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Sergei I. Golovatch & Robert Mesibov



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Robert Mesibov

RESEARCH ARTICLE



The millipede genus *Caucasodesmus* Golovatch, 1985, with the description of a new species from the Crimea, Ukraine (Polydesmida, Diplopoda, Trichopolydesmidae)

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Abstract

The hitherto monotypic genus *Caucasodesmus* is new to the Ukrainian list due to the discovery of *C. tauricus* **sp. n.** in a cave in the Crimea. The new species is easily distinguished from *C. inexpectatus* Golovatch, 1985, the type, and only other, known species of this genus, in the abundantly setose collum and following metaterga, and more elaborate gonopods. The status of *Caucasodesmus*, which shows in the superfamily Trichopolydesmoidea where it definitely belongs such evident generic-level apomorphies as the absence of bacilliform sensilla on antennomeres 5 and 7, of a cannula on the gonocoxite, and of a seminal groove on a biramous gononod telopodite (apparently, both latter characters are functionally correlated to each other), is refined by formally reassigning it to the family Trichopolydesmidae.

Keywords

millipede, Trichopolydesmidae, taxonomy, new species, cave, Crimea

Introduction

The millipede fauna of the Crimea has recently been reviewed (Golovatch 2008), with only 14 species from 11 genera, seven families and six orders being involved. Of these, only two or three species are possibly Crimean endemics, whereas most show more or less widely (Euro-)Mediterranean distributions.

The more so important is the present discovery of still another new millipede in a cave in the Crimea. Unlike all other faunal elements, this new species might prove to represent the first truly relict, palaeoendemic in the diploped list of that peninsula.

Material serving as the basis for the present contribution was captured with pitfall traps, later transferred into 75% alcohol and is currently deposited in the collection of the Zoological Museum, State University of Moscow, Russia. Specimens were studied and illustrated using standard stereomicroscopic, photographic and drawing equipment.

Systematics

Trichopolydesmidae Verhoeff, 1910

Caucasodesmus Golovatch, 1985

Caucasodesmus Golovatch, 1985: 40.

Type species: Caucasodesmus inexpectatus Golovatch, 1985, by original designation.

Caucasodesmus tauricus sp. n.

urn:lsid:zoobank.org:act:66FEBC49-89EC-432E-A0E2-561179B19B24 http://species-id.net/wiki/Caucasodesmus_tauricus Figs 1–8

Type material: Holotype ♂, Ukraine, Crimea, Mt Villya-Burun, Cave Villyaburunskaya, pitfall traps, 12.05.2008–12.10.2010, leg. A. Koval. – Paratype: 1 ♀, same locality, 19.07.2004–17.07.2006, leg. A. Koval.

Diagnosis: Easily distinguished from *C. inexpectatus* Golovatch, 1985, the type, and only other, known species of this genus, by the abundantly setose metaterga and more elaborate gonopods.

Description: Length of both sexes ca 8 mm, width of midbody pro- and metazona 0.8 and 1.5 mm, respectively. Coloration in alcohol from uniformly pallid to light yellowish.

Body with 20 segments. Tegument mainly dull, at most slightly shining, texture very delicately alveolate. Head densely pilose throughout; epicranial suture distinct



Figures 1–4. *Caucasodesmus tauricus* sp. n., holotype. 1, 2 anterior half of body, dorsal and lateral views, respectively 3, 4 posterior portion of body, dorsal and ventral views, respectively. Photographed not to scale.



Figures 5–8. *Caucasodesmus tauricus* sp. n., holotype. 5 leg 9 (setae not shown) 6 right gonopod, anteromesal view 7, 8, left gonopod, mesal, and lateral views, respectively. Scale bar: 0.4 (5) and 0.2 mm (6–8).

but thin; isthmus between antennae ca 1.5 times broader than length of antennomere 1, still broader than diameter of antennal socket. Antennae rather short, evidently clavate due to a considerably enlarged antennomere 6, slightly overreaching segment 2 dorsally; antennomeres 2, 3 and 6 longest, subequal in length (Figs 1, 2); only antennomere 6 with a large, compact, roundish, distodorsal group of bacilliform sensilla.

In width, collum < segment 2 = 3 < head = 4 < 5=16 (\Im) or head = collum = segment 2 = 4 < 5=16 (\Im), thereafter body gradually tapering towards telson. Paraterga moderately developed, starting from collum, subhorizontal to slightly declivous, set high but always lying slightly below a faintly convex dorsum, devoid of shoulders frontally (Figs 1–3). Caudal corner of postcollum paraterga invariably spiniform, pointed, starting from segment 4 extending increasingly further than rear tergal margin. Lateral edge of paraterga with neither marginal groove nor thickening, with 5–6 clear setigerous indentations. Pore formula normal, ozopores evident, round, located laterally in front of caudalmost incision. Collum and following metaterga beset with numerous medium-sized setae set on minute knobs, polygonal bosses missing (Figs 1–3). Stricture between pro- and metazona wide, shallow and smooth. Limbus very thin, microdenticulate. Pleurosternal carinae absent (Fig. 2). Epiproct short, conical, directed caudoventrally; preapical papillae small (Fig. 4). Hypoproct subtrapeziform, setiferous papillae at caudal corners evident, rather well separated.

Sterna without modifications, poorly setose. Epigynal ridge very low. Legs rather short (Figs 2, 5), ca 1.2–1.3 (\mathcal{J}) or 0.9–1.0 (\mathcal{Q}) times as long as midbody height; \mathcal{Q} legs slightly slenderer; \mathcal{J} legs with clearly enlarged prefemora and femora; tarsi especially long and slender, claw long, ca 1/4 length of tarsus; sphaerotrichomes missing (Fig. 5).

Gonopod aperture large, transversely oblong-oval, taking up nearly all of ventral part of metazonite 7. Gonopods (Figs 6–8) with large, globose, medially fused coxae carrying rather numerous setae laterally, but no trace of a cannula. Telopodite subfalcate, distally of a rather short prefemoral (= setose) portion split into two branches: exomere (ex) largest and longest, more simple, whereas endomere (en) shorter, more complex in shape; an evident, tooth-like, mesal process (d) at base between both ex and en; no trace of a seminal groove.

Remarks. This species is an unquestioned relict troglobite and, based on its zoogeographical traits, might well represent the first palaeoendemic in the diplopod fauna of the Crimea.

Only one species of *Caucasodesmus* has hitherto been known: *C. inexpectatus* from Cave Nyvjin Lagat (= Nyvdzhinlagat, = Tagardonskaya) in North Ossetia, central Caucasus Major (Golovatch 1984/85). The second congener, *C. tauricus* sp. n., shares with the type species such remarkable, clearly generic-level apomorphies as the absence of bacilliform sensilla on antennomeres 5 and 7, of a cannula on the gonocoxite, and of a seminal groove on a biramous gononod telopodite. Apparently, both latter characters are functionally correlated to each other, differing from the loss of a cannula alone which is observed in the families Dalodesmidae and Rhachodesmidae. The differences lie in *C. inexpectatus* showing a far more moniliform body, only three transverse rows of setae on the collum and following metaterga, and less strongly elaborate gonopod telopodites.

Systematic position of Caucasodesmus

Originally, *Caucasodesmus* was treated as a genus of the small Holarctic family Macrosternodesmidae (Golovatch 1984/85). However, Shear and Shelley (2007), in their recent reassessment of the Macrosternodesmidae, have ejected *Caucasodesmus* from that family, leaving it unclassified. These authors have also advanced a new terminology of the various parts of a polydesmidan gonopod. This has been further refined even more recently (Shear et al. 2009), in particular in accepting such denominations as exo- and endomere.

The superfamily Trichopolydesmoidea can be defined by its gonopod prefemoral (= setose) part orientated mostly transversely to the body's main axis, extending mesally across the entire width of the coxae (Hoffman 1982; Simonsen 1990). Within this superfamily, where *Caucasodesmus* undoubtedly belongs, there are several, mainly small families in addition to Macrosternodesmidae: Trichopolydesmidae, Neoarctodesmidae, Furhmannodesmidae and Mastigonodesmidae. To find a new, more suitable place for *Caucasodesmus*, their diagnoses must briefly be reiterated, especially as regards their gonopod conformation.

Macrosternodesmidae (Shear and Shelley 2007; Shear et al. 2009): In this Holarctic family, the gonopod aperture is large, transversely oval. The coxae completely fill the respective halves of the aperture, excavated mesad to accommodate the telopodites; the prefemora are horizontal or angling ventromesad, giving rise to the acropodite and often, but not always, to an additional projection; the acropodite part distal to the origin of a solenomere (distal zone) variably configured, sometimes folded, flattened, and not recognizable as such; the solenomere is long and narrow, arising subterminally, with neither a hairpad nor an accessory seminal chamber (= ampulla); the seminal groove opens terminally.

Nearctodesmidae (Shelley 1994; Shear et al. 2009): This small Nearctic group shares basically the same gonopod conformation with Macrosternodesmidae. No wonder it has sometimes been treated as only a subfamily or even a possible synonym of the latter family.

Trichopolydesmidae (Ceuca 1958; Mauriès 1983): This small, mainly Mediterranean family shows basically the same gonopod structure as the previous two groups, except in the prefemoral part sometimes being shortened (e.g. *Galliocookia* Ribaut, 1955, *Occitanocookia* Mauriès, 1980 and a few others), i.e. rather strongly resembling the condition observed in the family Polydesmidae (see Hoffman 1980; Simonsen 1990), while the telopodite is bi- or uniramous, far less elaborate, often with a long flagelliform solenomere. Yet I am inclined to follow Mauriès (1983) in treating such somewhat deviating genera as representing rather peculiar Trichopolydesmoidea.

Mastigonodesmidae (Mauriès 1980, 1982): This very small, purely western Mediterranean group of polydesmidean millipedes is sometimes regarded as only one of the numerous genera of Polydesmidae (Hoffman 1980; Simonsen 1990), apparently because the gonopod prefemoral part in *Mastigonodesmus* Silvestri, 1898, is also shortened, but, due to its globose gonocoxae and a peculiar, parabasal, long and coiled solenomere, it seems more similar to trichopolydesmoids. So I am again inclined to follow Mauriès (1980, 1982) in regarding this group as representing rather peculiar Trichopolydesmoidea as well.

Fuhrmannodesmidae (Golovatch 1994): This profoundly diverse, pantropical group of small polydesmideans shows a wide range of situations transitional in gonopod conformation between the typical Polydesmoidea and the typical Trichopolydesmoidea. At least in the Neotropical fauna, the gonopod coxae can be small and devoid of a gonocoel, with (sub)erect telopodites, yet more often the coxae are enlarged and deeply excavate for the accommodation of more stout, usually elaborate telopodites that can have a shortened to medially stretched prefemoral part supporting either crossing or parallel acropodites, the latter with or without a distinct solenomere. This highly heterogeneous assemblage certainly merits splitting into several natural families, but such a task is by necessity to be deferred because of the numerous genera and species involved, many of which still require revision.

Based on the above diagnoses and distributions, it appears to be quite difficult to unequivocally reallocate *Caucasodesmus*. The correlated absence of both a cannula and a seminal groove is probably a sufficiently strong apomorphy to erect still another family of Trichopolydesmoidea for the accommodation of solely this genus, but I refrain here from doing so pending more information becomes available. New taxa are still being regularly described, new synonymies established, and old types revised. Instead I reassign *Caucasodesmus* to Trichopolydesmidae as a family not only representing the oldest taxon in the superfamily, but also one which shows the same basic traits of gonopod structure and a coherent distribution pattern.

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I am most grateful to Alexandr Koval, St Petersburg, Russia, who has kindly allowed me to study his invaluable material, as well as to deposit it entirely in the Moscow Museum. I am also deeply obliged to Kirill Makarov, Moscow, Russia who skillfully took the pictures, and to Igor Muratov, Pietermaritzburg, Republic of South Africa for his kind technical assistance.

References

- Ceuca T (1958) Contribuții la cunoașterea diplopodelor din fauna Republicii Populare Romîne. III. Diplopode cavernicole. Studii și Cercetări de Biologie (Cluj) 2(9): 335–343.
- Golovatch SI (1984/85) Two new genera of cave-dwelling millipedes (Diplopoda), with remarks on the millipede fauna of West Caucasian caves. International Journal of Speleology 14: 39–50.

- Golovatch SI (1994) Further new Fuhrmannodesmidae from the environs of Manaus, Central Amazonia, Brazil, with a revision of *Cryptogonodesmus* Silvestri, 1898 (Diplopoda, Polydesmida). Amazoniana 13(1/2): 131–161.
- Golovatch SI (2008) On three remarkable millipedes (Diplopoda) from the Crimea, Ukraine. International Journal of Myriapodology 1: 97–110. doi:10.1163/187525408X316767
- Hoffman RL (1980) Classification of the Diplopoda. Muséum d'histoire naturelle, Genève, 237 pp. [for 1979].
- Hoffman RL (1982) Diplopoda. In: Parker SP (Ed) Synopsis and classification of living organisms 2. McGraw-Hill, New York & St Louis, 689–724.
- Mauriès JP (1980) Description d'une nouvelle espèce et d'un genre nouveau de diplopodes polydesmides hypogés récoltés dans l'arrondissement de Béziers (Héraults). Bulletin de la Société d'Histoire Naturelle de Toulouse 116(3/4): 228–234.
- Mauriès JP (1982) Un nouveau diplopode polydesmide cavernicole du Département du Gard : Manstigonodesmus fagniezi n. sp. (Polydesmidea, Mastigonodesmidae). Bulletin de la Société d'Histoire Naturelle de Toulouse 118: 141–144.
- Mauriès JP (1983) Le genre Galliocookia Ribaut, 1954. Deux espèces nouvelles des grottes de l'Ardèche et du Gard (Myriapoda, Diplopoda, Polydesmida). Bulletin de la Société d'Histoire Naturelle de Toulouse 119: 103–110.
- Shear WA, Shelley RM (2007) The milliped genus *Tidesmus* Chamberlin, 1943 (Polydesmida: Macrosternodesmidae). Zootaxa 1656: 51–68.
- Shear WA, Taylor ST, Wynne JJ, Krejca JK (2009) Cave millipeds of the United States. VIII. New genera and species of polydesmidan millipeds from caves in the southwestern United States (Diplopoda, Polydesmida, Macrosternodesmidae). Zootaxa 2151: 47–65.
- Shelley RM (1994) The milliped family Nearctodesmidae in northwestern North America, with accounts of *Sakophallus* and *S. simplex* Chamberlin (Polydesmida). Canadian Journal of Zoology 72: 470–495. doi:10.1139/z94-066
- Simonsen Å (1990) Phylogeny and biogeography of the millipede order Polydesmida, with special emphasis on the suborder Polydesmidea. Institute of Zoology, University of Bergen, Bergen, 114pp.

RESEARCH ARTICLE



The millipede family Polydesmidae in Taiwan, with descriptions of five new species (Polydesmida, Diplopoda)

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Abstract

Polydesmidae are represented in Taiwan by seven species in two genera. Neither of the genera is endemic to Taiwan, but six of the species are, including five new: *Nipponesmus minor* **sp. n.**, *Epanerchodus bispinosus* **sp. n.**, *E. curtigonopus* **sp. n.**, *E. flagellifer* **sp. n.** and *E. pinguis* **sp. n.** In addition, the diagnosis of the hitherto enigmatic genus *Nipponesmus* Chamberlin & Wang, 1953 is refined vis-à-vis the especially similar, Central Asian, Siberian and Eastern European genus *Schizoturanius* Verhoeff, 1931, chiefly based on new material of the type-species *N. shirinensis* Chamberlin & Wang, 1953; this species is adequately redescribed and represents still another Taiwanese endemic. A key to all three currently known species of *Nipponesmus* Chamberlin & Wang, 1953 is given. The highly speciose Central to East Asian genus *Epanerchodus* Attems, 1901 is represented in Taiwan by five species, all keyed, including *E. orientalis* Attems, 1901, which is long known to be highly variable in Japan and found particularly polymorphous and apparently allochthonous in Taiwan. The following synonymy is formalized: *E. orientalis orientalis* Attems, 1901 = *E. orientalis takakuwai* Verhoeff, 1913, **syn. n.** The genus *Usbekodesmus* Lohmander, 1932 is formally synonymized with *Epanerchodus* Attems, 1901, **syn. n.**, resulting in the following new formal transfers: *Epanerchodus redikorzevi* (Lohmander, 1932), *E. swatensis* (Golovatch, 1991), *E. varius*

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(Geoffroy & Golovatch, 2004), *E. anachoretus* (Golovatch, 1986), *E. buddhis* (Golovatch, 1986), *E. occultus* (Golovatch, 1986), *E. sacer* (Golovatch, 1987), *E. theocraticus* (Golovatch, 1990) and *E. theosophicus* (Golovatch, 1986), all **comb. n.** ex *Usbekodesmus*. The distributions of all seven species of Polydesmidae occurring in Taiwan are mapped and discussed.

Keywords

millipede, Polydesmidae, taxonomy, new species, new synonymy, key, Taiwan

Introduction

The millipede fauna of Taiwan is still quite poorly explored (Korsós 2004), with fewer than 70 species currently reported from this large, subtropical to tropical island. Many more species may be expected to occur there, to judge from the recent increase in the list of Taiwanese Glomerida from one species to five (Golovatch et al. 2010). This statement is easy to reconfirm with the large family Polydesmidae, order Polydesmida, taken as another example. Taiwan has hitherto been known to support only two polydesmid species: *Epanerchodus orientalis* Attems, 1901 and *Nipponesmus shirinensis* Chamberlin & Wang, 1953, both from a few localities only (see review: Korsós 2004).

Prompted by the abundant new material collected during the last couple of decades all over the island, below we offer a revision of the Taiwanese Polydesmidae. Already seven species appear to be involved, representing two genera. These new samples also allow for the diagnosis of one genus to be refined, and the synonymy of another one formalized.

Material and methods

Material serving as the basis for the present contribution was preserved in 75% alcohol and is currently shared between the collections of the National Museum of Natural Science, Taichung, Taiwan (NMNS), Taiwan Forest Research Institute, Taipei, Taiwan (TFRI), Department of Biological Sciences, National Sun Yat-Sen University, Kaohsiung, Taiwan (NSYSU), Zoological Museum, State University of Moscow, Russia (ZMUM), Natural History Museum of Denmark, University of Copenhagen, Denmark (ZMUC), Muséum national d'Histoire naturelle, Paris, France (MNHN), and Institute of Biology and Soil Science, Far Eastern Branch, Russian Academy of Sciences, Vladivostok, Russia (IBSS), as indicated hereafter. Specimens were studied and illustrated using standard stereomicroscopic, photographic and drawing equipment.

In the catalogue sections, which mostly refer to the fauna of Taiwan alone, D stands for the original description, N for additional descriptive notes, and R for a mere mention or record.

Systematics

Nipponesmus shirinensis Chamberlin & Wang, 1953 http://species-id.net/wiki/Nipponesmus_shirinensis

Figs 1-13

Nipponesmus shirinensis Chamberlin & Wang, 1953: 4 (D). Nipponesmus shirinensis – Golovatch 1991: 157 (N); Korsós 2004: 26 (R)

Material examined: 2 juv. (NSYSU), Taiwan, Taipei City, Wenshan Distr., Chih-Nan Temple, 03.2002, leg. C.C. Chen et al.; $2 \sqrt[3]{}, 2 \sqrt[9]{}$ (NMNS-6555-001), $1 \sqrt[3]{}$ (MNHN JC 331), Nantou County, Re-nai Township, Mei-Feng, 22.10.2001; 1 👌 (ZMUC), 1 👌 (NMNS-6555-002), same locality, 15.10.2001; 1 👌 (TFRI), same locality, 19.02.2002; 1 👌 (NMNS-6555-003), same locality, 15.10.2001; 1 👌 (ZMUM), Nantou County, Huisun timber land, 20.09.1997; 1 d (NMNS-6555-004), same locality, 10.1997; all leg. S.H. Wu; 3 ♂, 5 ♀ (TFRI), Nantou County, Lugu Township, Sitou, 15.11.2005, leg. J.D. Lee; 8 juv. (NSYSU), same locality, 6.07.2010, leg. H.W. Chang; $1 \stackrel{?}{\triangleleft}, 1 \stackrel{?}{\downarrow}$ (TFRI), Taitung County, Taimali Township, I-Ma forest road, 06.12.2004, leg. S.Y. Wu; 4 3, 1 9, 5 juv. (NSYSU), Chiavi County, Alishan Township, Nansi Forest road, ca 2,000 m a.s.l., 29.10.2010, leg. H.W. Chang; 1 3 (ZMUM), Hsinchu County, Wufeng Township, Sakaru (Shilu) trail, 30.09.2005; 1 🖒 (NMNS-6555-005), same locality, 22.09.2005, all leg. H.D. Zhu; 1 Å (NSYSU), Kaohsiung County, Liouguei, Shanping Workstation, 04.2004, leg. M.J. Hung; 1 & (NMNS-6555-006), Kaohsiung County, Taoyuan Township, Tengjhih, 1,550 m a.s.l., 17.11.2010, leg. S. Golovatch; 2 Q (NMNS-6555-007), Kaohsiung County, Taoyuan Township, Chungchihkuan, 15.03.2005, leg. Y.C. Chang; 1 juv. (NSYSU), same locality, Taiwania cryptomeroides plantation, 15.10.2005, leg. M.H. Hsu; 1 3, 1 2 (IBSS), Pingtung County, Chunri Township, Mt Dahan, 1,200 m a.s.l., 15.12.2009; 2 ♀ (NMNS-6555-008), same locality, ca 1,850 m a.s.l., 15.12.2009, all leg. M.H. Hsu.

Diagnosis: Differs from the other Polydesmidae in Taiwan by the larger body and often a dark coloration, from the only sympatric congener *N. minor* sp. n. also in the collum being broader than the head and in the gonopod showing a strongly elongate, slender and falcate telopodite (see also Key below).

Redescription: Length of both sexes ca 18–25 mm, usually about 20–23 mm; width of pro- and metazona varying between specimens from 1.5–2.2 to 2.9–4.8 mm, respectively, usually 1.8–2.0 and 3.0–4.3 mm, respectively. Usually $\partial \partial$ somewhat smaller than QQ. Coloration in alcohol from uniformly pallid (faded?) to dark chocolate-brown; in the latter case, sides, venter and legs (light) grey-brown to dark brown (Figs 1–6). Body with 20 segments. Tegument mainly dull, at most slightly shining, texture very delicately alveolate. Frons and labrum densely pilose, vertex bare; epicranial suture distinct but thin; a paramedian pair of evident, oblique ridges above antennal sockets; isthmus between antennae considerably broader than diameter of



Figures 1–5. *Nipponesmus shirinensis* Chamberlin & Wang, 1953, \bigcirc (1) and \bigcirc (2) from Mei-Feng, \bigcirc (3–5) from Tengjhih. 1, 2 habitus, lateral view 3–5 anterior portion of body, dorsal, lateral and ventral views, respectively. Photographed not to scale.



Figures 6–9. *Nipponesmus shirinensis* Chamberlin & Wang, 1953, $\overset{\circ}{\bigcirc}$ (6, 7) from Tengjhih and $\overset{\circ}{\ominus}$ (8, 9) from Mei-Feng. 6 middle portion of body, dorsal view 7, 9 posterior portion of body, dorsal view 8 anterior portion of body, dorsal view. Photographed not to scale.



Figures 10–13. *Nipponesmus shirinensis* Chamberlin & Wang, 1953, \mathcal{J} from Sitou. **10** leg 9 **11, 12** right gonopod, lateral and mesal views, respectively **13** distal part of gonopod telopodite, enlarged, mesal view. Scale bar: 0.5 mm (**10–12**) and 0.25 mm (**13**). See text for explanation of labels.

antennal socket (Fig. 5). Antennae rather long and only slightly clavate (Fig. 5), either slightly overreaching segment 3 dorsally (\Im) or slightly shorter (\Im); antennomere 3 longest (Figs 3–5); antennomeres 5 and 6 each with a small, compact, distodorsal group of bacilliform sensilla; antennomere 7 with a minute dorsoparabasal cone and a distodorsal group of microscopic sensilla.

In width, head < collum < segment 2 < 3 < 4 < 5=15(16), thereafter body gradually tapering towards telson. Paraterga strongly developed, starting from collum, subhorizontal, set high but always lying slightly below a faintly convex dorsum, drawn clearly forward only on metatergum 2 (Fig 3). Starting from segment 8 or 9 (\mathcal{S}) or 16 (\mathcal{Q}), paraterga extending increasingly beyond rear tergal contour, caudal corners invariably evidently rounded, only on paraterga 17–19 subspiniform, usually slightly more narrowly rounded in \mathcal{S} compared to \mathcal{Q} (Figs 3, 6–9). Paraterga more (\mathcal{Q}) or less (\mathcal{S}) evidently rounded laterally (Figs 3, 6–9); starting from segment 2, all poreless segments with three, all pore-bearing ones with four, minute, sometimes even obliterate incisions at lateral margin. Front edges of metaterga slightly bordered and upturned, straight, usually forming a distinct shoulder. Pore formula normal, ozopores evident, dorsal, located in front of posteriormost marginal indentation. Metatergal sculpture typical, well-developed, with three transverse rows of setiferous, polygonal bosses (Figs 3, 6–9). Tergal setae very short, mostly obliterate, partly retained only on collum and/ or metatergum 19. Stricture between pro- and metazona wide, shallow and smooth (Figs 3, 4, 6–9). Limbus very thin, microdenticulate. Pleurosternal carinae absent (Fig. 4). Epiproct rather short, conical, preapical papillae very evident (Figs 7, 9). Hypoproct semi-circular; caudal, paramedian, setiferous papillae small and well-separated.

Sterna without modifications, very densely (\eth) (Fig. 5) or poorly (\heartsuit) setose, \heartsuit ones often shining. Epigynal ridge very low. Legs rather long and slender (Figs 5, 10), ca 1.5–1.6 (\circlearrowright) or 1.1–1.2 (\heartsuit) times as long as midbody height; \circlearrowright legs evidently enlarged, prefemora only slightly swollen dorsally and, like femora and, partly, postfemora, ventrally beset with shorter bifid setae turning into short sphaerotrichomes on postfemora, tibiae and tarsi (Fig. 10).

Gonopods (Figs 4, 5, 11-13) with large, subquadrate, medially fused coxae carrying a few long setae ventrally. Telopodite elongated, slender, falcate, prefemoral (densely setose) portion almost half as long as entire telopodite; seminal groove running mesally over most of its extent, only distally moving frontally to recurve first laterad and then a little basad at base of both a somewhat shorter, more complex endomere (**en**) and a longer, simpler exomere (**ex**); **en** beset with long, bacilliform setae distally and supplied with an evident spine (**s**) mesally, as well as a prominent pulvillus near base, this pulvillus being likewise beset with bacilliform setae and marking the end of seminal groove devoid of any accessory seminal chamber; **ex** strongly unciform apically, with an additional lateral tooth distally to subapically.

Remarks. This species is the largest, as well as one of the most conspicuous and common among the polydesmids in Taiwan. It inhabits a wide range of habitats, mainly montane woodlands above 1,200 m a.s.l. (Map 1).

Nipponesmus minor sp. n.

urn:lsid:zoobank.org:act:225E19E9-CF6B-46A1-A16F-7EFAD3A91A58 http://species-id.net/wiki/Nipponesmus_minor Figs 14–23

Type material: Holotype \mathcal{F} (TFRI), Taiwan, Ilan County, Tatong Township, near Lakes Jialuohu, ca 2,250 m, 27.04.2003, leg. Y.M. Chen. Paratypes: 3 \mathcal{F} , 1 \mathcal{P} (TFRI), same locality, 14.03.2003; 12 \mathcal{F} , 8 \mathcal{P} , 1 fragm. (TFRI), same locality, 28.04.2003; 1 \mathcal{F} (TFRI), same locality, 27.04.2003; 2 \mathcal{F} (ZMUM), 1 \mathcal{F} (IBSS), 2 \mathcal{F} (NSYSU), same locality, 25.12.2002; 1 \mathcal{F} (ZMUC), 1 \mathcal{F} , 1 \mathcal{P} (TFRI), same locality, 7.11.2001; 1 \mathcal{F} , 1 \mathcal{F} fragm. (TFRI), same locality, 4.06.2003, all leg. Y.M. Chen; 1 \mathcal{F} (ZMUM), same locality, 24.10.2002, leg. J.T. Chao; 1 \mathcal{F} (TFRI), Taichung County, Shengguang, 24.09.2002; 1 \mathcal{F} (MNHN JC 332), same locality, 24.01.2003; 1 \mathcal{F} (TFRI), same locality, 24.09.2002, all leg. W.C. Yeh; 1 \mathcal{F} (NMNS-6556-001), Nantou County, Ren-ai Township, Mei-Feng, 19.02.2002; 1 \mathcal{F} (NMNS-6556-002), same locality, 11.07.2002; 4 \mathcal{F} (NMNS-6556-003), same locality, 15.04.2002, all leg. S.H. Wu.



Figures 14–19. *Nipponesmus minor* **sp. n.**, \circlearrowleft paratype from Jialuohu. **14** habitus, lateral view **15–17** anterior portion of body, dorsal, lateral and ventral views, respectively **18, 19** posterior portion of body, dorsal and ventral views, respectively. Photographed not to scale.



Figures 20–23. Left gonopods of *Nipponesmus minor* sp. n., \mathcal{J} paratypes from Mei-Feng (**20, 21**) and Jialuohu (**22, 23**), mesal, lateral, mesal and lateral views, respectively. Scale bar: 0.2 mm.

Name: To emphasize the smaller body size and the shorter gonopod telopodite.

Diagnosis: Differs from *N. shirinensis*, the only other congener known from Taiwan, in the smaller size, as well as in the collum being narrower than the head and in the gonopod telopodite being stouter and shorter (see also Key below).

Description: Length of both sexes ca 12–16 mm; width of pro- and metazona varying between specimens from 0.8-1.3 to 1.5-2.0 mm, respectively. Holotype ca 12 mm long, and 0.8 and 1.5 mm wide on pro- and metazona, respectively. Usually $\Im \Im$



Map 1. Distribution of *Nipponesmus* species in Taiwan. Borderlines show borders between the counties. *N. minor* sp. n.: filled red triangles; *N. shirinensis*: filled black circles.

somewhat smaller than $\bigcirc \bigcirc$. Coloration in alcohol from uniformly pallid (faded?) to yellowish to reddish-brown; in the latter case, sides, venter and legs light grey-brown (Figs 14–19).

All characters as in *N. shirinensis*, except as follows.

Antennae a little shorter, usually reaching midway of segment 3. In width, collum < head < segment 2 < 3 < 4 < 5=15(16), thereafter body gradually tapering towards telson. Starting from segment 16 (\bigcirc , \bigcirc), paraterga extending increasingly beyond rear tergal contour, caudal corners invariably evidently rounded, but even on paraterga 17–19 not spiniform (Figs 15, 18). Paraterga less evidently rounded laterally even in \bigcirc , lateral edges mostly subparallel in \bigcirc (Figs 15, 18), incisions being visible. Metatergal sculpture typical, rather superficial, with three transverse rows of setiferous, polygonal bosses (Figs 15, 18). Tergal setae very short, usually retained at least on collum and/or metatergum 19 (Figs 15, 16, 18).

Gonopod telopodite (Figs 20–23) much stouter; endomere (**en**) slightly longer than exomere (**ex**), beset with long, bacilliform setae nearly throughout, usually supplied with an evident spine (**s**) or tooth mesally, as well as a usually somewhat less prominent pulvillus near base; **ex** often not so strongly unciform apically, often with an additional lateral tooth in distal part.

Remarks. This species is not so widely distributed in Taiwan. Allopatry is prevailing, as it is only at Mei-Feng that both the congeners co-occur (Map 1). However, *N. minor* sp. n. quite often lives even syntopically together with *Epanerchodus orientalis* (see below).

A study of the ample material representing not only the type species *N. shirinensis*, but also the above new congener from Taiwan allows for the identity of *Nipponesmus* Chamberlin & Wang, 1953 to finally become clarified.

This genus has hitherto remained enigmatic, originally described too poorly (Chamberlin and Wang 1953) to shed any significant light on its affinities. It was only based on the gonopod conformation of the beautifully described *N. tangonis* (Murakami, 1973), a species from Honshu, Japan definitely most similar to *N. shirinensis*, that Golovatch (1991) suggested the relationships of *Nipponesmus* as a genus possibly somewhat intermediate between *Schizoturanius* Verhoeff, 1931 and *Epanerchodus* Attems, 1901.

In *N. shirinensis*, the gonopod telopodite (Figs 11–13) is indeed biramous only distally, being divided into subequally prominent endo- and exomere. Furthermore, the endomere (**en**) is beset with a characteristically bacilliform trichome, whereas the exomere (**ex**) is simple. The seminal groove runs mostly mesally to recurve neatly between **ex** and **en** and then to debauch somewhat basally into a prominent hairy pulvillus which is also beset with the same peculiar trichome, and is devoid of an accessory seminal chamber. The same general pattern is observed both in *N. tangonis* and *N. minor* (Figs 20–23). What we term here as endomere is the branch which Murakami (1973) erroneously referred to as solenomere in his *N. tangonis*. Yet it can hardly be called such, because the seminal groove ends somewhat basally of it and thus fails to support it at all. This is where one of the basic distinctions between *Nipponesmus*

and *Schizoturanius* seems to lie, because in *Schizoturanius* the recurvature point of the seminal groove between both distal branches **ex** and **en** is about level to the pulvillus (Golovatch 1979). So we can speak in this case about a true solenomere. In addition, in *Schizoturanius* an accessory seminal chamber, however small, is present. Another characteristic feature of *Nipponesmus* vis-à-vis not only *Schizoturanius*, but also all other genera of Polydesmidae is an abundant bacilliform trichome on the endomere. Although a similar trichome is known to occur in some European *Polydesmus* species as well, it is always located either on the exomere or on a solenomere. These three apomorphies distinguish *Nipponesmus* from the obviously most similar *Schizoturanius*, a genus encompassing several species in Central Asia, Siberia and the southern part of the Eastern European Plain (Golovatch 1979, 1991).

As regards Golovatch's (1991) placement of *Nipponesmus* also near *Epanerchodus*, following Hoffman (1980) who had synonymized these genera, this idea is false, as they appear to show too many profound differences in gonopod structure. Thus, in *Epanerchodus* the endomere is mostly absent, rarely present as only a rudimentary structure, while the seminal groove after the recurvature point still makes a long way basad to debauch into a prominent, simple-haired, accessory seminal chamber placed at the bottom of a profound parabasal cavity in the telopodite (see also below). Based on the gonopod conformation of one of the new Taiwanese species (see below), *Usbe-kodesmus* Lohmander, 1932, differing from *Epanerchodus* only in a somewhat better developed exomere, albeit also simple and more or less spiniform, is to be regarded as another junior synonym of *Epanerchodus*, syn. n. Arguments for synonymizing both these genera have long been put forth (Geoffroy and Golovatch 2004), but until now no formal synonymy has been advanced.

This results in the following new formal transfers: *Epanerchodus redikorzevi* (Lohmander, 1932), from Uzbekistan, Tajikistan and Afghanistan, *E. swatensis* (Golovatch, 1991), from Swat Province, northern Pakistan, *E. varius* (Geoffroy & Golovatch, 2004), from Hubei Province, southern China, as well as the Nepalese *E. anachoretus* (Golovatch, 1986), *E. buddhis* (Golovatch, 1986), *E. occultus* (Golovatch, 1986), *E. sacer* (Golovatch, 1987), *E. theocraticus* (Golovatch, 1990) and *E. theosophicus* (Golov vatch, 1986), all comb. n. ex *Usbekodesmus*.

The following key can serve to separate all three currently known species of *Nipponesmus*.

Key to Nipponesmus species

1	Adult body smaller, ≤ 10 mm long and ≤ 1.4 mm wide. Collum as wide as
	head. Endomere strongly enlarged, lobe-shaped, fringed by a very dense ba-
	cilliform trichome; exomere slender, much longer than endomere. Honshu,
	Japan
_	Adult body larger, at least 12 mm long and \geq 1.5 mm wide. Collum either
	broader or narrower than head. Endomere at most slightly enlarged digiti-

- 2 Adult body 18–25 mm long and 1.55–2.0 mm wide. Collum broader than head. Gonopod telopodite considerably longer (Figs 11–13) ..*N. shirinensis*
- Adult body 12–16 mm long and 2.9–4.8 mm wide. Collum narrower than head. Gonopod telopodite considerably stouter (Figs 20–23)...N. minor sp. n.

Epanerchodus orientalis Attems, 1901

http://species-id.net/wiki/Epanerchodus_orientalis Figs 24–36

Epanerchodus orientalis orientalis – Wang 1956: 155 (R); Wang 1963: 91 (R) *Epanerchodus orientalis takakuwai* – Wang 1958: 341 (R)

NB: Complete catalogue information referring to this species can be found in Murakami (1969)

Material examined: 10 \mathcal{F} (TFRI), 1 \mathcal{F} (NMNS-6557-001), 1 \mathcal{Q} (NSYSU), 2 \mathcal{F} (MNHN JC 333), Taiwan, Taichung County, Shengguang, 25.04.2003; 2 ♀ (TFRI), same locality, 26.03.2003; 1 ♀ (TFRI), same locality, 24.09.2002; 4 ♂ (TFRI), 1 ♂ (NMNS-6557-002), same locality, 24.07.2003, all leg. W.C. Yeh; 2 ♂, 1 ♀ (TFRI), 2 ♂, 1 ♀ (IBSS), Ilan County, Fushan, 23.03.2003; 2 ♀ (NMNS-6557-003), same locality, 18.05.2001; 5 $^{\circ}$, 1 $^{\circ}$ (TFRI), same locality, 19.06.2001; 1 $^{\circ}$ (TFRI), same locality, without date, all leg. J.T. Chao; 1 3 (ZMUM), same locality, 20.11.2001, leg. S.S. Lu; 52 ♂, 17 ♀, 4 fragm. (TFRI), 2 ♂ (ZMUC), 2 ♂ (NSYSU), Ilan County, Tatong Township, near Lakes Jialuohu, ca 2,250 m, 4.06.2003; 1 \bigcirc fragm. (TFRI), same locality, 28.04.2003; 8 $3, 6 \ (\text{TFRI})$, same locality, 20.06.2002; 1 3, (ZMUM), same locality, 25.04.2003; 1 ♂ (TFRI), same locality, 23.07.2002, all leg. Y.M. Chen; 1 ♀ (NSYSU), Taitung County, Yanping Township, Yanping Forest road, ca. 1,250 m, 3.06.2003, leg. M.H. Hsu; 2 🖉 (NSYSU), Hualien County, Fongbin Township, Guangfong Highway, ca 300 m, 6.05.2009; 1 Q (NSYSU), same County, Shoufang Township, ca. 230 m a.s.l., 5.05.2009, all leg. M.H. Shu; 2 🌻 (NMNS-6557-004), Pingtung County, Chaozhou Township, Si-Lin, 1.06.1999, leg. ?; 1 ♀ (NMNS-6557-005), Kaohsiung County, Taoyuan, Provincial Road No. 20, near 142.5 km road-sign, 3.09.2009, leg. C.Y. Huang.

Diagnosis: Differs from the other *Epanerchodus* species known from Taiwan in the variable, mostly medium size, coupled with the caudal corner of most of the paraterga being pointed, and in the gonopod telopodite being relatively slender, complex, highly variable in shape and armature (see also Key below).

Redescription: Length of both sexes ca 11–19 mm; width of pro- and metazona varying between specimens from 0.8–1.8 to 1.2–3.0 mm, respectively. Usually $\Im \Im$ somewhat smaller than $\Im \Im$. Coloration in alcohol from uniformly pallid (faded?) to light (reddish- to grey-) brown; in the latter case, venter and legs light grey to yellow (Figs 24–31). Body with 20 segments. Tegument mainly dull, at most slightly shining,



Figures 24–27. *Epanerchodus orientalis* Attems, 1901, from Fushan. **24** habitus, lateral view **25** anterior portion of body, subdorsal view **26** middle portion of body, dorsal view **27** posterior portion of body, dorsal view. Photographed not to scale.

texture very delicately alveolate. Labrum, frons and vertex densely pilose; epicranial suture clear but thin; no ridges above antennal sockets; isthmus between antennae considerably broader than diameter of antennal socket (Fig. 29). Antennae long and only slightly clavate (Figs 24, 25, 28), reaching behind end (\Im) or midway (\Im) of segment 4 dorsally; antennomere 3 longest, 5th highest (Figs 25, 28); antennomeres 5 and 6 each with a small, compact, distodorsal group of bacilliform sensilla; antennomere 7 with a minute dorsoparabasal cone and a distodorsal group of microscopic sensilla.

In width, either collum \leq segment 2 = 3 < 4 < head = 5(6)-15(16), or segment 2 = 3 < collum < head = 4 < 5 - 15(16) (both sexes), thereafter body gradually tapering towards telson. Paraterga strongly developed, starting from collum, subhorizontal, set high but always lying slightly below a faintly convex dorsum; front shoulders and caudal edge nearly straight on several postcollum metaterga, caudal corner always pointed. Collum (Fig. 28) nearly regularly elliptical, with an incision near caudal corner and three transverse rows of setae (6+6, 4+4 and 3+3). Starting from segment 5, paraterga extending increasingly beyond rear tergal contour, mostly subspiniform (Figs 25-28). Starting from segment 2, all poreless segments with three, all pore-bearing ones with four, small but evident incisions, each usually bearing a small seta on top at lateral margin. Pore formula normal, ozopores evident, dorsal, located in front of 4th indentation. Metatergal sculpture typical, rather well developed, with three transverse rows of setiferous, polygonal bosses (Figs 25-28). Tergal setae short, mostly retained, a little longer only on collum and in rear row on metatergum 19 (Figs 25, 27). Stricture between pro- and metazona rather obscure, wide, smooth and polished. Limbus very thin, microdenticulate. Pleurosternal carinae absent. Epiproct rather short, conical (Fig. 31), preapical papillae evident. Hypoproct semi-circular; caudal, paramedian, setiferous papillae evident and well-separated.

Sterna without modifications (Figs 29, 31), densely setose. Epigynal ridge very low, regularly rounded. Legs long and slender (Figs 28, 29), ca 1.8–1.9 (\Im) or 1.2–1.3 (\Im) times as long as midbody height; \Im legs evidently enlarged, prefemora only slightly swollen dorsally, femora ventro-parabasally with shorter bifid setae replaced by sphaero-trichomes in remaining parts of femora, as well as on entire postfemora, tibiae and tarsi.

Gonopods (Figs 32–36) with large, subquadrate, medially fused coxae carrying a few long setae ventrally. Telopodite stout to rather slender, subfalcate, prefemoral (densely setose) portion one-third to half as long as entire telopodite; seminal groove running mesally over much of its extent, only distally moving frontally to recurve first laterad and then mesad, squeezing neatly between a simple, more or less rudimentary to completely reduced exomere (**ex**) and a more complex, branching and always welldeveloped endomere (**en**), then groove continuing to a considerable extent basad to end into a large accessory seminal chamber lying near base of a prominent excavation, the latter carrying an evident hairy pulvillus; **en** often but not always with a strong mesal process (**s**), either slenderer and simple or larger and more complex in shape, as well as usually with a distinct, often again branching, laterobasal outgrowth (**p**); distal remainder of **en** elongate, often branching and enlarged, sometimes fringed with short setae or spines.



Figures 28–31. *Epanerchodus orientalis* Attems, 1901, \circlearrowleft from Jialuohu. **28,29** anterior portion of body, dorsal and ventral views, respectively **30** middle portion of body, lateral view **31** posterior portion of body, ventral view. Photographed not to scale.

Remarks. This species seems to be the most widespread and variable among congeners. It has heretofore been accepted as being split into two nominal subspecies: *E. orientalis orientalis* and *E. o. takakuwai* Verhoeff, 1913, but, given a similarly profound variation range in body size and shape, and, especially, in gonopod structure as observed in Japan alone, the subspecific status of *takakuwai* has long been questioned (e.g. Miyosi 1959, Murakami 1969, Nishikawa and Murakami 1993). Murakami (1993), in the latest checklist of the Japanese Diplopoda, treats *E. orientalis* without subspecies. Moreover, numerous samples from Hokkaido, Honshu and Shikoku, Japan, reveal that variation in gonopod conformation appears to be purely individual, failing to demonstrate any meaningful geographical patterns (Nishikawa and Murakami 1993). The same concerns the available samples from Taiwan. So we formalize here the long suspected synonymy: *E. orientalis orientalis* Attems, 1901 = *E. orientalis takakuwai* Verhoeff, 1913, syn. n.

It is noteworthy that, formally, *E. orientalis* fails to occur in southernmost Japan, i.e. on Kyushu Island and in the Ryukyus (Nishikawa and Murakami 1993, Nakamura and Korsós 2010), to reappear further south only in Taiwan. In northern Honshu, Japan, it is known to reach 26 mm in length and 3.4 mm in width, with the collum being slightly broader than the head (Murakami 1969). In Taiwan, as proven by our study of several abundant syntopic samples, the animals tend to be smaller, the collum is invariably narrower than the head, while rather often the gonopods are totally devoid of both an exomere remnant and process **s**, frequently with the distal, longest part of their endomere being slender, not expanded.

Looking at such a profound variation as observed in a number of peripheral and gonopod characters in *E. orientalis*, one cannot ignore several further nominal congeners described from Japan, including Kyushu, in which the gonopods look especially similar to those of E. orientalis: E. inferus Verhoeff, 1941, E. lobatus Verhoeff, 1941, E. satoi Takakuwa, 1954, E. tenuis Takakuwa, 1954, E. aculeatus Miyosi, 1954, E. etoi Miyosi, 1955, E. chichibensis Haga, in Takashima and Haga 1956, E. yoshidai Haga, in Takashima and Haga 1956, E. lacteus Shinohara, 1958, etc. (e.g. Takashima and Haga 1956, Shinohara 1958, Miyosi 1959). We suspect that some of them might well prove to represent junior synonyms of E. orientalis. Only future in-depth biological observations and such genetic investigations as bar-coding of such particularly similar forms can shed light on their true identities and statuses, because polymorphic variation has long been known in Epanerchodus. Thus, E. polymorphus Mikhaljova & Golovatch, 1981, widespread in the southern part of the Russian Far East and in northern Korea, shows two morphologically distinct morphs both in gonopod and peripheral structure in males, but a complete, overlapping range of the same somatic characters in females. Both male morphs invariably co-occur syntopically and either mates with any female variety (Mikhaljova and Golovatch 1981, Mikhaljova 2004). A similar situation is found in the nominate species E. acuticlivus Murakami, 1970 and E. aster Murakami, 1970, both described from the same cave in Shikoku, Japan. Murakami (1970) explicitly admitted that they were very close, with their females being indistinguishable, while the males showed small but stable differences in gonopod telopodite armature.



Figures 32–36. Right gonopods of *Epanerchodus orientalis* Attems, 1901, 33 from Shengguang (**32**), Jialuohu (**33–35**) and Guangfong Highway (**36**), mesal, lateral, mesal, sublateral and submesal views, respectively. Scale bar: 0.1 mm.

Based on the great variation observed in the populations of *E. orientalis* in Japan and, especially, Taiwan, the statuses of *E. polymorphus*, *E. acuticlivus* and *E. aster* as further congeners highly similar to *E. orientalis* are likewise to be questioned, as at least some of them might also prove to be the latter's junior synonyms. Yet no formal synonymies are advanced here as obviously being too premature at this purely descriptive taxonomic stage.

That not all of the congeners similar in gonopod structure to *E. orientalis* are synonyms of the latter is proven at least by *E. koreanus* Verhoeff, 1937, a species common throughout Korea, in Kyushu, Japan and in the southern Russian Far East. At least in Russia, it often occurs syntopically together with *E. polymorphus*. Yet *E. koreanus*, despite its minor variations in gonopod conformation, is easily recognizable even superficially through its much wider paraterga (3.3–3.8 versus 2.6–3.0 mm); in addition, these species never mate (Mikhaljova 2004). As another proof to the above statement may also serve *E. pinguis* sp. n., described below and representing still one more congener quite similar in gonopod structure to *E. orientalis*. In Taiwan, both are at least partly sympatric, but *E. pinguis* sp. n. differs markedly enough in a number of peripheral and gonopod characters to warrant recognition of a distinct species (see below).

In other words, several, but definitely not all, of the nominate species of *Epanerchodus* that show their gonopods particularly similar in structure to those of *E. orientalis* are jeopardized as potential junior synonyms of the latter species.

In Taiwan, *E. orientalis* occurs in various habitats ranging from lowlands to the mid-montane belt (up to 1,250 m a.s.l.) all over the island (Map 2).

Epanerchodus pinguis sp. n.

urn:lsid:zoobank.org:act:B0E8A6F1-335A-4961-9876-0328480D6D47 http://species-id.net/wiki/Epanerchodus_pinguis Figs 37–44

Type material: Holotype \mathcal{J} (head missing) (NMNS-6558-001), Taiwan, Nantou County, Huisun timber land, 15.04.2002, leg. S.H. Wu. Paratype \mathcal{J} (NMNS-6558-002), same locality, 24.03.1998, leg. S.H. Wu.

Name: To emphasize the stout gonopod telopodite.

Diagnosis: Differs from the other *Epanerchodus* species, in particular from the apparently especially similar *E. orientalis*, in the mostly square, broader and slightly upturned paraterga, coupled with the gonopod showing an unusually densely setose coxa and a remarkably stout telopodite (see also Key below).

Description: Length ca 16 (paratype) or 20 mm (holotype); width of midbody pro- and metazona 1.5 and 2.9 mm (paratype) or 1.5 and 3.0 mm (holotype), respectively. Coloration in alcohol uniformly light red-brown to red-brown; venter and legs yellowish (Figs 37–39).

All characters as in *E. orientalis* except as follows.

Antennae rather long, slender, only slightly clavate, reaching behind segment 3 dorsally; antennomere 3 longest, clearly longer than highest 5th; antennomeres 5 and 6 each with an evident, compact, distodorsal group of bacilliform sensilla; antennomere 7 with a minute dorsoparabasal cone and a distodorsal group of microscopic sensilla.

In width, collum < head \leq segment $2 \leq 3 < 4 < = 5-16$, thereafter body gradually tapering towards telson (Fig. 39). Paraterga strongly developed, starting from collum, slightly upturned, set high, mostly level to a very faintly convex dorsum, slightly below



Figures 37–41. *Epanerchodus pinguis* sp. n., \Diamond paratype. **37, 40** anterior portion of body, dorsal and ventral views, respectively; **38**, middle portion of body, dorsal view **39, 41** posterior portion of body, dorsal and ventral views, respectively. Photographed not to scale.



Figures 42–44. *Epanerchodus pinguis* sp. n., holotype. **42** leg 9 **43, 44** right gonopod, mesal and lateral views, respectively. Scale bar: 0.2 mm.

dorsum only on collum and segment 2; paraterga on collum small, subtriangular, a small lateral incision in front of a narrowly rounded caudal corner; front shoulders drawn forward only paraterga 2 and 3, straight and subrectangular on paraterga 4, onward straight but directed increasingly caudolaterad; caudal edge nearly straight on paraterga 2–7, thereafter caudal corner increasingly acutangular, nearly always narrowly rounded, only on segment 19 spiniform and nearly pointed, mostly lying nearly level to rear tergal contour until segment 15, onward extending increasingly beyond it (Figs 37–39). Paraterga



Map 2. Distribution of *Epanerchodus* species in Taiwan. Borderlines show borders between the counties. *E. bispinosus* sp. n.: empty black circle; *E. curtigonopus* sp. n.: blue cross; *E. flagellifer* sp. n.: filled green triangles; *E. orientalis*: filled grey squares; *E. pinguis* sp. n.: filled red circle.

2 with 3–4 small lateral incisions, all following poreless segments with three, all porebearing ones with four, small but evident incisions, each usually bearing a small seta on top at lateral margin. Metatergal sculpture typical, rather obliterate, with three indistinct transverse rows of setiferous, polygonal bosses (Figs 37–39). Tergal setae very short, mostly retained, a little longer only on collum and in rear row on metatergum 19 (Figs 37, 39). Stricture between pro- and metazona wide and smooth. Limbus very thin, microdenticulate. Epiproct rather short, conical (Fig. 39), preapical papillae prominent. Hypoproct semi-circular; caudal, paramedian, setiferous papillae evident and well-separated.

Sterna without modifications, very densely setose (Figs 40, 41). Legs long and slender, evidently enlarged (Figs 42), ca 1.6–1.7 times as long as midbody height, prefemora not swollen dorsally, acropodite (femur+postfemur+tibia+tarsus) with sphaerotrichomes ventrally (Fig. 42).

Gonopods (Figs 40, 43, 44) with large, subquadrate, medially fused coxae carrying numerous long setae ventromedially. Telopodite mostly hidden inside gonocoel, unusually stout, subfalcate, prefemoral (densely setose) portion about half as long as entire telopodite; endomere (**en**) short, simple, with a subapical knob laterally and a rounded tip, as well as with two subunciform processes (**s** and **p**); hairy pulvillus very evident, exomere totally suppressed.

Remarks. This species is apparently very local in distribution (Map 2) and seems to be allopatric with *E. orientalis*.

Epanerchodus bispinosus sp. n.

urn:lsid:zoobank.org:act:5944975E-495B-4578-8145-779D40B9C80A http://species-id.net/wiki/Epanerchodus_bispinosus Figs 45–53

Type material: Holotype \eth (NMNS-6559-001), Taiwan, Nantou County, Ren-ai Township, Mei-Feng, 15.04.2002, leg. S.H. Wu. Paratypes: 3 \circlearrowright , 1 \circlearrowright fragm., 4 \bigcirc , 1 \bigcirc juv. (NMNS-6559-002), 1 \circlearrowright , 1 \bigcirc (ZMUM), 1 \circlearrowright (without head), 1 \bigcirc (ZMUC), 1 \circlearrowright fragm., 1 \bigcirc (MNHN JC 334), 1 \circlearrowright (TFRI), 1 \circlearrowright (NSYSU), same locality, together with holotype.

Name: To emphasize the distal half of the gonopod telopodite being like two long spines.

Diagnosis: Due to the presence of a strong and spiniform exomere, this new species joins the few congeners hitherto referred to the erstwhile genus *Usbekodesmus* (see above the synonymy with *Epanerchodus*), but differs in the distal half of the gonopod telopodite being represented by only two spiniform branches showing no additional outgrowths (see also Key below).

Description: Length of both sexes ca 8–11 mm; width of pro- and metazona varying between specimens from 0.8–1.3 to 1.1–1.7 mm, respectively. Holotype ca 9 mm long, and 0.8 and 1.1 mm wide on pro- and metazona, respectively. Coloration in alcohol from pallid to uniformly light grey, yellow or very light red-brown, sometimes head faintly marbled light red-brown; venter and legs yellowish to greyish (Figs 45–49).



Figures 45–50. *Epanerchodus bispinosus* sp. n., ♂ paratype. **45** habitus, lateral view **46** anterior portion of body, dorsal view **47** middle portion of body, dorsal view **48, 49** posterior portion of body, dorsal and ventral views, respectively **50** gonopods, lateral view. Photographed not to scale.



Figures 51–53. *Epanerchodus bispinosus* sp. n., \Im paratype. **51** leg 9 **52, 53** left gonopod, submesal and sublateral views, respectively. Scale bar: 0.4 mm (**51**) and 0.2 mm (**52, 53**).

All characters as in *E. orientalis* except as follows.

Antennae rather long and evidently clavate, reaching behind end (\mathcal{E}) or midway (\mathcal{Q}) of segment 3 dorsally; antennomere 3 longest, considerably longer than a relatively stout, yet highest, 5th (Figs 45); antennomeres 5 and 6 each with a small, compact, distodorsal group of bacilliform sensilla; antennomere 7 with a minute dorsoparabasal cone and a distodorsal group of microscopic sensilla.

In width, collum < segment 2 = 3 < 4 < head = 5–15 (Fig. 46), thereafter body gradually tapering towards telson (\mathcal{J} , \mathcal{Q}) (Fig. 48). Paraterga moderately developed, starting from collum, set high but invariably lying slightly below a faintly convex dorsum; paraterga on collum small, subtriangular, with a small lateral incision in front of a rounded caudal corner; front shoulders drawn forward and slightly convex only paraterga 2–4, thereafter straight, increasingly well rounded and directed increasingly caudolaterad; caudal corner on pataterga 2–5 subrectangular and narrowly rounded, starting from 6th increasingly acutangular and beak-shaped, starting from segment 9 first faintly and then extending increasingly beyond rear tergal contour (Figs 45–48). All poreless segments with three, all pore-bearing ones with four, small but evident incisions, each usually bearing a small seta on top at lateral margin. Metatergal sculpture typical, moderately developed, with three indistinct transverse rows of setiferous, polygonal bosses (Figs 46–48). Tergal setae very short, mostly retained, a little longer only on collum and in rear row on metatergum 19. Stricture

between pro- and metazona wide and smooth. Limbus very thin, microdenticulate. Epiproct rather short, conical (Fig. 48), only slightly bent ventrad, preapical papillae evident. Hypoproct semi-circular; caudal, paramedian, setiferous papillae evident and well-separated.

Sterna without modifications, very densely setose. Legs rather short, slender, in \Im evidently enlarged (Figs 45), ca 1.5–1.6 (\Im) or 1.1–1.2 times (\Im) as long as midbody height, \Im prefemora not swollen dorsally, together with femora beset with bifid setae ventrally, acropodite (postfemur+tibia+tarsus) with sphaerotrichomes ventrally (Fig. 51).

Gonopods (Figs 50, 52, 53) with large, subquadrate, medially fused coxae carrying only a few long setae ventrally. Telopodite slender and simple, prefemoral portion relatively short, exomere (**ex**) spiniform, endomere (**en**) only a little longer than **ex**, apex bent unciform mesally, devoid of any outgrowths near base; hairy pulvillus evident.

Remarks. This species is remarkable in showing an exomere, albeit usual and spiniform, almost as long as a particularly simple endomere. This condition nicely bridges the weak distinction which has hitherto remained to formally keep *Usbekodesmus* and *Epanerchodus* as independent genera (Geoffroy and Golovatch 2004), with the gonopod structure in *E. bispinosus* sp. n. providing the final evidence to formally synonymize these genera (see also above).

E. bispinosus sp. n. in Taiwan is apparently very local in distribution, having been encountered only at a single locality (Map 2).

Epanerchodus curtigonopus sp. n.

urn:lsid:zoobank.org:act:CBDF0100-0AEF-4D12-B88A-3A59119AD5C0 http://species-id.net/wiki/Epanerchodus_curtigonopus Figs 54–60

Type material: Holotype ♂ (NMNS-6560-001), Taiwan, Nantou County, Ren-ai Township, Mei-Feng, 15.10.2001, leg. S.H. Wu.

Name: To emphasize the remarkably short gonopod telopodite.

Diagnosis: Differs from other *Epanerchodus* species in the distal half of the gonopod telopodite being particularly stout, with the endomere represented only by a short spine supplied with a similarly short spine at its base (see also Key below). This new species seems to be particularly similar to *E. pinguis* sp. n. in sharing the gonopod which shows a densely setose coxa and a very stout telopodite (apparently, both being synapomorphies), but differs in the entire leg telopodites (prefemur+femur+postfemu r+tibia+tarsus) being supplied with sphaerotrichomes ventrally, and the endomere and its basal process rudimentary and spiniform.

Description: Length ca 15 mm; width of pro- and metazona 1.3 and 2.5 mm, respectively. Coloration in alcohol pallid.

Superficially, also very similar to *E. pinguis* sp. n., except as follows.

In width, collum < head < segment 2 = 3 < 4 < 5 < 6-15 (Figs 54), thereafter body gradually tapering towards telson (Fig. 55). Paraterga strongly developed, starting



Figures 54–57. *Epanerchodus curtigonopus* sp. n., holotype. **54** anterior portion of body, dorsal view **55, 56** posterior portion of body, dorsal and ventral views, respectively **57** middle portion of body (with gonopods), ventral view. Photographed not to scale.



Figures 58–60. *Epanerchodus curtigonopus* sp. n., holotype. 58 leg 9 59, 60 left gonopod, dorsomesal and ventrolateral views, respectively. Scale bar: 0.2 mm.

from collum, set high, subhorizontal to very faintly upturned, lying slightly below dorsum only on collum and segment 2; mid-dorsum invariably extremely faintly convex, nearly flat; front shoulders mostly straight, drawn forward only on paraterga 2 and 3, thereafter directed increasingly caudolaterad and increasingly well rounded anterolaterally; caudal corner on paraterga 3–12 subrectangular and narrowly rounded, starting from 13^{th} increasingly acutangular and evidently extending increasingly beyond rear tergal contour, but nearly pointed and beak-shaped only on segment 19 (Figs 54, 55). Paraterga 2-5 and all following pore-bearing segments with four, following poreless ones with three, small but evident incisions, each usually bearing a small seta on top at lateral margin. Metatergal sculpture typical, moderately developed, with three indistinct transverse rows of setiferous, polygonal bosses (Figs 54, 55). Tergal setae very short, mostly retained, a little longer only on collum and in rear row on metatergum 19. Stricture between pro- and metazona wide and smooth. Limbus very thin, microdenticulate. Epiproct rather short, conical (Figs 55, 56), only slightly bent ventrad, preapical papillae evident. Hypoproct semi-circular; caudal, paramedian, setiferous papillae distinct and well-separated (Fig. 56).

Sterna without modifications, densely setose. Legs long and rather slender, only slightly enlarged (Figs 56, 57), ca 1.7–1.8 times as long as midbody height, prefemora not swollen dorsally, entire telopodite (prefemur+femur+postfemur+tibia+tarsus) with sphaerotrichomes ventrally (Fig. 58).

Gonopods (Figs 57, 59, 60) with large, subquadrate, medially fused coxae carrying numerous setae ventrally. Telopodite especially stout, prefemoral portion relatively prominent, taking up about one-third of telopodite length, endomere (**en**) like a short spine supplied with another, somewhat shorter spine (**p**) near base; both accessory seminal chamber and hairy pulvillus evident.

Remarks. This species is remarkable in showing an extremely short, simple, spiniform endomere (**en**), coupled with a single, even more rudimentary process (**p**) at **en** base.

In Taiwan, *E. curtigonopus* sp. n. occurs very locally, having been found only at a single locality (Map 2).

Epanerchodus flagellifer sp. n.

urn:lsid:zoobank.org:act:35EAB5D4-7E11-496E-8292-4ED5C0676C83 http://species-id.net/wiki/Epanerchodus_flagellifer Figs 61–68

Type material: Holotype $\overset{\circ}{\supset}$ (NMNS-6561-001), Taiwan, Nantou County, Huisun timber land, 24.04.1998, leg. S.H. Wu. Paratypes: 1 $\overset{\circ}{\supset}$ (NMNS-6561-002), same locality, together with holotype; 1 $\overset{\circ}{\supset}$ (NMNS-6561-003), same locality, 04.1998; 1 $\overset{\circ}{\supset}$ (ZMUM), same locality, 25.04.1999; 1 $\overset{\circ}{\supset}$ (TFRI), same locality, 24.04.1999, all leg. S.H. Wu.

Name: To emphasize the remarkably long, flagelliform distal part of the gonopod telopodite.

Diagnosis: Differs from other *Epanerchodus* species in the distal half of the gonopod telopodite being particularly long, flagelliform, coupled with the presence of two rounded teeth at the base of the endomere (see also Key below). From the other congeners known from Taiwan, this new species differs also in the absence of sphaerotrichomes on \Diamond legs.

Description: Length of both sexes ca 8–11 mm; width of pro- and metazona varying between specimens from 0.8–1.0 to 1.4–1.5 mm, respectively. Holotype ca 9 mm long, and 0.9 and 1.4 mm wide on pro- and metazona, respectively. Coloration in alcohol pallid to light grey- to red-brown (Figs 61–65).

All characters as in E. orientalis except as follows.

Antennae rather long and evidently clavate (Figs 61, 64), reaching behind segment 3 dorsally.

In width, collum < segment 2 < head = 3 = 4 < 5-15(16) (Fig. 62), thereafter body gradually tapering towards telson (Fig. 63). Paraterga well-developed, starting from collum, set high, subhorizontal to very faintly upturned, mostly nearly level to a very faintly convex dorsum, only on collum and segment 2 lying clearly below dorsum; paraterga on collum small, subtriangular, a small lateral incision in front of a rounded caudal corner; front shoulders drawn forward and slightly convex only paraterga 2 and 3, straight on paraterga 4, thereafter increasingly well rounded and directed increasingly ly caudolaterad; caudal edge straight on segments 2–4, thereafter increasingly bisinuate and acutangular caudolaterally; starting from segment 10, caudal corners extending



Figures 61–65. *Epanerchodus flagellifer* sp. n., \mathcal{O} paratype. **61** habitus, lateral view **62, 64** anterior portion of body, dorsal and ventral views, respectively **63, 65** posterior portion of body, dorsal and ventral views, respectively. Photographed not to scale.



Figures 66–68. *Epanerchodus flagellifer* sp. n., \mathcal{J} paratype. **66** leg 9 **67, 68** left gonopod, mesal and lateral views, respectively. Scale bar: 0.2 mm.

increasingly beyond rear tergal contour, spiniform on segments 17–19 (Figs 61–65). All poreless segments with three, all pore-bearing ones with four, small but evident incisions, each usually bearing a small seta on top at lateral margin. Metatergal sculpture typical, moderately developed, with three indistinct transverse rows of setiferous, polygonal bosses (Figs 62, 63). Tergal setae very short, mostly retained, a little longer only on collum and in rear row on metatergum 19. Stricture between pro- and metazona wide and smooth. Limbus very thin, microdenticulate. Epiproct rather short, conical (Fig. 65), only slightly bent ventrad, preapical papillae evident. Hypoproct semicircular (Fig. 65); caudal, paramedian, setiferous papillae evident and well-separated.

Sterna without modifications, very densely setose. Legs rather long, slender, only slightly incrassate (Figs 61, 64–66), ca 1.7–1.8 times (\bigcirc) as long as midbody height, prefemora not swollen dorsally, sphaerotrichomes missing (Fig. 66).

Gonopods (Figs 67, 68) with large, subquadrate, medially fused coxae carrying only a few long setae ventrally. Telopodite simple and especially slender, prefemoral portion relatively short, endomere (**en**) flagelliform, with two small dentiform outgrowths at base; hairy pulvillus evident.

Remarks. This small species is remarkable in showing a particularly long, flagelliform endomere, coupled with only two short outgrowths at its base.

In Taiwan, *E. flagellifer* sp. n. occurs very locally, having been encountered only at a single locality (Map 2).

Key to Epanerchodus species known from Taiwan (valid mostly for adult males)

1	Gonopod coxae unusually densely setose, while telopodite particularly stout:
	prefemiorar, selose part at least main as long as entire teropounte (Figs 45, 44,
	29, 60)
-	Gonopod coxae usual, with only a few strong setae, while telopodite elongate:
	prefemoral, setose part less than half as long as entire telopodite (Figs 32, 52,
	53, 67, 68) 3
2	\eth legs devoid of sphaerotrichomes (Fig. 66). Gonopod endomere (en) like a
	short spine (Figs 67, 68) E. curtigonopus sp. n.
_	all 🖒 telopoditomeres with sphaerotrichomes (Fig. 42). Gonopod endomere
	(en) like a strong tooth (Figs 40, 43, 44) <i>E. pinguis</i> sp. n.
3	Body usually larger, 11-19 mm long. Gonopod telopodite highly variable,
	complex: exomere (ex), if present, rudimentary, while endomere (en) branch-
	ing (Figs 29, 30, 32–36) <i>E. orientalis</i>
_	Body usually smaller, 8–11 mm long. Gonopod telopodite simple: exomere
	(ex), if present, strong and spiniform, while endomere (en) like a strong spine
	or a long flagellum
4	Gonopod telopodite biramous, exomere (ex) strong and spiniform, while en-
	domere (en) like a strong spine ending in a strong uncus (Figs 52, 53)
	E. bispinosus sp. n.
_	Gonopod telopodite uniramous, exomere absent, endomere (en) flagelliform
	(Figs 67, 68)
	J J J I

Conclusion

At present we can state that Taiwan supports a reasonably rich and quite peculiar polydesmid fauna represented by seven species in two genera. Of these, six species seem to be endemic, being largely restricted to the mountains in the central and northern parts of the island. Considering the distributions demonstrated by the Taiwanese Polydesmidae (Maps 1 and 2), allopatry is prevailing while sympatry, probably even syntopy, has only been observed in two places. Thus, the normally much larger *Nipponesmus shirinensis*, the slightly smaller *Epanerchodus pinguis* sp. n. and the smallest *E. flagellifer* sp. n. co-occur at Huisun. Similarly, *Nipponesmus shirinensis*, *N. minor* sp. n., *Epanerchodus orientalis* and *E. bispinosus* sp. n., which also form a comparable succession of size decrease, are sympatric if not syntopic at Mei-Feng. Such examples seem to be best explained in terms of local niche segregation long documented elsewhere for a number of insular groups of Diplopoda (e.g. Enghoff 1983, Enghoff and Báez 1993, Golovatch and Enghoff 2003), including those of Taiwan (Golovatch et al. 2010).

The only polydesmid that is remarkably widespread and polymorphous in Taiwan, *E. orientalis*, appears to be confined to lowland to foothill habitats (Map 2). For this reason alone, this species, which is also known to be extremely widely distributed,

variable and lowland-dwelling across at least most of Japan, seems to be the only allochthonous element in the fauna of Polydesmidae of Taiwan, likely a later colonizer from Japan.

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References

- Chamberlin RV, Wang YM (1953) Records of millipeds (Diplopoda) from Japan and other oriental areas, with descriptions of new genera and species. American Museum Novitates 1621: 1–13.
- Enghoff H (1983) Adaptive radiation of the millipede genus *Cylindroiulus* on Madeira: habitat, body size, and morphology (Diplopoda, Julida: Julidae). Revue d'Écologie et de Biologie du Sol 20(3): 403–415.
- Enghoff H, Báez M (1993) Evolution of distribution and habitat patterns in endemic millipedes of the genus *Dolichoiulus* (Diplopoda: Julidae) on the Canary Islands, with notes on distribution patterns of other Canarian species swarms. Biological Journal of the Linnean Society 49: 277–301.
- Geoffroy JJ, Golovatch SI (2004) Some polydesmidan millipedes from caves in southern China (Diplopoda: Polydesmida), with descriptions of four new species. Arthropoda Selecta 13(1/2): 19–28.
- Golovatch SI (1979) The composition and zoogeographical connections of the fauna of Diplopoda of Middle Asia. Communication 1. Zoologicheskiy Zhurnal 58(7): 987–1001. [in Russian, English summary]
- Golovatch SI (1991) The millipede family Polydesmidae in Southeast Asia, with notes on phylogeny. Steenstrupia 17(4): 141–159.

- Golovatch SI, Enghoff H (2003) Pill-millipedes of the Canary Islands: the *Glomeris alluaudi*group (Diplopoda, Glomeridae). Vieraea 31: 9–25.
- Golovatch SI, Mikhaljova EV, Chang HW (2010) Pill-millipedes (Glomerida, Diplopoda) in Taiwan. Zootaxa 2447: 1–20.
- Hoffman RL (1980) Classification of the Diplopoda. Muséum d'histoire naturelle, Genève, 237 pp. [for 1979]
- Korsós Z (2004) Checklist and bibliography of millipedes (Diplopoda) of Taiwan. Collection and Research 17: 11–32.
- Mikhaljova EV (2004) The millipedes of the Asian part of Russia. Pensoft, Sofia-Moscow, 292 pp.
- Mikhaljova EV, Golovatch SI (1981) Polymorphism in a new species of *Epanerchodus* (Diplopoda, Polydesmidae) from the USSR Far East. Zoologicheskiy Zhurnal 60(8): 1183–1189. [in Russian, English summary]
- Miyosi Y (1959) Über japanische Diplopoden. Arachnological Society of East Asia, Osaka, Special Number, 244 pp. [in Japanese]
- Murakami Y (1969) Myriapods found in limestone caves of northern Honshu, Japan. Bulletin of the National Science Museum 12(3): 557–582.
- Murakami Y (1970) More new species of *Epanerchodus* (Diplopoda, Polydesmidae) found in limestone caves in eastern Shikoku, Japan. Annotationes Zoologicae Japonenses 43(2): 151–157.
- Murakami Y (1973) Two new species of polydesmid millipeds from western Honshu, Japan. Annotationes Zoologicae Japonenses 44(4): 253–258.
- Murakami Y (1993) Diplopoda, Pauropoda, Symphyla. A list of Japanese species. Invertebrates 1. Shizen-Kankyô-Kenkyû Center. Environmental Agency Japan, Tokyo: 95–106. [in Japanese]
- Nakamura Y, Korsós Z (2010) Distribution and diversity of millipedes of the Ryukyu Archipelago, with the Senkaku and Daito island groups: A literature review (Arthropoda: Diplopoda). Acta Arachnologica 59(2): 73–86.
- Nishikawa Y, Murakami Y (1993) Distributional records on Japanese millipeds (II). Faculty of Letters Review of Otemon Gakuin University 27: 261–275. [in Japanese]
- Shinohara K (1958) Polydesmoidea millipeds from Chichibu. Bulletin of the Chichibu Museum of Natural History 8: 19–24. [in Japanese, with English abstract]
- Takashima H, Haga A (1956) A contribution towards the Japanese cave-dwelling species of the class Diplopoda. Miscellaneous Reports of Yamashina's Institute of Ornithology and Zoology 1: 329–343. [in Japanese]
- Wang Y-HM (1956) Serica 1e: Records of myriapods on Formosa with description of new species (2). Quarterly Journal of the Taiwan Museum 9(2): 155–159.
- Wang Y-HM (1958) Serica 1i: On Diplopoda from Taiwan with a new strongylosomids. Quarterly Journal of the Taiwan Museum 11(3–4): 340–344.
- Wang Y-HM (1963) Serica 1q: Millipedes and centipedes of Quemoy, Fukien Province and Taiwan Island, Botel Tobago (Lan Yu), Taiwan Province and of Singapore. Quarterly Journal of the Taiwan Museum 16(1–2): 89–96.

RESEARCH ARTICLE



New species of Asphalidesmus Silvestri, 1910 from Australia (Diplopoda, Polydesmida, Dalodesmidea)

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Abstract

Asphalidesmus allynensis **sp. n.** and A. dorrigensis **sp. n.** are described from New South Wales, A. otwayensis **sp. n.** from Victoria, and A. bellendenkerensis **sp. n.**, A. carbinensis **sp. n.**, A. magnus sp. n. and A. minor **sp. n.** from Queensland. The previously endemic Tasmanian genus Asphalidesmus Silvestri, 1910 is now known from 16°S to 43°S in eastern Australia, a north-south range of ca 3000 km. Asphalidesmus spp. throughout this range are very similar in overall appearance. Three of the new species are able to coil in a tight spiral.

Keywords

millipede, New South Wales, Queensland, Tasmania, Victoria

Introduction

Asphalidesmus Silvestri, 1910 is a genus of tiny, gregarious, slow-moving Polydesmida living in moist leaf litter and rotting logs. Juveniles are pure white in colour, while adults are yellow-brown (Fig. 1) and often encrusted with soil particles. The genus is currently placed in the suborder Dalodesmidea Hoffman, 1980 but has not yet been assigned to a family (Golovatch 2003, Mesibov 2009).

The three previously described species of *Asphalidesmus* are endemic to Tasmania (Mesibov 2002, 2009), where they occur in rainforest and wet eucalypt forest, and sometimes in caves. In this paper I describe seven new species of *Asphalidesmus* from the Australian mainland. The genus is now known to range from 16°03'S in tropical northern Queensland to 43°28'S in cool temperate southern Tasmania, or ca 3000 km north-south.

There are very wide gaps in the currently known distribution of *Asphalidesmus* in eastern Australia (Fig. 12). The gaps contain blocks of rainforest and wet eucalypt forest, and it is likely that some of those forests are home to undiscovered species of these cryptic millipedes. However, I have repeatedly searched for litter- and log-dwell-ing millipedes in the forested, high-rainfall Strzelecki Ranges in southeastern Victoria (Mesibov 2007 and unpublished observations) and have not collected an *Asphalidesmus* species there. It is also interesting that I recovered *Asphalidesmus* specimens from berlesates from northern Queensland rainforest, but not from rainforest in southeastern Queensland. The two regions have been intensively sampled by the same group of fieldworkers using the same methods, with roughly the same totals of collecting events (Fig. 3 in Mesibov 2008).

Asphalidesmus females from three eastern Australian sites remain unidentified because no males have yet been collected at those or nearby locations. The sites are shown on the distribution map (Fig. 12) and the females listed in the Appendix as 'Asphalidesmus sp.'

Methods

'Male' and 'female' in the text refer to adult, stadium 7 individuals. All specimens are stored in 75–80% ethanol in their respective repositories.

Gonopods were cleared and temporarily mounted in 60% lactic acid for optical microscopy. Preliminary drawings on graph paper were made using an eyepiece grid at 160X on a binocular microscope. Photomicrographs were taken with a Canon EOS 1000D digital SLR camera mounted on a Nikon SMZ800 binocular dissecting microscope equipped with a beam splitter. Measurements were made with the same microscope using an eyepiece scale. Specimens for scanning electron microscopy were air-dried, sputter-coated with platinum and examined with a Hitachi SU-70 operated in high-vacuum mode.

All images and drawings were prepared for publication using GIMP 2.6. Focusstacking was used to add depth of field to some photomicrographs. Maps were generated using ArcView GIS 3.2.

A list of all currently known localities for all *Asphalidesmus* species is given in the Appendix. Locality details there and in the text below are given in all cases with latitude and longitude based on the WGS84 datum. I also estimate a conservative uncertainty for each locality, expressed in metres as the radius of a circle around the stated position. Latitude and longitude data given below in italics are



Figure 1. A *Asphalidesmus leae* Silvestri, 1910, dorsal view of female, QVM 23:52009 **B** *A. dorrigensis* sp. n., lateral view of coiled adult paratype, AM KS61085 **C** *A. leae* Silvestri, 1910, lateral view of curled male, QVM 23:52009 **D** *A. magnus* sp. n., ventral view of male, ANIC 64-000204 **E, F** Anterior views of ring 6 of males of *A. leae* Silvestri, 1910 (**E**, QVM 23:41547) and paratype *A. magnus* sp. n. (**F**, QM S90026) **G** *A. otwayensis* sp. n., lateral view of last rings of paratype female, ANIC 64-000207. Scale bars: **A–D** = 1 mm, **E–G** = 0.25 mm.

based on museum collection databases, maps or Google Earth, as indicated in the Remarks sections.

Abbreviations: AM = Australian Museum, Sydney, NSW; ANIC = Australian National Insect Collection, Canberra, Australian Capital Territory; MV = Museum Victoria, Melbourne, Vic; NSW = New South Wales; Qld = Queensland; QM = Queensland Museum, Brisbane, Qld; QVM = Queen Victoria Museum and Art Gallery, Launceston, Tasmania; Vic = Victoria.

Results

Order Polydesmida Pocock, 1887 Suborder Dalodesmidea Hoffman, 1980

Asphalidesmus Silvestri, 1910

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

Asphalidesmus Silvestri 1910: 362. Attems 1914: 242, 1926: 153, 1931: 77, 1940: 205.
Brölemann 1916: 547. Verhoeff 1932: 1587, 1936: 12. Jeekel 1971: 313, 1982: 12, 1984: 85, 1986: 46. Hoffman 1980: 150. Mesibov 2002: 532, 2009: 67. Golovatch 2003: 53. Golovatch et al. 2009: 3. Mesibov 2009: 67.

Type species: Asphalidesmus leae Silvestri, 1910, by original designation.

Atopodesmus Chamberlin 1920: 153. Attems 1926: 134, 1940: 356. Verhoeff 1932: 1562. Jeekel 1971: 313, 1984: 85, 1986: 46. Hoffman 1980: 186. Mesibov 2002: 532 (synonymised). Golovatch et al. 2009: 3. Mesibov 2009: 67.

Type and only species: *Atopodesmus parvus* Chamberlin, 1920, by original designation.

Other included species: A. allynensis sp. n., A. bellendenkerensis sp. n., A. carbinensis sp. n., A. dorrigensis sp. n., A. golovatchi Mesibov, 2009, A. magnus sp. n., A. minor sp. n., A. otwayensis sp. n.

Diagnosis. Small Dalodesmidea (4–6 mm long as adults) with head + 19 rings; adults yellow-brown and often encrusted with soil particles, juveniles pure white and not encrusted; collum, metatergites and preanal ring with 3–6 transverse rows of small, uniform tubercles, each bearing a single seta with a slightly flared tip; ring 2 paranotum expanded, extending forward to partly cover collum edge and backward to lie under anterior edge of ring 3 paranotum; all paranota lying low on sides, flexed downward and covering legs, with a few indistinct outer marginal lobes; pore formula normal, each ozopore opening on short, columnar structure arising just dorsal to the centre of the paranotum base; legs short, without sphaerotrichomes; gonopod aperture transversely ovoid, posterior rim slightly raised; gonocoxae entirely contained within aperture, small, distally tapered, lightly joined (not fused) medially; gonopod telopodites slender, parallel and close together, more or less straight, reaching bases of legpair 4 or 5 when retracted.

Remarks. The genus description I offered nine years ago (Mesibov 2002) still largely applies to *A. golovatchi* and the seven new species described below. The only significant changes are in number of transverse rows of tubercles on midbody tergites (varying from 3–6 in the genus, rather than 5–6) and in gonopod telopodite structure, which varies considerably from species to species. An *Asphalidesmus* adult can be easily recognised by its colour, by the size and position of the ring 2 paranota, and by the characteristic dorsal tuberculation, and can be distinguished using these features alone from similar-looking Australian Pyrgodesmidae and species of *Agathodesmus* Silvestri, 1910. However, whereas each of the latter taxa has a distinctive telopodite form as well

as unique non-gonopodal features, *Asphalidesmus* telopodites are remarkably dissimilar (see descriptions and illustrations below).

In particular, there does not seem to be a common location on the telopodite for the opening of the prostatic groove. In the descriptions below I have avoided using the word 'solenomere' for the process with this opening, because doing so might suggest that those processes are homologous across the genus, and I doubt that they are. The prostatic groove opens on anterior and posterior branches in different *Asphalidesmus* species (with no sign of torsion in the course of the groove), on the tips of processes and subapically, and on the medial and lateral sides of the telopodite.

In his review of volvatory Polydesmida, Golovatch (2003) noted that the two Tasmanian *Asphalidesmus* species known at that time had only limited ability to coil (Fig. 1C), yet both had several anatomical features found in tightly-coiling 'oniscoid' polydesmidans in other families: short legs, downward-flexed paranota and a slight overlap of paranota on successive rings. Three of the new *Asphalidesmus* species are known to coil tightly (Fig. 1B), although in these species the paranota are short (on anterior-posterior axis) and do not overlap.

Asphalidesmus allynensis sp. n.

urn:lsid:zoobank.org:act:68732D56-5639-48F4-824C-676F98813319 http://species-id.net/wiki/Asphalidesmus_allynensis Figs 2A, 3A; map fig. 12

Holotype. Male, Allyn Stream, Barrington Tops, NSW, "32°14'S, 151°30'E" (label data, incorrect; see Remarks), 1 February 1975, P.M. Johns, in *Nothofagus moorei* [for-est], AM KS94167. Gonopods and remainder of body in two separate genitalia vials in the same sample tube.

Other material. None known.

Diagnosis. Gonopod telopodite branching at ca one-third telopodite height, 5 transverse rows of tubercles on midbody metatergites.

Description. Specimen somewhat decoloured and macerated, length ca 6 mm, ring 6 vertical diameter ca 0.6 mm and maximum width ca 0.9 mm. Midbody metatergites with 5 transverse rows of tubercles dorsally. Paranota narrow (Fig. 3A), margin clearly divided into 3 (occasionally 4) lobes.

Gonopod telopodite (Fig. 2A) divided at ca one-third telopodite height into anterior and posterior branches, below the division somewhat expanded posterolaterally, the base setose up to the division on posterior and posterolateral surfaces, the longest setae close to the division and directed distally. Posterior branch stout, curving first posteriorly, then distolaterally, mediolaterally flattening and expanding in distal half, the distal margin notched in anterior half, anterior to the notch the margin slightly bent medially and finely dentate. Posterior branch also with small, flat, near-rectangular process arising on medial surface of branch at ca one-half branch height and directed distally and slightly medially, the distal and posterior margins of the process



Figure 2. Gonopod telopodites, drawn to same scale; scale bar = 0.25 mm. Dashed lines indicate course of prostatic groove; setae not shown; **ab** = anterior branch, **pb** = posterior branch. **A** *Asphalidesmus allynensis* sp. n., holotype, AM KS94167, medial (left) and anteromedial views (right) of left gonopod telopodite. **B** *A. dorrigensis* sp. n., paratype, AM KS61085, posterolateral view of right gonopod telopodite **C** *A. magnus* sp .n., paratype, QM S90026, medial view of right gonopod telopodite **D** *A. otwayensis* sp. n., paratype, ANIC 64-000207, posteromedial view of right gonopod telopodite.



Figure 3. Anterior views of ring 6 (A–D, F) and ring 9 (E) of male *Asphalidesmus* spp., photographed at same scale; scale bar = 0.5 mm. A *A. allynensis* sp. n., holotype, AM KS94167 B *A. dorrigensis* sp. n., paratype, AM KS61085 C *A. otwayensis* sp. n., paratype, ANIC 64-000207 D *A. bellendenkerensis* sp. n., paratype, QM S90018 E *A. carbinensis* sp. n., holotype, QM S90023 F *A. minor* sp. n., paratype, ANIC 64-000205. (See Fig. 1 for comparable views of *A. leae* Silvestri, 1910 and *A. magnus* sp. n.)

roughened. Anterior branch more slender than posterior branch, curving smoothly posterodistally, tip slightly flattened mediolaterally and bent to lie medial to expanded tip of posterior branch and just anterodistal and lateral to tip of rectangular process on that branch. Prostatic groove following anterior surface of posterior branch, then curving posteriorly to terminate in small, conical projection on posteromedial surface of branch at origin of rectangular process.

Distribution. So far known only from cool temperate rainforest on the Barrington Tops in central, near-coastal New South Wales (Fig. 12; see also Remarks).

Etymology. For the Allyn River, type locality of this species.

Remarks. 'Allyn Stream' seems to be an obsolete local name for the Allyn River, whose tributaries flow through high-elevation *N. moorei* rainforest. The latitude/longitude on the printed specimen label marks the start of the Allyn River Road in long-cleared farmland at ca 220 m elevation. The latitude/longitude may have been added when the original handwritten label was replaced by a printed one (G. Milledge, pers. comm., 1 March 2011) The most likely collection sites are ca 10 km to the north-northwest, on forest roads through *N. moorei* forest above ca 700 m. My best guess is $32^{\circ}09$ 'S, $151^{\circ}27$ 'E ± 3 km (see Appendix).

Asphalidesmus bellendenkerensis sp. n.

urn:lsid:zoobank.org:act:C1B3140F-F571-4942-992F-2A5DFBC1D8B7 http://species-id.net/wiki/Asphalidesmus_bellendenkerensis Figs 3D, 4A, 4B; map fig. 12

Holotype. Male, Bellenden Ker Range, Qld, cable tower 3, 17°16'04"S, 145°53'00"E (see Remarks) ±0.25 km, 1000 m, 17–24 October 1981, Queensland Museum staff and 'Earthwatch' personnel, QM S90017.

Paratypes. 2 males, 2 females, details as for holotype but 25–31 October 1981, QM berlesate 324, rainforest, sieved litter, QM S90020; 5 males, 6 females, same details but QM berlesate 330, QM S90018; 4 males, 3 females, same details but QM berlesate 333, stick brushings, QM S90021; 1 male, 2 females, same details but summit TV station, *17°15'52"S*, *145°51'14"E* (see Remarks) ±0.25 km, 1560 m, 1–7 November 1981, QM berlesate 337, QM S90019.

Other material. 2 males, North Bell Peak via Gordonvale, Qld, *17°05'19"S*, *145°52'44"E* ±0.5 km, 900 m, 16 September 1981, G. Monteith and D. Cook, QM berlesate 300, rainforest, sieved litter and moss, QM S90022.

Diagnosis. Gonopod telopodite branches curling around and nested in plane at right angles to long axis of telopodite, 4 transverse rows of tubercles on midbody metatergites.

Description. Males and females approximately the same size, length ca 4 mm, ring 6 vertical diameter ca 0.4 mm and maximum width ca 0.7 mm. Midbody metatergites with 4 transverse rows of tubercles dorsally. Paranota wide (Fig. 3D); anterior and lateral margins in single convex curve, posterior margin straight; 3–4 weakly defined marginal lobes.

Gonopod telopodite (Figs 4A, 4B) upright, rounded-triangular in cross-section, tapering slightly and flattening distally, with small, scattered setae on posterior surface to ca two-thirds telopodite height; divided at ca seven-eighths telopodite height into complex, flattened anterolateral and posteromedial branches. Anterolateral branch with distal margin curving in plane at approximate right angle to telopodite long axis, extending in tight



Figure 4. *Asphalidesmus bellendenkerensis* sp. n., paratype, QM S90018. Views of gonopods in situ (**A**) and telopodite tips (**B**). **alb** = anterolateral branch, **pmb** = posteromedial branch, **o** = points to process on which prostatic groove opens. Scale bars: $\mathbf{A} = 0.05 \text{ mm}$, $\mathbf{B} = 0.025 \text{ mm}$.

arc posteriorly as blade-like process terminating in fold of posteromedial process close to inner (medial) side of telopodite. Posteromedial branch folded laterally on posterior margin of process, extending distally as flat process with truncate tip, the tip bluntly dentate with taller, triangular extension at posterior end. Posteromedial branch with two additional processes: (1) anterior process nested by, and curving to follow, anterolateral branch, terminating in fold of posteromedial branch just distal to tip of anterolateral branch process; (2) small lateral process arising ca halfway across diameter of 'circle' formed by anterolateral branch, directed posterolaterally, curling distally at tip where it reaches anterolateral branch. Prostatic groove on anteromedial surface, abruptly entering anterior process of posteromedial branch and following arc of process, opening at process tip.

Distribution. Known from tropical rainforest in far north Queensland on the Bellenden Ker Range and on the Malbon Thompson Range near Gordonvale; the two localities are ca 20 km apart (Fig. 12).

Etymology. For the type locality of this species. At the summit of the range is the wettest meteorological station in Australia (Australian Bureau of Meteorology site 31141), averaging more than 8 m of rain per year. Three of the *A. bellendenkerensis* specimens are from this site.

Remarks. *A. bellendenkerensis* is a striking exception to the dalodesmidean 'rule of thumb' that smaller species have simpler gonopods. The complex topology of the telopodite tip can only be clearly seen at high magnification using a scanning electron microscope (Fig. 4B).

This species can coil tightly in a spiral, but most of the specimens examined are only partly coiled.

Latitude/longitude data for the Bellenden Ker Range sites were obtained using Google Earth with advice from the Bellenden Ker cableway operator. The latitude/ longitude figures for North Bell Peak are from the QM collection database.

Asphalidesmus carbinensis sp. n.

urn:lsid:zoobank.org:act:747EE116-BC34-4F60-9BEF-05300EE8BC75 http://species-id.net/wiki/Asphalidesmus_carbinensis Figs 3E, 5A, 5B; map fig. 12

Holotype. Male, Mt Lewis Road, Qld, 29 km from highway, *16°30'44"S*, *145°16'10"E* ±0.5 km, 1210 m, 29 November 1997, D. Cook, QM berlesate 964, rainforest, leaf litter, QM S90023, ex QM S35904. Gonopods and remainder of body in two separate genitalia vials in the same sample tube.

Paratypes. 1 male, 1 female, 2 km SE of Mt Spurgeon via Mt Carbine, Qld, 16°27'17"S, 145°12'26"E ±0.5 km, 1100 m, 20 December 1988, G. Monteith and G. Thompson, QM berlesate 825, rainforest, sieved litter, QM S90024.

Other material. None known.

Diagnosis. Gonopod telopodite not obviously divided into branches, instead with 4 small, pointed apical processes; 4 transverse rows of tubercles on midbody metatergites.



Figure 5. *Asphalidesmus carbinensis* sp. n., paratype, QM S90024. Views of gonopods in situ (**A**) and telopodite tips (**B**). **1**, **2**, **3**, **4** = processes 1–4, respectively (see text for explanation), **o** = points to process on which prostatic groove opens. Scale bars: **A** = 0.05 mm, **B** = 0.025 mm.

Description. Males and females approximately the same size, length ca 5 mm, ring 6 vertical diameter ca 0.5 mm and maximum width ca 0.9 mm. Midbody metatergites with 4 transverse rows of tubercles dorsally. Paranota wide (Fig. 3E); anterior and lateral margins in single convex curve, posterior margin straight; 3–4 weakly defined marginal lobes.

Gonopod telopodite (Figs 5A, 5B) cylindrical, tapering distally, extended laterally at base as flange; basal one-quarter of telopodite with numerous minute, round bumps on posterior and posterolateral surfaces; sparse, strong setae to ca two-thirds telopodite height on posterior and posterolateral surfaces. Telopodite not evidently divided into branches, instead with cluster of 4 small, pointed processes at apex. From anterior to posterior: (1) short, spine-like process directed distally and very slightly medially; (2) short, spine-like process, slightly smaller than process (1), directed distally and slightly posteriorly; (3) longest process, directed distolaterally, tapering to sharp point curled medially to form 'fish-hook', with short, blunt, medial extension at ca two-thirds process height; (4) blade-like process, intermediate in length between (1) and (3), directed distally but bent posterolaterally at ca one-third process height. Prostatic groove on anteromedial surface of telopodite, entering process (3) and terminating on the short, blunt extension.

Distribution. So far known only from tropical rainforest on the Carbine Range in far north Queensland (Fig. 12).

Etymology. For the Carbine Range, type locality of this species.

Remarks. Latitude/longitude data are from the QM collection database.

Asphalidesmus dorrigensis sp. n.

urn:lsid:zoobank.org:act:9AF852C4-C859-4780-ABE2-97362164915D http://species-id.net/wiki/Asphalidesmus_dorrigensis Figs 1B, 2B, 3B, 6A, 6B; map fig. 12

Holotype. Male, Dorrigo National Park, NSW, west bank of Rosewood River, end of Little North Arm Road, 30°24'03"S, 152°46'18"E ±50 m, 110 m, 10–24 November 1999, M. Gray, G. Milledge and H. Smith, pitfall traps, Hotspots NE NSW site 7, AM KS114458, ex KS61085.

Paratypes. 7 males, 14 females, 29 adults tightly coiled and not checked for gender, details as for holotype, AM KS61085.

Other material. (All from NSW) 11 males, 3 females, Dorrigo National Park, 30°22'S, 152°43'E ±1 km, <1000 m, 7 November 1967, R.J. Bartell and L.B. Barton-Browne, ANIC berlesate 40, palm/rainforest, leaf mould, ANIC 64-000200; 6 males, 5 females, Cobcroft camp, Werrikimbe National Park, 31°15'S, 152°11'E ±1 km, 12 November 1982, J. Doyen, ANIC berlesate 858, closed rainforest litter, ANIC 64-000201; 8 males, 7 females, Cobcroft Creek, Werrikimbe National Park, 31°16'S, 152°11'E ±1 km, 13 June 1982, L. Hill, ANIC berlesate 832, closed forest litter, ANIC 64-000202; 2 males, Horseshoe Road, Scotchman State Forest, 3.5 km SE of Thora, 30°26'25"S, 152°47'30"E ±50 m, 100 m, 10–24 November 1999, M. Gray, G. Milledge and H. Smith, pitfall traps, Hotspots NE NSW site 18, AM KS61697.



Figure 6. *Asphalidesmus dorrigensis* sp. n., paratype, AM KS61085. Views of gonopods in situ (**A**) and telopodite tips (**B**). **lab** = anterior branch of left gonopod (broken at base, interlaced with right gonopod branches), **rab** = anterior branch of right gonopod, **lapb** = anterior process of posterior branch of left gonopod (broken at base, leaning laterally; medial arm bent over due to drying), **lppb** = posterior process of posterior branch of left gonopod (medial arm bent over due to drying), **rppb** = posterior process of posterior branch of right gonopod, **o** = points to process on which prostatic groove opens. Scale bars: **A** = 0.1 mm, **B** = 0.05 mm.

Diagnosis. Gonopod telopodite with anterior branch undivided, posterior branch divided into 2 bifid processes; 3–4 transverse rows of tubercles on midbody metatergites.

Description. Males slightly smaller than females, length ca 5 mm, ring 6 vertical diameter ca 0.5 mm and maximum width ca 0.9 mm. Midbody metatergites with 3–4 transverse rows of tubercles dorsally. Paranota wide (Figs 1B, 3B); anterior and lateral margins in single convex curve, posterior margin straight; 3–4 weakly defined marginal lobes.

Gonopod telopodite (Figs 2B, 6A, 6B) more or less cylindrical, tapering distally, divided at between two-thirds and three-quarters telopodite height into anterior and posterior branches, a few scattered setae basally on posterior and posteromedial surfaces. Anterior branch directed anterodistally, curving slightly medially, flattening apically, tip with thin, ovoid fringe (folded over in Fig. 5B). Posterior branch divided into Y-shaped anterior and posterior processes. Posterior process directed distally, with 'Y' in anteroposterior plane, both arms of 'Y' rounded at tip. Anterior process bent slightly laterally, with 'Y' in mediolateral plane, medial arm directed distally (curled over in Fig. 5B), lateral arm directed laterally with small tab near tip on anterior surface. Prostatic groove on anteromedial surface of telopodite, running to medial arm of anterior process of posterior branch and terminating at tip.

Distribution. Rainforest and wet eucalypt forest in northeastern, near-coastal New South Wales (Fig. 12).

Etymology. For Dorrigo National Park, type locality of this species.

Remarks. *A. dorrigensis* can coil tightly in a spiral (Fig. 1B).

The branches of the gonopod seem to be fairly fragile, and are broken near the base of the branch on several of the males examined. In the specimen illustrated in Figs 6A and 6B, the contralateral branches are interlaced as a result of breakage.

Latitude/longitude data in italics are from the ANIC collection database.

Asphalidesmus magnus sp. n.

urn:lsid:zoobank.org:act:FB9BD0E1-F23F-46E5-8422-58F4AB8C1830 http://species-id.net/wiki/Asphalidesmus_magnus Figs 1D, 1F, 2C, 7, 10A, 10B, 10C; map fig. 12

Holotype. Male, Mt Haig, Lamb Range, Qld, *17°05'52"S*, *145°36'09"E* ±0.5 km, 1000 m, 25 February 1997, G. Monteith, QM berlesate 918, rainforest, leaf litter, ex QM S37557, QM S90025.

Paratypes. 5 males, 5 females, details as for holotype, QM S90026.

Other material. (All from Qld) 2 males, 2 females, Cammoo Caves near Rockhampton (see Distribution), 23°10'S, 150°28'E ±1 km, 25 October 1976, R.W. Taylor and T.A. Weir, ANIC berlesate 535, dense low closed forest, ANIC 64-000204; 1 male, 1 female, 3 km W by S of Mt Haig, Lamb Range, Qld, 17°06'S, 145°34'E ±1 km, 1150 m, 3 April 1984, A. Calder and T.A. Weir, ANIC berlesate 952, rainforest, ANIC 64-000203; 1 male, Lambs Head, 10 km W of Edmonton, *17°01'23"S, 145°38'33"E* ±0.5 km, 1200 m, 4 December 1988, G. Monteith and G. Thompson,



Figure 7. *Asphalidesmus magnus* sp. n., paratype, QM S90026, gonopods in situ. **ab** = anterior branch, **pb** = posterior branch, **o** = points to process on which prostatic groove opens. Scale bar = 0.1 mm.

QM berlesate 806, rainforest, sieved litter, QM S90028; 2 males, Vine Creek, Majors Mountain, *17°40'58"S*, *145°32'02"E* ±0.5 km, 1050 m, 5 February 1999, G. Monteith and D. Cook, QM berlesate 987, rainforest, sieved litter, QM S90027.

Diagnosis. Dorsum distinctly flattened anteriorly; 2 small, rounded, paramedian swellings dorsally on rings 16–18; 3 transverse rows of tubercles on midbody metatergites; gonopod telopodite with posteriorly curving anterior branch and Y-shaped posterior branch directed posterodistally and slightly laterally.

Description. Males and females approximately the same size, length ca 5 mm, ring 6 vertical diameter ca 0.6 mm and maximum width ca 1.1 mm. Body strongly tapered from wide head to narrow telson (Fig. 1D); dorsum flattened anteriorly (Figs 1F, 10C); rings 16–18 with 2 small, rounded, paramedian swellings on (meta)tergites (Figs 10A,

10B). Midbody metatergites with 3 transverse rows of tubercles dorsally. Paranota wide (Fig. 1F); anterior and lateral margins in single convex curve, posterior margin straight; 3–4 weakly defined marginal lobes.

Gonopod telopodite (Figs 2C, 7) more or less cylindrical, tapering distally from laterally extended base, with a few strong setae on posterior surface, divided at ca threequarters telopodite height into anterior and posterior branches. Anterior branch somewhat flattened anteroposteriorly, with the lateral margin extended as rounded triangle basally; branch directed distally but curving posteriorly, the tip spade-like, pointed and slightly thickened. Posterior branch flattened mediolaterally, directed posterodistally and slightly laterally; branch Y-shaped, divided at ca one-half branch length into thin arms, one directed distally and the other laterally, both arms tipped with minute, variably positioned processes. Prostatic groove on anteromedial surface of telopodite, following posterior branch and terminating at tip of distally directed arm.

Distribution. Known from tropical rainforest in far north Queensland and from a single collection near Cammoo Caves in central coastal Queensland (Fig. 12). Cammoo Caves are ca 840 km from the type locality of *A. magnus*, but the four specimens from the Caves differ from the types mainly in being marginally larger; the gonopods are almost identical. If the specimens are indeed from forest near the Caves, then *A. magnus* may have been accidentally introduced to the area from far north Queensland. This record needs to be checked by further sampling in the Cammoo Caves area.

Etymology. Latin *magnus*, 'large', the name also containing Latin *agnus*, 'lamb'. *A. magnus* is the larger of the two *Asphalidesmus* species found on the Lamb Range.

Remarks. A. magnus can coil tightly in a spiral.

The dorsal flattening seen in this species (Figs 1F, 10C) contrasts strongly with the smoothly rounded cross-section of the type species *A. leae* (Figs 1E, 10D). Further, limbus elements in *A. magnus* are noticeably longer and more slender than limbus elements in the other nine *Asphalidesmus* spp. (Fig. 11) As the difference is only detectable at very high magnification, and because elements vary in length and width around the circumference of a body ring, I am reluctant to include this character state in the species diagnosis.

Latitude/longitude data in italics are from the QM collection database.

Asphalidesmus minor sp. n.

urn:lsid:zoobank.org:act:97FB1A5F-F95E-446A-BD35-0ABBDA950274 http://species-id.net/wiki/Asphalidesmus_minor Figs 3F, 8; map fig. 12

Holotype. Male, 3 km W by S of Mt Haig, Lamb Range, Qld, 17°06'S, 145°34'E ±1 km, 1150 m, 3 April 1984, A. Calder and T.A. Weir, ANIC berlesate 952, rainforest, ANIC 64-000209.

Paratypes. 2 males, details as for holotype, ANIC 64-000205; 1 female, Lamb Range, 19 km S of Mareeba, *17°06'39"S*, *145°34'04"E* ±0.5 km, 1200 m, 3 December 1988, G. Monteith and G. Thompson, QM berlesate 804, rainforest, sieved litter, QM S90029.



Figure 8. *Asphalidesmus minor* sp. n., paratype, ANIC 64-000205, gonopods in situ. **r** = posterior ridge, **st** = subquadrate tab, **o** = points to process on which prostatic groove opens. Scale bar = 0.05 mm.

Other material. None known.

Diagnosis. Gonopod telopodite sharply ridged posteriorly, not obviously divided into branches, instead extending apically as thin-walled, tube-like structure; 4 transverse rows of tubercles on midbody metatergites.

Description. Males and female approximately the same size, length ca 4 mm, ring 6 vertical diameter ca 0.4 mm and maximum width ca 0.6 mm. Midbody metatergites with 4 transverse rows of tubercles dorsally. Paranota wide (Fig. 3F); anterior and lateral margins in single convex curve, posterior margin straight; 4 weakly defined marginal lobes.

Posterior surface of gonopod telopodite (Fig. 8) abruptly produced as sharp ridge from ca one-quarter telopodite height. Numerous small bumps on posterior surface basal to ridge; larger, nearly contiguous bumps lateral to ridge to ca three-quarters telopodite height; surface medial to ridge nearly smooth, flat; a few scattered setae close to ridge to ca three-quarters telopodite height. Telopodite apex extending distally as thinwalled structure with narrow posterolateral opening; apical margin extended at medial end of wall as subquadrate tab with pointed extension at its posterior end; lateral end of apical wall extended as rhomboid with rounded distal corner and rounded notch near its anterior corner. Prostatic groove on anteromedial surface of telopodite, bending abruptly at anterior end of base of subquadrate tab and directed laterally, terminating in small process projecting into space surrounded by apical wall.

Distribution. So far known only from tropical rainforest on the Lamb Range in far north Queensland (Fig. 12).

Etymology. Latin *minor*, 'less'. *A. minor* is the smaller of the two *Asphalidesmus* species found on the Lamb Range.

Remarks. As with *A. bellendenkerensis* sp. n., the topology of the telopodite apex in this tiny species is surprisingly complex, and I have not yet had a clear view under the scanning electron microscope of the tiny process carrying the opening of the prostatic groove (Fig. 8). The course of the groove before it reaches this process, however, is clearly visible under a light microscope (not shown; see Description, above).

Latitude/longitude data in italics are from the QM collection database.

Asphalidesmus otwayensis sp. n.

urn:lsid:zoobank.org:act:A3771D42-9C7F-417E-93E8-C60C86A57D1A http://species-id.net/wiki/Asphalidesmus_otwayensis Figs 1G, 2D, 3C, 9; map fig. 12

Holotype. Male, Maits Rest, Otway Ranges, Vic, *38°45′S, 143°34′E*±1 km, 250 m, 24–25 December 1991, collector unknown (see Remarks), ANIC 64-000206.

Paratypes. 3 males, 2 females, details as for holotype, ANIC 64-000207.

Other material. (All from Otway Ranges, Vic) 4 males, 4 females, Phillips Road, 38°39'25"S, 143°30'E ±2 km, 25 December 1991, collector unknown (see Remarks), forest litter, ANIC 64-000208; 1 male, 1 stadium 5 female, Turtons Pass, 38°38'43"S, 143°40'36"E ±25 m, 420 m, 12 December 2003, R. Mesibov and T. Moule, MV K11142; 1 male, 1 female, same details but 38°38'39"S, 143°41'20"E ±25 m, 480 m, MV K11143; 1 male, 1 female, 1 stadium 6 female, Calder Ridge, 38°42'41"S, 143°34'03"E ±25 m, 380 m, 13 December 2003, R. Mesibov and T. Moule, MV K11141.

Diagnosis. Gonopod telopodites crossed at ca two-thirds telopodite height; apodous ring 18 produced dorsally as large, rounded swelling; 5 transverse rows of tubercles on midbody metatergites.

Description. Males and females approximately the same size, length ca 6 mm, ring 6 vertical diameter ca 0.6 mm and maximum width ca 1.1 mm. Midbody metatergites with 5 transverse rows of tubercles dorsally. Paranota wide (Fig. 3C); anterior and lateral margins in single convex curve, posterior margin straight with small round tab near base; 4–5 weakly defined marginal lobes. Ring 18 produced dorsally as large, rounded swelling (Fig. 1G) in both males and females.



Figure 9. *Asphalidesmus otwayensis* sp. n., paratype, ANIC 64-000207, gonopods in situ. Right gonopod telopodite is crossed anterior to left; view of left gonopod telopodite is down its long axis. \mathbf{ab} = anterior branch, \mathbf{pb} = posterior branch, \mathbf{o} = points to process on which prostatic groove opens. Scale bar = 0.2 mm.

Gonopod telopodite (Figs 2D, 9) divided into anterior and posterior branches at ca three-quarters telopodite height; telopodite widest just below division, bent posterodistally at ca one-half telopodite height, tapering basally to small base with small, rounded lobes directed posteriorly and posterolaterally, each lobe carrying a few small setae; a few small setae on posterior surface of telopodite just basal to division. Anterior branch anteroposteriorly flattened, directed posterodistally, expanded at tip into rhomboid, the central portion of the rhomboid thickened as finger-like process. Posterior branch similarly flattened, directed distally, the tip expanded into rhomboid lying just anterior to and parallel with rhomboid of anterior branch (leaving a small



Figure 10. A, B Lateral and dorsal views of last rings of paratype male *Asphalidesmus magnus* sp. n., QM S90026 **C** Ventral and slightly frontal view of head of paratype male *A. magnus* sp. n., QM S90026 **D** Ventral view of head of *A. leae* Silvestri, 1910, QVM 23:41547. Scale bars: **A, B** = 0.5 mm, **C, D** = 0.25 mm.



Figure 11. A, B Views of limbus on midbody metatergites; scale bars = 0.1 mm. **A** *Asphalidesmus magnus* sp. n., paratype male, QM S90026. **B** *A. otwayensis* sp. n., ANIC 64-000208. The form of the limbus elements in *A. otwayensis* sp. n. is typical for the genus, but as in all *Asphalidesmus* spp. the length and width of the elements varies around the circumference of a ring.

gap between), thus crossing anterior branch and terminating anterior to the latter's tip. Prostatic groove on anterior surface of telopodite, continuing on anterior branch to terminate at tip of finger-like process. Gonopod telopodites crossed near tips (see Remarks), with one telopodite nesting in bend on posterior surface of other telopodite.

Distribution. Known from cool temperate rainforest and wet eucalypt forest in the Otway Ranges in southwestern Victoria (Fig. 12).



Figure 12. A Outline map of Australia showing location of map **B**. **B** Localities for *Asphalidesmus otwayensis* sp. n. (crosses), *A. allynensis* sp. n. (star), *A. dorrigensis* sp. n. (filled triangles), all Queensland species (filled circles), unidentified *Asphalidesmus* (open squares) and questioned locality for *A. magnus* sp. n. (question mark). Rectangle at top shows location of map **C**. **C** Localities in far north Queensland for *A. bellendenkerensis* sp. n. (stars), *A. carbinensis* sp. n. (filled triangles), *A. magnus* sp. n. (open circles), *A. minor* sp. n. (filled circles) and unidentified *Asphalidesmus* (open squares). Scale bar = 50 km. **A** and **B** are geographic projections, **C** is Mercator projection.

Etymology. For the Otway Ranges, home to this species.

Remarks. The collector of the Maits Rest and Phillips Road samples from December 1991 is not named on the ANIC sample labels, which I copied when labelling specimens sorted from ANIC mixed holdings. Museum Victoria personnel collected at Otway Ranges sites at various times between October 1991 and March 1992, but there are no MV samples from 24 or 25 December 1991 (K. Walker, pers. comm., 4 March 2011). The ANIC database also has no collection records for other taxa from these places and dates (B. Mantle, pers. comm., 4 March 2011). The most likely possibility is that an entomological collector, not from MV, coincidentally sampled in the Otway Ranges during the 1991 Christmas holiday period and deposited the material in ANIC.

Latitude/longitude data in italics are based on local maps and Google Earth.

Crossing of gonopod telopodites (Fig. 9) is unusual in Dalodesmidea. In this species it may be facilitated by the remarkably small telopodite base articulating with the gonocoxa. The right telopodite crosses anterior to the left telopodite in six of the 11 *A. otwayensis* males examined, and posterior to the left telopodite in the other five.

Neither of the two juvenile females has a dorsal swelling on an apodous ring (ring 17 in stadium 6, rings 15 and 16 in stadium 5).

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References

- Attems C (1914) Die indoaustralischen Myriapoden. Archiv für Naturgeschichte (A) 80(4): 1–398.
- Attems C (1926) Myriopoda. In: Kükenthal W, Krumbach T (Eds) Handbuch der Zoologie. Eine Naturgeschichte der Stämme des Tierreiches. 4(1). Progoneata, Chilopoda, Insecta I. Walter de Gruyter and Co., Berlin and Leipzig, 1–402.
- Attems C (1931) Die Familie Leptodesmidae und andere Polydesmiden. Zoologica (Stuttgart) 30(3/4): 1–150.
- Attems C (1940) Das Tierreich. 70. Polydesmoidea. III. Fam. Polydesmidae, Vanhoeffeniidae, Cryptodesmidae, Oniscodesmidae, Sphaerotrichopidae, Peridontodesmidae, Rhachidesmidae, Macellolophidae, Pandirodesmidae. Walter de Gruyter and Co., Berlin, 577 pp.
- Brölemann HW (1916) Essai de classification des Polydesmiens (Myriapodes). Annales de la Société Entomologique de France 84: 523–608. (Online in Biodiversity Heritage Library)
- Chamberlin RV (1920) The Myriopoda of the Australian region. Bulletin of the Museum of Comparative Zoology 64(1): 1–269. (Online in Biodiversity Heritage Library)
- Golovatch SI (2003) A review of the volvatory Polydesmida, with special reference to the patterns of volvation (Diplopoda). African Invertebrates 44(1): 39–60.

- Golovatch SI, Geoffroy J-J, Mauriès J-P, VandenSpiegel D (2009) Review of the millipede family Haplodesmidae Cook, 1895, with descriptions of some new or poorly-known species (Diplopoda, Polydesmida). ZooKeys 7: 1–53. (Online through *ZooKeys* website) doi:10.3897/zookeys.7.117
- Hoffman RL (1980) ('1979') Classification of the Diplopoda. Muséum d'Histoire Naturelle, Genève, 237 pp.
- Jeekel CAW (1971) Nomenclator generum et familiarum Diplopodorum: a list of the genus and family-group names in the Class Diplopoda from the 10th edition of Linnaeus, 1758, to the end of 1957. Monografieën van de Nederlandse Entomologische Vereniging 5: i–xii, 1–412.
- Jeekel CAW (1982) Millipedes from Australia, 4: A new genus and species of the family Dalodesmidae from Australia (Diplopoda, Polydesmida). Bulletin Zoölogisch Museum, Universiteit van Amsterdam 9(2): 9–15.
- Jeekel CAW (1984) Millipedes from Australia, 7: The identity of the genus *Lissodesmus* Chamberlin, with the description of four new species from Tasmania (Diplopoda, Polydesmida, Dalodesmidae). Papers and Proceedings of the Royal Society of Tasmania 118: 85–101.
- Jeekel CAW (1986) Millipedes from Australia, 10: Three interesting new species and a new genus (Diplopoda: Sphaerotheriida, Spirobolida, Polydesmida). Beaufortia 36(3): 35–50.
- Mesibov R (2002) Redescriptions of Asphalidesmus leae Silvestri, 1910 and A. parvus (Chamberlin, 1920) comb. nov. from Tasmania, Australia (Diplopoda: Polydesmida: Haplodesmidae). Memoirs of Museum Victoria 59(2): 531–540. http://museumvictoria.com.au/pages/4094/59_2_mesibov.pdf
- Mesibov R (2007) The Trafalgar millipede *Lissodesmus johnsi* Mesibov, 2006 (Diplopoda: Polydesmida: Dalodesmidae). The Victorian Naturalist 124(4): 197–203.
- Mesibov R (2008) Diversity of Queensland paradoxosomatid millipedes (Diplopoda: Polydesmida: Paradoxosomatidae). Australian Entomologist 35(1): 37–46.
- Mesibov R (2009) A new millipede genus and a new species of Asphalidesmus Silvestri, 1910 (Diplopoda, Polydesmida, Dalodesmidea) from southern Tasmania, Australia. ZooKeys 7: 55–74. (Online through ZooKeys website) doi:10.3897/zookeys.7.111
- Silvestri F (1910) Descrizioni preliminari di nuovi generi di Diplopodi. I. Polydesmoidea. Zoologischer Anzeiger 35: 357–364. (Online in Biodiversity Heritage Library)
- Verhoeff KW (1932) Dr H. G. Bronn's Klassen und Ordnungen des Tier-Reichs wissentschaftlich dargestellt in Wort und Bild. 5(II)2. Gliederfüssler: Arthropoda. Klasse Diplopoda. Akademische Verlagsgesellschaft m.b.H., Leipzig, 2084 pp.
- Verhoeff KW (1936) Die Sphaerotrichopidae der südlichen Halbkugel und ihre Beziehungen. Zoologischer Anzeiger 114(1/2): 1–14.

Appendix I

Specimen records for the 10 currently known species of Asphalidesmus Silvestri, 1910.

Note: Specimen records for *Asphalidesmus* species are available on the *ZooKeys* website as a Microsoft Excel file (Appendix.xls, doi: 10.3897/zookeys.93.1255.app.1a) and a CSV file (Appendix.csv, doi: 10.3897/zookeys.93.1255.app.1b).