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## Morphology and natural history of the cryptogenic sponge associate *Polydora colonia* Moore, 1907 (Polychaeta: Spionidae)

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The polychaete *Polydora colonia* is a widely distributed symbiont of sponges that has been reported as introduced into the Mediterranean Sea. *Polydora colonia* is re-described based on specimens associated with the sponges *Microciona prolifera* and *Halichondria bowerbanki* from New York and aspects of its reproduction and feeding biology are described for the first time. The morphology of *P. colonia* agrees with previous reports of this species. Females of *P. colonia* deposited egg capsules (14–19 eggs/capsule) in their tubes on sponges and adelphophagy was observed. Larvae appear to be competent to settle on hosts at the 13-chaetiger stage. One commensal ciliate and one parasitic copepod were found associated with *P. colonia*. *P. colonia* as an introduced species is evaluated based on current evidence. Sponge material was observed in the gut of > 50% of the worms examined but further studies are needed to evaluate whether *P. colonia* is selectively feeding on *M. prolifera*.

**Keywords:** Porifera; introduced species; spionid; symbiosis

### Introduction

The Spionidae is a diverse family of polychaetes with a worldwide distribution. Members of this family are tubicolous, can be either free living or symbiotic and are adapted to a wide variety of habitats ranging from sandy and muddy sediments to calcareous substrates (Blake 1996). Within the Spionidae, the genus *Polydora* and nine related genera (termed polydorids) have been the focus of much attention. Polydorids are distinguished from other spionids by an enlarged fifth chaetiger that has large modified spines (Blake 1996). Although most spionids are free living, many polydorids are symbiotic with a variety of hosts, including sponges (Martin 1996; Martin and Britayev 1998; Williams 2000; Tinoco-Orta and Caceres-Martinez 2003; Radashevsky et al. 2006; Sato-Okoshi et al. 2008; Orensky and Williams 2009). Sponges have been documented to act as hosts to a wide range of polychaetes (Dauer 1974; Tzetlin et al. 1985; Martin and Britayev 1998; Martin 1996; Williams 2004; Walker 2009).

*Polydora colonia* Moore, 1907 is a widely distributed polydorid worm that is typically found associated with sponges but has also been reported from algae, including: *Corallina elongata* J. Ellis and Solander and *Padina pavonica* (Linnaeus) (Tena et al. 2000) and *Mesophyllum lichenoides* Elis (Aguirre et al. 1986). *Polydora colonia* was

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first described by Moore (1907) from pilings in the harbour of Vineyard Haven, Massachusetts based on incomplete specimens (pygidium absent). Hartman (1945) later reported the species from sponge masses collected on Pivers Island, North Carolina. Blake (1971) provided a re-description of *P. colonia* based on specimens from Massachusetts and concluded that *Polydora ancistra* (Jones 1962) from Jamaica and *Polydora hoplura inhaca* (Day, 1957) from South Africa were both synonyms of *P. colonia*. *Polydora colonia* has now been reported from other regions of the western Atlantic including Florida (Dauer 1974), Argentina (Blake 1983), and Brazil (Neves and Rocha 2008; Cangussu et al. 2010), and the Mediterranean Sea (Aguirre et al. 1986; Tena et al. 2000; Zenetos et al. 2010; Occhipinti-Ambrogi et al. 2010). Zachs (1933) reported the only Pacific population of *P. colonia* from the Sea of Japan. However, Radashevsky (1988) considered this as a misidentification of *Polydora uschakovi* Buzhinskaja, 1971, which was later synonymized as *Polydora spongicola* Berkeley and Berkeley, 1950 (Radashevsky 1993; Blake 1996), a closely related sponge symbiont.

The widespread distribution of *P. colonia* in the Atlantic Ocean could be the result of human-mediated introduction. The introduction of polychaetes (including sponionids) into different geographic regions through human influence has been well documented (Carlton 1985; Carlton and Geller 1993). Vectors for introduction of polydorids such as *P. colonia* include ballast water that can transport larvae, hull fouling of ships by sponge hosts that can harbour worms, floating debris with worms, and introduction of worms with aquaculture products such as mussels and oysters. At least 19 polydorid species have been introduced worldwide (mostly as borers of molluscs) and many additional species are of questionable status (see Carlton 1989; Radashevsky and Olivares 2005; Moreno et al. 2006; Radashevsky et al. 2006; Karhan et al. 2008; Simboura et al. 2008; Read 2010; Walker 2011; Zvyagintsev et al. 2011 and references therein). Because *P. colonia* is found on sponges that can attach to the hulls of ships and its larvae can be taken up into ballast water, it is a likely candidate for human-influenced introduction, especially in marinas where it has most often been recorded.

The problem becomes more complicated by the fact that introduced polychaetes may also consist of sibling species (Walker 2011). One example is the mud-blister worm, *Polydora cornuta* Bosc 1802 (formerly *Polydora ligni* Webster, 1880), which is also believed to be an introduced species in many regions (Radashevsky 2005; Williams 2007; Karhan et al. 2008; Neves and Rocha 2008; Simboura et al. 2008) via accidental introductions by shipping and possibly movement of aquaculture products. *Polydora cornuta* was described as a single cosmopolitan species by Blake and Maciolek (1987) but earlier studies by Rice and Simon (1980) showed that there may be sibling species among populations of *P. cornuta*, based on slight morphological, reproductive and physiological variations. Radashevsky (2005) later concluded that the variability observed in the different populations was insufficient evidence for cryptic species. However, Rice et al. (2008) and Rice and Rice (2009) showed substantial reproductive and genetic differences between geographically isolated specimens of *P. cornuta* using a combination of mitochondrial DNA sequences, allozyme patterns and experimental reproductive crosses.

Alternatively, the wide geographic range of *P. colonia* may represent a natural distribution; however, confirmation of natural cosmopolitan distributions of polydorids is difficult to assess (see Walker 2011). Based on the present evidence, *P. colonia* is best considered to be cryptogenic (i.e. “one that is not demonstrably native or introduced”; see Carlton 1996), as done by Neves and Rocha (2008) who investigated potential

introduced species in Brazil. Occhipinti-Ambrogi et al. (2010) and Zenetos et al. (2010) listed *P. colonia* on the Italian coast and the Western Mediterranean and Adriatic Sea respectively as a non-established alien species, though no morphological or molecular work were undertaken in these studies.

Specimens of *P. colonia* create burrows inside their host sponge that extend to the surface where they suspension feed with palps that protrude from the burrows. However, the diet and natural history of this worm are largely unknown. Studies have shown that other polychaetes associated with sponges (e.g. syllid worms) feed on sponge hosts and so exhibit parasitic tendencies (Martin and Britayev 1998; Lopez et al. 2001; Neves and Omena 2003; Lattig et al. 2007). A well-known example is *Haplosyllis spongicola*, which can reach high densities in a wide variety of sponges (Reiswig 1973; Magnino and Gaino 1998; Fiore and Jutte 2010). Magnino and Gaino (1998) used gut content analysis to show that *H. spongicola* fed on its sponge host. However, Lopez et al. (2001) indicated that feeding behaviour might differ over the geographic ranges of *H. spongicola*, with temperate worms being free living and the tropical worms being strict endosymbionts and most likely to exhibit parasitic behaviour. The reason for the difference is unknown, although some researchers have noted that *H. spongicola* may consist of sibling species (Licher 2000). Among polydorids, there are seven species that are symbionts of sponges and have been listed as commensals. However, the term “commensal” is used in the broad sense (Zapalski 2011) because it is doubtful that they have no impacts on sponges.

Sexual reproduction is common in polydorids and the mode of reproduction in *P. colonia* was thought to be similar to other polydorids that exhibit sexual reproduction with the production of a trochophore larva (see Blake and Arnofsky 1999; Blake 2006). Hartman (1945) documented the eggs of *P. colonia* and described two larval stages but did not provide figures. Aspects of sexual reproduction and larval development, including documentation of adelphophagy, are reported here for the first time in *P. colonia*. Asexual reproduction in polydorids is rare (Blake and Arnofsky 1999) and in fact has never been recorded in the field for the genus *Polydora*. However, asexual reproduction (via architomy) was found in *P. colonia* and is the subject of a separate study (David and Williams 2011).

The purpose of the present report is to re-describe *P. colonia* based on newly collected specimens from Long Island, New York using light and scanning electron microscopy. Museum specimens and all described populations of this species were compared from the literature to determine whether they can be distinguished morphologically and new data is presented here on the sexual reproduction, ecology and feeding biology of *P. colonia*.

## Materials and methods

Field collections of the red beard sponge *Microciona prolifera* (Ellis and Solander) were made during 2007–2010 on the east coast of the USA at the town of Hempstead East Marina, Point Lookout, New York. Specimens were collected during the months of September and October 2007; September, October and November 2008; October, January and March 2009; June, July, August, September, October and November 2010. The crumb of bread sponge *Halichondria bowerbanki* Burton was collected only once in November 2010 when a large colony of worms was noted. Sponges were removed from the side of the docks and transported in buckets filled with unfiltered seawater (33‰).

For removal of worms, *M. prolifera* was immersed in 7% MgCl<sub>2</sub> to anesthetize *P. colonia* inside its burrows. The sponge was then returned to seawater and examined with an Olympus SZX12 dissecting microscope. Metal probes were used to dislodge the burrow from the sponge and worms were forced out of the burrows with a stream of seawater from a 1-mm diameter pipette. Collected worms were placed in 60 × 15 mm Petri dishes and stored at 14°C for future examination. After extraction of *P. colonia*, sponges and additional worms were fixed in a 4% seawater/formalin solution for 24 hours, rinsed with warm tap water and placed in 70% ethanol for additional studies. Additional material of *P. colonia* was borrowed from the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C., USA and examined. Voucher specimens of *P. colonia* from New York were deposited in the USNM.

The gut contents of live *P. colonia* specimens were examined by squash preparation of 100 worms under an Olympus CX31 compound microscope and pictures were taken using an Olympus DP11 camera attachment. For scanning electron microscopy, the specimens were dehydrated in an ascending ethanol series (75%, 80%, 85%, 90% and 95%) for 10 minutes each followed by 100% ethanol three times for 15 minutes each. Specimens were critical point dried in carbon dioxide (Samdri – 795 critical point dryer), mounted on aluminium stubs, coated with gold (EMS-550 Sputter Coater), and then viewed with a Hitachi 2460N scanning electron microscope. The same protocol was followed for any symbionts found associated with *P. colonia*.

For examination of sexual reproduction, egg strings were dislodged from the worm burrows and placed in a Petri dish. Egg strings were ruptured using microscalpels and eggs plus any developing larvae were examined under the compound microscope. Egg strings were maintained at 23°C and water was changed daily to stimulate trochophore development. Egg and larval sizes were determined using an Olympus CX31 microscope and IMAGE J software calibrated with a micrometer.

## Results

### Family SPIONIDAE Grube, 1850

#### *Polydora* Bosc, 1802

#### *Polydora colonia* Moore, 1907

#### (Figures 1–6)

*Polydora colonia* Moore 1907: 199–201, fig. 18–23; Hartman 1945: 32–33; Blake 1971: 15–17, fig. 10a–10l; Dauer 1974: 193, 193 (Table), 194, 195; Read 1975: 404; Blake 1983: 254–255; Aguirre et al. 1986: 375–377, fig. 1A–1G; Radashevsky 1993: 21, 23; Blake 1996: 180; Martin 1996: 170 (Table); Radashevsky 1996: 691; Martin and Britayev 1998: 244 (Table); Tena et al. 2000: 65 (Table); Ruellet 2004: 356; Neves et al. 2007: 323 (Table); Neves and Rocha 2008: 625 (Table), 626, 627 (Table); Orensky and Williams 2009: 234; Occhipinti-Ambrogi et al. 2010: 218, 221 (Table); Cangussu et al. 2010: 227 (Table); Zenetos et al. 2010: 395 (Table); Simon 2011: 39; David and Williams 2011: 1–10, figs. 1–4, Table 1.

*Polydora hoplura inhaca* Day, 1957: 468, fig. 18.2N.

*Polydora ancistra* Jones, 1962: 185–187, fig. 55–65.

*Materials examined*

USA, New York, Point Lookout, Town of Hempstead East Marina (40°35'37.71" N, 73°35'07.09" W) from the red beard sponge *M. prolifera* attached to floating docks, September and October 2007, September, October, November and December 2008, January and March 2009, coll. J. Williams; July, September, October, November 2010, coll. J. Williams and A. David (USNM 1156935 and USNM 1156936), 780 specimens examined from *M. prolifera*; from crumb of bread sponge *Halichondria bowerbankii* from same location on November 2010, coll. J. Williams and A. David (USNM 1196937), 60 specimens examined in total from *H. bowerbanki*. USA, Massachusetts, Woods Hole, Hadley Harbor from pilings, coll. J. Blake 1967 (USNM 301179), 22 whole specimens, three regenerating specimens examined. Argentina, South Atlantic Ocean from sediment, coll. Oliver and Salanoure (USNM 345346), 12 specimens examined. Spain, Malaga, Mediterranean Coast, coll. G. San Martin 14 June 1983 (Museo Nacional de Ciencias Naturales, MNCN 16.01/10720), one specimen regenerating posterior end; Mediterranean Coast coll. G. San Martin 29 April 1983 (MNCN 16.01/10706), two posterior ends and two middle pieces.

*Adult morphology*

Largest specimen 8 mm in length and 51 chaetigers. In life, body light yellow with pigmentation absent in mature worms; preserved specimens white in colour. Eyes absent in adults except for one 24-chaetiger worm with two pairs of eyes. Prostomium rounded anteriorly to slightly bifid extending posteriorly as a short caruncle to the middle of chaetiger two, nuchal organ as ciliary band on either side of caruncle (Figure 1A,B). Palps long, extending posteriorly for approximately 13 chaetigers on adult specimens (Figures 1A, 2A), palps with frontal cilia lining food groove and non-motile cirri on papillae along lateral edges of food groove and scattered on abfrontal surface; presence of laterofrontal cirri not confirmed (Figure 2B).

Chaetiger 1 with neurochaetae; without notochaetae. Capillary notochaetae of chaetigers 2, 4, 6 and subsequent chaetigers in three successive rows, two vertical and one row positioned dorsally, posterior seven chaetigers with stout boat hooks except for specimens regenerating posterior ends (Figures 1C,G, 2E,F); generally two boat hooks per chaetiger and typically accompanied by two capillary chaetae, hooks variable in curvature from slightly curved tip to highly curved (Figure 2E). Capillary neurochaetae of chaetigers 2–4, 6 and subsequent chaetigers in two vertical rows. Hooded hooks begin on chaetiger 7 and extend to posterior chaetigers with three to five hooks per chaetiger, hooded hooks bidentate with large distal fang and smaller secondary tooth; shaft with manubrium and tapering to the base (Figure 1F). Glandular pouches in chaetigers 7–10, with largest glands from chaetiger 9–10; glands opening to exterior through small papillae ventral to rows of neurochaetae.

Chaetiger 5 modified; approximately twice the size of chaetigers 4 and 6, with three or four major modified spines decreasing in size posteriorly, each with a small and large apical tooth distal to a subterminal collar (Figures 1D, 2C,D), major spines alternating with pennoned companion setae; with dorsal fascicle of three capillary notochaetae (Figures 1E, 2C,D) and ventral fascicle of two capillary neurochaetae.

Branchiae from chaetiger 7 or 8, reaching maximum size on chaetiger 14, decreasing in size posteriorly (Figures 1A, 2A). Pygidium cup shaped with dorsal gap

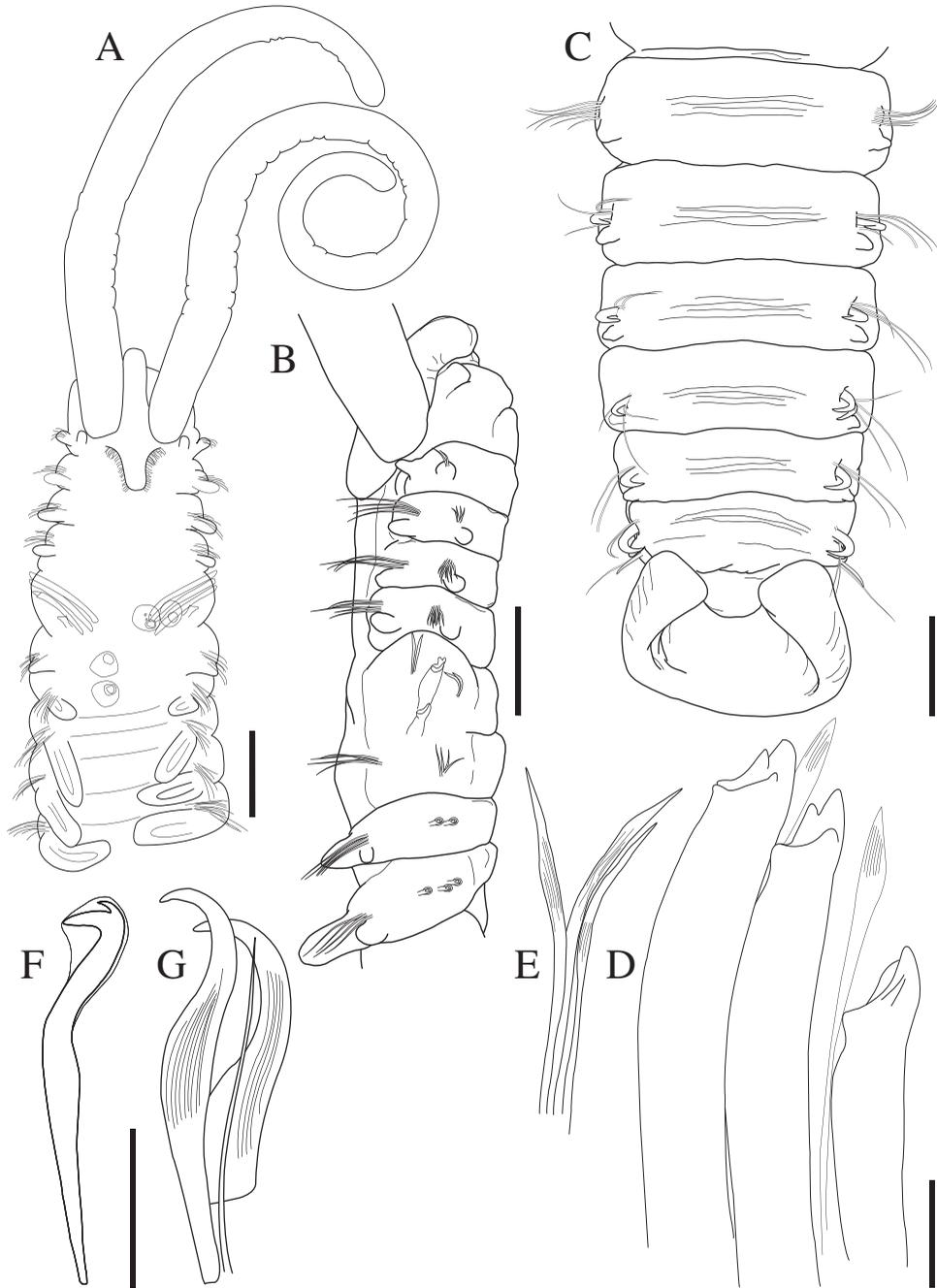


Figure 1. *Polydora colonia*, adult morphology based on light microscopy (USNM1156935, 1156936, 1156937). (A) Anterior end, dorsal view showing ciliates (arrow) attached to chaetigers 5, 6 and 7. (B) Anterior end, lateral view. (C) Posterior chaetigers and pygidium, dorsal view showing curved boat hooks. (D) Notochaetae from chaetiger 5. (E) Three modified fifth chaetiger spines with companion chaetae. (F) Bidentate hooded hooks from chaetiger 10. (G) Two boat hooks from the posterior end. Scale: 250  $\mu\text{m}$  (A); 100  $\mu\text{m}$  (B, C); 25  $\mu\text{m}$  (D–G).

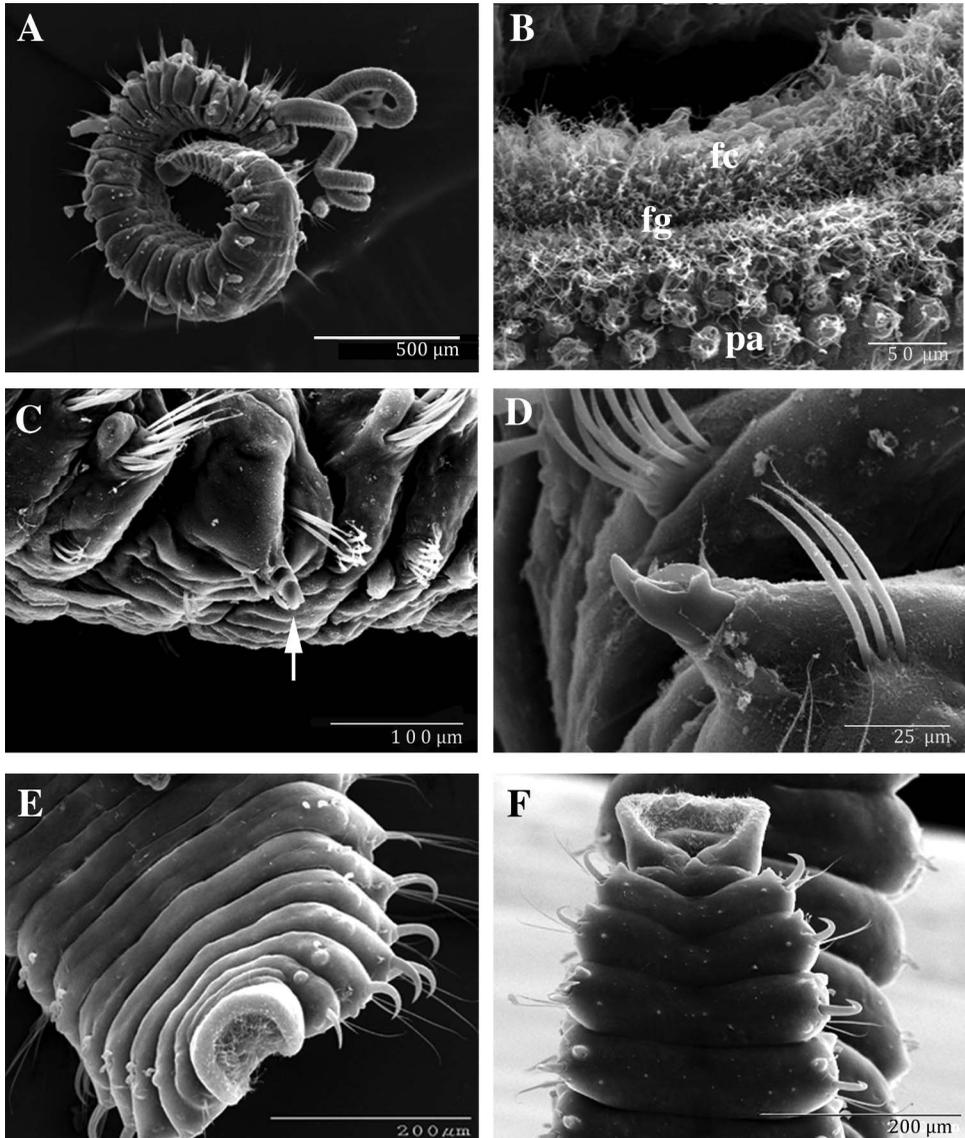


Figure 2. *Polydora colonia*, adult morphology based on scanning electron microscopy. (A) Overview of *P. colonia*. (B) Ventral view of palps showing the food groove lined by frontal cilia (fc) and papillae (pa). (C) Fifth chaetiger showing modified spines (arrow). (D) Single fifth chaetiger spine and dorsal fascicle of notochaetae. (E) Posterior end of worm showing cup-shaped pygidium along with boat hooks of varying curvature. (F) Posterior end and pygidium showing boat hooks on posterior chaetigers. Scale: 500 µm (A); 50 µm (B); 100 µm (C); 25 µm (D); 200 µm (E, F).

(Figures 1B, 2E,F). Table 1 summarizes major taxonomic features in *P. colonia* from geographical regions where it has been described and the distribution of the species is shown in Figure 3.

Table 1. Taxonomic features of *Polydora colonia* from several geographic regions.

	MA	NC	JAM	SA	MED	ARG	NY
Eyes	No	No	No	No	No	No	No*
Prostomium	Rounded to slightly bifid	Rounded to slightly bifid	Rounded	Rounded	Rounded to slightly bifid	Rounded	Rounded to slightly bifid
Caruncle	Extends to chaetiger 2	Extends to chaetiger 3	Extends to chaetiger 1	NR	Extends to the margin of chaetiger 1	Extends to the middle of chaetiger 3	Extends to the middle of chaetiger 2
Modified spines of 5th chaetiger	3 or 4 major spines with apical teeth; subterminal collar	NR	3 or 4 major spines bidentate with subterminal collar	Major spines with shelf/ large and small tooth attached too hooks	3 major spines with subterminal collar and unequal teeth at the top	3 or 4 major spines with small group of neuropodial spines	3 or 4 major spines with small and large apical teeth with subterminal collar
Boat hooks	Appear on chaetigers 6 or 7	Appear on last 7 chaetigers	Appear on last 2-4 chaetigers	NR	Appear on last 6 or 7 chaetigers	Appear on last 6 or 7 chaetigers	Appear on last 7 chaetigers
Hosts	Unidentified sponges and tunicates	Unidentified sponge	Unidentified sponge	NR	Encrusting algae <i>Mcsophyllum lichenoides</i> Elis	NR	Sponges, <i>Microciona prolifera</i> , <i>Halichondria bowerbanki</i>
References	Moore (1907), Blake (1971)	Hartman (1945)	Jones (1962)	Day (1957)	Aguirre et al. (1986)	Blake (1983)	Present study

These represent only records that were confirmed based on museum specimens or where a detailed written description and/or pictures of the species were provided.  
 MA, Massachusetts, USA; NC, North Carolina, USA; JAM, Jamaica; SA, South Africa; MED, Mediterranean, Spain; ARG, Argentina; NY, New York, USA.

\* A single recently metamorphosed individual had four eyes.

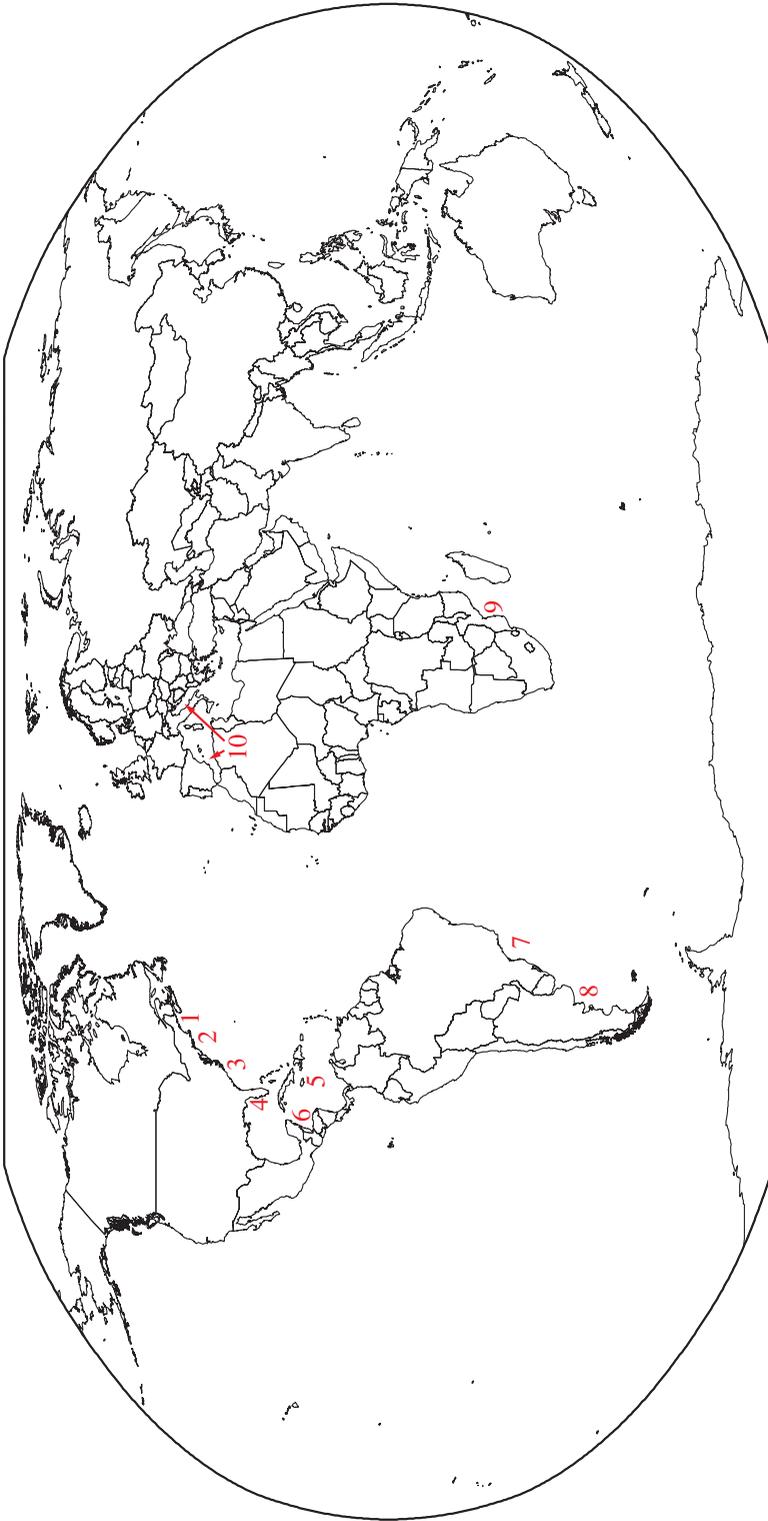


Figure 3. Map showing worldwide distribution of *Polydora colonia*. References for records: 1, Moore 1907, Blake 1971; 2, present study; 3, Hartman 1945; 4, Dauer 1974; 5, Jones 1962; 6, Radashevsky unpublished; 7, Neves and Rocha 2008, Cangussu et al. 2010; 8, Blake 1983; 9, Day 1957; 10, Aguirre et al. 1986, Tena et al. 2000, Zenetos et al. 2010, Occhipinti-Ambrogi et al. 2010.

*Ecology and feeding biology*

On Long Island, New York, *P. colonia* was found on the red beard sponge, *M. prolifera* and the crumb of bread sponge, *H. bowerbanki*. *Polydora colonia* and its sponge host, *M. prolifera* appear in the shallow subtidal area on pilings and floating docks approximately in late June. The worms reach densities as high as  $7.9 \pm 1.4$  worms/mm<sup>3</sup> ( $n = 16$ ) by mid-July to early August. Sponge colonies increase during September and October but are almost non-existent during the winter months (late December to February) when the host sponge (Figure 4A,B) can only be collected in the lower subtidal areas. Worms produce tubes on the surface of the sponge by cementing detritus material together with mucus; the worms can also extend their burrows into the tissue of the host sponge. The tubes can be intertwined to form compact masses; average length of a single tube was  $0.97 \pm 0.21$  cm ( $n = 20$ ). Heavily colonized sponges (Figure 4B) can have more than 200 individual tubes on the surface of a 100-cm<sup>2</sup> sponge branch. In this study, *M. prolifera* also harboured gammarids (*Corophium* sp.),

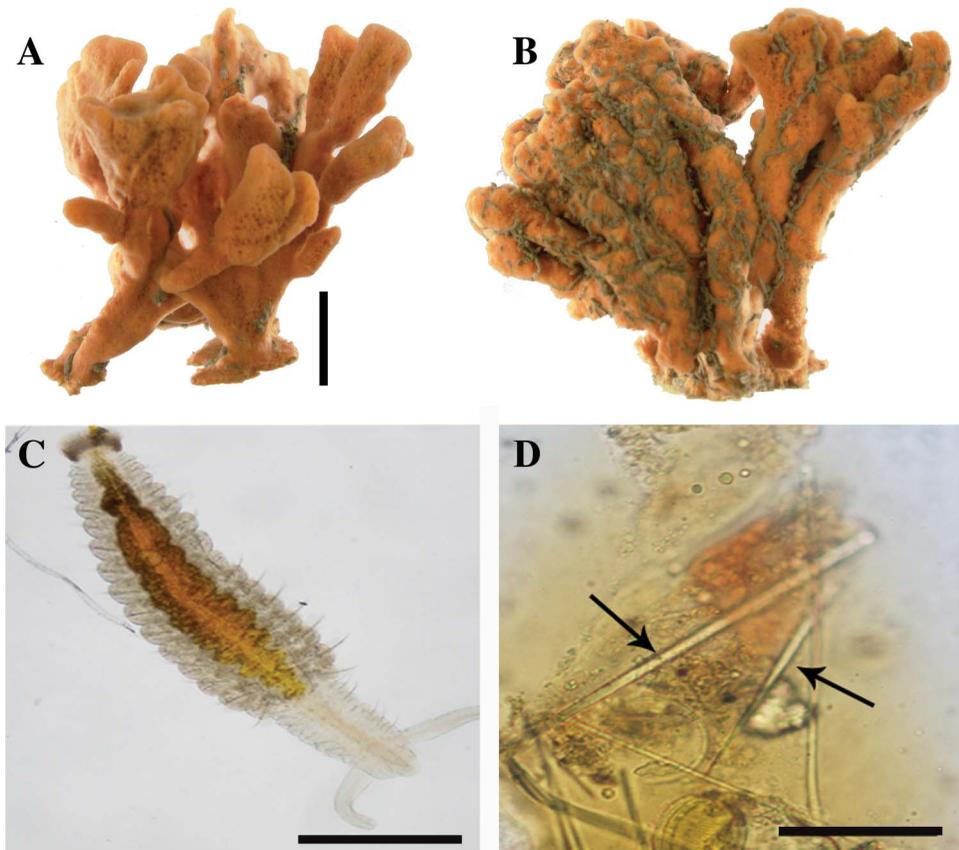


Figure 4. *Polydora colonia* and its sponge host *Microcionia prolifera*. (A) Uncolonized branch of *Microcionia prolifera*. (B) Colonized branch of *M. prolifera* showing the network of worm tubes on surface of the sponge. (C) Regenerating adult worm with gut containing sponge material. (D) Gut contents showing orange sponge material and two sponge spicules (arrows). Scale: 10 mm (A, B); 200  $\mu$ m (C); 50  $\mu$ m (D).

sabellid worms (*Sabella* sp.), nereid worms (*Nereis* sp.) and scaleworms (*Lepidonotus* sp.). *Polydora colonia* was the dominant polychaete worm inhabiting *M. prolifera*; the only other spionid associated with the host sponge was *Dipolydora socialis* (Schmarda 1861).

Gut contents of *P. colonia* were typically yellow to orange in appearance (Figure 4C). Materials from the gut included sand grains and partially digested sponge and spicules (Figure 4D). Around half (53 of 100) of the worms examined contained sponge, as evidenced by spicules and/or sponge material, in their gut and half of them (50 of 100) had sand grains in the gut. No sponge material was found in individuals associated with *H. bowerbanki*.

### Reproduction

Mean number of chaetigers in complete (non-regenerating) adult worms was  $30 \pm 6$  ( $n = 552$ ). Oviparous chaetigers begin as early as chaetiger 12 ( $14 \pm 1.2$ ;  $n = 30$ ) and end as early as chaetiger 20 ( $25 \pm 3.2$ ;  $n = 30$ ) with eggs crowding the coelomic spaces. Egg capsules and larvae of *P. colonia* were found in all months sampled. Egg capsules are arranged in a string attached to the inside of the mucous tubes by double filaments. Extracted egg strings had a mean number of egg capsules per string of  $7 \pm 2.9$  ( $n = 30$ ); however, complete strings were difficult to extract and these probably represent incomplete strings. Mean number of eggs per capsule was  $15 \pm 3$  ( $n = 30$ ). Based on the average number of oviparous chaetigers and eggs per capsule, the total fecundity of *P. colonia* is estimated to be 165 eggs per brood. Mean egg diameter was  $121.0 \pm 16.0 \mu\text{m}$  ( $n = 100$ ).

Of the 30 egg strings examined, 10% showed evidence of adelphophagia. Adelphophagic larvae were observed at the six- and seven-chaetiger stage. In one egg string about 25 nurse eggs were consumed by a single larva. Eggs were consumed whole by the larva and were broken down in the gut approximately 2–3 minutes after ingestion.

The earliest free-swimming larval stage found was a seven-chaetiger larva, 0.5 mm in length containing a large amount of yolk, presumably from ingestion of eggs (Figure 5A). Head of larva rounded with two pairs of eyes, with lateral eyes approximately twice the size of medial eyes. Prototroch divided and well developed. Melanophores present on chaetigers 4, 5 and 6 and pygidium. Chaetae as long bristles, longest in chaetiger one and decreasing in length posteriorly.

The 13-chaetiger larva (1 mm in length) was already settled on the surface of the sponge (Figure 5B). Prostomium rounded with two pairs of eyes; lateral eyes larger than medial. Palps long and flexible; caruncle absent. Pigmentation in irregular patches on most chaetigers. Nototrochs present on segments 2 and 3, lacking on segment 5. Chaetiger 5 well differentiated but major spines not visible externally. Lipid reserves restricted to the posterior region, from chaetigers 9 to 13. Pygidium rounded.

Asexual reproduction via architomy (fragmentation of the worm into an anterior and posterior end and subsequent regeneration to form two individuals) was commonly observed in the field based on specimens from New York (Figure 5C). This is the first record of architomy in the genus *Polydora*. In addition, architomy was observed in 12% (three of 25) of the specimens from Massachusetts and in the specimens from Spain. Morphogenesis during architomy and impacts of temperature on regeneration in specimens of *P. colonia* are reported separately (David and Williams 2011).

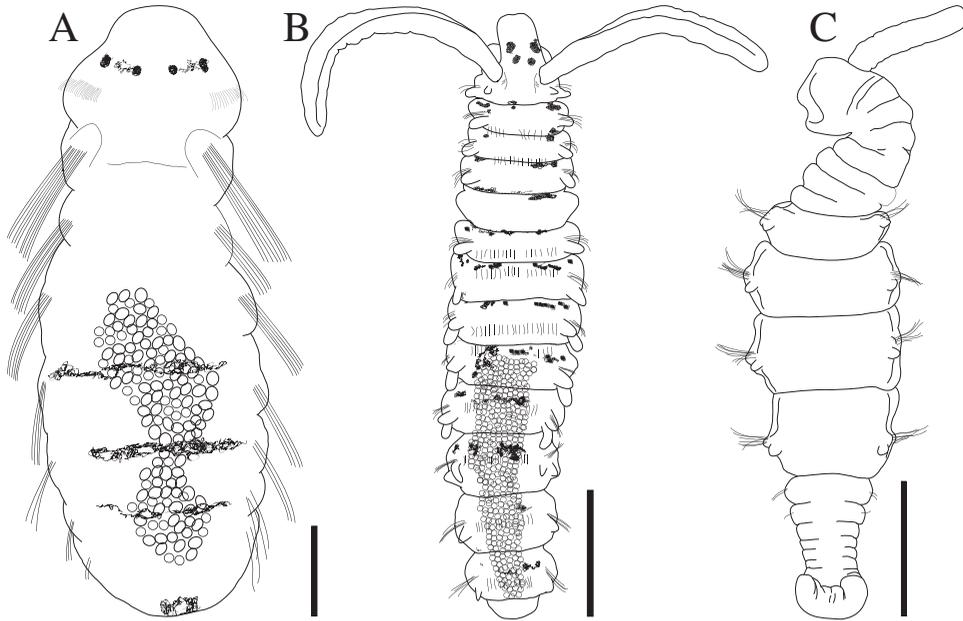


Figure 5. *Polydora colonia*, larvae and individual regenerating after architomic division. (A) Seven-chaetiger larva, dorsal view. (B) 13-chaetiger larva that settled on the sponge, dorsal view. (C) Individual with four original segments regenerating anterior and posterior ends. Scale: 100  $\mu\text{m}$  (A); 250  $\mu\text{m}$  (B, C).

### Symbionts

A species of ciliate of the genus *Urceolaria* (diameter 46  $\mu\text{m}$ ) was found attached to specimens of *P. colonia*. Ciliate prevalence was 25% (25 of 100) on the adult worms examined. The disc-shaped ciliate was found attached to the palps, anterior and posterior chaetigers and pygidium (Figure 6A). The basal disc of the ciliates had a band of radiating ribs (Figure 6B) and three or four concentric rings around the middle portion of the main body of the ciliate (Figure 6C). Specimens that harboured *Urceolaria* did not appear to be affected negatively compared with uninfected worms (e.g. females with eggs harboured the ciliates).

One endoparasitic copepod larva of the genus *Cymbasoma*, 1-mm in length (Figure 6D), was found inside the coelom of an incomplete worm at about chaetiger 14. Prevalence of *Cymbasoma* was 1% (1 of 100) in the worms examined. The larva of *Cymbasoma* possessed two pairs of antennae; one central pair of fused antennae and one non-fused pair (Figure 6D,E). The abdominal region is tubular and segmented, characterized by a protective sheath (0.5 mm in length), which encloses the thoracic appendages (Figure 6F). The protective sheath terminates in a cone with multiple vertical rows of short, blunt extensions.

### Discussion

*Polydora colonia* from New York was found to be morphologically indistinguishable from previous reports from other geographic regions with the exception that Moore

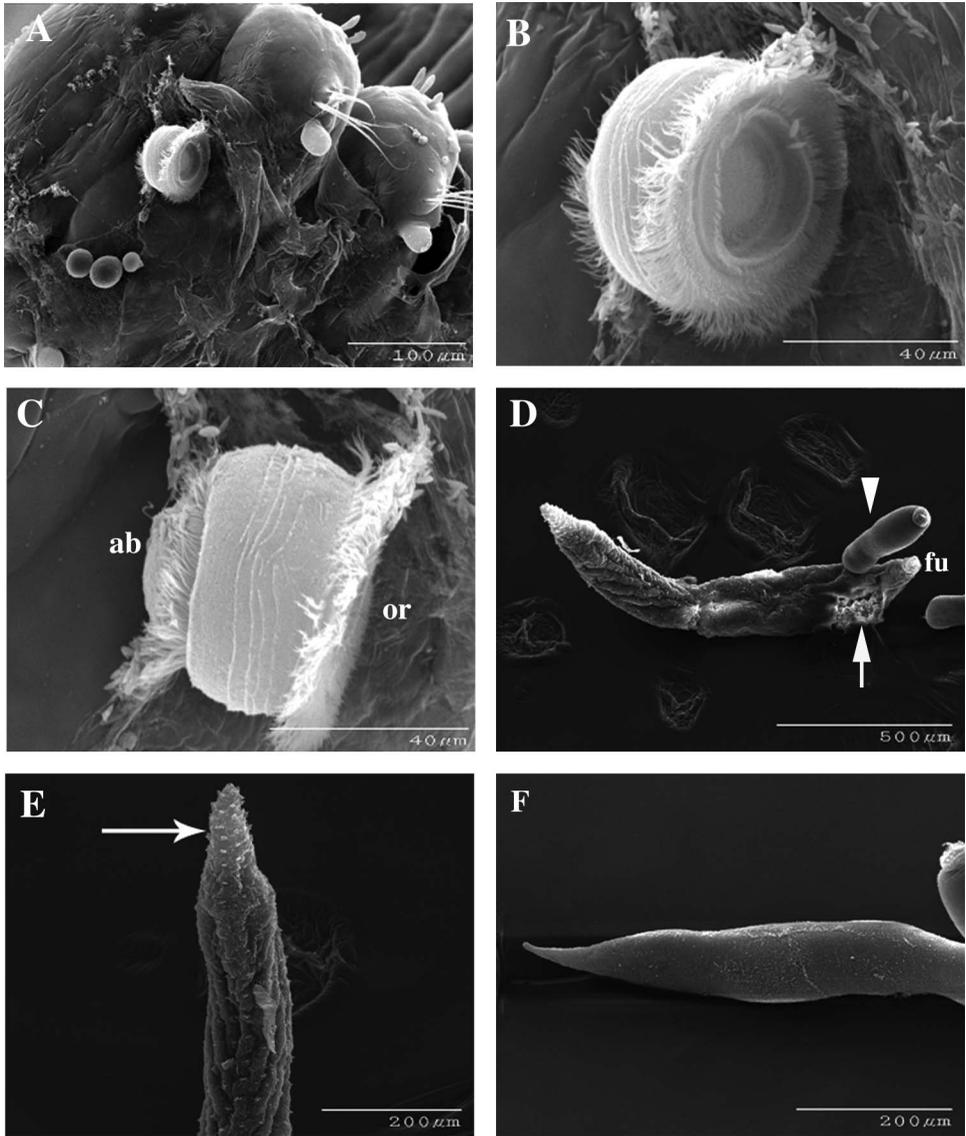


Figure 6. Symbionts of *Polydora colonia*, scanning electron micrographs. (A) The ciliate *Urceolaria* sp. attached to the posterior end of a regenerating worm. (B) Oblique lateral view of oral surface of *Urceolaria* sp. showing main ring. (C) Lateral view of *Urceolaria* sp. showing the oral (or) and aboral (ab) region. (D) Overview of the parasitic copepod *Cymbasoma* sp. with one pair of non-fused antennae (arrowhead showing intact non-fused antenna and arrow showing point of attachment of the second non-fused antenna) and one pair of fused antennae (fu). (E) Abdominal region showing protective sheath that houses the thoracic appendages, arrow pointing to posterior end of the sheath. (F) Lateral view of non-fused antenna. Scale: 100 μm (A); 40 μm (B, C); 500 μm (D); 200 μm (E, F).

(1907) reported that the branchiae could begin on chaetiger 9 in specimens from Massachusetts, which has not been reported in any other description of *P. colonia*. The only noted difference between the New York specimens and those from Argentina was in the caruncle length, which extended to chaetiger 3 in the Argentina specimens. There were no morphological differences between *P. colonia* from New York and type specimens obtained from the Mediterranean (Table 1). *Polydora colonia* is morphologically similar to *P. spongicola* and both species reside within tubes in sponges. However, *P. colonia* can be distinguished from *P. spongicola* based on the presence of eyes (four in *P. spongicola*) and the absence of boat hooks in *P. spongicola*. *Polydora spongicola* is distributed in the eastern and western Pacific (Blake 1996); its status as an introduced species in the Mediterranean is questionable (Arvanitidis 2000; Zenetos et al. 2010), especially as it can be confused with *P. colonia*.

*Polydora colonia* is a likely candidate for introduction because it is associated with sponges that can be encrusted on ships and can maintain colonies on docks in major shipping areas. Additionally, the larvae of *P. colonia* can be introduced into new areas via ballast water. Despite similarities in morphology of different populations of *P. colonia*, there is the possibility that it represents a species complex. Hence, molecular studies should be completed on this species based on specimens from all the geographic regions where it has been reported. We suspect that *P. colonia* is an introduced species but label it as cryptogenic until molecular data can be used to more fully evaluate its status and investigate its point of origin. In addition, because *P. colonia* can be confused with *P. spongicola*, records of the latter species should also be carefully evaluated.

The sponge host *M. prolifera* is present year round in temperate regions and reaches maximum growth during summer and autumn, providing that there are no competing sponges (Wells et al. 1964; Biernbaum 1981). Reproduction in *M. prolifera* occurs during early summer at intermediate temperatures (Wells et al. 1964). *Polydora colonia* is the first polydorid associated with sponges documented to ingest sponge material. However, the potential effects and extent of sponge feeding on hosts remain unknown. The presence of sand grains in the gut of *P. colonia* suggests that it often engages in deposit feeding and most likely switches between deposit and suspension feeding, as do many spionids (Dauer et al. 1981). Worms may be inadvertently ingesting sponge material when feeding on other deposited material. Alternatively, worms may actively feed on *M. prolifera* during periods of low food availability or as a means of supplementing its diet. As no spicules or sponge material were found in the gut of *P. colonia* specimens that inhabited *H. bowerbanki*, there is the possibility that *P. colonia* may show some degree of specificity in feeding on sponges.

The extent to which sponges are negatively affected by the burrow production and feeding of *P. colonia* is unknown and it is challenging to study in the field because many other organisms are associated with the sponge (Long 1968; Fiore and Jutte 2010). This makes it difficult to single out the effect of *P. colonia* unless isolated in the laboratory. It does appear that the worms influence the growth pattern of the sponges (Figure 4A,B) but quantitative studies are required to determine if their burrows influence growth and branching of hosts. Impacts of other polydorids associated with sponges (e.g. *P. spongicola*) should also be investigated, as they may also be predators on these hosts.

The reproduction of *P. colonia* is similar to other polydorid worms, with eggs deposited in capsule strings that are attached to the wall of the tube by double

filaments (Blake and Arnofsky 1999). The fecundity of *P. colonia* is relatively low compared with other polydorid species, some of which produce several thousand eggs per brood (Williams 2001) but is similar to other smaller polydorids such as *Dipolydora armata* that produce 50–100 eggs (Lewis 1998). Morphogenesis during architomy in *P. colonia* followed a very similar pattern to other polydorids that exhibit the process (Stock 1964; Gibson and Harvey 2000; Gibson and Paterson 2003). Posterior fragments produce an anterior blastema from which the prostomium, mouth, palps, chaetigers, caruncle and modified spines regenerate. Anterior fragments produce a posterior blastema from which the early pygidium forms and segments continue to be added along with chaetae, with the boat hooks forming last (David and Williams 2011).

Nurse-egg feeding (adelphophagia) is reported here for the first time in this species. Other members of the genus *Polydora* that produce nurse eggs include *P. hermaphroditica* Hannerz 1956, *P. hoplura* Claparede 1869, *P. nuchalis* Woodwick 1953, *P. spongicola* and *P. cornuta* (Blake 1969; Radashevsky 1988; Blake and Arnofsky 1999; Rice and Rice 2009). Rice and Rice (2009) demonstrated that as sperm become limited, the number of fertilized eggs in egg capsules decreases and this results in nurse-egg feeding by the larvae. In light of these findings, Rice and Rice (2009) suggested that adelphophagy in *P. cornuta* was a response to decreased levels of sperm rather than a reproductive strategy. A similar response may be found in *P. colonia* but further investigation is required to determine whether sperm limitation is involved or if the production of the nurse eggs is an active developmental process (Smith and Gibson 1999).

The ciliate *Urceolaria* sp. was common on adult worms. *Urceolaria* sp. most likely represents a commensal relationship, with some worms harbouring as many as eight ciliates. Douglass and Jones (1991) conducted a comprehensive survey of symbionts associated with spionid worms from California and showed that a species of *Urceolaria* was also associated with *P. cornuta*. They showed that these ciliates tended to have an affinity for polydorids versus other spionids. The only other symbionts ever recorded from *P. colonia* were intestinal gregarines (Hartman 1945); no gregarines were found in worms from New York.

Endoparasitic copepods of the family Monstrilloidae typically infect polychaetes and molluscs. The protelean life cycle of monstrilloids includes a free-living (and non-feeding) adult stage that lives in the water column, during which the females produce naupliar larvae (Malaquin 1901; Caullery and Mesnil 1914; Suarez-Morales et al. 2006; Huys et al. 2007). After reaching the last naupliar stage, the larvae invade the appropriate invertebrate host, produce a larval sheath within that host, and take up nutrients through anterior processes (Suarez-Morales et al. 2006). Development continues until they emerge from hosts in the last copepodid stage. Reports of monstrilloid infections in spioniform annelids are rare and they are the only endoparasitic copepods known to be associated with spionids. Caullery and Mesnil (1914) reported the larva of *Cymbasoma rigidium* Thompson, 1888 infecting *Dipolydora giardi* and Radashevsky (1996) and Williams (2004) reported unidentified endoparasitic copepods infecting *Polydorella dawydoffi* and *Polydorella stolonifera*, respectively. This is the first report of a monstrilloid infecting a member of the genus *Polydora*. The copepod larva found in this study matches the morphology reported by Caullery and Mesnil (1914) but is not identifiable to species without adult stages. The effect of *Cymbasoma* sp. on *P. colonia* is most likely similar to other endoparasitic copepods, i.e. parasitic castration. However, the effect of endoparasitic copepods on spionids and polychaetes in general is not well

studied and is an area ripe for experimental investigation. As suggested for other parasites of spionids (e.g. trematodes), they may impact the reproductive strategies of these worms (McCurdy 2001).

In conclusion, specimens of *P. colonia* from New York are morphologically indistinguishable from previous descriptions and museum specimens from various locations around the world. Reproduction is similar to other members of *Polydora* and adelphophagy is reported for the first time in this species. In addition, specimens of *P. colonia* ingested sponge tissue but their impact on the hosts requires additional studies. Worms were found to be parasitized by a monstrilloid copepod (*Cymbasoma* sp.) and harbouring ectocommensal protozoans (*Urceolaria* sp.). Although the host specificity of *P. colonia* is poorly known, it appears to be largely restricted to sponges and algae. In the Adriatic Sea and other regions of the Mediterranean the species is not considered to be established (*sensu* Blackburn et al. 2011). It is therefore conceivable that *P. colonia* could be targeted for eradication, as has been done for one polychaete (Culver and Kuris 2000; Moore et al. 2007). Although *P. colonia* is not of direct economic or ecological concern (as is the case with boring polydorids), it could have negative cascading effects through its impacts on host sponges. Further research on this species could fill in gaps in our knowledge of its natural history, its impacts on hosts and its status as an introduced species.

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