

# New light into the hormogastrid riddle: morphological and molecular description of *Hormogaster joseantonioi* sp. n. (Annelida, Clitellata, Hormogastridae)

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## Abstract

The earthworm family Hormogastridae shows a remarkable disjunction in its distribution in the Iberian Peninsula, with the *Hormogaster elisae* species complex isolated from the rest of the species. *Hormogaster joseantonioi* sp. n., a new species found in the intermediate area between the main ranges (in Teruel, Aragón), was described following the integrative approach, as it is suitable for earthworms due to their highly homoplastic morphology. The phylogenetic analysis of the molecular markers placed the new species as a sister taxon to *H. elisae*, thus showing the colonizing lineage of Central Iberian Peninsula could have originated near the *H. joseantonioi* sp. n. current range. External morphological characters revealed some degree of overlap with previously described species, but internal characters presented configurations/states unknown from other members of the family. These traits make the new species a key piece to understand the evolution of Hormogastridae.

## Keywords

Species description, earthworm, integrative taxonomy, phylogeny, disjunct distribution

## Introduction

The increasing availability of molecular and ecological data has placed the integrative taxonomy (as defined by Dayrat 2005) as a viable alternative to traditional species description. Several authors advocate its use in different animal groups (Padial and De La Riba 2010; Schlick-Steiner et al. 2010; Heethoff et al. 2011; but see Yeates et al. 2011 for iterative taxonomy instead) and particularly in earthworms (Blakemore and Kupriyanova 2010; Novo et al. 2012), whose taxonomy is in need of deep revision in the light of molecular phylogeny (Jamieson et al. 2002; Pop et al. 2003, 2007; Chang et al. 2008; Briones et al. 2009; Pérez-Losada et al. 2009, 2011; Novo et al. 2011; Fernández et al. 2012).

Fernández et al. (2014) have developed a new tool based in micro-computed tomography to study specimens in a non-destructive way which could help as an additional source of information.

Taxonomic characters traditionally used for the study of earthworms are few and sometimes present high intraspecific variability (Michaelsen 1900 and Stephenson 1930 on their global fauna; Pop et al. 2003 and Briones et al. 2009 about lumbricid earthworms). Recent findings show that cryptic diversity is common in these animals (but see critique in Blakemore et al. 2010), therefore earthworm taxonomy can particularly benefit from an integrative approach.

Novo et al. (2011) presented a molecular phylogeny of Hormogastridae (Oligochaeta, Annelida), whose taxonomy has historically been built on morphological characters, which highlighted some interesting evolutionary aspects. On one hand, hormogastrid distribution across the Western Mediterranean is biogeographically consistent, reflecting the geological events that affected the region in the Tertiary (which confirms previous studies, e.g Bouché 1972, Sbordoni et al. 1992). Two species -*Xana omodeoi* Díaz Cosin, Briones & Trigo, 1989 and the morphospecies *Hormogaster elisae* Álvarez, 1977 -, however, are found in locations far apart from the family main range in the Iberian Peninsula. While all the other Iberian species are distributed in Northeastern Spain, *X. omodeoi* inhabits Northwestern Spain and *H. elisae* is found in Central Spain (Segovia, Madrid and Guadalajara). The result is a disjunct distribution.

Novo (2010) found *Hormogaster elisae* complex to be monophyletic, and thus the likely result of a single colonisation event presumably from the North or the East of the Iberian Peninsula. There could be remaining populations of the migrating lineage in the geographic gap, which haven't been discovered yet.

On the other hand, it seems that most key characters used for hormogastrid traditional taxonomy and phylogeny (notably the shape, number and position of the spermathecae) are highly homoplastic, showing little or no phylogenetic signal across the family.



Due to its relevance for this subject, the intermediate area between the main ranges of hormogastrids in Spain has been subject to recent sampling campaigns. Both Zaragoza and Teruel (Aragón, Spain) were suitable regions as they have been poorly sampled for earthworms unlike the surrounding provinces. While no success was met in Zaragoza, a population assignable to a new species of Hormogastridae was recently found in Teruel.

This paper focuses on the description of *Hormogaster joseantonioi* sp. n. from an integrative point of view, following the example of Novo et al. (2012). The new molecular and morphological data are interpreted to gain insight into the diversification and morphological radiation of the family, with some considerations about its constituent genera.

## Materials and methods

### Earthworm specimens and sampling points

Specimens were collected by hand and fixed in the field in ca. 96% EtOH, with subsequent alcohol changes. Once in the laboratory, specimens were preserved at -20 °C.

The studied material includes 10 specimens (five mature specimens, one semimature specimen with tubercula pubertatis and four immatures) collected in a cleared holm-oak wood at the foothill of Sierra de Oriche, road A-2514 between Huesa del Común and Rudilla, Teruel (Spain) (41°0'55.68"N, 0°58'55.98"W) (Figure 1).



**Figure 1.** Map of the Iberian Peninsula showing the collection site of *H. joseantonioi* sp.n. (indicated by the white star). The northeastern hormogastrid range is shown in green, *H. elisae* range is shown in pink and *X. omodeoi* known location is indicated in yellow.

Specimens have been deposited in the Oligochaete collection of the Departamento de Zoología y Antropología Física, Universidad Complutense de Madrid (UCMLT), Spain with vouchers UCMLT 00001-00010.

Specimens available from previous studies (Novo et al. 2010, 2011, 2012) of all known hormogastrid species were used for comparison. Morphological characters include those features traditionally used for hormogastrids and other earthworms.

Molecular data generation

Total genomic DNA was extracted from ventral integument tissue samples using the DNeasy Tissue Kit (QIAGEN) with two consecutive steps of elution (70 µl of buffer). Seven molecular regions were amplified: mitochondrial subunit 1 of cytochrome *c* oxidase (COI), 16S rRNA and tRNA Leu, Ala, and Ser (16S t-RNAs), one nuclear ribosomal gene (a fragment of 28S rRNA) and one nuclear protein-encoding gene (histone H3). Primer sequences, polymerase chain reactions (PCR) and sequencing reactions are the same as in Novo et al. (2011). GeneBank accession numbers for the holo- and paragenotypes, following Chakrabarty (2010) for the markers analysed here are shown in Table 1.

Phylogenetic analyses

The new sequences were combined with all the hormogastrid information available from previous studies (Novo et al. 2010, 2011, 2012) in order to find their phylogenetic placement inside the family. *Pontodrilus litoralis* Grube, 1855, *Dichogaster saliens* Beddard, 1893, *Amyntas robustus* Perrier, 1872, *Lumbricus terrestris* Linnaeus, 1758 and *Aporrectodea trapezoides* Dugès, 1828 were used as outgroups (all the GenBank accession numbers are shown in Appendix). As hormogastrid individuals from

**Table 1.** Holo- and paragenotypes (sensu Chakrabarty, 2010) of *H. joseantonioi* sp. n., and their GenBank accession numbers. The hologenotype is shown in bold.

Specimen	Voucher	COI	16S-tRNAs	28S rRNA	H3
HRUD1	UCMLT 00001	KJ632674	KJ632684	KJ632686	KJ632688
HRUD2	UCMLT 00002	KJ632675	KJ632685	KJ632687	KJ632689
<b>HRUD3</b>	<b>UCMLT 00003</b>	<b>KJ632676</b>			
HRUD4	UCMLT 00004	KJ632677			
HRUD5	UCMLT 00005	KJ632678			
HRUD6	UCMLT 00006	KJ632679			
HRUD7	UCMLT 00007	KJ632680			
HRUD8	UCMLT 00008	KJ632681			
HRUD9	UCMLT 00009	KJ632682			
HRUD10	UCMLT 00010	KJ632683			

the same locality usually cluster together, one individual was analysed as representative per sampling site.

Sequences of each individual gene were aligned in MAFFT (Katoh and Standley 2013) with default settings and concatenated, resulting in a matrix of 2532 bp. jModelTest v. 2.1.3 (Darriba et al. 2012) was used to select the best-fit evolutionary model using the Akaike information criterion (AIC; Akaike 1973), and Bayesian information criterion (BIC; Schwarz 1978) which were GTR+I+G for COI, 16s and 28s, and HKY+I+G for H3.

Bayesian Inference (BI) of the phylogeny was estimated with MRBAYES v.3.1.2 (Ronquist and Huelsenbeck 2003) implemented in the CIPRES Science Gateway V. 3.3. (<http://www.phylo.org/index.php/portal/>). Unlinked nucleotide substitution models selected were specified for each gene fragment and the nucleotide substitution estimates were allowed to vary independently between each partition. Parameters were set to ten million generations and 10,000 trees were sampled for every 1000th generation, initiating the analysis from a random tree. After two analysis were performed 20% of the trees were discarded as burn-in, and the remaining trees were combined to find the maximum a posteriori probability estimate of phylogeny. Maximum likelihood analyses were performed with RAxML 7.2.7 (Stamatakis 2006) in the CIPRES Science Gateway with default settings, using GTR+I+G for each data partition and estimating the support for the resulting topologies by 100 bootstrap replicates.

Uncorrected pairwise differences for the mitochondrial regions were calculated between *H. joseantonioi* and the most closely related species with Arlequin 3.5 (Excoffier and Lischer 2010). To visualize the genetic distance we constructed networks with SplitsTree4 v.4.11.3 (Huson and Bryant 2006) for the more variable genes, including the former species plus *Hormogaster riojana* Qiu & Bouché, 1998 and *A. trapezoides* as outgroups. Default settings were used.

## Results

### Taxonomic results

**Phylum Annelida Lamarck, 1802**

**Subphylum Clitellata Michaelsen, 1919**

**Class Oligochaeta Grube, 1850**

**Superorder Megadrilacea Benham, 1890**

**Order Haplotaxida Michaelsen, 1900**

**Family Hormogastridae Michaelsen, 1900**

**Genus *Hormogaster* Rosa, 1887**

**Type-species.** *Hormogaster redii* Rosa, 1887.

***Hormogaster joseantonioi* Fernández Marchán, sp. n.**

<http://zoobank.org/1B7B13C0-FA56-466E-9FFE-AB985EB582BA>

[http://species-id.net/wiki/Hormogaster\\_joseantonioi](http://species-id.net/wiki/Hormogaster_joseantonioi)

**Material examined.** Holotype. Adult (UCMLT 00003), 41°0'55.68"N, 0°58'55.98"W, from a cleared holm-oak wood on the foothill of Oriche mountains, road A-2514 between Huesa del Común and Rudilla, Teruel (Spain), collectors D. Fernández Marchán and J.A. Fernández Fernández.

**Paratypes.** Nine individuals (UCMLT 00001, 00002, 00004–00010), with the same collection data of the holotype.

**Other material examined.** 16 hormogastrid species and several subspecies belonging to the UCMLT collection.

**Morphological description.** *External morphology* (Figure 2). \*Measures taken on the two only complete specimens, one being the holotype.

Length of mature specimens\*: 178–180 mm.

Maximum diameter (pre-clitellar, clitellar, post-clitellar) of mature specimens: 8–10, 9–11, 7–10 mm.

Number of segments\*: 305–369.

Weight (fixed specimens)\*: 7.05–11.57 g.

Colour: From light brown to dark chocolate brown varying between individuals, with orangeish-brown clitellum of a lighter shade on living specimens (Figure 2a). Beige with brown stripes or patches, mainly on the anterior end, with darker clitellum on fixed specimens (Figure 2b).

Prostomium prolobic, longitudinal striation on segments 1 and 2.

Closely paired chaetae; interchaetal ratio at segment 40, *aa*: 33, *ab*: 1.3, *bc*: 6, *cd*: 1, *dd*: 27. Nephridial pores in a row between chaetae *b* and *c* (very close to *b*), visible on fixed specimens as a brownish line.

Spermathecal pores at intersegments 9/10 and 10/11 at the level of *cd*.

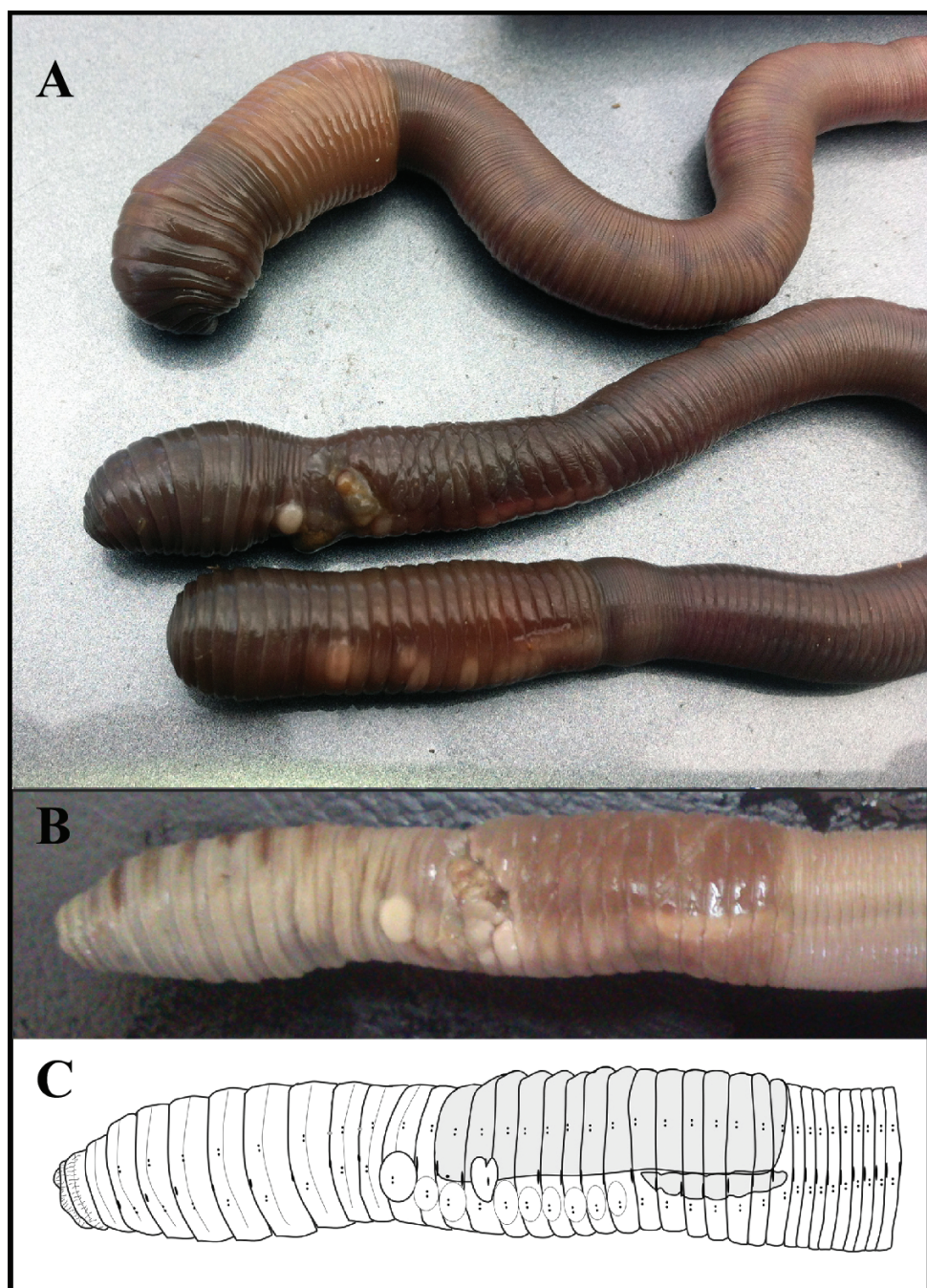
Male pores open over chaetae *ab* at the intersegment 15/16, surrounded by heart-shaped porophores which extend over most of segment 15 and at least half of 16. Female pores in segment 14 at the same level as male pores.

Clitellum saddle-shaped extending over segments (13) 14–28. Tubercula pubertatis on 1/n 22–27(1/n 28) as a continuous line. Papillae of chaetae *ab* in variable positions, usually between segments 12 and 28; papillae on 12 always showing an unusual degree of development in mature individuals, being very conspicuous both in live and fixed specimens (Figure 2a).

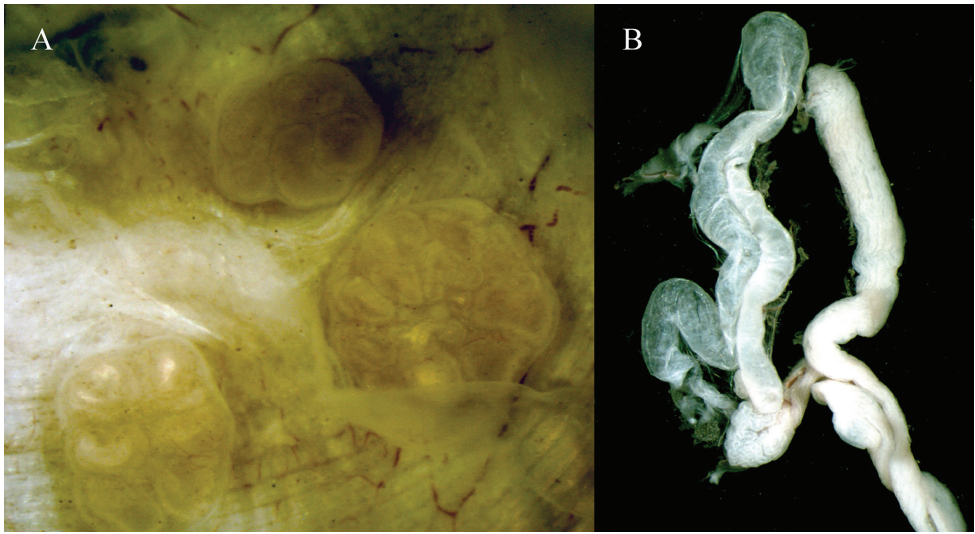
**Internal anatomy.** Funnel shaped, strongly thickened septa in 6/7, 7/8 and 8/9, septum 9/10 slightly thickened. The latter's attachment to the dorsal body wall is displaced two segments backwards, creating a mismatch between inner and outer segmentation with an internally very wide segment 9.

Last pair of hearts in segment 11. Three shiny, strongly muscular gizzards in 6, 7 and 8. Not apparent Morren's glands, even though small wrinkles exist in the oesophageal wall between segments 10 and 16.





**Figure 2.** (A) Live specimens of *H. joseantonioi* sp.n. External morphology of a fixed specimen, shown in a picture (B) and diagram (C).



**Figure 3. A)** Spermathecae in segments 9 and 10. Note the double spermathecae in segment 10 of this specimen. **B)** Nephridial bladder of segment 7.

A posterior gizzard is not well differentiated. There is a slight dilatation of the oesophagus between 14 and 16, but it lacks the muscular wall and reinforcements of a true gizzard. First section of the intestine is not dilated.

Typhlosole begins around segments 20 and 21 with seven lamellae, which around segments 26–27 increase to nine. From there they decrease gradually in number until segments 80–105, where they fuse in a single lamella. The latter extends until segments 218–230, where the typhlosole ends.

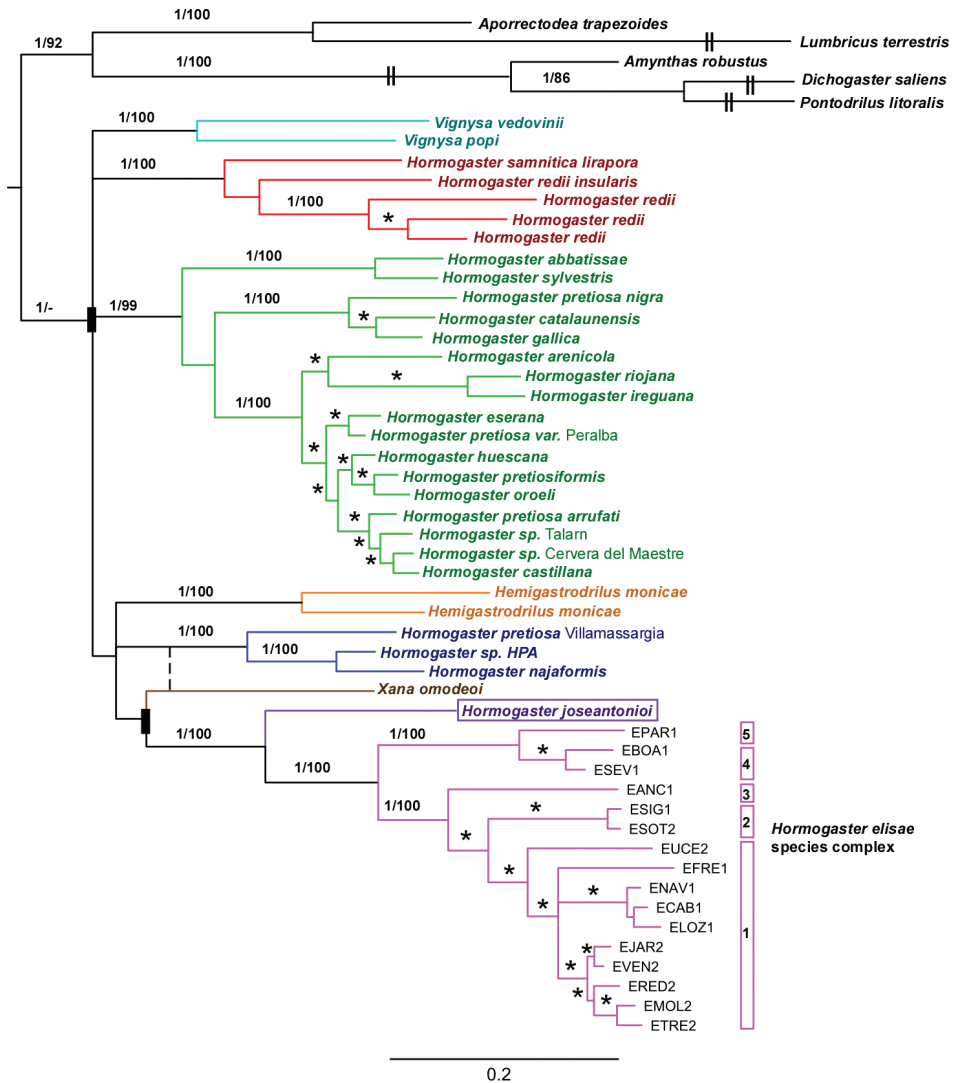
Fraying testes and iridescent seminal funnels in 10 and 11. Two pairs of voluminous, grainy seminal vesicles in 11 and 12. Ovaries and female funnels in 13, ovisacs in 14.

Two pairs of spermathecae in intersegments 9/10 and 10/11 (but apparently contained in segment 9 due to septum's backward displacement), the posterior pair bigger. They are sessile and disc-shaped, with multiple inner chambers which open to the exterior through a common pore, in the intersegments 9/10 and 10/11. Some individuals show double spermathecae (each multicameral and with own pore), either in 9/10 or 10/11 (Figure 3a).

Anterior nephridial bladders U-shaped with very close branches and no apparent cecum (Figure 3b). Bladders gradually flatten towards the end of the body, taking the usual elongated shape.

**Distribution.** Known only from its type locality.

**Habitat.** The specimens were collected at 10–20 cm deep in the soil in a cleared holm-oak wood, at the border between a dense forest of *Quercus rotundifolia* and a dryland farm. The soil had the following characteristics: 23.03% coarse sand, 8.06% fine sand, 5.33% coarse silt, 60.74% fine silt, and 2.84% clay, constituting a silty loam soil, carbon (C): 2.40%, nitrogen (N): 0.24%, C/N: 10.18, pH: 7.98. Mean annual



**Figure 4.** Bayesian inference of the phylogenetic tree on the concatenated sequence. Numbers above branches indicate posterior probability/bootstrap (of the Maximum Likelihood analysis) support values higher than 0.9/70 (shown as asterisks on terminal branches). Black rectangles show clades not recovered in both analyses (the alternative is shown with a dashed line). The cryptic species included in *H. elisae* are numbered from 1 to 5 (following Novo et al. 2010).

temperature is 12.7 °C and mean annual precipitation is 447.2 mm, as indicated by the nearest weather station (in Herrera de Los Navarros, Zaragoza-23 km away [http://www.aragon.es/DepartamentosOrganismosPublicos/Organismos/InstitutoAragon-esEstadistica/AreasTematicas/14\\_Medio\\_Ambiente\\_Y\\_Energia/ci.05\\_Clima\\_Datos\\_climatologicos.detalleDepartamento?channelSelected=ea9fa856c66de310VgnVCM2000002f551bacRCRD#section1](http://www.aragon.es/DepartamentosOrganismosPublicos/Organismos/InstitutoAragon-esEstadistica/AreasTematicas/14_Medio_Ambiente_Y_Energia/ci.05_Clima_Datos_climatologicos.detalleDepartamento?channelSelected=ea9fa856c66de310VgnVCM2000002f551bacRCRD#section1)).



**Etymology.** The species is named after Jose Antonio Fernández Fernández, father of the first author Daniel Fernández Marchán and important contributor during the sampling campaign in which this species was discovered.

**Molecular characters.** Analyses were conducted on sequences from loci COI (10 individuals), 16S (2 individuals), 28S (2 individuals) and H3 (2 individuals) of the new species, combined with similar sequences from other hormogastrid species.

The resulting Bayesian inference of the phylogenetic tree is shown in Figure 4. Its topology was congruent with that of the Maximum Likelihood inferred tree, except for the different placement of *X. omodeoi*. *H. joseantonioi* sp.n. was recovered as a monophyletic clade, with the *H. elisae* species complex as a sister clade.

Uncorrected pairwise distances for the genes COI and 16S-tRNA for *H. joseantonioi* and the species within the same clade (with *H. elisae* divided into its five cryptic species) are shown in Table 2.

## Discussion

Both morphological and molecular characters of *H. joseantonioi* sp.n. separate it clearly from all known hormogastrid species, the number of typhosole lamellae and the kind and location of the spermathecae being particularly distinctive. Those characters, while failing to resolve internal relationships within Hormogastridae, have been shown to be suitable for species diagnosis (Rota, 1993 on typhosole importance; Novo et al. 2012 on spermathecae number to separate *H. abbatissae* from *H. sylvestris*).

The species *H. riojana*, while distantly related according to molecular phylogeny, shows many similarities in morphology to *H. joseantonioi* (Table 3). However, *H. joseantonioi* differ by its lower number of lamellae in its typhosole and shorter tubercula pubertatis. Moreover it is longer and heavier. While the two species share a very similar position and shape of the spermathecae, some *H. joseantonioi* individuals show an additional spermatheca in segment 10 (on the right or left side). These cases don't seem to be teratologic, as the supernumerary spermathecae have their own pore in the body surface and contain sperm, thus being fully functional.

Other hormogastrid species possess double or multiple spermathecae, but never of the multicameral, disc shaped kind.

The geographically closest species, *H. castellana* (from Puerto Querol, Castellón), is neither morphologically nor phylogenetically closely related (Table 3).

*H. joseantonioi* sp. n. appears nested on a weakly supported clade on the phylogenetic tree, consisting in *Hemigastrodrilus monicae*, *Xana omodeoi*, *Hormogaster pretiosa* from Villamassargia, *Hormogaster najaformis* (and HPA from Omodeo, see Novo et al. 2011) and *Hormogaster elisae*. Genetic distances were high in all cases (16.47–19.08% for COI, 12.50–17.40% for 16S) according to the reference intervals given by Chang and James (2011). Aside from *H. elisae*, none of them showed significant morphological likeness to the new species, with the very different spermathecae configurations being noteworthy (Table 3).

**Table 2.** Uncorrected pairwise distances for the genes COI (below the diagonal) and 16S-rRNA (above the diagonal) for *H. joseantonioi* and the species on the same clade. XAN - *X. omdaeoi*, HPRE - *H. pretiosa*, HNAJ - *H. najiformis*, HEM - two populations of *He. monicae*. Intraspecific divergence for COI/16S is shown in the diagonal.

	HJOS	HE3	HE1	HE2	HE5	HE4	XAN	HPRE	HNAJ	HEM*	HEM**
HJOS	0.14/0	13.10	14.20	12.50	19.41	13.50	14.23	14.28	15.31	17.40	16.07
HE3	18.10	0.29/0	9.87	9.96	17.18	12.34	14.37	15.93	16.69	17.54	15.57
HE1	17.77	15.51	10.03/4.10	7.97	17.83	12.95	15.54	17.73	17.54	17.26	16.56
HE2	16.47	14.16	15.13	1.75/0.67	17.03	13.38	14.93	16.62	18.18	16.70	16.70
HE5	16.83	16.28	17.48	16.36	0.34/0	16.37	21.04	21.55	22.37	22.28	21.32
HE4	19.08	15.67	17.37	16.86	10.38	3.75/1.75	15.49	18.06	17.51	17.81	16.53
XAN	18.30	18.26	18.36	18.96	17.01	18.49	0.37/0.19	11.60	13.58	14.34	12.66
HPRE	18.61	20.17	20.34	19.74	18.92	19.52	17.76	0/2.14	10.74	16.47	13.69
HNAJ	18.92	18.39	19.77	18.19	18.64	19.17	19.92	17.31	0.10/0.18	16.69	14.86
HEM*	18.38	18.52	19.17	20.45	17.06	18.58	20.45	19.67	19.92	3.50/1.97	8.76
HEM**	18.11	18.19	18.10	17.79	16.14	16.55	18.31	19.24	18.93	17.63	6.30/2.07

**Table 3.** Comparison of the morphological characters of *H. joseantonioi* sp. n. and some of the phylogenetically closest species (*H. elisae*, *X. omodeoi* and *H. najaformis* Qiu & Bouché, 1998) plus the distantly related *H. riojana* and *H. castillana* Qiu & Bouché, 1998. N. segments: number of segments. N. typhlosole lamellae: number of typhlosole lamellae. Body length, weight and number of segments refer to adult specimens.

	<i>H. joseantonioi</i>	<i>H. elisae</i>	<i>X. omodeoi</i>	<i>H. najaformis</i>	<i>H. riojana</i>	<i>H. castillana</i>
Colour	Brownish	Colourless	Colourless	Slightly greyish	Dark brownish	Brownish grey
Clitellum	(13)14–28	(13)14(15)–26(27)28	14–26	13–31	13,14,17–27,28	1/14,15–29,1/2 30
Tubercula pubertatis	1/n 22–27 (1/n 28)	22(23)–25(26)	23–26	20–26	(20)21–27	22–28
Length (mm)	178–180	92–200	20–161	188–230	154	200–325
N. segments	305–369	205–300	190–230	395–523	243–278	320–429
Weight (g)	7.05–11.57	1.96–9.67	0.59–4.23	22.6–31.4	6.57	12.85–29.38
Spermathecae position (pores) and appearance	9 (see text) (9/10,10/11) Simple(double) Multicameral, disc shaped	9,10 (9/10,10/11) Simple Tubular	10,11 (9/10,10/11) Simple Small, globular	10,11 (10/11,11/12) Multiple Small, globular	9,10 (9/10,10/11) Simple Multicameral, disc shaped	9,10 (9/10,10/11) Simple Globular
N. typhlosole lamellae	9	5	12	15–17	15	21–23
Thickened septa	6/7,7/8,8/9, (9/10)	6/7,7/8,8/9, (9/10)	(6/7),7/8,8/9, 9/10,(10/11)	6/7,7/8,8/9, (9/10)	7/8,8/9,9/10, (10/11)	7/8,8/9,9/10, (10/11)

The *H. elisae* morphospecies was recovered as sister clade to *H. joseantonioi* sp. n. with high support. From a morphological point of view, most of their external characters overlap, except for a slightly longer clitellum and tubercula pubertatis, bigger average size and stronger pigmentation in *H. joseantonioi* sp. n. However, internal characters are very different and these species match neither in the number of lamellae in the typhlosole (five versus nine) nor in the structure of the spermathecae, which are tubular in *H. elisae* and disc-shaped and multicameral in *H. joseantonioi*. It’s worth noting that *H. elisae* shares the backwardly displaced disposition of the 9/10 septum.

Based on their phylogenetic and morphological relatedness, an origin of *H. elisae* from a common ancestor with *H. joseantonioi* sp. n. seems likely. This scenario is sensible from a biogeographical point of view, as the locality of the new species is intermediate between the ranges of *H. elisae* and the northeastern main hormogastrid range. A connection of emerged lands would have been possible from the Cretaceous-Tertiary boundary onwards (Andreweg 2002).

While *H. joseantonioi* status as a good species and its phylogenetic relationships seem quite clear, generic assignment is a more problematic matter. Novo et al. (2011) recovered the genus *Hormogaster* as paraphyletic in their molecular phylogeny, pointing out the need for a deep taxonomical revision of the family Hormogastridae, currently in preparation (author’s work in progress).

Based on its distinctive morphology and geographic range, high genetic divergence and consistent recovery as a well-defined clade, Novo (2010) suggested the *H. elisae*

species complex should be established as an independent genus. Due to the close phylogenetic position and morphological similarity of *H. joseantonioi* to this clade it could be argued they both should be included in the same genus.

At this stage it is more conservative to assign *H. joseantonioi* to the genus *Hormogaster* until the revision of the family is completed, which will allow to establish (if possible) a well-founded genera system on Hormogastridae. This work narrows the discontinuity between the North-Eastern and Central ranges of the Spanish hormogastrids. At the same time it highlights the importance of an intensive sampling of the area between Teruel and the center of the Iberian Peninsula (mainly zones of Soria and Guadalajara) to hopefully find new species along the hypothetical colonization route.

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## Appendix

**Supplementary material.** GenBank accession numbers for all sequences used in the phylogenetic analysis, including outgroups. RF: sequences provided by Rosa Fernández.

Species	COI	16S-tRNAs	28S-rRNA	H3
<i>H. castillana</i> QUE	HQ621989	HQ621883	HQ621960.1	HQ622028
<i>H. elisae</i> 3 ANC	EF653870	GQ409754.1	GQ409657.1	HQ622001
<i>H. elisae</i> 4 BOA	GQ409661.1	GQ409704.1	GQ409656.1	HQ622004
<i>H. elisae</i> 1 CAB	GQ409689.1	GQ409729.1	GQ409653.1	HQ622007
<i>H. elisae</i> 1 FRE	GQ409698.1	GQ409723.1	GQ409653.1	HQ622009
<i>H. elisae</i> 1 JAR	GQ409665.1	GQ409745.1	GQ409653.1	HQ622013
<i>H. elisae</i> 1 LOZ	EF653888	GQ409725.1	GQ409653.1	HQ622016
<i>H. elisae</i> 1 MOL	EF653875	GQ409732.1	GQ409653.1	HQ622019
<i>H. elisae</i> 1 NAV	GQ409683.1	GQ409730.1	GQ409653.1	HQ622021
<i>H. elisae</i> 5 PAR	EF653898	GQ409709.1	GQ409655.1	HQ622024
<i>H. elisae</i> 1 RED	EF653881	GQ409741.1	GQ409653.1	HQ622029
<i>H. elisae</i> 4 SEV	EF653905	GQ409707.1	GQ409656.1	HQ622031
<i>H. elisae</i> 2 SIG	EF653893	GQ409710.1	GQ409654.1	HQ622033
<i>H. elisae</i> 2 SOT	GQ409700.1	GQ409716.1	GQ409654.1	HQ622034
<i>H. elisae</i> 1 TRE	GQ409678.1	GQ409737.1	GQ409653.1	HQ622038
<i>H. elisae</i> 1 UCE	GQ409692.1	GQ409720.1	GQ409653.1	HQ622039
<i>H. elisae</i> 1 VEN	GQ409671.1	GQ409750.1	GQ409653.1	HQ622041
<i>H. pretiosa arrufati</i>	HQ621995	HQ621889	HQ621966.1	HQ622040
<i>H. pretiosa</i> var. PRB	HQ621987	HQ621881	HQ621958.1	HQ622026
<i>H. pretiosa</i> Villamassargia	HQ621998	HQ621893	HQ621969.1	HQ622045
<i>H. pretiosiformis oroeli</i>	HQ621984	HQ621877	HQ621955.1	HQ622022
<i>H. redii redii</i>	HQ621978	HQ621871	HQ621949.1	HQ622012
<i>H. redii redii</i>	HQ621971	HQ621863	HQ621942.1	HQ622000
<i>H. redii redii</i>	HQ621976	HQ621869	HQ621947.1	HQ622010
<i>H. redii insularis</i>	HQ621996	HQ621890	HQ621967.1	HQ622042
<i>H. samnitica lirapora</i>	HQ621993	HQ621887	HQ621964.1	HQ622036
<i>Hemigastrodriilus monicae</i>	HQ621979	HQ621872	HQ621950.1	HQ622014
<i>Hemigastrodriilus monicae</i>	HQ621982	HQ621875	HQ621953.1	HQ622018
<i>Hormogaster abbatisae</i>	HQ621990	HQ621884	HQ621961.1	HQ622030
<i>Hormogaster arenicola</i>	HQ621972	HQ621865	HQ621943.1	HQ622003
<i>Hormogaster catalaunensis</i>	HQ621973	HQ621866	HQ621944.1	HQ622005
<i>Hormogaster eserana</i>	HQ621977	HQ621870	HQ621948.1	HQ622011
<i>Hormogaster gallica</i>	HQ621974	HQ621867	HQ621945.1	HQ622006
<i>Hormogaster huescana</i>	HQ621980	HQ621873	HQ621951.1	HQ622015
<i>Hormogaster ireguana</i>	HQ621994	HQ621888	HQ621965.1	HQ622037
<i>Hormogaster najaformis</i>	HQ621985	HQ621878	HQ621956.1	HQ622023
<i>Hormogaster nigra</i>	HQ621988	HQ621882	HQ621959.1	HQ622027
<i>Hormogaster pretiosiformis</i>	HQ621983	HQ621876	HQ621954.1	HQ622020
<i>Hormogaster riojana</i>	HQ621970	HQ621862	HQ621941.1	HQ621999
<i>Hormogaster</i> sp. CER	HQ621975	HQ621868	HQ621946.1	HQ622008
<i>Hormogaster</i> sp. HPA	-	HQ621892	-	HQ622044
<i>Hormogaster</i> sp. TAL	HQ621992	HQ621886	HQ621963.1	HQ622035



Species	COI	16S-tRNAs	28S-rRNA	H3
<i>Hormogaster sylvestris</i>	HQ621981	HQ621874	HQ621952.1	HQ622017
<i>Vignysa popi</i>	HQ621991	HQ621885	HQ621962.1	HQ622032
<i>Vignysa vedovinii</i>	HQ621986	HQ621880	HQ621957.1	HQ622025
<i>Xana omodeoi</i>	HQ621997	HQ621891	HQ621968.1	HQ622043
<i>Amynthas robustus</i>	EF077569.1	EF490524.1	EF490529.1	-
<i>Dichogasters aliens</i>	-	AF406573.1	AY101560.1	-
<i>Pontodrilus litoralis</i>	-	AY340473.1	-	-
<i>Lumbricus terrestris</i>	HQ691222	U24570	HQ691218	HQ691227
<i>Aporrectodea trapezoides</i>	RF	HQ621864	RF	HQ622002



# Review of the millipede family Trichopolydesmidae in the Oriental realm (Diplopoda, Polydesmida), with descriptions of new genera and species

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## Abstract

In the Oriental Region, the large, basically Northern Hemisphere family Trichopolydesmidae is shown to currently comprise 18 genera and 43 species. Based mainly on gonopod structure, all of them, as well as the whole family, are (re)diagnosed, including five new genera and seven new species. These new taxa are keyed, also being the first to be described from Indochina in general and from Vietnam in particular: *Aporodesmella* **gen. n.**, with three species: *A. securiformis* **sp. n.** (the type species), *A. similis* **sp. n.** and *A. tergalis* **sp. n.**, as well as the following four monotypic genera: *Deharvengius* **gen. n.**, with *D. bedosae* **sp. n.**, *Gonatodesmus* **gen. n.**, with *G. communicans* **sp. n.**, *Helicodesmus* **gen. n.**, with *H. anichkini* **sp. n.**, and *Monstrodesmus* **gen. n.**, with *M. flagellifer* **sp. n.** In addition, *Cocacolaria hauseri* Hoffman, 1987, hitherto known only from New Ireland Island, Papua New Guinea, is redescribed based on material from Vanuatu whence it is recorded for the first time. One of the new genera, *Gonatodesmus* **gen. n.**, provides a kind of transition or evolutionary bridge between Trichopolydesmidae and Opisotretidae, thus reinforcing the assignment of these two families to the single superfamily Trichopolydesmoidea.

**Keywords**

Diplopoda, Trichopolydesmoidea, taxonomy, new genera, new species, key, Vietnam, Vanuatu

**Introduction**

The large, chiefly Northern Hemisphere millipede family Trichopolydesmidae has recently been rediagnosed and, together with the much smaller, Oriental and Papuan family Opisetretidae (Golovatch et al. 2013), shown to compose the superfamily Trichopolydesmoidea, suborder Polydesmoidea (Golovatch 2013). The bulk of trichopolydesmid diversity, both generic and species, is taken up by what has until recently been considered as an independent pantropical family Fuhrmannodesmidae. Hoffman (1980, 1982) counted about 80 species from over 50 genera as unequivocally belonging to Fuhrmannodesmidae while another eight species in five genera were included in that family only provisionally.

Because the present contribution focuses on the fauna of the Oriental realm alone, by default all tropical and subtropical Asian, plus the few known Papuan trichopolydesmids have hitherto been treated as fuhrmannodesmids. However, following the recent synonymization of Fuhrmannodesmidae and several other, smaller, Holarctic, Nearctic or Palaearctic families with Trichopolydesmidae (Golovatch 2013), the names “fuhrmannodesmids” or “Fuhrmannodesmidae” will be referred to here in quotation marks.

Golovatch (1992, 1994), when sorting out the rich “fuhrmannodesmid” fauna of the Neotropical realm, suggested the following evolutionary scenario. He accepted as the basalmost those genera showing rather small, subglobose gonopod coxae that form no significant gonocoel in which to hinge the largely exposed, usually rather simple and elongate telopodites. Moreover, as in some Holarctic Trichopolydesmoidea, the prefemoral (= setose) part of the gonopod is mostly orientated transversely to the body axis, extending fully mesally across the coxae. Following a series of transitional states, such forms ultimately culminate in having the gonopod coxae strongly enlarged, forming a large gonocoel in which to conceal the clearly shortened, usually highly complex and deeply sunken telopodites. Their prefemoral parts already tend to be positioned increasingly parallel to the body’s main axis, thus providing a transition between the usually small-sized Trichopolydesmoidea (= so-called “micropolydesmoids”) to the normally medium- to large-sized Polydesmoidea (= so-called “macropolydesmoids”).

Naturally, similar general trends can be surmised to have occurred in the “fuhrmannodesmids” of the Afrotropical and, especially, Oriental realms, which also support fairly diverse faunas of this family. Prompted by the need to identify and allocate several species from Vietnam and Vanuatu, the present paper is an attempt to review all Oriental Trichopolydesmidae, i.e. 36 species or subspecies from 13 genera, arranged in alphabetic order:

1. *Assamodesmus lindbergi* Manfredi, 1955, the type species of *Assamodesmus* Manfredi, 1954, by original designation, described from the Himalayas of Assam, northeastern India (Manfredi 1955), redescribed by Golovatch (1988b).

2. *Coonoorophilus monstruosus* Carl, 1932, the type species of *Coonoorophilus* Carl, 1932, by monotypy, described from a single gynandromorph (abnormal, with only one gonopod retained) from southern India (Carl 1932).
3. *Hingstonia beatae* Golovatch, 1990, described from Nepal, Himalayas (Golovatch 1990).
4. *Hingstonia dorjulana* Golovatch, 1988, described from Bhutan, Himalayas (Golovatch 1988a).
5. *Hingstonia eremita* Carl, 1935, the type species of *Hingstonia* Carl, 1935, by monotypy, described from Nepal, Himalaya (Carl 1935), redescribed by Golovatch (1986).
6. *Hingstonia falcata* Golovatch, 1986, described from Nepal, Himalaya (Golovatch 1986).
7. *Hingstonia fittkaui* Golovatch, 1990, described from Nepal, Himalaya (Golovatch 1990).
8. *Hingstonia gogonana* Golovatch, 1988, described from Bhutan, Himalayas (Golovatch 1988a).
9. *Hingstonia pahakholana* Golovatch, 1990, described from Nepal, Himalayas (Golovatch 1990).
10. *Hingstonia pelelana* Golovatch, 1988, described from Bhutan, Himalaya (Golovatch 1988a).
11. *Hingstonia perarmata* Golovatch, 1986, described from Nepal, Himalaya (Golovatch 1986).
12. *Hingstonia serrata* Golovatch, 1987, described from Nepal, Himalayas (Golovatch 1987).
13. *Hingstonia sympatrica* Golovatch, 1990, described from Nepal, Himalayas (Golovatch 1990).
14. *Hingstonia variata* Golovatch, 1987, described from Nepal, Himalayas (Golovatch 1987), a little later recorded in Nepal again (Golovatch 1990).
15. *Hingstonia yeti* Golovatch, 1988, described from Bhutan, Himalaya (Golovatch 1988a).
16. *Kukkalodesmus exiguus* Carl, 1932, the type species of *Kukkalodesmus* Carl, 1932, by monotypy, described from southern India (Carl 1932).
17. *Magidesmus affinis* Golovatch, 1988, described from Bhutan, Himalayas (Golovatch 1988a).
18. *Magidesmus bhutanensis* Golovatch, 1988, the type species of *Magidesmus* Golovatch, 1988, by original designation, described from Bhutan, Himalayas (Golovatch 1988a).
19. *Mastodesmus zehntneri* Carl, 1911, the type species of *Mastodesmus* Carl, 1911, by monotypy, described from Java, Indonesia (Carl 1911).
20. *Nasodesmus cognatus* (Humbert, 1865), originally described as *Polydesmus cognatus* Humbert, 1865, from Sri Lanka (Humbert 1865), first made the type species of *Nasodesmus* Cook, 1896, by monotypy by Cook (1896), then redescribed and made the type species of *Lankadesmus* Carl, 1932, by original designation by Carl (1932). *Lankadesmus* is thus only a junior objective synonym of *Nasodesmus*.

21. *Ootacadesmus humilis* Carl, 1932, the type species of *Ootacadesmus* Carl, 1932, by original designation, described from southern India (Carl 1932).
22. *Peronorchus parvicollis* Attems, 1907, the type species of *Peronorchus* Attems, 1907, by monotypy, described from Buitenzorg (= Bogor), Java, Indonesia (Attems 1907), redescribed from material from Mauritius, Indian Ocean and assigned to the family Trichopolydesmidae (Mauriès and Geoffroy 1999), but recently transferred to “Fuhrmannodesmidae” (Golovatch et al. 2013).
23. *Pseudosphaeroparia cardamoni* Carl, 1932, described from southern India (Carl 1932).
24. *Pseudosphaeroparia cavernicola* Turk, 1945, described from a series of ♀ or juvenile syntypes from a cave near Dehra Dun, Uttar Pradesh, Himalayas of India (Turk 1945).
25. *Pseudosphaeroparia nilgirensis* Carl, 1932, described from southern India (Carl 1932).
26. *Pseudosphaeroparia palnensis* Carl, 1932, the type species of *Pseudosphaeroparia* Carl, 1932, by original designation, described from southern India (Carl 1932).
27. *Pseudosphaeroparia palnensis soror* Carl, 1932, described from southern India (Carl 1932).
28. *Sholaphilus albidus* Carl, 1932, the type species of *Sholaphilus* Carl, 1932, by monotypy (not by original designation, as mistakenly stated by Jeekel (1970)), described from southern India (Carl 1932).
29. *Sholaphilus asceticus* Golovatch, 1986, described from Nepal, Himalayas (Golovatch 1986).
30. *Sholaphilus dalai* Golovatch, 1986, described from Nepal, Himalayas (Golovatch 1986).
31. *Sholaphilus gompa* Golovatch, 1990, described from Nepal, Himalayas (Golovatch 1990).
32. *Sholaphilus lama* Golovatch, 1986, described from Nepal, Himalayas (Golovatch 1986).
33. *Sholaphilus martensi* Golovatch, 1986, described from Nepal, Himalayas (Golovatch 1986).
34. *Sholaphilus monachus* Golovatch, 1990, described from Nepal, Himalayas (Golovatch 1990).
35. *Topalodesmus communis* Golovatch, 1988, the type species of *Topalodesmus* Golovatch, 1988, by original designation, described from the Himalayas of Darjeeling District, northern India (Golovatch 1988b).

We can also add here one more genus and species from the region concerned:

36. *Cocacolaria hauseri* Hoffman, 1987, the type species of *Cocacolaria* Hoffman, 1987, by original designation, described from New Ireland, Papua New Guinea by Hoffman (1987). He refrained from assigning it to a family, but placed it close to or inside the Haplodesmidae. Here we consider *Cocacolaria* as a genus of Trichopolydesmidae on account of body and gonopod structure, especially,

the shape of the collum and second tergite, these being drastically different from those observed in Haplodesmidae (Golovatch et al. 2009a, 2009b, 2010). Furthermore, below we provide the first record of this species in Vanuatu.

The following taxa must be excluded from *Trichopolydesmidae* or remain unclassified:

1. *Glenniea* Turk, 1945, with six species from the Himalayas of India, Nepal and Bhutan (Golovatch 1988a), as well as one species in Guangxi, southern China (Golovatch et al. 2012). A further two species, the first presumed troglobitic congeners, have been encountered in Sichuan, southern China (Golovatch & Geoffroy, in preparation). Hoffman (1980) listed this genus in Fuhrmannodesmidae, but Golovatch (1988a) transferred it to the Polydesmidae.
2. *Typhlopygmaeosoma hazeltonae* Turk, 1972, the type species of *Typhlopygmaeosoma* Turk, 1972, described from a cave near Shimla (formerly Simla), Himachal Pradesh, northern India (Turk 1972); first revised by Shear (1986) who equivocally assigned it to the family Opisotretidae, then by Golovatch (1988b) who placed it in the Polydesmidae.

In addition, closer unidentified “Fuhrmannodesmidae”, provisionally referred to as Gen. sp. 1, Gen. sp. 2 and Gen. sp. 3, have been recorded in the Cat Tien National Park, southern Vietnam (Golovatch et al. 2011). These species are described below.

As one can see from the above list, only one species, *Pseudosphaeroparia cavernicola*, is known too poorly (Turk 1945) to realistically become recognized. It is bound to remain enigmatic until a ♂ topotype has been obtained and properly described. In addition, *Coonoorophilus monstrosus* was based on a gynandromorph, thus strongly obscuring the identity both of the genus and species.

The main objective of the present paper is to address the generic classification of *Trichopolydesmidae* in the Oriental Region in order to identify and name a number of fresh samples from Vietnam and Melanesia.

### Abbreviations used:

<b>MNHN</b>	Muséum national d'Histoire naturelle, Paris, France
<b>SEM</b>	Scanning electron microscopy
<b>ZMUC</b>	Natural History Museum of Denmark, Copenhagen, Denmark
<b>ZMUM</b>	Zoological Museum, State University of Moscow, Moscow, Russia

### Material and methods

Most of the material treated below was taken by Louis Deharveng, Anne Bedos (MNHN) and/or their collaborators in Vietnam. Several samples derive from ZMUM, collected by Alexander Anichkin (Joint Russia-Vietnam Tropical Center, Ho Chi Minh City, Vietnam) in a national park in southern Vietnam.



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 in MNHN.

The course of the seminal groove was always checked and, if necessary, depicted using transmission light microscopy.

### The main characters used in the classification of Trichopolydesmidae

The following characters have been used for defining genera in Oriental Trichopolydesmidae (= “Fuhrmannodesmidae”). Note that there is nothing particular in the peripheral, non-gonopod features that would uniquely characterize the Trichopolydesmidae (Golovatch 2011, Golovatch et al. 2013). The family-level differences tend to lie solely in gonopod conformation (see discussion below).

#### - Number of body segments

Like in most other families in Polydesmida, the number is 18, 19 or 20, largely being sex-characteristic. Thus, 20 segments in both sexes are known in most of the Oriental Trichopolydesmidae, 19 in both sexes only in *Assamodesmus*, *Peronorchus*, *Aporodesmella* gen. n., *Gonatodesmus* gen. n. and *Helicodesmus* gen. n., 19 in the ♂, but 20 in the ♀ in *Cocacolaria*, at least 19 in the ♂ of *Coonoorophilus* and *Ootacadesmus*. *Deharvengius* gen. n. is the sole genus in Trichopolydesmoidea which has only 18 segments in both sexes.

#### - Metatergal setae

All known species of Trichopolydesmidae show 3 transverse rows of tergal setae. The setation pattern is typical of the Polydesmidea, being 3+3 or more setae per row, only exceptionally 2+2 (*Deharvengius* gen. n.), plus 2 or 3 setae at each lateral margin. However, the setae themselves are typically ribbed, often helicoid, varying from long and sharp, like in *Cocacolaria*, *Mastodesmus* or *Deharvengius* gen. n., through short and simple, like in *Nasodesmus* or *Ootacadesmus*, to long and bacilliform, like in *Assamodesmus*, *Deharvengius* gen. n., *Helicodesmus* gen. n. or *Gonatodesmus* gen. n., or short and clavate, like in *Magidesmus*, *Pseudosphaeroparia*, *Sholaphilus* or some species of *Aporodesmella* gen. n. At least the bacilli- and claviform setae seem to always be modified, ribbed all along (e.g. Figs 11L, 13L, M, 16N, O). However, similar setae occur in some other families of Polydesmida such as Opisetretidae or Paradoxosomatidae (e.g. Golovatch et al. 2013).

#### - Metatergal sculpture

The pattern of metatergal sculpturing is typical of the Polydesmidea, i.e. 3 transverse rows of polygonal bosses or rounded tubercles, either with a more or less deep sulcus separating the first row from the two following ones or with clear sulci between all 3 rows. Each boss or tubercle is typically surmounted by a seta sometimes borne on a small knob. Among the Oriental Trichopolydesmidae, only very few species show truly distinct bosses or tubercles, e.g. *Cocacolaria* or *Mastodesmus*, whereas in the vast

majority of cases the bosses are either flat or missing, and the transverse sulcus or sulci are largely superficial to wanting.

#### - Location and size of ozopores

Unlike species of *Opisotretidae* (Golovatch et al. 2013), Oriental *Trichopolydesmidae* usually show the ozopores small, opening flush on the dorsal surface and mostly located closer to the lateral margin of paraterga than to the caudal one. In *Cocacolaria* the ozopores are unusually prominent and, like in *Hingstonia*, *Mastodesmus* or *Nasodesmus*, placed just at or near the caudolateral paratergal corner. All other Oriental *Trichopolydesmidae* have the ozopores, albeit only rarely quite as large as in *Kukkalodesmus*, lying near the penultimate lateral incision of poriferous paraterga. So far as is known, the pore formula is always 5, 7, 9, 10, 12, 13, 15-17(18, 19), except in *Aporodesmella* gen. n., which is the sole genus in *Trichopolydesmoidea* which shows no ozopores whatever.

#### - Shape and size of paraterga

Variation in the degree of development of paraterga is considerable, ranging from fully wanting (some species of *Aporodesmella* gen. n.), through very poorly developed (nearly missing in *Cocacolaria*, *Peronorchus* or *Mastodesmus*) to evident or strong (*Nasodesmus*, *Magidesmus*, *Deharvengius* gen. n. or certain species of *Aporodesmella* gen. n.), usually varying between species in speciose genera. As in the other *Polydesmida*, paraterga tend to be slightly underdeveloped and set lower in ♀♀ and juveniles compared to ♂♂.

#### - Antennae

Normally, the antennae in *Trichopolydesmoidea* tend to be geniculate between antennomeres 5 and 6, these segments also usually bearing conspicuous apicodorsal groups of bacilliform sensilla. However, in a few Oriental *Trichopolydesmidae*, e.g. *Cocacolaria* or *Mastodesmus*, this geniculation is either feeble or totally wanting. Only exceptionally is ♂ antennomere 6 supplied with a conspicuous dorsoparabasal stump (some species of *Aporodesmella* gen. n.).

#### - ♂ head modifications

The ♂ vertex in Oriental *Trichopolydesmidae*, unlike that in some species from the Neotropical and Afrotropical realms (e.g. Golovatch 1994, Mauriès and Heymer 1996), usually remains unmodified. Only the ♂ of some species of *Aporodesmella* gen. n., as well as in *Gonatodesmus* gen. n. either shows a vertigial hump or the entire head in both sexes is clearly flattened dorsoventrally (*Deharvengius* gen. n.). Although the presence of such modifications is often considered as genus-characteristic (e.g. Mauriès and Heymer 1996), we believe they are only species-specific (e.g. Golovatch et al. 2013).

#### - Legs

Variation in leg length and armament in Oriental *Trichopolydesmidae* is quite pronounced, ranging from rather short and stout, sometimes also supplied with special ventral trichomes in the ♂, e.g. in some *Hingstonia*, to long and slender, e.g. in most of

*Hingstonia* species, but the bulk of species show medium-sized, moderately to considerably stout legs which are usually devoid of modified trichomes in the ♂ and thus fail to differ much between the sexes. This contradicts Simonsen (1990) who stated that ♂ legs in “fuhrmannodesmids” show sphaerotrichomes. Only in *Kukkalodesmus*, *Nasodesmus* and *Ootacadesmus* does the ♂ have clearly inflated and elongated legs 3. Claw length seems to vary proportionately to leg length. In *Gonatodesmus* gen. n., ♂ tarsi 1 are supplied with modified, mostly bi- or trifold setae on the ventral side (Fig. 12B).

### - Gonopod structure

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

The gonopods in Trichopolydesmidae appear to vary much more strongly than in the Opisetretidae, the sole other family of Trichopolydesmoidea, in agreement with the fact that Trichopolydesmidae is much larger and is widespread throughout the Northern Hemisphere. Moreover, a gonopod-based diagnosis of Trichopolydesmidae is still not entirely satisfactory (Simonsen 1990, Golovatch 2011, 2013). This family appears to unite the micropolydesmoids in which the gonopod coxae are subglobose, from rather small to very large, while the prefemoral part is often orientated transversely to the body axis, usually extending fully mesally across the coxae. However, as the gonopod prefemora in trichopolydesmids grow shorter, the acropodites become orientated increasingly along the body axis, thus providing transitions to the superfamily Polydesmoidea (Golovatch et al. 2013).

Simonsen (1990), in his cladistic analysis of the suborder Polydesmidea, allotted the Opisetretidae the rank of an independent superfamily, Opisetretoidea. He also distinguished the “Fuhrmannodesmidae” from the other “families” of Trichopolydesmoidea through the presence of a separate tooth (= solenomere) terminating the seminal groove. Even if a solenomere is present in some other trichopolydesmoids, it was said its position would not be apical.

Such a definition is basically correct, although a few Neotropical “fuhrmannodesmids” show no solenomere whatsoever (Golovatch 1994). The lack both of an accessory seminal chamber and a hairy pulvillus is typically also correct, but this is characteristic of nearly all Trichopolydesmoidea except Opisetretidae (at least as opposed to the Polydesmoidea). What is definitely wrong in Simonsen’s (1990, p. 81) diagnosis of “Fuhrmannodesmidae” is the statement that the gonopod coxae, however large, fail to form a gonocoel, while the telopodite is devoid of a mesal branch (endomere). In contrast, according to Golovatch (1992, 1994), the degree of development of the gonocoxae (and their gonocoel) seems to be instrumental in properly assessing the main evolutionary trends in the family. In addition, the gonotelopodite in various Trichopolydesmidae is usually supplied with additional branches or other outgrowths, including mesal ones.

Amongst the Oriental Trichopolydesmidae, like in the Neotropical ones (Golovatch 1992, 1994), the genera in which the gonopod coxae and their gonocoel are

still relatively small, leaving the telopodites strongly exposed, can be viewed as the basalmost. This condition is characteristic of *Assamodesmus*, *Cocacolaria* or *Mastodesmus*. In *Topalodesmus* and some *Sholaphilus*, the gonopod coxa has a strong frontal (= anterior) process which, like a rather deep gonocoel, is deemed to provide additional protection to the clearly exposed telopodites. Similar conditions have been noted in some Neotropical “Fuhrmannodesmidae” as well (Golovatch 1992, 1994). The deepest, maximally developed gonocoel, where the telopodites are extremely low, fully sunken and supplied with a tooth-shaped solenomere at the bottom of a mesal hollow, is found only in *Magidesmus*. Most of the remaining genera seem to represent intermediate states, whereas such species-rich genera as *Hingstonia*, *Pseudosphaeroparia* and *Sholaphilus* show a degree of intrageneric variation.

Only the gonopods of *Gonatodesmus* gen. n. stand apart in showing a kind of transition to Opisotretidae. Indeed, the gonocoel is small, the telopodites are strongly exposed and well separated, their basal parts are held parallel to the main axis, whereas their distal parts, following a clear midway geniculation, are directed abruptly laterad. Moreover, this genus demonstrates a strongly developed, hairy pulvillus and a small accessory seminal chamber so characteristic of most species of Opisotretidae (and Polydesmidae).

#### - Vulva

No special studies have been conducted on the conformation of the vulva in “Fuhrmannodesmidae”. Turk (1945) provided a crude sketch of an elongate and strongly setose vulva in *Pseudosphaeroparia cavernicola*. Mauriès and Heymer (1996) illustrated a rather short and poorly setose vulva of a *Sphaeroparia* species from Uganda, tropical Africa. The epigynal crest has never been described in any Trichopolydesmidae. Because these structures are too small and inconspicuous in the samples we have examined, they have been omitted from the descriptions.

### Generic reclassification

Based on the above information, as well as facing the need to properly allocate several new genera and species described below, we propose the following new diagnosis of Trichopolydesmidae and a new classification of the family's constituent Oriental genera.

#### Family Trichopolydesmidae Verhoeff, 1910

<http://species-id.net/wiki/Trichopolydesmidae>

**Diagnosis.** A family of the superfamily Trichopolydesmoidea, suborder Polydesmoidea with 18, 19 or 20 segments, sometimes varying between sexes. Body very small to

small (ca 2–20 mm long). Tegument microalveolate, limbus mostly microspiculate. ♂ head with or without vertigial modifications. Antennae often geniculate between segments 5 and 6, antennomeres 5 and 6 each usually with a compact group of bacilliform sensilla apicodorsally, rarely 6<sup>th</sup> in ♂ with a dorsoparabasal stump. Metaterga usually with 3 regular, more rarely with more and/or irregular, transverse rows of sharp (= simple), bacilliform or clavate setae sometimes borne on knobs; side margin of paraterga incised or tuberculate, with 2 or 3 setae. Paraterga from absent to strongly developed, usually only slightly indented laterally, only exceptionally deeply trilobate (*Trilobodesmus* Golovatch & Mauriès, 2007). Pore formula usually normal: 5, 7, 9, 10, 12, 13, 15–17 (18,19), but sometimes ozopores completely wanting, rarely unusually large, normally opening flush on dorsal or dorsolateral surface either near penultimate lateral incision or at caudal corner of paraterga. Legs rather short to long, ♂ ones often stouter and elongate, rarely modified, inflated, only sometimes with peculiar ventral setae, including sphaerotrichomes.

Gonopods with subglobose, medially fused coxae, these being rather small to quite large (with correspondingly large gonocoel), micropapillate and at most only slightly setose laterally, sometimes with a frontal (= anterior) process, each supporting a cannula medially (exception: *Caucasodesmus* Golovatch, 1987, in which there is no cannula) and a sack-shaped to elongate telopodite. The latter ranging from stout and short, deeply sunken inside a deep gonocoel, to slender and long, nearly fully exposed, strongly to modestly curved caudad or mesad, only exceptionally geniculate (distal half directed abruptly laterad: *Gonatodesmus* gen. n.) or perforating coxal wall with a prominent process (*Schizotelopus* Verhoeff, 1941), usually complex, with various processes or outgrowths, sometimes fringed; seminal groove normally terminating distally or apically on a separate branch or tooth (= solenomere), rarely on a tooth inside gonocoel, exceptionally absent (*Caucasodesmus*). Typically neither an accessory seminal chamber nor a hairy pulvillus (a few exceptions, e.g. *Gonatodesmus* gen. n.).

**Type genus.** *Trichopolydesmus* Verhoeff, 1910.

**Remarks.** Most of the above somatic and gonopod features of Trichopolydesmidae are in no way unique to the family, sometimes being also encountered, in various combinations, in the micropolydesmoid family Opisotretidae of the same superfamily Trichopolydesmoidea, as well as in certain macropolydesmoid members of the family Polydesmidae, superfamily Polydesmoidea (Golovatch et al. 2013, Golovatch 2013). The finely microspiculate limbus is also characteristic of most of the Polydesmoidea, and is another feature whose importance was obviously overestimated by Simonsen (1990). It is only the gonopod structure that seems to be characteristic of Trichopolydesmidae, at least so to a certain extent. Superficially, female and/or juvenile trichopolydesmids from the Oriental realm are not or only barely distinguishable from the often sympatric or even syntopic female or juvenile Opisotretidae or smaller Polydesmidae.

The following 13 nominate Oriental genera of Trichopolydesmidae seem to be valid, and are arranged and defined below in alphabetic order.

***Assamodesmus* Manfredi, 1954**

<http://species-id.net/wiki/Assamodesmus>

**Diagnosis.** 19 segments (♂, ♀), pore formula normal, ozopores placed closer to lateral than to caudal margin of paratergite; ♂ vertex unmodified, paraterga modest, 3 rows of bacilliform metatergal setae; gonopod telopodites subfalcate and clearly twisted, held parallel to main body axis, strongly exposed (gonocoel small); solenomere (**sl**) a long, simple, distal spine with an adjacent, distal, bipartite solenophore (**sph**) consisting of an apical spine and a massive velum.

**Type species.** *Assamodesmus lindbergi* Manfredi, 1955, by original designation.

**Remarks.** This well-defined Himalayan genus remains monobasic.

***Cocacolaria* Hoffman, 1987**

<http://species-id.net/wiki/Cocacolaria>

**Diagnosis.** 19 (♂) or 20 (♀) segments, pore formula normal, ozopores placed closer to lateral than to caudal margin of paratergite; ♂ vertex unmodified, paraterga poorly developed, 3 rows of sharp long metatergal setae, metatergal sculpture (bosses) unusually high; gonopod telopodites subfalcate, crossing mesally, very strongly exposed (gonocoel small); **sl** a small branchlet at midway along telopodite; **sph** distal to **sl** unipartite, large, bifid and rather simple.

**Type species.** *Cocacolaria hauseri* Hoffman, 1987, by original designation.

**Remarks.** This genus remains monobasic, its sole constituent species being quite widespread in Melanesia. *C. hauseri* is redescribed below, based on samples from Vanuatu.

***Coonorophilus* Carl, 1932**

<http://species-id.net/wiki/Coonorophilus>

**Diagnosis.** 19 segments (♂), ♀ unknown, much like *Ootacadesmus* (see below), but gonopods strongly resembling those of *Sholaphilus*.

**Type species.** *Coonorophilus monstrosus* Carl, 1932, by monotypy.

**Remarks.** This monobasic genus is retained only provisionally, because it combines the basic characters of *Ootacadesmus*, *Kukkalodesmus*, *Pseudosphaeroparia* and *Sholaphilus*. The gynandromorph ♂ holotype of *C. monstrosus* retained only a single gonopod.

***Hingstonia* Carl, 1935**

<http://species-id.net/wiki/Hingstonia>

**Diagnosis.** 20 segments (♂, ♀); pore formula normal, ozopores lying opposite 3<sup>rd</sup> incision, placed closer to lateral than to caudal margin of paratergite; ♂ vertex unmodified, paraterga

keel-shaped, rather well developed, 3 rows of short, bacilliform to clavate setae on knobs; ♂ legs nearly normal, often with sphaerotrichomes; gonopod coxae from modest to large (gonocoel also from modest to deep), telopodites strongly exposed, usually massive, never fringed; **sph** (distal part of telopodite) complex, at least with one process or outgrowth, usually more; **sl** a rather long, simple, apical or subapical branch.

**Type species.** *Hingstonia eremita* Carl, 1935, by monotypy.

**Remarks.** This relatively species-rich, well-defined, Himalayan genus mostly contains relatively large species (up to 20 mm long).

### ***Kukkalodesmus* Carl, 1932**

<http://species-id.net/wiki/Kukkalodesmus>

**Diagnosis.** 20 segments (♂, ♀); pore formula normal, ozopores lying opposite 2<sup>nd</sup> incision, placed closer to lateral than to caudal margin of paratergite; ♂ vertex unmodified, paraterga keel-shaped, rather well developed, 3 rows of short, bacilliform to clavate metatergal setae on knobs; ♂ femur 3 strongly enlarged; gonopod coxae not very large (gonocoel modest), telopodites strongly exposed; **sph** distal, complex, with 2 caudal lobes and a frontal process, **sl** a small, plumose, subapical branchlet.

**Type species.** *Kukkalodesmus exiguus* Carl, 1932, by monotypy.

**Remarks.** This monotypic genus seems to be rather poorly defined versus *Sholaphilus*, *Pseudosphaeroparia*, *Coonoorophilus* and *Ootacadesmus*, especially given the strong variation in gonopod structure in the relatively species-rich genera *Sholaphilus* and *Pseudosphaeroparia* (see also above and below).

### ***Magidesmus* Golovatch, 1988**

<http://species-id.net/wiki/Magidesmus>

**Diagnosis.** 20 segments (♂), ♀ unknown; pore formula normal, ozopores placed closer to lateral than to caudal margin of paratergite; ♂ vertex unmodified, paraterga well developed and set quite high, 3 rows of short clavate metatergal setae; gonopod coxae very large (gonocoel deep), telopodites deeply sunken and barely exposed, sac-shaped, hollow in the middle, apically somewhat fringed; a **sph** missing, **sl** a small denticle at bottom of this hollow.

**Type species.** *Magidesmus bhutanensis* Golovatch, 1988, by original designation.

**Remarks.** This small Himalayan genus is well-defined.

### ***Mastodesmus* Carl, 1911**

<http://species-id.net/wiki/Mastodesmus>

**Diagnosis.** 20 segments (♂, ♀); pore formula normal, ozopores placed closer to lateral than to caudal margin of paratergite; ♂ vertex unmodified, paraterga almost missing



and set low, 3 rows of long, curved, simple metatergal setae on unusually prominent tubercles; gonopod coxae modest (gonocoel not very deep), telopodites bipartite in distal half, well exposed, very simple; **sph** a simple exomere branch, **sl** a long, simple, caudal spine branching off from distal half of telopodite.

**Type species.** *Mastodesmus zehntneri* Carl, 1911, by monotypy.

**Remarks.** This monobasic genus strongly resembles *Peronorchus* and *Nasodesmus*, but seems to be sufficiently well defined.

### ***Nasodesmus* Cook, 1896**

<http://species-id.net/wiki/Nasodesmus>

**Diagnosis.** 20 segments (♂, ♀); pore formula normal, ozopores placed closer to lateral than to caudal margin of paratergite; ♂ vertex unmodified, paraterga well developed, 3 rows of short simple metatergal setae; ♂ legs 3 strongly elongate, the femur very strongly enlarged; gonopod coxae not very large (gonocoel not too deep); telopodites strongly exposed, simple, unipartite, slightly curved mesad; **sph** (exomere) simple, strong, with a small process at base; **sl** a small, subapical, mesal branchlet.

**Type species.** *Polydesmus cognatus* Humbert, 1865, by original designation.

**Remarks.** This monobasic genus strongly resembles *Peronorchus* and *Mastodesmus*, but seems to be sufficiently well defined.

### ***Ootacadesmus* Carl, 1932**

<http://species-id.net/wiki/Ootacadesmus>

**Diagnosis.** 19 segments (♂), ♀ unknown; pore formula normal, ozopores placed closer to lateral than to caudal margin of paratergite; ♂ vertex unmodified, paraterga well developed, 3 rows of very short and simple metatergal setae; ♂ legs 3 clearly elongate, the femur very strongly enlarged; gonopod coxae very large (gonocoel deep); telopodites deeply sunken and only very little exposed, with a parabasal process; **sph** bipartite, with various apical outgrowths, including a lateral velum, **sl** a small subapical branchlet.

**Type species.** *Ootacadesmus humilis* Carl, 1932, by original designation.

**Remarks.** This monotypic genus seems to be rather poorly defined versus *Sholaphilus*, *Pseudosphaeroparia*, *Coonoorphilus* and *Kukkalodesmus* (see also above and below).

### ***Peronorchus* Attems, 1907**

<http://species-id.net/wiki/Peronorchus>

**Diagnosis.** 19 segments (♂, ♀); pore formula normal, ozopores placed closer to lateral than to caudal margin of paratergite; ♂ vertex unmodified; paraterga very small, body nearly cylindrical, 3 rows of 3+3 or 4+4, rather long bacilliform metatergal setae (regard-

less of lateral setae on paraterga); gonopod coxae with gonocoel not deep; telopodites clearly exposed, without parabasal processes, moderately curved and held parallel to each other; **sph** bifid distally, with **sl** a rather long, flagelliform, apical branch lying in **sph** fork.

**Type species.** *Peronorchus parvicollis* Attems, 1907, by monotypy.

**Remarks.** This genus strongly resembles *Nasodesmus* and *Mastodesmus*, but seems to be sufficiently well defined.

### ***Pseudosphaeroparia* Carl, 1932**

<http://species-id.net/wiki/Pseudosphaeroparia>

**Diagnosis.** 20 segments (♂, ♀); pore formula normal, ozopores placed closer to lateral than to caudal margin of paratergite; ♂ vertex unmodified, paraterga modest to well developed, 3 rows of short clavate metatergal setae; gonopod coxae very large (gonocoel deep) to modest; telopodites from rather deeply sunken to rather clearly exposed, with or without parabasal processes; **sph** unipartite, with various outgrowths, **sl** a rather evident apical branch.

**Type species.** *Pseudosphaeroparia palnensis* Carl, 1932, by original designation.

**Remarks.** This small genus is quite poorly defined versus *Sholaphilus*, *Coonoorphilus*, *Ootacadesmus* and *Kukkalodesmus* (see also above and below).

### ***Sholaphilus* Carl, 1932**

<http://species-id.net/wiki/Sholaphilus>

**Diagnosis.** 20 segments (♂, ♀); pore formula normal, ozopores placed closer to lateral than to caudal margin of paratergite; ♂ vertex unmodified, paraterga modest to well developed, 3 rows of short clavate metatergal setae; gonopod coxae very large (gonocoel deep) to modest, sometimes with a strong frontal process; telopodites rather deeply sunken and usually only little exposed, but sometimes rather strongly exposed, with or without parabasal processes; **sph** uni- to only faintly bipartite, with various outgrowths, densely fringed, **sl** a small apical or subapical tooth or branchlet.

**Type species.** *Sholaphilus albidus* Carl, 1932, by monotypy.

**Remarks.** Even though this rather small genus is quite poorly defined versus *Ootacadesmus*, *Pseudosphaeroparia*, *Coonoorphilus* and *Kukkalodesmus* (see above), several species of *Sholaphilus* from the Himalayas have been described.

### ***Topalodesmus* Golovatch, 1988**

<http://species-id.net/wiki/Topalodesmus>

**Diagnosis.** 20 segments (♂, ♀); pore formula normal, ozopores placed closer to lateral than to caudal margin of paratergite; ♂ vertex unmodified, paraterga modest, 3 rows

of short simple/claviform metatergal setae; gonopod coxae massive, each with a prominent frontal process; gonocoel rather deep, but telopodites subfalcate and strongly exposed, tripartite, each with a strong, parabasal, unciform, caudomedial process, a short laterobasal stump-shaped exomere, and a prominent, elongate **sph** crowned with a small apical **sl**.

**Type species.** *Topalodesmus communis* Golovatch, 1988, by original designation.

**Remarks.** This monobasic Himalayan genus is well-defined (see also below under *Monstrodesmus* gen. n.).

## Descriptions

### *Cocacolaria hauseri* Hoffman, 1987

[http://species-id.net/wiki/Cocacolaria\\_hauseri](http://species-id.net/wiki/Cocacolaria_hauseri)

Figs 1, 2

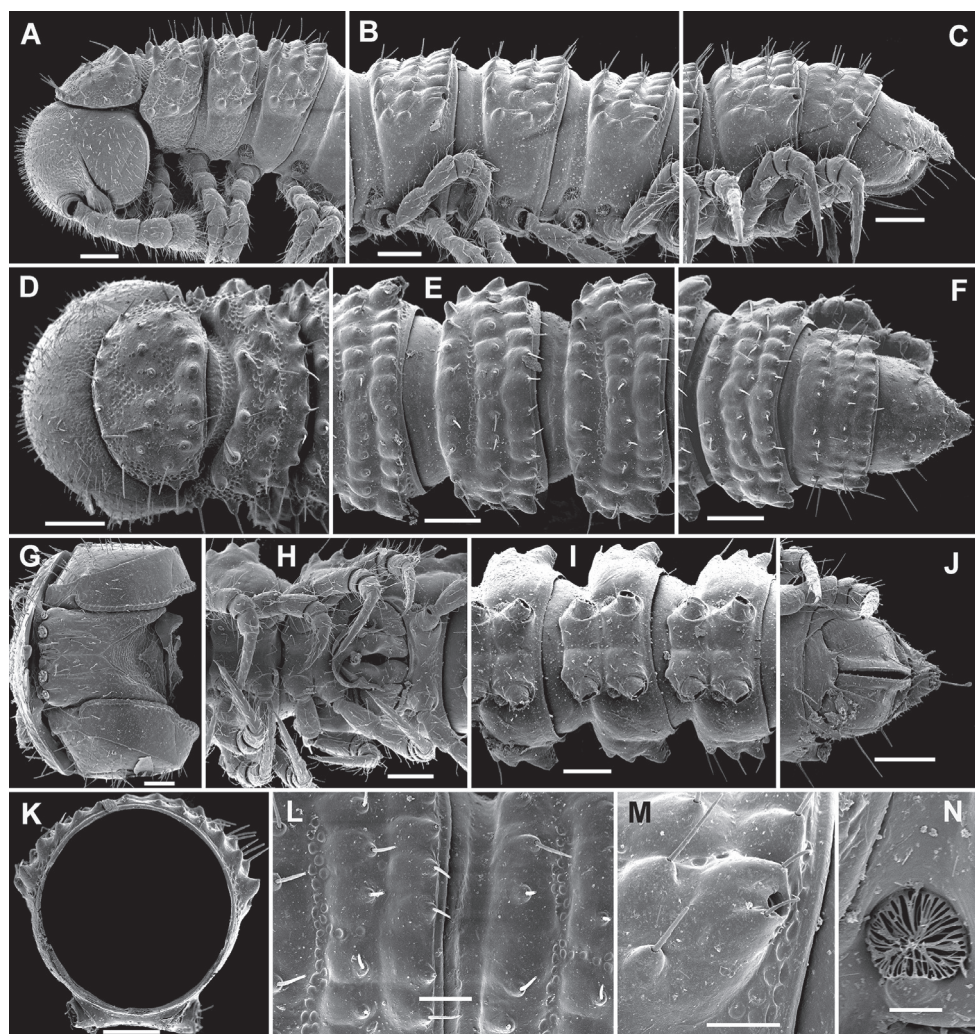
*Cocacolaria hauseri* Hoffman, 1987: 38.

**Material examined.** 1 ♂, 7 ♀, 1 fragment (MNHN JC 354), Vanuatu, Espirito Santo Island, Natawa forest, small doline Arifos, 167.183167E, 15.2962S, sieved litter & Berlese extraction, 24.09.2006, leg. L. Deharveng & A. Bedos (SK06-24-24); 1 ♂ (SEM), same locality, date and collectors (SK06-24-22); 3 ♀ (MNHN JC 354), Espirito Santo Island, Boutmas, forest near entrance to Cave Fapon, 166.9648833E, 15.33101667S, 380 m a.s.l., litter, Berlese extraction, 08.09.2006, leg. L. Deharveng & C. Rahmadi (SK06-08-24).

**Redescription.** Length of adults of both sexes 4–6 mm (♂, ♀), width of midbody pro- and metazonae ca 0.3 and 0.4 mm, respectively. Coloration in alcohol from uniformly pallid to light yellowish.

Body with 19 (♂) or 20 (♀) segments. Tegument mainly dull, at most slightly shining, texture very delicately alveolate. Head densely pilose throughout; epicranial suture superficial and thin (Fig. 1A); isthmus between antennae about 1.5 times as broad as diameter of antennal socket. Antennae short, reaching only behind (♂) or midway of collum (♀) when stretched dorsally, not geniculate, very clearly clavate, especially so due to largest antennomere 6, the latter with a small, but evident distodorsal group of bacilliform sensilla.

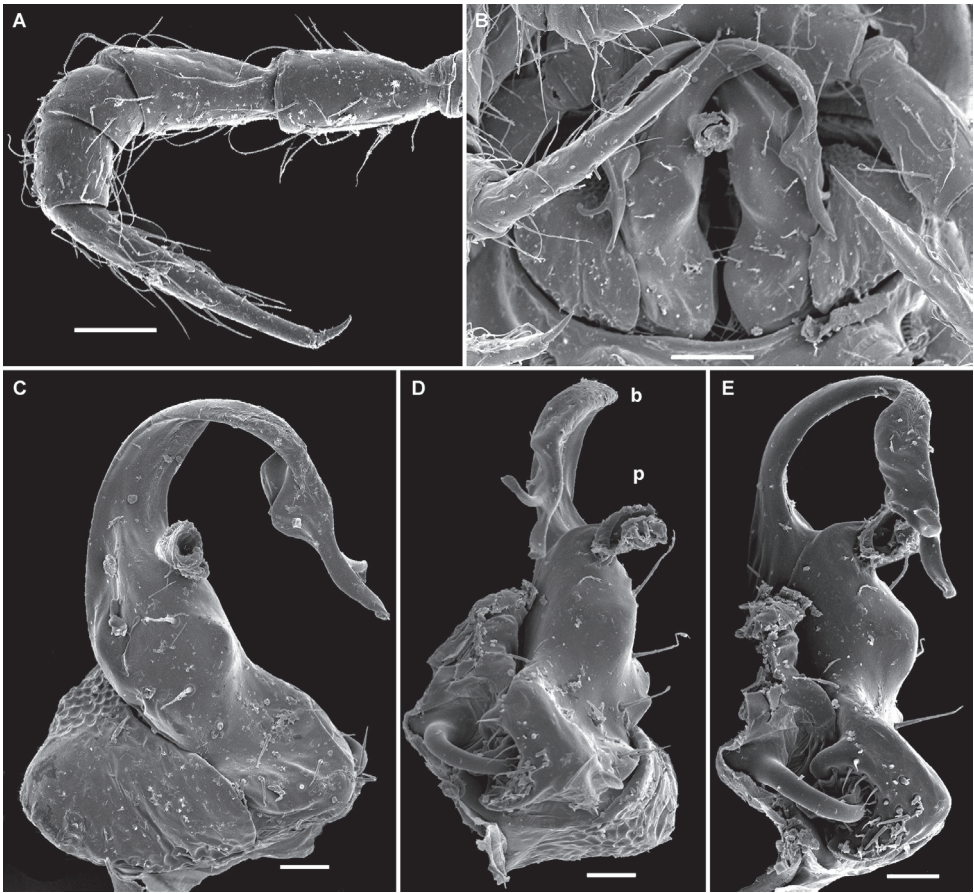
Body moniliform, especially so in ♂ (Fig. 1D–F). In width, collum << head < segment 2 < 3 = 4 < 5(6) = 15 (♂, ♀), thereafter body gradually tapering towards telson. Paraterga very poorly developed, mainly represented by setigerous tubercles (Fig. 1A–F, H–K), starting from collum, set rather low (at about upper 1/3–1/2 of segment's height), leaving a highly convex dorsum (Fig. 1A–C & K). Caudal corner of postcollum paraterga increasingly tuberculiform, mainly clearly rounded, not extending behind rear tergal margin. Pore formula normal; ozopores evident, round, lying dorsolaterally on top of caudolateral tubercle of paraterga very close



**Figure 1.** *Cocacolaria hauseri* Hoffman, 1987, ♂ from Natawa forest, Espirito Santo Island, Vanuatu; **A, D** anterior part of body, lateral and dorsal views, respectively **B, E, I** midbody segments, lateral, dorsal and ventral views, respectively **C, F, J** posterior part of body, lateral, dorsal and ventral views, respectively **G** head, ventral view **H** body segments 6 and 7, ventral view **K** cross-section of a midbody segment, caudal view **L** midbody tergal sculpture and setae, dorsal view **M** caudal part of a midbody pore-bearing paratergite, lateral view **N** midbody spiracle. Scale bars: **A–F, H–K** 0.1 mm; **G, L, M** 0.05 mm; **N** 0.02 mm.

to lateral margin, more remote from caudal margin (Fig. 1M). Collum subovoid, each following metatergum with 3 transverse rows of mostly long, pointed, very faintly ribbed, helicoid setae largely borne on 6+6 unusually high tubercles, these being especially prominent in last row (Fig. 1A–F). Stricture between pro- and metazonae deep, rather narrow and smooth. Limbus thin and entire, not microdentate. Pleurosternal carinae absent (Fig. 1A). Epiproct short, conical, directed





**Figure 2.** *Cocacolaria hauseri* Hoffman, 1987, ♂ from Natawa forest, Espirito Santo Island, Vanuatu; **A** midbody leg, lateral view **B** gonopod aperture with both gonopods *in situ*, ventral view **C** right gonopod, lateral view **D, E** left gonopod, caudomesal and mesal views, respectively. Scale bars: **A, B** 0.05 mm; **C–E** 0.02 mm. Designations of gonopod structures in text.

caudoventrally; pre-apical papillae evident (Fig. 1C, F, J). Hypoproct nearly semi-circular (Fig. 1J), setiferous papillae at caudal corners very clear, stalk-shaped and well separated.

Sterna without modifications, broad, flat, poorly setose (Fig. 1H–J). Stigma openings flat, beset with dense and long filaments (Fig. 1N). Legs in ♀ and juveniles clearly shorter and slenderer, ca 1.0–1.1 times as long as body height, in ♂ somewhat incrassate and ca 1.3–1.4 times as long as body height (Figs 1B, 2A); tarsi longest; sphaerotrichomes missing (Fig. 2A). Each ♂ coxa 2 with a short, cylindrical, dis-troventral gonapophysis.

Gonopod aperture transversely oblong-oval, taking up most of ventral part of metazonite 7, its edges nowhere elevated (Figs 1H, 2B). Gonopods (Fig. 2B–E) with rather moderately large, globose, bare, ventrolaterally papillate, medially fused coxae

carrying normal cannulae mesally. Telopodite strongly elongate and curved, subunciform, bipartite, directed mesad and crossing *in situ*, each at about midway with a short, mesal, calyciform process (**p**) (= solenomere) terminating a fully mesal seminal groove, with neither an accessory seminal chamber nor a hairy pulvillus. Main branch (**b**) (= solenophore) bifid and slightly expanded subterminally.

**Remarks.** This species, originally described from a single ♂ taken in a cave in Lelet Plateau, New Ireland, Papua New Guinea (Hoffman 1987), appears to be common and widespread in Vanuatu. However, among the literally hundreds of specimens taken on Espiritu Santo and Malo islands by the famous SANTO 2006 expedition, held by the MNHN (Bouchet et al. 2009, 2011, 2012), there were only two adult males. This might be evidence of seasonality or partial parthenogenesis, or both.

The original description is quite detailed and nicely illustrated (Hoffman 1987) and we are certain about the identity of our Vanuatu samples. We provide SEM images (Figs 1 and 2) to document the identity and to complement Hoffman's (1987) description.

### ***Aporodesmella* gen. n.**

<http://zoobank.org/3B37A67E-1F19-46E5-985C-E9AF3BD33826>

<http://species-id.net/wiki/Aporodesmella>

**Diagnosis.** 19 segments (♂, ♀); ozopores wanting; ♂ vertex modified or not; ♂ antennomere 6 sometimes with a conspicuous dorsoparabasal stump; paraterga absent to rather well developed, 3 rows of 3+3 or 4+4, short or long, bacilli- and/or claviform metatergal setae (regardless of lateral setae on or instead of paraterga); gonopod coxae with gonocoel not deep; telopodites clearly exposed, mostly or considerably represented by elongate prefemoral parts, at most only moderately curved, medially subcontiguous and held parallel to each other; acropodites, or solenophores (**sph**), lying distal to prefemoral parts shortened, only sometimes set off basally by a ventral sulcus, subtruncate, usually more or less coaxial with prefemoral parts, but sometimes extended laterad into a distinct process; solenomere (**sl**) subapical, rather long to vestigial.

**Name.** To emphasize the lack of ozopores, feminine.

**Type species.** *Aporodesmella securiformis* sp. n., by present designation.

**Remarks.** The new genus is unique among the Trichopolydesmoidea for its complete loss of ozopores. Among Oriental Trichopolydesmidae, *Aporodesmella* gen. n. seems to be especially similar to *Peronorchus*, sharing with it not only 19 body segments in both sexes, but also the gonopods demonstrating a modest gonocoel, elongate, clearly exposed and modestly curved telopodites which are (sub)contiguous medially and held parallel to each other (and to the main body axis), the solenophore being enlarged, more or less cup-shaped and membranous while the solenomere is a short subapical process or tooth. However, the prefemoral (= densely setose) part of the gonopod in *Peronorchus* is clearly shorter.

The following three new species are attributed to *Aporodesmella* gen. n.

***Aporodesmella securiformis* sp. n.**

<http://zoobank.org/A08E5C4F-B6E8-493B-A832-6C383E1FC438>

[http://species-id.net/wiki/Aporodesmella\\_securiformis](http://species-id.net/wiki/Aporodesmella_securiformis)

Figs 3, 4

**Type material.** Holotype ♂ (MNHN JC 355), Vietnam, Kien Giang Province, Kien Luong, Hon Chong, Nui Bai Voi, 104.618E, 10.218N, soil, Berlese extraction, 02.06.2008, leg. L. Deharveng & A. Bedos (Vn08-045).

Paratypes: 1 ♂, 4 ♀ (MNHN JC 355), 1 ♂, 1 ♀ (ZMUM 02346), 1 ♂ (SEM), same locality, together with holotype; 2 ♂, 1 ♀ (MNHN JC 355), 1 ♂ (SEM), same province, Kien Luong, Hon Chong, Nui Hang Tien, litter & soil, Berlese extraction, 02.06.2008, leg. Ly Ngoc Sam (Vn08-065); 3 ♂ (MNHN JC 355), 1 ♂ (SEM), same data (Vn08-066).

**Name.** To emphasize the axe-shaped solenophore.

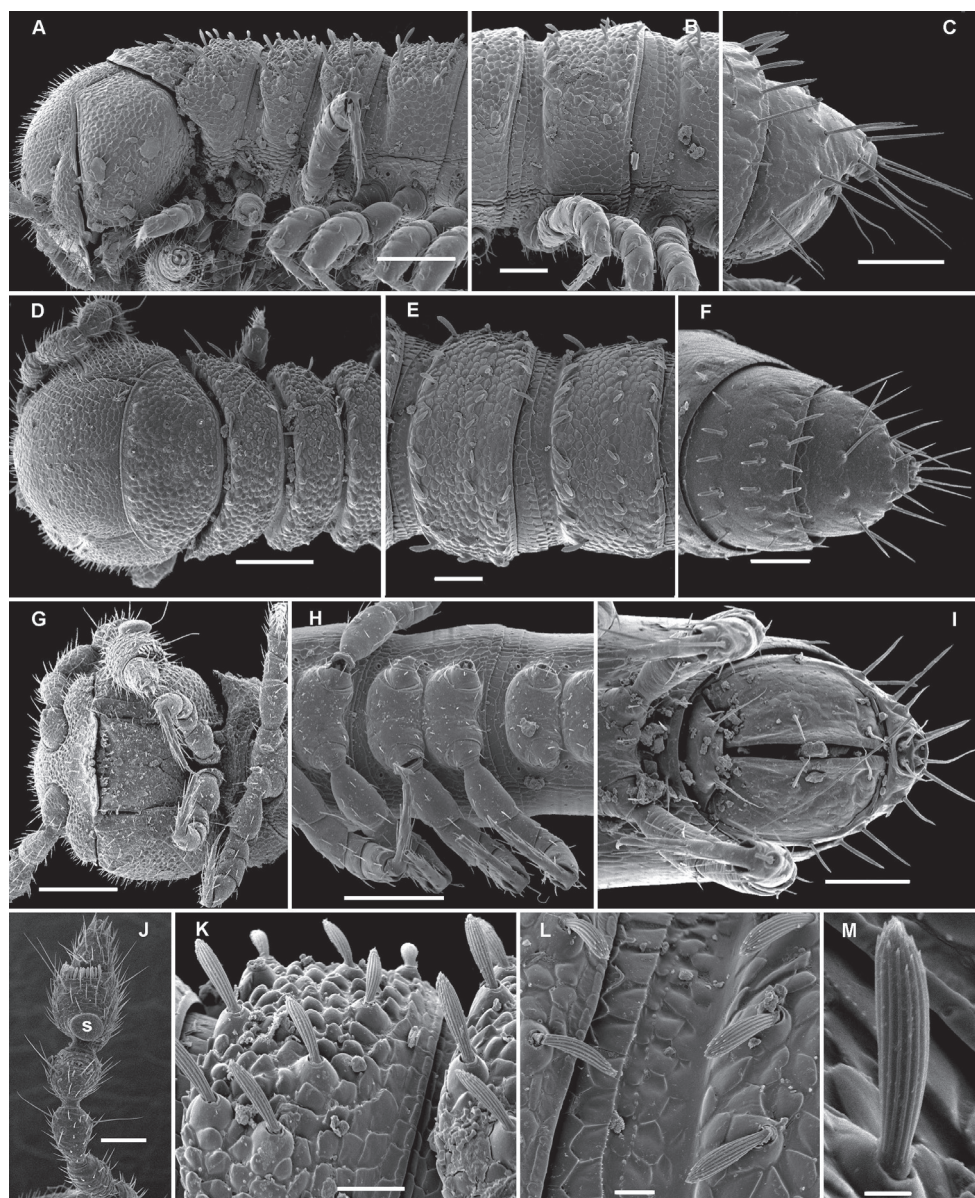
**Diagnosis.** Differs from congeners except *A. similis* sp. n. by the presence of a remarkable dorsoparabasal stump on ♂ antennomere 6, from *A. similis* sp. n. and other congeners by a peculiar, unusually short, axe-shaped solenophore and a simple, lanceolate, shorter and stout solenomere.

**Description.** Length of adults ca 2.8–2.9 mm (♂, ♀), up to 3.0 mm (♀), width of midbody pro- and metazonae 0.15 and 0.2 (♂, ♀), up to 0.2 and 0.25 mm (♀), respectively. Coloration in alcohol uniformly pallid, tegument translucent.

Body moniliform, with 19 segments (♂, ♀). Tegument mainly dull, at most slightly shining, texture very delicately alveolate and microgranulate. Head without modifications, densely pilose throughout except occiput; epicranial suture superficial and thin; genae squarish (Fig. 3A, D, G); gnathochilarium narrow, setae dense and short (Fig. 4A); isthmus between antennae about as broad as diameter of antennal socket (Fig. 3G). Antennae very short, reaching only behind collum (♂, ♀) when stretched dorsally, not geniculate, strongly clavate due to an abruptly and particularly enlarged antennomere 6, the latter with a usual, tight, distodorsal group of numerous bacilliform sensilla, but in ♂ also with a large, highly conspicuous, dorsoparabasal, rounded stump (**s**); antennomere 5 with a loose distodorsal group of only a few tiny sensilla, 7<sup>th</sup> with a tiny mid-dorsal knob (Figs 3G, J, 4A).

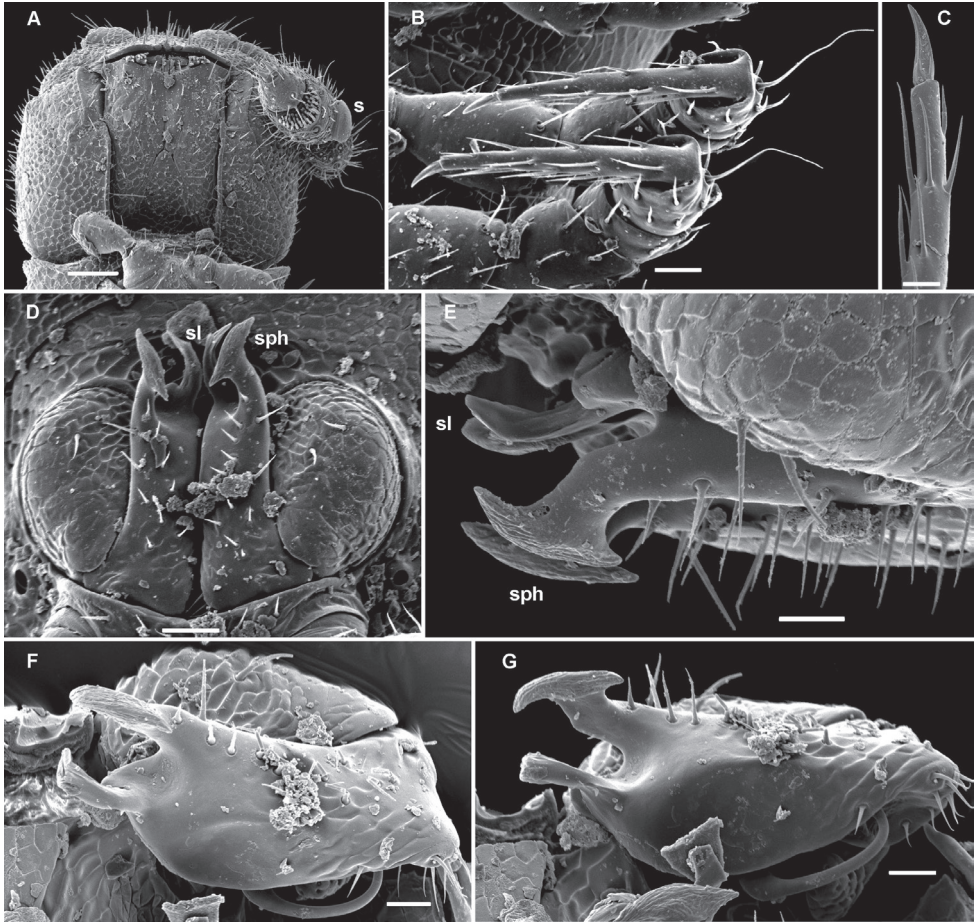
In width, head > segment 2 > collum = segment 3 = 4 > 5(6) = 16 (♂, ♀), thereafter body gradually tapering towards telson (Fig. 3D–F). Paraterga wanting, metazonae subcylindrical, dorsum strongly convex (Fig. 3A–I). Ozopores totally absent (Fig. 3A, B, D–F, K). Collum subovoid, each following metatergum mostly with 4+4 rather long, slightly blunted, subclavate to subbacilliform, thickened and longitudinally ribbed setae arranged in 3 transverse regular rows and borne on minute knobs (Fig. 3A–F, K–M). Stricture between pro- and metazonae rather wide and shallow, scaly like rear part of prozonae. Limbus very fine and microcrenulate (Fig. 3L). Pleurosternal carinae thin lines (Fig. 3A, B, H). Epiproct short, conical, directed caudoventrally; pre-apical papillae small (Fig. 3C, F, I). Hypoproct subtrapeziform, caudal setigerous papillae evident and well separated (Fig. 3I).





**Figure 3.** *Aporodesmella securiformis* sp. n., ♂ paratype from Nui Hang Tien; **A, D, G** anterior part of body, lateral, dorsal and ventral views, respectively **B, E, H** midbody segments, lateral, dorsal and ventral views, respectively **C, F, I** posterior part of body, lateral, dorsal and ventral views, respectively **J** antenna, dorsal view **K** tergal texture and setae, lateral view **L** tergal setae, limb and stricture region, sublateral view **M** tergal seta, lateral view. Scale bars: **A, D, H** 0.1 mm; **B, C, E–G, I, J** 0.05 mm; **K** 0.02 mm; **L** 0.01 mm; **M** 0.005 mm. Designation of antennal structure in text.

Sterna without modifications, rather broad and sparsely setose (Fig. 3H). Legs short, ca 1.3–1.4 (♂) or 1.1–1.2 times as long as midbody height (♀); ♂ prefemora, femora, postfemora and tibiae clearly incrassate, tarsi longest, slender, sphaerotri-



**Figure 4.** *Aporodesmella securiformis* sp. n., ♂ paratype from Nui Hang Tien; **A** head, ventral view **B** midbody legs, ventral view **C** midbody tarsus and claw, lateral view **D**, **E** gonopod aperture and gonopods *in situ*, ventral and lateral views, respectively **F**, **G** left gonopod, subventral and ventromedial views, respectively. Scale bars: **A** 0.05 mm; **B**, **D** 0.02 mm; **C**, **E–J** 0.01 mm. Designations of gonopod structures in text.

chomes missing (Figs 3A, B, 4B), claws simple, slightly curved (Fig. 4B, C); ♂ coxae 2 with short, membranous, cylindrical gonapophyses (Fig. 3G).

Gonopod aperture transversely oblong-oval, slightly subcordate, taking up most of ventral part of metazonite 7 (Fig. 4D). Gonopods (Fig. 4D–G) simple, with globose, scaly, medially fused coxae carrying a few setae on ventral face and a normal canula mesally. Telopodites nearly straight, mostly exposed, *in situ* held parallel to each other, contiguous medially, largely unipartite due to prominent, rather densely setose prefemoral parts, rather short and stout, only distal quarter distinctly divided into a peculiar, axe-shaped, lateral solenophore (**sph**) and a smaller, anteriorly lying, sublanceolate solenomere (**sl**) directed slightly laterad. Seminal groove running entirely mesally, terminating on top of **sl**.

***Aporodesmella similis* sp. n.**

<http://zoobank.org/7DE6B4E3-4698-4D44-8B74-7E7B60BE07D0>

[http://species-id.net/wiki/Aporodesmella\\_similis](http://species-id.net/wiki/Aporodesmella_similis)

Figs 5, 6

**Type material.** Holotype ♂ (MNHN JC 356), Vietnam, Kien Giang Province, Ha Tien, Nui Da Dung, valley, 104.477E, 10.4288N, secondary forest, litter, Berlese extraction, 29.11.2006, leg. L. Deharveng & A. Bedos (Vn06-102).

Paratypes: 1 ♂ (SEM), same locality, together with holotype; 1 ♂, 1 ♀ fragment (MNHN JC 356), 1 ♀ (SEM), same locality, soil, Berlese extraction, 05.12.2005, leg. L. Deharveng & A. Bedos (Vn05-107); 1 ♂ (ZMUM Q2347), same locality, litter, Berlese extraction, 05.12.2005, leg. L. Deharveng & A. Bedos (Vn05-112).

**Name.** To emphasize the particularly strong similarity to the previous new species.

**Diagnosis.** Differs from all congeners, except *A. securiformis* sp. n., in the presence of a peculiar, dorsoparabasal stump on ♂ antennomere 6, from *A. securiformis* sp. n. in the shape of the solenophore and solenomere.

**Description.** Length of adults ca 3.0 mm, width of midbody pro- and metazonae 0.2 and 0.25 mm (♂). Coloration in alcohol uniformly pallid, tegument nearly translucent.

Body moniliform, subcylindrical (Fig. 5A–J), with 19 segments (♂).

All characters as in *A. securiformis* sp. n. (Figs 5, 6A), except as follows.

Gonopods (Fig. 6B, C) more complex, especially due to an elaborate and subtruncate tip of a more elongate and slenderer telopodite. Solenophore branch (**sph**) long, membranous, somewhat spoon-shaped, directed laterad, with a long, caudolateral, similarly membranous, subspiniform process (**s**) starting at base of **sph** and remaining coaxial with a prominent prefemoral portion. Mesal part of telopodite tip divided into 2 small horns (**a** and **b**) bearing a very small, dentiform solenomere (**sl**) lying in front and in between.

***Aporodesmella tergalis* sp. n.**

<http://zoobank.org/4B5EB78A-B952-4DB6-A5F1-F984EC2ADFFE>

[http://species-id.net/wiki/Aporodesmella\\_tergalis](http://species-id.net/wiki/Aporodesmella_tergalis)

Figs 7, 8

Fuhrmannodesmidae gen. sp. – Golovatch et al. 2013: 73.

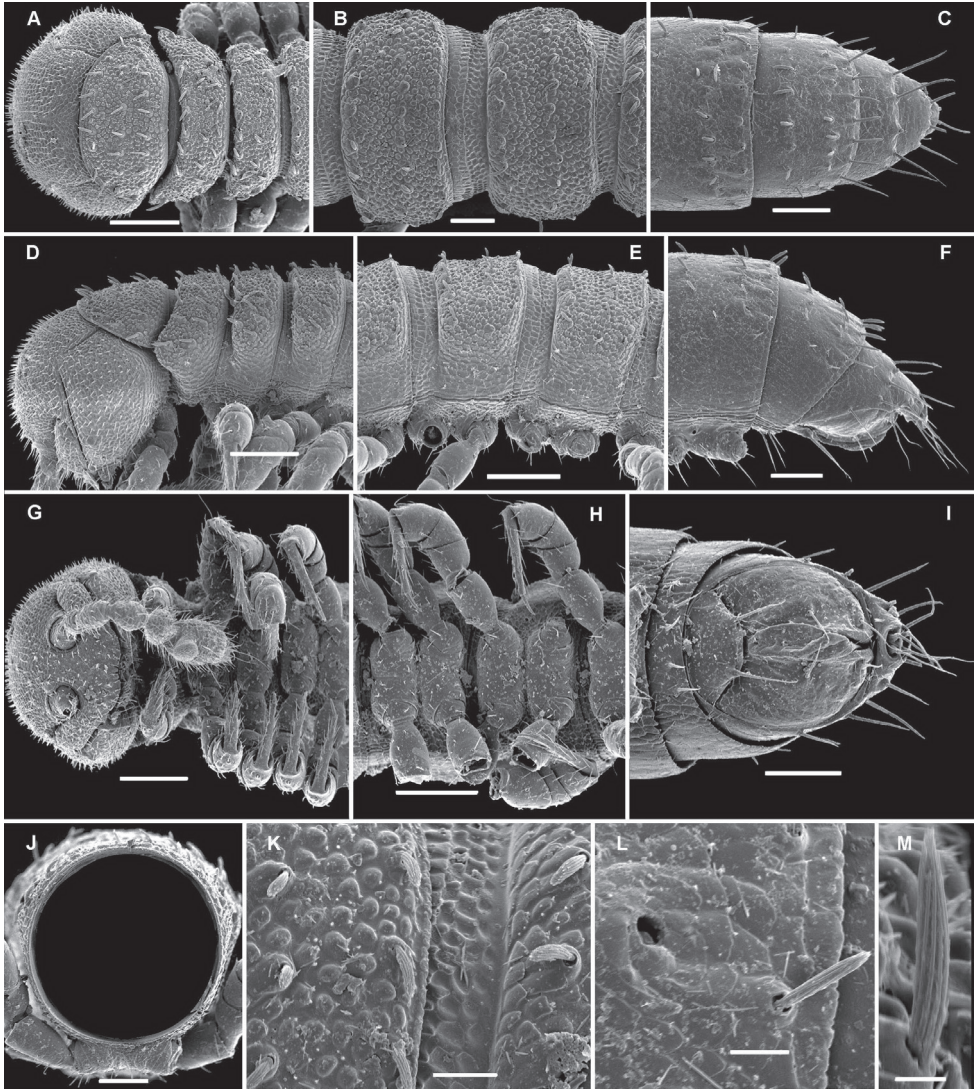
**Type material.** Holotype ♂ (MNHN JC 357), Vietnam, Kien Giang Province, Kien Luong, Hon Chong, Nui Bai Voi, cirque du Français, 104.618799E, 10.218541N, litter, Berlese extraction, 23.08.2003, leg. L. Deharveng & A. Bedos (Vn0308-112).

Paratypes: 1 ♂, 1 ♀ (SEM), same locality, together with holotype.

**Name.** To emphasize the well-developed paraterga.

**Diagnosis.** Differs from congeners by well developed paraterga, short tergal setae, the ♂ also by the presence of a peculiar, central hump above the antennae, the laterally bent, beak-shaped solenophore and the absence of a solenomere.

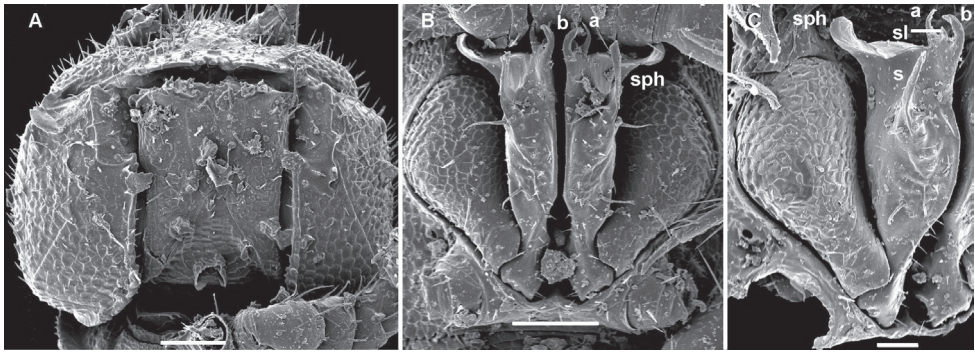




**Figure 5.** *Aporodesmella similis* sp. n., ♂ paratype; **A, D, G** anterior part of body, dorsal, lateral and ventral views, respectively **B, E, H** midbody segments, dorsal, lateral and ventral views, respectively **C, F, I** posterior part of body, dorsal, lateral and ventral views, respectively **J** cross-section of a midbody segment, caudal view **K, L** tergal setae, limb and stricture region, subdorsal views **M** tergal seta, lateral view. Scale bars: A, D, E, G, H 0.1 mm; B, C, F, I, J 0.05 mm; K 0.02 mm; L 0.01 mm; M 0.005 mm.

**Description.** Length of adults ca 4.0 mm, width of midbody pro- and metazonae 0.4 and 0.5 mm (♂). Coloration in alcohol uniformly pallid, tegument nearly translucent.

Body with 19 segments (♂). Tegument dull, texture delicately alveolate, a cera-tegument on metazonae well-developed (Fig. 8A). Head with an evident, round, very finely pilose, central hump above antennae (♂) (Fig. 7D, G), more roughly setose



**Figure 6.** *Aporodesmella similis* sp. n., ♂ paratype; **A** head, ventral view **B** gonopod aperture and both gonopods *in situ*, ventral view **C** right gonopod, ventrolateral view. Scale bars: **A**, **B** 0.05 mm; **C** 0.02 mm. Designations of gonopod structures in text.

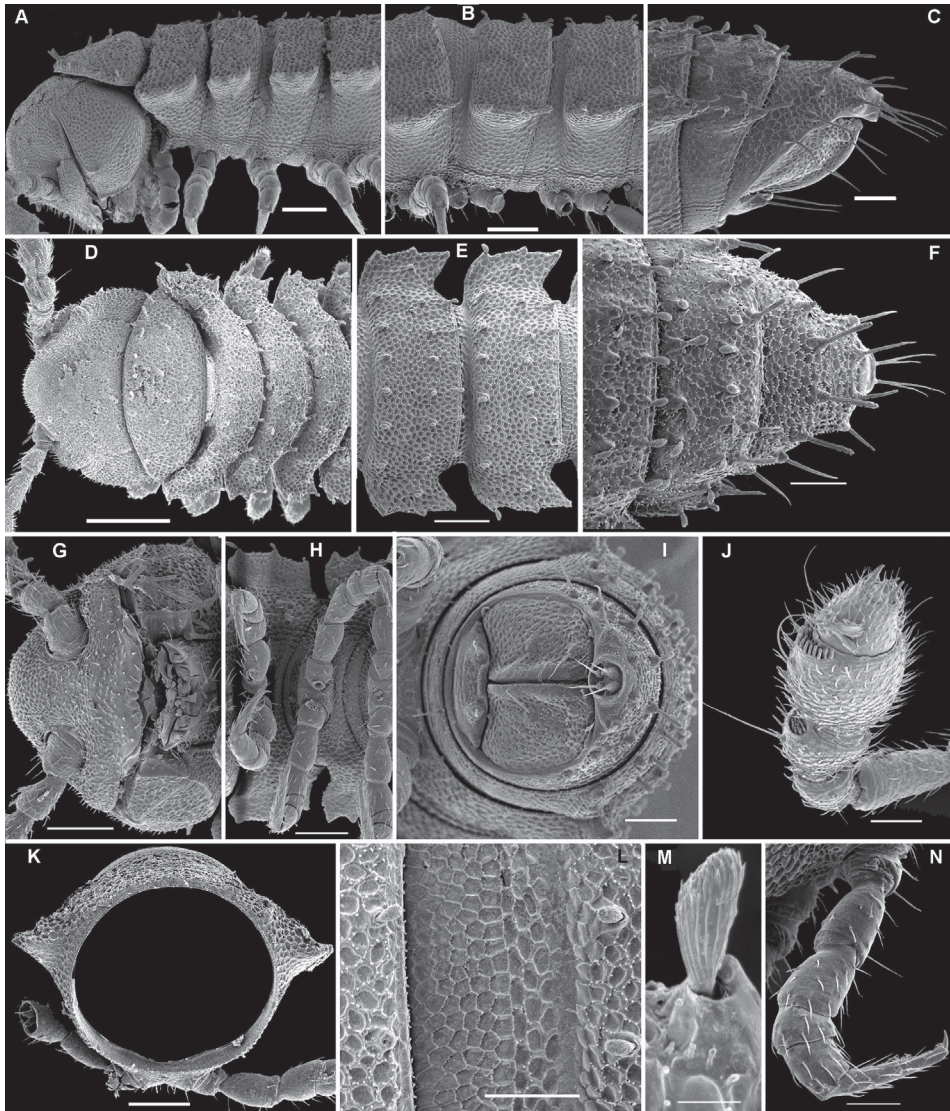
over remaining surface except occiput; epicranial suture superficial; genae squarish (Fig. 7A, D, G); gnathochilarium narrow, setae on lamellae linguales particularly strong (Fig. 8B); isthmus between antennae about 1.5 times as broad as diameter of antennal socket (Fig. 7G). Antennae very short, reaching only behind collum when stretched dorsally, not geniculate, strongly clavate due to an abruptly and particularly enlarged antennomere 6, the latter with a usual, tight, distodorsal group of numerous bacilliform sensilla, antennomere 5 with a smaller, but also compact, distodorsal group of only a few shorter sensilla, 7<sup>th</sup> with a tiny mid-dorsal knob (Fig. 7J).

In width, head = collum < segment 3 = 4 < 2 < 5 = 16 (♂), thereafter body gradually tapering towards telson (Fig. 7D–F). Paraterga well-developed, set low (at about upper 1/3–1/2 of body height), mostly clearly declined (Fig. 7A–F, K), front edges moderately convex and forming a shoulder, caudal edges increasingly strongly concave caudad, lateral edges mostly straight, on each side with 3 setigerous, equidistant knobs; caudal corners mostly nearly sharp, lying within rear tergal margin until segment 10, thereafter increasingly well produced behind the margin (Fig. 7A–F). Ozopores totally absent (Figs 7A–F, I, 8A). Collum biconvex, nearly sharp laterally on both sides, with 3 transverse rows of short setae (Fig. 7D). Each following metatergum mostly with 3+3 short, slightly blunted, clavate, thickened and longitudinally ribbed setae arranged in 3 transverse regular rows and borne on minute knobs; sulci between the rows absent (Figs 7A–F, M, 8A). Stricture between pro- and metazonae rather shallow and narrow, scaly like rear part of prozonae (Fig. 7E, L). Limbus very fine, very delicately and sparsely microdenticulate (Fig. 7L). Pleurosternal carinae absent (Fig. 7A, B, H). Epiproct short, conical, truncate, directed caudoventrally; pre-apical papillae large (Fig. 7C, F, I). Hypoproct subtrapeziform, caudal setigerous papillae well-developed and clearly separated (Fig. 7I).

Sterna without modifications, rather broad and sparsely setose. Legs short, ca 1.2–1.3 times as long as midbody height (♂); prefemora, femora, postfemora and tibiae clearly incrassate, tarsi longest, slender, sphaerotrichomes missing; claws simple, slightly curved (Fig. 7N); ♂ coxae 2 with very short, membranous, cylindrical gonapophyses (Fig. 7H).

Gonopod aperture transversely oblong-oval, slightly subcordate, taking up most of ventral part of metazonite 7 (Fig. 8C). Gonopods (Fig. 8C–F) rather complex, with

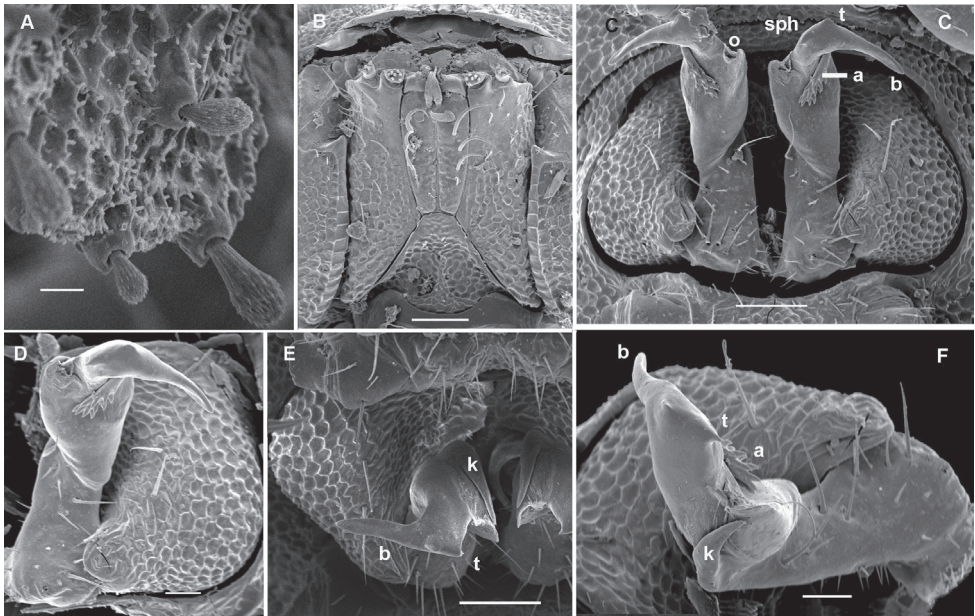




**Figure 7.** *Aporodesmella tergalis* sp. n., ♂ paratype; **A, D** anterior part of body, lateral and dorsal views, respectively **B, E** midbody segments, lateral and dorsal views, respectively **C, F, I** posterior part of body, lateral, dorsal and caudal views, respectively **G** head, ventral view **H** legs 1 and 2, ventral view **J** antenna, sublateral view **K** cross-section of a midbody segment, caudal view **L** tergal setae, limbus and stricture region, subdorsal view **M** tergal seta, lateral view **N** midbody leg. Scale bars: **D** 0.2 mm; **A, B, E, G, H, K** 0.1 mm; **C, F, I, J, L, N** 0.05 mm; **M** 0.005 mm.

globose, microgranulate, medially fused coxae carrying a few setae on ventral face and a normal cannula mesally. Telopodites mostly exposed, *in situ* held parallel to each other, nearly contiguous medially, each unipartite, with a rather large, densely setose prefemoral part clearly set off from acropodite by an oblique ventral sulcus and a curved dorsal spine (**k**); acropodite divided into 2 subequally long parts, each also about equal in





**Figure 8.** *Aporodesmella tergalis* sp. n., ♂ paratype; **A** cerategument and tergal setae, sublateral view **B** gnathochilarium, ventral view **C** gonopod aperture and both gonopods *in situ*, ventral view **D**, **F** left gonopod, subventral and submesal views, respectively **E** right gonopod, anteroventral view. Scale bars: **B**, **C**, **E** 0.05 mm; **D**, **F** 0.02 mm; **A** 0.01 mm. Designations of gonopod structures in text.

length to prefemoral portion; basal half of acropodite remaining coaxial with prefemoral portion, slightly broadened distad and carrying an evident orifice (**o**) of a fully mesally running seminal groove on a vestigial mesal solenomere (= tubercle), whereas distal half of acropodite, or solenophore (**sph**), acuminate, directed abruptly laterad, subflagelliform (**b**), carrying a parabasal apical tooth (**t**) and a conspicuous, curved, denticulate lamina (**a**) beginning from near **o** and turning around **b** on lateral side.

**Remarks.** This species served elsewhere (Golovatch et al. 2013) to illustrate a somewhat transitional condition in its gonopod structure, especially an elongate and laterad directed apical part, between the Trichopolydesmidae (= “Fuhrmannodesmidae”) and Opisetretidae within the same superfamily Trichopolydesmoidea. A far more spectacular example of the same trend is seen in *Gonatodesmus* gen. n. (see below).

### *Deharvengius* gen. n.

<http://zoobank.org/063BDEC3-966B-4AC3-98CF-CE76FDF85D86>

<http://species-id.net/wiki/Deharvengius>

**Diagnosis.** 18 segments (♂, ♀); pore formula normal: 5, 7, 9, 10, 12, 13, 15–17; head modified in both sexes in being somewhat flattened dorsoventrally; paraterga very poorly developed, serrate/microdentate at lateral edge, with 3 rows of 2+2, long,

simple setae (regardless of lateral setae); gonopod coxae with gonocoel not deep; telopodites clearly exposed, but lying tightly appressed and parallel to venter, strongly curved, semi-circular, unipartite, slender, directed mesad and strongly overlapping; prefemoral parts about half as long as telopodites, set off from acropodites neither by a sulcus nor a cingulum; acropodites with small solenophores (**sph**) lying basal to a spiniform, apical solenomere (**sl**). Seminal groove running mostly along ventral surface of subbasally obviously twisted acropodites.

**Name.** To honour Louis Deharveng (MNHN), one of the principal collectors, masculine.

**Type species.** *Deharvengius bedosae* sp. n., by present designation.

**Remarks.** In having only 18 body segments, this new genus is almost unique amongst the Trichopolydesmoidea. The same segment counts seem to solely concern *Moojenodesmus pumilus* Schubart, 1944, only one of the species of the rather small Neotropical genus *Moojenodesmus* Schubart, 1945, from the same family Trichopolydesmidae; *M. pumilus* is especially minute (< 2.5 mm long), and it seems to be parthenogenetic and quite widespread in Brazil (Golovatch 1992, 1994). Among the Oriental Trichopolydesmidae, partly globally as well, *Deharvengius* gen. n. stands well apart also in having a less convex head, only 2+2 tergal setae per row and very unusual gonopods. The latter are long, simple, unipartite, strongly curved and crossing medially, thus being quite similar to the condition observed in *Cocacolaria* (Fig. 2B–E). Yet in *Deharvengius* gen. n. the gonopods are much more strongly appressed to the venter while the seminal groove runs mostly on the ventral = lateral (not mesal) side to terminate apically on a simple and slender (not at about midway on a stout and calyciform) solenomere. By its habitus and even gonopod structure, *Deharvengius* gen. n. resembles some Euro-Mediterranean genera of Trichopolydesmidae as well (see reviews by Mauriès (1983) and Golovatch et al. (2013)). Some of them show a deeply bipartite and strongly curved gonopod telopodite, the prefemoral part of which is quite elongate, but lies more or less transversely to strongly angular, largely (sub)parallel telopodites and extends across the nearly entire ventral width of segment 7. Such are *Trichopolydesmus* Verhoeff, 1898 (together with the subgenus *Banatodesmus* Tabacaru, 1980), *Bacillidesmus* Attems, 1898, *Napocodesmus* Ceuca, 1974 and *Caucasodesmus* Golovatch, 1985. In contrast, the gonotelopodites in *Verhoeffodesmus* Strasser, 1959, *Cottodesmus* Verhoeff, 1936 and *Occitanocookia* Mauriès, 1980 have increasingly shortened prefemoral parts, being enlarged and laterally flattened distad and unipartite, but mostly less strongly curved, in *Cottodesmus* and *Occitanocookia* also devoid of a solenomere, but sometimes supplied instead with what can be seen as a primordial accessory seminal chamber. In *Trichopolydesmus*, *Heterocookia* Silvestri, 1898, *Ingurtidorgius* Strasser, 1974 and, especially, *Mastigonodesmus* Silvestri, 1898, the solenomere is almost to fully flagelliform, branching off near the base of the femorite. In all these genera, the gonotelopodites are strongly exposed, not sunken inside an obvious gonocoel (Golovatch et al. 2013).

*Deharvengius* gen. n. currently contains only one species.

***Deharvengius bedosae* sp. n.**

<http://zoobank.org/5C60DC06-021E-402F-8D03-871532155442>

[http://species-id.net/wiki/Deharvengius\\_bedosae](http://species-id.net/wiki/Deharvengius_bedosae)

Figs 9, 10

**Type material.** Holotype ♂ (MNHN JC 358), Vietnam, Kien Giang Province, Kien Luong, Hon Chong, Nui Bai Voi (cirque sud), 104.617E, 10.2199N, soil, Berlese extraction, 26.11.2008, leg. L. Deharveng & A. Bedos (Vn06-30).

Paratypes: 2 ♀, 4 juv. (subadults) (MNHN JC 358), same province, Kien Luong, Hon Chong, Nui Bai Voi (cirque sud), 104.617E, 10.2199N; soil, Berlese extraction, 02.06.2008, leg. L. Deharveng & A. Bedos (Vn08-055); 1 ♂, 2 ♀ (MNHN JC 358), 1 ♂ (ZMUM 02348), 1 ♂, 1 juv. (subadult) (SEM), same province, Hon Chong, Nui Khoe La, soil, Berlese extraction, 01.06.2008, leg. L. Deharveng & A. Bedos (Vn08-027).

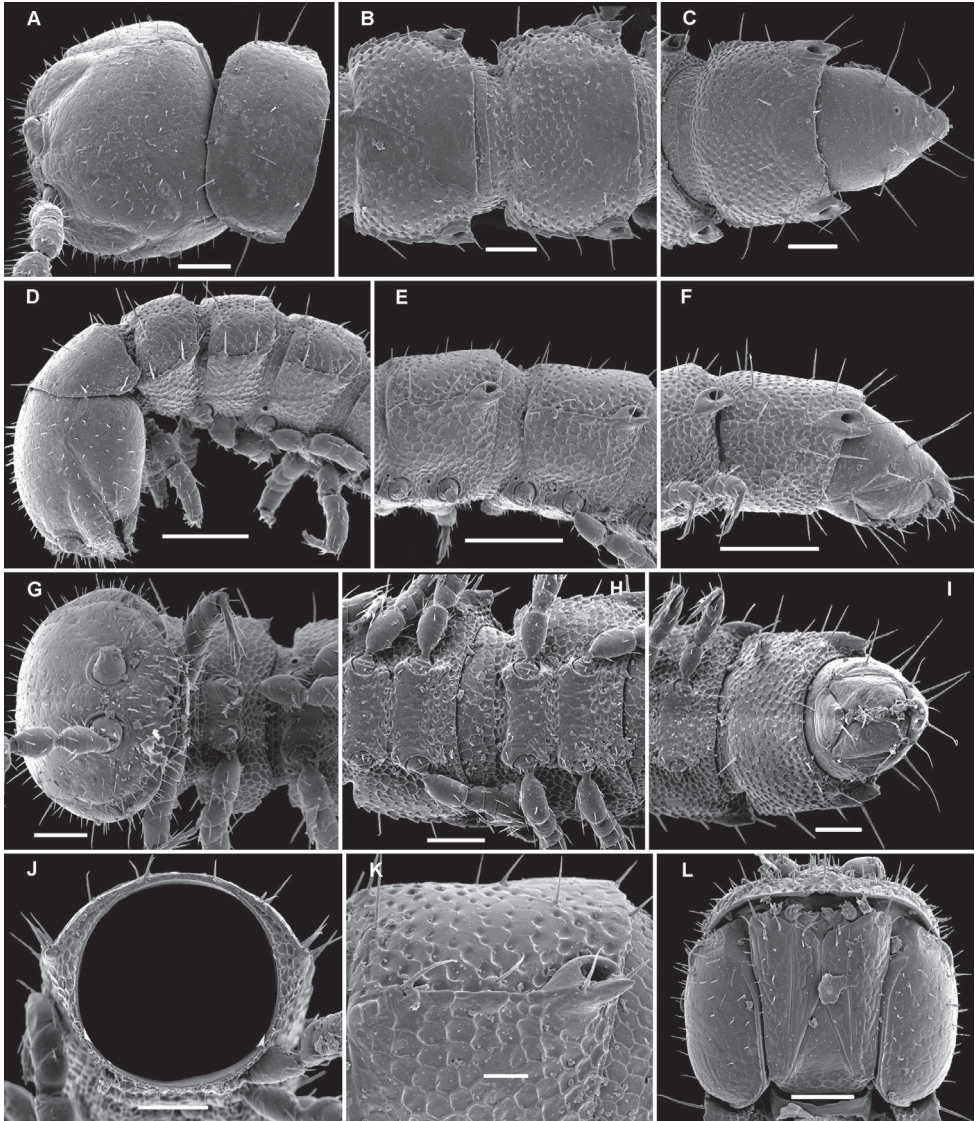
**Name.** To honour Anne Bedos (MNHN), one of the principal collectors.

**Description.** Length of adults ca 3.0 mm, width of midbody pro- and metazonae 0.3 and 0.45 mm (♂, ♀). Coloration in alcohol uniformly pallid, tegument often nearly translucent.

Body with 18 segments (♂, ♀). Tegument dull, texture of metazonae very delicately punctate on dorsum and sterna, but alveolate laterally below paraterga; collum smooth (Fig. 9A–K). Head relatively sparsely and finely pilose, less convex than usual (♂, ♀); epicranial suture superficial; genae squarish (Fig. 9A, D, G, L); gnathochilarium narrow, sparsely and uniformly setose (Fig. 9L); isthmus between antennae about 0.8 times as broad as diameter of antennal socket (Fig. 9A, G). Antennae very short (Fig. 10A), reaching only behind head when stretched dorsally, not geniculate, strongly clavate due to an abruptly and particularly enlarged antennomere 6, the latter with a usual, tight, distodorsal group of rather numerous, bacilliform sensilla; antennomere 7 with a smaller distodorsal group of only a few shorter and curved sensilla in front of a tiny mid-dorsal knob.

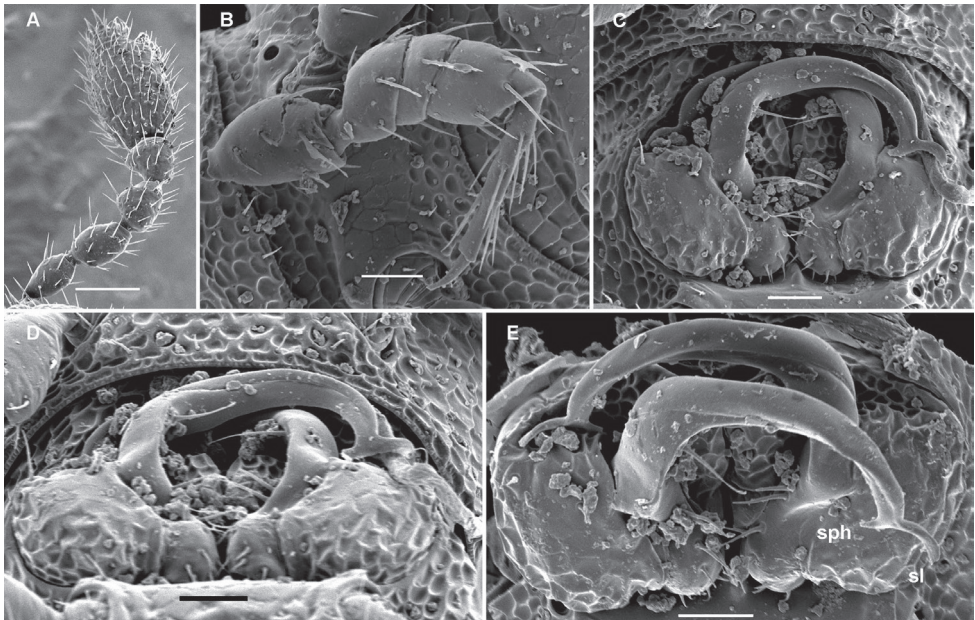
Body moniliform, subcylindrical (Fig. 9A–J). In width, head > segments 5–15 > 2 > 3 = 4 > collum; body gradually tapering on segments 16–18 (Fig. 9A–I). Paraterga very poorly developed, starting from collum, set low (at about upper 1/3–1/2 of body height), mostly represented by vestigial, delicately serrate ridges and sharp caudal teeth, the latter being clearly enlarged and slightly produced behind rear tergal margin in poriferous segments (Fig. 9A–K). Ozopores evident, ovoid, dorsolateral, lying about equally close to caudal corner and lateral edge (Fig. 9B, C, E, F, K). Collum roundly subquadrate, with 3 transverse rows of long setae dorsally and 2 similar setae on paraterga (Fig. 9A). Each following metatergum mostly with 2+2 long and pointed setae arranged in 3 transverse regular rows and not borne on knobs; sulci between the rows absent (Fig. 9B–F). Stricture between pro- and metazonae rather deep and narrow, scaly like rear part of prozonae (Fig. 9B, E). Limbus very fine, very delicately and sparsely microdenticulate (Figs 9J, K, 10D). Pleurosternal carinae absent (Fig. 9D–F). Epiproct short, conical, truncate, directed caudoventrally; pre-apical papillae small (Fig. 9C, F, I). Hypoproct subtrapeziform, relatively high and narrow, caudal setigerous papillae large and moderately separated, with a faintly convex edge in between (Fig. 9I).





**Figure 9.** *Deharvengius bedosae* sp. n., ♂ paratype from Nui Khoe La; **A, D, G** anterior part of body, dorsal, lateral and ventral views, respectively **B, E, H** midbody segments, dorsal, lateral and ventral views, respectively **C, F, I** posterior part of body, dorsal, lateral and ventral views, respectively **J** cross-section of a midbody segment, caudal view **K** poriferous midbody paratergite, tergal setae, tegument structure, limbus and stricture region **L** head, ventral view. Scale bars: **D–F** 0.1 mm; **A–C, G–J, L** 0.05 mm; **K** 0.02 mm.

Sterna without modifications, rather broad and sparsely setose (Fig. 9G–I). Legs short, ca 1.2–1.3 (♂) or 1.0–1.1 (♀) times as long as midbody height; prefemora, femora, postfemora and tibiae clearly incrassate, especially so in ♂ (Fig. 10B), tarsi longest, slender, sphaerotrichomes missing; claws simple, slightly curved; ♂ coxae 2 with very short, membranous, cylindrical gonapophyses (Fig. 9G).



**Figure 10.** *Deharvengius bedosae* sp. n., ♂ paratype from Nui Khoe La; **A** antenna, lateral view **B** midbody leg, lateral view **C–E** gonopod aperture and both gonopods *in situ*, ventral, ventrocaudal and anteroventral views, respectively. Scale bars: **A** 0.05 mm; **B–E** 0.02 mm Designations of gonopod structures in text.

Gonopod aperture transversely oblong-oval, taking up most of ventral part of metazonite 7 (Fig. 10C–E). Gonopod coxae with gonocoel not deep; telopodites clearly exposed, but lying tightly appressed and parallel to venter, strongly curved, semi-circular, unipartite, slender, directed mesad and strongly overlapping; prefemoral parts about half as long as telopodites, set off from acropodites neither by a sulcus nor a cingulum; each acropodite with a small solenophore (**sph**) lying basal to a spiniform, apical solenomere (**sl**). Seminal groove running mostly along ventral (= lateral) surface of a subbasally obviously twisted acropodite.

### *Gonatodesmus* gen. n.

<http://zoobank.org/7F9F0843-BD27-4A71-8995-91722D9CB039>

<http://species-id.net/wiki/Gonatodesmus>

**Diagnosis.** 19 segments (♂, ♀); pore formula normal: 5, 7, 9, 10, 12, 13, 15–18; ♂ head with a considerable, rounded, central hump above antennae; paraterga poorly developed, serrate/microdentate at lateral edge, with 3 rows of 3+3 or 4+4, long, bacilliform setae (regardless of lateral setae); gonopod coxae with gonocoel not deep; telopodites clearly exposed, but lying rather tightly appressed and mostly parallel to venter, unipartite, slender, abruptly geniculate and directed laterad distal to prefemoral

parts, the latter about half as long as telopodites, held parallel to main axis, each set off from a twisted acropodite by a geniculation cingulum (**c**); acropodites elongate, near midway with a remarkably large hairy pulvillus (**p**) on top of a small accessory seminal chamber; neither a separate solenophore branch nor a solenomere. Seminal groove (**sg**) running mostly on mesal side, turning caudad (= ventrad) only beyond geniculation.

**Name.** To emphasize the geniculated gonopod telopodite (γόνατο meaning “a knee” in Greek), masculine.

**Type species.** *Gonatodesmus communicans* sp. n., by present designation.

**Remarks.** This new genus is highly disjunct in being the sole member of the family which shows a remarkable midway geniculation of the gonopod telopodite. The gonopod tip being directed laterad is not unique in *Trichopolydesmidae*, shared also with *Aporodesmella tergalis* sp. n. However, the entire distal, post-geniculation half of the gonopod in *Gonatodesmus* gen. n. is obviously twisted and strongly elongate, also showing a remarkably distinct hairy pulvillus on top of a small, but evident accessory seminal chamber. Only vestiges of the latter are occasionally observed in a couple of Euro-Mediterranean genera of *Trichopolydesmidae* (Golovatch 2013), whereas an obvious hairy pulvillus seems to be singular in the family. In contrast, such a gonopod conformation vividly resembles the conditions largely characterizing the family *Opisotretidae* (Golovatch et al. 2013), but the prefemoral parts in *Gonatodesmus* gen. n. are clearly elongate and held parallel to the main axis while the acropodites distal to the unique geniculation are yet relatively short to be directed dorsolaterad. So the assignment of *Gonatodesmus* gen. n. to *Trichopolydesmidae*, not *Opisotretidae*, is preferred. However, one may justly regard *Gonatodesmus* gen. n. as a kind of transition or bridge between these two families of *Trichopolydesmoidea*. This new genus rather demonstrates an evolutionary trend from the more basal *Trichopolydesmidae* towards the advanced *Opisotretidae*.

***Gonatodesmus communicans* sp. n.**

<http://zoobank.org/3B7B82CD-75D0-4444-9E99-4FB6C7741F60>

[http://species-id.net/wiki/Gonatodesmus\\_communicans](http://species-id.net/wiki/Gonatodesmus_communicans)

Figs 11, 12

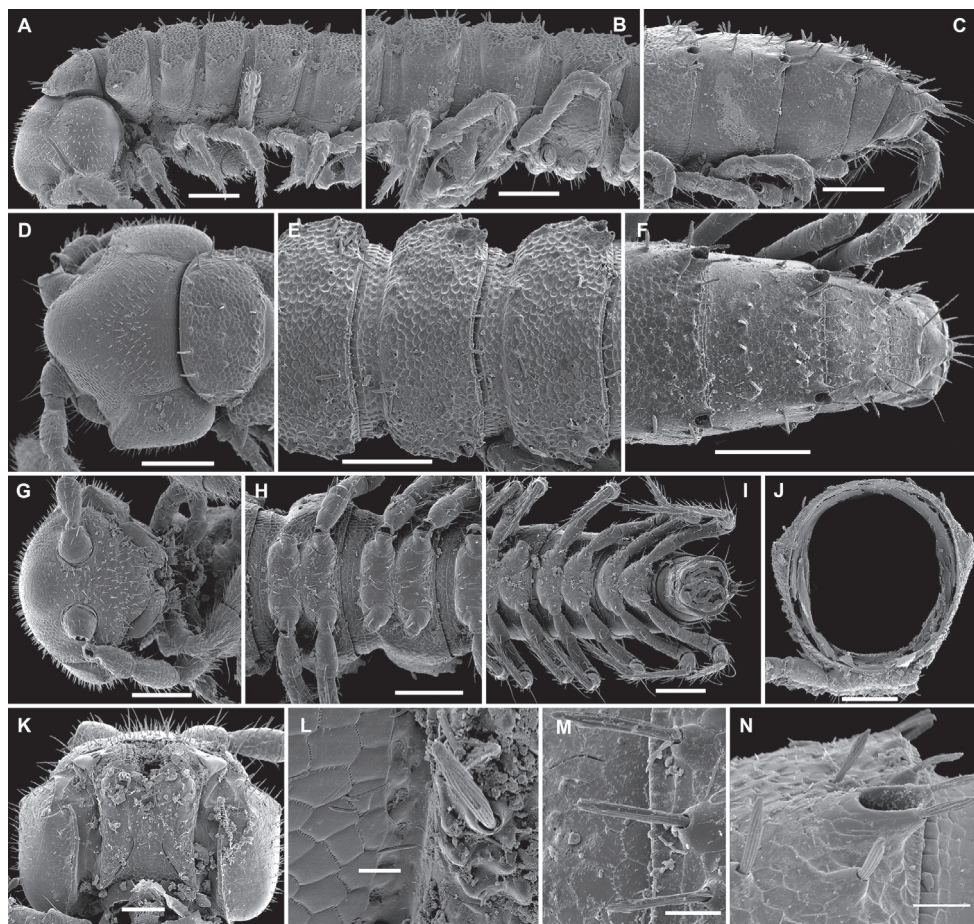
**Type material.** Holotype ♂ (MNHN JC 359), Vietnam, Dongnai Prov., Cat Tien National Park, 107°10'–107°34'E, 11°21'–11°48'N, lowland tropical forest, litter and topsoil, 01.06.2005, leg. A. Anichkin.

Paratypes: 5 ♂, 1 ♀ (MNHN JC 359), 9 ♂, 1 ♀, 1 juv. (ZMUM 2336–2339), 1 ♂ (SEM), 1 ♂ (ZMUC), same locality, together with holotype; 1 ♀ (MNHN JC 359), same locality, 15.07.2005, leg. A. Anichkin.

**Name.** The species epithet refers to the gonopod conformation somewhat transitional between the families *Trichopolydesmidae* and *Opisotretidae*.

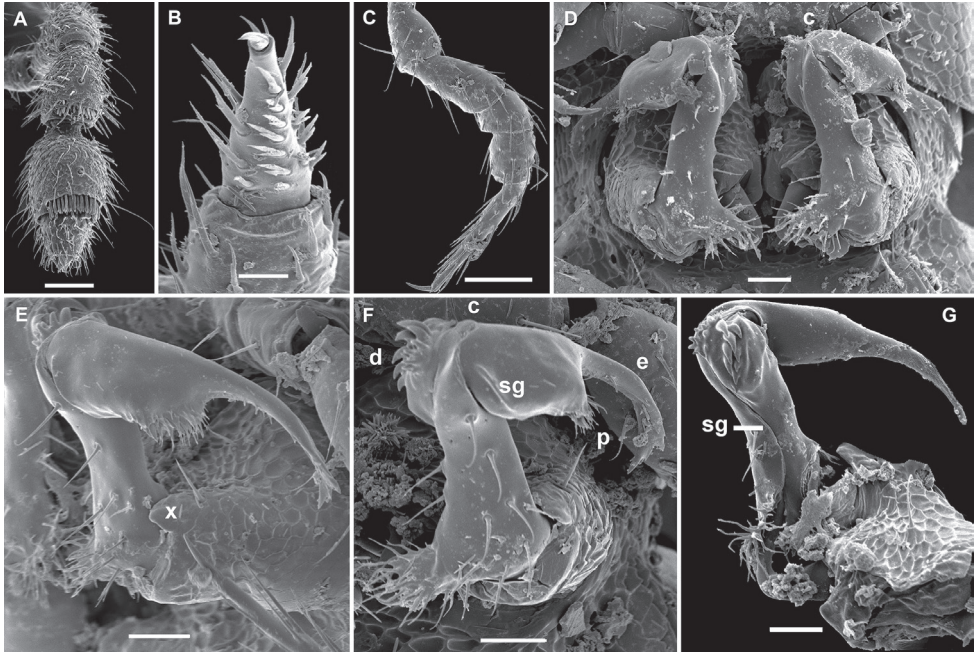
**Description.** Length of adults ca 2.8–3.7 mm, width of midbody pro- and metazonae 0.2–0.25 and 0.28–0.4 mm (♂, ♀). Coloration in alcohol uniformly pallid, tegument often nearly translucent.





**Figure 11.** *Gonatodesmus communicans* sp. n., ♂ paratype; **A, D, G** anterior part of body, lateral, dorsal and ventral views, respectively **B, E, H** midbody segments, lateral, dorsal and ventral views, respectively **C, F, I** posterior part of body, lateral, dorsal and ventral views, respectively **J** cross-section of a midbody segment, caudal view **K** head, ventral view **L, M** poriferous midbody paratergite, tergal setae, tegument structure, limb and stricture region **N** ozopore region of segment 16, subdorsal view. Scale bars: **A–D, F–J** 0.1 mm; **E, K** 0.05 mm; **N** 0.02 mm; **L, M** 0.01 mm.

Body with 19 segments (♂, ♀). Tegument dull, texture of pro- and metazonae delicately alveolate to scaly, metaterga a little more roughly alveolate, only sterna mostly smooth (Fig. 11A–I). Head very densely and finely pilose; epicranial suture absent (♂) or superficial (♀); genae squarish (Fig. 11A, D, G, K); gnathochilarium narrow, sparsely and uniformly setose (Fig. 11K); isthmus between antennae about 1.2 times as broad as diameter of antennal socket (Fig. 11G). Antennae short (Figs 11A, G, 12A), reaching only behind collum when stretched dorsally, not geniculate, rather strongly clavate due to a particularly enlarged antennomere 6, the latter with a usual, tight, distodorsal group of numerous, bacilliform sensilla; a similar, but



**Figure 12.** *Gonatodesmus communicans* sp. n., ♂ paratype; **A** antennomeres 4–8, dorsal view **B** tarsus 1, ventral view **C** midbody leg, lateral view **D** both gonopods *in situ*, ventral view **E–G** left gonopod, antero-ventral, ventral and submesal views, respectively. Scale bars: **A**, **C** 0.05 mm; **D–G** 0.02 mm; **B** 0.01 mm. Designations of gonopod structures in text.

smaller, also distodorsal group of sensilla on antennomere 5; antennomere 7 with a smaller distodorsal group of only a few shorter and curved sensilla in front of a tiny mid-dorsal knob.

In width, collum < segment 3 = 4 < 2 = 5 < 6–15 < head; body gradually tapering on segments 16–18 (Fig. 11A–I). Paraterga poorly developed, starting from collum, set rather low (at about upper 1/3 of body height, Fig. 11J), at most small ridges with 2–3 lateral, setigerous knobs, caudal corner never produced behind rear tergal margin even in poriferous segments (Fig. 11A–F, N). Ozopores evident, ovoid, dorsolateral, mostly lying closer to lateral edge, but in segments 15–18 slightly elevated and positioned closer to caudal edge between 2 subequal, setigerous stalks (Fig. 11N). Collum regularly rounded, transversely oblong-oval, with 3 transverse rows of 4+4, 2+2 and 3+3 rather long setae dorsally and 2 similar setae on paraterga (Fig. 11A, D). Each following metatergum with 3+3 or 4+4, similarly long, bacilliform, delicately ribbed setae arranged in 3 transverse regular rows and borne on knobs; sulci between the rows absent (Fig. 11A–F, L–N). Stricture between pro- and metazonae rather deep and narrow, micro-alveolate like metazonae (Fig. 11E, L, N). Limbus very fine, delicately and densely microcrenulate (Fig. 11E, N). Pleurosternal carinae absent (Fig. 11A–C). Epiproct short, conical, truncate, directed caudoventrally; pre-apical papillae very small (Fig. 11C, F).

Hypoproct subtrapeziform, caudal setigerous papillae large and well separated, with a faintly convex edge in between (Fig. 11I).

Sterna without modifications, rather broad and sparsely setose (Fig. 11H, I). Legs short and stout, ca 1.2–1.3 (♂) or 1.0–1.1 (♀) times as long as midbody height; prefemora, femora, postfemora and tibiae clearly incrassate, especially so in ♂ (Fig. 12C), tarsi longest, slender, sphaerotrichomes missing; claws simple, slightly curved; ♂ tarsi 1 with peculiar, bi- or trifid setae ventrally (Fig. 12B); ♂ coxae 2 with very short, membranous, cylindrical gonapophyses (Fig. 11G).

Gonopod aperture transversely oblong-oval, taking up most of ventral part of metazonite 7 (Fig. 12D). Gonopod coxae (Fig. 12D–G) rather small (gonocoel not deep), sparsely setose and clearly micropapillate laterally, each with a subtriangular ventral projection (**x**); telopodites clearly exposed, but lying rather tightly appressed and parallel to venter, unipartite, slender, abruptly geniculate and directed laterad distal to prefemoral parts, the latter about half as long as telopodites, held parallel to main axis, each with an apicomedian field of strong curved spines (**d**), set off from a twisted acropodite by a strong geniculation cingulum (**c**); acropodite elongate, near midway with a remarkably large hairy pulvillus (**p**) on top of a small accessory seminal chamber; acropodite distal to pulvillus particularly slender, slightly curved caudad, subacuminate; neither a separate solenophore branch nor a solenomere. Seminal groove (**sg**) running mostly on mesal side, turning caudad (= ventrad) only beyond geniculation.

### ***Helicodesmus* gen. n.**

<http://zoobank.org/77E87B7A-EABE-494E-A6C1-4BB38BA7E280>

<http://species-id.net/wiki/Helicodesmus>

**Diagnosis.** 19 segments (♂, ♀); pore formula normal: 5, 7, 9, 10, 12, 13, 15–18; head without modifications; paraterga poorly developed, metaterga with 3 rows of 3+3 or, more rarely, 4+4, long, bacilliform setae (regardless of lateral setae); gonopod coxae with gonocoel not deep; telopodites rather clearly exposed and transverse, but stout and remarkably complex, very strongly twisted, partly fimbriate/plumose distally, with several outgrowths of varying shapes; prefemoral part about half the height of telopodite, demarcated on lateral (not medial!) side by an oblique seminal groove running further mesad onto a medioventral outgrowth of acropodite to terminate distally, with neither a solenomere nor an accessory seminal chamber, nor a pulvillus.

**Name.** To emphasize the strongly helicoid gonopod telopodite, masculine.

**Type species.** *Helicodesmus anichkini* sp. n., by present designation.

**Remarks.** This new genus is remarkable within Trichopolydesmidae in showing particularly strongly twisted gonopods, including their prefemoral parts, such that the seminal groove turns ca 180° around the highly complex transverse acropodite. Also noteworthy is the complete lack of a solenomere.



***Helicodesmus anichkini* sp. n.**

<http://zoobank.org/981D48EE-2D59-4940-8954-4CA702DD2B5C>

[http://species-id.net/wiki/Helicodesmus\\_anichkini](http://species-id.net/wiki/Helicodesmus_anichkini)

Figs 13–15

**Type material.** Holotype ♂ (MNHN JC 360), Vietnam, Dongnai Prov., Cat Tien National Park, 107°10'–107°34'E, 11°21'–11°48'N, lowland tropical forest, litter and topsoil, 01.06.2005, leg. A. Anichkin.

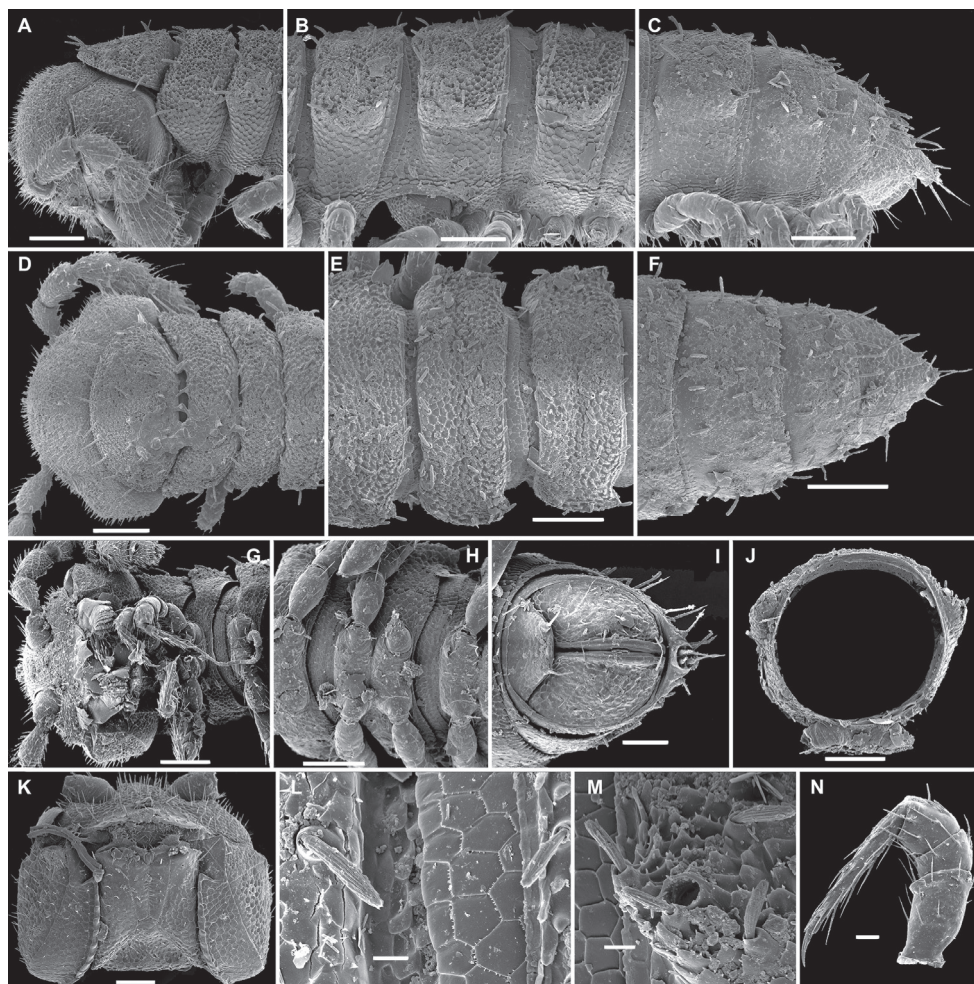
Paratypes: 2 ♂, 1 ♀ (ZMUM 02340, 02343), 1 ♂ (SEM), same locality, together with holotype; 1 ♂ (ZMUM 02342), same locality, 01.04.2005; 2 ♂ (MNHN JC 360), 1 ♂ (ZMUM 02341), same locality, 15.07.2005; 1 ♂, 1 ♀ (MNHN JC 360), 2 ♂ (ZMUM 02344, 02345), same locality, 23.11.2005; 1 ♂ (MNHN JC 360), same locality, 17.07.2005; 1 ♂ (ZMUC), same locality, 15.05.2005, all leg. A. Anichkin.

**Name.** To honour Alexander E. Anichkin, who provided for study all millipede material he had collected in Cat Tien National Park, including three trichopolydesmids described here.

**Description.** Length of adults ca 3.0–4.0 mm, width of midbody pro- and metazonae 0.28–0.32 and 0.4–0.45 mm (♂, ♀). Coloration in alcohol uniformly pallid, tegument often nearly translucent.

Body with 19 segments (♂, ♀). Tegument dull, texture of nearly entire body delicately alveolate to scaly, only sterna nearly smooth (Fig. 13A–I). Head very densely and finely pilose; epicranial suture highly superficial; genae squarish (Fig. 13A, D, G, K); gnathochilarium rather broad, sparsely and uniformly setose (Fig. 13K); isthmus between antennae about 1.2–1.3 times as broad as diameter of antennal socket (Fig. 13G, K). Antennae short (Fig. 13A, D, G), reaching only behind collum when stretched dorsally, not geniculate, rather strongly clavate due to a particularly enlarged antennomere 6, the latter with a usual, tight, distodorsal group of numerous, bacilli-form sensilla; a similar, but smaller, also distodorsal group of sensilla on antennomere 5; antennomere 7 with a smaller distodorsal group of only a few shorter and curved sensilla in front of a tiny mid-dorsal knob.

In width, collum = segment 3 = 4 < 5 < 2 < 6–15 < head; body gradually tapering on segments 16–18 (Fig. 13D–F). Paraterga mostly moderately wide, starting from collum, set rather low (at about upper 1/3 of body height, Fig. 13J), at most small ridges with 2–3 lateral, setigerous knobs, absent from segment 18, caudal corner never produced behind rear tergal margin even in poriferous segments (Fig. 13A–G, M). Ozopores evident, ovoid, dorsolateral, mostly lying closer to lateral edge (Fig. 13M). Collum biconvex, sides (= paraterga) narrowly rounded, dorsal surface with 3 transverse rows of 5+5, 3+3 and 4+4 rather long setae dorsally and 2 similar setae on paraterga (Fig. 13A, D). Each following metatergum with 3+3 or, more rarely, 4+4, similarly long, bacilliform, delicately ribbed setae arranged in 3 transverse regular rows and borne on knobs; sulci between the rows absent (Fig. 13A–G, L, M). Stricture between pro- and metazonae rather deep and narrow, microalveolate like adjacent metazonae

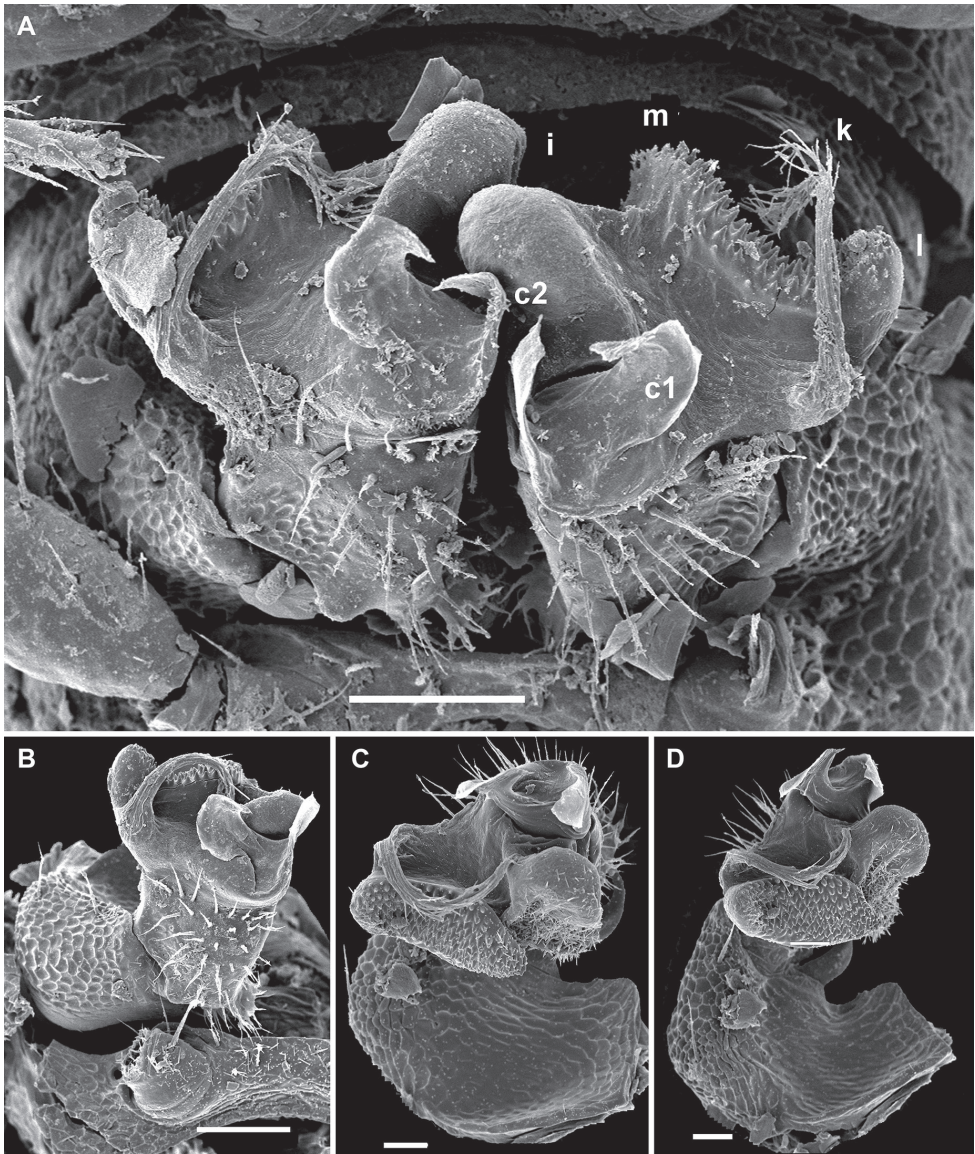


**Figure 13.** *Helicodesmus anichkini* sp. n., ♂ paratype; **A, D, G** anterior part of body, lateral, dorsal and ventral views, respectively **B, E, H** midbody segments, lateral, dorsal and ventral views, respectively **C, F, I** posterior part of body, lateral, dorsal and ventral views, respectively **J** cross-section of a midbody segment, caudal view **K** head, ventral view **L** tergal setae, tegument structure, limbus and stricture region **M** ozopore region of a midbody segment, sublateral view **N** midbody leg, lateral view. Scale bars: **A–J** 0.1 mm; **K** 0.05 mm; **N** 0.02 mm; **L, M** 0.01 mm.

(Fig. 13E, L). Limbus very fine, delicately and densely microcrenulate (Fig. 13L, M). Pleurosternal carinae absent (Fig. 13A–C). Epiproct short, conical, truncate, directed caudoventrally; pre-apical papillae evident (Fig. 13C, F, I). Hypoproct subtrapeziform, caudal setigerous papillae moderate and well separated (Fig. 13I).

Sterna without modifications, rather broad and sparsely setose (Fig. 13G, H). Legs short and stout, ca 1.1–1.2 (♂) or 0.9–1.0 (♀) times as long as midbody height; prefemora, femora, postfemora and tibiae clearly incrassate, especially so in ♂ (Fig. 13N),



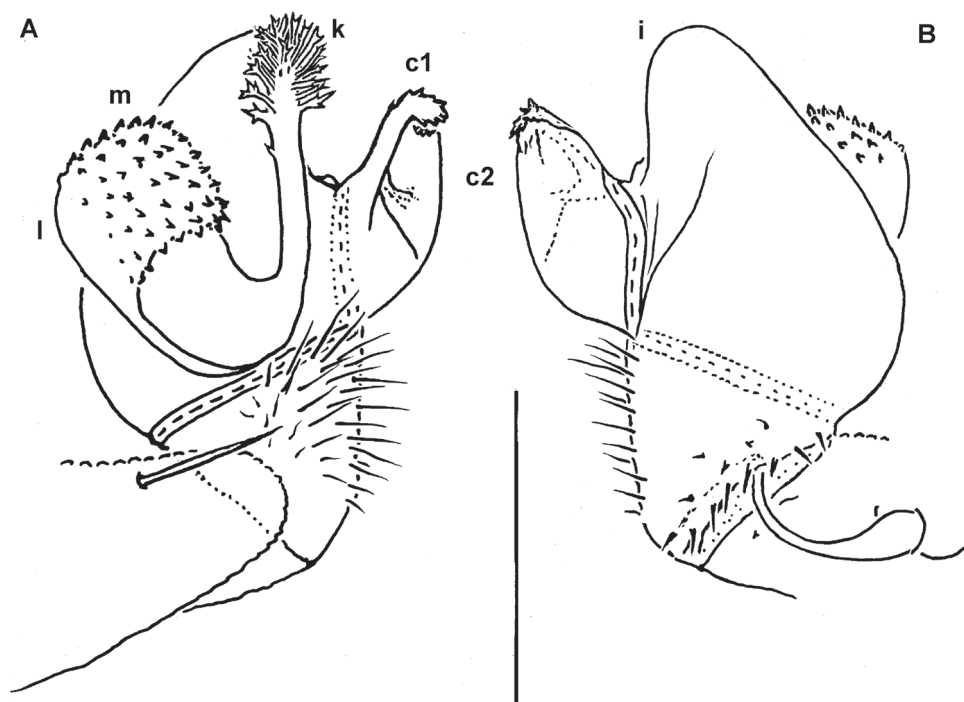


**Figure 14.** *Helicodesmus anichkini* sp. n., ♂ paratype; **A** both gonopods *in situ*, ventral view **B–D** right gonopod, anteroventral, ventrolateral and lateral views, respectively. Scale bars: **A, B, D** 0.05 mm; **C** 0.02 mm. Designations of gonopod structures in text.

tarsi longest, slender, sphaerotrichomes missing; claws simple, slightly curved; ♂ coxae 2 with very short, membranous, cylindrical gonapophyses (Fig. 13G).

Gonopod aperture transversely oblong-oval, taking up most of ventral part of metazonite 7 (Fig. 14A). Gonopod coxae rather small (gonocoel not deep), sparsely setose and clearly micropapillate laterally (Figs 14, 15); telopodites quite well exposed





**Figure 15.** *Helicodesmus anichkini* sp. n., ♂ paratype; **A, B** right gonopod, lateral and mesal views, respectively. Scale bar: 0.1 mm. Designations of gonopod structures in text.

and unusually transverse, but stout and remarkably complex, very strongly twisted, partly fimbriate (curved ventral projections **c1** and **c2**) or plumose (a long lateral process **k**), with several outgrowths of varying shapes (a stump-shaped, rounded, mesal **i** and 2 indistinctly separated, densely microdentate, also rounded **m** and **l**); prefemoral part about half the height of telopodite, demarcated on lateral (not medial!) side by an oblique seminal groove running further mesad onto a medioventral outgrowth of acropodite to terminate distally at joint base of **c1** and **c2**, with neither a solenomere nor an accessory seminal chamber, nor a pulvillus.

### *Monstrodesmus* gen. n.

<http://zoobank.org/71C607EC-50F6-49A5-8176-C57F3544EE7A>

<http://species-id.net/wiki/Monstrodesmus>

**Diagnosis.** 19 segments (♂), ♀ unknown; pore formula normal: 5, 7, 9, 10, 12, 13, 15–18; head without modifications; paraterga poorly developed, metaterga with 3 rows of 3+3 or, more rarely, 4+4, long, bacilliform setae (regardless of lateral setae); gonopod coxae large (gonocoel quite deep); telopodites rather well exposed, tripartite, without evidence of torsion, elongate, moderately curved caudad, subcontiguous medially and

held parallel to each other; acropodites lying distal to prefemoral parts much longer than and coaxial with the latter; solenomere (**sl**), or endomere, a strong, simple, frontal branch about as long as a lateral exomere (**ex**); a very long, flagelliform, mesal branch (**fl**) at base of both **sl** and **ex**; seminal groove (**sg**) running entirely along mesal side of **sl** to terminate on top with neither an accessory seminal chamber nor a pulvillus.

**Name.** To emphasize the monstrously long flagellum of the gonopod, masculine.

**Type species.** *Monstrodesmus flagellifer* sp. n., by present designation.

**Remarks.** This new genus seems to be particularly similar to *Topalodesmus* Golovatch, 1988, monobasic, from the Himalayas of India (Golovatch 1988b). Indeed, both share basically the same gonopod conformation: coxae quite massive; gonocel rather deep, but telopodites clearly exposed, deeply tripartite, untwisted, curved caudad, subcontiguous medially and held parallel to main axis; seminal groove running entirely mesally along a very strong frontal endomere branch (= solenomere, **sl**). However, the differences are definitely significant enough to keep these two genera separate. Unlike *Topalodesmus* which shows 20 segments in both sexes, the gonopod coxa in *Monstrodesmus* gen. n. is devoid of a frontal process, the exomere (**ex**) prominent (vs vestigial), the caudomesal branch (**fl**) unusually long and flagelliform (vs thick and unciform) while the solenomere (**sl**) a very long, strong, frontal branch.

***Monstrodesmus flagellifer* sp. n.**

<http://zoobank.org/46A8E604-6546-481A-A138-25C47E2323A6>

[http://species-id.net/wiki/Monstrodesmus\\_flagellifer](http://species-id.net/wiki/Monstrodesmus_flagellifer)

Figs 16–18

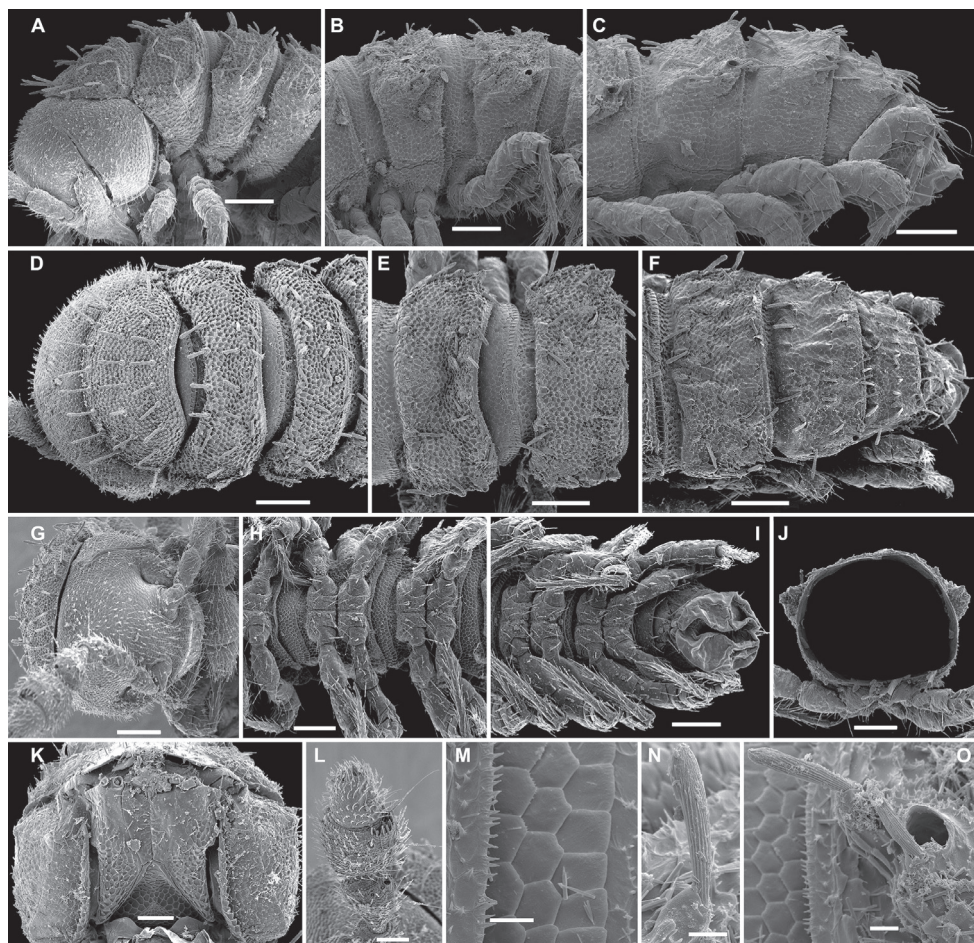
**Type material.** Holotype ♂ (MNHN JC 361), Vietnam, Dongnai Prov., Cat Tien National Park, 107°10'–107°34'E, 11°21'–11°48'N, lowland tropical forest, litter and topsoil, 01.06.2005, leg. A. Anichkin.

Paratype: 1 ♂ (SEM), same locality, together with holotype.

**Name.** The species epithet, a noun in apposition, is to emphasize the remarkably long gonopod flagellum.

**Description.** Length of adults ca 4.5 mm, width of midbody pro- and metazonae 0.33 and 0.4 mm (♂). Coloration in alcohol uniformly pallid, tegument often nearly translucent.

Body with 19 segments (♂). Tegument dull, texture of nearly entire body delicately alveolate to scaly, only sterna nearly smooth (Fig. 16A–I). Head very densely and finely pilose; epicranial suture highly superficial; genae squarish (Fig. 16A, D, G); gnathochilarium rather broad, sparsely and uniformly setose (Fig. 16K); isthmus between antennae about 1.2 times as broad as diameter of antennal socket (Fig. 16G). Antennae short (Fig. 16G, L), reaching only behind collum when stretched dorsally, not geniculate, rather strongly clavate due to a particularly enlarged antennomere 6, the latter with a usual, tight, distodorsal group of numerous, bacilliform sensilla; a similar, but smaller, also distodorsal group of sensilla on antennomere 5; antennomere

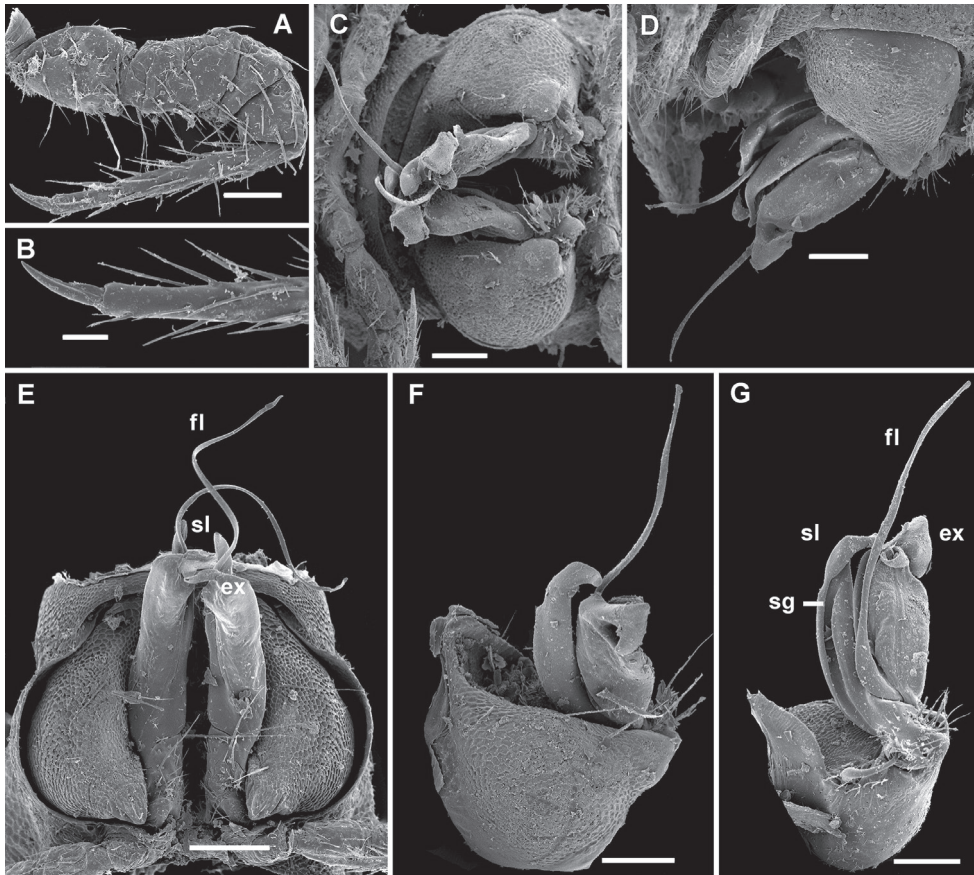


**Figure 16.** *Monstrodesmus flagellifer* sp. n., ♂ paratype; **A, D** anterior body part, lateral and dorsal views, respectively **B, E, H** midbody segments, lateral, dorsal and ventral views, respectively **C, F, I** posterior body part, lateral, dorsal and ventral views, respectively **G, K** head, frontal and ventral views, respectively **J** cross-section of a midbody segment, caudal view **L** antennomeres 4-8, sublateral view; tergal seta **M** tegument structure, limb and stricture region **N** tergal seta, lateral view **O** ozopore region of a midbody segment, sublateral view. Scale bars: **A-J** 0.1 mm; **K, L** 0.05 mm; **M-O** 0.01 mm.

7 with a smaller distodorsal group of only a few shorter and curved sensilla in front of a tiny mid-dorsal knob.

In width, collum < segment 3 = 4 < head = 2 < 5-15; thereafter body gradually tapering (Fig. 16D–F). Paraterga mostly moderate, starting from collum, set rather low (at about upper 1/3 of body height, Fig. 16J), at most small ridges with 2-3 lateral, setigerous knobs, absent from segment 18, caudal corner never produced behind rear tergal margin even in poriferous segments (Fig. 16A–I, O). Ozopores evident, ovoid, dorsolateral, mostly lying closer to lateral edge (Fig. 16B, C, E, F, O). Collum subovoid, sides (= paraterga) well rounded, dorsal surface with 3 transverse rows of

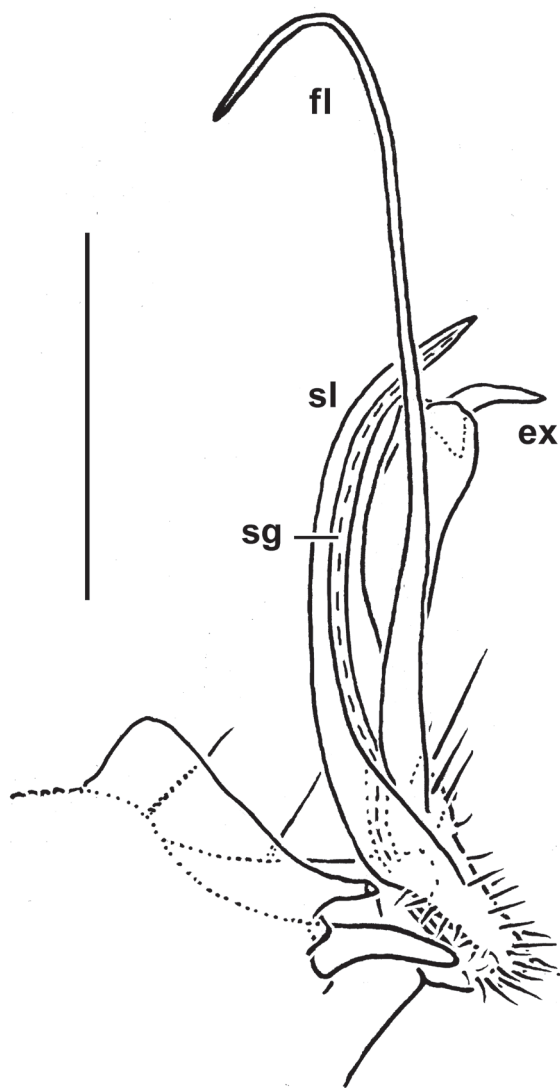




**Figure 17.** *Monstrodesmus flagellifer* sp. n., ♂ paratype; **A** midbody leg, lateral view **B** claw of a midbody leg **C–E** both gonopods *in situ*, ventral, lateral and ventrocaudal views, respectively **F** right gonopod, lateral view **G** left gonopod, mesal view. Scale bars: **C–G** 0.1 mm; **A** 0.05 mm; **B** 0.02 mm. Designations of gonopod structures in text.

4+4, 3+3 and 3+3 rather long setae dorsally and 2 similar setae on paraterga (Fig. 16A, D). Each following metatergum with 3+3 or, more rarely, 4+4, similarly long, bacilli-form, delicately ribbed setae arranged in 3 transverse regular rows and borne on knobs; sulci between the rows superficial (Fig. 16A–F). Stricture between pro- and metazonae rather deep and narrow, microalveolate like adjacent metazonae (Fig. 16A–F, M, O). Limbus very fine, delicately and densely microspiculate (Fig. 16M, O). Pleurosternal carinae absent (Fig. 16A–C). Epiproct short, conical, truncate, directed caudoventrally; pre-apical papillae small (Fig. 16C, F, I). Hypoproct subtrapeziform, caudal setigerous papillae moderate and well separated (Fig. 16I).

Sterna without modifications, rather broad and sparsely setose (Fig. 16H, I). Legs short and stout, ca 1.1–1.2 times as long as midbody height (♂); prefemora, femora, postfemora and tibiae clearly incrassate (Fig. 17A), tarsi longest, slender, sphaerotri-



**Figure 18.** *Monstrodesmus flagellifer* sp. n., ♂ holotype, right gonopod, mesal view. Scale bar: 0.2 mm. Designations of gonopod structures in text.

chomes missing; claws simple, slightly curved (Fig. 17B); coxae 2 with very short, membranous, cylindrical gonapophyses.

Gonopod aperture transversely obcordate, taking up most of ventral part of metazonite 7 (Fig. 17C, E). Gonopod coxae large (gonocoel rather deep), with 2 long setae and clearly micropapillate laterally, but without any frontal outgrowths (Fig. 17C–G, 18); telopodites quite well exposed, not twisted, tripartite, elongate, moderately curved caudad, subcontiguous medially and held parallel to each other; acropodites lying distal to prefemoral parts much longer than and coaxial with the latter; solenomere (**sl**)



(= endomere) a strong, simple, frontal branch about as long as an apically bifid lateral exomere (**ex**); an extremely long, flagelliform, mesal branch (**fl**) at base of both **sl** and **ex**; seminal groove (**sg**) running entirely along mesal side of **sl** to terminate on top with neither an accessory seminal chamber nor a pulvillus.

### A key to genera and species of *Trichopolydesmidae* currently known from Vietnam/Indochina, based mainly on male characters

Since brief diagnoses of all previously known Oriental trichopolydesmid genera are given above, and their scopes and statuses also considered, below we only present a key to the new genera and species, the first to be reported from Indochina in general and from Vietnam in particular.

- 1 Ozopores totally missing (Figs 3A–F, 5A–F, 7A–F) .... *Aporodesmella* gen. n., 2
- Pore formula normal..... 4
- 2 Paraterga strongly developed (Fig. 7A–F). ♂ head with an evident, round, very finely pilose, central hump above antennae (Fig. 7D, G). Antennomere 6 unmodified (Fig. 7J). Gonopods as in Fig. 8C–F ..... *A. tergalis* sp. n.
- Paraterga poorly developed to missing (Figs 3A–F, 5A–F). ♂ head unmodified. Antennomere 6 with a peculiar dorsoparabasal stump (**s**) (Figs 3J, 4A, 5G). Gonopods different ..... 3
- 3 Solenophore (**sph**) unusually short and axe-shaped, solenomere (**sl**) simple and lanceolate (Fig. 4D–G) ..... *A. securiformis* sp. n.
- Gonopod tip more elaborate, both **sph** and **sl** different (Fig. 6B, C) ..... *A. similis* sp. n.
- 4 ♂ head with an evident, round, central hump above antennae (Fig. 11A, D, G). Gonopod telopodites clearly geniculate due to a midway cingulum (**c**), distal half directed laterad, with an unusually strongly developed hairy pulvillus (**p**) (Figs 12D–G) ..... *Gonatodesmus* gen. n. (*G. communicans* sp. n.)
- ♂ head devoid of a hump. Gonopod telopodites non-geniculate, at most strongly, but regularly curved, distal parts never directed laterad; a hairy pulvillus absent ..... 5
- 5 Head in both sexes somewhat flattened dorsoventrally (Fig. 9A, D, G). Gonopod telopodites long and slender, semi-circular, *in situ* crossing medially, bifid subapically (Fig. 10C–E) .... *Deharvengius* gen. n. (*D. bedosae* sp. n.)
- Head clearly more convex dorsally. Gonopod telopodites far more elaborate .... 6
- 6 Gonopods especially complex, unusually strongly twisted, *in situ* clearly transverse, devoid of a solenomere (Figs 14, 15) ..... *Helicodesmus* gen. n. (*H. anichkini* sp. n.)
- Gonopod telopodites held parallel to main axis, each tripartite, including a remarkably long flagellum (**fl**) (Figs 17C–G, 18) ..... *Monstrodesmus* gen. n. (*M. flagellifer* sp. n.)

## A brief discussion and conclusions

As observed elsewhere (Golovatch et al. 2013), most of the Oriental Trichopolydesmidae seem to be moderately advanced. Only some show complex and strongly shortened gonopod telopodites deeply sunken inside the gonocoel formed by enlarged coxae, presumably a more advanced condition. In the majority of genera and species, however, the telopodites are strongly exposed, a more primitive situation. The orientation of the prefemoral part also varies, but it tends to be held parallel, not transversely, to the main axis of the body, a condition typical of the superfamily Polydesmoidea.

*Gonatodesmus* gen. n., in which the gonopods are considerably elongate, geniculate at about midway while their distal halves are directed laterad, provides a kind of transition or evolutionary bridge between Trichopolydesmidae and Opisotretidae, thus reinforcing the assignment of these two families to the single superfamily Trichopolydesmoidea. This is in contrast to the much more frequent condition of the gonotelopodites as observed in Trichopolydesmidae and most other groups of Polydesmida, which either cross mesally or are held parallel to each other. Based on this example, the Opisotretidae might well be viewed as a direct and disjunct derivative of the more basal Trichopolydesmidae, with their gonotelopodite growing increasingly elongate and orientated laterally (Golovatch et al. 2013).

There can be no doubt that many more species of Trichopolydesmidae await discovery and description. Representatives of this family might seem to be rare, but it is very likely that they are seriously under-collected due to their very small size and perhaps also to seasonality. Thus, most of the adults have been taken during or shortly after the rainy season (May to November), when the animals are surface-active. During the dry season, like most other Diplopoda in lowland tropical forests of Vietnam, the very small trichopolydesmoids seem to be dormant (Golovatch et al. 2011). At least in Vietnam, sympatry, even syntopy, of several ( $\geq$  three) different trichopolydesmid species also seems to be common.

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# Integrative revision of the giant pill-millipede genus *Sphaeromimus* from Madagascar, with the description of seven new species (Diplopoda, Sphaerotheriida, Arthrosphaeridae)

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## Abstract

The Malagasy giant pill-millipede genus *Sphaeromimus* de Saussure & Zehntner, 1902 is revised. Seven new species, *S. titanus* sp. n., *S. vatovavy* sp. n., *S. lavasoa* sp. n., *S. andohabela* sp. n., *S. ivohibe* sp. n., *S. saintelucei* sp. n., and *S. andrahomana* sp. n. were discovered, in one case with the help of sequence data, in the rainforests of southeastern Madagascar. The species are described using light- and scanning electron microscopy. A key to all 10 species of the genus is presented. All but one (*S. andohabela*) of the newly discovered species are microendemics each occurring in isolated forest fragments. The mitochondrial COI barcoding gene was amplified and sequenced for 18 *Sphaeromimus* specimens, and a dataset containing COI sequences of 28 specimens representing all *Sphaeromimus* species (except *S. vatovavy*) was analyzed. All species are genetically monophyletic. Interspecific uncorrected genetic distances were

moderate (4–10%) to high (18–25%), whereas intraspecific variation is low (0–3.5%). Sequence data allowed the correct identification of three colour morphs of *S. musicus*, as well as the identity of a cave specimen, which although aberrant in its morphology and colouration, was genetically identical to the holotype of *S. andrahoma*.

### Keywords

COI, Barcoding, soil arthropods, microendemism, Andrahomana, Lavasoa, Sainte Luce, Manombo

## Introduction

Madagascar, the world's third largest island, is famous for its endemic and endangered fauna and flora (Myers et al. 2000, Vences et al. 2009). Some representatives of the millipedes, class Diplopoda, represent quite charismatic invertebrate endemics of Madagascar. These include the large-bodied, strikingly red-black colored so-called 'Fire-Millipedes' of the order Spirobolida (Wesener et al. 2009a, Wesener et al. 2011a), and the giant pill-millipedes, locally called 'Tainkintana' (=star droppings), reaching the size of a small orange or a tennis ball when rolled-up.

Despite their conspicuousness, it was only recently that the millipede biodiversity on Madagascar became better known. Mauriès (1994, 1997) discovered and described the first African representatives of the order Chordeumatida from Madagascar, which belong to the same family Pygmaesomatidae as certain Indian endemics. Inventories of the 'classical' millipedes of the order Spirobolida led to the discovery of 13 new genera and 53 new species (Wesener et al. 2008, Wesener and Enghoff 2009, Wesener et al. 2009b). Recently the occurrence of the order Polyzoniida on Madagascar was reviewed, and was found to be diverse and indigenous (Wesener 2014a), while representatives of the order Siphonophorida were discovered on Madagascar for the first time (Wesener in press)

In giant pill-millipedes, all species known from Madagascar were redescribed (Wesener and Sierwald 2005, Wesener and Wägele 2008). New discoveries included the first dwarfed member of the giant pill-millipede order, the genus *Microsphaerotherium* Wesener & VandenSpiegel, 2007, as well as a surge of species in the genus *Zoo-sphaerium* Pocock, 1895, which now includes 62 described species (Wesener 2009), including the largest Sphaerotheriida by far, e.g. *Z. neptunus* (Butler, 1872) reaching the size of a tennis ball or small orange when rolled-up.

The third Malagasy giant pill-millipede genus *Sphaeromimus* de Saussure & Zehntner, 1902, is an unusual representative of the order. One characteristic of the genus is the presence of well-developed stridulation organs, the male 'harp' and the female 'washboard', which carry more stridulation ribs than in any other member of the Sphaerotheriida. These stridulation organs are still not well understood, but may play a role during courtship (Wesener et al. 2011b). The first species, *S. musicus* was described in 1897 (de Saussure and Zehntner 1897), with no additional specimens found for more than 100 years. The unusual morphology of *Sphaeromimus*, quite distinct from the majority of Malagasy giant pill-millipedes belonging to the genus

*Zoosphaerium* Pocock, 1895, let the experts to suggest that *S. musicus* might represent a “mislabelled or an introduced Indian sphaerotheriid” (Jeekel 1999). However, a century later, two additional species of *Sphaeromimus* were discovered in littoral rain-forest fragments in southeastern Madagascar, and its type species could be redescribed based on numerous samples taken from the southern Malagasy spiny forest ecosystem during general biodiversity inventory programs (Wesener and Sierwald 2005). A phylogenetic analysis of the Sphaerotheriida based on morphological (Wesener and VandenSpiegel 2009, Wesener 2014b) as well as molecular characters (Wesener et al. 2010) confirmed the sister-group relationship of *Sphaeromimus* to the Indian genus *Arthrosphaera* Pocock, 1895, the first time such a Madagascar-India relationship was discovered in soil arthropods. *Sphaeromimus* is more closely related to the Indian genus *Arthrosphaera* than to the other Malagasy giant pill-millipede genera *Zoosphaerium* and *Microsphaerotherium*, all of which belong to the family Arthrosphaeridae (Wesener 2014b).

An expedition to Madagascar conducted by TW in 2007, as well as sorting through different natural history collections, led to the discovery of 12 additional *Sphaeromimus* populations representing seven undescribed species of *Sphaeromimus*, all from humid forests in southeastern Madagascar. Many of the newly discovered species were only found in tiny rainforest vestiges/fragments, and one specimen was discovered in a cave located in the southern dry spiny forest ecosystem. While all known *Sphaeromimus* show a ‘normal’ size of 18–35 mm, one of the undescribed species shows gigantism. These findings highlight how little we still know about the biodiversity of one of the most striking invertebrate endemics on Madagascar.

## Methods

### Specimen collecting and conservation

*Sphaeromimus* specimens were collected by hand. Three of the seven newly discovered species were found in natural history collections: one historic and two obtained during general arthropod inventory programs on Madagascar. Specimens of the other four species were collected from eight localities during an expedition by TW and Kai Schütte (University of Hamburg). Between 12–20 hours were spent searching at each locality. Rarely were the *Sphaeromimus* individuals encountered in high numbers (spiny forest, Sainte Luce S9, Grande Lavasoa) and usually several hours of search were necessary to find an area where 3–5 specimens could be collected. The isolated occurrence patterns of *Sphaeromimus* species might be the main reason why no *Sphaeromimus* specimens were collected during general inventory programs, which targeted the same localities as we did in 2007. Legs were removed from several specimens and placed in 95% ethanol for DNA analysis, while the rest of the specimens was preserved in 80% ethanol, which was changed twice. A few months later, some of the specimens were transferred to 95% ethanol to facilitate future DNA work on the specimens.



**Table 1:** *Sphaeromimus* samples, Genbank code, and depository. Genbank numbers marked by an asterisk (\*) were published in a previous study (Wesener et al. 2010).

Species	Specimen Catalog #	Locality	Genbank #	GenSeq
<i>Procyliosoma leae</i> *	QVMAG 23:45801	Tasmania	FJ409910*	genseq-4
<i>Zoosphaerium neptunus</i> *	FMNH-INS 56005	Madagascar, Andasibe	FJ409929*	genseq-4
<i>Z. alluaudi</i> *	FMNH-INS 56000	Madagascar, Petriky	FJ409926*	genseq-3
<i>Arthrosphaera brandtii</i> *	FMNH-INS 8650	Tanzania, Usambara Hills	FJ409915*	genseq-4
<i>S. musicus</i> 01*	FMNH-INS 56016	Madagascar, Andrahomana	FJ409919*	genseq-4
<i>S. musicus</i> 02*	FMNH-INS 56016	Madagascar, Andrahomana	FJ409920*	genseq-4
<i>S. musicus</i> 03*	FMNH-INS 56008	Madagascar, Mangatsiaka	FJ409921*	genseq-4
<i>S. musicus</i> 04*	FMNH-INS 56212	Madagascar, Tsimelahy	FJ409922*	genseq-4
<i>S. musicus</i> 05 (red)	ZFMK MYR 2273	Madagascar, Tsimelahy	KJ13244	genseq-4
<i>S. musicus</i> 06 (red)	ZFMK MYR 2276	Madagascar, Tsimelahy	KJ13245	genseq-4
<i>S. splendidus</i> A*	FMNH-INS 6702	Madagascar, Sainte Luce S9	FJ409918*	genseq-3
<i>S. splendidus</i> B*	FMNH-INS 56031	Madagascar, Sainte Luce S9	FJ409917*	genseq-3
<i>S. inexpectatus</i> A*	FMNH-INS 56033	Madagascar, Enato	FJ409916*	genseq-4
<i>S. inexpectatus</i> B	FMNH-INS 61090	Madagascar, Enato	KJ13246	genseq-4
<i>S. titanus</i> sp. n.	CASENT 9032789	Madagascar, Manombo,	KJ13247	genseq-1
<i>S. ivohibe</i> sp. n.	FMNH-INS 8184	Madagascar, Ivohibe	KJ13248	genseq-1
<i>S. lavasoa</i> sp. n. A*	FMNH-INS 56208	Madagascar, Gr. Lavasoa	FJ409924*	genseq-2
<i>S. lavasoa</i> sp. n. B	FMNH-INS 61143	Madagascar, Gr. Lavasoa	KJ13249	genseq-2
<i>S. lavasoa</i> sp. n. C	FMNH-INS 61142	Madagascar, Gr. Lavasoa	KJ13250	genseq-2
<i>S. andohabeha</i> sp. n. 01	FMNH-INS 61135	Madagascar, Isaka-Ivondro	KJ13251	genseq-2
<i>S. andohabeha</i> sp. n. 02	FMNH-INS 61137	Madagascar, Isaka-Ivondro	KJ13252	genseq-2
<i>S. andohabeha</i> sp. n. 03	ZFMK MYR 2322	Madagascar, Isaka-Ivondro	KJ13253	genseq-1
<i>S. andohabeha</i> sp. n. 04	FMNH-INS 61136	Madagascar, Isaka-Ivondro	KJ13254	genseq-2
<i>S. andohabeha</i> sp. n. 05	FMNH-INS 61132	Madagascar, Manantantely	KJ13255	genseq-4
<i>S. andohabeha</i> sp. n. 06	FMNH-INS 61138	Madagascar, Manantantely	KJ13256	genseq-4
<i>S. andohabeha</i> sp. n. 07*	FMNH-INS 56210	Madagascar, Malio	FJ409923*	genseq-4
<i>S. andohabeha</i> sp. n. 08	FMNH-INS 56210	Madagascar, Malio	KJ13257	genseq-4
<i>S. andohabeha</i> sp. n. 09	ZFMK MYR 2323	Madagascar, Malio	KJ13258	genseq-4
<i>S. saintelucei</i> sp. n.	ZFMK MYR 889	Madagascar, Sainte Luce S8	KJ13259	genseq-1
<i>S. andrahomana</i> sp. n. Cave*	FMNH-INS 56211	Madagascar, Andrahomana	FJ409924*	genseq-4
<i>S. andrahomana</i> sp. n.	FMNH-INS 56214	Madagascar, Ankapaky Plateau	KJ13260	genseq-1
<i>S. sp.</i> , Vevembe <sup>c</sup>	CASENT 9032816	Madagascar, Vevembe	KJ13261	genseq-4

## Illustrations

Important structures of the *Sphaeromimus* specimens were drawn using a *camera lucida* mounted on an Olympus SZX12 stereo-microscope. Pencil drawings were later transferred to ink with pigma micron pens. For scanning electron microscopy, samples were dehydrated via an ethanol series (90%, 95%, 2× 100%), dried over night, and mounted on aluminium stubs before being sputter coated with gold. SEM images were taken using a Zeiss Leo EVO SEM (FMNH) and a Hitachi S-2460 SEM (ZFMK). All images were later modified using Adobe Photoshop CS2 and assembled into plates using Adobe Illustrator CS2.

## DNA extraction, sequencing

DNA was extracted from 18 specimens: 12 of them preserved in 95% ethanol, the remaining ones in 75% ethanol. The HCO/LCO primer pair (Folmer et al. 1994) was used to sequence a 674 bp fragment of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene. DNA extraction, PCR, purification, and sequencing protocols were identical to those used in a previous study (Wesener et al. 2010). While the COI gene, being a mitochondrial gene as well as containing little resolution at deeper evolutionary splits, does not allow a reconstruction of the phylogeny of the *Sphaeromimus* species, we aimed at finding a unique identifier allowing us to study and illustrate the genetic distances between the different species of the genus. All obtained sequences were checked via Blast searches (Altschul et al. 1997), no contaminations were discovered. The sequences were aligned by hand in BioEdit (Hall 1999) with those obtained during a previous study (Wesener et al. 2010) from other *Sphaeromimus* specimens, using as outgroup taxa a specimen of the basal family Procyliosomatidae (Wesener and VandenSpiegel 2009), as well as two species of the other Malagasy genus *Zoosphaerium*, including the type *Z. neptunus*, and a member of the closely related Indian genus *Arthrosphaera*. All newly sequenced *Sphaeromimus* sequences were uploaded to Genbank (Accession #: KJ13244–KJ13261, see Table 1).

## DNA analysis

To find the best substitution model, modeltest implemented in MEGA 5.05 (Tamura et al. 2011) was utilized. Codon positions included were 1st+2nd+3rd+Noncoding. All positions containing gaps and missing data were eliminated. There were a total of 567 positions in the final dataset. The lowest Bayesian Information Criterion score of 8149.1 was obtained by the GTR model plus invariant sites and gamma distribution to be best fitting (FreqA = 0.2694, FreqC = 0.2286, FreqT = 0.3304, FreqG = 0.1716, Invariant sites = 0.535, gamma shape = 1.29762). Maximum likelihood analyses were conducted in MEGA5 (Tamura et al. 2011). The bootstrap consensus tree (Fig. 20) from 1000 replicates (Felsenstein 1985) is taken to represent the evolutionary history of the analyzed taxa. All positions containing gaps and missing data were eliminated. There were a total of 570 positions in the final dataset. Mean uncorrected pairwise distances between terminals (transformed into percentages) were determined using MEGA5 (Tamura et al. 2011).

## Museum acronyms

<b>CAS</b>	California Academy of Sciences, San Francisco, California, U.S.A.
<b>FMNH</b>	Field Museum, Chicago, Illinois, U.S.A.
<b>MNHN</b>	Muséum national d'Histoire naturelle, Paris, France.

**QVMAG** Queen Victoria Museum and Art Gallery, Launceston, Australia.

**ZFMK** Zoologisches Forschungsmuseum A. Koenig, Bonn, Germany.

## Results

### Genus *Sphaeromimus* de Saussure & Zehntner, 1902

<http://species-id.net/wiki/Sphaeromimus>

*Sphaeromimus* de Saussure & Zehntner, 1902: 20 (first description); Attems 1926: 119 (list); Attems 1943: 60 (list); Jeekel 1971: 28 (list); Jeekel 1974: 45 (classification); Hoffman 1980: 63 (list); Jeekel 1999: 8 (catalogue, discussion); Enghoff 2003: 618 (list); Wesener and Sierwald 2005: 557 (redescription, additional species); Wesener and Wägele 2007: 147 (ecology); Wesener 2009: 8 (key); Wesener and VandenSpiegel 2009: 548 (morphological phylogenetic analysis); Wesener et al. 2010: 1185 (molecular phylogenetic analysis); Wesener 2014b: (morphological phylogenetic analysis).

**Type species.** *Sphaeropoeus musicus* de Saussure & Zehntner, 1897, by monotypy.

#### **Other species included (9).**

*Sphaeromimus splendidus* Wesener & Sierwald, 2005

*Sphaeromimus inexpectatus* Wesener & Sierwald, 2005

*Sphaeromimus titanus* sp. n. Wesener

*Sphaeromimus vatovavy* sp. n. Wesener

*Sphaeromimus lavasoa* sp. n. Wesener

*Sphaeromimus andohahela* sp. n. Wesener

*Sphaeromimus ivohibe* sp. n. Wesener

*Sphaeromimus saintelucei* sp. n. Wesener

*Sphaeromimus andrahomana* sp. n. Wesener

**Remarks.** See Wesener and Sierwald (2005) for a detailed revision of the genus. A phylogeny, highlighting the close relationship of *Sphaeromimus* to the Indian *Arthrosphaera* Pocock, 1895 is available based on morphological (Wesener and VandenSpiegel 2009; Wesener 2014b), and molecular characters (Wesener et al. 2010). A short re-diagnosis is presented so that fewer characters need to be mentioned in the species descriptions.

**New diagnosis.** Genus of small to medium-sized (15–45 mm length) Arthrosphaeridae. Colour variable, rarely pink or with a reddish-black pattern (Fig. 1A), but usually black to brown (Fig. 1B). Head with short antennae consisting of well-rounded antennomeres lacking cuticular scales. Antennomere 6 massive, only antennomere carrying sensilla basiconica. Apical disc with numerous apical cones (>20), number of cones sexual dimorphic, males with twice or even three times as many cones as females. Eyes consisting of 55–95 ocelli. Mandible with six or seven pectinate lamellae and a

3-combed internal tooth. Gnathochilarium typical of the order, rudimentary lateral palpi carrying three or four sensory cones. Tergites with a smooth surface, in some species polished. Legs short and broad, tarsus usually 2.5–4 times longer than wide. Leg pair 1 and 2 lacking an apical spine. Femur often with a well-developed toothed ridge. Coxae with a more or less well-developed sharp process carrying small triangular spines. Anal shield usually well-rounded, underside carrying a single, short, black locking carina located closely to the margin.

Male gonopore typical of Arthrosphaeridae, covered by a simple sclerotized plate.

Anterior telopod consisting of syncoxite plus four telopoditomeres. First telopoditomere enlarged, carrying the male stridulation organ (harp) consisting of 3–6 stridulation ribs, number of ribs independent of the size of the male, species specific. Second telopoditomere posteriorly with a process protruding up to the start of telopoditomere 4. Third telopoditomere short, sometimes with a spine juxtaposed to process of telopoditomere 2. Telopoditomere 4 larger than 3 and 4 combined, conical, basally with a field of sclerotized spots juxtaposed to process of telopoditomere 2, apically with a large, triangular lobe-like spine, usually three smaller spines distributed across the joint.

Posterior telopods always consisting of syncoxite with inner horns and inner lobes and pair of telopodites each consisting of three telopoditomeres forming chelae. First telopoditomere unremarkable, second telopoditomere forming the immovable finger of the chela. Immobile finger basally wide, apically tapering, always curved toward telopoditomere 3 (movable finger). Immobile finger as long as, or in some species overlapping movable finger. Membrane of telopoditomere 2 often extended into lobe, an anterior side juxtaposed to telopoditomere 3 with a dense field of sclerotized spots. Telopoditomere 3 curved or straight, relatively slender, margin juxtaposed to immovable finger with 20–40 small black crenulated teeth, three or four spines, and one, rarely two (*S. ivohibe* sp. n.) large membranous lobes.

Female vulva atypical for Arthrosphaeridae, with external and inner plate standing below operculum, not extending mesally. Operculum large and well-rounded, protruding at least up to basal half of prefemur. Female subanal plate greatly enlarged, in some species almost divided into two plates. Subanal plate carrying a washboard with 3–8 stridulation ribs on each side, number of ribs depending on female body size.

### Key to species of *Sphaeromimus*

- 1      Male harp on the anterior telopod with 3 stridulation ribs (Fig. 2E).....**2**
- Male harp on the anterior telopod with 4–6 stridulation ribs (Fig. 9A).....**7**
- 2      Body length <20 mm. Midbody legs without a coxal lobe (Fig. 17A). Endotergum with single row of marginal bristles (Fig. 16B). Immobile finger of posterior telopod slender, apically strongly curved like a hook (Fig. 17F). Colour pink or brown.....**3**
- Body length >20 mm. Midbody legs at least with weak coxal lobe (Fig. 2C). Endotergum usually with at least two (Fig. 12A), rarely only one (*S. titanus*)



- sp. n.) row of marginal bristles. Immobile finger of posterior telopod at least basally wide (Fig. 3B). Colour black or brown ..... **4**
- 3 Colour pink, surface shiny. Process of telopoditome 2 of anterior telopods in anterior view visible laterally. Littoral forest of Mandena and rainforest of Enato ..... ***S. inexpectatus***
- Colour light brown, surface dull. Process of telopoditome 2 of anterior telopods in anterior view not visible (Fig. 17B). Littoral forest of Sainte Luce, fragment S8 ..... ***S. saintelucei* sp. n.**
- 4 Body length >30 mm, light brown. Endotergum with single row of marginal bristles (Fig. 5A). Movable finger of posterior telopod straight (Fig. 3B). Lowland forest of Manombo ..... ***S. titanus* sp. n.**
- Body length 21–28 mm, black or dark brown. Endotergum with two rows of marginal bristles (Fig. 12A). Movable finger of posterior telopod curved (Fig. 11D) ..... **5**
- 5 Midbody legs with strongly developed coxal process. Tergite surface shiny. Littoral forest of Sainte Luce, fragment S9 ..... ***S. splendidus***
- Midbody legs with barely developed coxal process (Fig. 11A). Tergite surface dull ..... **6**
- 6 Endotergum with strongly developed cuticular patterns (Fig. 12A). Movable finger of posterior telopod without small pits, carrying 20–22 crenulated teeth (Fig. 14D). Andohahela mountain chain, Manantantely, Malio and Isaka-Ivondro ..... ***S. andohahela* sp. n.**
- Endotergum with weakly developed cuticular patterns (Fig. 16C). Movable finger of posterior telopod covered with small pits, carrying 23 or 24 crenulated teeth (Fig. 18F). Inside Grotte d’Andrahomana and in deep ravines N of Ankapaky ..... ***S. andrahomana* sp. n.**
- 7 Unique black pattern on orange-reddish basic colour (Fig. 1A). Harp with 5 ribs. Endotergum with three rows of marginal bristles. Widespread in the SW spiny forest ..... ***S. musicus***
- Colour different, either uniformly black or brown (Fig. 1B). Rainforest species ..... **8**
- 8 Harp with 4 stridulation ribs (Fig. 11B). Endotergum with two rows of marginal bristles, not reaching tergite margin (Fig. 12A). Operculum well-rounded (Fig. 11F). Lavaso Mountain ..... ***S. lavaso* sp. n.**
- Harp with 5 or 6 stridulation ribs (Fig. 9A). Endotergum with single row of marginal bristles (Fig. 5B) ..... **9**
- 9 Harp with 5 stridulation ribs (Fig. 9A). Marginal bristles of endotergum protruding beyond tergite margin (Fig. 5B). Operculum apically recessed (Fig. 9F). Movable finger of posterior telopod with single membranous lobe (Fig. 9E). Vevembe-Vatovavy area ..... ***S. vatovavy* sp. n.**
- Harp with 6 stridulation ribs (Fig. 15D). Marginal bristles sparse and very short (Fig. 16A). Movable finger of posterior telopod with two membranous lobes (Fig. 15H). Small, black species, red legs. Ivohibe mountain ... ***S. ivohibe* sp. n.**

***Sphaeromimus musicus* (de Saussure & Zehntner, 1897)**

[http://species-id.net/wiki/Sphaeromimus\\_musicus](http://species-id.net/wiki/Sphaeromimus_musicus)

Figure 1A

*Sphaeropoeus musicus* de Saussure & Zehntner, 1897: pl. 4, fig. 1 a-e (first description)  
*Sphaeromimus musicus*: de Saussure and Zehntner 1902: 75 (description); Jeekel 1999: 8 (list); Enghoff 2003: 618 (list); Wesener and Sierwald 2005: 564 (redescription); Wesener 2009: 131 (list); Wesener and VandenSpiegel 2009: 548 (morphological phylogenetic analysis); Wesener et al. 2010: 1185 (molecular phylogenetic analysis); Wesener 2014b: (morphological phylogenetic analysis).

**Additional specimen records.** 5 ♂ & ♀, ZFMK MYR2273, Madagascar, Province Toliara, PN Andohahela, Tsimelahy, 24°57.296'S, 046°37.214'E, 135 m, spiny forest, close to river, coll. Wesener & Schütte, 24.v.2007; 2 ♂, ZFMK MYR2276, PN Andohahela, Tsimelahy, 24°57.296'S, 046°37.214'E, 135 m, spiny forest, close to river, coll. Wesener & Schütte, 24.v.2007; 5 ♂ & ♀, FMNH-INS 56027, same data as previous; 7 ♂ & ♀, ZFMK MYR2274, Grotte Andrahomana, 24°51.006'S, 046°55.907'E, dry forest plateau, coll. Wesener & Schütte, 20.v.2007; 4 ♂ & ♀, FMNH-INS 56016, same data as previous; 6 ♂ & ♀, ZFMK MYR2279, PN Andohahela, Mangatsiaka, 24°58.051'S, 046°33.206'E, 90 m, spiny forest, coll. Wesener & Schütte, 23.v.2007; 5 ♂ & ♀, FMNH-INS 56008, same data as previous; 6 ♂ & ♀, FMNH-INS 7822, Province Antananarivo, Forêt de Analavelona, Antanimena, 12.5 km NW Andramoheza, 22.6783°S, 44.1917°E, 1050 m, coll. S. M. Goodman, 9–15.3.1998; 1 ♀, MNHN TW29, Madagascar, Province Toliara, Entree n°1, 1927, envoi G. Petit, Madagascar, Caisse 7 (tuite de lemoir la caisse 6), Petit, 1926, Bords du Fiherenana, P de Tulear, 3°Envoi, most likely “Bords du Fiherenana”, 23.01°S, 44.09°E; 1 ♂, MNHN TW120, Madagascar, Mission R. Decary, Fort Dauphin, Juin 1926, entree n°17, 1927.

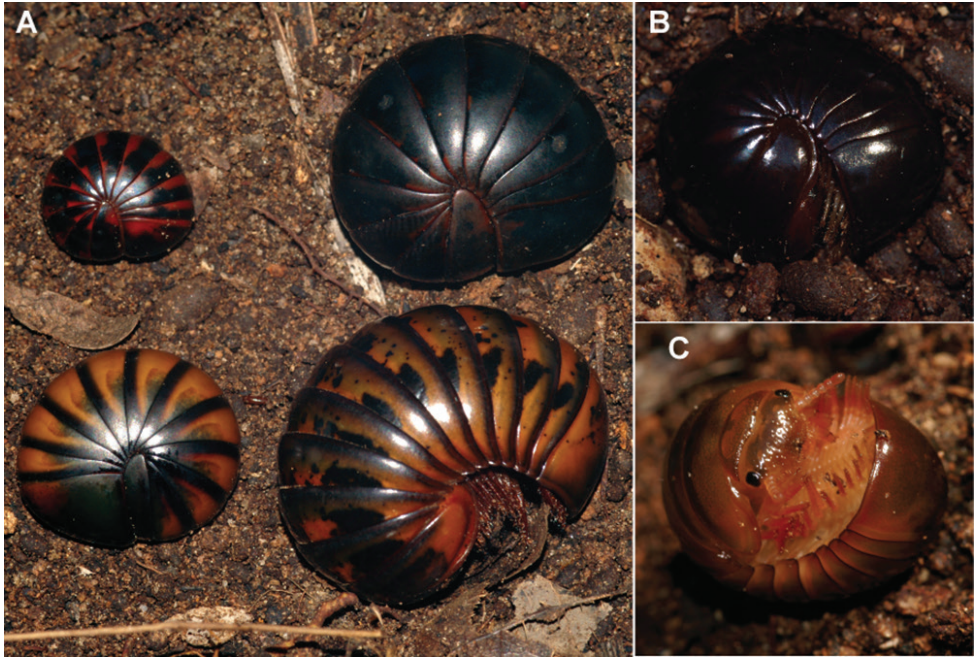
Localities. *S. musicus* is apparently widespread in the southern spiny forest ecosystem. Different colour morphs from the same locality (Fig. 1A) showed identical COI sequences (Fig. 20), while the intraspecific variation between two populations 35 km apart was 2%.

***Sphaeromimus splendidus* Wesener & Sierwald, 2005**

[http://species-id.net/wiki/Sphaeromimus\\_splendidus](http://species-id.net/wiki/Sphaeromimus_splendidus)

*Sphaeromimus splendidus* Wesener & Sierwald, 2005: 567 (first description); Wesener and Wägele 2007: 150 (ecology); Wesener 2009: 131 (list); Wesener and VandenSpiegel 2009: 548 (morphological phylogenetic analysis); Wesener et al. 2010: 1185 (molecular phylogenetic analysis); Wesener 2014b: (morphological phylogenetic analysis).

**Additional specimen records.** 1 ♀ paratype, ZFMK MYR2272 (transferred from FMNH), coll. T. Wesener, 06.iv.2003; 11 ♂ & ♀, ZFMK MYR2271, coll. Wesener



**Figure 1.** Photographs of living *Sphaeromimus*. **A** *Sphaeromimus musicus* (de Saussure & Zehntner, 1897) from Tsimelahy, upper left to lower left: red colour morph, black colour morph, normal colour morph, the similar looking sympatric *Zoosphaerium blandum* (de Saussure & Zehntner, 1902) **B** *Sphaeromimus lavasoa* sp. n. **C** *Sphaeromimus andrahomana* sp. n. cave specimen. Not to scale.

& Schütte, 01.vi.2007; 3 ♂ & ♀, ZFMK MYR2277, same data as previous; 19 ♂ & ♀, FMNH-INS 56031, same data as previous.

**Localities.** Only recorded from the littoral rainforest at Sainte Luce, fragment S9 (Wesener and Sierwald 2005). The two specimens from which the COI gene was sequenced differ by a single base pair substitution.

### *Sphaeromimus inexpectatus* Wesener & Sierwald, 2005

[http://species-id.net/wiki/Sphaeromimus\\_inexpectatus](http://species-id.net/wiki/Sphaeromimus_inexpectatus)

*Sphaeromimus inexpectatus* Wesener & Sierwald, 2005: 570 (first description); Wesener and Wägele 2007: 150 (ecology); Wesener 2009: 131 (list); Wesener and Vanden-Spiegel 2009: 548 (morphological phylogenetic analysis); Wesener et al. 2010: 1185 (molecular phylogenetic analysis); Wesener 2014b: (morphological phylogenetic analysis).

**Additional specimen records.** 3 ♂ & ♀, ZFMK MYR2275, Enato, 24°53'0.25"S, 046°59'2.77"E, rainforest, coll. Wesener & Schütte, 27.v.2007; 7 ♂ & ♀, ZFMK MYR2278, same data as previous; 1 ♂, FMNH-INS 61090, same data as previous; 1

♂, FMNH-INS 61091, same data as previous; 8 ♂ & ♀, FMNH-INS 56033, same data as previous.

**Localities.** Only recorded from the littoral rainforest of Mandena (Wesener and Sierwald 2005) and the rainforest of Enato (Wesener and Wägele 2007). The two specimens from which the COI gene was sequenced, both from Enato, differ in four base pair substitutions.

***Sphaeromimus titanus* Wesener, sp. n.**

<http://zoobank.org/A178FBE5-A0FD-43BF-B244-5FF116D8C720>

[http://species-id.net/wiki/Sphaeromimus\\_titanus](http://species-id.net/wiki/Sphaeromimus_titanus)

Figures 2–4, 5A

**Material examined.** Type material. *Holotype*: 1 ♂, BLF13962 (CASENT 9032789), Madagascar, Province Fianarantsoa, Réserve Speciale Manombo, 24.5 km 228°SW Farafangana, 23°00'57"S, 047°43'08"E, 30 m, rainforest, coll. Brian L. Fisher et al., 20.iv.2006, general collecting.

**Paratype.** 1 ♀, same data as holotype.

**Diagnosis.** By far the largest known *Sphaeromimus*, >30 mm. Differing from all other *Sphaeromimus* with three stridulation ribs on the male harp in the following characters: large size; first stigma-carrying plate with a well-rounded projecting apex; tarsus with few hairs, relatively slender, 4.5 times longer than wide; endotergum with single regular row of long setae that barely protrude up to posterior margin; chela of posterior telopod in posterior view almost glabrous, movable finger straight.

**Description. Measurements.** Male holotype: 33.5 long, 16.6 (2nd), 17.2 (8th) wide, 9.2 (2nd), 11.1 (9th - highest) height. Female: 46.9 mm long, 24.15 mm (2nd), 27.4 (8th - widest) wide, 13.1 (2nd), 19.5 mm (12th, highest) high (Fig. 2A).

Colouration of tergites dark brown with black posterior margin. Paratergite impressions and groove of thoracic shield orange. Legs, antennae and pleurites orange, head and collum dark brownish-black, eyes green.

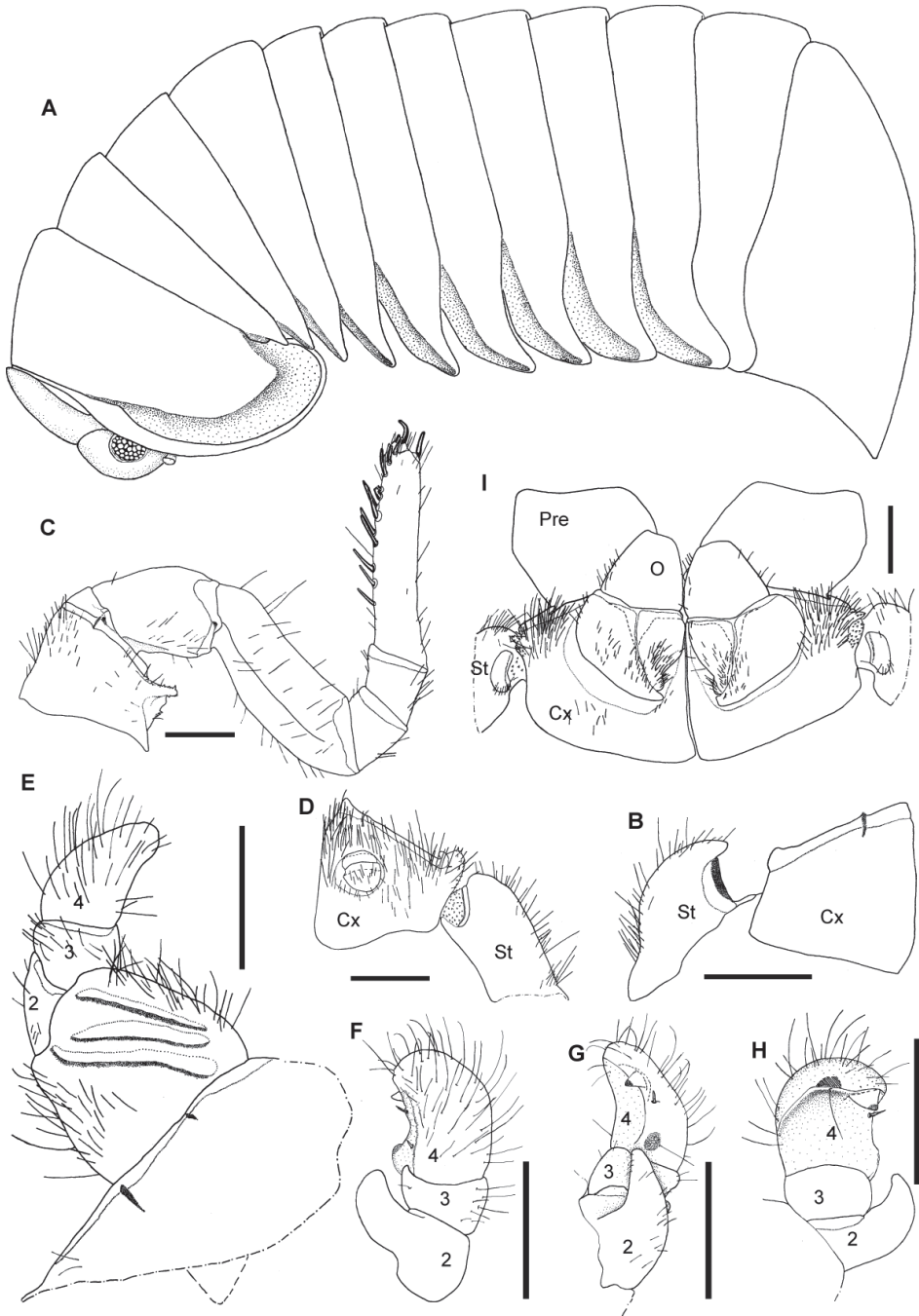
Head: Eyes with >70 ocelli. Antennae short, protruding back to coxa 6. Antennomeres 1–4 with few longer setae, 5 and 6 densely pubescent (Fig. 4A). Antennomere 6 towards disc with single row of sensilla basiconica (Fig. 4A). Female with 36/45, male with 79/81 apical cones (Fig. 4B). Mouthparts not dissected.

Collum glabrous except few setae at margins.

Thoracic shield smooth and glabrous, few setae in grooves. Grooves deep (Fig. 2A). Tergites 3–12 smooth, paratergite tips of midbody tergites strongly projecting posteriorly (Fig. 2A).

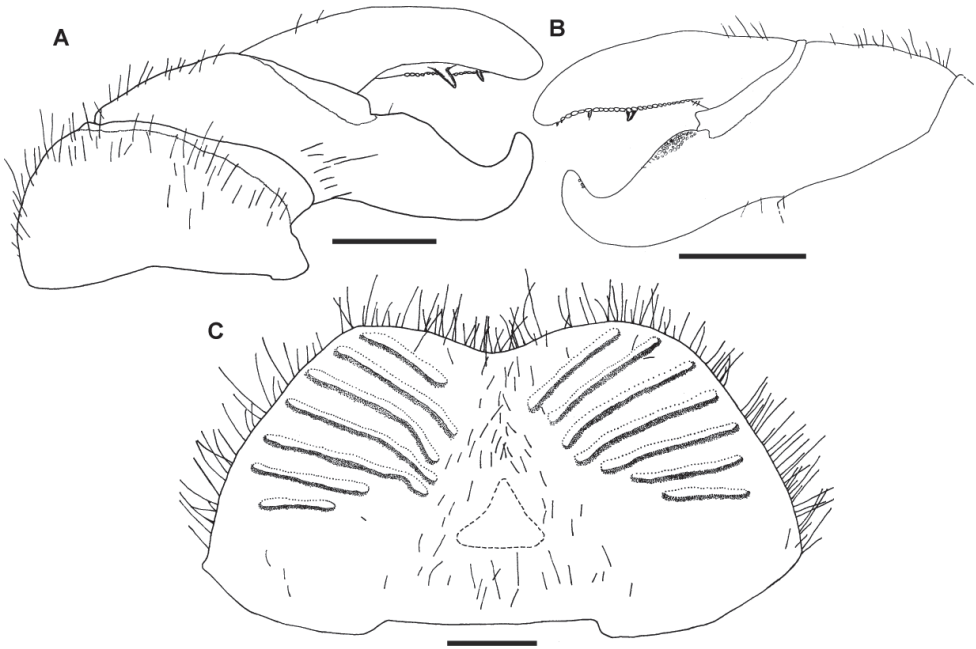
Anal shield massive, with a steep edge (Fig. 2A), lacking pubescent area.

Endotergum inner section with numerous short triangular spines and long setae (Fig. 5A). Between ridge and inner area two rows of weakly impressed, circular cuticular impressions. Externally single, sparse row of marginal bristles (Fig. 5A). Bristles short, barely reaching to tergite margin.

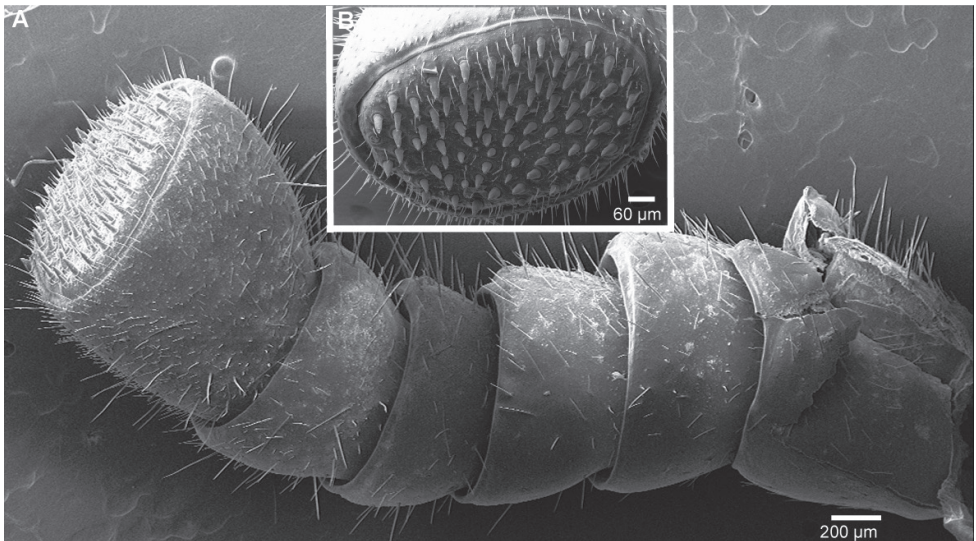


**Figure 2.** *Sphaeromimus titanus* sp. n., **A, I** female paratype **B–H** holotype **A** habitus **B** first right stigmatic plate and coxa 1 **C**: left leg 9 **D** left coxa 2 with gonopore and stigmatic plate 2 **E** left anterior telopod, anterior view ♀ left anterior telopod, mesal view **G** left anterior telopod, posterior view **H** left anterior telopod, lateral view **I** coxae and prefemora 2 with vulvae. Abbreviations: Cx = coxa; O = operculum; Pre = prefemur; St = stigmatic plate. Scale bars = 1 mm.

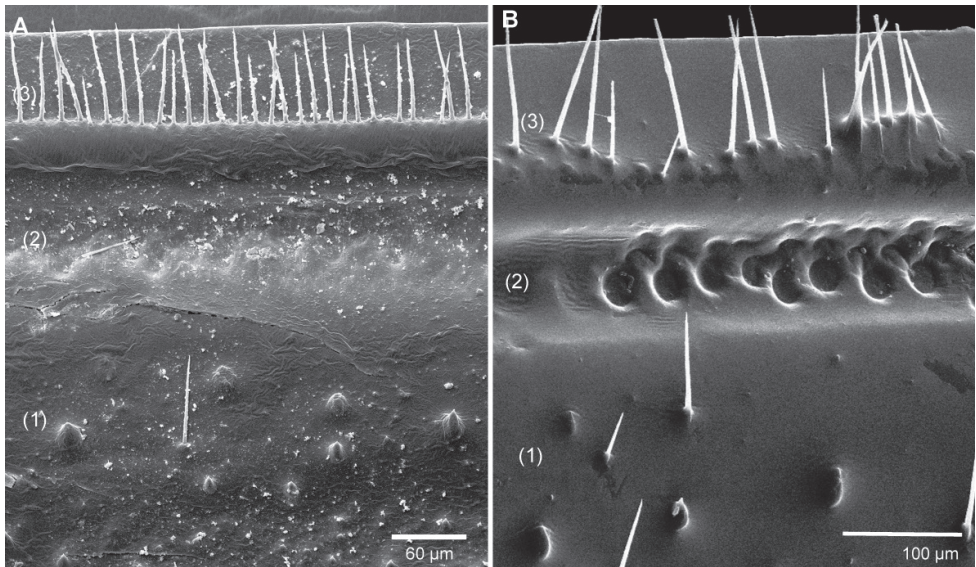




**Figure 3.** *Sphaeromimus titanus* sp. n., **C** female paratype, **A, B** holotype **A** left posterior telopod, anterior view **B** left posterior telopod, posterior view **C** female subanal plate with washboard. Scale bars = 1 mm.



**Figure 4.** *Sphaeromimus titanus* sp. n., holotype, SEM, left antenna. **A** lateral view **B** detail of disc with apical cones.



**Figure 5.** SEM, Endoterga of mid-body tergite. **A** *Sphaeromimus titanus* sp. n., holotype **B** *Sphaeromimus vatovavy* sp. n., holotype. Abbreviations: (1) = inner area with large spines and long setae; (2) = area with cuticular patterns; (3) = outer area with row(s) of marginal bristles and tergite margin.

First stigma-carrying plate with a well-rounded projecting apex (Fig. 2B).

Leg 1 with 2 or 3, 2 with 4–6, 3 with 10 ventral spines. Leg pairs 4–21 with 11–14 ventral spines. Coxa process strongly developed (Fig. 2C). Femur 2.1, tarsus 4.4 times longer than wide. All podomeres with only few setae (Fig. 2C).

Male gonopore typical for the genus (Fig. 2D).

Anterior telopod (Fig. 2E–H): Harp carrying three stridulation ribs (Fig. 2E). Shape usual for the genus, telopoditomere 4 with one large triangular spine and 2 or 3 smaller ones (Fig. 2F–H), apically with a weakly sclerotized spot (Fig. 2H).

Posterior telopod (Fig. 3A, B): Podomere 3 straight, 3.3 times longer than wide, slightly longer than immovable finger (Fig. 3A). Hollowed-out inner margin with one lobe and three sclerotized spines, posterior aspect with *ca.* 24 small crenulated teeth. Immovable finger basally wide, apically tapering, weakly curved towards podomere 3. Podomere 1 with few setae (Fig. 3A), podomere 2 only with few setae at anterior side, posterior side glabrous (Fig. 3B). Podomere 3 with only few marginal setae.

Female sexual characters: Vulva massive. Operculum well-rounded, protruding up to basal half of prefemur (Fig. 2I). Subanal shield massive, with shallow invagination at apical margin. Washboard with seven stridulation ribs on each side (Fig. 3C).

**Etymology.** ‘titanus’, adjective, referring to the large size of the species.

**Distribution.** Only known from the eastern lowland rainforest of Manombo, which is now isolated by vast areas of pseudosteppe from all other remaining rainforests.

***Sphaeromimus vatovavy* Wesener, sp. n.**

<http://zoobank.org/19F8614B-296B-44A0-A203-F1C38CE54FD3>

[http://species-id.net/wiki/Sphaeromimus\\_vatovavy](http://species-id.net/wiki/Sphaeromimus_vatovavy)

Figures 5B, 6, 7, 8, 9

**Material examined.** Type material. *Holotype*: 1 ♂, MNHN '39', Madagascar, Province Fianarantsoa, Forêt primitive de Tsianovoha (=Vatovavy-Fitovinany, Fort Carnot), rainforest, coll. Mission Heim á Madagascar, 1934-35, fin Sept. 34.

**Paratype.** 1 ♀, same data as holotype.

**Diagnosis.** Five stridulation ribs on the male harp, a character only shared with the spiny forest species *S. musicus*. Shape of female operculum unique, apically recessed. Endotergum with two rows of deeply impressed cuticular patterns and two dense, irregular rows of marginal bristles that protrude above tergite margin.

**Description.** Measurements: Female paratype: 21.1 mm long, 10.2 mm wide (2nd), 5.8 mm height (2nd), male broken, not measured but slightly smaller.

Colouration influenced by 70 years in preservative, faded dark brown without any discernable pattern (Fig. 6A). Antennae, legs and pleurites faded olive green, eyes green (Fig. 6A–D).

Head: Eyes with >60 ocelli (Fig. 6A). Posterior margin of head towards collum glabrous (Fig. 6A). Antennae short, protruding laterally slightly past margins of thoracic shield (Fig. 6A). Antennomeres 1–5 with few longer setae, only antennomere 6 densely pubescent (Fig. 7A). Antennomere 6 towards disc with single row of sensilla basiconica (Fig. 7A). Female with 63/65 (Fig. 7B), male with >90 apical cones. Gnathochilarium typical for the order (Fig. 7C), central pads mainly with single type of sensilla (Fig. 7D), rudimentary lateral palpi consisting of three sensilla (Fig. 7E). Mandible with the typical shape of the order, inner tooth 3-combed, with six long pectinate lamellae, condylus with a sharp groove at its apex (Fig. 8).

Collum glabrous, with few setiferous points at its margin (Fig. 6A). Thoracic shield smooth and glabrous, except for margin and lateral grooves (Fig. 6A). Grooves deep, anterior brim swollen. Tergites 3–12 smooth, paratergite tips of midbody tergites slightly projecting posteriorly. Anal shield massive, well-rounded, with single locking carinae, as typical for *Sphaeromimus* (Fig. 6C).

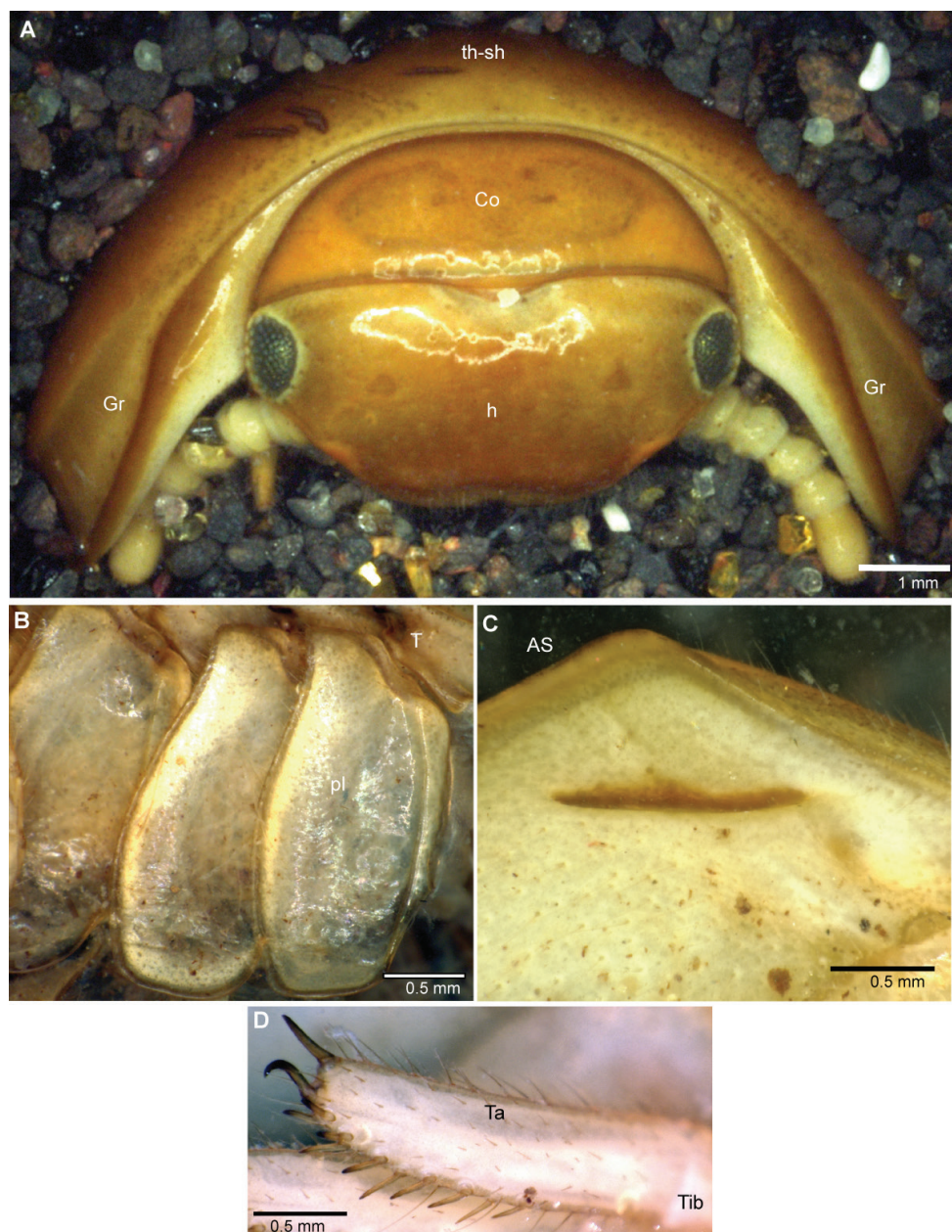
Endotergum inner section with numerous short triangular spines and long setae (Fig. 5B). Between ridge and inner area two rows of strongly impressed, circular cuticular impressions. Externally two dense but irregular rows of marginal bristles (Fig. 5B). Bristles long, protruding beyond tergite margin.

First stigma-carrying plate with a well-rounded apex.

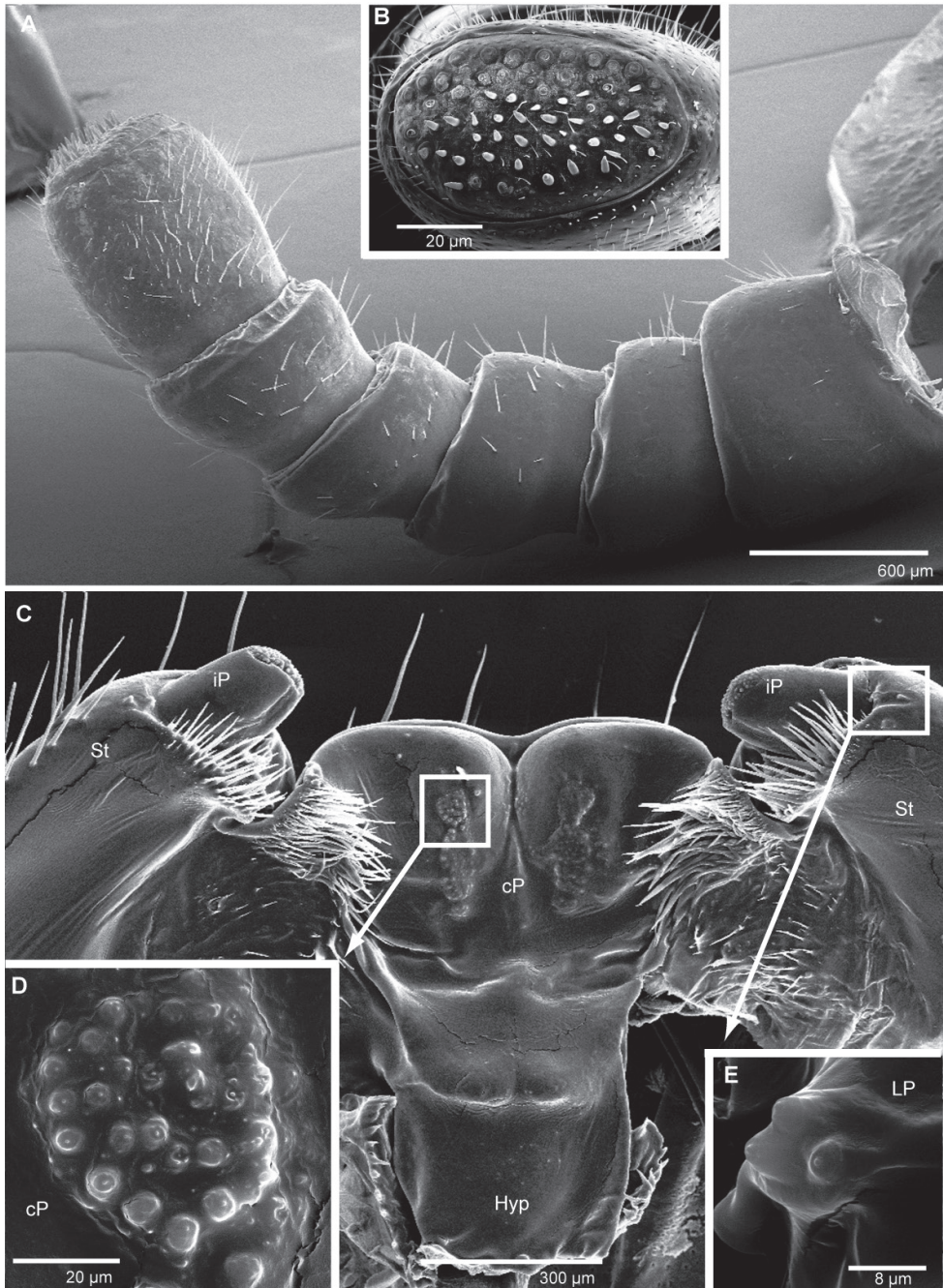
Leg 1 with 2–4, 2 with 3–5, 3 with 8 ventral spines. Leg pairs 4–21 with 10–12 ventral spines. Coxa process of midbody legs weakly developed. Femur 1.8, tarsus 3.3 times longer than wide (Fig. 6D).

Male gonopore inconspicuous.



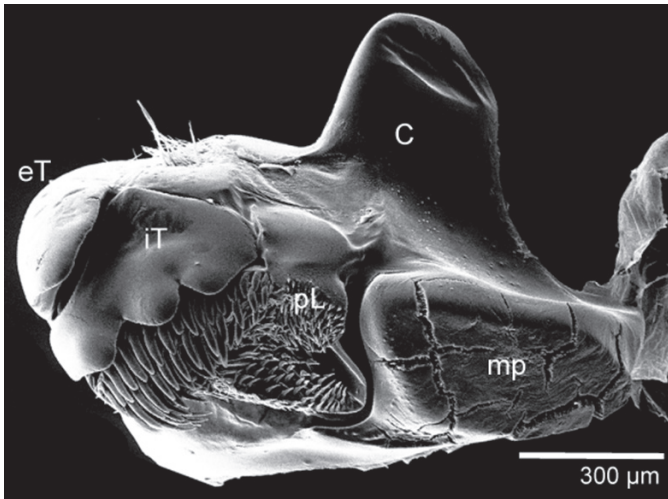


**Figure 6.** *Sphaeromimus vatovavy* sp. n., female paratype, multi-layer photographs. **A** head with collum and thoracic shield, frontal view **B** pleurites **C** underside of anal shield with black locking carina **D** tarsus of midbody leg. Abbreviations: AS = anal shield; Co = collum (tergite 1); Gr = lateral grooves of thoracic shield; h = head; pl = pleurite; T = tergite; Ta = tarsus; th-sh = thoracic shield (tergite 2); Tib = tibia.



**Figure 7.** *Sphaeromimus vatovavy* sp. n., female paratype, SEM. **A** right antenna, lateral view **B** antennomere 6 with disc **C** gnathochilarium, underside **D** detail of sensory cones on central pad **E** rudimentary right lateral palpus. Abbreviations: cP = central pads; Hyp = hypopharyngeal area; iP = inner palpus; LP = rudimentary lateral palpus; St = stipites.





**Figure 8.** *Sphaeromimus vatovavy* sp. n., female paratype, SEM. Right mandible. Abbreviations: C = condylus; eT = external tooth; iT = combed inner tooth; mp = molar plate; pL = pectinate lamellae.

Anterior telopod (Fig. 9A–C): Harp carrying five stridulation ribs (Fig. 9A). Shape usual for the genus, telopoditomere 4 massive, larger than two preceding joints, with one large triangular spine and 3 or 4 smaller ones (Fig. 9B, C).

Posterior telopod (Fig. 9D, E): Podomere 3 strongly curved, 3.1 times longer than wide, slightly longer than immovable finger (Fig. 9D). Hollowed-out inner margin with one lobe and four sclerotized spines, posterior aspect with *ca.* 26 small crenulated teeth (Fig. 9E). Immovable finger only slightly tapering apically, *ca.* 3 times longer than wide, apically strongly hooked towards podomere 3. Podomere 1 with few setae (Fig. 9D), podomere 2 and 3 glabrous.

Female sexual characters: Coxa process on leg 2 well-developed. Vulva massive. Operculum apically emarginate, protruding up to basal half of prefemur (Fig. 9F). Subanal partly reduced, with shallow invagination at apical margin. Washboard with 10 stridulation ribs on each side.

**Etymology.** ‘vatovavy’, noun in apposition, referring to the type locality, located in the area of Vatovavy-Fitovinany (Fort Carnot).

**Distribution.** Only known from the eastern lowland rainforest of Tsianovoha. Satellite images do not show much remaining natural vegetation in the area.

***Sphaeromimus lavasoa* Wesener, sp. n.**

<http://zoobank.org/8B359EBE-03AC-4367-96E7-D47F483447FE>

[http://species-id.net/wiki/Sphaeromimus\\_lavasoa](http://species-id.net/wiki/Sphaeromimus_lavasoa)

Figs 1B, 10, 11, 12A

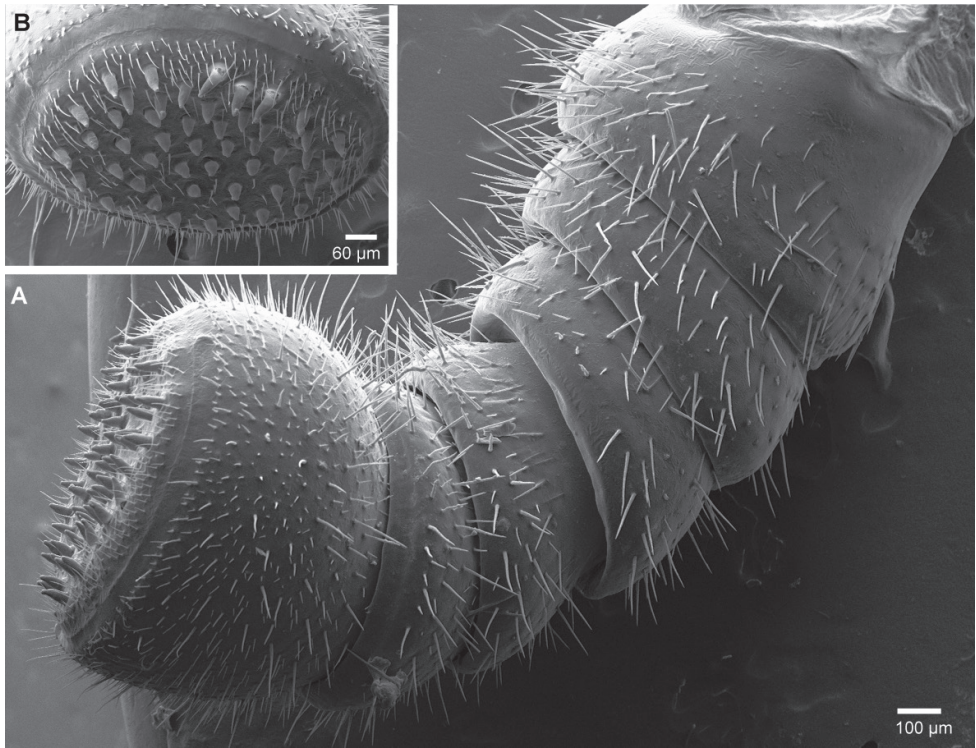
*Sphaeromimus* ‘sp. n. III G-Lavasoa’: Wesener et al. 2010: 1185 (molecular phylogenetic analysis).



**Figure 9.** *Sphaeromimus vatovavy* sp. n., A–E male holotype, ♀ female paratype, multi-layer photographs. **A** anterior telopods, anterior view **B** left anterior telopod, posterior view **C** left anterior telopod, lateral view **D** posterior telopods, anterior view **E** chela of right posterior telopod, posterior view ♀ coxa and prefemur 2 with vulvae. Abbreviations: Cx = coxa; Cx-P = coxal process; EP = external, lateral plate of vulva; IH = inner horns; IL = inner lobes; IP = inner, mesal plate of vulva; O = operculum; Pre = prefemur; syn = syncoxite.

**Material examined.** Type material. *Holotype*. 1 ♂, ZFMK MYR2320, Madagascar, Province Toliara, Grande Lavasoa, 25°5'10.23"S, 46°44'55.93"E, 524 m, rainforest, coll. Wesener & Schütte, 14.vi.2007.

**Paratypes.** 2 ♀, ZFMK MYR2321, same data as holotype; 1 ♂, FMNH-INS 61141, same data as previous; 1 ♂, FMNH-INS 61134 (Antenna removed); 1 ♀, FMNH-INS 61142; 1 ♀, FMNH 61143; ~ 35 ♂, ♀, juv., FMNH-INS 56208, all same data as holotype; 1 ♀, FMNH-INS 56213, Petit Lavasoa, 25°05.021'S, 046°46.110'E, 668 m, rainforest, coll. Wesener & Schütte, 21.v.2007.



**Figure 10.** *Sphaeromimus lavasoa* sp. n., male paratype, SEM, left antenna. **A** lateral view **B** detail of disc with apical cones.

**Other material.** ~ 50 ♂, ♀, juv., same data as holotype, sent as voucher specimens to the University of Antananarivo.

**Diagnosis.** Small shiny-black *Sphaeromimus* with brown collum and head. Male harp with four stridulation ribs. Midbody legs with weakly-developed coxal process.

**Description.** Measurements: male holotype: 21.7 long, 10.4 (2nd), 11.2 (8th - widest) wide, 5.6 (2nd), 6.8 (10th - highest) height. Largest female (with eggs): 23.1 mm long, 11.4 mm (2nd), 12.1 (8th - widest) wide, 6.35 (2nd), 8.55 mm (10th, highest) high.

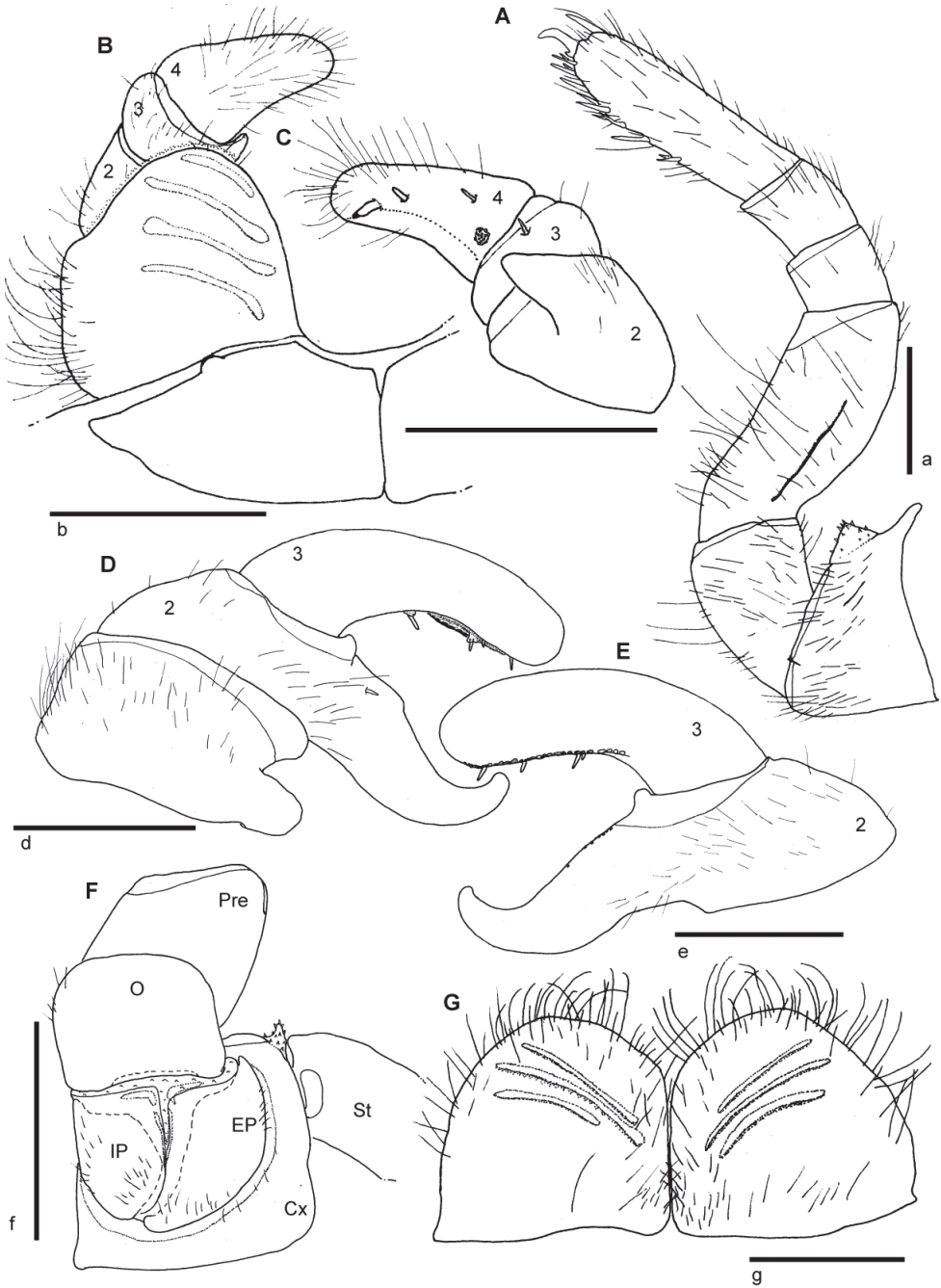
Colouration of tergites black. Collum and head light brown (Fig. 1B). Legs and antennae dark greenish-brown.

Head: Eyes with >60 ocelli. Antennae very short, protruding as far as leg 6. All antennomeres densely pubescent (Fig. 10A). Antennomere 6 towards disc with single row of sensilla basiconica (Fig. 10A). Female with 22/24 (largest), male with 62/65 apical cones (Fig. 10B). Mouthparts not dissected.

Collum glabrous except 3 or 4 short isolated setae on the surface and few at margin.

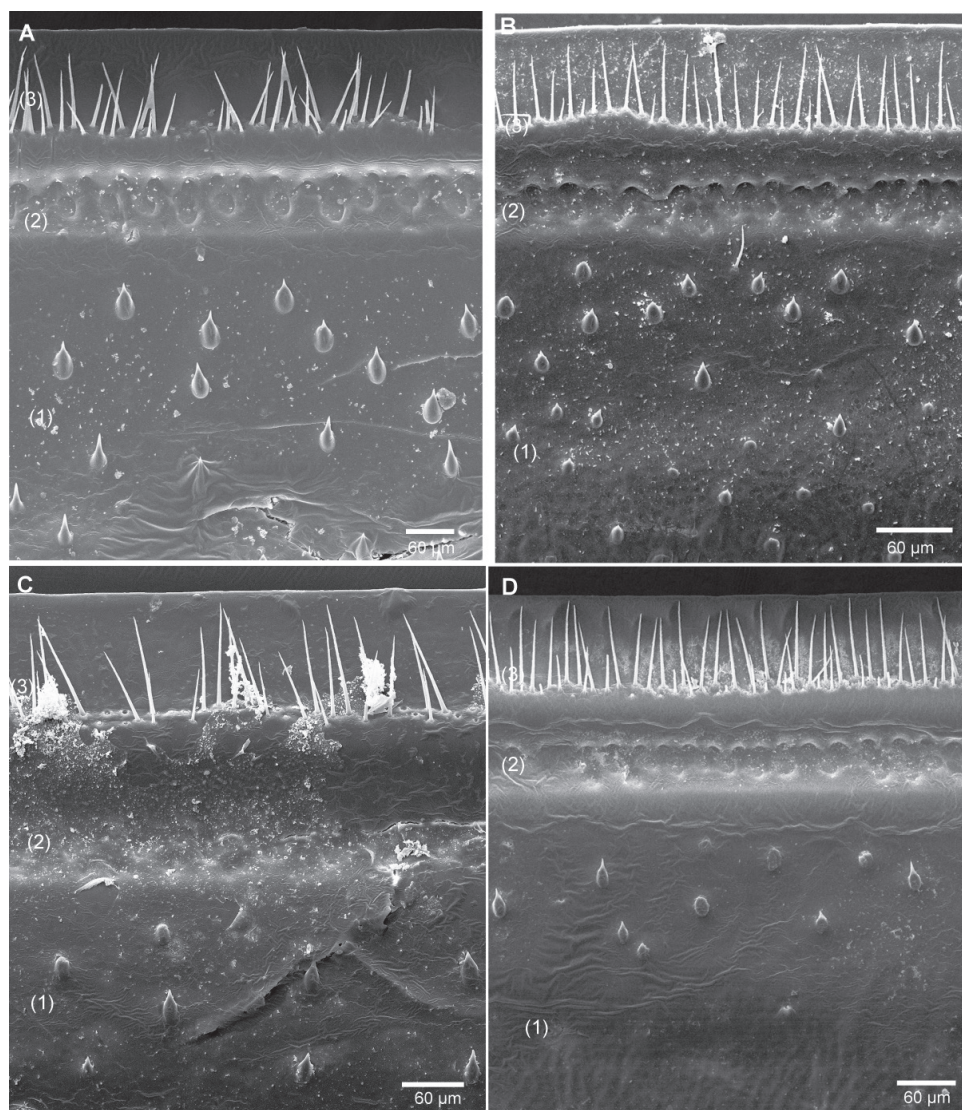
Thoracic shield smooth and glabrous, few setae in grooves. Tergites 3–12 smooth, paratergite tips of midbody tergites only weakly projecting posteriorly (Fig. 1B).

Anal shield massive, well-rounded, lacking pubescent area.



**Figure 11.** *Sphaeromimus lavasoa* sp. n., **A–E** male holotype ♀, **G** female paratype. **A** left leg 9 **B** anterior telopod, anterior view **C** left anterior telopod, posterior view **D** left posterior telopod, anterior view **E** chela of left posterior telopod, posterior view ♀ coxa and prefemur 2 with vulvae **G** female subanal plate with washboard. Abbreviations: Cx = coxa; EP = external, lateral plate of vulva; IP = inner, mesal plate of vulva; O = operculum; Pre = prefemur; St = stigmatic plate. Scale bars = 1 mm.





**Figure 12.** SEM, Endoterga of mid-body tergite. **A** *Sphaeromimus lavasoa* sp. n., paratype **B** *Sphaeromimus andohabela* sp. n., holotype from Isaka-Ivondro **C** specimen from Malio **D** specimen from Manantantely. Abbreviations: (1) = inner area with large spines and long setae; (2) = area with cuticular patterns; (3) = outer area with row(s) of marginal bristles and tergite margin.

Endotergum inner section with numerous short triangular spines and very few setae (Fig. 12A). Between ridge and inner area two rows of weakly impressed, circular cuticular impressions. Externally two irregular, dense rows of marginal bristles (Fig. 12A). Bristles short, ending well before tergite margin.

First stigma-carrying plate with a well-rounded apex.

Leg 1 with 3 or 4, 2 with 5 or 6, 3 with 8 or 9 ventral spines. Leg pairs 4–21 with 11–13 ventral spines. Coxa process weakly developed (Fig. 11A). Femur 2, tarsus 3.1 times longer than wide.

Male gonopore inconspicuous.

Anterior telopod (Fig. 11B, C): Harp carrying four stridulation ribs (Fig. 11B). Shape usual for the genus, telopoditomere 4 with one large triangular spine and 2 smaller ones (Fig. 11C). Telopoditomere 3 with a spine juxtaposed to process of telopoditomere 2 (Fig. 11C).

Posterior telopod (Fig. 11D, E): Podomere 3 curved, 3 times longer than wide, slightly longer than immovable finger (Fig. 11D). Hollowed-out inner margin with one lobe and four sclerotized spines, posterior aspect with *ca.* 29 small crenulated teeth. Immovable finger basally wide, apically tapering, 2.6 times longer than wide, strongly curved towards fixed finger. Podomere 1 and 2 with few setae on both sides (Fig. 11D), podomere 3 glabrous (Fig. 11E).

Female sexual characters: Second leg pair with well-developed coxal lobe. Vulva massive. Operculum well-rounded, protruding up to basal half of prefemur (Fig. 11F). Subanal shield almost divided into two, with strong invagination at apical margin (Fig. 11G). Washboard with three stridulation ribs on each side (Fig. 11G).

**Etymology.** ‘Lavaso’, noun in apposition, after the Lavaso (also called Ambatotsirongorongo) mountain, to which this species is endemic.

**Distribution.** Endemic to the Lavaso Mountain, where it could be recorded from two of the three remaining fragments. The species was common in the largest fragment of Grande Lavaso, but only a single female could be collected at Petit Lavaso.

***Sphaeromimus andohahela* Wesener, sp. n.**

<http://zoobank.org/CE4D941A-88F1-4D02-B08D-D141F8BDC7E5>

[http://species-id.net/wiki/Sphaeromimus\\_andohahela](http://species-id.net/wiki/Sphaeromimus_andohahela)

Figs 12B–D, 13, 14, 20

*Sphaeromimus* ‘sp. n. I Manantantely’; *Sphaeromimus* ‘sp. n. II Malio’-- Wesener et al. 2010: 1185 (molecular phylogenetic analysis)

**Material examined.** Type material. *Holotype*. 1 ♂, ZFMK MYR2322, Madagascar, Province Toliara, PN Andohahela, Isaka-Ivondro Nord, 24°46.302'S, 046°51.699'E, 571 m, rainforest, coll. Wesener & Schütte, 12.vi.2007.

**Paratypes.** 1 ♀, FMNH-INS 61135; 1 imm., FMNH-INS 61136; 1 ♀, FMNH 61137; 2 ♀, 2 imm., FMNH-INS 56212, all same data as holotype.

**Other material.** 6 ♂, ♀, Juv., FMNH-INS 56210, PN Andohahela, Malio, 24°55.810'S, 046°46.343'E, rainforest, coll. Wesener & Schütte, 30.v.2007; 1 ♂, ZFMK MYR2323, same data as previous; 9 ♂, ♀, imm., FMNH-INS 56209, Madagascar, Vohimena Chain, PR Manantantely, 24°59'17.14"S, 046°55'27.95"E, rainforest, coll. Wesener & Schütte, 06.vi.2007; 1 ♀, FMNH-INS 61140; 1 ♂, FMNH-INS

61132; 1 ♀, FMNH-INS 61138; 1 ♂, FMNH-INS 61139; 1 ♂, 2F, ZFMK MYR 2324, all same data as previous.

**Diagnosis.** Small matte-black pill millipede with a dark brown head and collum and light brown appendages. Male harp with three stridulation ribs.

**Description.** Measurements: male holotype: 20.2 long, 9.2 (2nd), 9.8 (8th) wide, 4.9 (2nd), 6.1 (10th = highest) high. Largest female (with eggs): 21.1 mm long, 9.6 mm (2nd), 10.75 (8th = widest) wide, 5.7 (2nd), 7.5 mm (10th = highest) high.

Colouration of tergites black, matte not shiny. Collum and head dark brown (Fig. 20). Depressions of paratergites as well as legs and antennae brownish.

Head: Eyes with >60 ocelli. Antennae quite long, protruding as far as leg 8. Antennomeres 1–5 with few setae, 6 densely pubescent (Fig. 13A). Antennomere 6 towards disc with single row of sensilla basiconica (Fig. 13B). Female with 54/56 (13B), male with 74/78 apical cones (Fig. 13C). Gnathochilarium typical for the genus (Fig. 13D), rudimentary lateral palpi with a field of four sensory cones (Fig. 13E). Mandible with the typical shape of the order, inner tooth 3-combed, with six long pectinate lamellae, condylus with a sharp and quite large groove at its apex (Fig. 13F).

Collum glabrous except few setae at its margin.

Thoracic shield smooth and glabrous, few setae in grooves. Tergites 3–12 smooth, but not glossy, paratergite tips of midbody tergites only weakly projecting posteriorly (Fig. 20).

Anal shield massive, well-rounded, lacking pubescent area.

Endotergum inner section with numerous short triangular spines and very few setae (Fig. 12B). Between ridge and inner area two rows of weakly impressed, circular cuticular impressions. Externally two irregular rows of marginal bristles (Fig. 12B–D). Bristles short, barely protruding up to tergite margin.

First stigma-carrying plate with a well-rounded apex.

Leg 1 with 2 to 4, 2 with 5 or 6, 3 with 10 or 11 ventral spines. Leg pairs 4–21 with 12–14 ventral spines. Coxa process weakly developed (Fig. 14A). Femur 2, tarsus 2.9 times longer than wide.

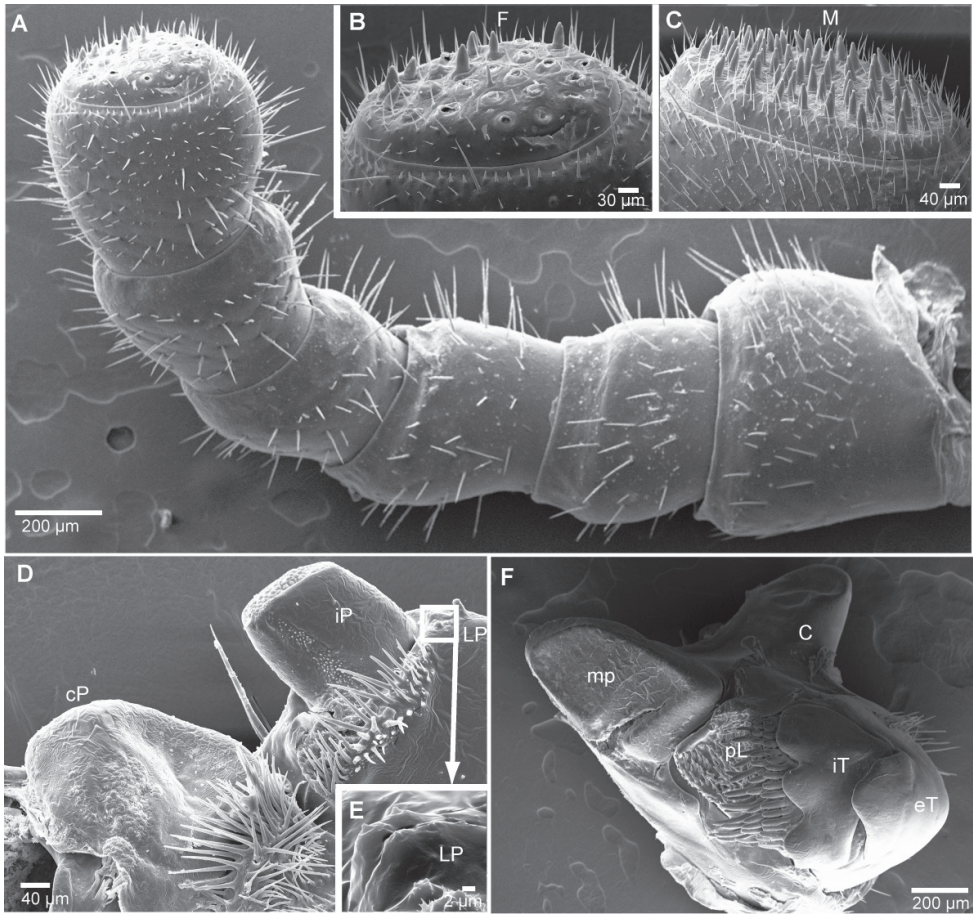
Male gonopore inconspicuous.

Anterior telopod (Fig. 14B, C): Harp carrying three stridulation ribs (Fig. 14B). Shape usual for the genus, telopoditomere 4 as long as 2 and 3 combined, with one large triangular spine and 4 smaller ones (Fig. 14C). Telopoditomere 3 with a spine juxtaposed to process of telopoditomere 2 (Fig. 14C).

Posterior telopod (Fig. 14D): Podomere 3 curved, 3 times longer than wide, slightly longer than immovable finger (Fig. 14D). Hollowed-out inner margin with one lobe and four sclerotized spines, posterior aspect with *ca.* 21 small crenulated teeth. Immobile finger basally wide, apically tapering, 3.1 times longer than wide, strongly curved towards fixed finger. Podomere 1 and 2 with few setae on both sides (Fig. 14D), podomere 3 with a few setae at its margins.

Female sexual characters: Second leg pair with well-developed coxal lobe. Vulva massive. Operculum well-rounded, protruding above basal half of prefemur (Fig. 14E). Subanal shield almost divided into two, with strong invagination at apical margin. Washboard with three stridulation ribs on each side.



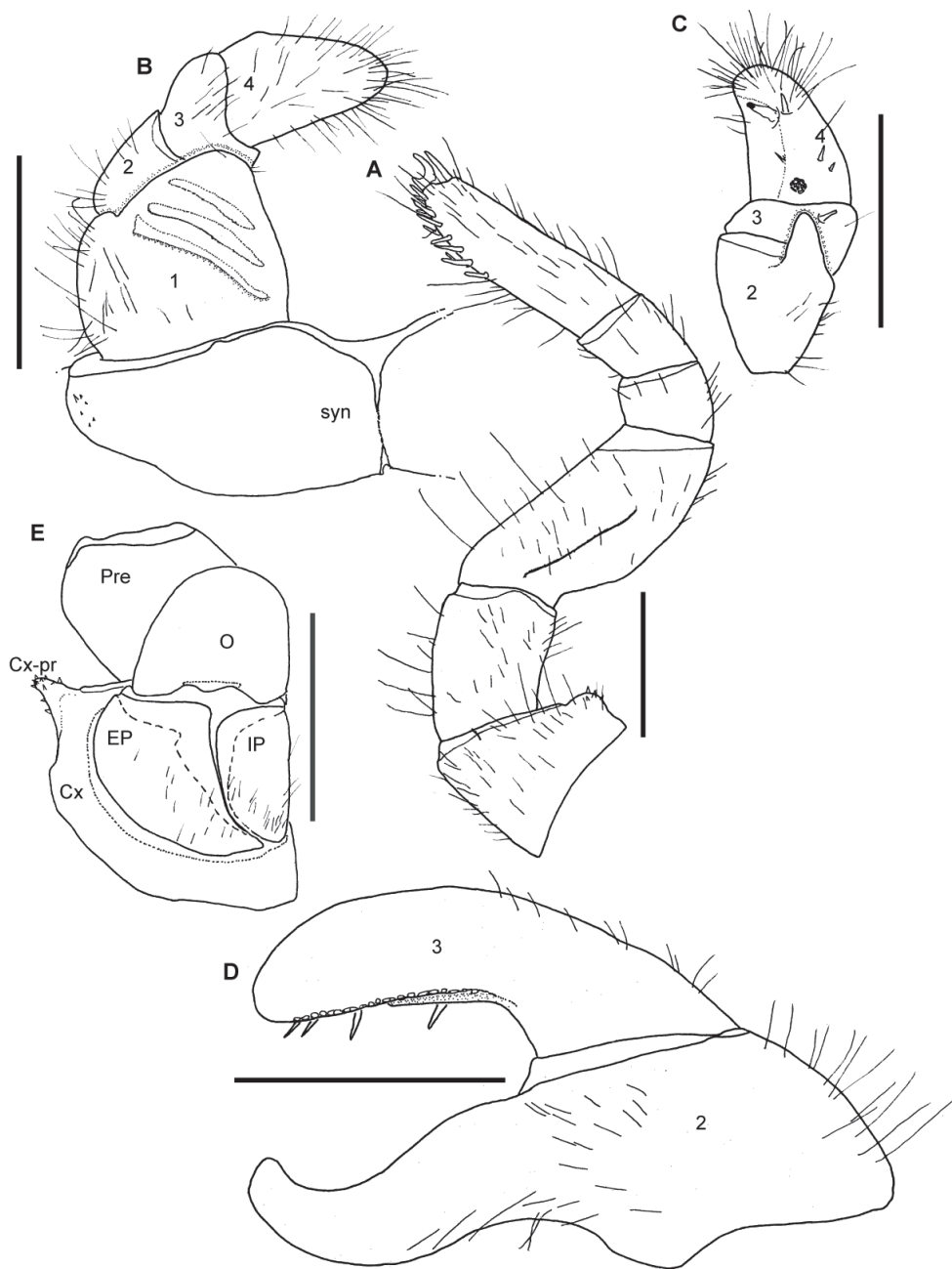


**Figure 13.** *Sphaeromimus andohabeha* sp. n., **A, B, D–F** female paratype **C** male paratype, SEM. **A** right female antenna, lateral view **B** female antennomere 6 with disc **C** male antennomere 6 with disc **D** gnathochilarium, right corner, inner surface **E** rudimentary right lateral palpus ♀ left mandible, mesal view. Abbreviations: C = condylus; cP = central pads; eT = external tooth; iP = inner palpus; iT = combed inner tooth; LP = rudimentary lateral palpus; mp = molar plate; pL = pectinate lamellae.

Intraspecific variation: The endotergum differs slightly in the development of the cuticular impressions between the specimens from Isaka-Ivondro (Fig. 12B), Malio (Fig. 12C) and Manantantely (Fig. 12D). The specimens from the three localities also differ slightly in their colour pattern: In specimens from Manantantely and Isaka-Ivondro, the head and collum are dark brown, while those from Malio have a brown thoracic shield too.

Genetic distances in the COI gene between the three populations are 2.9–4%, while even the two individuals from Malio show a variation at the population level of 3.6%. Future studies involving more localities and specimens should investigate whether or not gene flow occurs between the different populations of *S. andohabeha*.





**Figure 14.** *Sphaeromimus andohabela* sp. n., **A–D** male holotype **E** female paratype. **A** left leg 9 **B** anterior telopod, anterior view **C** right anterior telopod, posterior view **D** left posterior telopod, posterior view **E** coxa and prefemur 2 with vulvae. Abbreviations: Cx = coxa; Cx-pr = coxal process; EP = external, lateral plate of vulva; IP = inner, mesal plate of vulva; O = operculum; Pre = prefemur; syn = syncoxite. Scale bars = 1 mm.

**Etymology.** ‘andohahela’, noun in apposition, after the type locality, the rainforests of the national park Andohahela.

**Distribution.** Widespread in the lowland and montane rainforests of the northern Anosy and Vohimena mountain chains.

***Sphaeromimus ivohibe* Wesener, sp. n.**

<http://zoobank.org/E8220C56-2B68-414F-8949-27E207D3B0C2>

[http://species-id.net/wiki/Sphaeromimus\\_ivohibe](http://species-id.net/wiki/Sphaeromimus_ivohibe)

Figs 15, 16A

**Material examined.** Type material. *Holotype*. 1 ♂, FMNH-INS 8184, Madagascar, Province Fianarantsoa, extreme northern limit of Réserve Speciale de Ivohibe, along Hefitany Riv., ca. 7.5 km ENE Ivohibe, 22.4700°S, 46.9600°E, 1200 m, coll. S. M. Goodman, 03.–09.ix.1997.

**Diagnosis.** Small shining black pill millipede with orange-reddish appendages. Of all currently known *Sphaeromimus* with highest number of stridulation ribs, 6, on male harp. Posterior telopods unique, with two large membranous lobes.

**Description.** Measurements: male holotype: 20.6 long, 8.6 (2nd), 9.05 (8th = widest) wide, 5.2 (2nd), 6.1 (8th = highest) height.

Colouration of tergites shining black. Paratergite impressions and groove of thoracic shield dark greenish. Legs, antennae and pleurites orange-red, eyes green.

Head: Eyes with >60 ocelli. Antennae very short, protruding to coxa 5. Antennomeres 1–4 with few longer setae, 5 and 6 densely pubescent. Antennomere 6 towards disc with single row of sensilla basiconica. Male with 34/35 apical cones. Mouthparts not dissected.

Collum glabrous except few setae at margins.

Thoracic shield smooth and glabrous, few setae in grooves. Grooves deep. Tergites 3–12 smooth, except for paratergite depressions. Paratergite tips of midbody tergites weakly projecting posteriorly.

Anal shield well-rounded, lacking pubescent area.

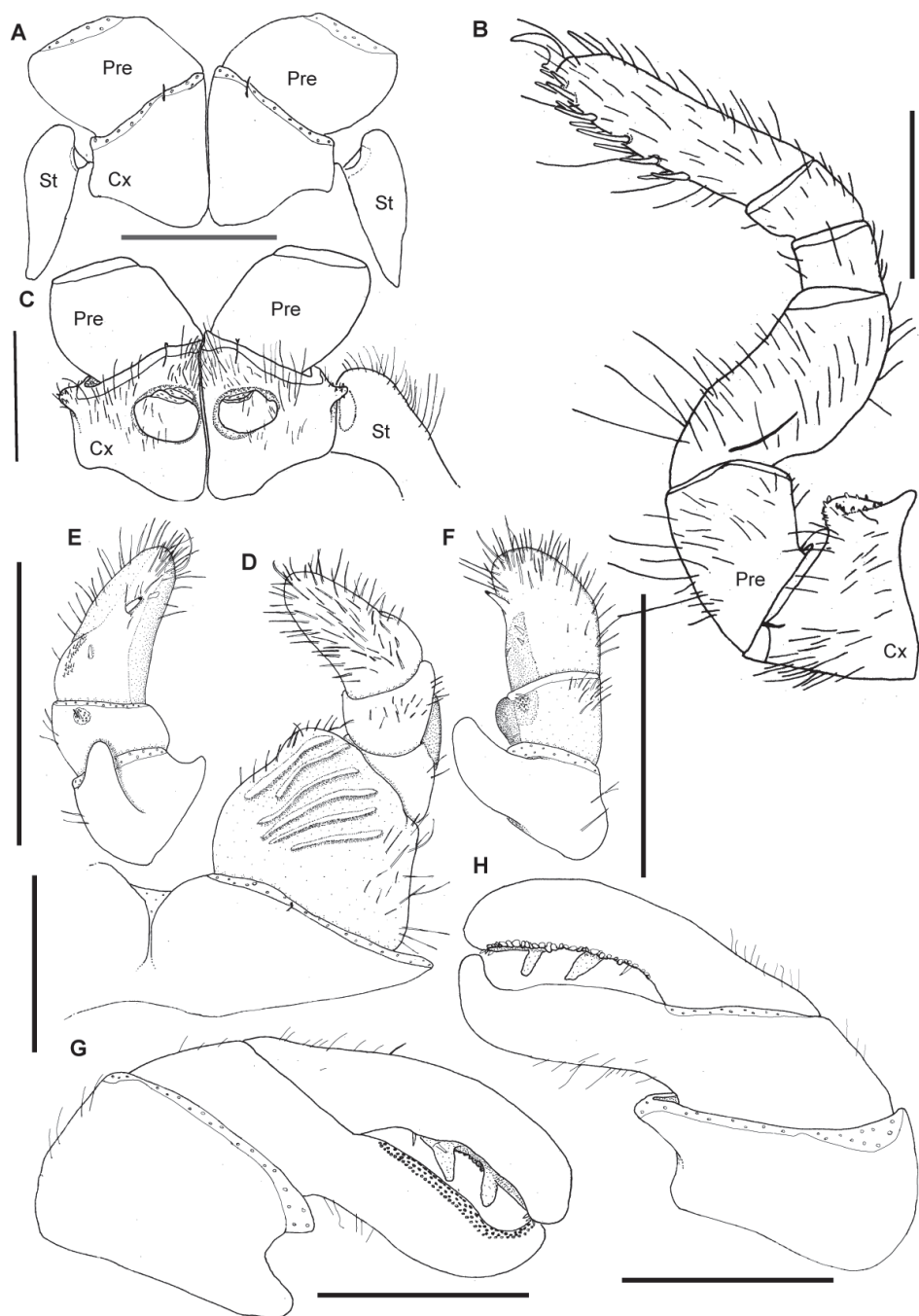
Endotergum inner section with numerous short triangular spines and long setae (Fig. 16A). Between ridge and inner area two rows of weakly impressed, circular cuticular impressions. Externally single, sparse row of marginal bristles (Fig. 16A). Bristles short, not protruding up to tergite margin.

First stigma-carrying plate with a well-rounded projecting apex (Fig. 15A).

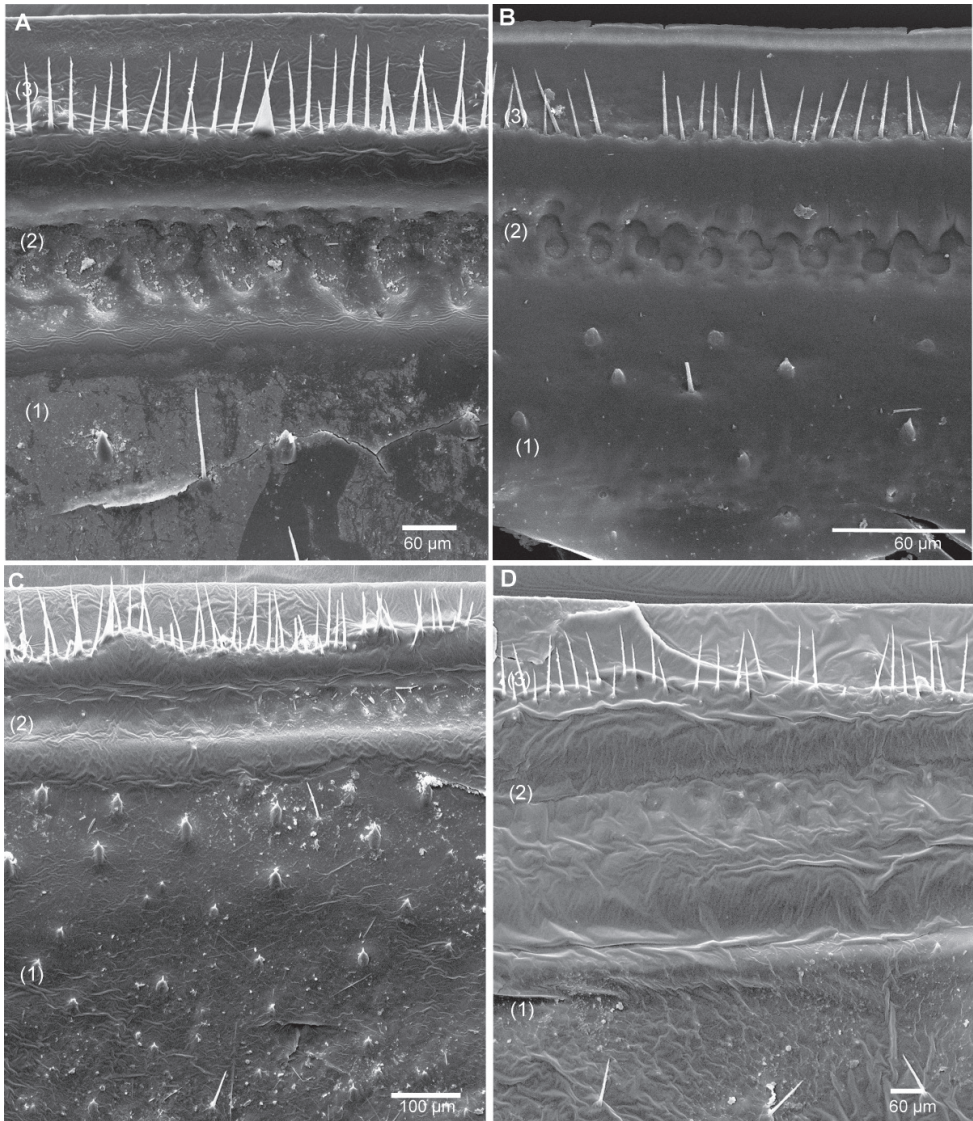
Leg 1 with 2, 2 with 3, 3 with 8 ventral spines. Leg pairs 4–21 with 12 ventral spines. Coxa process visible, but not as well developed as those of anterior legs (Fig. 15B). Femur 1.6, tarsus 2.9 times longer than wide (Fig. 15B).

Male gonopore typical for the genus (Fig. 15C).

Anterior telopod (Fig. 15D–F): Harp carrying six stridulation ribs (Fig. 15D). Shape usual for the genus, telopoditomere 4 longer than 2 and 3 combined, with one



**Figure 15.** *Sphaeromimus ivohibe* sp. n., holotype. **A** coxae and prefemora 1 with stigmatic plates **B** left leg 9 **C** coxae and prefemora 2 with gonopore and stigmatic plate **D** right anterior telopod, anterior view **E** right anterior telopod, posterior view **F** female right anterior telopod, lateral view **G** left posterior telopod, anterior view **H** left posterior telopod, posterior view. Abbreviations: Cx = coxa; Pre = prefemur; St = stigmatic plate. Scale bars = 1 mm.



**Figure 16.** SEM, Endoterga of mid-body tergite. **A** *Sphaeromimus ivohibe* sp. n., paratype **B** *Sphaeromimus saintelucei* sp. n., holotype from Isaka-Ivondro **C** *Sphaeromimus andrahomana* sp. n., holotype **D** *S. andrahomana* cave specimen. Abbreviations: (1) = inner area with large spines and long setae; (2) = area with cuticular patterns; (3) = outer area with row(s) of marginal bristles and tergite margin.

large triangular spine and 2 or 3 smaller ones (Fig. 15E, F), laterally with a field of sensory hair (Fig. 15E). Podomere 3 with several small spines juxtaposed to process of telopoditomere 2.

Posterior telopod (Fig. 15G, H): Podomere 3 straight, 4.4 times longer than wide, slightly longer than immovable finger (Fig. 15G). Hollowed-out inner margin with



two lobes and four sclerotized spines, posterior aspect with *ca.* 36 small crenulated teeth (Fig. 15H). Immovable finger apically only weakly tapering, only its apex curved towards podomere 3. Podomere 1–3 glabrous except for a few marginal hair with few setae (Fig. 15G, H).

Female unknown.

**Etymology.** ‘ivohibe’, noun in apposition, after the type locality, the national park Ivohibe.

**Distribution.** Only known from the type locality.

***Sphaeromimus saintelucei* Wesener, sp. n.**

<http://zoobank.org/EE026627-2CE4-4492-8141-9A841E794635>

[http://species-id.net/wiki/Sphaeromimus\\_saintelucei](http://species-id.net/wiki/Sphaeromimus_saintelucei)

Figs 16B, 17

**Material examined.** Type material. *Holotype*: 1 ♂, ZFMK MYR889, Madagascar, Province Toliara, Sainte Luce, fragment S8, 24°46.520'S, 047°09.074'E, 28 m, littoral forest on basaltic soil, coll. Wesener & Schütte, 29.v.2007.

**Paratypes.** 1 ♂, FMNH-INS 61089, same data as holotype; 1 ?, FMNH-INS 61088, same data as holotype.

**Diagnosis.** *S. saintelucei* sp. n. shares its small size (<20 mm), total absence of a coxal lobe at midbody legs in combination with slender posterior telopods of which the apex of the immovable finger is strongly curved only with *S. inexpectatus* Wesener & Sierwald, 2005. *S. saintelucei* differs from the latter in the dull brown colour (shiny pink in *S. inexpectatus*), and the anterior telopods. Both species differ genetically at 4–4.8% of their COI gene.

**Description.** Measurements: male holotype: 15.8 long, 6.6 (2nd) wide, 4.1 (2nd) high.

Colouration of tergites dull brown. Paratergite impressions and groove of thoracic shield slightly lighter. Legs, antennae and pleurites orange-red, eyes green.

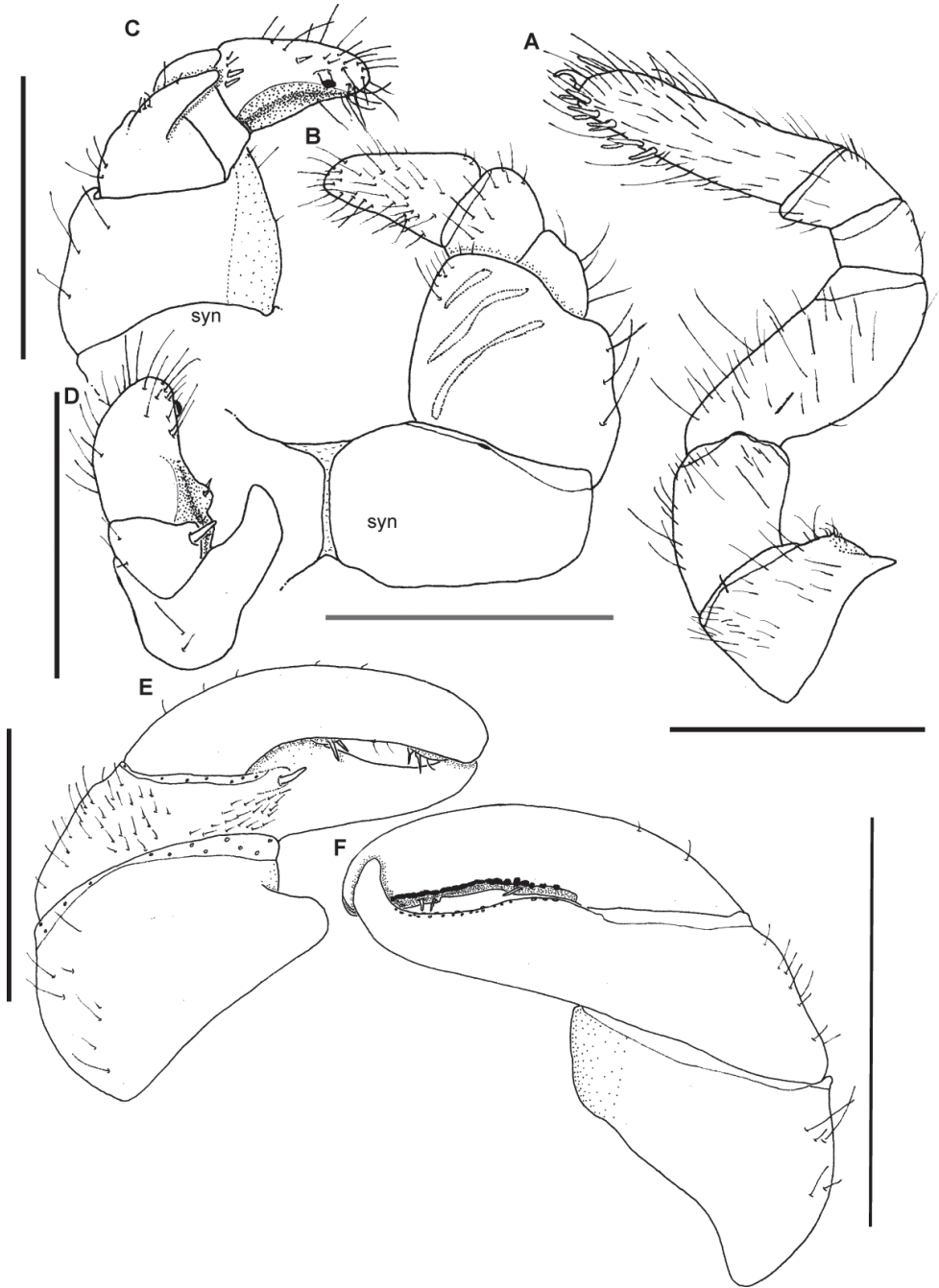
Head: Eyes with >45 ocelli. Antennae short, protruding to coxa 4. Antennomeres 1–5 with few longer setae, 6 densely pubescent. Antennomere 6 huge, large than 3 basal antennomere combined, towards disc with single row of sensilla basiconica. Male with 49/48 apical cones. Mouthparts not dissected.

Collum glabrous except few setae at margins.

Thoracic shield smooth and glabrous, few setae in grooves. Grooves deep. Tergites 3–12 smooth, except for paratergite depressions. Paratergite tips of midbody tergites weakly projecting posteriorly.

Anal shield well-rounded, lacking pubescent area.

Endotergum inner section with few short triangular spines and long setae (Fig. 16B). Between ridge and inner area two rows of weakly impressed, circular cuticular impressions. Externally single, extremely sparse row of marginal bristles (Fig. 16B). Bristles short, not protruding up to tergite margin.



**Figure 17.** *Sphaeromimus saintelucei* sp. n., holotype. **A** left leg 9 **B** right anterior telopod, anterior view **C** left anterior telopod, posterior view **D** right anterior telopod, lateral view **E** left posterior telopod, anterior view ♀ left posterior telopod, posterior view. Abbreviations: syn = syncoxite. Scale bars = 1 mm.

First stigma-carrying plate with a well-rounded not-projecting apex.

Leg 1 with 2, 2 with 2, 3 with 4 or 5 ventral spines. Leg-pairs 4–21 with 7–10 ventral spines. Coxa process invisible (Fig. 17A), only weakly developed at anterior legs. Femur 2, tarsus 3.2 times longer than wide (Fig. 17A).

Male gonopore typical for the genus.

Anterior telopod (Fig. 17B–D): Harp carrying three stridulation ribs (Fig. 17B). Shape usual for the genus, telopoditomere 4 as long as 2 and 3 combined, with one large triangular spine and 2 or 3 smaller ones (Fig. 15C, D). Podomere 3 with one large spine juxtaposed to process of telopoditomere 2 (Fig. 17D).

Posterior telopod (Fig. 17E, F): Podomere 3 weakly curved, 4.1 times longer than wide, longer than immovable finger (Fig. 17E). Hollowed-out inner margin with single lobe and four sclerotized spines, posterior aspect with *ca.* 24 small crenulated teeth (Fig. 17F). Immobile finger apically strongly tapering, its apex strongly curved and overlapping podomere 3. Immobile finger with single spine at its base (Fig. 17E). Podomere 1 and 3 glabrous except for a few marginal hair with few setae, podomere 2 on posterior side glabrous (Fig. 17F), on anterior side with several hairs (Fig. 17E).

Female unknown.

**Etymology.** ‘saintelucei’, adjective, after the type locality, and only area of occurrence, the littoral rainforest of Sainte Luce.

**Distribution.** Only known from the only remaining southern lowland forest on basaltic soil, the tiny fragment S8 of Sainte Luce. In the nearby fragments on sandy soil, *S. splendidus* occurs.

***Sphaeromimus andrahomana* Wesener, sp. n.**

<http://zoobank.org/DD6E47B7-56DB-44FB-8870-9380460B13F6>

[http://species-id.net/wiki/Sphaeromimus\\_andrahomana](http://species-id.net/wiki/Sphaeromimus_andrahomana)

Figs 1C, 16C, D, 18

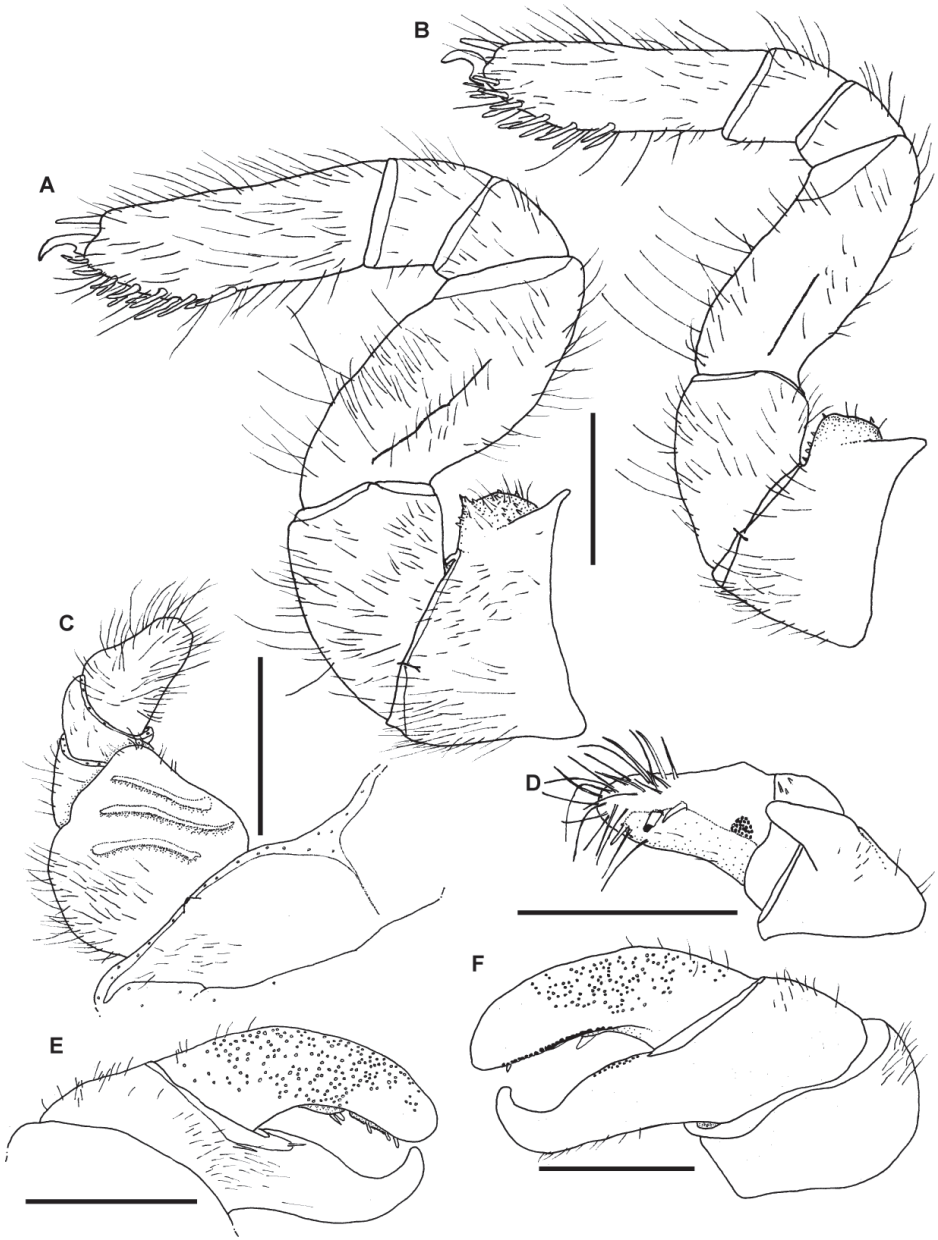
*Sphaeromimus* ‘sp. n. V Grotte’: Wesener et al. 2010: 1185 (molecular phylogenetic analysis)

**Material examined.** Type material. *Holotype*. 1 ♂, FMNH-INS 562214, N of village of N of Ankapaky, close to the Grotte d’Andrahomana, 25°11'18.87"S, 46°38'45.14"E, 70 m, dry forest plateau with deep ravines, coll. Wesener & Schütte, 20.v.2007

**Other material examined.** 1 ♂, FMNH-INS 56211, Grotte Andrahomana, 24°51.006'S, 046°55.907'E, inside humid cave, coll. Wesener & Schütte, 20.v.2007.

**Diagnosis.** Small matte-black pill millipede with a dark brown head and collum. Similar to *S. andohahela* but differs from the latter in weakly developed cuticular patterns and presence of numerous small pits on movable finger of posterior telopod. Genetical distance of the COI gene between both species is 10–11.4%.

**Description.** Measurements (holotype): 21.1 mm long, 9.8 mm (2nd), 10.7 mm (8th - widest) wide, 5.5 (2nd), 7.0 mm (10th, highest) height.



**Figure 18.** *Sphaeromimus andrahomana* sp. n.. **A** left leg 9, holotype **B** left leg 9, cave specimen **C** anterior telopod, anterior view **D** right anterior telopod, posterior view **E** left posterior telopod, anterior view **F** left posterior telopod, posterior view. Scale bars = 1 mm.

Colouration of tergites black, collum and head brown. Paratergite impressions light brown to olive-greenish, legs and antennae olive green (faded to white in ethanol), pleurites light brown, eyes green.



Head: Eyes with >55 ocelli. Antennae short, posteriorly protruding to coxa 5. Antennomeres 1–5 with few longer setae, 6 densely pubescent. Antennomere 6 towards disc with single row of sensilla basiconica. Male with 58/61 apical cones. Mouthparts not dissected.

Collum glabrous except few setae at margins.

Thoracic shield smooth and glabrous, few setae in grooves. Grooves deep. Tergites 3–12 smooth, except for paratergite depressions. Paratergite tips of midbody tergites weakly projecting posteriorly.

Anal shield well-rounded, lacking pubescent area.

Endotergum inner section with few short triangular spines and long setae (Fig. 16C). Between ridge and inner area two rows of weakly impressed, circular cuticular impressions. Externally two dense rows of marginal bristles (Fig. 16C). Bristles long, protruding above tergite margin.

First stigma-carrying plate with a well-rounded not-projecting apex.

Leg 1 with 2 or 3, 2 with 5 or 6, 3 with 10 or 11 ventral spines. Leg pairs 4–21 with 12–14 ventral spines. Coxa process well developed (Fig. 18A), only weakly developed at anterior legs. Femur 1.6, tarsus 3.0 times longer than wide (Fig. 18A).

Male gonopore typical for the genus.

Anterior telopod (Fig. 18C, D): Harp carrying three stridulation ribs (Fig. 18C). Shape usual for the genus, telopoditomere 4 as long as 2 and 3 combined, with one large triangular spine and 2 or 3 smaller ones (Fig. 18C, D). Podomere 3 with three small spines juxtaposed to process of telopoditomere 2 (Fig. 18D).

Posterior telopod (Fig. 18E, F): Podomere 3 weakly curved, 3 times longer than wide, longer than immovable finger (Fig. 18E). Both sides with conspicuous pits (Fig. 18E, F). Hollowed-out inner margin with single lobe and five sclerotized spines, posterior aspect with *ca.* 24 small crenulated teeth (Fig. 18F). Immovable finger apically strongly tapering, its apex strongly curved and overlapping podomere 3. Podomere 1 and 3 glabrous except for a few marginal hair with few setae, podomere 2 on posterior side glabrous (Fig. 18F), on anterior side with several hair (Fig. 18E).

Female unknown.

Etymology: ‘andrahomana’, noun in apposition, after the famous cave close to the type locality, the Grotte d’Andrahomana.

**Distribution.** Relic occurrence in the Grotte D’Andrahomana. The single individual found close to the village Ankapaky might be an indication of a more widespread occurrence in the little explored Vohisandria and Amboalaingo hills N. of Ankapaky and S. of Ranopiso.

**Discussion.** Intraspecific variations: The cave specimen shows a distinct colour pattern: tergites very light brown with dark brown posterior margins (Fig. 1C), head and collum light brown, legs and antenna, at least apically red. The endotergum shows fewer spines and hair in the cave specimen (Fig. 16D) when compared to the holotype (Fig. 16C). Furthermore, the leg of the cave specimen is distinctively slenderer at its basal joints (Fig. 18B), the femur being 2.2 (holotype 1.6), the tarsus 3 (holotype 3) times longer than wide. Despite their large morphological difference show both specimens the same COI haplotype.

### Undetermined *Sphaeromimus* spp. records

**Material examined.** 2 ♀, CAS ENT 9032816, Madagascar, Vevembe, Farafangana, Province Fianarantsoa, Forêt de Vevembe, 66.6 km 293°WNW Farafangana, 22°47'28"S, 047°10'55"E, 600 m, rainforest transitioning to montane forest, coll. B.L. Fisher et al., 23.iv.2006, general collecting; 1 ♀, MNHN '11', Madagascar, Ikongo, coll. G. Grandidier, 21.V.1901, potential locality: Province Fianarantsoa, Fort Carnot, 21°51'30"S, 47°26'30" E (similar to the type locality of *S. vatovavy*); 1 ♂ (broken), MNHN '53', Madagascar, Cap Diego, coll. R. Decary, Aug.-Sept. 1916, potential locality: Diego-Suarez (Antsiranana)?; 4 ♀ (together with 2 *Zoosphaerium libidinosum*), MNHN '114', Madagascar, envoi n°VI, 'Glomeris', coll. G. Petit, entree 24-1922.

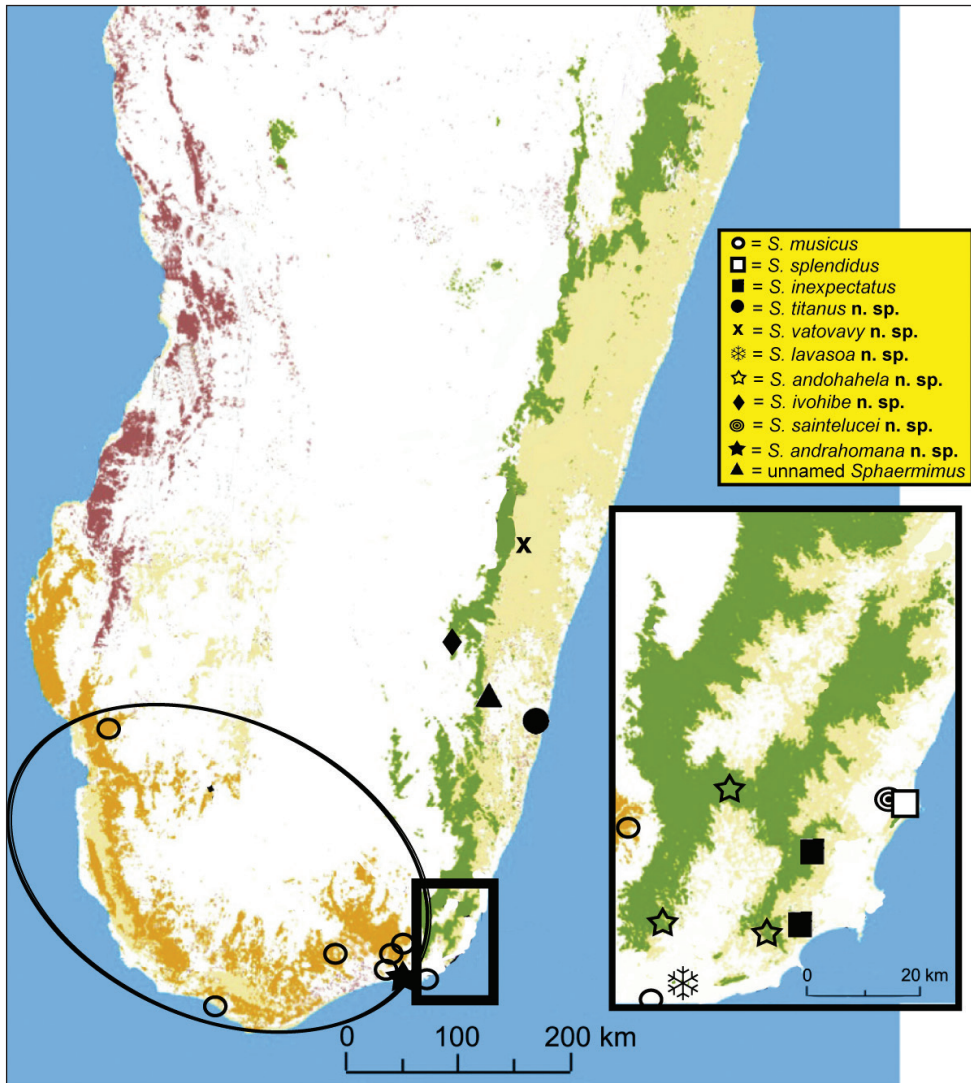
### Updated distribution of *Sphaeromimus*:

Despite the description of seven new species and numerous additional localities *Sphaeromimus* is still restricted to southeastern Madagascar (Fig. 19). Most species occur in the rainforest and littoral rainforest, with only the widespread *S. musicus* occurring in the spiny forest ecosystem. *Sphaeromimus* specimens could be discovered in every single explored southeastern Malagasy rainforest (Fig. 19), always in sympatry with species of the other Malagasy genus of giant pill-millipedes, *Zoosphaerium* (see Wesener 2009).

### Genetic distances between *Sphaeromimus* species

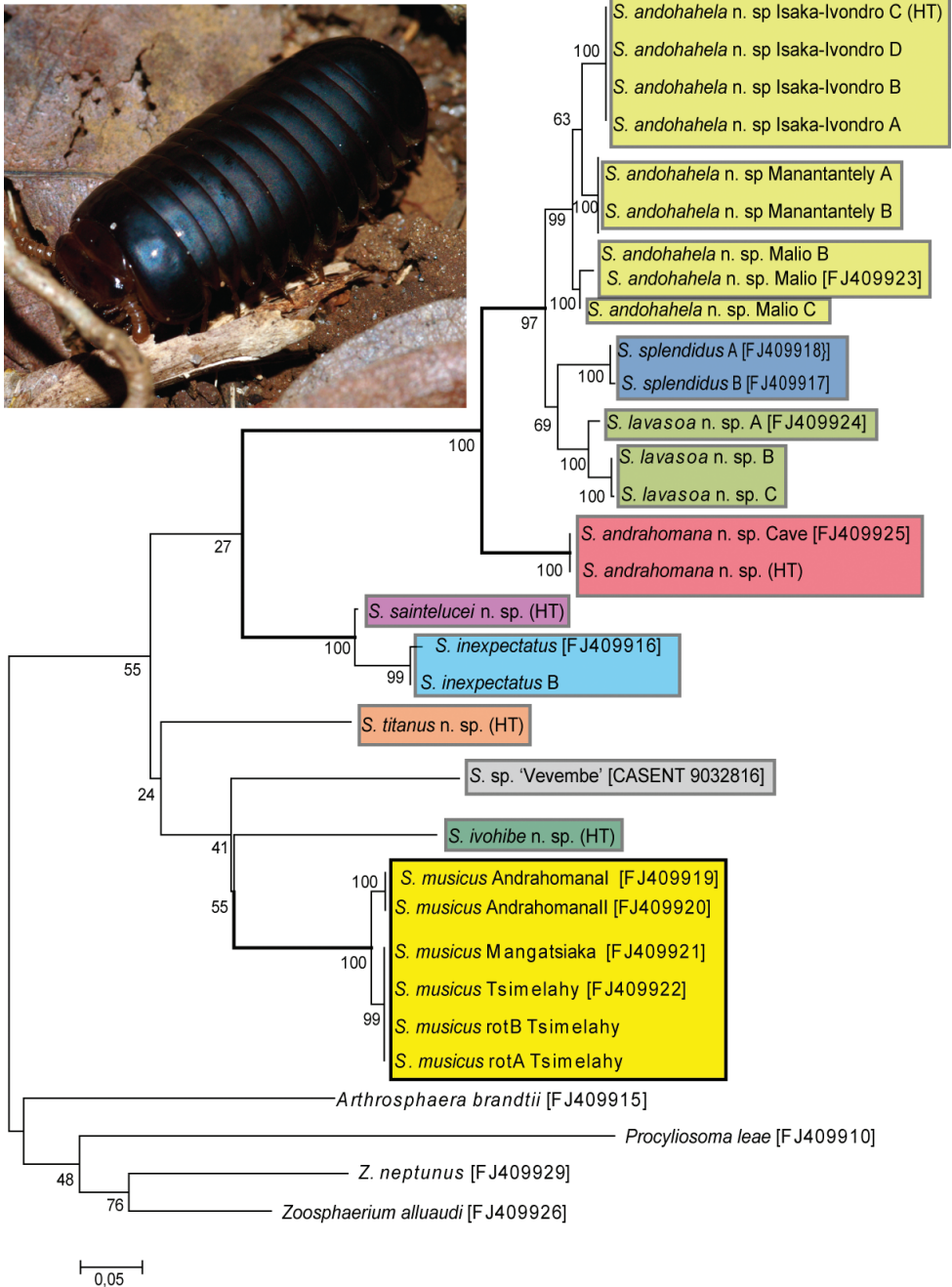
The analysis of the barcoding fragment of the COI gene provided a good resolution at the species level; all *Sphaeromimus* species are monophyletic and form well-supported terminals (Fig. 20). Genetic distances between the different *Sphaeromimus* species is 4.0% (*S. inexpectatus* and *S. saintelucei*) but mostly between 8–20% and up to 25.3% (*S. musicus* and *S. splendidus*). Based on their mitochondrial DNA, the species of the genus can be separated into two groups, albeit without any statistical support: (1) the extreme southeastern humid forest clade, and (2) a clade incorporating the spiny forest *S. musicus* together with the slightly more northern rainforest species from Ivohibe, Vevembe and Manombo (Fig. 20).

In the latter clade, all species show high genetic distances of 16–21% to one another and no sub-grouping receives any statistical support. More structure can be observed in the extreme southeastern clade. *S. inexpectatus* from the littoral rainforest of Mandena and the rainforest of Enato forms a well-supported monophyly with *S. saintelucei* from the nearby littoral rainforest fragment on basaltic soil at Sainte Luce S8. This monophyly is juxtaposed to a clade comprising *S. andrahomana*, *S. lavasoa*, *S. splendidus*, and *S. andohabela*. Within this clade, *S. andrahomana*, the southern-most



**Figure 19.** Distribution map of the genus *Sphaeromimus*. Map and vegetation types modified after Thiele et al. 2013.

taxon, is in the basal-most position differing by more than 10% of its base pairs from any other *Sphaeromimus* species (Fig. 20). *S. andohahela* from the Andohahela and Vohimena mountains is sister to a clade comprising the well-supported (69%) *S. splendidus* from the littoral rainforest sandy soil fragment S9 at Sainte Luce and *S. lavasoa* from the southern isolated Lavasoa Mountain.



**Figure 20.** Maximum likelihood tree obtained from the COI dataset after 1000 bootstrap replicates under the GTR+I+G model. Habitus photograph shows *S. andohahela* from Manantantely. Colours used to separate species. Green colours = mid-elevation rainforest; Blue & Red colours, littoral and lowland rainforests; Yellow colours = southern spiny forest. See table 1 for more details about sequenced specimens.



## Discussion

### Incorporating COI barcode data into the taxonomy of *Sphaeromimus*

Genetic distances between the species of *Sphaeromimus* are high, hinting at an old age of the speciation events shaping the current species of the genus (see also Wesener et al. 2010). This presumably old age is further highlighted by the fact that the deeper branches receive very little statistical support (Fig. 20). The COI gene probably already lost its resolution because too many reverse substitutions occurred.

Nevertheless, the COI gene is a powerful taxonomic tool, greatly improving our systematic understanding and has led to the description of new species in the family Zephroniidae from Asia (Wongthamwanich et al. 2012, Golovatch et al. 2012), and here also in the Malagasy genus *Sphaeromimus*. The incorporation of the COI barcoding gene allows a better separation of the small black taxa in the extreme southeastern clade which are more difficult to distinguish (Fig. 20). The COI data further led to the direct discovery of a pseudo-cryptic species, *S. saintelucei*. The few obtained *Sphaeromimus* specimens from the heavily degraded littoral rainforest fragment S8 at Sainte Luce (Fig. 19) were first mistaken for juveniles of *S. splendidus*. Only the very high genetic distances observed prompted a more close morphological study, which confirmed a closer morphological similarity with *S. inexpectatus*, matching the results from the analysis of the COI gene (Fig. 20). Additionally, the different colour morphs of *S. musicus* (Fig. 1A) could be correctly determined as just that, based on their identical COI sequences. The cave specimen of *S. andrahomana*, quite unusual in its colouration (Fig. 1C) and also morphology (Fig. 18B) would have been described as a separate species if not for the 0% difference in its COI sequence with those of the holotype of *S. andrahomana* (Fig. 20).

The interesting relationships and biogeographic patterns among the species of *Sphaeromimus*, with species like *S. splendidus* and *S. saintelucei* occurring in close proximity to one another (Fig. 19), but showing great genetic distances (21.7%) and no close relationship (Fig. 20), are further hints to the interesting biogeographic mechanisms shaping the current distribution of *Sphaeromimus* species in southeastern Madagascar. These patterns should be studied further using more molecular markers.

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Ubick (CAS), who loaned out the specimens of *S. titanus*. Kai Schütte (Zoological Museum Hamburg), the local field assistant Refaly Ernest and many local guides and helpers provided invaluable help during the field trip of 2007 which led to the discovery of *S. lavasoa*, *S. andohahela*, *S. saintelucei* and *S. andrahomana*. The support from the late O. Ramilijaona and D. Rakotondravony (Département de Biologie Animale, Université d'Antananarivo) is gratefully acknowledged. Special thanks goes to the Direction des Eaux et Forêts, Antananarivo for arranging collecting and export permits. Jacques Rakotondranary (Antananarivo) provided logical support. Other specimens of *Sphaeromimus* were collected during general inventories by the teams of Steven M. Goodman (FMNH) and Brian L. Fisher (CAS). We are very thankful for their laborious efforts of collecting millipedes and placing them in our care. Two reviewers, Sergei I. Golovatch and Henrik Enghoff, thankfully provided numerous comments that enhanced the quality of the here presented work. Funding for the Madagascar Field Expedition 2007 came from the German Science Foundation (DFG WA-530 37-1) and the Field Museum Collections Fund. The analysis of the data was funded by a NSF grant DEB 05-29715 to P. Sierwald, J. Bond and W. Shear. An internship of SL at the FMNH was funded via a REU site grant DBI 08-49958.

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# Open exchange of scientific knowledge and European copyright: The case of biodiversity information

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## Abstract

**Background.** The 7<sup>th</sup> Framework Programme for Research and Technological Development is helping the European Union to prepare for an integrative system for intelligent management of biodiversity knowledge. The infrastructure that is envisaged and that will be further developed within the Programme “Horizon 2020” aims to provide open and free access to taxonomic information to anyone with a requirement for biodiversity data, without the need for individual consent of other persons or institutions. Open and free access to information will foster the re-use and improve the quality of data, will accelerate research, and will promote new types of research. Progress towards the goal of free and open access to content is hampered by numerous technical, economic, sociological, legal, and other factors. The present article addresses barriers to the open exchange of biodiversity knowledge that arise from European laws, in particular European legislation on copyright and database protection rights.

We present a legal point of view as to what will be needed to bring distributed information together and facilitate its re-use by data mining, integration into semantic knowledge systems, and similar techniques. We address exceptions and limitations of copyright or database protection within Europe, and we point to the importance of data use agreements. We illustrate how exceptions and limitations have been transformed into national legislations within some European states to create inconsistencies that impede access to biodiversity information.

**Conclusions.** The legal situation within the EU is unsatisfactory because there are inconsistencies among states that hamper the deployment of an open biodiversity knowledge management system. Scientists within the EU who work with copyright protected works or with protected databases have to be aware of regulations that vary from country to country. This is a major stumbling block to international collaboration and is an impediment to the open exchange of biodiversity knowledge. Such differences should be removed by unifying exceptions and limitations for research purposes in a binding, Europe-wide regulation.

**Keywords**

Biodiversity knowledge, taxonomy, intellectual property rights, European copyright, European database protection right, data use agreement, Open Access to data and information

**Introduction**

Biodiversity data and information are important sources of knowledge for many biological, geological, and environmental research disciplines as well as for the development of policies relating to the natural environment and the management of natural resources (National Research Council 2009). The core knowledge about biodiversity has accumulated over hundreds of years in taxonomic literature, in natural history institutions, herbaria, botanic gardens; through ongoing biodiversity monitoring programs; and increasingly through digital initiatives.

Scientific names of organisms are an important component of biodiversity information. They act as a tally of how much biodiversity has been described. They are universally used to index biodiversity information (Patterson et al. 2010). Other sources of biodiversity information include hierarchical classifications of taxa; nomenclators and registries compiling information about names in the context of codes of nomenclature; taxonomic treatments being those parts of publications that include nomenclatural or taxonomic acts such as descriptions of species; checklists listing names in a particular context; and monographs or other taxonomic revisions that re-evaluate our understanding of biodiversity within a particular domain. In addition to scientific names, their origins, etymologies, histories, synonymies, and authorships, such sources contain descriptions of taxa, hierarchical classifications, information about specimens, citations of literature, reference to images and other media with information about species, information on distribution, ecology, uses, common names, conservation status, evolutionary history, and other aspects of the biology of species (Patterson et al. 2014).

The infrastructure for a system that will intelligently manage and integrate digital biodiversity information - an Open Biodiversity Knowledge Management System (OBKMS) - will need access to all names, taxonomic information, and other biodiversity data in formats that can be understood by both humans and computers (Dulong De Rosnay and Guadamuz 2013). If we are to realise the vision of Open Biodiversity Knowledge Management (OBKM), access to and re-use of data and information will need to be open, free, and independent of any individual authorisation by other persons or institutions. The system must allow intended and expected re-uses as well as unforeseen, innovative re-uses of the information.

The project “pro-iBiosphere”, financed through the European 7<sup>th</sup> Framework Programme for Research and Technological Development, and in the perspective of the EU Framework Programme for Research and Innovation “Horizon 2020”, has evaluated the requirements for an OBKMS that will: (i) offer a robust service-oriented architecture suited to working with taxon-level information distributed at multiple

sources; (ii) have a central registry of sources and services to help users find available data and services and to understand how to use them; (iii) provide open and free access to all names and taxonomic information for anyone with a requirement for biodiversity data, without depending on consent of other individuals or institutions; and (iv) facilitate the re-use of biodiversity data and information (pro-iBiosphere 2012).

At present, the access to and re-use of biodiversity data is hampered by an array of technical, economic, sociological, legal and other factors (Thessen and Patterson 2011). Many compilers of taxonomic content act as if or claim that they hold intellectual property rights over their data and information (Patterson et al. 2014), erecting legal barriers for access and re-use. Open and free access to biodiversity data and information will require a different attitude: there should be no legal provisions related to copyright that may prevent anyone whose activity requires biodiversity data from freely accessing and re-using such data from the place and at the time of their choice as well as in the technical form they prefer. This article addresses legal factors in Europe that will have to be overcome if we are to build an OBKMS.

## **The request for open access**

The political agenda for open access started with the Ministerial declaration of the high-level segment of the United Nations Economic and Social Council of 2000 “Development and international cooperation in the twenty-first century: the role of information technology in the context of a knowledge-based global economy” (United Nations 2000). In section 15, the declaration outlines “the importance of universal access to knowledge and information for promoting development”. This rather general assertion is re-expressed by the Budapest Open Access Initiative, which defines open access as the “free availability of scientific literature on the public internet, permitting any users to read, download, copy, distribute, print, search, or link to the full texts of these articles, crawl them for indexing, pass them as data to software, or use them for any lawful purpose, without financial, legal, or technical barriers other than those inseparable from gaining access to the internet itself” (Budapest Open Access Initiative 2001). The concept has been further developed in the 2003 Berlin Declaration (Berlin Declaration on Open Access to Knowledge in the Sciences and Humanities 2003). Open Access stresses the desirability of equitable access to knowledge across an economically and socially uneven world. The principle of open access to knowledge and information has been reaffirmed in numerous discipline-based, national, or international statements and declarations (Open Access Directory 2013). It is particularly important in sciences because of the importance of sharing data and information from which scientific insights are developed.

Open access should apply to the results of scientific research - such as raw data and metadata, source materials, processed data, results of analyses, and pictures, graphs and other diagrams derived from and representing the data. Open access should apply to every form of scholarly publication and other contributions to scientific knowledge.



In terms of the Berlin Declaration, open access contributions need to satisfy at least the following two conditions:

1. “The author(s) and right holder(s) of such contributions grant(s) to all users a free, irrevocable, worldwide, right of access to, and a license to copy, use, distribute, transmit and display the work publicly and to make and distribute derivative works, in any digital medium for any responsible purpose, subject to proper attribution of authorship (...), as well as the right to make small numbers of printed copies for their personal use.
2. A complete version of the work and all supplemental materials, including a copy of the permission as stated above, in an appropriate standard electronic format is deposited (and thus published) in at least one online repository using suitable technical standards (...) that is supported and maintained by an academic institution, scholarly society, government agency, or other well-established organisation that seeks to enable open access, unrestricted distribution, interoperability, and long-term archiving” (Berlin Declaration on open access to knowledge in the sciences and humanities 2003).

In the “Joint Declaration on Open Science for the 21st Century”, presented by the European Federation of Academies of Sciences and Humanities and the European Commission on 11th April, 2012, the vision of Open Science is summarised as follows:

“Open Science envisages optimal sharing of research results and tools: publications, data, software, and educational resources. It will rely on advanced e-infrastructures that enable online research collaboration. The potential to link cognate, and to re-use initially unrelated datasets will reveal unexpected relationships and will trigger new dynamics of scientific discovery. The collective intelligence of scientific communities will be unleashed through new collaborations across institutional, disciplinary, sectoral and national boundaries. The open science environment will help restore transparency and integrity to the scientific enterprise, for all to see. New points of exchange with non-academic end-users of scientific knowledge will be created, and progress will be made towards the vision of scientifically literate societies: this may require releasing scientific data in forms that are accessible to citizens” (ALLEA 2012).

In order to reach that goal, scientific publications must be made openly available, as soon after publication and as freely as possible. Restrictions should be based on specific justifications, such as to protect security, endangered species, or to protect the privacy of individuals. As a first step, the principles of open science should be applied to all content arising from – fully or partially – publicly funded research. Research proposals requesting public funds should include measures aimed at advancing open science and apply open access principles. Further steps will be necessary in order to extend these principles to all scientific research of general societal interest. A discussion, however, of how to balance commercial interests with societal interests is beyond the topic of the present contribution.

## **Why copyright can hamper the exchange of biodiversity knowledge**

Copyright protects works that are original, individual, new creations with respect of their form of presentation. It gives the owner the exclusive right to reproduce the work, to distribute it, to communicate it to the public, to make derivative versions, to transfer rights to others as well as several other rights (WIPO 1979). Copyright does not protect content in itself; the protection refers to the form of expression. Copyright protection applies only if the content is expressed in an original way. If content is presented in a pre-existing, familiar or standardised form, it does not qualify as work in the sense of copyright.

Scientific names of species follow a standardised format that was developed more than 250 years ago. This includes the latinisation of words and the use of a binomial name for species. Even when a name is new, the form of expression follows the well-established pattern. The same can be said about taxonomic treatments and much other taxonomic information which is expressed in standardised forms and language. The familiar nature of the information is valuable as it helps other scientists to understand the treatments, to compare them, and to draw their content together in their own scientific work. The familiar nature means that the material cannot be subject to copyright. Elements of taxonomic information that are 'familiar' to taxonomists were summarised as a 'blue list' that included: scientific names; etymology of names, authorities for names, nomenclatural information and opinions, rank and/or hierarchical organisation or classification; alphabetical, chronological, phylogenetic, palaeontological, geographical, ecological, host-based, or feature-based ordering of taxa; synonyms and taxonomic opinions; references to relevant literature, type material, and images; data about materials examined; information on overall distribution, ecology, conservation and uses and descriptions of the taxon (Patterson et al. 2014).

None-the-less, copyright statements are often associated with taxonomic information - especially on web sites. These refer to ownership and address the re-use of content. Most of these statements lack legal foundation because the data and information to which they refer do not qualify as works in the sense of copyright legislation. There are no legitimate copyright restrictions on the re-use of such information. A non-copyrightable publication remains non-copyrightable even if the author or others choose to mark it with a copyright statement, a copyright mark (such as ©), or with a Creative Commons license.

Biodiversity data and information are rarely presented as unembellished flat lists. They are parts of websites, articles, monographs, and other forms of publications. Even if the data or information are not copyrightable, the website or monograph as a whole may qualify as work and therefore be copyright protected. If the process of re-use requires the reproduction of copyright protected parts of the source, then authorisation of the copyright holder is required (Agosti and Egloff 2009).

European copyright legislation is well aware of the fact that copyright may present a barrier to scientific work. The EU-Directive 2001/29/EC on the harmonisation of certain aspects of copyright and related rights in the information society (European

Parliament and the Council of the European Union 2001) addresses the challenge and puts considerable weight on the importance of science by providing for exceptions and limitations to copyright. It grants to the author the rights to decide who shall be allowed to reproduce his work (“reproduction right”) or who shall be allowed to communicate it to the public (“communication right”), but it provides for restrictions (“exceptions and limitations”) to these rights in the general interest. Recital 34 to the Directive provides for exceptions and limitations for “educational and scientific purposes”. Recital 40 refers to exceptions and limitations “for the benefit of certain non-profit making establishments such as publicly accessible libraries and equivalent institutions, as well as archives”. Directive 2001/29/EC therefore gives member states the option of establishing their own laws for the following exceptions and limitations:

#### Article 5.2.

Member States may provide for exceptions and limitations to the reproduction right provided for in Article 2 in the following cases:

(...)

c) in respect of specific acts of reproduction made by publicly accessible libraries, educational establishments or museums, or by archives, which are not for direct or indirect economic or commercial advantage.

(...)”

#### Article 5.3

Member States may provide for exceptions and limitations to the rights provided for in Article 2 and 3 in the following cases:

a) use for the sole purpose of illustration for teaching or scientific research, as long as the source, including the author’s name, is indicated, unless this turns out to be impossible and to the extent justified by the non-commercial purposes to be achieved;

(...)

n) use by communication or making available, for the purpose of research or private study, to individual members of the public by dedicated terminals on the premises of establishments referred to in paragraph 2(c) of works and other subject-matter no subject to purchase or licensing terms which are contained in their collections;

(...)”

These exceptions and limitations are only applicable when they are transformed into national law by individual member states of the EU. Then, they apply only to that member state. Such transformations result in copyright provisions that differ from country to country. Therefore, scientists who rely on data from different EU member states or who collaborate internationally need to be aware that different legal frameworks may apply to the data they use. In the Communication on “Copyright in the

Knowledge Economy”, the EU Commission makes it clear that this situation is a major stumbling block to international scientific cooperation within the EU and declares that “limiting teaching and research to a specific location is considered to be contrary to the realities of modern life” (European Commission 2009).

In the context of the “Licenses for Europe – structured stakeholder dialogue 2013” (European Commission 2013), the European Commission established a special working group to discuss adaptations of the copyright framework regarding text and data mining (TDM). The Commission’s objective was to promote the efficient use of TDM for scientific research purposes. As TDM currently requires contractual agreements between users (e.g. research institutions) and rights holders (e.g. publishers of scientific journals) to establish the terms and conditions for technical access to the relevant data sets, the working group explored solutions such as standard licensing models as well as the design of technology platforms to facilitate TDM. The working group was unable to complete its mandate. Ten organisations representing interests within the research community concluded that progress was made impossible by the attitude of publishers who insisted on licensing models as the only acceptable solution and left the group.

## **The European database protection**

In 1996, the European Union introduced a special legal protection for databases (European Parliament and the Council of the European Union 1996). It applies to databases which show “that there has been qualitatively and/or quantitatively a substantial investment in either the obtaining, verification or presentation of the contents” (art. 7 of the Directive 96/9/EC). It allows owners to prevent extraction and/or re-use of the whole or of a substantial part, evaluated qualitatively and/or quantitatively, of the content of a database. The concept is unique to the EU. No similar rights exist in the U.S. or in European non-member states of the EU or the EEA.

As the European Court of Justice pointed out in several judgments, database protection concerns the creation of databases out of material that already exists, but does not deal with the creation of data as such (European court of Justice 2004a). The expression “investment in the obtaining of the contents” refers therefore to the resources used to find existing materials and collect them in the database, and not to the resources used to create materials. The expression “investment in the verification of the contents” refers to the resources used to monitor the accuracy of the materials collected when the database was created and during its operation, but does not refer to the resources used for verification during the creation of materials. The expression “investment in the presentation of the contents” concerns the resources used to process and deliver information (European Court of Justice 2004b).

According to the 48<sup>th</sup> recital of the preamble to Directive 96/9/EC, database protection has an economic justification, being to afford protection to the maker of a database and guarantee a return on the investment in the creation and maintenance of the database. “Investment” refers only to the investment of private or commercial



resources, but not to the use of public funding. In consequence, the protection applies exclusively to private databases. As most databases with relevant taxonomic information are mainly publicly funded, database protection for them is quite limited. However, there are databases containing biodiversity data which are protected by this so called “sui-generis-right”.

Database protection does not deal with individual data elements, but with databases as a whole. Database protection concerns the creation of databases but does not deal with the protection of data as such. It only prevents the extraction and re-utilisation of substantial parts of a database. Therefore, it cannot impede the access to a database, but only, in very particular circumstances, restrict the re-use of the whole or a substantial part of a database.

According to Art. 9 (b) of the Directive 96/9/EC, member states may stipulate that lawful users of a database may extract or re-utilise a substantial part of its contents for the purposes of scientific research. This exception is only applicable if transformed into national law by individual member states of the EU. Therefore, scientists in different EU member states have to be aware of different legal frameworks as far as database legislation is concerned.

## **The importance of data use agreements**

Access to and re-use of biodiversity data and information is not only regulated by copyright and database protection, but also through individual data use agreements (DUA). Such agreements can relate to data and information irrespective of whether copyright or databases rights apply. They can have the form of a written contract, or be a general “terms of use”-statement which the user has to accept before accessing protected data and information. Indeed, a DUA may simply be said to have been agreed as a result of accessing content. Such agreements are frequently called “licenses” although the term is, in many cases, inappropriate from a legal point of view.

A DUA is only valid if both parties have accepted the conditions of access or terms of use, and applies only to those parties. In many cases, it may be difficult to decide if there is an agreement or not and if a potential licensee has accepted it. An agreement requires an active expression of intent, whether spoken, written, or in fact. The mere action of accessing data and information on a website that is accompanied by a “terms of use”-statement or any similar declaration, will rarely be considered as consent.

Creative Commons licenses or similar are a form of data use agreement. They are declared unilaterally by a “licensor”, and they are valid under the condition that the licensee has accepted them. Their importance lies in the fact that they often declare a restriction to copyright and, with the new version 4, to database protection: The licensor declares to any interested user that he or she will not claim copyright or database rights as long as the material is re-used in a way that is explicitly authorised by the CC-license. Such terms of use appeal to licensors and licensees as it increases access to and use of works and databases.

In Europe, data use agreements can regulate the access to and the re-use of copyrighted works or protected databases only when there is no binding legal regulation in form of exceptions and limitations to copyright or database protection. The European Court of Justice ruled in a judgment of June 23, 2013, as follows: “Where a Member State has decided, pursuant to a provision in Article 5(2) and (3) of Directive 2001/29, to exclude, from the material scope of that provision, any right for the rightholders to authorise reproduction of their protected works or other subject-matter, any authorising act the rightholders may adopt is devoid of legal effects under the law of that State” (European Court of Justice 2013). Binding legal exceptions and limitations that allow certain uses of copyright protected works or of databases supersede any conflicting data use agreement, including Creative-Commons-licenses. Terms and conditions that contradict such legal regulations are void, as is clearly expressed for example in section 29A, par. 5, and section 50 D, par. 2, of the British CPDA, cited in the next section below. However, data use agreements can supersede legal regulations where this possibility is provided for in the same legal text, as in the cases, for example, of § 52b and 53a of the German copyright law or in Art. 71-ter of the Italian Copyright law, cited in the next section.

## **Examples of national regulations**

Exceptions and limitations to copyright and database protection apply if transformed into national law of member states of the European Union or the European Economic Area. The resulting national legislation differs from country to country (Dietrich et al. 2013). The following list illustrates the resulting diversity. The examples have been chosen with respect to: a) the special legal situations that are found in some countries (case law regulation in the United Kingdom, extended collective licenses in the Scandinavian countries, specific database regulations in Germany and Italy); b) the economic weight in the sector of scholarly publishing (United Kingdom, Germany, France); or c) the political status of the country (by including non-EU-members such as Norway and Switzerland).

### **Denmark**

Copyright and database protection in Denmark is provided for by the “LBK nr 202 af 27/02/2010 Gældende (Ophavsretsloven)” (Danske retsinformation 2010). The exceptions and limitations provided for in Directive 2001/29/EC und Directive 96/9/EC have in part been transformed into national law in the form of extended collective licenses (“aftalelicenser”). An extended collective license is an agreement between a qualified user (archive, libraries, and others) and an officially recognised collecting agency which represents “an essential part of authors whose works are used in Denmark” (§ 50). The following articles are particularly relevant:

## § 13 (referring to article 5.3.a of Directive 2001/29/EC):

Til brug i undervisningsvirksomhed kan der fremstilles eksemplarer af udgivne værker samt ved optagelse foretages eksemplar fremstilling af værker, som udsendes i radio eller fjernsyn, såfremt betingelserne for aftalelicens efter § 50 er opfyldt. (...)

## § 14 (referring to internal use in institutions and enterprises):

Offentlige eller private institutioner, organisationer og erhvervsvirksomheder kan til intern brug i deres virksomhed ved fotokopiering eller lignende fremstille eller lade fremstille eksemplarer af fagmæssige artikler i aviser, tidsskrifter og samleværker, af korte afsnit af andre udgivne værker af fagmæssig art, af musikværker samt af illustrationer, som er gengivet i tilslutning til teksten, såfremt betingelserne for aftalelicens efter § 50 er opfyldt. Sådanne eksemplarer må kun udnyttes inden for virksomhed, som omfattes af den i § 50 forudsatte aftale. (...)

## § 16 (referring to article 5.2.c of Directive 2001/29/EC):

<sup>1</sup>Offentlige arkiver, offentlige biblioteker og andre biblioteker, der helt eller delvis finanseres af det offentlige, samt statslige museer og museer, der er godkendt efter museumsloven, må gengive og sprede eksemplarer af værker til brug i deres virksomhed i overensstemmelse med bestemmelserne i stk. 2-6, såfremt det ikke sker i erhvervsøjemed. Dette gælder dog ikke for edb-programmer i digital form bortset fra computerspil.

<sup>2</sup>Institutionerne må fremstille eksemplarer i sikkerheds- og beskyttelsesøjemed.

<sup>3</sup>Såfremt et eksemplar i en institutions samling er ufuldstændigt, må institutionen fremstille eksemplarer af de manglende dele, medmindre værket kan erhverves i almindelig handel eller hos udgiveren.

<sup>4</sup>Biblioteker kan fremstille eksemplarer af udgivne værker, der bør være tilgængelige i bibliotekets samlinger, men som ikke kan erhverves i almindelig handel eller hos udgiveren. (...)

## § 16a (referring to article 5.3.n of Directive 2001/29/EC):

Offentliggjorte værker kan gøres tilgængelige for enkeltpersoner på de i § 16, stk. 1, nævnte institutioner til personligt gennemsyn eller studium på stedet ved hjælp af teknisk udstyr. (...)

## § 16b (referring to article 5.2.c and 5.3.n of Directive 2001/29/EC):

Offentlige biblioteker og andre biblioteker, der helt eller delvis finansieres af det offentlige, kan på bestilling i digital form gengive artikler fra aviser, tidsskrifter og samleværker, kortere afsnit af bøger og andre udgivne litterære værker samt illustrationer og noder, som er gengivet i tilslutning til teksten, såfremt betingelserne for aftalelicens efter § 50 er opfyldt. Bestemmelsen i 1. pkt. omfatter ikke udsendelse i radio eller fjernsyn eller tilrådighedsstillelse af værker på en sådan måde, at almenheden får adgang til dem på et individuelt valgt sted og tidspunkt (...).

§ 50 (referring to extended collective licenses):

<sup>1</sup>Aftalelicens efter §§ 13, 14 og § 16 b, § 17, stk. 4, og §§ 24, 30, 30 a og 35 kan påberåbes af brugere, der har indgået en aftale om den pågældende værksudnyttelse med en organisation, som omfatter en væsentlig del af ophavsmændene til en bestemt art af værker, der anvendes i Danmark.

<sup>2</sup>Aftalelicens kan desuden påberåbes af brugere, der inden for et nærmere defineret område har indgået aftale om værksudnyttelse med en organisation, der omfatter en væsentlig del af ophavsmændene til en bestemt art af værker, der anvendes i Danmark på det pågældende område. Dette gælder dog ikke, hvis ophavsmanden over for nogen af de aftalesluttende partner har nedlagt forbud mod værkets udnyttelse.

<sup>3</sup>Aftalelicensen giver brugeren ret til at udnytte andre værker af samme art, selv om ophavsmændene til disse værker ikke repræsenteres af organisationen. Aftalelicensen giver brugeren ret til at benytte de ikke-repræsenterede ophavsmænds værker på den måde og på de vilkår, som følger af den aftale, der er indgået med organisationen.

## **France**

Copyright and database protection in France is provided for by the 1<sup>st</sup> part of the “Code de la propriété intellectuelle (L. n° 92-597 du 1er juillet 1992)” (République Française 1992). The exceptions and limitations provided for in Directive 2001/29/EC and Directive 96/9/EC have been transformed into the following articles:

Art. L 122-5-8° (referring to article 5.2.c of Directive 2001/29/EC):

Lorsque l’oeuvre a été divulguée, l’auteur ne peut interdire:

(...)

8° La reproduction d’une œuvre et sa représentation effectuées à des fins de conservation ou destinées à préserver les conditions de sa consultation à des fins de recherche ou d’études privées par des particuliers, dans les locaux de l’établissement et sur des terminaux dédiés par des bibliothèques accessibles au public, par des musées ou par des services d’archives, sous réserve que ceux-ci ne recherchent aucun avantage économique ou commercial;

(...)

Art. L 122-5-3° (referring to paragraph 5.3.a of Directive 2001/29/EC):

Lorsque l’oeuvre a été divulguée, l’auteur ne peut interdire:

(...)

3° Sous réserve que soient indiqués clairement le nom de l’auteur et la source :

(...)

e) La représentation ou la reproduction d’extraits d’œuvres, sous réserve des œuvres conçues à des fins pédagogiques, des partitions de musique et des œuvres réalisés pour une édition numérique de l’écrit, à des fins exclusives d’illustration dans le cadre de l’enseignement et de la recherche, à l’exclusion de toute activité ludique

ou récréative, dès lors que le public auquel cette représentation ou cette reproduction est destinée est composé majoritairement d'élèves, d'étudiants, d'enseignants ou de chercheurs directement concernées, que l'utilisation de cette représentation ou cette reproduction ne donne lieu à aucune exploitation commerciale (...)

## Germany

Copyright and database protection in Germany is provided for by the “Gesetz über Urheberrecht und verwandte Schutzrechte (Urheberrechtsgesetz – UrhG) vom 9. September 1965” (Bundesministerium der Justiz und für Verbraucherschutz 2013). The exceptions and limitations provided for in Directive 2001/29/EC and Directive 96/9/EC have been transformed into the following articles:

§ 52b UrhG (referring to paragraph 5.3.n of Directive 2001/29/EC):

Zulässig ist, veröffentlichte Werke aus dem Bestand öffentlich zugänglicher Bibliotheken, Museen oder Archive, die keinen unmittelbar oder mittelbar wirtschaftlichen oder Erwerbszweck verfolgen, ausschliesslich in den Räumen der jeweiligen Einrichtung an eigens dafür eingerichteten elektronischen Leseplätzen zur Forschung und für private Studien zugänglich zu machen, soweit dem keine vertraglichen Regeln entgegenstehen. Es dürfen grundsätzlich nicht mehr Exemplare eines Werkes an den eingerichteten elektronischen Leseplätzen gleichzeitig zugänglich gemacht werden, als der Bestand der Einrichtung umfasst. Für die Zugänglichmachung ist eine angemessene Vergütung zu zahlen. (...)

§52a UrhG (referring to paragraph 5.3.a of Directive 2001/29/EC):

(1) Zulässig ist,

1. veröffentlichte kleine Teile eines Werkes, Werke geringen Umfangs sowie einzelne Beiträge aus Zeitungen oder Zeitschriften zur Veranschaulichung im Unterricht an Schulen, Hochschulen, nichtgewerblichen Einrichtungen der Aus- und Weiterbildung sowie an Einrichtungen der Berufsbildung ausschliesslich für den bestimmt abgegrenzten Kreis von Unterrichtsteilnehmern oder

2. veröffentlichte Teile eines Werkes, Werke geringen Umfangs sowie einzelne Beiträge aus Zeitungen oder Zeitschriften ausschliesslich für einen bestimmt abgegrenzten Kreis von Personen für deren eigene wissenschaftliche Forschung öffentlich zugänglich zu machen, soweit dies zu dem jeweiligen Zweck geboten und zur Verfolgung nicht kommerzieller Zwecke gerechtfertigt ist.

(2) Die öffentliche Zugänglichmachung eines für den Unterrichtsgebrauch an Schulen bestimmten Werkes ist stets nur mit Einwilligung des Berechtigten zulässig. Die öffentliche Zugänglichmachung eines Filmwerkes ist vor Ablauf von zwei Jahren nach Beginn der üblichen regulären Auswertung in Filmtheatern im Geltungsbereich dieses Gesetzes stets nur mit Einwilligung des Berechtigten zulässig. (...)



§53 UrhG (referring to paragraph 5.3.a of Directive 2001/29/EC):

(1) Zulässig sind einzelne Vervielfältigungen eines Werkes durch eine natürliche Person zum privaten Gebrauch auf beliebigen Trägern, sofern sie weder unmittelbar noch mittelbar Erwerbszwecken dienen, soweit nicht zur Vervielfältigung eine offensichtlich rechtswidrig hergestellte oder öffentlich zugänglich gemachte Vorlage verwendet wird. Der zur Vervielfältigung Befugte darf die Vervielfältigungsstücke auch durch einen anderen herstellen lassen, sofern dies unentgeltlich geschieht oder es sich um Vervielfältigungen auf Papier oder einem andern ähnlichen Träger mittels beliebiger photo-mechanischer Verfahren oder anderer Verfahren mit ähnlicher Wirkung handelt.

(2) Zulässig ist, einzelne Vervielfältigungsstücke eines Werkes herzustellen oder herstellen zu lassen

1. zum eigenen wissenschaftlichen Gebrauch, wenn und soweit die Vervielfältigung zu diesem Zweck geboten ist und sie keinen gewerblichen Zwecken dient,

2. (...)

(3) Zulässig ist, Vervielfältigungsstücke von kleinen Teilen eines Werkes, von Werken von geringem Umfang oder von einzelnen Beiträgen, die in Zeitungen oder Zeitschriften erschienen und öffentlich zugänglich gemacht worden sind, zum eigenen Gebrauch

1. zur Veranschaulichung des Unterrichts in Schulen, in nichtgewerblichen Einrichtungen der Aus- und Weiterbildung sowie in Einrichtungen der Berufsbildung in der für die Unterrichtsteilnehmer erforderlichen Anzahl oder

2. für staatliche Prüfungen und Prüfungen in Schulen, Hochschulen, in nichtgewerblichen Einrichtungen der Aus- und Weiterbildung sowie in der Berufsbildung in der erforderlichen Anzahl

herzustellen oder herstellen zu lassen, wenn und soweit die Vervielfältigung zu diesem Zweck geboten ist. Die Vervielfältigung eines Werkes, das für den Unterrichtsgebrauch bestimmt ist, ist stets nur mit Einwilligung des Berechtigten zulässig.  
(...)

§53a (referring to paragraph 5.3.n of Directive 2001/29/EC):

(1) Zulässig ist auf Einzelbestellung die Vervielfältigung und Übermittlung einzelner in Zeitungen und Zeitschriften erschienener Beiträge sowie kleiner Teile eines erschienenen Werkes im Wege des Post- oder Faxversands durch öffentliche Bibliotheken, sofern die Nutzung durch den Besteller nach § 53 zulässig ist. Die Vervielfältigung und Übermittlung in sonstiger elektronischer Form ist ausschliesslich als grafische Datei und zur Veranschaulichung des Unterrichts oder für Zwecke der wissenschaftlichen Forschung zulässig, soweit dies zur Verfolgung nicht gewerblicher Zwecke gerechtfertigt ist. Die Vervielfältigung und Übermittlung in sonstiger elektronischer Form ist ferner nur dann zulässig, wenn der Zugang zu den Beiträgen oder kleinen Teilen eines Werkes den Mitgliedern der Öffentlichkeit nicht offensichtlich von Orten und Zeiten ihrer Wahl mittels einer vertraglichen Vereinbarung zu angemessenen Bedingungen ermöglicht wird.

(...)

§87c (referring to art. 9(b) of Directive 96/9/EC):

(1) Die Vervielfältigung eines nach Art oder Umfang wesentlichen Teils einer Datenbank ist zulässig

1. (...)

2. zum eigenen wissenschaftlichen Gebrauch, wenn und soweit die Vervielfältigung zu diesem Zweck geboten ist und der wissenschaftliche Gebrauch nicht zu gewerblichen Zwecken erfolgt,

3. für die Benutzung zur Veranschaulichung des Unterrichts, sofern sie nicht zu gewerblichen Zwecken erfolgt.

In den Fällen der Nummern 2 und 3 ist die Quelle deutlich anzugeben.

(...)

## Italy

Copyright and database protection in Italy is provided for by Art. 2575 ss. of the Codice Civile and in the “Legge 22 Aprile 1941 n. 633 Protezione del diritto d’autore e di altri diritti connessi al suo esercizio” (Interlex 2008). The exceptions and limitations provided for in Directive 2001/29/EC and Directive 96/9/EC have been transformed into the following articles:

Art. 68 (referring to article 5.2.c of the Directive 2001/29/EC):

1. E’ libera la riproduzione di singole opere o brani di opere per uso personale dei lettori, fatta a mano o con mezzi di riproduzione non idonei a spaccio o diffusione dell’opera nel pubblico.

2. E’ libera la fotocopia di opere esistenti nelle biblioteche accessibili al pubblico o in quelle scolastiche, nei musei pubblici o negli archivi pubblici, effettuata dai predetti organismi per i propri servizi, senza alcun vantaggio economico o commerciale diretto o indiretto.

3. Fermo restando il divieto di riproduzione di spartiti e partiture musicali, è consentita, nei limiti del quindici per cento di ciascun volume o fascicolo di periodico, escluse le pagine di pubblicità, la riproduzione per uso personale di opere dell’ingegno effettuata mediante fotocopia, xerocopia o sistema analogo.

4. I responsabili dei punti o centri di riproduzione, i quali utilizzino nel proprio ambito o mettano a disposizione di terzi, anche gratuitamente, apparecchi per fotocopia, xerocopia o analogo sistema di riproduzione, devono corrispondere un compenso agli autori ed agli editori delle opere dell’ingegno pubblicate per le stampe che, mediante tali apparecchi, vengono riprodotte per gli usi previsti nel comma 3. La misura di detto compenso e le modalità per la riscossione e la ripartizione sono determinate secondo i criteri posti all’art. 181-ter della presente legge. Salvo diverso accordo tra la SIAE e le associazioni delle categorie interessate, tale compenso non può essere inferiore per ciascuna pagina riprodotta al prezzo medio a pagina rilevato annualmente dall’ISTAT per i libri.

Art. 70 (referring to article 5.3.a of the Directive 2001/29/EC):

1. Il riassunto, la citazione o la riproduzione di brani o di parti di opera e la loro comunicazione al pubblico sono liberi se effettuati per uso di critica o di discussione, nei limiti giustificati da tali fini e purché non costituiscano concorrenza all'utilizzazione economica dell'opera; se effettuati a fini di insegnamento o di ricerca scientifica l'utilizzo deve inoltre avvenire per finalità illustrative e per fini non commerciali.

1-bis. È consentita la libera pubblicazione attraverso la rete internet, a titolo gratuito, di immagini e musiche a bassa risoluzione o degradate, per uso didattico o scientifico e solo nel caso in cui tale utilizzo non sia a scopo di lucro. Con decreto del Ministro per i beni e le attività culturali, sentiti il Ministro della pubblica istruzione e il Ministro dell'università e della ricerca, previo parere delle Commissioni parlamentari competenti, sono definiti i limiti all'uso didattico o scientifico di cui al presente comma.

2. Nelle antologie ad uso scolastico la riproduzione non può superare la misura determinata dal regolamento, il quale fissa la modalità per la determinazione dell'equo compenso.

3. Il riassunto, la citazione o la riproduzione debbono essere sempre accompagnati dalla menzione del titolo dell'opera, dei nomi dell'autore, dell'editore e, se si tratti di traduzione, del traduttore, qualora tali indicazioni figurino sull'opera riprodotta.

Art. 71-ter (referring to article 5.3.n of the Directive 2001/29/EC):

1. E' libera la comunicazione o la messa a disposizione destinata a singoli individui, a scopo di ricerca o di attività privata di studio, su terminali aventi tale unica funzione situati nei locali delle biblioteche accessibili al pubblico, degli istituti di istruzione, nei musei e negli archivi, limitatamente alle opere o ad altri materiali contenuti nelle loro collezioni e non soggetti a vincoli derivanti da atti di cessione o da licenza.

Art. 64-sexies (referring to article 9(b) of Directive 96/9/EC):

1. Non sono soggetti all'autorizzazione di cui all'articolo 64-quinquies da parte del titolare del diritto:

a) l'accesso o la consultazione della banca di dati quando abbiano esclusivamente finalità didattiche o di ricerca scientifica, non svolta nell'ambito di un'impresa, purché si indichi la fonte e nei limiti di quanto giustificato dallo scopo non commerciale perseguito. Nell'ambito di tali attività di accesso e consultazione, le eventuali operazioni di riproduzione permanente della totalità o di parte sostanziale del contenuto su altro supporto sono comunque soggette all'autorizzazione del titolare del diritto;

b) l'impiego di una banca di dati per fini di sicurezza pubblica o per effetto di una procedura amministrativa o giurisdizionale.

2. Non sono soggette all'autorizzazione dell'autore le attività indicate nell'articolo 64-quinquies poste in essere da parte dell'utente legittimo della banca di dati o di una sua copia, se tali attività sono necessarie per l'accesso al contenuto della stessa banca di dati e per il suo normale impiego; se l'utente legittimo è autorizzato ad utilizzare solo una parte della banca di dati, il presente comma si applica unicamente a tale parte.

3. Le clausole contrattuali pattuite in violazione del comma 2 sono nulle ai sensi dell'articolo 1418 del codice civile.

4. Conformemente alla Convenzione di Berna per la protezione delle opere letterarie e artistiche, ratificata e resa esecutiva con legge 20 giugno 1978, n. 399, le disposizioni di cui ai commi 1 e 2 non possono essere interpretate in modo da consentire che la loro applicazione arrechi indebitamente pregiudizio al titolare del diritto o entri in conflitto con il normale impiego della banca di dati.

Art. 102-ter (referring to article 9(b) of Directive 96/9/EC):

1. L'utente legittimo della banca di dati messa a disposizione del pubblico non può arrecare pregiudizio al titolare del diritto d'autore o di un altro diritto connesso relativo ad opere o prestazioni contenute in tale banca.

2. L'utente legittimo di una banca di dati messa in qualsiasi modo a disposizione del pubblico non può eseguire operazioni che siano in contrasto con la normale gestione della banca di dati o che arrechino un ingiustificato pregiudizio al costituente della banca di dati.

3. Non sono soggette all'autorizzazione del costituente della banca di dati messa per qualsiasi motivo a disposizione del pubblico le attività di estrazione o reimpiego di parti non sostanziali, valutate in termini qualitativi e quantitativi, del contenuto della banca di dati per qualsivoglia fine effettuate dall'utente legittimo. Se l'utente legittimo è autorizzato ad effettuare l'estrazione o il reimpiego solo di una parte della banca di dati, il presente comma si applica unicamente a tale parte.

4. Le clausole contrattuali pattuite in violazione dei commi 1, 2 e 3 sono nulle.

## Norway

Copyright and database protection in Norway is provided for by the “Lov av 12. mai 1961 om opphavsrett til åndverk m.v. (åndverksloven)” (Lovdata 2013). The exceptions and limitations provided for in Directive 2001/29/EC und Directive 96/9/EC have been transformed into national law in form of extended collective licenses (“avtalelisenser”). An extended collective license is an agreement between a qualified user (archive, libraries and others) and an officially recognised collecting society which represents “an essential part of authors whose works are used in Norway” (§ 38a). The following articles are particularly relevant:

§ 16. (referring to paragraph 5.2.c and 5.3.n of Directive 2001/29/EC):

Kongen kan gi regler om rett for arkiv, bibliotek, museer og undervisnings- og forskningsinstitusjoner til å fremstille eksemplar av verk for konserverings- og sikringsformål og andre særskilte formål. Bestemmelsen gjelder ikke for ervervsmessig bruk. Kongen kan gi regler om at arkiv, bibliotek, museer og undervisningsinstitusjoner ved hjelp av terminaler i egne lokaler, kan gjøre verk i samlingene tilgjengelig for enkeltpersoner når det skjer til forskningsformål eller private studieformål.

(The institutions to which the regulations apply are specified in § 1-1 forskrift til åndverksloven as “arkiv under arkivverket, kommunale og fylkeskommunale arkiv, bibliotek under universiteter og høyskoler og andre vitenskapelige og faglige bibliotek som drives av det offentlige, fylkesbibliotekene og folkebibliotekene samt offentlige museer og museer som mottar offentlige tilskudd” [archives of institutional archives, communal and provincial archives, university and highschool libraries and other publicly organised scientific or specialised libraries, provincial and public libraries including public museums and publicly funded museums]. The authorization to make available protected works within the premises of these institutions is specified in § 1-9 forskrift til åndverksloven. Teaching and research institutions can be authorised by the state to produce copies in other formats than the original one [§ 1-4 forskrift til åndverksloven]).

§ 16a. (referring to paragraph 5.2.c and 5.3.n of Directive 2001/29/EC):

Arkiv, bibliotek og museer som angitt i § 16 første ledd kan fremstille eksemplarer av utgitte verk i samlingene og gjøre slike verk tilgjengelig for allmennheten når betingelsene for avtalelisens etter § 36 første ledd er oppfylt.

§ 36. (concerning extended collective licenses)

Når det foreligger avtale med organisasjon som nevnt i § 38a som tillater slik bruk av verk som nevnt i §§ 13b, 14, 16a, 17b, 30, 32 og 34, har bruker som omfattes av avtalen, overfor rettighetshaver som ikke er omfattet, rett til på samme område og på samme måte å utnytte verk av samme art som dem avtalen gjelder (avtalelisens). Bestemmelsen gjelder bare for bruk som skjer i samsvar med det avtalen fastsetter. Bestemmelsen gjelder ikke i forhold til kringkastingsforetaks rettigheter i sine sendinger.

§ 38a. (concerning extended collective licenses)

Avtale som skal ha virkning som nevnt i § 36 første ledd, må inngås av organisasjon som på området representerer en vesentlig del av opphavsmennene til verk som brukes i Norge, og som er godkjent av departementet. For bruk på nærmere angitte områder kan Kongen bestemme at den organisasjon som godkjennes, må være en felles organisasjon for de berørte rettighetshavere.

Kongen kan gi nærmere bestemmelser om kontroll med organisasjoner og fond som mottar vederlag til videre fordeling.

## Sweden

Copyright and database protection in Sweden is provided for by the “Lag (1960:729) om upphovsrätt till litterära och konstnärliga verk” (Sveriges Riksdag 1960). The exceptions and limitations provided for in Directive 2001/29/EC and Directive 96/9/EC have been transformed into the following articles:



## 16 § (referring to paragraph 5.2.c of Directive 2001/29/EC):

De arkiv och bibliotek som avses i tredje och fjärde styckena har rätt att framställa exemplar av verk, dock inte datorprogram,

1. för bevarande-, kompletterings- eller forskningsändamål,
2. för att tillgodose lånesökandes önskemål om enskilda artiklar eller korta avsnitt eller om material som av säkerhetsskäl inte bör lämnas ut i original, eller
3. för användning i läsapparater.

(...)

Rätt till exemplarframställning och spridning enligt denna paragraf har

1. de statliga och kommunala arkivmyndigheterna,
2. Statens ljud- och bildarkiv,
3. de vetenskapliga bibliotek och fackbibliotek som drivs av det allmänna samt
4. folkbiblioteken.

(...)

In addition, libraries and certain other institutions may make their collection available to the public on the basis of a so called extended collective licence (“avtalelicens”, 42 a–42 f §§). An extended collective licence is an agreement between a qualified user (the library) and a national collecting society which represents a considerable number of Swedish right-holders that oversee certain uses of protected works. The agreement applies not only to the use of works of represented authors but also to the use of any other work of the same kind:

“En avtalelicens som avses i 42 b–42 f §§ gäller för utnyttjande av verk på visst sätt, när ett avtal har ingåtts om utnyttjande av verk på sådant sätt med en organisation som företräder ett flertal svenska upphovsmän på området. Avtalelicensen ger användaren rätt att utnyttja verk av det slag som avses med avtalet trots att verkens upphovsmän inte företräds av organisationen” (42a §).

## Switzerland

Copyright and database protection in Switzerland is provided for by the “Bundesgesetz über das Urheberrecht und verwandte Schutzrechte (Urheberrechtsgesetz, URG) vom 9. Oktober 1992“ (Bundesversammlung der Schweizerischen Eidgenossenschaft 1992). As Switzerland is neither part of the EU nor the EEA, EU-Directives do not apply and they do not have to be transformed into national Swiss law. However, Switzerland’s national copyright law provides a series of regulations that seek the same objectives as the exceptions and limitations provided for in Directive 2001/29/EC and Directive 96/9/EC.

Switzerland does not provide for any database protection. Databases are protected only as far as they qualify as works in the sense of copyright. A specific database protection in form of a sui-generis-right does not exist.

Swiss copyright law provides no exceptions and limitations for scientific research. However, it provides exceptions for reproduction of copyrighted works within public li-

braries, educational institutions, museums and archives as well as exceptions for the private use of copyrighted works. As Swiss law applies, the concept of “private” includes the internal use in private entities and institutions, including commercial organisations and enterprises. Consequently, the exceptions for private use apply to a much wider set of subjects than in other countries. The regulations are to be found in the following articles:

#### Art. 19 Verwendung zum Eigengebrauch

<sup>1</sup>Veröffentlichte Werke dürfen zum Eigengebrauch verwendet werden. Als Eigengebrauch gilt:

- a. jede Werkverwendung im persönlichen Bereich und im Kreis von Personen, die unter sich eng verbunden sind, wie Verwandte und Freunde;
- b. jede Werkverwendung der Lehrperson in der Klasse;
- c. das Vervielfältigen von Werkexemplaren in Betrieben, öffentlichen Verwaltungen, Institutionen, Kommissionen und ähnlichen Einrichtungen für die interne Information und Kommunikation.

<sup>2</sup>Wer zum Eigengebrauch berechtigt ist, darf unter Vorbehalt von Absatz 3 die dazu erforderlichen Vervielfältigungen auch durch Dritte herstellen lassen; als Dritte im Sinne dieses Absatzes gelten auch Bibliotheken, andere öffentliche Institutionen und Geschäftsbetriebe, die ihren Benützern und Benutzerinnen Kopiergeräte zur Verfügung stellen.

<sup>3</sup>Ausserhalb des privaten Kreises nach Absatz 1 Buchstabe a sind nicht zulässig:

- a. die vollständige oder weitgehend vollständige Vervielfältigung im Handel erhältlicher Werkexemplare;
- b. die Vervielfältigung von Werken der bildenden Kunst;
- c. die Vervielfältigung von graphischen Aufzeichnungen von Werken der Musik;
- d. die Aufnahme von Vorträgen, Aufführungen oder Vorführungen eines Werkes auf Ton-, Tonbild- oder Datenträger.

(...)

#### Art. 24 Archivierungs- und Sicherungsexemplare

(...)

<sup>1bis</sup> Öffentlich zugängliche Bibliotheken, Bildungseinrichtungen, Museen und Archive dürfen die zur Sicherung und Erhaltung ihrer Bestände notwendigen Werkexemplare herstellen, sofern mit diesen Kopien kein wirtschaftlicher oder kommerzieller Zweck verfolgt wird.

(...)

### United Kingdom

Copyright and database protection in the UK is provided for by the “Copyright, Designs and Patents Act 1988” (CDPA) and in the “The Copyright and Rights in Databases

Regulations 1997” (United Kingdom Parliament 1988). The exceptions and limitations provided for in Directive 2001/29/EC and Directive 96/9/EC have been transformed into the following articles:

Section 29 CDPA (referring to article 5.3.a and 5.3.n of Directive 2001/29/EC):

- (1) Fair dealing with a work for the purposes of research for a non-commercial purpose does not infringe any copyright in the work provided that it is accompanied by a sufficient acknowledgement.
- (1B) No acknowledgement is required in connection with fair dealing for the purposes mentioned in subsection (1) where this would be impossible for reasons of practicality or otherwise.
- (1C) Fair dealing with a work for the purposes of private study does not infringe any copyright in the work.
- (3) Copying by a person other than the researcher or student himself is not fair dealing if—
  - (a) in the case of a librarian, or a person acting on behalf of a librarian, that person does anything which regulations under section 42A (copying by librarians: single copies of published works), or
  - (b) in any other case, the person doing the copying knows or has reason to believe that it will result in copies of substantially the same material being provided to more than one person at substantially the same time and for substantially the same purpose.

Section 29A CDPA (referring to article 5.2.c of Directive 2001/29/EC):

- (1) The making of a copy of a work by a person who has lawful access to the work does not infringe copyright in the work provided that—
  - (a) the copy is made in order that a person who has lawful access to the work may carry out a computational analysis of anything recorded in the work for the sole purpose of research for a non-commercial purpose, and
  - (b) the copy is accompanied by a sufficient acknowledgement (unless this would be impossible for reasons of practicality or otherwise).
- (2) Where a copy of a work has been made under this section, copyright in the work infringed if—
  - (a) the copy is transferred to any other person, except where the transfer is authorised by the copyright owner, or
  - (b) the copy is used for any purpose other than that mentioned in subsection (1) (a), except where the use is authorised by the copyright owner.
- (3) If a copy made under this section is subsequently dealt with—
  - (a) it is to be treated as an infringing copy for the purposes of that dealing, and
  - (b) if that dealing infringes copyright, it is to be treated as an infringing copy for all subsequent purposes.
- (4) In subsection (3) “dealt with” means sold or let for hire, or offered or exposed for ale or hire.

- (5) To the extent that a term of a contract purports to prevent or restrict the making of a copy which, by virtue of this section, would not infringe copyright, that term is unenforceable”.

Section 38 CDPA (referring to article 5.2.c of Directive 2001/29/EC):

- (1) The librarian of a prescribed library may, if the prescribed conditions are complied with, make and supply a copy of an article in a periodical without infringing any copyright in the text, in any illustrations accompanying the text or in the typographical arrangement.
- (2) The prescribed conditions shall include the following—
  - (a) that copies are supplied only to persons satisfying the librarian that they require them for the purposes of—
    - (i) research for a non-commercial purpose, or
    - (ii) private study, and will not use them for any other purpose;
  - (b) that no person is furnished with more than one copy of the same article or with copies of more than one article contained in the same issue of a periodical; and
  - (c) that persons to whom copies are supplied are required to pay for them a sum not less than the cost (including a contribution to the general expenses of the library) attributable to their production.

Section 39 CDPA (referring to article 5.2.c of Directive 2001/29/EC):

- (1) The librarian of a prescribed library may, if the prescribed conditions are complied with, make and supply from a published edition a copy of part of a literary, dramatic or musical work (other than an article in a periodical) without infringing any copyright in the work, in any illustrations accompanying the work or in the typographical arrangement.
- (2) The prescribed conditions shall include the following—
  - (a) that copies are supplied only to persons satisfying the librarian that they require them for the purposes of—
    - (i) research for a non-commercial purpose, or
    - (ii) private study,and will not use them for any other purpose;
  - (b) that no person is furnished with more than one copy of the same material or with a copy of more than a reasonable proportion of any work; and
  - (c) that persons to whom copies are supplied are required to pay for them a sum not less than the cost (including a contribution to the general expenses of the library) attributable to their production.

Section 40 CDPA (referring to article 5.2.c, 5.3.a and 5.3.n of Directive 2001/29/EC):

- (1) Regulations for the purposes of sections 38 and 39 (copying by librarian of article or part of published work) shall contain provision to the effect that a copy shall be supplied only to a person satisfying the librarian that his requirement is not related to any similar requirement of another person.

- (2) The regulations may provide—
  - (a) that requirements shall be regarded as similar if the requirements are for copies of substantially the same material at substantially the same time and for substantially the same purpose; and
  - (b) that requirements of persons shall be regarded as related if those persons receive instruction to which the material is relevant at the same time and place.

Section 42A CDPA (referring to article 5.3.a und 5.3.n of Directive 2001/29 EC):

- (1) A librarian of a library which is not conducted for profit may, if the conditions in subsection (2) are met, make and supply a single copy of—
  - (a) one article in any one issue of a periodical, or
  - (b) a reasonable proportion of any other published work, without infringing copyright in the work.
- (2) The conditions are—
  - (a) a copy is supplied in response to a request from a person who has provided the librarian with a declaration in writing which includes the information set out in subsection (3), and
  - (b) the librarian is not aware that the declaration is false in a material particular.
- (3) The information which must be included in the declaration is—
  - (a) the name of the person who requires the copy and the material which that person requires,
  - (b) a statement that the person has not previously been supplied with a copy of that material by any library,
  - (c) a statement that the person requires the copy for the purpose of research for a non-commercial purpose or private study, will use it only for those purposes and will not supply the copy to any other person, and
  - (d) a statement that to the best of the person's knowledge, no other person with whom the person works or studies has made, or intends to make, at or about the same time as the person's request, a request for substantially the same material for substantially the same purpose.

Section 50 D CDPA (referring to Article 9(b) of Directive 96/9/EC):

- (1) It is not an infringement of copyright in a database for a person who has a right to use the database or any part of the database, (whether under a licence to do any of the acts restricted by the copyright in the database or otherwise) to do, in the exercise of that right, anything which is necessary for the purposes of access to and use of the contents of the database or of that part of the database.
- (2) Where an act which would otherwise infringe copyright in a database is permitted under this section, it is irrelevant whether or not there exists any term or condition in any agreement which purports to prohibit or restrict the act (such terms being, by virtue of section 296B, void).



## Summary of national regulations

**Table 1.** Summary of national regulations.

	<b>D 2001/29 Art. 5.2.c</b>	<b>D 2001/29 Art. 5.3.a</b>	<b>D 2001/29 Art. 5.3.n</b>	<b>D 96/9 Art. 9(b)</b>
<b>Denmark</b>	allowed through extended collective license	allowed through extended collective license	legal license	no provision
<b>France</b>	legal license	legal license (except for school books)	no provision	no provision
<b>Germany</b>	legal license (restricted)	legal license (except for school books)	allowed within the premises, if no other data use agreement	legal license (except for commercial use)
<b>Italy</b>	legal license	legal license (restricted)	allowed within the premises, if no other data use agreement	legal license (except for commercial use)
<b>Norway</b>	legal license	no provision	allowed through extended collective license	no database protection
<b>Sweden</b>	legal license	no provision	allowed through extended collective license	no provision
<b>Switzerland</b>	legal license	no provision	no provision	no database protection
<b>United Kingdom</b>	legal license (restricted)	legal license (linked to "fair dealing")	legal license (linked to "fair dealing")	legal license

A legal license refers to the use of protected works allowed by law, normally linked to a levy. Legal licenses supersede individual data use agreements. Extended collective licenses are agreements between a qualified user (e.g. a library) and a national collecting society which represents a considerable number of national right-holders. The figures in the first line refer to the following provisions:

Directive 2001/29/EC of the European Parliament and of the Council of 22 May 2001 on the harmonisation of certain aspects of copyright and related rights in the information society.

Article 5.2: Member States may provide for exceptions or limitations to the reproduction right provided for in Article 2 in the following cases:

- (c) in respect of specific acts of reproduction made by publicly accessible libraries, educational establishments or museums, or by archives, which are not for direct or indirect economic or commercial advantage

Article 5.3. Member States may provide for exceptions or limitations to the rights provided for in Articles 2 and 3 in the following cases:

- (a) use for the sole purpose of illustration for teaching or scientific research, as long as the source, including the author's name, is indicated, unless this turns out to be impossible and to the extent justified by the non-commercial purpose to be achieved.
- (n) use by communication or making available, for the purpose of research or private study, to individual members of the public by dedicated terminals on the premises of establishments referred to in paragraph 2(c) of works and other subject-matter not subject to purchase or licensing terms which are contained in their collections

Directive 2001/29/EC of the European Parliament and of the Council of 11 March 1996 on the legal protection of databases. Article 9 Exceptions to the sui generis right:

Member States may stipulate that lawful users of a database which is made available to the public in whatever manner may, without the authorization of its maker, extract or re-utilize a substantial part of its contents:

- (b) in the case of extraction for the purposes of illustration for teaching or scientific research, as long as the source is indicated and to the extent justified by the non-commercial purpose to be achieved

## Conclusion

This review illustrates that national provisions in Europe on copyright and database protection regarding exceptions and limitations for research purposes differ not only in certain details but in substance. There is no consistency among national legislations despite Directive 2001/29/EC that aims to achieve harmonisation. In none of the regulations presented here is there a general exception or limitation to the copyright protection for the use of works for research purposes. In some countries, there are exceptions for some particular uses in the sector of scientific research. In Scandinavian countries, there is an exception linked to extended collective licence schemes. In the United Kingdom there is a very detailed exception for research purposes linked to a fair-dealing-clause. Exceptions to the sui-generis-database-protection are even more varied (Table 1).

Most national regulations seem to be oriented to a rather outdated concept of scientific work. Provisions that link copyright exceptions to the premises of certain institutions are incompatible with the current nature of scientific collaboration among institutions. Provisions that allow for the printing of copies but not for the storage on digital devices (as is the case in Germany), or that forbid the sharing of documents (as is the case in the recently introduced section 42A of the British CPDA), impair the efficiency of scientific work and confine researchers to outdated working methods.

Regulations that link exceptions and limitations to idiosyncratic definitions of works (for example, in Germany, Art. 53a par. 1 UrhG establishes that the exception for library copies is allowed if the same work cannot be purchased in a library or via the internet but is not allowed if the item can be purchased) make modern research techniques such as automated text generation and data mining difficult. It is not possible to search or analyse automatically a body of documents if there is no general rule about what can and cannot be done with all the documents. In the interests of efficient scientific research, exceptions and limitations of copyright and database protection should, therefore, apply to every object that is of interest to researchers.

There is no longer a clear distinction between commercial and non-commercial research (Hagedorn et al. 2011). Public-private partnerships and sponsored research render this distinction obsolete. A research institution that makes earnings from selling products or services cannot pretend to do non-commercial research. No institution can guarantee that the results of its research will not partly be commercialised by third persons. Regulations that restrict exceptions and limitations to the re-use of works for non-commercial research purposes misjudge the reality of science. The distinction is neither applicable nor useful and should be abandoned.

The emergence of an integrated system for the management of biodiversity knowledge will be hampered by current copyright and database protection. This hurdle should be removed by unifying exceptions and limitations for research purposes in a binding, Europe-wide regulation.

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# A replacement name for *Dayus* Gerken, 2001 (Crustacea, Peracarida, Cumacea), preoccupied by *Dayus* Mahmood, 1967 (Insecta, Hemiptera, Cicadellidae)

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## Abstract

A replacement name is proposed for genus *Dayus* Gerken, 2001 (Crustacea: Peracarida: Cumacea), preoccupied by *Dayus* Mahmood, 1967 (Insecta: Hemiptera: Cicadellidae). The following changes are proposed: *Jennidayus* **new replacement name** = *Dayus* Gerken, 2001 (nec Mahmood 1967); *Jennidayus pharocheradus* (Gerken, 2001), **comb. n.** = *Dayus pharocheradus* Gerken, 2001; *Jennidayus acanthus* (Gerken, 2001), **comb. n.** = *Dayus acanthus* Gerken, 2001; *Jennidayus makrokolosus* (Gerken, 2001), **comb. n.** = *Dayus makrokolosus* Gerken, 2001.

## Keywords

Crustacea, Peracarida, Cumacea, homonym, replacement name

## Introduction

The cumacean genus name *Dayus* Gerken, 2001 (Crustacea: Peracarida: Cumacea) is preoccupied by *Dayus* Mahmood, 1967 (Insecta: Hemiptera: Cicadellidae). The purpose of the present paper is to propose a replacement name.

## Nomenclatural changes and notes

### Genus *Jennidayus* nom. n.

*Dayus* Gerken, 2001: 9 (Crustacea: Peracarida: Cumacea). Preoccupied by *Dayus* Mahmood, 1967: 39 (Insecta: Hemiptera: Cicadellidae).

**Type species.** *Dayus pharocheradus* Gerken, 2001.

**Remarks on nomenclatural change.** The cumacean genus *Dayus* was established by Gerken (2001) with three species: *D. pharocheradus*, *D. acanthus* and *D. makrokolus* from Australia. *Dauys pharocheradus* was designated as the type species. However, *Dayus* Gerken, 2001 is preoccupied by *Dayus* Mahmood, 1967, established for a typhlocybinae leafhopper genus, with *Dayus elongatus* Mahmood, 1967 (from Singapore) as the type species (Insecta: Hemiptera: Cicadellidae). According to Article 60 of the International Code of Zoological Nomenclature (ICZN 1999), we propose the new replacement name *Jennidayus* nom. n. for *Dayus* Gerken, 2001. Accordingly, three new combinations are herein proposed for the species currently included in this genus: *Jennidayus pharocheradus* (Gerken, 2001), *Jennidayus acanthus* (Gerken, 2001) and *Jennidayus makrokolus* (Gerken, 2001).

**Etymology.** The genus name was meant to honor Jennifer Day of South Africa, for her work on South African Cumacea; gender masculine.

**Distribution.** Australia.

### Summary of nomenclatural changes

*Jennidayus* **new replacement name** = *Dayus* Gerken, 2001 (nec Mahmood, 1967).

*Jennidayus pharocheradus* (Gerken, 2001), **comb. n.** = *Dayus pharocheradus* Gerken, 2001.

*Jennidayus acanthus* (Gerken, 2001), **comb. n.** = *Dayus acanthus* Gerken, 2001.

*Jennidayus makrokolus* (Gerken, 2001), **comb. n.** = *Dayus makrokolus* Gerken, 2001.

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# Two new *Paraparatrechina* (Hymenoptera, Formicidae) species from the Seychelles, with notes on the hypogaedic *weissi* species-group

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## Abstract

Recent survey work in the Seychelles has revealed two new species of *Paraparatrechina* that are here described: *P. illusio* **sp. n.** and *P. luminella* **sp. n.** A revised key to the workers of *Paraparatrechina* for the Afrotropical and Malagasy regions is provided. The taxonomy of the hypogaedic *weissi* species-group is also reviewed in light of recent field collections. The species *P. sordida* is revived from synonymy and given new status (as a full species) and a discussion of the morphologically peculiar species-group is provided. With the description of the two species and the removal of another species from *weissi* synonymy there are now 16 *Paraparatrechina* species known from the Afrotropical and Malagasy regions.

## Keywords

Ants, Formicinae, *Prenolepis* genus-group, Seychelles, new species

## Introduction

The biology of the ant genus *Paraparatrechina* remains poorly known, but what is becoming clearer is that species diversity within the genus is certainly much higher than is currently recognized. LaPolla et al. (2010b) recently revised the Afrotropical and Malagasy species and found 8 new species (they found 13 total species within the two regions). While the Australasian species await taxonomic revision, preliminary data suggest that there are many undescribed species (S. Shattuck, pers. comm.). To emphasize this point of the genus having much higher species richness than is currently recognized, recent survey work in the Seychelles by BLF revealed two new species that were not included in LaPolla et al. (2010b). Here we describe those two species.

We also provide notes on a rather unusual group of *Paraparatrechina*, the Afrotropical *weissi* species-group (LaPolla 2004a; LaPolla et al. 2010a; LaPolla et al. 2010b). This group was last reviewed by LaPolla (2004a) and thought to contain two valid species (*P. bufona* and *P. weissi*). Recent collection work however in Uganda suggests that a third species, *P. sordida*, which is currently in synonymy with *P. weissi*, should be elevated to full species. Here we also discuss the taxonomic status of the *weissi* species-group and provide images for all three species.

## Materials and methods

Specimens examined for this study are deposited in the following institutions:

**CASC** California Academy of Sciences, San Francisco, CA, USA  
**MCZC** Museum of Comparative Zoology, Cambridge, MA, USA  
**USNM** National Museum of Natural History, Washington, DC, USA

All measurements were taken at 80× power with a Leica M125 microscope using an orthogonal pair of micrometers, recorded to the nearest 0.001 mm, and rounded to two decimal places for presentation. When more than one specimen was measured, minimum and maximum measurements and indices are presented. All measurements are given in millimeters. Digital color images were created using a Leica DFC425 digital camera. Leica Application Suite software (ver. 3.8) was used for images. Each imaged specimen is uniquely identified with a specimen-level unique identifier (e.g. CASENT0003099).

Morphological terminology for measurements and indices employed throughout are defined (following LaPolla et al. 2011a, b) as:

**EL** (Eye Length): maximum length of compound eye in full-face view.

**GL** (Gaster Length): the length of the gaster in lateral view from the anteriormost point of the first gastral segment (third abdominal segment) to the posteriormost point.

**HL** (Head Length): the length of the head proper, excluding the mandibles; measured in full-face view from the midpoint of the anterior clypeal margin to a line drawn across the posterior margin from its highest points.



**HW** (Head Width): the maximum width of the head in full-face view.

**PW** (Pronotal Width): the maximum width of the pronotum in dorsal view.

**SL** (Scape Length): the maximum length of the antennal scape excluding the condylar bulb.

**TL** (Total Length): HL+WL+GL

**WL** (Weber's Length): in lateral view, the distance from the posteriormost border of the metapleural lobe to the anteriormost border of the pronotum, excluding the neck.

**CI** (Cephalic Index):  $(HW/HL) \times 100$

**REL** (Relative Eye Length Index):  $(EL/HL) \times 100$

**SI** (Scape Index):  $(SL/HW) \times 100$

**Key to *Paraparatrechina* workers in the Afrotropical and Malagasy Regions (modified from LaPolla et al. 2010b)**

- 1 Eyes small relative to head length ( $REL \leq 16$ ) ..... **2**
- Eyes medium to large relative to head length ( $REL \geq 17$ ) ..... **6**
- 2 Eyes consisting of less than 10 facets; polymorphic, with clearly expressed major caste; Equatorial Africa; *weissi* species-group ..... **3**
- Eyes consisting of more than 10 facets; monomorphic; Madagascar ..... **5**
- 3 Scapes with numerous erect macrosetae; mesosoma with numerous erect macrosetae scattered across each segment (especially abundant on pronotum and mesonotum) ..... ***bufona***
- Scapes without erect macrosetae; few macrosetae on mesosoma (typically 2 on pronotum; 1 on mesonotum and 1 on propodeum) ..... **4**
- 4 Metanotal groove strongly impressed; head without paired macrosetae medially from posterior margin towards clypeus; no macrosetae on posterior margin ..... ***sordida* stat. n. & rev.**
- Metanotal groove not strongly impressed; head with paired macrosetae medially from posterior margin towards clypeus; at least four macrosetae on posterior margin ..... ***weissi***
- 5 Scape with decumbent pubescence; scapes surpass posterior margin by approximately length of the first 3–4 funicular segments ..... ***myops***
- Scape with appressed pubescence; scapes surpass posterior margin by approximately length of the first 2–3 funicular segments ..... ***ocellatula***
- 6 Mesosoma elongate in lateral view, with pronotum gently rising towards mesonotum ..... **7**
- Mesosoma compact in lateral view, with pronotum steeply rising towards mesonotum ..... **9**
- 7 Propodeum with a short, angular dorsal face, and a long declivitous face; scape length <0.6 mm; Madagascar ..... ***glabra***
- Propodeum with rounded dorsal face, not conspicuously longer than declivitous face; scape length >0.6 mm; Equatorial Africa ..... **8**

- 8 Scape length > 0.72 mm; tibiae same brown color as mesosoma; protrochanter brown as in mesosoma, but meso/metatrochanters may be lighter brown; mandibles and antennae typically same brown color as head..... ***splendida***
- Scape length < 0.72 mm; tibiae whitish to brownish-yellow; all trochanters white; mandibles and antennae yellowish-brown, contrasting with brown head..... ***concinata***
- 9 Mesosomal dorsum (primarily pronotum and mesonotum) much lighter (typically yellow against brown or white against dark brown) than remainder of mesosoma..... **10**
- Mesosomal dorsum not much lighter than remainder of mesosoma..... **11**
- 10 Dorsum of gaster with a distinctly yellow to white patch of color contrasting with remainder of gaster; Seychelles..... ***luminella* sp. n.**
- Dorsum of gaster solid dark brown in color; West Africa..... ***albipes***
- 11 Gaster brown, conspicuously contrasting with yellow head and mesosoma...  
..... ***umbranatis***
- Gaster brownish-yellow to yellow, not conspicuously contrasting with head and mesosoma ..... **11**
- 12 Dark brown species, with conspicuously lighter colored, contrasting antennae and legs ..... ***brunnella***
- Yellow species, with antennae and legs same color as remainder of body... **13**
- 13 Smaller species (HL & SL < 0.4 mm) ..... ***gnoma***
- Larger species (HL & SL > 0.4 mm) ..... **14**
- 14 Scares with appressed pubescence..... ***oreias***
- Scares with decumbent pubescence ..... **15**
- 15 Short, decumbent pubescence covers head, especially lateroposteriorly, where it is longer than remainder of head; pubescence on gaster longer, slightly decumbent, giving an “unkempt” appearance; West Africa ..... ***subtilis***
- Short, decumbent pubescence present lateroanteriorly around eyes; pubescence on gaster shorter, tightly appressed to gaster, with pubescence appearing in neat rows with a silky appearance; Seychelles ..... ***illusio* sp. n.**

## New species accounts

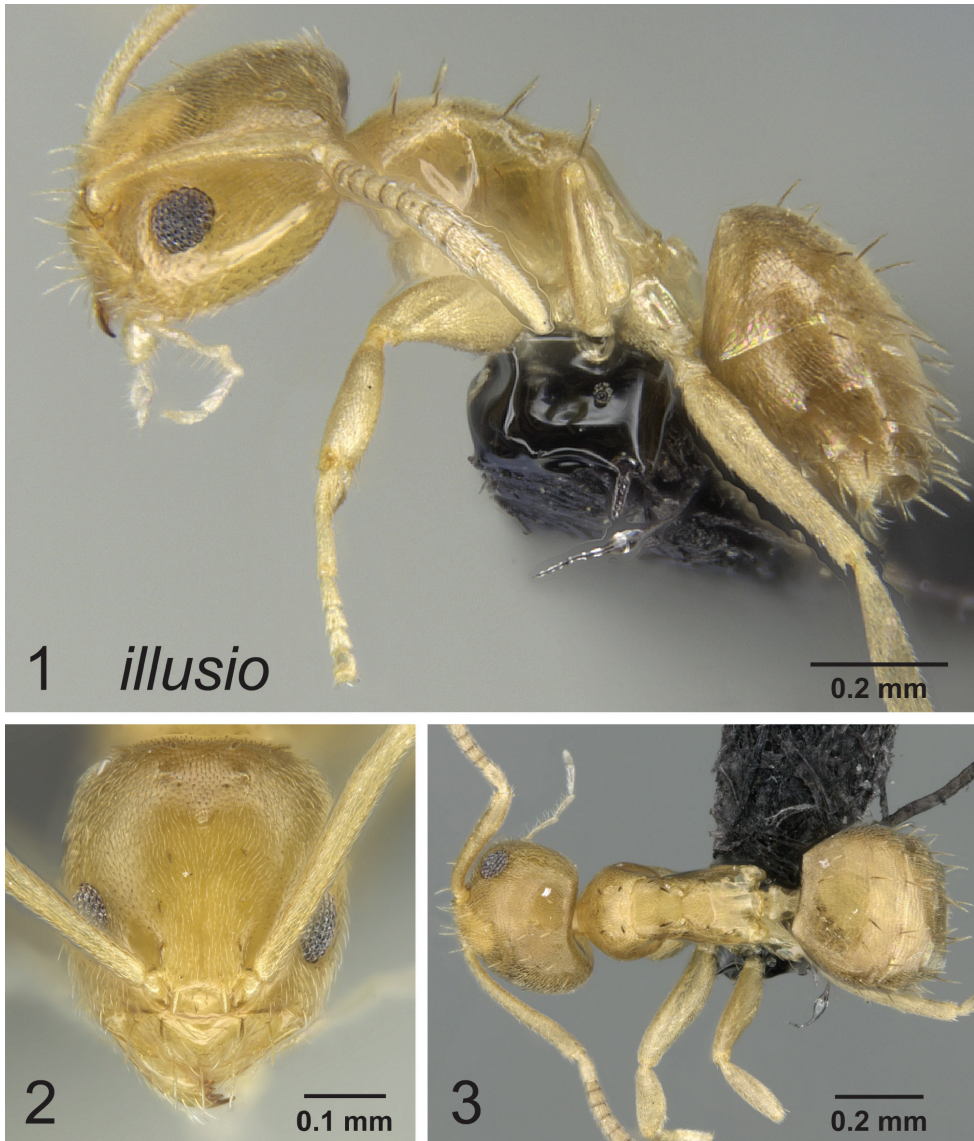
### ***Paraparatrechina illusio* sp. n.**

<http://zoobank.org/94A7F5B0-FAF1-477D-B697-71148BD9F5D4>

[http://species-id.net/wiki/Paraparatrechina\\_illusio](http://species-id.net/wiki/Paraparatrechina_illusio)

Figs 1–9

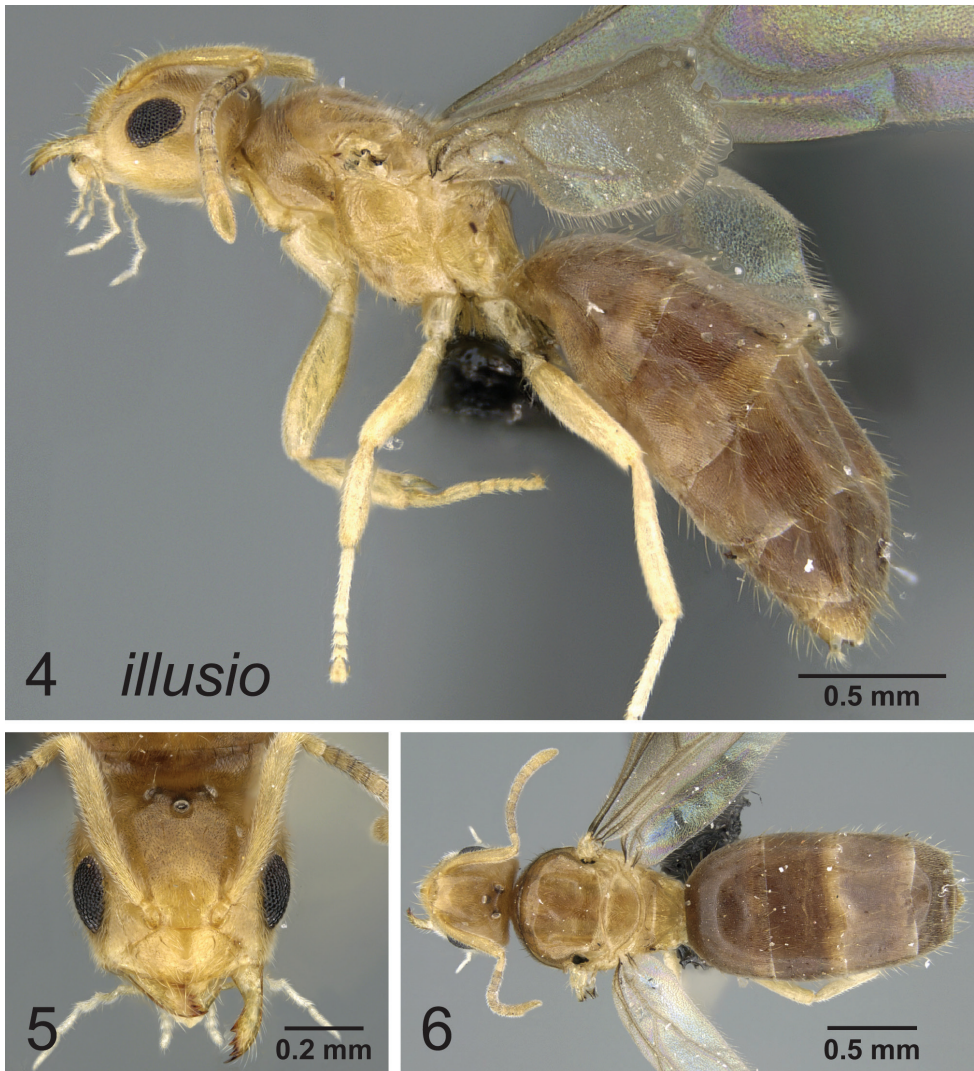
**Holotype worker.** SEYCHELLES: Praslin Island, 280m, 4.34725°S, 55.74743°E, 6.ii.2010, mixed palm forest, on low vegetation, B.L. Fisher et al. CASENT0159099 (CASC); 5 paratype workers, SEYCHELLES: Conception Island, 65 m, 4.66311°S, 55.36821°E, 12.ii.2010, mixed forest, B.L. Fisher et al. CASENT0160297 (CASC),



**Figures 1–3.** Lateral, full face and dorsal view of body. *Paraparatrechina illusio* holotype worker CASENT0159099.

CASENT0160331 (CASC), CASENT0160622 (USNM), CASENT0160625 (CASC), CASENT0160650 (CASC); paratype worker, SEYCHELLES: Curieuse Island, 5 m, 4.28364°S, 55.7269°E, 4.ii.2010, coastal scrub, B.L. Fisher et al. CASENT0160122 (CASC); paratype worker, SEYCHELLES: Praslin Island, Newcome, 130m, 4.390°S, 55.6926°E, 6.ii.2010, palm forest, B.L. Fisher et al. CASENT0158991 (USNM); paratype worker, SEYCHELLES: Sillhouette Island, 20 m, 4.49076°S, 55.25341°E, 21.i.2010, coastal scrub, B.L. Fisher et al., CASENT0159838 (CASC).





**Figures 4–6.** Lateral, full face and dorsal view of body. *Paraparatrechina illusio* queen CASENT0160097.

**Worker diagnosis.** Short, decumbent pubescence present lateroanteriorly around eyes; pubescence on gaster shorter, tightly appressed to gaster, with pubescence appearing in neat rows with a silky appearance.

Compare with: *P. gnoma*, *P. oreias*, and *P. subtilis*.

**Worker.** Measurements (n=8) TL: 1.20–1.67; HW: 0.35–0.38; HL: 0.39–0.42; EL: 0.10–0.11; SL: 0.37–0.40; PW: 0.23–0.26; WL: 0.41–0.44; GL: 0.39–0.81

*Indices:* CI: 86–95; REL: 25–27; SI: 101–112.

Yellow to brownish-yellow; legs and antennae lighter; short, decumbent pubescence present lateroanteriorly around eyes; pubescence on gaster short, tightly appressed to

gaster, with pubescence appearing in neat rows with a silky appearance. Head subquadrate with nearly straight posterior margin; scapes surpass posterior margin by first 2-3 funicular segments; three ocelli apparent. Mesosoma compact with steeply rising pronotum in lateral view; metanotal area indistinct, only slightly impressed; propodeum with short, flat dorsal face and much longer, steep declivitous face.

**Queen.** Measurements (n=3) TL: 2.92–3.23; HL: 0.54–0.55; HW: 0.58–0.61; EL: 0.20–0.21; SL: 0.53–0.53; PW: 0.62–0.66; WL: 0.97–1.03; GL: 1.34–1.70

*Indices:* CI: 110–111; REL: 36–38; SI: 86–88

As in worker, with modifications expected for queen caste and the following differences:

1. Pubescence distinctly across head and mesosoma.
2. Gaster darker (yellowish-brown) than remainder of body.

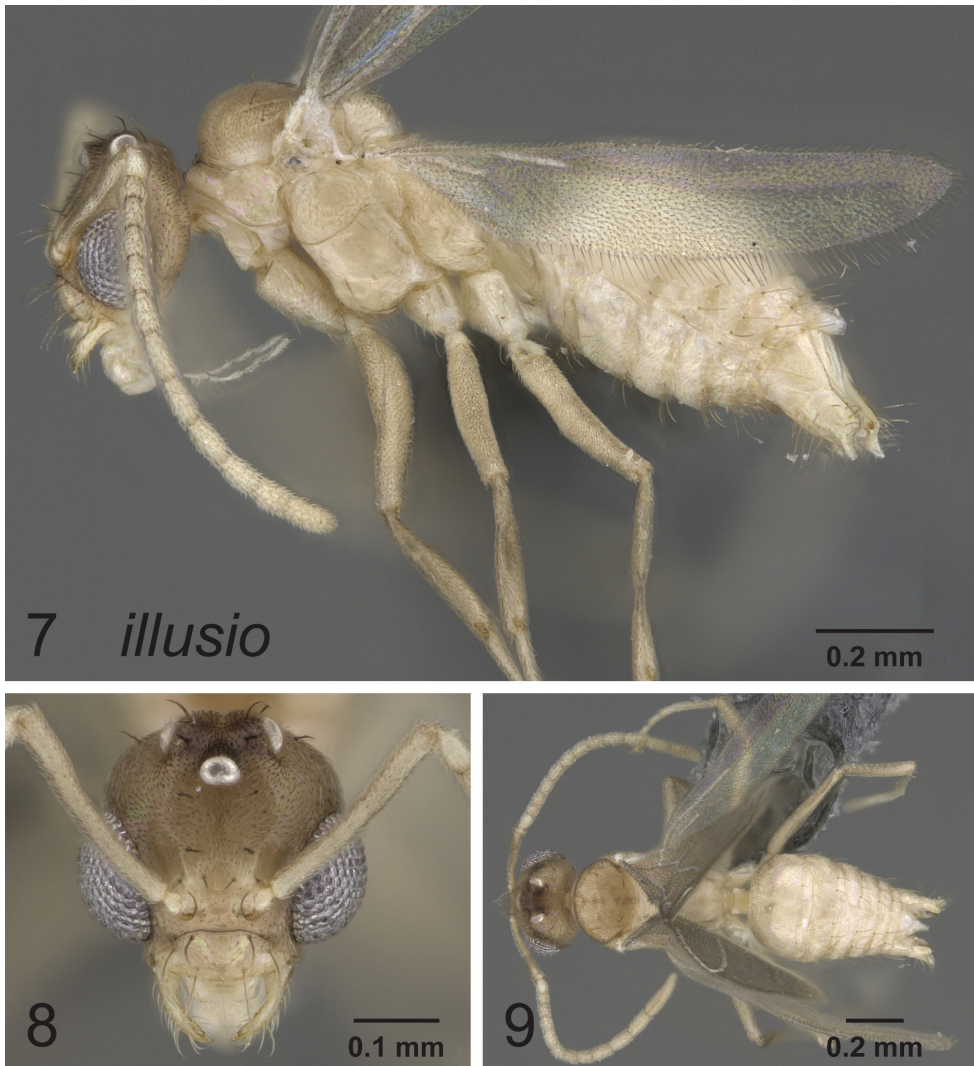
**Male.** Measurements (n=1) TL: 1.55; HL: 0.33; HW: 0.38; EL: 0.18; SL: 0.31; PW: 0.29; WL: 0.54; GL: 0.68

*Indices:* CI: 113; REL: 53; SI: 81

Head brown, with bulging large eyes that occupy most of the lateral region of the head; head slightly broader than long. Palps distinctly lighter than head in color. A dense layer of pubescence covers head, with scattered erect setae along mid-region, posterior margin and clypeus. Scapes surpass posterior margin by about length of the first 2 funicular segments; antennae 13-segmented. Mandible with apical tooth and an indistinct basal angle. Mesosoma same color as head; pronotum short and collar-like; mesonotum large, rounded anteriorly, overarching pronotum; mesosoma dorsum flat, with erect setae. Gaster slightly lighter brown than head and mesosoma, covered with pubescence and erect setae. Parameres relatively broad then with a steep angle towards last third of paramere length; last third of paramere thinner and elongated with rounded apex; paramere with scattered erect setae.

**Notes.** This species falls into the small, yellow *Paraparatrechina* worker phenotype range (typically workers of these species vary by only slight difference in setation and color tones of yellow and brownish-yellow) and therefore identification of the species can be difficult. It is morphological similar to three Afrotropical species: *P. gnoma*, *P. oreias*, and *P. subtilis*. In practice, a relatively straight forward, non-morphological way, to separate *P. illusio* is it is only known from the Seychelles, while the remaining three species are from West and Central Africa. Morphologically, it differs from *P. gnoma* in being slightly larger overall and in coloration (*P. gnoma* is brownish-yellow with lighter yellow patches). From *P. oreias* the main difference also lies in color. The gaster of *P. oreias* is brownish-yellow, contrasting slightly with the remainder of the body. The metanotal area of *P. oreias* is also more distinctly defined than is seen in *P. illusio*. From *P. subtilis*, the difference is in the pubescence. Whereas the pubescence on the head of *P. subtilis* is decumbent throughout, on *P. illusio* it is only decumbent lateroanteriorly around eyes. Additionally the gastral pubescence is different between the two: in *P. subtilis* it is longer and slightly decumbent, contrasting with the shorter, tightly appressed pubescence observed in *P. illusio*.





**Figures 7–9.** Lateral, full face and dorsal view of body. *Parapatrechina illusio* male CAsENT0914145.

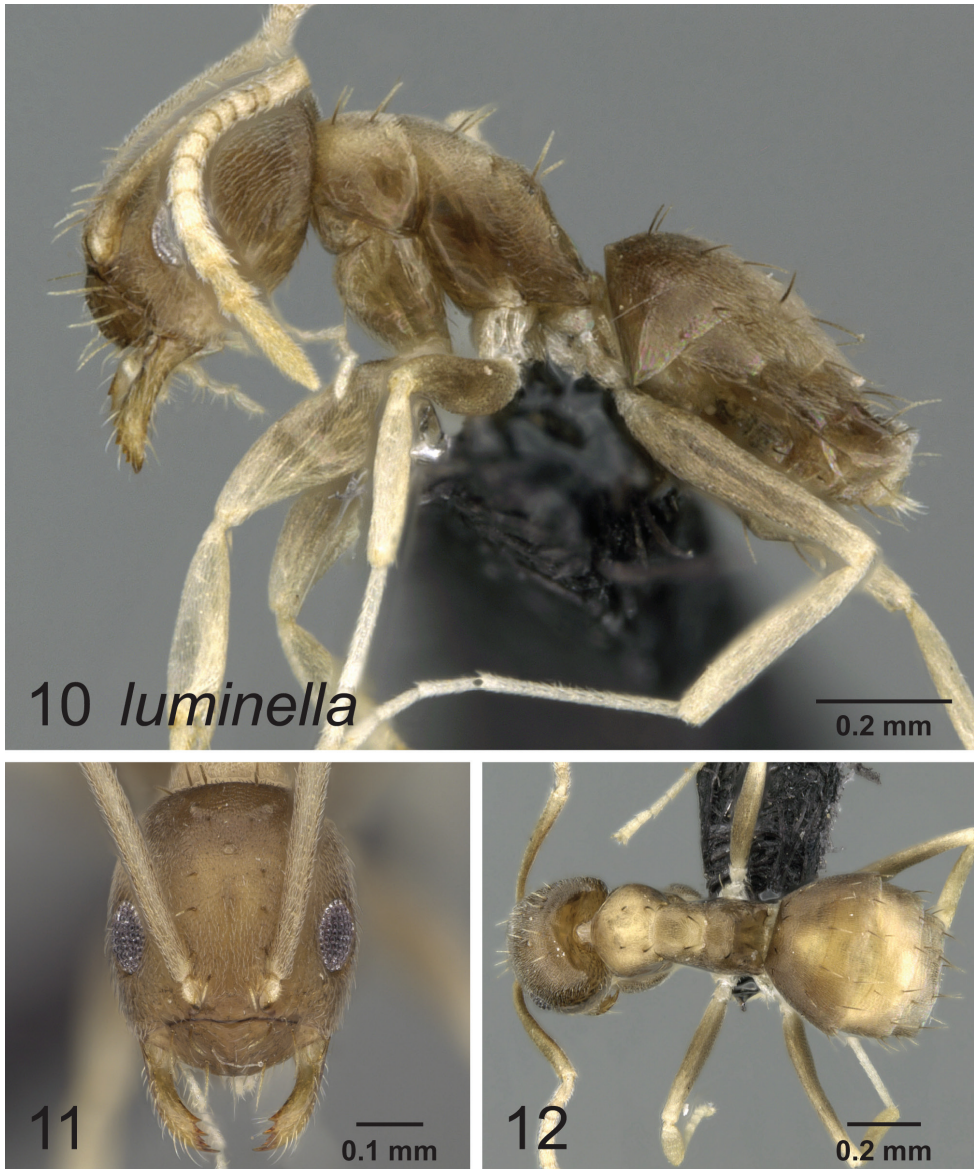
***Parapatrechina luminella* sp. n.**

<http://zoobank.org/4A4A4FCF-DFDD-462E-AB98-C707B61F7A31>

[http://species-id.net/wiki/Parapatrechina\\_luminella](http://species-id.net/wiki/Parapatrechina_luminella)

Figs 10–15

**Holotype worker.** SEYCHELLES: Silhouette Island, above Jardin Marron on crest to Mont Plaisir and Pot à Eau, 520m, 4.4867°S, 55.2341°E, 20.i.2010, forest, rotten log, B.L.Fisher et al. CAsENT0159693 (CASC); paratype worker, same locality as holotype (USNM); 2 paratype workers, SEYCHELLES: Mahé Island, Mont Copolia, 520m, 4.65121°S, 55.45835°E, 8.ii.2010, forest, sifted litter, B.L.Fisher et



**Figures 10–12.** Lateral, full face and dorsal view of body. *Paraparatrechina luminella* worker CASENT0160868.

al. CASENT0159361 (CASC), CASENT0159373 (CASC); paratype worker, SEYCHELLES: Mahé Island, Le Niol, 345m, 4.63067°S, 55.43159°E, 11.ii.2010, tree plantation, rotten log, B.L.Fisher et al. CASENT0159051 (CASC); paratype worker, SEYCHELLES: Mahé Island, Casse Dent, Morne Seychellois National Park, 465 m, 4.65284°S, 55.43735°E, 11.ii.2010, mixed forest, under rootmat, B.L.Fisher et al. CASENT0145383 (CASC); paratype worker, SEYCHELLES: Silhouette Is-

land, below Mont Cocos Marrons, 320m, 4.50248°S, 55.24395°E, 21.i.2010, forest, under rootmat, B.L.Fisher et al. CASENT0158936 (CASC); paratype worker, SEYCHELLES: Silhouette Island, on ridge toward Pot à Eau, 600m, 4.48213°S, 55.23408°E, 22.i.2010, moist rainforest, rotten log, B.L.Fisher et al. CASENT0158939 (CASC); paratype worker, SEYCHELLES: Silhouette Island, Jardin Marron, 395m, 4.48636°S, 55.23627°E, 27.i.2010, non-native forest, on low vegetation, B.L.Fisher et al. CASENT0159308 (CASC); paratype worker, SEYCHELLES: Silhouette Island, on ridge toward Mont Corgat, 445m, 4.49537°S, 55.23946°E, 25.i.2010, forest, ground nest, B.L.Fisher et al. CASENT0159944 (CASC); paratype worker & queen, SEYCHELLES: Silhouette Island, ridge from Mont Corgat to Mont Cocos Marron, 455m, 4.50126°S, 55.23985°E, 24.i.2010, forest, rotten log, B.L.Fisher et al. CASENT0159905 (USMN).

**Worker diagnosis.** Very distinct patches of lighter areas (ranging from yellow to white) on pronotum (that can extend onto mesonotum) and gastral tergites (typically from posterior of T1 through anterior portion of T4.)

Compare with: *P. albipes*.

**Worker.** Measurements (n=8) TL: 1.37–1.58; HW: 0.38–0.46; HL: 0.44–0.47; EL: 0.11–0.13; SL: 0.45–0.50; PW: 0.20–0.29; WL: 0.46–0.52; GL: 0.46–0.67

*Indices:* CI: 85–98; REL: 25–28; SI: 108–124;

Overall brown with patches of yellow to white; lighter area medially between eyes and above torulae; distinct patches of lighter areas (ranging from yellow to white) on pronotum (that typically extends onto mesonotum and occasionally onto dorsal face of propodeum) and gastral tergites (typically from posterior of T1 through anterior portion of T4; scapes proximally more brown becoming yellow to whitish midlength, lightening to white through apex of funiculus; procoxae golden yellow, meso/metacoxae and trochanters white; femur golden yellow then remainder of leg light yellow to white; body covered in dense, appressed pubescence; macrosetae placement as is typical in *Paraparatrechina*. Head ovate with nearly straight posterior margin; scapes surpass posterior margin by first 2-3 funicular segments; three ocelli apparent. Mesosoma compact with steeply rising pronotum in lateral view; mesonotum and metanotal area short; metanotal area indistinct, only slightly impressed; propodeum with short, flat dorsal face and much longer, steep declivitous face.

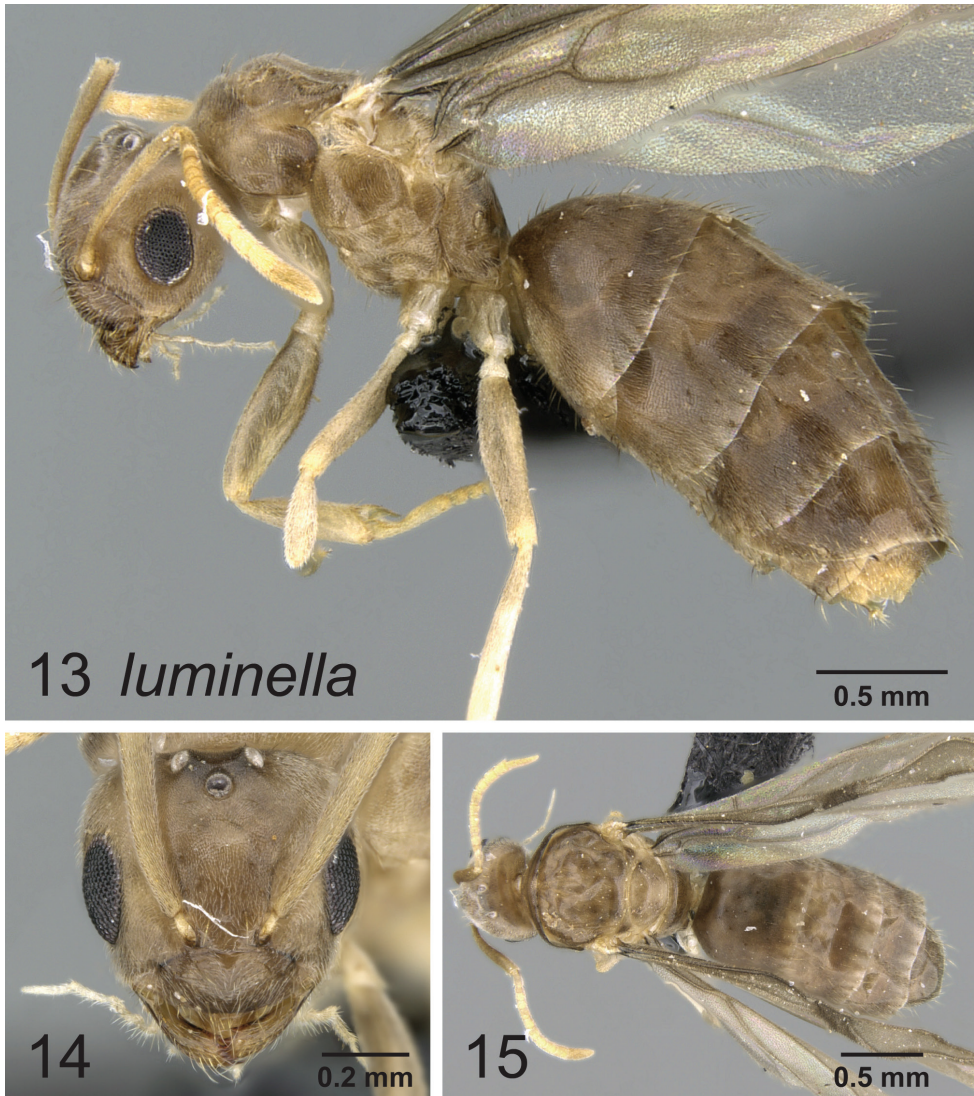
**Queen.** Measurements (n=3) TL: 3.34–3.75; HL: 0.61–0.63; HW: 0.66–0.69; EL: 0.25–0.26; SL: 0.61–0.62; PW: 0.66–0.74; WL: 1.13–1.22; GL: 1.52–2.02

*Indices:* CI: 104–111; REL: 39–41; SI: 91–92

As in worker, with modifications expected for queen caste and the following differences:

1. Coloration overall more brown than in worker, with no distinct yellow to white patches on mesosoma or gaster; lighter antennae and legs.
2. Head subcordate.
3. Legs generally as in worker, except coxae brown.





**Figures 13–15.** Lateral, full face and dorsal view of body. *Paraparatrechina luminella* queen CASENT0159313.

**Notes.** The coloration pattern seen in the worker of *Paraparatrechina luminella* is very distinct and is unlike any pattern seen in other species from either the Afrotropical or Malagasy regions. The most similar coloration pattern among *Paraparatrechina* is seen in *P. albipes*, in which workers typically have a light patch of whitish coloration on the posterior pronotum and mesonotum that contrasts with the generally overall dark brown color of the body. Whether this is indicative of a close relationship between these two species or is simply convergence is unclear.

### Synopsis of species in the *Paraparatrechina weissi* species-group

*Paraparatrechina bufona* (Wheeler, 1922)

*Paraparatrechina sordida* (Santschi, 1914), **stat. n. & rev.**

= *Paraparatrechina gowdeyi* (Wheeler, 1922)

= *Paraparatrechina bucculentus* (Wheeler, 1922)

*Paraparatrechina weissi* (Santschi, 1910)

= *Paraparatrechina bayonii* (Menozzi, 1924)

= *Paraparatrechina myersi* (Weber, 1943)

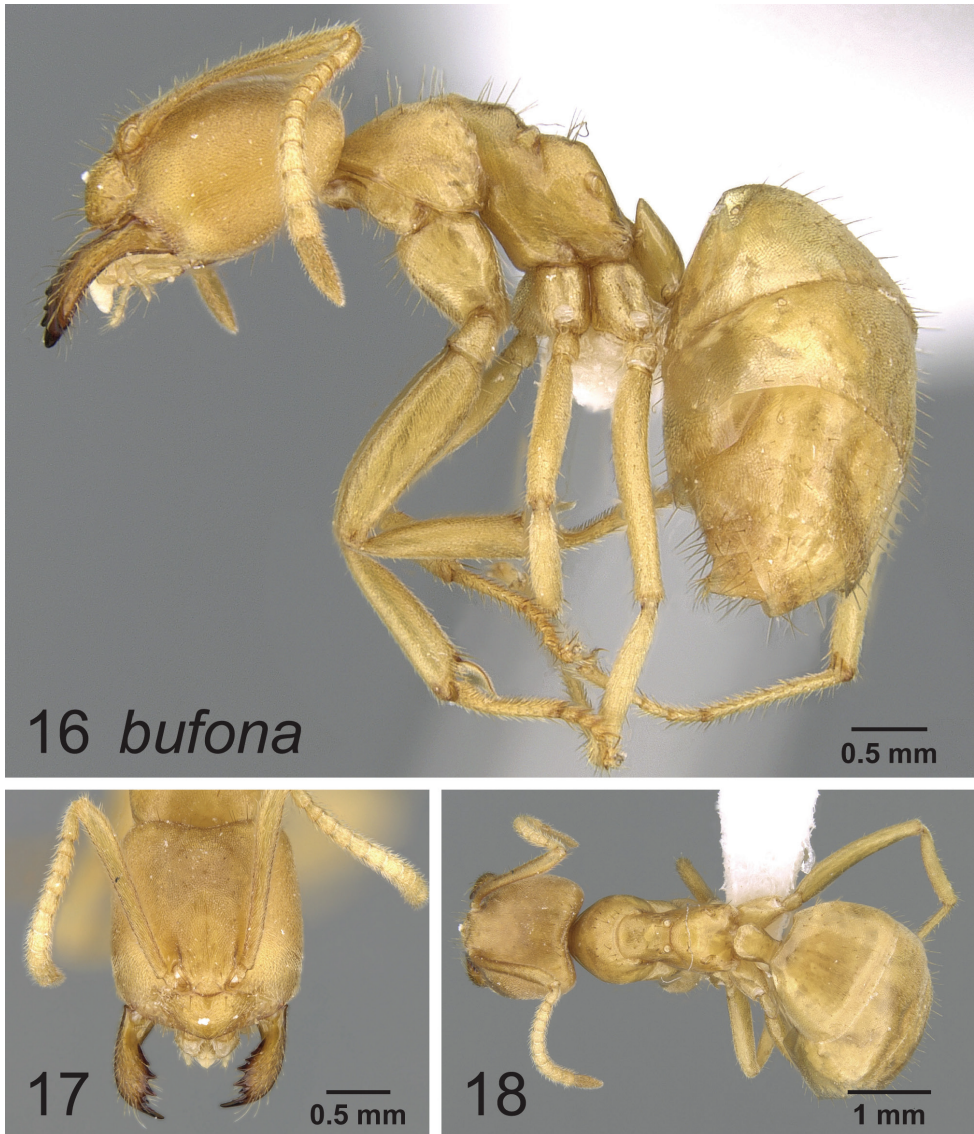
= *Paraparatrechina myersi occipitalis* (Weber & Anderson, 1950)

### Notes on the Afrotropical *weissi* species-group

The now called *weissi* species-group was last reviewed by LaPolla (2004a), where they were considered to belong to the genus *Pseudolasius*. Later, LaPolla et al. (2010a) found based on molecular evidence from 5 genes that these morphologically peculiar species in fact belonged in *Paraparatrechina*. In retrospect, there was some, albeit at the time seemingly rather weak morphological support for the placement within *Paraparatrechina* such as: the short, angular dorsal propodeal face (Figs 16, 19, 22), and although obscured in *P. bufona* by the presence of several erect macrosetae on the mesosoma, the typical *Paraparatrechina* mesosomal macrosetae pattern of 2:1:1 (pronotum, mesonotum and propodeum) is present on all species. Nonetheless, superficially the *weissi* species-group does resemble *Pseudolasius*. What this certainly reflects is that the *weissi* species-group species have become hypogaecic and have convergently taken on the suite of morphological characters common among subterranean formicines (for example see LaPolla 2004b). Of further interest is that like *Pseudolasius* at least two species of the *weissi* species-group have evolved majors (*P. bufona* and *P. weissi*). All *Pseudolasius* (of which most, if not all species are hypogaecic) presumably have majors (LaPolla et al. 2010a). There appears to be selection occurring in the *Prenolepis* genus-group among those with a hypogaecic lifestyle for the evolution of majors. For instance, the ground-dwelling and presumably largely hypogaecic (based on the morphology of the workers) *Nylanderia amblyops* known from Madagascar appears to be the only species in that genus to have evolved majors. In *Euprenolepis* at least one species, *E. procera*, has majors as well, although it is not hypogaecic (rather it appears to be nocturnal) (LaPolla 2009).

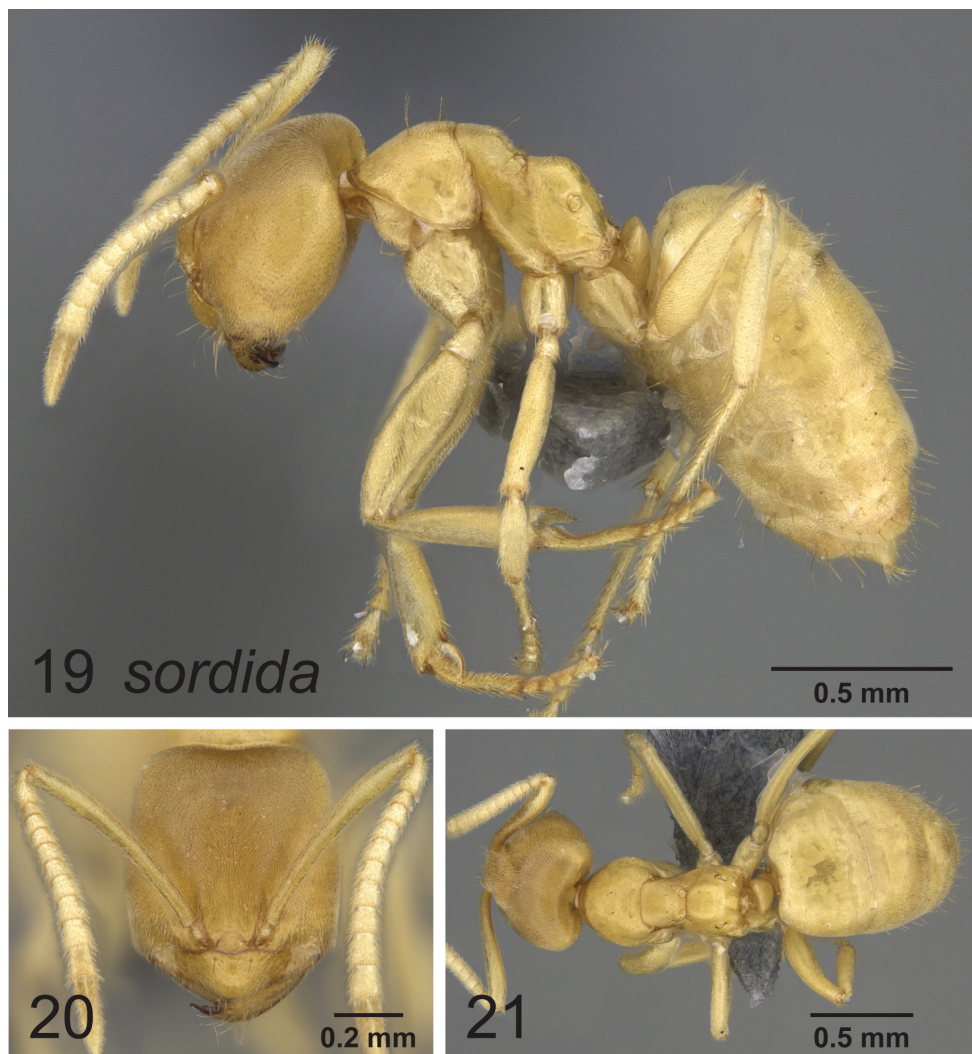
LaPolla (2004a) reviewed what would later be called the *weissi* species-group, and recognized only two valid species (*P. bufona* and *P. weissi*), the others of which were considered synonyms (all of *P. weissi*). The study was hindered in two ways: the lack of recent material from nest series and the confounding variable of worker polymorphism. Recent fieldwork (J. Longino, pers. comm.) however resulted in a small collection of





**Figures 16–18.** Lateral, full face and dorsal view of body. *Paraparatrechina bufona* worker CASENT0906212.

specimens of two species of the *weissi* species-group in sympatry with each other: *P. weissi* and another species that was clearly not *P. bufona*. Upon comparison with type material, we determined that the specimens clearly belonged to the species named *P. weissi sordida* (here treated as a full species), previously synonymized under *P. weissi*. *Paraparatrechina sordida* differs from *P. weissi* and *P. bufona* in several ways. *Paraparatrechina bufona* is distinct because of the presence of many erect macrosetae across



**Figures 19–21.** Lateral, full face and dorsal view of body. *Paraparatrechina sordida* worker CASENT0914143.

the scapes and mesosoma. The other two species *P. sordida* and *P. weissi* are more similar to each other but differ in that *P. sordida* possesses a strongly impressed metanotal groove, a head without paired macrosetae medially from the posterior margin towards the clypeus and has no macrosetae on the posterior margin of the head. We therefore propose a revived and new status of *P. sordida* as a full species. The synopsis of the *weissi* species-group provides a reinterpretation of the valid species and where the synonyms should properly be placed. These findings nicely demonstrate the continued need for collection in the very poorly sampled Afrotropical region.





**Figures 22–24.** Lateral, full face and dorsal view of body. *Paraparatrechina weissi* worker CASENT0906210.

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