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An Ectocommensal Polynoid Associated with
Indo-Pacific Echinoderms, Primarily Ophiuroids¹

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INTRODUCTION

Collection and observation of ophiuroids in the shallow waters of the Hawaiian Islands reveal the presence of a polynoid worm most often associated with three species of brittlestars in the family Ophiocomidae. The polynoid, identified as *Hololepidella nigropunctata* (Horst), represents a new faunal record for Hawaii.

The first part of this paper considers the systematic position of the polynoid, including its redescription, as well as specific and generic relationships. Additional sections are concerned with ecological, behavioral, and zoogeographical aspects of the commensal association. Finally, a review of other reported polynoid-ophiuroid associations is presented.

The occurrence of a polynoid living on an ophiuroid from Hawaii has been known for over 30 years (Edmondson, 1933).² In a revision of this earlier work the author stated: "Associated with the brittle star *Ophiocoma insularia* is a species [of polynoid] about 1 inch long with scales of uniform dark brown color" (1946, p. 106). Evidence presented in the following pages indicates that the polynoid referred to above is undoubtedly *H. nigropunctata*.

Recently, another reference to a Hawaiian polynoid-ophiuroid association has been cited by Hartman (1966) where an undetermined species is described as close to the genus *Acanthiclepis*. The relationship between *Acanthiclepis* and *Hololepidella* is discussed later in the present paper (p. 294).

¹ Contribution No. 271, Hawaii Institute of Marine Biology, University of Hawaii.

² Dates in parentheses refer to Literature Cited, p. 303.

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My sincere thanks are to Dr. Marian H. Pettibone of the Smithsonian Institution and to Dr. Olga Hartman of the Allan Hancock Foundation for their generous help in suggesting references and supplying materials which have helped to complete this work. I also wish to thank Mr. Marshall Youngbluth who assisted in collecting material for this study, and Gail Devaney for the illustrations presented in this paper.

Specimens of *Hololepidella nigropunctata* reported herein from Hawaii, Johnston Island, and Eniwetok have been deposited in Bernice P. Bishop Museum. Six specimens have been sent to the Smithsonian Institution, and several specimens are available in the collections of the Department of Zoology, University of Hawaii.

SYSTEMATICS³

PHYLUM ANNELIDA
CLASS POLYCHAETA
SUPERFAMILY APHRODITOIDES
FAMILY POLYNOIDAE
SUBFAMILY HARMOTHOINAE

Hololepidella nigropunctata (Horst).

Polynoe nigropunctata Horst, 1915, 20; 1917, 104, pl. 21, figs. 15-17.

Hololepidella nigropunctata (Horst): Day, 1957, 65, fig. 1, a-f.

Hololepidella nigropunctata (Potts) [error for Horst]: Macnae and Kalk, 1962, 118.

Near *Acanthicolepis* sp. Hartman, 1966, 174.

Size. Length, 4-18 mm.; width, excluding setae, 0.7-2.1 mm., including setae, 1.7-4.8 mm. Body widest in segments 11-21, tapering rapidly posteriorly, less anteriorly (Fig. 4, a). Minimum number of segments, 26 (specimen 4.2 mm. in length); maximum number, 53 (specimen 15.8 mm. in length).

Body pigmentation. Dorsum colorless, tan, very dark brown, or reddish. On dark specimens dorsum marked with central inverted triangle of dark color, each segment being divided by lighter transverse line into narrower anterior and wider posterior areas, terminating laterally near or on elyrophores or dorsal tubercles (Figs. 1, a; 4, c). Dorsal tubercles, ceratophores, and basal portions of dorsal cirri often with shades of dark color; base of ventral cirri to edge of

³ The terminology used in this paper to describe the morphology of the polynoid is based on Pettibone (1953, pp. 6-13).

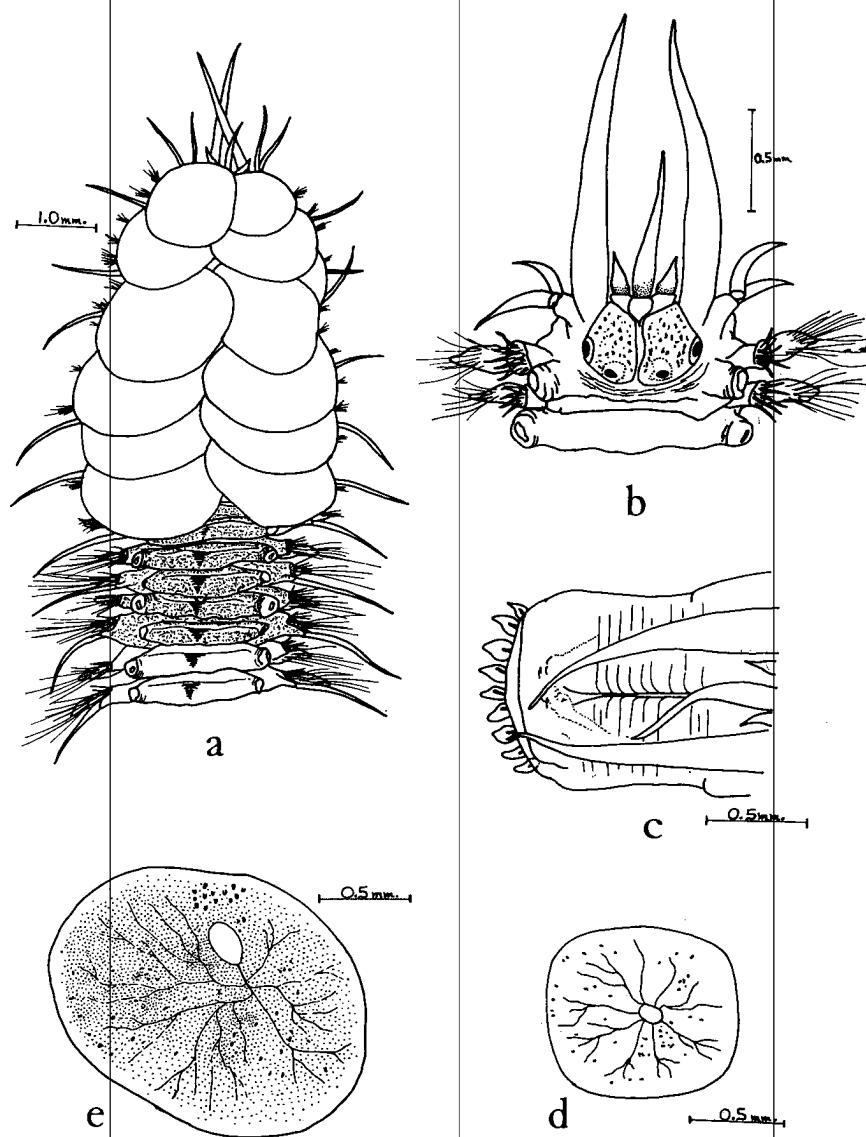


FIGURE 1.—*Hololepidella nigropunctata*: a, dorsal view of anterior region; b, prostomium and appendages; c, prostomium with proboscis everted; d, regenerating elytron; e, elytron from middle of body.

parapodium frequently the same. Pigment occurring as irregular spots or splotches; regenerating segments lacking pigmentation; occasionally very light specimens lacking dark pigmentation. Venter always lighter than dorsum; in most specimens, a noticeably lighter central longitudinal area (Fig. 4, *b*).

Elytra (Fig. 1, *d, e*) covering entire dorsum, moderately imbricated, easily detached. Subreniform in shape except for first pair, or those regenerating, which are circular (Fig. 1, *d*). Surface slick and smooth, except for characteristic small group of microtubercles at anterior curve adjacent to scar (Fig. 1, *e*); microtubercles often lacking in regenerating elytra; small channels radiating from one or more stems which leave scar. Elytra showing various degrees of pigmentation: where dorsum of body dark, elytra dark brownish red to tan; elytra light when dorsum lacks pigment; margin of pigmented elytra often lacking color (Fig. 1, *e*). Elytra on segments 2, 4, 5, 7, 9, . . . 23, 26, 29, 31, 34, 36, and then quite regularly on alternate segments to end; number of elytra depending on number of segments in given specimen. Maximum observed, 24 pairs, minimum 12 pairs.

Prostomium (Fig. 1, *b, c*): Prostomial lobes wider than long, with slight or moderate anterior peaks. Two pairs of eyes: anterior pair at lateral border in region of greatest width; posterior pair smaller, lying near medial border; both pairs usually visible from dorsal side, and in dark-pigmented specimens eyes sometimes surrounded by light circle. Light-colored central groove often between prostomial lobes, posterior to ceratophore of median antenna. Lateral antennae inserted ventral to prostomium and insertion of median antenna; ceratophores meeting midventrally; style arising from lateral border of ceratophore (Fig. 4, *b*); lateral antennae approximately one-fourth length of median antenna. Prostomial palps one-third again as long as median antenna and extending length of fully everted proboscis (Fig. 1, *c*). Proboscis with 18 terminal papillae besides two pairs of horny jaws.

Caudal region (Figs. 3, *b; 4, d*): Caudal (anal) cirri slightly longer than adjacent dorsal cirri; style attached by small peduncle (pygidium) to terminal segment.

Parapodia (Fig. 2), 1. Neuropodial branch. Neuropodium with elongated lobe enclosing distal end of neuropodial aciculum. Aciculum longer and thicker than notopodial aciculum. Neuropodial cirri only one-third length of notopodial cirri, not extending beyond neuropodial lobe. Neurosetae emerging on each side of neuropodial aciculum; subacicular group arising ventrally, supra-acicular group dorsally. From two to three times as many sub-acicular as supra-acicular setae (25-34); setae increasing in length dorsally. Sub-acicular setae characterized by change in shape from ventral to dorsal region (Fig. 3, *a, c, d*); ventral setae short with bidentate tip and minutely serrated along distal part of distinctly enlarged falcate blade (Fig. 3, *a*); dorsal setae longer, with lacinated fringes appearing in distal part arising below subterminal tooth (Fig. 3, *c, d*). Supra-acicular setae similar to preceding but longer; in anterior view, both sides of convex edge are serrated (Fig. 3, *e*); a few adjacent to notosetae shaped differently, rather slender distally, terminal and subterminal teeth reduced but approximately of same size, with serrations reduced or absent (Fig. 3, *f*).

2. Notopodial branch. Notopodium provided with pointed lobe into which distal end of notopodial aciculum extends (Fig. 2, *a, b*); lobe encloses aciculum eccentrically, greater portion ventral to aciculum. Style of notopodial cirrus about four times as long as neuropodial cirrus, 2.5 times as wide at base (Fig. 2, *a*). Notoetae as thick or thicker than neurosetae; of one kind arising in two clusters; slightly curved with definite spines (8-14) along convex border; tip

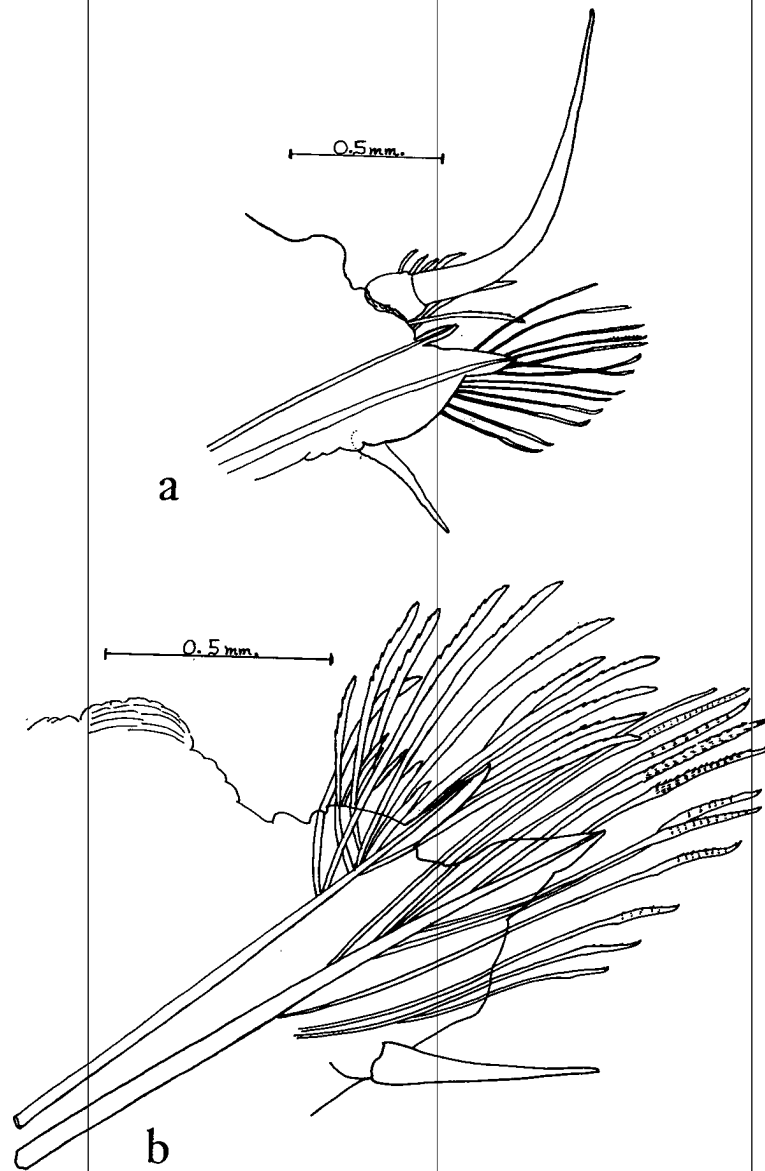


FIGURE 2.—*Hololepidella nigropunctata*: a, anterior view of cirriferous parapodium; b, posterior view of elytra-bearing parapodium.

of setae bluntly pointed; spines smaller near tip, first spine beginning below tip with space between spines increasing proximally. Notoetae and neuroetae light amber in color.

Material Examined. Over 60 specimens collected from Hawaiian echinoderm hosts were examined. Fifty-seven of these are deposited in Bishop Museum (Cat. nos. R277-R298, R300-R309). In addition, the specimen described by Hartman (1966, p. 174) as near *Acanthi-colepis* sp. from Station 391 is included as Bishop Museum Cat. no. R310. A single specimen from Johnston I. (BPBM Cat. no. R276) and one from Eniwetok (BPBM Cat. no. R299) were also examined.

Discussion. The Hawaiian specimens show a very close resemblance to the specimen described by Horst (1915, 1917) as *Polynoe nigropunctata*. The characteristic color pattern of the dorsum, arrangement of the elytra on identical segments, and the thickness and shape of the setae are among the most similar features. Although Horst (1917) described the prostomial palps as shorter than the median antenna, whereas most Hawaiian specimens show the palps typically longer than the antenna, little weight should be placed on this difference, owing to the contractile nature of the palps.

Day (1957) described a polynoid which he identified as *Hololepidella nigropunctata* (Horst) from the coast of Mozambique. He was the first to characterize the elytra. The presence of very evident dark stripes along the dorsum (1957, p. 65, and Fig. 1, a) and his description of the neuroetae are two characters which differ from both Horst's description and my examination of Hawaiian material.

The polynoid species which appears most closely allied to *H. nigropunctata* is the type species, *H. commensalis* described by Willey (1905). It differs from *H. nigropunctata* only in lacking the microtubercles on the elytra and in having neuroetae with simple rather than weakly bifid tips.

Concerning the generic status of *Hololepidella*, the genus is poorly differentiated from several other polynoid genera, but the Hawaiian specimens of *H. nigropunctata* appear to substantiate earlier descriptions pertaining to certain morphological features which may be of generic significance. Willey (1905) established *Hololepidella* to include one part of the genus *Polynoe* Savigny. He restricted the species to those in which the elytra were not limited to the anterior region of the body, the number of elytra was 15 pairs or more, and the lateral antennae arose ventral to the median antenna. Unfortunately these characters have not been sufficient to separate *Hololepidella* from sev-

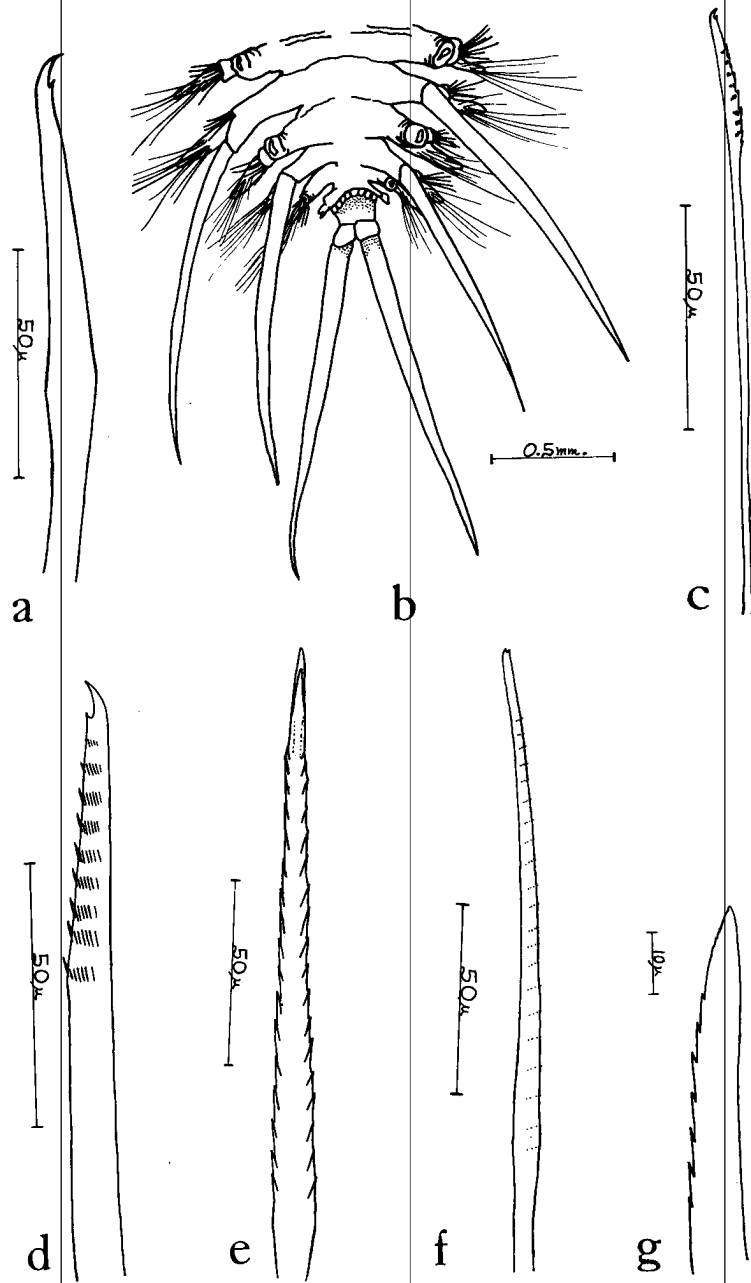


FIGURE 3.—*Hololepidella nigropunctata*: a, c, d, subacicular neurosetae; b, dorsal view of caudal region with cirri; e, f, supra-acicular neurosetae; g, notoseta.

eral other genera established before and since that time. Further characterization of the genus has been equally as general (see Fauvel, 1932), and has failed to take into account more diagnostic features.

A review of the original descriptions of *H. commensalis* Willey (1905) and *Polynoe nigropunctata* Horst (1915, 1917) reveals at least two additional characters which should be considered important generic criteria. First, the elytra are located on segments 2, 4, 5, 7, 9, . . . 23, 26, 29, 31, 34, 36, 38, 40, 42, and more or less regularly on posterior alternate segments. Horst specifically remarked on the unusual presence of the 15th pair of elytra on segment 31 rather than on 32 for *H. nigropunctata*, and Willey also indicated that *H. commensalis* has the same feature. Second, the notosetae are as thick or thicker than the neurosetae (Willey, 1905, pl. 1, figs. 17-19; Horst, 1917, pl. 21, figs. 16-17). The Hawaiian specimens attest to the consistency of both characters.

It appears then, in addition to the general diagnostic features reported by Willey, that the placement of the elytra on specific body segments and the relative thickness of the setae would provide additional characterization of the genus *Hololepidella*. It is suggested that other species in this genus be reexamined for these characters (for a list of species see Hartman, 1959, p. 81).

In the most complete review of Hawaiian polychaetes to date, Hartman (1966) has referred to a commensal polynoid associated with an ophiuroid as near to the genus *Acanthicolepis*. The diagnostic characters separating this genus, established by McIntosh (1900, p. 311) for *A. asperrima* (Sars), from *Hololepidella* are not conspicuous. For instance, *Acanthicolepis* was characterized in part by having 18 pairs of coarsely spinous elytra extending to the end of the body, a segmental count of about 41, a harmothoid prostomium, and notosetae thicker than neurosetae. *H. nigropunctata*, from Hawaii, passes through growth stages in which these characters are evident, except that the elytra are never spinous. The other diagnostic features serve both genera equally well. Unfortunately there was no mention of the elytra on specific body segments.

I have examined the three specimens reported by Dr. Hartman (1966) as near *Acanthicolepis* sp. The specimen listed from Station 391 (BPBM Cat. no. R310) from Halape, Hawaii, is in poor condition, without antennae or elytra. It has 37 segments and the elyrophores are located on the segments corresponding to *Hololepidella*. One specimen, from Johnston Island (BPBM Cat. no. R276) is in

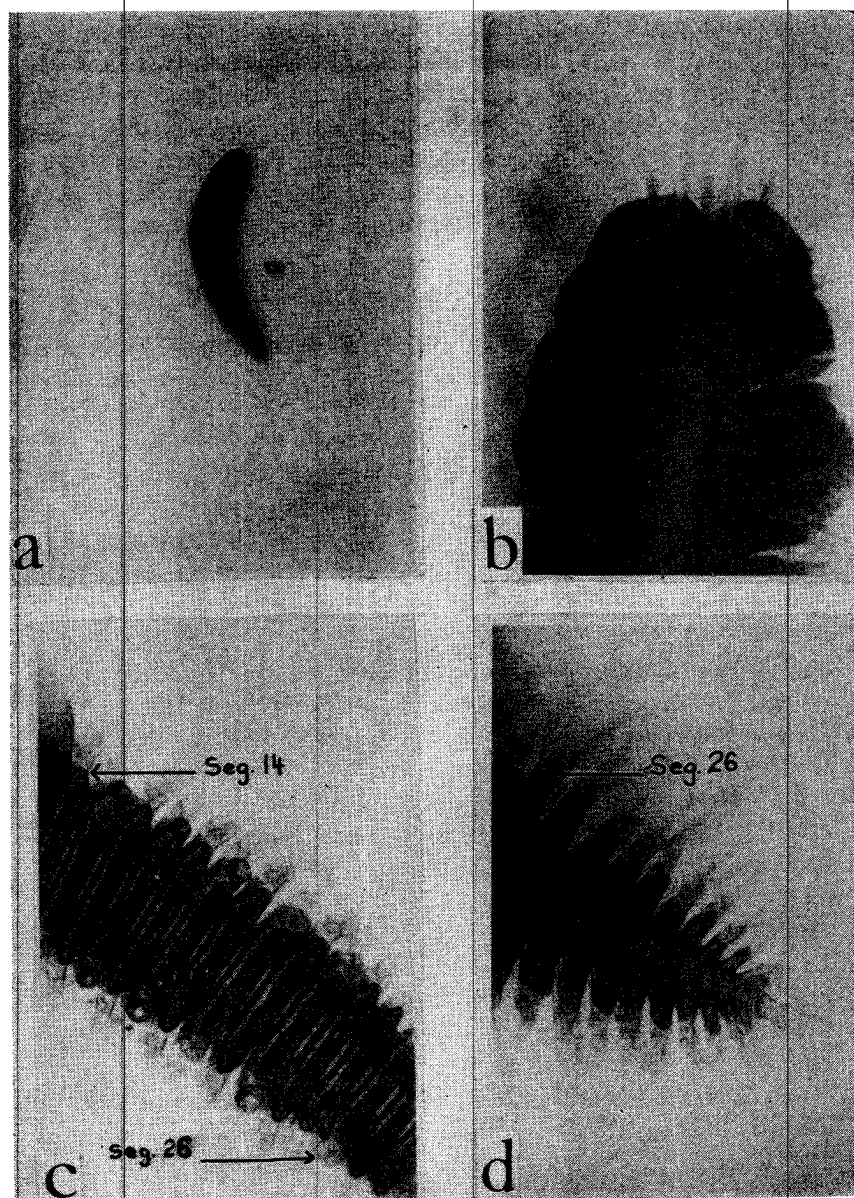


FIGURE 4.—*Hololepidella nigropunctata*: a, dorsal view of entire specimen, $\times 7$ (note free elytron); b, ventral view of anterior region, $\times 36$; c, dorsum with elytra absent, segments 14-28, $\times 35$; d, dorsum with elytra absent, caudal region, segments 26-37, $\times 35$.

good condition except for the lack of elytra, and differs only slightly from typical Hawaiian specimens of *H. nigropunctata* (see p. 290). A third specimen, listed by Hartman as coming from Johnston Island, actually was taken from an ophiuroid in Hawaii and does not differ from typical individuals of *H. nigropunctata*. With these considerations in mind, I do not hesitate in referring the specimens identified as near *Acanthicolepis* sp. by Dr. Hartman to *H. nigropunctata*.

DISTRIBUTION AND HABITAT

In Hawaii, the commensal polynoid has been observed on brittlestars in the family Ophiocomidae and the genus *Ophiocoma*. This genus contains, for the most part, the larger Hawaiian ophiuroids common in the shallow marine environment.

By far the largest number of commensal polynoid worms has been found associated with *Ophiocoma dentata* Müller and Troschel. This species has been most commonly referred to as *Ophiocoma insularia* Lyman, however recent examination of the type specimens of both species by the author shows that the two species are synonymous. Collections made at several localities along the coasts of Hawaii, Kauai, and Oahu reveal the association whenever this brittlestar is present. As many as 60 percent of the specimens collected near Kaena Point, Oahu, were found with commensals, whereas in Kaneohe Bay, Oahu, this figure dropped to a little more than 20 percent.

O. dentata is commonly found in the shallow sublittoral zone where lava or coral boulders cover a sandy or pebbly substratum to depths of 40 feet. This ophiuroid is uncommon or absent where silt or mud accumulate and form the predominant bottom deposit.

Another ophiuroid, *O. brevipes*, although far less common than *O. dentata* also serves as a host for the commensal polynoid. This brittlestar is smaller than adult specimens of *O. dentata* and none of the larger commensals has been observed with it. No data are available regarding the frequency of its association with the commensal worm.

O. brevipes is apparently more restricted in its habitat than *O. dentata*; it is usually found under boulders overlying sand where it can be seen partially buried. Furthermore, this species has not been observed where the bottom is composed of very coarse sand or cobble. The commensal polynoid has been collected from *O. brevipes* most often along the leeward side of Oahu, at Black Point and Hanauma Bay.

Many specimens of *O. erinaceus* were examined from many parts of Hawaii and relatively few commensals have been observed associated with it. This species is quite common to a depth of 100 feet and can be found in the same type of habitat as the two species mentioned above, although it is more prevalent within or around dead coral heads or under large living corals, and is not common on a sandy substratum. It is interesting that when both *O. dentata* and *O. erinaceus* have been collected together, only the former species harbored the commensal polynoid. It appears doubtful that *O. erinaceus* can be considered the major ophiuroid host in the Hawaiian Islands although there is some evidence that this species will be the host in areas where *O. dentata* is not common or is absent, both in Hawaii and elsewhere.

In 1964, a single polynoid was recovered from a sample of several specimens of *O. erinaceus* collected at Johnston Island. Examination of the polynoid revealed morphological characters in common with Hawaiian specimens of *H. nigropunctata*, although the specimen was very darkly pigmented and had unusually large prostomial peaks. Because neither *O. dentata* nor *O. brevipes* has been recorded from Johnston Island (A. H. Clark, 1949, p. 119), and since I have observed *O. erinaceus* as the dominant shallow-water ophiuroid there, it appears quite probable that it may serve as the major ophiuroid host for the polynoid.

Besides Johnston Island and the main Hawaiian islands, the polynoid identified as *H. nigropunctata* has been found along the east coast of Africa (Day, 1957). Balinsky (1957, p. 18) and Macnae and Kalk (1962, p. 118) report the polynoid commensal with the brittlestar, *Macrophiothrix hirsuta* (Ophiothricidae) from Inhaca Island, Mozambique. Interestingly enough, *Ophiocoma brevipes*, *O. erinaceus*, and *O. dentata* were also reported by Balinsky from Inhaca, but none of these has been found with the commensal. [I have examined specimens identified by Balinsky as *O. insularia* and find them to be *O. pusilla* (Brock).] Balinsky stated that *M. hirsuta* is the most common ophiuroid in the infralittoral fringe area of the main reef at Inhaca, with *O. erinaceus* and the species he called *O. insularia* infrequent or rare. These latter brittlestar species were reported being more abundant in another "more tropical reef area" (p. 31).

During the summer of 1966, another specimen of the polynoid was recovered from *Ophiocoma anaglyptica* Ely collected at Eniwetok Atoll, Marshall Islands, by Marshall Youngbluth. The commensal proved to be an ovigerous specimen of *H. nigropunctata*.

The single type specimen of *Polynoe nigropunctata* reported by Horst (1915) was collected on a reef at Amboina in the Moluccas group, Indonesia. However, there was no mention of an invertebrate host.

Recently, several specimens of the multirayed starfish, *Acanthaster planci*, collected in Oahu, have been found harboring a commensal polynoid which proved to be the same as that found on the ophiocomid brittlestars. Several of the starfishes carried from two to five polynoids. Table I summarizes the distribution of *H. nigropunctata* and its hosts.

Table I—Echinoderm hosts and distribution of *Hololepidella nigropunctata*.

Host	Hawaiian Islands	Johnston Island	Eniwetok Atoll	Amboina	Inhaca Island
Ophiuroidea					
Ophiocoma anaglyptica	-----	-----	Assoc. reported	-----	-----
O. brevipes	XX	-----	Assoc. not reported	Assoc. not reported	Assoc. not reported
O. erinaceus	X	Assoc. suspected	"	"	"
O. dentata	XXX	-----	"	"	"
Macrophiothrix hirsuta	-----	-----	-----	"	Assoc. reported
Asteroidea					
Acanthaster planci	Assoc. reported	Assoc. not reported	Assoc. not reported	"	Assoc. not reported

----- No record of host from locality.

X Association not common.

XX Association common.

XXX Association very common.

BIOLOGY

H. nigropunctata is most frequently found on the oral surface of the brittlestar, *O. dentata*, in contact with the oral arm plates near or below the disk, often with its head toward the oral cavity (Fig. 5, a). However Balinsky (1957, p. 18) noticed the commensal from Inhaca Island positioned in an interradius at the edge of the disk of the host, *Macrophiothrix hirsuta*. A similar position of the polynoid has also been noticed on Hawaiian specimens of *O. brevipes* and *O. erinaceus* as well (Fig. 5, b). In the case of *O. brevipes* this may be related to the tendency of the ophiuroid to bury in sand, thus exposing only the aboral surface to which the polynoid can attach.

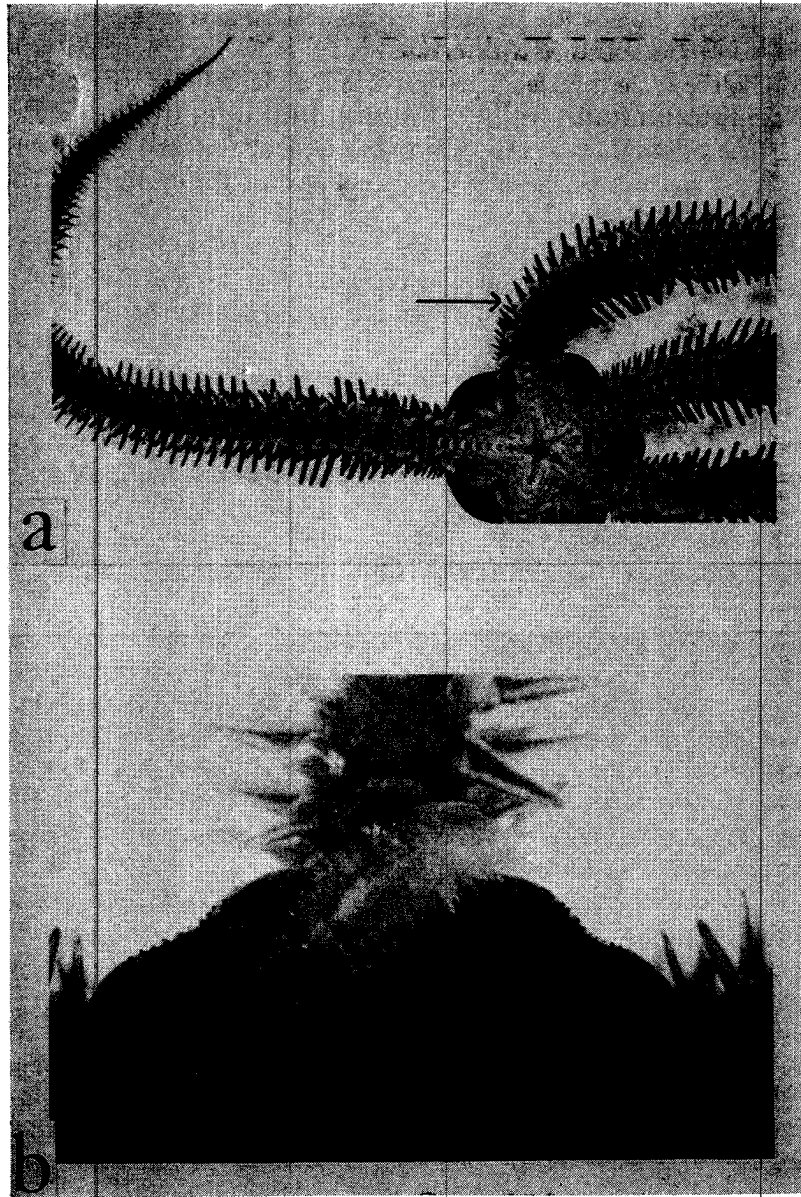


FIGURE 5.—Brittlestar hosts; **a**, ventral (oral) view of *Ophiocoma dentata* with commensal polynoid; **b**, dorsal (aboral) view of *O. erinaceus* with commensal in interradius and on disk.

The location of the polynoid on the oral surface or in an inter-radius of the ophiuroid disk would appear to be an adaptation protecting the commensal from predation, and also affording an excellent place to obtain food.

The polynoid does not appear to be cryptically colored on *O. dentata*, for the worm generally stands out against the oral plates. On the other hand, the color may be cryptic when the worm is associated with either *O. brevipes* or *O. erinaceus*. In general, only lightly pigmented specimens have been observed on *O. brevipes* and dark-brown or reddish specimens on *O. erinaceus*, corresponding closely to the background color of the hosts.

No more than one commensal has been recovered from a single ophiuroid host. This may be related to the fact that the polynoids have been noted to demonstrate rather aggressive behavior toward one another when two or more are placed in close proximity. In cases where several worms were removed from their hosts and placed in a petri dish, those that came in contact with one another would evert the proboscis and appear to strike each other. On more than one occasion elytra were shed after this contact.

Not only are elytra easily autotomized but in several instances it was noted that a polynoid, transferred from its host to a dish of sea water, would subsequently autotomize the caudal portion of the body. One specimen with 47 segments, autotomized at segment 28. This specimen was kept alive for over two months in a petri dish supplied with periodic changes of sea water and small pieces of the alga, *Ulva* sp. At the time the polynoid expired, six new segments had regenerated along with several elytra.

A series of studies was conducted on the possible taxic response of the commensal polynoid to its host. The basic experimental methods were patterned after those of Davenport (1950). Tests indicate that some stimulus, perhaps a diffusible chemical metabolite, may be released by the brittlestar hosts, *O. brevipes* and *O. dentata*. This metabolite may serve to attract the polynoid to the host as similar results obtained by Davenport (ibid.) using other polynoids and their invertebrate hosts suggested. Although the results of the experiments indicate a chemotaxic response by the polynoid to the brittlestars mentioned above, negative results were obtained with *O. erinaceus* and another Hawaiian ophiuroid, *Ophionereis porrecta*. Many more trials must be conducted however, before these preliminary results can be considered conclusive.

ADDITIONAL POLYNOID-OPHIUROID ASSOCIATIONS

It has been estimated that approximately two-thirds of all commensal polychaetes are members of the family Polynoidae and, of the many hosts, echinoderms are among the most common (R. B. Clark, 1956). The following review includes the reported polynoid commensals and their ophiuroid hosts.

Orton (1923) noted the commensal polynoid, *Harmothoe lunulata*, associated with the brittlestar, *Acrocnida* (as *Ophiocnida*) *brachiata* (Amphiuridae) along the coast of England. It was postulated that this relationship might be only temporary and the polynoid utilizes different invertebrate hosts at different stages in its life history. Davenport (1953) cited this as a case in which the factors of host recognition as well as adaptive changes which the polynoid must undergo in shifting hosts were virtually unknown.

Harmothoe lunulata has also been reported with *Ophionereis reticulata* (Ophionereididae) from Jamaica (Millott, 1953). The polynoid revealed adaptations in the morphology of the elytra, spines, and pigmentation which appeared relevant to this association. Moreover, the polynoid appeared to be negatively photographic, and this was also assumed to be adaptive.

At least three species of brittlestars in the genus *Ophiothrix* (Ophiothricidae) have been mentioned in connection with polynoid commensals. Along the French coast, Koehler (1894) reported *Scalisetosus pellucidus* (as *Hermadium pellucidum*) (sic) with cryptic coloration, against the oral side of the host, *O. echinata*. Cuénot (1912) also describes the same polynoid associated with *O. fragilis*. Chamberlin (1919) mentions the occurrence of the polynoid *Scalisetosus communis* (= *pellucidus*) with the ophiuroids, *O. fragilis* and *O. alopecurus*. These accounts probably represent only a fraction of the number of similar relationships which occur, and are in part reflections of collection techniques.

SUMMARY

1. A commensal polynoid from Hawaii and other Pacific localities is described and identified as *Hololepidella nigropunctata* (Horst).
2. The generic status of *Hololepidella* is reviewed and two additional morphological features are considered as possible criteria for separating this genus from other polynoid genera.

3. The polynoid is very commonly associated with the brittlestar *Ophiocoma dentata* and less frequently with *O. brevipes* and *O. erinaceus* in Hawaiian waters.

4. Biological observations indicate the following: a, Only single individuals are found on ophiuroid hosts, but more than one have been recovered from the asteroid, *Acanthaster planci*. b, The commensal does not appear cryptically pigmented with *O. dentata*, but may be with the other ophiuroid hosts. c, Chemotaxic responses have been initially indicated by the commensal to both *O. brevipes* and *O. dentata*, but negative results have been obtained with *O. erinaceus*.

5. Other commensal polynoid species and their associated ophiuroid hosts are reviewed.

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