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A new horsehair worm, *Chordodes formosanus* sp. n. (Nematomorpha, Gordiida) from *Hierodula* mantids of Taiwan and Japan with redescription of a closely related species, *Chordodes japonensis*

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Abstract

A new species of horsehair worm, *Chordodes formosanus* **sp. n.**, is described and compared to a closely related species, *C. japonensis*. Although both species possess the same six cuticular structures of areoles on the surface, the significantly longer filaments on the female crowned areoles can be used as diagnostic characters for the new species. The different taxonomic status of these two species was also confirmed after analyzing the partial cytochrome oxidase subunit I sequence, and the mantid hosts, which are respectively limited to the genus *Tenodera* for *C. japonensis* and *Hierodula* for *C. formosanus* **sp. n.** In addition, the immature stages of eggs and larvae of the new species are also described and discussed in detail.

Keywords

Nematomorpha, *Chordodes formosanus*, *C. japonensis*, new species, molecular analysis, immature stages, mantid hosts

Introduction

The host range of an organism is an important ecological character since it reflects the survival and reproduction of parasites (Onstad and McManus 1996). Parasite taxonomy can be clear only when the taxonomic status of both the parasites and their hosts are well understood. Horsehair worms are obligate parasites that pass through different hosts at various stages (Hanelt et al. 2005). Among the 350 described species of horsehair worms in 21 genera (Schmidt-Rhaesa and Lalramliana 2011), the genus *Chordodes* consists of about 90 species, and is one of the most diverse genera in the phylum Nematomorpha (Schmidt-Rhaesa et al. 2008). Members of *Chordodes* can be easily distinguished from those of other genera by their unique cuticular structures known as crowned areoles (Schmidt-Rhaesa 2002a). Nevertheless, the various structures of the areoles are not always clear at the species level.

Chordodes formosanus sp. n. which is morphologically similar to *C. japonensis* is hereby described as new to science. *Chordodes japonensis* was originally described by Inoue (1952) using light microscopy from specimens collected in Honsyu, Japan. At that time, this horsehair worm was known to parasitize the mantids *Tenodera sinensis* and *T. angustipennis*. Following that, Baek (1993) checked horsehair worms specimens deposited in Kon-Kuk University, Seoul, Korea (collected from Kyongsangbuk-do, Seoul, Chollabuk-do, and Kyunggi-do, Korea) and identified them as *C. japonensis* using scanning electron microscopy (SEM). Schmidt-Rhaesa (2004) checked horsehair worms (collected in Shiga, Japan) deposited in the Lake Biwa Museum, Shiga Prefecture, Japan. One female parasitized the mantid *Hierodula patellifera,* and one free-living male was considered to be *C. japonensis* after examining it with SEM. Although the descriptions in the previous three papers slightly differ (see Table 1 in Schmidt-Rhaesa 2004), those authors believed the similar morphologies still would not make them clearly separated species. In other words, *C. japonensis* was reported to be distributed in Japan and Korea and to have at least three mantid hosts, *T. sinensis, T. angustipennis,* and *H. patellifera*.

However, in April 2007 to February 2008, we conducted a field survey of horsehair worms in Taiwan and found that the mantids, *H. patellifera* and *H. formosana,* were infested by *C. japonensis*, but there was none in the 109 individuals of *T. sinensis* examined. This geographical difference in the host specificity of *C. japonensis* in Taiwan and Japan raised a question as to the taxonomic status of horsehair worms from the above three mantids. In order to answer this question, we examined morphological characters with both light and scanning electron microscopes, and the phylogeny was reconstructed using the mitochondrial (mt)DNA cytochrome oxidase subunit I (mtDNA-COI) gene of 40 adult horsehair worms collected from the three mantids, *T. sinensis*, *H. patellifera,* and *H. formosana,* in Taiwan and Japan. We believe that these horsehair worms actually consist of two distinct species: *Chordodes japonensis* Inoue, 1952 from *T. sinensis* in Japan, and a new species from *H. patellifera* and *H. formosana* in Japan and Taiwan. This paper deals with the new species of *C. formosanus* sp. n., and descriptions of its egg and larval morphologies are also provided.

Materials and methods

In total, the morphologies of 40 adult horsehair worms (including two females which laid eggs in the laboratory) were examined, and these worms were used for a DNA analysis. The morphologies of larvae laid in the laboratory were examined by light microscopy. Eggs and larvae collected in 2010 were examined by an SEM, and their COI sequences were analyzed to determine their taxonomic status. After studying the specimens, the partial bodies of these 40 samples were preserved in the Department of Entomology, National Taiwan University, Taipei; National Museum of Natural Science, Taichung, Taiwan; and Lake Biwa Museum, Shiga, Japan.

Collection and preservation of horsehair worms

Mantids (*H. formosana*, *H. patellifera*, and *T. sinensis*) infected with horsehair worms were collected from trees, shrubs, and grasses near water in Taiwan and Japan. Most of the adult horsehair worms emerged from the mantids after the hosts' abdomens were immersed in water. Some individuals inside the mantids were only found after we had dissected the mantids. In total, 30 mantids with 40 horsehair worms inside them were examined (23 hosts with a single worm, five with two, one with three, and one with four, see Table 1). We first fixed the horsehair worms (except for two females which laid eggs (see below for detail)) and their hosts in a 75% alcohol solution for several days and then kept them in a 95% alcohol solution to preserve the DNA. Collection data are given in Table 1 including the locality, date, and collector.

Two pairs of adult horsehair worms (two males from Sindian, New Taipei City, and two females from Taipei Zoo) were collected on August 2, 2007. They were reared together in a plastic container (20 cm in diameter and 10.5 cm high) filled with 800 ml of aerated tap water, and maintained at 27 ± 1 °C. The females were kept in water to lay eggs for 1 month, then fixed in a 75% alcohol solution and preserved in a 95% alcohol solution. Egg strings were found after 5 days and had hatched to larvae by 1 month later. Larvae were kept alive until being observed under light microscopy. Egg strings stuck on rocks were collected from Wufengqi Waterfalls, Yilan County, on July 21, 2010. They were brought back to the laboratory and kept in a tank with 20 L of tap water under the same conditions as described above. Eggs hatched about 8 weeks later and were then fixed and preserved as described above.

Morphological examination

For adult specimens, the body surface was examined under light microscopy (Olympus BH-2, PM-10AD, Tokyo, Japan). For each specimen, a fragment of about 1 cm long of the mid-body was removed and cut longitudinally. Instead of using a scalpel to directly remove the internal tissues, we dipped the fragment into a 1% KOH solution for

Table 1. Specimen information examined in the present study

Host					Horsehair worms			
Species	**Collecting date**	**Locality**	**Longitude and latitude**	**Collector**	**Species**	**Sex**	**GenBank no.**	**Deposition**
H. formosana[1/]	10-VII-2008	Xindian, New Taipei City, Taiwan	24°56'58.62"N, 121°34'2.90"E	Ming-Chung Chiu	*C. formosanus*	Male	HM044112	NTU
“	“	“	“	“	“	Female	HM044113	NTU
“	“	“	“	“	“	Female	HM044114	NTU
“	“	“	“	“	“	Female	HM044115	NTU
H. formosana	12-VII-2008	Xindian, New Taipei City, Taiwan	24°56'58.62"N, 121°34'2.90"E	Ming-Chung Chiu	*C. formosanus*	Female	HM044119	LBM
H. formosana	20-VII-2008	Xindian, New Taipei City, Taiwan	24°56'58.62"N, 121°34'2.90"E	Ming-Chung Chiu	*C. formosanus*	Male	HM044116	NMNS
“	“	“	“	“	“	Male	HM044104	NMNS
“	“	“	“	“	“	Female[2/]	**HM044105**	NMNS
H. formosana	10-VII-2009	Shimen, New Taipei City, Taiwan	NA	Chun-Kai Wang	*C. formosanus*	Male	HM044123	LBM
H. formosana	2-VIII-2007	Taipei Zoo, Taipei City, Taiwan	24°59'44.70"N, 121°34'49.49"E	Ming-Chung Chiu	*C. formosanus*	Female	HQ322115	NTU
“	“	“	“	“	“	Female	HQ322116	NTU
H. formosana[/3]	29-I-2008	Taipei Zoo, Taipei City, Taiwan	24°59'44.70"N, 121°34'49.49"E	Ming-Chung Chiu	*C. formosanus*	Male	HM044122	NTU
“	“	“	“	“	“	Female	HM044121	NTU
H. formosana	23-VII-2008	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	*C. formosanus*	Male	HM044111	NTU
H. formosana	23-VII-2008	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	*C. formosanus*	Male	HM044118	LBM
“	“	“	“	“	“	Female	HM044108	LBM
H. formosana	24-VI-2009	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	*C. formosanus*	Male[3/]	**HM044124**	NMNS

Host					Horsehair worms			
Species	**Collecting date**	**Locality**	**Longitude and latitude**	**Collector**	**Species**	**Sex**	**GenBank no.**	**Deposition**
“	“	“	“	“	“	Male	HM044125	NMNS
H. formosana	16-VII-2009	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	*C. formosanus*	Male	HM044126	NTU
H. formosana	3-VIII-2009	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	*C. formosanus*	Male	HM044127	NMNS
H. formosana	16-VII-2009	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	*C. formosanus*	Male	HM044128	NMNS
H. formosana	23-VII-2008	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	*C. formosanus*	Female	HM044117	NMNS
H. formosana	10-VII-2008	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	*C. formosanus*	Female	HM044120	NTU
H. formosana	23-VII-2008	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	*C. formosanus*	Female	HM044106	NTU
H. formosana	23-VII-2008	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	*C. formosanus*	Female	HM044109	NTU
H. formosana	23-VII-2008	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	*C. formosanus*	Female	HM044110	NTU
H. formosana	5-VII-2008	Taroko National Park, Hualien, Taiwan	NA	Tsung-Hung Yang	*C. formosanus*	Male	HM044107	NTU
H. patellifera	30-IX-2006	Taipei Zoo, Taipei City, Taiwan	24°59'44.70"N, 121°34'49.49"E	Ming-Chung Chiu	*C. formosanus*	Male	JF808204	NTU
H. patellifera	X-2008	Hsinchu City, Taiwan	NA	Ju-Chun Hsu	*C. formosanus*	Female	JF808197	NTU
H. patellifera[3/]	18-VII-2003	Lyudao, Taitung, Taiwan	NA	Hsing-Yu Chou	*C. formosanus*	Male	JF808203	NTU
“	“	“	“	“	“	Male	JF808205	NTU
H. patellifera	16-X-2010	Sakado, Saitama, Japan	35°96'44.87N, 139°40'27.39E	Etsuko Suzuki	*C. formosanus*	Female	JF808194	NTU
H. patellifera	1-XI-2010	Kijo, Miyazaki, Japan	32°13'30.59"N, 131°24'16.62"E	Yasukuni Ono	*C. formosanus*	Female	JF808198	LBM

Host					Horsehair worms			
Species	**Collecting date**	**Locality**	**Longitude and latitude**	**Collector**	**Species**	**Sex**	**GenBank no.**	**Deposition**
H. patellifera	1-XI-2010	Kijo, Miyazaki, Japan	32°13'30.59"N, 131°24'16.62"E	Yasukuni Ono	*C. formosanus*	Female	JF808199	NTU
H. patellifera	10-XI-2010	Kijo, Miyazaki, Japan	32°14'57.82"N, 131°23'3.93"E	Yasukuni Ono	*C. formosanus*	Female	JF808202	NTU
H. patellifera	11-XI-2010	Miyazaki, Miyazaki, Japan	31°56'54.15"N, 131°16'22.71"E	Yasukuni Ono	*C. formosanus*	Female	JF808200	NTU
H. patellifera	26-XI-2010	Kijo, Miyazaki, Japan	32°10'21.37"N, 131°27'36.53"E	Yasukuni Ono	*C. formosanus*	Male	JF808196	NTU
H. patellifera	26-XI-2010	Kijo, Miyazaki, Japan	32°12'55.36"N, 131°24'52.13"E	Yasukuni Ono	*C. formosanus*	Female	JF808201	NTU
H. patellifera	16-X-2010	Sakado, Saitama, Japan	5°96'44.87N, 139°40'27.39E	Wataru Toki	*C. formosanus*	Female	JF808195	NTU
T. sinensis	5-XI-2010	Kijo, Miyazaki, Japan	32°10'21.50"N, 131°27'36.53"E	Yasukuni Ono	*C, japonensis*	Male	JF808206	NTU

LBM: Lake Biwa Museum; NMNS: National Museum of Natural Science; NTU: National Taiwan University.

[1] No host specimen preserved.

[2] Allotype.

[3] Holotype.

2 h. The internal tissues became transparent and removable. The cuticles were placed on a microslide and observed under a microscope at a magnification of 40–200×. Eggs and newly hatched larvae were placed on the microslides, each with a drop of water and a cover glass. They were observed alive under the light microscope (at a magnification of 400×).

SEM was also used to examine adult and larval specimens. Its preparation protocol followed that of Schmidt-Rhaesa (2002b). Fragments of the anterior end, mid-body, and posterior end of preserved adult and larval specimens were dehydrated with a series of 75%, 95%, and 100% ethanol solutions and then replaced by acetone after using a series of alcohol/acetone mixtures of 2:1, 1:1, 1:2, and 0:1. Samples were then critical-point-dried, gold-sputter-coated, and examined under an SEM (JEOL JSM-5600, Tokyo, Japan) at a magnification of 100–15,000×.

The terminology of larvae follows that of Bohall et al. (1997), Hanelt and Janovy (2002), and Bolek et al. (2010).

Phylogenetic analysis

Genomic DNA was extracted from fragments of horsehair worms and whole larvae using an ALS Tissue Genomic DNA Extraction Kit (Kaohsiung, Taiwan). A partial COI sequence was amplified by a polymerase chain reaction (PCR) with a set of universal primers (LCO1490 and HC02198) (Folmer et al. 1994). The PCR was initiated at 95°C for 5 min, followed by 35 cycles at 95°C for 1 min, 40 °C for 1 min, and 72°C for 1 min, with a final extension at 72°C for 7 min. The PCR products were obtained by electrophoresis in 1.5% agarose gels and sequenced.

For the phylogenetic analysis, the COI sequence of *Paragordius* sp. (GenBank no. AY428843) was used as an outgroup. The 528 nucleotide base pairs of high quality were aligned using CLUSTALX 2.0.10 (Thompson et al. 1997). Pairwise genetic distances were calculated, and a phylogenic tree was reconstructed by the Neighbor-joining (NJ) method based on the Kimura 2-parameter model using MEGA 4.0.2 (Tamura et al. 2007). The support for the topology of the NJ tree was estimated by bootstrapping using 1000 replicates.

Results

Chordodes formosanus Chiu, 2011, sp. n.

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http://species-id.net/wiki/Chordodes_formosanus

Type locality. Wufengqi Waterfalls (24°49'55.62"N, 121°44'50.10"E), Jiaushi Township, Yilan County, Taiwan (Holotype). Dachijieu (24°56'59.21"N, 121°34'2.12"E), Sindian (New Taipei City) (allotypes). Paratypes collected from Taiwan and Japan:

Taipei Zoo (Taipei City), Sindian (New Taipei City), Taroko National Park (Hualien County), Wufengqi Waterfalls (Yilan County), Taiwan and Miyazaki Prefecture and Sakado (Saitama Prefecture), Japan. For detailed data, see Table 1.

Type material. Partial bodies of holotype (male, 167 mm), and allotype (female, 282 mm) deposited at the Department of Entomology, National Taiwan University with the hosts. Paratypes deposited at the Department of Entomology, National Taiwan University, Taipei, and National Museum of Natural Science, Taichung, Taiwan and Lake Biwa Museum, Shiga, Japan. For detailed information, see Table 1.

Type-host. *Hierodula formosana* Giglio-Tos (Mantodea: Mantidae). *Hierodula formosana* endemic to Taiwan, and the adult always emerging from late June to early August. Hosts of some samples belonging to *H. patellifera* which distributed in both Taiwan and Japan. Their adults usually emerging in late autumn, about 2 months later than *H. formosana*.

Etymology. The specific name refers to Taiwan, the collection locality of the type specimens.

Description. (Figs 1–5)

Male adult (*n* = 17) (Figs 1, 2). Body length 74–277 mm, width (widest) 0.7–1 mm (after dehydration). In alcohol-preserved specimens, body rough and flat with dorsal and ventral grooves; dark-brown with bright lengthwise regions on both dorsal and ventral sides and darkly pigmented line on ventral side in most specimens (Fig. 1D).

Posterior end (Fig. 1C) not lobed, with short spines (ca. 5–12 μm) among areoles on margin. Cloacal opening subterminal, oval, 27–78 μm long and 17–63 μm wide. A pair of oval regions without areoles posterior to cloacal opening, each with scattered bristles extending as two rows of ventral strips (155–160 μm wide), structured by cord-like folds or flat areoles; flat areoles ornamented with short filaments in a cluster on top or scattered on cord-like folds, or absent. Paired oval bristlefields (70–77 μm wide and 145–243 μm long) bearing bristles on borders between flat areoles and normal areoles on lateral side of cloacal opening; bristles in bristlefields varying among individuals; some bearing only shorter or thinner unbranched bristles and some with both branched and unbranched bristles (Figs 2D–F). Anterior end tapered, same color as body, with white tip (white cap) but no dark collar under a stereomicroscope. Under SEM, anterior end round with moderately flat areoles and short bristles on surface; about 10 of them elevated and cone-like near anterior terminal; long thick bristles scattered among areoles, some between areoles and some penetrating areoles (Fig. 2C). Anterior end on one individual with residual larval cuticle tapered but flat terminally (Fig. 2A); also flat surrounding ornamentations and bristles (Fig. 2B). Mouth opens terminally in some individuals.

Entire body covered by areoles with cord-like folds in between. Areoles characterized into five types (simple, tubercle, thorn, circumcluster, and crowned areoles). Simple areoles (Fig. 1A), most abundant, covering most of body surface except anterior end and ventral side of posterior end; each 5–8 μm in diameter, more or less circular or oval, generally with a smooth surface but some with dots, grooves, or short bristles on surface. Simple areoles varying in height and some significantly elevated areoles in

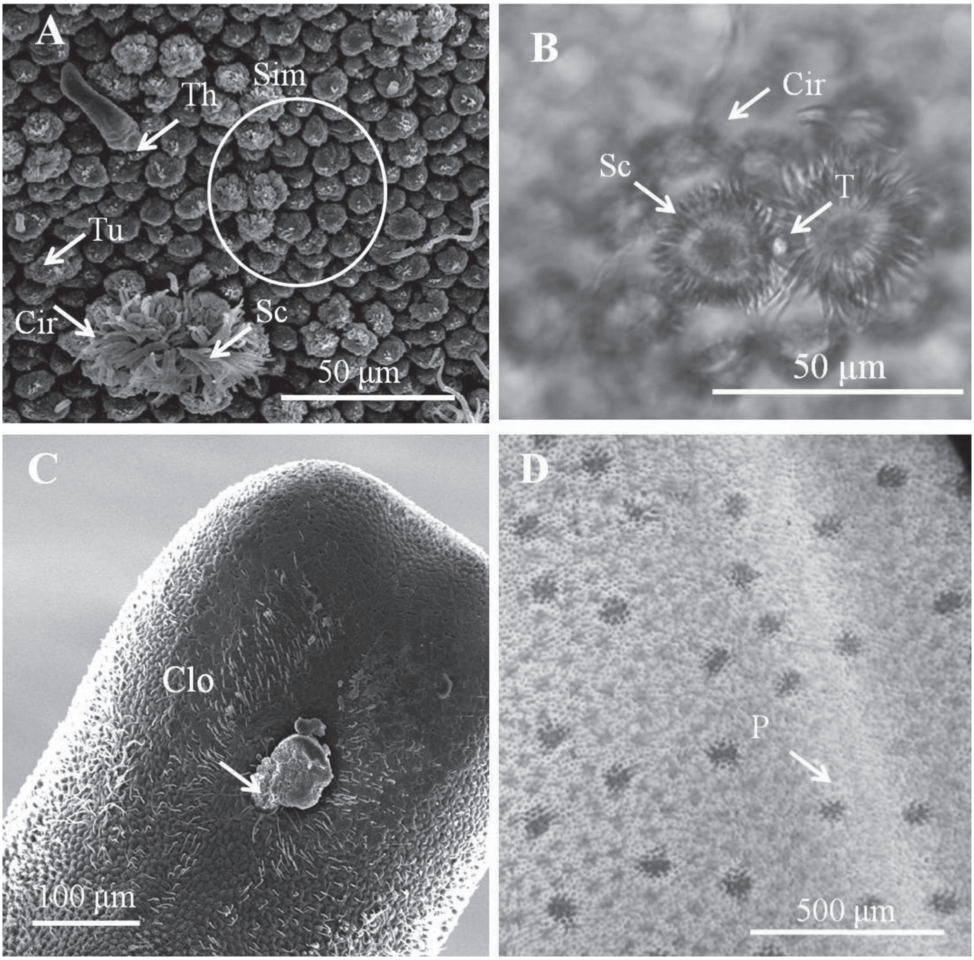


Figure 1. Male adult of *Chordodes formosanus* sp. n. **A** Cuticular surface with five types of areole **B** paired crowned areoles with a central tubercle **C** posterior end of the male **D** bright lengthwise regions with a darkly pigmented line on the ventral side of male body. Cir, circumcluster areole; Clo, cloacal opening; P, pigmented line; Sc, short-crowned areole; Sim, simple areoles; T, central tubercle; Th, thorn areole; Tu, tubercle areole.

clusters of two to ten, looking like bulging areoles as mentioned by Schmidt-Rhaesa et al. (2008); but darker under light microscopy (Fig. 1D). Tubercle areoles (Fig. 1A) scattered among simple areoles, each shaped similarly to simple areole but with a tubercle (6–9 µm long) on apically concave center. Thorn areoles (Fig. 1A) distributed slightly along dorsal and ventral middle lines, similar to tubercle areoles but with a long solid thorn (22–57 µm long) instead of a tubercle. Thorn areoles small or absent in two samples. Crowned areoles clustered in pair with a central tubercle in between and surrounded by 12–20 circumcluster areoles with short filaments on apical surface (short-crowned areoles) (Figs 1A, B); scattered over trunk except anterior and posterior ends; each with medium filaments (10–15 µm) originating from apical center and

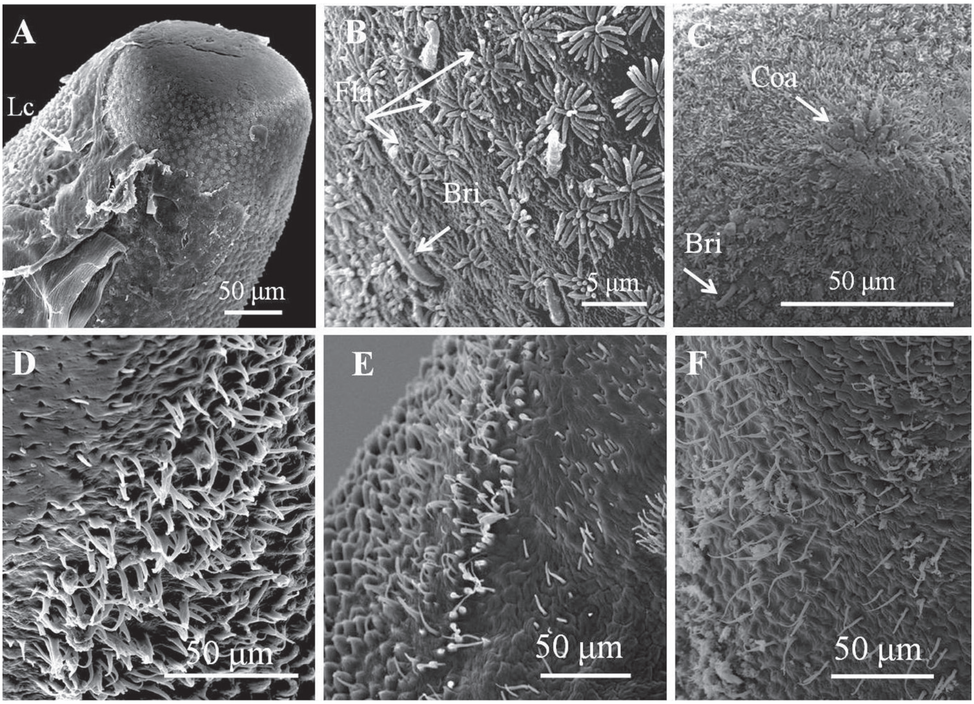


Figure 2. Details of ornamentations on anterior and posterior ends of male *Chordodes formosanus* sp. n. **A** Anterior end with larval cuticle **B** flat ornamentations and bristles on top of anterior end **C** cone-like areoles with bristles on top of anterior end **D–F** bristlefields with branched and unbranched bristles (D), short and unbranched bristles (E), or thin and unbranched bristles (F). Bri, bristle; Coa, cone-like areole; Lc, residual of larval cuticle; Fla, flat ornamentations.

sidelong to edges; only one male with a few crowned areoles containing a few filaments of around 100 µm.

Female adult (*n* = 14) (Fig. 3). Length 263.7 (78–440) mm; body width (widest) 1–1.5 mm (after dehydration); body rough, flattened, dorsal and ventral grooves present; light to dark-brown with lengthwise regions on both dorsal and ventral sides, and darkly pigmented line on ventral side in most specimens. Some individuals with dark patches on bodies.

Posterior end (Fig. 3B) rounded, slightly swollen, covered by moderately flat areoles with cord-like folds surrounding cloacal opening; short bristles (10–27 µm) scattered between borders of moderately flat areoles and cord-like folds. Cloacal opening on terminal end, circular, 18–33 µm in diameter, no circumcloacal spine.

Anterior end with similar structure and color to males except lower cone-like areoles; terminally flat anterior end also appearing in one individual. Pattern and distribution of areoles (Fig. 3A) also similar to those of males but much more crowded in most individuals. Thorns of areoles shorter than those of most males (11–30 µm) but small or absent in three females. Cord-like folds present between areoles. Crowned areoles

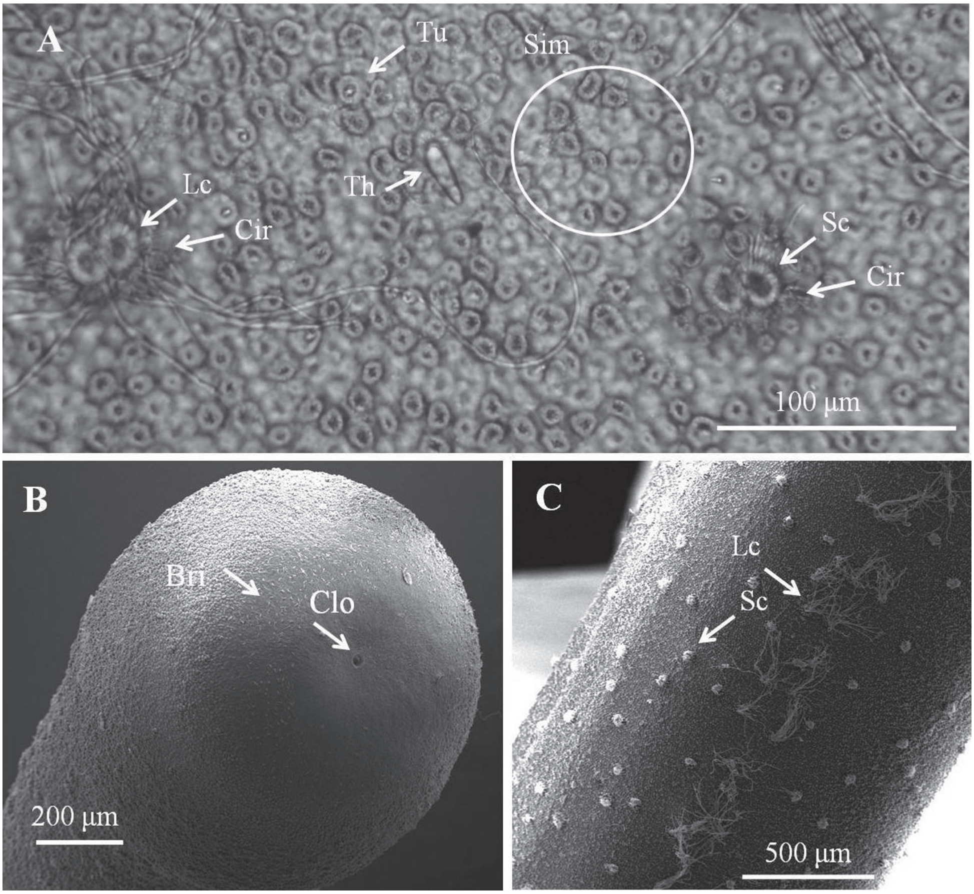


Figure 3. Female adult of *Chordodes formosanus* sp. n. **A** Cuticular surface with six types of areole **B** posterior end of female **C** ventral side of female body. Bri, bristle; Cir, circumcluster areole; Clo, cloacal opening; Lc, long crowned areole; Sc, short-crowned areole; Sim, simple areoles; Th, thorn areole; Tu, tubercle areole.

scattered over trunk as in males while roughly arranged in two lines on ventral and dorsal midlines, bearing significantly longer filaments (longest apical filaments ranging 65.57–392.25 μm (237.47 ± 66.22 μm, for details see "Diagnosis")) (Figs 3A, C).

Eggs (Fig. 4). In laboratory, egg strings stuck onto substrate or drifting on bottom. Eggs (6 days after being laid) (Fig. 4B) nearly circular, 30.39 ± 1.15 μm (*n* = 10) in diameter. Egg strings white when laid and becoming light-brown within 1 day, turning dark-gray just before hatching. Eggs collected in field (Fig. 4C) all stuck onto rocks; mostly brown to gray, but some light-brown as those just laid in laboratory.

Larvae (Figs 4, 5). Larvae remaining near egg strings after hatching, not active. Under light microscopy, larval preseptum (Fig. 4A) averaging 20.55 (16.32–24.78) μm long and 13.21 (10.93–16.34) μm wide; postseptum averaging 24.91 (22.52–27.44) μm long and 10.06 (9.25–11.49) μm wide, stylet averaging 11.04 (9.59–13.25) μm

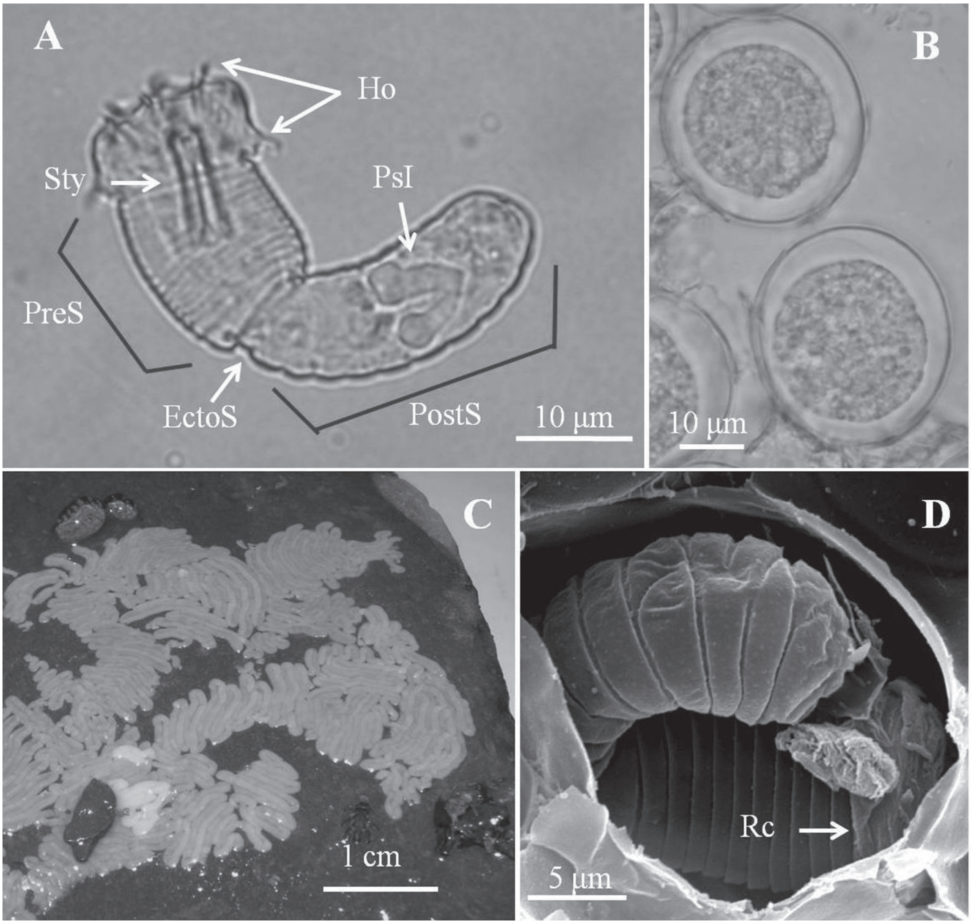


Figure 4. Eggs and larvae of *Chordodes formosanus* sp. n. **A** Live larva in water **B** eggs (6 days after being laid) **C** egg strings stuck onto a rock **D** larva in an egg with residual cuticle. EctoS, ectodermal septum; Ho, hooklet; PostS, postseptum; PreS, preseptum; PsI, pseudointestine gland; Rc, residual cuticle; Sty, stylet.

long and 3.36 (2.76–3.91) μm wide. Pseudointestines V-shaped (Fig. 4A) with one small and one large branch, both with a swelling on posterior ends. Large branch averaging 8.27 (7.28–9.82) μm, small branch averaging 6.70 (5.43–7.59) μm long. Under SEM, larvae superficially annulated with 13 segments on preseptum and 10 on postseptum, ectodermal septum as a single segment between them. Three sets of hooks arranged in three rings on anterior preseptum (Fig. 5A): outer ring containing seven hooks (outer hooks), two ventrally positioned and closely together on base (ventral double hook); six hooks on second ring located between each outer hook (middle hook); inner ring containing at least three inner spines, but real number unknown. A stylet (Figs 5A, C) appearing inside preseptum, ornamented with two sets of spines: nine spines on dorsal and ventral sides of stylet, five small lateral papillae on left side.

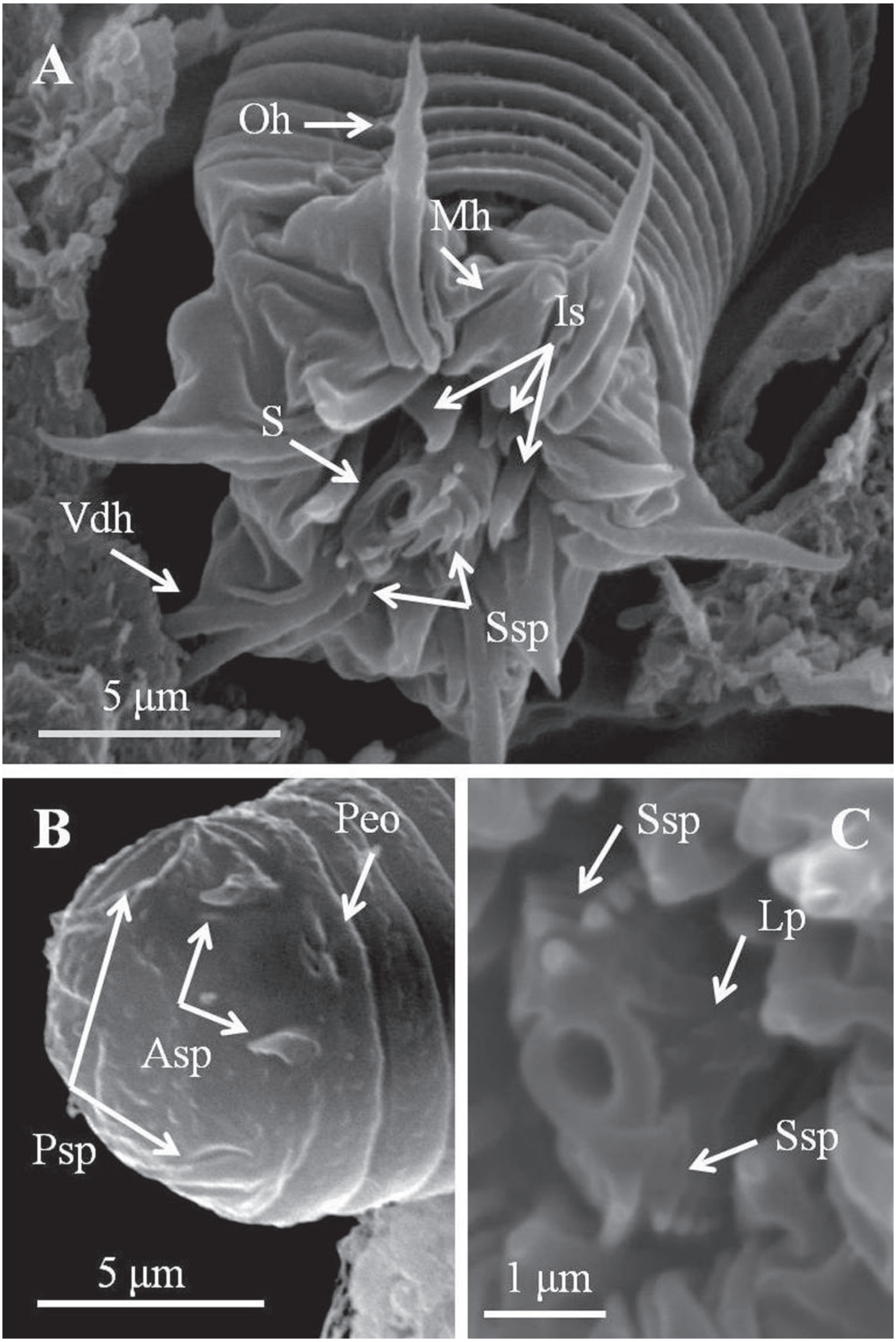


Figure 5. Detail of larvae of *Chordodes formosanus* sp. n. **A** Anterior view of a larva showing stylet and hook arrangement **B** posterior view of a larva **C** style with spines and lateral papillae. Asp, anterior terminal spine; Lp, lateral papillae; Is, inner spines; Mh, middle hook; Oh, outer hook; Peo, Pseudointestine exterior opening; Psp, posterior terminal spine; S, stylet; Ssp, stylet spines; Vdh, ventral double hook.

A pair of anterior and posterior terminal spines (Fig. 5B) on posterior of postseptum. Pseudointestine exterior opening (Fig. 5B) centrally located between anterior terminal spines on ventral body. Several larvae covered by residual skin: one observed in broken egg suggesting that molting had occurred before emergence (Fig. 4D).

Diagnosis. Horsehair worms from the mantids *H. formosana* and *H. patellifera* were characterized by all six types of areoles, including simple, tubercle, thorn, circumcluster, short-crowned, and long-crowned areoles in the female. The same six areole types are similar to those of *C. japonensis* described by Inoue (1952) and Baek (1993). Nevertheless, the significantly longer filaments on female crowned areoles suggest they belong to a new species, *C. formosanus* sp. n. By the way, the absence of long-crowned areoles in our male sample of *C. formosanus* sp. n. probably implies their potential for distinguishing these two different species. However, since the dimorphism of male crowned areoles has not been mentioned in *C. japonensis*, more studies are needed to uncover this phenomenon.

The crowned areole is an autapomorphy of the genus *Chordodes*. In *C. formosanus* sp. n. and *C. japonensis*, it is composed of two major areoles ornamented with apical filaments and several surrounding circumcluster areoles. The dimorphic length of the apical filaments divides the crowned areoles into two types, short-crowned areoles with short ornamental filaments and long-crowned areoles with long ones. All samples we checked (both sexes of *C. formosanus* sp. n. and one male *C. japonensis*) had short-crowned areoles scattered all over the body trunk, with the long-crowned areoles only appearing on the ventral and dorsal midlines of the female *C. formosanus* sp. n. and male *C. japonensis,* but not the male *C. formosanus* sp. n. We did not personally observe the female *C. japonensis,* but these dimorphic crowned areoles must be present according to the descriptions of Inoue (1952) and Baek (1993). Additionally, the apical filament lengths of long-crowned areoles were significantly longer on *C. formosanus* sp. n. We randomly chose two to five sets of long-crowned areoles from our female samples and measured each of their longest apical filaments. In the 68 sets of long crowned areoles, the longest apical filaments ranged 65.57–392.25 (237.47 ± 66.22) μm. Fifty-one of these 68 (75%) sets of crowned areoles had apical filaments of > 200 μm. The longest apical filaments in our male *C. japonensis* were 92.03–139.70 μm. Significantly shorter filaments in *C. japonensis* were also described by Inoue (1952) and Baek (1993). *Chordodes japonensis* has long-crowned areoles with filaments of around 50 μm (Inoue 1952; fig. 1a) and filaments of < 200 μm in the description by Baek (1993). For other differences and detailed comparisons, see Table 2 and the "Discussion".

Chordodes japonensis **Inoue, 1952**

http://species-id.net/wiki/Chordodes_japonensis

Material examined. Examined male collected with its host from Miyazaki Prefecture, Japan (32°10'21.50"N, 131°27'36.53"E) by Yasukuni Ono on 5-XI-2010. Partial body of horsehair worm deposited with its host at Department of Entomology, Na-

Table 2. Comparison of areolar types between *Chordodes formosanus* sp. n. (Schmidt-Rhaesa 2004, samples of which were considered to be *C. japonensis*), *C. japonensis* (Inoue 1952, Baek 1993) and in this investigation

Areolar type	***Chordodes formosanus* sp. n.**		***Chordodes japonensis***		
	This study	**Schmidt-Rhaesa (2004)**	**This study**	**Inoue (1952)**	**Baek (1993)**
Sample size	17 ♂♂, 22 ♀♀	1 ♂**, 1 ♀	1 ♂	49 ♂♂, 37 ♀♀	17 ♂♂, 7 ♀♀
Collecting locality	Taiwan, Japan	Japan	Japan	Japan	Korea
Host	*Hierodula formosana* and *H. patellifera*	*H. patellifera* (unknown for the male worm)	*Tenodera sinensis*	Not mentioned	Not mentioned
Crowned areoles with short projections	+	+	+	-	+
Crowned areoles with long projections	+ (most areoles with filaments > 200 µm)	+ (> 200 µm)	+ (mostly around 100 µm, maximum 140 µm)	+ (around 50 µm in Fig. 1a)	+ (< 200 µm)
Sexual dimorphism in crowned areoles	+	-	? (Only males were investigated)	-	-
Circumcluster areoles	+ (12-20)	+ (at least 12 in Fig. 2C)	+ (7-14)	+ (10 in Fig. 1a)	+ (7-17)
Tubercle areoles	+	+	+	+	+
Thorn areoles (spine areoles)	+ (small or absent in some samples; 9/40)	-	+	+	-
Bulging areoles	* (some elevated simple areoles in clusters of 2-10)	- (simple areoles elevated differently in Fig. 2A and 2D)	* (some elevated simple areoles in clusters of 2-5)	- (paired elevated areoles)	- (simple areoles elevated differently in Fig1)
Simple areoles	+	+	+	+	+

Terminology based on Schmidt-Rhaesa (2004) and Schmidt-Rhaesa et al. (2008).

+, present; -, absent; *, difficult to determine; ?, unknown.

**, According to the description, we consider the specimen not to be *Chordodes formosanus* sp. n.

tional Taiwan University, Taipei, Taiwan. Accession number of partial COI sequence in GenBank: JF808206.

Host. Chinese mantids, *Tenodera sinensis* (Mantodea: Mantidae), which are sometimes classified as *T. aridifolia*.

Redescription.(Fig. 6)

Male adult (*n* = 1). Body length 220 mm, width (widest) 0.94 mm (after dehydration). In alcohol-preserved specimens, body rough and flat with dorsal and ventral grooves, dark-brown with a darkly pigmented line on ventral side.

Posterior end (Fig. 6A) not lobed, with short spines (ca. 5–13 μm) among areoles on margin. Cloacal opening subterminal, oval 44 μm long and 25 μm wide, with circumcloacal spines. A pair of oval regions without areoles posterior to cloacal opening, each with scattered bristles extending as two rows of ventral strips (115–120 μm wide) structured by cord-like folds or flat areoles. Paired oval bristlefields (82 μm wide and 231 μm long) bearing numerous branched and unbranched bristles on borders between flat areoles and normal areoles on lateral side of cloacal opening. Anterior end tapered, same color as body, with white tip (white cap) but no dark collar under stereomicroscopy. Under SEM, anterior end (Fig. 6F) smooth with short, thick bristles and small spines; mouth open on cone at anterior extremity.

Entire body covered by areoles with slightly cord-like folds in between. Areoles characterized into six types (simple, tubercle, thorn, circumcluster, and two types of crowned areoles). Simple areoles (Fig. 6C), most abundant, covering entire body surface except anterior end and ventral side of posterior end; each 5–11 μm in diameter, more or less circular or oval, surface uneven, some areas with short bristles. Simple areoles varying in height and some significantly elevated areoles in clusters of two to five, appearing as bulging areoles but darker under light microscopy. Tubercle areoles (Fig. 6C) scattered among simple areoles, each similarly shaped to simple areole but with a tubercle (about 7 μm long) on apically concave center. Thorn areoles (Fig. 6E) similar to tubercle areoles but with a long solid thorn (15 μm long) instead of tubercle; number of thorn areoles much fewer than tubercle areoles. Crowned areoles (Figs 6B, D) clustered in pairs with a central tubercle in between and surrounded by 7–14 circumcluster areoles with short filaments on apical surface; scattered over trunk; each with medium filaments (12–20 μm) originating from apical center and sidelong to edges. Crowned areoles roughly arranged in two lines on ventral and dorsal midlines, bearing significantly longer filaments (most around 100 μm, none > 150 μm) (Figs 6B, C).

Phylogeny. A phylogenetic tree of the 40 samples of horsehair worms collected from three species of mantids *H. formosana*, *H. patellifera*, and *T. sinensis* from Taiwan and Japan with one outgroup (*Paragordius* sp.) is shown in Fig. 7.

Comparison of the 40 horsehair worm samples (39 *C. formosanus* and one *C. japonensis*) revealed there were 31 haplotypes with 432 invariable sites, 64 singletons, and 32 parsimoniously informative sites. Newly sequenced COI data were deposited in the GenBank database (see Table 1 for accession nos.). Samples from the host mantids of *Hierodula* and *Tenodera* (which are considered two species, *C. formosanus* sp. n. and *C. japonensis,* respectively) were significantly separated into two groups based

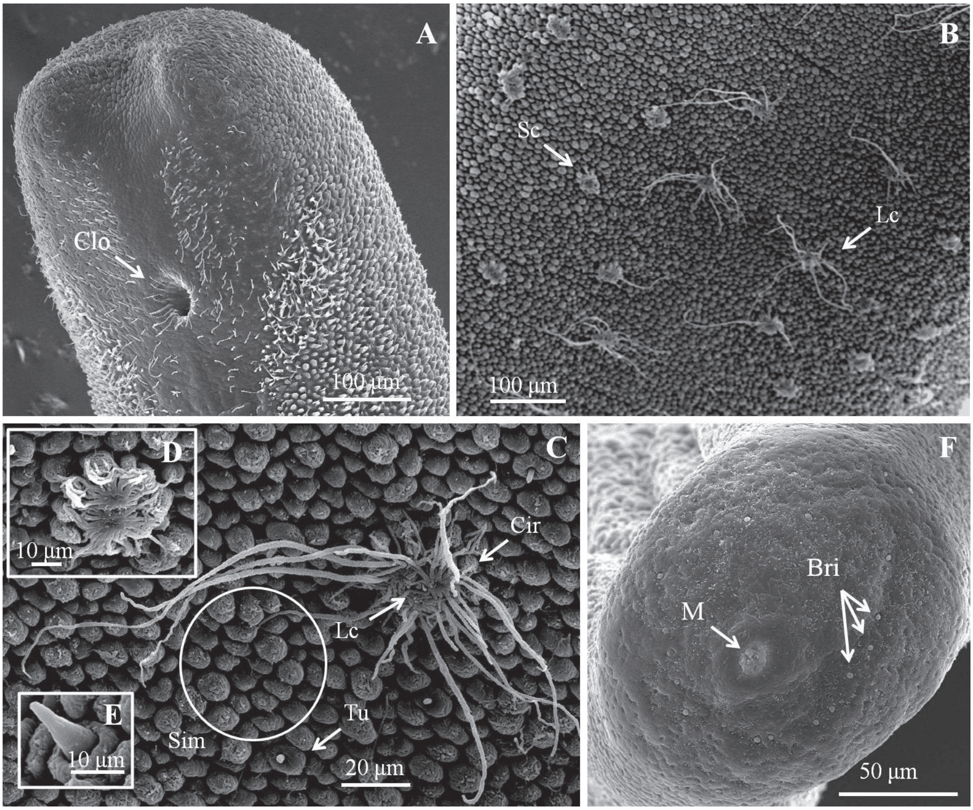
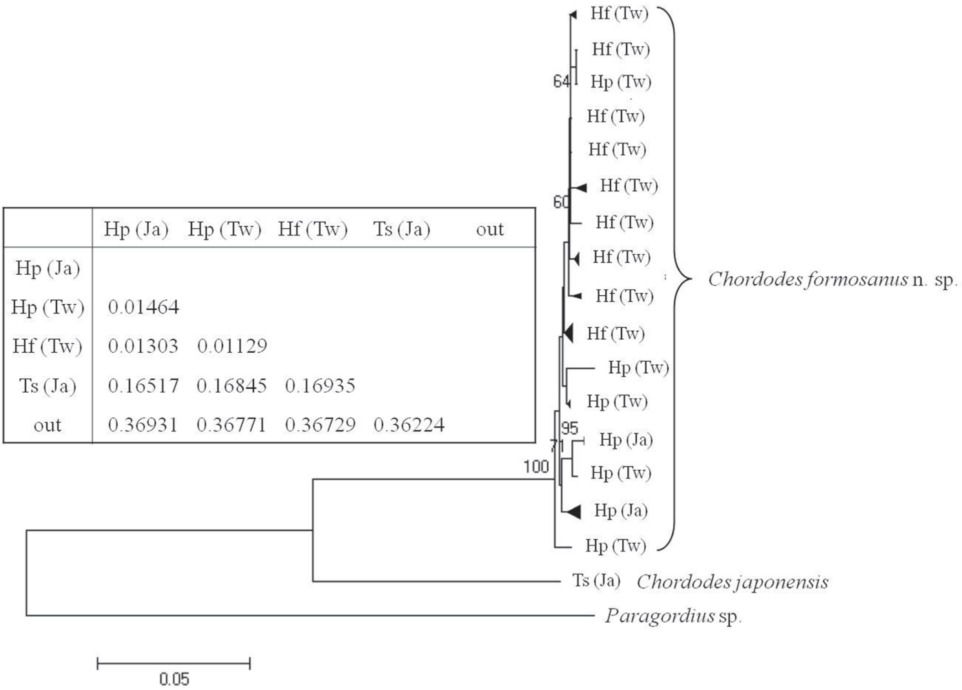


Figure 6. Male adult of *Chordodes japonensis*. **A** Posterior end of male **B** ventral side of male body **C** cuticular surface with four types of areole **D** short-crowned areoles **E** thorn areole **F** anterior end. Bri, bristle; Cir, circumcluster areole; Clo, cloacal opening; Lc, long crowned areole; M, mouth; Sc, short-crowned areole; Sim, simple areoles; Tu, tubercle areole.

on the phylogenetic tree restructured by the NJ method (Fig. 7). The genetic distance between these two groups was 0.16840. This result supports that they belong to different species as we suggested based on morphology. The phylogenetic tree also revealed a polytomic topology among the 39 horsehair worms parasitizing *Hierodula*. Although some clades were observed, they were not highly supported due to low bootstrap values and short genetic distances; the mean genetic distances among them was 0.00979 with a range of 0.000-0.01922. Since the genetic distance between the larvae collected in the field and *C. formosanus* was only 0.00759, we suggest that those larvae belong to the same species.

Discussion. In this article, a new species, *C. formosanus* sp. n., which parasitizes *H. formosana* and *H. patellifera,* was proposed and described including the morphology of the egg and larval stages. Because of a similar morphological description by Schmidt-Rhaesa (2004), we categorized the species in that study into *C. formosanus* sp. n. and also limited the mantid host range of *C. japonensis* to the genus *Tenodera*.



	Hp (Ja)	Hp (Tw)	Hf (Tw)	Ts (Ja)	out
Hp (Ja)					
Hp (Tw)	0.01464				
Hf (Tw)	0.01303	0.01129			
Ts (Ja)	0.16517	0.16845	0.16935		
out	0.36931	0.36771	0.36729	0.36224	

Figure 7. Neighbor-joining tree of *Chordodes formosanus* sp. n. and *C. japonensis* with genetic distances between each group. Abbreviations in the table indicate the horsehair worms' mantid hosts (Hf, *Hierodula formosana*; Hp, *H. patellifera*; Ts, *Tenodera sinensis*) and collecting localities (Tw, Taiwan; Ja, Japan). Numbers at the nodes represent the percentage of 1000 bootstrap values of > 70%. The outgroup (out) was a *Paragordius* sp.

Morphological comparison of *C. formosanus* sp. n. and *C. japonensis*

The two species, *C. formosanus* sp. n. and *C. japonensis*, can be distinguished by the presence of dimorphism in male crowned areoles and the length of long filaments on female crowned areoles. A comparison of areolar types in *C. formosanus* sp. n. and *C. japonensis* is given in Table 2. Both *C. formosanus* sp. n. and *C. japonensis* have two forms of crowned areoles on their cuticles, one with moderate attachments on the top (short-crowned areoles) and the other with significantly longer attachments (long-crowned areoles). Both types of crowned areoles were found on these two species except for the male *C. formosanus* sp. n. (the short-crowned areoles were not mentioned in the description of *C. japonensis* by Inoue (1952)), which indicates sexual dimorphism in *C. formosanus* sp. n. We believe the female worm which was previously considered to be *C. japonensis* by Schmidt-Rhaesa (2004) actually belongs to the species, *C. formosanus* n. sp, described here. The reason why the sexual dimorphism was not mentioned by Schmidt-Rhaesa (2004) is probably that the free-living male is not the same species as the female. In addition, the length of the filaments on the long-crowned areoles is also a significant character differentiating these two species; they are always > 200 µm in *C. formosanus* sp. n. (or > 6-fold that of paired crowned areoles) but < 200 µm in *C. japonensis* (or < 5-fold that of paired crowned areoles, and most of them are around 100 µm).

In addition to the crowned areoles, other minor differences in Table 2 (thorn areoles and bulging areoles) are much more difficult to use in discriminating these two species. Although the presence of thorn areoles is always questionable due to their small number, it is still considered a key character for distinguishing different species (Schmidt-Rhaesa et al. 2008). Thorn areoles were not reported by Schmidt-Rhaesa (2004) or Baek (1993) but appeared in the description by Inoue (1952). In our study, thorn areoles were not found in nine *C. formosanus* sp. n. but appeared in the other 31 *C. formosanus* sp. n. and one *C. japonensis*. Contrary to the thorn areoles which can be easily distinguished from other types of areoles, bulging areoles are much easier to be confused with simple areoles (Schmidt-Rhaesa et al. 2008). Although bulging areoles were consistently ignored in descriptions of *C. japonensis*, we observed various heights of simple areoles, and some of them clustered in groups similar to bulging areoles as described by Schmidt-Rhaesa et al. (2008). This renders the presence of bulging areoles in *C. japonensis* as well as *C. formosanus* sp. n. questionable.

Molting and environmental effects on morphology

About 90 species belong to the genus *Chordodes* which were proposed using only five characteristic types of areoles (Schmidt-Rhaesa et al. 2008). Unfortunately, most characters other than these areole types have seldom been mentioned. According to our observations, the complex ornamentations of the structure of the anterior end were previously considered to be smooth. A horsehair worm explores unknown environments with its head, and the head is also the first part which contacts outer environments when they emerge from a host. Schmidt-Rhaesa and Gerke (2006) suggested that the apical filaments of the crowned areoles may have sensory functions. It is rational that the anterior and posterior ends of horsehair worms with the complex ornamentations play important roles in exploration and mating. Therefore, the smooth anterior ends in some descriptions (e.g., de Villalobos and Zanca 2001) and some of our samples may have been caused by damage from the environment. In addition to the damage, some samples were found to have been covered by residual juvenile skins, indicating that the worms had just molted. Shapes of the ornamentations on the ends under the larval cuticle were flat. The molting of hairworms was observed (Schmidt-Rhaesa et al. 2003), and its potential effects on the morphology should be carefully considered in the future studies. Residual skin was also found on newly hatched larvae, and on a larva still inside an egg, indicating that molting occurred before it emerged from the egg. As a group of Ecdysozoa (Aguinaldo et al. 1997), horsehair worms molt between each instar. According to our observations of metamorphosis from cysts to wormlike juveniles and from juveniles to adults, we suspect those horsehair worms may proceed through at least three molts before maturing.

Host specificity

Compared to the wide range of paratenic hosts, horsehair worms' definitive host range is limited to one or a few species. Because nematomorphs are sometimes found after they have emerged from their hosts, definitive information on hosts is unknown in some species. *Chordodes japonensis* was reported to be parasites of the mantids, *T. sinensis*, *T. angustipennis* (Inoue 1952), *H. patellifera* (Schmidt-Rhaesa 2004), and longhorn grasshoppers, *Hexacentrus japonicus japonicus* (Inoue 1955) in Japan. Since the hairworm described by Schmidt-Rhaesa (2004) was here considered to be *C. formosanus* sp. n., the mantid host of *C. japonensis* is now limited to two species of *Tenodera*. Until now, we have no evidence to exclude *Hex. japonicus japonicus* from being a potential host of *C. japonensis*. However, in our investigation, the host range of these two species seems to be limited to the generic level. Therefore, we still question the ability of *C. japonensis* to develop inside hosts other than mantids.

Molecular approach and perspectives

In the 40 samples from Taiwan and Japan we examined, the taxonomic status was supported not only by their morphologies, but also by the partial COI sequences. COI sequences were used to study inter- and intraspecific relationships due to the high mutation rate (Hebert et al. 2003). The low genetic divergence among our hairworm samples suggests their conspecific relationship, and our samples can also be separated from those hairworms that emerged from *Tenodera* by their significantly divergent sequences. Since species of immature stages can only be conjectured by adults in the same area (Winterbourn 2005), molecular data were herein proven to be a useful tool for identifying both adults and immatures. As molecular information for the phylum Nematomorpha is still limited, we believe more molecular data would be helpful and can be used to uncover uncertain relationships among horsehair worms in the near future.

Acknowledgments

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Further records of non-cryptic New Zealand earthworms

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Abstract

Current descriptions add natives *Aporodrilus aotea* **sp. n.**, *A. ponga* **sp. n.** and *Notoscolex repanga* **sp. n.**, plus new exotic records to the numbers of megadrile earthworms known from New Zealand, which are now raised from 193 to 222 species in five families, *viz*: Acanthodrilidae, Octochaetidae and Megascolecidae, plus Lumbricidae and Glossoscolecidae for exotics. Overlooked spermathecal diverticula have been located for *Notoscolex equestris* Benham, 1942 and for *Megascolex animae* Lee, 1959 and non-tubular prostrates were misconstrued as tubular in *Megascolides tasmani* Lee, 1959. Of these latter three species, a lectotype is designated for *N. equestris* and holotypes of the other two are briefly redescribed. Whereas *M. tasmani* now belongs in *Notoscolex* Fletcher, 1887 and *M. animae* belongs in *Anisochaeta* Beddard, 1890, further lack of dorsal pores in *N. equestris* as with *Notoscolex esculentus* (Benham, 1904) and *N. mortenseni* (Michaelsen, 1924) newly qualifies all three as additional combs. novae in primarily Tasmanian genus *Aporodrilus* Blakemore, 2000.

Keywords

Eco-taxonomy, Annelida: Oligochaeta, new taxa, ICZN, island biodiversity

Introduction

The definitive earthworm study completed 50 years earlier (Lee 1959) was not taxonomically reviewed until Dr Ken Lee (1927-2007), my PhD assessor and mentor, kindly invited me to compile an update in 1999 for a *NZ Species 2000* meeting to be held around January, 2000 at Te Papa Museum in Wellington, New Zealand (NZ). This was, however, not finally published until 10 years later as modified under Glasby et al. (2009). Whereas the seminal works by Lee (1952, 1959) culminated in approximately 193 species in two families, subsequent lists by Blakemore (2000a, 2004, 2006, 2010) totaled 214 taxa in five families with some names removed and several others added.

Smith (1886) had earlier remarked that "*The habits of New Zealand earth-worms receive the smallest share of attention from naturalists of any group of our native fauna. This is to be expected, as the study of worms requires much time and patience*". Similarly, little attention has been shown to the native earthworms following Lee's detailed studies 50 yrs before. For exotics, the main additions to Lee (1959) were of *Aporrectodea tuberculata* (Eisen, 1874) and *Octolasion lacteum* (Örley, 1881) by Martin (1977), and three additions to the NZ alien species list following extensive searches of literature by the current author (e.g. Blakemore 2002, 2004, 2006, 2008). These were of records from NZ by Michaelsen (1900: 425, 1903: 132) of *Pontoscolex corethrurus* (Müller, 1857) that were seemingly overlooked by subsequent researchers; by Easton (1981: 53, 1984: 118) of *Amynthas hupeiensis* (Michaelsen, 1895) plus *Amynthas gracilis* (Kinberg, 1867) and *Amynthas corticis* (Kinberg, 1867) from Raoul Island. The latter was already described as widespread by Lee (1959) but under the synonymous names of "*Pheretima peregrina* (Fletcher)", *Pheretima clerica* Benham, 1947 and *Pheretima campestris* Lee, 1952. Additionally, *Perionyx excavatus* Perrier, 1872 and *Dendrobaena veneta* (Rosa, 1886) were identified by the current author around 2001 from vermicomposting operations in NZ (Blakemore 2002). Other new records of four or five other exotic species are pending (Blakemore submitted).

For natives, few had subsequent reports and because of this approximately 77 were automatically listed as "Threatened" or "Endangered" in the Department of Conservation (DoC) threatened species list (Anon. 2005). Details on three of these are given in McGuinness (2001) while 168 species from 173 qualified as "data deficient" in Hitchmough (2002) and Hitchmough et al. (2007). Terrestrial surveys continue to inexplicably languish. Further work such as that conducted by Springett and Gray (1998) is urgently required to determine the true status and ecology of natives and the extent of the relatively few species of introduced lumbricids and other exotics.

A study by Blakemore (2010) added twelve natives plus a new New Zealand record of *Octolasion tyrtaeum tyrtaeum* (Savigny, 1926), and synonymized genus *Eudinodriloides* Lee, 1959 with *Decachaetus* Lee, 1959. A taxonomic checklist gave natives separate family status to raise the numbers of megadrile earthworm families known from New Zealand from three to five, *viz.* Acanthodrilidae, Octochaetidae and Megascolecidae *sensu* Blakemore (2000c), plus exotic Glossoscolecidae (for *Pontoscolex*) and Lumbricidae, with species then totaling 214. In contrast, some contemporary online and public presentations (e.g. http://soilbugs.massey.ac.nz/oligochaeta.php, http://www.terranature.org/weta.htm, http://www.teara.govt.nz/en/1966/worms-earth/1, www.doc.govt.nz/upload/documents/science-and.../casn320a.pdf) yet claim just ~173 native species plus ~20 exotics in only two or three families.

Buckley et al. (2011) recently posited a phylogeny for the New Zealand earthworm fauna under (Oligochaeta: Megascolecidae) which they comprised as "Megascolecinae and Acanthodrilinae" based on approximately 33 newly collected known natives and about 48 unknown cryptic natives (total 81 taxa). However, their concepts of families and genera appear to be more than 50 yrs old reversions and, as no species/genera types were sourced, confidence in taxonomic acuity at even species level is reduced and their phylogenetic conclusions may be questionable. For instance, Buckley et al. (2011: 86) mention "a review of acanthodriles from Tasmania" when there are none. Moreover, their suggestions of cryptic taxonomic diversity in their 48 unknowns without consideration and analysis of types of all synonyms under ICZN Principals of Priority and of Typification may also be premature (see Blakemore et al. 2010). Speculations in Buckley et al. (2011), in particular a lengthy repetition of the merits of non-New Zealand *Terrisswalkerius* Jamieson, 1994 (they consistently misspell "*Terriswalkerius*"), were supported neither with analyses of type-specimens of genera nor of type-species of senior synonyms. This and other oversights are discussed in a summary endnote to this paper.

Changes invoked by Blakemore (2000a, 2000b, 2000c, 2004, 2006, 2008, 2010), and currently, compared to Lee's (1959) original, and clarifying some reversions/omission or errors in Buckley et al. (2011) concerning native species/genera are:

- Restatement of validity of Acanthodrilidae, Octochaetidae and Megascolecidae (plus Exxidae at one time thought from NZ) as separate families.
- Neoendemic *Microscolex macquariensis* (Beddard, 1896) is removed as Macquarie Island is now claimed by Australia (see Blakemore 2006), albeit still cited by Buckley et al. (2011) as a native but misspelt as "*Microscolex maquariensis*".
- Because *Rhododrilus disparatus* Lee is meroic it was transferred as a new combination in *Leucodrilus* Lee by Blakemore (2004, 2010).
- *Octochaetus* was proven to have native Australian representatives too, e.g. the native *Octochaetus ambrosensis* (Blakemore, 1997) and similar species in Queensland where *Adroitplema* Blakemore, 2006 (nom. n. pro *Neodiplotrema* Dyne, 1997 non Yamaguchi, 1938) is now a junior synonym (see Blakemore 2000c, 2006). [Cf. miscitation of the genus by Buckley et al. (2011)].
- *Sylvodrilus* Lee is retained as the type is anisochaetine, i.e., classed as non-lumbricine (cf. *Eudinodriloides*).
- *Plutellus* Perrier species are transferred to *Graliophilus* Jamieson which is said to have tubular prostates (as "flattened tubes") in its type species; those species having non-tubular prostates more appropriately belong in *Zacharius* Blakemore, 1997.
- *Megascolides* McCoy, 1878 is retained, although species with non-tubular prostates are returned or reallocated to *Notoscolex* Fletcher, 1886/7 for which its junior synonyms are: *Tokea* Benham, 1904; ?*Nelloscolex* Gates, 1939; ?*Lennoscolex* Gates, 1960; *Pseudonotoscolex* Jamieson, 1971; *Pseudocryptodrilus* :

Jamieson, 1974, 2000 (part. cf. *Megascolides*); *Oreoscolex* Jamieson, 1973; *Araucaridrilus*, Jamieson, 2000; ?*Plutelloides* Jamieson, 2000 (but cf. *Megascolides*) – synonyms from Blakemore (2000c, 2005a, 2006, 2010). *Megascolides* is a classical genus lacking nephridial bladders, cf. classical *Cryptodrilus* that retains and/or obtains them.

- Endemic *Perionyx* Perrier, 1872 spp go into originally defined *Perionychella* Michaelsen, 1907 [syn. *Terrisswalkerius* – for its putative type *Perichaeta canaliculata* Fletcher, 1887 and similar species with non-tubular prostates – see Blakemore (2000c) and cf. those species misplaced under that genus name that actually have tubular prostates and thus belong in *Diporochaeta* or *Reflechtodrilus*].
- *Diporochaeta* Beddard, 1890 is retained with its original definition [including the balance of *Terrisswalkerius* spp (part. – but not type or other species with non-tubular prostates – see Blakemore, 2000c and cf. *Perionychella*), some other erstwhile *Terrisswalkerius* interlopers properly belong in *Reflectodrilus* Blakemore, 2005 as per Blakemore (2005a, 2006)].
- *Perionychella shoeana* (Cognetti, 1912) position is rendered uncertain by its original description as: "Each prostate is a tongue-shaped body, not divided into lobes" being revised by Lee's (1959: 325) inspection of new material (the type not being located) to "Prostates short tongue-shaped organs, projecting laterally through xviii [18], surrounded by thin sheath and each consisting of a number of distinct lobes". Nevertheless, having non-tubular prostates qualify it for *Perionychella*; cf. Buckley et al.'s (2011: Appendix) inappropriate naming as "*Perionyx shoeanus*" (sic).
- *Megascolex* Templeton, 1844 species from Australia and New Zealand are now placed in *Anisochaeta* Beddard, 1890 for which *Trichaeta* Spencer, *Spenceriella* Michaelsen, *Gemascolex* Edmonds & Jamieson, *Pericryptodrilus* and *Propheretima* Jamieson are junior synonyms (see Blakemore 1997, 2000b, 2000c, 2002, 2005a, 2006, 2010).
- Species having tubular prostates and previously placed in *Spenceriella* (the neotype of which was stated to have racemose prostates, although this is possibly a mistake - see Blakemore 1997: 1823; 2000b, c) are now in the next available genus, *Celeriella* Gates, 1958 for which *Pericryptodrilus* Jamieson, 1977 would be a synonym if the prostates are indeed "thickly or flattened tubular" as claimed (but as they appear tubuloracemose then this name likely belongs in *Anisochaeta*). *Celeriella* is primarily an Indian genus and it is probable that its New Zealand species will eventually go into a separate genus (as noted by Blakemore, 2006).
- Monotypic *Eudinodriloides* Lee, 1959 was placed under *Decachaetus* Lee, 1959 in Blakemore (2010) with its perichaetine type-species, *Decachaetus forsteri* (Lee, 1959), comb. n.; cf. Buckley et al. (2011: Appendix A) with a single "*Eudinodriloides* n. sp. 2" (sic).

- Blakemore (2005a) noted that Lee (1962) made *Spenceriella shakespeari* (Benham) junior synonym of *Megascolex antarcticus* Baird, itself transferred to *Celeriella* Gates although this appears to have been overlooked or ignored by Buckley et al. (2011: Appendix A) who yet claim to have sampled "*Spenceriella shakespeari*" (WM93 from Waharau Pk, Hunua Range) but appear not to have sequenced its DNA.
- All "Michaelesen (1923)" species should be changed to Michaelsen (1924) according to the volume preface (see http://ia700402.us.archive.org/4/items/videnskabeligeme74dans/videnskabeligeme74dans_bw.pdf accessed Sept., 2011) and one of these, *N. mortenseni*, is considered herein.

Methods

Specimens were sketched, dissected and described under low power microscope using the techniques and conventions noted in Blakemore (2000, 2002, 2008). Tissue samples were taken from new type-species to attempt DNA/COI barcode analysis – any results are to be posted in GenBank. Classification follows Blakemore (2000) at family level and Blakemore (2002, 2008, 2010, 2000b) at genus and species levels. Discussion is confined to comments after species descriptions and endnote summaries of taxonomic conclusions.

Results

New species descriptions

Aporodrilus aotea sp. n.

urn:lsid:zoobank.org:act:F014AE5E-D434-4119-B949-E5AB86DB1E4E
http://species-id.net/wiki/Aporodrilus_aotea
Fig. 1

Material Examined. Holotype Auckland Museum; AMNZ 5254. Single complete specimen, now dissected, from New Zealand, Great Barrier Island, Little Windy Hill (ca. 36°10'S, 175°23'E). Coll: 2.IX.2001, J.W. Early & R.F. Gilbert. "*Under rock on forest floor. L11002*". "*W-025*" on lid. (Small tissue sample was taken for DNA analysis - code RJB09).

Etymology. After Maori name for Great Barrier Island; *Aporodrilus* is treated as masculine but this place name remains genderless as a noun in apposition.

Diagnosis. *Aporodrilus* having spermathecal pores paired segmentally in 6, 7 and 8; holandry with seminal vesicles in 9 and 12; oesophageal glands annular in 10–14; large genital markings paired in 17/18 and 18/19 on either side of male pores.

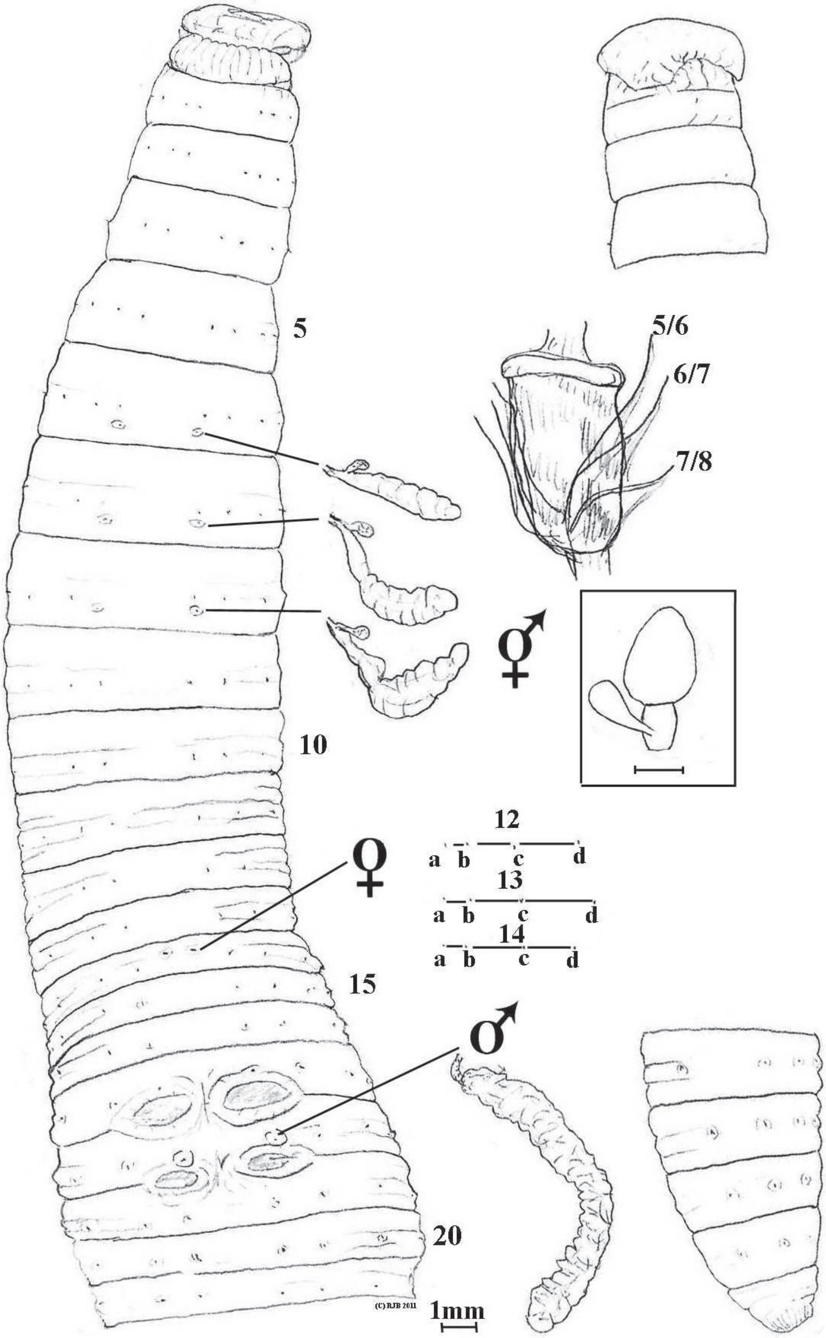

Figure 1. *Aporodrilus aotea* sp. n. ventral view with dorsal view of epilobous prostomium, spermathecae, prostate and gizzard in 5 *in situ*; and lumbricine setal ratios on 12–14; plus lateral view of tail end. [Boxed spermatheca is for comparison of *A. esculentus* (Benham, 1904) from Benham's fig. 67 and from Lee (1959: fig. 309)].

External characters. Body circular tapering at both ends. Dark, matt grayish pigment with iridescent cuticular sheen; paler intersegments and setal auriolae. Length 140 mm with 75 segments. Prostomium epilobous. Setae lumbricine, 8 per segment in rows becoming increasingly irregular further back. Clitellum not well marked. Dorsal pores absent. Nephropores not found (meroic). Spermathecal pores segmental, equatorial just below setae a on 6, 7 and 8. Female pores mid-ventral pair anteriormedian to setae a on 14. Male and prostatic pores combined on tiny mounds on 18 in position of deleted setae a. Penial setae not found. Genital markings large, longitudinally symmetrical pads, paired in 17/18 and smaller in 18/19.

Internal morphology. Pharyngeal mass to 4. Septa 4/5-10/11 thin, only 11/12/13 with slight thickening and thereafter membranous. Gizzard strong and elongate apparently in 6-7 but discernable in 5 by tracing septum 5/6 to near base despite dorsalwards displacement. Dorsal blood vessel single; hearts paired and increasingly large in 9-13; supra-oesophageal vessel in 10-13. Nephridia meroic with forests of avesiculate tubules on body wall. Spermathecae in 7, 8 and 9 each with elongate, flaccid ampulla and single, small, clavate diverticulum (inseminated) near base implicated with anterior septum which is transgressed. Holandric: minute funnels in 10 and 11 ventrally; seminal vesicles paired, racemose posteriorly in 9 and anteriorly in 12. Ovaries paired as free egg-string bunches ventrally in 13; ovisacs not found. Prostates tubuloracemose extending to ca. 22 from small flaccid ducts to male pores in 18. Oesophagus with oesophageal glands small in 10 and larger in 11-13 then small again in 14; glands more saccular than composite but dilated compared to extraneous oesophageal width. Intestinal origin in 16. Typhlosole and caeca not found (absent). Gut contains fine colloidal reddish soil.

Ecology. Lack of dorsal pores is usually associated with aquatic habitat, but possibly also with high rainfall/soil-moisture, however, the strong gizzard suggests a loamy diet. Further ecological and/or behavioural information is wanting.

Remarks. *Aporodrilus aotea* compares with *A. mortenseni* (Michaelsen, 1924) that differs, not least, by having its three pairs of spermathecal pores intersegmental in 6/7/8/9 and by lacking genital markings. However, in the review by Lee (1959) that did not routinely note presence or absence of dorsal pores (nor genital markings), the current species keys out nearest to Lee's *Megascolides* species now in *Notoscolex*, viz.: *N. sapidus* that differs in its spermatheal pores intersegmental in 6/7/8/9; or to those now in *Aporodrilus* viz. *A. equestris* (Benham, 1942), and edible *A. esculentus* (Benham, 1904) with which it perhaps comes closest as this too has spermathecae opening on 6-8. *A. equestris* as redescribed below has genital markings elongate in 17 & 19, exceptionally thickened septa, a gizzard in 6 and intestine from 17; while *A. esculentus* has genital markings paired midventrally in 16 and 17, thicker septa, a smaller gizzard, oesophageal dilations only in 15 and its spermathecae of a more spherical and compact form (see figures and compare Benham's original sketches http://www.archive.org/stream/proceedingsofzoo19042zool#page/240/mode/2up). A more distant contender is *N. urewerae* (Benham, 1904) "a short white worm" that has genital marking midventrally in 19/20 and last hearts in 12 amongst other differences (its dorsal pores are unrecorded and possibly it too belongs in *Aporodrilus*).

Aporodrilus ponga sp. n.

urn:lsid:zoobank.org:act:C7CD2EDF-0B2A-4EEA-A34B-4CF06F927A04
http://species-id.net/wiki/Aporodrilus_ponga
Fig. 2a, 2b

Material Examined. Holotype Auckland Museum; AMNZ 5255. Single mature, posterior amputee rather poorly preserved from Waitakere Ranges, Waiatarua. Coll: 9.V.1995, G. Ripley. "*Nikau/Ponga forest L761*"; "W-012" on lid. (Small tissue sample was taken for DNA analysis coded RJB10). [Two other specimens from the same jar are a posterior portion of a worm (AMNZ 5256) matching the dimensions and frayed edge of the current specimen is itself missing its tip; the other (AMNZ 5254) is a large mature, anterior amputee that is certainly different and probably a new species but which is inadequate for formal description here].

Etymology. After Maori name for silver fern *Cyathea dealbata* (G. Forster) Swartz, 1801, from the habitat detail and also the symbol commemorating the All Blacks victory in 2011 Rugby World Cup; *Aporodrilus* is masculine, but a noun in apposition is genderless.

Diagnosis. *Aporodrilus* having spermathecal pores paired intersegmentally in 7/8/9; metandric with seminal vesicles in 12; no oesophageal glands; genital marking as a distinct pad in 17/18 with male pores on lower rim replacing setae a.

External characters. Body robust, dorsally canaliculated in parts before amputation. Pale putty coloured in alcohol. Length 220+ mm anterior portion (a posterior fragment in jar is also 220mm and if from same specimen would give length = 440 mm). Prostomium much wrinkled prolobous. Setae lumbricine, obscure in anterior and mostly occluded on clitellum apparently converging towards male pores; further back the rows except for setal a lines become progressively irregular. Clitellum slightly more tumid and yellowy in ½13–17 (or thereabouts). Dorsal pores absent. Nephropores absent (meroic). Spermathecal pores intersegmental, detected by probe from interior and approximately in setal a lines in 7/8/9. Female pores large paired on 14 (setae obscure) in line with setae a of 13. Male pores superficial on 18 in place of deleted setae a on bottom rim of pad (detected by probe internally). Penial setae not found. Genital marking as a large pad in 17/18 distending both adjacent segments.

Internal morphology. Septa and pharyngeal mass absent before 5, septa 5/6–12/13 greatly thickened, thereafter membranous. Gizzard mucular barrel in 5. Dorsal blood vessel single; hearts sinuous in 9–13. Nephridia meroic forests on body wall. Spermathecae paired in 8 and 9 each with flask-shaped ampulla on equally long flat duct with multilocular diverticular frill (inseminated) near base. Probably metandric as paired seminal vesicle seen in 12 only. Testis and ovaries not located, probably minute and lost in musculature of septa and body wall. Prostates rounded but finely incised throughout so not as found in Acanthodrilidae and Octochaetidae (cf. Exxidae), i.e. tubuloracemose with small flaccid ducts in 18. Oesophagus without noticeable dilations (what I initially took as a hemispherical thickening of posterior of 9 was determined as a septum). Intestine substantial yet dilated and easily ruptured, origin appears

Figure 2a. *Aporodrilus ponga* ventral scan of Holotype (colour).

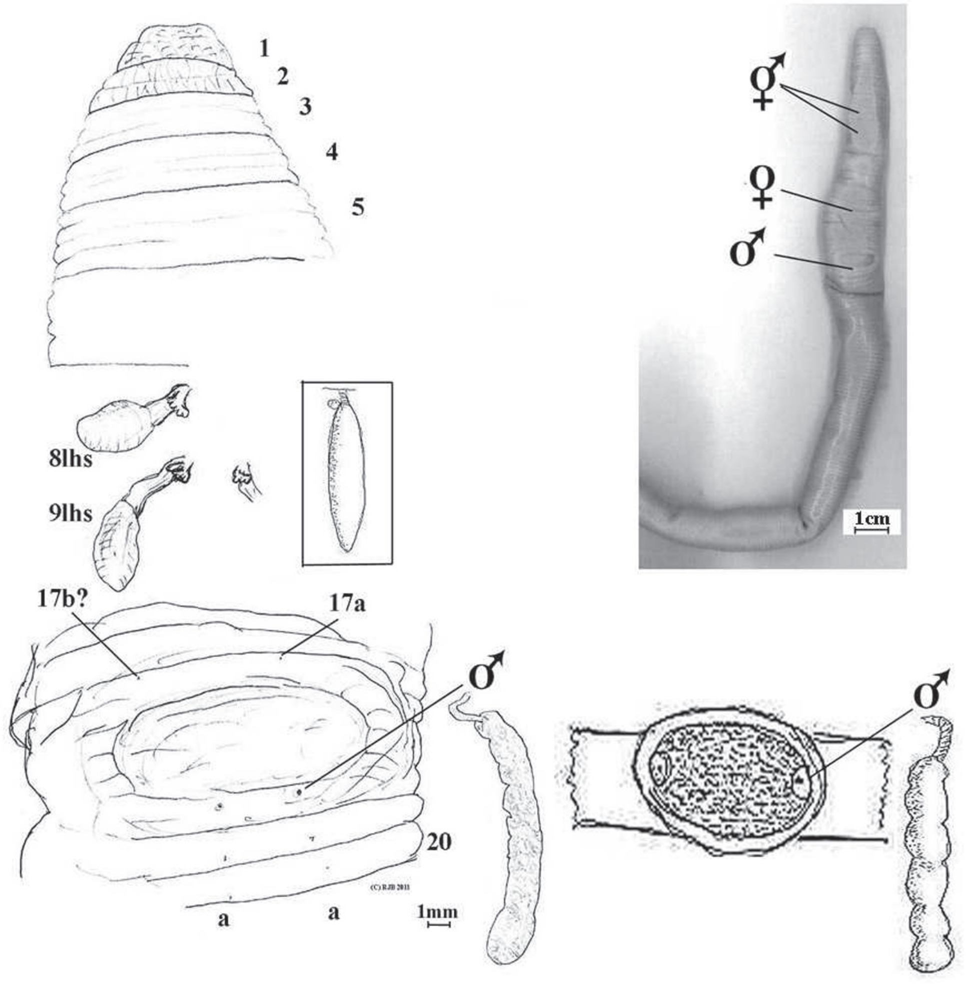

Figure 2b. *Aporodrilus ponga* dorsal view of prolobous prostomium, spermathecae (8lhs and 9lhs and part of 9rhs) and prostate in 18lhs *in situ*. Male field is shown with setae 17b? and 17a marked (setae a occluded by male pores on 18). [Boxed spermatheca of *Notoscolex hakeaphilus* Benham, 1949, with Benham's sketch of its male field and prostate shown for comparison].

in 15 or 16. Gut contains finely ground organic matter, organic soil plus coarse multicoloured grits.

Ecology. Anterior musculature and thickened septa are associated with strong burrowing, and lack of (anterior) dorsal pores may aid maintenance of hydroskeletal turgor pressure.

Remarks. *Aporodrilus ponga* differs from *A. aotea* on almost each specific point. According to Lee (1959), who often took tubuloracemose prostates to be tubular, this specimen keys to genus *Megascolides* but fails to match any known taxa from there. If more properly allowed into Lee's *Notoscolex* the similarity with *N. hakeaphilus* Benham, 1949 is remarkable: viz. large size (650–950 mm) with irregular setae, male pores on a median oval depression, septa absent before 5, spermathecae in 8 and 9, and metandry. Presumed differences however, are darker colour (current specimen bleached in alcohol?), epiloby and again much furrowed as here, tufted nephridia (how tufted?) in anterior, a thick-walled enlargement of oesophagus in 8 (possibly as I initially thought was in 9), prostates claimed as flat rather than rounded (although figured as rounded), spermathecae with "*a minute globular diverticulum*" (variation?), and male pores shown laterally within pad on 18 rather than on its rim as here. It is possible Benham mistook some of these points. His report of last hearts in segment 10 for this species is undoubtedly anomalous as invariably they are in either segments 12 or 13 in normal Megascolecidae; and intestine in 12 is also anterior to what is usual. No mention was made of dorsal pores by him. Benham's type was collected in 1946 from Kerikeri (A.48.31 – supposedly in poor condition but confirmation from Otago museum unforthcoming) that he thought imported from Australia as was the plant it was found under. This seems unlikely for such a large species: even if its cocoons were introduced, large species often have particular habitats unlike most small to medium cosmopolitans. Lee (1959: 318), presumably accepting Benham's characterization, has another specimen (current location unknown) from Pukehohe, suburb of Auckland, from subsoil collected by W. Cottier in 1951. (An online GBIF record of Australian Museum AM W.29352 at Taupo is unconfirmed http://data.gbif.org/occurrences/237279142 accessed November, 2011). A much smaller species but with remarkable superficial similarity of marking to Benham's *N. hakeaphilus* is his *N. maoricus* (Benham, 1904) (syn. *T. decipiens* Benham, 1905) that also comes from "*Waitakerei Bush*" (= Waitakere), near Auckland.

Without information to the contrary we must reluctantly accept the balance of Benham's earlier diagnosis, in which case a new name for this specimen has merit. Confirmation of independence of either species now depends on reinspection of Benham's type, apparently beyond the brief, budget and resources of successive workers for the last 62 years, including the present one.

Notoscolex repanga sp. n.

urn:lsid:zoobank.org:act:796E44B7-47A8-4D10-B491-8BBA8B6A85C3
http://species-id.net/wiki/Notoscolex_repanga
Fig. 3

Material Examined. Holotype Auckland Museum; AMNZ 5253. Single complete specimen, now dissected, from New Zealand, Cuvier Island (36°26'S, 175°46'E) SE catchment 40–60 m. Coll: 3.IV.2000, J.W. Early & R.F. Gilbert. "*Under rock in stream bed. L8229*" "*W-024*" on lid. (Small tissue sample was taken for DNA analysis coded RJB07).

Etymology. After Maori name for Cuvier Island; *Notoscolex* is treated as masculine but this place name remains genderless as a noun in apposition.

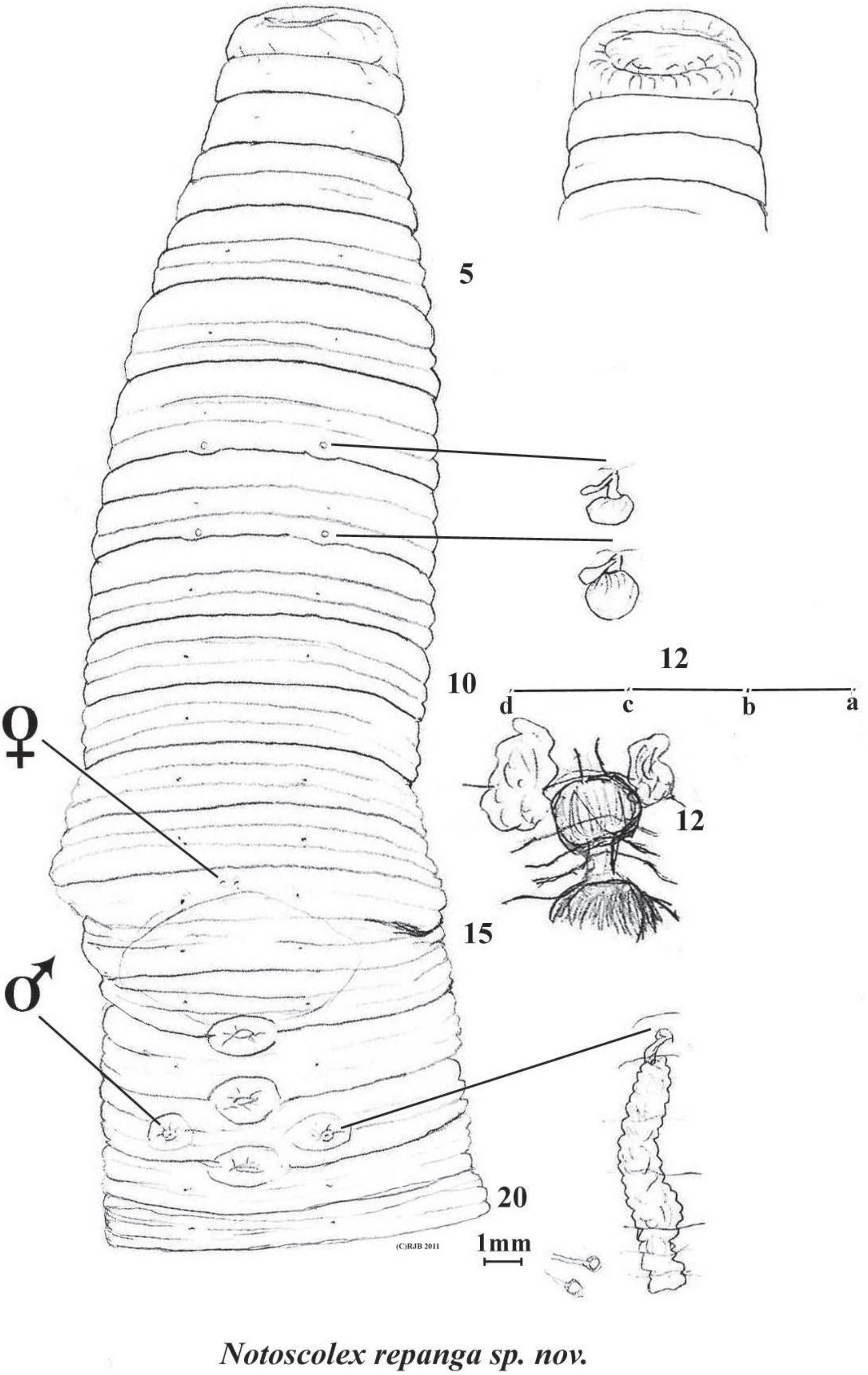

Figure 3. *Notoscolex repanga* ventral view with dorsal view of prolobous prostomium, spermathecae, prostate and oesophageal gland in 12 *in situ*; and lumbricine setal ratio in 12. (Small structures near scale bar are probable unidentified parasites, attached on intestine in region of 35–40).

Diagnosis. *Notoscolex* having spermathecal pores paired posteriorly in 7 and 8 but with clavate spermathecae anteriorly in 8 and 9; holandry with seminal vesicles in 9 and 12; oesophageal gland annular in 12; genital markings mid-ventral in 16/17/18/19.

External characters. Body circular. Pale unpigmented in alcohol. Length 135 mm with 149 segments. Prostomium prolobous. Setae lumbricine, 8 per segment in mostly regular rows and almost equidistant throughout. Clitellum not marked. Dorsal pores present but minute and difficult to detect, possibly commencing from 9/10 or 10/11. Nephropores not found (meroic). Spermathecal pores segmental, posteriorly just above intersegments in setal a lines on 7 and 8. Female pores difficult to detect with certainty, possibly mid-ventral pair anterio-median to setae a on 14. Male and prostatic pores combined on small tumescences on 18 in position of deleted setae a. Penial setae not found. Genital markings mid-ventral eye-shaped sucker pads in 16/17, 17/18 and 18/19; a yellowy midventral patch from ½14-16/17 may be artefactual.

Internal morphology. Septa increasingly thickening from 4/5–10/11; 11/12 thin and thereafter membranous. Gizzard large but weak in 5. Dorsal blood vessel single; commissurals in 5–8; hearts paired and small in 9, much larger in 10–13; supra-oesophageal vessel not found. Nephridia meroic with several avesiculate tubules almost evenly spaced in several rows on body wall in each segment. Spermathecae in 8 and 9 each with saccular ampulla and single, small clavate diverticulum (non inseminated). Holandric: testes and funnels minute in 10 and 11 ventrally; seminal vesicles paired, racemose in 9 and, larger, in 12. Ovaries paired as fine string masses ventrally in 13; ovisacs not found. Prostates flattened, tubuloracemose extending to ca. 24 from small ducts to male pores in 18. Sessile tumidity associated with genital markings internally. Oesophagus large and folded in on itself in anterior in 6–9 at least; with annular dilated oesophageal gland in 12. Intestinal origin in 16. Typhlosole and caeca not found (absent). Gut contains fine silt with few organic fragments. Intestine paler and concertinaed between 35–40 where several (gregarine?) parasitic cysts on stalks attach to it (see figure).

Ecology. Habitat location (under rocks in stream) would indicate an aquatic or semi-aquatic life style, a conclusion supported by the pale colouration plus reduced dorsal pores and gizzard; while the folded oesophagus in the anterior would allow considerable extension (for movement and feeding) and the gut contains silty (alluvial?) soil. Alternatively, this specimen may be an unintentional interloper washed into the stream from adjacent soil; more ecological information is needed to confirm or disconfirm this.

Remarks. *Notoscolex* is primarily an Australian genus with representatives in Sri Lanka and southern India as well as NZ. The current specimen although large is possibly subadult (it has genital markings but lacks a distinct clitellum and spermathecae uninseminated) yet appears to be a distinct species. Its morphology is comparable to the nine previously known regionally compatriot *Notoscolex* species, all confined to the north of the North Island, many of which were at some time placed in the cohesive genus *Tokea* Benham, 1904. This latter genus was made junior synonym of *Notoscolex* following Michaelsen (1916), Stephenson (1930: 837) and as herein compared to Lee (1959) who placed it within *Megascolides*.

Of the nine or so New Zealand species now known, *Notoscolex repanga* differs: from *N. sapidus*, *N. urewerae*, *N. huttoni* and *N. suteri*, all by Benham (1904) and each having three pairs of spermathecae; and from Benham's *N. kirki* and *N. maoricus* which share two pairs but differ in their arrangements of genital markings and spermathecae. Whereas *N. kirki* has intersegmental spermathecal pores in 7/8/9, *N. maoricus* has them segmentally but in posterior of 7 and 8, and not 8 and 9 as he originally stated and as inadvertently retained by Lee (1959: 302). [This correction according to Benham (1905: 240, pl XL, figs. 1–2, 8–9) – see http://www.archive.org/stream/transactionsproc38newz#page/240/mode/2up or http://rsnz.natlib.govt.nz/volume/rsnz_38/rsnz_38_00_002970.pdf where he unconventionally records segments 7 & 8 as "7/8" and 8 & 9 as "8/9"; see also http://rsnz.natlib.govt.nz/image/rsnz_38/rsnz_38_00_0736_0000f_ac_01.html for his original figures of *Tokea maorica* and its junior synonym *T. decipiens* Benham, 1905]. *N. hakeaphilus* (Benham, 1949) does have spermathecae in 8 and 9 (with pore locality indeterminate) but differs not least in its large (650 mm) dark body with irregular setae and metandry. *N. napierensis* (Benham, 1941) has its four pairs of spermathecal pores equatorial on 6–9, and was probably misdescribed by Benham as having two pairs of tubular prostates on 17 and 19, where the genital markings lie, while Lee (1959: 304), who thought it introduced, accords it a single pair of lobate prostates in 18; dorsal pores were unstated by both authors. A previous *Notoscolex* member, *N. mortenseni* (Michaelsen, 1924) is now moved to *Aporodrilus*.

Superficially, *N. repanga* is somewhat similar to several *Megascolides* spp., such as *M. viridis, M. raglani, M. irregularis, M. alba* and *M. novaezealandiae*, but it differs from all generically by its non-tubular prostates, and specifically by virtue of combination of segmental spermathecal pores and three mid-ventral genital markings, plus an oesophageal gland in 12 only and its last hearts in 13 rather than 12.

A further *Megascolides* species occurring in NZ and now possibly extinct was described by Schmarda in 1861 under the title of "*Hypogaeon orthostichon*," that is subjected to separate treatment in a forthcoming publication (Blakemore submitted.).

Redescription of original AMNZtypes

Types are redescribed for *Anisochaeta animae* (Lee, 1959) and *Notoscolex tasmani* (Lee, 1959) comb. n., and newly designated for *Aporodrilus equestris* (Benham, 1942) comb. n. As with Tasmanian *Notoscolex tasmanianus* Fletcher, 1887, the erstwhile representative of temporary genus *Pinguidrilus* Jamieson, 1974, that was found by Blakemore (2000c) to have had its spermathecal diverticula overlooked, a similar oversight applies to types for both *Notoscolex equestris* Benham, 1942 and *Megascolex animae* Lee, 1959. While *M. animae*, which belongs in *Anisochaeta*, has dorsal pores (from 4/5, pers. obs. – see separate description), *N. equestris* is found to lack them and thus, along with *N. esculetus* and *N. mortenseni*, belongs as comb. n. in *Aporodrilus* Blakemore, 2000.

***Anisochaeta animae* (Lee, 1959)**

http://species-id.net/wiki/Anisochaeta_animae
Fig. 4

Megascolex animae Lee, 1959: 281, figs. 301-304.
Anisochaeta animae; Blakemore, 2004, 2005, 2010.

Distribution. From Unuwhao Mt., nr Spirits Bay, northern extremity of Northland, NZ.

Description from type. AMNZ 5038 for *Megascolex animae* has the following label in jar: "*Unuwhao nr. Spirits Bay, N.Z. Coll: A.W.B.P. Feb 1946 AM8 1039*". It is a substantial specimen – 196 mm × 13.5 mm – collected by former director of Auckland Museum, A.W.B. Powell in Feb. 1946. Although the specimen in alcohol is now bleached of its earlier dark brown dorsal pigmentation and is wrinkled and hardened, it

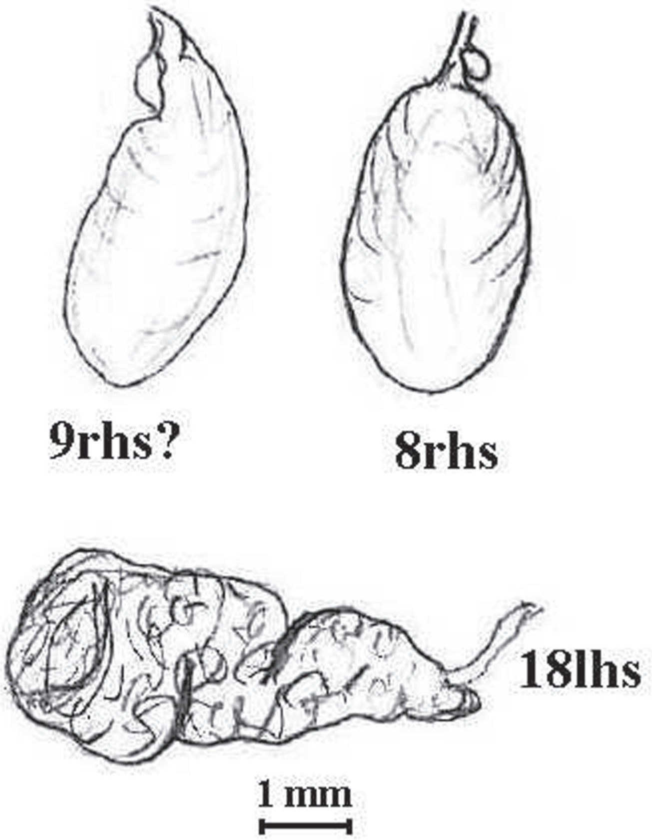

Figure 4. *Anisochaeta animae* (Lee, 1959). Holotype (AMNZ 5038); spermatheca labelled 9rhs? is from separate vial and is a broken off ampulla; that labelled 8rhs is *in situ* showing small iridescent diverticulum (no parasites were found internally); the tubuloracemose prostate is from 18lhs.

is yet well preserved. Reinspection of the type largely conforms to Lee's original except that his figured spermathecae (from 9rhs that he included in a separate vial) is broken off after the diverticulum, and diverticula are newly found to be present in the remaining *in situ* spermathecae (see figure). The peristomium was not obviously cleft ventrally and genital markings, rarely described by Lee, were not found, but dorsal pores were: small in 4/5 and more obvious afterwards. Specimen AMNZ 5038 is the monotypic holotype fixed by original designation under (ICZN, 1999: Art. 73.1.1); the only slight ambiguity is that Lee (1959: 282) also noted another specimen with "*Same data as type material*" that has not been subsequently located.

Notoscolex tasmani (Lee, 1959)

http://species-id.net/wiki/Notoscolex_tasmani
Fig. 5

Megascolides tasmani Lee, 1959: 313, figs. 326-328.
Megascolides tasmani; Blakemore, 2004, 2005, 2010; Buckley et al., 2011?

Distribution. Known only from Great Island, Three Kings Islands. Buckley et al. (2011) claim to have "*Megascolides tasmani*" (WM82), but this must be a mistake if they could not identify it as clearly belonging in *Notoscolex* with non-tubular prostates as herein from type inspection (or perhaps they failed to attempt specimen dissections?).

Description from type. Specimen AMNZ 5039 has the following labels in its jar: "*Auckland Museum Coll No. 13 Wet Greywacke gravel. Tasman Stm. Great Island. Three Kings 31.xii.52 J.S. Edwards*"; "*HOLOTYPE Megascolides tasmani Lee Tasman Stm, Great Is. Col. J.S. Edwards 30/12/52 1021. 3KI3*" [note slightly different dates], a further label is blank. Somewhere are two other non-type specimens from the same locality according to Lee's account (Lee, 1959: 314) with one collected "5.I.53".

The type specimen is dark and brittle, shrunken to 53 mm long. Lee has 67.5 mm with 132 segments but it is a posterior amputee so must naturally be greater (there is also a slight possibility it acquires more setae posteriorly). Dorsal pores, not noted by Lee, are present from 10/11, at least. It appears lumbricine with widely spread setae that converge slightly towards male pores. Lee has overlooked the penial setae which are protruding (due to shrinkage?) from each of the male pores on 18. In 17 in ab lines is a reddish patch that may be a residual genital artefact. The female and spermathecal pores are no longer obvious. Vascularization is mostly as described by Lee, i.e., commissurals are in 6–9, hearts are in 10–12 from dorsal blood vessel that loops between septa in 11, 12, (not 13) 14, 15 and 16 thereafter single (Lee, 1959: fig. 327 shows only in 14 and 15). Gizzard appears in 6 rather than 5 but being overlain by tufted pharyngeal glands it is difficult to discern. Seminal vesicles are in 9 and 12 as described. Prostates differ significantly as they are flattened tubuloracemose structures, rather than "tubular, convoluted" as Lee has them; the duct is not traceable in the

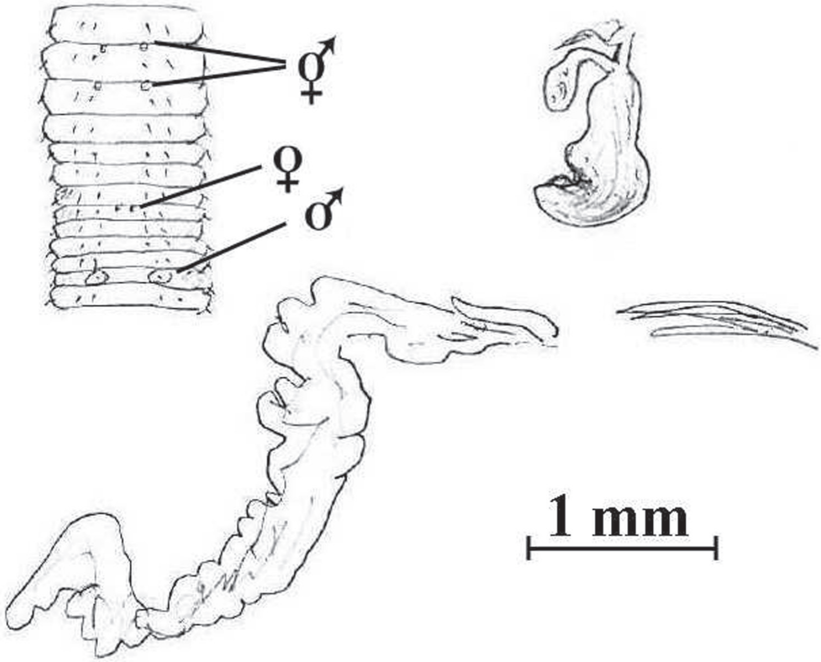

Figure 5. *Notoscolex tasmani* (Lee, 1959). Holotype (AMNZ 5039); sketch of anterior body (after Lee, 1959: fig. 326), a desiccated spermatheca from vial (cf. Lee, 1959: fig. 328) and flat, tubuloracemose prostate with penial setae *in situ* in 18lhs.

delicate specimen and, moreover, there is a bundle of long reddish penial setae more ventrally. An excised spermatheca is in a separate vial in the jar and, apart from being desiccated, complies with Lee's (1959) account and figure. The wide intestine contains organic matter and is full of coarse grits of various minerals.

Remarks. Having non-tubular prostates qualifies this taxon as a new combination in *Notoscolex*. The remote chance it acquires extra setae posteriorly after cut would permit it in *Anisochaeta*. Penial setae are unusual for New Zealand Megascolecidae, but it is interesting that they do not correspond well to the length of the spermathecal diverticula (see Blakemore 2000c; 2008). Further investigation is required for confirmation.

Aporodrilus equestris **(Benham, 1942), comb. n.**
http://species-id.net/wiki/Aporodrilus_equestris
Fig. 6

Notoscolex equestris Benham, 1942: 220-225, Pl. 17, figs. 1–5; 1949: 348; 1950: 33; Lee, 1952: 37; Blakemore, 2004, 2006, 2010.
Megascolides equestris; Lee, 1952b; 1959: 287, fig. 308 (of a spermatheca).

Distribution. Poor Knights Islands, New Zealand [an online report, along with several other New Zealand earthworms, as a Marine invertebrate from Mexico - http://mexinverts.lifedesks.org/pages/1545 (Oct. 2011) is clearly a mistake].

Description from types. Two specimens in jar: AMNZ 5040 a larger ~200mm specimen dissected previously, and AMNZ 5280 a smaller complete mature 140 mm long. Labelled "*TYPES Notoscolex equestris Benham 1942*"; "*Notoscolex Equestris Benham 1942*"; "*TAWHITI RAHI ISLAND, POOR KNIGHTS ISLANDS 26 November 1940 G.A. Buddle, R.A. Wilson, E.G. Turbott*".

There is some slight confusion with *Notoscolex equestris* Benham, 1942, in that Lee (1959) erroneously placed it in *Megascolides*, and Lee (1959: 296) said types were in Otago Museum (No. A.43.52 - two specimens in fair condition but confirmation from Otago museum unforthcoming), yet he also gives "4 specimens. (Auckland Museum Collection)". There are indeed two specimens in the Auckland Museum (pers. obs.) viz.: AMNZ 5040 with labels as above. Benham (1942: 220 - see http://rsnz.natlib.govt.nz/volume/rsnz_72/rsnz_72_03_002070.pdf) actually stated that Mr R.G. Turbott of the Auckland Memorial Museum had sent him two phials, one from Chatham Island that contained four earthworms, and these other two larger specimens collected from Poor Knights Islands by Majors G.A. Buddle and R.A. Wilson.

Both specimens are here inspected and described: the larger one – that entirely agrees superficially with Benham's figures – had been previously dissected with the 8lhs spermatheca, 18rhs prostate, and the anterior of the intestine removed and missing from the jar. Additions to Benham's and Lee's earlier descriptions are that the highly wrinkled prostomium is construed as pro-epilobous rather than prolobous, and no ventral cleft is present on the peristomium. Benham was "unable to detect the dorsal pores owing to the strongly contracted state of the body" and, for some reason, Lee omitted mention of them entirely except for exotic Lumbricidae. They are here confirmed as being absent throughout the body in both specimens (i.e., qualifying for *Aporodrilus*). Setae c and d are increasingly irregular. Spermathecae are in 7–9 but for 8lhs only the stub remains with the small diverticulum still attached (hence overlooked by earlier workers who also mistook slight folds in the soft duct as "excrescences"); as for other spermathecae, the small diverticula are visible by their slight iridescence just above the body wall at the base of the duct [see Fig. 6 and cf. Benham (1942: fig. 5), Lee (1959: fig. 308)]. Only the prostate 18lhs remains and is here construed as cylindrical tubulo-racemose i.e. non-tubular [see Fig. 6 and cf. Benham (1942: fig. 4)]. Genital markings agree as per original (Benham 1942: fig. 3) and the smaller undissected specimen (AMNZ 5280) is provided with a rough sketch showing how it conforms too. The gizzard appears more in 5 than 6 and oesophageal dilations are increasingly large in 10–14 (at least) but, as gut is removed, the intestinal origin cannot be confirmed. Although a typhlosole is absent and it is noted that the intestine below the break is filled with particularly coarse plant fragments only (no soil).

Remarks. Both specimens are surely syntypes (one dissected agrees and key organs removed suggests they were figured by Benham, although Lee also dissected a prostate)

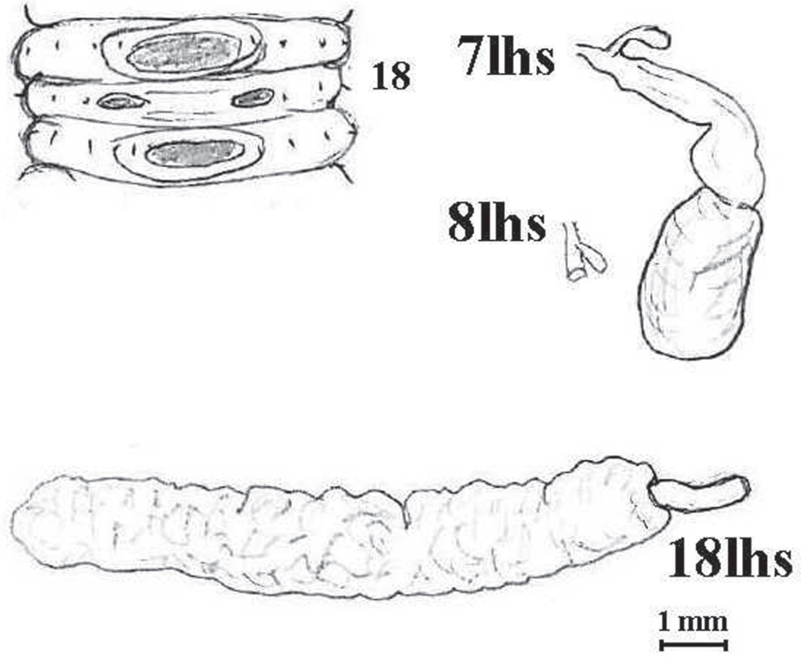

Figure 6. *Aporodrilus equestris* (Benham, 1942). Lectotype (AMNZ 5040); sketch of male field of paralectotype for comparison with Benham's figures; also spermathecae (7lhs, 8lhs as a stub with missed diverticulum, 9lhs not shown) and prostate *in situ*.

and, under ICZN (1999: Art. 74) I hereby expressly designate the larger dissected specimen AMNZ 5040 the lectotype of *Aporodrilus equestris* (Benham, 1942) leaving the remaining undissected specimen as paralectotype (AMNZ 5080). In compliance with "Declaration 44 – Amendment of Article 74.7.3 of ICZN" (1999 – see http://iczn.org/content/declaration-44-amendment-article-7473), this act is in order to provide stability in its taxonomic name coupled with the augmented description provided herein. Enquiries made to verify Otago Museum material (Email: cody.fraser@otagomuseum.govt.nz 15th Oct., 2011) were fruitless, but it is probable Lee (1959: 296) in his account confused the two lots that were sent to Benham, as commented on above.

Note on genus *Aporodrilus*

Meroic *Aporodrilus* has lumbricine setae, tubuloracemose prostates and typically an intestinal origin in 16 (or 17) – as do many other species referable to *Notoscolex* – but it definitively lacks dorsal pores. Previously, only sixteen species and one sub-species were known, all from Tasmania (Blakemore 2000b, c; 2006). Lee's (1952) species *Megascolides parvus* and *M. viridis*, for example, also lack dorsal pores, but they differ in having tubular prostates; yet Lee's statement that Michaelsen's *Megascolex mortenseni* is in *Megascolides* seems slightly askew due to its lumbricine setae (at least in the anterior of the damaged specimen available to Michaelsen) and non-tubular prostates [see Michaelsen (1924: fig. 8b) – reproduced here as Figure 7] that would more properly place it in *Notoscolex*. Based on Michaelsen's original description stating "Rückenporen sind nicht vorhanden", it apparently now belongs in *Aporodrilus*. Since *Aporodrilus mortenseni* was only ever found in a garden at Palmerston North, it may be a translocated native *sensu* Blakemore (1999, 2008) rather than an exotic introduction as intimated by Lee (1959) who considered it outside the normal *Megascolides* range; its conservation status is currently unknown. With addition of *Aporodrilus equestris*, *A. esculentus*, *A. mortenseni* plus *A. atoea* and *A. ponga* spp. novae, the genus total increases to twenty-one species and its range extends from Tasmania to New Zealand (with other expected Australian members in Victoria and southern New South Wales). Relationships within this group remain to be determined.

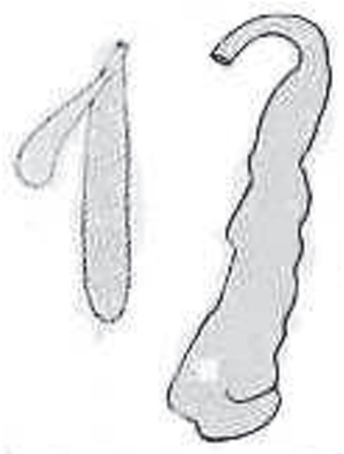

Figure 7. Spermatheca and prostate of *Aporodrilus mortenseni* from Michaelsen (1924: fig. 8).

Note on oversights in Buckley et al. (2011) cladistic phylogeny

While inexplicably ignoring the Australian genus *Reflectodrilus* Blakemore, 2005, Buckley et al. (2011) stated:

> *Australian Spenceriella were moved to Anisochaeta by Blakemore (2006), and they are in a weakly supported clade with Megascolex laingii, also transferred to Anisochaeta. The Anisochaeta concept has potential but needs revision based on more data. We provisionally reject the transfer (Blakemore 2006) of the Terriswalkerius species used here to Perionychella and/or to Diporochaeta because Terriswalkerius is a well-supported clade 5 nodes sister to the clade containing the other two genera.*

In actuality, Blakemore (2000c) was obliged – as any other taxonomist would be – to restore *Anisochaeta* Beddard, 1890 under ICZN priority as it had been overlooked and, rather than being a "concept" it is a valid and available prior genus with a tangible type-species, and hence acquires all similar species from *Spenceriella* Michaelsen, 1907 or any other synonymous genus. Genera strictly follow ICZN nomenclature and rather it is clades that are conceptual. Similar rules apply to genera *Diporochaeta* Beddard, 1890 and *Perionychella* Michaelsen, 1907 that take precedence over their successors for priority reasons as cogently explained by Blakemore (2000b, 2000c, 2005a). Thus, the phylogram by Buckley et al. (2011: fig. 2) merely confirms that all 15 species in the restricted group they call "a well-supported clade" should logically be folded into the earliest valid genus name which, in this particular case on a limited scope, they demonstrate to be *Didymogaster* Fletcher, 1887. The three proven NZ native families – Acanthodrilidae, Octochaetidae and Megascolecidae – may, by the same logic, be similarly telescoped back into family Ocnerodrilidae which is hardly a practical solution (see Blakemore, 2005b).

Proper generic resolution hinges on molecular testing of *Diporochaeta* type-species, *D. intermedia* (Beddard, 1888) from New Zealand. Whereas the four "*Diporochaeta*" samples these authors did test (SB 3 = *Diporochaeta chathamensis*?; WM5 an identical species they call "*Diporochaeta* n. sp. 1"; SB6 = *Diporochaeta brachysoma*, and an unidentified specimen from Tasmania) were partitioned into two separate "clades", with (WM20) what they call "*Perionyx shoeanus*" or "*Perionychella shoeanus*" (sic) and "*Megascolides tasmani*" (WM83) intervening (cf. its treatment within). The only other *Perionychella* in their analysis, "*Perionychella kershawi*" (AF406567/ AY048484), is not only a misidentification, it is also the wrong species in the wrong genus as its proper title is "*Diporochaeta* cf. *kershawi*". This last is certain as these specimens were personally collected, preserved and identified from Tasmania by the present author. Thus, rather than clarity we get further confusion and, as with several previous molecular phylogenetic works, the only errors in their otherwise informative study are the names.

Discussion of biogeography and phylogeny of NZ species is also somewhat invalidated by inability to differentiate genera when Buckley et al. (2011: 9) admit:

The first lineage (clade g) contains Megascolides and Spenceriella, the latter also labelled as Megascolides because they are intermingled with Megascolides proper.

Since the last decade, *Spenceriella* Michaelsen, 1907 species have been subsumed in prior *Anisochaeta* Beddard, 1890, as noted above, and most NZ *Megascolides* McCoy, 1878 have now also been shown to belong in Australian *Notoscolex* Fletcher, 1887.

Finally, Buckley et al.'s argument for phyogenetic relationships of off-shore island taxa representing geological history or ocean currents largely ignores the human component whereby earthworms are frequently transported to new areas, inadvertently or sometimes deliberately, especially when used by Māori for fishing bait or food source (Benham 1905, Lee 1959: 304, Blakemore 1999, 2009) and as noted herein.

Acknowledgements

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RESEARCH ARTICLE

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First record of the subgenus *Damaeus* (*Paradamaeus*) Bulanova-Zachvatkina (Oribatida, Damaeidae) from China, with description of a new species

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Abstract

A new species *Damaeus* (*Paradamaeus*) *yushuensis* **sp. n.** is described from Three Rivers' Headwaters National Natural Reserve, Qinghai province, China. This is the first record of this subgenus in China. A key is given to distinguish all species of the genus.

Keywords

Oribatida, *Damaeus*, *Paradamaeus*, new species, new record

Introduction

Bulanova-Zachvatkina (1957) proposed *Paradamaeus* to be a subgenus of *Damaeus* with *Damaeus* (*Paradamaeus*) *clavipes* Hermann, 1804 as type species, which is only single known species in the world. The diagnosis of this subgenus as given by Bulanova-

Zachvatkina (1957): large body size; rugged prodorsum with distinct ridges; apophysis *P* well developed; interlamellar setae(*in*) much shorter than sensillus (*ss*); prodorsal tubercles *Da*, *Ba* and *Bp* present; spinae adnatae (*s.a.*) well developed; companion seta *d* lost on genu III; setation of genua 4-4-2-3.

We firstly recorded the species of *Paradamaeus* from Three Rivers' Headwaters National Natural Reserve, Qinghai, China, which represented as new species, *Damaeus* (*Paradamaeus*) *yushuensis*. A key to the identification of all known species of *Damaeus* (*Paradamaeus*) is given.

Material and methods

Measurements and descriptions are based on specimens mounted in temporary cavity slides that were studied using a standard light microscope equipped with a drawing tube. In figures we used the following abbreviations: prodorsal and sejugal apophyses (*Ba*, *Bp*), lateral apophyses (*Sa*, *Sp*) and coxisternal apophyses (*E2a*, *E2p*, *Va*, *Vp*), spina adnatum (*s.a.*), discidium (*di*), prodorsal setae (*ro*, *le*, *in*, *ex*), bothridium (*bo*), sensillus (*ss*), notogastral or gastronotal setae (*c*-, *l*-, *h*-, *p*- series), adanal and anal setae (*ad*-, *an*- series), aggenital setae (*ag*), coxisternal setae (1*a*, 1*b*, 1*c*, 2*a*, 3*a*, 3*b*, 3*c*, 4*a*, 4*b*, 4*c*, *4d*), opisthonotal gland opening (*gla*), lyrifissures or cupules (*ia*, *im*, *ip*, *ian*, *iad*, *ips*, *ih*).

Terminology generally follows Grandjean (1949, 1954b, 1960), Miko (2006) and Norton & Behan-Pelletier (2009). The unit of measurement is micrometre (µm). All type specimens and other material studied are kept in alcohol and deposited in the Institute of Entomology, Guizhou University, Guiyang, China (GUGC).

Taxonomy

Damaeus (*Paradamaeus*) *clavipes* (Hermann, 1804)

Notaspis clavipes: Hermann 1804; Grandjean 1936, 1954a; Hammen 1952; Sellnick 1960.
Oribata clavipes: Oudemans 1900; Kulczyński 1902; Sellnick 1928.
Belba clavipes: Willmann 1931; Grandjean 1935; Schweizer 1956.
Damaeus (*Paradamaeus*) *clavipes*: Bulanova-Zachvatkina 1957; Balogh & Balogh 1992; Pérez-Íñigo 1997; Subías 2004; Miko 2006.
Paradamaeus clavipes: Bulanova-Zachvatkina 1967, 1975; Schatz 1983; Siepel 1996.

Distribution. China, Germany, Ireland, Southern Mediterranean, Faroe Islands, Norway, Latvia, Caucasus, Crimea, Ukraina, Czechoslovakia, Czech Republic, Belgium, Sweden, England, America, Finland, Azores Islands, France, Austria, Netherlands.

Keys to species of *Damaeus* (*Paradamaeus*)

1 With dorsosejugal tubercles *Da*, *Dp*; setae *in* short and thin; notogastral setae similar to one another .... ***Damaeus* (*Paradamaeus*) *clavipes***

– Without dorsosejugal tubercles *Da*, *Dp*; setae *in* long and thick; notogastral setae not similar to one another ....***Damaeus* (*Paradamaeus*) *yushuensis* sp. n. (Figs 1–6)**

***Damaeus* (*Paradamaeus*) *yushuensis* sp. n.**

urn:lsid:zoobank.org:act:9CA2E39F-5E98-43B2-87D5-DDD3F4119690
http://species-id.net/wiki/Damaeus_yushuensis
Figs 1–6

Material examined. Holotype: male (in alcohol, QHYS-XLX-8-5), China, Three Rivers' Headwaters Natural Reserve Area of Yushu Tibetan Autonomous Prefecture, Qinghai province (32°33'48.65''N , 97°39'55.66''E), from soil under the *Picea crassifolia*, 3464M, 5 Aug., 2009, col. Lixia Xie. Paratypes: Three females (in alcohol, QHYS-XLX-8-5), same data as holotype; Two males (in alcohol, QHYS-XLX-8-6), same data as QHYS-XLX-8-5, from soil under the *Kobresia pygmaea*.

Diagnosis. Propodolateral apophysis *P* distinct, with broader base and arched tip; setae *ro* slightly barbed, setae *le* heavily barbed, thick. Sensillus short, thick, heavily barbed and rod-like. Interlamellar setae long, rather thick and conspicuously barbed. Prodorsal tubercles *Da*, *Dp* absent, *Ba* well developed, *Bp* weakly developed. Spinae adnatae beak like, short, distinct, strongly curved inwards (about 30 µm in total), with broader base and quite sharp tip. Notogastral setae smooth, slender except *c*- series and *p*- series. *Setae of c*- series rather thick, with conspicuously barbed and frizzled tip, oriented forwards and the rest backwards.

Comparative length of notogastral setae: $lp < lm = ps3 < ps2 < la = h_3 = h_2 = h_1 < ps1 < c_1 < c_2$. Epimeral setae mostly smooth except 1*b*, 1*c*, 3*b*, 3c, 4*d* and hypostomal setae *a*, *m*, *h*. Seta 1*a*, 2*a* and 3*a* rather short. Epimeral setal formula: 3-1-3-4. Enantiophyses *E*2 and *V* present, *E*2p and *Vp* weakly developed, *E*2a and *Va* well developed. Parastigmatic tubercle *Sa* long, acuminate, with sharp tip; *Sp* small, triangular. Hypostomal setae *a*, *h* and *m* thin, slightly barbed. Legs rod-like and longer than body.

Description of adult. Dimensions. Holotype: Body length 980; length of prodorsum: 420, width 280, height 370, setae: *ss* 175, *in* 100, *le* 150, *ro* 125, *ex* 75, distance between setae: *ro-ro* 110, *in-in* 125, *le-le* 125, *in-le* 105, *le-ro* 40; length of notogaster: 700, width 670, height 780; setae: *c*1 135, *c2* 175, *la* 110, *lm* 95, *lp* 90, *h*3 110, *h*2 110, *h*1 110, *ps*1 125, *ps*2 105, *ps*3 95; *c*1-*c*2 75, *c2*-*c*2 275, *la-la* 375, *lm-lm* 435; ventral region: genito-aggenital plate 225×220, ano-adanal plate 190×175. Paratypes: length of prodorsum: 415-425, width 275-285, height 365-375; length of notogaster: 695-705, width 665-670, height 775-780; ventral region: genito-aggenital plate 220×215, ano-adanal plate 185×170.

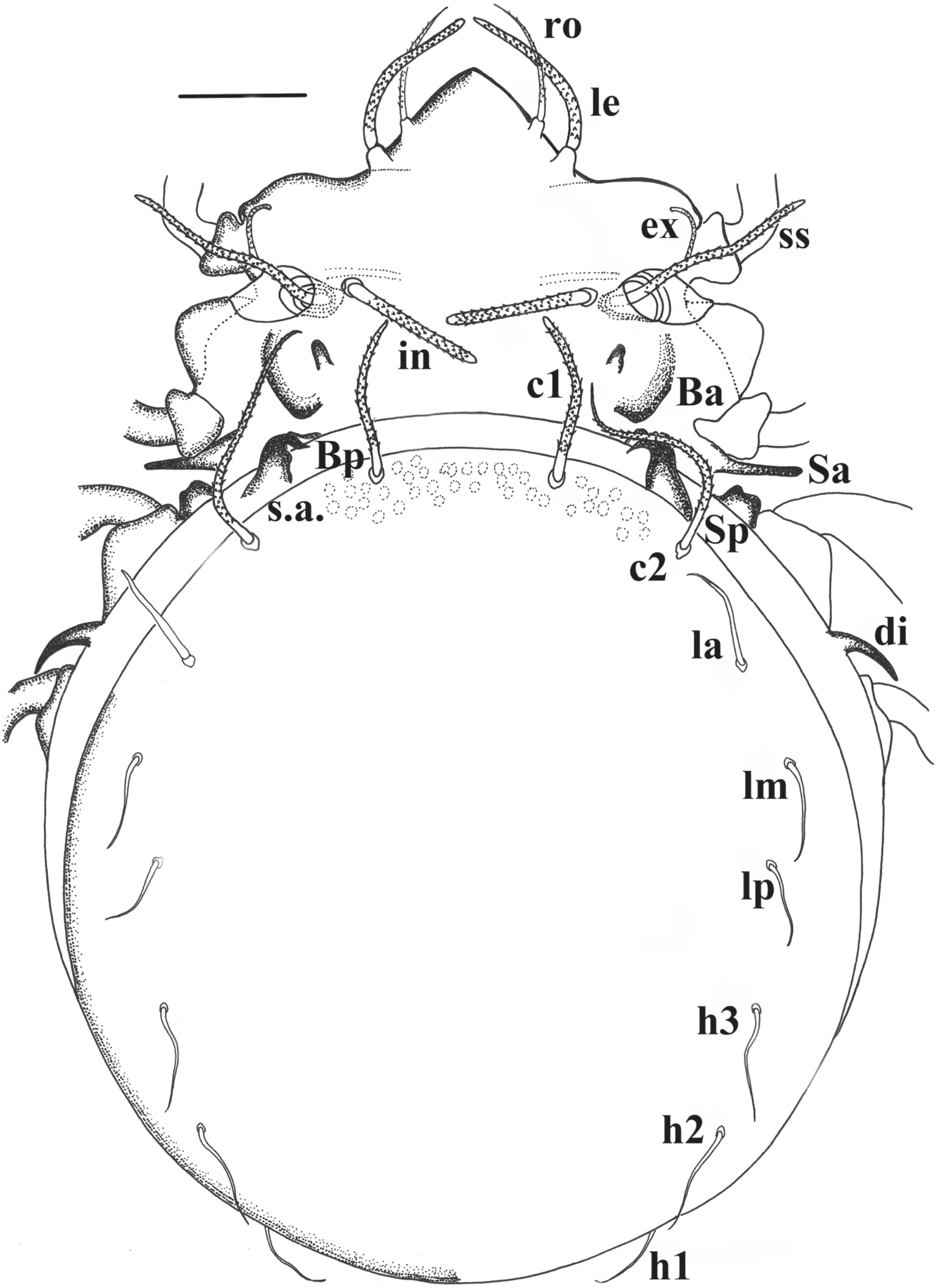

Figure 1. *Damaeus* (*Paradamaeus*) *yushuensis* sp. n.– dorsal view (100μm)

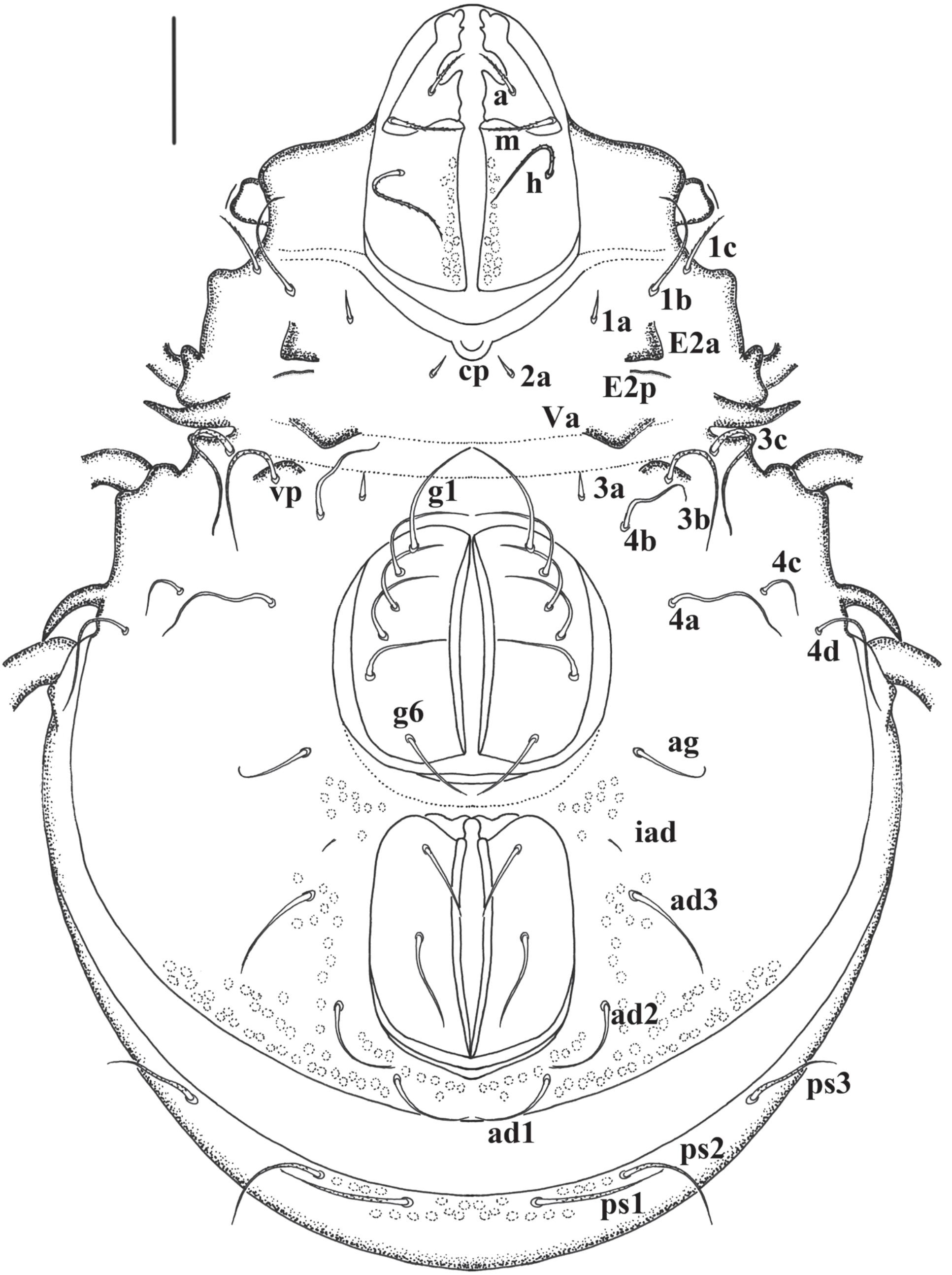

Figure 2. *Damaeus* (*Paradamaeus*) *yushuensis* sp. n. – Ventral view (100μm)

Figure 3. *Damaeus* (*Paradamaeus*) *yushuensis* sp. n. – lateral view (100μm)

Integument. Surface of body and leg segments with filamentous cerotegument. Conspicuous microtubercles present on prodorsum and around leg acetabula, legs with dense fungal mycelic.

Prodorsum (Fig. 1)**.** Triangular, propodolateral apophysis *P* distinct, with broader base and arched tip. Lamellar setae (*le*) and rostral setae (*ro*) both in dorsalaterad position, long, arched and tapered. Lamellar setae with obvious barbs, thick, being longer than slender, weakly barbed rostral pair. Bothridia well developed, funnel-like, with broad margin and pair of thick, heavily barbed sensillus. Interlamellar setae (*in*) long, thick and conspicuously barbed (specially in holotype). Exobothridial setae (*ex*) thick, with obvious barbs, frizzled. Comparative length of prodorsal setae: *ex*< *in*< *ro*< *le*< *ss.* Weakly developed transverse ridge connected to the base of bothridium and directed to median end of prodorsum. Prodorsal tubercles *Da* absent, *Ba* distinct; *Bp* weakly developed, usually as tuberculate sclerotised ridge, in light microscope sometimes discernible only in lateral view.

Notogaster. (Fig. 1). Circular viewed perpendicular to circumgastric scissure, length almost equivalent to wider. Spinae adnatae beak like, short, distinct, strongly curved inwards (about 30 μm in length), with broader base and quite sharp tip. Notogastral setae short, smooth, slender except *c*- series and *p*- series. Setae of *c*- series rather thick and long, with conspicuous barbed and frizzled tip, oriented forwards and the rest backwards. Comparative length of notogastral setae: *lp*< *lm*= *ps*3< *ps*2< *la*= *h*3= *h*2= *h*1< *ps*1< *c*1< *c*2. Pseudanal setae comparatively long, with obvious barbs, attenuate.

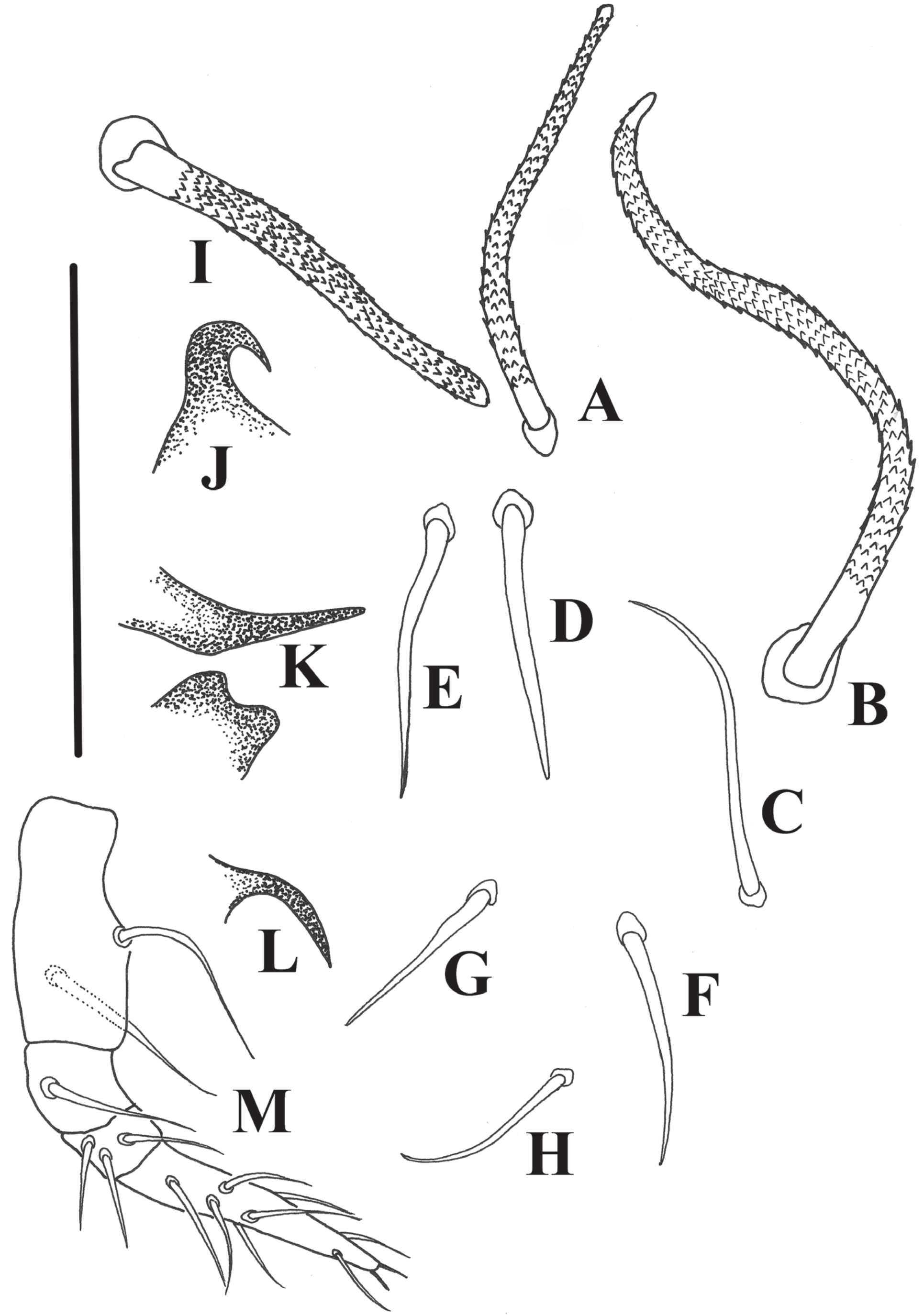

Figure 4. *Damaeus* (*Paradamaeus*) *yushuensis* sp. n. **A–H** notogastral setae (100μm) **I** interlamellar seta(100μm) **J** s.a.–spina adnata(100μm) **K** Sa –anterior sejugal apophysis(100μm), Sp –posterior sejugal apophysis(100μm) **L** di –discidium(100μm) **M** Pe. –pedipalp(100μm).

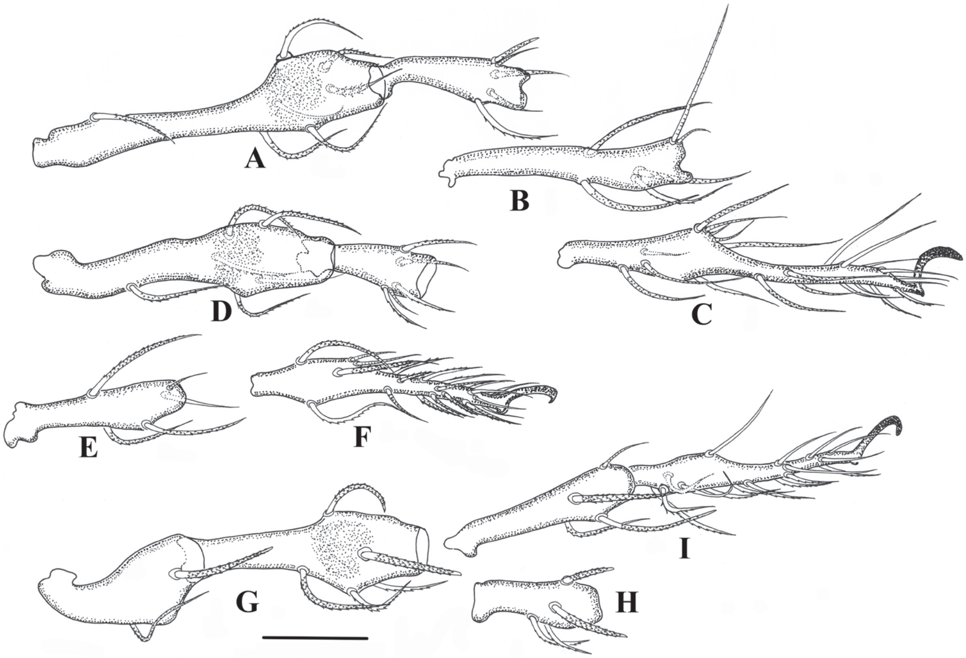

Figure 5. *Damaeus* (*Paradamaeus*) *yushuensis* sp. n. **A** femur, genu I (100μm) **B** tibia I (100μm) **C** tarsus I (100μm) **D** femur, genu II (100μm) **E** Tibia II (100μm) **F** tarsus II (100μm) **G** trochanter, femur III (100μm) **H** genu III (100μm) **I** tibia, tarsus III (100μm).

Ventral region. (Fig. 2)**.** Epimere I with medial pit (*cp*). Epimeral setae mostly smooth except 1*b*, 1*c*, 3*b*, 3*c*, 4*d*; setae 1*c*, 3*b*, 3c, 4*d* long, with obvious barbs; Seta 1*a*, 2*a* and 3*a* rather short, lanciform. Epimeral setal formula: 3–1–3–4. Ano-genital setal formula: 6–1–2–3. Enantiophyses *E*2 and *V* present, *E*2*a* triangular with pointed tip; *E*2*p* weakly developed, usually as tuberculate sclerotised ridge. Ventrosejugal tubercle *Va* large, strong, represented by broad ridge; *Vp* represented by low, broadly curved ridge, with setae 3*b* Parastigmatic tubercle *Sa* long, acuminate, with broader base and heavily pointed tip; *Sp* small, triangular; Discidium (*di*) long, acuminate, with broader base and heavily pointed tip, directed posterolaterad.

Gnathosoma. Infracapitular mentum without noticeable microtubercles. Hypostomal setae *a*, *m*, *h* slender, weakly barbed. Chelicera rather strong, fixed and movable digits with four blunt teeth; setae *cha* with obvious barbs and *chb* smooth. Palpal setation: 0–2–1–3–8, including solenidion *ω* (Fig. 4M).

Legs. (Figs 5–6)**.** Monodactylous, moderately long, leg I, III, IV longer than body, leg II shorter than body. Relative length of femur to tarsus of legs I to IV 1: 0.88: 1.01: 1.2. Leg IV 1.3 times ventral body length. Femur IV 1.4 times length of trochanter IV, proximal stalk 1.4 times length of bulb. Leg setae medium in length and thick, mostly with distinct short barbs on outer curvature. Setal formulas of legs as follows (from trochanter to tarsus, famulus and solenidia included): I: 1–7–4 (1)–4 (2)–20 (2); II: 1–6-4 (1)–4 (1)–18 (2); III: 2–4-3 (1)–3 (1)–16 (0); IV: 1–4-3 (1)–3 (1)–15 (0). Solenidia of genua I-II with compan-

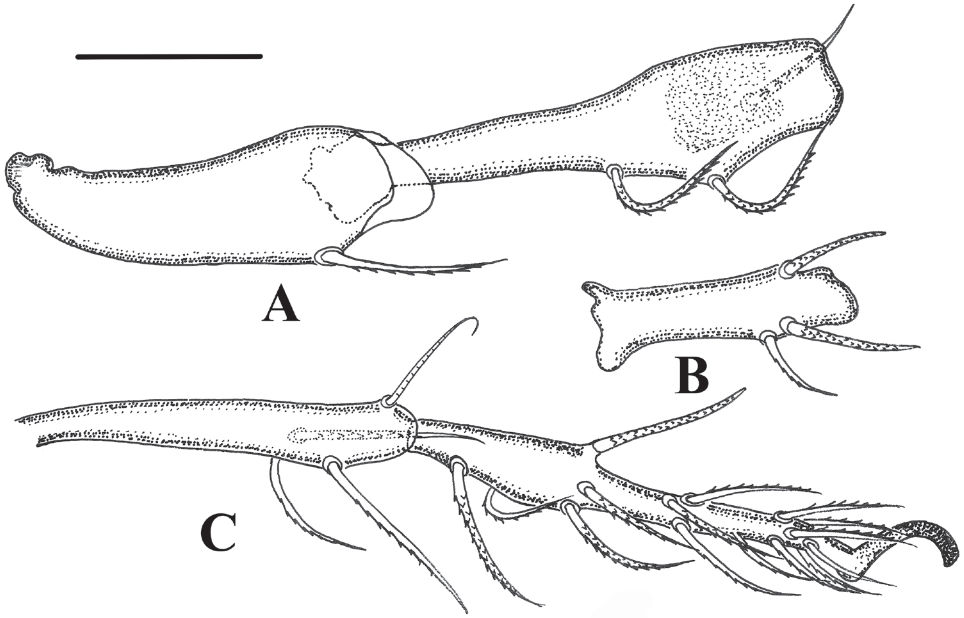

Figure 6. *Damaeus* (*Paradamaeus*) *yushuensis* sp. n. **A** trochanter, femur IV (100µm) **B** genu IV (100µm) **C** tibia, tarsus IV (100µm).

ion seta *d*. Solenidia *δ* equivalent to seta *d* on genua I, Solenidia *δ* shorter and thinner than seta *d* on genua II. Solenidion *φ*1 on tibia I 3 times longer than *φ*2. Seta *d* absent from all tibiae, solenidia on all tibiae free, as usual for genus.

Etymology. The specific name is derived from the type locality, Yushu Tibetan Autonomous Prefecture, Qinghai province.

Remarks. This new species is characterised by following characters: interlamellar setae (*in*) long, rather thick and conspicuously barbed; spinae adnatae beak like, short, distinct, strongly curved inwards; *c*-series rather thick, long with conspicuous barbed and frizzled tip, oriented forwards and the rest backwards, other notogastral setae smooth, slender and short, except *p*- series (see Table 1).

Table 1. Comparison of two species belonging to the subgenus *Paradamaeus*

Morphological character	***D.* (*Paradamaeus*) *clavipes***	***D.* (*Paradamaeus*) *yushuensis* sp. n.**
propodolateral apophysis *P*	with angular tip	with arched tip
Interlamellar setae (*in*)	short, thin	long, thick
Spinae adnatae (s.a.)	slender, medium long, triangular with sharp tip	beak like, short, quite sharp tip
Notogastral setae *c*1, *c*2	similar in length, slender	unequal length, thick
Number of setae on Femora III–IV	5	4
Prodorsal tubercles *Da*, *Dp*	present	absent
Parastigmatic tubercle *Sa*	small, indistinct	large, acuminate, with broader base and heavily pointed tip

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RESEARCH ARTICLE

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Descriptions of a new Brazilian *Tacora* species and the female of *T. saturata*, and a key to the species of the genus (Insecta, Hemiptera, Cicadellidae, Cicadellini)

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Abstract

Tacora johanni, a new species from Rondônia State, North Brazil, is described and illustrated. The new species can be recognized by the male genital features, especially the subgenital plates with the basal half distinctly expanded and with outer lateral margin round, the long and slender preapical pygofer process, and the styles with apical half strongly curved. Also, the genus is recorded for the first time from Venezuela, based on specimens of *T. saturata* Young, 1977, while the female of this species (here described in detail for the first time) shows two unusual features of the genitalia. A key to males of all known *Tacora* species and a map showing the known distribution of the genus are provided.

Keywords

Auchenorrhyncha, Cicadellinae, identification key, leafhopper, taxonomy, Venezuela

Introduction

The South American genus *Tacora* Melichar, 1926 is known from five species (Young 1977, Takiya and Mejdalani 2002, McKamey 2007): *T. dilecta* (Walker, 1851) (type species), *T. saturata* Young, 1977, *T. cavichiolii* Takiya & Mejdalani, 2002, *T. henriquesi* Takiya & Mejdalani, 2002, and *T. karipuna* Takiya & Mejdalani, 2002. This genus was recorded from Brazil (Acre, Amazonas, Mato Grosso, and Rondônia states), Colombia, and Peru, being restricted to the central and western portions of the Amazon region (Takiya and Mejdalani 2002). Among the Neotropical Cicadellini, *Tacora* species can be recognized by their distinctive color pattern: body yellow or orange with at least two conspicuous brown stripes on the forewings, one on clavus along the claval sulcus, the other transverse, transcommissural, located in the apical portion of clavus and extending over the corium towards the costal margin. Additional black, brown, red, lilac, or yellow markings are also present and vary interspecifically. According to a morphological cladistic analysis (Cavichioli 1992) of the 13 genera of the *Paromenia* group (established by Young 1977), *Tacora* is the sister group of *Dasmeusa* Melichar, 1926. The reader is referred to Takiya and Mejdalani (2002) for detailed comments on the taxonomy, phylogeny, and distribution of *Tacora*.

In the present paper, we describe a new *Tacora* species from Rondônia State (North Brazil). We also provide the first detailed description and illustrations of the female of *T. saturata*, including two unusual features of the genitalia. The genus is recorded from Venezuela (Amazonas and Bolivar states) for the first time (based on *T. saturata*). A new key to males of *Tacora* species and a map showing the known distribution of the genus, both modified from Takiya and Mejdalani (2002), are provided.

Material and methods

Techniques for preparation of male and female genital structures follow Oman (1949) and Mejdalani (1998), respectively. The dissected genital parts are stored in microvials with glycerin and attached below the specimens, as suggested by Young and Beirne (1958). The descriptive terminology adopted herein follows mainly Young (1977), except for the facial areas of the head (Hamilton 1981, Mejdalani 1998) and the female genitalia (Nielson 1965, Hill 1970). Mejdalani (1998) provided a detailed justification for the use of Hamilton's terminology for the head of the Cicadellinae and other leafhoppers. Use of the term gonoplac (= third ovipositor valvula) and the names for the processes of the dorsal and ventral sculptured areas of the first ovipositor valvula follow Mejdalani (1998).

Label data are given inside quotation marks with a reversed virgule (\) separating lines on the labels and a semicolon separating labels of a specimen. The specimens studied belong to the following institutions: American Museum of Natural History (AMNH; New York), Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ; Rio de Janeiro), and Museo del Instituto de Zoología Agrícola, Universidad Central de Venezuela (MIZA; Maracay).

The photographs of the body in dorsal view and of the general lateral views of the ovipositor valvulae were prepared with the software Automontage (Synoptics Inc., Frederick, Maryland) using a digital camera attached to a stereomicroscope. The photographs of the details of the ovipositor valvulae were taken with a digital camera attached to an optical microscope. Digital images of four of the five previously known *Tacora* species (body in dorsal view) are available in the internet site "Sharpshooter Leafhoppers of the World" (Wilson et al. 2009). These images were useful for the comparisons and identifications carried out in the present study. The orientation of the illustrations of male and female genital structures on the plates are in accordance with the monograph of Young (1977).

Results

Genus *Tacora* Melichar, 1926

Tacora johanni sp. n.

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http://species-id.net/wiki/Tacora_johanni
Figs 1a, 2, 3

Description of the male holotype. Length 15 mm from apex of head to apex of forewings at rest. Head (Fig. 2a, b) strongly produced anteriorly; median length of crown approximately 4/5 interocular width and 1/2 transocular width; anterior margin broadly rounded in dorsal view; without carina at transition from crown to face; ocelli located behind imaginary line between anterior eye angles, each ocellus slightly closer to median line of crown than to adjacent anterior eye angle; crown with concavity between eye and ocellus, without median fovea and without sculpturing or setae; frontogenal sutures extending onto crown and attaining ocelli; antennal ledges, in dorsal view, slightly protuberant, in lateral view with anterior margin broad and rounded; frons convex, muscle impressions distinct; epistomal suture obscure; clypeus not produced, its contour continuing profile of lower portion of frons.

Thorax (Fig. 2a, b) with pronotal width distinctly greater than transocular width; lateral pronotal margins convergent anteriorly; posterior margin slightly concave; dorsopleural carinae complete, rectilinear, distinctly declivous anteriorly; pronotal disk without sculpturing or pubescence; mesonotum with scutellum not swollen. Forewings (Fig. 2c) with membrane including all of apical cells except short basal portions of second, third, and fourth; veins mostly indistinct except at wing apical portion; with four apical cells, base of fourth more proximal than base of third (not shown in Fig. 2c); without anteapical plexus of veins. Hindlegs with femoral setal formula 2:1:1; length of first tarsomere greater than combined length of two more distal tarsomeres; plantar surface with two parallel rows of small setae.

Color (Fig. 1a) of anterior dorsum orange; pronotum with transverse brown stripe on posterior margin, this stripe distinctly broader medially; mesonotum with pair of large yellow maculae laterobasally. Forewings (Fig. 2c) with corium mostly translucent yellow, costal margin dark brown; clavus mostly yellow with two longitudinal brown stripes, both extending from basal portion to about middle area, one along claval sul-

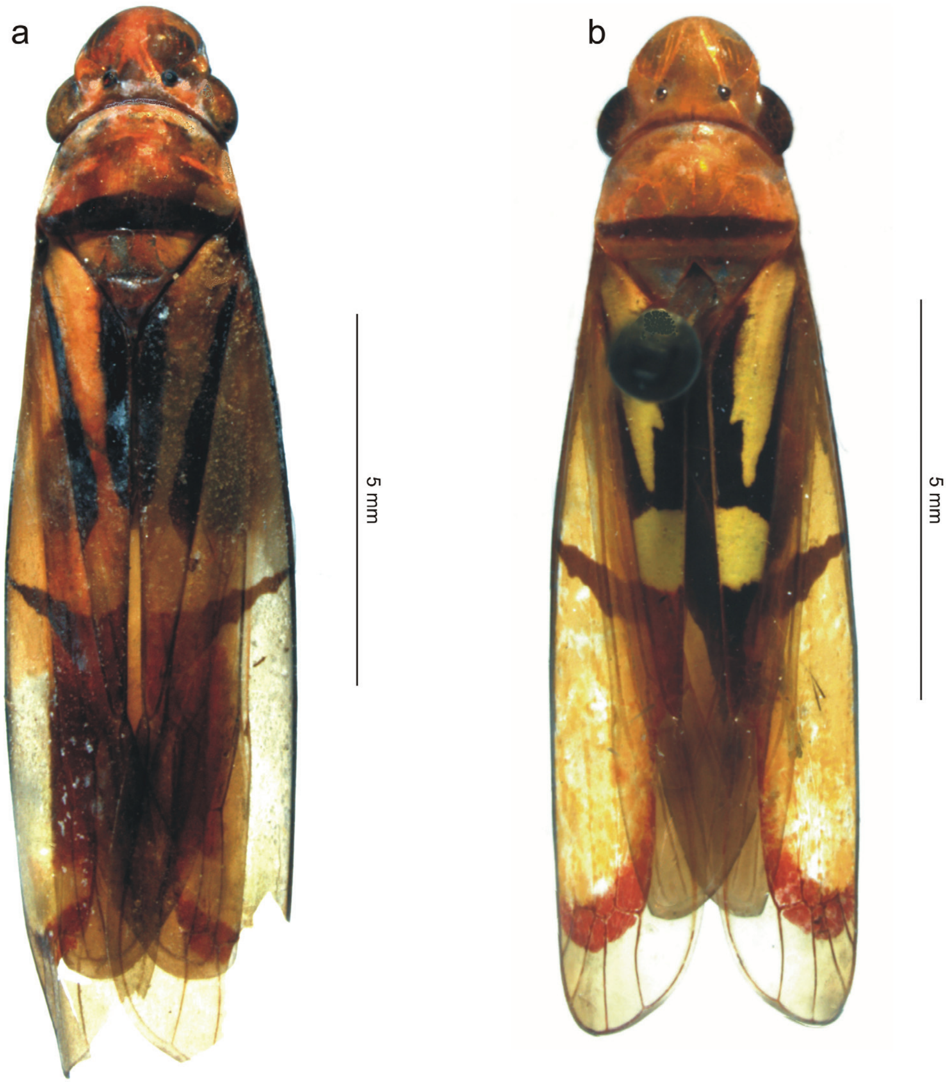

Figure 1. The two species treated in this paper, body in dorsal view (antennae and legs not depicted). **a** *Tacora johanni* sp. n., male holotype **b** *Tacora saturata* Young, 1977, female (pinned specimen).

cus (broadened posteriorly) and another along inner claval margin; posterior portion of clavus with transverse, oblique brown stripe extending over corium and reaching costal margin, this stripe distinctly narrowed towards costal margin; with red area behind transverse stripe covering apex of clavus, apexes of brachial and inner discal cells and large portion of corium adjacent to inner apical cell, this red area strongly constricted posteriorly and then forming stripe (evanescent towards costal margin) across bases of apical cells; corium region between red area and costal margin mostly depigmented. Face and venter orange-yellow with brown irregular areas on legs.

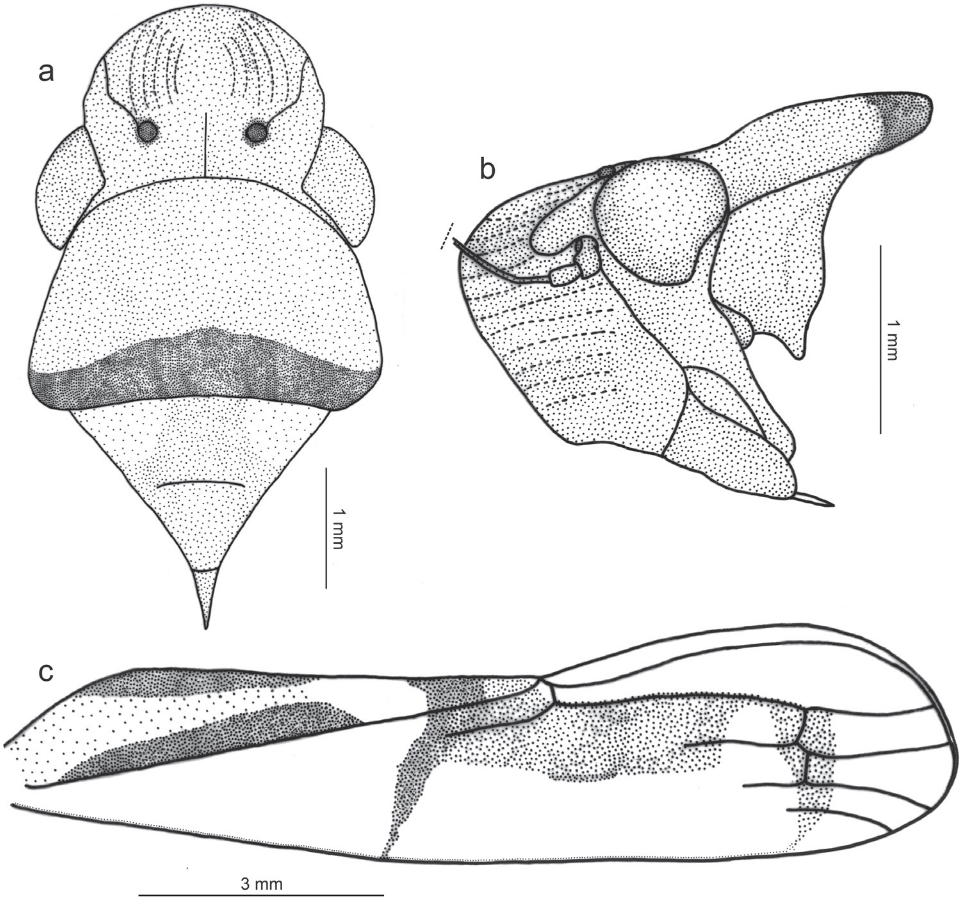

Figure 2. *Tacora johanni* sp. n., male holotype. **a** head, pronotum and mesonotum, dorsal view **b** anterior portion of body, lateral view **c** left forewing.

Genitalia with pygofer (Fig. 3a), in lateral view, strongly produced posteriorly; posterior margin narrowly rounded; distal third of dorsal margin with strong spiniform process, apex of process located slightly before pygofer apex, process (Fig. 3b), in dorsal view, directed inward, not attaining median body line; macrosetae distributed mostly on distal third of disk, some smaller macrosetae extending anteriorly along ventral margin. Subgenital plates (Fig. 3c), in ventral view, triangular but with basal half broad, expanded, with lateral margin round; distal half extremely narrow; plates not fused to each other basally; in lateral view, plates distinctly shorter than pygofer (Fig. 3a), extending posteriorly approximately as far as 2/3 of pygofer disk length; plates with uniseriate macrosetae (very large on basal half, very small on distal half), microsetae also present. Connective (Fig. 3d), in dorsal view, broadly T-shaped; stalk with strong median keel, the latter bifurcated basally and extending for short distance over arms. Styles (Fig. 3d), in dorsal view, extending almost as far poste-

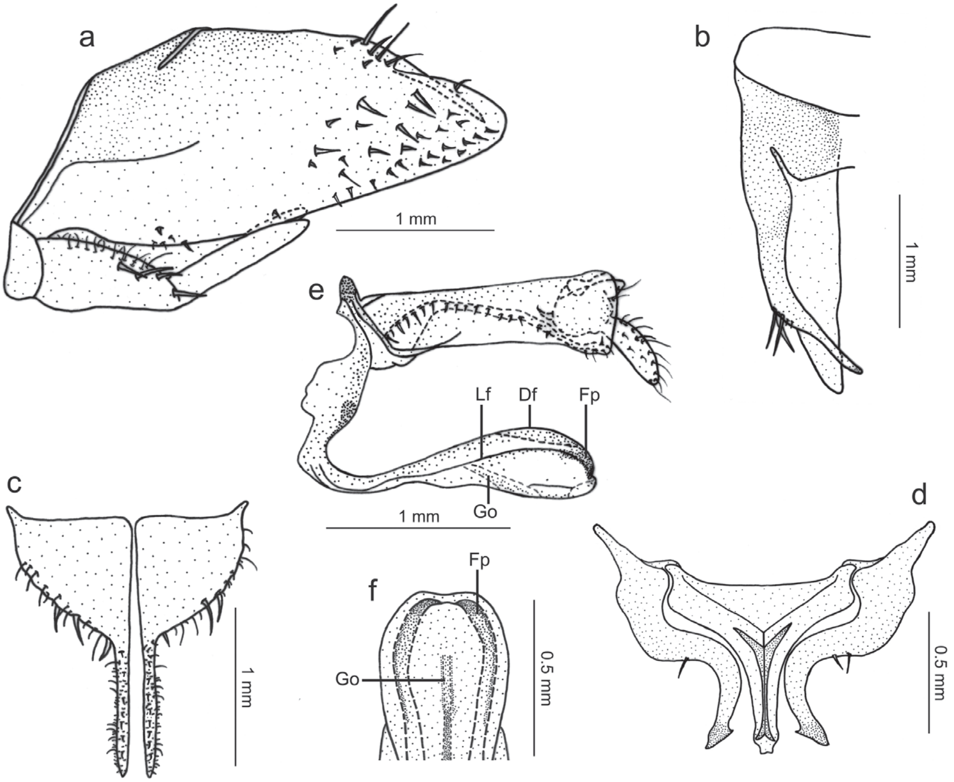

Figure 3. *Tacora johanni* sp. n., genitalia of male holotype. **a** pygofer, valve and subgenital plate, lateral view **b** pygofer, dorsal view **c** subgenital plates, ventral view **d** styles and connective, dorsal view **e** aedeagus and anal tube, lateral view (Df: dorsal flange, Fp: projection formed by flanges, Go: gonoduct, Lf: lateral flange) **f** apical portion of aedeagus, ventral view.

riorly as connective; strongly curved inward; without preapical lobe; apex slightly expanded, obliquely truncate, more sclerotized than remainder of apophysis; style median portion with a few setae on outer margin. Aedeagus (Fig. 3e, f), in lateral view, narrowest in basal third, gradually broader in distal two-thirds; shaft with two pairs of longitudinal flanges, one along lateral portion, another along dorsal margin; apical portion of shaft (Fig. 3f), in ventral view, with these flanges forming pair of projections directed medially; these projections covered by many tiny tegumentary processes; gonoduct distinctly visible in broadened portion of shaft (Fig. 3e), directed ventrally, gonopore located preapically.

Female. Unknown.

Material examined. Male holotype, "BRASIL: Rondônia, \ Ouro Preto d'Oeste [10°40'S, 62°18'W], \ 28.X.1983 \ J. Becker, O. Roppa & \ B. Silva" (MNRJ). The holotype is in good condition but the forewing apices are damaged (Fig. 1a).

Etymology. The new species is described in honor of the late Prof. Johann Becker (Museu Nacional, Universidade Federal do Rio de Janeiro) in recognition of his contribution to the development of Brazilian entomology. He was also one of the collectors of the holotype.

Remarks. *Tacora johanni* can be distinguished from the other known species of the genus by the following combination of features: (1) pronotum with a transverse brown stripe on posterior margin (Figs 1a, 2a); (2) subgenital plates extending posteriorly approximately as far as 2/3 of pygofer disk length (Fig. 3a); (3) subgenital plates with the basal half broad, expanded, with round lateral margin (Fig. 3c); (4) preapical pygofer process long and slender; (5) preapical pygofer process without pegs (Fig. 3a, b); (6) styles strongly curved inward (Fig. 3d); (7) aedeagus with two pairs of longitudinal flanges (Fig. 3e).

The male genitalia of the new species are similar to those of *T. dilecta* and *T. cavichiolii*. The presence of sculpturing (pegs) on the pygofer process of the male holotype of *T. dilecta* was mentioned and illustrated by Young (1977: 317 and Fig. 257p) as a diagnostic feature of this species. These pegs are not present in *T. johanni*. Other features that distinguish the new species (known only from the male) from *T. dilecta* include (1) the red color of the claval apex behind the transverse dark stripe (orange to yellow in *T. dilecta*) and (2) the rectilinear distal portion of the pygofer process in dorsal view (distinctly curved in *T. dilecta*). The above-mentioned features of the subgenital plates and styles of *T. johanni* are distinct from those of *T. dilecta* and *T. cavichiolii*. In addition, the pygofer process in *T. cavichiolii* is short and robust (Takiya and Mejdalani 2002: 239: Fig. 17), whereas it is long and slender in *T. johanni*.

Tacora saturata Young, 1977

http://species-id.net/wiki/Tacora_saturata
Figs 1b, 4, 5

Tacora saturata Young, 1977: 316, figure 258 (crown, pronotum, and male genitalia).

Description of the female. Length 13 mm from apex of head to apex of forewings at rest [male with about same length]; median length of crown approximately 9/10 interocular width and 1/2 transocular width. Head and thorax (Fig. 4a) much as in the above-described male holotype of *T. johanni* sp. n. Forewings extending well beyond apex of ovipositor.

Color (Fig. 1b) of anterior dorsum orange; pronotum with transverse, submarginal brown stripe on posterior portion, this stripe broader medially; mesonotum with pair of large brown maculae laterobasally. Forewings (Fig. 4b) with corium mostly translucent orange, costal margin dark brown; in rest position with transcommissural, brown W-shaped figure in basal half of clavi with anterior angles enclosing large, bright yellow maculae that extend to wing bases; large, bright yellow rounded transcommissural macula located just behind W-shaped figure, followed by transverse, oblique brown stripe extending over corium and reaching costal margin; apical portion of clavus red, with or without pair of small orange spots adjacent to claval sulcus just behind trans-

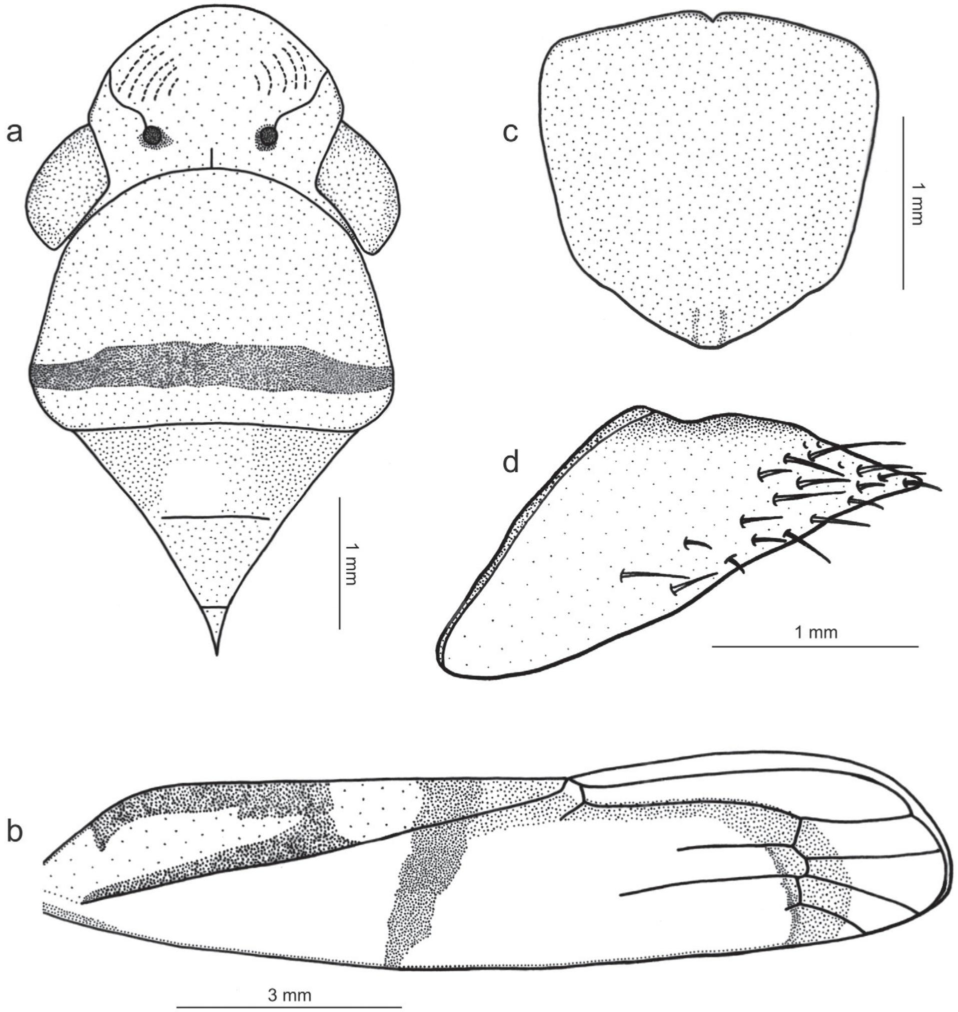

Figure 4. *Tacora saturata* Young, 1977, female. **a** head, pronotum and mesonotum, dorsal view (the white circle on the mesonotum delimits the pin perforation) **b** left forewing **c** sternite VII, ventral view **d** pygofer, lateral view.

verse brown stripe; distal half of corium with red stripe in inner anteapical cell (along outer margin of inner apical cell) and then descending across bases of apical cells.

Genitalia with abdominal sternite VII (Fig. 4c) broad, lateral margins convergent posteriorly, posterior margin broadly convex. Internal sternite VIII without distinct, well-defined sclerotized areas. Pygofer (Fig. 4d), in lateral view, well produced posteriorly, strongly narrowed towards apex; posterior margin very narrow, subacute; macrosetae located mostly on distal third, a few extending anteriorly along ventral margin. Valvifers I (Fig. 5a), in lateral view, of quadrate form, except for distinct lobe on posteroventral portion. Valvulae I, in ventral view, distinctly expanded basally; in lateral

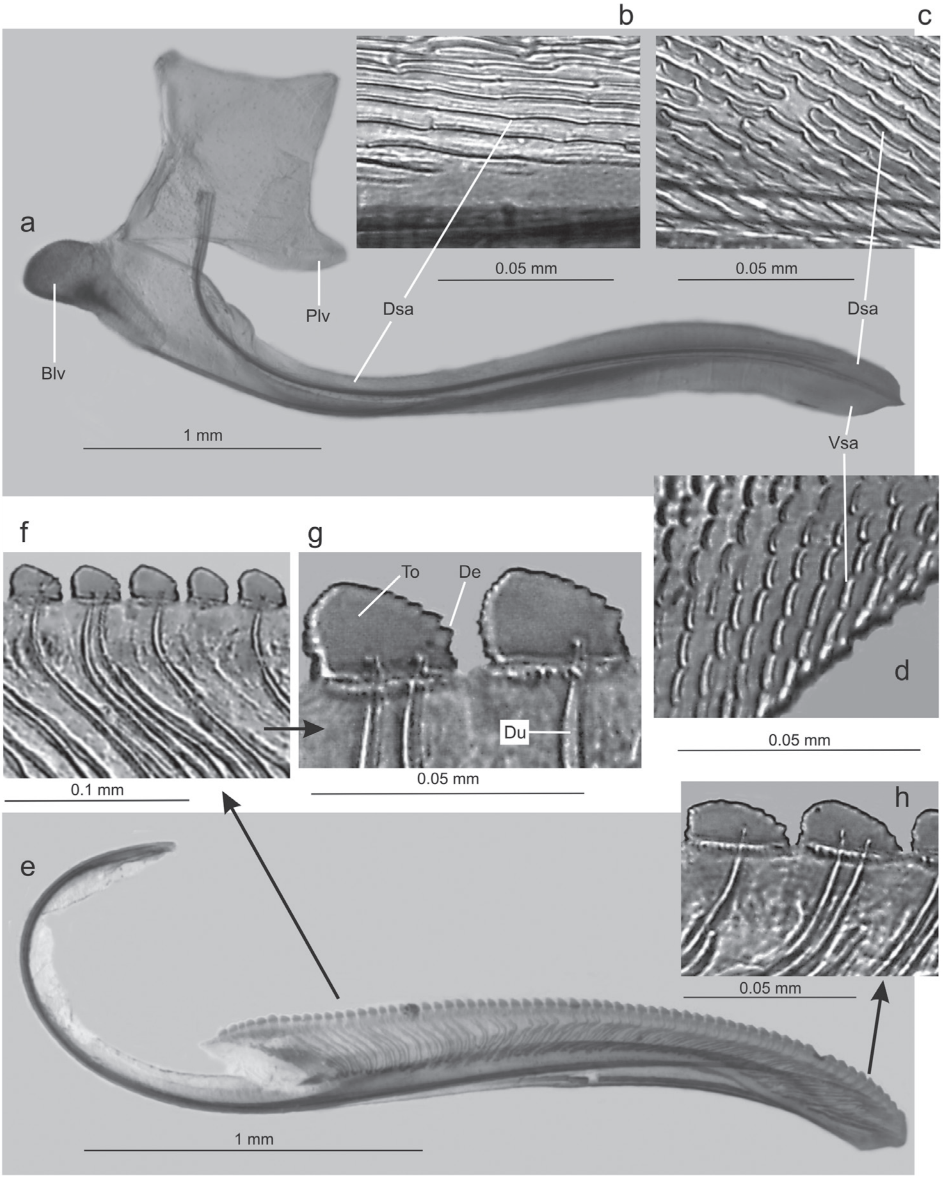

Figure 5. *Tacora saturata* Young, 1977, ovipositor. **a** valvifer I and valvula I, lateral view (Blv: basal lobe of valvula I, Dsa: dorsal sculptured area, Plv: posterior lobe of valvifer I, Vsa: ventral sculptured area) **b** dorsal sculptured area at basal portion **c** dorsal sculptured area at apical portion **d** ventral sculptured area **e** valvula II, lateral view **f-g** teeth at basal portion (De: denticle, Du: duct, To: tooth) **h** teeth at apical portion.

view (Fig. 5a), valvulae with broad basal lobe, blade distinctly expanded in distal half in comparison with basal half; dorsal sculptured area (mostly scale-like processes, except for linear processes basally, Fig. 5b, c) extending from basal portion of blade to apex, ventral sculptured area (scale-like processes, Fig. 5d) restricted to apical portion of blade; basal portion of blade with group of distinct setae located below ramus; apex of blade forming distinct dentiform projection (Fig. 5a); ventral interlocking device distinct, elongate, restricted to basal half of blade, located along ventral blade margin but with distal portion directed dorsally. Valvulae II (Fig. 5e), in lateral view, with dorsal margin regularly convex beyond basal curvature; without preapical prominence; apex obtuse; ventral outline of apical portion slightly concave; about 63 teeth (Fig. 5e, f, g, h), mostly subtriangular or subrectangular, distributed on dorsal portion of blade, with clear space between them; denticles (Fig. 5g) on posterior portions of teeth and on inferior half of apical portion; blade with numerous curved ducts (Fig. 5f, g) extending to teeth or terminating below the latter, ducts also extending towards apex (most teeth receive a single duct, others two or none). Gonoplacs, in lateral view, extending posteriorly slightly beyond pygofer apex; basal half with ventral margin convex and dorsal margin concave, the latter abruptly expanded towards distal half; ventral margin of distal half concave; apex of blade rounded; apical portion with few small setae and tiny tegumentary processes, the latter extending anteriorly along ventral margin.

Material examined. One male and one female, "Venezuela, T. F \ Amazonas Dpt \ Rio Negro"; "Rio Baria \ 140m. \ 0°55'N, 66°10'W"; "C. Padilla \ col. \ 28-II-84" (MIZA); one male, same as preceding, excepting "12-II-84" (MIZA); one male, same as preceding, excepting "7-III-84" (MIZA); one male, same as preceding, excepting "4-III-84" (MNRJ); one female, same as preceding, excepting "20-II-84" (MIZA); one male and one female, same as preceding, excepting "L. J. Joly \ A. Chacon \ 4–11-II-84" (MIZA); one male, same as preceding, excepting "Rio Mawari- \ numa 140m"; "3-III-84 \ C. Padilla \ col." (MIZA); one female, "Venezuela T. F. \ Amazonas. \ 25-XI-4-XII-1984"; "Rio Baria \ 140m. \ 0°55'N, 66°10'W"; "E. Osuna \ A. Chacón" (MNRJ); three males and one female, "VENEZUELA: Amazonas \ Cerro Unturan Camp, 65°14'W \ 01°33N, 1100m. 11–15/III/89"; "Phipps-FUDECI Exped. \ by Amer. Mus. Nat. Hist. \ D. A. Grimaldi, coll." (AMNH); one female, "Venezuela - Boli- \ var Rio Caura. \ 26-IV-1984"; "Salto Pará" [06°12'N, 64°28'W]; "B. Bechyne. \ leg." (MIZA).

Remarks. Young (1977) provided a detailed description of the male of *T. saturata*. Our identification is based on his description. The male genitalia and color pattern (male and female) of our Venezuelan specimens agree with the features and illustrations given by him. He recorded *T. saturata* from Colombia and Brazil. This species is the only one in the genus in which the transverse pronotal stripe is submarginal (Figs 1b, 4a).

Key to males of *Tacora* Melichar (modified from Takiya and Mejdalani 2002 to include *T. johanni* sp. n.)

1a Pronotum with posterior submarginal transverse stripe (Figs 1b, 4a; observed also in the female); subgenital plates extended posteriorly beyond pygofer apex (Young 1977: Fig. 258c) .... ***T. saturata* Young, 1977**

1b Pronotum with transverse stripe on posterior margin (Figs 1a, 2a); subgenital plates not extended posteriorly beyond pygofer apex.................................. **2**

2a Forewing corium with lilac band along claval sulcus basad of transverse brown band (observed also in the female); pygofer about five times longer than width on median portion in lateral view, dorsal preapical processes with short dentiform projection on inner margin in dorsal view. .... ***T. henriquesi* Takiya & Mejdalani, 2002**

2b Forewing with corium region along claval sulcus concolorous yellow or orange basad of transverse brown band (Fig. 1a, b); pygofer not more than three times longer than width on median portion in lateral view, dorsal preapical processes without conspicuous projection. **3**

3a Pygofer preapical dorsal processes bearing pegs on apical portion (Young 1977: Fig. 257p); aedeagus without flanges or processes (Young 1977: Fig. 257f) .... ***T. dilecta* (Walker, 1851)**

3b Pygofer preapical dorsal processes lacking sculpturing; aedeagus with dorsal and lateral carinate flanges. **4**

4a Aedeagus with four pairs of dorsolateral flanges, apical flanges very short and triangular in ventral view ....***T. karipuna* Takiya & Mejdalani, 2002**

4b Aedeagus with two pairs of lateral flanges... **5**

5a Subgenital plates with basal half distinctly expanded, with round outer lateral margin (Fig. 3c); preapical pygofer process long and slender (Fig. 3a, b); styles with apical half strongly curved (Fig. 3d) .... ***T. johanni* sp. n.**

5b Subgenital plates with basal half not expanded, with outer lateral margin more rectilinear, narrowing gradually towards median portion; preapical pygofer process short and robust; styles with apical half slightly curved. .... ***T. cavichiolii* Takiya & Mejdalani, 2002**

Concluding remarks

Six species of *Tacora* are now known. The most relevant features for the recognition of males from each of these species are given in our key, which provides an adequate comparison among the previously described species and *T. johanni* sp. n. These features are from the aedeagus and its flanges, pygofer and its processes, subgenital plates and styles, as well as from the color pattern.

Females of *Tacora* are of difficult identification when they can not be associated to males from the same collecting series, due perhaps to our still incomplete comparative knowledge of the female genitalia morphology and color pattern intraspecific variation. In addition to our description of *T. saturata*, the female genitalia of *T. dilecta*, *T. henriquesi*, and *T. cavichiolii* were described in detail (the first by Young 1977 and the second and third by Takiya and Mejdalani 2002). Our study of the *T. saturata* female revealed peculiar, previously undescribed genital features of potential taxonomic interest that deserve further comparative investigation, i.e. the lobe on the posteroventral portion of valvifer I and the dentiform projection on the apex of valvula I (Fig. 5a). Unfortunately, these parts of the female genitalia were not described for the other species.

The previously known distribution of *Tacora* (Brazil, Colombia, and Peru) is now extended to Venezuela (Fig. 6). Takiya and Mejdalani (2002) suggested that a vicariant event isolated the *Tacora* ancestor in Western Amazonia in an area that included the Napo and Inambari endemism centers, and possibly also the Imerí center (where no records of the genus were known at that time). Interestingly, the present results appear to support the proposal of Takiya and Mejdalani (2002), as we found that *T. saturata* is distributed in the Imerí center (Fig. 6).

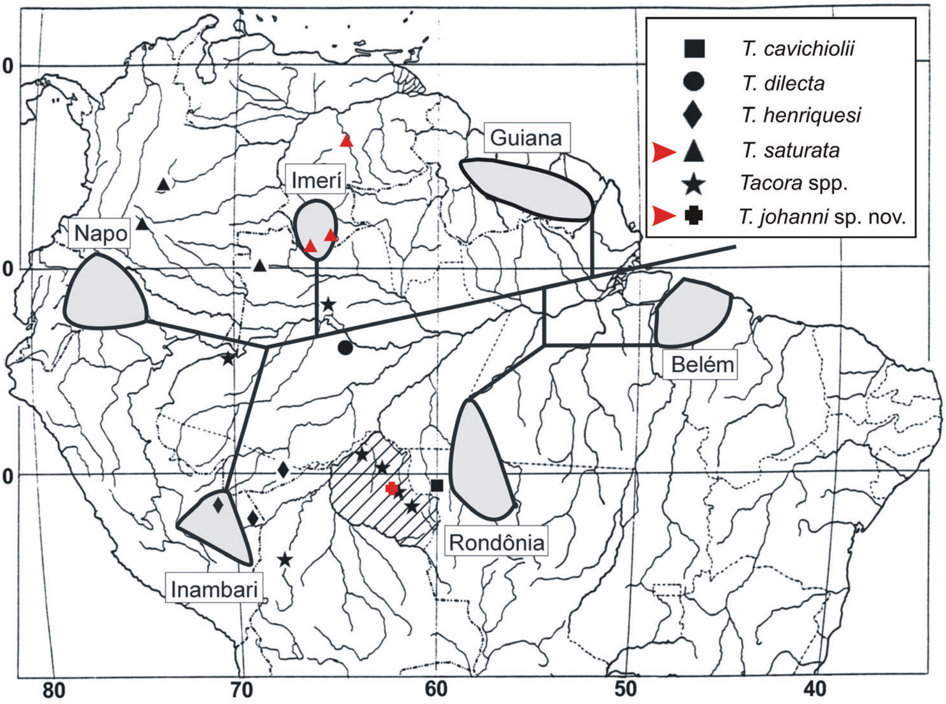

Figure 6. Distributional map of collecting sites of *Tacora* species (modified from Takiya and Mejdalani 2002). Records established in the present study are in red on the map. *Tacora* spp.: unidentified females. Rondônia State appears hatched due to the uncertain type locality of *T. karipuna*. Grey areas connected by black lines correspond to the central portions of six areas of endemism and their possible historical relationships (see details and additional references in Takiya and Mejdalani 2002).

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New genus and species of broad-nosed weevils from Baltic amber and notes on fossils of the subfamily Entiminae (Coleoptera, Curculionidae)

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Abstract

Arostropsis groehni **gen. et sp. n.** is described from Baltic amber and temporarily placed in the tribe Naupactini. It differs from all recent Naupactini genera with open corbels by very short and flattened scape, distinct lateral carina of the pronotum and elytra, and the rostrum distinctly narrower than the head capsule. The shape of head in the extinct genus is somewhat similar to that of the extant Naupactini genera with enclosed corbels (*Platyomus* Sahlberg, 1823 and *Aptolemus* Schoenherr, 1842), but differs in the slender body, open corbels, very short antennal scape and epifrons without a median sulcus (only a longitudinal depression is slightly visible). It is also similar to the Tanymecine genus *Pandeleteius* Schoenherr, 1834 in general appearance, but distinct by the straight anterior edge of the pronotum, lack of postocular spurs, lobes, and vibrissae, a slightly sloping elytral declivity, lateral ridges on the pronotum, subflattened antennal scape, elongate rostrum, and sparsely setose epistome. A new synonymy of the generic names *Protonaupactus* Zherikhin, 1971 and *Sucinophyllobius* Wanat & Borowiec, 1986, **syn. n.**, is established. The Madagascan genus *Corecaulus* Fairmaire, 1903 is transferred from the tribe Naupactini to the Brachyderini because of its connate claws and the similarity in chaetotaxy of the epistomal area with African and Madagascar Brachyderini genera. A key to the identification of known Baltic amber genera of Entiminae is proposed. A checklist of the prepleistocene fossil Entiminae, based on V.V. Zherikhin's data, with remarks and corrections, is presented.

Keywords
new genus and species, new synonymy, fossil Entiminae, Naupactini, Baltic amber, key, checklist

Introduction

Having examined the Baltic amber weevils from the collection of Mr. Carsten Gröhn, a new genus and species belonging to the subfamily Entiminae is described. However its tribal attribution was questioned because of the aberrant shape of the head capsule and inaccessibility of structures normally used for diagnostics (e.g. genitalia). In studying the various characters of Entiminae weevils, it became readily apparent that one of the most useful diagnostic features at the suprageneric level is the structure of the mandibular processes. They show some variability within Entiminae in general, but within certain tribes is usually rather stable. Besides, the mandibular process of fossils can be used, if available, as an additional character for identification of tribes.

In the course of the current study, mandibular processes of 35 extant genera in 17 tribes, including 6 genera of the tribe Naupactini Gistel, 1848, were examined (results of this comparison will be published in a forthcoming paper).

In addition, non-American genera treated in the Naupactini were also examined. As a result, the Madagascar genus *Corecaulus* Fairmaire, 1903 (type, female examined, MNHN) was transferred from the tribe Naupactini to Brachyderini, as its claws are connate in the basal third and similar to those in the genera *Podionops* Schoenherr, 1847 (South Africa) and *Lagocaulus* Fairmaire, 1903 (Madagascar) with the long median sulcus at the vertex and chaetotaxy of the epistomal area.

The type specimens of some poorly known taxa were re-examined. *Phyllobius sobrinus* Voss, 1972 was placed in the genus *Sucinophyllobius* (Wanat and Borovec 1986). A redescription of *Protonaupactus* is provided and a new taxonomic placement is proposed for this genus in accordance with the current knowledge of the Tertiary Entiminae fauna (Zherikhin 1971, 1992; and original data). This new information is included in the online catalogue (Ponomarenko et al. 2011).

Historical review of fossil Entiminae

The earliest descriptions of fossils from the subfamily Entiminae Schoenherr, 1823 were published by Heer (1847), Germar (1849), and Giebel (1856) in their reviews of "Tertiary" insects. One of the preceding publications includes a brief note on unrecognizable "*Naupactus*" species (Serres 1829). These authors assigned fossil species to recent genera. The oldest species treated as Entiminae (*Sitonites melanarius*) was dated from the Upper Jurassic (Heer 1864), but this assignment with the broad-nosed weevils is rather doubtful and it is not considered reliable. The fossil specimens reliably identified as Entiminae originated from the Middle Eocene

(Green River and Roan Mountain), the boundary between the Eocene and Oligocene, and also from the Lower Oligocene (Florissant and White River) (Scudder 1893). Exclusively rich American deposits with 47 genera and European deposits with 11 genera demonstrate the level of the Caenozoic diversity of this subfamily. The Middle Eocene deposits contain taxa resembling Entiminae but bear no mandibular processes, such as in Aterpini Lacordaire, 1866, usually assigned to the subfamily Cyclominae Schoenherr, 1826 (Oberprieler 2010). Some advanced genera of Entiminae have also been found with well developed postocular vibrissae and mandibles bearing mandibular processes, which are usually treated as members of the tribes Tanymecini Lacordaire, 1863 and Ophryastini Lacordaire, 1863. A rather large number of the taxa with free claws in the Caenozoic fossil weevils could be regarded as remarkable. Unfortunately, poor preservation of weevils from the Green River and most other American sediments make it difficult to determine generic or even tribal attributions, as most important characters (particularly legs and thin structures of the rostrum) seem to be rarely available for study. On the other hand, good preservation of some compression remnants makes it possible to provide precise systematic interpretations. In particular, the inprints of *Geralophus fossicius* Scudder, 1893 from Florissant, initially treated as Alophini LeConte, 1874, have the distinct transverse sulcus at the base of the epifrons, and the latter was transferred to Cylydrorhinini Lacordaire, 1863 or Aterpini (Cyclominae) (see Scudder 1893: plate II, Figs 16, 17 and 24); however, a more precise placement is scarcely possible due to the masking of fine structures of the mouthparts and epistomal area of the rostrum. Most Entiminae described from the Upper Eocene resin of Denmark, Poland and Russia (Voss 1953, 1972; Zherikhin 1971; Wanat and Boroviec 1986) are in quite good condition.

Baltic amber Entiminae and their systematic and biographic links

The Baltic amber weevils apparently share more similarity with recent groups occurring mostly in the Indo-Malayan (Oriental) and Neotropical Regions (Zherikhin 1971). The biotic similarity could be due to the more homogeneous Paleogene Euro-Asian biota which now mostly remains in the recent "Himalayan-Burmanian-Yunannian block" (Takhtajan 1970; Kirejtshuk and Kurochkin 2010), but the link between this Paleogene biota with the recent Neotropical fauna is still unclear. Nevertheless, the Baltic amber fauna of Entiminae comprises two fossil genera, *Paonaupactus* Voss, 1953 and *Protonaupactus* Zherikhin, 1971, linked to the Neotropics, versus *Sucinophyllobius* Wanat & Boroviec, 1986, linked to the Indo-Malayan Region. *Polydrusus* Germar, 1817, is the only confirmed recent genus known from Baltic amber. It was established by the paleoendemic, monotypic subgenus *Palaeodrosus* Zherikhin, 1971, and is highly diverse in the recent fauna of the warm-temperate zone of the Palaearctic where it comprises 204 species. Another recent Palaearctic genus recorded from Baltic amber may be *Trachyphloeus* Germar, 1824 (Klebs 1910), but this data is still not confirmed.

The genus *Paonaupactus* Voss, 1953 is monotypic and it is considered as a member of the tribe Anypotactini Champion, 1911 (Alonso-Zarazaga and Lyal 1999). *Protonaupactus* Zherikhin, 1971 is also monotypic and it was originally placed in the tribe Naupactini Gistel, 1856). The genus *Sucinophyllobius* Wanat & Boroviec, 1986 was proposed for *Phyllobius sobrinus* Voss, 1972 and another species (*Sucinophyllobius viridis* Wanat & Boroviec, 1986) was also described in it. According to the recent catalogue of weevil genera (Alonso-Zarazaga and Lyal 1999), *Sucinophyllobius* belongs to the tribe Cyphicerini Lacordaire, 1863. Preliminary study and a comparison of *Sucinophylobius* with *Cyphicerus* reveals that the characters of the head and prothorax make it questionable if *Sucinophyllobius* belongs within the subtribe Cyphicerina (see further discussion below under *Protonaupactus*).

Methods

The usual optic equipment was used for descriptions, including a Leica MZ 16.0 microscope provided with a CCD camera and camera lucida. Morphological terms mostly follow Thompson (1992), Emden (1944), and Doyen (1966). Special terms related to the rostrum structure follow Oberprieler 1988 and details of the epistomal area follow Morimoto et al. (2006).

Measurements. All measurements were taken with an ocular-micrometer. Body length was measured from the anterior margin of the eyes to the apex of the elytra, and rostrum length from the rostrum apex to the anterior margin of the eyes. Width of the rostrum is the maximum distance between the lateral edges of the pterygia.

Imaging. All outline illustrations were drawn using a camera-lucida and modified with a Wacom Graphire 4 Classic XL A5 tablet in Corel Draw (version 11.633) Corel®. Merging of layers was done with Helicon Focus (version 5.0) HeliconSoft®. Amber samples were photographed as under normal conditions as well as in sugar syrup to provide more suitable light refraction.

Abbreviations of depositories. **GPIH** Institute of Geology and Palaeontology and Museum (Geologo-Paläontologisches Institut u. Museum), University of Hamburg; **MNHN** National Museum of Natural History (Museum National d'Histoire Naturelle), Paris; **ZMUC** Zoological Museum (Zoologisk Museum), University of Copenhagen.

Abbreviations of morphological terms. **cb** corbel, **es** epistomal setae, **ed** elytral declivity, **fr** frons, **hp** humeral prominence, **ibt** intero-basal tooth, **ma** mandibular process, **lr** lateral ridge of pronotum, **pep** parepistome.

Abbreviations in table. **Agri** Agriento (=Girgenti), Sicilia, Italy, Upper Miocene; **Aix** Aix-en-Province, France, Lower Oligocene; **BalJ** Baltic Amber, Baltic and North Sea coast, Upper Eocene; **Boet** Böttinger Marmors, Germany, Miocene; **Cere** Céreste, west to Apt, Alpes-de-Haute, Basses Alp Department, Provence, France, Lower Oligocene; **Cela** Célas, railway Uzés - Saint-Julien-de-Casignac, Fumades, Corents, Bassein Ales, Gard Dept., France, Upper Eocene, previously Lower Oligocene (Sannosien); **Dece** Lava Camp Mine, Jumachuk River Valley, Seward peninsula, Alaska, Pleocene-Pleistocene (5.7 mln - 27 000 - Deceit Formation); **DomJ** Dominican amber, Dominican Republic and Haiti; Lower Miocene; **CerG** Cerro Guido, Ultima Esperanza, Magallanes, Upper Cretaceous; **Core** Corent, Gergovia Plateu, south of Clermon-Ferran, Puy-de-Dom Department, France, Upper Oligocene; **Flor** Florissant, south fork of Twin Creek, Front Range near Pike's Peak, Colorado, U.S.A., Lower Oligocene. **GreR** Green-River, 3-4 km western rail-way crossing of Green River; Utah, U.S.A, Middle Eocene; **N1** Neogene, Miocene; **N11** Neogene, Lower Miocene; **N13** Neogene, Upper Miocene; **N2** Neogene, Pliocene; **K2** Upper Cretaceous; **Dece** Lava Camp Mine, Jumachuk River Valley, Seward peninsula, Alaska, Pleocene-Pleistocene site (5.7 mln - 27 000 - Deceit Formation); **Oeni** Oeningen, near Baden lake, Baden-Württemberg, Germany, Upper Miocene; **Pg12** Paleogene, Middle Paleocene; **Pg2** Paleogene, Eocene; **Pg22** Paleogene, Middle Eocene; **Pg23** Paleogene, Upper Eocene; **Pg31** Paleogene, Lower Oligocene; **Pg33** Paleogene, Upper Oligocene; **RoaM** Roan Mountain, Colorado, USA, Middle Eocene; **Rott** Siebengebirge, Germany; Lower Miocene, Aquitanian or Upper Oligocene; **Sunc** Sunchal, La Mendieta, Jujuy Prov., northern Argentina; Upper Paleocene (Lower Eocene); **WhiR** White River Badlands, South Dakota, boundary Eocene and Oligocene.

Taxonomic treatment

Order Coleoptera Linnaeus, 1758
Family Curculionidae Latreille, 1802
Subfamily Entiminae Schoenherr, 1823

Arostropsis Yunakov & Kirejtshuk, gen. n.

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http://species-id.net/wiki/Arostropsis

Type species. *Arostropsis groehni* Yunakov & Kirejtshuk, sp. n.

Etymology. The name of the new genus is formed from the Greek negative prefix "a", "rōstron" (beak, bill, snout) and "opsis" (resembling a (specified) thing). Gender feminine.

Diagnosis. Body elongate, in general appearance similar to *Pandeleteius* Schoenherr, 1834. Antenna with scape short, as long as pedicel (first funicular article; term after Doyen, 1966) and 2nd funicular article (antennomere 3) together, reaching anterior margin of eye, strongly widened and flattened dorso-ventrally along apical third. Rostrum distinctly elongate and slender, about half as thick as frons. Vertex with small frontal fossa anterior of eyes. Buccal cavity completely covered by prementum; transverse sulcus absent. Epistome sparsely setose: only two pairs of short (internal) and long (external) setae (such composition of setae is not found among groups of Naupactini and Anypotactini); parepistome (term after Morimoto et al. 2006) weakly acute and gently extending beyond contour of rostrum (Fig. 14). Antennal scrobes entirely lateral, just swinging fossa (term after Morimoto et al. 2006) slightly visible from above, pterygia scarcely pronounced. Mandibular process resembling that in other Naupactini (this structure was examined for six genera of Naupactini), weakly curved inward, with distinct dorsal carina, without inner basal tooth (Fig. 18). Eyes strongly asymmetrically convex. Pronotal and elytral disk distinctly depressed dorsally. Pronotum with distinct lateral ridges; its posterior edge bisinuate. Elytra subparallel-sided, with humeral and distinct subapical prominences, elytral declivity gently sloping. Femora obtuse, weakly swollen. Metatibiae with open corbels. Claws free.

Arostropsis groehni **Yunakov & Kirejtshuk, sp. n.**

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http://species-id.net/wiki/Arostropsis_groehni
Figs 1–16

Material examined. *Holotype* “C 7968, GPIH 4516”, male (GPIH); the complete beetle with a clear integument is included in an irregular parallelepiped with the largest plane about 18.0 × 14.0 mm and the smallest one 11.0 × 7.0 mm; amber matter on right side from the beetle is rather homogeneous, but that from the left side of the inclusion consists of some layers, in which between the borders is a fine net of dark (almost blackish) organic matter.

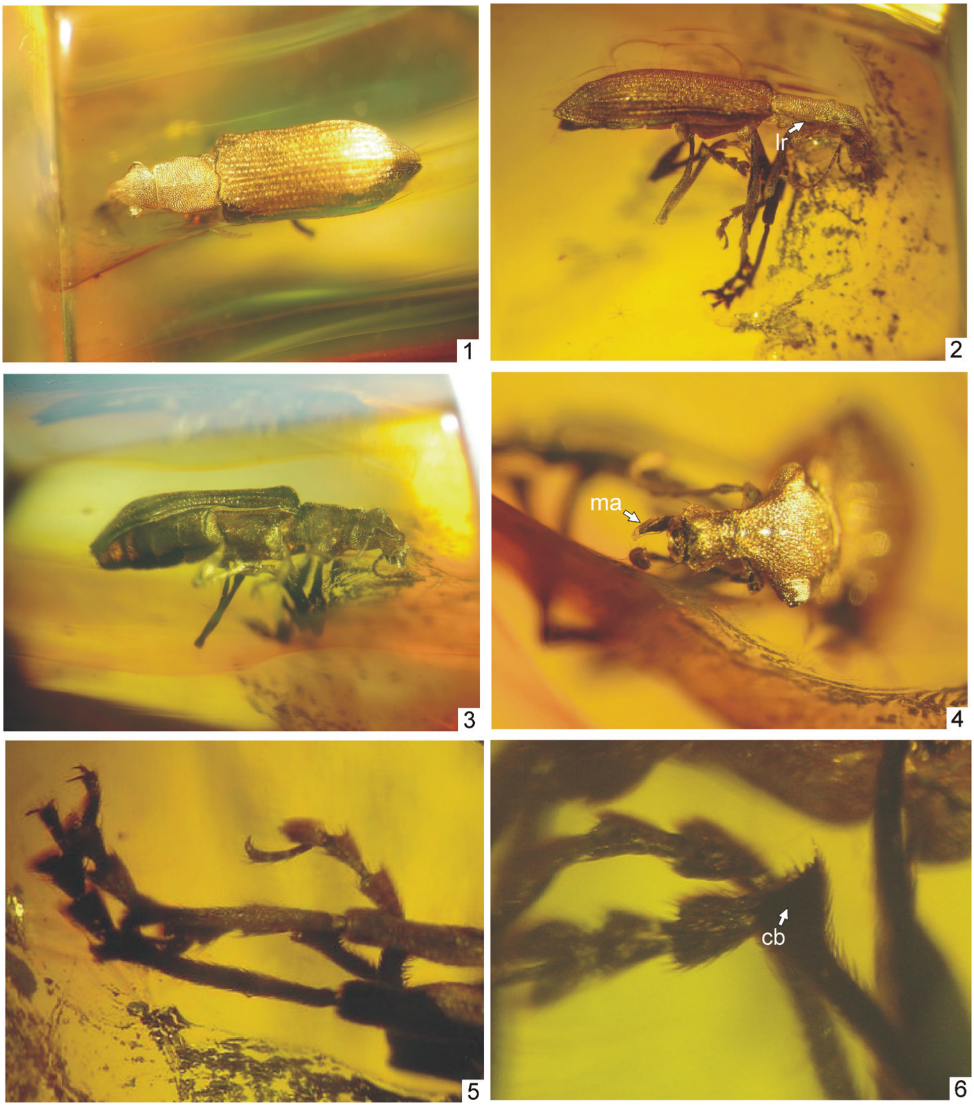
Etymology. The epithet of the new species is formed from the name of Carsten Gröhn, collector of its holotype.

Type strata. Baltic Amber; Upper Eocene, Prussian Formation.

Type locality. Baltic Sea coast and Amber quarry Jantarny near Kaliningrad (formerly Koenigsberg), Kaliningrad region, Russia.

Description. Length 6.4, width 1.8, height 1.3 mm. Body slender, distinctly depressed from above. Pronotum and elytra strongly carinate at sides. Integument densely covered with small, apparently metallic, lanceolate (apparently green) scales at both sides of body and legs.

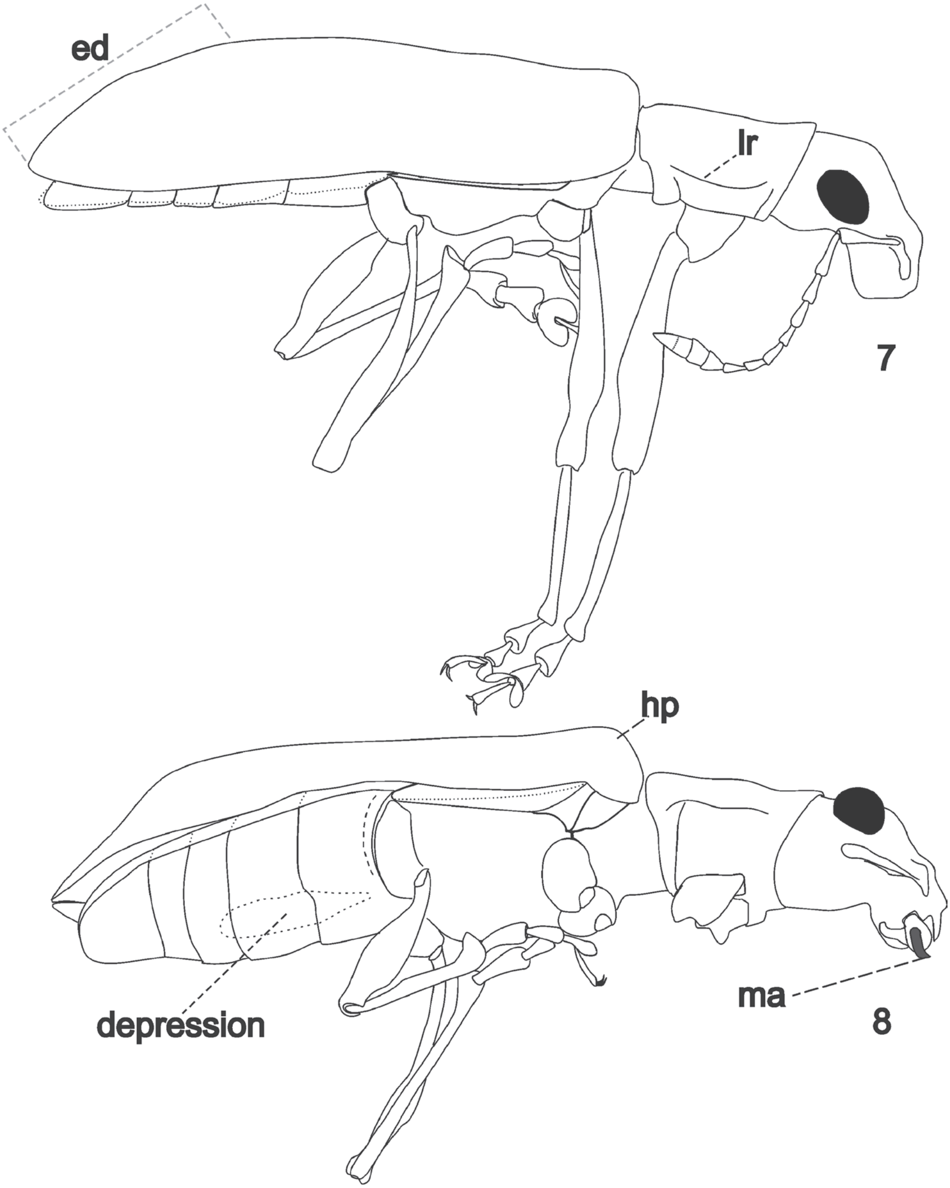
Head. Rostrum 1.5 times as long as wide, narrow, distinctly narrower than head capsule, laterally depressed. Pterygia weakly extending beyond lateral contour of rostrum. Epistomal area not depressed. Lateral edges of epifrons at middle convex, narrowed towards middle, then parallel-sided, without basal, transverse depression or sulcus. Median sulcus shallow, extending towards pit between eyes, not continuing towards vertex. Head capsule not constricted beyond eyes. Frons distinctly convex, almost twice as wide as epifrons at level of antennal insertions. Maximum width of head at posterior part of eyes. Scape comparatively short, about 1/4 as long as funicle, strongly expanded apically, somewhat compressed dorsoventrally, not extending beyond anterior third of eyes, directed obliquely downwards in folded state. Funicle slender; all segments elongate, funicular segment 1 about three times as long as wide, 2nd about two times as long as wide, 3rd about 1.5 times as long as wide; 4th-5th about two times as long as wide, segments



Figures 1–6. *Arostropsis groehni* gen. et sp.n. **1** body, dorsal view **2** body, lateral view **3** body, ventrolateral view **4** head, dorsal view **5** protarsi **6** metatibia apex. Abbreviations: **cb** – corbel, **ma** – mandibular process. Body length: 6.4 mm.

6-7 about 1.5 times as long as wide. Club spindle-shaped and comparatively thin, with distinctly separated segments, about as long as funicular segments 1-7 together. Mandibles entirely bare (without scales), moderately extended beyond buccal cavity. The only remaining left mandibular process knife-shaped, in apical third slightly curved inward, without internal prominences, about 1.5 times as long as protruding part of mandibles.

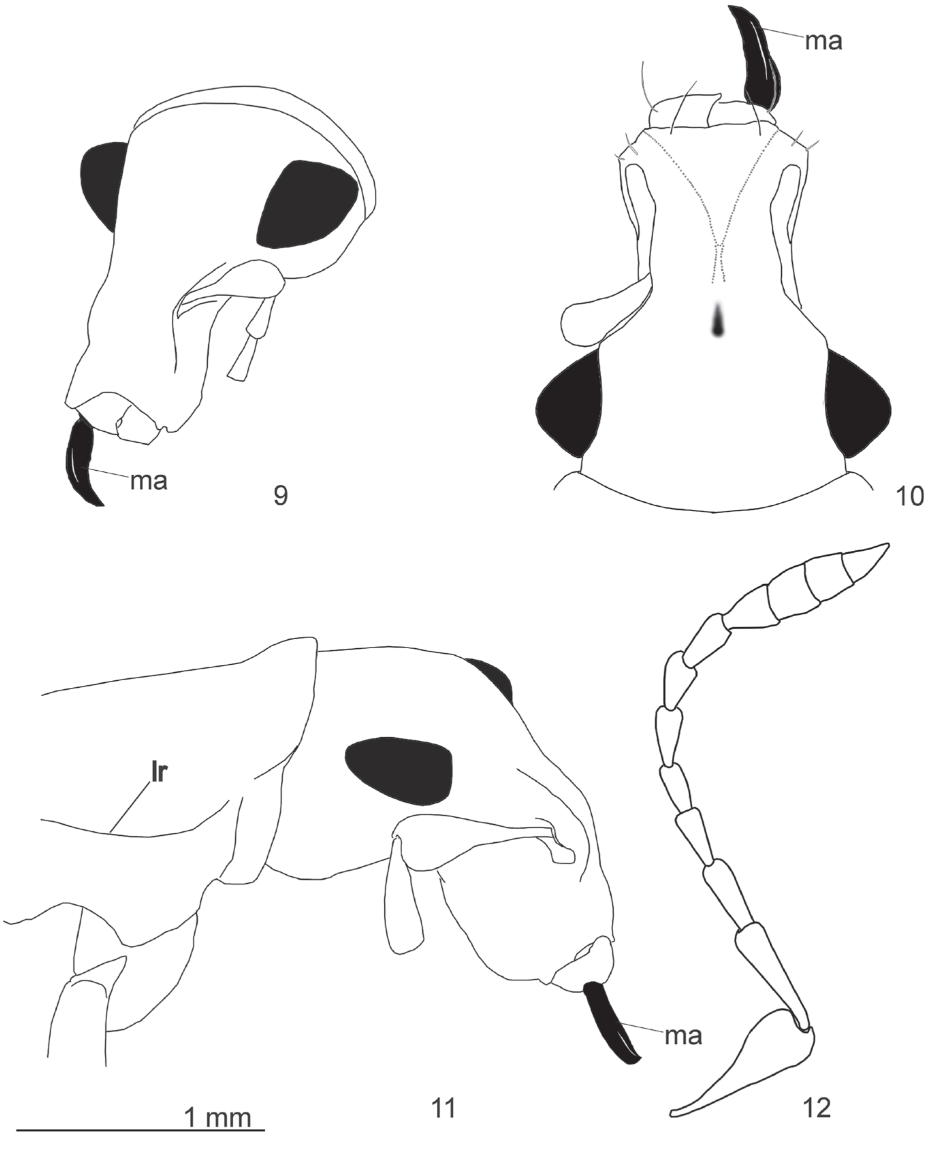
Pronotum elongate, almost parallel-sided, with anterior and posterior constrictions widely expressed, weakly and evenly convex at sides, with disc weakly convex transverse-



Figures 7–8. *Arostropsis groehni* gen. et sp.n. **7** body outline, lateral view **8** idem, ventro-lateral view (anterior and middle limbs removed). Abbreviations: **ed** elytral declivity, **hp** humeral prominence, **lr** lateral ridge, **ma** mandibular process. Body length: 6.4 mm.

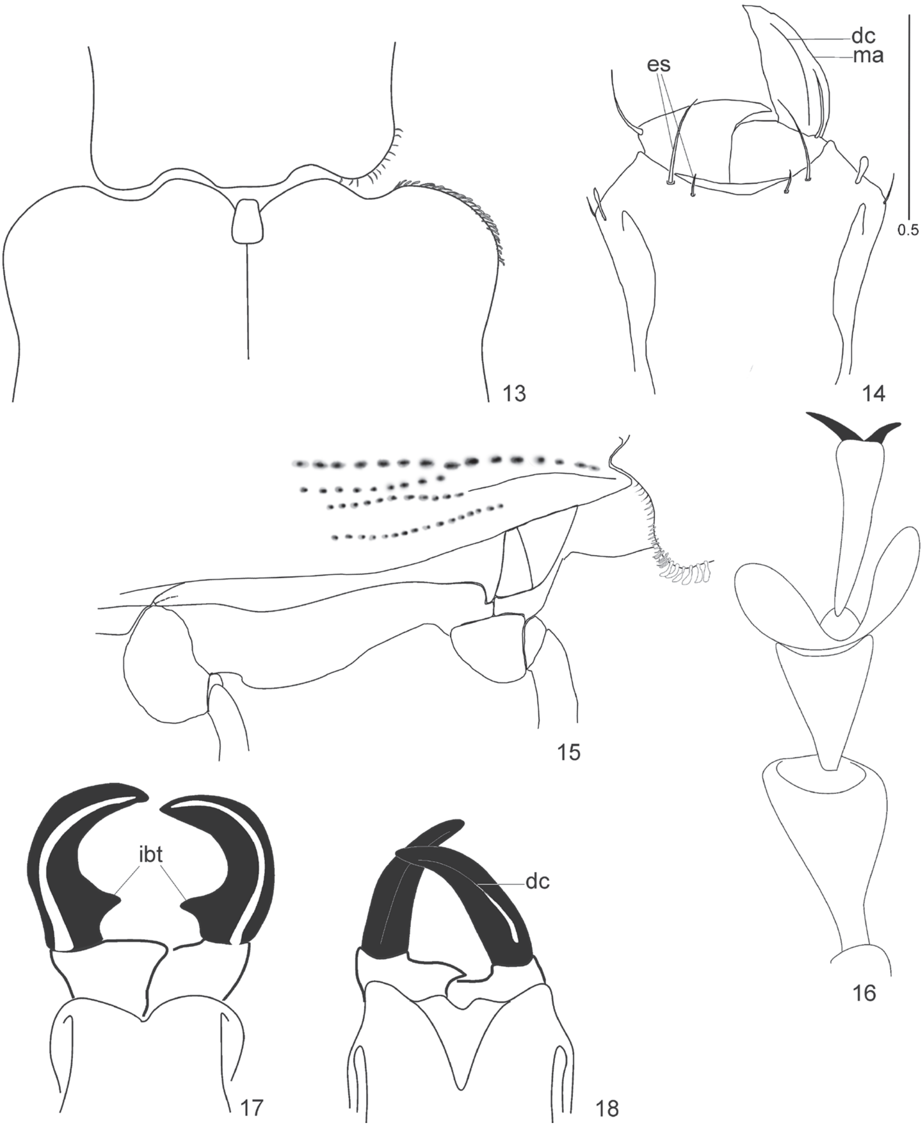
ly and anterior edge curving upward; posterior edge slightly bisinuate; posterior angles widely rounded and somewhat projecting posteriorly; anterior edge nearly straight.

Elytra elongate, about 4.5 times as long as wide, parallel-sided, humeral prominences distinct (Fig. 8, **hp**), basal edge of elytra biconvex opposite the posterior pronotal depressions. Elytral declivity gently sloping (Fig. 7).



Figures 9–12. *Arostropsis groehni* gen. et sp.n. **9** head, antero-lateral view **10** idem, antero-dorsal view **11** head and prothorax, lateral view **12** antenna, lateral view. Abbreviations: **lr** lateral ridge, **ma** mandibular process. Scale bar: 1 mm.

Legs slender. Femora slender, elongate, obtuse, weakly swollen in apical third. Tibiae slender and elongate. Protibiae gently curved inwards in apical third; with anterior row of thin spines. Metatibiae subflattened and with inner edge sinuate at apical third. Corbels open (Figs 6, **cb**; 8), without additional row of spines. Tarsi slender, setaceous, pelma well-developed (term after Doyen 1966). Tarsomere 1 almost as long as



Figures 13–18. Species of *Arostropsis, Lepropus,* and *Naupactus*, details. Figs 17 and 18 (modified from Thompson, 1992). **13**–**16**. *Arostropsis groehni* sp. n. **13** base of pronotum and elytra **14** epistome **15** epipleural margin of elytra **16** protarsus **17** *Lepropus rutilans* (Olivier, 1807) (Tanymecini), mandibular processes dentate **18** *Naupactus fatuus* Boheman, 1833, mandibular processes simple (Naupactini). Abbreviations: **dc** dorsal carina of mandibular process, **ibt** interobasal tooth of mandibular process, **es** epistomal setae, **ma** mandibular process. Scale bar: 1 mm (Figs **13, 15**); 0.5 mm (Figs **14, 16**); not in scale (Figs **17, 18**).

tarsomeres 2–3 combined. Ultimate tarsomere extended beyond lobes of tarsomere 3 by length of last one. Claws free. Procoxae comparatively small, situated in middle of prothorax (Fig. 8).

Comparison with recent genera. The new genus differs from all recent genera of Naupactini with open corbels and procoxae not completely separated from the prosternum (*Mesagroicus* Schoenherr, 1840, *Eurymetopus* Schoenherr, 1840, *Melanocyphus* Jekel, 1875, *Trichonaupactus* Hustache, 1939) in the following characters: short and depressed scape, rostrum narrow, epistomal area weakly setose, epifrons with a weakly developed median depression and vertex with very small fossa, not continuing to occiput.

Comparison with Baltic amber entimine genera. Since *Arostropsis* gen. n. has free claws, only two other fossil genera, *Paonaupactus* Voss, 1953 and *Protonaupactus* Zherikhin, 1971, share the same character state and can be compared with the new genus. *Arostropsis* gen. n. strongly differs from both *Paonaupactus* and *Protonaupactus* in the following characters given in the key below.

Key to Baltic amber genera of Entiminae with free claws

1 Scape short, reaching middle of eyes, strongly thickened apically; pedicel 1.5 times as long as or 2nd funicular article; 1st article of club similar in shape and size with 7th funicular article. Eyes irregularly convex, lateral, located significantly below level of frons (in lateral view). Epifrons without transverse sulcus before eyes. Lateral carina of prothorax developed. Pronotal disc depressed. Procoxae situated in middle of prosternum. Body length 6.4 mm................ .... ***Arostropsis* gen. n.**

– Scape long, reaching anterior edge of prothorax, not strongly thickened at apex; pedicel 0.7 time as long as 2nd funicular article; 1st article of club significantly different in shape from 7th funicular article. Eyes evenly convex, dorso-laterally, located almost at level of frons and somewhat extended above level of frons (in lateral view). Epifrons with more or less developed, transverse sulcus before eyes. Sides of prothorax evenly swollen, without carina. Pronotal disc moderately convex. Procoxae are closer to the anterior than to the posterior edge of prosternum. Body length 4.0-4.8 mm........................**2**

2 Antennal club oval. 4.5-4.8 mm. .... ***Protonaupactus* Zherikhin, 1971**

– Antennal club spindle-shaped. 4 mm..................***Paonaupactus* Voss, 1953**

Systematic position

This new genus is undoubtedly a member of Entiminae due to the presence of mandibular processes. Due to structural characters: mandibular processes long, knife-shaped (**ibt** not developed) - claws free, vertex and epifrons combined in uniform structure without transverse sulcus before eyes, the new genus could be assigned to the tribes Naupactini or Geonemini Gistel, 1848. Emden separated these groups from other ‘brachyderoid’ tribes of Entiminae with free claws (Tanymecini and Anypotactini) by the following characters (Table 1).

Table 1. Basic morphological characters of 'brachyderoid' tribes of Entiminae with free claws in comparison with the genus *Arostropsis* gen.n.

	Geonemini	Naupactini	Tanymecini	Anypotactini	Arostropsis
1. Postocular vibrissae	absent	absent	present	absent	absent
2. Claws	free	free	free/connate	free	free
3.Transverse sulcus	absent	present/ absent	present/ absent	present/ obsolete	absent
4. Eyes position	dorso-lateral	lateral	dorso-lateral	dorso-lateral	lateral
5. Mentum covers maxillae	yes	yes	yes	yes/no	unknown
6. Metatibial corbels	open/enclosed	open/ enclosed	open/ enclosed	open	open
7. Mandibular processes	without ibt	without ibt	with ibt	unknown	without ibt
8. Procoxae position	anterior	anterior/ median	median	median	median

The position of *Arostropsis* is tested following the table:

Presumption 1 (Geonemini). *Arostropsis* gen.n. lacks the key characters of Geonemini such as: evenly sloping lateral edges of epifrons, very narrow vertex and anterior position of procoxae. Consequently this genus cannot be assigned to this tribe..

Presumption 2 (Tanymecini). *Arostropsis* gen. n. could not be considered in the tribe Tanymecini, due to absence of postocular vibrissae at the prothorax. The amount of vibrissae varies from genus to genus within Tanymecini but at least a few vibrissae are present (some *Pandeleteius*). We do not know any case in which vibrissae are completely absent, so it is unlikely that *Arostropsis* belongs to Tanymecini.

Presumption 3 (Anypotactini). Due to absence of transverse sulcus between vertex and epifrons and U-shaped epistome in *Arostropsis* it is impossible to consider this genus within Anypotactini.

Presumption 4 (Naupactini). The strictly lateral position of the eyes, flattened epifrons and very broad vertex resembles that of *Arostropsis* within Naupactini, however, the shape of the rostrum is very different from that of any known member of this tribe. This transformation of rostrum probably resulted in reduction of the frontal fossa (Fig. 10) that is normally (in genera with broad rostrum) deep, long and continuing from the anterior portion of epifrons to the occiput. Such head shape together with the unusual slender body makes it difficult to recognize *Arostropsis* as a member of the tribe Naupactini.

Probable bionomy. The long legs and well developed tarsal pelma (term after Doyen 1966) of the new species suggests that this beetle was capable of running swiftly between leaves and, therefore, it was likely a canopy-dweller.

Genus *Protonaupactus* Zherikhin, 1971

= *Sucinophyllobius* Wanat & Borowiec, 1986: 243, syn. n.
Type species *Sucinophyllobius viridis* Wanat & Boroviec, 1986

Type species. *Protonaupactus microphthalmus* Zherikhin, 1971

Included species: *Protonaupactus microphthalmus* Zherikhin, 1971, *P. viridis* (Wanat & Boroviec, 1986), comb. n., *P. sobrinus* (Voss, 1972), comb. n.

Protonaupactus sobrinus **(Voss, 1972), comb. n.**

http://species-id.net/wiki/Protonaupactus_sobrinus
Figs 19–34

Phyllobius sobrinus Voss 1972: 174
Sucinophyllobius sobrinus Wanat & Borowiec 1986: 243

Material examined. Holotype: ZMUC903847, male (ZMUC); the complete beetle is included in a nearly regular amber piece, parallelepiped, with facets 14.0, 10.0 and 5.0 mm; one thin layer with wavy, light organic matter, small gas bubbles and small cracks located beneath the beetle.

Type strata. Baltic Amber; Upper Eocene, Prussian Formation.

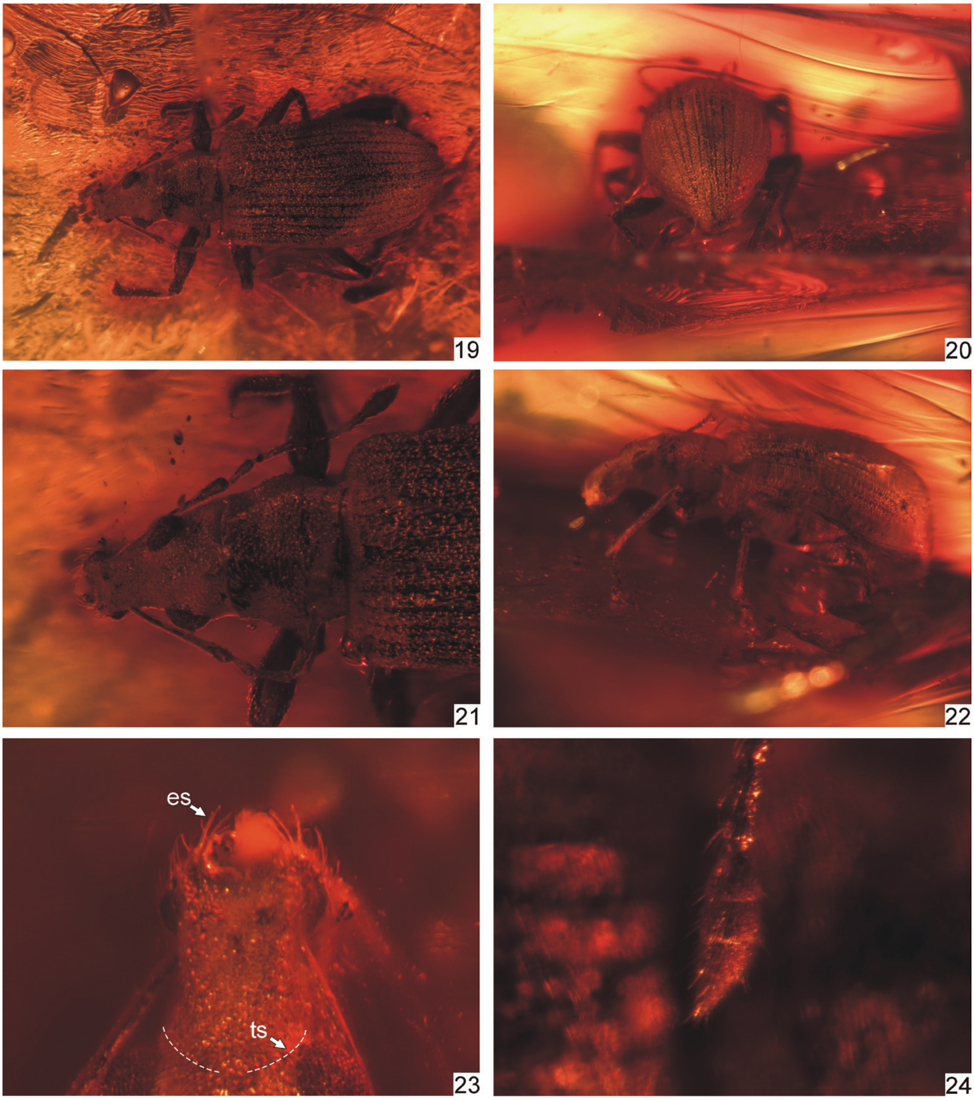
Type locality. Denmark "Bernschteinschluss, Versterhavet bei Thisted, 17.xii.1895, Madsen leg.".

Redescription. Length 4.5, width 1.75, and height 1.65 mm. Beetle densely covered with metallic, shining scales (apparently green).

Head. Rostrum 1.5 times as long as wide at level of pterygia. Epifrons subparallel-sided, at level of antennal insertions abruptly widened anteriorly, weakly convex longitudinally, separated from frons by a distinct depression indicating a transverse sulcus hidden by dense scales. Pterygia strongly extending beyond lateral contour of rostrum. Epistome well-defined by U-shaped keel. Epistomal setae grouped in dense bunches at anterior epistomal angles. Each bunch bearing at least 5 setae. Epistomal angles pronounced apically. Anterior edge of pterygia densely setose. Antennal furrows distinct only in their basal half and not continuing obliquely to underside of rostrum, their dorsal and ventral edges somewhat divergent posteriorly. Eyes dorso-lateral, round and evenly convex. Frons slightly convex, as wide as epifrons between antennal insertions. Frontal fossa not visible because masking by scales. Antennae long. Scape straight, evenly thickened apically, reaching anterior constriction of pronotum. Funicle thin: pedicel about 0.7 time as long as 2nd funicular article; 2nd article about 3.5 times as long as wide; 3rd –7th articles weakly oblong, about 1.5 times as long as wide. Club ovoid, about 2.3 times as long as wide, its 1st article significantly different in shape from 7th funicular article.

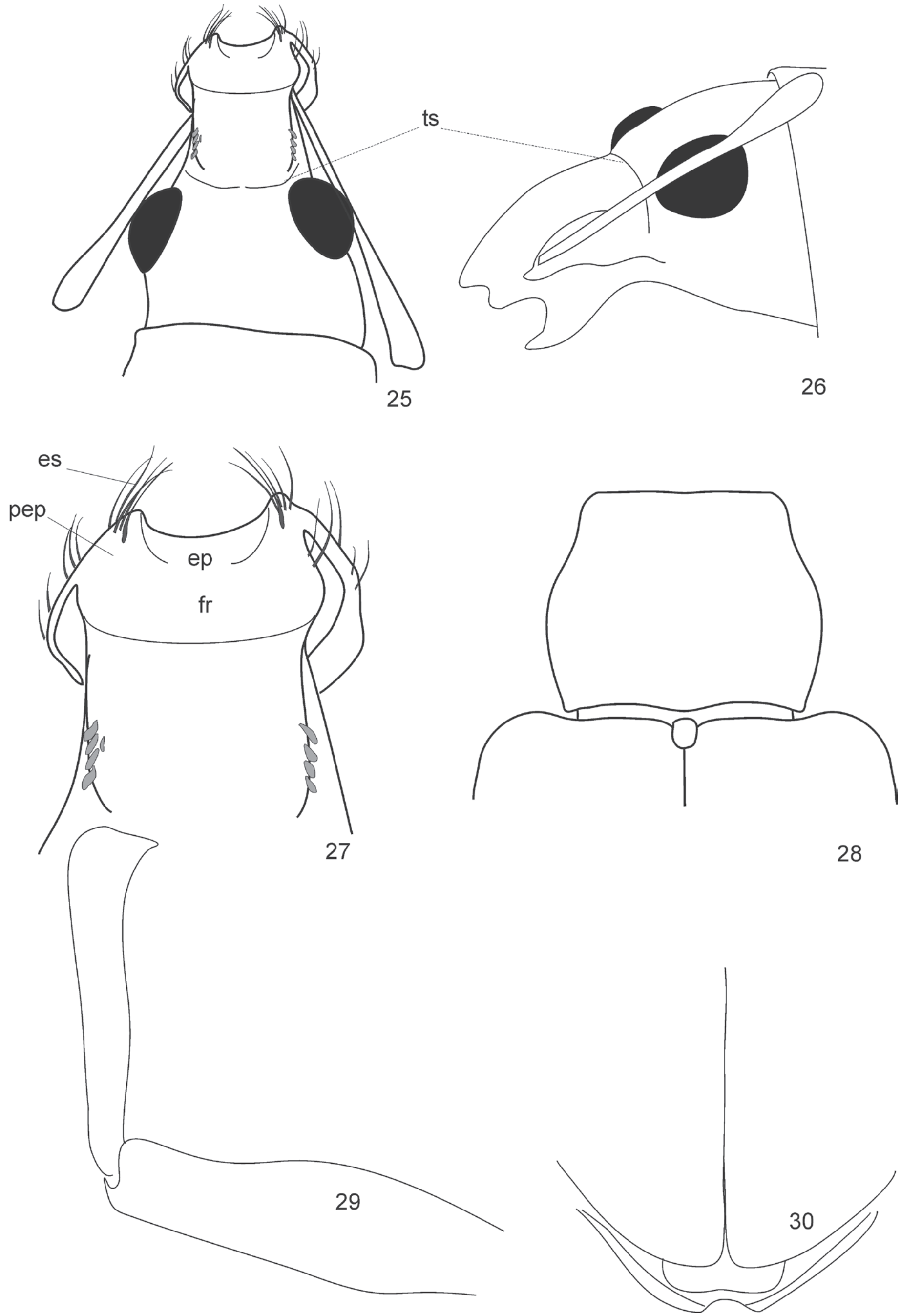
Pronotum transverse; evenly convex at sides and disc, strongly constricted anteriorly and posteriorly. Its base slightly bisinuate. Anterior edge of pronotum straight, without postocular lobes, spurs or vibrissae. Scutellum significantly pronounced, subquadrate.

Elytra subparallel, hardly widened in apical half, with pronounced humeral prominences. Epipleural edge weekly but distinctly S-shaped. Wings well-developed, beetle apparently capable of flying. Elytral declivity abruptly sloping. Anterior edge of anal ventrite (hypopygidium) emarginate (Fig. 30).

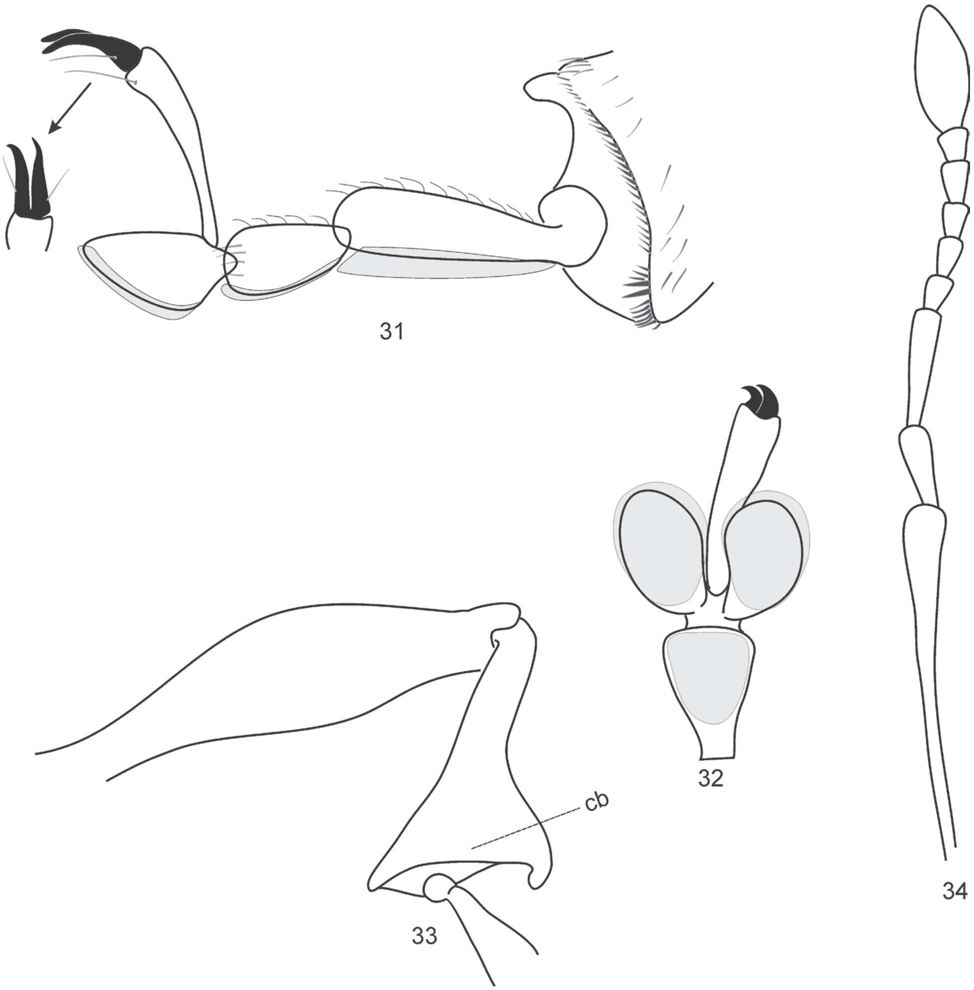


Figures 19–24. *Protonaupactus sobrinus* (Voss, 1972), holotype, male. **19** body, dorsal view **20** elytral declivity, posterior view **21** head and pronotum, dorsal view **22** body, lateral view **23** rostrum, dorsal view (transverse sulcus, indicated by dashed line, hidden by dense scale vestiture) **24** antennal club. Abbreviations: **es** epistomal setae, **ts** transverse sulcus. Body length: 4.5 mm.

Legs thin. Femora obtuse, weakly swollen in middle part. Protibiae straight at external edge, not widened at external apical angle. Metatibiae spatulate apically (Fig. 33), with open corbel but without additional setal row. Setal comb of all tibiae weakly-developed. Tarsi with well-developed setaceous pelma (term after Doyen 1966). Tarsomere 1 about as long as tarsomeres 2 and 3 combined. Tarsomere 3 with well-developed lobes. Ultimate tarsomere by 0.7 extending beyond lobes of tarsomere 3. Claws free.



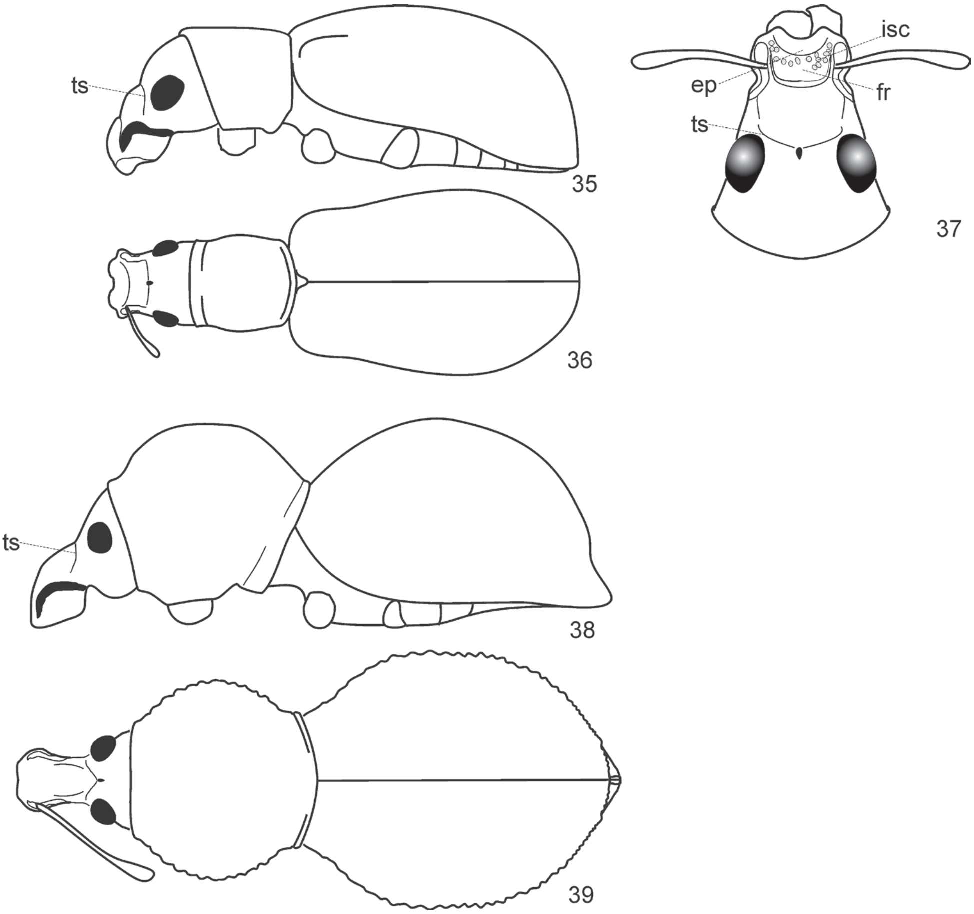
Figures 25–30. *Protonaupactus sobrinus* (Voss, 1972), holotype, male. **25** head with antennal scape, dorsal view **26** idem, lateral dorsal view **27** epistomal area of rostrum **28** pronotum and elytral base, dorsal view **29** anterior right leg, dorsal view **30** elytral apex with pygidium and anal ventrite. Abbreviations: **ts** transverse sulcus, **es** epistomal serae, **ep** epistome, **fr** frons, **pep** parepistome. Scale bar: 1 mm (Figs 25, 26, 28, 30); 0.5 mm (Figs **27, 29**).



Figures 31–34. *Protonaupactus sobrinus* (Voss, 1972), holotype, male. **31** metatibial apex and tarsus lateral view, and claws dorsal view **32** mesotarsus ventral view **33** posterior leg **34** antenna. **Remark**. Setose pelma (term after Doyen, 1966) indicated by grey color. Scale bar: 0.25 mm (Figs 31, 32); 0.5 mm (Figs **33, 34**).

Differential diagnosis. This species is distinguished from *P. microphthalmus* and *P. viridis* by the metatibiae being strongly spatulate apically. The re-examination of the holotype of *Phyllobius sobrinus* Voss, 1972 demonstrates the particular structure of the head, which is very similar to some genera of Anypotactini (mostly from tropical America) and Cyphicerini (mostly from Old World tropics, distinctly separated groups): epistome U-shaped, convex, weakly sinuate anteriorly, and claws free (Figs 27, 31). This species also shares a well-developed, transverse sulcus on the rostrum (Fig. 25, 26, 35–39) with other groups of Anypotactini.

Notes on synonymy. The comparison of *Sucinophyllobius sobrinus, S. viridis* and *Protonaupactus microphthalmus* shows they are closely related species of the same genus.



Figures 35–39. Anypotactini, details. 35, 38 body, lateral view; 36, 39 body, dorsal view; 37 head, dorsal view. **35**–**37** *Anypotactus exilis* Boheman, 1840, female (Venezuela); length 3,3 mm **38**, **39** *Hyphantus buccifer* Germar, 1824, female (Brazil); length 8,2 mm. Abbreviations. **isc** incrustation scales, **ep** epistome, **fr** frons, **ts** transverse sulcus.

They share almost the same characters of the rostrum, with moderately defined U-shaped epistome having apically pronounced angles, long and slender antennae with the scape extending behind the anterior margin of the pronotum, funicular article 1 about 0.7 × as long as article 2, and article 2 about 3.5 × as long as wide.

Systematic position of *Protonaupactus*

Anypotactini and Cyphicerini are the only tribes of Entiminae whose relationships with *Protonaupactus* still need to be tested. Both tribes contain genera with the following characters: (1) claws free, (2) epistome deeply sinuate, parepistome distinctly protruding and bearing dense bunches of long setae, (3) swinging fossae long, fully visible in dorsal view, (4) pterygia strongly extended beyond rostrum.

The tribe Cyphicerini consists of rather diverse genera which may be divided into two subgroups by the structure of the prothorax and underside of the head: (**1**) **a** prosternum subflattened with straight anterior edge; **b** pronotum with straight anterior edge; **c** rostrum and head united in a consolidated structure; **d** underside of rostrum densely covered with scales, its sculpture uniform; **e** rostrum directed forwards (Mylacorrhinina and Myllocerina) or (**2**) **a** prosternum with anterior edge sinuate; **b** pronotum with distinct postocular lobes; **c** head and rostrum distinctly separated by transverse constriction; **d** basal area of underside of rostrum with glabrous integument which has a bare stripe reaching the eyes; **e** rostrum directed downwards (Acanthotrachelina, Cyphicerina, and Phytoscaphina).

Anypotactini include a group of genera that share a character set characteristic of the subgroup I of Cyphicerini and distinct from this subgroup in the transverse sulcus on the rostrum. However, this tribe displays an enormous variety in rostrum shape, and also shows both dorsal and lateral positions of the antennal scape which is normally folded above the eyes, along the rostrum, or folded obliquely downwards in the scrobe if developed. Both the antennal scape and funicle are quite slender, hence the antennae resemble a brachyderoid rather than otiorhynchoid type, like in Cyphicerini.

Anypotactus Schoenherr 1840, *Polydacrys* Schoenherr, 1833 and other genera with short rostrum and large pterygia belong to Anypotactini subgroup 1, and *Prepodellus* Kirsch, 1867, *Hyphantus* Germar, 1824 and other genera with long rostrum with very small pterygia belong to Anypotactini subgroup 2.

Protonaupactus combines both character sets, Anypotactini and Cyphicerini. Nevertheless, it can be easily distinguished from Cyphicerini subgr. 2 in sharing the basic character set of Cyphicerini subgr. 1 and Anypotactini subgr. 1. From Cyphicerini subgr.1 *Protonaupactus* differs particularly in the transverse sulcus on the rostrum (Fig. 25, 26). The new data on this fossil genus show that the distinctness between these tribes is not very clear and needs a further investigation.

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Appendix

Checklist of prepleistocene fossil weevils of the subfamily Entiminae

(according to the taxonomic interpretation in Zherikhin and Egorov 1991 and Ponomarenko et al. 2011)

V.V. Zherikhin analyzed all available sources mentioning fossil Curculionoidea (Jurassic-Paleogene). Later the results of his analysis were published in the catalogue by Ponomarenko et al. (2011). In the list below (Table 1) the authors mostly follow his subdivisions pertaining to the subfamily Entiminae. Many references in the list provided here need to be checked re-examining the fossils. Most accounts regarded as doubtful Zherikhin were removed from the following list. Ponomarenko et al. (2011) treated them as 'Subfamilia incerta' or 'Familia incerta'.

Table 2. Checklist of prepleistocene fossil Entiminae.

Subfamilia Entiminae Schoenherr, 1823

NN	Species	age and site of finding
	Tribe Aterpini Lacordaire, 1863 (**see note 1 below this table**)	
1	Genus incertus *fossicius* Scudder, 1893:75 (*Geralophus*)	Pg31, Flor
	Tribe Tropiphorini Marseul, 1863	
2	*Vitavitus thulius* Kissinger, 1973	N2, Dece
3	*Rhytideres sexsulcatus* (Heer, 1856) (*Cleonus*) (= *Hipporhinus reynesii* Oustalet, 1874; *Brachycerus annosus* Oustalet, 1874)	Pg31st, Aix N13, Agri
	Tribe Cylydrorhinini Lacordaire, 1863	
4	*Dorotheus guidensis* Kuschel, 1959	K2, CerG
	Tribe Sitonini Gistel, 1848	
5	*Sitona* (subgenus incertus) *lata* Théobald, 1937	?Pg31, unknown
6	*Sitona* (subgenus incertus) sp. (Hieke and Pietrzeniuk, 1984)	Pg23, BalJ
	Tribe Entimini Schoenherr, 1823	
7	*Geralophus antiquarius* Scudder, 1893	Pg31, Flor
8	*Geralophus occultus* (Scudder, 1876) (*Eurhinus*)	Pg31, Flor
9	*Geralophus lassatus* Scudder, 1893	Pg31, Flor
10	*Geralophus scudderi* Wickham, 1911	Pg31, Flor
11	*Eudomus robustus* Scudder, 1893	Pg31, Flor
12	*Eudomus pinguis* Scudder, 1893	Pg31, Flor
13	*Hipporhinops sternbergi* Cockerell, 1926	Pg12, Sunc
14	Genus incertus *saxatilis* Scudder, 1876 (*Eudiagogus*)	Pg22, GreR
15	Genus incertus *effossus* Scudder, 1876 (*Eudiagogus*)	Pg22, GreR
16	Genus incertus *compactus* Scudder, 1878: 765 (*Ophryastes*)	Pg22, GreR
17	Genus incertus *heeri* Germar, 1849 (*Hipporhinus*) (= *matheroni* Nicolas, 1891; *similis* Nicolas, 1891; *intermedius* Nicolas, 1891; *marioni* Nicolas, 1891; *pertonii* Nicolas, 1891 (*Hipporhinus*))	Pg31, Aix
18	Genus incertus *brevis* Giebel, 1856 (*Hipporhinus*)	Pg31, Aix
19	Genus incertus *schaumi* Heer, 1856 (*Hipporhinus*)	Pg31, Aix

NN	Species	age and site of finding
20	Genus incertus *pumiceus* Scudder, 1893 (*Geralophus*)	Pg31, Flor
21	Genus incertus *repositus* Scudder, 1893 (*Geralophus*)	Pg31, Flor
22	Genus incertus *atavus* Oustalet, 1870 (*Bagous*)	Pg33, Core
	Tribe Tanymecini Lacordaire, 1863 (**see note 2 below this table**)	
23	Genus incertus *rugosus* Deichmüller, 1881 (*Thylacites*)	Pg3, Kucl
24	*Protainophthalmus asperulus* (Heer, 1856) (*Cleonus*) (including Théobald, 1937) (= *Brachyderes aquisextanus* Oustalet, 1874, *B. longipes* Heer in Oustalet, 1874, *Cleonus marcelli* Oustalet, 1874)	Pg31, Aix, Cere
25	*Protainophthalmus margarum* (Germar, 1849) (*Sitona*) (=*antiqua* Giebel, 1856) (*Sitona*)	Pg31, Aix
26	*Protainophthalmus punctulatus* (Nicolas, 1891) (*Desmidophorus*)	Pg31, Aix
27	*Protainophthalmus regularis* (Nicolas, 1891) (*Hipporhinus*)	Pg31, Aix
28	*Protainophthalmus rugicollis* (Heer, 1847) (*Lixus*)	N13, Oeni
29	*Protainophthalmus thaisi* Nicolas, 1891 (*Desmidophorus*)	Pg31, Aix
30	*Protainophthalmus tuberculatus* Nicolas, 1891 (*Desmidophorus*)	Pg31,Aix
31	*Lepropus* sp. (Zherikhin, 1992)	N13, Agri
32	Genus incertus *nudus* Wickham, 1912 (*Pandeleteius*)	Pg31, Flor
33	Genus incertus *secunda* Wickham, 1912 (*Paussopsis*)	Pg31, Flor
	Tribe Phyllobiini Schoenherr, 1826	
34	*Phyllobius* sp. (Spahr, 1981; Hieke and Pietrzeniuk, 1984 etc.)	Pg23, BalJ
	Tribe Polydrusini Schoenherr, 1823 (**see note 3 below this table**)	
35	*Polydrusus* (*Palaeodrosus*) *archetypus* Zherikhin, 1971	Pg23, BalJ
36	*Polydrusus* (Subgenus incertus) sp. (Burmeister, 1832; Hieke and Pietrzeniuk, 1984)	Pg23, BalJ
	Tribe Anypotactini Champion, 1911	
37	*Paonaupactus sitonitoides* Voss, 1953 (=*Polydrusus scheelei* Voss, 1953; *Otiorhynchus pellucidipes* Voss, 1972)	Pg23, BalJ
38	*Paonaupactus cephalotes* (Voss, 1972) (*Phyllobius*)	Pg23, BalJ
39	*Protonaupactus microphthalmus* Zherikhin, 1971	Pg23, BalJ
40	*Protonaupactus sobrinus* (Voss, 1972) (*Phyllobius* sbg. *Subphyllobius*); Wanat et Borowiec, 1986 (*Sucinophyllobius*)	Pg23, BalJ
41	*Protonaupactus viridis* (Wanat et Borowiec, 1986) (*Sucinophyllobius*)	Pg23, BalJ
	Tribe Hormorini Horn, 1876 (see note 4 below this table)	
42	*Hormorus undulatus* (Uhler, 1855) (*Chlorophanus*) (Alonso-Zarazaga and Lyal, 1999)	N1, USA
	Tribe Pristorhynchini Heer, 1847 (Pristorhynchiden)	
43	*Pristorhynchus ellipticus* Heer, 1847	N13, Oeni
	Tribe Naupactini Gistel, 1856	
44	Genus incertus *florissantensis* Wickham, 1914 (*Cyphus*)	Pg31, Flor
45	Genus incertus *subterraneus* Wickham, 1911 (*Cyphus*)	Pg31, Flor
	Tribe Otiorhynchini Schoenherr, 1826	
46	*Otiorhynchus boettingensis* van Emden in Zeuner, 1931	N13, Boet
	Tribe Trachyphloeini Lacordaire, 1863	
47	*Trachyphloeus* sp. (Klebs, 1910)	Pg23, BalJ
	Tribe Eudiagogini LeConte, 1874	
48	*Promecops tumidirostris* Poinar et Brown, 2011	N11, DomJ
	Tribe uncertain	

NN	Species	age and site of finding
49	*Laccopygus nilesii* Scudder, 1893	Pg31, Flor
50	*Evopes veneratus* Scudder, 1893	Pg31, Flor
51	*Oligocryptus sectus* (Scudder, 1893) (*Eucryptus*)	Pg31, Flor
52	Genus incertus *atavina* Heer, 1847 (*Sitona*)	N13, Oeni
53	Genus incertus *crassirostris* Heer, 1864 (*Naupactus*)	N13, Oeni
54	Genus incertus *dilapsus* Scudder, 1893 (*Phyxelis*)	Pg22, GreR
55	Genus incertus *durus* Scudder, 1893 (*Cryptorhynchus*)	Pg22, RoaM
56	Genus incertus *eradicatus* Scudder, 1893 (*Phyxelis*)	Pg22, RoaM
57	Genus incertus *evanidus* Scudder, 1893 (*Omileus*)	Pg31, Flor
58	Genus incertus *evigoratus* Scudder, 1893 (*Phyxelis*)	Pg22, WhiR
59	Genus incertus *exanimis* Scudder, 1876 (*Eudiagogus*, *Epicaerus*)	Pg22, GreR
60	Genus incertus *fortis* Cockerell, 1909 (?*Syntomostylus*)	Pg22, GreR
61	Genus incertus *manderstjernai* Heyden et Heyden, 1866 (*Tychius*)	N11, Rott
62	Genus incertus *margarum* Theobald, 1937 (*Sitona*) [HN]	Pg23, Cela
63	Genus incertus *obdurefactus* Scudder, 1893 (*Exomias*)	Pg22, RoaM
64	Genus incertus *occubatus* Scudder, 1893 (*Evopes*)	Pg31, Flor
65	Genus incertus *perditus* Scudder, 1876 (*Otiorhynchus*)	Pg22, GreR
66	Genus incertus *petrarum* Scudder, 1893 (*Ophryastes*)	Pg22, RoaM
67	Genus incertus *recuperatus* Scudder, 1893 (*Lachnopus*)	Pg31, Flor
68	Genus incertus *rhenanus* Meuner, 1923 (*Laccopygus*)	N11, Rott
69	Genus incertus *subteractus* Scudder, 1893 (*Otiorhynchus*)	Pg22, RoaM
70	Genus incertus *subterraneus* Scudder, 1893 (*Scythropus*)	Pg22, GreR, WhiR
71	Genus incertus *terrosus* Scudder, 1878 (*Eudiagogus*)	Pg22, RoaM, WhiR
72	Genus incertus *venustulus* Heyden et Heyden, 1866 (*Sitona*)	N11, Rott
73	Genus incertus sp. (Serres, 1829) (*Naupactus*)	Pg31, Aix

Notes to table 2.

1. In contrast to the interpretations of Zherikhin, the tribe Aterpini is traditionally treated as belonging to the subfamily Cyclominae (Alonso-Zarazaga and Lyal 1999, Oberprieler 2010, Bouchard et al. 2011) [in the classification proposed by Zherikhin and Egorov (1991) it is considered in 'Tropiphorinae']. Alonso-Zarazaga and Lyal (1999) consider the genus *Hipporhinops* in the subfamily Cyclominae.

2. According to V.V. Zherikhin's unpublished data, genus *Protainophthalmus* Zherikhin, 1992 comprises 7 species originally described within '*Cleonus*', '*Sitona*', '*Desmidophorus*', '*Hipporhinus*' and '*Lixus*' from the Late Paleogene of France and Germany. *Protainophthalmus asperulus* (Heer, 1856) known by three type prints (see Oustalet 1874: 259–263 + plate 3: Figs 20 and 21), two of them (from Aix) are types. We consider they belong to different species or even different genera: since the first print (see Oustalet 1874: Fig. 20) has a transverse sulcus behind the epifrons, but the second print (Oustalet 1874: Fig. 20) does not have such a transverse sulcus. The original description of *Protainophthalmus* (Zherikhin 1992 : 174) also includes two prints

(SMF VI 218 and SMF VI 220, Senckenberg Museum) from Agrigento (Italy) which are not types of *P. asperulus*.

3. The genus *Phyllobius* Germar, 1824 could not be placed in Polydrusini because of significant differences in head structure: long and closed swinging fossae, antennal scrobes not developed (foveiform) and scape not folding while in rest. V.V. Zherikhin, proposed that the tribes Polydrusini and Phyllobiini are synonyms. He considered that the number of mandibular setae is constant and may be used for discrimination of suprageneric groups (Zherikhin and Egorov 1991). Further study of Polydrusini and Phyllobiini genera showed a great variety of the number of mandibular setae. Recent molecular analysis based on two genes 16S rDNA and 18S rDNA, showed that Polydrusini and Phyllobiini are nested in different branches (Hundsdoerfer et al. 2009).

4. According to the current interpretation, the tribe Hormorini is assigned to Entiminae (Alonso-Zarazaga and Lyal 1999). This opinion corresponds to the results of our examination of mandibles, which revealed similarity between *Hormorus* and the North-Pacific genus *Byrsopages* Schoenherr, 1842. The abnormal shape of the mandibles, subflattened dorso-ventrally along the anterior edge and ventral position of the mandibular processes, led Zherikhin to refuse this opinion, and he treated *Hormorus* without subfamily placement as 'subfamilia incerta'.