far south as Brazil (Rathbun, 1879). Specimens have been collected from depths of one to over one hundred meters.

BEHAVIOR

Cowles (1910) used this species (as O. riisei) as an experimental animal along with O. echinata in performing tests which indicated that the podial appendages were important both in climbing and feeding. Other experiments concerned righting and locomotion methods.

DISCUSSION

Müller and Troschel's original description of Ophiocoma wendtii stated "unbekannt" [unknown] for the type locality. Later, Lyman (1882, p. 171) gave the locality as "South Seas". It was apparently this report in part which lead other workers to consider O. wendtii as an Indo-Pacific species. However, examination of the type specimen and comparison with other ophiocomid specimens makes it clear that O. wendtii is a senior synonum for O. riisei Lütken, a species found in the West Indian-Caribbean region. Lütken (1859, p. 245), in his original description of O. riisei, listed parenthetically

O. wendtii? as a synonym, but made no further comment.

Much of the difficulty in establishing the correct zoogeographic and taxonomic position of O. wendtii has been due to the very brief original description, which failed to pick out truly specific characters. Müller and Troschel failed to report the presence of only two arm spines on the first arm segment, one of the most important distinguishing characters of O. wendtii. Both Lyman (1865, p. 77) and A. H. Clark (1939b, p. 451) noted this feature but did not comment on its significance. No other member of the Scolopendrina group of Ophiocoma shares this character; all others have three spines on the first segment, typically. Examination of additional specimens identified as O. riisei from Caribbean areas confirms the presence of only two spines. In contrast, I found Koehler's (1922) specimens identified as O. wendtii from Samoa (deposited in the USNM) with three spines on the first segment. This indicates, together with other characters given below, that these specimens are not conspecific with the type.

The presence of an elongated upper (fourth) arm spine, while not limited to O. wendtii (also found in some specimens of O. erinaceus), is very typical of this species. None of the specimens identified by Koehler (1922) as O. wendtii have arm spines nearly as elongated and the spines are much thicker. Koehler's earlier description (1907b) of the arm spines of specimens reported as this species from several Indo-Pacific localities (Seychelles, Zanzibar, New Ireland, Fernando Velosa) indicated that the upper spine was swollen and even claviform. Hertz (1927) also described and figured the arm spines of two specimens, which he identified as O. wendtii from the Seychelles, as being rod-shaped and slightly thickened toward the tip. This condition has not been noted by me in Caribbean specimens nor the type, and the slender nature of the arm spines in this species (as O. riisei) was specifically mentioned by Verrill (1900, 1907).

In addition to the arm spines, the color pattern of the upper arm plates appears to be unique for this species. A photograph of an arm of a specimen from the Caribbean is given (Pl. XII, fig. 3) and compared with that of the type (Pl. XII, figs. 1, 5). Although this color pattern is not evident in all specimens its presence adds further evidence that Caribbean specimens identified as O. riisei are conspecific with O. wendtii. In contrast, Indo-Pacific specimens considered by Koehler (1905, 1907a, 1907b, 1922, 1927), H.L. Clark (1908, 1921), and Boone (1938) as O. wendtii are black, with or without variegated (black & white) arms which do not have the characteristic color pattern of the aboral arm plates.

Aside from the above characters, O. wendtii (as O. riisei) has been shown to differ from the closely related and syntopic species, O. echinata in several ways. Disc granules develop later in O. wendtii (H. L. Clark, 1921; A. H. Clark, 1939a). In this respect, as well as by the greater development of the arm spine length, the presence of two tentacle scales restricted to proximal segments, and the presence of only two arm spines on the first segment, O. wendtii can easily be distinguished from O. echinata.

Both Caribbean species share characters which link them to O. erinaceus in the Indo-Pacific. The polymorphic nature of this latter species suggests that perhaps both O. wendtii and O. echinata may have evolved, at different times, from O. erinaceus or an ancestral Scolopendrina species.

The erroneous records of O. wendtii from the Indo-Pacific have been shown in part by an examination of specimens Koehler described as this species in 1922: six specimens from Samoa (USNM: E4890) and one specimen from the Philippines (USNM: 40948) are polymorphs (schoenleinii form) of O. erinaceus (see p. 188). Koehler's records (1905, 1927) of this species from Indonesia, and the Fiji Islands, respectively, appear to represent similar polymorphs of

O. erinaceus, based on the descriptions and my comparison of similar specimens from the latter locality. H. L. Clark (1938, p. 336) may be correct in his assumption that Koehler's (1907a) record of O. wendtii from Shark Bay, West Australia is conspecific with O. occidentalis. Boone's (1938) record of O. wendtii from the Hawaiian Islands is certainly in error, considering her description and photographs which strongly indicate O. erinaceus. The color, large number of arm segments with two tentacle scales, and the arm spine sequence point to this.

Several lines of evidence however, suggest that another species, probably in the genus Ophiomastix, has also been mistakenly named O. wendtii in the Indo-Pacific. Koehler (1907b, Pl. 13, fig. 38) described and illustrated a specimen with enlarged claviform arm spines which were distinctly annulated. The disc cover revealed coarse granules. H. L. Clark (1921, pp. 129, 134) reported a similar specimen under the name O. wendtii from Zanzibar and the specimens reported by Hertz (1927) as this species are probably the same. Likewise, Ailsa M. Clark (pers. comm.) reported having two specimens from Zanzibar fitting this description. Since it is possible that Koehler's specimen(s) with the claviform arm spines could be from the same locality, it is reasonable to suggest that there might be a separate species, which combines the characters of _Ophiomastix_ (i.e. with claviform arm spines) and the Scolopendrina group of _Ophiocoma_ (i.e. with coarse disc granules). The very close relationship between several species of _Ophiomastix_ and species of _Ophiocoma_ in the Scolopendrina group is certainly evident from this form. If these specimens do represent a new species, it remains for more specimens, especially smaller individuals, to be examined before a satisfactory decision can be reached as to their taxonomic position. The type specimens of _Ophiocoma riisei_ are deposited in the Copenhagen Museum.

GENUS OPHIOCOMINA

The taxonomic position of the genus _Ophiocomina_ received attention during the early part of this century. Good reasons were presented by Mortensen (1920) and Koehler (1922) which favored the inclusion of _Ophiocomina nigra_ in the family Ophiocomidae. In large part generic evaluation at this time was stimulated by H. L. Clark's (1915, 1928) argument that _Ophiocomina_ should not be included in the Ophiocomidae, but in the Ophiacanthidae. However, the presence of paired peristomial plates and well defined dental papillae were convincing criteria for rejecting Clark's proposal (in the _Ophiacanthidae_ the peristomial plates are not paired, and dental papillae are absent), and serve as good characters of the Ophiocomidae.

The presence of hollow arm spines, the shape of the oral shields, and the fact that the adoral shields nearly or actually meet in front of the oral shields have been considered the most important features separating _Ophiocomina_ from other genera in the subfamily. In addition, Koehler (1922) indicated that the peristomial plates were thicker in _Ophiocomina nigra_ than those found in _Ophiocoma_ (_O. scolopendrina_ used for comparison).

Koehler (_op. cit._) and other investigators failed to note that two species of *Ophiocoma*, *bollonsi* and *canaliculata* shared several of the above features with *Ophiocomina*. In these two species, the oral and adoral shields bear the same relationship and the peristomial plates are intermediate in thickness between *Ophiocomina* and Scolopendrina Group of *Ophiocoma*. In addition, there is a very similar comparison in the size and nature of the disc granulation found in the Canaliculata species of *Ophiocoma* and *Ophiocomina*. In *Ophiocoma bollonsi* and *canaliculata* the arm spines are delicate, and together with their number and length resemble *Ophiocomina*. Further reduction in the degree of calcification of the arm spines in the two Canaliculata species would result in the hollow arm spine condition noted in *Ophiocomina*.

Mortensen (1920, p. 52) mentioned further, discussing the relationships of *Ophiocomina nigra*, that the "wings of the first vertebrae" although larger than in *Ophiacantha* were "not nearly so large as in *Ophiocoma*." This statement referred to the abradial side of the oral plates (the first arm vertebra was considered the third true vertebra, the first and second true vertebrae modified to form the oral plate), and was based on the condition noted in species of *Ophiocoma* in the Scolopendrina, Brevipes or even Pumila groups. In contrast however, it should be pointed out that the oral plates of *Ophiocoma bollonsi*, *O. canaliculata*, and *O. pusilla* show a much smaller abradial muscle area than in other species in the genus. In this respect the oral plate of these last three species comes closest to the condition indicated by Mortensen for *Ophiocomina nigra*. Morphologically therefore, *Ophiocomina* shows its greatest similarity to *Ophiocoma bollonsi*, *canaliculata*, and *pusilla*.

Within the genus *Ophiocomina* the difference in the number of tentacle scales is the best criterion for morphological separation of the two species, *O. australis* and *O. nigra*. Better diagnostic characters separating the two species must await future examination of specimens of both species. In the species analysis which follows, the DIAGNOSIS AND DISCUSSION section considers the two species of *Ophiocomina* together for comparative purposes.

Ophiocomina australis H. L. Clark

SYNONYMY

Ophiocomina australis H. L. Clark, 1928, p. 422, fig. 124; 1938, p. 372; 1946, p. 188.

Ophiocomina nigra (Abildgaard)

SYNONYMY

Asterias nigra Abildgaard, 1789, p. 20, Pl. XCIII, fix. 4.

Asterias tricolor Abildgaard, 1789, p. 28, Pl. XCVII, fig. 6.

Ophiura granulata Fleming, 1828, p. 488; Thompson, 1856, p. 438.

Ophiocoma granulata (Fleming): Forbes, 1839, p. 127; 1840, p. 50.

Ophiocoma nigra (Abildgaard): Müller and Troschel, 1842, p. 100, Pl. VIII, fig. 1; Gray, 1848, p. 26; Fjelstrup, 1890, p. 29, Pl. III, fig. 4; Lyman, 1882, p. 169; Mortensen, 1913, p. 12; 1931, p. 34; Pl. 4, fig. 1; Narasiharurti, 1933, p. 63; MacIntosh, 1903, p. 463; Bell, 1894, 129; 1900, p. 129.

Ophiocoma raschi G. O. Sars, 1872, p. 109.

? Ophiocoma tumida Müller and Troschel, 1842, p. 100; Koehler, 1922, pp. 316-319.

Ophiacantha sphaerulata (Pennant): H. L. Clark, 1915, p. 205; 1921, p. 121; 1928, p. 424.

Ophiocomina nigra (Abildgaard): Mortensen, 1920, p. 53; 1927, pp. 152, 178-179, Figs. 87, 88 (Larva and larval skeleton), Figs. 83, 100; Koehler, 1921, p. 93; 1922, p. 314; H. L. Clark, 1946, p. 188.

Ophiocoma nilssonii Müller and Troschel, 1842, p. 100.

MATERIAL EXAMINED

Norway (Bergen) - USNM: No. 8557 (1)

DIAGNOSIS AND DISCUSSION (Both Species)

Size. Ophiocomina nigra has been reported with a disc diameter 25 mm and arms 100 mm in length. O. australis has been reported to 12 mm (d.d.) with an arm length of 50-60 mm.

Disc cover. In both species granules covering disc completely aborally, but orally to variable extent, often to oral shields; but leaving the lateral areas bare. Granules evenly distributed and closely packed; in either species may extend upon several upper arm plates near disc.

Tentacle scales. O. nigra with two tentacle scales on proximal arm segments; number of segments with two scales increasing with size; distally number drops to one. O. australis with only one tentacle scale.

Arm spines. Both species having rather delicate arm spines that are hollow; no spines thickened; in larger specimens of O. nigra, proximal portion of arm may have middle spines of row with slightly broadened tip, but all distal spines acute.

There is apparently an increase in the number of spines with growth; toward the tip of the arm in both species there are only three spines; at the base of the arms, beyond the disc edge, up to eight spines have been noted on O. nigra on each side of a few segments. A maximum of six spines was reported on O. australis. The arm spine sequence has not been determined for either species.

Dental papillae. From twelve to fifteen dental papillae at base of each jaw from a specimen of O. nigra about 15 mm (d.d.). H. L. Clark (1928, p. 424) described O. australis with "an unpaired (rarely paired) papilla at the tip of each jaw and inside (toward the teeth) a pair of larger papillae". He also indicated that "rarely" another pair of papillae could also occur. Clark however, refused to consider these as true dental papillae, but there seems little doubt that they are attached to the dental plate and therefore should be considered dental papillae.

Teeth. Both species lacking the hyalinated tip characteristic of other genera in the Ophiocominae, except Ophiopteris. Teeth are narrow and rounded in O. nigra.

Peristomial plates. These internal radial supports have been found, in O. nigra to be paired and thicker than in Ophiocoma scolopendrina (Koehler, 1922, Pl. 73, fig. 5, 6). In shape, they appear nearly twice as long as broad, with the outer borders slightly curved. They have not been examined in _O. australis_.

Oral shields. In both species oral shields transversely broadened, and broader than long.

Adoral shields. In both species adoral shields extending along entire length of proximal (inner) border of oral shield where they nearly or actually come in contact.

Larva. The development and larva of _O. nigra_ have been discussed and described by Mortensen (1913, 1927). A reproduction of Mortensen's figure of the fully developed larval skeleton is given in this paper (Pl. XX, fig. 4). The larva of _O. australis_ is unknown.

Oral papillae. For both species usually five oral papillae along side of each jaw; outer and next scale-like, covering the opening of second buccal podium which appears near upper surface of jaw. The innermost papillae narrower and pointed.

Pigmentation. A considerable amount of variation in the color of _O. nigra_ has been reported. MacIntosh (1903) found the prevailing color to be dark brown; most of the time the color was uniform, but a lighter color pattern of various design was also noted, especially the aboral surface of the disc. Other notes on color are given by Mortensen (1927) and Bell (1900). Fontaine (1962) discussed the different shades of color in *O. nigra* in relation to its bathymetric distribution. He found that the color tones of the ophiuroid tended to match the color of bottom they lived on with the incidence of light-colored specimens apparently correlated with increasing depth. He postulated, on the basis of laboratory mortality experiments, that melanin, the component pigment in dark specimens, might act as a protective light screen. His tests showed light-colored forms tended to die more quickly than dark forms under constant illumination.

H. L. Clark (1928) reported a considerable diversity in the color of *O. australis*. The disc varied from brown to whitish with rosy or pinkish tinge, and the arms were lightly variegated, giving the impression of banding.

FUNCTIONAL MORPHOLOGY

Several workers, especially Fontaine, have contributed a great deal to our knowledge of the functional morphology of ophiuroids through the study of *Ophiocomina nigra*. In 1964, Fontaine discussed the possible roles of multicellular and unicellular mucous secreting glands associated with external skeletal ossicles and the tube feet. The multicellular glands, associated with the nervous system, occur abundantly in the disc granules, arm spines, and other skeletal parts. Fontaine suggested that the hollow interior of the arm spines appeared to be an adaptation to house the many cell bodies of the multicellular glands. Evidence was given to support the hypothesis that the acid mucous (pH 1) of these glands serves a protective function. Fenchel (1965) supports this hypothesis, noting that the starfish, Luidia sarsi, avoided Ophiocomina nigra while preying on two other species of ophiuroids.

The unicellular mucous glands of the skeleton widely distributed in aboral skeletal ossicles, were considered important in microphagous feeding. The tube feet, previously shown to play a role in locomotion by Smith (1936) also contributed mucous used in the feeding methods. Several types of feeding methods were elaborated by Fontaine (1965) using O. nigra as the primary experimental animal. Two mucous-net microphagous and three macrophagous methods of food capture were shown to be employed. One of the microphagous methods, the ability to use the air-water surface for feeding, is similar to that observed in Ophiocoma scolopendrina by Magnus (1962).

DISTRIBUTION

The two species of Ophiocomina are widely separated zoogeographically. O. nigra has been found extensively along the coast of Norway, the British Isles, as far south as Spain and the Azores Islands. This species also occurs in the northern Mediterranean Sea to Sicily. Bathymetrically, O. nigra has been taken at all depths from shallow sub-littoral to 200 meters.

O. australis has been collected only along the coast of South Australia in Spencer and St. Vincent Gulf. The bathymetric range is not known.

Both species are considered temperate water forms, and share the same type of peculiar discontinuous distribution shown by the two species of Ophiopteris.

The type specimens of Ophiocomina australis are deposited in the South Australian Museum, Adelaide, Australia.

The type specimen, Asterias nigra, is deposited in the Zoological Museum, Copenhagen, Denmark.

GENUS OPHIOMASTIX

The genus *Ophiomastix* was established by Müller and and Troschel in 1842. The presence of both oral and dental papillae suggested relationships with *Ophiocoma*. The presence of spinules instead of low rounded granules on the disc and a very noticeable thickening of the upper arm spine with the tip claviform (Pl. XVII, figs. 8, 10) were considered reasons enough to establish this genus. *Ophiomastix annulosa* was the type and only species originally included in the genus. In 1851, Peters described *Ophiomastix venosa*, a species with only a few disc spinules and claviform arm spines.

As more species were included in this genus, the desirability of restricting species to those having *both* distinguishing characters rather than either became questionable. Several changes in Müller and Troschel's generic diagnosis were proposed by Lütken (1869) after his discovery of three new species of *Ophiomastix* (*mixta*, *asperula*, and *caryophyllata*) and after observing that specimens of *O. venosa* could have a disc with no trace of disc spinules. Furthermore, he described a specimen of *O. annulosa*, with a disc diameter of only 14 mm, in which the upper arm spines were not claviform. *O. mixta* showed no club-shaped spines either, and showed further variation in having a disc cover of mixed spinules and granules. With these variations at hand, Lütken presented an emended generic diagnosis for *Ophiomastix*. Species were now not limited to only those with claviform arm spines, but included those allied to *Ophiocoma* with or without claviform arm spines in which the disc was covered with spinules, spinules and granules, or was entirely naked. Furthermore, he specified that for certain species of *Ophiomastix*, segments in the middle part of the arm had the upper spine modified into the form of a divided club at its apex, a character unique to the genus.

Lyman (1871) described another new species, *Ophiomastix flaccida* on the basis of a specimen (disc diameter 15 mm) lacking tentacle scales, and having a thick skin which obscured the lateral and upper arm plates. The disc had short (1.2mm), sparce, slender but rounded spines, as well as club-shaped arm spines every second to fourth joint on alternating sides of the arm. This species was unique in the absence of tentacle scales.

A species described by Smith (1878) as *Acantharachna mirabilis* was considered the type of a subgenus, of the same name, in the genus *Ophiomastix*. Comparison has shown that there was little except size to distinguish *A. mirabilis* from *Ophiomastix flaccida*. The use of Smith's subgeneric name, based primarily on the peculiar absence of tentacle scales, has not been adopted by other echinoderm workers. However, the merits of subgeneric division of _Ophiomastix_ may be warranted when other morphological features are better known, and in this paper I will point out that two groups of _Ophiomastix_ species can be distinguished (p. 240).

In 1882, in his report on the Ophiuroidea collected by the Challenger Expedition, Lyman reviewed the known species of _Ophiomastix_. In the form of a key (pp. 174-175) he separated them by the number of tentacle scales (two, one, or none), by the disc cover, and even by the shape of the under arm plates. He gave a generic description, emending Müller and Troschel's original description, and allowed more latitude with regard to the nature of the disc cover and shape of the arm spines (similar to Lütken's proposal in 1869). However, Lyman for the first time commented on the internal skeleton of the group. He compared _Ophiomastix_ with _Ophiocoma_ and noted in the latter that a) the radial shields were proportionately larger; b) there was a difference in the position of the oral plates with respect to one another; c) the genital plate was rounded and longer. For _Ophiomastix_ the scaling, presumably on the inside of the disc, was found to be variable (i.e. in O. venosa scales were minute and thin at the center of disc in opposition to O. annulosa in which scales were larger and lumpy). My own comparisons of these internal characters, and those by Murakami (1963) with regard to the oral plates, do not substantiate Lyman's generalizations and do not indicate generic differences. This is especially true with respect to new species in both genera, and variations due to growth changes in the various species. For example, the radial shields of Ophiocoma wendtii, O. erinaceus, and O. dentata are proportionately larger than those of Ophiomastix variablis. The genital plate of Ophiomastix venosa is no longer than that of Ophiocoma dentata. Furthermore, Murakami's (op. cit.) examination of the dental and oral plate of species in both Ophiomastix and Ophiocoma indicated the similarity between the two groups and showed no generic distinction.

A major review of the genus Ophiomastix was made by Brock (1888) in which two new species were described (O. pusilla and O. elegans). He reached his own conclusions regarding the generic status of Ophiomastix, placing emphasis on the form of the upper arm spine. He tried to show that the clubs (claviform arm spines) develop with age in the known Ophiomastix species and that the spines were a very characteristic mark of distinction in comparison with *Ophiocoma*. In addition, he indicated that each species has its own characteristic form and order of the claviform spines.

Of the species in which clubs were not known or considered present (i.e. *mixta* and *janualis*), Brock reported that one specimen of the former, found in the Göttinger Collection and identified by Lütken, had club-shaped arm spines. Brock believed that these spines might appear very late in the development of some species, especially after noticing the absence of claviform spines in a specimen of *O. caryophyllata* with a disc diameter 12 mm. Therefore he was not surprised at the absence of clubs in the case of Lyman's type of *O. janualis* with a disc diameter of only 5 mm. Brock spent some time describing the nature of the claviform spines for each of the species and the basis of his description was tabulated in the form of a key (as his TABLE I, p. 505).

In addition to placing great emphasis on the shape and position of the claviform arm spine, Brock arranged the species of *Ophiomastix* according to the nature of their disc cover. A key to the species based on the difference in disc cover was presented (as his TABLE II, p. 506).

Between 1888 and 1920, five additional species of *Ophiomastix* were described. Pfeffer's (1900) description of

O. luetkeni in many ways recalled O. januals, and aside from color (pointed out by H. L. Clark, 1921, p. 136) there was little to distinguish the two species. Koehler (1905) added two new species; Ophiomastix variabilis and O. ornata, the latter based on a single specimen (d.d. 9 mm) which showed thick, cylindrical, but pointed upper arm spines (i.e. not claviform), and small flattened spindle-shaped spinules on the disc. H. L. Clark (1915) described O. corallicola as having 3 and 4 alternating arm spines, two tentacle scales, and numerous disc spinelets. The fifth species, O. bispinosa, was described by H. L. Clark (1917) on the basis of 2 and 3 arm spines and the disc and upper arm plates covered by skin, recalling Lyman's O. flaccida and O. janualis, as well as Pfeffer's O. luetkeni.

In 1907, Koehler mistakenly described Ophiocoma wendtii from several Indo-Pacific localities apparently confusing two species. The larger specimens showed definite claviform upper arm spines recalling Ophiomastix, but the nature of the disc cover suggested Ophiocoma in its granulation. The taxonomic position of these specimens remains unknown at present, but in some ways recalls Brock's (1888) Ophiomastix elegans. Koehler pointed out that, based on these specimens, the distinction between Ophiomastix and Ophiocoma was very tenuous.

H. L. Clark (1921) made a review of the genus *Ophiomastix* attempting to distinguish the species primarily on the basis of pigmentation and a key to the species known at this time was given (p. 134) emphasizing this character. He excluded Brock's (1888) use of the nature of the claviform arm spines for not making, "sufficient allowance for individual diversity or for growth changes" (p. 134). Unfortunately, H. L. Clark did little more to verify his own use of characters. His emphasis of color as a specific character was amplified by several color drawings of species he encountered at Torres Strait (Mer Island) but included only seven of the thirteen previously recorded. In all, fifteen species had been described but Clark considered *O.* (*Acantharachna*) *mirabilis* (Smith) to be synonymous with *O. flaccida* (Lyman), and *Ophiomastix pusilla* (Brock) to be an *Ophiocoma*. No attempt was made toward unravelling the interrelationships between the species however. Based on a few small specimens available to him, Clark indicated that specific characters developed rather slowly. For specimens less than 10.0 mm (d.d.), he noted the upper and lower arm plates to be longer than wide and very different from adults of the same species (none designated). He noted in passing that the oral shields and adoral arm plates differed from the adult condition but did not state how. Likewise he noted that very young specimens might lack the characteristic claviform arm spines and disc spinelets of the adult. In this respect his findings agreed with Lütken and Brock.

Since 1921, three new species of Ophiomastix have been described. H. L. Clark (1938) described O. notabilis from Western Australia, Murakami (1943) described O. palaoensis from the Caroline Islands in the Pacific, and A. H. Clark (1952) described the only hexamerous species, O. sexradiata, from the Marshall Islands. Ailsa M. Clark (pers. comm.) found O. sexradiata to be like that of Ophiocomella and my examination of the type at MCZ confirmed this (see p. 124).

Aside from reports on the systematics of the genus, it has been suggested that the arm spines of at least one species of Ophiomastix may be toxic and produce paralysis and death in small animals (Ludwig and Hamann, 1901, based on Hamann, 1889; Hyman, 1955; Halstead, 1965). However, there has been little evidence to support the statements (Halstead, 1965).

New findings - relationships among Ophiomastix species

Phylogeny:

In an attempt to show the possible phylogenetic relationships between the species and genera in the subfamily Ophiocominae, I have indicated in my discussion on *Ophiocoma* (p. 158) the importance of the sequence and nature of the arm spines.

A review of the literature and examination of specimens of several species of *Ophiomastix* have made it apparent that most if not all species in this genus have been derived from the Scolopendrina group of *Ophiocoma*. The following evidence is presented to support this hypothesis.

Arm Spine Sequence. The arm spine sequence of many species of *Ophiomastix* shows that there is an alternation of arm spines either on opposite sides of the same arm segment, or on adjacent segments beyond the disc margin. Furthermore, it appears that we may divide the known species of *Ophiomastix* into two groups: those species in which the alternation is three and four spines in the middle parts of the arms; and those species in which two and three arm spines alternate. Species with an alternation of 3/4 arm spines and those with an alternation of 2/3 are listed below.

3/4 Arm Spines	2/3 Arm Spines
O. annulosa	*O. bispinosa*
O. asperula	*O. flaccida*
O. caryophyllata	*O. janualis*

O. corallicola

O. elegans

O. mixta

O. notabilis

O. palaoensis

O. variabilis

O. luetkeni

O. venosa

Those species of *Ophiomastix* with a 2/3 arm spine alternation also have a thick skin covering most of the scales on the disc and the upper arm plates. These species also have only widely placed disc spinules. In contrast, those species with a 3/4 alternation have the disc scales more exposed with no thick skin covering, and have numerous disc spinules or spinules and granules often closely packed.

Dental plate. Information concerning the oral and dental plates of a number of species of ophiocomids has been recorded including species of *Ophiomastix* (Murakami, 1963). I have already pointed out that several characteristics of the dental plate suggest differences between the proposed groups of *Ophiocoma* (see p. 36) which are positively correlated with other characters differentiating the groups in that genus. Murakami (*op. cit.*) stated, "The dental plate of *Ophiomastix* belongs to the same category as that of *Ophiocoma*, but the foramina on the upper portion number three, each of them being completely divided" (p. 27). In the case of *Ophiocoma*, I have found that the number of foramina varies in the same individual, is governed by the position of the teeth in each radius of the jaw, and is also a function of growth (i.e. fewer in smaller individuals). The same holds true for species of *Ophiomastix* which I have analyzed. Although it was not mentioned by Murakami, the septa dividing the teeth foramina have been found to be narrow and compressed. A comparison of Murakami's figures and my examination of the dental plates of *O. mixta*, *O. annulosa*, and *O. caryophyllata* has verified that the form of the septa is identical to that found in all of the species of *Ophiocoma* in the Scolopendrina group.

The length to breadth ratio (L/B) for each of Murakami's specimens of *Ophiomastix* and the percent of the total length occupied by the dental papillae (indicated by the dental bosses or projections) were analyzed. The data on *O. venosa* were supplied by me for a specimen from Mossambique. The data are presented below.

Species	L/B Ratio	% Dental Papillae of Total Length
O. annulosa	2.9:1	31
O. asperula	2.8:1	32
O. caryophyllata	2.8:1	28
O. leutkeni	2.8:1	33
O. mixta	2.6:1	33

O. palaoensis	2.8:1	18
O. variabilis	2.6:1	26
O. venosa	2.8:1	20

The length to breadth ratio is within the same range as that noted for specimens of *Ophiocoma* in the Scolopendrina group. Considerable variation was found with regard to the area (per cent) occupied by the dental papillae. *Ophiomastix palaoensis*, *O. variabilis*, and *O. venosa* have a percentage well below that noted in the Scolopendrina group of *Ophiocoma*, whereas the other five species are within the limits of the group. The dental plate of *Ophiomastix venosa* is shaped much like that of *Ophiarthrum pictum*. However, in the latter, the dental papillae occupy a far greater portion of the length of the plate (approximately 30%). Furthermore, there is a definite resemblance in the shape of the dental plate of *O. variabilis* to that of *Ophiocoma pusilla*.

Oral plate. The oral plate of *O. annulosa*, *O. leutkeni*, *O. mixta*, and *O. palaoensis* resembles *O. erinaceus* and *O. scolopendrina* in the condition of the indentations (scars) on the abradial side (Murakami, 1963).

Oral papillae. I have found that four oral papillae are typical in *Ophiomastix*. Most often the second oral papilla is the largest. The number and relative size of the oral papilla of _Ophiomastix_ resembles species of _Ophiocoma_ in the Scolopendrina group.

In summary, evidence presented on the basis of the arm spine sequence, dental and oral plates, and characteristics of the oral papillae, indicates a close relation between species of _Ophiomastix_ (with the possible exception of _variabilis_) and the Scolopendrina group of _Ophiocoma_. Although there is no fossil evidence to indicate which group is the older, the greater diversity in the shape of the upper arm spine, in the number of arm spines, and in the disc cover suggest that _Ophiomastix_ may be a specialized offshoot of the Scolopendrina line of _Ophiocoma_.

A key to the species in the genus _Ophiomastix_ is included in this work. The references given in the generic evaluation are sufficient for a review of the species in this group.

Distribution. Species of _Ophiomastix_ are limited to the Indo-Pacific area, whereas species in the Scolopendrina group of _Ophiocoma_ are found circum-tropically, suggesting a more ancient history for the latter. There is only one species of _Ophiomastix_ (_O. venosa_) which is distributed as far as the eastern coast of Africa. Another species, _O. mixta_, has been recorded as far north (350° N) as Sagami Bay, Japan (Utinomi, 1961). There is a reduction in the number of species eastward into the Pacific, with only _O. bispinosa_ being reported as far east as the Society Islands and Tuamotu's (H. L. Clark, 1917). There are not authentic records from the Line Islands nor the Hawiian Islands (A. H. Clark's 1949 record of _O. asperula_ from Hawaii has been shown to be based on _Ophiocoma macroplaca_, see p. 198).

Diagnostic characters of the genus Ophiomastix. Ophiocominae in which the upper arm spines are well developed, often forming a club-shaped spine with a divided apex, although elongate, tapering upper spines are present in several species; disc covered by few to many spinules, or by spinules and granules, but never by granules alone (one species, _Ophiomastix venosa_, may show the absence of any spinules and have the disc naked similar to the condition noted in _Ophiarthrum_; however, the presence of well defined claviform arm spines in _Ophiomastix venosa_ serves to distinguish it as a member of the genus _Ophiomastix_); the dental papillae are well developed in 2 to 4 rows; the teeth have hyalinated tips; the dental plate is from 2.5 times as long as broad or more, and the vertical septa dividing the teeth foramina are narrow and thin; the oral plate has well defined muscle scars on the aboral surface and a rather elongate adoral muscle region; all species are confined to the tropical Indo-Pacific area with the greatest concentration of species in the Indo-Malayan and Indo-Australian regions; shallow sublittoral to a depth of 60 meters. Type species: Ophiura annulosa Lamarck, 1816.

Synoptic key to species in the Genus Ophiomastix

1 Arm spines 3 or 4 on each side of basal arm segments, alternating irregularly 3 and 4 on opposite sides or adjacent segments............2

Arm spines 2 on each side of basal arm segments alternating irregularly 2 and 3 on opposite sides or adjacent segments...........11

2 (1) Disc covered with spinules and granules............3

Disc covered only with long or short spinules.......5

3 (2) Tentacle scales single, except on basal pores........................... O. asperula Lütken

Two tentacle scales..................................4

4 (3) Spinules rare, mixed irregularly among the granules, extending well into oral interradial part of disc; upper arm spines slightly thickened.................O. elegans Brock

Spinules numerous, mixed with closely packed granules in regular intervals;

with oral interradial part of disc (at least near genital opening) bare; upper arm spines not thickened............*O. mixta* Lütken

5 (2) Two tentacle scales..................................6

One tentacle scale, except on basal pores...........8

6 (5) Disc spinules 3 or more times as long as high, with blunt tip and of white color with dark brown bands; arms 7 to 12 times disc diameter..........*O. annulosa* Müller & Troschel

Disc spinules less than 3 times as long as high; with acute tip and of uniform color; arms about 5 times disc diameter..................7

7 (6) Upper arm plates broadly fan-shaped (distal border rounded), less than 2 times as broad as long; distal half of upper arm plate and lateral arm plates light, proximal halves very dark...................*O. caryophyllata* Lütken

Upper arm plates diamond shaped (distal border angular), 2 or more times as broad as long; upper arm plates uniformly light grey, lateral arm plates uniformly dark...................................*O. corallicola* H. L. Clark

8 (5) Spinules short, of uniform length; disc

marked with dark brown or black....................9

Spinules of two lengths, shorter ones more common; disc not marked with dark brown or black........................<u>O.</u> <u>variabilis</u> Koehler

9 (8) Spinules widely scattered over disc, more than three times as long as thick; upper enlarged arm spines thickened, but tip rounded not claviform..............................10

Spinules numerous, less than three times as long as thick; upper enlarged arm spines with claviform tip every 2 or 3 segments.......... .... <u>O.</u> <u>palaoensis</u> Murakami

10 (9) Color of disc jet black; upper arm plates also black but at intervals of 4-6 segments a light band crosses proximal half of upper arm-plate; arm spines uniform in color................. <u>O.</u> <u>notabilis</u> H. L. Clark

Color of disc light grey; arms not banded; arm spines annulated..............<u>O.</u> <u>ornata</u> Koehler

11 (1) Tentacle scales present...........................12

Tentacle scales absent.............<u>O.</u> <u>flaccida</u> Lyman

12 (11) Two tentacle scales.................<u>O.</u> <u>janualis</u> Lyman

(=<u>O.</u> <u>luetkeni</u> Pfeffer)

One tentacle scale (except basally)...............13

13 (12) Claviform upper arm spines present; arms with mid-longitudinal dark line on oral surface..........................*O. venosa* Peters

Claviform upper spines absent, but some upper spines are thickened; arms without mid-longitudinal dark line on oral surface......................*O. bispinosa* H. L. Clark

GENUS OPHIOPTERIS

Two species are included in the genus <u>Ophiopteris</u> proposed by Smith (1877). The morphological characters of both species are quite close and the two will be considered to gether for comparative purposes in a single DIAGNOSIS and DISCUSSION.

Re-examination of external characters and internal skeletal features have led to an emended generic diagnosis which follows.

<u>Generic Diagnosis: Ophiopteris E. A. Smith (emended)</u>

a. Disc covered with granules of uniform size.

b. Dental papillae numerous.

c. Dental plate elongated, much narrower aborally than orally.

d. Teeth without hyalinated tip, and relatively thin.

e. Oral papillae on jaw three to five, overlapping one another; additional outer oral papilla at base of ventral shield, quite small and separated from oral papillae on jaw by wide gap.

f. Oral shields broader than long.

g. Adoral shields nearly, or actually, meeting in front of oral shields.

h. Upper arm spine modified into compressed, broadened, scale-like form; other arm-spines compressed but elongated.

i. Oral plates with smooth, deeply concave, ear-shaped abradial muscular surface.

Ophiopteris bears its closest resemblance to the genus Ophiocomina and the Canaliculata group of Ophiocoma in the nature of the teeth, oral and adoral shields, and shape of the oral plate.

Synoptic key to species in the Genus Ophiopteris (after H. L. Clark, 1921)

Color black or very dark brown, more or less reddish orally; arm-plates, especially the upper, not very markedly wider than long; uppermost arm-spine nearly circular; New Zealand.............................. O. antipodum Smith

Color brown, often more or less variegated and arms distinctly banded; arm-plates markedly wider than long; uppermost arm-spines somewhat more elongated; West Coast North America.................... O. papillosa (Lyman)

Ophiopteris antipodum Smith

SYNONYMY

Ophiopteris antipodum Smith, 1877, p. 306, Pl. XV, figs. 1-5; Lyman, 1882, p. 168, 176; Farquhar, 1897, p. 192; 1898, p. 308; H. L. Clark, 1921, p. 132; Mortensen, 1924, p. 122, Fig. 10; Fell, 1949, p. 123.

MATERIAL EXAMINED

New Zealand: MCZ: No. 1787 (1)

Ophiopteris papillosa (Lyman)

(Plate XIX, figs. 1-4)

SYNONYMY

Ophiocoma papillosa Lyman, 1875, p. 11; 1882, p. 168, 173.

Ophiopteris papillosa (Lyman); McClendon, 1909, p. 49, Pl. 5, figs. 28-29; H. L. Clark, 1921, p. 132; 1940, p. 341; Campbell, 1921, p. 3, fig. 6; Nielsen, 1932, p. 249; Boolootian and Leighton, 1966, p. 6, fig. 25.

MATERIAL EXAMINED

California

Corona del Mar - BPBM: W1652a-b (2)

Portuguese Bend - BPBM: W1653a-c (3)

San Clemente Island - BPBM: W1651a-c (3)

San Miguel Island - BPBM: W1654 (1)

Santa Barbara - MCZ: No. 1788 (TYPE)

DIAGNOSIS (Both Species)

Size. Maximum disc diameter: O. antipodum, 26 mm; O. papillosa, 24 mm. Arm length between three and five times the disc diameter.

Oral papillae (Pl. XIX, fig. 1). Three to five oral papillae are typical along each side of the jaw in both species, although McClendon reported as many as six in O. papillosa. In addition to the oral papillae lying along the jaw edge, there is another pair of papillae which occur at the base of the ventral shield. There is a large gap between the oral papillae on the jaw and those on the ventral shield ossicles. The widely separated pair of papillae are directed downward into the mouth and lie to the outer side of the second buccal podium which is exposed in the gap. I consider these outer, downward directed oral papillae to be homologous to those which are more developed in other genera in the Ophiocominae, where they are adjacent to the oral papillae on the jaw. In very small specimens of O. papillosa which I examined there is very little separation between the outer and inner papillae; with growth, however, the separation between the papillae becomes evident, and the reduction in size of the outer papilla is most pronounced in

Ophiopteris among the Ophiocominae. Those oral papillae on the jaw overlap one another, rather than lying side by side; in this manner they differ from the condition noted in other ophiocomids. Mortensen (1924) mentioned this character for *O. antipodum* and the same condition has been found in *O. papillosa*.

Dental papillae (Pl. XIX, fig. 1). One of the most characteristic features of the genus is the presence of a large number of dental papillae extending deep into the mouth region. They develop very quickly, and Lyman (1875) counted fifteen in a specimen with a disc diameter of only 4 mm. I found only five in a specimen 3 mm however, whereas the largest specimen at my disposal (d.d. 24 mm) had between twenty-six and thirty. The outer dental papillae are larger than those in the center and are shaped like the oral papillae on the oral plate.

Teeth. Together with the genus *Ophiocomina*, both species of *Ophiopteris* lack the specialized hyalinated distal part of the tooth, characteristic of other ophiocomids. The teeth are quite flat as well.

Dental plate (Pl. XIX, fig. 3b). Examination of this plate in *O. papillosa* reveals it to be more than two times as long as broad and much narrower aborally in the area occupied by the teeth. The teeth foramina are small and show a very narrow vertical median septum. The oral portion of the plate is widened and spatulate, with a series of depressions for the dental papillae; the outer depressions are largest. The shape of this plate is quite different from any known in other ophiocomids, but comes closest to that seen in Ophiocoma bollonsi, or to several species of Ophiothrix figured by Murakami (1963).

Oral plate (Pl. XIX, fig. 4) In O. papillosa it shows a well developed ear-shaped abradial muscle area with a concave central portion and has a smooth surface; the adradial muscular area is limited to the oral, distal part. In these respects and in the general shape, the oral plate is very similar to that of Ophiocoma bollonsi.

Arm spines (Pl. XIX, figs. 2, 3). For both species, four to six rather flattened arm spines occur on each side of the arm segments. These spines are not pointed and are usually much compressed at the tip, even spatulate. In addition to these spines there are peculiar modified short, broad, and compressed scale-like spines which occur above the upper unmodified spines. H. L. Clark (1921, p. 132) described the uppermost arm spine of Ophiopteris antipodum as "nearly circular", and for O. papillosa, as "somewhat more elongated".

Observation of the number of arm spines in small specimens of O. papillosa as well as the number of spines on distal segments in larger specimens of both species revealed 3 arm spines developing first at approximately the same time; only with growth are more arm spines added, and always above these 3 spines. With exception of spines on those segments beneath the disc, most of the fourth, fifth, and sixth arm spines pass through a modified (scale-like) stage before elongating and developing into typical spines. Two methods can be used to demonstrate this. First, the development of the scale-like spines can be traced along one arm. In a specimen of O. antipodum 12.5 mm (d.d.) with well over eighty segments, I observed only 3 arm spines beyond segment seventy-eight and none was scale-like; a fourth spine was first noted at segment seventy-eight, slightly rounded; proximally the spine showed increasing elongation; at segment sixty-eight another spine was noted just beginning to develop above the fourth spine, it was scale-like at first but increased in length on more proximal segments; between the thirty-eighth and fortieth segment, a sixth spine was evident, at first scale-like, but like the fifth increasing in length on more proximal segments; finally quite near the disc a seventh scale-like spine was observed. Second, in order to show that additional arm spines do develop on a particular arm segment, with increase in size different sized specimens of _O. papillosa_ were examined and the number of arm spines on the tenth arm segment were counted. The following data were obtained:

Disc diameter (mm)	3	6.5	10.5	21
Number of arm spines on tenth segment	4	4+scale	5+scale	6+scale

It was evident from these observations that the scale-like upper arm spine increased in length with size, and additional spines, initially modified, developed above preexisting spines.

Eleven specimens of _O. papillosa_ with disc diameters ranging from 3 mm to 21 mm showed an arm spine sequence on each side of the first four segments of 3-4-5-5 respectively. Beyond segment four, the number of spines increases with the size of the specimen. Only one specimen of _O. antipodum_ was examined; it revealed a similar sequence on the proximal segments.

Tentacle scales (Pl. XIX, fig. 1). Only one scale is present on each pore for both species.

Aboral arm plates. These plates are transversely oblong, sharply pointed on each side, the points fitting between the lateral arm plates and lying on the distal side of the lateral plates and scale-like upper arm spines of the same segment. In the shape of the plates, *Ophiopteris* resembles the condition observed in both *Ophiocoma bollonsi* and *O. canaliculata*. H. L. Clark (1921, p. 132) considered the uppermost plates of *O. antipodum* as "not very markedly wider than long"; for *O. papillosa* as "markedly wider than long".

First arm vertebra (Pl. XIX, fig. 4,B). The first arm vertebra of *O. papillosa* shows the very characteristic ophiocomid feature with a calcareous septum forming an opening for the radial water canal, and separating it from the radial nerve.

Peristomial plates. These were observed in *O. papillosa*. They are quite large and double.

Pigmentation. The color of both species is generally dark brown, violet, or blackish. Both Smith (1877) and Farquhar (1897) give color descriptions of *O. antipodum*. In *O. papillosa* the disc is usually a deep brown, there may be on some individuals a large, lighter, central area as well; the upper arm plates are russet with deep purple-black arm bands; the lower side is brown; tube feet dark brown, almost black. Clark (1981, p. 132) used color to differentiate the two species: for O. antipodum, "black or very dark brown, more or less reddish orally; for O. papillosa, "brown often more or less variegated and arms distinctly banded".

HABITAT

O. antipodum has been collected beneath stones at the low water mark in several localities (Farquhar, 1897; Mortensen, 1924). Fell (1949) lists this species as "eulittoral", and rare.

Fred C. Ziesenhenne supplied me with the following data concerning O. papillosa: Found on rocky or kelp covered bottom in porous rock, often coiled in crevices with only one or two arms extended; often taken in large numbers from kelp holdfasts; to a depth of 95 fms. Nielsen (1932) recovered five specimens on the kelp Macrocystis which had washed ashore off La Jolla, California.

DISTRIBUTION

O. antipodum has been reported from Cook Strait and Tasman Bay, between the North and South Islands of New Zealand (Smith, 1877; Farquhar, 1897; Fell, 1949). Mortensen (1924) received specimens collected in Auckland Harbor on North Island.

O. papillosa has been collected from Monterey Bay, California to Cedros Island, Baja California, Mexico, based on specimens deposited in the Allan Hancock Foundation collection. Published records are within this range.

DISCUSSION (Both Species)

Certain morphological features have suggested relationship between *Ophiopteris* and *Ophiothrix* (fam. Ophiothricidae). The very large number of dental papillae and characteristic shape of the mouth region, led both Smith (1877) and Mortensen (1924) to consider the two genera related. The latter worker even considered it doubtful whether *Ophiopteris* really belonged to the Ophiocominae.

Until now, no one has reported the similarity of *Ophiopteris* to species of *Ophiocoma* in the Canaliculata group. In the foregoing diagnosis I mentioned that in the shape and structure of the oral plate, the form of the adoral shields (meeting in front of the oral shield) the tendency for reduction in the size of the outer oral papilla, the close approximation of the second buccal podia to the surface of the jaws, and in the shape of the regular arm spines, *Ophiopteris* and the Canaliculata species showed characters in common. The facts that the peristomial plates are double and the genital plates are not firmly fixed to the basal arm vertebrae in *Ophiopteris* argue against this genus being in the family Ophiothricidae or any other family in the order Gnathophiurida as defined by Matsumoto (1917). The shape of the first arm vertebra with a characteristic calcareous septum separating the radial water canal and nerve supports the decision to retain the genus *Ophiopteris* in the family Ophiocomidae.

Both species, *O. papillosa* and *O. antipodum* are quite similar morphologically. H. L. Clark (1921) separated the two on the basis of color, the length-breadth relationships of the upper arm plates, and the shape of the uppermost arm spine. But he states, "in the absence of more abundant material, it is difficult to determine what the essential differences are" (p. 132). I can add little to Clark's evaluation having had only one specimen of *O. antipodum* to compare with *O. papillosa*. Evaluation of more substantial specific morphological differences must await the analysis of additional material.

H. L. Clark (1921, p. 133) suggested *Ophiopteris antipodum* and *Ophiopteris papillosa* might represent specialized forms derived from *Ophiocoma erinaceus* and *O. aethiops*.

This seems unlikely considering the very different morphology in the oral skeleton and arm spines. My findings indicate that *Ophiocoma bollonsi* and *O. canaliculata* show more features in common with *Ophiopteris* than any other ophiocomid. Furthermore, these species are, like *Ophiopteris*, temperate water forms, and two of the species, *Ophiocoma bollonsi* and *Ophiopteris antipodum*, are confined to shallow sublittoral New Zealand waters. However, no member of the Canaliculata group of *Ophiocoma* has been recorded from the northeastern Pacific temperate waters where *Ophiopteris papillosa* is restricted.

I am inclined to believe that the two species of *Ophiopteris* are relic populations of previously widely distributed species. Yet present day temperature barriers and the apparent absence of any intermediate forms make it difficult to suggest the past distribution of the species.

SYSTEMATIC IMPLICATIONS OF THE OPHIOCOMID LARVA AND EGG

The characteristics of the egg and larvae of several ophiocomids are known (Pl. XX) and may be useful in supporting conclusions about the relationships of the taxa involved. Mortensen (1921b) described the larval form and skeleton of *Ophiocoma echinata*. He used the comparative features of the larval skeleton to separate the ophioplutei of suspected *Ophiocoma* species from the larvae of other brittlestars. On the basis of his study, three additional ophioplutei were considered to belong to *Ophiocoma* species. The larval form of one of these, "ophiopluteus of species *a*", suggested the condition known for *Ophiocomina nigra* more than for *Ophiocoma echinata*. The other two (species "b" and "c"), based on their larval form and skeleton, indicated the more typical *Ophiocoma* condition. These latter two ophioplutei had been recovered from plankton hauls made in the Gulf of Panama, near Taboga Island, a region in which *O. alexandri* and *O. aethiops* are known to occur.

Grave (1898) had previously mentioned that the egg of *O. echinata* formed a "tough prickly egg membrane soon after fertilization". Mortensen (*op. cit.*) stated that this peculiar membrane was probably a special adaptation, "serving as a floating apparatus" (p. 132).

In Bermuda, Mortensen (1931) verified Grave's description of the egg membrane in O. echinata and confirmed his earlier description of this species' larva. He described and figured the two-and-one-half, and six day larvae, noting in the latter a size and development similar to the larva of this species he had figured in 1921 (received from Grave and said to be eleven-and-one-half days).

Six years later, Mortensen (1937) described and figured the larva of three more tropical ophiocomids, Ophiocoma erinaceus, O. pica (as O. lineolata), and O. scolopendrina from the Indo-Pacific. He had been able to obtain natural fertilization of the eggs of these species in a laboratory near the Red Sea during April and May, 1936. The results of this work were important for they showed:

a. that a thorny membrane appeared around the egg of both O. erinaceus and O. scolopendrina (Pl. XX, fig. 6) after fertilization, but not around the egg of O. pica;

b. that the larval skeleton of the former two species (Pl. XX, figs. 1, 3) was nearly identical to that of O. echinata (Pl. XX, fig. 5) whereas the larval skeleton of O. pica was quite different. A comparison of Mortensen's figures shows that in the larval skeleton of O. erinaceus, O. scolopendrina, and O. echinata the body rods ((k), in his figures) were nearly horizontal, and the end rods (e) and transverse rods (t) were very short and broad, forming a knuckle-like projection where the two halves of the skeleton nearly meet in the midline. In O. pica, the body rods are nearly vertical and neither the end nor transverse rods are differentiated.

Mortensen also indicated that O. pica resembled Ophiocomina nigra in certain features of the larval form. However, the larval skeleton of these two species differed considerably (compare Pl. XX, figs. 2, 4).

In summary, at least three types of larval skeletons have been described for five ophiocomid species in two genera. Three species belonging to the Scolopendrina group of Ophiocoma (echinata, erinaceus, and scolopendrina) show larval and embryonic features which are quite similar. In contrast, the larval skeleton and fertilized egg of O. pica are quite different thus adding support to the separation of this species from species in the Scolopendrina group of Ophiocoma. The larval skeleton of Ophiocomina nigra differs from those noted for species of Ophiocoma.

The initial work, primarily by Mortensen, should be supplemented by more work on the larvae of other species in the subfamily; it is probable that further studies on the embryonic and larval forms of these species will help to further clarify interrelationships within the subfamily.

RELATIONSHIPS AMONG THE OPHIOCOMINAE

(Plate XXI)

The relationship of taxa in the subfamily Ophiocominae can be proposed on the basis of morphological characters supported in part by zoogeographical distribution.

The only attempt which has been made to indicate the evolution of the Ophiocominae was by H. L. Clark (1921). I have already discussed my views on his derivation of many of the species in the genus *Ophiocoma* from the species, *O. brevipes*, and his division of the genus into several groups (p. 35).

Clark commented briefly on the relationships of other genera in the subfamily. He considered *Ophiomastix* distinct from *Ophiocoma*, although he was aware that the criteria separating the two genera were not well defined. *Ophiarthrum* was regarded as a specialized offshoot of *Ophiocoma*, but Clark failed to indicate from which of his groups of *Ophiocoma* it was derived. The genus *Ophiopteris*, with two species showing a discontinuous distribution on opposite sides of the Pacific, was suggested to have been derived independently from two species of *Ophiocoma* in the Scolopendrina group.

The genus *Ophiocomina* was not considered by H. L. Clark in the subfamily Ophiocominae, but evidence given by Mortensen

(1921) and Koehler (1922) strongly support the inclusion of this genus in the subfamily (see p. 222).

My work with species in the genus *Ophiocoma* indicates that this genus is polyphyletic. In addition to three species complexes proposed by H. L. Clark (*op. cit.*) I have added another, the Canaliculata group, to account for two species which show obvious relationships to *Ophiopteris* and *Ophiocomina*, but are still within the limits of the genus *Ophiocoma*.

Among the most important criteria linking the Canaliculata group with these other genera are: a) the shape and structure of the oral plate; b) the nature of the adoral plates which meet in front of the oral shield; c) the separation of the outer and adjacent oral papillae, which leaves a distinct gap; d) the form of the arm spines which is thin and compressed; e) restriction of the species to temperate water regions in close geographical proximity. These morphological characters are not shared by other species in the genus *Ophiocoma*, with the exception of *O. pusilla*. This species does show similarity to the Canaliculata group in the nature of the arm spines and abradial surface of the oral plate, but in other respects differs.

Two features suggest that both *Ophiopteris* and *Ophiocomina* may be the most primitive of the Ophiocominae. The first is the absence of hyalinated grinding tips on the teeth. It is assumed that the presence of this feature is a specialization acquired during the evolution of the subfamily. Its presence, while not restricted to the Ophiocomidae, is limited to ophiuroid families considered by Matsumoto (1917) to be the most advanced. Second, both genera have two species which show very marked discontinuous distributions suggesting a very ancient history.

The presence of a scale-like upper arm spine and a much more pronounced development of the dental plate (in the oral region) serve to distinguish Ophiopteris from Ophiocomina but offer little in the way of suggesting which genus is the most primitive.

Other genera and species in the subfamily show marked differences from the groups just discussed primarily in the characteristics of the oral plate, shape of the first arm vertebra, thickness of the arm spines, nature of the oral papillae, and distribution.

Species in the genus Ophiocoma, aside from those in the Canaliculata group, as well as O. pusilla, and O. pica, can be separated into three groups. One of the major structural changes has occurred in the development of the arm spines. In the Scolopendrina group, the upper arm spines alternate on each side of the segment or on adjacent segments. These same characters are found in all species of *Ophiomastix* and *Ophiarthrum*, and together with similar characteristics of the dental and oral plates suggest a close relationship between these genera and the Scolopendrina group of *Ophiocoma*.

The far more specialized form of the aboral arm spine, developed into a clavate structure in many species of *Ophiomastix*, and the variation in the types of disc cover, suggest that this genus might be derived from the Scolopendrina line of *Ophiocoma*. Additional support of this hypothesis is suggested by the distribution of these groups: Species in the Scolopendrina group are widespread throughout the tropical Indo-Pacific, Caribbean, and Eastern Pacific, whereas species of *Ophiomastix* are restricted to the Indo-Pacific and show marked reduction in the east and west portions of this region.

I have suggested a division of the genus *Ophiomastix* into two groups on the basis of the number of arm spines and nature of the disc cover (p. 243).

Species of *Ophiarthrum* show characteristics in common with the group of *Ophiomastix* having predominantly 2 and 3 arm spines and thick integument covering the disc and arms. In these respects *Ophiarthrum* and this group are considered most closely related, and probably highly specialized.

The other groups of *Ophiocoma*, which are designated

Brevipes and Pumila appear to represent specialized branches of this genus with well defined species. H. L. Clark's (1921) suggestion that O. brevipes is the most primitive species in the genus cannot be maintained on the basis of the reduction in the number of dental papillae. This character can be considered a specialization rather than a primitive feature. Differences in the shape of the dental plate, shape of the arm spines, and nature of the disc granulation serve to distinguish the Brevipes group from others in the genus.

Ophiocoma pica may be considered a separate branch of the Ophiocoma line, sharing features present in the other groups.

Above the subfamily level, both Matsumoto (1917) and Murakami (1963) have considered the Ophiocominae among the most specialized groups of ophiuroids in the Order Chilophiura. The well developed mouth skeleton and arm spines have been mainly used to support this hypothesis. I do not propose to refute the considerations of these two workers and feel that a discussion of the relationships of the Ophiocominae to other ophiuroids must await additional comparative studies.

It should be pointed out however, that the characteristics of Ophiopteris, Ophiocomina, and the two species of

Ophiocoma in the Canaliculata group were not considered in their evaluation of the relationships of the Ophiocominae to other ophiuroids. The divergence of these groups from the more specialized groups in the subfamily shown in quite different characters, may lead to a clearer understanding of the broader relationships of these ophiuroids. The inferred relationships in the taxa comprising the Ophiocominae are presented in Pl. XXI.

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PLATE I

Ophiocoma dentata - First Arm Vertebra.

Fig. 1. Distal surface.

Fig. 2. Proximal surface.

Fig. 3. Oral surface.

Fig. 4. Aboral surface.

Fig. 5. Lateral surface.

List of abbreviations: a, upper muscular surface; a', lower muscular surface; b, upper lateral condyles; b', lower median condyle; c, upper median articular fossa; c', lower lateral articular fossa; d, opening for radial water canal; e, opening for lateral branch of water canal; f, upper muscular surface; f', lower muscular surface; g, upper median condyle; g', lower lateral condyle; g'', upper later condyles; h, opening for lateral branch of water canal; h', lower median articular fossa; l, podial recess; m, alar ridge; n, lateral alar papillae; o, pore to podium; p, oral groove; r, r', oral articular surfaces; s, aboral median furrow; t, furrow for nerve branch to podium; w, oblique ridges; y, pore from radial nerve.

PLATE I

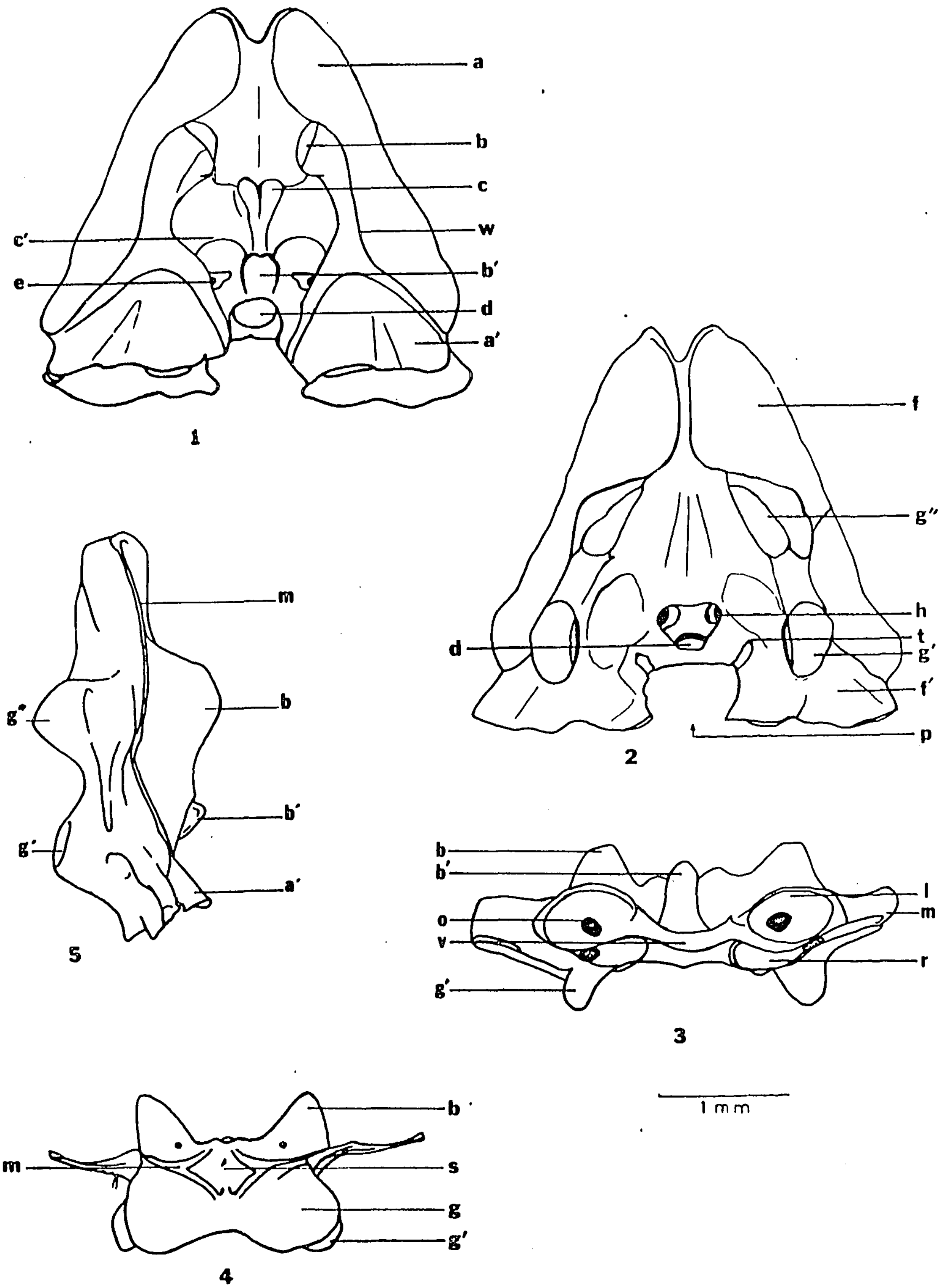


PLATE II

<u>Ophiocoma</u> <u>dentata</u>. Second Arm Vertebra.

Fig. 1. Distal surface.

Fig. 2. Proximal surface.

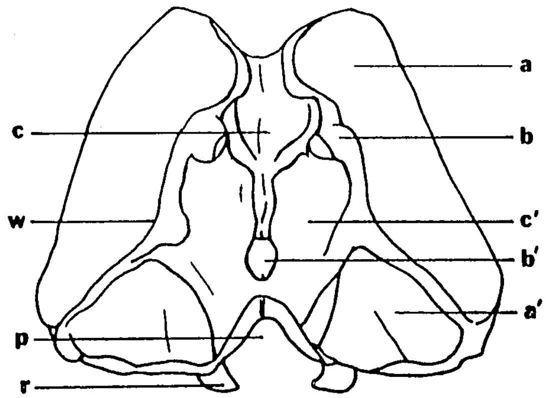
Fig. 3. Oral surface.

Fig. 4. Aboral surface.

Fig. 5. Lateral surface.

Legend for abbreviations given in Plate I.

PLATE II



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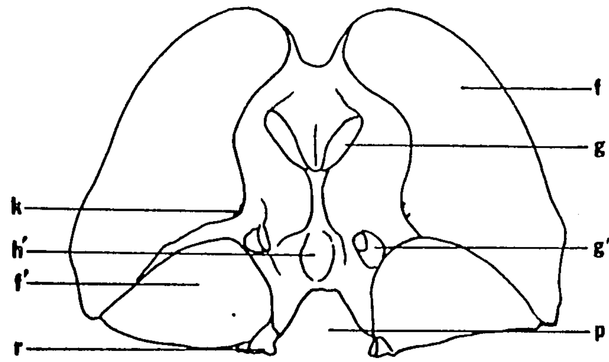

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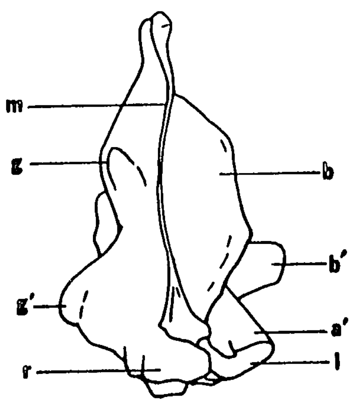

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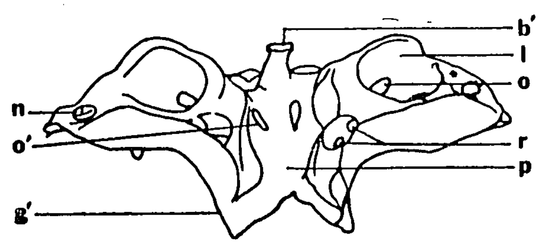

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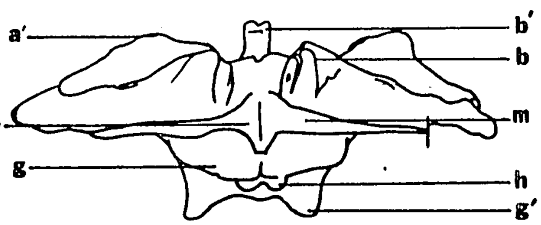


4

1 mm

PLATE III

Ophiocoma dentata. Third Arm Vertebra.

Fig. 1. Distal surface.

Fig. 2. Proximal surface.

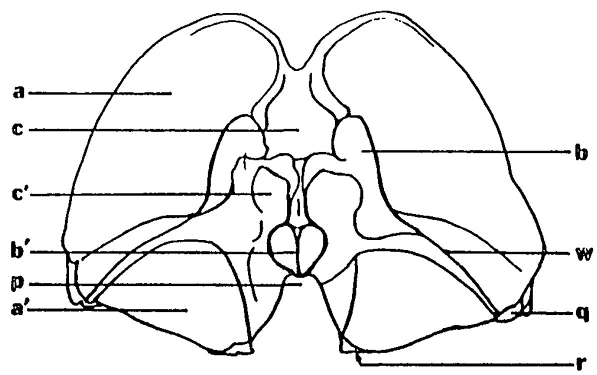
Fig. 3. Oral surface.

Fig. 4. Aboral surface.

Fig. 5. Lateral surface.

Legend for abbreviations given in Plate I.

PLATE III



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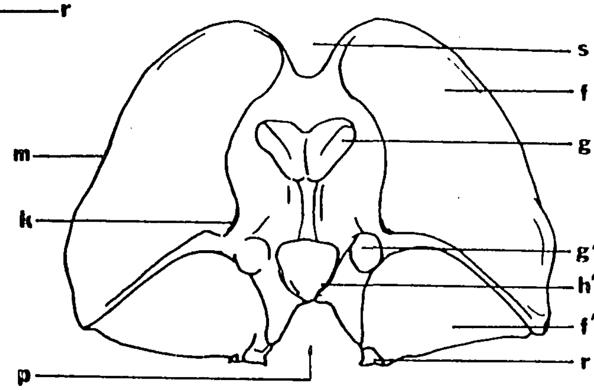

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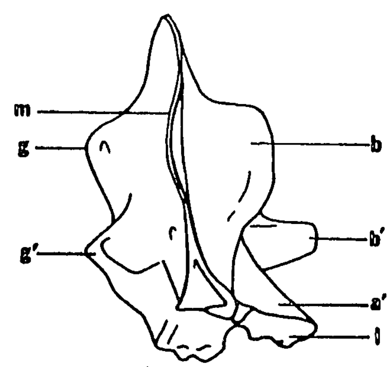

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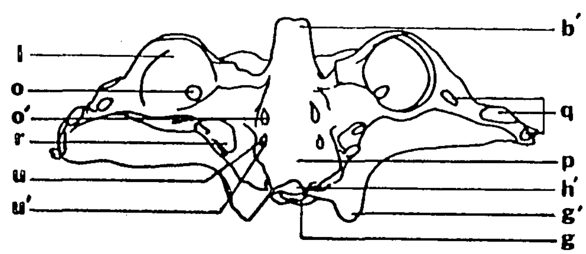

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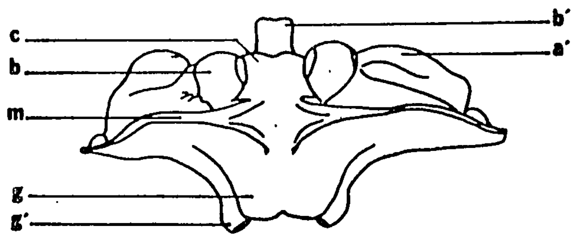

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PLATE IV

Ophiocoma dentata. Fourth Arm Vertebra.

Fig. 1. Distal surface.

Fig. 2. Proximal surface.

Fig. 3. Oral surface.

Fig. 4. Aboral surface.

Fig. 5. Lateral surface.

Legend for abbreviations given in Plate I.

PLATE IV

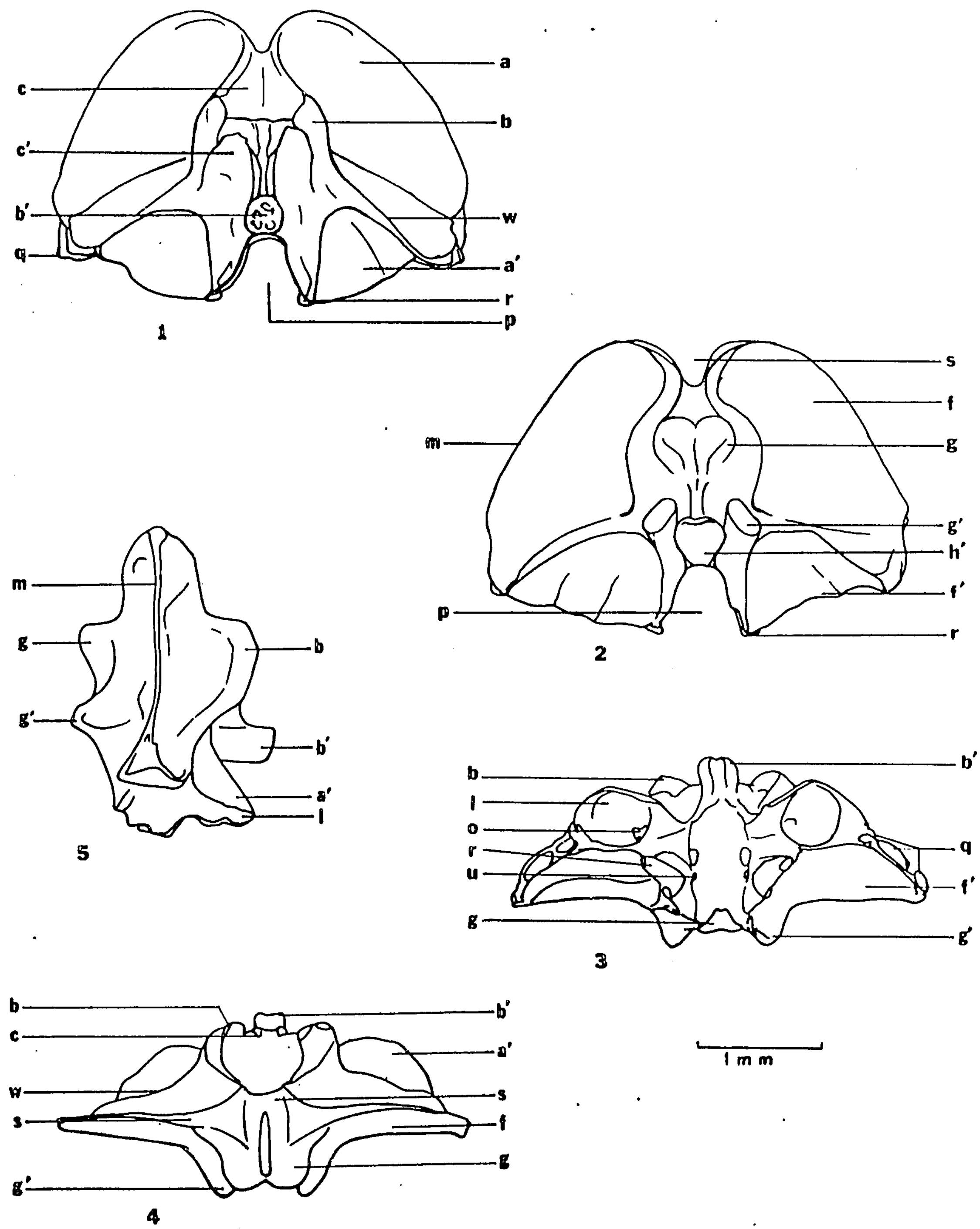

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PLATE V

Ophiocoma dentata. Fifth Arm Vertebra.

Fig. 1. Distal surface.

Fig. 2. Proximal surface.

Fig. 3. Oral surface.

Fig. 4. Aboral surface.

Fig. 5. Lateral surface.

Legend for abbreviations given in Plate I.

PLATE V

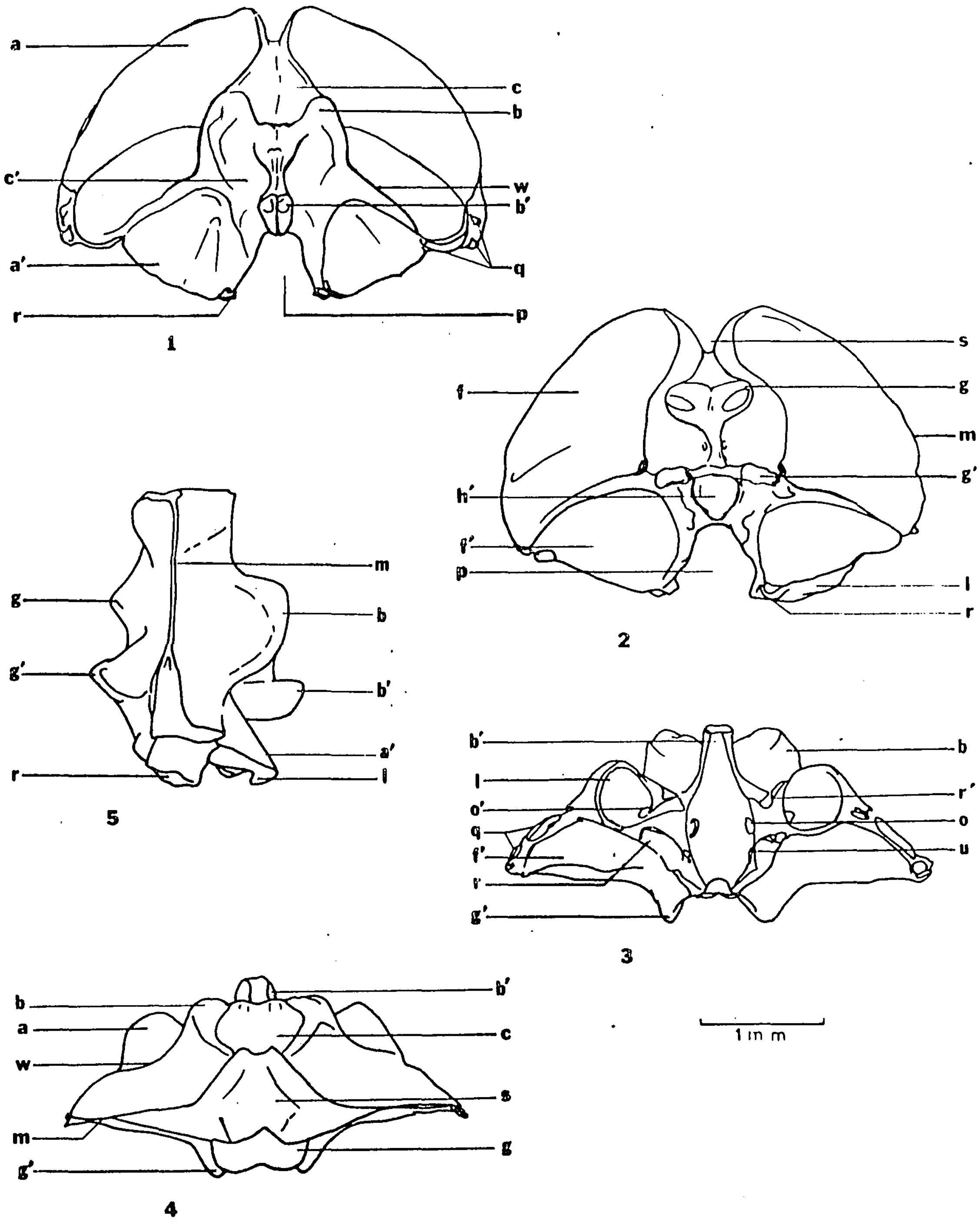
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PLATE VI

Ophiocoma dentata. Tenth Arm Vertebra.

Fig. 1. Distral surface.

Fig. 2. Proximal surface.

Fig. 3. Oral surface.

Fig. 4. Aboral surface.

Fig. 5. Lateral surface.

Legend for abbreviations given in Plate I.

PLATE VI

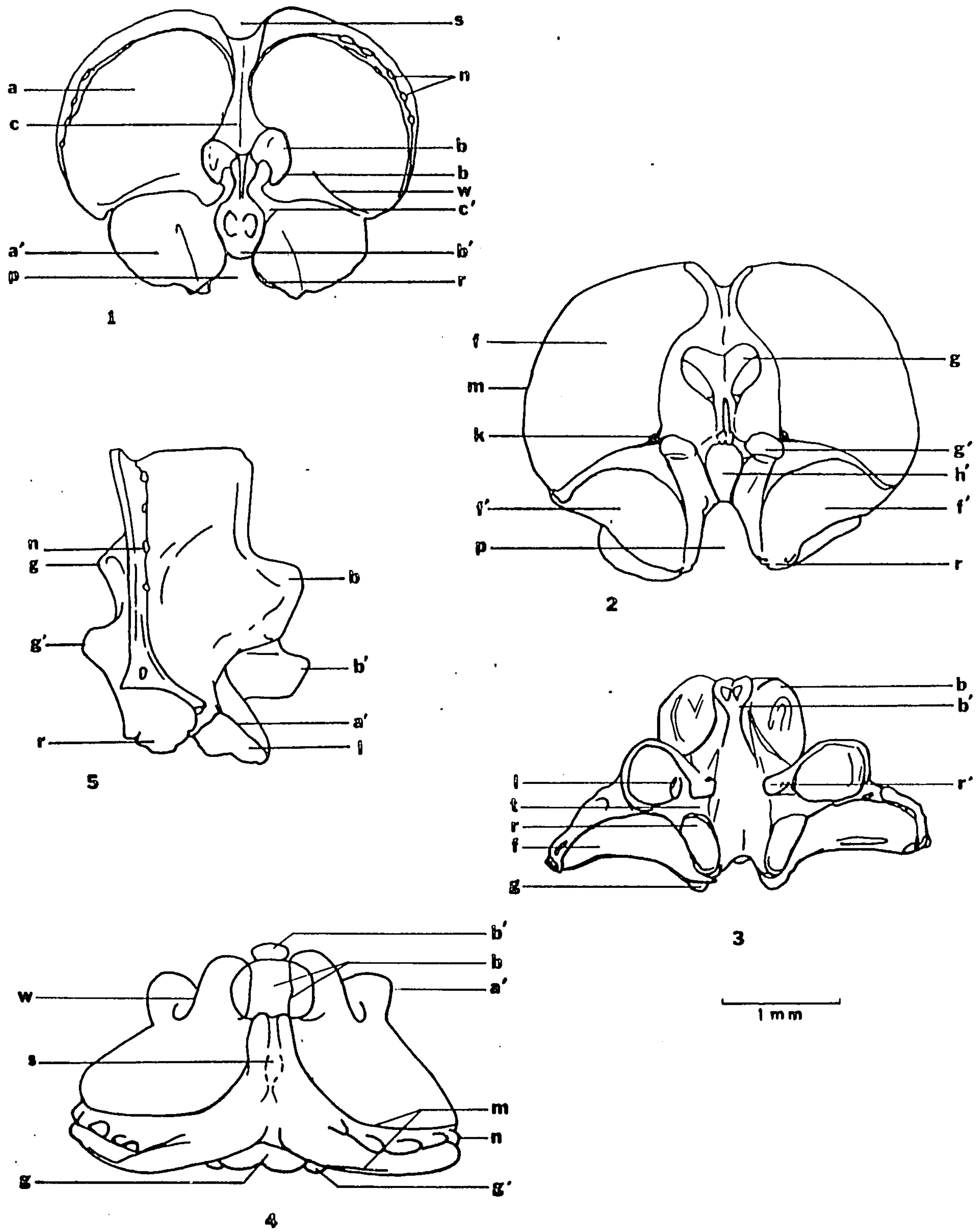

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PLATE VII

Ophiocoma brevipes.

Fig. 1. Skeletal plates: genital shield (a); genital scale (c); first arm vertebra (proximal surface) (g); oral shield (m); adoral shield (n). (Hawaiian specimen, d.d. 15 mm). X7.

Fig. 2. Aboral view, whole animal. (Hawaiian specimen, d.d. 12 mm). X0.5.

Fig. 3. Same as fig. 1 but opposite sides of same skeletal plates. X7.

Fig. 4. Tenth arm vertebra, aboral view (distal surface toward top of page). (Specimen 15.5 mm d.d.). X7.

Fig. 5. Tenth arm vertebra, aboral view (distal surface toward top of page). (Specimen 7.5 mm d.d.). X7.

Fig. 6. Dental plates, distal surface (left, from specimen 7 mm d.d.; right from specimen 15 mm d.d.). X7.

Fig. 7. Oral surface mouth region: oral shield (m). (Hawaiian specimen, d.d. 10 mm). X2.

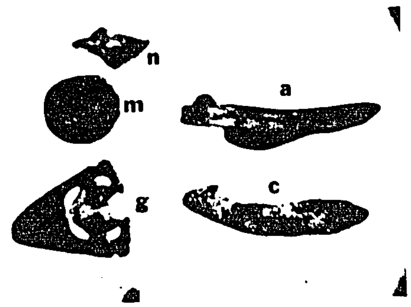
Fig. 8. First arm vertebra (right) and tenth arm vertebra (left) distal surface. (Specimen 15 mm d.d.). X7.

Fig. 9. Dental plate, proximal surface. (Specimen 15.5 mm d.d.). X13.5.

Fig. 10. First arm vertebra (right), and tenth arm vertebra (left) distal surface. (Specimen 7.5 mm d.d.). X7.

Fig. 11. Oral plates (d) adradial view (left) and abradial view (right); dental plate (b) distal surface. (Specimen 15 mm d.d.). X7.

PLATE VII



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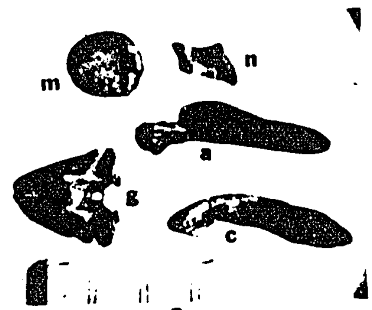

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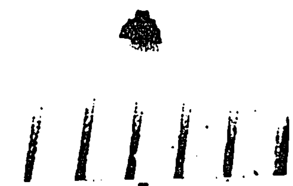

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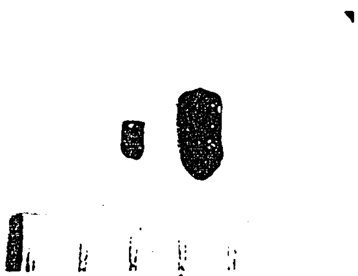

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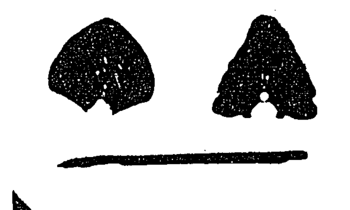

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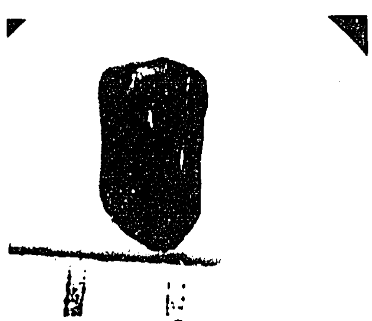

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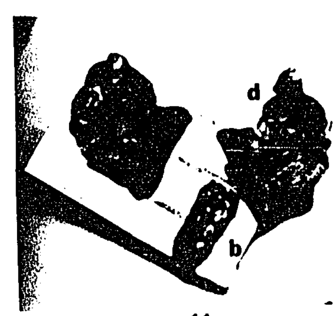

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PLATE VIII

Ophiocoma dentata and O. doederleini.

Fig. 1. Dental plate, O. doederleini (upper left, distal surface; upper right, proximal surface); O. dentata (lower left, distal surface; lower right, proximal surface). From Eniwetok specimens, d.d. 21 mm. X7.7.

Ophiocoma doederleini.

Fig. 2. Dental plate (left, proximal surface; right, distal surface). Specimen from Eniwetok, d.d. 9 mm. X7.7.

Ophiocoma dentata.

Fig. 3. Radial shields (left, from specimen 10 mm d.d.; right, specimen 21.5 mm d.d.). X9.

Fig. 4. Sixtieth arm vertebra, aboral view (distal surface above) d.d. 28 mm. X13.5.

Fig. 5. Fortieth arm vertebra (as above).

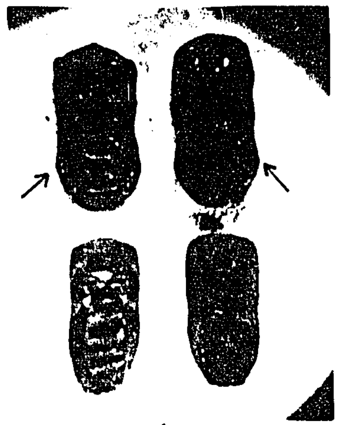
Fig. 6. Twentieth arm vertebra (as above).

Fig. 7. Arm plates from sixtieth arm segment; oral arm plate (u); lateral arm plate (l); aboral arm plate (r); vertebra (center). X4. d.d. 28 mm.

Fig. 8. Arm plates from fortieth arm segment; abbreviations as in Fig. 7, except tentacle scales (i). X4.

Fig. 9. Arm plates from twentieth arm segment; abbreviations as in Fig. 7, except tentacle scales (i). X4.

PLATE VIII



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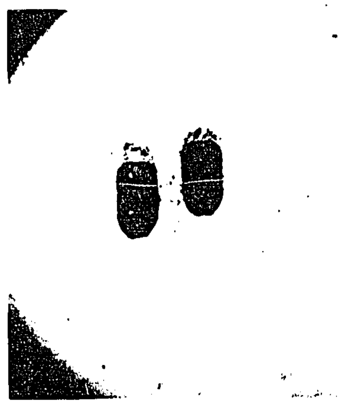

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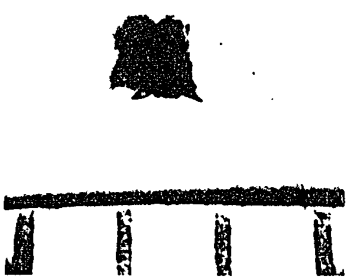

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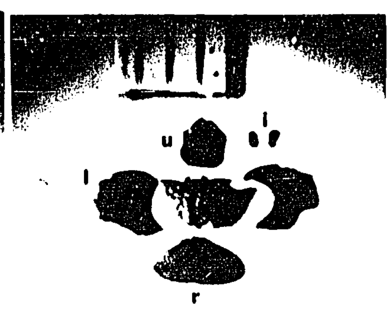

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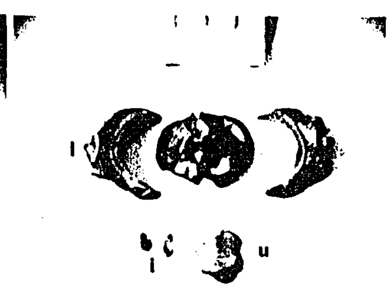

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PLATE IX

<u>Ophiocoma doederleini</u>.

Fig. 1. Aboral sector of disc. X4. (BPBM W1419b).

Fig. 2. Oral region of disc. X4. (as above).

Fig. 3. Aboral surface, entire. X1.8. (BPBM W1420).

Fig. 5. Aboral surface, nearly entire. X0.7. (BPBM W1662).

Fig. 6. Aboral surface, nearly entire enlarged. X2.4. (as above).

<u>Ophiocoma dentata</u>.

Fig. 4. Aboral surface, nearly entire. X0.6. (BPBM W1512).

Fig. 7. Aboral surface, nearly entire. X0.8. (USNM E7450).

Fig. 8. Oral surface, nearly entire. X0.8. (as above).

Fig. 9. Aboral surface, nearly entire. X0.5. (USNM E7450 another specimen).

PLATE IX


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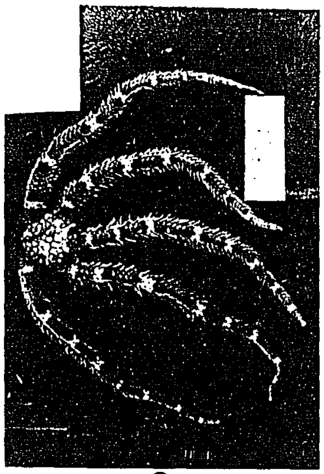
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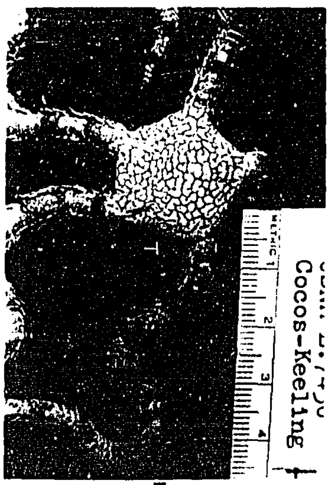

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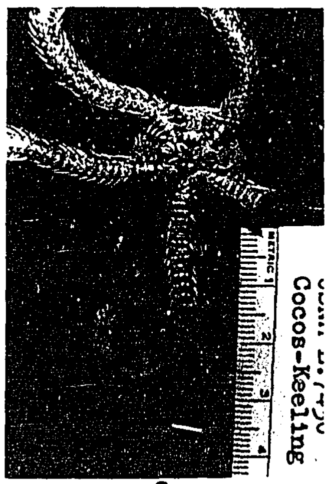

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PLATE X

Ophiocoma doederleini.

Fig. 1. Aboral view, entire specimen. X1. (BPBM W1509, d.d. 9 mm).

Fig. 2. Oral view, entire specimen. X1. (as above).

Fig. 5. Arm spines attached to lateral arm plate, tenth arm segment (upper arm spine to left). X8.3.

Fig. 7. Tenth arm segment, with arm spines attached on both sides, distal view. (upper spines above). X2.6.

Ophiocoma dentata.

Fig. 3. Arm spines attached to lateral arm plate, tenth arm segment (upper arm spine to left). X8.3.

Fig. 6. Tenth arm segment, with arm spines attached on both sides, distal view (upper spines above). X2.6.

Ophiocoma doederleini and O. dentata.

Fig. 4. Arm spines from one-half of arm attached to lateral arm plates (upper arm spine above); O. doederleini on right, O. dentata on left. X3.6.

PLATE X

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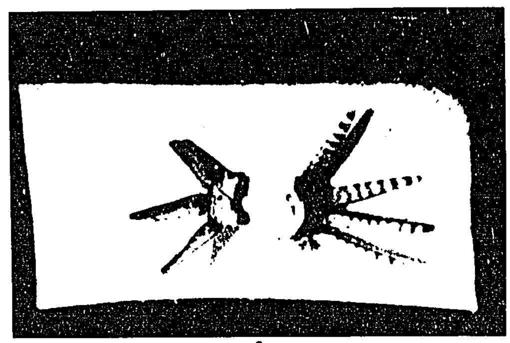

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PLATE XI

Ophiocoma anaglyptica.

Fig. 1. Skeletal plates: Genital plate (a); Dental plate (b), proximal surface; genital scale (c); radial shield (e); oral shield (m); upper arm spines (s). (BPBM W562a, d.d. 11 mm). X8.5.

Fig. 3. Tenth arm segment, with arm spines on both sides, showing alternation of spines (3/4) and very much enlarged upper spine. (same as specimen as fig. 1.). X6.

Fig. 5. Oral plate, abradial surface (d); first arm vertebra, proximal surface (g). (same specimen as above). X8.

Fig. 6. Oral plate, adradial surface (d); first arm vertebra, distal surface (g). (same as above). X8.

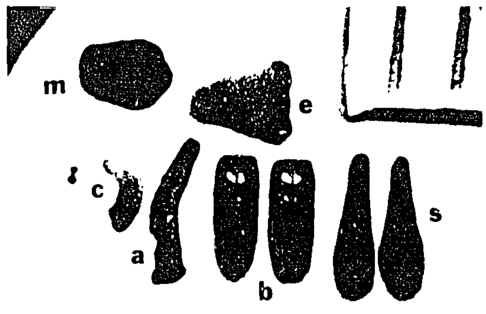
Fig. 7. Aboral arm plates, showing truncation of lateral border(s). X12.

Ophiocoma macroplaca.

Fig. 2. Skeletal plates: Genital plate (a); dental plate (distal surface, left, proximal surface, right) (b); genital scale (c); radial shield (e); adoral shield (n). X8.

Fig. 4. Oral plates (adradial surface, left, abradial surface, right). X8.

PLATE XI



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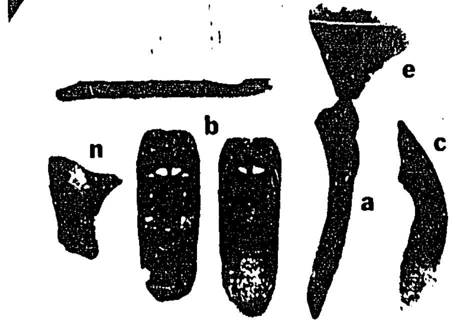

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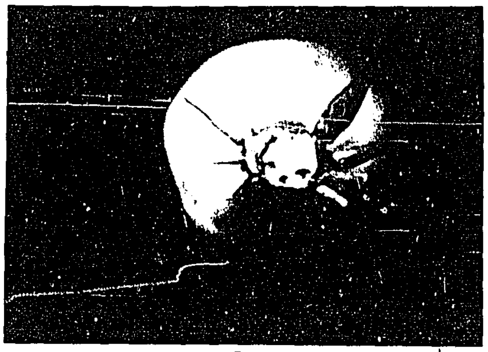

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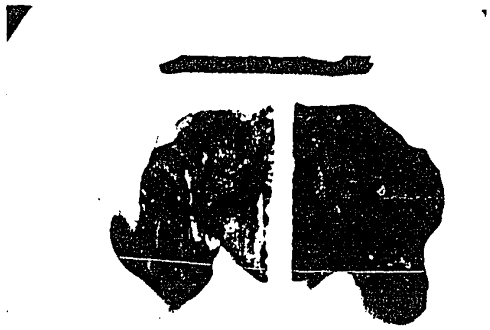

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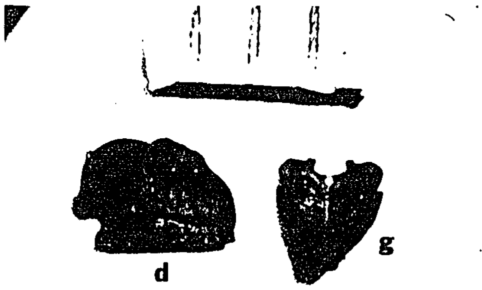

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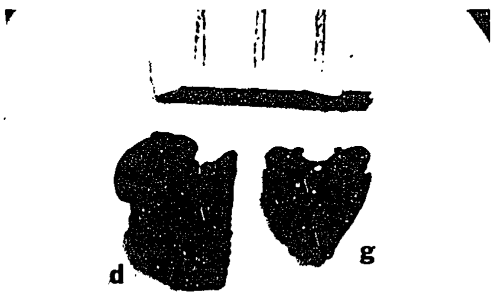

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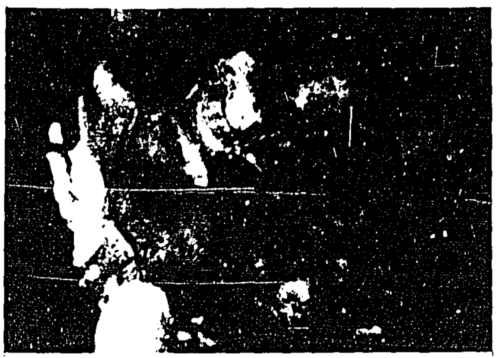

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PLATE XII

Ophiocoma wendtii.

Fig. 1. Portion of arm, aboral view. Xo.8. (type specimen, Berlin Zool. Mus. No. 929).

Fig. 3. Portions of three arms, aboral view. X1.2. (BPBM W1636a).

Fig. 5. Portion of disc and arms, aboral surface, X0.8. (Type specimen, same as Fig. 1).

Fig. 7. Oral view of disc and part of arms. X0.8 (same as Fig. 1).

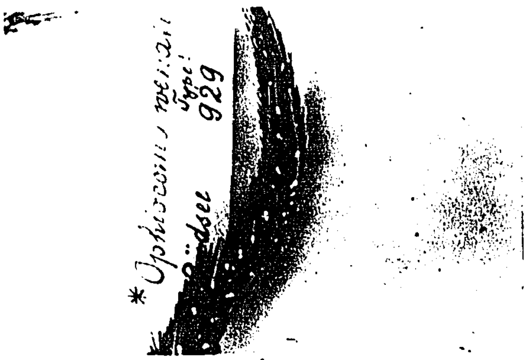
Ophiocoma erinaceus.

Fig. 2. Internal view, teeth (t) and tooth papillae (p), one sector of jaw. X7.2. (Hawaiian specimen, d.d. 21 mm).

Fig. 4. Internal view, three sectors of jaw, teeth (t), dental papillae (p), attached to dental plate (b). X6. (Hawaiian specimen, d.d. 28 mm).

Fig. 6. Oral view of mouth region, oral shield (m), adoral shield (n), and outer oral papilla (o). X6.7. (same specimen as Fig. 4).

PLATE XII



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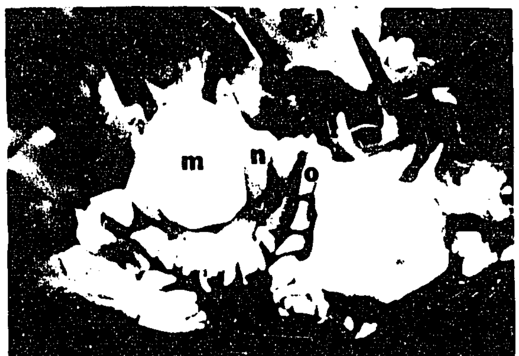

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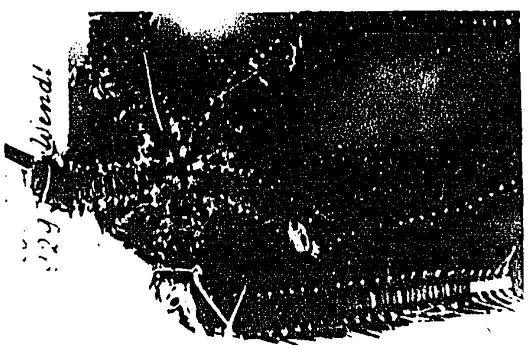

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PLATE XIII

Ophiocoma erinaceus.

Fig. 1. Tenth arm segment, with arm spines attached on both sides, distal view (upper spines to right). X6.

Fig. 2. Aboral arm plates, showing truncation of lateral borders. X6.

Fig. 3. Aboral view, tenth arm segment. X4.

Fig. 4. Arm plates from segment 15, specimen 1.5 mm in disc diameter. X33; oral arm plate (j), aboral arm plate (k), arm vertebra (g), and tentacle scale (r).

Fig. 5. Aboral view, specimen 3 mm d.d.. X4.

Fig. 6. Arm plates from segment 15, specimen 1.5 mm d.d.; X66. (abbreviations as in Fig. 4).

Fig. 7. Tenth arm vertebra, aboral view (distal surface below) from specimen with d.d. 21.5 mm. (distance between lines = 1 mm). X7.

Fig. 8. Seventy-fifth arm vertebra, aboral view (distal surface below) from same specimens as in Fig. 7. X7.

Fig. 9. Tenth arm vertebra, aboral view (distal surface below) from specimen with d.d. 8 mm. (distance between lines = 1 mm). X7.

PLATE XIII

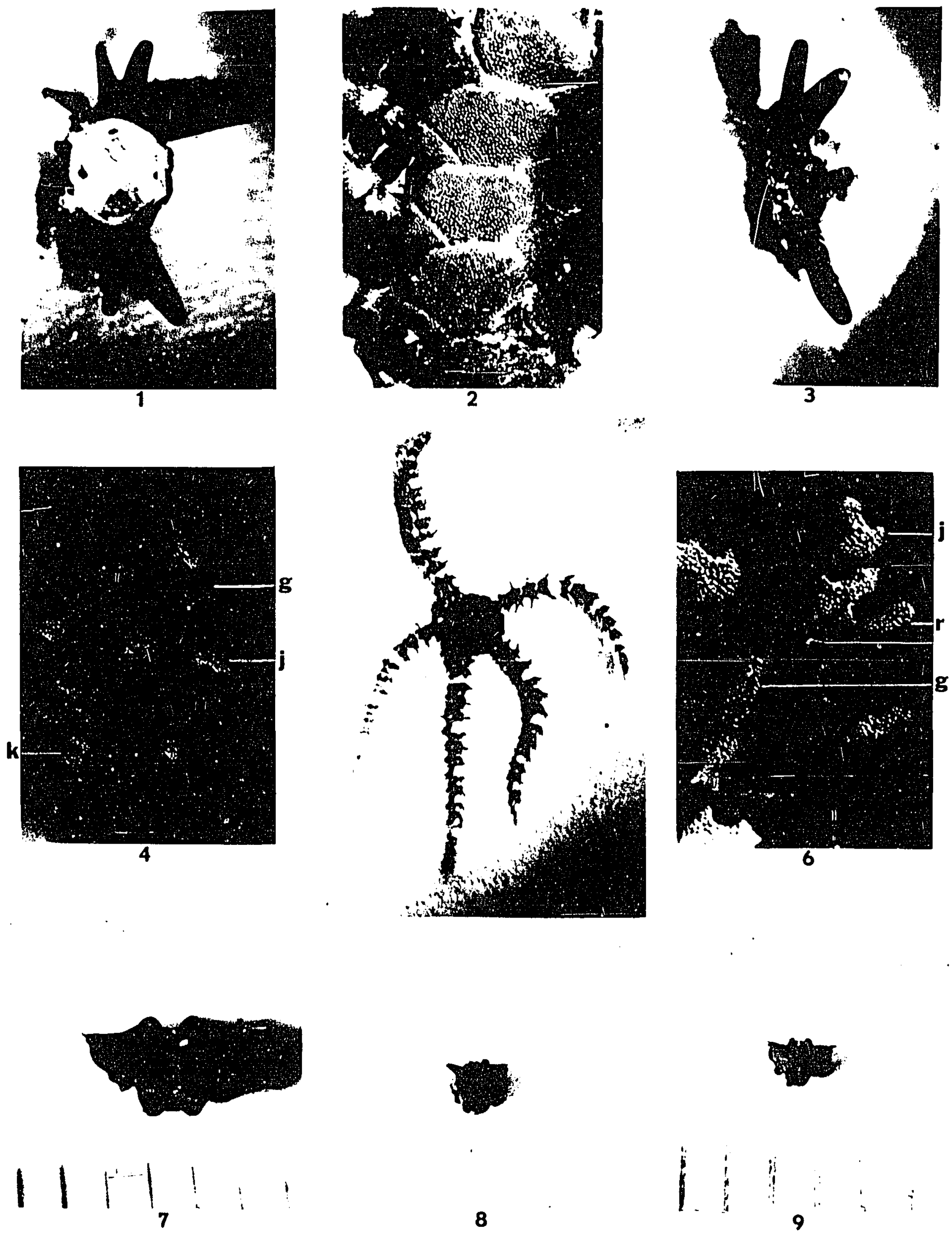

PLATE XIV

Ophiocoma canaliculata.

Fig. 1. Skeletal plates: genital plates (a); genital scales (c); dental plate (proximal surface) (b); oral plate (abradial to left, adradial to right) (d); radial shield (oral surface) (e). (MCZ: No. 3462, d.d. 18 mm). X4.5.

Fig. 2. Skeletal plates: as above, except only abradial surface of oral shield (d) shown. (MCZ: No. 3462, d.d. 6 mm). X8.5.

Fig. 6. First arm vertebra (g), proximal surface on right, distal surface on left. (MCZ: No. 3462, d.d. 6 mm). X13.5.

Fig. 7. First arm vertebra (h), proximal surface; second arm vertebra (g), distal surface. (MCZ: No. 3462, d.d. 18 mm). X8.5.

Fig. 8. First arm vertebra (g), distal surface; second arm vertebra (h), proximal surface. (same as Fig. 7).

Ophiocoma bollonsi.

Fig. 3. Oral plate (d), abradial surface; dental plate (b), distal surface. (BPBM W1611, d.d. 11 mm). X18.

Fig. 4. Skeletal plates: oral plate (d), as in Fig. 3; dental plate (b), as in Fig. 3; genital plate (a); adoral shield (n). (same specimen as Fig. 3). X9.

Fig. 5. Same as Fig. 3, except adoral surface of oral plate (d); and proximal surface of dental plate (b). X15.

PLATE XIV

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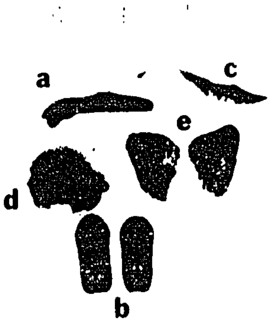

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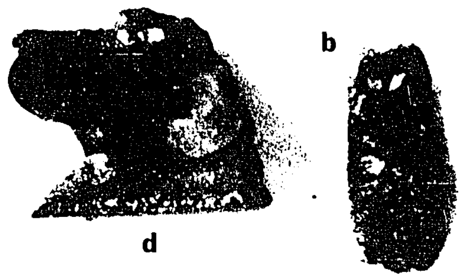

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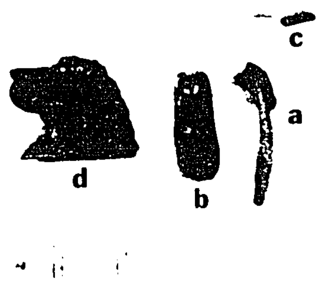

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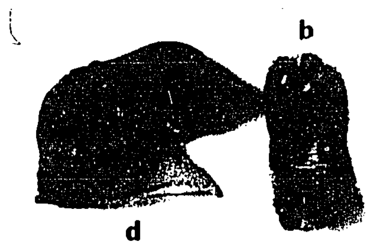

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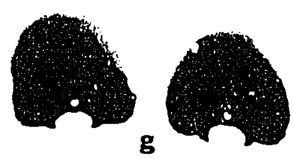

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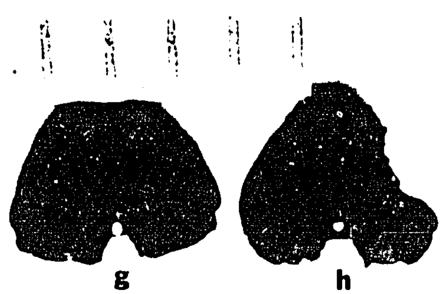

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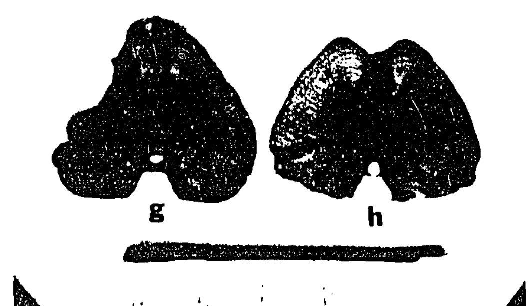

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PLATE XV

Ophiocoma pica.

Fig. 1. First arm vertebra, lateral aspect (distal side to left). (Hawaiian specimen, d.d. 18 mm). X13.5.

Fig. 2. Same, distal surface.

Fig. 3. Same, proximal surface.

Fig. 4. First arm vertebra, distal surface. (Hawaiian specimen, d.d. 10.5 mm). X13.5.

Fig. 5. Same as Fig. 4, proximal surface.

Fig. 6. First arm vertebra, distal surface. (Hawaiian specimen, d.d. 4.5 mm). X13.5.

Fig. 7. Same as Fig. 6, proximal surface.

Fig. 8. First arm vertebra, distal surface. (Hawaiian specimen, d.d. 2.0 mm). X13.5.

Fig. 9. Same as Fig. 8, proximal surface.

Fig. 10. Same as Fig. 8, but enlarged. X48.

Fig. 11. Same as Fig. 9, but enlarged. X48.

PLATE XV

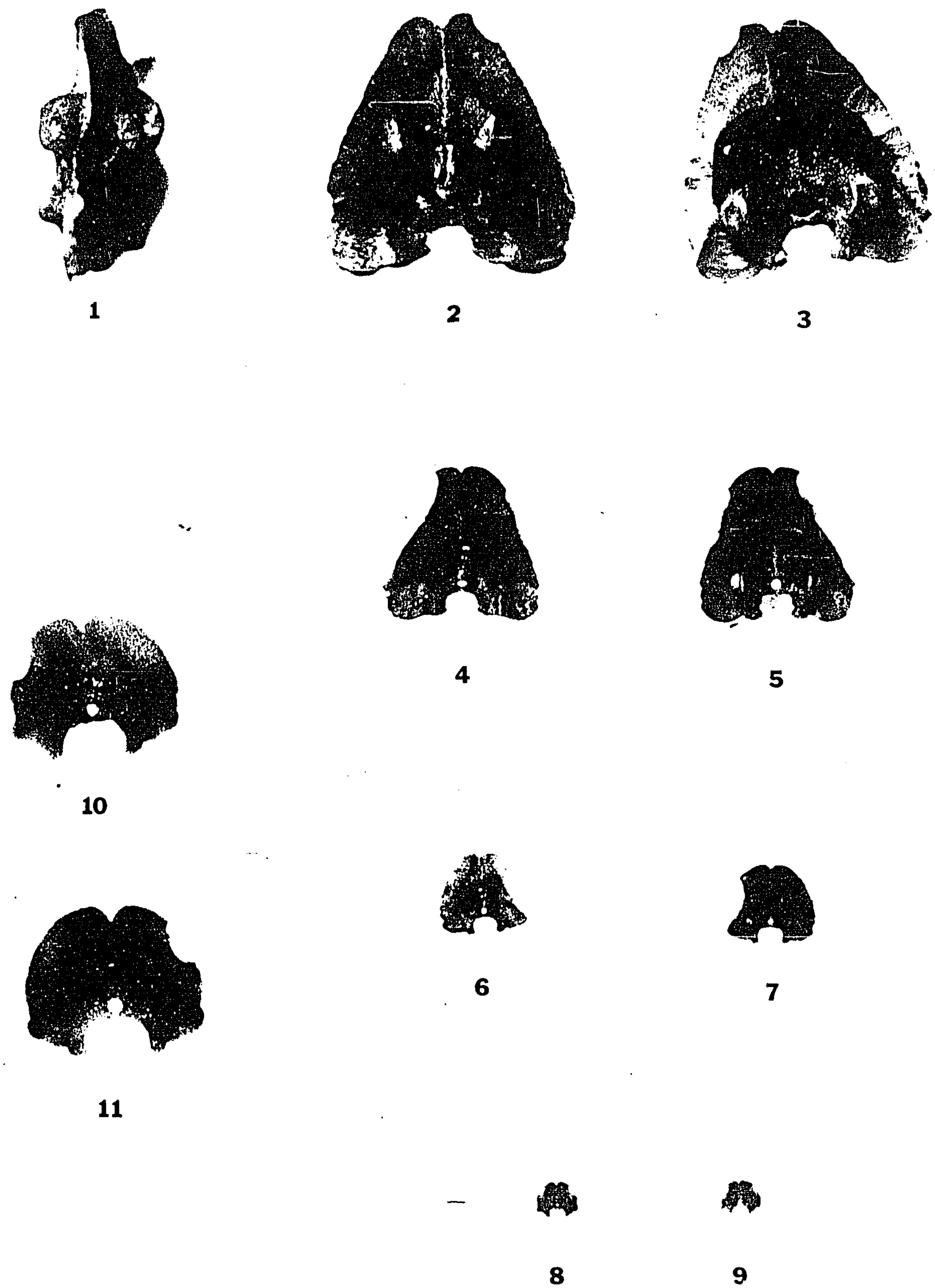

PLATE XVI

Ophiocoma pica.

Fig. 1. Dental plates from specimens between 15 and 23 mm (d.d.); distal view. X11.

Fig. 2. Same, from specimens between 8 and 14 mm (d.d.). X11.

Fig. 3. Same, from specimens between 2 and 7 mm (d.d.). X11.

Fig. 4. Same as Fig. 1; proximal view. X11.

Fig. 5. Same as Fig. 2; proximal view. X11.

Fig. 6. Same as Fig. 3; proximal view. X11.

Fig. 7. Internal view, three sectors of jaw, teeth (t), dental papillae to left; Hawaiian specimen, d.d. 21 mm. X6.

Fig. 8. Aboral view, entire specimen. X0.5.

Fig. 9. Oral view of mouth region, oral shield (m), adoral shield (n). X7.

Fig.10. Oral view, entire specimen; (same as Fig. 8). X0.5.

PLATE XVI

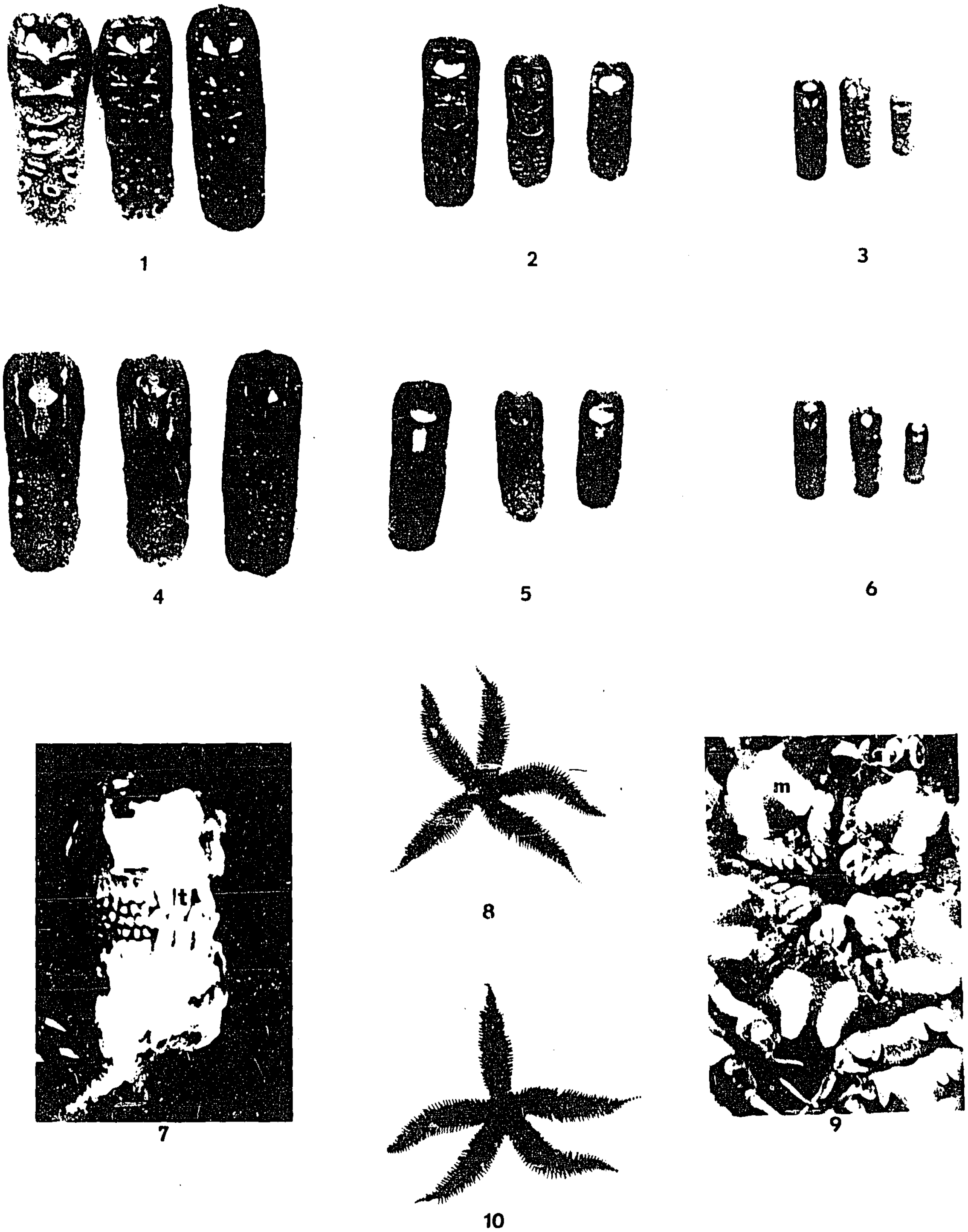

PLATE XVII

Ophiocoma sexradia.

Fig. 1. Oral shield (d), abradial surface. X4.2

Fig. 2. Same, adradial surface. X4.2.

Fig. 3. Genital plate (a), and scale (c). X4.2.

Fig. 4. Radial shields (e). X4.2.

Fig. 5. Genital plate (a), dental plate (b), and radial shield (e). X3.

Fig. 6. Same as Fig. 3. X4.2.

Fig. 7. Same as Fig. 4. X4.2.

Fig. 8. Aboral view, disc and arms, showing three smaller and three larger arms, indicative of fissiparous reproduction. X5.

Fig. 9. Same, oral view. X3.5.

PLATE XVII

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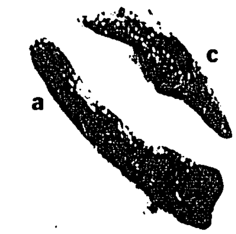

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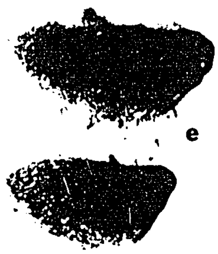

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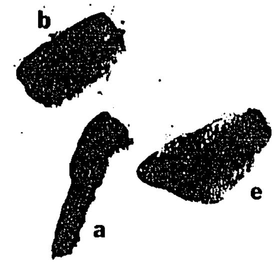

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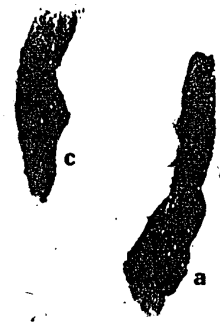

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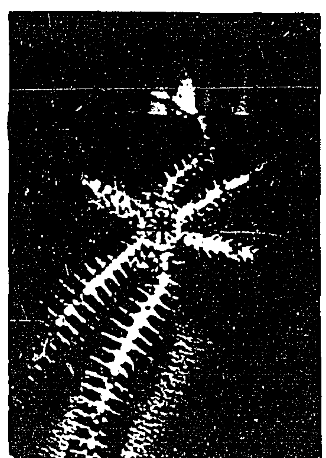

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PLATE XVIII

Ophiomastix venosa.

Fig. 1. Oral plate, abradial surface (BPBM W1586, d.d. 20 mm). X3.7.

Fig. 2. Skeletal plates: genital plate (a); genital scale (c); dental plate (b) (distal surface); radial shield (e). (same specimen as above). X4.

Fig. 3. Oral plate, adradial surface (same specimen as above). X3.7.

Fig. 4. Skeletal plates, same as Fig. 2, except proximal surface of dental plate (b). X4.

Ophiocoma macroplaca.

Fig. 5. Dental plate, distal surface. X11.

Ophiarthrum elegans.

Fig. 6. Oral plates, adradial surface (above), abradial surface (below). (BPBM W1465, d.d. 16 mm). X8.

Fig. 7. Skeletal plates: genital plate (a); genital scale (c); dental plate (b) proximal side; radial shield (e); oral shield (m); adoral shield (n); arm spines (x); tooth (t). (same specimen as Fig. 6). X8.

Fig. 9. First arm vertebrae, proximal surface (left); distal surface (right). (same specimen as Fig. 6). X8.

Ophiomastix annulosa.

Fig. 8. Tenth arm segment, showing arm spines, especially enlarged claviform upper arm spine (s). (BPBM W681, d.d. 18.5 mm). X4.

Fig. 10. Claviform arm spines, note variation in shape. (from different segments, same specimen as Fig. 8). X4.

PLATE XVIII

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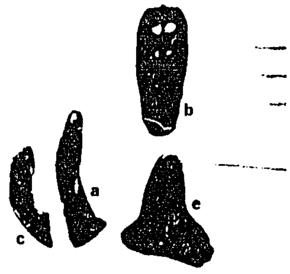

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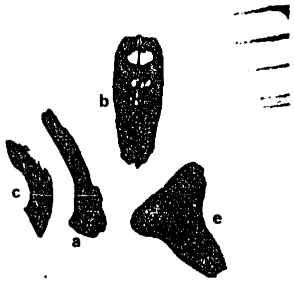

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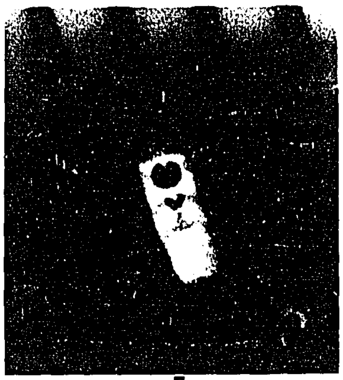

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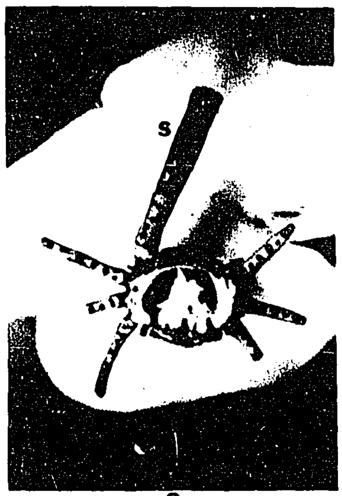

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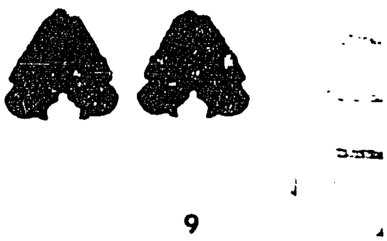

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PLATE XIX

Ophiopteris papillosa.

Fig. 1. Oral view, part of mouth region; oral shield (m), adoral shield (n). X12. d.d. 12 mm. (BPBM W1654).

Fig. 2. Aboral view, portion of disc and arm, showing scale-like upper arm spine. X3.3. (same specimen as Fig. 1).

Fig. 3. Skeletal plates: genital shield (a); adoral shield (n); ventral shield (q). X7.5. (BPBM W1655a, d.d. 12 mm).

Fig. 4. Oral plate (e), abradial surface; first arm vertebra (f), distal surface. X7. (same specimen as Fig. 3).

Ophiocoma canaliculata.

Fig. 5. *O. canaliculata* var. *pulchra*. Portion of arm. X1.5. (MCZ: No. 5237, d.d. 16 mm).

Fig. 7. Skeletal plates: three teeth (t); three arm spines (s); oral arm plate (u), (MCZ: No. 3462, d.d. 18 mm). X7.

Fig. 8. Dental plates, distal surface; same as Fig. 7.

Fig. 9. Aboral view of part of disc and arms. (MCZ: No. 5218, d.d. 16 mm). X2.

Ophiocoma pusilla.

Fig. 6. Skeletal plates: dental plate (distal surface) (b); first arm vertebra (proximal surface) (g); tooth (t). (BPBM W1585, d.d. 7.5 mm).

PLATE XIX

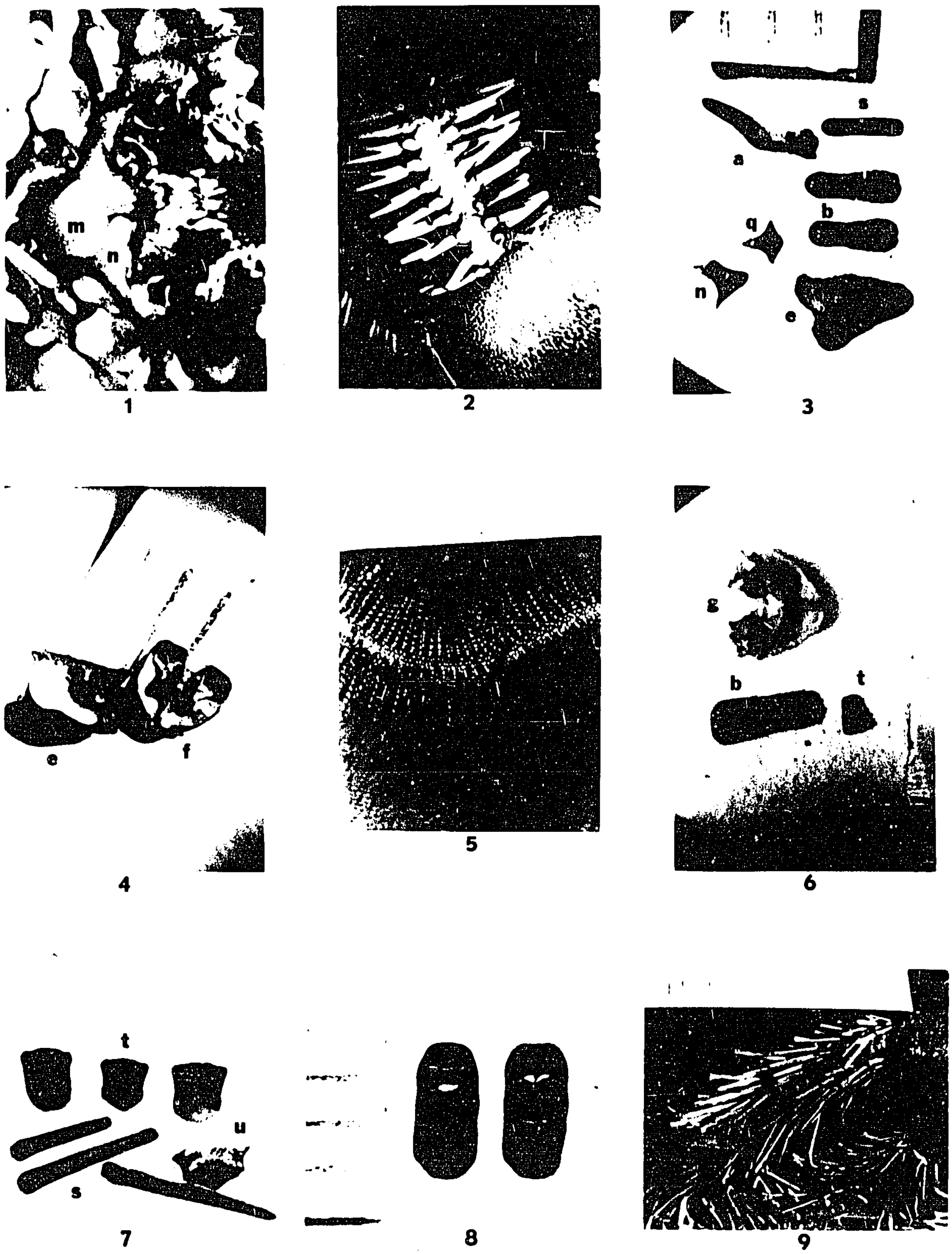


PLATE XX

<u>Ophiocominae, Larval Skeleton and Egg</u>.

Fig. 1. Larval skeleton, *Ophiocoma scolopendrina* (after Mortensen, 1937, Fig. 40) X250.

Fig. 2. Larval skeleton, *Ophiocoma pica* (after Mortensen, 1937, Fig. 41) X300.

Fig. 3. Larval skeleton, *Ophiocoma erinaceus* (after Mortensen, 1937, Fig. 37) X250.

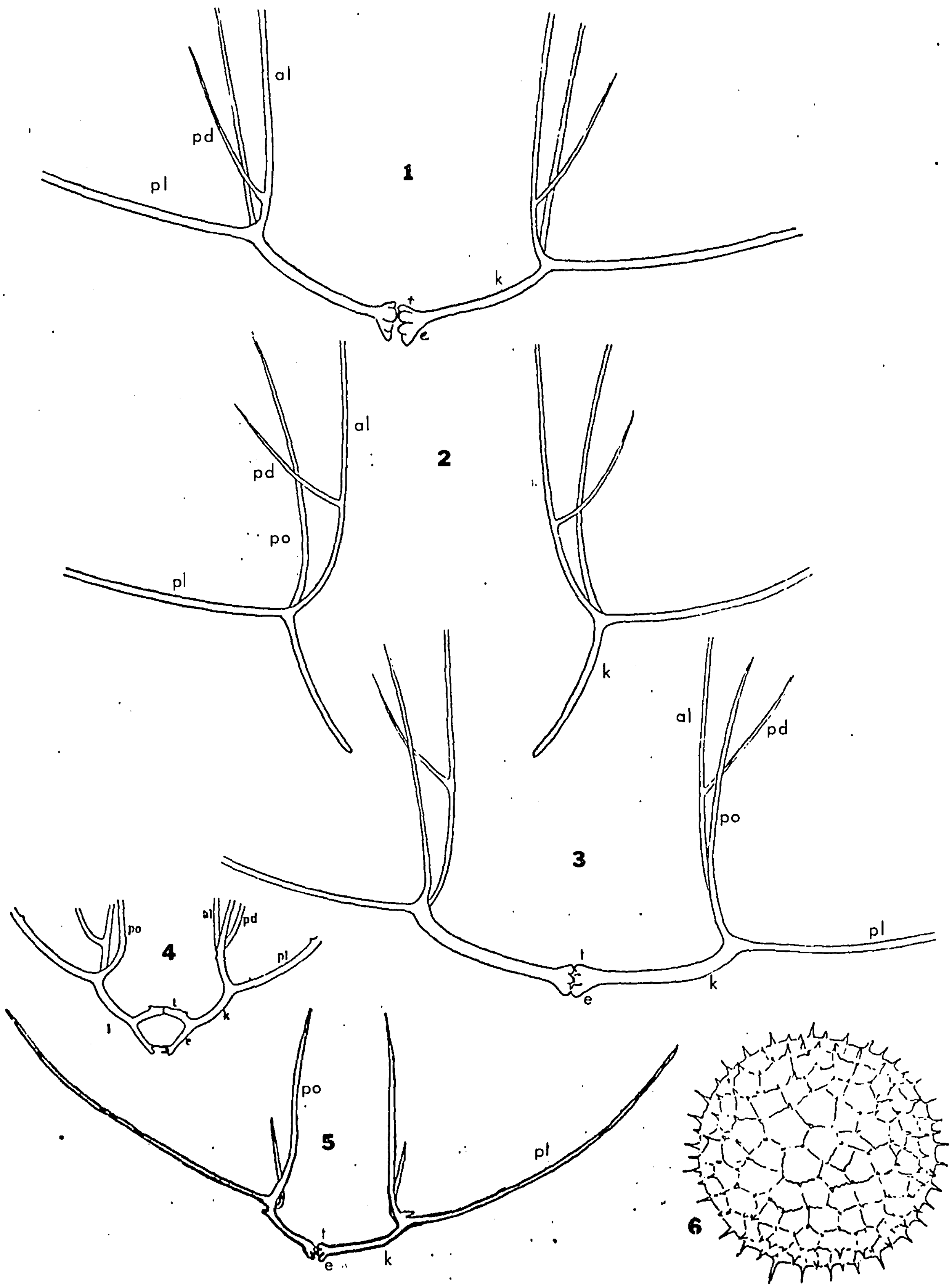
Fig. 4. Larval skeleton, *Ophiocomina nigra* (after Mortensen, 1927, Fig. 87) X145.

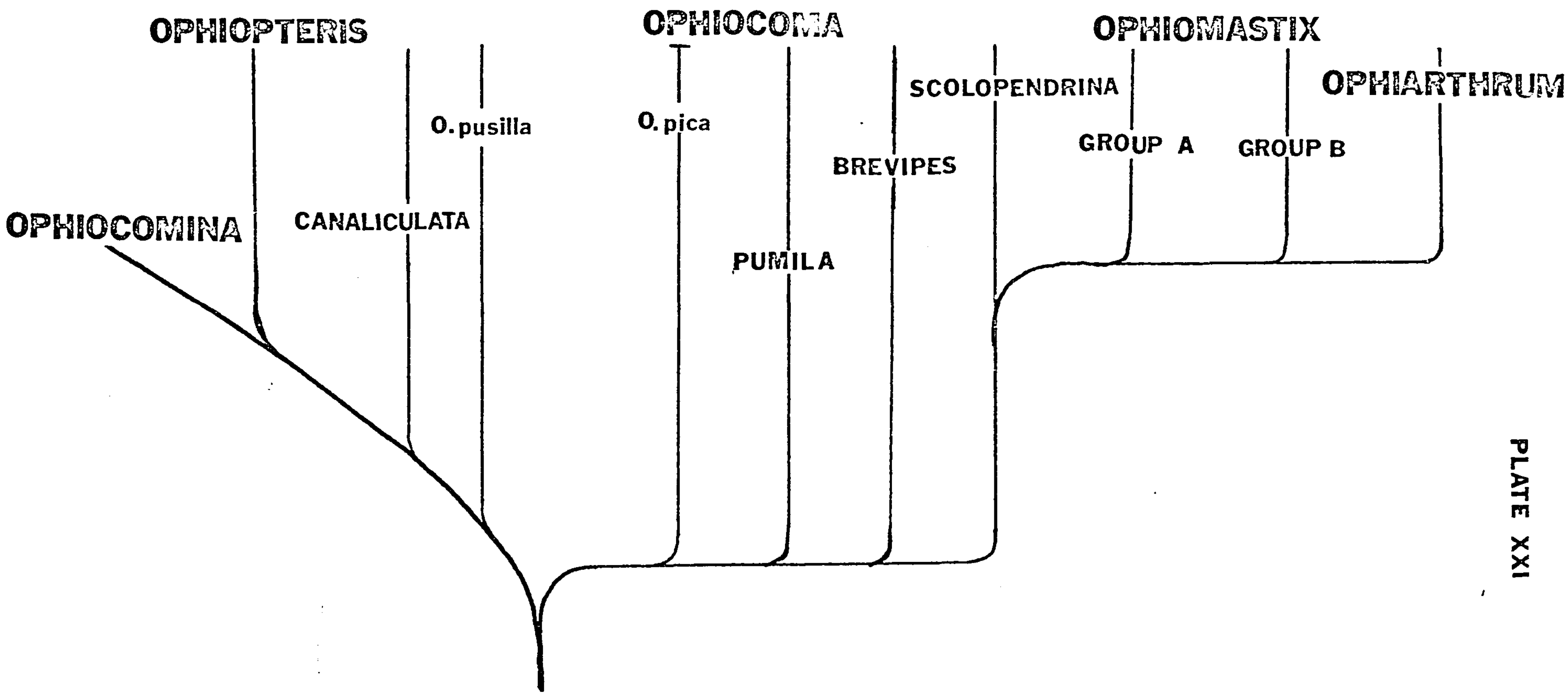
Fig. 5. Larval skeleton, *Ophiocoma echinata* (after Mortensen, 1921, Fig. 57) X250.

Fig. 6. Fertilized egg, *Ophiocoma scolopendrina* (after Mortensen, 1937, Fig. 38) X540.

List of abbreviations: al, anterior-lateral skeletal rod; e, end skeleton rod; t, transverse skeletal rod; k, body, skeletal rod; pd, posterior-dorsal skeletal rod; pl, posterior lateral skeletal rod; po, posterior oral skeletal rod.

PLATE XX





INFERRED RELATIONSHIPS in OPHIOCOMINAE

PLATE XXI