

MORPHOLOGY, ECOLOGY, AND REPRODUCTION OF A NEW *POLYDORA* SPECIES FROM THE EAST COAST OF NORTH AMERICA (POLYCHAETA: SPIONIDAE)

Jason D. Williams¹ & Vasily I. Radashevsky²

¹Department of Biological Sciences, 100 Flagg Road, University of Rhode Island, Kingston,
RI 02881-0816, USA

²Institute of Marine Biology, Vladivostok 690041, Russia

ABSTRACT

A new spionid polychaete species, *Polydora neocaeca*, is described from intertidal and shallow subtidal areas in Rhode Island on the east coast of North America. Adults bore into shells of living gastropods, gastropod shells occupied by hermit crabs, and bivalve shell fragments. Females deposit 13-24 egg capsules joined in a string from June-November. Each egg capsule is attached by two stalks to the inside wall of the burrow and contains 8-47 eggs, for a mean of 481 eggs per brood. The eggs have an average diameter of 116 µm. Development occurs within the egg capsules until the 3-segment stage at which time planktotrophic larvae are released. A series of adult morphological characters was examined and found to vary extensively in body pigmentation but less so in palp pigmentation, prostomium shape, presence of neurosetae and notosetae of the fifth segment, and caruncle length. *Polydora neocaeca* belongs to the *Polydora ciliata/websteri* species group and is characterized by palps crossed by black bars, incised prostomium, and caruncle extending up to the middle of segment 4. *Polydora* species with banded palps are reviewed and systematic revision of *P. agassizi* Claparède, 1869 and *P. limicola* sensu Hartman (1961) is proposed.

INTRODUCTION

Spionid polychaetes of the genus *Polydora* along the Atlantic coast of North America from Newfoundland to South Carolina were reviewed by Blake (1971) who recognized 12 species which he described and illustrated. Systematic and ecological studies of some *Polydora* species from the east coast of North America have been provided since that time, including new records of two known species and the description of a new species (Maciolek 1984). Blake (1996) has recently resurrected and redefined the genus *Dipolydora* Verrill, to which a number of former *Polydora* species have been referred. Thus, only four species in the newly restricted genus *Polydora* have been reported to occur along the east coast of North America: *P. aggregata* Blake, 1969, *P. colonia* Moore, 1907, *P. cornuta* Bosc, 1802, and *P. websteri* Hartman, 1943.

A *Polydora* species, distinct from these four species, was discovered during a survey of polydorids from Rhode Island. The species was found to match Webster's (1879) description of *Polydora caeca*, a borer of oyster shells from Virginia. However, *Polydora caeca* Webster is the permanently invalid secondary homonym for which Hartman (1943) proposed the replacement name *Polydora websteri*. Rediscovery of specimens matching Webster's description and examination of Hartman's material inspired a taxonomic revision which ultimately led to a change in the status of *Polydora websteri* (Radashevsky & Williams 1998; Radashevsky 1999). In order to serve taxonomic stability a new nominal species, *Polydora neocaeca*, is described to replace the permanently invalid name *P. caeca*. Until now, only the sperm ultrastructure of *Polydora neocaeca* has been described (Williams 1997).

The purpose of the present report is to describe and document the adult morphology and larval development of *Polydora neocaeca*. Variation within a series of adult morphological characters is quantified. Data on the ecology and reproduction of the species is also presented. A comparison of *Polydora neocaeca* is made with closely related species of the *Polydora ciliata/websteri* group.

We thank Kenneth A. Thomas and Paul W. Johnson for help in EM preparation and use of the JEOL electron microscope. We are greatly indebted to Mary E. Petersen (Zoological Museum, University of Copenhagen) and Linda Ward (Smithsonian Institution, Washington D.C.) for providing the literature. The comments and discussion of James A. Blake, Christopher B. Boyko, and three anonymous reviewers are greatly appreciated. The investigation was supported in part by the Research Grant 97-04-49731 from the Russian Foundation for Basic Research and by a Visiting Scientist Fellowship (to VIR) from the National Museum of Natural History, Smithsonian Institution.

MATERIALS AND METHODS

Field collections were made from two sites in Rhode Island, Atlantic coast of North America. Living gastropods, living bivalves, shell fragments and gastropod shells inhabited by hermit crabs were collected intertidally and shallow subtidally up to 2 m depth from September 1995 to November 1996. *Polydora* specimens were removed from their burrows by cracking the mollusc shells with a hammer or pliers.

Following removal of the worms, burrows were examined for the presence of egg capsules. Larvae were examined with video-microscopy and differential interference contrast microscopy (DIC) after relaxation in 3% magnesium chloride. Composite line-drawings of larvae were produced by a combination of camera lucida sketches and video-images. Adults, eggs, and larvae were measured using an ocular micrometer.

Adult worms were relaxed in 3% magnesium chloride prior to the production of camera lucida drawings. Variation in the following characters was quantified (mean \pm SD): 1) distribution of pigmentation, 2) caruncle length, 3) number of major spines of fifth segment, 4) number of eyes, 5) prostomium

shape, and 6) presence of neurosetae and notosetae on the fifth segment. The type material was fixed in 10% formaldehyde, stored in 70% ethyl alcohol, and deposited in the United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and in the Institute of Marine Biology, Vladivostok (IMBV).

Adult morphology was also examined with SEM. Specimens were fixed for 2 hr in 3% glutaraldehyde in Na-cacodylate buffer (pH 7.2) with 3% NaCl, rinsed with Na-cacodylate buffer (three 30 min changes), and dehydrated in an ascending ethanol series at 4°C. After warming to room temperature in 95% ethanol, the specimens were placed in four changes of 100% ethanol. Dehydration was achieved with Peldri II (Ted Pella, Inc.) by placing the specimens into a 1:1 mixture of 100% ethanol and Peldri II for 1 hr in a warm water bath (34°C). The specimens were transferred into 100% Peldri II for 1.5 hr and then placed into a cool water bath (15°C) and allowed to sublime overnight. Dried specimens were mounted on stubs, coated with gold-palladium mixture, and viewed in a JEOL 1200EX SEM.

RESULTS

Family Spionidae Grube, 1850

Genus *Polydora* Bosc, 1802 sensu Blake, 1996

Polydora neocaeca sp. nov.

Figs. 1-5

Polydora caeca Webster, 1879, pp. 252-253, pl. 9: figs. 119-122. ?Andrews, 1891, p. 291. Not *Leucodorum coecum* Örsted, 1843.

?*Polydora limicola*: Sato-Okoshi & Okoshi, 1997, p. 486. Not Annenkova 1934.

Material. – Collected by J. Williams, Rhode Island, Atlantic coast of North America: on the mudflat of Bluff Hill Cove ~26‰ (41°23'N, 71°30'W): from shell fragment of *Mya arenaria* Linné, 1 Oct 1996 (USNM 182878: holotype); from living *Crepidula fornicata* Linné, from *Busycotypus canaliculatus* Linné, *Ilyanassa obsoleta* Say, *Littorina littorea* Linné, and *Urosalpinx cinerea* Say inhabited by *Pagurus longicarpus* Say, 1 Oct 1996 (USNM 182879: 10 paratypes; USNM 182883: 2 paratypes, SEM stub); from *I. obsoleta*, *L. littorea*, and *Lunatia heros* Say inhabited by *P. longicarpus*, 21 Oct 1996 (USNM 182880: 8 paratypes); from shells of living *C. fornicata* and *L. littorea*, from shell fragment of *Mercenaria mercenaria* Linné, from shells of *L. littorea* and *I. obsoleta* inhabited by *P. longicarpus*, 12 Nov 1996 (USNM 182881: 39 paratypes); from living *C. fornicata*, 12 Nov 1996, (IMBV 549: 4 paratypes); along the bank of the Pettaquamscutt River underneath the Sprague Bridge in Narragansett ~24‰ (41°27'N, 71°27'W): from *L. littorea* inhabited by *P. longicarpus*, 11 Nov 1995 (IMBV 548: 2 paratypes); from *L. littorea* inhabited by *P. longicarpus*, 4 Jul 1996 (USNM 182882: 4 paratypes, SEM stub); from *L. littorea* inhabited by *P. longicarpus*, 15 Jul 1996 (USNM 182884: 1 para-

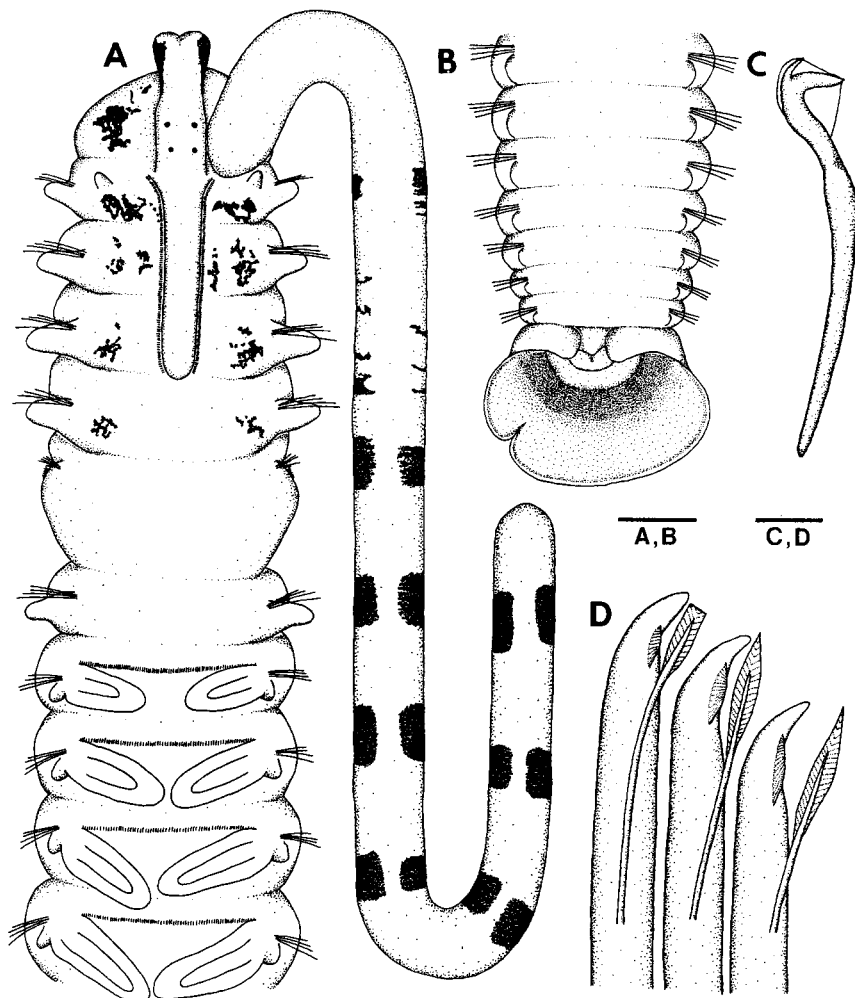


Fig. 1. *Polydora neocaeca* sp. nov.: holotype (USNM 182878). - A, anterior end, dorsal view. - B, posterior end, dorsal view. - C, neuropodial bidentate hooded hook. - D, major spines and pennoned companion setae of segment 5. Scale: A, B = 200 μ m; C, D = 20 μ m.

type); from *I. obsoleta* and *L. littorea* inhabited by *P. longicarpus*, 30 Aug 1996 (USNM 182885: 5 paratypes); from *L. littorea* inhabited by *P. longicarpus*, 21 Oct 1996 (USNM 182886: 1 paratype).

Diagnosis. – A moderate-sized *Polydora* with palps crossed by black bars; prostomium incised; caruncle up to middle of segment 4. Segment 1 with small notopodia, without notosetae. Segment 5 with falcate spines having lateral flange, with dorsal and ventral tufts of winged capillaries. Neuropodial hooded hooks

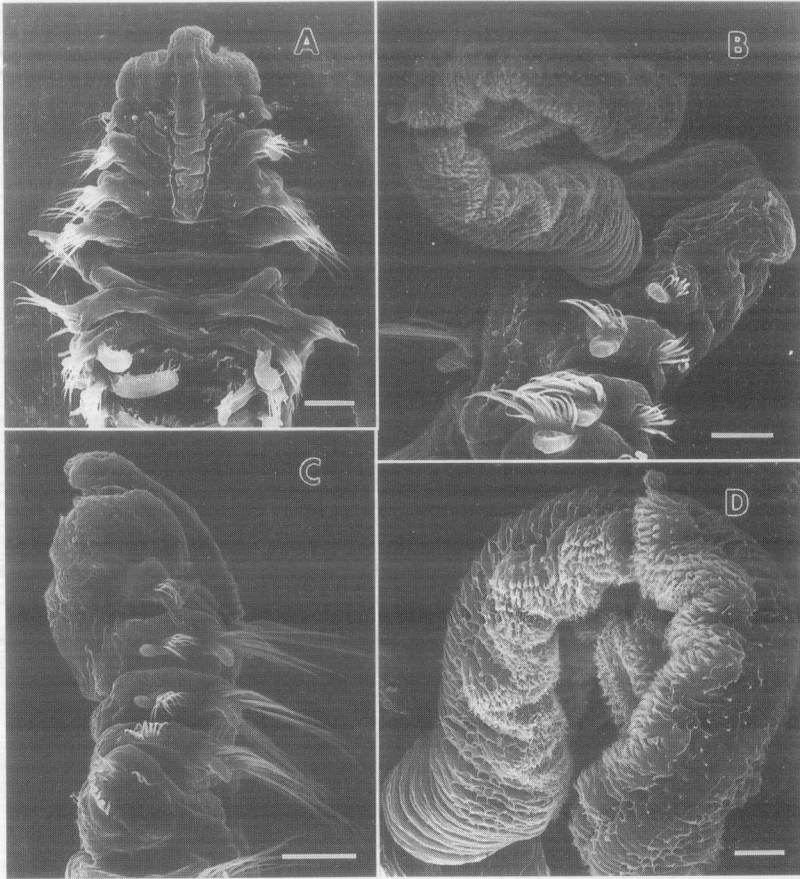


Fig. 2. *Polydora neocaece* sp. nov.: SEM micrographs of paratypes (USNM 182882). - **A**, anterior end, dorsal view. - **B**, anterior end, dorsolateral view with palps. - **C**, anterior end, lateral view. - **D**, lateral view of palp. Scale: A, C = 100 μ m; B = 50 μ m; D = 25 μ m.

bidentate, with constriction on shaft, from segment 7. Posterior segments without modified notosetae. Branchiae from segment 7 to almost end of body. Gizzard-like structure absent. Pygidium disc-like with distinct gap to narrow incision dorsally. Gonochoristic, development planktotrophic.

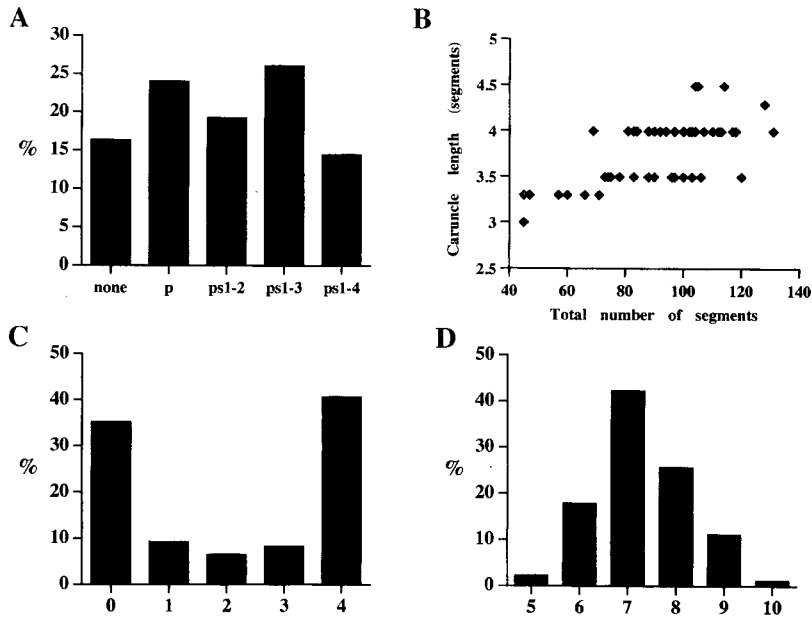
Holotype 22.0 mm long, 0.65 mm wide at segment 7, 107 segments. Black pigment present dorsally on either side of prostomium, peristomium and first 4 segments; ventrally on peristomium and segments 2-3; palps crossed by 7 distinct bars of black pigment (Fig. 1A). Prostomium incised anteriorly with two rounded lobes; caruncle straight in life (Fig. 1A) continuing posteriorly to end of segment 3, with ciliated groove on each side (Figs. 1A, 2A, 2B). Four eyes present; occipital tentacle absent. Palps extending posteriorly for 15-16 seg-



Fig. 3. *Polydora neocaeca* sp. nov.: SEM micrographs of paratypes (A, B - USNM 182882; C, D - USNM 182883). - **A**, fifth segment in left, lateral view. - **B**, fifth segment in right, lateral view. - **C**, bidentate hooded hook; apical end in lateral view. - **D**, bidentate hooded hook; apical end in frontal view. Arrowheads indicate the stalk of an attached peritrichous ciliate. Scale: A, B = 15 μ m; C = 2.5 μ m; D = 5 μ m.

ments. Laterofrontal cilia lining lateral edge of palp; frontal cilia covering the ventral median groove (Fig. 2D). Non-motile cilia extending from papillae concentrated dorsally along lateral edge of palps, above laterofrontal cilia; additional papillae in lower densities covering dorsal side of the palps (Fig. 2D).

Segment 1 with neurosetae, without notosetae, with weakly developed noto-



minishing through posterior half of body, absent from the posterior 8 segments. Nototrochs from segment 7, extending onto branchiae.

Pygidium disc-like with distinct dorsal gap and shallow ventrolateral notch (Fig. 1B); non-motile cilia present along edge and dorsal side of pygidium.

Glandular pouches from segment 7, larger in segments 8-10 and diminishing in size in posterior segments. Gizzard-like structure in digestive tract absent.

Variability. – The largest specimen measured 29.5 mm long and 0.7 mm in width at segment 7 with 133 segments. The prostomium was incised in most specimens, although 3 of the individuals examined ($n=66$) exhibited a rounded prostomium. Black pigmentation was highly variable (Fig. 4A) but was usually present to some degree dorsally on either side of the prostomium, peristomium and first four segments; 17% of the specimens examined had pigmentation on the ventral side of at least one of the first four segments. All specimens examined had black pigment bars along the palps; a mean number of 7.5 ± 3.4 ($n=86$) bars was observed; Webster (1879) reported 13 bands. No pigmentation was found on the posterior segments or pygidium of any specimens examined.

Caruncle length was size-dependent, extending from the posterior margin of segment 2 to the middle of segment 4 (Fig. 4B). The number of eyes was variable from 0 to 4; 1-3 eyes were rare (Fig. 4C). The fifth segment contained between 5-10 major spines with a mean of 7.3 ± 1.0 ($n=90$) (Fig. 4D). Notosetae and neurosetae of the fifth segment were present in all specimens examined ($n=68$). Branchiae of right and left sides meet middorsally. The pygidium was disc-like with distinct dorsal gap to narrow incision; 16% of the specimens examined ($n=50$) were found with a ventrolateral notch.

Ecology. – *Polydora neocaeca* bores into calcareous substrata. It has been found intertidally and shallow subtidally in shells of the gastropods *Busycotypus canaliculatus*, *Ilyanassa obsoleta*, *Littorina littorea*, *Lunatia heros*, and *Urosalpinx cinerea* occupied by *Pagurus longicarpus*; no worms were found to be associated with *Pagurus pollicaris* Say which was also collected in the field. The species has been found in shells of living gastropods, *Crepidula fornicata* and *Littorina littorea*, and in shell fragments of the bivalves *Mya arenaria* and *Mercenaria mercenaria*. Webster (1879) found his specimen boring into the upper valve of *Anomia simplex* d'Orbigny (= *Anomia glabra* Verrill). As many as 12 worms have been found boring in one shell. The worms reside in unbranched U-shaped burrows within the shell. The walls of the burrow are lined with detritus, forming a detrital tube within the burrow. The ends of the burrow are extended by a smooth silty tube, typically < 5 mm in length. *Polydora neocaeca* was found associated in the same shells with *P. websteri*.

A stalked peritrichous ciliate (Ciliophora: Oligohymenophorea) was found attached to 12.7% of the specimens examined ($n=126$). The peritrich attaches to the bidentate hooded hooks of the worms, usually 2-3 individuals per fascicle of hooks. The holdfast of the peritrich is attached to the hood of the bidentate

hooks on or below the main fang (Figs. 3C, 3D). In life the stalks of the peritrichs extend dorsally such that the main body and oral region are positioned near the branchiae of the worm.

Reproduction. – *Polydora neocaeca* is a gonochoristic species; 42 females and 30 males have been recognized within the specimens examined. The smallest female and male specimens with gametes in the coelom had 59 and 60 segments, respectively. Gametogenic segments were present in the middle portion of the body, in males from segments 18-45 to 40-83; in females from segments 19-46 to 40-92. The average number of segments containing developing gametes was 38.1 ± 14.9 ($n=11$) in males and 31.6 ± 10.2 ($n=26$) in females. The number of the first gametogenic segment and the total number of gametogenic segments per worm were slightly positively correlated with the total number of segments, $r^2 = 0.38$ and $r^2 = 0.51$ ($n=36$, $P<0.01$), respectively.

Spermatozoa have an elongate cylindrical nucleus and a bullet-shaped acrosome. The middlepiece of the sperm contains mitochondria closely aligned with the axoneme which is inserted into the nucleus in a short centriolar fossa. The spermatozoa have the following measurements: acrosome $0.9 \pm 0.1 \mu\text{m}$ ($n=10$), nucleus $4.8 \pm 0.4 \mu\text{m}$ ($n=11$), middlepiece $4.2 \pm 0.4 \mu\text{m}$ ($n=7$).

Females deposit eggs in 13-24 capsules (mean = 19.4 ± 3.2 ; $n=7$) joined in a string on the inside of the burrow (Fig. 5A). Each egg capsule is attached to the burrow wall by two thin stalks and contain 8-47 eggs (mean = 24.8 ± 1.3 , $n=21$), the mean number of eggs per brood is approximately 481. Eggs deposited within capsules had a mean diameter of $116.2 \pm 10.0 \mu\text{m}$ ($n=50$).

Larval development. – All eggs in capsules develop into larvae; no unfertilized or nurse eggs were found. The protrochophore measured $130 \mu\text{m}$ (Fig. 5B). The larvae have a blunt anterior end, a small ciliated vestibule, paired ventro-lateral ciliary patches and contain yolky macromeres in the center. Later in development the larvae exhibit the cilia of the telotroch and prototroch, 2 small lateral eyespots anterior to the prototroch and setae in the first segment (Fig. 5C). Larvae with 2 setigers containing observable setae are approximately $200 \mu\text{m}$ in length. The larvae have 3 sets of eyespots, a round median pair and a cup-shaped configuration of 2 pairs of lateral eyespots. The yolk has been partially depleted and the gut is beginning to form at this stage.

The early 3-segment larva (Figs. 5D, 5E, 5F) is $240 \mu\text{m}$ long. Large branched or ramified chromatophores are present between the lateral and median eyespots which are arranged in a row. The prototroch is developed and extends from the mouth vestibule almost to the median eyespots. The telotroch is composed of ciliary cells interrupted by a dorsal gap. Tactile cilia are present anteriorly on the head and posteriorly on the pygidium in number 4 and 2, respectively. The setae in segments 1, 2, and 3 are present in fascicles of approximately 9, 6, and 3 spines, respectively; those of segment 1 are the longest. A nototroch and grasping cilia are present on segment 3. A transverse band of black

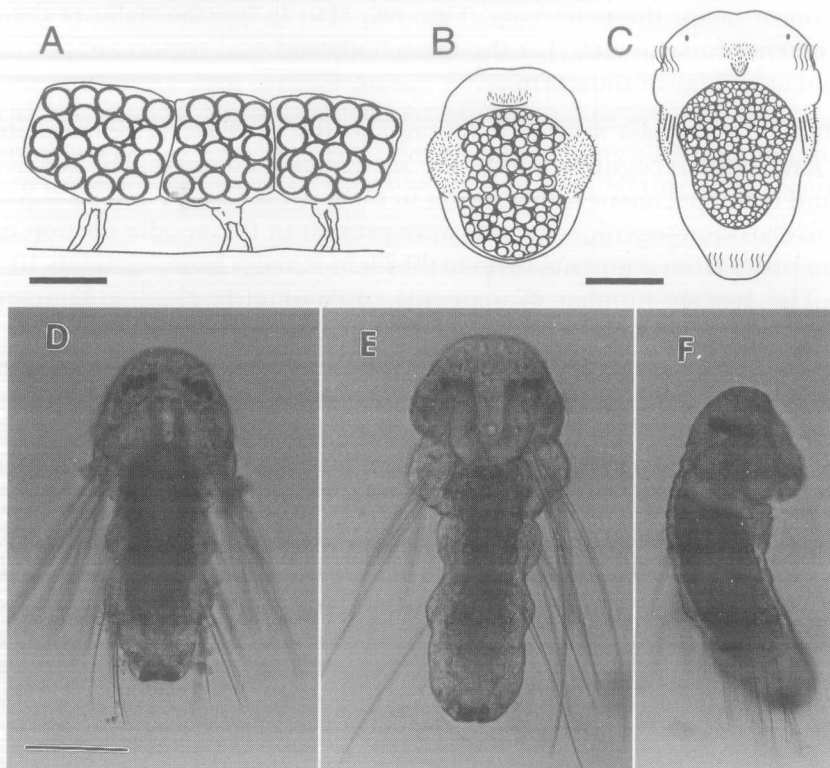


Fig. 5. *Polydora neocaeca* sp. nov: Larval development. - **A**, partial egg capsule string. - **B**, protochore larva in ventral view. - **C**, 1-setiger larva in ventral view. - **D**, 3-setiger larva in dorsal view. - **E**, 3-setiger larva in ventral view. - **F**, 3-setiger larva in lateral view. Scale: A = 300 μm ; B, C = 50 μm ; D-F = 100 μm .

pigment is present on the dorsal side of segment 3 in some larvae. Slight black pigment has developed on the pygidium.

The late 3-segment larvae grow to about 340 μm . The 2 lateral eyespots are slightly anterior to the median eyespots. The larvae contain little or no yolk at this stage and are capable of feeding and swimming. Attempts at culturing larvae beyond the 3-segment stage were unsuccessful.

Etymology. – The species name refers to *Polydora caeca* described by Webster (1879).

Distribution. – Atlantic coast of North America.

DISCUSSION

Polydora neocaeca belongs to the *Polydora ciliata/websteri* group as defined by

Blake (1996). It closely resembles *Polydora aggregata*, *P. ciliata* Johnston, 1838, *P. curiosa* Radashevsky, 1994, *P. limicola* Annenkova, 1934, and *P. websteri* in adult morphology. It differs from all these species in having palps crossed by black bars and in longer caruncle continuing to the middle of segment 4 rather than colorless or diffusely pigmented palps and caruncle typically extending to anterior border or end of segment 2. *Polydora neocaeca* resembles *P. agassizi* Claparède, 1869, *P. brevipalpa* Zachs, 1933, and *Polydora* sp. Blake (1996: 176-177) in pigmentation of the palps and caruncle length. *Polydora neocaeca* differs from the last two mentioned species in having an incised prostomium instead of entire, rounded prostomium; it also differs from *P. brevipalpa* in having, rather than lacking, dorsal capillaries on segment 5, and from *P. agassizi* and *Polydora* sp. by Blake (1996) in possessing a curved flange on the major spines instead of a large accessory tooth. Additionally, *Polydora neocaeca* differs from *P. agassizi* based on habitat. Morphological characters of these eight species of the *Polydora ciliata/websteri* group and *Polydora neocaeca* are compared in Table 1.

Several *Polydora* species have been reported to possess palps clearly pigmented with distinct bars or blotches of black pigment including *P. agassizi*, *P. alloporis* Light, 1970, *P. brevipalpa*, *P. limicola* by Hartman (1961) (not Annenkova, 1934), *P. maculata* Day, 1963, *P. narica* Light, 1969, *P. wobberi* Light, 1970, and *Polydora* sp. by Blake (1996). All of these species are from the North Pacific except *Polydora agassizi* from the Gulf of Naples and *P. maculata* from South Africa. *Polydora agassizi* was originally described by Claparède (1869) and was redescribed by Carazzi (1893) who provided the characters given in Table 1. Carazzi (1893) erroneously referred *Polydora agassizi* to synonymy with *P. ciliata* and this was accepted until the present (see Hartman 1959; Blake 1996) although *P. ciliata* has never been described as having banded palps.

Polydora limicola was originally poorly described by Annenkova (1934) as an intertidal and shallow subtidal tube-dweller in the Commander Islands and Kamchatka. Hartman (1961) provided a redescription based on her own material from California and greatly emended the diagnosis of the species. One of us (Radashevsky, unpublished) examined *Polydora* specimens from Kamchatka matching Annenkova's description and found that although Annenkova's and Hartman's specimens are close in some respects (e.g., tube-building) they clearly differ in other characters including palp pigmentation (see Table 1). Sato-Okoshi & Okoshi (1997) reported *Polydora limicola* from Vancouver Island as boring into mollusc shells and barnacles, in spite of the fact that they concluded boring activity to be a species specific trait. Information regarding deposited materials was not provided but a brief description of the specimens by the authors matches the diagnosis of *Polydora neocaeca*. Their report has therefore been included into questionable synonymy with *Polydora neocaeca*.

It is noteworthy that while diffuse body and palp pigmentation is variable within the genus *Polydora*, species with banded palps are invariably found with this unique pattern. Therefore, the palp banding pattern of *Polydora neocaeca*, in

Table 1. Morphological characters of some species of the *Polydora ciliata/websteri* group. References: 1) Johnston (1838); 2) Carazzi (1893); 3) McIntosh (1915); 4) Annenkova (1934); 5) Hartman (1961); 6) Blake (1971); 7) Radashkevsky (1993); 8) Radashkevsky (1994); 9) Blake (1996); 10) Radashkevsky (unpublished).

Species	Reference	Prostomium (anterior edge)	Caruncle (maximal length)	Palp pigmentation	Dorsal capillaries on segment 5	Accessory structures of major spines	Habitat
<i>P. agassizi</i>	2	incised	end of segment 3	black bands	present	small tooth	tube-dweller
<i>P. aggregata</i>	6	incised	end of segment 2	absent	present	small elevation	tube-dweller
<i>P. brevipalpa</i>	7	entire	end of segment 3	black bands	absent	flange or sheath	shell-borer
<i>P. ciliata</i>	1, 3	weak to distinct incision	end of segment 2	absent or diffuse black	present	large tooth	shell-borer and tube-dweller?
<i>P. curiosa</i>	8	entire	middle of segment 2	absent or diffuse black	absent	large tooth	shell-borer
<i>P. limicola</i>	4, 10	weak to distinct incision	end of segment 2	absent	present	small elevation	tube-dweller
<i>P. limicola</i>	5	weak to distinct incision	end of segment 3	black bands	present?	small tooth	tube-dweller
<i>P. neocacaea</i>	present study	incised	middle of segment 4	black bands	present	flange or sheath	shell-borer
<i>P. websteri</i>	6, 10	entire or weak to distinct incision	end of segment 2	absent or diffuse black	present	flange or sheath	shell-borer
<i>Polydora</i> sp.	9	entire	end of segment 3?	black bands	present	large tooth	borer of calcareous substrata

combination with other taxonomic characters, can be used to distinguish this species. Additional investigations are required to elucidate the systematics of both *Polydora agassizi* and *P. limicola* sensu Hartman. With the exception of *Polydora neocaeca*, no other *Polydora* species with banded palps have been described from the east coast of North America.

REFERENCES

- Andrews, E.A. 1891. Report on the Annelida Polychaeta of Beaufort, North Carolina. – *Proc. U.S. natn. Mus.* **14**: 277-302.
- Annenkova, N.P. 1934. Kurze Übersicht der Polychaeten der Litoralzone der Bering-Insel (Kommandor-Inseln), nebst Beschreibung neuer Arten. – *Zool. Anzeiger* **106**: 322-331.
- Blake, J.A. 1971. Revision of the genus *Polydora* from the east coast of North America (Polychaeta: Spionidae). – *Smithson. Contr. Zool.* **75**: 1-32.
- Blake, J.A. 1996. Family Spionidae Grube, 1850. Including a review of the genera and species from California and a revision of the genus *Polydora* Bosc, 1802. – In Blake J.A., B. Hilbig & P.H. Scott (eds): Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel, Vol. 6, pp. 81-223. Santa Barbara Museum of Natural History.
- Carazzi, D. 1893. Revisione del genere *Polydora* Bosc e cenni su due specie che vivono sulle ostriche. – *Mitt. Zool. Stn Neapel* **11**: 4-45.
- Claparède E. 1869. Les Annélides Chétopodes du Golfe de Naples. Seconde partie. Annélides sédentaires. – *Mém. Soc. Phys. Hist. nat. Genève* **20**: 1-225.
- Hartman, O. 1943. Description of *Polydora websteri*. In: Loosanoff, V.L. and J.B. Engle, *Polydora* in oysters suspended in the water. – *Biol. Bull.* **85**: 69-78.
- Hartman, O. 1959. Catalogue of the Polychaetous Annelids of the World. – *Occ. Pap. Allan Hancock Fdn* **23**: 1-628.
- Hartman, O. 1961. Polychaetous annelids from California. – *Allan Hancock Pacif. Exped.* **25**: 1-226.
- Johnston, G. 1838. Miscellanea Zoologica. The British Ariciadae. – *Mag. Zool. Bot.* **2**: 63-73
- Maciolek, N.J. 1984. A new species of *Polydora* (Polychaeta: Spionidae) from deep waters in the north-west Atlantic Ocean, and new records of other polydorid species. – *Sarsia* **69**: 123-131.
- McIntosh, W.C. 1915. *A monograph of the British Marine Annelids*. Vol.3. Part 1. – Text. Polychaeta. Opheliidae to Ammocharidae. – Ray Society, London. 368 pp.
- Örsted, A.S. 1843. *Annulorum danicorum conspectus*. Fasc. I. Maricolae. – Sumtibus Librariae Wahlianae, Hafniae. 52 pp.
- Radashevsky, V.I. 1993. Revision of the genus *Polydora* and related genera from the North West Pacific (Polychaeta: Spionidae). – *Publs Seto mar. biol. Lab.* **36**: 1-60.
- Radashevsky, V.I. 1994. Life history of a new *Polydora* species from the Kurile Islands and evolution of lecithotrophy in polydorid genera (Polychaeta: Spionidae). – *Ophelia* **39**: 121-136.
- Radashevsky, V.I. 1999. Description of the proposed lectotype for *Polydora websteri* Hartman in Loosanoff & Engle, 1943 (Polychaeta: Spionidae). – *Ophelia* **51**: 107-113.
- Radashevsky, V.I. & J.D. Williams 1998. Case 3080. *Polydora websteri* Hartman, 1943 (Annelida, Polychaeta): proposed ruling that the specific name is not to be treated as a replacement name for *P. caeca* Webster, 1879, and designation of a lectotype. – *Bull. zool. Nom.* **55**: 212-216.
- Sato-Okoshi, W. & K. Okoshi 1997. Survey of the genera *Polydora*, *Boccardiella* and *Boccardia* (Polychaeta, Spionidae) in Barkley Sound (Vancouver Island, Canada), with special reference to boring activity. – *Bull. Mar. Sci.* **60**: 482-493.
- Webster, H.E. 1879. Annelida Chaetopoda of the Virginian coast. – *Trans. Albany Inst. N.Y.* **9**: 202-269.
- Williams, J.D. 1997. Spermatozoon ultrastructure of a new species of *Polydora* (Polychaeta: Spionidae) from Rhode Island. – *Am. Zool.* **37**: 162A.