Advances in the Systematics of Diplopoda II

Edited by

Sergei I. Golovatch

&

Robert Mesibov

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Review of the millipede genus *Eutrichodesmus* Silvestri, 1910 (Diplopoda, Polydesmida, Haplodesmidae), with descriptions of new species

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Abstract

Eutrichodesmus, the largest genus in the Oriental family Haplodesmidae, is reviewed and shown to encompass 24 recognizable species, all keyed, including the following nine new species: *E. regularis* **sp. n.**, *E. aster* **sp. n.**, *E. filisetiger* **sp. n.**, *E. curticornis* **sp. n.**, *E. asteroides* **sp. n.** and *E. griseus* **sp. n.** from Vietnam, *E. distinctus* **sp. n.** from China, *E. multilobatus* **sp. n.** from Laos, and *E. reductus* **sp. n.** from Sulawesi, Indonesia. This genus is slightly redefined as follows: Gonopod coxae usually abundantly setose ventrolaterally; telopodite usually slender, not enlarged towards end of femorite, but typically with a more or less distinct process or outgrowth laterally, opposite recurvature point of seminal groove; solenomere thereafter usually comprising most of telopodite, sometimes elaborate; seminal groove normally terminating distally to subapically, with or without a hairpad; acropodite normally small to nearly absent.

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Keywords
Diplopoda, Haplodesmidae, *Eutrichodesmus*, taxonomy, new species, cave, China, Laos, Vietnam, Indonesia

Introduction

The millipede family Haplodesmidae Cook, 1895, which has only six component genera basically occurring (except for a few pantropical introductions) in East and Southeast Asia, as well as the southwestern Pacific region, has recently been reviewed (Golovatch et al. 2009).

The most speciose genus is *Eutrichodesmus* Silvestri, 1910, which contains 15 described species and ranges from southern Japan in the north, through southern China and Indochina, to Vanuatu, Melanesia in the south. The species are as follows (Golovatch et al. 2009):

Eutrichodesmus demangei Silvestri, 1910 (the type species), from Phu-Ly, Hanam Province, North Vietnam (Silvestri 1910);
Eutrichodesmus arcicollaris Zhang *in* Zhang & Wang, 1993, from Huayu Cave, Hekou County, Yunnan, China (Zhang and Wang 1993);
Eutrichodesmus armatocaudatus Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009, from Hang Lang Lua Cave, Pu Luong, Lung Cao, Thanh Hoa Prov., and a few more caves in and near Cuc Phuong National Park, Ha Nam Ninh Prov., northern Vietnam (Golovatch et al. 2009);
Eutrichodesmus basalis Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009, from Hang Bo Nau Cave, Dao Bo Hon, Vinh Ha Long Prov., northern Vietnam (Golovatch et al. 2009);
Eutrichodesmus cavernicola (Sinclair, 1901), from Cave Gua Tanan, Raman District and Cave Gua Glap near Biserat, Patani River, Patani District, southern Thailand (Hoffman 1977b);
Eutrichodesmus communicans Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009, from Vanuatu, Melanesia, southwestern Pacific (Golovatch et al. 2009);
Eutrichodesmus dorsiangulatus (Zhang *in* Zhang & Wang, 1993), from Baoniujiao Cave, Mengla County, Yunnan, China (Zhang & Wang 1993);
Eutrichodesmus gremialis (Hoffman, 1982), from "Chiang Dao caves" in northern Thailand (Hoffman 1982);
Eutrichodesmus incisus Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009, from caves near Hong Lin, Qianxi County, Guizhou Prov., China (Golovatch et al. 2009);
Eutrichodesmus latus Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009, from caves in Yachang Nature Reserve, Guangxi Prov., China (Golovatch et al. 2009);
Eutrichodesmus macclurei (Hoffman, 1977), from Batu Caves near Kuala Lumpur, Selangore State, Malaysia (Hoffman 1977a);
Eutrichodesmus monodentus (Zhang *in* Zhang & Wang, 1993), from Caiyun Cave, Mengla County, Yunnan, China (Zhang & Wang 1993);
Eutrichodesmus peculiaris (Murakami, 1966), from two epigean localities in Ehimé Prefecture, Shikoku, Japan (Murakami 1966);

Eutrichodesmus reclinatus (Hoffman, 1977), from Cave Gua Anak Takun at Templer Park near Kuala Lumpur, Selangore State, Malaysia (Hoffman 1977b); and
Eutrichodesmus similis Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009, from two caves in Mulun Nature Reserve, Guangxi Prov., China (Golovatch et al. 2009).

The present paper records another nine new species of *Eutrichodesmus*, thus improving our knowledge of the diversity of this Oriental genus. The descriptions below are arranged by countries in a more or less north-south direction.

Abbreviations used:

MNHN Muséum national d'Histoire naturelle, Paris, France
MZB Museum Zoologicum Bogoriense, Cibinong, Indonesia
SCAU South China Agricultural University, Guangzhou, China
SEM Scanning electron microscopy
ZMUM Zoological Museum, State University of Moscow, Moscow, Russia

Material and methods

The material serving as the basis for the present contribution derives mainly from subterranean collections made in Vietnam, China, Laos, and Indonesia by Anne Bedos and Louis Deharveng (MNHN). The bulk of this material, including most of the holotypes, has been deposited in MNHN, with two holotypes and a few paratypes from China and Indonesia shared between the collections of SCAU and MZB, respectively, and some further paratypes deposited in the collection of ZMUM, as indicated hereafter. The terms "doratodesmid" or "haplodesmid" are used hereafter only in their vernacular meaning, in order to concisely characterize a body shape, i.e. capable or nearly capable of volvation in the former informal group versus vermiform and definitely incapable of valvation in the latter.

SEM micrographs were taken using a JEOL JSM-6480LV scanning electron microscope. After examination, SEM material was removed from stubs and returned to alcohol, all such samples being kept at MNHN.

Systematics

***Eutrichodesmus distinctus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:5E777CD8-34D0-4820-9D76-0017195D53AD
Figs 1-3.

Type material: China, Guangxi Prov., Fushui, Bapen, Cave 4, 4.III.2005, leg. L. Deharveng & A. Bedos (CHIgx05-035), holotype ♂ (SCAU), paratypes: 1 ♀ (SCAU), 1 ♂ (MNHN JC 317), 1 ♂ (ZMUM), 1 ♂ (SEM).

Name: To emphasize the obvious distinctions from *E. latus* and *E. similis*, these being the only congeners hitherto known from Guangxi Province (Golovatch et al. 2009).

Diagnosis: Differs from all other congeners in the especially distinct metatergal tuberculation, coupled with the lack of tergal trichome, as well as only a few minor details of gonopod structure (in particular, the shape of the telopodite). In addition, it can be separated from the other species known from the same province, *E. latus* and *E. similis*, by the apparently perfect volvation (due to much shorter and more strongly declivous paraterga).

Description: Length of adults of both sexes *ca* 8.0-8.5 mm, width 1.35–1.40 mm, body broadest at segment 3 or 4. Holotype *ca* 8.0 mm long and 1.4 mm wide. Coloration uniformly pallid, shown pinkish because of a photographic artifact (Fig. 1).

Adults with 20 segments, body subcylindrical (Figs 1, 2A), conglobation complete, pattern of volvation typical, starting from segment 5 (cf. Golovatch 2003) (Fig. 2B). Head (Fig. 3C) slightly transverse (wider than high), rather densely pilose, microgranular and microvillose just below antennae and on vertex, with a pair of rounded,

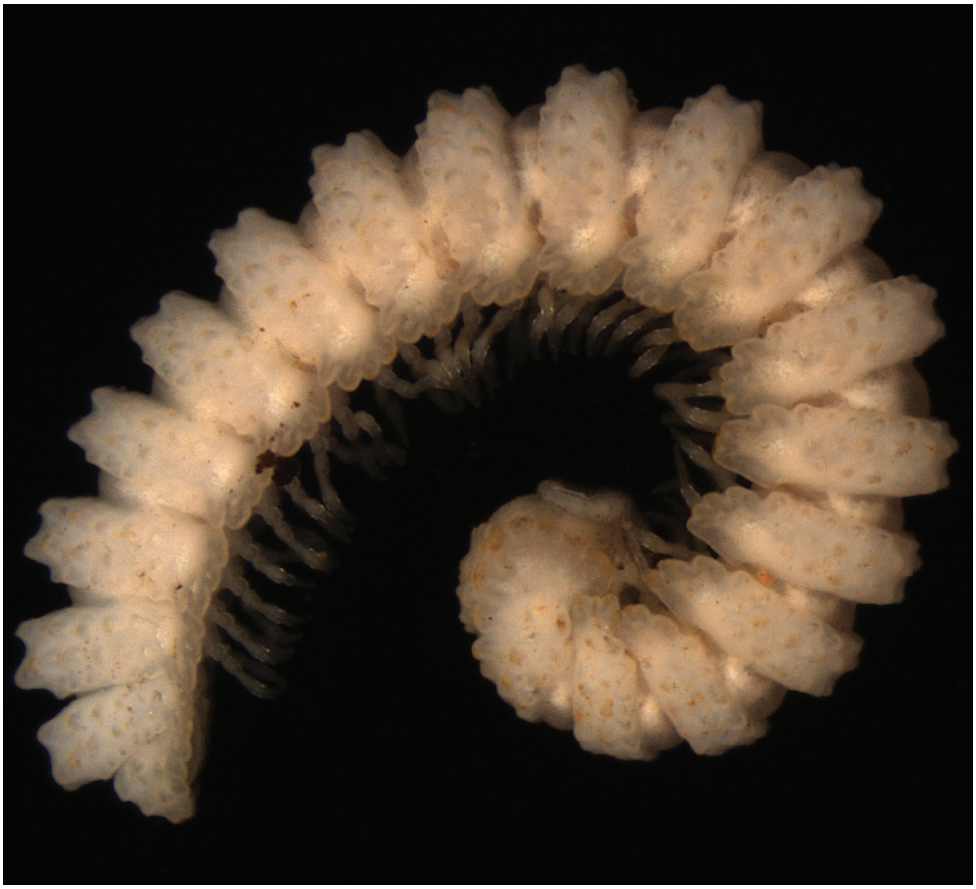

Figure 1. *Eutrichodesmus distinctus* sp. n., ♂ paratype; habitus, lateral view. (Photographed not to scale by L. Deharveng).

paramedian knobs; isthmus between antennal sockets about as wide as diameter of antennal socket. Antennae (Fig. 3C) rather long and slender; antennomere 6 longer than 5, both with an evident dorso-apical pit containing a tight group of minute bacilliform sensilla; antennomere 8 with the usual four sensory cones apically. Collum rather large, broader than head, distinctly flattened medially near front margin, not covering the head from above; entire surface microvillose, with several transverse rows of round tubercles (Fig. 2E). Prozona very finely alveolate, collum and metaterga covered with a cerotegumental crust held by abundant microvilli; stricture between pro- and meta-

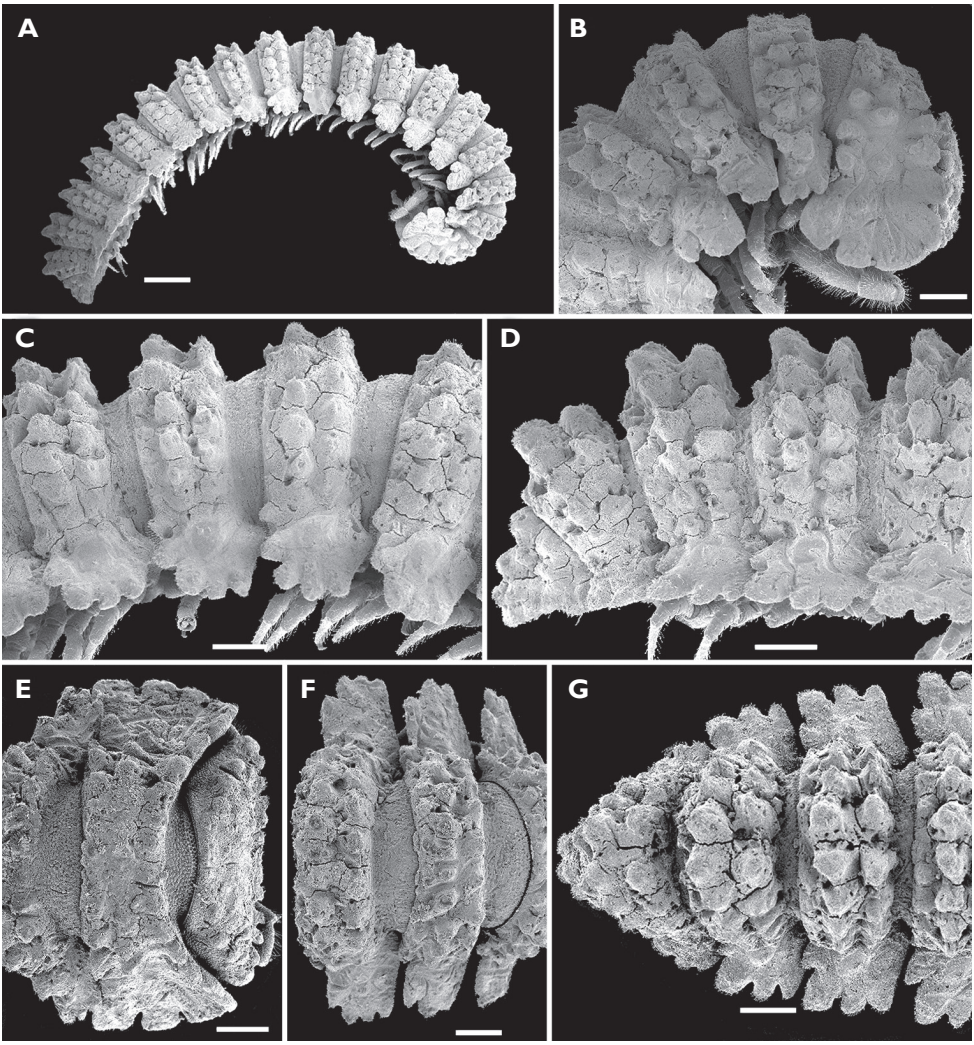

Figure 2. *Eutrichodesmus distinctus* sp. n., ♂ paratype; **A**, habitus, lateral view; **B & E**, anterior part of body, lateral and dorsal views, respectively; **C & F**, midbody segments, lateral and dorsal views, respectively; **D & G**, posterior part of body, lateral and dorsal views, respectively. – Scale bars: A, 0.5 mm; B-G, 0.2 mm.

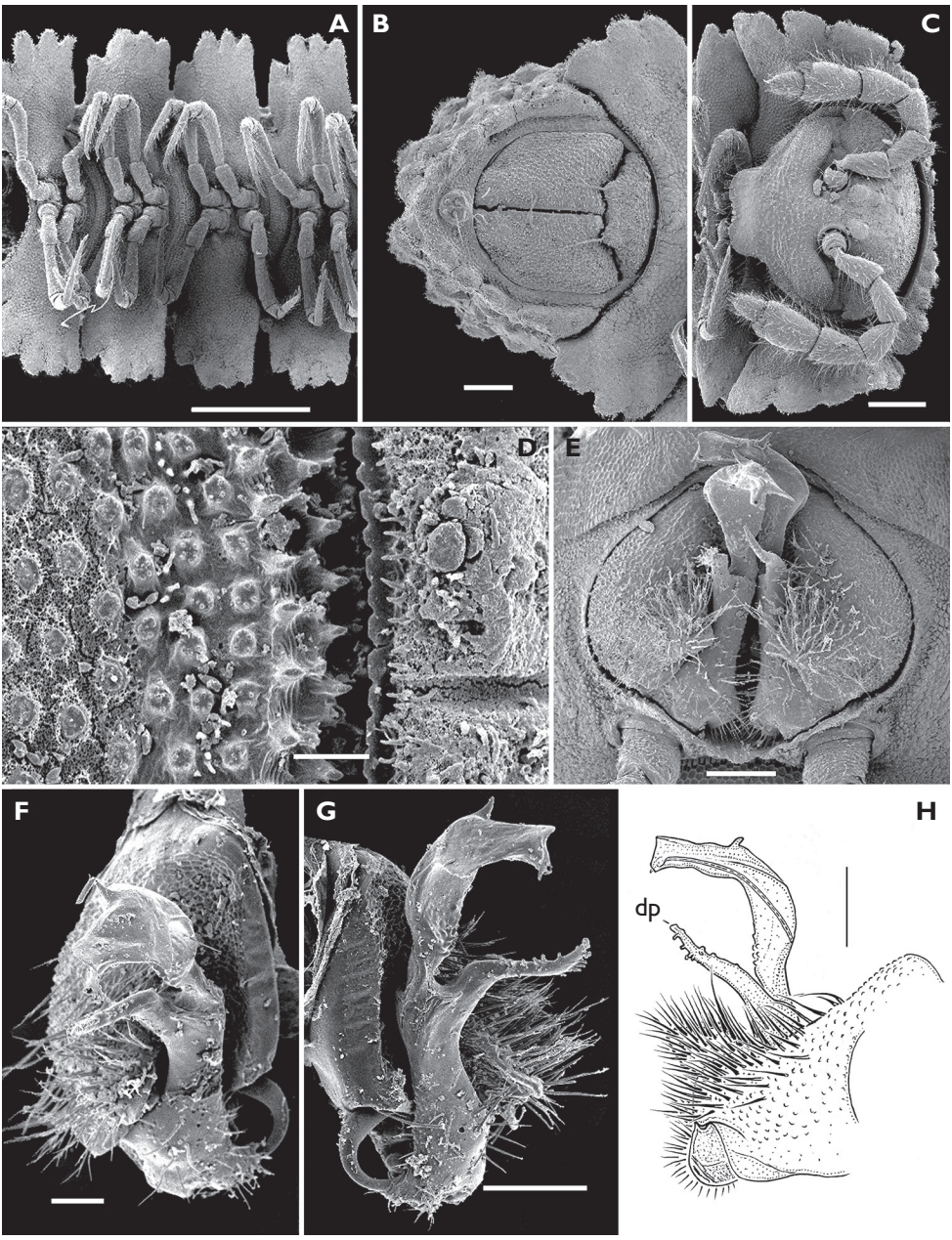

Figure 3. *Eutrichodesmus distinctus* sp. n., ♂ paratypes; **A**, midbody segments, ventral view; **B**, telson, ventral view; **C**, anterior part of body, ventral view; **D**, texture of tegument, dorsal view; **E**, both gonopods *in situ*, ventral view; **F-H**, gonopod, ventral, mesal and lateral views, respectively. – Scale bars: A, 0.5 mm; B, E & G, 0.1 mm; C & H, 0.2 mm; D, 0.02 mm; F, 0.05 mm.

zona broad and shallow, more finely alveolate-microgranular than prozona. Limbus microcrenulate, partly hidden by nearby abundant microvilli (Fig. 3D). Metaterga behind collum with three transverse and mixostictic (i.e. irregular in axial direction) rows of tubercles, second row being highest and best expressed in posterior part of body (Figs 1, 2A-G). Paraterga strongly declivous, rather broad and trilobate laterally, evidently surpassing level of venter, caudolaterally at base with 1-2 distinct lobulations (Figs 2A-G, 3A); middle and, especially, posterior parts of body set off laterally at base by a distinct impression, thus somewhat interrupting contour of convex dorsum; paraterga 2 strongly enlarged, with a series of lobulations anterolaterally, schism and hyposchism both very small; paraterga 3 and 4 slightly shorter than others (Fig. 2B), overlap of following paraterga typical. Pore formula normal (5, 7, 9, 10, 12, 13, 15-19), ozopores very indistinct, located near top of caudolateral lobulation. Metatergal setation wanting. Pleurotergal ridges absent. Epiproct short, also with differentiated tubercles, directed ventrocaudad, with the usual four cones just below tip. Hypoproct and paraprocts normal (Fig. 3B).

Sterna usually with a deep, narrow, transverse depression between coxae (Fig. 3A), only sterna between ♂ coxae 6, 7 and 9 much wider. Gonopod aperture suboval, relatively small, far from reaching lateral sides of segment 7 (Fig. 3E). Legs rather long and relatively slender, barely reaching tips of paraterga; femoral and tarsal segments longest, subequal in length; claw normal, simple, very slightly curved ventrad; some setae with microdenticulations (Fig. 3A).

Gonopods (Figs 3F-H) very simple. Coxae subquadrate, large, microtuberculate and abundantly setose ventrolaterally, with a conspicuous triangular lobe frontolaterally. Telopodite longer than coxite, slender throughout, setose in its basal half, with a conspicuous, denticulate, lateral, distofemoral process (dp) at about midway, seminal groove terminating subapically near a small spiniform prong.

Remarks: This pallid species shows differentiation of the metatergal tubercles in the second row growing steadily higher towards the telson, coupled with the absence of tergal setation. It is a typical "doratodesmid" (capable of volvation, see Golovatch et al. 2009), possibly a troglobite.

***Eutrichodesmus regularis* Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:5137C5B6-4F58-4BCC-A746-21705E195066
Figs 4-7.

Type material: Vietnam, Lao Cai Prov., Sa Pa, Hang Ta Phin Cave, hand collected, 11.VIII.2003, leg. L. Deharveng & Bedos (Vn0308-009), holotype ♂ (MNHN JC 318), paratypes: 1 ♂, 2 ♀, 1 subad., 1 juv. (MNHN JC 318), 1 ♀ (ZMUM), 1 ♂ (SEM).

Name: To emphasize the highly regular, isostictic (i.e. regular rows not only transversely, but also longitudinally) and almost undifferentiated pattern of metatergal tuberculation.

Diagnosis: Differs from congeners by the perfect volvation, coupled with faint metatergal lobulations, the especially regular, nearly undifferentiated and isostictic pattern of metatergal tuberculation, the peculiar, phylloid tergal setae and a few minor details of gonopod structure (in particular, the shape of the telopodite and distofemoral process).

Description: Length of adults of both sexes *ca* 9.0-10.0 mm, width 1.7-1.8 mm, body broadest at segment 3 or 4. Holotype *ca* 10 mm long and 1.7 mm wide. Coloration uniformly pallid, shown pinkish because of a photographic artifact (Fig. 4).

Adults with 20 segments, pattern of conglobation typical of "doratodesmids" (Figs 4, 5A). Head, antennae (Fig. 5E), tegument (Figs 6A-C), sterna (Fig. 6E), gonopod aperture (Fig. 6F) and many other characters (Figs 5F, 6D) much as in *E. distinctus* sp. n., but collum more regularly tuberculate and slightly flattened mid-dorsally (Fig. 5B). Metater-

Figure 4. *Eutrichodesmus regularis* sp. n., ♂ paratype; habitus, lateral view. (Photographed not to scale by L. Deharveng).

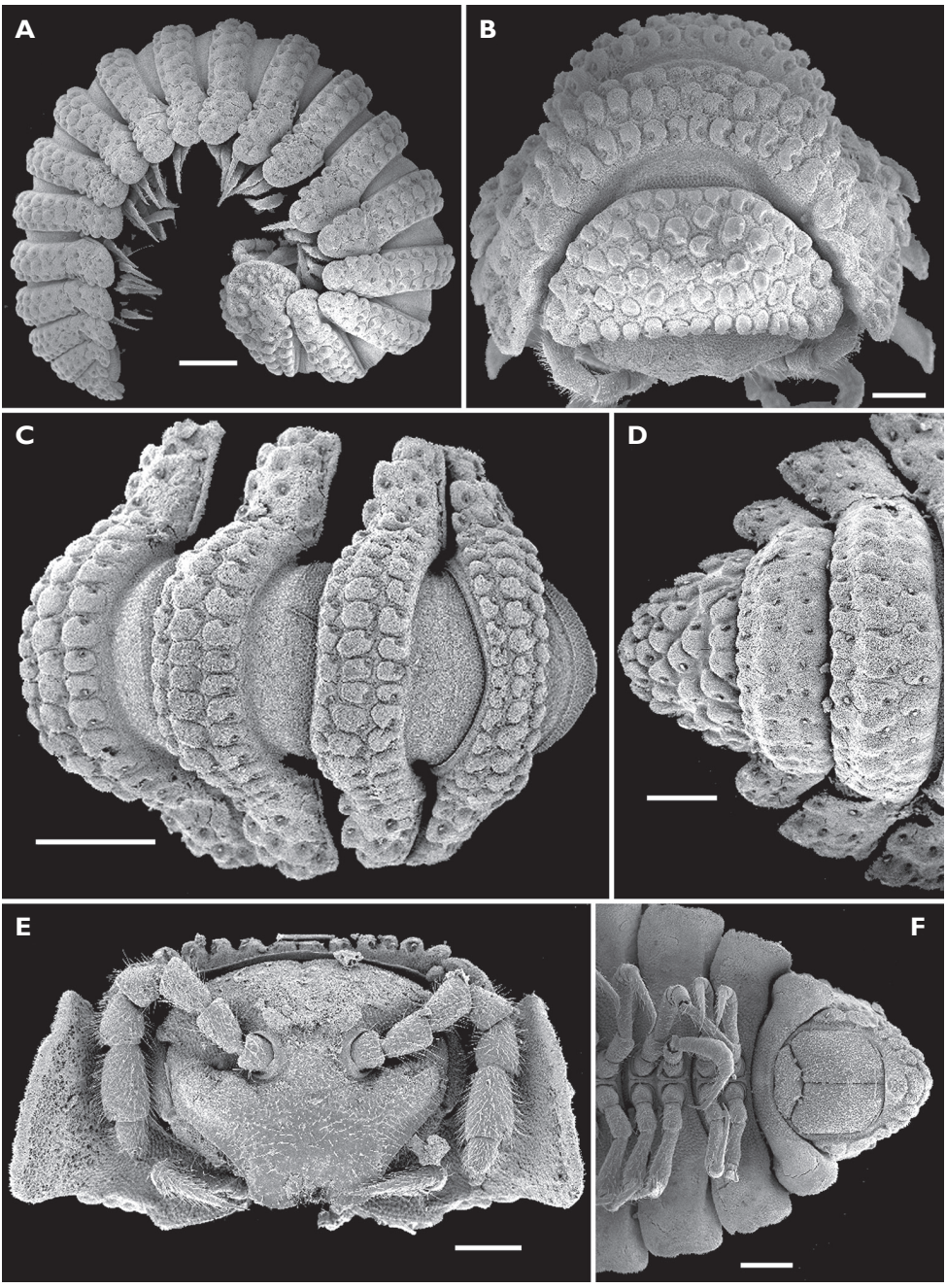

Figure 5. *Eutrichodesmus regularis* sp. n., ♂ paratype; **A**, habitus, lateral view; **B & E**, anterior part of body, frontodorsal and ventral views, respectively; **C**, midbody segments, dorsal view; **D & F**, posterior part of body, dorsal and ventral views, respectively. – Scale bars: A, C, 0.5 mm; B, D-F, 0.2 mm.

ga behind collum with three transverse, very regular and isostictic rows of subequally-sized, rounded, flat, nearly undifferentiated tubercles (Figs 5A-D), each crowned with a short, 2-segmented, phylloid seta (Fig. 6C). Paraterga directed ventrolaterad, rather broad, slightly surpassing level of venter, slightly interrupting general outline of convex dorsum (Figs 5A, C, 6D); paraterga 2 strongly enlarged, each margin nearly entire, with only very faint traces of a series of small lobulations anterolaterally (Figs 4, 5A, B, D). Following paraterga broadly rounded and slightly 3- or 4-lobate laterally and at least distinctly bilobate caudolaterally (Figs 5A, C, D, 6F). Limbus very faintly crenulate, almost

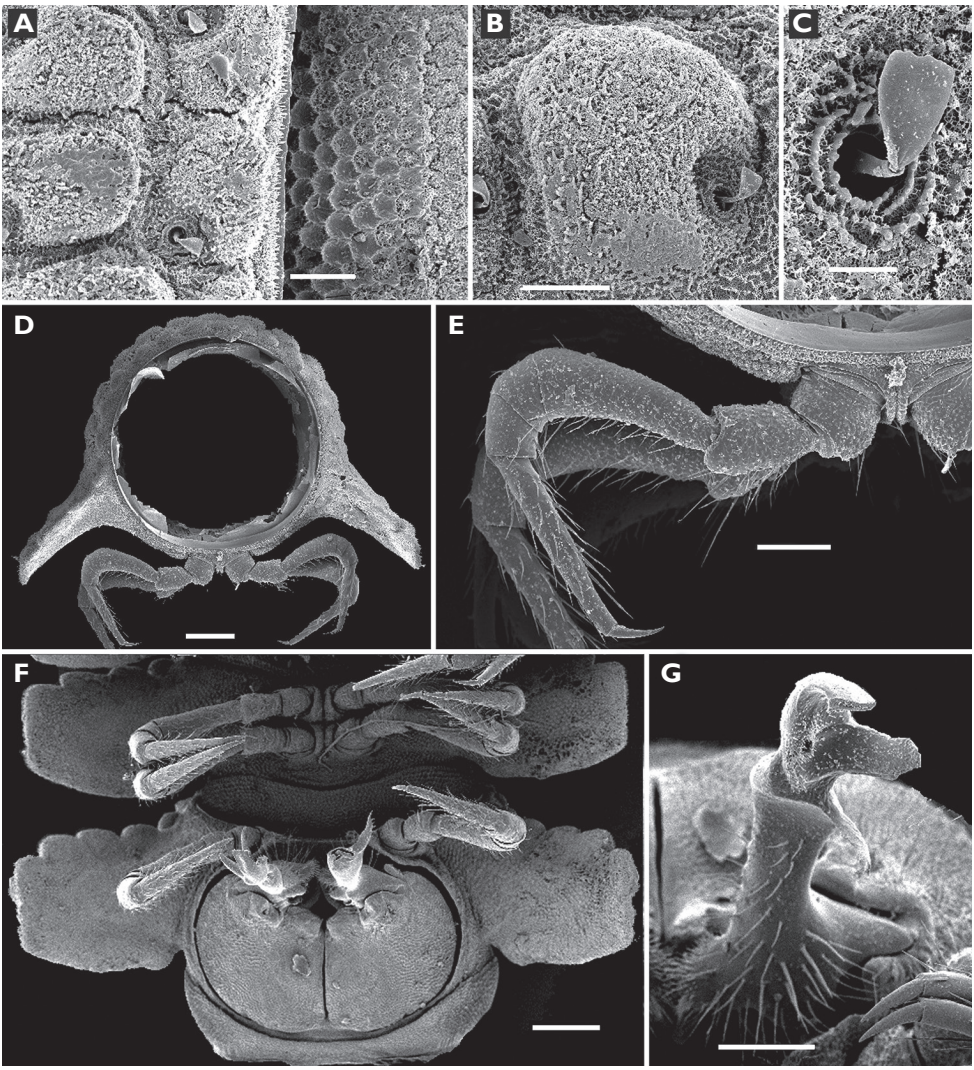

Figure 6. *Eutrichodesmus regularis* sp. n., ♂ paratype; **A**, texture of tegument, dorsal view; **B**, metatergal tubercle, dorsal view; **C**, metatergal seta, dorsal view; **D**, cross-section of a midbody segment, caudal view; **E**, midbody legs, caudal view; **F**, segments 7 and 8, ventral view; **G**, left gonopod *in situ*, caudoventral view. – Scale bars: A, B, 0.05 mm; C, 0.01 mm; D, F, 0.2 mm; E, G, 0.1 mm.

hidden by nearby abundant microvilli (Fig. 6A). Pore formula normal, ozopores poorly visible, located dorsally near tip of ventrocaudal lobulation (Figs 5C, D).

Legs relatively long, slightly surpassing edge of paraterga (Figs 6D, E).

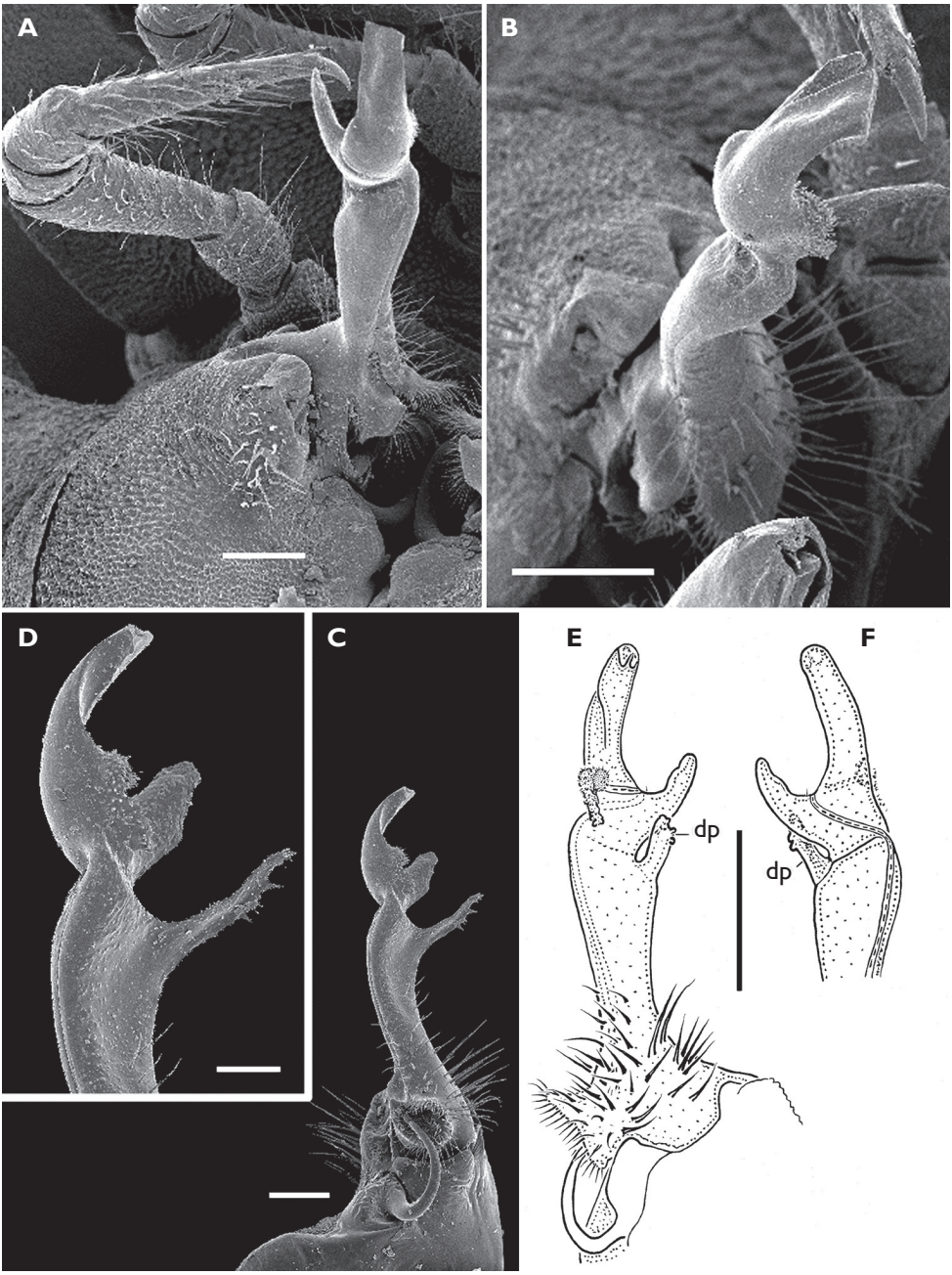

Figure 7. *Eutrichodesmus regularis* sp. n., ♂ paratypes; **A-F**, gonopods, frontoventral, submesal, mesal, mesal and lateral views, respectively. – Scale bars: A-C, 0.1 mm; D, 0.05 mm; E & F, 0.2 mm.

Gonopods (Figs 6F, G, 7A-E) relatively complex. Coxae subquadrate, large, microtuberculate, nearly bare, with only a few, mostly short setae on and near base of a small ventro-apical lobe. Telopodite considerably longer than coxite, slightly stouter and setose in its basal half, with an inconspicuous, digitiform, simple, lateral, distally papillate, distofemoral process (dp) at about midway, more distally with another simple outgrowth with its base marking recurvature point of a relatively short seminal groove; acropodite (= solenomere) relatively stout, lamelliform, slightly curved along main axis, with two small denticles apically and a conspicuous pilose-spinulate pulvillus near base (Figs 7E, F).

Remarks: This pallid species shows highly peculiar, phylloid but very short, tergal setae and undifferentiated metatergal tubercles. It is also a typical "doratodesmid", possibly another troglobite.

Eutrichodesmus aster **Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:B107B0B1-7423-466C-8E47-BE50F0EA0D5D
Figs 8-11.

Type material: Vietnam, Yen Bai Prov., Nghia Lo: Xa Som a, Tham Han Cave, hand collected, 20.XII.2003, leg. L. Deharveng, A. Bedos & Phuong (Vn0312-46), holo-

Figure 8. *Eutrichodesmus aster* sp. n., ♂ paratype from Tham Han Cave; habitus, lateral view. (Photographed not to scale by L. Deharveng).

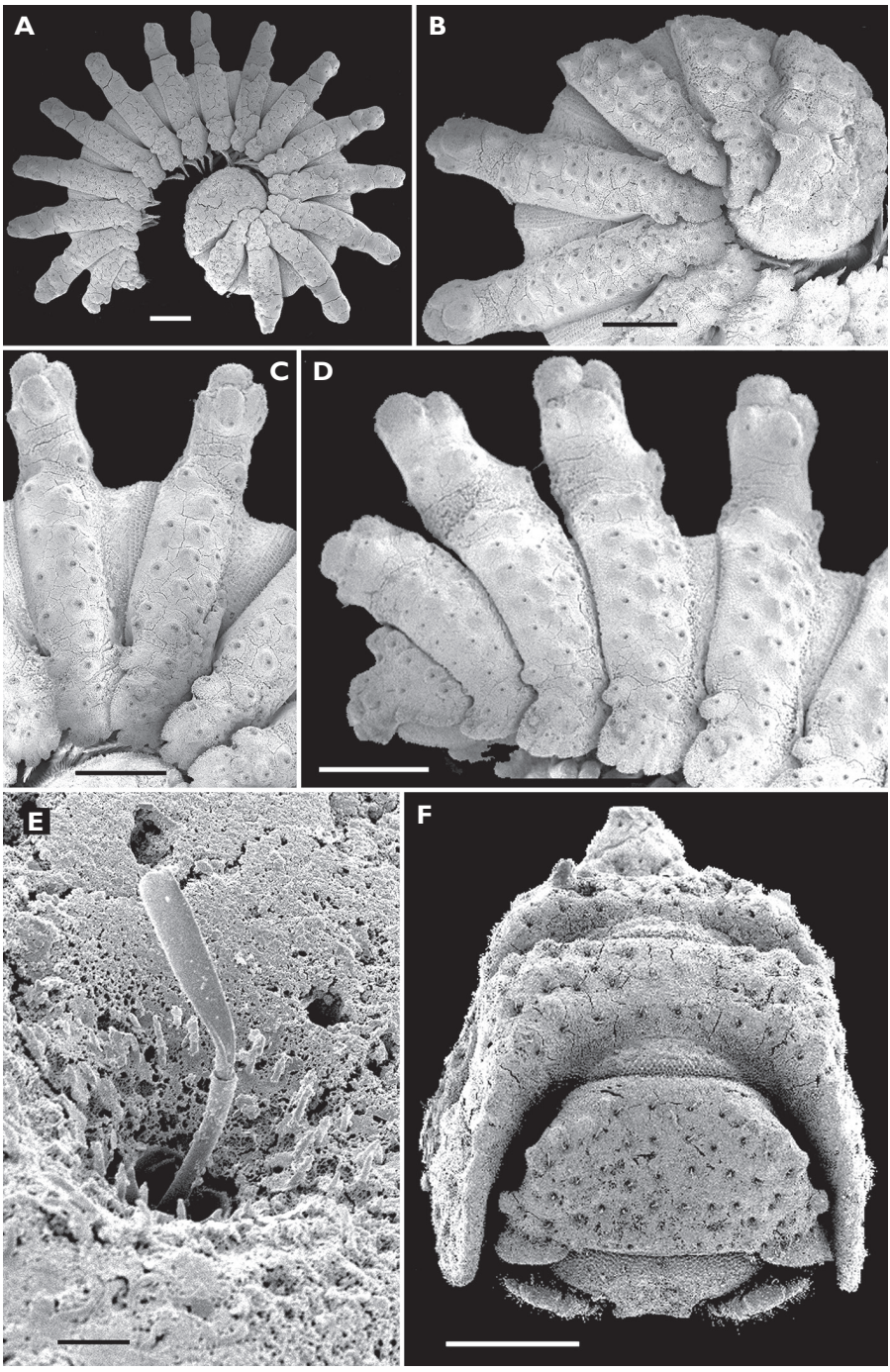

Figure 9. *Eutrichodesmus aster* sp. n., subadult paratype from Tham Han Cave; **A**, habitus, lateral view; **B**, anterior part of body, lateral view; **C**, midbody segments, lateral view; **D**, posterior part of body, lateral view; **E**, metatergal seta, sublateral view; **F**, anterior part of body, frontodorsal view. – Scale bars: A-D & F, 0.5 mm; E, 0.001 mm.

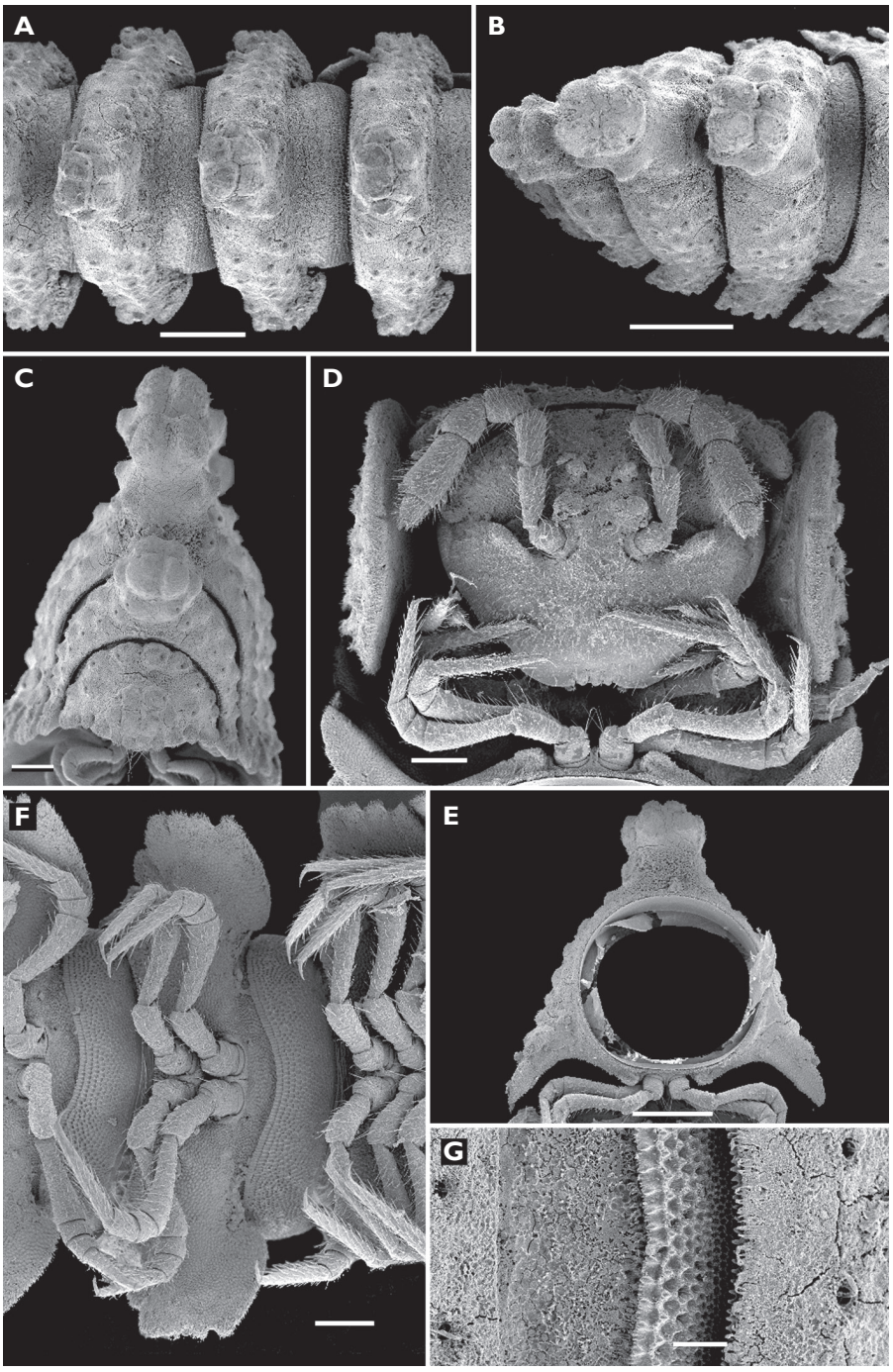

Figure 10. *Eutrichodesmus aster* sp. n., subadult paratype from Tham Han Cave; **A & E**, midbody segments, dorsal and ventral views, respectively; **B & C**, posterior part of body, dorsal and caudal views, respectively; **D**, anterior part of body, ventral view; **F**, cross-section of a midbody segment, caudal view; **G**, texture of tegument, dorsal view. – Scale bars: A, B & F, 0.5 mm; C-E, 0.2 mm; G, 0.05 mm.

type # (MNHN JC 319), paratypes: 1 ♂, 1 ♀, 2 subad., 1 juv. (MNHN JC 319), 1 ♂, 1 subad. (ZMUM), 1 subad. (SEM). Vietnam, Yen Bai Prov., Nghia Lo: Tham Lê Cave, hand collected, 19.XII.2003, leg. L. Deharveng, A. Bedos & Phuong (Vn0312-38), paratypes: 2 ♂ (MNHN JC 319). Vietnam, Yen Bai Prov., Nghia Lo: Hang Dan Khao Cave, hand collected, 20.XII.2003, leg. L. Deharveng, A. Bedos & Phuong (Vn0312-48), 1 ♂ (fragm.), 1 ♀ (MNHN JC 319), 1 ♀, 1 juv. (ZMUM).

Name: To reflect the star-shaped and discoid body of the volvated animal.

Diagnosis: Differs from all congeners, except *E. macclurei* and *E. reclinatus*, by the extremely high mid-dorsal crests on metaterga 5-19. In addition, it can be distinguished from *E. macclurei* and *E. reclinatus* in the presence of a mid-dorsal projection on metatergum 4, the slightly more strongly declivous and quadrilobate paraterga. The new species differs from all other species of the genus in minor details of gonopod structure (in particular, the shape of the telopodite and distofemoral process).

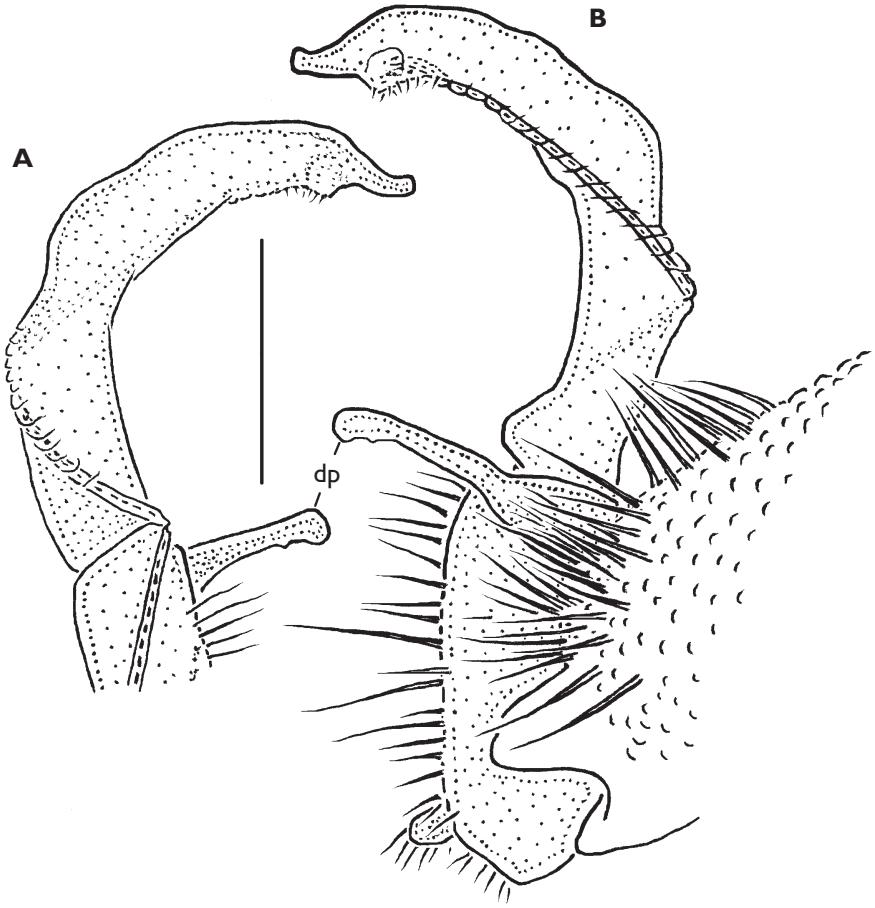

Figure 11. *Eutrichodesmus aster* sp. n., ♂ paratype from Tham Han Cave; **A & B**, left gonopod, mesal and lateral views, respectively. – Scale bar: 0.2 mm.

Description: Length of adults of both sexes *ca* 12-14 mm, width 2.1-2.3 mm, body broadest at segment 3 or 4. Holotype *ca* 12 mm long and 2.2 mm wide. Coloration uniformly pallid, shown pinkish because of a photographic artifact (Fig. 8).

Adults with 20 segments (Figs 8, 9A); body discoid, strongly flattened laterally; pattern of conglobation typical of "doratodesmids". Head, antennae (Fig. 10D), tegument (Fig. 10G), sterna (Fig. 10E), gonopod aperture and many other characters much as in *E. distinctus* sp. n.; collum rather irregularly tuberculate and only very slightly flattened medially at anterior edge (Fig. 9F). Metaterga behind collum with three transverse, rather irregular and mixostictic rows of rounded, flat, only slightly differentiated tubercles (Figs 9A-D), each crowned with a short, 2-segmented, flattened seta (Fig. 9E). Metaterga 4-19 each with a very high, slightly bifid, mid-dorsal process (Figs 8, 9A-D, 10A-C). Paraterga directed ventrolaterad up to subvertical, rather broad, surpassing level of venter (Fig. 10F); paraterga 2 strongly enlarged, very indistinctly lobulate anterolaterally (Fig. 9B). Following paraterga broadly rounded, evidently 4-lobate laterally and bilobate caudolaterally (Figs 9A-D, 10E). Limbus strongly denticulate, almost hidden by nearby abundant microvilli (Fig. 10G). Pore formula normal, ozopores poorly visible, located dorsally near base of ventrocaudal lobulation (Figs 10A, B). Epiproct short, with differentiated tubercles (Fig. 10C).

Legs relatively long, slightly surpassing edge of paraterga (Figs 10E, F).

Gonopods (Fig. 11) relatively simple. Coxae abundantly micropapillate and setose, with one normal, apicolateral lobe. Telopodite elongate, slender, slightly arcuate, with a short, bare, distofemoral process (dp) at about proximal one-third; seminal groove and acropodite (= solenomere) long, hairpad subapical.

Remarks: This pallid species shows peculiarly high mid-dorsal projections, coupled with short, distally flattened tergal setae. It is also a typical "doratodesmid", possibly another troglobite.

Eutrichodesmus filisetiger Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.

urn:lsid:zoobank.org:act:CC34CE29-FD03-4796-B19E-8EFD94686705

Figs 12-15.

Type material: Vietnam, Thanh Hoa Prov., Thanh Son: Lang Kho Muong, Hang Doi Cave, hand collected, 13.XII.2003, leg. L. Deharveng & team (Vn0312-27), holotype ♂ (MNHN JC 320), paratypes: 1 ♂, 2 subad. (MNHN JC 320), 1 ♂ (SEM). Vietnam, Thanh Hoa Prov., Lang Hang: Hang Bo Muoi Cave, hand collected, 14.XII.2003, leg. L. Deharveng & team (Vn0312-33), paratype ♀ (ZMUM).

Name: To emphasize the peculiar, filiform but rather short tergal setae.

Diagnosis: Differs from congeners by the perfect volvation, coupled with the filiform tergal setae, evident metatergal lobulations, a regular pattern of tergal tuberculation and a few minor details of gonopod structure (in particular, the shape of the telopodite and a rudimentary distofemoral process).

Figure 12. *Eutrichodesmus filisetiger* sp. n., ♂ paratype from Hang Doi Cave; habitus, lateral view. (Photographed not to scale by L. Deharveng).

Description: Length of adults of both sexes *ca* 12-13 mm, width 2.5–2.6 mm, body broadest at segment 3 or 4. Holotype *ca* 12 mm long and 2.5 mm wide. Coloration uniformly pallid, shown pinkish because of a photographic artifact (Fig. 12).

Adults with 20 segments (Figs 12, 13A), pattern of conglobation typical of "doratodesmids". Head, antennae (Fig. 14A), tegument (Figs 14E, F), sterna (Fig. 14C), gonopod aperture (Fig. 14G) and many other characters (Figs 14C, D) much as in *E. distinctus* sp. n.; collum rather irregularly tuberculate and slightly flattened medially at anterior edge (Figs 13E, 14B). Metaterga behind collum with three transverse, rather regular, mixostictic rows of rounded, flat, undifferentiated tubercles (Figs 13A-F), each crowned with a short, 2-segmented, filiform seta (often broken off) (Figs 14E, F). Only last two metaterga a little elevated compared to preceding ones (Figs 12, 13A, D). Paraterga directed ventrolaterad, nearly continuing general outline of convex dorsum, rather broad, slightly surpassing level of venter, most of them evidently lobulate (Figs 13A-F, 14C); paraterga 2 strongly enlarged, evidently lobulate only anterolaterally but

not laterally (Fig. 13B). Following paraterga broadly rounded, evidently 4-lobate laterally and 3-lobate caudolaterally (Figs 13A-D, 14G). Limbus very distinctly spiculate, almost hidden by nearby abundant microvilli (Fig. 14E). Pore formula normal, ozopores very poorly visible, located dorsally near base of ventrocaudal lobulation (Figs 13C, D). Epiproct short, with regular tuberculations (Fig. 13D).

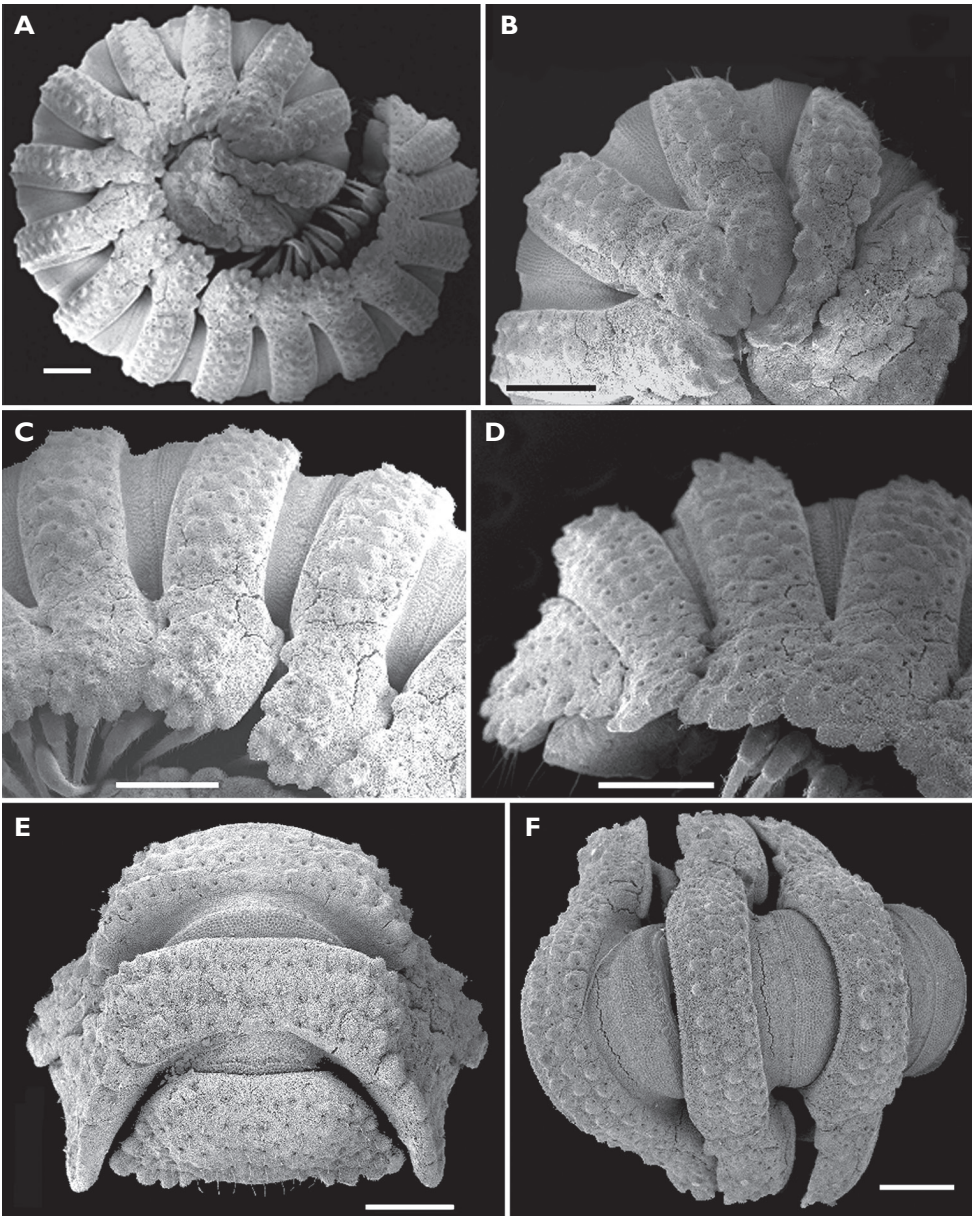

Figure 13. *Eutrichodesmus filisetiger* sp. n., ♂ paratype from Hang Doi Cave; **A**, habitus, lateral view; **B & E**, anterior part of body, lateral and frontodorsal views, respectively; **C & F**, midbody segments, lateral and dorsal views, respectively; **D**, posterior part of body, lateral view. – Scale bars: A-F, 0.5 mm.

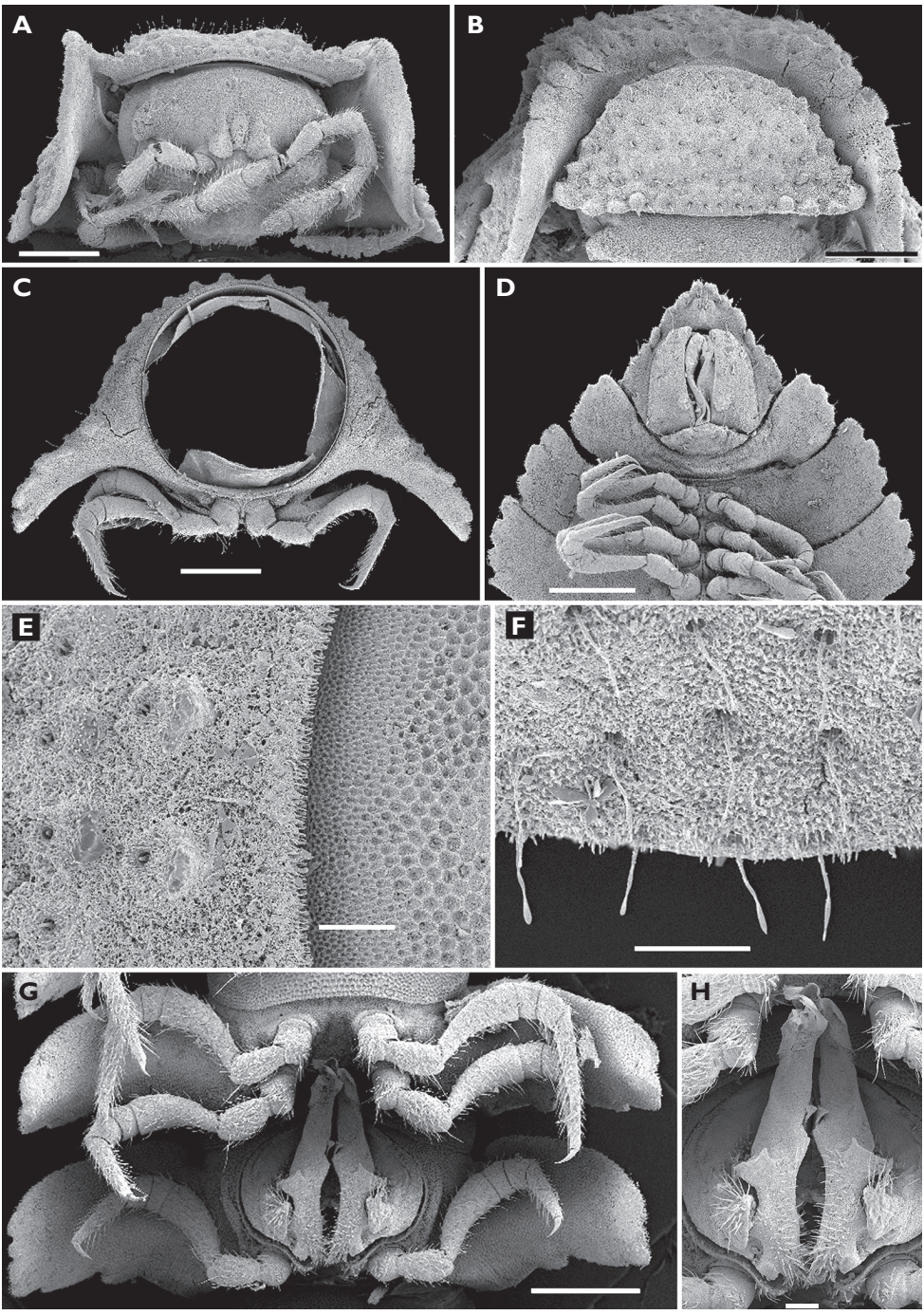

Figure 14. *Eutrichodesmus filisetiger* sp. n., ♂ paratype from Hang Doi Cave; **A**, head, dorsal view; **B**, collum, frontodorsal view; **C**, cross-section of a midbody segment, caudal view; **D**, posterior part of body, ventral view; **E**, texture of tegument, dorsal view; **F**, setae on collum; **G**, segments 6 and 7, ventral view; **H**, gonopods *in situ*. – Scale bars: A-D & G, 0.5 mm; E, F & H, 0.1 mm.

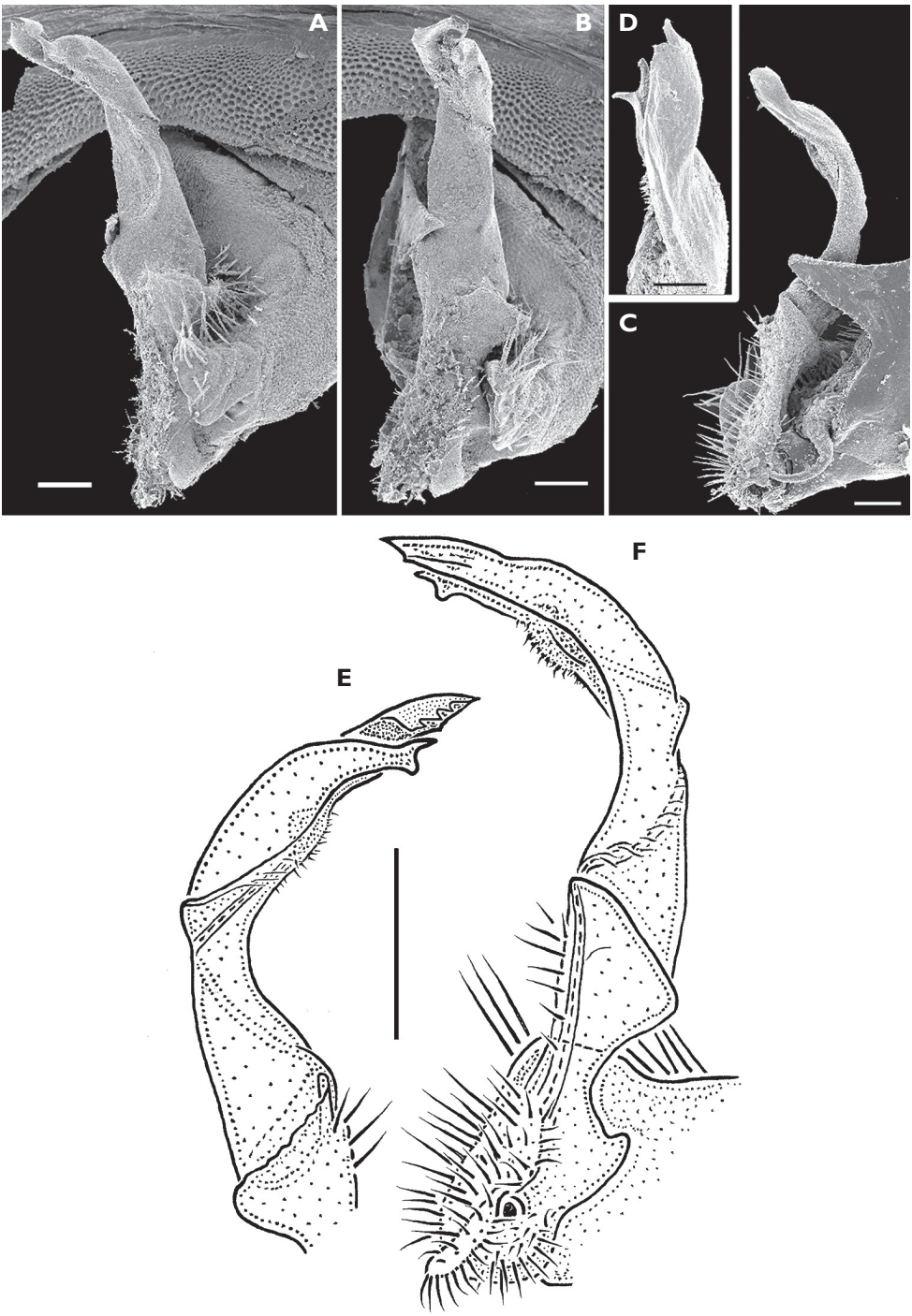

Figure 15. *Eutrichodesmus filisetiger* sp. n., ♂ paratypes from Hang Doi Cave; **A-F**, gonopod, subventral, ventral, sublateral, mesal, lateral and mesal views, respectively. – Scale bars: A-C, 0.01 mm; D, 0.05 mm; E & F, 0.2 mm.

Legs relatively long and slender, slightly reaching edge of paraterga (Figs 14C, G).

Gonopods (Figs 14G, H, 15A-F) relatively complex. Coxae abundantly micropapillate and setose, with two conspicuous lobes: one normal, apicolateral, the other unusual, subtriangular, median, both apparently to control telopodite movements. Telopodite elongate, slender, slightly arcuate, with only a rudimentary distofemoral process at about midway (barely seen in lateral view as a short prong in a kind of pocket) and an evident hairpad at distal one-third of acropodite (= solenomere), also marking a branching point of two long, slender, apical pieces, one lateral, bifid, a little shorter and well-sclerotized, the other lamellar, pointed and dentate.

Remarks: This rather large, pallid species shows filiform tergal setae and only poorly differentiated metatergal tubercles. It is also a typical "doratodesmid", possibly still another troglobite.

***Eutrichodesmus curticornis* Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:AEBAEF74-7FF7-4E99-8108-D0D85ACE06C3
Figs 16-18.

Type material: Vietnam, Nghê An Prov., Anh Son: Hoi Son, Hang Lung Bo Cave, hand collected, 19.I.2003, leg. L. Deharveng & A. Bedos (VIET-901), holotype ♂ (MNHN JC 321), paratypes: 1 ♀ (MNHN JC 321), 1 ♀ (SEM).

Figure 16. *Eutrichodesmus curticornis* sp. n., ♀ paratype; habitus, lateral view. (Photographed not to scale by L. Deharveng).

Name: To emphasize the unusually short antennae.

Diagnosis: Differs from congeners by the perfect volvation, coupled with the very short antennae, legs and paraterga, the contiguous paramedian tubercles above the antennal sockets, the regular mixostictic pattern of metatergal tuberculation and a few minor details of gonopod structure (in particular, the shape of the telopodite and distofemoral process).

Description: Length of adults of both sexes *ca* 4.7-5.3 mm, width 0.65–0.7 mm, body broadest at segment 3 or 4. Holotype *ca* 4.7 mm long and 0.65 mm wide. Coloration uniformly pallid, shown pinkish because of a photographic artifact (Fig. 16).

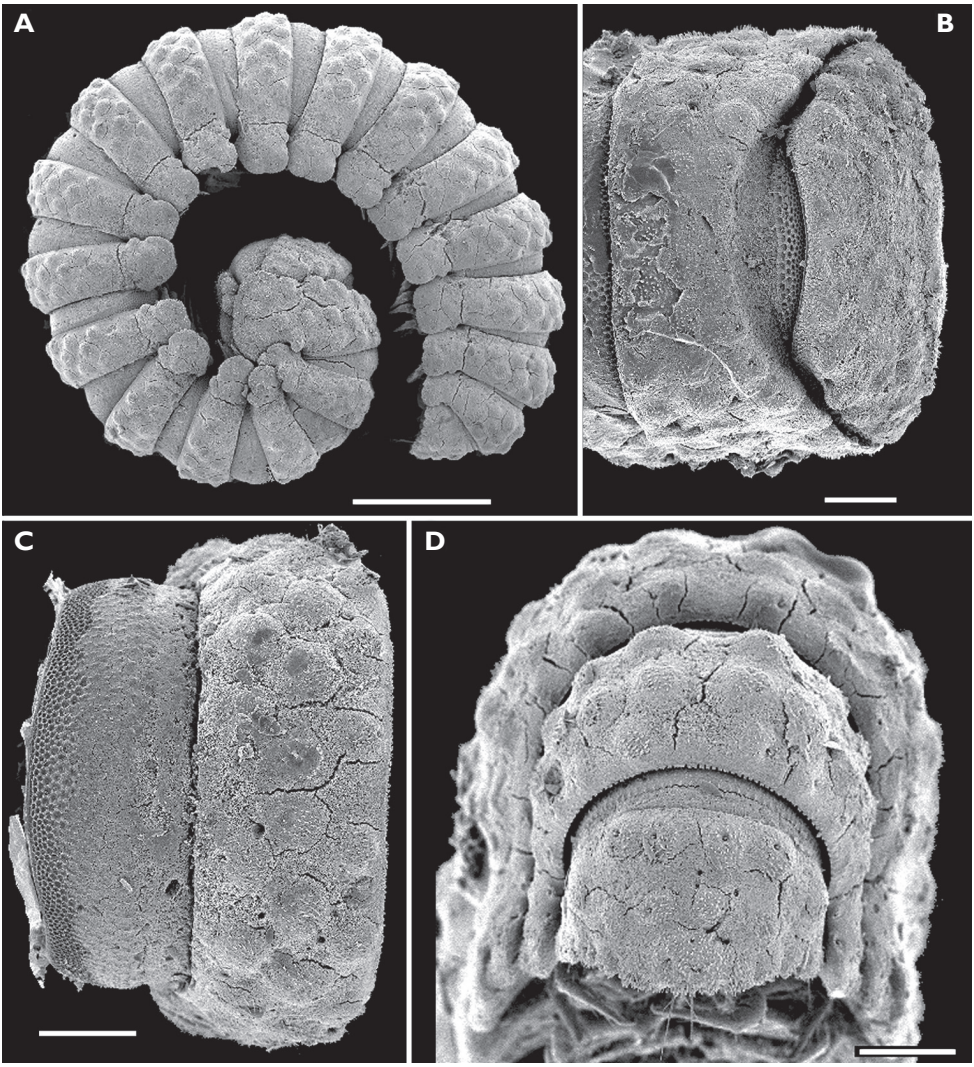

Figure 17. *Eutrichodesmus curticornis* sp. n., ♀ paratype; **A**, habitus, lateral view; **B**, anterior part of body, dorsal view; **C**, midbody segment, dorsal view; **D**, posterior part of body, caudal view. Scale bars: A, 1.0 mm; B-D, 0.1 mm.

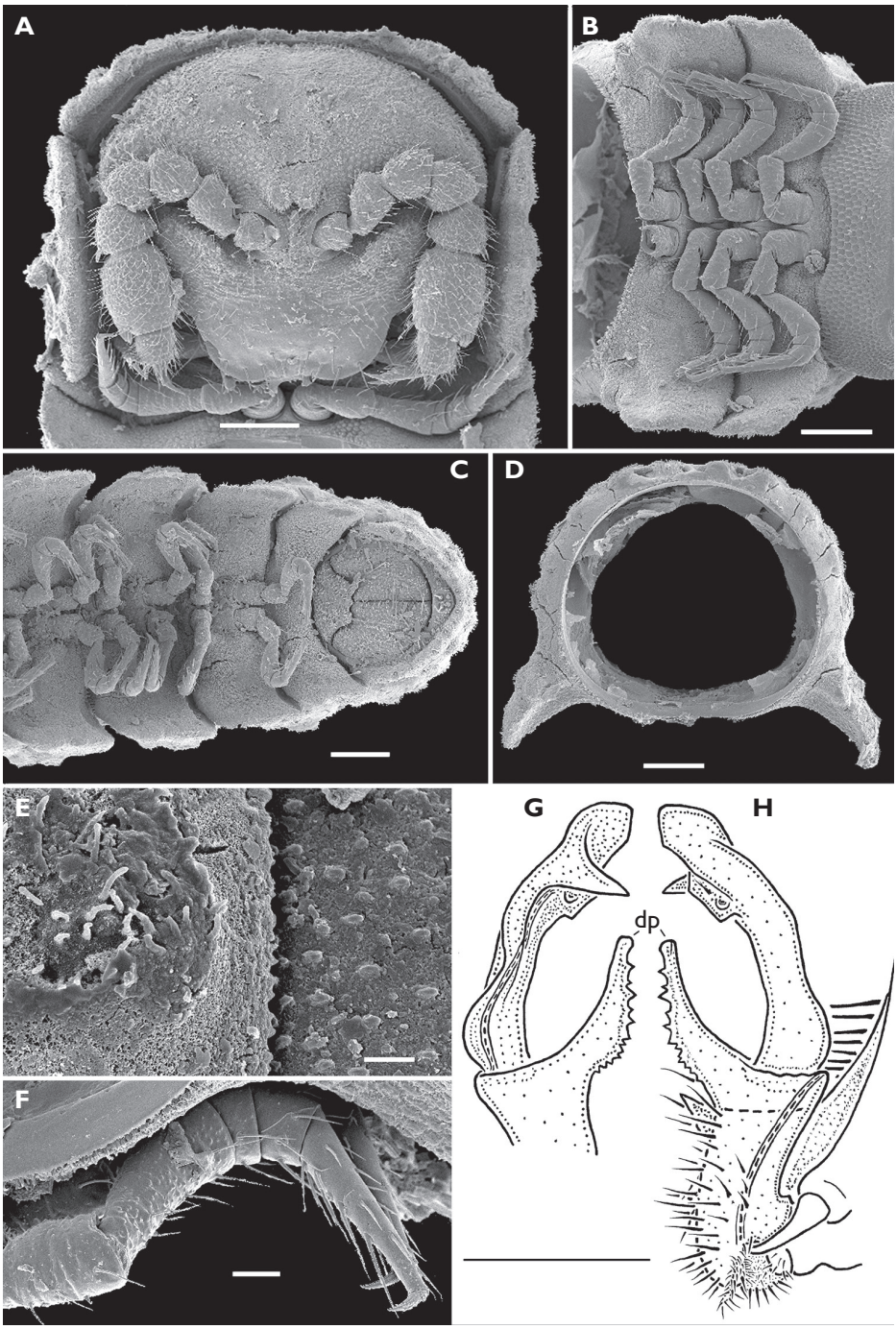

Figure 18. *Eutrichodesmus curticornis* sp. n., ♀ paratype (A-F) & ♂ holotype (G-H) ; **A**, anterior part of body, ventral view; **B**, midbody segments, ventral view; **C**, posterior part of body, ventral view; **D**, cross-section of a midbody segment, caudal view; **E**, texture of tegument; **F**, legs, caudal view; **G & H**, right gonopod, lateral and mesal views, respectively. – Scale bars: A-D & G, 0.1 mm; E, 0.01 mm; F & H, 0.02 mm.

Adults with 20 segments (Figs 16, 17A), pattern of conglobation typical of "doratodesmids". Head (Fig. 18A) with a contiguous pair of paramedian tubercles above antennal sockets; antennae very short and clavate, but tegument (Fig. 18E) and many other characters (Figs 18B, C, F) much as in *E. distinctus* sp. n.; collum rather regularly tuberculate (Fig. 17B). Metaterga behind collum with three transverse, regular, mixostictic rows of rounded, flat, undifferentiated tubercles (Figs 17A, C), each crowned with a broken-off seta (Fig. 18E). Paraterga subvertical, rather wide, slightly surpassing level of venter, with only a slight impression at base and nearly continuing general outline of convex dorsum (Fig. 18D); paraterga 2 (Figs 17A, 18A) evidently lobulate only anterolaterally but not laterally (Fig. 17A). Following paraterga broadly rounded, very slightly bilobate laterally and unilobate caudolaterally (Figs 17A, 18B). Limbus rather irregularly crenulate, almost hidden by nearby abundant microvilli (Fig. 18E). Pore formula normal, ozopores poorly visible, located dorsally near base of ventrocaudal lobulation (Fig. 17A). Epiproct short, with only slightly differentiated tubercles (Fig. 17D).

Legs very short and stout, barely reaching edge of paraterga (Fig. 18F).

Gonopods (Figs 18G, H) relatively complex. Coxae abundantly micropapillate and setose, with a usual, apicolateral lobe. Telopodite elongate, slender, only very slightly arcuate, with a marked, denticulate distofemoral process (dp) at about midway and an evident distolateral tooth; seminal groove terminating without hairpad at base of the tooth.

Remarks: This pallid species shows short antennae, legs and paraterga, all these traits apparently being related to the small body size. It is also a typical "doratodesmid", possibly yet one more troglobite.

***Eutrichodesmus asteroides* Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:C1DBB0D8-E640-42A8-9307-7E0CFB894BC5
Figs 19-22.

Type material: Vietnam, Quang Binh Prov., Cha Noi: Hang Cha Noi Cave, hand collected, 8.I.1995, leg. L. Deharveng & A. Bedos (VIET-064), holotype ♂ (MNHN JC 322), paratypes: 1 ♂ (MNHN JC 322), 1 ♀ (SEM). Vietnam, Quang Binh Prov., Dong Hoi: Grotte de Troc, hand collected, 15.III.1997, leg. A. Bedos & Long (VIET-407), paratypes: 3 ♂, 2 ♀, 2 juv. (MNHN JC 322), 1 ♂ (ZMUM).

Name: To emphasize the nearly star-shaped but broad body of the volvated animal.

Diagnosis: Differs from congeners by the peculiar, subtriangular, rather high, mid-dorsal crests on metaterga 4-18, coupled with 19 body segments, the relatively wide paraterga and a few minor details of gonopod structure (in particular, the shape of the telopodite and a rudimentary distofemoral process).

Description: Length of adults of both sexes *ca* 8.0-8.5 mm, width 2.1-2.5 mm, body broadest at segment 3 or 4. Holotype *ca* 8.0 mm long and 1.9 mm wide. Coloration uniformly pallid, shown pinkish because of a photographic artifact (Fig. 19).

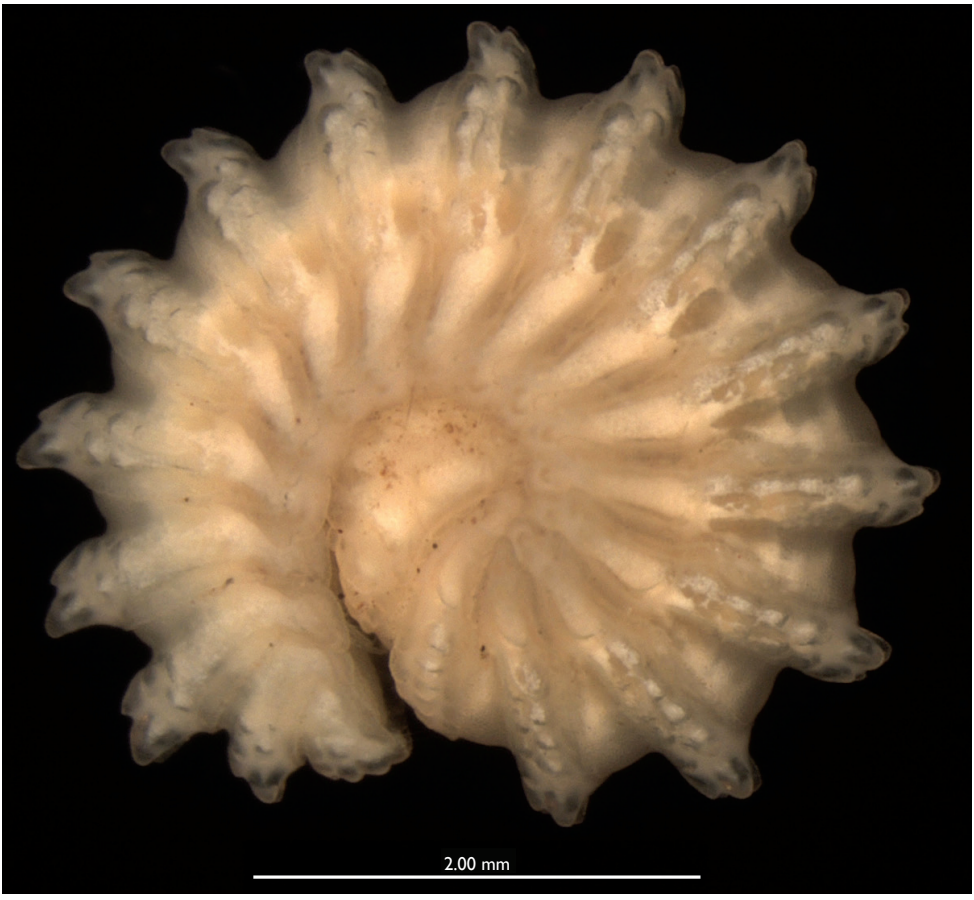

Figure 19. *Eutrichodesmus asteroides* sp. n., ♂ paratype from Hang Cha Noi Cave; habitus, lateral view. (Photographed by L. Deharveng).

Adults with 19 segments (Figs 19, 20A); body subasteriform but relatively broad, non-discoid; volvation complete even though paraterga relatively wide. Head (Fig. 21C) with a very distinctly separated pair of paramedian tubercles above antennal sockets; antennae relatively long and slender; tegument (Figs 22A, C) and many other characters (Figs 21D, E, 22A-D) much as in *E. distinctus* sp. n.; collum very faintly tuberculate, almost smooth (Fig. 20E). Metaterga behind collum with three transverse, rather regular, mixostictic rows of rounded, flat, well-differentiated tubercles, mid-dorsal ones in anterior and middle rows being especially high and fused into a high double club of subtriangular shape in lateral view (Figs 20A-F, 21A, B); tergal setation missing (Figs 22A-C). Paraterga directed ventrolaterad, rather long and broad, well reaching level of venter (Figs 21B, D-F); paraterga 2 rather poorly lobulate only anterolaterally and caudally (Fig. 20B). Following paraterga broadly rounded, unilobate only caudolaterally. Limbus with very broad crenulations (Figs 22B). Pore formula normal, ozopores poorly visible, located dorsomedially of lateral margin of paraterga (Fig. 22A).

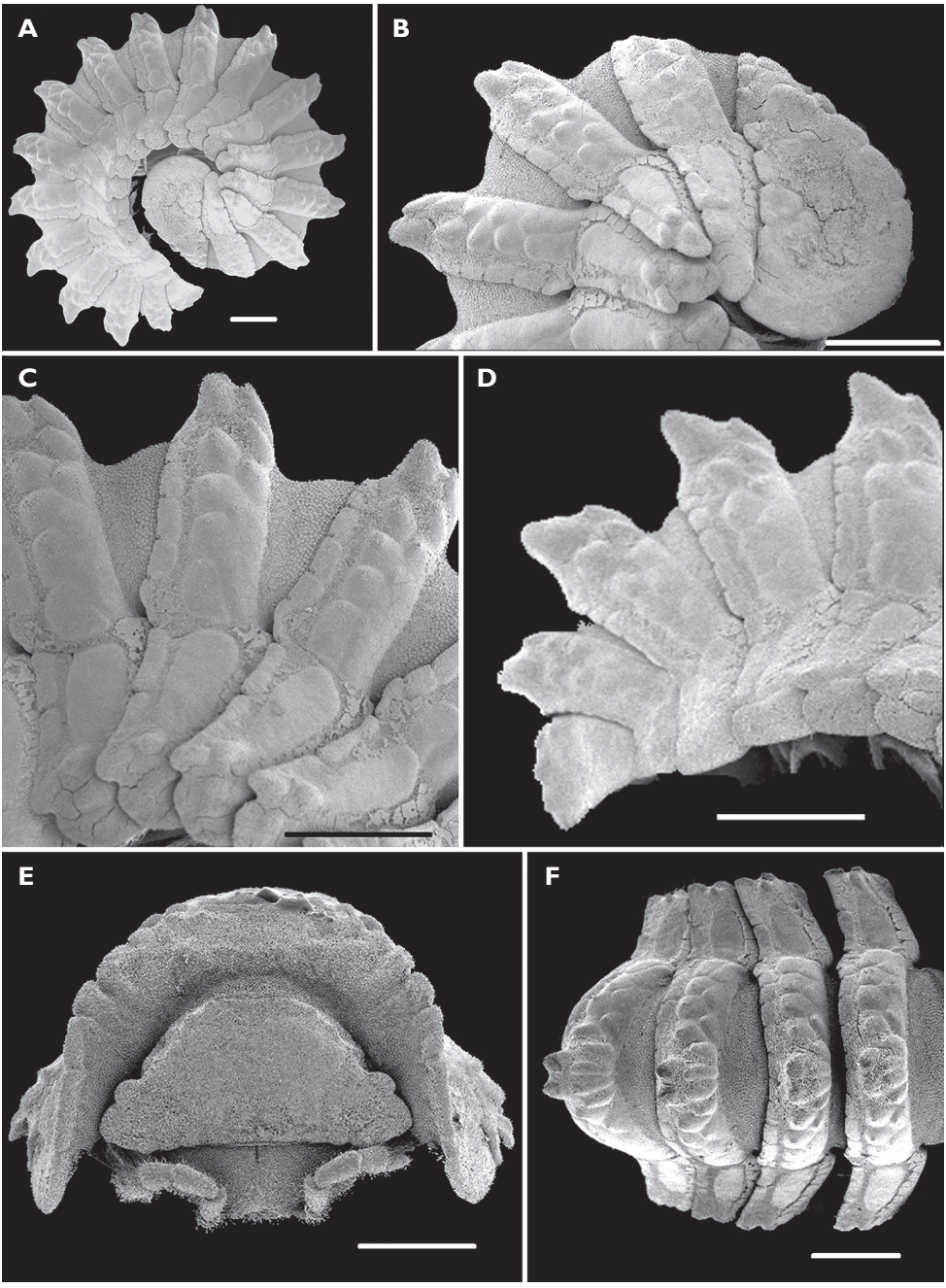

Figure 20. *Eutrichodesmus asteroides* sp. n., ♀ paratype from Hang Cha Noi Cave; **A**, habitus, lateral view; **B & E**, anterior part of body, lateral and frontal views, respectively; **C & F**, midbody segments, lateral and dorsal views, respectively; **D**, posterior part of body, lateral view. – Scale bars: A-F, 0.5 mm.

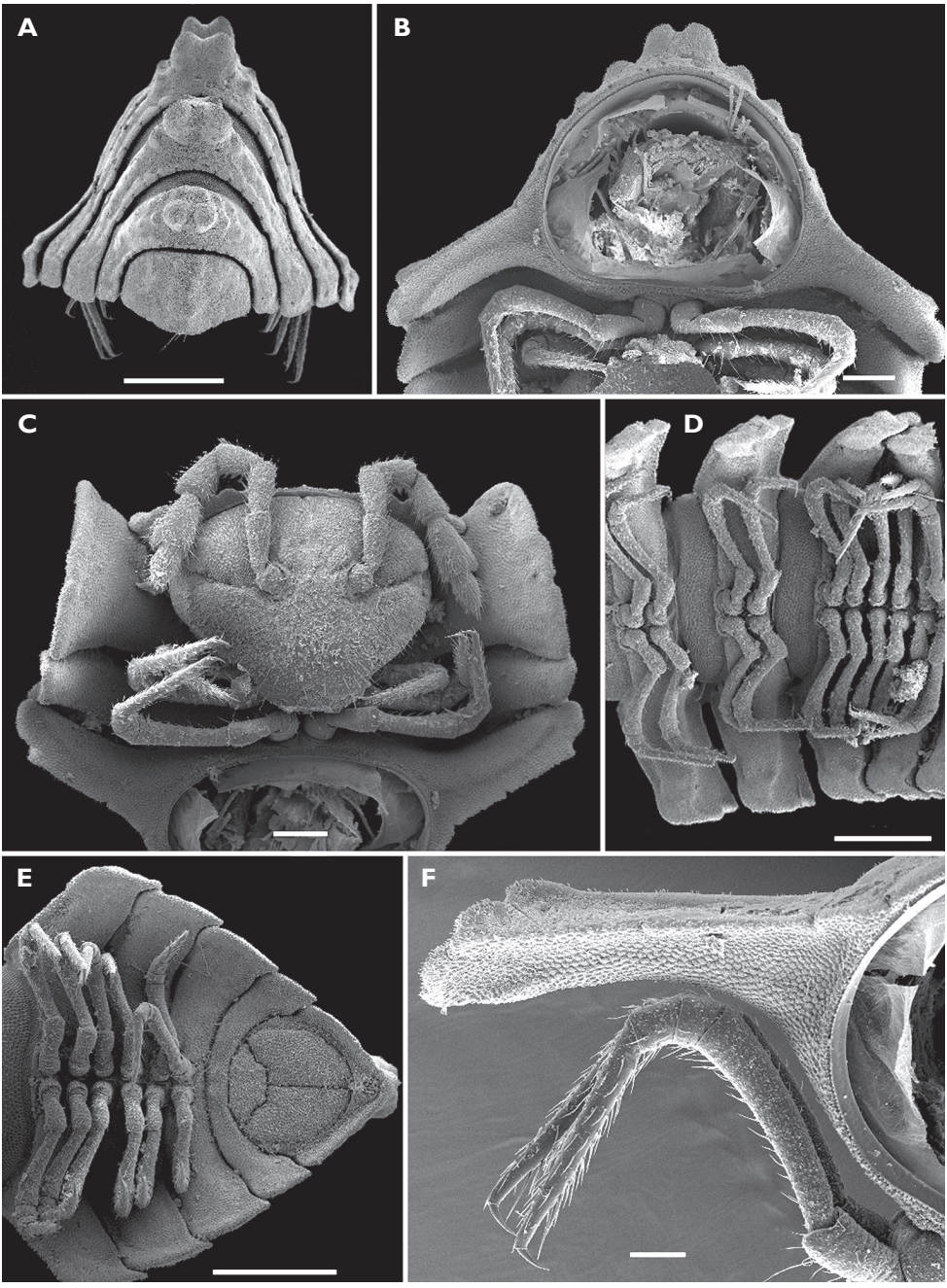

Figure 21. *Eutrichodesmus asteroides* sp. n., ♀ paratype from Hang Cha Noi Cave; **A & E**, posterior part of body, caudal and ventral views, respectively; **B**, cross-section of a midbody segment, caudal view; **C**, anterior part of body, ventral view; **D**, midbody segments, ventral view; **F**, midbody paratergum and legs, caudal view. – Scale bars: A, D & E, 0.5 mm; B & C, 0.2 mm; F, 0.1 mm.

Legs relatively long and slender, reaching edge of paraterga (Figs 21B, D-F).

Gonopods (Figs 22E, F) relatively simple. Coxae abundantly micropapillate but only with two macrosetae near base a small apicolateral lobe. Telopodite elongate, slender, evidently arcuate, with a rudimentary, prong-shaped distofemoral process (dp) at about midway, an evident, mesal, rounded lobe at about midway of acropodite (= solenomere), and a bipartite apical part starting at a hairless pad terminating seminal

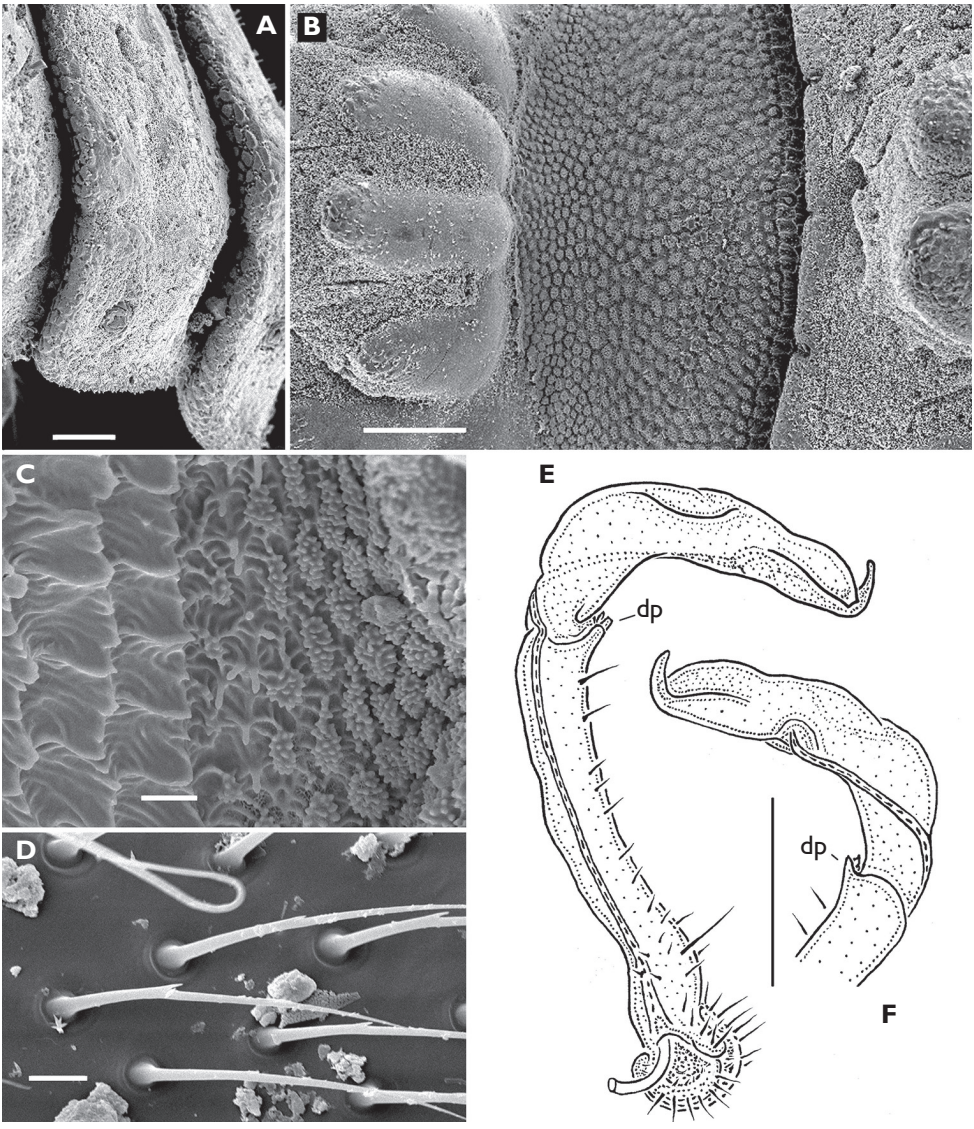

Figure 22. *Eutrichodesmus asteroides* sp. n., ♀ (A-D) and ♂ (E-F) paratypes from Hang Cha Noi Cave; **A**, midbody metaterga, sublateral view; **B & C**, texture of tegument, dorsal view; **D**, setae on antennae; **E & F**, left gonopod, mesal and lateral views, respectively. – Scale bars: A, 0.05 mm; B, 0.1 mm; C, 0.01; D, 0.005 mm; E & F, 0.2 mm.

groove; mesal of apical branches shorter and digitiform, whereas lateral one a little longer and unciform.

Remarks: Because this species has only been taken from caves, it can possibly be considered as a troglobite.

***Eutrichodesmus griseus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:E7EB907C-AA5B-4612-B292-403142A55D5B
Figs 23-26.

Type material: Vietnam, Kien Giang Prov., Kien Luong: Hon Chong, Nui Hon Chong, outside Cave 2 near Hang Hai Côt, grasses, soil, Berlese extraction, 27.I.2003, leg. L. Deharveng & A. Bedos (VIET-923), holotype ♂ (MNHN JC 323), paratypes: 1 ♂, 1 ♀ (MNHN JC 323), 1 ♀ (SEM).

Name: To emphasize the greyish coloration of the vertex, collum, metaterga and most of the telson.

Diagnosis: Differs from congeners by the peculiar, grey to blackish coloration, coupled with the relatively short and high paraterga (thus the body apparently not capable of complete volvation) and a few minor details of gonopod structure (in particular, the shape of the telopodite and distofemoral process).

Figure 23. *Eutrichodesmus griseus* sp. n., ♀ paratype; habitus, lateral view. (Photographed not to scale by L. Deharveng).

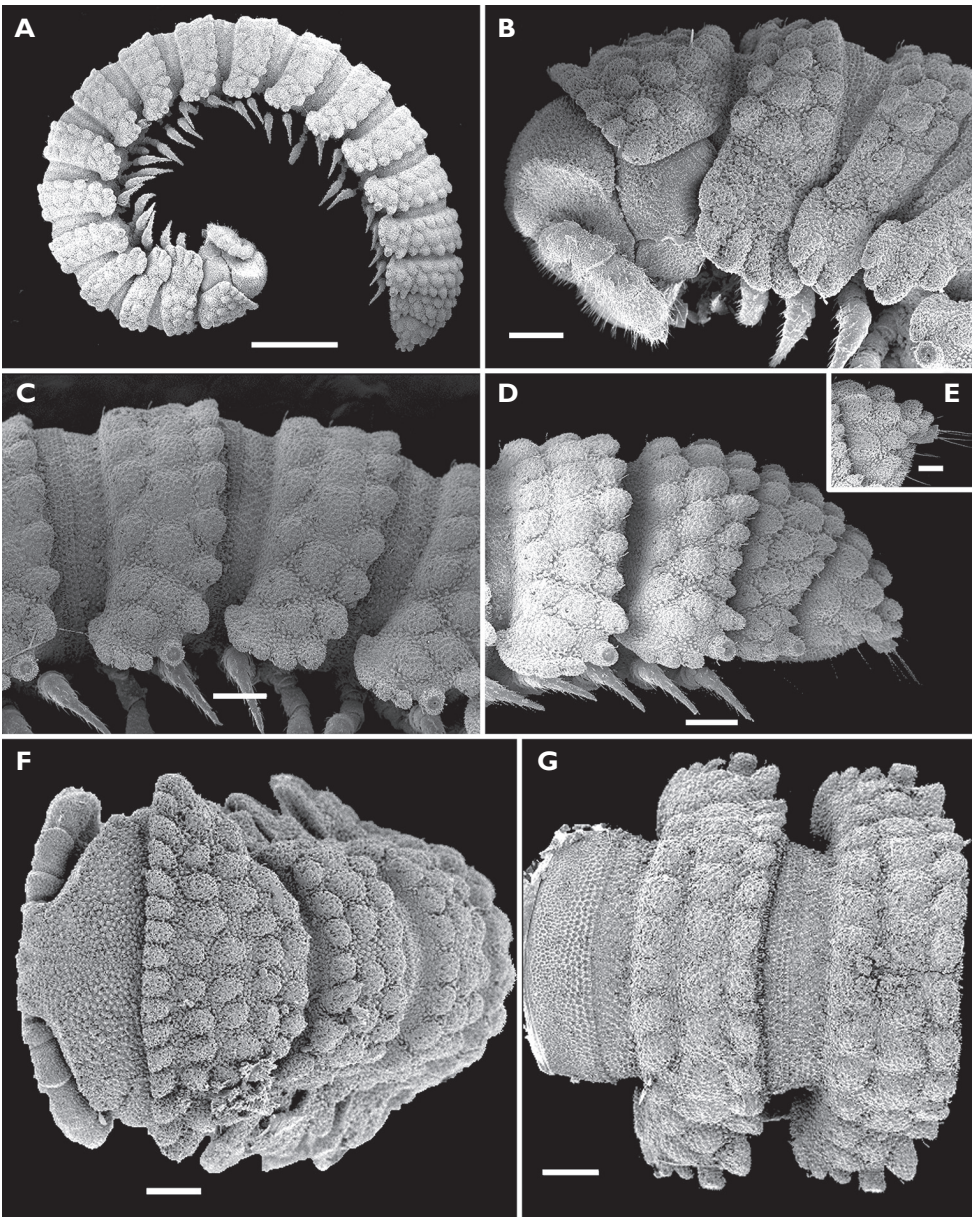

Figure 24. *Eutrichodesmus griseus* sp. n., ♀ paratype; **A**, habitus, lateral view; **B & F**, anterior part of body, lateral and frontal views, respectively; **C & G**, midbody segments, lateral and dorsal views, respectively; **D**, posterior part of body, lateral view; **E**, epiproct, dorsolateral view. – Scale bars: A, 0.5 mm; B-G, 0.1 mm.

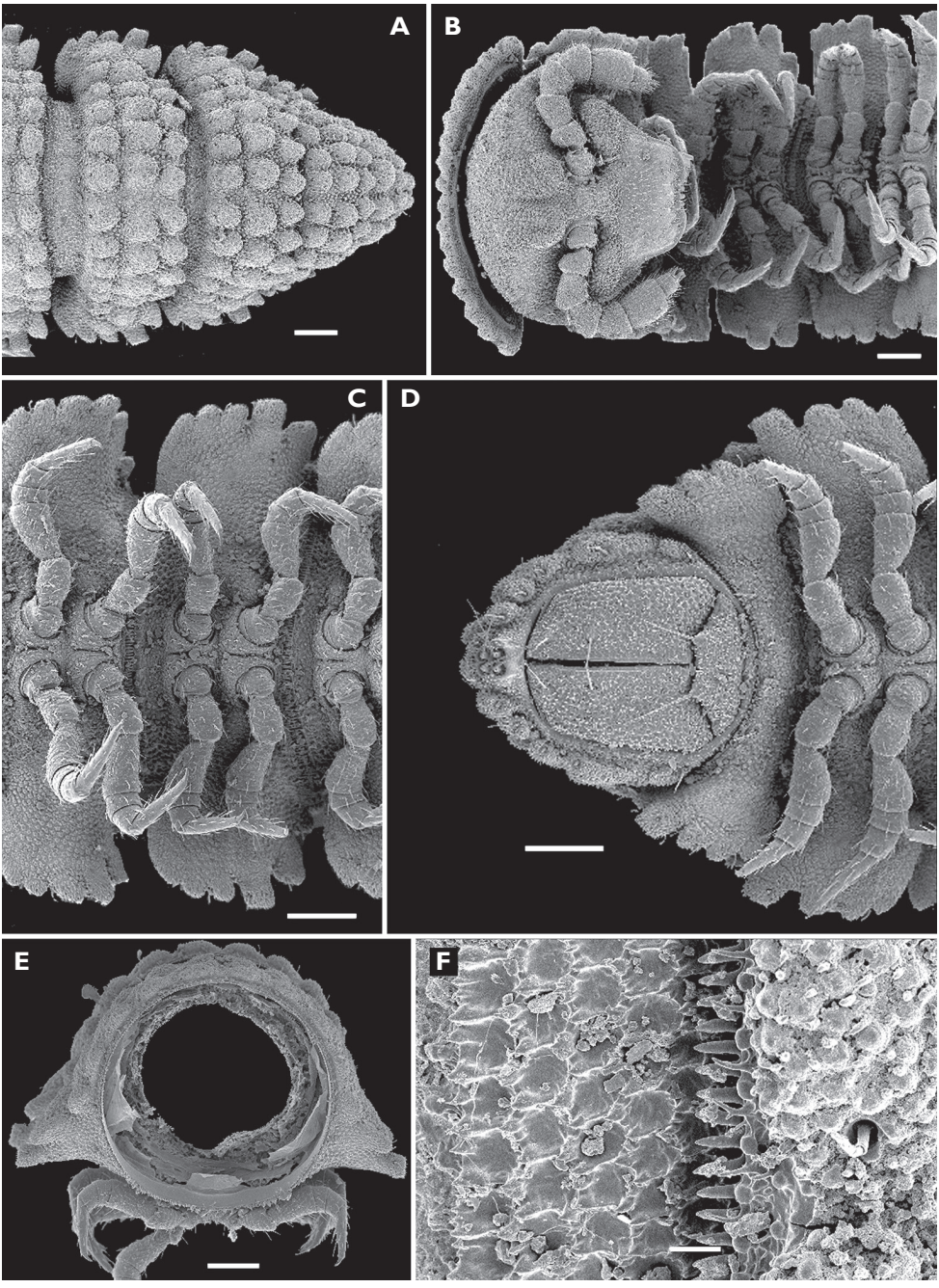

Figure 25. *Eutrichodesmus griseus* sp. n., ♀ paratype; **A & D**, posterior part of body, dorsal and ventral views, respectively; **B**, anterior part of body, ventral view; **C**, midbody segments, ventral view; **E**, cross-section of a midbody segment, caudal view; **F**, texture of tegument, dorsal view. – Scale bars: A-E, 0.1 mm; F, 0.01 mm.

Description: Length of adults of both sexes *ca* 6.0-6.5 mm, width 0.7–0.75 mm, body broadest at segment 3 or 4. Holotype *ca* 4.5 mm long and 2.5 mm wide. Coloration of vertex, collum, following metaterga, and of dorsal and lateral parts of telson greyish to dark grey. Clypeolabral part of head, venter and legs contrastingly pallid (Fig. 23). Holotype light grey.

Adults with 20 segments (Figs 23, 24A), volvation apparently incomplete due to relatively short paraterga. Head (Fig. 25B) with a poorly separated pair of paramedian tubercles above antennal sockets; antennae relatively short and clavate; tegument (Fig. 25F) and many other characters (Figs 25C-E) much as in *E. distinctus* sp. n.; collum

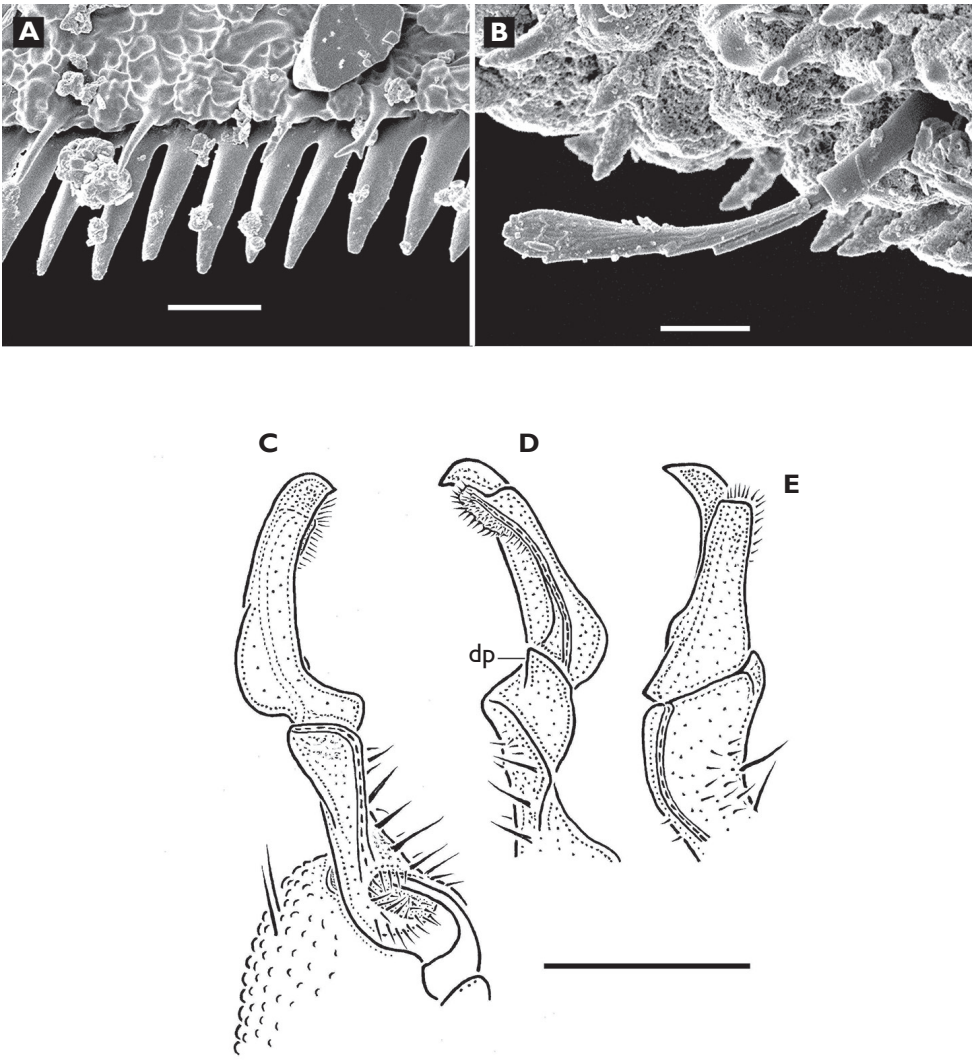

Figure 26. *Eutrichodesmus griseus* sp. n., ♀ (A, B) & ♂ (C, D, E) paratypes; **A**, limbus, dorsal view; **B**, metatergal seta, sublateral view; **C-E**, left gonopod, mesal, lateral and subfrontal views, respectively. – Scale bars: A, 0.01 mm; B, 0.005 mm; C-E, 0.2 mm.

rather regularly tuberculate, anterior row of tubercles especially dense and directed dorsofrontally, thus slightly resembling a pyrgodesmid condition (Figs 24A, B, F). Metaterga behind collum with three transverse, regular, nearly isostictic rows of rounded, flat, undifferentiated tubercles (Figs 24A-G), each crowned with a short, 2-segmented, conspicuously denticulate and slightly claviform seta (Fig. 26B). Paraterga directed ventrolaterad, short but rather broad, barely reaching level of venter, nearly continuing general outline of convex dorsum (Figs 24A-D, 25E); paraterga 2 (Fig. 24B) evidently lobulate only laterally. Following paraterga broadly rounded, evidently 3- to 5-lobate laterally, at least bilobate also caudolaterally (Figs 24A-D, G). Limbus distinctly spinulate (Fig. 26A), almost hidden by nearby abundant microvilli (Fig. 25F). Pore formula normal, ozopores located on top of porosteles (always caudalmost lateral lobulation) (Figs 24A-D, G). Epiproct rather heavily tuberculate (Figs 24D, E).

Legs relatively short and stout, barely reaching edge of paraterga (Figs 25C-E).

Gonopods (Figs 26C-E) relatively simple. Coxae abundantly micropapillate but only with two macrosetae near base of a small apicolateral lobe. Telopodite elongate, rather slender, evidently arcuate, with a rudimentary, subtriangular, distofemoral process (dp) at about midway and an evident lateral, digitiform solenomere bearing a large hairpad apically and subapically, and a simple dentiform acropodite mesally.

Remarks: Because this pigmented species obviously shows incomplete volvation, it is not a typical "doratodesmid", definitely epigean. Moreover, because of the elevated anterior row of tubercles on the collum, superficially it slightly resembles certain Pyrgodesmidae.

***Eutrichodesmus multilobatus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:9236AEA3-5110-48E6-BD00-2ABB1CBAADC2
Figs 27-30.

Type material: Laos, Luang Prabang Prov., Nong Kiaw: Tham Pha Kouang, Cave B, hand collected, 22.XII.1999, leg. L. Deharveng & A. Bedos (LAO-099), holotype ♂ (MNHN JC 324), paratypes: 1 ♂ (MNHN JC 324), 1 # M (ZMUM), 1 ♀ (SEM).

Name: To emphasize the mostly 5-lobulated paraterga.

Diagnosis: Differs from congeners by the peculiar, evidently and only laterally 5-lobulated paraterga, coupled with very distinct but only slightly differentiated metatergal tuberculation and a few minor details of gonopod structure (in particular, the shape of the telopodite and distofemoral process).

Description: Length of adults of both sexes *ca* 6.0-6.5 mm, width 1.1-1.2 mm, body broadest at segment 3 or 4. Holotype *ca* 6.0 mm long and 1.1 mm wide. Coloration uniformly pallid, shown pinkish because of a photographic artifact (Fig. 27).

Adults with 20 segments (Figs 27, 28A), volvation complete, although paraterga relatively short. Head (Fig. 28G) with a poorly separated pair of paramedian tubercles above antennal sockets; antennae relatively short and clavate (Fig. 29D); tegument (Figs 29E, F) and many other characters (Figs 28F, G, 29A, B) much as in *E. distinc-*

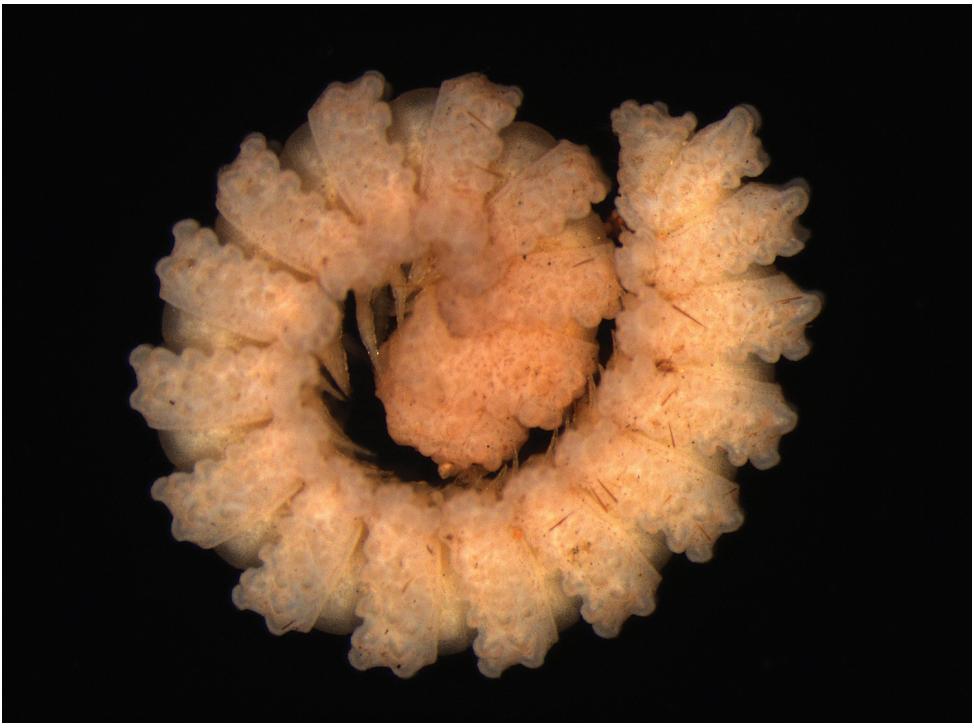

Figure 27. *Eutrichodesmus multilobatus* sp. n., ♀ paratype; habitus, lateral view. (Photographed not to scale by L. Deharveng).

tus sp. n.; collum and following metaterga heavily tuberculate (Figs 28A, C, D, G). Metaterga behind collum with three transverse, irregular, mixostictic rows of rounded, mostly very clear, differentiated tubercles slightly but steadily growing higher in anterior and, especially, middle rows both toward axial line and telson (Figs 27, 28A-F), and becoming particularly evident on segments 18 and 19 (Fig. 28F). Metatergal setae mostly broken off, otherwise short, filiform, helically striate as in Fig. 29F. Paraterga directed ventrolaterad, yet markedly interrupting contour of convex dorsum, rather short but broad, reaching level of venter (Figs 28F, 29C); paraterga 2 evidently lobulate only anteriorly and laterally (Figs 28A, C, G). Following paraterga narrowly rounded caudally, always subtruncated and quite evidently 5-lobate laterally, non-lobate caudolaterally (Figs 28A, B, D, 29A). Limbus distinctly crenulate, almost hidden by nearby abundant microvilli (Fig. 29E). Pore formula normal, ozopores located on top of porosteles (always penultimate lateral lobulation) (Figs 28A, B, D, E).

Legs relatively short and stout, barely reaching edge of paraterga (Figs 29A, C).

Gonopods (Fig. 30) relatively simple. Coxae abundantly micropapillate, but only with a few macrosetae. Telopodite elongate, slightly arcuate, with a large, papillate, distofemoral process (dp) at about midway and a very simple solenomere bearing a small group of minute hairs (but no pad!) subapically at base of a tiny, rounded, terminal hook.

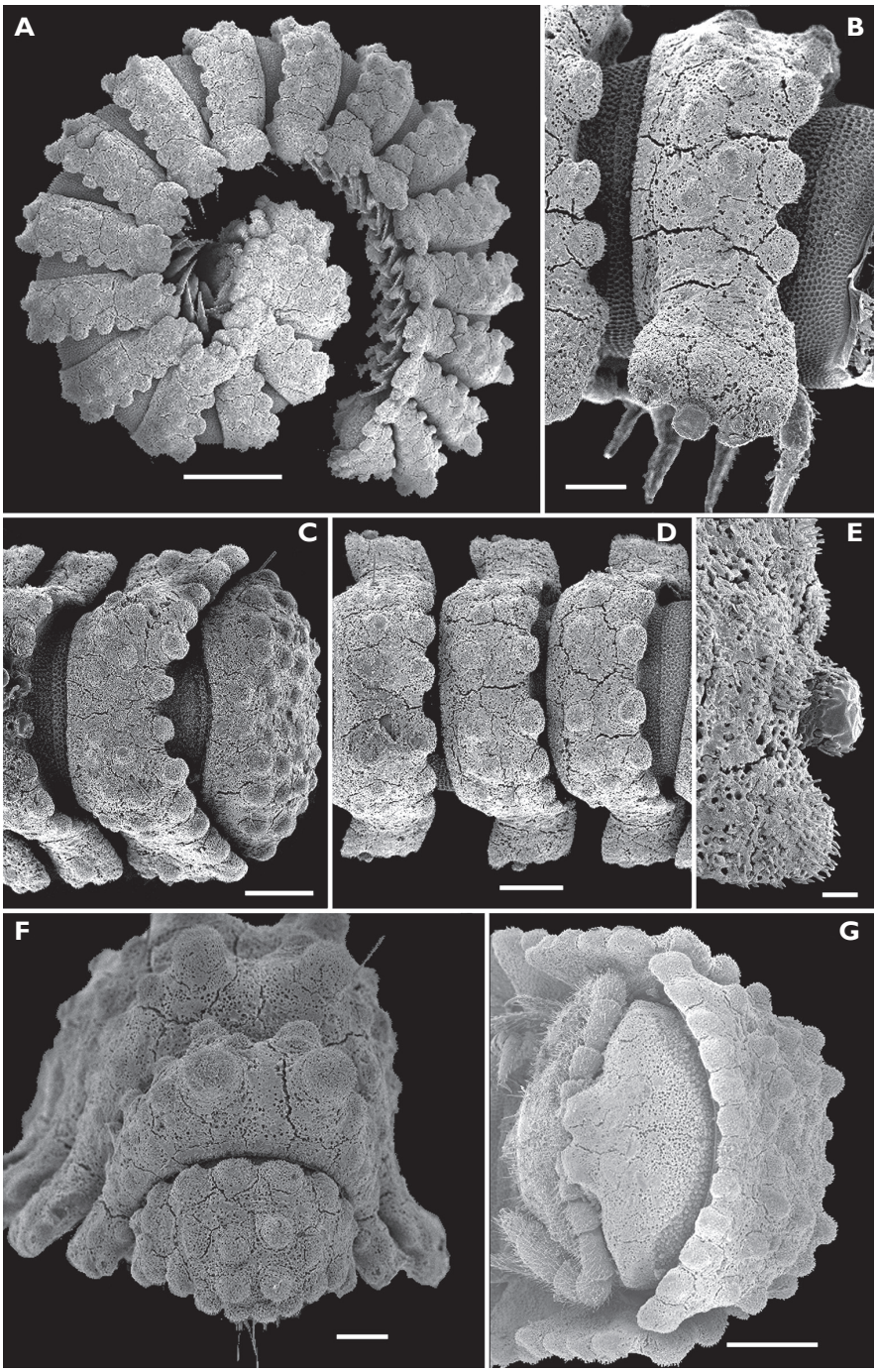

Figure 28. *Eutrichodesmus multilobatus* sp. n., ♀ paratype; **A**, habitus, lateral view; **B & D**, midbody segments, lateral and dorsal views, respectively; **C & G**, anterior part of body, dorsal and ventral views, respectively; **E**, lateral edge of paratergum with ozopore, dorsal view; **F**, posterior part of body, caudal view. – Scale bars: A, 0.5 mm; B & F, 0.1 mm; C, D & G, 0.2 mm; E, 0.02 mm.

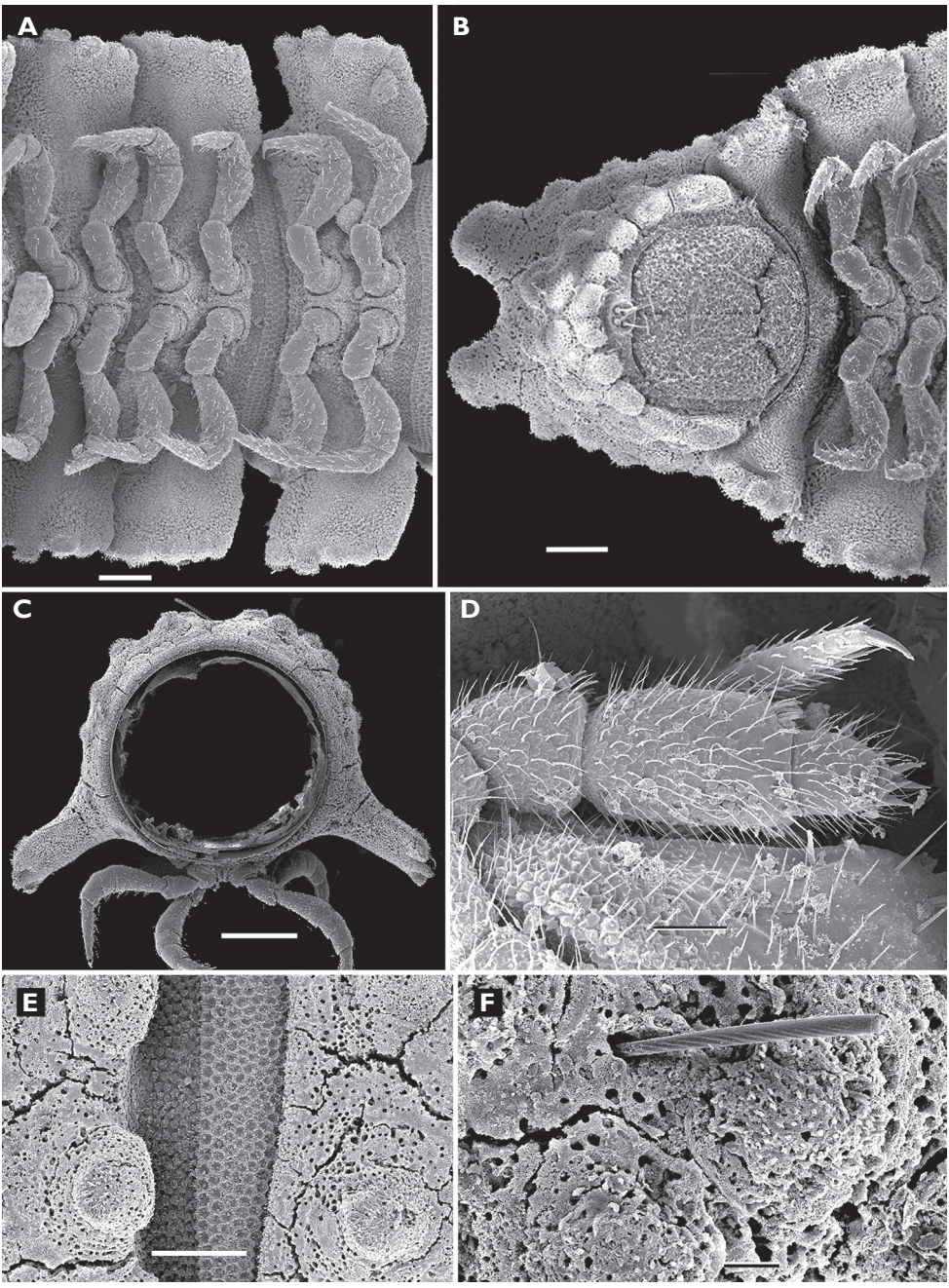

Figure 29. *Eutrichodesmus multilobatus* sp. n., ♀ paratype; **A**, midbody segments, ventral view; **B**, posterior part of body, ventral view; **C**, cross-section of a midbody segment, caudal view; **D**, part of head with left antenna, subdorsal view; **E**, texture of tegument, dorsal view; **F**, metatergal seta. – Scale bars: A, B & E, 0.1 mm; C, 0.2 mm; D, 0.05 mm; F, 0.02 mm.

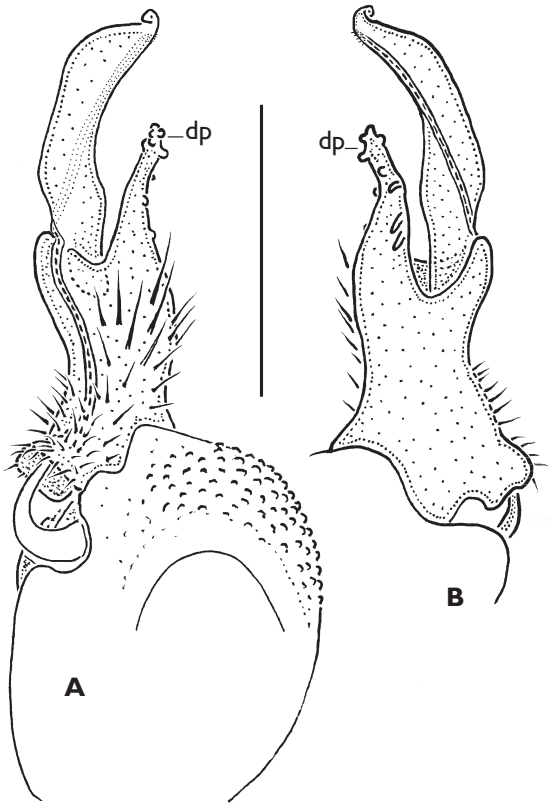

Figure 30. *Eutrichodesmus multilobatus* sp. n., ♂ paratype; **A & B**, right gonopod, mesal and lateral views, respectively. – Scale bar: 0.3 mm.

Remarks: This small-bodied, pallid species shows peculiar patterns of metatergal tuberculation and paratergal lobulation. It is a typical "doratodesmid", possibly still one more troglobite.

***Eutrichodesmus reductus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:1726A727-8FC2-4BF8-807D-8DFC1C54380C
Figs 31-33.

Type material: Indonesia, Sulawesi Selatan, kab. Maros: Samanggi, Gua Saripa Cave, hand collected, 18.VIII.1990, leg. A. Bedos & L. Deharveng (SULS-214), holotype ♂ (MZB), paratypes: 1 ♂ (MNHN JC 325), 1 ♀ (SEM).

Name: To emphasize the strongly underdeveloped paraterga 2 and lack of metatergal tuberculation.

Diagnosis: Differs from congeners except *E. communicans* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009 by the strongly underdeveloped paraterga 2, coupled

Figure 31. *Eutrichodesmus reductus* sp. n., ♂ & ♀ paratypes; habitus, lateral view. (Photographed not to scale by L. Deharveng).

with 19 body segments and the absence of metatergal tuberculation; from *E. communicans* by a very short tergal trichome, from it and other congeners in a few minor details of gonopod structure (in particular, the shape of the telopodite).

Description: Length of adults of both sexes *ca* 4.0-4.2 mm, width 0.45-0.5 mm, body broadest at midbody segments. Holotype *ca* 4.0 mm long and 0.45 mm wide. Coloration uniformly pallid, shown pinkish because of a photographic artifact (Fig. 31).

Adults with 19 segments, body subcylindrical (Figs 31, 32A), volvation apparently incomplete due to insufficiently wide and low paraterga. Head (Fig. 33A) slightly transverse, with a poorly separated pair of very low, paramedian tubercles above antennal sockets; antennae relatively short and clavate, antennomere 6 longest; tegument (Figs 33C-E) and many other characters (Figs 32F, 33B) much as in *E. distinctus* sp. n.; collum and following metaterga devoid of tuberculation, beset with numerous, irregularly arranged, extremely short setae (Fig. 32B-F, 33C-E). Paraterga directed ventrolaterad, slightly interrupting contour of convex dorsum, short, not reaching level of venter (Figs 32A-D); paraterga 2 (Fig. 32B) only a little enlarged compared to following ones, indistinctly lobulate both anterolaterally and laterally, with only a single noticeable lobe forming a schism ledge, both schism and hyposchism very small; paraterga 3 and 4 not narrower than others, overlap typical already from paraterga 4, not paraterga 5 as in preceding congeners. Paraterga broadly rounded caudally, very indistinctly lobulate laterally

and with a single evident lobulation caudolaterally (Figs 32C-E, 33C). Limbus distinctly denticulate, almost hidden by nearby abundant microvilli (Fig. 33D, E). Pore formula normal, ozopores located dorsally near base of caudal corner of paraterga (Fig. 33C).

Legs relatively long and slender, evidently surpassing edge of paraterga (Fig. 33B).

Gonopods (Fig. 33F, G) relatively complex. Coxae abundantly micropapillate, but only with a few macrosetae. Telopodite elongate, only slightly arcuate, with a large, papillate, peculiar, distofemoral outgrowth (dp) in distal one-third and a slender but short solenomere bearing a few small setae (but no pad!) subapically at base of a very

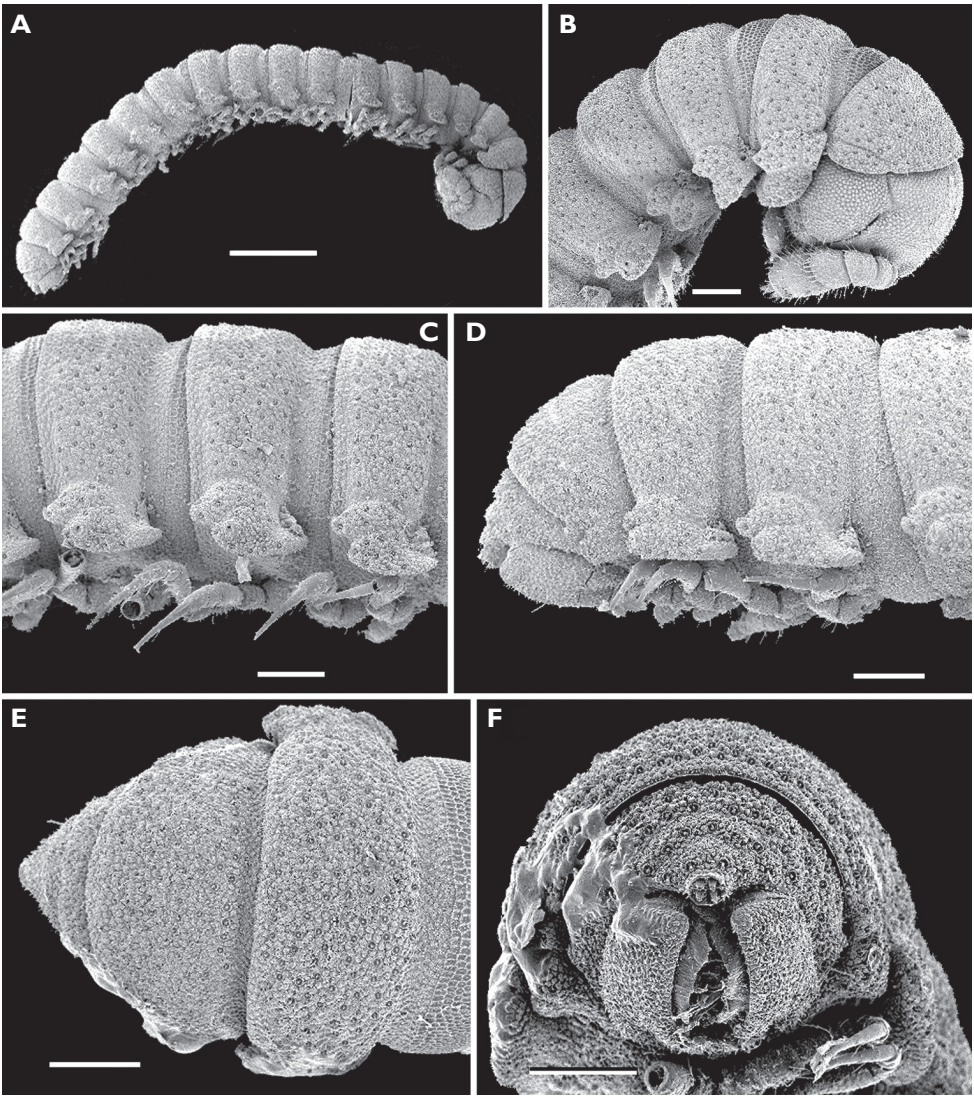

Figure 32. *Eutrichodesmus reductus* sp. n., ♀ paratype; **A**, habitus, lateral view; **B**, anterior part of body, lateral view; **C**, midbody segments, lateral view; **D-F**, posterior part of body, lateral, dorsal and caudal views, respectively. – Scale bars: A, 0.5 mm; B-F, 0.1 mm.

complex tip represented by two erect teeth, a longer uncus and a group of minute outgrowths.

Remarks: This small-bodied, pallid, non-volvatory (= "haplodesmid", see Golovatch et al. 2009) species seems to be especially close, morphologically as well as geographically, to *E. communicans* from Vanuatu, Melanesia, southwestern Pacific (Golovatch et al. 2009), possibly representing still one more troglobite.

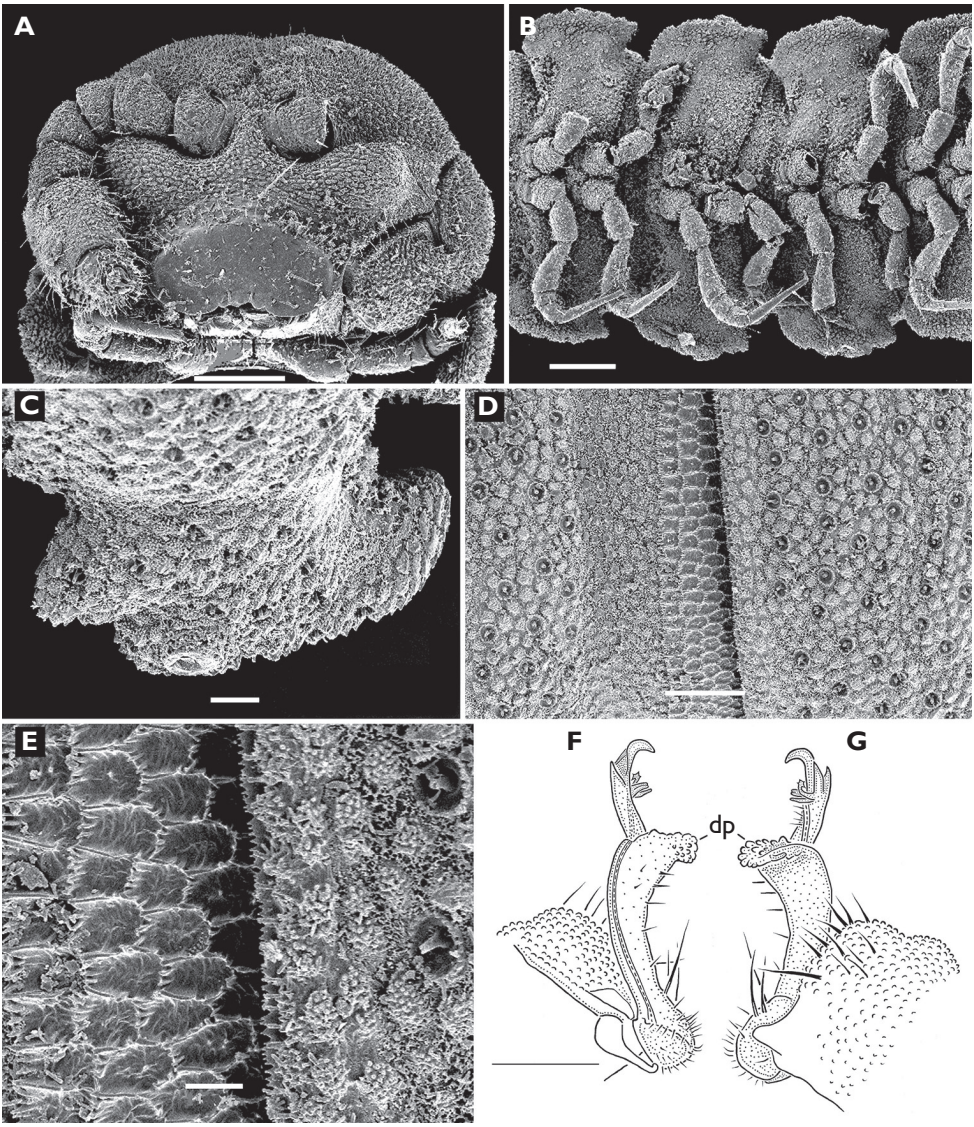

Figure 33. *Eutrichodesmus reductus* sp. n., ♀ (A-E) & ♂ (F-G) paratypes; **A**, head, ventral view; **B**, midbody segments, ventral view; **C**, midbody paratergum with ozopore, dorsal view; **D & E**, texture of tegument, dorsal view; **F & G**, left gonopod, mesal and lateral views, respectively. – Scale bars: A & B, 0.1 mm; C, 0.02 mm; D, 0.05 mm, E, 0.01 mm; F & G, 0.1 mm.

Discussion

Now that *Eutrichodesmus* has grown even more speciose, containing 24 species and no doubt with more still remaining to be discovered, it seems appropriate to redefine it and provide an updated key.

The definition of the genus (cf. Golovatch et al. 2009) is therefore amended as follows:

Eutrichodesmus Silvestri, 1910
Type-species: *Eutrichodesmus demangei* Silvestri, 1910, by original designation.

New diagnosis
Body usually "doratodesmid", with or without mid-dorsal projections; conglobation usually complete, only seldom imperfect due to underdeveloped or hypertrophied paraterga. Collum and metaterga often (micro)setose, usually tuberculate, only rarely smooth. Gonopod coxae usually abundantly setose ventrolaterally; telopodite usually slender, not enlarged towards end of femorite, but typically with a more or less distinct process or outgrowth laterally, opposite recurvature point of seminal groove; solenomere thereafter usually comprising most of telopodite, sometimes elaborate; seminal groove normally terminating distally to subapically, with or without a hairpad; acropodite normally small to nearly absent.

Key to the species of *Eutrichodesmus*

1 At least some metaterga with an evident mid-dorsal outgrowth or projection (Figs 9A-D; 20A-D)..... **2**
– All metaterga subequal, devoid of an evident mid-dorsal outgrowth or projection (Figs 2A-F, 5A-D; 17A-D)..... **9**
2 Only last 3-8 metaterga in front of telson with a very evident mid-dorsal outgrowth. Body with 20 segments..... **3**
– Most of metaterga, including some of anterior body portion, with a high, often tuberculated projection (Figs 9A-D; 20A-D). Body with 19 or 20 segments..... **5**
3 Metaterga 12-19 each with an increasingly evident, subtriangular, mid-dorsal outgrowth. Cave in Yunnan Prov., China..... ***E. dorsiangulatus***
– Only metaterga 16(17)-19 each with an evident, rather rounded, mid-dorsal outgrowth..... **4**
4 Paraterga narrower. Gonopod process dp less than one-quarter length of acropodite. North Vietnam ..... ***E. armatocaudatus***
– Paraterga broader. Gonopod process dp much longer, more than half length of acropodite. Cave in Yunnan Prov., China..... ***E. monodentus***

5 Mid-dorsal projections relatively low, not club-shaped, increasingly evident on metaterga 3–17(18) (Fig. 20A) **6**

– Mid-dorsal projections especially prominent, club-shaped, present on metaterga (4)5-19, only slightly lower on metatergum 19 ..... **7**

6 Body with 19 segments. Subtriangular mid-dorsal projections evident on metaterga 3-17, only slightly smaller on metatergum 18 (Fig. 20A). Gonopod process dp rudimentary (Figs 22E, F). Vietnam ..... ***E. asteroides* sp. n.**

– Body with 20 segments. Clearly tridentate mid-dorsal projections evident on metaterga 3-18, abruptly smaller on metatergum 19. Gonopod process dp small but evident. Malaysia ..... ***E. cavernicola***

7 Metatergum 4 with a high mid-dorsal projection (Fig. 9A). Paraterga strongly declivous and quadrilobate (Figs 9A-D, 10E). Gonopods as in Fig. 11. Vietnam ..... ***E. aster* sp. n.**

– Mid-dorsal projections absent from metatergum 4. Paraterga less strongly declivous. Gonopods different. Malaysia **8**

8 Mid-dorsal projections on metaterga 5 and 6 straight in lateral view ..... ***E. macclurei***

– Mid-dorsal projections on metaterga 5 and 6 slightly inclined anteriorly in lateral view ..... ***E. reclinatus***

9 Body with 19 segments. Collum and metaterga virtually smooth, non-tuberculate, beset with long or short trichome (Fig. 32A-F, 33C-E). Paraterga too short to allow complete body volvation (Fig. 32A). Gonopod telopodite with a complex, lobiform dp (Fig. 33F, G). Southwestern Pacific **10**

– Body with 20 segments. Collum and metaterga clearly tuberculate, trichome (if present) usually short (Figs 25F, 29F). Paraterga much broader, mostly reaching level of venter, so volvation usually complete. East and Southeast Asia **11**

10 Collum and metaterga beset with long, 2-segmented, tactile setae. Tip of gonopod telopodite without teeth. Vanuatu ..... ***E. communicans***

– Collum and metaterga beset with very short trichome (Figs 32B-E, 33C-E). Tip of gonopod telopodite with a few teeth (Figs 33F, G). Sulawesi, Indonesia ..... ***E. reductus* sp. n.**

11 Paraterga mostly especially wide and only slightly declivous. Caves in Guangxi Province, China **12**

– Paraterga not so wide, strongly declivous (Figs 2A, 5A, 13A, 17A, 28A) ... **13**

12 Collum with a row of conspicuous teeth along fore edge of collum ..... ***E. similis***

– Collum with only minute teeth at fore edge of collum ..... ***E. latus***

13 Most metaterga with two transverse rows of bosses. Epiproct very strongly flattened dorsoventrally, subquadrate, spatuliform, with unincised margins. Gonopod telopodite particularly slender, about twice as long as coxa. Shikoku, Japan ..... ***E. peculiaris***

– Most metaterga with three transverse rows of bosses or conical tubercles. Epiproct never so strongly flattened. Gonopod telopodite usually shorter. Southeast Asia **14**

14 Paraterga mostly set off laterally at base by a clear sulcus. Metaterga with three mixostictic rows of evident, conical tubercles, each surmounted by a long, 2-segmented seta. Gonopod telopodite with a particularly small, dentiform dp. Thailand ..... ***E. gremialis***

– Paraterga less markedly (if at all) set off laterally at base (Figs 2A, 5A, 13A, 17A, 28A), largely continuing general outline of metaterga or nearly so (Figs 18D, 29C). Metatergal trichome very short or missing. Gonopod telopodite different **15**

15 Paraterga relatively short, volvation apparently imperfect (Fig. 24A). Body small, up to 6.5 mm long. Vietnam **16**

– Paraterga broad enough to allow complete volvation (Figs 17A, 28A). Body usually larger **17**

16 Entire body pallid, up to 5.0 mm long. Gonopods simple ..... ***E. basalis***

– Vertex, collum, metaterga and much of telson grey, this strongly contrasting with pallid venter and legs (Fig. 23). Body 6.0-6.5 mm long. Gonopods more elaborate (Figs 26C-E) ..... ***E. griseus* sp. n.**

17 Pattern of metatergal tuberculation isostictic (Figs 5A-D). Seminal groove terminating on a very evident, pilose-spiculate pulvillus near base of a relatively shortened, lamellar acropodite (Figs 6F, G, 7A-F) .... ***E. regularis* sp. n.**

– Metatergal tuberculation mixostictic (Figs 13A-F, 24A). Seminal groove terminating distally to subapically, mostly without a pulvillus (seldom with a hairpad) (Figs 18G, H, 30) **18**

18 Distofemoral process of gonotelopodite bare, subunciform, pointed **19**

– Distofemoral process of gonotelopodite nearly always conspicuously papillate (Figs 18G, H, 30), seldom redumentary (Figs 15A-F), never pointed **20**

19 Body *ca* 8.0 mm long. Gonopod tip bifid. Vietnam ..... ***E. demangei***

– Body *ca* 14.0 mm long. Gonopod tip simple, unciform. Cave in Yunnan Prov., China ..... ***E. arcicollaris***

20 Paraterga mostly bilobate laterally and unilobate caudolaterally (Fig. 17A). Very small: 4.7-5.3 mm long and 0.65-0.7 mm wide. Gonopods as in Figs 18G, H. Vietnam ..... ***E. curticornis* sp. n.**

– Paraterga mostly 3- or 4-lobate laterally (Figs 13A-D). Length ≥ 6.0 mm, width ≥ 1.1 mm. Gonopods different **21**

21 Metaterga 18 and 19 not elevated dorsally. Caudolateral lobulations mostly deeply incised. Distofemoral process of gonopod bipartite. Caves in Guizhou Prov., China ..... ***E. incisus***

– Metaterga 18 and 19 slightly elevated dorsally (Figs 28A-F). Caudolateral lobulations not incised, tuberculiform. Distofemoral process of gonopod unipartite (Fig. 30) **22**

22 Body 6.0-6.5 mm long and 1.1-1.2 mm wide. Ozopores opening on top of porosteles representing penultimate of five lateral lobulations of respective paraterga, with caudolateral lobulations missing. Gonocoxae with only few macrosetae. Gonopods as in Fig. 30. Laos..... ***E. multilobatus* sp. n.**

– Body ≥ 8.0 mm long and 1.35 mm wide. Ozopores opening dorsally on caudalmost of 3-4 lateral lobulations of respective paraterga, caudolateral lobulations present. Gonocoxae with abundant macrosetae. Gonopods different.... ..... **23**

23 Body 8.0-8.5 mm long and 1.35-1.4 mm wide. Paraterga mostly 3-lobate (Figs 2A-G). Gonopods as in Figs 3E-H. Cave in Guizhou Prov., China..... ..... ***E. distinctus* sp. n.**

– Body 12-13 mm long and 2.5-2.6 mm wide. Paraterga mostly 4-lobate (Figs 13A-D). Gonopods as in Figs 15A-F. Caves in Thanh Hoa Prov., Vietnam... ..... ***E. filisetiger* sp. n.**

Conclusion

As stated recently (Golovatch et al. 2009), there seem to be almost no coherent patterns in the distribution of the various non-genitalic and gonopodal characters in *Eutrichodesmus*. The same concerns geographic patterns. Only a few pairs of particularly similar species can be distinguished in this speciose genus: e.g. *E. macclurei* and *E. reclinatus*, *E. latus* and *E. similis*, *E. demangei* and *E. arcicollaris*, and *E. communicans* and *E. reductus* sp. n. However, it is still too early to attempt to discriminate species groups, because many more new species of *Eutrichodesmus* can be expected to occur at least in East and Southeast Asia, as well as in the Indo-Australian archipelago, which seem to represent the centre of diversity of this genus (Fig. 34), and of the entire family Haplodesmidae.

That most of the *Eutrichodesmus* species have been found and described from cave material alone does not necessarily mean their obligate cavernicoly, even though many of them exhibit troglomorphic features. Most of the caves are simply better explored than the adjacent, much less prospected, epigean habitats.

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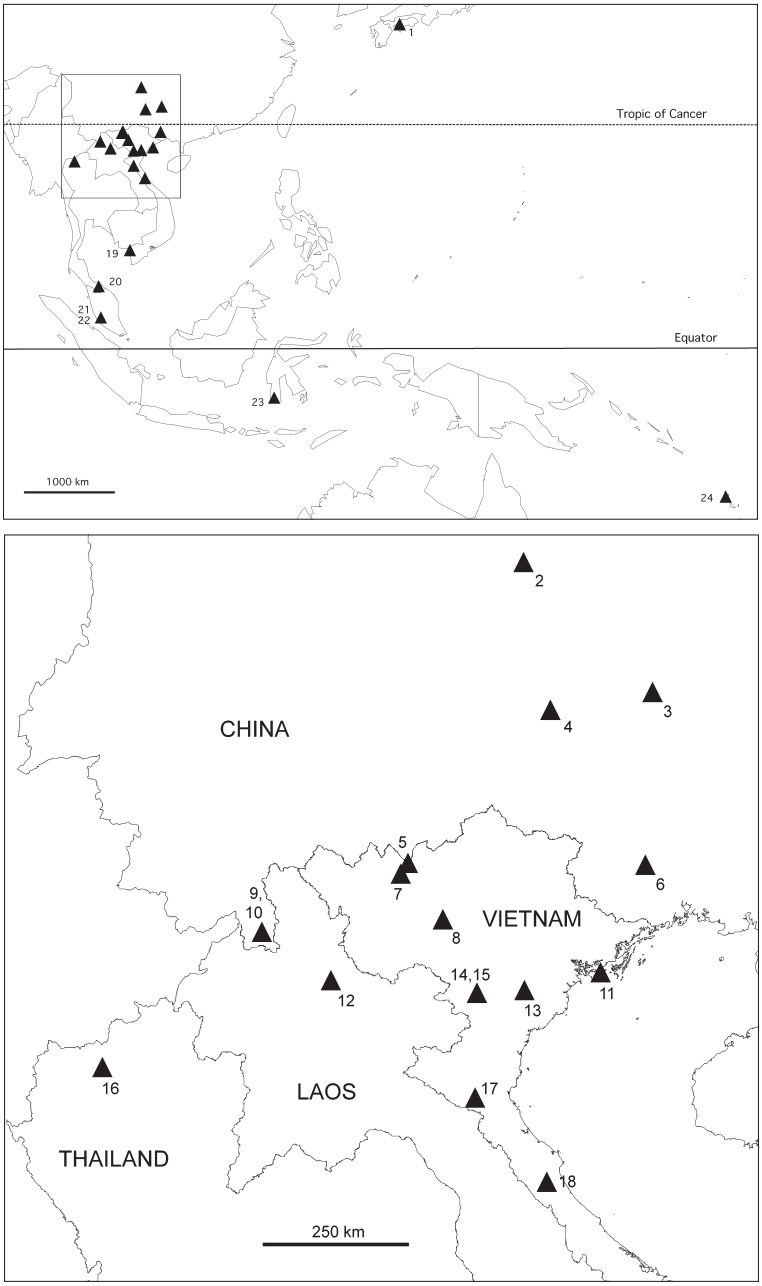

Figure 34. Map showing the general distribution of *Eutrichodesmus* species (A) and an enlarged section thereof showing the distribution of species in southern China and northern Indochina (B).
1 – *E. peculiaris*; 2 – *E. incisus*; 3 – *E. similis*; 4 – *E. latus*; 5 – *E. arcicollaris*; 6 – *E. distinctus* sp. n.; 7 – *E. regularis* sp. n.; 8 – *E. aster* sp. n.; 9 – *E. dorsiangulatus*; 10 – *E. monodentus*; 11 – *E. basalis*; 12 – *E. multilobatus* sp. n.; 13 – *E. demangei*; 14 – *E. filisetiger* sp. n.; 15 – *E. armatocaudatus*; 16 – *E. gremialis*; 17 – *E. curticornis* sp. n.; 18 – *E. asteroides* sp. n.; 19 – *E. griseus* sp. n.; 20 – *E. cavernicola*; 21 – *E. macclurei*; 22 – *E. reclinatus*; 23 – *E. reductus* sp. n.; 24 – *E. communicans*.

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RESEARCH ARTICLE

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The millipede genus *Glomeris* Latreille, 1802 (Diplopoda, Glomerida, Glomeridae) in North Africa

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Abstract

In North Africa, the genus *Glomeris* is shown to encompass 11 species, all of which are keyed. These include: *G. troglokabyliana* **sp. n.** from several caves in Algeria; *G. monostriata* **sp. n.** from a cave in Libya; *G. colorata* **sp. n.**, an epigean species from Tunisia; *G. anisosticta* Brandt, 1841 (still a *nomen inquirendum*) from Algeria; *G. brolemanni* Schubart, 1960 from Morocco; *G. carthaginiensis* Schubart, 1953 (stat. n., elevated from subspecific rank) from Tunisia; *G. flavomaculata* Lucas, 1846 from Algeria; *G. klugii* Brandt, 1833 (with *G. marmorata* Brandt, 1833, *G. fuscomarmorata* Lucas, 1846 and *G. maculosa* Verhoeff, 1921 as new junior subjective synonyms) from Algeria and Tunisia; *G. mohamedanica* Attems, 1900 from Tuni-

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sia; *G. punica* Attems, 1900 (with *G. numidia* Verhoeff, 1921 as a new junior subjective synonym) from Tunisia; and *G. sublimbata* Lucas, 1846 from Algeria and Tunisia.

Keywords
Diplopoda, Glomerida, *Glomeris*, taxonomy, new species

Introduction

The millipede order Glomerida is basically a temperate to warm temperate Holarctic group which contains about 30 genera and some 450 species (Mauriès 2006). Only six genera and about 80 species occur in the Oriental or Neotropical realms, reaching Sulawesi and Guatemala in the South, respectively. The genus *Glomeris* Latreille, 1802, with the type-species *G. pustulata* (Fabricius, 1781), is the largest, numbering about 100 species and a few hundred subspecies, varieties, forms or aberrations, largely from Europe, but marginally also in the Canaries, North Africa and northwestern Anatolia. Like all Glomerida, in Africa *Glomeris* species only occur north of the Sahara, along a relatively narrow strip of the Mediterranean coast, in rather humid habitats. This genus is characterized by a subquadrate shape of the telopod femur, which is not markedly hypertrophied in relation to the adjacent podomeres and is supplied with a broad distocaudal lobe instead of a distinct process (Mauriès 2006).

The taxonomy of *Glomeris* has only recently been improved. In particular, the Central European and Macaronesian faunas were reviewed and keyed (Hoess 2000; Golovatch & Enghoff 2003), with the main species-specific characters currently recognized as lying in colour patterns and, to a lesser extent, telopod structure. The identities of several Central European congeners were clarified with the use of allozyme electrophoresis (Hoess & Scholl 1999; Hoess 2000), whereas scanning electron microscopy was quite extensively applied to the study of the *alluaudi*-group of *Glomeris* endemic to the Canary Islands (Golovatch & Enghoff 2003).

The first *Glomeris* ever to have been recorded in Africa seems to be *G. klugii* Brandt, 1833, a species originally described from a single female from "Egypt or Syria" (Brandt 1833), but later rectified as coming from "Syria" (Brandt 1840b). The holotype, still housed in the Berlin Museum (Moritz & Fischer 1973), was found to have been mislabeled, and *G. klugii* proved to be a senior synonym of the common European species *G. undulata* C. L. Koch, 1844 (Golovatch 2003).

Glomeris, as well as a few other myriapod genera, was then simply listed as present in Algeria (Brandt 1840a). A few months later, two much more detailed accounts appeared. The first of these, Brandt's (1840b) review of *Glomeris*, mentioned two forms of *G. pustulata* found in Algeria and Germany, which were described or referred to as "var. *microstemma* n." and "var. *marmorata*" Brandt, 1833, respectively. Brandt also stated that both these varieties were very common in Algeria, but occurred much less frequently in Germany. The second publication (Brandt 1841a) was an essay specifically focusing on the fauna of Algeria. It largely repeated the same information, but the same varieties

were instead referred to as *G. pustulata* "var. *anisosticta* n." and "var. *marmorata*"! Just like *microstemma*, the variety *anisosticta* was stated to differ from the European samples of *G. pustulata* in showing both median spots on the thoracic shield smaller than the lateral ones. Unfortunately, this information was omitted from both the Brandt bibliography and the list of Brandt's diplopod taxa in Golovatch & Hoffman (2001), otherwise this confusion would have already been corrected. It is now apparent that these names are strictly synonymous, with *microstemma* Brandt, 1840 having priority over *anisosticta* Brandt, 1841 and representing the first truly African glomeridan to have been named. In contrast, *marmorata* was downgraded from a full species (Brandt 1833) to a variety of *G. pustulata*, while the samples from Algeria were found to be typical var. *marmorata* (Brandt 1840b, 1841a, b), in no way differing from their European counterparts.

At the present, the type material of *microstemma* and *anisosticta* seems to be lost, since it is missing from the collections of the Berlin (Moritz & Fischer 1973, 1978) and St. Petersburg (Golovatch & Hoffman 2001) museums. A neotype designation would therefore be necessary to revive either name as a taxon. Verhoeff (1906) was apparently the last author to use the name *microstemma*, still as a variety (this time of *G. pustulata norica* Latzel, 1884), and even incorporated it into a key. In contrast, because *anisosticta* has since been elevated to the rank of a full species (Brolemann 1921), despite having been published slightly later, we use *anisosticta* as the valid name.

Although the identity of *G. marmorata* might appear to lie beyond the scope of the present study, because it was first described from Hercynia (= Harz), Germany (Brandt 1833), it will be resolved below due to its relevance to the North African fauna. This taxon has hitherto remained dubious (Golovatch & Hoffman 2001), even though the type material has long been available in the Berlin Museum (Moritz & Fischer 1978). It is highly regrettable that Hoess (2000) did not attempt to revise type material of numerous Central European *Glomeris* when preparing his otherwise very useful review and key. Otherwise he could not have overlooked the great similarity between *G. marmorata*, as redescribed and beautifully illustrated by Koch (1863) from samples taken in southern Germany (and probably also based in part on a restudy of type material), and *G. undulata* which Hoess also very skillfully depicted himself.

Shortly after Brandt's contributions appeared, Lucas (1846) described three new species of *Glomeris* from Algeria: *G. sublimbata* Lucas, 1846, *G. fuscomarmorata* Lucas, 1846 and *G. flavomaculata* Lucas, 1846, all listed, redescribed and nicely illustrated after in his atlas (Lucas 1849). Among these species, only *G. flavomaculata* was found to be abundant, being represented by five varieties. Since these received no names (they were simply denominated A to E), they have no nomenclatural status. Because type material of all three species is still available in the Paris Museum, they could be revised and, when necessary, lectotypes selected (see below). Brölemann (1913a) provided a brief redescription of *G. sublimbata*, based on new samples from Algeria.

Pocock (1892) referred some fresh specimens from Algeria to *G. fuscomarmorata* and *G. flavomaculata*, but emphasized that probably both were at most only varieties of the European *G. conspersa* C. L. Koch, 1844 and *G. connexa* C. L. Koch, 1844, respectively. In contrast, Silvestri (1896) identified new material from Tunisia as *G. sublimbata*

and *G. flavomaculata*, already formally treating both as just varieties of *G. connexa*. Thereafter, Attems (1900), violating all rules of priority, described a new subspecies, *Glomeris europaea striata* n., within which he distinguished several varieties, including the var. *pustulata* (Fabricius, 1781), var. *transalpina* C. L. Koch, 1836 etc., as well as the newly described var. *punica* n. and var. *mohamedanica* n., both from Tunisia. Soon after that, Attems (1908) transferred his var. *punica* to *G. connexa* and added *G. conspersa* C. L. Koch, 1844, forma *genuina* (= *conspersa*) to the Tunisian list. Both of the originally infrasubspecific names by Attems, however, have since become validated as species-group taxa. Thus, in his list of North African millipedes, Brolemann (1921) reported three species of *Glomeris* from Algeria: *G. anisosticta* Brandt, 1841, *G. fuscomarmorata* Lucas, 1846 and *G. pustulata* Latreille, 1804 (sic!); one from Tunisia: *G. connexa punica* Attems, 1900; and another three from both these countries: *G. conspersa* C. Koch, 1847 (= *marmorata*), *G. flavomaculata* Lucas, 1846 and *G. sublimbata* Lucas, 1846. He must have either forgotten to include *G. mohamedanica* or considered it as a variety not worth mentioning. Schubart (1953), when revising Brolemann's (1921) checklist, treated both *G. mohamedanica* Attems, 1900 and *G. punica* Attems, 1900 as full species.

Verhoeff (1921) described a further two species from Algeria: *G. maculosa* Verhoeff, 1921 and *G. numidia* Verhoeff, 1921. Brolemann (1925) added to the confusion by describing from Tunisia the new subspecies *G. pustulata trisulcata* n., a long pre-occupied name (*G. intermedia trisulcata* Rothenbühler, 1899). To eliminate this homonymy, Schubart (1953) renamed it as *G. pustulata carthaginiensis* Schubart, 1953. He also described the first congener from Morocco: *G. brolemanni* Schubart, 1960, and provided some useful comments on the *Glomeris* fauna of North Africa in relation to a new record of *G. flavomaculata* in Algeria (Schubart 1960, 1963). Finally, Abrous-Kherbouche & Mauriès (1996) reported two *Glomeris* species from a nature reserve in Algeria, and provided an updated checklist of the Diplopoda of that country.

Superficially, all *Glomeris* species, including those from North Africa, can more or less easily be separated into two groups, formerly invalidly treated as subgenera. One group, *Eurypleuromeris* Verhoeff, 1906, includes the species with a laterally broadened tergum 3 (tergum 4 as counted by Verhoeff (1906, 1921), who considered the thoracic shield to be composed of two terga, 2nd and 3rd). The other, *Stenopleuromeris* Verhoeff, 1909, includes the species with a laterally narrowed tergum 3, in particular its anterior (condylar) part shortened in relation to its posterior part, the two parts being separated by a stria. This distinction may still be useful, but it was only after Jeekel's (1971) typification that both these names could be correctly applied. Despite this, all of the numerous nominate subgenera or synonyms of *Glomeris* (see Mauriès 2006) remain hopelessly heterogeneous. Thus, *Glomeris conspersa* C. L. Koch, 1847 (= *G. klugii* Brandt, 1833) became the type-species of *Eurypleuromeris* and, like *Glomeris connexa* C. L. Koch, 1847, the type-species of *Euglomeris* Verhoeff, 1906, shows a broadened condylar part of tergum 3. The type-species of *Stenopleuromeris* was designated as *Glomeris pulchra* C. L. Koch, 1847 which, like *G. pustulata*, the type-species of *Glomeris* s. str., or *G. dorsosanguine* Verhoeff, 1906, the type-species of *Xestoglomeris* Verhoeff, 1906, has a shortened anterior part of tergum 3. So at the present, follow-

ing Hoess (2000), it seems best not to use a formal subgeneric division of *Glomeris*, referring instead to informal groups in quotation marks. In addition, this character/distinction appears to be subject to a degree of variation (see below).

Taking into account the two other glomeridans described from North Africa—*Eupeyerimhoffia algerina* Brölemann, 1913 from Algeria (Brölemann 1913b) and *Glomerellina convolvens africana* Ceuca, 1988 from Tunisia (Ceuca 1988)—all previous knowledge of the regional fauna of Glomerida can be summarized in the following checklist (Table 1). *G. conspersa*, reported from Tunisia and Algeria (Attems 1908; Abrous-Kherbouche & Mauriès 1996), is listed under the name *G. klugii* because it is just a colour morph of the latter (Hoess 2000; Golovatch 2003).

Rich material, including type material of Brandt, Lucas, Attems, Verhoeff and Brolemann, has been amassed from various sources for the present review. The following acronyms are adopted here for the relevant repositories:

FMNH Field Museum of Natural History, Chicago, U.S.A.
HNHM Hungarian Natural History Museum, Budapest, Hungary
MNHN Muséum national d'Histoire naturelle, Paris, France
MSNF Museo di Storia naturale, "La Specola", Florence, Italy
NHMW Naturhistorisches Museum Wien, Austria
NMNH National Museum of Natural History, Sofia, Bulgaria
ZMUB Museum für Naturkunde, Humboldt Universität, Berlin, Germany
ZMUC Natural History Museum of Denmark (Zoological Museum), University of Copenhagen, Denmark
ZMUM Zoological Museum, State University of Moscow, Russia
ZSM Zoologische Staatssammlung, Munich, Germany

Table 1. A checklist of the Glomerida in North Africa, based on literature records (A: Algeria, M: Morocco, T: Tunisia).

Species	A	T	M
Eupeyerimhoffia algerina Brölemann, 1913	+		
Glomerellina convolvens africana Ceuca, 1988		+	
Glomeris anisosticta Brandt, 1841	+		
G. brolemanni Schubart, 1960			+
G. flavomaculata Lucas, 1846	+	+	
G. fuscomarmorata Lucas, 1846	+		
G. klugii Brandt, 1833 (= *G. conspersa* C. L. Koch, 1844)	+	+	
G. maculosa Verhoeff, 1921	+		
G. numidia Verhoeff, 1921	+		
G. mohamedanica Attems, 1900		+	
G. punica Attems, 1900		+	
G. pustulata carthaginiensis Schubart, 1953		+	
G. sublimbata Lucas, 1846	+	+	

In the catalogue sections, D stands for the original description, R for a redescription or descriptive notes, F for new faunistic records, N for a new name, and L for simple listings.

Systematics

***Glomeris troglokabyliana* Golovatch & Mauriès, sp. n.**
urn:lsid:zoobank.org:act:36F30A02-E19F-4B99-8468-B75A52A771EC
Fig. 1.

Type material. Algeria, Algiers, "dept. Alger", Michelet-Djurdjura road, Azerou Tidjer, entrance of Ifri Mareb Cave, 19.XI.1912, leg. P. de Peyerimhoff (Biospeologica 704A), holotype ♂ (MNHN CC 165), paratypes: 2 ♂, 3 ♀, 8 juv. (MNHN CC 165). Same locality, Azerou Tidjer, Ifri bou-Amane Cave, 19.XI.1912, leg. P. de Peyerimhoff (Biospeologica 706), paratypes: 1 ♂, 2 ♀ (ZMUM). Same locality, 29.VII.1913, leg. P. de Peyerimhoff (Biospeologica 707), paratypes: 6 ♂ & juv. ♂, 23 ♀ & juv. ♀ (MNHN CC 165), 1 ♂, 1 ♀ (ZMUC), 3 ♀ (NMNH), 3 ♀ (FMNH), 3 ♀ (NHMW 7779). Same locality, Michelet-Djurdjura road, douar Aït-Boudrar, Anou Tahalouant Cave, 11.VII.1914, leg. P. de Peyerimhoff (Biospeologica 710), 1 ♂ (MNHN CC 165). Algeria, "dept. Alger", Bouïra, douar Haïzer, Ifri Yacoub Cave, 30.X.1912, leg. P. de Peyerimhoff (Biospeologica 915), paratypes: 3 ♂, 5 ♀, 7 juv. (MNHN CC 165). Algeria, "dept. Alger", douar Ben-bou-Ouakour, canton Beni Mansour Maillot, n'Tarzout Cave, 8.III.1914, leg. P. de Peyerimhoff (Biospeologica 906), 1 ♀ (MNHN CC 165).

Name: To emphasize the provenance of material from caves in the High Kabylia, Algeria.

Diagnosis: Differs from all congeners except *G. albida* Mauriès & Vicente, 1978 and *G. monostriata* sp. n. in the clear troglomorphy (in particular, the lack of pigmentation), coupled with two striae crossing the collum and 1-2 striae crossing the thoracic shield, and usually with (6)7+1 ocelli.

Description: Length of extended adults of both sexes ranging between 13.5-14.0 (♂) and 15.0-17.5 mm (♀), width 3.4-4.2 (♂) and 5.0-5.8 mm (♀), body broadest at thoracic shield. Holotype *ca* 13.5 mm long and 3.65 mm wide (extended), or *ca* 9.5 and 3.5 mm, respectively (unextended). Juveniles with 12 segments (like adults) and 5 ocelli, *ca* 4.8 mm long and 2.2 mm wide. Juveniles with 11 segments and 5 ocelli, *ca* 4.5 mm long and 2.2 mm wide. Juveniles with 10 segments and 3 ocelli, *ca* 3.4 mm long and 1.75 mm wide. Juveniles with 8 or 9 segments and 2-3 ocelli, *ca* 2.7-2.8 mm long and 1.13-1.40 mm wide.

Coloration entirely pallid.

Head usual, transverse; Tömösváry's organ transversely oval, strongly elongate (Fig. 1A); antennae long, antennomere 6 longest, 2.5-2.8 times longer than wide (Fig. 1B); ocelli usually 7+1, rather convex but usually transparent and thus poorly visible (Fig. 1A), only rarely pigmented (5+1 or 6+1 grey ocelli in ♂♂ from Anou Tahalouant and n'Tarzout caves, respectively).

Collum with two transverse striae.

Thoracic shield with a narrow hyposchism reaching the caudal tergal contour (Fig. 1C); 3-4 transverse striae, of which 1-2 anterior, starting well in front of schism, crossing entire dorsum, while the others, starting just above schism, are abbreviated (Fig. 1C).

Tergal surface very finely punctate. Terga 3 and 4 rather broadly rounded laterally, tergum 3 being only slightly narrower (Fig. 1C). Tergal pilosity and mid-dorsal sinuosity lacking. Pygidium usually with a completely regularly rounded caudal margin, only rarely extremely faintly sinuated medially at margin.

♂ leg 17 (Fig. 1D) with a medium-sized, regularly rounded, outer coxal lobe; telopodite 4-segmented.

♂ leg 18 (Fig. 1E) with a broadly ogival syncoxital notch; telopodite 4-segmented.

Telopods (Figs 1F, G) with a rather high, regularly rounded, bare, central syncoxital lobe flanked by two setose horns, each crowned with a very small bulb and a long, setiform filament. Femur with a large caudomedial outgrowth, subquadrate at base. Tibia with a caudomedial unciform process. Tarsus rather broadly rounded apically.

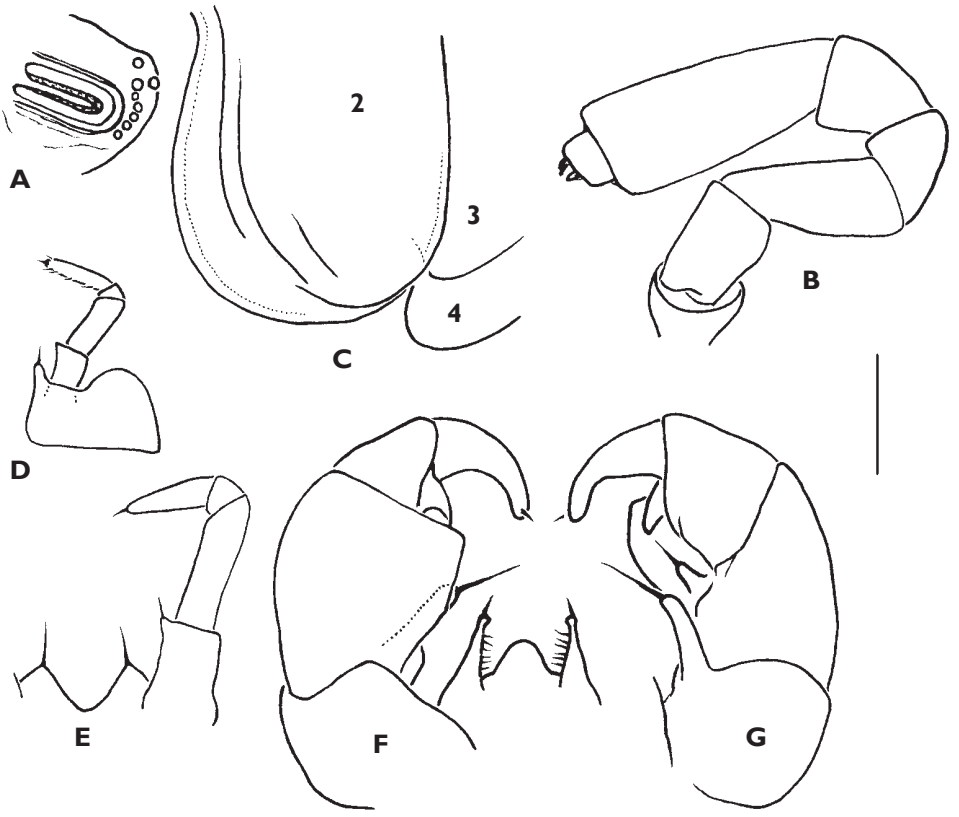

Figure 1. *Glomeris troglokabyliana* sp. n., ♂ paratype; **A,** left part of head showing ocelli and Tömösváry's organ, dorsal view; **B,** antenna, lateral view; **C,** thoracic shield and terga 3 & 4, lateral view; **D,** leg 17; **E,** leg 18; **F & G,** leg 19 (telopod), caudal and frontal views, respectively. – Scale bar: 0.3 mm (D-G); drawn not to scale (A-C).

Remarks: This species is the only clearly troglomorphic congener to be reported from Algeria. It is noteworthy that some specimens show rudimentary pigmentation of the ocelli.

Based on the shape of tergum 3, this new species can be regarded as somewhat intermediate between the "*Stenopleuromeris*" and "*Eurypleuromeris*" types, although closer to the former.

Glomeris monostriata **Golovatch & Mauriès, sp. n.**
urn:lsid:zoobank.org:act:B6C89F7D-F1BF-44C1-AE72-15016BC6F8D2
Fig. 2.

Type material. Libya, Cyrenaica, Ayn Dabusia, cave near Al Qubbah, 280 m, 32°50'00.9"N, 22°16'49.6"E (WGS84), 8.IV.2008, leg. S. Taiti, holotype ♂ (MNHN CC 166), paratypes: 1 ♂, 2 ♀ (MNHN CC 166), 1 ♂, 1 ♀ (MSNF), 1 ♂, 1 ♀ (ZMUM).

Name: To emphasize the collum and the thoracic shield each being crossed by only a single stria.

Diagnosis: Differs from all congeners except *G. albida* Mauriès & Vicente, 1978 in being troglomorphic, coupled with only a single stria crossing the collum and thoracic shield; differs from *G. albida* in the evidently bifid horns and a lower central lobe of the telopod syncoxite.

Description: Length of adults of both sexes (unextended, alcohol material) ranging between 8.0 and 9.0 mm, width between 3.0 and 3.2 mm, up to *ca* 11 and 3.5 mm, respectively (extended animals); body broadest at thoracic shield. Holotype (unextended) *ca* 8.2 mm long and 3.2 mm wide. Coloration entirely pallid.

Head usual, transverse; Tömösváry's organ transversely oval, slightly less extended transversely than in *G. troglokabyliana* sp. n.; antennae long, antennomere 6 longest, 2.4-2.5 times longer than wide; distance between antennal sockets 1.95 times greater than socket diameter; ocelli 4+1, rather convex, but transparent and thus poorly visible.

Collum with one (anterior) transverse stria.

Thoracic shield with a narrow hyposchism reaching the caudal tergal contour (Fig. 2A); two transverse striae, of which the one starting well in front of the schism crosses the entire dorsum, the other, starting just above the schism, is abbreviated (Fig. 2A).

Tergum 3 relatively narrowly (Fig. 2A) and tergum 4 broadly rounded laterally. Tergal pilosity and mid-dorsal sinuosity missing. Pygidium usually with a completely regularly rounded caudal margin, only rarely extremely faintly sinuated medially at margin.

♂ leg 17 (Fig. 2B) with a low, slightly irregularly rounded, outer coxal lobe; telopodite 4-segmented.

♂ leg 18 (Fig. 2C) with an ogival syncoxital notch; telopodite 4-segmented.

Telopods (Figs 2D, E) with a low, regularly rounded, bare, central syncoxital lobe flanked by two setose and evidently bifid horns. Prefemur micropapillate distolaterally. Femur with a large caudomedial outgrowth, subquadrate at base. Tibia with a tuber-

culiform caudomedial outgrowth and a strong caudolateral seta near base. Tarsus quite narrowly rounded apically.

Remarks: This species is the first glomeridan to be recorded in Libya and, given that it is troglobitic, may represent a relictual element.

In general, the condition of having just one stria, rather than two, crossing the collum is extremely rare in *Glomeris* species. The only other congener showing this condition that we are aware of is *G. albida* Mauriès & Vicente, 1978, a troglobite from Málaga, Spain (Mauriès & Vicente, 1978). Both these species are evidently regressive, apparently in response to cavernicoly. Similarly, *G. albida* also demonstrates two striae on the thoracic shield, only the anteriormost of which crosses the dorsum. In addition, both these species are pallid, of about the same size, with the same number (5) of ocelli and the same proportions (L/D 2.5) of antennomere 6, and both are devoid of tergal or pygidial sinuosity. The main differences concern the shape of the telopod syncoxite,

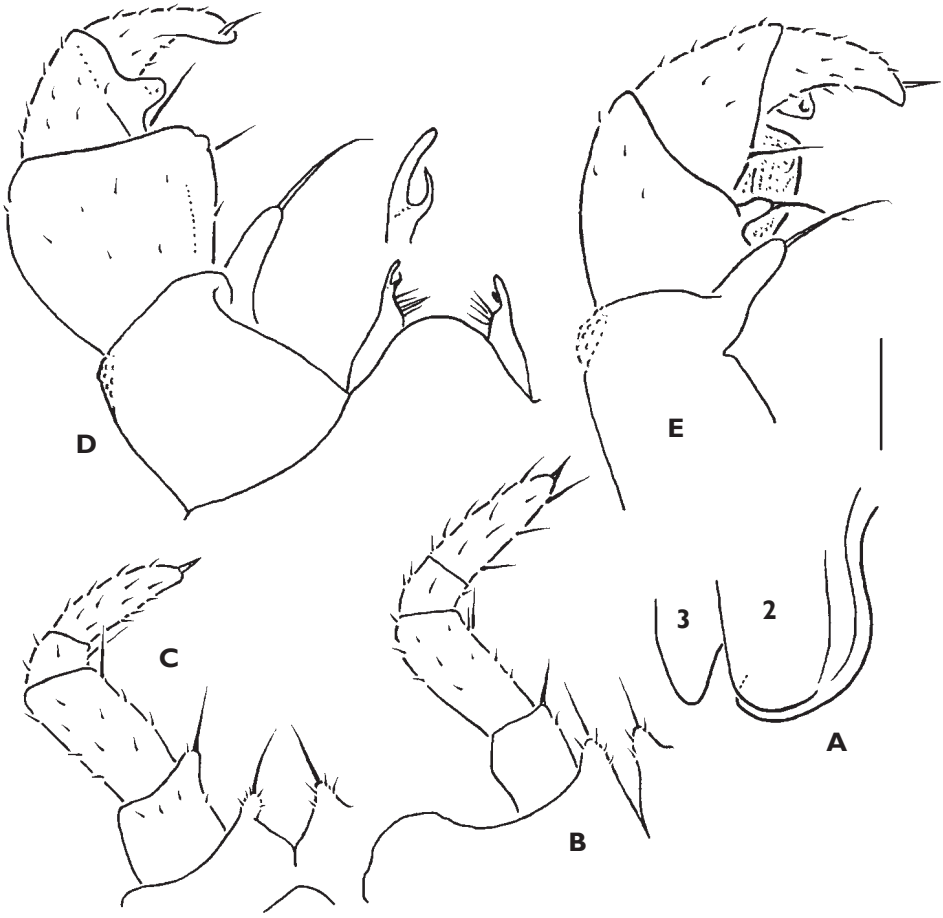

Figure 2. *Glomeris monostriata* sp. n., ♂ paratype; **A,** thoracic shield and tergum 3, lateral view; **B,** leg 17; **C**, leg 18; **D & E,** leg 19 (telopod), caudal and frontal views, respectively. – Scale bar: 0.2 mm (B-E); drawn not to scale (A).

being strongly marked in the bifid tip of the horns and the relatively low and regularly rounded central lobe in *G. monostriata* sp. n.

Even more regressive appears to be *G. dionysii* (Strasser, 1961), a troglobite from Sicily, Italy, which totally lacks striae on the collum (Strasser 1961).

Based on the narrow tergum 3, *G. monostriata* sp. n. can readily be attributed to the "*Stenopleuromeris*" type.

Glomeris colorata Golovatch, Mauriès, Akkari & Stoev, sp. n.

urn:lsid:zoobank.org:act:672AFB57-3269-4D2C-89FB-BCDAA16D3DFC
Figs 3-5.

Type material. Tunisia, Siliana Gov., Jebel Sidi Aouidet (47 km from Siliana, road El Fahs-Siliana), 36°15'81"N, 9°46.46"E, alt. approx. 440 m, slope overgrown by conifers close to road, under stones, leaf litter, 28.III.2008, leg. P. Stoev & N. Akkari, holotype ♂ (MNHN CC 167), paratypes: 3 ♀ (MNHN CC 167), 2 ♀ (ZMUM), 1 ♀ (NMNH), 1 ♀ (ZMUC). Tunisia, Zaghouan Gov., Jebel Mansour, near Sidi Aouidet Village, 36°12'31"N, 9°45'59"E, alt. approx. 510 m. *Pinus* forest with *Rosmarinus officinalis* bushes, under stones and leaf litter, 28.III.2008, leg. N. Akkari & P. Stoev, paratypes: 6 ♀ (FMNH), 4 ♂, 1 ♀ (NMNH).

Name: To emphasize the colourful tergal pattern.

Diagnosis: Especially similar to *G. punica* and *G. flavomaculata*, based on the characteristic colour pattern (2+2 rows of spots on terga 2-11), but differs in the presence of a light axial line, of medially coalesced 1+1 spots on the pygidium and the lighter background coloration.

Figure 3. *Glomeris colorata* sp. n., ♀ paratype from Tunisia, Siliana Gov.; habitus, dorsal view. (Photographed not to scale by I. Muratov).

Description: Length of adults of both sexes (extended, alcohol material) ranging between 9.5 (♂) and 10.0-13.5 mm (♀), width between 4.7 (♂) and 5.0-6.7 mm (♀); body broadest at thoracic shield. Holotype *ca* 9.5 mm long and 4.7 mm wide.

Coloration (Figs 3, 4) variegated, mostly rather vivid, background usually dark brown, but sometimes mostly yellow due to expanded light spots. Head mostly light brown, evidently marbled near ocelli, with 1+1 and 2+2 small pallid spots against a light brown background just above antennal sockets; labrum pale yellowish; antennae largely dark brown, only tip pallid. Collum with a large, mostly marbled, yellowish central spot (Figs 3, 4). Thoracic shield with 2+2 large light spots, sometimes interconnected with a transversely oval marbled area in-between, but separated by a more or less evident, often incomplete, light axial line. Subsequent terga, except pygidium, with 1+1 more or less wide, light paramedian spots, usually arranged into clear stripes, a mostly interrupted and sometimes vague, light, axial line, and a pair of marbled, transversely oval, lateral areas. Pygidium with 1+1 light, paramedian, mostly coalesced spots (Fig. 4), less frequently nearly entirely light grey-brown. Venter and legs contrastingly light yellow.

Head usual, transverse; Tömösváry's organ transversely oval, slightly shorter than in *G. troglokabyliana* sp. n.; antennae long, antennomere 6 longest, 2.4-2.5 times longer than wide; ocelli (4)5 black + 1 transparent, all convex.

Collum with two transverse striae.

Thoracic shield with a narrow hyposchism almost reaching caudal tergal contour (Fig. 5A); four transverse striae, of which 1-2 anteriormost starting well in front of

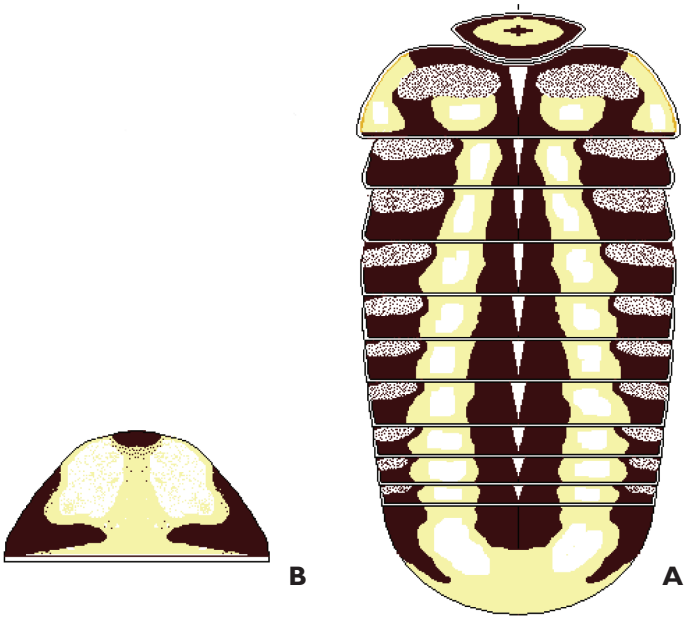

Figure 4. *Glomeris colorata* sp. n., ♂ holotype; **A,** habitus, dorsal view; **B,** pygidium, caudal view. A schematic, slightly too bright presentation of the colour pattern (del. J.-P. Mauriès).

schism and crossing entire dorsum, the other two always abbreviated (Fig. 5A); anteriormost stria only rarely slightly interrupted dorsally.

Tergum 3 relatively narrowly (Fig. 5A) and tergum 4 broadly rounded laterally. Tergal pilosity and mid-dorsal sinuosity absent. Pygidium usually with a completely regularly rounded caudal margin, only rarely extremely faintly sinuated medially at margin.

♂ leg 17 (Fig. 5B) with a low outer coxal lobe; telopodite 4-segmented.

♂ leg 18 (Fig. 5C) with a broadly subtriangular syncoxital notch; telopodite 4-segmented.

Telopods (Figs 5D) with a high, rather regularly rounded, bare, central syncoxital lobe flanked by two setose horns, latter each crowned with a minute bulb and a short setoid filament. Tarsus quite narrowly rounded apically.

Remarks: Based on the narrow tergum 3, *G. colorata* sp. n. can be attributed to the "*Stenopleuromeris*" type.

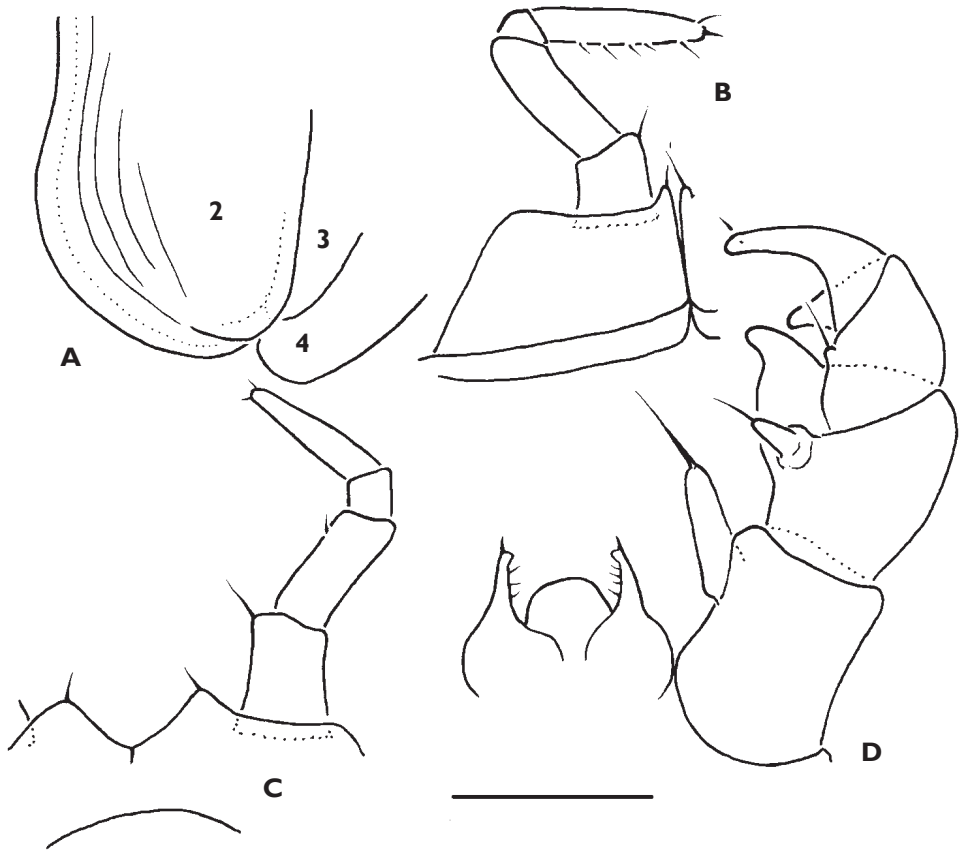

Figure 5. *Glomeris colorata* sp. n., ♂ holotype; **A,** thoracic shield and terga 3 & 4, lateral view; **B,** leg 17; **C,** leg 18; **D,** leg 19 (telopod), frontal view. – Scale bar: 0.5 mm (B-D); drawn not to scale (A).

Glomeris anisosticta Brandt, 1841

Glomeris pustulata Latr., var. *microstemma* Brandt, 1840b: 42 (D).
Glomeris pustulata Latr., var. *microstemma* – Brandt 1841b: 148 (R); Gervais 1847: 72 (R).
Glomeris pustulata Latr., var. *anisosticta* Brandt, 1841a: 284 (D).
Glomeris pustulata genuina (= *pustulata*), var. *microstemma* – Verhoeff 1906: 180 (R).
Glomeris anisosticta – Brolemann 1921: 100 (L); Schubart 1953: 218 (L).
Glomeris pustulata anisosticta – Abrous-Kherbouche & Mauriès 1996: 586 (L).

Remarks: Unfortunately, no new material of this species could be obtained for study. It is stated to be close to *G. pustulata*, but differs in the paramedian spots on the thoracic shield being much smaller than each lateral spot (Brandt 1840b, 1841a, b). For the time being, we treat this taxon as a full species, but its separation from *G. pustulata* remains to be confirmed.

Glomeris brolemanni Schubart, 1960

Glomeris brolemanni Schubart, 1960: 164, figs 1-3 (D).

Remarks: Unfortunately, no new material of this species could be obtained for study. It is stated to differ from congeners in having a black-brown ground coloration, with the thoracic shield showing only a single, large, pale spot in the anterior part, each of the subsequent terga showing a pair of light, lateral, transverse-oval spots, and the pygidium completely dark (except for the usual pale margin, which is slightly wider laterally) (Schubart 1960). It belongs to the "*Stenopleuromeris*" type.

Glomeris flavomaculata Lucas, 1846
Figs 6-9.

Glomeris flavomaculata Lucas, 1846: 284 (D).
Glomeris flavo-maculata (sic!) – Gervais 1847: 74 (R); Lucas, 1849: 326, plate 1, fig. 5 (R); Pocock 1892: 27 (F); Brolemann 1921: 101 (L); Schubart 1963: 80 (R).
Glomeris connexa C. Koch, v. *flavo-maculata* (sic!) – Silvestri 1896: 157 (F).
Glomeris flavomaculata – Schubart 1953: 218 (L); Abrous-Kherbouche & Mauriès 1996: 572, 586 (F, L).

Type material examined: Algeria, environs of Algiers, date ?, leg. & det. H. Lucas, ♂ lectotype (here designated) (MNHN CC 042), paralectotypes: 14 ♂, 19 ♀, 4 ♀ juv. (MNHN CC 042). Algeria, environs of Oran, 1846, leg. ?, det. H. Lucas, paralectotypes: 1 ♂, 2 ♀ (MNHN CC 042). The designation of a lectotype seems advisable in order to fix the type locality and to ensure that the name-bearing type shows the diag-

Figure 6. *Glomeris flavomaculata* Lucas, 1846, ♂ ?paralectotype; habitus, dorsal view. (Photographed not to scale by I. Muratov).

nostically important characteristics of the male sex, particularly as Lucas (1846) spoke about this species being common throughout Algeria.

Other material: Algeria, 1850, leg. H. Lucas, ?paralectotype ♂ (MNHN CC 042, entry 67-96). Algeria, Vallée des Singes, leg. & det. H. Ribaut, 2 ♂, 3 ♀ (MNHN CC 042).

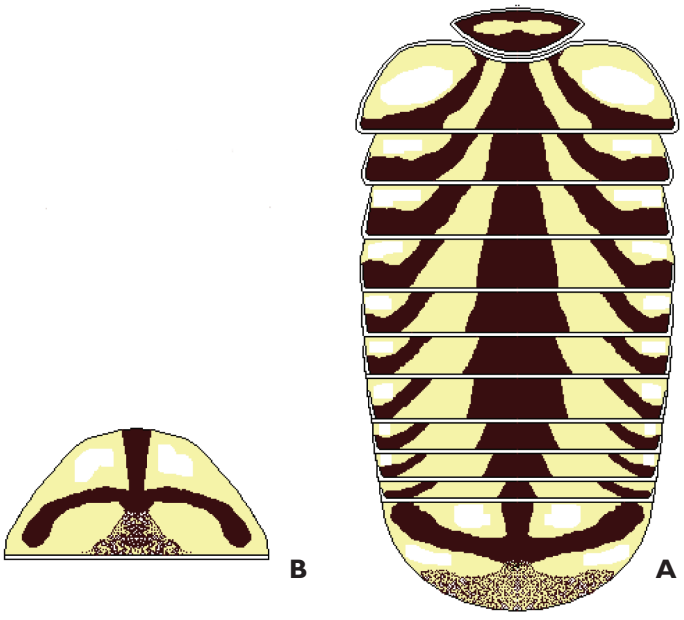

Figure 7. *Glomeris flavomaculata* Lucas, 1846, ♂ paralectotype; **A,** habitus, dorsal view; **B,** pygidium, caudal view. A schematic, slightly too bright presentation of the colour pattern (del. J.-P. Mauriès).

Figure 8. *Glomeris flavomaculata* Lucas, 1846, syntype; habitus, dorsal view. (After Lucas 1849).

Brief redescription: Length up to 15 mm, width up to 6.25 mm. Coloration vivid, pattern as in Figs 6-8. ♂ legs 17, 18 and 19 (telopods) as in Figs 9A-D.

Remarks: Nearly the entire type series of *G. flavomaculata* has faded completely, probably due to the long preservation in alcohol. Fortunately, however, the paralectotypes from near Oran and the ?paralectotype ♂ from Lucas' collection (1850) have retained their coloration (Figs 6, 7), which matches quite closely the pattern well depicted by Lucas (1849), based on a then rather freshly collected syntype (Fig. 8). We are certain, however, that all diplopods printed in colour by Lucas (1849) in Plate 1 are too dark and red compared to their natural coloration, not only because pertinent alcohol material shows this, but also in view of the specific name itself, *flavomaculata*, clearly indicating the presence of light spots on the body. The most likely explanation is that Lucas used dry material of *G. flavomaculata* which had become somewhat darkened (see also below).

This species belongs to the "*Stenopleuromeris*" type.

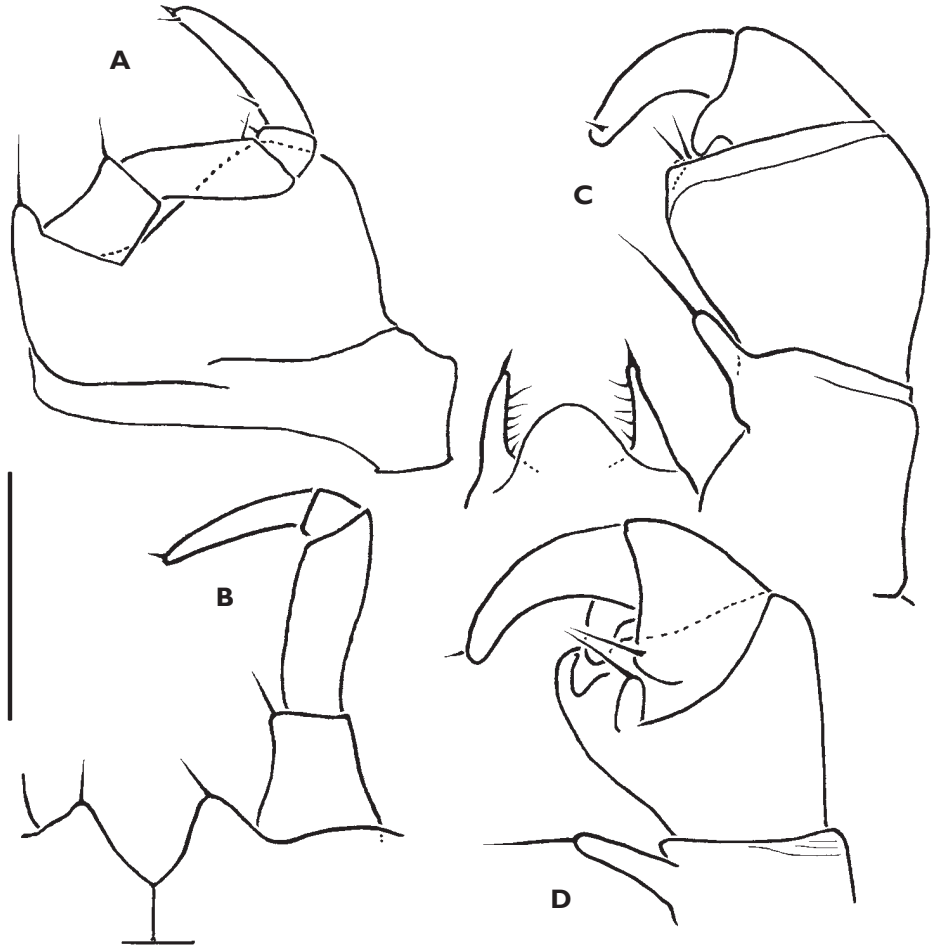

Figure 9. *Glomeris flavomaculata* Lucas, 1846, ♂ lectotype; **A,** leg 17; **B,** leg 18; **C & D,** leg 19 (telopod), caudal and frontal views, respectively. – Scale bar: 0.5 mm.

Glomeris klugii **Brandt, 1833**

Figs 10-14.

Glomeris klugii Brandt, 1833: 195 (D).
Glomeris marmorata Brandt, 1833: 196 (D), **syn. n.!**
Glomeris fuscomarmorata Lucas, 1846: 284 (D), **syn. n.!**
Glomeris pustulata Latr., var. *marmorata* – Brandt 1840b: 42 (R); 1841b: 148 (R); Gervais 1847: 73 (R).
Glomeris fusco-marmorata (sic!) – Gervais 1847: 74 (R); Lucas, 1849: 327, plate 1, fig. 4 (R); Pocock 1892: 27 (F); Brolemann 1921: 101 (L).
Glomeris conspersa forma *genuina* (sic!) – Attems 1908: 105 (F).

Glomeris fuscomarmorata – Schubart 1953: 218 (L); Abrous-Kherbouche & Mauriès 1996: 586 (L).
Glomeris maculosa Verhoeff, 1921: 27, fig. 3 (D), **syn. n.!**
Glomeris maculosa – Schubart 1953: 218 (L).
Glomeris conspersa – Abrous-Kherbouche & Mauriès 1996: 572, 586 (F, L).

Type material examined: Germany, "Hercynia", leg. Zimmermann, 2 ♀ ?syntypes of *Glomeris marmorata* Brandt, 1833 (ZMUB 39). No lectotype designation has been made here, particularly as we did not directly examine the material.

Algeria, Philippeville (now Skikda), date ?, leg. & det. H. Lucas, 1 ♀ syntype ("type") of *Glomeris fuscomarmorata* (MNHN CC 043).

Algeria, Gorges de la Chiffa, date ?, leg. H. Ribaut, ♂ "type" of *Glomeris maculosa* Verhoeff, 1921 (ZSM A20070924 + micropreparation A20032085). The ♂ represents only part of the syntype series, which was said to consist of 2 ♂ and 1 ♀ (Verhoeff 1921).

Other material (nearly all previously identified as *Glomeris fuscomarmorata*): Algeria, "Bona" (now Annaba), leg. F. Meinert, 5 ♀ (ZMUC). Algeria, le Ruisseau (environs of Algiers), 18.XII.1892, leg. P. Lesne, 2 ♀ (MNHN CC 168, entry 6-97). Algeria, Ravin de la Femme Sauvage (environs of Algiers), XII.1892, leg. P. Lesne, 2 ♂, 2 ♀ (MNHN CC 168, entry 6-97). Algeria, loc. ?, 1898, leg. Noucelhier, 1 ♂, 3 ♀ (MNHN CC 168). Algeria, Massif de l'Edough, VII-VIII.1918, leg. Ed. Ch. (?), 1 ♂ juv., 4 ♀ (MNHN CC 168). Algeria, near Algiers, ruisseau des Singes, date ?, leg. & det. H. Ribaut, 1 ♂, 1 ♀, 1♀ juv. (MNHN CC 043). Algeria, Algiers, 3.IV.1907, leg. & det. H. Ribaut, 2 ♀ (MNHN CC 043). Tunisia (Khroumirie), Jendouba Gov., Aïn Draham, V-VI.1906, leg. H. Gadeau de Kerville, 1 ♂ (MNHN CC 043). Same locality, Aïn Draham, Col des Ruines, 36°47'N, 8°41'E, 19.XI.2003, leg N. Akkari, 1 ♀ (NMNH). Same locality, 5.II.2004, leg N. Akkari, 3 ♀ (ZMUM). Same locality, 19.XI.2003, leg N. Akkari, 1 ♀ (NMNH). Same locality, 18.IV.2004, leg. N. Akkari, 1

Figure 10. *Glomeris klugii* Brandt, 1833, ♀ from Tunisia, Aïn Draham area (ZMUC 200107); habitus, dorsal view. (Photographed not to scale by I. Muratov).

juv. (ZMUM). Same locality, alt. approx. 735 m, 9.III.2009, leg. N. Akkari & H. Enghoff, 1 ♀ (ZMUC). Same locality, alt. approx. 710 m, 11.III.2009, leg. N. Akkari & H. Enghoff, 3 ♂, 1 ♂ juv., 11 ♀ (ZMUC). Same locality, Aïn Draham area, 5-18.V.1988, leg. Z. M. Cop. Exp., 3 ♂, 2 ♀ (ZMUC 200107). Same locality, 7 km S of Aïn Draham, Les Chênes, 22.03.1986, leg. Z. M. Cop. Exp., 2 ♂, 6 ♀ (ZMUC 200109). Same locality, Fernana, 36°43'59"N, 8°40'43"E, alt. approx. 750 m, *Quercus-Erica* forest,

Figure 11. *Glomeris klugii* Brandt, 1833, both ♀ ?syntypes of *G. marmorata* Brandt, 1833 from "Hercynia" (ZMUB); **A & B,** habitus, dorsal view. (Photographed not to scale by A. Friederichs).

9.III.2009, leg. N. Akkari & H. Enghoff, 2 ♂ juv., 3 ♀ (ZMUC). Same locality, Aïn Draham, Beni M'Tir, 36°43'51"N, 8°42'19"E, alt. approx. 590 m, *Quercus-Erica* forest, 10.III.2009, leg. N. Akkari & H. Enghoff, 2 ♂, 1 ♂ juv., 2 ♀ (ZMUC).

Brief redescription: Length up to 13.5 mm, width up to 6.25 mm. Coloration mostly vivid, very distinctly marbled, pattern as in Figs 10-13. Syncoxite of telopods as in Figs 14A, B, with only minor variations in shape of central lobe and in delicately bifid coxal horns.

Remarks: The presumed type series of *G. marmorata*, even though represented by two dry, pinned specimens, has still preserved its colour pattern sufficiently well (Fig. 11) to compare it with the beautiful illustrations by Koch (1863) and hence to unequivocally synonymize this species here with *G. klugii*, the holotype of which has been revised elsewhere (Golovatch 2003). This formalizes Brolemann's (1921) informal synonymy "*G. conspersa* C. Koch, 1847 (= *marmorata*)" proposed in his checklist.

The syntype of *G. fuscomarmorata* examined here has faded completely, apparently due to the long preservation in alcohol. Fortunately, most of the other samples from North Africa, especially fresh ones, have retained their coloration (Figs 10, 12), which matches quite closely the pattern depicted by Lucas (1849), based on a then recently collected syntype (Fig. 13). We are certain, however, that this species must also have been printed somewhat too dark and red compared to its natural coloration in Lucas' (1849) Plate 1, likely because Lucas used dry material (*cf* Figs 11 and 13). On the other hand, *G. klugii* in Europe is known to exist in two colour morphs, the dark "*undulata*" and the light "*conspersa*" (Hoess 2000), of which "*conspersa*" is much more widespread

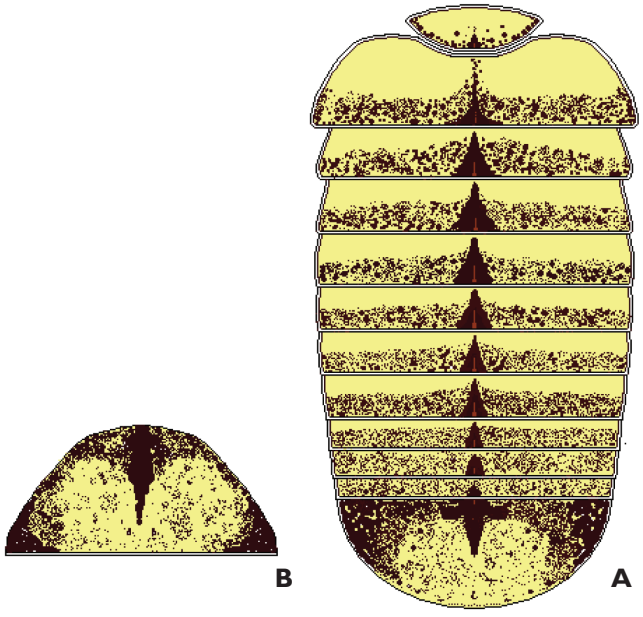

Figure 12. *Glomeris klugii* Brandt, 1833, ♀ from Tunisia, Aïn Draham area (MNHN CC 168); **A,** habitus, dorsal view; **B,** pygidium, caudal view. A schematic, slightly too bright presentation of the colour pattern (del. J.-P. Mauriès).

Figure 13. *Glomeris klugii* Brandt, 1833, ♀ syntype of *G. fuscomarmorata* Lucas, 1846 from Algeria. (After Lucas 1849).

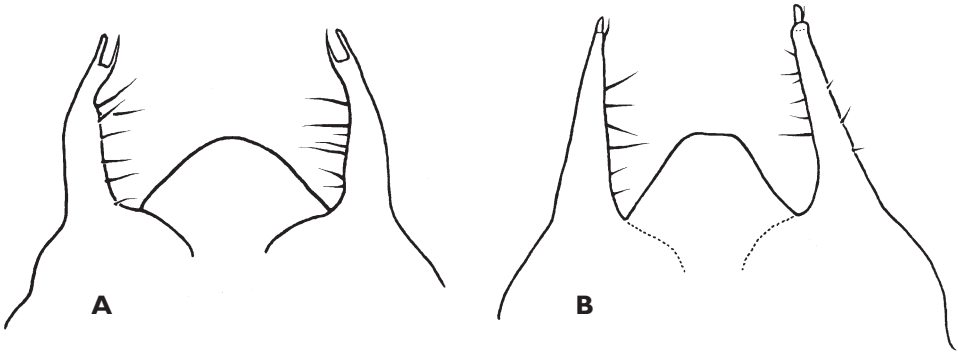

Figure 14. Telopod syncoxite of *Glomeris klugii* Brandt, 1833; **A,** ♂ from near Algiers, ruisseau des Singes (MNHN CC 043); **B,** ♂ from Tunisia, Aïn Draham area (ZMUC 200107), both previously identified as *G. fuscomarmorata* Lucas, 1846. – Drawn not to scale.

and occupies peripheral parts of the species' distribution area, including North Africa. Could material of "*undulata*" have served, at least in part, for Lucas' (1846, 1849) descriptions and illustrations? Hoess (2000) marked as questionable populations of "*conspersa*" from a few small, outlying areas in the Balkans, near Algiers and Tunis, but we can confirm the presence of *G. klugii* in North Africa. We suggest that it could well have arrived there, particularly at the largest sea ports, through commercial activities, which have been going on since prehistoric times throughout the Mediterranean. The synonymy of *G. klugii* and *G. fuscomarmorata* proposed here therefore appears fully justified.

Furthermore, we must give due tribute to Brandt (1840b, 1841a, b) who, already at the very beginning of diplopodological explorations in North Africa, wrote that his *G. marmorata* from Germany and Algeria were identical. Although he failed to recognize that his own *G. klugii* and *G. marmorata* actually represented the same species—apparently because the holotype of *G. klugii* (surprisingly) did not show any striae on the thoracic shield, retained (in alcohol) its generally light coloration and was thought to have come from Egypt or Syria—he was essentially correct in thinking that the same species could exist on both continents. Likewise correct have been the very few subsequent records of "*conspersa*" in Algeria and Tunisia (Attems 1908; Abrous-Kherbouche & Mauriès 1996), whereas most other authors believed that the North African fauna, including that of *Glomeris*, is fully endemic.

The syntype of *G. maculosa* is a "*conspersa*" specimen of *G. klugii*, with the colour pattern still well traceable. Hence the synonymy of these names is also proposed here.

The fact that *G. klugii* belongs to the "*Eurypleuromeris*" type provides an additional indication of its probable introduction to North Africa from Europe. Moreover, even though *G. conspersa* is the type-species of *Eurypleuromeris*, Verhoeff (1921) mistakenly attributed his *G. maculosa* to the "*Stenopleuromeris*" type. Indeed, the anterior part of tergum 3 in the syntype of *G. maculosa* that we have examined is probably a little narrower than is usual for European or other North African "*conspersa*" specimens of *G. klugii*, but this variation seems too modest to be considered a reliable distinction, perhaps even reflecting individual rather than geographical variation. This is another good reason to abandon the subgeneric division of *Glomeris*.

Glomeris sublimbata **Lucas, 1846**

Figs 15-19.

Glomeris sublimbata Lucas, 1846: 284 (D).
Glomeris sublimbata – Gervais 1847: 74 (R); Lucas, 1849: 324, plate 1, fig. 3 (R); Brolemann 1913a: 388, fig. 1 (R); 1921: 101 (L); Schubart 1953: 218 (L); Abrous-Kherbouche & Mauriès 1996: 586 (L).
Glomeris connexa C. Koch, v. *sublimbata* (sic!) – Silvestri 1896: 156 (F).

Type material: Algeria, Philippeville (now Skikda), date ?, leg. & det. Lucas ?, ♂ lectotype (here designated) (MNHN CC 094), paralectotypes: 1 ♂, 4 ♀ (MNHN CC

Figure 15. *Glomeris sublimbata* Lucas, 1846, ♂ from Tunisia, Aïn Draham area; habitus, lateral view. (Photographed not to scale by N. Akkari).

094). The designation of a lectotype seems advisable in order to fix the type locality and to ensure that the name-bearing type shows the diagnostically important characteristics of the male sex, particularly as Lucas (1846) spoke about this species being recorded from several localities in Algeria.

Other material: Algeria, loc. ?, date ?, leg. H. Lucas?, ?paralectotypes: 1 ♂, 4 ♀ (MNHN CC 094). Algeria, loc. ?, 1850, leg. Lucas, 1 M (MNHN CC 094, entry 67-96). Algeria, "Bona" (now Annaba), leg. F. Meinert, 4 ♂, 22 ♀ (ZMUC). Algeria, Constantine, date ?. leg. M. Hénon, 1 ♀ (MNHN CC 094). Algeria, Philippeville (now Skikda), 1902, leg. Théry, 2 ♀, 1 juv. (MNHN CC 094). Algeria, Mt Babor, between Sétif and Bougie (now Béjaia), date ?, leg. P. de Peyerimhoff , 1 ♀ (MNHN CC 094). Algeria, Guerrounchi Forest, date ?, leg. ?, 5 ♂, 20 ♀ (MNHN CC 094). Algeria, date ?, leg. I. de Gaulle, 1 ♀ (MNHN CC 094). Algeria, ruisseau des Singes, date ?, leg. ?, 2 ♀ juv. (MNHN CC 094). Tunisia, Béja Gov., Jebel El Jouza, close to Amdoun Village, mixed oak forest dominated by *Quercus suber*, 36°49'N, 9°E, alt. approx. 560 m, under stone, 25.V.2005, leg. N. Akkari, 1 ♀ (NMNH). Same locality, in litter and under barks, 5.II.2004, leg. N. Akkari, 8 ♂, 7♀, 1 juv. (NMNH). Same locality, 4.XI.2003, leg. N. Akkari, 1 ♀, 1 juv. (ZMUM). Same locality, 25.XII.2003, leg. N. Akkari, 3 ♂, 1 ♀ (ZMUM). Tunisia, Jendouba Gov., Aïn Draham, Col des Ruines, in litter, 19.XI.2003, leg. N. Akkari, 2 ♀

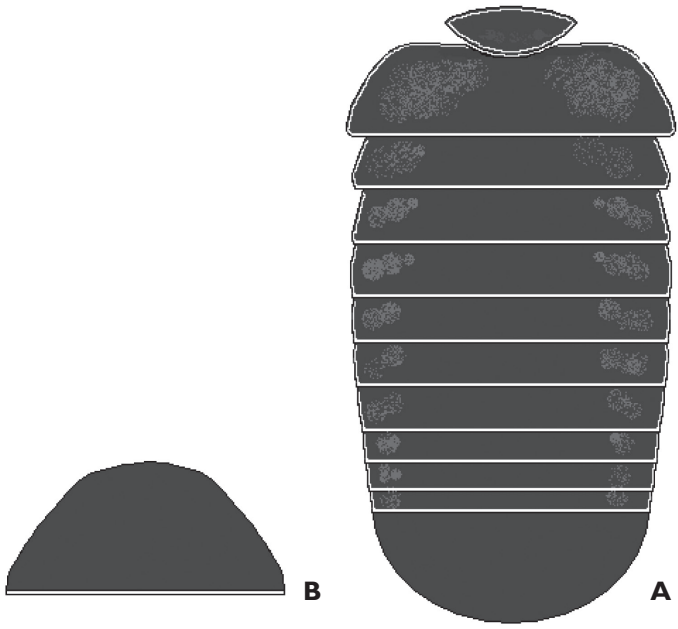

Figure 16. *Glomeris sublimbata* Lucas, 1846, ♂ from Algeria, Guerrounchi Forest (MNHN CC 094); **A,** habitus, dorsal view; **B,** pygidium, caudal view. A schematic, slightly too vague presentation of the colour pattern (del. J.-P. Mauriès).

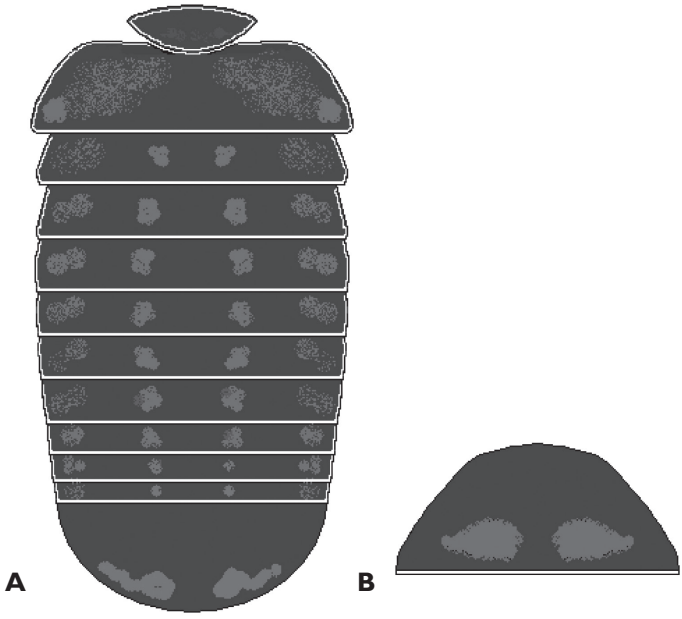

Figure 17. *Glomeris sublimbata* Lucas, 1846, juvenile ♀ from Algeria, ruisseau des Singes (MNHN CC 094); **A,** habitus, dorsal view; **B,** pygidium, caudal view. A schematic, slightly too vague presentation of the colour pattern (del. J.-P. Mauriès).

(NMNH). Same locality, in litter, 18.IV.2004, leg. N. Akkari, 1 ♀ (NMNH). Tunisia, Jendouba Gov., Feija National Park, oak forest with mixed *Quercus faginea* & *Q. suber*, 36°29'N, 8°18'E, in litter, 7.III.2004, leg. N. Akkari, 2 ♂, 1 ♀ (MNHN CC 094). Same locality, alt. approx. 690 m, in litter, 26.XII.2003, leg. N. Akkari, 2 ♂ (NMNH). Tunisia, Jendouba Gov., 15 km of Tabarka, 36°49'97"N, 8°42'34"E, alt. approx. 230 m, *Quercus* forest, slope, under stones and barks, 21.III.2008, leg. N.A. & P. Stoev, 3 ♂, 3 ♀ (MNHN CC 094). Tunisia, Béja Gov., Djebel El Jouza, 10.III.2005, leg. & det. N. Akkari, 2 ♂, 1 ♀ (ZMUC 200112). Tunisia, Jendouba Gov., Aïn Draham area, 5-18.V.1988, leg. Z. M. Cop. Exp., 1 ♀ (ZMUC 200107). Tunisia, Jendouba Gov., 7 km S of Aïn Draham, Les Chênes, 22.III.1986, leg. Z. M. Cop. Exp., 1 ♀ (ZMUC 200109). Tunisia, Béja Gov., Djebel Jouza, Amdoun, 2003, coll. N. Akkari, 2 ♀ (MNHN CC 094). Tunisia, Jendouba Gov., 15 km of Tabarka, 36°49'97"N, 8°42'34"E, alt. approx. 230 m, *Quercus suber* forest, slope, under stones and barks, 21.III.2008, coll. P. Stoev & N. Akkari, 2 ♂, 1 ♀ (FMNH). Tunisia, Jendouba Gov., 9 km of Hammam Bourguiba (W of Aïn Draham), 36°48'05"N, 8°39'54"E, alt. approx. 380 m, humid *Pinus* forest, close to river, under stones, logs and in leaf litter, 22.III.2008, leg. P. Stoev & N. Akkari, 8 ♂, 10 ♀, 1 ♀ juv.

Figure 18. *Glomeris sublimbata* Lucas, 1846, syntype from Algeria. (After Lucas 1849).

Figure 19. *Glomeris sublimbata* Lucas, 1846, ♂ lectotype; **A,** leg 17; **B,** leg 18; **C,** leg 19 (telopod), frontal view. – Scale bar: 0.5 mm.

(FMNH). Tunisia, Jendouba Gov., 4 km of Tabarka (direction to Melloula), 36°57'48"N, 8°43'78"E, alt. approx. 225 m, *Eucalyptus* and *Pinus* forest, under stones, 22.III.2008, leg. P. Stoev & N. Akkari, 1 ♂ 1 ♀ (FMNH). Tunisia, Béja Gov., 13 km of Nefza (road Tabarka-Nefza), 36°57'61"N, 8°56'51"E, alt. approx. 150 m, *Pinus* forest, under stones, 23.III.2008, leg. P. Stoev & N. Akkari, 3 ♂, 3 ♀, 1 ♀ juv. (FMNH). Tunisia, Jendouba Gov., W of Babouch (near frontier to Algeria), 36°48'20"N, 8°39'29"E, alt. approx. 400 m, *Erica-Pinus* or *-Quercus* forest, 11.III.2009, leg. N. Akkari & H. Enghoff, 1 ♂ juv., 1 ♀ (ZMUC). Tunisia, Jendouba Gov., Aïn Draham, Col des Ruines, 11.III.2009, leg. N. Akkari & H. Enghoff, 1 ♀ (ZMUC). Tunisia, Jendouba Gov., Aïn Snoussi, close to Tabarka, 36°50'12"N, 8°54'41"E, alt. approx. 420 m, *Erica-Quercus* forest, 11.III.2009, leg. N. Akkari & H. Enghoff, 3 ♀ (ZMUC). Tunisia, Jendouba Gov., Tbainia (on road Béja-Aïn Draham), 36°47'06"N, 8°45'08"E, alt. approx. 575 m, *Erica-Quercus* forest, 11.III.2009, leg. N. Akkari & H. Enghoff, 3 ♀ (ZMUC).

Short description: Length up to 20 mm, width up to 10 mm. Coloration always brown-blackish, with 1+1 (adults) or 2+2 (some adults and all juveniles), more or less vague, greyish to brownish, marbled, lateral spots on terga 2(3)-11(12), pattern as in Figs 15-18. ♂ legs 17, 18 and 19 (telopods) as in Figs 19A-C.

Remarks: The type series of *G. sublimbata* has faded completely, probably due to the long preservation in alcohol. Fortunately, most of the other samples from North Africa, especially fresh ones, have retained their coloration (Figs 15-17), which matches quite closely the pattern depicted by Lucas (1849), based on a then recently collected syntype (Fig. 18). We are certain, however, this species in Lucas' (1849) Plate 1 was also printed or painted too dark compared to its natural coloration, since most probably Lucas used dry material which had become somewhat darkened.

This species is certainly among the largest and darkest in North Africa. It resembles the widespread and similarly uniformly very dark Western European *G. marginata* (Villers, 1789), yet *G. sublimbata* belongs to the "*Stenopleuromeris*" type. On the other hand, the degree of development of the anterior part of tergum 3 in relation to its posterior part may again prove to vary even intraspecifically, as is apparently the case in *G. klugii* (see above).

Glomeris carthaginiensis Schubart, 1953

Figs 20-23.

Glomeris pustulata trisulcata Brolemann, 1925: 65 (D), nom. praeoc.
Glomeris pustulata carthaginiensis Schubart, 1953: 222 (N), nom. nov.

Type material: Tunisia, Bizerte Gov., Djebel Ichkheul (near Mateur), 29.IX.1924, leg. L. Seurat, ♂ lectotype of *Glomeris pustulata trisulcata* Brolemann, 1925 (here designated) (MNHN CC 098, Brolemann n° 2629), paralectotypes: 1 ♂, 3 ♀ (MNHN CC 098, Brolemann n° 2629), det. H. Brolemann. The designation of a lectotype seems advisable in order to ensure that the name-bearing type shows the diagnostically important characteristics of the male sex.

Other material: Tunisia, Bizerte Gov., Ichkeul National Park (plain of Mateur), inside the park, 37°08'30"N, 9°41'03"E, under stones, 7.I.2005, leg. N. Akkari, 3 ♀, 1 juv. (ZMUC). Same locality, under stones, 24.IX.2006, leg. N. Akkari, 1 ♂, 1 ♀ (NMNH). Same locality, alt. approx. 50 m, under stones, 23.III.2008, leg. N. Akkari & P. Stoev, 1 ♂, 10 ♀, 4 juv. (MNHN CC 098), 1 ♂, 4 ♀, 2 juv. (ZMUC), 3 ♀, 2 juv. (NHMW 7780). Same locality, under stones, 8.III.2004, leg. N. Akkari, 1 ♂, 7 ♀, 1 juv. (ZMUM). Same locality, under stones, 3.XII.2006, leg. N. Akkari, 3 ♀ (ZMUM). Same locality, 12.III.2009, leg. N. Akkari & H. Enghoff, 3 ♂, 8 ♀ (ZMUC). Same locality, 27.III.2007, leg. F. Vilisics, 1 ♂ (HNHM).

Short description: Length up to 17 mm, width up to 7.5 mm. Coloration blackish, with a characteristic pattern of 2+2 light spots on thoracic shield and, occasionally, also on terga 3 and 4, but always with a pair 1+1 light and especially large spots both on tergum 6 and pygidium; no light markings on terga 7-11 (Figs 20-22). ♂ legs 17, 18 and 19 (telopods) as in Figs 23A-C.

Remarks: This taxon is here considered to be a full species. The type series, said to have originally consisted of 13 specimens of both sexes (Brolemann 1925), is now

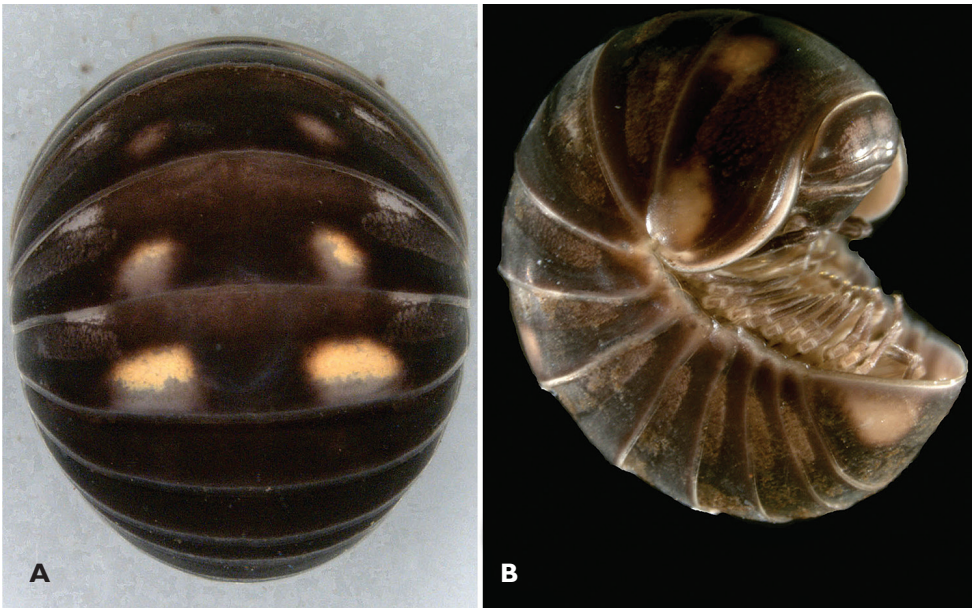

Figure 20. *Glomeris carthaginiensis* Schubart, 1953, ♂ topotype; **A & B,** dorsal and lateral views, respectively, of a rolled animal. (Photographed not to scale by N. Akkari).

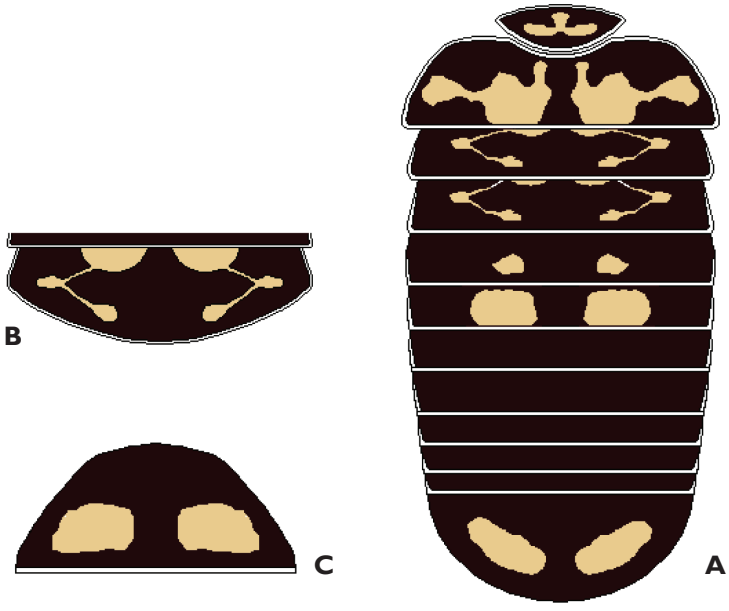

Figure 21. *Glomeris carthaginiensis* Schubart, 1953, ♂ topotype; **A,** habitus, dorsal view; **B,** pygidium, dorsal view; **C,** pygidium, caudal view. A schematic, slightly too bright presentation of the colour pattern (del. J.-P. Mauriès).

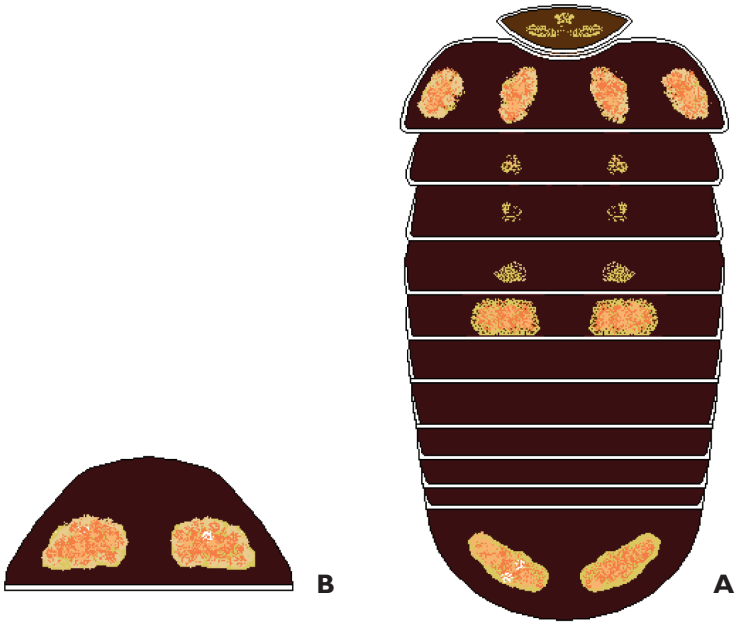

Figure 22. *Glomeris carthaginiensis* Schubart, 1953, ♂ topotype; **A,** habitus, dorsal view; **B,** pygidium, caudal view. A schematic, slightly too bright presentation of the colour pattern (del. J.-P. Mauriès).

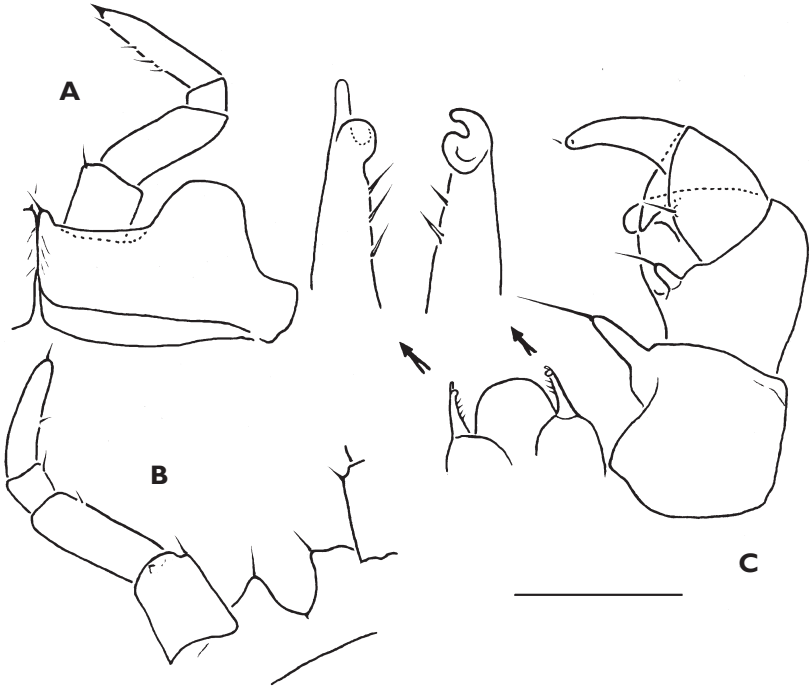

Figure 23. *Glomeris carthaginiensis* Schubart, 1953, ♂ lectotype; **A,** leg 17; **B,** leg 18; **C,** leg 19 (telopod), frontal view. – Scale bar: 0.5 mm.

incomplete (only 5 specimens left), and strongly faded, but still with a detectable colour pattern. Variation in coloration and pattern modest, the most characteristic feature being the presence of a paramedian pair of especially large, light spots on tergum 6 and a complete absence of lighter markings thereafter until the pygidium (Figs 20-22).

This species belongs to the "*Stenopleuromeris*" type.

***Glomeris mohamedanica* Attems, 1900**

Figs 24, 25.

Glomeris europaea striata var. *mohamedanica* Attems, 1900: 303 (D).
Glomeris mohamedanica – Schubart 1953: 218 (L).

Type material: Tunisia, Béja Gov., Medjez El Bab (now Mejez El Bab), date ?, leg. ?, ♂ lectotype (here designated) (NHMW 3913), paralectotypes: 3 ♂, 2 ♀ (NHMW 3913), 1 ♂ (MNHN CC 153). The designation of a lectotype (from 350 syntypes, see Attems 1900) seems advisable in order to ensure that the name-bearing type shows the diagnostically important characteristics of the male sex.

Other material: Tunisia, Béja Gov., Nefza (30 km of Béja), 2003, leg. N. Akkari, 1 ♂, 1 ♀ (MNHN CC 153). Same locality, 36°57'61"N, 8°56'51"E, open area with scattered vegetation, under stones, 27.II.2004, leg. N. Akkari, 3 ♂, 5 ♀, 3 juv. (MNHN CC 153). Same locality, 2.X.2005, leg. N. Akkari, 1 ♂, 3 ♀ (NMNH). Tunisia, Jen-

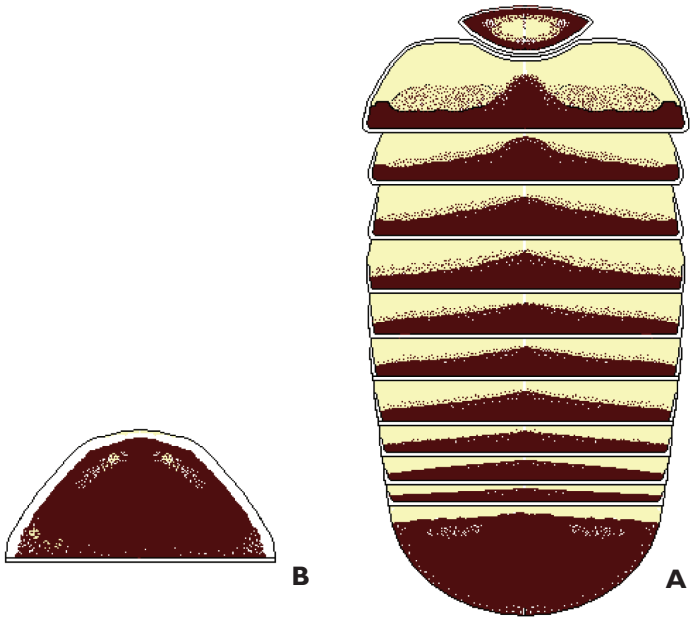

Figure 24. *Glomeris mohamedanica* Attems, 1900, ♂ from Tunisia, Nefza; **A,** habitus, dorsal view; **B,** pygidium, caudal view. A schematic, slightly too bright presentation of the colour pattern (del. J.-P. Mauriès).

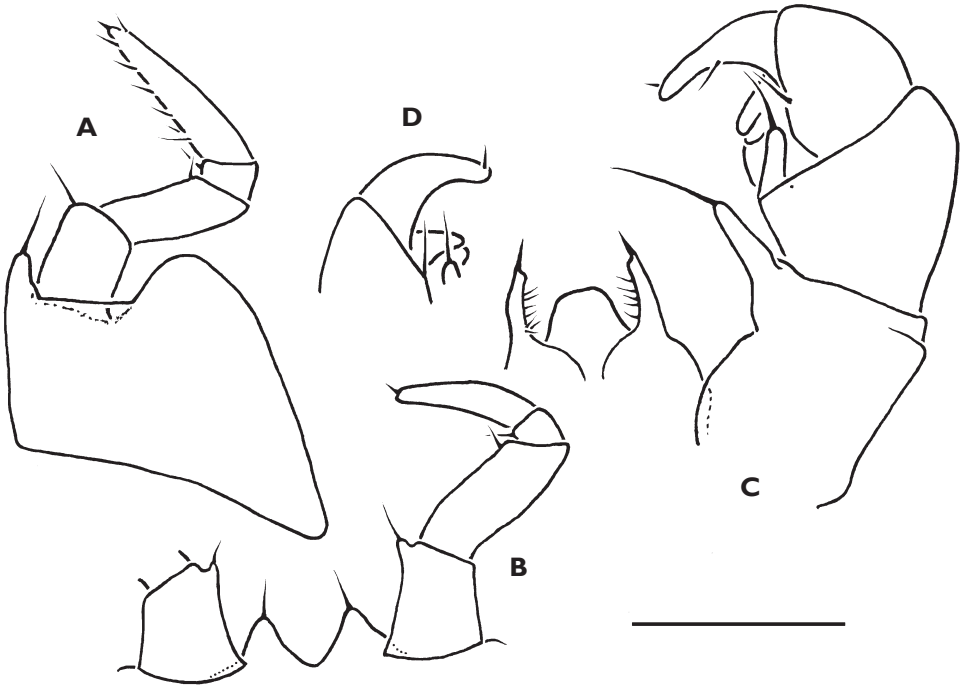

Figure 25. *Glomeris mohamedanica* Attems, 1900, ♂ lectotype; **A,** leg 17; **B,** leg 18; **C,** leg 19 (telopod), frontal view; **D**, distal part of telopod, caudal view. – Scale bar: 0.5 mm.

douba Gov., Beni Mtir (8 km S of Aïn Draham), mixed oak forest dominated by *Quercus suber*, slope, under stones, 19.II.2007, leg. N. Akkari, 10 ♂ (MNHN CC 153), 3 ♂ (ZMUM), 2 ♂ (NMNH), 2 # (FMNH). Same locality, alt. approx. 500 m, 19.II.2007, leg. N. Akkari, 2 ♂, 2 ♀ (ZMUC 200113). Tunisia, Jendouba Gov., Tabarka, 10.XII.2003, leg. N. Akkari, 1 ♀ (FMNH). Tunisia, Jendouba Gov., 40 km of Jendouba, near frontier, 17.V.1988, leg. Z. M. Cop. Exp., 2 M (ZMUC 200108).

Short description: Length up to 12 mm, width up to 6.0 mm. Coloration dark brown to blackish, with contrasting yellow bands, pattern as in Figs 24A, B. ♂ legs 17, 18 and 19 (telopods) as in Figs 25A-D.

Remarks: This species is unusual among the presumably native North African *Glomeris* in belonging to the "*Eurypleuromeris*" type.

Glomeris punica Attems, 1900

Figs 26-28.

Glomeris europaea striata var. *punica* Attems, 1900: 302 (D).
Glomeris connexa var. *punica* – Attems 1908: 105 (F).
Glomeris connexa punica – Brolemann 1921: 100 (L).

Glomeris numidia Verhoeff, 1921: 28 (D), **syn. n.!**
Glomeris numidia – Schubart 1953: 218 (L).
Glomeris punica – Schubart 1953: 218 (L).

Type material: Tunisia, Bou-Kournine (now Bou Kornine), date ?, leg. ?, ♂ lectotype of *G. punica* Attems, 1900 (here designated) (NHMW 3910), paralectotypes: 5 ♂, 1 ♀ (NHMW 3910). The designation of a lectotype (of 60 syntypes, see Attems 1900) seems advisable in order to ensure that the name-bearing type shows the diagnostically important characteristics of the male sex.

Algeria, Gorges de la Chiffa, date ?, leg. H. Ribaut, 2 ♂ syntypes of *Glomeris numidia* Verhoeff, 1921 (♂ "type", ZSM A20070944 + micropreparation A20032086 and ♂ "?type", A20091438). Both ♂♂ represent only part of the type series stated to have consisted of 2 ♂ and 2 ♀ (Verhoeff 1921).

Other material: Algeria, La Chiffa, date ?, leg. Ch. Alluaud (219), 2 ♂, 5 ♀ (MNHN CC 018, collection Brolemann CCXIX). Algeria, le Ruisseau (environs

Figure 26. *Glomeris punica* Attems, 1900, ♂ from Tunisia, Amdoun; **A & B,** habitus, dorsal and lateral views, respectively. (Photographed not to scale by N. Akkari).

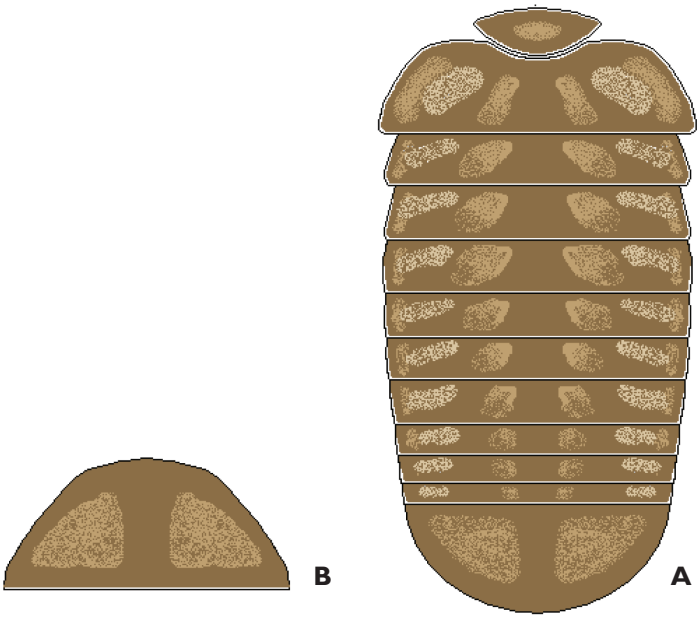

Figure 27. *Glomeris punica* Attems, 1900, ♂ from Tunisia, Amdoun; **A,** habitus, dorsal view; **B,** pygidium, caudal view. A schematic, slightly too vague presentation of the colour pattern (del. J.-P. Mauriès).

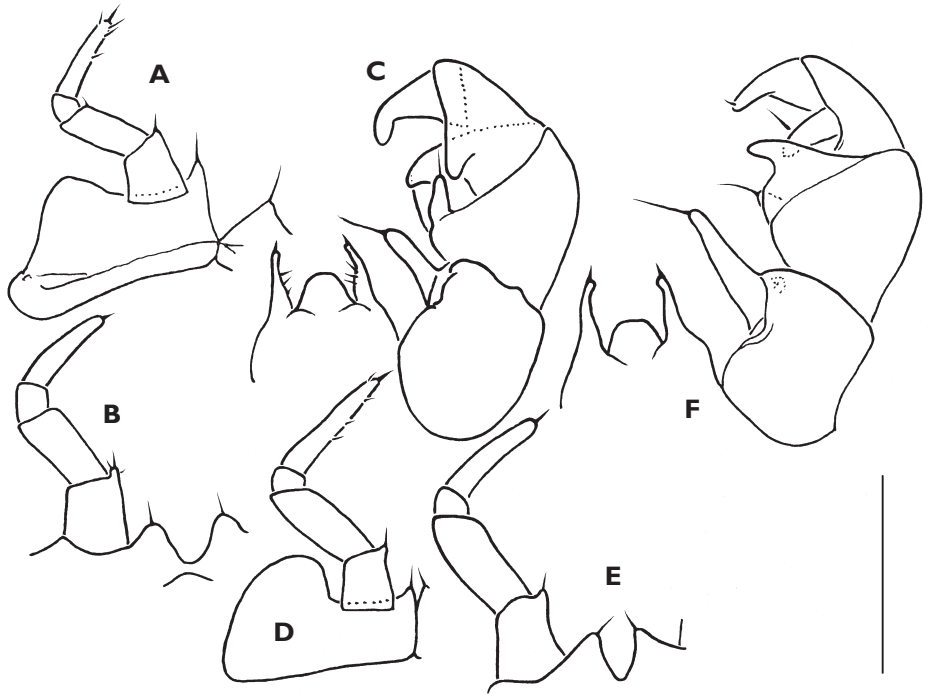

Figure 28. *Glomeris punica* Attems, 1900, ♂ lectotype (A-C) & ♂ from Sakiet Sidi Youssef (D-F); **A & D,** leg 17; **B & E,** leg 18; **C & F,** leg 19 (telopod), frontal and caudal views, respectively. – Scale bar: 0.5 mm.

of Algiers), 18.XII.1892, leg. P. Lesne, 1 ♂ (MNHN CC 018, entry 6-97). Algeria, Yakouren (Kabylia), 10.VI.1893, leg. P. Lesne, 1 ♂ (MNHN CC 018, entry 6-97). Tunisia (Kroumirie), Jendouba Gov., Aïn Draham, V-VI.1906, leg. H. Gadeau de Kerville, 6 ♂, 19 ♀ (MNHN CC 018). Tunisia, Béja Gov., Jebel El Jouza, close to Amdoun Village, under stones, 10.III.2005, leg. N. Akkari, 2 juv. (MNHN CC 018). Same locality, under stones and barks, 25.V.2005, leg. N. Akkari, 2 ♂, 1 ♀ (NMNH). Tunisia, Jendouba Gov., Aïn Draham, Col des Ruines, mixed oak forest with *Quercus faginea* and *Q. suber*, 36°47'N, 8°41'E, under stone, 19.XI.2003, leg. N. Akkari, 1 juv. (MNHN CC 018). Tunisia, Le Kef Gov., Sakiet Sidi Youssef, coniferous forest dominated by *Pinus halepensis*, under stones, 24.X.2003, leg. N. Akkari, 4 ♂, 5 ♀ (ZMUM). Tunisia, Zaghouan Gov., Jebel Zaghouan, alt. 350-390 m, 25.II.2007, leg. N. Akkari, 2 ♂, 2 ♀ (ZMUC 200114). Tunisia, Jendouba Gov., 15 km E of Tabarka, 25.III.1986, leg. Z. M. Cop. Exp., 1 ♂ (ZMUC 200111). Tunisia, Thala Gov., 12 km S of Thala, 10.III.1986, leg. Z. M. Cop. Exp., 1 ♂ (ZMUC 200110). Tunisia, Zaghouan Gov., 3 km SE of Zaghouan, NE side of Djebel Zaghouan, 1.XII.1974, leg. H. Waldén, 1 ♀ (Museum Göteborg). Tunisia, Tunis Gov., Bou Kornine National Park, 18 km SE of Tunis, close to Hammam Lif Town, 36°42'53"N, 10°20'68"E, alt. 105-150 m, *Thuya* & *Eucalyptus* grove, dry river bed, under stones and logs, 4.III.2008, leg. P. Stoev & N. Akkari, 2 ♂, 9 ♀ (FMNH), 6 ♂, 4 ♀, 1 juv. (NMNH). Tunisia, Zaghouan Gov., Jebel Zaghouan, surroundings of "Temple des Eaux", 36°23'40"N, 10°08'09"E, alt. approx. 300 m, forest close to road, under stones and in leaf litter, 19.III.2008, leg. N. Akkari & P. Stoev, 2 ♂, 4 ♀ (FMNH), 4 ♂, 2 ♀, 1 juv. (NMNH). Tunisia, Jendouba Gov., 15 km of Tabarka, 36°49'97"N, 8°42'34"E, alt. approx. 230 m, *Quercus suber* forest, slope, under stones and barks, 21.III.2008, leg. P. Stoev & N. Akkari, 1 ♂, 2 ♀, 1 ♀ juv. (FMNH), 1 ♀ (NMNH). Tunisia, Béja Gov., 13 km of Nefza (road Tabarka-Nefza), 36°57'61"N, 8°56'51"E, alt. approx. 150 m, *Pinus* forest, under stones, 23.III.2008, leg. P. Stoev & N. Akkari, 2 ♂, 1 ♀ (FMNH). Tunisia, Jendouba Gov., close to Aïn Draham, Fernana, 9.III.2009, leg. N. Akkari & H. Enghoff, 1 ♂ juv., 3 ♀ (ZMUC). Tunisia, Zaghouan Gov., Jebel Zaghouan, 13.III.2009, leg. N. Akkari & H. Enghoff, 4 ♂, 2 ♀, 1 ♂ juv. (ZMUC). Tunisia, Jendouba Gov., 9 km of Hammam Bourguiba (W of Aïn Draham), 36°48'05"N, 8°39'54"E, alt. approx. 380 m, humid *Pinus* forest, close to river, under stones, logs and in litter, 22.III.2008, leg. P. Stoev & N. Akkari, 1 ♂, 1 juv. (NMNH).

Short description: Length up to 12 mm, width up to 6.0 mm. Coloration light to dark brown, terga 2-11 each with 2+2, rather vague, paramedian spots; pattern as in Fig. 27. ♂ legs 17, 18 and 19 (telopods) as in Figs 28A-F. An always high lateral lobe of ♂ coxite 17 is remarkable (Fig. 28A).

Remarks: This species belongs to the "*Stenopleuromeris*" type. Schubart (1963) mistakenly attributed it to the "*Eurypleuromeris*" type.

Discussion

Interestingly, the proportion of *Glomeris* species and populations with a ventrolaterally narrowed tergum 3 increases towards the South. In Central and Eastern Europe, most (if not all) species show a broadly rounded tergum 3, i.e. belonging to the "*Eurypleuromeris*" type, whereas in the Mediterranean area, including North Africa, the majority of species have a shorter anterior part of tergum 3, i.e. they belong to the "*Stenopleuromeris*" type. A ventrolaterally narrower tergum 3 can be seen as an adaptation for tighter body enrolment, possibly providing better protection from desiccation in the South. In North Africa, only *G. mohamedanica* and most (if not all) of the *G. klugii* populations have a somewhat broadened tergum 3, whereas it is considerably narrower in the other species, including even the somewhat intermediate *G. troglokabyliana* sp. n.

Most of the North African species of *Glomeris* demonstrate the same or a very similar structure of the telopod syncoxite, in which the central lobe is rather high to very high, bare and rounded, whereas the coxal horns are crowned with a small bulb/lobule and a setoid filament, the latter either rounded or pointed at its apex. Only two species, *G. klugii* and *G. monostriata* sp. n., show evidently bifid tips of the coxal horns, a character state which may be evidence of closer ties to European rather than North African counterparts. In the case of *G. klugii*, we are rather inclined to admit its early introduction from Europe, naturally from "*conspersa*"-type populations, through human agency to the major sea ports of Algeria and Tunisia. Active trade throughout the Mediterranean has begun at latest with the Phoenicians, *ca* 3,500 years ago. In the case of *G. monostriata* sp. n., the closest relatives are probably *G. albida* (Spain) and *G. dyonisii* (Sicily), although this might just reflect convergent adaptations to the cave environment.

As elsewhere, there are two striae on the collum in most of the North African *Glomeris* species, reduced to one in *G. monostriata* sp. n. The number of striae on the thoracic shield is more variable, typically ranging from two to four, of which the anterior one or two (rarely none) cross the dorsum.

The distribution of *Glomeris* in North Africa (Figs 29-32) shows that all of the species are, as would be expected, confined to a narrow strip along the Mediterranean coast. The distribution of *G. anisosticta* remains unmapped because we only know it occurs, and is common, in Algeria (Brandt 1840b, 1841a). The proportion of cavernicoles (most likely troglobites) is increased (two of 11 species), which is hardly surprising given the predominantly harsh environments these normally meso- to hygrophilous Diplopoda face in North Africa. Among the *ca* 100 *Glomeris* species known to date, very few occur obligatorily in caves, i.e. only two from Europe (one in Spain, the other in Sicily) and only another two from North Africa (one in Algeria, the other in Libya).

Much more material is required to properly assess the North African glomeridan fauna. Despite the long history of exploration in Algeria, several taxonomic problems remain, such as the status of *G. anisosticta*. On the other hand, a country like Morocco, which includes most of the Atlas Mountains, will certainly be found to contain more species of *Glomeris*

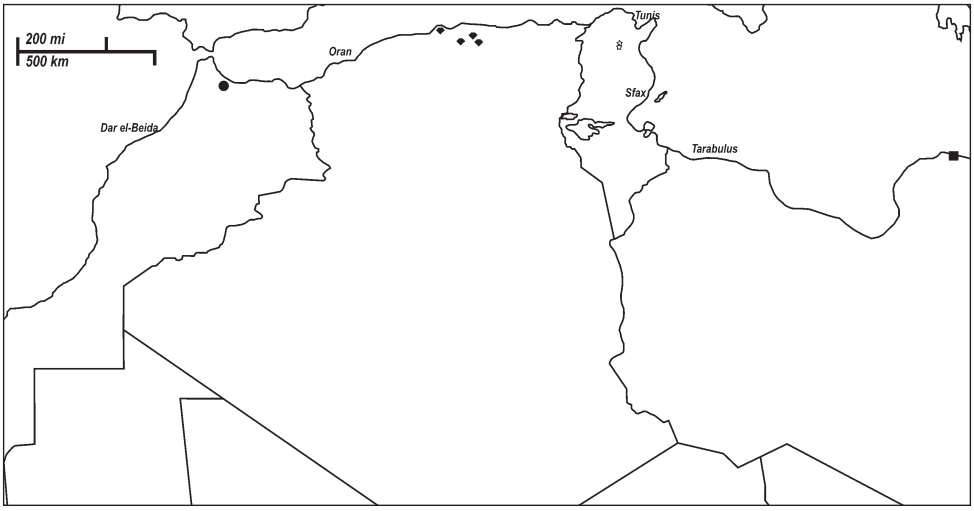

Figure 29. A map showing the distribution of *Glomeris brolemanni* (filled circle), *G. troglokabyliana* (filled diamond), *G. colorata* (open star) and *G. monostriata* (filled square).

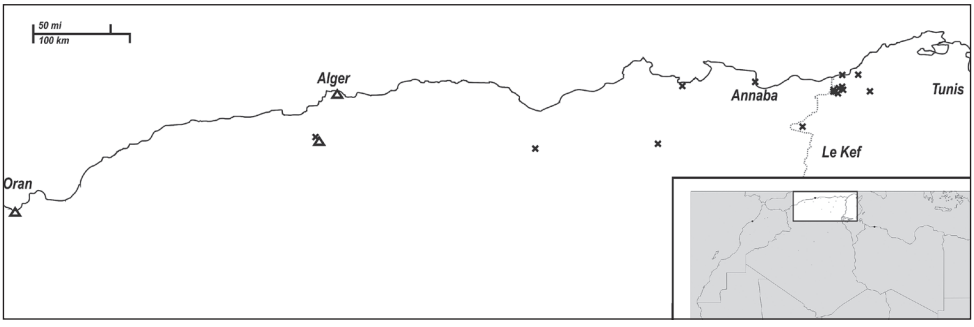

Figure 30. A map showing the distribution of *Glomeris sublimbata* (cross) and *G. flavomaculata* (open triangle).

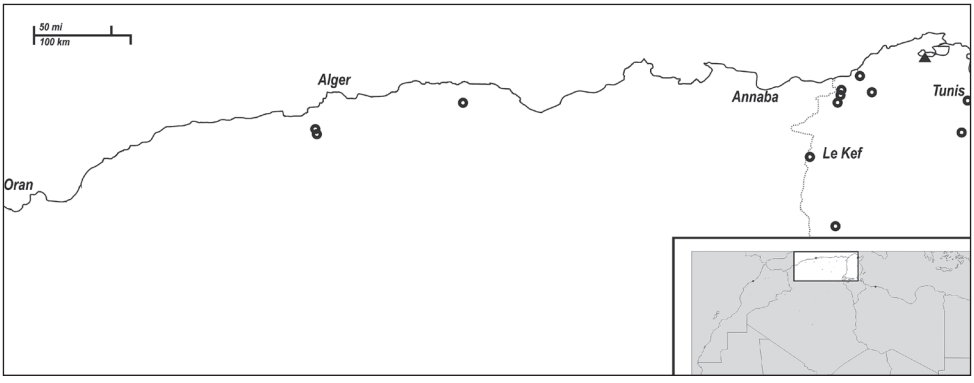

Figure 31. A map showing the distribution of *Glomeris punica* (open circle) and *G. carthaginiensis* (filled triangle).

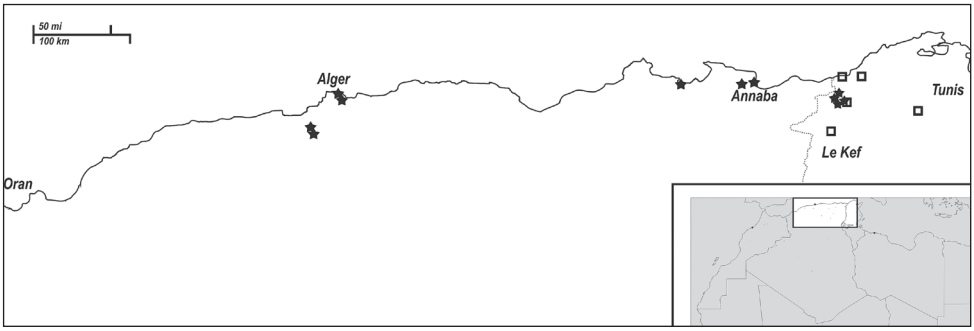

Figure 32. A map showing the distribution of *Glomeris mohamedanica* (open square) and *G. klugii* (filled star).

than just *G. brolemanni*. In addition, the discovery of *G. monostriata* sp. n. in Libya hints that this country might well harbour a richer fauna of *Glomeris*, particularly in caves. Only the relatively small country of Tunisia can claim to be fairly adequately prospected.

Genetic investigations, e.g. allozyme analyses which have been very successfully applied to the study of European *Glomeris* by Hoess & Scholl (1999), might provide further insights into the taxonomy and relationships of the North African species. Scanning electron microscopy can also prove very useful in search for new characters (Golovatch & Enghoff 2003).

An updated checklist of the Glomerida in North Africa is given in Table 2, followed by a key to the species of *Glomeris* occurring in the region.

Table 2. An updated checklist of the Glomerida in North Africa (M: Morocco, A: Algeria, T: Tunisia, L: Libya).

Species	M	A	T	L
Eupeyerimhoffia algerina Brölemann, 1913		+		
Glomerellina convolvens africana Ceuca, 1988			+	
Glomeris anisosticta Brandt, 1841		+		
G. brolemanni Schubart, 1960	+			
G. carthaginiensis Schubart, 1953			+	
G. colorata sp. n.			+	
G. flavomaculata Lucas, 1846		+		
G. klugii Brandt, 1833		+	+	
G. mohamedanica Attems, 1900			+	
G. monostriata sp. n.				+
G. punica Attems, 1900		+	+	
G. sublimbata Lucas, 1846		+	+	
G. troglokabyliana sp. n.		+		

Key to the known *Glomeris* species of North Africa

1 Tegument entirely pallid, rarely only ocelli dark. Cavernicoles **2**
– Head and terga distinctly pigmented, colour pattern evident, coloration mostly vivid. Epigean **3**
2 Collum with a single transverse stria. Syncoxital horns of telopod clearly bifid (Fig. 2D, E). Libya ..... ***G. monostriata* sp. n.**
– Collum with the usual two transverse striae. Syncoxital horns of telopod surmounted with a setoid filament (Fig. 1F). Kabylia, Algeria..... ..... ***G. troglokabyliana* sp. n.**
3 Colour pattern of terga 2-11 without evident, light, paramedian spots, but with alternating light and dark transverse bands (Figs 10, 12, 24) **4**
– Colour pattern of terga 2-(6)11 with 1+1 or 2+2 more or less evident light spots (Figs 3, 4, 7, 15-17, 20-22, 26, 27) **5**
4 Coloration of caudal halves of terga distinctly marbled throughout (Figs 10, 12) ..... ***G. klugii***
– Transverse bands on terga at most only slightly marbled in contact zones (Fig. 24) ..... ***G. mohamedanica***
5 Unusually large yellowish to orange spots on tergum 6, following terga 7-11 uniformly blackish (Figs 20-22) ..... ***G. carthaginiensis***
– Spots on tergum 6 of same size as on adjacent terga **6**
6 Median spots on tergum 2 much smaller than lateral ones ..... ***G. anisosticta***
– Either both pairs of spots on tergum 2 comparable in size or lateral ones (if present) smaller than median ones 7
7 Coloration uniformly blackish, lighter spots (1+1 or 2+2) very vague, marbled (Figs 15-18)..... ***G. sublimbata***
– Background coloration brown to blackish, lighter spots more distinct..... **8**
8 Tergum 2 with a single central light spot against a black-brown background. Pygidium uniformly black-brown. Morocco ..... ***G. brolemanni***
– Tergum 2 with 2+2 light spots **9**
9 Background coloration light to dark brown, drab, pattern as in Figs 26, 27 ..... ***G. punica***
– Background coloration dark brown to blackish, pattern vivid **10**
10 Light axial stripe absent (Figs 6-8)..... ***G. flavomaculata***
– Light axial stripe present (Figs 3, 4)..... ***G. colorata* sp. n.**

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Revision of *Agathodesmus* Silvestri, 1910 (Diplopoda, Polydesmida, Haplodesmidae)

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Abstract

Agathodesmus Silvestri, 1910 includes *A. baccatus* (Carl, 1926) **comb. n.** from New Caledonia, *A. bucculentus* (Jeekel, 1986) **comb. n.** from Queensland, Australia, and *A. johnsi* **sp. n.** and *A. steeli* Silvestri, 1910 (type species) from New South Wales, Australia. *A. baccatus* and *A. bucculentus* were formerly placed in *Atopogonus* Carl, 1926 **syn. n.** The identity of the apparently congeneric *Inodesmus jamaicensis* Cook, 1896 sensu Loomis, 1969 from Jamaica is still uncertain, and *Inodesmus* Cook, 1896 remains a nomen inquirendum.

Keywords

Diplopoda, Polydesmida, Haplodesmidae, Australia, New South Wales

Introduction

Filippo Silvestri (1910) erected the polydesmidan genus *Agathodesmus* Silvestri, 1910 for a single female specimen from Australia. Because millipede taxonomy is based largely on male genitalia, the classification of *Agathodesmus* and its type species *A. steeli* Silvestri, 1910 has been uncertain for almost 100 years.

Neither Silvestri (1910), nor Attems (1914, 1940) nor Brölemann (1916) assigned the genus to a family. Hoffman (1980) placed *Agathodesmus* in Dalodesmidae Cook, 1896 (suborder Dalodesmidea Hoffman, 1980) without explanation. On the basis of

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Silvestri's brief description of non-genitalic characters, Jeekel (1985) assigned *Agathodesmus* to Haplodesmidae Cook, 1895 (suborder Polydesmidea Pocock, 1887). Jeekel later qualified his assignment, saying that *Agathodesmus* was a "potential" haplodesmid, but in the absence of males "as yet no certainty can be obtained" (Jeekel 1986, p. 46). Simonsen (1990) also placed *Agathodesmus* in Haplodesmidae, while Golovatch et al. (2009), in a revision of Haplodesmidae, excluded *Agathodesmus* from the family, arguing that its type species was a nomen inquirendum, i.e. more information was needed.

In this paper I redescribe *A. steeli* from the holotype and from recently collected, nearly topotypical males and females. A second *Agathodesmus* species is described from a site ca. 180 km from the *A. steeli* type locality. The two species are shown to be congeneric with species of *Atopogonus* Carl, 1926 in Haplodesmidae.

Materials and methods

The type locality of *A. steeli*

Silvestri (1910) reported that the *A. steeli* holotype was collected by Thomas Steel at Avoca, New South Wales (see Appendix). No additional information is on the holotype slide label (Fig. 1). At the beginning of the 20th century there were three New South Wales places called "Avoca": one in the dry southwestern corner of the State, one in the highlands west of Wollongong and one on the coast near Gosford. The latter "Avoca" is today known as Avoca Beach.

Independent evidence that the type locality is the highlands Avoca comes from records concerning Thomas Steel (1858-1925). Steel was an industrial chemist and was based in Sydney from 1893 to 1918 (Carter 1926). In his spare time Steel was a field naturalist with a taxonomic interest in Onychophora and terrestrial flatworms; he donated many specimens to the Australian Museum in Sydney (G. Milledge, pers. comm.). The Museum's collection database lists earthworms, onychophorans, terrestrial flatworms, frogs, lizards and snakes collected by Steel between 1895 and 1908

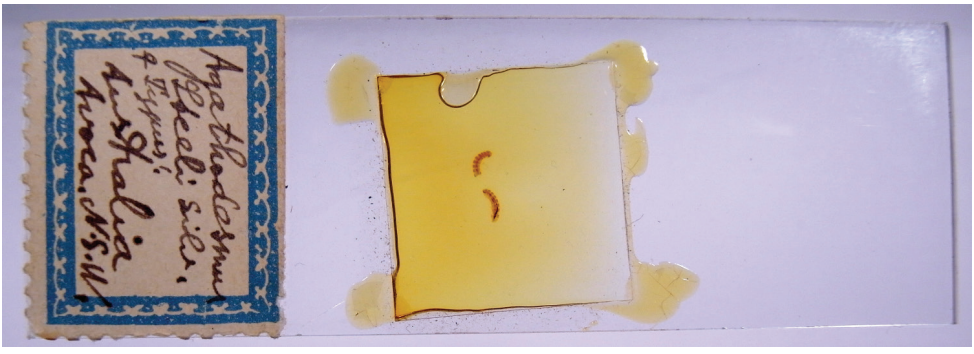

Figure 1. Holotype slide, photographed 1 May 2009. The label reads 'Agathodesmus / Steeli Silv. / ♀ Typus! / Australia / Avoca. N.S.W.'

from Bundanoon, Moss Vale, "Avoca, near Moss Vale", Wildes Meadow and Robertson. These five localities are clustered in the southern highlands of New South Wales (Fig. 2C). In Steel's time they were easily accessed by train from Sydney, and the area

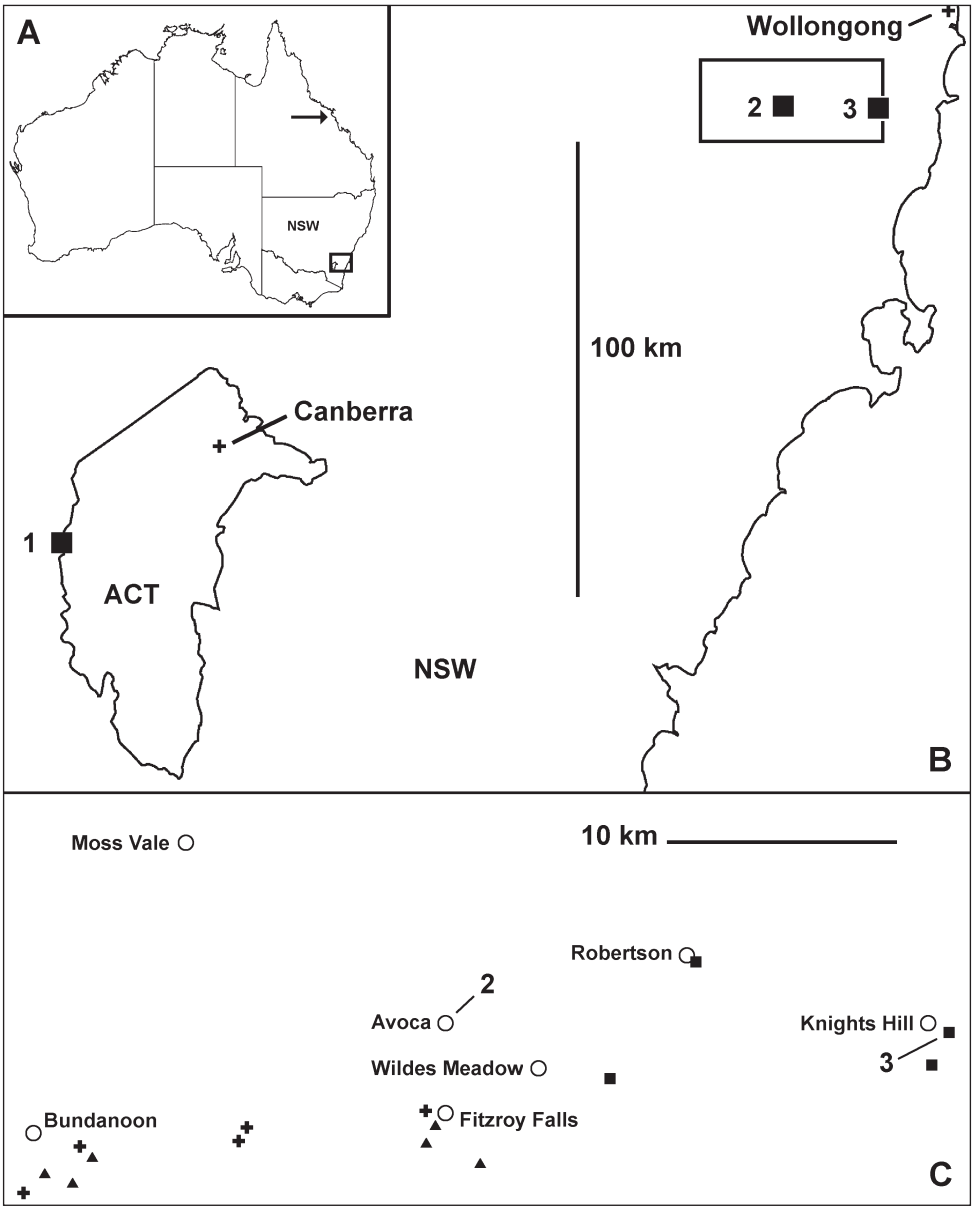

Figure 2. *Agathodesmus* localities. (A) Australia with rectangle indicating extent of map B; arrow points to type locality of *A. bucculentus*. (B) New South Wales localities (squares). 1 = Mt Aggie, *A. johnsi* **sp. n.**; 2 = Avoca, 3 = Knights Hill, *A. steeli* Silvestri, 1910; rectangle around 2 and 3 indicates extent of map C. (C) Southern highlands places (open circles), approximate sites for ANIC berlesates (triangles), 2009 search sites on sandstone and shale (crosses) and basalt (squares). Mercator projections.

had been popular with rail tourists since the 1880s (Garran 1886). There are no Steel collections in the Australian Museum from either of the other two "Avoca" localities in New South Wales (G. Milledge, pers. comm.)

The date of the *A. steeli* collection is unknown, but the Australian Museum collection database lists a terrestrial flatworm collected by Steel at Avoca in February 1905, and a leech, an onychophoran and flatworms collected by Steel at Avoca in January 1907. Both dates are consistent with the 1910 date for Silvestri's description. I have been unable to locate any correspondence between Steel and Silvestri, nor have I found any other information indicating how Silvestri acquired Steel's specimen.

Fig. 2C shows that Avoca (a named locality, not a town) is only ca. 4 km and 14 km, respectively, from the Steel localities Wildes Meadow and Moss Vale, and only 4 km from Fitzroy Falls, a tourist destination that was as well known by that name in Steel's time (Garran 1886) as it is today. It is likely, then, that the place name "Avoca" as used by Steel refers to a small area, perhaps only a few square kilometres.

2009 search for *A. steeli*

The Avoca locality today is cleared farmland on a small patch of Tertiary basalt (Fig. 9 in Bowie 2006). Although closed rainforest grew on basalt further to the east, the isolated Avoca basalt patch is thought to have carried open eucalypt forest, not rainforest, prior to clearing in the mid- to late 19th century (K. Mills, pers. comm.; Fig. 3.1 in Mills and Jakeman 1995). Thomas Steel may have collected *A. steeli* in an intact forest remnant at Avoca, or among logs and other woody residues of clearing operations.

On 6 and 7 April and 14 May 2009, I searched for *A. steeli* at the forested places near Avoca marked in Fig. 2C. I looked under stones, under loose bark on fallen trees, in and under rotting wood on the ground, and in fallen leaf and bark litter.

The five April sites carried open eucalypt forest on soils derived from shale and sandstone. These soils are relatively infertile and there is a large area of never-cleared forest on shale and sandstone south and west of Avoca. Spirobolida, Spirostreptida and paradoxosomatid Polydesmida were abundant at the five sites, with scattered occurrences of dalodesmid Polydesmida, Siphonophorida and Polyzoniida. I saw no Polydesmida in the *A. steeli* size range (ca. 6 mm long) other than early-stadium juvenile paradoxosomatids and dalodesmids.

The four May sites were all on basalt and carried either closed rainforest or tall eucalypt forest with a variably dense understorey of small trees. Uncleared forest on fertile basalt soil is rare in the area, and the remnants I searched have survived largely because the ground under the trees is too stony for farming. The millipede fauna appeared to be the same at the basalt sites as at the sandstone and shale sites, but the dalodesmid *Orthorhachis christinae* Mesibov, 2008 was noticeably more abundant. I found 11 adults and four juveniles of *A. steeli* in a single rotting log in eucalypt forest at Knights Hill, ca. 20 km east of Avoca. No other small, adult Polydesmida were seen at the basalt sites.

Other specimens

The Australian Museum in Sydney holds many millipede samples from New South Wales, mostly sorted to Order or below. As part of a paradoxosomatid mapping project in 2006-07 (Mesibov 2008), all samples sorted to Polydesmida were examined by Cathy Car (Charles Sturt University) or myself. We sorted these further to Dalodesmidae, Paradoxosomatidae and "other". Among the latter samples I found specimens of a second *Agathodesmus* species collected in 1966 from the Brindabella Ranges west of Canberra, at a site ca. 180 km west and south of Avoca (Fig. 2B).

The Australian National Insect Collection in Canberra holds a small number of unsorted samples obtained from Berlese extraction of forest litter from the area I searched (Fig. 2C). I examined these samples but found no *Agathodesmus*.

Note on geography

The new *Agathodesmus* species described below was found on the summit of Mt Aggie. According to the Australian Museum database, Mt Aggie is in the Australian Capitol Territory, which is embedded within the much larger Australian state of New South Wales (Fig. 2B). The Commonwealth of Australia gazetteer (searchable online at http://www.ga.gov.au/place-name/) locates Mt Aggie in both the Australian Capitol Territory and New South Wales, because the mountain straddles the border between the two, and the border crosses the summit. The new species undoubtedly occurs on both sides of the border on Mt Aggie, and for practical reasons is here regarded as a New South Wales species.

Specimen treatment

"Male" and "female" in the text refer to stadium VII individuals unless otherwise indicated. Specimens are stored in 80% ethanol in the Australian Museum. Some specimens were cleared in 80% lactic acid, then temporarily mounted in 60% lactic acid for optical microscopy. SEM images were acquired digitally using an FEI Quanta 600 operated in high-vacuum mode; alcohol-preserved individuals and body parts were air-dried before sputter-coating with gold.

Abbreviations:

ACT Australian Capitol Territory
AM Australian Museum, Sydney
MCSN Museo Civico di Storia Naturale "Giacomo Doria", Genova
NSW New South Wales.

Results

Order Polydesmida Pocock, 1887
Suborder Polydesmidea Pocock, 1887
Haplodesmidae Cook, 1895

Agathodesmus Silvestri, 1910

Agathodesmus. Silvestri 1910:362. Attems 1914:282, 1940:487. Brölemann 1916:547,587. Jeekel 1971:310; 1982:11; 1983:146; 1985:50,51; 1986:46. Hoffman 1980:184. Simonsen 1990:57. Golovatch et al. 2009:2.

Atopogonus. Carl 1926:386. Attems 1940:477. Verhoeff 1941:406. Jeekel 1971:314, 1984:88, 1986:46. Hoffman 1980:186, 1999:480. Simonsen 1990:57. Golovatch et al. 2001:185, 2009:2,44. **New synonymy.**

Type species. *Agathodesmus steeli* Silvestri, 1910, by original designation; of *Atopogonus*, *A. baccatus* (Carl, 1926) **comb. n.**, by monotypy.
Other included species: *A. bucculentus* (Jeekel, 1986) **comb. n.**, *A. johnsi* **sp. n.**

Diagnosis. Small Polydesmida with head and 19 or 20 rings; body not curling in spiral; head and telson facing downwards; metatergites with numerous tubercles of different sizes, the largest sometimes bearing a single seta; ring 2 tergite extended laterally, basally and anteriorly, and edged with large tubercles; no paranota on posterior rings, sometimes replaced by short row of large tubercles just above leg bases; gonopod with neither cannula nor prostatic groove, telopodite consisting of more or less cylindrical basal portion with broad, flattened structure arising posterodistally on basal portion of telopodite and bent basally or basolaterally.

Agathodesmus steeli Silvestri, 1910

Figs 1, 3A-D, 4A-D, 5A, 5B, 6A-C, 7A

Agathodesmus steeli. Silvestri 1910:362. Attems 1914:283, 1940:488. Chamberlin 1920:137. Jeekel 1971:310, 1985:50. Golovatch et al. 2009:3.

Holotype. Female, permanently mounted on microscope slide in two pieces, with a break between rings 9 and 10 (Figs 1, 3A). Avoca, NSW, Australia, Thomas Steel, date not known. In MCSN.

Paratypes. None designated.

Other material examined. 7 males, 4 females, 1 stadium VI female, 2 stadium V females, 1 stadium IV female, Knights Hill, NSW, 34°37'07"S 150°42'38"E ±25 m, 720 m, 14 May 2009, R. Mesibov and T. Moule, wet eucalypt forest, AM KS107964 (three males, two females dissected).

Diagnosis. Head + 19 rings; gonopod telopodite with distal portion directed basally and slightly laterally near origin and with broad lateral branch apically expanded and divided into three anterobasally curving lobes.

Description. The original description (Silvestri 1910) is quoted in the Appendix. What follows is based on my examination of both the holotype and the Knights Hill material.

Adult with head + 19 rings (Fig. 4A). Live and freshly preserved adults pale with faint reddish pigmentation dorsally; in some individuals, pigment concentrated in transverse band at rear of metazonite. Male/female approximate dimensions: length

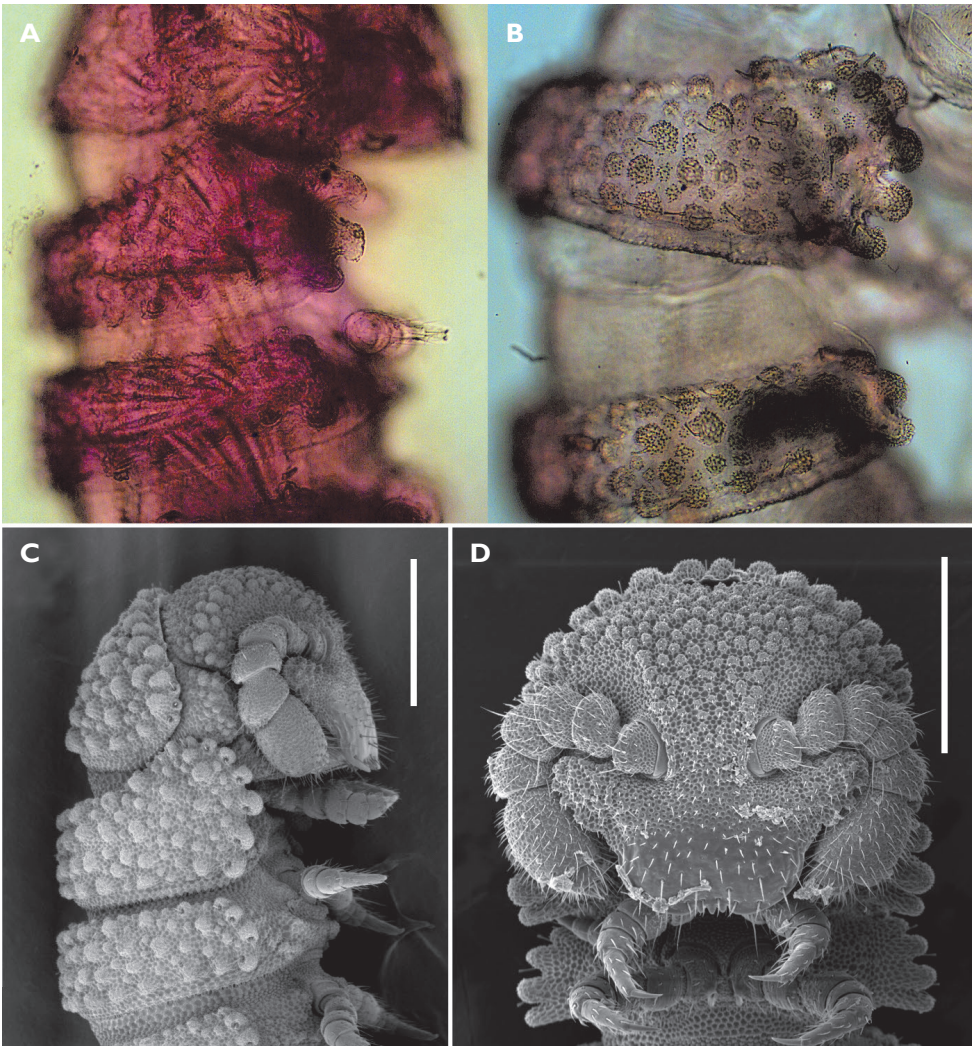

Figure 3. *Agathodesmus steeli* Silvestri, 1910. (A)-(C) Right lateral views of anterior end; (A) female holotype, (B) female (cleared specimen), (C) male. (D) Male, ventral view of head. (B)-(D) ex AM KS107964. (A), (B) to same unknown scale; scale bars in (C), (D) = 0.25 mm.

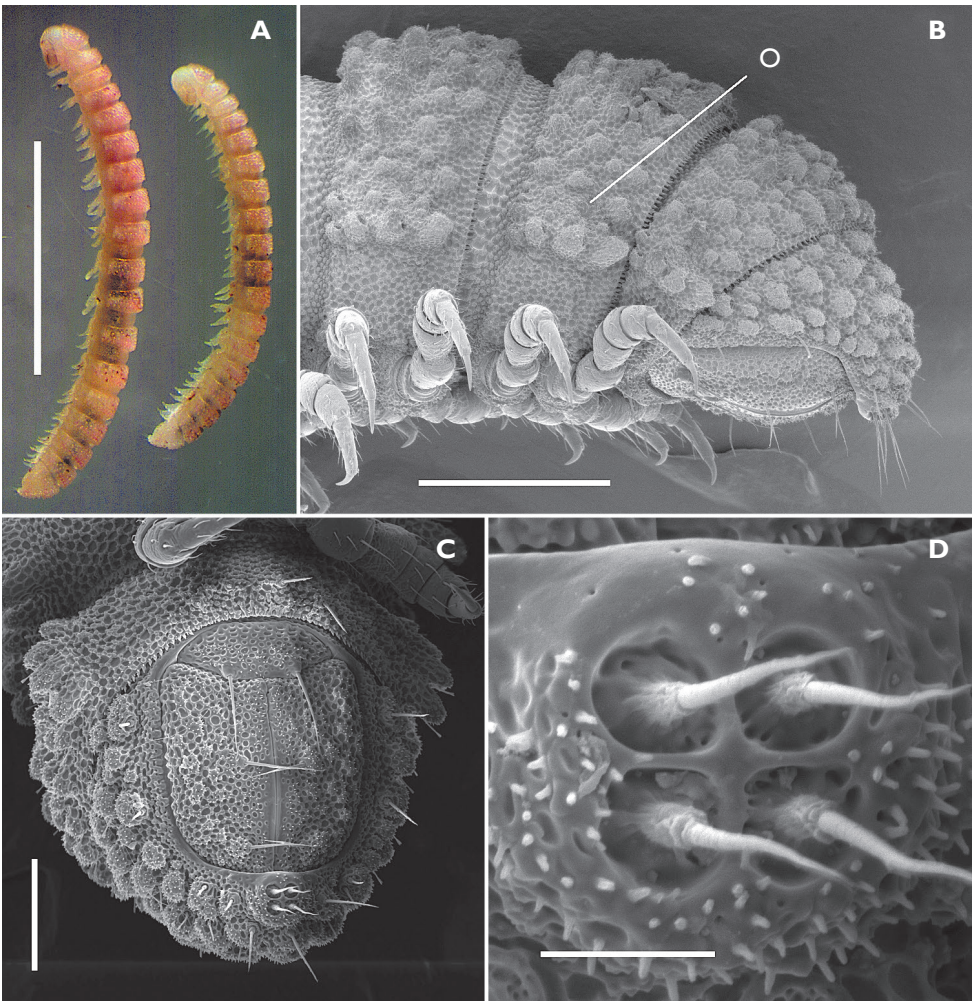

Figure 4. *Agathodesmus steeli* Silvestri, 1910, ex AM KS107964. (A) Female (left) and male (right); red colour is imaging artifact. (B) Male, left lateral view of posterior end; o = ozopore area. (C) Male, ventral view of telson. (D) Enlargement of (C) showing spinnerets. Scale bars: (A) = 2.5 mm, (B) = 0.25 mm, (C) = 0.1 mm, (D) = 0.02 mm.

4.5/5.5 mm, maximum width with paranota 0.5/0.6 mm, midbody vertical diameter 0.4/0.4 mm. Head (Figs 3C, 3D) about as wide as collum, overall body width almost uniform, tapering only slightly posteriorly from collum. Head facing downwards (Fig. 3C), with clypeus, frons and ventral part of vertex almost parallel to substrate and only slightly convex. Antenna (Fig. 3D) short, stout, clavate, held close to head, antennomeres 2 and 3 lying in broad, shallow excavation on head; antennomere 6 widest and longest; antennomeres 2-5 about equal in length, decreasing slightly in diameter from 5 to 2. Collum with slightly convex anterior margin and broadly convex posterior margin; corners rounded (Fig. 3C). Ring 2 tergite largest, extending basally, later-

ally and anteriorly well below collum corner (Figs 3A, 3B, 3C). Ring 2 and 3 tergites edged with 5-6 and 4 large tubercles, respectively (Figs 3A, 3B, 3C); posterior rings, including apodous ring 18, with row of 4 large tubercles just above leg bases forming all or part of lateral extension of metatergite, the anteriormost tubercle smaller than the posterior 3. Prozonites sharply demarcated from metazonites (Figs 3C, 4B, 6C). Ozopore (Fig. 4B) very small, not raised, in small, non-tuberculated area just above middle of group of 4 larger tubercles forming lateral metatergal extension; pore formula 5, 7, 9, 10, 12, 13, 15-18. Sternites on diplosegments (Fig. 5A) longer than wide, not setose, with distinct longitudinal and transverse impressions. Legs short, stout; relative podomere lengths tarsus>(prefemur, femur)>(postfemur, tibia); claw large, about two-thirds tarsus length. Spiracles not evident. Telson facing downwards (Fig. 4B), anal valves parallel to substrate and almost flat. Hypoproct trapezoidal (Fig. 4C); spinnerets in square array (Figs 4C, 4D); spinneret setae with single, low sheath, each seta in deep, walled depression.

Integument richly and densely sculptured (Figs 3D, 4C, 5A, 5C, 6A-C, 7A, 7B). Most of body covered with cuticle raised in cellular mesh of narrow folds, often with minute bumps (adorned with even smaller bumps) at or near fold junctions. Integument raised further as tubercles (Fig. 6A) of varying sizes on head, collum, tergites, metatergites and telson, the largest tubercles forming paranotum-like extensions on posterior rings; tubercles and some other parts of integument with minute, finger-like projections (Figs 4D, 6A, 6B), often arising along 'mesh-cell' boundaries. Cell boundaries at rear of metazonite extended as lappets, forming secondary limbus above primary limbus of uniform, triangular elements (Fig. 6C). Setae of normal type on legs and some other surfaces; a bisegmented seta with flattened, expanded tip (Fig. 6B) on each 'paranotum' tubercle and in association with some dorsal tubercles.

Male with gonopore opening at tip of cylindrical projection about 1/3 the length of leg 2 coxa, arising distomedially on the coxa. First legs somewhat swollen (Fig. 3C), no other anterior legs enlarged; neither sphaerotrichomes nor brush setae on any legs. Leg 7 bases well separated; leg 6 bases slightly separated, with a pair of short, rounded projections between coxae. Gonopod aperture oval (Fig. 7A), rim a little raised laterally. Gonocoxae (Fig. 7A) occupying full width of aperture; tapering a little distally; with mesh-like integumental sculpture and without setae; firmly joined medially near distal end. Telopodite (Fig. 7A) short, compact, when retracted reaching leg 7 base; broadly joined to gonocoxa (Figs 5B, 7A); no trace of cannula or prostatic groove; no integumental sculpturing; divided into more or less cylindrical basal portion and flattened distal portion. Basal portion of telopodite with blunt, basally directed projection arising posteromedial to junction with gonocoxa; portion terminating in flat, rounded tab bending posteriorly; with a few short setae on basal half of posterior surface of portion and three large setae in a row on lateral edge of posterior surface of terminal tab. Distal portion of telopodite a large, flattened structure arising on posterior surface of basal portion of telopodite just below terminal tab; curving basally and slightly laterally; divided near base into narrow medial branch, flattened apically with minute, spine-like protrusions on posterior and medial surfaces, and much larger lateral branch, the latter

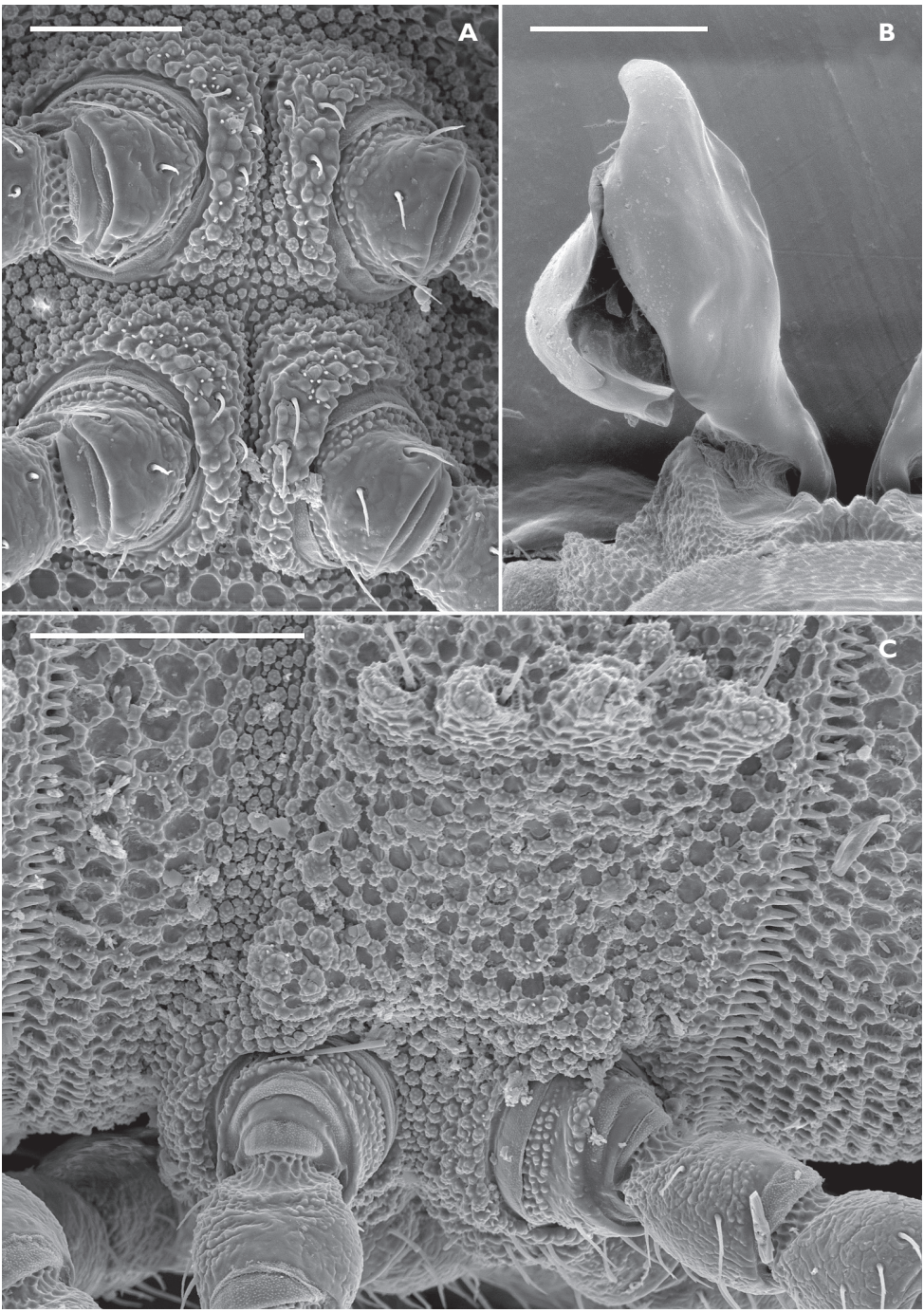

Figure 5. *Agathodesmus steeli* Silvestri, 1910, ex AM KS107964. (A) Male midbody sternite (anterior towards top). (B) Anterior view of extended left gonopod. *Agathodesmus johnsi* **sp. n.**, ex AM KS94156. (C) Left ventrolateral view of male midbody ring (anterior towards left); no spiracles are evident above leg bases. Scale bars: (A) = 0.5 mm; (B), (C) = 0.1 mm.

much expanded, curving anterobasally and divided by two deep notches into three broad, rounded lobes (Figs 5B, 7A).

Female longer and more robust than male (Fig. 4A); epigynum inconspicuous, posterior margin barely raised; cyphopods not examined.

Distribution and habitat. Known so far from eucalypt forest (historically in the case of Avoca) at two localities ca. 20 km apart in southeastern New South Wales

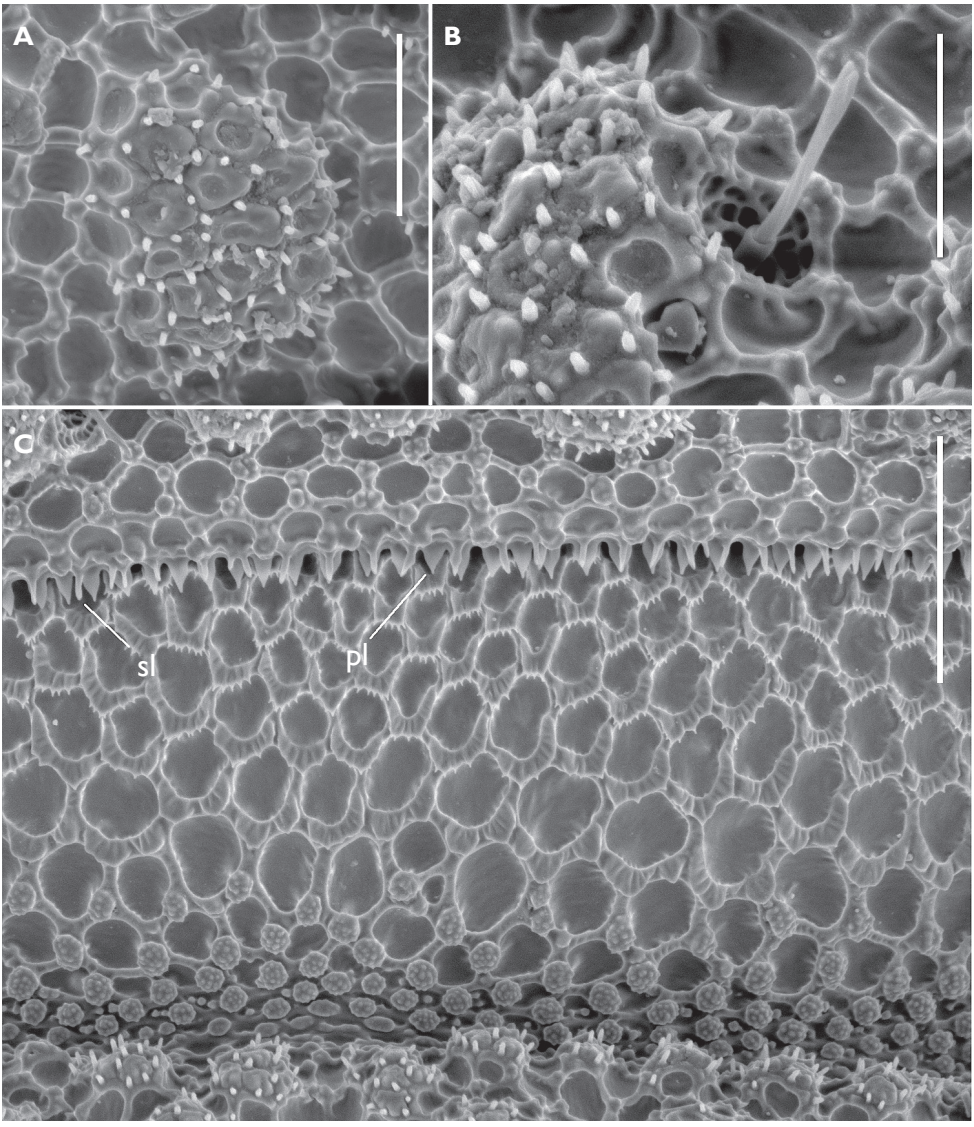

Figure 6. *Agathodesmus steeli* Silvestri, 1910, female ex AM KS107964. (A) Tubercle on midbody metatergite. (B) Bisegmented seta adjoining tubercle on midbody metatergite. (C) Dorsal view of midbody prozonite; limbus on next anterior ring at top, edge of metazonite at bottom; pl = primary limbus element, sl = secondary limbus element. Scale bars: (A) = 0.025 mm, (B) = 0.02 mm, (C) = 0.05 mm.

(Figs 2B, 2C). Both sites are above 700 m with annual rainfall probably >900 mm, in a temperate climate with cool winters. At the Knights Hill site, the 15 *A. steeli* specimens were found in narrow spaces in part of a large, moist, well-rotted log, either a *Eucalyptus* species or *Acacia melanoxylon*. Also in that part of the log were Siphonophorida, Symphyla, *Cryptops* sp. centipedes, fly and beetle larvae and terrestrial isopod crustaceans.

Remarks. Live *A. steeli* are very slow-moving and do not curl up, even when disturbed. Unlike adults of the morphologically, ecologically and behaviourally similar species of *Asphalidesmus* Silvestri, 1910 (Mesibov 2002, 2009), *A. steeli* adults are not heavily encrusted with soil particles.

The apparent absence of well-defined spiracles in *A. steeli* is remarkable. I have so far been unable to detect spiracles either with light microscopy (cleared specimens) or scanning electron microscopy (see also Fig. 5C). A histological study is needed to determine whether the tracheal system is also modified from the norm in Polydesmida.

Agathodesmus johnsi Mesibov, sp. n.

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Figs 5C, 7B

Holotype. Male. Mt Aggie, Brindabella Ranges, ACT, Australia, 35°27'S 148°46'E, 5000', 24 August 1966, P.M. Johns, snow sclerophyll, AM KS107965.

Paratypes. 12 males, 12 females, details as for holotype, AM KS94156 (two males dissected).

Diagnosis. Head + 19 rings; gonopod telopodite with distal portion directed laterally near origin and with broad lateral branch without notches, apically tapering and curving basally rather than anterobasally.

Description. Colour uniformly light yellow-brown after long preservation. Males and females as for *A. steeli* in all details so far noted, including apparent absence of spiracles (Fig. 5C), but male gonopod telopodite (Fig. 7B) with more short setae on posterior surface of basal portion, terminal tab narrower and less bent posteriorly, and distal portion directed laterally near base rather than posterolaterally, with narrow medial branch curving to lie against broad lateral branch, the latter undivided, curving basally and tapering to bluntly rounded tip.

Distribution and habitat. The only known locality is the summit of Mt Aggie at ca. 1500 m, where according to the collector, "The site was in scrubby high altitude *Eucalyptus*, a few bits of snow were around and the ground was quite damp" (P.M. Johns, in litt.).

Etymology. Adjective, genitive singular, for the collector Peter M. Johns.

Figure 7. Ventral views of retracted male gonopods. (A) *Agathodesmus steeli* Silvestri, 1910, ex AM KS107964. (B) *Agathodesmus johnsi* **sp. n.**, ex AM KS94156. Scale bars = 0.1 mm.

Discussion

Identification of *A. steeli*

The *A. steeli* type is mounted on its side and has evidently degraded over 100 years; not all of its characters are clearly visible. However, the type agrees with adult Knights Hill females in size, number and shape of rings, orientation of head and telson, and sizes and shapes of antennomeres and podomeres. More importantly, both the type and the Knights Hill specimens have variably sized tubercles with microsculpture, bisegmented setae, 5-6 large tubercles edging the ring 2 tergite (Figs 3A-C) and paranotum-like, four-tubercle lateral extensions on rings 3-18.

The Knights Hill specimens are clearly in the same genus as the type. It is still possible that they are not conspecific with *A. steeli*, which was collected ca. 20 km to the west in forest habitat lost many years ago. If the Knights Hill form also occurs in the remnant forests south and west of Avoca, where so far no *Agathodesmus* specimens have been found (Fig. 2C), I would be more confident in its identification with *A. steeli*.

It is curious that Silvestri (1910; see Appendix) noted setae arising laterally in the type, but did not record the more obvious fact that the lateral extensions and the ring 2 tergite have lobed margins.

Agathodesmus and *Atopogonus* as synonyms

As indicated in the *Agathodesmus* diagnosis (above), *A. johnsi* and *A. steeli* share several non-genitalic apomorphies with the two species described under *Atopogonus.* All four species also have inconspicuous ozopores located in non-tuberculated 'clear' zones low on the metatergites (Fig. 4B; Fig. 24 in Carl 1926; Jeekel 1986, p. 47). The most striking similarities, however, are in details of gonopod telopodite structure, as seen in Figs 8A-8E. These include a rounded terminal tab on the basal portion with three long setae on the posterolateral surface, and the division of the distal portion by notches into lobes in *A. baccatus*, *A. bucculentus* and *A. steeli*. The similarity in telopodite structure of the last two species is particularly striking (compare Fig. 7A with Figs 8D and 8E), and justifies placing them in the same genus.

Like *Agathodesmus*, the pyrgodesmid genus *Poratia* Cook and Cook, 1894 contains species with either 19 or 20 body rings (Golovatch and Sierwald 2001). Adis et al. (2001) suggested that the 19-ringed *Poratia digitata* (Porat, 1889) form could have evolved by neoteny from a larger, 20-ringed ancestor. Similarly, the 19-ringed ancestor of the miniscule *A. johnsi* and *A. steeli* might have evolved from a 20-ringed lineage represented today by the larger *A. baccatus* and *A. bucculentus*.

Family placement of *Agathodesmus*

Carl (1926) assigned his *A. baccatus* to Rhachidesmidae Carl, 1903. The remarkable lack of both a cannula and a prostatic groove inspired Verhoeff (1941) to establish Atopogonidae Verhoeff, 1941 for this species within the superfamily Rhachidesmidea Verhoeff, 1941, which also included Rhachidesmidae. Hoffman (1980) regarded *Atopogonus* as a genus of uncertain family position within the suborder Polydesmidea, but Jeekel (1986) placed it in Haplodesmidae. Hoffman (1999) agreed, but nevertheless felt that "the gonopods present a singular and highly disjunct pattern that invites taxonomic recognition at a level no less than subfamily (or family)" (p. 483). Golovatch et al. (2009) were unwilling to distinguish *Atopogonus* in this way, and listed it as one of six genera in Haplodesmidae after a careful revision of the family.

Here I follow Golovatch et al. (2009) in leaving *Atopogonus*, now synonymised with *Agathodesmus*, in Haplodesmidae. A haplodesmid character state demonstrated here for *A. johnsi* and *A. steeli* is bisegmentation of setae on the tergites (Golovatch et al. 2009); whether the other two described species in the genus have bisegmented setae is yet to be determined.

The *Inodesmus* problem

The name *Agathodesmus* may fall into synonymy with *Inodesmus* Cook, 1896 if "an intriguing and very difficult problem" (Hoffman 1999, p. 483) can be resolved. The problem has been briefly discussed by Jeekel (1986) and Hoffman (1999). Here I explore the problem in more detail.

In his self-published journal *Brandtia*, O.F. Cook added the new genus *Inodesmus* to Comodesmidae Cook, 1896 with the following words (Cook 1896b, p. 25):

> *From a cave in Jamaica I have specimens of a genus related to* Comodesmus.
>
> *Genus* Inodesmus, nov.
>
> *Differing from* Comodesmus *in the somewhat more slender, moniliform body, obsolete carinae, more projecting last segment, and normal pore-formula, the pores located in shallow depressions in the lateral middle of the segments, not in front of the middle as in* Comodesmus. *The only known species,* I. jamaicensis, *is about equal in size to* Comodesmus lanatus, *and is lighter brown in color, but may be faded.*

Since Cook assigned *Inodesmus* to Comodesmidae Cook, 1896 and compared it with the the type species of *Comodesmus* Cook, 1896, it is worth examining what Cook wrote about these taxa. I have corrected minor spelling and typographical errors in the following extracts:

Family Comodesmidae, new.

The type of this family is a small, reddish-brown, subcylindrical form, very rare, and also inhabiting the denser parts of the forest [in Liberia]. *The pore formula is unique: 5, 7, 9, 12, 15, 17, 18. The pores are located in the front part of the posterior subsegments. The dorsal surface is beset with conic piliferous granules, giving a woolly appearance. The last segment is scarcely produced beyond the anal valves, but is rounded off at apex as in many Iulidae. The head is not concealed by the first segment, which is narrower than the second and somewhat included between the carinae of the latter, much as in* Scytonotus granulatus *(Say)*. (Cook 1896a, p. 415)

Comodesmus lanatus.
Antennae distinctly clavate; last segment decurved, the immediate apex small, projecting, truncate; lateral carinae present only as a longitudinal row of large tubercles, above which the tubercles are gradually smaller; length 8 mm., width 1 mm. (Cook 1896c, p. 258)

The location of the types of *I. jamaicensis* Cook, 1896, if they still exist, is not known. It is particularly ironic that the types may have been lost, considering that Cook understood the value of type specimens:

The importance of preserving type specimens with special care is now recognized throughout the scientific world, and where specific types are lacking, naturalists are endeavoring to supply their place by specimens collected in the original localities. This may be taken as a general admission of the obvious fact that purely descriptive methods are generally insufficient for scientific accuracy and need to be supplemented by actual specimens if correct identifications are to be permanently assured. (Cook 1900, p. 481)

Nearly 40 years after the establishment of *Inodesmus*, H.F. Loomis (1934) described another species in the genus from a set of females collected in Dutch Guiana (now Suriname). At the same time Loomis synonymised the monotypic *Lasiodesmus* Silvestri, 1908 with *Inodesmus*. There were now three species in *Inodesmus*: *I. jamaicensis* (Jamaica), *I. peduncularis* Loomis, 1934 (Suriname) and *I. caraibicus* Silvestri, 1908 (Puerto Rico). Discussing the new synonymy, Loomis wrote

After comparing the present species, from a generic standpoint, with Silvestri's description of Lasiodesmus *and with the brief characterization of* Inodesmus *Cook, there appears to be no reason for maintaining Silvestri's genus... The question of the distinctness of* Inodesmus jamaicensis *Cook and* I. caraibicus *(Silvestri) cannot be decided until comparison is made of the types or of specimens undoubtedly similar to the types*. (Loomis 1934, p. 65)

It seems clear from these statements that Loomis had not examined the types of *I. jamaicensis*. He was confident that his *I. peduncularis* and *L. caraibicus* were conge-

neric, because he had specimens of the former and a clear, beautifully illustrated description of the latter (Silvestri 1908). However, he was also confident that both were congeneric with *I. jamaicensis*, for which he had neither specimens, nor illustrations, nor an adequate description.

Thirty years later Loomis (1964) added another species to the genus, *I. globulosus* Loomis, 1964 from Panama, with only minor differences distinguishing it from *I. peduncularis*.

It is not clear whether Cook (1896b) had examined males of *I. jamaicensis*, but we know from the original descriptions that the three species assigned by Loomis to *Inodesmus* were based on all-female samples. In the late 1960s, samples of *Inodesmus* spp. including males were collected by Stewart Peck in Jamaica and Panama. The Jamaican millipedes, from two caves, were identified by Loomis (1969) as *I. jamaicensis* and redescribed. The gonopods of the Jamaican species were very different from those of the males collected by Peck in Panama and identified by Loomis as *I. globulosus*, so Loomis (1969) transferred the latter species to a new genus, *Hypsoporus* Loomis, 1969.

There is no evidence that Loomis compared the new Jamaican specimens with types of *I. jamaicensis*, but he was confident that they were conspecific:

> *Also present* [in the Peck collection] *were both sexes of the genotype species,* Inodesmus jamaicensis*, which O.F. Cook (1896) diagnosed very briefly in erecting the genus and which species has not been reported since*. (Loomis 1969, p. 141)

> *The exceedingly brief description of this species, its type locality given merely as "a cave in Jamaica," failed to mention many of the following characters which are of importance*. (Loomis 1969, p. 144)

The other two *Inodesmus* species, *I. caraibicus* and *I. peduncularis*, have since been shown to be synonyms, like *Hypsoporus globulosus*, of the pantropical "tramp" species *Cylindrodesmus hirsutus* Pocock, 1889 (Golovatch et al. 2001). The question remains: did Loomis (1969) describe Cook's *I. jamaicensis*, or a species in a different genus?

The descriptions of *I. jamaicensis* by Cook and Loomis agree only in body length (8-9 mm) and in the position of the ozopore (near the transverse midline of the metazonite). If we assume that Cook's *I. jamaicensis* shares with his *Comodesmus lanatus* those features not said to be different, then Cook's *I. jamaicensis* appears to agree with Loomis' *I. jamaicensis* in having the dorsal surface covered with more or less conical tubercles bearing long setae, and in having the paranota of ring 2 extending slightly forward. It does not seem enough on which to base an identification, and the fact that both came from Jamaican caves is hardly relevant, since Loomis (1969) says that his specimens have no "modifications indicating restriction to cave life" (p. 141), and Cook's specimens were pigmented.

The identity question became important when it was recognised by C.A.W. Jeekel that the gonopod of Loomis' *I. jamaicensis* (Fig. 8F) closely resembled that of the two *Atopogonus* species: "it is quite obvious that *Inodesmus jamaicensis* sensu Loomis, 1969,

is a species congeneric with *Atopogonus baccatus* and the presently described species [*A. bucculentus*]" (Jeekel 1986, p. 46). However, Jeekel (1986) was not convinced that Loomis had redescribed *I. jamaicensis*, and he refrained from synonymising *Atopogonus* with *Inodesmus*.

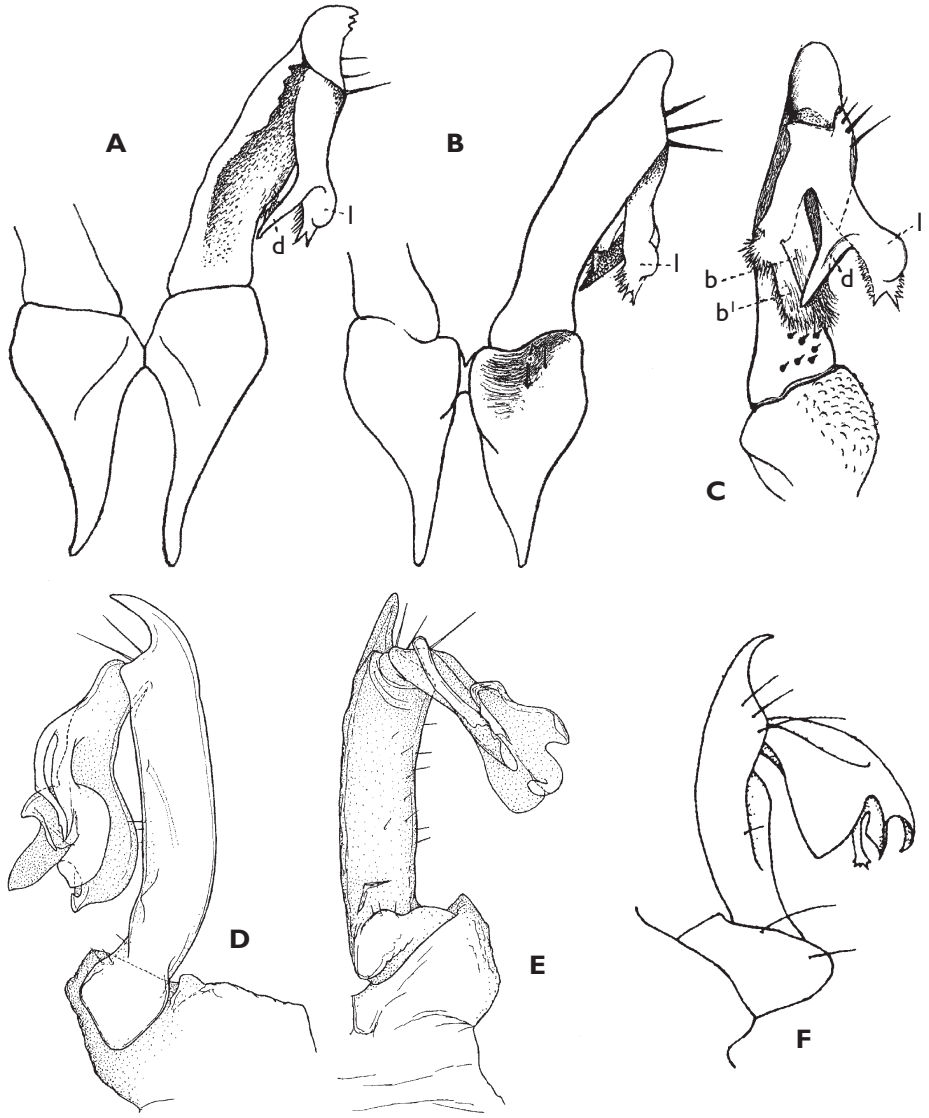

Figure 8. Gonopod drawings. (A)-(C) *Agathodesmus baccatus* (Carl, 1926) **comb. n.**, Figs 26-28 from Carl (1926); (A) posterior view with left telopodite detail, (B) anterior view with right telopodite detail, (C) left telopodite, posterolateral view. (D), (E) *Agathodesmus bucculentus* (Jeekel, 1986) **comb. n.**, Figs 16 and 17 from Jeekel (1986), reproduced with permission; (D) right gonopod, medial view, (E) left gonopod, posterior view. (F) *Inodesmus jamaicensis* Cook, 1896 sensu Loomis, 1969, Fig. 7 from Loomis (1969); right gonopod, lateral view.

R.L. Hoffman (1999) was also unconvinced by Loomis' identification. Further, he was puzzled by the geographic disjunction between Australian and New Caledonian *Atopogonus* and Jamaican *Inodesmus* sensu Loomis, 1969. Jeekel (1986) had suggested that the genus was "in essence...a continental Australian taxon" (p. 46) which might have been carried by humans to New Caledonia and Jamaica. Hoffman (1999) reported that there was a second, undescribed species of *Inodesmus* sensu Loomis, 1969 in Jamaica's Blue Mountains rainforest, and argued: "While a multiple transport of rare and localized species from the Antipodes to a single West Indian island is not impossible, it does appear improbable. How else, then, can this distribution be accounted? If natural, it can only represent an astonishing case of reliction of a formerly widespread parental lineage." (p. 483).

If Cook's *I. jamaicensis* types are indeed permanently lost, then *I. jamaicensis* sensu Loomis, 1969 could be renamed as a species of *Agathodesmus*, leaving *Inodesmus* as a nomen inquirendum. Alternatively, it could be assumed that Cook's types are lost and that Loomis' identification is correct. A neotype of *I. jamaicensis* Cook, 1896 could then be selected from among the specimens examined by Loomis (1969), as suggested by Golovatch et al. (2009), and *Agathodesmus* would become a junior subjective synonym of *Inodesmus*.

A third and more satisfying possibility would be to first make a thorough inventory of Jamaican Polydesmida, both in and out of caves. If it could be shown that the only Jamaican genus fitting Cook's description is the one represented by the species described by Loomis (1969), then the three known *Agathodesmus* species should be moved into the older genus *Inodesmus*. I suspect, however, that there are other genera of small Jamaican Polydesmida with dorsal tuberculation and an anteriorly extended ring 2 tergite, and it is possible that Cook (1896) may in fact have redescribed *Cylindrodesmus hirsutus* as *I. jamaicensis*.

In this paper I leave the *Inodesmus* problem unresolved.

Key to described species of *Agathodesmus* Silvestri, 1910

1	Head + 19 rings **2**
–	Head + 20 rings **3**
2	Gonopod telopodite with broad lateral branch of distal portion apically expanded, notched and curving anterobasally (Avoca area, New South Wales, Australia) ..... ***Agathodesmus steeli* Silvestri, 1910**
–	Gonopod telopodite with broad lateral branch of distal portion tapering to apex, without notches and curving basally (Brindabella Ranges, New South Wales, Australia) ..... ***A. johnsi* sp. n.**
3	Body width ca. 2 mm; distal portion of telopodite with toothed fringes; New Caledonia ..... ***A. baccatus* (Carl, 1926) comb. n.**
–	Body width <1 mm; distal portion of telopodite without toothed fringes; Queensland, Australia ..... ***A. bucculentus* (Jeekel, 1986) comb. n.**

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Appendix

Original description of *Agathodesmus steeli* from Silvestri (1910), pp. 362-363, with translation.

8. Gen. *Agathodesmus* nov.

(F) Corpus capite, collo, segmento anali et segmentis aliis 18 constitutum, longum, subcylindraceum, postice paullulum angustatum, carinis minimis, dorso tuberculis parvis, lateraliter breviter setigeris, instructo, in spiram contractile.

Caput manifestum, ab antennarum radicibus ad marginem externum fovea transversali excavatum, clypeo in parte postica laterali aliquantum inflato et tuberculis aucto.

Antennae breviores, articulo sexto quam ceteri multo longiore et crassiore.

Collum subellipticum, convexum, caput latitudine subaequans.

Trunci segmentum primum metazonae lateribus quam carinae segmentorum sequentium multo longioribus et latioribus, antrorsum extensis et late rotundatis.

Carinae minimae, parum supra ventris libellam orientes, transversales.

Pori in segmentis 4, 6, 8, 9, 11, 12, 14-17 (= 5, 7, 9, 10, 12, 13, 15-18 Auct.), in parte mediana laterali segmentorum, sat longe a carinarum margine laterali, sese aperientes.

Segmentum praeanale lateraliter utrimque sinuatum, parte postica crassa, apice truncato valvulas anales paullulum superans.

Sterna inter pedum basim valde angusta. Pedes breviores, articulo secundo quam tertus parum longiore.

Mas latet.

Typus:

Agathodesmus steeli sp. n.

Subochraceus.

Long. corp. mm 6, lat. segmenti noni cum carinis 0,60, sine carinis 0,46; long. antennarum 0,54, pedum 0,45.

Habitat: Avoca (Nova Hollandia: N.S. Wales. Thomas Steel legit).

8. Gen. *Agathodesmus* nov.

(F) Body composed of head, collum, anal segment and 18 other segments, long, subcylindrical, a little narrowed posteriorly, keels very small, dorsally with small tubercles, laterally with short setae, curling spirally.

Head distinct, excavated from the antennal base to the outer margin with a transverse pit, clypeus a little inflated posterolaterally and provided with tubercles.

Antennae quite short, sixth article much longer and thicker than others.

Collum subelliptical, convex, subequal to head in width.

Sides of first trunk segment metazona much longer and wider than keels of subsequent segments, extended anteriorly and broadly rounded.

Keels very small, arising just above the level of the venter, transverse.

Pores in segments 4, 6, 8, 9, 11, 12, 14-17 (= 5, 7, 9, 10, 12, 13, 15-18 of other authors), opening in median lateral portion of segments, some distance from the lateral margin of the keel.

Preanal segment sinuous on both sides, posteriorly inflated, apex truncate, extending a little past the anal valves.

Sternites between leg bases very narrow. Legs short, second article just longer than third.

Male unknown.

Type:

Agathodesmus steeli sp. n.

Almost ochre-coloured.

Body 6 mm long, segment 9 0.60 mm wide with keels, 0.46 mm without; antenna 0.54 mm long, leg 0.45 mm.

Habitat: Avoca (New Holland: N.S. Wales. Collected by Thomas Steel).