

Six new species of *Grania* (Oligochaeta, Enchytraeidae) from the Ross Sea, Antarctica

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Abstract: Six new species of marine Enchytraeidae, *Grania hirsuticauda* sp.n., *G. acanthochaeta* sp.n., *G. carchinii* sp.n., *G. angustinasus* sp.n., *G. antarctica* sp.n. and *G. algida* sp.n., are described from benthic material collected in McMurdo Sound during 1959–61 and Terra Nova Bay in 1988. They represent the first records of this family from below the Antarctic circle and, together with tubificids, the first oligochaetes from the Ross Sea. *G. hirsuticauda*, apparently the most widespread species in McMurdo Sound, is distinguished by having setae abruptly larger in the posterior third of the body and almost nodulate; a T-shaped prostomial bifurcation of the dorsal vessel, short sperm funnels and sperm sac, and thick-walled spermathecae. *G. acanthochaeta* possesses a unique, thorn-like, setal morphology and diverticulate spermathecal ampullae. *G. carchinii*, the only new species lacking lateral setae, is also distinguished by a remarkably high development of the chloragogen tissue and the possession of nephridia at 6/7. *G. angustinasus*, the most abundant species in the sampling area in Terra Nova Bay, and *G. antarctica*, have the same setal distribution, size and (curved) shape, but show different forms of penial bulbs (more complex in *G. angustinasus*) and spermathecal structures (the ampullae being larger and the external pores more posterior in *G. antarctica*). *G. algida* is distinguished by its L-shaped setae and carrot-shaped, diverticulate, spermathecal ampullae. All the new species lack cuticular penial stylets as well as spermathecal ectal glands. All species but *G. carchinii* are peculiar in possessing, in front of the brain, a middorsal vesicular body of specific shape and size containing a few refractile inclusions; a sensory (possibly a statocyst-like) function is suggested for this 'head organ', which has not been previously reported in the Oligochaeta.

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Key words: Antarctica, benthos, distribution, Enchytraeidae, *Grania*, head organ, Ross Sea, taxonomy

Introduction

There have been several records of marine and terrestrial enchytraeids from the subantarctic region, particularly from South Georgia (Michaelsen 1888, 1905a, 1905b, 1921, Ude 1896, Benham 1905, 1922, Stephenson 1932, Tétry 1947, Block & Christensen 1985). Surprisingly, however, only one collection is known from the High Antarctic, i.e. three littoral species of *Lumbricillus* [*L. griseus* (Stephenson, 1932), *L. lineatus* (Müller, 1774) and *L. maximus* (Michaelsen, 1888)] from the Palmer Archipelago, off the east coast of the Antarctic Peninsula (Stephenson 1932).

The six new species of *Grania* Southern, 1913 described here are the first records of Enchytraeidae from above the Antarctic circle and along with members of the family Tubificidae (Erséus & Rota 1996), also the first oligochaetes ever reported from the Ross Sea.

All material comes from the south-western corner of the Ross Sea. A part of it was collected in 1959–61 by Stanford University researchers under the auspices of the US Antarctic Research Program (USARP) near the Naval Air Facility at McMurdo Sound (77°51'S, 166°39'E). Another part was obtained within the Italian National Research Programme in Antarctica (ENEA-PNRA) during the third expedition

(December 1987–February 1988) to the Italian Base at Terra Nova Bay (74°41'S, 164°07'E), north Victoria Land.

Material and methods

Alcohol preserved worms from McMurdo Sound were sent to C. Erséus by the former Smithsonian Oceanographic Sorting Center (SOSC). They were stained in paracarmine and mounted whole in Canada balsam.

Material from Terra Nova Bay, including both alcohol preserved specimens (samples A35 and A39) and unsorted, formalin preserved (7%, non neutralized) sediments (samples B79, B95 and B100), was passed to E. Rota by the Italian PNRA Programme. Unsorted samples were extracted in December 1994 using flotation and subsequent filtering on a sieve with 150 µm mesh size. Sorting was done using a stereomicroscope. Most of the Terra Nova Bay worms were then stained in borax carmine, Mayer's hemalum or paracarmine (the last proving the most successful after long storage in formalin) and mounted whole in Canada balsam. The remainder (presumably all specimens of *G. angustinasus*) was kept, unstained, in alcohol.

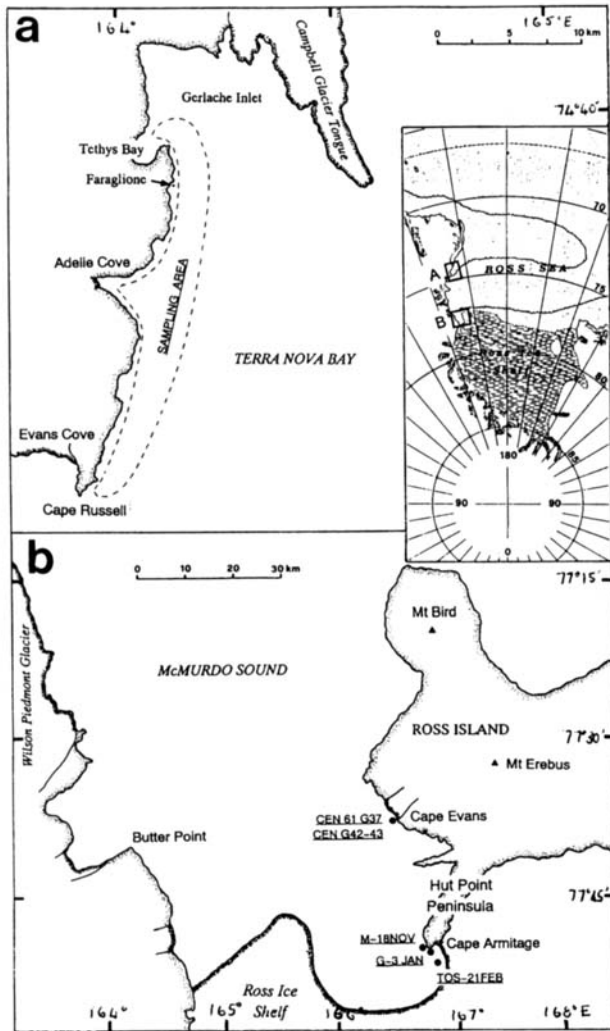


Fig. 1. a. Sites sampled in Terra Nova Bay. b. Sites sampled in McMurdo Sound. Inset shows locations of the two areas in the Ross Sea. Distance between a and b about 300–350 km.

Type material of the new species is deposited in the US National Museum of Natural History (USNM), Smithsonian Institution, Washington DC; in the Museo Civico di Zoologia di Roma (MCZR), Via Aldrovandi 14, Rome; and in the Swedish Museum of Natural History (SMNH), Stockholm.

All measurements refer to whole-mounted, more or less compressed specimens; the length of the setae was measured in a straight line from the ectal tip to the farthest ental point; their ental bend is hereafter described as the angle between the long axis of the shaft and the underside of the ental hook (as illustrated in the figures). The length of the penial bulbs is defined as their diameter parallel to the longitudinal axis of the worm. The types of the penial bulbs are according to Coates' (1984) definitions. The bulbs of the new species described here all fall within Type 3, i.e., they have glandular bodies attached medially to male pores, and male invaginations

forming more or less prominent lateral outpocketings. However, the latter are markedly different in size in the various species and only in one case (*G. angustinasus*) can be regarded as 'aglandular sacs'. A redefinition of the bulb types, based on the many new species that have been described since 1984, appears urgent (K.A. Coates personal communication). All segment counts include the (postsegmental) pygidium.

Figures were drawn with the aid of a camera lucida. Photographs of "head organs" were taken with Ilford Pan F Plus using interference contrast on a Leitz Aristoplan microscope.

Collecting sites (Fig. 1)

Details of US collections were drawn from Dearborn (1967); information on Italian samples was supplemented by data in Argano & Carchini (1991). All Terra Nova Bay stations were situated between Gerlache Inlet and Cape Russell; in most cases, however, their exact position is not known.

McMurdo Sound

G-3 JAN - Near tip of Cape Armitage (Ross Island), 77°51'S, 166°40'E; January 1959; 5 m depth; volcanic gravel and sandy mud. Coll. J.H. Dearborn, H.H. De Witt, D.E. Wohlschlag. Open crack in the ice. *G. hirsuticauda*.

M-18NOV 1 / M-18NOV 2 - South of Hut Point (Ross Island), 77°51'S, 166°39'E; 18 November 1959; 38 m depth; greyish brown gravelly mud with sponge spicules and *Limatula* valves. Coll. J.H. Dearborn. Hole blasted in the ice. *G. acanthochaeta*, *G. hirsuticauda*.

TOS-21FEB - Tressler Oceanographic Station. South of Cape Armitage (Ross Island); 77°53'S, 166°44'E; 21 February 1961; 565–585 m depth; gravel, small rocks, ectoproct and sponge debris. Coll. S.B. Haven, A.M. Ommundsen, W.L. Tressler. Hole cut in ice. Grab. *G. hirsuticauda*.

CEN 61 G37; CEN G42-43 - Off beach in front of Scott's Hut, northern shore of Cape Evans (Ross Island); 77°38'S, 166°24'E; 4 September 1961; 14 m depth; volcanic gravel and cobble. Coll. J.H. Dearborn, J.L. Littlepage, J.S. Pearse. Holes cut in ice. *G. algida*, *G. antarctica*.

Terra Nova Bay

A35 - 100 m off the coast between Faraglione (a large rock near the coastline, 5 km south of the Italian Base) and Adélie Cove (=Penguin Bay), i.e. between the latitudes 74°43'–74°46'S and the longitudes 164°01'–164°08'E; 27 January 1988; 40 m depth. Coll. G. Carchini. Dredge (1 cm mesh) and grab. *G. algida*.

A39 - Off beach in Adélie Cove (=Penguin Bay) (about 74°46'S, 164°01'E); 4 February 1988; 31 m depth. Coll. G. Carchini. Grab. *G. antarctica*.

B79 - Sea between Faraglione (74°43'S) and Cape Russell (74°54'S), between longitudes 163°55'–164°09'E; 10 February 1988; 126 m depth. Fine sand containing mica shales and

Table I. Distinguishing features of the new species of *Grania* from the Ross Sea.

	<i>hirsuticauda</i>	<i>acanthochaeta</i>	<i>carchinii</i>	<i>angustinasus</i>	<i>antarctica</i>	<i>algida</i>
Body length (mm)	9–10	12 (at least)	8	6–9	10–11	5.5
Width at V; XII (mm)	0.26–0.32; 0.32–0.42	0.15–0.22; 0.17–0.29	0.19; 0.21	0.13–0.18; 0.14–0.20	0.14–0.18; 0.17–0.21	0.09–0.10; 0.15
Segment number	33–35	48 or 49 (at least)	47	45–65	55, 68	49–51
Setae						
from (ventrals, laterals)	IV, XV	IV, XVII–XVIII	IV	IV, XIV–XVI	IV, XV–XVII	IV, XIV
preclit. length (range)	49–63 μm	54–82 μm	38–52 μm	38–49 μm	34–45 μm	35–43 μm
postclit. length (max)	103 μm	105 μm	72 μm	66.5 μm	66 μm	82 μm
size (anter. to poster.)	discontinuously larger	continuously larger	contin. larger	contin. larger	contin. larger	contin. larger
form: shaft	thick	thick	thin	very thin	very thin	thin
ental hook	'babouche'	expanded anter. and poster.	tiptoe foot	curved	curved	L-shaped
Brain length	120–130 μm	92 μm	92–95 μm	80–90 μm	100–115 μm	68–82 μm
Head organ	+	+	-	+	+	+
shape of vesicle	subtriangular	subtriangular	-	bilobed	chestnut-like	globular
size of inclusions	minute	varying in size	-	large	large	varying in size
First nephridia at	7/8	7/8	6/7	7/8	7/8	?
Sperm sac to	XIII	XVI	16/17	$\frac{1}{2}$ XIV or $\frac{1}{2}$ XVII– $\frac{1}{2}$ XIX	XV– $\frac{1}{2}$ XVIII	XV
Sperm funnels (length:width)	3:1	6-7:1	4:1	6.5-9:1	5.5-7.5:1	7:1
Male ducts (width)	7–8 μm	5–7 μm	9–5 μm	7–8 μm	5–8 μm	4 μm
Penial invagination	crescent-shaped, simple	with lateral outpocketing	?	with aglandular sac	conical, deep	with lateral outpocketing
Egg sac to	XVI– $\frac{1}{2}$ XVIII	XVII	?	$\frac{1}{2}$ XVIII–XX	XIX	XVI or XVII
Spermathecae						
ectal pores	near 4/5	near 4/5	near 4/5	near 4/5	a little behind 4/5	a little behind 4/5
ectal ducts	stout, reaching ampullae on anterior aspect	long, narrow	enlarging entally	spindle-shaped, joining ampullae on lateral aspect	thinner ectally, joining ampullae on lateral aspect	long, narrow, ventrally connecting to ampullae
ampullae	heart-shaped	diverticulate	pear-shaped	pear-shaped	large, heart-shaped	diverticulate

rich in sponge spicules, diatom skeletons, sand tubes and organic debris. Coll. G. Carchini, M. Taviani. Grab. *G. angustinasus*.

B95 - Sea between Faraglione (74°43'S) and Cape Russell (74°54'S), between longitudes 163°55'–164°09'E; 10 February 1988; 35 m depth. Fine sand with mica shales and shell debris; some pebbles. Coll. G. Carchini, M. Taviani. Grab. *G. angustinasus*, *G. carchinii*.

B100 - Sea between Faraglione (74°43'S) and Cape Russell (74°54'S), between longitudes 163°55'–164°09'E; 10 February 1988; 61 m depth. Fine sand mixed with shell fragments, diatom skeletons and abundant organic debris. Coll. G. Carchini, M. Taviani. Grab. *G. angustinasus*.

Taxonomic descriptions

Family Enchytraeidae

Genus *Grania* Southern, 1913

Grania hirsuticauda sp. n. (Figs 2, 3a, Table I)

Holotype: USNM 172136, whole-mounted specimen.

Type locality: McMurdo Sound, near tip of Cape Armitage (Ross Island) (St. G-3 JAN).

Paratypes: USNM 172137, whole-mounted specimen from St. TOS-21FEB. USNM 172138, whole-mounted specimen from type locality.

Other material examined: USNM 172139, 1 subadult from type locality; USNM 172140, 1 juvenile from St. TOS-

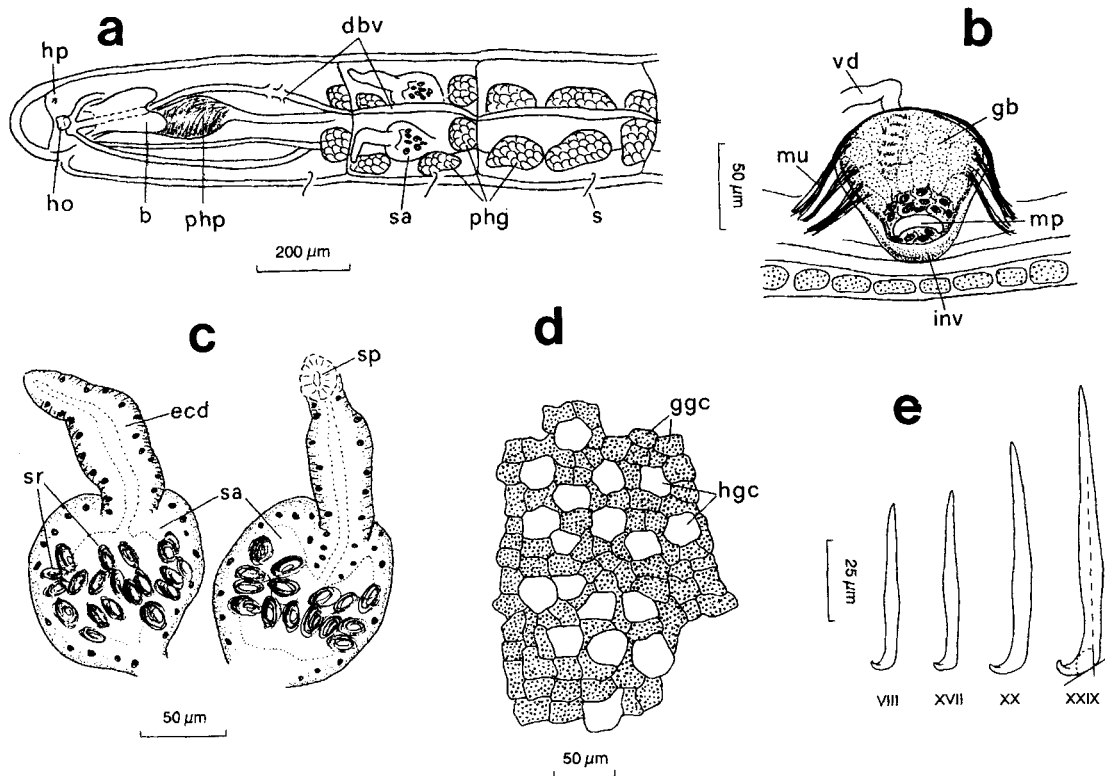


Fig. 2. *Grania hirsuticauda* sp. n. **a.** Anterior segments (dorsolateral view). **b.** Penial bulb and ectal portion of male duct (ventral view). **c.** Spermathecae. **d.** Arrangement of clitellar gland cells near anterior border of XII (left). **e.** Setae from different segments (indicated by Roman numerals).

21FEB; USNM 172141, 1 juvenile from St. M-18NOV 2.
Description: Body 9–10 mm long, 0.26–0.32 mm wide at V, 0.32–0.42 mm at clitellum. Segment number 33–35. Prostomium broad, rounded (hemispherical) (Figs 2a, 3a), 165–190 μm across at 0/1, 104–116 μm long. Peristomium (segment I) 0.20–0.23 mm wide. Setae (Fig. 2e) occurring from IV (V in one specimen) ventrally, from XV or XVII laterally. Setal shaft almost nodulate with maximum thickness a little below midpoint of shaft; ental hook with upturned tip which makes it resemble a ‘babouche’ (a kind of oriental shoe); in most specimens ‘babouche’ bent at about 110° to the shaft, but in caudal setae of some specimens bent a little less sharply (at 120° – 130° to the shaft) (Fig. 2e). Setae 49–63 μm long in preclitellar segments, 55–70 μm in midbody segments, increasing suddenly to 80–90 μm at around XIX–XXI and reaching as much as 103 μm in more posterior segments. Setae also abruptly thicker in hind third of body (even in juveniles): maximum thickness 4 μm in anterior and midbody segments, 6 μm in posterior segments. Epidermis highly glandular on prostomium and segments I–II. Clitellum over XII– $\frac{1}{2}$ XIII, formed by irregular clusters of small granular cells separated by larger hyaline cells (Fig. 2d). Male pores ventrolateral in middle of XII. Unpaired small copulatory gland midventral in XIV. Spermathecal pores lateral, immediately posterior to septum 4/5.

Brain 120–130 μm long, 92–110 μm wide. Head organ (see Discussion) present: vesicle subtriangular, anteriorly truncate, wider than long ($l = 20$ – 38.5 μm ; $w = 25$ – 42 μm), with conspicuous inner compartments and nuclei and containing maximally 4 minute inclusions (diameter 1.5–2 μm) (Fig. 3a). Pharyngeal glands at 4/5–6/7, not united dorsally; ventral lobes in V–VI only, largest in VI. First pair of nephridia at 7/8. Coelomocytes of various shapes (oval to elongate) and sizes (18–27 μm long), containing pale, non-staining granules. Dorsal blood vessel appears to commence in XVI; its anterior end distinctly T-shaped (rectangular) in that the roots of the ventral branches are sharply bent backwards (Figs 2a, 3a). Sperm sac extending posteriad to XIII only. Sperm funnels 3 times longer than wide (244–306 by 80–97 μm). Male ducts muscular, 7–8 μm wide, extending posteriad into XIV. Penial bulbs (Fig. 2b) 67–86 μm long, with no separate aglandular sacs; narrow opening at each male pore expanding inwards into a crescent-shaped invagination lined with cuticle bordering lateral side of bulb (type 3 *sensu* Coates 1984); no stylet present. Egg sac extending into XVI– $\frac{1}{2}$ XVIII. Spermathecae (Fig. 2c) attached to oesophagus in posterior half of V; Large, thick-walled, each consisting of a heart-shaped ampulla (92–122 μm long, 86–113 μm wide) and a stout, 135–153 μm long, ectal duct connecting with ampulla on its anterior aspect; ampullae

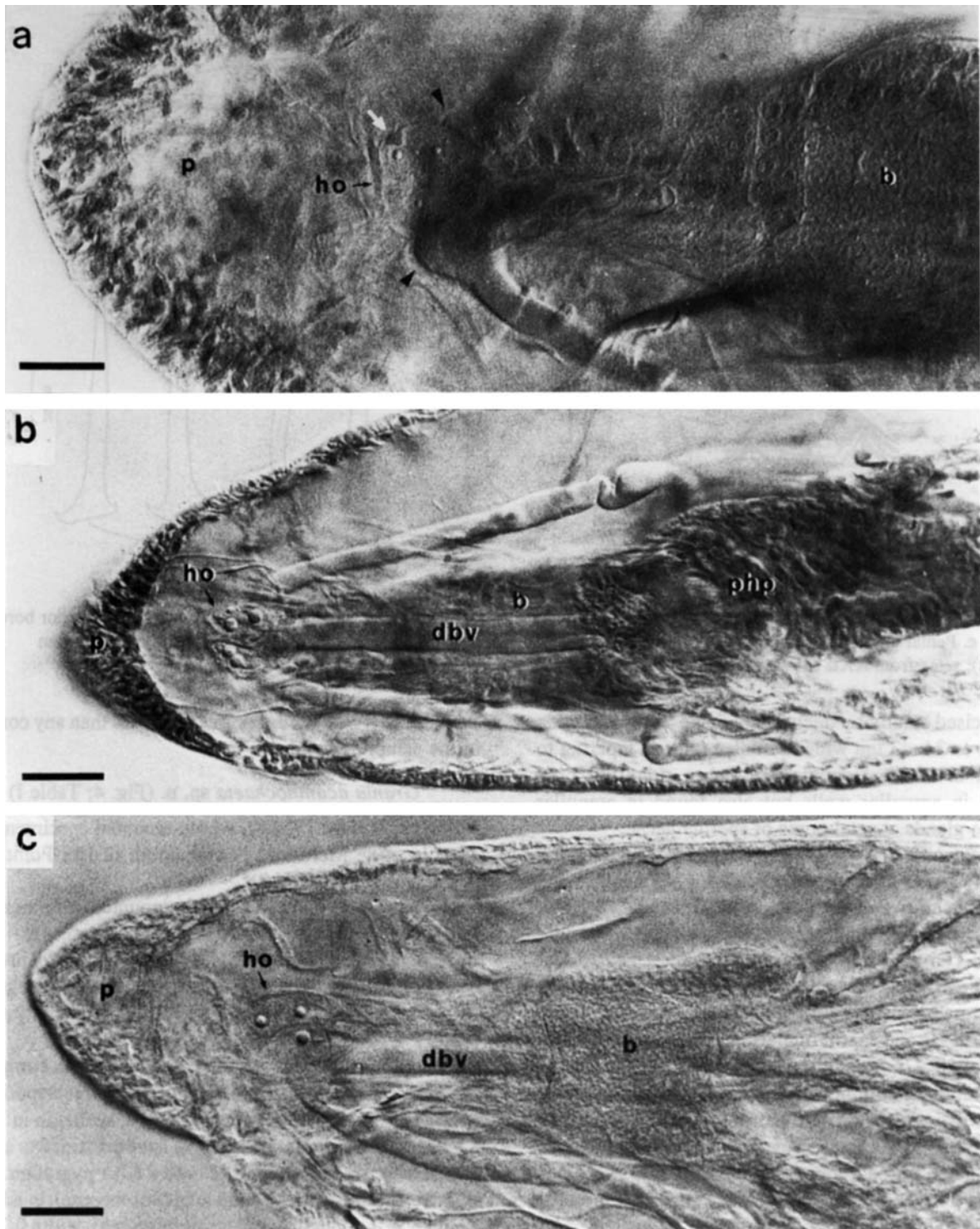


Fig. 3. Cephalic regions of three Antarctic species of *Grania*, showing location of the 'head organ'. **a.** *Grania hirsuticauda* (dorsolateral view). Note the nucleus bulging inwards from the peripheral wall of the head organ (white arrow), and the enlarged, cornered, anterior end of the dorsal blood vessel (black arrow-heads). **b.** *Grania angustinasus* (dorsal view). Prostomium only partly visible, pointing downwards. **c.** *Grania antarctica* (dorsolateral view; specimen possessing only three inclusions in the head organ). Scales = 25 μm .

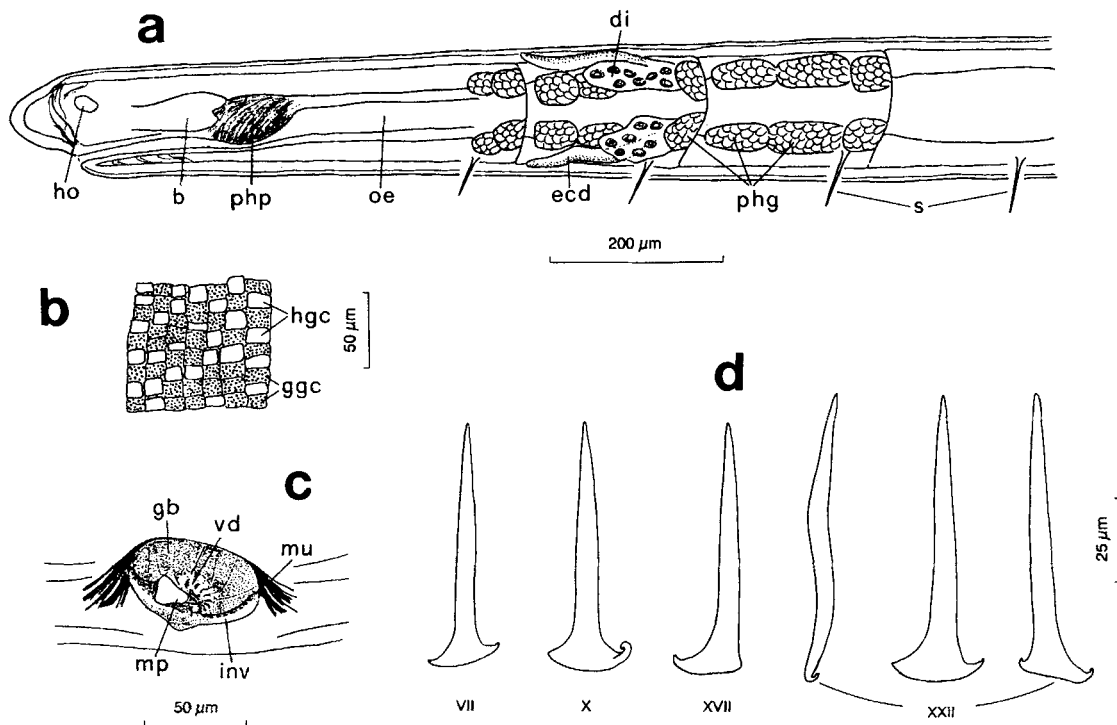


Fig. 4. *Grania acanthochaeta* sp. n. **a.** Anterior segments (dorsolateral view). **b.** Arrangement of clitellar gland cells (anterior border on the left). **c.** Penial bulb and ectal portion of male duct (ventral view). **d.** Setae from different segments (indicated by Roman numerals); setae from XXII shown in three different views (that on the left in a frontal view).

slightly incised ectally by ducts; ectal ducts 31–37 μm wide entally, up to 34–43 μm wide at midlength, and tapering to 21–24 μm at external openings. Sperm rings not only embedded in ampullar walls but also found in ampullar lumen. No glands at ectal pores of spermathecae.

Derivatio nominis: The specific name refers to the possession of distinctly larger-sized setae in posterior segments, using the Latin ‘hirsutus’ (= hairy, shaggy) and ‘cauda’ (= tail).

Remarks: The almost nodulate setae, the low segment number relative to (large) body size, the T-shaped prostomial bifurcation of the dorsal vessel, as well as the stout, thick-walled spermathecae (devoid of ectal glands) combined with a short sperm sac and sperm funnels, distinguish this species from any other *Grania* hitherto described having similar setal distribution and simple penial bulbs. *Grania hirsuticauda* is further distinguished from the new species described herein (Table I) by its setal shape and ‘discontinuous’ size distribution, and a broad, rounded prostomium. The brain is also 1/4 longer than in most other Antarctic species, whilst the head organ always contains very small inclusions.

Distribution and habitat: Only known from stations in McMurdo Sound, Ross Sea. In volcanic gravel and sandy mud, 5 m depth (St. G-3 JAN); in greyish brown gravelly mud with sponge spicules and *Limatula* valves, 38 m depth (St. M-18NOV 2); in gravel, small rocks, ectoproct and sponge debris, 565–585 m depth (St. TOS-21FEB). So far it seems to be the most widespread species of *Grania* in McMurdo

Sound, and it also occurs at greater depths than any congener in the sampling area.

Grania acanthochaeta sp. n. (Fig. 4; Table I)

Holotype: USNM 172142, whole-mounted specimen.

Type locality: McMurdo Sound, south of Hut Point (Ross Island) (St. M-18NOV 2).

Paratype: USNM 172393, whole-mounted specimen from type locality.

Other material examined: USNM 172394–172397, 3 juveniles and 1 posterior fragment (7 mm long, comprising 30 segments, all with 4 setae, and pygidium) from type locality (St. M-18NOV 1/M-18NOV 2).

Description: Holotype and paratype incomplete, comprising 24–25 anterior segments. Juveniles (only complete specimens) with 25 to 33 segments. Since lateral setae begin in XVII–XVIII, the posterior fragment must have pertained to a worm with at least 47–48 segments (17–18 + 30) + pygidium. Body length at least 12 mm (= body length of incomplete adults to XVII–XVIII + length of posterior fragment); width 0.22 mm at V, 0.29 mm at clitellum in most compressed adult (holotype), 0.15 mm at V, 0.17 mm at clitellum in paratype. Prostomium small, rounded or dome-shaped (Fig. 4a), 67 μm long, 80–90 μm wide at 0/1. Peristomium 0.12 mm wide. Setae (Fig. 4d) occurring from IV ventrally, from XVII–XVIII laterally. Ental end as much as 18–27 μm wide, anteriad and posteriad expanded, sometimes in such a symmetrical manner

as to resemble the rake used by croupiers. As a result, setae possess a thorn-like silhouette in a lateral view, while they resemble a crochet hook in a frontal view (Fig. 4d). All setae fairly long, 54–82 μm in preclitellar segments, 74–105 μm in postclitellar segments (same range observed in a juvenile 35 segments long which had already shed the setae in XII). Setal shaft stout; in a lateral view, proximal third almost cylindrical, 6–8 μm thick, distal two thirds gradually tapering. Clitellum extending over XII– $\frac{1}{2}$ XIII; granular cells quadrangular (9–12 μm wide), arranged in regular transverse rows (Fig. 4b). Position of male pores and possible copulatory glands not determined due to poor conditions of clitellar and adjacent segments in both mature specimens. Spermathecal pores opening immediately behind septum 4/5.

Body wall with thick longitudinal muscles (up to 18 μm thick, even in juveniles). Brain 92 μm long. Head organ (see Discussion) present: vesicle subtriangular, anteriorly truncate, longer than wide ($l = 27\text{--}28.5 \mu\text{m}$; $w = 23\text{--}27 \mu\text{m}$), containing maximally four inclusions of equal or different diameter (range: 1.5–5 μm). Pharyngeal glands at 4/5–6/7, not united dorsally; ventral lobes in IV–VI. First pair of nephridia at 7/8. Coelomocytes elongate (up to 27 μm long), containing pale granules and a large, deeply staining nucleus. Dorsal vessel not seen. Sperm sac extending to XVI. Sperm funnels 6–7 times longer than broad (366 by 49–67 μm); collar covered with long sperm (heads longer than 60 μm). Male ducts 5–7 μm wide, extending posteriad to XV. From each male pore a crescent-shaped, cuticle-lined invagination with small lateral outpocketing flanks (laterally) a simple, glandular, 61 μm long, penial bulb (type 3 *sensu* Coates 1984) (Fig. 4c); no stylet observed. Egg sac extending into XVII. Spermathecal ectal ducts 148 μm long, unequally wide (15 μm in distal and proximal portions, 34 μm in midportion). Each ampulla with a large (100 μm by 61 μm), thin-walled diverticulum, broadly connected entally to, but lying dorsally on ectal duct; communication with oesophagus near 5/6. Sperm rings within diverticula (Fig. 4a). No glands at ectal pores of spermathecae.

Derivatio nominis: Named for the thorn-like outline of the setae, using the Greek nouns ‘acantha’ (= spine, thorn) and ‘chaeta’ (= bristle).

Remarks: In addition to the unique setal shape, the new species is recognized by the dorsal diverticulum of the spermathecal ampullae. The latter is reminiscent of that of *G. postclitellochaeta* (Knöllner, 1935), *G. pacifica* Shurova, 1979, *G. reducta* Coates & Erséus, 1985, *G. atlantica* Coates & Erséus, 1985, *G. monochaeta* (Michaelsen, 1888) as redescribed by Erséus & Lasserre (1977), *G. ascophora* Coates, 1990, and *G. integra* Coates & Stacey (in press). However, in *G. postclitellochaeta* and *G. reducta* the lateral setae are absent, and the ventral setae occur only in postclitellar segments; moreover, in *G. postclitellochaeta* the penial bulb is surrounded by a very large, dorsomedial gland (bulb of type 2 *sensu* Coates 1984) and in *G. reducta* the sperm funnels are only three times longer than wide. *G. integra* also lacks

lateral setae, has long sperm funnels (up to 10 times longer than wide and extending posteriad as far as XVIII) and penial bulbs with stylets (Coates & Stacey in press). In *G. atlantica* the lateral setae begin 4–11 segments more posteriorly than in *G. acanthochaeta*, whilst the ventral setae occur irregularly. In *G. monochaeta* the lateral setae begin preclitellarly, and all preclitellar setae are smaller and sperm funnels shorter than in the new species (see Erséus & Lasserre 1977). Short sperm funnels (2–2.5 times longer than wide) also distinguish *G. ascophora*, which, furthermore, possesses complex penial bulbs with stylets. *G. pacifica* has not only shorter sperm funnels but also thicker male ducts and shorter spermathecal ducts than *G. acanthochaeta*; moreover, it entirely lacks lateral setae. Diverticulate ampullae are reported also for *G. algida* sp. n. (see below), which, however, appears to be very distinct from *G. acanthochaeta* with regard to body size, setal features, and shape and dimensions of internal organs (cf. Table I).

Distribution and habitat: Only known from the type locality in McMurdo Sound, Ross Sea. In greyish brown gravelly mud with sponge spicules and *Limatula* valves, 38 m depth.

Grania carchinii sp. n. (Fig. 5, Table I)

Holotype: MCZR OLIGOCHAETA 0057, whole-mounted specimen (adult, postreproductive).

Type locality: Terra Nova Bay, between Faraglione and Cape Russell (St. B95).

Paratype: MCZR OLIGOCHAETA 0058, whole-mounted specimen (subadult) from type locality.

Description: Body of adult specimen 8 mm long, 0.19 mm wide at V, 0.21 mm at clitellum. Segments 47 (36 in paratype). Prostomium 80 μm long, 98 μm wide at 0/1, distinctly set off (Fig. 5a) from peristomium which is 135 μm wide. Ventral setae only, beginning in IV (Fig. 5a). Setae 38–52 μm long in anteclitellar segments, up to 72 μm posteriorly. Setal shaft maximally 4 μm thick in segments IV–XXI, maximally 5 μm thick in following segments, gradually tapering towards ectal end; ental hook of posterior setae may be bent at as much as 130° to shaft resembling a nearly tiptoe foot, with a more or less pronounced heel; distal portion of shaft slightly curved backwards in posterior segments (Fig. 5c). Epidermal gland cells visible on prostomium and foremost segments. Clitellum extending over XII– $\frac{2}{3}$ XIII; granular gland cells of postreproductive specimen irregularly shaped, probably due to regression. Male pores ventrolateral, at 2/3 of XII. Unpaired copulatory gland midventral in XIV, at setal level. Spermathecal pores opening laterally, immediately posterior to septum 4/5 (Fig. 5b).

Brain 92–95 μm long. Head organ absent; in corresponding position, an oval swelling with no inclusions and of same fibrous appearance as the circumpharyngeal connectives running on its sides. Pharyngeal glands at 4/5–6/7, not united dorsally; ventral lobes in IV–VI, lobes in VI largest, compact. First pair of nephridia at 6/7. Coelomocytes not

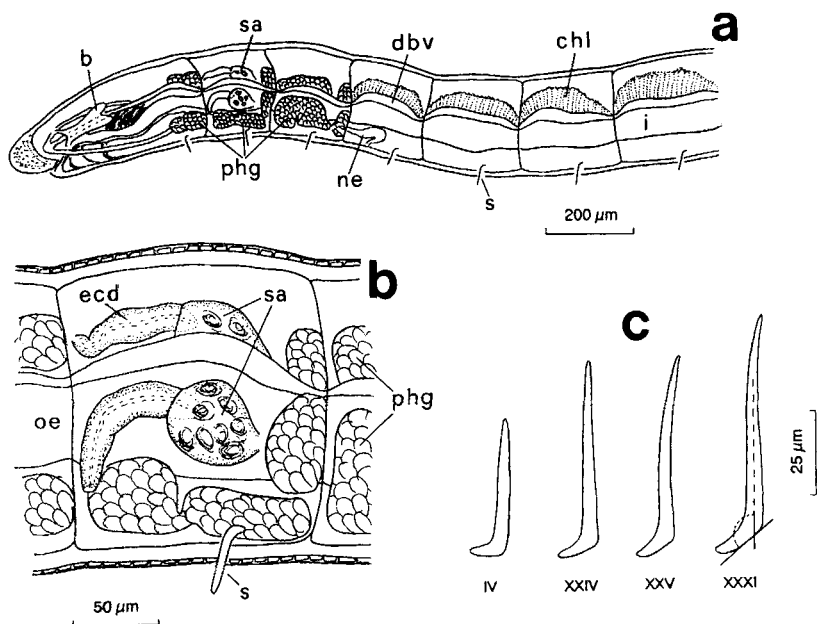


Fig. 5. *Grania carchinii* sp. n. a. Preclitellar segments (dorsolateral view). b. Detail of segment V showing the spermathecae and pharyngeal glands. c. Setae from different segments (indicated by Roman numerals).

seen. Dorsal vessel commencing in XXI. Chloragogen tissue conspicuous in both subadult and postreproductive specimens, dense from VI–VII (Fig. 5a); cells extend as much as 50 µm above gut wall and are filled with yellow to pale brown, refringent granules. Sperm sac extending to 16/17 in (subadult) paratype, not clearly seen in (postreproductive) holotype. Sperm funnels 85 by 23 µm in paratype. Male ducts muscular, extending into XVI, 9.5 µm wide at mid-course. In holotype, penial bulbs absent (regressed?), but epidermis glandular around male pores; in paratype, penial bulbs small (not fully developed?), glandular, opening behind setae of XII, which are still present. Penial stylets absent (but see Remarks). Egg sac not visible. Spermathecal ectal ducts 87 µm long, 15 µm thick ectally, expanding to 19–23 µm entally; ampullae pear-shaped, 57 µm long, 49 µm wide, distinctly set off from ectal ducts, attached to oesophagus near 5/6; sperm rings embedded in ampullar walls (Fig. 5b). No glands at ectal pores of spermathecae.

Derivatio nominis: The species is dedicated to Prof Gianmaria Carchini, collector of all the Terra Nova Bay material.

Remarks: Because of the nature of the available material, the description of *G. carchinii* remains incomplete with regard to details of the male apparatus (sperm funnels, penial bulbs, etc.). For instance, the absence of penial stylets might not be significant, since such structures could normally be missing in both subadult and postreproductive specimens (see Coates & Stacey in press). Nevertheless, the absence of lateral setae, the distribution of nephridia and the great development of the chloragogen tissue (regardless of age) substantiate the separation of this species not only from all other Antarctic species herein described, but also from any other congener

previously known. More specifically, in the absence of lateral setae, the distribution and length, but not the shape, of ventral setae, and the possession of a copulatory gland in XIV, *G. carchinii* resembles the northern Australian *G. integra* Coates & Stacey (in press). Although *G. carchinii* has a body length within the range reported for the latter, its body width is larger and its segment number lower. Male pores have a different location in the two species (at mid XII in *G. integra*). Setal shape in *G. carchinii* is reminiscent of that of *G. stilifera* Erséus, 1990 from Hong Kong and of a second northern Australian species, *G. eurystila* Coates & Stacey (in press). However, in contrast to *G. carchinii*, *G. stilifera* possesses lateral setae, whilst in *G. eurystila*, ventral setae occur only postclitellarly and no copulatory glands are observed (Coates & Stacey in press). The spermathecae of both forementioned Australian species also are remarkably different from those of *G. carchinii*: in one case, the saccate ampulla extends mediodorsally to the ectal duct (like a diverticulum); in the other, the subrectangular, thick-walled ampulla surrounds the ectal duct for most of its length (Coates & Stacey in press).

A thick chloragogen tissue such as that described for *G. carchinii* has never been mentioned for *Grania* before. Records of distribution of nephridia in *Grania* spp. are rather scanty and incomplete in the literature, probably because such organs are not always easily detectable in mounted material. However, nephridia seem to start at 7/8 in the majority of species for which information is available, while nephridia beginning at 6/7 are reported so far only for the northwestern Atlantic *G. levis* Coates & Erséus, 1985 and for *G. inermis* Erséus, 1990 from Hong Kong. In contrast

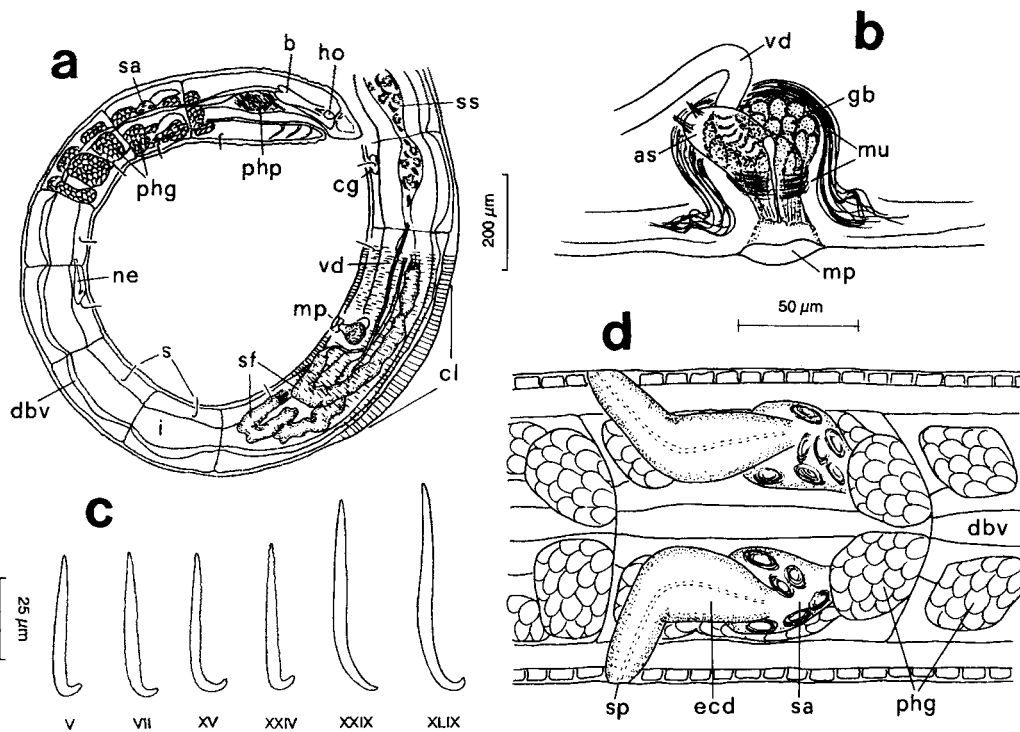


Fig. 6. *Grania angustinasus* sp. n. **a.** Lateral view of prostomium, anterior segments and clitellum. **b.** Penial bulb and ectal portion of male duct (lateral view). **c.** Setae from different segments (indicated by Roman numerals). **d.** Detail of segment V showing the spermathecae and pharyngeal glands (dorsal view). **b** and **d** drawn to same scale.

to *G. carchinii*, *G. levis* lacks setae entirely and has complex penial bulbs with stylets, while *G. inermis* has both lateral and ventral setae and elongate glandular bodies at male openings.

Grania carchinii is the only species described here in which the head organ is absent.

Distribution and habitat: Only known from the type locality in Terra Nova Bay, Ross Sea. In fine sand with mica shales, shell debris and some pebbles, 35 m depth.

Grania angustinasus sp. n. (Figs 3b, 6, Table I)

Holotype: MCZR OLIGOCHAETA 0059, whole-mounted specimen.

Type locality: Terra Nova Bay, between Faraglione and Cape Russell (St. B100).

Paratypes: MCZR OLIGOCHAETA 0060–0061, two whole-mounted specimens from type locality. MCZR OLIGOCHAETA 0062, whole-mounted specimen from St. B95. MCZR OLIGOCHAETA 0063, whole-mounted specimen from St. B79. SMNH Type coll. 4759–4761, three whole-mounted specimens from type locality.

Other material examined: Rota's collection, 11 whole-mounted specimens: 4 adults, 3 subadults and 2 juveniles from type locality; 1 adult and 1 juvenile from St. B79. Ten more adults and 15 subadults and juveniles from type locality preserved in alcohol, identified as *G. angustinasus* from their general appearance.

Description: Body length about 6–9 mm; width 0.13–0.18 mm

at V, 0.14–0.20 mm at clitellum. Segments 45, 47, 48, 49 (2 specimens), 52, 55, 60, 61 (2 specimens), 65. Prostomium 57–85 μm wide at 0/1, 53–68 μm long, conical, pointing forwards or downwards (Fig. 6a); peristomium 80–110 μm wide, well demarcated from prostomium. Marked secondary annulation in II–III. Ventral setae beginning in IV, lateral setae beginning in XIV–XVI. Setae sharp and straight ectally, broadest (maximal diameter 3–4 μm) at shaft base, where they curve into a long hook (Fig. 6c). Setae increasingly longer from anterior to caudal region; preclitellar setae ranging between 38–49 μm (longest in V–VII), postclitellar setae between 39–66.5 μm . Epidermal gland cells usually conspicuous (occasionally orange-coloured) in prostomium and I–VII. Clitellum extending over XII–2/3 XIII, interrupted midventrally in XII; granular gland cells square to rectangular (6–9 by 6–15 μm), arranged in about 40 regular rows (Fig. 6a). In most unstained specimens, clitellum distinctly reddish. Male pores ventrolateral in middle of XII, anterior to midpoint of clitellum. Unpaired copulatory gland midventral in XIV at setal level (Fig. 6a). Spermathecal pores lateral, immediately posterior to 4/5 (Fig. 6d).

Brain 80–90 μm long, 40–60 μm wide. Head organ (see Discussion) present: vesicle 23–27 μm long, 22–25 μm wide, divided into two main compartments somewhat diverging anteriorly (bilobed), containing maximally 4 inclusions, often of conspicuous diameter (total range: 2–6 μm) (Fig. 3b). Pharyngeal glands at 4/5–6/7, not united dorsally; ventral lobes in IV–VI, largest in VI. First pair of nephridia at 7/8.

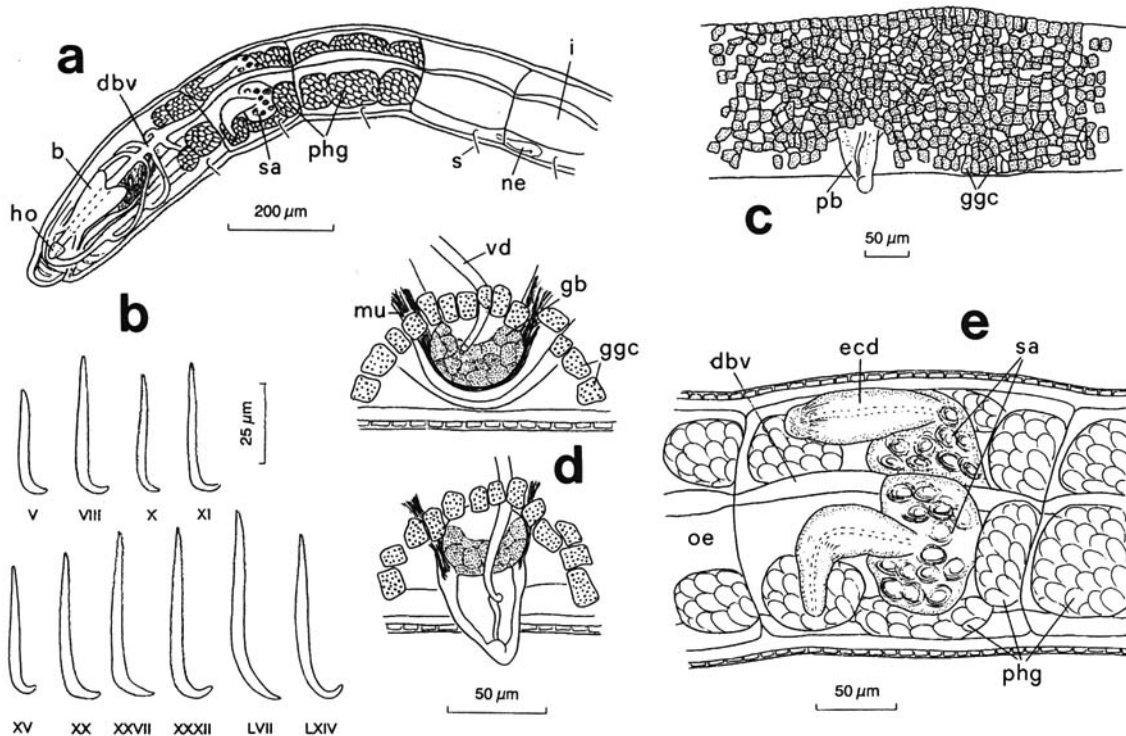


Fig. 7. *Grania antarctica* sp. n. **a.** Anterior segments (dorsolateral view). **b.** Setae from preclitellar (top) and postclitellar segments (bottom); segments indicated by Roman numerals. **c.** Clitellum (anterior border on the left), showing the arrangement of gland cells, and position of male pore (penial bulb everted) at mid XII. **d.** Lateral view of penial bulb when invaginated (top) and everted (bottom). **e.** Dorsolateral view of segments one-half IV through half VI, showing the spermathecae and pharyngeal glands.

Coelomocytes round to narrow oval, 15–19 μm long, with large nuclei (diameter 4 μm) and pale, non-staining granules. Dorsal blood vessel commencing in (XVII, XVIII) XX–XXIII. Chloragogen tissue thin. Sperm sac extending posteriad to $\frac{1}{2}$ XIV or $\frac{1}{2}$ XXVII– $\frac{1}{2}$ XIX. Sperm funnels 6.5–9 times longer than wide (288–380 by 37–57 μm), with irregular outline except at proximal and distal ends (Fig. 6a); collars 21 μm wide. Male ducts 7–8 μm thick, extending posteriad into XV–XVIII. Each penial bulb (Fig. 6b) 43–49 μm long, enclosed in muscles and stalked (constricted basally by muscle fibres), the glandular part appearing drop-shaped; broad, deep invagination at male pore expanding laterally as an elongate aglandular sac (type 3 *sensu* Coates 1984); stylets not seen. Egg sac extending to $\frac{1}{2}$ XVIII–XX. Spermathecal ectal ducts 74–100 μm long, widest (25–32 μm) at midlength, generally tapering gradually both entally and ectally (13–15 μm wide at external pores); longitudinal muscle fibres occasionally conspicuous. Ampullae pear-shaped, 61–68 μm wide, attached to gut near 5/6; ectal ducts reaching ampullae in middle of their lateral aspects; sperm arranged in rings in the ampullar walls (Fig. 6d). No glands at pores of spermathecae.

Derivatio nominis: Named for the shape of the prostomium, from the Latin 'angustus' (= thin, narrow) and 'nasus' (= nose).

Remarks: The shape, distribution and size of setae of *G. angustinasus* are identical with those of *G. antarctica* sp. n. (described below), but the two species appear distinctly different in other respects, e.g. in the arrangement of clitellar glands (irregular in *G. antarctica*), the structure of the penial bulbs (with compact, not stalked, glandular bodies, and no separate aglandular sacs in *G. antarctica*), the size of spermathecal ampullae (larger in *G. antarctica*), and the position of spermathecal pores (shifted slightly posteriad in *G. antarctica*) (see also Table I). With regard to setal features, segment number, position of male pores, and some other morphological traits, both these Antarctic species are similar to the southwestern Australian *G. hyperoadenia* Coates, 1990. However, *G. hyperoadenia* possesses a completely different penial bulb endowed with a large accessory gland (type 2 *sensu* Coates 1984).

Distribution and habitat: Only known from three sampling localities between Faraglione and Cape Russell in Terra Nova Bay, Ross Sea. In fine sand, 35–126 m depth. This species appears so far the most widespread and also the most abundant in the sampling area in Terra Nova Bay.

Grania antarctica sp. n. (Figs 3c, 7, Table I)

Holotype: USNM 172400, whole-mounted specimen.

Type locality: McMurdo Sound, off beach in front of Scott's

Hut, northern shore of Cape Evans (Ross Island) (St. CEN G42-43).

Paratypes: USNM 172401-172402, two whole-mounted specimens from type locality. MCZR OLIGOCHAETA 0064, whole-mounted specimen from St. A39.

Other material examined: USNM 172403-172406, four whole-mounted specimens from type locality (St. CEN G42-43/CEN 61 G37).

Description: Body length 10–11 mm; width 0.14–0.18 mm at V, 0.17–0.21 mm at clitellum. Segments 55, 68 (only two specimens complete). Prostomium ogival (Fig. 3c, 7a), 74–84 μm across at its basis, 61–72 μm long; peristomium 112–122 μm wide. Epidermal gland cells inconspicuous, visible only laterally, at setal level. Ventral setae beginning in segment IV; lateral setae beginning in XV (2 specimens), XVI (3 specimens) or XVII (2 specimens). Setae (Fig. 7b) broadest entally, ental end curving into a long hook; tapering and straight ectally; maximum thickness of shaft 3.5–4.2 μm ; thinnest setae (3 μm) in VIII–XI, XIII–XXV. Setae increasingly longer from anterior to caudal region; 34–45 μm long in preclitellar segments, 39–66 μm long in postclitellar segments (both ventrally and laterally). Clitellum (Fig. 7c) extending over XII–2/3XIII, elevated; large, round to rectangular (up to 24 μm long), granular gland cells prevailing, arranged irregularly, denser dorsolaterally to male pores and around female pores. Male pores ventrolateral in middle of XII (anterior to midpoint of clitellum). Unpaired copulatory gland midventral in XIV. Spermathecal pores lateral, somewhat posterior to septum 4/5.

Brain 100–115 μm long, 61–68 μm wide. Head organ (see Discussion) present: vesicle chestnut-shaped (posterior margin asymmetrically pointed), 27–32 μm long, 25–36 μm wide, divided into compartments; up to 4 inclusions, 3–6 μm wide (Fig. 3c). Pharyngeal glands at 4/5–6/7, not united dorsally; ventral lobes in IV–VI, largest in VI. First pair of nephridia at 7/8. Coelomocytes oval (24 by 12 μm), filled with pale, non-staining granules. Dorsal blood vessel from XX–XXII; blood vessels in segments I–IV conspicuous (Fig. 7a). Sperm sac extending posteriad to XV–1/2XVIII. Sperm funnels restricted to XI–XII, with an irregular outline, about 5.5–7.5 times longer than broad (295–465 by 53–62 μm), narrower at both ends; collar 32–38 μm wide. Male ducts extending into XV–XVI, 5–8 μm wide. Each penial bulb (Fig. 7c, d) 50–73 μm long, compact, with a muscular sheath, attached medially to a deep, conical, cuticle-lined invagination on the tip of which opens the male duct; no lateral outpocketing visible; cuticular stylets absent (bulbs of type 3 *sensu* Coates 1984). Egg sac extending to XIX (some yolk in XXI, external to sac, in one specimen). Spermathecal ectal ducts with conspicuous longitudinal muscles, 95–135 μm long, widest at midpoint (23–30 μm), gradually tapering towards ampullae and connecting with them on lateral aspects; ectal third often distinct, uniformly narrow (13–18 μm at external pores); ampullae heart-shaped, 61–85 μm long, 55–86 μm wide, attached to gut in posterior half of V; sperm arranged in rings

in the thin ampullar walls (Fig. 7e). No glands at ectal pores of spermathecae.

Remarks: This species is similar to *G. angustinasus* sp. n. described above in shape, size and distribution of setae and general spermathecal structure, but it has a larger body size, a different arrangement of clitellar glands (regular in *G. angustinasus*), larger prostomium and brain, different structure of the head organ, simpler penial bulbs, and its spermathecal ectal pores are shifted posteriad. Body dimensions, segment number, shape and maximal size of setae and of spermathecal ampullae are the same as in *G. hyperoadenia* from south-western Australia. The latter, however, is characterized by a very conspicuous gland surrounding the penial bulb (type 2 *sensu* Coates 1984); it also possesses a different distribution of nephridia (only present in posterior segments), and longer sperm funnels (9–10 times longer than broad), and its spermathecal ectal ducts are uniformly thick.

Distribution and habitat: Known from both McMurdo Sound and Terra Nova Bay. In volcanic gravel and cobble, 14 m depth (St. CEN G42-43, CEN 61 G37). In unspecified sediment, 31 m depth (St. A39).

Grania algida sp. n. (Fig. 8, Table I)

Holotype: USNM 172398, whole-mounted specimen.

Type locality: McMurdo Sound, off beach in front of Scott's Hut, northern shore of Cape Evans (Ross Island) (St. CEN 61 G37).

Paratype: MCZR OLIGOCHAETA 0065, whole-mounted specimen from St. A35.

Other material: USNM 172399, whole-mounted specimen (incomplete subadult) from type locality.

Description: Body 5.5 mm long (2 specimens), 0.09–0.10 mm wide at V, 0.15 mm at XII. Segment number 49, 51. Prostomium small, thick-walled, pointed (Fig. 8a), 42–47 μm long, 53–66 μm wide at 0/1; peristomium 97–113 μm wide. Setae occurring from IV ventrally, from XIV laterally, almost L-shaped. Setal shaft sharply pointed distally, gradually broadening towards ental end; ental hook sharply bent at 90–125° to shaft and with slightly upturned tip (Fig. 8d). Setal length and thickness increasing from anterior to posterior segments: length 35–43 μm in anterior ventrals, 40–82 μm in posterior ventrals (longer than 60 μm posterior to XX–XXII), 41–78 μm in laterals. Shaft of anterior and midbody setae thinner than 3 μm at midpoint, up to 4.5 μm in posterior segments. Width of ental hook (length of 'foot') from 12 μm in anteriormost setae to 17.5 μm in posterior setae. Setae laterally compressed in their ental portion, cylindrical at midlength, tapering (conical) ectally; as a result, they show a sigmoid silhouette when seen in a somewhat frontal view (parallel to long axis of 'foot'). Clitellum extending over XII–1/2XIII; granular gland cells arranged irregularly. Male pores in middle of XII. Unpaired copulatory gland seen midventrally in XIV. Spermathecal pores lateral, a little behind septum 4/5.

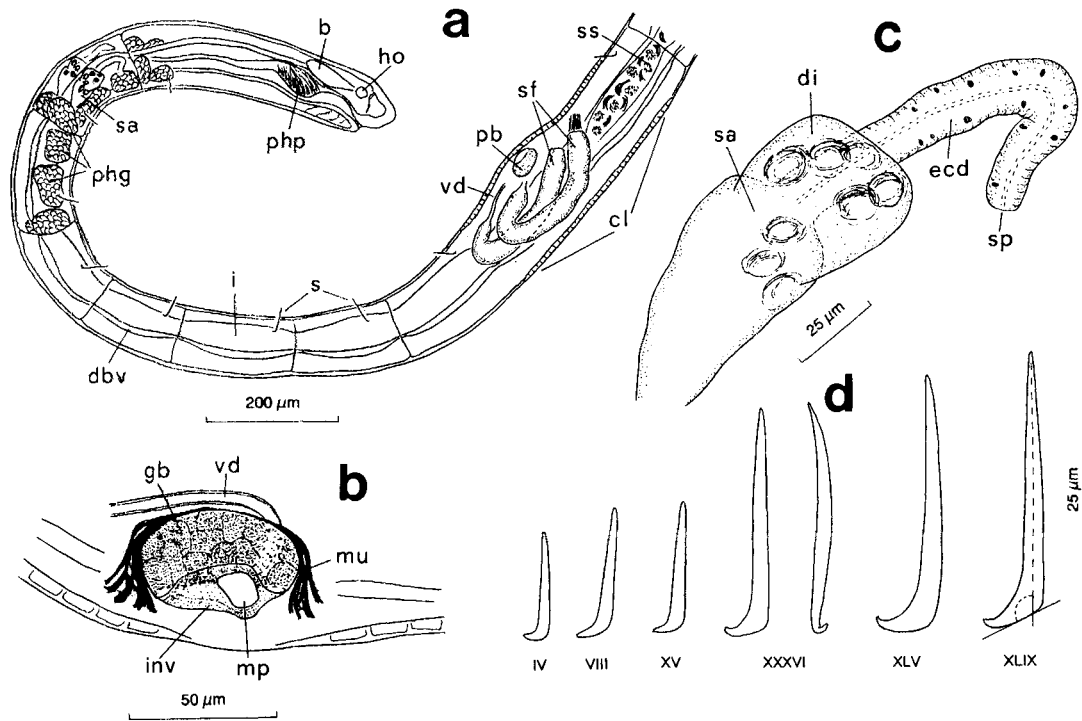


Fig. 8. *Grania algida* sp. n. **a.** Lateral view of anterior and clitellar body regions. **b.** Penial bulb and ectal portion of male duct (ventral view). **c.** Spermatheca. **d.** Setae from various segments (indicated by Roman numerals); right seta from XXXVI in a somewhat frontal view.

Brain 68–82 μm long. Head organ (see Discussion) present: vesicle globular ($l = 23\text{--}27 \mu\text{m}$), without evident compartments, containing maximally four inclusions of equal or different size (diameter 1.5–4 μm). Pharyngeal glands at 4/5–6/7, not united dorsally; one pair of ventral lobes in V, two pairs in VI. Nephridia not seen. Coelomocytes not seen. Dorsal vessel not seen. Chloragogen tissue inconspicuous. Sperm sac extending into XV. Sperm funnels seven times longer than wide (310 by 43 μm in holotype). Male ducts extending posteriad into $\frac{1}{2}$ XVIII, thin (4 μm wide). Penial bulbs (Fig. 8b) 49–53 μm long, each consisting of a simple glandular body attached medial to male invagination; the latter with a small lateral outpocketing (type 3 *sensu* Coates 1984). Egg sac extending into XVI or XVII. Spermathecae attached to oesophagus near 5/6: ectal ducts long (130 μm) and thin (11–19 μm in diameter), thickest at midlength, tapering at both ends; ampullae thin-walled, carrot-shaped (68 μm long, 38 μm wide), each ectally giving off a dorsal diverticulum (38 μm long, 42 μm wide) resting above ectal duct. Sperm rings in ampullar diverticula (Fig. 8c). No glands at ectal pores of spermathecae.

Derivatio nominis: Named from the Latin 'algidus' (= ice cold, frosty).

Remarks: The shape of the setae is possibly similar to that described for *G. inermis* from Hong Kong (Erséus 1990) and

for *G. eurystyla* from Darwin Harbour, northern Australia (Coates & Stacey in press). In *G. inermis*, however, nephridia begin at 6/7, the sperm sac extends only to XIII, male ducts are thicker (8–11 μm), sperm funnels are only three times longer than wide, spermathecal pores open dorsally and just behind 4/5, the ectal ducts are ectally widened and the ampullae without diverticula. In *G. eurystyla*, lateral setae are lacking and ventrals occur only postclitellarly, sperm and egg sacs extend much further posteriad, sperm funnels are 15 times longer than wide, male ducts have terminal stylets, and spermathecal ampullae surround the ectal ducts for most of their length. The setal features as well as the shape of spermathecal ampullae are reminiscent of those of *G. monochaeta* as redescribed by Erséus & Lasserre (1977); the latter species, however, has a larger body size, lateral setae beginning preclitellarly, shorter sperm funnels, and entally enlarged spermathecal ectal ducts. With regard to the spermathecal form, *G. algida* is also very similar to the south-western Australian *G. ascophora* which, however, has shorter sperm funnels and more complex structure of the penial bulbs (type 5 *sensu* Coates 1984) (Coates 1990). Important differences exist also between *G. algida* and *G. acanthochaeta*, another Antarctic species (described above) possessing diverticulate spermathecal ampullae (see also Table I).

Distribution and habitat: Only known from two localities in McMurdo Sound and Terra Nova Bay. In volcanic gravel and cobble, at 14 m depth and in unspecified sediment, at 40 m depth, respectively.

Discussion

Head organ (Fig. 3)

With one exception (*G. carchinii*), all *Grania* species described here possess a peculiar structure located within the peristomium in front of the brain (Figs 2a, 4a, 6a, 7a, 8a). This 'head organ' is a middorsal vesicular body containing a certain number of conspicuous, refractile inclusions (Fig. 3a–c). The anterior border of the vesicle corresponds roughly to the position of the head pore (0/1), but in a lateral view it appears to be deeper inside the segment, just dorsal to the anterior end of the dorsal vessel. The vesicle lies between the proximal tracts of the two circumpharyngeal connectives (or the roots of the prostomial nerves) and is often so close to them — and its walls so similar in light microscopy to the sheaths of the adjacent connectives, as to appear like an anterior extension of the cerebral ganglion. No visible connections exist with the blood system. A muscular lamina loosely anchors the anterior border of the organ to the dorsal body wall. The lumen of the vesicle is more or less distinctly subdivided into a number of hollow compartments of varying size. The refractile inclusions are seen as rounded, smooth globules in the middle of the larger compartments, the smaller compartments appearing empty. In one species (*G. hirsuticauda*), a number of nuclei are seen on the peripheral walls of both the vesicle and its inner compartments, suggesting a cellular nature of the organ (Fig. 3a).

In all species there seem to be maximally four inclusions; some damaged specimens showed fewer inclusions or none, but in most cases the vesicle was still visible. The shape and size of the vesicle appear to be specific (cf. species descriptions and Table I). The size of the inclusions is not so consistent; they are mostly large in *G. angustinasus* and *G. antarctica*, but vary greatly, even within the same individual, in *G. acanthochaeta* and *G. algida*. *G. hirsuticauda* is exceptional in having minute inclusions in all specimens examined.

The exact nature of the inclusions is unknown, but they appear to be solid and resistant to both the fixation and the standard mounting procedures. In the case of most Terra Nova Bay samples, they endured for six years in 7% (non neutralized) formalin, and still had an identical appearance to those of alcohol fixed and preserved conspecific specimens. It may be worth noting that at least in one species (see above) the dimensions of the inclusions are constant, regardless of the depth at which specimens were sampled (5 to 565–585 m).

The function of the head organ is not clear, although its cephalic position and proximity to the nervous system suggest that it is a sensory organ. The solid inclusions are reminiscent

of statoliths and the whole structure may indeed appear like a complex statocyst. Among the Annelida, statocysts are known only in some burrowing and tubicolous polychaetes, where they appear as epidermal or subepidermal vesicles, often communicating with the exterior through ciliated canals (Mill 1978, Storch & Schlötzer-Schrehardt 1988). In this phylum, no such structure has ever been observed as deep inside the body and closely adjacent to the cerebral ganglion as the *Grania* head organ, whilst statocyst-like vesicles embedded in the brain or very close to it are known to occur in the Platyhelminthes (Hyman 1951, Ferrero 1973, Rieger *et al.* 1991). A closer histological and ultrastructural study of the head organ is planned.

Distributional and systematic considerations

Grania, which now contains over 40 described species, is by far the largest and most common enchytraeid genus inhabiting the subtidal zone (Erséus 1990). The genus has been recorded, more or less intensively, from around all continents but also in deep-sea sediments and at some oceanic islands (Erséus 1980, Coates 1984, Coates & Erséus 1985). The great majority of the described species have been collected in lower intertidal or nearshore subtidal waters (less than 100 m deep) and show relatively restricted geographical distributions, but one deep-sea species, *G. atlantica*, has been recorded in a 750–1800 m depth range and from about 40°N through 10°S latitudes in the Atlantic Ocean (Coates & Erséus 1985).

Of course, most of the distribution patterns are likely to reflect the areas from which collections have been made rather than the actual biological distributions of species. Up to the 1980s, the taxonomic and faunistic literature on *Grania* was concentrated on the European and North American coasts, but in the last few years an effort has been made to study the fauna of the eastern hemisphere, particularly that inhabiting the Indo-West Pacific area (Erséus 1990, Coates 1990, Coates & Stacey 1993, Coates & Stacey *in press*). In two such surveys, conducted at the southwestern corner of Australia, Coates (1990) and Coates & Stacey (1993) found a remarkable area diversity and a possible high degree of endemism of the genus in intertidal and shallow subtidal habitats.

Prior to our study, the southernmost records of *Grania*, all originally identified as one species (*G. monochaeta*), were from South Georgia (Michaelsen 1888, 1921, Stephenson 1932, Erséus & Lasserre 1977). The present information demonstrates that *Grania* is well established even in High Antarctic waters and probably, given the numerous species yielded by the two small areas investigated, with a fairly rich fauna. Indeed, the richness of the whole Antarctic *Grania* assemblage looks all the more promising, since many more thoroughly investigated benthic groups exhibit a relatively 'low' faunal diversity in the Ross Sea (e.g. polychaetes: Knox 1977, molluscs: Dell 1990, isopods: Brandt 1992).

As to the bathymetric distribution, it might not be a

coincidence that the shallowest records of *Grania* reported here were in 5 and 14 m at McMurdo Sound sites, and no oligochaetes at all (see also Erséus & Rota 1996, for tubificids) were found in less than 30 m in Terra Nova Bay. The paucity of sessile benthic communities in shallow Antarctic waters is a well-known phenomenon determined by the formation of ice around all shores during winter, and by the abrasion of the sediments by ice in spring and summer and the formation of anchor ice on the sea floor (White 1984). In the same coastal stretch adjacent to the Italian Base in Terra Nova Bay, Gambi & Castelli (1994) found minimal numbers of species and individuals in polychaete communities at depths less than 50 m, those occurring being all restricted to large, errant taxa (families Polynoidae, Nephtyidae). Most infaunal groups are effectively eliminated from the intertidal and shallow subtidal zone (cf. also Dell 1990 for molluscs). Due mainly to the particular current regime and length of the ice-free season, the same does not hold true in the eastern, eutrophic part of McMurdo Sound: at depths of only 20–30 m, Dayton & Oliver (1977) have demonstrated the existence of extremely dense infaunal populations, “denser than almost any other benthic assemblage in the world”.

Due to the lack of information from most of the Southern Hemisphere and the subantarctic region, and from the other Antarctic districts, any speculation on the affinities of the Ross Sea fauna appears premature. Nevertheless, some comments on the morphology of the Antarctic species as a group and relative to other congeners may be of general taxonomic interest. For example,

- 1) all the new species except *G. carchinii* show a common pattern of setal distribution, i.e. with ventral setae from IV (as in many *Grania* spp.), and lateral setae from immediately or a few segment behind the clitellum through all posterior segments.
- 2) They all share the same setal size distribution, with setae becoming, more or less gradually, longer and stouter towards the posterior body region.
- 3) A midventral copulatory gland in XIV has been observed in all but one species.
- 4) No species bears glands at the spermathecal orifices.
- 5) Penial bulbs are all basically similar, with the glandular body attached medially to the male invagination (type 3 *sensu* Coates 1984) and no cuticular stylets.

Most of these shared features (points 1, 3, 4, plus others mentioned in the individual Remarks paragraphs) are also found in *Grania* species described from Australia (the lack of lateral setae, which distinguishes *G. carchinii*, is found in some Australian taxa too). However, many Australian species show the opposite pattern of setal size distribution, with larger setae occurring in front of the clitellum, and are characterized by complex penial bulbs endowed with cuticular stylets. When the character polarities have been more

thoroughly assessed within *Grania* (i.e. on the basis of a proper outgroup comparison), a study that remains to be undertaken, it may be possible to conclude whether the Antarctic taxa, or at least the bulk of them, constitute a monophyletic group.

The possession of the head organ, which makes the assemblage of new Antarctic species so peculiar, is common to all Ross Sea species except *G. carchinii*. It is reported here for the first time, but we have found it also in *G. atlantica*, in material of *G. monochaeta* (a further revision of this taxon being in preparation) and in other still undescribed species from the subantarctic (in C.E. collection). In contrast, the organ seems to be lacking in at least ten known species from various geographic areas (northern Europe, North America, southern China, south-western Australia) which have been tentatively re-examined by us, and in some additional undescribed material from the subantarctic. Details of this screening and a more thorough reexamination of the genus with regard to this character will appear in a future paper, aiming at establishing its geographical distribution and possible zoogeographical implications as well as addressing its use as a synapomorphy for a larger group.

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References

- ARGANO, R. & CARCHINI, G. 1991. Raccolte faunistiche nell'area della Base Italiana a Terra Nova Bay (Antartide, Victoria Land). *Atti I Convegno Biologia Antartica (Roma, CNR, 22–23 Giugno 1989)*. *Scienza e Cultura*, No. Speciale, 87–109. [English summary]
- BENHAM, W.B. 1905. On the Oligochaeta from the southern islands of the New Zealand region. *Transactions of the New Zealand Institute*, 37, 285–297.
- BENHAM, W.B. 1922. Oligochaeta of Macquarie Island. *Australasian Antarctic Expedition 1911–1914. Scientific Report*, 6, 1–38.
- BLOCK, W. & CHRISTENSEN, B. 1985. Terrestrial Enchytraeidae from South Georgia and the maritime Antarctic. *British Antarctic Survey Bulletin*, No. 69, 65–70.
- BRANDT, A. 1992. Origin of Antarctic Isopoda (Crustacea, Malacostraca). *Marine Biology*, 113, 415–423.

- COATES, K.A. 1984. Specific criteria in *Grania* (Oligochaeta, Enchytraeidae). *Hydrobiologia*, **115**, 45-50.
- COATES, K.A. 1990. Marine Enchytraeidae (Oligochaeta, Annelida) of the Albany area, Western Australia. In WELLS, F.E., WALKER, D.I., KIRKMAN, H. & LETHBRIDGE, R., eds. *Proceedings of the Third International Marine Biological Workshop: The marine flora and fauna of Albany, Western Australia*, Vol. 1. Perth: Western Australian Museum, 13-41.
- COATES, K.A. & ERSÉUS, C. 1985. Marine enchytraeids (Oligochaeta) of the coastal Northwest and Mid USA. *Zoologica Scripta*, **14**, 103-116.
- COATES, K.A. & STACEY, D.F. 1993. The marine Enchytraeidae (Oligochaeta, Annelida) of Rottnest Island, Western Australia. In WELLS, F.E., WALKER, D.I., KIRKMAN, H. & LETHBRIDGE, R., eds. *Proceedings of the Fifth International Marine Biological Workshop: The marine flora and fauna of Rottnest Island, Western Australia*, Vol. 2. Perth: Western Australian Museum, 391-414.
- COATES, K.A. & STACEY, D.F. In press. Enchytraeids (Oligochaeta: Annelida) of the lower shore and shallow subtidal of Darwin Harbour, Northern Territory, Australia. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences*.
- DAYTON, P.K. & OLIVER, J.S. 1977. Antarctic soft-bottom benthos in oligotrophic and eutrophic environments. *Science*, **197**, 55-58.
- DEARBORN, J.H. 1967. Stanford University invertebrate studies in the Ross Sea 1958-61: general account and station list. In BULLIVANT, J.S. & DEARBORN, J.H., eds. *The fauna of the Ross Sea*. Part 5. General accounts, station lists, and benthic ecology. *New Zealand Department of Scientific and Industrial Research Bulletin*, **176**, 31-47. (also, *Memoirs of the New Zealand Oceanographic Institute*, No. 32, 31-47).
- DELL, R.K. 1990. Antarctic Mollusca: with special reference to the fauna of the Ross Sea. *Bulletin of the Royal Society of New Zealand*, **27**, 1-311.
- ERSÉUS, C. 1980. A new species of *Grania* (Oligochaeta, Enchytraeidae) from Ascension Island, South Atlantic. *Sarsia*, **65**, 27-28.
- ERSÉUS, C. 1990. Marine Oligochaeta of Hong Kong. In MORTON, B., ed. *Proceedings of the Second International Marine Biological Workshop: The marine flora and fauna of Hong Kong and Southern China, Hong Kong, 1986*, Vol. 1. Hong Kong: Hong Kong University Press, 259-335.
- ERSÉUS, C. & LASSERRE, P. 1977. Redescription of *Grania monochaeta* (Michaelsen) a marine enchytraeid (Oligochaeta) from South Georgia (SW Atlantic). *Zoologica Scripta*, **6**, 299-300.
- ERSÉUS, C. & ROTA, E. 1996. Tubificidae (Oligochaeta) from the Ross Sea (Antarctica), with descriptions of one new genus and two new species. *Polar Biology*, **14**.
- FERRERO, E. 1973. A fine structural analysis of the statocyst in Turbellaria Acoela. *Zoologica Scripta*, **2**, 5-16.
- GAMBI, M.C. & CASTELLI, A. 1994. First quantitative data on coastal soft bottoms populations off Terra Nova Bay (Ross Sea, Antarctica): Polychaetes. *National Scientific Commission Antarctic Oceanographic Campaign 1989-1990, Data Report*, III, 179-186.
- HYMAN, L.H. 1951. *The Invertebrates*. Vol. 2, *Platyhelminthes and Rhynchocoela: the acoelomate Bilateria*. New York: McGraw-Hill, 550 pp.
- KNÖLLNER, F.H. 1935. Ökologische und systematische Untersuchungen über litorale und marine Oligochäten der Kieler Bucht. *Zoologische Jahrbücher (Systematik)*, **66**, 425-512.
- KNOX, G.A. 1977. The Antarctic Polychaete fauna: its characteristics, distribution patterns and evolution. In LLANO, G.A., ed. *Adaptations within Antarctic ecosystems. Proceedings of the Third SCAR Symposium on Antarctic Biology*. Washington DC: Smithsonian Institution, 1111-1126.
- MICHAELSEN, W. 1888. Die Oligochaeten von Süd-Georgien nach Ausbeute der deutschen Station von 1882-83. *Jahrbuch der Hamburgischen wissenschaftlicher Anstalten*, **5**, 53-73.
- MICHAELSEN, W. 1905a. Die Oligochaeten der schwedischen Südpolar-Expedition. *Wissenschaftliche Ergebnisse der schwedischen Südpolar-Expedition 1901-1903*, **5**, Zoologie I, Lief 3, 1-12.
- MICHAELSEN, W. 1905b. Die Oligochaeten der deutschen Südpolar-Expedition 1901-1903. *Deutsche Südpolar-Expedition 1901-1903*, **9**, Zoologie I, 1-58.
- MICHAELSEN, W. 1921. Neue und wenig bekannte Oligochäten aus skandinavischen Sammlungen. *Arkiv för Zoologi*, **13**, 1-25.
- MILL, P.J. 1978. Sense organs and sensory pathways. In MILL, P.J., ed. *Physiology of annelids*. London: Academic Press, 63-114.
- MÜLLER, O.F. 1774. Vermium terrestrium et fluviatilium, seu Animalium Infusoriorum, Helminthicorum et Testaceorum, non marinorum, succincta Historia. *Havniae et Lipsiae: Hieneck et Faber*, **1**, (1), 1-30.
- RIEGER, R.M., TYLER, S., SMITH, J.P.S.III & RIEGER, G.E. 1991. Platyhelminthes: Turbellaria. In HARRISON, F.W. & BOGITSH, B.J., eds. *Microscopic Anatomy of Invertebrates*, Vol. 3: *Platyhelminthes and Nemertinea*. New York: Wiley-Liss, 7-140.
- SHUROVA, N.M. 1979. Enchitreidy (Oligochaeta) dal'nevostocnych morej SSSR [Enchytraeids of the far eastern seas of the USSR]. In *Issledovannija pelagiceskich i donnych organizmov dal'nevostocnych morej*. Vladivostok, 75-90.
- SOUTHERN, R. 1913. Clare Island Survey. Part 48: Oligochaeta. *Proceedings of the Royal Irish Academy*, **31**, 1-48.
- STEPHENSON, J. 1932. Oligochaeta. Part I. Microdrili. *Discovery Reports*, **4**, 233-264.
- STORCH, V. & SCHLÖTZER-SCHREHARDT, U. 1988. Sensory structures. In WESTHEIDE, W. & HERMANS, C.O., eds. *The ultrastructure of Polychaeta*, Vol. 4. *Microfauna marina*. Stuttgart: Fischer, 121-133.
- TÉTRY, A. 1947. Croisière du Bougainville aux îles australes françaises. XVIII. Oligochètes. *Mémoires du Muséum National d'Histoire naturelle de Paris*, **20**, 101-110.
- UDE, H. 1896. Enchytraeiden. *Ergebnisse der Hamburger Magelhaensischen Sammelreise*, **1**, 1-43.
- WHITE, M.G. 1984. Marine Benthos. In LAWS, R.M., ed. *Antarctic Ecology*, Vol. 2. London: Academic Press, 421-461.

Abbreviations used in the figures

as	aglandular sac
b	brain
chl	chlorogentissue
cg	copulatory gland
cl	clitellum
dbv	dorsal blood vessel
di	diverticulum of spermathecal ampulla
ecd	spermathecal ectal duct
gb	glandular body of penial bulb
ggc	granular gland cell of clitellum
hgc	hyaline gland cell of clitellum
ho	head organ
hp	head pore
i	intestine
inv	invagination at male pore
mp	male pore
mu	muscle fibres
ne	nephridium
oe	oesophagus
p	prostomium
pb	penial bulb
phg	pharyngeal gland
php	pharyngeal pad
s	seta
sa	spermathecal ampulla
sf	sperm funnel
sp	spermathecal pore
sr	sperm ring
ss	sperm sac
vd	male duct (vas deferens)