



A new species of *Polydora* (Polychaeta: Spionidae) from the Indo-West Pacific and first record of host hermit crab egg predation by a commensal polydorid worm

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A new spionid polychaete, *Polydora robi*, is described from intertidal and shallow subtidal areas in the Philippine Islands and Bali, Indonesia. *Polydora robi* belongs to the *Polydora ciliata/websteri* species group and is characterized by a rounded prostomium, triangular occipital tentacle, needlelike posterior notosetae, and a pygidium with digitiform composite cirri surrounding the anus. Adults burrow into empty gastropod shells inhabited by hermit crabs. The burrows of the worms typically extend from an external opening in the apex of the shells to an opening in the central body whorls along the columella. The species was found to ingest the fertilized eggs and developing embryos attached to the pleopods of host hermit crabs. The occurrence of egg predation and the symbiotic relationship between polydorids and hermit crabs is discussed. Known egg predators of hermit crabs are reviewed.

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ADDITIONAL KEY WORDS:—Annelida – Paguridae – symbiosis – commensalism – feeding – egg predation.

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INTRODUCTION

The Spionidae is one of the largest polychaete families, occupying a variety of marine habitats from sandy bottoms to calcareous substrates worldwide. Blake (1996)

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has reviewed the family and provided a revision of *Polydora* and related genera (termed polydorids, spionid genera that contain a modified fifth segment). Polydorids feed with a pair of peristomial palps and have been classified as deposit, suspension, and combined deposit-suspension feeders (Dauer, Maybury & Ewing, 1981), enabling them to persist in a wide range of habitats. Polydorids from the northwestern Pacific (Japan to the Bering Strait) have been studied in detail (e.g. Radashevsky, 1993). In the southwestern Pacific most work has concentrated on material from Australia and New Zealand (Rainer, 1973; Read, 1975; Blake & Kudenov, 1978; Hutchings & Turvey, 1984).

In spite of the amount of work completed in the north- and southwestern Pacific, little is known of polydorids from tropical and subtropical Indo-West Pacific areas such as the Philippines. Basic studies on the polychaetes from these areas include Grube (1878), Hoagland (1920), and Treadwell (1920, 1942, 1943). Only one polydorid has been identified from the Philippines (Pillai, 1965), although a number of faunistic surveys of polychaetes from the Philippines have been completed (Rosita, 1980, 1983; Palpal-latoc, 1981, 1990, 1994; Palpal-latoc & Gonzales, 1981; Natividad & Palpal-latoc, 1986). Polydorids from Hong Kong (Shin, 1980), the Marshall Islands (Hartman, 1954; Woodwick, 1964), the Solomon Islands (Gibbs, 1971), and the Hawaiian Islands (Hartman, 1966; Ward, 1981, 1987) have been described.

The present study describes a new species of *Polydora* which bores into gastropod shells inhabited by hermit crabs. Data on the adult morphology, ecology, and feeding biology of the species are presented. The worm is documented as a predator of host hermit crab embryos and the nature of the symbioses between polydorids and hermit crabs is discussed. A review of known egg predators of hermit crabs is provided.

MATERIAL AND METHODS

Hermit crabs inhabiting gastropod shells were collected in intertidal and shallow subtidal (<5 m) areas in Batangas (Anilao, 13°46'N, 120°56'E; Sombrero Island, 13°42'N, 120°50'E; Sepoc Point, 13°41'N, 120°50'E), Cebu (Mactan Island, 10°18'N, 123°58'E; Olango Island, 10°16'N, 124°03'E), and Oriental Mindoro (Big Lalaguna Beach, 13°30'N, 120°57'E) provinces of the Philippines and in Bali (Sanur, 8°41'S, 115°15'E) Indonesia from June to August 1997. Specimens were relaxed in 3% magnesium chloride, fixed in 4% formalin-seawater solution (1 part 39% formalin and 9 parts seawater), rinsed in tapwater and stored in 70% ethanol. Worms were removed from burrows by cracking the gastropod shells with a hammer or pliers. Camera lucida drawings were made of adult specimens after fixation. Measurements were made to 0.1 mm using an ocular micrometer. Notes on feeding behaviour and documentation of egg predation were made on live specimens collected at the marine station of the University of San Carlos in Cebu.

Adult morphology was examined with scanning electron microscopy (SEM). Specimens stored in 70% ethanol were dehydrated in an ascending ethanol series followed by four changes of 100% ethanol. Material was dehydrated with Peldri II (Ted Pella, Inc.) by placing the specimens into a 1:1 mixture of 100% ethanol and Peldri II for 1 h at 34°C. The specimens were transferred to 100% Peldri II for 3 h and then placed in a cool water bath and allowed to sublime overnight. Dried specimens were mounted on a copper stub, coated with gold-palladium mixture, and viewed in a JEOL 1200EX SEM.

For histological preparation, worms stored in 70% ethanol were dehydrated in an ascending ethanol series. The specimens were cleared with HemoDE and infiltrated and embedded in Paraplast. Paraplast blocks were sectioned at 5–10 μm (Spencer 820 microtome) and the sections were stained for the presence of yolk with Pantin Trichrome stain.

Specimens are deposited in the Department of Invertebrates, American Museum of Natural History (AMNH) and in the Department of Invertebrates, National Museum of Natural History (USNM).

RESULTS

Family Spionidae Grube, 1850
Genus *Polydora* Bosc, 1802 *sensu* Blake, 1996
***Polydora robi*, sp. nov.**
(Figs 1–4)

Material examined

Collected by J. Williams, Philippines, Batangas: Anilao (13°46'N, 120°56'E): from *Terebra* sp. inhabited by an unidentified hermit crab, 20 Jun 1997 (USNM 186472: 1 paratype); from *Cymatium rubeculum* (Linné), *Latirus turritus* (Gmelin) and *Pisania fasciculata* (Reeve) inhabited by *Clibanarius* sp., *Clibanarius cruentatus* (Milne Edwards), and *Dardanus* sp., 28 Jun 1997 (USNM 186473: 8 paratypes); Philippines, Batangas: Sombrero Island (13°42'N, 120°50'E): from *Drupella cornus* (Röding), *Gyrineum gyrinum* (Linné) and *Latirus turritus* inhabited by *Calcinus latens* (Randall), 5 Jul 1997 (USNM 186474: 5 paratypes); from *Drupella cornus* and *Thais mancinella* (Linné) inhabited by *Calcinus minutus* Buitendijk, 1937 and *Dardanus* sp., 13 Jul 1997 (USNM 186475: 3 paratypes and USNM 186476: 4 paratypes, SEM stub); Philippines, Batangas: Sepoc Point (13°41'N, 120°50'E): from *Cypraea* sp., *Drupa rubusidaeus* (Röding), *Drupella cornus*, *Gyrineum gyrinum* and *Latirus turritus* inhabited by *Calcinus latens*, 5 Jul 1997 (AMNH 4219: 13 paratypes); Philippines, Cebu: Mactan Island (10°18'N, 123°58'E): from *Conus* sp. and *Strombus minimus* (Linné) inhabited by *Calcinus latens*, *Dardanus* sp., and *Diogenes* sp., 7 Jul 1997 (USNM 186477: 5 paratypes); from *Clypeomorus moniliferus* (Kiener) inhabited by *Clibanarius cruentatus*, 8 Jul 1997 (USNM 186478: 1 paratype); Philippines, Cebu: Olango Island (10°16'N, 124°03'E): from *Astraliu rhodostoma* (Lamarck), *Bursa* sp., *Pisania fasciculata*, *Cerithium echinatum* (Lamarck), *Conus* sp., *Cymatium rubeculum*, *Drupella cornus*, *Latirus turritus*, *Oliva* sp., *Tectus conus* (Gmelin) and *Turbo petholatus* (Linné) inhabited by *Calcinus gaimardii* (Milne Edwards), *Calcinus latens*, *Calcinus pulcher* Forest, *Clibanarius* sp., and *Dardanus* sp., 9 Jul 1997 (AMNH 4218: 27 paratypes); Philippines, Puerto Gaera: Big Lalaguna Beach (13°30'N, 120°57'E): from *Drupella cornus* inhabited by *Calcinus minutus*, 21 Jul 1997 (USNM 186471: holotype); from *Cymatium rubeculum* inhabited by *Calcinus gaimardii* and *Clibanarius* sp., 21 Jul 1997 (USNM 186479: 2 paratypes, SEM stub); from *Coralliophila neritoidea* (Lamarck), *Drupella cornus*, *Latirus turritus*, *Morula granulata* (Duclos), *Fasciolaria trapezium* (Linné), *Thais mancinella* and *Turbo petholatus* inhabited by *Calcinus gaimardii*, *Calcinus latens* and *Calcinus minutus*, 31 Jul 1997 (USNM 186480: 49 paratypes); Indonesia, Bali: Sanur (8°41'S, 115°15'E): from *Cerithium echinatum* inhabited by *Calcinus gaimardii*, 6 Aug 1997 (USNM 186481: 1 paratype).

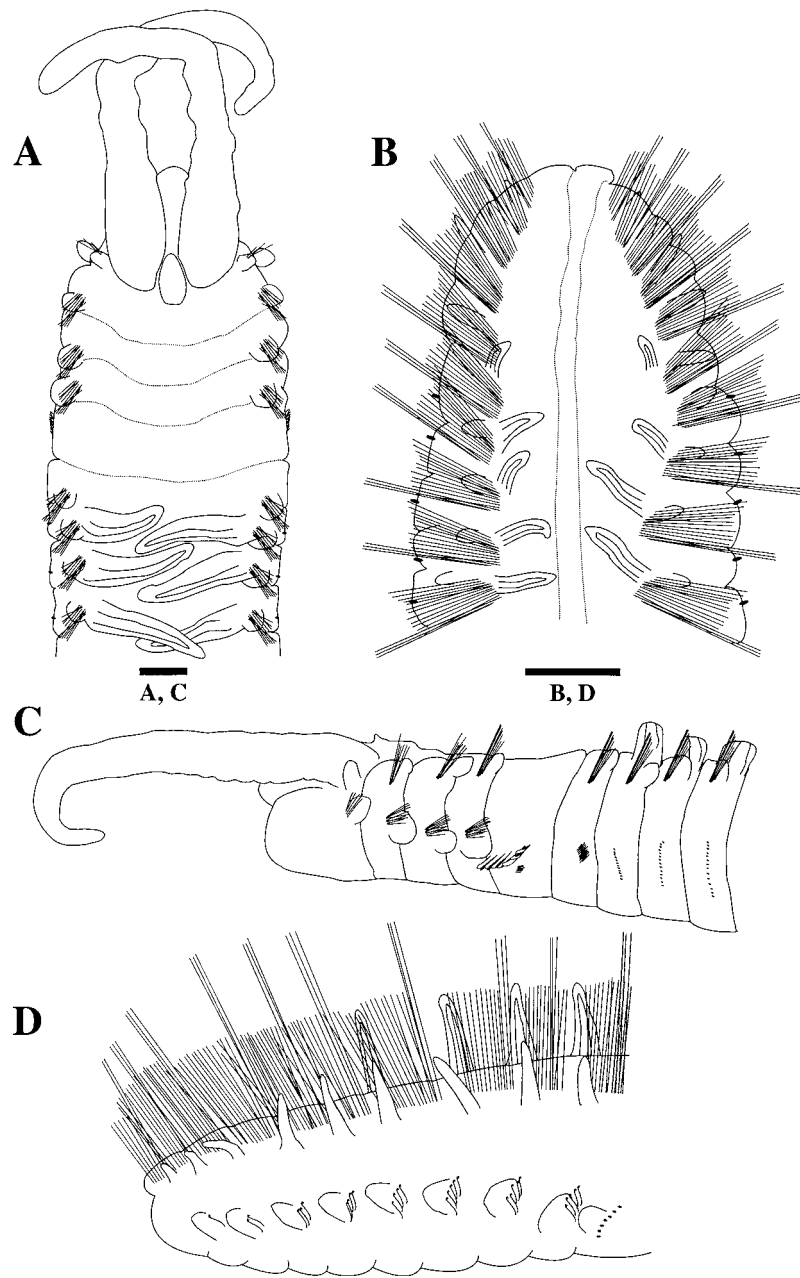


Figure 1. *Polydora robi*, sp.nov. Holotype (USNM 186471). A, anterior end, dorsal view. B, posterior end, dorsal view. C, anterior end, lateral view. D, posterior end, lateral view. Scale bars = 200 μm.

Diagnosis

A moderate-sized *Polydora*; prostomium rounded; caruncle to end of segment 2; occipital tentacle short, triangular. Segment 1 with small notopodia, without notosetae. Segment 5 with falcate spines containing small lateral flange, with ventral

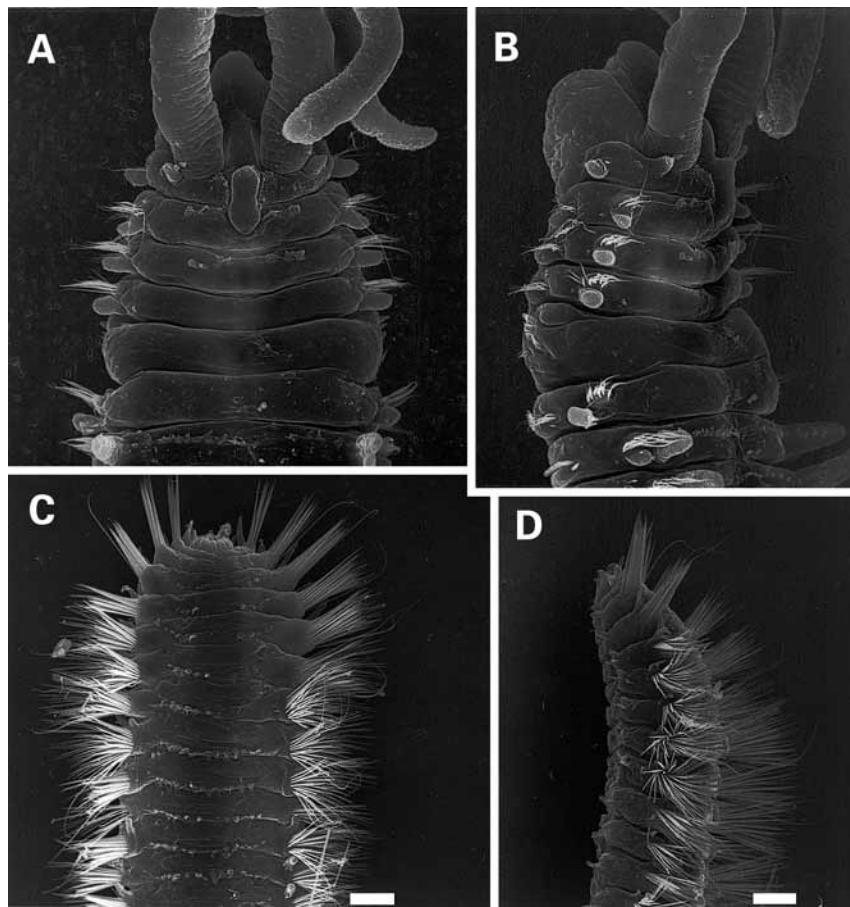


Figure 2. *Polydora robi*, **sp.nov.** SEM micrographs of paratypes. A, anterior end, dorsal view. B, anterior end, lateral view. C, posterior end, dorsal view. D, posterior end, lateral view. Scale bars = 100 μ m. A,B: USNM 186476; C,D: USNM 186479.

tuft of capillaries, notosetae absent. Neuropodial hooded hooks bidentate, present from segment 7. Segments of posterior one-third of body each with few long, thin capillaries anterior to a bundle of 85–95 shorter notosetae. Branchiae from segment 7 to end of body. Pygidium with variable number of digitiform composite anal cirri surrounding anus.

Description

Holotype 25.0 mm long, 1.0 mm wide at segment 7; 117 segments; ovigerous female with developing eggs in segments 20–64. Prostomium rounded; caruncle extending to middle of segment 2; short triangular occipital tentacle at anterior margin of segment 1; eyes absent (Figs 1A,B, 2A,B). Palps extend posteriorly for 10 segments. In life, palps and body pale yellow, without pigmentation.

Segment 1 with neurosetae, without notosetae. Winged capillary notosetae of segments 2–4, 6 and subsequent segments arranged in two vertical rows and a superior group of longer and thinner setae; notosetae from segment 80 to last

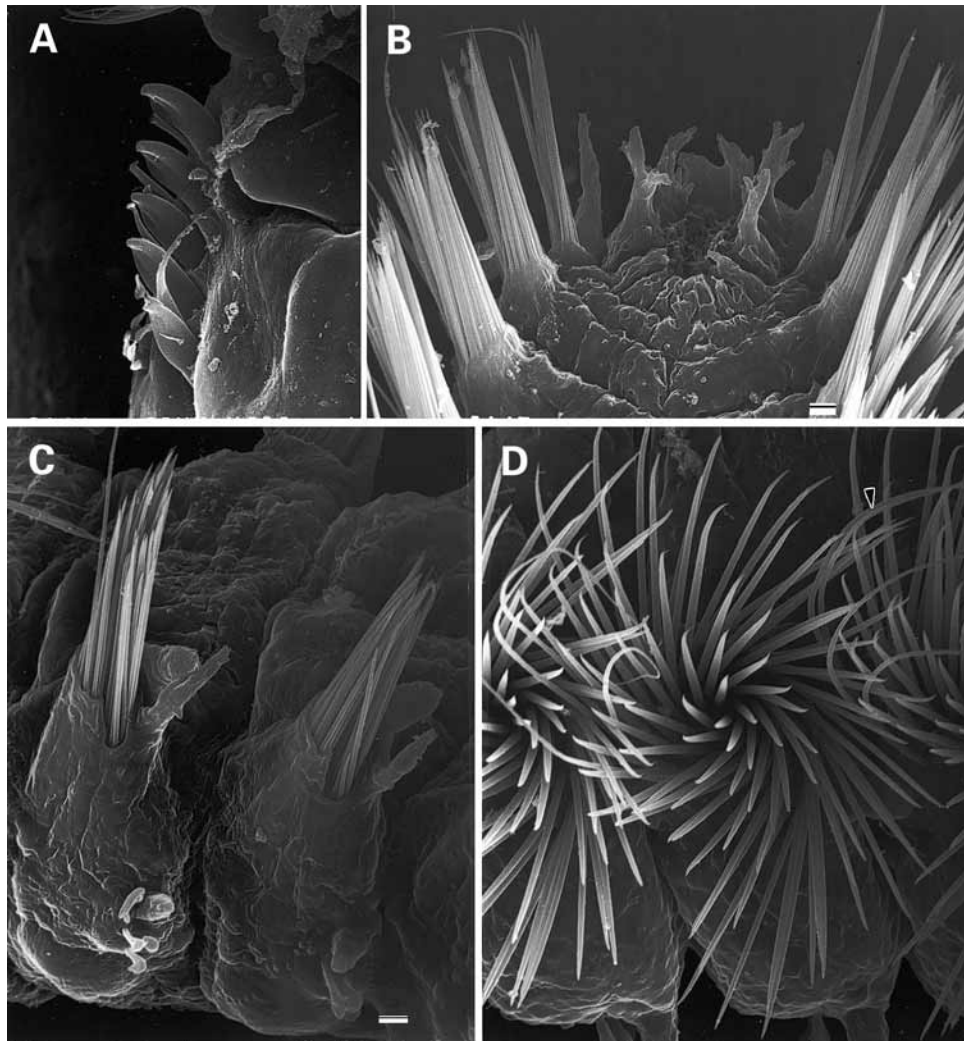


Figure 3. *Polydora robi*, sp.nov. SEM micrographs of paratypes. A, heavy spines and companion setae of fifth segment, dorsal view. B, terminal segments and pygidium, dorsal view. C, posterior notosetae, lateral view. D, posterior notosetae, dorsal view. Arrowhead indicates two of the longer anterior notosetae. Scale bars = 10 μ m. A,D: USNM 186479; B,C: USNM 186476.

segment in flared bundles of fine needlelike spines protruding through cuticle; approximately 95 spines in segment 110 with 2–4 longer anterior notosetae (Figs 1B,D, 2C,D, 3B–D). Winged capillary neurosetae of segments 2–4, 6 and subsequent segments arranged in two vertical rows and an inferior tuft of capillaries. Bidentate hooded hooks from segment 7, not accompanied by capillaries, up to 27 in series at segment 21; hooks with wide angle between main fang and apical tooth, with constriction on shaft (Fig. 4C).

Segment 5 almost twice as large as segments 4 and 6, with slightly curved row of 5 exposed major spines and 2 developing spines alternating with pennoned companion setae; with posteroventral fascicle of 6 winged neurosetae; notosetae

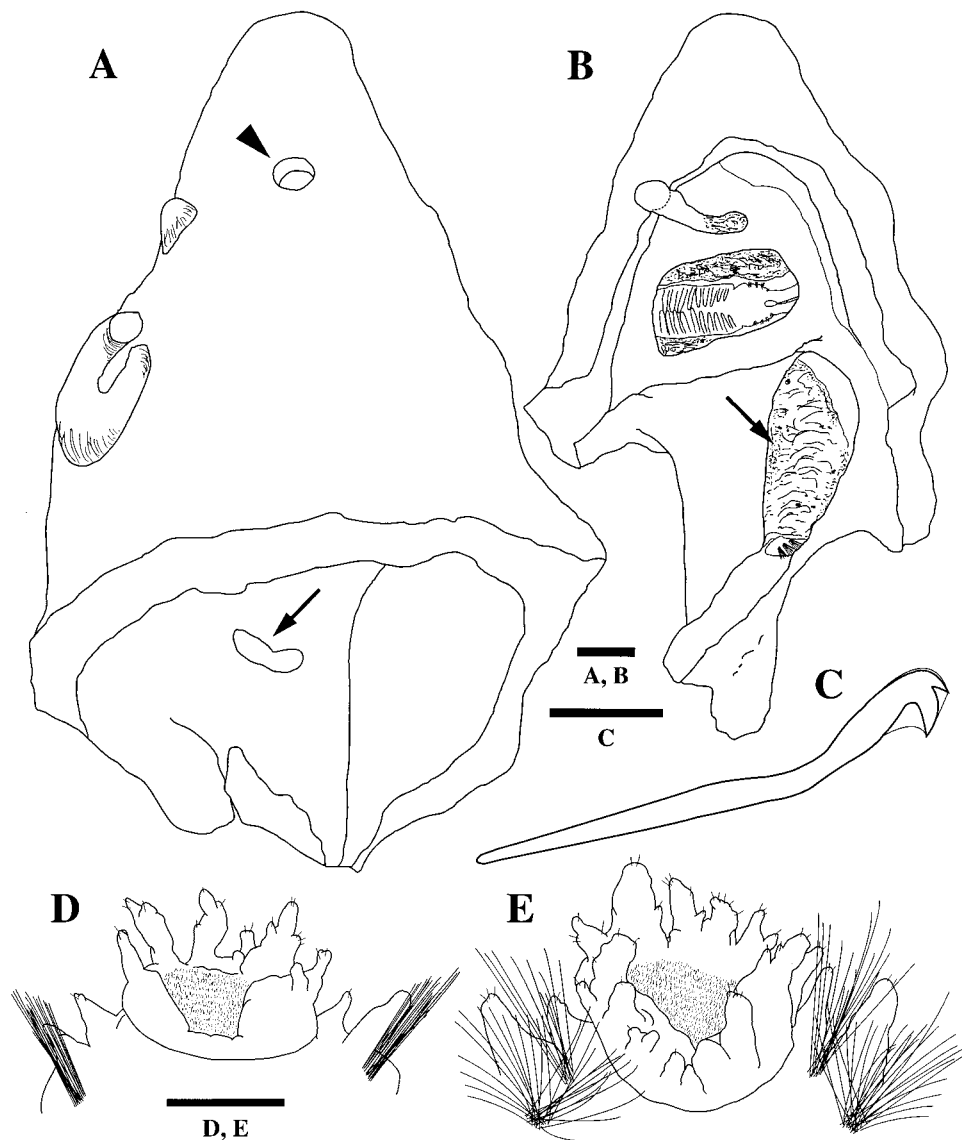


Figure 4. *Polydora robi*, **sp.nov.** Burrow morphology, hooded hook, and pygidium. A, burrow showing openings in apex (arrowhead) and along the columella (arrow). B, exposed burrow showing body of worm and covering of cemented detritus material (arrow). C, neuropodial bidentate hooded hook of holotype (USNM 186471). D,E, pygidium, dorsal views. Scale bars: A,B=1000 µm; C=20 µm; D,E=100 µm.

absent (Fig. 3A). Major spines falcate, with lateral obliquely curved flange (Fig. 3A).

Branchiae from segment 7, continuing to terminal segments of body, small at first, attaining full size by segment 10, diminishing in size in posterior segments. Dorsal ciliary bands present from segment 7. Posterior segments with well developed digitiform notopodia and enlarged neuropodia (Figs 1B,D, 3C).

Pygidium small, with digitiform composite cirri surrounding anus (Figs 2C,D, 3B,

4D,E); anal cirri longer on ventral side of pygidium, with irregular knoblike projections and non-motile cilia (Figs 3B, 4D,E).

Variability

The largest specimen found was that of the holotype; the smallest specimen measured 2.2 mm long and 0.3 mm wide at segment 7 with 36 segments. The prostomium was rounded in all specimens examined. The number of eyes present varied from 0 to 4; 0 and 4 eyes were most common (59.0% and 30.8% respectively, $n=39$). The caruncle length ranged from the middle to end of segment 2. Notosetae were absent on segment 5 of all specimens examined while 4–9 neurosetae were present posteroventrally to 4–8 falcate major spines with a curved flange ($n=39$). Hooded hooks began on segment 7 except in the smallest specimen examined where the hooks began on segment 8. The fine needlelike posterior notosetae are consistent in number and arrangement over the posterior segments, indicating they are true posterior spines and not replacement setae for the longer anterior capillaries. In all specimens examined the posterior notosetae were found to protrude through the cuticle; in some specimens the notosetae are in tight bundles (Fig. 3B,C) while in others the notosetae exhibit a flared, spiral pattern (Figs 2C,D, 3D). Composite anal cirri were variable in number and shape; typically 4–10 digitiform cirri with irregular knoblike projections and non-motile cilia were present.

Ecology

Polydora robi is found in burrows within gastropod shells and appears to be an obligate commensal of hermit crabs. The species was not found in live gastropod shells or dead bivalve shells examined from the sites where hermit crabs were collected. The species has been found intertidally and shallow subtidally to a depth of 5 m in empty shells of the gastropods *Astrarium rhodostoma*, *Cerithium echinatum*, *Clypeomorus moniliferus*, *Conus* sp., *Coralliophila neritoidea*, *Cymatium rubeculum*, *Cypraea* sp., *Drupa rubusidaeus*, *Drupella cornus*, *Fasciolaria trapezium*, *Gyrineum gyrinum*, *Latirus turritus*, *Morula granulata*, *Oliva* sp., *Pisania fasciculata*, *Strombus minimus*, *Tectus conus*, *Terebra* sp., *Thais mancinella* and *Turbo petholatus* occupied by *Calcinus gaimardii*, *Calcinus latens*, *Calcinus minutus*, *Calcinus pulcher*, *Clibanarius cruentatus*, *Clibanarius* sp., *Dardanus woodmasonii* (Alcock), *Dardanus* sp., and *Diogenes* sp. Up to 5 worms have been found in one shell; typically one large female and one smaller male occupy a burrow in the apex. Worms produce a shallow burrow along the columella in the lumen of the central whorls, which is covered by a thin layer of detritus and sand grains (Fig. 4A,B). The tube extends to an opening near the apex of the shell (Fig. 4A,B). The species has been found associated with *Dipolydora armata* (Langerhans).

Feeding

One live specimen of *Polydora robi* was found having ingested the newly fertilized eggs attached to the pleopods of the hermit crab *Clibanarius cruentatus*. Approximately 25 eggs were evacuated from the gut of the worm upon removal from the shell and additional eggs remained in the anterior portion of the gut. The hermit crab had a shield length of 4.05 mm and 1384 eggs attached to pleopods 2 to 4 (pleopod 5 lacking eggs). The 4th pleopod had hairs devoid of eggs, suggesting that the worm removed eggs from this region. Among the preserved worms, 7 additional specimens were found with distended orange guts, the same colour as preserved host hermit

crab eggs. Histological sectioning of two of these worms confirmed the presence of embryos of *Calcinus gaimardii* and *Calcinus pulcher* within the gut. Developing eyes and yolk granules were observed in the hermit crab embryos within the gut of these worms, the same stage of development as the embryos being brooded by the host hermit crabs.

The worms were also observed to suspension feed by extending their palps from the burrow opening in the apex. The palps are moved through the water and transport particles to the mouth for ingestion, primarily by ciliary action along the oral groove. The worms can reverse direction in the burrows allowing access to the lumen of the shell. The eggs attached to the pleopods of the crab are within reach of the palps while the anterior end of the worm is at the tube opening along the columella (Fig. 4B).

Etymology

The species is named in memory of my brother, Robert L. Williams, Jr, who supported this work but sadly missed its completion. His encouragement will always be remembered.

Distribution

Philippines: Batangas, Cebu, and Mindoro Provinces; Indonesia: Bali.

DISCUSSION

Polydora robi belongs to the *Polydora ciliata/websteri* group as defined by Blake (1996). The species resembles *Polydora aura* Sato-Okoshi, *P. latispinosa* Blake and Kudenov, and *P. vulgaris* Mohammad in lacking dorsal notosetae on segment 5 and posterior spines. It differs from these species in possessing a rounded prostomium and a pygidium with anal cirri instead of an incised prostomium and a disc-shaped pygidium. It further differs from *P. aura* in possessing distinct, protruding needlelike posterior notosetae instead of bundles of imbedded needlelike posterior notosetae. Needlelike posterior notosetae have been found in groups of distinct setae or dense flattened packets in a number of polydorids (see Blake, 1979 for summary of forms of posterior notosetae). The distinctive flaring, rotation of the posterior notosetae of *Polydora robi* has not been previously documented in the genus *Polydora* although similar patterns are found in *Dipolydora armata* and *D. rogeri* (Martin, 1996; Williams, pers. obs.).

This is the first record of a polydorid ingesting the eggs of host hermit crabs. *Polydora robi* can be classified as an egg predator (Kuris, 1991) where the term egg is used to indicate embryonic development within an egg membrane attached via a stalk (funiculus) to the pleopodal hairs of brooding hermit crabs. The worm's association with hermit crabs is not species specific and to date the worm has been documented to ingest the eggs of *Calcinus gaimardii*, *Calcinus pulcher*, and *Clibanarius cruentatus*. The mechanics of egg capture and ingestion remain unknown. However, observations of live specimens and histological sections have shown that the worms are able to feed on recently attached eggs up to embryos which are close to hatching. The palps may be used to remove the embryos attached to the pleopodal hairs of

the crab or the worm may feed by pressing the pharynx against the embryos and ingesting (i.e. mouth feeding *sensu* Woodin, 1995). The mechanics and prevalence of egg predation is currently being investigated and will be discussed in subsequent publications (Williams, in prep.).

As suggested by Fotheringham (1976), the potential for egg predation should be examined in polydorids and additional invertebrates with access to the lumen of gastropod shells where the abdomen of host hermit crabs is located. *Nereis fucata* (Savigny), a non-burrowing commensal of hermit crabs, was found to ingest the eggs of *Pagurus prideauxi* Leach and *Pagurus bernhardus* (Linné) (Matthews, 1959; Goerke, 1971). This represents the only other documented case of egg predation by a polychaete worm. Matthews (1959) found the cnidarians *Adamsia palliata* (Müller) and *Podocoryne carnea* (Sars) ingested eggs of *Pagurus prideauxi* under laboratory conditions. Hermit crab egg predation has been found in the turbellarian flatworm, *Stylochus zebra* (Verrill), which ingests the eggs and embryos of *Pagurus pollicaris* (Say) (Lytwyn, 1976, 1979). Nemertean worms are well documented egg predators of decapod crustaceans, but have not been found associated with hermit crabs (e.g. Wickham & Kuris, 1985, 1988; Wickham, 1986; Kuris, 1991). Thus, there are presently 5 species (representing 3 phyla) known to be egg predators of hermit crabs.

Dipolydora commensalis (Andrews), the only other obligate commensal polydorid of hermit crabs (Martin & Britayev, 1998), produces burrows in gastropod shells which extend from the columella and along the inner spiral to the apex. A U-shaped burrow ending in the apex was found in shells occupied by *Pagurus longicarpus* Say examined from the Delaware Bay which may allow access to hermit crab eggs (Williams, unpublished data). Feeding experiments with *Dipolydora commensalis* have shown this worm can ingest particles within the size range of host hermit crab eggs (Williams & McDermott, 1997). Thus, it would not be surprising for this species and other polydorids associated with hermit crabs (e.g. *Polydora biocipitalis* Blake & Woodwick) to prey upon eggs of host female hermit crabs. However, McDermott (1999) reported no apparent relationship between the presence of *Dipolydora commensalis* and the clutch size of *Pagurus longicarpus*.

The present findings of egg predation indicate that the nature of the symbiotic relationship between polydorids and hermit crabs must be reexamined. Additionally, research has shown that hermit crabs inhabiting gastropod shells infested by polydorids may have increased susceptibility to predation due to reduction in the shell strength (Buckley & Ebersole, 1994). The symbiotic association between hermit crabs and polydorids depends on a number of ecological factors, including the reproductive state of the host hermit crabs and the presence of hermit crab predators. Future research directed at the percentage of hermit crab shells infested by polydorids and occurrence of egg predation will help to more accurately define the nature of polydorid/hermit crab symbioses.

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