

New phallodrilines (Annelida: Clitellata: Tubificidae) from Western Australian groundwater

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Abstract

Four species of phallodriline tubificids (Clitellata: Tubificidae) from karst aquifers and caves along the west coast of the state of Western Australia are the first records of this subfamily from non-marine waters in the southern hemisphere. *Akteredrilus parvithecatus* (Erséus 1978) and *Pectinodrilus ningaloo* **n. sp.** occur in anchialine groundwater of Cape Range, along with other taxa of marine affinity. *Akteredrilus leeuwinensis* **n. sp.** and *Akteredrilus podeilema* **n. sp.** occur in caves of the Leeuwin-Naturaliste Ridge and Perth Basin respectively and are the first taxa of marine lineage to have been collected from these systems.

Key words: Clitellata, oligochaete, Tubificidae, Phallodrilinae, stygofauna, cave fauna, groundwater, Western Australia

Introduction

Surveys over the last decade have revealed the presence of diverse aquatic invertebrate communities in caves and groundwater aquifers of Western Australia (e.g. Eberhard *et al.* 2005; Eberhard *et al.* 2004; Humphreys 1999a, 2000; Humphreys & Harvey 2001; Jasinska *et al.* 1996; Leys *et al.* 2003). Examination of oligochaetes from these surveys has revealed numerous new undescribed species, including three species of the tubificid subfamily Phallodrilinae, belonging to *Akteredrilus* and *Pectinodrilus*, described below. The mostly marine *Akteredrilus parvithecatus* (Erséus 1978), was also recorded. Phallodrilines are primarily marine interstitial worms, although some estuarine and freshwater species are known, especially in Europe (e.g. Erséus *et al.* 1992; Giani *et al.* 2001; Juget & Chatelliers 2001; Sambugar *et al.* 1999). Erséus (1990a; 1990b; 1993; 1997a; 1997b) and

Erséus and Wang (in press) have documented a rich phallodriline fauna from Australian marine waters, but the species dealt with below, collected from near-coastal karst aquifers, are the first from the continent's inland waters.

Study area

Along the west coast of Western Australia, broad coastal plains overlie the Carnarvon and Perth sedimentary basins that abut older (Precambrian/Cambrian) elements of the continental crust (the Yilgarn and Pilbara Cratons and the intervening Capricorn Orogen) (Fig. 1). Cave and karst development has occurred within Quarternary dune limestones (Tamala Limestone Formation (Playford *et al.* 1976)) deposited along the coastal margins of these basins. Subterranean fauna, including stygofauna, occur in these caves and karst aquifers.

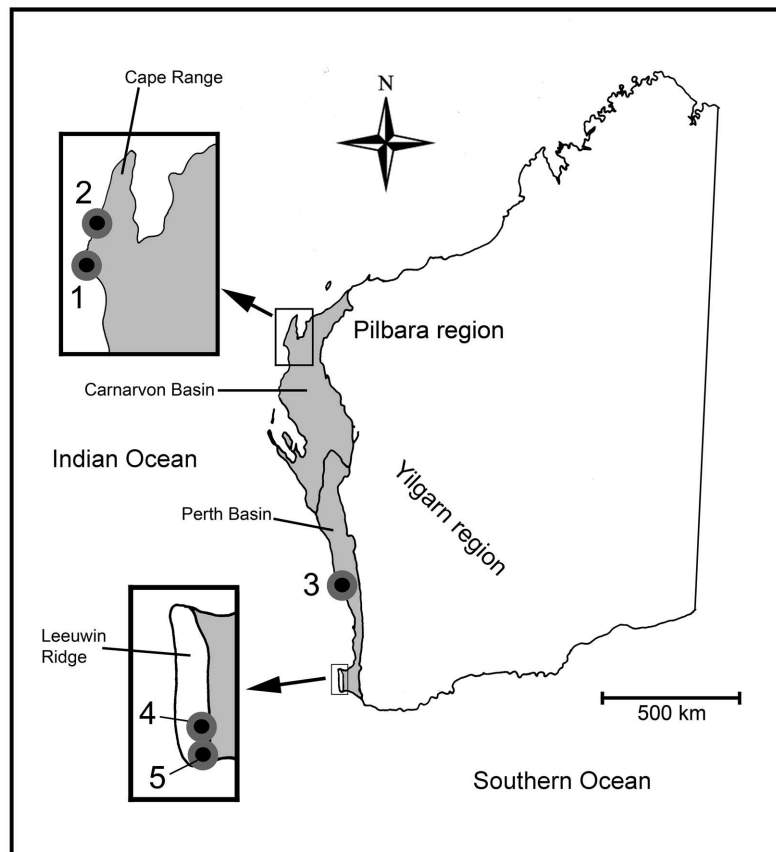


FIGURE 1. Map of Western Australia showing major geological units and localities for 1) *Pectinodrillus ningaloo*, 2) *Aktedrilus parvithecatus*, 3) *Aktedrilus podeilema*, 4) *Aktedrilus leeuwinensis* and 5) *Aktedrilus* sp.

The late Pleistocene Bundera Calcarenite, one of many named correlatives of the Tamala Limestone, extends along the west coast of Cape Range (Fig. 1) and contains an anchialine ecosystem, exposed naturally at a few caves, sinkholes and small karst windows, and in artificial bores and wells (Humphreys 1999b, 2001). In places, such as Bundera Sinkhole (Humphreys 2000), the cave development extends into the deeper Miocene Tulki Limestone. Phallogrillines were found in two sites within the Bundera Limestone: an artificial well and small karst window. Further south, Tombstone Rocks Cave is formed in a wide band of Tamala Limestone within the Perth Basin, 9 km from the current seashore (Fig. 1).

The two remaining sites, Budjur Mar Cave and Turners Spring, are developed in Tamala Limestone overlying granite-gneiss of the Leeuwin Block, immediately west of the southern-most part of the Perth Basin (Fig. 1). Budjur Mar Cave is about 3 km inland from the Indian Ocean. The cave is not associated with a water-table aquifer, but a perennial stream in the cave is fed by diffuse rainfall derived seepage through the limestone directly above the cave, and from a small epigeal catchment to the east of the cave. As is characteristic of stream caves in the Leeuwin-Naturaliste Ridge, the stream flows westwards towards the sea, along a channel in the underlying basement rocks, probably eroded prior to deposition of the overlying limestone (Eberhard 2004). The perennial Turners Spring is only 1 km from the coast and feeds a small intermittent stream which flows into the sea near the confluence of the Southern and Indian Oceans. The spring is not hydrologically connected to Budjur Mar Cave.

Materials and methods

Specimens were collected using a hand net or a phreatobiological haul net (mesh sizes 250–350 μm) and preserved in 75% methylated ethanol. The interstitial fauna of Turners Spring was sampled by the Bou–Rouch method (Bou & Rouch 1967) as described in Pospisil (1992), with pumped water filtered through a 250 μm mesh net. Worms were whole-mounted in Permout™ after staining with Grenacher's Borax Carmine and clearing in Histoclear™. Drawings were made freehand or with a drawing tube attached to a Zeiss compound microscope and measurements were made on slide-mounted specimens using Auto-Montage software (The Synoptics Group 2003) calibrated with a stage micrometer. Collections are deposited with the Western Australian Museum (WAM) or retained by the senior author (AP colln). Abbreviations on figures: a, atrium; e, egg; o, ovary; p, penis; pr, prostate gland; pc, penial chaetae; ps, penis sheath; sa, spermathecal ampulla; v, vas deferens.

Systematics

Pectinodrillus ningaloo Pinder n. sp. (Fig. 2)

Holotype. WAM V 4442. Specimen whole-mounted under right coverslip on same slide as paratype WAM V 4443, from groundwater in Ningaloo Homestead Well, about 500 m from the ocean, Ningaloo Station, Cape Range, Western Australia (Fig. 1), 22°42'S 113°41'E, 11 June 1993. Temperature 22.8°C, conductivity 0.66 mS cm⁻¹, total dissolved solids 360 mg L⁻¹. Coll. R.D. Brooks, WAM collection # BES 2230).

Paratypes. WAM V 4443 and 4444. One mature with head and tail missing, whole-mounted under left coverslip on same slide as holotype and 1 mature with tail missing, whole-mounted on separate slide, collection details as for holotype.

Other material. WAM V 4445. Two immature of uncertain identity in alcohol, collection details as for holotype.

Description. Length and number of segments of holotype 8.2 mm and 61 respectively, maximum width of slide-mounted worms 0.14–0.20 mm at segment XI. Clitellum from posterior 1/3 of X to 12/13, more glandular, but not thicker, than epidermis of pre-clitellar segments. Post-clitellar segments with epidermis thinner than anterior segments. Male pores ventro-lateral on XI about 4/5 distance between 10/11 and 11/12. Spermathecal pores ventro-lateral immediately behind 9/10. Female funnels ventro-lateral at 11/12.

Prostomium elongate oval, length:height at base 1.5, with large round clusters of cells with nuclei on the periphery, lying beneath the epidermis and projecting into the coelom. Pharynx in II/III. Pharyngeal glands, consisting of large irregular cells, mostly lateral and dorsal to the gut in IV–VI. Rest of ciliated digestive tract of variable width but not enlarging in pre-genital segments. Large dorsal and smaller ventral blood vessels connected by commissural vessels in II–V and by a plexus of capillaries surrounding the gut from VI. From VI or VII onwards, gut surrounded dorsally and laterally by large chlorogogue cells with non-staining cytoplasm occupying up to half of the coelom in many segments. Coelomocytes not observed. Chaetae 3(4–5)/bundle anteriorly, reduced to 2 posteriorly, 32–40 µm long x 1.5–1.8 µm wide at nodulus, bifid with sharp teeth, the upper tooth about half as long as lower, the nodulus distinctly distal. Straight penial chaetae 10–19/bundle in XI, protruding from body wall on a rounded papilla anterior to the male pores. Penial chaetae 32–36 µm long x ~ 1–1.5 µm wide at the base, tapering slightly towards their tips which appear to be slightly swollen and minutely hooked, but tips difficult to see as chaetae facing outwards.

Genitalia paired. Testes antero-ventral in X with sperm sacs from IX to XIII. Ovaries antero-ventral in XI with egg sacs extending to XIV. Asymmetrical sperm funnels ventro-lateral on 9/10. Vasa deferentia ciliated and tripartite: a short, thin (7–8 µm wide) ental section with thin muscle layer, a longer, thicker (maximum width 20–27 µm) middle section with thick (2–3 µm) muscle layer and thicker lining tissue and an ectal section (11–17 µm wide) with thinner muscle layer and lining tissue intermediate in width

between the ental and middle sections. Atria short (50–58 μm), upright and moderately muscular, leading to simple male pore in a shallow invagination (at least in preserved specimens) behind penial chaetae. Two small ovoid prostates associated with each set of male ducts, one ventral to the middle part of vasa deferentia and one posterior to atrium, connections with the male ducts not seen. Spermathecae variable in shape, size and expansion of the lumen, but ampullae about 3 times longer than maximum width (about 50 μm in 2 mated specimens), with a short constriction between the ampulla and a small ectal vestibule. Sperm in loose masses in ampullae.

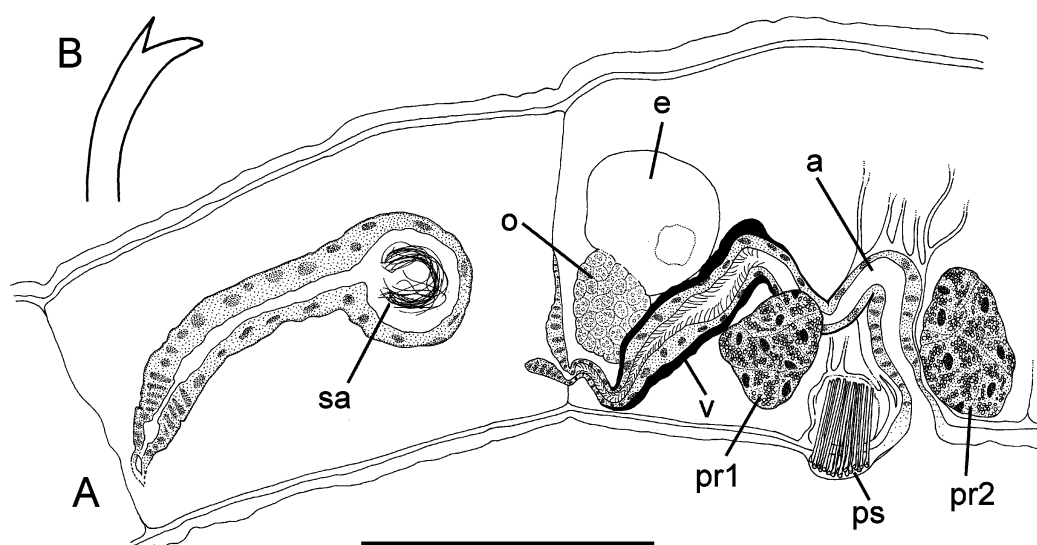


FIGURE 2. *Pectinodrilus ningaloo* n. sp. A, Genitalia of holotype (scale bar 100 μm); B, anterior chaeta.

Remarks. Members of the genus *Pectinodrilus* are united by the presence of small upright atria and the large number of penial chaetae, both characters that are clearly present in the new species. All previously described *Pectinodrilus* are marine meiobenthic and most have simple male ducts with a thin vasa deferentia leading directly into the atria. The new species, however, resembles a small number of species from the Southern Indian Ocean, Western Australia and south-east Asia (Hong Kong) that Erséus (1992a; 1997a) considered to constitute a monophyletic group within *Pectinodrilus*. Members of this group share ‘multiple club-shaped and hooked penial chaetae’ and ‘various modifications and elaborations of the vasa deferentia’. Of these, *Pectinodrilus multiplex* (Erséus 1990) and *Pectinodrilus hoihaensis* Erséus 1992 have a tripartite vas like the new species but with the middle muscular section even more developed and forming a broad sperm storage organ and with *P. multiplex* also possessing another ampulla (atrium *sensu* Erséus 1992a) between the vas and a copulatory sac. The male ducts of the new species are not this complex but are more differentiated than some other species in the group such as *P. marionensis* (Erséus 1979) and *P. nervosus* (Erséus 1990), which have a small non-

muscular section of vas followed by a longer extremely muscular section leading directly into a muscular atrium. Other members of this subgroup are *P. glomeriductus* Erséus 1997, which has highly coiled vasa and *P. vitreus* Erséus 1993 which has bi-partite vasa that are not as muscular as those of *P. marionensis* and *P. nervosus*).

Etymology. Named for the type locality: a bore next to the homestead on Ningaloo Station.

***Aktedrilus parvithecatus* (Erséus 1978) (Fig. 3)**

Bacescuella parvithecata Erséus, 1978: 264

Bacescuella pilicrepus Erséus, 1984b: 153

Aktedrilus parvithecatus (Erséus, 1978); Erséus (1987: 117); Erséus (1992: 21)

Material examined. WAM V 4446. Two specimens whole-mounted on same slide, from a small anchialine karst window (#C-510) about 500 m from the sea, Cape Range, Western Australia (Fig. 1), 22°20'S 113°49'E, 8 Aug 1993. Conductivity 3.30 mS cm⁻¹, total dissolved solids 1800 mg L⁻¹. Coll. W.F. Humphreys and R.D. Brooks (WAM collection # BES 2502).

Description of new material. Length and number of segments 6.3–6.6 mm and 48–53 respectively, width of slide-mounted worms 0.15–0.21 mm at segment XI. Clitellum from posterior 1/3 of X to 12/13, more glandular, but not distinctly thicker than epidermis of other segments. Male pores ventro-lateral on XI, about one third of the distance between 10/11 and 11/12. Single spermathecal pore mid-dorsal behind 9/10. Female funnels ventro-lateral on 11/12.

Prostomium bluntly oval, length:height at base 1.1–1.3, with large round clusters of cells below the epidermis, projecting into, and occupying up to half of the prostomial coelom. Pharynx in II/III. Pharyngeal glands, consisting of large irregular cells, associated with gut in IV–V (or anterior of VI). Rest of ciliated digestive tract narrow anteriorly, wider from XIV–XVII. Dorsal and ventral blood vessels connected by commissural vessels in at least IV and V and by a plexus of capillaries surrounding the gut from about VI. Large chlorogogue cells with non-staining cytoplasm almost filling coelom from VI or VII. Coelomocytes not observed. Chaetae bifid with sharp teeth, the upper tooth about half as long as the lower, 4–7/bundle in pre-genital segments and 3–5/bundle posteriorly, located at about two-thirds of the distance between anterior and posterior septa, 33–48 µm long x 1.3–1.5 µm wide at nodulus, largest in pre-genital segments, the nodulus slightly distal. Ventral chaetae present but not modified on X, absent on XI.

Genitalia paired, except for spermatheca. Testes antero-ventral in X with sperm sacs extending posteriad to XIV. Ovaries antero-ventral in XI, egg sacs not present. Sperm funnels ventro-lateral on 9/10 leading to very short thin (8 µm) vasa deferentia (ciliation uncertain) joining apical end of tubular atria. Atria about 300 µm long, width about 17 µm

with sperm present in the lumen (not shown on Fig. 3). Cytoplasm of atrial lining cells with numerous vesicles, much more so in ectal $2/3^{\text{rds}}$, of a similar size and shape to those in the prostate glands. Muscle layer of atrium mostly thin, but in one specimen this is somewhat thicker around the ental part of the atrium with less abundant cellular vesicles. Atria joining ovoid penes apically, leading to a pore on the inner side of the penes. Penis sacs opening to exterior ventro-laterally. Two large prostate glands associated with each set of male ducts. Anterior prostates lying medial to the atria but connection to male duct not visible. Posterior prostates lying medial to penis sacs in front of 11/12, almost as tall as the segment and connected to the male duct where the atria join the penis sacs, sometimes protruding into XII. One spermatheca present with a small ampulla (28–31 x 16 μm) connected to mid-dorsal pore by thick duct (25–32 μm long, 13–14 μm wide) narrowing towards pore with narrow lumen. Loose sperm present in ampulla.

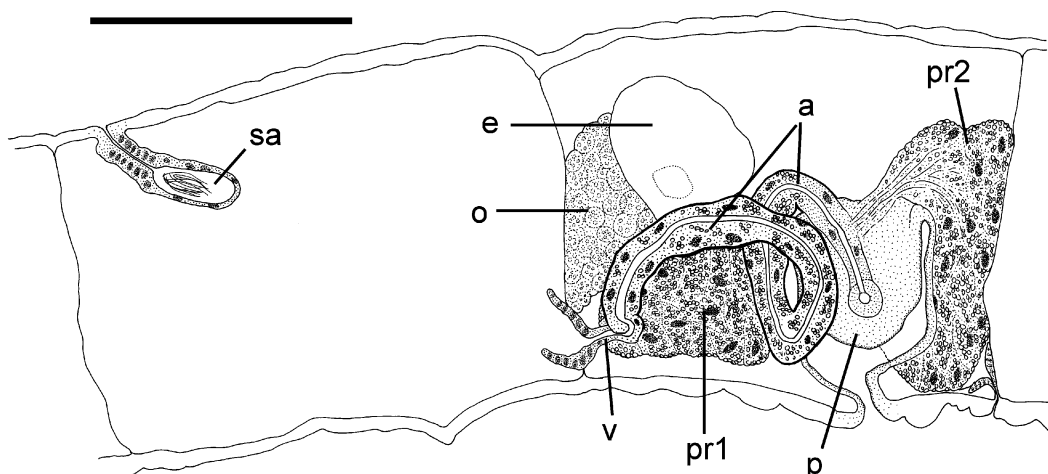


FIGURE 3. *Aktedrilus parvithecatus* (Erséus, 1978). Genitalia (scale bar 100 μm).

Remarks. Apart from lacking external spermatophores, the new specimens conform well to descriptions and illustrations of *A. parvithecatus* by Erséus (1978; 1984a; 1984b; 1987) and Erséus and Cantú-Martínez (1984). The spermatophores are placed on the exterior body wall during reproduction in some species of *Aktedrilus*, including *A. parvithecatus*, although their absence in these three specimens is not of great significance: they were absent on 4 of 8 specimens from Rottneest Island collected by Erséus (1993). This species has mostly been collected from intertidal and barely subtidal sands (Erséus 1987, 1993), although Erséus (1992b) also recorded it from brackish anchialine waters in the Cabo Verde Islands off north-west Africa. This species is obviously capable of living in a wide range of salinities as the population described above was collected in water with tds only 1800 mg L^{-1} . Occurrence in both marine littoral and brackish hypogean water (a mineral spring) has similarly been reported for *Aktedrilus cuneus* Erséus, 1984. *Aktedrilus parvithecatus* is circumtropical in distribution, with records from Pacific Mexico,

Galapagos, France, Canary and Cabo Verde Islands, Saudi Arabia, Hong Kong, Bermuda and south-western Australia (Rottnest Island).

Aktedrilus podeilema Pinder n. sp. (Fig. 4)

Holotype. WAM V 4447. Incomplete specimen whole-mounted, from Tombstone Rocks Cave, about 9 km from the ocean, Nambung region, Western Australia (Fig. 1), 30°41'S 115°14'E, 9 June 1998. Collected from sand and fine black silt with organic matter in a deep clear pool of freshwater. Coll. S. Eberhard (collection BES 5984).

Description. Body > 4.9 mm, number of segments > 40, width of slide-mounted worm 0.19 mm at segment XI. Body wall of genital segments not thicker or more glandular than that of somatic segments. Male pores ventro-lateral, each antero-medial to a small papilla, located about 2/3 of the distance between 10/11 and 11/12. Single mid-dorsal spermathecal pore located within lobes of the body wall (which may be partially everted walls of a vestibule). Female funnels not seen.

Prostomium bluntly conical, length:height at base 1.1, with thin lining tissue. Pharynx in II/III. Pharyngeal glands, consisting of irregularly shaped cells, dorsal to gut on posterior of 3/4 and lateral to gut on posterior of 4/5 and 5/6. Rest of ciliated digestive tract narrow with thin walls in III to X, slightly wider with thicker walls in genital region and much wider with even thicker lobed walls from XIV. Circulatory system not discernable. Chlorogogue tissue consisting of a single layer of cells with non-staining cytoplasm unevenly along the gut from VI. Coelomocytes not observed. Chaetae 4–6/bundle anteriorly, reduced to 3–4/bundle posteriorly, 33–48 µm long x 1–1.5 µm wide at nodulus, all bifid with sharp teeth, the upper tooth 1/2 to 3/4 the length of the lower and the nodulus slightly distal. Chaetal bundles of first few segments located 1/2 to 2/3 of the distance between anterior and posterior intersegmental furrows but most segments with bundles closer to the posterior septa. Ventral chaetae present but not modified on X, absent on XI.

Genitalia paired except for spermatheca. Testes antero-ventral in X with sperm sacs from IX to XIII. Ovaries antero-ventral in XI with egg sacs to XIV. Sperm funnels ventro-lateral on 9/10. Ciliated, non-glandular vasa deferentia about 340 µm long x 7–11 µm wide with thin muscle layer. Vasa deferentia joining atria subapically. Atria broad (50 x 95 µm) with muscle layer (1.5 µm). Numerous muscle fibres attach atria to dorso-lateral body wall (especially the ectal portion of atria) and with muscle layer of atria binding atrium to penis sac walls. Atria opening apically into stout and asymmetrical penes which are covered by a distinct cuticular sheath with a pointed antero-ventral projection. Penis sacs opening to exterior ventro-laterally. Two prostate glands associated with each set of male ducts. Posterior prostates smaller than anterior ones, lying posterior to penis sacs and communicating with male duct where the atria join the penes. Anterior prostates lying anterior to atria in vicinity of vasa deferentia but connection to male duct not visible. One

spermatheca present in X, consisting of a swollen vestibule with a narrow pore ectally and connected entally to an elongate ampulla via a constriction. Loose sperm in ampulla.

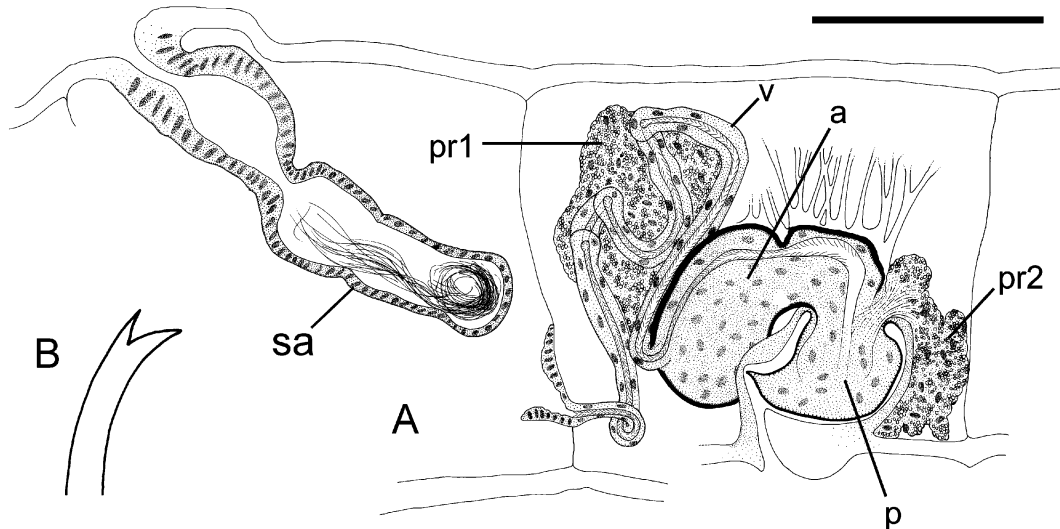


FIGURE 4. *Aktedrilus podeilema* n. sp. A, Genitalia of holotype (scale bar 100 μ m); B, anterior chaeta..

Remarks. Numerous other *Aktedrilus* possess cuticular penis sheaths. In particular, the asymmetrical sheaths of *A. podeilema* resembles those of two marine intertidal species: *A. dentatus* Erséus 1983b (from Brazil) and *A. paradentatus* Erséus 1984c (from Saudi Arabia). These two species, however, have other features (long tubular atria, posterior prostates attached broadly to the penis sacs and spermathecal pores posteriorly in IX or in intersegmental furrow 9/10) absent in the new species. Otherwise, *A. podeilema*, possessing a combination of asymmetrical penis sheaths, broad bipartite atria, long vasa deferentia and restricted connection between the posterior prostate and penis sacs, does not especially resemble any of its congeners.

Etymology. From the Greek *podos* (foot) and *eilema* (sheath) referring to the foot-shaped penis sheath.

***Aktedrilus leeuwinensis* Pinder n. sp. (Figs 5 and 6a)**

Holotype. WAM V 4448. Specimen whole-mounted, from sand and root mats (gently disturbed and caught in a net) in a pool area of a stream within Budjur Mar Cave, 34°06'00"S 115°02'50"E, 25 m asl, Leeuwin-Naturaliste Ridge, Western Australia (Fig. 1), 29 June 2002, coll. S. Eberhard.

Paratypes. WAM V 4449 and 4450. Two mature whole-mounted, collection data as for holotype.

Description. Length and number of segments 2.4–5.5 mm and 39–42 respectively, width of slide-mounted worms at segment XI 0.11–0.16 mm. Clitellum from posterior 1/3 of X to end of XII, epidermis of genital segments not thicker, but more glandular, than that of somatic segments. Anterior-most somatic segments with a distinct secondary annulation about 1/4 of the distance from anterior to posterior intersegmental furrow. Male pores ventro-lateral, about 1/3 of the distance from 10/11 to 11/12, in the form of crescent-shaped slits medial to small papillae. Single spermathecal pore mid-dorsal behind 10/11, often with ectal part of vestibule partially protruding. Female pores not seen.

Prostomium not much longer than tall, length:height at base 1.0–1.1, with loose clusters of cells below the epidermis. Pharynx in II/III. Pharyngeal glands, consisting of groups of large irregular cells, mostly lateral and dorsal to the gut in IV–VI. Digestive tract enlarging substantially between XI and XIV. Chlorogogue tissue present around gut but extent and distribution variable. Coelomocytes not observed. Chaetae 4–5/bundle anteriorly, reduced to 2(3)/bundle in post-clitellar segments, 25–30 μm long x 1.1–1.5 μm wide at nodulus, bifid with sharp teeth, the upper tooth 1/2 to 3/4 as long as lower, the nodulus distinctly distal.

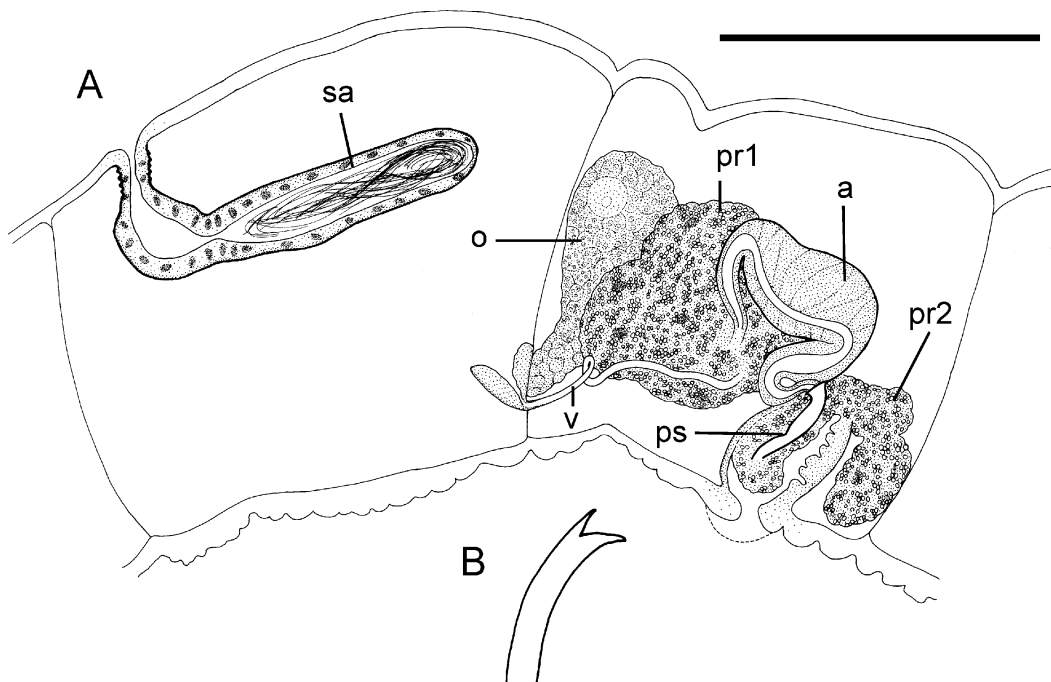


FIGURE 5. *Aktedrilus leeuwinensis*. n. sp. A, Genitalia of holotype (scale bar 100 μm); B, anterior chaeta.

Genitalia paired, except for spermatheca. Male funnels ventro-lateral on 10/11, feeding narrow (4 μm) ciliated vasa deferentia (ciliation not illustrated). Vasa deferentia partially obscured by anterior prostate, presumably joining narrow ental end of atria, but

union not seen. Atria narrow entally, expanding abruptly into a broad sac (length 70 μm , width = 34 μm) then tapering ectally to form a short ejaculatory duct which joins penes apically. Atrial muscle layer thin, lining tissue cells particularly large but position of lumen unclear — possibly towards one side of widest part of atria in holotype but more central in some other specimens (apparent position perhaps depending on aspect of view). Penes lying in deep penis sacs and enclosed by narrow, tapering and curved cuticular sheaths (Fig. 6), with the ental ends lateral to the gut and curving inwards (ventro-medially) so full extent of curve not seen from lateral view. Diagonal length of penis sheaths 20–25 μm . Penis sheaths of holotype presumably bent during lateral compression of specimen on slide (Fig. 5). Details of penis sacs difficult to discern (Fig. 5 is the authors' interpretation) but each seeming to have a glandular lobe at least partially enclosing the penis but with uncertain attachment to the sac walls and of similar glandular histology to the prostate tissue, especially entally. Anterior prostates voluminous but connection to male ducts uncertain. Posterior prostate glands between the penis sac and septa 11/12, joining the male duct at the atrial/penis sac union. Spermatheca single, with a long ampulla (up to 141 x 37 μm), connected to the mid-dorsal pore by a smaller vestibule (up to 37.5 μm long x 29 μm). Loose sperm present in ampulla. Female funnels not seen. Egg sacs extending to XIII, sperm sacs from VIII–XIII.

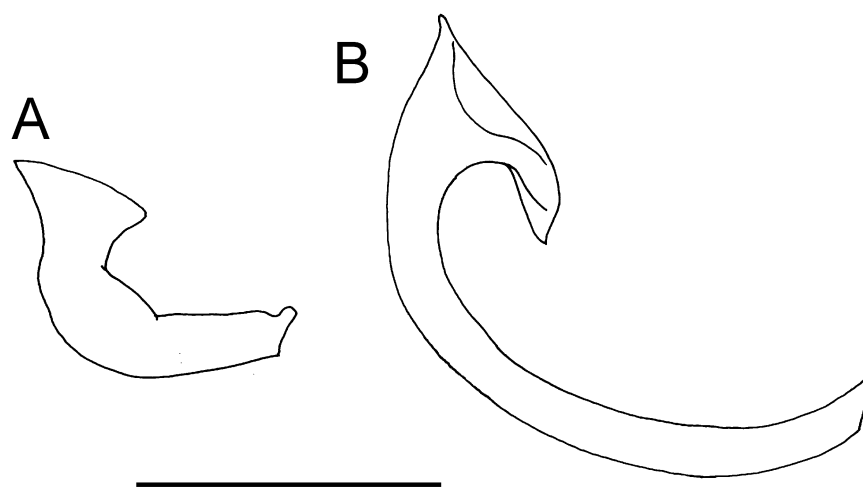


FIGURE 6. Penis sheaths of A) *Aktedrilus leeuwinensis* n. sp. and B) *Aktedrilus* sp. from Turners Spring. Scale bar 25 μm .

Remarks. Details of the male genitalia of this species needs to be confirmed further when new material becomes available. Nevertheless, this species most closely resembles a number of *Aktedrilus* which share narrow and frequently curved and/or tapering penis sheaths: *A. argatxae* Giani and Rodriguez 1988, *A. mortoni* Erséus 1984b, *A. ruffoi* Sambugar *et al.* 1999, *A. svetlovi* Finogenova 1976, *A. longitubularis* Finogenova and

Shurova 1980, *A. oregonensis* Strehlow 1982, *A. brevis* Erséus 1980 and *A. martiniquensis* Erséus 1983b. The last four of these also have a glandular pad on the penis sac wall (*longitubularis*, *brevis*, *martiniquensis*) and/or a glandular lobe of tissue within the sac (*brevis*, *oregonensis*) associated with, or even representing the full extent of (*longitubularis*, *martiniquensis*), the posterior prostate gland. The precise anatomy of the penis sac and its interaction with the posterior prostate is not clear in the new species, but the narrow curved penis sheath and the suggestion of a glandular region within the penis sac indicates that *A. leeuwinensis* is allied with these marine intertidal species. Numerous features of these other species, however, distinguish them from *leeuwinensis*: *martiniquensis* and *longitubularis* have reduced posterior prostates and the former has simple-pointed chaetae posteriorly; *longitubularis*, *oregonensis* and *brevis* have more tubular atria; only *oregonensis* has a spermatheca with a well-defined duct/vestibule ectal to an ampulla (but with a much smaller ampulla than is present in *leeuwinensis*) and all except *brevis* have sperm partly embedded within the ampulla walls. In addition, the shape and/or size of the penis sheath differs in all of these species. *Aktedrilus longitubularis* is widespread and has been recorded from Rottneest Island off the south-west coast of Australia whereas *oregonensis*, *martiniquensis* and *brevis* are known only from the coasts of the north-east Pacific, the West Indies and the south-west Atlantic respectively.

Etymology. Named after the geographical feature close to where the type material was collected: Cape Leeuwin.

Aktedrilus sp. (Fig. 6b)

Material examined. WAM V 4451, one mature and one immature whole-mounted, Turners Spring, 34°21'00"S 115°09'15"S, 25m asl, Leeuwin-Naturaliste region, Western Australia (Fig. 1), 27 Feb 2002, coll. S. Eberhard. AP colln, several immature specimens in alcohol or whole-mounted, collection details as above.

Remarks. What little of the genitalia that can be seen in the poorly preserved and obliquely mounted mature specimen resembles that of *A. leeuwinensis*, except that the penis sheaths (Fig. 6B) are almost twice the size (curved length 60 µm, height 41 µm) than those of *A. leeuwinensis* (Fig. 6A). The chaetae are also slightly larger (up to 38 µm anteriorly), although the mature worm (width 0.15 mm at XI and length 5.4 mm) is of about the same size as *A. leeuwinensis*. The penis sheaths are similar in shape to (but shorter than) those of the marine species *Aktedrilus longitubularis* Finogenova and Shurova 1980 which is widespread but known from south-western Australia. More specimens are required determine the identity of this species.

Discussion

Ten species of non-marine phallo-drilines have been described previously (Farara & Erséus 1991; Giani & Martínez-Ansemil 1981; Giani *et al.* 2001; Juget 1987; Rodriguez & Giani 1989; Sambugar *et al.* 1999), most of which are from hyporheic zones, wells, caves and springs of southern Europe. The only non-marine species recorded outside Europe are two surface water species from North America (Cook & Hiltunen 1975; Farara & Erséus 1991), one of which also occurs in Europe, and the species dealt with in this paper. The overseas fauna includes two species of *Akteredrilus* but these do not appear to be more closely related to the two new Australian species than are a number of marine species. In Western Australia, the genus *Akteredrilus* appears to be disproportionately well-represented in groundwater compared to its richness in the Australian marine littoral (5 out of a total of 73 phallo-driline species in 12 genera). However, the diversity of *Akteredrilus* in the region's intertidal sands is likely to be much greater than revealed to date (Erséus pers. comm).

All of the Western Australian groundwater localities from which phallo-drilines have been reported are within a few kilometres of the coast. While more inland regions of the state, such as the Pilbara and Yilgarn, have rich groundwater oligochaete faunas, these do not include phallo-drilines (Eberhard *et al.* 2004, unpublished data: AP and Dept Conservation and Land Management). By contrast, some polychaetes of marine affinity have been collected in groundwater up to 350 km from the coast in the Pilbara region (*ibid*) and the largely marine harpacticoid copepod families Diosaccidae Sars and Ameirinae Monard occur widely in inland groundwaters, even in inland areas long emergent from the sea (Karanovic 2004).

Holsinger (2000) summarised theories of colonisation of stygal environments and mechanisms of stygobiont evolution. Four evolutionary pathways were envisaged: 1) Evolution of marine or brackish water stygobionts (= thalassostygobionts) by adaptive shift or vicariance (e.g. sea-level change) following active invasion of marine or anchialine interstitial, crevicular or cavernous habitats; 2) Evolution of freshwater stygobionts (= limnostygobionts) from marine ancestors by adaptive shifts in freshening aquifers following stranding during marine regressions; 3) Evolution of limnostygobionts from marine ancestors by adaptive shift following active invasion of limnic aquifers via interstitial routes; 4) Evolution of limnostygobionts from epigeal limnic species by local vicariance events following active or passive invasion of hypogean waters.

The first of Holsinger's mechanisms is the most parsimonious explanation for the thalassostygobionts found in the anchialine system of Cape Range. Most marine oligochaetes are interstitial species and invasion of anchialine systems via sediments and crevices is easily envisaged. *Pectinodrillus ningaloo* may be a thalassostygobiont, though adjacent marine littoral environments have not been surveyed for oligochaetes. As discussed above, *Akteredrilus parvithecatus* is opportunistically stygal. Numerous other taxa present in the Cape Range system, including other annelids, also attest to marine connections. The spionid polychaete *Prionospio thalanji* (Wilson 2001) from Bundera

Sinkhole is apparently a sister taxon to a marine species (Wilson & Humphreys 2001). *Sphaerosyllis centroamericana* Hartmann-Schröder, 1959 (Syllidae) occurs widely in karst windows and *Typosyllis (Ehlersia) cf. broomensis* Hartmann-Schröder, 1979 (Syllidae) was found in a deep pastoral well. Both species were characterized as 'normal' marine forms (Dr G. Hartmann-Schröder, pers. comm. to WH) so are also opportunistically stygal. A new species of harpacticoid copepod in the genus *Phyllopodopsyllus* occurs in this anchialine system at the northern end of the Cape Range peninsula (Karanovic *et al.* 2001). It is the only known occurrence of the genus outside strictly marine habitats but it displays clear stygomorphies, being colourless and lacking the nauplius eye (Karanovic *et al.* 2001).

Anchialine habitats are not present within the Leeuwin-Naturaliste Ridge and Tombstone Rocks areas and no other fauna of recent marine origin are known from these systems, though the latter is poorly sampled for stygofauna. The ancestor of *Akteredrilus leeuwinensis* may have colonised Budjur Mar Cave by moving up the permanent underground stream which is presumed to have a submarine discharge (Eberhard 2004). This equates to Holsinger's pathway 3. Similarly, the *Akteredrilus* population at Turners Spring may be derived from an ancestor that moved up the creek that flows from it, presumably during wetter times when the creek may have had a more persistent flow regime. In the Leeuwin-Naturaliste region, Pleistocene marine shoreline deposits indicate sea-level rises of 3–8 m (eg. Fairbridge & Teichert 1952; Lowry 1967; Wyrwoll *et al.* 1993), while Kendrick *et al.* (1991) infer some 20 m of uplift in the southern Perth Basin since the middle Pleistocene. These eustatic sea level rises would have brought an ancestral marine species closer to both sites via Holsinger's pathway 2. No obvious lotic colonisation pathway can be envisaged for the Tombstone Rocks site, but the superficial groundwaters in this area discharge to the ocean above a saltwater interface (Nidagal 1994), while open conduits within the karst terrane may have provided colonisation routes to groundwater from the ocean, which would have been closer at times.

Another phalloporine, listed as tubificid WA9 in Pinder *et al.* (2004), from non-marine waters, was collected from the brackish (tds 6.9 g L⁻¹) Lake Mortijinup near Esperance on the south-coast of Western Australia. This resembles species belonging to *Gianius* but the available material was not sufficient for description.

Acknowledgements

Collection of material from the Cape Range area was made under funding to WH from the National Estate Program, a Commonwealth financed grants scheme administered by the Australian Heritage Commission and the Heritage Council of Western Australia, the Western Australian Water Authority, the National Estate Grants Scheme and the W.H. Butler Trust. Collection of material from the Leeuwin-Naturaliste Ridge by SE was funded

by the Augusta-Margaret River Tourism Association (CaveWorks). Christer Erséus (Göteborg University, Sweden) provided valuable advice on the generic identity of these worms and on the diversity and anatomy of phallo-drilines and Emilia Rota (University of Sienna, Italy) advised on nomenclature.

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