New species of *Doliodrilus* and other Limnodriloidinae (Oligochaeta, Tubificidae) from Hainan and other parts of the north-west Pacific Ocean

HONGZHU WANG† and CHRISTER ERSEUS‡

† State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China; e-mail: wanghai@ihb.ac.cn
‡ Department of Invertebrate Zoology, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden

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Thirteen species of Limnodriloidinae (Tubificidae) are recorded from marine and brackish-water habitats of Hainan Island, southern China, including 11 species of *Doliodrilus* and two species belonging to *Limnodriloides*. Eight species are new to science: *D. bisaccus* sp. n. (types from Japan), *D. longidentatus* sp. n. (types from Hong Kong), *D. ciliatus* sp. n., *D. adiacens* sp. n., *D. fbrisaccus* sp. n. (also from Fiji), *D. brachydactus* sp. n., *D. bidolium* sp. n. and *D. chinensis* sp. n. In addition, material of *D. puertoricensis* Erseus and Milligan, 1988, from New Caledonia, is briefly described. This study shows that *Doliodrilus* is unexpectedly species-rich in Asian seas, in particular, around Hainan. Including an unnamed species from this island, the known members of this genus increase from three to 12.

**KEYWORDS:** *Doliodrilus*, Limnodriloidinae, Oligochaeta, taxonomy, new species, southern China, Japan, Fiji, New Caledonia.

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Introduction

The marine oligochaetes of the South China Sea have been rather well studied inasmuch as a diverse fauna of these worms has been described from Hong Kong and its close surroundings in southern China (Erseus, 1984, 1990a, 1992a, 1992b, 1997a; Sundberg et al., 1992; Erseus and Diaz, 1997). The Hong Kong area, however, is greatly impacted by the activities of a multi-million human population, including the effects of heavy pollution, land reclamation and other physical removal of natural habitats, and it can be assumed that these studies cover only a part of the oligochaete species present along the Chinese coasts of the South China Sea. To broaden the basis of our knowledge, the present authors therefore made a collecting effort for marine and brackish-water oligochaetes on the island of Hainan in southernmost China, in March 2000. The Hainan coastline is less disturbed than that of the Hong
Kong region, and it extends through a slightly more tropical range of latitudes. Sampling was done in the vicinities of the two cities of Sanya (in the south) and Haikou (in the north), and special attention was paid to the oligochaete fauna of mangrove forests (see Erséus, 2002).

In a first account (Wang and Erséus, 2001), a number of species belonging to the tubificid subfamily Phalodrilininae, found in this material, were reported. In the present paper, we describe the members of the Limnodriloidinae (Tubificidae) encountered in Hainan, including eight new species of *Doliodrilus* Erséus, 1984. In this study also, we include material of *Doliodrilus* from Japan, Hong Kong, Fiji and New Caledonia.

**Material and methods**

All specimens from Hainan were collected from intertidal and subtidal sediments. The samples were repeatedly stirred with habitat water, and the organic suspensions decanted into a fine-mesh sieve (250–300 μm). Some samples were treated by the wet-funnel method (O'Connor, 1955; Healy and Rota, 1992). Live oligochaetes were sorted under dissecting microscopes. Only sexually mature specimens were fixed in Bouin’s fluid. After about 1 day in the fixative, they were transferred into 70% ethanol. Worms were stained with paracarmine, cleared in xylene and mounted whole in Canada balsam.

The type specimens of *Doliodrilus bisaccus* sp. n. and *D. longidentatus* sp. n were collected in Japan by Dr K. Ogawa and in Hong Kong by C. Erséus, respectively; the Hong Kong material was previously identified as *D. tener* (Erséus, 1990a). Specimens of *D. longidentatus* from Hong Kong were also provided by A. Mackie and G. Oliver. Additional material of *D. fibriscaccus* sp. n. and new specimens of *D. puertoricensis* Erséus and Milligan, 1988 were collected by C. Erséus from Fiji and New Caledonia, respectively. Type material and other reference specimens in the Swedish Museum of Natural History (SMNH), Stockholm, were re-examined.

Holotypes, some paratypes and other reference specimens are deposited in the Institute of Hydrobiology (IHB), Chinese Academy of Sciences (CAS), Wuhan; the remaining material, including type specimens of *Doliodrilus bisaccus* sp. n. and *D. longidentatus* sp. n., is lodged in SMNH.

When not stated otherwise, material listed in the Systematic account, measurements, and drawings refer to fixed, whole-mounted and slightly compressed specimens.

**Abbreviations used in the figures**

a, atrium; aa, atrial ampulla; ad, atrial duct; at1, first ‘lobe’ of atrial ampulla; at2, second ‘lobe’ of atrial ampulla; bs, blind sac of atrial duct; cs, copulatory sac; ead, ectal atrial dilatation; ed, efferent duct of atrium; mp, male pore; ncc, nuclei clusters close to prostatic pad; nco, nuclei cluster opposite to prostatic pad; od, oesophageal diverticulum; ppd, prostatic pad; pr, prostate gland; s, spermatheca; sf, sperm funnel; sp, spermathecal pore; sz, spermatozeugma; vd, vas deferens.

**List of stations in Hainan**

The following stations were sampled by the authors; omitted are sites yielding no Limnodriloidinae. The species of the subfamily encountered are listed for each station.

*Station SY00-2A.* Main flow of Sanya River, at children’s park in middle of
Sanya City, 18°15.34' N, 109°30.25' E, soft organic sediment, 14 March 2000; *Doliodrilus tener*, *D. diverti culatus*.

*SY00-6.* Fish pond at road to Teng Hai, E of Sanya City, 18°17’N, 109°44’E, brackish-water, coarse sand with black mud, 16 March 2000; *Doliodrilus bisaccus* sp. n., *D. fibriscus* sp. n., *D. brachydactus* sp. n., *D. bidolium* sp. n., *D. chinensis* sp. n.

*SY00-8A.* The West Coral Islet (Ximaozhou) (W of Sanya City), reef flat at NW side of island close to tourist resort, 18°14.56’N, 109°21.97’E, barely subtidal, poorly oxygenated coarse sand with smell of H₂S, 17 March 2000; *Limnodriloides macinnesi*.

*SY00-9C.* Lower end of estuary SE of Teng Qiao Town, 18°23.18’N, 109°45.71’E, lower intertidal, silty medium sands with black mud, 18 March 2000; *Doliodrilus tener*, *D. adiacepp* sp. n., *D. fibriscus* sp. n., *Limnodriloides parahastatus*.

*SY00-10.* Brackish-water shrimp pond connected with estuary SE of Teng Qiao Town, 18°22.93’N, 109°45.57’E, lower intertidal, medium to coarse sand with black mud and filamentous algae, 18 March 2000; *Doliodrilus fibriscus* sp. n.

*HU00-14A.* Dong Zhai Harbour nature reserve E of Haikou, edge of mangrove channel immediately N of dock located at end of concrete walkway from off nature reserve gate, 19°57.00’N, 110°34.01’E, subtidal, about 1 m, mud, 21 March 2000; *Doliodrilus tener*.

*HU00-14B.* Same as *HU00-14A*, but under branches of mangrove trees N of dock, lower intertidal, clay and mud, 21 March 2000; *Doliodrilus longidentatus* sp. n., *D. ciliatus* sp. n.

*HU00-19A.* Haikou City, bay (surrounded by wall) in Wan Lu Yuan Park, 20°02.10’N, 110°18.66’E, subtidal, mud with some sand, 22 March 2000; *Doliodrilus tener*, D. sp., *D. diverti culatus*.

**Systematic account**

**Family TUBIFICIDAE**

**Subfamily LIMNODRILOIDINAE**

**Genus Doliodrilus** Erséus, 1984

**Remarks.** This genus was established by Erséus (1984) with *D. tener* Erséus, 1984 from Hong Kong as type species, and then expanded to accommodate *D. diverti culatus* Erséus, 1985 from Saudi Arabia (Erséus, 1985). Later, a third species, *D. puertoricensis* Erséus and Milligan, 1988, was added from Puerto Rico (Erséus and Milligan, 1988). In this paper, we describe eight new species belonging to this genus, but some of them do not conform completely with the previous diagnosis, which thus needs to be revised, and this will be done in a more comprehensive study of the subfamily Limnodriloidinae elsewhere. As a rule, the members of *Doliodrilus* are characterized by: (1) a modified, enlarged, tract of oesophagus in IX (sometimes involving also a part of VIII) bearing a reticulate blood plexus (see Gustavsson and Erséus, 1999); (2) distinct prostatic pads, each restricted to a limited region of the atrial ampulla (see Erséus, 1982); (3) weakly granulated atrial ducts (see Erséus, 1982), generally provided with blind sacs or ectal dilatations, and terminating in simple male pores; (4) large, deeply staining, nucleus-like bodies in the prostate glands of some species, their true nature being unknown; and (5) vestibules at the ectal orifices of the spermathecal ducts.
**Doliodrilus tener** Erseus, 1984

*(figure 1)*


![Diagram](image)

**Fig. 1.** *Doliodrilus tener* Erseus, 1984. Male ducts of two specimens, with triangular (A) or hemispherical (B) prostatic projections, respectively.
New material. IHB HANA2000003b–e, HANA2000017c, HANA2000022a–e, HANA2000029c–f, 14 specimens: four from SY00-2A, one from SY00-9C, five from Station HU00-14A, four from HU00-19A. SMNH Main Coll. 43665–43677, 13 specimens: three from SY00-2A, seven from HU00-14A, three from HU00-19A.

Brief description of new material. Six complete specimens 5.1–9.8 mm long, 28–45 segments. Diameter at XI about 0.4 mm. Prostomium usually conical. Clitellum extending over XI–XII. Chaetae 50–75 µm long, about 2.5 µm thick, with upper teeth 1–1.5 times as long as, and thinner than or as thick as, lower; two to five per bundle anteriorly, one to three per bundle in post-clitellary segments. Chloragogen cells from VI onwards. Oesophagus in IX barrel-shaped, thick-walled and granulated, with or without chloragogen cells; semi-embedded blood plexus permeating dorsal region, with regular transverse vessels and less regular longitudinal ones. Vasa deferentia (figure 1A; vd) about 135 µm long, 12–19 µm wide. Atria totally 200–220 µm long, 14–36 µm wide; ental end of atrial ampullae thin-walled and distinctly dilated; ventral projections on ampullae either (1) triangular (figure 1A), each with small (only 10–17 µm long) prostatic pad (ppd) at bottom, and with numerous spindle-shaped nuclei (ncc) along both sides of pad (especially ental to pad), or (2) hemispherical (figure 1B), with large (29–34 µm long) prostatic pad (ppd), and with dense, but smaller patches of slender nuclei (ncc) around pad. Dense cluster of nuclei also present in dorsal wall of ampulla opposite to prostatic pad; these nuclei slender and regularly arranged when ventral projection triangular (figure 1A: nco), but oval and less regular when projection hemispherical (figure 1B: nco). Prostate glands (figure 1A, B: pr) usually medium to large, sometimes small, with small nuclei and large nucleus-like bodies, latter oblong to round, maximally 12 µm long, 11 µm wide. Atrial ducts (figure 1A, B: ad) each with (1) posterior blind sac (bs), 25–50 µm long, 15–30 µm wide, and (2) efferent duct (ed), 25–35 µm long, 19–27 µm wide. Sperm sac in one to five segments within IX–XIII, when developed at all. Egg sac in one to three segments within XI–XIII, when developed. Spermathecal ducts 45–95 µm long, 24–44 µm wide, with ectal vestibules; ampullae 85–175 µm long, 30–95 µm wide, with sperm arranged in bundles or masses in lumina.

Remarks. This species was originally described from Hong Kong (Erséus, 1984). In 1990, Erséus reported it from Hong Kong again, noting some morphological variation, but a form with unusually long upper teeth on the chaetae is now regarded as a separate taxon (see D. longidentatus sp. n. below). The other known distributional areas of D. tener are Qingdao (Erséus et al., 1990) and Taiwan (Erséus and Hsieh, 1997).

The most prominent character of D. tener, not specifically noted in the previous descriptions, is the conspicuous thickening of the dorsal wall opposite to the prostatic pad in the atrium, and the clusters of nuclei in this wall and around the pad. We observed this character in all the material from Hainan, as well as in numerous old specimens from Hong Kong [treated by Erséus, 1984, 1990a (partim)]. However, there are two different appearances of the ventral projections on the atria; they are either triangular (figure 1A) or hemispherical (figure 1B) (see above description). In the former state, the small prostatic pads seem to have discharged secretion into the atria, and the nuclei around the pads are widely distributed. In the latter state, the large pads appear to be full of secretion, and the nuclei are more restricted in distribution.

The prostate glands were stated to be small in the Hong Kong material (Erséus, 1984, 1990a), but a re-examination shows that the glands in the specimens from
Hong Kong and Taiwan (Erséus and Hsieh, 1997), as well as in the new material, vary considerably, i.e. from small to large.

Distribution and habitat. Known only from China [Hainan (new record), Hong Kong, Jiaozhou Bay (at Qingdao), Taiwan]. Brackish-water, intertidal and subtidal soft mud and muddy sand.

**Doliodrilus bisaccus** sp. n.

(figure 2)

**Holotype.** SMNH Type Coll. 5457, whole-mounted specimen.

**Type locality.** Japan, Honshu, Mie Prefecture, Gokasho Bay, brackish-water; 16 May 1990, coll. K. Ogawa.

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Fig. 2. *Doliodrilus bisaccus* sp. n. (A) Chaetae; (B) spermatheca; (C, D) male ducts of two specimens.
New species of *Doliodrilus* from Hainan 275

*Paratypes.* SMNH Type Coll. 5458–5460, three specimens from type locality.

*Other material.* IHB HANA2000009al, one specimen from Hainan Island, Station SY00-6.

*Etymology.* The specific name *bisaccus* is Latin for ‘with two sacs’, and refers to the bilobed atrial ampullae, a feature unique within the genus.

*Description of type material.* Two complete specimens, holotype 9.7 mm with 43 segments, one paratype 8.4 mm with 41 segments. Diameter at XI 0.3–0.5 mm. Prostomium usually conical. Clitellum well developed over XI–XII. Chaetae bifid, with upper teeth more or less as long as, and thinner than, or sometimes as thick as, lower (figure 2A). Chaetae 45–60 μm long, about 2.5 μm thick; (zero) one to two (three) per bundle anteriorly, zero to two per bundle in post-clitellar segments. Ventral chaetae absent in XI. Male pores, paired in line with ventral chaetae in posterior part of XI (figure 2B). Spermathecal pores paired in line with ventral chaetae in anterior part of X.

Pharyngeal glands well developed in IV–V. Chloragogen cells from VI onwards. Oesophagus in IX barrel-shaped, thick-walled and granulated, without chloragogen cells; semi-embedded blood plexus permeating entire region, with regular transverse vessels and less regular longitudinal ones.

Male genitalia (figure 2C, D) paired. Vas deferens (figure 2C, D: vd) short and wide, about 70 μm long, 19–22 μm wide, entering atrium apically. Ental part of atrial ampulla bilobed, thin-walled and dilated; lobes separated by constriction. First ‘lobe’ of ampulla (figure 2C, D: at1) conical or oval, 35–65 μm long, maximally 39–53 μm wide. Second ‘lobe’ oval (at2), 35–50 μm long, maximally 39–44 μm wide. Ectal part of atrial ampulla more duct-like, thick-walled, with numerous slender nuclei close to (figure 2C, D: nce) and opposite to (nco) prostatic pad. This part 150–155 μm long, 16–48 μm wide. Prostatic pad (figure 2C, D: ppd) round, 46–48 μm long, ventrally attached to middle of duct-like part of atrial ampulla (aa), bulging out from atrium. Prostate gland (figure 2C, D: pr) large, with small nuclei and large nucleus-like bodies, latter oblong or round, maximally 16 μm long, 15 μm wide. Atrial duct (figure 2C, D: ad) with (1) posterior blind sac (bs), 25–50 μm long, 15–48 μm wide, and (2) efferent duct (ed), 45–55 μm long, 31–48 μm wide, opening directly to exterior through simple pore. Sperm sac in IX–XII, or XI–XII. Egg sac in XII–XIII or absent. Spermathecae (figure 2B) large; ducts 75–105 μm long, 36–48 μm wide, with ectal vestibules; ampullae oblong, thin-walled, 145–195 μm long, 50–75 μm wide, with sperm masses in lumina.

*Brief description of specimen from Hainan.* Specimen complete, 5 mm long, 39 segments. Chaetae 45–55 μm long, about 2.5 μm thick, bifid, with equal teeth; one to two (three) per bundle anteriorly, one to two per bundle in post-clitellar segments. Male pores posterior to middle of XI. Male ducts somewhat twisted and difficult to make out. Spermathecae with oblong ampullae, but without sperm; specimen appears pre-copulatory.

*Remarks.* This species is easily distinguished from all its congeners by its bilobed atrial ampullae, and low number of chaetae; latter usually no more than two per bundle or even absent. The atria have dorsal thickenings and clusters of slender nuclei around the prostatic pads, as well as blind sacs, suggesting a close relationship to *D. tener*. In the new species, however, the vasa deferentia are shorter than those of the latter, and the prostatic pads are situated at mid-point of the atrium, as opposed to the more ental location in *D. tener*.

Although not all its features were clearly seen, the specimen from Hainan has
fewer chaetae than *D. tener*, and appears to have blind sacs and clusters of slender nuclei in the atria. Therefore, it is identified as *D. bisaccus*, at least for the time being.

*Distribution and habitat.* Japan and southern China. Brackish-water, muddy sands.

*Doliolirulus longidentatus* sp. n.

(figures 3)


*Non Doliolirulus tener* Erséus, 1984: 159–160, figure 15.

*Holotype.* SMNH Type. Coll. 5461, whole-mounted specimen.

*Type locality.* China, Hong Kong, mangroves at Mai Po, edge of dredged channel, mid-intertidal mud (Station HK86-26 = ‘Station 70’ in Erséus, 1990a); 9 April 1986, coll. C. Erséus.

*Paratypes.* SMNH Type. Coll. 5462–5466, five specimens from type locality. SMNH Type Coll. 5467–5468, two (sectioned) specimens from type locality. SMNH Type Coll. 5469–5470, two from Hong Kong, Deep Bay, mudflat just off mangroves at Mai Po marshes (Station HK86-25 = ‘Station 69’ in Erséus, 1990a); 9 April 1986, coll. C. Erséus. SMNH Type Coll. 5471, one specimen from Hong Kong, Deep Bay, Tsim Bei Sui, intertidal mudflat (Station HK86-31 = ‘Station 76’ in Erséus, 1990a); 10 April 1986, coll. C. Erséus.

*Other material.* SMNH Main Coll. 43678–43679, two specimens from Hong Kong, Deep Bay, mangroves at Mai Po marshes, intertidal mud; 22 April 1989, coll. A. Mackie and G. Oliver. IHB HANA2000023a, one specimen from Hainan Island, Station HU00-14B.

*Etymology.* The specific name *longidentatus* is Latin for ‘with long teeth’, and refers to the long upper teeth of the chaetae.

*Description.* No complete specimen in material from Hong Kong. Hainan specimen 9.3 mm long, about 50 segments. Diameter at XI 0.4–0.6 mm. Prostomium conical. Clitellum well developed over XI–XII. Chaetae bifid, with upper teeth 2–2.5 times as long as, and as thick as, lower (figure 3A). Chaetae 70–85 µm long, about 3 µm thick; (two) three to four (five) per bundle anteriorly, two (three) per bundle in post-clitellar segments. Ventral chaetae absent in XI. Male pores paired, in line with ventral chaetae in posterior part of XI (figure 3B). Spermaticheal pores paired, in line with ventral chaetae in anterior part of X.

Pharyngeal glands well developed in IV–V. Chloragogen cells from VI onwards. Oesophagus in IX barrel-shaped, thick-walled and granulated, without or with few chloragogen cells; semi-embedded blood plexus permeating dorsal region, with regular transverse vessels and less regular longitudinal ones.

Male genitalia (figure 3C, D) paired. Vas deferens (figure 3C, D: vd) 160–255 µm long, 19–22 µm wide, entering atrium apically. Atrium totally 190–340 µm long, 14–48 µm wide; ental part of ampulla thin-walled and dilated, ectal part tubular and with more nuclei (figure 3C, D: aa), but without clusters of dense slender nuclei around prostatic pad; when atrium not stretched (figure 3C), dorsal wall opposite to prostatic pad somewhat thicker than other parts of ampullar wall. Prostatic pad (figure 3C, D: ppd) round, 17–24 µm long, bulging out from atrial ampulla, usually situated at middle or ectal to middle of atrium (figure 3C), but slightly ental to middle of atrium when latter is stretched (figure 3D). Prostate gland (figure 3C, D:
Fig. 3. *Doliodrilus longidentatus* sp. n. (A) Chaetae; (B) spermatheca of specimen from Hainan; (C, D) male ducts of holotype (C) and one paratype (D).
medium-sized, with small nuclei and large nucleus-like bodies, latter oblong to round, maximally 14 μm long, 10 μm wide. Atrial duct (figure 3C, D: ad) with (1) large posterior blind sac (bs), 95–120 μm long, 15–40 μm wide, and (2) short efferent duct (ed), about 35 μm long, 31–48 μm wide. Sperm sac in one to two segments within IX–XI, when developed at all. Egg sac in one to two segments within XI–XIII, when developed. Spermathecae (figure 3B) variable in size; ducts about 50 μm long, 22–31 μm wide, with ectal vestibules; ampullae oblong, 95–205 μm long, 60–75 μm wide, with sperm masses in lumina.

Remarks. This species was previously regarded as a form of *D. tener* (Erseus, 1990a), but as the result of a more careful assessment of the male genital ducts, it is now recognized as a separate taxon. It is distinguished from *D. tener* by the distinctly longer upper teeth of its chaetae, the absence of clusters of slender nuclei in the atria, the more ectal location of the prostatic pads on the atria, and, generally, the larger size of external and internal structures. The long upper teeth on the chaetae are shared by *D. ciliatus* sp. n. (described below), but otherwise this feature discriminates *D. longidentatus* from all congeners.

The specimen from Hainan was studied from a dorsal view, and its identification is mainly based upon the features of the chaetae and the absence of nuclei clusters.

Distribution and habitat. Southern China. Usually intertidal in mangroves, clay and mud.

*Doliodrilus ciliatus* sp. n.

(figure 4)

Holotype. IHB HANA2000023b, whole-mounted specimen.

Type locality. China, northern Hainan, mangroves of Dong Zhai Harbour nature reserve (Station HU00-14B).

Etymology. The specific name *ciliatus* is Latin for ‘furnished with cilia’ and refers to the ciliated atria.

Description. Specimen complete, 12.0 mm, 69 segments. Diameter at XI 0.5 mm. Prostomium conical. Clitellum extending over XI–1/2XII. Chaetae bifid, with upper teeth about twice as long as lower (figure 4A). Chaetae 70–85 μm long, about 2.5 μm thick; two to five per bundle anteriorly, two to three per bundle in post-clitellar segments. Ventral chaetae absent in XI. Male pores paired, in line with ventral chaetae in posterior part of XI (figure 4B). Spermathecal pores paired, in line with ventral chaetae in X, at about one-third of segment from anterior septum (figure 4B).

Pharyngeal glands well developed in IV–V. Chloragogen cells from VI onwards. Anterior third of oesophagus in IX unmodified, with wall only 25–35 μm thick. Posterior two-thirds of oesophagus in IX barrel-shaped, granulated, with wall up to 70 μm thick, but without chloragogen cells; semi-embedded blood plexus present, but inconspicuous, with regular transverse vessels and less regular longitudinal ones.

Male genitalia (figure 4B) paired. Vas deferens not clearly visible, estimated to be about as long as atrium, entering latter subapically (?). Atrium tubular, totally 230 μm long, 17–27 μm wide; ental part of atrial ampulla densely ciliated, thin-walled and somewhat dilated; ectal part of ampulla more thick-walled, and with wall containing more nuclei (figure 4B: aa). Prostatic pad (ppd) oval, 31 μm long, ventrally situated, bulging out from middle of atrium. Prostate gland (pr) large,
with small nuclei and large nucleus-like bodies, latter oblong, round or irregularly polygonal, maximally 14 μm long, 10 μm wide. Atrial duct (figure 4B: ad) with (1) posterior blind sac (bs), about 30 μm long, 10–15 μm wide, and (2) short efferent duct (ed), about 30 μm long, 25 μm wide, opening directly to exterior through simple pore. Sperm sac extending through IX–X. Egg sac in XII–XIII. Spermathecae (figure 4B: s) club-shaped; ducts 110 μm long, 27–34 μm wide, with small, but distinct ectal vestibules; ampullae oval, thin-walled, 120 μm long, up to 77 μm wide, with sperm bundles in lumina.

Remarks. Initially, we hesitated to assign this species to the genus Doliodrilus, as the ental parts of its atria are ciliated, a character formerly considered to be an autapomorphy of Smithsonidrilus Brinkhurst, 1966 (Limnodriloidinae) (Erséus, 1990b). However, D. ciliatus has a dilated oesophagus in segment IX, and although indistinct, there is an oesophageal blood plexus in this segment. This type of modification as well as the atrial blind sacs are characteristic of most Doliodrilus, and thus, it is reasonable to conclude that this species belongs to the latter genus. With regard to the chaetal morphology and male ducts, D. ciliatus appears to be closely related to D. longidentatus sp. n. described above, but it is easily differentiated from the latter and other congeners by its ciliated atria, and the short length of the modified part of the oesophagus in segment IX.

Distribution and habitat. Known only from type locality, southern China. Lower intertidal in mangroves, clay and mud.
Doliodrilus sp.  
(figure 5)

Material examined. IHB HANA2000029a–b, two whole-mounted specimens from Station HU-19A. SMNH Main Coll. 43680, one specimen from HU-19A.

Description. Two complete specimens, 5.6–6.8 mm long, 45–46 segments. Diameter at XI 0.2–0.3 mm. Prostomium blunt. Clitellum well developed over XI–1/2 XII (XII). Chaetae bifid, with upper teeth thinner than, and as long as, lower (figure 5A). Chaetae 50–65 μm long, about 2.5 μm thick; two to four per bundle anteriorly, (one) two to three per bundle in post-clitellar segments. Ventral chaetae absent in XI. Male pores paired, in line with ventral chaetae in posterior part of XI (figure 5C). Spermathecal pores paired, in line with ventral chaetae in anterior part of X.

Pharyngeal glands in IV–V. Chloragogen cells from VI onwards. Oesophagus in IX barrel-shaped, thick-walled and granulated, with reticulate blood plexus but without chloragogen cells.

Male genitalia (figure 5C) paired. Vas deferens inconspicuous, estimated to be about as long as atrium, but unclear whether it enters latter apically or subapically. Atrium totally about 150 μm long, 15–30 μm wide, somewhat club-shaped; ental part of atrium dilated but not thin-walled; wall opposite prostatic pad somewhat

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**Fig. 5.** Doliodrilus sp. (A) Chaeta; (B) spermatheca; (C) male duct.
thicker than other part of ampullar wall, but thickening without clusters of slender nuclei (figure 5C: aa). Prostatic pad (ppd) large and round, 36 μm long, situated ventrally one-third down atrium from apical end. Prostate gland (pr) large, with small nucleli and large nucleus-like bodies, latter oblong to round, maximally 12 μm long, 10 μm wide. Atrial duct (figure 5C: ad) with (1) small posterior blind sac (bs), about 20 μm long, 12–17 μm wide, and (2) short efferent duct (ed), about 20 μm long, 14 μm wide. Sperm sac in XI. Egg sac in XII. Spermathecae (figure 5B) small; ducts short, about 27 μm long, up to 24 μm wide, with ectal vestibules; ampullae oblong, 90 μm long, 30–50 μm wide, with sperm masses in lumina.

Remarks. With regard to the male ducts, this form appears closely related to D. tener. However, there are substantial differences. First, the ental parts of its atria are not thin-walled and dilated as in the latter. Second, its prostatic pads are more entally located and somewhat bigger than those of D. tener. Third, there are no clusters of slender nuclei around its prostatic pads. Hence, this form is likely to be a separate species. However, considering that two of the specimens are partly damaged, and the male ducts of the other are obscured by food particles, we do not name it for the time being.

In one of the studied specimens, the posterior end bears commensal ciliates, similar to those reported by Erséus (1990a: 295, figure 15H).

Distribution and habitat. Known only from one locality in Hainan, China. Brackish-water, subtidal, sandy mud.

Doliodrillus adiacens sp. n.

(figure 6)

Holotype. IHB HANA2000017b, whole-mounted specimen.

Type locality. China, southern Hainan, lower end of estuary SE of Teng Qiao Town (Station SY00-9C).

Paratype. IHB HANA2000017c–d, two specimens from type locality. SMNH Type Coll. 5472–5474, three specimens from type locality.

Etymology. The specific name ‘adiacens’ is Latin for ‘adjacent’, and alludes to the position of the spermathecal pores, which are located immediately behind the anterior septum of segment X.

Description. Two complete specimens, holotype 4.6 mm with 43 segments, one paratype 7.0 mm with 53 segments. Diameter at XI 0.3–0.4 mm. Prostomium blunt. Clitellum well developed over XI–XII. Chaetae bifid, with upper teeth variable in length (ranging from longer to shorter than lower teeth), and thinner than, or sometimes as thick as, lower (figure 6A). Chaetae 40–60 μm long, about 2.5 μm thick; (one) two to four (five) per bundle anteriorly, (one) two to three per bundle in post-clitellar segments. Ventral chaetae absent in XI. Male pores paired, in line with ventral chaetae in posterior part of XI (figure 6C, D). Spermathecal pores paired in line with ventral chaetae, immediately behind septum 9/10 (figure 6B).

Pharyngeal glands in IV–V; those in V sometimes indistinct. Chloragogen cells from VI onwards. Oesophagus in IX barrel-shaped, thick-walled and granulated, with chloragogen cells; semi-embedded blood plexus permeating dorsal region, with regular transverse vessels and less regular longitudinal ones.

Male genitalia (figure 6C, D) paired. Vas deferens (figure 6C, D; vd) 120–155 μm long, about 18 μm wide, entering atrium subapically. Atrium tubular, totally 150–180 μm long, 16–24 μm wide; ental ampulla dilated but not thin-walled; dorsal wall
Fig. 6. Doliodrilus adiacens sp. n. (A) Chaetae; (B) spermatheca of one paratype; (C, D) male ducts of one paratype (C) and holotype (D).

opposite prostatic pad thin, and clusters of slender nuclei around pad absent (figure 6C, D: aa). Prostatic pad (ppd) small, oval to round, 16–24 μm long, situated at middle or ectal to middle of atrium. Prostate gland (pr) medium-sized, with oblong to round nuclei, latter maximally 8 μm long, 5 μm wide. Atrial duct (figure 6C, D: ad) with (1) posterior blind sac (bs), varying in size mainly with regard to extent of evagination of male pore, 15–50 μm long, 10–20 μm wide, and (2) efferent duct (ed), also variable, 10–40 μm long, 12–17 μm wide. Spermathecal ducts (figure 6B) about 30 μm long, about 23 μm wide, with ectal vestibules; ampullae cylindrical, 70–100 μm long, 25–35 μm wide, with more or less sigmoid spermatozeugmata (figure 6B: sz) in lumina.

Remarks. This species has two distinguishing characters. First, its spermathecal
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pores are adjacent to the anterior septum of segment X, whereas those of all the congeneres are well separated from the septum. Second, in *D. adiacens* sp. n., the vasa deferentia enter the atria at a considerable distance from the apical ends of the latter, while the vasa join the atria apically in most of the congeres (vasa slightly subapical in *D. brachyductus* sp. n. and, probably, also in *D. ciliatus* sp. n.). With regard to the male ducts, it seems likely that *D. adiacens* is closely related to *D. tener* and *D. longidentatus* sp. n. In addition to the above-mentioned features, *D. adiacens* differs from *D. tener* by its lack of clusters of slender atrial nuclei and the more ectal location of its prostatic pads, and from *D. longidentatus* sp. n. by the shorter upper teeth of its chaetae, and the thicker walls of the ental part of the atria.

**Distribution and habitat.** Known only from type locality, Hainan, China. Brackish-water, lower intertidal, muddy sand.

**Doliodrilus divorticulatus** Erős, 1985

*(figure 7)*


**New material.** IHB HANA2000003a, one specimen from SY00-2A. SMNH Main Coll. 43681, one specimen from HU00-19A.

**Brief description of new material.** One complete specimen 3.5 mm long, about 30 segments. Diameter at XI 0.3–0.4 mm. Prostomium conical. Clitellum extending over XI-XII. Chaetae 50–55 μm long, about 2.5 μm thick, with upper teeth variable in length, ranging from longer to shorter than lower teeth (figure 7A); (two) three to four (five) per bundle anteriorly, one to three per bundle in post-clitellar segments. Chloragogen cells from VI onwards. Unpaired ventral diverticulum in IX variable; in specimen from SY00-2A, diverticulum (figure 7F: od) only about 85 μm long, 40–50 μm wide, covered with cell projections, and without reticulate blood plexus; in specimen from HU00-19A, diverticulum (figure 7E: od) larger, about 200 μm long, 80–90 μm wide, with conspicuous, more or less regular, blood plexus; moreover, in latter specimen, although less distinct, plexus developed also on other parts of the gut in IX–XII. Vasa deferentia (figure 7D: vd) about 100 μm long, 10 μm wide. Atria slender, totally 135–160 μm long, 7–22 μm wide; ental part not thin-walled, tapering off on to vasa. Prostatic pads (figure 7D: ppd) somewhat triangular, about 24 μm long. Prostate gland (pr) medium-sized, with oblong or round nuclei, latter maximally 7 μm long and 6 μm wide. Atrial ducts (figure 7D: ad) each with (1) posterior blind sac (bs), 20–25 μm long, 10–35 μm wide, and (2) efferent duct (ed), 15–25 μm long, 17–24 μm wide. Spermathecal ducts 30–35 μm long, 12–29 μm wide; ampullae 50–55 μm long, 10–35 μm wide (figure 7B, C); only the specimen from HU00-19A post-copulatory, with a few scattered spermatozoa in lumina of ampullae (figure 7B).

**Remarks.** This species was originally described from Saudi Arabia, and subsequently reported also from Darwin Harbour (Erős, 1997b) and Montebello Islands (Erős, 1997c) in Australia. The new material conforms to the previous descriptions (Erős, 1985, 1997b, 1997c) in most aspects, particularly, with regard to male ducts.

The unpaired diverticulum was first described as ‘dorsal’ (Erős, 1985), but was later shown to be attached to the ventral side of the oesophagus and from there to
Fig. 7. *Doliodrilus diverticulatus* Erseus, 1985. (A) Chaetae; (B, C) spermathecae of specimens from Stations HU00-19A (B) and SY00-2A (C); (D) male duct of specimen from Station SY00-2A; (E, F) side views of oesophagus in segment IX of specimens from Stations HU00-19A (E) and SY00-2A (F).

run upwards along one lateral side of the segment (Erseus, 1997c; Gustavsson and Erseus, 1999). The new material conforms with the latter description. However, the diverticulum is variable in size, a large one being over twice as long as a small one. Such a variation was confirmed also by re-examination of the specimens from Saudi
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Arabia (treated by Erseús, 1985) and Darwin Harbour (treated by Erseús, 1997b), which all have similar body size. In the Saudi Arabia material, the diverticulum is 100–180 μm long, 40–70 μm wide, and in that from Darwin Harbour, it is about 250 μm long, 100 μm wide.

Referring to the blood plexus, it is absent or present in the diverticulum of the new material, and when present it may even extend more broadly on to the gut. Gustavsson and Erseús (1999) noted the irregular blood plexus in the diverticulum of Darwin Harbour worms, but on re-examination of that material, we found it also to be present in other parts of the gut in segments IX–1/3X. In the Saudi Arabian form, we also observed the irregular blood plexus in the diverticulum. Hence, a blood plexus is generally present in the diverticulum in *D. diverticulatus*, but it is less regular than in other species.

In the original description by Erseús (1985), the clitellum is stated to extend over XI–1/2XII, but a re-examination of his material showed that it actually reaches the end of XII in some specimens. The new material falls within this variation.

**Distribution and habitat.** Southern China (new record), Western Australia and Northern Territory in Australia, and Saudi Arabia. Brackish-water to marine, intertidal and subtidal in mangroves, sand and mud.

*Doliodrilus fbrisaccus* sp. n.

*(figure 8)*

**Holotype.** IHB HANA2000018a, whole-mounted specimen.

**Type locality.** China, southern Hainan, brackish-water pond SE of Teng Qiao Town (Station SY00-10).

**Paratypes.** IHB HANA2000009a–d, HANA2000017a, five specimens: four from SY00-6, one from SY00-9C. SMNH Type Coll. 5475–5479, five specimens: one from type locality, four from SY00-6.

**Other material.** IHB HANA2000009e–h, four specimens from SY00-6. SMNH Main Coll. 43682–43685, four specimens from SY00-6. SMNH Main Coll. 43686–43695, 10 specimens from Fiji, Viti Levu, Lauthala Bay (E of Suva), Rewa River Delta at N end of Lauthala Island, mangrove swamp, mud, intertidal, oligohaline brackish-water; 3 December 1982, coll. C. Erseús (Station FI82-16).

**Etymology.** The specific name *fbrisaccus*, Latin meaning 'with fibrous sac', refers to the muscular ectal part of the male duct.

**Description of material from Hainan** (figure 8A–C). Six complete specimens 3.5–9.7 mm long (holotype: 6.5 mm), 23–57 segments (holotype: 33). Diameter at XI 0.3–0.4 mm. Prostomium more or less conical. Clitellum more or less developed over XI–XII. Chaetae (figure 8A) bifid, with upper teeth thinner, and shorter than, or as long as, lower. Chaetae 45–60 μm long, about 2.5 μm thick, (one) two to four (five) per bundle anteriorly, (one) two (three) per bundle in post-clitellar segments. Ventral chaetae absent in XI. Male pores paired, in line with ventral chaetae in posterior part of XI (figure 8C). Spermatical pores paired, in line with ventral chaetae in anterior part of X (figure 8B).

Pharyngeal glands in IV–V; those in V sometimes indistinct or absent. Chloragogen cells from VI onwards. Oesophagus in IX barrel-shaped, thick-walled and granulated, usually with few chloragogen cells; semi-embedded blood plexus permeating entire region, with regular transverse vessels and less regular longitudinal ones.
Male genitalia (figure 8C) paired. Vas deferens (figure 8C; vd) longer than atrium, 155–200 μm long, 4–7 μm wide, straight or irregularly coiled, entering atrium apically. Atrium tubular, totally 150–190 μm long; ental (shorter) part of ampulla (figure 8C; aa) thin-walled and somewhat dilated, oval to round, about 25 μm wide; middle (longer) duct-like part of atrium 14–16 μm wide, with thicker inner epithelium. Prostatic pad (figure 8C; ppm) oval to round, 35–60 μm long, ventrally attached to atrium, ental to middle of duct-like part. Prostate gland (pr) small, posteriorly situated, with oval to round nuclei, latter maximally 7 μm long and 5 μm wide. Ectal
part of atrium saciform (figure 8C: ead), 70–80 μm long, maximally 40–65 μm wide, with 10–12 μm thick muscular layer. Sperm sac, when developed, extending through one of segments IX–XI. Egg sac, when developed, extending through one to two segments within XI–XIII. Spermatothecae (figure 8B) slender; ducts 45–80 μm long, 15–30 μm wide, with ectal vestibules; ampullae oval to round, thin-walled, 55–60 μm long, 20–45 μm wide, with scattered spermatozoa in lumina.

Brief description of material from Fiji (figure 8D, E). Four complete specimens 3.0–8.5 mm long, 17–52 segments. Diameter at XI 0.2–0.3 mm. Chaetae 45–55 μm long, about 2.5 μm thick, with upper teeth thinner and shorter than lower; (two) three to four per bundle anteriorly, usually two per bundle in post-clitellar segments. Vasa deferentia (figure 8E: vd) 160–195 μm long, about 12 μm wide. Atria totally 160–200 μm long, with ental part of ampullae (figure 8E: aa) 19–22 μm wide, middle duct-like part 15–17 μm wide. Prostatic pads (figure 8E: ppd) about 30 μm long. Prostate glands (pr) broadly attached to pads, with nuclei maximally 7 μm long, about 5 μm wide. Ectal saciform parts of atria (figure 8E: ead) 75–100 μm long, maximally 36–48 μm wide, with 3–10 μm thick muscular layer. Spermatothecal ducts about 60 μm long, 24–27 μm wide; ampullae oval, 55–65 μm long, 25–30 μm wide, containing sperm masses (figure 8D).

Remarks. This taxon has a heavily muscular, dilated, ectal part in each male duct, which is not present in any other species of Doliodrilus. It is not conclusive whether this structure is a proper copulatory sac, i.e. a secondary ectodermal invagination associated with the male pore, or whether it is homologous to the ectal part of the atrial duct, but the latter hypothesis is implied in the description above. In several other species of Doliodrilus, such as D. tener and D. diverticulatus, the ectal most part of the atrium is modified and includes a posterior blind sac. In most of our specimens of D. fibriscaccus, the irregularity in the outline of the muscular sac (i.e. with the posterior face of the sac bulging more than the anterior face; see figure 8C, E: ead) appears to suggest homology with the ‘blind sac’ of other species.

The material from Fiji is similar to that from Hainan. However, in the Fijian worms, the vasa deferentia are thicker, and the ectal dilatations on the atria are somewhat longer and generally thinner, than the corresponding features in the Hainanese material.

Distribution and habitat. Southern China and Fiji. Brackish-water, lower intertidal, muddy sand.

Doliodrilus brachyductus sp. n.

(figure 9)

Holotype. IHB HANA200009ak, whole-mounted specimen.

Type locality. China, southern Hainan, brackish-water pond near Teng Hai (E of Sanya City) (Station SY00-6).

Etymology. The specific name brachyductus is Greek for ‘with short duct’, and alludes to the short, simple male duct.

Description. Holotype 6.7 mm long, 53 segments. Diameter at XI about 0.2 mm. Prostomium blunt. Clitellum inconspicuous. Chaetae bifid, with upper teeth as long as but much thinner than lower (figure 9A). Chaetae 45–50 μm long, about 2.5 μm thick; two to three per bundle anteriorly, (one) two to three per bundle in post-clitellar segments. Ventral chaetae absent in XI. Male pores paired, in line with
ventral chaetae, posterior to middle of XI (figure 9B). Spermathecal pores paired, in line with ventral chaetae, anterior to middle of X (figure 9B).

Pharyngeal glands in IV–V. Chloragogen cells from VI onwards. Oesophagus in IX barrel-shaped, thick-walled and granulated, with few chloragogen cells; semi-embedded blood plexus permeating entire region, with regular transverse vessels and less regular longitudinal ones.

Male genitalia (figure 9B) paired. Vas deferens (figure 9B: vd) longer than atrium, about 100 μm long, 5 μm wide, entering atrium slightly subapically. Atrium tubular or somewhat spindle-shaped, ental part (figure 9B: aa) somewhat dilated but not thin-walled, ectal part (ead) distinctly dilated but opening to exterior through simple pore; atrium totally 70–80 μm long, 15–17 μm wide for most part, 25–30 μm wide at ectal dilatation. Prostatic pad (figure 9B: ppd) oval to round, 22–24 μm long, ventrally attached to atrium, distinctly ental to middle of latter. Prostate gland (pr) small, with oval nuclei, latter maximally 5 μm long, 3 μm wide. Spermathecae (figure 9B: s) small; ectal ducts short, indistinct; ampullae oval and thick-walled, 50–95 μm long, 25–45 μm wide, each with a few spermatozoa in lumina.

Remarks. This new species resembles *D. fibrisaccus* sp. n. in certain aspects of the atria, i.e. the ectal parts are dilated, the ental parts are short, the prostatic pads are entally located, and the prostate glands are small. In *D. brachydactus* sp. n., however, the ectal dilatations of the atria have no distinct musculature, as opposed to the thick muscular layers in *D. fibrisaccus*. Moreover, the spermathecal ducts of
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*D. brachydactus* are indistinct, whereas those of *D. fibrisaccus* are about as long as the spermathecal ampullae (cf. figure 8B, D).

**Distribution and habitat.** Known only from type locality, southern China. Brackish-water, muddy sand.

*Doliodrilus bidolium* sp. n.  
(figure 10)

**Holotype.** IHB HANA2000009af, whole-mounted specimen.

**Type locality.** China, southern Hainan, brackish-water pond near Teng Hai (E of Sanya City) (Station SY00-6).

**Paratypes.** IHB HANA2000009ag–aj, four specimens from type locality. SMNH Type Coll. 5480–5484, five specimens from type locality.

**Etymology.** The specific name bidolium, Latin meaning ‘two small barrels’, alludes to the modified oesophagus, which in VIII–IX is thick-walled, granulated, and bearing a reticulate blood plexus.

**Description.** Two complete specimens, holotype 11.0 mm with 58 segments, one paratype 9.8 mm long, 50 segments. Diameter at XI about 0.5 mm. Prostomium blunt. Clitellum more or less developed over XI–XII. Chaetae (figure 10A) bifid, with upper teeth thinner and shorter than, or as long as, lower. Chaetae 45–55 μm long, about 2.5 μm thick; (one) two to four per bundle anteriorly, one to three per bundle in post-clitellar segments. Ventral chaetae absent in XI. Male pores paired, in line with ventral chaetae in mid-XI (figure 10D). Spermathecal pores paired in line with ventral chaetae in anterior part of X.

Pharyngeal glands in IV–V. Chloragogen cells from VI onwards. Oesophagus in posterior two-thirds of VIII and whole of IX thick-walled and granulated, constricted at septum 8/9, without or with chloragogen cells; semi-embedded blood plexus permeating entire region, with regular transverse vessels and less regular longitudinal ones.

Male genitalia (figure 10D) paired. Vas deferens (figure 10D: vd) short, 50–60 μm long, 7–10 μm wide, entering atrium apically. Atrium (figure 10D: a) slender and somewhat spindle-shaped, about 185 μm long, 12–27 μm wide; ental part tapering off on to vas but not thin-walled; ental part slightly dilated and opening to exterior through simple pore. Prostatic pad (figure 10D: ppd) round, about 30 μm long, entally situated, i.e. about one-third up atrium from male pore; pad bulging out from atrium. Prostate gland (pr) medium-sized, with small nuclei and large nucleus-like bodies, latter oval to round, maximally 10 μm long, 7 μm wide. Sperm sac inconspicuous. Egg sac in XI–XII or XI. Spermathecae (figure 10B, C) small; ducts about 50 μm long, 17–27 μm wide, with ental vestibules; ampullae oval and thick-walled, about 35 μm long, 30–40 μm wide, with few scattered sperm (figure 10B) or distinct sperm bundles (figure 10C) in lumina.

**Remarks.** In this new species, the modification of the oesophagus extends forward into, and through a large part of, VIII, which is a feature unique within the subfamily Limnodriloidinae. With regard to the simple atria and the position of the male pores, *D. bidolium* is similar to *D. puertoricensis*, but it differs from the latter by its shorter vasa deferentia and its more ental position of the prostatic pads in the atria.

**Distribution and habitat.** Known only from type locality, southern China. Brackish-water, muddy sand.
Fig. 10. *Doliodrilus bidolium* sp. n. (A) Chaetae; (B, C) spermathecae with few scattered sperm (B) and sperm bundles (C), respectively; (D) male duct.

*H. Wang and C. Erséus*

*Fig. 10. Doliodrilus chinensis* sp. n. (figure 11)

*Holotype.* IHB HANA2000009i, whole-mounted specimen

*Type locality.* China, southern Hainan, brackish-water pond near Teng Hai (E of Sanya City) (Station SY00-6).

*Paratypes.* IHB HANA20000009j–n, five specimens from type locality. SMNH Type Coll. 5485–5489, five specimens from type locality.

*Other material.* IHB HANA2000009o–ae, 17 specimens from type locality. SMNH Main Coll. 43696–43712, 17 specimens from type locality.
**Fig. 11.** *Doliodrilus chinensis* sp. n. (A) Chaetae; (B–D) spermathecae with one spermatozeugma (B), several spermatozeugmata (C) and sperm masses (D); (E) male duct.
Etymology. This species is known only from China so far, and its name is Latin for ‘of China’.

Description. Seven complete specimens 8.2–12.0 mm (holotype: 10.6 mm), 53–66 segments (holotype: 58). Diameter at XI 0.4–0.6 mm. Prostomium blunt or conical. Clitellum extending over XI–XII. Chaetae (figure 11A) bifid, with upper teeth usually thinner and shorter than lower, teeth sometimes equal in length. Chaetae 50–75 μm long, about 2.5 μm thick; two to four per bundle anteriorly, one to three per bundle in post-clitellar segments. Ventral chaetae absent in XI. Male pores paired, in line with ventral chaetae in posterior part of XI (figure 11E). Spermathecal pores paired, in line with ventral chaetae in anterior part of X.

Pharyngeal glands in IV–V, those in V sometimes indistinct or absent. Chloragogen cells from VI onwards. Oesophagus in IX barrel-shaped, thick-walled and granulated, with chloragogen cells absent, scarce or (sometimes) abundant; semi-embedded blood plexus permeating entire region, with regular transverse vessels and less regular longitudinal ones.

Male genitalia (figure 11E) paired. Vas deferens (figure 11E: vd) shorter than atrium, 80–100 μm long, about 16 μm wide, entering atrium apically. Atrium (figure 11E: a) altogether somewhat spindle-shaped, 205–235 μm long, 31–43 μm wide, opening to exterior through simple pore. Ental end of atrium neither thin-walled nor dilated, somewhat tapering off on to vas. Prostatic pad (figure 11E: ppd) round, 44–53 μm long, ventrally attached ental to middle of atrium; pad bulging out from atrium. Prostate gland (pr) large, with small nuclei and large nucleus-like bodies, latter oval to round, maximally 14 μm long and 12 μm wide. Ectal part of atrium simple, with neither blind sac nor dilatation (figure 11E). Sperm sac large, extending through two to five segments in IX–XIII. Egg sac when developed, restricted to one segment within XII–XIII. Spermathecae (figure 11B–D) large; ducts 40–80 μm long, 24–51 μm wide, with small ectal vestibules; ampullae oval and thin-walled, 175–195 μm long, 65–115 μm wide, sperm in lumina usually as dense, somewhat sea-horse-shaped spermatozogmata (figure 11B, C), sometimes in random masses (figure 11D).

Remarks. This new species is characteristic, as it usually has somewhat sea-horse-shaped spermatogmata. Considering the simple male ducts, with rather short vasa deferentia, D. chinensis sp. n. shows similarities to, and is possibly closely related to, D. bidolium sp. n. However, in addition to the difference with regard to the oesophageal modifications (see Remarks for D. bidolium), the prostatic pads of D. chinensis are situated more entally on the atria, and the male pores are located posteriorly in segment XI, not in mid-XI as in D. bidolium.

Distribution and habitat. Known only from type locality, southern China. Brackish-water, muddy sand.

**Doliodrillus puertoricensis** Erséus and Milligan, 1988

*(figure 12)*


New material. SMNH Main Coll. 43713–43714, two whole-mounted specimens from New Caledonia, Touhou, N of E end of point at Kombounou, 20°46.6'S, 165°14.4'E, mid-intertidal, pebbles, gravel, sand and black mud; 18 September 1993, coll. C. Erséus (Station NC93-45).
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Fig. 12. *Doliodrilus puertoricensis* Erséus and Milligan, 1988. (A) Chaetae; (B) spermatheca; (C) male duct.

**Brief description of new material.** One complete specimen 7.7 mm long, 51 segments. Diameter at XI about 0.4 mm. Prostomium blunt. Clitellum extending over XI–XII. Chaetae 40–45 μm long, about 2.5 μm thick, with upper teeth variable in length but thinner than lower (figure 12A); (one) two to four per bundle anteriorly, (one) two (three) per bundle in post-clitellar segments. Pharyngeal glands in IV–V. Chloragogen cells from VI onwards. Oesophagus in IX barrel-shaped, thick-walled and granulated; semi-embedded blood plexus permeating dorsal region. In the complete specimen, irregular blood plexus also present in posterior third of oesophagus in VIII. Vasa deferentia (figure 12C: vd) about 5 μm wide, longer than atria. Atria (figure 12C: a) tubular, 120–175 μm long, 17–19 μm wide; ental part of ampullae somewhat dilated but not thin-walled. Prostatic pads (figure 12C: ppd) somewhat triangular, 34–44 μm long. Prostate gland (pr) small, with irregular to round nuclei, latter maximally 7 μm long, 6 μm wide. Sperm sac inconspicuous. Egg sac in XI. Spermathecae (figure 12B) small; ducts 25–30 μm long, maximally 29–31 μm wide, with wide ectal vestibules; ampullae spherical, 35 μm long, maximally 35–40 μm wide, with sperm scattered or as bundles in lumina.

**Remarks.** This species was originally described from Puerto Rico (Erséus and Milligan, 1988), and then reported from Belize (Erséus, 1990b). The new material conforms well to the previous descriptions, except that its sperm are sometimes scattered in the spermathecae; they were originally stated to be in bundles only (Erséus and Milligan, 1988). In addition, we here supplement the description with
details regarding the beginning of chloragogen cells, and the nature of the blood plexus associated with the oesophagus.

In one of the specimens, the irregular blood plexus is present also in the posterior part of the oesophagus in segment VIII. A similar situation was observed in some specimens of *Doliodrilus diverticulatus* (see above). Thus, the presence or absence of an irregular oesophageal blood plexus around segment IX may be an intraspecific variation.

*Distribution and habitat.* New Caledonia (new record), Belize, and Puerto Rico Intertidal and subtidal, mud and sandy mud; at least in Puerto Rico subject to fluctuating salinities.

**Genus Limnodriloides** Pierantoni, 1903

*Limnodriloides parahastatus* Erséus, 1985

(figur 13)


*New material.* IHB HANA2000017f, one specimen from Station SY00-9C.

*Brief description of new material.* Specimen incomplete, 5.1 mm long with 39 (anterior) segments. Prostomium blunt. Clitellum not developed. Somatic chaetae (figure 13A) 45–50 µm long, 2.0–2.5 µm thick, with upper teeth shorter and thinner than lower; two to three per bundle anteriorly, (one) two per bundle in post-clitellar segments. All chaetae absent in XI. Spermathecal chaetae 55 µm long, about 3.0 µm thick, with ectal third grooved. Chloragogen cells from VI onwards. Vasa deferentia coiled, shorter than atria. Atria tubular; ampullae 130 µm long, 17–22 µm wide; atrial ducts 75 µm long, 10 µm wide, opening to exterior through complex bodies of tissue. Prostatic pads oval, about 24 µm long. Nuclei of prostatic glands oblong, maximally 7 µm long, 5 µm wide. Spermathecae (figure 13B) small; ducts 30 µm long, 24 µm wide; ampullae oval, 50 µm long, 30 µm wide, with a few sperm bundles in lumina.

*Remarks.* This post-copulatory specimen fits well the description of a single precopulatory worm reported from Hong Kong (Erséus, 1990a), but in the Hainan worm, the upper teeth of the somatic chaetae are shorter than the corresponding lower teeth, while in the Hong Kong material, the upper and lower teeth were of about same length (Erséus, 1990a: figure 16A). Erséus (1990a) listed five differences between the Hong Kong specimen and the type specimen from Saudi Arabia. He

![Fig. 13. *Limnodriloides parahastatus* Erséus, 1985. (A) Chaetae; (B) spermatheca.](image-url)
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pointed out that the Chinese form may be separate, but more specimens are needed from both localities to enable a comprehensive comparison. Erséus (1990a) also stated that the atrial ducts of his Hong Kong material were poorly granulated, whereas those of the holotype were heavily granulated (see also Erséus, 1985). However, a re-examination of the holotype shows that the granules of the atrial ducts almost cannot be observed; the heavy granulation was simply inferred from the irregularity of the inner epithelium. Thus, it now seems even more likely that the form from southern China indeed is conspecific with the original material of L. parahastatus.

*Distribution and habitat.* Southern China (new record for Hainan) and Saudi Arabia. Shallow subtidal and lower intertidal, sandy mud.

*Limnodriloides macinnesi* Erséus, 1990

(figure 14)


**New material.** IHB HANA2000012a–b, two specimens from SY00-8A. SMNH Main Coll. 43715–43716, two specimens from SY00-8A.

**Brief description of new material.** Two complete specimens 8.8–9.3 mm long, 69–70 segments. Diameter at XI 0.3–0.4 mm. Prostomium conical or blunt. Clitellum more or less developed in XI–XII. Chaetae 45–50 µm long, about 2.2 µm thick, with upper teeth shorter and much thinner than lower; (two) three to four per bundle anteriorly, (one) two per bundle in post-clitellar segments. Ventral chaetae absent in X–XI. Male pores in mid-XI (figure 14: mp). Chloragogen cells from VI–VII onwards. Vasa deferentia (figure 14: vd) about 200 µm long, 17 µm wide. Atrial ampullae (figure 14: aa) heavily muscular and contractile, about 90 µm long, maximally 73 µm wide when relaxed, but only about 75 µm long, maximally 60–65 µm wide when contracted. Atrial ducts (ad) 70–95 µm long, 19–44 µm wide. Prostatic pads (ppd) 36 µm long. Nuclei of prostatic glands round to oblong, maximally 7 µm long, 5 µm wide. Copulatory sacs (figure 14: cs) 70–75 µm long, 44–53 µm wide. Sperm sac extending through one to three segments within IX–XII. Egg sac absent, or extending through two to six segments in XII–XVII. Spermathecae absent.

**Remarks.** This species was previously reported from Hong Kong (type locality) and Hawaii (Erséus, 1990a). The new material fits well the original description, but the new specimens are longer than the paratype from Hawaii (about 9 mm, 70 segments versus 6 mm, 53 segments) (the holotype was not intact). The atrial ampullae of the present material are somewhat wider than those of previously studied worms (up to 73 µm wide versus maximally 60 µm wide).

**Distribution and habitat.** Southern China (new record for Hainan) and Hawaii. Subtidal sands.

**Discussion**

Prior to this study, only three species of Doliodrilus were known (Erséus, 1984, 1985; Erséus and Milligan, 1988). It was therefore somewhat unexpected that our limited sampling effort in Hainan would add eight new species, plus one unnamed form, to this genus. In a single brackish-water pond near Sanya (Station SY00-6), as many as five of these species occurred together.

Our study shows that the detailed morphology of the male ducts, and the modification of the ectal parts of the atria in particular, is crucial for the
discrimination between different species in *Doliodrilus* (table 1). For convenience of identification, three species groups can be distinguished, groups that, however, may not be monophyletic: (1) the 'tener group', including all the species with blind sacs on their atria (*D. tener*, *D. bisaccus*, *D. longidentatus*, *D. ciliatus*, *D. adiacens*, *D. diverticulatus*); (2) the 'fbrisaccus group', comprising the members with ectal atrial dilatations (*D. fbrisaccus*, *D. brachyductus*); and (3) the 'bidolium group', consisting of the taxa lacking ectal atrial modifications altogether (*D. bidolium*, *D. chinensis*, *D. puertoricensis*).

Among the other diagnostic characters of the *Doliodrilus* species (table 1), some are particularly noteworthy. First, the morphology of the ental part of the atria is taxonomically useful. In eight species, the innermost ends of the atrial ampullae are more or less dilated, these regions being either thin-walled or thick-walled; in the other species, the atria entally taper off and appear continuous with the vasa deferentia. Further, as discussed in the Remarks for *D. tener*, an important atrial feature, not previously specified (see Er séus, 1984, 1990a), is the mid-dorsal
Table 1. Principal distinguishing characteristics of the species of *Doliodrilus*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Upper/ lower teeth of chaetae</th>
<th>Male pores, position in segment</th>
<th>Vasa deferentia</th>
<th>Junction of vasa on to atria</th>
<th>Ental parts of atria</th>
<th>Position of prostatic pads in atria</th>
<th>Ectal atrial modification</th>
<th>Mid-dorsal atrial thickening and nuclei clusters around prostatic pads</th>
<th>Spermatozeugmata</th>
<th>Other important characters</th>
</tr>
</thead>
<tbody>
<tr>
<td>tener</td>
<td>&lt;1.5</td>
<td>Posterior</td>
<td>About as long as atria</td>
<td>Apical</td>
<td>Thin-walled, dilated</td>
<td>Ental</td>
<td>Blind sacs</td>
<td>Present</td>
<td>Absent</td>
<td></td>
</tr>
<tr>
<td>bisaccus</td>
<td>&lt;1.5</td>
<td>Posterior</td>
<td>Distinctly shorter than atria</td>
<td>Apical</td>
<td>Bilobed, thin-walled, dilated</td>
<td>Middle</td>
<td>Blind sacs</td>
<td>Present</td>
<td>Absent</td>
<td>Chaetae generally no more than two per bundle</td>
</tr>
<tr>
<td>longidentatus</td>
<td>&gt;2</td>
<td>Posterior</td>
<td>About as long as atria</td>
<td>Apical</td>
<td>Thin-walled, dilated</td>
<td>Mid-ectal</td>
<td>Blind sacs</td>
<td>Absent</td>
<td>Absent</td>
<td>Oesophageal modification shorter than one segment</td>
</tr>
<tr>
<td>ciliatus</td>
<td>&gt;2</td>
<td>Posterior</td>
<td>About as long as atria</td>
<td>Apical</td>
<td>Ciliated, thin-walled, somewhat dilated</td>
<td>Middle</td>
<td>Blind sacs</td>
<td>Absent</td>
<td>Absent</td>
<td>Spermathecal pores in anteriormost part of X</td>
</tr>
<tr>
<td>adiacens</td>
<td>&lt;1.5</td>
<td>Posterior</td>
<td>About as long as atria</td>
<td>Subapical</td>
<td>Not thin-walled, dilated</td>
<td>Mid-ectal</td>
<td>Blind sacs</td>
<td>Absent</td>
<td>Sigmoid</td>
<td>Unpaired oesophageal diverticulum</td>
</tr>
<tr>
<td>diverticulatus</td>
<td>&lt;1.5</td>
<td>Posterior</td>
<td>About as long as atria</td>
<td>Apical</td>
<td>Not thin-walled, tapering</td>
<td>Middle</td>
<td>Blind sacs</td>
<td>Absent</td>
<td>Absent</td>
<td></td>
</tr>
<tr>
<td>fibrisaccus</td>
<td>&lt;1.5</td>
<td>Posterior</td>
<td>About as long as atria</td>
<td>Apical</td>
<td>Thin-walled, somewhat dilated</td>
<td>Ental</td>
<td>Muscular dilatations</td>
<td>Absent</td>
<td>Absent</td>
<td>Spermathecal ducts indistinct</td>
</tr>
<tr>
<td>brachydactus</td>
<td>&lt;1.5</td>
<td>Mid-posterior</td>
<td>About as long as atria</td>
<td>Slightly subapical</td>
<td>Not thin-walled, dilated</td>
<td>Ental</td>
<td>Dilatations</td>
<td>Absent</td>
<td>Absent</td>
<td>Oesophageal modification extends to VIII</td>
</tr>
<tr>
<td>bidolium</td>
<td>&lt;1.5</td>
<td>Middle</td>
<td>Distinctly shorter than atria</td>
<td>Apical</td>
<td>Not thin-walled, somewhat tapering</td>
<td>Ectal</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Generally sea-horse-shaped</td>
</tr>
<tr>
<td>chinensis</td>
<td>&lt;1.5</td>
<td>Posterior</td>
<td>Distinctly shorter than atria</td>
<td>Apical</td>
<td>Not thin-walled, somewhat dilated</td>
<td>Mid-ental</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td></td>
</tr>
<tr>
<td>puertoricensis</td>
<td>&lt;1.5</td>
<td>Middle</td>
<td>About as long as atria</td>
<td>Apical</td>
<td>Not thin-walled, somewhat dilated</td>
<td>Middle</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td></td>
</tr>
</tbody>
</table>
thickening opposite to, and the clusters of elongate cell nuclei around, the prostatic pads. This condition is shared by *D. tener* and *D. bisaccus*, but not by the other known congeners. Finally, the length of the oesophageal modification is species-specific. It is shortest in *D. ciliatus*, extending over only about two-thirds of segment IX, and longest in *D. bidolium*, in which it extends over all of IX plus two-thirds of VIII; in the other species, it occupies most of IX. The visibility of the oesophageal blood-plexi is different in various specimens. This is probably related to the condition of the live worms when they are fixed, as well as to the fixation itself.

It is very likely that the knowledge of the distribution and diversity of *Doliodrilus* is still far from complete, considering that in a general global perspective marine oligochaetes are still fragmentarily known. Most of the *Doliodrilus* species are recorded from only a few places in Asia, and now in particular from around Hainan Island. *Doliodrilus diverticulatus* and *D. puertoricensis* appear more widely distributed and may be circumtropical. Regarding habitats, many of the members of this genus seem to prefer tropical brackish water, where they can be dominant taxa, e.g. in mangrove sediments (Hsieh and Hsu, 1999).

Among the 13 Hainanese species described above, nine, all belonging to *Doliodrilus* (and this includes *D. sp.*), have not been recorded from Hong Kong to date, and yet 25 species of Limnodriloidinae have already been identified among the oligochaetes collected from over 200 sites in the Hong Kong area (Erseus, 1984, 1990a, 1992a, 1997a; present study). Considering that we spent only 9 days collecting specimens in Hainan and we mainly concentrated on intertidal habitats, Limnodriloidinae as well as other subfamilies may be more species-rich in the southern part of the South China Sea than they are in Hong Kong (see also Wang and Erseus, 2001).

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References


New species of *Doliolirulus* from Hainan


