RESEARCH ARTICLE

A new Ingolfiellid (Crustacea, Amphipoda, Ingolfiellidae) from an anchialine pool on Abd al Kuri Island, Socotra Archipelago, Yemen

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Abstract

Ingolfiella arganoi **sp. n.** from Abd al Kuri Island in the Arabian Sea is described from two specimens, a male and a female. The western shore of the Indian Ocean was hitherto a vacant spot in the distribution of circumtropical shallow marine interstitial ingolfiellids and therefore the location of the new species fills a meaningful gap in the geography of the family. Morphologically, the new species shows close affinities with *I. xarifae* from the Maldives.

Keywords

Taxonomy, meiofauna, subterranean thalassoid amphipods, beach environment, mesopsammon, Arabian Sea

Introduction

During sampling of aquatic fauna from the Socotra Archipelago conducted by Roberto Argano and co-workers (Taiti and Ferrara 2004), two specimens of a new species of *Ingolfiella* were found in the mesopsammon of an anchialine pool on Abd al Kuri Island (Fig. 1a, b). Anchialine water bodies are well known to offer a great potential of unique species (Becking et al. 2011 and references herein). Ingolfiellid amphipods are sporadically found and are confined to fresh, brackish, and marine ground- and cave waters, and even ocean floor habitats (Ruffo 1950; Spooner 1959, 1960; Vonk and Schram 2003). They are seldom observed in great numbers and the specimens from the small island of Abd al Kuri are no exception to this rule; only two specimens were found. Their discovery points to a long-awaited geographic link in the chain of locality records in this group, as they bridge a gap in the so often presumed Tethys distribution. Until now, no ingolfiellid has been reported between the coasts of Greece in the west and the beaches of the Maldives in the east – a stretch well over 6000 km.

The late Sandro Ruffo, curator of the natural history museum of Verona, started the work on the two specimens from Abd al Kuri, helped by one of us (V.I.), but did not finish it because he was not confident about the status of a new species based on so little material and the presence of only few available distinctive morphological characters. A few years later we decided to take up this work and bring it to fruition because it provides relevant new information on the geographic range of ingolfiellids and on new combinations of character states as shown by these specimens from an anchialine environment in the Arabian Sea.

Material and methods

The two specimens were collected on a beach on the north coast of Abd al Kuri Island, Republic of Yemen, (12°11.988'N, 52°15.943'E), close to a little village called Bait
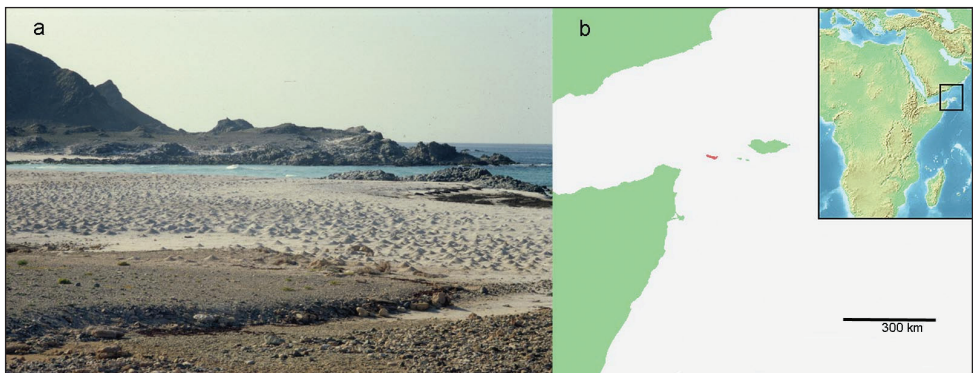

Figure 1. a Abd al Kuri, beach, with gully in foreground, scoured in the sand by rainwater during the wet season (photograph taken while standing at the collection site by R. Argano). Pointed hills on the white beach sand are *Ocypode* crab burrows **b** position of Abd al Kuri Island (red color) in the Arabian Sea.

Eesa. Sampling was done with a micro-creel in coarse sand at the bottom of a pool in an otherwise dry wadi, running as a slight depression to the sea (pers. comm. R. Argano). The approximate position of the pool with unknown salinity from which the ingolfiellids were collected on 7 February 2000 is shown in Fig. 1a .

Taxonomy

Order AMPHIPODA Latreille, 1802
Suborder INGOLFIELLIDEA Hansen, 1903
Family Ingofiellidae Hansen, 1903
Genus *Ingolfiella* Hansen, 1903

Ingolfiella arganoi **sp. n.**
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http://species-id.net/wiki/Ingolfiella_arganoi
Figs 2–5

Material examined. Two specimens: one male **holotype**, 1.4 mm, dissected and mounted in Faure's liquid on slide MSNVRCr nr. 434; one preparatory female **paratype** on two slides MSNVRCr nr. 470 in Museo di Storia Naturale di Verona, Italy.

Diagnosis. Lateral lobes on frontal margin of head developed. Maxillule, basal endite (= outer lobe) left and right with asymmetrical seta. Gnathopods 1 and 2 carpochelate with oblique palm, dactyli with a serrated inner margin with four teeth. Female with extra palmar margin robust seta. Oöstegites on pereiopod 3 and 4, with three regularly placed small button-like processes. Gills present on P3-5. Dactylus of P3 and P4 with slender trifid unguis; P5-7 with thicker bifid unguis, not clearly separated from dactylus. Pleopods 1-3 subtrapezoidal and similar, except first pleopod in male which is flexed and has a broadened tip. Uropod 1 with inner ramus about 1.5 times as long as outer ramus; uropod 2 peduncle without basofacial spine and with two diagonal rows of sturdy rectangular setae, three rows in female, individual setae mostly bifid but with some of them trifid at the tip.

Etymology. The new species is named after Roberto Argano (University of Rome "la Sapienza") who collected the specimens and gave them to the Verona Museum for study.

Description. *Body* elongate, without coloration, all segments laterally compressed. *Head* (Fig. 2a) with lateral margin rounded; lateral or 'ocular lobes' present on frontal margin, well developed, suboval. *Pleonites* I-III with diffusely developed posteriorly rounded epimeral plates adorned with simple seta, a superficial marginal edge slightly visible. *Urosomite* III subcilindrical, slightly longer than deep, enclosing base of telson and uropod III.

Antennule (Fig. 2a), peduncular article slightly shorter than head; article ratio 1:0,42:0,42; flagellum of 4 articles, half the length, articles 2-4 with 1 aesthetasc; accessory flagellum slightly shorter than flagellar articles 1+2, three articles.
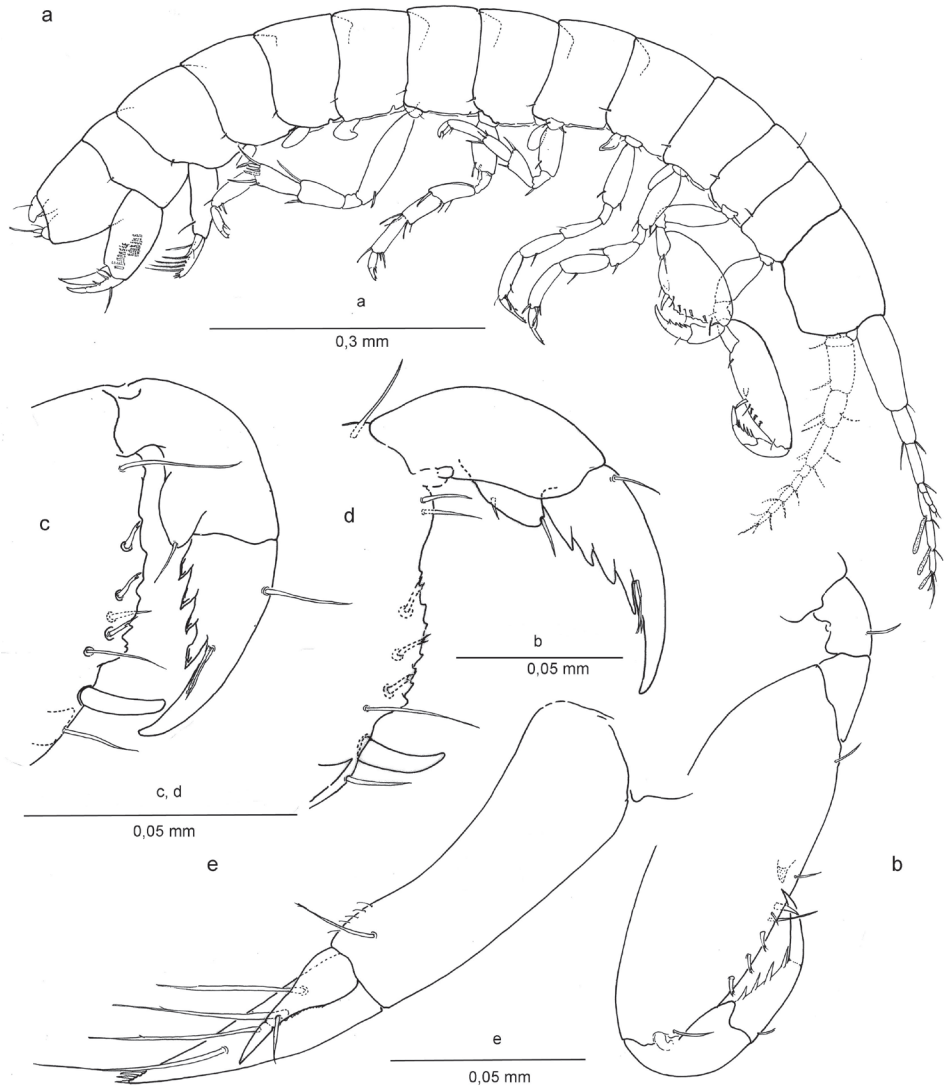
Figure 2. *Ingolfiella arganoi* sp. n., male holotype 1.4 mm. **a** habitus, male 1.4 mm **b** left gnathopod I, lateral **c** right gnathopod II, lateral **d** left gnathopod II, medial **e** right uropod I, lateral.

Antenna (Fig. 2a) subequal in length to antennule; flagellum of 5 articles, slightly shorter than half the length of peduncle, the last article bearing one aesthetasc (antenna drawn by S. Ruffo but not present in mounted slides).

Mandibles with non-triturative molar process, spiniform. Left mandible (Fig. 5d) with broad incisor, right mandible (Fig. 5c) with fine serrations on lacinia and molar process margin.

Maxillule (Figs 5a, e) coxal endite (= inner lobe) with 3 simple setae; basal endite (= outer lobe) with six robust setae of which the second one on the medial side has

four teeth in the left maxillule and three teeth in the right one. Endopod (= palp) two-segmented, distal segment with two setae.

Maxilla (Fig. 5b) with short, equally long plates, each bearing four distal setae.

Maxilliped (Fig. 5f) basal endite slender, with one simple seta; ischium with two setae; merus and carpus without setae; propodus with one seta; dactylus with one lateral robust seta and distally two long setae, unguis not discernible.

Oöstegites on pereiopods III-IV (Figs 3d, e), suboval, without setae and with 3 button-like processes.

Coxal gills on pereiopods III-V.

Gnathopod I (Figs 2b, 3b) carpo-subchelate, palm strongly oblique, carpus 2.4 times as long as wide, palm margin smooth, not serrated, and with three short, bifid flagellate setae along lateral side of margin, and one simple seta on palm angle in male. In female two of such setae of which one placed closer to the row of three bifid setae. Just posterior to the palmar angle seta is a broad triangular spine on the medial side in the male, and three spines in the female: two smaller ones and a larger, more pointed one. Dactylus with four long spines along posterior margin and thin setules or grooves at the base of the unguis.

Gnathopod II (Figs 2c,d; 3c) Carpo-subchelate, palm oblique, carpus stronger than in gnathopod I, subtrapezoidal, carpal index = 4.6, palm angle defined by one large seta and one smaller spine in female (Fig. 3c), one seta in male (Figs 2c,d), and with triangular tooth proximal to the palmar angle seta, palm margin with irregular serrations; propodus strong with lobe on lateral side ending in a setule, less pronounced in female; dactylus with four strong teeth enforced with thick margins on lateral side and a groove or bundled setules at the base of the unguis.

Pereipods III - IV (Figs 3d,e) with two distal setae on dactylus at the base of the unguis, and three distal setae on propodus, one of them long and apically bifid, unguis apically trifid. Oöstegites with in both pereiopods regularly placed series of 3 button-like processes.

Pereiopods V – VII (Figs 4a,b,c) progressively longer towards P7; basis of P5 broad, that of P7 slender; carpus of P5 with two long and stout distal setae, others shorter; carpus of P7 with broad, curved and modified comb setae; merus of P7 with long distal seta; dactyli with two small setae distally; unguis bifid.

Pleopods I-III (Fig. 2a) subtrapezoidal, without setae. Pleopod I in male deformed or broadened distally.

Uropod I (Figs 2e, 4e) male: protopod with one seta and a row of fine setules on anterolateral margin; exopod with very feeble segment suture and one seta placed at two-thirds the length; endopod with terminal row of spines and four long setae laterally. In female protopod with three setae; endopod with six long setae laterally.

Uropod II (Figs 3a, 4d), protopod with two oblique comb rows in male, and three in female; setae of rows more or less rectangular with bifid or trifid, or even comb-like tips; endopod slightly longer than exopod, sharper, and with four setae.

Uropod III (Fig. 2a) short, 2 segmented, with one ramus, protopod with 2 distal setae, ramus short with 1 distal seta.
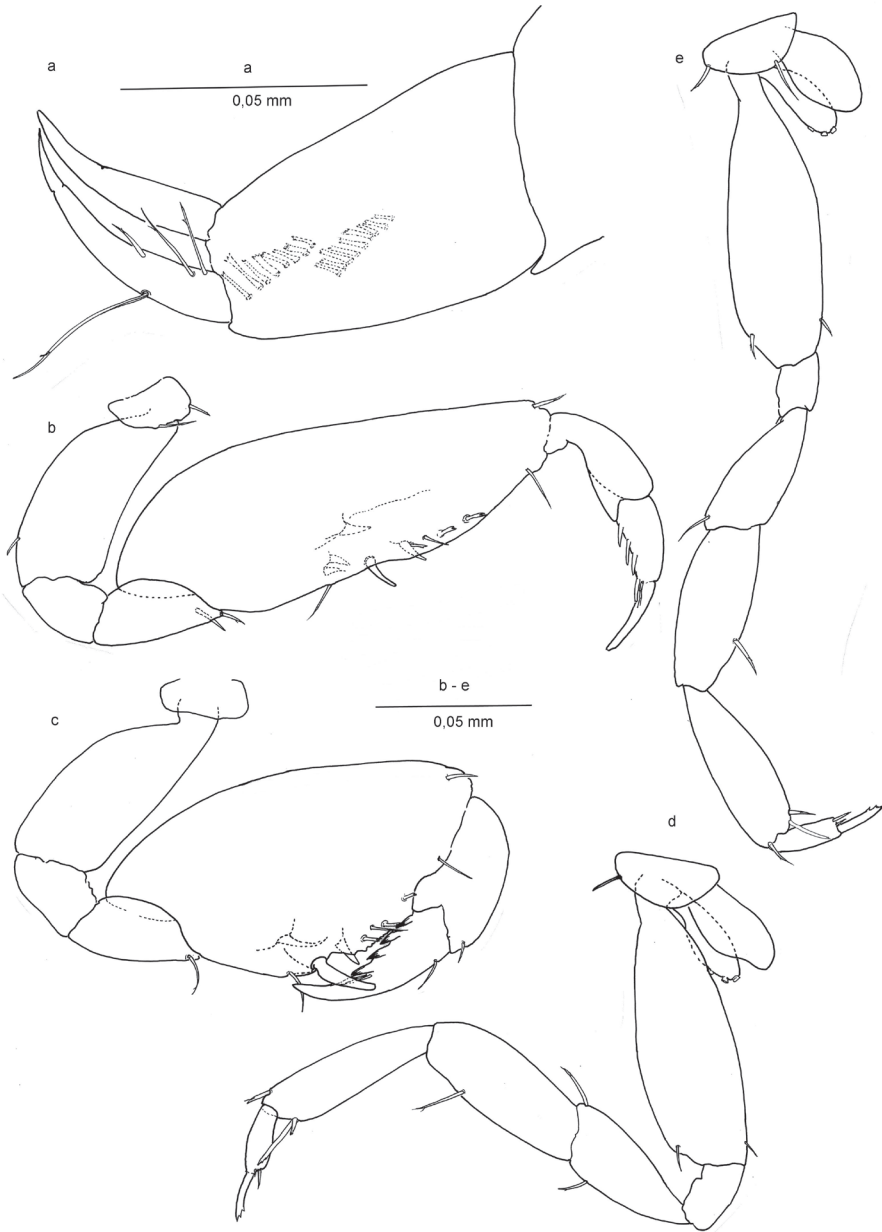
Figure 3. *Ingolfiella arganoi* sp. n., male holotype 1.4 mm. **a** right uropod II, lateral; female paratype 1.5 mm. **b** right gnathopod I, lateral **c** right gnathopod II, lateral **d** right pereiopod III, lateral **e** right pereiopod IV, lateral.

Telson (Fig. 2a) globose, with 1 pair of long dorsal setae.

Differences between male and female: gnathopods without extra palmar seta in male, and uropod II without a third comb row in male. Pleopod I in the male has a broadened tip.
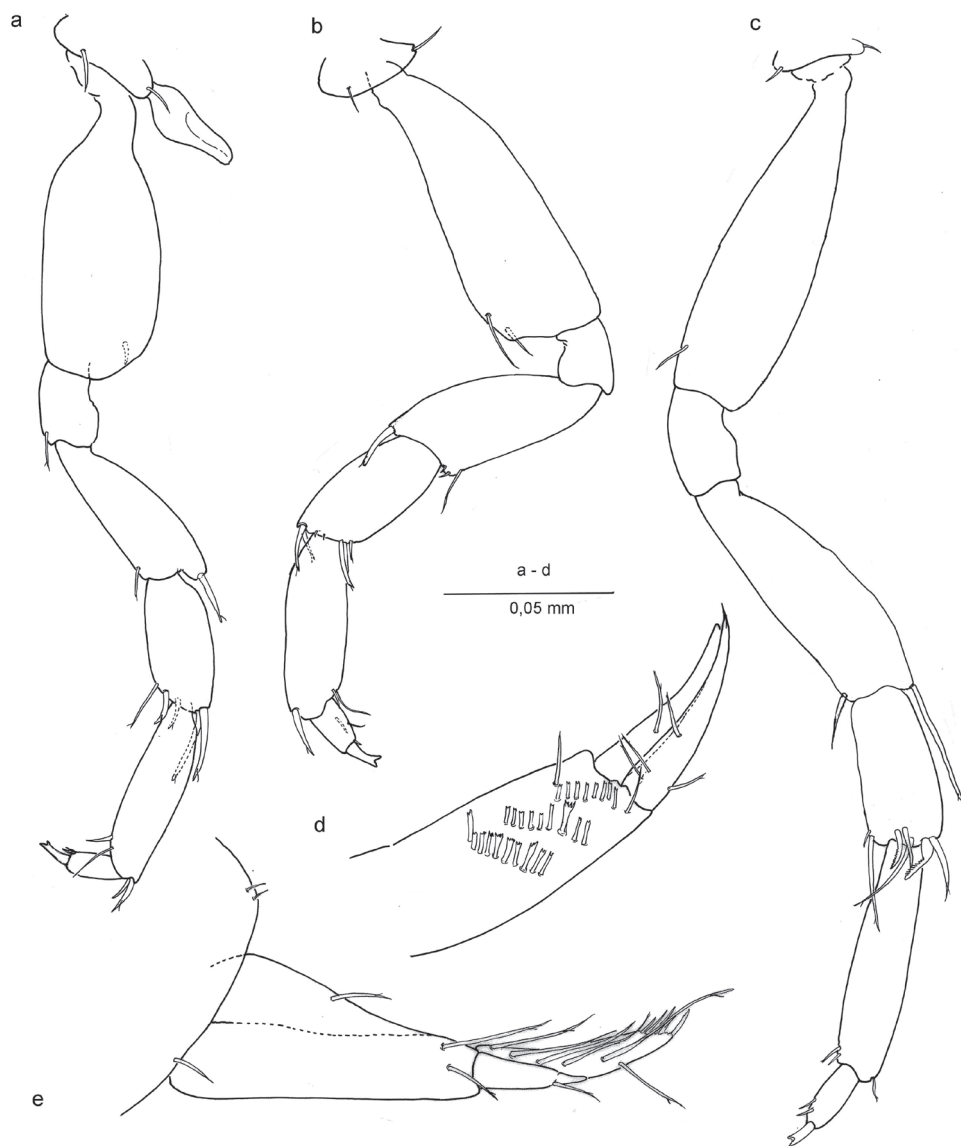
Figure 4. *Ingolfiella arganoi* sp. n., female paratype. **a** pereiopod V **b** pereiopod VI **c** pereiopod VII **d** right uropod II, medial **e** left uropod I, lateral.

Remarks. *Ingolfiella arganoi* sp. n. shares most morphological character states with a species found 2500 km southeastward across the Indian Ocean, on the Maldives, namely *I. xarifae* (Ruffo, 1966), from washed-out broken coral pieces (*Favites* sp.). Species ranges of stygobionts have not been reported to exceed such large distances in the past and molecular work on cryptic lineage diversity of populations of groundwater crustaceans have even diminished existing ranges to distances of less than 1000 km (Trontelj et al. 2009).
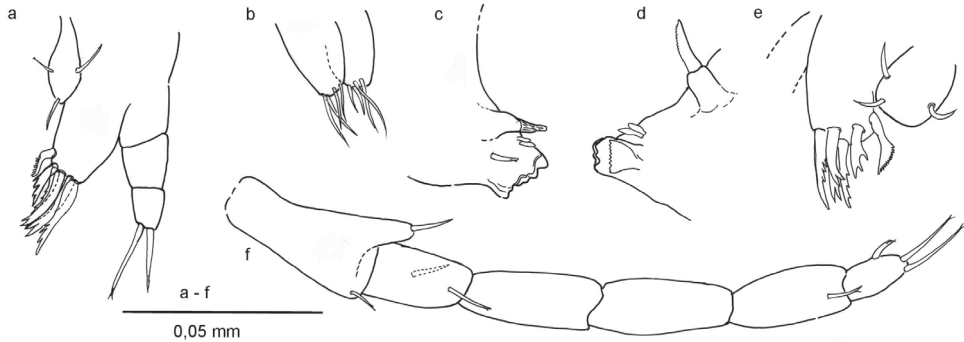
Figure 5. *Ingolfiella arganoi* sp. n., female paratype. **a** left maxillule **b** maxilla **c** right mandible **d** left mandible **e** right maxillule **f** right maxilliped.

For now, five clear morphological differences justify the designation of a new species that also is geographically quite far away from its nearest congeners. These differences can be observed in the four spines on the medial margin of the propodus of gnathopod I – three spines in *I. xarifae*; subtrapezoidal carpus of gnathopod 2 – elongate oval in *xarifae*; palmar index of gnathopod 2 is 4.6 – against 6.4 in xarifae; palm of gnathopod 2 strongly serrate – almost smooth in *xarifae*; pereiopod VII with specialized, combed, robust setae distally on carpus – not present in *xarifae*.

The differences in the placement, form and number of setae have shown to be quite consistent in the case of the poorly setose ingolfiellids (Vonk and Sanchez 1991). The spines and setae that have remained, are perhaps critically functional due to selective reductive factors in the underground environment.

The oöstegites have 3 small button-like processes. The same character was described in *Ingolfiella alba* Iannilli et al., 2008, where also three small button-like processes are present, but here from P3 to P5. Re-examination of *I. xarifae* typus by Sandro Ruffo and V.I. allowed them to observe also on the oöstegites of this species the button-like processes, as described for *I. alba.* Something similar was described in *Metaingolfiella mirabilis* Ruffo, 1969, although the processes were smaller and more numerous. These structures are probably present in other *Ingolfiella* species but have yet to be observed and described (Iannilli et al., 2008). Stock (1979) observed in *I. quadridentata* Stock, 1979, that oöstegites found on P3 and P4 were: "curved, truncate at tip, provided with 3 apical teeth, but without setae."

In other amphipods with preparatory females (females in a moult stage in between two brooding periods), these structures are sometimes present on the oöstegites (pers. comm. D. Jaume). Slattery (1985) mentions the development of oöstegites in infaunal amphipod families of Phoxocephalidae and Haustoriidae undergoing three stages of development: buds (of the oostegite itself), preparatory (moderately long oöstegites with some setae), and mature (long oöstegites, curved, and setose to form a brood-carrying pouch or marsupium). If the buttons, that occur in threesomes on the oöstegites of pereiopods III and IV in *I. arganoi*, can be observed in other ingolfiellids as being present at the same time with setae this might prove their precursory role. On the other

hand, in contradiction to these observations, are our studies of abundant material of *I. alba*, that shows this character. The material consists of several individuals collected in different years (from 1992 to 2004) and in different months of the year. We could verify that the structure is always the same, namely the presence of only three button-like processes, and we did not find setae on the oöstegites. So an interpretation of these structures being preparatory setae seems not convincing for *Ingolfiella* species.

In agreement with Ruffo and Vigna Taglianti 1989 the new species could be placed in the subgenus *Tethydiella,* although Vonk and Schram (2003), basing their phylogeny on more characters, did not use the splitting of *Ingolfiella* into genus and subgenera as several taxa are poorly described when compared to recent taxonomic descriptions and only few species have both sexes well known.

However, the species-groups in sensu Ruffo (1970) and Ruffo and Vigna Taglianti (1989) may still be of practical taxonomic use and the geographical location as well as the morphological diagnosis fits the *Tethydiella* group. Of course, more detailed biogeographic data are required to reconstruct the history of the actual distribution of Ingolfiellidae (Iannilli et al. 2008).

Subterranean thalassoid crustaceans of the region

The present discovery represents the westernmost record of ingolfiellids in the Indo-Pacific Oceans. The Red Sea shores, Gulf of Aden, and the shores of the Arabian sea are relatively unknown areas for stygobiont and marine interstitial crustaceans. Geographically it is an interesting region as it forms the corridor between the better known Mediterranean and south east Asian/Australian stygofaunas. Sampling by Stock and Nijssen (1965) on Entedebir Island in the southern Red Sea revealed the presence of the circumtropical marine groundwater amphipod genus *Psammogammarus* (Vonk and Stock 1987; Vonk 1990; Van der Ham and Vonk 2003; Tomikawa et al. 2010; Vonk et al. 2011), suggesting the possible occurrence of the usual inhabitants of the present coastal groundwater biotope. In this respect also *Angeliera xarifae* Siewing, 1959 can be mentioned. This is a microparasellid isopod, sampled from coastal groundwater of Abd al Kuri during the Xarifa expedition of 1957 (Wallace and Zahir 2007). In 2005 Iannilli et al. described the bogidiellid amphipod *Nubigidiella theresiae*, from a freshwater well at Bin Aissa, on Abd al Kuri Island. Until 2005 the only amphipod species known from the subterranean waters of Socotra was *Indoweckelia superstes* Holsinger & Ruffo, 2002, from a water well on the main island of Socotra. These are mainly freshwater subterranean amphipods with well investigated marine affinities. Recently the coastal aquifer waters of Oman showed to contain *Metacrangonyx* (Jaume & Vonk, 2012), a stygobiont amphipod with proven marine origins (Bauzà-Ribot et al. 2012), distributed in marine and freshwaters from the Caribbean to its current eastern border, the Indian Ocean. On Socotra and Abd al Kuri new cyclopoid copepods were described from brackish wells and caves (Mirabdullaev et al. 2002) showing the island's isolated status. The first inland, freshwater ingolfiellid of the region, as well as those from deep marine sediments, are still to be discovered.

Acknowledgements

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RESEARCH ARTICLE

Review of the millipede family Opisotretidae (Diplopoda, Polydesmida), with descriptions of new species

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Abstract

The small, basically Oriental family Opisotretidae is rediagnosed, reclassified, and shown to comprise the following seven genera, all keyed: *Carlotretus* Hoffman, 1980, with two species, including *C. triramus* **sp. n.** from southern China; *Corypholophus* Attems, 1938, with two species, one in Vietnam, the other in the Ryukyus, Japan; *Martensodesmus* Golovatch, 1987, with eight species, all keyed, including *M. cattienensis* **sp. n.** from southern Vietnam, as well as *M. bedosae* **sp. n.** and *M. spiniger* **sp. n.** from southern China; *Opisotretus* Attems, 1907, with seven species, all keyed, including *O. beroni* **sp. n.** and *O. hagen* **sp. n.**, both from Papua New Guinea, *O. deharvengi* **sp. n.** from Sulawesi, Indonesia, and *O. spinosus* **sp. n.** from Nusakambangan Island, off Java, Indonesia; *Opisthoporodesmus* Silvestri, 1899, with six nominate species; *Retrodesmus* Chamberlin, 1945, with two species, i.e. the type-species *R. dammermani* Chamberlin, 1945, from Java, Indonesia, revised from the holotype, and *R. cavernicola* **sp. n.**, from Papua New Guinea; and *Solaenaulus* Attems, 1940, with two species. Comments are presented on the family's possible relationships and palaeogeographic history. Instead of being considered as the sole component of the superfamily Opisotretoidea, the Opisotretidae is believed here to form one of the families of the diverse superfamily Trichopolydesmoidea, perhaps the sister-group to,

if not immediately derived from, the pantropical family Fuhrmannodesmidae. The origin of Opisotretidae, previously dated as far back as the Triassic (220 Ma) in relation to the fragmentation of eastern Gondwanaland, mainly in the region of present-day Indonesia, could have had nothing to do with Gondwanaland. Opisotretids might have originated in mainland Southeast Asia well within the Cenozoic, with subsequent dispersals along the Himalayas in the West and across Indonesia (including New Guinea) in the East, also reaching as far north as the Ryukyus, Japan and Guangxi, southern China.

Introduction

The small millipede family Opisotretidae was first proposed by Hoffman (1980) as a member of the superfamily Polydesmoidea, suborder Polydesmidea, to incorporate the following genera: *Opisotretus* Attems, 1907, *Corypholophus* Attems, 1938, *Solaenaulus* Attems, 1940 and *Carlotretus* Hoffman, 1980. Another two genera were also included, but only with qualifications: *Opisthoporodesmus* Silvestri, 1899 and *Retrodesmus* Chamberlin, 1945. Soon after that Hoffman (1982) firmly assigned all these six genera to Opisotretidae. Golovatch (1987) added one more genus, *Martensodesmus* Golovatch, 1987. Simonsen (1990), based on the results of a cladistic analysis, not only unequivocally included all these genera except *Carlotretus* (likely just forgotten) in Opisotretidae, but he also considered this family as the sole component of a separate superfamily, Opisotretoidea, in the infraorder Polydesmoides, suborder Polydesmidea.

Opisotretidae have hitherto been known to contain the following 20 species, arranged in alphabetic order:

1. *Carlotretus setosus* (Carl, 1922)
    Opisotretus setosus Carl, 1922: 574.
    Solaenaulus setosus – Attems 1940: 173.
    Carlotretus setosus – Hoffman 1980: 188.
    The type species of *Carlotretus* Hoffman, 1980, which Hoffman (1980) erected, based on certain gonopod traits alone. Originally described as *Opisotretus setosus* Carl, 1922, from Sumatra, Indonesia (Carl 1922).

2. *Corypholophus minutus* Attems, 1938
    Corypholophus minutus Attems, 1938: 249.
    Corypholophus minutus – Attems 1940: 190; Golovatch 1987: 205.
    The type species of *Corypholophus*, originally described from near Nhatrang, southern Vietnam (Attems 1938), later recorded and clearly depicted from material taken from a locality in northern Vietnam (Golovatch 1987).

3. *Corypholophus ryukyuensis* Murakami, 1975
    Corypholophus ryukyuensis Murakami, 1975: 108.

Corypholophus ryukyuensis – Golovatch 1987: 205; Nakamura and Korsós 2010: 82. Described from several islands of the Ryukyu Archipelago, Japan (Murakami 1975), whence all later records have been summarized by Nakamura & Korsós (2010). Based on gonopod conformation, the assignment of *ryukyuensis* to *Corypholophus* was questioned by Golovatch (1987).

4.   *Martensodesmus bicuspidatus* Golovatch, 1988
      Martensodesmus bicuspidatus Golovatch, 1988: 32.
      Described from Bhutan, Himalaya (Golovatch 1988).

5.   *Martensodesmus excornis* Golovatch, 1988
      Martensodesmus excornis Golovatch, 1988: 30.
      Described from Bhutan, Himalaya (Golovatch 1988).

6.   *Martensodesmus himalayensis* Golovatch, 1987
      Martensodesmus himalayensis Golovatch, 1987: 205.
      The type species of *Martensodesmus* Golovatch, 1987, described from Nepal, Himalaya (Golovatch 1987).

7.   *Martensodesmus nagarjungicus* Golovatch, 1987
      Martensodesmus nagarjungicus Golovatch, 1987: 207.
      Described from Nepal, Himalaya (Golovatch 1987).

8.   *Martensodesmus sherpa* Golovatch, 1987
      Martensodesmus sherpa Golovatch, 1987: 206.
      Described from Nepal, Himalaya (Golovatch 1987).

9.   *Opisotretus euthus* Chamberlin, 1945
      Opisotretus euthus Chamberlin, 1945: 4.
      Rather poorly described from near Tjibodas (now Cibodas), Java, Indonesia (Chamberlin 1945).

10.   *Opisotretus kraepelini* Attems, 1907
      Opisotretus Kraepelini Attems, 1907: 113.
      Opisotretus kraepelini – Attems 1940: 150.
      The type species of *Opisotretus* Attems, 1907, described from Mount Pangerango, Java, Indonesia (Attems 1907).

11.   *Opisotretus mimus* Chamberlin, 1945
      Opisotretus mimus Chamberlin, 1945: 4.
      Very poorly described from ♀ material from near Tjibodas (now Cibodas), Java, Indonesia (Chamberlin 1945).

12.   *Opisthoporodesmus anandrus* Chamberlin, 1945
       Opisthoporodesmus anandrus Chamberlin, 1945: 3.
       Very poorly described from a ♀ holotype from Doormanpad, Irian Jaya, central
       mountains, 1410–1450 m a.s.l., 3°24'S, 138°38'E, New Guinea, Papua Prov-
       ince, Indonesia (Chamberlin 1945).

13.   *Opisthoporodesmus bacillifer* Carl, 1912
       Opisthoporodesmus bacillifer Carl, 1912: 153.
       Opisthoporodesmus bacillifer – Attems 1940: 152.
       Very poorly described from two presumably subadult ♀♀ from Masarang,
       northern Sulawesi, Indonesia (Carl 1912).

14.   *Opisthoporodesmus conservandus* Chamberlin, 1945
       Opisthoporodesmus conservandus Chamberlin, 1945: 3.
       Very poorly described from Prauwenbivak, Mamberamo River, 3°15'S,
       138°35'E, ca 40 km SW of Sukarnapura, Irian Jaya, New Guinea, Papua Prov-
       ince, Indonesia (Chamberlin 1945).

15.   *Opisthoporodesmus obtectus* Silvestri, 1899
       Opisthoporodesmus obtectus Silvestri, 1899: 206.
       Opisthoporodesmus obtectus – Attems 1940: 151.
       The type species of *Opisthoporodesmus* Silvestri, 1899, described from Tamara
       Island, near Berlinhafen (now Aitape), 3°13'S, 142°35'E, North Sepik Prov-
       ince, Papua New Guinea (Silvestri 1899).

16.   *Opisthoporodesmus silvestri* Chamberlin, 1945
       Opisthoporodesmus. silvestri Chamberlin, 1945: 2.
       Very poorly described from a ♀ holotype from Pionierbivak, 4°19'S, 141°55'E,
       Irian Jaya, New Guinea, Papua Province, Indonesia (Chamberlin 1945).

17.   *Opisthoporodesmus simplex* Chamberlin, 1945
       Opisthoporodesmus simplex Chamberlin, 1945: 4.
       Very poorly described from ♀ and juvenile material from near Tjibodas (now
       Cibodas), Java, Indonesia (Chamberlin 1945).

18.   *Retrodesmus dammermani* Chamberlin, 1945
       Retrodesmus dammermani Chamberlin, 1945: 5.
       The type species of *Retrodesmus* Chamberlin, 1945, quite poorly described from
       Tjibodas (now Cibodas), Java, Indonesia (Chamberlin 1945), briefly rede-
       scribed and properly illustrated below.

19.   *Solaenaulus birmanicus* Carl, 1941
       Solaenaulus butteli, ssp. *birmanica* Carl, 1941: 374.
       Solaenaulus butteli – Jeekel 2006: 162.

Solaenaulus birmanicus – Golovatch et al. 2010: 143.

Originally described as *S. butteli*, ssp. *birmanicus* (incorrectly spelled as "*birmanica*"), from Irawadi, Myanmar (Carl 1941). Golovatch et al. (2010) consider it a full species, as opposed to Jeekel (2006) who believed it was only a variety of the type species, thus deserving no taxonomic rank.

20. *Solaenaulus butteli* (Carl, 1922)
    Opisotretus butteli Carl, 1922: 573.
    Solaenaulus butteli – Attems 1940: 172; Carl 1941: 374; Jeekel 2006: 61; Golovatch et al. 2010: 140.

    The type species of *Solaenaulus* Attems, 1940, which Attems (1940) erected, based on certain gonopod traits alone. Originally described as *Opisotretus butteli* Carl, 1922, from Sumatra, Indonesia (Carl 1922), since then recorded in Christmas Island, Indian Ocean, Australia (Jeekel 2006) and redescribed in due detail from material from Lae, Morobe Province, Papua New Guinea (Golovatch et al. 2010). Apparently, introduced to both latter localities.

In addition, unidentified Opisotretidae, provisionally referred to as ?*Crypholophus* sp. or *Martensodesmus* sp., respectively, occur also in Taiwan (Golovatch et al. 2011a) and southern Vietnam (Golovatch et al. 2011b).

As one can see from the above list, several species have been described too poorly to realistically become recognized. This holds especially true of what Chamberlin (1945) described in *Opisthoporodesmus*, making the compilation of even a superficial key to *Opisthoporodesmus* species impossible. The few he described from ♂ material must be revised, whereas the identities of the species which were based on ♀ and/or juvenile samples are bound to remain enigmatic until ♂ topotypes have been obtained and properly described. Since the main objective of the present paper is to address the generic classification of Opisotretidae in order to identify and name a number of fresh samples ranging from continental southern China, through Indochina and Indonesia, to Papua New Guinea, only *Retrodesmus dammermani*, fortunately an intact ♂ holotype, has been revised here.

Abbreviations used

AMNH   American Museum of Natural History, New York, U.S.A.
IZAS   Institute of Zoology, Academia Sinica, Beijing, China
MNHN   Muséum national d'Histoire naturelle, Paris, France
MZB   Museum Zoologicum Bogoriense, Cibinong, Indonesia
NMNHS   National Museum of Natural History, Sofia, Bulgaria
SCAU   South China Agricultural University, Guangzhou, China
SEM   Scanning electron microscopy
ZMUC   National Museum of Natural History, Copenhagen, Denmark
ZMUM   Zoological Museum, State University of Moscow, Moscow, Russia

Material and methods

The bulk of the material treated below was taken by Louis Deharveng and Anne Bedos (MNHN) in Indonesia and China, as well as nearly entirely by Petar Beron (NMNHS) in Papua New Guinea. A few samples derive from ZMUM. The holotype of *Retrodesmus dammermani* was received on loan from AMNH. The holotypes from Indonesia have been housed in MZB, those from China in the collection of IZAS, whereas a few paratypes from China have been deposited in SCAU. Much of the material has been kept at MNHN, a few duplicates have also been donated to ZMUC and NMNHS, as indicated below.

SEM micrographs were taken using a JEOL JSM-6480LV scanning electron microscope.

After examination, SEM material was removed from stubs and returned to alcohol, all such samples from Papua New Guinea being kept in NMNHS, from the remaining places in MNHN.

The main characters used in the classification of Opisotretidae

The following characters have been used for defining the genera in Opisotretidae, the only family in the entire order Polydesmida in which the gonopods are directed dorsolaterad, curving very strongly around coxae 8 along the sides of segment 7:

Number of body segments.

Like in most other families in Polydesmida, the number varies from 19 to 20, mostly being sex-characteristic. Thus, in *Carlotretus setosus, Corypholophus minutus* and *Opisotretus kraepelini*, the type species of their respective genera, the ♂ has 19 segments, whereas ♀♀ are unknown. Regrettably, Chamberlin (1945) did not care to mention the number of body segments in the ♀♀ of his *Opisotretus mimus* and *O. euthus. Opisthoporodesmus* species, perhaps including also *O. bacillifer* which was described from presumably subadult ♀♀ with 19 segments (Carl 1912), show equally 20 segments in both sexes. All of the remaining genera and species seem to have 19 segments in the ♂ versus 20 segments in the ♀.

Number of rows of setae on body metaterga.

Only two known species show two transverse rows on the metaterga: *Carlotretus setosus* and *Corypholophus ryukyuensis*, as opposed to the other species which clearly have three transverse rows of bacilliform setae, these sometimes being evidently shifted caudad. However, this character appears to be only species-specific, as one of the new species of *Martensodesmus* described below also has only two rows of tergal setae.

These setae are longitudinally ribbed (Figs 5F, 14I, 19L, 22J, 24J, 28B, 30L, 34B, C, 37J, 40B). However, similar setae occur in certain Fuhrmannodesmidae as well. For example, a still unpublished fuhrmannodesmid from Vietnam shows tergal setae of

two types, one claviform (Fig. 42M), the other bacilliform (Fig. 42F), both ribbed the same way. Moreover, some, but not all, species of the genus *Boreviulisoma* Brolemann, 1928, representing the distantly related family Paradoxosomatidae, also have similarly ribbed bacilliform setae (Reboleira and Enghoff 2013).

Metatergal sculpture.

The pattern of metatergal sculture is that typical of the Polydesmidea, i.e. three transverse rows of polygonal bosses, with a more or less deep sulcus separating the first row from the two following ones. Each boss is typically surmounted by a seta sometimes borne on a small knob, the pattern being 3+3 per row (see above). In Opisotretidae, only few species show very distinct bosses, like those observed in *Solaenaulus butteli* (Figs 4, 5) or *Opisotretus beroni* sp. n. (Figs 17A–F), whereas in most species the bosses tend to be poorly visible to virtually untraceable (Figs 24A–F), whereas the transverse sulcus is largely superficial.

Location of ozopores.

The location of ozopores is often quite peculiar in species of Opisotretidae. The pore formula always being normal, 5, 7, 9, 10, 12, 13, 15-18(19), the ozopores are normally placed near the caudolateral corner of paraterga, very to quite close to the caudal margin of the tergite (Figs 1A, 5B, G, 8A, B, 11A, B, 14B, G, K, 17C, L, 22C, E, M, 24B, C, K, 26B, C, 30B, C, E, F, K, 31B, 33B, C, F, 34B, 36, 37B, E, F, 39B–E, 40B). Chamberlin (1945) paid special attention to this character when assigning his species to either *Opisotretus* or *Opisthoporodesmus*, or *Retrodesmus*. In particular, he tended to treat all species with ozopores placed especially close to the caudal metatergal margin in *Opisotretus*, apparently following Attems (1907), whereas the species with the ozopores slightly more strongly removed forward from the caudal margin he placed in *Opisthoporodesmus*. In the type species of *Retrodesmus*, the ozopore is well removed from the caudal corner of paraterga, lying closer to their lateral margin, but in a new congener described below the ozopores lie just at the caudal margin, this being more typical of the family.

However, this feature must be admitted as not being unique to and characteristic of some Opisotretidae alone. Thus, many species of Fuhrmannodesmidae possess ozopores which also flush open at the caudolateral corner of poriferous paraterga quite close to very close to the caudal margin, in South America (Golovatch 1994) and Vietnam (Figs 42C, F). In general, this condition strongly depends on the degree of development of paraterga which varies between species, as well as between segments. The more strongly the caudal corner of a paratergum is drawn caudad, this being increasingly marked towards the telson, the closer the ozopore to the caudal margin.

In other words, the distinctions based on ozopore location are species-specific at most and clearly fail to characterize opisotretid genera.

Shape of paraterga.

Variation in the degree of development of paraterga is great, ranging from very poorly developed, e.g. in *Solaenaulus butteli* (Figs 4, 5), to very broad and upturned, e.g. in *Retrodesmus cavernicola* sp. n. (Figs 14A–E, G, H). Paraterga tend to be more strongly developed, up to directed dorsolaterad, only in *Opisthoporodesmus* and *Ret-*

rodesmus species, where the midbody paraterga usually show considerable shoulders anterolaterally and a no less considerable emargination caudally (Figs 11A, B, 12). In the remaining Opisotretidae, however, the paraterga tend to be modest to very modest (Figs 1A, 3E, 8A–C, 33A–F, H, 34A, 37A–F, 39A–E, H, J), especially in ♀♀ and juveniles.

The presence of especially prominent shoulders seems to correlate positively with a shift caudad of the transverse rows of tergal setae. In such species, the frontal row of setae is situated close to the metatergite's midway sulcus, whereas both following rows are considerably shortened in extent, strongly shifted to the caudal margin of the tergite and placed very close to each other (Figs 11A, B).

♂ head modifications.

The ♂ vertex of several Opisotretidae is modified. In particular, *Martensodesmus*, among other things, was first distinguished by ♂ vertigial modifications usually traceable as humps or tubercles above the antennal sockets (Golovatch 1987). Later this feature had to be abandoned as a generic-level character after the discovery of *M. excornis* which lacks any such modifications. Moreover, sexual dimorphism in *M. bicuspidatus* was found to concern not only a complex structure (a fossa with two cusps of filaments) on the ♂ vertex, but also the shape of the collum (Golovatch 1988). ♂ vertigial modifications are also known in *Corypholophus minutus* (a hump with a tuft, Fig. 2A) and two new *Opisotretus* described below.

However, like in the case of ozopore location (see above), similar vertigial modifications in the ♂ concern numerous species of Fuhrmannodesmidae, including those occurring in South America (Golovatch 1994) and Vietnam (Figs 42D, G).

Legs.

Variation in leg length and armament in Opisotretidae is pronounced, ranging from short and stout, sometimes also supplied with special ventral trichomes in the ♂, e.g. in *Solaenaulus butteli* (Fig. 5H), to extremely long and slender, e.g. in *Retrodesmus cavernicola* sp. n. (Figs 15B, 16A), but most species show medium-sized, moderately stout legs which are usually devoid of special trichomes in the ♂ and thus fail to differ much between the sexes. Claw length seems to vary proportionately to leg length (Figs 5H, I, 8C, 15B, 16A, 27K, 28D).

Gonopod structure.

As usual in the systematics of any subgroup of Polydesmida, the gonopods offer most of the characters deemed useful, if not crucial, for the discrimination of genera and species. This fully applies to Opisotretidae as well.

As noted above, the gonopods in Opisotretidae are really unique in obviously having rather small, subglobose, medially fused and nearly fully exposed coxae, these being only very poorly sunken into an unusually small gonocoel. The gonopod aperture is invariably obcordate (Fig. 6B). The coxae support the usual cannulae medially and elongated, sometimes strongly curved telopodites laterally. The telopodites are directed dorsolaterad, curving, often very strongly, around coxae 8 along the sides of segment 7. The seminal groove runs along most of the telopodite's extent to termi-

nate distally either on a special branch or tooth (= solenomere), or flush open on the surface, or debauch inside an accessory seminal chamber which normally is supplied with a hairy pulvillus.

Against this general pattern, various species and genera show several important modifications. Species in two of the genera are recognized for the presence of a very peculiar frontobasal process placed on the ventral side of the femorite: in *Crypholophus minutus*, this process (**p**) is neatly attached to a rather slender, unipartite and suberect gonotelopodite, and it carries an additional groove (Fig. 2B), whereas **p** in *Solaenaulus* is devoid of a groove, being well separated from a strongly unciform, bipartite telopodite beset with bacilliform structures distally (Figs 6A, C–F, 7). Because *Crypholophus ryukyuensis* has no process **p** (Fig. 3), its generic assignment has been questioned (Golovatch 1987). However, since a well-developed **p** also occurs in a new species of *Martensodesmus* described below, this character must be regarded as being only species-specific. This clearly supports maintaining *Crypholophus ryukyuensis* in *Crypholophus*, even though *C. minutus* has a **p** (Fig. 2B).

Carlotretus seems to be the only genus in Opisotretidae in which the distal part of a unipartite gonotelopodite is totally free from fringes or bacilli, including a long, erect and simple solenomere (**sl**) (Figs 1B, C, 40D–H, 41). *Solaenaulus*, in addition to **p**, also shows a prominent solenomere (**sl**) attached closely to a similarly long exomere (**ex**), both the branches being curved and abundantly ornamented with bacilli (Figs 6, 7). In all other opisotretid genera and species, the solenomere is a rather small denticle or lobule at most. The gonopods of *Opisotretus*, of *O. kraepelini* at least (Fig. 8D), look very similar to those of *Solaenaulus*, especially as regards the unciform appearance and the distal ornamentation of the telopodite, but the latter in *Opisotretus* is unipartite, sometimes being also devoid even of a vestigial solenomere (Figs 26F, G). *Opisthoporodesmus*, at least *O. obtectus*, *Martensodesmus* and *Retrodesmus* share the gonopod telopodite being rather short, poorly curved and, in the former two genera, modestly ornamented distally. The gonotelopodite in *Martensodesmus* species is often more or less hollow or flattened on the caudal face and carries considerable lobes or processes, sometimes including **p**. In *Opisthoporodesmus obtectus*, the gonopod telopodite (Fig. 11C) is very simple, attenuating distad and virtually fully devoid of a trichome other than the one on a subterminal hairy pulvillus. In contrast, *Retrodesmus* has an enlarged, bifid and elaborate tip of the gonotelopodite, one of its apical branches being beset with bacilliform ornamentations, but showing neither a solenomere nor an accessory seminal chamber, nor a hairy pulvillus.

Vulva.

No special studies have been conducted on the conformation of the vulva in Opisotretidae. Only Chamberlin (1945) depicted the vulva of *Opisthoporodesmus silvestri* as showing a remarkable subelliptic lobe. The epigynal crest has never been described either. Because these structures are too small and inconspicuous in the samples we have examined, they have been omitted from the descriptions.

Generic reclassification

Based on the above information, as well as facing the need to properly allocate several new species described below, we propose the following new classification of Opisotretidae.

Family Opisotretidae Hoffman, 1980
http://species-id.net/wiki/Opisotretidae

Opisotretidae Hoffman, 1980: 176, 188.
Opisotretidae – Hoffman 1982: 722; Simonsen 1990: 53, 82.

Diagnosis. A family of the suborder Polydesmidea with 19 (♂) or 20 (♂, ♀) segments. Body small to very small (3–16 mm long). Tegument microalveolate, limbus microspiculate. ♂ head with or without vertigial modifications. Antennae geniculate between segments 5 and 6, antennomeres 5 and 6 each with a compact group of bacilliform sensilla distodorsally. Metaterga with 2 or 3 regular, transverse rows of bacilliform, longitudinally ribbed setae sometimes borne on minute knobs; frontal margin of midbody paraterga only seldom forming clear-cut shoulders; side margin of paraterga often slightly incised, with 2 or 3 bacilliform setae. Pore formula normal, ozopores flush open dorsally, usually near to very near caudolateral corner of paraterga, only seldom clearly removed from caudal margin. Legs rather short to long, ♂ ones often stouter and longer, sometimes with peculiar, bi- or trifid ventral trichomes, but sphaerotrichomes missing.

Gonopods peculiar in having rather small, subglobose, medially fused coxae nearly fully exposed in a small gonocoel; coxae at most only slightly setose ventrally, supporting usual cannulae medially and elongated, sometimes strongly curved telopodites laterally; the latter directed dorsolaterad, curving, often very strongly, around coxae 8 along sides of segment 7; seminal groove running along most of telopodite on caudal face to terminate distally either on a special branch or tooth (= solenomere), or flush open on caudal surface, or debauching inside an accessory seminal chamber which normally, but not always, is supplied with a hairy pulvillus.

Type genus. *Opisotretus* Attems, 1907.

Remarks. The above somatic features of Opisotretidae are in no way unique to the family, at least sometimes being also encountered, in various combinations, in the other families of the micropolydesmoid superfamily Trichopolydesmoidea, such as Fuhrmannodesmidae, Trichopolydesmidae, Macrosternodesmidae, Mastigonodesmidae and Nearctodesmidae (e.g. Golovatch 1994, 2011). This can also be said about the basically finely microspiculate limbus obviously characteristic of most of the Polydesmidea. It is only the gonopod structure that is truly characteristic of Opisotretidae, the family formally representing a superfamily of its own, the Opisotretoidea (Simonsen 1990). Superficially, female and/or juvenile Opisotretidae are not or only barely distinguishable from the often sympatric or even syntopic female or juvenile Fuhr-

mannodesmidae, the latter family dominating most of the tropical micropolydesmoid faunas. In this connection, we rather believe that Opisotretidae is also a family of Trichopolydesmoidea, probably the closest to Fuhrmannodesmidae (see below).

Genus *Carlotretus* Hoffman, 1980

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

Carlotretus Hoffman, 1980: 176, 188.
Carlotretus – Hoffman 1982: 722.

Diagnosis. A genus of Opisotretidae with 19 (♂) or 20 (♀) body segments. ♂ head without modifications. Metaterga with two regular, transverse rows of bacilliform setae. Frontolateral margin of midbody paraterga devoid of evident shoulders. Ozopore lying close to caudal margin of paratergite's caudolateral corner.

Gonopod telopodite rather stout, unipartite, at best slightly hollow on caudal face; distal part devoid of ornamentations (spines or setae), being a long and simple solenomere (**sl**) supplied with lobes or processes either subtending it or lying at its base. Neither an accessory seminal chamber nor a hairy pulvillus (Figs 1B, C, 38B–E, 40D–H, 41).

Type species. *Opisotretus setosus* Carl, 1922, by original designation of Hoffman (1980).

Remarks. In addition to the type species, this genus includes a new congener described below. The differences are depicted in Fig. 1 and Figs 38, 40, 41, being also mentioned in the diagnosis of *C. triramus* sp. n.

Genus *Corypholophus* Attems, 1938

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

Corypholophus Attems, 1938: 249.
Corypholophus – Attems 1940: 190; Murakami 1975: 108; Hoffman 1980: 176, 188; 1982: 722; Golovatch 1987: 205; Simonsen 1990: 53.

Diagnosis. A genus of Opisotretidae with 19 (♂) or 20 (♀) body segments. ♂ vertex with or without modifications. Metaterga with 2 or 3 regular, transverse rows of bacilliform setae. Frontolateral margin of midbody paraterga devoid of shoulders. Ozopore lying close to caudal margin of paratergite's caudolateral corner.

Gonopod telopodite slender, unipartite, slightly hollow on caudal face only distally; basal frontoventral process (**p**) either present or absent; distal part devoid of ornamentations (spines, bacilli or setae), lobes or prominent processes, at most microdenticulate near both a small accessory seminal chamber and a hairy pulvillus (Figs 2B, 3).

Type species: *Corypholophus minutus* Attems, 1938, by original designation.

Remarks. This genus also includes *C. ryukyuensis* from the Ryukyus, Japan (and Taiwan?). The differences between these two species are depicted in Fig. 2B and Fig. 3.

Genus *Martensodesmus* Golovatch, 1987

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

Martensodesmus Golovatch, 1987: 203.
Martensodesmus – Golovatch 1988: 34; Simonsen 1990: 53.

Diagnosis. A genus of Opisotretidae with 19 (♂) or 20 (♀) body segments. ♂ head often, but not always, with modifications on vertex, collum rarely enlarged. Most of metaterga with 2 (more rarely) or 3 (more usually) regular, transverse rows of bacilliform setae. Frontolateral margin of midbody paraterga usually without evident shoulders, in any event not so strongly developed as to cause a caudad shift of the rows of tergal setae. Ozopore lying from close to, to rather far in front of caudal margin of paratergite's caudolateral corner.

Gonopod telopodite rather stout, at least basal half so, unipartite, usually only faintly curved, slightly, more usually clearly, hollow/excavate/flattened on caudal face all along; parabasal and/or distal parts with lobes or processes, sometimes including **p**; both accessory seminal chamber and hairy pulvillus wanting, but a very short, dentiform solenomere usually ornamented with a few bacilli- or setiform structures nearby often present (Figs 9, 10C, D, 28E–I, 29, 31E–H, 32, 35).

Type species. *Martensodesmus himalayensis* Golovatch, 1987, by original designation.

Remarks. In addition to the type species, the genus currently contains further four Himalayan congeners: *Martensodesmus bicuspidatus* Golovatch, 1988, *M. excornis* Golovatch, 1988, *M. nagarjungicus* Golovatch, 1987 and *M. sherpa* Golovatch, 1987, as well as one new species in Vietnam and two more in southern China. A key to *Martensodesmus* species is given below.

Genus *Opisotretus* Attems, 1907

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

Opisotretus Attems, 1907: 113.
Opisotretus – Attems 1940: 150; Chamberlin 1945: 4; Hoffman 1980: 176, 188; 1982: 722; Simonsen 1990: 53.

Diagnosis. A genus of Opisotretidae with 19 (♂) or 20 (♀) body segments. ♂ vertex with or without modifications. Metaterga with three regular, transverse rows of bacilliform setae. Frontal margin of midbody paraterga devoid of obvious shoulders. Ozopore usually lying close to very close to caudal margin of paratergite's caudolateral corner.
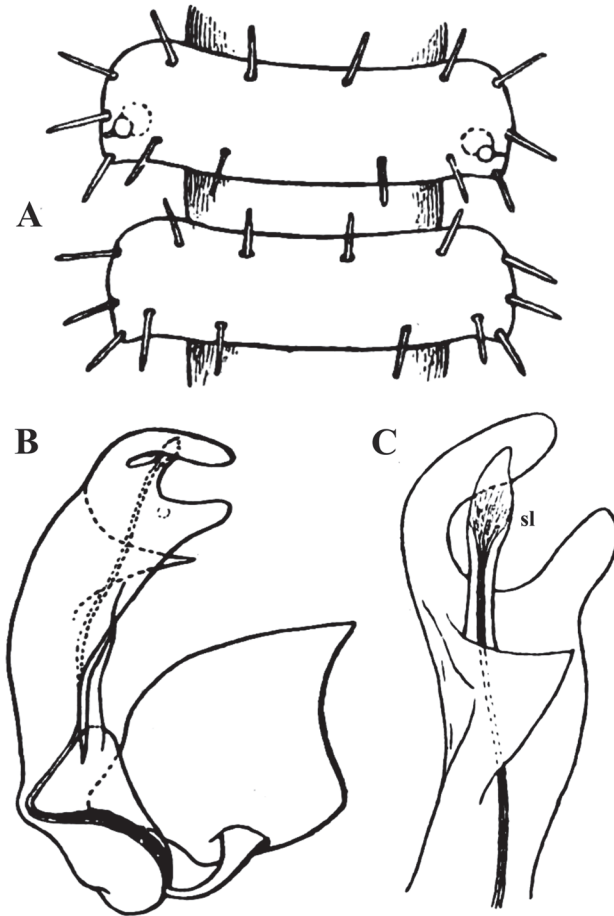
Figure 1. *Carlotretus setosus* Carl, 1922; ♂ holotype from Sumatra, Indonesia; **A** midbody segments, dorsal view **B, C** right gonopod and its apical part, mesal and lateral views, respectively. Depicted not to scale. After Carl (1922).

Gonopod telopodite elongate, unciform, unipartite; distal part beset with ornamentations (small spines, bacilli or setae) and at least with one evident process, either devoid of or supplied with a short solenomere, but with both an evident accessory seminal chamber and a hairy pulvillus (Figs 8D, 18B–D, 20C, D, 21, 23C, D, 25, 26F, G).

Type species. *Opisotretus kraepelini* Attems 1907, by monotypy.

Remarks. In addition to the type species, the genus currently contains two described congeners: *Opisotretus euthus* Chamberlin, 1945 and *O. mimus* Chamberlin, 1945. Because the gonopods of *O. euthus* are indeed very similar to those of *O. kraepelini* as depicted by Chamberlin (1945), the former species is definitely congeneric with the latter one. The identity of *O. mimus*, however, remains uncertain, but superficially it strongly reminds of *Peronorchus parvicollis* Attems, 1907, a species we think belongs in the family Fuhrmannodesmidae. It was originally described from Buitenzorg (= Bogor), Java, Indonesia
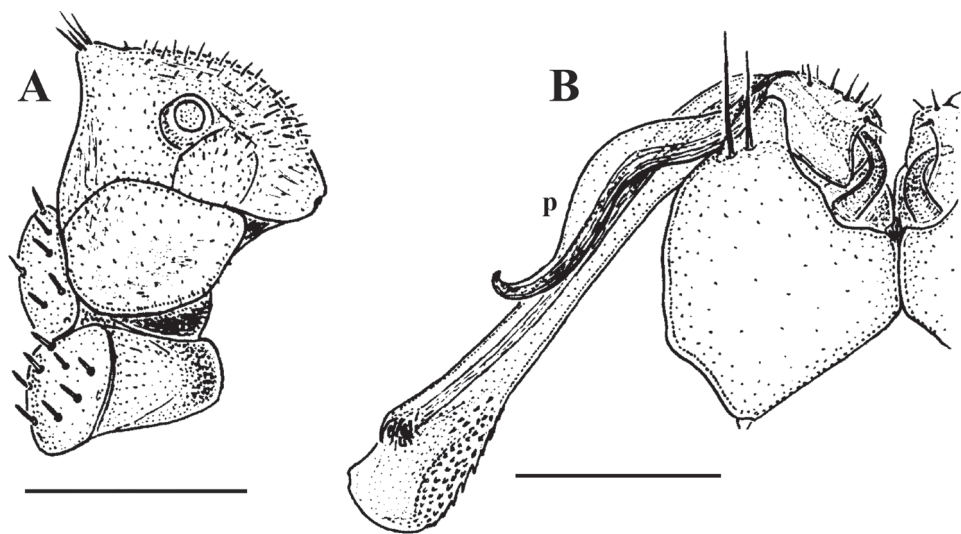
Figure 2. *Corypholophus minutus* Attems, 1938, ♂ from left bank of Ma River, Von Mai, Mai Tiao Distr., Hoa Binh Prov., northern Vietnam; **A** head, lateral view **B** left gonopod, caudal view. – Scale bars: **A** 0.3 mm; **B** 0.1 mm. After Golovatch (1987).
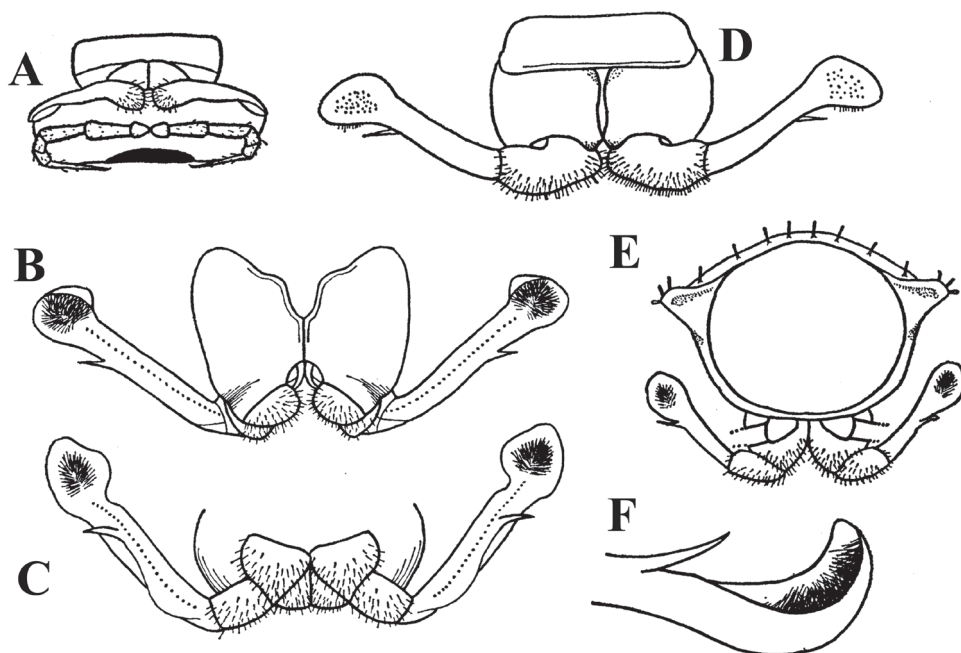

Figure 3. *Corypholophus ryukyuensis* Murakami, 1975, ♂ paratype from Ryukyu Islands, Japan; **A–E** both gonopods *in situ*, ventral, caudal, subcaudal and caudal views, respectively **F** gonopod tip, dorsal view. Depicted not to scale. After Murakami (1975).
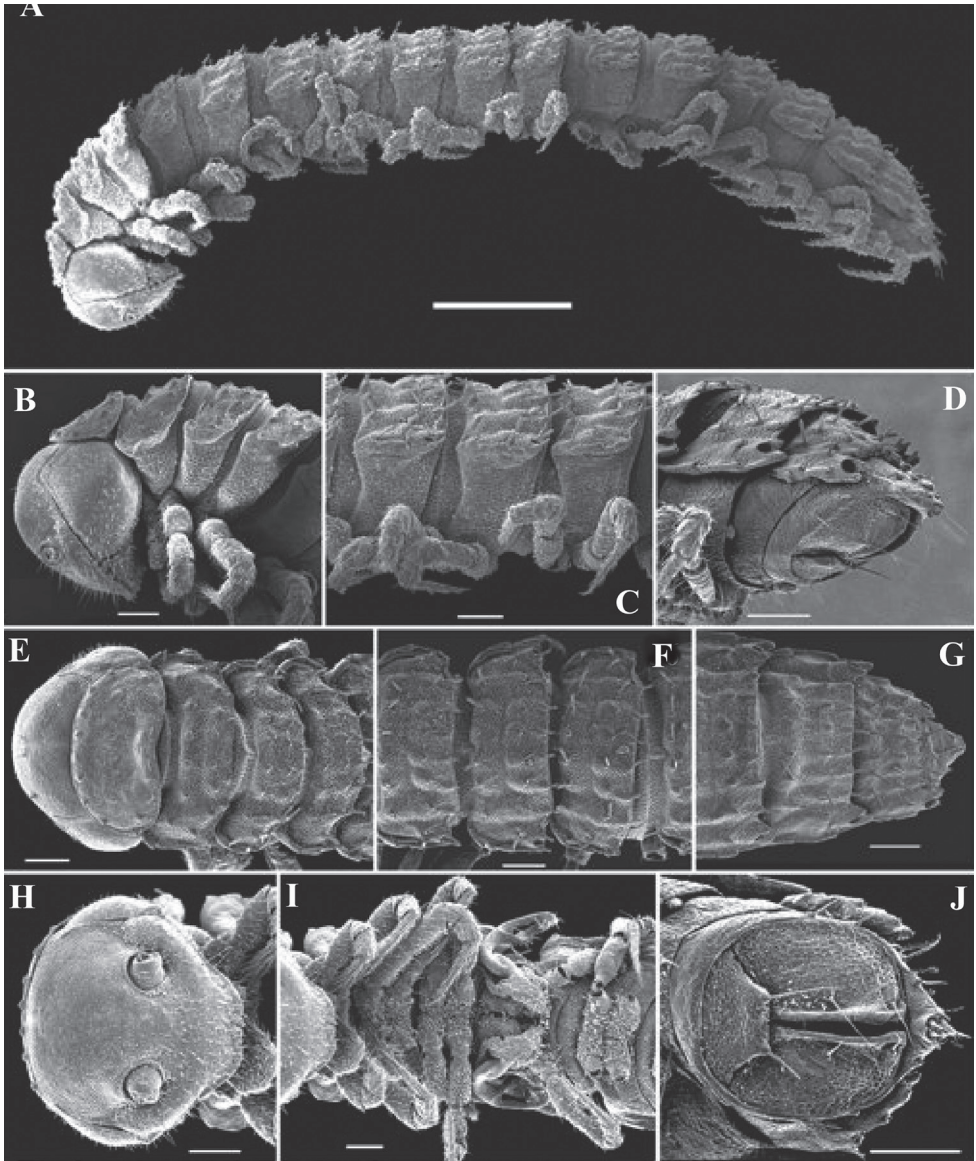
Figure 4. *Solaenaulus butteli* (Carl, 1922), ♂ from Lae, Papua New Guinea; **A** habitus, lateral view **B, E, H** anterior body part, lateral, dorsal and ventral views, respectively **C, F, I** midbody segments, lateral, dorsal and ventral views, respectively **D, G, J** posterior body part, lateral, dorsal and ventral views, respectively. – Scale bars: **A** 0.5 mm; **B–I** 0.1 mm; J, 0.12 mm. After Golovatch et al. (2010).

(Attems 1907) and seems to be very similar to an opisotretid in showing long bacilliform tergal setae arranged in three transverse rows, notably reduced paraterga, and the ozopores located near the paratergite's caudal corner. Interestingly, Mauriès and Geoffroy (1999), when redescribing *P. parvicollis* from material taken on Mauritius, Indian Ocean, assigned
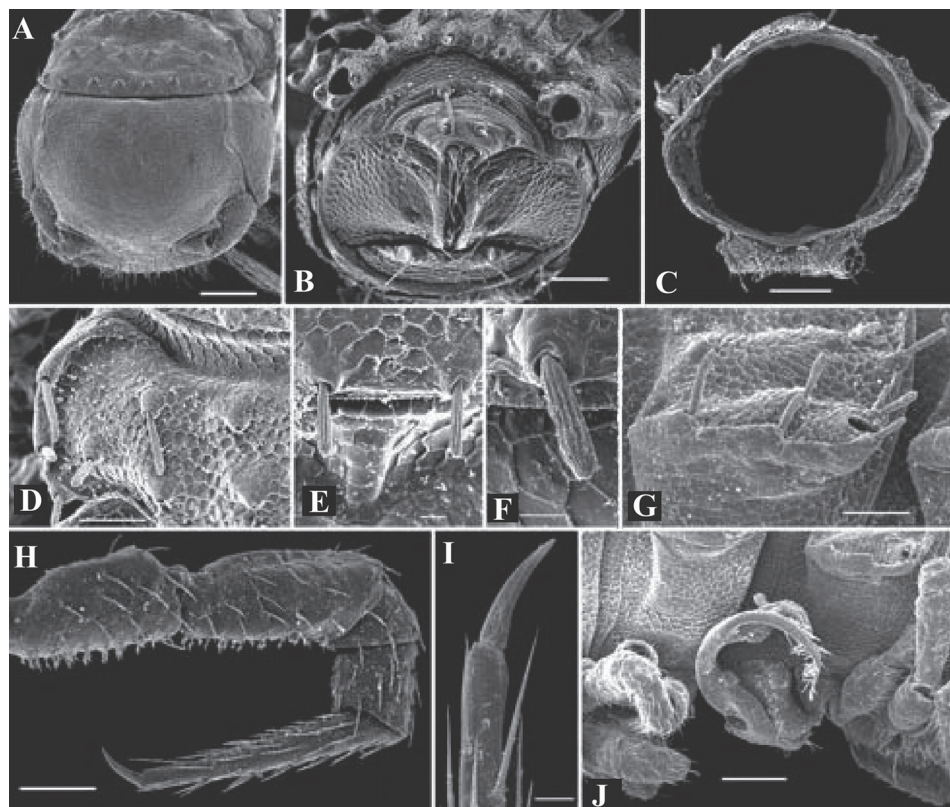
Figure 5. *Solaenaulus butteli* (Carl, 1922), ♂ from Lae, Papua New Guinea **A** head and collum, dorsal view **B** metatergum 18 and telson, caudal view **C** cross-section of a midbody segment, caudal view **D–G** tegument texture and tergal setae, dorsal, dorsal, dorsal and lateral views, respectively **H** midbody leg **I** claw **J** segment 7 with left gonopod *in situ*. – Scale bars: **A, C, J** 0.1 mm; **B, D, G, H** 0.05 mm; **E** 0.02 mm; **F, I** 0.01 mm. After Golovatch et al. (2010).

this genus to the family Trichopolydesmidae, as opposed to Hoffman (1980) who had left *Peronorchu*s among the genera of Polydesmidea of uncertain status and family position.

Four new species described below also belong in *Opisotretus*. A key to all seven *Opisotretus* species, including *O. mimus*, is given below.

Genus *Opisthoporodesmus* Silvestri, 1899
http://species-id.net/wiki/Opisthoporodesmus

Opisthoporodesmus Silvestri, 1899: 206.
Opisthoporodesmus – Attems 1940: 151; Chamberlin 1945: 2-4; Hoffman 1982: 722; Simonsen 1990: 53.

Diagnosis. A genus of Opisotretidae with 20 body segments (♂, ♀). ♂ vertex without modifications. Metaterga with three regular, transverse rows of bacilliform setae,
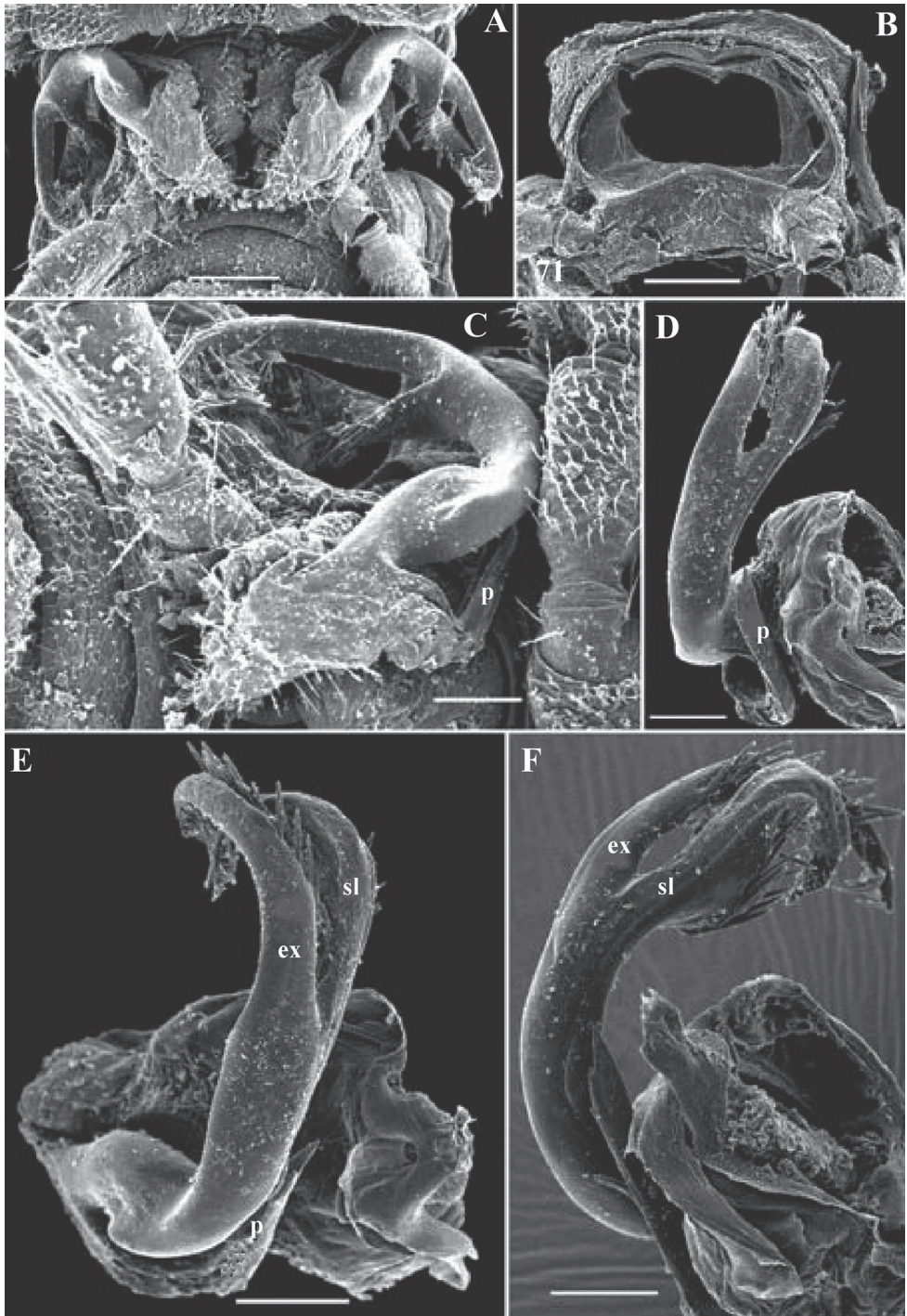
Figure 6. *Solaenaulus butteli* (Carl, 1922), ♂ from Lae, Papua New Guinea **A** both gonopods *in situ*, ventral view **B** gonopod aperture, ventral view **C–F** individual gonopods, subventral, subfrontal, lateral and mesal views, respectively. – Scale bars: **A, B** 0.05 mm; **C–F** 0.01 mm. After Golovatch et al. (2010).
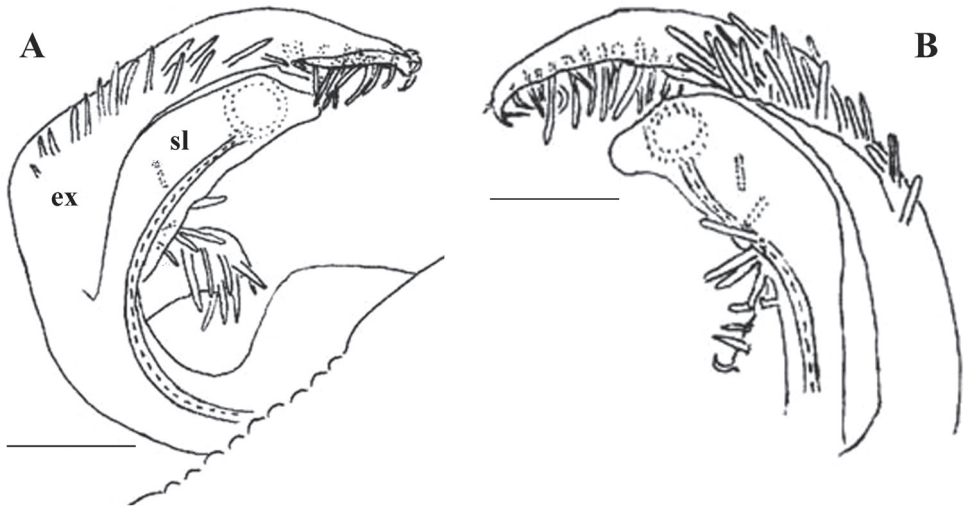
Figure 7. *Solaenaulus butteli* (Carl, 1922), ♂ from Lae, Papua New Guinea; **A, B** left gonopod, lateral and submesal views, respectively. – Scale bars: A, 0.4 mm; B, 0.1 mm. After Golovatch et al. (2010).

but, probably in conjunction with frontolateral margin of midbody paraterga bearing prominent shoulders, at least sometimes all three rows strongly shifted caudad, last two being also abbreviated. Ozopore usually lying close to caudal margin of paratergite's caudolateral corner.

Gonopod telopodite elongate, subunciform, unipartite, markedly attenuating distad; distal part with only a few small outgrowths at best, devoid of both bacilliform ornamentations and a solenomere, but supplied with both a small accessory seminal chamber and a hairy pulvillus (Fig. 11C).

Type species. *Opisthoporodesmus obtectus* Silvestri, 1899, by monotypy.

Remarks. In addition to the type species, the genus currently contains five formal congeners: *Opisthoporodesmus anandrus* Chamberlin, 1945, *O. bacillifer* Carl, 1912, *O. conservandus* Chamberlin, 1945, *O. silvestri* Chamberlin, 1945 and *O. simplex* Chamberlin, 1945. As these five species require revision and their identities remain uncertain, no key to *Opisthoporodesmus* species is possible for the time being.

Genus *Retrodesmus* Chamberlin, 1945
http://species-id.net/wiki/Retrodesmus

Retrodesmus Chamberlin, 1945: 4.
Retrodesmus – Hoffman 1982: 722; Simonsen 1990: 53.

Diagnosis. A genus of Opisotretidae with 19 (♂) or 20 (♀) body segments. ♂ vertex without modifications. Metaterga with three regular, transverse rows of bacilliform setae, but, in conjunction with frontolateral margin of midbody paraterga bearing
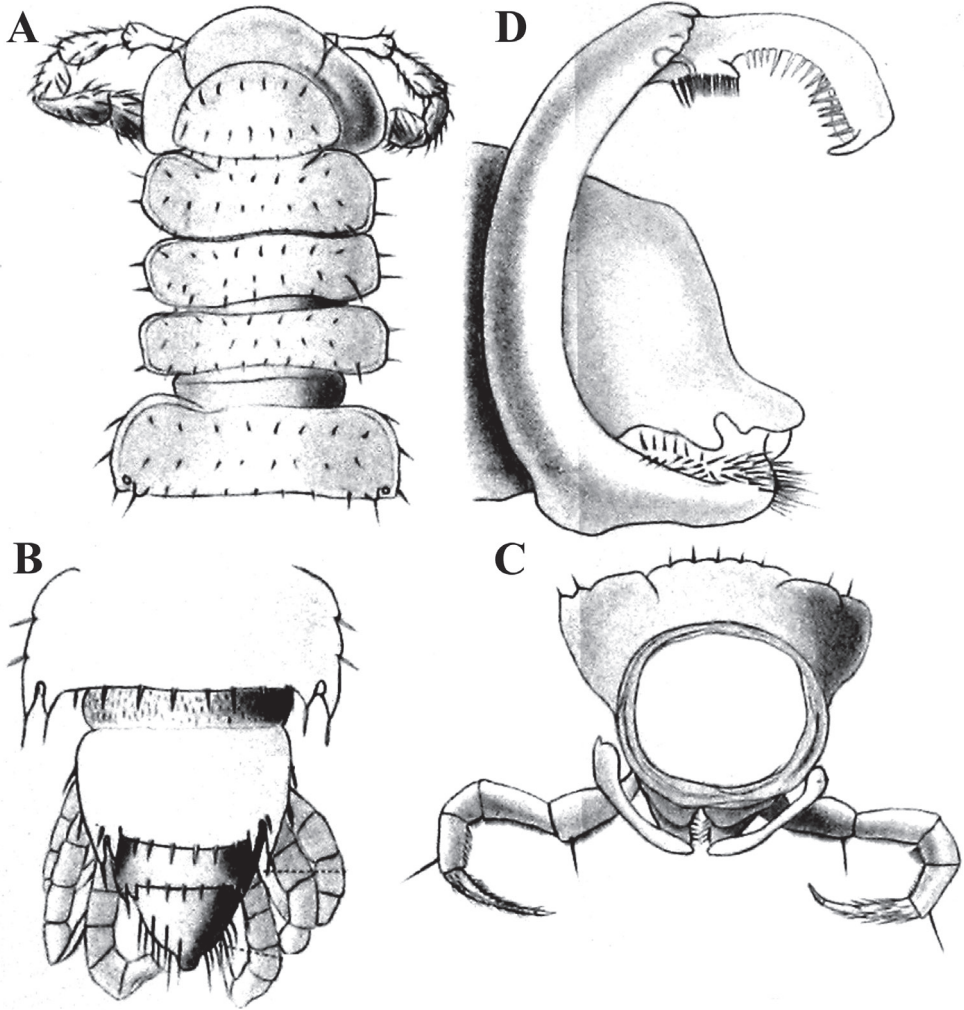
Figure 8. *Opisotretus kraepelini* Attems, 1907, ♂ holotype from Java, Indonesia **A, B** anterior and posterior body parts, respectively **C** cross-section of segment 7, frontal view **D** left gonopod, sublateral view. Depicted not to scale. After Attems (1907).

evident shoulders, all three rows strongly shifted caudad, last two being also abbreviated. Ozopore from well removed from, to very near caudal margin of paratergite's caudolateral incision.

Gonopod telopodite rather stout, only slightly curved, unipartite, divided only distally into a frontal stump heavily beset with bacilliform ornamentions and a simple to complex caudal branch; seminal groove terminating near base of both these branches; neither a solenomere nor a hairy pulvillus (Figs 13B, 15C, D, 16B, C), only sometimes with a visible accessory seminal chamber.

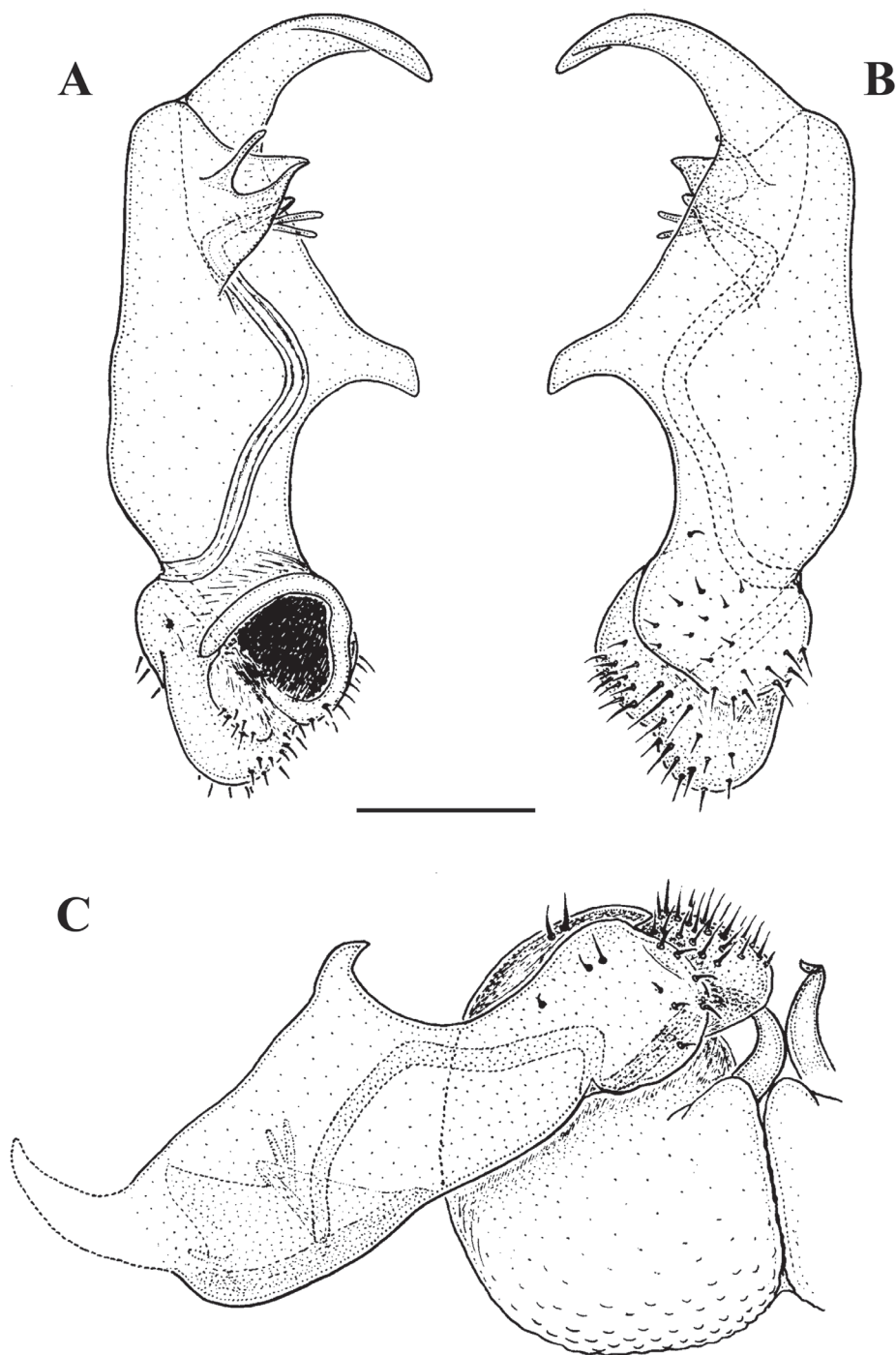**Type species.** *Retrodesmus dammermani* Chamberlin, 1945, by original designation.

Figure 9. *Martensodesmus himalayensis* Golovatch, 1987, ♂ paratype from Nepal; **A, B** right gonopod, subcaudal and subfrontal views, respectively **C** left gonopod, frontal view. – Scale bar: 0.1 mm. After Golovatch (1987).
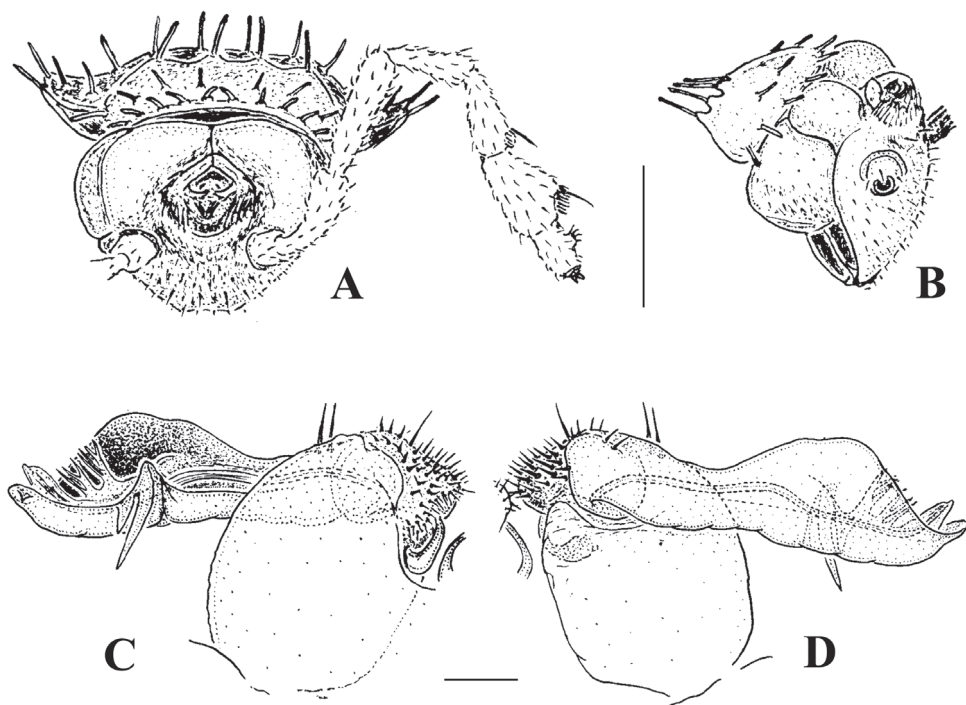
Figure 10. *Martensodesmus bicuspidatus* Golovatch, 1988, ♂ paratype from Bhutan; **A, B** head and collum, frontal and lateral views, respectively **C, D** right gonopod, caudal and frontal views, respectively. – Scale bars: **A, B** 0.5 mm; **C, D** 0.1 mm. After Golovatch (1988).

Remarks. The holotype of this species has been examined in order to shed light on the identity of both the genus and species. A new species is added as well. The differences between both are clear from Figs 12, 13 and Figs 14–16, as well as from the diagnosis of *R. cavernicola* sp. n.

Retrodesmus dammermani Chamberlin, 1945
http://species-id.net/wiki/Retrodesmus_dammermani
Figs 12, 13

Holotype ♂ (AMNH), Java, Tjibodas, 1400 m, Aug. 1921, Dammerman [on label].

Descriptive notes and remarks. The series also contains a microvial with several fragments of a presumed ♀ labeled "♀ allotype", but, having not been mentioned in the original description (Chamberlin 1945), this ♀ cannot be considered as part of the type series.

The holotype, an intact ♂, has been restudied, with several colour pictures taken to show the habitus (Fig. 12), and line drawings executed of a midbody paratergite and the gonopods *in situ* (Fig. 13).
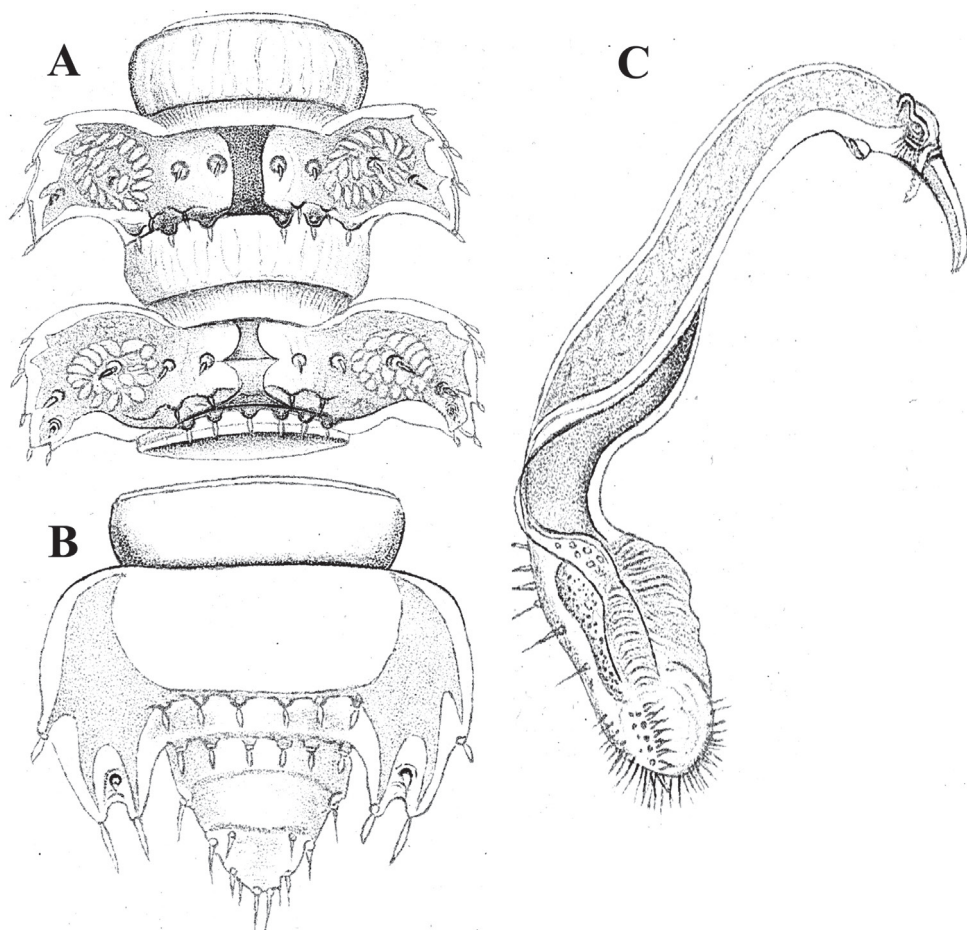
Figure 11. *Opisthoporodesmus obtectus* Silvestri, 1899, ♂ ?holotype from Papua New Guinea; **A** segments 8 and 9, dorsal view **B** posterior body part, dorsal view **C** right gonopod, subcaudal view. Depicted not to scale. After Silvestri (1899).

Chamberlin's (1945) succinct description is basically correct in showing quite broad and mostly slightly upturned paraterga with 2 or 3 minute, lateral, setiferous incisions; the caudal corners of postcollum paraterga until the 17th are produced increasingly well behind the rear tergal margin, roundly dentiform; the metaterga support three rather regular, transverse rows of short to medium-sized bacilliform setae; the ozopores are located rather close to the lateral margin of ozoporiferous paraterga, but quite far from the caudal corner (Fig. 13A). Body length ca 6 mm, width 0.55 mm.

The gonopods (Fig. 13B), contrary to Chamberlin's (1945) sketch (his fig. 20), show only a slightly curved telopodite devoid of a drastic parabasal geniculation. The coxae bear several setae on the ventral side. The telopodite is rather stout,

Figure 12. *Retrodesmus dammermani* Chamberlin, 1945, ♂ holotype from Java, Indonesia; **A–C** habitus, dorsal, lateral and ventral views, respectively.

uniparttite, slightly hollow on the caudal face, only subterminally subdivided into a frontal stump (**s**) beset with bacilliform ornamentations and surmounted by a long spine (**sp**), and a simple, similarly spinigerous branch (**b**). The seminal groove runs along the caudal face to flush open on the surface, with neither a solenomere nor an accessory seminal chamber, nor a hairy pulvillus, terminating near the base of both **s** and **b**.
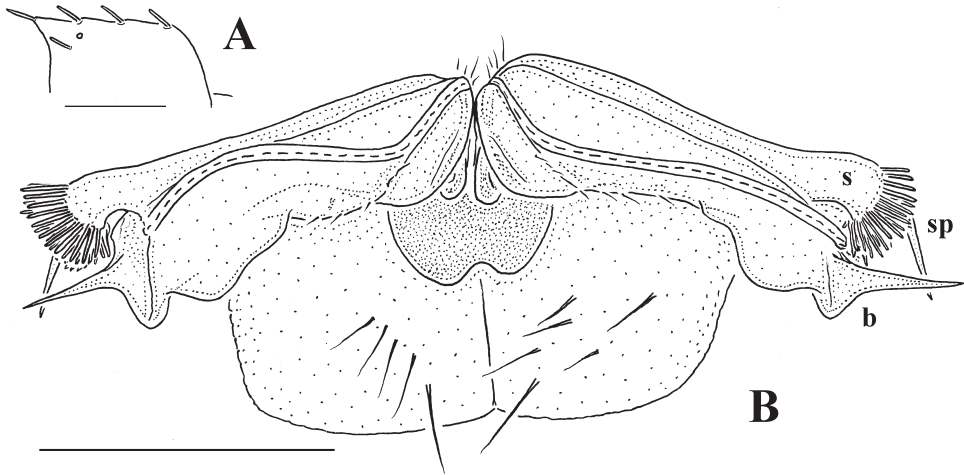
Figure 13. *Retrodesmus dammermani* Chamberlin, 1945, ♂ holotype from Java, Indonesia **A** left paratergite 10, dorsal view **B** both gonopods *in situ*, ventral view. – Scale bars: 0.2 mm.

As Hoffman (2005, p. 75) once put it quite sarcastically as regards the quality of Chamberlin's (1945) paper, "There is no evidence that Professor Chamberlin invested much time in consultation of available literature sources". Nevertheless, his *Retrodesmus* remains a valid genus sufficiently distinct from the other opisotretid genera.

In addition to the type species, *Retrodesmus* also includes *R. cavernicola* sp. n., a presumed troglobite from Papua New Guinea.

Genus *Solaenaulus* Attems, 1940
http://species-id.net/wiki/Solaenaulus

Diagnosis. A genus of Opisotretidae with 19 (♂) or 20 (♀) body segments. ♂ vertex without modifications. Metaterga with three regular, transverse rows of bacilliform setae. Frontolateral margin of midbody paraterga without shoulders. Ozopore usually lying very close to caudal margin of paratergite's caudolateral corner (Figs 4C, D, F, 5B, G).

Gonopod telopodite elongate, subunciform, bipartite; basal process (**p**) on frontoventral face of femorite prominent, removed from femorite proper; distal part of telopodite usually beset with bacilliform ornamentations both over a prominent solenomere (**sl**) and an even more prominent exomere (**ex**); a small accessory seminal chamber present, but a hairy pulvillus absent (Figs 6A, C–F, 7).

Type species. *Opisotretus butteli* Carl, 1922, by original designation of Attems (1940).

Remarks. In addition to the type species, the genus currently contains only one known species: *S. birmanicus* Carl, 1941 (Golovatch et al. 2010), which, however, is sometimes treated as a variety of the type species (Jeekel 2006).

Descriptions of new species

Retrodesmus cavernicola sp. n.

urn:lsid:zoobank.org:act:F9034C5B-EC1B-4AD8-968D-7F77FF1AD0EB
http://species-id.net/wiki/Retrodesmus_cavernicola
Figs 14–16

Type material. Holotype ♂ (NMNHS), Papua New Guinea, Western Prov., Finim tel Plateau, Peep Hole Cave, 18.08.1975, leg. P. Beron (British Speleological Expedition).

Paratypes: 1 ♂, 1 ♀, 1 ♂ (incomplete), 5 juv. (17 segments) (NMNHS), 1 juv. (17 segments) (ZMUC), 1 ♀ subadult (19 segments) (MNHN JC 338), Papua New Guinea, Western Prov., Telefomin, Cave Bem Tem (No. 1), 31.07.1975, leg. British Speleological Expedition; 1 ♀ subadult (19 segments) (ZMUM), 1 ♀ subadult (19 segments) (SEM), 1 juv. (17 segments) (NMNHS), Finim tel Plateau, Upper Bitip Cave, west chamber, 21.11.1975, leg. British Speleological Expedition, FT-11; 1 ♀ (fragments) (NMNHS), Finim tel Plateau, bottom of a 150 m shaft near Girtoil, 08.08.1975, leg. British Speleological Expedition; 1 ♀ (fragments) (NMNHS), Chimbu Prov., Goglme Village, Cave Ogon I, 1975, leg. P. Beron (British Speleological Expedition).

Diagnosis. Differs readily from *R. dammermani* Chamberlin, 1945, the only other known species of *Retrodesmus*, by the particularly broad paraterga, several clearly troglomorphic features such as especially long and slender antennae, legs and metatergal setae, the latter also being very dense, the subcaudal position of the ozopores, and the shape and ornamentation of the gonopod apex.

Name. To emphasize the obvious troglomorphic traits strongly suggesting obligate cave-dwelling; a noun in apposition.

Description. Length of adults of both sexes ca 12 (♂) or 16 mm (♀), width of midbody pro- and metazona 0.95–1.0 and 2.0 mm (holotype and ♂ paratype) or 1.5 and 2.8 mm (♀ paratypes), respectively. Coloration in alcohol from uniformly pallid to light yellowish.

Body with 19 (♂) or 20 (♀) segments. Tegument mainly dull, at most slightly shining, texture very delicately alveolate. Head densely pilose throughout; epicranial suture superficial and thin; isthmus between antennae about twice the diameter of antennal socket. Antennae very long and slender, reaching behind segment 2 when stretched dorsally, geniculate between antennomeres 5 and 6, each latter with an apicodorsal group of tiny sensilla; antennomere 7 with a tiny mid-dorsal knob; antennomeres 2-6 subequal in length (Fig. 15A).

In width, collum << head < segment 2 < 3 = 4 < 5(6)=15 (♂, ♀), thereafter body gradually tapering towards telson. Paraterga very strongly developed, starting from collum, invariably slightly to clearly upturned, set high, but always lying slightly below a faintly convex dorsum, with shoulders frontolaterally (Figs 14A–C). Caudal corner of postcollum paraterga invariably spiniform, pointed, extending increasingly behind rear tergal margin. Lateral edge of paraterga with 2 or 3 clear and deep seti-
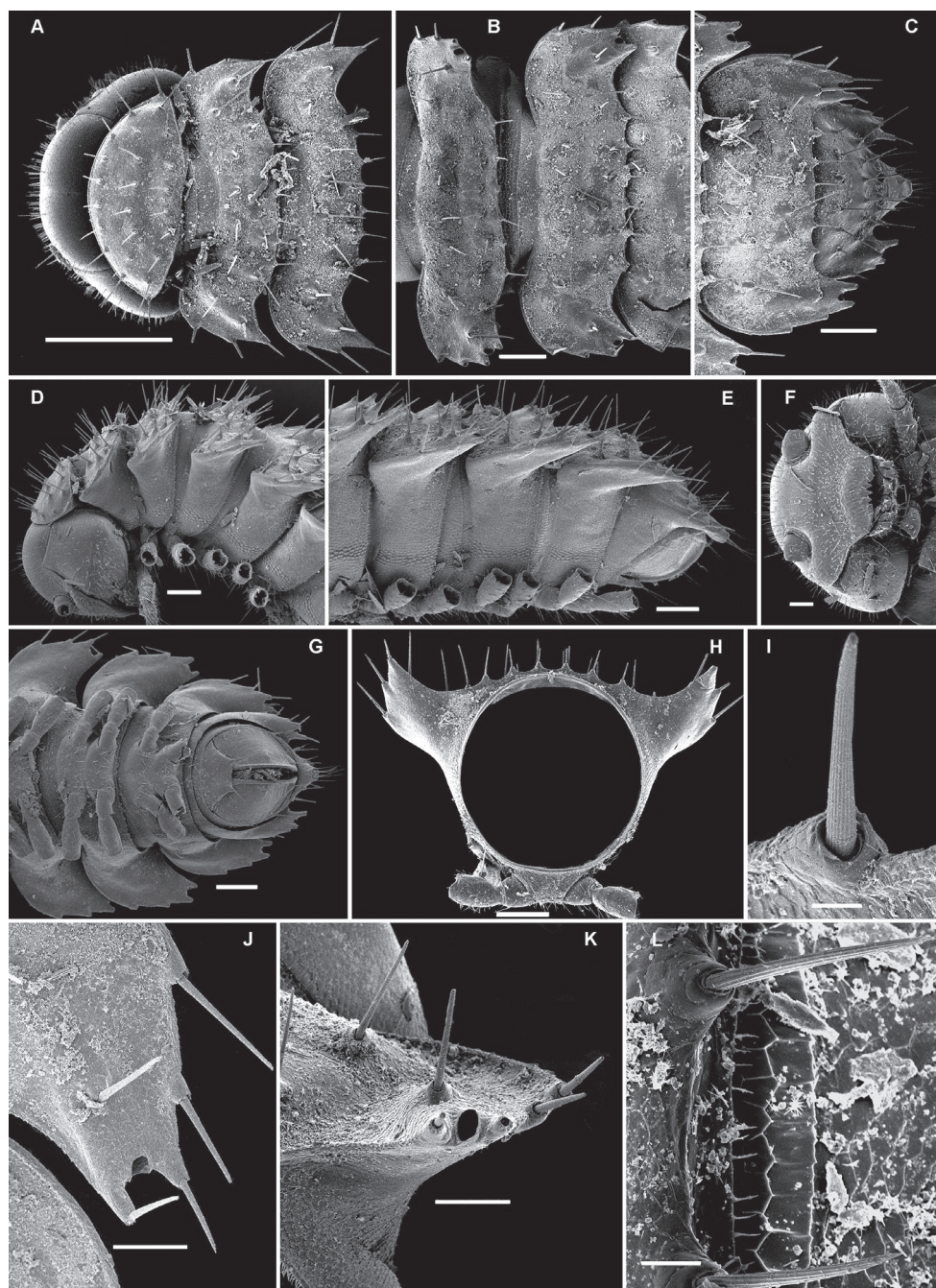
Figure 14. *Retrodesmus cavernicola* sp. n., ♀ subadult, paratype; **A, D** anterior body part, dorsal and lateral views, respectively **B** midbody segments, dorsal view **C, E, G** posterior body part, dorsal, lateral and ventral views, respectively **F** head, ventral view **H** cross-section of a midbody segment, caudal view **I** tergal seta **J, K** paratergite 15, dorsal and subcaudal views, respectively **L** limbus, dorsal view. – Scale bars: **A** 0.5 mm; **B–E, G, H** 0.2 mm; **F, J, K** 0.1 mm; **I, L** 0.02 mm.
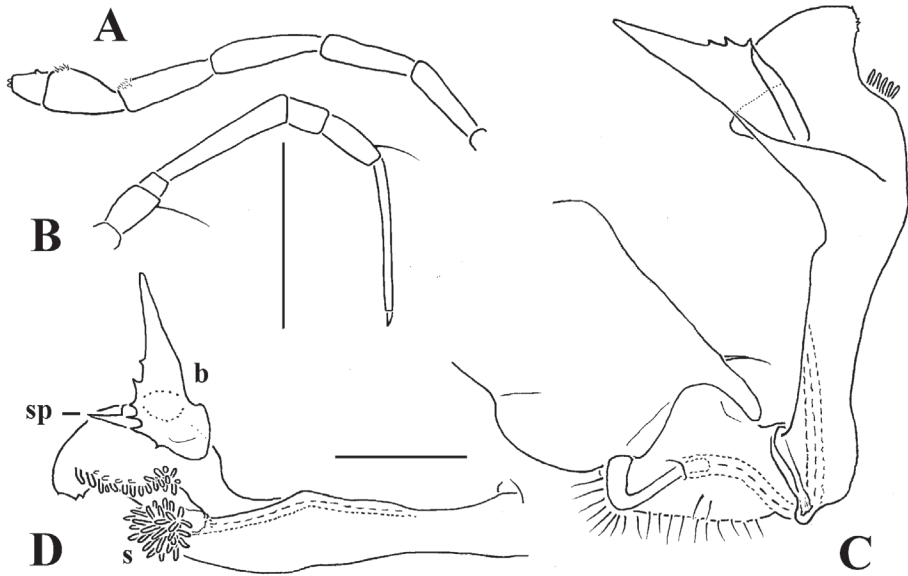
Figure 15. *Retrodesmus cavernicola* sp. n., ♂ paratype from Cave Bem Tem; **A** antenna, lateral view **B** midbody leg **C** left gonopod, submesal view **D** right gonopod, subfrontal view. – Scale bars: **A, B** 1.0 mm; **C, D** 0.2 mm.

gerous indentations in poreless and poriferous segments, respectively. Pore formula normal; ozopores evident, round, flush open on dorsal surface, located very close to caudal margin at bottom of caudalmost lateral incision (Fig. 14J), lateral tooth being considerably shorter than medial one. Collum and each following metatergum with mostly 3+3 long, nearly pointed, but ribbed and subbacilliform setae arranged in three transverse, rather regular rows and borne on small stalks; polygonal bosses very flat; both rear rows of setae more irregular, placed very close to each other (Figs 14A–E, H). Stricture between pro- and metazona wide, shallow and smooth. Limbus very fine, microspiculate, the spikes mostly being rather sparse and irregular. Pleurosternal carinae absent (Figs 14D, E). Epiproct short, conical, directed caudoventrally; pre-apical papillae small (Figs 14C, E, G). Hypoproct trapeziform (Fig. 14G), setiferous papillae at caudal corners very small and well separated.

Sterna without modifications, rather broad, strongly setose (Fig. 14G). Epigynal ridge very low. Legs very long and slender, growing slightly slenderer towards telson (Figs 15B, 16A), ca 1.5 (♂) times as long as midbody height; femora and tarsi longest, subequal in length; sphaerotrichomes missing.

Gonopod aperture evident, transversely oblong-oval, taking up most of ventral part of metazonite 7. Gonopods (Figs 15C, D, 16B, C) with globose, medially fused coxae carrying a few setae on ventral face and a normal cannula mesally. Telopodite nearly straight, unipartite, rather short and stout. Distal part of telopodite split into a shorter frontal stump (**s**) (= solenomere?) beset with bacilliform ornamentations and
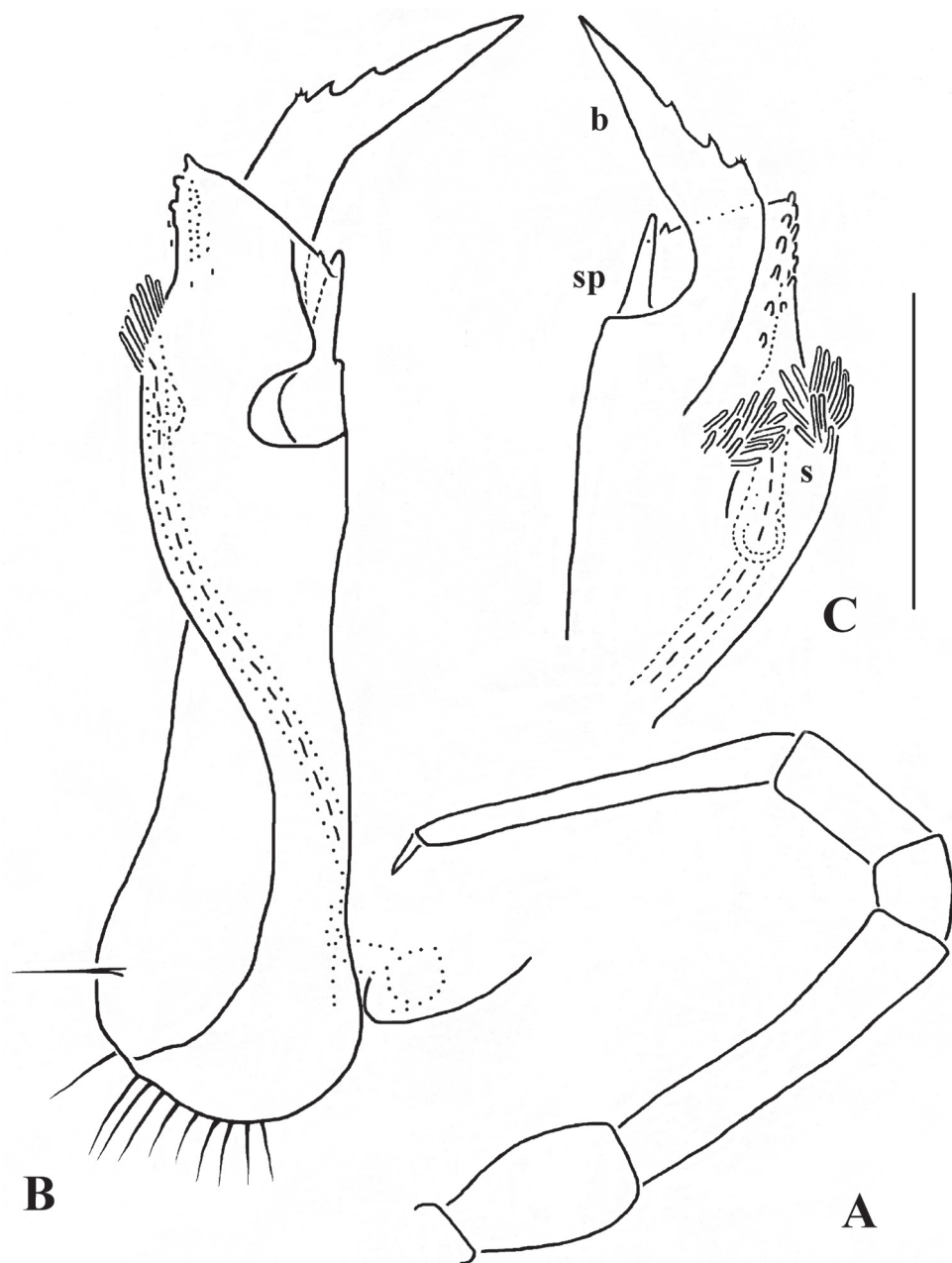
Figure 16. *Retrodesmus cavernicola* sp. n., ♂ holotype; **A** leg 9 **B, C** left gonopod, subdorsal and subventral views, respectively. – Scale bars: **A** 0.5 mm; **B, C** 0.2 mm.

a quite complex, subtriangular, pointed, caudal branch (**b**) with a spine (**sp**) at base. Seminal groove terminating near base of both **s** and **b**, with neither a distinct solenomere nor a hairy pulvillus, but with a small accessory seminal chamber.

Remarks. Because of several apparent troglomorphic traits, this species seems to be a troglobite. Surprisingly, it appears to be rather widespread in western Papua New Guinea, occurring in places like Finim tel and Goglme which are separated from each other by >200 km.

It is the gonopod conformation, not the location of the ozopores, that clearly indicates the true affinities of *R. cavernicola* sp. n. to *R. dammermani*, despite the great geographical gap between Java and New Guinea that also separates these species.

Opisotretus beroni sp. n.

urn:lsid:zoobank.org:act:8B8C4BC4-80C2-4243-916A-057600056EFA
http://species-id.net/wiki/Opisotretus_beroni
Figs 17–21

Type material. Holotype ♂ (NMNHS), Papua New Guinea, Western Prov., Mount Fugilil, at camp, 2980 m a.s.l., 09.10.1975, leg. P. Beron (British Speleological Expedition).

Paratype. 1 ♀ subadult (19 segments) (ZMUC), same locality, together with holotype; 1 ♂, 1 ♀, 1 ♀ subadult (19 segments) (NMNHS), 1 ♂, 1 ♀ (ZMUM), 1 ♂ (SEM), same locality, Mount Fugilil, summit, 3150 m a.s.l., 29.09.1975, leg. P. Beron (British Speleological Expedition); 1 ♂, 1 ♀ (MNHN JC 339), Western Prov., Finim tel Plateau, Selminum doline, 2300 m a.s.l., forest litter, 02.10.1975, leg. Ph. Chapman & P. Beron (British Speleological Expedition); 1 ♀ (NMNHS), Papua New Guinea: Mount Wilhelm, Lake Pinde, 3480 m, 25.10.1975, leg. P. Beron (British Speleological Expedition); 1 ♂, 1 ♀ (NMNHS), 1 ♀ subadult (19 segments) (SEM), same locality, Mount Wilhelm, from 4260 m a.s.l. (14000 feet) to summit (4694 m a.s.l.), 24.10.1975, leg. P. Beron (British Speleological Expedition).

Diagnosis. Differs readily from congeners by the shorter and bifid apical piece of the gonopod telopodite devoid of a spine level to a short solenomere, coupled with a deeper caudalmost incision of paraterga harbouring the ozopore in poriferous segments.

Name. Honours Petar Beron (NMNHS), the principal collector of material.

Description. Length of adults of both sexes ca 10-11 mm, width of midbody pro- and metazona 1.0 and 1.4 mm (holotype), 0.95 and 1.3 mm (♂ paratypes) or 1.1–1.2 and 1.5–1.6 mm (♀ paratypes), respectively. Coloration in alcohol from uniformly pallid to light yellowish.

Body with 19 (♂) or 20 (♀) segments. All characters like in *R. cavernicola* sp. n., except as follows.

Antennae medium-sized, strongly clavate, extending behind segment 2 when stretched dorsally (Figs 17K, 20A).

In width, collum << segment 2 < 3 < head = 4 < 5(6)=15 (♂, ♀), thereafter body gradually tapering towards telson. Paraterga of adults rather strongly developed, considerably smaller and set lower in ♀ subadults (Figs 17J, 19I), starting from collum, mostly subhorizontal to slightly declivous, set high, but always lying slightly below a faintly convex dorsum, with very faint shoulders frontolaterally (Figs
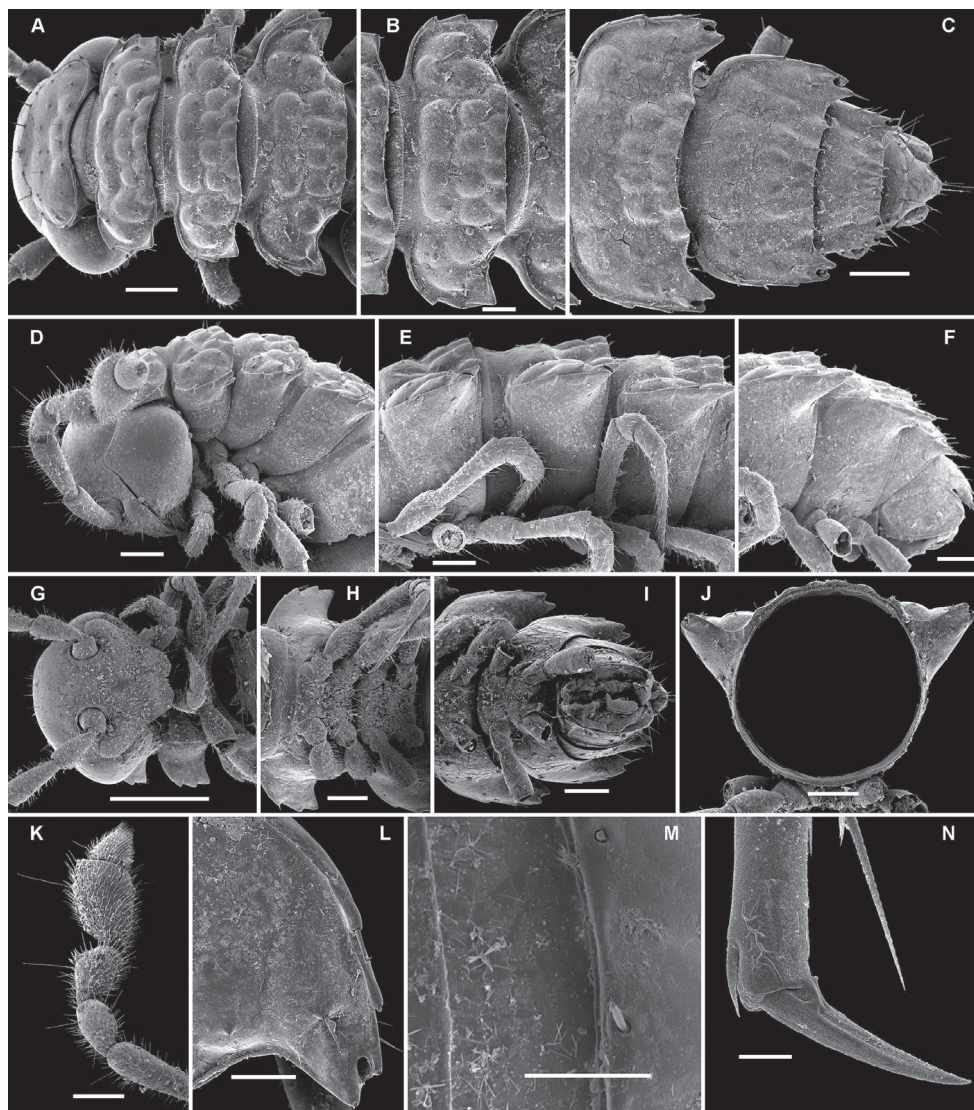
Figure 17. *Opisotretus beroni* sp. n., ♂ paratype from Mount Fugilil (summit); **A, D, G** anterior body part, dorsal, lateral and ventral views, respectively **B, E, H** midbody segments, dorsal, lateral and ventral views, respectively **C, F, I** posterior body part, dorsal, lateral and ventral views, respectively **J** cross-section of a midbody segment **K** antenna, lateral view **L** right paratergite 13, dorsal view **M** tergal setae **N** claw. – Scale bars: **G** 0.5 mm; **A, C–F, H–K** 0.2 mm; **B, L** 0.1 mm; **M** 0.05 mm; **N** 0.01 mm.

17A–C). Caudal corner of postcollum paraterga dentiform, narrowly rounded to nearly pointed, extending increasingly behind rear tergal margin only in a few caudalmost segments. Lateral edge of paraterga with 2 or 3 small setigerous indentations in poreless and poriferous segments, respectively. Ozopores evident, round, flush
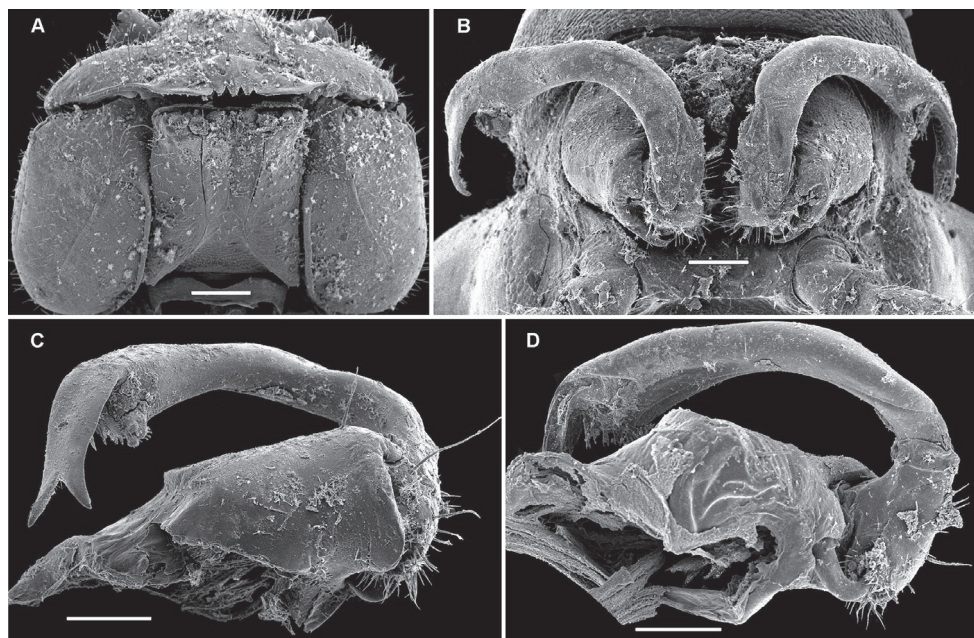
Figure 18. *Opisotretus beroni* sp. n., ♂ paratype from Mount Fugilil (summit); **A** head, ventral view **B** both gonopods *in situ*, ventral view **C, D** left gonopod, sublateral and submesal views, respectively. – Scale bars: 0.01 mm.

open on dorsal surface, located very close to caudal margin at bottom of caudalmost lateral incision (Figs 17C, L), lateral tooth being considerably shorter than medial one. Collum and each following metatergum with 3+3 very short bacilliform setae arranged in three regular transverse rows; polygonal bosses evident, transverse sulcus superficial (Figs 17A–F).

Sterna without modifications, rather broad, strongly setose (Fig. 17H). Epigynal ridge very low. Legs rather long, clearly incrassate in ♂ (Figs 17D–F), ca 1.2–1.3 (♂) or 1.0–1.1 times (♀, juveniles) as long as midbody height; femora and tarsi longest, subequal in length; sphaerotrichomes missing, but ♂ prefemora and femora beset with short spiniform setae ventrally (Fig. 20B).

Gonopod telopodite (Figs 18B–D, 20C, D, 21) only slightly curved, unipartite, rather long and slender; apical piece (**a**) distal to a very short solenomere (**sl**) elongate, more strongly curved, clearly bifid, on caudal face with a few to several denti- or spiniform ornamentations, but devoid of a strong parabasal spine level to **sl**. An accessory seminal chamber at base of **sl** evident, crowned with a hairy pulvillus.

Remarks. The gonopod structure of this new species has already been illustrated by mistake elsewhere (Golovatch et al. 2010, figs 78 & 80), in connection with documenting the record of *Solaenaulus butteli* in Papua New Guinea. The same drawings (Fig. 21) are reproduced here again.

Opisotretus hagen sp. n.

urn:lsid:zoobank.org:act:9CD9B717-7849-4122-B437-ABCF2AC79C48

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

Figs 22, 23

Type material. Holotype ♂ (NMNHS), Papua New Guinea, Western Highlands Prov., Mount Hagen, ca 1990 m a.s.l., in town, 22.10.1975, leg. P. Beron (British Speleological Expedition).

Paratypes. 1 ♀ subadult (19 segments), 1 juv. (fragments) (NMNHS), 1 ♀ subadult (19 segments) (SEM; MNHN JC 340), same locality, together with holotype.

Diagnosis. Differs readily from congeners by a modified ♂ head (two prominent paramedian tubercles above the antennal sockets), coupled with a less strongly curved, nearly suberect gonopod telopodite, with its apical piece crowned with several peculiar, mostly digitiform outgrowths.

Name. Referring to the type locality; a noun in apposition.

Description. Length of holotype (and of subadult ♀ paratypes) ca 9 mm, width of midbody pro- and metazona 0.8 and 1.15 mm, respectively. Coloration in alcohol from uniformly pallid to light yellowish.

Body with 19 (♂) or 20 (♀) segments. All characters like in *R. cavernicola* sp. n., except as follows.

♂ head with two round, paramedian, rather high tubercles (**t**) above antennal sockets (Fig. 23A). Antennae medium-sized, strongly clavate, extending behind segment 2 when stretched dorsally (Figs 22D, 23A).

In width, collum << segment 2 < head = 3 < 4 < 5(6)=15 (♂), thereafter body gradually tapering towards telson. Paraterga rather strongly developed, starting from collum, mostly subhorizontal to slightly declivous, set high, but always lying slightly below a moderately (♀, juv.) to weakly (♂) convex dorsum, with rather faint shoulders frontolaterally (Figs 22A–C). Caudal corner of postcollum paraterga dentiform, always pointed and extending increasingly well behind rear tergal margin. Lateral edge of paraterga with 2 or 3 small setigerous indentations in poreless and poriferous segments, respectively. Ozopores evident, round, flush open on dorsal surface, located very close to caudal margin at bottom of caudalmost lateral incision (Figs 22C, E, M), lateral tooth being very considerably shorter than medial one. Collum and each following metatergum with 3+3 long bacilliform setae arranged in three regular transverse rows; polygonal bosses flat, but visible (Figs 22A–F).

Sterna without modifications, rather broad, strongly setose (Fig. 22H). Legs long, incrassate in ♂ due to prefemora alone (Figs 22N, 23B), ca 1.5 times (♂) as long as midbody height; femora and tarsi longest, subequal in length; sphaerotrichomes or other modified setae missing.

Gonopod telopodite (Figs 23C, D) only very slightly curved, nearly suberect, unipartite, rather long and slender; apical piece (**a**) distal to a very short solenomere (**sl**) rather short, on caudal face with a few finger-shaped ornamentations and a strong,
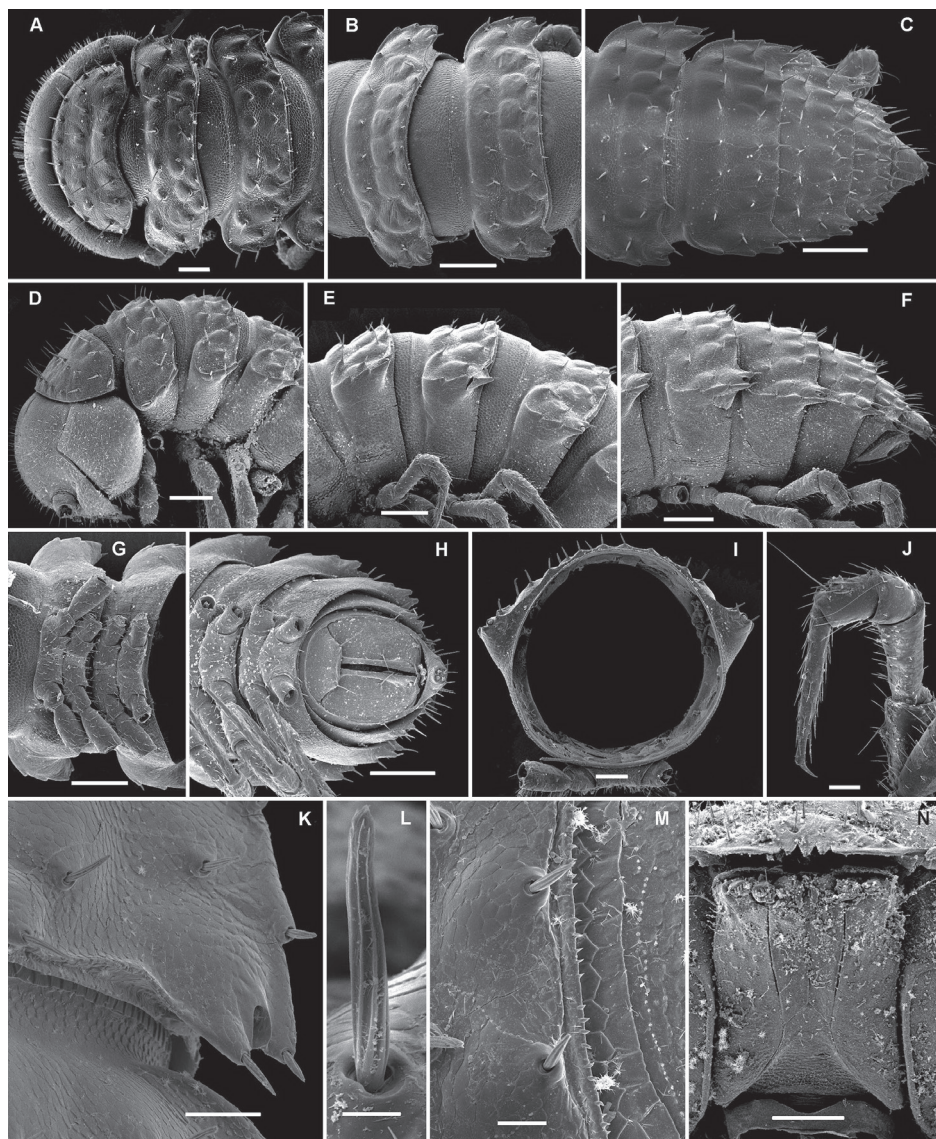
Figure 19. *Opisotretus beroni* sp. n., ♀ subadult, paratype from Mount Fugilil (summit); **A, D** anterior body part, dorsal and lateral views, respectively **B, E, G** midbody segments, dorsal, lateral and ventral views, respectively **C, F, H** posterior body part, dorsal, lateral and ventral views, respectively **I** cross-section of a midbody segment **J** midbody leg **K** right paratergite 13, dorsal view **L, M** tergal setae **N** gnathochilarium, ventral view. – Scale bars: **B–H**,0.2 mm; **A, I, N** 0.1 mm; **J, K** 0.05 mm; **M** 0.02 mm; **L** 0.01 mm.

parabasal, subspiniform process (**pr**). An accessory seminal chamber at base of **sl** evident, crowned with a hairy pulvillus.

Remarks. This is the first *Opisotretus* showing ♂ head modifications, thus confirming the character as being only species-specific (Golovatch 1988).
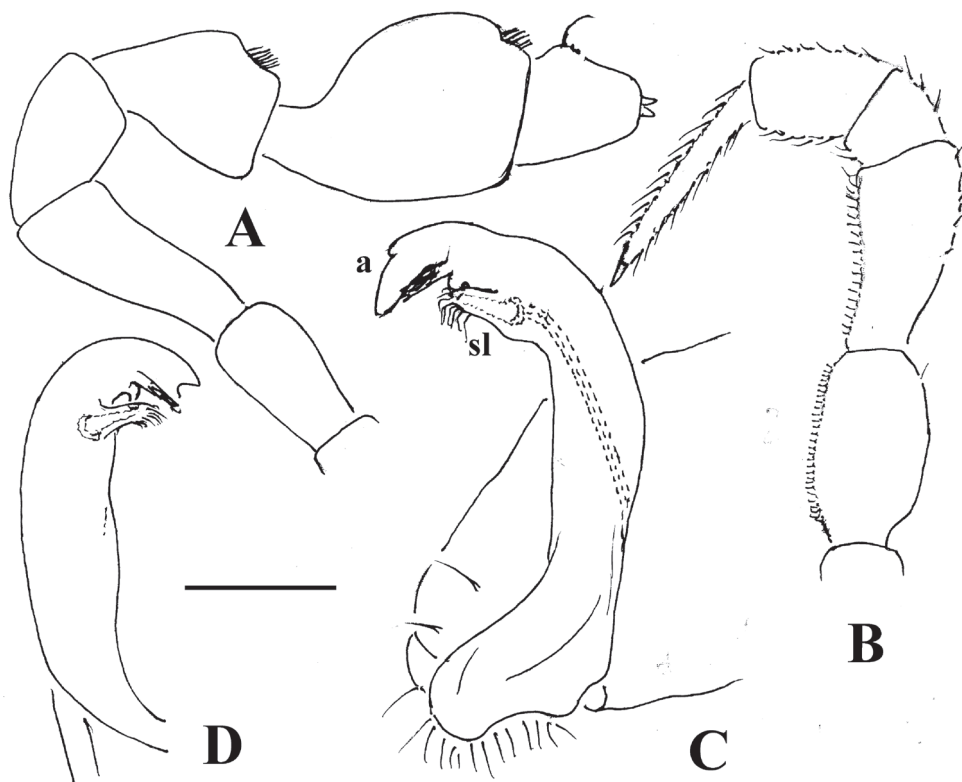
Figure 20. *Opisotretus beroni* sp. n., ♂ paratype from Mount Fugilil (summit); **A** antenna, lateral view **B** midbody leg **C, D** left gonopod, sublateral and submesal views, respectively. – Scale bar: 0.2 mm.

Opisotretus deharvengi sp. n.

urn:lsid:zoobank.org:act:3BE21451-287B-47B4-BE42-0CBB5FC8AB8D
http://species-id.net/wiki/Opisotretus_deharvengi
Figs 24, 25

Type material. Holotype ♂ (MZB), Indonesia, Sulawesi Selatan, Bone (Watampone), Taccipi, Cave Gua Karabice, inside cave, hand collection, 30.07.1989, leg. L. Deharveng (SULS-068).

Paratype. 1 ♀ (SEM; MNHN JC 341), same locality, together with holotype.

Diagnosis. Differs readily from congeners both by tergal sculpture and lateral paratergal incisions being rather poorly developed, coupled with the presence of a short solenomere and a peculiar ornamentation in the apical piece (**a**) of the gonopod telopodite.

Name. Honours Louis Deharveng, the collector.

Description. Length of holotype ca 9 mm, width of midbody pro- and metazona 0.7 and 1.0 mm, respectively. Coloration in alcohol uniformly pallid.

Body with 19 (♂) or 20 (♀) segments. All characters like in *R. cavernicola* sp. n., except as follows.
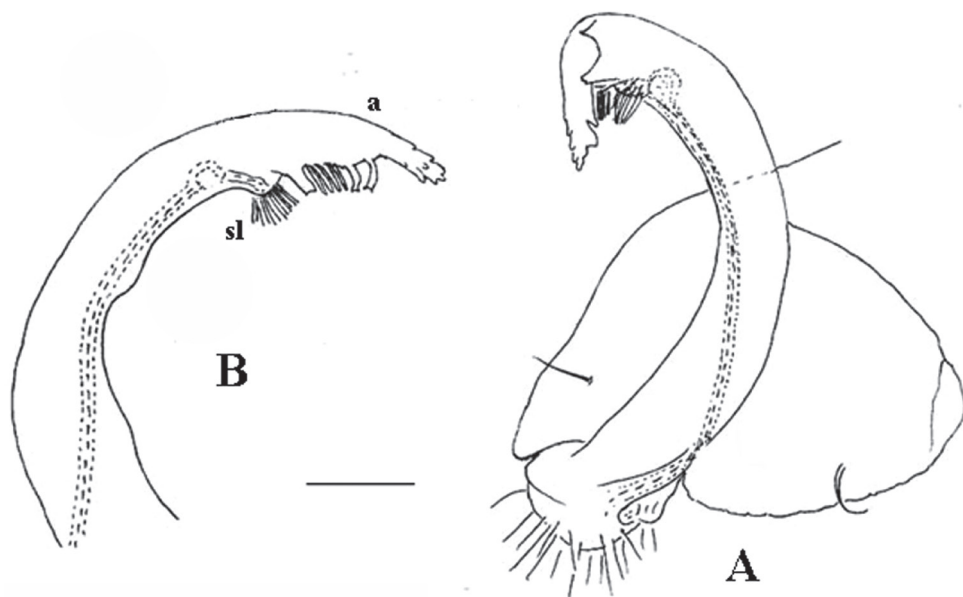
Figure 21. *Opisotretus beroni* sp. n., ♂ paratype from Selminum doline; **A, B** left gonopod, submesal and sublateral views, respectively. – Scale bar: 0.2 mm. After Golovatch et al. (2010).

Antennae broken off, but likely long and slender.

In width, collum << segments 2-4 < 5 < 6=15 < head (♂); after 15th, body gradually tapering towards telson. Paraterga strongly developed, starting from a kidney-shaped collum, mostly subhorizontal, largely set high, almost level to (♂) or only very slightly below a weakly convex dorsum (♀), with faint shoulders frontolaterally (Figs 24A–C). Caudal corner of postcollum paraterga dentiform, always narrowly rounded and extending increasingly well behind rear tergal margin only in segments 16-18(19). Lateral edge of paraterga with 2 or 3 small setigerous indentations in poreless and poriferous segments, respectively. Ozopores evident, round, flush open on dorsal surface, located very close to caudal margin at bottom of caudalmost lateral incision (Fig. 24B, C, I, K), lateral tooth being only slightly shorter than medial one. Collum and each following metatergum with 3+3 long bacilliform setae arranged in three regular transverse rows; polygonal bosses flat, but visible (Figs 24A–F).

Legs long and very slender (Fig. 24M), ca 2.0-2.1 (♂) or 1.5-1.6 times (♀) as long as midbody height; ♂ prefemora not incrassate, femora and tarsi longest, subequal in length, but tarsi especially slender; sphaerotrichomes or other modified setae missing.

Gonopod telopodite (Fig. 25) clearly curved, unipartite, long and slender; apical piece (**a**) distal to a short solenomere (**sl**) rather long due to a terminal uncus (**u**) bearing near its base a strong subcaudal spine (**sp**) and a short field of subspiniform, mostly curved ornamentations. An accessory seminal chamber at base of **sl** evident, crowned with a hairy pulvillus.

Remarks. This is the first formal encounter of an *Opisotretus* species in Sulawesi, Indonesia. Due to its long legs and uncoloured tegument, *O. deharvengi* sp. n. is

Figure 22. *Opisotretus hagen* sp. n., ♀ subadult, paratype; **A, D, G,** anterior body part, dorsal, lateral and ventral views, respectively **B, E, H** midbody segments, dorsal, lateral and ventral views, respectively **C, F, I** posterior body part, dorsal, lateral and caudal views, respectively **J** tergal seta, lateral view **K** tegument texture, dorsal view **L** limbus, dorsal view **M** midbody paratergite, subcaudal view **N** midbody leg; **O,** claw. – Scale bars: **A, G** 0.2 mm; **B–F, H, I, K, N** 0.1 mm; **M** 0.05 mm; **J, L, O** 0.01 mm.

likely to represent a troglobite. *Opisthoporodesmus bacillifer*, the only other opisotretid known from Sulawesi, differs readily in having only two, not three, lateral incisions on the parterga (Carl 1912).
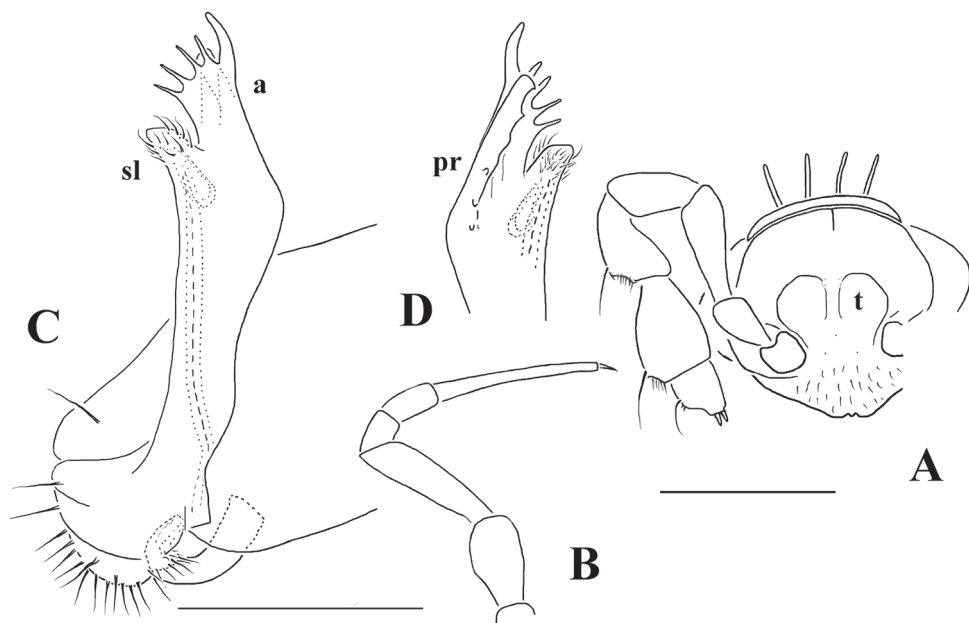
Figure 23. *Opisotretus hagen* sp. n., ♂ holotype; **A** head, frontal view **B** midbody leg **C, D** right gonopod, mesal and lateral views, respectively. – Scale bars: **A** 1.0; **B** 0.5 mm; **C, D** 0.2 mm.

Opisotretus spinosus sp. n.

urn:lsid:zoobank.org:act:155B2375-F1DF-46D8-A194-3FD75766B75D
http://species-id.net/wiki/Opisotretus_spinosus
Fig. 26

Type material. Holotype ♂ (MZB), Indonesia, Java, Jawa Tengah, Cilicap, Nusakambangan Island, near Cave Goa Kali Empat, litter, sieving and Berlese extraction, 19.02.2011, leg. L. Deharveng & Dito (JAVA-NK32).

Paratype. 1 ♀ (MNHN JC 342), same locality, together with holotype.

Diagnosis. Differs readily from congeners by the presence of a clear, bare hump on the ♂ vertex, coupled with the presence both of only a rudimentary solenomere and a peculiar spination of the apical piece (**a**) of the gonopod telopodite.

Name. To emphasize the highly spinose apical piece of the gonopod telopodite.

Description. Length of holotype ca 4 mm, width of midbody pro- and metazona 0.3 and 0.5 mm, respectively. Length of paratype ca 5 mm, width of midbody pro- and metazona 0.45 and 0.6 mm, respectively. Coloration in alcohol uniformly pallid.

Body with 19 (♂) or 20 (♀) segments. All characters like in *R. cavernicola* sp. n., except as follows.

♂ head with an evident, bare, rounded vertigial hump (Fig. 26A, **h**). Antennae broken off, but obviously medium-sized.
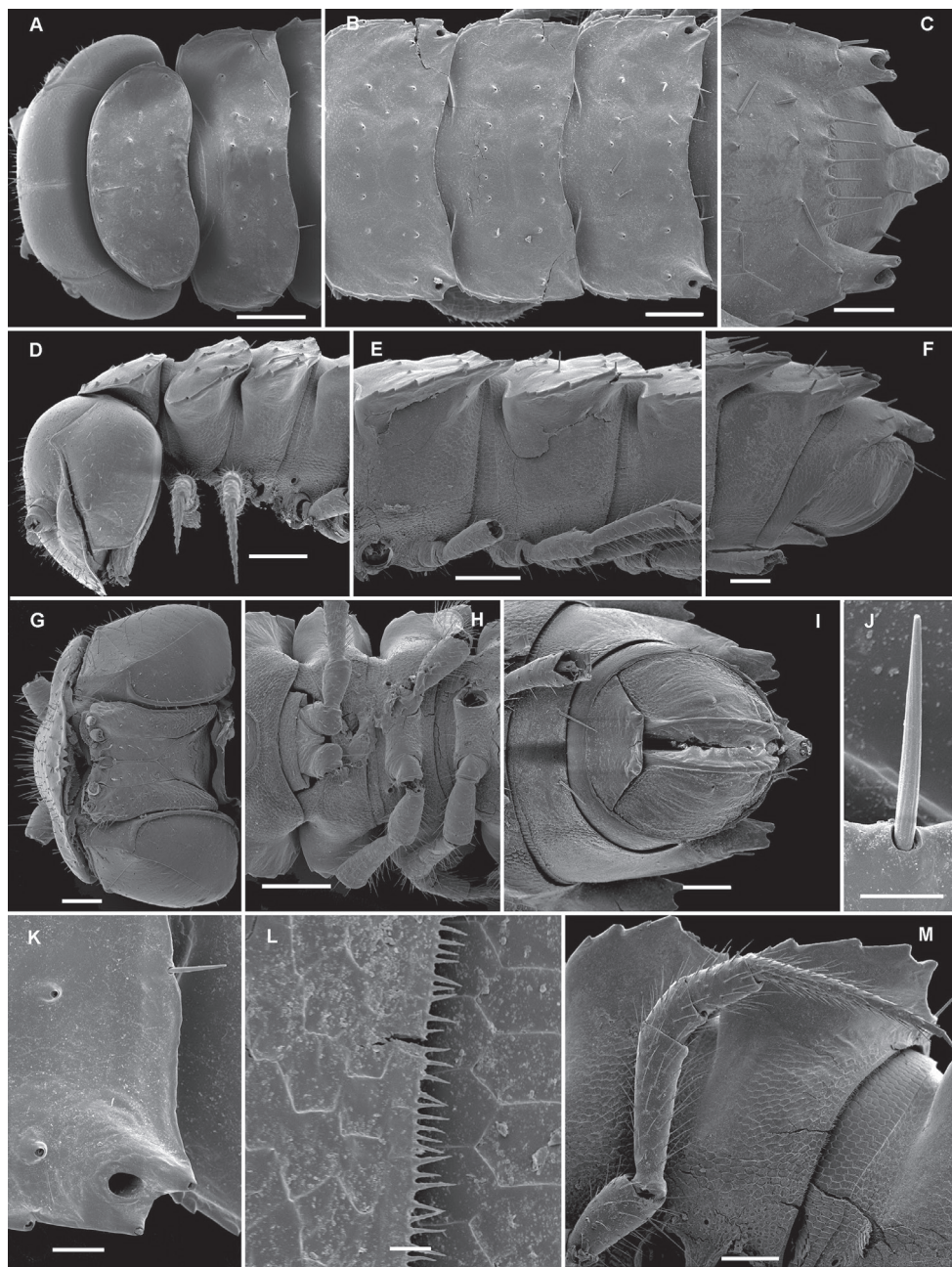
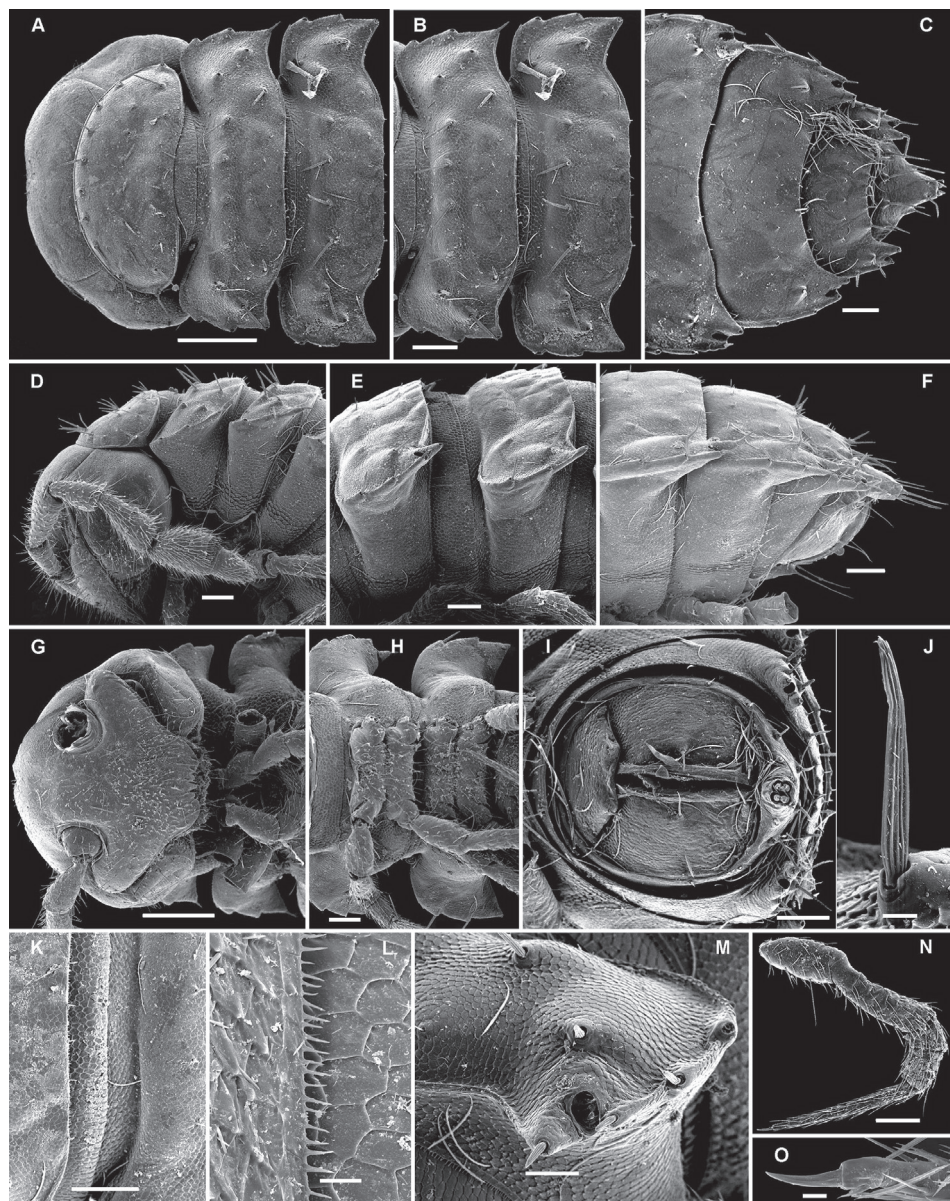**Figure 24.** *Opisotretus deharvengi* sp. n., ♀ paratype; **A, D** anterior body part, dorsal and lateral views, respectively **B, E, H** midbody segments, dorsal, lateral and ventral views, respectively **C, F, I** posterior body part, dorsal, lateral and caudal views, respectively **G** head ventral view **J** tergal seta, lateral view **K** left paratergite 13, dorsal view **L** tegument texture and limbus, dorsal view **M** midbody paratergite and leg *in situ*, ventrolateral view. – Scale bars: **A, B, D, E, H** 0.2 mm; **C, F, G, I, M** 0.1 mm; **K** 0.05 mm; **L** 0.01 mm.
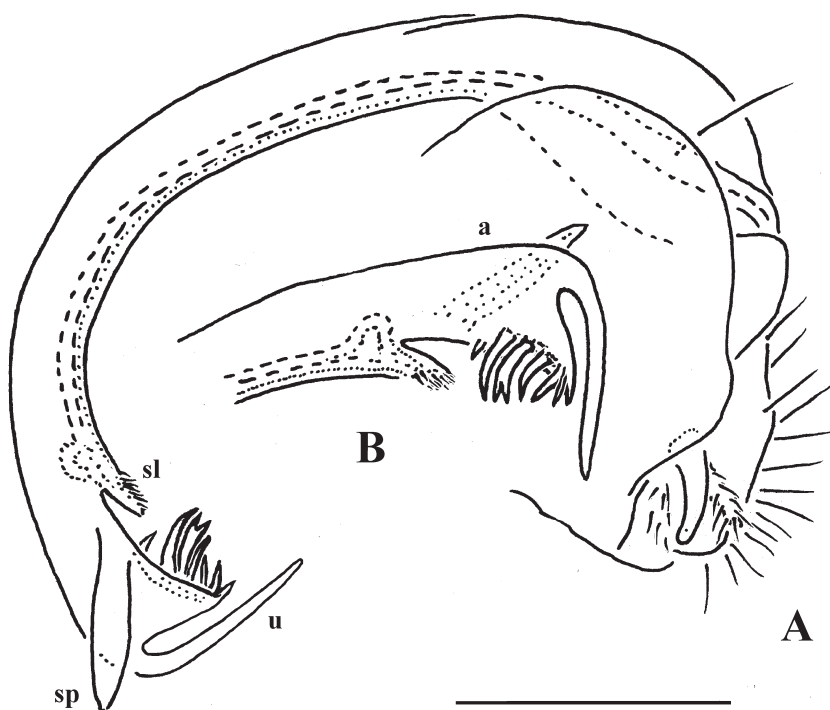
Figure 25. *Opisotretus deharvengi* sp. n., ♂ holotype; **A, B** left gonopod, subventral and subdorsal views, respectively. – Scale bar: 0.1 mm.

In width, collum << segments 2 & 3 < head = 4 ≤ 5 < 6=15 < (♂, ♀); thereafter body gradually tapering towards telson. Paraterga rather poorly developed (Figs 26B, C), starting from a subcordiform, broadly rounded collum, mostly faintly declivous and continuing the outline of a quite convex dorsum (especially so in ♀), largely set rather high, at about ¼ to 1/3 of midbody height, with faint shoulders frontolaterally (Figs 26B, C). Caudal corner of postcollum paraterga dentiform, always narrowly rounded and extending increasingly well behind rear tergal margin in segments 12-18 (♂) or 15-19 (♀). Lateral edge of paraterga with 2-3 or 3-4 small setigerous indentations in poreless and poriferous segments, respectively. Ozopores evident, round, flush open on dorsal surface, lying clearly in front of caudal margin at bottom of caudalmost lateral incision, both lateral and medial teeth being subequal (Figs 26B, C). Collum and each following metatergum with 3+3, rather long, bacilliform setae arranged in three regular transverse rows; polygonal bosses flat, poorly visible. Hypoproct subtrapeziform, as in Fig. 26D.

Legs rather short and stout, ca 1.2-1.3 (♂) or 1.0-1.1 times (♀) as long as midbody height; tarsi longest and particularly slender (Fig. 26E), sphaerotrichomes or other modified setae missing.

Gonopod telopodite (Figs 26F, G) clearly curved, unipartite, long and slender; apical piece (**a**) distal to a vestigial solenomere strongly curved due to a terminal uncus (**u**) bearing near its base a strong subcaudal spine (**sp**) and a field of spiniform orna-
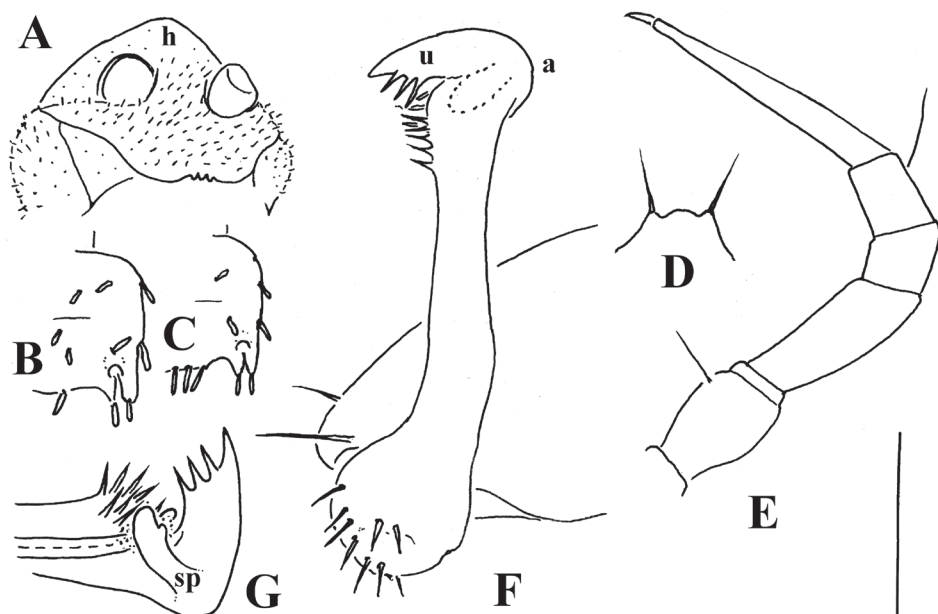
Figure 26. *Opisotretus spinosus* sp. n., ♂ holotype; **A** head, frontolateral view **B, C** right paratergites 15 and 18, respectively, dorsal view **D** hypoproct, ventral view **E** midbody leg **F, G** right gonopod, subventral and subdorsal views, respectively. – Scale bar: **A–C** 0.2 mm; **D, E** 0.1 mm; **F, G** 0.05 mm.

mentations. An accessory seminal chamber at base of solenomere rather evident, but probably devoid of a hairy pulvillus.

Remarks. This new *Opisotretus* species has been taken together with several immature females (18 segments) of a different, somewhat larger and slightly pigmented (reddish metaterga and antennae) opisotretid with somewhat broader paraterga and a different location of the ozopores (these being placed close to the caudal tergal margin) which could not be identified in the absence of adult male material.

Martensodesmus cattienensis sp. n.

urn:lsid:zoobank.org:act:6B037C95-B3CB-4016-80C3-68CFB46E1BF2
http://species-id.net/wiki/Martensodesmus_cattienensis
Figs 27–29

Martensodesmus sp. – Golovatch et al. 2011b: 81.

Type material. Holotype ♂ (MNHN JC 343), Vietnam, Dongnai Prov., Cat Tien National Park, lowland semi-deciduous tropical monsoon forest, ca 150 m a.s.l., 107°10'–107°34'E, 11°21'–11°48'N, 08-22.11.2005, leg. A. E. Anichkin.

Paratypes. 1 ♂, 1 ♀ (MNHN JC 343), 1 ♂, 1 ♀, 1 ♀ fragment (ZMUM), 1 ♂ (ZMUC), same locality, together with holotype; 1 ♂, 1 ♀, 1 ♀ subadult (MNHN JC

343), 1 ♂ , 1 ♀ (SEM), 1 ♂, 1 ♀, 1 ♀ subadult (ZMUM), same locality, 01.06.2005, leg. A. E. Anichkin; 1 ♂ (MNHN JC 343), 1 ♂ (NMNHS) same locality, 15.07.2005, leg. A. E. Anichkin.

Diagnosis. Differs readily from congeners by the missing modifications on the ♂ vertex, coupled with quite well developed shoulders on metaterga, the high and broad paraterga, as well as the presence near the gonopod telopodite's midpoint of three strong spines proximally to a considerably attenuating acropodite.

Name. To emphasize the type locality.

Description. Length of holotype ca 5.5 mm, width of midbody pro- and metazona ca 0.8 and 1.0 mm, respectively. Length of ♂ paratypes ca 5.5–6.0 mm, width of midbody pro- and metazona ca 0.75–0.8 and 1.0–1.1 mm, respectively. Length of ♀ paratypes ca 7.0-8.0 mm, width of midbody pro- and metazona ca 0.9–0.95 and 1.1–1.15 mm, respectively. Coloration in alcohol from nearly uniformly light yellowish to head and several anterior segments slightly infuscate, light yellow-brown, more rarely with a rusty reddish tint.

Body with 19 (♂) or 20 (♀) segments. All characters like in *R. cavernicola* sp. n., except as follows.

Antennae very long, but strongly clavate (Fig. 27G), extending behind segment 4 (♂) or 3 (♀) when stretched dorsally.

In width, collum << head = segments 2 & 3 < 4 < 5 < 6=15(16); thereafter body gradually tapering towards telson. Paraterga well-developed (Fig. 27), starting from a broadly rounded, kidney-shaped collum, mostly only very faintly declivous to continue the outline of a rather slightly convex dorsum, largely set high, at about ¼ of midbody height, with quite strong shoulders frontolaterally (Figs 27D, E). Caudal corner of postcollum paraterga mostly dentiform, always narrowly rounded and extending increasingly well behind rear tergal margin only in segments 15-18 (♂) or 16-19 (♀). Lateral edge of paraterga with 2 or 3 small setigerous indentations in poreless and poriferous segments, respectively. Ozopores very evident, round, flush open on dorsal surface, clearly removed from caudal margin and lying anteriorly to bottom of caudalmost lateral incision (Figs 27A–C, E, F, H, I, L), lateral tooth being clearly shorter than medial one. Each postcollum metatergum with 3+3, long, bacilliform setae arranged in three regular transverse rows; polygonal bosses flat, but visible, while transverse sulcus mostly rather deep (Figs 27A–I).

Legs rather long and slender, ca 1.4–1.5 (♂) or 1.2–1.3 (♀) times as long as midbody height (♂); tarsi longest and particularly slender (Figs 27A, B, G–I, K, 28D), sphaerotrichomes or other modified setae missing.

Gonopod telopodite (Figs 28E–I, 29) clearly curved, but stout, unipartite; basal half voluminous and supplied with three strong spines, distal half gradually attenuating, apical piece (**a**) distal to a vestigial solenomere with a number of short spinules. Neither bacilliform ornamentations nor an accessory seminal chamber, nor a hairy pulvillus.

Remarks. This species has already been referred to as *Martensodesmus* sp. elsewhere (Golovatch et al. 2011b).
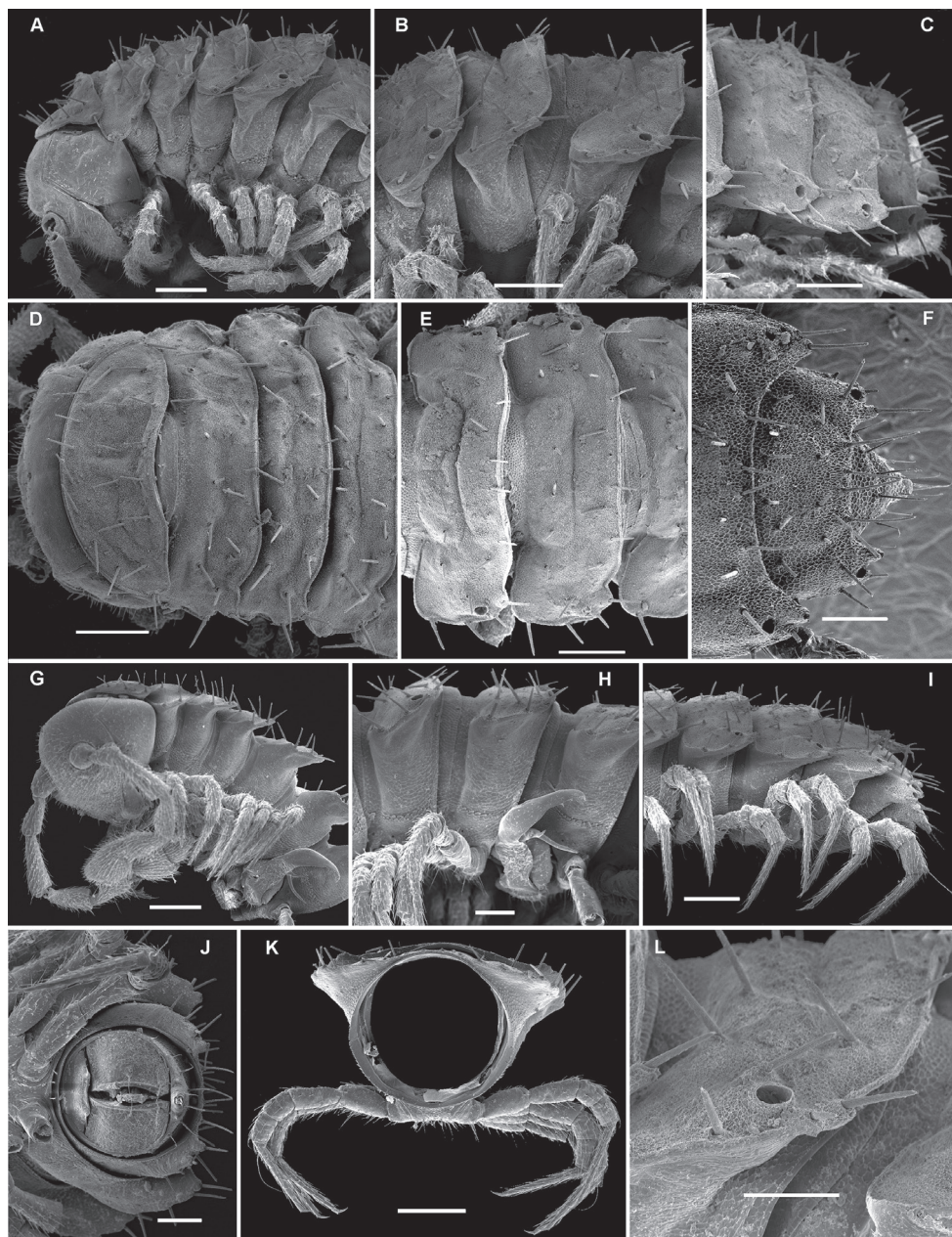
Figure 27. *Martensodesmus cattienensis* sp. n., ♂ paratype; **A, D, G** anterior body part, lateral, dorsal and ventrolateral views, respectively **B, E** midbody segments, lateral and dorsal views, respectively **C, F, I, J** posterior body part, dorsolateral, dorsal, lateral and caudal views, respectively **H** segments 5-7 with an exposed left gonopod, lateral view **K** cross-section of a midbody segment, caudal view **L** midbody paratergite with setae and an ozopore, lateral view. – Scale bars: **A–E, G, I, K** 0.2 mm; **F, H, J, L** 0.1 mm.

Martensodesmus bedosae **sp. n.**

urn:lsid:zoobank.org:act:4CE2CCEE-F30A-4E9D-88FE-757C874FD3E8
http://species-id.net/wiki/Martensodesmus_bedosae
Figs 30–32

Type material. Holotype ♂ (IZAS), China, Guangxi, Hechi County, Duan Xian, Baling karst hill, disturbed forest, 109.07333°E, 23.98171°N, litter, sieving and Berlese extraction, 26.04.2010, leg. L. Deharveng & A. Bedos (CHIgx10-61).

Paratypes. 1 ♂ fragmented, 1 ♀ fragment (SCAU), 1 ♂, 1 ♀ (MNHN JC 344), 1 ♂ (SEM), same locality, together with holotype.

Diagnosis. Differs readily from congeners by the presence of a well-developed frontobasal process **p** on the ventral side of the gonopod femorite, coupled with no modifications on the ♂ vertex.

Name. Honours Anne Bedos, one of the collectors.

Description. Length of holotype and ♂ paratypes ca 4.0 mm, width of midbody pro- and metazona ca 0.4 and 0.6 mm, respectively. Length of ♀ paratypes ca 5.5 mm, width of midbody pro- and metazona ca 0.6-0.65 and 0.8-0.9 mm, respectively. Coloration in alcohol from nearly uniformly pallid to head, collum and following metazona (especially their caudal halves) light rusty brown, anterior body portion in ♂♂ being clearly more infuscate, rusty brown, compared to ♀♀.

Body with 19 (♂) or 20 (♀) segments. All characters like in *R. cavernicola* sp. n., except as follows.

Antennae medium-sized, strongly clavate, extending behind segment 3 (♂, broken off in the sole complete ♀) when stretched dorsally.

In width, collum << segments 2 & 3 < head = 4 < 5 < 6=15(16); thereafter body gradually tapering towards telson. Paraterga well-developed (Figs 30A–F, H, J), starting from a rather broadly rounded, kidney-shaped collum, mostly only faintly declivous to continue the outline of a rather slightly convex dorsum, largely set high, at about 1/3 of midbody height, with evident shoulders frontolaterally (Figs 30A–C). Caudal corner of postcollum paraterga mostly broadly rounded, obtuse-angular, more narrowly rounded and very slightly extending behind rear tergal margin only in segments 16-18 (♂) or 17-19 (♀). Lateral edge of paraterga with 2 or 3 small setigerous indentations in poreless and poriferous segments, respectively. Ozopores very evident, round, flush open on dorsal surface, clearly removed from caudal margin and lying anteriorly to bottom of caudalmost lateral incision (Figs 30B, C, E, F, K, 31B), lateral tooth being clearly shorter than medial one. Each metatergum with 3+3, long, bacilliform setae arranged in 2 or 3 regular transverse rows; polygonal bosses invisible, transverse sulcus very shallow (Figs 30A–F, K).

Legs rather long and slender, ca 1.3-1.4 (♂) or 1.1-1.2 (♀) times as long as midbody height (♂); tarsi longest and particularly slender, with modified, dense, bifid setae ventrally (Fig. 31D), but sphaerotrichomes missing.

Gonopod telopodite (Figs 31E–H, 32) clearly curved, but stout, unipartite; basal half especially voluminous due to an unciform frontoventral process (**p**), more distally

Figure 28. *Martensodesmus cattienensis* sp. n., ♀ (**A–F**) & ♂ (**G–L**) paratypes; **A** tegument texture, dorsal view **B** tergal seta, sublateral view **C** gnathochilarium, ventral view **D** midbody leg **E** right gonopod *in situ*, ventral view **F** tip of gonopod telopodite, ventral view **G–I** dissected left gonopod, subdorsal, frontal and submesal views, respectively. – Scale bars: **C, D** 0.1 mm; **E, G–I** 0.05 mm; **A, F** 0.02 mm; **B** 0.01 mm.

on caudal face with a strong subtriangular tooth (**z**) and two long spines (**x** and **y**), distal half with a short, finger-shaped, caudal process (**d**). Neither bacilliform ornamentations nor an accessory seminal chamber, nor a hairy pulvillus, seminal groove ending at base of a small subapical tooth.
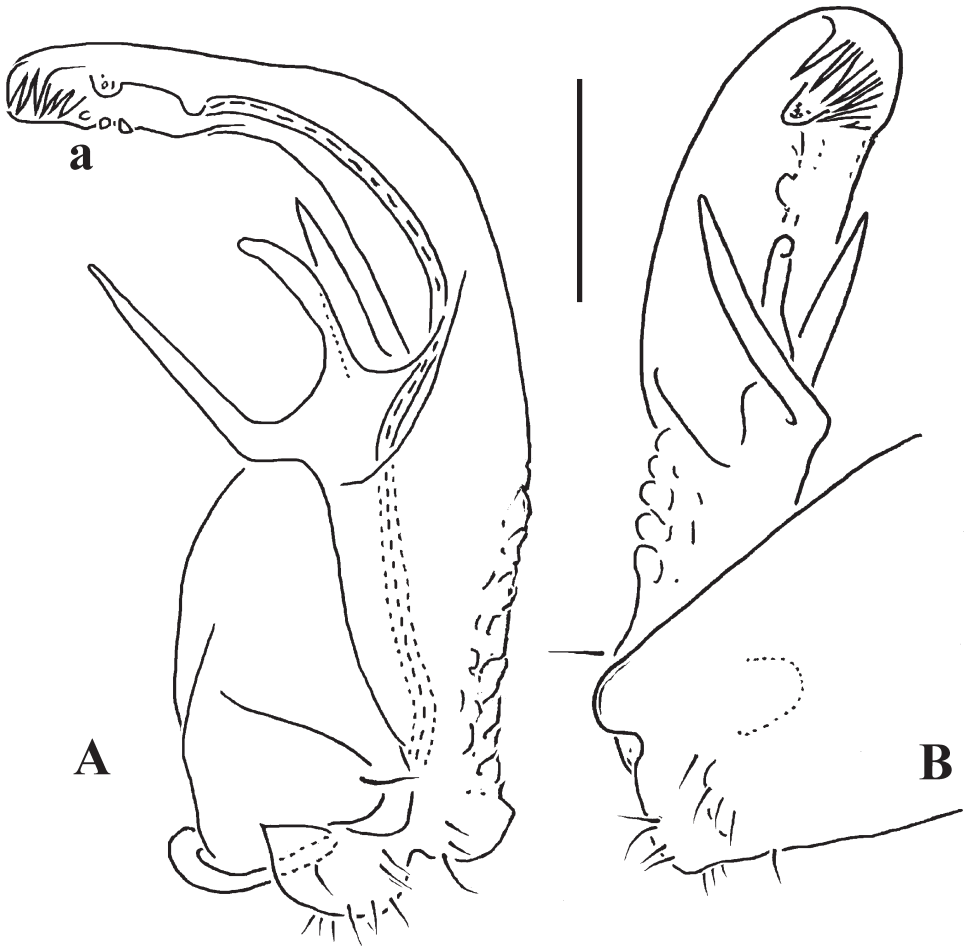
Figure 29. *Martensodesmus cattienensis* sp. n., ♂ paratype; **A, B** right gonopod, subventral and subfrontal views, respectively. – Scale bar: 0.1 mm.

Remarks. This new species is still unique in showing a marked process **p** at the base of the gonotelopodite.

Martensodesmus spiniger **sp. n.**
urn:lsid:zoobank.org:act:4BB13E54-F108-46E3-A603-B45F0F67BCA1
http://species-id.net/wiki/Martensodesmus_spiniger
Figs 33–36

Type material. Holotype ♂ (IZAS), China, Guangxi, Chongzuo County, Longzhou Xian, Shanglong Xiang, Lenglei, Nonggang Forest, 106.964835°E, 22.467175°N, litter, Berlese extraction, 07.03.2005, leg. L. Deharveng & A. Bedos (CHIgx05-062).
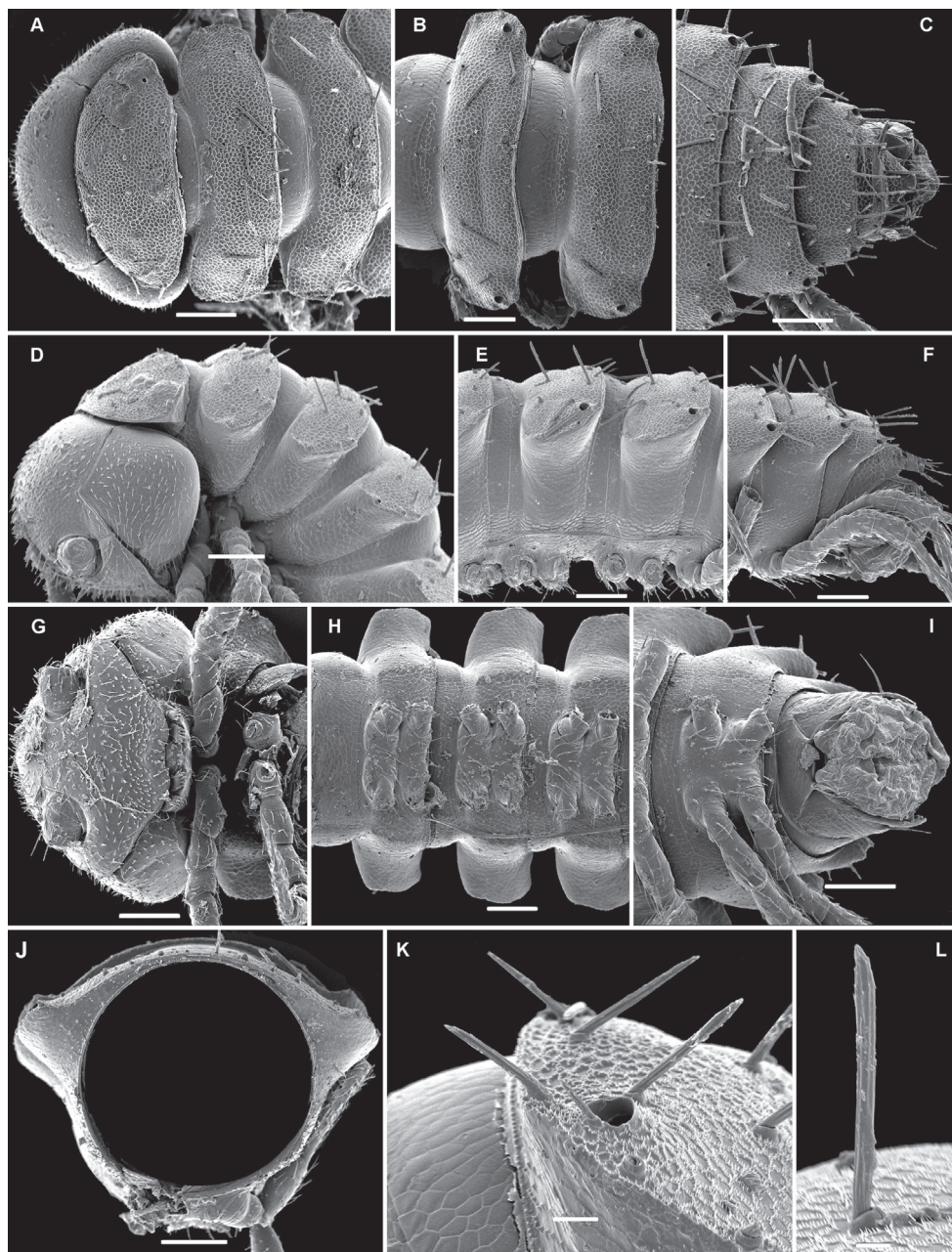
Figure 30. *Martensodesmus bedosae* sp. n., ♂ paratype; **A, D, G** anterior body part, dorsal, lateral and ventral views, respectively **B, E, H** midbody segments, dorsal, lateral and ventral views, respectively **C, F, I** posterior body part, dorsal, lateral and ventral views, respectively **J** cross-section of a midbody segment, caudal view **K** midbody paratergite with setae and an ozopore, lateral view **L** tergal seta, lateral view. – Scale bars: **A–J** 0.1 mm; **K** 0.02 mm; **L** 0.01 mm.

Figure 31. *Martensodesmus bedosae* sp. n., ♂ paratype; **A, B** tegument texture, tergal setae and ozopore, dorsal view **C** head, frontoventral view **D** midbody leg, subventral view; **E,** both gonopods *in situ*, ventral view; **F,** right gonopod, ventral view **G, H** dissected left gonopod, subdorsal and frontal views, respectively. – Scale bars: **C, E** 0.1 mm; **D, F–H** 0.05 mm; **A, B** 0.02 mm.

Paratypes. 1 ♂ (SCAU), same locality, together with holotype; 1 ♂ (MNHN JC 345), same locality, Shanglong Xiang, Nonghang, Nonggang Forest, 106.90575°E, 22.48617°N, litter, sieving and Berlese extraction, 14.04.2010, leg. L. Deharveng & A. Bedos (CHIgx10-07).

Figure 32. *Martensodesmus bedosae* sp. n., ♂ paratype; **A, B** left gonopod, ventral and dorsal views, respectively. – Scale bar: 0.1 mm.

Non-type: 1 ♀ (MNHN JC 345), 1 ♂ subadult, 1 ♀ (SEM), same locality (CHIgx10-07); 1 ♂ subadult (SEM), same data as holotype (CHIgx05-062).

Diagnosis. Differs readily from congeners by the presence of only two transverse rows of setae on metaterga, combined with five strong spines on the caudal face of a rather strongly curved gonopod telopodite which lacks even traces of a solenomere.

Name. To emphasize the highly spinose gonopod telopodite.

Description. Length of holotype ca 4.0 mm, width of midbody pro- and metazona ca 0.35 and 0.5 mm, respectively. Length of paratype ♂ ca 4.5 mm, width of midbody pro- and metazona ca 0.4 and 0.6 mm, respectively. Length of adult ♀ ca 4.7 mm, width of midbody pro- and metazona ca 0.5 and 0.6 mm, respectively. Coloration in alcohol from uniformly pallid to head, several anterior segments and following metaterga clearly infuscate, rusty reddish, increasingly poorly pigmented towards telson.

Body with 19 (♂) or 20 (♀) segments. All characters like in *R. cavernicola* sp. n., except as follows.

Antennae broken off, but obviously medium-sized.

In width, collum << segments 2 & 3 < head = 4 ≤ 5 < 6=15(16); thereafter body gradually tapering towards telson. Paraterga medium-sized, keel-shaped (Figs 33A–F, 34A, 36C, D), a little better developed in ♂ compared to ♀, starting from a broadly rounded collum, mostly faintly declivous and continuing the outline of a rather convex dorsum, largely set rather high, at about ¼ to 1/3 of midbody height, with faint shoulders frontolaterally (Figs 33D–F, H). Caudal corner of postcollum paraterga mostly dentiform, always clearly rounded to narrowly rounded and extending increasingly well
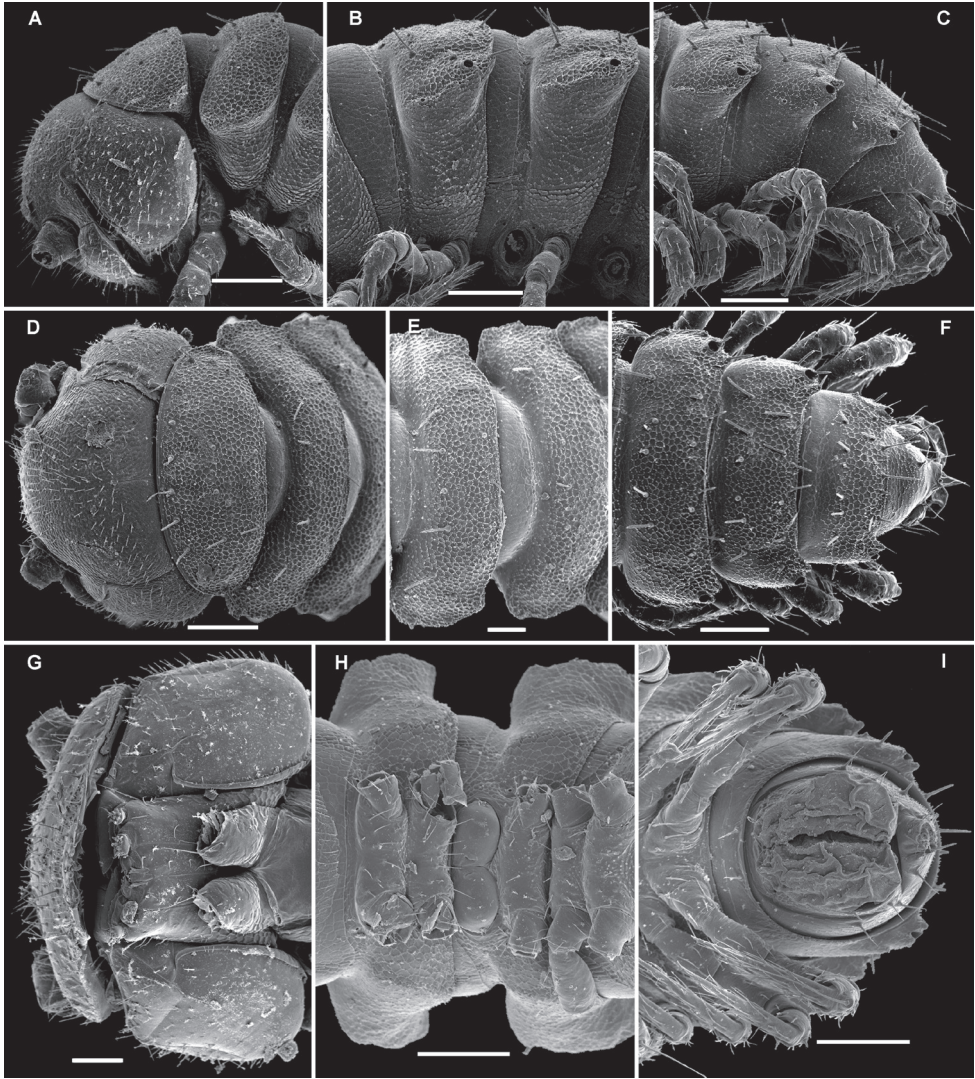
Figure 33. *Martensodesmus spiniger* sp. n., ♂ subadult, non-type; **A, D** anterior body part, lateral and dorsal views, respectively **B, E** midbody segments, lateral and dorsal views, respectively **C, F, I** posterior body part, lateral, dorsal and ventral views, respectively **G** head, ventral view **H** segments 6 and 7, ventral view. – Scale bars: **A–D, F, H, I** 0.1 mm; **E, G** 0.05 mm.

behind rear tergal margin only in segments 15-18 (♂) or 16-19 (♀). Lateral edge of paraterga with 2 or 3 small setigerous indentations in poreless and poriferous segments, respectively. Ozopores evident, round, flush open on dorsal surface, mostly clearly removed from caudal margin, lying slightly above and close to caudalmost lateral incision (Figs 33B, C, F, 34B, 36C, D), lateral tooth being shorter than medial one, in segment 17 clearly lateral, in 18th caudal (Figs 36C, D). Each postcollum metatergum until 18th (♂) or 19 (♀) with 3+3, long, bacilliform setae arranged in two regular transverse rows,
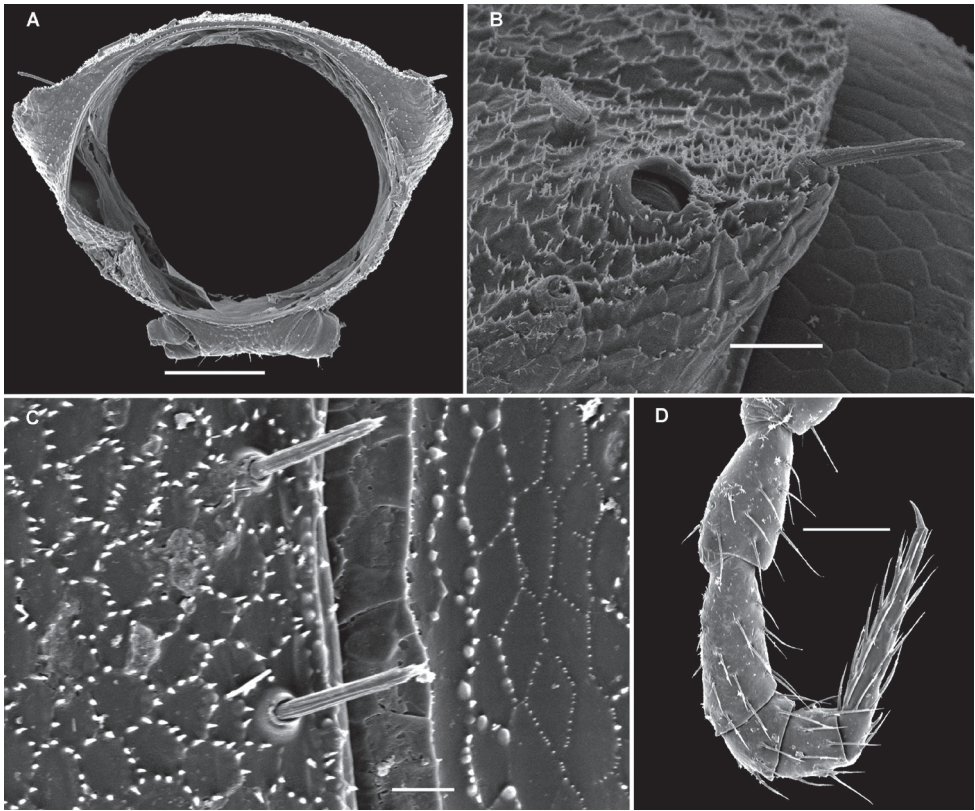
Figure 34. *Martensodesmus spiniger* sp. n., ♂ subadult, non-type; **A** cross-section of a midbody segment, caudal view **B** midbody paratergite with setae and an ozopore, lateral view **C** tegument texture, limbus and setae **D** midbody leg. – Scale bars: **A** 0.1 mm; **D** 0.05 mm; **B** 0.02 mm; **C** 0.01 mm.

only collum and segment 18 with three transverse rows of bacilliform setae, in segment 18 (♂) or 19 (♀) both posterior rows being placed close to each other; polygonal bosses flat, barely visible, even transverse sulcus very faint (Figs 33A–F).

Legs rather long, but stout, ca 1.4-1.5 times as long as midbody height (♂); tarsi longest and particularly slender (Fig. 34D), sphaerotrichomes or other modified setae missing.

Gonopod telopodite (Fig. 35) clearly curved, but stout, unipartite; apical piece (**a**) distal to orifice of seminal groove complex, consisting of a very strong apical spine (**sp**) protected in its basal half by a membranous ventral velum (**ve**) with a faintly fringed apical margin and a similarly membranous, apically spinigerous, dorsal lobe (**k**); caudal face below **a** with three distinct spines (**x**, **y** and **z**), **z** being longest. Neither bacilliform ornamentations, nor accessory seminal chamber, nor even traces of a solenomere, nor a hairy pulvillus.

Remarks. This new *Martensodesmus* species appears to co-occur, even syntopically, together with another opisotretid, *Carlotretus triramus* sp. n., described just below. Moreover, these two species are superficially so similar that only adult males can be separated with confidence. We therefore prefer to regard the females and juveniles as non-type material.
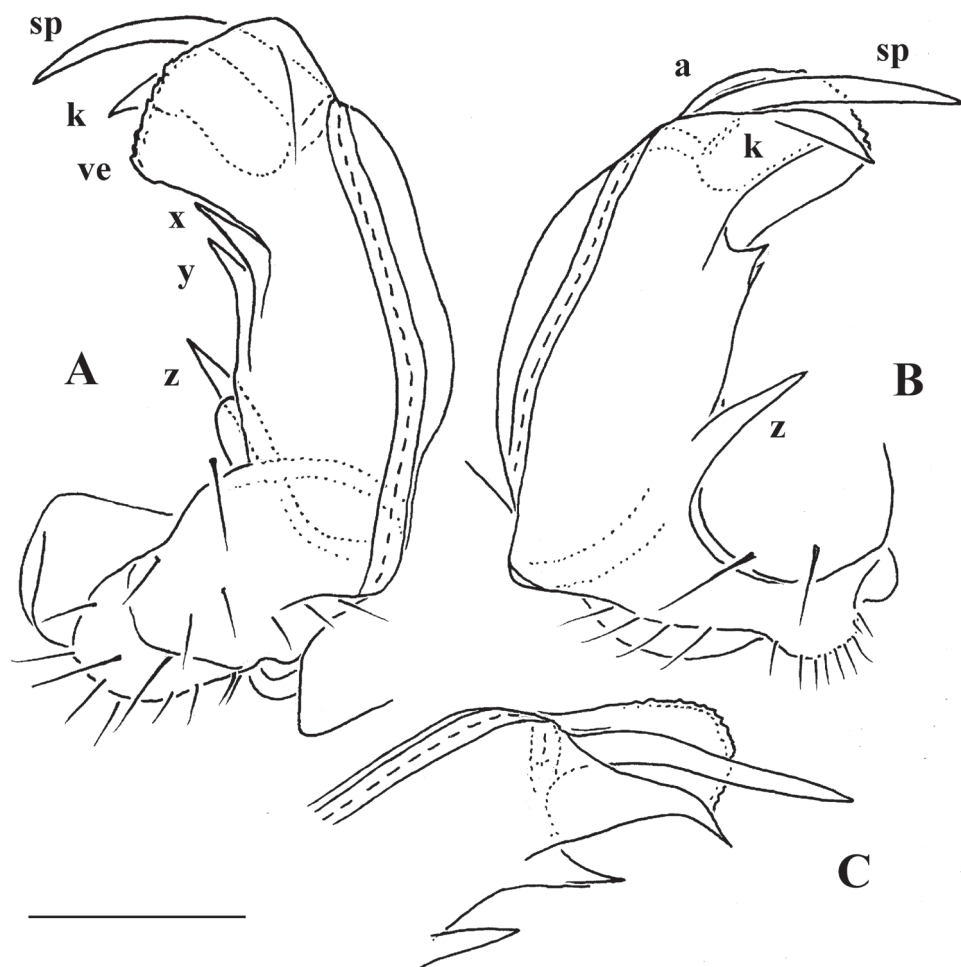
Figure 35. *Martensodesmus spiniger* sp. n., ♂ paratype; **A** right gonopod, ventral view **B, C** left gonopod, frontodorsal and subdorsal views, respectively. – Scale bar: 0.1 mm.

Carlotretus triramus **sp. n.**

urn:lsid:zoobank.org:act:62FEDFD9-45E8-4B52-BDAD-7511C98AD4D3
http://species-id.net/wiki/Carlotretus_triramus
Figs 36–41

Type material. Holotype ♂ (IZAS), China, Guangxi, Chongzuo County, Longzhou Xian, Shanglong Xiang, Lenglei, Nonggang Forest, 106.964835°E, 22.467175°N, litter, Berlese extraction, 07.03.2005, leg. L. Deharveng & A. Bedos (CHIgx05-068).

Paratypes. 1 ♂ (SEM), same data as holotype (CHIgx05-066); 1 ♂ (SCAU), same locality, Shanglong Xiang, Nonghang, Nonggang Forest, 106.90575°E, 22.48617°N,
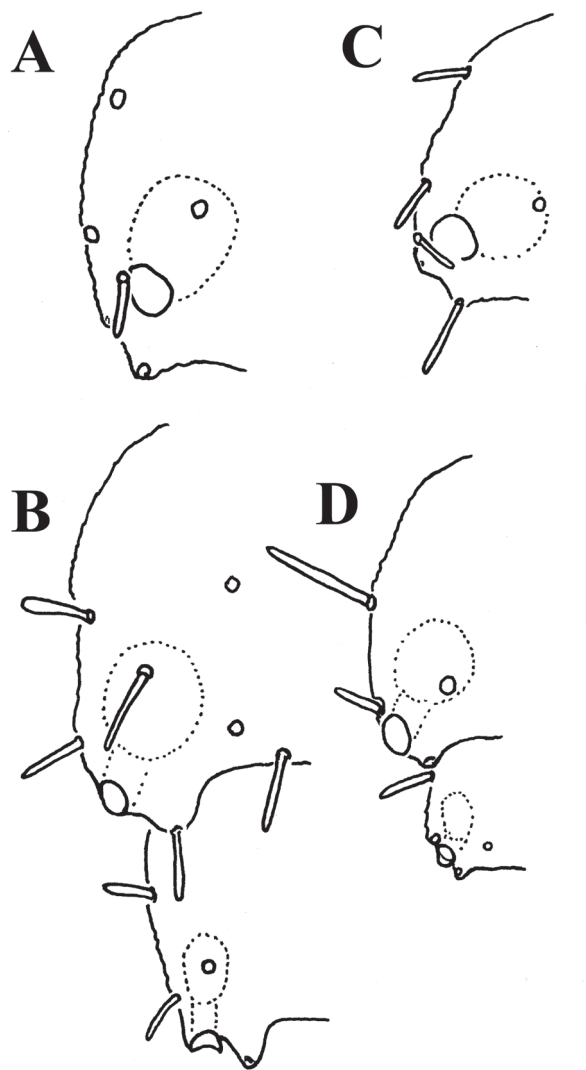
Figure 36. *Martensodesmus spiniger* sp. n., ♂ holotype (**A, B**), and *Carlotretus triramus* sp. n., ♂ paratype (**C, D**) **A, C** left paratergite 13, dorsal view **B, D** left paratergites 17 and 18, dorsal view. – Scale bar: 0.1 mm.

litter, sieving and Berlese extraction, 14.04.2010, leg. L. Deharveng & A. Bedos (CHIgx10-07).

Non-types. 1 ♂ subadult (SEM), same locality, together with holotype (CHIgx05-068); 1 ♀ (SEM), same data as holotype (CHIgx05-064); 1 ♀, 3 ♀ subadults (MNHN JC 346), same locality (CHIgx10-07).

Diagnosis. Differs readily from *C. setosus*, the only known congener, by the much longer, strong and totally unprotected solenomere branch, whereas the parabasal branches are slender and subunciform.
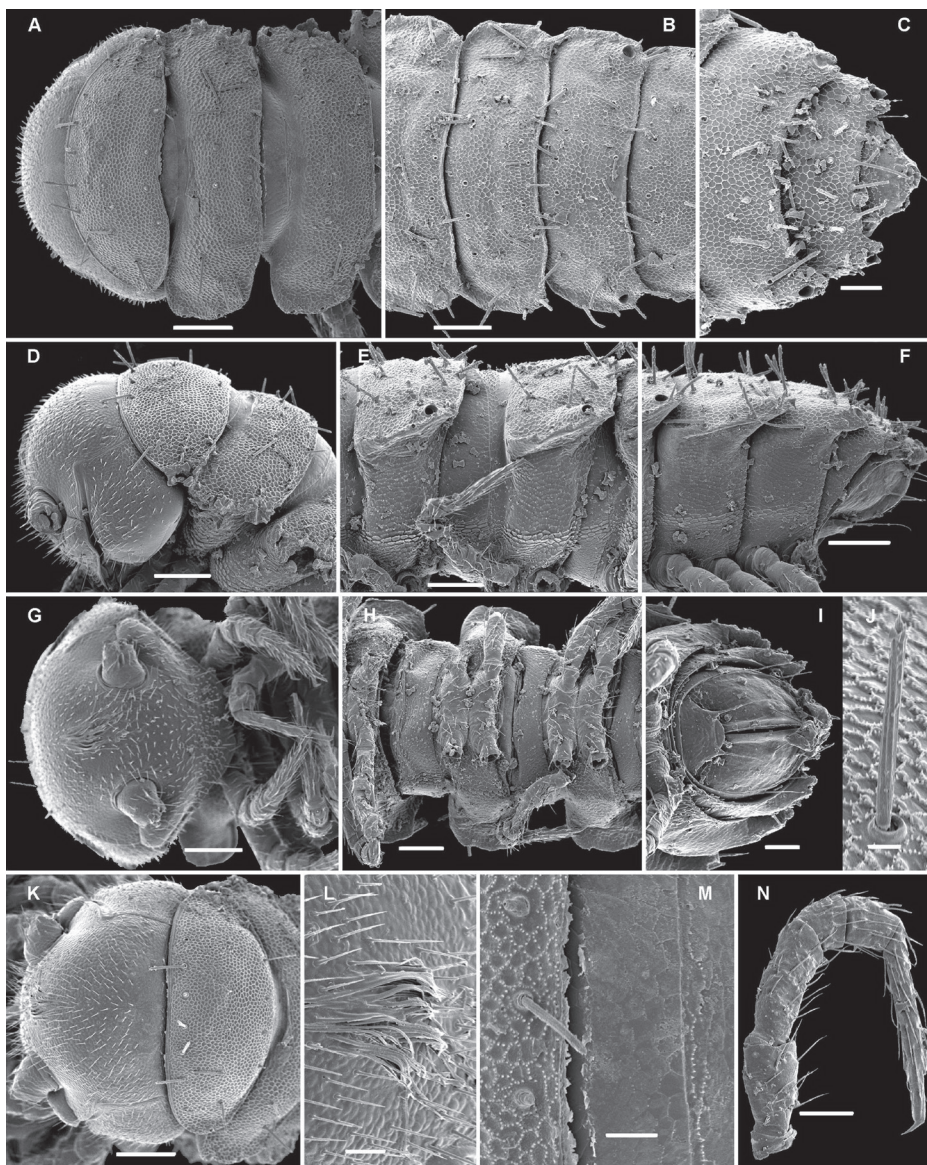
Figure 37. *Carlotretus triramus* sp. n., ♂ paratype (CHIgx10-07); **A, D, G, K** anterior body part, dorsal, lateral, ventral and frontodorsal views, respectively **B, E, H** midbody segments, dorsal, lateral and ventral views, respectively **C, F, I** posterior body part, dorsal, lateral and ventral views, respectively **J** tergal seta, lateral view **L, M** tegument texture, limbus and tergal seta, dorsal view **N** midbody leg. – Scale bars: **A, B, D–H, K** 0.1 mm; **C, I, N** 0.05 mm; **L, M** 0.02 mm.

Name. To emphasize the clearly triramous midlength process of the gonopod telopodite.

Description. Length of holotype ca 4.3 mm, width of midbody pro- and metazona ca 0.4 and 0.55 mm, respectively. Length of paratype ♂ ca 4.6 mm,
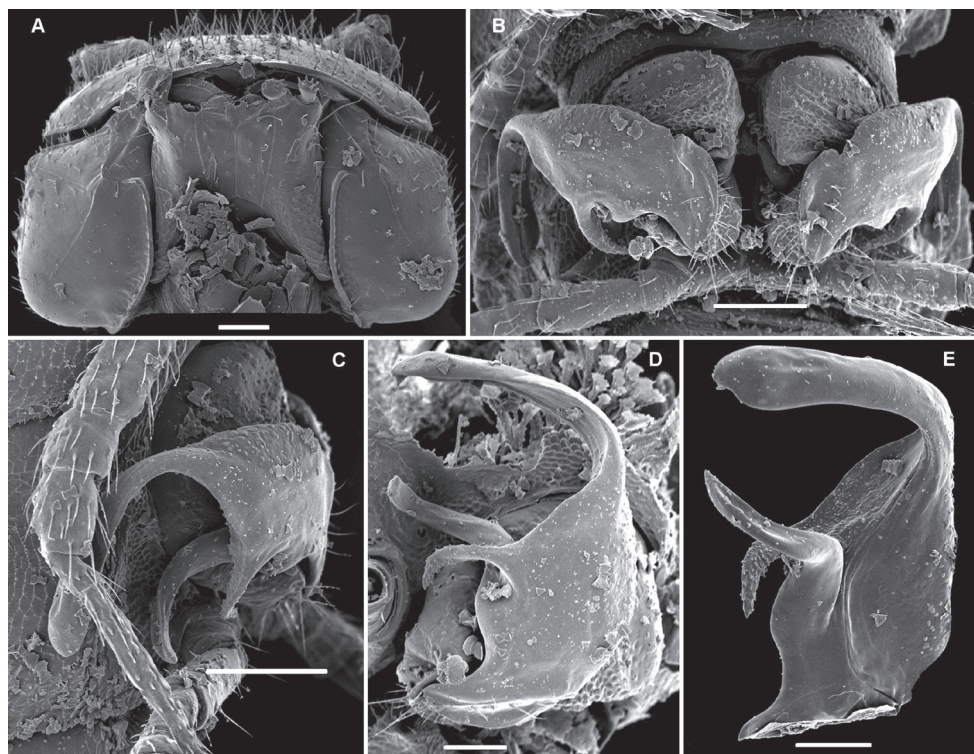
Figure 38. *Carlotretus triramus* sp. n., ♂ paratype (CHIgx10-07); **A** head, ventral view **B–D** gonopods *in situ* **E** dissected left gonopod, subdorsal view. – Scale bars: **B, C** 0.1 mm; **A, D, E** 0.05 mm.

width of midbody pro- and metazona ca 0.45 and 0.6 mm, respectively. Length of adult ♀ ca 6.0 mm, width of midbody pro- and metazona ca 0.6 and 0.7 mm, respectively. Coloration in alcohol from uniformly pallid to head and metaterga faintly rusty reddish.

Body with 19 (♂) or 20 (♀) segments. All characters like in *M. spiniger* sp. n., except as follows.

Antennae medium-sized, extending behind segment 2 when stretched dorsally.

Caudal corner of postcollum parateterga mostly dentiform, always clearly rounded and extending increasingly well behind rear tergal margin only in segments 15-18 (♂) or 16-19 (♀), a little better produced behind than in *M. spiniger* sp. n. (Figs 36A, B).

Gonopod telopodite (Figs 38B–E, 40D–H, 41) clearly curved, but its basal half quite stout, unipartite; solenomere (**sl**) very long, slender and simple, only faintly curved, orifice of seminal groove placed on a small subapical tooth, with neither bacilliform ornamentations, nor accessory seminal chamber, nor a hairy pulvillus. Two large, subunciform processes, **m** and **n**, at base of **sl**, process **n** lying more dorsally and being slightly larger than a ventral, very finely and densely microspinulate **m**.
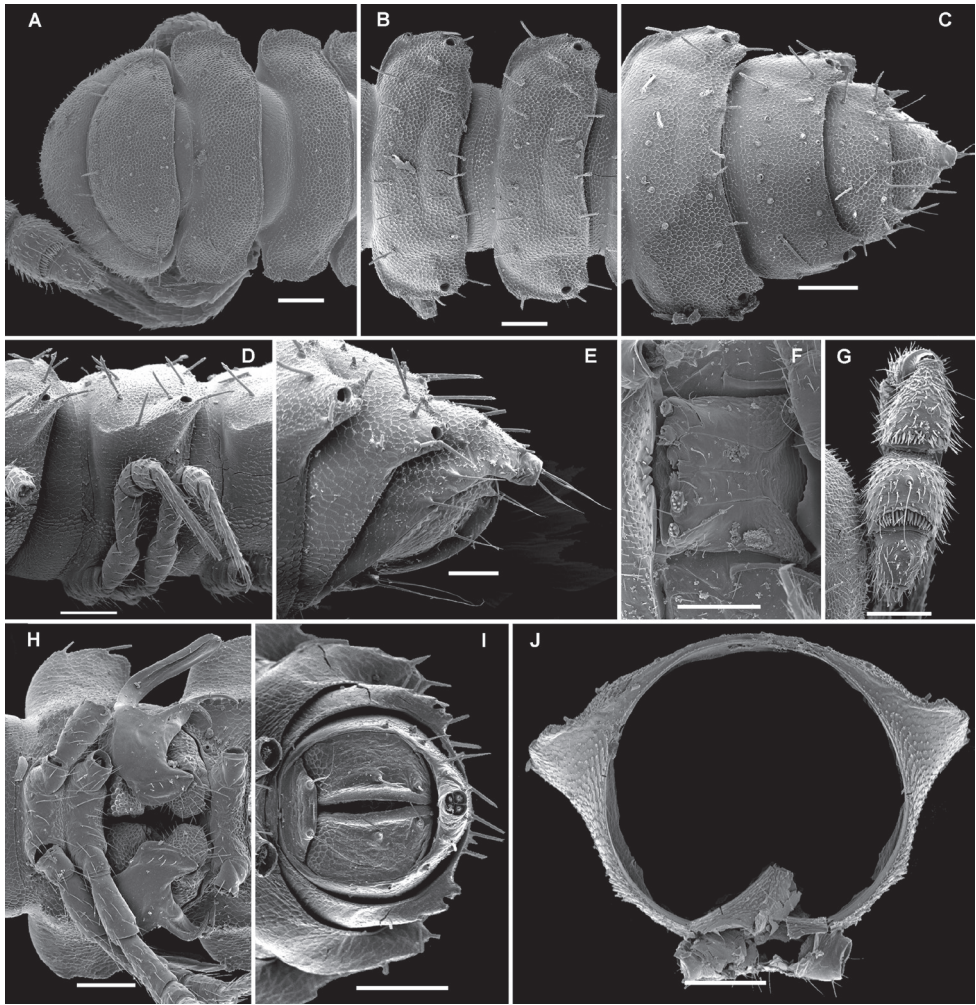
Figure 39. *Carlotretus triramus* sp. n., ♂ paratype (CHIgx05-068); **A** anterior body part, dorsal view **B, D** midbody segments, dorsal and lateral views, respectively **C, E, I** posterior body part, dorsal, lateral and ventrocaudal views, respectively **F** gnathochilarium, ventral view **G** antennomeres 5-8, dorsal view **H** segments 6 and 7 with gonopods *in situ*, ventral view **J** cross-section of a midbody segment, caudal view. – Scale bars: **A–D, F–J** 0.1 mm; **E** 0.05 mm.

A key to genera of Opisotretidae, based mainly on male characters

1   Adults of both sexes with 20 body segments (including telson). Prominent shoulders of paraterga causing a caudad shift of all three rows of tergal setae (Figs 11A, B). Gonopod telopodite (Fig. 11C) very simple, attenuating distad and virtually fully devoid of a trichome other than the one of a subterminal hairy pulvillus ....***Opisthoporodesmus***
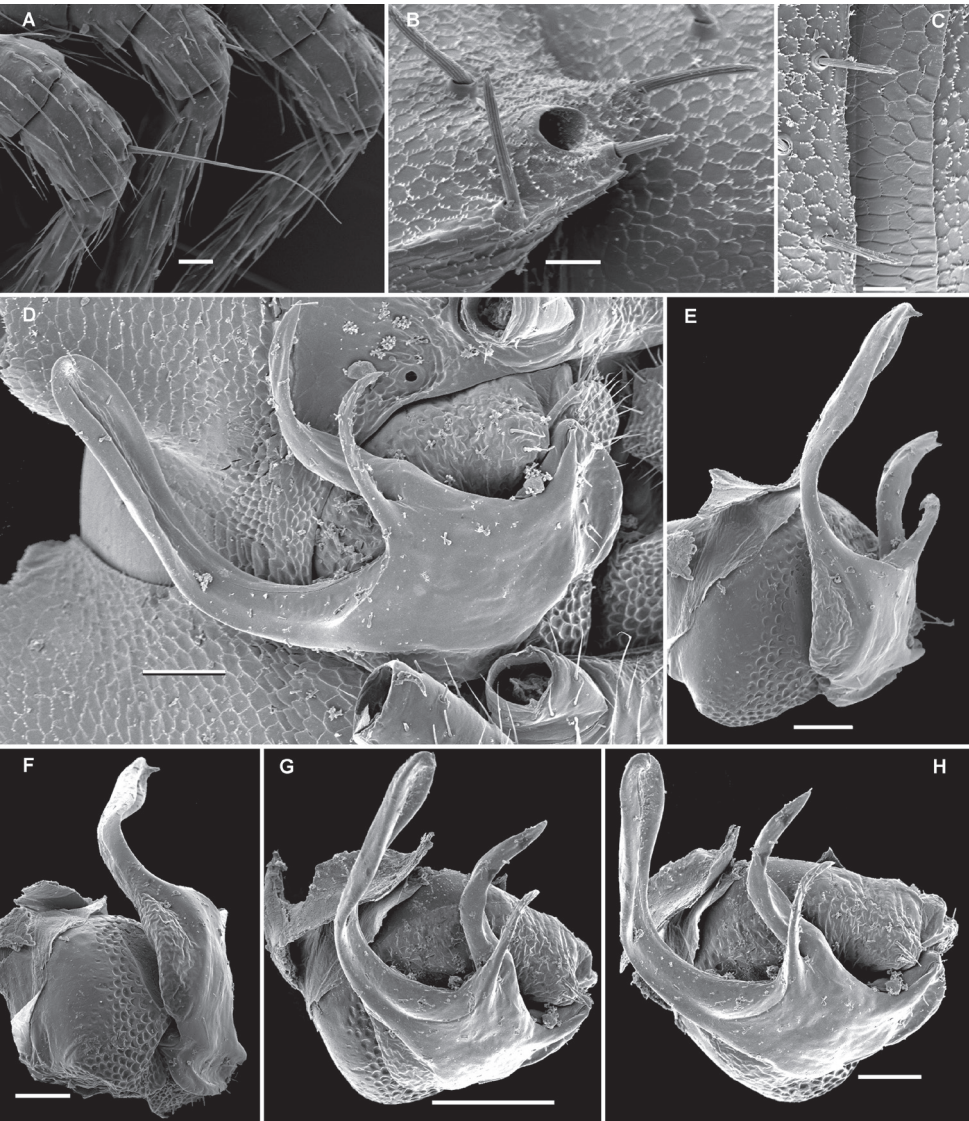
Figure 40. *Carlotretus triramus* sp. n., ♂ paratype (CHIgx05-068); **A** long tactile distodorsal seta on a midbody tibia **B** caudolateral corner of a midbody ozoporiferous paratergite **C** tegument texture, limbus and setae, dorsal view **D** left gonopod *in situ*, ventral view **E–H** dissected left gonopod, frontomesal, frontal, subventral and ventral views, respectively. – Scale bars: **G** 0.1 mm; **D–F, H** 0.05 mm; **A–C** 0.02 mm.

– Females with 20, males with 19 body segments. Shoulders of paraterga usually not so prominent. Gonopod telopodite usually more complex **2**

2 Gonopod telopodite bipartite (**sl** and **ex**), with a strong, frontobasal process **p** on ventral face (Figs 6, 7) .... ***Solaenaulus***

– Gonopod telopodite unipartite, usually devoid of such a basal process **p** on ventral face **3**
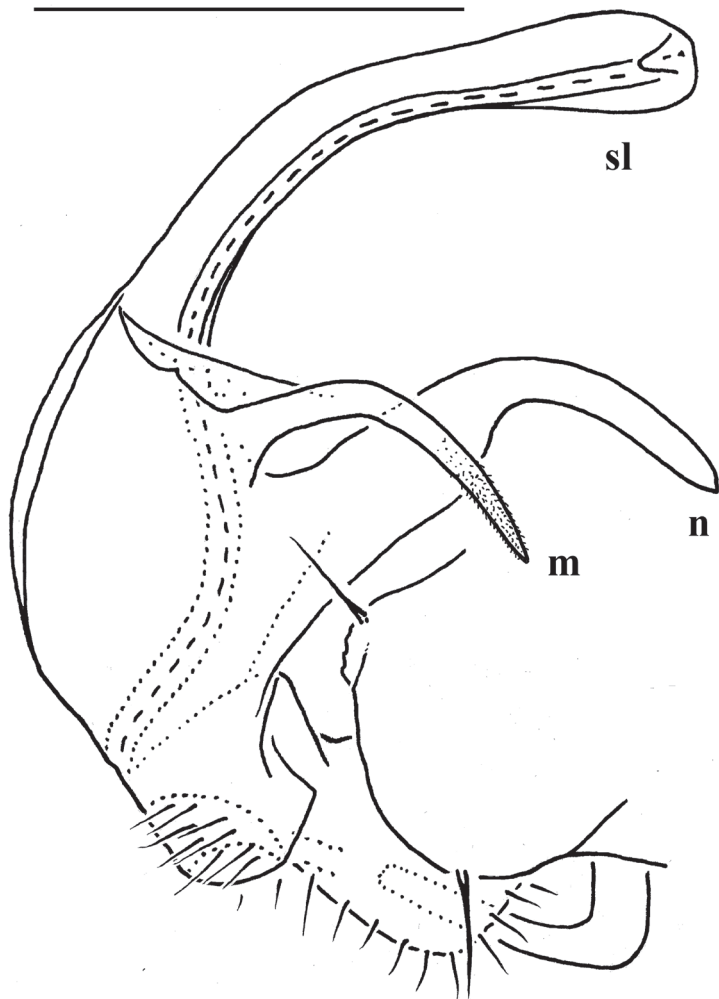
Figure 41. *Carlotretus triramus* sp. n., ♂ paratype (CHIgx10-07), right gonopod, mesal view. – Scale bar: 0.1 mm.

3   Gonopod telopodite rather stout, its distal part devoid of ornamentations (spines or setae), being a long and simple solenomere (**sl**), either with lobes or processes to subtend **sl** or with processes near **sl** base. Neither an accessory seminal chamber nor a hairy pulvillus (Figs 1B, C, 40D–H, 41) ....***Carlotretus***

–   Gonopod telopodite variable, often with bacilliform ornamentations distally, but solenomere never so conspicuous and simple.......................................**4**

4   Gonopod telopodite slender and suberect, devoid both of prominent outgrowths and distal ornamentations, at most microdenticulate near both a small accessory seminal chamber and a hairy pulvillus, with or without process **p** (Figs 2B, 3)..***Corypholophus***

– Gonopod telopodite usually either clearly curved when elongate and slender or nearly straight at least in basal half when thick and stout, often with various evident outgrowths, sometimes also with bacilliform ornamentations distally.......**5**

5 Gonopod telopodite (at least its basal half) rather stout, its basal and/or distal parts with lobes or processes, sometimes including a **p**; both accessory seminal chamber and hairy pulvillus wanting, but a very short, dentiform solenomere usually ornamented with a few bacilli- or setiform structures nearby often present (Figs 9, 10C, D, 29, 32, 35) ....***Martensodesmus***

– Gonopod telopodite with abundant bacilli- and/or setiform ornamentations distally **6**

6 Gonopod telopodite rather stout, only slightly curved; distal part divided into a frontal stump heavily beset with bacilliform ornamentions and a simple to complex caudal branch (Figs 13B, 15C, D, 16B, C) ....***Retrodesmus***

– Gonopod telopodite slender, more clearly curved; distal part beset with ornamentations (small spines, bacilli or setae) and at least with one evident process, either devoid of or supplied with a short solenomere, but with both an evident accessory seminal chamber and a hairy pulvillus (Figs 8D, 18B–D, 20C, D, 21, 23C, D, 25, 26F, G).. ***Opisotretus***

A key to species of *Martensodesmus*

1 ♂ vertex with modifications. Himalaya...**2**

– ♂ vertex without modifications...**5**

2 ♂ vertex with a fossa supporting two cusps of filaments; 2+2 long bacilliform setae at the caudal edge of an elongated ♂ collum (Figs 10A, B). Gonopod as in Figs 10C, D. Bhutan ....***M. bicuspidatus***

– ♂ vertex with a hump. Gonopods different. Nepal **3**

3 Gonopods as in Fig. 9...***M. himalayensis***

– Gonopods different...**4**

4 Apex of gonopod telopodite with a long slender process ....***M. sherpa***

– Apex of gonopod telopodite with a broad, bifid, membranous lobe, devoid of any prominent processes ....***M. nagarjungicus***

5 Gonopod telopodite with a basal **p**, as in Figs 31E–H, 32. Guangxi, China . ...***M. bedosae*** **sp. n.**

– Process **p** absent...**6**

6 Metaterga 2-17 (♂) or 2-18 (♀) with two transverse rows of bacilliform setae. Gonopods as in Fig. 35. Guangxi, China..........................***M. spiniger*** **sp. n.**

– All metaterga with three transverse rows of bacilliform setae. Gonopods different...**8**

7 Gonopod telopodite suberect, with a broadened apex, no process proximal to apical part. Bhutan .... ***M. excornis***

– Gonopod telopodite with a strongly attenuating and curved apical half, three strong processes parabasally (Figs 28E–I, 29). Vietnam ...***M. cattienensis*** **sp. n.**

A key to species of *Opisotretus*

1   ♂ vertex with modification **2**
–   ♂ vertex without modifications..**3**
2   ♂ vertex with two paramedian tubercles (Fig. 23A). Gonopods as in Figs
         23C, D. Papua New Guinea..***O. hagen* sp. n.**
–   ♂ vertex with a bare hump (Fig. 26A). Gonopods as in Figs 26F, G. Nu-
         sakambangan Island south off Java, Indonesia...................***O. spinosus* sp. n.**
3   ♀ paraterga 18 and 19 with caudal teeth nearly obsolete, not extending be-
         hind rear tergal margin. Gonopod structure unknown. Java, Indonesia ....
         ....***O. mimus***
–   Caudal teeth of two last paraterga at least slightly produced behind rear tergal
         margin. Gonopod structure known..**4**
4   Lateral tooth of caudalmost incision in a few last paraterga considerably long-
         er than median one. Gonopods as in Fig. 8D. Java, Indonesia **5**
–   Lateral tooth of caudalmost incision in a few last paraterga clearly shorter
         than median one. Gonopods different **6**
5   Body about 8 mm long and 1.25 mm wide (♀)............................ ***O. euthus***
–   Body about 12 mm long and 1.5 mm wide (♂)...................... ***O. kraepelini***
6   Gonopods as in Figs 18B–D, 20C, D. Papua New Guinea...***O. beroni* sp. n.**
–   Gonopods as in Fig. 25. Sulawesi, Indonesia .... ***O. deharvengi* sp. n.**

Evolutionary and biogeographic implications

The family Opisotretidae appears to range from the Ryukyu Islands, Japan and southern China, through Indochina and Indonesia, to Papua New Guinea. Simonsen (1992) dates the origin of Opisotretidae back to the Triassic (220 Ma) in relation to the geological history and fragmentation of eastern Gondwanaland, placing it mainly in the region of present-day Indonesia. However, such a reconstruction fails to account for the presence of opisotretid species all over Indonesia, including Sulawesi and New Guinea, only parts of which might have been derived from Gondwanaland. Even less convincing is the attribution of such remote and outlying areas as the Ryukyus and southern China to Gondwanaland. Thus there is no compelling reason to suppose that the evolution of Opisotretidae is linked to Gondwanaland. It seems far more logical to consider Opisotretidae as a purely Oriental family, probably the sister-group to, or even a disjunct offshoot of, the pantropical family Fuhrmannodesmidae. Opisotretids might well have originated in mainland Southeast Asia, with subsequent dispersals along the Himalayas in the West and across Indonesia (including New Guinea) in the East. Such patterns do not need to be dated as far back as the early Mesozoic, but could have instead become established much more recently, well within the Cenozoic. Moreover, Southeast Asia hosts the largest number of higher diplopod taxa, including all sixteen Recent orders of the class, and it provides many other examples, at various taxonomic levels,

of connections with the Himalayas and Southeast Asian expansions to Indonesia/
East Indies (Shelley & Golovatch 2011).

In the present work we place Opisotretidae in the superfamily Trichopoly-
desmoidea, as recently reviewed by Golovatch (2011), considering them to be close
to, if not immediately derived from, the still poorly defined, highly diverse and mostly
pantropical family Fuhrmannodesmidae. The reasons for this view of the relationships
between them are as follows. Golovatch (1994) provided an evolutionary scenario for
the genera of Fuhrmannodesmidae known from the Neotropical realm, accepting
as the basalmost those genera showing rather small, subglobose gonopod coxae that
form no significant gonocoel in which to hinge the largely exposed, usually rather
simple and elongate telopodites. Moreover, as in some true Trichopolydesmoidea,
the prefemoral (= setose) part of the gonopod is mostly orientated transversely to
the body axis, extending mesally across the entire width of the coxae. Following a
series of transitional states, such forms ultimately culminate in having the gonopod
coxae strongly enlarged, forming a large gonocoel in which to conceal the clearly
shortened, usually highly complex and deeply sunken telopodites. Their prefemoral
parts already tend to be positioned increasingly parallel to the body's main axis, thus
providing a transition between the usually small-sized Trichopolydesmoidea (= so-
called "micropolydesmoids") to the normally medium- to large-sized Polydesmoidea
(= so-called "macropolydesmoids"). In this respect, Fuhrmannodesmidae might well
prove to be a paraphyletic group.

Naturally, similar general trends can be surmised to have occurred in the fuhrman-
nodesmids of the Afrotropical and, especially, Oriental realms, which support fairly
diverse faunas of this family.

Based on the published record and the available collections of Fuhrmannodes-
midae (largely kept at MNHN) from Southeast Asia and adjacent regions, including
southern China, Indonesia and Melanesia (Golovatch et al., in preparation), most of
the Oriental Fuhrmannodesmidae are indeed highly advanced, showing complex and
strongly shortened gonopod telopodites deeply sunken inside the gonocoel formed by
enlarged coxae. The orientation of the prefemoral part also varies, but it tends to be
held parallel, not transversely, to the main axis of the body. However, amongst the
Asian fuhrmannodesmids, there are certain genera and species that instead show quite
primitive conditions, i.e. long, usually less complex gonopod telopodites that remain
strongly exposed above a relatively small gonocoel. At least some of these have the
prefemoral parts orientated strictly parallel to the main axis, a condition typical of the
sister-superfamily Polydesmoidea. Moreover, one of these species (Figs 42, 43), from
Vietnam, yet to be described, shows the distal parts of the gonopod telopodites elon-
gated and directed laterad. This is in contrast to the much more frequent condition of
the gonotelopodites in Fuhrmannodesmidae and most other groups of Polydesmida,
which either cross mesally or are held parallel to each other. Based on this example, the
evolution of the Opisotretidae might well be viewed as a case when the gonotelopodite
of fuhrmannodesmids grows increasingly elongate and orientated laterally, while the
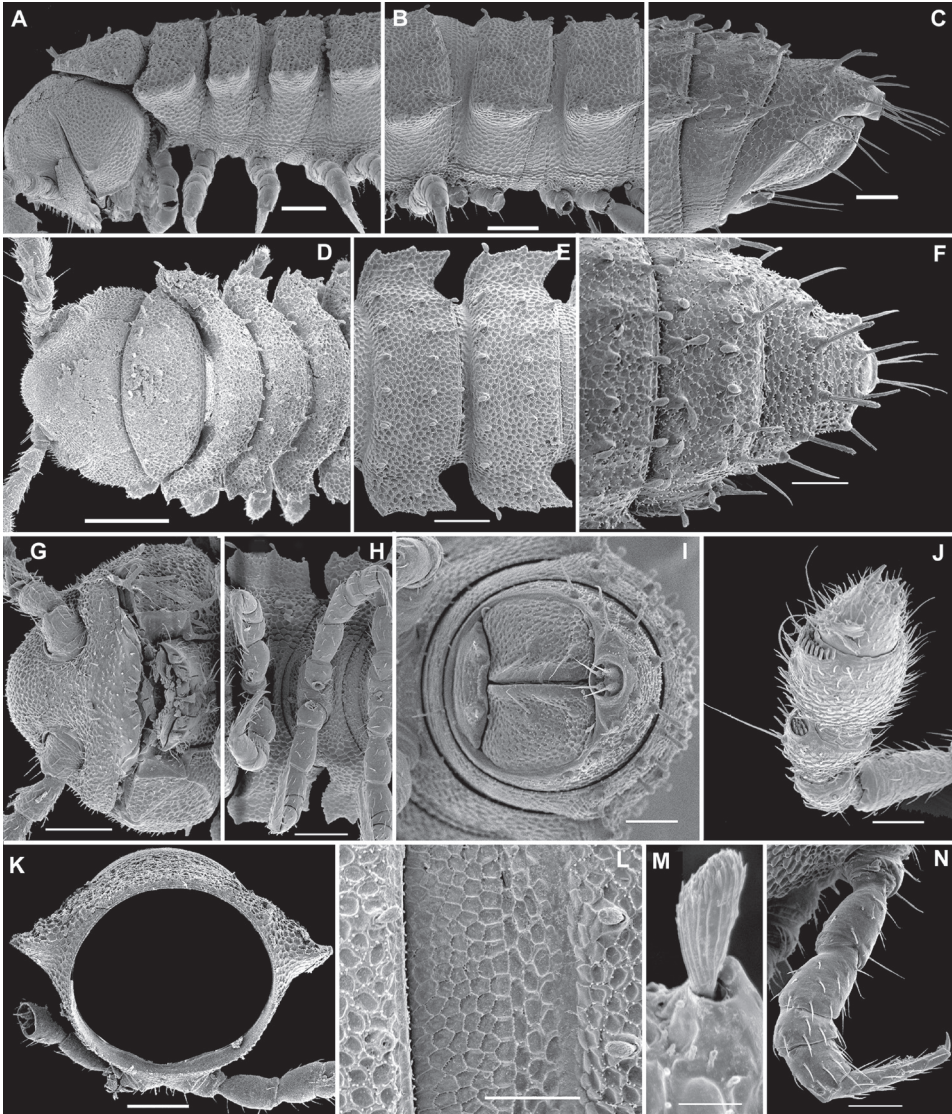coxae remain rather small and do not form a significant gonocoel. Against this back-

Figure 42. Fuhrmannodesmidae gen. sp., ♂ from near Kien Luong, Kien Giang Prov., Vietnam (Vn0308-112); **A, D** anterior body part, lateral and dorsal views, respectively **B, E, H** midbody segments, lateral, dorsal and ventral views, respectively **C, F, I** posterior body part, lateral, dorsal and ventrocaudal views, respectively **G** head, frontoventral view **J** antennomeres 3-8, subdorsal view **K** cross-section of a midbody segment, caudal view **L** tegument texture, limbus and setae, dorsal view **M** tergal seta, lateral view; **N,** midbody leg. – Scale bars: **D** 0.2 mm; **A, B, E, G, H, K** 0.1 mm; **C, F, I, J, L, N** 0.05 mm; **M** 0.005 mm.

ground, we would again emphasize that none of the peripheral, non-gonopod features of Opisotretidae seems to characterize this family alone.

To summarize, the Opisotretidae could have originated directly from a disjunct member of Fuhrmannodesmidae in which the gonopod coxae would have remained
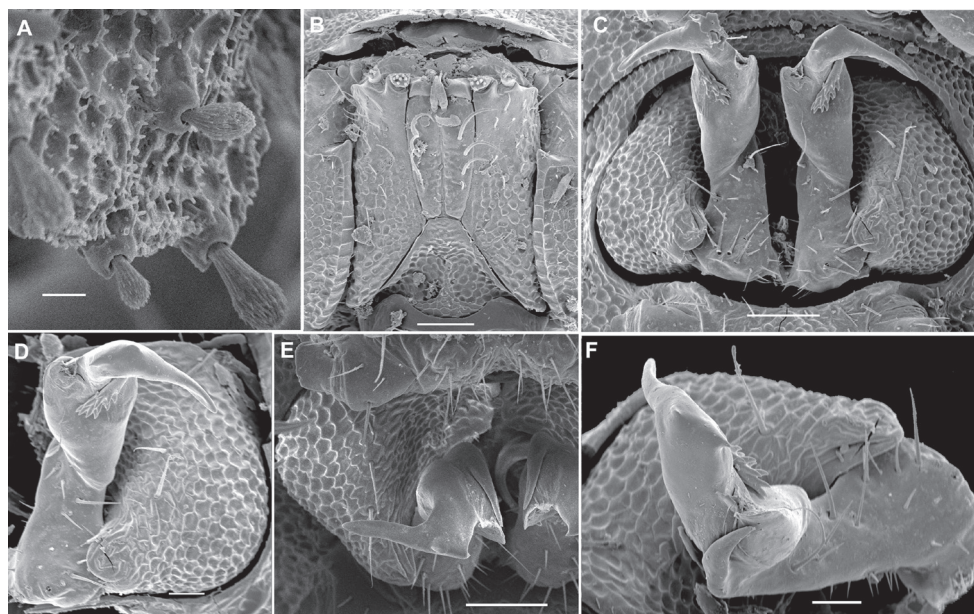
Figure 43. Fuhrmannodesmidae gen. sp., ♂ from near Kien Luong, Kien Giang Prov., Vietnam (Vn0308-112); **A** tegument texture and tergal setae, subdorsal view **B** gnathochilarium, ventral view **C, E** gonopods *in situ*, ventral and frontoventral views, respectively **D, F** left gonopod, subventral and sublateral views, respectively. – Scale bars: **B, C, E** 0.05 mm; **D, F** 0.02 mm; **A** 0.01 mm.

small and probably been held parallel to the main axis of the body, but the development of the telopodite would have culminated in its considerable elongation and fully dorsolaterad orientation. In addition, the gonopods of this stem species must have been equipped with an accessory seminal chamber and a hairy pulvillus, the apomorphies which are absent from present-day Fuhrmannodesmidae, but retained in most of the Polydesmoidea and a few Trichopolydesmoidea, including Opisotretidae. So the ancestor of Opisotretidae might have also been a species of Polydesmoidea or even a common stem member of the Polydesmoidea+Trichopolydesmoidea. A clear-cut trend to having these apomorphies (as well as ♂ sphaerotrichomes) reduced is evident, apparently along with body miniaturization, not only in Opisotretidae, but also in some typical Polydesmidae, e.g. within the Siberian genus *Uniramidesmus* Golovatch, 1979 (Mikhaljova 2004, 2006), and Trichopolydesmidae, e.g. within the western Mediterranean genus *Cottodesmus* Verhoeff, 1936 (Verhoeff 1936, Mauriès and Vicente 1977, Mauriès 1983).

Conclusions

There can be no doubt that many more species of Opisotretidae await discovery and description. Representatives of this family seem to be rare, but it is likely that they are

seriously under-collected due to their small size. Even in caves, they seem never to be abundant, making them easy to overlook, which is in strong contrast to most diplopod groups common in tropical caves, including those of the Oriental realm (Deharveng & Bedos 2012). Sympatry, even syntopy, of two different opisotretid species also seems to be common.

Acknowledgements

References

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RESEARCH ARTICLE

Three new species in the genus *Wilkinsonellus* (Braconidae, Microgastrinae) from the Neotropics, and the first host record for the genus

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Abstract

The genus *Wilkinsonellus* Mason is a poorly sampled but widely distributed tropical genus of Microgastrinae (Braconidae), parasitoid wasps that exclusively attack caterpillars (Lepidoptera). Currently, species of *Wilkinsonellus* have been described only from the Palaeotropics, but the genus was known to occur in the Neotropics. Here we describe the first three species from Central and South America: *Wilkinsonellus alexsmithi* **sp. n.**, *Wilkinsonellus kogui* **sp. n.**, and *Wilkinsonellus panamaensis* **sp. n.** These species descriptions confirm that *Wilkinsonellus* is a Pantropical genus. A dichotomous key for the three new Neotropical species is given. The first recorded host for the genus, *Microthyris prolongalis* (Crambidae), is also reported, for *Wilkinsonellus alexsmithi*.

Resumen

Wilkinsonellus es un género tropical de microgastrinos (Braconidae) que ha sido poco muestreado aunque presenta una distribución amplia. Estas avispas parasitoides únicamente utilizan como hospederos larvas (orugas) de lepidópteros. Hasta el momento, las especies de *Wilkinsonellus* han sido descritas solo a partir

de material colectado en la región Paleotropical (trópico del viejo mundo), aunque su presencia en el Neotrópico ya se conocía. En esta publicación se describen las primeras tres especies Neotropicales, dos de Centroamérica y una de Suramérica: *Wilkinsonellus alexsmithi* **sp. n.**, *Wilkinsonellus kogui* **sp. n.**, *Wilkinsonellus panamaensis* **sp. n.** Estas descripciones de especies Neotropicales confirman la distribución Pantropical del género. Una clave taxonómica para la identificación de las tres nuevas especies es propuesta. El primer hospedero para el género, *Microthyris prolongalis* (Crambidae), se reporta para *Wilkinsonellus alexsmithi*.

Keywords

Biodiversity, caterpillars, parasitoid wasps, tropical rain forest lowlands

Palabras clave

Avispas parasitoides, biodiversidad, bosque lluvioso de tierras bajas tropicales, larvas, orugas

Introduction

The genus *Wilkinsonellus* was erected by Mason (1981) to accommodate four Palaeotropical species that Nixon (1965) included in the *Apanteles henicopus* and *Apanteles daira* groups. The former of those two species-groups contained three species, *Apanteles henicopus* (de Saeger 1944) from Kenya and Rwanda, *A. iphitus* (Nixon 1965), and *A. thyone* (Nixon 1965) both from the Philippines, and the *daira*-group is monotypic, with *A. daira* (Nixon 1965) being from Papua New Guinea. In both species-groups, tergite I exhibits a distinctively narrow petiole, which is constricted medially and also with a deeply median groove (Nixon 1965).

After its origin as a recognized genus, the frequency of additional new *Wilkinsonellus* species descriptions has been spasmodic. Eleven years after its acceptance as a new genus, three new species were described from Papua New Guinea and Australia (Austin and Dangerfield 1992); the latter country was added as a new continental record of distribution. In the early twenty-first century, two more species were described, but this time from Northwest Vietnam (Long and van Achterberg 2003). Between 2005-2007, two additional species were described, one from India (Ahmad et al. 2005) and a further one from Vietnam (Long 2007). The most recent descriptions are from Taiwan and Vietnam (Long and van Achterberg 2011), when another four new species were added. Thus, the genus currently contains 15 described species, mainly from the Palaeotropics: Africa, south and Southeast Asia, Indonesia and Australia. The presence of *Wilkinsonellus* in the Neotropics was reported more than a decade ago during the elaboration of a key to Microgastrinae (Whitfield 1997), published in the Manual of the New World Genera of the family Braconidae. However, no Neotropical species were formally described at that time.

Currently, there is no information available about which families of Lepidoptera are used by these wasps as hosts, except that newly reported here. However, they are assumed to be koinobiont endoparasitoids of caterpillars (larvae of Lepidoptera), as are all genera of Microgastrinae. Only one of the previously described species, *W. daira*,

has natural history data associated. It was labeled as bred from the plant *Hibiscus,* Malvaceae (Nixon 1965), which is obviously incomplete without an insect host.

Three undetermined species of *Wilkinsonellus* were reported in Kalimantan (Indonesia: Borneo island) during a study that assessed braconid parasitoid wasps diversity after the reforestation of degraded *Imperata* grassland (*Imperata cylindrica,* Poaceae) with *Acacia mangium,* Fabaceae (Maeto et al. 2009). In that study, one undetermined species was reported in matured *Acacia* plantations (aged 5–12 years), and two other unidentified species were found in old secondary logged dipterocarp forests.

The phylogenetic position of the genus within Microgastrinae is unclear. However, some authors have used comparative morphology to suggest a close relationship with *Diolcogaster* Ashmead. Two *Diolcogaster* species-groups have been proposed as close relatives. One of them is the *xanthaspis*-group (Austin and Dangerfield 1992). As with *Wilkinsonellus*, this species-group is characterized by its narrow petiole of tergite I, but the petiole has more or less parallel sides, while that of *Wilkinsonellus* (Nixon 1965) is constricted laterally. The other species-group is the *fasciipennis*-group (Mason 1981), which differs from *xanthaspis* only in that tergites II and III show no delimited median area (Nixon 1965). At the present time, the phylogenetic position of *Wilkinsonellus* within Microgastrinae remains an open question, largely due to little effort having been expended in representing all relevant groups in phylogenetic analyses.

After a brief mention of Dr. Wilkinson's contribution to the knowledge of Microgastrinae, the first three Neotropical species of *Wilkinsonellus* are described. A Pantropical distribution for the genus is confirmed, along with the first host data for the genus, and we offer a key for the three new species.

Douglas Shipton Wilkinson (1890–1941)

In 1981, William R. M. Mason named the genus in honor of D. S. Wilkinson, a renowned British entomologist at the Natural History Museum in London - then known as the British Museum (Natural History), who dedicated his entire career to the study of Microgastrinae. Wilkinson was a significant contributor to Microgastrinae taxonomy. He concentrated his efforts in understanding the morphological variability of *Apanteles* not only regionally, but also on a global scale. His vast knowledge of *Apanteles* helped him to design a morphology-based classification (Papp 1976). He proposed six groups; each one was named with arbitrarily chosen letters [A, F, G, S, U, & M] (first developed in Wilkinson 1932). This system of letter-designated groups was adopted, modified and extended from the previous four sections proposed by Marshall (1885) for the British *Apanteles* fauna (Nixon 1965). He was the first European entomologist to recognize the necessity of critically reviewing the classification of the Palaearctic *Apanteles* species. Wilkinson enlisted in the navy during World War II and was killed at sea in 1941, terminating his intention of attaining a world classification of Microgastrinae (Papp 1976, Whitfield et al. 2002).

Wilkinson's later work on the Palaearctic fauna was published after his death, with the aid of Gilbert Nixon, who became his successor in studying the group (Wilkinson 1945). In this monumental work he re-described 58 European *Apanteles* species in a highly detailed way, and included nomenclatural comments and extensive information on natural history. The detailed critical analysis of host-ranges was due to his proficient collaborator Richard Laurence Edward Ford, who could replicate in the laboratory the conditions of rearing parasitoids and their hosts.

Methods

Specimens used by this revision were obtained on loan from the following institutions, which are identified in the text by their acronyms:

- Canadian National Collection of Insects (CNC). Ottawa, Canada.
- Entomological collection, Jorge Ignacio Hernández Camacho, Institute of Biological Resources Alexander von Humboldt (IAvH-E). Villa de Leyva, Colombia.
- Inventory Collection of D. H. Janzen and W. Hallwachs (DHJWH) destined for the CNC or National Museum of Natural History, Smithsonian Institution, Washington, D.C.

The specimens from the IAvH–E collection are the result of the project "Insect Survey of a Megadiverse Country Phase I and II: Colombia" conducted from 2002 to 2006. More than 25 natural protected areas managed by the Colombian government were sampled (Arias-Penna 2007). Specimens from the DHJWH collection are the result of "the caterpillar and parasitoid inventory of the Área de Conservación en Guanacaste (ACG)" Costa Rica (Janzen and Hallwachs 2009, Janzen et al. 2009), a large-scale on-going rearing project. Caterpillars were collected directly in the field and subsequently reared in laboratory conditions. Information about taxonomic identification for caterpillar, host plant and parasitoids as well as data of parasitoid eclosion is available. Each caterpillar is tagged with a voucher code: YY-SRNP-XXXX. The prefix refers to the last two digits of the year that caterpillar was discovered in the field. SRNP stands for Santa Rosa National Park, and the suffix is a unique number assigned within the year. When a parasitoid emerged from its host, the same caterpillar voucher code is assigned, but also a unique DNA wasp voucher code is assigned: DHJPARxxxxxxxx (Janzen and Hallwachs 2009, Janzen et al. 2009).

Morphology and taxonomic characters

Initial identification to genus level followed the key to the Neotropical microgastrine genera (Whitfield 1997). The original *Wilkinsonellus* species descriptions from Papua New Guinea (Nixon 1965), Australasian Region (Austin and Dangerfield 1992), Vietnam (Long and Achterberg 2003, 2011), India (Ahmad et al. 2005) and China (Zeng

et al. 2011) were consulted to confirm that the new species matched the generic aspects of those descriptions. The cuticular sculpturing terminology utilized in this revision follows Harris (1979). Morphological terms for body structures as well as venation are a variation of the Comstock-Needham system that was used by Sharkey and Wharton (1997, Fig. 15). Photos were taken with a Leica DFC425 digital microscope camera mounted on a Leica M205 stereomicroscope, (Wetzlar, Germany). The LAS (Leica Application Suite) multifocus module integrated within the Leica microscope was used for taking the pictures. The stack of images at different focus positions was processed with Zerene Stacker version 1.04 (http://zerenesystems.com/cms/stacker).

Results

Wilkinsonellus **Mason, 1981**
http://species-id.net/wiki/Wilkinsonellus

Type species: *Apanteles iphitus*, Nixon 1965

   Diagnosis. *Wilkinsonellus* can be differentiated from other Microgastrinae genera by the combination of the following characters: body coloration largely yellowish (Figs 1A, L; 3A; 4A); propodeum with a median carina, spiracles surrounded by carinae (Figs 1F, 3G, 4H); propleuron with a posterior flange (Figs 1D, 3F, 4B); scutellum sculptured medio-posteriorly and often with subapical carina (Figs 1M–N, 3G, 4H); lunulae of scutellum wide (Figs 1E–F, 3G, 4G–H) (Long and Achterberg 2011), fore wing with second submarginal cell ("areolet") open distally, thus vein r-m absent (Fig. 3J); vein 1-1A strongly curved, laying very close to posterior margin of the fore wing (Fig. 3J) (Long and Achterberg 2003); tergite I with petiole 4–5 times as long as its apical width, more or less constricted medially and deeply grooved almost to apex (Figs 1H, Q–R; 3H; 4H–I) (Zeng et al. 2011); median longitudinal area of metasomal tergite II slightly raised, usually poorly delimited (Figs 1G–H, Q–R; 3H, L; 4I), tergite II as long as tergite III, both smooth (Figs 2G–H, Q–R; 3H, L; 4I) (Whitfield 1997); hind coxa enlarged (Figs 1A, I, L, Q; 3A, H, L,) rarely short except in *W. flavicrus* (Long and Achterberg 2011); ovipositor sheaths short (Figs 1A, G, J, 4A, J) (Whitfield 1997).

Key to Neotropical *Wilkinsonellus* Mason

1   Scutellar sulcus with seven carinate foveae (Fig. 4G). Axillary trough of metanotum with complete parallel carinae (Fig. 4H). Eyes and ocelli appearing reddish in preserved specimens (Figs 4A–D) ...... ***W. panamaensis* sp. n.**
–   Scutellar sulcus with five carinate foveae (Figs 1E ,M–N; 3E). Axillary trough of metanotum with some incomplete parallel carinae (Figs 1F; 3G). Eyes and ocelli silver in preserved specimens (Figs 1A–C, L; 3A–D, F).....................**2**
2   Fore wing and hind wing infuscate (Figs 3A, J–K)............... ***W. kogui* sp. n.**
–   Fore wing and hind wing not infuscate (Figs 1A, L)......***W. alexsmithi* sp. n.**

Descriptions of new species

Wilkinsonellus alexsmithi Arias-Penna & Whitfield, sp. n.
urn:lsid:zoobank.org:act:7D233175-9A75-4850-BB55-E314F705F906
http://species-id.net/wiki/Wilkinsonellus_alexsmithi
Figs 1A–R

Material examined. Type material. Holotype, 1 female, COSTA RICA: Alajuela, Area de Conservación Guanacaste, Sector Rincon Rain Forest, Estación Llanura, lat 10.93332, long -85.25331, 135 m, 17.ix.2009, M. Moraga, 09-SRNP-75793, parasitoid voucher DHJPAR0039932. Paratypes: 2 males same data as holotype except for collecting dates and voucher codes as follow: 10.x.2009, 09-SRNP-76107, parasitoid voucher DHJPAR0039933; and 09.x.2009, 09-SRNP-76084, parasitoid voucher DHJPAR0039931. All specimens deposited in DHJWH temporarily, for later transfer to CNC.

Diagnosis. Eyes silver mottled with gray, ocelli silver (Figs 1A–C, L). Curvature of pronotum with a deep groove that has semicircular rugae. Scutellar sulcus with five deep, carinated foveae of heterogeneous size (Figs 1E–F, M–N). Axillary trough of scutellum (ATS) with several parallel carinae that are close to each other (Figs 1F, M–N). Fore wing longer than body length.

Holotype female. Body length 4.56 mm, fore wing length 4.87 mm, hind wing length 3.99 mm

Coloration (Figs 1A–R). General body pale yellow, except posterior half of hind coxa with an infuscated ventral band (Fig. 1I). Flagellum, trochanter, trochantellus, apex of both femur and tibia brown, hind tarsi, and tarsal claws of all legs completely brown. Scape and pedicel yellow-brown. Eyes silver mottled with gray, ocelli silver (Figs 1A–C, L). Membrane and microtrichiae of both fore and hind wings light brown (Figs 1A, L).

Head (Figs 1B–C). Scape longer than wide (0.26:0.17 mm); pedicel wider than long (0.12:0.10 mm), first antennal flagellomeres not sub-equal in length (0.30:0.36:0.34 mm). Antennal scrobes deep, smooth, far above middle level of eyes (Fig. 1B), carinated dorsally (Fig. 1C); in frontal view, medial area between antennal scrobes with a sharp, short projection carrot-shaped (Fig. 1B), antennal scrobes in contact with inner eye margin (Fig. 1B). Face with small, sparse and homogeneous punctures, face with a median-longitudinal carina running from antennal scrobes to clypeus, fronto-clypeal suture absent (Fig. 1B). Distance between each anterior tentorial pit and closest inner compound eye margin equal to diameter of a tentorial pit (0.06:0.06 mm); anterior tentorial pits far away from each other (0.30 mm) (Fig. 1B). Mandible with two teeth, inferior tooth thinner, longer than superior. Maxillary palps longer than labial palps (Fig. 1B). Distance between a posterior ocellus and adjacent eye margin sub-equal in length equal to diameter of lateral ocellus (0.10:0.10 mm), distance between lateral ocelli shorter than diameter of lateral ocellus (0.06:0.10 mm) (Fig. 1C). Vertex narrow with small, sparse punctuations, but medially smooth and concave (Fig. 1C).
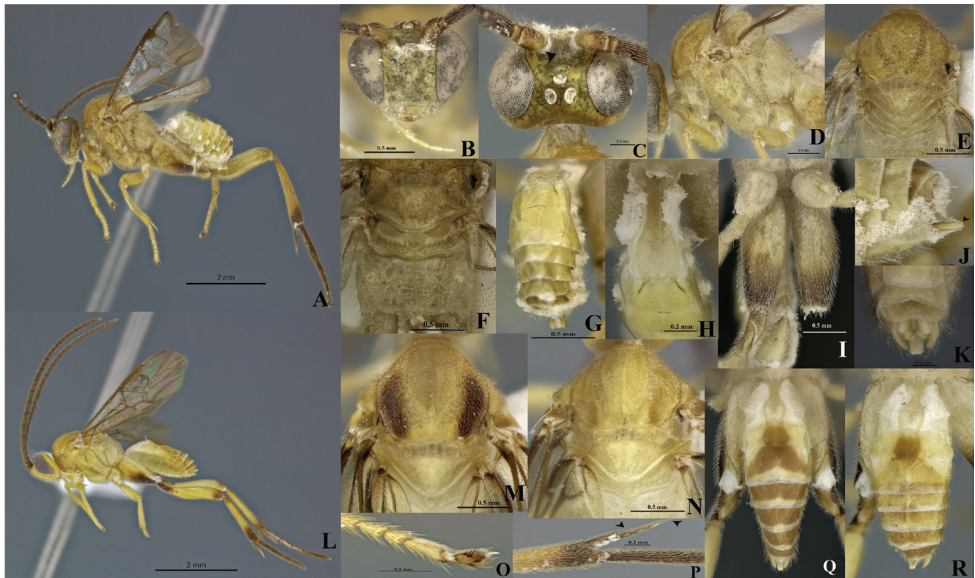
Figure 1. *Wilkinsonellus alexsmithi* Arias-Penna & Whitfield, **A–J** female & **K–R** male **A** Habitus **B–C** Head **B** Frontal view **C** Dorsal view **D–E** Mesosoma **D** Lateral view **E** Dorsal view **F** Scutellum, metanotum & propodeum, dorsal view **G** Last tergites, dorsal view **H** Petiole & Tergites I-II, dorsal view **I** Hindcoxa, ventral view **J** Hypopygium & ovipositor sheaths, lateral view **K–R** Male: **K** Genitalia **L** Habitus **M–N** Mesonotum, dorsal view **O** Claw of hind tarsus **P** Spines of hind tibia **Q–R** Metasoma, dorsal view.

Mesosoma (Fig. 1A, D–F, L–N). Mesosoma dorsoventrally convex (Figs 1A, D). Pronotum shiny, smooth; curvature of pronotum with a deep groove that has semicircular rugae. Mesopleuron convex, extended, smooth except margins lateral and ventro-lateral that form a L-shaped area that possesses small, homogeneous punctuations (Fig. 1D), mesopleuron with a deep dent just above L-shaped area, dent with elongated foveae bordering the L-shape area, mesosternum slightly flat with distinctive groove of deep, homogeneous foveae. Metepisternum and metepimeron separated by a groove with several deep foveae throughout (Fig. 1D), metepisternum narrower than metepimeron, metepisternum just above hindcoxa outlined by a wide and flat carina, and apical half with several short cariane. Mesoscutum as wide as head with small and homogenous punctures. Notauli clearly impressed, broad, but not reaching the transscutal articulation (Fig. 1E). Scutellar sulcus with five deep, carinated foveae of heterogeneous size (Figs 1E–F, M–N). Scutellum shiny, almost smooth with sparse, fine punctures and surrounded by a strong carina (Figs 1E–F, M–N). ATS with several parallel carinae which are close to each other (Figs 1E, N). Axillary trough of metanotum (ATM) with a few, incomplete parallel carinae, only present basally (Figs 1E, N). Lunule of scutellum (L) and medioposterior band of scutellum (BS) smooth and shiny. Medioposterior band of metanotum (BM) short and crossed by a carina aligned with the median longitudinal carina of propodeum (Fig. 1F). Medioanteror pit of metano-

tum (MPM) hexagonal, and delimited by a strong carina (Fig. 1F). Posterior rim of metanotum (PRM) thin and smooth (Fig. 1F). Propodeum with a complete median-longitudinal carina dividing the propodeum in two halves, plus one divergent carina at each half of propodeum, area between carinae basally shorter than apically, divergent carinae crossed by semicircular carinae (Fig. 1F).

Wings (Figs 1A, L). Fore wing with vein r straight (0.30 mm) arising just beyond middle of pterostigma; vein 2RS as long as r (0.30:0.30 mm), but longer than 2M and (RS+M)b veins (0.30:0.15:0.20 mm). Hind wing with vannal lobe reduced, slightly convex; edge with sparse setae throughout. Costal and basal cell infuscate.

Legs (Figs 1A, I, L, O–R). Hind coxa surpassing apex of tergite III (Figs 1A, L, Q–R), outer dorsal surface of hind coxa delimiting an area surrounded by a strong longitudinal carina running from base to apex, but last third apically the carina turns inward (Fig. 1Q); that area with rugulose punctuations and with an extra strong basal carina inclined and reaching only the first third basally; hind tibia with outer spur half as long as inner spur (0.34:0.66 mm); inner spur more than half as long as hind basi-tarsus (0.66:0.90 mm) (Fig. 1P); hind tibia and hind tarsi both with spines throughout, hind tarsal claw with a short comb (Fig. 1O).

Metasoma (Figs 1G–H, J–K, Q–R). Petiole of tergite I narrow (Figs 1H, Q–R), length 0.56 mm, distinctly constricted at anterior half (minimum width 0.09 mm), but subapically wider (maximum width 0.25 mm) and with a few sculpturations, petiole with a deep groove extending more of two thirds tergite I length; hypopygium not protruding at apex of metasoma (Figs 1A, J); hypopygium plate with truncate apex (Fig. 1J), ovipositor sheath length 0.20 mm, glabrous, slightly protruding apex of metasoma (Fig. 1J).

Males (Figs 1K–R). Males differ in coloration from the female: lateral mesonotal lobes pale or dark brown (Figs 1M–N). Tergite II with a brown median area which is longer than wide (Figs 1Q–R); tergite III with a brown (Fig. 1Q) or yellow-brown area (Fig. 1R) anteriorly narrower than posteriorly; tergites IV brown but subapically with a thin transversal yellow apical band (Figs 1Q–R). The infuscate areas on hind legs are darker than in females (Fig. 1L). Antennae length = 5.0-5.2 mm, body length = 4.2-4.5 mm. Last antennal segment gradually narrowing at the apex. Tergite I, minimum width = 0.10 mm, maximum width = 0.22 mm, total length = 0.60-0.70 mm.

Etymology. This species is named in honor of Dr. M. Alex Smith of the University of Guelph, Canada, in recognition of his decade of deep intellectual, laboratory and logistic support for the DNA barcoding of the parasitoid wasps and flies of ACG.

Distribution. The species is only known from the original rain forest collection site, Sector Rincon Rain Forest, in Área de Conservación Guanacaste in northwestern Costa Rica. In 1999, ACG was inscribed as a UNESCO World Heritage site containing the best-preserved and regenerating dry forest habitats from Central America to northern Mexico.

Host. *Wilkinsonellus alexsmithi* has been reared from the leaf-roller *Microthyris prolongalis,* Crambidae (Figs 2A, C–D) three times, while feeding on the rain forest leaves of *Ipomoea phillomega* or sweet potatoes *I. batatas* (Convolvulaceae) (http://janzen.
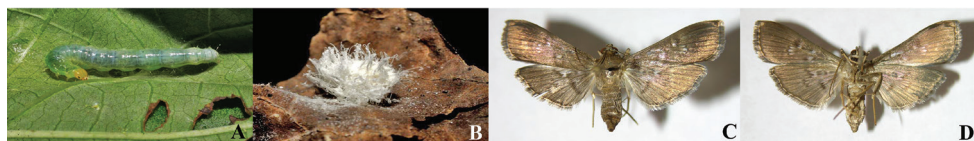
Figure 2. A *Microthyris propongalis* (Guenée, 1854) Crambidae: Larva (07-SRNP-41608, Photo: DHJ422561) **B** Silk and wax cocoon of *Wilkinsonellus alexsmithi* sp. n. (09-SRNP-75793, DHJ-PAR0039932, photo: DHJ476579) **C–D** Adults of *Microthyris propongalis* **C** Dorsal view **D** Ventral view (06-SRNP-41780 Photos: DHJ349728 & DHJ349729).

bio.upenn.edu/caterpillars/database.lasso). The larva of *M. prolongalis* lives inside of the leaf roll that it constructs, eating leaf tissue there. It is therefore likely that oviposition takes place through the leaf into the moth larva. The wasp cocoon (Fig. 2B) is lightly silked to the inner wall of the leaf roll and the larva dies at about the time that the wasp larva exits the cadaver.

Comments. The last three antennal segments are missing from the holotype. *W. alexsmithi* is a parasitoid of a crambid leaf roller larva, *Microthyris prolongalis* (Crambidae). In ACG, this moth larva feeds only on Convolvulaceae (410 rearing records, Janzen & Hallwachs 2009a). Within the subfamily Microgastrinae besides *Wilkinsonellus*, members of two other genera, *Apanteles* and *Diolcogaster*, are parasitoids only on this species of moth. The taxonomic range of insect parasitoids that use *M. prolongalis* as a host entails two insect orders, Hymenoptera and Diptera. Within Hymenoptera the chalcidoid family Encyrtidae (genus not reported), and two additional subfamilies of Braconidae, Orgilinae (*Stantonia*) and Agathidinae (*Alabagrus maya*) were reported; for the Diptera parasitoids, two genera of Tachinidae, *Actia* and *Argyrophylax* also parasitize this caterpillar (Janzen and Hallwachs 2009).

Wilkinsonellus kogui Arias-Penna & Whitfield, sp. n.
urn:lsid:zoobank.org:act:FC7BA3D2-3503-4DD9-B9F7-AADC34BF13CB
http://species-id.net/wiki/Wilkinsonellus_kogui
Figs 3A–L

Material examined. Type material. Holotype. Male, COLOMBIA Magdalena, PNN [Parque Nacional Natural] Tayrona Pueblito, lat 11.33333, long -74.03333, 225m, Malaise, 03-22.i.2001, R. Henriquez leg. M.1212. Paratype. 1 Male, COLOMBIA Chocó, PNN [Parque Nacional Natural] Utría, Cocalito, 6º1'N 77º20'W, 20m, Malaise, 26.xii.2000–01.ii.2001, J. Pérez, Leg. M.1342. Holotype and paratype deposited in IAvH-E.

Diagnosis. Eyes and ocelli silver (Figs 3A–D, F). Scutellar sulcus with five deep, heterogeneous and carinated foveae (Fig. 3E). Axillary trough of metanotum with a few striated grooves defined at least posteriorly (Fig. 3G). Body longer than fore wing (Fig. 3A).

Holotype male. Body length 4.30 (4.30-4.55 mm), fore wing length 4.15mm, hind wing length 3.59 mm.
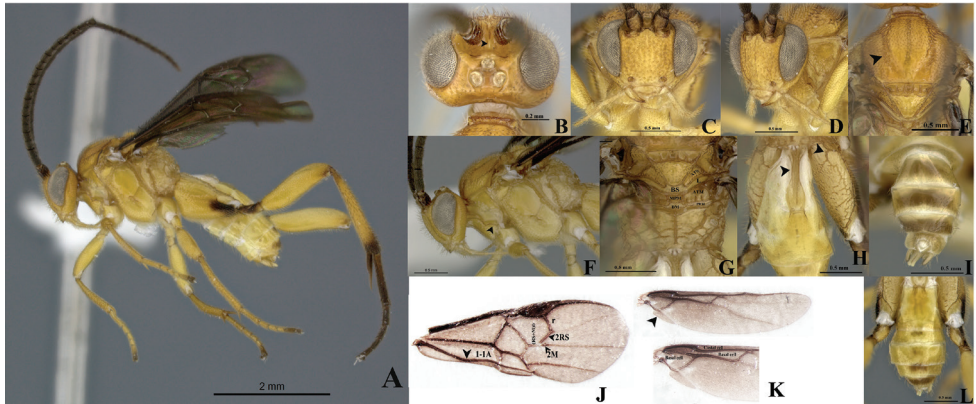
Figure 3. *Wilkinsonellus kogui* Arias-Penna & Whitfield, male. **A** Habitus **B–D** Head **B** Dorsal view **C** Frontal view **D** lateral view **E** Mesosotum, dorsal view **F** Head and mesosoma, lateral view **G** Scutellum, metanotum & propodeum, dorsal view **ATM** = axillary through of metanotum; **ATS** = axillary trough of scutellum; **BM** = Medioposterior band of metanotum; **BS** = medioposterior band of scutellum; **L** = Lunule, **MPM** = Medioanteror pit of metanotum & **PRM** = Posterior rim of metanotum. **H** Tergites I-III & hind coxa, dorsal view **I** Last tergites of metasoma, dorsal view **J** Fore wing veins **K** Hind wing cells **L** Metasoma, dorsal view.

Coloration (Figs 3A–L). General body dark yellow; all legs yellow, except hind leg: coxa infuscated at the apex forming a ventral, wide brown band; apex of trochanter, and trochantellus, base of tibia and tarsi brown (Fig. 3A). Scape and pedicel brown both with thin apical yellow ring. Flagellum dark brown. Eyes and ocelli silver (Figs 3A–D, F.) Tergite IV and beyond mostly brown, but subapically and subbasally with a transverse yellow band (Figs 3I, L). Membrane and microtrichiae of fore and hind wing infusctate (Figs 3J–K).

Head (Figs 3A–D). Scape slightly longer than wide (0.20:0.18 mm); pedicel wider than long (0.12:0.08 mm); first three flagellomeres subequal in length (0.32:0.30:0.34). Antennal scrobes smooth, dorsally carinate (Fig. 3B), positioned far above middle level of eyes (Figs 3C–D); median part between antennal scrobes with a short carina (Fig. 3B). Face with sparse, homogeneous and medium-sized punctures, interspaces wavy; face with a median-longitudinal carina running from antennal scrobes to fronto-clypeal suture (Fig. 3D). Distance between each anterior tentorial pit and closest inner compound eye margin longer than diameter of tentorial pit (0.10:0.06 mm) (Figs 3C–D); anterior tentorial pits far away from each other (0.26 mm) (Fig. 3C). Fronto-clypeal suture absent (Figs 3C–D). Mandible with two teeth, inferior tooth thinner and longer than superior (Fig. 3C). Suture malar present (Fig. 3D). Maxillary palps longer than labial palps (Fig. 3C). Distance between lateral ocellus and adjacent compound eye margin longer than diameter of lateral ocellus (0.11:0.08 mm) (Fig. 3B), distance between lateral ocelli equal to diameter of lateral ocellus (0.08:0.08 mm) (Fig. 3B). Vertex medially smooth, but laterally with some sparse and small punctuations. Occiput slightly concave with a median short grove basally.

Mesosoma (Figs 3A, E–G). Mesosoma dorsoventrally convex (Figs 3A, F). Pronotum shiny, smooth, but curvature of pronotum with elongate areolae. Mesopleuron shiny, smooth medially, but margins lateral and ventro-lateral forming a L-shaped area which small, dense and homogeneous sculptures (Fig. 3F); mesopleuron just above of L-shape area with a dent with some large wave-like sculpturing. Mesosternum slightly flat with a deep row of deep foveae. Metepisternum and metepimeron outlined by a groove with several deep foveae throughout (Fig. 3F), metepisternum inverted triangular, smooth and narrower than metepimeron (Fig. 3F), apical margin metepisternum (above hindcoxa) delimited by a wide, flat carina (Fig. 3F). Mesoscutum as wide as head with small, dense, and homogenous sculptures. Notauli clearly impressed, but not reaching the transscutal articulation (Fig. 3E). Scutellar sulcus heterogeneous, with five deep, heterogeneous and carinated foveae (Figs 3E, G). Scutellum shiny, medially smooth, but with sparse fine punctures and surrounded by carina (Figs 3E, G). Axillary trough of scutellum with several homogeneous striated grooves (Fig. 3G). Axillary trough of metanotum with a few striated grooves defined at least posteriorly (Fig. 3G). Medioposterior band of scutellum slightly wider than lunule of scutellum both smooth and shiny (Fig. 3G). Medioposterior band of metanotum hexagonal and crossed by a median carina aligned with the median longitudinal carina of propodeum (Fig. 3G). Medioanteror pit of metanotum pentagonal-shape surrounded by carina (Fig. 3G). Posterior rim of metanotum thin, wavy and smooth (Fig. 3G). Propodeum with a complete median-longitudinal carina dividing in two halves, each half with one divergent carina wider as they go away from propodeal foramen, space among all carinae intercepted by transverse semicircular carinae (Fig. 3G).

Wings (Figs 3A, J–K). Fore wing with vein r length 0.26 mm slightly curved, arising beyond middle of pterostigma, arising just beyond middle of stigma (Fig. 3J); vein 2RS as same length as r (0.26:0.26 mm), but 2RS vein longer than 2M and (Rs+M)b veins (0.26:0.10:0.20 mm) (Fig. 3J). Hind wing with vannal lobe reduced, slightly convex; edge with sparse setae throughout (Fig. 3K). Costal and basal cells infuscate (Fig. 3K).

Legs (Figs 3A, H, L). Hind coxa very long, reaching apex of tergite III (Fig. 3H), outer dorsal surface of hind coxa delimited by a strong carina, area coarsely rugulose and with a short, strong basal carina (Fig. 3H); hind tibia with outer spur more than half as long as inner spur (0.40:0.66 mm), inner more than half as long as hind basitarsus (0.66:0.88 mm) (Fig. 3A), hindtibia and tarsi with spines throughout.

Metasoma (Figs 3A, H–I, L). Petiole of tergite I narrow (Fig. 2H), length 0.70 mm, distinctly constricted at upper middle (minimum width 0.09 mm) and wider subapically (maximum width 0.20 mm) with sculpturations, petiole with a deep groove extending more of two third of the tergite I length (Fig. 3H). Male genitalia externally visible (Fig. 3I).

Female. Unknown

Etymology. From Kogui = jaguar in the Kogui language. The Kogui are indigenous in the Colombia Caribbean coast at the foot of the Sierra Nevada de Santa Marta, the highest coastal mountains in the world and not directly attached to the Andean mountain range.

Distribution. Colombia, from PNN Tayrona and PNN Utría, both being marine ecosystems protected by the Colombian government and belonging to the National Natural systems. Tayrona is located on the Caribbean coast in Magdalena Department, whereas Utría is located on Colombia's Pacific coast, in Chocó Department.

Host. Unknown

Comments. Holotype lacks the last antennal flagellomeres. The specimens from Utría with antennae length = 4.8 mm, body length 4.3 mm. Last antennal flagellomere length = 0.35 mm, penultimate flagellomere antennae length = 0.30 mm. Male from Chocó shows hind legs with the same pattern of coloration but darker and Tergite VI and beyond with brown spots (Fig. 3L).

Wilkinsonellus panamaensis **Arias-Penna & Whitfield, sp. n.**
urn:lsid:zoobank.org:act:A3274FC6-02B2-4292-9A5B-B37D142516D1
http://species-id.net/wiki/Wilkinsonellus_panamaensis
Figs 4A–J

Material examined. Type material. Holotype. Female, PANAMA Provincia Panamá, Distrito de Panamá, Las Cumbres. Malaise 20.i-02.ii.1982. M. Wolda. DNA Voucher CNCHYM03459. Specimen deposited in CNC.

Diagnosis. Eyes and ocelli appearing reddish in preserved specimens (Figs 4A–D). Metasoma curve (Fig. 4J). Fore wing longer than body length. Vein 2M as long as (Rs+M)b. Scutellar sulcus with seven carinated foveae heterogeneous in size (Fig. 4G). Axillary trough of scutellum and axillary trough of metanotum both with complete parallel carinae (Fig. 4H).

Holotype female. Body length 4.18 mm, fore wing length 4.44 mm, hind wing length 3.43 mm.

Coloration (Figs 4A–J). General body dark yellow, except hind leg infuscated at the base and apex of tibia; hind coxa, trochanter and trochantellus with a narrow dorsal band (Fig. 4J). Hind tarsi completely brown (Fig. 4A). Scape half basal brown and half apical yellow (Fig. 4D). Pedicel brown with yellow apical ring (Fig. 4D). Flagellum brown (Fig. 4E), ocelli and eyes appearing reddish in preserved specimens (Figs 4A–D).

Head (Figs 4A–D). Antenna longer than body (4.44:4.18 mm); scape longer than wide (0.22:0.16 mm); pedicel wider than large (0.12:0.10 mm); first antennal flagellomeres sub-equal in length (0.34:0.32:0.32 mm); penultimate flagellomere as same length than apical segment (0.11:0.11mm); but with flat, abruptly acute in apex. Antennal scrobes smooth, far above middle level of eyes (Fig. 4D) and carinate dorsally (Fig. 4C), median part between antennal scrobes with a short carina (Fig. 4C). Face with small, sparse and homogeneous punctures, face with a median-longitudinal carina running from antennal scrobes to clypeus (Fig. 4D), fronto-clypeal suture absent (Fig. 4D). Distance between an anterior tentorial pit and inner compound eye margin equal to diameter of a tentorial pit (0.06:0.07 mm); anterior tentorial pits far away from each other (0.24 mm) (Fig. 4D). Mandible with two teeth, inferior tooth thinner and longer than superior.
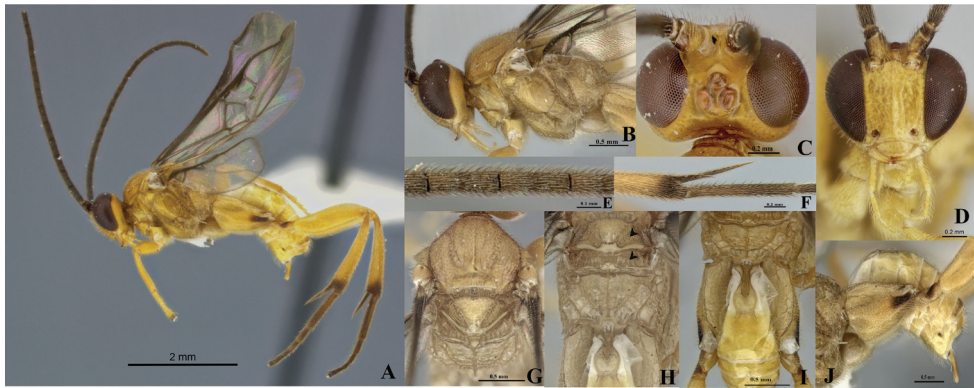
Figure 4. *Wilkinsonellus panamaensis* Arias-Penna & Whitfield, female. **A** Habitus **B** Head & mesosoma, lateral view **C–D** Head **C** Dorsal view **D** Frontal view **E** Antennal flagellomeres **F** Spines on hindtibia **G** Mesosoma, dorsal view **H** Scutellum, metanotum & propodeum, dorsal view **I** Propodeum, Tergites I-V & hindcoxa, dorsal view **J** Metasoma and hindcoxa, lateral view.

Maxillary palps longer than labial palps (Fig. 4D). Distance between lateral ocellus and adjacent compound eye margin sub-equal in length to the diameter of the lateral ocellus (0.09:0.10 mm), distance between lateral ocelli shorter than diameter of lateral ocellus (0.06:0.10 mm) (Fig. 4D). Vertex narrow, medially with a smooth area, but laterally with small and sparse punctuations. Occiput slightly concaved with a short grove medially.

Mesosoma (Figs 4A–B, G–H). Mesosoma dorsoventrally convex (Figs 4A–B). Pronotum shiny, smooth, but curvature of pronotum with a deep grove. Mesopleuron convex, extended smooth except margins lateral and ventro-lateral that form a L-shaped region that possesses small, dense and homogeneous punctuations (Fig. 4B); mesopleuron with a deep dent just above of L-shaped area, demarcating the border of the area with elongate foveae (Fig. 4B). Mesosternum slightly flat with a median row of foveae. Metepisternum and metepimeron separated by a groove with several deep foveae throughout (Fig. 4B), metepisternum smooth and narrower than metepimeron, apical margin metepisternum just above hindcoxa outlined by a wide, flat carina (Fig. 4B). Mesoscutum as wide as head, with small, sparse and homogenous punctures. Notauli clearly impressed, but not reaching the transscutal articulation (Fig. 4G). Scutellar sulcus with seven deep, carinated foveae of heterogeneous size (Fig. 4G). Scutellum shiny with fine, sparse punctures and delimited by carina. Axillary trough of scutellum and axillary trough of metanotum both with vertical parallel carinae (Fig. 4H); space among ATM carinae wider than ATS carinae (Fig. 4H). Lunule of scutellum and medioposterior band of scutellum smooth and shiny (Fig. 4H). Medioposterior band of metanotum and medioanterior pit of metanotum forming a pentagonal-shaped delimited by carinae (Fig. 4H). Posterior rim of metanotum thin and smooth (Fig. 4H). Propodeum with a complete median-longitudinal carina dividing the propodeum in two halves, each half with one additional carina that does not branch basally at the same point than median-longitudinal carina (Figs 4H–I); space between median and an additional carina wider as they become more

distant from propodeal foramen (Figs 4H–I), and all three carinae crossed by transverse semicircular carinae, although apically less transverse carinae than basally.

Wings (Fig. 4A). Fore wing with vein r straight (0.27 mm), arising just beyond middle of stigma; vein 2RS longer than 2M and (Rs+M)b veins (0.24:0.10:0.10 mm). Hind wing with vannal lobe reduced, slightly convex; edge with sparse setae throughout. Costal and basal cell infuscate.

Legs (Figs 4A, F, I–J). Hind coxa reaching apex of tergite III (Fig. 4I), outer dorsal surface of hind coxa with an area delimited by a strong longitudinal carina running from base to apex, but last third apically the carina turns inward (Fig. 4I); area surrounded by the carina with rugulose punctuations that are more visible in dorsal view, and with an additional basal carina which splits and runs only the first third basally (Fig. 4I); hind tibia with outer spur half as long as inner spur (0.36:0.72 mm); inner spur more than half as long as hind basitarsus (0.72:0.92 mm) (Fig. 4F); outer dorsal side of hind tibia moderately spinose (Fig. 4F).

Metasoma (Figs 4A, I–J). Petiole of tergite I narrow (Fig, 4I), length 0.52 mm, distinctly constricted at anterior half (minimum width 0.10 mm), but subapically wider (maximum width 0.26 mm); petiole with a deep groove extending more of two thirds tergite I length (Fig. 4I); hypopygium not protruding beyond apex of metasoma (Fig. 4J), hypopygium plate with truncate apex (Fig. 4J); ovipositor sheaths length 0.36mm, glabrous, with apex rounded protruding apex of metasoma (Fig. 4A, J)

Males. Unknown.

Etymology. The name is based on the country of Panamá, where the holotype was collected.

Distribution. The species is only known from the original collecting site in Panamá.

Host. Unknown.

Conclusions

Neotropical *Wilkinsonellus* range from 4.0 to 4.8 mm in length, excluding antennae, and all specimens were collected in lowland tropical rain forest 500 m.a.s.l. or lower in elevation. Palaeotropical *Wilkinsonellus* range from 2.5 to 4.8 mm in length, and occur at altitudes up to 1700 m.a.s.l.

Wilkinsonellus has not been the only genus within Microgastrinae that was initially believed to be confined to a specific zoogeographical region. This is also true for *Austrocotesia* Austin and Dangerfield and *Parapanteles* Ashmead, each of which has turned out to have a much wider distribution. *Austrocotesia* was erected as a new genus in 1992. In that time, it was considered restricted to Papua New Guinea and the adjacent Australian region of North Queensland (Austin and Dangerfield 1992). However, the first two species from South America–Colombia and Ecuador– were described thirteen years later (Valerio and Whitfield 2005). Equally, *Parapanteles* was originally recorded only from the Australian and American continents. Ashmead proposed the genus in 1900. However, after little more than a century, *Parapanteles* was reported in South Africa –Western

Cape province, Cederberg (Valerio et al. 2005). *Austrocotesia* was also reported from the Neotropics at the same time as *Wilkinsonellus* in a chapter on Microgastrinae (Whitfield 1997) included in the Manual of the New World genera of the family Braconidae (Hymenoptera). Another genus mentioned in that manual was the Afrotropical genus *Beyarslania,* formerly known as *Xenogaster* (Koçak and Kemal 2009). However, those undescribed Neotropical *Beyarslania* species possibly belong to *Mariapanteles,* a genus recently erected (Whitfield et al. 2012). Thus, *Beyarslania* is still restricted to the Afrotropical region. In brief, all the new records point suggest that *Wilkinsonellus* as well as *Austrocotesia* and *Parapanteles* have a more extensively Gondwanan distribution.

The new distribution of *Wilkinsonellus* has been discovered thanks to large-scale rearing projects as well as arthropod diversity surveys undertaken in recent decades in the Neotropical region. The importance of rearing projects lies in the fact the associations across more than two trophic levels are possible. The identification of parasitized larval hosts implies the use of external morphological characteristics present on the larvae combined with the food plant and microlocation, because the caterpillar host is often destroyed when the larval parasitoid emerges. In contrast, specimens collected by malaise trap contribute mainly to inventory of biological diversity, except that most ecological information is lacking. Notwithstanding the current efforts, the extreme richness of the Neotropics means that both taxonomic and biological records continue to be highly incomplete (Whitfield et al. 2002) and more studies are considered necessary in order to improve understanding of the distribution patterns of the Neotropical Microgastrinae fauna. This situation also applies to other critical areas in the planet (i.e., Wallacea, New Guinea, Solomon Islands) that are still unexplored; consequently the understanding of the global distribution patterns remains incomplete.

Acknowledgments

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