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Seven new species of *Grania* (Annelida: Clitellata: Enchytraeidae) from New Caledonia, South Pacific Ocean

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Abstract

In meiofauna of the intertidal and subtidal zones (to 20 m depth) of New Caledonia seven species of the marine enchytraeid genus *Grania* were found, all of which were previously undescribed: *G. novacaledonia* **sp.n.**, *G. cinctura* **sp. n.**, *G. galbina* **sp. n.**, *G. curta* **sp. n.**, *G. fustata* **sp. n.**, *G. papillata* **sp. n.** and *G. fiscellata* **sp. n.** On the basis of morphology, these new species seem to have a phylogenetic affinity to congeners in Australia and possibly Antarctica, although little is known about the enchytraeid fauna of the surrounding areas.

Key words: *Grania*, Enchytraeidae, New Caledonia, meiofauna, new species, taxonomy

Introduction

Grania Southern, 1913, is without doubt the enchytraeid genus most adapted to marine life, with species living from the intertidal zone to the deep-sea floor, either in heterogeneous sand, most often with coarse particles (e.g. Erséus & Diaz, 1995; Coates & Stacey, 1997; Locke & Coates, 2000; Rota & Erséus, 2003), or in fine sediments (Erséus & Lasserre, 1976; Coates & Erséus, 1980). A few species, such as *Grania postclitellochaeta* (Knöllner, 1935) and *G. dolichura* Rota & Erséus, 2000, have also been encountered in brackish-water environments. The genus is cosmopolitan, although the distribution of individual species seems fairly limited to specific geographic regions; one exception is the deep-sea *G. atlantica* Coates & Erséus, 1985, which is widely distributed in the Atlantic Ocean (Coates & Erséus, 1985). To date, 57 species have been described, mostly from the Atlantic coasts of Europe and North America, as well as Western and Southern Australia (e.g. Lasserre, 1971; Erséus, 1977; Coates & Erséus, 1985; Coates, 1990; Rota & Erséus, 2000, 2003). These mostly temperate regions reflect where the scientific efforts have been concentrated, and it is safe to assume that there is a high number of yet undescribed species inhabiting tropical waters, especially in the Indo-Pacific which generally is accredited with the highest degree of marine biodiversity and endemism in the world. Little has been done, however, in this region with regard to the study of the marine enchytraeid fauna. Efforts have been concentrated to Hong Kong (Erséus, 1990; Erséus & Diaz, 1997), the Great Barrier Reef (Jamieson, 1977), north and north-western Australia (Coates & Stacey, 1997; Rota, Erséus & Wang, 2003), while the immense regions between Australia and continental Asia, as well as eastwards throughout the oceanic islands of the South Pacific, remain unexplored.

This paper attempts to chart the *Grania* species of the archipelago of New Caledonia, which is situated in the southern part of the tropical Indo-Pacific, bordering to temperate waters. Seven new species are described from localities both on the main island (Grande Terre) of New Caledonia and in the Loyalty Islands, and all taxa are unknown from any other part of the world.

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Material and methods

The interstitial fauna of New Caledonia was sampled by the second author during two workshops: The "Atelier Biodiversité Récifale – Expédition Montrouzier", arranged by Prof. Philippe Bouchet (Muséum national d'Histoire naturelle, Paris) and ORSTOM, Nouméa, in the vicinity of Touho on Grande Terre in September 1993, and the "Atelier Biodiversité LIFOU 2000" workshop on Lifou, one of the Loyalty Islands, in November 2000 (Figure 1). Clitellates were obtained from sediment samples, collected by hand or scooped by divers, and stirred with seawater followed by decantation through a 0.25 mm mesh-sized sieve. The sieved fractions were sorted using a stereo microscope and worms were fixed in Bouin's fluid, thereafter transferred to 80 % ethanol, stained in alcoholic paracarmine and mounted whole in Canada balsam. The whole-mounted specimens determined to belong to the genus *Grania* were given to the first author, together with similarly prepared but formalin-fixed *Grania* material obtained during the Centre National de Tri D'Oceanographie Biologique (CENTOB, Brest, France) expedition "Nouvelle Calédonie 78" (principal investigator: Dr. Bernard Thomassin) in the vicinity of Nouméa, New Caledonia, in May – June, 1978.

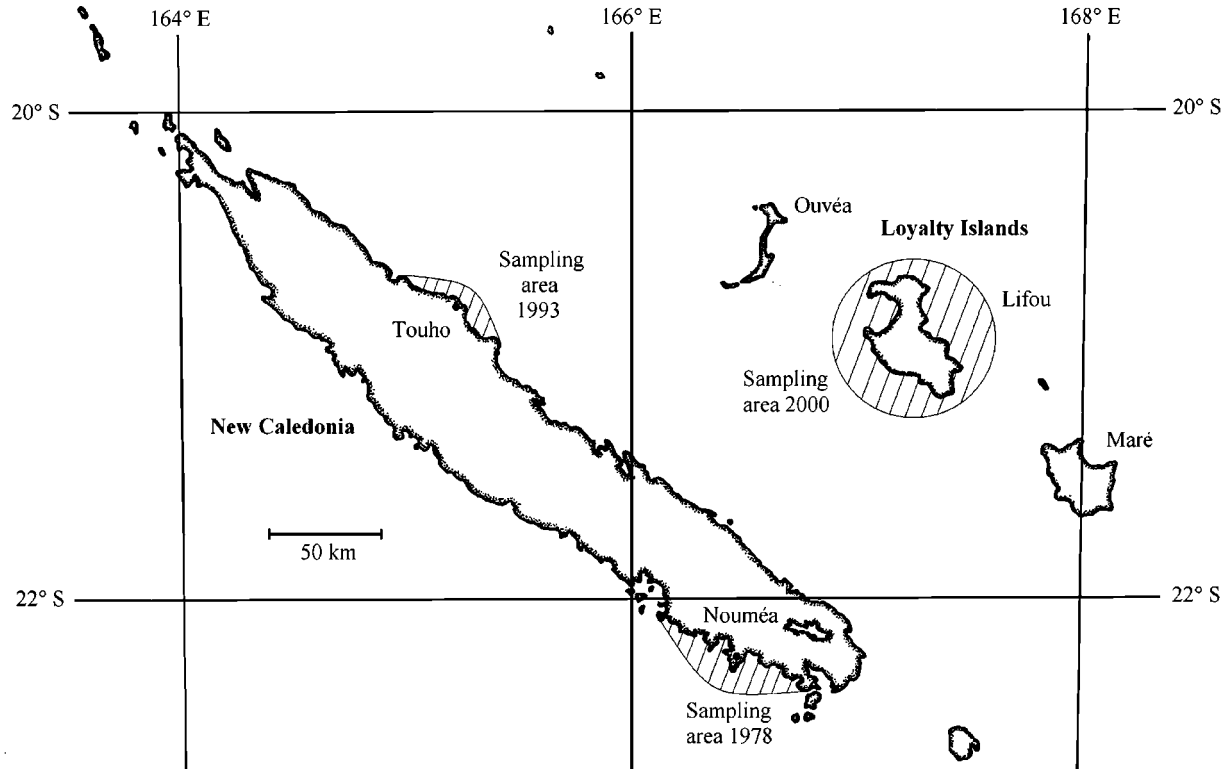


FIGURE 1. Map of New Caledonia showing sampling areas from three different expeditions in 1978, 1993 and 2000.

Mature specimens were observed with light transmission and interference contrast microscopy, using an Olympus BX60 microscope and a Nikon DXM1200 digital camera; the Olympus software MicroImage 4.0 was used for measurements. Chaetal measurements were taken from the chaetal tip in a straight line through the middle of the shaft to the base (chaetal length), and from the tip of the "foot" in a straight line through the middle of the foot to a point on the "heel", maximizing the width of the ental end (chaetal foot length). The "chaetal index" (Rota & Erséus, 2003) was calculated for chaetae with distinct "heels" by dividing the chaetal length by the chaetal foot length and calculating the mean and standard deviation. Penial bulb lengths are understood as the lengths parallel to the long body axis, and the widths are meant as the size of the penial bulbs perpendicular to the long body axis. Head organ and penial bulb type definitions (type 2, 3 and 6) are from Rota & Erséus (1996) and Coates (1984), respectively. Drawings were made using a camera lucida. The

type series and other material of the new species were deposited in the Swedish Museum of Natural History (SMNH), Stockholm.

Abbreviations used in the figures: amp, spermathecal ampulla; av, anterior vesicle; br, brain; bv, blood vessel; ch, chaeta; ed, spermathecal ectal duct; eg, ectal gland; ei, epidermal invagination; fs, free sperm; gb, glandular bulb; gc, glandular cell; ggc, granular gland cell; gvd, glandular vas deferens; hgc, hyaline gland cell; m, muscular tissue; mp, male pore; mvd, muscular vas deferens; pap, epidermal papilla; phg, pharyngeal gland; phx, pharynx; pro, prostomium; sp, spermatheca; spp, spermathecal pore; sr, sperm ring; vd, vas deferens.

Collecting sites

1978 (M. Segonzac [CENTOB], *personal communication*)

NC78-26B: Channel between l'Île aux Goélands and Récif Abore (N of the wreck), 13 m, coarse sand with film of reddish-brown diatoms, 13 May.

NC78-31: Récif de Va, 16 m, rich growth of sponges and corals (Alcyonaria*)* at the sediment surface, 18 May.

NC78-42: S corner of Récif Tetembia (barrier reef), towards lagoon, 4–6 m, coarse sediment, finer at depth, with corals (*Acropora branchus*, *Diplostrea heliopora)*, *Nassarius graniferus* (Gastropoda) and numerous filamentous black algae, 24 May.

NC78-43: Bottom of lagoon of Récif Tetembia, near N slope of underwater valley, 21 m, bottom consisting of dying patch reefs covered by coarse sediment with ophiurans, 24 May.

NC78-49A: Reef of M'Ba lagoon, 10 m, sea grass meadow with *Didemnum moseleyi* (Ascidiacea) and coral (*Trachyphyllia*, small Madreporaria*)*, 29 May.

NC78-51A: Reef of Ndué lagoon, 21 m, border of the sea grass meadow with bottom of algae (*Sargassum)* and coral (Madreporaria*)*, 30 May.

1993

NC93-8: Off Touho, S end of Grand Récif Mengalia, E side of Ilot Ain, coarse sand and gravel, lower intertidal, 20° 45.1'S, 165° 16.0'E, 14 Sep.

NC93-9: Off Touho, S end of Grand Récif Mengalia, E of Ilot Ain, coarse greyish sand, barely subtidal (0.5 m), 20° 45.1'S, 165° 16.0'E, 14 Sep.

NC93-10: Off Touho, S end of Grand Récif Mengalia, E of Ilot Ain, coarse clean sand, barely subtidal (0.5 m), 20° 45.1'S, 165° 16.0'E, 14 Sep.

NC93-11: Off Touho, S end of Grand Récif Mengalia, W side of Ilot Ain, coarse sand, lower intertidal (0.5 m), 20° 45.1'S, 165° 16.0'E, 14 Sep.

NC93-12: Off Touho, S end of Grand Récif Mengalia, W side of Ilot Ain, medium to coarse sand, lower intertidal between parallel beach rocks, 20° 45.1'S, 165° 16.0'E, 14 Sep.

NC93-13: Off Touho, S end of Grand Récif Mengalia, S of Ilot Ain, greyish coarse sand, protected behind beach rock, 20° 45.1'S, 165° 16.0'E, 14 Sep.

NC93-14: Off Touho, S end of Grand Récif Mengalia, back reef E of Ilot Ain, heterogeneous sand under dead coral clumps, barely subtidal (0.5 m), 20° 45.1'S, 165° 16.3'E, 14 Sep.

NC93-15: Off Touho, S end of Grand Récif Mengalia, middle of back reef E of Ilot Ain, small patches of heterogeneous sand, barely subtidal (0.5 m), 20° 45.1'S, 165° 16.3'E, 14 Sep.

NC93-16: Off Touho, S end of Grand Récif Mengalia, outer barrier E of Ilot Ain, coarse sand and rubble under dead coral, barely subtidal (0.5 m), 20° 45.1'S, 165° 16.3'E, 14 Sep.

NC93-23: Touho, E of Baie de Touho, middle of large intertidal bank N of Kombounou, heterogeneous, largely fine sand with seagrass, lower intertidal, 20° 46.2'S, 165° 14.2'E, 16 Sep.

NC93-24: Touho, E of Baie de Touho, N side of middle of large intertidal bank N of Kombounou, rubble and sand, lower intertidal, 20° 46.1'S, 165° 14.2'E, 16 Sep.

NC93-25: Touho, E of Baie de Touho, N side of middle of large intertidal bank N of Kombounou, solid platform of reef with lots of living corals, small patches of heterogeneous sand and rubble under dead coral, lower

intertidal, 20° 46.0’S, 165° 14.2’E, 16 Sep.
NC93-26: Touho, E of Baie de Touho, N side of middle of large intertidal bank N of Kombounou, solid platform of reef with mostly dead corals, heterogeneous sand and coral rubble, lower intertidal, 20° 46.0’S, 165° 14.2’E, 16 Sep.
NC93-29: N of Touho, SE corner of Ilot Ouao, intertidal sand bank on large flat, coarse greyish sand, lower intertidal, 20° 43.3’S, 165° 08.7’E, 17 Sep.
NC93-31: N of Touho, SE corner of Ilot Ouao, intertidal flat, greyish sand with sparse seagrass, lower intertidal, 20° 43.3’S, 165° 08.7’E, 17 Sep.
NC93-33: N of Touho, reef platform NE of Ilot Ouao, coarse, poorly oxygenated sand, lower intertidal, 20° 42.9’S, 165° 09.1’E, 17 Sep.
NC93-34: N of Touho, reef platform NE of Ilot Ouao, coarse, poorly oxygenated sand, barely subtidal (0.5 m), 20° 42.9’S, 165° 09.1’E, 17 Sep.
NC93-37: N of Touho, SE corner of Ilot Ouao, seagrass bed near beach, with heterogeneous sand, lower intertidal, 20° 43.3’S, 165° 08.7’E, 17 Sep.
NC93-49: Touho, reef crest N of Ilot Atit, small pools on reef crest, in lower intertidal, with coarse sand and coral rubble, 20° 46.4’S, 165° 14.8’E, 19 Sep.
NC93-50: Touho, reef crest N of Ilot Atit, pool on reef crest, with medium sand (0.3 m), 20° 46.4’S, 165° 14.8’E, 19 Sep.
NC93-53: Touho, near reef crest N of Ilot Atit, patch of coarse sand, lower intertidal, 20° 46.4’S, 165° 14.7’E, 19 Sep.
NC93-54: Touho, near reef crest N of Ilot Atit, coarse to medium sand, lower intertidal, 20° 46.4’S, 165° 14.7’E, 19 Sep.
NC93-55: Touho, N of Ilot Atit, NW tip off reef flat, greyish, heterogeneous sand, lower intertidal, 20° 46.5’S, 165° 14.6’E, 19 Sep.
NC93-56: Touho, sand flat NW of Ilot Atit, edge of seagrass bed, poorly oxygenated coarse sand, with lots of sipunculids, lower intertidal, 20° 46.0’S, 165° 14.0’E, 19 Sep.
NC93-59: Between Touho and Hienghene, Point Bounou, near bridge at Tiouandé, coarse, muddy sand, with lots of sipunculids, barely subtidal (0.5 m), 20° 43.8’S, 165° 02.5’E, 20 Sep.
NC93-60: Between Touho and Hienghene, Point Bounou, near bridge at Tiouandé, rubble and muddy sand, lower intertidal, 20° 43.8’S, 165° 02.5’E, 20 Sep.
NC93-61: Between Touho and Hienghene, Point Bounou, near bridge at Tiouandé, reef platform with rubble and heterogeneous sand, lower intertidal, 20° 43.8’S, 165° 02.5’E, 20 Sep.
NC93-62: Between Touho and Hienghene, about 200 m N of bridge at Tiouandé, E side of river mouth, rubble and muddy sand, barely subtidal (0.5 m), 20° 43.8’S, 165° 02.5’E, 20 Sep.
NC93-66: Between Tiéti and Poindimié, reef flat N of a public beach, small pool in reef flat, with heterogeneous, largely coarse sand, lower intertidal, 20° 56.0’S, 165° 19.0’E, 21 Sep.
NC93-69: Between Tiéti and Poindimié, reef flat N of a public beach, seagrass and fine sand, lower intertidal, 20° 56.0’S, 165° 19.0’E, 21 Sep.
NC93-70: Between Tiéti and Poindimié, reef flat N of a public beach, pool in reef platform with heterogeneous sand and rubble, barely subtidal (0.5 m), 20° 56.0’S, 165° 19.0’E, 21 Sep.
NC93-72: S of Touho, N side of Anse Ponandou, about 300 m from bridge across River Ponandou, clean coarse sand and gravel, barely subtidal (0.5 m), 20° 49.0’S, 165° 15.0’E, 21 Sep.
NC93-73: S of Touho, N side of Anse Ponandou, about 250 m from bridge across River Ponandou, poorly oxygenated, heterogeneous sand, with seagrass, lower intertidal, 20° 49’S, 165° 15’E, 21 Sep.
NC93-82: Off Touho, W of S end of Grand Récif Mengalia, heterogeneous, largely fine sand (7 m), 20° 44.4’S, 165° 15.7’E, 23 Sep. (coll. P. Scaps).
2000

NC00-12: Lifou, Baie du Santal, Baie d´Hunete, W of Pte de Easo, poorly sorted sand (4–5 m), 20° 47.0'S, 167° 07.0'E, 17 Nov.
NC00-17: Lifou, Baie de Chateaubriand, reef flat at Traput (SW of Wé), small patches of sand in reef platform, fine to coarse sand (1–1.5 m), 20° 55.0'S, 167° 18.0'E, 20 Nov.
NC00-18: Lifou, Baie de Chateaubriand, reef flat at Traput (SW of Wé), sand and coral rubble, lower intertidal, 20° 55.0'S, 167° 18.0'E, 20 Nov.
NC00-20: Lifou, Baie de Chateaubriand, Luecilla Beach, fine sand with freshwater springs, (0.5–1 m), 20° 54.0'S, 167° 16.0'E, 21 Nov.
NC00-25: Lifou, E side of island, Luengoni, E end of sand beach, poorly sorted sand (1–1.5 m), 21° 02.0'S, 167° 25.5'E, 22 Nov.
NC00-27: Lifou, Baie du Santal, Chépénéhé, immediately off rocky shore W of pier, small patches of coarse sand (1–1.5 m), 20° 47.0'S, 167° 08.5'E, 23 Nov.
NC00-35: Lifou, W side of island, SE of Pointe Lefèvre (S of Baie du Santal), between Jua Wekutr and Jua Wajez, medium sand (20–22 m), 20° 56.8'S, 167° 02.7'E, 25 Nov.
NC00-36: Lifou, Baie du Santal, Chépénéhé, W of pier, silty fine sand (3 m), 20° 47.0'S, 167° 08.5'E, 25 Nov.
NC00-43: Lifou, E side of island, Ejengen (off village of St. James), medium sand at lower end of sandy beach, immediately inside extensive reef flat (0.5 m), 20° 47'S, 167° 17'E, 27 Nov.

Taxonomy

Grania novacaledonia sp. n.

(Figure 2, Table 1)

Holotype: SMNH type coll. 6549, whole-mounted specimen from Touho, stn. NC93-25.

Paratypes: SMNH type coll. 6550-6558, 9 whole-mounted specimens from Touho, 4 of which from type locality, and 1 from each of stns. NC93-14, NC93-15, NC93-49, NC93-50 and NC93-82.

Other material examined: SMNH Main coll. 87841-87847, 7 specimens from CENTOB collected off Nouméa, New Caledonia, during the Nouvelle Calédonie 78 excursion in 1978 (stns. NC78-31, NC78-43, NC78-49A and NC78-51A); SMNH main coll. 87848-87860, 13 whole-mounted specimens from Touho (stns. NC93-14, NC93-15, NC93-25, NC93-26, NC93-49).

Description of type material: Body 5.7–7.7 mm long (n=8), 0.14–0.17 mm wide at III, 0.14–0.19 mm at clitellum (n=10). Segment number 41–50 (n=8). Prostomium rounded, 70–85 μm wide, 35–60 μm long (n=10); epidermis 15–23 μm thick on occipital lobes, 10–18 μm on upper lip (n=9), 5–15 μm at front side (n=10). Peristomium 118–143 μm wide at 1/2 (n=10). Chaetal distribution irregular, with preclitellar ventral chaetae frequently occurring only in VII and sometimes VI and VIII, although sometimes completely absent; ventral chaetae occurring at all postclitellar locations; lateral chaetae commencing in XVII–XXI. Chaetae increasing in size posteriorly, 43–55 μm long pre-clitellum (n=7), 58–73 μm near posterior end (n=10); chaetae L-shaped; sharply pointed with distinct heel, foot 8–15 μm long (chaetal index=5.38, n=14, sd=0.78) (Figure 2A). Epidermal gland cells inconspicuous, interspersed irregularly. Clitellum 13–23 μm thick, starting in anterior of XII and extending to chaetal position of XIII, consisting of transverse cell rows with granular gland cells interspersed with hyaline cells at a ratio of about 2:1 (Figure 2B), except around male pores where hyaline cells are absent. "Copulatory glands" present midventrally in XIV. Spermathecal pores lateral, located right behind 4/5. Male pores located ventrolaterally in mid XII.

Brain in II–III, posteriorly indented in "head" region. No true "head organ" present, but bilobed vesicle present immediately behind 0/1, dorsal to the anterior furcation of blood vessel, between the circumpharyngeal commissures; no inclusions present, but hollow compartments visible with internal whorls of cilia. Pha-

ryngeal glands located from 4/5 to 6/7, not united dorsally; dorsal lobes present in IV–VI, ventral lobes present in IV (1 pair), V (2 pairs) and VI (2 pairs), largest in VI (Figure 2C). First pair of nephridia at 7/8.

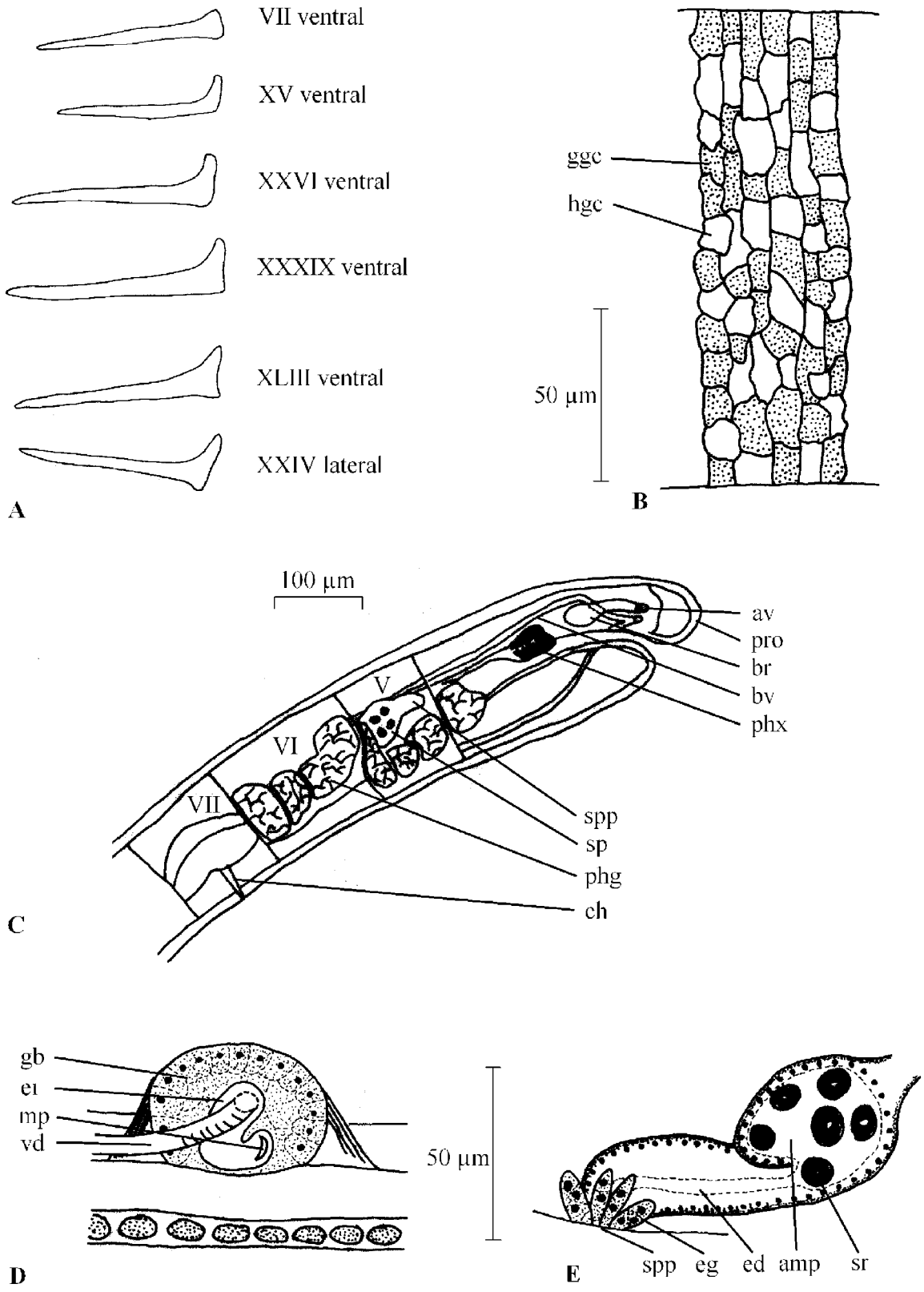


FIGURE 2. *Grania novacaledonia* **sp. n.**. A: Chaetae. B: Clitellar cell pattern. C: Overview of I– VII. D: Penial apparatus. E: Spermatheca.

Dorsal blood vessel commencing in XVII–XXII. Chloragogen cells small (5–7 μm tall). Coelomocytes not observed. Sperm sac extending posteriorly from clitellum as far back as XVII. Sperm funnels of uniform width, 40–50 μm wide, 5 times as long as wide. Heads of spermatozoa about 20 μm long. Vasa deferentia long, loosely coiled in XII and XIII; 6 μm wide, internally ciliated. Penial apparati (Figure 2D) with uniform oval glandular structures, 48–58 μm long, 25–35 μm wide; vas deferens opening into epidermal invagination (Penial bulbs type 3). Stylets absent. Egg sac extending as far back as XVIII. Spermathecae (Figure 2E) attached to oesophagus near 5/6; ampullae pear-shaped, 53–58 μm wide, with small diverticulum on anterior side of each ampulla, ectal ducts uniform in thickness, 40 μm long and 25 μm wide; 4–8 sperm rings per spermatheca, 13–18 μm in diameter, located throughout ampullae; 4 ectal glands present at each spermathecal pore.

Etymology: Named after New Caledonia.

Remarks: The irregular pre-clitellar chaetal distribution with chaetae present in only one to three segments (VI, VII and/or VIII) is unusual, yet not unique to this species. Similar distributions have been described for *Grania variochaeta* Erséus & Lasserre, 1976, and in *G. ocarina* Rota, Erséus & Wang, 2003, the latter existing in Western Australian waters. *Grania novacaledonia* is different from *G. ocarina* and *G. variochaeta* in its chaetal shape (*G. ocarina* has no distinct heel; *G. variochaeta* has upturned tips on the ental "feet") and the presence of ectal glands at the spermathecal pores. The lack of penial stylets also distinguishes *G. novacaledonia* from *G. ocarina*. Ectal glands by the spermathecal pores have also been recorded in Western Australian species [*G. ersei* Coates, 1990 and *G. darwinensis* (Coates & Stacey, 1997)], as well as in North Pacific waters [*G. paucispina* (Eisen, 1904) and *G. americana* Kennedy, 1966]. *Grania novacaledonia* differs from all of these, however, in its chaetal distribution.

The bilobed vesicle present anterior to the brain in this and two other species described herein is peculiar, as it has the same apparent structure as the "head organ" recently described in a number of *Grania* species (Rota & Erséus, 1996; Rota & Erséus, 1997; Locke & Coates, 1999; Rota & Erséus, 2000, 2003), yet it contains no inclusions. This has previously been noted in descriptions of only two species: *G. aquitana* Rota & Erséus, 2003 and *G. monochaeta* (Michaelsen, 1888) (see Rota & Erséus, 1997). Rota *et al.* (1999), however, noted that some other species (e.g. *G. maricola* Southern, 1913) also possess this feature. Upon re-examination, it seems as if this could be the case in a considerable number of species of the genus (De Wit, *personal observation*) (see Discussion).

Another feature worth noting is the apparent lack of coelomocytes in this and several other species from New Caledonia. This has also been reported for *G. algida* Rota & Erséus, 1996 and in *G. carchinii* Rota & Erséus, 1996, both inhabiting Antarctic waters. This could, possibly, be an artifact caused by the fixation or staining procedure. However, the presence or lack of coelomocytes has frequently been omitted in literature, which might justify further investigation and re-examination of poorly described species.

Distribution and habitat: Touho and Nouméa areas, New Caledonia, lower intertidal and subtidal (to 21 m), heterogeneous sand.

***Grania cinctura* sp.n.**
(Figure 3, Table 1)

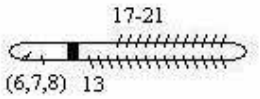
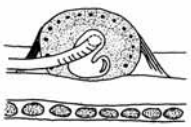
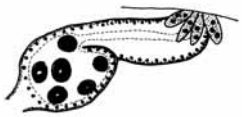
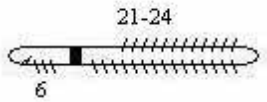
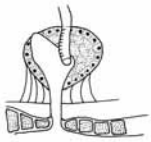
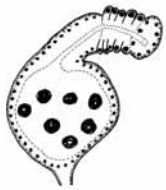
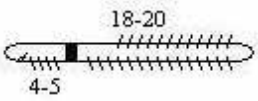
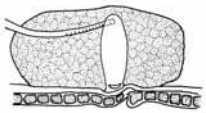
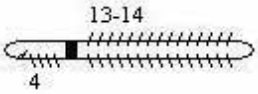
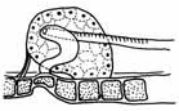
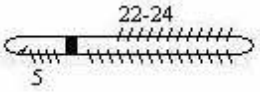
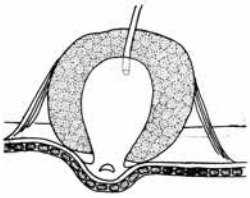
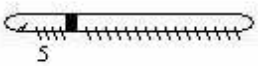
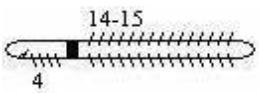
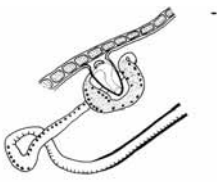
Holotype: SMNH type coll. 6559, whole-mounted specimen from Lifou, stn. NC00-17.

Paratypes: SMNH type coll. 6560-6564, 5 whole-mounted specimens from Lifou, 4 of which from type locality, and 1 from stn. NC00-18; SMNH type coll. 6565-6568, 6572, 5 whole-mounted specimens from Touho: 1 from each of stns. NC93-10, NC93-12, NC93-13, NC93-29 and NC93-33.

Other material examined: SMNH main coll. 87866-87882, 17 specimens from CENTOB collected off Nouméa, New Caledonia, during the Nouvelle Calédonie 78 excursion in 1978 (stn. NC78-42); SMNH main

coll. 87884-87924, 41 specimens from Touho (stns. NC93-9, NC93-10, NC93-11, NC93-12, NC93-13, NC93-14, NC93-16, NC93-25, NC93-29, NC93-33, NC93-50 and NC93-59); SMNH main coll. 87927-87956, 30 specimens from Lifou (stns. NC00-17 and NC00-18).

TABLE 1. Distinguishing characters of the new species of *Grania* from New Caledonia. Segment numbers for chaetal distribution refers to commencement of lateral and ventral chaetae, respectively.

Species	Chaetal distribution	Penial bulb shape	Spermathecal shape
Grania novacaledonia			
Grania cinctura			
Grania galbina			
Grania curta			
Grania fustata			
Grania papillata			
Grania fiscellata			

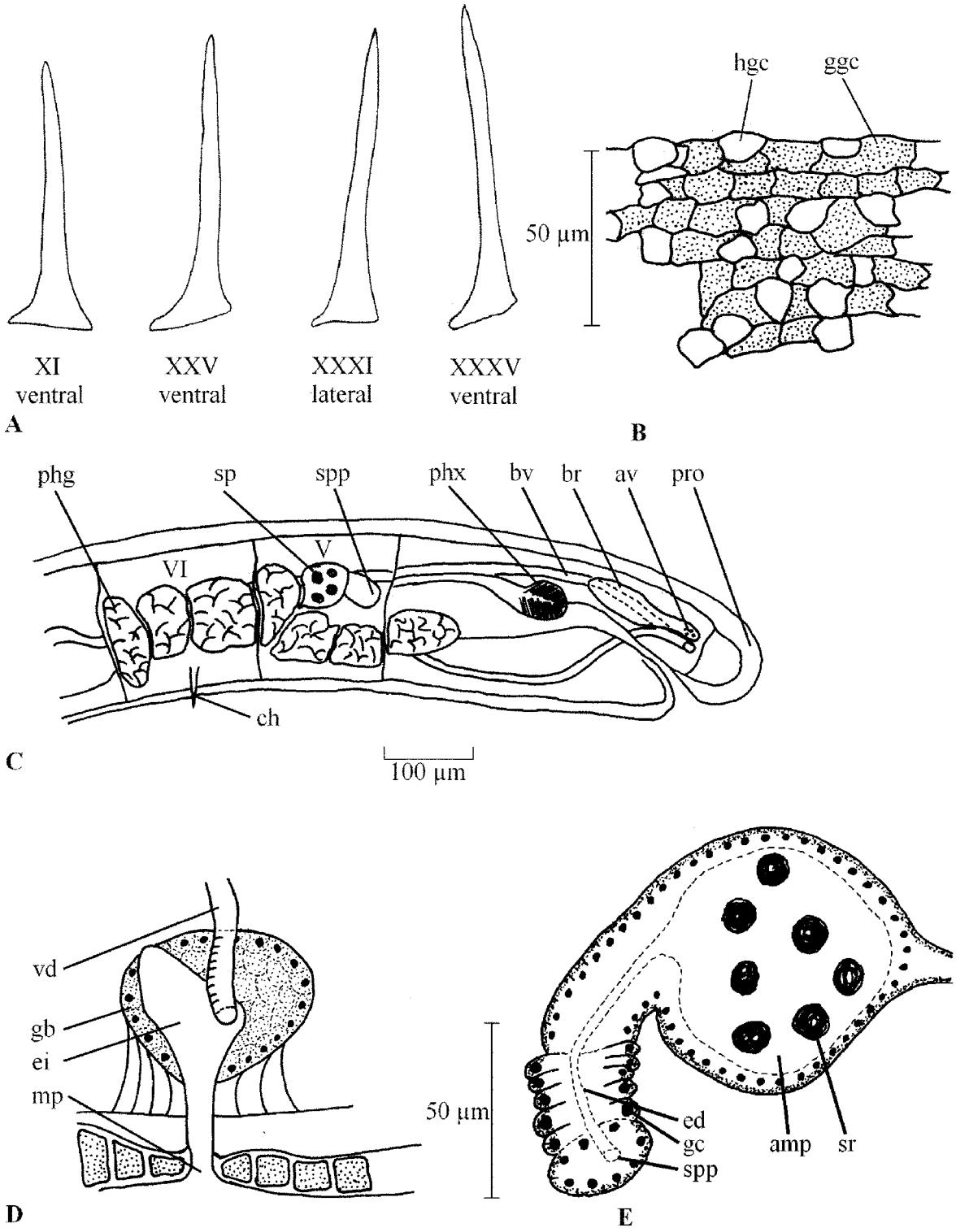


FIGURE 3. *Grania cinctura* **sp. n.**. A: Chaetae. B: Clitellar cell pattern. C: Overview of I–VI. D: Penial apparatus. E: Spermatheca.

Description of type material: Body 7.4–9.5 mm long (n=11), 0.21–0.26 mm wide at III, 0.23–0.27 mm at clitellum (n=10). Segment number 42–54 (n=11). Prostomium rounded, 90–120 µm wide, 70–75 µm long (n=10); epidermis 23–28 µm thick on occipital lobes, 15–25 µm on upper lip (n=9), 5–18 µm at front side (n=8). Peristomium 165–205 µm wide at 1/2 (n=9). Preclitellar chaetal distribution highly variable, ventral chaetae commencing in VI but frequently missing from one or more segments, most often IX and X; chaetae

absent in XII; lateral chaetae commencing in XXI–XXIV. Chaetae of uniform size throughout body, 65–80 μm long (n=15); chaetae L-shaped with conspicuous heel, in pre-clitellar segments almost T-shaped due to size of heel; foot 17–27 μm long (chaetal index=4.78, n=15, sd=0.98) (Figure 3A). Epidermal gland cells inconspicuous. Clitellum 20–25 μm thick, starting in XII and extending to mid XIII, in the shape of uneven transverse rows consisting of granular gland cells interspersed with hyaline cells at a ratio of about 2:1, except near male pores where hyaline cells are absent (Figure 3B). "Copulatory glands" not observed in XIV. Spermathecal pores lateral, located right behind 4/5. Male pores located ventrolaterally in mid XII.

Brain in II–III, posteriorly indented in "head" region. No true "head organ" present, but bilobed vesicle present immediately behind 0/1, dorsal to the anterior furcation of blood vessel, between the circumpharyngeal commissures; no inclusions present, but hollow compartments visible which seem to be internally ciliated. Pharyngeal glands located from 4/5 to 6/7, not united dorsally; dorsal lobes present in IV – VI, ventral lobes present in IV (1 pair), V (2 pairs) and VI (2 pairs); largest in VI, indenting septum 6/7 slightly into VII (Figure 3C). First pair of nephridia at 7/8. Dorsal blood vessel commencing in XXIII–XXVI. Chloragogen cells small (5–7 μm tall). Coelomocytes not observed. Sperm sac extending posteriorly from clitellum as far back as XV. Sperm funnels of uniform width, 40–50 μm wide, 6–7 times as long as wide. Heads of spermatozoa 15–20 μm long. Vasa deferentia long, unmodified, loosely coiled in XII to XIV; 6 μm wide, internally ciliated. Penial apparati (Figure 3D) uniform oval glandular structures, 50–65 μm long, 45–50 μm wide, with vasa deferentia opening into epidermal invagination (Penial bulb type 3). Stylets absent. Egg sac reaching as far back as XIX. Spermathecae (Figure 3E) attached to oesophagus near 5/6; ampullae roughly spherical, 50–55 μm in diameter, ectal ducts bipartite, with ental part of uniform width, 40–45 μm long and 25 μm wide, ectal part covered by glandular cells; 4–8 sperm rings per spermatheca, 13–18 μm in diameter, located throughout ampullae; no glands at spermathecal pores.

Etymology: Named by the Latin *cinctura*, which is a form of Roman girdle. This refers to this species having a thick clitellum which obscures the male genitalia in many specimens.

Remarks: As in *G. novacaledonia*, the pre-clitellar chaetal distribution is irregular. *Grania cinctura*, however, is most frequently equipped with chaetae in all segments but one or two (IX–X), which is a distribution resembling that of *G. atlantica* Coates & Erséus, 1985 and *G. mira* Locke & Coates, 1998. In addition, the penial bulb structure is similar to that of *G. atlantica*, which is an Atlantic deep-sea species. The spermatheca, however, is distinct with its bipartite ectal duct, where the ectal part is covered by glandular cells. Neither *G. atlantica* nor *G. mira* possess any gland cells on the spermathecal duct.

Other characters in common with *G. novacaledonia* are the bilobed vesicles present anterior to the brain (see Remarks under *G. novacaledonia* and Discussion), and the apparent lack of coelomocytes (see Remarks under *G. novacaledonia*). The two are easily distinguished from each other, however, by the size difference (*G. cinctura* is much larger), and by the shape of the spermatheca.

Distribution and habitat: Touho and Nouméa areas, New Caledonia, and Lifou, Loyalty Islands, lower intertidal to shallow subtidal (6 m), medium to coarse sand.

***Grania galbina* sp.n.**
(Figure 4, Table 1)

Holotype: SMNH type coll. 6573, whole-mounted specimen from Lifou, stn. NC00-17.

Paratypes: SMNH type coll. 6574-6582, 9 whole-mounted specimens from Lifou, 5 of which from type locality, and 1 from each of stns. NC00-18, NC00-20, NC00-25 and NC00-27.

Other material examined: SMNH main coll. 87958-87978, 21 whole-mounted specimens from Lifou (stns. NC00-17, NC00-18, NC00-27); SMNH main coll. 87979, 1 specimen from CENTOB, collected off Nouméa, New Caledonia, during the Nouvelle Calédonie 78 excursion in 1978 (stn. NC78-26B).

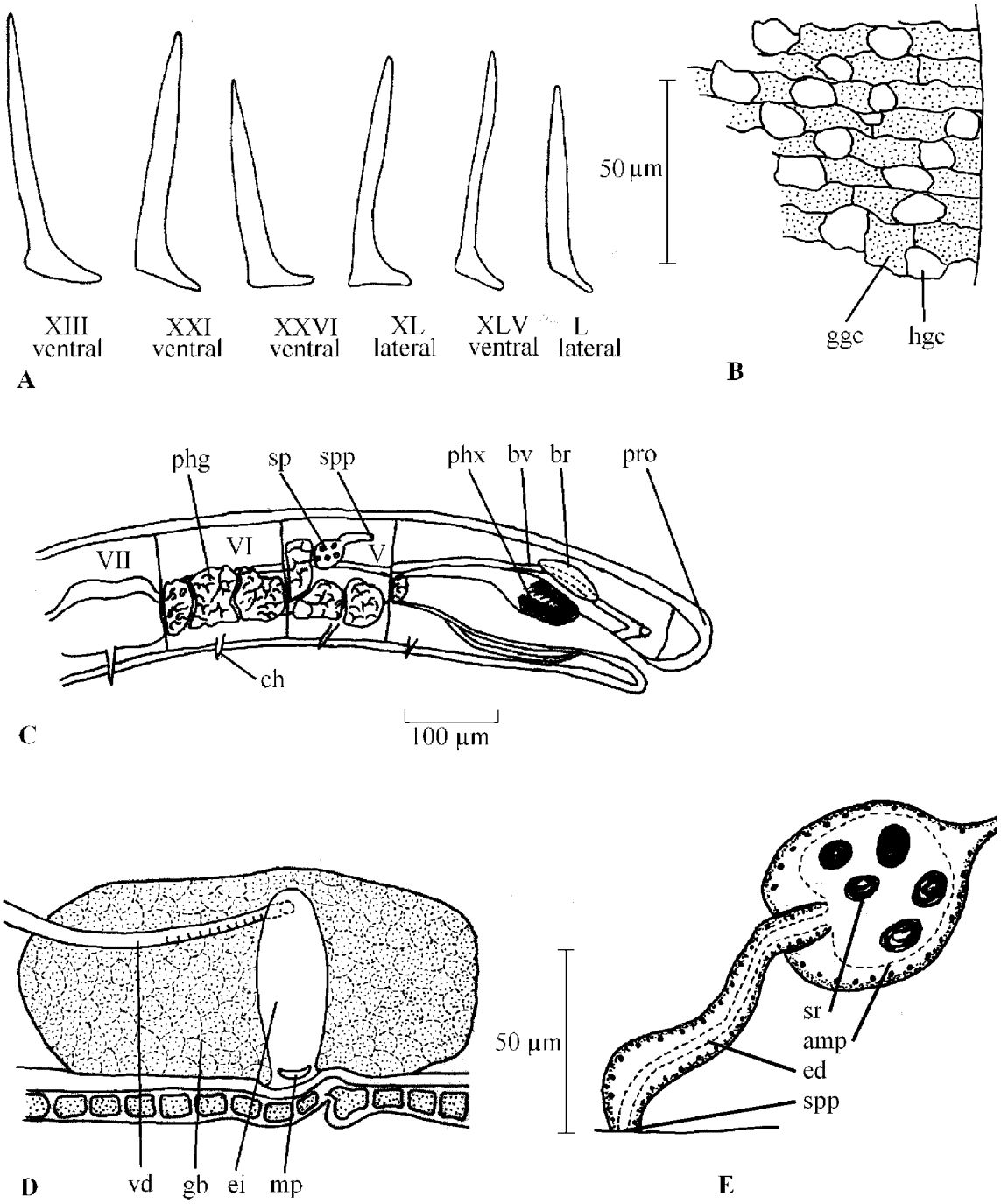


FIGURE 4. *Grania galbina* **sp. n.**. A: Chaetae. B: Clitellar cell pattern. C: Overview of I–VII. D: Penial apparatus. E: Spermatheca.

Description of type specimens: Living specimens greenish yellow. Body 6.4–7.8 mm long (n=10), 0.16–0.20 mm wide at III, 0.16–0.22 mm at clitellum (n=10). Segment number 51–56 (n=10). Prostomium rounded, 65–85 µm wide, 45–75 µm long (n=9); epidermis 13–23 µm thick on occipital lobes and upper lip (n=7), 8–18 µm thick at front side (n=10). Peristomium 125–145 µm wide at 1/2 (n=10). Ventral chaetae commencing in IV or V, absent in XII**,** laterals commencing in XVIII–XX. Chaetae larger post-clitellum, 43–50 µm long in preclitellar segments (n=5), 50–60 µm post-clitellarly (n=9); chaetae L-shaped, sharply pointed with distinct heel, foot 13–20 µm long (chaetal index=3.92**,** n=14, sd=0.66) (Figure 4A). Epidermal gland cells inconspicuous, interspersed irregularly. Clitellum 10–20 µm thick, starting at anterior end of XII and extending to chaetal position in XIII, consisting of unevenly shaped transverse cell rows with granular gland cells and hyaline cells

at a ratio of about 3:1 (Figure 4B), except around male pores where hyaline cells are absent. "Copulatory glands" not observed in XIV. Spermathecal pores lateral, as far back as one quarter into V. Male pores ventrolateral in mid XII.

Brain in II–III, posteriorly indented in "head" region. Head organ absent. Pharyngeal glands located from 4/5 to 6/7, not united dorsally; dorsal lobes present in IV–VI, ventral lobes present in V (2 pairs) and VI (2 pairs); no ventral lobes present in IV (Figure 4C). First pair of nephridia at 7/8. Dorsal blood vessel generally commencing in XIX–XXII, in one specimen in XVII. Chloragogen cells small (5–7 μm tall). Coelomocytes not observed. Sperm sac extending posteriorly from clitellum as far back as XIX, in most specimens to XV or XVI. Sperm funnels 25–35 μm wide at collar, tapering to 15–25 μm wide at other end, 4–5 times as long as wide. Heads of spermatozoa about 15 μm long. Vasa deferentia long, unmodified, loosely coiled posteriorly from XII to XIV; 6 μm wide, internally ciliated. Penial apparati (Figure 4D) with oval, uniform glandular structures, 120–155 μm long, 60–80 μm wide, extending through most of XII, surrounding epidermal invaginations at male pores, 20–30 μm in diameter, vasa deferentia opening into invaginations (Penial bulb type 2 or 3). Stylets absent. Egg sac extending as far back as XXI. Spermathecae (Figure 4E) attached to oesophagus near 5/6; ampullae roughly pear-shaped, 40–45 μm wide, ectal ducts narrow, 50–60 μm long, 10–15 μm wide, incising ampullae slightly; 5–10 sperm rings per spermatheca, 13–18 μm in diameter, located throughout ampullae; ectal glands on spermathecal ducts absent.

Remarks: When alive, this species is discernable from other *Grania* species by its distinct coloration. Whereas most other members of this genus are translucent or whitish in color, this species is brightly greenish yellow; this could, however, be the case for some other species as well, considering that the coloration is lost after fixation.

A spermathecal pore location at some distance from 4/5 has been described for some 15 species of *Grania* to date, mostly Atlantic, but also Western Australian (*G. vacivasa* Coates & Stacey, 1993) and Antarctic taxa (*G. algida* Rota & Erséus, 1996; *G. antarctica* Rota & Erséus, 1996). *Grania galbina* differs from all of the above, however, in the possession of large glandular masses surrounding the male pores, structures which resemble those of *G. postclitellochaeta* (Knöllner, 1935) (see Coates, 1984), with the difference of having more conspicuous epidermal invaginations at the male pores. This is a morphology resembling that in *G. fortunata* Rota & Erséus, 2003 and *G. hylae* Locke & Coates, 1999, both which are North Atlantic species. *Grania hylae*, however, possesses stylets, which is not the case in *G. galbina*. The spermathecal structure of *G. galbina* also resembles that of *G. fortunata* and *G. hylae*, but *G. galbina* differs from these two by its lack of a head organ and in the presence of a distinct heel at the base of the chaetae.

Etymology: From the Latin word *galbinus*, which translates into greenish yellow.

Distribution and habitat: Nouméa area, New Caledonia, and Lifou, Loyalty Islands, intertidal and subtidal (13 m), heterogeneous sand.

***Grania curta* sp.n.**
(Figure 5, Table 1)

Holotype: SMNH type coll. 6583, whole-mounted specimen from Lifou, stn. NC00-43.

Paratypes: SMNH type coll. 6584-6588, 5 whole-mounted specimens from type locality.

Description: Body 2.6–4.1 mm long (n=6), 0.16–0.18 mm wide at III, 0.17–0.20 mm at clitellum (n=6). Segment number 26–34 (n=6). Prostomium rounded, 65–75 μm wide, 50–60 μm long (n=6); epidermis 15–25 μm thick on occipital lobes, 15–20 μm on upper lip, 10–15 μm at front side (n=6). Peristomium 110–130 μm wide at 1/2 (n=6). Ventral chaetae commencing in IV, absent in XII; lateral chaetae commencing in XIII or XIV. Chaetae increasing in size posteriorly, 25–35 μm long in preclitellar segments, 45–65 μm long near posterior end (n=6); chaetae sharply pointed, proximal end curved, hook 5–13 μm long (Figure 5A). Epidermal

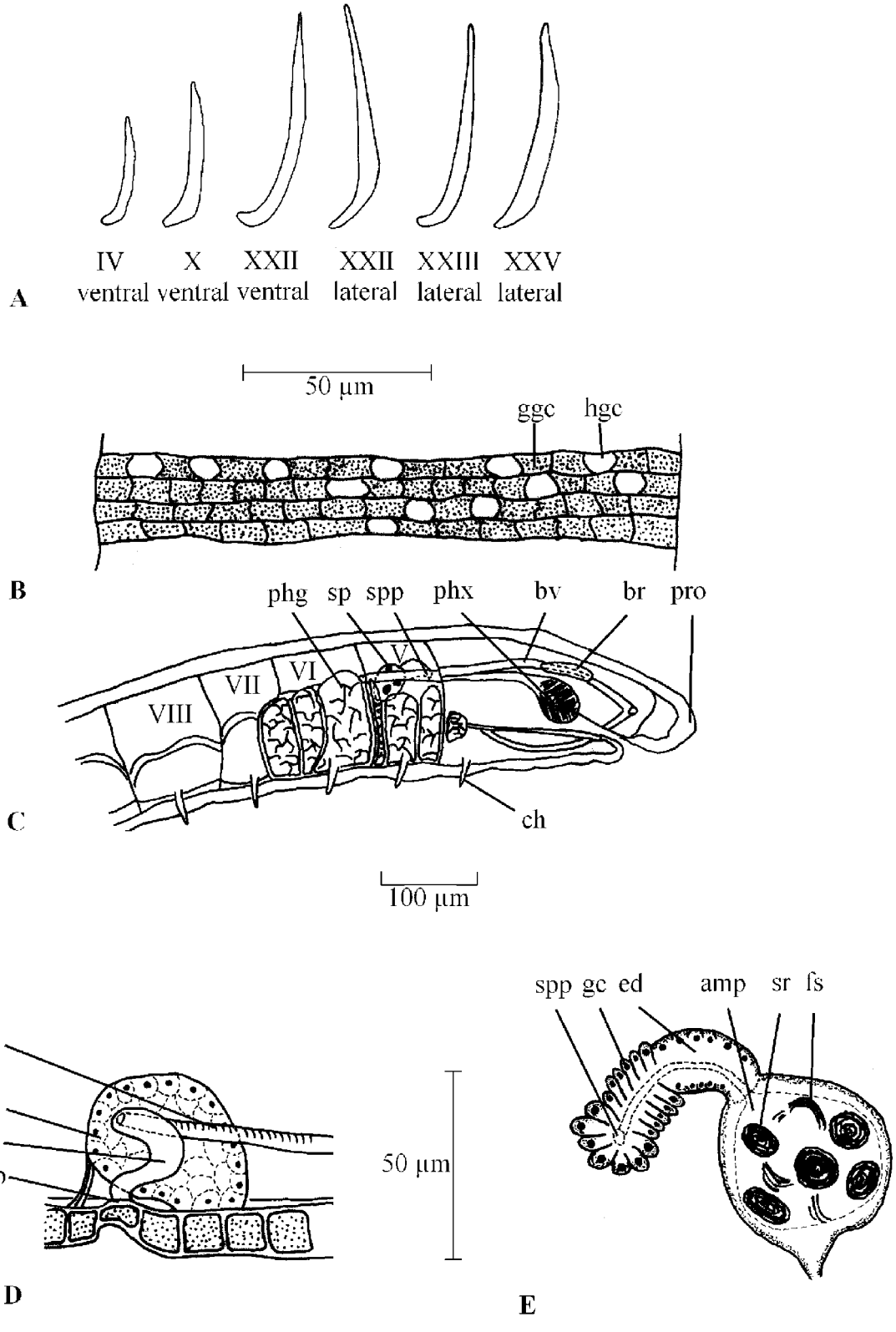


FIGURE 5. *Grania curta* **sp. n.**. A: Chaetae. B: Clitellar cell pattern. C: Overview of I– VIII. D: Penial apparatus. E: Spermatheca.

gland cells inconspicuous, interspersed irregularly. Clitellum 15–20 µm thick, starting at anterior end of XII and extending to chaetal position in XIII, consisting of transverse rows of granular gland cells irregularly interspersed with hyaline cells at a ratio of about 4–5:1 (Figure 5B), except around male pores where hyaline

cells are absent. “Copulatory glands” not observed in XIV. Spermathecal pores lateral, located immediately behind 4/5. Male pores located ventrolaterally in mid XII.

Brain in II–III**,** posteriorly indented in “head” region. Head organ absent. Pharyngeal glands located from 4/5 to 6/7, not united dorsally; dorsal lobes present in IV–VI, ventral lobes present in V (2 pairs) and VI (2 pairs), in VI ventrally pressing septum 6/7 as far back as chaetal position of VII); no ventral lobes present in IV (Figure 5C). First pair of nephridia at 7/8. Dorsal blood vessel commencing in XIV–XVI. Chloragogen cells small (5–7 μm tall). Coelomocytes not observed. Sperm sac extending posteriorly from clitellum as far back as XV. Sperm funnels bell-shaped, 65–70 μm wide at collar, 2 times as long as wide. Heads of spermatozoa about 20 μm long. Vasa deferentia long, loosely coiled in XII–XVI; 6 μm wide, internally ciliated. Penial apparati (Figure 5D) with oval glandular structures, 35–45 μm long, 25–30 μm wide, vasa deferentia opening into epidermal invagination from male pores (Penial bulb type 3). Stylets absent. Egg sac extending to XVI. Spermathecae (Figure 5E) attached to oesophagus near 5/6; ampullae roughly spherical, 50–55 μm in diameter, ectal ducts bipartite, ental part uniformly 15 μm wide, 20 μm long, ectal part covered by glandular cells, 20–25 μm long; somewhat larger glandular cells also surrounding spermathecal pores; sperm present freely in ampullae as well as in rings; 4–8 sperm rings per spermatheca, 13–18 μm in diameter, located throughout ampullae.

Etymology: *Curta* is a Latin word meaning “too short” or “mutilated”. This refers to the short, stubby body shape of this species.

Remarks: This is one of the shortest species of *Grania* described up to date. Other short taxa, such as *G. papillinasus* Rota & Erséus, 2003, from the Atlantic deep sea, are typically also thin (and thus slender), but this is not the case in *G. curta*, which gives an impression of it being mutilated. However, as the appearance (also of the pygidium) is similar in all observed specimens, the specimens are most likely intact. The peculiar spermathecal ectal duct structure, with glandular cells covering the ectal part of the duct, is similar to that of *G. cinctura* **sp.n.**, with the difference that in *G. curta* the spermathecal pores are also surrounded by glandular cells. This kind of gland arrangement along the spermathecal ectal duct is similar to what has been described in *G. parvitheca* Erséus, 1980, a South Atlantic species. However, while in *G. curta* and *G. cinctura* the ectal duct is bipartite, with the ental part lacking glandular cells, in *G. parvitheca* the entire duct is covered by such cells.

Distribution and habitat: Loyalty Islands, New Caledonia, shallow subtidal (0.5 m), heterogeneous sand.

***Grania fustata* sp.n.**
(Figure 6, Table 1)

Holotype: SMNH type coll. 6589, whole-mounted specimen from Touho, stn. NC93-9.

Paratypes: SMNH type coll. 6590-6598, 9 whole-mounted specimens from Touho, 4 of which from stn. NC93-8, 2 from type locality, and 3 from stn. NC93-10.

Other material examined: SMNH main coll. 87982-87999, 18 specimens from Touho (type locality, and stns. NC93-8 and NC93-10).

Description of type material: Body 12.1–15.3 mm long (n=10), 0.25–0.28 mm wide at III, 0.24–0.27 mm at clitellum (n=10). Segment number 61–71 (n=10). Prostomium rounded, 120–140 μm wide, 65–85 μm long (n=10); epidermis 25–28 μm thick on occipital lobes, 18–23 on upper lip, 8–13 μm at front side (n=9). Peristomium 205–225 μm wide at 1/2 (n=10). Ventral chaetae commencing in V, absent in XII; lateral chaetae commencing in XXII–XXIV. Chaetae stout, of uniform size throughout body, 100–140 μm long (n=16); chaetae L-shaped, sharply pointed, foot 20–33 μm long, with slight heel (chaetal index=4.54, n=16, sd=0.67) (Figure 6A). Epidermal gland cells inconspicuous, interspersed irregularly. Clitellum 20–25 μm thick, starting at

anterior of XII and extending to chaetal position of XIII, consisting of uneven transverse rows of granular gland cells irregularly interspersed with smaller hyaline cells at a ratio of around 2:1 (Figure 6B) except around male pores where hyaline cells are absent. “Copulatory glands” present ventrally in XIV. Spermathecal pores lateral, located immediately posterior to 4/5. Male pores ventrolateral in XII.

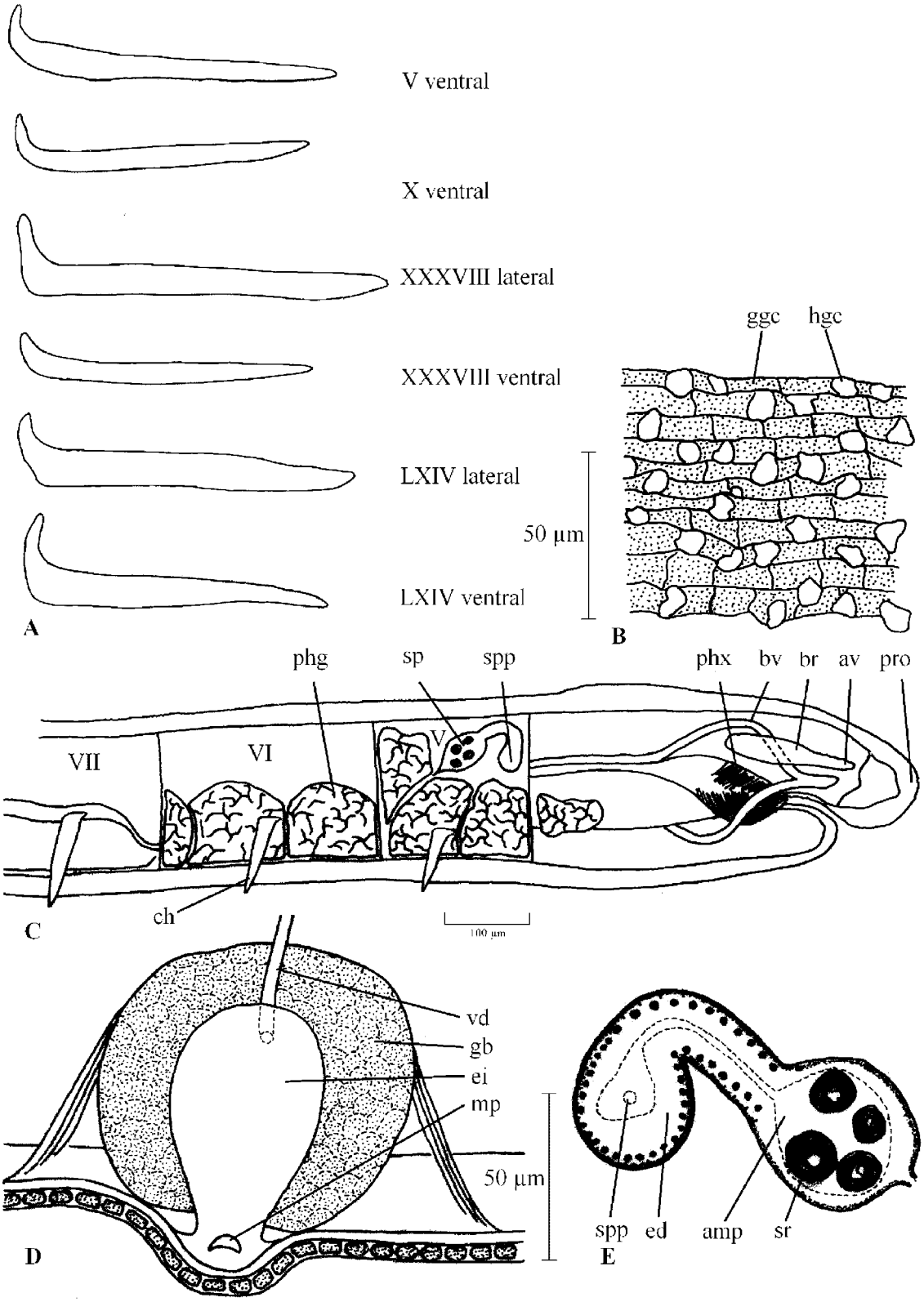


FIGURE 6. *Grania fustata* **sp. n.**. A: Chaetae. B: Clitellar cell pattern. C: Overview of I– VII. D: Penial apparatus. E: Spermatheca.

Brain in II–III, posteriorly indented in "head" region. No true "head organ" present, but bilobed vesicle present immediately behind 0/1, dorsal to the anterior furcation of blood vessel, between circumpharyngeal commissures; no inclusions present, but hollow compartments visible which seem to be internally ciliated. Pharyngeal glands located from 4/5 to 6/7, not united dorsally; dorsal lobes present in IV–VI, ventral lobes present in IV (1 pair), V (2 pairs) and VI (2 pairs) (Figure 6C). First pair of nephridia at 7/8. Dorsal blood vessel commencing in XXVI–XXIX (n=10). Chloragogen cells small (extending 5–7 μm above gut wall). Coelomocytes abundant, flattened, circular to slightly oval in shape with irregular surfaces, about 15 μm in diameter, granular with stained nuclei. Sperm sac extending posteriorly from clitellum as far back as XXI. Sperm funnels of uniform width, 50–60 μm, 3 times as long as wide. Heads of spermatozoa about 15–17 μm long. Vasa deferentia long, loosely coiled in XII and XIII, 5 μm wide, internally ciliated. Penial apparati (Figure 6D) granulated oval structures, 80–95 μm long, 50–70 μm wide, each consisting of glandular body surrounding invagination of epidermal tissue at male pore; epidermal invagination forming large aglandular sac 15–20 μm wide, 70–90 μm deep (penial bulb type 3). Stylets absent. Egg sac extending as far back as XXI–XXIV. Spermathecal ampullae (Figure 6E) rounded, 50–55 μm in diameter, ectal ducts bipartite, with ental parts cylindrical, 35–40 μm long and 10–15 μm wide, ectal ends bulbous, 25–30 μm thick at widest point; 4–5 sperm rings per spermatheca, 10–20 μm in diameter, located throughout ampullae; ectal glands on spermathecal ducts absent.

Etymology: Named using the Latin word *fustus* and the suffix *–ata*, which translates into "armed with a club". This refers to *G. fustata* being equipped with penial bulbs with large aglandular sacs which are often everted in mounted specimens.

Remarks: The shape of the spermathecal ectal duct of *G. fustata*, with a bulbous ectal part and a narrow ental part, is rather unusual in this genus. A similar feature has been described for *G. laxarta* Locke & Coates, 1990, known from the Atlantic waters of Bermuda and Belize. *Grania fustata* is different from *G. laxarta*, however, in that its penial bulbs lack stylets, but rather have large epidermal invaginations at the male pores.

As in *G. novacaledonia* **sp.n.** and *G. cinctura* **sp.n.**, *G. fustata* possesses a bilobed vesicle anterior to the brain which contains hollow compartments, but no inclusions as a head organ proper would have (see Remarks under *G. novacaledonia*; and Discussion). Other characters shared with *G. cinctura* are the bipartite spermathecal ectal ducts, and the large size, although *G. fustata* clearly is the larger of the two. *Grania fustata* also differs from *G. cinctura* in lacking glandular cells around the spermathecal ectal duct, and in the larger size of the epidermal invaginations at the male pores.

Distribution and habitat: Touho area, New Caledonia, lower intertidal to barely subtidal, heterogeneous sand.

***Grania papillata* sp.n.**
(Figure 7–8, Table 1)

Holotype: SMNH type coll. 6599, whole-mounted specimen from Lifou, stn. NC00-35.

Paratypes: SMNH type coll. 6600-6602, 3 whole-mounted specimens from Lifou, 1 of which from stn. NC00-12 and 2 from stn. NC00-25; SMNH type coll. 6603-6606, 6608-6609, 6 whole-mounted specimens from Touho, 2 of which from stn. NC93-50 and 1 each from stns. NC93-37, NC93-54, NC93-59 and NC93-61.

Other material examined: SMNH main coll. 88001-88003, 3 specimens from Lifou (type locality and stn. NC00-25); SMNH main coll. 88004-88076, 73 specimens from Touho (stns. NC93-23, NC93-24, NC93-31, NC93-33, NC93-34, NC93-37, NC93-50, NC93-53, NC93-54, NC93-55, NC93-56, NC93-59, NC93-60, NC93-62, NC93-69, NC93-70, NC93-72, NC93-73).

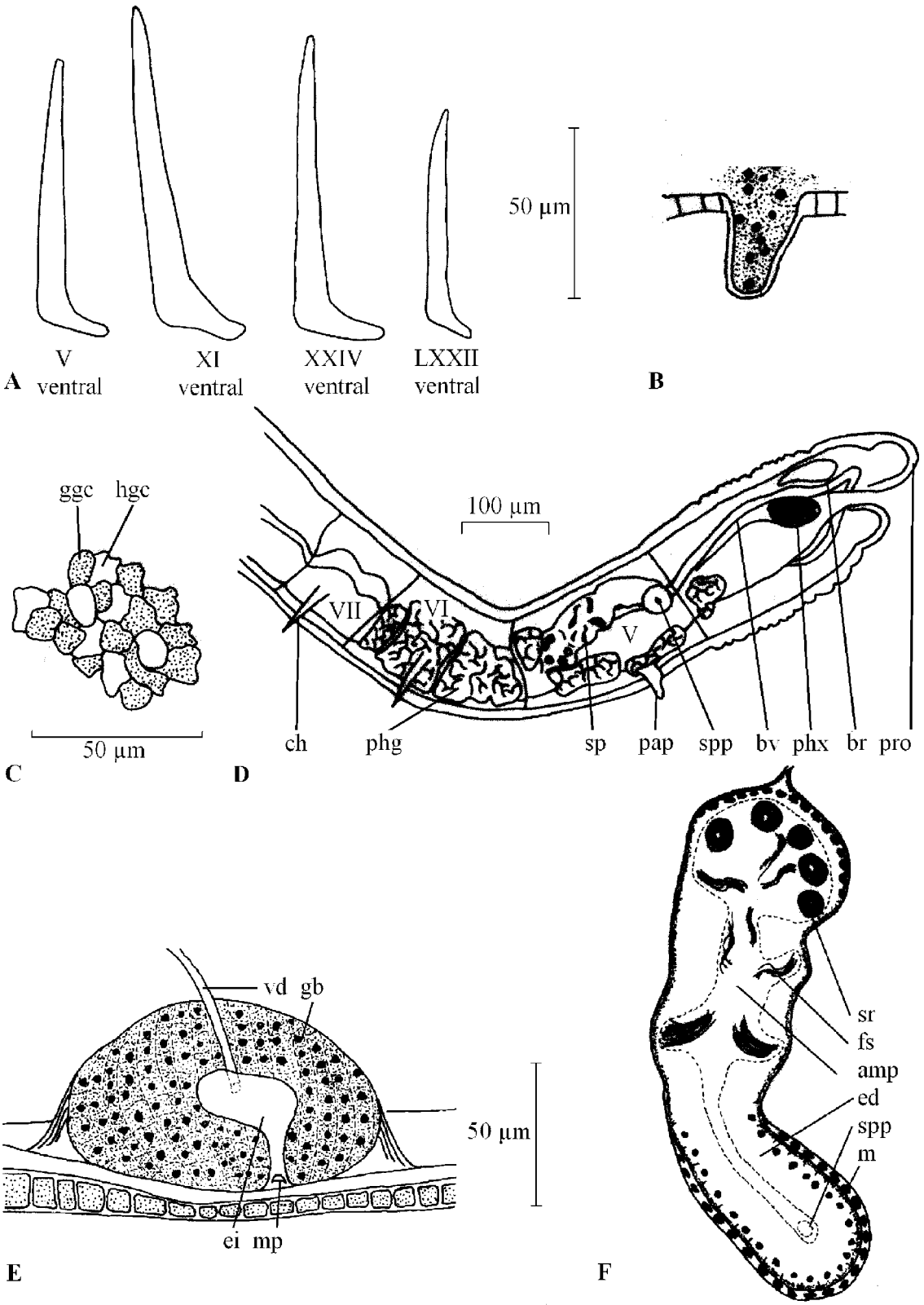


FIGURE 7. *Grania papillata* **sp. n.**. A: Chaetae. B: Clitellar cell pattern. C: Epidermal papilla in V. D: Overview of I–VII. E: Penial apparatus. F: Spermatheca.

Description of type material: Body 9.4–13.1 mm long (n=10), 0.16–0.20 mm wide at III, 0.17–0.22 mm at clitellum (n=10). Segment number 62–82 (n=10). Prostomium rounded, 75–110 µm wide, 55–80 µm long (n=10); epidermis 17–25 µm thick on occipital lobes and upper lip (n=7), 8–20 µm thick at front side (n=10).

Peristomium 133–185 μm wide at 1/2 (n=10). Ventral chaetae commencing in V, absent in XII; laterals completely absent. Preclitellar chaetae 60–80 μm long, post-clitellar chaetae of uniform length, 85–100 μm long (n=16); chaetae L-shaped with distinct heel, sharply pointed, foot 20–25 μm long (chaetal index=3.40, n=16, sd=0.25) (Figure 7A). A pair of conspicuous body wall papillae present ventrolaterally in mid-V in all specimens, extending 35–45 μm from epidermis, 15–20 μm wide at base (Figures 7B; 8). Epidermal gland cells conspicuous in I–IV only, interspersed irregularly. Clitellum 10–23 μm thick, starting at anterior end of XII and extending to chaetal position of XIII, consisting of granular gland cells interspersed irregularly with hyaline cells at a ratio of about 2:1 (Figure 7C), except around male pores where hyaline cells are absent, only forming regular rows at anterior and posterior end of clitellum. "Copulatory glands" not observed in XIV. Spermathecal pores lateral, immediately behind 4/5. Male pore ventrolateral in mid XII.

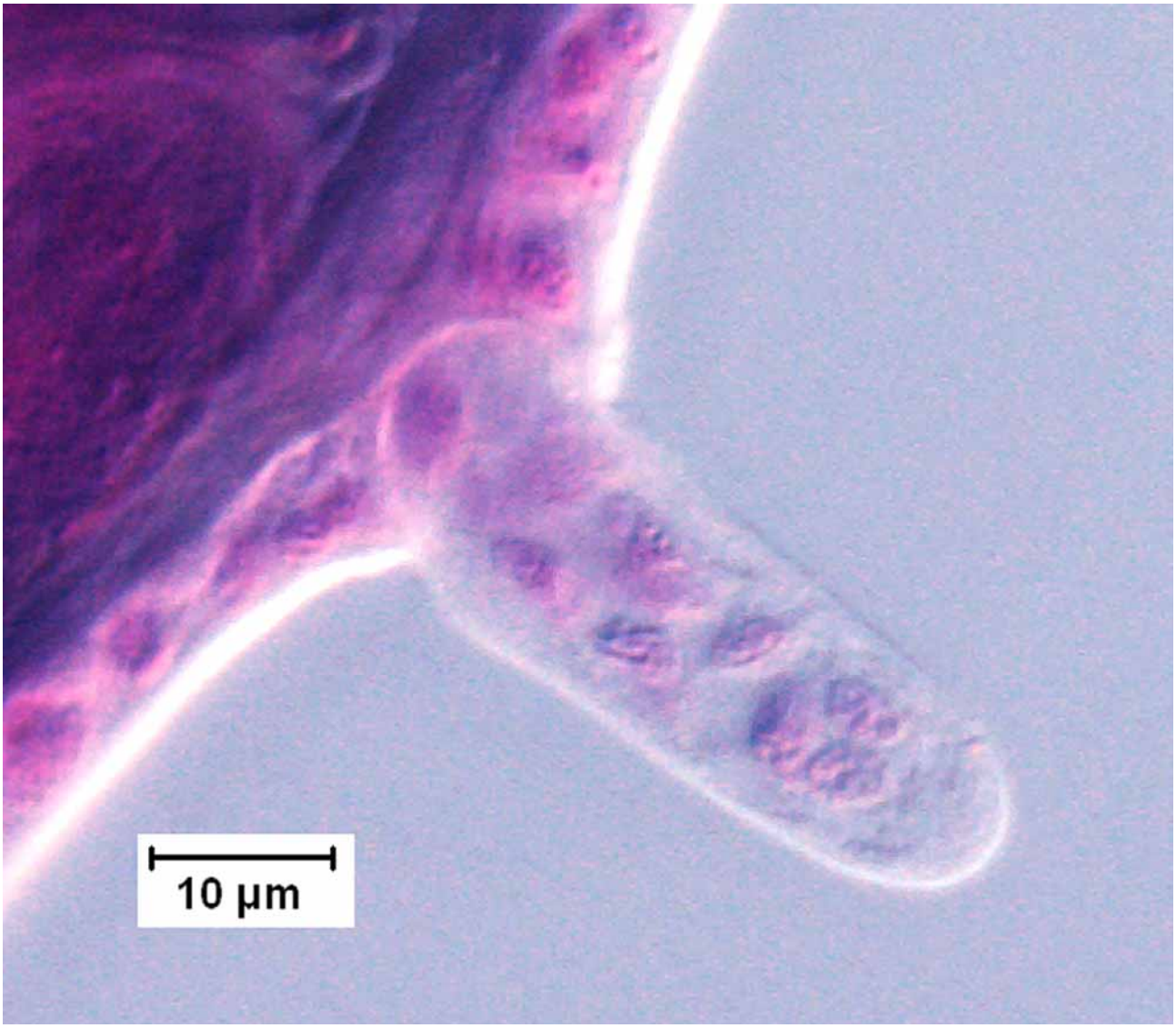


FIGURE 8. Interference contrast microscopy photo of epidermal papilla of *G. papillata* **sp. n.**.

Brain in II–III, posteriorly indented in "head" region. Head organ absent. Pharyngeal glands located from 4/5 to 6/7, not united dorsally; dorsal lobes present in IV–VI, ventral lobes present in IV (1 pair), V (2 pairs) and VI (2 pairs); ventral lobes in V compressed ventrally (Figure 7D). First pair of nephridia at 7/8. Dorsal blood vessel commencing in XXXVIII–XLII (n=7). Chloragogen cells small (5–7 μm tall). Coelomocytes abundant, oval (10–12 μm long), cytoplasm coarsely granular, nuclei unstained. Sperm sac extending posteriorly from clitellum as far back as XIX. Sperm funnels of uniform width, 40–60 μm wide, 4–5 times as long as

wide. Heads of spermatozoa 20 μm long. Vasa deferentia long, loosely coiled posteriorly from XII to XV–XVIII; 7 μm wide, internally ciliated. Penial apparati (Figure 7E) with oval, uniform glandular structures, 100–120 μm long, 65–85 μm wide, surrounding smaller, sac-like invaginations of epidermis at male pores, 10 μm wide, 60–70 μm deep (Penial bulb type 3). Stylets absent. Egg sac ending as far back as XXIII. Spermathecae (Figure 7F) large, attached to oesophagus near 5/6; ampullae, sac-like, 75–120 μm long, 50–70 μm wide, lumen funnel-shaped at ectal end; ectal ducts thick-walled and covered by muscle cells, uniform in diameter (30–45 μm), 60–80 μm long; 4–7 sperm rings per spermatheca, 13–18 μm in diameter, located in inner end of ampullae, as well as large bundles of spermatozoa in free form throughout ampullae; ectal glands on spermathecal ducts absent.

Etymology: Named after the characteristic papillae in segment V, which have only been observed in this species.

Remarks: This species is easily distinguished from all members of this genus described to date by the paired ventrolateral papillae in V (Figure 8). These papillae do not seem to be attached to any muscle tissue internally, nor do they seem to be connected to any glandular tissue (see Discussion). The spermathecae which fill almost all of V are also unique to this species and are very easy to identify with their large, sac-like ampullae and muscular ectal ducts. Muscular ectal ducts have been described previously, in *G. longiducta* Erséus & Lasserre 1976, but in that species they are long and narrow, while in *G. papillata* the ectal ducts are much wider and shorter. *Grania papillata* can also be discerned from other members of this genus in that its vas deferens is coiled as far back as XVIII, and the egg sac stretches as far as XXIII, which has previously only been reported for a few North and West Australian *Grania* species (*G. vacivasa* Coates & Stacey, 1993, *G. conjuncta* Coates & Stacey, 1993, *G. eurystila* Coates & Stacey, 1997 and *G. integra* Coates & Stacey, 1997).

The dorsal blood vessel location is interesting in that it commences further back (XXXVII–XLII) than has been reported for most species of the genus. The only instance where something similar has been noted is in *G. dolichura* Rota & Erséus, 2000, a Tasmanian species, in which the dorsal blood vessel commences in XXXVIII–LXXVIII. Furthermore, *G. papillata* possesses large epidermal cells in I–IV, creating an uneven body surface in these segments. This is not the case for any other species described in this paper, but it resembles a species described from Tasmania, *G. dolichura* Rota & Erséus, 2003. The structure of *G. papillata*'s clitellum also suggests a relationship with the Tasmanian species, since the irregular form is unique in the New Caledonian taxa, yet shared with *G. tasmaniae***,** as well as with *G. antarctica* Rota & Erséus, 1996, *G. carchinii* and *G. hirsuticauda*, all from Antarctic waters.

Distribution and habitat: Touho area, New Caledonia, and Lifou, Loyalty Islands, lower intertidal and subtidal (22 m), heterogeneous sand.

***Grania fiscellata* sp.n.**
(Figure 9, Table 1)

Holotype: SMNH type coll. 6610, whole-mounted (incomplete) specimen from Touho, stn. NC93-66.

Paratypes: SMNH type coll. 6611-6613, 3 mounted specimens (2 of which are incomplete) from Touho, stn. NC93-25; SMNH type coll. 6617, whole-mounted specimen from Lifou, stn. NC00-36.

Description: Body 3.4 mm long (n=1), 0.11–0.12 mm wide at III, 0.10–0.12 mm at clitellum (n=3). Segment number 42 in the only complete specimen. Prostomium rounded**,** 55–65 μm wide, 35–45 μm long (n=3); epidermis 8–20 μm thick on occipital lobes and upper lip, 5–10 μm at front side (n=3). Peristomium 90–100 μm wide at 1/2 (n=3). Ventral chaetae commencing in IV; lateral chaetae commencing in XIV–XV. Chaetae of uniform size throughout body, 40–45 μm long (n=4); chaetae sharply pointed, entally curved into a hook 8–10 μm long (Figure 9A). Epidermal gland cells inconspicuous, interspersed irregularly. Clitellum 15–25 μm thick, starting at anterior of XII and extending to chaetal position of XIII, consisting of transverse rows of

granular gland cells interspersed with hyaline cells at a ratio of about 4:1 (Figure 9B), except around male pores where hyaline cells are absent. “Copulatory glands” not observed in XIV. Spermathecal pores lateral, located right behind 4/5. Male pores located ventrolaterally in mid XII.

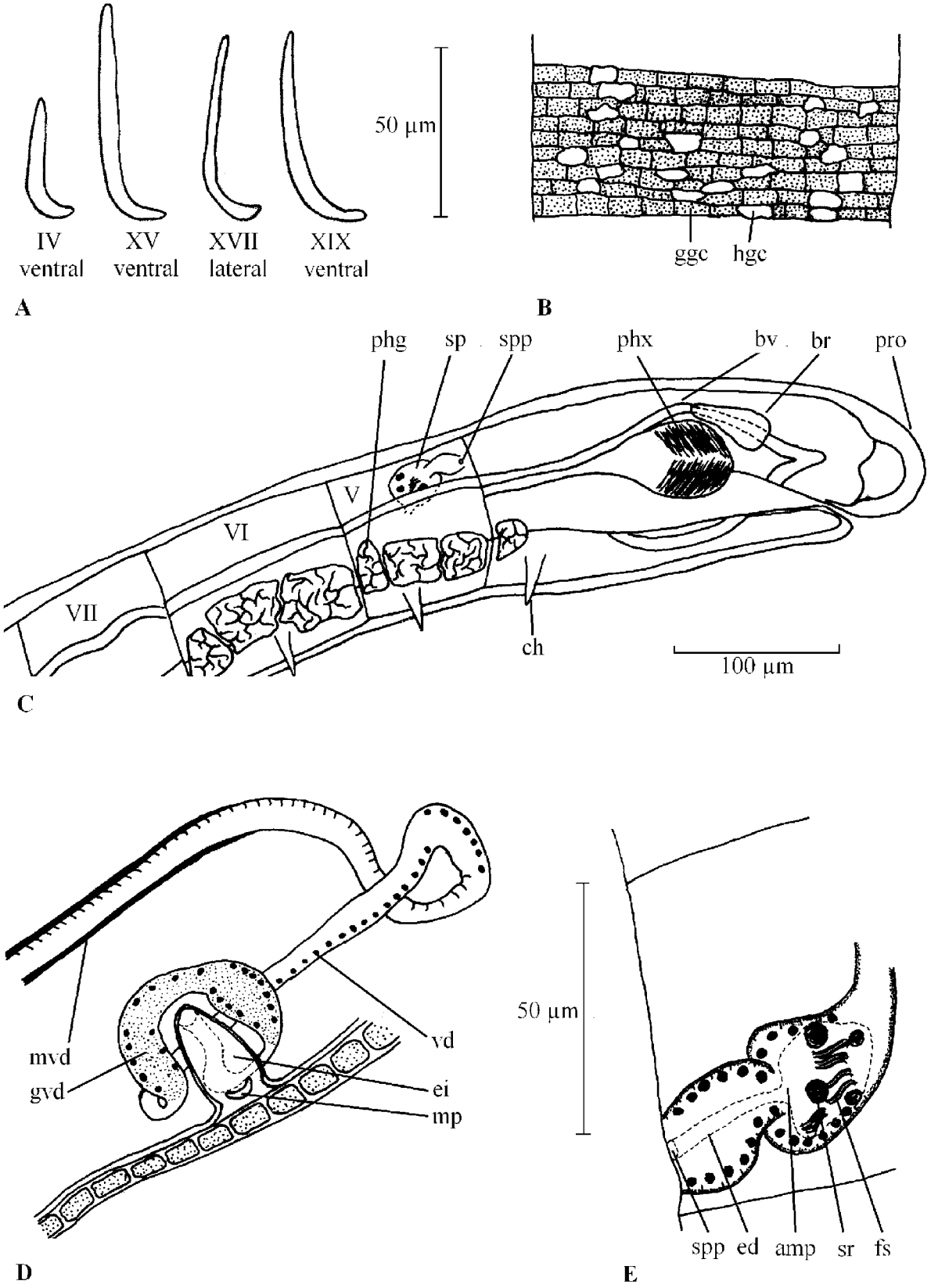


FIGURE 9. *Grania fiscellata* **sp. n.**. A: Chaetae. B: Clitellar cell pattern. C: Overview of I–VII. D: Penial apparatus. E: Spermatheca.

Brain in II–III, posteriorly indented in "head" region. Head organ absent. Pharyngeal glands located from 4/5 to 6/7, not united dorsally; dorsal lobes present in IV–VI, ventral lobes present in V (2 pairs) and VI (2 pairs); no ventral lobes in IV (Figure 9C). First pair of nephridia at 7/8. Dorsal blood vessel commencing in XVI (visible in one specimen only). Chloragogen cells small (5–7 μm tall). Coelomocytes abundant, slightly oval, flattened, granular with irregular surface, about 10 μm wide at the widest point. Sperm sac extending posteriorly to XIII or XIV. Sperm funnels of uniform width, 15–25 μm, 3–4 times as long as wide. Heads of spermatozoa about 8–10 μm long. Vasa deferentia in XII, strongly muscularized entally, 6–7 μm wide. Penial apparati (Figure 9D) consisting of a glandular widening of the most ectal end of vas deferens (diameter 9–10 μm), which is curved around, and attached to, a small aglandular invagination of epidermal tissue from male pore, 20–30 μm deep, 5–10 μm wide (Penial bulb type 6, without stylet). Stylets absent. Egg sac extending as far back as XIX. Spermathecal ectal ducts bulbous, about 15 μm wide at widest point, projecting slightly into ampullae, ampullae pear-shaped, 20-25 μm wide, 25–30 μm long, connected to gut in middle of V, sperm existing in ampullae both in loose form in the lumen and as small sperm rings embedded in walls, 3–5 μm in diameter; ectal glands on spermathecal ducts absent (Figure 9E).

Etymology: *Fiscella* is a Latin word for a small basket, and *–ata* translates into "equipped with", indicating that this species indeed is equipped with a small basket, i.e. spermatheca.

Remarks: A spermathecal connection to the gut in mid V is unusual in *Grania*. It has hitherto been described in 7 species, which include a few species from Hong Kong (*G. hongkongensis* Erséus, 1990, *G. inermis* Erséus, 1990 and *G. stilifera* Erséus, 1990) and also, interestingly enough, *G. mira* Locke & Coates, 1998 (see below).

The male genital system of *G. fiscellata* is different from that of most other species of *Grania* in that it has a thick and muscularized vas deferens and a reduced gland at the male pore, yet it bears no stylet. Thus, the penial apparatus of this species does not fit any of the penial bulb types defined by Coates (1984). Some muscular modifications of the vas deferens in conjunction with a penial bulb of this shape has been described in several species, e.g. *G. mira*, *G. canaria* Rota & Erséus, 2003, *G. fortunata* Rota & Erséus, 2003 and *G. aquitana* Rota & Erséus, 2003, but *G. mira*, an Irish taxon, is the only species with vasa deferentia that are muscularized throughout as well as small epidermal invaginations, and at the same time the species lacks penial stylets.

The peculiar widening of the vas deferens forming a curved structure around the male pore resembles a glandular penial bulb in low magnification; the vas deferens is rather coiled which makes it very difficult to follow. However, at high magnification it becomes clear that the vas deferens is glandular while a separate glandular bulb is absent, which to date is a feature unique to *G. fiscellata*.

Distribution and habitat: Touho area, New Caledonia, and Lifou, Loyalty Islands, lower intertidal and shallow subtidal (3 m), heterogeneous sand.

Discussion

Epidermal papillae

The unique epidermal papillae of *G. papillata* **sp.n.** are intriguing, as their function is unknown. They are not connected to any glandular tissue, so a secretory function is unlikely. Their position ventrolaterally in mid V, however, suggests that they might have a function in copulation. A sensory function is possible, and could be associated with copulation as well as with locomotion. The papillae seem to consist of epidermal tissue which projects through the thick cuticle of the surrounding body wall, and must be vulnerable to abrasion. Interestingly, they do not seem to be associated with any muscle tissue, in which case they are probably not retractable. How they manage to exist without being torn off is an issue worth further study. A possible explanation would be that these structures are internal and only become projected outward at fixation, but to investigate this, *in vivo* studies of the species are necessary.

Apparent lack of coelomocytes

An issue to be raised here is the apparent lack of coelomocytes in some of the New Caledonian species. It is possible that this is an artifact from fixation (ejection of all coelomocytes upon contact with fixative) or the staining procedure, and that these species in fact do possess coelomocytes. Within the material studied, coelomocytes are never present in some individuals and absent in the others of the same species, however, which strengthens the argument that this is an intrinsic character of the species. If this is indeed the case, it would suggest a phylogenetic affinity to Antarctic species, for which this has also been mentioned (*G. carchinii* Rota & Erséus, 1996 and *G. algida* Rota & Erséus, 1996). Coelomocytes are rarely noted in older literature on *Grania*, which makes it difficult to conclude that lack of coelomocytes is unique to a few species only, but a common origin of New Caledonian, Australian and Antarctic species is feasible, considering that New Caledonia is a continental Australian island, and as such was connected to Antarctica as late as 33 million years ago (Kennett *et al.*, 1975).

Anterior vesicles

The compartments found anterior to the brain of three of the new species (*G. novacaledonia*, *G. cinctura* and *G. fustata*) are interesting, since they might be homologous to the "head organ" or statocyst found in some *Grania* species, an organ thought to be a georeceptor (Rota & Erséus, 1996; Rota *et al.*, 1999; Locke, 2000). With the lack of inclusions, however, it cannot function as such. As mentioned earlier (remarks under *G. novacaledonia*), this feature has been noted in descriptions of *G. monochaeta* and *G. aquitana*, which are found in the South and North Atlantic, respectively. Neither of the articles describing these features goes into any length discussing the possibility of this being a structure analogous to the head organ, rather they assume homology (Rota & Erséus, 1997, 2003). Rota *et al.* (1999) noted that a possible hypothesis could be that some cerebral cells have migrated forward to be organized as an independent structure, and *G. maricola* was mentioned as an intermediary form with vesicles but no inclusions. The ultrastructure of the head organ has been studied by Rota *et al.* (1999) and Locke (2000); it would also be interesting to study the empty compartments reported in the literature and in the present study under an electron microscope to confirm similarity to the true head organs.

Upon re-examination of *Grania* species found in Sweden, we found structures indicating that anterior vesicles also exist in *G. pusilla* Erséus, 1974, *G. variochaeta* Erséus & Lasserre, 1976 and *G. vikinga* Rota & Erséus, 2003, neither of which contain any inclusions. The presence of an anterior vesicle in *G. maricola* Southern, 1913 (Rota *et al.*, 1999), which is the type species of *Grania* was also re-confirmed (De Wit, *personal observation*). The structure was found in many, but not all *Grania* species re-examined, possibly making this a useful diagnostic character phylogenetically (in this study, only *G. cinctura*, *G. fustata* and *G. novacaledonia* possess the anterior vesicle). Re-examinations of species from other locations are needed before any conclusions can be made regarding how wide-spread the vesicle is within the genus.

As mentioned above, it is possible that some New Caledonian species are related to Antarctic and Australian species of *Grania*. All but one of the Antarctic species possess head organs; *Grania carchinii* Rota & Erséus, 1996, instead possesses "in corresponding position, an oval swelling with no inclusions and of same fibrous appearance as the circumpharyngeal connectives running on its sides" (Rota & Erséus, 1996, p. 175). This might be a similar structure to the anterior vesicles described in this paper, but a re-examination is needed for confirmation. Unfortunately, the few descriptions of species in the neighbouring regions of the South China Sea and the Great Barrier Reef (*G. hongkongensis* Erséus, 1990 and *G. trichaeta* Jamieson, 1977) lack this diagnostic feature, making a comparison difficult.

Biogeography

There are other indications of a possible Australian and Antarctic affinity of the New Caledonian *Grania* species. For instance, *G. galbina* has its spermathecal pores located distinctly posterior to the 4/5 septum,

which is a character also found in the Antarctic species *G. antarctica* and *G. algida*. Furthermore, the penial bulb morphology is similar in Antarctic species (see Rota & Erséus, 1996) and most of the taxa described in this paper (type 3 *sensu* Coates, 1984). This feature is also shared with *G. trichaeta*, the only *Grania* species described from the Great Barrier Reef.

Grania papillata shares some unusual features with Tasmanian species (see Rota & Erséus, 2000), such as the large anterior epidermal cells also present in *G. dolichura*, the posterior commencement of the dorsal blood vessel (as in *G. dolichura*), and the irregular pattern of the clitellum (as in *G. tasmaniae*). *Grania papillata* also shares the posterior placement of the egg sac with species described from Darwin (North Australia), and Rottnest Island (Western Australia) (Coates & Stacey, 1993; 1997).

The tropical position of New Caledonia in the South Pacific predicts that elements in its oligochaete fauna have phylogenetic links with the rest of the west Indo-Pacific region. So far, little is known about the *Grania* fauna of Eastern Australia, including the Great Barrier Reef, but it is possible that taxa similar to the species described herein could be found there, as well as in the immense regions of Indonesia, Papua New Guinea, and Polynesia.

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