

## Reproduction and morphology of *Polydorella* (Polychaeta: Spionidae), including the description of a new species from the Philippines

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A new spionid polychaete, *Polydorella kamakamai*, associated with sponges is described from the Philippines. *Polydorella kamakamai* is characterized by acicular neurosetae in segments 2–7, a fifth segment containing a ventral row of spines with digitiform bosses, and lack of branchiae. As in all members of the genus, *P. kamakamai* undergoes asexual reproduction via paratomy; the process of paratomy is examined through scanning electron and light microscopy. This species exhibits a growth zone following segment 10, leading to the production of stolon individuals budding from the stock individual; five or more individuals can thus be formed in a single chain. Paratomic division typically occurs in chains containing four to five individuals and as a result colonies are dominated by chains of two individuals. Sexual reproduction is documented for only the second time in the genus; *P. kamakamai* produces eggs in segments 13–15. Asexual reproduction and fine morphological structure of the ventral spines of the fifth segment are examined by SEM in *P. dawydoffi* and *P. stolonifera*. *Polydorella dawydoffi* is recorded for the first time from the Philippines and the Red Sea and these are compared to type specimens from Vietnam. The ventral spines of *P. dawydoffi* contain eight or nine rounded or pointed teeth along the apical end and a capillary extension not previously observed with light microscopy. Notes on feeding biology, parasitism by copepods, and a discussion of the evolutionary relationships of *Polydorella* and other polydorids are provided.

**KEYWORDS:** Polychaeta, Spionidae, asexual reproduction, commensalism, Porifera.

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### Introduction

A variety of polychaete families are documented as associates of sponges, either living on or within the tissue of host sponges (Martín and Britayev, 1998). Within the family Spionidae all members of the genus *Polydorella* Augener, 1914 are associates of sponges, constructing mud tubes on the surface of hosts. Currently, the genus *Polydorella* contains four species, all known from the Indo-West Pacific: *P. dawydoffi* Radashevsky, 1996, *P. prolifera* Augener, 1914, *P. smurovi* Tzetlin and Britayev, 1985 and *P. stolonifera* (Blake and Kudenov, 1978). Gibbs (1971)

described an additional species, *Polydorella novaegraegiae*, from the Solomon Islands but Radashevsky (1996) indicated the species belongs to the genus *Pseudopolydora* and his conclusion is followed here. Some authors (Blake and Kudenov, 1978; Hsieh, 1992; Blake, 1996) have placed the genus *Polydorella* in synonymy with *Pseudopolydora* Czerniavsky, 1881. However, Tzetlin and Britayev (1985) indicated that *Polydorella* forms a distinct group based on morphology and Radashevsky (1996) supported this finding with research on the ecology and reproduction. Thus, there are presently nine polydorid genera (an informal grouping within the Spionidae that possess a modified fifth segment) that exhibit a worldwide distribution and are known from a wide range of marine habitats.

Asexual reproduction via paratomy is relatively uncommon within the Spionidae and has been documented in only five species (Blake and Arnofsky, 1999). All members of the genus *Polydorella* reproduce by paratomy in which a growth zone develops following segment 10 or 11, eventually leading to the formation a new individual (stolon) joined to the parental (stock) individual. As many as five individuals can thus be joined in a chain prior to division. As a result of this form of asexual reproduction, single specimens of *Polydorella* species exhibit a small and relatively constant number of segments (14–16 segments). Paratomic division has best been studied in *P. dawydoffi* and *P. smurovi* (Tzetlin and Britayev, 1985; Radashevsky, 1996) but was also documented in *Dipolydora tetrabranchia* (Hartman, 1945) (Campbell, 1955). A similar process of asexual reproduction via architomy (production of offspring through fragmentation of a parental individual into segments followed by subsequent regeneration) has been examined in detail for the spionid, *Pygospio elegans* Claparède, 1863 (Gibson and Harvey, 2000). Stock (1965) documented architomy and regeneration in six spionids.

The purpose of the present study is to examine the morphology and reproduction of *Polydorella* species, including two species associated with sponges from coral reef areas in the Philippines. The study includes the description of a new species and examination of adult morphology and reproduction of these species with scanning electron microscopy (SEM). Data on the proportion of individuals in colonies exhibiting asexual reproduction is reported. Discussion of the phylogenetic relationships and reproduction of the genus *Polydorella* is provided.

## Materials and methods

Sponges were collected shallow subtidally (<5 m) by snorkelling in coral reef areas of the Oriental Mindoro province (Puerto Galera: Big and Small La Laguna Beaches, 13°30'N, 120°57'E; Puerto Galera: Agus Beach, 13°32'N, 121°57'E) of the Philippines from June to August 2000 (see figure 1 in Williams, 2001). All Philippine specimens were collected by the author.

Specimens were relaxed in 3% magnesium chloride in seawater, fixed in 4% formalin-seawater solution (one part 39% formalin and nine parts seawater) and stored in 70% ethyl alcohol. Sketches of live and preserved specimens were completed using a compound microscope with a drawing tube attachment. These sketches were scanned into a Macintosh<sup>™</sup> computer and images were prepared using the programs Adobe Photoshop<sup>™</sup> and Adobe Illustrator<sup>™</sup>. Measurements were made with an ocular micrometer or from drawing tube sketches and all means are reported with standard deviations (SD).

For SEM, specimens were fixed as described above and dehydrated in an ascending ethanol series followed by four changes of 100% ethanol. Dehydration

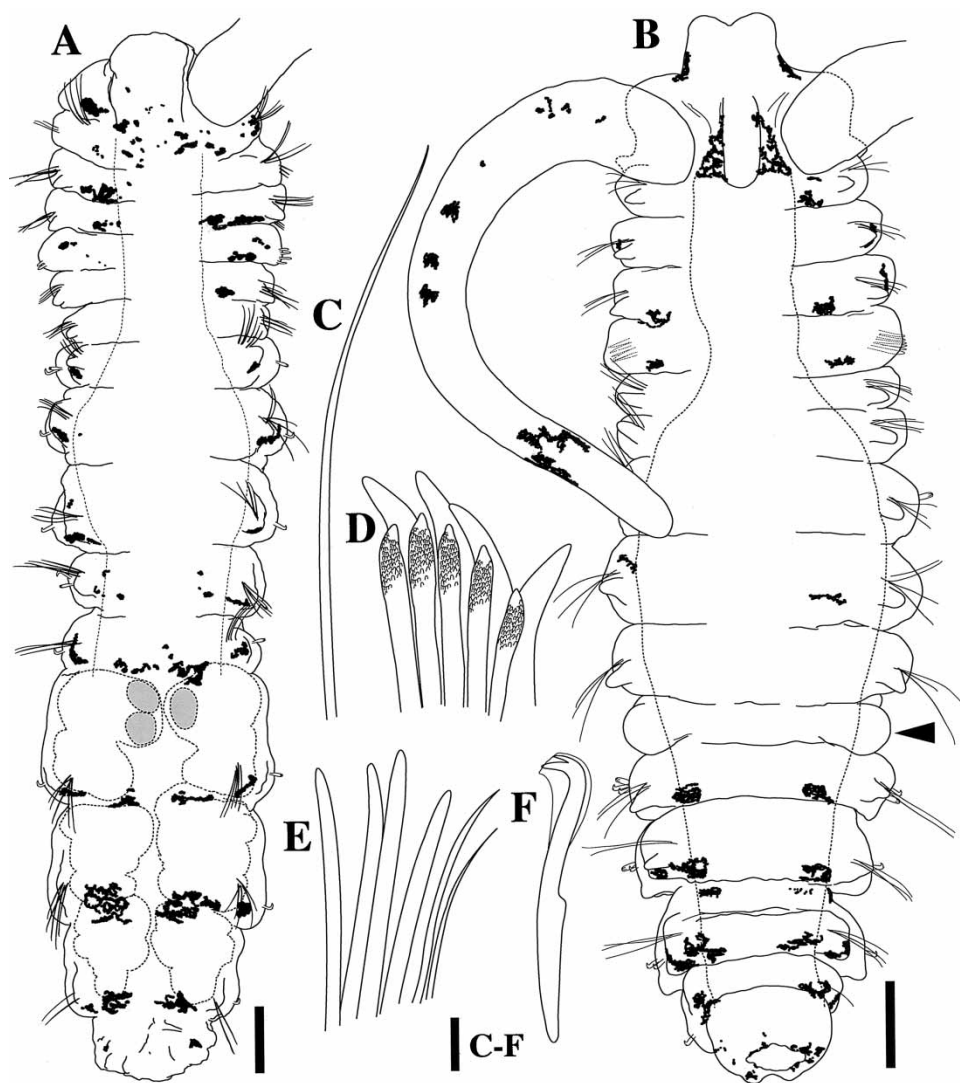


FIG. 1. *Polydorella kamakamai* new species: holotype (USNM 1008710) and paratypes (AMNH 4347). (A) Dorsal view of paratype exhibiting sexual reproduction (developing eggs in segments 13–15 outlined in dotted lines; three single eggs shown via shading); (B) dorsal view of holotype, arrowhead indicating growth zone following segment 10; (C) capillary neurosetae from segment 4; (D) spines of fifth segment, ventral view; (E) four acicular and two capillary neurosetae from segment 4; (F) hooded hook from segment 8. Scale: 100  $\mu$ m (A, B); 10  $\mu$ m (C–F).

was completed with a Samdri 795 Critical Point Drier or with Peldri II (Ted Pella, Inc.) by placing the specimens into a 1:1 mixture of 100% ethanol and Peldri II for 1 h at 34°C. The specimens were transferred to 100% Peldri II for 3 h and then placed in a cool water bath and allowed to sublime overnight. Dried specimens were mounted on a copper stub, coated with gold or gold–palladium mixture, and viewed with JEOL 1200EX and Hitachi S-2640N SEMs. Type material of *Polydorella dawydoffi* borrowed from the National Museum of Natural History,

Smithsonian Institution, Washington, DC, USA (USNM) and *P. stolonifera* borrowed from the Museum Victoria, Melbourne, Australia (NMV) were examined and prepared for SEM as described above. Type and voucher specimens are deposited in the Division of Invertebrate Zoology, American Museum of Natural History, New York, USA (AMNH) and USNM.

### Systematic account

**Family SPIONIDAE** Grube, 1850

**Genus *Polydorella*** Augener, 1914

*Polydorella* Augener, 1914. Type species: *Polydorella prolifera* Augener, 1914, by monotypy.

*Diagnosis.* Body short, consisting of 14–16 segments. Prostomium with anterior incision or rounded; caruncle short, extending posteriorly to segment 2 or absent. Segment 1 with small notopodia or notopodia absent, without notosetae; neuropodia present, with minute neurosetae or neurosetae absent. Segments 2–4 with simple, capillary neurosetae or acicular spines accompanied by capillaries. Segment 5 modified with two types of spines arranged in a double row: dorsal row simple, falcate; ventral row with expanded distal end, bearing denticulate edge, bristles or digitiform bosses; with or without capillary notosetae; with neurosetae in form of acicular spines and/or capillaries. Bidentate hooded hooks begin on segment 8; approximately right angle between main fang and shaft, narrow angle between main fang and apical tooth, with constriction on shaft; without accompanying capillaries. One or two pairs of branchiae beginning on segment 7 or absent. Pygidium reduced. Asexual reproduction via paratomy; growth zone between segments 10 and 11 or 11 and 12. Constructs tubes on surface of sponges.

***Polydorella kamakamai*, sp. n.**

(figures 1–5)

**HOLOTYPE:** Philippines, Puerto Galera, Agus Beach, ~3 m, 1 July 2000, from *Clathria (Thalysias) cervicornis* (Thiele, 1903) (USNM 1008710).

**PARATYPES:** same data as for holotype (USNM 1008711: 270+ paratypes; USNM 1008712: 10 paratypes, on nine SEM stubs). Philippines, Puerto Galera, Small La Laguna Beach, ~3 m, 24 July 2000, from *Clathria (Thalysias) cervicornis* (AMNH 4347: 180+ paratypes).

*Etymology.* The specific name *kamakamai* is derived from the Filipino word for supernatural beings that are small, human-like creatures possessing long beards and nails used to pinch offending children (Jocano, 1969), reminiscent of the acicular neurosetae of anterior segments in this species.

### Description

*Holotype.* 1.3 mm long, 0.3 mm wide at segment 7; 14 segments. Prostomium bifid; caruncle short, terminating between posterior margin of segment 1 and middle of segment 2; occipital tentacle and eyes absent (figures 1–3). Palps extend posteriorly for 10–12 segments. Black pigmentation in irregular patches on palps, sides of peristomium, prostomium, along caruncle, dorsal and ventral sides of all segments and pygidium (figures 1, 3).

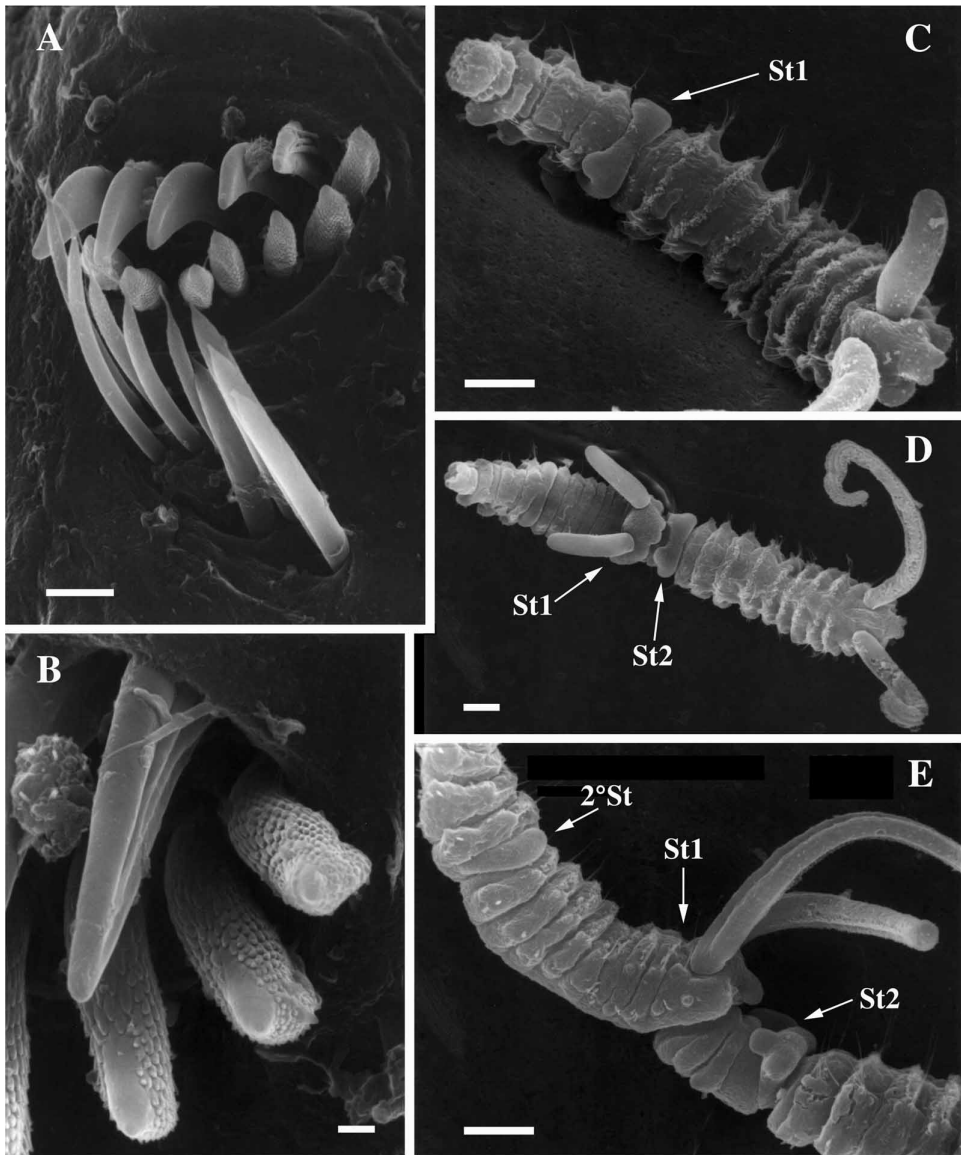


FIG. 2. *Polydorella kamakamai* new species: paratypes (USNM 1008712), SEM micrographs. (A) Spines of fifth segment, lateral view; (B) magnified view of spines in (A), showing digitiform bosses on ventral row of spines; (C) dorsal view of individual with developing stolon 1; (D) dorsal view of paratomic chain with stock, stolon 2 (St2) and stolon 1 (St1); (E) lateral view of paratomic chain with stock, stolon 2, stolon 1 and developing secondary stolon (2°St). Scale: 5  $\mu$ m (A); 1  $\mu$ m (B); 100  $\mu$ m (C–E).

Segment 1 without notopodial lobes or notosetae; neuropodia lobes present and neurosetae absent. Capillary notosetae of segments 2–4, 6 and subsequent segments in two rows; no specialized posterior notosetae. Neurosetae of segments 2–5 of two types, arranged in two rows; dorsal row composed of up to three acicular spines on

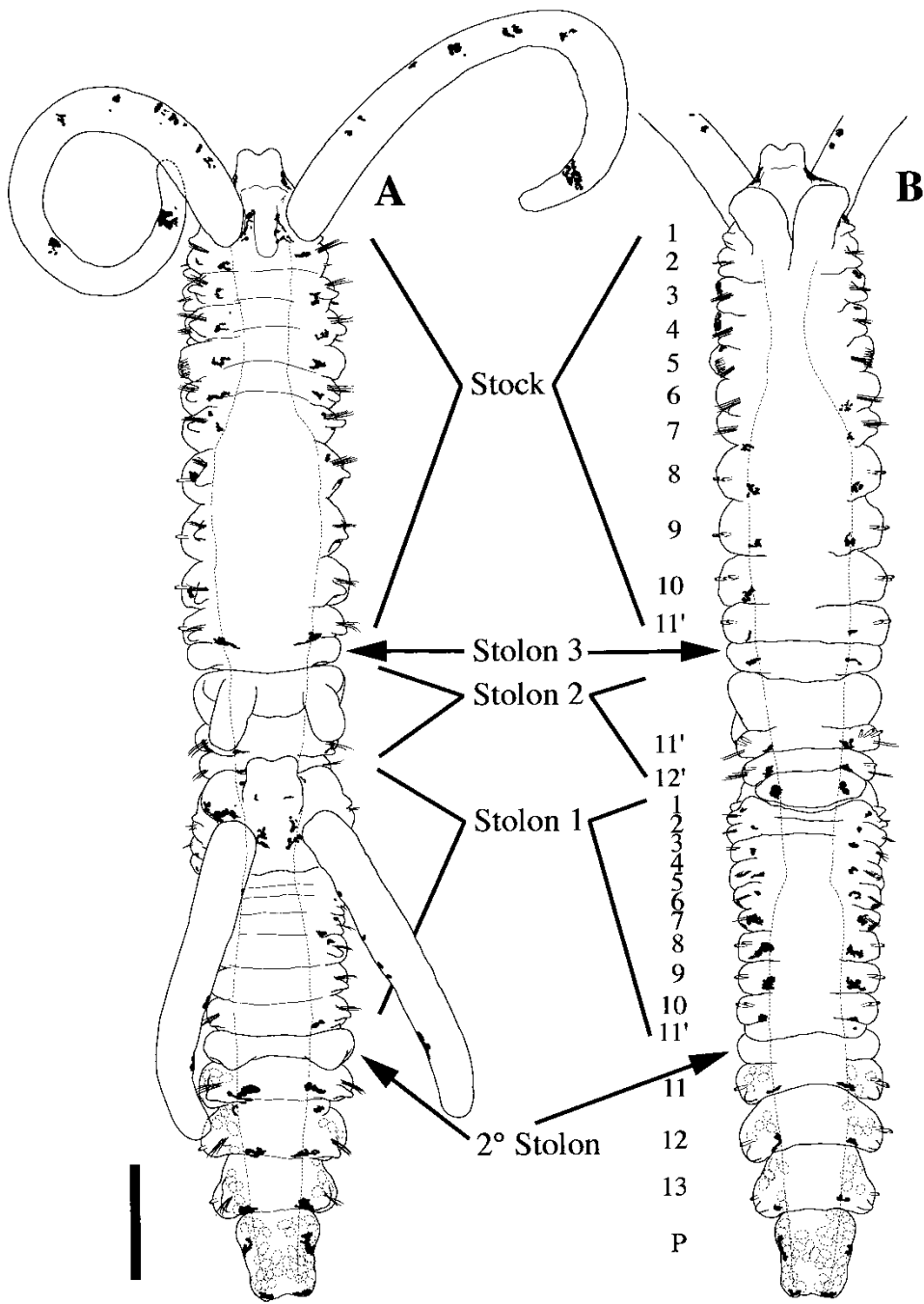


FIG. 3. *Polydorella kamakamai* new species: paratype (USNM 1008711). Paratomic chain with five developing individuals. (A) Dorsal view; (B) ventral view. Segment numbers of stock, stolon 2 and stolon 1 indicated to left of ventral view. P, pygidium. Scale: 250  $\mu$ m.

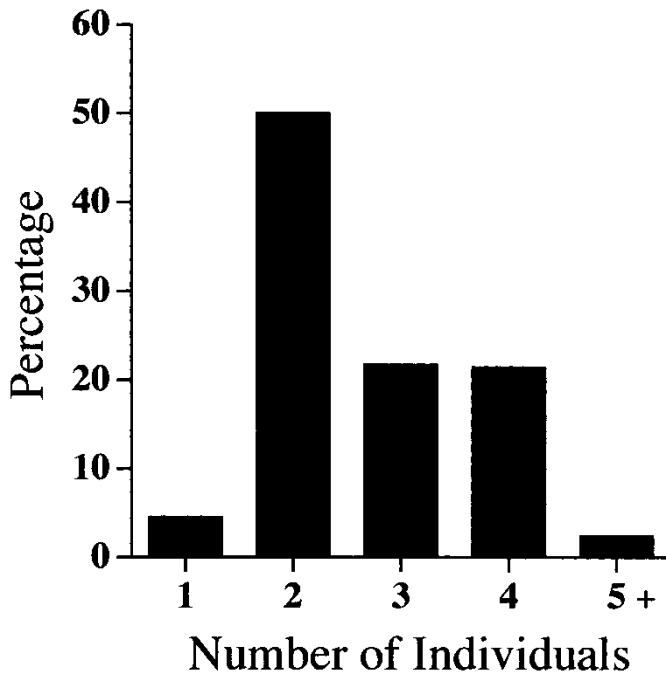


FIG. 4. *Polydorella kamakamai* new species. Percentages of single individuals and paratomic chains of two, three, four and five or more individuals in colonies from the Philippines ( $N=290$ ).

segment four, ventral row composed of up to four capillaries on segment four (figure 1C, E); segments 6 and 7 with reduced number of acicular spines and capillaries; three bidentate hooded hooks begin on segment 8, not accompanied by capillaries; hooks with approximately right angle between main fang and shaft, narrow angle between main fang and apical tooth, with constriction on shaft (figure 1F).

Segment 5 slightly modified, about the same size as segments 4 and 6, with acicular spines and capillary neurosetae in same arrangement as on segments 2–4; notosetae absent (figure 2A). Two types of major spines on segment 5 in approximately straight, horizontal rows; ventral row of four acicular spines with small digitiform bosses ( $\sim 0.3 \mu\text{m}$ ) closely applied to the apical ends of the spines, lacking on tips of the spines (figures 1D, 2A, B), and a dorsal row of four falcate spines (figures 1D, 2A, B).

Branchiae absent. Dorsal ciliary bands apparent from segment 3 continuing to terminal segments of stock individual (figure 2C–E).

Narrow pharynx to segment 7 leading to broad intestine, narrowing in posterior segments; without gizzard-like structure in digestive tract.

Pygidium reduced, knob-shaped (figure 1B); with large cells ( $\sim 30 \mu\text{m}$ ) within pygidium and terminal segments (figure 3).

*Variability.* All specimens examined exhibited black pigmentation on the palps, peristomium, prostomium, surrounding the caruncle, sides of anterior and posterior segments, and on the pygidium. Pigmentation was most prominent on the dorsal side but was also present on the ventral side of segments. A bifid

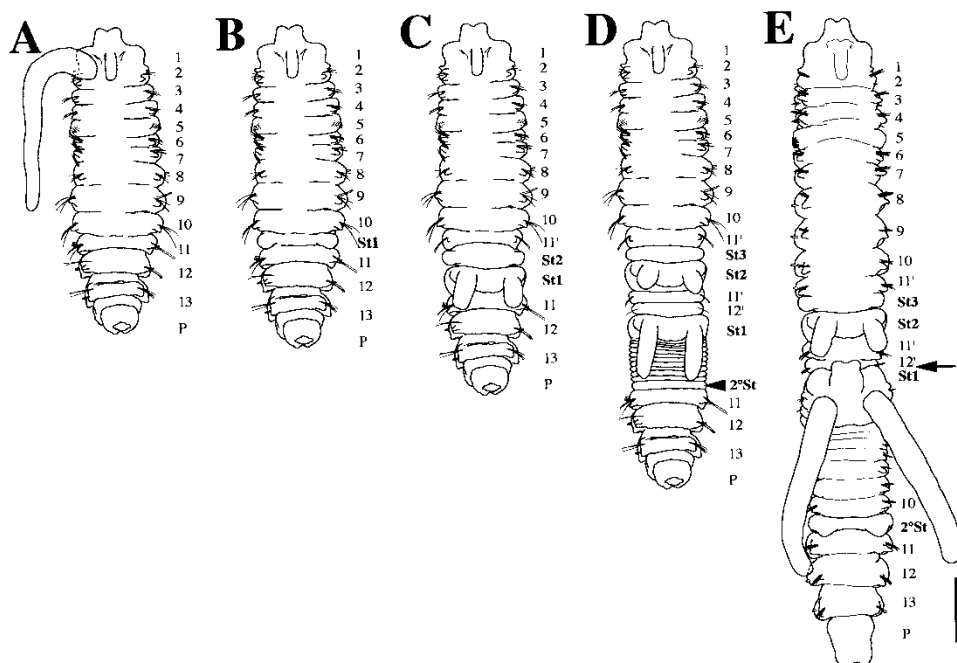


FIG. 5. *Polydorella kamakamai* new species. Semi-diagrammatic view of process of asexual reproduction via paratomy. (A) Single stock individual without growth zone (left palp shown for comparison with developing palp buds; palps removed from remaining figures); (B) development of stolon 1 (St1) growth zone; (C) development of stolon 2 (St2) growth zone; (D) development of first 10 segments of stolon 1 and stolon 3 (St3) growth zone; secondary stolon (2°St) indicated by arrowhead; (E) paratomic chain of five developing individuals just prior to paratomic division between stolon 2 and stolon 1; site of paratomic division indicated by arrow. Scale: 250  $\mu$ m.

prostomium and caruncle extending to middle of segment two was observed in all specimens; no specimens possessed branchiae. Acicular neurosetae were found in approximately vertical rows reaching four in number on segment 5, accompanied by a dorsal row of typically four to six capillary neurosetae. The number of acicular neurosetae was reduced to two or three in segments 6 and 7, accompanied by one or two capillary neurosetae.

The fifth segment contained four to seven major spines in both the dorsal and ventral rows; 20% of the specimens examined ( $N=50$ ) possessed one more additional spine in the ventral row than the dorsal row; all other specimens possessed equivalent numbers of spines in both rows. Hooded hooks numbered three or four on segment 8, reaching a maximum of three to five hooded hooks on segments 8–11. The pygidium was variable, from a reduced, knob-shape (figures 1B, 2C, D) to a more elongate conical shape (figure 3); small bumps were often observed surrounding the anus.

#### Distribution

Philippines: Oriental Mindoro.



### Remarks

*Polydorella kamakamai* is unique within the genus in possession of acicular neurosetae in segments 2–7 and the fifth segment containing ventral row of major spines with digitiform bosses. The species is further differentiated from *P. dawydoffi*, *P. prolifera* and *P. stolonifera* by the lack of branchiae.

### Ecology

*Polydorella kamakamai* was found to construct small mud tubes (up to 5 mm) on the surface of the sponge, *Clathria (Thalysias) cervicornis*. The worms were found in fairly high abundance, with approximately 280 worms on a sponge consisting of eight main branches approximately 100 mm long and 7 mm in diameter ( $\sim 1892.0 \text{ cm}^2$ ). Some specimens contained material in the gut the same colour as the preserved sponge; additional behavioural and histological studies are required to determine if the worms feed on the tissue of sponges as has been documented in some other polychaetes (see Martín and Britayev, 1998). Many tubes contained two individuals with dorsal sides apposed and anterior ends facing in opposite directions; tubes containing greater than two individuals were not observed. When disturbed, worms were able to move quickly out of their tubes and efficiently crawl across the surface of the sponge.

### Asexual reproduction

Most specimens examined ( $N=290$ ) exhibited some stage of asexual reproduction via paratomy (figure 4). Single parental or stock individuals consist of 13–15 segments (figure 5A). Stock individuals then exhibit a growth zone which follows segment 10 (figures 1B, 2C, 5B). The growth zone is distinct from anterior and posterior segments in its opaque colouring and smooth form. The opaque colouring of the growth zone may come from the breakdown of muscular material as the zone prepares for the formation of a new stolon body (Schroeder and Hermans, 1975). The growth zone exhibits two sections: an anterior section that will become the new segment 11 (denoted as 11', following Radashevsky (1996) where ' indicates newly developed stock segments) and the posterior portion which produces the developing stolon 1.

After further development of the growth zone, palp buds are formed and the new stock segment anterior to the head of the developing stolon 1 exhibits setae. New segments of the stolon body then appear to form simultaneously (overt distinction of 10 segments displayed at once from subdivision of the elongated growth zone). Ultimately, stolon 1 consists of 10 new anterior segments and three to four posterior segments derived from the stock individual (figure 5D). Stolon 2 is formed following 11'. Prior to complete development of the first 10 segments of stolon 1 (i.e. lacking externally observable setae), a secondary growth zone is formed following segment 10. Formation of stolon 2 proceeds as described above and the secondary growth zone of stolon 1 then exhibits palp buds (figures 2D, E, 5D). A third stolon (stolon 3) is observed in some individuals behind 11'. In this way, a chain of five developing individuals is formed (stock, stolon 3, stolon 2, stolon 1 and the secondary stolon) (figures 3A, B, 5E). The process of asexual reproduction is shown in figure 5.

It appears that in most cases paratomic division takes place when four or five individuals are present in a chain. Stolon 1 (with secondary stolon) breaks from the

stock individual (stolon 3 and stolon 2) (figure 5E). Prior to division, the posterior segments of stolon 2 are found in a wedge-shape under the head of stolon 1 (figures 2E, 3B). At this time, palps of stolon 1 are approximately one-half to three-quarters the length of stock individuals. Following division, the pygidium is fully formed on the posterior end of stolon 2. Stolon 1 (with secondary stolon) and stock (with stolon 3 and stolon 2) individuals then repeat the course of asexual reproduction described above. Following division, the worms apparently do not immediately leave their original tubes and construct new ones, as evidenced by tubes containing two individuals. The division of paratomic chains with stock individuals lacking a stolon 3 or stolon 2 leads to the presence of single individuals within the population. In only seven (2.4%) cases were the stock individuals within paratomic chains observed to possess 13–15 stock segments prior to division; this low number explains the relative rarity of single individuals lacking growth zones (figure 4).

The colonies were dominated by specimens composed of chains of two individuals (sometimes with developing growth zones); chains of three and four individuals were approximately half as abundant as chains of two individuals (figure 4). Only rarely were single individuals and chains of five individuals or greater observed (figure 4).

### *Sexual reproduction*

In addition to asexual reproduction, one specimen composed of 15 segments was found with eggs (figure 1A). Segments 10–12 of the specimen were narrower than preceding segments (no growth zone was exhibited), while segments 13–15 were expanded and contained yolky eggs. Eggs were oval in shape;  $43.3\ \mu\text{m}$  ( $\pm 5.8$ ) by  $62.2\ \mu\text{m}$  ( $\pm 6.8$ ) ( $N=11$ ). Based on the volume of the eggs within this specimen, segments 13–15 are estimated to contain 36–42, 26–34 and 15–20 eggs, respectively.

### *Polydorella dawydoffi* Radashevsky, 1996 (figures 6, 7)

*Polydorella dawydoffi* Radashevsky, 1996: 684–693, figures 2, 3.

*Material examined.* *Polydorella dawydoffi*: 10 paratypes from Thailand, Gulf of Thailand, Thom Island of Anthoi Archipelago, 7 m, 2 February 1986, from *Xestospongia testudinaria* (Lamarck, 1815) (USNM 148722; one prepared for SEM); 60+ specimens from Philippines, Puerto Galera, Small La Laguna Beach, ~3 m, 30 June 2000, from *Chalinula* sp., (USNM 1008713); 50+ specimens from same locality and sponge as above, 1 July 2000, (AMNH 4348); 18 specimens from same locality and date as above, from *Niphates* sp. (USNM 1008714); 60+ specimens from Philippines, Puerto Galera, Agus Beach, ~3 m, 1 July 2000, from *Niphates* sp. (AMNH 4349); 30 specimens from same locality and sponge as above, 25 July 2000 (USNM 1008715: 24 specimens; USNM 1008716: six specimens, on three SEM stubs); seven specimens from Philippines, Puerto Galera, Big La Laguna Beach, ~3 m, 24 July 2000, from *Petrosia* sp. (USNM 1008717); 37 specimens from Red Sea: Egypt, Hurghada, 0.1 m, November 2001, from *Xestospongia* sp. (USNM 1008718: 32 specimens; USNM 1008719: five specimens, on two SEM stubs), coll. Pliascheva.

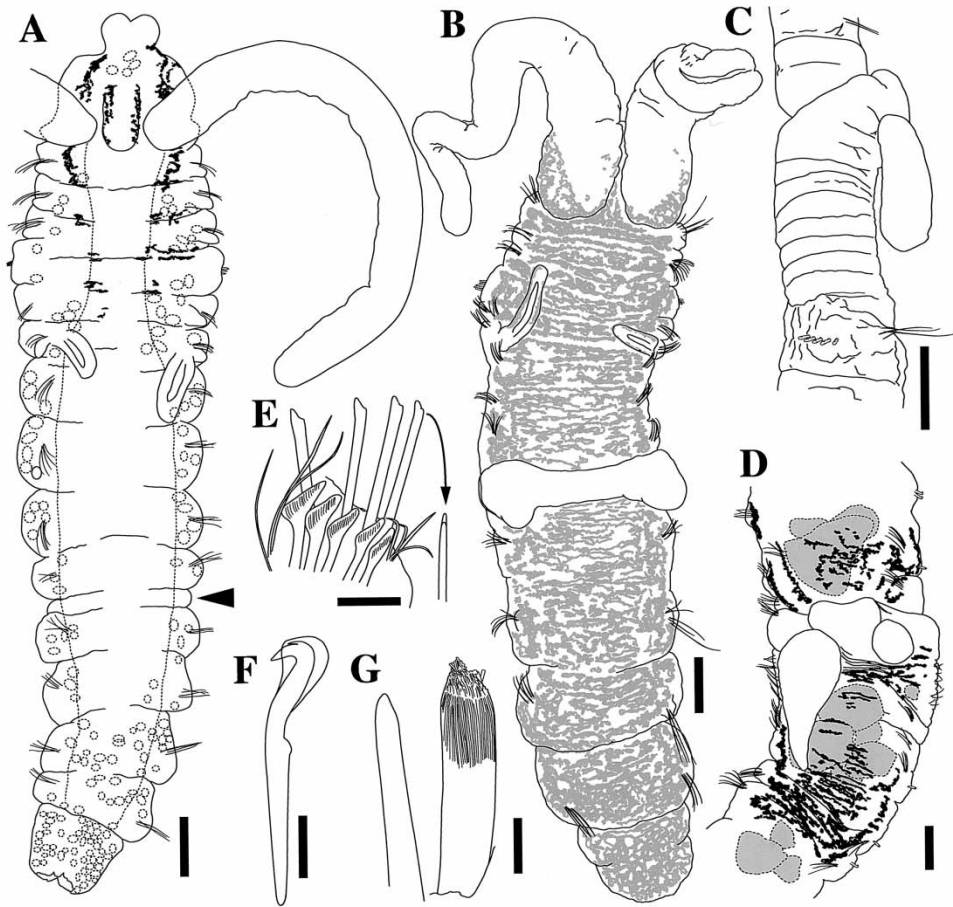


FIG. 6. *Polydorella dawydoffi* (AMNH 4348) (A), (USNM 1008717) (B, D, F), (USNM 1008716) (C), (USNM 148722) (E) and *P. stolonifera* (NMV F42898) (G). (A) Dorsal view of specimen from the Philippines; (B) dorsal view of specimen from the Red Sea; extensive black pigmentation is indicated by grey shading; (C) lateral view showing 10 developing segments of stolon 1; (D) dorsal view of posterior end of stock and anterior end of stolon 1 of an individual containing sand grains (shaded structures) within intestine; (E) dorsolateral view of fifth segment spines; (F) hooded hook; (G) lateral view of dorsal (to left) and ventral (to right) major spines of segment 5. Scale: 100  $\mu$ m (A–D); 25  $\mu$ m (E); 12.5  $\mu$ m (F); 5  $\mu$ m (G).

### Description

Single individuals with 14–15 segments; approximately 1.5 mm in length and 0.4 mm in width at segment 5. Prostomium bifid; caruncle short, reaching anterior margin or middle of segment 2; occipital tentacle absent; two round, white eyes observable in life only. Palps extend posteriorly for 8–12 segments. Pigmentation variable, present on dorsal and ventral sides of anterior and posterior segments or absent (figure 6A, B).

Segment 1 without notopodial lobes or notosetae; neuropodial lobe present without neurosetae (figure 6A). Unilimbate capillary notosetae of segments 2–4, 6 and subsequent segments in two rows. Unilimbate capillary neurosetae of segments

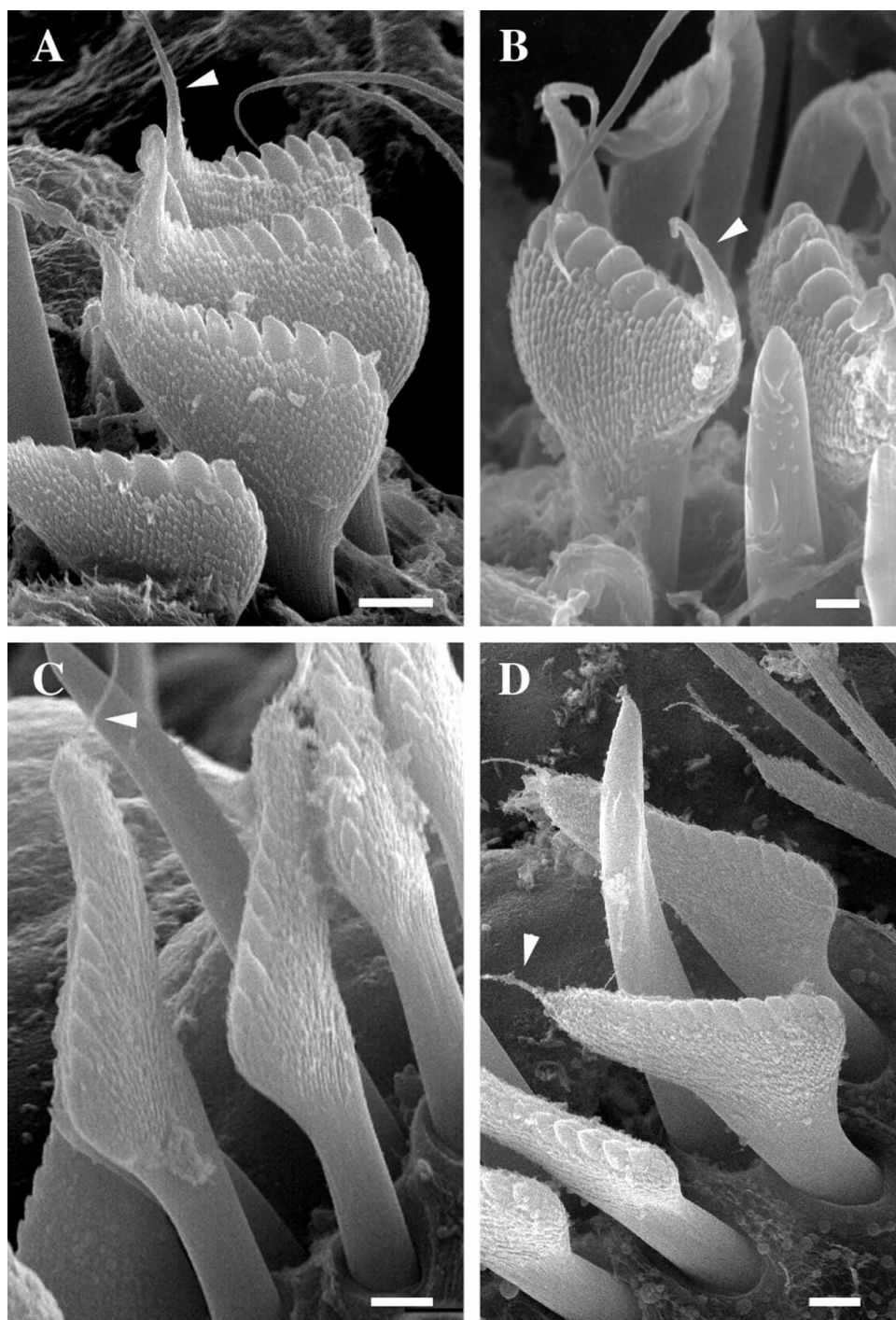


FIG. 7. *Polydorella dawydoffi* (USNM 1008716) (A, B), (USNM 148722) (C) and (USNM 1008719) (D). (A) Lateral view of ventral row of fifth segment major spines, Philippine specimen; note separated teeth along edge; (B) oblique view of ventral row of fifth segment major spines, Red Sea specimen; note acicular spine of dorsal row; (C) lateral view of ventral row of fifth segment major spines, Vietnam specimen; (D) oblique view of ventral row of fifth segment major spines, Red Sea specimen; note acicular spine of dorsal row. In all figures arrowheads indicate apical capillary extension of spines. Scale: 2.5  $\mu$ m (A, C, D); 1  $\mu$ m (B).

2–4, 6 and 7 arranged in two rows; up to six bidentate hooded hooks begin on segment 8, not accompanied by capillaries; hooks with approximately right angle between main fang and shaft, narrow angle between main fang and apical tooth, with constriction on shaft (figure 6F).

Segment 5 slightly modified, about the same size as segments 4 and 6, with posteroventral fascicle of unilimbate capillary neurosetae in two rows; with anterodorsal fascicle of unilimbate notosetae. Two types of major spines of segment 5 in approximately horizontal curved row; ventral row of up to four to six spines with distally enlarged ends, with small digitiform bosses on sides and main shaft, approaching apical edge with eight to nine rounded or pointed teeth, posterior end of spines with capillary extension (figures 6E, 7A–D) and dorsal row of up to three to four acicular spines with an apical shelf (figures 6E, 7B).

Single pair of branchiae present on segment 7 (figure 6A, B). Dorsal ciliary bands from segment 2 continuing to terminal segments.

Posterior segments with large cells ( $\sim 20\text{--}30\ \mu\text{m}$ ); pygidium cylindrical, slightly tapering to distal end (figure 6A, B).

#### *Asexual reproduction*

The sequence of stolon body formation closely follows that described by Radashevsky (1996), although the growth zone position may vary between segments 10 and 11. Eighteen specimens examined from the Philippines and the Red Sea exhibited a growth zone that appeared to follow segment 10 (these individuals possessed a recently formed growth zone corresponding to stolon 1). Radashevsky (1996) noted that the growth zone may be incorrectly interpreted to form after segment 10 during secondary stolon formation. Yet even during formation of stolon 1 specimens exhibited a growth zone following segment 10. Thus, it appears that the growth zone can form following segment 10, soon after which the anlage of segment 11 is formed. Individuals later in development (with stolon 1 possessing new thoracic segments and newly formed palps) possess a fully developed segment 11 and often a developing segment 12. Records of specimens possessing a growth zone following segment 11 may represent individuals later in development rather than initial position of the growth zone. SEM examination confirmed that 10 segments simultaneously arise in developing stolons (figure 6C); early in this stage the setae of the developing segments are not visible externally and develop later in segment formation.

#### *Feeding*

Examination of specimens collected from the Red Sea showed that nearly all individuals contained sand grains within the digestive tract. The sand grains were of considerable size ( $164.5 \pm 100.3\ \mu\text{m}$ , mean maximal length  $\pm$  SD;  $N=20$ ) compared to the digestive tract and distributed throughout the digestive tract of paratomic chains (figure 6D). These sand grains indicate the worms have the ability to ingest large food particles; their mode of feeding (deposit, suspension, or deposit and suspension) remains unknown but it is likely that they exhibit a combination of deposit and suspension feeding as documented in other polydorids (e.g. Dauer *et al.*, 1981; Williams and McDermott, 1997). If the worms remove sand grains and other deposited material on the surface of sponges they could be benefiting sponges

by keeping their surfaces free of debris, as documented in other polychaetes associated with sponges (Martín *et al.*, 1992).

#### *Distribution*

South China Sea: south-eastern coast of Vietnam, Philippines; Red Sea.

#### *Remarks*

SEM examination has allowed more detailed analysis of the fifth segment spine morphology, leading to the observation of the capillary extension at the apical end of the spines and the digitiform bosses (both difficult to observe with light microscopy). The spine morphology of *P. dawydoffi* specimens from the Philippines differs slightly from those collected in the Red Sea and Vietnam. The Philippine specimens exhibit spines which are more squat on the denticulate edge and possess a thicker capillary extension (figure 7A, B); Vietnam and Red Sea specimens exhibit spines which are more elongate along the denticulate edge and have a rounded distal end with a thinner distal capillary (figure 7C, D). No other morphological differences were noted between specimens from the three localities and without further morphological or molecular evidence, the distinctions in the spines do not appear to warrant the erection of a new species. The Philippine specimens exhibited slight pigmentation on anterior and posterior segments while those of the Red Sea were heavily pigmented (figure 6A, B); Radashevsky (1996) found no pigmentation on specimens collected from Vietnam. One of the paratypes examined was composed of 18 segments and contained an endoparasitic copepod within segments 11–15; additional parasitic copepods were found in specimens from Vietnam (Radashevsky, 1996). This is the first record of the species from the Red Sea and the Philippines.

#### *Polydorella stolonifera* (Blake and Kudenov, 1978)

(figures 6, 8)

*Polydorella stolonifera* (Blake and Kudenov, 1978): 269–271, figure 50a–j.

*Material examined.* Twelve paratypes from Australia, Victoria, Westernport Bay, Crawfish Rock, 5 m, 3 January 1972, from *Ancorina cordicata* (Carter, 1879) (NMV F42898, previously registered as G2898; two prepared for SEM).

#### *Description*

Largest single individual 3.8 mm long and 0.6 mm wide at segment 7; 16 segments, with endoparasitic copepod (see Remarks); single individuals with developing growth zone of stolon 1 and 16 segments 2.5 mm long and 0.4 mm wide at segment 7 (figure 8A). Prostomium bifid; caruncle short, terminating at posterior margin of segment 1; occipital tentacle and eyes absent (figure 8A, B). Palps extend posteriorly for 8–12 segments. Pigmentation absent.

Segment 1 with small notopodial lobe without notosetae; neuropodial lobe with two or three winged capillary neurosetae (figure 8A, B). Unilimbate capillary notosetae of segments 2–4, 6 and subsequent segments in two rows. Unilimbate capillary neurosetae of segments 2–4, 6 and 7 arranged in two rows; up to eight bidentate hooded hooks begin on segment 8, not accompanied by capillaries

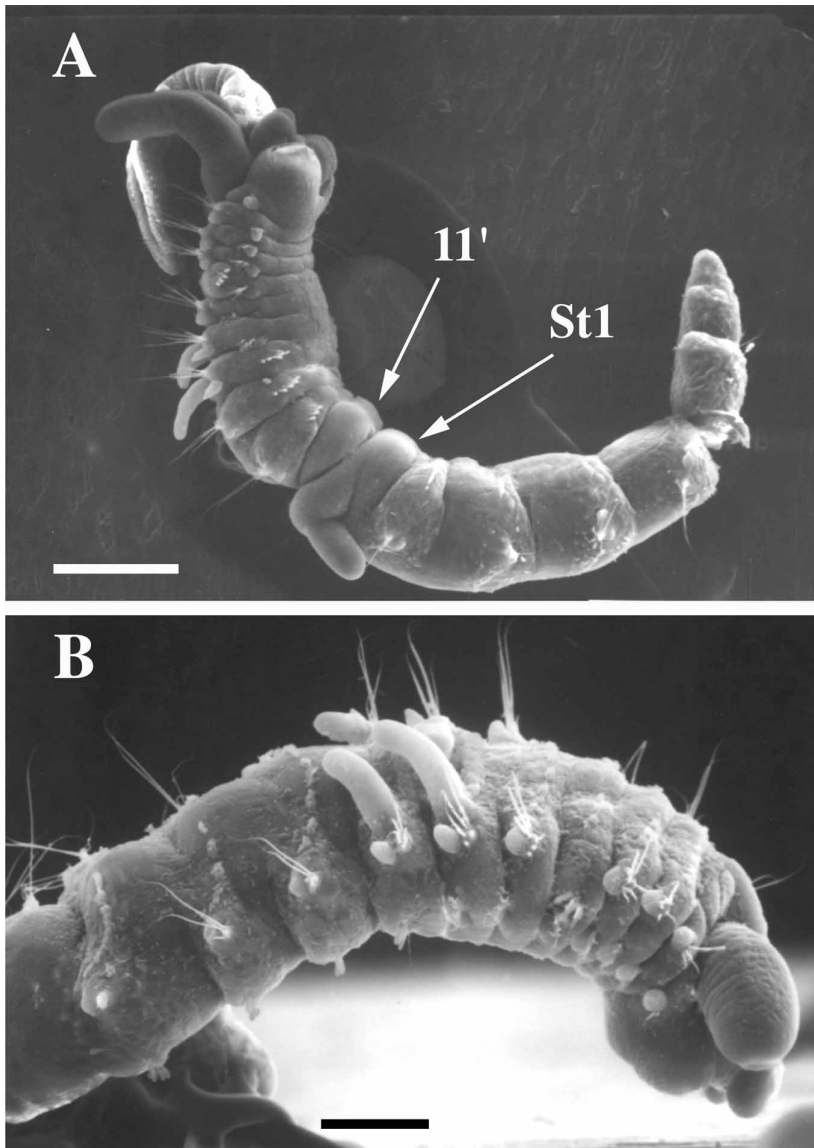


FIG. 8. *Polydorella stolonifera* (NMV F42898). (A) Lateral view of paratomic chain containing a developing stolon 1 (St1) and a newly developed segment 11 (11'); (B) dorsolateral view of anterior end of single specimen containing 16 segments; note branchiae on segments 7 and 8. Scale: 250  $\mu$ m (A); 100  $\mu$ m (B).

(figure 8A, B); hooks with approximately right angle between main fang and shaft, narrow angle between main fang and apical tooth, with constriction on shaft.

Segment 5 slightly modified, about the same size as segments 4 and 6, with posteroventral fascicle of bilimbate capillary neurosetae in two rows; notosetae absent. Two types of major spines of segment 5 in approximately horizontal curved row; ventral row of three to six spines with expanded tips covered by fine bristles and a dorsal row of up to five simple acicular spines (figure 6G).

Branchiae present on segments 7 and 8 (figure 8A, B). Dorsal ciliary bands from segment 2 continuing to terminal segments (figure 8B).

Pygidium with small cirri surrounding terminal anus (figure 8A).

#### *Asexual reproduction and parasitism*

Of 12 individuals examined, 10 exhibited asexual reproduction with two individuals joined in a chain (figure 8A). The two single individuals consisted of up to 16 segments; both possessed endoparasitic copepods within segments 8–12. Individuals undergoing asexual reproduction contain a growth zone that developed after segment 10. Formation of new posterior stock segments is apparent in side and ventral views (figure 8A). The sequence of stolon body formation appears to be similar to that described for *Polydorella kamakamai*, although no specimens were composed of more than two individuals.

#### *Distribution*

South China Sea: south-eastern coast of Vietnam, Philippines; Red Sea.

#### *Remarks*

Blake and Kudenov (1978) indicated that brown pigmentation was present on the branchiae, peristomium and sides of anterior segments; this pigmentation has been lost from the specimens stored in alcohol for 29 years. This is the first report of parasitic copepods within *Polydorella stolonifera*, although Radashevsky (1996) noted such parasites in *P. dawydoffi*. The copepod parasites apparently interfere with the process of asexual reproduction in *Polydorella*. These parasites may induce larger numbers of segments and longer length in infected individuals; 16 segments in *P. stolonifera* that contained parasites versus 15 segments in those lacking parasites and 17–18 segments in parasitized *P. dawydoffi* versus 15 segments in those lacking parasites. The present findings are in contrast to those of McCurdy (2001), who found earlier fragmentation in asexual reproduction via architomy by *Pygospio elegans* Claparède, 1863 when parasitized by trematode metacercariae. Such differences are not unexpected because host responses to parasites could be influenced by a variety of factors including mode of asexual reproduction (i.e. paratomy versus architomy) and type of parasite (crustacean versus trematode).

#### **Discussion**

*Polydorella kamakamai* is unique among the polydorids in possession of acicular neurosetae in the anterior body segments. *Lindaspio dibranchiata* Blake and Maciolek, 1992 contains similar heavy neurosetae in the anterior segments and also exhibits heavy spines in the notopodia of segments 2–4 (Radashevsky and Fauchald, 2000); the function of these spines remains unknown (Blake and Maciolek, 1992). Additional spionids possess acicular spines in posterior body segments, typically restricted to the notopodia, although *Dipolydora aciculata* (Blake and Kudenov, 1978) exhibits acicular spines in both the notopodia and neuropodia of posterior segments (see Blake, 1979 and Sato-Okoshi and Takatsuka, 2001 for discussion of posterior modified notopodial spines). In addition, the major spines of segment 5 in *Polydorella kamakamai* include a ventral row of spines with small digitiform bosses not previously observed in the genus. However, these bosses



are similar to those found along the sides of the ventral row of major spines in *P. dawydoffi*.

SEM investigations have provided more detailed morphological observations of the spines in *P. dawydoffi*, including the possession of digitiform bosses around the expanded portion of the spines, an edge containing eight or nine sharp to rounded teeth and a distal capillary extension. The digitiform bosses and distal extensions were not previously noted in *P. dawydoffi* by Radashevsky (1996), who showed the spines as having a rounded distal end. The capillary extension in *P. dawydoffi* is similar to that found in the ventral row of major spines in *Pseudopolydora paucibranchiata* (Okuda, 1937) which also contains what Radashevsky and Hsieh (2000) described as 'tilelike' structures on the distal end of the posterior row of falcate spines of the fifth segment (similar in morphology to the digitiform bosses described here). This fact, together with the reduced modification of the fifth segment and morphology of the hooded hooks with apical spine closely applied and constriction on the shaft, indicates a close relationship between the genera *Polydorella* and *Pseudopolydora*. A close relationship between these genera was also found in a preliminary cladistic analysis by Williams (2000).

Radashevsky and Fauchald (2000) showed that homology of chaetae in spionids could be shown based on positional criteria and subsequently used in cladistic analyses. Within *Polydorella* spp., the fifth segment exhibits dorsal (falcate) and ventral (denticulate, bristled or with digitiform bosses) notochaetae positioned in two horizontal rows; these two rows correspond to the dorsal posterior and dorsal anterior rows of notochaetae, respectively (Radashevsky and Fauchald, 2000: figures 3, 4). The two vertical rows of neurochaetae are more difficult to homologize. *P. kamakamai* is unique in possessing a dorsal row of acicular neurochaetae and a ventral row of capillary neurochaetae. Acicular spines are reduced in number on segments 6–7 and bidentate hooded hooks replace both acicular and capillary neurosetae from segment 8 and posterior; the hooks appear to correspond with the posterior row of neurochaetae. Recent investigations of palp ciliation patterns (Worsaae, 2001) provide additional structures that also will enhance future cladistic analyses of polydorids; unfortunately such information is currently lacking for many species.

The process of paratomic division in *Polydorella kamakamai* is similar to that found in all members of the genus. *Polydorella kamakamai*, *P. stolonifera*, *P. prolifera* and *P. smurovi* all produce a growth zone between segments 10 and 11 while *P. dawydoffi* typically exhibits a growth zone following segment 11. In *P. kamakamai* and *P. dawydoffi*, 10 segments in the developing stolon appear to form simultaneously from subdivision of the growth zone. This is probably the case in all members of the genus but needs to be confirmed by examining the process of paratomic division in live specimens and detailed histological examination. Specificity in the number of thoracic segments produced during asexual reproduction has also been shown in *Pygospio elegans* where 10–12 anterior segments are formed after architomic division (Gibson and Harvey, 2000) and in *Dipolydora armata* where 12 segments are formed (Bick, 2001). A similar mode of subdivision of anlage was documented during larval development in *Chaetopterus* sp.; this species does not exhibit overt segmentation of segments A1–A9 until the L5 stage (approximately 60 days in development) (Irvine *et al.*, 1999). Formation of these segments is through subdivision of the anlage rather than by sequential addition of segments from a growth zone as is typical during larval development in polychaetes (Irvine *et al.*,

1999). Expression patterns of Hox genes in *Chaetopterus* sp. have been correlated with segment formation (Irvine and Martindale, 2000) and, as suggested by Gibson and Harvey (2000), these and other genes may be involved in segment formation during asexual reproduction in *Polydorella* and other spionids.

The process of paratomic division in *Polydorella* species also closely matches that of *Dipolydora tetrabanchia* described by Campbell (1955). In specimens of *D. tetrabanchia* the growth zone develops between segments 15 and 18 in individuals that possessed approximately 28 total segments; the posterior portion of the growth zone gave rise to 10 segments of the developing stolon. Campbell (1955) showed that five separate individuals of *D. tetrabanchia* were produced from a paratomic chain consisting of two individuals within 15 days; specimens exhibited paratomic division during all seasons. This high rate of reproduction accounts for the large numbers of *D. tetrabanchia* found within the colonies formed in mollusc shells. Similarly, regeneration of fragments produced through architomy in *Pygospio elegans* requires 8 days (Gibson and Harvey, 2000). Some colonies of *P. elegans* reproduce exclusively by architomic division and can reach high population densities (Anger, 1984). Bick (2001) indicated asexual reproduction (via architomy) favours *D. armata* in competition for limited space on shell surfaces, particularly during early colonization. Data on the development time of stolons during asexual reproduction in *Polydorella* species are lacking but clearly paratomy allows for effective utilization of sponge surfaces.

Sexual reproduction appears to be rare or transient among *Polydorella kamakamai* and other species within the genus. Only one of 290 specimens (0.3%) of *P. kamakamai* were found with eggs and no egg capsules were found within the burrows of the worms. As Radashevsky (1996) noted for *P. dawydoffi* from Vietnam, no Philippine or Red Sea specimens of *P. dawydoffi* were found to exhibit sexual reproduction. Tzetlin and Britayev (1985) found some specimens of *P. smurovi* with egg capsules containing approximately 30 developing embryos; other specimens were found with developing eggs within the body but measures of eggs or percentage of worms exhibiting sexual reproduction were not noted, although based on their figure 1 (Tzetlin and Britayev, 1985: 178), developing eggs within the body are approximately 29–43  $\mu\text{m}$  in diameter. The estimated number of eggs produced in *Polydorella kamakamai* (36–42, 26–34 and 15–20 eggs in segments 13–15, respectively) closely matches that provided for *P. smurovi*.

*Polydorella kamakamai* and *P. smurovi* are the only members of the genus documented to produce eggs and there are no data on the larval development within the genus. It has been suggested that planktotrophic larvae would need to be produced in order for colonization of new sponges (Radashevsky, 1996) and the egg size of *P. kamakamai* is in the size range of spionids exhibiting planktotrophic development (Blake and Arnofsky, 1999). In the present investigation, *P. kamakamai* were also noted to move efficiently across the surface of sponges and may have the ability to move to neighbouring sponges as adults. In addition, single individuals of 13–15 segments are within the size range of planktotrophic larval stages of polydorids (Blake and Arnofsky, 1999). It is possible that these single individuals could move out of their burrows following paratomic division and be released from the surface of the sponge, thereby allowing dispersal as adults. Such a mode of dispersal is purely speculative but would partly explain the lack of sexual reproduction observed in *P. dawydoffi*, *P. prolifera* and *P. stolonifera*, in spite of the examination of hundreds of individuals. Further studies are needed to document

the complete life-cycle of these species and to determine the cues (e.g. food availability and temperature) responsible for switching from reproduction via paratomy to sexual reproduction (as completed for architomy in *Pygospio elegans*: Anger, 1984; Wilson, 1985). In addition, research on live specimens would illuminate critical aspects of the biology of *Polydorella* species, including the development time in stolon formation and paratomic division (also behaviour during this process), sexual reproductive potential (number of eggs per brood), timing and morphology of larval development, and planktotrophic development (if present).

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