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POLYDORA ALLOPORIS, NEW SPECIES, A COMMENSAL SPIONID (ANNELIDA, POLYCHAETA) FROM A HYDROCORAL OFF CENTRAL CALIFORNIA

By

William J. Light

Department of Biological Sciences Simon Fraser University Burnaby 2, British Columbia

ABSTRACT: A new species of polychaetous annelid, *Polydora alloporis* (Spionidae), is described from central California. It is always abundantly found in burrows bored into the coenosteum of the hydrocoral *Allopora californica* Verrill, 1866, and is one of the largest of the polydorids, reaching a length of 75 mm. or more. It is related to *Polydora hornelli* Willey, 1905, from India, and to *P. cavitensis* Pillai, 1965, and *P. pacifica* Takahashi, 1937, both from the western Pacific.

INTRODUCTION

Biologists have long known that the subtidal hydrocoral *Allopora californica* Verrill, 1866, from central California is always found to harbor a burrowing spionid, whose paired burrow-openings are scattered throughout the branches of both the orange-red and the purple color phases of the hydocoral. Its identity, however, has until now remained obscure. Preserved material of *Allopora californica* collected by Mr. Dennis Sullivan, then of the California Academy of Sciences, in August, 1962, off San Jose Creek Beach (Monastery Beach), Carmel, Monterey County, California, in 35 to 40 feet of water, was deposited in the Academy's collections in the Department of Invertebrate Zoology (CASIZ). This material was examined and the worms it contained were diagnosed simply as *Polydora* species, inasmuch as only a few isolated fragments could be with-

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drawn from the preserved hydrocoral. This, however, was sufficient for a generic determination.

On 19 September 1968, Mr. Don Wobber of San Francisco State College secured live material with scuba equipment from the same general vicinity near Carmel, California, from a depth of 80 feet. We were able to obtain entire living worms from this sample of *Allopora* by carefully crushing it with a pair of vice-grip pliers. It was readily apparent that these polychaetes represented an undescribed species closely allied to *Polydora cavitensis* Pillai, 1965, from the Philippine Islands and to *P. hornelli* Willey, 1905, from India. Further investigation also revealed affinities with *Polydora pacifica* Takahashi, 1937, from Palau Island, Caroline Islands, in the Philippine Sea. The last mentioned is a species commonly found burrowing in a species of *Montipora*, a branched coral growing in the reefs of that region, as well as in the shells of the pearl oyster, *Pinctada margaritifera* (Linné, 1758).

On 26 October 1968, Mr. Wobber and I returned to the Monterey area and obtained additional living material off 17-Mile Drive near Carmel, California from 125 feet of water in an area of submerged seastacks known locally to scuba divers as "the Pinnacles." The type series contains material from all three of the above collections, and includes the holotype and 12 paratypes.

Family Spionidae Grube, 1850 Genus **Polydora** Bosc, 1802

Polydora alloporis Light, new species.

DIAGNOSIS. Length to 75 mm. or more. Modified major spines of fifth setiger simple and falcate, with hollowed out distal ends; companion setae situated immediately ventrad of the major spine series, normally lanceolate, but when worn resembling narrow clubs with many small spiny projections. Fifth setiger heavily folded and creased, dorsally. A prominent band of cilia running transversely across the dorsum of each segment from the seventh setiger to the pygidium; similar cilia on the medial surfaces of the branchiae. Prostomium anteriorly entire, formed of two membranes, a superior one forming a dorsal sheath over an inferior process which projects anteriorly beyond the forward margin of the superior membrane; prostomial caruncle narrow, extending posteriorly to the middle of the fourth or the anterior border of the fifth setiger. Median and posterior segments ventrally marked with distinctive greenish-or reddish-brown butterfly or fleur-de-lis pattern, the "wings" of which may form open rings, two or more parallel lines, or even more or less solid blotches. Pygidium a widely flaring dusky silver, fleshy disc with a deep dorsal cleft and many small papillae on the posterior surface. Found exclusively and in large numbers in deep burrows in the coenosteum of Allopora californica at subtidal depths.

Type Material. The holotype and six paratypes have been placed in the California Academy of Sciences, Department of Invertebrate Zoology (CASIZ) Type Series as numbers 381 (the holotype) through 387, inclusive. Additional material, including the modified spines of the fifth setiger, neuropodial crotchets, palpi, and longitudinal and cross sections of various segments and parapodia have been mounted separately as CASIZ microscope slide numbers 353 through 364, inclusive. Paratypes have also been deposited in the British Museum (Natural History), American Museum of Natural History, the Zoological Institute of the Academy of Sciences (Leningrad), United States National Museum, and the Allan Hancock Foundation at the University of Southern California.

DISTRIBUTION. *Polydora alloporis* has been recovered only from samples of *Allopora californica* taken at various subtidal depths off the Carmel area, Monterey County, California.

Habitat. This polychaete lives as a commensal in deep burrows in the coenosteum of *Allopora californica* where it may form large colonies. The paired openings of the burrows are distinctive and the worms may be seen in living material with the palpi projecting from one of the apertures, and the pygidium just visible below the lip of the other (fig. 1). There is a distinctive fauna associated with this hydrocoral, including the gastropod *Pedicularia californica* Newcomb, 1864, which matches the color of its host, and a variety of small reddish caprellids and other amphipods. A distinctive balanomorph barnacle, *Balanus (Armatobalanus) nefrens* Zullo, 1963, was also recovered from the same samples of *Allopora* as were the worms. This barnacle, which was identified by Dr. Victor A. Zullo, California Academy of Sciences, is only known to exist in the coenosteum of *Allopora californica* and *Errinopora pourtalesi* Dall, 1884, from Monterey Bay and the Channel Islands, California (Zullo, 1963, p. 593). It has its closest affinities with animals from the Australasian region (Zullo, 1966, p. 142).

In addition, a number of nonhost specific organisms have been taken from these samples, including the following polychaetes: *Halosydna johnsoni* (Darboux, 1899) and *H. brevisetosa* Kinberg, 1855 (Polynoidae), and *Anaitides* species (Phyllodocidae).

EXTENDED DESCRIPTION. *Polydora alloporis* is extremely long for the genus and specimens commonly attain lengths of 65 to 70 mm. The longest specimen, the holotype with 188 segments, measured 75 mm. in length by 2 mm. wide. The greatest number of segments (236), was noted in an individual measuring 67 mm. in overall length. The most striking features of the living animals are the prominent dorsal and ventral blood vessels through which pulsates bright-red blood. The dorsal vessel bifurcates anteriorly and is continued in the palpi, where it forms convoluted loops proximally. The ground color is fleshy but there is often a faint greenish tinge to the body in living specimens. Distinctive



FIGURE 1. Polydora alloporis, new species. Living animal protruding from paired holes in coenosteum of Allopora californica. Photograph by Allyn G. Smith.

patterns of pigmentation are exhibited on the venter and the palpi. These are discussed below. The pygidium is a striking dusky silver in complete contrast to the rest of the body.

The animal is somewhat dorsoventrally compressed in the anterior third of its length, but the somites become gradually attenuated and laterally swollen posteriorly, where they acquire a barrel-like configuration. The sixth to about the twelfth setigers appear to be affixed to the modified fifth segment at a lower level than are the preceding somites in many individuals, so that the animals appear to be ventrally distended over this region (fig. 5).

Prostomium. The prostomium projects well beyond the anterior border of the lateral cephalic lobes of the peristomium. It is bluntly rounded and entire at its anterior margin where it forms a small roll of tissue passing from one side of the prostomium to the other, imparting a "hognosed" appearance to the snout (fig. 5). Immediately behind this lies the anterior border of a superior membrane which forms a sheath over the prostomium that extends laterally onto the lateral cephalic lobes on either side of the prostomium for about one-fourth of the width

of these lobes (figs. 2, 5). Posteriorly, this sheath passes back to the point of insertion of the palpi. This membrane is medially continuous with the prostomial caruncle and appears to represent a forward extension of that structure. The prostomial portion underlying this superior sheath is widest distally and tapers evenly to the level of the first setiger, or to the midpoint of insertion of the palpi. At this point are situated one pair of small, but prominent eyespots, which are overlain by the superior prostomial sheath.

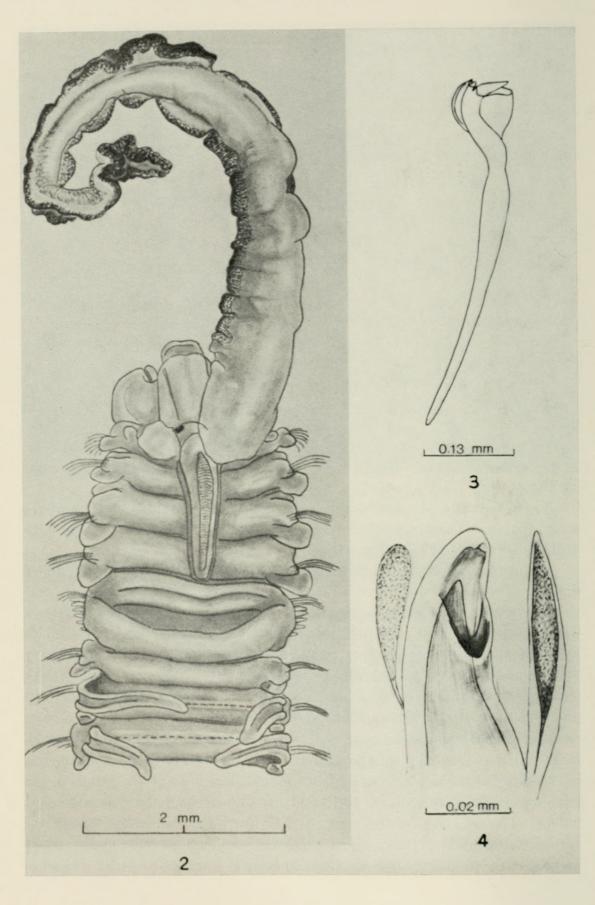
At the level of the eyespots the caruncle forms two successive dorsally projecting humps or bosses and then passes posteriorly as a rather narrow band of raised tissue to the middle of the fourth or the anterior border of the fifth setiger (to the anterior margin of the third in one specimen). The caruncle is dorsally raised into a strip of corrugated glandular tissue extending from the posterior border of the palpi to the posterior tip of the caruncular extension (figs. 2, 5). From a dorsal perspective the two anterior dorsal bosses appear to project slightly forward, but there is no trace whatsoever of an occipital cirrus.

Peristomium. The peristomium is laterally projected on either side of the prostomium into two widely flaring cephalic lobes which are not fused with the first setiger, contrary to the condition occurring in some polydorids. Anteriorly, it sweeps downward to enclose a converging U-shaped buccal opening, which is lined on each side by two fleshy strips of tissue (figs. 2, 5). These two fleshy borders are confluent with a folded and lobulated eversible proboscidial mass which lies inside the oral cavity. This proboscis is well extended in one of the paratypes.

Posteroventrally, the peristomium extends to a point below the level of the second parapodia and generally, though not always, completely supresses the ventral development of the first setiger.

The palpi are thick, long, and highly lobulated along the longitudinal ciliated grooves. They are densely studded over their entire surface with minute, bell-shaped, cellular protuberances, each of which bears a single whip-like flagellum. The median longitudinal groove is heavily ciliated and is bordered on each side by thick pads of mucus-secreting glandular tissue which are raised into heavy mounds and ridges. This glandular region is densely colored with a sooty-black pigment which forms a more or less continuous border on either side of the groove in most specimens, but which in some animals forms discrete blotches or rectangular bars along the groove (figs. 1, 2). The proximal sixth of the palpi lacks both pigment and glands and the grooves at this level are nonciliated.

Modified fifth setiger. The modified fifth setiger is twice the length of the segments immediately adjacent to it, and two and one-half times as wide as it is long. The dorsum of this segment is heavily ridged and folded. From the region of attachment of the modified spines and setae, a large fold passes dorsally and somewhat posteriorly over the dorsum, extends along the posterior margin of



the somite, and is continuous with its companion from the opposite side (figs. 2, 5). A slightly smaller fold extends transversely across the segment along its anterior border, and the two folds enclose a central spindle-shaped depression (fig. 2).

The modified spine series forms a dorsally concave anteroposteriorly sweeping arc and the spines themselves project far out from the body wall. There are usually six or seven of these spines (rarely eight) which are visible externally, but six or seven additional embryonic spines are generally found embedded in the tissues.

These spines are quite long and laterally expanded along the mid-portion of their lengths; they are distally falcate and quite pointed at their tips when unworn. Each spine bears a deep, hollowed-out, subdistal concavity, which is bordered laterally and ventrally by a continuous slightly raised flange (fig. 4). This condition is very similar to that found in both *Polydora cavitensis* and *P. hornelli*. The embedded proximal tips of these spines are heavily striated with transverse ridges which become obscure distally. The core is considerably expanded in the middle part of the spine and fills the greater part of the cavity. It extends beyond the distal concavity almost to the terminal point.

Each spine alternates with a clear transparent companion seta. These setae project laterally from the body wall in an even row lying immediately adjacent, but inferior to the major spine series. These setae are generally quite worn and closely resemble those figured by Takahashi (1937, p. 160) for *Polydora pacifica* in forming narrow, club-shaped, distal tips (the "lancet-like forms" of Takahashi) which are covered by many minute spiny projections (fig. 4). These setae taper proximally into a long, thin, whip-like, medial stalk. It is apparent, however, that these club-shaped companion setae are but worn versions of the lanceolate setae which remain unmodified in some animals. One or two such unworn setae can also be found farther posteriorly among the younger spines of most individuals.

A vertical tuft of from seven to nine lanceolate setae emerges from near the base of the anteriormost modified major spine, and a much smaller fascicle of four or five similar setae projects from an isolated position ventral to the major spine series.

Unmodified segments and parapodia. Both the dorsal and ventral lamellae are well developed on the first four setigers, but the entire parapodium of the first setiger has moved somewhat dorsally, so that the neuropodium lies at an

FIGURE 2. Polydora alloporis, new species. Dorsal view of animal with left palp removed. FIGURE 3. Polydora alloporis, new species. Neuropodial hooded crotchet.

FIGURE 4. Polydora alloporis, new species. Distal tip of major spine of fifth setiger, showing worn (left) and unworn (right) companion setae.

intermediate position between the notopodia and neuropodia of the succeeding somites. This differs from the situation in most members of this genus, in which the first neuropodium lies approximately at the same level as the following notopodia. There are no notosetae on the first setiger and only a small fascicle emerges from the neuropodium. This somite is generally ventrally supressed by the posterior prolongation of the peristomium. The postsetal lamellae of both rami are well developed from setigers two to four, but the notopodial postsetal lobes are distinctly larger than those in the neuropodia.

The notosetae from setigers two to about fourteen emerge in two, closely appressed, vertical rows as a prominent light-colored, U-shaped fascicle. The superior portion of the anterior row consists of long capillaries which merge ventrally with unilimbate setae of an intermediate length. The latter are abruptly bent in a posterior direction shortly after emerging from the body wall and the wings are distinctly striated. At the base of the U-shaped fascicle appear very small spearshaped setae, which again blend into unilimbate setae of the intermediate type in the posterior vertical row of the fascicle. These setae resemble those found in the more generalized genus, *Pseudopolydora*, Czerniavsky, 1881, although the arrangement is somewhat different in the latter. From about the fourteenth somite, the smaller bladed setae drop out and the long capillaries and unilimbate setae become reduced in number. The two rows of the fascicle are reduced to one, and in the posterior segments the capillaries alone remain.

The neuropodial setae of the first six setigers (including the small ventral tuft on the fifth) consist of bladed lanceolate forms.

Simple hooded neuropodial crotchets appear on setiger seven where they are usually seven or eight in number, but occasionally as few as five or as many as ten. Within a very few segments they increase to 10 or 11 per row, this number persisting over from 6 to 10 somites. Thereafter, they gradually decrease by one crotchet per row (this may fluctuate by one or two hooks in a given series), each number being maintained over a long region, up to the segments immediately preceding the pygidium, which usually contain from two to five each.

These crotchets resemble those of *Polydora cavitensis* in having a bidentate tip in which the beak forms an angle of slightly less than 90° back against the main shaft (fig. 3). As in *P. cavitensis*, the point where the beak emerges from the shaft is smoothly rounded, and the apical tooth is more closely appressed against the beak than is usual among members of this genus considered in the strict sense. Below the level of the transparent hood, the shaft forms a curved neck and waist, followed by a slight swelling which then tapers evenly to the pointed proximal tip. The neck is much shorter than in the hooks of *P. cavitensis*, so that the waist lies at the distal fourth of the shaft, rather than at the distal third, as in Pillai's species. The crotchets are extremely small for so large an

animal, measuring less than 0.5 mm. in length, and the neurosetal lamellae are poorly developed.

The branchiae are well developed from the outset, beginning on the seventh setiger and continuing to the pygidium. The inner or medial surfaces are heavily ciliated and this ciliary band is continued over the dorsum of each segment on a raised transverse ridge, where it merges with the cilia of the opposite gill. A well developed postsetal lobe arises at the posterior edge of each gill.

Dorsolateral nephridial openings are evident just behind the septa dividing the somites in a position anteroventral to the branchiae. These openings are surrounded by a highly glandular epithelial ridge which runs dorsally parallel to the intersegmental septum, and which terminates in the vicinity of the dorsal transverse ciliary band. The glandular regions surrounding the nephridial openings are often pigmented and appear as reddish spots along the sides of the animal. They begin on the eighth segment and continue over as many as 40 somites in some individuals.

The dorsum in preserved material exhibits a series of longitudinal, dark, reddish-brown, rectangular blotches over many of the segments, but this appears to be due to coagulated material in the massive dorsal blood vessel.¹ A conspicuous and typical pattern commonly appears on the ventral surfaces of the median and posterior segments, however. This consists of either a sooty-green or reddish-brown butterfly or fleur-de-lis configuration made up of closely parallel lines of pigment (fig. 6). The lateral "wings" of this pattern may form more or less open rings, consist of two or more longitudinal lines, or even appear as a solid blotch. This pigmentation is absent on some animals.

Pygidium. The pygidium is a widely flaring, thick, fleshy disc, with a deep dorsal notch (figs. 6, 7). The fleshy pad is flattened on the posterior surface and is densely studded with many minute papillae. There is no posterior cuplike invagination so characteristic of the polydorids, and the anus opens somewhat dorsally. *Polydora cavitensis* also has a flattened anal disc which, however, is triangular in shape and which bears projecting dorsolateral lobes.

Discussion. *Polydora alloporis* is closely related to *P. cavitensis* and *P. hornelli* by virtue of the specialized spines on the fifth setiger, which in all three species have hollow distal concavities. *Polydora hornelli*, however, has a distinct neck proximal to the concavity which is not found in the other two forms. The arrangement of the setae of the fifth setiger is similar in all of these species. The heavy dorsal folding of this segment seen in *Polydora alloporis* is not mentioned for either of the Asian forms. However, it is indicated in the illustrations of *P. cavitensis* and appears to be in an incipient stage in the figures of *P. hornelli*. An examination of paratypic material of *P. cavitensis* reveals the

¹Pillai (1965, p. 152) mentions a similar pigmentation on the dorsum of *P. cavitensis*, but an examination of two paratypes on loan from the British Museum (Natural History) indicates that this is also due to the dorsal aorta and its contents.

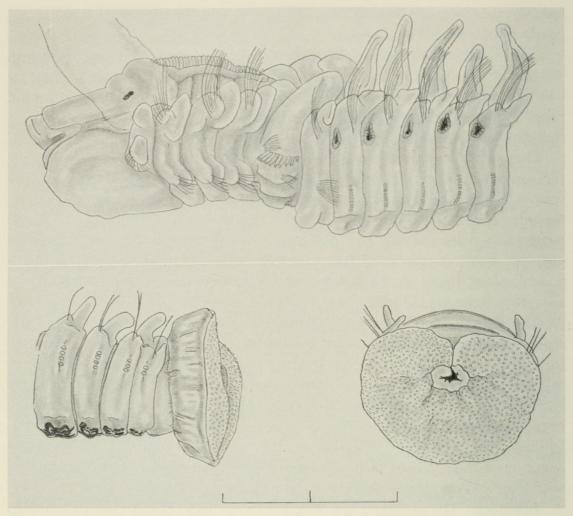


FIGURE 5. Polydora alloporis, new species. Left lateral view of anterior end.

FIGURE 6. Polydora alloporis, new species. Lateral view of pygidium, showing papillae.

FIGURE 7. Polydora alloporis, new species. Posterior view of pygidium, showing papillae.

Scale indicates 2 mm.

dorsal folding to be present, although poorly developed. The neuropodial crotchets are very similar to those of *P. cavitensis*; to a lesser extent they also resemble those of *P. hornelli*. The prostomium is distinctly bifurcated anteriorly in *P. cavitensis* and slightly notched in *P. hornelli*, whereas it is distally entire and exhibits a distinctive superior caruncular sheath in *Polydora alloporis*. The caruncle extends to the end of the second or third setiger in *P. hornelli* and to the end of the third in *P. cavitensis*. In *Polydora alloporis* it is almost always found as far back as the middle of the fourth or anterior border of the fifth setiger.

Polydora cavitensis possesses an occipital cirrus and two pairs of eyes, as compared with no such cirrus and but one pair of eyes in P. alloporis. There is no evidence of an occipital cirrus or eyes in P. hornelli, but all three species

show one or more raised bosses in this region. The anal segments of both *P. alloporis* and *P. cavitensis* are described above; that of *P. hornelli* remains unknown.

Polydora alloporis also shows affinities with P. pacifica from Palau Island. In size, it approaches the latter species and reaches 75 mm. or more in length, as against 85 mm. for the Palau animals. Both Polydora hornelli (31 mm. for an incomplete specimen of 92 segments) and P. cavitensis (15 mm.) are considerably smaller. The prostomium of P. pacifica is anteriorly notched and the caruncle reaches the anterior margin of the third setigerous segment. No eyes are indicated and the fifth segment does not appear to exhibit the dorsal folding of the other three forms. The modified major spines of the Palau specimens are described as having a lateral subdistal spur, as in Polydora ciliata (Johnston, 1838), and the companion setae appear much like the worn companion setae of P. alloporis, being termed "lancet-like" by Takahashi. As we have seen, these setae, at least in P. alloporis, are but the worn lanceolate setae of the same basic design generally found in polydorids.

The hooded crotchets of *Polydora pacifica* are described as possessing a distally directed spine on the main shaft at the lower point of attachment of the transparent hood. In these crotchets, the portion of the hood which shields the beak is less pronounced, and that covering the apical fang more flared than in any of the other three species in this complex. It is of interest, however, that one slide containing the crotchets of *P. alloporis* which were distorted by improper mounting of the coverslip, showed a very similar configuration to those described for *P. pacifica*.

The pygidium of *P. pacifica* more nearly resembles that of *P. alloporis* than does that of *P. cavitensis*, except that the dorsal lobes in *P. pacifica* do not approach one another so closely and the dorsal cleft is much wider, leaving the anus directly exposed above.

Both *Polydora pacifica* and *P. alloporis* are found burrowing in branched corals and hydrocorals, *Montipora* species and *Allopora californica*, respectively, but the former is also commonly known to burrow into the inner nacreous layer of the pearl oyster, *Pinctada margaritifera* (Linné, 1758). *Polydora hornelli* is known only from crevices in oyster shells from fresh water at Manikpatna, Chilka Lake near Calcutta, India, and the Gulf of Manaar, Ceylon. *Polydora cavitensis* was collected from the Government Oyster Farm in Binakayan, Cavite, Manila Bay, Luzon, Philippine Islands, likewise from among oysters. We have, then, two marine and two estuarine populations.

According to Fisher (1938, p. 496), *Allopora californica* occurs at temperatures between 46° F. and 52° F. (7.7° C. to 11.1° C.) from the Farallon Islands south to Lower California at depths of up to 25 fathoms. It would not be surprising to find a similar distribution for *Polydora alloporis*. In this connection,

however, it is noteworthy that a sample of *Allopora*, near *A. californica* from an unknown depth off Anacapa Island near Santa Barbara, California, in the dry collections of the Department of Invertebrate Zoology, California Academy of Sciences, shows no evidence of the characteristic burrow-openings made by these animals.

Allopora venusta Verrill, 1868, another hydrocoral which ranges from Washington to Monterey Bay and which is also represented in the dry collections of the Academy, does exhibit the paired holes of *Polydora*, as do several other hydrocorals from Vancouver Island and Alaska. These holes are much smaller than those typically found in the coenosteum of *Allopora californica*, and since none of the polychaetes are available for study, it is uncertain whether these other hydrocorals harbor *Polydora alloporis*, another previously described polydorid, or an as yet new and undescribed species.

An examination of the plates in a monographic work on northern Pacific hydrocorals (Fisher, 1938) reveals paired burrow openings in the coenosteum of the following species: *Allopora porphyra* (Fisher, 1931, pl. 59, fig. 2), *A. stejnegeri* Fisher, 1938 (pl. 56, fig. 2), and *A. boreopacifica* (Broch, 1932 [pl. 56, fig. 3]).

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I wish to express my gratitude to Messrs. Dennis Sullivan and Don Wobber for their collections of the *Allopora* from which the polychaetes were extracted. I am also indebted to Miss Gay Little of the Department of Zoology, University of California at Berkeley, for verifying the identity of *Allopora californica*, and to Dr. Victor A. Zullo and Mr. Allyn G. Smith, both of the California Academy of Sciences, for identifying the barnacle, *Balanus (Armatobalanus) nefrens*, and the gastropod, *Pedicularia californica*, respectively. Mr. Smith also took the remarkable photograph of the living specimen of *Polydora alloporis* (fig. 1).

I am especially grateful to Dr. J. David George, Curator of the Porifera and Polychaeta Section of the British Museum (Natural History) for his generous loan of two paratypes of *Polydora cavitensis*.

NOTE. After the manuscript had gone to press, additional spionids were recovered from specimens of *Allopora venusta* from Monterey County, California (kindly provided by Gay Little), as well as from samples of an encrusting hydrocoral, *Allopora* species near *A. petrograpta* Fisher, 1938, from the lower littoral of the west coast of Vancouver Island, British Columbia. These worms are, in both cases, referred to *Polydora alloporis*.

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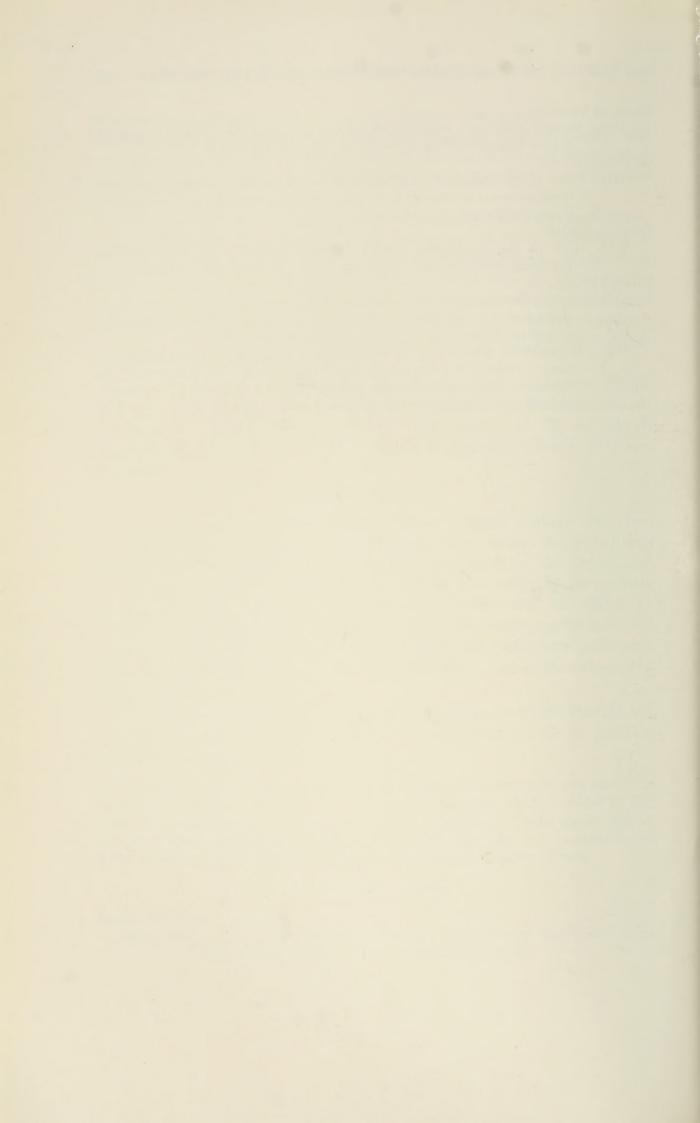
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