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Morphology and ecology of a new sexually dimorphic species of *Polydora* (Polychaeta: Spionidae) associated with hermit crabs from Jamaica, West Indies

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Abstract

A new commensal species of *Polydora* was found associated with hermit crabs from shallow subtidal coral reefs in Jamaica, West Indies, in 2005 and 2006. *Polydora nanomon* sp. nov**.** is the third known obligate commensal polydorid of hermit crabs. The species is found in approximately 20% of the gastropod shells, most commonly *Leucozonia nassa leucozonalis* (Lamarck, 1822), inhabited by *Calcinus tibicen* (Herbst, 1791) and other hermit crab hosts. *P. nanomon* sp. nov. produces a hole in the apex of the shell, enters the lumen of the uppermost whorl, and connects to the columella with a tube of mucus and detritus. One large female (up to 70 setigers) is found in the apex with up to four smaller males (generally <30 setigers). Females are distinguished from other species of *Polydora* by the morphology of the major spines of setiger 5. In addition to a horizontal row of major spines with two lateral teeth, companion setae, and ventral capillaries, setiger 5 contains a group of superior accessory spines, including one large falcate spine with a channel extending down the shaft, one spine with a low rounded tooth, and one companion seta. *P. nanomon* sp. nov. exhibits sexual dimorphism with the males being much smaller than females, having a reduced first segment, and lacking accessory spines on setiger 4 (= setiger 5 on females). The occurrence of sexual dimorphism within the family Spionidae is reviewed.

Key words: polychaete, spionid, taxonomy, commensalism, sexual dimorphism

Introduction

The Spionidae is a large family of approximately 450 species of polychaetes, members of which occupy a multitude of marine habitats from the intertidal to the deep sea. Many spionids produce tubes in soft bottom sediments whereas others bore into calcareous substrates. The spionid genus *Polydora* includes species that build tubes in sediment or bore into calcareous substrates such as coral, algae, or mollusc shells (Blake 1996). *Polydora* species are characterized by a modified fifth setiger. Eight additional spionid genera possess a modified fifth setiger with major spines and collectively these genera are termed polydorids.

Over 373 species of polychaetes have been documented as symbionts of other invertebrates (Martin & Britayev 1998). Within the family Spionidae, 43 symbionts are known, all of which are polydorids. These species are associated with various hosts including bivalves, gastropods, sponges, and decapods. In particular, 26 species of polydorids are known to be associated with hermit crabs, boring into the empty gastropod shells occupied by the hosts (Williams & McDermott 2004). Most of these polydorids are facultative symbionts of hermit crabs; only two described were previously known to be obligate symbionts, *Dipolydora commensalis* (Andrews, 1891) and *Polydora robi* Williams, 2000. In addition, Ishikawa & Kase (2007) examined bore

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holes of an undescribed species of *Dipolydora* that presumably is an obligate symbiont of hermit crabs inhabiting gastropod shells from the Philippines.

Hermit crabs from Jamaica were examined for polydorids and found to contain a new species of *Polydora* that bores into the apex of inhabited shells. The gastropod shells typically contained one female worm and 1–4 smaller males. The dwarf males have a much reduced first segment and lack the accessory spines of setiger 5 that are found in females. This type of sexual dimorphism has not been described in any other polydorid species. The present study describes the new species of *Polydora* and provides data on adult morphology, ecology, and sexual dimorphism of the species based on a combination of light and scanning electron microscopy (SEM).

Materials and methods

Hermit crabs inhabiting gastropod shells were collected in shallow subtidal (<5 m) areas in St. Ann's Bay province of Jamaica from May 2005 to August 2006 (Fig. 1). Specimens were relaxed in 7% magnesium chloride, fixed in 4% formalin-seawater solution (1 part 39% formalin and 9 parts seawater), rinsed in warm tap water, and stored in 70% ethanol. Worms were removed by cracking the gastropod shells with a small hammer. The shield length (SL) of host hermit crabs was measured using a vernier caliper or stage micrometer to the nearest 0.1 mm. Notes were made on live specimens collected at the Hofstra University Marine Laboratory in St. Ann's Bay, Jamaica, in August 2006.

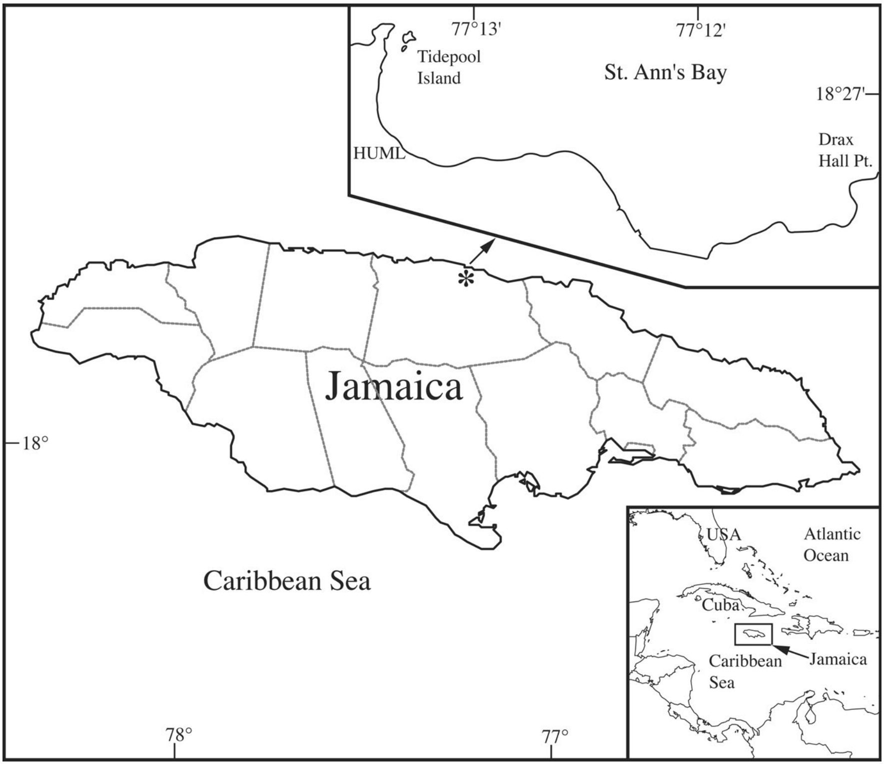


FIGURE 1. Map of Jamaica, West Indies. Asterisk indicates St. Ann's Bay shown in detail at upper right (HUML = former site of the Hofstra University Marine Laboratory).

Sketches of specimens were completed using a compound light microscope with drawing tube attachment; sketches were then scanned into a Macintosh computer and images were prepared using Adobe Illustrator and Adobe Photoshop. Specimens were prepared for viewing with SEM by dehydrating through an ascending series of ethanol concentrations (75%, 80%, 85%, 90%, 95%) for 10 minutes each and 100% ethanol three times for 15 minutes each. Dehydrated specimens were critical-point dried in carbon dioxide using a Samdri 798 Critical Point Dryer. Specimens were mounted on SEM stubs with mounting adhesive, coated with gold in an EMS-550 Sputter Coater and viewed using an S-2460N Hitachi SEM. Type specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D. C., U.S.A. (USNM) and the Goodbody Collection, The Mona Institute of Applied Sciences (an affiliate of the University of the West Indies), Kingston, Jamaica.

Results

Family Spionidae Grube, 1850
Subfamily Spioninae Söderström, 1920
Genus *Polydora* Bosc, 1802
Polydora nanomon sp. nov.

Figures 2–5

Material examined. Holotype. Jamaica, St. Ann’s Bay (18°27' N, 77°12' W), Drax Hall, coral reef, from *Leucozonia nassa leucozonalis* (Lamarck, 1822) inhabited by *Calcinus tibicen* (Herbst, 1791), coll. J. Williams & L. Orensky, 11 Aug 2006 (USNM 1110102).—Allotype. Same data as holotype (USNM 1110103) .—Paratypes. Same location as holotype, from *L. nassa leucozonalis* and *Strombus gigas* Linnaeus, 1758 inhabited by *C. tibicen*, *Phimochirus holthuisi* (Provenzano, 1961), and an unidentified hermit crab, coll. J. Williams, 14 May 2005 (2 female and 2 male paratypes in ethanol, Goodbody Collection 2906); Christopher Cove, coral reef, from *L. nassa leucozonalis* and unidentified gastropod shells inhabited by *C. tibicen*, *Paguristes* sp., and unidentified hermit crabs, coll. J. Williams, 15 May 2005 (11 female and 20 male paratypes in ethanol 1110104; 6 female and 5 male paratypes on SEM stubs, USNM 1110105); Tide Pool Island, muddy sand, from *L. nassa leucozonalis*, *Tegula fasciata* (Born, 1778), and *Cerithium* sp. inhabited by *C. tibicen*, coll. J. Williams, 23 Nov 2005 (4 female paratypes in ethanol, USNM 1110106); same location as holotype, from *L. nassa leucozonalis*, *T. fasciata*, and an unidentified gastropod shell inhabited by *C. tibicen*, coll. J. Williams & L. Orensky, 11 Aug 2006 (7 female and 1 male paratype in ethanol 1110107; 1 female paratype on SEM stub, USNM 1110108); Urchin Cove, coral reef, from *L. nassa leucozonalis*, *Cymatium nicobarium* (Röding, 1798), and unidentified gastropod shells inhabited by *C. tibicen*, *Paguristes* sp., and unidentified hermit crabs, coll. J. Williams & L. Orensky, 12 Aug 2006 (9 female and 2 male paratypes in ethanol 1110109; 1 female paratype on SEM stub, USNM 1110110).

Etymology. The species epithet *nanomon* (derived from the Greek *nano* for dwarf and the Jamaican slang *mon* for man) refers to the dwarf males in this species.

Diagnosis. Female: Moderately sized ~12 mm (up to 79 setigers) *Polydora* species that bores into gastropod shells inhabited by hermit crabs. Prostomium weakly incised on anterior margin, two eyes present or both eyes lacking; caruncle extending to end of setiger 2; triangular occipital tentacle present between base of palps. Setiger 1 with small notopodia, lacking notosetae. Setiger 5 modified, with falcate spines possessing two lateral teeth, group of accessory spines dorsal to major spines, with ventral group of capillary neurosetae. Neuropodial hooded hooks bidentate, present from setiger 7. Branchiae from setiger 7 on first two thirds of the body. Pygidium cup-shaped.

Male: Small ~4 mm (up to 31 setigers) with reduced segment 1 lacking notosetae, neurosetae and corresponding lobes. No observable caruncle or occipital tentacle. Setiger 4 modified (= setiger 5 on females) containing falcate spines with two lateral teeth, lacking accessory spines and ventral group of neurosetae.

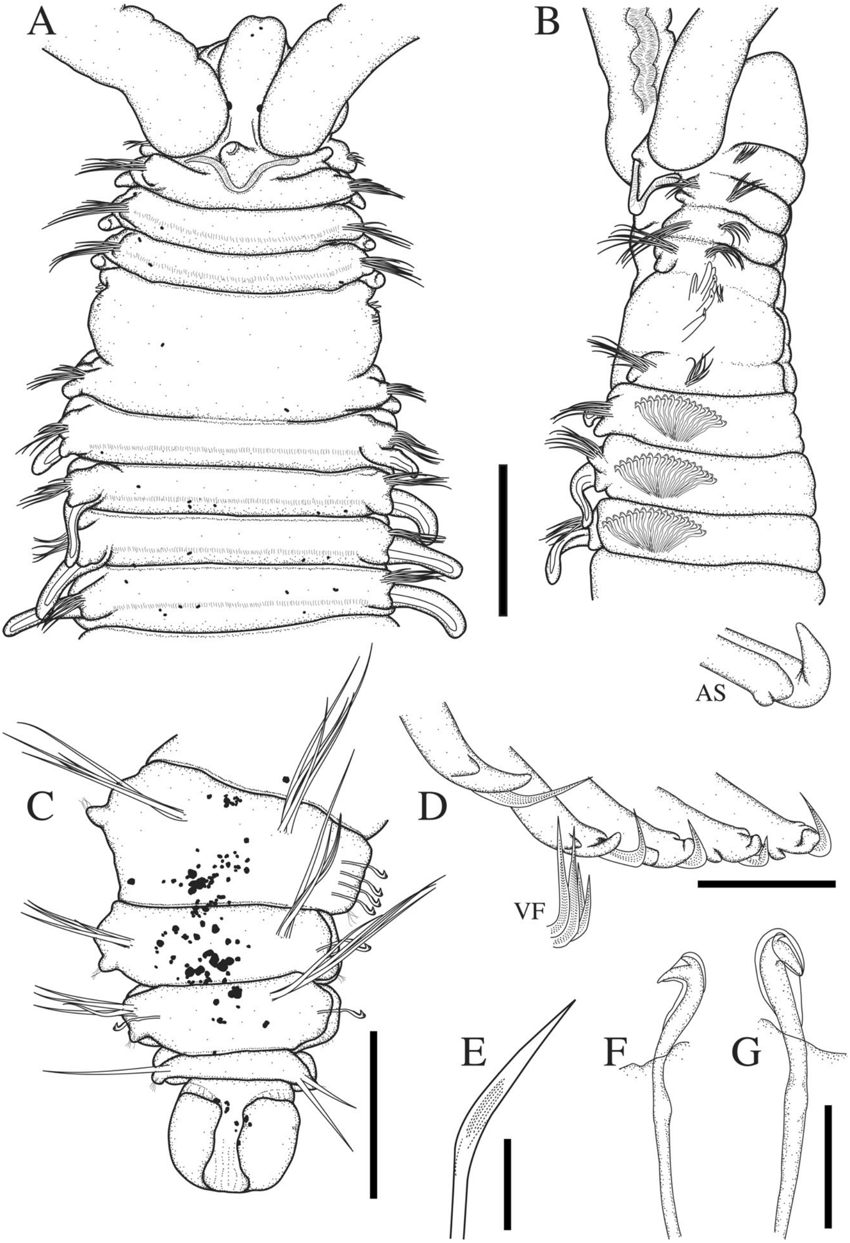


FIGURE 2. *Polydora nanomon* sp. nov. A–B, E, holotype (USNM 1110102); D, female paratype (USNM 1110109); C, F–G, female paratype (USNM 1110104). A, anterior end, dorsal view; B, anterior end, lateral view; C, posterior end and pygidium, dorsal view; D, major spines of setiger 5, lateral view (AS = accessory spines, VT = ventral fascicle of notosetae); E, notoseta from setiger 5; F, neuropodial hooded hook from setiger 31, lateral view; G, neuropodial hooded hook from setiger 31, oblique-lateral view. Scale bars: A–B = 500 µm; C = 100 µm; D = 50 µm; E–G = 25 µm.

Neuropodial hooded hooks bidentate, present from setigers 6 or 7. Branchiae from setigers 6 or 7. Pygidium reduced, nub-like.

Description. Holotype: complete female specimen of 68 setigers, 12.04 mm long, and 0.57 mm wide at setiger 7. Prostomium weakly incised on anterior margin; caruncle extending to posterior margin of setiger 2; two round black eyes present; triangular occipital tentacle present behind eyes and between base of palps (Figs. 2A–B, 3A–C). Palps extending posteriorly for approximately 20 setigers, palps with a longitudinal food groove lined by frontal cilia, presumably non-motile cirri on papillae along lateral edges of food groove and scattered on the abfrontal surface (lack of motility of cirri and presence of laterofrontal cilia needs to be confirmed in live specimens) (Fig. 3A). Color in alcohol opaque white, no pigmentation.

Setiger 1 with neurosetae, without notosetae, with notopodial lobes (Figs. 2A–B, 3B, D). Winged capillary notosetae of setigers 2–4, 6 and subsequent setigers in 2 vertical rows (Fig. 3D); without specialized posterior notosetae. Fifteen bidentate hooded hooks from setiger 7, not accompanied by capillaries, increasing to 21 hooks in series at setiger 14; hooks with nearly right angle between main fang and shaft and wide angle between main fang and apical tooth, with constriction on shaft (Fig. 2F–G).

Setiger 5 approximately twice as large as setigers 4 and 6, with slightly curved row of six exposed major spines, major spines alternating with pennoned companion setae; with ventral fascicle of two winged capillary neurosetae (Figs. 2D–E, 3F–G). Major spines falcate, with two lateral teeth (Figs. 2D, 3F–G). Group of accessory spines superior to major spines, consisting of one large falcate spine with a channel extending along shaft, second spine smaller, with low, rounded tooth and one companion seta (Fig. 3H).

Branchiae from setiger 7, free from notopodial postsetal lamellae, continuing to posterior setigers; branchiae overlapping from setiger 8 to middle setigers, decreasing in length posteriorly (Figs. 2A, 3A–C). Bands of dorsal cilia extending between notopodia of setigers 3 and 4, ciliary bands between branchiae of setiger 7 and subsequent setigers (Figs. 2A, 3C). Lateral organs present between notopodial and neuropodial lamellae on setigers 1–4, 6 and subsequent setigers, lateral organs largest on setiger 1 (Fig. 3D). Cilia on notopodia of posterior setigers. Pygidium broad, cup-shaped with dorsal gap (Figs. 2C, 5A–B).

No gizzard-like structure present in digestive tract. Glandular pouches in setigers 7–10, largest in setiger 8.

Allotype. Complete male specimen of 27 setigers, 3.67mm long and 0.20mm wide at setiger 7. Prostomium rounded (slightly bifid in other specimens); no observable caruncle; eyes lacking; occipital tentacle lacking (Figs. 4A–C, 5C–E). Palps extending posteriorly for approximately eight setigers, ciliation pattern as in holotype. Color in alcohol opaque white, with diffuse black pigmentation on prostomium between palps.

Segment 1 without notosetae, neurosetae or associated lobes (Figs. 4B–C, 5D–E), appearing to be coalesced with prostomium. Winged capillary notosetae of setigers 1–3, 5 and subsequent setigers in two vertical rows. Four bidentate hooded hooks begin on setiger 7 (= segment 8), not accompanied by capillaries, up to five in series at setiger 13; hooks with nearly right angle between main fang and shaft, wide angle between main fang and apical tooth, with constriction on shaft (Fig. 4D).

Setiger 4 (= segment 5 on females; see Remarks) approximately twice as large as setigers 3 and 5, with slightly curved row of three exposed major spines, major spines alternating with pennoned companion setae; notosetae and neurosetae absent (Figs. 4E, 5F–G). Major spines simple, falcate, with one large and one shallow lateral flange (Figs. 4E, 5F–G); accessory spines found in females are lacking.

Branchiae from setiger 6 (= segment 7), free from notopodial postsetal lamellae, continuing to posterior setigers; branchiae short, not overlapping, decreasing in length posteriorly and absent from middle to posterior setigers (Figs. 4B, 5D). Pygidium reduced, nub-like (Figs. 4F, 5H).

No gizzard-like structure present in digestive tract. Glandular pouches in setigers 6–9, largest in setiger 8.

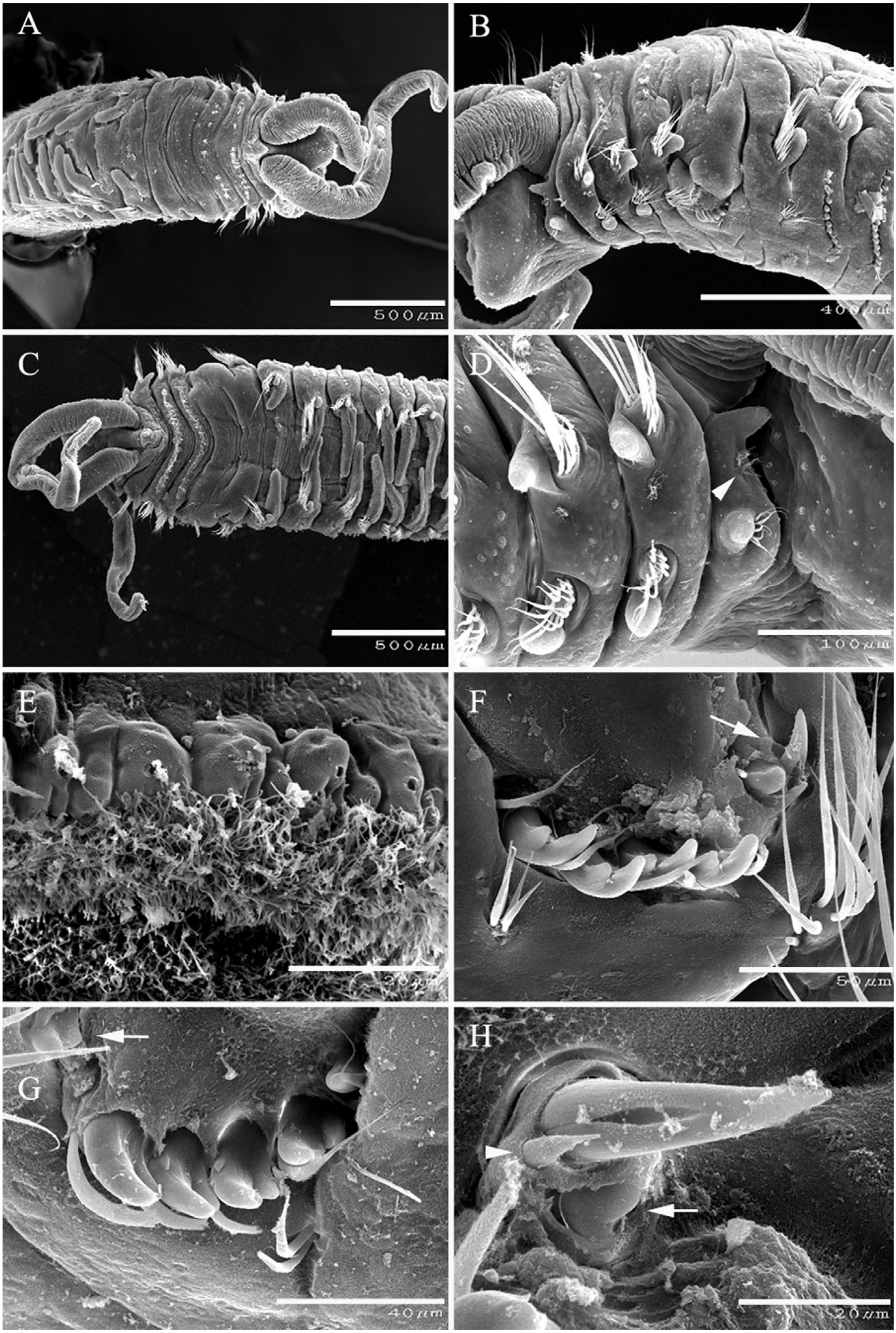
Variation. Females sometimes exhibit slight irregular pigmentation patches on the dorsal side of anterior and posterior segments. Females contain 39–79 setigers (55.9 ± 10.8 setigers, n = 23) with eggs in setigers 21–37; males contain 19–34 setigers (27.9 ± 3.5 setigers, n = 29) with sperm in setigers 11–22. Both males and females typically possess two eyes but individuals with one eye have been found. In males, hooded hooks begin on setiger 6 or 7 (= segments 7 or 8), sometimes accompanied by a capillary neuroseta; 3–6 hooded hooks begin on setiger 6 or 7 and up to six are found by segment 17 (average maximum number of hooded hooks, 4.67 ± 0.87, n = 24). In females, 5–16 hooded hooks begin invariably on setiger 7 and up to 21 hooded hooks are found by segment 16 (average maximum number of hooded hooks, 14.11 ± 3.69, n = 24). Males possess 2–4 major spines (3.04 ± 0.65, n = 27) and lack accessory spines; females possess 3–6 major spines (4.69 ± 0.85, n = 33) plus accessory spines.

Remarks. The only polydorid previously documented from Jamaica was the sponge associate *Polydora colonia* Moore, 1907 [see Delgado-Blas (2008) for a review of polydorids from the Caribbean Sea]. *P. colonia* was found in Jamaica by Jones (1962) who described a new species (*P. ancistrata*), but later Blake (1971) considered the species to be synonymous with *P. colonia*. *P. nanomon* sp. nov. is distinct from all members of the genus based on the morphology of setiger 5; female worms exhibit a horizontal row of major spines with two lateral teeth, companion setae, and ventral capillaries. The fifth setiger also contains a group of accessory spines, consisting of one large falcate spine with a channel extending down the shaft, one spine with a low, rounded tooth, and one companion seta. These spines can be difficult to see because they often protrude only slightly through the cuticle. The large falcate spines are similar in morphology to the provisional spines found in juvenile *P. heterochaeta* Rioja, 1939 and other polydorids (Blake 1996); however, in the Jamaican species the spines are retained in adult females. Radashevsky & Fauchald (2000) mentioned a species of *Polydora* from Vietnam that retains provisional setae of setiger 5 until the 50-setiger stage but the species remains undescribed (Radashevsky, pers. comm.). The provisional spines of *P. heterochaeta* have a channel extending down the shaft, similar to that found in *P. nanomon* sp. nov. It is possible that the channel functions in the delivery of acidic secretions used in dissolving the shell matrix during the boring process [see Blake (1996) and Sato-Okoshi & Kenji (2000) for review of the shell boring process in polydorids].

Polydora nanomon sp. nov. can also be distinguished from other *Polydora* species by its sexual dimorphism. Males are much smaller than the females and have a reduced first segment that lacks setae. The reduction of segment 1 can create confusion when comparing arrangement of setae between males and females. Males possess major spines on setiger 4 (= segment 5) homologous with the setiger 5 spines of females (see Fig. 4B for designation of segments/setigers in males). Males possess fewer major spines, branchiae, and hooded hooks, their pygidium is nub-like rather than cup-shaped, and hooded hooks begin on setiger 7 (= segment 8). The digestive tract of males was often filled with lipid droplets, with setigers 11–20 containing the largest droplets, which decreased in size posteriorly.

Ecology. *Polydora nanomon* sp. nov. is found in burrows within gastropod shells inhabited by hermit crabs from shallow subtidal coral reef areas. Overall, 23.0% (37/161) of shells contained this species in 2005 and 17.3% (24/139) of shells contained the worm in 2006. Of the shells with *P. nanomon* sp. nov., 45.9 % were inhabited by *C. tibicen* (mean SL, 3.9 ± 0.7 mm, n = 25), 37.7 % were inhabited by *Paguristes* sp. (mean SL, 4.1 ± 0.8 mm, n = 14), and the rest (16.4%) were inhabited by *P. holthuisi* and unidentified species of hermit crabs. The worms were not found in live gastropod shells examined from sites where hermit crab shells were collected; thus, the species appears to be an obligate commensal of hermit crabs. The species was found subtidally to a depth of 5 m in empty shells of *L. nassa leucozonalis*, *T. fasciata*, *C. nicobarium*, *Cerithium* sp., and other unidentified gastropods occupied by hermit crabs. In shells that contained the polydorid, typically one large female and 1–4 smaller males were found per shell.

FIGURE 3. *Polydora nanomon* sp. nov. A–G, female paratypes (USNM 1110105); H, female paratype (USNM 1110108) SEM micrographs. A, anterior end, dorsal view; B, anterior end, lateral view; C, anterior end, dorsal view; D, setigers 1–3, lateral view (arrowhead indicates lateral organ of setiger 1); E, midsection of palp, oblique-lateral view with dorsal food groove on bottom; F, major spines of setiger 5, lateral view (arrow indicates accessory spines); G, major spines of setiger 5, lateral view, arrow indicates accessory spines; H, accessory spines of setiger 5, falcate spine with channel down shaft shown at top (arrowhead indicates companion seta; arrow indicates spine with low rounded tooth). Scale bars: A, C = 500 µm; B = 400 µm; D = 100 µm; E, H = 20 µm; F = 50 µm; G = 40 µm.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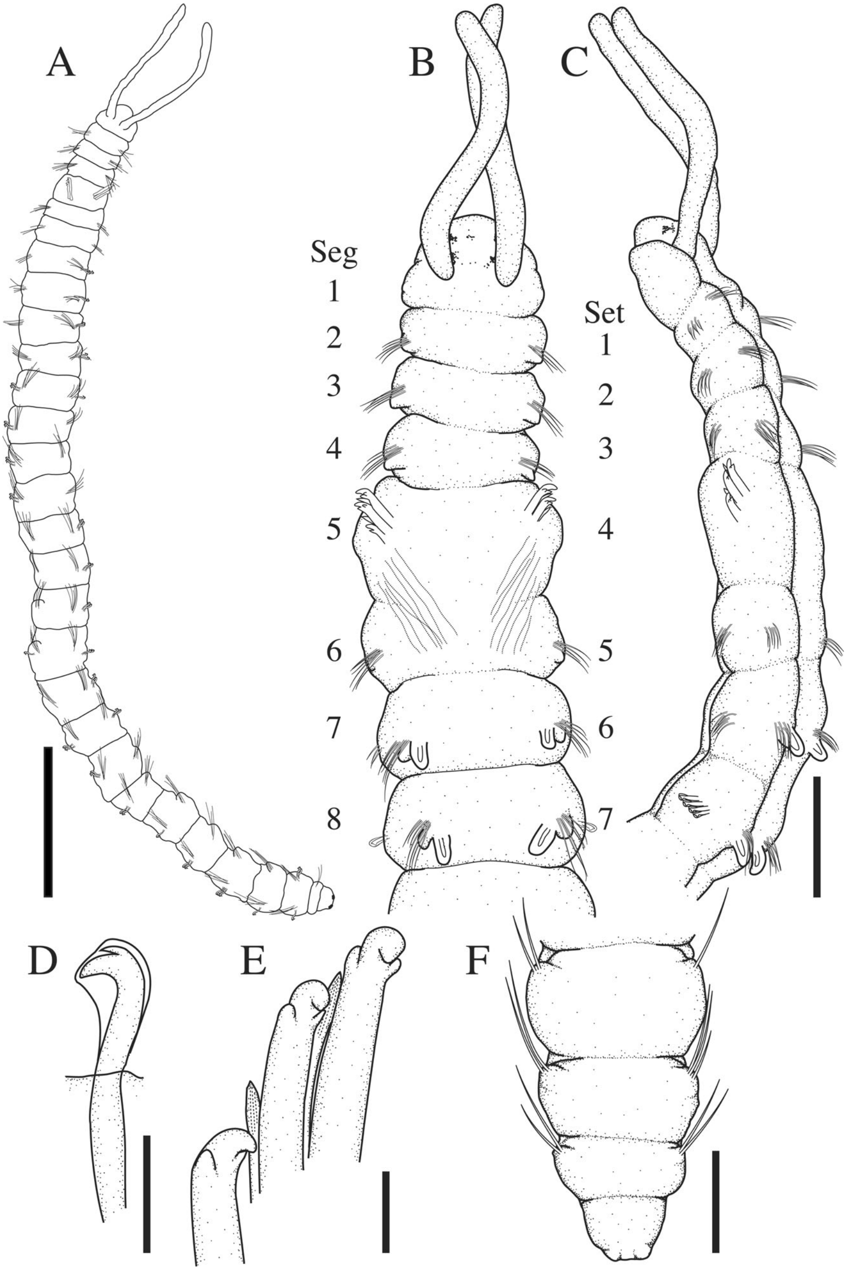

FIGURE 4. *Polydora nanomon* sp. nov. A, D–F, male paratypes (USNM 1110104); B–C, allotype (USNM 1110103). A, complete specimen, dorsal view (branchiae not shown); B, anterior end, dorsal view (numbers to left indicate segments [SEG], numbers to right indicate setigers [SET]; C, anterior end, lateral view; D, neuropodial hooded hook from setiger 17; E, major spines of setiger 5, dorsal view; F, posterior end and pygidium, dorsal view. Scale bars: A = 500 µm; B–C = 75 µm; D–E = 12.5 µm; F = 125 µm.

Burrow openings were observed on the external surface of the gastropod shells near the apex. Females of *P. nanomon* sp. nov. typically produce a hole near the apex of the shell that enters the shell lumen in the uppermost whorl. The hole connects to the columella of the shell with a tube of detritus and mucus that winds around the columella, opening in the lumen of the shell. In life, palps of the worms were observed extending from the hole in the apex in order to suspension feed or to deposit feed on the surface of the shell surrounding the hole. The males create burrows within the detrital matrix of the females' tube. Although females were not able to crawl when removed from their burrows, males crawled rapidly among the detrital tubes associated with the female burrows and also along the bottom of glass dishes when isolated. The ability to crawl has been suggested as a character to distinguish between boring and non-boring polydorid species (Sato-Okoshi 1999) but the present findings indicate that this behavior can also vary between sexes. The males of *P. nanomon* sp. nov. appear to be mobile within the detritus burrows associated with females; their feeding biology and mode of fertilization remain unknown.

Discussion

Polydora nanomon sp. nov. is the third known obligate commensal of hermit crabs: *Dipolydora commensalis* and *P. robi* are the two previously described obligate polydorids (Williams & McDermott 2004). Both *P. nanomon* sp. nov. and *P. robi* create burrows that begin with a hole near the apex, enter the lumen, and wind around the columella as a mucus/detritus tube and end in the upper whorls of the shell (Williams 2000). In contrast, females of *D. commensalis* create a burrow in the gastropod shell that begins on the columella near the aperture and winds around it before reaching the apex where it may loop over onto itself (Williams, pers. obs.). Presumably, as found in *D. commensalis* and *P. robi*, females of *P. nanomon* sp. nov. are able to reverse directions in their burrows. Although *D. commensalis* and *P. robi* are known to be egg predators of host hermit crabs (Williams 2000; Williams & McDermott 2004), the feeding biology of *P. nanomon* sp. nov. remains unknown. No evidence of hermit crab eggs were found in the guts of *P. nanomon* sp. nov. in spite of over 20 occasions where they inhabited shells occupied by ovigerous hermit crabs.

P. nanomon sp. nov. is similar to *D. commensalis* in having multiple worms per shell, including a large female and multiple smaller males. Although *D. commensalis* exhibits sexual size dimorphism [see Vollrath (1998) for review of dwarf males in other phyla], no studies have shown differences in morphological features of males and females as in *P. nanomon* sp. nov. In addition to *P. nanomon* sp. nov. and *D. commensalis*, sexual dimorphism has been reported in only one other polydorid, *Pseudopolydora primigenia* Blake, 1983, a species in which males possess an extra pair of branchiae on setiger 2 (Blake 1983). Males of *Pygospio elegans* Claparède, 1863 and *P. californica* Hartman, 1936 also possess additional structures on setiger 2. These were first thought to be auxillary branchiae (Foster 1971; Light 1978) but were later shown to be paired dorsal appendages with a ciliary groove (Schlötzer-Schrehardt 1986, 1987, 1991). Schlötzer-Schrehardt (1991) proposed that males use the dorsal appendages in combination with dorsal organs to transfer spermatophores to females. Males of *Scolelepis vazaha* Eibye-Jacobsen & Soares, 2000 sometimes exhibit additional notopodial hooks on setigers 5 and 6 (found only in setiger 4 of females) as well as swollen notopodial lobes from setiger 5–8 and dorsal organs on setigers 11–20, whereas females do not exhibit such structures (Eibye-Jacobsen & Soares 2000). Finally, *Scolelepis laonicola* (Tzetlin, 1985) has a unique form of sexual dimorphism in which males are dwarf ectoparasites of females (Tzetlin 1985). Originally the males were described as a new species of the parasitic genus *Asetocalamyzas* parasitizing *Laonice cirrata* (Tzetlin 1985); since that time it has been determined that the "host" females belong to the genus *Scolelepis* (Vortsepneva et al. 2006, 2008). Sexual dimorphism is rare within spionids, to our knowledge having only been documented in the seven species described above. Unlike the examples described above, where males exhibit extra branchiae or appendages, the dwarf males of *P. nanomon* sp. nov. are reduced and lack features found in females. The small size of the males and lipid content in the gut suggests paedomorphosis, as found in other polychaetes (Rouse et. al. 2004, 2008; Struck 2006). However, since the larvae of *P. nanomon* sp. nov. are unknown, developmental studies are needed to address questions on the apparent loss of these features in males.

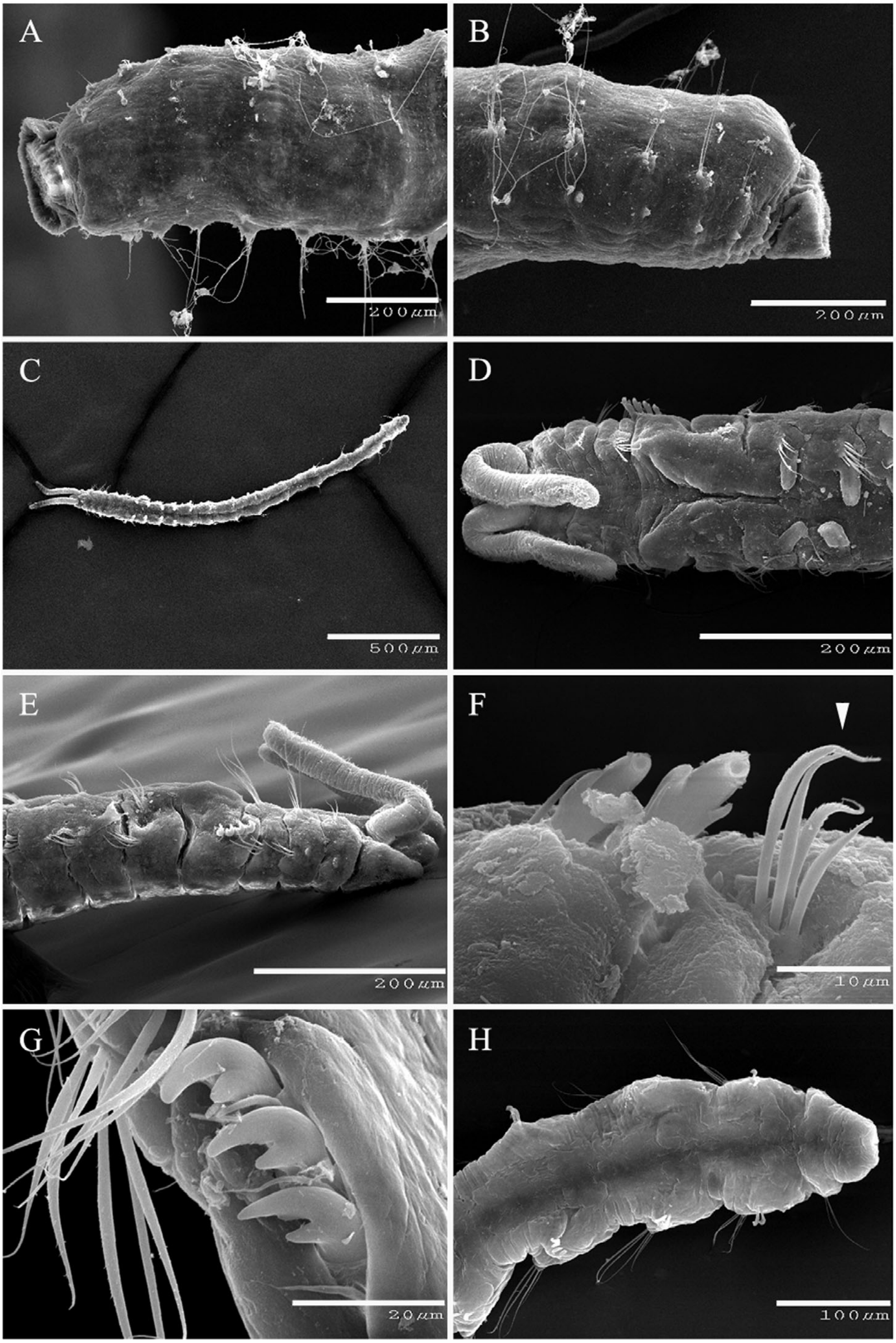
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FIGURE 5. *Polydora nanomon* sp. nov. A–B, female paratype (USNM 1110105); C–H, male paratypes (USNM 1110105) SEM micrographs. A, posterior end, dorsal view; B, posterior end, lateral view; C, complete specimen, dorsal view; D, anterior end, dorsal view; E, anterior end, lateral view; F, major spines of setiger 5, dorsal view (arrowhead indicates notosetae of setiger 4); G, major spines of setiger 5, lateral view; H, posterior end, dorsal view. Scale bars: A–B, D–E = 200 µm; C = 500 µm; F = 10 µm; G = 20 µm; H = 100 µm.

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