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## A new *Polygordius* (Annelida: Polychaeta) from Terra Nova Bay, Ross Sea, Antarctica

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**Abstract** *Polygordius antarcticus* sp. nov. is described from benthic material collected at depths ranging between 31 and 61 m in Terra Nova Bay, Ross Sea, during the 1987–1988 and 1988–1989 expeditions of the Italian National Research Program in Antarctica. This is the first named species of the genus from Antarctic waters. Although no fully mature specimens were available, the new species appears unique in combining the following features: a regular pygidium, inflated and with a single ring of round adhesive pads, a conical prostomium with short antennae (only half as long as the prostomium) and shallow head fold, and a well-developed circulatory apparatus, with circumoesophageal commissures entering the prostomium and long intersegmental commissures insinuating into the ventrolateral compartments of the trunk. These and other significant features were investigated by light and scanning electron microscopy. In the construction of the head and the scheme of the blood system, the new species resembles *Polygordius triestinus* Woltereck, described by Hempelmann in 1906, an aberrant species inhabiting muddy, anoxic sediments in the Adriatic Sea, but it differs significantly from it in the shape of the mouth (in *P. triestinus* the upper lip is hypertrophied and strongly protruding) and the pygidium (in *P. triestinus* this region is stump-like and non-adhesive). The pygidium of *P. antarcticus* sp. nov. is encircled by 28–30 small adhesive pads, each with 15–20 glandular openings. Preterminal cirri are lacking, as are perianal appendages. The anus is surrounded by six to seven lobes of which the midventral is largest and longest. A world distribution map of the genus is provided.

### Introduction

Members of the Polygordiidae are common inhabitants of marine coastal sands at various latitudes (Fig. 1). Their bodies are elongate and cylindrical, tapering at both ends. The prostomium has a pair of solid, non-grooved projections innervated from the anterior part of the brain (antennae; Fauchald 1977). The pygidium is generally expanded and encircled by adhesive glands; behind these glands, preterminal cirri or perianal papillae may be present (Table 1). The trunk surface is smooth, almost nematode-like, and shows little sign of external segmentation. All members of the family are classified in the genus *Polygordius* Schneider, 1868, which lacks parapodia and chaetae. The chaetate *Chaetogordius canaliculatus* Moore, 1904 described “from a couple of fragmented specimens in association with marine Oligochaeta on Cape Cod”, yet never re-discovered (Hermans 1969), is regarded today as an invalid taxon (Westheide 1990).

Like the protodrilids and saccocirrids, but unlike all other interstitial polychaetes, *Polygordius* worms develop with pelagic planktotrophic larvae (Hermans 1969; Westheide 1990). These are of two types: in the “exolarva” the larval body becomes gradually elongated by addition of new segments; in the “endolarva” the developing segments remain folded up inside the hyposphere until a more or less abrupt metamorphosis (Woltereck 1902; Remane 1932; Dawydoff 1959). Until recently (Lenihan and Oliver 1995; Rota and Carchini 1996), the collection of giant endolarvae in the South Atlantic during the German Deep Sea Expedition aboard the *Valdivia* (1898–1899) (Woltereck 1905) represented the southernmost record of these animals.

During the third (1987–1988) and fourth (1988–1989) expeditions of the PNRA (Italian National Research Program in Antarctica) to the Ross Sea, one of the authors (GC) collected abundant benthic material of *Polygordius* at various depths in the coastal stretch adjacent to the Italian Base in Terra Nova Bay (Rota and

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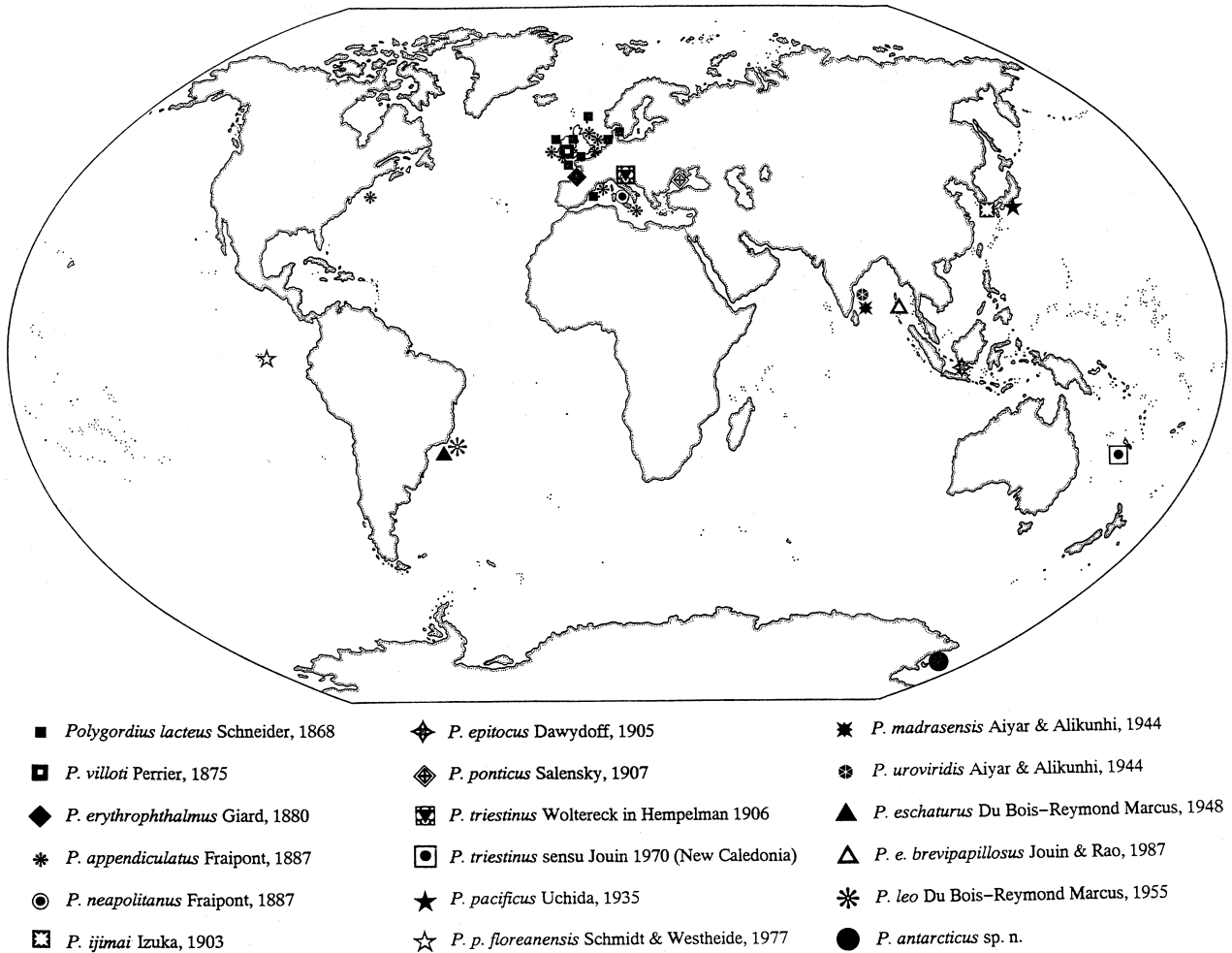


Fig. 1 Distribution of the genus *Polygordius* Schneider, 1868

Carchini 1996; Rota et al. 1997). This discovery and an immediately preceding record (undescribed and unnamed) in shallow waters in McMurdo Sound (Lenihan and Oliver 1995) have extended the known range of the genus to latitudes well south of the Antarctic circle. In spite of the absence of mature specimens, the Terra Nova Bay worms display a combination of somatic traits that does not match any of the known species, thus allowing the description of a new species.

## Materials and methods

Soft-bottom sediments were sampled during January/February 1988 and January 1989 at various locations between the Italian Base and Cape Russell (Fig. 2), in an 18- to 126-m depth range, using a grab from a motorboat (station series "a" and "b", collector G. Carchini) and from aboard M/S *Finnpolaris* (station series "B", collectors G. Carchini and M. Taviani). The substrates ranged from medium to fine sands, often mixed with mica or mollusc shell fragments and diatom skeletons; a coarser mineral component (gravel and pebbles) was frequent in shallow samples (35–41 m), whereas organic debris, foraminiferan shells and sponge spicules prevailed in the deepest ones. These collections have provided material of endofaunal annelid groups not previously reported

from the Ross Sea (Erséus and Rota 1996; Rota and Erséus 1996; Rota et al. 1997). Details of the samples containing *Polygordius* are as follows.

*Sample a33.* Sea between Tethys Bay (74°40'S) and Adélie Cove (74°46'S), between longitudes 164°01' and 164°08'E; 24 January 1988; 50 m depth, 35 specimens.

*Sample a35.* Off the coast (100 m) between Faraglione (a large rock near the coastline, 5 km south of the Italian Base) and Adélie Cove, i.e. between latitudes 74°43' and 74°46'S and longitudes 164°01' and 164°08'E; 27 January 1988; 40 m depth, 25 specimens.

*Sample a39.* Off beach in Adélie Cove (about 74°46'S, 164°01'E); 4 February 1988; 31 m depth, 30 specimens.

*Sample b76.* Off the coastal area named Campo Icaro (74°43'S, 164°07'E); 30 January 1989; 50- to 100-m depth, 50 specimens.

*Sample B98.* Sea between Faraglione (74°43'S) and Cape Russell (74°54'S), between 163°55'E and 164°10'E; 10 February 1988; 41 m depth, medium to coarse sand with mica, 150 specimens.

*Sample B100.* Sea between Faraglione (74°43'S) and Cape Russell (74°54'S), between 163°55'E and 164°10'E; 10 February 1988; 61 m depth, fine to medium sand mixed with shell fragments, diatom skeletons and abundant organic debris, over 300 specimens.

A part of the material (samples "a" and "b") was sorted while alive, fixed in formalin and subsequently transferred to alcohol. Another part (samples "B") was extracted in Italy in 1994 from formalin-preserved (7%, non neutralised) sandy sediments using elutriation and filtering on a sieve with 0.15 mm mesh size, and transferred to 70% alcohol. The whole collection comprised more than 600 specimens (anterior ends counted). Unfortunately, the majority of the worms were fragmented and in a rather poor condition. All measurements reported in the following description refer to the largest (subadult) specimens in the collection, which

**Table 1** Principal features distinguishing the species of *Polygordius*. Data from the literature and own observations. For the geographic location of the species see Fig. 1

Species	Body size (mm)	Segment number	Prostomium shape	Antennae	Length ratio antennae: prostomium	Eyes	Head fold	Pygidium shape	Adhesive glandular pads	Pygidial appendages	Anal opening	Circulatory apparatus	First fertile segments	Larva	External motile cilia
<i>Polygordius lacteus</i> Schneider, 1868 = <i>P. apogon</i> (McIntosh, 1875)	40–100 by 0.6–1.5	150–185	Rounded	Stiff, l = 600–780 µm	≥1:1	0 or 2	Deep	Bulb-like	26–28, round, 35–43 pores each	None	Central with 8 lobes	Dorsal and ventral vv. linked by circumoesoph. (peristomial) and intersegmental commissures; a gut sinus and blind lateral branches of commissures in mature fertile segments	males: 50–70, females: 40–60	Endo-larva	No
<i>P. villoti</i> Perrier, 1875	≥100 by 1					0		Bulb-like		None		Dorsal and ventral vv. linked by intersegmental commissures			Yes (mouth + posterior end)
<i>P. erythrophthalmus</i> Giard, 1880	≥100					2		Bulb-like		None		Dorsal and ventral vv. linked by intersegmental commissures			Yes (tufts)
<i>P. neapolitanus</i> Fraipont, 1887	25–50 by 0.3–0.5		Rounded	Short, separate	≥1:1	0	Deep	Bulb-like	Round	None	Ventral, with 8 lobes	As in <i>P. lacteus</i> but with intersegmental commissures giving off blind lateral branches in most segments	4?	Exo-larva	No
<i>P. appendiculatus</i> Fraipont, 1887	20–45 by 0.12–0.31	95–125	Rounded or blunt	Long, narrow, l = 240–410 µm	> 1:1	1 or 2	Deep	Bulb-like	30, round, 25–35 pores each	pre-terminal	Central, with 5 lobes	As in <i>P. lacteus</i>	males: 25–35, females: 25–40	Endo-larva	No

Table 1 (continued)

Species	Body size (mm)	Segment number	Prostomium shape	Antennae	Length ratio antennae: prostomium	Eyes	Head fold	Pygidium shape	Adhesive glandular pads	Pygidial appendages	Anal opening	Circulatory apparatus	First fertile segments	Larva	External motile cilia
<i>P. ijimai</i> Izuka, 1903	70–77 by 0.6–0.8			Long, horn-like, l = 1000 µm		0		Bulb-like	Elongate	3 (1 dors., 2 ventr.) preterminal	With 8 lobes	As in <i>P. lacteus</i> but with adjacent intersegmental commissures anastomosing through lateral longitudinal vessels	At 1/4 of body length		No
<i>P. triestinus</i> Woltereck in Hempelmann 1906	30		Conical	Short, very close	<0.5:1	0	Shallow	Cylindr.	None	None	Central	Circumoes. commissures entering prostomium; intersegmental ones very long and winding; dorsal gut sinus in fertile region	Herma-phroditic	Exo-larva	No
<i>P. triestinus</i> sensu Jouin 1970 (New Caledonian population)	10–12 (adult males)	60	Conical	Short	0.5:1	0	?Shallow	Elongate, tapering	Round, arranged in several circles	None	Central	As in typical <i>P. triestinus</i> , but with longest intersegmental commissures in forebody and no anterior anastomoses	Males: 22–24		
<i>P. pacificus</i> Uchida, 1935	30–35 by 0.4–0.5			Short	≥1:1	0		Bulb-like	Ca. 40, elongate	None	Central, with 6–8 lobes				
<i>P. p. floreanensis</i> Schmidt & Westheide, 1977	4.9–23 by 0.11	35–75	Conical	l = 100–225 µm, close	≥1:1	0		Bulb-like (160 µm)	Elongate, with 2 lines of pores	None	Central	Dorsal vessel bifurcating behind peristomium; intersegmental commissures present	Males: 17		No
<i>P. madrasensis</i> Aiyar & Alikunhi, 1944	7–15 by 0.12–0.18	40–75	Conical	l = 150 µm	≥1:1	0		Bulb-like (150 µm)	14–18, round	2 (80 µm) terminal	With no lobes				
<i>P. uroviridis</i> Aiyar & Alikunhi, 1944	4–6 (immature)	25–35 (immature)	Rounded	Tapering	1:1	2 or 4		Swollen (125 µm)	None, pigment only	None	With no lobes				

<i>P. eschaturus</i> Du Bois-Reymond Marcus, 1948	40 by 0.21	120–180	Rounded	l = 150–220 $\mu$ m, close	2:1	0	Deep	Bulb-like (300 $\mu$ m)	> 50, elongate	2 (50–70 $\mu$ m) terminal	Central	As in <i>P. lacteus</i> ; dorsal gut sinus in fertile region	20–28	No
<i>P. e. brevipapillosus</i> Jouin & Rao, 1987	30–50 by 0.25–0.5	120–205	Rounded	l = 200–250 $\mu$ m		0		Bulb-like (530 $\mu$ m)	Many, elongate	2 (30 $\mu$ m) terminal			20–30	No
<i>P. leo</i> Du Bois-Reymond Marcus, 1955	40 by 0.5	200	Rounded	l = 300 $\mu$ m	> 1:1	0		Bulb-like (460 $\mu$ m)	40, elongate	8–15 (300 $\mu$ m) preterminal	Central, lobed	Broad dorsal sinus over intestine in most segments		No
<i>P. antarcticus</i> sp. nov.	20 by 0.22–0.32 (subadult)	82–98 (subadult)	Conical	l = 75 $\mu$ m, very close	0.5:1	0	Shallow	Bulb-like (165 $\mu$ m)	28–30, round, 15–20 pores each	None	Dorsal, with 6–7 lobes	As in <i>P. irie-stinus</i> , but with longest intersegmental commissures in forebody and no anterior anastomoses		No

*Polygordius epitocus* Dawydoff, 1905 and *P. ponticus* Salensky, 1907, both morphologically similar to *P. lacteus*, have been omitted; one reproduces by epitoky, the other has a modified endolarva

were mounted on slides and more or less compressed under a coverslip. Any different dimensions of the material photographed under scanning electron microscopy are explained by the lack of compression and different age of the specimens.

Photographs of whole mounts (stained in paracarmine and embedded in Canada balsam) were taken using interference contrast on a Leitz Aristoplan microscope. Photographs of serial sections (4  $\mu$ m thick, stained in ferric haematoxylin) of specimens from stations a33 and B100 were obtained either on the same microscope or (Fig. 6d only) on a Leitz Dialux 20 microscope. For ultrastructural studies, specimens from stations B98 and B100 were rinsed in abundant distilled water, dehydrated in ethanol, critical point dried, mounted on aluminium stubs and sputter-coated with gold. They were examined and photographed with a Philips XL 20 scanning electron microscope.

The holotype and some paratypes of the new species are deposited in the Museo Civico di Zoologia di Roma (MCZR). Other paratypes are deposited at the Swedish Museum of Natural History, Stockholm, Sweden (SMNH).

For comparative purposes, material of *Polygordius lacteus* Schneider, 1868 (from Kristineberg Zoological Station, western Sweden, July 1896) and *Polygordius appendiculatus* Fraipont, 1887 (from the Institute of Biology of Helgoland, North Sea) were borrowed from SMNH.

## Results

Family *Polygordiidae* Czerniavsky, 1881

Genus *Polygordius* Schneider, 1868

*Polygordius antarcticus* sp. nov. (Figs. 3–6)

*Holotype*. MCZR POLYCHAETA 0001, whole-mount (a complete specimen cut into two pieces).

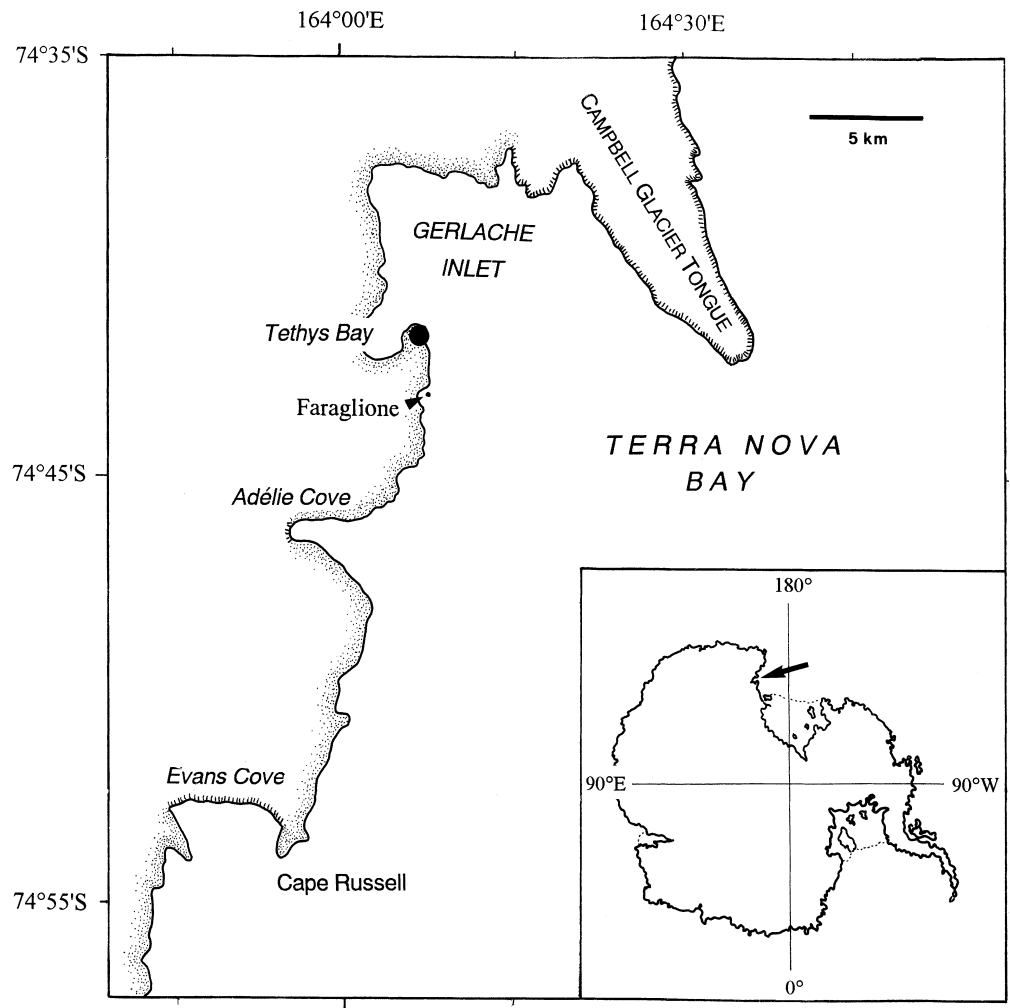
*Type locality*. Ross Sea, Terra Nova Bay, sea between Tethys Bay (74°40'S) and Adélie Cove (74°46'S) between longitudes 164°01'E and 164°08'E; 24 January 1988; 50 m depth.

*Paratypes*. MCZR POLYCHAETA 0002–0006, five whole-mounted specimens (two posteriorly amputated) from type locality; MCZR POLYCHAETA 0007–0008, two posteriorly amputated whole-mounted specimens from station B100. SMNH Type Coll. 5043–5045, three whole-mounted specimens (one complete) from type locality. SMNH Type Coll. 5046–5048, three whole-mounted specimens (all posteriorly amputated) from stations a39, B98 and B100, respectively.

*Other material*. Numerous other whole-mounts, as well as the series of transverse and longitudinal sections of both body ends, the SEM preparations, and the rest of the samples preserved in 70% alcohol, are kept in the first author's collection.

*Diagnosis*. Head conical, with weak external demarcation between prostomium and peristomium. Antennae small, only half as long as the prostomium. A highly developed circulatory system, with anterior commissures penetrating the prostomium and long intersegmental vessels entering the ventrolateral compartments of the trunk; the length of the intersegmental loops maximal in the anteriormost segments. A typical bulbous pygidium with a single ring of rounded adhesive pads and no elongate appendages. Anal opening dorsally directed (Table 1).

**Fig. 2** Topography of the coastal area sampled in Terra Nova Bay. The filled circle indicates location of the Italian Base. Inset shows position in the Ross Sea

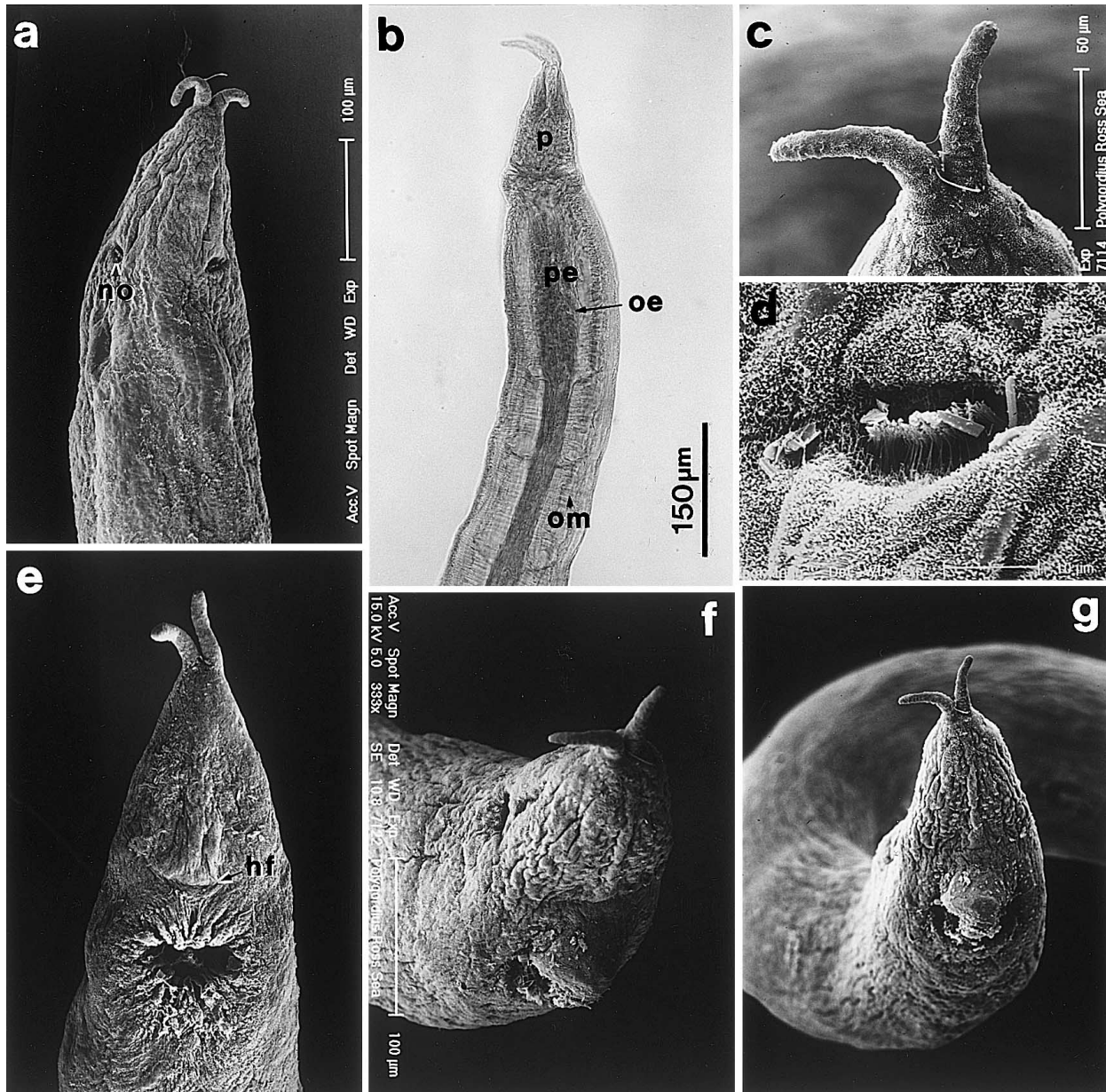


Holotype (the largest complete specimen in the collection) 20 mm long, with 98 segments. Largest complete paratypes up to 19 mm long, with 82–85 segments. Segment dimensions maximal between segments 20 and 40 (length,  $l = 375\text{--}422\ \mu\text{m}$ ; width,  $w = 225\text{--}320\ \mu\text{m}$ ); caudal segments very small ( $l = 60\text{--}80\ \mu\text{m}$ ;  $w = 150\text{--}200\ \mu\text{m}$ ).

Head conical (Figs. 3, 4), comprising a pointed prostomium ( $l = 148\text{--}152\ \mu\text{m}$ ; maximal  $w = 100\text{--}125\ \mu\text{m}$ ) and a long, composite peristomium ( $l = 296\text{--}355\ \mu\text{m}$ ; maximal  $w = 200\text{--}207\ \mu\text{m}$ ); ventral transverse groove separating these two regions (“head fold”) poorly marked and shallow (Fig. 3e). Antennae short (maximally  $75\ \mu\text{m}$  long), half as long as prostomium (this same proportion observed in all specimens, regardless of age), attached close to each other (Figs. 3c,e,g, 4, Table 1), with inconspicuous sensory cilia; antennal ganglia connected to anterolateral sides of cerebral ganglion. Eyes absent. Nuchal organs appearing externally as large (up to  $45\ \mu\text{m}$  long,  $15\ \mu\text{m}$  wide) dorsolateral slits, somewhat oblique to the transversal body axis, densely ciliated (Fig. 3a,d). Beneath them, the paired nuchal ganglia, connected to posterodorsal pro-

jections of the cerebral ganglion, are clearly visible (Fig. 4). Perioesophageal connectives meeting ventrally in the middle of peristomium to form the suboesophageal ganglion, the only ganglion occurring along the basiepidermal nerve cord (Fig. 4).

Mouth located somewhat behind the head fold, crescent-shaped (concave anteriorly). Upper buccal lip slightly protrusible (Fig. 3f–g), so as to show the anterior middorsal ridge of pharynx; lower lip followed by a thin-walled pharyngeal sac (Fig. 4). In front and behind the mouth (till the suboesophageal ganglion), the body wall comprises a midventral pad of strong transverse muscle fibres (buccal muscles; Fig. 4); the posterior part of these buccal muscles was also described by Fraipont (1887) in *Polygordius neapolitanus* and by Hempelmann (1906) in *Polygordius lacteus*. There is no muscular pharyngeal apparatus. Oesophagus thick-walled, densely ciliated, occupying the whole length of peristomium (this region was in fact named “Schlunddoppelsegment” by Woltereck (1905)). Intestine intersegmentally constricted throughout its length; its lumen is narrow and its wall contracted in the first 10–15 segments behind the peristomium

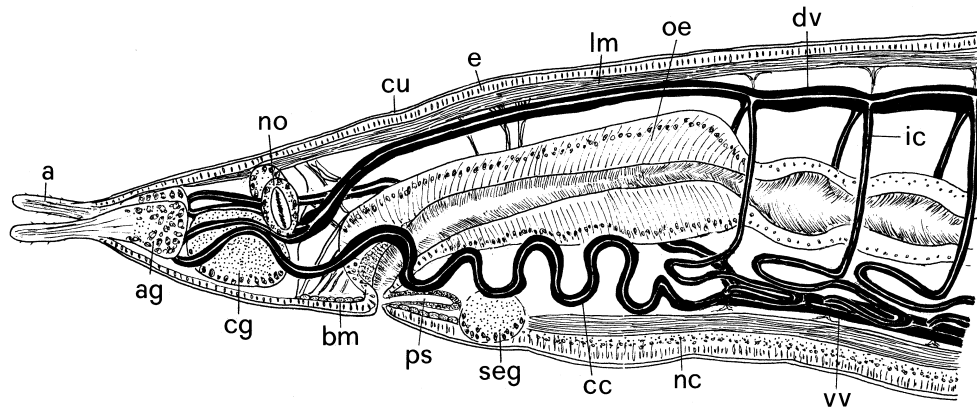


**Fig. 3a–g** Photographs of the anterior end of *Polygordius antarcticus* sp. nov. showing details of the head region (all specimens from formalin-preserved samples, **b**, light microscopy, others, scanning electron microscopy). **a,b** Dorsal views of head and anterior segments. **c** Enlargement of the antennae. **d** Ciliated slit of a nuchal organ. **e–g** Views of the ventral side of prostomium and peristomium. Note that the upper buccal lip, even when everted (**f,g**), has a small size by comparison with the prostomium (*hf* head fold; *no* nuchal organ, *oe* oesophagus, *om* oblique muscles, *p* prostomium, *pe* peristomium)

(Fig. 5a–b); lumen considerably broader and often showing a ventral ridge of high epithelial cells in midbody and posterior segments (Fig. 5c–e). Gut contents consisting of organic debris, diatom skeletons and sand grains. Occasionally a large sand grain trapped in the rectum.

Cuticle thin throughout. No circular muscles in the trunk body wall. Longitudinal musculature commencing dorsally from the sides of prostomium (Fig. 4), which makes it possible for the head to be held high (Fig. 3f–g), and ventrally behind the mouth. Ventrolateral longitudinal fibres generally thicker (Fig. 5). Oblique muscles beginning in the anterior of peristomium and comprising 10–15 bundles of fibres per segment (Fig. 3b). In many specimens the contraction of these muscles has produced two ventrolateral longitudinal folds in the trunk wall, thus dividing the segment cavity into three rounded compartments (Fig. 5).

In some specimens, strands of young germinal tissue could be seen within the ventrolateral compartments (Fig. 5d) and hanging from the body wall in the proximity of septa.



**Fig. 4** Internal organisation of the anterior body region of *Polygordius antarcticus* sp. nov. (schematic). The connections between the cerebral ganglion, the antennal ganglia and the nuchal ganglia, as well as the sinuous lower tracts of the intersegmental blood commissures on the right side of the body, and the oblique muscles, have been omitted for clarity (*a* antenna, *ag* antennal ganglion, *bm* buccal muscles, *cc* circumoesophageal blood commissure, *cg* cerebral ganglion, *cu* cuticle, *dv* dorsal blood vessel, *e* epidermis, *ic* intersegmental blood commissure, *lm* longitudinal muscles of body wall, *nc* nerve cord, *no* nuchal organ, *oe* oesophagus, *ps* pharyngeal sac, *seg* suboesophageal ganglion, *vv* ventral blood vessel)

A blood sinus extends over the dorsal side of the intestine in midbody and posterior segments (Fig. 5c–e). Serial sections show that the sinus prolongs further ventrad through a network of narrow channels (Fig. 5c). Towards the pygidium the ventral vessel may also have the character of a sinus. The dorsal vessel arises from the intestinal sinus around segment 20, but still adheres to the gut upto segment 10, and then lifts upwards and continues within the dorsal mesentery through the peristomium (Figs. 4, 5a–b). In front of the mouth, the vessel divides into two long loops (circumoesophageal commissures), which enter the prostomium, pass over the cerebral ganglion and descend to the base of the antennal ganglia; here they curve backwards and, after a very winding course, meet at the posterior border of the peristomium to form the ventral vessel (Fig. 4). Intersegmentally, paired transverse commissures come down from the dorsal towards the ventral vessel enclosed in the septa (Fig. 5a). In the first 20 segments, these commissures are extremely long and in their lower tract they form tortuous loops that insinuate into the ventrolateral compartments of adjacent segments (Figs. 4, 5a,b), to run then ventrad and join the ventral vessel. The length of the loops is maximal in the anteriormost segments. In the ventrolateral compartments of genital segments, thin blood vessels run through the gonadic tissue (Fig. 5d).

The structure of nephridia has not been discerned with certainty nor has their distribution along the body, but these organs are possibly lacking in the anteriormost segments.

Pygidium bulb-like, more or less inflated ( $w = 130$ – $165 \mu\text{m}$ ) depending on the degree of muscular contraction (Fig. 6a,b,e). It carries a slightly irregular, somewhat prominent, crown of 28–30 small, round glandular

pads, each possessing 15–20 pores (Fig. 6c). No elongate pygidial papillae or appendages are present. The anal opening is surrounded by six or seven lobes asymmetrically developed: the midventral lobe is the largest and longest and makes the anal opening slightly eccentric and directed upwards (Fig. 6b,e).

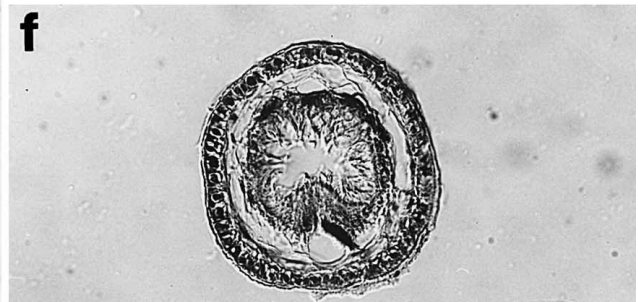
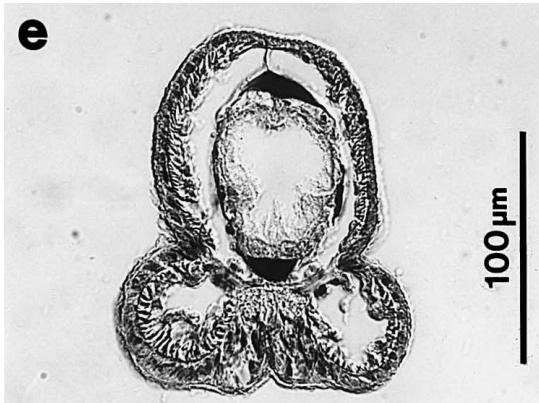
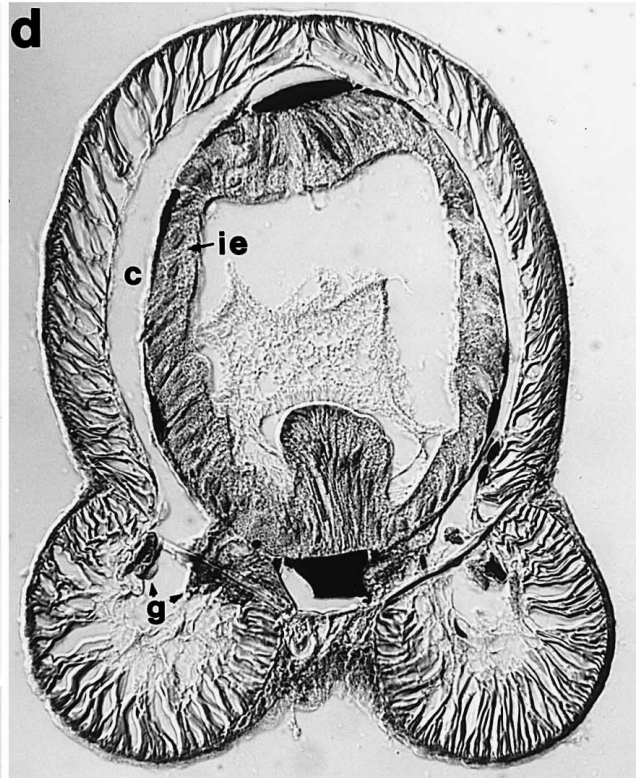
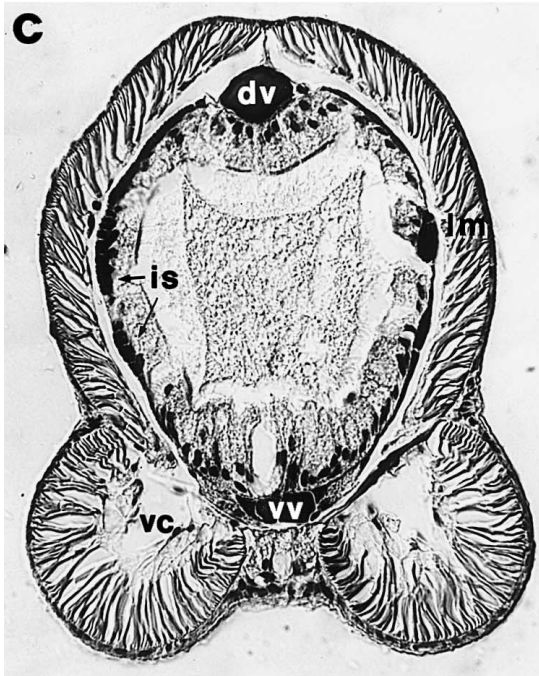
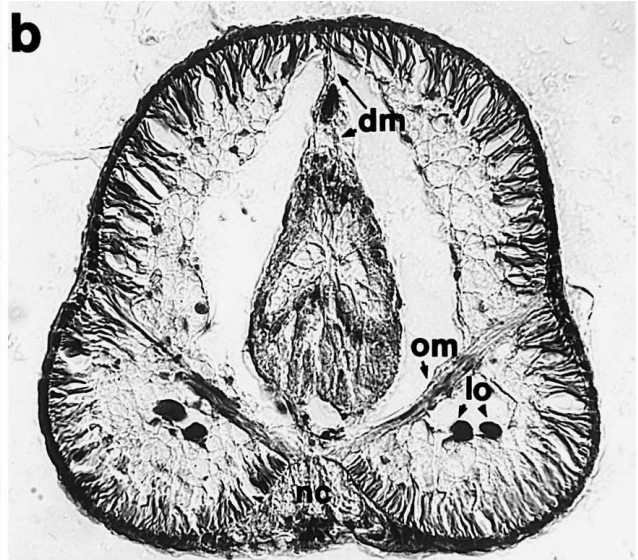
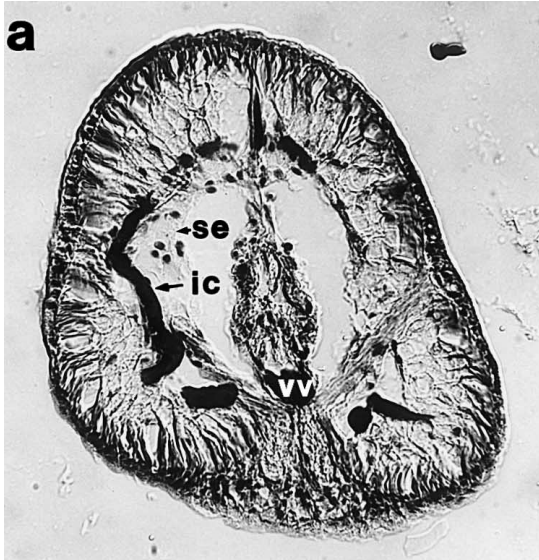
Serial sections indicate that the nerve cord, the oblique muscles and the mesenteries terminate in succession at the anterior margin of the pygidium. The epidermis becomes thickest just in front of the glandular crown; the longitudinal muscles get gradually thinner, while internal to them a circular sphincter intervenes (Fig. 6d). Behind the crown, the longitudinal muscles disappear completely (Fig. 5f), followed by the dorsal and ventral blood sinuses.

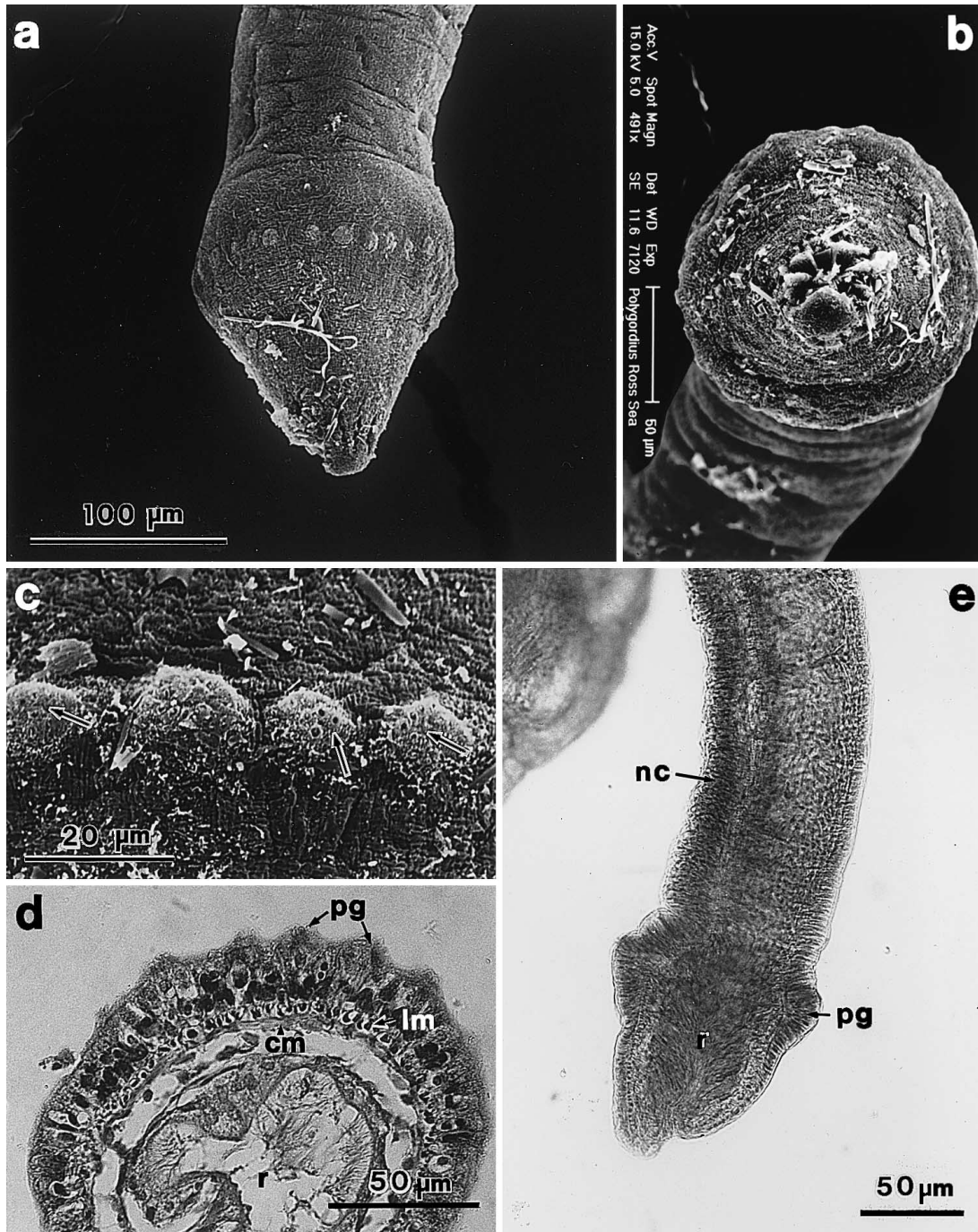
**Ecology.** *Polygordius antarcticus* sp. nov. inhabits a range of fine to coarse sandy sediments, often mixed with mica, at least down to a depth of 61 m. The Terra Nova Bay stations probably represent the greatest depths at which polygordiids have been reported. Specimens were most abundant at 61 m depth, where sand was mixed with shell fragments, diatom skeletons and abundant organic debris. It is worth mentioning that no specimen was found instead in a similarly grained sample from 126 m, rich in sponge spicules and inhabited by many tubicolous polychaetes and large-sized oligochaetes (tubificids; Erséus and Rota 1996), nor in two other organic-rich samples from 18 m and 50 m largely dominated by nematodes. Indeed, little habitat overlap is observed generally between *Polygordius* and large marine oligochaetes, even in warmer seas (C. Erséus, personal communication).

Several specimens had the coelom of their anterior or posterior body regions heavily infected by parasites. The

**Fig. 5a–f** Photographs of cross sections through the trunk and tail of *Polygordius antarcticus* sp. nov. (alcohol-preserved specimens; light microscopy). **a,b** Intersegment and middle of a segment in the postoesophageal region. **c,d** Midbody region. **e** Tail region. **f** Pygidium, just before the anus. All to same scale (*c* coelomic cavity, *dm* dorsal mesentery, *dv* dorsal blood vessel, *g* germinal tissue, *ic* intersegmental blood commissure, *ie* intestinal epithelium, *is* intestinal blood sinus, *lm* longitudinal muscles, *lo* loops of intersegmental commissure, *nc* nerve cord, *om* oblique muscles, *se* septum, *vc* ventrolateral compartment, *vv* ventral blood vessel)







**Fig. 6a–e.** Photographs of the posterior end of *Polygordius antarcticus* sp. nov. (a–d specimens from formalin-preserved samples, e specimen preserved in alcohol; a–c scanning electron microscopy, d,e light microscopy). a Ventrolateral view of the pygidium. b Posterior view of the pygidium (note the larger midventral lobe of the anal opening). c Enlargement of the adhesive pads, showing glandular pores (arrows). d Cross section of the pygidium through the glandular crown. e Lateral view of the tail in a whole mounted specimen (cm pygidial circular muscles, lm longitudinal muscles, nc nerve cord, pg pygidial adhesive glands, r rectum)

most common were elongate foliaceous eugregarines, similar to those reported by Fraipont (1887) in the intestine of *P. neapolitanus*.

## Discussion

Although no fully mature specimens were available, the description of a new species is justified by three considerations. Firstly, the morphology of grown polygordiids does not change with sexual maturity, except of course for body size. Characters present only in adults are the internal sexual characters, i.e. the location of the fertile segments along the body, the intrasegmental position of the reproductive cells, and the structure of gametes. At present such data are unknown for half the species of the

genus (Table 1). Secondly, like most of the Antarctic seas (Clarke 1988; Pearse et al. 1991), the coastal waters at Terra Nova Bay are characterised by a strong summer pulse of primary production, with little or no production from late autumn to early spring (see Gambi et al. 1994). A markedly seasonal reproductive activity is indicated for the Antarctic benthic invertebrates with pelagic planktotrophic development (White 1977; Pearse et al. 1991; Knox 1994) as a response to such extreme seasonality. The absence of mature *Polygordius* worms from Antarctic midsummer collections (i.e. at a time of the year when reproductive activity would be most intense in species living in temperate and tropical areas; Aiyar and Alikunhi 1944; Von Nordheim 1984) suggests that at these extreme latitudes gonad maturation and spawning may be limited to an earlier (possibly very short) period, as an adaptation for coupling the long development of planktotrophic larvae with the seasonal availability of primary production. Under these circumstances, it will be difficult to obtain sexually mature specimens in the near future. Thirdly, there is a wide geographic separation between the Ross Sea and the areas whence the putative closest relatives of the new species (see below) were described. This separation and their significant somatic divergence are sufficient justifications for regarding them as separate species.

#### State of *Polygordius* taxonomy and position of the new species within the genus

While always having an important role in debates on the phylogeny and comparative morphology of Polychaeta (Hermans 1969; Anderson 1973; Clark 1978; Fransen 1980; Sensenbaugh and Franzén 1987; Purschke and Tzetlin 1996), *Polygordius* worms have not aroused the interest of modern taxonomists. The simplicity of their body creates a paucity of morphological characters that can be used for species discrimination, and this has probably discouraged many students from reviewing the group and attempting a supraspecific ranking.

Including the new species, the genus *Polygordius* currently comprises 15 named species and 2 subspecies. As is evident from Table 1, for many of these taxa knowledge is very scanty and restricted to general traits such as the body size and colour, the shape of the head and pygidium, the occurrence of eyes and ciliation of the body surface, the pattern of the circulatory apparatus, or the type of larval development. At some stage in the past, distinctions based on the latter two features became highly controversial (e.g. Woltereck 1902, 1925; Hempelmann 1906, 1908; Söderström 1924a,b), reinforcing the impression of great uniformity of features throughout the genus, but they were eventually retained as real (Fauvel 1927; Du Bois-Reymond Marcus 1948). With the increasing number of species discovered, descriptions became more accurate, focusing on fine details of the pygidium and its associated structures, the location of the fertile region and, in some cases, the

sperm structure (e.g. Aiyar and Alikunhi 1944; Du Bois-Reymond Marcus 1948, 1955; Jouin and Rao 1987). Unfortunately, these and other potentially informative features remain unexplored for most members of the genus (Table 1). A careful revision of the whole group should be undertaken, with redescrptions of the types or of new material from the type areas.

Jouin and Rao (1987) suggested some affinity among the species possessing a belt of elongate glandular pads on the pygidium (Table 1), as opposed to the species with rounded pads or those lacking such adhesive structures. Indeed, this 'elongate pads' group encompassed all species described from the southern hemisphere (Fig. 1). *Polygordius antarcticus* sp. nov., with its rounded glandular pads on the pygidium, is obviously excluded from this group.

Among the few congeners having a conical head and lacking pygidial appendages (Table 1), the new species appears very similar to *P. triestinus* Woltereck (in Hempelmann 1906), an aberrant form living in muddy bottoms in the Adriatic Sea (Hempelmann 1906, 1908). The most remarkable correspondences between the two concern the unusually short antennae and the elaborate vascular system (Table 1). The totally different arrangements of both these features in *P. lacteus* and *P. appendiculatus* (Table 1) are confirmed by observations during the present study. The thin blood vessels flanking the strands of germinal tissue and the well-developed intestinal blood sinus seen in the largest individuals of *P. antarcticus* indicate that they are close to maturity. *P. antarcticus* therefore probably also resembles *P. triestinus* in adult body size.

Details of the vascular systems differ, however, with *P. triestinus* having each circumoesophageal commissure forming an anastomotic anterior loop that closes just outside the prostomium (Hempelmann 1906). The variation in length of the intersegmental commissural vessels also differs, with *P. triestinus* having the shortest vessels in the anterior segments. In other respects the two species are even more notably distinct. The Adriatic species, the sole hermaphroditic in the genus, possesses a very large upper lip overhanging the mouth (this lip is larger than the prostomium and probably works as an anchor during locomotion), and its tail is gently tapering (unswollen) and non-adhesive (Hempelmann 1906).

The significance of the strong similarities between the Adriatic and the Antarctic species is not obvious. *Polygordius* is generally associated with medium- to coarse-grained, well-oxygenated sands, and all the special traits of *P. triestinus*, including the short antennae and the rich vascularisation of the body, were interpreted as adaptations to life in an exceptionally fine, oxygen-depleted substratum (Hempelmann 1906). A similar specialisation could hardly be suggested for *P. antarcticus* sp. nov., as the oxygen levels are generally high at the bottom of the Southern Ocean (Knox 1994), even where sands are muddy and seasonally enriched with organic detritus (Dayton 1990). Moreover, anthropogenically contaminated sediments are definitely avoided

by (conspecific?) *Polygordius* populations living in McMurdo Sound (Lenihan and Oliver 1995). On this basis, a convergent evolution of *P. antarcticus* and *P. triestinus* should be excluded.

Unfortunately, no direct comparison with *P. triestinus* has been possible, as its type series (if still existing) can no longer be located, nor does any material of this species exist in the Laboratory of Marine Biology of Trieste (S. Dolce, personal communication). Enquiries to other centers for marine research on the Adriatic coasts and to institutions where Woltereck and Hempelmann worked have received no reply. Thus further points of difference or similarity between the two species cannot be detailed at this time.

In 1970 Jouin recorded *P. triestinus* from New Caledonia at 22°S 166°E, i.e. at about the same longitude as Terra Nova Bay but slightly to the north of the Tropic of Capricorn in the South Pacific (Fig. 1). The worms were taken from muddy coral sand at 6- to 7-m depth in an area with strong currents, variable salinity and high organic content. They were identified on the basis of their conical head, short antennae, non-swollen tail and the general pattern of the circulatory apparatus (Table 1). However, they clearly differed from the material described by Hempelmann (1906) in body size, in the shape of the mouth, in having several rings of adhesive pads on the pygidium, and in being gonochoristic (only males were found) (Jouin 1970). Interestingly, the scheme of their anterior blood vessels was identical with that described herein for *P. antarcticus*.

There is no doubt that the worms from New Caledonia and the typical *P. triestinus* are closely related, and we agree with Jouin (1970) that the scheme of the circulatory system may provide an excellent taxonomic criterion for species recognition and discrimination, but we regard the marked differences in body size, morphology of the mouth and pygidium, and sexual characters as sufficient justifications for separating the Adriatic and the New Caledonian taxa at species level. Differences in body size and pygidial morphology also separate the New Caledonian taxon from *P. antarcticus*. Other (unpublished) material sharing the same general plan of the circulatory system as these three taxa was found in collections from the east coast of the United States (Cape Cod and Florida; C. Jouin-Toulmond, personal communication). We suggest here that the possession of this particular circulatory scheme, possibly combined with a conical head and short antennae, may indicate phylogenetic membership in a distinct, geographically widespread, subgroup of polygordiids which would deserve subgeneric ranking. However, we are also inclined to believe that in this family some similarities in the pygidial morphology may simply indicate convergent adaptations to similar habitats.

The description of the reproductive characters of the new species, postponed to the time when fully mature specimens become available, and a comparative study involving also the material collected in McMurdo Sound should help to shed more light on the subject.

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## References

- Aiyar RG, Alikunhi KH (1944) On some archiannelids of the Madras Coast. *Proc Natl Inst Sci India* 10:113–140
- Anderson DT (1973) Embryology and phylogeny in annelids and arthropods. *Int Ser Monogr pure appl biol, zool*, vol 50. Pergamon Press, Oxford
- Clark RB (1978) Composition and relationships. In: Mill PJ (ed) *Physiology of annelids*. Academic Press, London, pp 1–32
- Clarke A (1988) Seasonality in the Antarctic marine environment. *Comp Biochem Physiol* 90B:461–473
- Dawydoff C (1905) On the morphology of the Archiannelida. Biological observations on the epitocous form of *Polygordius*. Scientific results of a travel to Java, III (in Russian). *Bull Acad Imp Sci St-Petersbourg* 22:51–56
- Dawydoff C (1959) Ontogenèse des Annelides. In: Grassé P-P (ed) *Traité de Zoologie*, vol 5. Masson, Paris, pp 594–686
- Dayton PK (1990) Polar benthos. In: Smith WO (ed) *Polar oceanography, part B. Chemistry, biology, and geology*. Academic Press, San Diego, pp 631–685
- Du Bois-Reymond Marcus E (1948) Further archiannelids from Brazil. *Comun Zool Mus Hist Nat Montevideo* 2: 1–27
- Du Bois-Reymond Marcus E (1955) On Turbellaria and *Polygordius* from the Brazilian Coast. *Bol Fac Filos Cienc Letr Univ Sao Paulo Zool* 20:19–65
- Erséus C, Rota E (1996) Tubificidae (Oligochaeta) from the Ross Sea (Antarctica), with descriptions of one new genus and two new species. *Polar Biol* 16:491–496
- Fauchald K (1977) The polichaete worms. Definitions and keys to the orders, families and genera. *Nat Hist Mus Los Angeles Cty Sci Ser* 28:1–188
- Fauvel P (1927) Archiannelides. *Faune France* 16:413–445
- Fraipont J (1887) Le genre *Polygordius*. *Fauna Flora Golf's Neapel* 14:1–125
- Fransen ME (1980) Ultrastructure of coelomic organization in annelids. I. Archiannelids and other small polychaetes. *Zoomorphologie* 95:235–249
- Gambi MC, Lorenti M, Russo GF, Scipione MB (1994) Benthic associations of the shallow hard bottoms off Terra Nova Bay, Ross Sea: zonation, biomass and population structure. *Antarct Sci* 6:449–462
- Giard A (1880) On the affinities of the genus *Polygordius* with the annelids of the family Opheliidae. *Ann Mag Nat Hist Ser* 5, 6:324–326
- Hempelmann F (1906) Zur Morphologie von *Polygordius lacteus* Schn. und *Polygordius triestinus* Woltereck, nov. spec. *Z Wiss Zool* 84:527–618
- Hempelmann F (1908) Neuere Arbeiten über *Polygordius*, und einige an diesen Anneliden anknüpfende theoretische Erörterungen aus der Literatur der letzten Jahre. *Zool Zentralbl* 15:649–672
- Hermans CO (1969) The systematic position of the Archiannelida. *Syst Zool* 18:85–102
- Izuka A (1903) On a new *Polygordius* from Misaki (*P. ijimai* n. sp.). *Annot Zool Jpn* 4:137–139

- Jouin C (1970) Archiannelides interstitielles de Nouvelle-Calédonie. In: Expédition française sur les récifs coralliens de la Nouvelle Calédonie, 1960–1963. Editions de la Fondation Singer-Polignac, Paris, 4:147–167
- Jouin C, Rao GC (1987) Morphological studies on some Polygordiidae and Saccocirridae (Polychaeta) from the Indian Ocean. *Cah Biol Mar* 28:389–402
- Knox GA (1994) The biology of the Southern Ocean. Studies in polar research. Cambridge University Press, Cambridge
- Lenihan HS, Oliver JS (1995) Anthropogenic and natural disturbances to marine benthic communities in Antarctica. *Ecol Appl* 5:311–326
- McIntosh WC (1875) On a new example of the Opheliidae (*Lino-trypaenae apogon*) from Shetland. *Proc R Soc Edinb* 8:386–390
- Moore P (1904) A new generic type of Polygordiidae (*Chaetogordius*). *Am Nat* 38:519–520
- Pearse JS, McClintock JB, Bosch I (1991) Reproduction of Antarctic benthic marine invertebrates: tempos, modes, and timing. *Am Zool* 31:65–80
- Perrier E (1875) On a new intermediate type of the subkingdom vermes (*Polygordius?*, Schneider). *Ann Mag Nat Hist Ser 4*, 16:295–298
- Purschke G, Tzetlin AB (1996) Dorsolateral ciliary folds in the polychaete foregut: structure, prevalence and phylogenetic significance. *Acta Zool Stockholm* 77:33–49
- Remane A (1932) Archiannelida. In: Grimpe G (ed) *Die Tierwelt Nord- und Ostsee*. Akad Verlag, Leipzig, 6a: pp 1–36
- Rota E, Carchini G (1996) Prima segnalazione di *Polygordius* in acque antartiche. In: 57° Congresso Nazionale dell'Unione Zoologica Italiana, San Benedetto del Tronto, Riassunti dei contributi scientifici. University of Camerino, Camerino, p 12
- Rota E, Carchini G, Erséus C (1997) Taxonomy and biogeography of smaller marine infaunal Annelida from Antarctica. In: Di Prisco G, Focardi S, Luporini P (eds) *Proc 3rd Meeting on Antarctic Biology*, S. Margherita Ligure. University of Camerino, Camerino, pp 317–320
- Rota E, Erséus C (1996) Six new species of *Grania* (Oligochaeta, Enchytraeidae) from the Ross Sea, Antarctica. *Antarct Sci* 8:169–183
- Salensky U (1907) Morphogenetische Studien an Würmern, II–IV. *Mém Acad Imp Sci St-Petersbourg Ser 8*, 19:103–451
- Schmidt P, Westheide W (1977) Interstitielle Fauna von Galapagos. 17. Polygordiidae, Saccocirridae, Protodrilidae, Nerillidae, Dinophilidae (Polychaeta). *Mikrofauna Meeresboden* 62:1–38
- Schneider A (1868) Über Bau und Entwicklung von *Polygordius*. *Arch Anat Physiol Wiss Med Leipz* 10:51–60
- Sensenbaugh T, Franzén Å (1987) Fine structural observations of the apical organ in the larva of *Polygordius* (Annelida: Polychaeta). *Scanning Microsc* 1:181–189
- Söderström A (1924a) Über die 'katastrophale' Metamorphose der *Polygordius*-Larve. *Universitets Arsskrift*, Uppsala
- Söderström A (1924b) Das Problem der *Polygordius*-Endolarve. Eine Gegenantwort an Prof. Richard Woltereck. *Almqvist & Wiksell*, Stockholm
- Uchida T (1935) Eine neue Urannelidenart, *Polygordius pacificus* n. sp. *Proc Imp Acad Tokyo* 11:119–120
- Von Nordheim H (1984) Life histories of the subtidal interstitial polychaetes of the families Polygordiidae, Protodrilidae, Nerillidae, Dinophilidae, and Diurodrilidae from Helgoland (North Sea). *Helgol Meeresunters* 38:1–20
- Westheide W (1990) Polychaetes: interstitial families. *Synopsis Br Fauna* 44:1–152
- White MG (1977) Ecological adaptations by Antarctic poikilotherms to the polar marine environment. In: Llano GA (ed) *Adaptations within Antarctic ecosystems*. Gulf, Houston, pp 197–208
- Woltereck R (1902) Über zwei Entwicklungstypen der *Polygordius* Larve. *Verh Int Zool Congr Berl* 5:729–736
- Woltereck R (1905) Zur Kopffrage der Anneliden. *Verh Dtsch Zool Ges Leipz* 15:154–186
- Woltereck R (1925) Neue und alte Beobachtungen zur Metamorphose der Endolarve von *Polygordius*. *Zool Anz* 65:49–60