

***Grania ocarina* sp. n., *G. darwinensis* (Coates and Stacey) comb. n., and other marine Enchytraeidae (Oligochaeta) from the Dampier area, Western Australia**

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Abstract – The study reports on four species of marine Enchytraeidae collected from intertidal and subtidal sites (down to 16 m) near the town of Dampier and in the Dampier Archipelago, in northern Western Australia. One species, *Grania ocarina*, is new to science. It is diagnosed by its unique chaetal distribution (preclitellar chaetae present only ventrally from V to VIII), complex penial apparatus endowed with unusually broad cylindrical penial stylets, and the characteristic ocarina-shaped ectal ducts of its spermathecae. The descriptions of *Grania integra* Coates and Stacey, 1997 and *Randidrilus darwinensis* Coates and Stacey, 1997, previously known only from Darwin Harbour, Northern Territory, Australia, are augmented, and the habitat range of the latter is expanded to include subtidal sediments at 16 m depth. The taxonomy of *Randidrilus* Coates and Erséus, 1985 is reviewed to justify the present reallocation of *R. darwinensis* in *Grania*. Only the fourth species recorded, the intertidal *Marionina coatesae* Erséus, 1990, is known to occur outside Australia.

Key words: Marine Oligocheta, Enchytraeidae, taxonomy, new species, *Grania*, *Randidrilus*, *Marionina*

INTRODUCTION

Previous studies of the Australian marine Enchytraeidae were based on material from the west and the southwest (Albany area: Michaelsen, 1907; Coates, 1990; Rottnest Island: Coates and Stacey, 1993), the northern coast (Darwin Harbour: Coates and Stacey, 1997; Healy and Coates, 1997), the Great Barrier Reef (Jamieson, 1977), and Tasmania (Rota and Erséus, 2000). The present paper describes taxa collected near the town of Dampier and in the Dampier Archipelago, in northern Western Australia. The sampling was carried out during a biodiversity

inventory organised by the Western Australian Museum, aiming to promote the conservation of this coastal area.

MATERIAL AND METHODS

A range of intertidal and shallow-water subtidal sites in the Dampier area were visited by the third author. At each station, a sediment sample of on average a few litres was collected by hand. Each sample was repeatedly (four times or more) stirred in seawater in a bucket, and the suspensions of organic material thus obtained were decanted into a 0.25 mm sieve, after which the sieved material was brought live into the laboratory for further examination. Ninety-four sexually mature enchytraeids, present in nine of the samples, were sorted out under a dissecting microscope. The worms were fixed in Bouin's fluid for one or two days and then transferred into 80% ethanol. An additional enchytraeid specimen was sorted from a subtidal sediment sample (included in list below) collected by a SCUBA diver (Mr. Clay Bryce) and preserved *in toto* in formalin. Later, the individuals were all stained in alcoholic paracarmine, dehydrated and cleared through an ethanol/xylene series and mounted whole in Canada balsam. All morphological studies reported herein were performed on these mounted specimens using light transmission and interference contrast microscopy.

In the descriptions, specific segments are referred to by Roman numerals. Segment counts include the peristomium (segment I). Measurements were obtained by using an eyepiece micrometer. The length of the chaetal shaft was measured in a straight line from the distal tip to the furthest proximal point. The length of the ental hook (or foot) is meant as the projection of the maximal breadth of the chaeta at its ental end. The "chaetal index" (Rota and Erséus, *in press*), used to discriminate between different types of L-shaped chaetae, expresses the average ratio between the total chaetal length and the foot length (average calculated on *n* chaetae). The length of the glandular bulbs in the penial apparatus was measured as their extension parallel to the longitudinal axis of the body. Figures were drawn with the aid of a camera lucida.

Types and other reference material are deposited in the Western Australian Museum (WAM), Perth, the Swedish Museum of Natural History (SMNH), Stockholm and the Museo Civico di Zoologia di Roma (MCZR), Italy.

LIST OF STATIONS

All stations were in the vicinity of Dampier, Western Australia. The oligochaete species found at each station are listed too (including members of Tubificidae, in parentheses, reported separately by Erséus and Wang, 2003).

- DP00-2. Burrup Peninsula, Withnell Bay, SW of mangroves; medium sand, lower intertidal; 20°35'S, 116°47'E; 3 August 2000. *Grania ocarina* sp.n. (*Heterodrilus devexus*, *Olavius clavatus*.)
- DP00-4. Dampier, W of Hamersley Cottages and Western Australian Laboratory of Australian Institute of Marine Science, rocky area; medium to coarse sand, lower intertidal; 20°39'S, 116°43'E; 4 August 2000. *Grania darwinensis*. (*Heterodrilus devexus*.)
- DP00-5A. E part of Nickol Bay, E of Cleaverville, rocky platform, intertidal pool; medium to coarse sands, lower intertidal; 20°40'S, 117°03'E; 5 August 2000. *Grania ocarina* sp.n. (*Heterodrilus decipiens*, *H. devexus*, *H. carinatus*.)

- DP00-8C. W end of Dampier Archipelago, near Cape Preston, N of Sand Pit, rocky area; medium to coarse sand with black silt among or underneath rocks, lower intertidal; 20°56'S, 116°19'E; 6 August 2000. *Grania darwinensis*. (*Heterodrilus devexus*, *Limnodriloides armatus*, *Smithsonidrilus grandiculus*, *S. edgari*.)
- DP00-11C. Nickol Bay, Karratha Beach, rocky area; clay with medium to coarse sand, lower intertidal; 20°44'S, 116°54'E; 7 August 2000. *Grania darwinensis*. (*Duridrilus piger*, *Heronidrilus* cf. *gravidus*, *Limnodriloides armatus*.)
- DP00-14B. Nickol Bay, E side of Burrup Peninsula, Watering Cove, N rocky platform; heterogeneous sand with silt, lower intertidal pool; 20°36'S, 116°48'E; 8 August 2000. *Grania integra*. (*Heronidrilus* cf. *gravidus*.)
- DP00-14C. Nickol Bay, E side of Burrup Peninsula, N of Watering Cove, near mangrove trees; yellow clay with fine to medium sand, upper intertidal; 20°36'S, 116°48'E; 8 August 2000. *Marionina coatesae*.
- DP00-16A. Dampier, NW of shopping center, rocky area; medium to coarse sand, barely subtidal, 0.5 m; 20°39'S, 116°43'E; 9 August 2000. *Grania darwinensis*. (*Heterodrilus devexus*.)
- DP00-16E. Dampier, NW of shopping center, rocky area; medium to coarse sand, barely subtidal, 0.5 m (a site very similar and close to DPOD-16A); 20°39'S, 116°43'E; 9 August 2000. *Grania darwinensis*, *Grania ocarina* sp.n. (*Heterodrilus devexus*, *Pectinodrilus multiplex*, *Bathydrius paramunitus*, *Smithsonidrilus grandiculus*, *S. edgari*.)
- DP00-22. E of Dampier Archipelago, NE corner of Delambre Island; subtidal sediment, 16 m; 20°25.11'S, 116°05.11'E; 7 August 2000; sediment collected by C. Bryce. *Grania darwinensis*.

ABBREVIATIONS USED IN THE FIGURES

agb, accessory glandular body of penial bulb; as, aglandular sac; b, brain; bw, body wall; co, collar; dbv, dorsal blood vessel; ecd, ectal duct of spermatheca; ecg, ectal gland of spermatheca; gb, glandular body of penial bulb; mi, invagination from male pore; mp, male pore; mu, muscle fibres; oe, oesophagus; p, prostomium; phg, pharyngeal glands; sa, spermathecal ampulla; sp, spermathecal pore; sr, sperm ring; st, stylet; vd, vas deferens.

SYSTEMATIC ACCOUNT

Genus *Grania* Southern, 1913

Grania integra Coates and Stacey, 1997

Figure 1

Grania integra Coates and Stacey, 1997:74–76, figure 3.

New material

WAM V 4350, one specimen from Station DP00-14B. SMNH Main Coll. 49472, one specimen from Station DP00-14B.

Description of new material

Only complete specimen 8 mm long, with 66 segments. Width 0.15–0.16 mm at V, 0.15 mm at XII. Prostomium 55–60 μm long and about 95 μm wide, with epidermis thinning at front tip (Figure 1a). Peristomium 115–125 μm wide at 1/2, glandular. Ventral chaetae from IV, laterals absent. Chaetae L-shaped (Figure 1b); maximal lengths 70–74 μm , recorded around segment XL. Shaft straight, proximal half thicker (4–5.5 μm), almost cylindrical, distal half tapering. Chaetal foot slender, with low instep and no heel, perpendicular (anterior chaetae) or oblique to shaft, relatively long (13–17 μm); chaetal index (see Rota and Erséus, in press): 4.34 ($n = 8$, $s = 0.499$). No detached chaetae in coelom. Epidermal gland cells inconspicuous. Clitellum comprising 35 transversal rows of gland cells, extending from 11/12 to chaetae of XIII, rows interrupted midventrally in front of and between male pores; behind latter, only granular cells ventrally in XII. Male pores slightly lateral to line of ventral chaetae. Female pores aligned with male pores. Midventral “copulatory gland” in XIV; (glandular?) bulges observed on nerve cord also in II and V, but without connection to epidermis. Spermathecal pores in lateral lines, somewhat behind 4/5 (Figure 1d).

Brain indented posteriorly (Figure 1a). Head organ (Rota & Erséus, 1996, 1997; Rota *et al.*, 1999) absent; circumpharyngeal connectives with prominent anterior ganglionic swellings (see Rota *et al.*, 1999). Pharyngeal glands with well developed ventral lobes in IV–VI. Nephridia not seen. Dorsal blood vessel from XXVII. Chloragogen cells low, particularly so in preclitellar segments, reaching 10 μm above gut wall only in caudal segments. Coelomocytes (Figure 1c) abundant, irregularly outlined, roughly elliptic, elongate (10–20 by 5–7.5 μm); cytoplasm with coarse granular inclusions (the largest 1.5 μm wide) obscuring the 2–2.5 μm wide nucleus. Sperm sac extending posteriad to XX, egg sac reaching XXII–XXIV. Vasa deferentia 13 μm wide for most length, thinning to 8 μm only near junction with penial apparatus. Latter (Figure 1e–f) consisting of an oval glandular bulb, 70–75 μm long, a typical stylet, and a small aglandular sac. Stylet 44–50 μm long, ental one-fifth enclosed inside vas deferens and 2.5 μm wide; free portion with bottleneck at midcourse attenuating diameter to 1–1.5 μm ; ectal tip somewhat flared (Figure 1e–f). Spermathecae (Figure 1d) conspicuous, occupying anterior half of V; ectal ducts sharply bent at pores; ampullae large, saccate, thin-walled, with sperm rings (diameter 10–14 μm) mostly embedded in anterior walls; ental connection to oesophagus at 2/3 of V. No glands at spermathecal ectal pores.

Remarks

This species, originally described from the Darwin area, Northern Territory (Coates and Stacey, 1997), is easily recognized by the lack of lateral chaetae, the unique shape of the penial stylet, and (we add here) the confinement of the spermathecal ampullae to the anterior part of V (a trait not specified for the original material). Additional amendments to Coates and Stacey’s description and drawings (1997: figure 3) concern the brain shape (posteriorly indented, as in most known congeners; see Rota and Erséus, in press), the form of the spermathecal ectal ducts (distinctly angular near junctions to body wall), and the location of the spermathecal pores (somewhat posterior to 4/5) and the female pores (in line with male pores).

Distribution and habitat

Northern Territory (a number of locations around Darwin Harbour; Coates and Stacey, 1997) and Western Australia (Dampier area: Nickol Bay; new record). In mid to lower intertidal heterogeneous sediments.

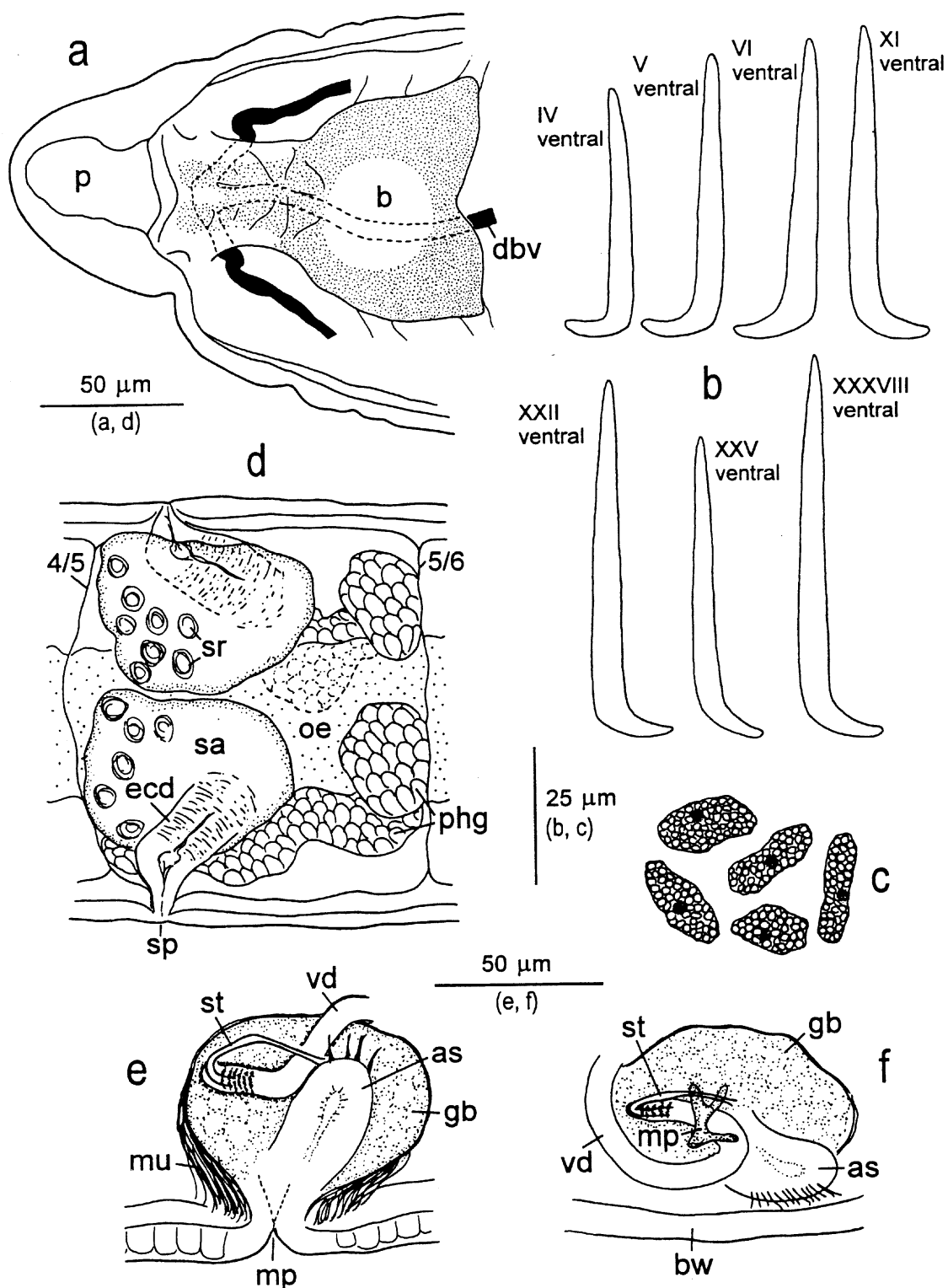


Figure 1 *Grania integra* Coates and Stacey, 1997. a, cephalic region (dorsal view); b, chaetae from different segments, indicated by Roman numerals; c, coelomocytes; d, laterodorsal view of segment V, showing anterior position of the spermathecae; e, left penial apparatus in lateral view; f, right penial apparatus in ventral view.

Grania ocarina sp.n.

Figure 2

Holotype

WAM V 4351, whole mounted specimen.

Type locality

Western Australia, Dampier area, Burrup Peninsula, Withnell Bay (Station DP00-2).

Paratypes

WAM V 4352, one specimen from type locality. SMNH Type Coll. 5868, one specimen from Station DP00-5A. MCZR Oligochaeta 0128, one specimen from Station DP00-16E.

Description

Body 5.2–6.2 mm long, 0.12–0.14 mm wide at V, and 0.15–0.17 mm at clitellum. Segment number 46–61 ($n = 4$). Prostomium rounded, 48–55 μm long, about 75 μm wide at 0/1; epidermis slightly thinner at front side (Figure 2a). Peristomium 88–113 μm wide at 1/2. Preclitellar chaetae occurring only ventrally and in segments V–VIII. Behind clitellum, ventral chaetae commencing in XIII, laterals in XVI ($n = 3$) or XVII ($n = 1$). Chaetae L-shaped (Figure 2b); shaft straight, distally pointed, proximally bending into a slender foot without heel. Length of chaetae minimal in V (45 μm), maximal in VI–VIII (72–90 μm); chaetae still large (65–70 μm long) immediately behind clitellum (XIII–XV), thereafter shorter (51–67 μm), particularly so around segment XX and at posterior body end. Feet 18–22 μm long in VI–VIII and XIII–XV, 9–14 μm long in other segments; thus, chaetal index (see Rota and Erséus, in press): 3.57 ($n = 8$, $s = 0.160$), in forebody except segment V; index increasing to 4.89 ($n = 15$, $s = 0.292$) in other regions. Shaft thickest at midpoint, 3.5 μm in V, 6.5 μm in VI–VIII, 3.8–5 μm in other segments. Epidermal gland cells numerous in I–IV, elsewhere arranged in at most 1–3 rows per segment. Clitellum up to 17 μm thick, extending from anterior border of XII to behind chaetae of XIII, absent midventrally in front of and between male pores; with granular and hyaline gland cells interspersed in about 37 rows; only granular cells lateral to male pores and ventrally in posterior of XII. In one specimen, clitellar gland cells distributed from XII through XV. Male pores as short, deep slits in middle of XII. A midventral “copulatory gland” in XIV. Spermathecal pores in lateral lines, somewhat behind septum 4/5 (Figure 2d); an epidermal glandular field in anterior of V below each spermathecal pore (extending from lateral line to chaetal line).

Brain posteriorly indented; head organ (Rota and Erséus, 1996, 1997; Rota *et al.*, 1999) absent (Figure 2a). Pharyngeal glands at 4/5–6/7, not united dorsally; ventral lobes well developed in IV and VI, somewhat reduced in V. First pair of nephridia at 7/8, inconspicuous. Dorsal blood vessel commencing between XVIII and XX. Chloragogen cells from IV, finely granular, in some segments projecting 10 μm above gut wall. Coelomocytes (Figure 2c) oval to irregularly elliptic, mostly 10–14 μm long, with granular refractive cytoplasm. Sperm sac extending posteriad to XV–XVIII. Sperm funnels stout, about 2 times longer than wide (125 by 63–70 μm), with low, narrow (38–50 μm) collar covered with short spermatozoa (heads of latter about 13 μm long). Vasa deferentia forming prominent coils but never extending behind 13/14; with conspicuous inner ciliation and large, constant diameter (12–16 μm), slightly narrowing (11–12 μm) at junction with penial apparatus; vas walls not markedly muscular. Glandular penial

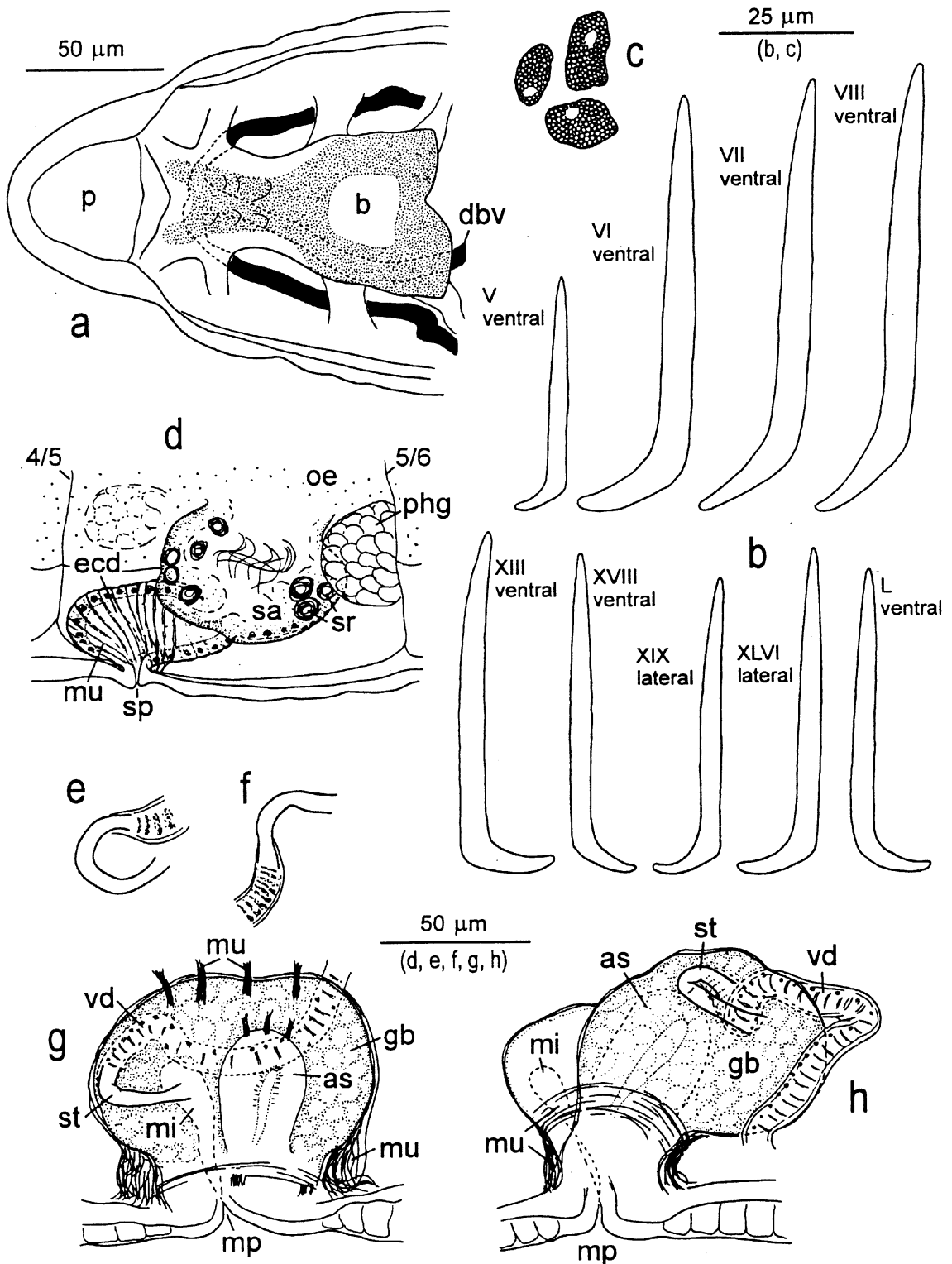


Figure 2 *Grania ocarina* sp.n. a, cephalic region (dorsal view); b, chaetae from different segments, indicated by Roman numerals; c, coelomocytes; d, left spermatheca (dorsolateral view); e–f, penial stylet in two different views; g, left penial apparatus, lateral view; h, right penial apparatus from a more contracted specimen, medial view.

bulb (Figure 2g–h) relatively large (85–110 μm long), oval, basally encircled by robust muscle fibres and medially housing a broad cylindrical stylet originating inside terminal part of vas deferens. Bulb laterally flanked by a well-developed aglandular sac and deep invagination from male pore; both sac and invagination secured to body wall by muscle fibres. Stylet (Figure 2e–h) at least 40 μm long, 6.5–8 μm wide throughout, slightly expanded at both ends, sharply bending against dorsal periphery of bulb; not extending into lateral aglandular sac (? penial type “4” *sensu* Coates, 1984). Egg sac extending into XVII–XX. Female ducts inconspicuous, opening behind 12/13. Spermathecae (Figure 2d) conspicuous (total length 90–110 μm), with broad connection to oesophagus in posterior half of V. Each ectal duct 30 μm wide, egg-shaped, with long axis lying parallel to body wall but distally resembling an ocarina (due to lateral, subterminal opening to exterior), fastened by robust muscle fibres to body wall; no accessory glands at ectal pores. Ducts joining ampullae on ventrolateral aspects, constricted at junction; both duct and ampulla enclose a wide inner lumen (Figure 2d). Ampullae rounded to oval, in latter case 61–75 by 50–65 μm , their anterior border 35–50 μm far from the duct’s anterior border. Sperm rings of various diameter (up to 15 μm) embedded in walls but also many spermatozoa loose in ampullar lumen.

Etymology

Named for the peculiar form of the spermathecal ectal duct resembling an *ocarina*, an Italian, terra-cotta, wind instrument having the mouthpiece as a spout on the side.

Remarks

This new species can be distinguished from all known congeners by its unique chaetal distribution (preclitellar chaetae present only ventrally from V to VIII) and the complex penial apparatus. The latter comprise unusually broad cylindrical penial stylets, well-developed aglandular sacs, and large glandular bulbs basally constricted by muscles. The form of the spermathecal ectal ducts is also characteristic and only similar to that originally depicted (Pierantoni, 1903: pl. 16, figure 25) for *G. macrochaeta* (Pierantoni, 1901). Interestingly, *G. ocarina* shares with the latter also the shape of the chaetae and their size distribution (larger in anterior segments) (see Pierantoni, 1903: pl. 15, figures 4–5). However, in *G. macrochaeta* the ventral chaetae are continuously distributed from IV to the caudal region (Pierantoni, 1901, 1903), and according to Locke and Coates (1998), *G. macrochaeta* is devoid of penial stylets. In a forthcoming redescription of this Italian species (Rota and Erséus, in preparation) the affinities of the two species will be thoroughly assessed.

Distribution and habitat

Known only from the Dampier area (Burrup Peninsula, Withnell Bay; Nickol Bay; Dampier), Western Australia. In medium to coarse sand, intertidal to barely subtidal (0.5 m).

Grania darwinensis (Coates and Stacey, 1997) comb.n.

Figure 3

Randidrilus darwinensis Coates and Stacey, 1997:70–72, figure 1.

New material

WAM V 4353 to V 4359, seven specimens from Station DP00-4. WAM V 4360, one

specimen from Station DP00-8C. WAM V 4361 to V 4363 three specimens from Station DP00-11C. WAM V 4364 to V 4367, four specimens from Station DP00-16A. WAM V 4368 to V 4372, five specimens from Station DP00-16E. SMNH Main Coll. 49473-49497, 26 specimens (two of them on the same slide) from Station DP00-4. SMNH Main Coll. 49498, one specimen from Station DP00-11C. SMNH Main Coll. 49499-49523, 25 specimens from Station DP00-16A. SMNH Main Coll. 49524-49533, 10 specimens from Station DP00-16E. SMNH Main Coll. 49534, one specimen from Station DP00-22. MCZR Oligochaeta 0129-0130, two specimens from Station DP00-11C. MCZR Oligochaeta 0131-0132, two specimens from Station DP00-16A. MCZR Oligochaeta 0133, one specimen from Station DP00-16E.

Description of new material (based on 26 specimens)

Body 3.8, 5.5–7.7 mm long ($n = 8$), 0.16–0.19 mm wide at V, 0.18–0.21 mm at clitellum. Segment number 34, 42–60 ($n = 17$). Prostomium (Figure 3a) 70–83 μm wide at 0/1, 53–58 μm long ($n = 6$), its wall thinning to as little as 3–5 μm at front, in correspondence of pointed inner cavity. Peristomium 105–128 μm wide at 1/2 ($n = 5$). Ventral chaetae consistently from V, laterals from XVII ($n = 1$), XVIII ($n = 2$), XIX ($n = 13$), or XX ($n = 1$). Chaetae (Figure 3b) L-shaped, shaft thickest (4–7 μm) at midpoint, entally curving into a 10–27 μm long foot with slight heel. Length of anterior ventral chaetae: 49–55 μm in V ($n = 3$), 86–90 μm in VI–VIII ($n = 8$), 72–77 μm in IX–XI ($n = 6$), 77–81 μm in XIII–XV ($n = 3$). Chaetae shortest in XVI–XXI; from about XX to caudal segments, ventral and lateral chaetae 56–69 μm long. Chaetal index (see Rota and Erséus, in press): 3.58 ($n = 6$, $s = 0.409$). Epidermal gland cells dense over peristomium; on rest of body, scattered, at most forming three equidistant rows per segment; nowhere arranged as mid-dorsal pads. Clitellum 16 μm thick, with gland cells arranged in 41 or 42 transverse rows; anteriormost 4(5) rows, as well as posteriormost 4(5) (located behind the chaetae of XIII), comprise hyaline and finely granular cells, whereas the intervening rows form a regular mosaic of hyaline and coarsely granular cells. Clitellum not developed midventrally in front of and between male pores; only granular cells on lateral and posterior aspects of male pores. Male pores in line with female pores, ventrolateral in middle of XII. Two (glandular?) bulges often present beneath nerve cord in II ($n = 6$) and III ($n = 11$) but a clear connection between them and epidermis could not be ascertained. An ordinary “copulatory gland” in XIV. Spermathecal pores (Figure 3d) located well behind 4/5 (at about 1/3 of V) and slightly below lateral lines; a broad, oval, field of glandular epidermis around each pore.

Brain deeply indented posteriorly (Figure 3a). Head organ (Rota and Erséus, 1996, 1997; Rota *et al.*, 1999) absent, but architecture of cerebral ganglion and annexed supraoesophageal nervous structures as typical of *Grania* (see Rota *et al.*, 1999). Pharyngeal glands at 4/5–6/7, not united dorsally; ventral lobes in IV well developed. First nephridium at 7/8 (seen in at least 10 specimens); a few nephridia seen also around segment XXX. Anterior end of dorsal blood vessel incised by a notch; this vessel may commence as far back as XX. Chloragogen tissue mostly low (3–5 μm), but in caudal part of body projecting about 7 μm above gut wall. Coelomocytes (Figure 3c) oval, small (11–21 by 7–8 μm), often with irregular outline, containing coarse refractile granules. Heads of spermatozoa short, extending 10 μm above collars of sperm funnels. Vasa deferentia long (may reach XV within egg sac), thick (18–20 μm) and granular at ental origin (initial 50–65 μm behind septum 11/12), narrower (8 μm) and translucent through most of following course, only 6 μm thick when approaching penial apparatus. Latter (Figure 3e–f) paired, each with a centrally located bulb (50–55 μm long, globular in lateral view) and two equally large, one anterior and one posterior, accessory

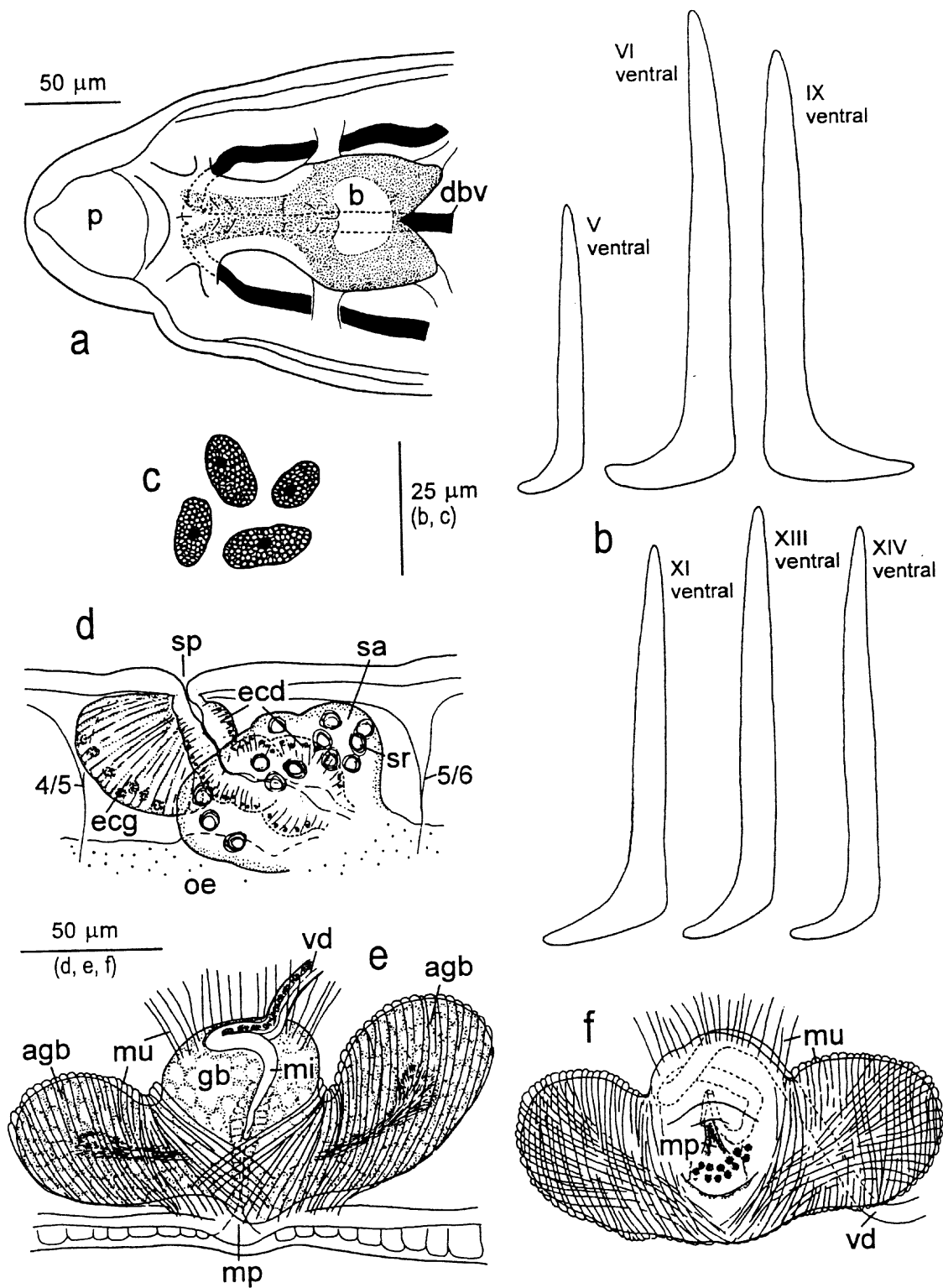


Figure 3 *Grania darwinensis* (Coates and Stacey, 1997) comb.n. a, cephalic region (dorsal view); b, chaetae from different segments, indicated by Roman numerals; c, coelomocytes; d, right spermatheca (dorsal view); e, right penial apparatus in ventromedial view; f, left penial apparatus from a different specimen in ventral view.

glandular bodies, whole complex attaining a length of 143–175 μm along worm axis; fascicles of gland cell extensions travel from centre of each accessory body toward ventral side of bulb, to finally open into male pore. A complex of variously oriented (mostly transverse) muscle slings surround the accessory bodies and anchor them to body wall medially to male pore (the oblique insertions of such slings produce a herring-bone pattern on body wall). Vas deferens reaches central bulb on dorsolateral side and, with a superficial half turn, merges with elongate conical, winding, cuticle-lined invagination that ascends from male pore. In some worms such details made conspicuous by travelling sperm. A true penial stylet absent. Spermathecae (Figure 3d) connected to oesophagus in posterior half of V. Ectal ducts contractile but not heavily muscular, 33–40 μm thick entally, 20 μm ectally, reaching body wall on posterior side of prominent (58–65 μm long) multicellular gland. Ampullae irregularly shaped, their walls non-granular, enclosing about 15 sperm rings, latter 9–13 μm in diameter (Figure 3d).

Remarks

When originally described from Darwin Harbour, Northern Territory (Coates and Stacey, 1997), this species was regarded as a member of *Randidrilus* Coates and Erséus, 1985, a genus otherwise known only from the eastern shores of the United States and diagnosed by a unique combination of features (see Coates and Erséus, 1985): (1) chaetae single, ectally pointed, entally J-shaped, (2) their first occurrence in II; (3) lateral chaetae absent; (4) mid-dorsal pads of modified epidermal cells present in postclitellar segments; (5) dorsal lobes of pharyngeal glands united; (6) seminal vesicle unlobed, unpaired, extending anteriad and posteriad from XI; (7) penial bulbs each with two separate glandular masses, one anterior and one posterior; (8) vasa deferentia unmodified, opening lateral to central part of bulb “onto tip of small medial papilla which extends into epidermal invagination”; (9) spermathecae with glands at ectal pores; (10) sperm not embedded in ampullar walls of spermathecae. The species *darwinensis* is incompatible with that diagnosis in many relevant points: (i) it has robust, entally expanded, chaetae that are distributed ventrally and laterally, but completely absent in I–IV; (ii) all pairs of its pharyngeal glands are dorsally separated; (iii) “well-defined sperm rings” are embedded in the walls of its saccate spermathecal ampullae. Such character states are likely to be apomorphic, and are typically combined in *Grania*. Coates and Stacey (1997) justified their taxonomic decision by “the unique apomorphic form of the penial bulb, with large, separate, accessory anterior and posterior glands, seen in the new species [*darwinensis*] and other nominal species of *Randidrilus* but not recognised in any of the species described in *Grania*, as well as the presence of a large gland at the ectal pore of the spermatheca”. They admitted that amendments were required to the original diagnosis of *Randidrilus* for it to accommodate *darwinensis*, but only with regard to the chaetal distribution (i.e., lateral chaetae can be present; chaetae can be missing in segments anterior to IV) and the sperm arrangement in the spermathecal ampullae (i.e., sperm can be stored as rings in pockets of the ampullar walls). Thus, divergence was implicitly assumed by these authors to be possible within *Randidrilus* in the chaetal shape and distribution, the sperm arrangement in the spermathecae, and the dorsal separation of the pharyngeal glands (the latter generally being intragenerically conservative in enchytraeids), but not in the glandular equipment of the spermathecae and the form of the penial apparatus. We find, however, that morphological evidence rather suggests that *Randidrilus* is phylogenetically incoherent if *darwinensis* is included in it, and that this species is more likely to be phylogenetically positioned within *Grania*. In fact, spermathecal ectal glands are not infrequently described in *Grania*; some species even develop them all along the ectal ducts (see

Coates and Erséus, 1980; Erséus, 1980; Rota and Erséus, 1997, in press; Locke and Coates, 1999). The assumption that *darwinensis* exclusively shares the form of the penial apparatus with *R. codensis* (Lasserre, 1971) and *R. quadrithecatus* Coates and Erséus, 1985 (i.e., the two North American species) is also questionable. First, and most important, the architecture of the male opening in *darwinensis*, as redescribed above, appears much more complex than in the two North American *Randidrilus* (where the vas deferens directly abuts a comparatively shallow male invagination; Coates and Erséus, 1985, and pers. obs.). Second, penial bulbs with two accessory glands are not unique to the three species in question: a similar construction occurs in the terrestrial enchytraeid *Fridericia isseli* Rota, 1994 (see also Rota, 1995; Rota and Healy, 1999), and a *convergent* form of bulb could have evolved in *Grania*, especially considering the remarkable morphological diversity recognised in the penial apparatus of this genus. Our observations on the coelomocytes and the brain structure of the Dampier material provide further elements pro the inclusion of this species in *Grania*. The elliptic, irregularly outlined, coarsely granular, coelomocytes of *darwinensis* resemble those of *G. integra*, and show a size range that is virtually identical to those of most *Grania* species investigated in such respect (see Rota and Erséus, 1996, 1997, 2000, in press; Rota *et al.*, 1999). The overall length range of these cells in *Grania* is 10–27 μm ; only *G. tasmaniae* Rota and Erséus, 2000 shows more elongate (22–40 by 5–9 μm), spindle-shaped, coelomic cells (interpreted, with some reservation, as coelomocytes by Rota and Erséus, 2000). In *Randidrilus*, the coelomocytes look different, foliaceous, broadly oval to pear-shaped, and clearly larger (25–40 by 10–22 μm in *R. codensis*; Lasserre, 1971, and pers. obs.). The rostral part of the brain of *darwinensis* shows the characteristic partitioned appearance that appears unique to *Grania* (see Rota *et al.*, 1999). Finally, it is noteworthy that the two anterior midventral glands (?) detected beneath the nerve cord of *darwinensis* are reported herein also for *G. integra*.

In conclusion, we find the allocation of *darwinensis* in *Grania* to be well supported, although it makes the morphological differentiation of this genus (see Rota and Erséus, in press) more and more impressive. In fact, *G. darwinensis* appears as a highly derived species, whose intrageneric affinities cannot be easily determined. In addition to the complex muscular and glandular equipment of the penial apparatus, the species has an unprecedented displacement of the spermathecal pores (toward 1/3 V and slightly below the lateral lines) and spermathecal glands of an extraordinary size.

With regard to the phylogenetic affinities between *Randidrilus* and *Grania*, Coates and Stacey (1997) did not express any clear hypothesis, but commented that the new generic record and the characteristics of the new species [*Randidrilus darwinensis*] “raised questions about the relationships among species of *Grania* and *Randidrilus* as they are now found to share setal form and distribution characteristics that are otherwise unique among the enchytraeids”. However, we suggest that their classification of *darwinensis* implies two possible hypotheses. Either the two North American species of *Randidrilus* are advanced members of a taxon that shares its roots with *Grania* (*darwinensis* thus being a plesiomorphic species), or the (advanced) species *darwinensis* has diverged from the North American members of *Randidrilus* to become similar to some *Grania* species by convergence. Having re-examined part of the original material of *Randidrilus*, as well as of other marine taxa attributed to *Marionina* Michaelsen, 1889 (all available in C.E. collection), we conclude that the two North American *Randidrilus* species are unlikely to be the sister group to any part or the whole of *Grania*. Their structural similarities to species of *Grania* are limited to plesiomorphic (or convergent) features that occur in some nominal *Marionina* as well. This applies, for example, to the simple structure of the

chaetae, but also to the possession of mid-dorsal pads of epidermal glands (which are absent in *G. darwinensis*), described in *G. reducta* Coates and Erséus, 1985, *G. levis* Coates and Erséus, 1985, *G. longiducta* Erséus and Lasserre, 1976, and in *Marionina diazi* Coates and Erséus, 1985 (see Coates and Erséus, 1985). In fact, with respect to chaetal shape, structure of the male openings, and features of the clitellar gland cells and coelomocytes, the two American *Randidrilus* are closer to *M. diazi* and *M. welchi* Lasserre, 1971, or to other marine species currently ascribed to *Marionina* (*sensu lato*). This suggests that it is rather in this heterogeneous assemblage (see Xie and Rota, 2001) that one should search for the (probably independent) origins of *Randidrilus* and *Grania*.

Distribution and habitat

Northern Territory (Darwin area; Coates and Stacey, 1997) and Western Australia (Dampier area; new record). Common in both areas, found in various types of substrates (medium to coarse sand, clayey or silty sediments). Previously known from lower intertidal to water pools in mid-upper beach, at salinities as high as 57‰ (Coates and Stacey, 1997); in the Dampier area occurring from lower intertidal to 16 m depth.

Genus *Marionina* Michaelsen, 1889 (*sensu lato*)

Marionina coatesae Erséus, 1990

Marionina coatesae Erséus, 1990:318–319, figure 26A–G; Erséus *et al.*, 1990:117–118, figure 6A–B; Coates and Stacey, 1993:411, figure 12; Healy and Coates, 1997:93.

New material

WAM V 4373, one specimen from Station DP00-14C.

Description of new material (focusing on additions to or deviations from previously published descriptions)

Body 2 mm long, with 32 segments. Width 0.15 mm at III, 0.17 mm at V, 0.21 mm at XII. Chaetae absent in XII, 27–40 µm long in preclitellar segments, 37–52 µm in postclitellar segments, their length gradually increasing along body. Distance between male pores 92 µm. Coelomocytes 19–27 µm long, with pale, finely granular cytoplasm. Nephridia present at 7/8, 8/9 and, segmentally, from 16/17. Vasa deferentia 7 µm wide. Penial bulbs extending 32 µm along worm long axis. Spermathecae with variously sized glands around the ectal orifices, ampullae 35 µm wide, each with a few loose spermatozoa in the central cavity and 4–9 sperm rings embedded in walls.

Remarks

This specimen conforms well to the original description (Erséus, 1990) but all its morphometric characters appear a bit smaller than those previously noted.

Distribution and habitat

Known from Hong Kong (Erséus, 1990), northern China (Yellow Sea: Erséus *et al.*, 1990), the Northern Territory (Darwin area: Healy and Coates, 1997), Western Australia (Rottnest

Island: Coates and Stacey, 1993; Dampier area: new record). Intertidal, previously found in coarse sandy substrates, now in clay mixed with fine to medium sand.

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