Proceedings of the 18th International Congress of Myriapodology, Budapest, Hungary

Edited by

Zoltán Korsós, László Dányi

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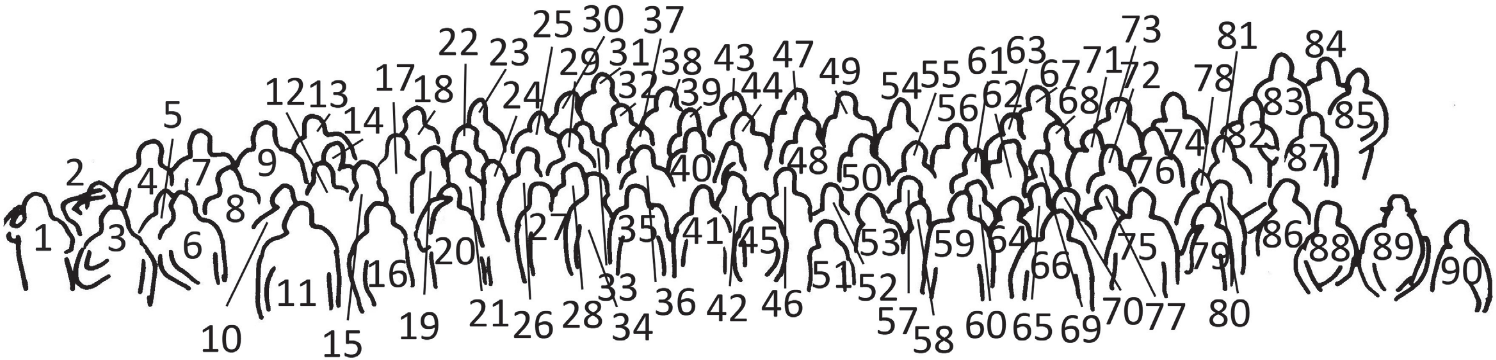

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EDITORIAL

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Editorial

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It was a great honour when the International Society for Myriapodology (Centre International de Myriapodologie) accepted our proposal to organize the 18th International Congress of Myriapodology at the Hungarian Natural History Museum in Budapest, between August 25–31, 2019. We had a successful meeting: 92 scientific participants (plus 13 accompanying persons) from 32 countries, all around the world from Brazil and Uruguay through Europe and South Africa to China and Australia. During the four scientific days we had 48 lectures (including four invited plenary presentations – one each morning) and 55 posters, which covered a wide range of our field, myriapodology, from the zoological subjects of morphology, anatomy, taxonomy, systematics, physiology, biogeography and nature conservation. We also had a joint full day excursion to the nearby Buda Hills, where participants could encounter some representatives of the local soil fauna. In the name of the organizing committee we would like to thank our 16 Hungarian colleagues who helped to make the congress really enjoyable.

From the presentations, we are presenting here 11 scientific papers in this Special Issue of Zookeys. We are grateful to Pensoft Publishers and to the editorial board of Zookeys for providing the opportunity to publish a cross-section of the 18th International Congress of Myriapodology.

Dr. Zoltán Korsós and Dr. László Dányi
Guest editors

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RESEARCH ARTICLE

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The millipedes collected by the Museum "La Specola" on Madagascar 1989/1991, with the description of three new species of giant pill-millipedes (Diplopoda, Sphaerotheriida, Arthrosphaeridae)

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Abstract

A large collection of millipedes (Diplopoda) from Madagascar, belonging to the Museum “La Specola” in Florence, Italy were investigated. The collection includes three new species of the giant pill-millipede genus *Zoosphaerium* Pocock, 1895 which are described here as *Zoosphaerium mangabe* Wesener, **sp. nov.,** *Z. bartolozzii* Anilkumar & Wesener, **sp. nov.,** and *Z. taitii* Anilkumar & Wesener, **sp. nov.,** all belonging to the *Z. coquerelianum* species group. The latter two are currently only known from a single site. Other specimens belonging to eight orders (Polyxenida, Sphaerotheriida, Polyzoniida, Siphonophorida, Chordeumatida, Polydesmida, Spirobolida, and Spirostreptida) are listed. Three tropical tramp species, *Pseudospirobolellus avernus* (Butler, 1876), *Glyphiulus granulatus* Gervais, 1847, and *Chondromorpha xanthotricha* (Attems, 1898) are recorded for the first time from Madagascar. New locality data is provided for *Zoosphaerium neptunus* (Butler, 1872), *Z. villosum* Wesener & Sierwald, 2005, *Z. blandum* (de Saussure & Zehntner, 1897), *Sphaeromimus musicus* (de Saussure & Zehntner, 1897), *Rhinotus purpureus* (Pocock, 1894), *Hylekobolus andasibensis* Wesener, 2009, *Aphistogoniulus infernalis* Wesener, 2009, *Ostinobolus rufus* Wesener, 2009, *Ostinobolus subterraneus* Wesener, 2009, *Dactylobolus bivirgatus* (Karsch, 1881), and *Eumekius antimena* (de Saussure & Zehntner, 1901).

Keywords

Biodiversity, *COI*, introduced species, Madagascar, museum collection

Introduction

Madagascar, the fourth largest island lying 400 km east of Africa in the Indian Ocean, is one of the world's biodiversity hot-spots, great for the studies of endemism, species richness, and island gigantism (Myers et al. 2000, Goodman and Benstead 2005, Wesener and VandenSpiegel 2009). Madagascar with India were the first landmasses to be separated from Gondwana approximately 170 million years ago, subsequently split from India around 90-85 million years ago (Ali and Aitchison 2008). The long isolation of Madagascar has given rise to an enormous level of endemism, resulting in 96% of plants, 86% of macro-invertebrates (Goodman and Benstead 2005), 51% of birds, 90% of mammals, 99% of amphibians, and more than 90% of reptiles (Harper et al. 2007) being endemic. Madagascar harbors various forest types, humid rainforests on the east coast (Harper et al. 2007), the montane forests at the center, tropical dry forests in the west, desert spiny forests in the southwest and tropical littoral forests on the eastern shore. Such an insularity and habitat diversity aided the micro-endemism and the speciation observable in different plant and animal taxa on Madagascar (Goodman 2007).

Soil fauna is a species-rich component of terrestrial ecosystems, where one of the major faunal elements is arthropods, especially terrestrial insects (Giller 1996). Flightless arthropods are more prone to speciation because of their light body weight, shorter generation time, and smaller size requirements of habitat compared to other animal groups (Brühl 1997). Millipedes (class Diplopoda) are major detritivores in all types of forests (Golovatch and Kime 2009) and one of the eye-catching macro-invertebrate group on Madagascar (Wesener 2009, Sagorny and Wesener 2017). The giant pill-millipedes (order Sphaerotheriida) are the most diverse myriapod group on Madagascar with 81 known strictly endemic species. They also show micro-endemism and island gigantism (Wesener and Wägele 2008, Wesener et al. 2010a, b). Among the Sphaerotheriida family Arthrosphaeridae, three of the four genera, *Zoosphaerium* Pocock, 1895, *Microsphaerotherium* Wesener & VandenSpiegel, 2007, and *Sphaeromimus* de Saussure & Zehntner, 1902 are endemic to Madagascar while the genus *Arthrosphaera* Pocock, 1895 occurs in southern India and Sri Lanka (Wesener and VandenSpiegel 2009, Golovatch and Wesener 2016).

Morphological and molecular studies show that the Malagasy genus *Sphaeromimus* is more closely related to the Indian genus *Arthrosphaera*, which reflects an Indian-Malagasy biogeographical affinity (Wesener and VandenSpiegel 2009, Wesener et al. 2010a, 2014, Moritz and Wesener 2017). Within the family Arthrosphaeridae, the endemic Malagasy genus *Zoosphaerium* has the highest number of known species (67) (Wesener 2016, Sagorny and Wesener 2017). Some species of *Zoosphaerium* show island gigantism; thus, the female of *Z. neptunus* (Butler, 1872), with a length of 80.9 mm and when rolled-up the size of a tennis ball, is the largest described species of all Sphaerotheriida (Wesener and Wägele 2008).

Deforestation is a key cause of species extinction on Madagascar (Harper et al. 2007). Madagascar has undergone an enormous amount of deforestation in the past years, resulting in only 9.9% of natural forests remaining (Myers et al. 2000). The arrival of humans on Madagascar dates back to 2000 years and has changed the land structure especially by forest fragmentation for agriculture and charcoal production (Burney 2003). During the past 50 years, approximately 40% of the remaining forests on Madagascar were deforested (Harper et al. 2007) and this destruction is still continuing today. The region prone to highest percentage of deforestation is the spiny forest, with a reduction of 28% in last two decades (Harper et al. 2007). Because of this massive deforestation, 65 species of *Zoosphaerium* are listed on the IUCN Red List (IUCN 2019), where seven are critically endangered, three are endangered, three are vulnerable, and 18 are nearly threatened, mainly because of habitat loss (Rudolf and Wesener 2017a-d).

This study is about a millipede collection of the Museum “La Specola”, the Natural History Museum of Florence located in central Italy, collected by Dr. Luca Bartolozzi and Dr. Stefano Taiti during two expeditions to Madagascar in 1989 and 1991. A total of 24 millipede species was identified, of which 17 are indigenous to Madagascar, and seven are introduced species. Among the seven introduced species, three are new records. New locality data is provided for eleven species, of which ten are indigenous. The most spectacular find was the presence of three undescribed giant pill-millipede species. Numerous additional specimens were also present, but species-level determination was impossible as they were females or immatures.

Here, we describe the three new species of endemic giant pill-millipedes of the genus *Zoosphaerium*. The three new species belong to the *Z. coquerelianum* species group, making it the most diverse species group with 22 representatives (Sagorny and Wesener 2017).

Material and methods

Abbreviations:

MZUF	Museum "La Specola", Florence, Italy.
ZFMK	Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany

Illustrations

The first and second right legs, ninth left leg, as well as the anterior and posterior telopods were dissected and drawn using a *camera lucida* mounted on an Olympus SZX12 stereo-microscope and later transferred to ink using Pigma Micron pens of widths 0.20 mm and 0.40 mm. For scanning electron microscopy (SEM) imaging, the right antenna and a small part of the endotergum from a mid-body tergite were dissected, cleaned, undergone a dehydration ethanol chain procedure (1 x 90%, 2 x 96%, 2 x 100%), then dried for 24 h, and mounted on aluminum stubs. The stubs with samples were coated with gold for 240 seconds in a sputter coater. SEM images were taken using a

Supra VR 300VP (Carl Zeiss AG) scanning electron microscope utilizing the Software SmartSEM V05.00 based at the ZFMK. The SEM samples were returned to ethanol after the study. All ink drawings and images were edited using Adobe Photoshop CS2, later labelled and assembled into plates in Adobe Illustrator CS2.

DNA extraction attempts

DNA extraction, amplification, and sequencing were conducted under identical conditions to those of earlier studies (Sagorny and Wesener 2017, Moritz and Wesener 2017, Wesener 2018), with the COI JJ primer (Astrin and Stüben 2008) being used for both PCR and sequencing. A translation into amino acids showed a similar composition to those of related species. Only a single sequence of one of the species *Zoosphaerium bartolozzii* sp. nov. (P_05) could be successfully sequenced due to the old age of the material. The sequence has been uploaded to GenBank under the accession number MN783351.

This one sequence was added to a fasta file containing COI sequences of all available *Zoosphaerium* sequences from GenBank ($N = 14$), as well as two sequences of the related Malagasy genus *Sphaeromimus*, as the near outgroup and a species of the unrelated family Procyliosomatidae from Australia as the far outgroup (Wesener and VandenSpiegel 2009, Wesener et al. 2010, 2014), bringing the total number of terminals to 18.

Genetic analyses

Sequences were aligned by hand in Bioedit (Hall 1999). The final dataset consisted of 18 sequences and 657 base pairs. Pairwise distances: The number of base differences per site between sequences is shown in Table 1. The analysis involved 18 nucleotide sequences. Codon positions included were 1^{st}+2^{nd}+3^{rd}. All ambiguous positions were removed for each sequence pair.

The best-fitting substitution model for maximum-likelihood analysis was calculated with Model test (Tamura and Nei 1993) as implemented in MEGA6 (Tamura et al. 2013). The best-fitting model was the General Time Reversal (GTR)-Model (Tavaré 1986) with gamma distribution and Invariant sites (GTR+G+I) (lnL = -3600.757, Invariant = 0.50, Gamma = 0.9659, R = 4.09; Freq A: 0.30, T: 0.339, C: 0.204, G: 0.157).

The evolutionary history was inferred by using the Maximum Likelihood method based on the General Time Reversible model. The tree with the highest log likelihood (-3590.0809) is shown in Fig. 1. The percentage of trees in which the associated taxa clustered together is shown next to the branches. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Joining and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. A discrete Gamma distribution was used to model evolutionary rate differences among

Table 1. Genetic *p*-distances between species of *Zoosphaerium* Pocock, 1895. Variation among sites was modeled with gamma distribution with shape parameter = 0.9659. Included were codon positions $1^{st}+2^{nd}+3^{rd}$.

Procyliosoma sp. (*FJ409911.1*)																	
Sphaeromimus musicus (*KJ713245.1*)	0.234																
Sphaeromimus musicus (*KJ713244.1*)	0.234	0.000															
Zoosphaerium villosum (*KY399028.1*)	0.228	0.180	0.180														
Zoosphaerium sp. green (*KY399027.1*)	0.237	0.191	0.191	0.116													
***Zoosphaerium mangabe* sp. nov. (*KY399026.1*)**	0.209	0.200	0.200	0.135	0.116												
Zoosphaerium sp. (*KY399025.1*)	0.237	0.197	0.197	0.047	0.135	0.136											
Zoosphaerium sp. (*KY399024.1*)	0. 239	0.199	0.199	0.046	0.047	0.135	0.001										
Zoosphaerium minutus (*KY399023.1*)	0.200	0.196	0.196	0.129	0.046	0.091	0.122	0.120									
Zoosphaerium minutus (*KY399022.1*)	0.208	0.193	0.193	0.131	0.129	0.095	0.123	0.122	0.012								
Zoosphaerium bemanevika (*KY399021.1*)	0.227	0.169	0.169	0.108	0.131	0.141	0.117	0.119	0.131	0.131							
Zoosphaerium bemanevika (*KY399020.1*)	0.231	0.172	0.172	0.110	0.108	0.144	0.114	0.116	0.131	0.134	0.010						
Zoosphaerium bemanevika (*KY399019.1*)	0.227	0.169	0.169	0.108	0.110	0.141	0.117	0.119	0.131	0.131	0.000	0.010					
Zoosphaerium sp. brown (*FJ409931.1*)	0.203	0.194	0.194	0.163	0.108	0.150	0.166	0.165	0.129	0.129	0.150	0.153	0.150				
Zoosphaerium neptunus (*FJ409929.1*)	0.208	0.194	0.194	0.151	0.163	0.148	0.154	0.153	0.139	0.145	0.150	0.156	0.150	0.151			
Zoosphaerium alluaudi (*FJ409927.1*)	0.202	0.171	0.171	0.148	0.151	0.131	0.151	0.153	0.120	0.120	0.151	0.156	0.151	0.114	0.148		
Zoosphaerium alluaudi (*FJ409926.1*)	0.208	0.178	0.178	0.151	0.148	0.141	0.160	0.162	0.129	0.129	0.160	0.165	0.160	0.123	0.157	0.013	
***Zoosphaerium bartolozzii* sp. nov. (P_05)**	0.215	0.199	0.199	0.144	0.151	0.131	0.139	0.141	0.122	0.119	0.150	0.151	0.150	0.134	0.147	0.113	0.122

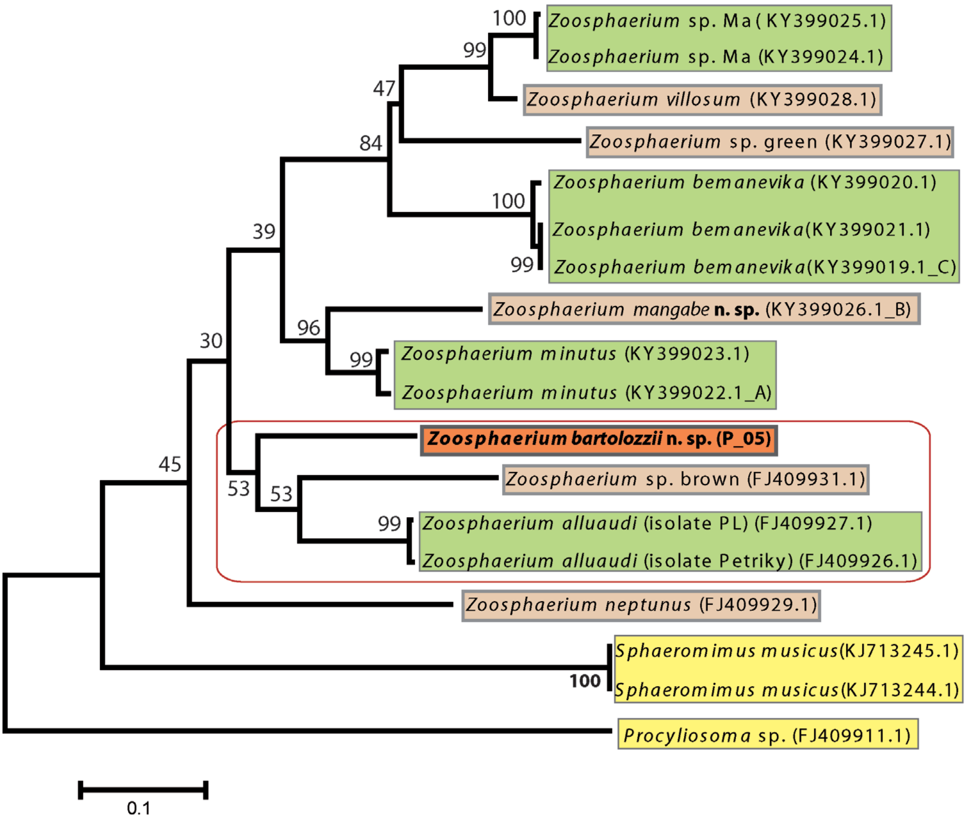

Figure 1. Maximum likelihood tree inferred from the COI dataset with 1000 bootstrap pseudoreplicates implementing the GTR+I+G model. Colors used to separate species. The circle indicates weakly supported sister-group relationships.

sites (five categories (+G, parameter = 0.9659)). The rate variation model allowed for some sites to be evolutionarily invariable ([+I], 49.3492% sites). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. All positions with less than 5% site coverage were eliminated. That is, fewer than 95% alignment gaps, missing data, and ambiguous bases were allowed at any position. Evolutionary analyses were conducted in MEGA6.

Results

Genetic distances:

Zoosphaerium bartolozzii sp. nov. differs from all other analyzed species of the genus by a minimum of 11% uncorrected p-distance. The smallest genetic distances are shown towards *Z. alluaudi* (de Saussure & Zehntner, 1902) belonging to the *Z. coquerelianum* species group in which *Z. bartolozzii* sp. nov. is currently placed. Comparably low genetic distances of 11.9% are shown towards *Z. minutus* Sagorny & Wesener, 2017, which is currently not placed in any species group. A similar pattern is observed for *Z. mangabe* sp. nov. which shows a distance of 9.1–9.5% to *Z. minutus*. Genetic distances to other members of the *Z. coquerelianum* species group such as *Z. bemanevika* Sagorny & Wesener, 2017 and *Z. villosum* Wesener & Sierwald, 2005 are within 15%, similar to species belonging to different species groups such as *Z. neptunus*. In the phylogenetic tree, *Z. bartolozzii* sp. nov. is placed in a weakly supported clade together with an undescribed gigantic species from the Andohahela national park and *Z. alluaudi*.

Taxonomy

Genus *Zoosphaerium* Pocock, 1895

See Wesener (2016) and Sagorny and Wesener (2017) for a recent catalogue and key to the species.

Zoosphaerium mangabe Wesener, sp. nov.

http://zoobank.org/F9D03D6A-2AEB-4208-B64A-80554641BE6A
Figures 2, 3A–H, 5A

Material examined. 1 ♂ *holotype* (MZUF), Nosy Mangabe (Maroantsetra), 15°29'43.4''S, 49°46'07.6''E, Mag 1313, R. Nicheri, 24 Apr 1990.

Other material examined. 1 ♂ (**ZMUCXXXX**), Madagascar, Province Antsiranana, Marojejy Res., 8.4 km NNW Manantenina, 14°26'S, 49°45'E, 700 m, 10-16 Nov 1991, leg. J. Coddington, N. Scharff, S. Larcher, C. Griswold, R. Andriamasimanana; 1 ♂ (**ZFMK MYR8915**), same data as previous; 1 ♀ (**FMNH-INS 2858681B**), VS-2642, Madagascar, Antsiranana, SAVA, Parc National de Marojejy, 6.5 km NW Manantenina village, 14°27'21.2'' S, 49°46'29.8''E, 780 m, disturbed lowland humid forest, pitfalls, coll. 31 May 2016, Voahangy Soarimalala, GenBank #KY399026.

Etymology. The word *mangabe* is a noun in apposition, after the type locality of the species, the island of Nosy Mangabe at the NE coast of Madagascar.

Diagnosis. *Zoosphaerium mangabe* sp. nov. shares the large body size, surface structure (like the peel of an orange), presence of only one stridulation rib on the male harp, and > 10 apical cones on the antenna only with *Z. coquerelianum* (de Saussure & Zehntner, 1897) and *Z. tainkintana* Wesener, 2009. *Zoosphaerium mangabe* sp. nov. differs from *Z. coquerelianum* in the long second locking carina on the anal shield (> times longer than the first), the hairy anal shield, and the presence of sclerotized teeth on the anterior telopods. The former differs from *Z. tainkintana* in the much shorter marginal bristles of the endotergum (reaching only 1/3 of the distance towards margin), the female operculum (two widely separated tips vs. fused tips), and in structures

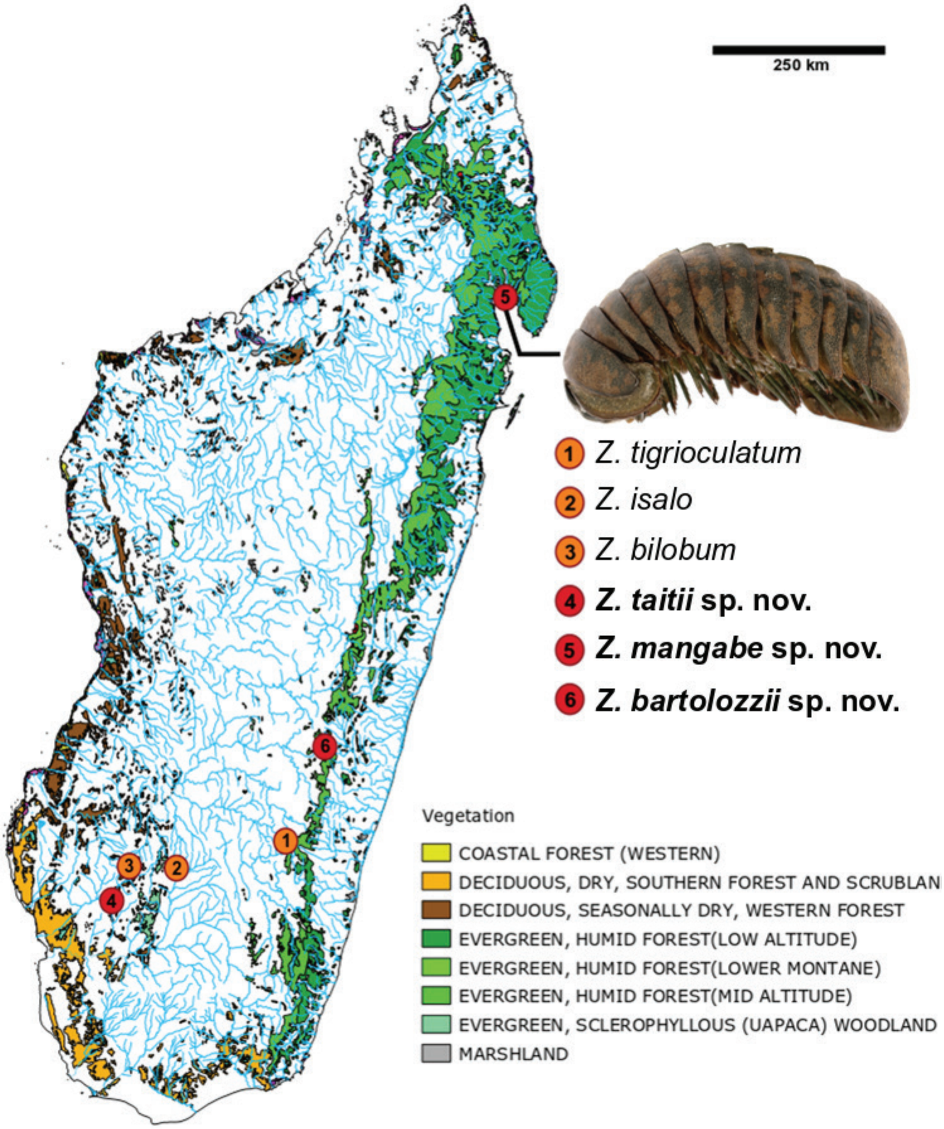

Figure 2. Distribution map of the three new *Zoosphaerium* species and the morphologically related species. Photograph shows the holotype of *Zoosphaerium mangabe* sp. nov., male.

of the anterior telopod (e.g., three or four large teeth in *Z. mangabe* sp. nov. but seven in *Z. tainkintana*).

Description (all measurements in mm). Body length: Male holotype: length 49.3, width 27.4 (2nd), 27.9 (8th = widest), height 13.7 (2nd), 15.5 (8th = highest). Female from Marojejy (broken): length ca. 50, width 27.9 (2nd = widest), height 14.6 (2nd), 18.1 (8th = highest).

Coloration: Color in some parts faded to a lighter brown than other parts after almost 30 years in ethanol. Younger and better-preserved female from Marojejy (FMNH-INS 2858681B) shows dark grey tergites with a thin dark brown posterior margin. Clypeus, base of legs and tip of antennae lighter brown, other parts of appendages dark green. Head except clypeus, collum, thoracic shield, body tergites, and anal shield dark olive green.

Head: Eyes consisting of 65/68 ommatidia. Antennae with 36/48 apical cones, part of left tip apparently regenerated.

Gnathochilarium: Sensory cones of palpi in single field. Inner parts of gnathochilarium not dissected.

Mandible not dissected.

Stigmatic plate: First stigmatic plate slender, apically narrow but well-rounded.

Pleurite: First pleurite laterally sharp-edged but not projecting.

Collum: Anterior and posterior margins with a sparse row of short setae . Inner part with a few isolated short setae.

Thoracic shield: Grooves deep, with few long setae. Remaining surface of thoracic shield similar to following tergites.

Tergites: Surface orange-like, each pit carrying a tiny seta. Tergite tips strongly projecting posteriorly.

Endotergum: Inner area with conical spines, broad at base with numerous setae and numerous small sharp spines in between. Single row of interchanging elliptical and smaller circular cuticular impressions. Smooth marginal ridge. Two rows of very short marginal bristle, protruding towards 1/4–1/2 margin (Fig. 5A).

Anal shield: Well-rounded, well-visible dorsally. Completely and regularly covered by small setae, underside carrying two locking carinae, second more than four times as long as first.

Legs: Leg one with three or five, leg two with six, leg three with seven ventral spines. First two leg pairs without an apical spine. Legs 4–21 with 8–10 ventral spines and one apical spine (Fig. 3A). In leg nine femur 1.9, tarsus 4.1 times longer than wide.

Female sexual characters: Vulva large, covering 3/4 of coxa, not extending to prefemur but protruding to apical margin of coxa. Operculum rounded, medially deeply invaginated, apical margin extended into two well-rounded lobes. Inner mesal plate long and slender and extending to apex of coxa and operculum. Lateral margin covered by hairs. External mesal plate broader and only extending to base of operculum, lateral margins also covered by hair (Fig. 3G).

Subanal plate: Large and wide, with shallow invagination at apical margin. Washboard with two short but well-developed stridulation ribs on each side. Margins and median part densely covered with hair (Fig. 3H).

Male sexual characters: Gonopore slightly oval, rounded apically, apical 1/4 covered by semicircular membranous plate, basal 3/4 by sclerotized plate, with few setae.

Anterior telopod: Harp carrying one stridulation rib positioned medially with end pointing laterad. Podomere one wide with few setae in anterior aspect (Fig. 3B). Podomere two, process not visible in anterior view, reaching half of length of podomere three (Fig. 3C, D), with sclerotized nubs along mesal margin. Podomere three taper-

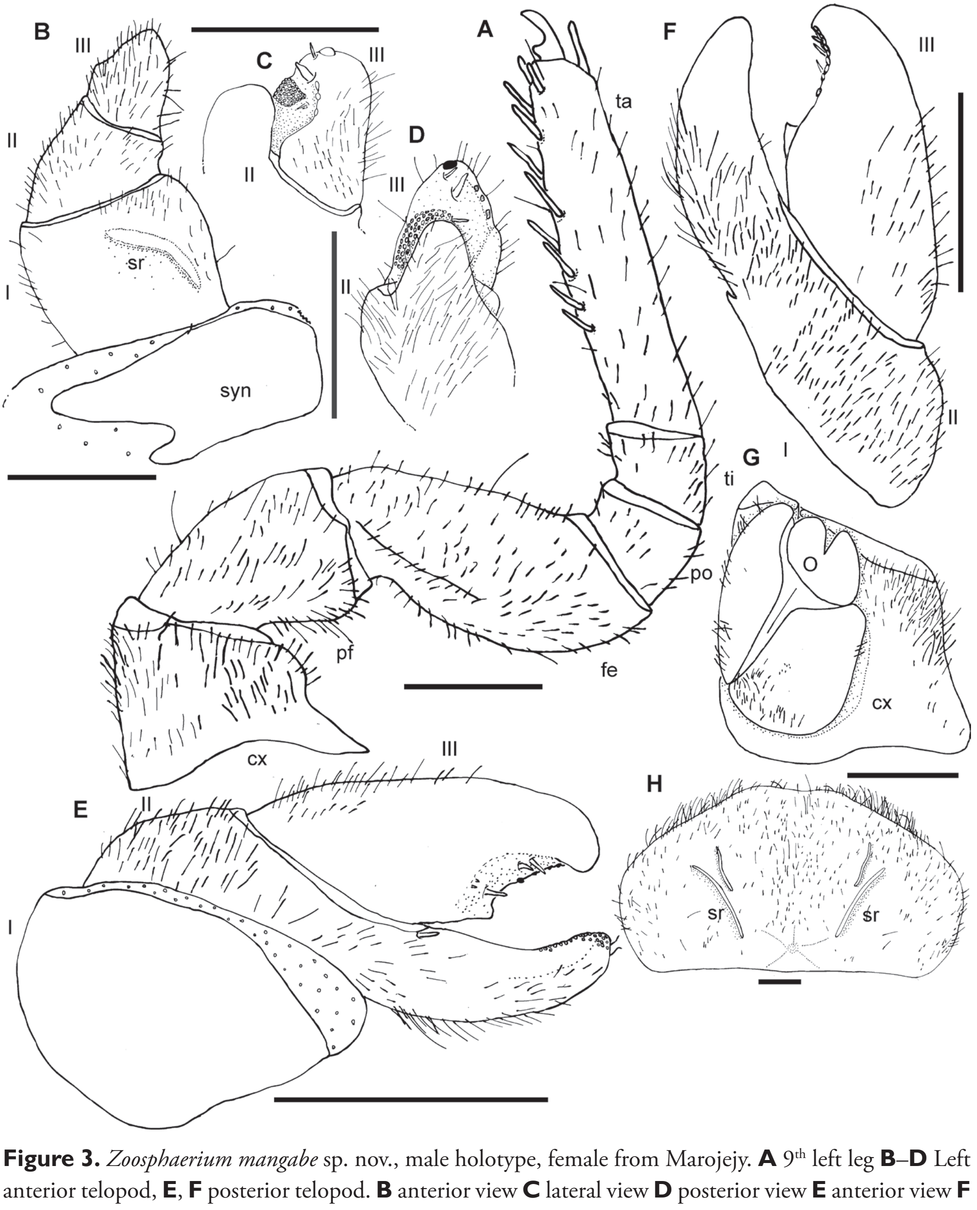

Figure 3. *Zoosphaerium mangabe* sp. nov., male holotype, female from Marojejy. **A** 9th left leg **B–D** Left anterior telopod, **E**, **F** posterior telopod. **B** anterior view **C** lateral view **D** posterior view **E** anterior view **F** posterior view **G** female vulva **H** female washboard. Abbreviations: cx = coxa; fe = femur; O = operculum; pf = prefemur; po = postfemur; sr = stridulation rib; syn = syncoxite; ta = tarsus; ti = tibia; roman numerals refer to telopoditomere number. Scale bars: 1 mm.

ing, as long as podomere two, with a rounded apex carrying one dark sclerotized spot near tip (Fig. 3C, D). Field of sclerotized spots run along apical-basal margin with three spines (Fig. 3C, D). Three or four crenulated teeth at lateral margin (Fig. 3C, D).

Posterior telopod: Movable finger 2.4 times longer than wide with tip slightly curving towards the immovable finger. Apical tip with ten sclerotized crenulated teeth, three spines, and a shallow mesal cavity with one triangular membranous lobe (Fig. 3E, F).

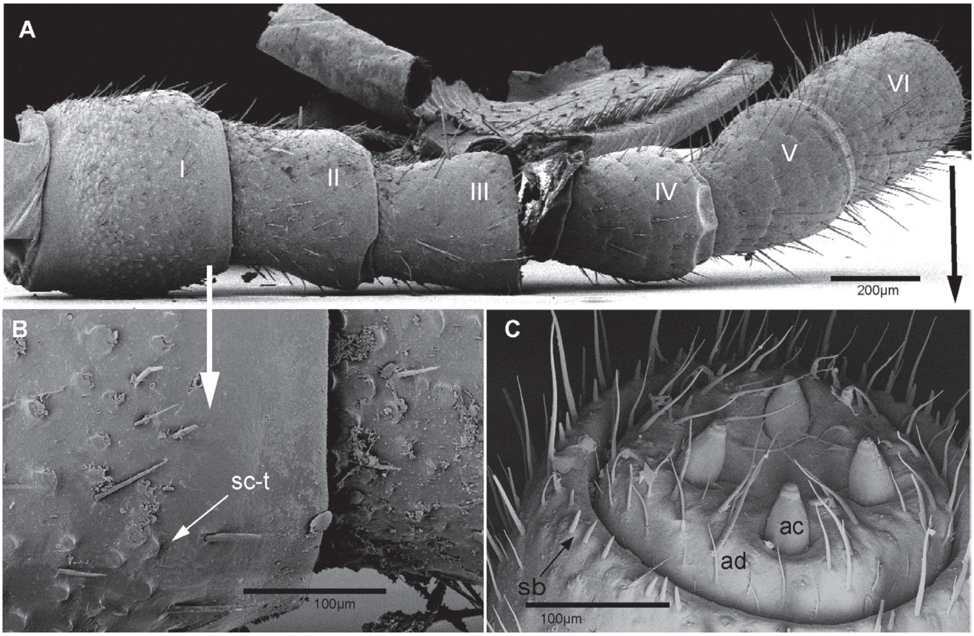

Figure 4. *Zoosphaerium bartolozzii* sp. nov., male holotype, SEM, Right antenna. **A** lateral view **B** antennomeres 1 and 2 with sclerotized teeth **C** apical disc with four sensory cones. Abbreviations: ac = apical cone; ad = apical disc; sb = sensilla basiconica; sc-t = sclerotized teeth.

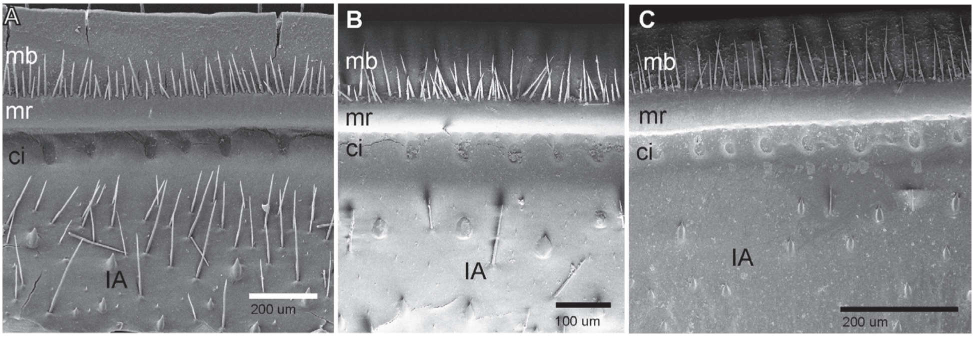

Figure 5. SEM, Endotergum of mid body tergites, ventral view. **A** *Zoosphaerium mangabe* sp. nov., male from Marojejy **B** *Zoosphaerium bartolozzii* sp. nov., male holotype **C** *Zoosphaerium taitii* sp. nov., male holotype. Abbreviations: IA = inner area; ci = cuticular impressions; mr = marginal ridge; mb = marginal bristles.

Immovable finger basally with one spine (Fig. 3E); slender, 3.4 times longer than wide, reaching as far as movable finger, tip curved towards movable finger with a row of small sclerotized spots along apical part of mesal margin. Podomere one glabrous, podomere two in both aspects densely covered with setae, apical part of immovable finger glabrous. Movable finger with few setae in latero-basal part in both aspects (Fig. 3E, F).

Intraspecific variation. Surprisingly, the specimens from Marojejy are in almost all aspects identical to the one studied from Nosy Mangabe. The genetic barcode comes from the female, and was previously published as "*Zoosphaerium* sp. Grey" (Sagorny and Wesener 2017).

Remarks

The following two new species are closely related to *Z. isalo* Wesener, 2009, *Z. bilobum* Wesener, 2009, and *Z. tigrioculatum* Wesener & Bespalova, 2010, of the *Z. coquerelianum* species group. All five species share the presence of a single stridulation rib on the male harp, four apical cones on the antenna, and, uniquely for species of the *Z. coquerelianum* species group, the presence of two instead of a single membranous lobe on the movable finger of the posterior telopod.

Determination key

1 Process of second podomere of anterior telopod not visible in anterior view. Fifth antennomere with field of sensilla basiconica. Collum with isolated, long setae. Endotergum with row of large cuticular impressions and second row of much smaller impressions, bristles long, strongly protruding above tergite .... ***Z. bilobum* Wesener, 2009**

– Process of second podomere of anterior telopod visible in anterior view **2**

2 Podomere three of anterior telopod with crenulated teeth **3**

– Podomere three of anterior telopod without crenulated teeth **4**

3 Collum glabrous with few setae at corners on either side of head. Endotergum with two rows of regularly distributed circular impressions, marginal bristles strongly protruding above tergite. Sensilla basiconica present on antennomere one and two. Anal shield weakly bell shaped ..... ***Z. trigrioculatum* Wesener & Bespalova, 2010**

– Collum glabrous, anterior margin with two rows of setae. Endotergum with single row of elliptical cuticular impression, marginal bristles protruding to margin. Sensilla basiconica absent. Anal shield well rounded........ ***Z. bartolozzii* sp. nov.**

4 Collum glabrous. Endotergum with single row of large cuticular impressions, marginal bristles slightly protruding above tergite. 2nd leg with four or five ventral spines. Anal shield tapering .... ***Z. isalo* Wesener, 2009**

– Collum glabrous. Endotergum with single row of slightly rounded elliptical cuticular impressions, marginal bristle protruding to margin. 2nd leg with six or seven ventral spine. Anal shield well rounded. .... ***Z. taitii* sp. nov.**

Zoosphaerium bartolozzii Anilkumar & Wesener, sp. nov.

http://zoobank.org/15D3E6C0-73DE-4939-B3E3-AEB577711707
Figures 4, 5B, 6, 7

Etymology. Adjective, the species is named after the Italian beetle expert Dr. Luca Bartolozzi who collected this species.

Material examined. 1 ♂ *Holotype* (MZUF), Madagascar: 5 km S di Ambalamanakana, (strada Ambositra – Fianarantsoa) in forests, 20°46'49.2"S, 47°10'48.5"E, n. Mag. 1107. Legit: Bartolozzi, S. Taiti, C. Raharimina, 10 May 1991.

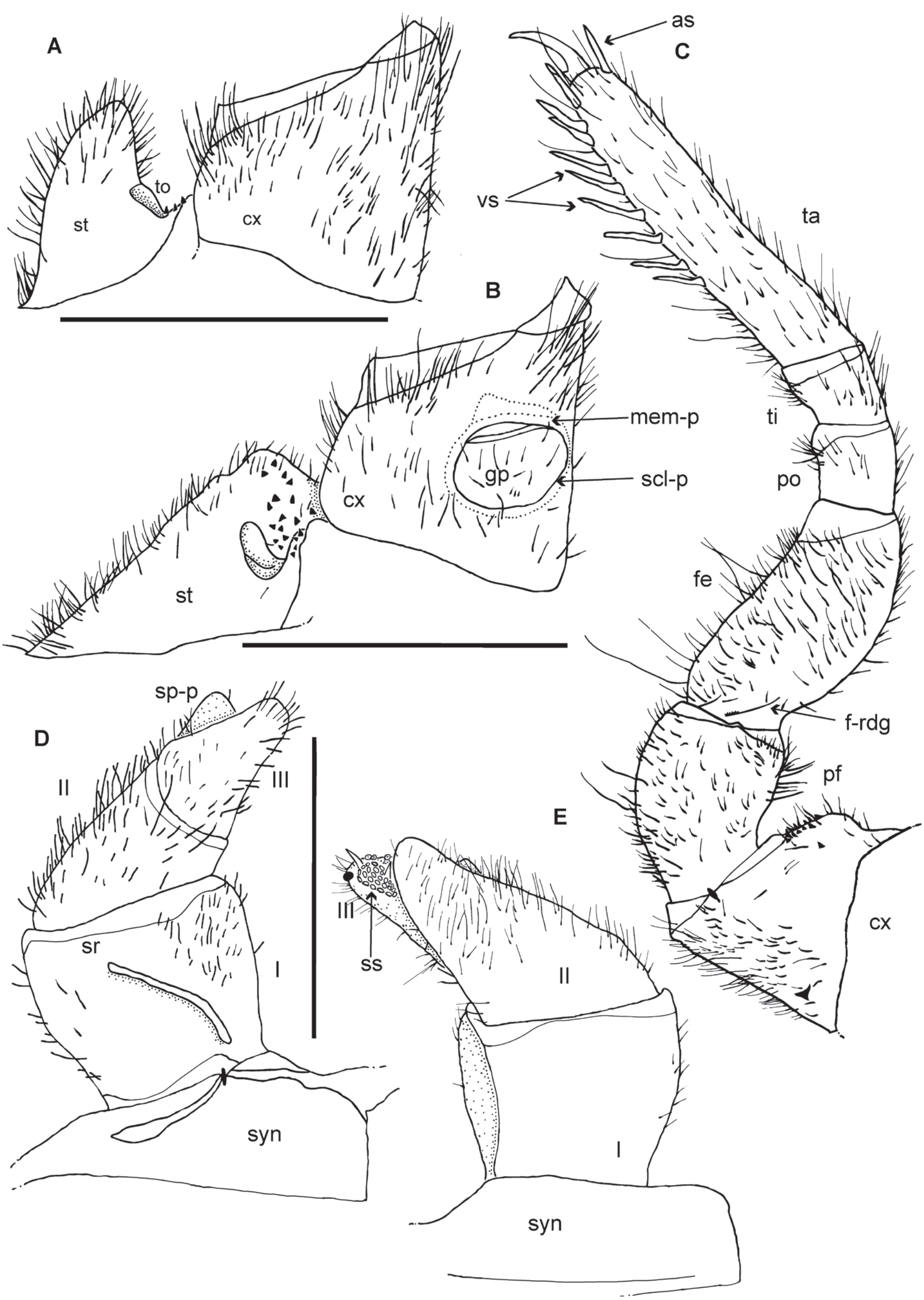

Figure 6. *Zoosphaerium bartolozzii* sp. nov., male holotype. **A**, **B** Coxae of first and second right legs, **D**, **E** Left anterior telopod. **A** first stigmatic plate **B** second stigmatic plate **C** 9th left leg **D** anterior view **E** posterior view. Abbreviations: as = apical spine; cx = coxa; fe = femur; f-rdg = femur ridge; gp = gonopore; mem-p = apical membranous part of plate covering gonopore; pf = prefemur; po = postfemur; scl-p = sclerotized plate; sp-p = second podomere process; sr = stridulation rib; ss = sclerotized spot; st = stigmatic plate; syn = syncoxite; ta = tarsus; ti = tibia; to = tracheal opening. Scale bars: 1 mm.

Diagnosis. *Zoosphaerium bartolozzii* sp. nov. is most similar to *Z. tigrioculatum* due to the presence of three sclerotized crenulated teeth on the podomere three of the anterior telopod, and also in the visibility of the process of the 2nd podomere in anterior view (Figs 6D, 7G). *Zoosphaerium bartolozzii* sp. nov. differs from *Z. tigrioculatum* in the presence of a single row cuticular impression on the endotergum (two rows in the latter), the absence of sensilla basiconica on antennomeres one and two, and the presence of a well-rounded anal shield which is slightly bell-shaped in *Z. tigrioculatum*.

Description (all measurements in mm):

Body length: holotype male: length 24.2, width 11 (2nd = widest), height 6.2 (2nd = highest).

Coloration: Faded due to 27 years of preservation in alcohol. Legs and antennae dark green. Head and collum dark olive-green. Tergites and anal shield faded dark green-brown.

Head: Eyes with 90–100 ommatidia. Antennae long and protruding up to leg pair six. Size of antennomeres 1>2<3=4<5<6 (Fig. 4A). Antennomere 1 broad, antennomeres 1–3 with large rounded protuberant sclerotized teeth (Fig. 4B). Antennomeres 3–6 covered with large setae. Antennomere 6 with a single row of sensilla basiconica surrounding the apical disc, with four apical sensory cones (Fig. 4C).

Gnathochilarium: Lateral stipites and central mentum with long setae, setae absent at center of lamellae linguales. Inner palpi protruding to medial side of gnathochilarium bearing single field of sensory cones. Rudimentary lateral palpi sharing a well-developed base bearing four sensory cones. Hypopharynx with single row of marginal teeth. Central pads apically protruding from lamellae linguales, with a median triangular incision on each pad. Posterior half of underside with single field of large sensory cones interspersed with longer, slimmer structures.

Mandible not dissected.

Stigmatic plates: First stigmatic plate triangular, with marginal setae and some extra setae at elliptical apex, three spines near tracheal opening (Fig. 6A). Second stigmatic plate triangular, with a slightly curved apex. Marginal setae dense at base, 19 spines near tracheal opening (Fig. 6B).

Pleurite: First pleurite with a rounded tip protruding backwards.

Collum: Surface glabrous, anterior margin with two rows of setae. Posterior margin laterally with few isolated setae.

Thoracic shield: Lateral grooves shallow, setae only present in lateral grooves.

Tergites: Surface glabrous and slightly chagrined. Tips of paratergites slightly extending posteriorly.

Endotergum: Inner area with conical spines, broad at base with few setae and numerous small sharp spines in between. Single row of elliptical cuticular impressions. Smooth marginal ridge. Two rows of marginal bristles, majority protruding 1/4–1/2, a few to 3/4 of distance to margin (Fig. 5B).

Anal shield: Large and well rounded, completely covered with tiny setae, underside carrying two locking carinae, second 3.5 times longer than first.

Legs: Leg 1 with three or four, leg 2 with six or seven, leg 3 with seven ventral spines. Legs 1 and 2 without an apical spine. Legs 4–21 with eleven ventral spines and

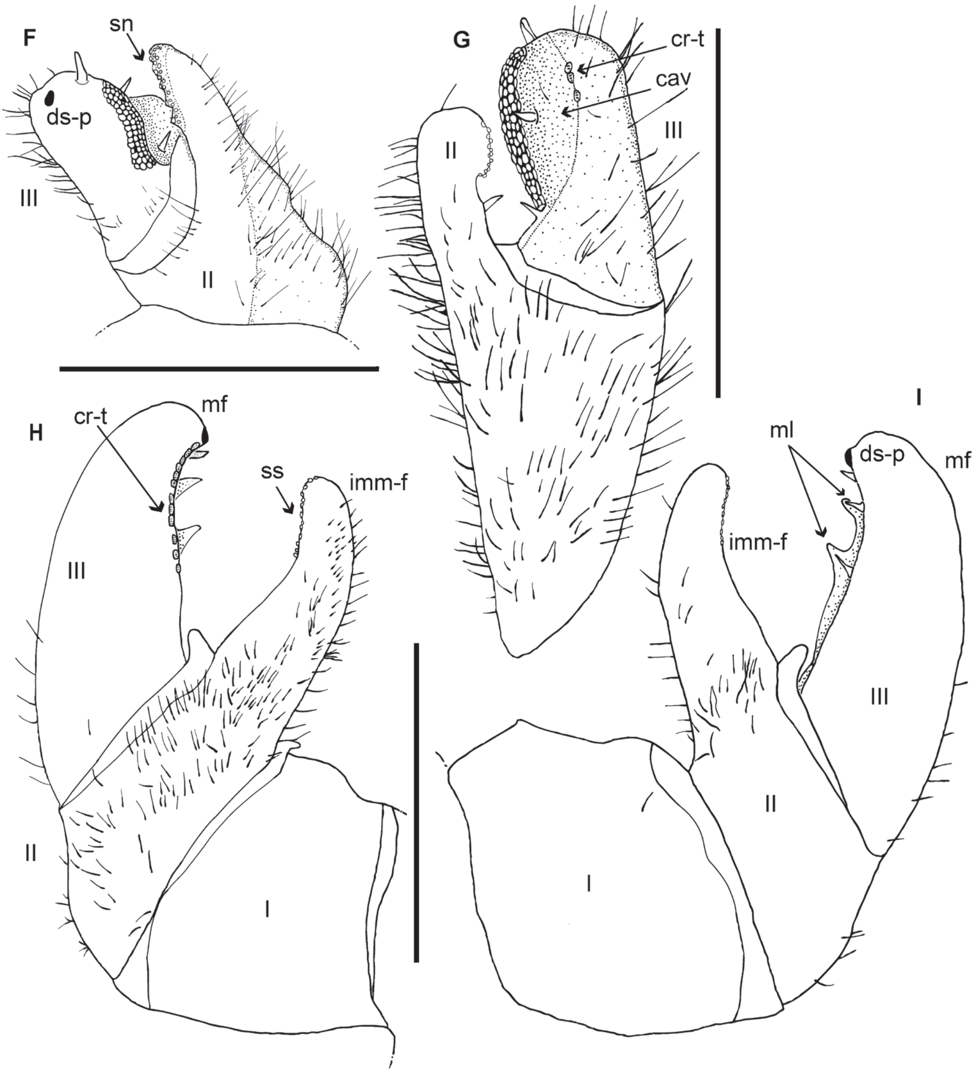

Figure 7. *Zoosphaerium bartolozzii* sp. nov., male holotype. **F**, **G** Left anterior telopod, **H**, **I** posterior telopod. **F** mesal view **G** lateral view **H** posterior view **I** anterior view. Abbreviations: cav = cavity; cr-t = crenulated teeth; ds-p = dark sclerotized spot; imm-f = immovable finger; mf = movable finger; ml = membranous lobes; sn = sclerotized nubs; **ss** = sclerotized spot. Scale bars: 1 mm.

one apical spine (Fig. 6C). In leg 9 femur 1.7, tarsus 5.4 times longer than wide. Coxa with few spines. Femur ridge present. All podomeres covered with setae.

Female unknown.

Male sexual characters: Gonopore rounded, slightly divided near to apex, covered by 1/4 membranous plate apically and 3/4 sclerotized plate basally with few setae. Gonopore covering 1/4 height and 1/2 width of coxa (Fig. 6C).

Anterior telopod: Harp carrying one stridulation rib. Podomere 1 with few marginal and apical setae (Fig. 6D), and a shallow mesal cavity laterally (Fig. 6E). Podomere 2, process visible in anterior view, reaching 2/3rd of length of podomere 3 (Fig. 6D). Podomere 2 process slightly slender apically, with sclerotized nubs along apical-mesal margin and a basal spine present below field of spots (Fig. 7F, G). Podomere 3 apically wide, visible as small triangular lobe in anterior aspect (Fig. 6D), with one dark sclerotized spot near apical margin (Figs 6E, 7F) and a broad mesal cavity with sclerotized spots running along apical-basal margin, with four spines and three sclerotized crenulated teeth at meso-apical margin of cavity (Fig. 7F, G). Two spines merged at apical margin above field of spots, one at center of cavity with tip protruding to sclerotized spots, one basal spine below field of spots. Podomeres 2 and 3 covered with setae (Fig. 7F, G).

Posterior telopod: Movable finger thicker (2.5 times longer than wide) and slightly longer than immovable finger, carrying one spine just below dark sclerotized spot along apical margin (Fig. 7H). Hollowed-out margin with two membranous lobes, each with one marginal spine centrally (Fig. 7I). 12 sclerotized crenulated teeth present marginally. Six teeth apically positioned together, three at center of margin (between two membranous lobes), and last three separated by a short distance, two directly at base and one near base of posterior membranous lobe (Fig. 7H). Movable finger with few basal marginal setae. Tips of podomeres 2 and 3 slightly curved towards one another. Immovable finger slender (3.2 times longer than wide) with sclerotized spots running from apical to mid margin. Immovable finger covered with setae in posterior aspect, one membranous lobe present between podomeres 2 and 3. Podomere 1 large, rectangular with no setae in anterior or posterior aspect (Fig. 7H, I).

Zoosphaerium taitii **Anilkumar & Wesener, sp. nov.**

http://zoobank.org/DA735EC5-8612-4C13-A42E-910718F6ED4C
Figures 5C, 8–10

Etymology. Adjective, the species is named after the land isopod expert Dr. Stefano Taiti who collected this species.

Material examined. 1 ♂ *Holotype* (MZUF), Madagascar: SW 17 km Edi Sakaraha, forêt de Zombitsy, foresta secca, 22°52'47.1'' S, 44°36'41.1'' E, n. Mag. 1107. Legit: Bartolozzi, S. Taiti, C. Raharimina, 15 May 1991.

Other material. 1 ♂, **CAS BLF Mei-99 Ma-14**, Province Toliara, Zombitse Nature Reserve, 16 km E Sakaraha, 825 m, tropical forest on sand, 22.88231°S, 44.70062°E, coll. E. L. Schlinger, M. E. Irwin, 15–18 Dec 1999.

Diagnosis. *Zoosphaerium taitii* sp. nov. is mostly similar to *Z. isalo*, both differing from all other species in the anterior telopod where sclerotized teeth are absent on the third podomere. *Zoosphaerium taitii* sp. nov. differs from *Z. isalo* in the shorter marginal bristles of the endotergum (protruding above the tergite margin in *Z. isalo*), the higher number of ventral spines on leg 2 (four or five versus six or seven) and the slightly differently shaped anal shield (tapering in *Z. isalo*, well-rounded in *Z. taitii* sp. nov.).

Description (all measurements in mm):

Body length: holotype male: length 20.4, width 9.4 (2nd) up to 9.9 (tergite 9 = widest), height 5.4 (2nd = highest).

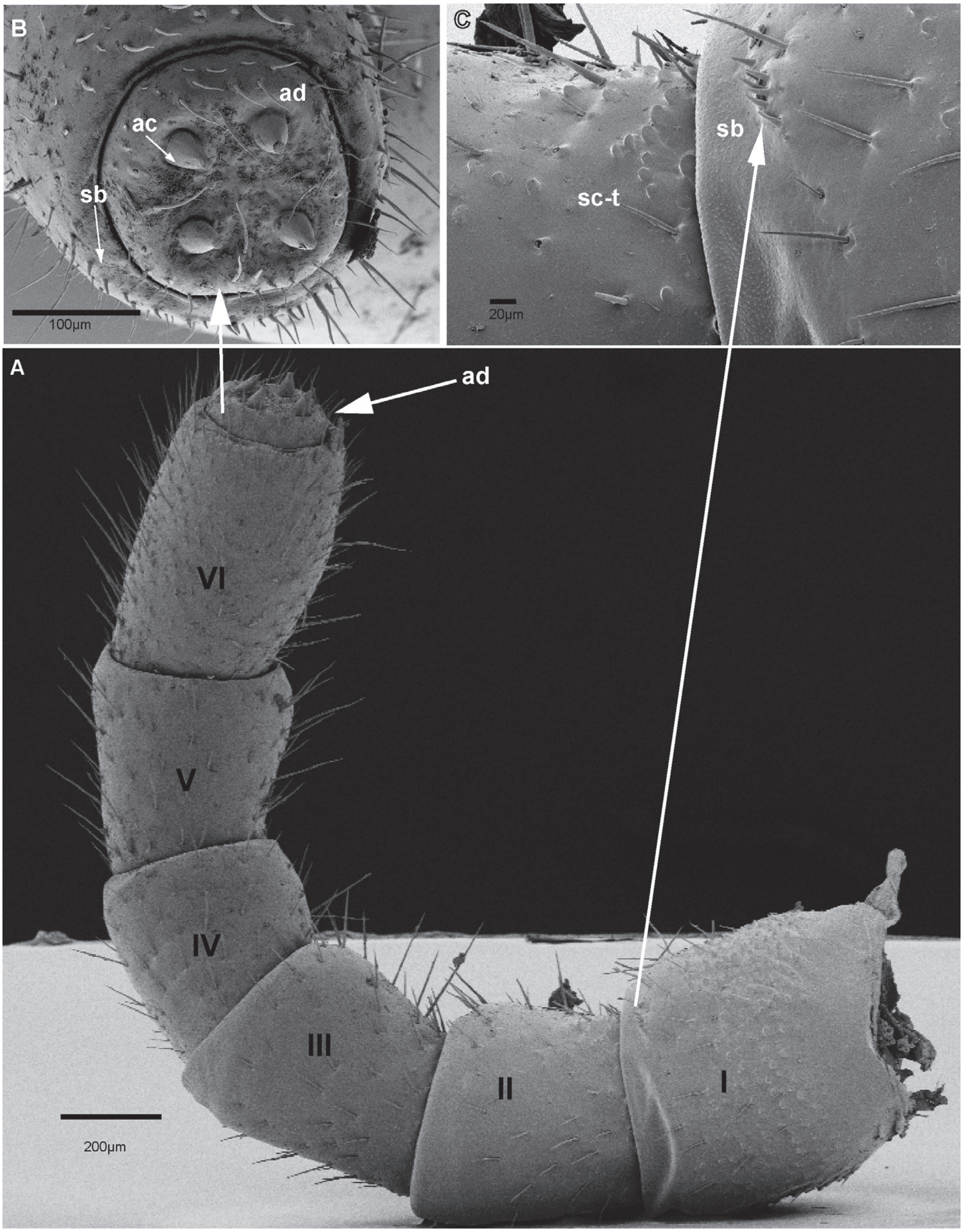

Figure 8. *Zoosphaerium taitii* sp. nov., male holotype, SEM, Right antenna. **A** lateral view **B** antennomeres 1 and 2 with sclerotized teeth **C** apical disc with four sensory cones. Abbreviations: ac = apical cone; ad = apical disc; sb = sensilla basiconica; sc-t = sclerotized teeth.

Coloration: Strongly faded due to exposure to alcohol. Antennae dark green. Legs basally brown and apically green. Head and collum light green. Tergites and anal shield faded light brown.

Head: Eyes with 60–70 ommatidia. Antennae short, protruding up to leg 3 or 4. Size of antennomeres 1>2<3>4<5<6 (Fig. 8A). Antennomeres 1–3 with sclerotized teeth. Antennomeres 1 and 6 with a single row of sensilla basiconica (Fig. 8B, C). Antennomeres 3–6 with long setae. Antennomere 6 with an apical disc containing four apical sensory cones (Fig. 8B).

Gnathochilarium: Stipites and central mentum with long setae, setae absent at center of lamellae linguales. Inner palpi protruding to medial side of gnathochilarium, bearing single field of sensory cones. Rudimentary lateral palpi sharing a well-developed base bearing four sensory cones. Hypopharynx with one row of marginal teeth. Central pads apically protruding from lamellae linguales, with a median triangular incision on each pad. Posterior half of underside with single field of large sensory cones interspersed with longer, slimmer structures.

Mandible not dissected.

Stigmatic plates: First stigmatic plate apically elliptical with marginal setae, lateral end pointed (Fig. 9A). Second stigmatic plate trapezoidal with nine spines near tracheal opening, covered with tiny setae inside and few long marginal setae (Fig. 9B).

Pleurite: First pleurite weakly extending posteriorly with a well-rounded tip.

Collum: Glabrous, anterior and posterior margin with sparse rows of isolated setae.

Thoracic shield: Glabrous expect for narrow lateral grooves.

Tergites: Surface glabrous and shiny, chagrined. Paratergite tips not projecting.

Endotergum: Inner area with narrow conical spines, very few isolated setae. A single row of rounded-elliptical cuticular impressions. Broad smooth marginal ridge. Two rows of marginal bristle protruding towards marginal brim, few reaching tip, other few reaching 1/4–3/4 of distance to margin (Fig. 5C).

Anal shield: Large and well rounded, surface glabrous. Two locking carinae, second carina 2.3 times longer than first, close to anal shield margin.

Legs: Leg 1 with four or five spines, leg 2 with six or seven spines, leg 3 with seven or eight ventral spines and an apical spine, legs 4–21 with nine ventral spines and one apical spine. In leg 9 femur 2.0, tarsus 4.7 times longer than wide. Uniform distribution of setae on all podomeres. Prefemur and femur with few long setae. Femur ridge length reaching 1/4 of femur length (Fig. 9C).

Female unknown.

Male sexual characters: Gonopore slightly oval, rounded apically, divided, reaching 1/2 length and 1/4 width of coxa, covered by 1/4 semicircular membranous plate apically and 3/4 sclerotized plate basally with few setae (Fig. 9B).

Anterior telopod: Harp carrying one stridulation rib positioned medially with one end pointing laterad. Podomere 1 broad with marginal setae, few setae above stridulation rib (Fig. 9D) and a shallow mesal cavity laterally (Fig. 9E). Podomere 2, process visible in anterior view, reaching 2/3rd of length of podomere 3 (Fig. 9D), with sclerotized nubs along apical-mesal margin and one basal spine present below field of spots (Fig. 9F). Podomere 3 apically broad, rounded, longer than podomere 2 (Figs 9F, 10G), and carrying one dark sclerotized spot at apical tip (Fig. 9F). Field of sclerotized spots run along apical-basal margin with four spines out of six visible (Figs 9F, 10G). Three spines positioned at apical margin above field of spots, one in middle of cavity

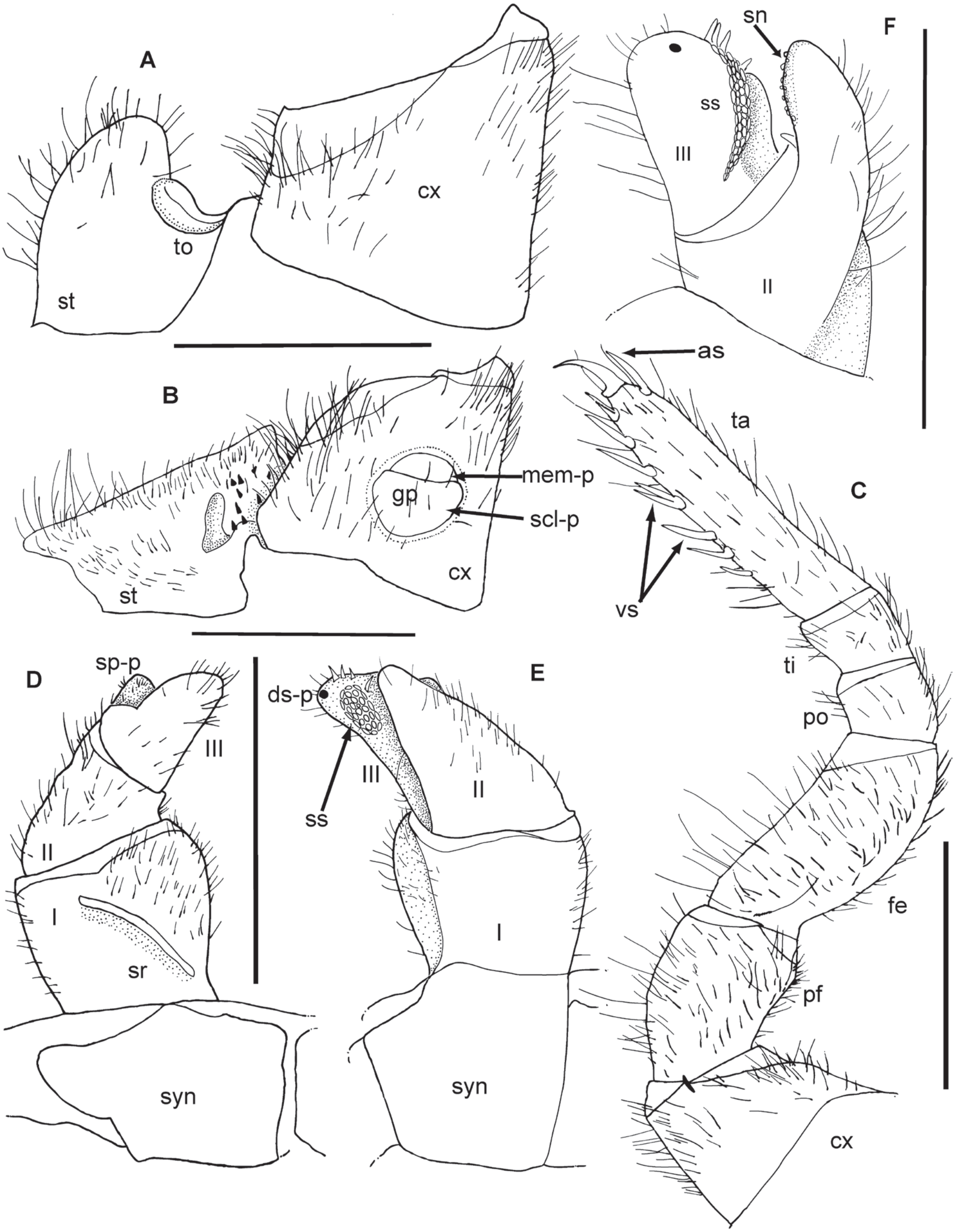

Figure 9. *Zoosphaerium taitii* sp. nov., male holotype. **A**, **B** Coxae of first and second right legs, **D**–**F** Left anterior telopod. **A** first stigmatic plate **B** second stigmatic plate **C** 9th left leg **D** anterior view **E** posterior view **F** mesal view. Abbreviations: as = apical spine; cx = coxa; ds-p = dark sclerotized spot; fe = femur; f-rdg = femur ridge; gp = gonopore; mem-p = apical membranous part of plate covering gonopore; pf = prefemur; po = postfemur; scl-p = sclerotized plate; sp-p = second podomere process; sr = stridulation rib; ss = sclerotized spot; st = stigmatic plate; syn = syncoxite; ta = tarsus; ti = tibia; to = tracheal opening. Scale bars: 1 mm.

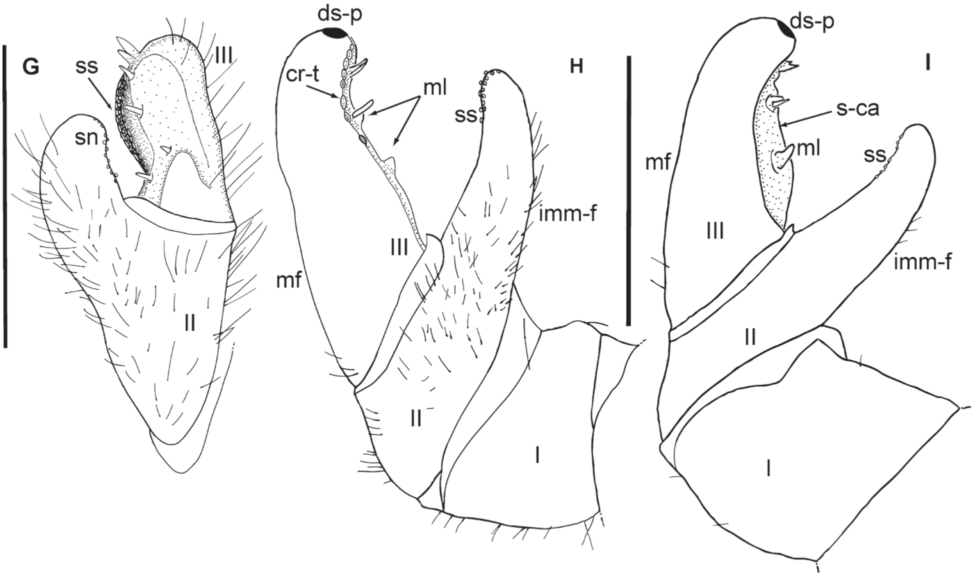

Figure 10. *Zoosphaerium taitii* sp. nov., male holotype, left anterior telopod. **G** lateral view. **H**, **I** Left posterior telopod. **H** posterior view **I** anterior view. Abbreviations: cr-t = crenulated teeth; ds-p = dark sclerotized spot; imm-f = immovable finger; mf = movable finger; ml = membranous lobes; s-ca = shallow cavity sn = sclerotized nubs; ss = sclerotized spot. Scale bars: 1 mm.

with tip protruding to sclerotized spot, one small single spine in lateral projected area slightly towards base, and one spine at base of field of spots (Fig. 10G). Podomeres 2 and 3 covered with setae except mesally (Fig. 10G).

Posterior telopod: Movable finger 2.5 times longer than wide with tip slightly curving towards immovable finger. Apical tip with a dark sclerotized spot, eight sclerotized crenulated teeth (arranged in three groups), three mesal spines (two merged at tip), with very few setae at base and a shallow mesal cavity with two membranous lobes (Fig. 10H, I). First five teeth positioned below apically merged spines, other two teeth below middle spine, located in middle of first membranous lobe, two isolated single tooth located between both membranous lobes (Fig. 10H). Immovable finger 4.3 times longer than wide, reaching 3/4th of length of movable finger, slender, tip curved towards movable finger with a row of small sclerotized spots along 1/4 apical mesal margin, covered with setae in posterior aspect (Fig. 10H). Podomere 1 glabrous except for very few marginal setae.

Remarks. This species was described as a population of *Z. isalo* in a previous study, already with a remark that the status of the population should be evaluated when more male specimens become available (Wesener 2009). With the additional male specimen available from the collections of the "La Specola" Museum, we feel more confident in describing the Zombitse specimens as a species separate from *Z. isalo*. The species lives in sympatry with *Z. album* Wesener, 2009, a species belonging to a different species group (Wesener 2016).

Table 2. Comparison of *Z. isalo* Wesener, 2009, *Z. bilobum* Wesener, 2009, *Z. tigrioculatum* Wesener & Bespalova, 2010, *Z. bartolozzii* sp. nov., and *Z. taitii* sp. nov. Abbreviations: ANT – Antenna; aT – anterior telopod, bas – basiconica, Endo – endotergum. Modified after Wesener et al. 2010b.

Character	*Z. isalo*	*Z. bilobum*	*Z. tigrioculatum*	*Z. bartolozzii* sp. nov.	*Z. taitii* sp. nov.
Shape of anal shield	Tapering	Tapering	Weakly bell shaped	Well rounded	Well rounded
Locking carinae	2nd 3×1st	2nd 2.5×1st	2nd 4×1st	2nd 3.5 ×1st	2nd 2.3× 1st
1st leg no. of ventral spines	3 or 4	6 or 7	4 or 5	3 or 4	4 or 5
2nd leg no. of ventral spines	4 or 5	8 or 9	6 or 7	6 or 7	6 or 7
aT, 2nd podomere in av	visible	Not visible	visible	visible	visible
aT, 3rd podomere in av	without crenulated teeth	without crenulated teeth	with crenulated teeth	with crenulated teeth	without crenulated teeth
ANT, sclerotized teeth	on antennomeres 1-4	on antennomeres 1-5	on antennomeres 1-3	on antennomeres 1-3	on antennomeres 1-3
ANT, sensilla bas.	only on 1st	only on 1st and 5th	on 1st and 2nd	absent	only on 1st
Endo, marginal bristle	protruding slightly above margin	extending beyond margin	extending beyond	protruding to margin	protruding to margin
Endo, cuticular patterns	single row	two rows	two rows	single row	single row

New locality data

Order Polyxenida

Polyxenidae sp.

1; **Fi-xx**; Col des Tapia, fra Ambositra e Antsirabe, 1400 m, foresta di Tapia (Uapaca bojeri), 9 May 1991.

Order Sphaerotheriida

Zoosphaerium neptunus (Butler, 1872)

7 immatures; **Fi-19B**; Perinet, 29 May 1991 (foresta pluviale).

Remarks: This species is known to show swarming behavior near Perinet/Andasibe (Wesener and Schütte 2010).

Zoosphaerium villosum Wesener & Sierwald, 2005

1 M, 2 F; **Fi-01A**; Madagascar, Stat. For. Tampolo, 10 km N. Fenerive, foresta costiera, 1 Jun 1991.

Zoosphaerium blandum (de Saussure & Zehntner, 1897)

2 F; **Fi-03A**; Andohahela pII, foresta secca, 26 May 1991.

Zoosphaerium cf. *pseudoblandum* Wesener, 2009

2 F; **Fi-06B**; Andohahela pI, versante E, NW Ft. Dauphin, ca. 300 m, foresta pluviale, lettiera vagliata, 24-26 May 1991. 4 immatures; **Fi-24F**; RNI Andohahela, pI, versante E, ca. 300 m, lettiera vagliata, 24-26 May 1991.

Zoosphaerium cf. *aureum* Wesener, 2009

Juveniles; **Fi-Mag1058**; Mt d'Ambre, 1000-1200 m, 24 Sep 1989.

Zoosphaerium cf. *album* Wesener, 2009

2 F; **Fi-08A**; 17 km E. Sakaraha, Zombitsy, 15 May 1991.

Sphaeromimus musicus (de Saussure & Zehntner, 1897)

2 M; **Fi-02**; Ifaty, 20 km N. di Tulear, sotto corteccia, 16 May 1991.

Remarks: The following three species are distinct from any described ones, but cannot be formally named because no mature males are known.

Zoosphaerium sp. 1

2 F, 2 immatures; **Fi Mag 1058**; Tsaramandroso, Ankarafantsika, 13 Sept 1989.

Zoosphaerium sp. 2

2 F, 2 immatures; **Fi-05A**; PN Ranomafana, foresta, 11 May1991. 1 F; **Fi-X**; Ranomafana, NE Fianarantsoa, 950-1100 m, ettiera e sotto tranchi, 11-12 May 1991. 1 immature M; **Fi-Y**; Ranomafana, foresta secondaria, 1100 m, 12 May 1991.

Zoosphaerium sp. 3
1 F; **Fi-xx**; Mt d'Ambre, 1000 m, 23 Sept 1989.

Zoosphaerium spp.
Juveniles; **Fi-07D**; Andohahela pI, versante E, NW Ft. Dauphin, ca. 300 m, foresta pluviale, lettiera vagliata, 24-26 May 1991. 2 immatures; **Fi-xx**. Mt. d'Ambre 1000 m, 25 Sept 1989. 7 immatures; **Fi-29A**; Mt. d'Ambre 1100 m, 25 Sept 1989. 5 immatures; **Fi-11A**; Andohahela, pI, 500-600 m, foresta lettiera vagliata, 25 May 1991. 3 immatures; **Fi-14B**; Mahavelona (= Foulpointe), N. die Tamatave, foresta litorale, lettiera vagliata, 31 May 1991. 2 immatures; **Fi-xx**; Marojejy 1200 m, 28 Sept1989. 5 immatures; **Fi-32C**; Perinet, 1000 m, 8 Oct1989. 2 immatures F; **Fi-20A**; Manjakatompo, c/o station Pisciculture, 1700 m, 5 Oct1989. 1 immature; **Fi-31A**; 7 km NE di Ankaramena, SW di Ambalavao, boschetto di manghi lungo un torrente, 13 May1991. 5 immatures; **Fi-37D**; Montagne d'Andrangoatra (a N. diSambava), 29 Sept1989.

Order Polyzoniida
Rhinotus purpureus (Pocock, 1894)
6?; **Fi-35B**; Ranomafana, sotto cortecce di alteri morti, giardini, 12 May1991. 3?; **Fi-17D**; Nosy Be, spioggia Ambatoloaka, 15. Sept1989. 5?; **Fi-25B**; Nosy Be, c/o Cascata, 18 Sept1989. 5?; **Fi-23A**; Tampolo, foresta costiera. 12?; **Fi-15B**; Mahavelona (=Foulpointe), N. die Tamatave, foresta litorale, lettiera vagliata, 31 May1991. 4?; **Fi-18B**; Valle del Sambirano, 10 km SE Ambanja, 21 Sept1989. 1?; **Fi-32D**; Perinet, 1000 m, 8 Oct1989.
Remarks: This introduced species is very common in humid forests on Madagascar. Potential indigenous species of other siphonotid genera also exist, but are rare and unnamed (Wesener 2014a).

Order Siphonophorida
Siphonorhinus sp.
1?; **Fi-19E**; Perinet, 29 May1991 (foresta pluviale).
Remarks: Specimens of this order were previously known from 18 humid forest sites on Madagascar; none of the species has been named (Wesener 2014b).

Order Chordeumatida
Betscheuma spp.
1 M; **Fi-04C**; 5 km S. di Ambalamanakana (strada Ambositra-Fianarantsoa), in foresta, coll. 10 May1991. 1 F; **Fi-24D**; RNI Andohahela, pI, versante E, ca. 300 m, lettiera vagliata, 24-26 May1991. 1 M, 1 F; **Fi-14A**; Mahavelona (=Foulpointe), N. die Tamatave, foresta litorale, lettiera vagliata, 31 May1991. 2 M; **Fi-16B**; Mahavelona (= Foulpointe), N. die Tamatave, foresta litorale, lettiera vagliata, 31May1991. 4 M; **Fi-32B**; Perinet, 1000 m, 8 Oct1989. 2 larvae; **Fi-28D**; Is. Sainte Marie, foreste di Kalalao, 3 Oct1989. 3 larvae; **Fi-xx**; Manjakaptompo, 2000 m, 6 Oct1989.

Remarks: Representatives of the Chordeumatida, a group absent from sub-Saharan Africa, were first recorded from Madagascar in the 1990s (Mauriès 1994; 1998). Currently, only species of the genus *Betscheuma* Mauriès, 1994 is known from the island. The endemic genus *Betscheuma* Mauriès, 1994 is closely related to Indian taxa (Enghoff et al. 2015).

Order Polydesmida

Remarks: Numerous specimens are females or larvae and could not be determined; therefore, only species which could be determined at least to genus are listed.

Family Dalodesmidae

Dalodesmus spp.

1 F; **Fi-30A**; Mt d'Ambre 900 m, c/o grande cascade, 26 Sept1989. 1 M; **Fi-24E**; RNI Andohahela, pI, versante E, ca. 300 m, lettiera vagliata, 24-26 May1991. 1 M, 1 F; **Fi-zz**; Grotta di Anjohibe, 12 Sept1989. 1 M, 1 F; **Fi-zz**; Grotta di Anjohibe, 12 Sept1989. 5 juveniles; **Fi-37B**; Montagne d'Andrangoatra (a N. diSambava), 29 Sept1989.

Remarks: *Dalodesmus* Cook, 1896 species are the only Polydesmida (except for *Phymatodesmus*) which are indigenous to the island (Enghoff 2003). The remaining Polydesmida fauna constitutes introduced taxa.

Family Paradoxosomatidae

Oxidus gracilis (Koch, 1847)

> 30?; **Fi-33A**; Ranomafana, NE Fianarantsoa, foresta, 11May1991. 3 immatures; **Fi-35C**; Ranomafana, sotto cortecce di alteri morti, giardini, 12 May1991. > 5?; **Fi-12B**; Nosy Be, foresta di Lokobe, 16 Sept1989. 5 ♂ & F; **Fi-17C**; Nosy Be, spioggia Ambatoloaka, 15 Sept1989. 5?; **Fi-18A**; Valle del Sambirano, 10 km SE Ambanja, 21Sept1989. 30?; **Fi-32A**; Perinet, 1000 m, 8 Oct1989. 4?; **Fi-20B**; Manjakatompo, c/o station Pisciculture, 1700 m, 5 Oct1989. >5; **Fi-x1**; Antananarivo, Parco Tsimbazaza, 7 Sept 1989. 1 M; **Fi-27B**; Nosy Komba, spiaggi e dint. 17.Sept 1989. 6?; **Fi-x2**; Antsirabe, in giardini di citta, 9 May 1991.

Orthomorpha coarcata (de Saussure, 1860)

5 F; **Fi-29B**; Mt. d'Ambre 1100 m, 25 Sept 1989.

Chondromorpha xanthotricha (Attems, 1898) **new record for Madagascar**

1 F; **Fi-32F**; Perinet, 1000 m, 8 Oct 1989.

Remarks: All three paradoxosomatids are common tropical tramp species (Shelley and Lehtinen 1998, Likhitrakarn et al. 2017).

Order Spirobolida

Family Spirobolellidae

Hylekobolus andasibensis Wesener, 2009

4 immatures; **Fi-19D**; Perinet, 29 May 1991 (foresta pluviale).

Hylekobolus spp.

3 F, 1 immature; **Fi-05E**; PN Ranomafana, foresta, 11 May 1991.

Family Pseudospirobolellidae

Pseudospirobolellus avernus (Butler, 1872) **new record for Madagascar**

1 M; **Fi-35E**; Ranomafana, sotto cortecce di alteri morti, giardini, 12 May 1991.

Remarks: Tropical tramp, also known from the Comoros (VandenSpiegel and Golovatch 2007) and the Seychelles (Golovatch and Korsós 1992).

Family Pachybolidae

Aphistogoniulus infernalis Wesener, 2009

1 F, 1 immature; **Fi-06A**; Andohahela pI, versante E, NW Ft. Dauphin, ca. 300 m, foresta pluviale, lettiera vagliata, 24-26 May 1991.

Remarks: This locality fits very well in the known distribution of the species (Wesener et al. 2009b, Wesener et al. 2011). This species has been classified as "endangered" in the IUCN Red List (Rudolf and Wesener 2017a).

Ostinobolus rufus Wesener, 2009

1 F; **Fi-07B**; Andohahela pI, versante E, NW Ft. Dauphin, ca. 300 m, foresta pluviale, lettiera vagliata, 24-26 May 1991. 1 F, 1 immature, **Fi-11B**; Andohahela, p1, 500-600 m, foresta lettiera vagliata, 25 May1991; 1 immature M; **Fi-24G;** RNI Andohahela, p1, versante E, ca. 300 m, lettiera vagliata, 24-26 May1991.

Remarks: This species is widespread in SE Madagascar, apparently being present in every humid forest that was sampled (Wesener et al. 2009b). This species is classified as "near threatened" in the IUCN Red List (Rudolf and Wesener 2017b).

Ostinobolus subterraneus Wesener, 2009

1 F; **Fi-09D**; SE Tolagnaro, dint. Spiaggia Libanona, 23 May 1991.

Remarks: This species, only known from lowland forests surrounding Fort Dauphin (Wesener et al. 2009) is currently classified as "critically endangered" in the IUCN Red List (Rudolf and Wesener 2017c). The presence of this species in a habitat slightly modified by humans (although almost 30 years ago) is an indication of a higher resilience than expected of this species to forest removal and human disturbance.

Granitobolus cf. *andohahelensis* Wesener, 2009

1 M, 4?; **Fi-11A**; Andohahela, p1, 500-600 m, foresta lettiera vagliata, 25 May 1991.

Remarks: This species has already been recorded from the area, albeit at higher elevations (Wesener et al. 2009a). The species is listed as "near threatened" in the IUCN Red List (Rudolf and Wesener 2017d).

Granitobolus spp.

1 F; **Fi-07E**; Andohahela pI, versante E, NW Ft. Dauphin, ca. 300 m, foresta pluviale, lettiera vagliata, 24-26 May 1991. 1 immature male; **Fi-22A**; dint Evatra, 25 km NE Fort Dauphin, foresta litorale, 23 May 1991.

Riotintobolus spp.

1 F; **Fi-09B**; SE Tolagnaro, dint. Spiaggia Libanona, 23 May 1991. 1 M, 1 immature; **Fi-10A**; Andohahela, 6-12Jun-Dec 1991, leg B. Randriamampionona.

Trigoniulus corallinus (Gervais, 1847)

1 F; **Fi-17B**; Nosy Be, spioggia Ambatoloaka, 15 Sept 1989.

Remarks: Widespread tropical tramp (Shelley and Lehtinen 1999).

Dactylobolus bivirgatus (Karsch, 1881)

1 F; **Fi-17A**; Nosy Be, spioggia Ambatoloaka, 15 Sept 1989. MK & F; **Fi-x3**; Sambava, 29 Sept 1989.

Remarks: The only indigenous Malagasy Spirobolida that is not a strict endemic to Madagascar. Also occurs in the Comoros (Rollard and Golovatch 2012) and Seychelles (Golovatch and Korsós 1992). On Madagascar only known from humid forests in coastal areas in the northern half of the island.

Order Spirostreptida

Remarks: Numerous specimens are females or larvae and could not be determined; therefore, only species which could be determined are listed.

Suborder Cambalidea

Glyphiulus granulatus (Gervais, 1847) **new record**

2 M; **Fi-25A**; Nosy Be, c/o Cascata, 18 Sept 1989.

Remarks: This is a tropical tramp species, already recorded from the Comoros (VandenSpiegel and Golovatch 2007) and Seychelles Islands (Golovatch and Korsós 1992).

Cambalidea indet. cf. Iulomorphinae.

1 M, 5 F; **Fi-33B**; Ranomafana, foresta, 11 May 1991. 1 M, 5?; **Fi-34A**; Vohiparara, 13 km W. die Ranomafana, foresta secondaria, 10 May 1991. 2 M, 11 F; **Fi-07F**; Andohahela pI, versante E, NW Ft. Dauphin, ca. 300 m, foresta pluviale, lettiera vagliata, 24-26 May 1991. 1 M, 5?; **Fi-09C**; SE Tolagnaro, dint. Spiaggia Libanona, 23 May .1991. 12?; **Fi-11A**; Andohahela, pI, 500-600 m, foresta lettiera vagliata, 25 May 1991. 9?; **Fi-24C**; RNI Andohahela, pI, versante E, ca. 300 m, lettiera vagliata, 24-26 May 1991. 2 M; **Fi-14A**; Mahavelona (=Foulpointe), N. die Tamatave, foresta litorale, lettiera vagliata, 31May 1991. 8?; **Fi-13B**; Tampolo, 10 km N. Fenerive, foresta, lettiera, 1Jun 1991. 1?; **Fi-22A**; dint Evatra, 25 km NE Fort Dauphin, foresta litorale, 23 May 1991. 2?; **Fi-36B**; S. fra Ampanihy e Beloha, ca. 20 km d. Beloha, boscaglia, 22 May 1991.

Remarks: Undetermined Iulomorphine specimens, already mentioned previously (Enghoff 2003), seem to be widespread on Madagascar. The occurrence in disturbed habitats, often alongside introduced tropical tramp species, suggest that they may belong to one (or more?) introduced species.

Suborder Spirostreptidea, family Spirostreptidae

Eumekius antimena (de Saussure & Zehntner, 1901)
1 M; **Fi-12A**; Nosy Be, foresta di Lokobe, 16.ix.1989. 3 M; **Fi-27A**; Nosy Komba, spiaggi e dint. 17 Sept 1989.

Discussion

Relationships and biogeography of the newly described species

Zoosphaerium mangabe sp. nov. shows an unusual distributed pattern, linking lowland rainforest of the island Nosy Mangabe to the nearby mountain forest of Marojejy. The close link (9.9% p-distance in the COI) of *Z. mangabe* sp. nov. to the morphologically very different (Sagorny and Wesener 2017) *Z. minutus* from northern Madagascar is surprising.

Zoosphaerium bartolozzii sp. nov. seems most closely related to *Z. tigrioculatum* based on morphological characters such as the presence of three sclerotized crenulated teeth on podomere 3 of the anterior telopod. Both species were collected from the humid evergreen forests present in the south-east of Madagascar, at specific small microclimatic refugees. *Zoosphaerium taitii* sp. nov. seems more similar to *Z. isalo* due to the absence of sclerotized crenulated teeth on podomere 3 of the anterior telopod (Wesener 2009, Wesener et al. 2010a). *Zoosphaerium taitii* sp. nov. was recorded from the Zombitse forest and *Z. isalo* from the Isalo National Park which both lie in the south-west of Madagascar. *Zoosphaerium taitii* sp. nov. occurs in sympatry with *Z. album*, a species belonging to a different species group (Wesener 2016).

Notes on introduced species

Among the Diplopoda collection of the museum "La Specola" from Madagascar, 30% of the specimens represent introduced species. They belong to four orders: Polyzoniida, Polydesmida, Spirobolida, and Spirostreptida.

Order Polyzoniida: *Rhinotus purpureus* is a worldwide introduced species (see Peck and Shear 2000, Shelley and Golovatch 2011), native to Central America and Caribbean islands (Golovatch and Korsós 1992). In Madagascar, they have actively conquered the majority of the vegetated land areas except dry ecosystems (Wesener 2014a).

Order Polydesmida: So far eleven species have been recorded from Madagascar, of which only the seven members of the genus *Dalodesmus* and the single species of *Phymatodesmus* are indigenous, while four are introduced species (Enghoff 2003). Among the collections of the Museum “La Specola” there were three of the introduced species, of which two are common tramps *Oxidus gracilis* and *Orthomorpha coarcata* (see Stoev 2004, Kime and Enghoff 2012, Rollard and Golovatch 2012, Jovanović et al. 2016, Nguyen et al. 2017). The third species, *Chondromorpha xanthotricha* is also a common tropical tramp (Likhitrakarn et al. 2017), but this is the first record for Madagascar.

Order Spirobolida: Madagascar hosts the highest diversity of Spirobolida in the world, with a good degree of endemism (15 endemic genera, Wesener et al. 2009, Wesener 2011). Aside from the previously recorded *Trigoniulus corallinus*, a widespread tramp (see Shelley 1998, Korsós 2004, Shelley et al. 2006), one other common Spirobolida tramp species is recorded for the first time from Madagascar, *Pseudospirobolellus avernus*, as is the spirostreptid *Glyphiulus granulatus*.

Impact of introduced species

The seven tropical tramp species found in the collections of the Museum "La Specola" have been introduced on this island by human activity. Millipedes are often introduced along with soil or plants (Decker and Tertilt 2012). The previously known tramp species are widespread on Madagascar (Enghoff 2003, Wesener 2014a) and along with the three new records, they account for > 25% of the millipede collection of the Museum "La Specola", which clearly demonstrates human influence on this island. These seven tramp species are recorded worldwide as introduced species. Studies have suggested that introduced species may have chances to replace the indigenous species existing in that region (Shelley and Golovatch 2011, Wesener 2014a). In addition to the continuous deforestation, the widespread presence of these introduced millipede species could be an understudied but severe threat to the endemic and unique millipede fauna of Madagascar.

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Some new or poorly-known Zephroniidae (Diplopoda, Sphaerotheriida) from Vietnam

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Abstract

Three new species of the giant pill-millipede family Zephroniidae are described from southern Vietnam: *Sphaerobelum pumatense* **sp. nov.**, *Sphaeropoeus honbaensis* **sp. nov.** and *Sphaeropoeus bidoupensis* **sp. nov.** Two species, *Sphaerobelum bicorne* Attems, 1938 and *Sphaeropoeus maculatus* (Verhoeff, 1924), are redescribed, the former from new material, the latter from type material with lectotype designation. A new transfer is proposed: *Zephronia manca* Attems, 1936, to the genus *Sphaeropoeus* Brandt, 1833, giving the new combination, *Sphaeropoeus manca* (Attems, 1936) **comb. nov.**

Keywords

biological observations, giant pill-millipede, *Sphaerobelum*, *Sphaeropoeus*, taxonomy

Introduction

The giant pill-millipede fauna (order Sphaerotheriida) of Southeast Asia is dominated by members of the family Zephroniidae (Wesener 2016a). This family is the only one in the order that occurs in Indochina. According to the latest review (Semenyuk et al.

2018), the Vietnamese fauna is particularly rich in zephroniids and currently contains six species of *Sphaerobelum* Verhoeff, 1924, five species of *Zephronia* Gray, 1832, three species of *Prionobelum* Verhoeff, 1924, and one species each in *Cryxus* Leach, 1814 and *Sphaeropoeus* Brandt, 1833.

The present paper puts on record another three new zephroniid species from Vietnam, provides redescriptions of two previously described species, and establishes a new combination.

Material and methods

Collecting, dissecting and drawing

Field work of author IS was conducted in accordance with Agreement 37/HD for the scientific cooperation between the Joint Russian-Vietnamese Tropical Centre and the Bidoup Nui Ba National Park and Hon Ba Nature Reserve, according to Agreement 1700/UBND.VX for the Pu Mat National Park, and to Agreement 308/SNgV-LS for the Song Thanh National Park. The Animal Care and Use Protocol Review No. 1723018 was strictly followed.

Material was collected in the Bidoup Nui Ba National Park during three field trips: 5–16 January, 12–21 June and 22–27 November 2018. The field work in the Hon Ba Nature Reserve was carried out from 23–29 June 2018, that in the Pu Mat National Park from 11–24 April 2018, while that in the Song Thanh National Park was from 23 April to 11 May 2019. Millipedes were obtained in forest or rural habitats by hand-sorting the leaf litter, visual spotting on open places, and through the examination of spaces under logs and stones. Collecting was performed in daylight, as well as at night. Ecological and behavioral data were recorded while collecting. Pictures of living animals were taken with a Panasonic DMC-TZ80 - LUMIX Digital Camera. Animals were preserved in 75% ethanol.

For illustrations, the 9th legs and both anterior and posterior telopods were removed from males with forceps. Female vulvae were dissected from leg-pair 2 on one side of the body (not dissected in one species). Antennae were examined for all species where females were available, and male antennae were illustrated without removing the head. An Olympus SZ61 stereo microscope was used for observation and capturing images for the line drawings; sketches were scanned with a CanoScan Lide 60 scanner and then edited with Corel Photo-Paint X5 software. The terminology of morphological characters follows Wesener and Sierwald (2005) and Wesener (2016a). New specimens, including types, were shared between the collections of the Zoological Museum, State University of Moscow, Russia (**ZMUM**) and the Zoological Research Museum A. Koenig, Bonn, Germany (**ZFMK**), as indicated below. Types of existing species were borrowed and/or used from the collections of the Natural History Museum in Vienna (**NHMW**) and the Hungarian Natural History Museum in Budapest (**NHMB**).

Scanning electron microscopy (SEM)

Left antennae, endoterga and terga were dissected. The samples were cleaned and dehydrated via an ethanol series (2× 96%, 3× 100%) prior to mounting on aluminum SEM stubs. The samples were coated with gold for 240 seconds in a sputter coater. SEM images were then taken using a Supra VR 300VP (Carl Zeiss AG, Oberkochen, Germany) scanning electron microscope utilizing SmartSEM V05.00 software based at the ZFMK. Dry-coated SEM material was then removed after study from the stubs and returned to alcohol. All images were later edited using Adobe Photoshop CS2 and assembled into plates with Adobe Illustrator CS2 (San Jose, USA).

Results

Taxonomy

Class Diplopoda de Blainville in Gervais, 1844
Order Sphaerotheriida Brandt, 1833
Family Zephroniidae Gray in Jones, 1843

Genus *Sphaerobelum* Verhoeff, 1924

See Wesener (2016a) for a recent diagnosis of the species, and Wesener (2019) for a key.

Sphaerobelum bicorne Attems, 1938

Figs 1A–C, 3A, 4A, 5

Sphaerobelum bicorne Attems, 1938: 200; Enghoff et al. 2004: 32 (list); Jeekel 2001: 17 (list); Wongthamwanich et al. 2012: 34 (key); Wesener 2019: 211 (key).

Material examined. 1 ♂, 1 ♀ (ZFMK MYR8860), 2 ♂, 5 ♀, 2 juv. (ZMUM Rd 4636), Vietnam, Quang Nam Prov., Song Thanh National Park, 15°33'N, 107°23'E, 1000 m a.s.l., tropical forest in a narrow river valley, on forest floor (♂) and in leaf litter (♀), daytime, V.2019, I. I. Semenyuk leg. ***Syntypes*** 1 ♂, 1 ♀ (NHMW 2196), Vietnam, South Annam (Tourane = Da Nang), Ba Na Hills, C. Dawydoff leg. Studied only from numerous photographs by author TW.

New diagnosis. *Sphaerobelum bicorne* belongs to the group of congeners in which the mesal margin of the femur is extended into several teeth. *Sphaerobelum bicorne* shares only with *S. bolavensis* Wesener, 2019, from Laos (Wesener 2019), the presence of such an extension in the apical part of the femur, but differs from the latter species in several characters: ♀ operculum projecting into two conspicuous processes (Fig. 5H)

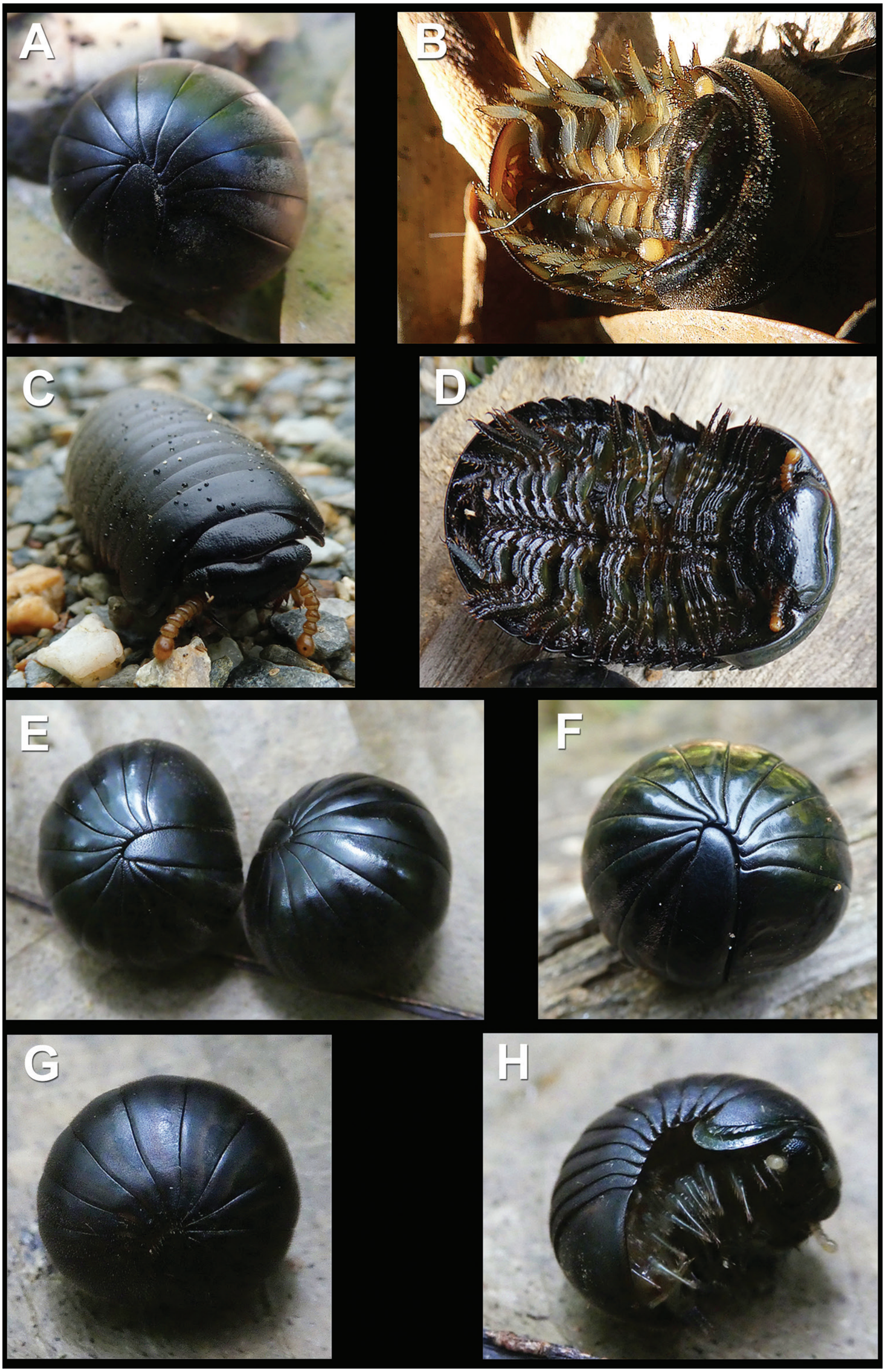

Figure 1. Live *Sphaerobelum pumatense* sp. nov. (**A–C**) and *Sphaerobelum bicorne* Attems, 1938 (**D–H**) in the field **A–C** adult, enrolled, ventral view and walking, respectively **D–F** adults, ventral view, and enrolled, respectively **G, H** juvenile, enrolled and unrolling, respectively. Pictures taken not to scale.

(vs. one process in *S. bolavensis*), telopoditomere 4 of posterior telopod straight, apically with a recessed hook (Fig. 5A, B) (vs. no hook in *S. bolavensis*), and locking carina of anal shield long (vs. short in *S. bolavensis*).

Redescription (mostly based on ZFMK material). ***Body length:*** ♂ length ca. 40.9 mm, width of thoracic shield 21.3 mm, of tergite 8, 21.9 mm (= broadest), height of thoracic shield, 12.1 mm, of tergite 8, 13.3 mm (= highest); ♀ length ca. 42.7 mm, width of thoracic shield, 23.5 mm, of tergite 7, 24.3 mm (= broadest), height of thoracic shield 11.9 mm, of tergite 8, 15.1 mm (= highest). ZMUM adults 18 (♂) to 23 mm wide (♀). ***Coloration:*** both in vivo and in vitro, after several months of preservation in ethanol, uniformly black to blackish, shining. Head and collum also black. Antennae orange, legs in life mainly blackish as well (Fig. 1D–F), but in alcohol dark olive, usually with several basal segments and tarsi or their distal halves orange, only juveniles a little lighter, dark brown to blackish, some with very vague variegated tergal patterns (Fig. 1G, H). ***Head:*** eyes with >70 ocelli. Aberrant ocellus located inside antennal groove. Antennae short (Fig. 5G), with rounded joints, protruding posteriorly to leg-pair 3. All antennomeres densely pubescent, sensilla basiconica surrounding apical disc. Shape of antennae sexually dimorphic, cylindrical in ♀, thickened, apically broadened and slightly flattened in ♂. Apical disc with ca. 74/76 (♂) or 56/51 (♀) apical cones, respectively. Apical cones typical of Diplopoda. Organ of Tömösváry located inside antennal groove. ***Gnathochilarium:*** structure typical of the order. Palpi with sensory cones arranged in clusters. ***Mandibles:*** not dissected. ***Stigmatic plates:*** first stigmatic plate broadly rounded, apex clearly rounded, weakly curved towards coxa 1. ***Laterotergites:*** laterotergite 1 strongly projecting into a well-rounded tip. Laterotergite 2 well-rounded, like following laterotergites. ***Collum:*** with a glabrous surface, margins with few isolated setae. ***Thoracic shield:*** surface glabrous like tergites, setae only in grooves. Shallow grooves beset with numerous long setae, sloping towards groove with 5 or 6 continuous lateral and posterior keels. ***Tergites:*** surface of anterior half of tergites setose, with very small setae and small pits, posterior half of tergite smooth (Fig. 4A). Tips of midbody paratergites projecting posteriorly. ***Endotergum:*** inner section lacking any spines or setae. Middle area with a single row of large, dense, elliptical, cuticular impressions. Distance between impressions shorter than half their diameter. Apically, 3–4 dense rows of long marginal bristles, tips of longest setae clearly protruding beyond tergal margin (Fig. 3A). Bristles not smooth, but with numerous small spinicles. ***Anal shield:*** large, sexually dimorphic: in ♀ well-rounded, in ♂ weakly bell-shaped. Surface in ♀ only in anterior half, in ♂ completely covered with tiny setae. Underside with a single, long, black, locking carina, this being slightly longer than width of last laterotergite, locking carina located close to last laterotergite. ***Legs:*** leg 1 with 4, leg 2 with 5, leg 3 with 6 or 7 ventral spines. First two leg-pairs each without an apical spine. Leg-pairs 4–21 with 7–9 ventral spines and one dorso-apical spine (Fig. 5F). In leg 9, femur 1.7, tarsus 3.8 times longer than wide (Fig. 5F). All podomeres densely setose. Coxa with a large and well-rounded process. Coxa process sharp in legs 1 and 2. Prefemur apico-mesally with a weak projection. Femur in apical part extended mesally into a dentate margin featuring 4–6 teeth. ***Female sexual characters:*** vulva large, covering 2/3 of coxa, extending mesally to anterior half of prefemur (Fig. 5H). Operculum centrally deeply recessed, apical margin projecting into two rounded lobes, 2–3 times as high as remaining operculum (Fig. 5H). Subanal plate well-rounded, almost circular. ***Male sexual characters:*** gonopore covered with a single, undivided, circular, sclerotized plate. ***Anterior telopods*** (Fig. 5C–E): consisting of only 3 telopoditomeres distal to syncoxite, telopoditomeres 3 and 4 partly fused. Telopoditomere 1 cylindrical, slightly longer than wide. Telopoditomere 2 large, without process as long as telopoditomere 3. Process of telopoditomere 2 located posteriorly, visible in anterior view. Process slender, projecting to 2/3 of telopoditomere 3, conspicuously curved, with an almost sharp apex. Telopoditomere 3 massive, cylindrical, straight, apically slightly tapering. Posterior side with a black sclerotized spot and a small, triangular spine. Telopoditomere 1 in apical view covered with long setae. In posterior view all telopoditomeres setose. ***Posterior telopods*** (Fig. 5A, B): telopoditomere 1 large and cylindrical, twice as long as wide, reaching the length of telopoditomere 3. Immovable finger (process of telopoditomere 2) shorter than movable finger, consisting of telopoditomeres 3 and 4. Immovable finger with a characteristic, distally swollen apex, clearly rounded, apex therefore wider as base, projecting especially strongly at lower margin. Telopoditomere 3 rectangular, clearly rounded, with a sharp process directed towards immovable finger. Telopoditomere 4 as long as, but slightly more slender than, telopoditomere 3, 2.5 times longer than wide, apically weakly tapering, with a tiny curved hook directed towards immovable finger. Telopoditomere 1 on both sides covered with setae, remaining telopoditomeres in posterior view almost glabrous, in anterior view with few isolated setae except for immovable finger which is more densely setose.

Remarks. In the field, these millipedes were found in a very wide range of habitats, from 700 to 1200 m a.s.l., including extremely humid forest on river banks and in valleys with abundant *Cyathea* sp. tree ferns, on sandy soils and in sparse leaf litter; on hill slopes covered with rich broadleaved tropical forest and a thick leaf litter layer; as well as on very dry ridges and interfluves with broadleaved forest with admixtures of coniferous trees, and in open places colonized by *Dicranopteris* sp. ferns and *Melastoma* sp. bushes. A similar number of males and females were recorded during the expedition (30 adult individuals in total). Two-thirds of the females were hidden in leaf litter inside their “living chambers”, the remaining were spotted walking on the forest floor. All males were likewise walking on the forest floor, most probably searching for mates. The few recorded juveniles of both sexes were hidden in leaf litter. During the expedition, the day temperature on the leaf litter surface averaged 24 °C, compared to 19 °C in the night, with occasional nights when the temperature dropped down to 17.5 °C. Heavy, but rather short showers took place almost every day, quite often also with fogs in the evening. The abundance of the millipedes did not change drastically under rains, only slightly decreasing on non-rainy days in open habitats.

According to local knowledge, April is the driest month in the Park, while the rest of the year is extremely humid. Surprisingly, we noticed the lack of Diplopoda during the expedition with very little millipede activity, but *S. bicorne* was abundant at different age stadia. It may be a strategy for avoiding competition with other millipede species, as *Sphaerobelum* is a quite robust and well-protected diplopod capable of surviving difficult conditions.

Sphaerobelum pumatense sp. nov.

http://zoobank.org/180236D4-C6AD-4682-B2C2-911BE419F552
Figs 1A–C, 3B, 6

Material examined. ***Holotype*** ♂ (ZMUM Rd 4647), Vietnam, Nghe An Prov., Pu Mat National Park, 18°56'N, 104°38'E, 200 m a.s.l., mixed tropical forest on steep slopes, on forest floor, daytime, IV.2018, I.I. Semenyuk leg. ***Paratypes*** 1 ♂, 1 ♀ (ZMUM Rd 4632), 1 ♂, 2 ♀ (ZMUM Rd 4648), 1 ♂, 1 ♀ (ZFMK MYR8942), same data as holotype.

Diagnosis. *Sphaerobelum pumatense* sp. nov. belongs to the group of congeners in which the mesal margin of the femur is extended into several teeth (Fig. 6F). In addition, *S. pumatense* sp. nov. shares only with *S. spinatum* Wesener, 2019 and *S. nigrum* Wesener, 2019, both from Laos, and with *S. cattiense* Semenyuk et al., 2018 and *S. konkakinhense* Semenyuk et al., 2018, both from Vietnam, a straight telopoditomere 4 of the posterior telopod (Fig. 6A, B). *Sphaerobelum pumatense* sp. nov. differs in several unique characters from the four other species: vulval operculum not projecting mesally into a strong tip (Fig. 6H); telopoditomere 4 of posterior telopods exceptionally slender, >5× as long as wide (Fig. 6A, B).

Description. ***Body length:*** holotype ♂ length ca. 27.2 mm, width of thoracic shield 15.61 mm, of tergite 7 (= broadest), 15.5 mm, height of thoracic shield, 7.9 mm, of tergite 7 (= highest), 8.2 mm; ♀ length ca. 34.8 mm, width of thoracic shield, 17.2 mm, of tergite 7, 17.9 mm (= broadest), height of thoracic shield, 9.5 mm, of tergite 7, 9.9 mm (= highest). Width of paratypes 14–17 (♂) or 15–17 mm (♀). ***Coloration:*** both in vivo and in vitro, after >1.5 years of preservation in ethanol, similar, uniformly dark blackish brown, dark chestnut, dark grey-brown or dark reddish brown, in alcohol with posterior margin usually dark brown, paratergite depressions, groove of thoracic shield and legs dark olive to olive-brown, but several basal podomeres and distal halves of tarsi considerably lighter, orange. Antennae blackish to dark brown, but antennomeres 5 and 6 lighter, light brown to nearly orange. Tegument mosly dull to poorly shining (Fig. 1A–C). ***Head:*** eyes with >75 ommatidia. Aberrant ocellus located inside antennal groove. Antennae short (Fig. 6G), with rounded joints, protruding posteriorly to leg-pair 3. Lengths of antennomeres: 1 = 2 = 3 = 4 = 5 << 6. All antennomeres densely pubescent, sensilla basiconica surrounding apical disc. Shape of antennae sexually dimorphic, cylindrical in ♀, thickened, apically broadened and flattened in ♂. Apical disc with ca. 63/67 (♂) or 48/45 (♀) apical cones, respectively. Organ of Tömösváry located inside antennal groove. ***Gnathochilarium:*** palpi with sensory cones arranged in a single field. ***Mandibles:*** not dissected. ***Stigmatic plates:*** first stigmatic plate rounded, apex well-rounded, straight towards coxa 1. ***Laterotergites:*** laterotergite 1 strongly elongated into a well-ronded tip. Laterotergite 2 with a broad, stout, much shorter projection. ***Collum:*** with few setae on surface, anterior and posterior margins with 3–4 rows of short setae. ***Thoracic shield:*** surface like tergites, longer setae only in grooves. Slope towards groove without anterior, but with 3 or 4 posterior keels. ***Tergites:*** surface densely setose with short setae standing in pits. Tips of paratergites of midbody tergites slightly projecting posteriorly. ***Endotergum:*** inner section lacking any spines or setae. Middle area with a single row of large, sparse, elliptical, cuticular impressions. Distance between impressions >2× their diameter. Apically, two sparse rows of marginal bristles, tips of longest setae slightly protruding beyond tergal margin (Fig. 3B). Bristles not smooth, but barbed, with numerous small spinicles. ***Anal shield:*** large, in both sexes regularly rounded. Surface in both sexes completely covered with tiny setae located in small pits. Underside with a single, long, black, locking carina 2× as long as width of last laterotergite. Carina located close to last laterotergite. ***Legs:*** leg 1 with 6, leg 2 with 7, leg 3 with 7 or 8 ventral spines. First two leg-pairs without an apical spine. Leg-pairs 4–21 with 10–12 ventral spines and one dorso-apical spine. In leg 9, femur 1.6, tarsus 4.5 times longer than wide (Fig. 6F). All podomeres densely setose. Coxa with a large and process dentate at margins. Coxa process absent from first and sharply projecting in second leg. Prefemur at apical margin with a projection mesally. Femur extended mesally into a dentate margin featuring 12–14 teeth. ***Female sexual characters:*** vulva large, covering half of coxa, extending mesally to anterior third of prefemur (Fig. 6H). Operculum rounded, very slightly invaginated medially, mesal margin slightly projecting into a well-rounded lobe slightly higher than remaining operculum. ***Subanal plate:*** large and wide, centrally recessed. ***Male sexual characters:*** gonopore covered with a single, undivided, circular, sclerotized plate. ***Anterior telopods*** (Fig. 6C–E): consisting of 4 telopoditomeres distal to syncoxite. Telopoditomere 1 rectangular, as long as wide. Telopoditomere 2 large, without process, as long as telopoditomere 1. Process of telopoditomere 2 located posteriorly, visible mesally in anterior view. Process wide, well-rounded, projecting to basal part of telopoditomere 3. Telopoditomeres 3 and 4 slightly curved mesally. Telopoditomere 3 small, cylindrical, slightly shorter than telopoditomere 4, with a spine juxtaposed to process of telopoditomere 2. Telopoditomere 4 cylindrical, well-rounded, posterior side with 2–4 small spines. All telopoditomeres covered with long setae. ***Posterior telopods*** (Fig. 6A, B): telopoditomere 1 narrow, as long as wide. Immovable finger (process of telopoditomere 2) slightly shorter than movable finger, consisting of telopoditomeres 3 and 4. Immovable finger with a characteristic, distally swollen apex, clearly rounded apically, apex only slightly wider than base. Swelling only slightly expressed basally. Telopoditomere 3 rectangular, well-rounded, apically with a clearly rounded extension carrying three small spines. Telopoditomere 4 only slightly shorter and much more slender than telopoditomere 3, 5.2× as long as wide, apically weakly tapering, straight, not curved, with 23 small spines at margin towards immovable finger close to tip. In anterior view, telopoditomeres 1–3 covered with setae, in posterior view telopoditomeres 2–4 more glabrous except for numerous setae at margins.

Etymology. To emphasize the provenance from the Pu Mat National Park, adjective.

Remarks. In the field, the weather was fluctuating between very dry and hot days and several rainy days, with day temperature above the leaf litter averaging 24 °C, and night temperature averaging 21 °C, not dropping below 18.5 °C. *Sphaerobelum pumatense* were quite rare in any weather conditions. The millipedes were found in forests ranging from 150 m to 400 m a.s.l., the forest canopy appeared to have been free of this species. Females were mostly hidden in leaf litter in small patches of litter on very steep slopes (60–70°), forming "living rooms", choosing places with water oozing from beneath shale so that the leaf litter was constantly wet. Males were found mainly on the forest floor at night. No juveniles were seen.

Genus *Sphaeropoeus* Brandt, 1833

See Wesener (2016b) for a redescription, a diagnosis and a phylogenetic analysis of the genus.

Remarks. A large gap between the tarsal claw and apical spine as observed in the three species of *Sphaeropoeus* studied here, as well as in the two (including the type species *S. hercules* Brandt, 1833) redescribed recently (Wesener 2016b); this may represent another feature characteristic of the genus. Another leg character that is conspicuous in all five recently studied species of the genus is the very long femoral ridge.

Sphaeropoeus manca (Attems, 1936), comb. nov.

Zephronia manca Attems, 1936: 169; Sundara 1970: 127 (list); Golovatch 1983 (list); Enghoff et al. 2004: 32 (list); Jeekel 2001: 20 (list); Wesener 2016b: 33 (list).

Syntypes. ♂ and ♀, NHMW 2239 (not examined).

Distribution. Vietnam: D'Ran, Lam Dong Prov., near Dalat; Peak Lang Biang, Lam Dong Prov., S. Annam. India: Dhobie Jhora, Kurseong, eastern Himalayas (Attems 1936).

Remarks. The drawings of the telopods, as well as the extremely enlarged operculum of the ♀ vulva as depicted in the original description (Attems 1936) clearly show this species to be a member of the genus *Sphaeropoeus*, related to the other species mentioned below. Only a full revision of the type series, which contains syntypes from several localities in Vietnam and India, may clarify whether several species are actually hidden under the name *S. manca*. The posterior telopods and other characters are clearly different in *S. manca* compared to the two other species, as well as to *Sphaeropoeus maculatus* (Verhoeff, 1924) which is redescribed below.

Sphaeropoeus maculatus (Verhoeff, 1924)

Figs 3C, 7, 10

Tonkinobelum maculatum Verhoeff, 1924: 62; Attems 1936: 192 (list); Wang 1967: 484 (list); Korsós 1983: 118 (list); Golovatch 1983 (list)

Sphaeropoeus maculatus—Jeekel 2001: 23 (list); Enghoff et al. 2004: 32 (list); Wesener 2016a: 40 (list); Wesener 2016b: 146 (list).

Material examined. ***Lectotype*** ♂ (HNMB 2858/1), designated here to fix the name for future studies and to avoid taxonomic confusion. Vietnam, 'Tonkin', Mau Son (= Mau Son Mountains, Lang Son Province), H. Fruhstorfer leg.

Redescription. ***Measurements:*** ca. 58 mm long, 23.1 mm (2nd), up to 23.9 mm (8th) wide, 13.5 mm (2nd) up to 15.1 mm height (8th the highest). ***Coloration:*** apparently faded after more than 90 years in ethanol. Head, collum and appendages dark green, remaining tergites castaneous brown. ***Head:*** eyes with >70 ocelli. Antennae very short, protruding up to centre of head. Antennomeres 1–5 with few longer setae, 6th densely pubescent. Antennomere 6 towards disc with a single row of sensilla basiconica. Antennomere 6 strongly axe-shaped, twice as wide as antennomeres 1–5. ♂ with >140 apical cones. Palpi of gnathochilarium located in a single field. ***Collum:*** glabrous except for anterior edges. ***Thoracic shield:*** with wide and deep grooves, 3 or 4 weak crests present at posterior corner. ***Tergites:*** surface glabrous and smooth except for paratergite depressions. Midbody paratergite tips projecting posteriorly. ***Anal shield:*** well-rounded, glabrous. Locking carinae rudimentary, very short, located close to last laterotergite. ***Endotergum:*** inner section lacking any spines or setae. Middle area lacking discernible cuticular impressions. Apically, 3–4 very dense rows of short marginal bristles, tips of longest setae barely protruding beyond midpoint towards tergal margin (Fig. 3C). Bristles not smooth, but barbed, with numerous small spinicles. ***Stigmatic plates:*** first well-rounded, not triangular in shape. ***Laterotergites:*** first elongated into a strongly tapering sharp process. Laterotergite 2 also extended, with a very sharp tip. Laterotergites 3 and following not extended, well-rounded. ***Legs:*** first with 2, second with 5, third with 8 ventral and a single apical spine. Leg-pairs 4–21 with 10–12 ventral spines. Coxa process visible, well-rounded (Fig. 7A). Femur 2.1, tarsus 4 times longer than wide. Femur with a very long ridge (Fig. 7A). ***Male gonopore:*** opening covered with a single, apically membranous plate. ***Anterior telopod*** (Fig. 7B–D): four podomeres, first two of equal length, 3rd half as long as 2nd discarding its process, 4th slightly shorter and more slender than 3rd. Telopoditomere 2 with a strong, curved process. Telopoditomere 3 posteriorly with a shorter process juxtaposed to apex process of telopoditomere 2. Telopoditomere 4 conical, lacking any spines, lobes or teeth. ***Posterior telopod*** (Fig. 7E, F): podomeres 3 and 4 longer than process of podomere 2. Podomere 4 short, conical, with a membranous ledge and no visible spines. Podomere 3, 2.8 times longer than wide. Its excavated inner margin with a membranous ledge, in posterior aspect with ca. 4 small crenulated teeth. Immovable finger wide, apically tapering, tip curved towards movable finger. Membranous area with at least one large membranous lobe. Podomeres 1–3 in anterior view with numerous setae, in posterior view telopoditomere 3 with few setae mainly located at margins. Podomere 4 in both aspects glabrous, except for 3 or 4 long setae at mesal margin.

Remarks. Verhoeff described the species based on four syntypes. Only one syntype could be relocated; the others may be considered as likely lost. As the sole available syntype is a mature ♂ in very good condition, this specimen has been designated as the lectotype. ♀ unknown.

Jeekel (2001) thought the specimen had been mislabeled, because no other species of the genus was then known from Vietnam or continental Asia north of Singapore. However, with the new combination of *Zephronia manca* (see above), and the two new species described below, the provenance of *S. maculatus* may well be correct.

***Sphaeropoeus honbaensis* sp. nov.**

http://zoobank.org/8C6B0566-6BEE-4A06-B59F-BDA14A90892B
Figs 2F–H, 3E, 8

Material examined. ***Holotype*** ♂ (ZMUM Rd 4644), Vietnam, Khanh Hoa Prov., Hon Ba Nature Reserve, 12°07'N, 108°56'E, 1550 m a.s.l., mixed mossy tropical forest on mountain ridge, on forest floor, night time, VI.2018, I.I. Semenyuk leg. ***Paratypes*** 2 ♂ (ZMUM Rd 4633), 1 ♂ (ZFMK MYR8943), same locality as holotype. 1 ♀ (ZMUM Rd 4645), same locality, 1450 m a.s.l., mixed tropical forest on mountain slope, in leaf litter, day time, VI.2018, I.I. Semenyuk leg.

Diagnosis. *Sphaeropoeus honbaensis* sp. nov. differs from all other known continental species of the genus in the presence of very few (< 30) apical cones on the ♂ antenna (usually at least >70, often >120). The anterior telopod also shows a very short, almost completely reduced telopoditomere 4, a character only shared with *S. bidoupensis* sp. nov. *Sphaeropoeus honbaensis* sp. nov. differs from *S. bidoupensis* sp. nov. in the lack of a spine in the inner area of the large telopoditomere 3 (vs. present in *S. bidoupensis* sp. nov.), in the endotergum, where the distances between the cuticular impressions are wider than the diameter (vs. slightly narrower than diameter in *S. bidoupensis* sp. nov.), the ♂ anal shield being weakly bell-shaped (vs. well-rounded in *S. bidoupensis* sp. nov.), and in leg structure, with leg-pair 3 lacking an apical spine (vs. present in *S. bidoupensis* sp. nov.), the prefemur lacking a dentate mesal margin (vs. present in *S. bidoupensis* sp. nov.), and the coxa process being strongly developed and well-rounded (vs. weakly developed and partly sharp in *S. bidoupensis* sp. nov.).

Description. ***Measurements:*** holotype ♂ ca. 27 mm long, 12.1 mm (2nd), up to 12.2 mm (7th) wide, 7.8 mm (2nd) up to 15.1 mm height (8th the highest); ♂ paratypes 8–11 mm wide. Paratype ♀ ca. 29 mm long, 13.1 mm (2nd), up to 13.3 mm (7th) wide, 7.8 mm (2nd) up to 8.4 mm height (7th the highest). ***Coloration:*** both in vivo and in vitro, after >1.5 years of preservation in ethanol, similar, in life uniformly dark violet brown to violet blackish with vague infuscate bands near caudal margin (Fig. 2F–H), in alcohol dark brown to brown, in places marbled, only dorsalmost part of anal shield sometimes lighter centrally, light brown. Antennae orange. Legs mostly grey- or olive-brown, but tarsi yellow-brown. Tegument mosly dull to poorly shining. ***Head:*** eyes with ca. 65 ocelli. Antennae short (Fig. 8A), protruding beyond centre of head. Antennomeres 1–5 with few longer setae, 6th densely pubescent. Antennomere 6 towards disc with single row of sensilla basiconica. Antennomere 6 slightly swollen in ♂, cylindrical in ♀, twice as long as, but only slightly wider than, antennomeres 1–5. ♂ with 26/27, ♀ with 22/24 apical cones. Palpi of gnathochilarium located in a single field. ***Collum:*** completely covered with long setae, like

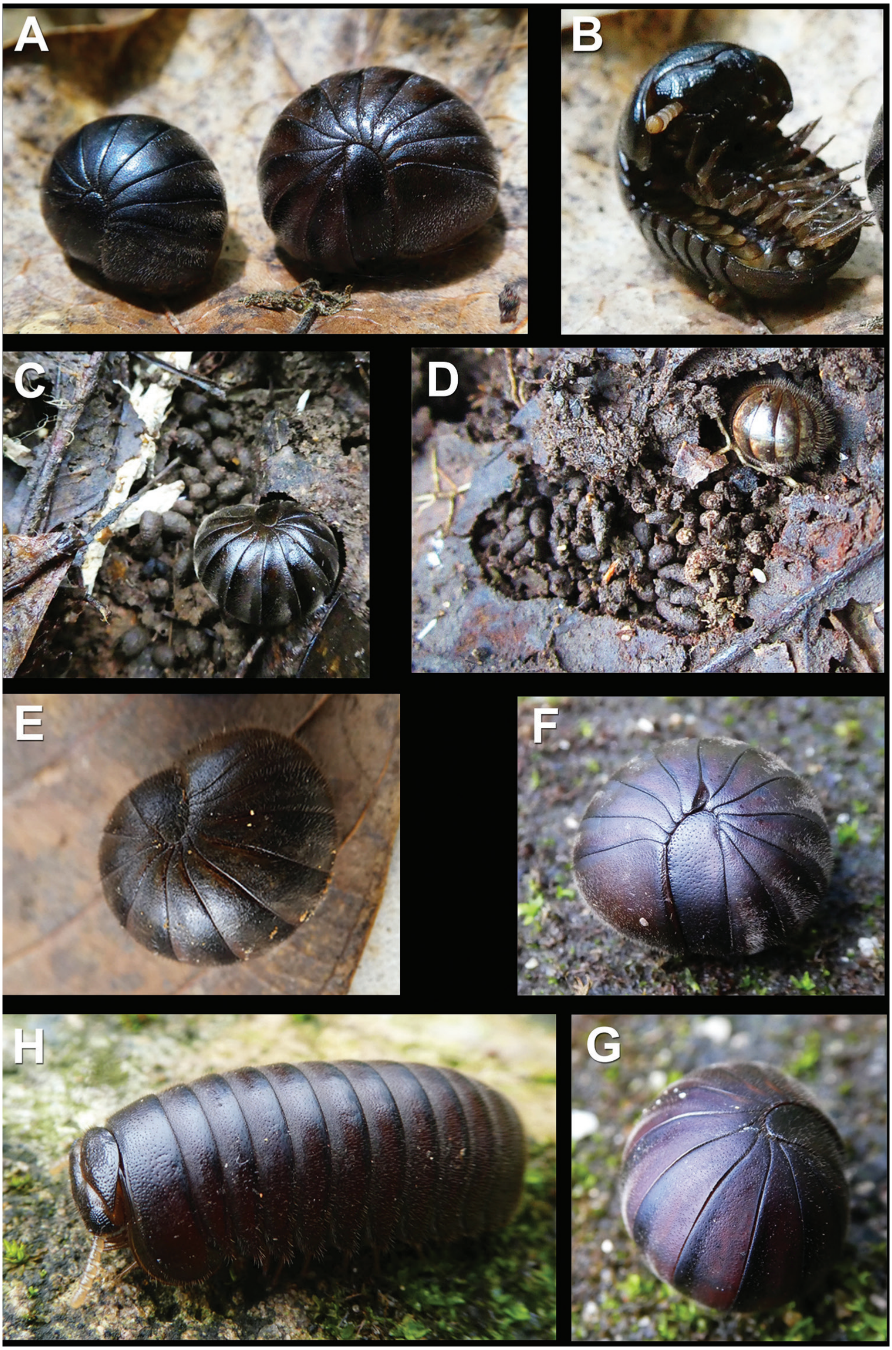

Figure 2. Live *Sphaeropoeus bidoupensis* sp. nov. (**A–E**) and *Sphaeropoeus honbaensis* sp. nov. (**F–H**) in the field **A** enrolled male (left) and female (right) **B** adult, ventral view **C** adult and its excrements in a "living room" in leaf litter **D** early instar juvenile enrolled in its "living room", with surrounding dead leaves eaten and excrement used to shape the room **E** enrolled middle-sized instar juvenile **F–H** adult, enrolled and walking, respectively. Pictures taken not to scale.

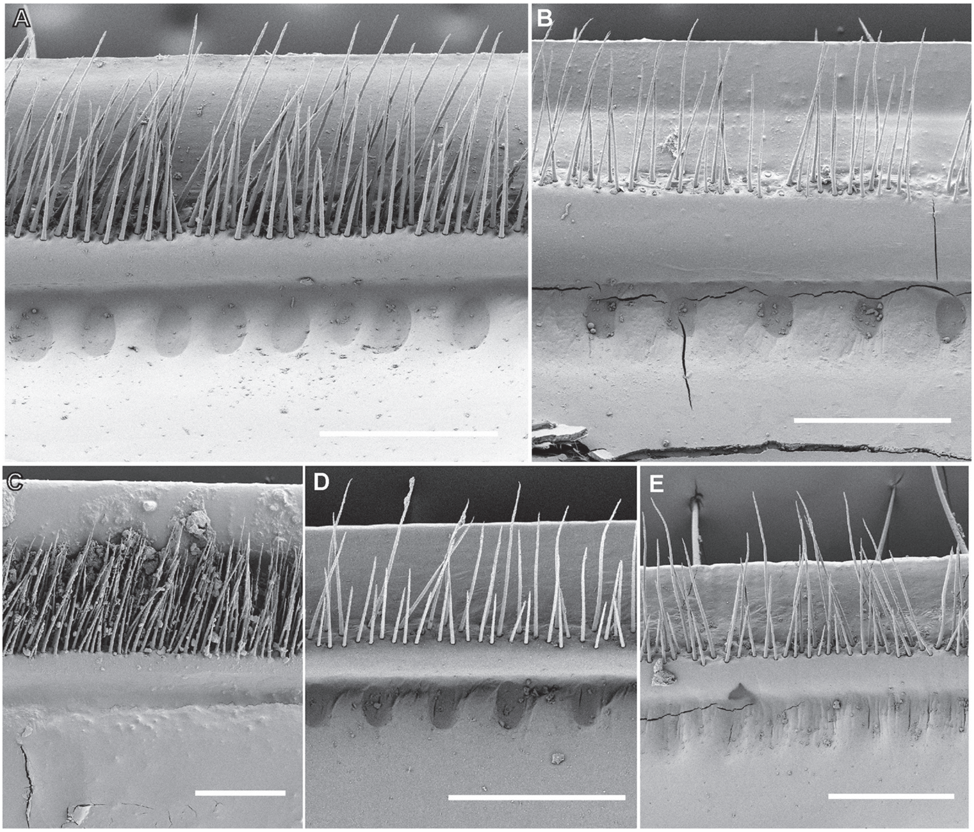

Figure 3. Endoterga of midbody segments, SEM micrographs. **A** *Sphaerobelum bicorne* Attems, 1938, ♂ (ZFMK) **B** *Sphaerobelum pumatense* sp. nov., ♂ holotype **C** *Sphaeropoeus maculatus* (Verhoeff, 1924), ♂ lectotype **D** *Sphaeropoeus bidoupensis* sp. nov., ♂ holotype **E** *Sphaeropoeus honbaensis* sp. nov., ♂ holotype. Scale bars: 0.2 mm.

the tergites. ***Thoracic shield:*** with wide and shallow grooves, 3 or 4 weak crests present at posterior corner. ***Tergites:*** surface covered with longer setae, most innervating in small pits. Midbody paratergite tips projecting posteriorly (Fig. 10). ***Anal shield:*** well-rounded in ♀, weakly bell-shaped in ♂. In both sexes completely covered with longer setae. Locking carina long, twice as long as width of last laterotergite, located close to margin. ***Endotergum:*** inner section lacking any spines or setae. Middle area with a single row of large, sparse, elliptical, cuticular impressions. Distance between impressions greater than their diameter. Apically, two rows of long marginal bristles, tips of longest setae clearly protruding beyond tergal margin (Fig. 3E). Bristles not smooth, but with numerous small spinicles. ***Stigmatic plates:*** first well-rounded, triangular. ***Laterotergites:*** first with a slightly projecting, well-rounded process. Laterotergites 2 and following not extended, well-rounded. ***Legs:*** first with 2 or 3, second with 3 or 4, third with 8 ventral and lacking an apical spine. Leg-pairs 4–21 each with 10–12 ventral spines and a single apical spine. Coxa process visible, well-rounded (Fig. 8B). Femur 1.7, tarsus 5.2× as long as wide. Femur with a very long ridge (Fig. 8B).

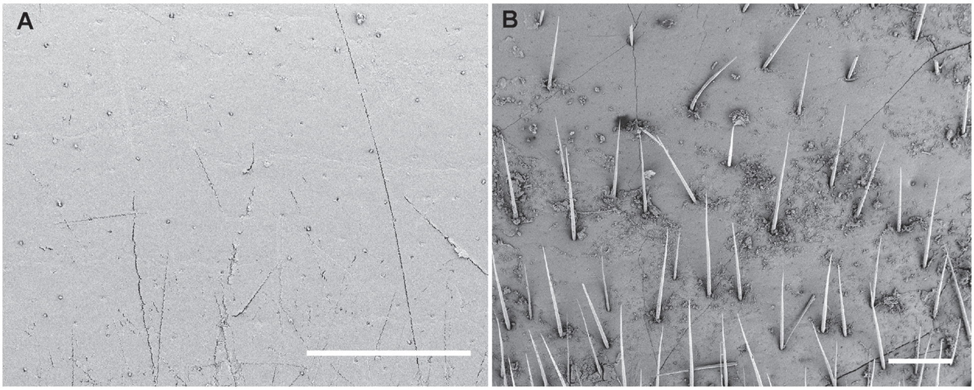

Figure 4. Tergal surface of midbody segments, SEM micrographs. **A** *Sphaerobelum bicorne* Attems, 1938, ♂ (ZFMK) **B** *Sphaeropoeus bidoupensis* sp. nov., ♂ holotype. Scale bars: 0.2 mm.

Mesal margin of femur completely extended into 12–14 teeth, lateral margin of prefemur, juxtaposed to coxal process, slightly extended into 2–4 teeth (Fig. 8B). ***Female sexual characters:*** vulva large, covering 2/3 coxa, a conspicuous operculum extending to basal half of prefemur (Fig. 8H). Operculum massive, larger than bursa, wider than prefemur, apically rounded, mesal margin very slightly projecting and slightly higher than remaining operculum. ***Subanal plate:*** large and wide, triangular. ***Male gonopore:*** opening covered with a single, apically membranous plate. ***Anterior telopod*** (Fig. 8E–G): four podomeres, first three of equal length regardless of the processes, podomere 4 rudimentary, conical. Telopoditomere 2 with a strong, curved process overreaching telopoditomere 4. Telopoditomere 3 posteriorly with a longer process juxtaposed to apex process of telopoditomere 2, clearly protruding above telopoditomere 4, as well as process of telopoditomere 2. Telopoditomere 4 conical, with two spines. ***Posterior telopod*** (Fig. 8C, D): Podomeres 3 and 4 slightly longer than process of podomere 2. Podomere 4 short, conical, with two spines, slightly curved towards immovable finger. Podomere 3 slender, 4.2 times longer than wide. Its excavate inner margin with a membranous lobe and a single spine, posterior aspect with ca. 12 small crenulated teeth. Immovable finger slender, apically tapering, tip curved towards movable finger. Membranous area apically with a large membranous lobe. Podomeres 1–3 in anterior and posterior views with few setae. Podomere 4 in both aspects glabrous.

Etymology. To emphasize the provenance from the Hon Ba Nature Reserve, adjective.

Remarks. During the expedition, more than ten males of this species were recorded, all walking on the forest floor in the night, mainly on the mountain ridge. Only one adult female was found despite special searching efforts: it was hidden in leaf litter, which is typical of sphaerotheriidans. The female was encountered in a forest at an elevation considerably lower than the where abundant males were observed. Although confusing, this may be accounted for by high population abundance at the onset of a season. During the expedition, it was raining almost every day, the temperature in the daytime above leaf litter averaging 20 °C and dropping down to 17.5 °C (minimum 16.8 °C) at night. Fog was very often seen on the top of the mountain. No juveniles were recorded.

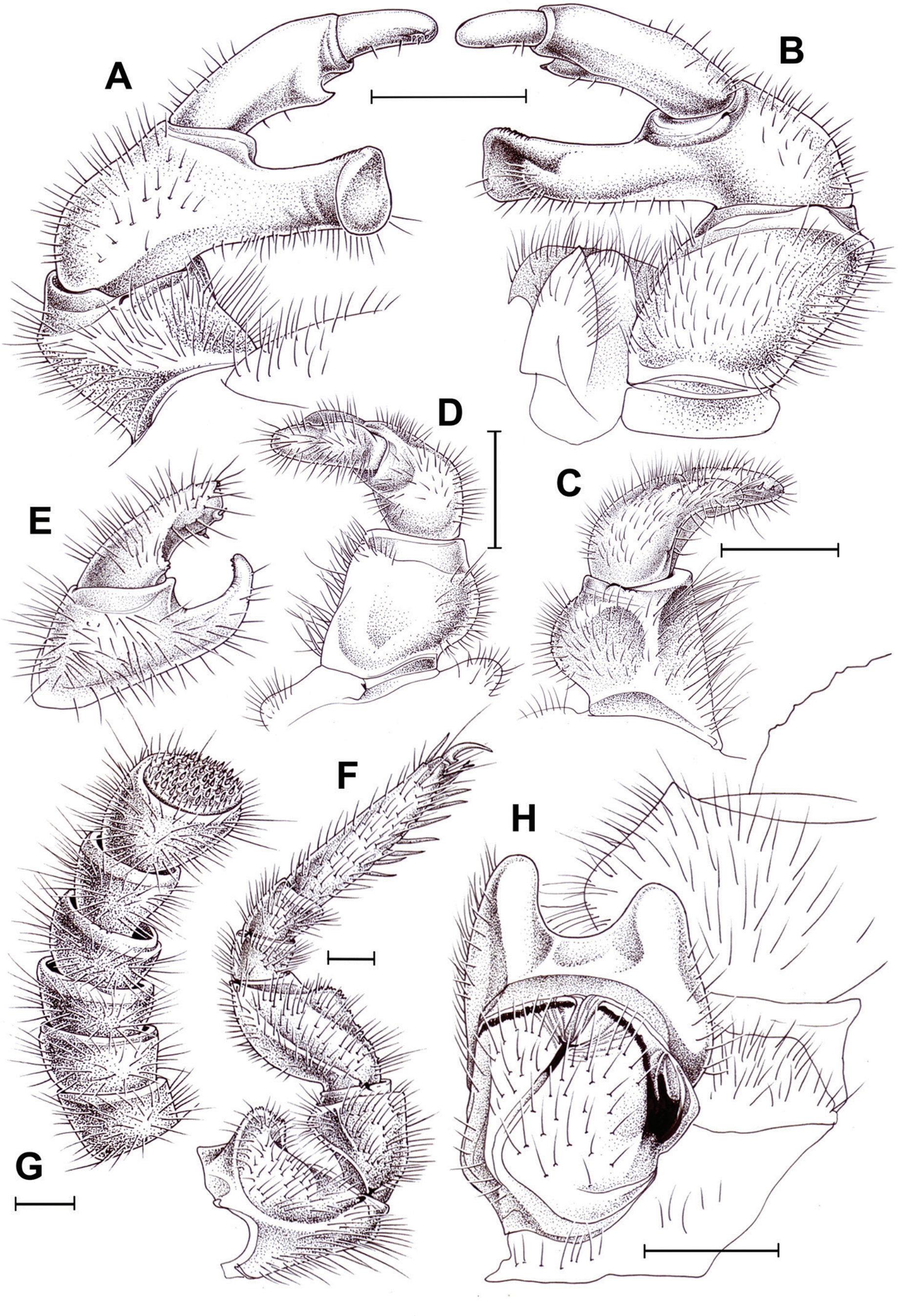

Figure 5. *Sphaerobelum bicorne* Attems, 1938, ♂ (**A–G**) and ♀ (**H**) from Song Thanh National Park. **A, B** Right posterior telopod, anterior and posterior views, respectively **C, D** right anterior telopod, posterior and anterior views, respectively **E** telopoditomeres 2 and 3 of right anterior telopod, lateral view **F** left leg 9, anterior view **G** left antenna **H** left coxa and prefemur 2 with vulva, posterior view. Scale bars: 1.0 mm, **E** drawn not to scale.

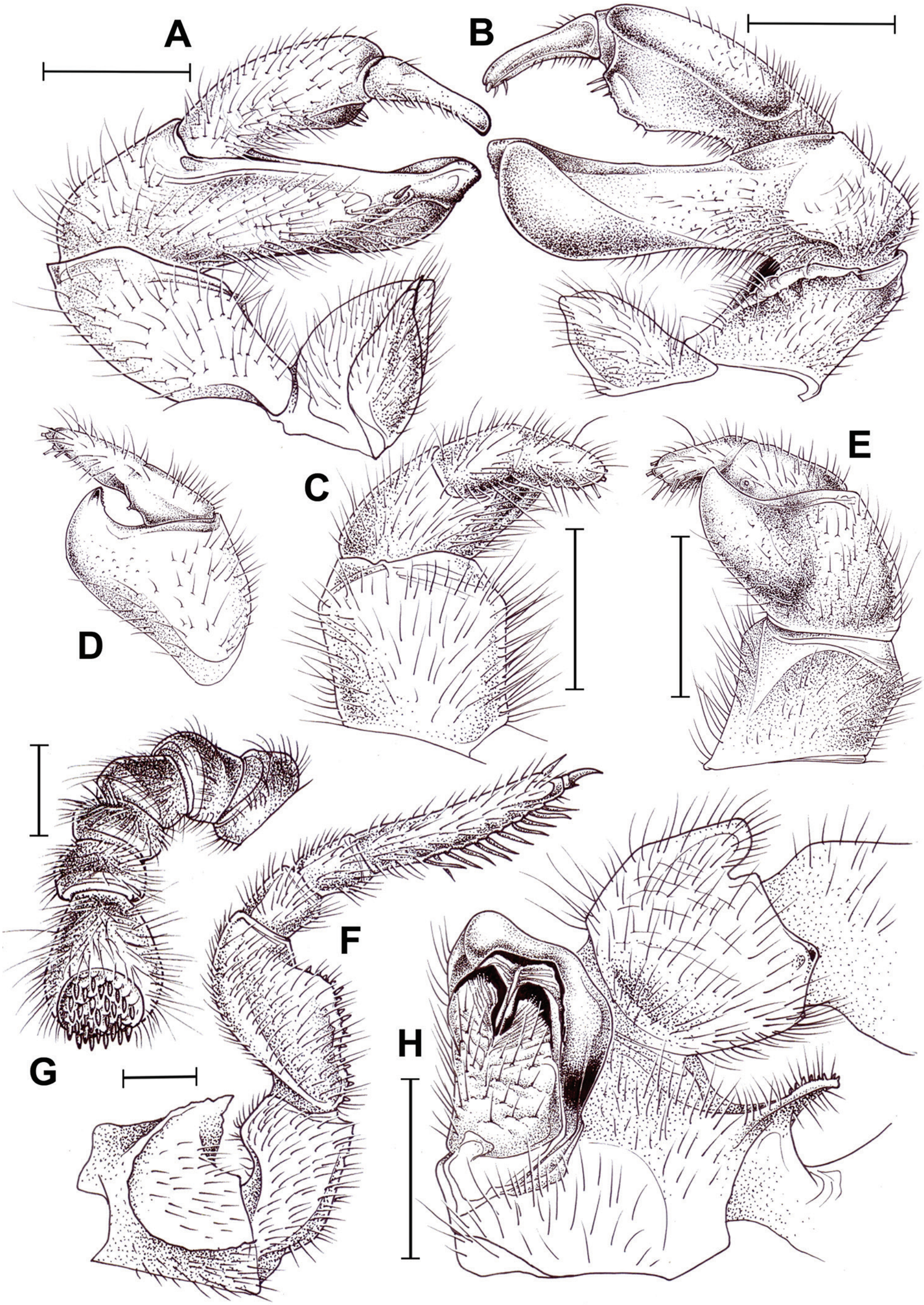

Figure 6. *Sphaerobelum pumatense* sp. nov., ♂ holotype (**A–G**) and ♀ paratype (**H**). **A, B** Left posterior telopod, anterior and posterior views, respectively **C–E** left anterior telopod, anterior, lateral and posterior views, respectively **F** left leg 9, anterior view **G** left antenna **H** left coxa and prefemur 2 with vulva, posterior view. Scale bars: 1.0 mm, **D** drawn not to scale.

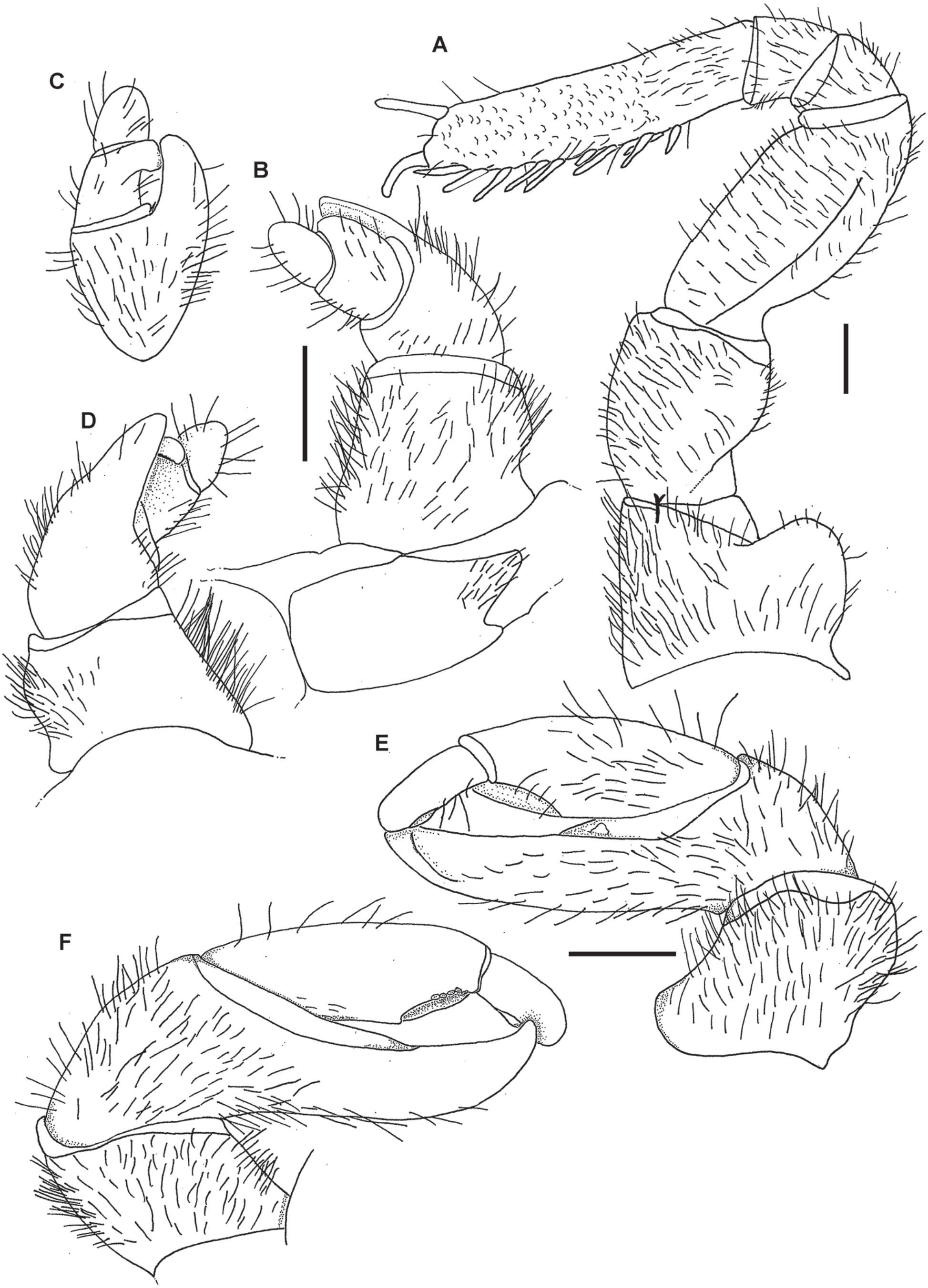

Figure 7. *Sphaeropoeus maculatus* (Verhoeff, 1924), ♂ lectotype. **A** Left leg 9, posterior view **B–D** right anterior telopod, anterior, lateral and posterior views, respectively **E, F** right posterior telopod, anterior and posterior views, respectively. Scale bars: 1.0 mm.

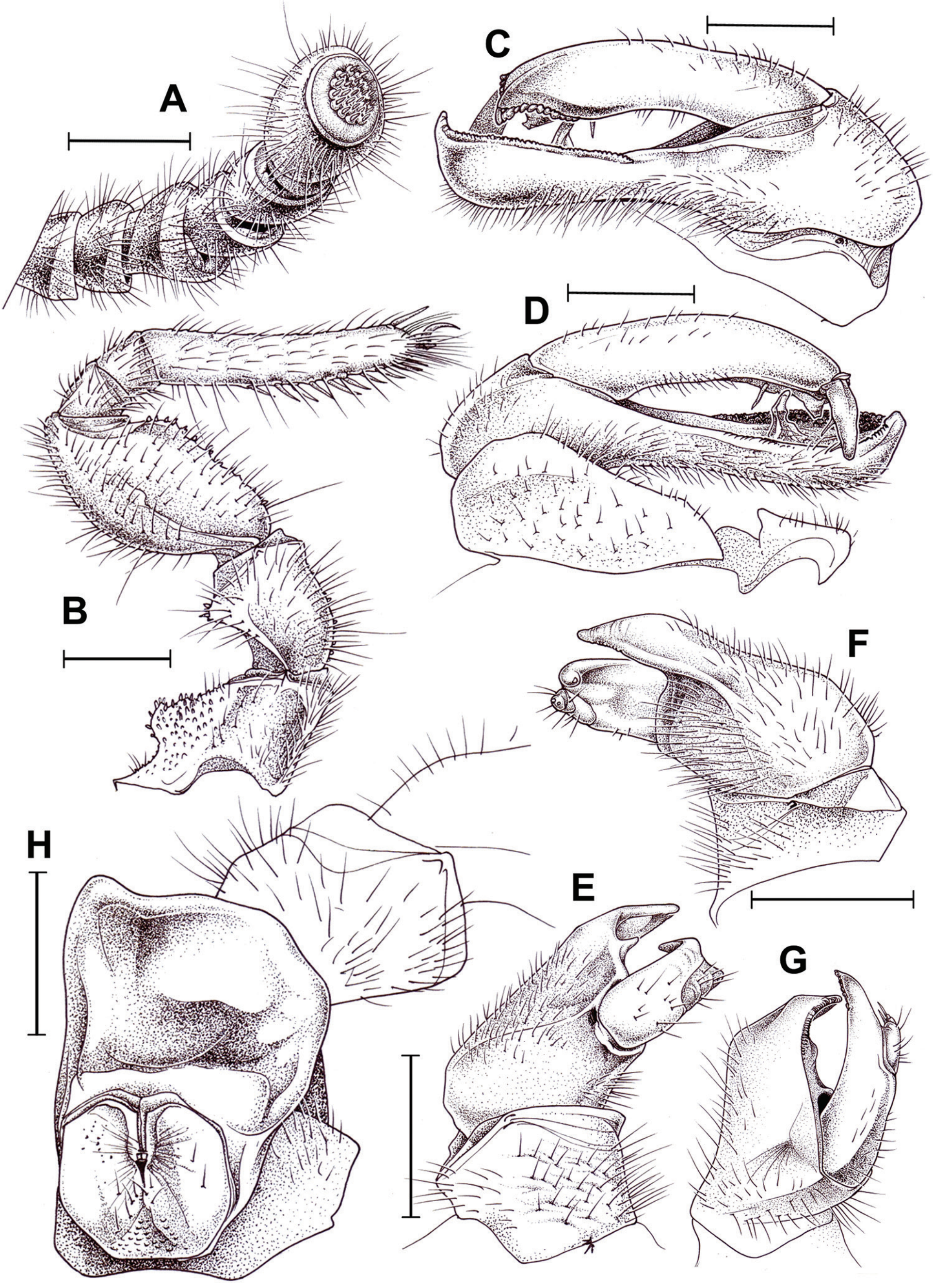

Figure 8. *Sphaeropoeus honbaensis* sp. nov., ♂ holotype (**A–G**) and ♀ paratype (**H**). **A** Left antenna, **B** left leg 9, anterior view **C, D** left posterior telopod, posterior and anterior views, respectively **E–G** left anterior telopod, anterior, posterior and lateral views, respectively **H** left coxa and prefemur 2 with vulva, posterior view. Scale bars: 1.0 mm, **G** drawn not to scale.

Sphaeropoeus bidoupensis sp. nov.

http://zoobank.org/F68EE25F-CEF3-4816-B94C-D5050AE5B5C5

Figs 2A–E, 3D, 4B, 9

Material examined. ***Holotype*** ♂ (ZMUM Rd 4646), Vietnam, Lam Dong Prov., Bidoup Nui Ba National Park, 12°10'N, 108°41'E, 1500 m a.s.l., mixed tropical forest on hills, in leaf litter, daytime, VI.2018, I.I. Semenyuk leg. ***Paratypes*** 1 ♂, 2 ♀ (ZMUM Rd 4634), 1 ♂ (ZFMK MYR8944), 1 ♀ (ZFMK MYR8859), same data as holotype.

Diagnosis. *Sphaeropoeus bidoupensis* sp. nov. differs from almost all other known continental species of the genus in the anterior telopod showing a very short, almost completely reduced telopoditomere 4, a character only shared with *S. honbaensis* sp. nov. *Sphaeropoeus bidoupensis* sp. nov. differs from *S. honbaensis* sp. nov. in the presence of a spine in the inner area of the large telopoditomere 3 (vs. absent in *S. honbaensis* sp. nov.), in the endotergum, where the distances between the cuticular impressions are slightly smaller than the diameter (vs. wider than diameter in *S. honbaensis* sp. nov.), the ♂ anal shield being well-rounded (weakly bell-shaped in *S. honbaensis* sp. nov.), and in leg structure, with leg-pair 3 having an apical spine (vs. absent in *S. honbaensis* sp. nov.), the prefemur showing a dentate mesal margin (vs. smooth in *S. honbaensis* sp. nov.), and the coxa process being weakly developed and partly sharp (vs. strongly developed and well-rounded in *S. honbaensis* sp. nov.).

Description. ***Measurements:*** holotype ♂ ca. 24 mm long, 11.2 mm (2nd), up to 12.3 mm (7th) wide, 7.1 mm high (2nd the highest). Paratype ♀ (ZFMK): ca. 29 mm long, 13.5 mm (2nd), up to 14.3 mm (7th) wide, 7.7 mm (2nd) up to 9.1 mm in height (7th the highest). ZMUM paratypes 10 mm (♂), 11 mm (♀) or 13 mm wide (♀). ***Coloration:*** both in vivo and in vitro, after >1.5 years of preservation in ethanol, similar; in life, adults uniformly dark brown to blackish brown, juveniles lighter and showing vague or clear variegated tergal patterns (Fig. 2C, D), antennae in adults orange, legs in adults mostly dark or lighter olive-brown (Fig. 2B); in alcohol, adults likewise uniformly dark brown to blackish brown, antennae orange, legs light grey-brown to olive-grey-brown with a little lighter tarsi. Tegument mostly dull to poorly shining (Fig. 2A, B). ***Head:*** eyes with ca. 65 ocelli. Antennae short (Fig. 9H), protruding beyond centre of head. Antennomeres 1–5 with few longer setae, 6th densely pubescent. Antennomere 6 towards disc with a single row of sensilla basiconica. Antennomere 6 swollen in ♂, cylindrical in ♀, twice as long as, but only slightly wider than, antennomeres 1–5. ♂ with 36/40, ♀ with 17/24 apical cones. Palpi of gnathochilarium located in a single field. ***Collum:*** completely covered with long setae, like the tergites. ***Thoracic shield:*** with wide and shallow grooves, 3 or 4 weak crests present at posterior corner. ***Tergites:*** surface covered with longer setae, most innervating in small pits (Fig. 4B). Paratergite tips of midbody tergites projecting posteriorly (Fig. 2A). ***Anal shield:*** well-rounded. In both sexes completely covered with longer setae. Locking carina long, 2× as long as width of last laterotergite, located close to margin. ***Endotergum:*** inner section lacking any spines or setae. Middle area with a single row of large, sparse, elliptical, cuticular impressions. Distance between impressions shorter than their diameter. Apically, two rows of long

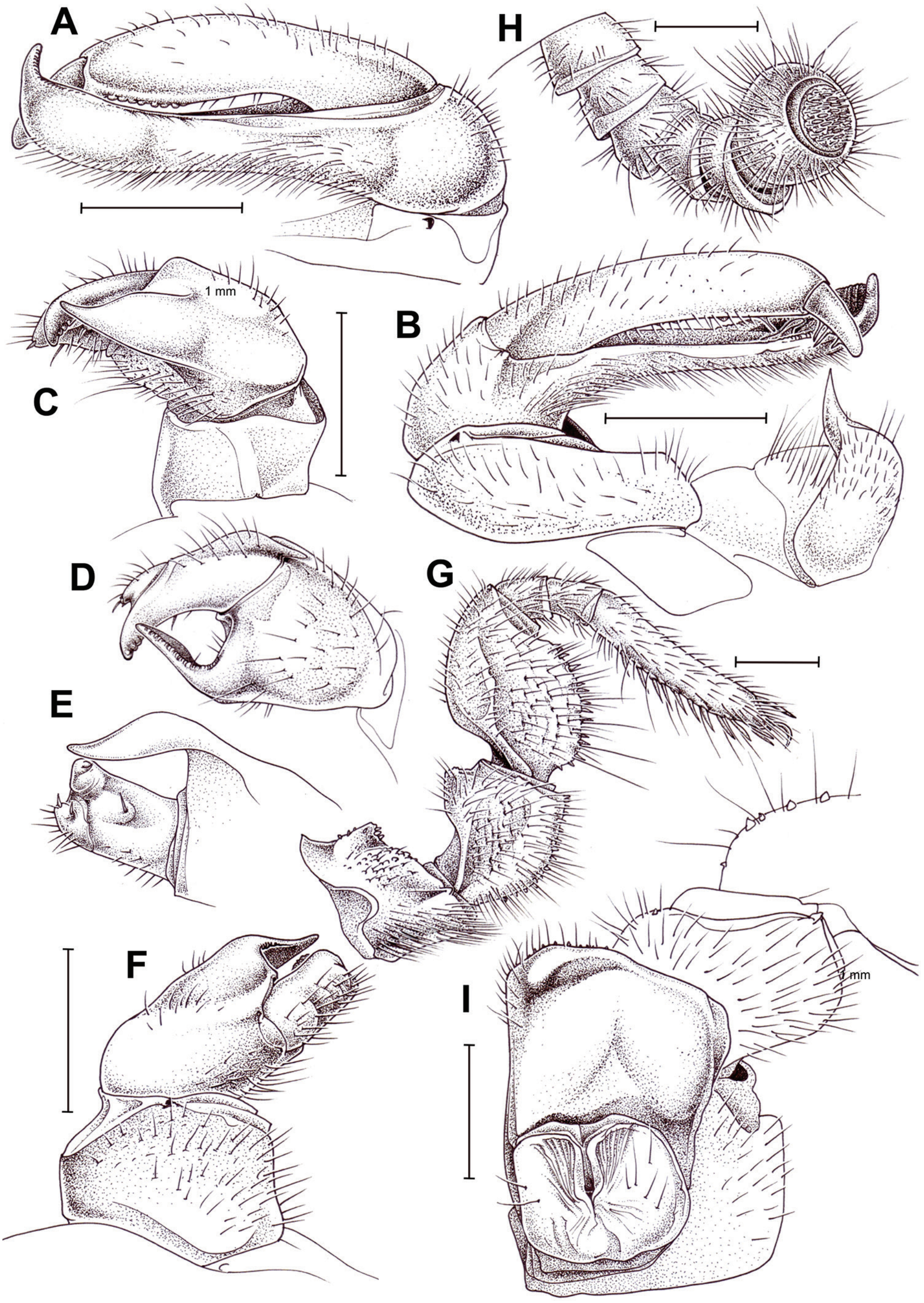

Figure 9. *Sphaeropoeus bidoupensis* sp. nov., ♂ holotype (**A–H**) and ♀ paratype (**I**). **A, B** Left posterior telopod, posterior and anterior views, respectively **C–F** left anterior telopod, posterior, sublateral, lateral and anterior views, respectively **G** left leg 9, anterior view **H** left antenna **I** left coxa and prefemur 2 with vulva, posterior view. Scale bars: 1.0 mm, **D** drawn not to scale.

marginal bristles, tips of longest setae clearly protruding beyond tergal margin (Fig. 3D). Bristles not smooth, but with numerous small spinicles. ***Stigmatic plates:*** first well-rounded, triangular. ***Laterotergites:*** first with a slightly projecting, well-rounded process. Laterotergites 2 and following not extended, well-rounded. ***Legs:*** first with 2 or 3, second with 5 (one of them basal), third with 8 ventral and an apical spine. Leg-pairs 4–21 each with 12–14 ventral spines and a single apical spine. Coxa process visible, partly sharp (Fig. 9G). Femur 1.5, tarsus 4.7 times longer than wide. Femur with a very long ridge (Fig. 9G). Mesal margin of femur completely extended into 12–14 teeth, prefemur at mesal margin with 5–8 teeth (Fig. 9G). ***Female sexual characters:*** vulva large, covering 2/3 coxa, a conspicuous operculum extending above basal half of prefemur (Fig. 9I). Operculum massive, larger than bursa, wider than prefemur, apically rounded. ***Subanal plate:*** large and wide, triangular. ***Male gonopore:*** opening covered with a single, apically membranous plate. ***Anterior telopod*** (Fig. 9C–F): four podomeres, first three of equal length regardless of the processes, podomere 4 rudimentary, conical. Telopoditomere 2 with a strong, curved process overreaching telopoditomere 4. Telopoditomere 3 posteriorly with a longer process juxtaposed to apex process of telopoditomere 2, clearly protruding above telopoditomere 4, as well as both process of telopoditomere 2 and a large spine in the central area. Telopoditomere 4 conical, with a single spine. ***Posterior telopod*** (Fig. 9A, B): podomeres 3 and 4 slightly longer than process of podomere 2. Podomere 4 short, conical, with two spines, slightly curved towards immovable finger. Podomere 3 slender, 3.6 times longer than wide. Its excavate inner margin with a membranous lobe and a single spine, posterior face with ca. 10 small crenulated teeth. Immovable finger slender, apically tapering, tip curved towards movable finger. Membranous area apically with a large, bifid, membranous lobe. Podomeres 1–3 in anterior and posterior views with few setae. Podomere 4 in both aspects glabrous.

Etymology. To emphasize the provenance from the Bidoup Nui Ba National Park, adjective.

Remarks. This new species was very abundant in the Park area and could be found almost throughout the year. In January, juveniles lived under logs, but no adults were recorded. The daytime temperature above the leaf litter averaged 17 °C, dropping down to 14 °C (minimum 12.5 °C) at night; rains were quite abundant. In June, juveniles colonized decaying wood, leaf litter, suspended soils in *Asplenium* sp. ferns, and spaces under logs. Adults lived in leaf litter and the suspended soil of ferns, only occasionally and only males walking openly on the forest floor. Juveniles and some adults were often recorded hiding inside their “living chambers” (Fig. 2C, D), just like those observed in *Sphaerobelum bicorne* (see above). The daytime temperature above the leaf litter averaged 20 °C, compared to 16.5 °C (minimum 14.9 °C) at night; rains were likewise quite abundant. In November, the millipedes were mainly hidden in leaf litter. The daytime temperature above the leaf litter averaged 22 °C, vs. 14.5 °C (minimum 11.2 °C) at night; rains were particularly heavy, as a typhoon came in.

Sphaeropoeus bidoupensis sp. nov. seems only to occur in forests at about 1500 m a.s.l.. This was a riparian, very wet, broadleaved forest with abundant *Asplenium* sp. ferns on tree trunks starting from the ground level and a thick leaf litter layer on the floor, as well as a forest with dominating Fagaceae trees mixed with several coniferous

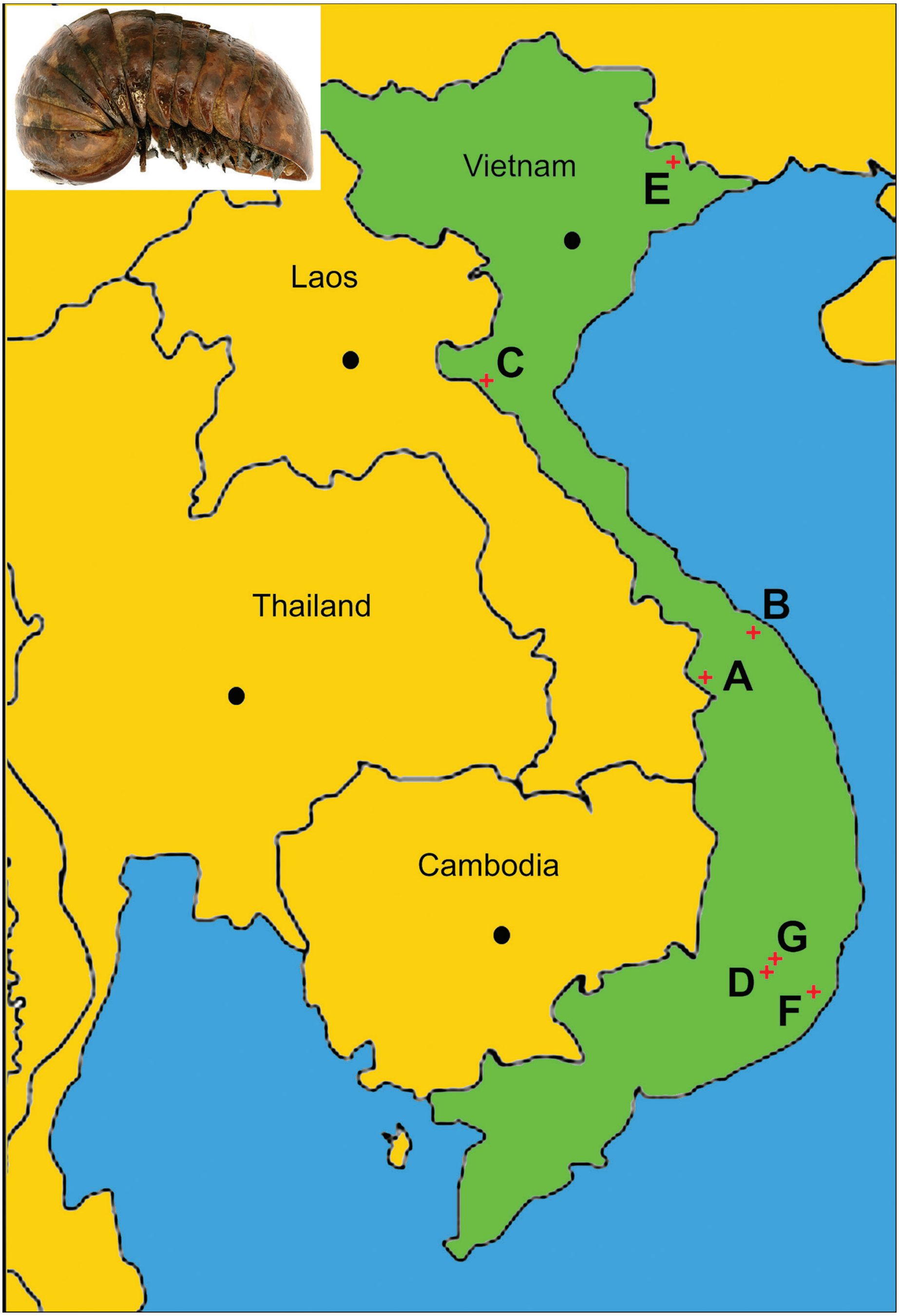

Figure 10. Habitus photograph of the lectotype (HNHM 2858/1) of *Sphaeropoeus maculatus* (Verhoeff, 1924), lateral view, and a distribution map of all other relevant zephroniid species in Vietnam. **A** *Sphaerobelum bicorne* Attems, 1938 (new record) **B** *Sphaerobelum bicorne* Attems, 1938 (old record) **C** *Sphaerobelum pumatense* sp. nov. **D** *Sphaeropoeus manca* (Attems, 1936) **E** *Sphaeropoeus maculatus* (Verhoeff, 1924) **F** *Sphaeropoeus honbaensis* sp. nov. **G** *Sphaeropoeus bidoupensis* sp. nov.

species on slopes, the leaf litter layer being thick and to a significant proportion formed by coniferous needles. The species was not located in the adjacent mossy elfin forest up to 2000 m a.s.l. with a much cooler and wet weather.

Conclusions

Zephroniidae in Vietnam, currently amounting to seven species of *Sphaerobelum*, five species in *Zephronia*, four in *Sphaeropoeus*, three in *Prionobelum* and one species in *Cryxus*, are distributed in the north as well as the south of the country (Fig. 10). They tend to show a remarkable pattern of each species being very narrowly endemic and mostly confined to a single locality, although more inventories in numerous unexplored areas need to be conducted. This has been observed in Laos (Wesener 2019) and Thailand (Wongthamwanich et al. 2012). In Vietnam, examples of syntopically coexisting species or even genera are likewise very few, e.g., *Sphaerobelum konkakinhense* Semenyuk, Golovatch & Wesener, 2018, *Zephronia konkakinhensis* Semenyuk, Golovatch & Wesener, 2018 and *Z. montis* Semenyuk, Golovatch & Wesener, 2018 in the montane forests of the Kon Ka Kinh National Park, Gia Lai Province or *Cryxus ovalis* Leach, 1814, *Sphaerobelum cattiense* Semenyuk, Golovatch & Wesener, 2018 and *Zephronia ovalis* Gray, 1832 in the monsoon lowland forest patch of the Nam Cat Tien National Park, Dong Nai Province, both in southern Vietnam (Golovatch et al. 2012, Semenyuk et al. 2018).

Our contribution reinforces the impression that Vietnam, together with the adjacent parts of Laos, represents one of the main hotspots of zephroniid/sphaerotheriidan diversity not only in Indochina, but also in the entire Southeast Asia. Despite the considerable recent progress achieved in the study of Sphaerotheriida in Indochina (Golovatch et al. 2012, Wesener 2016a, 2016b, 2019, Semenyuk et al. 2018), there can be little doubt that future investigations will reveal many more new species and records of giant pill-millipedes in the region. Revisionary work remains topical as well.

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RESEARCH ARTICLE

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The millipede genus *Globanus* Attems, 1914, endemic to São Tomé and Príncipe, with the description of a new species (Diplopoda, Spirostreptida, Spirostreptidae)

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Abstract

During a soil zoological expedition to São Tomé and Príncipe in 2010 by the California Academy of Sciences, millipedes of the genus *Globanus* were collected. Samples of *G. marginescaber* (Karsch, 1884) and *G. integer* (Karsch, 1884) were recovered in addition to those containing a new species. *Globanus drewesi* **sp. nov.** is described and additional records, illustrations, and descriptive notes are given for the other two species. A key to all three species of the genus is provided, and a distribution map is presented. The monotypic genus *Lobogonus* Demange, 1971, which includes *L. trilobatus* Demange, 1971, from Sierra Leone, mainland western Africa, is revalidated and removed from synonymy under *Globanus*. *Lobogonus* is illustrated from a type specimen.

Keywords

Africa, Diplopoda, Gulf of Guinea, key, *Lobogonus*, taxonomy

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[†] Deceased

Introduction

São Tomé and Príncipe are two volcanic islands in the Gulf of Guinea straddling the Equator ca 250 km west off the coast of Gabon. Together with Annobon and Bioko, they belong to the Cameroon volcanic chain. These are classical oceanic islands long known for their peculiar biota. Although the bird fauna is relatively well documented (Christy and Clarke 1998) and a flora exists since the 1920s (Liberato and Espirito Santo 1972–1982) that describes the major elements of the islands' botany, many other important animal groups remain badly understudied, with Diplopoda, or millipedes, being one of them.

The first diplopods recorded from São Tomé and Príncipe were two species, *Spirostreptus* (*Nodopyge*) *integer* Karsch, 1884, and *Spirostreptus* (*Nodopyge*) *marginescaber* Karsch, 1884, described as new by Karsch (1884) in anecdotal "descriptions" accompanied by no illustrations whatsoever. Later, *S. integer* was relegated to the new genus *Globanus* Attems, 1914, while *S. marginescaber* was considered as a species *incertae sedis* because its holotype was a female (Attems 1914). Spelda (1993) summarized the myriapod fauna of São Tomé Island, reporting six centipede and five millipede species. Amongst the Diplopoda, only two species of Spirostreptidae were considered indigenous: *G. integer* and *G. marginescaber*. All others were likely introductions, either pantropical: *Paraspirobolus lucifugus* (Gervais, 1836) (Spirobolida, Spirobolellidae) and *Orthomorpha coarctata* (de Saussure, 1860) (Polydesmida, Paradoxosomatidae) or widespread and western African: *Teloidenopus sulcatus* (Voges, 1878) (Spirostreptida, Spirostreptidae). A number of spirostreptid samples remained unidentified, but Spelda (1993) assigned them all unequivocally to *Globanus*. The only hitherto known diplopod truly endemic to Príncipe seems to be *Monachodesmus feae* Silvestri, 1927, the type species of *Monachodesmus* Silvestri, 1927, a large Afrotropical genus with 18 species, which are mostly western African (Silvestri 1927; Golovatch et al. 2015).

The genus *Globanus* had been considered endemic to São Tomé and Príncipe until Krabbe (1982), in her global revision of Spirostreptidae, synonymized *Globanus* with *Lobogonus* Demange, 1971, and thus extended the distribution of *Globanus* to mainland western Africa. She only recognized two valid species, *G. integer* and *G. trilobatus* (Demange, 1971). The latter species is from Sierra Leone, even though Brolemann (1935), albeit cryptically inside an introductory part to his *Faune de France* monograph, had beautifully depicted the gonopod of *Aulonopyge marginescaber* (= *Globanus marginescaber*).

In 2010, R.C. Drewes (California Academy of Sciences) collected millipedes in addition to his herpetology speciality for six weeks on São Tomé and Príncipe, but the samples consist of only one order, family, and genus: Spirostreptida, Spirostreptidae, *Globanus* Attems, 1914. *Globanus integer* (Karsch, 1884) and *G. marginescaber* (Karsch, 1884) were both recovered on each island, along with one new species. This suggests that a *Globanus* "species swarm" exists on both São Tomé and Príncipe islands.

The present paper is a review of *Globanus*, with the description of a new species endemic to São Tomé Island. The Sierra Leone genus *Lobogonus* is revalidated and removed from synonymy under *Globanus*.

Material and methods

This study is based on material collected in 2010 by R.C. Drewes. Some additional samples were obtained from the Muséum national d'Histoire naturelle (MNHN), Paris, France and the Royal Museum for Central Africa (MRAC), Tervuren, Belgium.

All samples are stored in 70% ethanol. Photographs were made with a Leica DFC 500 digital camera mounted on a Leica MZ16A stereo microscope. Images were processed with a Leica Application Suite program. Specimens for scanning electron microscopy (SEM) were air-dried, mounted on aluminium stubs, coated with gold and studied using a JEOL JSM-6480LV scanning electron microscope.

The terminology used to describe the gonopod conformations follows that of Hoffman (2008).

Museum acronyms

CAS	California Academy of Sciences, San Francisco, U.S.A.
MNHN	Muséum national d'Histoire naturelle, Paris, France
RMCA	Royal Museum for Central Africa, Tervuren, Belgium
ZMB	Zoological Museum, Humboldt University, Berlin, Germany

Systematics

Family SPIROSTREPTIDAE

Genus *Lobogonus* Demange, 1971

Type species. *Lobogonus trilobatus* Demange, 1971, by original designation.

Diagnosis (after Demange 1971, with modifications). A genus of large millipedes (up to ca 200 mm long) with relatively long legs (80% of maximum body diameter). Gonocoxite stout and large, ending with a thick apicolateral projection (Fig. 1C, lap); telopodite thick and short, distally characterized by three well-differentiated lobes and a thin seminal branch (Fig. 1D, E, sb).

Lobogonus trilobatus Demange, 1971

Figure 1

Globanus trilobatus: Krabbe 1982: 146–147.

Material observed. Syntypes: 10 ♂♂, 6 ♀♀, 5 juv, Sierra Leone, Mt Loma, 02.XI.1964 (MNHM-MY-MY 6531).

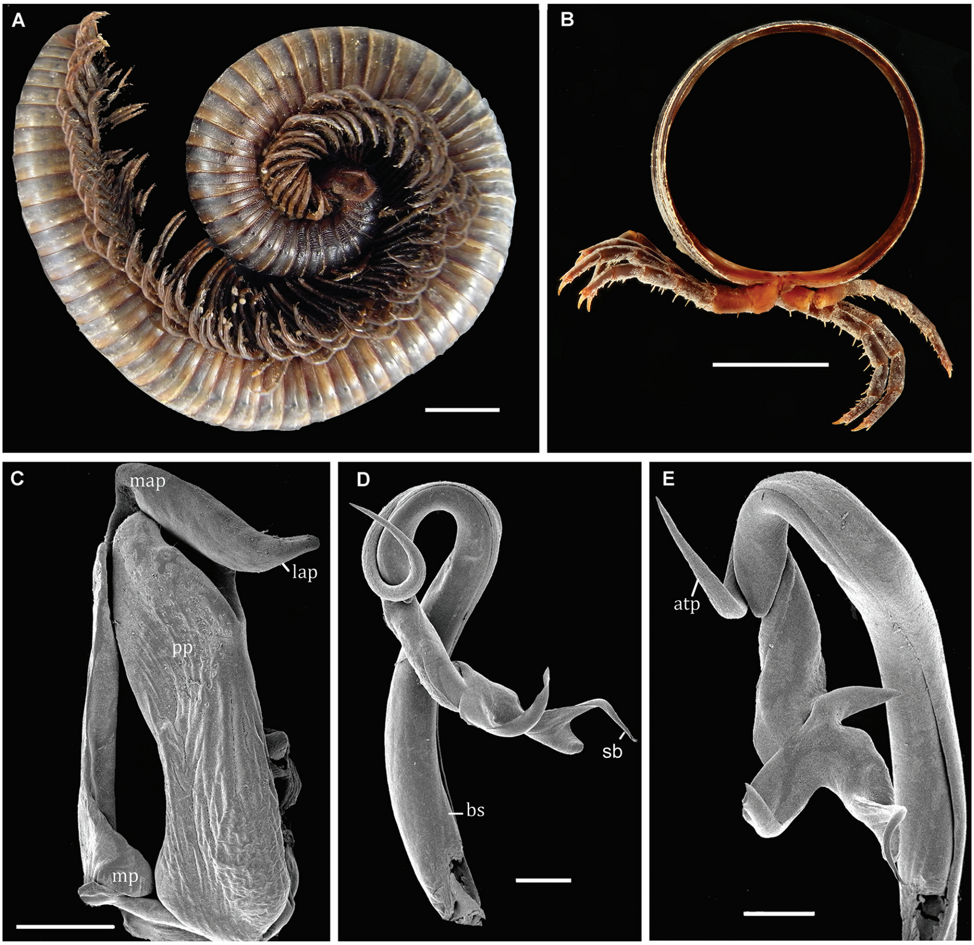

Figure 1. *Lobogonus trilobatus* Demange, 1971, ♂ syntype. **A** habitus, lateral view **B** transverse section of midbody segment **C** right gonopod, posterior view **D** left telopodite, anterior view **E** tip of telopodite. Abbreviations: atp = antetorsal process, bs = basomere, lap = latero-apical process, map = meso-apical metaplical process, mp = metaplica, pp = proplica, sb = seminal branch. Scale bars: 10 mm (**A**); 1 mm (**C**); 500 µm (**D**, **E**).

Remarks. Having studied the original description, closely examined the type species of the genus *Lobogonus* Demange, 1971 (Mt Loma region, Sierra Leone, MNHN, types), and compared its gonopods to those of *Globanus* spp., we disagree with the decision of Krabbe (1982) to merge *Lobogonus* with *Globanus*. Krabbe synonymized these two genera on account of similarities in gonopod structure, but the similarities appear to be rather superficial. In addition, both of the genera show different, totally disjunct distributions; *Globanus* is confined to São Tomé and Príncipe, whereas *Lobogonus* occurs in the Mont Loma region, Sierra Leone. *Lobogonus trilobatus* is a large millipede (ca 200 mm long) with long legs (80% of maximum body diameter; Fig.

1A, B), *vs. Globanus* species, which are considerably smaller and show relatively short legs (ca 60% of maximum body diameter; Fig. 2A, E). *Lobogonus trilobatus* has a pilose gnathochilarium, in contrast to the poorly setose one observed in *Globanus* species (Fig. 2D). Similarities of the gonopods are also superficial and only concern the post-torsal process of the gonotelopodites, with 2 or 3 lobes or processes observed in both genera. In *Globanus* these lobes are subapical lobes, whereas in *Lobogonus* they are apical. The gonocoxite of *L. trilobatus* is rather stout and large (Fig. 1C–E) compared to the slender gonocoxite observed in *Globanus* species.

Genus *Globanus* Attems, 1914

Type species. *Spirostreptus integer* Karsch, 1884, by original designation.

Diagnosis (after Krabbe 1982, with modifications). A genus of moderate-sized millipedes (up to 65 mm long with relatively short legs (ca 60% of maximum body diameter)). Gnathochilarium notable in that the surface sculpture of the mentum shows a submedian transverse groove (Fig. 2D, sg). Gonopod metaplica extended into an apicolateral projection, proplica slender, with or without a distolateral spine. Telopodite with a long, slender, antetorsal process, with a post-torsal process situated more distally, with 2 or 3 lobes proximal to an attenuating and slender tip.

Distribution. São Tomé and Príncipe islands.

Species included. *Globanus integer* (Karsch, 1884), *G. marginescaber* (Karsch, 1884), *G. drewesi* sp. nov.

Key to *Globanus* species

1 Median lamella of telocoxite without distal proplica spine (Fig. 5B, C)......... .... ***G. integer* (Karsch, 1884)**

– Median lamella of telocoxite with a distal proplica spine (ps)......................**2**

2 Apical part of telopodite without subtriangular projection (Fig. 4C)............ .... ***G. marginescaber* (Karsch, 1884)**

– Apical part of telopodite with a subtriangular projection (sp) (Fig. 3D, F).... ....***G. drewesi* sp. nov.**

Globanus drewesi sp. nov.

http://zoobank.org/6A51E9E2-E585-4003-B4AA-90CFDF04F05C

Figures 2, 3

Type material. Holotype ♂, Republic of São Tomé and Príncipe, São Tomé Island, Morro Provaz Ridge, road to Lagoa Amelia, alt. 1475 m, 3.III.2010, 0°16’58”N, 6°35’12.5”E, Bob Drewes leg. (CASENT9032626).

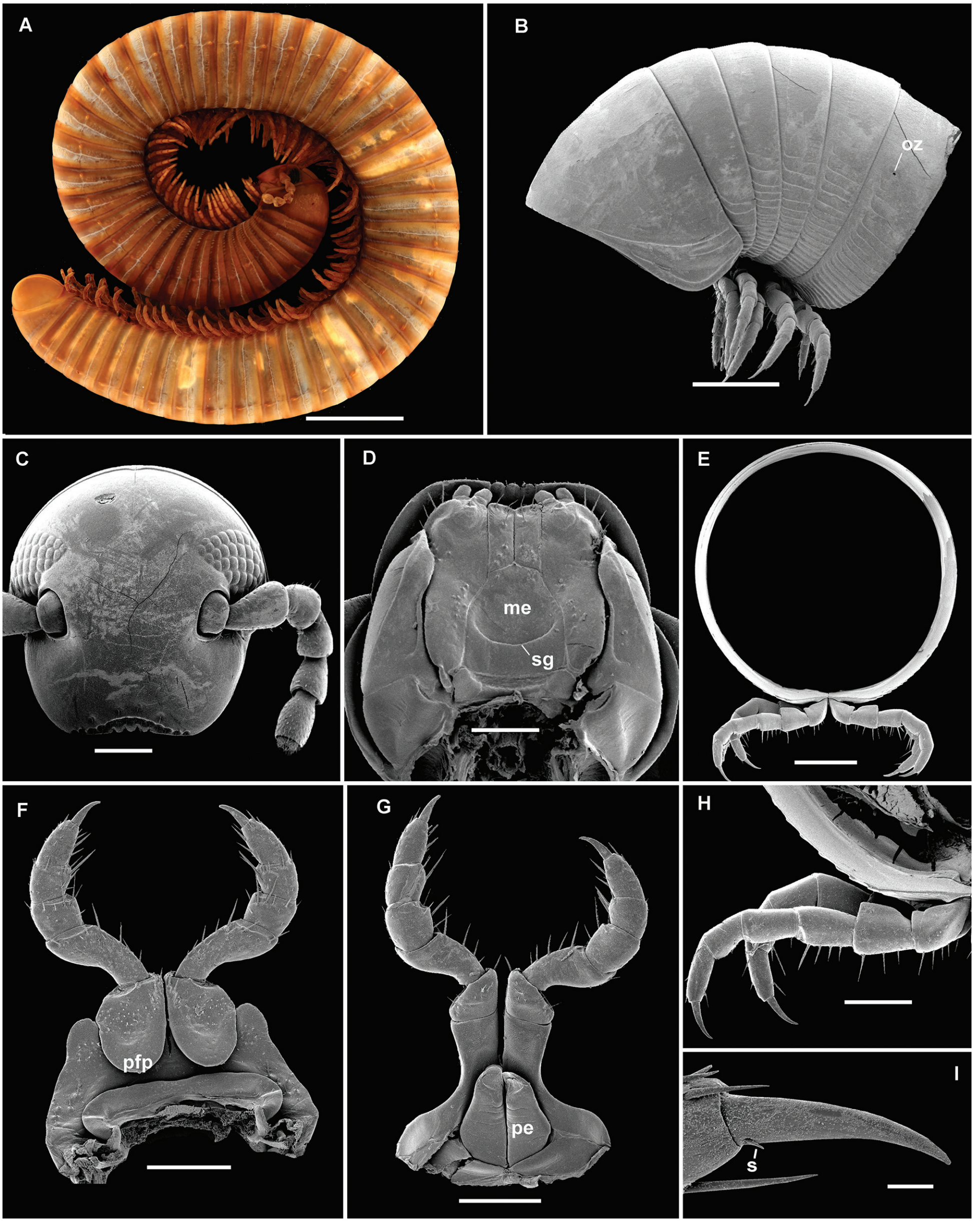

Figure 2. *Globanus drewesi* sp. nov., ♂ paratype. **A** habitus, lateral view **B** collum and segments 2–6, lateral view **C** frontal view of head **D** gnathochilarium **E** midbody transversal section **F** first pair of legs, oral view **G** second pair of legs, oral view **H** midbody legs, oral view **I** midbody claw, caudal view. Abbreviations: me = mentum, pe = penes, pfp = prefemoral process, s = seta at base of claw, sg = submedian transverse groove. Scale bars: 5 mm (**A**); 1 mm (**B**) 1mm (**D, E**); 500µm (**C, D, F, G**); 200µm (**H**); 50µm (**I**).

Paratypes: 1 ♂, 6 ♀♀, Republic of São Tomé and Principe, São Tomé Island, Morro Provaz Ridge, Headwaters of Rio do Oro, alt. 1240 m, 3.III.2010, 0°17’3.8”N, 6°35’57.5”E, Bob Drewes leg. (CASENT9032626).

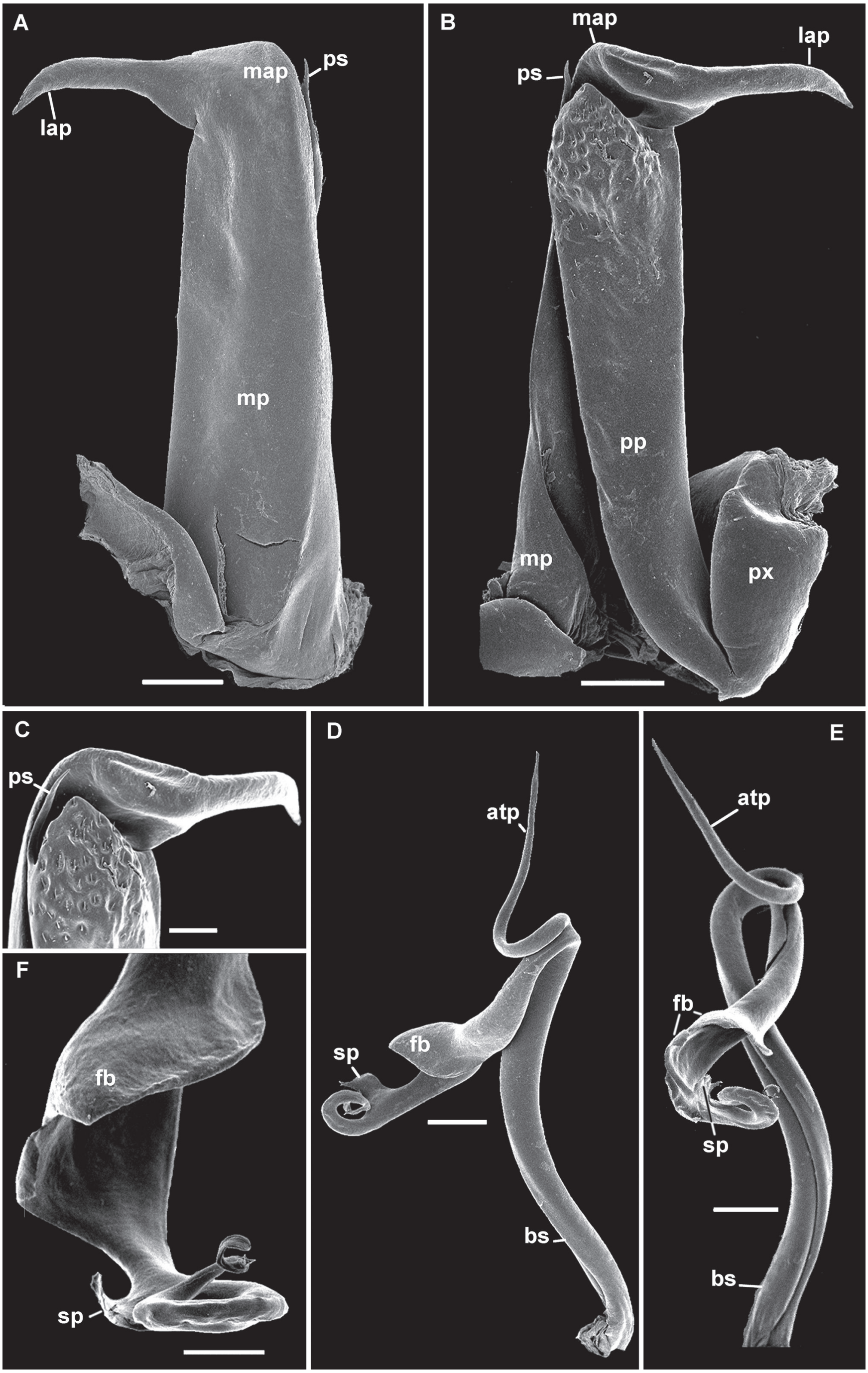

Figure 3. *Globanus drewesi* sp. nov. ♂ paratype. **A, B** left coxite, oral and caudal views, respectively **C** tip of left coxite, caudal view **D, E** left telopodite detached, anterior and posterior views, respectively **F** tip of left telopodite, posterior view. Abbreviations: atp = antetorsal process, bs = basomere, fb = flattened blade, lap = latero-apical process, map = meso-apical metaplical process, mp = metaplica, pp = proplica, ps = proplica spine, px = paracoxite, sp = subtriangular projection. Scale bars: 200 µm (**A**, **B**, **D**, **E**); 100 µm (**C**, **F**).

Etymology. Honours Bob Drewes, the collector.

Diagnosis. Distinguished from other species of the genus by the acuminate distal prolongation of the gonopod proplica. Post-torsal process of telopodite with two attached lamellae; apex rotated 360°ending in a tongue-shaped process.

Description. Holotype, adult male with 52 body rings (including preanal ring), length ca 65 mm (curved and broken), maximum body diameter 4.23 mm.

Colour (in alcohol) predominantly brownish; prozonae yellowish brown; metazonae, legs, and antennae dark brown.

Head without modifications, smooth and polished, interantennal isthmus 1.11 mm, interocellarial isthmus 1.15 mm; antennae short (55% of maximum body diameter), extending up to posterior edge of collum; sensory pits on antennomeres 5 and 6 present, on 5th antennomere smaller. Eyes reniform, ommatidia arranged in five series: 9-8-7-6-4 = 34, counted from behind (Fig. 2C). Gnathochilarium with a transverse row of about 10 setae along distal margin and 6 large setae on each lingual lamella; mentum elongate-triangular with a few setae and a well-marked submedian transverse groove (Fig. 2D, sg).

Collum subcylindrical, smooth, lateral ends with three submarginal striae (Fig. 2B).

Body rings circular (height/width ratio of midbody rings 0.98–1.0), no legless body rings in front of telson. Prozonae smooth, suture between pro- and metazonae straight. Metazonae equal in diameter to prozonae; metazonital striae present below ozopore level; ozopores starting with segment 6, rather vague, located just behind suture on midbody segments (Fig. 2B, oz). Paraprocts convex, distal margins set off by a submarginal groove. Hypoproct not fused to preceding segment.

First pair of male Iegs as shown in Fig. 2F, with 5 or 6 setose tubercles laterally; each prefemur with a prominent basal projection on anterior side and with short setae medially. Second pair of legs and penes as in Figure 2E. Walking legs rather short (length 61% of midbody diameter, only tarsi visible from above when stretched; Fig. 2E, H), distal third with ventral tibial pads extending to proximal third of tarsi. Tarsal claws long and curved, each with a small basal seta (Fig. 2I, s).

Gonopods with a small sternum; proplica (pp) slender, with an acuminate distolateral spine and a field of short setae proximal to it. Metaplica (mp) slender proximally, expanded distally to form a latero-apical metaplical process (lap), slightly projecting outside the body when at rest (Fig. 3A–C). Telopodite as shown in Figure 3D, E, placed on anterior side of gonopod, antetorsal process (atp) long and slender, originating near arculus. Torsate region comprising less than half of telopodite length, distal third giving rise to a flattened blade (fb) and, beyond this, to a subtriangular projection (sp) (Fig. 3D). Apex rotated 360° ending in a tongue-shaped process. Prostatic groove running straight to tip of solenomere, ending just before the tongue-shape process level to a small digit (Fig. 3F).

Paratype male agrees with holotype in all structural details, but females larger (up to 80 mm in length and ca 6 mm in diameter), with short legs (ca 60% of midbody diameter) devoid of tibial pads; the number of body rings also varies between specimens (up to 56 body rings including preanal ring). Vulvae placed vertically inside segment 3; no setae on vulvae.

The other characters agree with those of the holotype.

Distribution. The species seems to be endemic to São Tomé Island.

Relationships. Although the three species of *Globanus* are externaly very similar, the gonopod structure suggests that the new species is closer to *G. marginescaber*. In both species, the median lamella of the telocoxite shows a well-marked distal proplica spine, which is absent in *G. integer*.

***Globanus marginescaber* (Karsch, 1884)**

Figure 4

Spirostreptus (*Nodopyge*) *marginescaber* Karsch 1884: 58–59
Aulonopyge marginescaber Brolemann 1935: 63.
Globanus marginescaber: synonymy after Spelda (1993).

Material examined. Type material: not *Globanus marginescaber*, revised.

Other material: 13 ♂♂, 15 ♀♀, 1 juv., Príncipe Island, Bela vista, alt. 40 m, 1°37’10.8”N, 7°24’49.7”E, 9.II.2010, B. Drewes leg. (CAS 9032625); 6 ♂♂, 14 ♀♀, Principe, E side, road to Infante Henrique, alt. 115–150 m, 1°36’2.4”N, 7°24’56”E, 9.II.2010, B. Drewes leg. (CAS 9032624); 1 ♂, Príncipe, E side, road to Infante Henrique, alt. 115–150 m, 1°36’2.4”N, 7°24’56”E, 9.II.2010, B. Drewes leg. (CAS 9032437); 2 ♂♂, 7 ♀♀, Príncipe, slope of Pico Papagaio, alt. 315–550 m, 1°37’10”N, 7°23’28”E, 8.III.2010, B. Drewes leg. (CAS 9032621); 1 ♂, São Thomé, Morro Provaz Ridge, headwaters of Rio do Oro, alt. 1240 m, 0°17’38.8”N, 6°35’57.5”E, 3.III.2010, B. Drewes leg. (CAS 9032483); 1 ♂, Principe, Bela vista, alt. 40 m, 1°37’10.8”N, 7°24’49.7”E, 11.III.2010, B. Drewes leg. (CAS 9032482); 1 ♂, Príncipe, Morro Provaz ridge, alt. 1275 m, 0°7’20.9”N, 6°35’50.9”E; 5.III.2010, B. Drewes leg. (CAS 9032432); 1 ♂, Príncipe, slope of Pico Papagaio, alt. 315–550 m, 1°37’10”N, 7°23’28”E, 8.III.2010, B. Drewes leg. (CAS 9032488).

Diagnosis. Differs from *G. integer* by the presence of a distal proplica spine and from *G. drewesi* by the absence of a subtriangular projection in the distal third of the telopodite.

Description (based on specimens CAS 9032625). Length of males ca 55 mm, width of midbody metazonae ca 0.5 mm, length of females ca 55 mm, width of midbody ca 5 mm. Colour in alcohol brown, prozonae usually light brown; antennae and clypeolabral region light yellow-brown; venter and legs yellowish.

Somatic characters as in previous species (Fig. 4A).

Gonopods with a small sternum; proplica slender, with an acuminate distolateral spine and a field of short setae proximal to it. Metaplica slender proximally, expanded distally to form a lateral cone, slightly projecting outside body when at rest (Fig. 4B). Telopodite as shown in Figure 4D, placed on anterior side of gonopod; antetorsal process long and slender, originating near arculus. Torsate region comprising approximately half of telopodite length, proximal third giving rise to an acute lateral process; beyond this, telopodite slightly flattened and attenuating regularly towards tip (Fig. 4C). Prostatic groove running straight to tip of solenomere, ending just before telopodite apex.

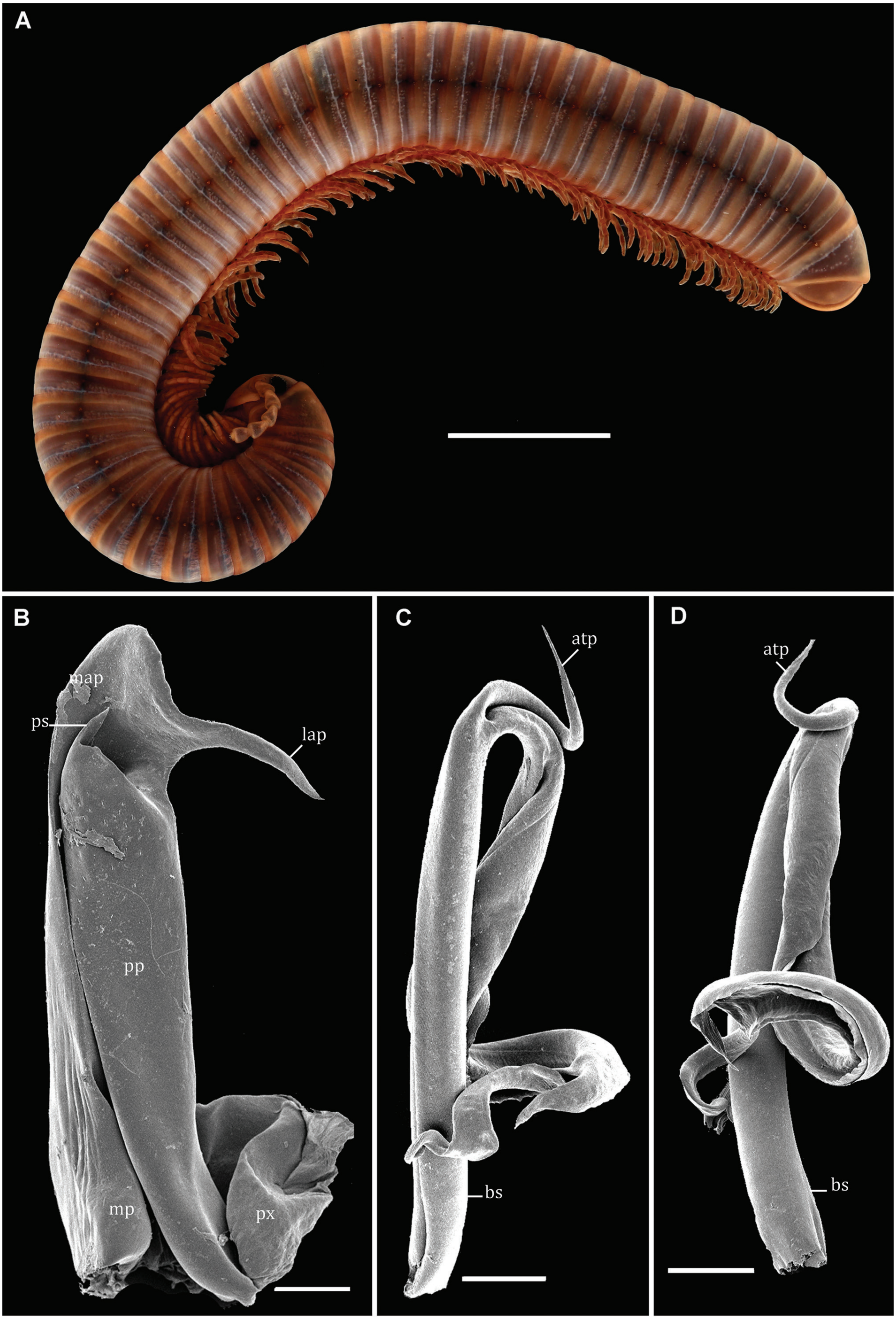

Figure 4. *Globanus marginescaber* (Karsch, 1884), ♂ topotype from Príncipe Island. **A** habitus, lateral view **B** left coxite, posterior view **C, D** right telopodite, posterior and mesal views, respectively. Abbreviations: atp = antetorsal process, lap = latero-apical process, , map = mesapical metaplical process, mp = metaplica, pp = proplica, ps = proplica spine, px = paracoxite. Scale bars: 5 mm (**A**); 200 µm (**B**, **C**, **D**).

Remarks. This species was originally described so poorly by Karsh (1884) from the female holotype that Attems (1914) considered it as a species *incertae sedis*. The holotype is still in the Berlin Museum (ZMB), but its revision reveals that actually it belongs to the family Harpagophoridae and is definitely not the true type of *marginescaber*. This was already observed by Richard Hoffman (pers. comm.), who suggested some mixing of labels, which must have occurred when the collection was re-organized. The first illustration of the gonopods was published in a text book by Brolemann (1935: 63), simply to show the complex conformation of a spirostreptid gonopod. Krabbe (1982), in her revision of the family Spirostreptidae, did not mention the species, but Spelda (1993) did and provided new drawings of the gonopods of both *Globanus* species then known from São Tomé and Príncipe. The gonopod structure of the specimen observed here agrees with the drawing presented by Spelda (1993) for *G. marginescaber*, except that our male shows no small spine beyond the lateral process. Another difference is the body size; the samples from the MNHN are much larger compared to the specimens collected by R.C. Drewes: males to only 11 cm long (maximum body diameter 0.9 cm) and females to 13.5 cm long (maximum body diameter 1 cm).

This species occurs both on São Tomé and Príncipe.

Globanus integer (Karsch, 1884)

Figure 5

Spirostreptus (*Nodopyge*) *integer* Karsch 1884: 57–58
Spirostreptus (*Nodopyge*) *molleri* Verhoeff 1892: 193–199
Scaphiostreptus molleri Attems 1914: 39
Rhopaloditius molleri Verhoeff 1938: 20
Globanus molleri Attems 1950: 188
Globanus integer: synonymies after Demange (1970).

Material examined. Type material: 1 ♂ syntype, São Thomé, Greeff leg. (ZMB 933).

Other material: 1 ♂, 1 ♀, São Thomé, Neves, 0°22'N, 06°34'E, in litter, cocoa plantation, 27.X.1999, W. Tavernier leg. (MRAC 18.531); 2 ♂♂, 8 ♀♀, 2 juv., São Thomé, Morro Provaz Ridge, alt. 1275 m, 0°17'20.9"N, 6°35'50.9"E, III.2010, B. Drewes leg. (CAS 9032433); 1 ♂, São Thomé, Nova Moca, alt. 920 m, 0°17'25.8"N, 6°37'58.1"E, 27.II.2010, B. Drewes leg. (CAS 9032435); 1 ♂, 1 ♀, São Thomé, Nova Moca, alt. 920 m, 0°17'25.8"N, 6°37'58.1"E, 27.II.2010, B. Drewes leg. (CAS 9032485); 8 ♀♀, São Thomé, Nova Moca, alt. 900 m, 0°17'25.8"N, 6°37'58.1"E; 27.II.2010, B. Drewes leg. (CAS 9032434); 2 ♂♂, 1 ♀, São Thomé, Nova Moca, alt. 900 m, 0°17'25.8"N, 6°37'58.1"E, 27.II.2010, B. Drewes leg. (CAS 9032436); 4 ♀♀, São Thomé, Nova Moca, alt. 920 m, 0°17'25.8"N, 6°37'58.1"E, 27.II.2010, B. Drewes leg. (CAS 9032484); 2 ♂♂, 8 ♀♀, 1 juv., São Thomé, Nova Moca, alt. 920 m, 0°17'25.8"N, 6°37'58.1"E, 27.II.2010, B. Drewes leg. (CAS 9036824).

Diagnosis. Differs from congeners by the absence of a distal proplica spine, telopodite distally stout and with attached, large, plate-like lamellae.

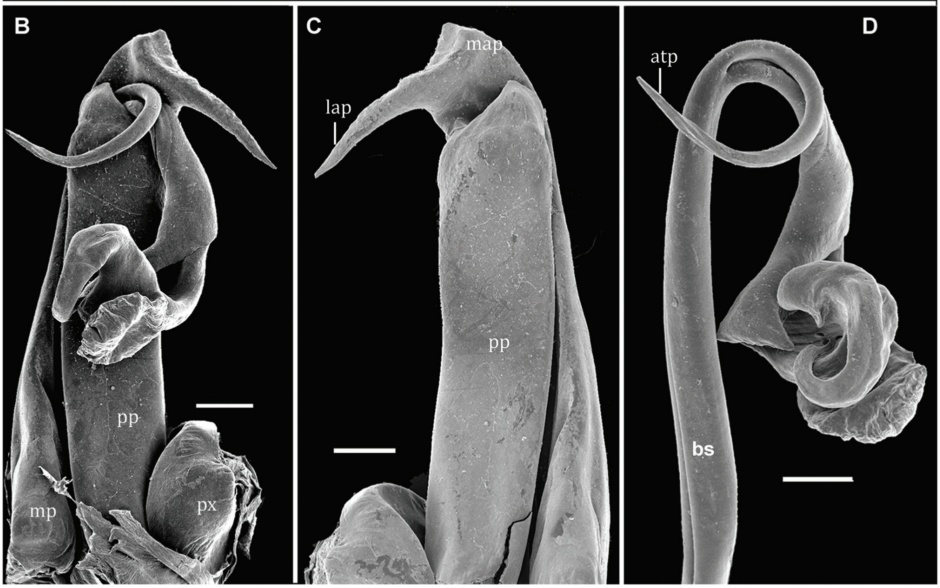

Figure 5. *Globanus integer* (Karsch, 1884), ♂ topotype. **A** habitus, lateral view **B** right gonopod, posterior view **C** left coxite, posterior view **D** right telopodite, posterior view. Abbreviations: atp = antetorsal process, bs = basomere, lap = latero-apical process, map = meso-apical metaplical process, mp = metaplica, pp = proplica, ps = proplica spine, px = paracoxite. Scale bars: 5 mm (**A**); 200 µm (**B**–**D**).

Figure 6. Distribution of *Globanus* species in São Tomé and Príncipe.

Remark. The gonopod structure of a topotype (Fig. 5) agrees closely with the drawings presented by Spelda (1993).

This species seems to be restricted to São Tomé Island.

Conclusion

Globanus trilobatus, originally described in the monotypic *Lobogonus* (Demange 1971) and then relegated to *Globanus* by Krabbe (1982), is returned to *Lobogonus* with that genus revalidated. A close examination of type specimens of *L. trilobatus* (in the MNHN) shows that species of these two genera are strikingly different both in habitus and gonopod structure and also have completely disjunct distributions. Thus, there is clear support for the separation of *Globanus* and *Lobogonus*.

The oligotypic genus *Globanus* currently encompasses three species and seems to be endemic to São Tomé and Príncipe islands. Among the species, only *G. marginescaber* occurs on both islands, while *G. integer* and *G. drewesi* sp. nov. apparenty are restricted to the larger São Tomé Island (Fig. 6). The trio may well be regarded as another example of "insular species swarms" among Diplopoda, however small, much like several others long reported from all main archipelagos of Macaronesia, as well as the Hawaiian Islands and New Caledonia (e.g. Enghoff 1992, 1993).

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We are most grateful to Dr R.C. Drewes, California Academy of Sciences, who made the material available for treatment and to Dr Jason A. Dunlop for sending us the type material of *G. marginoscaber*. We are also greatly obliged to Miss Aurore Mathys for taking the colour pictures.

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RESEARCH ARTICLE

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Sexual size and shape dimorphism in *Brachydesmus troglobius* Daday, 1889 (Diplopoda, Polydesmida)

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Abstract

Until now, morphological trait variation has been investigated in several millipede species using geometric morphometrics. The present study is the first attempt to explore sexual shape and size dimorphism (SShD and SSD) of morphological structures in Polydesmida. We here analyse antennal, head, and leg SShD and SSD in *Brachydesmus troglobius* Daday, 1889. Our results show that SSD exists in all of the analysed structures, while SShD is present only in the legs. In comparison with females, males possess longer and wider legs, as well as longer antennae and a shorter head. Contrary to previous findings in some Julida, in *B. troglobius* SSD of the antennae and legs varies more than SShD in these morphological structures.

Keywords

flat-backed millipedes, geometric morphometrics, intersexual morphological differences, polydesmidan millipedes, sexual shape dimorphism

Introduction

Sexual dimorphism (SD) is frequently studied in many biological fields and refers to any morphological, behavioural, physiological, and lifespan differences between the sexes (Fairbairn et al. 2007; Austad and Fischer 2016; Janicke et al. 2016). Besides sexual selection, the origin and maintenance of various forms of SD can be related to ecological factors (i.e., sex-specific interactions with the natural environment) or different behavioural traits (i.e., parental care, locomotor activity before mating, etc.) (Slatkin 1984). Intersexual morphological differences have been widely investigated in many arthropods (Walker and Rypstra 2002; Cooper 2014, 2016, 2017, 2018a, b; Virginio et al. 2015; Bidau et al. 2016; Medina et al. 2016; Ilić et al. 2017, 2019; Rohner et al. 2018). Secondary sexual traits were mostly investigated in these studies (Markow 1994; Watson and Simmons 2010).

Both sexual size and shape dimorphism (SSD and SShD, respectively) of morphological traits represent components of SD since both of them may be under different evolutionary pressures in females and males. To describe SD precisely, it is necessary to analyse both of the mentioned components (Berns 2013). Despite this fact, SShD was rarely investigated in comparison with SSD in numerous zoological studies (Cheng and Kuntner 2015). Like intersexual differences in size, shape differences can result from sex-specific behavioural peculiarities and ecological differences arising from specific ecological demands of the sexes (Butler and Losos 2002).

Millipedes represent one of the first arthropods colonizing terrestrial habitats. There is a need for better understanding of the morphological intersexual architecture of these ancient animals. Intersexual differences in the following traits have been investigated in several groups of millipedes: number of leg pairs and body segments (Verhoeff 1928; Mauriès 1987; Minelli and Michalik 2015); morphology and setation of the metaterga (Minelli and Michalik 2015; VandenSpiegel and Golovatch 2015); body size and body mass (Enghoff 1982; Adolph and Geber 1995; Rowe 2010; Cooper 2014, 2018a,b; Ilić et al. 2017); antennal length (Enghoff 1982; Ilić et al. 2017); leg length (Enghoff 1982; Rowe 2010; Ilić et al. 2017); head and trunk size (Ilić et al. 2017); morphology of anterior legs and mandibles (Minelli and Michalik 2015) and the gnathochilarium (Ilić et al. 2017); and that of the coxal glands (Hopkin and Read 1992). Further, SSD of body length, body mass, trunk height, trunk width, and antennal and leg centroid size (CS) was investigated in three diplopod species: *Pachyiulus hungaricus* (Karsch, 1881), *Megaphyllum unilineatum* (C.L. Koch, 1838), and *M. bosniense* (Verhoeff, 1897) (Ilić et al. 2019). In previous studies, shape differences of morphological traits were analysed using different methods. Specifically, in some julid species, Enghoff (1982) described body shape as the ratio between certain linear measurements, while Ilić et al. (2019) used the geometric morphometric technique (GM) to explore SShD. However, GM has never before been used to describe SShD of morphological traits in other diplopod groups, including Polydesmida.

In the present work, *Brachydesmus troglobius* Daday, 1889 was selected as a model-system to analyse SSD and SShD of three morphological structures, namely antennae, heads, and legs. Bearing in mind that it was previously shown that individuals of the sampled population of *B. troglobius* were in different phases of the life cycle in the Lazareva Pećina Cave (Ćurčić and Makarov 1998), we here analysed whether such life history differences influence the SSD and SShD of some morphological traits in this millipede species. The Lazareva Pećina Cave represents a complex underground system consisting of three levels (the two upper levels are fossilized, while the lowest one still functions as a permanent stream). The main corridors of this cave originated at the end of the Pliocene (Petrović 1958), but formation of the underground karst relief in this region had started already in the Lower Miocene. It is possible that colonization of the population of *B. troglobius* in the Lazareva Pećina Cave is not a recent event.

To our knowledge, this study represents the first attempt to analyse SSD and SShD of the head in Polydesmida. Bearing in mind the role that these body parts have during mating behaviour in Polydesmida (Snider 1981; Rowe 2010), we hypothesized that SSD and SShD exist in all of the aforementioned traits.

Materials and methods

Brachydesmus troglobius (Fig. 1A–C) is frequently found in caves, but also in epigean habitats in some European countries (Fig. 2) (Strasser 1971; Mršić 1985, 1988, 1994; Ćurčić and Makarov 1998; Tabacaru et al. 2002–2003; Makarov et al. 2004; Korsós et al. 2006; Antić et al. 2013; Angyal and Korsós 2013; Angyal et al. 2017). The analysed species belongs to the genus *Brachydesmus* Heller, 1858, which includes numerous species and subspecies (in many cases with dubious validity) with great diversity on the Balkan Peninsula (Makarov et al. 2004; Antić et al. 2013). In the present study, samples were collected at the main corridor (300 m from the entrance) of Lazareva Pećina Cave (eastern Serbia). The samples were collected during the 1997/1998 season. All specimens used in this study were preserved in 70% ethanol immediately after collecting and deposited in collections of the Institute of Zoology, University of Belgrade – Faculty of Biology. Three morphological structures (antennae, heads, and legs) were dissected and further used for analysing SSD and SShD.

Size and shape of the left and right antennae (average value of both antennae, in 28 females and 21 males), heads (in 27 females and 22 males), and both legs from the anterior leg-pair of the 10th body ring (average value of both legs in 28 females and 21 males) were analysed. First of all, each morphological structure was dissected using a Carl Zeiss Stemi-2000 binocular stereomicroscope. Photos of all morphological structures were taken with a Carl Zeiss Axiocam MRc camera. The Make Fan program (available at http://www3.canisius.edu/~sheets/IMP%208.htm) was used to create fans on each picture of the heads. In the TpsDig program (Rohlf 2008, available at http://life.bio.sunysb.edu/morph/soft-dataacq.html), 32 landmarks were positioned on pictures of antennae, 10 semi-landmarks and 5 landmarks were positioned on pictures of heads (lateral view), and 26 landmarks were positioned on each picture of legs (Fig. 3A–C). Centroid size (CS) for each morphological structure was calculated in the CoordGen6 program (Sheets 2003, available at http://www3.canisius.edu/~sheets/IMP%208.htm). Sexual shape differences were analysed using Canonical Variate Analysis (CVA), performed in the MorphoJ program (Klingenberg 2011, available at http://www.flywings.org.uk/morphoj_page.htm). Statistica 7 (StatSoft, Tulsa, OK, USA) was used to test intersexual differences in the CS of antennae, heads, and legs. The R program (R Core Team 2013) was used to visualize differences in CS values of the aforementioned traits. The distribution map was created using Google Earth Pro (version 7.3.2.5776).

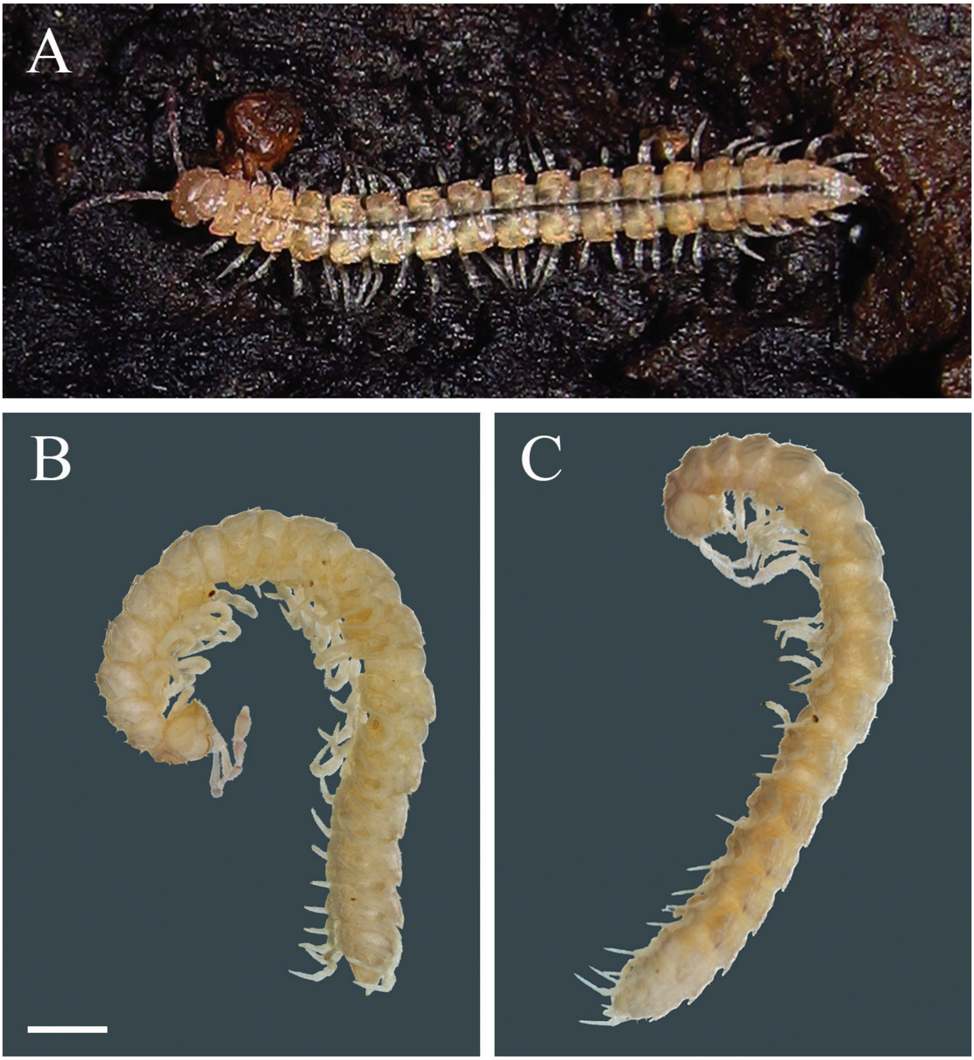

Figure 1. *Brachydesmus troglobius* Daday, 1889 **A** male photographed in Lazareva Pećina Cave **B** male **C** female. Photo credit: D. Antić (**A**), V. Vujić and B. Ilić (**B, C**). Scale bar: 1 mm (**B, C**).

Results

Intersexual differences of CS were present in all analysed structures (antennae: p = 0.0081; heads: p = 0.0481; legs: $p < 0.0001$) (Fig. 4A–C). Sexual shape dimorphism was present only in legs (antennae: p = 0.6319; heads: p = 0.0882; legs: p = 0.0008) (Figs 5–7). Males possess longer and wider legs in comparison with females (Figs 4C, 7), as well as longer antennae (Fig. 4A), while the opposite pattern was observed in analysis of intersexual differences in head CS (Fig. 4B).

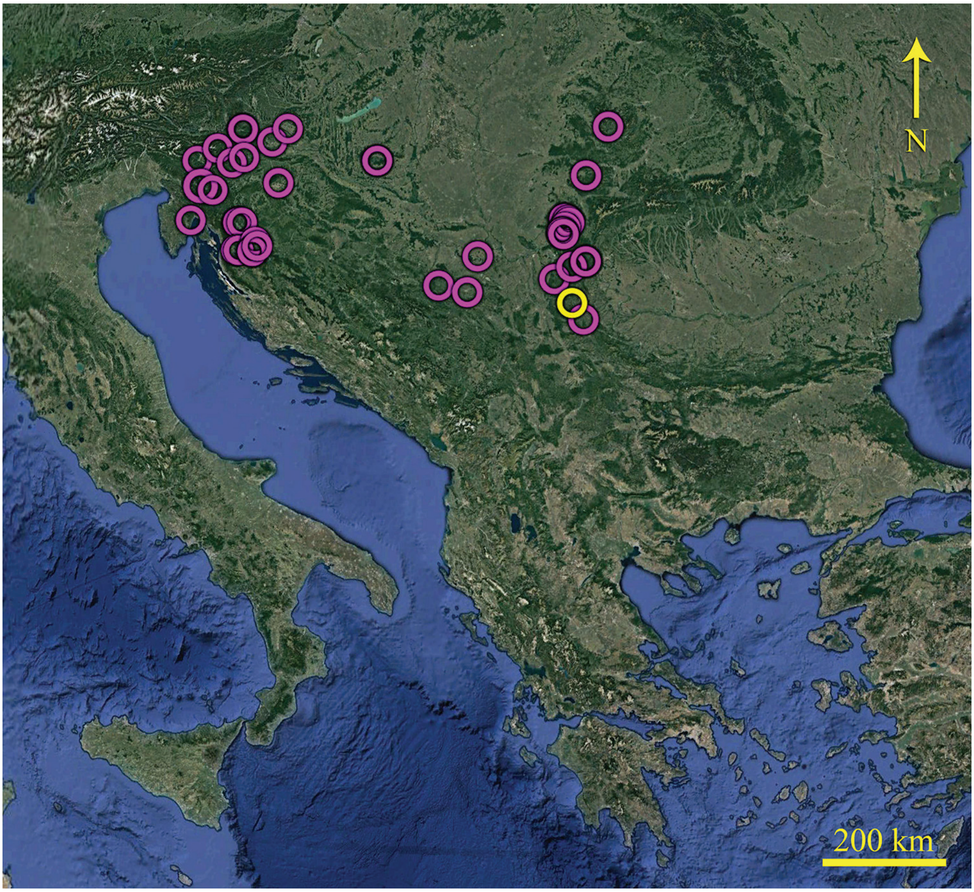

Figure 2. Distribution of *B. troglobius* (yellow circle- Lazareva Pećina Cave, and purple circles- literature records of *B. troglobius*).

Discussion

In polydesmidan millipedes, SShD has never been studied using both traditional and GM techniques. However, SSD in polydesmidan species has been investigated using linear body measurements (length and width), body mass, and leg length (Adolph and Geber 1995; Rowe 2010). Sexual size dimorphism in the aforementioned morphological traits has been examined in some millipede species. Intersexual differences of body dimensions and mass were investigated in two polydesmidan species, viz., *Nyssodesmus python* (Peters, 1864) (Adolph and Geber 1995) and *Cladethosoma clarum* (Chamberlin, 1920) (Rowe 2010); the callipodidan species *Apfelbeckia insculpta* (C.L. Koch, 1867) (Ilić et al. 2017); the julidan species *Cylindroiulus* sp. (Enghoff 1982) and *Pachyiulus hungaricus*, *Megaphyllum bosniense*, and *M. unilineatum* (Ilić et al. 2019); and the spirobolidan species *Chersastus* sp. (Cooper 2014) and *Centrobolus*

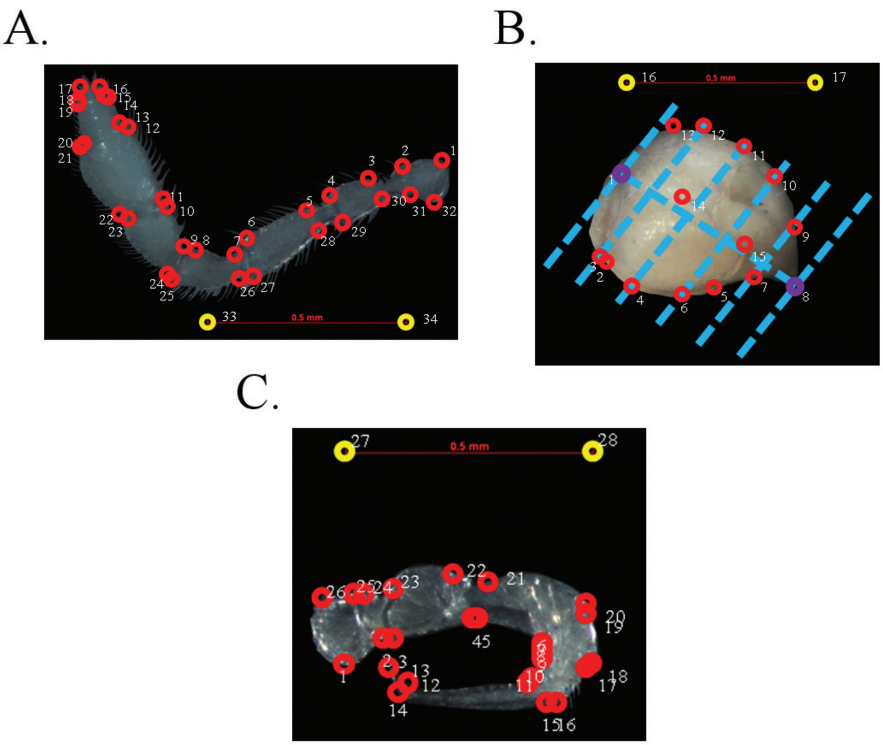

Figure 3. Position of landmarks and semi-landmarks (3, 4, 6, 7, 9–12 on the picture of head) on the analysed morphological structures **A** antenna **B** head **C** leg.

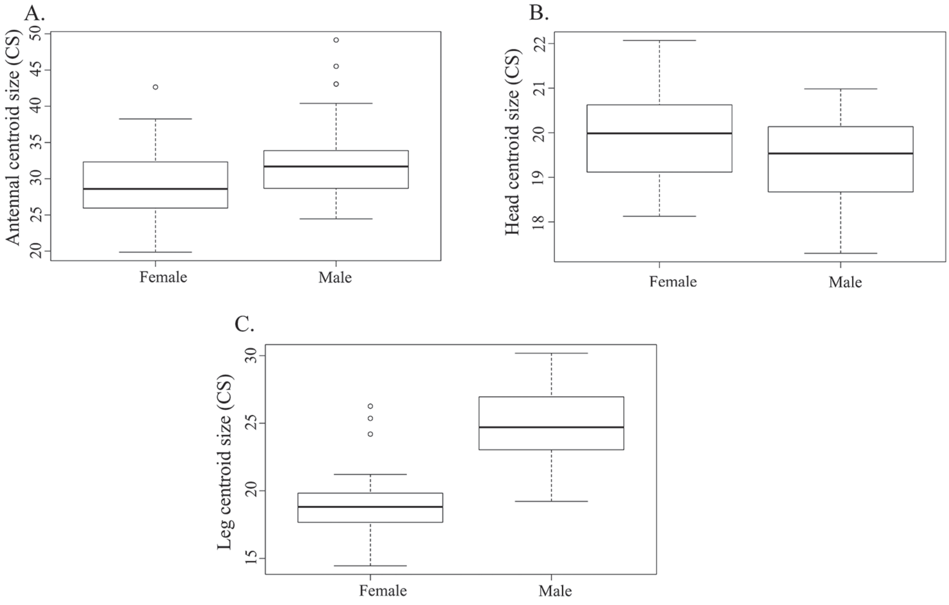

Figure 4. Intersexual differences in CS of: **A** antennae **B** heads **C** legs.

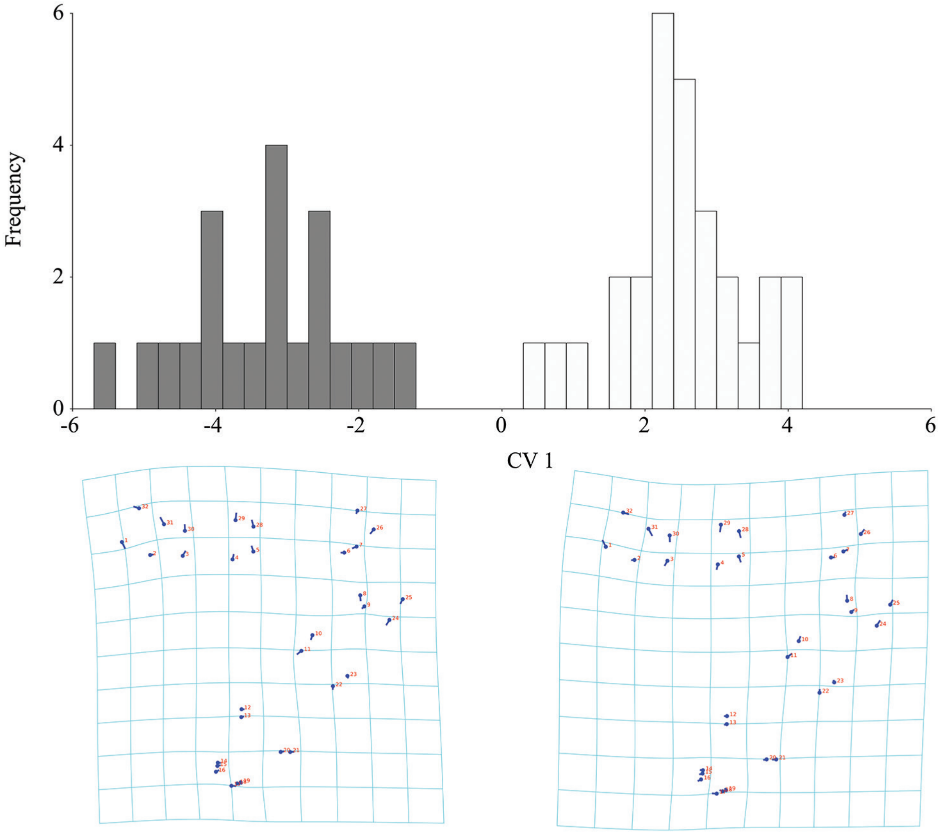

Figure 5. Intersexual differences of antennal shape in *B. troglobius* illustrated using Canonical Variate Analysis (CVA). Position and size of the vectors' influence on a thin-plate spline deformation grid and illustration of the pattern of intersexual differences of antennal shape (white bars indicate females; grey bars indicate males).

inscriptus (Attems, 1928), *Ce. fulgidus* (Lawrence, 1967), *Ce. ruber* (Attems, 1928), and *Ce. diagrammus* (Pocock, 1893) (Cooper 2018c). Also, SD of trunk dimensions was studied in *A. insculpta* (Ilić et al. 2017); and in *P. hungaricus*, *M. bosniense*, and *M. unilineatum* (Ilić et al. 2019). Sexual dimorphism of leg length, which is described as total length and/or length of individual podomeres, was investigated in *Cl. clarum* (Rowe 2010); in *A. insculpta* (Ilić et al. 2017); and in *P. hungaricus*, *M. bosniense*, and *M. unilineatum* (Ilić et al. 2019), as well as in several species of the genus *Cylindroiulus* (Enghoff 1982). Likewise, SD of antennal length has been analysed in all of the aforementioned species with the exception of *Cl. clarum*. Also, SD of the head and gnathochilarium was studied using traditional morphometric technique in the case of *A. insculpta* (Ilić et al. 2017). Additionally, in some of these studies, the shape of several morphological structures was described using different techniques. Thus, shape was described using only linear measurements in callipodidan species (Ilić et al. 2017), while shape variation was described using both ratios of linear measurements

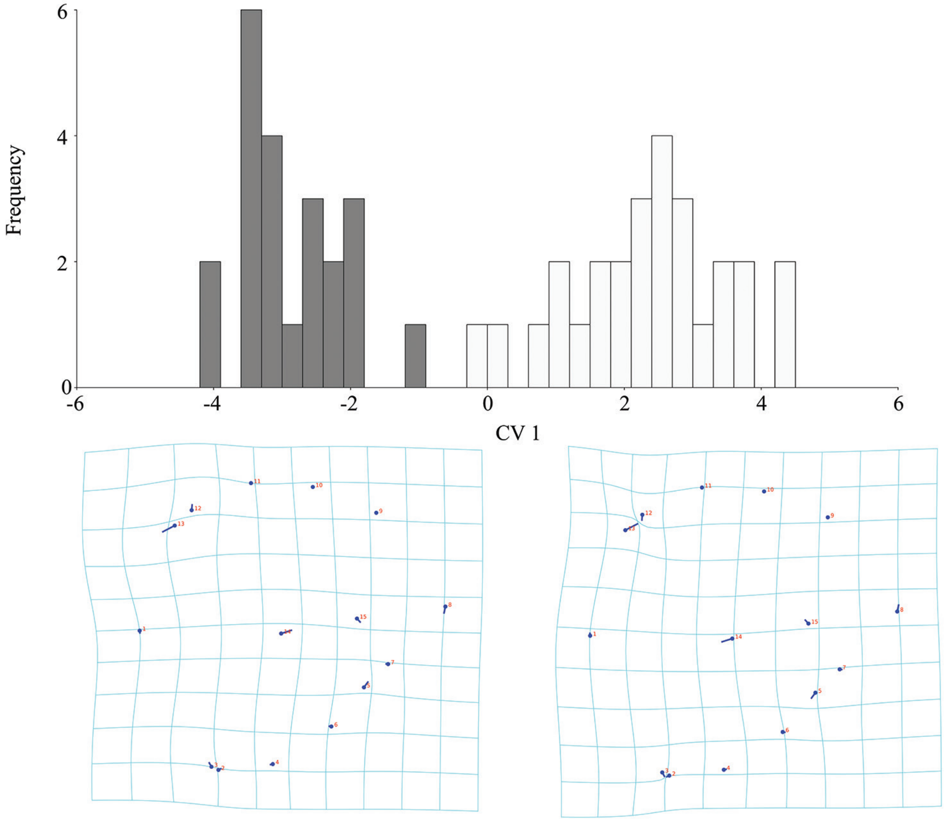

Figure 6. Intersexual differences of head shape in *B. troglobius* illustrated using Canonical Variate Analysis (CVA). Position and size of the vectors' influence on a thin-plate spline deformation grid and illustration of the pattern of intersexual differences of head shape (white bars indicate females; grey bars indicate males).

and the GM approach in some julidan species (Enghoff 1982; Ilić et al. 2019). Results obtained using the GM technique in the present study revealed that in *B. troglobius* SSD is present in all of the examined structures (antennae, heads, and legs), while SShD is present only in the legs. Our results indicated that females have shorter and narrower legs as well as shorter antennae than males. Rowe (2010) provided an explanation for the presence of longer legs in males based on positive correlations between leg length and motion speed, i.e., between leg length and the mate encounter rate. Thus, males with longer legs can find a suitable partner for mating more quickly. Also, longer legs in Polydesmida species could be important for mating success, since the male during mating firmly grasps the female with his legs (e.g., Harz 1962; Snider 1981; Tanabe and Sota 2008).

In addition, we found that females possess higher values of head CS in comparison with males, which is in agreement with the previously reported situation in the case of *A. insculpta* (Ilić et al. 2017). This result can be attributed to the presence of fecundity selection, implying that females spend more time feeding and/or nest building

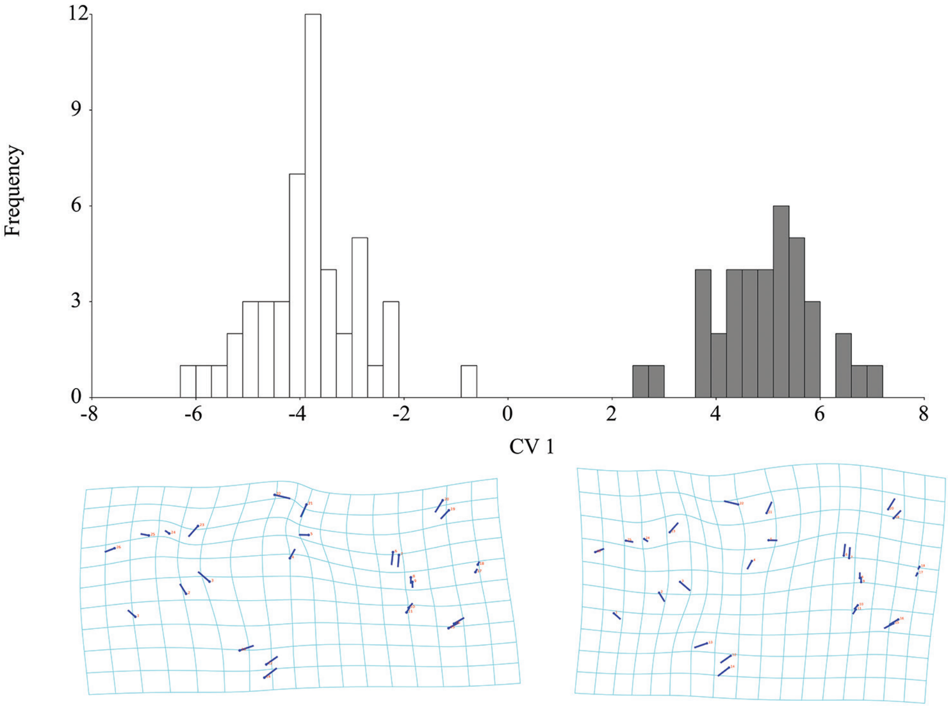

Figure 7. Intersexual differences of leg shape in *B. troglobius* illustrated using Canonical Variate Analysis (CVA). Position and size of the vectors' influence on a thin-plate spline deformation grid and illustration of the pattern of intersexual differences of leg shape (white bars indicate females; grey bars indicate males).

in comparison with males, which spend more time finding suitable mating partner. The females of *B. troglobius* are the larger sex and we presume that they invest more in offspring. Besides SSD, in the present study we also analysed SShD of the antennae, heads, and legs. Although intersexual differences of antennal and leg shape were previously studied using GM (Ilić et al. 2019), this is the first GM-based report on intersexual differences of head shape in millipedes.

The GM approach has been widely used to describe intersexual differences of morphological traits in arthropods (Benítez 2013; Fernández-Montraveta and Marugán-Lobón 2017; Gushki et al. 2018; Vesović et al. 2019). In millipedes, intersexual morphological differences were previously described by Ilić et al. (2019) using the GM technique. Our results indicated leg SShD in *B. troglobius*. This finding is in line with previously reported results indicating that leg SShD exists in some other julidan species, ones such as *P. hungaricus*, *M. unilineatum*, and *M. bosniense* (Ilić et al. 2019). In the case of antennal SShD, the results of our study are not concordant with previous findings in millipedes. In the present study, the presence of antennal SShD was not obtained in *B. troglobius*, whereas this pattern of SD was previously detected in two julidan species, *P. hungaricus* and *M. bosniense* (Ilić et al. 2019). As for antennal length SD, *B. troglobius* males possess longer antennae in comparison with females, whereas *P.*

hungaricus and *M. unilineatum* males possess shorter antennae than females (Ilić et al. 2019). *Brachydesmus troglobius* males possess longer legs in comparison with females, whereas leg SD was not detected in three julidan species, *P. hungaricus*, *M. unilineatum*, and *M. bosniense* (Ilić et al. 2019). In our opinion, this discordance in leg length between our findings and previously reported results could be associated with the different life histories of julidan (mostly iteroparous) and polydesmidan (all semelparous) species (Blower 1985; Bhakat et al. 1989; David 1992 and references therein; Hopkin and Read 1992; Minelli 2015). As semelparous species seek to maximize fitness by investing all energy and gametes in a single breeding season (Narum et al. 2008), it is reasonable to expect a tighter relationship between mating success and morphological traits associated with it. Furthermore, longer legs in polydesmidan males could be linked with the presence of scramble competition polygyny in millipedes (Telford and Dangerfield 1993; Rowe 2010; Holwell et al. 2016). One of the male behavioural types included in this system is maximization of fitness through investment in mate acquisition (Herberstein et al. 2017). This explanation is also supported by the fact that there is a positive correlation between speed and leg length in millipedes (Manton 1973). Apart from analysis of SD using GM, there are several studies of SD based on analyses of linear measurements (Rowe 2010; Cooper 2016; Ilić et al. 2017). Our results are in agreement with previously reported findings in *Cl. clarum*, in which males possess wider and longer legs in comparison with females (Rowe 2010), and with results reported for the callipodidan species *A. insculpta* indicating that females possess shorter legs than males (Ilić et al. 2017).

With respect to the head, no SShD was observed in *B. troglobius.* Our results also showed that females of *B. troglobius* have a longer head than males, which is in agreement with the previously reported situation in the case of *A. insculpta* (Ilić et al. 2017). For antennal SSD, Ilić et al. (2017) noted that males of *A. insculpta* possess longer antennae than females, the same as the pattern detected in *B. troglobius*.

Conclusion

No antennal SShD or head SShD was observed in the present study, although antennal and head SShD was present in some previously studied julidans, as well as head SShD in some callipodidans. However, leg SShD was detected in *B. troglobius*, in some julidan species, and one callipodidan species. The same patterns of intersexual differences of antennal and head length were detected in both *B. troglobius* and the callipodidan species *A. insculpta*.

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A second remarkable case of parapatry in a Tasmanian millipede genus (Diplopoda, Polydesmida, Dalodesmidae)

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Abstract

Tasmaniosoma armatum Verhoeff, 1936 and *T. orientale* Mesibov, 2010 are parapatric in northeast Tasmania, Australia. The parapatric boundary is ca 50 km long and mainly follows streamlines. Three sections of the boundary were intensively sampled. Two gonopod variants of *T. orientale* also appear to be parapatric.

Keywords

parapatry, *Tasmaniosoma*, Tasmania, Australia

Introduction

The endemic Tasmanian dalodesmid genus *Tasmaniosoma* Verhoeff, 1936 currently contains 22 species (http://www.millibase.org/aphia.php?p=taxdetails&id=892720 accessed 2019-07-03), some of which are distributed in mosaic parapatry. In a previous publication I documented a parapatric boundary ca 230 km long between *T. compitale* Mesibov, 2010 and *T. hickmanorum* Mesibov, 2010 in northwest Tasmania (Mesibov 2011). Here I document sections of a parapatric boundary ca 50 km long in eastern Tasmania between *T. armatum* Verhoeff, 1936 and *T. orientale* Mesibov, 2010. While the *compitale*/*hickmanorum* boundary crosses numerous streams and vegetation ecotones, the well-sampled sections of the *armatum*/*orientale* boundary mainly follow streamlines. Evidence is also presented for parapatry in two *T. orientale* gonopod variants.

Materials and methods

Millipede species

Tasmaniosoma armatum and *T. orientale* are very similar in size and coloration (Fig. 1) and females of the two species are currently indistinguishable. Adult males are readily identified to species by inspection of the gonopods under low magnification (Fig. 2). On the *T. armatum* telopodite, processes 1 and 2 (Fig. 2A) are both Y-shaped, often with a small tooth inside either Y. In *T. orientale*, process 1 is Y-shaped in some populations (Fig. 2B) and simply acute in others (Fig. 2C). Process 2 in *T. orientale* is never Y-shaped but varies in length and in the shape of the apex. In most populations process 2 is gently curved medially and has a slightly expanded, flattened apex with a few small marginal teeth (Fig. 2B, C).

Tasmaniosoma armatum occurs over ca 25000 km^2 on Tasmania's main island from sea level to ca 1100 m but is absent from both the western third and the northeast corner of the island (Fig. 3A). *Tasmaniosoma orientale* is restricted to ca 3000 km^2 in the northern portion of Tasmania's East Coast region (Fig. 3A), where it is found from sea level to at least 1000 m. Both millipede species are more abundant in open eucalypt forest and woodland than in wet eucalypt forest with a dense understory. Adults can be collected at any time of year during wet weather, but are more easily found in the cooler months (May to September). Both species wander at night as adults. During the day they shelter in loose-structured leaf, bark, and woody litter, under loose bark on standing trees, and occasionally under stones. When sheltering, *Tasmaniosoma* species rest full-length (not coiled) on damp surfaces largely free of dirt and fungal growth.

Millipede sampling

I searched for *Tasmaniosoma* spp. on 76 field days from 2012 to 2019 at 335 sites in the western portion of the *T. orientale* range (Fig. 3B). Another 17 sites on five field days were sampled by W. and L. Clarkson in 2012 and 2013. Searches were concentrated in the neighbourhood of the presumed parapatric boundary as its location became more apparent.

Most of the searching was done in the days immediately following rainy weather. In wet periods I sometimes found several adult *Tasmaniosoma* within the first 5–10 minutes at a site. During the prolonged dry periods of the last three years of the sampling (2017–2019), I often searched a suitable site for an hour or more without success.

Millipedes were usually collected live in the field in small, screw-capped, plastic vials loosely packed with damp paper or bark fragments. Specimens were later identified, preserved in 80% ethanol and deposited as registered lots (one lot per species per collection site) in the Queen Victoria Museum and Art Gallery, Launceston, Tasmania (QVM).

Figure 1. Adult males of *Tasmaniosoma armatum* Verhoeff, 1936 (top, QVM:2018:23:0093) and *T. orientale* Mesibov, 2010 (bottom, QVM:2018:23:0089). **g** indicates gonopods. The two males are from the Hop Pole Creek area (see Results section) and were collected at sites ca 0.5 km apart on the same day, 6 August 2018. Scale bar: 5 mm.

Most search sites were located in the field with a Garmin Etrex 10 GPS and the locations later checked by reference to aerial photography or satellite imagery on the LISTmap website (https://maps.thelist.tas.gov.au/listmap/app/list/map). The smallest coordinate uncertainty recorded for all sites was ±25 m, to allow for the area searched around the GPS latitude/longitude. For sites yielding only a single specimen, however, the uncertainty was closer to the GPS uncertainty, ca 15 m.

Locality data and graphics

Locality records for *T. armatum*, *T. clarksonorum*, *T. orientale* and unidentified *T. armatum/orientale* to 3 July 2019 are in Supplement 1 with the Darwin Core fields institutionCode, catalogNumber, phylum, class, order, family, genus, specificEpithet, scientificName, typeStatus, organismRemarks, identifiedBy, identificationRemarks, locality, country, stateProvince, decimalLatitude, decimalLongitude, geodeticDatum, coordinateUncertaintyInMeters, georeferenceSources, georeferencedBy, verbatimCo-

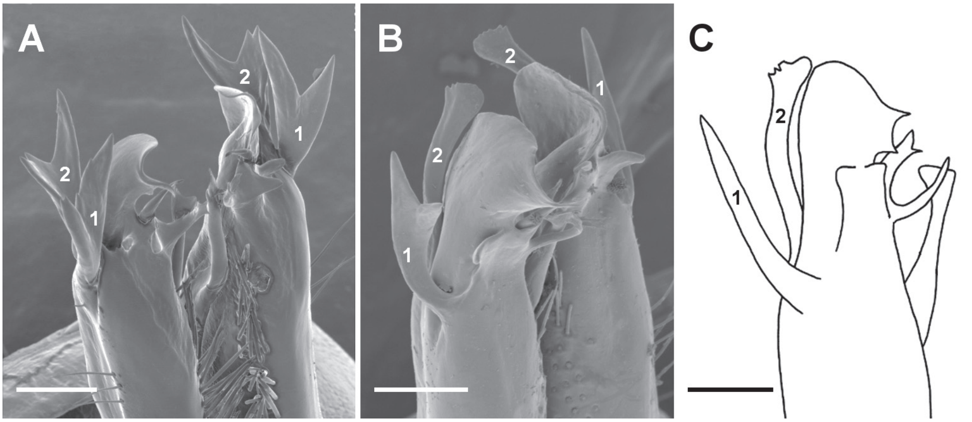

Figure 2. Posterolateral views of gonopod telopodite tips of *Tasmaniosoma armatum* Verhoeff, 1936 (**A** QVM:23:46567) and *T. orientale* Mesibov, 2010 (**B** QVM:23:46018 **C** QVM:23:51550, paratype). **1** = process 1, **2** = process 2. **C** shows left gonopod but is right-left reversed for easier comparison with **B**. **A–C** modified from Mesibov (2010). Scale bars: 0.1 mm.

ordinates, verbatimSRS, minimumElevationInMeters, maximumElevationInMeters, recordedBy, eventDate and eventRemarks.

The locality maps were generated using LISTmap tools from *theLIST* (https://maps.thelist.tas.gov.au/listmap/app/list/map), State of Tasmania. The background images (topographic maps, hillshaded maps and aerial photographs) are LISTmap background layers and the plotted points are from the author's KML files, imported into LISTmap as external services. Habitat photographs are by the author.

Results

Overview

The *T. armatum* and *T. orientale* distributions meet in a zone ca 50 km long running southeast from the Ben Lomond area at ca 700 m a.s.l. to the lower Swan River valley north of Swansea at ca 30 m a.s.l. (Fig. 3B). Enough native forest and woodland remains in three portions of the zone to allow fine-scale *Tasmaniosoma* mapping: (1) near Rossarden, (2) at the northern end of the Old Coach Road, and (3) near the West Swan River/Swan River junction (areas numbered 1, 2 and 3 in Fig. 3B). Distributions in these three areas are reported separately below.

Clearing of native vegetation for farms in the South Esk River, St Pauls River and lower Swan River valleys has largely eliminated *Tasmaniosoma* populations on the wider river flats. The present-day distributions (Fig. 3B) indicate that in pre-European times the zone may have followed the South Esk downstream to its junction with the St Pauls River, then followed the latter river upstream.

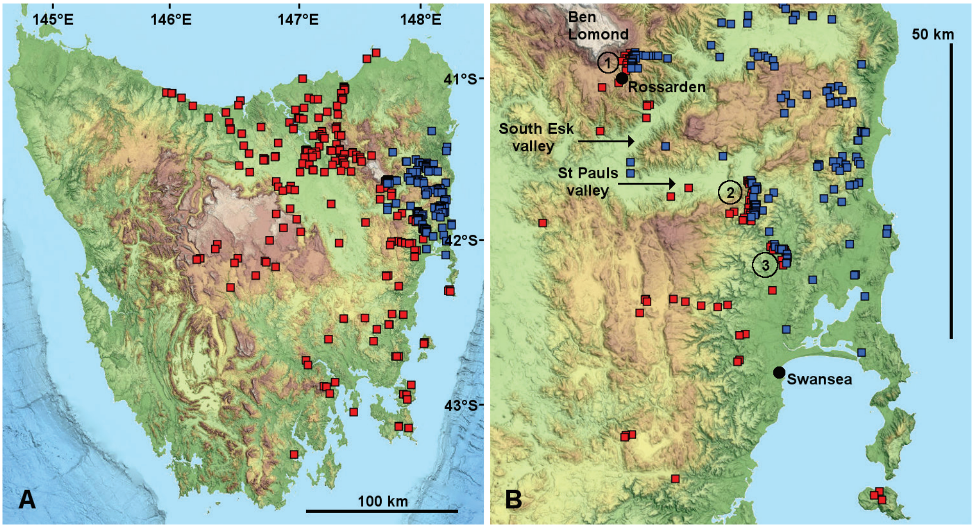

Figure 3. Known localities for *Tasmaniosoma armatum* Verhoeff, 1936 (red squares) and *T. orientale* Mesibov, 2010 (blue squares) as of 3 July 2019. **A** Overview of species ranges **B** Overview of parapatric zone. 1, 2 and 3 in **B** are the three areas shown in closer view in following figures.

I did not find *T. armatum* and *T. orientale* together at the same site anywhere in the area searched. Males with "anomalous" gonopods were collected at two sites; these are discussed below.

Near Rossarden

In dry eucalypt forest near Rossarden, *T. armatum* and *T. orientale* are parapatric along Aberfoyle Creek upstream to its junction with Mistletoe Creek (Fig. 4A). The parapatric boundary follows Mistletoe Creek upstream to ca 700 m a.s.l. in wet eucalypt forest, where the two *Tasmaniosoma* species are either absent or at very low abundance.

Mistletoe Creek is divided in the upper end of the parapatric zone into an ephemeral eastern branch and a perennial western branch. Between the two branches is a deposit of rocky rubble ("boulder bed" in Fig. 4A), lightly forested and up to ca 3 m deep. I did not find either *T. armatum* or *T. orientale* on this deposit, although *T. clarksonorum* and other native millipede species were present there in surface litter.

Tasmaniosoma clarksonorum Mesibov, 2010 is the dominant *Tasmaniosoma* species in wet eucalypt forest and rainforest at higher elevations in northeast Tasmania (Mesibov 2010). It is abundant at the northern, high-elevation end of the parapatric zone (Fig. 4B). *Tasmaniosoma clarksonorum* co-occurs with *T. armatum* and *T. orientale* in the riparian zones of both Aberfoyle and Mistletoe Creeks down to ca 550 m elevation.

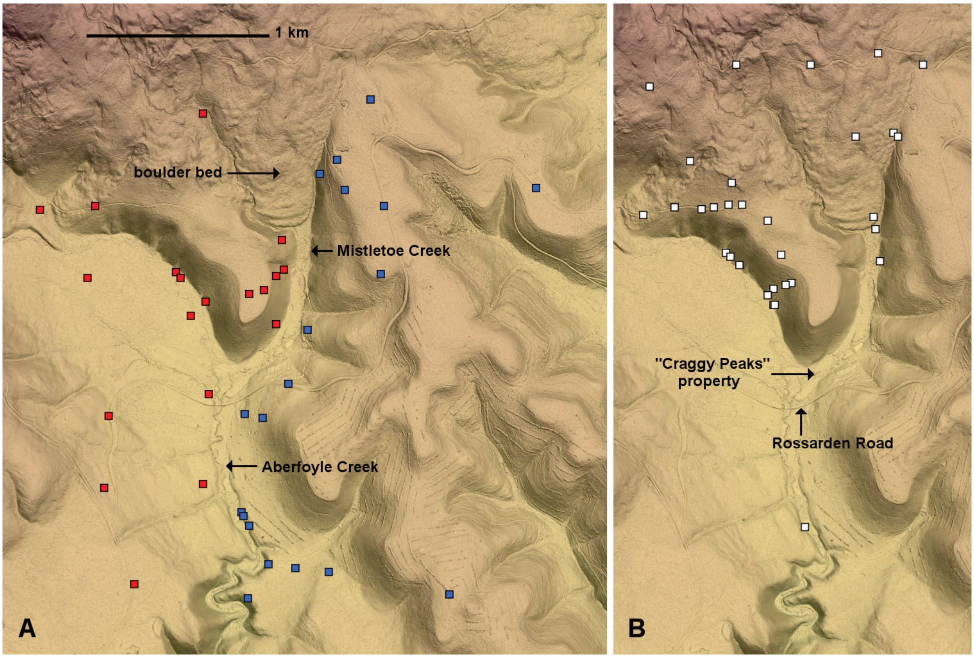

Figure 4. Known localities for *Tasmaniosoma* spp. near Rossarden as of 3 July 2019, on hillshaded terrain map. **A** *Tasmaniosoma armatum* Verhoeff, 1936 (red squares) and *T. orientale* Mesibov, 2010 (blue squares) **B** *T. clarksonorum* Mesibov, 2010 (white squares).

The south-facing hillslopes south of the Rossarden Road (Fig. 4B) to the South Esk River flat have been frequently burned, and *Tasmaniosoma* spp. are very hard to find in the dry eucalypt forest on these slopes. I found scattered *T. armatum* populations east of the lower portion of Aberfoyle Creek near the South Esk River flat, which may mean that the parapatric zone in that area (if it exists) is also further east.

The parapatric zone north of the Rossarden Road is on the “Craggy Peaks” private property (Fig. 4B), which in 2019 is a holiday resort with self-contained cabins. The Mistletoe Creek flat and part of the Aberfoyle Creek flat on “Craggy Peaks” were developed in the 20th century for a small golf course (labelled “Ben Lomond Golf Course” on some maps). The dry eucalypt forest on the hills sloping down to the grassy flats is in good condition (Fig. 5A) and supports a diverse native invertebrate fauna.

Northern end of the Old Coach Road

At the eastern end of the St Pauls River valley (Fig. 3B), the parapatric zone follows Hop Pole Creek and Marshes Creek upstream to the low watershed crossed by McKays Road (Fig. 6). From here the zone descends along Spratts Creek towards the junction with the West Swan River.

Figure 5. Views of dry eucalypt forest habitat. **A** Slope east of Mistletoe Creek (see Fig. 4), 12 June 2019 **B** Slope west of Hop Pole Creek (see Fig. 6), 2 July 2019.

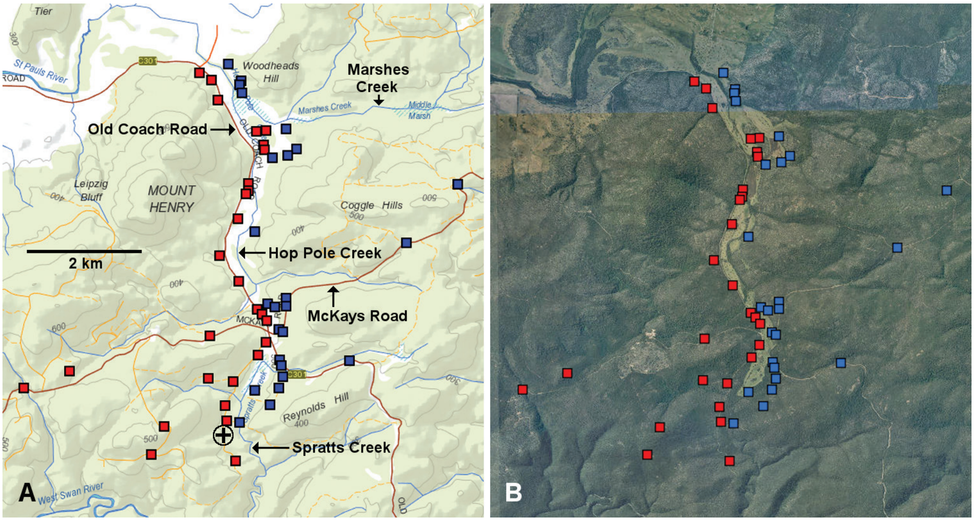

Figure 6. Known localities for *Tasmaniosoma armatum* Verhoeff, 1936 (red squares) and *T. orientale* Mesibov, 2010 (blue squares) at the northern end of the Old Coach Road as of 3 July 2019. **A** Topographic map with named features **B** Aerial photograph taken 25 February 2010. Circled black cross in **A** marks locality of *Tasmaniosoma* male with "anomalous" gonopods (QVM:2017:23:0173).

The Hop Pole Creek/Marshes Creek flat (= "Hop Pole Bottom" on some maps) and the upper portion of the Spratts Creek flat were cleared for farming in the 19th century and are privately owned. Despite many years of grazing by sheep, the surrounding low, rocky hills carry dry eucalypt forest in fairly good condition (Fig. 5B).

South of the Spratts Creek flat, the creek descends towards the West Swan River in a deep, narrow valley on Crown land. The deeper parts of the valley carry denser, somewhat wetter eucalypt forest and have not been sampled.

Near the West Swan River/Swan River junction

Tasmaniosoma armatum and *T. orientale* are separated by the Swan River for at least 3 km below its junction with the West Swan River (Fig. 7). Very little native vegetation remains in the Swan River valley below the junction and close to the river. I found a few specimens of *Tasmaniosoma* spp. in riparian and near-riparian remnants below the West Swan River/Swan River junction, but none downstream from the Blacks Creek junction with the Swan.

For at least 3 km above the junction, *T. armatum* and *T. orientale* are mainly separated by the West Swan River. In 2017, however, I collected a male *T. armatum* on the north bank, i.e. on the *T. orientale* side of the river (Fig. 7). Millipedes are very hard to find on the north bank, which carries sparse dry eucalypt forest on stony ground (Fig. 8A).

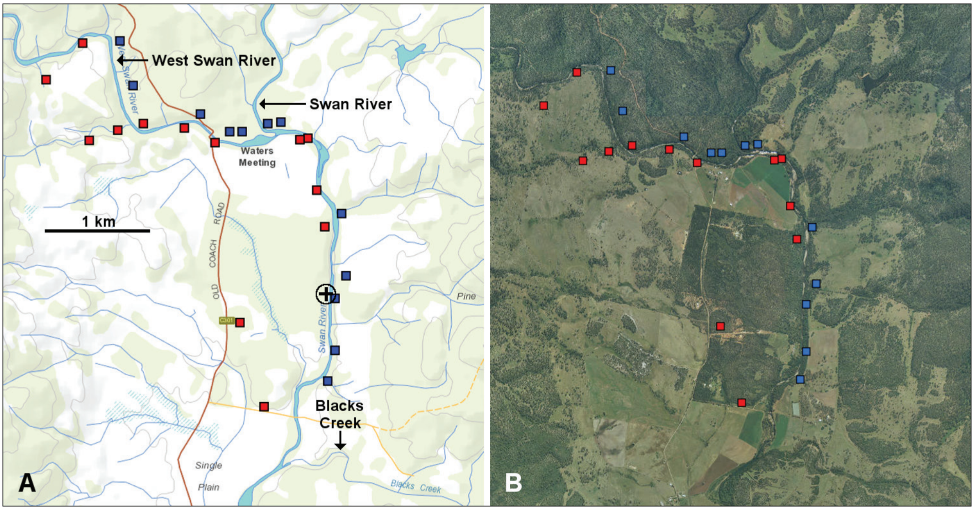

Figure 7. Known localities for *Tasmaniosoma armatum* Verhoeff, 1936 (red squares) and *T. orientale* Mesibov, 2010 (blue squares) near the West Swan River/Swan River junction as of 3 July 2019. **A** Topographic map with named features **B** Aerial photograph taken 1 December 2006. Circled black cross in **A** marks locality of *Tasmaniosoma* male with "anomalous" gonopods (QVM:23:54570).

This section of the parapatric zone is entirely on an assortment of private property blocks, with clearing for farms on the blocks beginning in the first half of the 19th century.

Males with "anomalous" gonopods

On gonopod morphology I was readily able to assign 325 males to *T. armatum* and 204 males to *T. orientale*. Two other males had a Y-shaped process 2 but a simply acute process 1 (QVM:23:54570) and a Y-shaped process 1 and a somewhat spear-shaped process 2 (QVM:2017:23:0173) (see also Fig. 2). Both were found in the parapatric zone (circled black crosses in Figs 6A, 7A) and may be hybrids.

Gonopod variants of *T. orientale*

The geographical distributions of Y-shaped and simply acute variants of gonopod process 1 in *T. orientale* are shown in Figure 8B, C. The two distributions are largely discrete, and there are several areas in the *T. orientale* range where the variants have been collected near each other and may be parapatric: near Scamander, in the Douglas-Apsley National Park, along the Coles Bay Road and at the junction of the West Swan and Swan rivers. In the latter case the two variants appear to be separated by the Swan River (Fig. 8C).

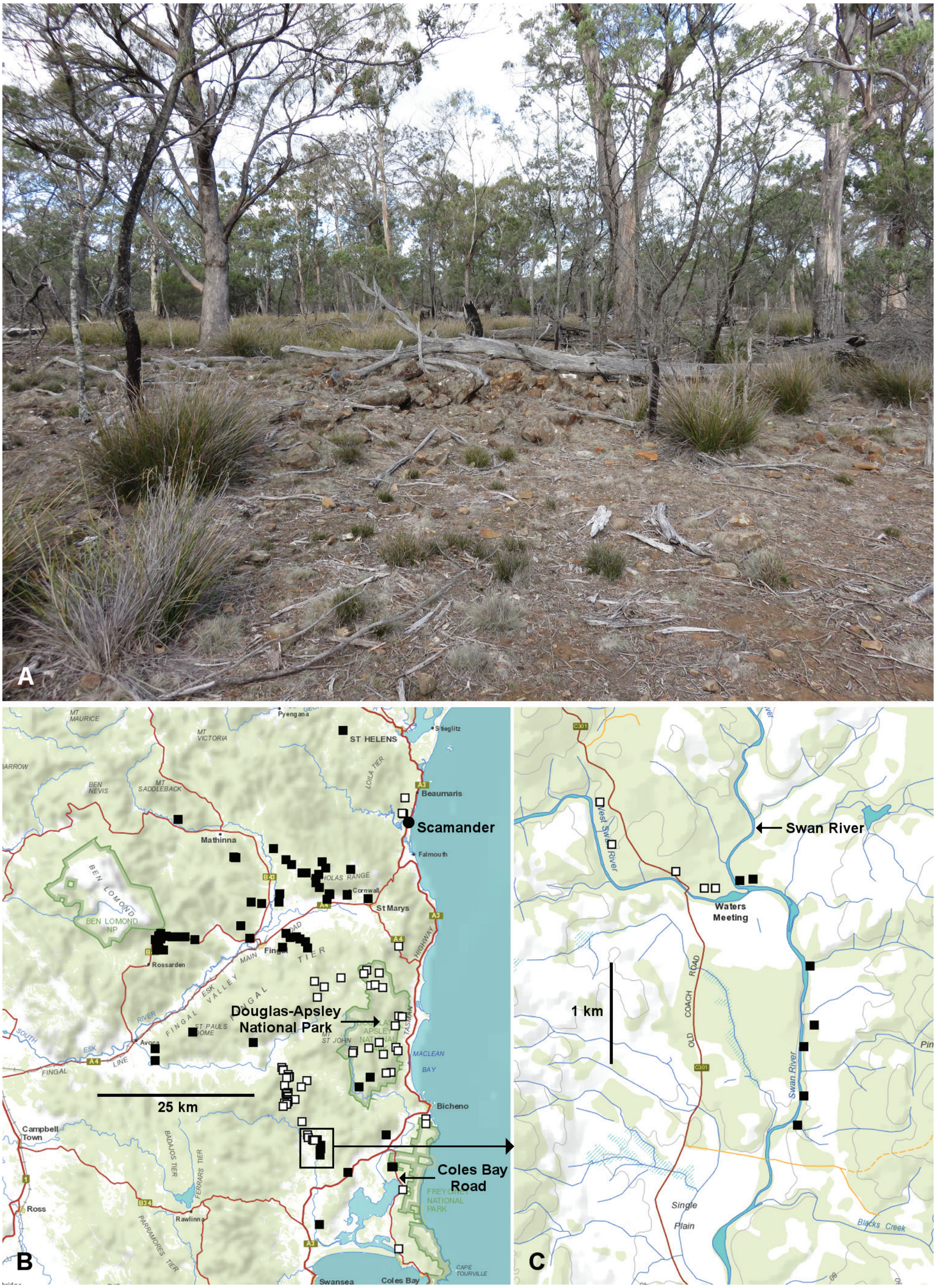

Figure 8. A View of dry eucalypt forest habitat on the north bank of the West Swan River near the West Swan River/Swan River junction (see Fig. 7), 1 July 2019 **B, C** Distributions of "Y-shaped" (black squares) and "simply acute" (white squares) process 1 variants of *Tasmaniosoma orientale* Mesibov, 2010 as of 3 July 2019 **B** Overview of *T. orientale* range **C** Near the West Swan River/Swan River junction.

Discussion

Tasmaniosoma armatum/*T. orientale* parapatry

I documented parapatry in *T. compitale* and *T. hickmanorum* (Mesibov 2011) as a knowledge base for future studies of millipede parapatry and speciation. The mapping of the *T. armatum* and *T. orientale* parapatric zone had a similar aim but was not as successful. Most of the native forest and woodland has long been cleared for farming in what might have been the parapatric zone in pre-European times, eliminating *Tasmaniosoma* populations. The mapping study was also limited by unfavourably dry weather during six of the seven sampling years, 2012–2019, and especially in the last three.

However, the maps presented here show that *armatum*/*orientale* parapatry in northeast Tasmania differs in one important respect from *compitale*/*hickmanorum* parapatry in northwest Tasmania. The northwest parapatric zone crosses numerous streams (Mesibov 2011: fig. 7B), while the northeast parapatric zone mainly follows streamlines. In northwest Tasmania there are numerous patches of continuous native forest within which *T. compitale* and *T. hickmanorum* are relatively abundant, and within which the parapatric zone can be crossed with a sampling transect. I found no such patches along the *armatum*/*orientale* boundary, although it is possible one exists in the lower Spratts Creek catchment (Fig. 6).

T. orientale gonopod variants

Gonopod variation in *T. orientale* may represent an ongoing lineage split or splits that will eventually result in two or more reproductively isolated species. The splitting may be occurring at more than one location in the *T. orientale* range, to judge from the somewhat complicated map of variant distributions (Fig. 8B). Genetic evidence is needed in future to determine whether the variants are already isolated in areas of close parapatry.

Future work

Besides the difference between the northwest and northeast *Tasmaniosoma* parapatric zones with respect to streamlines, three groups of more fundamental questions remain to be answered in each case: how is the parapatric boundary maintained; how, when and where did the parapatry originate; and how and when did the boundary arrive at its present position in the landscape?

Unfortunately, none of these questions can be answered from mapping evidence alone, as presented here. I have now retired from millipede studies, but I encourage other zoologists to study with genetic methods the tight parapatry documented in

Tasmaniosoma and a number of other well-mapped Tasmanian polydesmidan genera, including *Atrophotergum* Mesibov, 2004 (Mesibov 2004), *Dasystigma* Mesibov, 2003 (Mesibov 2003a), *Gasterogramma* Jeekel, 1982 (Mesibov 2003b), and *Lissodesmus* Chamberlin, 1920 (Mesibov 2006). Much of the Tasmanian landmass still carries native vegetation in good condition and the native litter fauna (especially of millipedes) is remarkably diverse. The island is a natural laboratory awaiting investigators interested in millipede biogeography on a fine scale.

Acknowledgements

For specimens and for assistance in the field in 2012 and 2013 I thank Wade and Lisa Clarkson (Riverside, Tasmania). I am very grateful to the many private landowners and land managers who gave me access to private properties for millipede collecting, especially Alastair Crisp ("Lewis Hill"), Adam Greenhill (Cranbrook), Paddy and Steph McShane ("Waters Meeting"), and the operators of the "Craggy Peaks" property.

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Supplementary material 1

Specimen data for *Tasmaniosoma armatum* Verhoeff, 1936, *T. clarksonorum* Mesibov, 2010, *T. orientale* Mesibov, 2010 and specimens not yet identifiable as *T. armatum* or *T. orientale*

Authors: Robert Mesibov

Data type: Occurrence

Explanation note: Data file Tasmaniosoma_specimen_data_2019-07-03.tsv. The file is a tab-separated table in UTF-8 encoding with the following Darwin Core fields: institutionCode, catalogNumber, phylum, class, order, family, genus, specificEpithet, scientificName, typeStatus, organismRemarks, identifiedBy, identificationRemarks, locality, country, stateProvince, decimalLatitude, decimalLongitude, geodeticDatum, coordinateUncertaintyInMeters, georeferenceSources, georeferencedBy, verbatimCoordinates, verbatimSRS, minimumElevationInMeters, maximumElevationInMeters, recordedBy, eventDate and eventRemarks.

Link: https://doi.org/10.3897/zookeys.930.38031.suppl1

ZooKeys 930: 103–115 (2020)
doi: 10.3897/zookeys.930.48438
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RESEARCH ARTICLE

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No Tömösváry organ in flat backed millipedes (Diplopoda, Polydesmida)

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Abstract

The Tömösváry organ is a sensory structure of the head in myriapods and some other terrestrial arthropods. Due to its variable shape, size, and position in millipedes (Diplopoda) the Tömösváry organ is commonly used as diagnostic character in taxonomic descriptions and often included in phylogenetic analyses. For the Polydesmida, the largest millipede order, the Tömösváry organ is inconsistently stated as being either absent or present as a pear-shaped pit covered by a membrane or cuticular disc. In order to resolve this inconsistency, we investigated the morphology of the presumable Tömösváry organ in four polydesmidan species based on paraffin-histology, semi-thin sections and micro-computed tomography. Our results unambiguously favor the view that the articulation of the cephalic tentorium with the head capsule was misidentified as the Tömösváry organ in previous studies, and thus that the Tömösváry organ indeed is absent in the Polydesmida. The pear-shaped pit proved to represent the distal roundish expansion of the incisura lateralis, to which – similarly as in julidan millipedes – the tentorial transverse bar is articulated. The absence of the Tömösváry organ in the Polydesmida does not affect the topology of the interrelationships among the millipede orders retrieved in previous cladistic analyses based on morphology. As a character shared by Colobognatha and Juliformia, however, absence of a Tömösváry organ in Polydesmida favors the optimization of its presence in nematophoran millipedes as a reversal. Further studies are needed to clarify whether among chilognathan millipedes a Tömösváry organ really exists in taxa such as Stemmiulida, and whether the Tömösváry organs are homologous across millipedes.

Keywords
Anatomy, Histology, Micro-Computed Tomography, Morphology, Tentorium

Introduction

The Tömösváry organ is a paired sensory organ, situated on the head of millipedes (Diplopoda) and other Myriapoda posterior of the antennal base. It is also referred to as postantennal organ (e.g., Altner and Thies 1976), temporal organ (e.g., Bedini and Mirolli 1967; Yamana et al. 1986) or in German as either "Schläfenorgan" (e.g., Tömösváry 1883; Latzel 1884; Verhoeff 1926–1928; Seifert 1932) or "Schläfengrube" (e.g., Vom Rath 1886) or as "foveae lateralis capitis" (e.g., Vom Rath 1886). The function of the Tömösváry organ is still unclear and several competing hypotheses exist, as discussed in detail by Müller and Sombke (2015), such as reception of vibration (e.g., Pflugfelder 1933; Meske 1961), olfaction (e.g., Zograf 1899; Bedini and Mirolli 1967), gravitation (e.g., Krishnan 1968), or humidity (e.g., Bedini and Mirolli 1967).

Tömösváry organs can be present in various shapes, forming a groove, pit or tube (Hennings 1906; Müller and Sombke 2015), and possess a sensory cavity with a thin and porous cuticle formed by a peg-like or hemispherical epidermis (Müller and Sombke 2015). In addition to studies on the physiology and morphology of the Tömösváry organ it is also used as an important taxonomic and phylogenetic character due to the variation in its shape, position or size (e.g., Hennings 1906; Attems 1926; Sierwald and Bond 2007; Blanke and Wesener 2014; Müller and Sombke 2015; Bouzan et al. 2017a, b). This is also true for the Polydesmida, where it has been coded in phylogenetic analyses as present and small (Blanke and Wesener 2014, characters 6 and 7) or as small pit (Sierwald and Bond 2007, character 18).

The order Polydesmida is the most diverse order of the millipedes (Diplopoda), with more than 5000 described species (Brewer et al. 2012) in 30 families (Shelley 2002), which contribute to over a third of the more than 12,000 known millipede species. The flat body of the blind Polydesmida consists of usually 17 or 18 fully fused body-rings (plus one apodous ring and telson) with large paranota (Enghoff et al. 2015), a habitus known as litter-splitter (Golovatch and Kime 2009).

There is uncertainty about the absence or presence of the Tömösváry organ in the Polydesmida. Its presence in Polydesmida was first stated by Attems (1899) and subsequently reported by him repeatedly (e.g., Attems 1926, 1937). Since the first detailed description of the presumable Tömösváry organ in the Polydesmida by Hennings (1906), this peculiar organ has not been re-examined for the order. Attems (1926) questioned its presence in some genera of the Polydesmida (Attems 1926, p. 55), while Verhoeff (1926–1928) depicted the Tömösváry organ for *Coromus thomsonii* (Verhoeff 1926–1928, p. 771, fig. 364), and Snodgrass (1952) described a Tömösváry organ for *Apheloria coriacea*. Seifert (1932), in contrast, stated its absence in the Polydesmida

(Seifert 1932, p. 436), without referring to previous records. Apparently Richard L. Hoffman likewise affirmed absence of the Tömösváry organ in the Polydesmida in an unpublished manuscript (P. E. Marek, pers. comm. December 2019). Although it seems to be mostly accepted among some taxonomic experts that the Tömösváry organ is absent in the Polydesmida (W. A. Shear and P. E. Marek, pers. comm. 12th May 2017) it is still stated as being present in recent cladistic analyses and taxonomic descriptions (e.g., Sierwald and Bond 2007; Blanke and Wesener 2014; Enghoff et al. 2015; Müller and Sombke 2015; Bouzan et al. 2017a, b), usually with reference to Hennings (1906) or Attems (1926).

In this study we aim to clarify whether the Tömösváry organ is present or absent in the Polydesmida, and which structure was originally described by Hennings (1906).

Material and methods

Specimens and data deposition

Four species representing four families (Polydesmidae, Paradoxosomatidae, Oxydesmidae, Gomphodesmidae) and three suborders (Polydesmidea, Strongylosomatidea, Leptodesmidea) were investigated. Specimens of *Polydesmus angustus* (Latzel, 1884) were collected in April 2015 in the Kottenforst (50°41'05.3"N, 07°05'19.4"E, Bonn, Germany) and fixed in Bouin-solution for paraffin-histology and micro-CT scanning, or in Karnovsky fixative (2.5% glutaraldehyde, 3.2% paraformaldehyde in 0.1M salted phosphate buffer, pH 7.2) for semi-thin sections. Furthermore, for investigations with micro-CT only, specimens of *Oxidus gracilis* (Koch, C. L., 1847) (collected in the Botanical Garden of the University of Bonn, Germany in April 2018), *Coromus vittatus* (Cook, 1896) (obtained via the pet trade from Nigeria) and *Tymbodesmus* sp. (obtained via the pet trade from Cameroon) were fixed in Bouin-solution. Micro-CT data and histological images of *Polydesmus angustus* are deposited on Morphobank (O'Leary and Kaufman 2011, 2012) under project number 3582 (http://morphobank.org/permalink/?P3582). The specimens studied by micro-CT are stored in the Zoological Research Museum Alexander Koenig (ZFMK) as vouchers (see Table 1).

Table 1. Taxon sampling and scanning parameters for micro-computed tomography.

	ID	Location	Voltage	Current	Pixel size	Exposure	Rotation steps	Rotation	Averaging
Polydesmus angustus	ZFMK-MYR08922	Kottenforst, Bonn, Germany	40 kV	200 µA	2.6 µm	1659 ms	0.1°	180°	7
Oxidus gracilis	ZFMK-MYR08923	Botanical garden, Bonn, Germany	50 kV	200 µA	1.2 µm	500 ms	0.1°	180°	7
Coromus vittatus	ZFMK-MYR08924	Pet trade, Nigeria	60 kV	166 µA	3.6 µm	500 ms	0.1°	180°	7
***Tymbodesmus* sp.**	ZFMK-MYR08925	Pet trade, Cameroon	43 kV	200 µA	1.8 µm	1800 ms	0.15°	360°	10

Histology

Following Hennings (1906) histological sections were acquired of specimens embedded in paraffin wax. Specimens fixed with Bouin-solution were decalcified in 5% nitric acid for 6 hours before embedding in paraffin (Paraplast, Sigma-Aldrich). Sections with a thickness of 7 µm were obtained with a Leica RM2165 microtome and stained with a trichrome Azan-staining. To obtain semi-thin sections, specimens fixed in Karnovsky fixative for one hour and decalcified in 5% nitric acid were embedded into an Epon-Araldite epoxy resin (Electron Microscopy Science). Semi-thin sections of the specimen's head with a thickness of 1 µm were made with a Diatome Histojumbo Hj4237 diamond knife at a Reichert Ultracut S ultramicrotome (Leica). The semi-thin sections were stained with Toluidine blue. Sections were photographed with a dotSlide Olympus BX51 light microscope and the software dotSlide 2.5 (Olympus Soft Imaging Solutions GmbH). The digital images were aligned in an image stack with the software Imodalign (B. Quast, https://www.q-terra.de/biowelt/3drekon/tools/imodalign/imodalign.htm).

Micro-computed tomography (micro-CT) and visualization

For micro-CT scanning one specimen each fixed in Bouin-solution of *Polydesmus angustus* (Latzel, 1884), *Oxidus gracilis* (Koch, C. L., 1847), *Coromus vittatus* (Cook, 1896) and *Tymbodesmus* sp. were transferred to 96% ethanol via an ascending ethanol series and stained with 3% Iodine solution for 24 hours. The specimens were washed in 100% ethanol and critical point dried using a Leica EM CPD 300. Micro-CT scanning was performed at the ZFMK using a SKYSCAN 1272 (Bruker micro-CT) with random movement = 15 and flat-filed correction and geometric correction switched on. For varying scanning parameters see Table 1. Post-alignment, ring-artefact reduction, beam-hardening correction and reconstruction were performed in NRecon 1.7.1.6 (Bruker microCT). The image stacks were modified using Fiji ImageJ 1.50e (Schindelin et al. 2012). Volume rendering was performed in Drishti Version 2.6.3 (Limaye 2012). Segmentation was done in ITK-SNAP 3.6.0 (Yushkevich et al. 2006). Images were edited in GIMP version 2.10.6 (https://www.gimp.org) and Inkscape 0.92 (www.inkscape.org).

Results

In all studied species the structure described as Tömösváry organ (Fig. 1A, *) in previous studies demarcates the distal roundish expansion of the incisura lateralis (Fig. 1B, C). At this point of the incisura lateralis the transverse bar of the tentorium projects through the head capsule. From the outside the tip of the transverse bar appears oval in shape and is surrounded by a rim (Figs 1C; 2A–C) formed by the cephalic cuticle

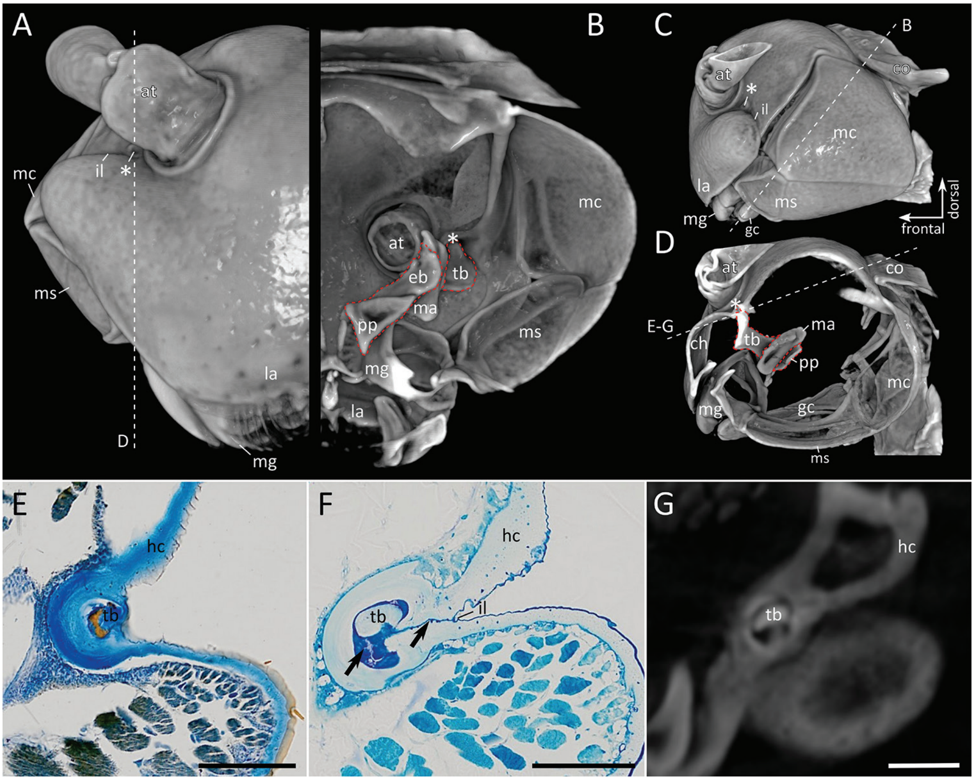

Figure 1. *Polydesmus angustus*, head **A–D** volume rendering based on micro-CT data: **A** Frontal view **B** cross-section, posterior view, plane indicated in C **C** lateral view **D** sagittal view, cutting plane indicated in A **E–G** details of connection of tentorial transverse bar to head capsule at incisura lateralis, plane as indicated in D: **E** histological section (Paraffin, Azan-staining) **F** histological section (Araldite, Toluidine blue) **G** optical section of micro-CT scan. Abbreviations: at = antenna, co = collum, eb = epipharyngeal bar of tentorium, gc = gnathochilarium, gls = gnathal lobe sclerite, hc = head capsule, il = incisura lateralis, la = labrum, mc = mandibular cardo, mg = mandibular gnathal lobe, ms = mandibular stipes, pp = posterior process of tentorium, tb = transverse bar of tentorium. Asterisk (*) indicates structure previously interpreted by Hennings (1906) as the Tömösváry organ in the Polydesmida. In the volume renderings the tentorium is marked with a red dotted line. Scale bar: 100 µm (**E–G**).

(Figs 1D; 2D–F). The cuticle of the head capsule is soft in this region and surrounds the tip of the transverse bar completely (Figs 1E, F; 2G–J). While in *Polydesmus angustus* and *Oxidus gracilis* the transverse bar does not project over the level of the surrounding cuticle (Figs 1A, D; 2A, D), it is more exposed in *Coromus vittatus* and *Tymbodesmus* sp. (Fig. 2B, C, E, F). No structure similar to a Tömösváry organ in other millipedes is associated with the flexible connection of the transverse bar to the head capsule.

The general structure of the tentorium of the studied species is the same as described by Seifert (1932) for *Strongylosoma pallipes*. The transverse bar (tb) extends from the incisura lateralis (Fig. 3A) posteriorly and bends mesially off about 90°, where

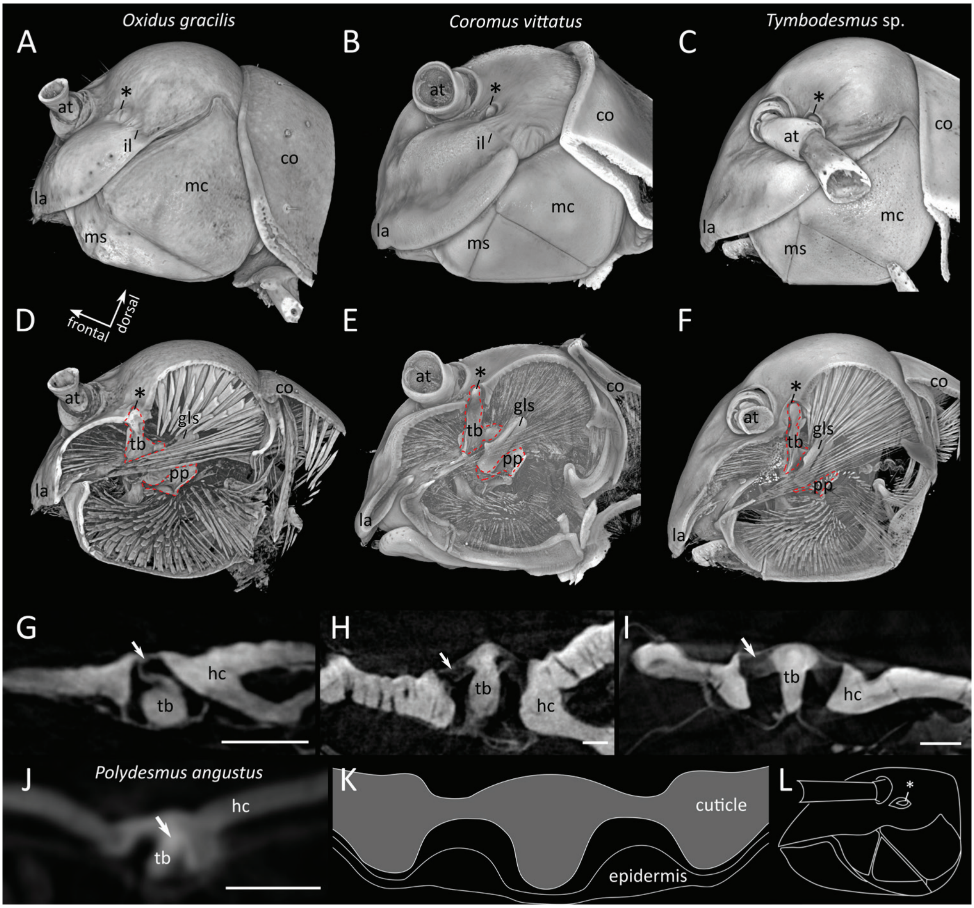

Figure 2. Articulation of the tentorial transverse bar to the head capsule in the Polydesmida **A–C** head in lateral view (anterior is left), volume rendering **D–F** head, sagittal section through tentorial transverse bar, volume rendering **A, D, G** *Oxidus gracilis* **B, E, H** *Coromus vittatus* **C, F, I** *Tymbodesmus* sp. **J** *Polydesmus angustus* **G–J** optical cross sections **K, L** the Tömösváry organ in *Eurydesmus laxus* after Hennings (1906): **K** cross-section, modified from Hennings (1906, plate XXXI, fig. 11) **L** head in lateral view, modified from Hennings (1906, plate XXXI, fig. 9). Abbreviations: at = antenna, co = collum, gls = gnathal lobe sclerite, hc = head capsule, la = labrum, mc = mandibular cardo, ms = mandibular stipes, tb = transverse bar of tentorium, pp = posterior process of tentorium. Asterisk (*) indicates the structure previously interpreted by Hennings (1906) as Tömösváry organ. In the volume renderings the tentorium is marked with a red dotted line. Arrows indicate the flexible connection of transverse bar and head capsule. Scale bars: 100 µm (**G–J**).

it becomes plate-like. Along its mesal extension towards the preoral chamber the tb serves as insertion for the anterior tentorial muscle (t1) which originates from the head capsule. Antero-laterally the transverse bar passes over into the epipharyngeal bar (eb) (Fig. 3B). On its distal tip the dorsal tentorial muscle (t2) inserts, which originates from the head capsule mesal of t1. Posteriorly the epipharyngeal bar passes

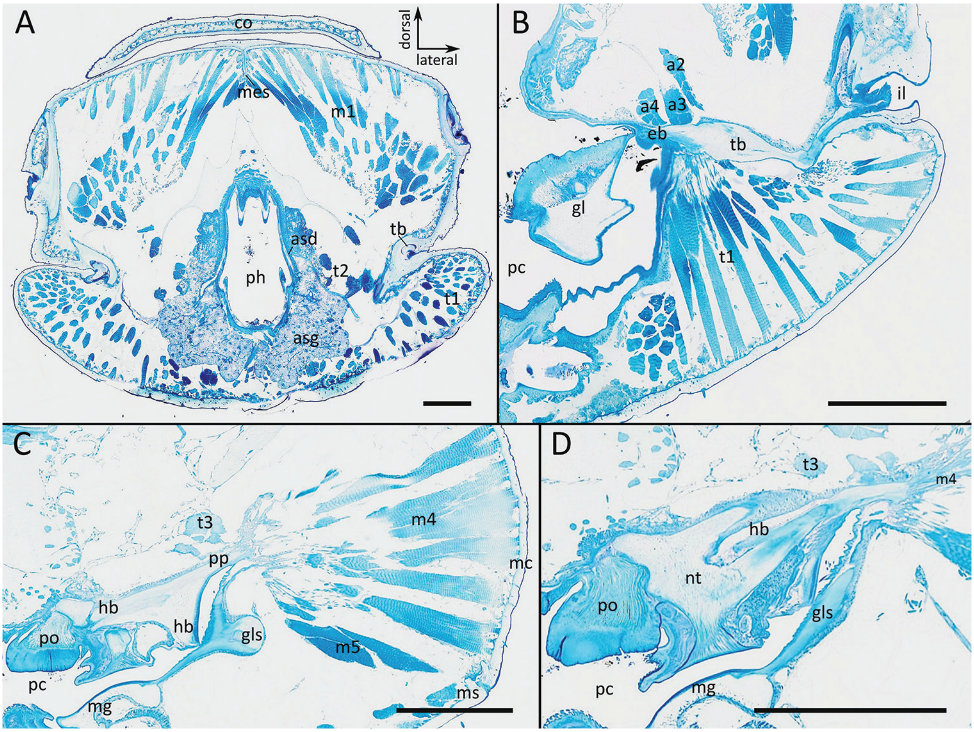

Figure 3. *Polydesmus angustus*, histological sections from anterior (**A**) to posterior (**D**) **A** articulation of tentorial transverse bar to head capsule **B** tentorial transverse bar and epipharyngeal bar **C** tentorial hypopharyngeal bar and posterior process **D** articulation of tentorium to "Nebententorium". Abbreviations: a2 = medial antennal muscle, a3 = lateral antennal muscle, a4 = anterior antennal muscle, asd = duct of anterior salivary gland, asg = anterior salivary gland, co = collum, eb = epipharyngeal bar of tentorium, gl = mandibular gnathal lobe, gls = gnathal lobe sclerite, hb = hypopharyngeal bar of tentorium, m1 = gnathal lobe sclerite muscle, m4 = anterior mandibular cardo muscle, m5 = posterior mandibular cardo muscle, mc = mandibular cardo, mes = median septum, mg = mandibular gnathal lobe, ms = mandibular stipes, nt = 'Nebententorium', pc = preoral chamber, ph = pharynx, po = 'Presshöcker', t1 = anterior tentorial muscle, t2 = dorsal tentorial muscle, tb = transverse bar of tentorium. Scale bars: 200 µm.

over into the hypopharyngeal bar (hb), which is located within the hypopharyngeal wall and distally articulated to the 'Nebententorium' (Fig. 3C, D). At the point where epipharyngeal bar and hypopharyngeal bar meet, the plate-like posterior process (pp) projects posteriorly into the head capsule. The posterior process serves as origin of three (medial, lateral and anterior) antennal muscles (a2, a3, a4) inserting on the antennal base, and of the tentorial pharyngeal dilator muscle (p5), which inserts laterally on the pharyngeal wall. Furthermore, the mandibular muscles m4/m5 originate from the posterior margin of the tentorial posterior process and insert at the mandibular base.

Attached on the distal margin of the posterior process is the posterior tentorial muscle (t3), which originates from the postoccipital flange, and the ventral tentorial muscle (t4), which originates from the transverse mandibular tendon (see Suppl. material 1: file S1).

Discussion

No Tömösváry organ in Polydesmida

Hennings (1906) described the alleged Tömösváry organ of the polydesmid *Eurydesmus laxus* Gerstaecker, 1873 as a pear-shaped pit covered by a membrane with a median hard swelling (Fig. 2K, L; compare also to Hennings 1906, p. 593). Snodgrass (1952) also described the Tömösváry organ of the Polydesmida as oval groove with a thickened central disc, beneath which sensory cells lie. Such a structure cannot be observed in the studied species. A structure resembling the general appearance of the Tömösváry organ in millipedes, with a sensory cavity lined by a thin porous cuticle and a peg-like epithelium is not present in the Polydesmida. All previous descriptions as well as the accompanying graphical depictions provided by Attems (1899, 1937), Verhoeff (1926–1928) and Snodgrass (1952) for the Polydesmida unambiguously refer to a structure we identified as the projection of the tentorial transverse bar through the head capsule. Snodgrass (1951) stated that the tentorial transverse bar (fulturae sensu Snodgrass 1951) attaches to the central disc of a horseshoe-shaped Tömösváry organ in the Polydesmida, but in the studied species no separate disc-like structure was found. Instead a knob-like distal tip of the tentorial transverse bar is present. Based on our data it is now obvious that the connection of the tentorial transverse bar to the head capsule was misidentified as the Tömösváry organ in Polydesmida. Hennings (1906) stated that the alleged Tömösváry organ only varies in size in the seven species of Polydesmida he studied (*Oranmorpha guerini*, *Orthomorpha coarctata*, *Orthomorpha tenuipes*, *Polydesmus complanatus*, *Spanobrachium collaris*, *Fontaria* sp., *Aphelidesmus uncinatus*), among which is one congener of *Polydesmus angustus* (*P. complanatus*), while being absent in species capable of volvation (i.e., *Lignydesmus rubriceps*, *Oniscodesmus aurantiacus* and *Aporodesmus gabonicus*).We accordingly hypothesize that the Tömösváry organ is generally absent in the Polydesmida.

This conclusion (absence of the Tömösváry organ in the Polydesmida) is further supported by previous doubts on the presence of a nervus tömösváryi in the Polydesmida (Sombke and Rosenberg 2015). The nerve innervating the Tömösváry organ in other myriapods could not be identified either in our histological studies, in contrast to Hennings (1906) who stated its presence, but absence of the nervus opticus. The absence of the alleged Tömösváry organ in *Lignydesmus rubriceps*, *Oniscodesmus aurantiacus* (Hennings 1906) and in *Cyclodesmus* (Attems 1899) can straightforwardly be related to their ability to volvate (Golovatch 2003). In the same context of volvation, the lateral connection of the tentorium to the head capsule via the transverse bar is also lost in Sphaerotheriida (Moritz and Wesener 2017; Moritz et al. 2018).

Phylogenetic significance of the Tömösváry organ

The absence of the Tömösváry organ in the Polydesmida is a character shared with the Colobognatha, Stemmiulida, Juliformia and Siphoniulida among the chilognathan millipedes (Sierwald and Bond 2007; Blanke and Wesener 2014). The phylogenetic analyses based on morphological data by Sierwald et al. (2003) and Blanke and Wesener (2014) suggest a sister-group relationship of Polydesmida and Nematophora. Other phylogenetic analyses resolve the Polydesmida as more closely related to either Juliformia (Enghoff et al. 1993; Cong et al. 2009), Stemmiulida (Rodriguez et al. 2018), or Colobognatha (Sierwald and Bond 2007), all of which do not possess a Tömösváry organ. Although Silvestri (1903) depicts the Tömösváry organ for the stemmiulid *Stemmiulus ortonedae*, its apparent presence likewise requires re-consideration according to Müller and Sombke (2015). The correction of the character coding related to the Tömösváry organ for Polydesmida in the character matrix compiled by Blanke and Wesener (2014) does not alter its topology, in which the Polydesmida is the sister group of the Nematophora. The resolution of the chilognathan orders in this analysis, however, now questions the homology of the Tömösváry organ across millipedes, since its presence in (some) Nematophora optimizes most parsimoniously as a reversal. Based on the available data, the question of whether the Tömösváry organ among chilognathans is exclusively maintained or instead regained in Nematophora remains an issue of debate. Therefore, detailed investigations of the head morphology for all millipede orders are needed combining various techniques including developmental studies.

Conclusion

Contrary to several old and recent publications (e.g., Hennings 1906; Verhoeff 1926–1928; Snodgrass 1951, 1952; Blanke and Wesener 2014; Müller and Sombke 2015; Bouzan et al. 2017a, b) the Polydesmida do not seem to possess a Tömösváry organ. Indeed, the connection of the tentorial transverse bar laterally to the head capsule has been misinterpreted as the Tömösváry organ, as we show here. The absence of the Tömösváry organ in the Polydesmida, Juliformia and Colobognatha may be due to multiple losses, but parsimony favors its sole presence in Nematophora among Chilognatha as a reversal. To further clarify the distribution, homology and evolution of the Tömösváry organ in the Diplopoda more detailed studies are needed.

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Supplementary material 1

***Polydesmus angustus*, head capsule and tentorium with associated musculature**

Authors: Leif Moritz, Markus Koch

Data type: multimedia

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RESEARCH ARTICLE

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Subterranean biodiversity and depth distribution of myriapods in forested scree slopes of Central Europe

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The paper is dedicated to Christian Juberthie (12 Mar 1931–7 Nov 2019),
the author of the concept of MSS (milieu souterrain superficiel)
and the doyen of modern biospeleology

Abstract

The shallow underground of rock debris is a unique animal refuge. Nevertheless, the research of this habitat lags far behind the study of caves and soil, due to technical and time-consuming demands. Data on Myriapoda in scree habitat from eleven localities in seven different geomorphological units of the Czech and Slovak Republics were processed. Based on previous studies, as well as knowledge of cave and soil fauna, it was hypothesised that the occurrence of a varied and peculiar fauna would show a pattern of depth distribution with variations due to local specificities. From 2005–2016 (at least one year on each site), macrofauna was collected via sets of three long-term exposed subterranean traps consisting of 110 cm long perforated tube, with ten cups located in a gradient at 5–95 cm below the soil surface. In total, 14 symphylans (not identified to species level), 271 centipedes (23 spp.) and 572 millipedes (32 spp.) were sampled. The overall depth distribution of centipedes and millipedes appeared to have relatively similar pattern, with both groups being found at all depth levels. Nevertheless, this pattern depends on locations. The depth distribution trend lines are mostly in the form of an asymmetric 'U', with decreased abundance until the middle of the gradient, followed by increase in the deepest levels. Epigeic species were sporadically distributed along the whole depth gradient, but concentrated at the soil surface, while some subterranean species, such as the centipede *Lithobius lucifugus* and the millipedes *Geoglomeris subterranea*, *Cibiniulus slovacus* and *Archiboreoiulus pallidus*, were recorded in the deepest parts of the gradient. This characterises the debris community as a mixture of soil and subterranean species with an absence of species exclusively found in caves. The use of different fixation methods in traps had a significant and selective impact on samples; millipedes were either attracted by ethylene glycol or repelled by formaldehyde. Centipedes were also captured more frequently in ethylene glycol; however, the species composition varied in each of the fixatives. Depth distribution of myriapods was similar in both fixative solutions. Traps with these fixatives could be recommended for similar ecological studies.

Keywords
Chilopoda, Diplopoda, Myriapoda, MSS, subterranean traps

Introduction

Forested scree slopes (slope deposits) represent a unique type of shallow subterranean domain, which are frequently labelled in literature as shallow subterranean habitat (SSH; Culver and Pipan 2014) or meso-void shallow substratum (milieu souterrain superficiel, MSS of Juberthie et al. 1980; preferred abbreviation for this paper). The main condition for the existence of MSS is the presence of stone deposits forming in the underground environment. Weathered rock fragments and sediments accumulate in several layers, which are subsequently covered by the soil. Due to this isolation from the surface, MSS serves as a stable habitat with conditions similar to those in caves (Juberthie 2000; Giachino and Vailati 2010). Cracks and air-filled voids create a network of interconnected corridors that provide suitable shelter for various groups of invertebrates, but also serve as a refugium for relic fauna (Růžička and Klimeš 2005; Zacharda et al. 2005; Mock et al. 2015; Kováč et al. 2016; Růžička et al. 2016; Nitzu 2016; Tuf et al. 2017; Nitzu et al. 2018b; Mammola 2018). Shallow subterranean habitats can be defined as a habitat on a transition zone with the ongoing adaptation of organisms to underground life (Pipan et al. 2011; Ortuño et al. 2013; Nitzu et al. 2014; Mammola et al. 2017). The presence of invertebrate life forms possessing convergent morphological adaptations (depigmentation, eye absence, reduction of size, etc.) to subterranean life is one of the main criteria for distinguishing surface from underground habitats.

The study of deeper layers of forested scree slopes reveals that refugia of rare fauna add another dimension of environmental heterogeneity affecting overall biodiversity. Rather numerous studies on the ecology of various groups of fauna in MSS in Europe were conducted (reviewed in Mammola et al. 2018), some of them focusing on scree slopes of Slovakia and the Czech Republic (Růžička and Klimeš 2005; Laška et al. 2011; Rendoš et al. 2012, 2014, 2016a; Mock et al. 2015; Růžička and Dolanský 2016; Rudy et al. 2018; Jakšová et al. 2019; Jureková et al. 2019). Subterranean diversity of Myriapoda inhabiting underground of scree slopes has been investigated as well (Nitzu et al. 1999; Ilie 2003a, 2003b; Rendoš et al. 2012, 2016a; Jiménez-Valverde et al. 2015; Mock et al. 2015; Tuf et al. 2017); some studies even have described new myriapod taxa (e.g., Stoev 2008; Gilgado et al. 2015; Akkari et al. 2018). Attention should also be paid to the results of studies testing the reliability of the use of a set of subterranean traps inserted to the substrate through plastic pipe and other methodological aspects. The type of fixative solution and trap exposure duration can also affect species assemblages (Mammola et al. 2016; Jureková et al. 2019). Additionally, environmental variables affect the distribution pattern of invertebrates below the surface of stone debris (Rendoš et al. 2016b; Nitzu et al. 2018a). Our contribution completes the knowledge from a number of little or unstudied sites of Slovak and the Czech republics. The aims of our study were to (1) analyse the structure and diversity of myriapods dwelling in forested scree slopes, and (2) to generalise the distribution of myriapods along the depth gradient at selected locations in Central Europe.

Materials and methods

Study sites

The study was carried out from 2005 to 2016 at various locations situated in different geomorphological units of Slovakia and the Czech Republic. Five of the forested scree slopes were situated in four geomorphological units in Slovakia; six study sites were part of two geomorphological units in the Czech Republic (Fig. 1 and Table 1).

1. Forested scree slope in the karst doline (sinkhole) were close to the collapse entrance of the Silická ľadnica Ice Cave, Slovak Karst National Park (site 1; Fig. 1). Situated on limestone bedrock, the site is characterised by dense vegetative cover, forested by linden-hornbeam and maple trees (*Tilio-Aceretum* with *Carpinus betulus*, *Urtica* sp., *Lunaria* sp., *Galium* sp. in herb layer). Scree profile is divided to leaf litter and humus (0–10 cm), organo-mineral layer (10–30 cm) and rock fragments layer (30–110 cm).
2. Forested scree slope of the Vysoká Hill is situated approximately 30 m from the entrance of Ardovská jaskyňa Cave, Slovak Karst National Park (site 2; Fig. 1). Situated on limestone bedrock, the vegetative cover on the slope is poor, with the presence of dogwood-maple trees (*Corno-Carpinetum*) and bryophytes. Scree profile is characterised by a layer of leaf litter and humus (0–15 cm), organo-mineral layer mixed with tiny rocks (15–75 cm) and a large rock layer (75–110 cm).
3. Northern limestone scree slope in the Drienok Valley is located a few meters below the entrance to the Špaňopoľská Cave, Revúcka vrchovina Highlands (site 3; Fig. 1). The slope is overgrown with beech-hornbeam forest (*Fago-Caripetum*) and the scree slope profile is characterised by a layer of leaf litter and humus (0–5 cm), organo-mineral layer (5–25 cm), a layer of a mixture of soil and rocks (25–70 cm) and layer of weathered rock fragments (70–110 cm).

4. Southwestern scree slope is in the Belinské skaly National Nature Monument, Cerová vrchovina Highlands (site 4; Fig. 1). Situated on basalt bedrock, the slope is covered with xerophilous oak-hornbeam trees (*Querco-Carpinetum*). Scree profile consists of litter and humus (0–5 cm), organo-mineral layer (5–30 cm) and scree with mineralised soils (30–110 cm).
5. Forested south scree slope is on the Okopanec Hill, Malé Karpaty Mountains (site 5; Fig. 1). The granitoid slope characterised by poor vegetative cover with the presence of beech trees and bryophytes. Scree slope profile consists of leaf litter and humus (0–5 cm), organo-mineral layer (5–20 cm), a layer of rock segments and mineralised soil (20–75) and scree partially filled with soil and tree roots (75–110 cm).
6. Limestone scree slope is a part of the Zbrašov Aragonite Caves National Natural Reserve, Moravian-Silesian Foothills (site 6; Fig. 1). The site is situated 50 m from the administration building. Vegetative cover is represented by deciduous trees, predominantly *Acer* sp., *Fraxinus excelsior* and *Tilia* sp. with occasional occurrence of *Quercus* sp. and *Robinia pseudacacia*. Soil profile consists of scree made up of stone fragments ranging from a few centimetres in diameter to larger rocks. The interspace between the limestone rock fragments is filled with humus formed by leaf litter decomposition.
7. Limestone scree slope is located above the right bank of the Bečva River, southern part of the Hůrka u Hranic National Natural Reserve, Moravian-Silesian Foothills (site 7; Fig. 1). The slope is overgrown with old trees of *Fagus sylvatica* and *Quercus* sp.; occasionally *Carpinus betulus*, *Acer* sp., and *Fraxinus excelsior* are present. Due to close proximity to the limestone wall, the soil contains many small limestone fragments of various sizes with interspace filled with yellow clay.
8. Limestone scree slope is located above the right edge of the Bečva River, southern part of the Hůrka u Hranic National Natural Reserve, Moravian-Silesian Foothills (site 8; Fig. 1); this site is close to study site 7, but further away from the limestone wall. Vegetative cover is the same as at study site 7. The size of the debris particles ranges from a few centimetres to tens of centimetres. Scree profile is formed by larger fragments on the surface, the spaces between them filled with humus; the lowest layer consists of smaller fragment, with spaces filled with yellow clay.
9. Sandstone scree slope is at the edge of a beech forest, cadastral area of the Hluboká village, Chrudim region, Železné hory (Iron Mountains; site 9; Fig. 1). Vegetative cover consists predominantly of *Trifolium pratense*, *Impatiens noli-tangere*, *Impatiens parviflora*, *Anemone nemorosa*, *Convallaria majalis*, *Asperula odorata*, and *Polygonatum multiflorum.* The greatest relative abundance of the tree community is represented by *Fagus sylvatica*, with the presence of *Abies alba* and *Picea abies*. The scree profile is characterised by beech leaf litter with undecomposed leaves at the surface (10 cm), sandy soil (20 cm) and a layer of clay (> 20 cm).

10. Basalt scree slope is in the vicinity of the Hněvětice village, Chrudim region, Železné hory (Iron Mountains; site 10; Fig. 1). The average stone fragment size is about 10 cm in diameter. The slope is overgrown with mixed forest, predominantly *Betula pendula*, *Carpinus betulus*, *Picea abies*, and *Fagus sylvatica*. The scree was covered with a thin layer of undecomposed leaves on the surface. The soil was homogeneous throughout the whole depth gradient. Stone fragments were few centimetres in diameter. The spaces between the stones were filled clay.
11. Scree slope was situated next to a former basalt quarry in the cadastral area of the Hněvětice village, Chrudim region, Železné hory (Iron Mountains; site 11; Fig. 1). The area is treeless. Poor vegetative cover is represented mainly by *Tussilago farfara* and *Crepis biennis*, with the presence of some ruderal weeds (e.g., *Atriplex patula*, *Rumex acetosa*, *Rumex obtusifolius*). Soil on the study site was almost homogeneous to the depth of 60 cm and consisted of clay with a large amount of stone fragments. With increasing depth, the presence of clay particles intensified.

Sampling

To capture myriapods, subterranean pitfall traps were used, constructed by Schlick-Steiner and Schlick. These traps were finely modified according to the available construction material and there was little difference between those used in the Czech and Slovak study sites. These differences should not have affected the monitored parameters of the myriapod communities.

At study sites 1–5, the traps consisted of 110 cm long PVC tube, 10 cm in diameter, perforated at 10 horizontal levels (5, 15, 25…95 cm), circumferentially. Perforations were 0.7 cm in diameter and served as an entrance to the traps for studied fauna. Inside the plastic tube, ten plastic cups (volume 500 ml) were inserted, connected with threated rod (forming 10 cm spacing between each cup) and aligned directly under the perforations to allow animals to be trapped at particular level. We used 4% formaldehyde a fixative solution in two traps at each site and either 50% ethylene glycol in one trap at study sites 1–4 or 11% ethylene glycol in one trap at study site 5. Traps at study sites 6–11 were constructed according to the same design, with a few differences. Instead of drilled perforations at ten levels, three transverse cuts were made in the plastic tube at each of the depth levels, so that three pillars remained in between the cuts to keep the tube together. The cuts were 0.4 cm wide and 9 cm long and served as an entrance for animals to the traps. Inside the plastic cups, only 4% formaldehyde was used as a fixative. All fixatives were diluted in water to the appropriate concentrations.

At each of the study sites, we installed a set of three traps, 1–2 m apart. The plastic pipes with the traps were inserted in a horizontal line into a dug longitudinal pit. The excavated substrate was returned to the pit roughly in layers as it was dug. Approximately 1 month after placing traps into the substrate, they were controlled, and the fixation solution was replaced to avoid the effect of mixing the substrate when digging pits for deep invertebrate distribution.

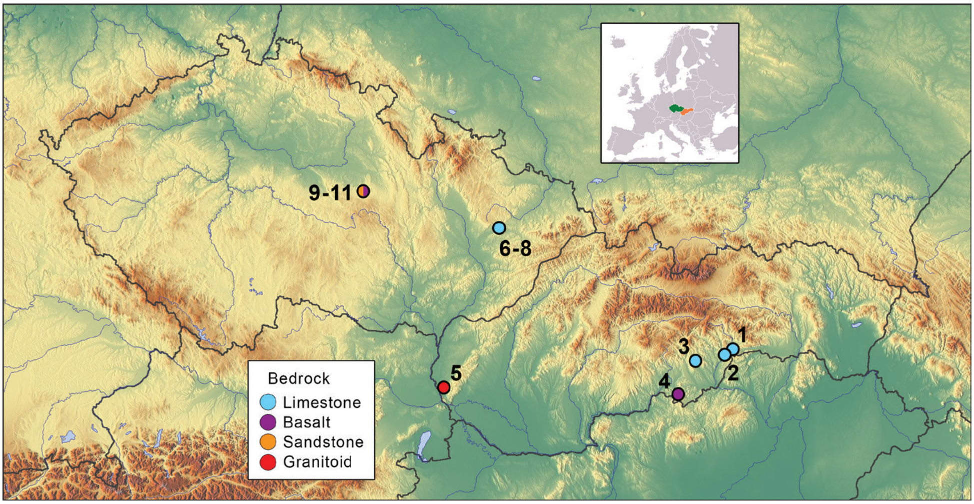

Figure 1. Location of the study sites. **1** Doline next to Silická ľadnica Ice Cave **2** Vysoká Hill (both sites in Slovak Karst National Park) **3** Drienok Valley (Revúcka Highlands) **4** Belinské skaly (Cerová vrchovina Highlands) **5** Okopanec Hill (Malé Karpaty Mts.) **6–8** Three localities near the Zbrašov Aragonite Caves and Hůrka u Hranic (Moravian-Silesian Foothills) **9–11** Three localities in Chrudim region (Iron Mts.).

Subterranean traps were exposed for approximately one year at each of the 11 study sites and controlled regularly. Sampling intervals varied for each study site (Table 1). The plastic cups were pulled out to retrieve the sampled specimens; the content was collected and transported to laboratory. Myriapods were fixed in ethyl alcohol and identified to species level.

Community characteristics and data analysis

In order to describe myriapod communities, we calculated dominance (D), constancy (C), Shannon's diversity index (*H'*), and Pielou's evenness index (*J'*) for centipedes and millipedes separately; indices were estimated separately for each of the study sites. In addition, *H'* was calculated for each depth of the gradient, for centipedes and millipedes separately. Patterns of depth distribution in overall material of millipedes and centipedes were tested using fitted Generalised Additive Models (GAM) in Canoco 5.0 program. Distributions of species with more than two trapped specimens were tested; only species with significant pattern of its distribution were illustrated in figures.

Results

Myriapoda were recorded at all eleven study sites and were one of the less frequent groups of arthropods. In total, 857 individuals were identified to 55 species. Diplopo-

Table 1. Characteristics of the scree slopes study sites. The numbers indicating particular study are presented in Fig. 1. Key: Alt. = altitude, Expo. days = trap exposure time.

Study site	Coordinates	Alt. (m)	Bedrock	Slope aspect	Sampling period	Expo. days
1	48°33'N, 20°30'E	489	Limestone	W	11 Jun 2014–29 Apr 2015	322
2	48°31'N, 20°25'E	328	Limestone	SW	11 Jun 2014–29 Apr 2015	322
3	48°32'N, 20°07'E	315	Limestone	N	15 May 2012–17 Oct 2013	520
4	48°13'N, 19°52'E	460	Basalt	SW	15 May 2012–17 Oct 2013	520
5	49°77'N, 17°66'E	410	Granitoid	SW	15 Jan 2015–16 Jan 2016	365
6	49°31'N, 17°44'E	325	Limestone	E	1 Feb 2005–1 Mar 2006	393
7	49°32'N, 17°44'E	375	Limestone	W	1 Feb 2005–1 Mar 2006	393
8	49°32'N, 17°44'E	375	Limestone	W	1 Feb 2005–1 Mar 2006	393
9	49°50'N, 16°04'E	460	Sandstone	SE	7 Mar 2005–24 Mar 2006	382
10	49°49'N, 16°02'E	400	Sandstone	NW	7 Mar 2005–24 Mar 2006	382
11	49°50'N, 16°02'E	455	Basalt	W	7 Mar 2005–24 Mar 2006	382

da, unlike to ever-present Chilopoda, were missing at study site 11; however, it was the richest represented class of myriapods, regarding both individuals and species. Symphyla were represented only by 14 individuals at four study sites. The fourth myriapod class, Pauropoda, was not documented at any of the study sites. Species diversity and depth distribution showed geographical differences, but overall, two dominant groups demonstrated similar indicators. Alternation of two fixative solutions in traps resulted in significant differences in both the number of individuals and the species composition, with Diplopoda and Chilopoda responding differently to the type of fixation.

Representatives of Symphyla were captured at four of the study sites. All collected individuals (not identified to species level) were distributed unevenly along the depth gradient, present at almost every depth of the top half of the gradient. One third of all captured symphylans were present in the bottom half of the gradient, at depths of 65 and 95 cm. Almost two-thirds of Symphyla specimens were captured in traps with formaldehyde.

Centipedes

Overall, 271 specimens of Chilopoda were sampled, belonging to 23 species and five families (See Suppl. material 1: Table S1). The number of centipede species sampled on individual study sites varied from 1–8 species, with an average of 5.2 species sampled per site. The highest value of Shannon's diversity index (*H'* = 1.58) was recorded on the scree slope at the edge of the Bečva River (site 7), while the highest value of Pielou's evenness index (*J'* = 1) was recorded at the scree slope near Silická ľadnica Ice Cave (site 1) (Fig. 2B). At the scree slope next to the quarry of the village of Hněvětice (site 11), only one species, *Lamyctes emarginatus*, was caught in the traps. Among collected Chilopoda, two species can be classified as eudominant, *Lithobius forficatus* (D = 47%) and *Lithobius lucifugus* (D = 14%); *Lithobius forficatus* represented the species with the highest constancy (C = 82%), occurring at nine of eleven sites.

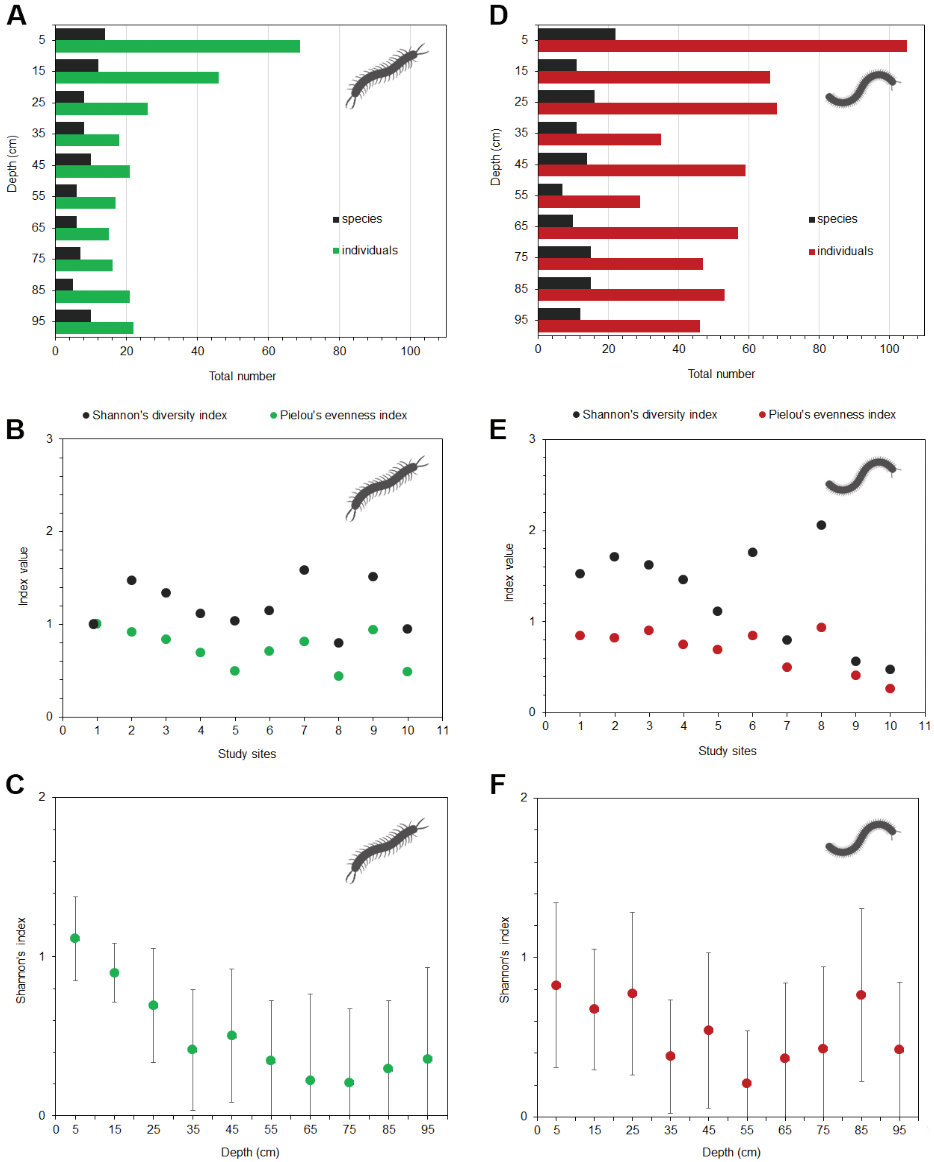

Figure 2. A Overall depth distribution of centipede individuals and species **B** values of Shannon's diversity index and Pielou's evenness index, calculated for centipedes, at each of the study sites **C** mean values of Shannon's diversity index (±SD) calculated for centipedes, at each depth of the gradient (summarised data from all localities) **D** overall depth distribution of millipede individuals and species **E** values of Shannon's diversity index and Pielou's evenness index, calculated for millipedes, at each of the study sites **F** mean values of Shannon's diversity index (±SD) calculated for millipedes, at each depth of the gradient.

Regarding depth distribution of centipedes, the highest numbers of individuals and species were captured near the surface; however, the overall distribution curve resembled U-shape with decreasing abundances in upper part of profile replaced by

Table 2. A summary overview of the centipede depth distribution in the eleven scree slopes of Slovakia and the Czech Republic.

Depth (cm)	5	15	25	35	45	55	65	75	85	95	Σ
Clinopodes flavidus	2	–	–	1	–	–	–	–	–	–	3
Cryptops parisi	1	1	–	1	2	2	–	1	2	1	11
Geophilus electricus	1	–	–	–	–	–	–	–	–	–	1
Geophilus insculptus	–	1	–	–	–	1	–	–	–	–	2
Geophilus flavus	1	–	1	1	–	3	1	–	–	–	7
Harpolithobius anodus	4	–	–	–	1	–	–	–	–	1	6
Lamyctes emarginatus	3	3	–	–	–	–	–	–	–	–	6
Lithobius agilis	–	2	–	1	–	1	–	–	–	–	4
Lithobius austriacus	–	1	–	–	–	–	–	–	–	1	2
Lithobius cyrtopus	–	1	–	–	–	–	–	–	–	–	1
Lithobius dentatus	–	–	–	–	1	–	–	–	–	–	1
Lithobius forficatus	29	25	14	9	8	8	5	9	14	5	126
Lithobius lucifugus	9	4	4	3	2	2	5	1	3	4	37
Lithobius macilentus	–	–	–	–	2	–	–	–	–	1	3
Lithobius microps	–	–	–	–	1	–	–	–	–	–	1
Lithobius mutabilis	2	5	1	–	–	–	1	–	–	–	9
Lithobius muticus	6	–	–	–	1	–	–	1	–	–	8
Lithobius nodulipes	2	1	–	1	–	–	–	–	–	–	4
Lithobius tenebrosus	–	–	–	1	–	–	–	–	–	–	1
Lithobius t. fennoscandius	1	–	1	–	1	–	1	2	1	1	8
Strigamia acuminata	4	1	1	–	2	–	–	1	–	5	14
Strigamia crassipes	–	–	1	–	–	–	–	–	–	1	2
Strigamia transsilvanica	4	1	3	–	–	–	2	1	1	2	14
Σ	69	46	26	18	21	17	15	16	21	22	271

opposite pattern in deepest layers (Fig. 2A). More than half of the species were sampled only in the first half of the depth profile (5–45 cm), while four species were collected exclusively in the uppermost levels (5–15 cm). None of the species were observed solely in the deeper half of the gradient (Table 2). Shannon's diversity index (*H'*) was highest at a depth of 95 cm; however, at 5 cm depth, the value was really similar (Fig. 2C). *Lithobius forficatus* and *L. lucifugus* were the only two Chilopoda species with an occurrence at all layers of the depth profile; *L. forficatus* showed a significant affinity to the surface (F = 17.2, $p < 0.01$), while none of the species showed significant positive relation to deepest layers of the depth gradient (Fig. 3A).

Millipedes

Diplopoda were represented by 572 individuals (including unidentified juveniles), belonging to 32 species and 12 families (see Suppl.material 2: Table S2). The highest number of species (nine species) was recorded at study site 8, with the complete absence of millipedes at one of the study sites (quarry, locality 11). On average, 5.5 species per site were sampled. The highest value of both Shannon's diversity index and Pielou's evenness index (*H'* = 2.06 and *J'* = 0.94) was recorded on the scree slope at the

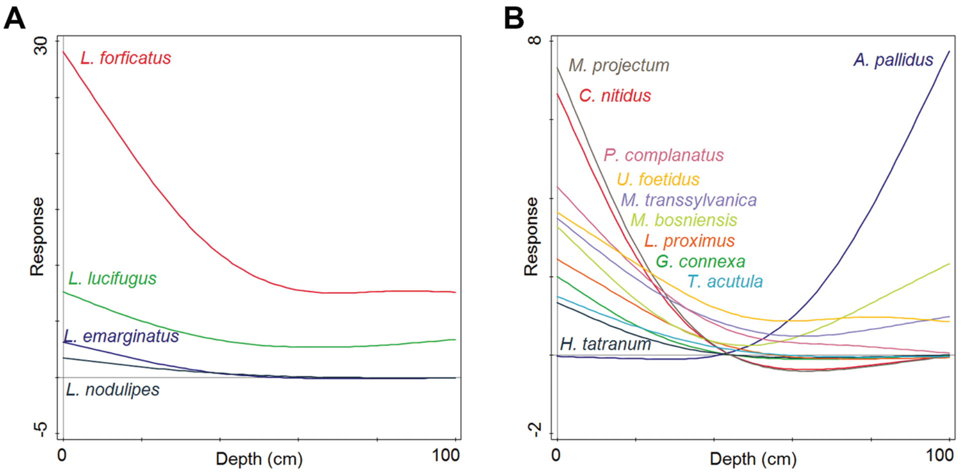

Figure 3. Generalised Additive Models of depth distribution pattern of **A** centipedes and **B** millipedes. Only species with significant pattern are illustrated. (F-values, * $p < 0.05$, ** $p < 0.01$): **A** *Lamyctes emarginatus* (13.1**), *Lithobius forficatus* (17.2**), *Lithobius lucifugus* (5.0*), *Lithobius nodulipes* (9.7**) **B** *Archiboreoiulus pallidus* (22.7**), *Cylindroiulus nitidus* (5.4*), *Glomeris connexa* (5.4*), *Hylebainosoma tatranum* (5.4*), *Leptoiulus proximus* (7.3*), *Mastigona bosniensis* (10.5**), *Megaphyllum projectum* (5.4*), *Melogona transsylvanica* (15.2**), *Polydesmus complanatus* (13.1**), *Trachysphaera acutula* (5.4*), *Unciger foetidus* (4.9*).

edge of the Bečva River (site 8; Fig. 2E). The only eudominant species of Diplopoda was *Ochogona caroli* (D = 40%). None of the species occurred on more than half of the study sites, with *Unciger foetidus* representing the species with the highest constancy (C = 46%; occurred at five of eleven sites).

The distribution of millipedes along the depth profile was non-uniform. The highest numbers of individuals and species were sampled at the depth of 5 cm (Fig. 2D). One third of the species were captured solely in the top half of the depth gradient (5–45 cm), with five species sampled exclusively in the uppermost layers (5–15 cm). Shannon's diversity index was highest at a depth of 5 cm; the value was lowest at 65 cm (Fig. 2F). Three species, *Craspedosoma transsylvanicum*, *Polyzonium germanicum*, and *Trachysphaera costata* occurred solely in the deeper half of the depth gradient (85–95 cm); however, they were represented by low number of individuals (Table 3). *Megaphyllum projectum* and *Cylindroiulus nitidus* showed a significant positive correlation to the surface (both species F = 5.4, $p < 0.05$); other species with affinity for the upper part of the depth gradient are depicted in the left part of the Fig. 3B. The millipedes *Mastigona bosniensis* and *Melogona transsylvanica* were abundant on the surface as well as in deepest layers. The only species significantly more abundant at lower depths was *Archiboreoiulus pallidus* (F = 22.7, $p < 0.01$). Nevertheless, another species of the same morphotype (thin blind julid without pigment), *Cibiniulus slovacus* was also sampled exclusively in deeper zones of scree habitats.

Table 3. A summary overview of the millipede depth distribution in the eleven scree slopes of Slovakia and The Czech Republic. Seven juvenile individuals could not be identified to species level.

Depth (cm)	5	15	25	35	45	55	65	75	85	95	Σ
Archiboreoiulus pallidus	–	–	1	–	–	–	–	2	4	9	16
Blaniulus guttulatus	2	3	2	2	3	–	2	1	3	5	23
Brachydesmus superus	–	2	1	–	–	–	1	–	1	–	5
Cibiniulus slovacus	–	–	–	–	4	1	–	6	4	–	15
Craspedosoma transsylvanicum	–	–	–	–	–	–	–	–	–	1	1
Cylindroiulus nitidus	10	–	–	–	–	–	–	–	–	–	10
Geoglomeris subterranea	–	–	–	–	1	1	–	–	–	–	2
Glomeris connexa	3	–	–	–	–	–	–	–	–	–	3
Glomeris tetrasticha	–	–	–	–	2	–	–	–	1	1	4
Haasea flavescens	2	12	2	1	1	3	–	1	4	–	26
Haplogona oculodistincta	3	8	16	4	4	7	3	–	4	2	51
Hungarosoma bokori	1	–	–	–	1	–	–	–	–	–	2
Hylebainosoma tatranum	2	–	–	–	–	–	–	–	–	–	2
Leptoiulus baconyensis	1	–	–	–	–	–	–	–	–	–	1
Leptoiulus proximus	2	3	–	–	–	–	–	–	–	–	5
Leptoiulus trilobatus	3	–	–	2	–	1	–	–	–	–	6
Listrocheritium septentrionale	5	–	1	2	2	1	2	2	1	1	17
Mastigona bosniensis	4	2	–	–	–	–	–	2	2	2	12
Megaphyllum projectum	11	–	–	–	–	–	–	–	–	–	11
Melogona transsylvanica	4	2	1	1	1	–	–	1	1	1	12
Melogona voigtii	2	–	3	2	1	–	–	1	1	–	10
Ochogona caroli	21	21	24	18	33	15	41	21	17	18	229
Ommatoiulus sabulosus	1	–	–	–	–	–	–	1	–	–	2
Polydesmus complanatus	5	2	2	–	–	–	1	1	–	–	11
Polydesmus denticulatus	9	7	8	1	4	–	2	4	7	3	45
Polyxenus lagurus	–	–	1	1	–	–	–	–	–	1	3
Polyzonium germanicum	–	–	–	–	–	–	–	1	–	–	1
Trachysphaera acutula	2	–	1	–	–	–	–	–	–	–	3
Trachysphaera costata	–	–	–	–	–	–	–	1	–	–	1
Trachysphaera gibbula	9	–	2	–	1	–	1	–	1	2	16
Unciger foetidus	3	4	2	1	–	–	1	2	2	–	15
Unciger transsilvanicus	–	–	1	–	1	–	3	–	–	–	5
Σ	105	66	68	35	59	29	57	47	53	46	565

Effects of fixative solutions on diversity and activity of myriapods along the depth gradient of screes

At five of the study sites (sites 1–5; all situated in Slovakia), formaldehyde (two trap sets) and ethylene glycol (one trap set) were used in parallel. At all of these five study sites, much greater numbers of individuals and species of myriapods were recorded in subterranean traps with ethylene glycol than in the traps with formaldehyde; however, each of the systematic groups of Myriapoda responded specifically to the type of fixation.

For centipedes, ethylene glycol appears to be more attractive (or less repellent) than formaldehyde. Higher numbers of individuals were collected in traps with ethylene glycol. However, regarding species composition, the effect of both fixatives seems to be

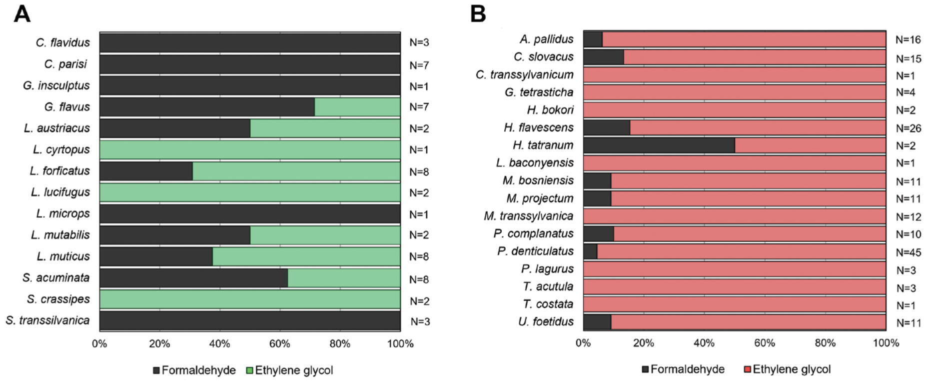

Figure 4. Graphical presentation of myriapod community characteristics in different fixative solutions (N = number of individuals). **A** Formaldehyde to ethylene glycol ratio of sampled centipede species from all study sites, where both fixating solutions were used **B** formaldehyde to ethylene glycol ratio of sampled millipede species from all study sites, where both fixating solutions were used.

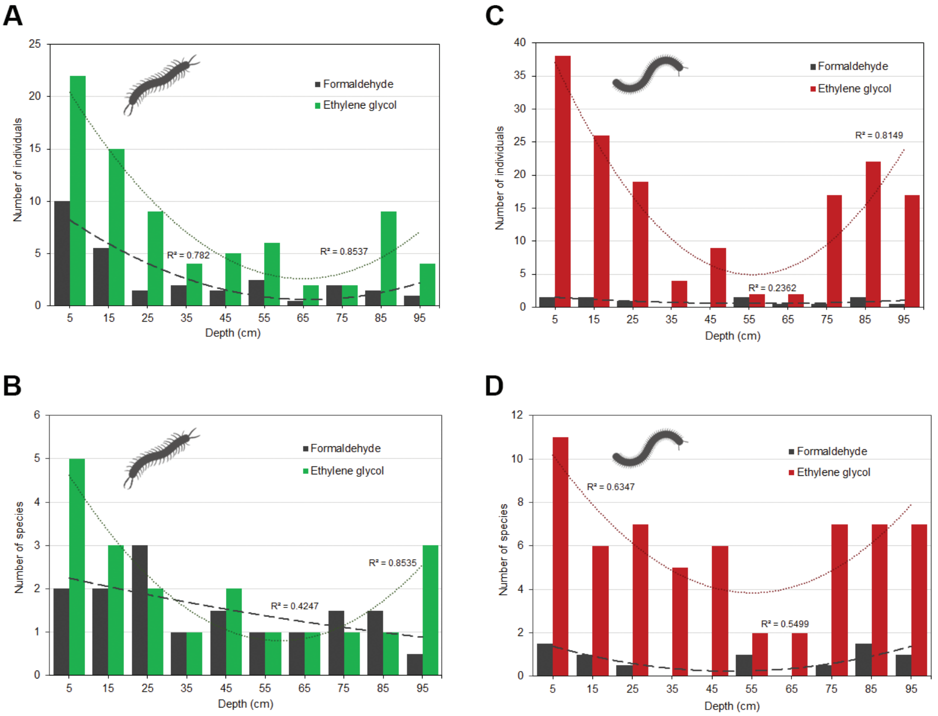

Figure 5. Vertical distribution of myriapods along the depth gradient in different fixative solutions (data recalculated for the same number of traps). Trend line: dashed = formaldehyde, dotted = ethylene glycol. **A** Vertical distribution of Chilopoda specimens along the depth gradient (5–95 cm) at five scree slopes in different fixative solutions **B** vertical distribution of centipede species along the depth gradient at five scree slopes in different fixative solutions **C** vertical distribution of Diplopoda specimens along the depth gradient (5–95 cm) at five scree slopes in different fixative solutions **D** vertical distribution of millipede species along the depth gradient at five scree slopes in different fixative solutions.

complementary, as each of the solutions contained some species exclusive for particular fixative too (Fig. 4A). Vertical distribution of centipedes along the depth gradient at five scree slopes was characterised by strong decline and later small increase in deepest layers in the number of individuals in formaldehyde as well as ethylene glycol fixative solution, resembling its general U-shape curve of abundances (cf. Figs 2A, 5A). On the other hand, and contrary to ethylene glycol fixative, a simple decreasing trend in number of species was recorded in traps with formaldehyde fixative (Fig. 5B).

Regarding millipedes, ethylene glycol showed significantly higher activity and species diversity compared to formaldehyde. All collected species preferred traps with ethylene glycol; almost half of the millipede species occurred exclusively in this type of fixative solutions (Fig. 4B). Number of species and individuals decreased with depth in ethylene glycol fixation (down to 35 cm) and increased again at depths of 75–95 cm. Vertical distributions of millipedes in formaldehyde showed no particular trend (Fig. 5C). Similar patterns were recognized for number of species too (Fig. 5D).

Discussion

Scree habitats serve as a prospective source of information on species habitat preference, diversity and potential migration between the shallow underground environment and the cave environment. Interspaces of forested scree slopes are inhabited by various groups of invertebrates, predominantly arthropods, represented by both edaphic and subterranean species (Juberthie 2000; Nitzu et al. 2014; Jiménez-Valverde et al. 2015). Our study confirmed that Central European myriapods colonise belowground zones in scree habitats covered with soil. It also indicates that there are some differences in diversity and distribution of centipede and millipede assemblages along depth profiles. The majority of myriapod species captured using subterranean traps represent common epigeic or edaphic fauna, occurring predominantly in the nutrient-rich uppermost layers of soil and litter. Some subterranean forms were captured, as well as species preferring scree slope habitats, including *Archiboreoiulus pallidus* and *Cibiniulus slovacus* (Antić et al. 2015; Mock et al 2015); these species are also cave-dwellers. However, some cave dwelling species known from the study region are absent in scree samples (Kováč et al. 2014).

The distribution pattern was characterised by typical sharp decline at the beginning of the measured depth gradient culminated near the middle zone, and increased occurrence and diversity of myriapods in the deeper parts of the gradient. Such decrease in abundance of the studied groups has been confirmed by several studies in different invertebrates (e.g., Laška et al. 2011; Rendoš et al. 2012, 2016a). Among other factors, the decline in upper layers may be due to the decreasing availability of organic resources as well as available spaces up to 50 cm (Gers 1998; Rendoš et al. 2012; Nitzu et al. 2014). On the other hand, from the depth of 70 cm we can see numerous communities of subterranean species that do not move to the upper layers. Some of the studies (Růžička et al. 1990; Růžička 1999; Laška et al. 2008) highlight the effect of substrate porosity, layer depth and vegetation on vertical distribution in soil. Regional surface species congregate deeper underground in screes similarly to caves especially in territories with rare obligate subterranean dwellers (Rendoš et al. 2016a; Fernandes et al. 2019).

The structure of centipede assemblage in scree habitats along the depth gradient has been described by various authors. In Querner and Gereben-Krenn (2005), the centipedes were distributed vertically only to a depth of 20 cm, while in our study, centipedes occurred at each depth of the gradient. Almost half of our collected centipedes were represented by *Lithobius forficatus*. The species is known for its wide ecological valency, characterised by Pan-European and Palearctic distribution. It has been documented from subterranean environment by Nitzu et al. (1999) from the caves of Romania (Ilie 2003a, 2003b) and caves of the Slovak Karst (Országh et al. 1994; Országh 2000). *Lithobius forficatus* is also known to penetrate deeper parts of the scree slope habitats (Rendoš et al. 2012, 2016a). The second-most abundant species of centipedes captured along the depth gradient was *Lithobius lucifugus*. This species was previously recorded at different karstic areas (e.g., Folkmanová 1951; Ilie et al. 2003a, Ilie 2004) and is known to inhabit various underground habitats, including caves (Novák and Dányi 2011; Dvořák and Dvořáková 2015; Růžička et al. 2016; Tuf et al. 2017).

Relative abundance and diversity of millipedes captured using subterranean traps was higher in comparison to centipedes. Majority of the sampled species can be described as epigeic and edaphic. The most abundant species, collected only on the scree slopes of the Czech Republic, was *Ochogona caroli*. This species inhabits mainly higher altitudes of Central European mountains confirming its higher activity for the colder part of the year (Kocourek et al. 2017). Some important representatives of edaphic or subterranean forms were captured, including two species of family Blaniulidae, *Archiboreoiulus pallidus* and *Cibiniulus slovacus*; these species were captured in the deepest parts of depth gradient. Both species represent blind relict millipedes with similar ecological demands, known for their preference of shallow subterranean habitats. *Archiboreoiulus pallidus*, characterised by cryptic behaviour, has so far been documented only from the subterranean environment, for the studied area (Mock et al. 2015). Another blind relict species, *Cibiniulus slovacus*, was described only recently from caves in Slovakia (Antić et al. 2015); the species shows considerable affinity to forested scree habitats. The presence of similar species (morphotypes) that may coexist on a single site (e.g., chordeumatid diplopods of *Ochogona caroli* and *Listrocheritium septentrionale*) or that alternate similarly in the depth gradient (e.g., blind blaniulid millipedes and *Blaniulus guttulatus*, *Archiboreoiulus. pallidus*, and *Cibiniulus slovacus*) emphasises the need for precise taxonomic work. Another representative of subterranean millipede fauna captured in scree slopes is *Geoglomeris subterranea*. The species is morphologically well-adapted to subterranean environment and is known to inhabit various western-European caves (Gruber 1985; Kocourek et al. 2017). Its occurrence in soil has been documented (Wesener et al. 2019) even from artificial MSS habitat from the Czech Republic (Riedel et al. 2009). Apart from common European species, a few endemic species of millipedes were determined such as *Cibiniulus slovacus*, *Hungarosoma bokori*, *Hylebainosoma tatranum*, and *Listrocheritium septentrionale*. Some relict species with wider distribution include millipedes (*Geoglomeris subterranea*, *Archiboreoiulus pallidus*, *Trachysphaera* spp.) and centipedes (*Harpolithobius anodus*, *Lithobius cyrtopus*, *Lithobius forficatus*, *Lithobius nodulipes*) (Tuf and Tufová 2008; Kováč et al. 2014).

Nitzu et al. (2018a) emphasise, in addition to the geographical differences on the sites, the significant influence of the geological subsoil on the abundance and diversity of calciphile diplopods in favour of carbonate rocks. Although their study suggests a strong correlation of the calcareous geological substratum with an invertebrate species assemblage, our study found no statistically significant differences between assemblage abundance on limestone and non-limestone study sites either in Chilopoda or in Diplopoda (Chi-square test results).

Generalised additive models helped identify significant patterns of distribution, i.e., to find species, for which depth is useful predictor of its abundance. This analysis can record species with some preferences. A non-significant pattern of distribution could be evidence for either random distribution or equal distribution. Some species with equal depth distribution can be important and stable members of MSS, too. Such notable species in our material seem to be millipedes *Cibiniulus slovacus*, *Haasea flavescens*, *Ochogona caroli*, *Polydesmus denticulatus*, and *Trachysphaera gibbula*.

Five of the study sites used of two types of fixative solutions in parallel and brought different results. For millipedes, traps with ethylene glycol show much higher efficiency in comparison to those with formaldehyde. This is consistent with other studies referring to the effectiveness of fixative solutions on some invertebrates in forested scree slopes (Rendoš et al. 2014, 2016a; Mock et al. 2015; Rudy et al. 2018; Jureková et al. 2019). This phenomenon seems to be caused by the repellent effect of formaldehyde solution on some species, observed by several authors (e.g., Renner 1982; Gerlach et al. 2009; Rendoš et al. 2016a). However, some fixative solutions could serve as attractants for different species (Skvarla et al. 2014). Regarding species composition, each of the millipede species preferred ethylene glycol, with some species collected exclusively in this fixative. Altogether, for millipedes there is no benefit to using formaldehyde in comparison to ethylene glycol. Regarding millipedes, it seems there is no sense in using formaldehyde as a fixative. On the contrary, ethylene glycol has been proved to be a suitable fixation. As an inexpensive alternative to ethylene glycol, propylene glycol can be used (Skvarla et al 2014). Propylene glycol is practically non-toxic and has the same preservation properties as ethylene glycol (Jud and Schmidt-Engling 2008; Aristophanous 2010). In addition, it is suitable for molecular studies, as the quality of DNA conservation in undiluted propylene glycol seems to be similar to DNA preserved in ethanol (Moreau et al. 2013).

Positive effects of ethylene-glycol were also observed in centipedes, with higher abundance in ethylene glycol traps documented at majority of the study sites with two fixative liquids used. Species composition, however, showed selective effects of both fixative solutions, as some of the centipede species were collected only in formaldehyde and others only in ethylene glycol. An attractive effect of formaldehyde was observed only in case of symphylans, with more individuals collected in traps using this fixative solution. Any small change in traps, including using different fixatives, can affect results. In our study, we generalise the main features, yet each of the study sites has specific characteristics. For a long-term depth gradient study, it would be advisable to use a completely neutral fixative solution (water); however, this is in principle impossible. After a short period of time, in any type of solution, the carcasses of captured animals accumulate and become attractant or repellent for other animals. The types of subterranean traps used in this study have limitations; however, it is effective for comparison of results to other methods of collecting of soil fauna and does not require excessive and time-consuming effort.

Conclusions

Subterranean diversity of Myriapoda inhabiting scree slopes has been investigated at various localities of mountainous Central Europe to the depth of one meter. Our study represents the first study with a larger number of sites dealing with the issue. Forested scree slopes in the region are usually lacking exclusively subterranean myriapod species and are largely colonised by surface-dwelling species of centipedes and millipedes. Deeper zones of screes are apparently parts of MSS and are clearly preferred only by two blind blaniulid millipedes, *Archiboreoiulus pallidus* and *Cibiniulus slovacus*. However, a relatively diverse community of relict myriapod fauna uses debris habitats as a climatic refugium. Although all studied locations and studied groups of invertebrates have their distinctive specifics, general depth distribution of Myriapoda has its pattern as well.

The design of subterranean traps had a significant effect on the findings. This was verified using two different fixative solutions in traps in parallel. The use of ethylene glycol in traps superimposed data obtained by formaldehyde; however, it did not provide a completely different picture of the depth distribution of myriapods. Any of the types of subterranean traps used in this study can only be recommended for any similar study.

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Supplementary material 1

Table S1

Authors: Beáta Haľková, Ivan Hadrián Tuf, Karel Tajovský, Andrej Mock

Data type: Species data

Explanation note: List of sampled centipede species and community characteristics. Abbreviations: D-Dominance, C-Constancy. Coloured boxes indicate number of individuals in given depth. The numbers indicating particular studied scree slopes are stated in Fig. 1.

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Supplementary material 2

Table S2

Authors: Beáta Haľková, Ivan Hadrián Tuf, Karel Tajovský, Andrej Mock

Data type: Species data

Explanation note: List of sampled millipede species and community characteristics. Abbreviations: D-Dominance, C-Constancy. Coloured boxes indicate number of individuals in given depth. The numbers indicating particular studied scree slopes are stated in Fig. 1.

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Character of woodland fragments affects distribution of myriapod assemblages in agricultural landscape

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Abstract

Fragments of woodland fulfil many irreplaceable functions in the agricultural landscape including being the main source of biodiversity of soil invertebrates. Due to intensive farming and land use changes, especially in the second half of the 20th century, fragments of woodland in agricultural landscape almost disappeared. This has led to a decrease in the diversity of invertebrates, especially those for which the presence of these woodland habitats in the landscape is a key element for survival. The aim of this study was to evaluate the importance of fragments of woodland (characterised by their area, vegetation structure, the amount of leaf litter layer and soil moisture) on the distribution of centipedes and millipedes (Myriapoda) in the agricultural landscape of South Moravia (Czech Republic). Myriapods were collected using pitfall traps during summer in 2016 and 2017. Results showed that activity-density of myriapods is positively correlated with thickness of the leaf litter layer. Moreover, the species richness of centipedes is positively correlated with increasing size of fragments of woodland although higher centipedes' activity-density was found in rather uniform woodlands in term of diversity of tree species.

Keywords

activity-density, area, Chilopoda, Diplopoda, landscape elements, species richness

Introduction

Hedgerows, wood fragments, windbreaks, and other wood elements represent an integral part of the agricultural landscape, defined as a mosaic of fields and uncultivated natural or semi-natural areas (Burel 1996). They were created by human planting primarily or they are remnants of formerly wooded landscape (Burel and Baudry 1989). The species composition of flora and fauna of these forest elements differs based on historical rural development and agricultural practices (Burel 1996). In the agricultural landscape, these elements fulfil many important functions. In addition to their importance in protecting against water and wind erosion (Burel and Baudry 1989; Baudry et al. 2000; Stašiov et al. 2017), they also represent a major source of invertebrates' biodiversity in the landscape (Diekötter et al. 2007).

The presence of invertebrates is very important as they provide many irreplaceable ecosystem services. One of the major groups of ground dwelling invertebrates in this regard are myriapods (Myriapoda). Millipedes (Diplopoda) are in most cases detritovores, saprophages or phytophages (Kime and Golovatch 2000). They consume decaying plant residues that break into smaller particles, thereby mediating this dead material to microbial decomposition (David and Handa 2010; Riutta et al. 2012; David 2014; Bogyó et al. 2015; De Smedt et al. 2016, 2017, 2018). Centipedes (Chilopoda) are soil predators that feed on larvae and adults of other small invertebrates and thus significantly reduce the abundance of other invertebrates (Voigtländer 2011). Both these groups of myriapods are also sources of food for other animals (Stašiov et al. 2017).

For ground dwelling invertebrates, that use uncultivated areas, hedgerows and fragments of woodland are indispensable as they provide suitable habitats for the survival of their populations in the agricultural landscape (Agger and Brandt 1988). They are especially important for species that are strictly bound to these habitats, but also for species that spend a certain part of their life cycle on them (Burel and Baudry 1990, 2005). Higher heterogeneity, undisturbed habitats and the presence of vegetation cover also affects the availability of food sources for invertebrates (Previati et al. 2007).

Fragments of woodland and hedgerows were for centuries under the influence of transformations by farmers, who often evaluated them as being worthless and thus they eliminated them (Burel and Baudry 1989). The main change in European landscapes occurred in the second half of the 20th century (50s–80s) (Burel and Baudry 1990), particularly in terms of the structure of agricultural landscapes (Weibull et al. 2003). In countries in which agriculture collectivization was applied (e.g., former Czechoslovakia) such changes were even more dramatic (Šarapatka and Štěrba 1998; Havlíček et al. 2018). Under the influence of specialization and intensification, there was simplification of the landscape and redistribution of land, where emphasis was placed on the extension of arable land. This management led to a change in the structure of landscape (fragmentation, decrease and uneven distribution of hedgerows and fragments of woodland) and habitat quality, which was reflected also in local species richness (Agger and Brandt 1988; Wade et al. 2003; Dauber et al. 2005; Previati et al. 2007).

Such long-term landscape management caused many negative effects, which also manifested themselves in the ground dwelling invertebrates. Previati et al. (2007) point to the increased impact of disturbances associated with intensive field cultivation that have been recognized to reduce the species richness of invertebrates. Moreover, loss of habitats, their fragmentation or reduction of size lead to the species extinction or increased susceptibility to their disappearance (Fahrig 2003; Ewers and Didham 2005; Honnay et al. 2005).

Quality natural resources and ecosystem services that directly provide fragments of woodland and hedgerows or invertebrates, which are supported through presence of these habitats, are indispensable for agriculture. Their rational use and proper management in the landscape should therefore be given special attention (Meeus 1993; De Smedt et al. 2017). Based on this, we tried to evaluate the relationship between fragments of woodland (their size, vegetation characteristics, thickness of leaf litter and moisture) and the activity-density and species richness of myriapods.

Materials and methods

Description of study sites

Research was realized in agricultural landscape of Southern Moravia in the vicinity of the villages of Šardice (48°58'N, 17°2'E), Stavěšice (49°0'N, 17°2'E), Čejč (48°57'N, 16°58'E), and Hovorany (48°57'N, 17°0'E). The studied sites consisted of 38 preselected isolated wood fragments and hedgerows. The surrounding matrix of these habitats consisted mainly of arable land, vineyards and partly permanent or temporary grasslands.

Wood fragments represented the remains of lowland broadleaf forests, coastal tree vegetation around the streams, or artificially planted orchards, or wood linear elements forming the natural boundaries between lands. Many patches were largely invaded by self-seeding black locust (*Robinia pseudacacia*), blackthorn (*Prunus spinosa*) and elderberry (*Sambucus nigra*). Remains of large wood stands were mostly made up of linden (*Tilia* spp.), birch (*Betula pendula*), ash (*Fraxinus excelsior*), pine (*Pinus silvestris*), chestnut (*Aesculus hippocastanum*), oak (*Quercus* spp.) or maple (*Acer* spp.). Other hedgerows were often made of walnut (*Juglans regia*), cherry (*Prunus* spp.) or poplar (*Populus* spp.).

Five pitfall traps were placed at each site, these consisting of a plastic cup of a volume of 3 decilitres (diameter 7 cm, high 13 cm) buried uniformly with the soil surface. The traps were half filled with 4% formaldehyde as a fixative solution and were covered by metal sheets. The pitfall traps were arranged in line spacing 10 m inside a wood patch. Some linear wood strips were only ca 10 m wide; in this situation a line of traps passing through the middle of the strip. In larger patches, the line was placed at least 10 m far from the edge. Traps were installed on the sites for three weeks during June to August of 2016 or 2017. Caught centipedes and millipedes were identified to species level.

Environmental variables

The distribution of invertebrates in the landscape was assessed in relation to several selected environmental variables:

(1) *size of the sites*, which ranged from 0.04 to 7 ha (measured using Google Earth software),
(2) *density of the canopy of trees*, evaluated at scale 1–4, when level 1 is for canopies covering sky from 0–25%, level 2 for sky covered by canopies at level 26–50%, level 3 for covering sky at level 51–75% and level 4 for canopy covering sky by 76–100%, covering was mean of estimations by naked eyes of three independent persons,
(3) *the percentage coverage of surface by herb layer*, estimated as mean of three independent estimations (rounded to tens of percent),
(4) *dominance of grasses in herb layer*, evaluated by the same methods as previous parameter,
(5) *thickness of leaf litter layer*, measured in centimetres as the mean of three measures on different points at each site,
(6) *soil moisture*, measured gravimetrically during installation of traps,
(7) *species richness of trees*, expressed as number of tree species creating evaluated wood fragment and
(8) *black locust dominance* in tree layer, estimated as the mean of three independent estimations with 10% accuracy.

Data analysis

Constrained ordination and canonical correspondence analysis (CCA) were used to analyse the activity-density and species richness of the invertebrates (dependent variables) in relation to individual environmental factors (independent variables). To assess the trends of the ordination diagrams, we used a generalized additive model (GAM). All analyses were performed using the CANOCO 5 program (Šmilauer and Lepš 2014).

Results

Altogether 245 individuals of centipedes (Chilopoda) in 11 species were caught, and 304 individuals of millipedes (Diplopoda) in 7 species (Tab. 1). The mean catch is 0.4 centipede and 0.5 millipede per trap per week, respectively. The most dominant centipede species, *Lithobius forficatus* and *Lithobius microps*, represented together 85% of caught individuals. Among the millipedes, *Polydesmus complanatus* showed the highest activity (96% of all sampled millipedes). Number of species of trapped centipedes per site usually reached values of 1 or 2 with minimum 0 (three localities) and maximum 5 (once). Due to dominance of *P. complanatus*, this millipede was usually the only species caught and 14 sites were without surface-dwelling millipede activity during our research.

Table 1. List of the centipedes and millipedes caught on 38 studied localities, total number of individuals caught by 5 traps during 3 weeks and number of localities, at which species was recorded.

Taxon	Individuals	Localities
Chilopoda	**245**	**37**
Geophilus electricus (Linnaeus, 1758)	3	3
Lamyctes emarginatus Newport, 1844	3	3
Lithobius aeruginosus L.Koch, 1862	2	2
Lithobius austriacus Verhoeff, 1937	1	1
Lithobius crassipes L.Koch, 1862	2	2
Lithobius cyrtopus Latzel,1880	1	1
Lithobius erythrocephalus C.L.Koch, 1847	8	6
Lithobius forficatus Linnaeus, 1758	164	32
Lithobius micropodus (Matic, 1980)	2	2
Lithobius microps Meinert, 1868	45	18
Lithobius mutabilis L.Koch, 1862	14	9
Diplopoda	**304**	**24**
Blaniulus guttulatus (Fabricius, 1798)	1	1
Brachyiulus bagnalli (Curtis, 1845)	1	1
Brachyiulus lusitanus Verhoeff, 1898	1	1
Cylindroiulus boleti (C.L. Koch, 1847)	1	1
Enantiulus nanus (Latzel, 1884)	1	1
Polydesmus cf. *denticulatus* C.L. Koch, 1847	6	3
Polydesmus complanatus (Linnaeus, 1761)	293	22

Using canonical correspondence analysis (CCA) and subsequent generalized additive models (GAM), we tested the species richness and activity-density of both myriapods in total, and centipedes and millipedes independently in relation to individual measured environmental characteristics.

In independent evaluation of centipedes' distribution, the measured environmental variables explained 22.2% of the pattern of distribution. From the tested environmental characteristics, the size of fragments of woodland ($F = 3.8$, $p = 0.031$), the thickness of the leaf litter ($F = 3.4$, $p = 0.045$) and species richness of the tree floor ($F = 3.6$, $p = 0.038$) proved to be significant (Tab. 2). The number of recorded species of centipedes increased with the increasing size of the fragments of woodland (Fig. 1a), although their activity-density was not affected ($p > 0.05$). Activity-density but not species richness of centipedes was positively correlated with increasing leaf litter thickness (Fig. 1b). On the other hand, a significant decrease in activity-density was observed in localities with higher species richness of the tree floor (Fig. 1c). There was also a decline in species richness of centipedes, but the statistical model in this case came out slightly above the significance level ($F = 2.9$, $p = 0.07$).

In independent analysis of millipedes' distribution, the measured variables explained 23.5% of variability in their distribution pattern. A significant response of millipedes was to leaf litter thickness ($F = 4.2$, $p = 0.023$) in terms of their activity-density, i.e., with increasing thickness of leaf litter the number of captured individuals increased (Fig. 1d). Analysis of species response curves showed that effect of leaf litter

Table 2. The effect of measured environmental factors to myriapod communities. Effects to its activity-density and species richness for both taxa are presented independently.

	Chilopoda				**Diplopoda**			
	Activity-density		**Species richness**		**Activity-density**		**Species richness**	
	F	**p**	**F**	**p**	**F**	**p**	**F**	**p**
area of wood fragment	1.60	0.208	3.80	0.031	1.40	0.257	2.40	0.104
canopy coverage	0.07	0.931	0.45	0.643	2.40	0.105	2.50	0.101
herb layer coverage	1.40	0.257	0.60	0.556	0.38	0.687	1.50	0.248
grasses dominance	2.10	0.144	1.50	0.237	1.50	0.229	0.69	0.506
leaf litter thickness	3.40	0.045	1.10	0.336	4.20	0.023	0.56	0.576
soil moisture	0.91	0.588	2.30	0.113	0.44	0.650	0.42	0.659
tree diversity	3.60	0.038	2.90	0.071	1.10	0.341	1.20	0.326
black locust dominance	0.63	0.538	1.10	0.343	2.50	0.095	0.62	0.543

was reflected only in *P. complanatus* (F = 4.4, p = 0.019). No other factor significantly affected millipede activity-density (Tab. 2). In addition, the species richness of millipedes was not affected by any factor.

Discussion

We studied the distribution of millipedes and centipedes inhabiting fragments of woodland and hedgerows in intensively used agricultural landscape. We focused on several characteristics of the environment, which, as we supposed, could affect the species richness and abundance of these myriapods. Leaf litter thickness, area size and species richness of tree species affected myriapod assemblages.

Although number of trapped individuals seems to be rather low, very similar number of trapped centipedes (0.45 per trap per week) and millipedes (0.52 respectively) were recorded in hedgerows in Slovakia (Stašiov et al. 2017) too. Moreover, the design of study, i.e., methods (the solely pitfall trapping) and term of study (dry summer months), was chosen with respect to more groups of soil macrofauna (spiders, ground beetles, woodlice) and was not aimed to describe myriapod communities in all details (Tuf 2015). It is possible there are other species of millipedes and centipedes living in the soil and less tolerant to desiccation, but such isolated sites are able to colonize surface active species more easily (De Smedt et al. 2018). High activity and dominance of *P. complanatus* among millipedes is not surprising. This species is one of the largest millipedes among Central European species and is more resistant to desiccation. It can stay active during summer months (when research was done) (De Smedt et al. 2017).

Leaf litter

Myriapods usually occur in the leaf litter layer, typically in deciduous forests and benefit from its greater thickness and soil surface coverage. For millipedes, leaf litter is a direct source of food, while centipedes are affected indirectly through the availability

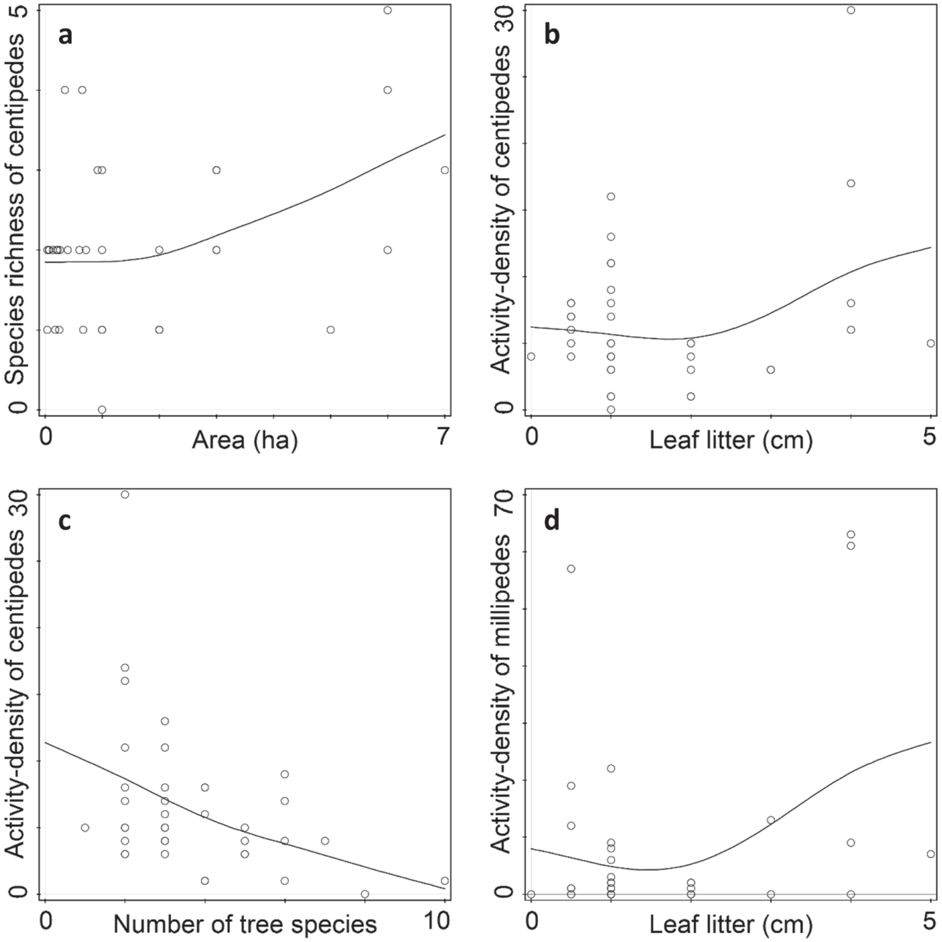

Figure 1. GAM plots evaluating effect of selected measured environmental factors to communities of centipedes and millipedes **a** relationship between size of wood fragments and number of centipedes' species trapped **b** relationship between thickness of leaf litter and number of centipedes trapped **c** relationship between species richness of trees in sites and number of centipedes trapped **d** relationship between thickness of leaf litter and number of millipedes trapped. Circles on diagram represent individual fragments of woodland.

of prey (Voigtländer 2011; Riutta et al. 2012; Bogyó et al. 2015). Moreover, predatory centipedes are mostly generalist, not dependent on the availability of a specific diet (Blackburn et al. 2002; Scheu et al. 2003) and thicker leaf litter layer can provide them a wider range of prey (Voigtländer 2011). This was also confirmed in our case, in which the thickness of leaf litter was correlated positively with activity-density of both millipedes and centipedes. This conclusion is also supported by Gava (2004), reporting that myriapods were more densely located in the lower layers of the litter, which are more favourable because of more stable microclimatic conditions. The litter layer is most important during the dry season, and this research was done in dry summer months.

Diversity of trees

Millipedes are influenced by the quality of leaf litter consumed, while higher tree species diversity often contributes to greater variability in food supply (Stašiov et al. 2012, 2017). However, we have not observed any positive effect of tree species diversity on the improvement of activity-density or species richness of millipedes. On the contrary, with increasing number of tree species, activity-density of millipedes had a tendency to decrease, although this relationship was not significant. Despite the higher diversity of trees, in the habitats may dominate tree species, which are not preferred as a source of food by millipedes. Therefore, the expected positive effect of higher species richness of tree species may be limited (Stašiov et al. 2017). On the other hand, when almost all millipedes belonged to one species, the effect on diversity cannot be correctly tested. It is also necessary to point out that those artificial fragments were usually of highest tree diversity (e.g., abandoned gardens with diverse fruit trees) and more nature-similar woods were forested by few tree species.

Centipedes showed that with increasing richness of tree species their activity-density decreased. At the same time, in habitats with a lower number (2–4) of tree species black locust dominated. Similarly, Štrobl et al. (2019) noted a positive effect of black locust on some invertebrates, especially the species of open habitats, which benefited from the specific microclimatic conditions of these stands. Moreover, black locust, due to its ability to fix atmospheric nitrogen, has an increased content of nitrogen and other nutrients in leaf litter (Rahmonov 2009), although Berthold et al. (2009) state it may be more difficult to degrade. Thus, the rate of decomposition between acacia leaves and leaves of other tree species may not be entirely comparable. Despite this, an increase in food supply for predatory centipedes may result, as e.g., Stašiov et al. (2012) noted higher species richness and equability of millipedes with increasing nitrogen content, and they also mention the positive effect of leaf litter quality on the abundance of these decomposers. Also, in our case, the activity-density of millipedes correlated positively with black locust, although this dependence was not significant. On the other hand, the long-term effect of black locust leads to acidification and decrease of nutrients in soil (Berthold et al. 2009) and, as reported by Scheu and Poser (1996), with increasing acidity the density of soil macrofauna generally decreases. However, this negative effect of black locust can be mitigated through a higher nitrogen content in the litter, which improves the quality of food for decomposers and supports microbial activity (Vasconcelos and Laurance 2005; Stašiov et al. 2012; De Smedt et al. 2018). Scheu and Poser (1996) also mention an increase in the density of the springtails (Collembola) with higher soil acidity, which may increase the food supply for centipedes.

Size of area

The increase in species richness with area size is mostly attributed to increasing environmental heterogeneity (Tews et al. 2004; Báldi 2008). However, in many cases, the species richness of individual taxonomic groups can be influenced by their different life strategies or specific habitat factors (Báldi 2008). In our case, the influence of the area size was recorded only in terms of species richness of centipedes, which positively correlated with increasing area size. One explanation could be the effect of specific microclimatic conditions of fragments of woodland in the agricultural landscape. Since humidity and temperature are the main limiting factor for centipedes (Voigtländer 2011, Kicaj and Qirjo 2014), the more favourable and more stable conditions provided from this point of view, were rather larger areas, which were typically more forested with greater shading. Smaller areas often had a more open character and due to their size and shape, acted as a drier forest edge habitat throughout their area (De Smedt et al. 2017).

Accordingly, Young and Mitchel (1994) state that as the habitat decreases, the area acting as the inner part of the forest (more stable temperature and light conditions) also decreases and the edge effect becomes more significant. The habitat smaller than 1 hectare then acts as a marginal habitat. As well, Riutta et al. (2012) mention the differences in microclimatic conditions between the edge and the interior of the fragments, where evapotranspiration grows at the edges and thus reduces the moisture of the soil and leaf litter. On the other hand, forest edges host the most abundant (or active) communities of millipedes (Bogyó et al. 2015; De Smedt et al. 2017) contrary to forest interiors. Due to these two factors affecting communities of myriapods in contradiction, finding a simple effect of forest site area on myriapods is not easy.

Other habitat characteristics

None of the other environmental characteristics investigated has been shown to be significant, although, for example, moisture is one of the major factors affecting the distribution of myriapods, as reported by many authors (Gava 2004; Tajovský and Wytwer 2009; Wytwer et al. 2009; Voigtländer 2011; Stašiov et al. 2017).

However, there were no substantial differences in moisture within the sites (moisture of soil ranged from 10 to 41% as measured during installation of traps), which may be one of the reasons why moisture did not significantly affect myriapod distribution (Riutta et al. 2012). Similarly, Lazorík and Kula (2015) also did not confirm the significant effect of moisture on centipede and millipede assemblages. Myriapod assemblages can also be influenced by other characteristics such as temperature (Voigtländer 2011), pH or organic carbon and nitrogen content in the soil (Scheu and Poser 1996; Stašiov et al. 2012, 2017). According to Grgič and Kos (2005), the heterogeneity of the internal horizontal structure of the stand is a key factor that also affects centipede diversity. Nevertheless, these characteristics were not the subject of our research. Finally, we must also consider the effects of the surrounding intensively used agricultural landscape that can specifically reflect on the characteristics of fragments of woodland and hedgerows (Paoletti et al. 2010).

Conclusions

The results of our study show that the leaf litter layer may be one of the important characteristics affecting the surface dwelling myriapod assemblages inhabiting the fragments of woodland in the agricultural landscape. In addition, the size of individual fragments of woodland and the species richness of the tree canopy also have a noticeable effect. These habitat characteristics work together with many other factors, and the interpretation of particular conclusions is often difficult. However, we believe that specific environmental conditions of fragments of woodland are a key element for distribution of myriapod assemblages in intensively cultivated agricultural landscape.

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Diversity, distribution patterns, and fauno-genesis of the millipedes (Diplopoda) of mainland China

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Abstract

Based on all available information, 339 species from 71 genera, 26 families, and eleven orders of Diplopoda have hitherto been recorded from mainland China, the fauna thus being very rich, albeit far from completely known, comprising various zoogeographic elements and populating very different environments. Diplopods mainly occur in various woodlands, in caves, and high in the mountains. Most species (> 90 %, usually highly localised, including 160 cavernicoles), 18 genera, and one family are strictly endemic to continental China. Mapping not only the horizontal, but also the vertical distributions of Diplopoda in China shows the bulk of the fauna to be expectedly restricted to forested lowland and mountain biomes or their remnants. Yet some Chordeumatida, Callipodida, Polydesmida, Julida, and even Spirobolida seem to occur only in the subalpine to alpine environments and thus may provisionally be considered as truly high-montane. The long-acknowledged notions of China being a great biogeographic zone transitional between the Palaearctic and Oriental regions generally find good support in millipede distributions, in particular at the higher taxonomic levels (generic, familial, and ordinal). While the Palaearctic/Holarctic components expectedly dominate the fauna of the northern parts of the country, the Oriental ones prevail in its south and along the Pacific coast. Both realms are increasingly mixed and intermingled towards China's centre. However, in addition to the above traditional views, based on distribution patterns alone, southern China seems to harbour a rather small, but highly peculiar faunal nucleus or origin centre of its own, whence Himalaya, Myanmar, Thailand, Indochina and/or Taiwan could have become populated by younger lineages. The millipede fauna of continental China is thus a tangled mixture of zoogeographic elements of various origins and ages, both relict and more advanced. The few anthropochores must have been the latest faunal "layer" to populate China.

Keywords
continental China, Diplopod fauna, zoogeography

Introduction

Millipedes (Diplopoda) form a highly diverse, yet strongly understudied arthropod class with > 11,000 described species (Minelli 2015). Apparently, only ca. 20 % of the global species diversity of millipedes are currently known, with the actual number of species being estimated between 50,000 and 80,000 species (Minelli and Golovatch 2013). Being mainly represented by mesophilous forest-dwelling detritivores, millipedes have long been recognised as playing important ecological roles, mostly in temperate and tropical land ecosystems where their diversity is especially pronounced (Golovatch and Kime 2009).

The class encompasses 16 extant orders, 140+ families, and ca. 2,000 genera (Minelli and Golovatch 2013), while the distributions of higher taxa fully agree with the major biogeographic divisions of Earth into the Holarctic (Palaearctic + Nearctic), Afrotropical, Oriental, Neotropical and Australian regions which are accepted since Alfred Russel Wallace and Joseph Dalton Hooker. Antarctica is completely devoid of diplopods, whereas the Oriental Region appears to be the sole one to harbour all 16 orders. Being very ancient (Silurian, early Palaeozoic) and diverse taxonomically, widespread (present on all continents except Antarctica), virtually fully terrestrial (even fossils show spiracles), poorly vagile (with highly limited dispersal capacities) and highly limited in compensatory ecological faculties (strongly restricted by a single limiting ecological factor even if the others are favourable), Diplopoda have long been considered as an exemplary group for biogeographic studies and reconstructions (e.g. Shelley and Golovatch 2011).

China has long been considered as a huge territory lying between and linking the Palaearctic and Oriental realms, with very considerable areas of southern China representing not only a marked transitional zone (e.g. Wulf 1944; Zherikhin 2003; Holt et al. 2012), but also the largest karst belt of the world particularly rich in cavernicoles, including millipedes (Golovatch 2015a). Continental China as conventionally understood here includes Hainan and Hong Kong but excludes Taiwan. The territory in question covers ca. 9,326 million sq. km, spanning ca. 5,500 km from north to south and ca. 5,200 km from west to east. China's topography is very complex. The outline descends step by step from west to east: mountains, high plateaus and hilly land prevail and take up nearly 70 % of the total area, with deserts also located in the west, but mostly plains, deltas and hills in the east. The climates are likewise varied, ranging from sharply continental in the north, through temperate in the middle, to monsoon subtropical and tropical in the south, with a warm humid influence along the eastern sea coasts (https://en.wikipedia.org/wiki/Geographic_information_systems_in_China).

China with its highly varied climates and relief (ca. 70 % national land area being mountains or plateaus) is exceptionally rich in ecological conditions and it supports as many as 18 natural latitudinal belts or biomes (Ni et al. 2000). They range from Polar desert and Alpine tundra in Tibet, through grasslands (savanna, steppe) or desert in the northern parts, to various woodlands (scrub, boreal forest, temperate forest, tropi-

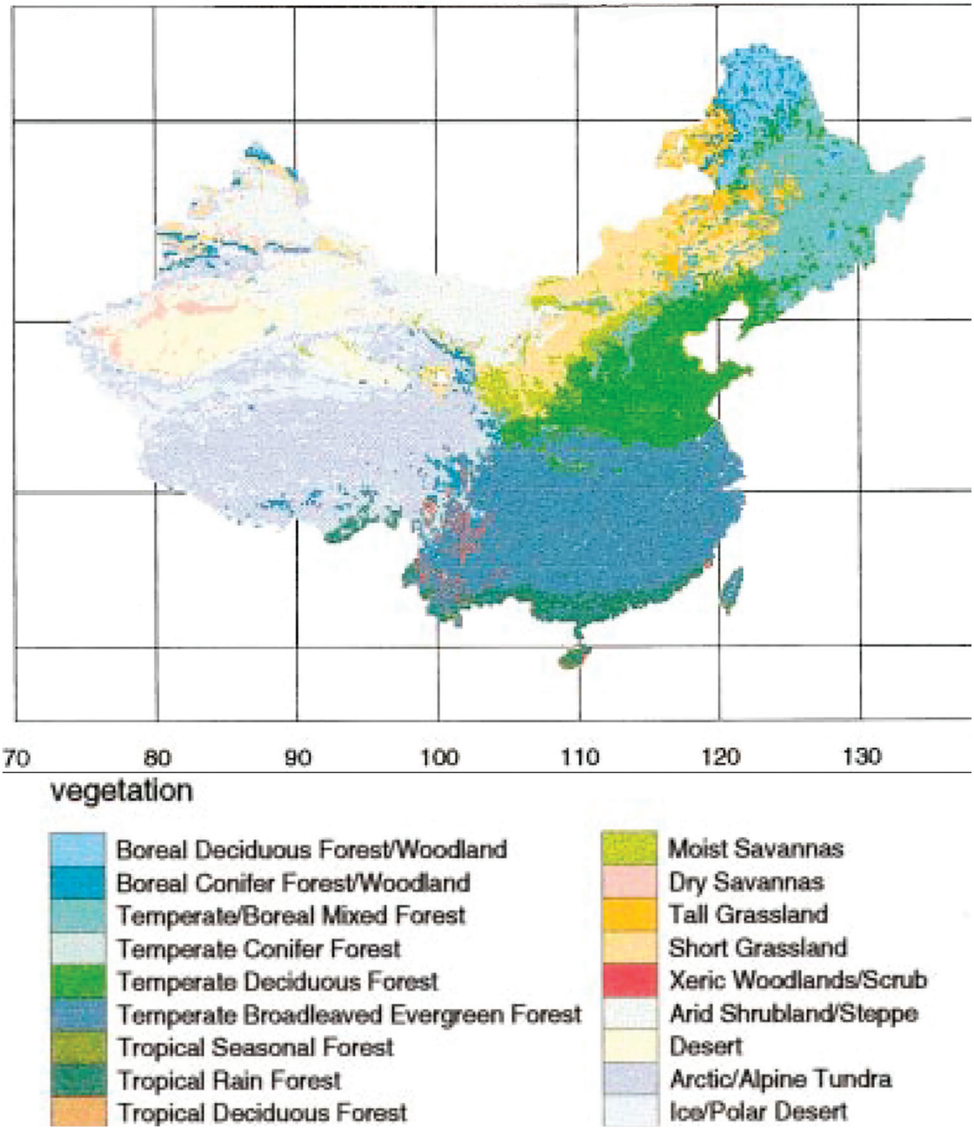

Figure 1. Nature zonation and the main biomes of China (after Ni et al. 2000).

cal forest etc.) (Fig. 1). Nature zonation is generally well-expressed, forested biomes prevailing in total area and forming a succession of boreal forest in the north, through temperate (conifer, deciduous and evergreen), to tropical rainforest in the far south. Altitudinal zonation follows the same general pattern which varies depending on location and grows increasingly complex from seven vegetation or eco-geographic belts in the Tianshan Mountains in the northwest or Tibetan Plateau in the southwest to 14 in Yunnan in the south (review by Zhang et al. 2004).

Even though the millipede fauna of China enjoys a very long history of taxonomic study, dating back to 1833 (Wang and Mauriès 1996), it still remains far from well-known. Based on all available information, 339 species from 71 genera, 26 families, and eleven orders of Diplopoda have hitherto been recorded from mainland China (Table 1), but there can be no doubt that our review will soon be out of date.

The present paper is an attempt not only to summarise the Chinese species list (as of the end of 2019), but also to provide an analysis of the distribution patterns revealed, both altitudinal and horizontal, and to hypothesise the main sources, routes and stages of fauno-genesis. A very similar approach has recently been applied to treating the millipedes of the Himalaya (Golovatch and Martens 2018).

Materials and methods

Only described species and published records are considered in our paper, while dubious taxa and those not identified to the species level have been omitted from both checklist and bibliography.

Several broken transects have been chosen to grossly reflect the macro relief of mainland China that accompanies the usual mapped distributions (Figs 2–15). The maps and their corresponding transects at the bottom show both horizontal and vertical distributions of all or most species in a number of largely speciose genera from different families and of various origins across China. The species on the maps and along transects are arranged from west to east and/or north to south. The generic level has been chosen as the most suitable to be accepted in historical biogeography (Kryzhanovsky 2002). The above novel approach to a graphic presentation of faunistic data allows us to combine the horizontal and vertical distributions of millipedes in the easiest and most vivid way on the same map. Mapping largely concerns endemic species and only the territory of mainland China.

The colour maps were generated using Google Earth Pro version 7.3.2.5495 and Adobe Photoshop CS6. The final images were processed with Adobe Photoshop CS6.

Results

The diplopod fauna of continental China at any higher level is basically a mixture of various zoogeographic elements. At the species level, most diplopods encountered in China are not only endemic to the country, but they are also more or less narrowly localised. This holds especially true for cave-dwellers which are usually presumed troglobionts restricted to a single or few adjacent caves. Generally, as the real diversity of millipedes in China has been estimated to amount to no less than 1,000 species (Golovatch 2015a), the list in Table 1, however impressive, seems to represent only ca. 1/3 of the fauna. It is thereby noteworthy that epigean Diplopoda remain especially badly understudied, since much of the collecting and taxonomic exploration efforts still focus on cavernicoles (Golovatch 2015a).

As noted above, according to the ordinal and supra-ordinal distributions in the Diplopoda and a purely biogeographic reconstruction of their origins and early evolution by Shelley and Golovatch (2011), the Oriental Region is the only biogeographic realm of the globe that supports all 16 extant orders of the class. Amongst them, eleven orders are known to occur in mainland China, with the distribution patterns of their constituent families and genera available in Table 1. The remaining five orders, albeit formally excluded from consideration, are added to the roster (Table 2), because representatives of the orders Glomeridesmida, Siphonophorida, Siphonocryptida, Siphoniulida, and Stemmiulida occur or occurred in the adjacent parts of East, Southeast and/or Central Asia. Thus, one extant species of Glomeridesmida and Siphonocryptida each is known from northern Thailand and Taiwan, respectively (Shelley and Golovatch 2011, Golovatch 2015a), several Siphonophorida have been recorded from Vietnam, Laos and northern Pakistan (Jeekel 2001), while fossil Siphoniulida have recently been described from northern Myanmar (Liu et al. 2017c). Two very small orders, Siphoniulida and Siphonocryptida, are considered relict, in a stage of evolutionary decline, whereas most if not all of the remaining orders of Diplopoda are far more diverse and currently in an expansive stage of their evolution (Shelley and Golovatch 2011, Shelley 2011, Golovatch 2015a).

The greatest and about equal shares in the diplopod fauna of mainland China expectedly belong to Holarctic/Palaearctic or Oriental elements, with the former naturally dominating the northern, the latter the southern, parts of the country, and both thoroughly mixed and intermingled mainly in the more central parts. The orders Polyxenida, Polyzoniida, Platydesmida, Glomerida, Callipodida, Chordeumatida, and Julida, the families Polydesmidae and Xystodesmidae, as well as certain genera of Paradoxosomatidae seem best to be attributed to Holarctic/Palaearctic components in the fauna of China. In contrast, most of the remaining higher taxa such as the largely tropical orders Sphaerotheriida, Spirobolida, and Spirostreptida, the families Cryptodesmidae, Haplodesmidae, Opisotretidae, and Pyrgodesmidae, as well as several genera of Paradoxosomatidae seem to represent the Oriental stem. Only two families (of 25, or 8%) are endemic or subendemic to China: the monobasic Guizhousomatidae (Chordeumatida), an apparently relict troglobiont from Guizhou Province, and the Paracortinidae (Callipodida) with two genera (maybe just one, see Stoev and Geoffroy 2004) and a handful of species (including two from northern Vietnam). The number of endemic genera is quite high, 16 (of 65, or ca. 25 %): *Sinostemmiulus* (Julida), *Parabilingulus*, *Agaricogonopus*, *Junceustreptus*, *Prominulostreptus* (all Spirostreptida), *Lipseuma* (Chordeumatida), *Angulifemur* (Callipodida), *Belousoviella*, *Gonobelus*, *Mandarinopus*, *Orthomorphella*, *Sigipinius*, *Sinomorpha*, *Wulingina*, *Yuennanina* (all Polydesmida: Paradoxosomatidae), and *Kiulinga* (Polydesmida: Xystodesmidae). One might think the higher the altitude, the more likely the taxon's Holarctic or Palaearctic origin and, *vice versa*, the lower the elevation, the more probable a tropical descent. However, the vertical distributions usually fail to provide a clear-cut support to attributing a higher taxon to this or that stem. The following examples can serve to show this.

Table 1. The millipede fauna of continental China, with data on distributions and basic literature sources.

Taxa	Altitude (m a.s.l.)	Distribution, province/region (main reference/s)
Order Polyxenida Verhoeff, 1934		Global
Family Polyxenidae Lucas, 1840		Global
Genus *Eudigraphis* Silvestri, 1948		East Asia
1. *Eudigraphis sinensis* Ishii & Liang, 1990	ca. 100	Zhejiang, Hangzhou, Lake Xihu (Ishii and Liang 1990)
Genus *Polyxenus* Latreille, 1802–03		Global
2. *Polyxenus hangzoensis* Ishii & Liang, 1990	ca. 100	Zhejiang, Hangzhou, Lake Xihu (Ishii and Liang 1990)
Order Glomerida Brandt, 1833		Holarctic and SE Asia
Family Glomeridae Leach, 1816		Holarctic and SE Asia
Genus *Hyleoglomeris* Verhoeff, 1910	145–2810	Balkans, Anatolia, Caucasus, Central, E and SE Asia
3. *Hyleoglomeris albicorporis* Zhang & Zhang, 1995	ca. 1660	Yunnan, Baoshan City, Cave Shihua Dong (Zhang and Zhang 1995)
4. *H. aschnae* Makhan, 2010	ca. 730	Chongqing, Beibei, Mt. Jinyunshan (Makhan 2010b)
5. *H. baxian* Liu & Tian, 2015	ca. 145	Guangxi, Du'an County, Chengjiang Town, Cave Baxian Park Dong (Liu and Tian 2015a)
6. *H. bicolor* (Wood, 1865)	210	Hong Kong, Mt. Taimoshan (Golovatch et al. 2006b)
7. *H. curtisulcata* Golovatch, Liu & Geoffroy, 2012	420	Guangxi, Huanjiang County, Mulun, Cave Gang Lai Dong (Golovatch et al. 2012b)
8. *H. emarginata* Golovatch, 1981	310	Jiangsu, Nanjing City, Mt. Zijinshan (Golovatch 1981, Golovatch et al. 2006b)
9. *H. eusulcata* Golovatch, Geoffroy & Mauriès, 2006	ca. 410	Guizhou, Libo County, caves Latai Dong and Shuijiang Dong (Golovatch et al. 2006b)
10. *H. generalis* Liu & Tian, 2015	550	Guizhou, Cengong County, Shuiwei Town, Cave Jiangjun Dong (Liu and Tian 2015a)
11. *H. getuhensis* Liu & Tian, 2015	ca. 910	Guizhou, Ziyun County, Getuhe National Geopark, Cave Miaoting Dong (Liu and Tian 2015a)
12. *H. grandis* Liu & Tian, 2015	ca. 280	Guangxi, Dahua County, Qibainong Geopark, Cave Qiaoxu Dong (Liu and Tian 2015a)
13. *H. gudu* Golovatch, Liu & Geoffroy, 2012	1365	Guizhou, Anlong County, Cave Hei Dong (Golovatch et al. 2012b)
14. *H. heshang* Golovatch, Liu & Geoffroy, 2012	ca. 700	Guangxi, Xilin County, Cave Zhoubang Dong (Golovatch et al. 2012b)
15. *H. kunnan* Golovatch, Liu & Geoffroy, 2012	420	Guangxi, Huanjiang County, Mulun, Cave Ganxiao Dong (Golovatch et al. 2012b)
16. *H. lii* Golovatch, Liu & Geoffroy, 2012	190	Guangxi, Fuchuan County, Cave Baifu Dong (Golovatch et al. 2012b)
17. *H. maculata* Golovatch, Geoffroy & Mauriès, 2006	ca. 1315	Yunnan, Mengzi County, Cave Laoshao Dong (Golovatch et al. 2006b)
18. *H. mashanorum* Golovatch, Liu & Geoffroy, 2012	ca. 210	Guangxi, Huanjiang County, Mulun, Cave Mashan Dong (Golovatch et al. 2012b)
19. *H. multistriata* Liu & Tian, 2015	ca. 400	Guizhou, Jiangkou County, Nuxi Town, Cave I Dong (Liu and Tian 2015a)
20. *H. mulunensis* Golovatch, Liu & Geoffroy, 2012	ca. 210	Guangxi, Huanjiang County, Mulun, Cave Xia Dong (Golovatch et al. 2012b)
21. *H. nigu* Golovatch, Liu & Geoffroy, 2012	ca. 1120	Guizhou, Qianxi County, Cave Luo Sai Dong (Golovatch et al. 2012b)
22. *H. qiyi* Golovatch, Liu & Geoffroy, 2012	ca. 210	Guangxi, Huanjiang County, Mulun, Cave MinLi Dong (Golovatch et al. 2012b)
23. *H. reducta* Golovatch, Geoffroy & Mauriès, 2006	ca. 1315	Yunnan, Jianshui County, Cave Yan Dong (Golovatch et al. 2006b)

Taxa	Altitude (m a.s.l.)	Distribution, province/region (main reference/s)
24. *H. rhinoceros* Liu & Tian, 2015	ca. 1025	Guizhou, Anlong County, Dushan Town, Cave Xiniu Dong (Liu and Tian 2015a)
25. *H. rukouqu* Liu & Wynne, 2019	190	Guangxi, Yangshuo County, Cave Shangshuiyan Dong (Liu and Wynne 2019)
26. *H. sinensis* (Brölemann, 1896)	1540–2810	Sichuan, Kangding County, and Tibet (Golovatch et al. 2006b, Liu and Tian 2015a); New record: Sichuan, W of Ningnan County, 3.3 km WSW of Xiaotiancun village
27. *H. tiani* Golovatch, Liu & Geoffroy, 2012	ca. 300	Hunan, Linwu County, Huatang Town, Cave Long Dong (Golovatch et al. 2012b)
28. *H. variabilis* Liu & Tian, 2015	830	Guizhou, Cengong County, Pingle Town, Cave Wanfuchangcheng Dong (Liu and Tian 2015a)
29. *H. wuse* Golovatch, Liu & Geoffroy, 2012	ca. 425	Guizhou, Maolan County, Cave Dongge Dong (Golovatch et al. 2012b)
30. *H. xia* Golovatch, Liu & Geoffroy, 2012	ca. 300	Hunan, Linwu County, Sanhe Town, Tianhe Village, Cave 1 Dong (Golovatch et al. 2012b)
31. *H. xueju* Golovatch, Liu & Geoffroy, 2012	ca. 140	Guangxi, Du'an County, Cave Yaonan Dong (Golovatch et al. 2012b)
32. *H. xuxiakei* Liu & Wynne, 2019	190	Guangxi, Yangshuo County, Cave Guanshan No. 4 Dong (Liu and Wynne 2019)
33. *H. yinshi* Golovatch, Liu & Geoffroy, 2012	1205	Guizhou, Kaiyang County, Cave Xianyan Dong (Golovatch et al. 2012b)
34. *H. youhao* Golovatch, Liu & Geoffroy, 2012	ca. 300	Hunan, Linwu County, Sanhe Town, near Changshali Village, Cave 2 Dong (Golovatch et al. 2012b)
Order Sphaerotheriida Brandt, 1833		S and E Africa, Madagascar, Seychelles, Sri Lanka, S India, Himalayas, E China, SE Asia, Australia, New Zealand
Family Zephroniidae Gray, in Jones, 1843		Seychelles, Himalayas, E China, SE Asia, Sumatra, Java, Borneo, Sulawesi, Philippines
Genus *Prionobelum* Verhoeff, 1924	10–1500	Vietnam, E China
35. *Prionobelum hainani* (Gressitt, 1941)	375	Hainan, Tai-Pin-ts'uen (Dwa Bi), foot of Mt. Loi Mother (Mauriès 2001)
36. *P. joliveti* Mauriès, 2001	145	Hainan, W of Danzhou (Mauriès 2001)
37. *P. maculosum* (Attems, 1935)	10	Fujian, Fuzhou City (Attems 1935, Mauriès 2001, Wesener 2016)
38. *P. majorinum* (Zhang & Li, 1982)	1200	Hainan, Mt. Diaoluoshan (Zhang and Li 1982c, Mauriès 2001)
39. *P. multidentata* (Wang & Zhang, 1993)	1500	Fujian, Jiangle County, Mt. Longqi (Wang and Zhang 1993b, Wesener 2016)
Genus *Zephronia* Gray, 1832		Himalayas, Myanmar, E China, Indochina, Thailand, Malaysia
40. *Zephronia profuga* Attems, 1936	?	Hong Kong (Attems 1936, Wesener 2016)
Order Platydesmida Cook, 1895		Mediterranean, Near East, E and SE Asia, Nearctic, Central America
Family Andrognathidae Cope, 1869		E and SE Asia, USA, Mexico
Genus *Brachycybe* Wood, 1964		E and SE Asia, USA
41. *Brachycybe cooki* (Loomis, 1942)	ca. 1090	Jiangxi, S of Jiujiang, Lushan City, Guling Town (Loomis 1942, Shelley et al. 2005)
Order Polyzoniida Cook, 1895		Global
Family Polyzoniidae Gervais, 1844		Holarctic
Genus *Angarozonium* Shelley, 1997		N Asia
42. *Angarozonium amurense* (Gerstfeldt, 1859)	100–1800	Heilongjiang, mouth of Songari River; also Siberia and Mongolia (Mikhaljova 2017)

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Order Julida Brandt, 1833		Holarctic, E and SE Asia
Family Julidae Leach, 1814		Holarctic, E and SE Asia
Genus *Anaulaciulus* Pocock, 1895	10–3350	Himalaya and E Asia
43. *Anaulaciulus enghoffi* Korsós, 2001	2700	Gansu, Karyn Valley, S wall of Latshi-san Pass (Korsós 2001)
44. *A. otigonopus* Zhang, 1993	ca. 200	Hunan, Changsha City, Mt. Yuelushan (Zhang 1993a)
45. *A. paludicola* (Pocock,1895)	10	Zhejiang, 25 mi of Ningo (Ningbo), Lake Wo-Lee (Causey 1966)
46. *A. tibetanus* Korsós, 2001	2700–3350	Tibet, Dü Chu Valley; Assam, India, 11,000 feet (Korsós 2001)
47. *A. tonginus* (Karsch, 1881)	?	Hong Kong; Taiwan; ? Hunan (Korsós 1994)
48. *A. vallicola* (Pocock, 1895)	?	Zhejiang, 60 mi inland from Sam-moon Bay, Da-zeh Valley (Causey 1966)
Genus *Nepalmatoiulus* Mauriès, 1983	275–3650	Himalaya, E and SE Asia
49. *Nepalmatoiulus brachymeritus* Enghoff, 1987	2810	Sichuan, Kangding (Enghoff 1987b)
50. *N. eulobos* Enghoff, 1987	320	Guangdong, Meizhou City, Mt. Qingliangshan (Enghoff 1987b)
51. *N. fraterdraconis* Enghoff, 1987	ca. 1045	Jiangxi, Jiujiang City, Mt. Lushan, road to Guling (Enghoff 1987b)
52. *N. polyakis* Enghoff, 1987	ca. 275	Sichuan, Suining City (Enghoff 1987b)
53. *N. rhaphimeritus* Enghoff, 1987	2810	Sichuan, Kangding City (Enghoff 1987b)
54. *N. tibetanus* Enghoff, 1987	2750–3650	SE Tibet, Do-Chu Valley, Pasho Distr., near Rombe Gompa (Enghoff 1987b)
55. *N. yunnanensis* Enghoff, 1987	?	Yunnan (Enghoff 1987b)
Genus *Pacifiiulus* Mikhaljova, 1982		Siberia
56. *Pacifiiulus amurensis* (Gerstfeldt, 1859)	100–2500	Heilongjiang, between mouths of Ussuri and Garyn rivers; also Siberia and the Russian Far East (Mikhaljova 2017)
Family Mongoliulidae Pocock, 1903		E Asia
Genus *Skleroprotopus* Attems, 1901	125–1190	E Asia
57. *Skleroprotopus confucius* Attems, 1901	ca. 490	Hebei, Zhangjiakou City (Attems 1901)
58. *S. laticoxalis* Takakuwa, 1942	395	Liaoning, Shenyang City (Takakuwa 1942)
59. *S. membramipedalis* Zhang, 1985	ca. 125–150	Beijing, Fangshan, caves Shihua and Yunshui (Zhang 1985a, Vagalinski et al. 2018)
60. *S. serratus* Takakuwa & Takashima, 1949	ca. 1190	Shanxi, Yantou village (Takakuwa and Takashima 1949)
Family Nemasomatidae Bollman, 1893		Holarctic
Genus *Orinisobates* Lohmander, 1933		Holarctic E of Ural Mountains
61. *Orinisobates gracilis* (Verhoeff, 1934)	?	Xinjiang, Urumqi, Mt. Tianshan (Verhoeff 1934, Enghoff 1985)
Genus *Sinostemmiulus* Chamberlin & Wang, 1953		China
62. *Sinostemmiulus simplicior* Chamberlin & Wang, 1953	?	Zhejiang, Chenghsien (Cheng County?) (Chamberlin and Wang 1953, Hoffman 1966)
Family Parajulidae Bollman, 1893		Nearctic and E Asia
Genus *Karteroiulus* Attems, 1909		Nearctic and E Asia
63. *Karteroiulus niger* Attems, 1909	?	Jiangxi, Tai-an-Long (Enghoff 1987a)

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Order Spirobolida Cook, 1895		Pantropical
Family Spirobolidae Bollman, 1893		E Asia
Genus *Spirobolus* Brandt, 1833	305–3350	E Asia
64. *Spirobolus bungii* Brandt, 1833	?	North of Beijing (Keeton 1960)
65. *S. cincinnalis* Wang & Zhang, 1993	1500	Fujian, Jiangle County, Mt. Longqi (Wang and Zhang 1993b)
66. *S. grahami* Keeton, 1960	ca. 305–3350	Sichuan, Suifu; S of Suifu on the Yunnan border; Mupin; near Yueh-Shi, Granham; Mt. Omeishan; Kweichow: Shih Men Kan (Keeton, 1960); Hubei, Jianshi County (Wang and Zhang 1993b)
67. *S. umbobrochus* Keeton, 1960	ca. 915	Sichuan, Yongshien; Kueichow, Shih Men Kan (Keeton 1960)
68. *S. walkeri* Pocock, 1895	ca. 150–760	Zhejiang, Chusan Island, "Da-laen-Saen", 30 mi SW of Ningpo (Keeton 1960)
Order Spirostreptida Brandt, 1833		Pantropical
Family Cambalopsidae Cook, 1895		Himalaya, E and SE Asia, Java, Borneo
Genus *Glyphiulus* Gervais, 1847	105–4150	E and SE Asia, Java, Borneo
69. *Glyphiulus acutus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011	ca. 210	Guangxi, Huanjiang County, Mulun, caves Ganglai Dong and Huobayun Dong (Golovatch et al. 2011a)
70. *G. adeloglyphus* Zhang & Li, 1982	ca. 120	Guangxi, Yangshuo County, Xingping Town (Zhang and Li 1982b)
71. *G. anophthalmus* (Loksa, 1960)	ca. 105	Guangxi (Loksa 1960)
72. *G. balazsi* (Loksa, 1960)	ca. 990 or 835	Guizhou, Luodian County or Longping Town (Loksa 1960)
73. *G. basalis* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2007	ca. 4150	Sichuan, Xinlong County, Cave Ganchuan Dong (Golovatch et al. 2007a)
74. *G. beroni* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2007	ca. 1315	Yunnan, Jianshui County, Cave Baguo Dong; and Tonghai County, Cave Xianren Dong (Golovatch et al. 2007a)
75. *G. calceus* Jiang, Guo, Chen & Xie, 2018	900	Guangxi, Tian'e County, Bala Town, Madong village, Hanyaotun, Cave Xianren Dong (Jiang et al. 2018)
76. *G. deharvengi* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2007	730	Hunan, Longshan County, Huoyan Village, Cave Feihu Dong, Cave Baiyan Dong, Cave Remi Dong (Golovatch et al. 2007a)
77. *G. difficilis* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011	ca. 925	Guangxi, Leye County, Yachang Town, Huaping, Cave She Dong and Cave Xiayan Dong (Golovatch et al. 2011b)
78. *G. echinoides* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011	ca. 270	Guangxi, Fushui County, Bapen village, Cave II Dong (Golovatch et al. 2011b)
79. *G. foetidus* Jiang, Guo, Chen & Xie, 2018	690–820	Guangxi, Xilin County, Zhoubang village, Cave Zhoubang Dong; Yunnan, Guangnan County, Bamei Town, Ake village, Cave Miaopu Dong (Jiang et al. 2018)
80. *G. formosus* (Pocock, 1895)	ca. 135	Hong Kong (Pocock 1895)
81. *G. granulatus* Gervais, 1847	135–440	Pantropical; Guangxi, Longzhou; Hong Kong; Taiwan (Golovatch et al. 2007a)
82. *G. guangnanensis* Jiang, Guo, Chen & Xie, 2018	690	Yunnan, Guangnan County, Bamei Town, Ake village, Cave Miaopu Dong (Jiang et al. 2018)
83. *G. impletus* Jiang, Guo, Chen & Xie, 2018	320–830	Guangxi, Lingyun County, caves (Jiang et al. 2018)
84. *G. intermedius* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2007	ca. 485	Sichuan, Chengdu, Cave Huanlong Dong (Golovatch et al. 2007b)

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85. *G. latellai* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2007	ca. 1495	Guizhou, Qianxi County, Honglin village, Cave Hangtu Dong, Cave Xiao Dong, Cave Xixiang Dong, Cave Dayan Dong, Cave Tiaoshui Dong, Cave Ludiaoai Dong, Cave Shuhuayan Dong, Cave Shuiluo Dong (Golovatch et al. 2007a)
86. *G. latus* Jiang, Lv, Guo & Chen, 2017	ca. 410	Sichuan, Leshan City, Muchuan County, Cave Longgong Dong (Jiang et al. 2017)
87. *G. liangshanensis* Jiang, Lv, Guo & Chen, 2017	ca. 470–1155	Sichuan, Liangshan Yi Autonomous Prefecture, Xichang City, Xixi, Xianren Cave; Miyi County, Baima Town, Cave Zhuanxulong Dong (Jiang et al. 2017)
88. *G. lipsorum* Mauriès & Nguyen Duy-Jacquemin, 1997	ca. 430	Hubei, cave (Mauriès and Nguyen Duy-Jacquemin 1997)
89. *G. maocun* Liu & Wynne, 2019	180	Guangxi, Lingchuan County, Maocun Village, Cave Liangfeng Dong (Liu and Wynne 2019)
90. *G. melanoporus* Mauriès & Nguyen Duy-Jacquemin, 1997	ca. 180	Guangxi, near Guilin, cave (Mauriès and Nguyen Duy-Jacquemin 1997); Xiufeng District, Cave Maomaotou (Liu and Wynne 2019)
91. *G. mulunensis* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011	ca. 270	Guangxi, Huanjiang County, Mulun, caves Mashan Dong and Ganglai II Dong (Golovatch et al. 2011a)
92. *G. obliteratoides* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2007	1400	Guizhou, Anshun City, Liangshuijing, Cave Tianxian Dong (Golovatch et al. 2007b)
93. *G. obliteratus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2007	ca. 1315	Yunnan, Mile County, caves Bailong Dong and Houshan Dong (Golovatch et al. 2007b)
94. *G. paracostulifer* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2007	ca. 1495	Guizhou, Qianxi County, Honglin Town, Cave Laohu Dong (Golovatch et al. 2007b)
95. *G. paragranulatus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2007	ca. 1315	Yunnan, Jianshui County, Cave Yan Dong (Golovatch et al. 2007a)
96. *G. paramulunensis* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011	211	Guangxi, Huanjiang County, Mulun, caves Shui Dong and Xialan Dong (Golovatch et al. 2011a)
97. *G. parobliteratus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2007	ca. 725–860	Guizhou, Suiyang County, Wenquan Town, Shuanghe, Cave Dafeng Dong (Golovatch et al. 2007b)
98. *G. pergranulatus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2007	ca. 1065	Guizhou, Guanling County, Huajiang, Cave Da Dong and Cave Anjiada Dong (Golovatch et al. 2007a)
99. *G. proximus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011	ca. 210	Guangxi, Huanjiang County, Mulun, caves Ganxiao Dong and Dongtu Dong (Golovatch et al. 2011a)
100. *G. pulcher* Loksa, 1960	ca. 105	Guangxi, Daxin County, Fulong Town, a cave (Loksa 1960, Jiang et al. 2018)
101. *G. quadrohamatus* Chen & Meng, 1991	ca. 1110	Guizhou, Zhenning County, several caves (Chen and Meng 1991)
102. *G. rayrouchi* Mauriès & Nguyen Duy-Jacquemin, 1997	ca. 390	Guizhou, Maguan, Cave Heiyan Dong (Mauriès and Nguyen Duy-Jacquemin 1997)
103. *G. recticullus* Zhang & Li, 1982	ca. 325	Zhejiang, Qingyuan County (Zhang and Li 1982b)
104. *G. semigranulatus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2007	ca. 1315	Yunnan, Mile County, Cave Bailong Dong; Jianshui County, Cave Yanzi Dong (Golovatch et al. 2007a)

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105. *G. septentrionalis* Murakami, 1975	ca. 170	Guangxi, Guilin; Japan, Ryukyus, Okinawa Island (Golovatch et al. 2007a)
106. *G. sinensis* (Meng & Zhang, 1993)	ca. 1065	Guizhou, Guanling County, cave (Meng and Zhang 1993)
107. *G. speobius* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011	ca. 310	Guangxi, Huanjiang County, caves Xialan Dong and Shenlong Dong (Golovatch et al. 2011a)
108. *G. subgranulatus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2007	1313	Yunnan, Mengzi County, cave near footpath to plateau, Pothole No. 2 (Golovatch et al. 2007a)
109. *G. subobliteratus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2007	ca. 1685	Yunnan, Shilin County, Cave Zhiyun Dong (Golovatch et al. 2007b)
110. *G. tiani* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011	ca. 210	Guangxi, Huanjiang County, Mulun, Cave Dongzai Dong (Golovatch et al. 2011a)
111. *G. zorzini* Mauriès & Nguyen Duy-Jacquemin, 1997	ca. 1105	Guizhou, Shuicheng County, Cave Anjia Yan (Mauriès and Nguyen Duy-Jacquemin 1997)
Genus *Hypocambala* Silvestri, 1897		SE Asia
112. *Hypocambala polytricha* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011	ca. 110	Guangxi, Longzhou County, Nonggang, Cave Biji Dong (Golovatch et al. 2011c)
Family Pericambalidae Silvestri, 1909		China, Indochina
Genus *Bilingulus* Zhang & Li, 1981		China, Vietnam
113. *Bilingulus sinicus* Zhang & Li, 1981	165	Guangxi, Guilin City, a cave (Zhang and Li 1981a); Yangshuo County, Cave Shangshuiyan; Xiufeng District, Cave Maomaotou; Lingchuan County, Cave Liangfeng Dong (Liu and Wynne 2019)
Genus *Parabilingulus* Zhang & Li, 1981	105–120	China
114. *Parabilingulus aramulus* Zhang & Li, 1981	ca. 120	Guangxi, Yangshuo County, Xingping Town (Zhang and Li 1981a)
115. *P. simplicius* Mauriès & Jacquemin-Nguyen Duy, 1997	ca. 105	Guangxi, Gongcheng County, Cave Heiyan Dong (Mauriès and Nguyen Duy-Jacquemin 1997)
Family Harpagophoridae Attems, 1909		Afrotropical, Himalaya, Sri Lanka, S India, E and SE Asia, Sunda Archipelago
Genus *Agaricogonopus* Zhang & Zhang, 1997		China
116. *Agaricogonopus acrotrifoliolatus* Zhang & Zhang, 1997	ca. 870	Yunnan, Xishuangbanna, Mengla County, tropical rainforest (Zhang and Zhang 1997; Pimvichai et al. 2010)
Genus *Junceustreptus* Demange, 1961	650–1895	China
117. *Junceustreptus brevispinus* Zhang, 1985	ca. 650	Yunnan, Xishuangbanna, Mengman (Zhang 1985b; Pimvichai et al. 2010)
118. *J. browningi* Demange, 1962	ca. 1895	Yunnan (Demange 1962; Pimvichai et al. 2010)
119. *J. retrorsus* Hoffman, 1980	ca. 1890	Sichuan, Ning Gyuen Nfu (Hoffman 1980; Pimvichai et al. 2010)
Genus *Prominulostreptus* Pimvichai, Enghoff & Panha, 2010	?	China
120. *Prominulostreptus prominulus* (Demange, 1962)	?	Yunnan, Lou-Fou-Tsouen (Ing-Ka-Tsoue) (Demange 1962; Pimvichai et al. 2010)
Genus *Uriunceustreptus* Zhang & Chang, 1990	650–1750	China, Vietnam

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121. *Uriunceustreptus afemorispinus* Zhang & Chang, 1990	ca. 1750	Yunnan, Gejiu City (Zhang and Chang 1990; Pimvichai et al. 2010)
122. *U. bilamellatus* Zhang, 1997	ca. 650	Sichuan (now Chongqing), Youyang County (Zhang et al. 1997)
Order Chordeumatida Pocock, 1894		Mostly Holarctic, but also Central and SW South America, Madagascar, Sri Lanka, S India, E and SE Asia, Sunda Archipelago, Philippines, New Guinea, Australia, New Zealand
Family Guizhousomatidae Mauriès, 2005		China
Genus *Guizhousoma* Mauriès, 2005	ca. 1495	China
123. *Guizhousoma latellai* Mauriès, 2005	ca. 1495	Guizhou, Qianxi County, Honglin, caves Changtu Dong, Shujiayan, Luosai Dong, Shuiluo Dong, Tiaoshui Dong; and Dafang County, Cave Hei Dong (Mauriès 2005)
Family Kashmireumatidae Mauriès, 1982		Himalaya, E and SE Asia
Genus *Lipseuma* Golovatch, Geoffroy & Mauriès, 2006	435–1405	China
124. *Lipseuma bernardi* Golovatch, Geoffroy & Mauriès, 2006	ca. 435	Sichuan, Xinlong County, Three Eyes Cave (Golovatch et al. 2006a, 2007)
125. *L. josianae* Golovatch Geoffroy & Mauriès, 2006	1405	Hubei, Banqiao Town, Cave ChuanDongZi (Golovatch et al. 2006a)
Genus *Vieteuma* Golovatch, 1984	2100–2300	China, Vietnam
126. *Vieteuma hubeiense* Mauriès & Nguyen Duy-Jacquemin, 1997	ca. 2130	Hubei, Shennongjia, Yanziya, Cave Yanzi Dong (Mauriès and Nguyen Duy-Jacquemin 1997)
127. *V. longi* Shear, 2002	2100–2300	Yunnan, Baoshan City, Mt. Gaoligongshan, Nankang, 36 air km SE of Tengchong; and LuoshuiDong, 28 air km SE of Teng Chong (Shear 2002)
Family Megalotylidae Golovatch, 1978		Himalaya, Myanmar, E and SE Asia
Genus *Nepalella* Shear, 1979	750–4530	Himalaya, Myanmar, E and SE Asia
128. *Nepalella caeca* Shear, 1999	1795	Guizhou, Shuicheng County, Cave Anjia Yan (Shear 1999, Liu, Wesener et al. 2017c)
129. *N. grandis* Golovatch, Geoffroy & Mauriès, 2006	ca. 1670	Yunnan, Zhenxiong County, Cave Baiyin Dong (Golovatch et al. 2006a)
130. *N. grandoides* Golovatch, Geoffroy & Mauriès, 2006	ca. 750	Sichuan, Beichuan County, caves Yuan Dong and Black Wind Dong (Golovatch et al. 2006a, Liu, Wesener et al. 2017d)
131. *N. griswoldi* Shear, 2002	2100–2300	Yunnan, Baoshan City, Mt. Gaoligongshan, Luoshuidong, 28 air km of Tengcheng (Shear 2002)
132. *N. jinfoshan* Liu, in Liu, Wesener et al., 2017 2017	1500–2100	Chongqing, Jinfoshan, Cave Houshan Dong; Cave Lingguan Dong (Liu, Wesener et al. 2017d)
133. *N. kavanaughi* Shear, 2002	2500	Yunnan, Nujiang, Pianma, native forest on Mt. Gaoligongshan (Shear 2002)
134. *N. lobata* Liu, in Liu, Wesener et al., 2017	1000	Sichuan, Mianyang City, Beichuan County, Cave Liangshui Dong (Liu, Wesener et al. 2017d)
135. *N. magna* Shear, 2002	2300	Yunnan, Baoshan City, Mt. Gaoligongshan, Luoshuidong, 28 air-km of Tengchong (Shear 2002)
136. *N. marmorata* Golovatch, Geoffroy & Mauriès, 2006	ca. 4350	Sichuan, Xinlong County, caves Snake Mouth Dong and Three Eyes Dong (Golovatch et al. 2006a, 2007)
137. *N. pianma* Shear, 2002	2500	Yunnan, Nujiang, Pianma, Mt. Gaoligongshan, native forest (Shear 2002)
138. *N. troglodytes* Liu, in Liu, Wesener et al., 2017	1200–1300	Guizhou, Guiyang City, Xifeng County, Hejiadong village, Cave Hejia Dong; same County, Mushan village, Cave Zhangkou Dong; Guizhou, Qiannan, Longli County, Cave Feilong Dong; Guizhou, Qiannan, Fuquan County, Cave Sanlou Dong (Liu, Wesener et al. 2017d)

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139. *N. wangi* Liu, in Liu, Wesener et al., 2017	1300	Chongqing, Wulong County, Huangying Town, Qimenxia, Cave I Dong (Liu, Wesener et al. 2017d)
Order Callipodida Pocock, 1894		Holarctic, E and SE Asia
Family Caspiopetalidae Lohmander, 1931		Central Asia and China
Genus *Bollmania* Silvestri, 1896		Central Asia and China
140. *Bollmania beroni* Stoev & Enghoff, 2005	ca. 1315	Yunnan, Jianshui County, Cave Yan Dong (Stoev and Enghoff 2005)
Family Paracortinidae Wang & Zhang, 1993		China and Vietnam
Genus *Angulifemur* Zhang, 1997	1315	China
141. *Angulifemur tridigitis* Zhang, 1997	ca. 1315	Yunnan, Mengzi City, Cave Niupeng-yanzi Dong (Zhang 1997)
142. *A. unidigitis* Zhang, 1997	ca. 1315	Yunnan, Mengzi City, caves Longbaopo Dong and Laoxiao Dong (Zhang 1997)
Genus *Paracortina* Wang & Zhang, 1993	865–3300	China and N Vietnam
143. *Paracortina carinata* Wang & Zhang, 1993	3300	Yunnan, Shangrila (= Zhongdian) County (Wang and Zhang 1993a)
144. *P. chinensis* Stoev & Geoffroy, 2004	ca. 1670	Yunnan, Zhenxiong County, caves Ke Ma Dong, Da Hei Dong and Liao Jun Dong (Stoev and Geoffroy 2004)
145. *P. leptoclada* Wang & Zhang, 1993	3300	Yunnan, Shangrila (= Zhongdian) County (Wang and Zhang 1993a)
146. *P. serrata* Wang & Zhang, 1993	ca. 1845	Yunnan, Deqin County (Wang and Zhang 1993a)
147. *P. stimula* Wang & Zhang, 1993	3300	Yunnan, Shangrila (= Zhongdian) County (Wang and Zhang 1993a)
148. *P. thallina* Wang & Zhang, 1993	3300	Yunnan, Shangrila (= Zhongdian) County; Sichuan, Batang County (Wang and Zhang 1993a)
149. *P. viriosa* Wang & Zhang, 1993	3300	Yunnan, Shangrila (= Zhongdian) County (Wang and Zhang 1993a); Tibet, Mangkang County (Stoev et al. 2008)
150. *P. voluta* Wang & Zhang, 1993	ca. 2690	Sichuan, Yajiang County (Wang and Zhang 1993a)
151. *P. yinae* Liu & Tian, 2015	ca. 865	Guangxi, Baise City, Longlin County, Tianshengqiao Town, Yanchang village, Cave I (Liu and Tian 2015c)
152. *P. zhangi* Liu & Tian, 2015	ca. 965	Guizhou, Qianxinan Autonomous Prefecture, Ceheng County, Rongdu village, Cave Qiaoxia Dong (Liu and Tian 2015c)
Family Sinocallipodidae Zhang, 1993		China and Indochina
Genus *Sinocallipus* Zhang, 1993	1860	China, Laos and Vietnam
153. *Sinocallipus simplopodicus* Zhang, 1993	1860	Yunnan, Hehou City, Cave Xiao Dong (Zhang 1993b)
Order Polydesmida Pocock, 1887		Global
Family Cryptodesmidae Karsch, 1880		Pantropical
Genus *Trichopeltis* Pocock, 1894	165–1890	Himalaya, E and SE Asia, Malaysia, Sunda Archipelago
154. *Trichopeltis bellus* Liu, Golovatch & Tian, 2017	1530	Yunnan, Qujing City, Luoping County, Machang village, Cave Shuiyuan Dong (Liu et al. 2017a)
155. *T. intricatus* Liu, Golovatch & Tian, 2017	1890	Yunnan, Kunming City, Shilin County, Guishan Town, Cave Haiyi I Dong (Liu et al. 2017a)
156. *T. latellai* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2010	ca. 1495	Guizhou, Qianxi County, Honglin Town, caves Tiaoshui Dong and Changtu Dong (Golovatch et al. 2010c)
157. *T. liangfengdong* Liu & Wynne, 2019	180	Guangxi, Lingchuan County, Cave Liangfeng Dong (Liu and Wynne 2019)

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158. *T. reflexus* Liu, Golovatch & Tian, 2017	ca. 165	Hunan, Chenzhou City, Linwu County, Xianghualing Town, II Dong Cave (Liu et al. 2017a)
Family Haplodesmidae Cook, 1895		Himalaya, Myanmar, E and SE Asia, Malaysia, Sunda Archipelago, New Guinea, Melanesia, Australia
Genus *Doratodesmus* Cook, 1895		Sunda Archipelago, China
159. *Doratodesmus grandifoliatus* Zhang, in Zhang & Wang, 1993	ca. 1315	Yunnan, Mengzi County, Cave Longbaopo Dong (Zhang and Wang 1993)
Genus *Eutrichodesmus* Silvestri, 1910	65–1495	E and SE Asia, Sunda Archipelago, Melanesia
160. *Eutrichodesmus anisodentus* (Zhang, 1995)	ca. 385	Fujian, Mt. Wuyishan (Zhang 1995b)
161. *E. apicalis* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2015	ca. 75	Hubei, Yichang, Yichang County, Grotte des Araignées (Golovatch et al. 2015)
162. *E. arcicollaris* Zhang, in Zhang & Wang, 1993	ca. 170	Yunnan, Hekou County, Cave Huayu Dong (Zhang and Wang 1993, Golovatch et al. 2009a, 2009b)
163. *E. digitatus* Liu & Tian, 2013	ca. 65	Guangdong, Qingyuan City, Jintan Town, Cave Mi Dong (Liu and Tian 2013)
164. *E. distinctus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009	ca. 105	Guangxi, Fusui County, Bapen, Cave 4 Dong (Golovatch et al. 2009b)
165. *E. dorsiangulatus* (Zhang, in Zhang & Wang, 1993)	ca. 635	Yunnan, Mengla County, Cave Baoniujiao Dong (Zhang and Wang 1993, Golovatch et al. 2009a, 2009b)
166. *E. incisus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009	ca. 1495	Guizhou, Qianxi County, Honglin, caves Tiaoshui Dong, Cave Liaojingling Dong, Jiayan Dong, Dakong Dong and Luosai Dong (Golovatch et al. 2009a)
167. *E. jianjia* Liu & Wynne, 2019	190	Guangxi, Yangshuo County, Cave Guanshan No. 4 (Liu and Wynne 2019)
168. *E. latellai* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2015	1060	Guizhou, Zhenfeng County, Beipanjiang Town, Cave Shui Chi Dong (Water Pool Cave) (Golovatch et al. 2015)
169. *E. latus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009	ca. 560	Guangxi, Leye County, Yachang Nature Reserve, caves Yanwu Dong, Xiayan Dong, Xiaoshui Dong and She Dong (Golovatch et al. 2009a)
170. *E. lipsae* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2015	ca. 160	Guangxi, Guilin, Grotte des Squelettes (Golovatch et al. 2015)
171. *E. monodentus* (Zhang, in Zhang & Wang, 1993)	ca. 650	Yunnan, Mengla County, Cave Caiyun Dong (Zhang and Wang 1993, Golovatch et al. 2009a, 2009b)
172. *E. obliteratus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2015	ca. 1065	Guizhou, Guanling County, Huajiang Town, Cave Huashiban Dong (Slippery Cave) (Golovatch et al. 2015)
173. *E. pectinatidentis* (Zhang, 1995)	ca. 1010	Zhejiang, Lin'an County, Mt. Tianmu (Zhang 1995a)
174. *E. planatus* Liu & Tian, 2013	ca. 550	Guangxi, Hechi City, Liujia Town, Cave Zhenzhuyan Dong (Liu and Tian 2013)
175. *E. sketi* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2015	730	Hunan, Longshan County, Huoyan, Cave Feihu Dong (Golovatch et al. 2015)
176. *E. similis* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009	ca. 310–420	Guangxi, Huanjiang County, Mulun Nature Reserve, caves Gui II Dong and Shenlong Dong (Golovatch et al. 2009a)
177. *E. simplex* Liu & Tian, 2013	130	Jiangxi, Fenyi County, Cave Taoyuan Dong (Liu and Tian 2013)
178. *E. soesilae* Makhan, 2010	ca. 735	Chongqing, Beibei, Mt. Jinyunshan (Makhan 2010a)
179. *E. spinatus* Liu & Tian, 2013	ca. 875	Hunan, Guidong County, Sidu Town, Sidu Caves (Liu and Tian 2013)

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180. *E. tenuis* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2015	ca. 1065	Guizhou, Guanling County, Yongning Town, Cave Yun Dong (Cloud Cave) (Golovatch et al. 2015)
181. *E. triangularis* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2015	ca. 750	Sichuan, Beichuan County, Cave Yan Dong (Golovatch et al. 2015)
182. *E. troglobius* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2015	1205	Guizhou, Kaiyang County, Cave Xianyan Dong (Golovatch et al. 2015)
183. *E. trontelji* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2015	ca. 410	Guizhou, Libo County, caves Shui Jiang Dong, Shuipu Da Dong, Shuipa, Latai Dong, Jia Ban and Feng Dong (Golovatch et al. 2015)
Family Paradoxosomatidae Daday, 1889		Global except for N America
Genus *Anoplodesmus* Pocock, 1895		S, E and SE Asia
184. *Anoplodesmus chinenis* Golovatch, 2013	1700–2400	Shaanxi, Mt. Taibaishan, southern slopes, above Houshenzi, primary broadleaved forest (Golovatch 2013a)
Genus *Antheromorpha* Jeekel, 1968		E and SE Asia
185. *Antheromorpha rosea* Golovatch, 2013	1200–1700	Yunnan, S of Pianma; Baoshan District, near Hemu, Mt. Gaoligongshan, near Cave Bianfu II Dong (Golovatch 2013a, 2013b); also N Thailand and Laos (Likhitrakarn et al. 2019)
Genus *Belousoviella* Golovatch, 2012		China
186. *Belousoviella kabaki* Golovatch, 2012	3360	Sichuan, SW of Mianning, right tributary of Yalongjiang River canyon (Golovatch 2012)
Genus *Cawjeekelia* Golovatch, 1980	100–2110	E and SE Asia
187. *Cawjeekelia nova* Golovatch, 2011	2110	Chongqing, Dabashan Mt. Range, NE of Heyu, *Betula* forest (Golovatch 2011)
188. *C. pallida* Golovatch, 1996	100–200	Hong Kong, Tai Po Kau Nature Reserve (Golovatch 1996)
189. *C. propria* (Mikhaljova & Korsós, 2003)	500	Jilin, Mt. Changbaishan National Park; also N Korea (Mikhaljova and Korsós 2003, Golovatch 2013a)
Genus *Desmoxytes* Chamberlin, 1923		E and SE Asia
190. *Desmoxytes planata* (Pocock, 1895)	560	Nearly pantropical; Yunnan, Xishuangbanna, Menglun, Tropical Botanical Garden (Srisonchai et al. 2018; Golovatch 2018)
Genus *Enghoffosoma* Golovatch, 1993		E and SE Asia
191. *Enghoffosoma longipes* Golovatch, 2011	3150	Yunnan, NW slope of Mt. Yulongxueshan (Golovatch 2011)
Genus *Gonobelus* Attems, 1936	995–2615	China
192. *Gonobelus belousovi* Golovatch, 2014	995	Sichuan, NE of Shimian, Xiangshuigou River, Tianpingzi (Golovatch 2014a)
193. *G. martensi* Golovatch, 2013	1700–2600	Shaanxi, Mt. Taibaishan (Golovatch 2013a)
194. *G. pentaspinus* Golovatch, 2013	2475	Sichuan, NW of Mianning (Golovatch 2013b)
195. *G. sinensis* Attems, 1936	2615	Yunnan, Mt. Laojunshan, 3.7 km ENE of Segengsheng (Golovatch 2017)
Genus *Hedinomorpha* Verhoeff, 1934	1300–4490	Central Asia and China
196. *Hedinomorpha affinis* Golovatch, 2014	2870	Gansu, Mt. Lianhuashan (Golovatch 2014a)
197. *H. altiterga* Golovatch, 2019	1445	Gansu, WWS of Longnan (Wudu), 2.4 km NW of Zhongzhaixiang (Golovatch 2019a)

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198. *H. bifida* Golovatch, 2019	3665	Sichuan, 7.3 km S of Ganzi (Golovatch 2019a)
199. *H. biramipedicula* Zhang & Tang, 1985	ca. 1360	Shaanxi, Qinling, Mt. Taibaishan (Zhang and Tang 1985)
200. *H. circofera* Golovatch, 2013	ca. 2735	Qinghai, Beishan National Park, 120 km N of Xining (Golovatch 2013a)
201. *H. circularis* (Takakuwa & Takashima, 1949)	?	Shanxi, Chinkaiji (Takakuwa and Takashima 1949, Golovatch 2019a)
202. *H. crassiterga* Golovatch, 2019	4490	Sichuan, 16.8 km SSW Ganzi (Golovatch 2019a)
203. *H. flavobulbus* Golovatch, 2019	3650	Gansu, WWS of Longnan (Wudu), Yin Duoguosa & Aounang divide (Golovatch 2019a, 2019b)
204. *H. hummelii* Verhoeff, 1934	?	Gansu, Tan-Chang (Verhoeff 1934)
205. *H. jeekeli* (Golovatch, 2009)	1300–2600	Shaanxi, Foping Nature Reserve, Panda area (Golovatch 2009); Shaanxi, Mt. Taibaishan, S slopes, above Houshenzi, primary and secondary broadleaved forests (Golovatch 2013a)
206. *H. martensi* Golovatch, 2014	3510	Sichuan, Langmusi, remnants of a moist *Abies* forest above town (Golovatch 2014a)
207. *H. montana* Golovatch, 2016	3080–3695	Yunnan, NNE of Weixi City, 8.15 km ESE of Shajiama; N of Weixi City, 2.95 km NW of Xugongqingshang Village; NW of Jianchuan, 4.7 km WNW of Damaidi; Mt. Laojunshan, NE of Liming, 4.2 km S of Muzhengdu (Golovatch 2016b, 2017)
208. *H. nigra* Golovatch, 2013	3530–4000	Sichuan, Jiuzhaigou County, N of Dajisi (Golovatch 2013b)
209. *H. proxima* Golovatch, 2016	3570	Yunnan, Mt. Tianbaoshan between Shangrila and Mt. Habaxueshan, E slope, NW of Bengla (Golovatch 2016b)
210. *H. reducta* Golovatch, 2012	2900	Sichuan, SW of Mianning, Right tributary of Yalongjiang River canyon, ca. 9 km SW of Mofanggou (Golovatch 2012)
211. *H. subnigra* Golovatch, 2013	3910	Yunnan, W of Lake Lugu (Golovatch 2013b)
212. *H. yunnanensis* Golovatch, 2016	3480	Yunnan, NNE of Weixi City, right tributary of Lapugon River, 5.2 km ENE of Jizong (Golovatch 2016b)
Genus *Helicorthomorpha* Attems, 1914		E and SE Asia
213. *Helicorthomorpha holstii* (Pocock, 1895)	340	Widespread in SE Asia; Yunnan; Guangdong, Dinghushan Mt., 86 km W of Guangzhou (Attems 1936, Golovatch 1981)
Genus *Hirtodrepanum* Golovatch, 1994		Himalaya and China
214. *Hirtodrepanum chinense* Golovatch, 2014	1990–2015	Yunnan, Deqin, Dewei Line, E of Aqiku; Mekong Valley, 2 km E of Yezhixiang (Golovatch 2014a, 2019a)
Genus *Hylomus* Cook & Loomis, 1924	ca. 140–910	E and SE Asia
215. *Hylomus cornutus* (Zhang & Li, 1982)	ca. 140	Guangxi, Guilin, Yangshuo (Zhang and Li 1982a)
216. *H. draco* Cook & Loomis, 1924	ca. 400	Jiangxi, Jiujiang City, Mt. Lushan (Cook and Loomis 1924, Srisonchai et al. 2018)
217. *H. eupterygotus* (Golovatch, Li, Liu & Geoffroy, 2012)	ca. 260	Hunan, Linwu County, Tianhe, Cave I Dong and Changshali Cave I Dong (Golovatch et al. 2012a)
218. *H. getuhensis* (Liu, Golovatch & Tian, 2014)	ca. 910	Guizhou, Ziyun County, Getuhe National Geopark, caves Suidao Dong and Taiyang Dong (Liu et al. 2014)
219. *H. laticollis* (Liu, Golovatch & Tian, 2016)	450	Guangdong, Yingde City, Huanghua Town, Yanbei village, Cave Yangyan Dong (Liu et al. 2016)
220. *H. lingulatus* (Liu, Golovatch & Tian, 2014)	ca. 140	Guangxi, Guilin, Pingle County, Cave Chaotianyan (Liu et al. 2014)
221. *H. longispinus* (Loksa, 1960)	?	Guangxi, a cave (no exact locality known) (Loksa 1960)
222. *H. lui* (Golovatch, Li, Liu & Geoffroy, 2012)	ca. 155	Guangxi, Yongfu County, Shangxiao, Cave Dachong Dong (Golovatch et al. 2012a)

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223. *H. minutuberculus* (Zhang, 1986)	ca. 295	Guangxi, Tianlin County (Zhang 1986)
224. *H. nodulosus* (Liu, Golovatch & Tian, 2014)	ca. 350	Guangxi, Du'an County, Xia'ao Town, near Xia'ao Middle School, Cave II Dong; same county, Yong'an Town, Yong'an village, Cave I Dong; same town, Anju Village, Cave Suidao Dong; same county, Longwan Town, Qunle village, entrance to Cave I Dong (Liu et al. 2014)
225. *H. parvulus* (Liu, Golovatch & Tian, 2014)	ca. 350	Guangxi, Du'an, Xia'ao (Liu et al. 2014)
226. *H. phasmoides* (Liu, Golovatch & Tian, 2016)	ca. 445	Guangxi, Lingyun County, Jiayou Town, Yangli village, Cave Fengliu Dong (Liu et al. 2016)
227. *H. scolopendroides* (Golovatch, Geoffroy & Mauriès, 2010)	ca. 210–350	Guangxi, Huanjiang County, Dacai Town, Cave Shenlong Dong; Du'an County, Gaoling Town, Jinzhu village, Cave I Dong, Cave II Dong; Xia'ao Town, Cave I Dong (Golovatch et al. 2010b, Liu et al. 2014)
228. *H. scutigeroides* (Golovatch, Geoffroy & Mauriès, 2010)	ca. 310	Guangxi, Huanjiang County, Cave Ganglai Dong, Cave Mashan II Dong, Cave Gonglu Dong, Cave Shui Dong, and Du'an County, Disu Town, Dading village, Cave II Dong, same county, Longwan Town, Nongqu village, Cave I Dong, (Golovatch et al. 2010b, Liu et al. 2014)
229. *H. similis* (Liu, Golovatch & Tian, 2016)	230	Guangdong, Yingde City, Qingkeng Town, Bangjiao village, Cave Bangjiao Dong (Liu et al. 2016)
230. *H. simplipodus* (Liu, Golovatch & Tian, 2016)	140	Guangdong, Qingyuan City, Yangshan County, Chengjia Town, Dabei Village, Cave Kuangzhanyan (Liu et al. 2016)
231. *H. spinissimus* (Golovatch, Li, Liu & Geoffroy, 2012)	190	Guangxi, Fuchuan County, Guanyuan, Cave Guanyuan Dong (Golovatch et al. 2012a)
232. *H. spinitergus* (Liu, Golovatch & Tian, 2016)	ca. 210	Guangxi, Huanjiang County, near Cave Gui DongII, secondary forest (Liu et al. 2016)
233. *H. variabilis* (Liu, Golovatch & Tian, 2016)	500	Guangxi, Fengshan County, numerous caves (Liu et al. 2016)
234. *H. yuani* Liu & Wynne, 2019	180	Guangxi, Lingchuan County, Cave Liangfeng (Liu and Wynne 2019)
Genus *Inversispina* Zhang, 1997	510–4150	China and Taiwan
235. *Inversispina erectispina* Golovatch, 2012	2400–4150	Sichuan, SW of right tributary of Yalongjiang River, canyon; Sichuan, NW of Mianning, broadleaved forest; Sichuan, Jiulong County, SW of Wulaxixiang, broadleaved forest; Yunnan, between Tianbaoshan and Luzilashan, between Shuimofang and Xipazi; Yunnan, N of Lijiang, NW of Baoshanxiang, W of Bengluo village (Golovatch 2012, 2013b, 2016a, 2016b)
236. *I. multispina* Golovatch, 2016	2360	Sichuan, SSE of Shimian, S of Zhuma (Golovatch 2016a)
237. *I. tortiapicalis* Zhang, 1997	510	Hubei, Hefeng Tu jiazu County, Yien (Zhang et al. 1997)
238. *I. trispina* Golovatch, 2013	1050	Sichuan, Mt. Emeishan, Wannian Monastery (Golovatch 2013a)
Genus *Kronopolites* Attems, 1914	35–3600	Himalaya, E and SE Asia
239. *Kronopolites biagrilectus* Hoffman, 1963	35–3600	Jiangxi, 10 mi S of Jiujiang (oHoffman 1963); Sichuan, SSE of Shimian, S of Zhuma; Yunnan, Mt. Laojunshan,NE Liming, 2.5 km SE of Yankuluo; N of Lanping, 10.3 km SW of Hexi; N of Lanping, 11.3 km SW of Hexi; Yunnan, SE of Deqen City, 3.3 km S of Gejiancun; Yunnan, Mt. Laojunshan, NE Liming, 2.5 km SE of Yankuluo; N of Lanping, 10.3 km SW of Hexi; N of Lanping, 11.3 km SW of Hexi (Golovatch 2016a, 2016b, 2017)
240. *K. davidiani* Golovatch, 2014	3365	Sichuan, Wenchuan City, 214 National Road, WSW of Edi (Golovatch 2014a)

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241. *K. swinhoei* (Pocock, 1895)	1300–1700	Shaanxi, Mt. Taibaishan (oHoffman 1963); Shaanxi, Panda area, Foping Nature Reserve; Gansu, WWS of Longnan (Wudu), 2.4 km NW of Zhongzhaixiang (Golovatch 2017, 2019a)
Genus *Mandarinopus* Verhoeff, 1934	700–2955	China
242. *Mandarinopus corticinus* (Attems, 1936)	?	Yunnan (Attems 1936, Golovatch 2019a)
243. *M. gracilipes* Verhoeff, 1934	700–2195	Gansu, Baishui Jiang River; WWS of Longnan (Wudu), 3 km W of Jiejiaonuocun, Yin Duoguosa (Verhoeff 1934, Golovatch 2019a)
244. *M. hirsutus* Golovatch, 2019	2315	Yunnan, NW of Lijiang, W of Chang Jiang (= Yangtze) River, NW of Jinzhuang, 2.5 km N of Tuozhi village (Golovatch 2019a)
245. *M. rugosus* (Golovatch, 2013)	2400	Yunnan, N of Lijiang (Golovatch 2013a, 2019a)
246. *M. semirugosus* (Golovatch, 2013)	2955	Sichuan, NW of Mianning (Golovatch 2013b, 2019a)
Genus *Nedyopus* Attems, 1914	170–450	E and SE Asia
247. *Nedyopus beroni* (Golovatch, 1995)	350–450	Jiangsu, Nanjing City, Mt. Zijin (Golovatch 1995)
248. *N. picturatus* (Golovatch, 1995)	ca. 170	Guangxi, Guilin (Golovatch 1995)
Genus *Orthomorpha* Bollman, 1893		E and SE Asia, Sunda Archipelago
249. *Orthomorpha coarctata* (de Saussure, 1860)	ca. 20	Pantropical; Hainan, Sanya (Golovatch 1994)
250. *"Orthomorpha" endeusa* Attems, 1898	?	China (Attems 1898)
Genus *Orthomorphella* Hoffman, 1963		China
251. *Orthomorphella pekuensis* (Karsch, 1881)	ca. 40–165	Hebei, Shanlin, 70 km of Peking (Golovatch 1981); Hunan, Yuanling County, Mumaling (Zhang et al. 1997); New record: Jilin, Changchun City.
Genus *Oxidus* Cook, 1911		E and SE Asia
252. *Oxidus gracilis* C. L. Koch, 1847	200–1300	Subcosmopolitan, anthropochore; near Beijing; Shaanxi, Xi'an City; Guangxi, near Guilin; Sichuan, Maoxian County, NE of Shimian (Golovatch 2013a, 2014a)
Genus *Piccola* Attems, 1953		China and Vietnam
253. *Piccola golovatchi* Liu & Tian, 2015	ca. 840	Guangxi, Baise City, Tianlin County, Langping Town, Cave Shizikou Dadong (Liu and Tian 2015b)
Genus *Polylobosoma* Jeekel, 1980	10–1600	China and Vietnam
254. *Polylobosoma panda* (Golovatch, 2009)	1600	Shaanxi, Foping Nature Reserve, Panda area (Golovatch 2009, 2014a)
255. *P. roseipes* (Pocock, 1895)	10	Zhejiang, Ningpo (Jeekel 1980)
Genus *Sellanucheza* Enghoff, Golovatch & Nguyen, 2004	995–3155	E and SE Asia
256. *Sellanucheza jaegeri* Golovatch, 2013	1300–1700	Shaanxi, Mt. Taibaishan (Golovatch 2013a)
257. *S. tenebra* (Hoffman, 1961)	?	Sichuan, Wushan (Hoffman 1961)
258. *S. typica* Golovatch, 2013	995–3155	Sichuan, Maoxian County, SE of Nanxizhen (Golovatch 2013b); Sichuan, NE of Shimian, Xiangshuigou River, Tianpingzi (Golovatch 2014a)
Genus *Sigipinius* Hoffman, 1961	2810–4195	China
259. *Sigipinius campanuliformis* Golovatch, 2013	3910	Yunnan, W of Lake Lugu, N of Dajisi (Golovatch 2013b)

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260. *S. complex* Golovatch, 2013	3780–4120	Sichuan, S of Muli (Golovatch 2013b)
261. *S. dentiger* Golovatch, 2016	3570	Yunnan, Mt. Tianbaoshan between Shangrila and Habaxue Shan, E slope, NW of Bengla (Golovatch 2016b)
262. *S. grahami* Hoffman, 1961	2810–4170	Sichuan, Lixi County, SW of Tonghua; Jiuzhaigou County, N of Dajisi; Maoxian County, SE of Nanxizhen; Lixian, NNW of Xuecheng, Ertaizi; N of Lixian, Mengdonggou & Lianghekou divide, W of Xing Fanweizi; Gansu, WWS of Longnan (Wudu), Yin Duoguosa & Aounang divide; WWS of Longnan (Wudu), Yin Duoguosa & Yaxielu, W of Zhagazu, WWS of Longnan (Wudu), Wushenggou & Line Chaping divide; NNE Zhugqu, Minjiang Bas, 3 km ENE Xiaohuangya, Qinyugou (Golovatch 2013b, 2019a)
263. *S. kabaki* Golovatch, 2013	3330–3550	Xinjiang, Koeksu Basin (Golovatch 2013b)
264. *S. montanus* (Golovatch, 2011)	3710–4090	Yunnan, S of Nixi, near upper timber-line of a humid montane *Abies* forest; WNW of Zhongdian, humid mid-montane *Abies* forest with admixture of broad-leaved hardwood species (Golovatch 2011, 2013b)
265. *S. pinnifer* Golovatch, 2016	3625	Sichuan, SSE of Shimian, S of Zhuma (Golovatch 2016a)
266. *S. simplex* Golovatch, 2013	3915–4195	Sichuan, Jiulong County, SW of Wulaxixiang; Muli County, SW of Wulaxixiang (Golovatch 2013b); Sichuan, Kangding NNE of Yalaxiang, Shuangyanwo (Golovatch 2014a)
267. *S. spiniger* Golovatch, 2014	3690–3960	Yunnan, from Lijiang to Shangrila, 214 National Road, WSW of Edi (Golovatch 2014a)
Genus *Sinomorpha* Golovatch, 2013		China
268. *Sinomorpha setosa* Golovatch, 2013	1050	Sichuan, Mt. Emeishan, Wannian Monastery (Golovatch 2013a)
Genus *Tetracentrosternus* Pocock, 1895		Myanmar, Thailand and Indochina
269. *Tetracentrosternus hoffmani* Golovatch, 2013	1610	Yunnan, Mt. Gaolinggongshan, S of Pianma (Golovatch 2013a)
Genus *Tonkinosoma* Jeekel, 1953	500–1250	China and Vietnam
270. *Tonkinosoma flexipes* Jeekel, 1953	500	Guangxi, Hechi City, Fengshan County, Jinya Town, Hangdong village (Liu and Golovatch 2018a); also N Vietnam (Jeekel 1953)
271. *T. tiani* Liu & Golovatch, 2018	1250	Guizhou, Qianxinan, Anlong County, Sayu Town, Ganhan Dong Cave (Liu and Golovatch 2018a)
Genus *Tylopus* Jeekel, 1968	350–4025	Myanmar, China, Thailand and Indochina
272. *Tylopus deharvengi* Liu & Luo, 2013	350	Guangxi, Du'an County, Xia'ao Town, Cave I Dong (Liu and Luo 2013)
273. *T. kabaki* Golovatch, 2014	3575–4025	Yunnan, Deqen, Tuoxia Highway, Mt. Xiaruolisuzuxiang & Yezhizhen; same province, NW of Lijiang, W of Chang Jiang (Yangtze River), NW of Jinzhuang, 6 km of Tuozhi village; N of Lijiang, W of Maguwa, 4.2 km SE of Shanggaohan village; N of Lijiang, W of Maguwa, 4.4 km ENE of Shanggaohan village; Mekong Valley, ENE of Yezhixiang, 3 km NE of Houqing (Golovatch 2014a, 2019b)
274. *T. nigromarginatus* Golovatch, 2018	835	Chongqing, Mt. Jinyunshan, secondary forest, stump, trees, small cave (Golovatch 2018)
275. *T. reductus* Golovatch, 2013	1600–1800	Yunnan, Mt. Gaoligongshan, S of Pianma (Golovatch 2013a)
276. *T. schawalleri* Golovatch, 2013	2500–2700	Yunnan, Mt. Dincangshang, above Dali (Golovatch 2013a)
277. *T. similis* Golovatch, 2014	1670	Yunnan, from Lijiang to Shangrila, E of Guojie Luocun (Golovatch 2014a)

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278. *T. sinensis* Golovatch, 1995	1315	Yunnan, Mengzi County, Cave Hafatiao Dong (Golovatch 1995)
Genus *Wulingina* Zhang, 1997		China
279. *Wulingina macroloba* Zhang, 1997	510	Hubei, Hefeng Tu jiazu County (Zhang 1997)
280. *W. miniloba* Zhang, 1997	510	Hubei, Hefeng Tu jiazu County (Zhang 1997)
Genus *Yuennanina* Attems, 1936	1915–1920	China
281. *Yuennanina aceratogaster* Zhang & Li, 1977	1920	Yunnan, Kunming City (Zhang and Li 1977)
282. *Y. ceratogaster* Attems, 1936	1920	Yunnan, Kunming City (Attems 1936)
283. *Y. petalolobodes* Chang & Zhang, 1989	1915	Yunnan, Kunming, Chenggong County (Chang and Zhang 1989)
Family Polydesmidae Leach, 1815		Palaearctic and SE Asia
Genus *Epanerchodus* Attems, 1901	35–3090	Central and E Asia, marginally N Vietnam
284. *Epanerchodus belousovi* Golovatch, 2014	2810	Sichuan, Kangding City (Golovatch 2014c)
285. *E. chutou* Liu & Golovatch, 2018	680	Guizhou, Shiqian County, Cave Feng Dong (Liu and Golovatch 2018b)
286. *E. coniger* Liu & Golovatch, 2018	ca. 1620	Guizhou, Bijie City, Zhijin County, Chengguan Town, Dongshan village, Cave Houshan Dong (Liu and Golovatch 2018b)
287. *E. draco* Geoffroy & Golovatch, 2004	ca. 1670	Yunnan, Zhenxiong County, a cave; Guizhou, Liupanshui City, Shuicheng County, Cave Shendongmigong Dong (Geoffroy and Golovatch 2004, Liu and Golovatch 2018b)
288. *E. eurycornutus* Zhang & Wang, 1992	885	Zhejiang, Mt. Tianmu (Zhang and Wang 1992)
289. *E. frater* Geoffroy & Golovatch, 2004	ca. 1670	Yunnan, Zhenxiong County, Cave Dahei Dong (Geoffroy and Golovatch 2004)
290. *E. fuscus* Golovatch, 2015	ca. 2450	Yunnan, Lanping County (Golovatch 2015b)
291. *E. gladiatus* Liu & Golovatch, 2018	920	Guizhou, Wuchuan County, Huangdu Town, Gaodong village, Cave Yinshi Dong (Liu and Golovatch 2018b)
292. *E. jaegeri* Golovatch, 2014	ca. 2345	Shaanxi, Mt. Taibaishan (Golovatch 2014b)
293. *E. jiangxiensis* Liu & Golovatch, 2018	475	Jiangxi, Lianhua County, Gaotan village, Cave Shuilian Dong (Liu and Golovatch 2018b)
294. *E. koreanus* Verhoeff, 1937	2230	Jilin, Mt. Changbaishan (Golovatch 2014b)
295. *E. latus* Liu & Golovatch, 2018	ca. 1330	Chongqing, Wushan County, Luoping Town, Qinglong village, Cave Qinglong Dong (Liu and Golovatch 2018b)
296. *E. lipsae* Golovatch & Geoffroy, 2014	ca. 750	Sichuan, Beichuan and Jiangyou counties, numerous caves (Golovatch and Geoffroy 2014, Liu and Golovatch 2018b)
297. *E. martensi* Golovatch, 2014	ca. 2345	Shaanxi, Mt. Taibaishan (Golovatch 2014b)
298. *E. orientalis* Attems, 1901	ca. 205	Guangxi, Fuchuan County, Cave Banbianshan Dong (Golovatch et al. 2012c), also Japan and Taiwan
299. *E. parvus* Liu & Golovatch, 2018	830	Guizhou, Cengong County, Pingzhuang Town, Cave Wanfuchangcheng Dong (Liu and Golovatch 2018b)
300. *E. potanini* Golovatch, 1991		Sichuan, Gansu and Yunnan provinces (Golovatch 1991a, 2014b)
301. *E. schawalleri* Golovatch, 2014	ca. 1550	Sichuan, Mt. Emeishan (Golovatch 2014b)
302. *E. soror* Geoffroy & Golovatch, 2004	ca. 1670	Yunnan, Zhenxiong County, caves Hama Dong, Dahei Dong and Xianren Dong (Geoffroy and Golovatch 2004, Liu and Golovatch 2018b)
303. *E. sphaerisetosus* Zhang & Chen, 1983	ca. 35	Zhejiang, 10 mi S of Jinhua City, Gaocun village (Zhang and Chen 1983)

Taxa	Altitude (m a.s.l.)	Distribution, province/region (main reference/s)
304. *E. stylotarseus* Chen & Zhang, 1990	ca. 1220	Guizhou, Guanling County, several caves (Chen and Zhang 1990, Golovatch et al. 2007, 2012)
305. *E. tujiaphilus* Liu & Golovatch, 2018	730	Hunan, Longshan County, Huoyan village, Cave Tujiamei Dong (Liu and Golovatch 2018b)
306. *E. typicus* Golovatch, 2014	ca. 3030	Yunnan, Deqin County (Golovatch 2014c)
307. *E. varius* (Geoffroy & Golovatch, 2004)	ca. 755–3090	Numerous caves in Hubei, Banqiao Town; and Sichuan, Xinlong and Beichuan counties (Geoffroy and Golovatch 2004, Golovatch et al. 2007, Golovatch and Geoffroy 2014)
308. *E. yunnanensis* Golovatch, 2014	1995	Yunnan, Dali City (Golovatch 2014b)
Genus *Glenniea* Turk, 1945	170–1510	Himalaya and China
309. *Glenniea blanca* Golovatch & Geoffroy, 2014	600	Sichuan, Tongjiang County, Cave Lou Fang Dong (= Grotte de la Maison) (Golovatch and Geoffroy 2014)
310. *G. lagredae* Golovatch & Geoffroy, 2014	1360–1510	Sichuan, Beichuan County, Cave Yuan Dong (= La grotte du Rocher); Sichuan, Huajiaoling County, Cave Zhangjiayankoukeng Dong (Golovatch and Geoffroy 2014)
311. *G. prima* Golovatch, Li, Liu & Geoffroy, 2012	ca. 170	Guangxi, Longzhou County, Shanglong Town, Lenglei Nonggang Forest (Golovatch et al. 2012c, Golovatch and Geoffroy 2014)
Genus *Pacidesmus* Golovatch, 1991	ca. 180–1865	China and N Thailand
312. *Pacidesmus armatus* Golovatch, Geoffroy & Mauriès, 2010	ca. 310	Guangxi, Huanjiang County, Cave Xialan Dong, caves Shui Dong and Shenglong Dong (Golovatch et al. 2010a)
313. *P. bedosae* Golovatch, Geoffroy & Mauriès, 2010	ca. 310	Guangxi, Huanjiang County, caves Dongtu Dong, Huoka Dong and Ganxiao Dong (Golovatch et al. 2010a)
314. *P. bifidus* Golovatch & Geoffroy, 2014	ca. 495	Guangxi, near Fengshan County, Cave Henglixin Dong (Golovatch and Geoffroy 2014, Liu and Golovatch 2019)
315. *P. martensi* Golovatch & Geoffroy, 2006	ca. 1495	Guizhou, Dafang County, Cave Hei Dong; Qianxi County, Honglin Town, caves Luoshui Dong and Luosai Dong (Golovatch and Geoffroy 2006, Golovatch et al. 2007, Liu and Golovatch 2019)
316. *P. sinesis* (Golovatch & Hoffman, 1989)	ca. 1285	Guizhou, Zhenning County, Cave Kaikou Dong (Loksa 1960, Golovatch and Hoffman 1989, Chen and Meng 1990, Liu and Golovatch 2019)
317. *P. superdraco* Golovatch, Geoffroy & Mauriès, 2007	ca. 410	Guizhou, Libo County, Cave Laitai Dong (Golovatch et al. 2007)
318. *P. tiani* Golovatch, Geoffroy & Mauriès, 2010	ca. 310	Guangxi, Huanjiang County, caves Ganglai Dong I and II (Golovatch et al. 2010a)
319. *P. trifidus* Golovatch & Geoffroy, 2014	ca. 180	Guangxi, Guilin City, Cave Kulou Dong (Golovatch and Geoffroy 2014); Yangshuo County, Cave Guanshan No. 4; Xiufeng District, Cave Maomaotou; Yangshuo County, Cave Shangshuiyan (Liu and Wynne 2019)
320. *P. trilobatus* Liu & Golovatch, 2020	ca. 1315	Yunnan, Wenshan County, Liujing Town, Laozhai village, Cave I Dong (Liu and Golovatch 2020)
321. *P. uncatus* Liu & Golovatch, 2020	ca. 1865	Yunnan, Qujing City, Zhanyi County, Cave Tianshengqiao Dong (Liu and Golovatch 2020)
322. *P. whitteni* Liu & Golovatch, 2020	ca. 755	Guangxi, Fengshan County, Jinya Town, Hangdong village, Cave I Dong (Liu and Golovatch 2020)
Genus *Polydesmus* Latreille, 1802–03		Amphi-Palaearctic
323. *Polydesmus liber* Golovatch, 1991	ca. 140	Hong Kong (Golovatch 1991a)
Family Pyrgodesmidae Silvestri, 1896		Pantropical

Taxa	Altitude (m a.s.l.)	Distribution, province/region (main reference/s)
Genus *Cryptocorypha* Attems, 1907		Old World, up to Melanesia in the east
324. *Cryptocorypha spinicoronata* (Zhang & Li, 1981)	ca. 1110	Guangxi, Tianlin County, Langping Town (Zhang and Li 1981b)
Family Xystodesmidae Cook, 1895		Holarctic, E and SE Asia up to N Vietnam in the south
Genus *Kiulinga* Hoffman, 1956	10–1080	China
325. *Kiulinga jeekeli* Hoffman, 1956	1080	Jiangxi, Jiujiang City, Jiguling (Hoffman 1956, Zhang and Mao 1984)
326. *K. lacustris* (Pocock, 1895)	10	Zhejiang, 25 mi S of Ninghsien, Lake Wo-Lee (Hoffman 1956)
327. *K. lobosa* Zhang & Mao, 1984	ca. 30	Zhejiang, Zhoushan City, Daishan Island (Zhang and Mao 1984)
Genus *Riukiaria* Attems, 1938	170–4440	E Asia up to N Vietnam in the south
328. *Riukiaria belousovi* Golovatch, 2014	4100	Sichuan, Muli County, SW of Wulaxixiang (Golovatch 2014d)
329. *R. capaca* Wang & Zhang, 1993	170	Fujian, Jiangle County (Wang and Zhang 1993b)
330. *R. chinensis* Tanabe, Ishii & Yin, 1996	885	Zhejiang, Mt. Tianmu (Tanabe et al. 1996)
331. *R. davidiani* Golovatch, 2014	2810	Sichuan, Lixian County, SW of Tonghua (Golovatch 2014d)
332. *R. kabaki* Golovatch, 2014	4440	Sichuan, Kangding City, NNE of Walaxiang, NE of Yusicun (Golovatch 2014d)
333. *R. korolevi* Golovatch, 2014	2900	Sichuan, W of Jiuzhaigou (Golovatch 2014d)
334. *R. martensi* Golovatch, 2014	1700	Shaanxi, Mt. Taibaishan, southern slopes, above Houzhenzi, primary broadleaved forest (Golovatch 2014d)
335. *R. spatuliformis* Golovatch, 2015	2525	Sichuan, N of Luding City, N of Lanan (Golovatch 2015b)
336. *R. tianmu* (Tanabe, Ishii & Yin, 1996)	885	Zhejiang, Mt. Tianmu (Tanabe et al. 1996, Golovatch 2014d)
Family Opisotretidae Hoffman, 1980		Himalaya, Myanmar, Indochina, Indonesia, New Guinea, Ryukyu Islands, Japan and Christmas Island, Australia, Indian Ocean (Golovatch et al. 2013)
Genus *Carlotretus* Hoffman, 1980		S China and Sumatra, Indonesia (Golovatch et al. 2013)
337. *Carlotretus triramus* Golovatch, Geoffroy, Stoev & VandenSpiegel, 2013	ca. 200	Guangxi, Chongzuo City, Longzhou County, Shanglong Town, Nonggang Forest (Golovatch et al. 2013)
Genus *Martensodesmus* Golovatch, 1987	150–200	Himalaya, Indochina and S China (Golovatch et al. 2013)
338. *Martensodesmus bedosae* Golovatch, Geoffroy, Stoev & VandenSpiegel, 2013	ca. 150	Guangxi, Hechi City, Du'an County, Baling karst hill (Golovatch et al. 2013)
339. *M. spiniger* Golovatch, Geoffroy, Stoev & VandenSpiegel, 2013	ca. 200	Guangxi, Chongzuo City, Longzhou County, Shanglong Town, Nonggang Forest (Golovatch et al. 2013)

The huge, Eurasian, warm-temperate to tropical genus *Hyleoglomeris* (Glomeridae, Glomerida) currently contains 100+ species, including numerous cavernicoles. Unlike the glomerid fauna of the adjacent Indochina which harbours a considerable proportion of endemic genera (60 % in Vietnam), continental China currently supports only 32 species of *Hyleoglomeris*, most of which occur in caves alone (Golovatch 2015a). The genus ranges from the Balkans in the west, though Anatolia, the Caucasus, Central Asia, the Himalaya, Myanmar and Indochina, to Taiwan, the Philippines and Sulawesi,

Table 2. Distribution patterns of all 16 extant millipede orders, those presently known to occur in mainland China being marked with an asterisk.

Orders	Distribution pattern	Orders	Distribution pattern
Polyxenida*	Cosmopolitan	Siphonophorida	Pantropical
Glomeridesmida	Pantropical	Chordeumatida*	Holarctic + Neotropical + Oriental
Glomerida*	Holarctic + Oriental	Callipodida*	Holarctic + Oriental
Sphaerotheriida*	Old World	Julida*	Holarctic + Oriental
Platydesmida*	Subcosmopolitan	Stemmiulida	Pantropical
Polyzoniida*	Subcosmopolitan	Spirostreptida*	Pantropical
Siphoniulida	Neotropical + Oriental	Spirobolida*	Pantropical
Siphonocryptida	Palaearctic + Oriental	Polydesmida*	Cosmopolitan

Indonesia in the east. Importantly, a fossil congener is known from Baltic amber (Eocene, 44 Mya) (Wesener et al. 2019). *Hyleoglomeris* spp. are widespread across China and occur at various elevations, from nearly sea-level to high mountains (Fig. 2), the highest record belonging to *H. sinensis* (2810 m a.s.l.) (Table 1). In the Himalaya of Nepal, one species occurs even higher in the mountains, being high-montane: *H. khumbua* Golovatch, 1987 (3250–3300 m a.s.l.) (Golovatch and Martens 2018).

A very similar pattern is demonstrated by the subendemic genus *Paracortina* (Paracortinidae, Callipodida), with 12 species, of which ten (Fig. 3) are confined to the mountains of southwestern China (Liu and Tian 2015c), mostly high-montane (3300 m a.s.l., Table 1). Only a few are cavernicoles.

Nepalmatoiulus (Julidae, Julida) is another very large genus which presently comprises 55 species that span from the central Himalaya in the west, through Bhutan, Myanmar, Indochina, Thailand and West Malaysia, to the Ryukyus, Japan and Taiwan in the east (Enghoff 1987b). Seven species range across the southern parts of China (Fig. 4), including two high-montane ones (2750–3650 m a.s.l., Table 1). Although Beron (2008) reported closer unidentified Diplopoda from up to 5300 m a.s.l. from Nepal, the world's highest record for a known species belongs to *N. ivanloebli* Enghoff, 1987, also from Nepal: 4800 m a.s.l. (Enghoff 1987b, Shelley and Golovatch 2011). The same general pattern is observed in the similarly speciose (ca. 50 spp.), but more boreal genus *Anaulaciulus* (Julidae), the distribution of which covers northern Pakistan and India, the Himalaya, northern Myanmar, the Far East of Russia, all Japan and Korea, Taiwan, as well as central and eastern China. The highest record belongs to *A. bilineatus* Korsós, 2001 from Nepal: 3600–4300 m a.s.l. (Korsós 2001). Unlike *Nepalmatoiulus*, no *Anaulaciulus* spp. are known to occur in southern China, both these genera being allo- to parapatric. Among the Julidae in China, only very few are cavernicoles.

Particularly clear Palaearctic origins are observed in the large genus *Skleroprotopus* (Mongoliulidae, Julida), most species of which inhabit the Russian Far East, Korea, Japan and China (Table 1), the small Siberian genus *Angarozonium* (Polyzoniidae, Polyzoniida) only marginally encountered in northern China (Table 1), the rather small Siberio-Nearctic genus *Orinisobates* (Nemasomatidae, Julida) represented in China by a single species endemic to the southern Tianshan Mountains (Table 1) (Mikhaljova 2017). The

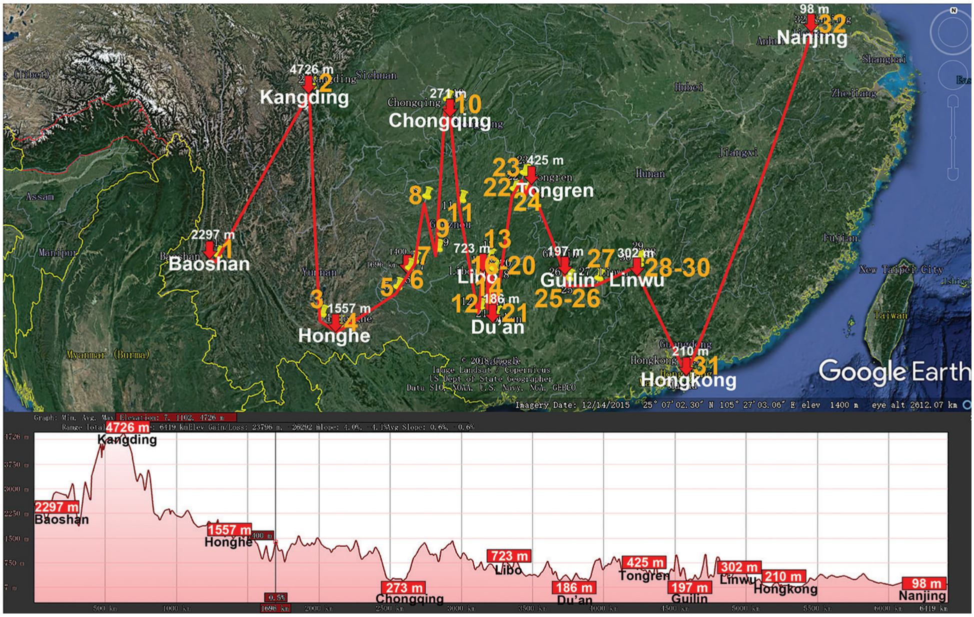

Figure 2. Distribution of the family Glomeridae, genus *Hyleoglomeris* in mainland China. Red lines show the transect Baoshan – Kangding – Honghe – Chongqing – Libo – Du'an – Tongren – Guilin – Linwu – Hong Kong – Nanjing, along which the elevations are crudely indicated below. **1** *H. albicorporis* **2** *H. sinensis* **3** *H. reducta* **4** *H. maculata* **5** *H. heshang* **6** *H. gudu* **7** *H. rhinceros* **8** *H. nigu* **9** *H. getuhensis* **10** *H. aschnae* **11** *H. yinshi* **12** *H. grandis* **13** *H. eusulcata* **14** *H. xueju* **15** *H. wuse* **16** *H. qiyi* **17** *H. curtisulcata* **18** *H. mulunensis* **19** *H. kunnan* **20** *H. mashanorum* **21** *H. baxian* **22** *H. variabilis* **23** *H. multistriata* **24** *H. generalis* **25** *H. rukouqu* **26** *H. xuxiakei* **27** *H. lii* **28** *H. xia* **29** *H. youhao* **30** *H. tiani* **31** *H. bicolor*, **32** *H. emarginata*.

same concerns *Polydesmus* (Polydesmidae, Polydesmida), a very large genus with ca. 80 species, most of which occur in Europe, the Mediterranean area, Anatolia and the western Caucasus, but a few are known from Japan, and one each in northern Vietnam and Hong Kong (Table 1) (Golovatch 1991a, Nguyen 2009).

The large genus *Nepalella* (Megalotylidae, Chordeumatida), with its 27 species spanning from Nepal (10 species) in the west, through Myanmar (two species) and Thailand (two species), to Vietnam (one species) in the south, and southwestern China (12 species, including several presumed troglobionts) in the north (Liu, Wesener et al. 2017d), shows the same general pattern (Fig. 5). Most congeners are mid-montane, but one, *N. marmorata*, has been recorded from ca. 4350 m a.s.l. (Table 1).

Basically the same picture is revealed in the distribution of the huge Central to East Asian genus *Epanerchodus* (Polydesmidae, Polydesmida) which presently encompasses 118 species or subspecies, both epi- and endogean, including 25 across almost entire continental China (Liu and Golovatch 2018b) (Table 1, Fig. 6). Their vertical distributions range from nearly sea-level to high-montane (3090 m a.s.l.), but a few congeners from the Himalaya occur even up to 4250 m a.s.l. (Golovatch and Martens 2018).

The genus *Pacidesmus* (Polydesmidae, Polydesmida) shows a highly peculiar distribution (Fig. 7), with all of its eleven Chinese species being low- to mid-montane

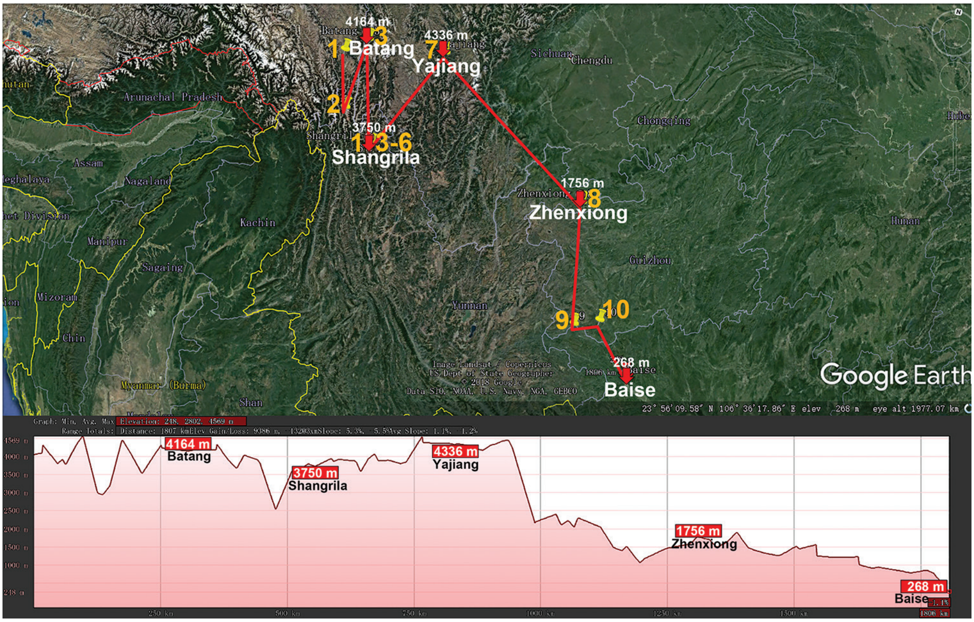

Figure 3. Distribution of the family Paracortinidae, genus *Paracortina* in mainland China. Red lines show the transect Batang – Shangrila – Yajiang – Zhenxiong – Baise, along which the elevations are crudely indicated below. **1** *P. viriosa* **2** *P. serrata* **3** *P. thallina* **4** *P. carrinata* **5** *P. leptoclada* **6** *P. stimula* **7** *P. voluta* **8** *P. chinensis* **9** *P. yinae* **10** *P. zhangi*.

Figure 4. Distribution of the family Julidae, genus *Nepalmatoiulus* in mainland China. Red lines show the transect Linzhi – Kangding – Suining – Jiujiang – Meizhou, along which the elevations are crudely indicated below. **1** *N. tibetanus* **2** *N. brachymeritus* **3** *N. rhaphimeritus* **4** *N. polyakis* **5** *N. fraterdraconis* **6** *N. eulobos*. *Nepalmatoiulus yunnanensis* is not mapped because no exact locality in Yunnan is known.

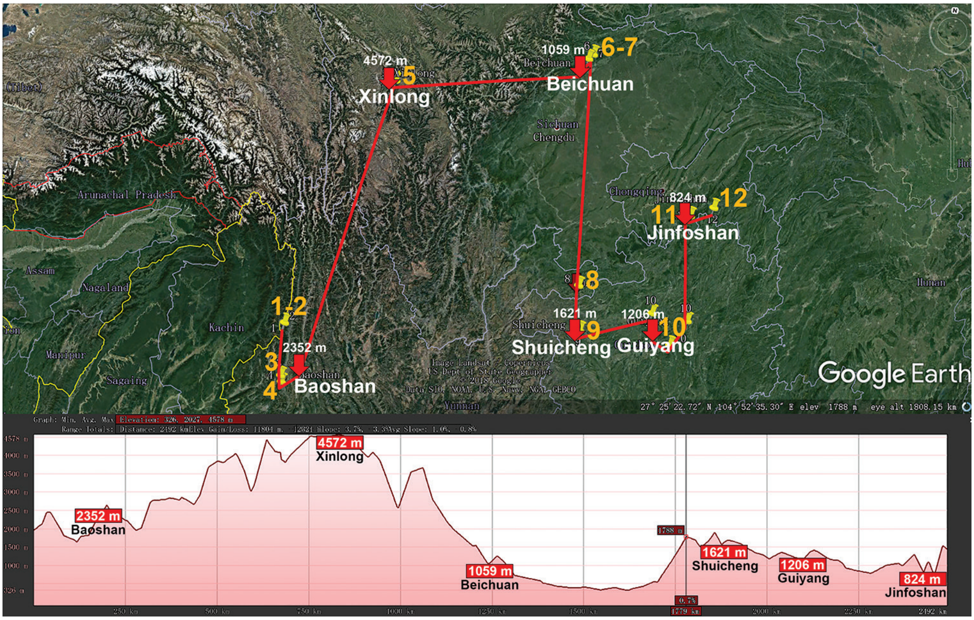

Figure 5. Distribution of the family Megalotylidae, genus *Nepalella* in mainland China. Red lines show the transect Baoshan – Xinlong – Beichuan – Shuicheng – Guiyang – Jinfoshan, along which the elevations are crudely indicated below. **1** *N. kavanaughi* **2** *N. pianma* **3** *N. magna* **4** *N. griswoldi* **5** *N. marmorata* **6** *N. lobata* **7** *N. grandoides* **8** *N. grandis* **9** *N. caeca* **10** *N. troglodytes* **11** *N. jinfoshan* **12** *N. wangi*.

and restricted to karst caves in the south (Liu and Golovatch in press), whereas the type species, *P. shelleyi* Golovatch, 1991, comes from the summit (2200–2500 m a.s.l.) of Mount Doi Inthanon, northern Thailand (Golovatch 1991a). Similarly, the small genus *Glenniea* (Polydesmidae) contains five lowland to mid-montane epigean species from the Himalaya of India and Bhutan (Golovatch and Martens 2018), as well as another three species (including two cavernicoles) from southern China (Golovatch and Geoffroy 2014) (Table 1, Fig. 8).

The great Holarctic family Xystodesmidae (Polydesmida) presently encompasses 66 genera and ca. 410 species, most of which occur in the Nearctic. Only few genera and species are known from Central and northern South America (to Ecuador in the south), the Antilles, the Mediterranean region and East Asia (Shelley and Smith 2018). The largest East Asian genus *Riukiaria* currently contains 35 species or subspecies from southern Japan, southern Korea, Taiwan and China (Korsós et al. 2011, Golovatch 2014d, 2015b, Nguyen 2016). We disagree with Nguyen (2016), who split *Riukiaria* into two genera and created a new genus, *Parariukiaria* Nguyen, 2016, to accommodate a new species from northern Vietnam and three previously described ones from China. To our mind, *Riukiaria* and *Parariukiaria* show all transitional stages in the reduction of a gonoprefemoral process and, albeit without formal synonymy advanced here, both may well be regarded as representing a single large genus, in which several peripheral, southernmost congeners demonstrate a more or less strongly suppressed process on the

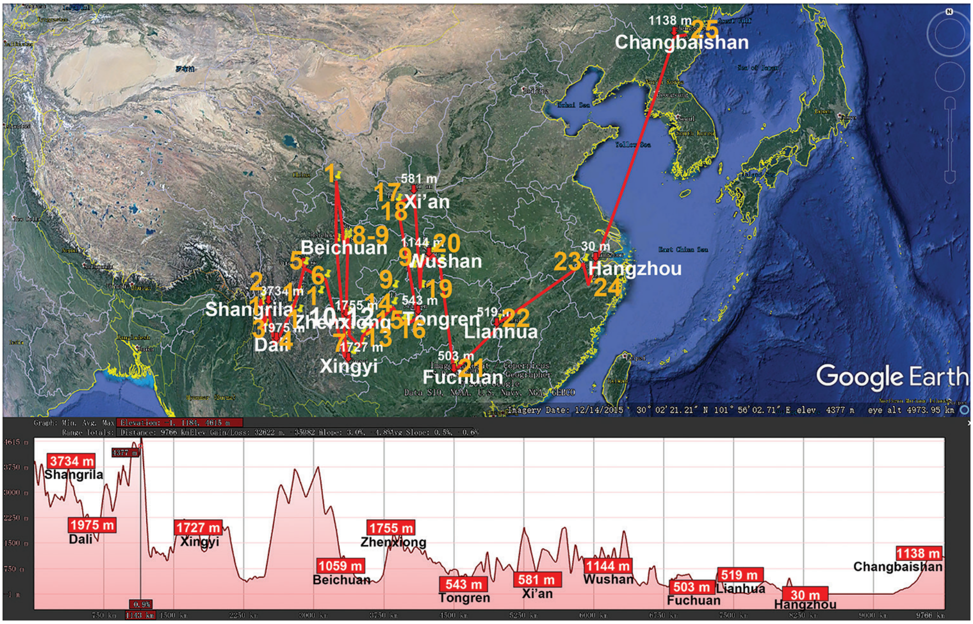

Figure 6. Distribution of the family Polydesmidae, genus *Epanerchodus* in mainland China. Red lines show the transect Shangrila – Dali – Xingyi – Beichuan – Zhengxiong – Tongren – Xi'an – Wushan – Fuchuan – Lianhua – Hangzhou – Changbaishan, along which the elevations are crudely indicated below. **1** *E. potanini* **2** *E. typicus* **3** *E. fuscus* **4** *E. yunnanensis* **5** *E. belousovi* **6** *E. schawalleri* **7** *E. stylotarseus* **8** *E. lipsae* **9** *E. varius* **10** *E. frater* **11** *E. soror* **12** *E. draco* **13** *E. coniger* **14** *E. gladiatus* **15** *E. chutou* **16** *E. parvus* **17** *E. jaegeri* **18** *E. martensi* **19** *E. tujiaphiulus* **20** *E. latus* **21** *E. orientalis* **22** *E. jiangxiensis* **23** *E. enrycornutus* **24** *E. sphaerisetosus* **25** *E. koreanus*.

gonopodal prefemur, from relatively small to totally missing. All nine *Riukiaria* species in China are epigean and span across the central and southern parts of the country, occurring in lowland to high-montane habitats (170–4440 m a.s.l., Table 1, Fig. 9).

As noted above, in China the great family Paradoxosomatidae, which is amongst the largest in the class (200+ genera, 1,000+ species), dominates most of the tropical faunas across the world, but is absent from the Nearctic, contains remarkably few troglobionts (Golovatch 2015a) and comprises genera of various origins. Some seem to be rooted in the Palaearctic (including several endemic or subendemic ones), the others are likely to be Oriental. Among the former elements, the following two rather species-rich genera can be taken as examples.

The genus *Hedinomorpha* is subendemic to China, with most of its 17 species known from the country being high-montane (up to 4490 m a.s.l., Table 1, Fig. 10), and only one more restricted to Tajikistan, Central Asia (Golovatch 2019b). The genus *Sigipinius* is strictly endemic to mainland China and contains nine high-montane species (2810–4195 m a.s.l., Table 1, Fig. 11). Such paradoxosomatid genera as *Cawjeekelia*, *Kronopolites*, *Mandarinopus* and *Orthomorphella* likewise seem best to be attributed to Palaearctic elements in the fauna of China.

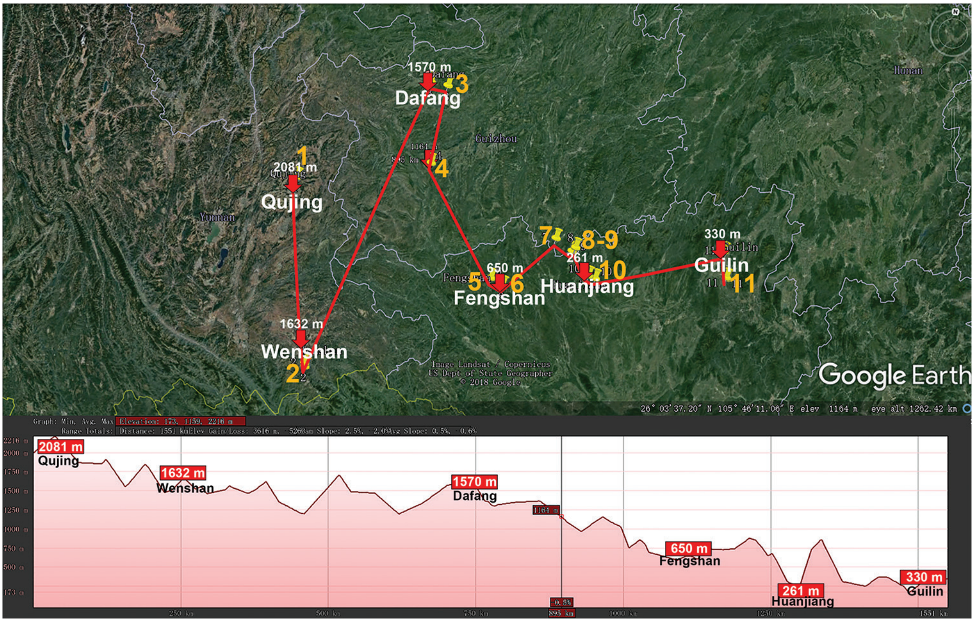

Figure 7. Distribution of the family Polydesmidae, genus *Pacidesmus* in mainland China. Red lines show the transect Qujing – Wenshan – Dafang – Fengshan – Huanjiang – Guilin, along which the elevations are crudely indicated below. **1** *P. uncatus* **2** *P. trilobatus* **3** *P. martensi* **4** *P. sinensis* **5** *P. whitteni* **6** *P. bifidus* **7** *P. superdraco* **8** *P. tiani* **9** *P. bedosae* **10** *P. armatus* **11** *P. trifidus*.

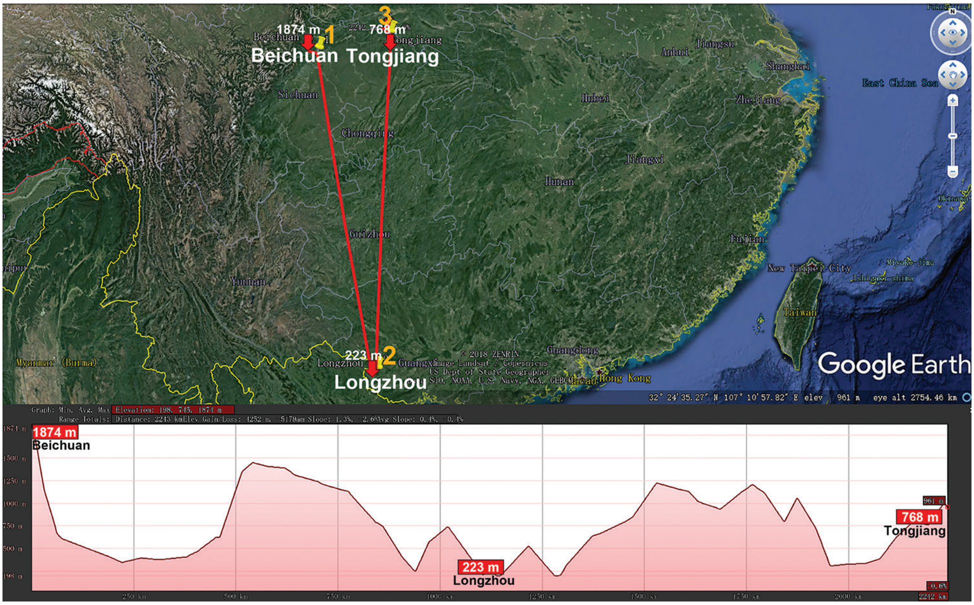

Figure 8. Distribution of the family Polydesmidae, genus *Glenniea* in mainland China. Red lines show the transect Beichuan – Longzhuan – Tongjiang, along which the elevations are crudely indicated below. **1** *G. lagredae* **2** *G. prima* **3** *G. blanca*.

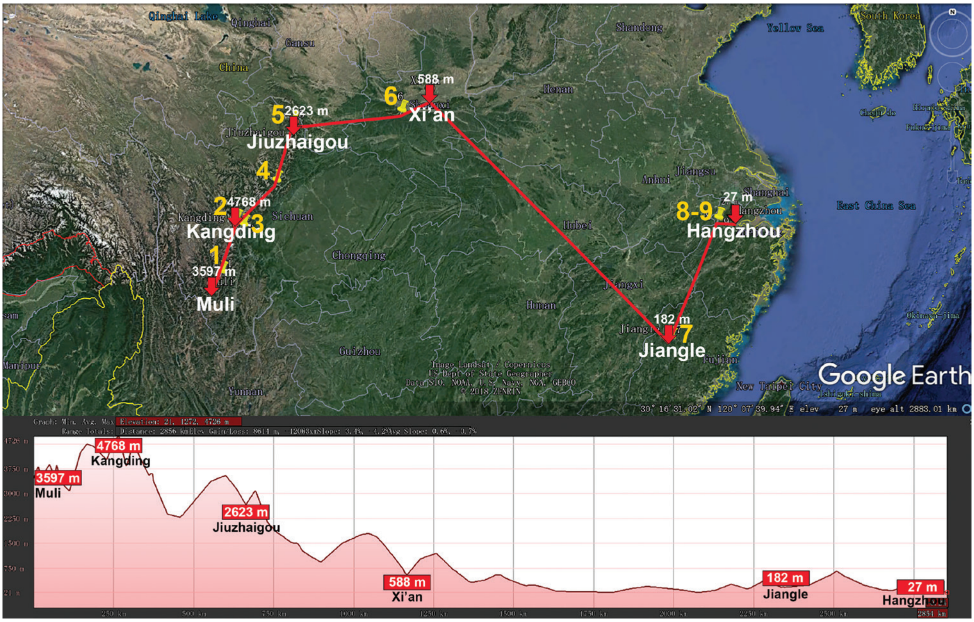

Figure 9. Distribution of the family Xystodesmidae, genus *Riukiaria* in mainland China. Red lines show the transect Muli – Kangding – Jiuzhaigou – Xi'an – Jiangle – Hangzhou, along which the elevations are crudely indicated below. **1** *R. belousovi* **2** *R. kabaki* **3** *R. spatuliformis* **4** *R. davidiani* **5** *R. korolevi* **6** *R. martensi* **7** *R. capaca* **8** *R. chinensis* **9** *R. tianmu*.

In contrast, Paradoxosomatidae also contain a good number of presumed Oriental components, mostly tropical to subtropical. Thus, the genus *Hylomus* presently comprises 36 species from Myanmar, Thailand, Laos, Vietnam and China (Srisonchai et al. 2018, Liu and Wynne 2019, Golovatch 2019b). Many of them are presumed troglobionts. The distributions of all 20 *Hylomus* spp. recorded from China cover much of the southern and eastern parts of the country and are only confined to lowland to mid-montane habitats (ca. 140–910 m a.s.l., Table 1, Fig. 12). At the moment, with its 73 species (Golovatch 2019b) that range from southern China in the north, through most of Indochina, to Myanmar in the south, *Tylopus* remains the largest genus of Paradoxosomatidae globally. However, the altitudinal distributions vary from lowland to high-montane (350–4025 m a.s.l., Table 1), cavernicoles are few, while the Chinese congeners mark the northern range limit of the genus and are confined to the southwestern parts of the country (Fig. 13). Because *Tylopus* and *Hedinomorpha* seem to be particularly similar morphologically and co-occur, albeit probably never strictly sympatric, in southwestern China (at least Yunnan, Figs 10, 13), these areas seem to mark the southern range limit of *Hedinomorpha*.

The relatively large genera *Anoplodesmus*, *Antheromorpha*, *Enghoffosoma*, *Nedyopus* and *Sellanucheza* also seem best to refer to as Oriental components in the fauna of China, because it is southern China that marks their northern range limits. The same concerns the small genera *Hirtodrepanum*, *Inversispina*, *Piccola*, *Polylobosoma* and *Tetracentrosternus*, all of which show one or a few congeners either in the Himalaya and/or Myanmar,

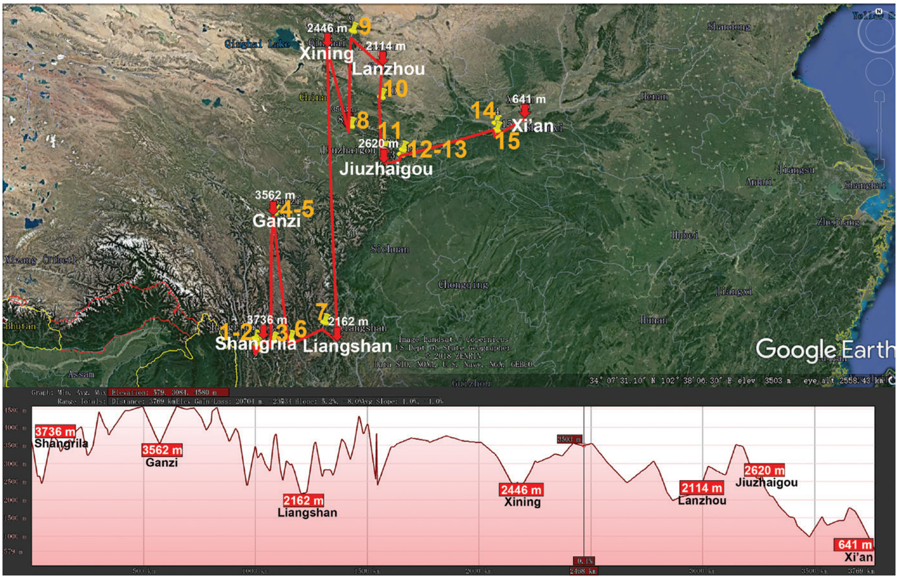

Figure 10. Distribution of the family Paradoxosomatidae, genus *Hedinomorpha* in mainland China. Red lines show the transect Shangrila – Ganzi – Liangshan – Xining – Lanzhou – Jiuzhaigou – Xi'an, along which the elevations are crudely indicated below. **1** *H. montana* **2** *H. yunnanensis* **3** *H. proxima* **4** *H. crassiterga* **5** *H. bifida* **6** *H. subnigra* **7** *H. reducta* **8** *H. martensi* **9** *H. circofera* **10** *H. affinis* **11** *H. nigra* **12** *H. altiterga* **13** *H. flavobulbus* **14** *H. biramipedicula* **15** *H. jeekeli*; neither *H. circularis* nor *H. hummelii* is mapped because their exact type localities remain unknown.

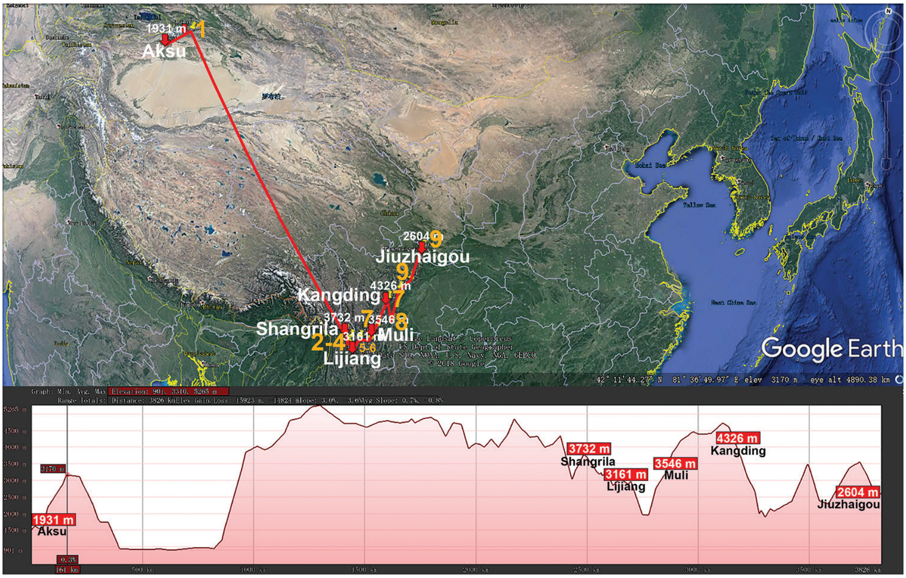

Figure 11. Distribution of the family Paradoxosomatidae, genus *Sigipinius* in mainland China. Red lines show the transect Aksu – Shangrila – Lijiang – Kangding – Jiuzhaigou, along which the elevations are crudely indicated below. **1** *S. kabaki* **2** *S. montana* **3** *S. spiniger* **4** *S. dentiger* **5** *S. campanuliformis* **6** *S. complex* **7** *S. simplex* **8** *S. pinnifer* **9** *S. grahami*.

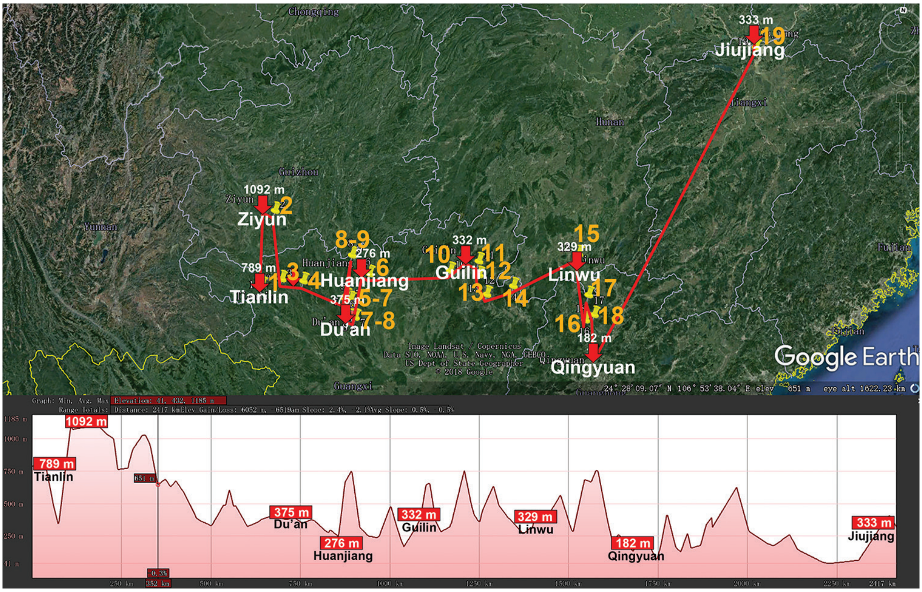

Figure 12. Distribution of the family Paradoxosomatidae, genus *Hylomus* in mainland China. Red lines show the transect Tianlin – Ziyun – Du'an – Huanjiang – Guilin – Linwu – Qingyuan – Jiujiang, along which the elevations are crudely indicated below. **1** *H. minutuberculus* **2** *H. getuhensis* **3** *H. phasmoides* **4** *H. variabilis* **5** *H. parvulus* **6** *H. scolopendroides* **7** *H. nodulosus* **8** *H. scutigeroides* **9** *H. spinitergus* **10** *H. lui* **11** *H. yuani* **12** *H. cornutus* **13** *H. lingulatus* **14** *H. spinissimus* **15** *H. eupterygotus* **16** *H. laticollis* **17** *H. simplipodus* **18** *H. similis* **19** *H. draco*; *H. longispinus* is not mapped because its exact type locality remains unknown.

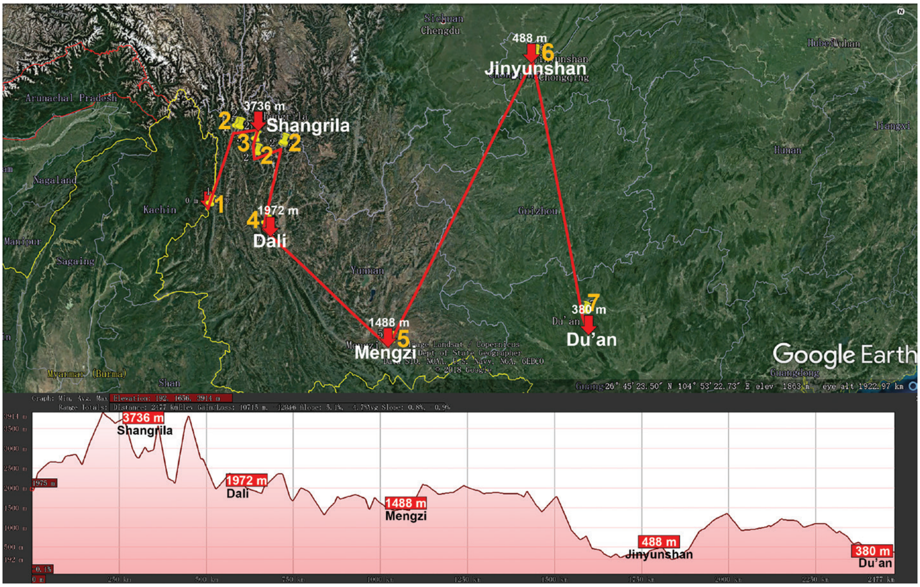

Figure 13. Distribution of the family Paradoxosomatidae, genus *Tylopus* in mainland China. Red lines show the transect Shangrila – Dali – Mengzi – Jinyunshan – Du'an, along which the elevations are crudely indicated below. **1** *T. reductus* **2** *T. kabaki* **3** *T. similis* **4** *T. schawalleri* **5** *T. sinensis* **6** *T. nigromarginatus* **7** *T. deharvengi*.

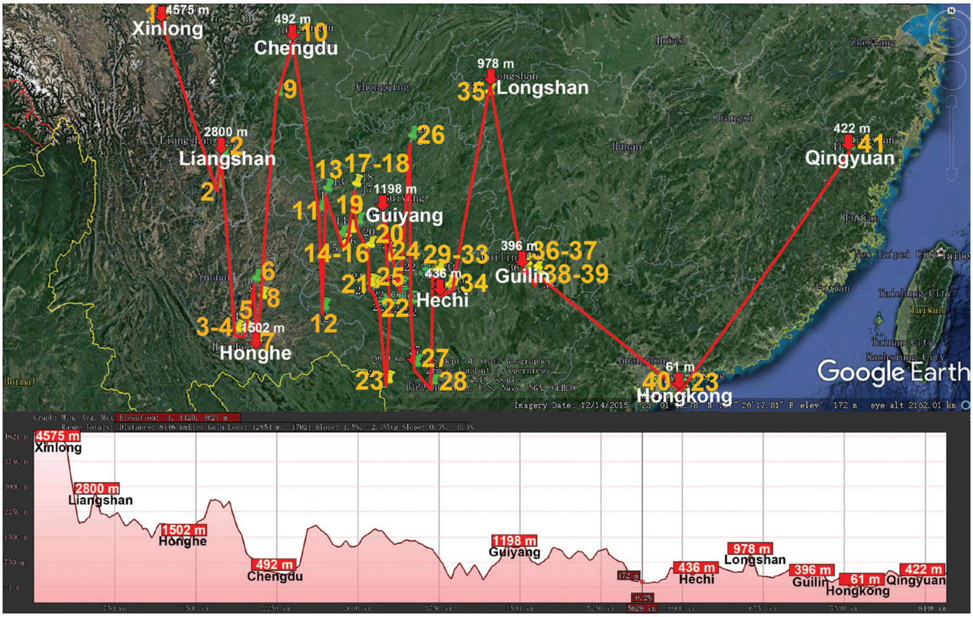

Figure 14. Distribution of the family Cambalopsidae, genus *Glyphiulus* in mainland China. Red lines show the transect Xinlong – Liangshan – Honghe – Chengdu – Guiyang – Hechi – Longshan – Guilin – Hong Kong – Qingyuan, along which the elevations are crudely indicated below. **1** *G. basalis* **2** *G. liangshanensis* **3** *G. beroni* **4** *G. paragranulatus* **5** *G. semigranulatus* **6** *G. subobliteratus* **7** *G. subgranulatus* **8** *G. obliteratus* **9** *G. latus* **10** *G. intermedius* **11** *G. zorzini* **12** *G. guangnanensis* **13** *G. foetidus* **14** *G. sinensis* **15** *G. pergranulatus* **16** *G. quadrohamatus* **17** *G. paracostulifer* **18** *G. latellai* **19** *G. obliteratoides* **20** *G. rayrouchi* **21** *G. difficilis* **22** *G. impletus* **23** *G. granulatus* **24** *G. basazsi* **25** *G. calceus* **26** *G. parobliteratus* **27** *G. pulcher* **28** *G. echinoides* **29** *G. acutus* **30** *G. mulunensis* **31** *G. proximus* **32** *G. tiani* **33** *G. paramulunensis* **34** *G. speobius* **35** *G. deharvengi* **36** *G. melanoporus* **37** *G. septentrionalis* **38** *G. adeloglyphus* **39** *G. maocun* **40** *G. formosus* **41** *G. recticulus*; *G. anophthalmus* and *G. lipsorum* are not mapped because their exact type localities remain unknown, whereas *G. granulatus* is mapped, but it is pantropical.

or northern Vietnam, or Taiwan. The mono- or oligotypic *Belousoviella*, *Gonobelus*, *Sinomorpha*, *Wulingina*, and *Yuennanina* are all strictly endemic to China, mostly to its southwestern parts, but their Oriental stem is clear-cut due to their closest affinities.

The immediately above paradoxosomatid genera endemic or subendemic to southern China which all seem to be of Oriental stock, together with some other polydesmidans like *Carlotretus* and *Martensodesmus* (both Opisotretidae), *Glenniea* and *Pacidesmus* (both Polydesmidae, Figs 7, 8), as well as several others (e.g. Cryptodesmidae, Haplodesmidae, Pyrgodesmidae), regardless of whether they are Oriental or Palaearctic in origin, seem to be sufficiently numerous and manifest to warrant the recognition of a separate, albeit secondary, subordinate, southern Chinese diversity and faunogenetic centre which must have seriously contributed to at least the faunas of the adjacent parts of the Himalaya, Myanmar, Thailand, Indochina and Taiwan. The influence of that southern Chinese centre in the Himalaya has recently been emphasized (Golovatch and Martens 2018).

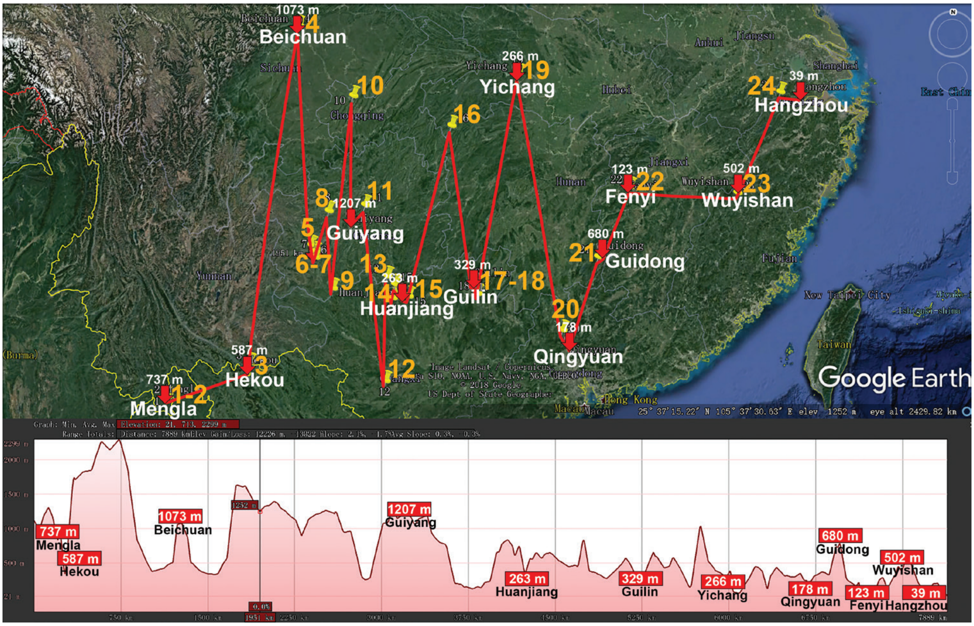

Figure 15. Distribution of the family Haplodesmidae, genus *Eutrichodesmus* in mainland China. Red lines show the transect Mengla – Hekou – Beichuan – Guiyang – Huanjiang – Guilin – Yichang – Qingyuan – Guidong – Fenyi – Wuyishan – Hangzhou, along which the elevations are crudely indicated below. **1** *E. dorsiangulatus* **2** *E. monodentus* **3** *E. arcicollaris* **4** *E. triangularis* **5** *E. tenuis* **6** *E. latellai* **7** *E. obliteratus* **8** *E. incisus* **9** *E. latus* **10** *E. soesilae* **11** *E. triglobius* **12** *E. distinctus* **13** *E. trontelji* **14** *E. planatus* **15** *E. similis* **16** *E. sketi* **17** *E. lipsae* **18** *E. jianjia* **19** *E. apicalis* **20** *E. digitatus* **21** *E. spinatus* **22** *E. simplex* **23** *E. anisodentus* **24** *E. pectinatidentis*.

The Oriental realm as one of the main sources for the formation of the millipede fauna of China can also be exemplified by the basically tropical to subtropical orders Sphaerotheriida, Spirobolida and Spirostreptida, as well as the families Cryptodesmidae, Haplodesmidae, Opisotretidae, Pyrgodesmidae (all Polydesmida) and Sinocallipodidae (Callipodida), some of which often vary a lot in altitudinal distributions just like numerous Holarctic/Palaearctic groups. The often presumed rule "tropical elements for low elevations only" does not always work.

The genus *Glyphiulus*, the largest in the family Cambalopsidae (Spirostreptida), presently comprises 60+ species in East and Southeast Asia (to Borneo in the east), 42 of which are encountered at 105–4150 m a.s.l. across China (Fig. 14). Most of them are cavernicoles (Liu and Wynne 2019). A similarly large and even more widespread genus, *Eutrichodesmus* (Haplodesmidae), presently encompasses 50 species (Liu et al. 2017b, Liu and Wynne 2019) which range from southern Japan and Taiwan in the north, through entire Southeast Asia, to Vanuatu, Melanesia in the south. The distributions of all 24 species that populate continental China seem to be more typical, much better agreeing with the above rule: 65–1495 m a.s.l. (Table 1, Fig. 15). At least half of them are also cavernicoles.

Discussion

The diversity estimates presented in Table 1, i.e. 339 species, 71 genera, 26 families, and eleven orders, are much or significantly higher than those reported from the main adjacent areas. The similarly huge territories of Siberia and the Russian Far East that lie north of China support only ca. 130 species, 46 genera, 18 families and five orders of Diplopoda, while the fauna is reasonably well known (Mikhaljova 2017). This is hardly surprising because the prevailing permafrost and sharply continental climates of Asian Russia are largely too harsh to sustain a rich millipede fauna. The even harsher, mostly arid Mongolia is extremely poor in millipedes, with some nine species, five genera and families, and three orders involved (Mikhaljova 2012, Nefediev et al. 2015).

In contrast, the great Himalayan Range spanning for >2,300 km from northwest to southeast and mostly lying south of China supports >275 species, 53 genera, 23 families and 13 orders of diplopods (Golovatch and Martens 2018). Similarly, the fauna of India presently amounts to > 270 species, at least 90 genera, 25 families, and eleven orders (Golovatch and Wesener 2016), *vs.* 92 species from 34 genera, 13 families, and eight orders recorded from Myanmar (Likhitrakarn et al. 2017) or ca. 230 species in Thailand (Likhitrakarn et al. 2019). A direct correlation between area and latitude is clear: the larger the area and the closer it lies to the equator, the richer the biota, including the diplopod faunas. However, the more southerly, the greater the diversity, and the more incomplete and fragmentary is our knowledge.

Certainly the Chinese millipede fauna still remains strongly understudied, given the country's great size and habitat diversity, including the globe's greatest karst areas. It may well amount to 1,000 species (Golovatch 2015a), chiefly due to the still particularly poorly studied micropolydesmidans, as well as cavernicoles. Southern China's karsts are unique in often harbouring up to 5–6 diplopod species per cave (Golovatch 2015a). At least some of the remaining orders such as Glomeridesmida, Siphonocryptida, Siphonophorida, Siphoniulida, and Stemmiulida that occur in the Oriental Region (Table 2), including areas immediately adjacent to mainland China, may also be expected to populate the country. For example, Jiang et al. (2019) have recently described a fossil Siphonophorida from Cretaceous amber (ca. 99 Mya) in northern Myanmar, and an extant species is long known to occur in northern Pakistan (Golovatch 1991b). In addition, the same Burmese amber contains still undescribed Stemmiulida (Stoev et al. 2019) and two described species of Siphoniulida (Liu et al. 2017c). Likewise, as noted above, an extant species of Siphonocryptida and Glomeridesmida each is known from Taiwan and northern Thailand, respectively (Korsós et al. 2008, Shelley 2011).

While the Palaearctic/Holarctic components expectedly dominate the fauna of the northern parts of the country, the Oriental ones prevail in its south and along the Pacific coast. Both realms are increasingly mixed and intermingled towards China's centre. However, in addition to the above traditional views, based on millipede distribution patterns alone, southern China seems to harbour a subordinate, but highly peculiar faunal nucleus, or origin centre of its own, whence the adjacent Himalaya, Indochina and/or Taiwan could have become populated by younger lineages. The presence of a family (the monobasic Guizhousomatidae) and numerous genera endemic or subendemic to southern China, both apparently relict and relatively advanced, seems to be evidence of this. Within the order Callipodida alone, the family Sinocallipodidae seems to be the basalmost and representing a suborder of its own, the Paracortinidae is a more advanced subendemic, same as the mostly Central Asian Caspiopetalidae (Stoev and Geoffroy 2004, Stoev and Enghoff 2011). More importantly, a fossil family representing a separate suborder has recently been discovered in the Cretaceous Burmese amber, ca. 99 Mya (Stoev et al. 2019).

The millipede fauna of mainland China is thus a tangled mixture of zoogeographic elements of various origins and ages, apparently both relict and more advanced. The few anthropochores/introductions must have been the latest faunal "layer" to populate China.

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RESEARCH ARTICLE

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Diversity and distribution of the millipedes (Diplopoda) of Georgia, Caucasus

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Abstract

The diplopod fauna of Georgia, Transcaucasia, is very rich given the country's relatively small territory; it presently comprises 103 species from 44 genera, 12 families, and 7 orders. Most of the Diplopoda known from Georgia (86 species, or 83%) demonstrate Caucasian distribution patterns, 36 and 46 species, as well as 8 and 9 genera being endemic or subendemic to the country, respectively. A single Holarctic family, Anthroleucosomatidae (order Chordeumatida), contains 44 Caucasian species and 20 genera, of which 27 species and 14 genera are endemic or subendemic to Georgia. Likewise, all species from the orders Polyzoniida, Siphonocryptida, Glomerida and Chordeumatida, as well as most species of Julida and Polydesmida are native, also endemic or subendemic to the Caucasus, but the genera and families they represent are widely distributed at least across the Euro-Mediterranean Realm. Most of the presumed troglobionts in the Caucasus appear to be confined to western Georgia's karst caves (14 species, 5 genera). Within Georgia, the fauna of the western part (= Colchis) is particularly rich and diverse, while that of the central and eastern parts of the country grows increasingly depauperate inland following the gradual climatic aridisation from west (Black Sea coast) to east (Armenia and Azerbaijan). The vertical distribution of the Diplopoda in Georgia, as well as the Caucasus generally, shows the bulk of the fauna restricted to forested lowland to mountain biomes or their remnants. Only very few Chordeumatida and *Julus* species seem to occur solely in the subalpine to alpine environments and thus may provisionally be considered as high-montane elements. Ongoing and future research on the millipedes of the Caucasus, especially in cave and montane environments, will undoubtedly allow for many more novelties and details of the diversity and distribution of Georgia's Diplopoda to be revealed or refined.

Keywords
checklist, Colchis, endemism, fauna, Myriapoda

Introduction

Georgia is one of the main countries in the Caucasus, lying between western Asia and Eastern Europe. It is bounded in the west by the Black Sea, in the north by Russia, in the south by Turkey, and in the southeast and east by Armenia and Azerbaijan (Fig. 1). The area is mainly montane to high montane, situated between 41° and 44°N, and 40° and 47°E. The Greater Caucasus Mountain Range, or Caucasus Major, forms the northern border of Georgia, while the southern border is bounded by the Lesser Caucasus Mountains, or Caucasus Minor. The Caucasus Major is much higher in elevation (more than 5000 m a.s.l.) than the plateau-like Caucasus Minor, both being connected by the submeridional Surami (= Likhi) Mountain Range which divides Georgia into the western and central + eastern parts. Both parts are quite varied in climate and biota. Western Georgia's landscape ranges from lowland marsh-forests, swamps, and temperate rainforests within the Colchis Plain to eternal snows and glaciers, while the eastern part of the country even contains a small segment of semi-arid plains. Forests cover around 40% of Georgia's territory, while the alpine/subalpine zone accounts for approximately 10% of the land. The climate of Georgia is extremely diverse, considering the nation's small size, but is largely mild to warm. There are two main climatic zones, roughly corresponding to the eastern and western parts of the country. The Greater Caucasus Mountain Range plays an important role in moderating Georgia's climate and protects the nation from the penetration of colder air masses from the north. The Lesser Caucasus Mountains partially protect the region from the influence of dry and hot air masses from the south (Bondyrev et al. 2015).

The millipede fauna of Georgia has recently been reviewed and shown to comprise 95 species from 42 genera, 12 families, and 7 orders (Kokhia and Golovatch 2018). A few relevant faunistic papers have, or will have, appeared since (Golovatch 2018, Golovatch and Turbanov 2017, Antić et al. 2018, Evsyukov et al. 2018, 2020, Vagalinski and Lazányi 2018, Short et al. 2020), allowing for the previous checklist to be rectified and updated, as well as the previous reference list to be considerably shortened. The present checklist contains 103 species from 44 genera, 12 families, and 7 orders (Table 1). Data on the elevations at which the species occur, both within and beyond Georgia, are also added, representing the basic information for our analysis of millipede vertical distributions.

Material and methods

Only described species and published records are considered in our paper, while dubious taxa and those not identified to the species level have been omitted both from the checklist and reference list. Only one important exception has been made: *Calyptophyllum* sp. as the only record of this genus in the Caucasus (Table 1).

Figure 1. Geographic division of Georgia.

Three zigzag transects chosen to grossly reflect the north-to-south lie of the macro relief of Georgia, extending from the Caucasus Major in the north to the Caucasus Minor in the south (Figs 2–5), have been drawn, one each for the western, central and eastern parts of the country (Fig. 1). The transect across western Georgia connects Pitsunda – Arabika Plateau – Khaishi – Bagdati – Batumi (427 km long), that in central Georgia connects Roki Tunnel – Tskhinvali – Tbilisi – Tsalka Reservoir – Ninotsminda – Javakheti National Park (275 km), and the eastern Georgia one connects Omalo – Tianeti – Akhmeta – Shilda – Kvareli – Lagodekhi – Tamariani (186 km) (Fig. 2). Both at the bottom of the maps and on the maps themselves, each transect is accompanied by the respective altitudes given for each of the turn localities and thus provides a clear generalized picture of the macro relief (Figs 3–5). These three transects thus cover all major variations in millipede vertical distribution across entire Georgia. This novel approach to a graphic presentation of faunistic results allows us to combine the horizontal and vertical distributions of millipedes in the easiest and most vivid way on the same map. Mapping largely concerns endemic or subendemic species and concerns only the territory of Georgia.

Most of the colour maps were generated using Google Earth Pro version 7.3.2.5495 and Adobe Photoshop CS6. The final images were processed with Adobe Photoshop CS6.

Results

The diplopod fauna of the Caucasus region, including Georgia, is basically Euro-Mediterranean in its composition (Table 1). This also concerns the relatively few widespread,

Table 1. A revised checklist of the Diplopoda of Georgia, with data on species distributions, both within and beyond the country, their statuses, and the main relevant literature sources. Designations: i – introduced; G – entire Georgia; W – western Georgia; C – central Georgia; E – eastern Georgia; R – Russian Caucasus; T – Turkey; Ar – Armenia; Az – Azerbaijan; Cr – Crimean Peninsula; (+) – present; e – endemic to Georgia; se – subendemic to Georgia; t – presumed troglobiont; sc – subcosmopolitan; EuM – Euro-Mediterranean; M – Mediterranean; EM – eastern Mediterranean; EE – eastern European; Ca – Caucasian.

Fauna	G	R	T	Ar	Az	Cr	Elevations (m a.s.l.) and status	Distribution pattern	Main relevant references
Class Diplopoda									
Order Polyxenida									
Family Polyxenidae									
Genus *Polyxenus* Latreille, 1803									
1. *Polyxenus lagurus* (Linnaeus, 1758)	W	+				+	20–1700, i	sc	Issaev 1911, Short et al. 2020
2. *Polyxenus lankaranensis* Short, Vahtera, Wesener & Golovatch, 2020	E	+			+		100–800	Ca	Short et al. 2020
Genus *Propolyxenus* Silvestri, 1948	W								
3. *Propolyxenus argentifer* (Verhoeff, 1921)	G	+	+	+	+	+	20–1700	EM	Short et al. 2020
Family Lophoproctidae									
Genus *Lophoproctus* Pocock, 1894									
4. *Lophoproctus coecus* Pocock, 1894	G					+	20–900	EM	Short 2015, Short et al. 2020
Order Polyzoniida									
Family Hirudisomatidae									
Genus *Hirudisoma* Fanzago, 1881									
5. *Hirudisoma roseum* (Victor, 1839)	G	+	+		+		20–1100, se	EM	Golovatch et al. 2015
Order Siphonocryptida									
Family Siphonocryptidae									
Hirudicryptus Enghoff & Golovatch, 1985									
6. *Hirudicryptus abchasicus* Golovatch, Evsyukov & Reip, 2015	W	+					600–1500, se	Ca	Golovatch et al. 2015, Zuev 2017
Order Glomerida									
Family Glomeridae									
Genus *Hyleoglomeris* Verhoeff, 1910									
7. *Hyleoglomeris awchasica* (Brandt, 1840)	W	+					20–2100, se	Ca	Golovatch 1975, 1976a, 1989b
8. *H. specialis* Golovatch, 1989	E	+					500–1400, se	Ca	Golovatch 1989b
Genus *Trachysphaera* Heller, 1858									
9. *Trachyspaera costata* (Waga, 1857)	G	+	+	+	+	+	20–2000	EuM	Golovatch 1990, 2008
10. *T. fragilis* Golovatch, 1976	G	+					80–460, t, e	Ca	Golovatch 1976c,1990, Golovatch and Turbanov 2017
11. *T. minuta* Golovatch, 1976	G	+	+	+			20–1700, se	Ca	Golovatch 1976c, 1990
12. *T. orientalis* Golovatch, 1976	W						800–1100, t, e	Ca	Golovatch 1976c, 1990
13. *T. radiosa* (Lignau, 1911)	W	+					20–1800, se	Ca	Golovatch 1976a, 1990
14. *T. solida* Golovatch, 1976	W, C						20–2020, se	Ca	Golovatch 1976c, 1976c, 1990, 1993

Fauna	G	R	T	Ar	Az	Cr	Elevations (m a.s.l.) and status	Distribution pattern	Main relevant references
Family Glomeridellidae									
Genus *Typhloglomeris* Verhoeff, 1898									
15. *Typhloglomeris lohmanderi* (Golovatch, 1989)	C, E	+		+			600–1450, se	Ca	Golovatch 1989a, 2003
16. *Typhloglomeris palatovi* Golovatch & Turbanov, 2018	W						650, t, e	Ca	Golovatch and Turbanov 2017
Order Chordeumatida									
Family Anthroleucosomatidae									
Genus *Acanthophorella* Antić & Makarov, 2016									
17. *Acanthophorella barjadzei* Antić & Makarov, 2016	W						1120–1200, t, e	Ca	Antić and Makarov 2016
Genus *Adshardicus* Golovatch, 1981									
18. *Adshardicus strasseri* Golovatch, 1981	W		+				20–530, se	Ca	Enghoff 2006, Antić and Makarov 2016
Genus *Alpinella* Antić & Makarov, 2016									
19. *Alpinella waltheri* Antić & Makarov, 2016	E						2860, e	Ca	Antić and Makarov 2016
Genus *Brachychaetosoma* Antić & Makarov, 2016									
20. *Brachychaetosoma turbanovi* Antić & Makarov, 2016	W						300, t, e	Ca	Antić and Makarov 2016
Genus *Caucaseuma* Strasser, 1970									
21. *Caucaseuma kelasuri* Antić & Makarov, 2016	W						190, e	Ca	Antić and Makarov 2016
22. *C. variabile* Antić & Makarov, 2016	C	+					100–2500, se	Ca	Antić and Makarov 2016
Genus *Cryptacanthophorella* Antić & Makarov, 2016									
23. *Cryptacanthophorella manubriata* Antić & Makarov, 2016	W, C						800–1700, e	Ca	Antić and Makarov 2016
Genus *Dentatosoma* Antić & Makarov, 2016									
24. *Dentatosoma denticulatum* Antić & Makarov, 2016	W						400–900, e	Ca	Antić and Makarov 2016
25. *D. magnum* Antić & Makarov, 2016	W	+					20–2200, se	Ca	Antić and Makarov 2016
26. *D. zeraboseli* Antić & Makarov, 2016	W						20–1700, e	Ca	Antić and Makarov 2016
Genus *Georgiosoma* Antić & Makarov, 2016									
27. *Georgiosoma bicornutum* Antić & Makarov, 2016	W						2000, t, e	Ca	Antić and Makarov 2016
Genus *Herculina* Antić & Makarov, 2016									
28. *Herculina oligosagittae* Antić & Makarov, 2016	W						1500–1700, e	Ca	Antić and Makarov 2016
29. *H. polysagittae* Antić & Makarov, 2016	C						1750, e	Ca	Antić and Makarov 2016
Genus *Heterocaucaseuma* Antić & Makarov, 2016									
30. *Heterocaucaseuma deprofundum* Antić & Makarov, 2018	W						2000–2100, t, e	Ca	Antić et al. 2018
31. *H. longicorne* Antić & Makarov, 2016	W						100–350, t, e	Ca	Antić and Makarov 2016, Antić et al. 2018
32. *H. mauriesi* (Golovatch & Makarov, 2011)	W						215, t, e	Ca	Golovatch and Makarov 2011, Antić and Makarov 2016, Antić et al. 2018

Fauna	G	R	T	Ar	Az	Cr	Elevations (m a.s.l.) and status	Distribution pattern	Main relevant references
Genus *Metamastigophorophyllon* Ceuca, 1976									
33. *Metamastigophorophyllon giljarovi* (Lang, 1959)	W	+					20–1850, se	Ca	Antić and Makarov 2016
34. *M. hamatum* Antić & Makarov, 2016	W	+					150–2200, se	Ca	Antić and Makarov 2016
35. *M. lamellohirsutum* Antić & Makarov, 2016	W						700–800, e	Ca	Antić and Makarov 2016
36. *M. torsivum* Antić & Makarov, 2016	G				+		800–1700, se	Ca	Antić and Makarov 2016
Genus *Paranotosoma* Antić & Makarov, 2016									
37. *Paranotosoma attemsi* Antić & Makarov, 2016	W						1500–1800, e	Ca	Antić and Makarov 2016
38. *P. cordatum* Antić & Makarov, 2016	W						20–800, e	Ca	Antić and Makarov 2016
39. *P. subrotundatum* Antić & Makarov, 2016	W, C	+					350–850, se	Ca	Antić and Makarov 2016
Genus *Pseudoflagellophorella* Antić & Makarov, 2016									
40. *Pseudoflagellophorella eskovi* Antić & Makarov, 2016	C, E			+	+		100–2080, se	Ca	Antić and Makarov 2016
41. *P. mirabilis* Antić & Makarov, 2016	W						20–130, e	Ca	Antić and Makarov 2016
42. *P. papilioformis* Antić & Makarov, 2016	E				+		850–2100, se	Ca	Antić and Makarov 2016
Genus *Ratcheuma* Golovatch, 1985									
43. *Ratcheuma excorne* Golovatch, 1985	W						1180, t, e	Ca	Golovatch 1984/85, Antić and Makarov 2016
Order Julida									
Family Blaniulidae									
Genus *Cibiniulus* Verhoeff, 1927									
44. *Cibiniulus phlepsii* (Verhoeff, 1897)	W		+				20–130	EuM	Enghoff 1984, 2006
Genus *Nopoiulus* Menge, 1851									
45. *Nopoiulus brevipilosus* Enghoff, 1984	W						130, t, e	Ca	Enghoff 1984, Golovatch and Enghoff 1990
46. *N. densepilosus* Enghoff, 1984	W		+		+		1500–1700	Ca	Enghoff 1984, Golovatch and Enghoff 1990
47. *N. golovatchi* Enghoff, 1984	W		+				20–130, se	Ca	Enghoff 1984, 1990
48. *N. kochii* (Gervais, 1847)	G	+	+	+	+		10–2200, i?	sc	Enghoff 1984, Golovatch and Enghoff 1990
Family Nemasomatidae									
Genus *Nemasoma* C.L. Koch, 1847									
49. *Nemasoma caucasicum* (Lohmander, 1932)	G	+	+	+	+		20–2000, se	Ca	Kobakhidze 1965, Enghoff 1985
Family Julidae									
Genus *Archileucogeorgia* Lohmander, 1936									
50. *Archileucogeorgia abchasica* Lohmander, 1936	W						130, t, e	Ca	Lohmander 1936
51. *A. satunini* Lohmander, 1936	W						130, e	Ca	Lohmander 1936
Genus *Brachyiulus* Berlese, 1884									
52. *Brachyiulus lusitanus* Verhoeff, 1898`	C				+		100, i	M	Lohmander 1936

Fauna	G	R	T	Ar	Az	Cr	Elevations (m a.s.l.) and status	Distribution pattern	Main relevant references
Genus *Byzantorhopalum* Verhoeff, 1930									
53. *Byzantorhopalum rossicum* (Timotheew, 1897)	W?	+			+	+	30–1500	EE	Lohmander 1936, Vagalinski and Lazányi 2018
Genus *Catamicrophyllum* Verhoeff, 1900									
54. *Catamicrophyllum caucasicum* (Attems, 1901)	G	+	+	+			700–2000, se	Ca	Lohmander 1936, Enghoff 1995
Genus *Calyptophyllum* Brolemann, 1922									
55. *Calyptophyllum* sp.	W						100?	?	Lohmander 1936, Enghoff 1995
Genus *Chaetoleptophyllum* Verhoeff, 1898									
56. *Chaetoleptophyllum flexum* Golovatch, 1979	G	+					15–2200, se	Ca	Golovatch 1979, Evsyukov et al. (2020)
Genus *Cylindroiulus* Verhoeff, 1894									
57. *Cylindroiulus bellus* (Lignau, 1903)	W?	+				+	100	EM	Lignau 1903, Read 1992, Chumachenko 2016
58. *C. crassiphylacum* Read, 1992	W, C		+				600–1700, se	Ca	Read 1992
59. *C. kacheticus* Lohmander, 1936	E	+					500–1250, se	Ca	Lohmander 1936, Read 1992
60. *C. olgainna* Read, 1992	W						300–1100, e	Ca	Read 1992
61. *C. parvus* Lohmander, 1928	C, E				+		500–2100, se	Ca	Lohmander 1936, Read 1992
62. *C. placidus* (Lignau, 1903)	W, C	+					20–2200, se	Ca	Lignau 1903, Read 1992
63. *C. pterophylacum* Read, 1992	W, C	+					20–1600, se	Ca	Read 1992, Zuev 2014
64. *C. quadrus* Read, 1992	W, C						700–1000, e	Ca	Read 1992
65. *C. ruber* (Lignau, 1903)	W	+					100–2000, se	Ca	Lignau 1903, 1915, Read 1992
66. *C. schestoperovi* Lohmander, 1936	W	+					400–1800, se	Ca	Lohmander 1936, Read 1992
67. *C. truncorum* (Silvestri, 1896)	W	+	+				130, i	sc	Read 1992
Genus *Grusiniulus* Lohmander, 1936									
68. *Grusiniulus redikorzevi* Lohmander, 1936	C						800–900, e	Ca	Lohmander 1936, Vagalinski and Lazányi 2018
Genus *Julus* Linnaeus, 1758									
69. *Julus colchicus* Lohmander, 1936	G	+	+				20–2850, se	Ca	Lohmander 1936, Enghoff 2006, Evsyukov et al. 2018
70. *J. kubanus* Lohmander, 1936	W, E	+					300–2100, se	Ca	Lohmander 1936, Kobakhidze 1965, Evsyukov et al. 2018
71. *J. lignaui* Verhoeff, 1910	W	+					1500–2800, se	Ca	Evsyukov et al. 2018
72. *J. lindholmi* Lohmander, 1936	W	+					450–2200, se	Ca	Lohmander 1936, Evsyukov et al. 2018

Fauna	G	R	T	Ar	Az	Cr	Elevations (m a.s.l.) and status	Distribution pattern	Main relevant references
Genus *Kubaniulus* Lohmander, 1936									
73. *Kubaniulus gracilis* Lohmander, 1936	W	+					20–700, se	Ca	Lohmander 1936, Evsyukov et al. 2020
Genus *Leptoiulus* Verhoeff, 1894									
74. *Leptoiulus hastatus* Lohmander, 1932	C		+				800–1530, se	Ca	Lohmander 1936, Enghoff 2006, Evsyukov et al. 2020
75. *L. tanymorphus* (Attems, 1901)	C, E	+		+	+		80–1800, se	Ca	Lohmander 1936, Evsyukov et al. 2020
Genus *Leucogeorgia* Verhoeff, 1930									
76. *Leucogeorgia longipes* Verhoeff, 1930	W						170, t, e	Ca	Verhoeff 1930, Barjadze et al. 2019
77. *L. rediviva* Golovatch, 1983	W						330, t, e	Ca	Golovatch 1983, Barjadze et al. 2019
Genus *Megaphyllum* Verhoeff, 1894									
78. *Megaphyllum dioscoriadis* (Lignau, 1915)	W	+					130–1400, se	Ca	Lignau 1915, Lohmander 1936, Kobakhidze 1965, Chumachenko 2016, Vagalinski and Lazányi 2018
79. *M. hercules* (Verhoeff, 1901)	W	+					20, i	EM	Lazányi and Vagalinski 2013
80. *M. spathulatum* (Lohmander, 1936)	W?	?					?	Ca	Lohmander 1936, Lazányi and Vagalinski 2013
Genus *Omobrachyiulus* Lohmander, 1936									
81. *Omobrachyiulus adsharicus* (Lohmander, 1936)	W						20–30, e	Ca	Lohmander 1936, Vagalinski and Lazányi 2018
82. *O. brachyurus* (Attems, 1899)	G	+	+	+	+		20–2500	EM	Lohmander 1936, Kobakhidze 1965, Enghoff 2006, Vagalinski and Lazányi 2018
83. *O. curvocaudatus* (Lignau, 1903)	W	+					30–1700, se	Ca	Lohmander 1936, Kobakhidze 1965, Vagalinski and Lazányi 2018
84. *O. divaricatus* (Lohmander, 1936)	G			+			600 –2000, se	Ca	Lohmander 1936, Kobakhidze 1965, Vagalinski and Lazányi 2018
85. *O. hortensis* (Golovatch, 1981)	W						150, e	Ca	Golovatch 1981, Vagalinski and Lazányi 2018
86. *O. implicitus* Lohmander, 1936 (= *O. i. ritsensis* (Golovatch, 1981))	W	+					400–1800, se	Ca	Lohmander 1936, Chumachenko 2016, Vagalinski and Lazányi 2018, Vagalinski in litt.

Fauna	**G**	**R**	**T**	**Ar**	**Az**	**Cr**	**Elevations (m a.s.l.) and status**	**Distribution pattern**	**Main relevant references**
87. *O. macrourus* (Lohmander, 1928) (= *O. m. abchasicus* (Lohmander, 1936))	W, C						130–2000, e	Ca	Lohmander 1936, Kobakhidze 1965, Vagalinski and Lazányi 2018, Vagalinski in litt.
Genus *Pachyiulus* Berlese, 1883									
88. *Pachyiulus flavipes* (C.L. Koch, 1847)	W					+	30, i	M	Lohmander 1936
89. *P. krivolutskyi* Golovatch, 1977	W	+					20–1800, se	Ca	Golovatch 1977, Evsyukov 2016
Genus *Syrioiulus* Verhoeff, 1914									
90. *Syrioiulus adsharicus* (Lohmander, 1936)	W						120, e	Ca	Lohmander 1936, Golovatch 2018
91. *S. georgicus* (Lohmander, 1932)	C						800–900, e	Ca	Lohmander 1932, Golovatch 2018
Order Polydesmida									
Family Paradoxosomatidae									
Genus *Oxidus* Cook, 1911									
92. *Oxidus gracilis* (C.L. Koch, 1847)	W	+					20–100, i	Ca	Lignau 1915, Lohmander 1936, Chumachenko 2016
Genus *Strongylosoma* Brandt, 1833									
93. *Strongylosoma kordylamythrum* Attems, 1898	G	+		+			20–2200	Ca	Lohmander 1936, Kobakhidze 1965, Evsyukov et al. 2016
94. *S. lenkoranum* Attems, 1898	C		+	+	+		80–1650	Ca	Lohmander 1936, Kobakhidze 1965, Evsyukov et al. 2016
Family Polydesmidae									
Genus *Brachydesmus* Heller, 1858									
95. *Brachydesmus assimilis* Lohmander, 1936	C, E	+		+	+		600–2800, se	Ca	Golovatch et al. 2016
96. *B. furcatus* Lohmander, 1936	W	+					20–1900, se	Ca	Golovatch et al. 2016
97. *B. kalischewskyi* Lignau, 1915	G	+	+	+	+		50–2400, se	Ca	Golovatch et al. 2016
98. *B. kvavadzei* Golovatch, Evsyukov & Reip, 2016	W						70–1520, e	Ca	Golovatch et al. 2016
99. *B. simplex* Golovatch, Evsyukov & Reip, 2016	W	+					20–1100, se	Ca	Golovatch et al. 2016
100. *B. superus* Latzel, 1884	W	+					150–450, i	sc	Golovatch et al. 2016
Genus *Polydesmus* Latreille, 1803									
101. *Polydesmus abchasius* Attems, 1899	W, C	+					10–2230, se	Ca	Golovatch et al. 2016
102. *P. lignaui* Lohmander, 1936	W	+					100–2200, se	Ca	Golovatch et al. 2016
103. *P. mediterraneus* Daday, 1889	W					+	100, i	EM	Golovatch et al. 2016

likely introduced species from the orders Polyxenida, Julida and Polydesmida that occur in the Caucasus. Even among the few unquestioned introductions, only *Oxidus gracilis* (C.L. Koch, 1847) is an Oriental or East Asian alien element.

All species of Polyzoniida, Siphonocryptida, Glomerida and Chordeumatida, as well as most species of Julida and Polydesmida appear to be native, endemic or subendemic, but the genera and families they represent are widely distributed across the Euro-Mediterranean Realm. As a result, endemism is profound at the species and, to a lesser degree, generic levels. Most of the species (86, or 83%) show a Caucasian distribution pattern, thus being endemic or subendemic to the Caucasus region. The same pattern was found at the generic level, with 18 genera being endemic or subendemic to the Caucasus, including all 14 genera of the order Chordeumatida that inhabit the region (Antić and Makarov 2016, Antić et al. 2018). There are neither families nor orders of Diplopoda that are confined to the Caucasus region alone.

Our analysis of the distribution of Georgia's millipedes is largely based on strictly endemic and subendemic species (36 and 46, respectively: Table 1) and genera (8 and 9, respectively: *Alpinella*, *Brachychaetosoma*, *Cryptacanthophorella*, *Georgiosoma*, *Grusiniulus*, *Herculina*, *Leucogeorgia* and *Ratcheuma*, vs. *Adshardicus*, *Acanthophorella*, *Archileucogeorgia*, *Caucaseuma*, *Dentatosoma*, *Heterocaucaseuma*, *Omobrachyiulus*, *Paranotosoma* and *Pseudoflagellophorella*). It shows that western Georgia, including Abkhazia and Ajaria – which are shown separately (Figs 9, 10) to more clearly depict the localities/distributions and thus to avoid an "overcrowded" picture – supports the richest and most diverse fauna (Figs 7–10). This is also the area where all 14 presumed troglobionts are found in Georgia, all confined to karst caves (Barjadze et al. 2019). Abkhazia, northwestern Georgia, is the richest subregion both in epigean and troglobitic Diplopoda (Figs 7–9), hosting, among others, *Heterocaucaseuma deprofundum* Antić & Makarov, 2018. This species is the world's deepest record of a millipede, found at 60–1980 m below the surface in the Krubera-Voronja and Sarma caves, Arabika Massif, Abkhazia (Fig. 3). Both these caves are among the deepest globally and support the second and third deepest subterranean invertebrate communities, respectively. Furthermore, both harbour still one more diplopod species, a yet undescribed *Leucogeorgia* sp. (Antić et al. 2018).

This picture is hardly surprising, as due to the proximity to the Black Sea the climate of western Georgia is largely humid warm temperate. More easterly, the climate is increasingly dry and hot, already dominating eastern Georgia (Bondyrev et al. 2015). Following this trend, the millipede fauna is increasingly depauperate: at least 79 diplopod species occur in western Georgia (= Colchis), but this number drops down to 37 in the central and to 25 in the eastern parts of Georgia (Table 1, Figs 7–12). Millipedes are mainly confined to forests in the Caucasus and in Georgia reflecting their terrestrial, meso- to hygrophilous, largely also calciphilous, arthropod relationships which are historically, trophically and ecologically closely associated with forested biomes (Golovatch and Kime 2009). Dry steppes and arid light forests in central and eastern Georgia (Table 2), as well as the Colchidan swamps of western Georgia support only very few millipede species. Especially tolerant to xeric conditions

Figure 2. Map of Georgia with three transects (light blue), one each in the western, central and eastern parts of the country, to crudely show both horizontal and vertical distributions of millipedes endemic or subendemic to the country.

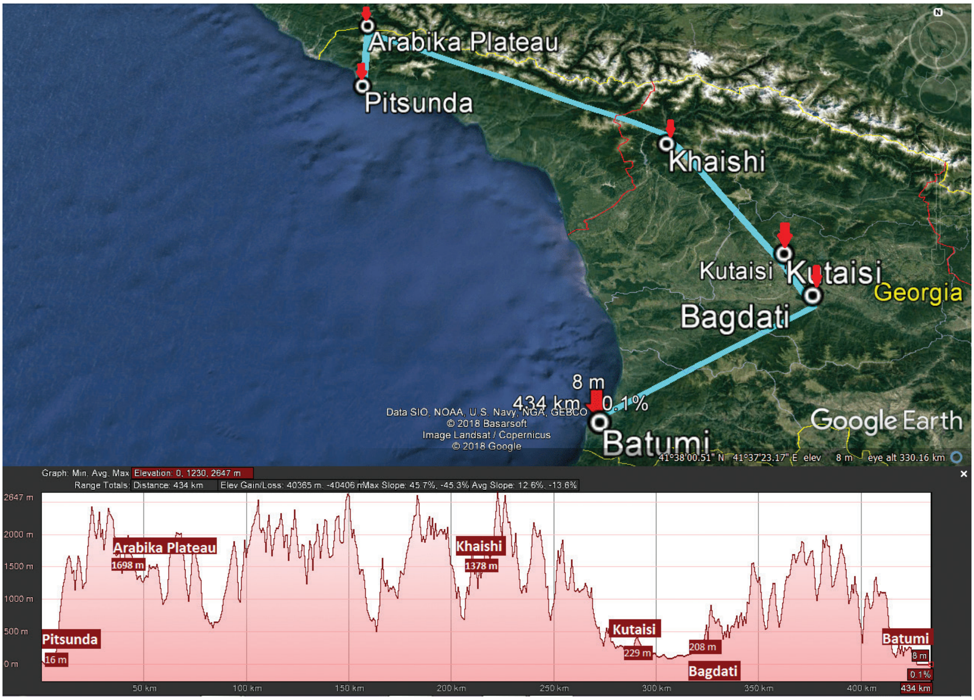

Figure 3. Map of western Georgia with its transect (light blue), Pitsunda – Arabika Plateau – Khaishi – Bagdati – Batumi, and macro relief (bottom).

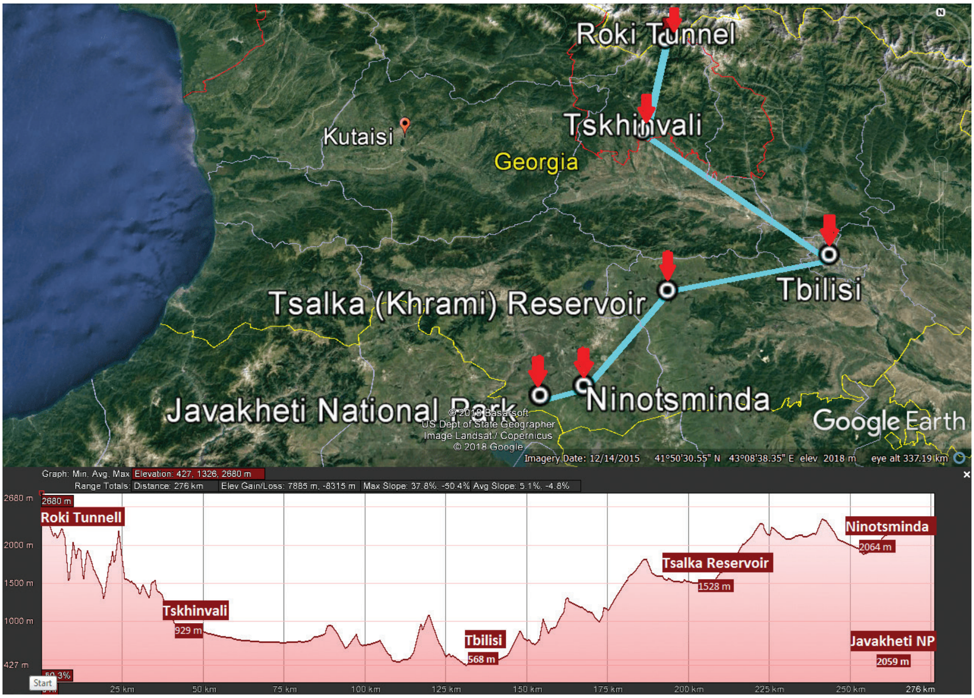

Figure 4. Map of central Georgia with its transect (light blue), Roki Tunnel – Tskhinvali – Tbilisi – Tsalka Reservoir – Ninotsminda – Javakheti National Park, and its macro relief (bottom).

Table 2. Vertical zonation of Georgia's vegetation belts.

Vegetation belts	Western Georgia, altitude (m a.s.l.)	Eastern Georgia, altitude (m a.s.l.)
deserts, dry steppes and arid light forests		150–600
forests	0–1900	600–1900
subalpine	1900–2500	1900–2500
alpine	2500–3100	2500–3000
subnival and nival	3100–3600 and > 3600	3000–3500 and > 3500

seems to be *Leptoiulus tanymorphus* (Attems, 1901) (Fig. 12), whereas both *Hirudisoma roseum* (Victor, 1839) and *Julus colchicus* Lohmander, 1936 (Fig. 6), as well as several Chordeumatida tend to represent particularly hydrophilous epigean species. Nearly all cavernicoles (e.g., *Leucogeorgia* spp.) are likewise highly hydrophilous.

As noted above, due to the quite extensive karsts that blanket much of western Georgia, in particular Abkhazia, Samegrelo, Racha Lechkhumi and Imereti, a large proportion of the total fauna is taken up by true cavernicoles (14 species, or 13%). The bulk, however, remains forest-dwelling millipedes and their woody habitats mainly are more or less montane. Present-day Georgia enjoys a remarkable network of nature reserves and national parks, with more than 1/3 of the entire national territory still

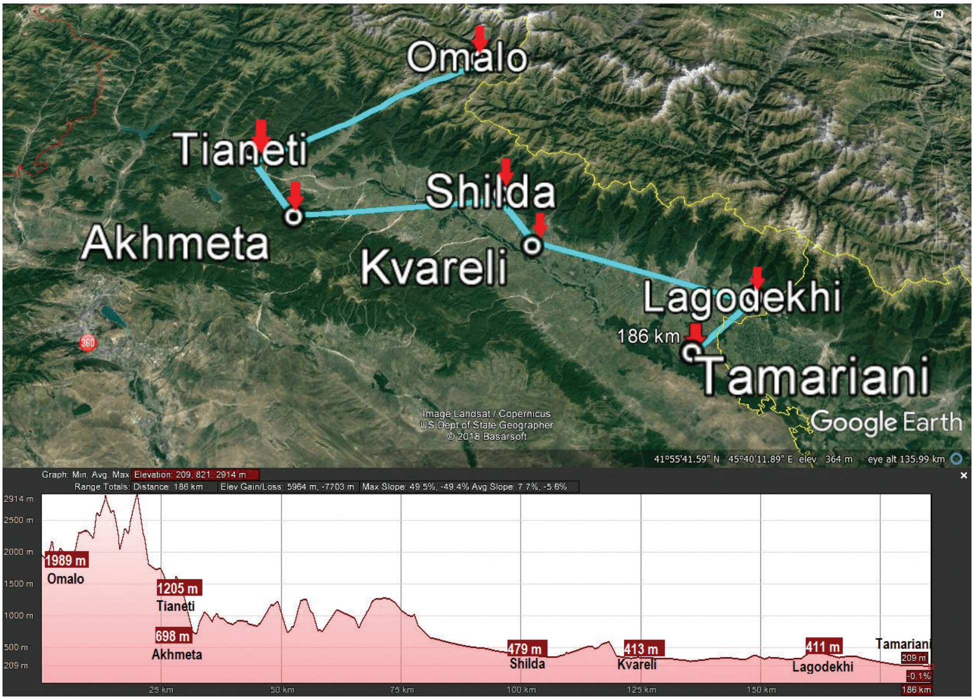

Figure 5. Map of eastern Georgia with its transect (light blue), Omalo – Tianeti – Akhmeta – Shilda – Kvareli – Lagodekhi – Tamariani, and its macro relief (bottom).

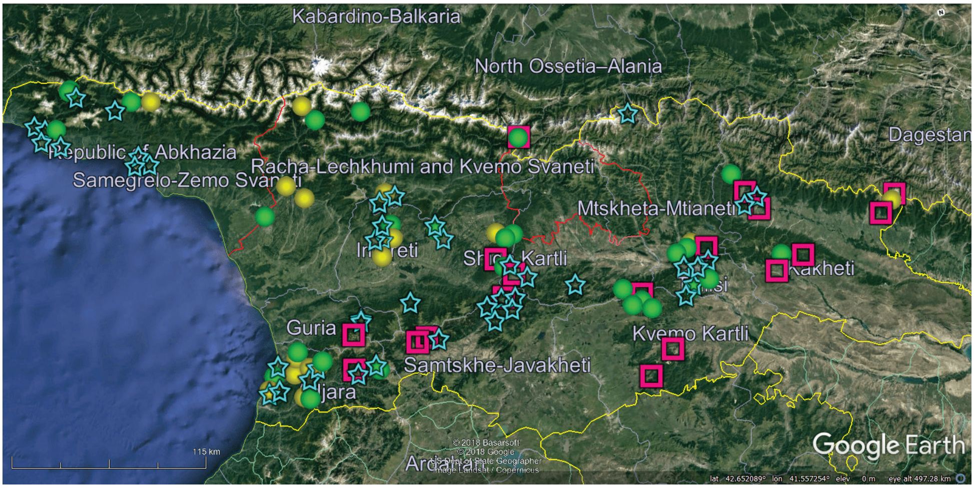

Figure 6. Map showing the distributions of four particularly widespread millipedes endemic or subendemic to Georgia. Designations: yellow ball (*Hirudisoma roseum*), green ball (*Chaetoleptophyllum flexum*), pink square (*Metamastigophorophyllon torsivum*), blue star (*Julus colchicus*).

Figure 7. Map of western Georgia (= Colchis) showing the distributions of some endemic or subendemic species. Designations: orange ball (*Hyleoglomeris awchasica*), red ball (*Nopoiulus golovatchi*), green triangle (*Cylindroiulus pterophylacum*), red ring (*Cylindroiulus ruber*), white ball (*Polydesmus abchasius*), blue ball (*Trachysphaera fragilis*), green star (*Trachysphaera radiosa*), pink ring (*Cylindroiulus schestoperovi*), yellow ring (*Hirudicryptus abchasicus*).

covered with mountain forests. In contrast, its lowland woodlands have largely been destroyed and long replaced by agri- or sylvicultures, as well as orchards and vineyards (https://apa.gov.ge/en/protected-areas/national-park).

Following Gulisashvili (1964) and Nakhutsrishvili (2013), the altitudinal nature zonation of Georgia can crudely be presented in a tabular form (Table 2). The zonation varies quite clearly in different parts of Georgia (Fig. 1) in relation to climatic gradients. Central Georgia (Figs 1, 4), which is climatically closer to the eastern part of the country, warrants recognition as a separate entity based at least on the distribution of several endemic or subendemic species of Diplopoda (Fig. 11).

No transects are contained in Figures 6–12 to avoid an "overcrowded" presentation of the numerous species distributions; however, these are easy to extrapolate from the figures and thus to follow the general trends and variations in the macro relief of the corresponding parts of Georgia. Only relatively few millipedes occur in subalpine to alpine environments (usually ≥ 2200 m a.s.l.) in Georgia (Table 2). Yet nearly none of them can be considered as being characteristic of the high altitudes, because the same species appear to populate lower elevations as well, down to almost sea-level: *Caucaseuma variabile* Antić & Makarov, 2016, *Dentatosoma magnum* Antić & Makarov, 2016,

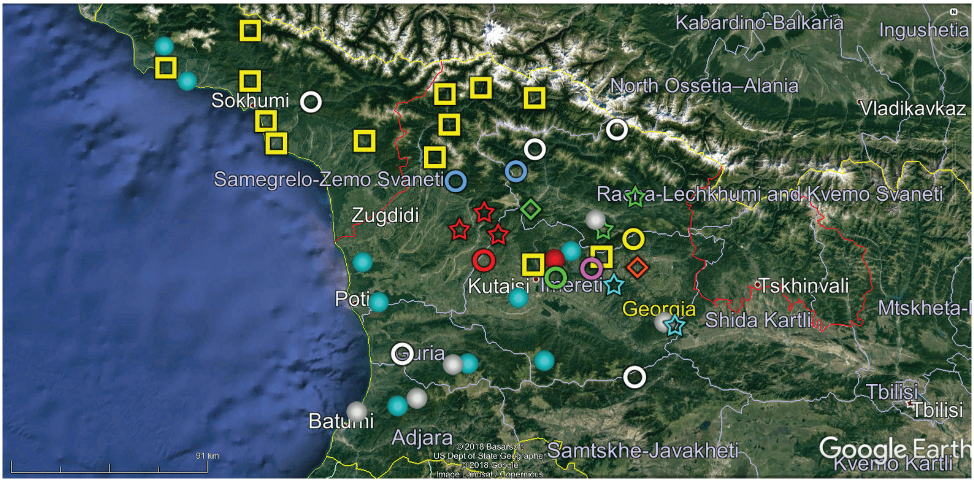

Figure 8. Map of western Georgia (= Colchis) showing the distributions of some other endemic or subendemic species. Designations: green diamond (*Georgiosoma bicornutum*), white ball (*Trachysphaera minuta*), orange diamond (*Trachysphaera orientalis*), red ball (*Trachysphaera solida*), red star (*Typhloglomeris palatovi*), red ring (*Paranotosoma cordatum*), blue star (*Cylindroiulus quadrus*), blue ball (*Cylindroiulus placidus*)**,** yellow square (*Pachyiulus krivolutskyi*), green star (*Acanthophorella barjadzei*), pink ring (*Metamastigophorophyllon lamellohirsutum*), blue ring (*Paranotosoma attemsi*), yellow ring (*Ratcheuma excorne*), white ring (*Nemasoma caucasicum*), green ring (*Leucogeorgia longipes*).

Metamastigophorophyllon hamatum Antić & Makarov, 2016, *Chaetoleptophyllum flexum* Golovatch, 1979, *Cylindroiulus placidus* (Lignau, 1903), *Strongylosoma kordylamythrum* Attems, 1898, *Brachydesmus assimilis* Lohmander, 1936, *B. kalischewskyi* Lignau, 1915, *Polydesmus abchasius* Attems, 1899 and *P. lignaui* Lohmander, 1936. The same concerns *Omobrachyiulus brachyurus* (Attems, 1899) and *Catamicrophyllum caucasicum* (Attems, 1901), both of which occur also at ≤ 2500 m a.s.l. in the Caucasus Minor of Armenia and Azerbaijan; the former species also in Dagestan, Russia, Caucasus Major (personal observations). *Nopoiulus kochii* (Gervais, 1847) is a subcosmpolitan species, common also throughout the Caucasus (10–2200 m a.s.l., Table 1), but because the entire genus *Nopoiulus* is particularly diverse in the Caucasus region, the latter could well have also been the origin centre of *N. kochii* (Golovatch and Enghoff 1990).

At the present, the only exception that may possibly be referred to as a high-montane element in the fauna of Georgia, as well as the entire Caucasus, seems to be *Alpinella waltheri* Antić & Makarov, 2016 (2860 m a.s.l., Table 1, Map 12). Even though some species of *Julus*, i.e., *Julus colchicus* Lohmander, 1936 (20–2850 m a.s.l.), *J. kubanus* Lohmander, 1936 (300–2100 m a.s.l.) and *J. lindholmi* Lohmander, 1936 (450–2200 m a.s.l., Table 1, Figs 9, 12), mostly occur over a wide range of altitudes, *J. lignaui* Verhoeff, 1910 (1500–2800 m a.s.l.) is perhaps the sole congener that seems to be inclined to dwelling in high-mountain environments. However, the paucity or even absence of unequivocally high-mountain elements in the Caucasus generally, and in Georgia in particular, requires confirmation, as our knowledge of the millipede fauna of the regions concerned is still far from complete.

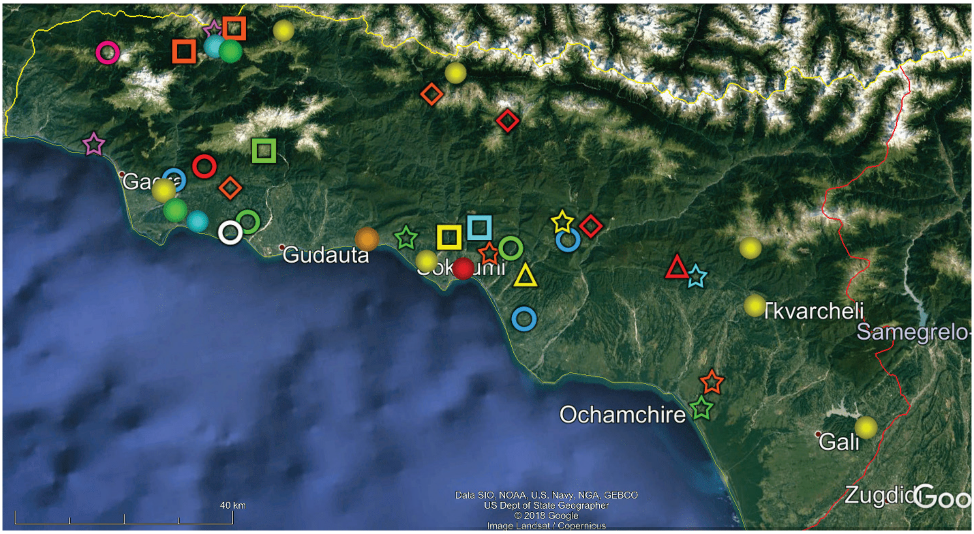

Figure 9. Map of Abkhazia showing the distributions of some endemic or subendemic species. Designations: red triangle (*Brachychaetosoma turbanovi*), blue square (*Caucaseuma kelasuri*), orange star (*Archileucogeorgia abchasica*), pink star (*Omobrachyiulus implicitus*), orange square (*Cylindroiulus olgainna*), blue ring (*Paranotosoma subrotundatum*), yellow star (*Julus lindholmi*), green star (*Leucogeorgia rediviva*), green ring (*Dentatosoma magnum*), pink ring (*Heterocaucaseuma deprofundum*), orange diamond (*Metamastigophorophyllon giljarovi*), white ring (*Kubaniulus gracilis*), blue star (*Metamastigophorophyllon hamatum*), red ring (*Pseudoflagellophorella mirabilis*), red diamond (*Megaphyllum dioscoriadis*), yellow square (*Nopoiulus brevipilosus*), yellow triangle (*Archileucogeorgia satunini*), orange ball (*Heterocaucaseuma longicorne*), red ball (*Omobrachyiulus hortensis*), blue ball (*Brachydesmus furcatus*), green ball (*Brachydesmus simplex*), yellow ball (*Polydesmus lignaui*), green square (*Heterocaucaseuma mauriesi*).

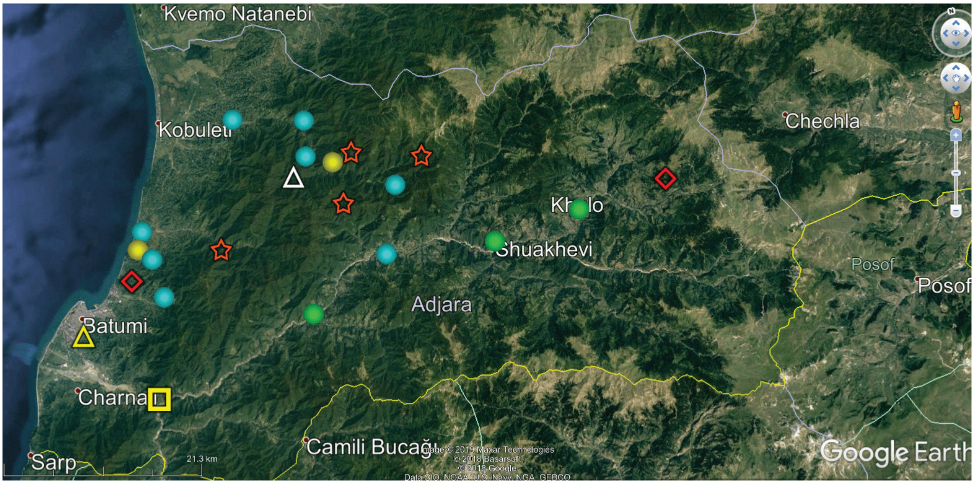

Figure 10. Map of Ajaria showing the distributions of some endemic or subendemic species. Designations: blue ball (*Adshardicus strasseri*), red diamond (*Brachydesmus kvavadzei*), green ball (*Dentatosoma denticulatum*), orange star (*Dentatosoma zeraboseli*), yellow square (*Omobrachyiulus adsharicus*), white triangle (*Omobrachyiulus divaricatus*), yellow ball (*Paranotosoma cordatum*), yellow triangle (*Syrioiulus adsharicus*).

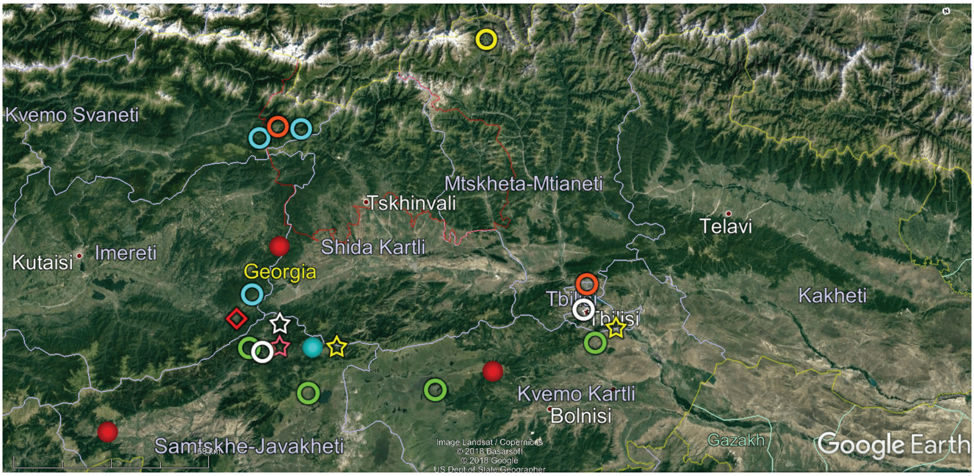

Figure 11. Map of central Georgia showing the distributions of some endemic or subendemic species. Designations: blue ring (*Brachydesmus kalischewskyi*), yellow ring (*Caucaseuma variable*), green Ring (*Catamicrophyllum caucasicum*), red ball (*Cylindroiulus crassiphylacum*), orange ring (*Cylindroiulus pterophylacum*), white ring (*Grusiniulus redikorzevi*), yellow ball (*Herculina oligosagittae*), blue ball (*Herculina polysagittae*), pink star (*Leptoiulus hastatus*), red diamond (*Metamastigophorophyllon martensi*), yellow star (*Omobrachyiulus macrourus* (= *O. m. abchasicus*)), white star (*Syrioiulus georgicus*).

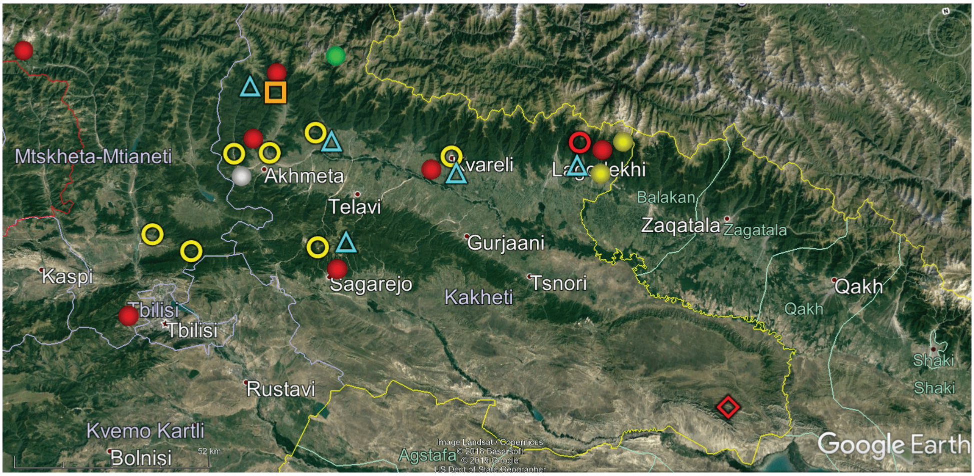

Figure 12. Map of eastern Georgia showing the distributions of some endemic or subendemic species. Designations: green ball (*Alpinella waltheri*), red ball (*Brachydesmus assimilis*), blue triangle (*Cylindroiulus kacheticus*), yellow ball (*Cylindroiulus parvus*), yellow ring (*Hyleoglomeris specialis*), orange square (*Julus kubanus*), red diamond (*Leptoiulus tanymorphus*), white ball (*Pseudoflagellophorella eskovi*), red ring (*Pseudoflagellophorella papilioformis*).

Conclusion

Ongoing research on the diplopod fauna of Georgia will undoubtedly reveal many more species and refine their distributions. This particularly concerns several genera of Julidae, including new cavernicolous and epigean ones (D. Antić, A. Evsyukov, B. Vagalinski, personal communications). As a result, the present paper must only be taken as provisional, marking the present state of the art and is certain to be updated in the near future.

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Conservation of terrestrial invertebrates: a review of IUCN and regional Red Lists for Myriapoda

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Abstract

Red Listing of Threatened species is recognized as the most objective approach for evaluating extinction risk of living organisms which can be applied at global or national scales. Invertebrates account for nearly 97% of all animals on the planet but are insufficiently represented in the IUCN Red Lists at both scales. To analyze the occurrence of species present in regional Red Lists, accounts of 48 different countries and regions all over the world were consulted and all data about myriapods (Myriapoda) ever assessed in Red Lists at any level assembled. Myriapod species assessments were found in eleven regional Red Lists; however, no overlap between the species included in the global IUCN Red List and the regional ones was established. This means that myriapod species considered threatened at regional level may not be eligible for international funding specific for protection of native threatened species (more than US$ 25 million were available in the last decade) as most financial instruments tend to support only threatened species included in the IUCN Red List. As the lack of financial resources may limit protection for species in risk of extinction, it is urgent to increase the possibilities of getting financial support for implementation of measures for their protection. A Red List of all Myriapoda species recorded in Red Lists at national or local (596) and global (210) scales totaling 806 species is presented. This list shows for the first time an overview of the current conservation status of Myriapoda species. Here, the urgent need of establishing a Myriapoda Specialist Group in the Species Survival Commission of IUCN is also stressed.

Keywords
Arthropoda, Chilopoda, Diplopoda, extinction, national red lists, Pauropoda, risk assessment, Symphyla, threatened species

Introduction

Biodiversity conservation is an applied science which involves several tools and approaches to avoid species extinction and protect environment as a whole. The approaches for conservation planning may vary in scale and extent (Pressey and Bottrill 2009), but they need to rely on rigorous evidence on species and ecosystems involved (Cook et al. 2010). Specifically, evidence-based wildlife management requires reliable information on the conservation status and the extinction risk of species (Charra and Sarasa 2018).

The most widely recognized assessment of the conservation status of species is the Red List of Threatened Species, established by the International Union for Conservation of Nature (IUCN) in 1964 (Charra and Sarasa 2018). Since then, IUCN has been developing and updating a global list of threatened species and a methodology for species assessments. The organization has also been investing efforts in expanding its taxonomic expertise. The IUCN Red List of Threatened Species plays an important role of a global database of the conservation status of various organism groups (IUCN 2019a).

In the past decades, several countries have elaborated own lists of threatened species, often based on IUCN guidelines for species assessments (IUCN 2012; IUCN 2019b). The national and regional lists are essential for the implementation of local conservation actions, where policy is often implemented (IUCN 2019a). They also supply national governing bodies with information of both scientific and political relevance regarding the state of biodiversity, and as such could be a valuable resource for conservation planning (Zamin et al. 2010). Red Lists that focus on specific areas are of particular importance in aiding national reporting to international conventions with specific biodiversity targets, such as the Convention on Biological Diversity and the Sustainable Development Goals (IUCN 2019a). Furthermore, the information from local species assessments is important for developing species and ecosystem-based strategies for climate change adaptation (Zamin et al. 2010).

To meet the needs of the scholars, some scientific journals have developed specific publication types compliant with the IUCN Red List species assessments (Cardoso et al. 2016). Among the invertebrate experts, arachnological community is especially active in publishing species assessments at various scales in the form of academic papers (Seppälä et al. 2018, Branco et al. 2019, Fukushima et al. 2019). Similar surveys have recently been published for moths, cave-dwelling arthropods (Borges et al. 2018, 2019) and an endangered species of rattan palm from Africa (Cosiaux et al. 2017) to name a few. Specific software has also been developed to ease the species assessments (Cardoso 2017).

The IUCN global species conservation assessments are based on objective criteria which classify taxa into nine clearly defined categories (Fig. 1). Of them, three

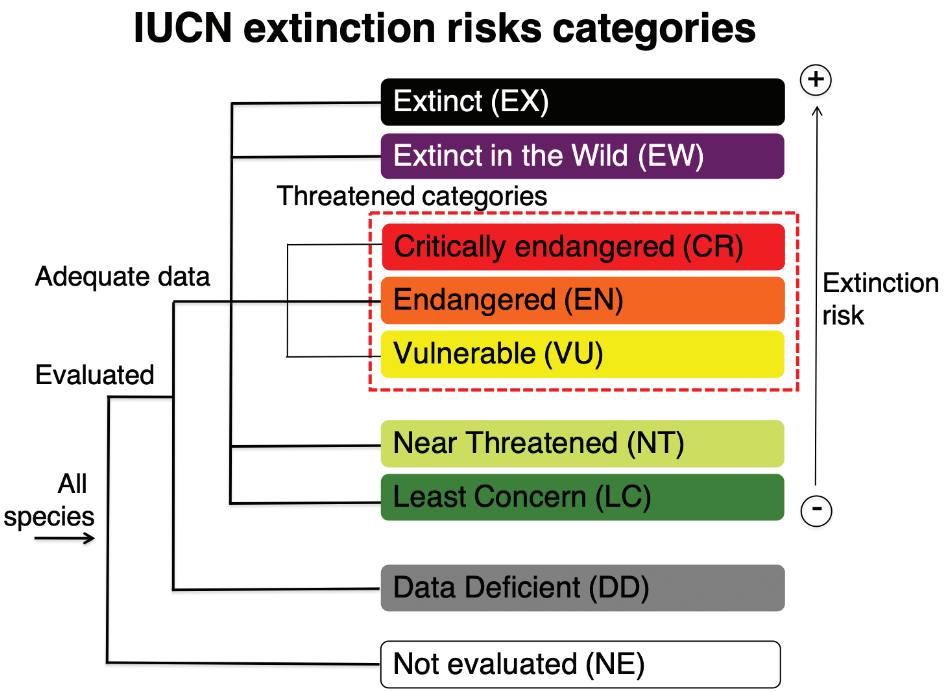

Figure 1. IUCN extinction risks categories for global assessments. Threatened categories are within dashed red line. (Modified from IUCN 2019).

categories concern species with higher extinction risk: Critically Endangered (CR), Endangered (EN), and Vulnerable (VU). The other categories refer to Extinct (EX) or Extinct in the Wild (EW) species; species that are close to become threatened (Near Threatened – NT); species that do not qualify for threatened nor NT categories (Least Concern – LC); species without sufficient data available for assessment (Data Deficient – DD); and Not Evaluated species (NE). At smaller scale, two other categories are being introduced: Regionally Extinct (RE), for species extinct in the wild within the respective region, and Not Applicable (NA), for species that do not qualify for assessment at a regional level (i.e., introduced taxa).

Until 2019, IUCN Red List had already assessed 71% of vertebrate species, 11% of plant species, and 2% of invertebrate species in the world (IUCN 2019a). In latest IUCN report (2019a) 49% of the species considered as threatened are animals and 51% are plants (fungi account for less than 1%). Among threatened fauna, 63% are vertebrates and 37% are invertebrates. The species groups covered by the IUCN Red List are biased towards terrestrial and in particular forest ecosystems (IUCN 2019a). Estimated to represent around 97% of all animals on the planet, invertebrates are the least conservational explored group and currently form only 31% of all animal assessments in the Red List (IUCN 2019a). There is a taxonomic bias in IUCN Red List that excludes species with small body sizes, narrow distribution ranges and low dispersal abilities, which constitute the vast majority of the planet's biota, particularly local endemics (Cardoso et al. 2011). At national level, invertebrates are also among the least represented as regards the taxonomic coverage (Zamin et al. 2010). The low number of experts working with the group and, consequently, the lack of data on historic population and distribution trends may help to explain the taxonomic bias towards the invertebrates in Red Lists.

Myriapoda is a group of terrestrial arthropods of high ecological importance. It comprises four, well defined classes: Diplopoda (millipedes), Chilopoda (centipedes), Symphyla (symphylans), and Pauropoda (pauropodans). As top invertebrate predators, centipedes drive ecosystem function, for example, by regulating decomposer populations (Phillips et al. 2019). Millipedes are important ecosystems decomposers, as their impact on fragmenting leaf litter increases surface area for microbial processing and, consequently, soil development and mineralization of nutrients for plant growth (Snyder and Hendrix 2008). The other two classes are less diverse and while symphylans could be pests, especially by eating seeds and roots of young crops, pauropodans are of little agricultural importance. In contrast to many other Arthropoda, myriapods show a very low tendency to disperse, which results in high species endemism (Voigtländer et al. 2011). The current version of IUCN Red List (2019a) comprises 210 myriapods assessments (200 millipede species and 10 centipede species), which represents only 1% of all described species (circa 17 000 species; Sierwald and Spelda 2019). Among assessed species, 44% are listed in categories of higher threat and 16% are considered Data Deficient (IUCN 2019a). However, the actual number of threatened species for any group is often uncertain because it is not known whether Data Deficient species are actually threatened or not.

Several countries have assessed and listed myriapod species in their own national or regional census (Gärdenfors 2010; MMA 2014; Henriksen and Hilmo 2015). Although regional lists are essential for presenting evidences for local conservation decisions and therefore must be presented primarily in local language, they are often published in obscure outlets or exclusively in local languages, which makes their finding and comprehension difficult for a meta-analysis. In general, when pertinent information on biological diversity is too sparse or scattered it may not to be of practical use for a global scale analysis. In such cases the information needs to be gathered through systematic efforts to strengthen the entire research process (National Research Council 1992). The IUCN Red List accepts only global level assessments, but regional evaluations can also be included if they refer to single-country endemics for instance and the applied assessment process follows strictly the IUCN guidelines. As a whole, local red lists are not taken into consideration by the global database of IUCN. For instance, myriapod endemic species listed in the Brazilian Red List are not included in IUCN global database (Karam-Gemael et al. 2018a). Since Brazil's list was elaborated under the IUCN guidelines, why the endemic species assessed are not included in the IUCN Red List? There is no mechanism that IUCN SSC evaluate already existing national or regional Red Lists or at least this seem not to be in the agendas of the expert groups.

The addition of endemic species assessed regionally in the IUCN Red List has two major applications and benefits. On one hand, it would expand the taxonomic coverage of a given organism group, thus having direct implications for the species management both at local and global levels. On the other hand, it also allows endemic threatened species to be eligible for international funding (Karam-Gemael et al. 2018a). There are several specific funding schemas for conservation of threatened species listed by IUCN. Increasing the possibility of getting financial support for applied research and conservation measures is especially important as naturally this is an integral limitation for species in risk of extinction (Zamin et al. 2010). This may be particularly true for terrestrial invertebrates which are usually of lower conservation priority. The invertebrate protection usually concerns the conservation of habitats, and thus the whole community occurring in a given habitat could benefit the measures. Attracting funds for “umbrella species” which some invertebrate species could be, would mean to invest in the protection of the habitat as a whole for the benefit of other threatened taxa. In Brazil alone, the occurrence of the threatened endemic velvet worm *Epiperipatus acacioi* (Marcus & Marcus, 1955) in Minas Gerais (Brazil) justified the creation of the first Ecological Station in the state (ESEC Tripuí), a very restrictive category of federal protected area according to the Brazilian legislation (FEAM 1995). Another similar case in Brazil is a protected area created for dragonflies (RVS Libélulas da Serra de São José; Diário do Executivo 2004). Having a mechanism for getting species assessed at regional/national/local scale on the IUCN Red List would boost such surveys.

The main aim of the present study is to analyze the congruence between the invertebrate species assessed in regional Red Lists against the IUCN Red List, using Myriapoda as a case study.

Materials and methods

We have assembled a global list of Myriapoda species in Red Lists irrespective of their scale. For data collection, we conducted a global survey for national/regional lists between May and July 2019. First, we searched for Myriapoda species in the Red Lists available at the National Red List website database (Zoological Society of London 2019). We also used the snowball sampling method to obtain a sample of eligible countries from different continents. This method helps to increase the diversity of sampling (Rossi et al. 2004), but its limitations prevent the estimation of how representative a sample is (Walsh et al. 2015). Once we found an eligible Regional Red List, we looked for Myriapoda species assessed. From each list we collected the species name, extinction risk category, language of publication, and the methodology used for assessment (based on IUCN guidelines or not). To avoid missing regional Red Lists with Myriapoda species listed due to the limitation of snowball sampling, we carried out an online survey asking the experts associated to the International Society for Myriapodology if their country/region had ever assessed myriapod species in their Red Lists. Finally, for IUCN Red List data we performed an advanced search at its website and then downloaded all myriapods assessments in an Excel spreadsheet with all species assessed and its extinction risk categories (version 2019-2).

For data analysis, we joined data from all regional Red Lists where myriapod species were found and the results from the IUCN Red List search to create a unique database with all the species names of Myriapoda assessed, the current valid taxon name, its extinction risk categories according to IUCN, the original category (if differing to IUCN), methodology used and the (literature) source of the data. We then analyzed: a) which species from the IUCN Red List were also present in regional Red Lists (congruence among the lists); b) which species are represented in more than one Regional Red List; c) the proportion of each extinction risk category; d) correlations between: growth in GDP (World Bank 2019), protected areas network coverage (World Bank 2019), deforestation rate (Mongabay 2019), CO2 emission rates (World Bank 2019) for each country included as well as the proportion of threatened species recorded for that country; e) which species are endemic; we considered endemic a species occurring only in the country where it is listed. Taxonomic and geographic data for most species were gathered from the taxonomic online catalogues Millibase (Sierwald and Spelda 2019) and Chilobase (Bonato et al. 2016).

The German Red List uses some additional refined categories which have no analogue in the IUCN Red List. The categories “extreme rare species with geographic restriction” (R) and “threat of unknown extant” (G), which are situated between the IUCN “near threatened” (NT) and “vulnerable” (VU) are translated according to Ludwig et al. (2009) to NT for the former and VU for the latter. In the Slovenian Red List, the categories “rare species” (R) and “undetermined species” (I) were translated with IUCN NT, and the category “unknown species” (K) with data deficient (DD).

Results

We consulted regional Red Lists of 48 countries from: South America (12), Europe (19), Africa (3), Asia (7), North America (3), Central America (3), and Oceania (1) (Fig. 2). We found Myriapoda species assessments in 23% of them (Table 1).

The survey resulted in assembling a spreadsheet comprising 596 taxa assessed in regional lists. On the other hand, the IUCN Red List of Threatened Species records 210 species of Myriapoda. There are no species in common between the local lists and the global one, therefore, there is no congruence among the lists analyzed at species level (Table 2).

A global list with all myriapod assessments is presented in Suppl. material 1. It considers both the species present in regional Red Lists and in the IUCN Global Red List, and totals 806 species belonging to the four Myriapoda classes: Diplopoda (81%), Chilopoda (16%), Pauropoda (2%), and Symphyla (1%). Among the Diplopoda, species from 13 orders (out of 16 worldwide) have been assessed, of which Polydesmida (27%) and Spirobolida (16%) are the most assessed orders. Among Chilopoda, species from four (out of five) orders have been assessed: Lithobiomorpha (46%), Geophilomorpha (41%), Scolopendromorpha (11%), and Scutigeromorpha (2%). Only the order Craterostigmomorpha, which is restricted to Tasmania and New Zealand, was not assessed.

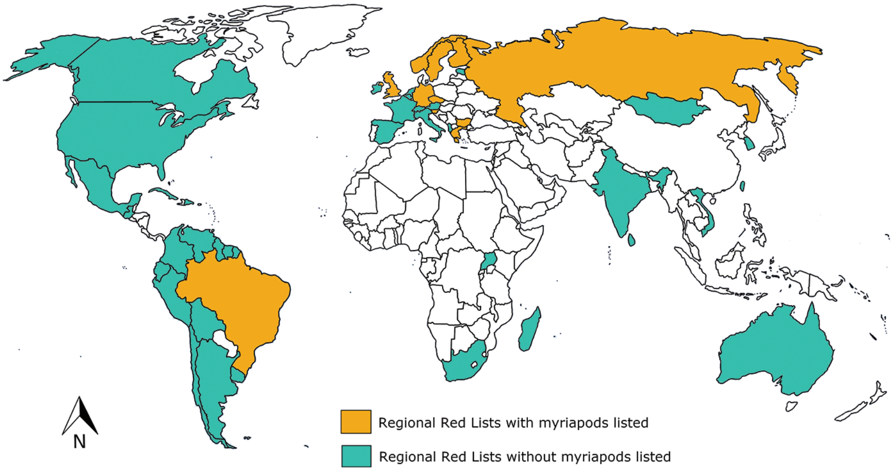

Figure 2. Countries included in this study. In orange, countries consulted that have their own local lists and myriapods are listed: Brazil, Bulgaria, Czech Republic, Finland, Germany, Greece, Norway, Slovenia, Russia, Sweden, UK. In green, countries consulted that have their own local lists, but there are not myriapods listed: Albania, Argentina, Australia, Austria, Belgium, Bolivia, Canada, Chile, Colombia, Cuba, Dominican Republic, Ecuador, Estonia, France, French Guiana, Guatemala, Guiana, India, Italy, Ireland, Mexico, Madagascar, Mongolia, Netherlands, Peru, Republic of Korea, South Africa, Spain, Sri Lanka, Suriname, Switzerland, Taiwan, Uganda, Uruguay, USA, Venezuela, Vietnam.

Table 1. National/regional Red Lists with Myriapoda species assessments included in this study. Documents are presented in order of publication year. Complete literature information of each one is given in Suppl. material 1.

Country	Region	Year	References
Brazil		2003, 2014	MMA (2003), MMA (2014)
Bulgaria		2011	Golemansky (2011)
Czech Rep.		2005, 2017	Kocourek (2005), Hejda et al. (2017)
Finland		2019	Hyvärinen et al. (2019)
Germany		2016	Decker et al. (2016), Reip et al. (2016)
	Baden-Württemberg	1998	Spelda (1998)
	Bavaria	2004	Spelda (2004)
	Saxony-Anhalt	2004; in press	Voigtländer (2004a), Voigtländer (2004b), Lindner et al. (in press), Voigtländer et al. (in press)
Greece		2009	Legakis and Maragos (2009)
Norway		2006, 2010, 2015	Djursvoll and Meidell (2006), Dursvoll (2010), Henriksen and Hilmo (2015)
Russia	Altai	2016	Altai University (2016)
	Republic of Komi	2019	The Red Data Book of the Rep. of Komi (2019)
	Sevastopol	2019	The Red Data Book of Sevastopol (2019)
	Tver Area	2016	The Red Data Book of the Tver Area (2016)
Slovenia		1992, 2002	Kos (1992), Mrsic (1992), Official Gazette of RS No. 82/2002 (2002a/b)
Sweden		2010	Gärdenfors (2010)
Great Britain		2015	Natural England (2015)

Table 2. Diversity of Myriapoda in the worldwide Red List of threatened species presented here. Includes data from IUCN Red List (2019) and from Regional Red Lists from eleven countries compiled for this study (for countries included see Fig. 2).

Class	Taxonomic level	IUCN Red List	Regional Red Lists	Shared taxa
Diplopoda	Families	12	50	4
	Genera	35	207	0
	Species	200	654	0
Chilopoda	Families	5	13	4
	Genera	5	32	0
	Species	10	130	0
Pauropoda	Families	0	1	0
	Genera	0	6	0
	Species	0	14	0
Symphyla	Families	0	2	0
	Genera	0	4	0
	Species	0	8	0

Although the number of species assessed is 806, the total of assessments found is 1289, due to: a) species assessed in two, three or four countries; b) species reassessed in the same country; and c) species listed in NE (Not Evaluated) and NA (Not Applicable) categories in Germany's and Norway´s list (even not being assessments itself, species listed in these categories are included in the list).

Among all myriapods assessed (local lists and IUCN Red List), 24% are considered as threatened (Critically Endangered (CR), Endangered (EN) or Vulnerable (VU)). According to the assessments three species are considered extinct. Species assessed as Data Deficient account for 19% (Fig. 3). A significant number of myriapods classified as Least Concern (LC) (32%; Fig. 3) comes from the regional Red Lists analyzed (91%), rather than from the IUCN Red List (9%). Brazil and Germany are responsible for 80% of all species assessed as LC. Among the species assessed only by regional lists, 36% are in threatened categories (CR, EN, VU; Table 3). Brazil and Germany are the countries with more myriapods assessed.

The proportion of threatened myriapod species in the regional Red Lists analyzed was significantly and positively correlated with the growth in GDP from the countries included (r-value = 0.71) (those countries which have assessed Myriapoda in their national Red Lists; see the list in Fig. 2). Correlations between threatened species and: protected areas network coverage (r-value = 0.84), deforestation rate (r-value = 0.02), and CO2 emissions (r-value = 0.05) were also all positive.

Among the eleven countries, eight applied the IUCN methodology for the assessments. Russia and Slovenia applied their own methodology, but former used methodology corresponding to the categories of IUCN. Slovenia's methodology is also based on equivalent categories. The methodology used by Germany is a modified IUCN version. Among the Red Lists of eleven countries with myriapods assessed, 54% were published only in the native language of the country, with no English version or abstract available.

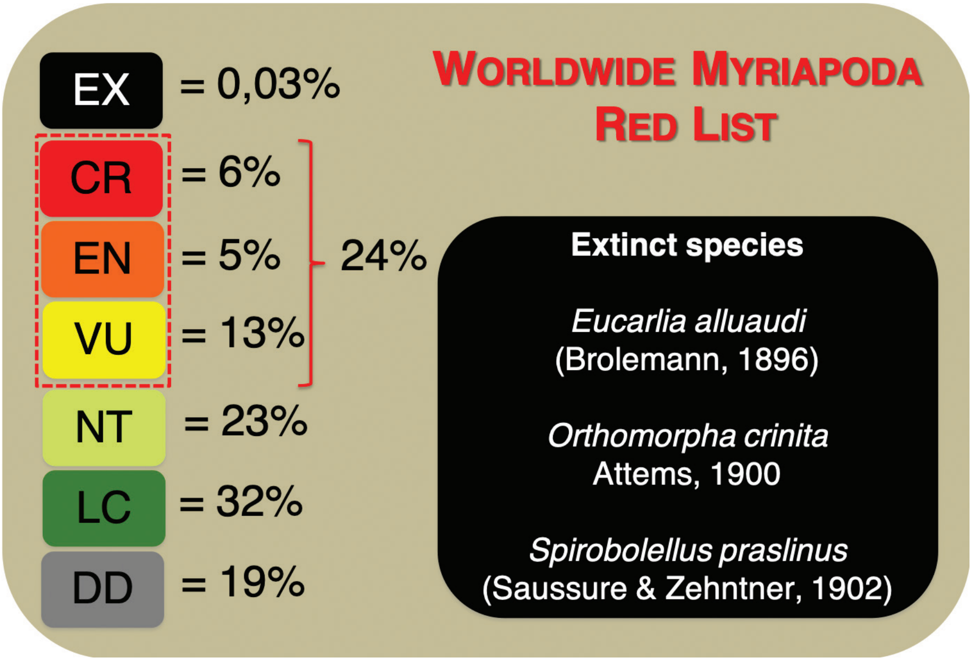

Figure 3. Proportion of extinction risk categories of the Worldwide Myriapoda Red List presented here. Includes data from regional Red Lists from eleven countries and from IUCN Red List of Threatened Species. Threatened categories are within dashed red lines.

Table 3. Total of Myriapoda assessments per country per extinction risk category. The column Total threatened species sums up the CR, EN, and VU categories. Table is sorted according to Total Threatened Species in decreasing order. Brazil's assessments include data from the 2014 Red List plus the troglobitic species assessed in 2018 but not published yet.

Country	EX	CR	EN	VU	NT	LC	DD	NA	NE	Total threatened species	Total assessments
Slovenia		4		86	117		17			90	224
Germany		4	13	11	85	207	51		3	28	374
Czech Republic		5	2	25	15		9			32	56
Brazil		11	9	12	1	119	98			32	250
Russia		2	1	8						11	11
Bulgaria		4								4	4
Greece		3	1							4	4
UK			2	2	6		9			4	19
Sweden		1		2	6		6			3	15
Norway			1	6	18	49	17	11	10	7	112
Finland		1			3		6			1	10
IUCN	**3**	**37**	**37**	**19**	**42**	**35**	**37**			**93**	**210**
Total	3	72	66	171	293	410	250	11	13	309	1289

Discussion

The analysis of similarity of regional Red Lists and the IUCN Red List for myriapods showed that endemic species already assessed at national/local level have not been included in IUCN global database. Also, there is no congruence on species level between regional lists and the IUCN Red List for myriapods. The data presented here increase the awareness about the dissimilarity between regional Red Lists and the IUCN Red List, as it corroborates the results found for Brazilian myriapods (Karam-Gemael et al. 2018a).

Two main points arise from the incongruity between regional Red Lists and IUCN Red List found here. Firstly, Myriapoda seem to be largely neglected by the terrestrial invertebrate censuses of IUCN, which may be true also for other arthropod groups. Another reason probably is that only very few specialists working on Myriapoda worldwide. Then, the few species specialists existing have the responsibility to work on regional and/or global assessments, even if they only assess members of their scope taxa. Besides that, it is also relevant to consider that the scientific evidences presented in regional lists are scattered in several documents with different formats and languages worldwide. Of course, regional Red Lists should be presented primarily to the national politics, decision makers and NGOs without any language burdens and in official governmental publication. However, in Germany, for example, the nationwide Red List experts have put pressure on the responsible federal office so that an English abstract will be available in the next version of the German Red Lists and the publication will now also be freely available as a PDF. Easy access and English language will help to integrate data resources and to abroad IUCN Red List coverage. As IUCN list works as an objective indicator of the health of the world's biodiversity showing which wild species are threatened, one of its urgent targets is to fund the assessment of taxa not yet well represented on The IUCN Red List (IUCN 2019a). The worldwide list presented here can help to partially fill in IUCN Red List gap in invertebrate's coverage, as current version of IUCN Red List presents only 1% of known myriapods, and the total number of worldwide assessed species (806) presented here represents 5% of all species known for the group. This will help expand coverage to a more representative subset of the planet's biodiversity.

In fact, it is expected that taxonomic groups not represented among the IUCN Specialists Groups will receive less attention and consequently will be less represented in the IUCN Red List. Currently there are 13 terrestrial invertebrates Specialists Groups, besides Cave Invertebrate, South Asian Invertebrate, Terrestrial and Freshwater Invertebrate, and Mid Atlantic Islands Invertebrate groups (IUCN 2019a). When submitted for evaluation to IUCN, myriapod species assessments would be handled by one of the groups focused on invertebrate mentioned above. Otherwise, the assessments are forwarded to the Invertebrate Sub-Committee. The Species Survival Commission Specialist Groups are considered the Red List Authorities (RLA) for the species in their remit within IUCN (IUCN 2019a). Among the responsibilities of RLA specific for taxonomic groups are establishing mechanisms for assessing and regularly reassessing species, undertaking assessments at the global level. Considering the diversity of terrestrial invertebrates and their poor representation in the IUCN Red List, it is strongly recommended the designation of more invertebrate specialist groups, and in particular Myriapoda Specialist Group.

The second main point that arises from the incongruity between the lists is that endemic myriapod species assessed as threatened in regional Red Lists that followed IUCN guidelines are currently not eligible for international funding. Most international funding organizations support conservation activities only directed to IUCN listed threatened species. Among 596 Myriapoda species compiled from regional Red Lists, 36% are assessed in threatened categories (CR, EN, and VU). It means that these species could be eligible for international funding if they were also listed by IUCN. In the last decade, international biodiversity conservation organizations directed more than US$ 25 million specifically to fund projects with species assessed as threatened by IUCN Red List (Karam-Gemael et al. 2018a). Considering the significant taxonomic gap for invertebrates in IUCN Red List, it is likely that a large amount of species of other invertebrate groups may also be find in threatened categories in regional lists but are missing in the IUCN Red List. Then, the scenario discussed here may be helpful when discussing terrestrial invertebrate's conservation in general.

Brazil and Germany are together responsible for 80% of all species currently assessed as Least Concern (LC) in the worldwide list of Myriapoda presented here. The category is applied to taxa that do not qualify as Threatened or Near Threatened. However, it is important to emphasize that "least concern" simply means that, in terms of extinction risk, these species are of lesser concern than species in other threat categories. It does not imply that these species are of no conservation concern (IUCN 2019b). According to IUCN criteria, species known only from the type locality may be classified as LC if the area is relatively well known and there are no plausible threats. However, it also could be a product of insufficient data about the species or the area where it occurs. Then, similarly to Data Deficient species (which may hide threatened species in function of no information about them), species assessed as LC may be considered as threatened in a near future when more information about the group or the area is brought up.

More than half of the lists where we found myriapods assessments were published in the native language of the country only, with no English version. This is an important barrier to biodiversity conservation and science in general, which has English as its universal language. We have also found several different formats of publishing the data. Although some countries (Russia, Slovenia, and Germany) apply similar categorization, no IUCN standardized protocols for assessments were used. It means that data from these countries' red lists may be informative and sufficient for inform local management needs, but cannot be linked to or incorporated in the IUCN Red List. Therefore, using different methodologies to assess species extinction risks does not allow comparability and no sharing of information between lists, because including species assessed locally in IUCN Red List demands that assessments followed IUCN guidelines strictly. IUCN categories and criteria have a history of versions throughout the decades, as it has been revised under extensive consultation processes and workshops in several occasions (IUCN/UNEP et al. 1987, Mace and Lande 1991, IUCN 2001, IUCN 2003, IUCN 2019b). Hence, it is important to keep in mind that even IUCN Red Lists are not really 100% comparable and regional Red Lists according to the IUCN need to be carefully checked about which version and if modified differences need to be mentioned. And even when assessments follow the same methodology, the publication format may vary in: the associated data included; the arrangement of presenting species (by taxonomic group or by assessed category); the format itself (a downloadable PDF, listed in a webpage or not available online). Altogether, these publications variations and the native language were very time consuming to overcome when gathering data. When science data is freely and easily available (in English, gathered and standardized, with online open access) it creates new opportunities for integrating data between research projects and analyzing data in additional ways. The long-term availability of data is especially important in conservation science because field data can be costly to collect. In addition, historic data, especially on threatened species and their associated biota, become more valuable over time (Costello and Wieczorek 2014).

Although it may seem illogical, the countries with higher number of threatened myriapods are also those with bigger proportion of protected areas (PAs). This is also supported by the notion that PAs are not designed to really make a difference in conservation (Pressey et al. 2015). The reasons for this discrepancy could be that those countries are more sensitized about habitat loss and spend more money on biodiversity surveys and/or have better research infrastructure to assess endangerment of habitats and taxa. Likewise, in Brazil alone, current PAs network fails to protect the majority of endemic species as demonstrated by vertebrates, arthropods, and angiosperms (Oliveira et al. 2017). On the other hand, it was expected that correlations among myriapods threatened species and deforestation and CO_2 emissions rates would be positive, as deforestation accurately predicts threat to endemic species (Brooks et al. 1999). Similarly, GDP growth is also higher where there are the majority of threatened species. In fact, it is expected that emerging economies present a high number of threatened species, as they are in general in tropical areas with high endemism levels and facing the pressure of human population growth, intense urbanization processes and increase area of intensive land use.

Connecting regional Red Lists

Analyzing several regional Red Lists showed that it may turn out being isolated from other local lists, even when considering neighboring countries. In continents like Europe, for example, Red Lists of countries with low (or no) endemism may assess the same population of a given species considering data and threats specific for its area, but missing information that impacts the same population from its neighboring countries.

Our results show that some species were classified in different categories in neighboring countries. For example, the millipede *Leptoiulus cibdellus* (Chamberlin, 1921) is assessed as Least Concern (LC) in Germany (Reip et al. 2016), as Endangered (EN) in the federal state Saxony-Anhalt in Germany (Voigtländer et al. in press), and Vulnerable (VU) in the Czech Republic (Hejda et al. 2017). Considering that Germany and Czech Republic share a border, it is possible that both countries assessed the same population simultaneously. Therefore, local conservation management may need to broaden the targets of actions and programs to a regional level, as interactions among sub-units should be carefully considered when planning conservation actions (IUCN 2019b). It is also interesting to note the different threats operating in each country, as the threats also impact conservation status assessments. Although the IUCN methodology and criteria may be applied at any geographical scale (considering the guidelines for regional assessments), application within very restricted geographical areas is strongly discouraged by IUCN (IUCN 2012). In a small region, a wide-ranging taxon will frequently exchange individuals with neighboring regions, leading to unreliable assessments (IUCN 2012). Then, expanding the geographic range of the assessment brings a broader overview of the group and may be a stronger evidence to inform conservation decision, even in local, regional or global scales. It means that local assessments should always be interpreted alongside other available assessments in the region/continent.

It is necessary and important to reassess species every five to ten years, as risk of extinction may change due to increase of data (e.g., distribution, ecology), change in land use or habitat size. Such case can be illustrated in the case of *Thalassisobates littoralis* (Silvestri, 1903) on the Red List of Norway. In 2006 it was assessed as Vulnerable (VU), 2010 as Near Threatened (NT) and 2015 as Endangered (EN) (Djursvoll 2006, Djursvoll and Meidell 2010, Henriksen and Hilmo 2015).

Connecting regional and global Red Lists

Both local and global lists are essential for informing evidence-based conservation management. Joined, they can lead to new possibilities to work with threatened species, including increasing financial resources. But who is responsible for connecting local and global lists?

Scientists working with endemic species could take their part in this task, as they are often those who participate of species assessments in regional/national level. Scientists are (or should be) aware that including species in Red Lists may help to approximate evidence-based science to practice, once Red Lists assessments are based on evidences and also that threatened species may inform the process of priority setting for conservation management (see next section). Research groups working with endemic species (usually coordinated by scientists) would be directly impacted with the potential raise in projects funding. Then, we suggest two ways that scientists could contribute with the connection between local and global lists. First, scientists could collectively demand from the environmental agency in charge of the national lists workshops in a given country that the final assessments files are translated into English for publication in the IUCN Red List. In general, the communication between academia and environmental managers is poor and conservation decisions often lack scientific evidences (Karam-Gemael et al. 2018b). Then, this would be an opportunity of narrowing the flow of demands and information between science and practice. Second, scientists could help to improve taxonomic gaps in IUCN List by including the assessment of the species they are working with in their research projects. When it is not a large amount of species, the assessment process and its preparation in the standardized IUCN assessment file may not be a huge task. Also, scientists working with ecology and biodiversity conservation usually are familiar with the literature, the language and the methods applied in the assessment process.

IUCN welcomes Red Lists assessments of endemic species resulting from projects carried out by academia and from national Red List initiatives. The process for submitting data is formalized and follows several steps of revisions, data validation and final checks by IUCN staff before publication in the IUCN Red List. The "Guidelines for application of IUCN Red List criteria at regional and national levels" is available online in several different languages. It allows for experts working with endemic species include the assessment of its targeted species in their projects. Adding more species assessments in the IUCN Red List would result in increasing: 1) taxonomic coverage of the group knowledge; 2) coverage of the global list; 3) funding opportunities; 4) scientific evidences for conservation science.

Besides scientists, the governments and institutions supporting national Red Lists initiatives could also take their part on helping to connect local and global lists. When planning national assessments workshops, they could include in the project budget the translation of the files and the supporting information to English.

It is important to notice that the connection between Red Lists (among Regional lists and between Regional and IUCN Red List) based on IUCN methodology depends on using the same updated methodology and standards when analyzing and publishing data. It helps to ensure that local lists are comparable and promotes the sharing of species information between neighboring countries. Using a comparable methodology also allows an easier flow of information between the regional and global levels. A regional approach to identifying threatened species complements the global Red List and provides information at an appropriate scale for international conservation treaties (for example, the Bern Convention) and legislation (e.g., the EU Habitats Directive) that have a regional focus (IUCN 2019a).

Priority for conservation action

Although the species listed in threatened categories may be those for which the risk of extinction is higher, it is essential to point out that assessment of extinction risk and the process of setting conservation priorities are related but different processes. The extinction risk assessment shows the likelihood of extinction of the taxon, and as such it is part of the process of setting conservation priorities, but alone it is not sufficient to determine conservation priorities. Setting conservation priorities should also takes into account other factors rather than the extinction risk, such as ecological traits, economic and cultural values, the probability of success of conservation actions, availability of funds and specialists to carry out the actions, legal context for conservation of threatened species (IUCN 2012).

Especially when considering regional/national/local assessments for non-endemic species, priorities setting should also take into account not only conditions within the region but also the status and population size of the taxon at the global level. Then, IUCN recommends that the publication of regional assessments of non-endemic taxa should include the global assessment and the proportion of the global population occurring within the region (IUCN 2012).

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Supplementary material 1

Worlwide Myriapoda assessments

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