

**Proceedings of the  
17th International Congress  
of Myriapodology, Krabi, Thailand**

*Edited by*

Pavel Stoev, Gregory D. Edgecombe

ZooKeys 741 (SPECIAL ISSUE)

PROCEEDINGS OF THE 17TH INTERNATIONAL CONGRESS OF MYRIAPODOLOGY, KRABI, THAILAND

*Edited by* Pavel Stoev, Gregory D. Edgecombe

First published 2018

ISBN 978-954-642-919-3 (paperback)

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[www.pensoft.net](http://www.pensoft.net)

Printed in Bulgaria, March 2018



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# Proceedings of the 17<sup>th</sup> International Congress of Myriapodology, Krabi, Thailand

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Received 21 February 2018 | Accepted 21 February 2018 | Published 7 March 2018

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<http://zoobank.org/053B1791-9A17-42A9-A327-393ABBDf1005>

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**Citation:** Stoev P, Edgecombe GD (2018) Proceedings of the 17<sup>th</sup> International Congress of Myriapodology, Krabi, Thailand. In: Stoev P, Edgecombe GD (Eds) Proceedings of the 17<sup>th</sup> International Congress of Myriapodology, Krabi, Thailand. ZooKeys 741: 1–2. <https://doi.org/10.3897/zookeys.741.24612>

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This special issue of ZooKeys assembles a collection of contemporary research devoted to myriapods presented at the 17<sup>th</sup> International Congress of Myriapodology, held from 23 to 26 July 2017 in Krabi, Thailand. The congress was organised by Prof. Somsak Panha and his team from the Animal Systematics Research Unit of Chulalongkorn University in Bangkok. This is the third ZooKeys special issue emerging from a myriapodological congress following those of the 15<sup>th</sup> and 16<sup>th</sup> congresses in Australia and the Czech Republic, respectively: Mesibov R & Short M (2011) Proceedings of the 15<sup>th</sup> International Congress of Myriapodology. ZooKeys 156: 139 pp. and Tuf IH & Tajovský K (2015) Proceedings of the 16<sup>th</sup> International Congress of Myriapodology. ZooKeys 510: 278 pp.

The current issue comprises 13 articles by 35 authors from 10 countries (Austria, Australia, Brazil, China, Czech Republic, Georgia, Germany, Russia, Taiwan, UK). Two articles are devoted to the biogeography of myriapods of the Himalayas and lowland Altai (Golovatch and Martens, Nefedev et al., respectively). Reip and Wesener investigate the haplotype diversity and biogeography of the familiar Black Pill Millipede, *Glomeris marginata*, throughout Europe and draw conclusions on the taxonomic status of a number of subspecies and colour morphs known in this widespread, model millipede species. Kokhia and Golovatch provide an annotated checklist of the millipedes of Georgia.



**Figure 1.** Group photo of the 17<sup>th</sup> International Congress of Myriapodology.

Two papers focus on anatomical structures of the head capsule and their phylogenetic significance. These involve documenting the tentorium of sphaerotheriid millipedes (Moritz et al.) and the epipharynx and hypopharynx in the centipede genus *Lithobius* Leach, 1814 (Ganske et al.). Another paper deals with the conservation status of Brazilian myriapods based on recent assessments following the IUCN criteria and discusses some practical implications for their conservation (Karam-Gemael et al.). One contribution (Decker et al.) describes the online platform VIRMISCO (Virtual Microscope Slide Collection) – a digital archive for microscope slides that enables users to view, search, rotate, zoom, measure, etc., important type objects.

Five papers in this special issue are devoted to systematic description of altogether nine new myriapod species from East Asia and Australia, these belonging to the centipede genus *Lithobius* (Chao et al., Ma et al., Pei et al.), and the millipede genera *Lophoturus* (Huynh and Veenstra) and *Glyphiulus* (Jiang et al.).

We are grateful to the referees of contributions to this issue for careful and prompt work that improved the quality of the accepted manuscripts.

We look forward to the next International Congress of Myriapodology, which will be held in 2019 and hosted by Prof. Zoltan Korsós and his team at the Hungarian Natural History Museum.

Pavel Stoev, Gregory D. Edgecombe

# Distribution, diversity patterns and faunogenesis of the millipedes (Diplopoda) of the Himalayas

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Academic editor: P. Stoev | Received 4 August 2017 | Accepted 7 September 2017 | Published 7 March 2018

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<http://zoobank.org/74400373-2CB8-45D6-935A-E8333DDB3B50>

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**Citation:** Golovatch SI, Martens J (2018) Distribution, diversity patterns and faunogenesis of the millipedes (Diplopoda) of the Himalayas. In: Stoev P, Edgecombe GD (Eds) Proceedings of the 17<sup>th</sup> International Congress of Myriapodology, Krabi, Thailand. ZooKeys 741: 3–34. <https://doi.org/10.3897/zookeys.741.20041>

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## Abstract

The Himalayas support a highly rich, diverse, multi-layered, mostly endemic diplopod fauna which presently contains >270 species, 53 genera, 23 families and 13 orders. This is the result of mixing the ancient, apparently Tertiary and younger, Plio-Pleistocene elements of various origins, as well as the most recent anthropochore (= man-mediated) introductions. At the species and, partly, generic levels, the fauna is largely autochthonous and sylviculous, formed through abounding *in situ* radiation and vicariance events. In general, the species from large genera and families tend to occupy a wide range of altitudes, but nearly each of the constituent species shows a distribution highly localized both horizontally and altitudinally, yet quite often with sympatry or even syntopy involved. The bulk of the fauna is Indo-Malayan in origin, with individual genera or families shared with those of SE Asia (mostly) and/or S India (few). Sino-Himalayan and, especially, Palearctic components are subordinate, but also clearly distinguishable.

## Keywords

Diplopoda, faunistics, Plio-Pleistocene, Asia, Palearctic

## Introduction

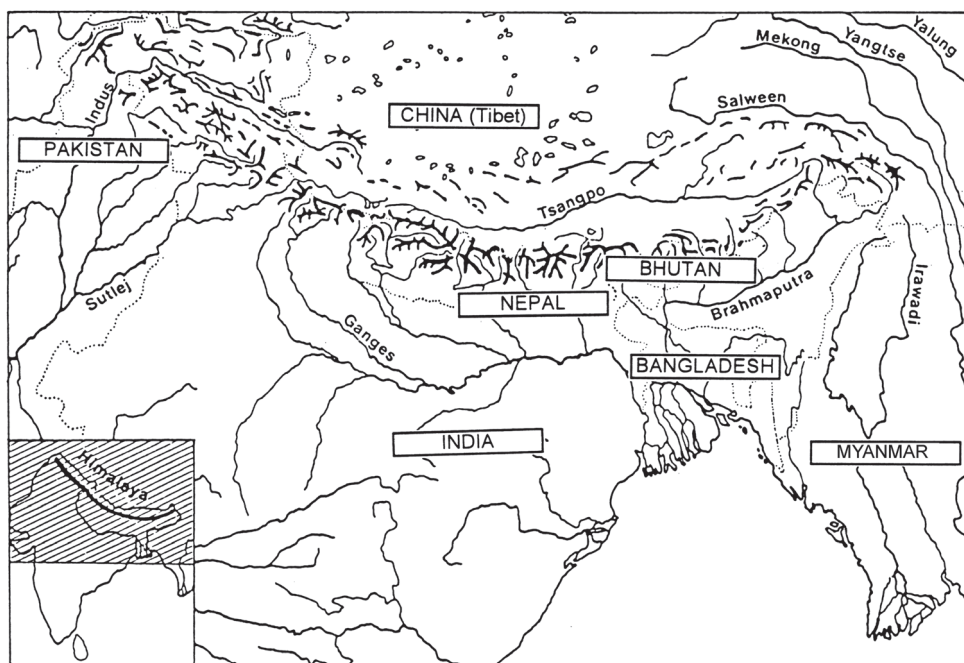
The Himalaya Range, or Himalayas for short, meaning “the abode of snow” in Sanskrit, is the mountain range in Asia that separates the Indian subcontinent from the Tibetan Plateau. Sometimes by extension, it is also the name of a massive mountain system that includes the Karakoram, the Hindu Kush, and other, lesser, ranges that reach out from the Pamir Knot (<http://maps.thefullwiki.org/Himalayas>). However, below the Himalayas is treated in the strict sense. The main Himalayan Range runs, northwest to southeast, from the Indus River valley to the Brahmaputra River valley, forming an arc which varies in width from 400 km in the western Kashmir-Xinjiang region to 150 km in the southeastern Tibet-Arunachal Pradesh region. The range consists of three extensive sub-ranges, with the northernmost, and highest, known as the Great Himalayas.

The Himalayan mountain system is the Earth’s highest and home to the world’s highest peaks, the Eight-thousanders, which include Mount Everest and K2. The system, which includes various outlying sub-ranges, stretches across five countries: India, Nepal, Bhutan, China and Pakistan. The Himalayan Range is bordered on the northwest by the Karakoram and Hindu Kush ranges, on the north by the Tibetan Plateau, and on the south by the Indo-Gangetic Plain. The region is roughly delimited by 74°E in the west and 95°E in the east. Some of the world’s major rivers, the Indus, the Ganges, and the Tsangpo-Brahmaputra, rise in the Himalayas, and their combined drainage basin is home to some 600 million people. The Himalayas have profoundly shaped the cultures of South Asia, having united and separated them as well; many Himalayan peaks are sacred in Hinduism and Buddhism (<https://en.wikipedia.org/wiki/Himalayas>). An orographic map of the Himalayas is presented in Fig. 1.

From a biologist’s viewpoint, the Himalayas represent a highly important biogeographical barrier between the cold and arid uplands of Central Asia and the largely tropical South and Southeast Asia. During the southwestern monsoon period, precipitation mainly occurs on the southern slopes, being greatly reduced on the northern ones. This picture is especially typical of the Central Himalayas, more or less within Kumaon, Nepal, Sikkim and Bhutan, as more to the west the aridity of Central Asia extends across the southern slopes while in the eastern parts of the system heavy monsoon rains, though declining in amount and frequency, reach beyond the main ridge as far as southeastern Tibet (Troll 1967, Miehe 2015).

The drastic climatic gradient within the Central Himalayas is of utmost importance in affecting the distribution of various organisms. Although phyto- and zoogeographical regions delimited differ to some degree, they both emphasize the role of the Himalayas as a contact zone between two major biogeographical realms, the Palearctic and Oriental, which meet and intermesh here in various combinations. All areas lying north of the Central Himalayas obviously belong to the Palearctic, as do the highest parts of the inhabited southern macroslope. The lower and lowest elevations of the southern macroslope are largely attributable to the Oriental, or Indo-Malayan realm. In addition, a third realm, the Sino-Himalayan biogeographical region, can be distinguished, bringing old faunal elements into the Himalayan chain. However, the border





**Figure 1.** Orographic map of the Himalayan region.

between both regions is generally neither striking nor abrupt, forming more (especially in the eastern Himalayas) or less (in their central parts) vast transition areas, numerous inversions or anomalies. In other words, the otherwise manifest rule “(sub)tropical organisms for (sub)tropical environments only” is very often violated in the Himalayas, particularly in the central parts of the system and as regards animals in general (Martens 1984, 1993, 2015). Even the pattern of vertical zonation of the tree plant cover in the region is rather conventional (Dobremez 1972) (Fig. 2).

The first, provisional review of the millipede fauna of the Himalayas (Golovatch and Martens 1996) was based on a fauna of approximately 200 species or subspecies. Now, the list has reached more than 270 species or subspecies belonging to 53 genera distributed in 23 families and 13 orders (Table 1). As before, several species and even genera remain unidentified. The main increase is due to the omnipresent family Paradoxosomatidae, especially as regards the fauna of Nepal. The objective of this paper is to critically list the actually known Himalayan diplopod fauna and to discuss the different faunal and evolutionary influences that made this fauna so rich and complex.

## Material and methods

These results mostly rely on published records, which have grown considerably over the past two decades. The resultant checklist (Table 1) is not just a literature compila-

						m
						6000
	nival stage					
	subnival stage	scattered patches of vegetation			eternal snow	5500
						5000
alpine zone	upper alpine level			alpine meadows		4500
	lower alpine level			heath with dwarf <i>Rhododendron</i> and junipers	heath with dwarf <i>Rhododendron</i>	4000
		thorn steppes				
subalpine zone	upper subalpine level			birch forest		3600
	lower subalpine level			fir forest	forest of tree <i>Rhododendron</i> and fir ( <i>Abies</i> )	3000
temperate zone	upper mountain zone	mountain region	<i>Cedrus</i> , <i>Cupressus</i> and <i>Juniperus</i> forest	coniferous ( <i>Pinus</i> , <i>Picea</i> ) and deciduous ( <i>Quercus</i> ) forest	hygrophilic <i>Quercus</i> forest	2600
	lower mountain zone	hill region		forest of evergreen oaks and laurels		2000
subtropical zone	upper subtropical level	<i>Olea</i> forest		pine forest ( <i>Pinus roxburghii</i> )	subtropical deciduous forest ( <i>Schima</i> , <i>Castanopsis</i> )	1500
	lower subtropical level					1000
tropical zone	upper tropical level			tropical forests, mainly <i>Shorea</i>		400
	lower tropical level					0
		northwest: IV	west: III	central: II	east: I	

**Figure 2.** The vegetation belts and most important plant communities in the Nepal Himalayas. The Roman numerals at the bottom indicate the floral regions of Nepal (modified, after Dobremez 1972).

tion, as it is largely based on the vast experience of the first author who has described numerous diplopod species from the Himalayas. Most of the recent advance has appeared, based on material collected by the second author and/or his collaborators during numerous, often long-term expeditions to Nepal, India and elsewhere. The trips to Nepal covered all seasons, focused on the exploration of local forest soil/litter fauna and concerned all forest biomes ranging from the terai lowlands to and beyond the timber line.



**Table 1.** Diplopoda of the Himalayas. In addition to the taxonomic composition of the fauna, data on the vertical and geographical distribution of species in the region are also presented, largely with key references.

Fauna	Altitude (m a.s.l.)	Country/state and main reference(s)
<b>Order Polyxenida</b>	1585–2400	
<b>Family Polyxenidae</b>	1585–2400	
Genus <i>Polyxenus</i> Latreille, 1802–03		
1. <i>Polyxenus</i> sp.	1585	India, Jammu & Kashmir (Silvestri 1936)
Genus <i>Monographis</i> Attems, 1907		
2. <i>Monographis mira</i> (Turk, 1947)	1600–2400	Nepal <sup>1</sup> & India, Almora (Turk 1947, Condé 1962, Golovatch and Wesener 2016)
Genus <i>Unixenus</i> Jones, 1944		
3. <i>Unixenus</i> sp.	2400–4550	Nepal <sup>2</sup> (Condé and Jacquemin-Nguyen Duy 1968, Golovatch and Martens 1996)
<b>Order Sphaerotheriida</b>	140–2700	
<b>Family Zephroniidae</b>	140–2700	
Genus <i>Indosphaera</i> Attems, 1935		
4. <i>Indosphaera feae</i> Attems, 1935	?	India, Assam (Attems 1936, Golovatch and Wesener 2016)
Genus <i>Kophosphaera</i> Attems, 1935	1650–2100	
5. <i>Kophosphaera brevilamina</i> Attems, 1936	1700	India, West Bengal & Darjeeling Distr. (Golovatch and Martens 1996, Golovatch and Wesener 2016)
6. <i>K. devolvens</i> Attems, 1936	1700–2050	India, Sikkim & Darjeeling Distr. (Golovatch and Martens 1996, Golovatch and Wesener 2016)
7. <i>K. excavata</i> (Butler, 1874)	?	Nepal, Chitlang; India, Sikkim, Darjeeling Distr. & Assam (Golovatch and Martens 1996, Golovatch and Wesener 2016)
8. <i>K. mammifera</i> Attems, 1936	?	India, Darjeeling Distr. & Assam (Golovatch and Martens 1996, Golovatch and Wesener 2016)
9. <i>K. martensi</i> Wesener, 2015	2100	Nepal (Wesener 2015)
10. <i>K. politissima</i> Attems, 1935	1650–1870	India, Darjeeling Distr. & Nepal (Wesener 2015)
11. <i>K. shivapuri</i> Wesener, 2015	1700–2100	Nepal (Wesener 2015)
Genus <i>Zephronia</i> Gray, 1832	140–2700	
12. <i>Zephronia alticola alticola</i> Attems, 1936	400–1700	India, Darjeeling Distr. & Assam (Attems 1936, Golovatch and Martens 1996)
13. <i>Z. alticola bengalica</i> Attems, 1936	?	India, West Bengal (Attems 1936, Golovatch and Martens 1996)
14. <i>Z. debilis</i> Attems, 1936	1700	India, Darjeeling Distr. (Attems 1936, Golovatch and Martens 1996)
15. <i>Z. densipora</i> Attems, 1936	?	India, Assam (Attems 1936, Golovatch and Martens 1996)
16. <i>Z. disparipora</i> Attems, 1936	140	India, Assam (Attems 1936, Golovatch and Martens 1996)
17. <i>Z. hirta</i> Attems, 1936	1700	India, Darjeeling Distr. (Attems 1936, Golovatch and Martens 1996)
18. <i>Z. hysoiphila</i> Attems, 1936	?	India, Assam (Attems 1936, Golovatch and Martens 1996)
19. <i>Z. juvenis</i> Attems, 1936	?	India, Assam (Attems 1936, Golovatch and Martens 1996)
20. <i>Z. lignivora</i> Attems, 1936	180–330	India, Assam (Attems 1936, Golovatch and Martens 1996)
21. <i>Z. manca</i> Attems, 1936	1000–1700	Vietnam & India, Darjeeling Distr. (Attems 1936, Golovatch and Martens 1996)
22. <i>Z. montana</i> (Karsch, 1881)	?	“Himalaya” (Wesener 2015)
23. <i>Z. nepalensis</i> Wesener, 2015	1700–2600	Nepal (Wesener 2015)

Fauna	Altitude (m a.s.l.)	Country/state and main reference(s)
24. <i>Z. nigrinota</i> Butler, 1872	2300–2700	India, Darjeeling Distr. (Golovatch and Martens 1996, Golovatch and Wesener 2016)
25. <i>Z. specularis</i> Attems, 1936	?	India, Assam (Attems 1936, Golovatch and Martens 1996)
26. <i>Z. tigrina</i> Butler, 1872	?	India, Darjeeling Distr. (Golovatch and Wesener 2016)
27. <i>Z. tigrinoides</i> Attems, 1936	170	India, Darjeeling Distr. (Attems 1936, Golovatch and Martens 1996)
28. <i>Z. tumida</i> Butler, 1882	?	India, Assam & Darjeeling Distr.; Myanmar (Wesener 2015)
<b>Order Glomerida</b>	150–3300	
<b>Family Glomeridae</b>	150–3300	
Genus <i>Hyleoglomeris</i> Verhoeff, 1910	150–3300	
29. <i>Hyleoglomeris crassipes</i> Golovatch, 1987	2450–2720	Nepal (Golovatch 1987b, Golovatch and Martens 1996)
30. <i>H. electa</i> (Silvestri, 1917)	500–1700	India, Darjeeling Distr. (Attems 1936, Golovatch and Martens 1996)
31. <i>H. gorkhalis</i> Golovatch, 1987	1200	Nepal (Golovatch 1987b, Golovatch and Martens 1996)
32. <i>H. khumbua</i> Golovatch, 1987	3250–3300	Nepal (Golovatch 1987b, Golovatch and Martens 1996)
33. <i>H. modesta</i> Silvestri, 1917	150	India, Assam (Golovatch and Martens 1996)
34. <i>H. nagarjunga</i> Golovatch, 1987	1600–2100	Nepal (Golovatch 1987b, Golovatch and Martens 1996, Golovatch et al. 2006)
35. <i>H. tinjurana</i> Golovatch, 1987	2450	Nepal (Golovatch 1987b, Golovatch and Martens 1996)
36. <i>H. venustula</i> Silvestri, 1917	?	India, Assam (Golovatch and Martens 1996)
<b>Order Siphonophorida</b>		
<b>Family Siphonorhinidae</b>	500–1700	
Genus <i>Siphonorhinus</i> Pocock, 1894	500–1700	
37. <i>Siphonorhinus cingulatus</i> (Attems, 1936)	500–1700	Vietnam and India, Darjeeling Distr. (Attems 1936, Golovatch and Wesener 2016)
38. <i>S. coniceps</i> (Attems, 1936)	1700	India, Darjeeling Distr. (Attems 1936, Golovatch and Wesener 2016)
39. <i>S. larwoodi</i> (Turk, 1947)	1600	India, Almora (Golovatch and Martens 1996, Golovatch and Wesener 2016)
<b>Order Siphonocryptida</b>		
<b>Family Siphonocryptidae</b>	2450	
Genus <i>Hirudicryprus</i> Enghoff & Golovatch, 1995		
40. <i>Hirudicryprus quintumelementum</i> Korsós, Geoffroy & Mauriès, 2009	2450	Nepal (Korsós et al. 2009)
<b>Order Platydesmida</b>	<2000	
<b>Family Andrognathidae</b>	<2000	
Genus <i>Pseudodesmus</i> Pocock, 1887		
41. ? <i>Pseudodesmus</i> sp.	<2000	Nepal (Golovatch and Martens 1996)
<b>Order Polyzooniida</b>	4700–4800	
<b>Family Hirudisomatidae</b>	4700–4800	
Genus <i>Nepalozonium</i> Shelley, 1996		
42. <i>Nepalozonium trimaculatum</i> Shelley, 1996	4700–4800	Nepal (Shelley 1996)
<b>Order Chordeumatida</b>	900–4100	
<b>Family Kashmireumatidae</b>	2600–4100	
Genus <i>Kashmireuma</i> Mauriès, 1982	2600–4100	

Fauna	Altitude (m a.s.l.)	Country/state and main reference(s)
43. <i>Kashmireuma nepalensis</i> Mauriès, 1988	3600–4100	Nepal (Mauriès 1988, Golovatch and Martens 1996)
44. <i>K. nielsenii</i> Mauriès, 1982	2600–3500	India, Kashmir (Mauriès 1982, Golovatch and Martens 1996)
45. <i>K. schawalleri</i> Shear, 1987	3450–3600	Nepal (Shear 1987, Golovatch and Martens 1996)
<b>Family Cleidogonidae</b>	900–3900	
Genus <i>Tianella</i> Attems, 1904	900–3900	
46. <i>Tianella ausobskyi</i> Shear, 1987	2500–3050	Nepal (Shear 1987, Golovatch and Martens 1996)
47. <i>T. bobanga</i> Shear, 1979	2460–2500	Nepal (Shear 1979, 1987, Golovatch and Martens 1996)
48. <i>T. daamsae</i> Shear, 1987	3600–3900	Nepal (Shear 1987, Golovatch and Martens 1996)
49. <i>T. gitanga</i> Shear, 1987	2550	Nepal (Shear 1987, Golovatch and Martens 1996)
50. <i>T. jaljalensis</i> Mauriès, 1988	2350	Nepal (Mauriès 1988, Golovatch and Martens 1996)
51. <i>T. kathmandua</i> Mauriès, 1988	1700	Nepal (Mauriès 1988, Golovatch and Martens 1996)
52. <i>T. lughla</i> Shear, 1979	2950–3300	Nepal (Shear 1979, 1987, Golovatch and Martens 1996)
53. <i>T. managa</i> Shear, 1987	2550	Nepal (Shear 1987, Golovatch and Martens 1996)
54. <i>T. mangsingma</i> Mauriès, 1988	2250	Nepal (Mauriès 1988, Golovatch and Martens 1996)
55. <i>T. martensi</i> Shear, 1979	1150–2900	Nepal (Shear, 1979, 1987, Golovatch and Martens 1996)
56. <i>T. smetanai</i> Mauriès, 1988	3250	Nepal (Mauriès 1988, Golovatch and Martens 1996)
57. <i>Tianella</i> sp.	900–1400	India, Darjeeling Distr. (Golovatch and Martens 1996)
<b>Family Megalotyidae</b>	1900–4100	
Genus <i>Nepalella</i> Shear, 1979	1900–4100	
58. <i>Nepalella deharvengi</i> Mauriès, 1988	2900–3500	Nepal (Mauriès 1988, Golovatch and Martens 1996)
59. <i>N. gairiensis</i> Mauriès, 1988	3000	Nepal (Mauriès 1988, Golovatch and Martens 1996)
60. <i>N. gunsae</i> Shear, 1987	3600–3800	Nepal (Shear 1987, Golovatch and Martens 1996)
61. <i>N. jaljalae</i> Mauriès, 1988	2200	Nepal (Mauriès 1988, Golovatch and Martens 1996)
62. <i>N. khumbua</i> Shear, 1979	3350–3300	Nepal (Shear 1979, 1987, Golovatch and Martens 1996)
63. <i>N. phulcokia</i> Mauriès, 1988	2250	Nepal (Mauriès 1988, Golovatch and Martens 1996)
64. <i>N. ringmoensis</i> Mauriès, 1988	2750–3000	Nepal (Mauriès 1988, Golovatch and Martens 1996)
65. <i>N. taplejunga</i> Shear, 1987	3000–3300	Nepal (Shear 1987, Golovatch and Martens 1996)
66. <i>N. thodunga</i> Shear, 1979	3200	Nepal (Shear 1979, 1987, Golovatch and Martens 1996)
67. <i>N. tragsindola</i> Mauriès, 1988	2450–3300	Nepal (Mauriès 1988, Golovatch and Martens 1996)
68. <i>Nepalella</i> sp.	1900–4100	Nepal (Golovatch and Martens 1996)
<b>Order Callipodida</b>	650	
<b>Family Caspiopetalidae</b>	650	
Genus <i>Bollmania</i> Silvestri, 1896		
69. <i>Bollmania kohalana</i> (Attems, 1936)	650	Pakistan, Punjab (Attems 1936, Golovatch and Wesener 2016)
<b>Order Julida</b>	1680–4800	
<b>Family Julidae</b>	1680–4800	
Genus <i>Anaulaciulus</i> Pocock, 1895	1900–4500	
70. <i>Anaulaciulus acaudatus</i> Korsós, 1996	3990	India, Sikkim (Korsós 1996, Golovatch and Martens 1996)
71. <i>A. bilineatus</i> Korsós, 1996	3300–4300	Nepal (Korsós 1996, Golovatch and Martens 1996)
72. <i>A. kashmirensis</i> Korsós, 1996	3100–3200	India, Kashmir (Korsós 1996, Golovatch and Martens 1996)
73. <i>A. nepalensis</i> Korsós, 1996	2600–3400	Nepal (Korsós 1996, Golovatch and Martens 1996)
74. <i>A. niger</i> Korsós, 1996	2600–4500	Nepal (Korsós 1996, Golovatch and Martens 1996)

Fauna	Altitude (m a.s.l.)	Country/state and main reference(s)
75. <i>A. tibetanus</i> Korsós, 1996	3700	China, Tibet; India, Assam (Korsós 1996, Golovatch and Martens 1996)
76. <i>A. topali</i> Korsós, 1996	2300	India, Kashmir (Korsós 1996, Golovatch and Martens 1996)
Genus <i>Nepalmatoiulus</i> Mauriès, 1983	1680–4800	
77. <i>Nepalmatoiulus appendiculatus</i> Enghoff, 1987	1900–2100	India, Uttar Pradesh (Enghoff 1987, Golovatch and Martens 1996)
78. <i>N. deharvengi</i> (Mauriès, 1983)	2550–3350	Nepal (Mauriès 1983, Golovatch and Martens 1996)
79. <i>N. dhaulagiri</i> Enghoff, 1987	3000–3350	Nepal (Enghoff 1987, Golovatch and Martens 1996)
80. <i>N. generalis</i> Enghoff, 1987	3400	Nepal (Enghoff 1987, Golovatch and Martens 1996)
81. <i>N. hyalilobus</i> Enghoff, 1987	3600–3800	Nepal (Enghoff 1987, Golovatch and Martens 1996)
82. <i>N. ivanloebli</i> Enghoff, 1987	2200–4800	Nepal (Mauriès 1983, Enghoff 1987, Golovatch and Martens 1996)
83. <i>N. juctapositus</i> Enghoff, 1987	2800–3050	Nepal (Mauriès 1983, Golovatch and Martens 1996)
84. <i>N. martensi</i> Enghoff, 1987	3250–3300	Nepal (Enghoff 1987, Golovatch and Martens 1996)
85. <i>N. mauriesi</i> Enghoff, 1987	3600	Nepal (Enghoff 1983, Golovatch and Martens 1996)
86. <i>N. nigrescens</i> Enghoff, 1987	2300	Bhutan (Enghoff 1983, Golovatch and Martens 1996)
87. <i>N. pineti</i> Enghoff, 1987	2900	Nepal (Enghoff 1987, Golovatch and Martens 1996)
88. <i>N. rugiflagrum</i> Enghoff, 1987	3300	Bhutan (Enghoff 1987, Golovatch and Martens 1996)
89. <i>N. smetanai</i> (Mauriès, 1983)	1900–2700	Nepal (Enghoff 1983, Golovatch and Martens 1996)
90. <i>N. sympatricus</i> Enghoff, 1987	3000	Nepal (Enghoff 1987, Golovatch and Martens 1996)
88. <i>N. uncus</i> Enghoff, 1987	2550	Nepal (Enghoff 1987, Golovatch and Martens 1996)
91. <i>N. wuermlii</i> Enghoff, 1987	1680–2600	Bhutan (Enghoff 1987, Golovatch and Martens 1996)
92. <i>N. zachonoides</i> Enghoff, 1987	2450–2600	Nepal (Enghoff 1987, Golovatch and Martens 1996)
<b>Order Spirostreptida</b>	200–2500	
<b>Family Cambalopsidae</b>	<1000–1200	
Genus <i>Podoglyphiulus</i> Attems, 1909	<1000–1200	
93. <i>Podoglyphiulus elegans nepalensis</i> Mauriès, 1983	<1000	Nepal <sup>3</sup> (Mauriès 1983, Golovatch and Martens 1996)
Genus <i>Trachyjulus</i> Peters, 1864		
94. <i>Trachyjulus mimus</i> Silvestri, 1924	1200	India, Assam (Silvestri 1924, Golovatch and Martens 1996, Golovatch and Wesener 2016)
95. <i>T. wilsonae</i> Mauriès, 1983	<1000	Nepal (Mauriès 1983, Golovatch and Martens 1996)
<b>Family Harpagophoridae</b>	200–2500	
Genus <i>Dametis</i> Attems, 1942		
96. <i>Dametis falcatus</i> (Attems, 1936)	400–500	India, Assam (Attems 1936, Golovatch and Wesener 2016)
Genus <i>Gonoplectus</i> Chamberlin, 1921	200–2500	
97. <i>Gonoplectus alius</i> Demange, 1961	?	India, Assam (Demange 1961, Golovatch and Martens 1996)
98. <i>G. bhutanensis</i> Demange, 1988	350–450	Bhutan (Demange 1988, Golovatch and Martens 1996)
99. <i>G. broelemanni</i> Demange, 1961	1800–2300	Nepal (Demange 1961, Golovatch and Martens 1996)
100. <i>G. corniger</i> (Attems, 1936)	?	India, Assam (Attems 1936, Golovatch and Martens 1996)
101. <i>G. gracilis</i> (Attems, 1936)	1200	India, Darjeeling Distr. (Attems 1936, Golovatch and Martens 1996)
102. <i>G. hyatti</i> Demange, 1961	1200	Nepal (Demange 1961, Golovatch and Martens 1996)

Fauna	Altitude (m a.s.l.)	Country/state and main reference(s)
103. <i>G. malayus malayus</i> (Carl, 1909)	200–2500	Indonesia, Java; Nepal, Bhutan & India, Madhya Pradesh, Uttar Pradesh, Himachal Pradesh, West Bengal (Golovatch and Martens 1996, Golovatch and Wesener 2016)
104. <i>G. malayus lindbergi</i> (Carl, 1909)	350	Bhutan & India, Darjeeling Distr. (Golovatch and Martens 1996, Golovatch and Wesener 2016)
105. <i>G. probus</i> (Attems, 1936)	1000	India, Darjeeling Distr. (Attems 1936, Golovatch and Martens 1996, Golovatch and Wesener 2016)
106. <i>G. remyi</i> Demange, 1961	?	India, Assam (Demange 1961, Golovatch and Martens 1996, Golovatch and Wesener 2016)
107. <i>G. repertus</i> (Attems, 1936)	900	India, Darjeeling Distr. (Attems 1936, Golovatch and Wesener 2016)
108. <i>G. sulcatus</i> (Attems, 1936)	2400	India, Darjeeling Distr. (Attems 1936, Golovatch and Wesener 2016)
<b>Order Spirobolida</b>	<1000–1800	
<b>Family Pachybolidae</b>		
Genus <i>Trigoniulus</i> Pocock, 1894	<1000	
109. <i>Trigoniulus corallinus</i> (Gervais, 1847)	<1000	Pantropical, in India nearly throughout, including Assam (Golovatch and Wesener 2016)
<b>Family Pseudospirobolellidae</b>		
Genus <i>Physobolus</i> Attems, 1936		
110. <i>Physobolus olivaceus</i> Attems, 1936	1800	India, Darjeeling Distr. (Attems 1936, Golovatch and Wesener 2016)
<b>Order Polydesmida</b>	150–4500	
<b>Family Cryptodesmidae</b>		
Genus <i>Trichopeltis</i> Pocock, 1894	350–1000	
111. <i>Trichopeltis watsoni</i> Pocock, 1895	350–1000	Bangladesh, Myanmar, Bhutan and India, Darjeeling Distr., West Bengal, Assam & near Kolkata (Attems 1936, Golovatch and Martens 1996, Golovatch and Wesener 2016)
<b>Family Haplodesmidae</b>	150–1750	
Genus <i>Koponenius</i> Golovatch & VandenSpiegel, 2014	150–1750	
112. <i>Koponenius biramus</i> Golovatch & VandenSpiegel, 2014	1750	Nepal (Golovatch and VandenSpiegel 2014)
113. <i>K. schawalleri</i> Golovatch & VandenSpiegel, 2016	150	Nepal (Golovatch and VandenSpiegel 2016)
114. <i>K. unicornis</i> Golovatch & VandenSpiegel, 2014	880	India, Darjeeling Distr. (Golovatch and VandenSpiegel 2014, Golovatch and Wesener 2016)
<b>Family Opisotretidae</b>	1100–2440	
Genus <i>Martensodesmus</i> Golovatch, 1987	1100–2440	
115. <i>Martensodesmus bicuspidatus</i> Golovatch, 1988	1650–2000	Bhutan (Golovatch 1988a, Golovatch and Martens 1996, Golovatch et al. 2013)
116. <i>M. excornis</i> Golovatch, 1988	2440	Bhutan (Golovatch 1988a, Golovatch and Martens 1996, Golovatch et al. 2013)
117. <i>M. himalayensis</i> Golovatch, 1987	1100–1300	Nepal (Golovatch 1987a, Golovatch and Martens 1996, Golovatch et al. 2013)

Fauna	Altitude (m a.s.l.)	Country/state and main reference(s)
118. <i>M. nagarjungicus</i> Golovatch, 1987	1900–2100	Nepal (Golovatch 1987a, Golovatch and Martens 1996, Golovatch et al. 2013)
119. <i>M. sherpa</i> Golovatch, 1987	1200	Nepal (Golovatch 1987a, Golovatch and Martens 1996, Golovatch et al. 2013)
120. <i>Martensodesmus</i> sp.	1300–2150	Nepal, Bhutan (Golovatch and Martens 1996)
<b>Family Paradoxosomatidae</b>	150–4500	
Genus <i>Anoplodesmus</i> Carl, 1932	1000–3600	
121. <i>Anoplodesmus affinis</i> (Golovatch, 1990)	2475–2700	Nepal (Golovatch 1990a, Golovatch and Martens 1996)
122. <i>A. cylindricus</i> (Carl, 1935)	1650–2850	Nepal & India, Darjeeling Distr. (Carl 1935, Golovatch 1984, Golovatch and Martens 1996, Golovatch and Wesener 2016)
123. <i>A. elongissimus</i> (Golovatch, 1984)	1000	India, Darjeeling Distr. (Golovatch 1984, Golovatch and Martens 1996, Golovatch and Wesener 2016)
124. <i>A. magnus</i> Golovatch, 2015	2700	Nepal (Golovatch 2015a)
125. <i>A. martensi</i> (Golovatch, 1990)	2250–3600	Nepal (Golovatch 1990a, 2014b, 2016a, Golovatch and Martens 1996)
126. <i>A. schawalleri</i> (Golovatch, 1990)	2050–2150	Nepal (Golovatch 1990a, Golovatch and Martens 1996)
127. <i>A. similis</i> (Golovatch, 1990)	2300–3000	Nepal (Golovatch 1990a, Golovatch and Martens 1996)
128. <i>A. spinosus</i> Golovatch, 2016	2500	Nepal (Golovatch 2016a)
129. <i>A. subcylindricus</i> (Carl, 1932)	?	S India & Nepal (Nguyen 2010 <sup>4</sup> , Golovatch and Wesener 2016)
Genus <i>Beronodesmoides</i> Golovatch, 2015	1650–4250	
130. <i>Beronodesmoides anteriporus</i> Golovatch, 2015	1650–3350	Nepal (Golovatch 2015a, 2016c)
131. <i>B. bifidus</i> Golovatch, 2015	3100	Nepal (Golovatch 2015a)
132. <i>B. lobatus</i> Golovatch, 2015	4000–4250	Nepal (Golovatch 2015a, Golovatch et al. 2016)
133. <i>B. longifemoratus</i> Golovatch, 2015	2700–2800	Nepal (Golovatch 2016a)
134. <i>B. martensi</i> Golovatch, 2016	2700	Nepal (Golovatch 2016c)
135. <i>B. montigena</i> Golovatch, 2016	3550	Nepal (Golovatch 2016c)
136. <i>B. typicus</i> Golovatch, 2016	3400	Nepal (Golovatch 2016c)
Genus <i>Beronodesmus</i> Golovatch, 2014	1650–4500	
137. <i>Beronodesmus curtispinus</i> Golovatch, 2015	4500	Nepal (Golovatch 2015a)
138. <i>B. distospinosus</i> Golovatch, 2015	1650–3080	Nepal (Golovatch 2015a, 2016c)
139. <i>B. gorkhalis</i> Golovatch, 2015	3050–3600	Nepal (Golovatch 2015a, Golovatch et al. 2016)
140. <i>B. latispinosus</i> Golovatch, 2015	1900–3500	Nepal (Golovatch 2015a, 2016c, Golovatch et al. 2016)
141. <i>B. longispinus</i> Golovatch, 2015	2550–4270	Nepal (Golovatch 2015a, 2016c, Golovatch et al. 2016)
142. <i>B. martensi</i> Golovatch et al., 2016	2650	Nepal (Golovatch et al. 2016)
143. <i>B. minutus</i> Golovatch, 2015	3300–3500	Nepal (Golovatch 2015a)
144. <i>B. pallidus</i> Golovatch, 2014	3800–4100	Nepal (Golovatch 2014b)
145. <i>B. serratus</i> Golovatch et al., 2016	3300–3500	Nepal (Golovatch et al. 2016)
146. <i>B. simplex</i> Golovatch, 2016	2100	Nepal (Golovatch 2016c, Golovatch et al. 2016)
147. <i>B. sinuatospinus</i> Golovatch, 2015	2150–2250	Nepal (Golovatch 2015a, 2016c)

Fauna	Altitude (m a.s.l.)	Country/state and main reference(s)
Genus <i>Delarthrum</i> Attems, 1936	600–4100	
148. <i>Delarthrum aberrans</i> (Golovatch, 1996)	1000–2600	Nepal (Golovatch 1996, 2014b, 2016a, Golovatch and Martens 1996)
149. <i>D. affine</i> (Golovatch, 1994)	1400	Nepal (Golovatch 1994a, 2014b, Golovatch and Martens 1996)
150. <i>D. alatum</i> (Golovatch, 1996)	1900–2100	Nepal (Golovatch 1996, 2014b, Golovatch and Martens 1996)
151. <i>D. andreevi</i> Golovatch, 2014	1800	Nepal (Golovatch 2014b)
152. <i>D. arunense</i> (Golovatch, 1994)	1850–2150	Nepal (Golovatch 1994a, 2014b, 2016a, Golovatch and Martens 1996)
153. <i>D. beroni</i> Golovatch, 2014	600–1000	Nepal (Golovatch 2014b)
154. <i>D. bifidum</i> (Golovatch, 1996)	2550–2650	Nepal (Golovatch 1996, 2014b, Golovatch and Martens 1996)
155. <i>D. chulingense</i> (Golovatch, 1994)	3000–3700	Nepal (Golovatch 1994a, 2014b, Golovatch and Martens 1996)
156. <i>D. communicans</i> (Golovatch, 1992)	2650	Nepal (Golovatch 1992, 2014b, Golovatch and Martens 1996)
157. <i>D. curtisoma</i> Golovatch, 2015	2050–2150	Nepal (Golovatch 2015a)
158. <i>D. curtum</i> Golovatch, 2014	600–1000	Nepal (Golovatch 2014b)
159. <i>D. densesetosum</i> Golovatch, 2015	2400	Nepal (Golovatch 2015a)
160. <i>D. elegans</i> (Golovatch, 1992)	1350	Nepal (Golovatch 1992, 2014b, Golovatch and Martens 1996)
161. <i>D. extremum</i> (Golovatch, 1996)	2450	Nepal (Golovatch 1996, 2014b, Golovatch and Martens 1996)
162. <i>D. facile</i> (Golovatch, 1996)	2200–2400	Nepal (Golovatch 1996, 2014b, Golovatch and Martens 1996)
163. <i>D. fechteri</i> (Golovatch, 1990)	2330–3150	Nepal (Golovatch 1990a, 2014b, Golovatch and Martens 1996)
164. <i>D. foveatum</i> (Golovatch, 1996)	1800–2000	Nepal (Golovatch 1992, 2014b, Golovatch and Martens 1996)
165. <i>D. furcatum</i> (Golovatch, 1996)	600–2000	Nepal (Golovatch 1996, 2014b, 2016c, Golovatch and Martens 1996)
166. <i>D. gracile</i> Golovatch, 2015	1750	Nepal (Golovatch 2015a)
167. <i>D. granulosum</i> (Golovatch, 1994)	2000	Nepal (Golovatch 1994a, 2014b, 2016c, Golovatch and Martens 1996)
168. <i>D. heterotergale</i> Golovatch, 2014	600–1000	Nepal (Golovatch 2014)
169. <i>D. hingstoni</i> (Carl, 1935)	3400	China, Tibet (Carl 1935, Golovatch and Martens 1996)
170. <i>D. hirsutum</i> (Golovatch, 1994)	2400–4100	Nepal (Golovatch 1994a, 2014b, 2015a, Golovatch and Martens 1996)
171. <i>D. intermedium</i> (Golovatch, 1994)	1000–1100	Nepal (Golovatch 1994a, 2014b, Golovatch and Martens 1996)
172. <i>D. invocatum</i> (Golovatch, 1996)	2600–2800	Nepal (Golovatch 1996, 2014b, Golovatch and Martens 1996)
173. <i>D. kuznetsovi</i> (Golovatch, 1994)	3000	Nepal (Golovatch 1994a, 2014b, Golovatch and Martens 1996)
174. <i>D. longisetum</i> (Golovatch, 1994)	1400–1600	Nepal (Golovatch 1994a, 2014b, 2016c, Golovatch and Martens 1996)



Fauna	Altitude (m a.s.l.)	Country/state and main reference(s)
175. <i>D. longispinum</i> (Golovatch, 1996)	2150–2250	Nepal (Golovatch 1996, 2016c, Golovatch and Martens 1996)
176. <i>D. modestum</i> (Golovatch, 1996)	3450–3600	Nepal (Golovatch 1996, 2014b, Golovatch and Martens 1996)
177. <i>D. nyakense</i> (Golovatch, 1992)	2270–2400	Nepal (Golovatch 1992, 2014b, Golovatch and Martens 1996)
178. <i>D. obscurum</i> Attems, 1936	ca 2800	N Pakistan, Punjab (Attems 1936, Golovatch and Wesener 2016)
179. <i>D. philosophicum</i> (Golovatch, 1994)	1650–2450	Nepal (Golovatch 1994a, 2014b, Golovatch and Martens 1996)
180. <i>D. planifemur</i> Golovatch, 2015	2200	Nepal (Golovatch 2015a)
181. <i>D. prolixum</i> (Golovatch, 1996)	2550–2650	Nepal (Golovatch 1996, 2014b, Golovatch and Martens 1996)
182. <i>D. pumilum</i> (Attems, 1944)	?	India, Uttar Pradesh (Attems 1944, Golovatch and Wesener 2016)
183. <i>D. quadridentatum</i> Golovatch, 2016	2600–2800	Nepal (Golovatch 2016b)
184. <i>D. schawalleri</i> (Golovatch, 1992)	1000–2150	Nepal (Golovatch 1992, 1994a, 2014, Golovatch and Martens 1996)
185. <i>D. setosum</i> Golovatch, 2014	?	Nepal (Golovatch 2014b)
186. <i>D. silvestre</i> (Golovatch, 1994)	2000–3400	Nepal (Golovatch 1994a, 2014b, 2016a, Golovatch and Martens 1996)
187. <i>D. simile</i> (Golovatch, 1992)	2300–2700	Nepal (Golovatch 1992, 2014b, Golovatch and Martens 1996)
188. <i>D. simplex</i> (Golovatch, 1996)	1650	Nepal (Golovatch 1996, 2014b, Golovatch and Martens 1996)
189. <i>D. simulans</i> (Carl, 1935)	3700	Nepal & China, Tibet (Carl 1935, Golovatch and Martens 1996)
190. <i>D. spectabile</i> (Golovatch, 1994)	2650	Nepal (Golovatch 1994a, 2014b, 2016c, Golovatch and Martens 1996)
191. <i>D. spiniger</i> (Attems, 1936)	1000–2200	India, West Bengal & Darjeeling Distr. (Attems 1936, Golovatch 1984, Golovatch and Wesener 2016)
192. <i>D. spinigerum</i> (Golovatch, 1992)	600–1400	Nepal (Golovatch 1992, 2014b)
193. <i>D. splendens</i> (Golovatch, 1992)	1650–2150	Nepal (Golovatch 1992, 1994a, 2014, Golovatch and Martens 1996)
194. <i>D. subalatum</i> (Golovatch, 1996)	2600–2800	Nepal (Golovatch 1996, 2014b, Golovatch and Martens 1996)
195. <i>D. subsimulans</i> (Golovatch, 1996)	3100–3300	Nepal (Golovatch 1996, 2014b, Golovatch and Martens 1996)
196. <i>D. tenuitergale</i> Golovatch, 2014	3250	Nepal (Golovatch 2014)
197. <i>D. tergale</i> (Golovatch, 1994)	2650	Nepal (Golovatch 1994a, 2014b, Golovatch and Martens 1996)
198. <i>D. tuberculatum</i> (Golovatch, 1994)	3000–3300	Nepal (Golovatch 1992, 1994a, 2014b, Golovatch and Martens 1996)
199. <i>D. typicum</i> Golovatch, 2014	3100	Nepal (Golovatch 2014)
200. <i>D. unicum</i> (Golovatch, 1996)	2100–3420	Nepal (Golovatch 1996, 2014, 2015a, Golovatch and Martens 1996)
201. <i>D. unicolor</i> (Attems, 1936)	1200–1700	India, Assam & Darjeeling Distr. (Attems 1936, Golovatch and Wesener 2016)



Fauna	Altitude (m a.s.l.)	Country/state and main reference(s)
Genus <i>Hirtodrepanum</i> Golovatch, 1994		
202. <i>Hirtodrepanum latigonopum</i> Golovatch, 1994	2100–2600	Nepal (Golovatch 1994b, 2015a, Golovatch et al. 2016)
Genus <i>Kaschmiriosoma</i> Schubart, 1935	1000–3300	
203. <i>Kaschmiriosoma contortipes</i> Schubart, 1935	2000–3300	N Pakistan & India, Jammu & Kashmir (Schubart 1935, Silvestri 1936, Golovatch 1983, Golovatch and Martens 1996, Jeekel 2003, Shelley 2014)
204. <i>K. nulla</i> (Attems, 1936)	1000	India, Himachal Pradesh (Attems 1936, Golovatch and Martens 1996, Jeekel 2003, Golovatch and Wesener 2016)
205. <i>K. pleuropterum</i> (Attems, 1936)	2800	N Pakistan, Punjab (Attems 1936, Golovatch and Martens 1996, Jeekel 2003, Golovatch and Wesener 2016)
Genus <i>Kronopolites</i> Attems, 1914		
206. <i>Kronopolites coriaceus</i> Golovatch, 2015	2000	Nepal (Golovatch 2015a)
207. <i>K. occidentalis</i> Golovatch, 1983	1500	India, Jammu & Kashmir (Golovatch 1983, Golovatch and Martens 1996, Golovatch and Wesener 2016)
Genus <i>Orthomorpha</i> Bollman, 1893		
208. <i>Orthomorpha coarctata</i> (de Saussure, 1860)	600–650	Nepal & India, pantropical anthropochore (Golovatch and Martens 1996, Golovatch and Wesener 2016)
209. “ <i>O. almorensis</i> ” Turk, 1947	1600	India, Almora (Turk 1947, Golovatch and Martens 1996, Golovatch and Wesener 2016)
Genus <i>Oxidus</i> Cook, 1911		
210. <i>Oxidus gracilis</i> (C.L. Koch, 1847)	570–1200	Nepal & India, subcosmopolitan anthropochore (Golovatch and Martens 1996, Golovatch and Wesener 2016)
Genus <i>Pocockina</i> Jeekel, 1965		
211. <i>Pocockina schawalleri</i> Golovatch, 2016	150	Nepal (Golovatch 2016a)
Genus <i>Streptogonopus</i> Attems, 1914		
212. <i>Streptogonopus phipsoni</i> (Pocock, 1892)	≤2700	Pakistan, Bangladesh, Nepal & India, West Bengal (Golovatch 2015a, Golovatch and Wesener 2016)
Genus <i>Substrongylosoma</i> Golovatch, 1984	1000–2200	
213. <i>Substrongylosoma bifurcatum</i> Golovatch, 2016	2000	Nepal (Golovatch 2016a)
214. <i>S. distinctum</i> Golovatch, 1984	1200–1500	India, Darjeeling Distr. (Golovatch 1984, Golovatch and Martens 1996, Golovatch and Wesener 2016)
215. <i>S. falcatum</i> Golovatch, 1984	1000–1400	India, Darjeeling Distr. (Golovatch 1984, Golovatch and Martens 1996, Golovatch and Wesener 2016)
216. <i>S. exiguum</i> Golovatch, 2016	1900	Nepal (Golovatch 2016a)
217. <i>S. montigena</i> (Carl, 1935)	1200–2200	India, Darjeeling Distr. (Carl 1935, Golovatch 1984, Golovatch and Martens 1996, Golovatch and Wesener 2016)
218. <i>S. schawalleri</i> Golovatch, 1993	1620–2000	Nepal (Golovatch 1993, Golovatch and Martens 1996)
Genus <i>Sundanina</i> Attems, 1914		
219. “ <i>Sundanina</i> ” <i>septentrionalis</i> Turk, 1947	ca 1700	India, Almora (Turk 1947, Golovatch and Wesener 2016)

Fauna	Altitude (m a.s.l.)	Country/state and main reference(s)
Genus <i>Topalosoma</i> Golovatch, 1984	900	
220. <i>Topalosoma setiferum</i> Golovatch, 1984	900	India, Darjeeling Distr. (Golovatch 1984, Golovatch and Martens 1996, Golovatch and Wesener 2016)
Genus <i>Trogodesmus</i> Pocock, 1895		
221. <i>Trogodesmus uncinatus</i> (Attems, 1936)	?	India, Assam (Attems 1936, Golovatch and Wesener 2016 <sup>5</sup> )
Genus <i>Touranella</i> Attems, 1937	2300–2800	
222. <i>Touranella himalayaensis</i> Golovatch, 1994	2300–2700	Nepal (Golovatch 1994b, Golovatch and Martens 1996)
223. <i>T. pilosa</i> Golovatch, 2016	2600–2800	Nepal (Golovatch 2016b)
<b>Family Polydesmidae</b>	350–4250	
Genus <i>Bhutanodesmus</i> Golovatch, 1988		
224. <i>Bhutanodesmus velatus</i> Golovatch, 1988	350–450	Bhutan (Golovatch 1988, Golovatch and Martens 1996)
Genus <i>Epanerchodus</i> Attems, 1901	2300–4250	
225. <i>Epanerchodus buddis</i> (Golovatch, 1986)	3300–3400	Nepal (Golovatch 1986, Golovatch and Martens 1996, Golovatch et al. 2011)
226. <i>E. occultus</i> (Golovatch, 1986)	2300–2800	Nepal (Golovatch 1986, Golovatch and Martens 1996, Golovatch et al. 2011)
227. <i>E. sacer</i> (Golovatch, 1987)	3300–3400	Nepal (Golovatch 1987a, Golovatch and Martens 1996, Golovatch et al. 2011)
228. <i>E. theocraticus</i> (Golovatch, 1990)	2600–2800	Nepal (Golovatch 1990b, Golovatch and Martens 1996, Golovatch et al. 2011)
229. <i>E. theosophicus</i> (Golovatch, 1986)	3200	Nepal (Golovatch 1986, Golovatch et al. 2011, Golovatch and Martens 1996)
230. <i>Epanerchodus</i> sp.	3450–4250	Nepal & Bhutan (Golovatch and Martens 1996)
Genus <i>Glenniea</i> Turk, 1945	350–2800	
231. <i>Glenniea bhotiaensis</i> Golovatch, 1988	350–450	Bhutan (Golovatch 1988a, Golovatch and Martens 1996)
232. <i>G. indica</i> Turk, 1945	2800	India, Himachal Pradesh (Turk 1945a, 1945b, Golovatch 1988a, Golovatch and Martens 1996, Golovatch and Wesener 2016)
233. <i>G. martensi</i> (Golovatch, 1987)	1200	Nepal (Golovatch 1987b, 1988a, Golovatch and Martens 1996)
234. <i>G. minuscula</i> Golovatch, 1988	1900–2300	Bhutan (Golovatch 1988a, Golovatch and Martens 1996)
235. <i>G. perarmata</i> Golovatch, 1988	1680	Bhutan (Golovatch 1988a, Golovatch and Martens 1996)
Genus <i>Himalodesmus</i> Golovatch, 1986	1000–3400	
236. <i>Himalodesmus audax</i> Golovatch, 1986	2650	Nepal (Golovatch 1986, Golovatch and Martens 1996)
237. <i>H. benefactor</i> Golovatch, 1987	2600–3400	Nepal (Golovatch 1987a, Golovatch and Martens 1996)
238. <i>H. faustus</i> Golovatch, 1987	1000–1750	Nepal (Golovatch 1987a, Golovatch and Martens 1996)
239. <i>H. parvus</i> Golovatch, 1987	2200	Nepal (Golovatch 1987a, Golovatch and Martens 1996)
240. <i>H. prosperus</i> Golovatch, 1990	2600–2800	Nepal (Golovatch 1990b, Golovatch and Martens 1996)
241. <i>H. pulcher</i> Golovatch, 1987	2450	Nepal (Golovatch 1987a, Golovatch and Martens 1996)
242. <i>H. pygmaeus</i> Golovatch, 1986	3300–3400	Nepal (Golovatch 1986, Golovatch and Martens 1996)
243. <i>H. vigens</i> Golovatch, 1987	2150–2250	Nepal (Golovatch 1987a, Golovatch and Martens 1996)

Fauna	Altitude (m a.s.l.)	Country/state and main reference(s)
Genus <i>Typhlopygmaeosoma</i> Turk, 1972		
244. <i>Typhlopygmaeosoma hazeltonae</i> Turk, 1972	1850	India, Himachal Pradesh (Turk 1972, Shear 1986, Golovatch 1988b, Golovatch et al. 2014)
<b>Family Trichopolydesmidae</b>	450–4500	
Genus <i>Assamodesmus</i> Manfredi, 1955		
245. <i>Assamodesmus lindbergi</i> Manfredi, 1954	?	India, Assam (Manfredi 1954, Golovatch 1988b, Golovatch and Martens 1996, Golovatch et al. 2014)
Genus <i>Hingstonia</i> Carl, 1935	2000–4500	
246. <i>Hingstonia beatae</i> Golovatch, 1990	2400–3500	Nepal (Golovatch 1990b, Golovatch and Martens 1996, Golovatch et al. 2014)
247. <i>H. dorjulana</i> Golovatch, 1988	2450–3100	Bhutan (Golovatch 1988a, Golovatch and Martens 1996, Golovatch et al. 2014)
248. <i>H. eremita</i> Carl, 1935	2000	Nepal (Carl 1935, Golovatch 1986, Golovatch and Martens 1996, Golovatch et al. 2014)
249. <i>H. falcata</i> Golovatch, 1986	2650	Nepal (Golovatch 1986, Golovatch and Martens 1996, Golovatch et al. 2014)
250. <i>H. fittkaui</i> Golovatch, 1990	3350–3450	Nepal (Golovatch 1990b, Golovatch and Martens 1996, Golovatch et al. 2014)
251. <i>H. gogonana</i> Golovatch, 1988	3650–4000	Bhutan (Golovatch 1988a, Golovatch and Martens 1996, Golovatch et al. 2014)
252. <i>H. pahakholana</i> Golovatch, 1990	2600–2800	Nepal (Golovatch 1990b, Golovatch and Martens 1996, Golovatch et al. 2014)
253. <i>H. pelelana</i> Golovatch, 1988	3300–3400	Bhutan (Golovatch 1988a, Golovatch and Martens 1996, Golovatch et al. 2014)
254. <i>H. perarmata</i> Golovatch, 1986	3150	Nepal (Golovatch 1986, Golovatch and Martens 1996, Golovatch et al. 2014)
255. <i>H. serrata</i> Golovatch, 1987	3400–3600	Nepal (Golovatch 1987a, Golovatch and Martens 1996, Golovatch et al. 2014)
256. <i>H. sympatrica</i> Golovatch, 1990	3550–3650	Nepal (Golovatch 1990b, Golovatch and Martens 1996, Golovatch et al. 2014)
257. <i>H. variata</i> Golovatch, 1987	2600–4500	Nepal (Golovatch 1987a, 1990b, Golovatch and Martens 1996, Golovatch et al. 2014)
258. <i>H. yeti</i> Golovatch, 1988	1600–2600	Bhutan (Golovatch 1988a, Golovatch et al. 2014)
259. <i>Hingstonia</i> sp.	2200–3900	Nepal (Golovatch and Martens 1996)
Genus <i>Magidesmus</i> Golovatch, 1988	3100–3400	
260. <i>Magidesmus affinis</i> Golovatch, 1988	3300–3400	Bhutan (Golovatch 1988a, Golovatch et al. 2014)
261. <i>M. bhutanensis</i> Golovatch, 1988	3100	Bhutan (Golovatch 1988a, Golovatch et al. 2014)
Genus <i>Pseudosphaeroparia</i> Carl, 1932		
262. <i>Pseudosphaeroparia cavernicola</i> Turk, 1945	2800	India, Uttar Pradesh (Turk 1945a, 1945b, Golovatch and Martens 1996, Golovatch et al. 2014)
Genus <i>Sholaphilus</i> Carl, 1932	1100–2200	
263. <i>Sholaphilus asceticus</i> Golovatch, 1986	1300–1650	Nepal (Golovatch 1986, Golovatch and Martens 1996, Golovatch et al. 2014)
264. <i>S. dalai</i> Golovatch, 1986	2400	Nepal (Golovatch 1986, Golovatch and Martens 1996, Golovatch et al. 2014)
265. <i>S. gompa</i> Golovatch, 1990	2000–2100	Nepal (Golovatch 1990b, Golovatch and Martens 1996, Golovatch et al. 2014)
266. <i>S. lama</i> Golovatch, 1986	1800–2000	Nepal (Golovatch 1986, Golovatch and Martens 1996, Golovatch et al. 2014)

Fauna	Altitude (m a.s.l.)	Country/state and main reference(s)
267. <i>S. martensi</i> Golovatch, 1986	1100–1850	Nepal (Golovatch 1986, Golovatch and Martens 1996, Golovatch et al. 2014)
268. <i>S. monachus</i> Golovatch, 1990	2050–2150	Nepal (Golovatch 1990b, Golovatch and Martens 1996, Golovatch et al. 2014)
Genus <i>Topalodesmus</i> Golovatch, 1988		
269. <i>Topalodesmus communis</i> Golovatch, 1988	2000–2200	India, Darjeeling Distr. (Golovatch 1988b, Golovatch and Martens 1996, Golovatch et al. 2014)
Family <b>Pyrgodesmidae</b>	450–1200	
270–275? Several genera and species (including at least 2 species of <i>Cryptocorypha</i> Attems, 1907)	450–1200	Nepal (Golovatch and Martens 1996)

<sup>1</sup> A large, still unidentified species of *Monographis* is available from E Nepal, taken at 2400 m a.s.l. (M. Short, in litt.). Because the genus is feminine in gender, the species (adjective) must be named “*mira*”.

<sup>2</sup> A still unidentified species of *Unixenus* is available from E Nepal, taken at 3600–3900 m a.s.l. (M. Short, in litt.).

<sup>3</sup> The nominal subspecies is known only from S India (Silvestri 1923).

<sup>4</sup> The first record by Nguyen (2010) of this south Indian species from Nepal seems to be erroneous, based on no evidence whatsoever.

<sup>5</sup> Nguyen and Sierwald (2013) erroneously stated this species as deriving from Myanmar.

Results

Species of Diplopoda

Species concepts are only little addressed in diplopod taxonomy. To think about species limits and species definitions is not at all trivial; in nearly every case, a morphological species concept is used with the background idea that these entities, defined by external characters, fit well to the Biological Species Concept. In practical alpha-taxonomy it circumscribes reproductively isolated groups of specimens. Diplopod taxonomists largely base their identifications on adult male samples. Differences in male genitalic structure usually provide the basic characters that allow us to safely determine millipede species. In most cases this raises no problems. In the Himalayas, however, we have to tackle with numerous populations in a wide array of forest habitats found at various altitudes and in remote and secluded valleys. Hardly surprisingly, the Himalayas do support quite a number of examples of species swarms among Diplopoda as well. Species delimitation may then cause problems like those described by Martens (1978) for the polymorphous biantid harvestman *Biantes pernepalicus* Martens, 1978. Such situations also resemble the few known cases of insular species swarms in millipedes of Macaronesia (e.g. Enghoff 1992).

The following examples can be given and easily added to the roster of similar observations that Martens (2015) made or compiled for Himalayan mammals, birds, arachnids, insects and several other animal groups. Such a distribution pattern can be termed fanned (see below) and is also found in the endemic Himalayan diplopod genera *Beronodesmus* and *Beronodesmoides* containing 11 and seven species, respectively

(Golovatch 2016c, Golovatch et al. 2016). The main species-specific characters are in minor details of gonopodal structure, in particular, the shapes of the various outgrowths (Fig. 3). Vicariance speciation must have taken place *in situ*, with several of the congeners forming pairs or trios that can occur sympatrically or even syntopically and thus implying a series of secondary dispersal events.

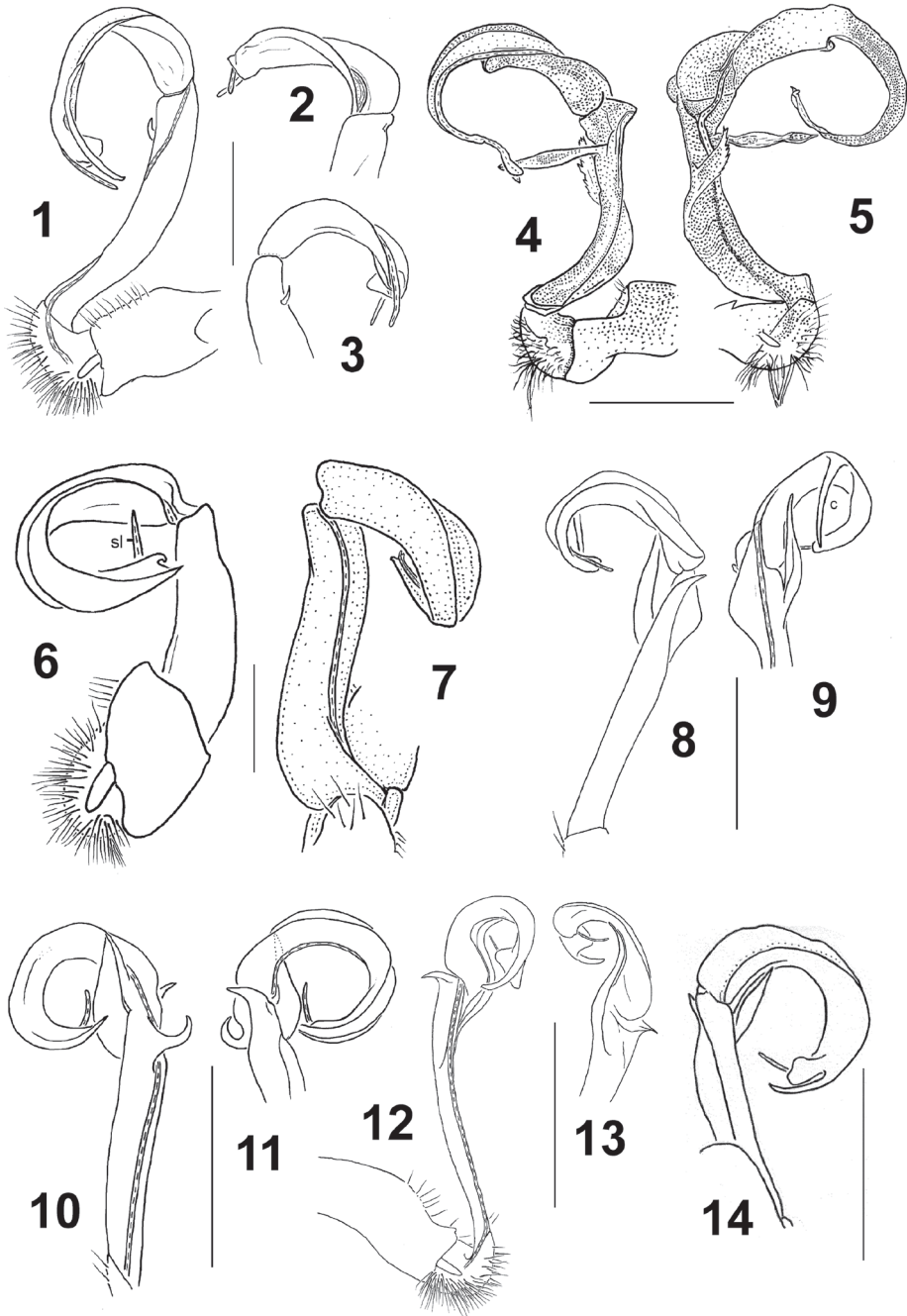
## Zoogeographical patterns and origins

### Ecology and dispersal abilities

The vast majority of Himalayan diplopod species are highly localized in distribution, both geographical and altitudinal. There are only few relatively widespread species like *Zephronia manca*, *Siphonorhinus cingulatus* (both recorded from Vietnam & Darjeeling District, India) or *Trichopeltis watsoni* (Bangladesh, Myanmar, Bhutan and India, Darjeeling Distr., West Bengal, Assam & near Kolkata). Despite extended collection activities over most parts of Nepal during several decades, most millipedes in the Himalayas remain known from only a single or very few localities. This particularly concerns the best-explored fauna of Nepal, Central Himalayas (ca 160 spp.), including species of the dominant family Paradoxosomatidae (82 spp., or >50%).

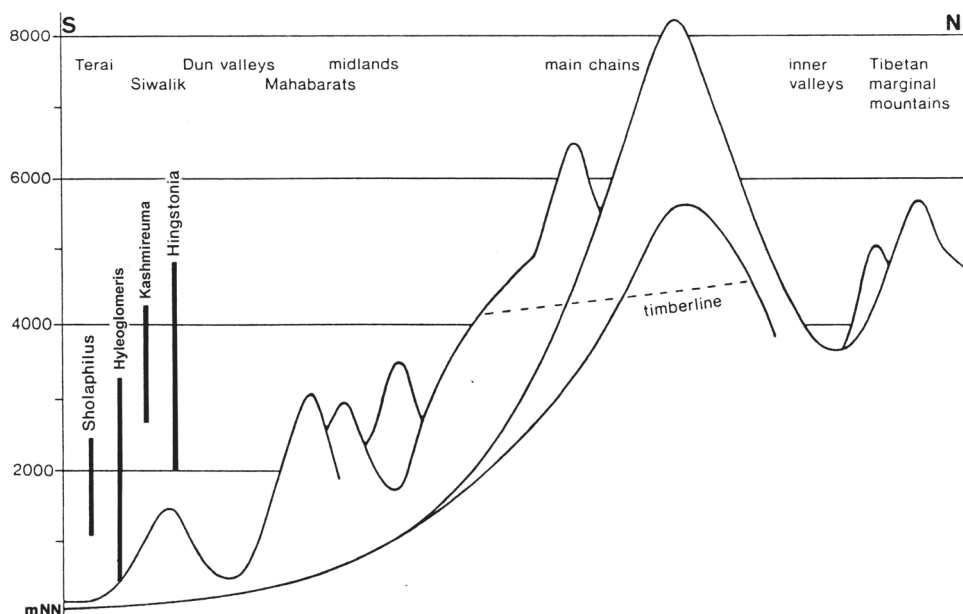
In contrast, most genera occur through a range of altitudes (Fig. 4), but are more or less restricted to forest habitats. The alpine (= nival) zone of the Central Himalayas which lies above closed forests appears to only marginally be populated by Diplopoda (Table 1, Figs 2, 4), the bulk of the fauna being confined to the tropical and subtropical forest belts. The highest records belong to *Nepalozonium trimaculatum* and *Nepalmatoiulus ivanloebli*, both found at 4800 m a.s.l. This pattern conforms to general knowledge that millipedes are basically a class of forest-dwelling terrestrial arthropods both trophologically and historically largely associated with woodlands and ranging from nemoral (= broadleaved forest) and coniferous forest in temperate regions in the north to rainforest tropical areas in the south (Golovatch 1997a, 1997b). Such a background is accepted and it serves as the basis for faunogenetic reconstructions using phyto- and palaeogeographical evidence.

According to Martens (1993, 2015), broad vertical distribution belts appear to be exceptional in animals at least in the Central Himalayas, in contrast to fanned ones which are especially characteristic of species-rich groups, both vertebrates and invertebrates. Yet the vertical width of a distributional belt varies very considerably between taxa. Diplopods in their natural habitats seem to be particularly restricted to their forest habitats, with little capacity for enlarging their areas, both vertically and horizontally. There is hardly any other larger land arthropod group that shows a similarly strong specialization and relation to a habitat. In many cases, congeners occupy only limited vertical belts and such patterns are the result of multi-layered speciation processes that occurred in secluded valleys and mountain massifs. There are obvious altitudinal adaptations resulting from the interaction between Pliocene/Pleistocene climate oscillations and speciation processes. Whilst species of different clades occupy narrow vertical



**Figure 3.** Gonopodal structural variations between several species of *Beronodesmus*: *B. martensi* Golovatch et al., 2016 (1–3), *B. serratus* Golovatch et al., 2016 (4, 5), *B. simplex* Golovatch, 2016 (6, 7), *B. distospinosus* Golovatch, 2015 (8, 9), *B. latispinosus* Golovatch, 2015 (10, 11), *B. sinuatospinus* Golovatch, 2015 (12, 13) and *B. gorkhalis* Golovatch, 2015 (14). Scale bars: 1.0 mm (4–5, 14), 0.5 mm (1–3, 8–13) or 0.4 mm (6, 7). After Golovatch (2015a, 2016c) and Golovatch et al. (2016).





**Figure 4.** Vertical distribution of several genera of Diplopoda in the Himalayas (modified, after Golovatch and Martens 1996).

belts, close congeners, i.e. sister species, are mostly horizontally allopatric because of their allopatric vicariance speciation. Sympatry or syntopy are quite common among congeners (see above for *Beronodesmus*, Fig. 3), this alone implying a series of secondary dispersal events. On the other hand, all 13 species of *Nepalmatoiulus* known from Nepal and Bhutan are nearly exclusively allopatric in distribution (Engelhoff 1987).

Narrow belts seem to be rare, when each individual species has been recorded from a single or very few localities, but even the whole species set combined remains restricted to a narrow altitudinal range. Much more common, rather usual are the situations when the vertical and horizontal distribution of a species is highly restricted, but that of the corresponding species-group or genus is very considerable (Table 1, Fig. 4).

Among the Diplopoda of the Himalayas, most if not all of the rather to highly species-rich genera show fanned vertical distribution patterns. Such are all genera at least in the orders Sphaerotheriida, Glomerida, Chordeumatida, Julida and Spirostreptida, as well as most in the order Polydesmida. Their origins seem to be very different, but profound *in situ* speciation is their general characteristic. No evident narrow belts seem to be distinguishable in the combined vertical distribution of millipede congeners in the Himalayas (Table 1, Figs 2, 4). Even within Nepal, a gradual east-west decline in diplopod diversity is clearly observed towards the country's central regions, apparently following the climate aridity gradient and increased absence of humid forest.

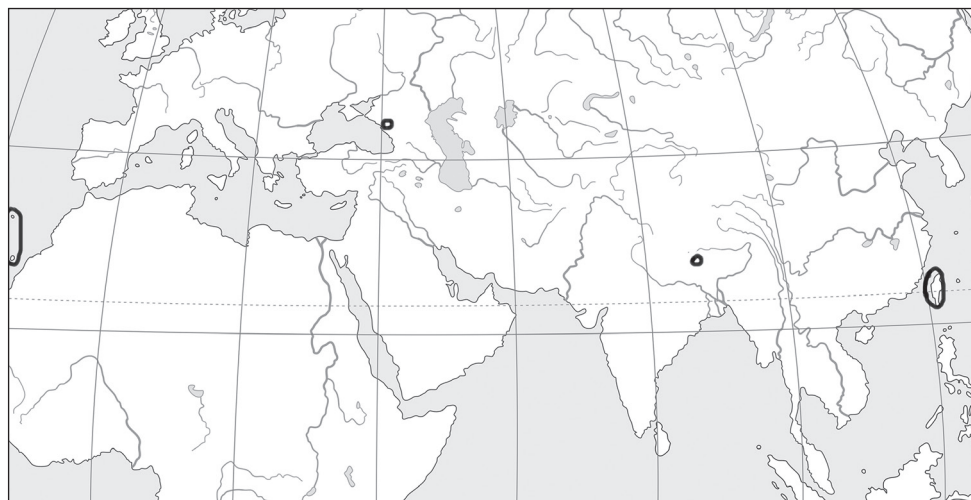
As noted above, zoogeographically the Himalayas are traditionally viewed as a vast, yet clear-cut transitional zone between the Palearctic and Oriental (= Indo-Malayan) realms. Martens (2015, p. 212) writes that "The renowned species diversity of the

Himalayan fauna results from the area's position between tropical SE Asia to the south and southeast, temperate High Asia to the north and dry Central Asia to the northwest, in addition to its proximity to endemic-rich SW China, which harbours many Tertiary relicts. Elements from all these areas contributed to and influenced the present faunal composition, creating one of the world's 25 biodiversity hotspots, Indo-Burma and the adjacent South Central China." He discriminated a predominantly immigrant fauna with five main sources: SW Chinese Himalayan from the northeastern Himalayan Arc; Indochinese Himalayan from the southeast; tropical Indian from the south; central Asian from the north via Tibet; and W Asian Himalayan from mountain ranges westwards to the Mediterranean. This fauna is mainly composed of species with good dispersal abilities such as bats, birds, butterflies, dragonflies and many other groups. Since millipedes are poor dispersers and only relatively few species are anthropochores, we refrain from enlisting any as belonging to this category, even though a few widespread Oriental species do reach the Himalayas from the east and/or southeast (e.g. the above *Zephronia manca*, *Siphonorhinus cingulatus*, *Streptogonopus phipsoni*, *Gonoplectus malayus malayus* or *Trichopeltis watsoni*). Human introductions cannot be excluded in such cases, these being especially apparent as regards the few unquestioned anthropochores like *Trigoniulus corallinus*, *Orthomorpha coarctata* or *Oxidus gracilis*.

In addition, a Sino-Himalayan fauna (or even a Sino-Himalayan region) is distinguished, which is characterized by remarkable diversity, partially of Indo-Malayan origins and partially Palaearctic in nature, but with marked peculiarities. Holt et al. (2012), based on the modern distributions and phylogenies of amphibians, birds and non-marine mammals, defined 20 distinct zoogeographic regions grouped into 11 realms, including a Sino-Japanese realm which appears to show closer phylogenetic affinities to the Palaearctic than to the Oriental realm. It includes Japan, Tibet and nearly all of China. Eventually, that paper represents one of the most consistent, but no less unsuccessful attempts at uncritically combining the landscape-typological (= zonal) and faunogenetic approaches to biogeography which, however, must be clearly separated at least as regards the biotas of older biomes (e.g. Chernov 1975, Golovatch 2015b). To reiterate Chernov (1975) briefly, from the "viewpoint" of a biome or more local landscape it only matters whether the constituent species properly function as its biotic elements, regardless of their origins. In contrast, from a faunogenetic point of view, the more ancient the biome or landscape, the more ancient its biota and the more complex its history. Thus both approaches must be clearly distinguished, especially as regards the relatively younger zonal biomes like tundra or taiga (= boreal forest) from the particularly ancient, rather regional than zonal, subtropical and tropical ones.

In terms of its faunal composition, the Sino-Himalayan region represents a mixed zone of elements derived from both the Palaearctic and Oriental realms, but it includes moreover a wealth of endemics with surprisingly small and often relict distributions (Martens 2015). It is within this category that many of the Himalayan Diplopoda seem best to place. Perhaps the most conspicuous example of such a pattern is represented by the definitely relict order Siphonocryptida which globally contains only two genera and seven species. Thus, the genus *Siphonocryptus* Pocock, 1894, comprises





**Figure 5.** Distribution of the genus *Hirudicryptus* (Siphonocryptidae, Siphonocryptida). After Golovatch et al. (2015).

three species: one in Sumatra, Indonesia, the other two in continental Western Malaysia. In contrast, the distribution pattern of *Hirudicryptus* Enghoff & Golovatch, 1995 is trans-Palaearctic (Fig. 5). The type species occurs only on Madeira and the Canaries, where it is largely confined to the relict, subtropical, laurisilva biome. One species each is endemic to Taiwan, to Nepal and to the NW Caucasus (Golovatch et al. 2015, Zuev 2017). It may well be that the distribution pattern under consideration dates back at least to the Oligocene times of the so-called “Warm Earth” to have highly probable explanations rooted in palaeobotanical evidence. These imply a gradual shrinkage and disruption ever since of the previously dominating and continuous subtropical biome (Golovatch 1997a, 1997b, Zherikhin 2003). Being so vastly disjunct, the present-day distribution of Siphonocryptida is best accounted for by extinction events (Shelley and Golovatch 2011).

### Genus- and species-level relations

Further possible examples of the Sino-Himalayan pattern seem to be represented by *Glenniea* (Polydesmidae, a largely Holarctic family), with five species from the Himalayas of Nepal and Bhutan, and three in S China (Golovatch 2015b), *Nepalella* (Megalotylidae, the genus being the westernmost in that temperate to tropical Asian family), with 23 species or subspecies from Nepal, S China and SE Asia (Minelli 2015, Table 1), *Hirtodrepanum* (Paradoxosomatidae, a subcosmopolitan family absent only from N America) with one species each in Nepal and S China (Golovatch 2014a), and *Martensodesmus* (Opisotretidae, the genus being the westernmost in that Indo-Australian family), with at least five species from the Himalayas of Nepal and Bhutan, two in S China, and one in S Vietnam (Golovatch et al. 2013). The latter example, however, may likewise illustrate the predominating zoogeographical connections of

the Himalayan fauna with the Indo-Malayan one. Such are also the genera *Cryptocorypha* (Pyrgodesmidae), with 14 described species from S India, Myanmar, S China and Australasia, eastwards to Vanuatu, Melanesia (Golovatch and VandenSpiegel 2015, Golovatch and Wesener 2016), *Zephronia* (Sphaerotheriida), with 38 species or subspecies from Nepal, NE India, Myanmar, Thailand, Cambodia, Vietnam, Western (= mainland) Malaysia and Hong Kong (Wesener 2016), *Siphonorhinus* (Siphonophorida), with eight species from Indonesia, Vietnam, Cambodia, Laos, India and Madagascar (Minelli 2015) and *Pocockina* (Paradoxosomatidae), with three species from Nepal and Myanmar (Golovatch 2016b). The small genus *Trichopeltis* (Cryptodesmidae) includes nine described species, largely from Indochina, Sumatra, Indonesia, Myanmar and S China; only the much more widespread *T. watsoni* and *Gonoplectus malayus malayus* reach as far west as the Himalayas of India (Table 1). Similarly, amongst the Paradoxosomatidae the genus *Trogodesmus* contains four species in Myanmar and one more in Assam, India (Nguyen and Sierwald 2013); *Touranella* harbours two species from Nepal and further four from Vietnam (Golovatch 2016b); *Kronopolites* has one species in Jammu & Kashmir, India, one in Thailand, one in Laos, and another nine in China, including one in Taiwan (Likhitrakarn et al. 2015, Golovatch 2015a); *Anoplodesmus* is a large genus which, regardless of a few pantropical anthropochores, comprises approximately 35 species in S (India and Sri Lanka), E (Taiwan) and SE Asia (eastwards up to Sumatra, Indonesia), including nine congeners confined to the Himalayas (Golovatch 2016a, Table 1); *Streptogonopus* contains not only *S. phipsoni*, a species quite widespread in the Himalayas and certain adjacent countries (Table 1), but also two more in India, and one each in Eritrea, Thailand and Vietnam (Nguyen et al. 2016); *Delarthrum* is one of the most species-rich genera of Diplopoda (56 spp.), with most (55 spp.) of its diversity confined to the Himalayas of Pakistan, Nepal and India (Table 1), and only one outlier congener in S India (Golovatch and Wesener 2016, Golovatch 2016b). Much like *Delarthrum*, the genus *Sholaphilus* demonstrates faunal connections between the Himalayas (6 spp., Table 1) and S India (1 sp., Golovatch and Wesener 2016).

### Suprageneric relations

At these taxonomic levels, the fully to largely tropical orders Sphaerotheriida, Siphonophorida and Spirostreptida, as well as most of Spirobolida, Platydesmida and Polydesmida (at least some Haplodesmidae, Cryptodesmidae, Paradoxosomatidae, Pyrgodesmidae and Trichopolydesmidae) seem to represent Indo-Malayan elements in the Himalayan millipede fauna. A siphonophoridan and a cryptodesmid species, both have been recorded as far north as N Pakistan (Golovatch 1991). However, at the species level the bulk of diversity is endemic and highly localized, both horizontally and vertically, clearly due to allopatric vicariance (cf. Golovatch and Martens 1996). There are several Himalayan endemic to subendemic diplopod genera, but not a single suprageneric taxon: *Kophosphaera* (Sphaerotheriida, seven species, Wesener 2016 & Table 1), *Koponenius* (Polydesmida, four species from Nepal, NW India and Myanmar (Golovatch and VandenSpiegel 2014, 2016), *Kashmireuma* (Chordeumatida), with three

species from Nepal and N India (Table 1), *Himalodesmus* (Polydesmidae, Table 1), *Beronodesmoides*, *Beronodesmus*, *Substrongylosoma* (all Paradoxosomatidae, Table 1), *Magidesmus* (Trichopolydesmidae, Table 1), as well as the monotypic *Assamodesmus*, *Bhutanodesmus*, *Topalodesmus*, *Topalosoma* and *Typhlopygmaeosoma* (Table 1).

Faunal connections to the northwest and/or north are demonstrated by a few examples only. Even at the generic level, not all of them could unequivocally be treated as likely Palaearctic components in the Himalayan millipede fauna. Thus, the genus *Kaschmiriosoma* (Paradoxosomatidae) is composed of three species endemic to N Pakistan, and one to both N Pakistan and N India (Jeekel 2003). Such a pattern might seem to have been accounted for by an originally northwestwards dispersal. Even in the absence of a phylogenetic reconstruction, the gonopodal structure in *Kaschmiriosoma*, especially the particularly complex, strongly coiled and thus apomorphic solenophores as observed in the southernmost, Himalayan *K. contortipes* and *K. nulla*, may rather be evidence of a Palaearctic origin of the genus. Its deemed closest relatives within the tribe Sulciferini, also often showing particularly complex and strongly twisted gonopodal solenophores, are observed in the genera *Gonobelus* Attems, 1936, *Inversispina* Zhang, in Zhang et al. 1997 and a few others, all confined to southern China, occasionally including Taiwan (Jeekel 1980, Golovatch 2012, 2016b).

Ties to the north are much better pronounced, e.g., in the genera *Tianella* (Cleidogonidae), *Epanerchodus* (Polydesmidae), *Bollmania* (Caspiopetalidae) and *Anaulaciulus* (Julidae). *Tianella* has two described and a number on still undescribed species in Kyrgyzstan and Kazakhstan, Central Asia, as well as 11 named species in Nepal and a few undescribed ones from both Nepal and N India (Mauriès 1988, Read and Golovatch 1994, Table 1). *Epanerchodus* is a very large genus comprising 70+ species from Central and E Asia: Russian Far East, Korea, China, Taiwan and Japan, as well as several species from Nepal (Minelli 2015, Table 1). *Bollmania* is composed of eight described and a few undescribed species ranging from Turkmenistan, Iran, Uzbekistan, Tajikistan and Afghanistan in Central Asia to S China; one species is known from the Himalayas of Pakistan (Stoev et al. 2008, Table 1). *Anaulaciulus* is also a highly speciose Asian genus which contains nearly 50 species ranging from across the Himalayas, through China, to the Russian Far East, Korea, Japan and Taiwan (Korsós 2001, Table 1). It is partly sympatric with still another, similarly large, Asian genus *Nepalmatoiulus* (Julidae), which harbours 55 species also distributed across the Himalayas, but then extending more to the east and southeast (S China, Taiwan, S Ryukyus, Myanmar, Indochina and peninsular Malaysia) (Enghoff 1987, Korsós and Lazányi 2013, Table 1). In the Himalayas, many species from these genera are high-montane (Table 1), thus reinforcing their presumed Palaearctic origins. The occurrence of the sole known species of *Nepalozonium* (Polyzoniida) at 4700–4800 a.s.l., i.e. among the highest records in the entire class, coupled with the family Hirudisomatidae where it belongs being strictly Holarctic (Minelli 2015), is clearly evidence of its Palaearctic roots.

The pattern demonstrated by the very large genus *Hyleoglomeris* (Glomeridae) strongly resembles that of the family Siphonocryptidae (see above and Fig. 5), but in no way is it relictual. Indeed, its 100+ species range from the Balkans and Greek

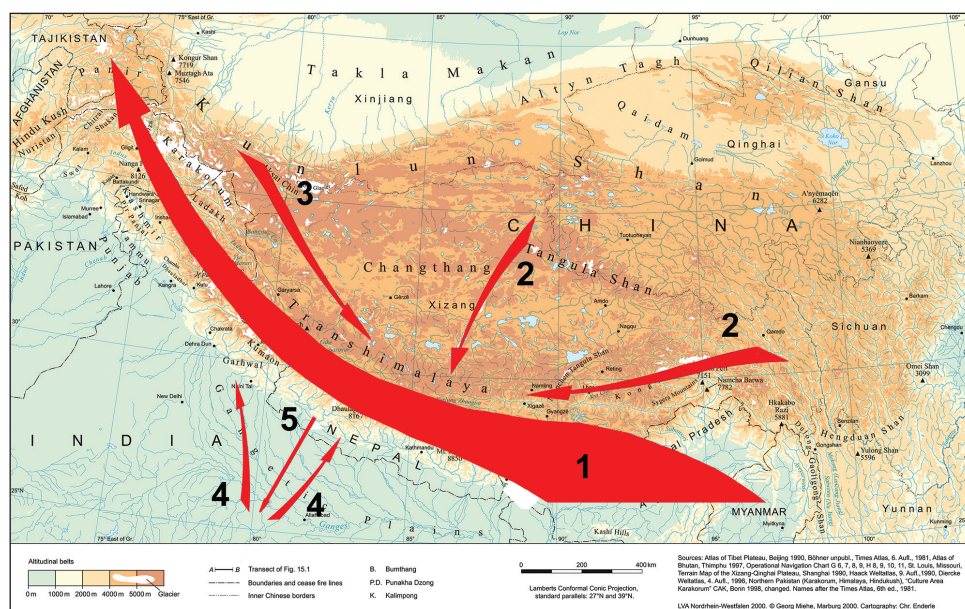
islands in the west, through Anatolia, the Caucasus, Central Asia and the Himalayas, to China, Korea, Japan, and Taiwan in the east, and through Indochina to the Philippines and Sulawesi, Indonesia in the southeast (Golovatch et al. 2006, Table 1). This picture actually reflects one of the fundamental patterns of historical biogeography as evidenced in the entire class Diplopoda (Shelley and Golovatch 2011). Generally, west-east trans-Himalayan faunal connections are traced in numerous millipede higher taxa: Glomerida, Julida, Chordeumatida, Callipodida, Siphonocryptida, Spirostreptida, Polydesmida etc. Southeast Asia is the only corner in the world where all 16 extant orders of Diplopoda are still to be found. In many cases, the Himalayas might have served as a paramount stepping stone and refugium in linking, much more in the past than at present, the faunas of SE Asia to those of Europe and W Asia. In the past, the Himalayas started rising and absorbing surrounding faunal elements often already present in the area. After having gained a certain height, the Himalayas functioned more as a trap, a “prison”, mountain ridges and deep valley systems hindering further faunal exchange, with the tremendous speciation process that came into action. Old migration routes both ways are thereby evident, although the influence of the Oriental fauna is by far greater. Since the uplift of the Himalayas started in the early Oligocene (about 27 Mya), the diplopod fauna of the region has gradually acquired its own, highly characteristic, very rich and diverse composition, multi-layered and very complex, with profound *in situ* radiations and vicariance events (cf. Golovatch and Martens 1996, Martens 2015). At least some of the oldest components are presently highly disjunct and clearly relict, as is the order Siphonocryptida (see above & Fig. 5). The most recent faunal layer is certainly represented by the few pantropical or subcosmopolitan introductions like *Trigoniulus corallinus*, *Orthomorpha coarctata* or *Oxidus gracilis*.

## Conclusions

Since the previous review of millipede chorology and faunogenesis in the Himalayas (Golovatch and Martens 1996), our knowledge of the Himalayan fauna has become considerably enriched (ca 200 vs >270 spp.) and often refined taxonomically. This is particularly true of the composition of the dominant family Paradoxosomatidae. However, the main results and trends remain unchanged.

The Himalayas support a highly rich, diverse, multi-layered, mostly endemic diplopod fauna. This is the result of mixing the ancient, apparently Tertiary and younger, Plio-Pleistocene elements of various origins, as well as the most recent anthropochore introductions. At the species and, partly, generic levels, the fauna is largely autochthonous and sylvicolous, formed through abounding *in situ* radiation and vicariance events, when overall the species from large genera and families tend to occupy a wide range of altitudes, but nearly each of the constituent species shows a distribution highly localized both horizontally and altitudinally, yet quite often with sympatry or even syntopy involved. The bulk of the fauna is Indo-Malayan in origin, with individual genera or families shared with those of SE Asia (mostly) and/or S India (few) (Fig. 6).





**Figure 6.** General schematic picture of the faunogenesis of Himalayan Diplopoda. Arrows reflect the main pathways of faunal migration or exchange, their thickness roughly corresponding to the degree of influence. The thickest arrow 1 clearly emphasizes the dominant roles the Indo-Malayan core fauna may have played in the present-day composition of the Himalayan fauna, its most ancient layers extending westwards to reach central and western Asia, as well as Europe (by default also northwards up to eastern Asia and even North America). The considerably less thick arrows 2 and 3 are to reflect the more subordinate roles the Sino-Himalayan and Palearctic elements, respectively, could have played in the modern Himalayan fauna. Arrows 4 and, especially, 5 are even less thick and demonstrate the relatively minor faunal exchanges to be presumed between the Indian and Himalayan faunas.

Their constituent species tend to be lowland to mid-montane, but the general rule “(sub)tropical organisms for (sub)tropical environments only” fails very often.

The Palearctic influence is modest (Fig. 6), but still can be traced in several genera and families. Collectively, their species tend to be high montane, but with numerous exceptions as well. The trans-Himalayan faunal connections at higher taxonomic levels, generic to ordinal, that link SE Asia to Europe are manifest. They show routes and directions of ancient dispersal both ways, but the one from SE Asia seems to have prevailed over the opposite one. Moreover, certain fragments or offshoots of such ancient, obviously Tertiary, opposite migrations more or less along the southern coasts of the receding Tethys Sea may have been left *en route* in S and SW China, as well as in N Pakistan and Central Asia.

One must also take into account that a number of presumably Himalayan species groups might have originated from the times when Tibet was still forest-covered and the Himalayan chain still in its infancies. According to Schmidt (2006), stem species invaded the raising Himalayas from the north where they developed to presently known spe-

cies swarms. After the Himalayas and Tibetan Plateau had raised sufficiently high, Tibet became drier and the forests vanished including their fauna, the Himalayas becoming their exile. Schmidt coined the term “Tibeto-Tertiary element” of paleo-Tibetan origin with present Himalayan distributions (Schmidt 2006, Schmidt et al. 2012).

The particularly rich Himalayan diplopod fauna with its numerous small-ranging species confined to permanent forest sheds new light on a much disputed controversy among geographers, zoologists, taxonomists, climatologists and glaciologists (Kuhle 1982, 2015 and figure 4 therein). Was the central Himalayan chain, at least at certain sections of the Pleistocene, covered by a complete shield of ice? Taxonomists dealing with low-dispersal soil/litter-dwelling arthropods have a clear response. Any ice cover would have been detrimental to the local soil arthropod fauna and would have driven its larger part or entirely to extinction. Only a long and steady evolution under more or less constant, albeit slightly varying, conditions would have allowed the biota to develop gradually over long geological periods (Martens 2015). This scenario certainly applies to all Himalayan Diplopoda.

The above picture of faunal connections (Fig. 6) is consistent both with general wisdom (e.g. Martens 2015) and our previous analysis (Golovatch and Martens 1996), the salient aspects of Diplopoda, contrary to many other animal groups in the Himalayas, being their pronounced sylvicoly, extremely diverse and small-ranging species endemism, and mostly Oriental and/or Indian origins, while some of the rather ostensible influence of the Palaearctic may have come not only from the north and/or northwest, but also from the currently subtropical regions of S China. Reciprocal migrations from the Himalayan faunal knot as a major refugium and secondary diversification centre also seem quite plausible, but documenting such requires detailed phylogenies which unfortunately are still almost missing.

## Acknowledgements

J.M. thanks all of the many co-workers who accompanied him and made the various expeditions as successful as they finally turned out. His wife Beate especially is to be mentioned; she participated in the 1983 extended expedition and, most importantly, encouraged him to leave for Asia nearly annually for many weeks. The Feldbausch-Stiftung and the Wagner-Stiftung at the Fachbereich Biologie of Mainz University granted financial aid to J.M. We both heartily thank all colleagues, friends and institutions.

## References

- Attems C (1936) Diplopoda of India. *Memoirs of the Indian Museum* 11(4): 133–323.
- Attems C (1944) Neue Polydesmoidea. *Zoologischer Anzeiger* 144(11/12): 223–251.
- Carl J (1935) Polydesmiden gesammelt von Major R.W. Hingston auf der III. Everest-Expedition, 1924. *Revue suisse de Zoologie* 42(10): 325–340. <https://doi.org/10.5962/bhl.part.118945>

- Chernov YI (1975) [Nature zonation and terrestrial animal life]. Mysl, Moscow, 222 pp. [In Russian]
- Condé B (1962) Révision d'un polyxenidé indien décrit par F. A. Turk. Bulletin de la Société zoologique de France 87(4): 452–458.
- Condé B, Jacquemin-Nguyen Duy M (1968) Diplopodes pénicillates et diploures campodéidés. Khumbu Himal 3: 4–8.
- Demange JM (1961) Matériaux pour servir à une révision des Harpagophoridae (Myriapodes – Diplopodes). Mémoires du Muséum national d'Histoire naturelle, Sér. A, Zoologie, 24: 1–274.
- Demange JM (1988) Myriapodes diplopodes de l'expédition zoologique du Muséum d'histoire naturelle de Bâle au royaume du Bhoutan (Spirostreptoidea : Harpagophoridae et Polydesmoidea). Entomologica Basiliensia 12: 7–14.
- Dobremez JF (1972) Les grandes divisions phytogéographiques du Népal et de l'Himalaya. Bulletin de la Société botanique de France 119: 111–120. <https://doi.org/10.1080/00378941.1972.10839010>
- Enghoff H (1987) Revision of *Nepalmatoiulus* Mauriès, 1983 – a Southeast Asiatic genus of millipedes (Diplopoda: Julida: Julidae). Courier Forschungsinstitut Senckenberg 93: 241–331.
- Enghoff H (1992) Macaronesian millipedes (Diplopoda) with emphasis on endemic species swarms on Madeira and the Canary Islands. Biological Journal of the Linnean Society 46: 153–161. <https://doi.org/10.1111/j.1095-8312.1992.tb00857.x>
- Golovatch SI (1983) Two Paradoxosomatidae from the Kashmir Himalayas (Diplopoda). Senckenbergiana biologica 63(3/4): 297–302 (for 1982).
- Golovatch SI (1984) Some new or less known Paradoxosomatidae (Diplopoda, Polydesmida) from India. Acta Zoologica Hungarica 30(3–4): 327–352.
- Golovatch SI (1986) Diplopoda from the Nepal Himalayas: Polydesmidae, Fuhrmannodesmidae. Senckenbergiana biologica 66(4/6): 345–369.
- Golovatch SI (1987a) Diplopoda from the Nepal Himalayas. Opisetretidae, additional Polydesmidae and Fuhrmannodesmidae. Courier Forschungsinstitut Senckenberg 93: 203–217.
- Golovatch SI (1987b) Diplopoda from the Nepal Himalayas. Glomeridae, additional Opisetretidae. Courier Forschungsinstitut Senckenberg 93: 219–228.
- Golovatch SI (1988a) On the first Polydesmidae, Opisetretidae and Fuhrmannodesmidae from Bhutan (Diplopoda, Polydesmida). Entomologica Basiliensia 12: 15–48.
- Golovatch SI (1988b) On three remarkable genera of Polydesmoidea (Diplopoda: Polydesmida) from the Himalayas of India. Folia Entomologica Hungarica 49: 41–47.
- Golovatch SI (1990a) Diplopoda from the Nepal Himalayas. The first Paradoxosomatidae (Polydesmida). Spixiana 13(1): 9–24.
- Golovatch SI (1990b) Diplopoda from the Nepal Himalayas. Several additional Polydesmidae, and Fuhrmannodesmidae (Polydesmida). Spixiana 13(3): 237–252.
- Golovatch SI (1991) On a small collection of millipedes (Diplopoda) from northern Pakistan and its zoogeographic significance. Revue suisse de Zoologie 98(4): 865–878. <https://doi.org/10.5962/bhl.part.79815>
- Golovatch SI (1992) Diplopoda from the Nepal Himalayas. Some additional Paradoxosomatidae. Senckenbergiana biologica 72(1–3): 183–203.

- Golovatch SI (1993) On several new or poorly-known Oriental Paradoxosomatidae (Diplopoda Polydesmida). *Arthropoda Selecta* 2(1): 3–14.
- Golovatch SI (1994a) Diplopoda from the Nepal Himalayas. Further Paradoxosomatidae (Polydesmida). *Senckenbergiana biologica* 73(1–2): 163–182.
- Golovatch SI (1994b) Diplopoda from the Himalayas. Two new Alogolykini (Polydesmida: Paradoxosomatidae). *Senckenbergiana biologica* 73(1–2): 183–187.
- Golovatch SI (1996) Diplopoda from the Nepal Himalayas. Review of the genus *Orophosoma* Jeekel 1980 (Polydesmida: Paradoxosomatidae). *Senckenbergiana biologica* 76(1–2): 163–184.
- Golovatch SI (1997a) On the main patterns of millipede diversity in Eurasia (Diplopoda). *Senckenbergiana biologica* 77(1): 101–106.
- Golovatch SI (1997b) On the main traits of millipede distribution and faunogenesis in Eurasia (Diplopoda). *Entomologica Scandinavica*, Suppl. 51: 199–208.
- Golovatch SI (2012) On several new or poorly-known Oriental Paradoxosomatidae (Diplopoda: Polydesmida), XII. *Arthropoda Selecta* 21(1): 1–12.
- Golovatch SI (2014a) On several new or poorly-known Oriental Paradoxosomatidae (Diplopoda: Polydesmida), XV. *Arthropoda Selecta* 23(1): 1–19.
- Golovatch SI (2014b) On several new or poorly-known Oriental Paradoxosomatidae (Diplopoda: Polydesmida), XVI. *Arthropoda Selecta* 23(3): 227–251.
- Golovatch SI (2015a) On several new or poorly-known Oriental Paradoxosomatidae (Diplopoda: Polydesmida), XVII. *Arthropoda Selecta* 24(2): 127–168.
- Golovatch SI (2015b) Cave Diplopoda of southern China with reference to millipede diversity in Southeast Asia. *ZooKeys* 510: 79–94. <https://doi.org/10.3897/zookeys.510.8640>
- Golovatch SI (2016a) On several new or poorly-known Oriental Paradoxosomatidae (Diplopoda: Polydesmida), XVIII. *Arthropoda Selecta* 25(1): 1–18.
- Golovatch SI (2016b) On several new or poorly-known Oriental Paradoxosomatidae (Diplopoda: Polydesmida), XIX. *Arthropoda Selecta* 25(2): 131–152.
- Golovatch SI (2016c) On several new or poorly-known Oriental Paradoxosomatidae (Diplopoda: Polydesmida), XX. *Arthropoda Selecta* 25(3): 219–240.
- Golovatch SI, Martens J (1996) On the distribution and faunogenesis of Himalayan millipedes (Diplopoda): Preliminary results. *Mémoires du Muséum national d'Histoire naturelle* 169: 163–174.
- Golovatch SI, VandenSpiegel D (2014) *Koponenius* gen. nov., a new genus of the millipede family Haplodesmidae from the Himalayas of India and Nepal (Diplopoda: Polydesmida). *Zootaxa* 3894(1): 141–151. <https://doi.org/10.11646/zootaxa.3894.1.11>
- Golovatch SI, VandenSpiegel D (2015) A new species of the millipede genus *Cryptocorypha* Attems, 1907, from Myanmar (Diplopoda: Polydesmida: Pyrgodesmidae). *Arthropoda Selecta* 24(1): 27–31.
- Golovatch SI, VandenSpiegel D (2016) A new species of the millipede genus *Koponenius* Golovatch et VandenSpiegel, 2014, from Nepal (Diplopoda: Polydesmida: Haplodesmidae). *Russian Entomological Journal* 25(2): 219–223.
- Golovatch SI, Wesener T (2016) A species checklist of the millipedes (Myriapoda, Diplopoda) of India. *Zootaxa* 4129(1): 001–075. <https://doi.org/10.11646/zootaxa.4129.1.1>



- Golovatch S, Evsyukov A, Reip HS (2015) Colobognatha millipedes in the Caucasus (Diplopoda: Polyzoniida, Platydesmida, Siphonocryptida). *Zootaxa* 3972(2): 250–266. <https://doi.org/10.11646/zootaxa.3972.2.6>
- Golovatch SI, Geoffroy JJ, Mauriès JP (2006) Review of the millipede genus *Hyleoglomeris* Verhoeff, 1910 (Diplopoda, Glomerida, Glomeridae), with descriptions of new species in Southeast Asia. *Zoosystema* 28(4): 887–915.
- Golovatch SI, Geoffroy JJ, VandenSpiegel D (2014) Review of the millipede family Trichopolydesmidae in the Oriental realm (Diplopoda, Polydesmida), with descriptions of new genera and species. *ZooKeys* 414: 19–65. <https://doi.org/10.3897/zookeys.414.7671>
- Golovatch SI, Mikhaljova EV, Chang HW (2011) The millipede family Polydesmidae in Taiwan, with descriptions of five new species (Polydesmida, Diplopoda). *ZooKeys* 93: 9–42. <https://doi.org/10.3897/zookeys.93.1167>
- Golovatch SI, VandenSpiegel D, Semenyuk II (2016) On several new or poorly-known Oriental Paradoxosomatidae (Diplopoda: Polydesmida), XXI. *Arthropoda Selecta* 25(4): 335–354.
- Golovatch SI, Geoffroy JJ, Stoev P, VandenSpiegel D (2013) Review of the millipede family Opisotretidae (Diplopoda, Polydesmida), with descriptions of new species. *ZooKeys* 302: 13–77. <https://doi.org/10.3897/zookeys.302.5357>
- Holt BG, Lessard JP, Borregaard MK, Fritz SA, Araújo MB, Dimitrov D, Fabre PH, Graham CH, Graves GR, Jönsson KA, Nogués-Bravo D, Wang ZH, Whittaker RJ, Fjeldså J, Rahbek C (2012) An update of Wallace's zoogeographic regions of the world. *Science Express*: 1–191. <https://doi.org/10.1126/science.1228282>
- Jeekel CAW (1980) The generic allocation of some little-known Paradoxosomatidae from South-East Asia (Diplopoda, Polydesmida). *Revue suisse de Zoologie* 87(3): 651–670. <http://dx.doi.org/10.5962/bhl.part.85538>
- Jeekel CAW (2003) Paradoxosomatidae from North Pakistan, collected by Cl. Besuchet and I. Löbl in 1983 (Diplopoda, Polydesmida). *Myriapod Memoranda* 6: 12–27.
- Korsós Z (1996) An approach to the revision of the East Asian millipede genus *Anaulaciulus*. *Mémoires du Muséum national d'Histoire naturelle* 169: 35–43.
- Korsós Z (2001) Diplopoda from the Nepal Himalaya: Towards the clarification of the genus *Anaulaciulus* Pocock 1895 (Diplopoda, Julida, Julidae, Brachyiulini). *Senckenbergiana biologica* 81(1/2): 61–81.
- Korsós Z, Lazányi E (2013) Three new species of the millipede genus *Nepalmatoiulus* (Diplopoda: Julidae) from Taiwan and Japan, with notes on its biogeography. *Edaphologia* 92: 1–6.
- Korsós Z, Geoffroy JJ, Mauriès JP (2009) The fifth element: reconnection of the disjunct distribution of the members of Siphonocryptida (Diplopoda) with the description of a new species from Nepal. *Journal of Natural History* 43(7-8): 435–445. <https://doi.org/10.1080/00222930802610428>
- Kuhle M (1982) Der Dhaulagiri- und Annapurna-Himal. Ein Beitrag zur Geomorphologie extremer Hochgebirge. *Zeitschrift für Geomorphologie, Suppl.* 41: 1–229.
- Kuhle M (2015) The Glacial (LGP, MIS 3-2) Marsyandi Nadi-icestream network between the junction of the Nar Khola glacier (Damodar Himal) and the junction of the Ngadi Khola (Manaslu Himal) with its Dudh-, Dana-, and Myardi-tributary glaciers from east-north-east up to south-east of Annapurna II. S. 9-61. In: Hartmann M, Weipert J (Hrsg.)

- Biodiversität und Naturausstattung im Himalaya V, Verein der Freunde und Förderer des Naturkundemuseums Erfurt e.V., Erfurt, 580 pp.
- Likhitrakarn N, Golovatch SI, Panha S (2015) Review of the millipede genus *Kronopolites* Attems, 1914 (Diplopoda, Polydesmida, Paradoxosomatidae), with the description of a new species from Laos. *ZooKeys* 472: 27–41. <https://doi.org/10.3897/zookeys.472.9001>
- Manfredi P (1954) Un nouveau polydesmien cavernicole de l'Assam (Inde). *Notes Biospéologiques* 9: 141–144.
- Martens J (1978) Opiliones aus dem Nepal-Himalaya. IV. Biantidae (Arachnida). *Senckenbergiana biologica* 58(5–6): 347–414.
- Martens J (1984) Vertical distribution of Palaearctic and Oriental faunal components in the Nepal Himalayas. *Erdwissenschaftliche Forschung* 18: 321–336.
- Martens J (1993) Bodenlebende Arthropoda im zentralen Himalaya: Bestandsaufnahme, Wege zur Vielfalt und ökologische Nischen. *Erdkundliches Wissen* 112: 231–249.
- Martens J (2015) 10. Fauna – Himalayan patterns of diversity. In: Miehle G, Pendry C, Chaudhary R (Eds) *Nepal. An introduction to the natural history, ecology and human environment of the Himalayas*. Royal Botanic Garden Edinburgh, 211–249.
- Mauriès JP (1982) Une famille nouvelle et deux genres nouveaux de Cleidogonoidea, avec notes sur la classification de la superfamille (Diplopoda, Craspedosomida). *Steenstrupia* 8(6): 165–176.
- Mauriès JP (1983) Myriapodes du Népal (Mission I. Löbl et A. Smetana 1981). I. Diplopodes iuliformes (Iulida, Cambalida et Spirostreptida): *Nepalmatoiulus* nov. subgen. *Revue suisse de Zoologie* 90(1): 127–138.
- Mauriès JP (1988) Myriapodes du Népal. II. Diplopodes craspedosomides nouveaux de l'Himalaya et de la région indo-malaise (Craspedosomidea et Chordeumidea). *Revue suisse de Zoologie* 95(1): 3–49. <https://doi.org/10.5962/bhl.part.79638>
- Miehle G (2015) Landscapes of Nepal. In: Miehle G, Pendry C, Chaudhary R (Eds) *Nepal. An introduction to the natural history, ecology and human environment of the Himalayas*. Royal Botanic Garden Edinburgh, 561 pp.
- Minelli A (Ed.) (2015) *Treatise on Zoology – Anatomy, Taxonomy, Biology. The Myriapoda*. 2. Brill, Leiden–Boston, 482 pp.
- Nguyen DA (2010) The millipede genus *Anoplodesmus* Pocock, 1895 in Vietnam (Diplopoda: Polydesmida: Paradoxosomatidae). *Zootaxa* 2649: 52–60.
- Nguyen DA, Sierwald P (2013) A worldwide catalog of the family Paradoxosomatidae Daday, 1889 (Diplopoda: Polydesmida). *Check List* 9(6): 1132–1353. <https://doi.org/10.15560/9.6.1132>
- Nguyen DA, Jang KH, Hwang UW (2016) The first record of the millipede genus *Streptogonopus* Attems, 1914 from Vietnam, with description of a new species (Diplopoda, Polydesmida, Paradoxosomatidae). *ZooKeys* 601: 111–118. <https://doi.org/10.3897/zookeys.601.9165>
- Read H, Golovatch SI (1994) A review of the Central Asian millipede fauna. *Bulletin of the British Myriapod Group* 10: 59–70.
- Schmidt J (2006) Die *Pterostichus*-Arten des Subgenus *Pseudethira* Sciaky, 1996, in Zentral- und West-Nepal (Coleoptera: Carabidae). In: Hartmann M, Weipert J (Eds) *Biodiversität*

- und Naturausstattung im Himalaya II“, Verein der Freunde und Förderer des Naturkundemuseums Erfurt e.V., Erfurt, 179–243.
- Schmidt J, Opgenoorth L, Höll S, Bastrop R (2012) Into the Himalayan exile: The phylogeography of the ground beetle *Ethira* clade supports the Tibetan origin of forest-dwelling Himalayan species groups. *PloS ONE* 7: e45482. <https://doi.org/10.1371/journal.pone.0045482>
- Schubart O (1935) Diplopoda (über Diplopoden Nr. 22). In: Visser CC, Visser-Hooft J (Hsgeb.) Wissenschaftliche Ergebnisse der niederländischen Expeditionen in der Karakorum und die angrenzenden Gebiete 1922, 1925 und 1929/30. Zoologie. FA Brockhaus, Leipzig, 187–193.
- Shear WA (1979) Diplopoda of the Nepal Himalayas. Chordeumida with comments on the Asian chordeumid fauna. *Senckenbergiana biologica* 60(1/2): 115–130.
- Shear WA (1986) Identity of the Indian cave milliped *Typhlopygmaeosoma hazeltonae* Turk (Polydesmidae, Opistretidae?): another case of ordinal misplacement in the Diplopoda. *Myriapodologica* 2(2): 7–12.
- Shear WA (1987) Chordeumatid Diplopoda from the Nepal Himalayas, II. *Courier Forschungsinstitut Senckenberg* 93: 229–240.
- Shelley RM (1996) *Nepalozonium trimaculatum*, n. gen., n. sp. (Diplopoda: Polyzoniida: Hirudisomatidae): first record of the order and family from Central Asia. *Proceedings of the Entomological Society of Washington* 98(4): 677–680.
- Shelley RM (2014) A summary of the milliped faunas of Pakistan, Bangladesh, and Kashmir (Arthropoda: Diplopoda). *Insecta Mundi* 0368: 1–7.
- Shelley RM, Golovatch SI (2011) Atlas of myriapod biogeography. I. Indigenous ordinal and supra-ordinal distributions in the Diplopoda: Perspectives on taxon origins and ages, and a hypothesis on the origin and early evolution of the class. *Insecta Mundi* 0158: 1–134.
- Silvestri F (1917) Contributions to a knowledge of Oriental Diplopoda Oniscomorpha. I. The family Glomeridae. *Records of the Indian Museum* 13(3 & 9): 103–151.
- Silvestri F (1923) Descriptions of some Indian and Malayan Myriapoda Cambaloidea. *Records of the Indian Museum* 25(2): 181–193.
- Silvestri F (1924) Myriapoda from the Siju Cave, Garo Hills, Assam. *Records of the Indian Museum* 26(1): 71–79.
- Silvestri F (1936) Yale North India Expedition. Article XIII. Report on myriapods. *Memoirs of the Connecticut Academy of Arts and Sciences* 10(13): 241–252.
- Stoeb P, Sierwald P, Billey A (2008) An annotated world catalogue of the millipede order Callipodida (Arthropoda: Diplopoda). *Zootaxa* 1706: 1–50.
- Troll C (1967) Die klimatische und vegetationsgeographische Giedering des Himalaya-Systems. *Khumbu Himal* 1: 353–388. [https://doi.org/10.1007/978-3-642-92945-8\\_1](https://doi.org/10.1007/978-3-642-92945-8_1)
- Turk FA (1945a) On two diplopods of the family Vanhoeffeniidae from Indian caves, with the description of a new genus. *Annals and Magazine of Natural History* (11) 12: 38–42. <https://doi.org/10.1080/00222934508527486>
- Turk FA (1945b) A correction and additional data to two former papers on opilionids and diplopods from Indian caves. *Annals and Magazine of Natural History* (11) 12: 420. <http://dx.doi.org/10.1080/00222934508654738>

- Turk FA (1947) On a collection of diplopods from North India, both cavernicolous and epigeal. Proceedings of the Zoological Society of London 117: 65–78. <http://dx.doi.org/10.1111/j.1096-3642.1947.tb00498.x>
- Turk FA (1972) A new blind millipede (*Typhlopygmaeosoma hazeltonae* n. gen., n. sp.) from a Himalayan cave with notes on its zoogeographical significance. Transactions of the Cave Research Group of Great Britain 14(4): 195–198.
- Wesener T (2015) The giant pill-millipedes of Nepal (Diplopoda, Sphaerotheriida, Zephroniidae). Zootaxa 3964(3): 301–320. <https://doi.org/10.11646/zootaxa.3964.3.1>
- Wesener T (2016) The giant pill-millipedes, order Sphaerotheriida – An annotated species catalogue with morphological atlas and list of apomorphies. Bonn Zoological Bulletin, Suppl. 63: 1–104.
- Zherikhin VV (2003) [A history of biomes]. In: Selected Works. KMK Scientific Press, Moscow, 98–188. [In Russian]
- Zuev RV (2017) The relict millipede *Hirudicryptus abchasicus* Golovatch, Evsyukov et Reip, 2015, represents a species, genus, family and order new to the fauna of Russia (Diplopoda: Siphonocryptida: Siphonocryptidae). Russian Entomological Journal 26(3): 283–286.

# A checklist of the millipedes of Georgia, Caucasus (Diplopoda)

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Academic editor: P. Stoev | Received 4 August 2017 | Accepted 9 November 2017 | Published 7 March 2018

<http://zoobank.org/7B60748C-1972-4952-A133-7F28B5B6BBD3>

**Citation:** Kokhia MS, Golovatch SI (2018) A checklist of the millipedes of Georgia, Caucasus (Diplopoda). In: Stoev P, Edgecombe GD (Eds) Proceedings of the 17<sup>th</sup> International Congress of Myriapodology, Krabi, Thailand. ZooKeys 741: 35–48. <https://doi.org/10.3897/zookeys.741.20042>

## Abstract

The diplopod fauna of Georgia, Transcaucasia, is very rich given the country's relatively small territory, presently comprising 95 species from 42 genera, 12 families, and seven orders. Most of the Diplopoda known from Georgia are subendemics (39 species, or 38%), shared with one or more neighbouring countries, but another 33 species (33%) are strict endemics, nearly all highly localized, including 12 presumed troglobites. Several genera are likewise endemic to Georgia, including a few troglobionts. Within Georgia, the fauna of the western part (= Colchis) is particularly rich and diverse, the faunas of the central and eastern parts of the country growing increasingly depauperate inland and apparently following a rather gradual climatic aridisation gradient from west (the Black Sea coast) to east (Armenia and Azerbaijan). Much more work to include alpine and cave environments is required in order to reveal and refine the real diversity of Georgia's Diplopoda.

## Keywords

Colchis, distribution, endemism, fauna, Myriapoda

## Introduction

Georgia is one of the main countries in the Caucasus, lying between western Asia and Eastern Europe. It is bounded to the west by the Black Sea, to the north by Russia, to the south by Turkey, and to the southeast and east by Armenia and Azerbaijan



**Figure 1.** Crude geographical division of Georgia.

(Fig. 1). The area is largely montane to high montane, situated between latitudes  $41^{\circ}$  and  $44^{\circ}\text{N}$ , and longitudes  $40^{\circ}$  and  $47^{\circ}\text{E}$ . 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 (up to more than 5,000 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, but largely mild to warm, considering the nation's small size. 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 history of diplopodological research in the Caucasus generally, and in Georgia in particular, started with the works of Victor (1839), Brandt (1840) and Karsch (1881), followed by faunistic contributions by Timotheew (1897), Attems (1898, 1899, 1901, 1903, 1907), Lignau (1903, 1907, 1911, 1915, 1924), Muralewicz (1907, 1911, 1913,

1927) and Issaev (1911). Muralewicz (1911) was the first to thoroughly review the fauna of Caucasian Myriapoda known to that date. Verhoeff (1921, 1930), Jawłowski (1929) and Lohmander (1928, 1932) had added a few more species of Caucasian millipedes before a real milestone synthesis appeared. That historical stage culminated with Lohmander's (1936) monograph which still serves, however outdated taxonomically, as one of the main sources of our knowledge of the Diplopoda of the Caucasus.

Several checklists, partly containing new faunistic records of Caucasian Diplopoda, appeared since then (Lang 1959, Kobakhidze 1964, 1965, Lokšina and Golovatch 1979, Talikadze 1984), but marked progress in the taxonomic study of millipedes in the region resumed only with contributions by Golovatch (1975, 1976a, 1976b, 1976c, 1977, 1979, 1980, 1981a, 1981b, 1984/85). Sporadic descriptions have since been upgraded to regional reviews of certain higher taxa such as genera, families and orders, with few exceptions only. These reviews mostly covered not only the Caucasus proper, but also the faunas of the adjacent parts of Turkey and Iran, e.g. the families Blaniulidae (Enghoff 1984, 1990, Golovatch and Enghoff 1990), Nemasomatidae (Enghoff 1985) and several tribes and genera of Julidae (Read 1992, Enghoff 1995, Evsyukov 2016b, Vagalinski and Lazányi 2018), all from the order Julida. The order Glomerida (Golovatch 1989a, 1989b, 1990, 1993, Golovatch and Chumachenko 2013), three orders of the subterclass Colobognatha (Golovatch et al. 2015, Zuev 2017), as well as the orders Polyxenida (Short 2015, Short et al. 2018), Polydesmida (Golovatch et al. 2016, Evsyukov et al. 2016) and Chordeumatida (Antić and Makarov 2016) have also been revised in the scope of the entire Caucasian fauna, sometimes even broader. The faunas of two larger areas in Ciscaucasia have also been reviewed and updated (Evsyukov and Golovatch 2013, Evsyukov 2016a, Zuev 2014). A couple of nature reserves at the Black Sea coast of the Russian Caucasus have likewise been thoroughly surveyed for their local millipede faunas, with some data on ecology and distribution (Chumachenko 2016, Korobushkin et al. 2016).

The present paper provides an up-to-date checklist (Table 1) of the millipede fauna of Georgia, based on all available publications. It shows very considerable progress achieved since the latest lists by Kobakhidze (1964, 1965), who grossly repeated Lohmander's (1936) and added many new faunistic records, and by Talikadze (1984), who only considered the Colchidian part of the Caucasus, including the Black Sea coast area of Russia. Cave fauna has been reviewed within the entire former Soviet Union, including the Diplopoda of the Caucasus together with Georgia (Turbanov et al. 2016).

Georgia is conventionally divisible into three main parts: western, central, and eastern (Figure 1). This division is followed in the checklist below. Data are also given on the presence or absence of relevant species in the immediately neighbouring countries, including the Crimean Peninsula, as well as the distribution patterns and main literature sources. The checklist is arranged in alphabetic order per family, omitting subgeneric categories. All accepted designations are explained at the bottom of Table 1.



## Results

**Table 1.** 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. Dp = Distribution pattern.

Taxonomic composition	G	R	T	Ar	Az	Cr	St	Dp	Main relevant references
Class Diplopoda									
Order Polyxenida									
Family Polyxenidae									
Genus <i>Polyxenus</i> Latreille, 1803									
1. <i>Polyxenus argentifer</i> Verhoeff, 1921	G	+		+	+	+		AM	Short et al. 2018
2. <i>P. lagurus</i> (Linnaeus, 1758)	W, E					+		sc	Short et al. 2018
Family Lophoproctidae									
Genus <i>Lophoproctus</i> Pocock, 1894									
3. <i>Lophoproctus coecus</i> Pocock, 1894	G	+				+		EM	Short 2015, Short et al. 2018
Order Polyzoniida									
Family Hirudisomatidae									
Genus <i>Hirudisoma</i> Fanzago, 1881									
4. <i>Hirudisoma roseum</i> (Victor, 1839)	G	+	+		+		se	EM	Golovatch et al. 2015
Order Siphonocryptida									
Family Siphonocryptidae									
Genus <i>Hirudicryptus</i> Enghoff & Golovatch, 1985									
5. <i>Hirudicryptus abchasicus</i> Golovatch, Esvyukov & Reip, 2015	W	+					se	Ca	Golovatch et al. 2015, Zuev 2017
Order Glomerida									
Family Glomeridae									
Genus <i>Hyleoglomeris</i> Verhoeff, 1910									
6. <i>Hyleoglomeris awchasia</i> (Brandt, 1840)	W	+					se	Ca	Golovatch 1976a, 1989b
7. <i>H. specialis</i> Golovatch, 1989	E	+					se	Ca	Golovatch 1989b
Genus <i>Trachysphaera</i> Heller, 1858									
8. <i>Trachysphaera costata</i> (Waga, 1857)	G	+	+	+	+	+		EuM	Golovatch 1990, 2008
9. <i>T. fragilis</i> Golovatch, 1976	G						t, e	Ca	Golovatch 1990, Golovatch and Turbanov 2017
10. <i>T. minuta</i> Golovatch, 1976	G	+	+	+			se	Ca	Golovatch 1990
11. <i>T. orientalis</i> Golovatch, 1976	W						t, e	Ca	Golovatch 1976c, 1990
12. <i>T. radiosa</i> (Lignau, 1911)	W	+					se	Ca	Golovatch 1976c, 1990
13. <i>T. solida</i> Golovatch, 1976	W, C						se	Ca	Golovatch 1976c, 1990, 1993
Family Glomeridellidae									
Genus <i>Typhloglomeris</i> Verhoeff, 1898									
14. <i>Typhloglomeris lohmanderi</i> (Golovatch, 1989)	C, E	+		+			se	Ca	Golovatch 1989a, 2003
Order Chordeumatida									
Family Anthroleucosomatidae									
Genus <i>Acanthophorella</i> Antić & Makarov, 2016									
15. <i>Acanthophorella barjadzei</i> Antić & Makarov, 2016	W						t, e	Ca	Antić and Makarov 2016
Genus <i>Adshardicus</i> Golovatch, 1981									
16. <i>Adshardicus strasseri</i> Golovatch, 1981	W		+				se	Ca	Enghoff 2006, Antić and Makarov 2016
Genus <i>Alpinella</i> Antić & Makarov, 2016									
17. <i>Alpinella waltheri</i> Antić & Makarov, 2016	E						e	Ca	Antić and Makarov 2016
Genus <i>Brachychaetosoma</i> Antić & Makarov, 2016									
18. <i>Brachychaetosoma turbanovi</i> Antić & Makarov, 2016	W						t, e	Ca	Antić and Makarov 2016

Taxonomic composition	G	R	T	Ar	Az	Cr	St	Dp	Main relevant references
Genus <i>Caucaseuma</i> Strasser, 1970									
19. <i>Caucaseuma kelasuri</i> Antić & Makarov, 2016	W						e	Ca	Antić and Makarov 2016
20. <i>C. variabile</i> Antić & Makarov, 2016	C	+					se	Ca	Antić and Makarov 2016
Genus <i>Cryptacanthophorella</i> Antić & Makarov, 2016									
21. <i>Cryptacanthophorella manubriata</i> Antić & Makarov, 2016	W, C						e	Ca	Antić and Makarov 2016
Genus <i>Dentatosoma</i> Antić & Makarov, 2016									
22. <i>Dentatosoma denticulatum</i> Antić & Makarov, 2016	W						e	Ca	Antić and Makarov 2016
23. <i>D. magnum</i> Antić & Makarov, 2016	W	+					se	Ca	Antić and Makarov 2016
24. <i>D. zeraboseli</i> Antić & Makarov, 2016	W						e	Ca	Antić and Makarov 2016
Genus <i>Georgiosoma</i> Antić & Makarov, 2016									
25. <i>Georgiosoma bicornutum</i> Antić & Makarov, 2016	W						t, e	Ca	Antić and Makarov 2016
Genus <i>Herculina</i> Antić & Makarov, 2016									
26. <i>Herculina oligosagittae</i> Antić & Makarov, 2016	W						e	Ca	Antić and Makarov 2016
27. <i>H. polysagittae</i> Antić & Makarov, 2016	C						e	Ca	Antić and Makarov 2016
Genus <i>Heterocaucaseuma</i> Antić & Makarov, 2016									
28. <i>Heterocaucaseuma longicorne</i> Antić & Makarov, 2016	W						t, e	Ca	Antić and Makarov 2016
29. <i>Heterocaucaseuma mauriesi</i> (Golovatch & Makarov, 2011)	W						t, e	Ca	Golovatch and Makarov 2011, Antić and Makarov 2016
Genus <i>Metamastigophorophyllon</i> Ceuca, 1976									
30. <i>Metamastigophorophyllon giljarovi</i> (Lang, 1959)	W	+					se	Ca	Antić and Makarov 2016
31. <i>M. hamatum</i> Antić & Makarov, 2016	W	+					se	Ca	Antić and Makarov 2016
32. <i>M. lamellohirsutum</i> Antić & Makarov, 2016	W						e	Ca	Antić and Makarov 2016
33. <i>M. torsivum</i> Antić & Makarov, 2016	G				+		se	Ca	Antić and Makarov 2016
Genus <i>Paranotosoma</i> Antić & Makarov, 2016									
34. <i>Paranotosoma attemsi</i> Antić & Makarov, 2016	W						e	Ca	Antić and Makarov 2016
35. <i>P. cordatum</i> Antić & Makarov, 2016	W						e	Ca	Antić and Makarov 2016
36. <i>P. subrotundatum</i> Antić & Makarov, 2016	W	+					se	Ca	Antić and Makarov 2016
Genus <i>Pseudoflagellophorella</i> Antić & Makarov, 2016									
37. <i>Pseudoflagellophorella eskovi</i> Antić & Makarov, 2016	C, E			+	+		se	Ca	Antić and Makarov 2016
38. <i>P. mirabilis</i> Antić & Makarov, 2016	W						e	Ca	Antić and Makarov 2016
39. <i>P. papilioformis</i> Antić & Makarov, 2016	E				+		se	Ca	Antić and Makarov 2016
Genus <i>Ratcheuma</i> Golovatch, 1985									
40. <i>Ratcheuma exorne</i> Golovatch, 1985	W						t, e	Ca	Golovatch 1984/85, Antić and Makarov 2016
Order Julida Family Blaniulidae Genus <i>Cibiniulus</i> Verhoeff, 1927									
41. <i>Cibiniulus phlepsii</i> (Verhoeff, 1897)	W		+					EuM	Enghoff 1984, 2006
Genus <i>Nopoiulus</i> Menge, 1851									
42. <i>Nopoiulus brevipilosus</i> Enghoff, 1984	W						t, e	Ca	Enghoff 1984
43. <i>N. densepilosus</i> Enghoff, 1984*	W				+			Ca	Enghoff 1984, Golovatch and Enghoff 1990
44. <i>N. golovatchi</i> Enghoff, 1984	W		+					Ca	Enghoff 1984, 1990
45. <i>N. kochii</i> (Gervais, 1847)	G	+	+	+	+			sc	Enghoff 1984, Golovatch and Enghoff 1990

Taxonomic composition	G	R	T	Ar	Az	Cr	St	Dp	Main relevant references
Family Nemasomatidae									
Genus <i>Nemasoma</i> C.L. Koch, 1847									
46. <i>Nemasoma caucasicum</i> (Lohmander, 1932)	G	+	+	+	+		se	Ca	Enghoff 1985
Family Julidae									
Genus <i>Amblyiulus</i> Silvestri, 1896									
47. <i>Amblyiulus adsharicus</i> Lohmander, 1936	W						e	Ca	Lohmander 1936
48. <i>A. georgicus</i> Lohmander, 1932	C						e	Ca	Lohmander 1932
Genus <i>Archileucogeorgia</i> Lohmander, 1936									
49. <i>Archileucogeorgia abchasica</i> Lohmander, 1936	W						t, e	Ca	Lohmander 1936
50. <i>Archileucogeorgia satunini</i> Lohmander, 1936	W						e	Ca	Lohmander 1936
Genus <i>Brachyiulus</i> Berlese, 1884									
51. <i>Brachyiulus lusitanus</i> Verhoeff, 1898	C				+			M	Lohmander 1936
Genus <i>Catamicrophyllum</i> Verhoeff, 1900									
52. <i>Catamicrophyllum caucasicum</i> (Attems, 1901)	G	+	+	+			se	Ca	Lohmander 1936, Enghoff 1995
Genus <i>Calyptophyllum</i> Brolemann, 1922									
53. <i>Calyptophyllum</i> sp.	W						?	?	Lohmander 1936, Enghoff 1995
Genus <i>Chaetoleptophyllum</i> Verhoeff, 1898									
54. <i>Chaetoleptophyllum flexum</i> Golovatch, 1979	G	+					se	Ca	Golovatch 1979, Chumachenko 2016, Korobushkin et al. 2016
Genus <i>Cylindroiulus</i> Verhoeff, 1894									
55. <i>Cylindroiulus bellus</i> (Lignau, 1903)	W?	+				+		EM	Lignau 1903, Read 1992, Chumachenko 2016
56. <i>C. crasiphylacum</i> Read, 1992	G	+					se	Ca	Read 1992
57. <i>C. kacheticus</i> Lohmander, 1936	E	+					se	Ca	Read 1992
58. <i>C. olgaimna</i> Read, 1992	W						e	Ca	Read 1992
59. <i>C. parvus</i> Lohmander, 1928	C, E				+		se	Ca	Read 1992
60. <i>C. placidus</i> (Lignau, 1903)	W, C	+					se	Ca	Read 1992
61. <i>C. pterophylacum</i> Read, 1992	W, C	+					se	Ca	Read 1992, Zuev 2014
62. <i>C. quadrus</i> Read, 1992	G	+					se	Ca	Read 1992
63. <i>C. ruber</i> (Lignau, 1903)	W	+					se	Ca	Read 1992
64. <i>C. schestoperoi</i> Lohmander, 1936	W	+					se	Ca	Lohmander 1936, Read 1992
65. <i>C. truncorum</i> (Silvestri, 1896)	W							sc	Read 1992
Genus <i>Grusiniulus</i> Lohmander, 1936									
66. <i>Grusiniulus redikorzevi</i> Lohmander, 1932	C						e	Ca	Lohmander 1936, Vagalinski and Lazányi 2018
Genus <i>Julus</i> Linnaeus, 1758									
67. <i>Julus colchicus</i> Lohmander, 1936	W	+	+				se	Ca	Lohmander 1936, Enghoff 2006
68. <i>J. kubanus</i> Verhoeff, 1921	W	+					se	Ca	Lohmander 1936, Kobakhidze 1965
69. <i>J. lindholmi</i> Lohmander, 1936	W						e	Ca	Lohmander 1936
Genus <i>Leptoiulus</i> Verhoeff, 1894									
70. <i>Leptoiulus disparatus</i> Lohmander, 1936	C	+					se	Ca	Lohmander 1936, Enghoff 2006
71. <i>L. tanyomorphus</i> (Attems, 1901)	C, E				+			Ca	Lohmander 1936
Genus <i>Leucogeorgia</i> Verhoeff, 1930									
72. <i>Leucogeorgia longipes</i> Verhoeff, 1930	W						t, e		Verhoeff 1930
73. <i>L. rediviva</i> Golovatch, 1983	W						t, e	Ca	Golovatch 1983
Genus <i>Megaphyllum</i> Verhoeff, 1894									
74. <i>Megaphyllum dioscoriadis</i> (Lignau, 1915)	W	+					e	Ca	Lignau 1915, Lohmander 1936, Chumachenko 2016, Vagalinski and Lazányi 2018
75. <i>M. hercules</i> (Verhoeff, 1901)	W	+						EM	Lazányi and Vagalinski 2013

Taxonomic composition	G	R	T	Ar	Az	Cr	St	Dp	Main relevant references
76. <i>M. spathulatum</i> (Lohmander, 1936)	W?	?						Ca	Lohmander 1936, Lazányi and Vagalinski 2013
Genus <i>Omobrachiulus</i> Lohmander, 1936									
77. <i>Omobrachiulus adsharicus</i> (Lohmander, 1936)	W						e	Ca	Lohmander 1936, Vagalinski and Lazányi 2018
78. <i>O. brachyurus</i> (Attems, 1899)	G	+	+	+	+			EM	Lohmander 1936, Enghoff 2006, Vagalinski and Lazányi 2018
79. <i>O. curvicaudatus</i> (Lignau, 1903)	W	+					se	Ca	Lohmander 1936, Vagalinski and Lazányi 2018
80. <i>O. divaricatus</i> (Lohmander, 1936)	G			+			se	Ca	Lohmander 1936, Vagalinski and Lazányi 2018
81. <i>O. hortensis</i> (Golovatch, 1981)	W						e	Ca	Golovatch 1981, Vagalinski and Lazányi 2018
82. <i>O. implicitus</i> Lohmander, 1936 (= <i>O. i. ritsensis</i> (Golovatch, 1981))	W	+					se	Ca	Lohmander 1936, Chumachenko 2016, Vagalinski and Lazányi 2018
83. <i>O. macrourus</i> (Lohmander, 1928) (= <i>O. m. abchasicus</i> (Lohmander, 1936))	W, C						e	Ca	Lohmander 1936, Kobakhidze 1965, Vagalinski and Lazányi 2018
Genus <i>Pachyiulus</i> Berlese, 1883									
84. <i>Pachyiulus flavipes</i> (C.L. Koch, 1847)	W					+		M	Lohmander 1936
85. <i>Pachyiulus krivolutskyi</i> Golovatch, 1977	W	+					se	Ca	Evsyukov 2016
Order Polydesmida									
Family Paradoxosomatidae									
Genus <i>Oxidus</i> Cook, 1911									
86. <i>Oxidus gracilis</i> (C.L. Koch, 1847)	W	+						sc	Lignau 1915, Lohmander 1936, Chumachenko 2016
Family Polydesmidae									
Genus <i>Brachydesmus</i> Heller, 1858									
87. <i>Brachydesmus assimilis</i> Lohmander, 1936	C, E	+					se	Ca	Golovatch et al. 2016
88. <i>B. furcatus</i> Lohmander, 1936	W	+					se	Ca	Golovatch et al. 2016
89. <i>B. kalischevskyi</i> Lignau, 1915	G	+	+	+	+		se	Ca	Golovatch et al. 2016
90. <i>B. kvavadzei</i> Golovatch, Evsyukov & Reip, 2016	W						e	Ca	Golovatch et al. 2016
91. <i>B. simplex</i> Golovatch, Evsyukov & Reip, 2016	W	+					se	Ca	Golovatch et al. 2016
92. <i>B. superus</i> Latzel, 1884	W	+						sc	Golovatch et al. 2016
Genus <i>Polydesmus</i> Latreille, 1803									
93. <i>Polydesmus abchasius</i> Attems, 1899	W	+					se	Ca	Golovatch et al. 2016
94. <i>P. lignaii</i> Lohmander, 1936	W	+					se	Ca	Golovatch et al. 2016
95. <i>P. mediterraneus</i> Daday, 1889	W					+		EM	Golovatch et al. 2016

**Designations:** 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; St – status; e – endemic to Georgia; se – subendemic to Georgia; t – presumed troglobiont; sc – subcosmopolitan; AM – Ancient Mediterranean; EuM – Euro-Mediterranean; M – Mediterranean; EM – eastern Mediterranean; EE – eastern European; Ca – Caucasian.

## Discussion

As is evident from the above list, the millipede fauna of Georgia is, surprisingly, very diverse, especially so given the relatively small territory it covers. This is hardly surprising, because Diplopoda are largely mesophilous forest-dwellers (e.g., Kime and Golovatch 2000, Golovatch and Kime 2009). Georgia with its mostly mild climate and large

woodland areas supports the richest millipede fauna in the entire Caucasus, nearly twice as rich as neighbouring Azerbaijan (Bababekova 1996, a quite poorly compiled list) or Iran (Enghoff and Moravvej 2005), and approximately 2/3 as diverse as the fauna of the so much larger Turkey (Enghoff 2006, 135 species), for all of which rather modern country checklists are available. Although the bulk of the fauna of Georgia is represented by epigeal taxa, the abundant limestone massifs, primarily those lying at the northern and northeastern peripheries of the Colchis, harbour numerous karstic caves with their own fauna. Troglobionts do account for a considerable proportion (12 species, or 14%) of Georgia's millipede species (Barjadze et al. 2015, Turbanov et al. 2016).

Western Georgia, the Colchis (Fig. 1), is especially rich in millipedes, apparently due to the moist and mild climate near the warm Black Sea, highly varied, but largely forested habitats, and abundant karst caves. The Colchidian millipede fauna is also the richest in endemics, both at the species and generic levels. The orders Chordeumatida and Julida are particularly strongly diversified in Georgia. As well the country supports also *Hirudicryptus abchasicus*, a subendemic representing one of the most relict diplopod orders, Siphonocryptida, which presently comprises only seven species in two genera and a single family (Golovatch et al. 2015, Zuev 2017). Central and eastern parts of Georgia are increasingly drier, in places even semi-arid, and the millipede fauna generally demonstrates a decline in diversity from the Black Sea coast inland, appearing to follow rather gradual climatic aridisation gradient from west to east.

Most of the Diplopoda known from Georgia are subendemics (40 species, or 42%), shared with one or more neighbouring countries, but another 33 species (34%) are strict endemics, nearly all highly localized, including 12 presumed troglobites. Several genera are likewise endemic to Georgia, including a few troglobionts. The proportions of the remaining, more widely distributed, species are rather modest, represented by Mediterranean, Euro-Mediterranean, eastern Mediterranean, eastern European or ubiquitous elements, but even among the latter the subcosmopolitan *Nopoiulus kochii* may have originated in the Caucasus, because the remaining congeners (from all subgenera) seem to be endemic to the Caucasus region (Golovatch and Enghoff 1990).

The present checklist must be understood as temporary, far from complete, marking only the state of knowledge of diplopodological research in Georgia. Several of Lohmander's *nomina nuda* listed by Kobakhidze (1964) are thereby omitted. Much more work is required to reveal the real diversity of Georgia's Diplopoda. Discoveries and descriptions of numerous new taxa, both species and probably even genera, can still be expected in the future. Further faunistic records are necessary to refine not only the taxonomy and the above list, but also the distributions, both horizontal and vertical. Very little is known yet concerning high-montane millipedes, in particular, whether strictly alpine Caucasian/Georgian endemics exist at all, like those few recorded from the Pyrenees and Alps. Finally, cave explorations in Georgia will undoubtedly reveal many more new troglobionts, including diplopods.

## Acknowledgements

Thanks are due to Boyan Vagalinski (Sofia, Bulgaria) and Megan Short (Melbourne, Australia) for kindly sharing published and unpublished information on their current research relevant to our topic, as well as acknowledgements to them and Dragan Antić (Belgrade, Serbia) and Elena Mikhajlova (Vladivostok, Russia) for their helpful reviews of the manuscript. MK is grateful for the support rendered through the Project “Georgia’s Natural and Agricultural Ecosystems: Animal Diversity, Monitoring, Biocontrol”, funded by the Ministry of Science and Education of Georgia.

## References

- Antić DŽ, Makarov SE (2016) The Caucasus as a major hotspot of biodiversity: Evidence from the millipede family Anthroleucosomatidae (Diplopoda, Chordeumatida). *Zootaxa* 4211(1): 1–205. <https://doi.org/10.11646/zootaxa.4211.1.1>
- Attems C (1898) System der Polydesmiden. I. Theil. Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Classe 67: 221–482.
- Attems C (1899) Neues über paläarktische Myriopoden. *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Thiere* 12: 286–336. <https://doi.org/10.5962/bhl.part.2032>
- Attems C (1901) Myriopoden. – Horvath G (Hrsg), *Zoologische Ergebnisse der dritten asiatischen Forschungsreise des Grafen Eugen Zichy*, Budapest 2: 275–310.
- Attems C (1903) Beiträge zur Myriopodenkunde. *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Thiere* 18: 63–154.
- Attems C (1907) Myriopoden aus der Krim und dem Kaukasus von Dr. A. Stuxberg gesammelt. *Arkiv för Zoologi* 3(25): 1–16.
- Bababekova LA (1996) The subphylum of tracheates – Tracheata. In: Aliev SV, Kasymov EG (Eds) *Animal life of Azerbaijan 2: The phylum of arthropods*. Elm Publishers, Baku, 89–97. [in Russian]
- Barjadze S, Murvanidze M, Arabuli T, Mumladze L, Pkhakadze V, Djanashvili R, Salakaia M (2015) Annotated list of invertebrates of the Georgian karst caves. *Georgian Academic Book*, Tbilisi, 119 pp.
- Bondyrev IV, Davitashvili ZV, Singh VP (2015) Natural Resources. The Geography of Georgia, Problems and Perspectives. *World Regional Geography Book Series*. Springer, Cham, 227 pp. [https://doi.org/10.1007/978-3-319-05413-1\\_11](https://doi.org/10.1007/978-3-319-05413-1_11)
- Brandt JF (1840) Remarques critiques sur les espèces qui composent le genre *Glomeris*, suivies de quelques observations sur leur distribution géographique. *Bulletin scientifique publié par l’Académie Impériale des Sciences de Saint-Petersbourg* 7(148, 149): 37–44.
- Chumachenko YA (2016) [Millipede (Diplopoda) populations in a yew-boxtree grove in the Caucasian Nature Reserve, Russia]. *Zoologicheskii Zhurnal* 95(4): 406–416. <https://doi.org/10.7868/S004451341604005X> [In Russian, English summary]



- Enghoff H (1984) A revision of the Nopoiulinae, with notes on the classification of blaniulid millipedes (Diplopoda: Julida: Blaniulidae). *Senckenbergiana biologica* 64 (4–6): 393–427.
- Enghoff H (1985) The millipede family Nemasomatidae. With the description of a new genus, and a revision of *Orinisobates* (Diplopoda: Julida). *Entomologica scandinavica* 16: 27–67. <https://doi.org/10.1163/187631285X00045>
- Enghoff H (1990) A new species of *Nopoiulus* Menge 1851, subgenus *Paranopoiulus* Lohmander, 1939, from the Caucasus, with records of consubgeneric species, and the systematic position of *Thassoblaniulus* Mauriès 1985 (Diplopoda: Julida: Blaniulidae). *Senckenbergiana biologica* 70(4/6): 323–330.
- Enghoff H (1995) A revision of the Paectophyllini and Calyptophyllini: millipedes of the Middle East (Diplopoda: Julida: Julidae). *Journal of Natural History* 29: 685–786. <https://doi.org/10.1080/00222939500770241>
- Enghoff H (2006) The millipedes of Turkey (Diplopoda). *Steenstrupia* 29(2): 175–198.
- Enghoff H, Moravvej SA (2005) A review of the millipede fauna of Iran (Diplopoda). *Zoology in the Near East* 35: 61–72. <https://doi.org/10.1080/09397140.2005.10638104>
- Evsyukov AP (2016a) A new species of the millipede genus *Julus* from the Rostov-on-Don Region, southern Russia (Diplopoda: Julida: Julidae). *Arthropoda Selecta* 25(3): 241–245. [http://kmkjournals.com/upload/PDF/ArthropodaSelecta/25/25\\_3\\_241\\_245\\_Evsyukov\\_for\\_Inet.pdf](http://kmkjournals.com/upload/PDF/ArthropodaSelecta/25/25_3_241_245_Evsyukov_for_Inet.pdf)
- Evsyukov AP (2016b) The millipede *Pachyiulus krivolutskyi* Golovatch, 1977, the easternmost species of the eastern Mediterranean genus *Pachyiulus* Berlese, 1883, endemic to the western Caucasus (Diplopoda: Julida: Julidae). *Russian Entomological Journal* 25(3): 299–306. [http://kmkjournals.com/upload/PDF/REJ/25/ent25\\_3\\_299\\_306\\_Evsyukov\\_for\\_Inet.pdf](http://kmkjournals.com/upload/PDF/REJ/25/ent25_3_299_306_Evsyukov_for_Inet.pdf)
- Evsyukov AP, Golovatch SI (2013) Millipedes (Diplopoda) from the Rostov-on-Don Region, southern Russia. *Arthropoda Selecta* 22(3): 207–215. [http://kmkjournals.com/upload/PDF/ArthropodaSelecta/22/22\\_3%20207\\_215%20Evsyukov%20Golovatch%20for%20Inet.pdf](http://kmkjournals.com/upload/PDF/ArthropodaSelecta/22/22_3%20207_215%20Evsyukov%20Golovatch%20for%20Inet.pdf)
- Evsyukov AP, Golovatch SI, Reip H (2016) The millipede genus *Strongylosoma* Brandt, 1833 in the Caucasus (Diplopoda, Polydesmida, Paradoxosomatidae). *Acta Societatis Zoologicae Bohemicae* 80: 7–16.
- Golovatch SI (1975) [Two genera of Oniscomorpha (Diplopoda) new to the USSR fauna, found in Transcaucasia, and their zoogeographical relations]. *Zoologicheskii Zhurnal* 54(10): 1566–1571. [In Russian, English summary]
- Golovatch SI (1976a) [New or little-known species of Glomeridae (Diplopoda, Oniscomorpha)]. *Zoologicheskii Zhurnal* 55(6): 931–935. [In Russian, English summary].
- Golovatch SI (1976b) [New species of polydesmidans (Polydesmida, Diplopoda) of the USSR]. *Zoologicheskii Zhurnal* 55(10): 1567–1570. [In Russian, English abstract]
- Golovatch SI (1976c) [Description of new species of *Trachysphaera* (Oniscomorpha; Diplopoda) from caves of Transcaucasia with remarks on *T. rotundata* (Lignau) 1911]. *Bulletin de la Société des Naturalistes de Moscou, Section Biologique* [Byulleten Moskovskogo obshchestva ispytateley prirody, Otdel biologicheskii] 81(5): 30–43. [In Russian, English summary]

- Golovatch SI (1977) [New or little-known Julida (Diplopoda) of the Sataplia Nature Reserve (SSR Georgia)]. Bulletin de la Société des Naturalistes de Moscou, Section Biologique [Byulleten Moskovskogo obshchestva ispytateley prirody. Otdel biologicheskii] 82(4): 46–51. [In Russian, English summary]
- Golovatch SI (1979) [Three genera of Diplopoda-Chilognatha new to the USSR fauna]. Zoologicheskii Zhurnal 58(3): 336–343. [In Russian, English summary]
- Golovatch SI (1980) [A new species of the millipede genus *Fioria* (Diplopoda, Platydesmidae) from Transcaucasia]. Zoologicheskii Zhurnal 59(3): 458–460. [In Russian, English summary]
- Golovatch SI (1981a) A review of the cavernicolous millipede fauna (Diplopoda) of the western Caucasus. Caves of Georgia [Peshchery Gruzii], Tbilisi 9: 108–111. [In Russian]
- Golovatch SI (1981b) Some new forms of millipedes (Diplopoda) from the Caucasus. Annales Zoologici 36(5): 105–116.
- Golovatch SI (1983) Une nouvelle espèce cavernicole du genre *Leucogeorgia* de la Transcaucasie (Diplopoda, Julidae). Fragmenta Entomologica 17(1): 47–50.
- Golovatch SI (1984/85) Two new genera of cave-dwelling millipedes (Diplopoda), with remarks on the millipede fauna of West Caucasian caves. International Journal of Speleology 14(1/4): 39–50.
- Golovatch SI (1989a) Diplopoda of the Caucasus, 1. Glomeridellidae, with contributions to the fauna of Turkey. Senckenbergiana biologica 69(4/6): 405–419.
- Golovatch SI (1989b) Diplopoda of the Caucasus, 2. Glomeridae, with contributions to the fauna of Turkey. Senckenbergiana biologica 69(4/6): 421–440.
- Golovatch SI (1990) Diplopoda of the Caucasus, 3. Trachysphaeridae, with contributions to the fauna of Turkey. Senckenbergiana biologica 70(4/6): 331–358.
- Golovatch SI (1993) *Trachysphaera solida* Golovatch, 1976, a revalidated Caucasian millipede species (Diplopoda Glomerida Trachysphaeridae). Arthropoda Selecta 2(4): 19–20.
- Golovatch SI (2003) Two new species of Glomeridellidae (Diplopoda: Glomerida) from the Middle East. Arthropoda Selecta 11(4): 255–258.
- Golovatch SI (2008) On three remarkable millipedes (Diplopoda) from the Crimea, Ukraine. International Journal of Myriapodology 1: 97–110. <https://doi.org/10.1163/187525408X316767>
- Golovatch SI, Chumachenko YA (2013) The millipede *Typhloglomeris caucasica* Golovatch, 1975 found epigeically (Diplopoda, Glomerida, Glomeridellidae). Biodiversity Data Journal 1: 1–3, e981. <https://doi.org/10.3897/BDJ.1.e981>
- Golovatch SI, Enghoff H (1990) [The millipede *Nopoiulus kochii* (Gervais, 1847) in the Caucasus (Diplopoda, Julida, Blaniulidae)]. In: Striganova BR (Ed.) Fauna of Terrestrial Invertebrates of the Caucasus. Nauka Publishers, Moscow, 114–118. [In Russian]
- Golovatch SI, Kime RD (2009) Millipede (Diplopoda) distributions: A review. Soil Organisms 81(3): 565–597.
- Golovatch SI, Makarov S (2011) Two new, easternmost species of the millipede genus *Anamastigona* Silvestri, 1898 from Israel and the Caucasus (Diplopoda, Chordeumatida, Anthroleucosomatidae). Arthropoda Selecta 20(1): 11–20. [http://kmkjournals.com/upload/PDF/ArthropodaSelecta/20/20\\_1%20011\\_020%20Golovatch%2C%20Makarov%20for%20Inet.pdf](http://kmkjournals.com/upload/PDF/ArthropodaSelecta/20/20_1%20011_020%20Golovatch%2C%20Makarov%20for%20Inet.pdf)

- Golovatch SI, Turbanov IS (2017) The cave millipede *Trachysphaera fragilis* Golovatch, 1976, new to the fauna of Abkhazia, western Caucasus (Diplopoda: Glomerida: Glomeridae). Russian Entomological Journal 25(1): 101–102. [http://kmkjournals.com/upload/PDF/REJ/26/ent26\\_1\\_101\\_102\\_Golovatch\\_Turbanov\\_for\\_Inet.pdf](http://kmkjournals.com/upload/PDF/REJ/26/ent26_1_101_102_Golovatch_Turbanov_for_Inet.pdf)
- Golovatch SI, Evsyukov AP, Reip HS (2015) Colobognatha millipedes in the Caucasus (Diplopoda: Polyzoniida, Platydesmida, Siphonocryptida). Zootaxa 3972(2): 250–266. doi.org/10.11646/zootaxa.3972.2.6
- Golovatch SI, Evsyukov AP, Reip HS (2016) The millipede family Polydesmidae in the Caucasus (Diplopoda: Polydesmida). Zootaxa 4085(1): 1–51. <https://doi.org/10.11646/zootaxa.4085.1.1>
- Issaev VM (1911) [Observations of millipedes Diplopoda at the Black Sea coast of the Caucasus]. Travaux de la Société Impériale des Naturalistes de Saint-Petersbourg [Trudy Imperatorskogo Sankt-Peterburgskogo obshchestva estestvoispytateley] 42(1): 292–310. [In Russian]
- Jawłowski H (1929) Über einige neue Diplopoden-Arten aus Kleinasien und Transkaukasien. Annales Musei Zoologici Polonici 8(1): 49–53.
- Karsch F (1881) Neue Juliden des Berliner Museums, als Prodrum einer Juliden-Monographie. Zeitschrift für die gesammten Naturwissenschaften 54: 1–79.
- Kime RD, Golovatch SI (2000) Trends in the ecological strategies and evolution of millipedes (Diplopoda). Biological Journal of the Linnean Society 69: 333–349.
- Kobakhidze DN (1964) [Myriopoda]. In [Animal Life of Georgia 2: Arthropoda. Institute of Zoology, SSR Georgia Academy of Sciences, Tbilisi, 186–195. [In Georgian]
- Kobakhidze DN (1965) [A list of millipedes (Diplopoda) of SSR Georgia]. Fragmenta Faunistica 11(21): 390–398. [In Russian, summaries in Polish and German]
- Korobushkin DI, Semenyuk II, Tuf IH (2016) An annotated checklist of the Chilopoda and Diplopoda (Myriapoda) of the Abrau Peninsula, northwestern Caucasus, Russia. Biodiversity Data Journal 19(4): e7308. <https://doi.org/10.3897/BDJ.4.e7308>
- Lang J (1959) [To the knowledge of millipedes (Diplopoda) of the USSR territory] // Zoologicheskii Zhurnal 38(12): 1790–1796. [In Russian, a summary in English]
- Lazányi E, Vagalinski B (2013) Redefinition of the millipede subgenus *Megaphyllum* sensu stricto Verhoeff, 1894 and neotype designation for *Megaphyllum austriacum* (Latzel, 1884) (Myriapoda: Diplopoda: Julida: Julidae). Zootaxa 3741: 55–100. <http://dx.doi.org/10.11646/zootaxa.3741.1.2>
- Lignau N (1903) [Myriapods of the Black Sea coast of the Caucasus]. Die Myriopoden am Kaukasischen Schwarzmeerufer. Mémoires de la Société Impériale des Naturalistes de la Nouvelle-Russie [Zapiski Imperatorskogo Novorossiyskogo obshchestva estestvoispytateley. Odessa] 25(1): 82–149. [In Russian and German]
- Lignau N (1907) [To the myriapod fauna of the Caucasus]. Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de Saint Pétersbourg [Ezhegodnik zoologicheskogo muzeya Imperatorskoy akademii nauk. Sankt-Peterburg] 12: 195–200.
- Lignau N (1911) Neue Beiträge zur Myriopodenfauna des Kaukasus. Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de Saint Pétersbourg [Ezhegodnik zoologicheskogo muzeya Imperatorskoy akademii nauk. Sankt-Peterburg] 16: 38–59.

- Lignau N (1915) Vielfüssler aus Abchasien. Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de Petrograd [Ezhegodnik zoologicheskogo muzeya Imperatorskoy akademii nauk. Petrograd] 19: 349–401 (for 1914).
- Lignau N (1924) Les nouveaux représentants du genre *Polyxenus*. Journal of Research Chairs in Odessa [Zhurnal nauchno-issledovatel'skikh kafedr v Odesse] 1(10/11): 191–201. [In Russian and French]
- Lohmander H (1928) Neue Diplopoden aus Ukraine und dem Kaukasus. Mémoires de la Classe des Sciences Physiques et Mathématiques, Académie des Sciences de l'Ukraine [Trudy Fizichno-matematichnogo viddilu, Ukrainska akademiya nauk. Kyiv] 4(3): 529–550.
- Lohmander H (1932) Neue transkaukasische Diplopoden. 4. Aufsatz über Diplopoden aus Sowjet-Union. Zoologischer Anzeiger 98(7/8): 171–182.
- Lohmander H (1936) Über die Diplopoden des Kaukasusgebietes. Göteborgs Kungliga Vetenskaps- och Vitterhets-Samhälles Handlingar, Series 5B, 5(1): 1–196.
- Lokšina IE, Golovatch SI (1979) Diplopoda of the USSR fauna. Pedobiologia 19: 381–389.
- Muralewicz WS (1907) Zur Myriapodenfauna des Kaukasus. Zoologischer Anzeiger 31(11/12): 329–351.
- Muralewicz WS (1911) [Essay on the fauna of Myriopoda of the Caucasus]. Mitteilungen des Kaukasischen Museums [Izvestiya Kavkazskogo muzeya] 5: 1–80. [in Russian]
- Muralewicz WS (1913) [Arthropods.—Arthropoda. Chapter VII. Class of myriapods.—Myriapoda]. Proceedings of the Society for the Study of the Black Sea Coast [Trudy Obshchestva izucheniya Chernomorskogo poberezhya] 2: 215–221. [in Russian]
- Muralewicz WS (1927) [To the fauna of Myriopoda of the Caucasus]. Acta Societatis Entomologicae Stauropolitanae [Izvestiya Stavropolskogo entomologicheskogo obshchestva] 3(1): 1–7. [in Russian]
- Read H (1992) The genus *Cylindroiulus* Verhoeff 1894 in the faunas of the Caucasus, Turkey and Iran (Myriapoda: Diplopoda: Julidae). Senckenbergiana biologica 72(4/6): 373–433.
- Short M (2015) New records of *Lophoproctus coecus* Pocock, 1894 (Diplopoda, Polyxenida, Lophoproctidae) extend the range of the genus *Lophoproctus*. ZooKeys 510: 209–222. <https://doi.org/10.3897/zookeys.510.8668>
- Short M, Vahtera V, Golovatch SI (2018) The millipede order Polyxenida in the faunas of the Crimean Peninsula and Caucasus, with notes on some other Polyxenidae. Zootaxa.
- Talikadze DA (1984) [On the millipede fauna (Diplopoda) of the Colchidan Province of the Caucasus]. Zoologicheskii Zhurnal 63(1): 124–145. [in Russian, a summary in English]
- Timotheew TE (1897) [Two new species of Diplopoda]. Bulletin de la Société des Naturalistes à l'Université Impériale de Kharkov [Trudy Obshchestva ispytateley prirody pri Imperatorskom Kharkovskom Universitete] 31: 1–19. [in Russian]
- Turbanov IS, Palatov DM, Golovatch SI (2016) The state of the art of biospeleology in Russia and other countries of the former Soviet Union: A review of cave (endogean) invertebrate fauna. 2. Arachnida – Acknowledgements. Zoologicheskii Zhurnal 95(11): 1283–1304. [in Russian; English translation: Entomological Review, 2016, 96(9): 1297–1333]. <https://doi.org/10.7868/S0044513416110064>

- Vagalinski B, Lazányi E (2018) Revision of the millipede tribe Brachyiulini Verhoeff, 1909 (Diplopoda: Julida: Julidae) with description of new taxa. Zootaxa.
- Verhoeff KW (1921) Chilognathen-Studien (91. Diplopoden-Aufsatz). Archiv für Naturgeschichte 85A: 23–80.
- Verhoeff KW (1930) Eine cavernicole Symphyognathen-Gattung aus Georgien, Transcaucasien. Mitteilungen über Höhlen- und Karstforschung 1930: 33–39.
- Victor T (1839) Insectes du Caucase et des provinces Transcausiennes recueillis et décrits par T. Victor. Bulletin de la Société Impériale des Naturalistes de Moscou 12: 44–67.
- Zuev RV (2014) Preliminary data on the millipedes (Diplopoda) from the Stavropol Territory, northern Caucasus, Russia. Arthropoda Selecta 23(4): 347–354. [http://kmkjournals.com/upload/PDF/ArthropodaSelecta/23/23\\_4\\_347\\_354\\_Zuev\\_for\\_Inet.pdf](http://kmkjournals.com/upload/PDF/ArthropodaSelecta/23/23_4_347_354_Zuev_for_Inet.pdf)
- Zuev RV (2017) The relict millipede *Hirudicryptus abchasicus* Golovatch, Evsyukov et Reip, 2015, new to the fauna of Russia (Diplopoda: Siphonocryptida: Siphonocryptidae). Russian Entomological Journal 26(3): 281–286.

# The peristomatic structures as a source of systematic characters in the genus *Lithobius* Leach, 1814 (Myriapoda, Chilopoda)

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Academic editor: P. Stoev | Received 17 October 2017 | Accepted 29 November 2017 | Published 7 March 2018

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<http://zoobank.org/514BFAB6-5BAE-4C73-A98D-18A16B6273BE>

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**Citation:** Ganske A-S, Edgecombe GD, Akkari N (2018) The peristomatic structures as a source of systematic characters in the genus *Lithobius* Leach, 1814 (Myriapoda, Chilopoda). In: Stoev P, Edgecombe GD (Eds) Proceedings of the 17<sup>th</sup> International Congress of Myriapodology, Krabi, Thailand. ZooKeys 741: 49–75. <https://doi.org/10.3897/zookeys.741.21706>

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## Abstract

Morphological characters have been widely used in centipede systematics. Here, we aim to obtain morphological information from the preoral chamber and peristomatic structures of lithobiomorph centipedes, with taxonomic sampling focused on the species-rich genus *Lithobius* Leach, 1814. Towards this goal, we (i) examined the epipharynx and hypopharynx of 32 species belonging to four subgenera of the genus *Lithobius*, viz. *Lithobius* Leach, 1814, *Monotarsobius* Verhoeff, 1905, *Sigibius* Chamberlin, 1913 and *Ezembius* Chamberlin, 1919 using light and scanning electron microscopy, (ii) searched for phylogenetically informative characters and (iii) described interspecific variation. Three species of the lithobiid genera *Eupolybothrus* Verhoeff, 1907, *Disphaerobius* Attems, 1926 and *Neolithobius* Stuxberg, 1875 were additionally examined and considered as likely outgroups. New characters and character states are proposed as additions to current phylogenetic datasets. Similarities in the peristomatic structures ally *Disphaerobius* with *Lithobius* (*Ezembius*), suggesting that the subfamily Pterygoterginae is nested within Lithobiinae and *Lithobius*.

## Keywords

Lithobiomorpha, Lithobiidae, epipharynx, hypopharynx, phylogeny, systematics



## Introduction

The peristomatic structures – the epipharynx and hypopharynx – of Chilopoda have hitherto been studied in the orders Scutigeromorpha, Lithobiomorpha, Geophilomorpha (Koch and Edgecombe 2006, 2008, 2012, respectively), and Scolopendromorpha (Edgecombe and Koch 2008, 2009) revealing numerous characters bearing phylogenetically useful information (see also Koch et al. 2010, Vahtera et al. 2013). Two characters of the peristomatic structures, viz. ‘bottle-shaped’ epidermal glandular shafts on the epipharynx and a characteristic shape of the hypopharynx, support the monophyly of the order Lithobiomorpha, whereas paired oblique rows of spines on the clypeal part of the epipharynx are thought to be apomorphic for the family Lithobiidae (Koch and Edgecombe 2008). Until now, *Lithobius*, the most diverse genus in Chilopoda, with more than 500 described species (Zapparoli and Edgecombe 2011, Bonato et al. 2016), is resolved as non-monophyletic on the basis of morphological data. Particular species were recovered in cladistic analysis as most closely related to the genera *Australobius* Chamberlin, 1920, *Hessebius* Verhoeff, 1941, and *Pleurolithobius* Verhoeff, 1899 (Koch and Edgecombe 2008), and this likely applies to other genera of Lithobiinae as well, if not even some of other five subfamilies of Lithobiidae (for current classification of this family see Zapparoli and Edgecombe 2011). However, broad information on species-interrelationships is still missing and the monophyly of subgenera remains questionable, being based on combinations of the same set of characters (Edgecombe 2007). Aiming to obtain further morphological information from the peristomatic structures of *Lithobius* to evaluate whether those might be useful for identifying clades within this very large genus, we study the epipharynx and hypopharynx of 32 species of *Lithobius*, including the subgenera *Lithobius* (23 spp.), *Sigibius* (3 spp.), *Monotarsobius* (5 spp.), and *Ezembius* (1 sp.) using light and scanning electron microscopy. We describe the variation of the microstructures between species and propose new characters for which patterns of variability suggest a potential for phylogenetic analyses. Additionally, we examine species of the lithobiid genera *Neolithobius* Stuxberg, 1875 (Lithobiinae), *Eupolybothrus* Verhoeff, 1907 (Ethopolyinae), and *Disphaerobius* Attems, 1926 (Pterygoterginae), for comparison with *Lithobius*.

## Material and methods

### Material

The studied material consists of 61 specimens belonging to 35 species preserved in 70% or 95% EtOH (Table 1), deposited at the Natural History Museum Vienna (NHMW), the Natural History Museum London (BM/NHMUK) and the Hungarian Natural History Museum Budapest (HNHMB). All material was examined with light and scanning electron microscopy.

**Table 1.** List of studied material deposited in the NHMW, BM/NHMK and HNHMB.

Species	Studied material
<i>Lithobius (Lithobius) agilis</i> C.L. Koch, 1847	2 females, NHMW 9123, 9124, <b>Austria</b> , Niederösterreich, Gaming, F. Feiller leg.
<i>L. (L.) calcaratus</i> C.L. Koch, 1844	1 male, NHMW 9132; 1 female, NHMW 9133, <b>France</b> , Normandie, 1919, H. Gadeau de Kerville leg.
<i>L. (L.) carinatus</i> L. Koch, 1862	1 female, NHMW 9125, <b>Croatia</b> , Jabuka Island, Pomo, April 1934, F. Werner & O. Wettstein leg.
<i>L. (L.) castaneus</i> Newport, 1844	1 female, NHMW 9194, N36°12'18", E 9°45'35", <b>Tunisia</b> , Zaghuan District, Jebel Mansour Mountain, close to (south to) Sidi Aouidette village, pine forest, <i>Rosmarinus</i> , under stones and leaf litter, 514 m, 28 March 2008, N. Akkari & P. Stoev leg.
<i>L. (L.) cyrtopus</i> Latzel, 1880	1 female, NHMW 1081, <b>Poland</b> , Galizien (früher zu Ungarn), 1919, R. Latzel leg.
<i>L. (L.) dentatus</i> C.L. Koch, 1844	2 females, NHMW 9134, 9135, <b>Austria</b> , Wiener Wald
<i>L. (L.) erythrocephalus</i> C.L. Koch, 1847	2 females, NHMW 9136, 9137, <b>Hungary</b> , Simontornya, F. Pillich leg.
<i>L. (L.) fagei</i> Demange, 1961	1 male, NHMUK, <b>Spain</b> , Majorca, Inca, 1974.242.
<i>L. (L.) forficatus</i> (Linnaeus, 1758)	1 male, NHMW 9138; 1 female, NHMW 9139, <b>Austria</b> , Kärnten, Friedlach, 16 October 2001, V. Stagl leg.
<i>L. (L.) lapidicola</i> Meinert, 1872	1 female, NHMW 9196, N 35°32.796' E 11°1.662', <b>Tunisia</b> , Mahdia District, Mahdia, touristic area, scattered palm trees and shrubs close to the road, polluted area not far from agricultural land, under stones, 0 m, 16 March 2008, N. Akkari & P. Stoev leg.
<i>L. (L.) latro</i> Meinert, 1872	2 females, NHMW 9140, 9141, <b>Austria</b> , Tirol, Zillertal, 1950, Schmöller leg.
<i>L. (L.) lucifugus</i> L. Koch, 1862	2 females, NHMW 9142, 9143, <b>Italy</b> , Südtirol, Sellajoch, 8 August 1896, C. Attems leg.
<i>L. (L.) macilentus</i> L. Koch, 1862	1 male, NHMW 9144, <b>Austria</b> , Wien, Niederösterreich, Wiener Wald, 18 December 1892; 25 March 1894; 5 October 1924, C. Attems leg.
<i>L. (L.) mutabilis</i> L. Koch, 1862	2 females, NHMW 9126, 9127, <b>Czech Republic</b> , Sudetenländer, 1919, R. Latzel leg.
<i>L. (L.) muticus</i> C.L. Koch, 1847	1 male, NHMW 9145, <b>Slovenia</b> , Maribor (Marburg), C. Attems leg.
<i>L. (L.) nodulipes</i> Latzel, 1880	2 females, NHMW 9146, 9147, <b>Croatia</b> , Küstenland Kroatien, 1919, R. Latzel leg.
<i>L. (L.) peregrinus</i> Latzel, 1880	1 male, NHMW 9129, <b>Serbia</b> , Šar planina mountain range, Ljubeten (=Ljuboten mountain), upper beech forest, 4 June 1906, C. Attems leg.
<i>L. (L.) piceus</i> L. Koch, 1862	1 female, NHMW 9128, <b>Austria</b> , österreichische Alpenlande, R. Latzel leg.
<i>L. (L.) pelidnus</i> Haase, 1880	1 male, NHMW 9148, <b>Austria</b> , Wiener Wald, Buch leg. 1male, NHMW 9149, N 48°16'45", E 016°20'10", <b>Austria</b> , Wien, 19. Bezirk, Kastralgemeinde Josefsdorf, Kahlenberg Nordosthang, ca. 400 m (Wald, unter Holz), 15 June 1980, J. Gruber leg.
<i>L. (L.) pyrenaicus</i> Meinert, 1872	1 male, NHMW 9130; 1 female, NHMW 9131, <b>France</b> , Pyrénées-Orientales, J. Chalande leg.
<i>L. (L.) tenebrosus</i> Meinert, 1872	2 females, NHMW 9151, 9152, <b>Austria</b> , Kärnten, Bezirk Sankt Veit an der Glan, Gemeinde Hüttenberg, Pressen (mountain)

Species	Studied material
<i>L. (L.) tricuspis</i> Meinert, 1872	2 females, NHMW 9153, 9154, <b>Austria</b> , Steiermark, Graz, Platte
<i>L. (L.) validus</i> Meinert, 1872	1 female, NHMW 9150, <b>Austria</b> , Steiermark, Weiz, Weizenklamm, 1948, H. Franz leg.
<i>L. (Monotarsobius) aeruginosus</i> L. Koch, 1862	2 females, NHMW 7546, <b>Austria</b> , Steiermark, Bezirk Liezen, Admont, Kemmatgraben, 1949, Franz H. leg.
<i>L. (M.) austriacus</i> (Verhoeff, 1937)	1 male, HNHMB 5980, <b>Hungary</b> , Felsőszőlőnk, Hármaskok, beech-hornbeam forest, 04 August 1948, I. Loksa leg.
	2 males, HNHMB 5983, 5984, <b>Hungary</b> , Salgóhánya, next to Hotel Medves, oak-beech forest, 30 March 2003, L. Dányi leg.
<i>L. (M.) crassipes</i> L. Koch, 1862	2 females, NHMW 9157, 9158, <b>Germany</b> , Leipzig, Sturany leg.
	2 females, HNHMB 5981, 5982, <b>Hungary</b> , Abaliget, Török-pince Cave (in a forest), at 8 m from the entrance, 14 January 2012, D. Angyal & L. Dányi leg.
<i>L. (M.) curtipes</i> C.L. Koch, 1847	1 female, HNHMB 5985; 1 male, HNHMB 5986, <b>Hungary</b> , Győrzámoly, under a woodstem at the side of the dam, 05 October 2000, L. Dányi, Z. Korsós & A. Seres leg.
<i>L. (M.) franciscorum</i> Dányi & Tuf, 2012	2 males, HNHMB 5987, 5988, <b>Kazakhstan</b> , Altai Mts., Arshaty, wood near village, 1200 m a.s.l., 30 June 2007, I.H. Tuf leg.
<i>L. (Sigibius) burzenlandicus</i> Verhoeff, 1931	2 males, HNHMB 5989, 5990, N 47°53.456', E 24°31.089', <b>Romania</b> , Maramureş Mts, Poienile de Sub Munte, Socolău valley, mixed forest, 825m a.s.l., 24 May 2007, Cs. Csuzdi, L. Dányi, J. Kotschán & D. Murányi leg.
	1 female, 1 male, NHMW 7413, <b>Hungary</b> , Siebenbürgen, 1919, R. Latzel leg.
<i>L. (S.) microps</i> Meinert, 1868	1 female, HNHMB 5991; 1 male, HNHMB 5992, N 46.1586°, E 8.8804°, <b>Switzerland</b> , Magadino, Bolle di Magadino, 195m, under <i>Reynoutria japonica</i> , pitfall trap, 2005-2006, M. Moretti leg.
<i>L. (S.) trebinjanus</i> Verhoeff, 1900	1 male, NHMW 9155; 1 female, NHMW 9156, <b>Albania</b> , Kukes county/Qarku i Kukësit, Has district/Rrethi i Hasit, Pashtrik mountain range/Mali i Pashtrikut, 1900 m, 1918, A. Penther leg.
<i>L. (Ezembius) electus</i> Silvestri, 1935	1 female, NHMUK, <b>China</b> , Kara-Korum, Aghill Dabam (Pass), 4700-4800 m, 30 August 1988, P. Beron leg.
<i>Neolithobius aztecus</i> (Humbert & Saussure, 1869)	1 female, NHMUK, BM1894.4.1.75-77, <b>Guatemala</b> , Dr. Stoll leg.
<i>Disphaerobius loricatus</i> (Sselivanoff, 1881)	1 male, NHMW 9204, <b>Kazakhstan</b> , East-Kazakhstan Area, Kaigutty River Valley, 32 km NW Ayagos, Saline-lend, 15 April 2016, A.A. Fomichev, R.Yu. Dudko leg.
<i>Eupolybothrus (Eupolybothrus) grossipes</i> (C.L. Koch, 1847)	1 male, NHMW 9176, N 46.4916°, E 14.3488°, <b>Austria</b> , Kärnten, Bezirk Klagenfurt-Land, Gemeinde Ferlach, Katastralgemeinde Waidisch, 602 m, rocky beech forest with spruce, under stones, logs and from leaf litter, 25 June 2017, Akkari N., Ganske A.-S. & Dányi L. leg.

## Sample preparation

The epipharynx and hypopharynx were dissected from the preoral chamber as described in Koch and Edgecombe (2008) in one to four adult male or female individuals per species. Multifocus images of the sclerotized parts of the epipharynx and hypopharynx were obtained with a Nikon SMZ25 stereomicroscope equipped with a Nikon DS-F2.5 camera using NIS-Elements Microscope Imaging Software with an Extended

Depth of Focus (EDF) patch. For scanning electron microscopy (SEM), the specimens were: (1) cleaned in an ultrasonic bath (50–60 Hz) for 5 to 10 seconds (maximum), occasionally in a solution of 15% hydrogen peroxide for 2 hours; (2) dehydrated in an ascending alcohol series (70%, 80%, 90%, 96% EtOH, 2 × 10–15 min each); (3) air dried overnight (or covered with HMDS) or critical point dried (Leica 300 CPD). Specimens were mounted on aluminium stubs equipped with a sticky aluminium tape, glued with conductive silver, coated with platinum (Leica EM SCD500) and studied with a JEOL JSM 6610-LV at an accelerating voltage of 15 kV. Figures were processed with Adobe Photoshop CS6 and assembled in Adobe InDesign CS6.

Terminology follows Koch and Edgecombe (2008).

### List of abbreviations

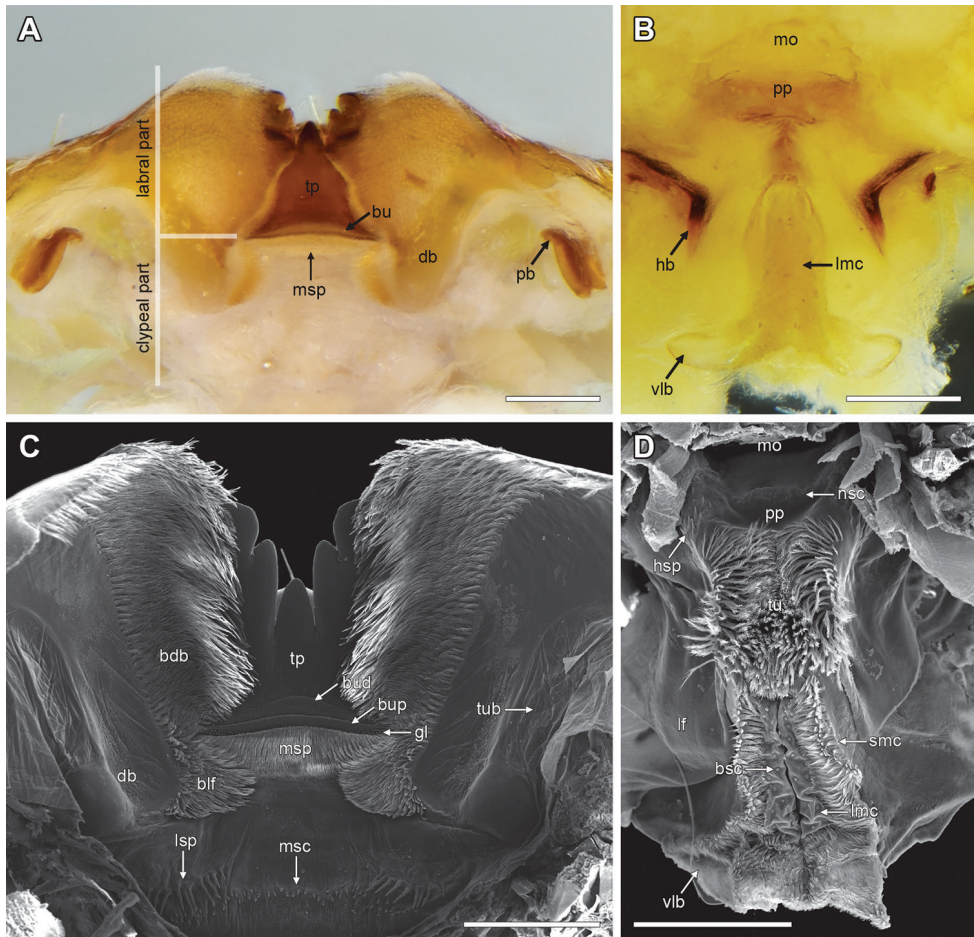
bdb – labral bristles on distal bar; blf – labral bristles on lateral flap; bsc – ‘button-shaped’ sensilla; bu – single transverse bulge; bud – distal transverse bulge; bup – proximal transverse bulge; db – distal bar; gl – ‘bottle-shaped’ epidermal glandular shafts; hb – hypopharyngeal bar; hsp – hypopharyngeal spine field; lf – lateral flap; lsp – lateral spine field; lmc – paired lips forming median crest; mo – mouth opening; msc – median sensilla cluster; msp – median spine field; nsc – cluster of ‘nipple-shaped’ sensilla; pb – proximal bar; pp – pharyngeal plate; smc – spines flanking median crest; tu – tuft of bristles; tub – tubercles on distal bar; vlb – ventrolateral bar.

## Results

### Epipharynx

The epipharynx is distally and proximally bordered by the inner walls of the labrum and the clypeus, respectively (Fig. 1A). Except for *D. loricatus* (Fig. 2A), the labral and clypeal parts of the epipharynx are generally divided by one or two transverse bulges (distal and proximal transverse bulge) (Figs 1A, C, 2B–F, 3: bu, bud, bup). The transverse bulge occurs with a stronger or less pronounced curvature of the furrowed distal and proximal margins bordering the ‘bottle-shaped’ epidermal glandular shafts (Figs 1C: gl, 2B–F, 3A–B). The margins can be parallel or not, curved distally and proximally (Fig. 2B–C) or curved distally and straight proximally (Figs 2D–F, 3A–B). The bulge always narrows laterally (Figs 2B–F, 3A–B, D, 4D–F, 5A). The surface of the bulge(s) is generally smooth (Figs 3A, 4A) but in some species it may show longitudinal striae laterally (Fig. 4D). In *L. tenebrosus* and *L. lucifugus*, the surface of the bulges is longitudinally striated and shows scattered pores (Figs 3C, 4B–C). In other species, a weak transverse furrow occurs on the tooth plate distally to the transverse bulge (Fig. 3A–B).

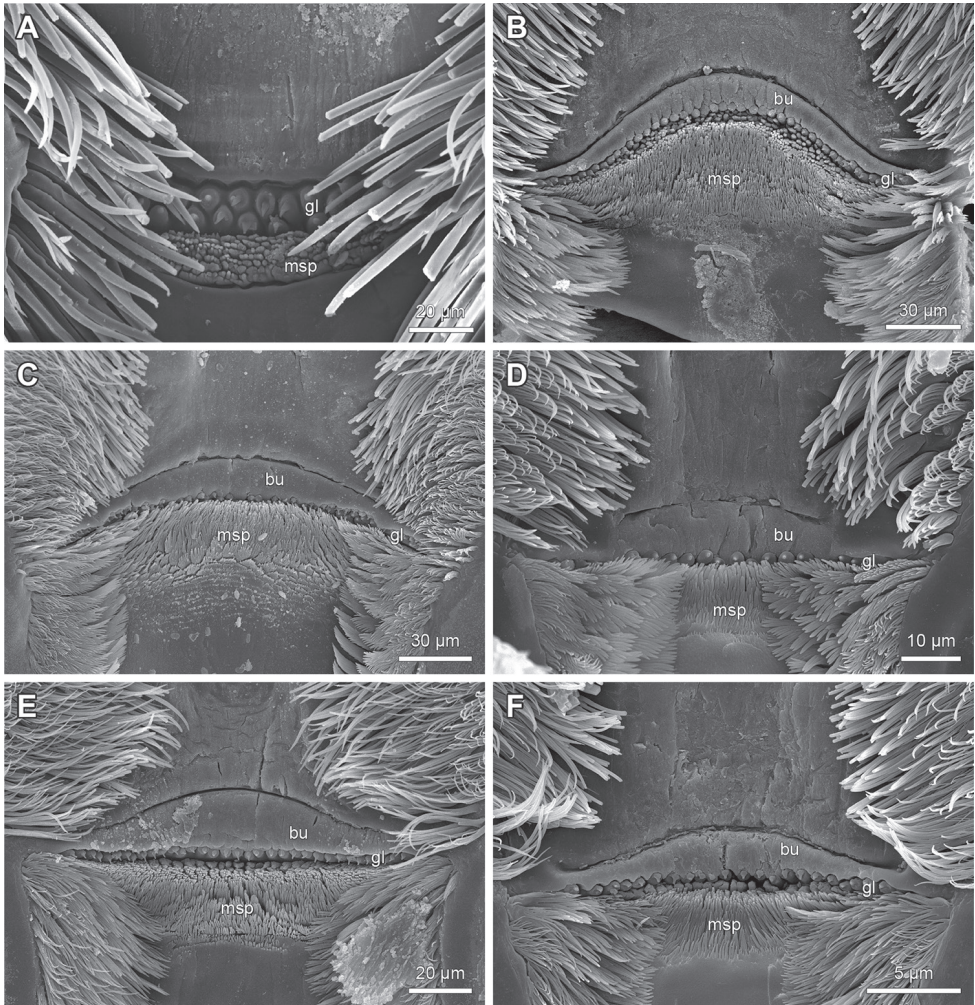
‘Bottle-shaped’ epidermal glandular shafts always occur proximal to the transverse bulge (Fig. 1C: gl). They can be arranged in one row (Figs 2B, E–F, 5A), one row medi-



**Figure 1.** Multifocus light-micrographs and SEM-photographs of peristomatic structures in Lithobiidae. **A** Epipharynx of *Lithobius* (*Lithobius*) *validus*; posterior view (top is ventral) **B** Hypopharynx of *Lithobius* (*Lithobius*) *carinatus*; anterior view (top is dorsal) **C** Epipharynx of *Eupolybothrus* (*Eupolybothrus*) *grossipes*; posterior view (top is ventral) **D** Hypopharynx of *Lithobius* (*Lithobius*) *forficatus*; anterodorsal view (left ventrolateral bar broken). bdb – labral bristles on distal bar, blf – labral bristles on labral flap, bsc – ‘button-shaped’ sensilla, bu – single transverse bulge, bud – distal transverse bulge, bup – proximal transverse bulge, db – distal bar, gl – ‘bottle-shaped’ epidermal glandular shafts, hb – hypopharyngeal bar, hsp – hypopharyngeal spine field, lf – lateral flap, lsp – lateral spine field, lmc – paired lips forming median crest, mo – mouth opening, msc – median sensilla cluster, msp – median spine field, nsc – cluster of ‘nipple-shaped’ sensilla, pb – proximal bar, pp – pharyngeal plate, smc – spines flanking median crest, tp – tooth plate, tu – tuft of bristles, tub – tubercles on distal bar, vlb – ventrolateral bar. Scale bars: 200  $\mu$ m.

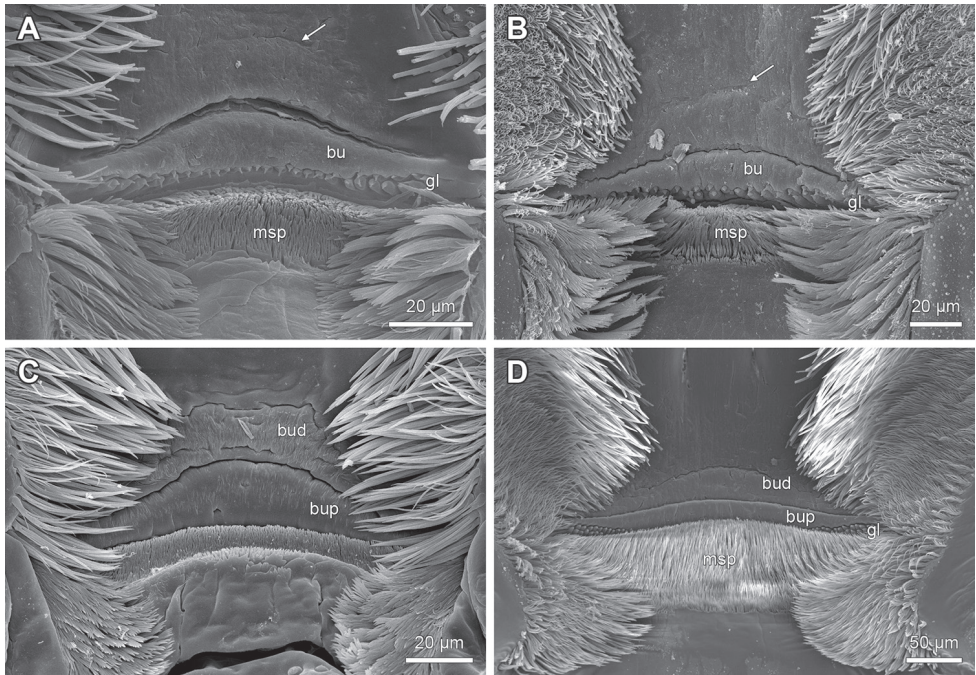
ally with up to two or more rows on the lateral sides (Figs 2C, 3A, 4A, 5B), or consistently two to more rows (Figs 2A, 3B). The number of glandular shafts varies from 19 in *L. microps* to more than 80 in *L. validus* and is generally higher in larger species. The number of glandular shafts can also differ between individuals of the same species, e.g. 20–22 in *L. aeruginosus* or 42–48 in *L. pyrenaicus*.





**Figure 2.** Details of transverse bulge, 'bottle-shaped' epidermal glandular shafts and median spine field of the epipharynx of Lithobiidae. **A** *Disphaerobius loricatus*; no transverse bulge; consistently two rows of 'bottle-shaped' epidermal glandular shafts; narrow and slightly medially widening median spine field **B** *Lithobius* (*Lithobius*) *pyrenaicus*; parallel aligned margins of a single transverse bulge; one row of 'bottle-shaped' epidermal glandular shafts; rhomboid and medially widening median spine field **C** *Lithobius* (*Lithobius*) *fagei*; single transverse bulge with parallel margins; more than one row of 'bottle-shaped' epidermal glandular shafts laterally; laterally widening median spine field **D** *Lithobius* (*Sigibius*) *microps*; single transverse bulge with non-parallel margins; subequal width of median spine field **E** *Lithobius* (*Lithobius*) *mutabilis*; single transverse bulge with non-parallel margins; one row of 'bottle-shaped' epidermal glandular shafts; subequal width of median spine field **F** *Lithobius* (*Monotarsobius*) *aeruginosus*; single transverse bulge with non-parallel margins; one row of 'bottle-shaped' epidermal glandular shafts; subequal width of median spine field. bu – transverse bulge, gl – 'bottle-shaped' epidermal glandular shafts, msp – median spine field.

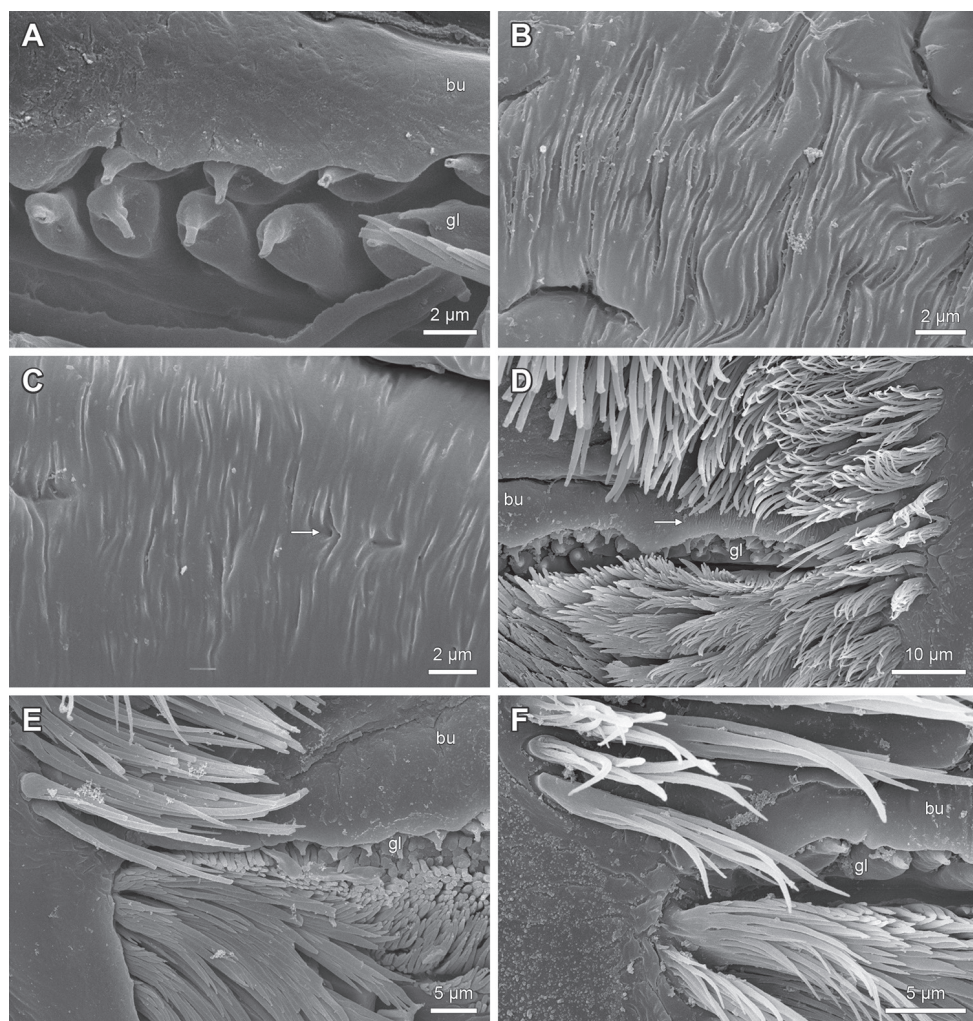




**Figure 3.** Details of transverse bulge, ‘bottle-shaped’ epidermal glandular shafts and median spine field of the epipharynx of Lithobiidae. **A** *Lithobius (Lithobius) macilentus*; single transverse bulge with smooth surface (see Fig. 4A) and non-parallel aligned margins; one row of ‘bottle-shaped’ epidermal glandular shafts medially with a transition to two rows laterally (see Fig. 4A); weak transverse furrow distally to the transverse bulge (arrow); laterally widening median spine field **B** *Lithobius (Lithobius) piceus*; weak transverse furrow (arrow) distally to the single transverse bulge (non-parallel margins); irregular two rows of ‘bottle-shaped’ epidermal glandular shafts; subequal width medially and laterally of median spine field **C** *Lithobius (Lithobius) lucifugus*; distal and proximal transverse bulges with surface striation (see Fig. 4B–C) **D** *Eupolybothrus (Eupolybothrus) grossipes*; distal and proximal transverse bulges; medially widening median spine field. bu – transverse bulge, bud – distal transverse bulge, bup – proximal transverse bulge, gl – ‘bottle-shaped’ epidermal glandular shafts, msp – median spine field.

Proximal to the ‘bottle-shaped’ epidermal glandular shafts is a median spine field arranged as a wide or a narrow band with a subequal width, medially or laterally widened and consisting of a variable number of branching spines (Figs 1A, C, 2, 3A–B, D: msp, 5D, 6A, D). The spines are always directed towards the labral part of the epipharynx but differ in shape, size and texture. The shape can be scaly, apically furcated or not (Figs 5D, 6).

Paired labral bristle bands occur on the distal bars on each side of the tooth plate (Fig. 1C: bdb). The bristle bands consist of long, simple bristles medially with a gradual transition to branching bristles laterally (Fig. 7). The branching bristles occur with a few or several outer rows, more or less covering the distal bar (Fig. 7A–B). The bristles point dorsomedial towards the transverse bulge. The branching bristles on the distal bar of the outer rows are generally ‘hassock-like’ (Fig. 8A–C), but they can also be ‘palmleaf-

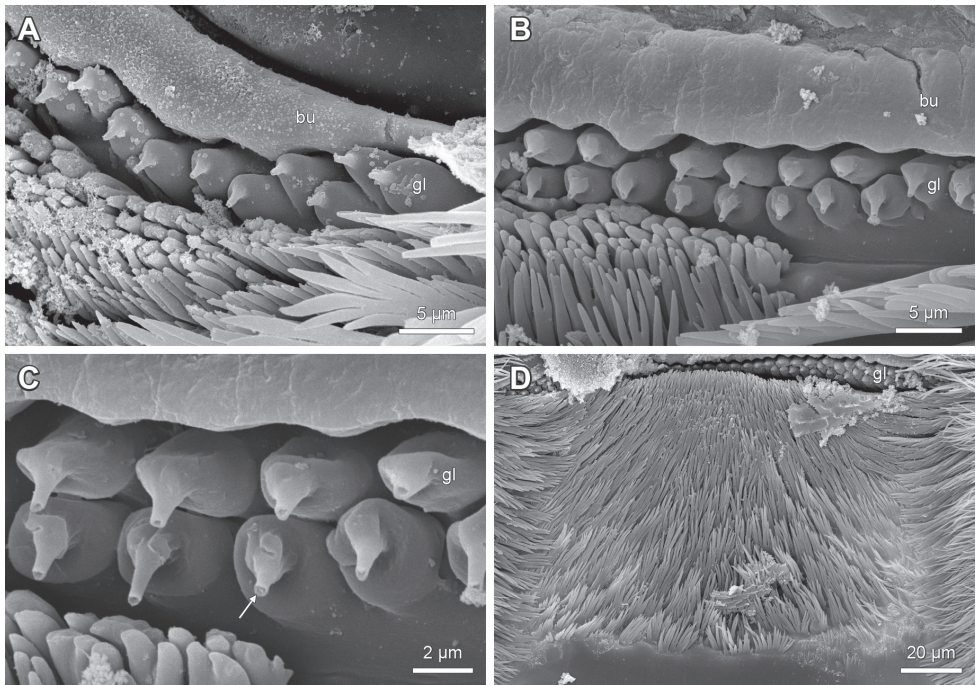


**Figure 4.** Epipharyngeal structures of *Lithobius*. **A** *Lithobius (Lithobius) macilentus*; transverse bulge with a smooth surface; two rows of epidermal glandular shafts at the lateral border of the transverse bulge **B** *Lithobius (Lithobius) lucifugus*; distal transverse bulge with longitudinal striae **C** *Lithobius (Lithobius) lucifugus*; proximal transverse bulge with longitudinal striae and pores (arrow) **D** *Lithobius (Lithobius) fagei*; longitudinal striae on the lateral part of the transverse bulge (arrow); continuous branching bristle band from the distal bar to the lateral flap at the margin of the transverse bulge **E** *Lithobius (Lithobius) cyrtopus*; distinct break of branching bristle band from the distal bar to the lateral flap **F** *Lithobius (Monotarsobius) crassipes*; distinct break of branching bristle band from the distal bar to the lateral flap. bu – transverse bulge, gl – ‘bottle-shaped’ epidermal glandular shafts.

like’ as for *L. validus* (Fig. 8D) or ‘comb-like’ in *L. trebinjanus* (Fig. 8E). The base of the branching bristles ranges from narrow to wide, with intermediate forms (Fig. 8).

The labral branching bristles on the distal bar expand towards the proximal part in a continuous manner (Fig. 4D) or with a distinct break (Fig. 4E–F) across the transverse





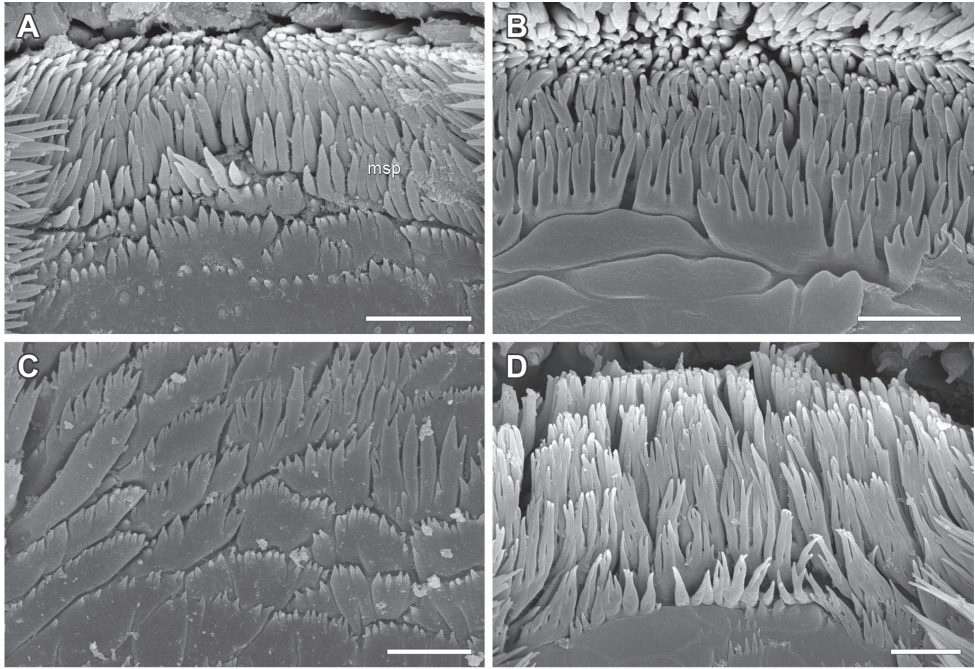
**Figure 5.** Epipharyngeal structures of *Lithobius*. **A** *Lithobius* (*Lithobius*) *pyrenaicus*; one row of ‘bottle-shaped’ epidermal glandular shafts; laterally narrowing transverse bulge **B–C** *Lithobius* (*Lithobius*) *validus* **B** two rows of ‘bottle-shaped’ epidermal glandular shafts **C** pore of an epidermal glandular shaft (arrow) **D** *Lithobius* (*Ezembius*) *electus*; broad median spine field with several rows of branching bristles and a sub-equal width medially and laterally. bu – transverse bulge, gl – ‘bottle-shaped’ epidermal glandular shafts.

bulge to the labral flap margins (Fig. 1C: blf). On the lateral flap, the structure of labral bristles changes gradually from laterally plumose to medially ‘fan-shaped’ (Fig. 9A–C) or it is consistently plumose (Fig. 9D), ‘fan-shaped’ only (Fig. 9E), or they can show just as simple bristles (Fig. 9F).

On the lateral borders of the distal bar, ovoid tubercles are observed in nearly all investigated species (Figs 1C: tub, 10H).

The median sensilla cluster (Fig. 1C: msc) on the clypeal part is always transversely aligned. It displays a highly variable interspecific arrangement of the sensilla. These sensilla can be arranged in line (Fig. 10A inset), in an offset-pattern (Fig. 10A, C–D) or symmetrical (Fig. 10B). The number of sensilla in the studied species varies between five in *L. aeruginosus* to 65 in *E. grossipes* (Fig. 10D). Variation of the arrangement and number of sensilla is also recorded in individuals of the same species (e.g. *L. tenebrosus* and *L. aeruginosus*).

Proximal to the clypeal part pairwise lateral spine fields are present bordering the median sensilla cluster except for *N. aztecus* (Fig. 10C), *D. loricatus* and *E. grossipes* (Fig. 10D) in which the sensilla overlap with the spine fields (Fig. 1C: lsp). The lateral spine fields are arranged in one oblique row or more than one row (Fig. 10A–G). If there is more than



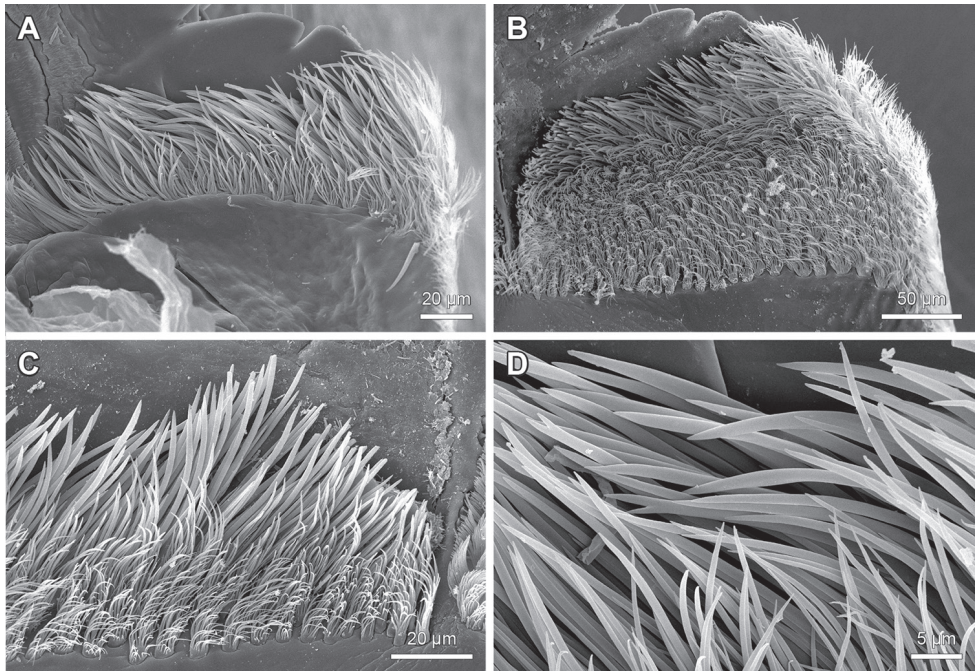
**Figure 6.** Details of spines from the median spine field on the epipharynx of *Lithobius*. **A** *Lithobius* (*Monotarsobius*) *aeruginosus*; narrow median spine field with a few rows of branching spines **B** *Lithobius* (*Lithobius*) *macilentus* **C** *Lithobius* (*Lithobius*) *peregrinus* **D** *Lithobius* (*Lithobius*) *tricuspis*. msp – median spine field. Scale bars: 5  $\mu$ m.

one row there is a tendency for spines to cluster or form small groups (Fig. 10E). These spines are surrounded by pores (Fig. 10E) and vary in number from two per side in *L. peregrinus* to approximately 17 in *L. crassipes*. They always point proximomedial towards the mouth opening and show a dissimilarity in number and distribution per side within a single individual. The spines are mainly long and tapering, with shorter ones in between (Fig. 10A–G). In some other species, they can be bi- or trifurcate (Fig. 10B, E).

## Hypopharynx

The hypopharynx is a subtriangular outgrowth consisting of paired lips forming a median crest (Fig. 1B, D: lmc). In front of the mouth opening lies the pharyngeal plate (*Schlundplatte* after Verhoeff 1902–1925) (Figs 1B, D, 11A: mo, pp). The latter shows transversely arranged ‘nipple-shaped’ sensilla on its median part (Figs 1D, 11A: nsc). The number of these sensilla varies from five in *L. aeruginosus* (Fig. 11B) to 25 in *L. validus* (Fig. 11D). The distribution pattern of ‘nipple-shaped’ sensilla varies from one clear line (Fig. 11A–B), zig-zag (Fig. 11C) to clusters of sensilla (Fig. 11E–F) but also displays intermediate forms (Fig. 11D).



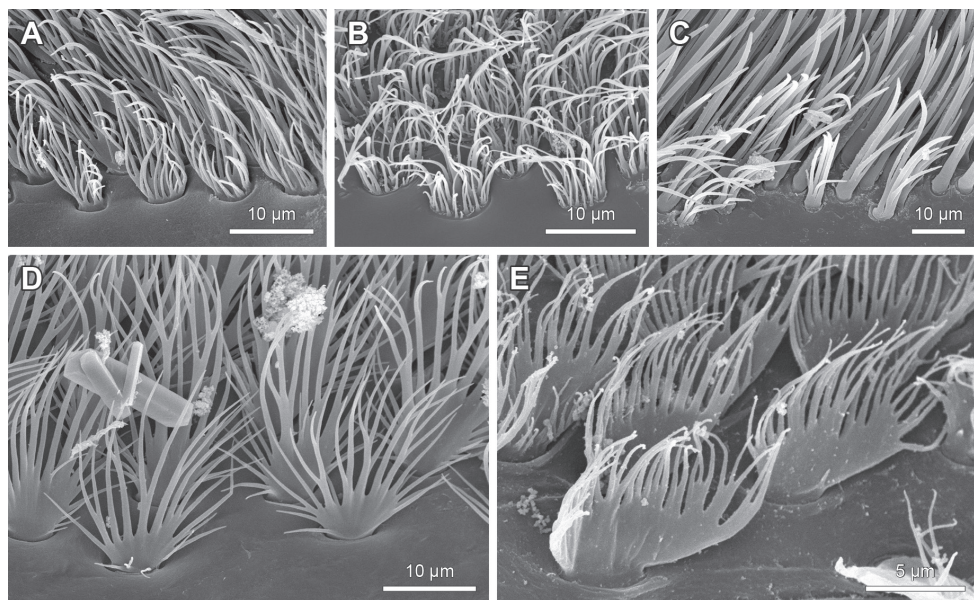


**Figure 7.** Labral bristle bands on the distal bar of the epipharynx of *Lithobius*. **A** *Lithobius* (*Lithobius*) *lucifugus*; transition of simple to branching bristles from medial to lateral with a few rows of branching bristles **B** *Lithobius* (*Lithobius*) *peregrinus*; transition of simple to branching bristles from medial to lateral with several rows of branching bristles **C** *Lithobius* (*Lithobius*) *erythrocephalus*; detail of the transition of simple to branching bristles from medial to lateral **D** *Lithobius* (*Lithobius*) *lucifugus*; simple bristles on the medial part of the distal bar (top is medial).

Distal to the pharyngeal plate appears a ‘tuft-like’ cluster of branching bristles (Fig. 1D: tu). The shape of these branching bristles varies from ‘fan-shaped’ to ramified, with a more flattened or roundish shaft occurring with several intermediate forms (Figs 12, 13C).

Lateral to the pharyngeal plate, hypopharyngeal spines are always present (Figs 1D, 11A, 12A: hsp). They are arranged in clusters of five to 37 spines unilaterally (Fig. 13A–C) and they are surrounded with single or clustered pores (up to six) from apparently epidermal glands (Fig. 13A–B, D, F). The spines mainly taper (Figs 11A, 13A–D, F), sometimes with ridges along the lateral side of the spine shaft (Fig. 13E) or are apically furcate (Fig. 13A). They can be long or short, sometimes with a more flattened appearance (Figs 11A, 13). The hypopharyngeal spines may occur with a continuous transition distomedially to the tuft area (Fig. 13A) or with a distinct break (Fig. 13C).

‘Button-shaped’ sensilla are arranged in continuous clusters on the lips of the median crest medially up to the ventrolateral bars within the branching bristles and are present in all examined species (Figs 1D: bsc, 14, 16B–D). The median crest is flanked by intergrading rows of branching bristles (Fig. 1D: smc), which can be stout and short (Fig. 15D) or slender and long (Fig. 15E). In several species, we observed a



**Figure 8.** Details of branching bristles on the outer row of the labral bristle bands on the distal bar of the epipharynx of *Lithobius*. **A–B** ‘hassock-like’ branching bristles with a broad base **A** *Lithobius* (*Lithobius*) *mutabilis* **B** *Lithobius* (*Ezembius*) *electus* **C** *Lithobius* (*Lithobius*) *pyrenaicus*; ‘hassock-like’ branching bristles with a narrow base **D** *Lithobius* (*Lithobius*) *validus*; ‘palmleaf-like’ bristles **E** *Lithobius* (*Sigibius*) *trebinjanus*; ‘comb-like’ bristles (top is medial).

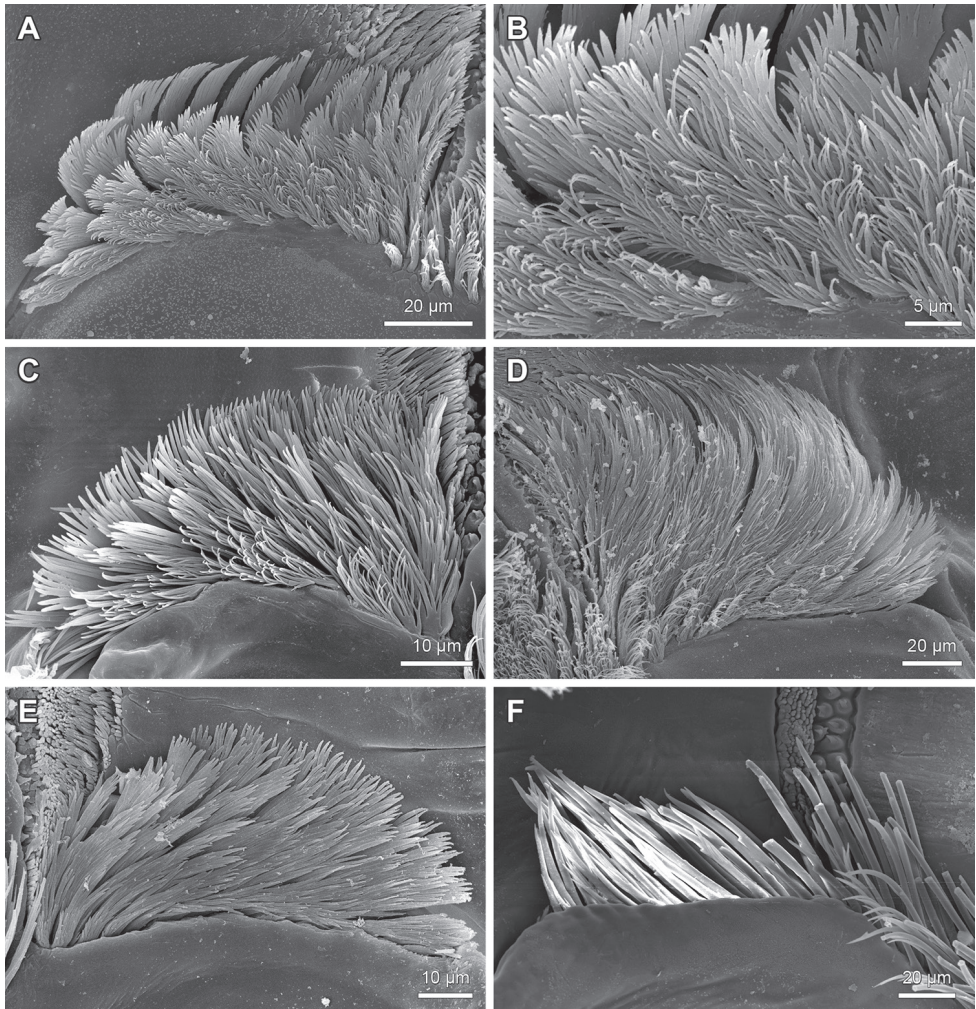
transition from branching bristles to flattened spines on the outermost rows (Figs 14A, 15A–C, F). The flattened spines show a structured surface (Fig. 15C).

The trichomes on the paired lips forming the median crest exhibit an intergrading transition from the tuft area proximal to distal up to the tips of the ventrolateral bars and medially to the proximoventral parts of the hypopharynx (Fig. 1D). At the border to the tuft area, there are generally ‘fan-shaped’ or plumose branching bristles, which mostly shorten in length, transitioning to ‘brush-’, ‘tuft-’, ‘feather-like’ or simple bristles (Figs 14A, 15A, E–F, 16A–C, E–F, 17A–D, F). On the proximoventral part, the bristles change over into clearly separated brush-tufts that are intermingled by ‘button-shaped’ sensilla (Fig. 16D). The shape of trichomes varies greatly between species. In *D. loricatus*, for example, there are scales on the distal tips of the lips bordered by the margin of the ventrolateral bar (Fig. 17E) in comparison to other species showing bristles in this area (Fig. 17A–D, F).

### Peristomatic characters with phylogenetic significance

In the following, eight peristomatic characters are proposed for the genus *Lithobius*, three of which are newly described (see char. 4, 6, 7). Additionally, we verified the consistency of two characters (see char. 2, 8) and adjusted three (see char. 1, 3, 5) from those indicated by Koch and Edgecombe (2008). Codings are provided in Appendix 1.

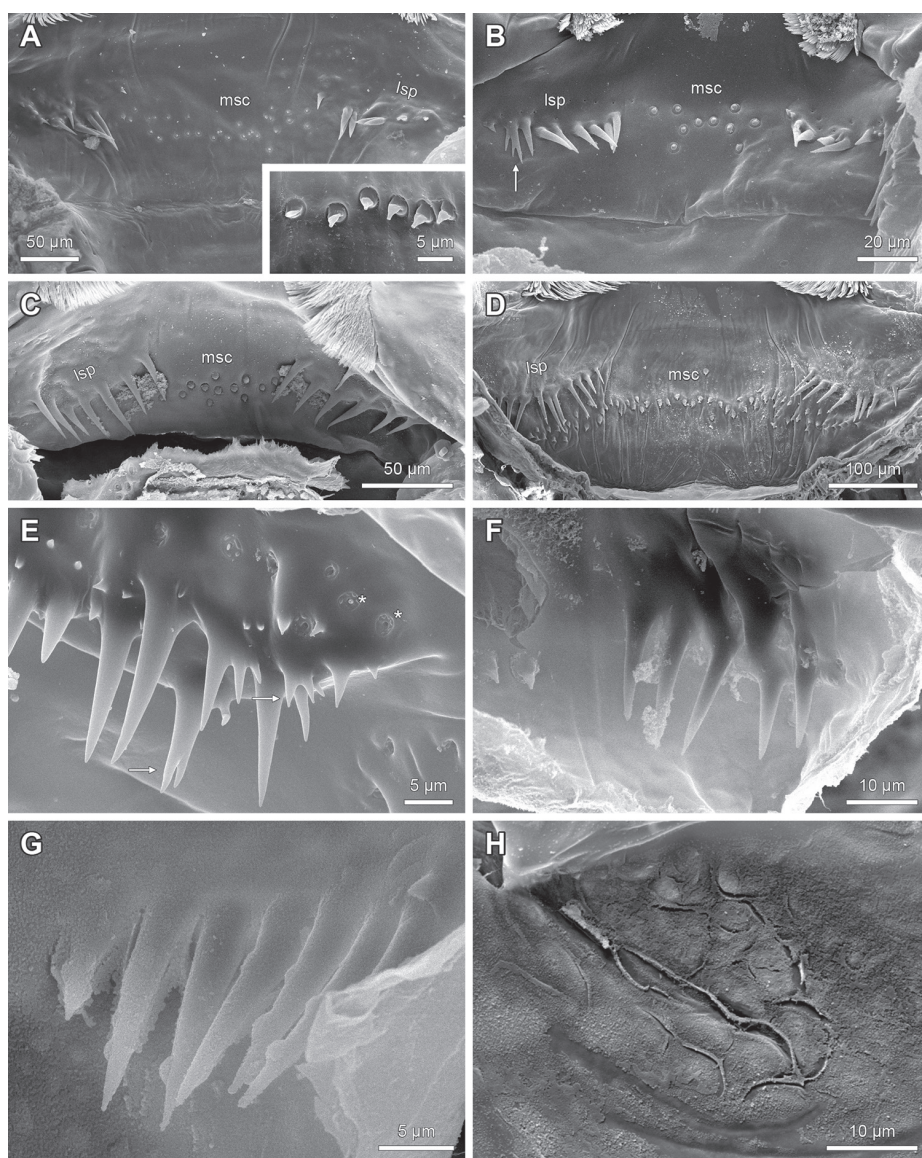




**Figure 9.** Details of branching bristles on the lateral flap on the distal bar of the epipharynx of *Lithobius*. **A–B** *Lithobius (Lithobius) fagei* **A** bristles changing from plumose laterally to ‘fan-shaped’ medially **B** detail of 9A **C** *Lithobius (Monotarsobius) aeruginosus*; bristles changing from plumose laterally to ‘fan-shaped’ medially **D** *Lithobius (Lithobius) peregrinus*; plumose bristles only **E** *Lithobius (Lithobius) cyrtopus*; ‘fan-shaped’ bristles only **F** *Disphaerobius loricatus*; simple bristles only (top is medial).

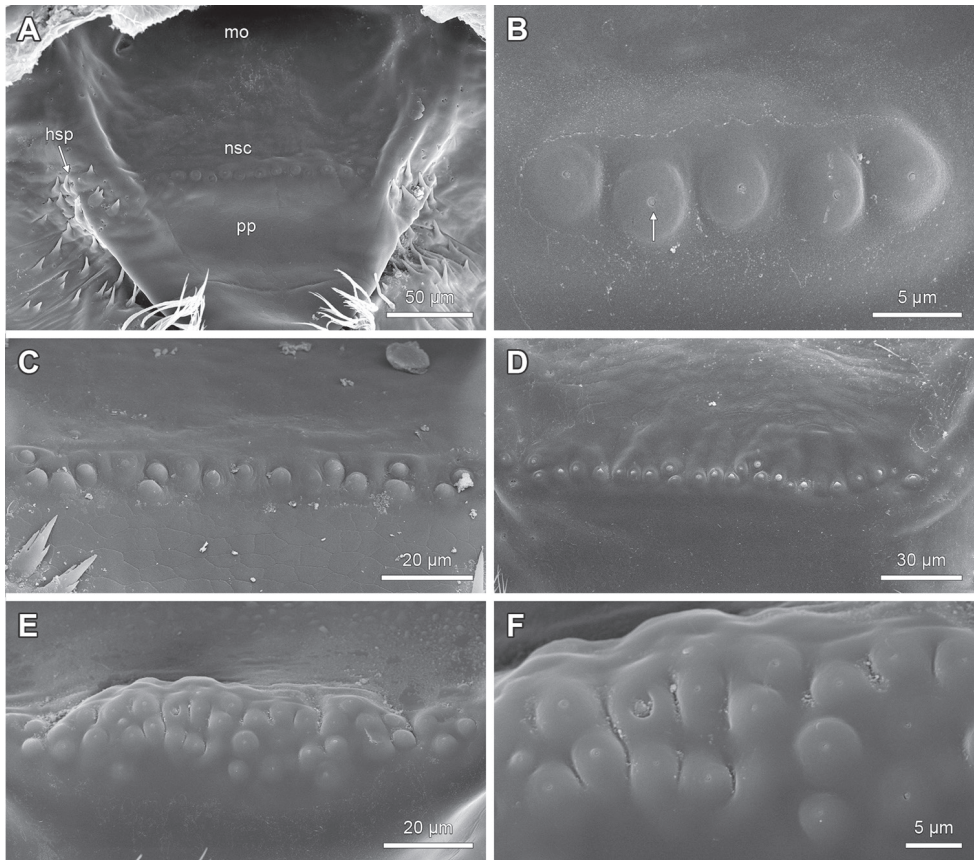
## Epipharynx

1. ‘Bottle-shaped’ glandular shafts at the border between labral and clypeal part of epipharynx: (0) one distinct regular row; (1) more than one regular or irregular row. All the investigated lithobiomorph species possess ‘bottle-shaped’ epidermal glandular shafts at the border between the labral and clypeal parts of the epipharynx. The latter can be in one regular row (Figs 2B, D–F, 5A) or with a variable arrangement, e.g. one regular row medially, which expands to two



**Figure 10.** Median sensilla cluster and lateral spine fields on the epipharynx of *Lithobiidae*. **A** *Lithobius* (*Lithobius*) *validus*; sensilla cluster arranged in an offset pattern; spine field arranged as single oblique row; Inset: *Lithobius* (*Monotarsobius*) *aeruginosus*; sensilla cluster arranged in line **B** *Lithobius* (*Lithobius*) *tenebrosus*; sensilla cluster arranged symmetrically; spine field arranged as single oblique row with trifurcate spines (arrow) **C** *Neolithobius aztecus*; sensilla cluster arranged in an offset pattern; spine field arranged as single oblique row **D** *Eupolybothrus* (*Eupolybothrus*) *grossipes*; sensilla cluster arranged in an offset-pattern and strongly overlapping with lateral spine field proximolaterally; spine field arranged as single oblique row **E** *Lithobius* (*Lithobius*) *pelidnus*; spine field arranged as two rows (tendency of clustering) with bi- or trifurcate spines (arrows) and pores (asterisks) **F** *Lithobius* (*Monotarsobius*) *curtipes*; spine field arranged as single oblique row **G** *Lithobius* (*Monotarsobius*) *aeruginosus*; spine field arranged as single oblique row **H** *Lithobius* (*Monotarsobius*) *aeruginosus*; tubercles on distal bar. lsp – lateral spine field, msc – median sensilla cluster.

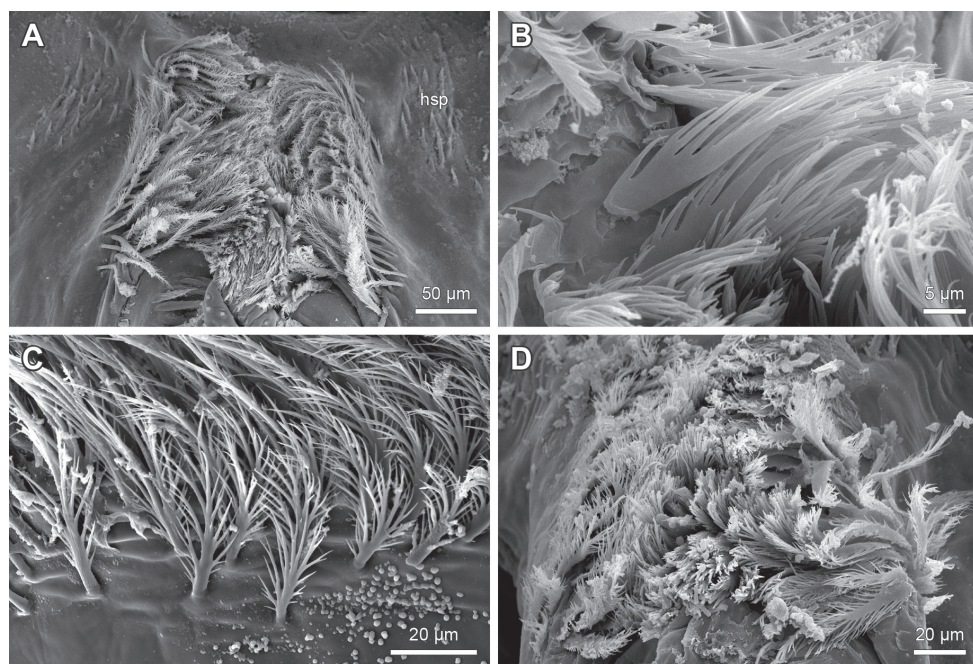




**Figure 11.** ‘Nipple-shaped’ sensilla on pharyngeal plate and hypopharyngeal spines of hypopharynx of *Lithobius*. **A** *Lithobius* (*Lithobius*) *dentatus*; pairwise hypopharyngeal spine fields laterally to pharyngeal plate; transverse line of several ‘nipple-shaped’ sensilla **B** *Lithobius* (*Monotarsobius*) *aeruginosus*; transverse line of a few ‘nipple-shaped’ sensilla on the pharyngeal plate; arrow indicates a pore **C** *Lithobius* (*Lithobius*) *pyrenaicus*; ‘nipple-shaped’ sensilla arranged in a zig-zag-pattern **D** *Lithobius* (*Lithobius*) *validus*; several ‘nipple-shaped’ sensilla arranged in a transverse line with some offset sensilla **E–F** *Lithobius* (*Lithobius*) *forficatus* **E** clustered ‘nipple-shaped’ sensilla **F** high magnification of ‘nipple-shaped’ sensilla from Fig. 11E. hsp – hypopharyngeal spine field, mo – mouth opening, nsc – cluster of ‘nipple-shaped’ sensilla, pp – pharyngeal plate.

or three regular or irregular rows laterally (Figs 2C, 3A, 4A, 5B). A regular or irregular arrangement of consistently two or more rows along the whole width is present, for example, for *D. loricatus* and *L. piceus* (Figs 2A, 3B). Both states were identified across all subgenera of *Lithobius* with state (0) being underrepresented in the subgenus *Lithobius* (6 of 23 examined species). *N. aztecus*, *D. loricatus* (Fig. 2A) and *E. grossipes* (Fig. 3D) share state (1).

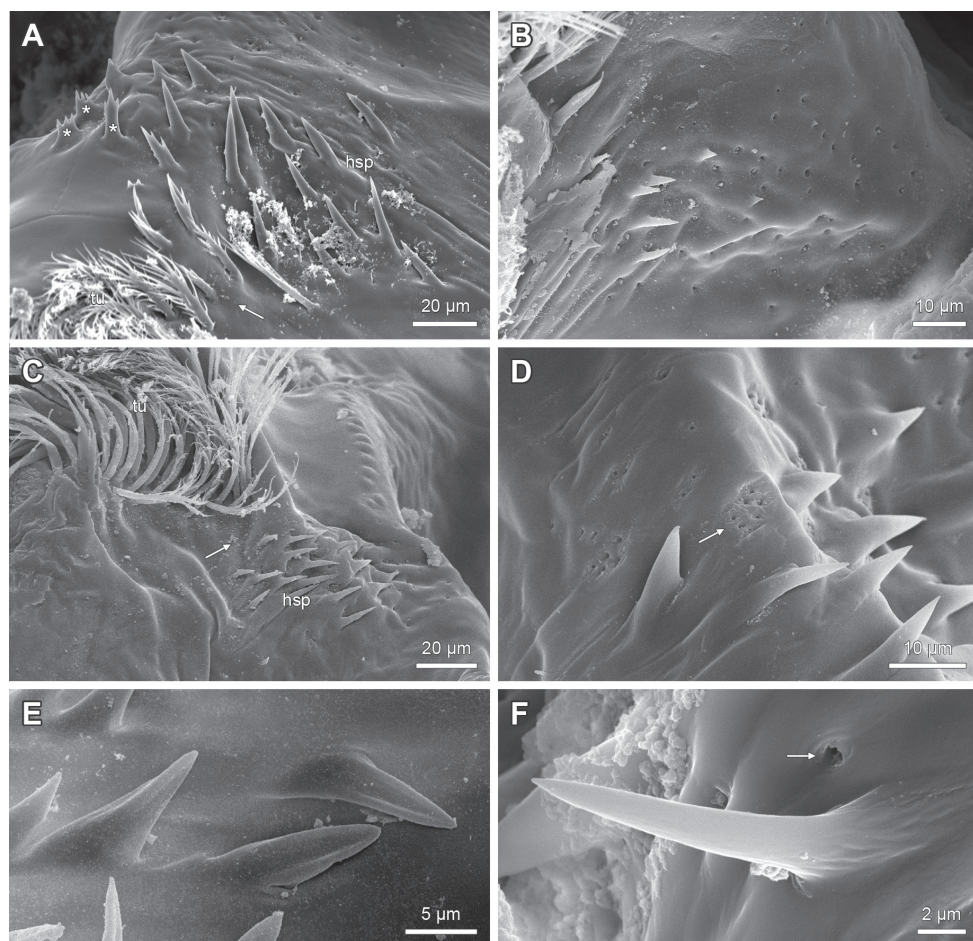
2. Labral bristle bands of epipharynx: (0) bristle bands continuous across transverse bulge; (1) distinct break in bristle bands proximal and distal to transverse bulge. (Character 31 in Koch and Edgecombe 2008).



**Figure 12.** Shapes of branching bristles forming a tuft distally to the pharyngeal plate of the hypopharynx of Lithobiidae. **A** *Lithobius (Lithobius) forficatus*; ramified branching bristles with a roundish shaft and hypopharyngeal spines laterally to pharyngeal plate (top is dorsal) **B** *Lithobius (Lithobius) calcaratus*; close-up of 'fan-shaped' and flattened branching bristles (top is medial) **C** *Eupolybothrus (Eupolybothrus) grossipes*; ramified and more flattened branching bristles (top is dorsal) **D** *Lithobius (Lithobius) latro*; ramified and flat branching bristles (top is medial). hsp – hypopharyngeal spine field.

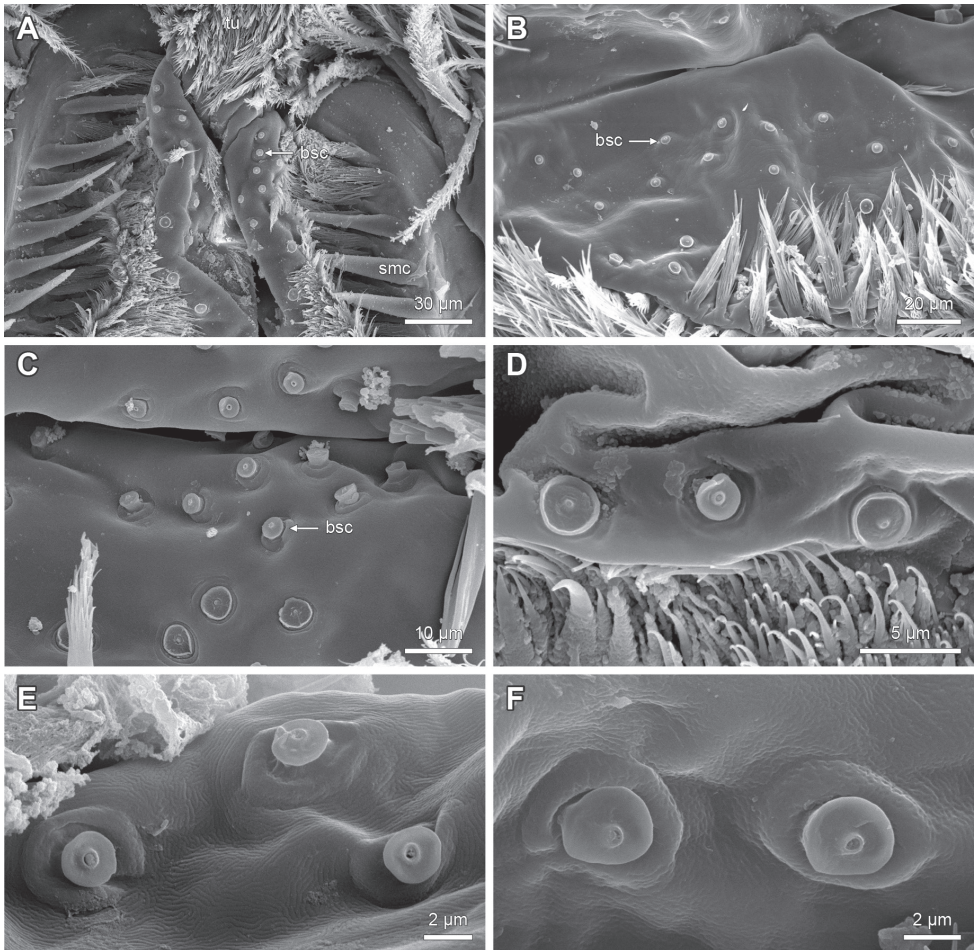
- The subgenera of *Lithobius* and other lithobiid genera show labral bristle bands that are either continuous (Fig. 4D) or are interrupted at the transverse bulge (Fig. 4E–F). All studied species of the subgenus *Sigibius* share state (1) (e.g. Fig. 2D).
3. Number of transverse bulge(s) at border between labral and clypeal parts of epipharynx: (0) none; (1) one; (2) two.  
The presence of one or two transverse bulges is common for the genera *Lithobius*, *Neolithobius* and *Eupolybothrus* (e.g. Figs 2B–F, 3). The bulges are absent only in the genus *Disphaerobius* (Fig. 2A). Two bulges are shared by *L. calcaratus*, *L. lucifugus*, *L. tenebrosus* and *E. grossipes* only (e.g. Fig. 3C–D).
  4. Direction of distal and proximal furrowed margins of transverse bulge or transverse bulges on epipharynx: (0) parallel; (1) non-parallel.  
Both states occur in all studied genera, state (0) e.g. in *L. pyrenaicus*, *L. fagei*, *L. lucifugus* and *E. grossipes* (Figs 2B–C, 3C–D) or state (1) e.g. in *L. microps*, *L. mutabilis*, *L. aeruginosus*, *L. macilentus* and *L. piceus* (Figs 2D–F, 3A–B). All species of the subgenus *Sigibius* share a non-parallel alignment (state (1)) of the transverse bulge margins (e.g. *L. microps*; Fig. 2D).





**Figure 13.** Examples of number and shape of the hypopharyngeal spines and surrounding pores of Lithobiidae. **A** *Eupolybothrus* (*Eupolybothrus*) *grossipes*; several tapering spines with trifurcate spines (asterisks) in between and a continuous transition to the tuft area (arrow) **B** *Lithobius* (*Lithobius*) *agilis*; few short tapering spines; several single pores **C** *Lithobius* (*Lithobius*) *muticus*; long and tapering spines; distinct break (arrow) between hypopharyngeal spine field and branching bristles of tuft **D** *Lithobius* (*Lithobius*) *validus*; hypopharyngeal spines surrounded by cluster of up to six pores (arrow) **E** *Lithobius* (*Lithobius*) *cyrtopus*; flattened and ridged spines **F** *Lithobius* (*Lithobius*) *castaneus*; detail of a long tapering spine close to a single pore (arrow). hsp – hypopharyngeal spine field, tu – tuft of bristles.

5. Median field of branching spines immediately proximal to the border between labral and clypeal parts of epipharynx: (0) rhomboid, widening medially; (1) widening laterally; (2) subequal width medially and laterally. State (2) is most common throughout the subgenus *Lithobius* and occurs in the other subgenera of *Lithobius*, e.g. *L. microps*, *L. piceus* and *L. electus* (Figs 2D, 3B, 5D). The genera *Eupolybothrus*, *Disphaerobius* and *Neolithobius* share state (0) but show variation in the number of rows of branching spines



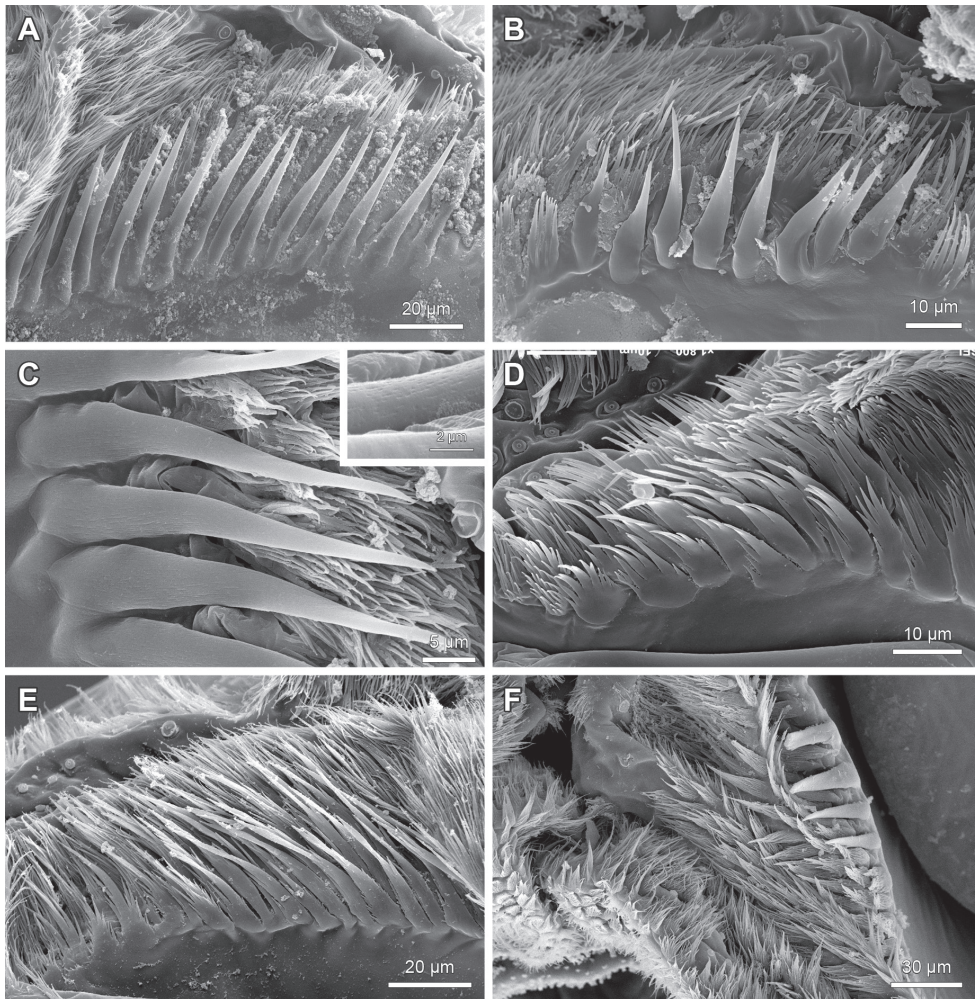
**Figure 14.** Examples of 'button-shaped' sensilla on the lips of hypopharynx of Lithobiidae. **A** *Lithobius (Lithobius) forficatus*; proximal part of lips forming median crest with cluster of 'button-shaped' sensilla; flattened spines flanking median crest margin **B** *Eupolybothrus (Eupolybothrus) grossipes*; left lip with cluster of 'button-shaped' sensilla **C** *Lithobius (Lithobius) validus* **D** *Lithobius (Sigibius) burzenlandicus* **E** *Lithobius (Lithobius) muticus* **F** *Lithobius (Lithobius) carinatus*. bsc – 'button-shaped' sensilla, smc – spines flanking median crest, tu – tuft of bristles. **A** top is dorsal; **B–F** top is medial.

(e.g. Figs 2A, 3D). All states occur with a narrower or wider band having a few or several rows of branching spines.

6. Shape of branching bristles on labral flap of epipharynx: (0) lateral to medial transition from plumose to 'fan-shaped' bristles; (1) 'fan-shaped' bristles only; (2) plumose bristles only; (3) simple bristles only.

A transition of branching bristles from plumose laterally to 'fan-shaped' medially is the most common state (0) across the genus *Lithobius*, and also pertains to *Neolithobius* and *Eupolybothrus* (e.g. Fig. 9A–C). State (1) was observed in

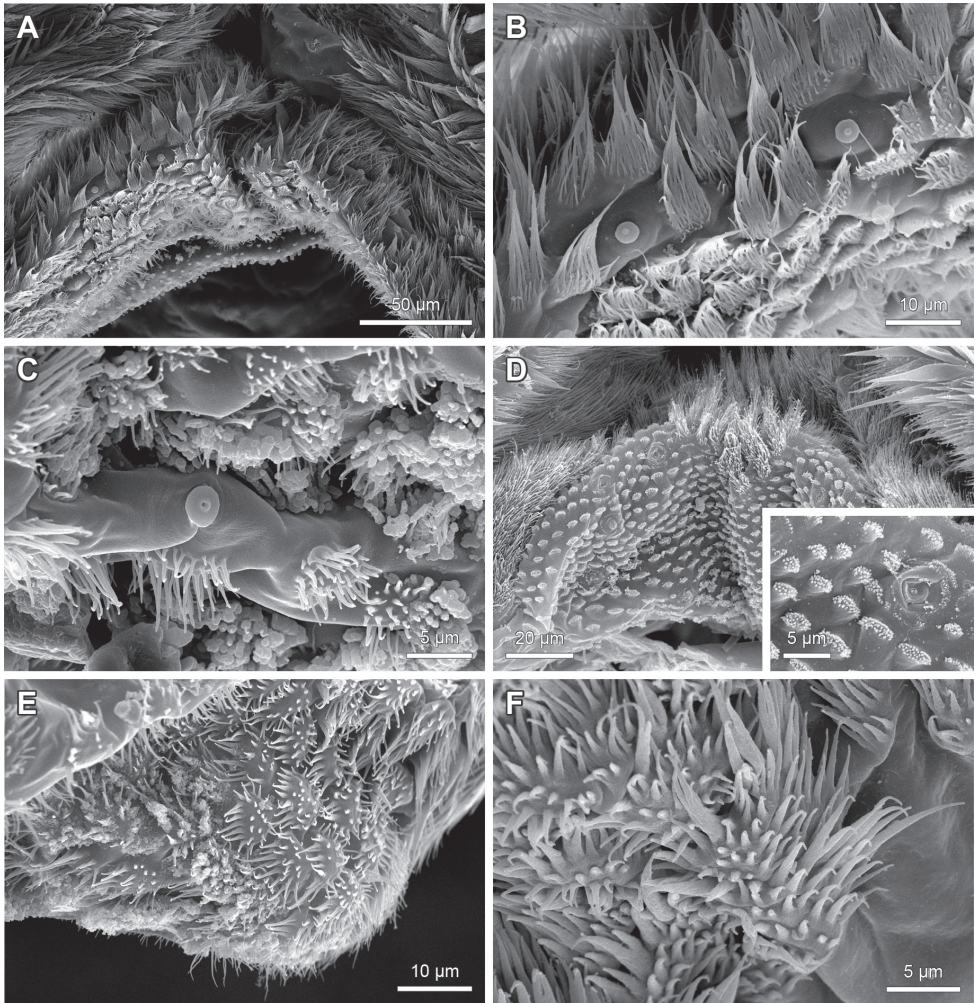




**Figure 15.** Examples of spines and bristles flanking the median crest margins of hypopharynx of *Lithobius*. **A–C** flattened spines with a transition to branching bristles on the inner rows **A** *Lithobius* (*Lithobius*) *pelidnus* **B** *Lithobius* (*Monotarsobius*) *franciscorum* **C** *Lithobius* (*Lithobius*) *muticus*; Inset: detail of structured surface of flattened spines **D–E** continuously branching bristles flanking the median crest **D** *Lithobius* (*Sigibius*) *microps*; stout and short branching bristles **E** *Lithobius* (*Lithobius*) *piceus*; slender and long branching bristles **F** *Lithobius* (*Lithobius*) *forficatus*; flattened spines flanking median crest margin. **A–B, D–E** top is medial; **C** top is ventral; **F** top is dorsal.

*L. cyrtopus* (Fig. 9E), *L. lucifugus*, *L. pelidnus* and *L. microps*. State (2) was present in *L. peregrinus* (Fig. 9D), *L. piceus* and *L. tricusps*, and state (3) in *D. loricatus* only (Fig. 9F).

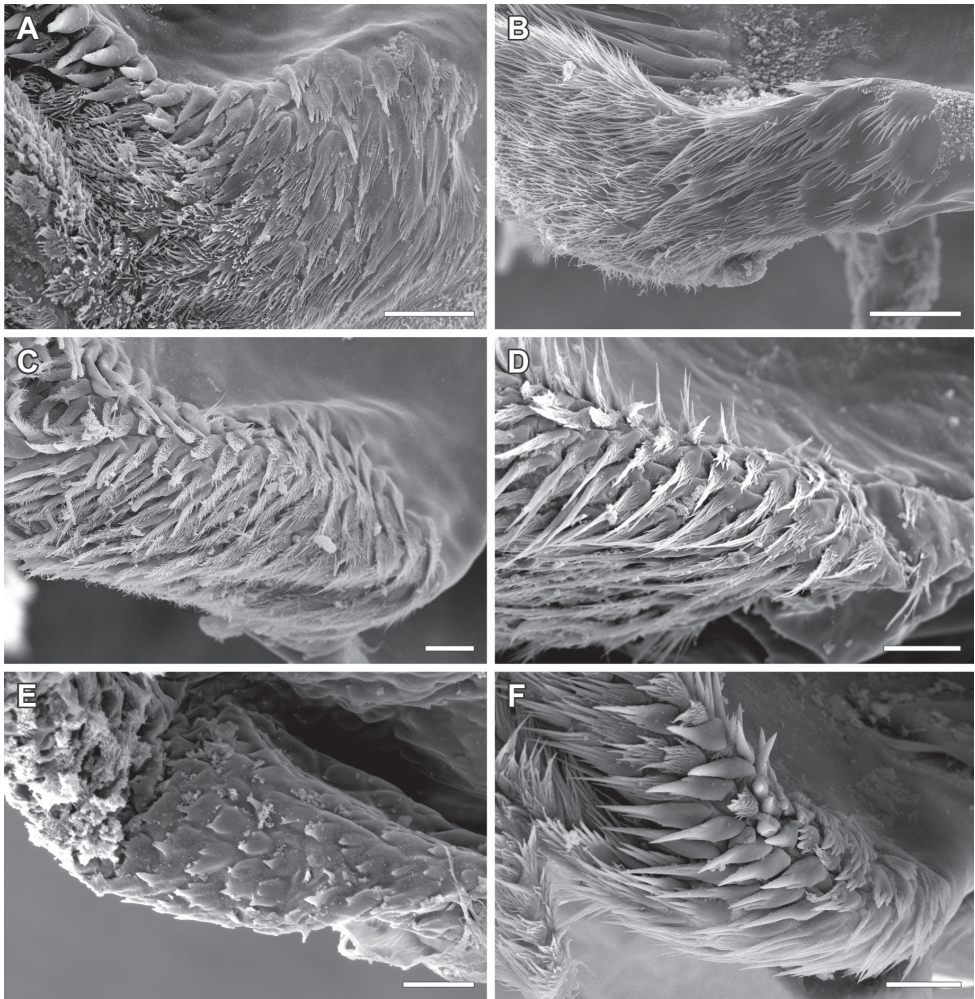
7. Lateral expansion of median sensilla cluster of epipharynx: (0) isolated from the lateral spine fields; (1) partly overlapping with the lateral spine fields.



**Figure 16.** Examples of bristles transitioning in shape and length along the median crest margin on hypopharynx of *Lithobius*. **A–B** *Lithobius (Lithobius) forficatus* **B** ‘button-shaped’ sensilla between branching bristles on the distal part of the lips **C** *Lithobius (Lithobius) pyrenaicus* **D** *Lithobius (Lithobius) erythrocephalus*; Inset: detail of brush-tufts surrounding ‘button-shaped’ sensilla **E** *Lithobius (Lithobius) pelidnus* **F** *Lithobius (Lithobius) carinatus*.

In all *Lithobius* species we examined (except for *L. tricuspis* and *L. nodulipes* for which the samples were damaged), the median sensilla cluster is bordered laterally by fields of spines (state (0); Fig. 10A–B). The sensilla in *D. loricatus* and *N. aztecus* slightly overlap with the lateral spine fields medially (state (1); e.g. Fig. 10C). In *E. grossipes* the sensilla of the median sensilla cluster strongly overlap with the lateral spine fields proximolaterally (state (1); Fig. 10D).





**Figure 17.** Bristles and scales on the distal tips of the lips on hypopharynx of Lithobiidae. **A** *Lithobius* (*Lithobius*) *cyrtopus* **B** *Lithobius* (*Lithobius*) *pelidnus* **C** *Lithobius* (*Lithobius*) *validus* **D** *Eupolybothrus* (*Eupolybothrus*) *grossipes* **E** *Disphaerobius loricatus*; scales **F** *Lithobius* (*Lithobius*) *forficatus*. Scale bars: 20  $\mu\text{m}$ .

8. Differentiation of spines flanking median crest of hypopharynx: (0) intergrading rows of branching bristles; (1) single outer row of simple flattened spines with abrupt transition to multifurcating inner rows of branching bristles. (Character 39 in Koch and Edgecombe 2008)

Species of the subgenus *Monotarsobius* always display state (1) (e.g. *L. franciscorum*; Fig. 15B). The *Ezembius* species *L. electus* studied here displays state (1), which differs from *Lithobius* (*Ezembius*) *giganteus* Sseliwanoff, 1881, stated by Koch and Edgecombe (2008). State (1) (Fig. 15A–C, F) is more common throughout the other subgenera of *Lithobius* and species of the other examined genera compared to state (0) (Fig. 15D–E).

## Discussion

Studies on the external morphology and microanatomy of the peristomatic structures of centipedes have hitherto unveiled phylogenetically useful information (Koch and Edgecombe 2006, 2008, 2012, Edgecombe and Koch 2008, 2009). The 'bottle-shaped' epidermal glandular shafts of the epipharynx and the discrete shape of the hypopharynx support the monophyly of the order Lithobiomorpha and paired oblique rows of lateral spines on the clypeal part of the epipharynx is, for example, considered as an apomorphic character for the family Lithobiidae (Koch and Edgecombe 2008). The inclusion of characters from these structures in a morphological dataset that also included other (mostly external) parts of the body further revealed the genus *Lithobius* as a non-monophyletic taxon (Koch and Edgecombe 2008). Within the genus *Lithobius*, five out of eleven described characters of the peristomatic structures display different states (Koch and Edgecombe 2008), which might give hints on species-interrelationships within the genus. These data from the peristomatic structures are presented as a set of coded characters (Appendix 1) that will be analysed cladistically with characters from other character systems in a later study.

## Phylogenetic significance of the peristomatic structures of Lithobiidae

While studying the peristomatic structures of Lithobiomorpha and Scutigleromorpha, Koch and Edgecombe (2008) compared the presence of the 'bottle-shaped' epidermal glandular shafts between the labral and clypeal part of the epipharynx. These glandular shafts were reported to be constantly present in Lithobiomorpha (Koch and Edgecombe 2008) and absent in other chilopods (Koch and Edgecombe 2006, 2008, 2012, Edgecombe and Koch 2008). We confirmed the presence of glandular shafts in the specimens we examined in the lithobiid genera *Lithobius*, *Neolithobius*, *Eupolybothrus* and *Disphaerobius* and further recorded differences in number and regularity of rows (character 1).

The same authors (Koch and Edgecombe 2008) described the presence of a transverse bulge dividing the labral and clypeal part on the epipharynx for all Lithobiomorpha except for *Hessebius plumatus* Zaleskaja, 1978 and *L. (Ezembius) giganteus* displaying no bulge at all. This study confirms the absence of the bulge in the species *D. loricatus* (Fig. 2A) and for the first time the presence of a second bulge (distal transverse bulge) as recorded for the species *L. calcaratus*, *L. lucifugus*, *L. tenebrosus* and *E. grossipes* as well as *E. fasciatus* (Newport, 1845) (specimens used by Koch and Edgecombe 2008). The alignment of the bulges is further described and proposed as an additional character state (character 4).

The examination of additional taxa within Lithobiidae revealed more variation in the shape of the median spine field than previously described and having surveyed more species we include additional character states to those already described by Koch and Edgecombe (2008) (character 5).

Although differences in shape of the bristles on the labral flap were briefly mentioned by Koch and Edgecombe (2008), our study unveiled four consistent states in the shape of bristles and transition of those from laterally to medially, which serves as a new multistate character for Lithobiidae (character 6). A transition of bristles from plumose to 'fan-shaped' was described for *Pleuroolithobius patriarchalis* (Berlese, 1894) (Koch and Edgecombe 2008), as in the majority of the investigated species in the present study. In contrast, only 'fan-shaped' bristles are observed in the lithobiid *Harpolithobius anodus* (Latzel, 1880) and the henicopid *Lamyctes* (*Lamyctes*) *emarginatus* (Newport, 1844). On the other hand, the interpretation that *Lithobius* (*Monotarsobius*) *holstii* (Pocock, 1895) possesses only 'fan-shaped' bristles (Fig. 6E in Koch and Edgecombe 2008) seems erroneous as their figure reveals a pattern in accordance with the other examined *Monotarsobius*-species, which exhibit a transition from plumose to 'fan-shaped' bristles (e.g. *L. aeruginosus*, Fig. 9C).

Generally, the median sensilla cluster borders or overlaps marginally with the lateral field of spines in Lithobiomorpha (Koch and Edgecombe 2008). However, we observed a median sensilla cluster considerably expanding along the length of the lateral spine fields on the epipharynx in *E. grossipes* for Lithobiomorpha (Fig. 10D). This was also verified in *E. fasciatus* (specimens used by Koch and Edgecombe 2008), which also displays a large but partial overlap.

As mentioned in the introduction, the hypopharynx as a short outgrowth with a median crest is an apomorphic character for Lithobiomorpha. This is verified in all examined lithobiid species. Moreover, the median crest margin of all studied species of the subgenus *Monotarsobius* displays flattened spines (character 8) as previously described for *L. holstii* (Koch and Edgecombe 2008).

### Variability of the peristomatic structures in Lithobiidae

Besides the well-defined characters listed in the previous paragraph, our investigation also yielded several structures with high variability in appearance and/or intermediate forms between and even within species. For example, the branching bristles of (i) the labral bristle band on the distal bar, (ii) the spines of the median spine field of the epipharynx and (iii) the branching bristles as a tuft on the hypopharynx occur with several non-definable forms. Koch and Edgecombe (2008) described a smooth transverse bulge for Lithobiidae, which we confirmed for most of the examined species. However, we also observed a longitudinal striation of the whole bulge surface or at least on the lateral parts of the bulge for some species (Figs 3C, 4D). A similar description of the latter state was observed for the henicopid *Lamyctes emarginatus*, where more defined longitudinal grooves occur (Koch and Edgecombe 2008).

The paired oblique rows of elongated lateral spines on the clypeal part of the epipharynx were also considered as an apomorphic character for Lithobiidae (Koch and Edgecombe 2008). This is also confirmed in all examined lithobiid species we

studied. However, the proposed character states, i.e. (2): oblique rows of single spines and (3): a few small groups of branching spines for the lateral field of spines on Lithobiidae were not consistent across the species we examined and showed many intermediate states. On this basis we excluded the character for conclusions on the systematics in Lithobiidae, especially *Lithobius*, in our study.

Koch and Edgecombe (2008) recorded groups of lateral fields of spines in the subgenus *Monotarsobius* in contrast to pairs of oblique rows in the rest of Lithobiidae (character 32, state (3)). These spines seem to be arranged in oblique rows as in the rest of Lithobiidae in the species *L. (Monotarsobius) aeruginosus* and *L. (Monotarsobius) curtipes* (Fig. 10F–G).

A correlation between the number of 'bottle-shaped' epidermal glandular shafts of Lithobiomorpha and body size was also mentioned by Koch and Edgecombe (2008), implying that larger species tend to have higher numbers. Here, we suggest the same for the number of glandular shafts, sensilla in the median sensilla cluster and the 'nipple-shaped' sensilla cluster, lateral spines, and the hypopharyngeal spines. This size correlation needs to be confirmed by morphometrics and statistical analysis but the phylogenetic significance of these characters is cast into doubt.

### **Assumptions on the relationship of *Disphaerobius* with (sub)genera *Lithobius* and *Ezembius***

The peristomatic structures of *H. plumatus* and *L. (Ezembius) giganteus* described by Koch and Edgecombe (2008) and *D. loricatus* examined in this study, i.e. a missing transverse bulge (character 3), simple bristles on the labral flap of the epipharynx (character 6) and scales on the distal tips of the lips of the hypopharynx (Fig. 17E), differ from all other studied species of *Lithobius*, including *L. (Ezembius) electus*, even if the latter is correctly placed in the subgenus *Ezembius*. Several taxa in Central Asia, also species of the *giganteus*-group of *Lithobius* (Eason 1983, 1986) and of the genus *Hesebius* Verhoeff, 1941 share some morphological characters with the genus *Disphaerobius* Attems, 1926, as mentioned by Farzalieva et al. (2017): "... functionally biarticulated tarsi of leg 1–13, the antennae composed of 20 antennomeres, the rounded posterior angles of all tergites, the 1-segmented male gonopods, and Tömösváry's organ being equal in size to the nearest ocellus or smaller." In contrast to the three other species of the *giganteus*-group of *Lithobius*, *L. (Ezembius) giganteus* displays secondary sexual modifications of the tergites in males similar to *Disphaerobius* (Farzalieva et al. 2017). Here, we assume that the epipharyngeal and hypopharyngeal structures may confirm a closer relationship of *L. (Ezembius) giganteus* to *D. loricatus* than to *L. (Ezembius) electus*. This relationship is inconsistent with the classification of *Disphaerobius* as a separate subfamily, Pterygoterginae Verhoeff, 1933, because that classification would render Lithobiinae, as well as *Lithobius* and *L. (Ezembius)* as paraphyletic groups.



## Acknowledgements

This project has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No 642241. Critical point drying (Leica 300CPD) for some specimens was performed at the Core Facility Cell Imaging and Ultrastructure Research, University of Vienna. Thanks are due to Dan Topa for support with the SEM and the sputter coater and to Edmund Schiller for inventorying and incorporating the specimens in the collections. We are grateful to László Dányi (HNHM Budapest) and Gyulli Farzalieva (Perm State University) for providing specimens for research. Andy Sombke, Markus Koch and Marzio Zapparoli provided helpful comments on a previous version of the manuscript and Markus Koch shared additional unpublished SEM images of *E. fasciatus*.

## References

- Bonato L, Chagas Junior A, Edgecombe GD, Lewis JGE, Minelli A, Pereira LA, Shelley RM, Stoev P, Zapparoli M (2016) ChiloBase 2.0 – A World Catalogue of Centipedes (Chilopoda) <http://chilobase.biologia.unipd.it>
- Eason EH (1983) On the synonymy of *Lithobius giganteus* Sseliwanoff, 1881 and the taxonomic status of *Porobius* Attems, 1926 (Chilopoda). *Annalen des Naturhistorischen Museums in Wien* 87: 181–192.
- Eason EH (1986) The Lithobiidae of Afghanistan with descriptions of three new species of the *giganteus*-group of *Lithobius* subgenus *Ezembius*, and a key to the central Asiatic species of this group (Chilopoda, Lithobiomorpha). *Steenstrupia* 12: 49–60.
- Edgecombe GD (2007) Centipede systematics: progress and problems. In: Zhang Z-Q, Shear WA (Eds) *Linnaeus Tercentenary: Progress in Invertebrate Taxonomy*. *Zootaxa* 1668: 327–341.
- Edgecombe GD, Koch M (2008) Phylogeny of scolopendromorph centipedes (Chilopoda): Morphological analysis featuring characters from the peristomatic area. *Cladistics* 24: 872–901. <https://doi.org/10.1111/j.1096-0031.2008.00220.x>
- Edgecombe GD, Koch M (2009) The contribution of preoral chamber and foregut morphology to the phylogenetics of Scolopendromorpha (Chilopoda). *Soil Organisms* 81: 295–318.
- Farzalieva GSH, Nefediev PS, Tuf IH (2017) Revision of *Disphaerobius* Attems, 1926 (Chilopoda: Lithobiomorpha: Lithobiidae: Pterygoterginae), a centipede genus with remarkable sexual dimorphism. *Zootaxa* 4258: 121–137. <http://www.mapress.com/j/zt/article/view/zootaxa.4258.2.2>
- Koch M, Edgecombe GD (2006) Peristomatic structures in Scutigleromorpha (Chilopoda): A comparative study, with new characters for higher-level systematics. *Zoomorphology* 125: 187–207. <https://doi.org/10.1007/s00435-006-0027-8>
- Koch M, Edgecombe GD (2008) The peristomatic structures of Lithobiomorpha (Myriapoda, Chilopoda): Comparative morphology and phylogenetic significance. *Journal of Morphology* 269: 153–174. <https://doi.org/10.1002/jmor.10578>

- Koch M, Edgecombe GD (2012) The preoral chamber in geophilomorph centipedes: Comparative morphology, phylogeny, and the evolution of centipede feeding structures. *Zoological Journal of the Linnean Society* 165: 1–62. <https://doi.org/10.1111/j.1096-3642.2011.00803.x>
- Koch M, Edgecombe GD, Shelley RM (2010) Anatomy of Ectonocryptoides (Scolocryptoidae: Ectonocryptooiinae) and the phylogeny of blind Scolopendromorpha (Chilopoda). *International Journal of Myriapodology* 3: 51–81. doi:10.1163/187525410X1257862960344
- Vahtera V, Edgecombe GD, Giribet G (2013) Phylogenetics of scolopendromorph centipedes: Can denser taxon sampling improve an artificial classification? *Invertebrate Systematics* 27: 578–602. <https://doi.org/10.1071/IS13035>
- Verhoeff KW (1902–1925) Chilopoda. In: Bronn HG (Ed.) *Klassen und Ordnungen des Tierreichs*. 5, Abt. 2, Buch 1. Akademische Verlagsgesellschaft, Leipzig, 1–725.
- Zapparoli M, Edgecombe GD (2011) Chilopoda – taxonomic overview: Order Lithobiomorpha. In: Minelli A (Ed) *Treatise on Zoology – Anatomy, Taxonomy, Biology. The Myriapoda*, Volume 1. Brill, Leiden, 371–389.

## Appendix I

Data matrix of 8 peristomatic characters of Lithobiidae, numbered as in the text.

Species	Characters
	12345678
<i>L. (L.) agilis</i>	111(0?)1000
<i>L. (L.) calcaratus</i>	11212000
<i>L. (L.) carinatus</i>	10111000
<i>L. (L.) castaneus</i>	10102000
<i>L. (L.) cyrtopus</i>	01110101
<i>L. (L.) dentatus</i>	11112000
<i>L. (L.) erythrocephalus</i>	11112001
<i>L. (L.) fagei</i>	10101000
<i>L. (L.) forficatus</i>	10100001
<i>L. (L.) lapidicola</i>	01112001
<i>L. (L.) latro</i>	11112001
<i>L. (L.) lucifugus</i>	11202101
<i>L. (L.) macilentus</i>	11111001
<i>L. (L.) mutabilis</i>	01112001
<i>L. (L.) muticus</i>	00110001
<i>L. (L.) nodulipes</i>	111110?1
<i>L. (L.) peregrinus</i>	10100200

Species	Characters
<i>L. (L.) piceus</i>	10112200
<i>L. (L.) pelidnus</i>	11102101
<i>L. (L.) pyrenaicus</i>	00100001
<i>L. (L.) tenebrosus</i>	0121200?
<i>L. (L.) tricuspis</i>	101022?0
<i>L. (L.) validus</i>	10101001
<i>L. (M.) aeruginosus</i>	01112001
<i>L. (M.) austriacus</i>	01111001
<i>L. (M.) crassipes</i>	01112001
<i>L. (M.) curtipes</i>	10111001
<i>L. (M.) franciscorum</i>	(1?)1110001
<i>L. (S.) burzenlandicus</i>	0111?000
<i>L. (S.) microps</i>	01112100
<i>L. (S.) trebinjanus</i>	11111001
<i>L. (E.) electus</i>	10102001
<i>N. aztecus</i>	11100011
<i>D. loricatus</i>	100–0311
<i>E. (E.) grossipes</i>	10200010



# An apparently non-swinging tentorium in the Diplopoda (Myriapoda): comparative morphology of the tentorial complex in giant pill-millipedes (Sphaerotheriida)

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Academic editor: *G.D. Edgecombe* | Received 29 October 2017 | Accepted 20 December 2017 | Published 7 March 2018

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<http://zoobank.org/8F4AEFD3-9943-42D5-9E08-11C0F1D94FB4>

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**Citation:** Moritz L, Wesener T, Koch M (2018) An apparently non-swinging tentorium in the Diplopoda (Myriapoda): comparative morphology of the tentorial complex in giant pill-millipedes (Sphaerotheriida). In: Stoev P, Edgecombe GD (Eds) Proceedings of the 17th International Congress of Myriapodology, Krabi, Thailand. ZooKeys 741: 77–91. <https://doi.org/10.3897/zookeys.741.21909>

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## Abstract

The presence of a swinging tentorium is a key apomorphy of Myriapoda, but this character has been studied in detail in only few species. Here the tentorium, i.e., the peristomatic skeleton of the preoral chamber, is comparatively studied in three species of the millipede order Sphaerotheriida Brandt, 1833. Since dissections of the fragile tentorial components proved to be difficult, despite the large head size, they were analysed mainly in situ via micro-computed tomography. Our results confirm previous observations of large differences in the tentorial construction in the giant pill-millipedes compared to chilognathan diplopods. The tentorium of Sphaerotheriida consists of a curved, plate-like epipharyngeal bar with distal projections, an elongate and thin hypopharyngeal bar, and a plate-like triangular posterior process; a transverse bar is absent. Only seven muscles attach at the tentorium in giant pill-millipedes, including two antennal muscles and two muscles of the gnathochilarium. Within the order Sphaerotheriida, the composition of the tentorium and its muscular equipment seems to be conserved, except for some vari-

ability in the shape of the epipharyngeal bar. As the transverse bar has been considered essential for the mobility of the tentorium in myriapods, its absence in Sphaerotheriida may indicate that their tentorium is not capable of performing a swing. Loss of tentorial mobility may also pertain to the order Glomerida Brandt, 1833, inferred here from the absence of a posterior process. An apparently immobile tentorium in Glomerida and Sphaerotheriida can straightforwardly be correlated with transformations of the head related to their ability of volvation. The different transformations of the tentorium, here hypothesised to cause immobility, may support current assumptions that the ability of volvation evolved convergently in Glomerida and Sphaerotheriida. This conclusion, however, still requires more detailed studies of the head anatomy in Glomerida and Glomeridesmida Cook, 1895.

## Keywords

Arthrosphaeridae, micro-CT, 3D-reconstruction, swinging tentorium, volvation

## Introduction

Recent molecular studies (Gai et al. 2006, Regier et al. 2010, Miyazawa et al. 2014, Fernández et al. 2016) as well as studies combining molecular and morphological data (Lee et al. 2013, Giribet et al. 2001) consistently retrieve the Myriapoda as a monophylum. Unique synapomorphies shared by its taxa Chilopoda, Symphyla, Pauropoda, and Diplopoda, however, are sparse. The most striking character in favour of myriapod monophyly is the so-called swinging tentorium, i.e. an apparently mobile skeleton of the head supporting the preoral chamber and movements of the mandibles (Edgecombe and Giribet 2002, Koch 2003, Edgecombe 2004, Shear and Edgecombe 2010, Edgecombe 2011, Koch et al. 2015). The tentorial complex consists of sclerotised exoskeletal bars and endoskeletal processes (Koch 2003, Koch 2015). This complex provides stability to the largely membranous epi- and hypopharynx and serves as muscle attachment sites. The tentorium is considered essential for the movement of the mandibles and the gnathochilarium, although the mechanism is not yet understood (Manton 1964, Fechter 1961, Koch 2015). In general the tentorium of the Diplopoda is composed of four parts: the exoskeletal (1) hypopharyngeal bar, (2) the epipharyngeal bar, (3) the transverse bar, and (4) the endoskeletal posterior process (sensu Koch 2003). Associated with the tentorial complex is an additional sclerite, the nebententorium (sensu Attems 1926, Verhoeff 1928, Koch 2015) or hypopharyngeal lateral sclerite (sensu Wilson 2002), also serving as an attachment site for musculature (Verhoeff 1928). Details on the structure of the tentorium and its musculature have been described for only few representatives of the Diplopoda. Four descriptions for members of the order Sphaerotheriida date back more than 100 years, and three of them (vom Rath 1886, Silvestri 1903, Attems 1926) describe the state for *Sphaeropoeus* Brandt, 1833 (Zephroniidae Gray, 1843). There is only one description for the Arthrosphaeridae Jeekel 1974 by Verhoeff (1928) for *Arthrosphaera dentigera* Verhoeff, 1930. Recently, the tentorium of *Zoosphaerium bemanevika* Sagorny & Wesener, 2017 from Madagascar was visualised in 3D using volume renderings of a  $\mu$ CT scan (Sagorny and

Wesener 2017), but it was not described in detail. The Arthrosphaeridae are the second largest family with 119 species and 4 genera within the order Sphaerotheriida. The Arthrosphaeridae have a very interesting biogeography with *Arthrosphaera* from the Indian sub-continent, and the three genera *Sphaeromimus*, *Zoosphaerium* and *Microsphaerotherium* Wesener & VandenSpiegel, 2007 only known from Madagascar (Wesener and VandenSpiegel 2009, Wesener et al. 2010). All descriptions indicate that the tentorium in the Sphaerotheriida deviates markedly from the pattern described for other myriapods. In order to reveal the deviating characteristics more comprehensively, the tentorium of three representatives of the Arthrosphaeridae genera *Arthrosphaera* Pocock, 1895, *Sphaeromimus* de Saussure & Zehntner, 1902 and *Zoosphaerium* Pocock, 1895 are described and compared.

## Materials and methods

Vouchers are stored in natural history collections of the Zoological Research Museum A. Koenig (ZFMK) and the California Academy of Science (CAS). One head of *Zoosphaerium* sp. was used for light microscopy of the skeletal components with a Keyence VHX 700 digital stack imaging system. For this purpose the mandibles were removed with micro-scissors and the head bisected by slicing along the mouth with a razor blade. Micro-CT scans were taken from the heads of the three giant pill-millipede species *Arthrosphaera brandtii* (Humbert, 1865) (ZFMK MYR 06265), *Sphaeromimus kalambatritra* Moritz & Wesener, 2017 (CAS ENT 9058301) and *Zoosphaerium bemanevika* Sagorny & Wesener, 2017 (ZFMK MYR 6144), all belonging to the family Arthrosphaeridae Jeekel, 1974. The heads were dissected and critical point dried (CPD) after dehydration via an ascending ethanol series. X-ray micro-computed tomography ( $\mu$ CT) was performed with a SKYSCAN 1272 (Bruker microCT, Kontich, Belgium), using the following settings: source voltage = 60 kV, source current = 166  $\mu$ A, exposure = 915 ms, rotation of 180° in rotational steps of 0.2°, frame averaging = 6, random movement = 15 px, filter = Al 0.25 mm. Isotropic voxel resolution varied in the following manner: *Arthrosphaera brandtii*: 5.99  $\mu$ m; *Sphaeromimus kalambatritra*: 7.86  $\mu$ m; *Zoosphaerium bemanevika*: 7.99  $\mu$ m. Reconstruction and thermal drift correction was performed in NRecon 1.7.0.4 (Bruker microCT, Kontich, Belgium). Reduction of the data size by scaling to 50 % and conversion from 16- to 8-bit grey-scale, and the adjustment of contrast and brightness was performed in IMAGE J 1.50e (Schneider et al. 2012). The resulting image stacks are deposited in MorphoBank as Project 2795 (<http://morphobank.org/permalink/?P2795>) Automated segmentation with subsequent manual corrections and 3D visualisation of the studied structures was performed in ITK-SNAP 3.6.0 (Yushkevich et al. 2006). Terminology follows Koch (2015) for components of the endoskeleton, and Wilson (2002) for the musculature. Illustrations and figure plates were prepared with Adobe Photoshop CS2 and Adobe Illustrator CS2.



## Results

### Skeletal elements of the tentorium in the Sphaerotheriida

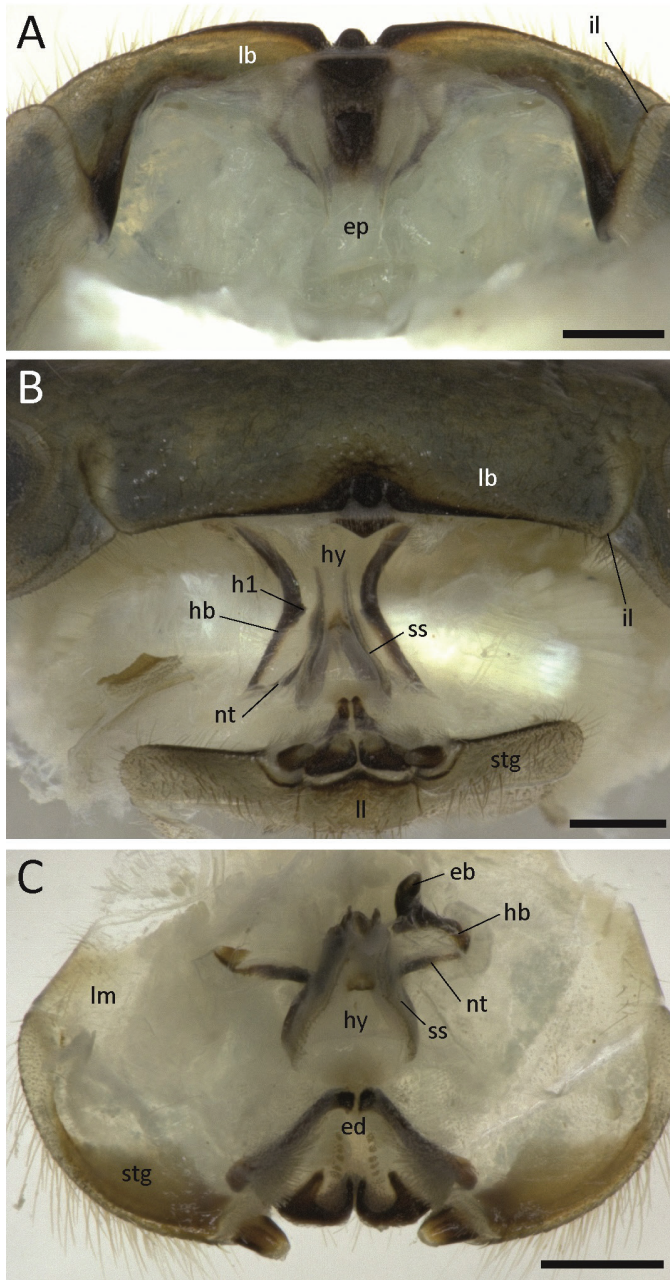
A connection of the tentorium to the head capsule by a transverse bar (sensu Koch 2003) is missing in the three analysed species, despite the presence of an incisura lateralis (Fig. 1A). The paired tentorial complex consists of only four major parts: the epipharyngeal bar (Fig. 1C, eb), the hypopharyngeal bar (Fig. 1B, hb), the posterior process (Fig. 2, pp), which forms a single tripartite sclerite (the tentorium sensu stricto) along the mouth opening, and the separate nebententorium (nt; hypopharyngeal lateral sclerite sensu Wilson 2002) located on the hypopharynx (Fig. 1B, hy).

#### (1) The epipharyngeal bar:

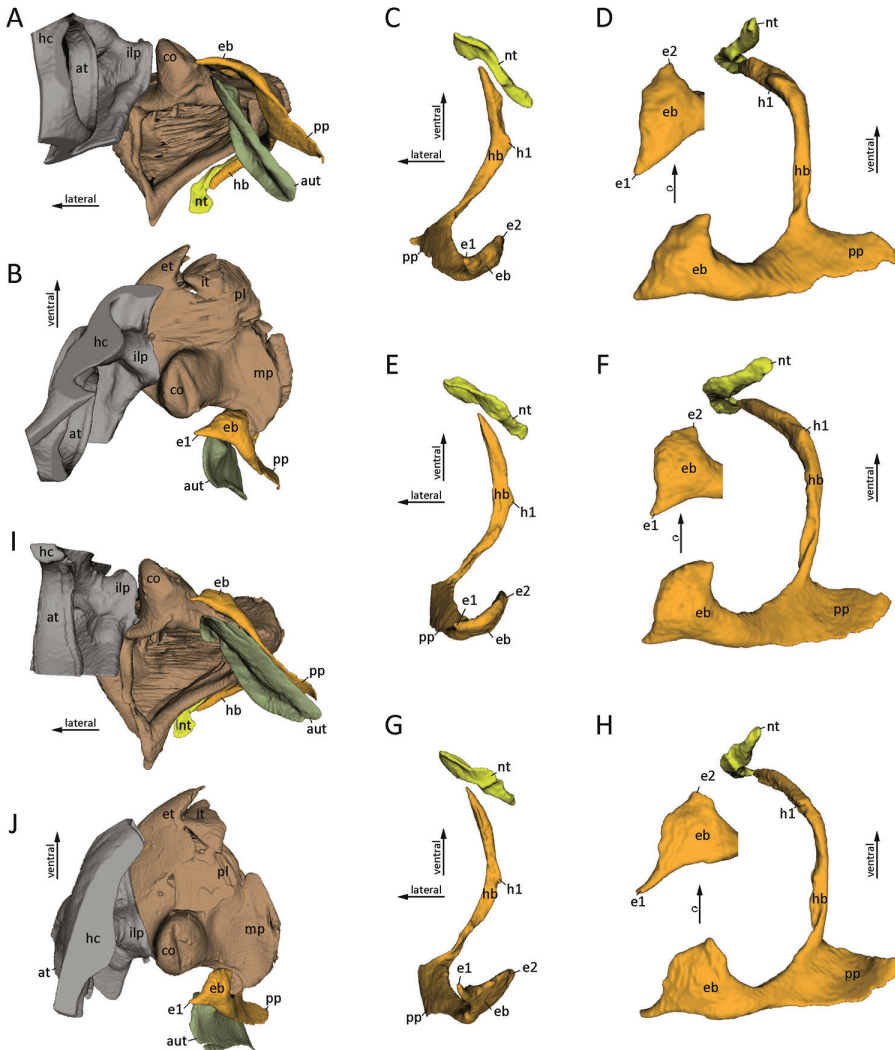
The plate-like epipharyngeal bar (eb) is in connection with the wall of the epipharynx (Fig. 2A–J, ep). The distal part of the epipharyngeal bar is a triangular plate with one slightly curved lateral projection (e1) and a stout median projection (Fig. 1C, D, e2). The shape of the projections of the epipharyngeal bar is variable within the Arthrosphaeridae (Fig. 2D, F, H): the lateral projection (e1) is rather stout and short in *Sphaeromimus kalambatritra* (Fig. 2F), more elongate in *Arthrosphaera brandtii* (Fig. 2D) and long, slender and curved in *Zoosphaerium bemanevika* (Fig. 2H). The median projection (e2) is triangular in *A. brandtii* (Fig. 2D) and *S. kalambatritra* (Fig. 2F), and rectangular in *Z. bemanevika* (Fig. 2H). The distal part of the epipharyngeal bar (eb) is curved, following in shape the curvature of the mandible condyles (Fig. 2A, B, I, J, co) in all analysed specimens. The proximal part of the epipharyngeal bar (eb) is a rectangular plate, which is wider in *A. brandtii* (Fig. 2D) and *S. kalambatritra* (Fig. 2F), while it is more slender in *Z. bemanevika* (Fig. 2H).

#### (2) The hypopharyngeal bar:

In the three analysed species, the epipharyngeal bar (eb) of the tentorium (Fig. 2A–J) passes over into the hypopharyngeal bar (hb) posteriorly to the pharyngeal opening. The hypopharyngeal bar is elongate and rod-like (Fig. 2A–J, hb). The bar is strongly curved inward and extends ventrally on the hypopharynx towards the gnathochilarium where it is associated to the nebententorium (nt) via a membranous connection (Fig. 2C, E, G). A small cone-shaped medial projection (h1) close to the center of the hypopharyngeal bar is present (Fig. 2C–H), pointing to the hypopharyngeal suspensorial sclerites (Fig. 1B, ss) (Stützgerüst sensu Attems, 1926; Verhoeff, 1928). Although the hypopharyngeal bar of *A. brandtii* (Fig. 2C) is slightly shorter in relation to its width than in *S. kalambatritra* (Fig. 2E) and *Z. bemanevika* (Fig. 2G), its general rod-like appearance can be seen in all analysed species.



**Figure 1.** *Zoosphaerium* sp., light micrographs of peristomatic structures. **A** Epipharynx, showing absence of the tentorial transverse bar **B** Preoral chamber, frontal view on hypopharynx (mandibles removed) **C** Hypopharynx and endochilarium, dorsal view (hypo- and epipharyngeal bar of right tentorium broken off). Scale bars: 500  $\mu$ m. **Abbreviations:** eb = epipharyngeal bar of left tentorium; ed = endochilarium; ep = epipharynx; h1 = projection of hypopharyngeal bar; hb = hypopharyngeal bar of tentorium; hy = hypopharynx; il = incisura lateralis; lb = labrum; ll = lamella lingualis; lm = lamella-mentum; nt = nebententorium; ss = suspensorial sclerite; stg = stipes of gnathochilarium.



**Figure 2.** The tentorial complex of the Sphaerotheriida, 3D visualization. GREY = Head capsule; BROWN = mandible; ORANGE = tentorium; YELLOW = neotentorium; OLIVE = außtentorium. **A–D** *Arthrosphaera brandtii* (Humbert, 1865), ZFMK MYR6265 **E, F, I, J** *Sphaeromimus kalambatritra*, CASENT 9058301 **G, H** *Zoosphaerium bemanevika* Sagorny & Wesener, 2017, ZFMK MYR6144. **A** tentorial complex and its association with the mandibular gnathal lobe and the head capsule of *A. brandtii*, dorsal view **B** same as A frontal view **C** tentorial complex of *A. brandtii*, frontal view **D** same as C medial view, with rotated epipharyngeal bar **E** tentorial complex of *S. sp.*, frontal view **F** same as E medial view, with rotated epipharyngeal bar **G** tentorial complex of *Z. bemanevika*, frontal view **H** same as G medial view, with rotated epipharyngeal bar **I** tentorial complex and its association with the mandibular gnathal lobe and the headcapsule of *S. sp.*, dorsal view **J** same as I, frontal view. **Abbreviations:** at = antennal socket; aut = mandibular gnathal lobe sclerite (außtentorium); co = condylus of mandible; e1 = lateral projection of epipharyngeal bar; e2 = medial projection of epipharyngeal bar; eb = epipharyngeal bar; et = external tooth; h1 = projection of hypopharyngeal bar; hb = hypopharyngeal bar; hc = head capsule; ilp = projection arising from incisura lateralis; it = internal tooth; mp = molar plate; nt = neotentorium; pl = pectinate lamellae; pp = posterior process.

### **(3) The posterior process:**

The posterior process (pp) is a large triangular plate projecting posteriorly into the head capsule parallel to the mandibular gnathal lobe sclerite (sensu Wilson 2002; äußeres Tentorium sensu Voges 1916, Attems 1926; Außententorium sensu Seifert 1932; (German for "outer tentorium")) (Fig. 2A, B, I, J, aut). It arises from the transition point between the epi- (eb) and hypopharyngeal bars (hb). There is no variation in the shape of the posterior process (pp) within the studied Arthrosphaeridae (Fig. 2C–H).

### **(4) The nebertentorium:**

The nebertentorium (nt) is a short, flat sclerite parallel to the distal portion of the hypopharyngeal bar (hb) of the tentorium (Fig. 2A, B, I, J, YELLOW). It bypasses the distal tip of the hypopharyngeal bar slightly and broadens, forming an articulation with the tentorium (Fig. 2C–H).

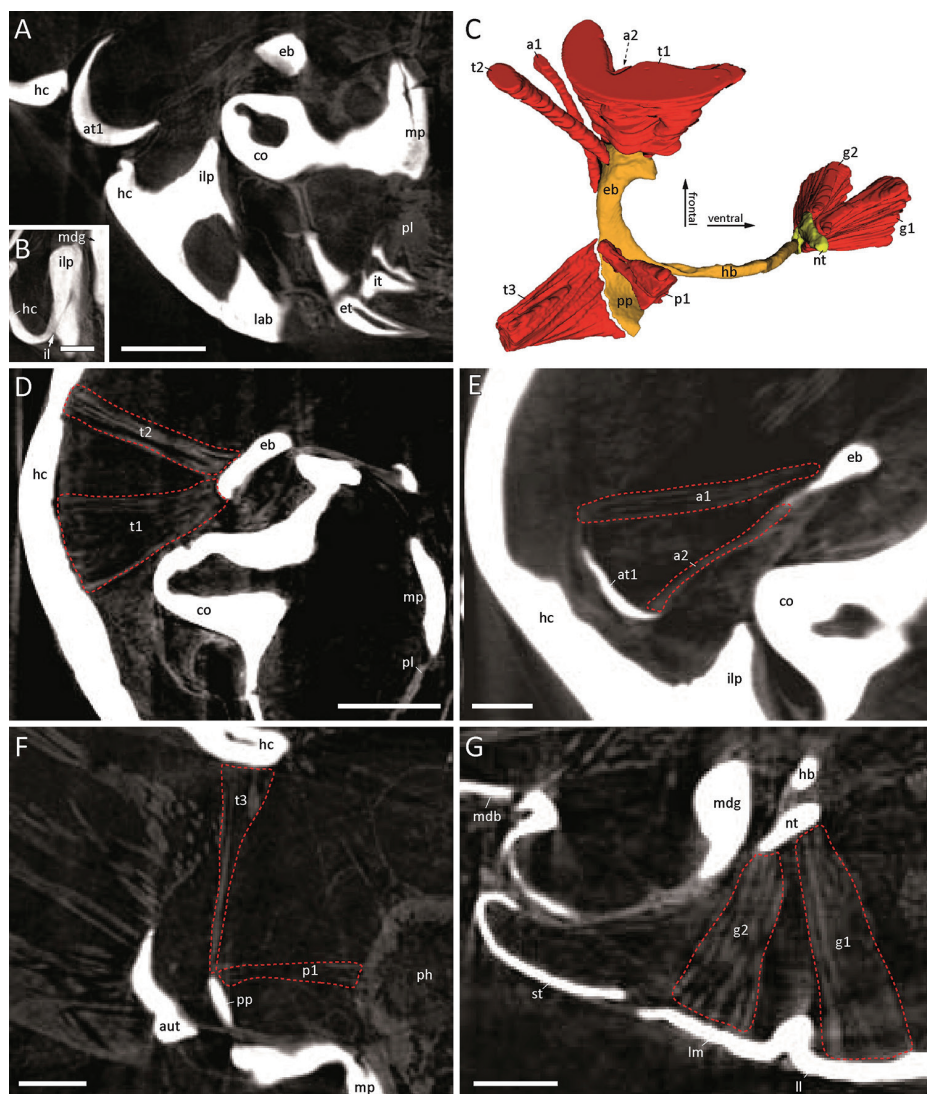
## **The connection of the mandible to the tentorium in Arthrosphaeridae**

The strong condylus (co) of the mandibular gnathal lobe (Fig. 2A, B, I, J, BROWN) is not in direct contact with the tentorium, but medially faces the epipharyngeal bar (Fig. 2A, B, I, J, eb). Lateral of the condylus arises a sclerotised socket-shaped projection (Fig. 3A, ilp) from the incisura lateralis (il) of the head capsule (Fig. 3B, hc). The mandibular condylus hence appears to be encompassed by both the epipharyngeal bar and the sclerotised projection of the incisura lateralis.

## **Musculature of the tentorium in Arthrosphaeridae**

The tentorial complex of the Arthrosphaeridae is associated with a set of seven muscles (Fig. 3C), which do not vary in the studied species. The proximal part of the epipharyngeal bar (eb) gives rise to the anterior tentorial muscle (t1), which inserts on the anterior part of the head, and to the dorsal tentorial muscle (t2), which inserts medial of the antennal socket (Fig. 3D). The posterior tentorial muscle (t3) inserts on the whole length of the posterior margin of the posterior process (pp) and originates from the postoccipital flange close to the transition to the collum (Fig. 3C, F). The lateral antennal muscle (a1) originates from the posterior margin of the transitional area between the epipharyngeal bar (eb) and the posterior process (pp), anteriorly of t3, and inserts on the posterior margin of the first antennomere (at1). The anterior antennal muscle (a2) inserts on the anterior margin of the first antennomere (at1) and originates from the epipharyngeal bar (eb) lateral of t3 (Fig. 3E). Median to t3, the pharyngeal dilator muscle (p1), which inserts on the lateral pharyngeal wall (ph),





**Figure 3.** Head musculature of *Sphaeromimus kalambatritra*. **A, B, D–G** micro-CT images **C** 3D segmentation. **A** Arrangement of mandible, tentorium and head capsule, frontal section **B** Incisura lateralis in detail, frontal section **C** 3D segmentation of the isolated tentorium and its muscles, medial view **D, E** Muscles of the epipharyngeal bar, fronto-medial view **F** Muscles of the posterior process, frontal section **G** Muscles of the nevententorium, frontal section. Top is frontal, left is lateral. Scale bars: **A, D** 1000  $\mu\text{m}$  **B, E–G** 500  $\mu\text{m}$  **C** not to scale. **Abbreviations:** a1 = lateral antennal muscle (m.); a2 = anterior antennal m.; at1 = first antennomere; co = condyle of mandibular gnathal lobe; eb = epipharyngeal bar; et = external tooth of mandible; g1 = lamella lingualis m.; g2 = lamello-mentum m.; aut = mandibular gnathal lobe sclerite (außerententorium); hb = hypopharyngeal bar; hc = head capsule; il = incisura lateralis; ilp = projection arising from incisura lateralis; it = internal tooth of mandible; lab = labrum; ll = lamella lingualis of gnathochilarium; lm = lamello-mentum; mdb = mandibular base; mdg = mandibular gnathal lobe; mp = molar plate; nt = nevententorium; p1 = pharyngeal dilator m.; ph = pharynx; pl = pectinate lamellae of mandible; pp = posterior process; st = stipes of gnathochilarium; t1 = anterior tentorial m.; t2 = dorsal tentorial m.; t3 = posterior tentorial m.

originates from the frontal anterior portion of the posterior process (Fig. 3F, pp). The nebententorium (nt) gives rise to a muscle (g1) inserting medially on the lamella lingualis (ll) of the gnathochilarium. Another muscle (g2) of the gnathochilarium passes from the lamello-mentum (lm) to the posterior surface of the nebententorium (nt) lateral to g1 (Fig. 3G).

## Discussion

### Structure of the tentorium in the Sphaerotheriida

The tentorium of the three studied representatives of Sphaerotheriida shows the same basic structure (Fig. 2C–H), as already described by vom Rath (1886), Silvestri (1903) and Attems (1926) for *Sphaeropoeus*, and by Verhoeff (1928) for *Arthrosphaera dentigera*. Vom Rath (1886) stated that the tentorium of the Sphaerotheriidae *Sphaerotherium* Brandt, 1833 resembles that of the Zephroniidae *Sphaeropoeus* Brandt, 1833, without a detailed description. Therefore, the general structure of the tentorium seems to be highly conserved within the Sphaerotheriida.

The most striking character of the giant pill-millipede tentorium is the absence of the transverse bar (Fig. 1C), which is present in all other millipede orders as far as known. Although the transverse bar differs among millipedes in its shape and articulation to the head capsule, it is known to be present in the Polyxenida (Koch 2003), Glomerida (vom Rath 1886, Silvestri 1903, Voges 1916), Julida (vom Rath 1886, Silvestri 1903, Voges 1916, Attems 1926, Verhoeff 1928, Fechter 1961), Spirobolida (vom Rath 1886, Snodgrass 1950), Spirostreptida (vom Rath 1886, Silvestri 1903, Manton 1964), Polydesmida (vom Rath 1886, Silvestri 1903, Verhoeff 1928, Seifert 1932, Snodgrass 1950), Chordeumatida (vom Rath 1886, Verhoeff 1928), Callipodida (Verhoeff 1928) and Platydesmida (Koch 2015). The state of the transverse bar (or the tentorium in general) for Glomeridesmida, Stemmiulida, Siphoniulida and most Colobognatha has not been documented yet. A transverse bar can nevertheless be assumed for the ground pattern of Diplopoda. Its reduction can be viewed as a derived state of the Sphaerotheriida.

### Impact on tentorial mobility

The general function of the transverse bar is the connection of the tentorial complex to the head capsule at the incisura lateralis (= clypeal notch), around which the tentorium is deemed to perform its swinging movements (Manton 1964). Furthermore, the transverse bar is the insertion site for tentorial protractor muscles (Manton 1964, Wilson 2002). Along with the reduction of the transverse bar in Sphaerotheriida, the mobility of the tentorium must have undergone tremendous changes and must differ from the mechanism assumed by Fechter (1961) and Manton (1964) for Juliformia, as the muscular equipment of the tentorium in Sphaerotheriida (Fig. 3 C) varies greatly

from that of Juliformia. While Wilson (2002) reported 13 muscles attached to the tentorium in Spirostreptida, Sphaerotheriida only maintain seven muscles (Fig. 3C). In Sphaerotheriida, the anterior tentorial muscle and the dorsal tentorial muscles originating on the epipharyngeal bar (Fig. 3D), as well as the posterior tentorial muscle and pharyngeal dilator muscles originating from the posterior process (Fig. 3F) correspond to the state in Juliformia (Wilson 2002). The tentorial protractor muscles, however, apparently shifted their position from the transverse bar (as described by Wilson 2002) to the distal part of the epipharyngeal bar. Further differences concern the antennal muscles that arise from the posterior process of the tentorium in Juliformia, but from the epipharyngeal bar in Sphaerotheriida (Fig. 3E). In Sphaerotheriida, contrarily to Juliformia (Silvestri 1903, Manton 1964, Wilson 2002), no mandibular muscles arise from the tentorium. In the Sphaerotheriida all muscles of the mandibular base instead originate from the transverse mandibular tendon and cranial wall, respectively. Among the three gnathochilarial muscles arising from the nebententorium in Juliformia, only two are present in Sphaerotheriida, i.e., the one (g1) inserting on the lamella-mentum, and the one (g2) inserting on the lamellae linguales (Fig. 3G). The muscle extending from the gnathochilarial stipes to the nebententorium is apparently reduced in giant pill-millipedes. This reduction of gnathochilarial muscles is likely due to strong modifications of the gnathochilarium in Sphaerotheriida, which are considered as autapomorphies of this taxon (Wesener 2016).

Despite these differences, the main muscles considered essential for movements of the tentorial complex are present. Manton (1964) states that the movement of the tentorium in Spirostreptida results from the tension of the protractor tentorii (anterior tentorial muscle sensu Wilson 2002, t1) and the depressor tentorii, which correspond to the lamella lingualis muscle (g1) and the lamello-mentum muscle (g2) of Sphaerotheriida.

The differences in the composition of the tentorium and in its muscular equipment might not only be correlated with the absence of the tentorial transverse bar, but also with the presence of a strong condylus on the mandibular gnathal lobes of Sphaerotheriida that unquestionably impacts on the mandibular mechanism. In Juliformia, the connection of the transverse bar to the incisura lateralis is deemed to fix a swing of the tentorium, causing the mandibular gnathal lobe to abduct (Fechter 1961, Manton 1964). In Sphaerotheriida, we propose that abduction of the mandibular gnathal lobes instead is caused by forces exerted from the epipharyngeal bar on the condylus of the gnathal lobes. The shape of the epipharyngeal bar indicates that it interlinks to the notch present on the condylus (Fig. 2A, J) to cause abduction of the gnathal lobe by pushing its condylus into the projection of the incisura lateralis. The theory about this movement is further corroborated by the shape correlation between the shape of the notch and the curvature of the epipharyngeal bar. The curvature of the epipharyngeal bar is more shallow in *A. brandtii*, where the notch forms a larger plateau (Fig. 2A) than in *S. kalambatritra*, in which the notch of the condylus is more strongly curved (Fig. 2I). The projections of the incisura lateralis and the epipharyngeal bar appear to form an anchor around which the mandibular gnathal lobe rotates during its abduction. According to this interpretation, the tentorial protractor and retractor muscles

likely do no longer cause the tentorium to swing. The modified muscles instead likely serve to stabilise the tentorium in a position enabling the condylus of the gnathal lobe to rotate between the incisura lateralis and the epipharyngeal bar.

### **Correlations of the shape of the tentorium with volvation: a comparison with Glomerida**

The tentorium of Sphaerotheriida contributes more characters to the list of head modifications that likely correlate with adaptations to volvation (see, e.g., Golovatch 2003, Blanke and Wesener 2014, Tuf et al. 2016). These adaptations include a reduction of the head lumen and coincident size reduction or entire loss of endoskeletal formations (surveyed by Koch 2015). Among Pentazonia, both Sphaerotheriida and Glomerida are able to roll themselves up into a ball, but their tentorium displays different transformations: as inferred from *Glomeris marginata*, the transverse bar is primarily maintained (e.g., Voges 1916, Dohle 1964), albeit with a remarkably loose connection to the head capsule. However, unlike in Sphaerotheriida, in the Glomerida the posterior process of the tentorium seems to be absent (Koch 2015). Since the posterior process provides the origin of the tentorial retractor muscle (t3), the loss of the posterior process may indicate that the tentorium in Glomerida is, as in Sphaerotheriida, no longer capable of performing swinging movements. The different modifications of the tentorium, the reduction of the transverse bar in Sphaerotheriida and of the posterior process in Glomerida, corroborate the view that anatomical adaptations to volvation are non-homologous (Sierwald and Bond 2007, their Supplemental Appendix 1), i.e., that volvation evolved convergently in Glomerida and Sphaerotheriida. This view is particularly supported by recent molecular analyses (Regier et al. 2005, Fernández et al. 2016), as well as by characters of the gnathochilarium (Wesener and Van den Spiegel 2009) favouring a sister group relationship between Glomerida and Glomeridesmida over the traditional classification of Glomerida and Sphaerotheriida in the taxon Oniscomorpha. Our ongoing studies focus on a detailed comparison of the cephalic musculature in Glomerida and Glomeridesmida to test the hypothesis of convergent loss of a swinging tentorium in correlation with convergent gain of volvation in Glomerida and Sphaerotheriida.

### **The tentorium as a taxonomic character inside Sphaerotheriida**

Although the general appearance of the tentorium is conserved within Arthrosphaeridae there are some differences in details. These mainly concern the epipharyngeal bar, with its projections varying in their shape and length (Fig. 2D, F, H). Slight variations in shape are also displayed by the hypopharyngeal bar and the nebententorium (Fig. 2C, E, G). The tentorium of *Sphaeromimus* (Fig. 2E, F) is more similar to the state in *Arthrosphaera* (Fig. 2C, D) than in *Zoosphaerium* (Fig. 2G, H). This corresponds to the interrelationship within Arthrosphaeridae retrieved by Wesener et al.

(2010) from molecular analyses, according to which the Malagasy genus *Sphaeromimus* is more closely related to the Indian genus *Arthrosphaera* than to the other Malagasy genera *Zoosphaerium* and *Microsphaerotherium*. The structure and shape of the tentorium accordingly might also serve as an informative character not only for phylogenetic reconstructions, but also for taxonomic studies, which can be assessed quite rapidly with high-throughput techniques like  $\mu$ CT and automated 3D-segmentation. However, not investigated yet were the changes in the structure of the tentorium in different life stages of millipedes and intraspecific variations. We recommend that internal characters should more often be considered in taxonomic descriptions.

## Conclusions

The reduction of the transverse bar of the tentorial complex as well as the presence of the mandible condyles in Sphaerotheriida must have an enormous impact on the mandibular abduction, resulting in a probably non-swinging tentorium. The reduction of the transverse bar in Sphaerotheriida is probably correlated to the volvation and suggests a convergent evolution of volvation in the pentazonian orders Sphaerotheriida and Glomerida. In Glomerida the posterior process of the tentorial complex is reduced as an adaptation to volvation. This could furthermore support a previously suggested (Regier et al. 2005, Fernández et al. 2016, Wesener and van den Spiegel 2009) closer relationship between Glomerida and Glomeridesmida. Furthermore the tentorium offers taxonomic characters to distinguish at least genera. Therefore we recommend considering internal characters more often in taxonomic descriptions. Despite its importance as apomorphy, supporting the monophyly of Myriapoda, and its functional role, the tentorial complex is largely understudied and the knowledge on it throughout the Myriapoda is only fragmentary. This study can be seen as first step towards a broader assessment of the tentorial complex in the Diplopoda.

## Acknowledgements

We thank Thorsten Klug and Hans-Joachim Krammer (both ZFMK) for technical assistance with the preparation of the specimens, and Alexander Ziegler (University of Bonn, Germany) for recommendations on the processing of the imagery. The studied material was provided by Petra Sierwald, Crystal Maier (both FMNH), and Darrel Ubick (CAS), and collected by Steven M. Goodman, Toky Randriamora and Brian L. Fisher, to whom we are grateful. Christina L. Sagorny (University of Bonn) conducted the scan of the head of *Zoosphaerium bemanevika* and allowed us to utilise her data for the analysis of the tentorium. Furthermore we thank the editor Gregory Edgecombe and the reviewers Nesrine Akkari and Andy Sombke for their comments, which greatly helped us to improve the quality of our manuscript.



## References

- Attems C (1926) Myriapoda. In: Kükenthal W, Krumbach T (Eds) Handbuch der Zoologie. Eine Naturgeschichte der Stämme des Tierreiches. Progoneata, Chilopoda, Insecta. Walter de Gruyter & Co, Berlin and Leipzig, 1–402.
- Blanke A, Wesener T (2014) Revival of forgotten Characters and modern imaging Techniques help to produce a robust phylogeny of the Diplopoda (Arthropoda, Myriapoda). *Arthropod structure & development* 43(1): 63–75. <https://doi.org/10.1016/j.asd.2013.10.003>
- Brandt IF (1833) Tentaminum quorundam monographicorum Insecta Myriapoda Chilognatha Latreillii spectantium Prodromus. *Bulletin de la Société impériale des naturalistes de Moscou* 6: 194–209.
- Cook OF (1895) Introductory note on the families of Diplopoda. The Craspedosomatidae of North America. *Annals of the New York Academy of Sciences* 9: 1–100. <https://doi.org/10.1111/j.1749-6632.1896.tb55430.x>
- De Sassure HLF, Zehntner L (1902) Myriapodes de Madagascar. In: Grandidier A (Ed.) Histoire physique, naturelle et politique de Madagascar. *Mémoires du Muséum national d'Histoire naturelle* 27(53): 1–356.
- Dohle W (1964) Die Embryonalentwicklung von *Glomeris marginata* (Villers) im Vergleich zur Entwicklung anderer Diplopoden. *Zoologische Jahrbücher. Abteilung für Anatomie und Ontogenie der Tiere* 81: 241–310.
- Edgecombe GD (2004) Morphological data, extant Myriapoda, and the myriapod stem-group. *Contributions to Zoology* 73(3): 207–252.
- Edgecombe GD (2011) Phylogenetic relationships of Myriapoda. In: Minelli A (Ed.) *The Myriapoda*, Volume 1. Brill, Leiden, 1–20. [https://doi.org/10.1163/9789004188266\\_002](https://doi.org/10.1163/9789004188266_002)
- Edgecombe GD, Giribet G (2002) Myriapod phylogeny and the relationships of Chilopoda. In: Llorente Bousquets JE, Morrone JJ (Eds) *Biodiversidad, taxonomía y biogeografía de artrópodos de México: Hacia una síntesis de su conocimiento*. Prensas de Ciencias, Universidad Nacional Autónoma de México, Mexico-City, Mexico, 143–168.
- Fechter H (1961) Anatomie und Funktion der Kopfmuskulatur von *Cylindroiulus teutonicus*. *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere*: 479–582.
- Fernández R, Edgecombe GD, Giribet G (2016) Exploring Phylogenetic Relationships within Myriapoda and the Effects of Matrix Composition and Occupancy on Phylogenomic Reconstruction. *Systematic Biology* 65(5): 871–889. <https://doi.org/10.1093/sysbio/syw041>
- Gai YH, Song DX, Sun HY, Zhou KY (2006) Myriapod Monophyly and Relationships among Myriapod Classes based on nearly complete 28S and 18S rDNA Sequences. *Zoological Science* 23(2): 1101–1108. <https://doi.org/10.2108/zsj.23.1101>
- Giribet G, Edgecombe GD, Wheeler WC (2001) Arthropod phylogeny based on eight molecular loci and morphology. *Nature* 413: 157–161. <https://doi.org/10.1038/35093097>
- Golovatch SI (2003) A review of the volvatory Polydesmida, with special Reference to the patterns of Volvation (Diplopoda). *African Invertebrates* 44(1): 39–60.
- Gray EJ (1842) Myriapoda In: Jones TR, Todd RB (Eds) *Cyclopedia of anatomy and physiology* 3: 544–560.

- Humbert A (1865) Essai sur les Myriapodes de Ceylan. Mémoires de la Société de Physiques et d'Histoire naturelle de Genève 18: 1–63.
- Jeekel CAW (1974) The group taxonomy and geography of the Sphaerotheriida (Diplopoda). Symposia of the Zoological Society of London 32: 41–52.
- Koch M (2003) Monophyly of the Myriapoda? Reliability of current arguments. African Invertebrates 44(1): 137–153.
- Koch M (2015) Diplopoda – general morphology. In: Minelli A (Ed.) The Myriapoda, Volume 2. Brill, Leiden, 7–68. [https://doi.org/10.1163/9789004188273\\_003](https://doi.org/10.1163/9789004188273_003)
- Koch M, Schulz J, Edgecombe GD (2015) Tentorial mobility in centipedes (Chilopoda) revisited: 3D reconstruction of the mandibulo-tentorial musculature of Geophilomorpha. Zookeys 510: 243–267. <https://doi.org/10.3897/zookeys.510.8840>
- Lee MSY, Soubrier J, Edgecombe GD (2013) Rates of phenotypic and genomic evolution during the Cambrian explosion. Current Biology 23(19): 1889–1895. <https://doi.org/10.1016/j.cub.2013.07.055>
- Manton SM (1964) Mandibular mechanisms and the evolution of arthropods. Philosophical Transactions of the Royal Society of London B 247: 1–183. <https://doi.org/10.1098/rstb.1964.0001>
- Miyazawa H, Ueda C, Yahata K, Su ZH (2014) Molecular phylogeny of Myriapoda provides insights into evolutionary patterns of the mode in post-embryonic development. Scientific reports 4: 1–9. <https://doi.org/10.1038/srep04127>
- Moritz L, Wesener T (2017) Integrative description of two new species of Malagasy chirping giant pill-millipedes, genus *Sphaeromimus* (Diplopoda: Sphaerotheriida: Arthrosphaeridae). European Journal of Taxonomy 381: 1–25. <https://doi.org/10.5852/ejt.2017.381>
- Pocock RI (1895) XLIII.-Report upon the Chilopoda and Diplopoda obtained by PW Bassett-Smith, Esq., Surgeon RN, and JJ Wallcer, Esq., RN, during the cruise in the Chinese Seas of HMS 'Penguin,' Commander WU Moore commanding. Journal of Natural History 15(88): 346–369. <https://doi.org/10.1080/00222939508677895>
- Regier JC, Wilson HM, Shultz JW (2005) Phylogenetic analysis of Myriapoda using three nuclear protein-coding genes. Molecular Phylogenetics and Evolution 34(1): 147–158. <https://doi.org/10.1016/j.ympev.2004.09.005>
- Regier JC, Shultz JW, Zwick A, Hussey A, Ball B, Wetzer R, Martin JW, Cunningham CW (2010) Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. Nature 463: 1079–1083. <https://doi.org/10.1038/nature08742>
- Sagorny C, Wesener T (2017) Two new giant pill-millipede species of the genus *Zoosphaerium* endemic to the Bemanevika area in northern Madagascar (Diplopoda, Sphaerotheriida, Arthrosphaeridae). Zootaxa 4263(2): 273–294. <https://doi.org/10.11646/zootaxa.4263.2.4>
- Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. Nature Methods 9: 671–675. <https://doi.org/10.1038/nmeth.2089>
- Seifert B (1932) Anatomie und Biologie des Diplopoden *Strongylosoma pallipes*. Zoomorphology 25(2): 362–507. <https://doi.org/10.1007/BF00446714>
- Shear WA, Edgecombe GD (2010) The geological record and phylogeny of the Myriapoda. Arthropod Structure & Development 39: 174–190. <https://doi.org/10.1016/j.asd.2009.11.002>

- Sierwald P, Bond JE (2007) Current status of the myriapod class Diplopoda (millipedes): taxonomic diversity and phylogeny. *Annual Review of Entomology* 52: 401–420. <https://doi.org/10.1146/annurev.ento.52.111805.090210>
- Silvestri F (1903) Classis Diplopoda. Anatome: Pars I, Segmenta, Tegumentum, Musculi. In: Berlese A (Ed.) *Acari, Myriapoda et Scorpiones hucusque in Italia reperta*, Portici, 1–272.
- Snodgrass RE (1950) Comparative Studies on the Jaws of Mandibulate Arthropods. *Smithsonian Miscellaneous Collections* 116(1): 1–85.
- Tuf IH, Cmielova L, Sipos J (2016) Conglobation as a defensive behavior of pill millipedes (Diplopoda: Glomerida). *Acta Societatis Zoologicae Bohemicae* 80: 39–44.
- Verhoeff KW (1928–1932) *Diplopoda I. Bronns Klassen und Ordnungen des Tierreichs*, vol. 5. Akademischer Verlag, Leipzig, 1–1071.
- Voges E (1916) *Myriapodenstudien*. *Zeitschrift für Wissenschaftliche Zoologie* 116: 75–135.
- vom Rath O (1886) *Beitraege zur Kenntnis der Chilognathen*. Doctoral thesis, Strasbourg, France, Kaiser-Wilhelms-Universität Strasburg.
- Wesener T (2016) The Giant Pill-Millipedes, order Sphaerotheriida – An annotated species catalogue with morphological atlas and list of apomorphies (Arthropoda: Diplopoda). *Bonn Zoological Bulletin (Supplementum 63)*: 1–104.
- Wesener T, van den Spiegel D (2007) *Microsphaerotherium ivohibiensis*, a new genus and species of Giant-Pill Millipedes from Madagascar (Diplopoda, Sphaerotheriida, Arthrosphaerinae). *Journal of Afrotropical Zoology* 3: 153–160.
- Wesener T, van den Spiegel D (2009) A first phylogenetic analysis of Giant Pill-Millipedes (Diplopoda: Sphaerotheriida), a new model Gondwanan taxon, with special emphasis on island gigantism. *Cladistics* 25: 545–573. <https://doi.org/10.1111/j.1096-0031.2009.00267.x>
- Wesener T, Raupach MJ, Sierwald P (2010) The origins of the giant pill-millipedes from Madagascar (Diplopoda: Sphaerotheriida: Arthrosphaeridae). *Molecular Phylogenetics and Evolution* 57(3): 1184–1193. <https://doi.org/10.1016/j.ympev.2010.08.023>
- Wilson HM (2002) Muscular anatomy of the millipede *Phyllogonostreptus nigrolabiatus* (Diplopoda: Spirostreptida) and its bearing on the millipede “thorax”. *Journal of Morphology* 251(3): 256–275. <https://doi.org/10.1002/jmor.1087>
- Yushkevich PA, Piven J, Hazlett HC, Smith RG, Ho S, Gee JC, Gerig G (2006) User-guided 3D active contour segmentation of anatomical structures: Significantly improved efficiency and reliability. *Neuroimage* 31(3):1116–28. <https://doi.org/10.1016/j.neuroimage.2006.01.015>



# Intraspecific variation and phylogeography of the millipede model organism, the Black Pill Millipede *Glomeris marginata* (Villers, 1789) (Diplopoda, Glomerida, Glomeridae)

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Academic editor: P. Stoev | Received 29 October 2017 | Accepted 15 February 2018 | Published 7 March 2018

<http://zoobank.org/6E3C67E2-2568-4CCB-971C-9191B223D62F>

**Citation:** Reip HS, Wesener T (2018) Intraspecific variation and phylogeography of the millipede model organism, the Black Pill Millipede *Glomeris marginata* (Villers, 1789) (Diplopoda, Glomerida, Glomeridae). In: Stoev P, Edgecombe GD (Eds) Proceedings of the 17<sup>th</sup> International Congress of Myriapodology, Krabi, Thailand. ZooKeys 741: 93–131. <https://doi.org/10.3897/zookeys.741.21917>

## Abstract

The Black Pill Millipede, *Glomeris marginata*, is the best studied millipede species and a model organism for Diplopoda. *Glomeris marginata* is widespread, with numerous colour morphs occurring across its range, especially in the south. This study investigates whether colour morphs might represent cryptic species as well as the haplotype diversity and biogeography of *G. marginata*. The results of the COI barcoding fragment analysis include 97 *G. marginata*, as well as 21 specimens from seven potentially related species: *G. intermedia* Latzel, 1884, *G. klugii* Brandt, 1833 (*G. undulata* C.L. Koch, 1844), *G. connexa* Koch, 1847, *G. hexasticha* Brandt, 1833, *G. maerens* Attems, 1927, *G. annulata* Brandt, 1833 and *G. apuana* Verhoeff, 1911. The majority of the barcoding data was obtained through the German Barcode of Life project (GBOL). Interspecifically, *G. marginata* is separated from its congeners by a minimum uncorrected genetic distance of 12.9 %, confirming its monophyly. Uncorrected intraspecific distances of *G. marginata* are comparable to those of other widespread *Glomeris* species, varying between 0–4.7%, with the largest genetic distances (>2.5 %) found at the Mediterranean coast. 97 sampled specimens of *G. marginata* yielded 47 different haplotypes, with identical haplotypes occurring at large distances from one another, and different haplotypes being present in populations occurring in close



proximity. The highest number of haplotypes was found in the best-sampled area, western Germany. The English haplotype is identical to northern Spain; specimens from southern Spain are closer to French Mediterranean specimens. Analyses (CHAO1) show that approximately 400 different haplotypes can be expected in *G. marginata*. To cover all haplotypes, it is projected that up to 6,000 specimens would need to be sequenced, highlighting the impossibility of covering the whole genetic diversity in barcoding attempts of immobile soil arthropod species.

### Keywords

biogeographic regions, COI, Europe, haplotype analysis, haplotype richness estimation

## Introduction

In recent decades the Black Pill Millipede, *G. marginata* (Glomerida, Glomeridae) has become a model organism of the Diplopoda. The Black Pill Millipede is morphologically the best studied species of the millipedes (see examples in Koch 2015). Studies include muscle supercontraction (Candia Carnevali and Valvassori 1982), the digestive tract (Schlüter 1980, Martin and Kirkham 1989), the tracheal system (Verhoeff 1895, Wernitzsch 1910, Hilken 1998, Hilken et al. 2015), the Malpighian tubule system (Johnson and Riegel 1977a, 1977b), the postgonopodial glands (Juberthie-Jupeau 1978) and sensorial system (Sahli 1966, Seifert 1966, Müller and Sombke 2015). Additionally, numerous studies on the chemical composition of the integument of millipedes are based on *G. marginata* (Ansenne et al. 1990, Compère et al. 1996, Makarov 2015).

After discovering a new chemical compound in *G. marginata* (Glomerin: Schildknecht et al. 1966), further studies on the defensive secretions of *G. marginata* were conducted by several authors (Meinwald et al. 1966, Schildknecht et al. 1967, Schildknecht and Wenneis 1967, Carrel 1984). For a long time (see Shear et al. 2011) *G. marginata* was the only animal species known to sequester quinazolinone alkaloids. *Glomeris marginata* is the only millipede species in which the embryonic and postembryonic development is thoroughly known (Dohle 1964, Juberthie-Jupeau 1967, Enghoff et al. 1993, Janssen 2004, Prpic 2004).

The unusual mating behaviour of pill millipedes (involving the sperm ejaculation on a piece of soil before the transfer to the female) was studied extensively in the Black Pill Millipede (e.g., Haacker 1964). The ecology of the species was also the subject of numerous studies (for single aspects e.g., Nicholson et al. 1966, Van der Drift 1975, David and Gillon 2002, Rawlins et al. 2006; for the role in species communities e.g., Dunger and Steinmetzger 1981 and Voigtländer 2011). The Black Pill Millipede was also the first myriapod species in which the pheromone producing postgonopodial glands were studied (Juberthie-Jupeau 1976).

*Glomeris marginata* is commonly included in arthropod phylogenetic analyses (e.g., Regier 2001, 2005). The Black Pill Millipede is the only species of the Diplopoda in

which gene expressions of different genes, including Hox genes, were widely researched (e.g., Prpic and Tautz 2003, Prpic 2005, Prpic et al. 2005, Janssen et al. 2006, Janssen and Damen 2006). Recently, the embryonic expression of Wnt genes was studied for the first time in myriapods (Janssen and Posnien 2014) in this species. Additionally, the embryonic development, especially the embryonic development of the segmentation inside the Myriapoda, is currently nowhere as well known as in *G. marginata* (Enghoff et al. 1993, Janssen 2011, 2013, Fusco and Minelli 2013, Minelli and Fusco 2013, Minelli 2015). The same applies to the neurogenesis (Dove 2003).

Despite the high importance of *G. marginata* for general studies of millipedes, and arthropod segmentation patterns in general, little to no taxonomic studies or population genetic studies of the species were conducted in recent decades. Recent genetic studies in congeneric pill millipedes allowed the detection of several synonymies as well as cryptic species, and clarified the taxonomic status of several *Glomeris* species (Hoess and Scholl 1999, 2001, Wesener 2015a, 2015b, Conrad and Wesener 2016).

The lack of taxonomic studies in *G. marginata* is even more surprising considering the unusual wide distribution of the species (Kime and Enghoff 2011). *Glomeris marginata* is the only pill millipede reaching northern Europe. Its southernmost distribution is the south-eastern part of Spain alongside the southern border of the Pyrenees. The area of distribution of *G. marginata* covers France, England/Wales and Ireland, the whole of Germany except southern Bavaria and Saxony and extends north through Denmark to southern Sweden/Norway (Hoess 1999, Kime and Enghoff 2011: p. 104). *Glomeris marginata* is the most common pill millipede species in Germany (Reip et al. 2016).

While adult *G. marginata* normally can be easily distinguished from their congeners by their shiny completely black-brown colour with brightly coloured creamy-white tergal margins (see Schubart 1934: 32, Hoess 2000, Figure 1A), several unusual specimens (grey or reddish, with prominent white marks, or with orange or reddish margins, see Figures 1B–E, 2A, B), currently interpreted as colour morphs, are often encountered. Such unusual specimens resemble other species of the genus, such as *G. intermedia* Latzel, 1884 (Figure 2B, C), which shares a similar, but more western, distribution pattern than *G. marginata*, or *G. annulata* Koch, 1847 (Figure 2D), a local endemic in southern France (Hoess 2000, Kime and Enghoff 2011). Two other local endemic species, *G. apuana* Verhoeff, 1911 (see Wesener 2015b) and *G. maerens* Attems, 1927 (Figures 2E–G) not only occur in areas directly bordering the known distribution of *G. marginata*, but also show a similar colour pattern. Furthermore, the species *G. klugii* Brandt, 1833 / *G. undulata* C.L. Koch, 1844 and *G. connexa* Koch, 1847 sometimes also appear in dark-brown colour forms.

In this work, it is tested whether *G. marginata* and its different colour variants form a monophyletic taxon based on barcoding mt-DNA COI data. The phylogeographic relationship and the possible origin of the species are also ascertained. Finally, the relationship of the Black Pill Millipede to the other, similar coloured congeneric species, *G. annulata*, *G. apuana*, and *G. maerens* is clarified.



**Figure 1.** *Glomeris marginata* (Villers, 1789) colour morphs. **A** main coloration form, center immature specimens showing the perplexa colour pattern; Germany, Landskrone **B** strongly lightened adult perplexa pattern, France, Pays de la Loire **C** red mutant, Germany, Bonn **D** strongly red-banded form, from France, Montauroux **E** more weakly red-brown banded form, France, same population as D. **A, D, E** photographed by Jan Philip Oeyen **B** by ZFMK **C** by Dennis Rödder.





**Figure 2.** **A** *G. marginata*, brown and black form occurring in sympatry, Germany, Rügen, 2016. **B–G** Similar coloured species of *Glomeris* analyzed in this study **B** *G. marginata*, with a single specimen of *G. intermedia* in the upper left part, Germany, Landskrone, 2015 **C** *G. intermedia* Latzel, 1884, with sympatric *G. marginata*, Germany, Landskrone, 2015 **D** *G. annulata* Brandt, 1833, France, Gard, Courry, 2015 **E** *G. cf. lugubris* Attems, 1952, Spain, Cádiz/ Sierra de Grazalema, 2008, preserved specimen **F** *G. cf. maerens* Attems, 1927, Spain, Aragón/Teruel, 2010, preserved specimen **G** *G. maerens*, Spain, Tarragona/Montsià, 2017; **B–D** photographed by Jan Philip Oeyen.

## Material and methods

### *Selection of specimens*

Based on the project German Barcoding of Life (GBOL, <http://www.bolgermany.de>), 80 specimens of *G. marginata* from different locations were selected from the collection of the ZFMK (Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany). All specimens of *G. annulata*, *G. apuana* and the *G. maerens* species-group came from the collection of the ZFMK, while the two specimens of *G. hexasticha* were collected by the first author. Six additional COI-sequences of *G. marginata* were obtained from former projects of the authors (see Spelda et al. 2011 and Wesener et al. 2010). These sequences are available from GenBank (see Table 1 for accession numbers). Also, the COI-sequences of the outgroup species *G. intermedia*, *G. klugii undulata*, and *G. connexa* were obtained from the work of Spelda et al. (2011). An additional 11 French COI-sequences of *G. marginata* were available in BOLD (downloadable at the Public Data Portal, <http://www.boldsystem.org>, see Table 1 for BOLD-numbers) by end of November 2015. In total 97 COI-sequences of *G. marginata* and 21 of the seven outgroup species were obtained for this study (93 newly sequenced, 14 from GenBank and 11 from BOLD).

The specimens of *G. marginata* were collected from a major part of the distribution region in NW Europe, covering the region from NE Spain to northern Germany (Figure 3). Material from the north-eastern part of the range (Denmark-Sweden-Norway) was not available. For the different analyses, two datasets were created, one which contained the 97 *G. marginata* sequences only, and a second one combining the *G. marginata* sequences with the 21 outgroup specimens.

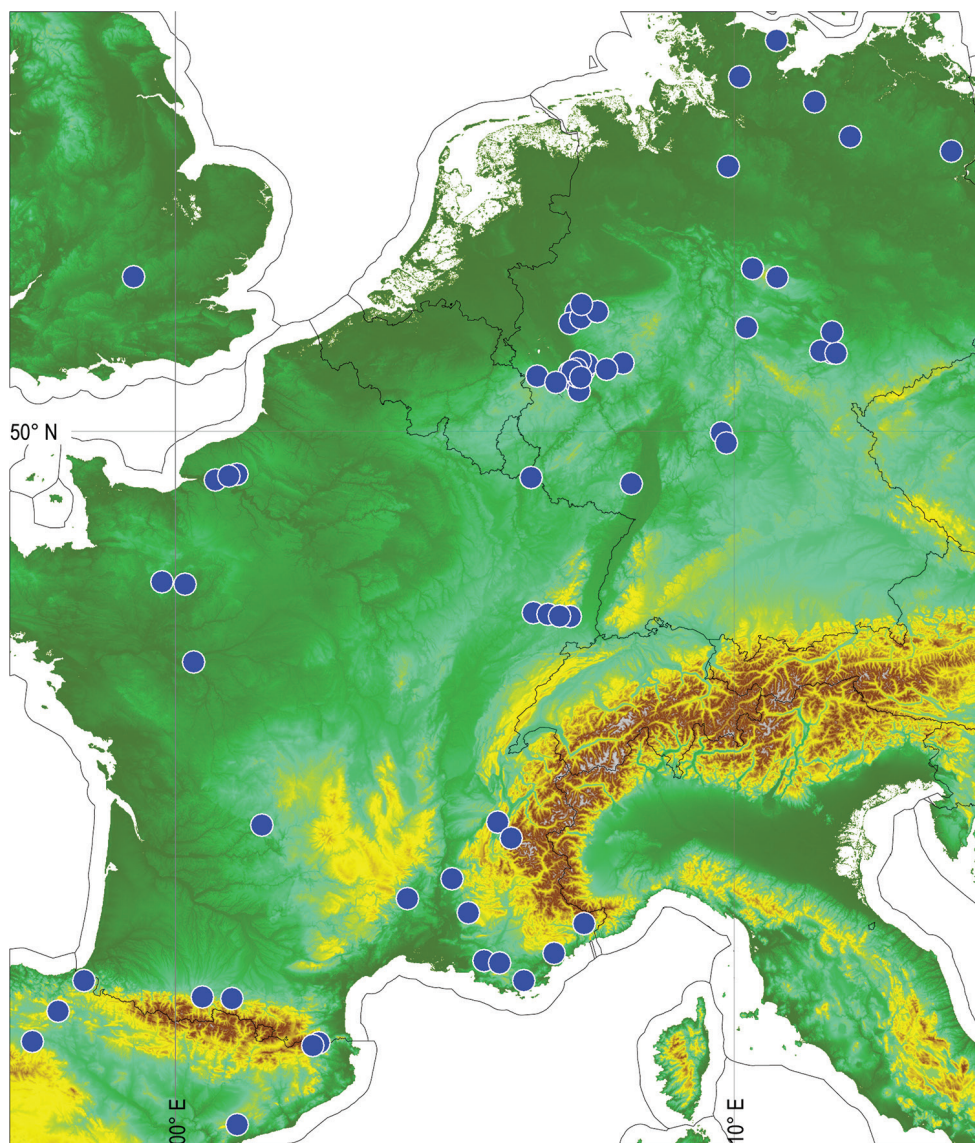
### *DNA extraction, PCR, and sequencing*

From the analysed specimens, genomic mtDNA (the barcoding region of COI) was extracted from muscle tissue applying a standard extraction protocol (see e.g., Wesener et al. 2015) at the ZFMK. Also, the PCR and sequencing protocols were identical to those used in a previous work (Wesener et al. 2015). All specimens and the aliquots of the DNA extractions were deposited in the collection of the ZFMK. All new sequences (80 *G. marginata*, two *G. annulata*, and nine *G. maerens* sp. as *Glomeris* sp.) were deposited in GenBank (see Table 1 for accession numbers).

### *Aligning and control*

Sequences were aligned by hand in BIOEDIT (Hall 1999), version 7.2.5 (for final data set see Suppl. material S1). To rule out the accidental amplification of nuclear copies of the mitochondrial COI gene, the whole dataset was translated into amino





**Figure 3.** Distribution map of all successfully sequenced samples of *G. marginata* (blue dots). Base map: Shuttle Radar Topography Mission elevation data of the Deutsche Zentrum für Luft- und Raumfahrt (SRTM-3), accessed with GLOBALMAPPER v17.

acids following the ‘invertebrate’ code in MEGA 7 (Tamura et al. 2013); internal stop codons were absent in our dataset. There were in total 657 positions in the final dataset, gaps were absent. Voucher specimens and aliquots of the DNA extractions were stored in natural history collections and are available for each analysed sequence (see Table 1).

**Table 1.** Analysed specimens, voucher and Genbank code, collection locality and bioregion (see Table 2).

SpecimenID	Voucher #	GenBank #		Lat./Lon.	BioRegion
<i>Glomeris marginata</i>					
G.mar.01	GBOL33714	MG892112	Germany, Sachsen-Anhalt, Wernigerode, Königshütte	N51.743, E10.767	DE.MGSO
G.mar.02	ZFMK100409275	MG892115	Germany, Sachsen-Anhalt, Wernigerode, Königshütte	N51.744, E10.767	DE.MGSO
G.mar.03	ZFMK1634	MG892119	Germany, Niedersachsen, Goslar, Bockswiese	N51.841, E10.326	DE.MGSO
G.mar.04	ZFMK1909	MG892123	Germany, Thüringen, Saale-Holzland-Kreis, Schöngleina	N50.895, E11.753	DE.MGSO
G.mar.05	ZFMK19531	MG892146	Germany, Thüringen, Saale-Holzland-Kreis, Schöngleina	N50.895, E11.753	DE.MGSO
G.mar.06	ZFMK2503693	MG892153	Germany, Thüringen, Jena	N50.919, E11.548	DE.MGSO
G.mar.07	ZFMK2503694	MG892154	Germany, Thüringen, Jena	N50.919, E11.548	DE.MGSO
G.mar.08	ZFMK2542470	MG892173	Germany, Thüringen, Stadtroda, Hermsdorf	N50.892, E11.821	DE.MGSO
G.mar.09	ZFMK2542471	MG892174	Germany, Thüringen, Stadtroda, Hermsdorf	N50.892, E11.821	DE.MGSO
G.mar.10	ZFMK2542541	MG892175	Germany, Sachsen-Anhalt, Burgenland, Bad Kösen	N51.133, E11.749	DE.MGSO
G.mar.11	ZFMK2542542	MG892176	Germany, Sachsen-Anhalt, Burgenland, Bad Kösen	N51.133, E11.749	DE.MGSO
G.mar.12	ZFMK18967	MG892124	Germany, Nordrhein-Westfalen, Bonn, Wachtberg	N50.663, E7.103	DE.MGSW
G.mar.13	ZFMK18987	MG892126	Germany, Nordrhein-Westfalen, Königswinter	N50.666, E7.216	DE.MGSW
G.mar.14	ZFMK18988	MG892127	Germany, Nordrhein-Westfalen, Quirrenbach	N50.687, E7.300	DE.MGSW
G.mar.15	ZFMK18991	MG892128	Germany, Nordrhein-Westfalen, Hennef, Blankenberg	N50.767, E7.367	DE.MGSW
G.mar.16	ZFMK19003	MG892129	Germany, Nordrhein-Westfalen, Hagen-Holthausen	N51.361, E7.550	DE.MGSW
G.mar.17	ZFMK19005	MG892130	Germany, Nordrhein-Westfalen, Hagen-Holthausen	N51.361, E7.550	DE.MGSW
G.mar.18	ZFMK19029	MG892132	Germany, Nordrhein-Westfalen, Bad Münstereifel	N50.560, E6.808	DE.MGSW
G.mar.19	ZFMK19031	MG892133	Germany, Nordrhein-Westfalen, Wuppertal, Krutscheid	N51.230, E7.054	DE.MGSW
G.mar.20	ZFMK19044	MG892136	Germany, Nordrhein-Westfalen, Siegburg	N50.803, E7.242	DE.MGSW
G.mar.21	ZFMK19045	MG892137	Germany, Nordrhein-Westfalen, Hattingen, Felderbachtal	N51.359, E7.170	DE.MGSW
G.mar.22	ZFMK19046	MG892138	Germany, Nordrhein-Westfalen, Wuppertal, Krutscheid	N51.230, E7.054	DE.MGSW
G.mar.23	ZFMK19047	MG892139	Germany, Nordrhein-Westfalen, Bonn, Oberkassel	N50.714, E7.177	DE.MGSW

SpecimenID	Voucher #	GenBank #		Lat./Lon.	BioRegion
G.mar.24	ZFMK19048	MG892140	Germany, Nordrhein-Westfalen, Bonn, Röttgen	N50.672, E7.047	DE.MGSW
G.mar.25	ZFMK19049	MG892141	Germany, Nordrhein-Westfalen, Wuppertal, NSG Im Hölken	N51.291, E7.252	DE.MGSW
G.mar.26	ZFMK19051	MG892142	Germany, Rheinland-Pfalz, Ahrweiler, Heppingen	N50.551, E7.172	DE.MGSW
G.mar.27	ZFMK19054	MG892143	Germany, Rheinland-Pfalz, Niederzissen, Bausenberg	N50.465, E7.223	DE.MGSW
G.mar.28	ZFMK19057	MG892144	Germany, Nordrhein-Westfalen, Hagen-Holthausen	N51.361, E7.550	DE.MGSW
G.mar.29	ZFMK19539	MG892147	Germany, Nordrhein-Westfalen, Heimbach, Meuchelberg	N50.632, E6.473	DE.MGSW
G.mar.30	ZFMK19550	MG892148	Germany, Nordrhein-Westfalen, Neunkirchen, Hellerberg	N50.780, E8.009	DE.MGSW
G.mar.31	ZFMK19555	MG892149	Germany, Nordrhein-Westfalen, Neunkirchen, Hellerberg	N50.780, E8.009	DE.MGSW
G.mar.32	ZFMK19558	MG892150	Germany, Rheinland-Pfalz, Altenkirchen, Giesenhausen	N50.709, E7.713	DE.MGSW
G.mar.33	ZFMK19560	MG892151	Germany, Rheinland-Pfalz, Altenkirchen, Giesenhausen	N50.709, E7.713	DE.MGSW
G.mar.34	ZFMK19561	MG892152	Germany, Rheinland-Pfalz, Altenkirchen, Giesenhausen	N50.709, E7.713	DE.MGSW
G.mar.35	ZFMK2516208	MG892156	Germany, Nordrhein-Westfalen, Bad Honnef, Kasselbachtal	N50.625, E7.194	DE.MGSW
G.mar.36	ZFMK2516209	MG892157	Germany, Nordrhein-Westfalen, Bad Honnef, Kasselbachtal	N50.625, E7.194	DE.MGSW
G.mar.37	ZFMK2557907	MG892181	Germany, Hessen, Eschwege, Wanfried	N51.182, E10.221	DE.MGSW
G.mar.38	ZFMK2557908	MG892182	Germany, Hessen, Eschwege, Wanfried	N51.182, E10.221	DE.MGSW
G.mar.39	ZFMK100409283	MG892116	Germany, Schleswig-Holstein, Segeberg, Bockhorn	N53.919, E10.098	DE.NDTO
G.mar.40	ZFMK2538190	MG892171	Germany, Schleswig-Holstein, Weissenhaus	N54.303, E10.756	DE.NDTO
G.mar.41	ZFMK2538253	MG892172	Germany, Brandenburg, Pfingstberg, Schorfheide	N53.124, E13.884	DE.NDTO
G.mar.42	ZFMK2553394	MG892177	Germany, Mecklenburg-Vorpommern, Schwerin, Schweriner Innensee	N53.653, E11.437	DE.NDTO
G.mar.43	ZFMK2553395	MG892178	Germany, Mecklenburg-Vorpommern, Schwerin, Schweriner Innensee	N53.653, E11.437	DE.NDTO
G.mar.44	ZFMK2553405	MG892179	Germany, Brandenburg, Pritzwalk, Putlitz	N53.279, E12.077	DE.NDTO
G.mar.45	ZFMK100409272	MG892114	Germany, Niedersachsen, Soltau-Fallingb., Hebenbrock	N52.960, E9.893	DE.NDTW
G.mar.46	ZFMK19472	MG892145	Germany, Nordrhein-Westfalen, Bochum, Botanical Garden	N51.442, E7.267	DE.NDTW

SpecimenID	Voucher #	GenBank #		Lat./Lon.	BioRegion
G.mar.47	ZFMK100409123	MG892113	Germany, Bayern, Main-Spessart, Karlstadt	N49.983, E9.768	DE.SSL
G.mar.48	ZFMK100409296	MG892117	Germany, Bayern, Würzburg, Erlabrunn	N49.864, E9.857	DE.SSL
G.mar.49	ZFMK1861	MG892120	Spain, La Rioja, Navarrete	N42.430, W2.562	ES.CC
G.mar.50	ZFMK1863	MG892121	Spain, Navarra, Etxalar	N43.234, W1.638	ES.CC
G.mar.51	ZFMK1893	MG892122	Spain, Navarra, Etxalar	N43.234, W1.638	ES.CC
G.mar.52	ZFMK2517202	MG892159	Spain, Cataluña, Tarragona, Farena	N41.315, E1.104	ES.PYRS
G.mar.53	BGI12GEU183	MG892183	France, Auvergne-Rhône-Alpes, Isere, Grenoble	N45.273, E5.766	FR.ALP
G.mar.54	ZFMK2517217	MG892168	France, Auvergne-Rhône-Alpes, Isere, Oisans	N45.071, E6.008	FR.ALP
G.mar.55	ZFMK2553457	MG892180	France, Pays de la Loire, Mayenne, Saint-Pierre-sur-Orthe	N48.201, E0.171	FR.ATLN
G.mar.56	ZFMKTW163	MG931019	France, Pays de la Loire, Mayenne, Saint-Martin-de-Connée	N48.230, W0.242	FR.ATLN
G.mar.57	ZFMKTW164	MG931020	France, Centre-Val de Loire, Chinon, Rigny-Ussé	N47.261, E0.326	FR.ATLN
G.mar.58	ZFMK100410157	MG892118	France, Alsace, Haut-Rhin, Col du Hundsruck, Thann	N47.812, E7.065	FR.CONN
G.mar.59	ZFMK18996	MG931021	Luxemburg, , Schengen	N49.461, E6.364	FR.CONN
G.mar.60	ZFMK2517315	MG892169	France, Bourgogne-Franche-Comté, Luxeuil-les-Bains	N47.859, E6.404	FR.CONN
G.mar.61	ZFMK2517322	MG8921701	France, Elsas, Ballons des Vosges, Faucogney-et-la-Mer	N47.839, E6.667	FR.CONN
G.mar.62	ZFMKTW161	MG892184	France, Elsas, Ballons des Vosges, Faucogney-et-la-Mer	N47.839, E6.667	FR.CONN
G.mar.63	ZFMKTW162	MG892185	France, Elsas, Ballon d'Alcas, Sewen	N47.817, E6.874	FR.CONN
G.mar.64	ZFMK2517209	MG892160	France, Haute-Vienne-Corrèze-Creuse, Limousin, Correze	N45.235, E1.545	FR.CONNS
G.mar.65	ZFMK18977	MG892125	France, Provence-Alpes-Côte d'Azur, Bédoin, Vaucluse	N44.114, E5.241	FR.MED
G.mar.66	ZFMK19021	MG892131	France, Provence-Alpes-Côte d'Azur, Bédoin, Vaucluse	N44.114, E5.241	FR.MED
G.mar.67	ZFMK19037	MG892134	France, Provence-Alpes-Côte d'Azur, Bédoin, Vaucluse	N44.114, E5.241	FR.MED
G.mar.68	ZFMK2516203	MG892155	France, Rhône-Alpes, Drôme, La Bégude-de-Mazenc	N44.551, E4.949	FR.MED
G.mar.69	ZFMK2517213	MG892164	France, Provence-Alpes-Côte d'Azur, Var	N43.494, E5.521	FR.MED
G.mar.70	ZFMK2517214	MG892165	France, Provence-Alpes-Côte d'Azur, Var	N43.464, E5.800	FR.MED

SpecimenID	Voucher #	GenBank #		Lat./Lon.	BioRegion
G.mar.71	ZFMK2517215	MG892166	France, Provence-Alpes-Côte d'Azur, Pierrefeu	N43.232, E6.234	FR.MED
G.mar.72	ZFMK2517216	MG892167	France, Provence-Alpes-Côte d'Azur, Lantosque	N43.974, E7.311	FR.MED
G.mar.73	ZFMKTW102	MG892186	France, Languedoc-Roussillon-Midi-Pyrénées, Courry	N44.297, E4.152	FR.MED
G.mar.74	ZFMKTW165	MG892187	France, Alpes-Côte d'Azur, Var, Montauroux, Fondurane	N43.589, E6775	FR.MED
G.mar.75	ZFMKTW166	MG892188	France, Alpes-Côte d'Azur, Var, Montauroux, Fondurane	N43.589, E6775	FR.MED
G.mar.76	ZFMK2517199	MG931022	Spain, Pirineos, Le Grau	N42.412, E2.566	FR.PYRN
G.mar.77	ZFMK2517210	MG892161	France, Languedoc-Roussillon-Midi-Pyrénées, Ariège, Bas-Couserans	N42.997, E1.010	FR.PYRN
G.mar.78	ZFMK2517211	MG892162	France, Languedoc-Roussillon-Midi-Pyrénées, La Vallée de la Barousse	N43.017, E0.480	FR.PYRN
G.mar.79	ZFMK2517212	MG892163	France, Languedoc-Roussillon-Midi-Pyrénées, Le Canigou	N42.375, E2.456	FR.PYRN
G.mar.80	ZFMK19038	MG892135	Great Britain, England, Buckinghamshire	N51.750, W0.750	GB.EM
<b>Sequences from BOLD</b>					
G.mar.81	BOLDECHUB974		France, Haute Normandie, Seine-Maritime, Rouen, Forêt verte	N49.500, E1.100	FR.ATLN
G.mar.82	BOLDECHUB975		France, Haute Normandie, Seine-Maritime, Rouen, Forêt verte	N49.500, E1.100	FR.ATLN
G.mar.83	BOLDECHUB978		France, Haute Normandie, Seine-Maritime, Rouen, Forêt verte	N49.500, E1.100	FR.ATLN
G.mar.84	BOLDECHUB979		France, Haute Normandie, Seine-Maritime, Rouen, Forêt verte	N49.500, E1.100	FR.ATLN
G.mar.85	BOLDGENHP020		France, Haute Normandie, Seine-Maritime, Forêt de Brotonne	N49.434, E0.714	FR.ATLN
G.mar.86	BOLDGENHP021		France, Haute Normandie, Seine-Maritime, Forêt de Brotonne	N49.434, E0.714	FR.ATLN
G.mar.87	BOLDGENHP022		France, Haute Normandie, Seine-Maritime, Forêt de Brotonne	N49.434, E0.714	FR.ATLN
G.mar.88	BOLDGENHP023		France, Haute Normandie, Seine-Maritime, Forêt de Brotonne	N49.434, E0.714	FR.ATLN
G.mar.89	BOLDGENHP024		France, Haute Normandie, Seine-Maritime, Forêt de Brotonne	N49.434, E0.714	FR.ATLN
G.mar.90	BOLDGENHP025		France, Haute Normandie, Seine-Maritime, Forêt de Brotonne	N49.434, E0.714	FR.ATLN
G.mar.91	BOLDGENHP317		France, Haute Normandie, Seine-Maritime, Forêt Henouville	N49.480, E0.954	FR.ATLN
<b>Sequences from GenBank</b>					
G.mar.92		FJ409909	Germany, Nordrhein-Westfalen, Bonn, Venusberg	N50.692, E7.100	DE.MGSW



SpecimenID	Voucher #	GenBank #		Lat./Lon.	BioRegion
G.mar.93		HM888107	Germany, Rheinland-Pfalz, Rheinbreitbach	N50.619, E7.254	DE.MGSW
G.mar.94		HM888108	Germany, Nordrhein-Westfalen, Bad Münstereifel	N50.560, E6.808	DE.MGSW
G.mar.95		HM888109	Germany, Rheinland-Pfalz, Rheinbreitbach	N50.619, E7.254	DE.MGSW
G.mar.96		HQ966136	Germany, Rheinland-Pfalz, Neustadt an der Weinstraße, Klausental	N49.392, E8.158	DE.SSL
G.mar.97		JQ350444	Spain, Navarra, Sierra De Urbasa	N42.830, W2.100	ES.CC

#### Outgroup species/specimens

##### *Glomeris intermedia*

G.int.1	see Spelda et al. 2011	HM888099	Germany, Rheinland-Pfalz, Neuwied		
G.int.2		HQ966138	Germany, Rheinland-Pfalz, Neustadt		

##### *Glomeris klugii*

G.und.1	see Spelda et al. 2011	HM888106	Germany, Bayern, Lindau		
G.und.2		HQ966135	Germany, Bayern, Solnhofen		

##### *Glomeris connexa*

G.con.1	see Spelda et al. 2011	HM888096	Germany, Bavaria, Andechs		
G.con.2		JN271879	Italy, Lombardia, Sondrio		

##### *Glomeris hexasticha*

G.hex.1	ZFMK2542473	MG931024	Germany, Thüringen, Hermsdorf		
G.hex.2	ZFMK19526	MG931023	Germany, Bayern, Neumarkt		

##### *Glomeris maerens* species group

G.mae.1	ZFMK2517198	MG892103	Spain, Valencia, Pego		
G.mae.2	ZFMK2517200	MG892104	Spain, Castellon, l'Alcora		
G.mae.3	ZFMK2517201	MG892105	Spain, Tarragona, Vandellos		
G.mae.4	ZFMK2517203	MG892106	Spain, Tarragona, Llaberia		
G.mae.5	ZFMK2517204	MG892107	Spain, Castellon, l'Alcora		
G.mae.6	ZFMK2517205	MG892108	Spain, Valencia, Pego		
G.mae.7	ZFMK2517206	MG892109	Spain, Tarragona, Reus, La Riba		
G.mae.8	ZFMK2517207	MG892110	Spain, Castellon, Atzeneta del Maestrat		
G.mae.9	ZFMK2517208	MG892111	Spain, Barcelona, Castellet, El Vendrell		

##### *Glomeris annulata*

G.ann.1	ZFMKTW100	MG892190	France, Gard, Courry, 280-300 m		
G.ann.2	ZFMKTW101	MG892189	France, Gard, Courry, 280-300 m		

##### *Glomeris apuana*

G.apu.1	ZFMKMYR752	KT188943	Italy, Liguria, Cinque Terre	see Wesener 2015	
G.apu.2	ZFMKMYR753	KT188944	Italy, Liguria, Cinque Terre		

## Assignment to biogeographic regions

All specimens of *G. marginata* were assigned to a biogeographic region of the main sub-country level (bioregion) (see Table 1, column BioRegion and Table 2). The structuring of the specimens with their origin in Germany is based on the official map of natural regions of Germany, the “Großregionen”, 1<sup>st</sup> level (Meynen and Schmithüsen 1953–1962, see also “Naturräumliche Großregionen Deutschlands” at <http://de.wikipedia.org>). Due to their disproportionately large size, the regions “Norddeutsches Tiefland” and “Mittelgebirgsschwelle” are additionally each divided into a western and eastern part according to Figure 4. The structuring of the specimens with their origin in France is based on the “régions biogéographiques pour l’évaluation de l’état de conservation en France” (see <http://inpn.mnhn.fr/programme/rapportage-directives-nature/presentation>). Additionally, the regions “France Atlantique” and “France Continentale” – due to their size – are each divided into a northern and southern part as shown in Figure 5. The ecological region “France alpine” is geographically divided into France Alps and France Pyrenees. The single specimen from Great Britain is located in southern England. For Spain, we used the regions of southern Pyrenees and the Cantabrian Mountains. In total 14 biogeographic regions were assigned in four countries (see Table 2).

**Table 2.** Biogeographic regions (bioregions) and their code.

Region code	Region
<b>Germany</b>	
DE.NDTW	“Norddeutsches Tiefland” western part, Norddeutsche Geest west of river Elbe
DE.NDTO	“Norddeutsches Tiefland” eastern part, east of river Elbe
DE.MGSW	“Mittelgebirgsschwelle”, western part, Niedersächsisch-Hessisches Bergland, Rheinisches Schiefergebirge, Kölner Bucht
DE.MGSO	“Mittelgebirgsschwelle”, eastern part, Harz, Thüringer Becken, Östliche Mittelgebirgsschwelle
DE.SSL	“Schichtstufenland” on both sides of the Oberrheingraben
<b>France</b>	
FR.CONN	France Continentale, northern part
FR.CONS	France Continentale, southern part
FR.MED	France Méditerranéenne
FR.ATLN	France Atlantique, north of La Rochelle
FR.ALP	Alps of France
FR.PYRN	Pyrenees of France
<b>Spain</b>	
ES.PYRS	Pyrenees of Spain
ES.CC	Cordillera Cantábrica (Navarre, Sierra de Urbasa)
<b>Great Britain</b>	
GB.EM	Middle England



**Figure 4.** Modified biogeographic regions of Germany, based on Naturräumliche Großregionen of Germany, Meynen and Schmithüsen (1953–1962) and [http://commons.wikimedia.org/wiki/File:Deutschland\\_Naturraumliche\\_Grossregionen.png](http://commons.wikimedia.org/wiki/File:Deutschland_Naturraumliche_Grossregionen.png)

### Phylogenetic and distance analysis

Analyses were conducted in MEGA 7 (Kumar et al. 2015). The uncorrected pairwise distances (p-distances) were calculated with all codon positions included. Ambiguous positions were removed for each sequence pair. The distance matrix was exported to



**Figure 5.** Modified biogeographic regions of France, based on <http://inpn.mnhn.fr/programme/rapportage-directives-nature/presentation>.

MICROSOFT EXCEL for further calculations of minimum interspecific and maximum intraspecific distances (see Suppl. material S2).

A model test, as implemented in MEGA 7, was performed to find the best fitting maximum likelihood substitution model for the complete sequence set. The model with the lowest AICc value (Akaike Information Criterion, corrected) are considered to describe the best substitution pattern. Codon positions included were 1<sup>st</sup> + 2<sup>nd</sup> + 3<sup>rd</sup>. The model test selected the General Time Reversible model (Tavaré 1986) with gamma distribution and invariant sites (GTR+G+I) as the best fitting model (AIC: 7988, lnL: -3750).

The evolutionary history was inferred by using the maximum likelihood method based on the selected GTR+G+I model. Initial tree(s) for the heuristic search were obtained automatically by applying NJ/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. The discrete gamma distribution was used with five categories to model evolutionary rate differences among sites. The analysis involved the complete sequence set (*G. marginata* + out-group species). Codon positions included were “1st+2nd+3rd” (Missing Data: partial deletion). The bootstrap consensus tree inferred from 1,000 replicates (Felsenstein 1985) is taken to represent the evolutionary history of the analysed taxa. Trees were built with FIGTREE 1.4.2 and drawn to scale, with branch lengths measured in the number of substitutions per site.

## Spatial relationship

Besides the genetic p-distances (see above) for all *G. marginata* specimen pairs (4656 pairs) the geographical distances were calculated based on the more exact method of calculation, the Euclidean geometry:

$$\text{distance} = \arccos\left(\sin\left(\text{Lat1} * \frac{\pi}{180}\right) * \sin\left(\text{Lat2} * \frac{\pi}{180}\right) + \cos\left(\text{Lat1} * \frac{\pi}{180}\right) * \cos\left(\text{Lat2} * \frac{\pi}{180}\right) * \cos\left(\text{Lon2} * \frac{\pi}{180} - \text{Lon1} * \frac{\pi}{180}\right)\right) * \text{er}$$

The earth’s radius (= er) in central Europe is 6,367 km. Lat1 and Lon1 are the latitude and longitude of the location of specimen 1, Lat2 and Lon2 those of specimen 2. For the full dataset see Suppl. material S3. A chart was plotted to show the relationship between the genetic and geographical distance.

## Haplotype analysis

A haplotype analysis was conducted with DNASP (Librado and Rozas 2009) by assigning the genetic code to “mtDNA *Drosophila*” for invertebrates. The *G. marginata* sequences were grouped to haplotypes (DNASP / Generate / HaploType Data File, excluding sites with missing data). The haplotypes were marked by geography.

In a second run the sequences were grouped again by considering only non-synonymous changes. In this second step all synonymous changes were discarded. For this an interim sequence set with only non-synonymous changes was created (DNASP / Generate / Polymorphic Data File / “only Non-synonymous”) and afterwards the Haplotype file was built. Because of the unequal sampling with a bias to the German fauna within the GBOL-project, no comparative population analysis was possible.

The previous first haplotype data file was used as a basis for a TCS Networks analysis (Clement et al. 2002). A TCS-network was created with the software POPART (Leigh 2015). For this a frequency matrix of haplotypes to bioregions was created in MICROSOFT EXCEL and according the software manual transformed to the POPART-nexus format (see Suppl. material S4).



## Haplotype richness estimation

The potential number of haplotypes for the complete distribution area was estimated with ESTIMATES 9.1.0 (Colwell 2013). For this, the CHAO1-estimator (Chao 1984) based on the haplotype distribution (instead of a species distribution) was calculated (for the underlying data file see Suppl. Material S5). Together with the ACE-index the CHAO1-estimator is the main estimator for individually based abundance data (Gotelli and Colwell 2010). It is based on the number of all OTUs (operational taxonomic units, in this study the haplotypes) with one sequence in relation to the number of all OTUs with two sequences. With 10,000 randomized runs the haplotype accumulation curve (rarefaction curve) and the 95 % lower and upper boundaries of confidence intervals were calculated and additionally also their extrapolation curves (formulas in detail see Colwell et al. 2012).

## Results

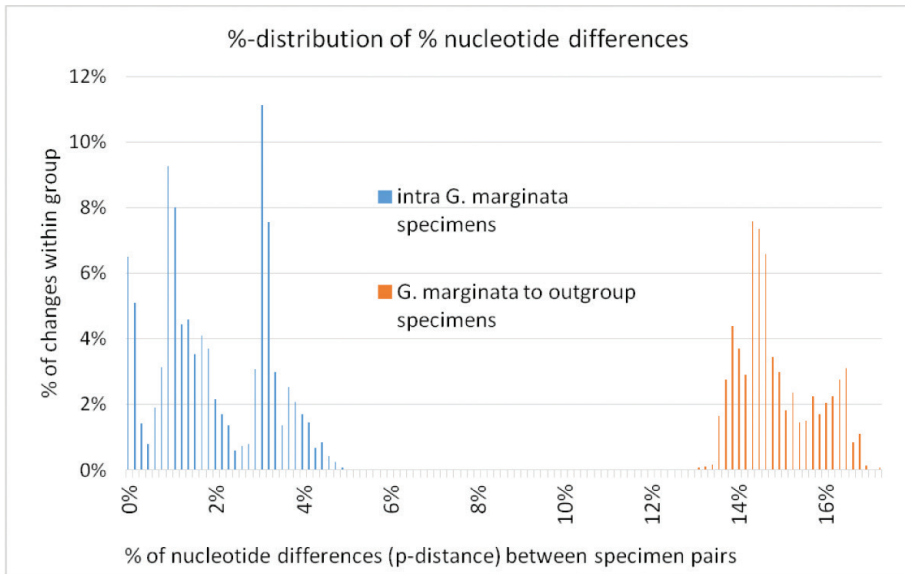
### Phylogenetic relationship of *G. marginata* with similar species

The minimum interspecific distance of *G. marginata* to other *Glomeris* species ranges from 12.9–15.9 % (see Table 3). There is a clear barcoding gap between the maximum intraspecific distance (5.0 %) and the minimum interspecific distance (12.9 %) (see also Figure 6). *Glomeris connexa* and the *G. maerens* species-group are closest to *G. marginata*. The separation of the outgroup species to *G. marginata* is clearly visible in the graphical mapping of the phylogenetic analyses (see Figure 7). The *G. marginata* specimens, together with *G. connexa*, *G. apuana*, and the *G. maerens*-group, form a distinct clade separate from the other species. The other four species (*G. hexasticha*, *G. klugii/undulata*, *G. intermedia*, and *G. annulata*) form a single clade. Statistical support for both clades is rather low, not exceeding 82 %.

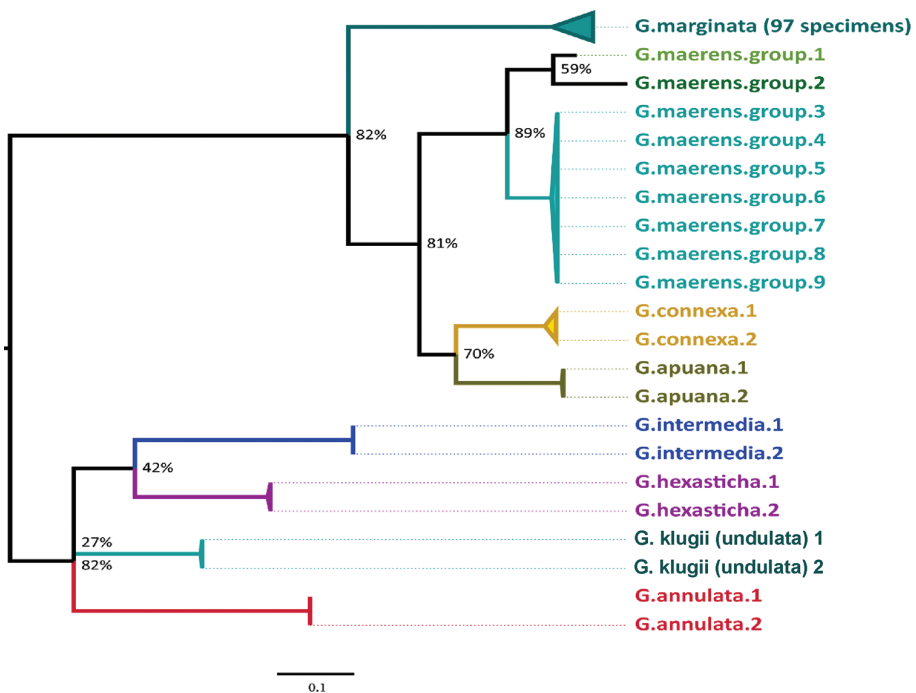
The specimens of the *G. maerens* species-group cluster together with a minimum interspecific distance (10.5 %) to the other species, but the *G. maerens* specimens fall into three clades with a maximum intraspecific distance of up to 9.1 % (see Figure 7).

**Table 3.** Minimum p-distance of *G. marginata* to other species.

Species	Min. p-distance to <i>G. marginata</i>
<i>Glomeris connexa</i>	12.9 %
<i>Glomeris maerens</i> -group	13.1 %
<i>Glomeris klugii/undulata</i>	13.4 %
<i>Glomeris apuana</i>	14.2 %
<i>Glomeris intermedia</i>	14.8 %
<i>Glomeris hexasticha</i>	14.9 %
<i>Glomeris annulata</i>	15.9 %



**Figure 6.** Distribution of nucleotide differences in % between specimen pairs of *Glomeris marginata* and to outgroup specimens.



**Figure 7.** Molecular phylogenetic analysis of *Glomeris* species by the maximum likelihood method. Midpoint rooted. Bootstrap values in % at nodes. All collapsed nodes have a bootstrap value of 100%. Scale bar: 10 % genetic ML distance.

### Intraspecific variation of *G. marginata*

All 97 specimens of *G. marginata* form a well-supported clade (bootstrap value 100 %, not shown in Figure 7). The 97 specimens of *G. marginata* have a maximum intraspecific distance of 5.0 %. The intraspecific distance chart (Figure 6, blue bars) shows three peaks (at: 0 %, 0.9 % and 3.0 %) within the p-distances of the *G. marginata* specimens; within the range every p-distance value is present. There is no gap in the distribution of the p-distance values.

### Geographical relationship of *G. marginata* specimens

The specimens from northern Germany and eastern France show the lowest genetic distance ( $\approx 1$  %) to the rest of all samples. The specimens from western and southern France show the highest median distance ( $\approx 3\text{--}4$  %) to those of other populations (see Table 4 and Suppl. Material S2).

The maximum and the mean p-distance of *G. marginata* within the north-eastern part of the distribution ( $\approx 4$  % or  $\approx 1$  %, respectively) is lower than in the south-western part ( $\approx 5$  % or  $\approx 3\text{--}4$  %, respectively). Specimens from Mediterranean France group most distantly from the rest, with a maximum p-distance of 5.0 %.

The plot of the genetic p-distance to the geographical distances of all samples (4,656 possible pairs) shows no distinct relationship between both values (see Figure 8). There is a small and negligible trend of  $+0.00001$  % p-distance/km-distance. The coefficient of determination  $R^2$  with  $\approx 0.1$  is extremely low. For example, two specimens collected only 43 km apart (77 to 78, see Figure 8: green circle and Table 5) show a genetic p-distance of 3.8 %, while contrarily two specimens with a geographical distance of more than 1,000 km (43 to 54, see Figure 8, grey circle and Table 5) belong to an identical haplotype (0 % p-distance). The geographically most distant analysed specimens (41 to 49, Figure 8: red circle) show a p-distance of 2.1 %.

### Haplotypes/regions

Within the 657 sites of the 97 sequences of *G. marginata*, 74 were polymorphic which resulted from a total number of 81 mutations. The total number of synonymous changes is 71 and the total number of replacement changes is six. In the haplotype analysis, within the 97 samples, 47 haplotypes were detected, with 79 polymorphic sites. Haplotype diversity is 0.93, nucleotide diversity  $\Pi$  is 0.017.

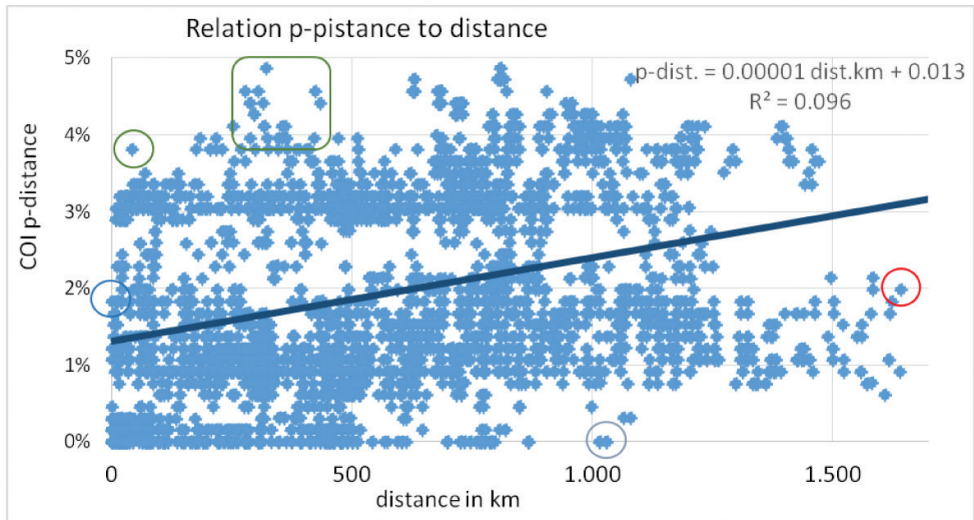
38 haplotypes (81 % of all haplotypes) consist of only one specimen ( $\hat{=} 38$  specimens  $\hat{=} 39$  % of all specimens) and 42 haplotypes (89 % of all haplotypes) represents only specimens from one bioregion ( $\hat{=} 48$  specimens  $\hat{=} 49$  % of all specimens). Nine haplotypes are represented in our dataset with two or more specimens ( $\hat{=} 59$  specimens  $\hat{=} 61$  % of all specimens).

**Table 4.** The 10 specimens with smallest and greatest median p-distance to the rest of samples.

SpecimenID	BioRegion	p-Distance		
		Median	Max	Mean
G.mar.40	DE.NDTO	0.6 %	3.5 %	1.2 %
G.mar.17	DE.MGSW	0.9 %	4.0 %	1.3 %
G.mar.58	FR.CON	0.9 %	3.8 %	1.4 %
G.mar.59	FR.CON	0.9 %	3.8 %	1.4 %
G.mar.61	FR.CON	0.9 %	3.8 %	1.4 %
G.mar.95	DE.MGSW	0.9 %	3.8 %	1.4 %
G.mar.04	DE.MGSO	1.1 %	3.8 %	1.4 %
G.mar.05	DE.MGSO	1.1 %	3.8 %	1.4 %
G.mar.06	DE.MGSO	1.1 %	3.8 %	1.4 %
G.mar.07	DE.MGSO	1.1 %	3.8 %	1.4 %
...	...	...	...	...
G.mar.85	FR.ATLN	3.2 %	4.9 %	2.8 %
G.mar.86	FR.ATLN	3.2 %	4.9 %	2.8 %
G.mar.68	FR.MED	3.3 %	4.7 %	3.4 %
G.mar.65	FR.MED	3.5 %	4.6 %	3.4 %
G.mar.66	FR.MED	3.5 %	4.6 %	3.4 %
G.mar.67	FR.MED	3.5 %	4.6 %	3.4 %
G.mar.79	FR.PYRN	3.8 %	4.9 %	3.7 %
G.mar.77	FR.PYRN	3.8 %	4.6 %	3.8 %
G.mar.76	FR.PYRN	4.0 %	5.0 %	3.9 %
G.mar.71	FR.MED	4.0 %	5.0 %	3.9 %

**Table 5.** Examples of specimen pairs with small and great ratio of p-distance (p-dist.) to geographical distance (geo-dist in km). Green marked: specimen pairs with exceptionally high p-dist. but low geo-dist. (representative for dots of upper-left side of Figure 8: green box). Light-blue marked: specimens of the same location with the highest p-dist (Figure 8: blue circle). Orange marked: specimen pair with exceptionally low p-dist. but high geo-dist. (representative for dots of lower-right side of Figure 8: red circle). Grey-blue marked: most distant specimen pair with identical haplotype (Figure 8: grey circle).

SpecimenID	SpecimenID	geo-dist	p-dist	p-dist./geo-dist.
G.mar.71 (FR.MED)	G.mar.79 (FR.PYRN)	322	4.9 %	0.000151
G.mar.77 (FR.PYRN)	G.mar.78 (FR.PYRN)	43	3.8 %	0.000883
G.mar.26 (DE.MGSW)	G.mar.93 (DE.MGSW)	9	3.0 %	0.003204
G.mar.26 (DE.MGSW)	G.mar.36 (DE.MGSW)	8	2.9 %	0.003486
G.mar.30 (DE.MGSW)	G.mar.31 (DE.MGSW)	0	1,8 %	–
...	...	...	...	...
G.mar.57 (FR.ATLN)	G.mar.74 (FR.MED)	647	0.2 %	0.000002
G.mar.01 (DE.MGSO)	G.mar.54 (FR.ALP)	820	0.2 %	0.000002
G.mar.44 (DE.NDTO)	G.mar.84 (FR.ATLN)	868	0.0 %	–
G.mar.43 (DE.NDTO)	G.mar.54 (FR.ALP)	1031	0.0 %	–
G.mar.40 (DE.NDTO)	G.mar.52 (ES.PYRS)	1610	0.6 %	0.000004



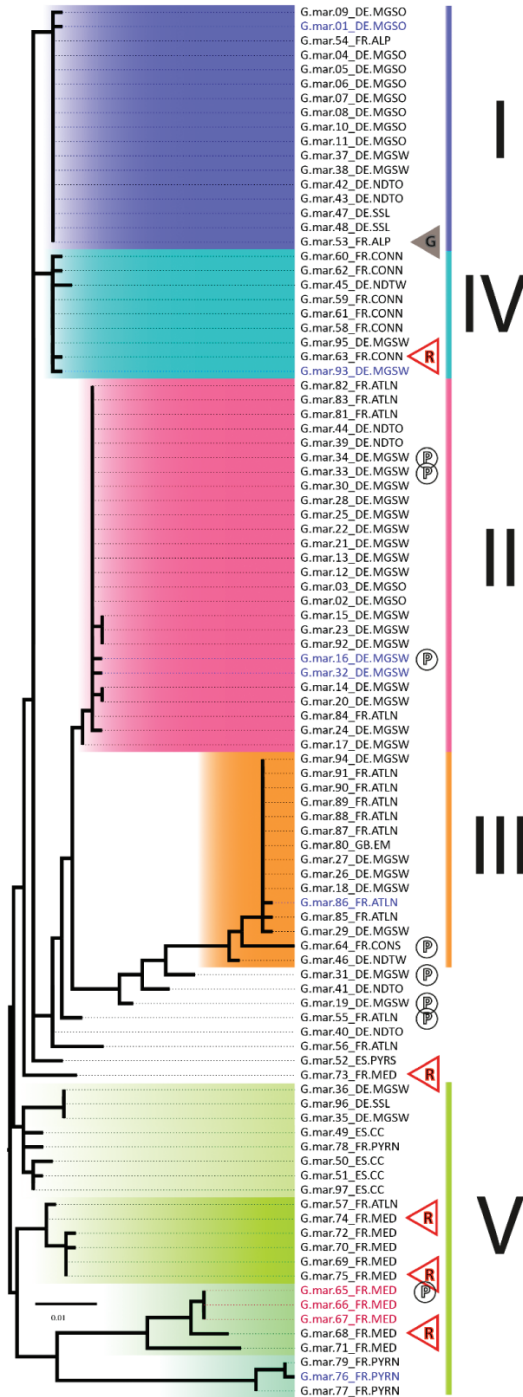
**Figure 8.** Mapped genetic p-distance to geographical distance of all analysed specimen-pairs (4,656) of *Glomeris marginata*. Solid line: linear trend line with linear function and coefficient of determination  $R^2$ . Circles: see text below and Table 5.

The dataset was divided into five major haplotype lineages (see Figure 9 and partially Table 6). The major haplotype lineage V is basal to all other and shows a higher internal genetic variability (to their member subgroups and specimens:  $\emptyset$  2.4 %) than the other haplotype lineages of *G. marginata*. Haplotype lineage V consists of several loosely connected subgroups, mainly from the French Mediterranean, the French Pyrenees and Spanish Cantabria (FR.MED, FR.PYR and ES.CC) (see Figure 9, Figure 10, black circled). This basal group is connected to the bioregion DE.MGSW via specimens 35 and 36 (Figure 8, Table 1). The area occupied by lineage V excludes all other major haplotype lineages, which do not extend to the two South French regions (FR.MED and FR.PYR), or to the more western Spanish Cantabrian Mountains (ES.CC).

The other four haplotype lineages I–IV show a wider area of distribution, but genetically less diversity. Major haplotype lineages I and IV are closely related (see Figure 9). Together this joint lineage (I+IV) covers almost the complete northern distribution range of *G. marginata* (seven bioregions: DE.MGSO, DE.MGSW, DE.NDTO, DE.NDTW, DE.SSL, FR.CONN, and FR.ALP see Table 6).

Haplotype lineage I occurs in an area reaching from the French Alps to NE Europe, with the main haplotype diversity in the German “Mittelgebirgsschwelle“, eastern part (DE.MGSO). Haplotype lineage II shows a central distribution with a high proportion of specimens in the German “Mittelgebirgsschwelle“, western part (DE.MGSW). Lineage II has the greatest distribution area and includes several subordinated haplotypes in the region DE.MGSW. Haplotype lineage III occurs in NW Europe with the most specimens in the France Atlantique, northern part (FR.ATLN). Additionally, the specimen from Great Britain (GB.EM) belongs to this group and has even





**Figure 9.** Maximum likelihood tree based on the mtDNA COI gene of 97 *Glomeris marginata*. Mid-point rooted. Roman numerals: Haplotype lineages I–V. Colour morphs of *G. marginata*: Common black = none; G = grey; R = red border; P = perplexa-markings. Scale bar = 1 % genetic ML distance.

**Table 6.** Number of samples and bioregions (BioR) to major haplotypes (mHapT) and lineages.

Number of lineages in Figure 9	Number of Samples in mHapT	Number of BioR/mHapT BioR/lineage	Covered BioR	Number of Samples/ lineages
I	15	5	DE.MGSW – DE.MGSO – DE.ND TO DE.SSL – FR.ALP	17
II	17	4	DE.MGSW – DE.MGSO – DE.ND TO FR.ATLN	26
III	10	3/5	DE.MGSW – FR.ATLN – GB.EM DE.ND TW – FR.CON S	15
IV	4	2/3	DE.MGSW – FR.CONN – DE.ND TW	9

the same haplotype as the majority specimens of this lineage. Haplotype lineage IV has a more narrow distribution range, with its main samples in France Continentale, northern part (FR.CONN). None of those four lineages are found in southern France or northern Spain (the distribution area of lineage V), but the distribution areas of the lineages I–IV overlap in DE.MGSW.

Haplotype lineages I–III and partially lineage IV are especially poor in haplotypes. Four haplotypes, one in each lineage (see Table 6), are especially rich in specimens, 17, 15, 10, and 4, respectively, together representing 47 % (46 specimens) of all analysed *G. marginata*. Additional haplotypes can be added to those four main haplotypes, differing only by a few basepairs. 65 specimens can therefore be grouped into these haplotype lineages (I–IV in Table 6 and Figure 8,  $\triangleq$  67 % of all specimens).

Every well-sampled bioregion has many haplotypes. The haplotype/specimen-rate is always higher than 0.3 (see Table 7). The less sampled a region is, the higher the haplotype/samples rate is. At the French Pyrenees and the Spanish Cantabrian Mountains, every sample of *G. marginata* represents a different haplotype. The three especially well-represented major haplotypes of lineages I–III were collected in 5, 4 or 3 different bioregions (see Table 6). These three haplotypes/lineages each cover a large geographical range, with all three overlapping centrally in the bioregion DE.MGSW, our best-sampled region.

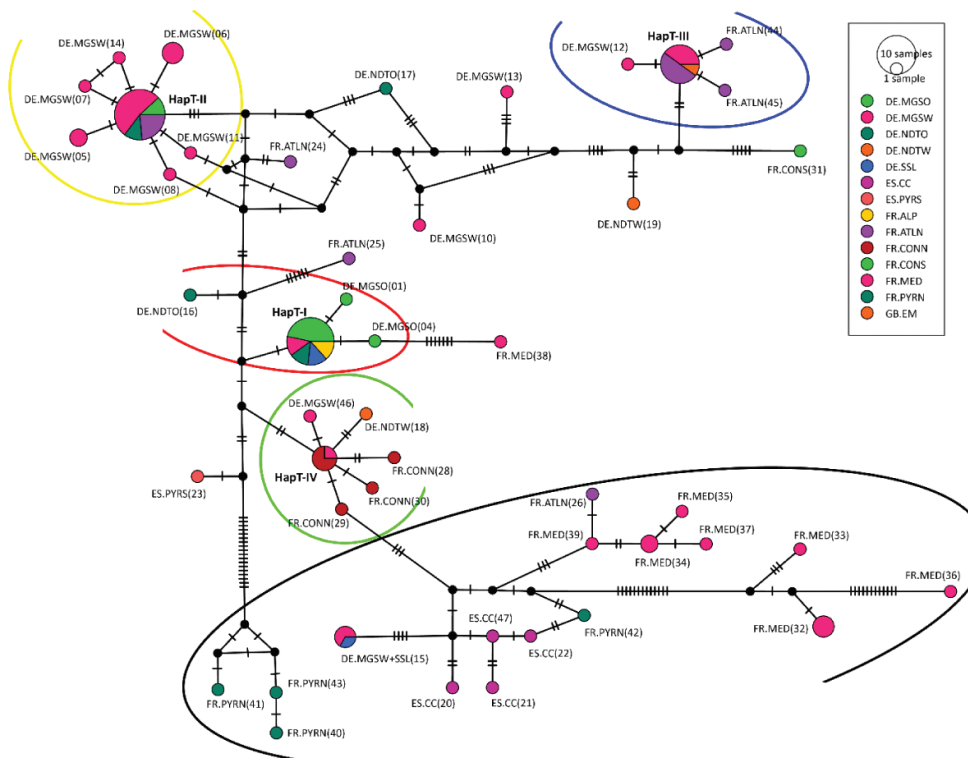
The haplotype lineage III mainly connects the northern French bioregion (FR.ATLN) with central Germany (DE.MGSW). One direct connection exists between the southern French/Spanish (FR.MED, FR.PYR and ES.CC) and the northern French populations (specimen 57, FR.ATLN, Table 1).

### Haplotype network of *G. marginata*

Based on the 47 haplotypes the TCS analysis shows a complex net of different possible evolutionary pathways between the haplotypes (see Figure 10). The clustering of the main four haplotypes (four largest filled circles in Figure 10) is similar to our phylogenetic tree

**Table 7.** Rates of haplotypes (HapT) and haplogroups (HapG) per samples in major sampled bioregions (BioR).

BioRegion	Samples in BioR	HapT in BioR	HapT/ Samples	Mean p-distance	HapG in BioR	HapG/ Samples
Total	97	47	0.5	1.9 %	8	0.1
DE.MGSW	31	15	0.5	1.4 %	4	0.1
FR.ATLN	14	7	0.5	1.9 %	2	0.1
DE.MGSO	11	4	0.4	0.4 %	2	0.2
FR.MED	11	8	0.7	2.2 %	2	0.2
DE.NDTO	6	4	0.7	0.8 %	1	0.2
FR.CONN	6	4	0.7	0.2 %	1	0.2
ES.CC	4	4	1.0	0.6 %	1	0.3
FR.PYRN	4	4	1.0	2.1 %	2	0.5
N-Europe	77	30	0.4	1.8 %	6	0.1
S-Europe	20	17	0.9	2.5 %	3	0.2



**Figure 10.** TCS-Network of haplotypes of *Glomeris marginata* with distribution region. Numbers behind region = consecutive haplotype number of DNASP-output. Haplotype accumulations: Red oval = Haplotype lineage I; Yellow oval = Haplotype lineage II; Blue oval = Haplotype lineage III; Green circle = Haplotype lineage IV; Black oval = Haplotype lineage V. Dashes on node connecting lines are representing single nucleotide mutations.

(Figure 9), with adjacent and closely related haplotypes forming distinct lineages (coloured oval lines in Figure 10). The haplotypes of the southern Mediterranean France and southern Spain are building a complex, highly disjunctive net (black oval line in Figure 10).

### Haplotype number estimation

The rarefaction curve shows no saturation for the number of haplotypes (see Figure 11, 12). The estimation of CHAO1 shows that there could be overall 404 haplotypes in *G. marginata* (95 % confidence interval: 140–1,426 haplotypes). By extrapolation with rarefaction curves (Colwell et al. 2012) we estimate that a mean of 6,612 samples would be needed to be analysed to find all potential 404 different haplotypes. To reach the 95 % lower boundary (140 haplotypes) at least an additional 274 specimens need to be included.

### Colour morphs of *G. marginata*

The dataset contains one specimen of the grey colour morph, eight with the “perplexa” pattern and four with red margins. Those 13 distinctly coloured specimens are marked in our specimen tree (see Figure 9 with symbols “G”, “P”, and “R”). The grey specimen belongs to the major haplotype of the lineage I. The specimens with the red margin are scattered in the tree and therefore do not cluster together. They are mainly found in Mediterranean France, therefore placed mainly in the lumping group V, but one specimen groups with lineage IV (Figure 9). The “perplexa” form is even more scattered over the tree, occurring in several bioregions.

## Discussion

### *Glomeris annulata*, *G. apuana*, and *G. maerens*

The three local endemic species, despite some similarities in the coloration (Figures 2D–G), are genetically clearly distinct from *G. marginata*, separated by p-distances of more than 13 %.

Further studies should investigate the *G. maerens*-group in northern Spain. All three species (*G. maerens*, *G. lugubris* Attems, 1927, and *G. obsoleta* Attems, 1952) of the group were described by Attems from Spain (*G. maerens*: Tarragona and Lérida; *G. lugubris*: Cádiz; *G. obsoleta*: Barcelona) and show a similar obscure black-brown colouration (see examples in Figure 2E–G). Due to their geographically close type locations and quite similar colour, as well as thoracic shield striation pattern (both with two main striae) *G. maerens* and *G. obsoleta* may be synonyms. Therefore, the examined specimens could not be assigned to either species. However, our analysis recovers a considerable variation inside the species-group, with p-distances of 7.5–9.1 % which hints at the existence of several independent species in the *G. maerens* complex.

## Monophyly of *G. marginata*

*Glomeris marginata* is genetically distant but related to *G. connexa*, with a p-distance of 12.9 %. Based on the COI-data, the *G. maerens* species group is more closely related to *G. connexa*/*G. apuana* than to *G. marginata*. The genetic distance of *G. marginata* to the other tested species (*G. klugii/undulata*, *G. intermedia*, *G. hexasticha*, and *G. annulata*) is, with a p-distance up to 15.9 %, even more pronounced.

In comparison to vertebrate species (e.g., fishes: 0.32 %, Keskin and Atar 2013 or rodents: 2.1 %, Li et al. 2015) a maximum intraspecific variation of a p-distance of 5 % is rather high. However, such an intraspecific variation of 5 % was also found in another widespread central European *Glomeris*, *G. klugii/undulata* (Wesener and Conrad 2016). A minimum p-distance of 12.9 % of *G. marginata* to the most closely related species (a factor of 2.6 to the maximum intraspecific p-distance), shows a clear barcoding gap to the nearest congener, *G. connexa*.

The known colour morphs of *G. marginata* do not represent single lineages or even subspecies. The conspicuously red borders in specimens from southern France (Figures 1D, E) are present in several lineages and sub-lineages (Figure 9, marked with R). The same applies to the perplexa-form (Figures 1A, B, 9, marked with P). The grey form is even a member of the main haplotype of the eastern lineage I (Figure 9, marked with G). Unfortunately, specimens of the brown form of northern Germany could not yet be sequenced, but they appear always syntopically with specimens of the black form (Figure 2A). Therefore, any relevant divergence from those haplotypes cannot be expected.

The COI-gene is clearly working as a barcoding gene to identify and discriminate *G. marginata* specimens from the other *Glomeris* species.

## Geographical relationship of *G. marginata* specimens

Syntopical specimens as well as specimens with a maximum geographical distance of 1,701 km (Germany, Brandenburg to Spain, La Rioja) were analysed. There is no obvious relationship between geographical and genetic distance. There are specimen pairs of the same haplotype (p-distance = 0) which were collected more than 1,000 km apart. This distance of 1,000 km seems to be the maximum distance *G. marginata* could spread without experiencing genetic changes. Specimen pairs with a geographical distance larger than 1,000 km experienced at least a few mutations in the COI gene, with a minimum p-distance of  $\approx 0.8$  % in our dataset (see Figure 7).

On the other hand, local specimens can show high genetic variation. Even from nearby locations specimen pairs show a p-distance as high as 3 %. Such a mutation rate is unlikely to have happened locally, but is more likely the result of a different geographical origin of the source populations. As such large genetic distances between different populations of *G. marginata* are common, a human-influenced dispersal seems not to be the reason behind the regular high COI-variance.



## Haplotype regions, origin and potential migration patterns

The haplotype analysis shows five main haplotype lineages in *G. marginata* (Figure 9). Four of those (I–IV) show a wide distribution in northern Europe, one (lineage V) is restricted to southern Europe.

The haplotype lineage V is highly genetically variable, therefore a combination into a single group is not justified. Four rather distinct lineages not forming a monophylum could be seen in Figure 9 (coloured in different shades of green). Additionally, a block with unrelated singular haplotypes (see Figure 9 between lineage III and V) could be assigned to this fifth major haplotype lineage. Most of the specimens of these unrelated singular haplotypes are coming from the Mediterranean. These unrelated haplotypes are linked to the region DE.MGSW (specimens 19 and 31; Figure 8).

The examined northern European regions are mainly inhabited by specimens of the haplotype lineages I–IV, showing a low variance in their p-distance to one another (see Table 7). The specimen pairs within the whole North European area have a mean p-distance of 1.8 %. In contrast the French Mediterranean and French Pyrenees specimens of *G. marginata* show a higher p-distance (FR.MED: 2.2 % and FR.PYRN: 2.1 %). The specimen pairs of *G. marginata* within the geographically smaller South European bioregions (FR.MED, FR.PYRN, ES.PYRS, and ES.CC) have a mean p-distance of 2.5 %, higher than those observed in the entire North of Europe (1.8 %). With further sampling in southern Europe and collecting of similar haplotypes those values might decrease, however, further sampling will also reveal new haplotypes (see Figure 11). A saturation of the number of haplotypes is not detectable (see Figures 11, 12).

With the before mentioned mean p-distance of 2.5 %, the small south European area of bioregions contains a much higher genetic diversity in *G. marginata* than the much larger northern Europe. To develop such a higher genetic diversity, the south European populations of *G. marginata* must be older than the northern European populations. Northern Europe must have been colonized by *G. marginata* more recently. The main dispersal into those northern areas could only have been started after the last glaciation retreated during the early Holocene starting around 11,000 years ago (Roberts 2014).

Our data does not reveal how far north the distribution of *G. marginata* reached and how high any genetic diversity of the species was before the ice age. However, the south European mixed populations could be regarded as a remnant of old haplotype lineages of *G. marginata*, which are not any more present in the north European populations.

The geographical coverage of our analysed specimens is biased towards western Germany (MGSW, see Figure 3). For the colonization of northern Europe there are two possible scenarios. The new dispersal could have started from the south, or the dispersal could have started from a glacial refugium in northern Europe. The two scenarios are, however, not mutually exclusive and could have been concurrent. From a genetic point of view the northern populations differ from the southern populations. There are only a few and weak links between north and south. Therefore, a single or main colonization from the south to the north is not plausible.

Contrarily, all main haplotype lineages I–IV, which are exclusively found in northern Europe are linked to the bioregion DE.MGSW (Figure 3). The main redistribution over northern Europe could have been started from central Germany, which shows high haplotype diversity in *G. marginata*. From the bioregion DE.MGSW four major migrations could have led to the current distribution of the main haplotype lineages I–IV. Haplotype lineage I might have spread mainly to the north-east, haplotype lineage III to the North-West and haplotype lineage II only westwards. Haplotype-lineage IV spread to the bioregion FR.CONN. The colonisations by the haplotype lineages were probably independent.

### Haplotype number estimation

With this work, for the first time, a survey of almost 100 barcodes is presented for a diplopod species. On average, every haplotype in our study is based on two specimens (97 specimens / 47 haplotypes). In reality, the majority of haplotypes (38 haplotypes  $\pm$  81 %) are represented by only one specimen. The haplotype number estimation has shown that these 97 successfully sequenced specimens are just providing an overview of the real haplotype diversity in *G. marginata*. With the current data we are still far away from a complete collection of all haplotypes of the species. Many more specimens need to be collected to reach at least the lower estimated boundary of 140 haplotypes.

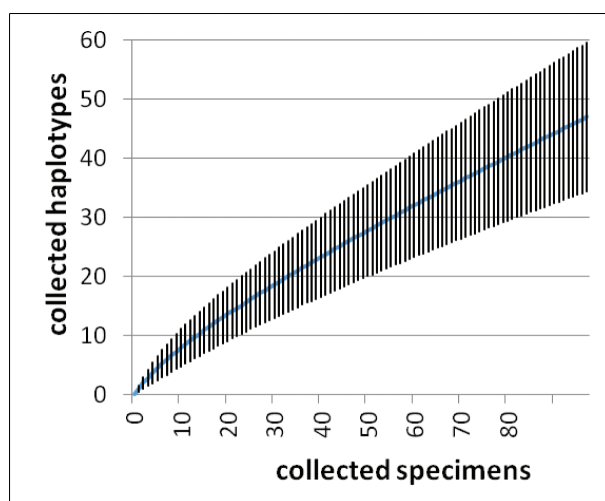
In general, this also means that haplotype analysis should not be based on few specimens and not only on specimens of a certain region, but always from specimens covering the whole distribution area of a species (Elias et al. 2007, Bergsten et al. 2012, Jordal and Kambestad 2014). With the current data we should have a good base to cover the whole range of haplotypes. Further new haplotypes should mainly cluster within the current main lineages I to IV or should end up within the haplotype complex V with its four subgroups.

Many new haplotypes would simply represent the missing mutation steps present in the TCS-network of Figure 10 by dashes between the nodes. Probably most of the haplotypes representing end nodes in the current TCS-network are not representing the real end nodes of the mutation chains.

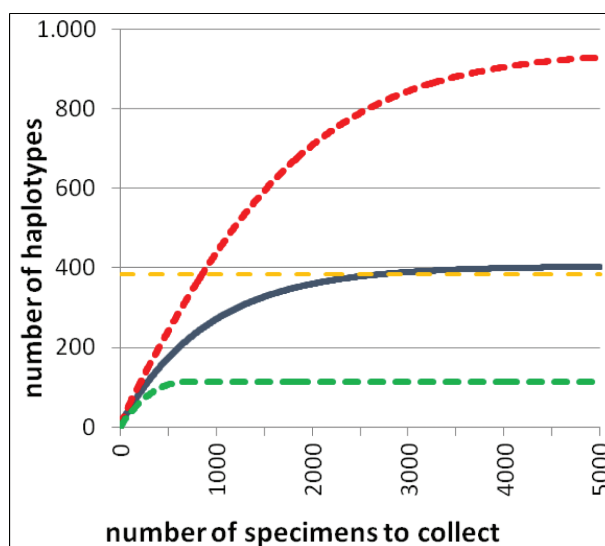
### Nomenclatorial acts

In the year 1789 the species with the common name Cloporte bordé (bordered woodlouse) was first described by the French naturalist Charles Joseph de Villers (1724–1810) as *Oniscus marginatus*. He used few, but descriptive words: “niger, segmentis corporis luteo marginatis” [black, segments of the body with yellow margin].

Within a few years the species has been named and described four times again (see below). Thirteen years after the description the French zoologist Pierre André Latreille (1762–1833) placed the species in his new genus *Glomeris* Latreille, 1802.



**Figure 11.** Individual based rarefaction curve calculated with ESTIMATES and with 10,000 replicates (simulated collections) of the COI sequences of *Glomeris marginata*. Vertical lines indicating 95% lower and upper boundary.



**Figure 12.** Extrapolation of rarefaction curves with ESTIMATES of the COI sequences of *Glomeris marginata*. Blue line = estimation with premise of mean number (404 haplotypes); Horizontal yellow line = 95% satisfaction of mean number (384 haplotypes); Green and red line = curve at the 95% upper and lower boundary.

Almost one hundred years later several subspecies or variations were added by Verhoeff, Latzel, and Attems. Those taxa represent different versions of the pale form which was first named *G. perplexa* by Latzel (1895), all now regarded as synonyms of the nominate species.

We do not recognize any subspecies of *G. marginata*. Therefore the subspecies *Glomeris marginata ponentina* Verhoeff, 1911 and *Glomeris marginata leridana* Attems, 1927 are synonymised under the nominal species.

Only initial new naming acts are listed. Due to the numerous mentions of *G. marginata* in the literature, a comprehensive list of all citations is not provided.

### ***Glomeris marginata* (Villers, 1789)**

*Oniscus marginatus* Villers, 1789: 187 (first description, type locality “Gallia australiori” – south France)

*Glomeris marginata* – Latreille, 1802: 66 (placing the taxon in the genus *Glomeris*)

### **Synonyms**

*Julus limbatus* Olivier, 1792: 414 = *Glomeris limbatus* (Latreille, 1802: 66)

*Armadillo marginalis* Culver, 1792: 30, fig. 23–25, new synonym

*Oniscus zonatus* Panzer, 1793: Heft 9, chapter 25

*Julus oniscoides* Steward, 1802, chapter V: 307

*Glomeris marginata* var. *lucida* Latzel, 1890: 365 and 367

*Glomeris perplexa* Latzel, 1895: 7 and 11, new synonym

*Glomeris connexa perplexa* Verhoeff, 1906: 152

*Glomeris connexa perplexa* aberr. *rhenanorum* Verhoeff, 1906: 152 and 153

*Glomeris connexa perplexa* var. *rhenana* Verhoeff, 1906: 152

*Glomeris marginata* aut. *genuina* Verhoeff, 1911: 121

*Glomeris marginata* var. *marginata* Verhoeff, 1911: 121

*Glomeris marginata* var. *perplexa* Verhoeff, 1911: 121

*Glomeris marginata ponentina* Verhoeff, 1911: 122, new synonym

*Glomeris marginata leridana* Attems, 1927: 250, new synonym

The description of *Oniscus variegatus* Villers, 1789: 188, fig. 16 (“niger, segmentis corporis nigris, albo marginatis ...” - black, the segments of the body black, white framed) also perfectly fits *G. marginata* and therefore could potentially be treated as a junior synonym of it. However, with the case 2909 of the International Commission on Zoological Nomenclature it was already treated as a senior synonym of *Armadillidium vulgare* Latreille, 1804 and placed on the Official Index of Rejected and Invalid Species Names in Zoology (Lehtinen and Holthuis 1995, ICZN 1998).

### **Analysis software used in this study**

BIOEDIT 7.2.5: <http://www.mbio.ncsu.edu/bioedit/bioedit.html>

DNASP 5.10.1: <http://www.ub.edu/dnasp>

ESTIMATES 9.1.0:	<a href="http://viceroy.eeb.uconn.edu/estimates">http://viceroy.eeb.uconn.edu/estimates</a>
FIGTREE 1.4.2:	<a href="http://tree.bio.ed.ac.uk/software/figtree">http://tree.bio.ed.ac.uk/software/figtree</a>
GLOBALMAPPER 17:	<a href="http://www.bluemarblegeo.com/products/global-mapper.php">http://www.bluemarblegeo.com/products/global-mapper.php</a>
MEGA 7.14 GUI:	<a href="http://www.megasoftware.net">http://www.megasoftware.net</a>
MICROSOFT EXCEL 2013:	<a href="http://www.microsoftstore.com">http://www.microsoftstore.com</a>
POPART 1.7:	<a href="http://popart.otago.ac.nz">http://popart.otago.ac.nz</a>

## Acknowledgements

B. Rulik, J. Thormann, and L. von der Mark from the GBOL-Team in Bonn who photographed, extracted and sequenced the *G. marginata* ZFMK specimens; their invaluable help is greatly appreciated. M. Geiger assisted with the upload of the sequence data to GenBank. Specimens of the outgroup taxa were thankfully prepared and sequenced by Claudia Etzbauer (ZFMK). Specimens were thankfully provided by Peter Kautt, Axel Schönhofer, Helen Read, and Robin Duborget. We thank Michaël Aubert of the University of Rouen for providing us the sequences and data of specimens from France, Haut Normandie (via BOLD).

We also thank Jörg Spelda (Munich) and Hans Pohl (Jena) for discussions on the earlier version of the manuscript, Henrik Enghoff (Copenhagen) and an anonymous reviewer provided numerous comments that greatly enhanced the quality of the here presented work. We are indebted to Steve Gregory (Oxford) for improving our English. This is a publication of the German Barcode of Life (GBOL) project of the Humboldt Ring, financed by the German Federal Ministry for Education and Research (FKZ 01LI1101A and FKZ 01LI1101B).

## References

- Aho K, Derryberry D, Peterson T (2014) Model selection for ecologists: the worldviews of AIC and BIC. *Ecology* 95: 631–636. <https://doi.org/10.1890/13-1452.1>
- Ansenne A, Compère P, Goffinet G (1990) Ultrastructural organization and chemical composition of the mineralized cuticle of *Glomeris marginata* (Myriapoda, Diplopoda). In Minelli A (Ed.) *Proceedings of the 7<sup>th</sup> International Congress of Myriapodology*. Brill, Leiden, 125–134.
- Attems C (1927) Myriopoden aus den nördlichen und östlichen Spanien, gesammelt von Dr. F. Haas in den Jahren 1914–1919. Nebst Beiträgen zur Kenntnis der Lithobiiden, Glomeriden sowie der Gattungen *Brachydesmus* und *Archiulus*. *Abhandlungen der Senckenbergischen naturforschenden Gesellschaft* 39(3): 233–289.
- Attems C (1952) Myriopoden der Forschungsreise Dr. H. Franz in Spanien 1951 nebst Übersicht über die gesamte iberische Myriopodenfauna. *EOS, Revista Espanola de Entomologia* 28(4): 323–366.
- Bergsten J, Bilton DT, Fujisawa T et al. (2012) The effect of geographical scale of sampling on DNA barcoding. *Systematic Biology* 61: 851–869. <https://doi.org/10.1093/sysbio/sys037>



- Candia Carnevali MD, Valvassori R (1982) Active supercontraction in rolling-up muscles of *Glomeris marginata* (Myriapoda, Diplopoda). *Journal of Morphology* 172(1): 75–82. <https://doi.org/10.1002/jmor.1051720107>
- Carrel JE (1984) Defensive secretion of the pill millipede *Glomeris* [*Glomeris*] *marginata*. 1. Fluid production and storage. *Journal of Chemical Ecology* 10(1): 41–51. <https://doi.org/10.1007/BF00987642>
- Chao A (1984) Nonparametric Estimation of the Number of Classes in a Population. *Scandinavian Journal of Statistics* 11(4): 265–270.
- Clement M, Snell Q, Walker P, Posada D, Crandall K (2002) TCS: Estimating gene genealogies. *Parallel and Distributed Processing Symposium, International Proceedings* 2: 184. <https://doi.org/10.1109/IPDPS.2002.1016585>
- Colwell RK (2013) EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. <http://purl.oclc.org/estimates>
- Colwell RK, Chao A, Gotelli NJ, Lin SY, Mao CX, Chazdon RL, Longino JT (2012) Models and estimators linking individual-based and sample-based rarefaction, extrapolation, and comparison of assemblages. *Journal of Plant Ecology* 5: 3–21. <https://doi.org/10.1093/jpe/rtr044>
- Compère PS, Defise S, Goffinet G (1996) Cytochemistry of the tergite epicuticle of *Glomeris marginata* (Villers) (Myriapoda, Diplopoda): preliminary experimental results. *Mémoires du Muséum national d'Histoire naturelle* 169: 395–401.
- Cuvier G (1792) Mémoire sur les cloportes terrestres. *Journal d'Histoire naturelle (Paris)* 2(13): 18–31.
- David JF, Gillon D (2002) Annual feeding rate of the millipede *Glomeris marginata* on holm oak (*Quercus ilex*) leaf litter under Mediterranean conditions. *Pedobiologia* 46(1): 42–52. <https://doi.org/10.1078/0031-4056-00112>
- Dohle W (1964) Die Embryonalentwicklung von *Glomeris marginata* (Villers) im Vergleich zur Entwicklung anderer Diplopoden. *Zoologische Jahrbücher / Abteilung für Anatomie und Ontogenie der Tiere* 81: 241–310.
- Dove H, Stollewerk A (2003) Comparative analysis of neurogenesis in the myriapod *Glomeris marginata* (Diplopoda) suggests more similarities to chelicerates than to insects. *Development* 130: 2161–2171. <https://doi.org/10.1242/dev.00442>
- Dunger W, Steinmetzger K (1981) Ökologische Untersuchungen an Diplopoden einer Rasen-Wald-Catena im Thüringer Kalkgebiet. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere* 108(4): 519–553.
- Elias M, Hill RI, Willmott KR et al. (2007) Limited performance of DNA barcoding in a diverse community of tropical butterflies. *Proceedings of the Royal Society B: Biological Sciences* 274: 2881–2889. <https://doi.org/10.1098/rspb.2007.1035>
- Engelhoff H, Dohle W, Blower JG (1993) Anamorphosis in millipedes (Diplopoda) - the present state of knowledge with some developmental and phylogenetic considerations. *Zoological Journal of the Linnean Society* 109: 103–234. <https://doi.org/10.1111/j.1096-3642.1993.tb00305.x>
- Fusco G, Minelli A (2013) Arthropod Segmentation and Tagmosis. In: Minelli A (Ed.) *Arthropod Biology and Evolution*, 91–122. [https://doi.org/10.1007/978-3-662-45798-6\\_9](https://doi.org/10.1007/978-3-662-45798-6_9)
- Gotelli NJ, Colwell RK (2010) Estimating species richness. In: *Biological Diversity: Frontiers In: Magurran AE, McGill BJ (Eds) Measurement and Assessment*. Oxford University Press, Oxford, 39–54.

- Haacker U (1964) Das Paarungsverhalten des Saftkuglers *Glomeris marginata*. Natur und Museum 94: 265–272.
- Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series 41: 95–98.
- Hilken G (1998) Vergleich von Tracheensystemen unter phylogenetischem Aspekt. Verhandlungen des naturwissenschaftlichen Vereins Hamburg (N.F.) 37: 5–94.
- Hilken G, Sombke A, Müller CHG, Rosenberg J (2015) Diplopoda - tracheal system. In: Minelli A (Ed.) Treatise on zoology - anatomy, taxonomy, biology. The Myriapoda 2(6): 129–152. [https://doi.org/10.1163/9789004188273\\_007](https://doi.org/10.1163/9789004188273_007)
- Hoess R (2000) Bestimmungsschlüssel für die *Glomeris*-Arten Mitteleuropas und angrenzender Gebiete (Diplopoda: Glomeridae). Jahrbuch des Naturhistorischen Museums Bern 13: 3–20.
- International Commission on Zoological Nomenclature (1998) *Glomeris* Latreille, 1802 (Diplopoda), *Armadillo* Latreille, 1802, *Armadillidium* Brandt in Brandt and Ratzeburg, (1831) and *Armadillo vulgaris* Latreille, 1804 (currently *Armadillidium vulgare*) (Crustacea, Isopoda): Generic and specific names conserved. Bulletin of Zoological Nomenclature 55(2): 124–12.
- Janssen R (2004) Untersuchungen zur molekularen Grundlage der Segmentbildung im Saftkugler *Glomeris marginata* (Myriapoda: Diplopoda). Inaugural-Dissertation zur Erlangung des Doktorgrades an der Mathematisch-Naturwissenschaftlichen Fakultät der Universität zu Köln, 313 pp.
- Janssen R, Prpic NM, Damen WGM (2006) Dorso-ventral differences in gene expression in *Glomeris marginata* (Villers, 1789) (Myriapoda: Diplopoda). Norwegian Journal of Entomology 53(2): 129–137.
- Janssen R, Damen WGM (2006) The ten Hox genes of the millipede *Glomeris marginata*. Development, Genes and Evolution 216(7–8): 451–465. <https://doi.org/10.1007/s00427-006-0092-5>
- Janssen R (2011) An abnormally developed embryo of the pill millipede *Glomeris marginata* that lacks dorsal segmental derivatives. Development, Genes and Evolution 221: 351–355. <https://doi.org/10.1007/s00427-011-0377-1>
- Janssen R (2013) Developmental abnormalities in *Glomeris marginata* (Villers 1789) (Myriapoda: Diplopoda): implications for body axis determination in a myriapod. Naturwissenschaften 100: 33–43. <https://doi.org/10.1007/s00114-012-0989-y>
- Janssen R, Posnien N (2014) Identification and embryonic expression of Wnt2, Wnt4, Wnt5 and Wnt9 in the millipede *Glomeris marginata* (Myriapoda: Diplopoda). Gene Expression Patterns 14: 55–61. <https://doi.org/10.1016/j.gep.2013.12.003>
- Johnson IT, Riegel JA (1977a) Ultrastructural studies on the Malpighian tubule of the pill millipede, *Glomeris marginata* (Villers). Cell and Tissue Research 180(3): 357–366. <https://doi.org/10.1007/BF00227601>
- Johnson IT, Riegel JA (1977b) Ultrastructural tracer studies on the permeability of the Malpighian tubule of the pill millipede, *Glomeris marginata* (Villers). Cell and Tissue Research 182(4): 549–56. <https://doi.org/10.1007/BF00219837>
- Jordan HB, Kambestadt M (2014) DNA barcoding of bark and ambrosia beetles reveals excessive NUMTs and consistent east-west divergence across Palearctic forests. Molecular Ecology Resources 14: 7–17. <https://doi.org/10.1111/1755-0998.12150>
- Juberthie-Jupeau L (1967) Les oothèques de quelques Diplopodes Glomeridia. Revue d'Ecologie et de Biologie du Sol 4: 131–142.

- Juberthie-Jupeau L (1978) Fine structure of postgonopodial glands of a myriapod *Glomeris marginata* (Villers). Tissue and Cell 8(2): 293–304. [https://doi.org/10.1016/0040-8166\(76\)90053-7](https://doi.org/10.1016/0040-8166(76)90053-7)
- Lehtinen PT, Holthuis LB (1995) *Glomeris* Latreille, 1802 (Diplopoda): Proposed conservation; *Armadillo vulgaris* Latreille, 1804 (Crustacea, Isopoda): Proposed conservation of the specific name; and *Armadillo* Latreille, 1802 (Crustacea, Isopoda): Application for a ruling on its status. Bulletin of Zoological Nomenclature 52(3): 236–243. <https://doi.org/10.5962/bhl.part.6782>
- Librado P, Rozas J (2009) DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. Bioinformatics 25: 1451–1452. <https://doi.org/10.1093/bioinformatics/btp187>
- Keskin E, Atar HH (2013) DNA barcoding commercially important fish species of Turkey. Molecular Ecology Resources 13: 788–797. <https://doi.org/10.1111/1755-0998.12120>
- Kime RD, Enghoff H (2011) Atlas of European Millipedes (Class Diplopoda), Vol. 1 - Orders Polyxenida, Glomerida, Platydesmida, Siphonocryptida, Polyzoniida, Callipodida, Polydesmida. Series: Fauna Europaea Evertabrata #3, Pensoft Publishers, 282 pp.
- Koch M (2015) Diplopoda - general morphology. In: Minelli A (Ed.) Treatise on zoology - anatomy, taxonomy, biology. The Myriapoda 2(2): 7–68. [https://doi.org/10.1163/9789004188273\\_003](https://doi.org/10.1163/9789004188273_003)
- Kumar S, Stecher G, Tamura K (2015) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33(7): 1870–1874. <https://doi.org/10.1093/molbev/msw054>
- Latzel R (1890) Description d'une variété nouvelle du *Glomeris marginata* Villers. In: Gadeau de Kerville H (1890) Deuxième addenda à la faune des myriopodes de la Normandie. Bulletin de la Société des Amis des Sciences naturelles de Rouen 1889(1): 363–367.
- Latzel R (1895) Die Myriopoden aus der Umgebung Hamburgs. Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten, Beiheft 12: 99–109.
- Latreille PA (1802) Histoire naturelle, générale et particulière des Crustacés et des Insectes. 3 + 7. (= Tom 95 + 99), Dufart, Paris, 467 pp.
- Li J, Zheng X, Cai Y, Zhang X, Yang M, Yue B, Li J (2015) DNA barcoding of Murinae (Rodentia: Muridae) and Arvicolinae (Rodentia: Cricetidae) distributed in China. Molecular Ecology Resources 15: 153–167. <https://doi.org/10.1111/1755-0998.12279>
- Martin JS, Kirkham JB (1989) Dynamic role of microvilli in peritrophic membrane formation. Tissue and Cell 21: 627–638. [https://doi.org/10.1016/0040-8166\(89\)90013-X](https://doi.org/10.1016/0040-8166(89)90013-X)
- Meynen E, Schmithüsen J (1953–1962) Handbuch der naturräumlichen Gliederung Deutschlands. Bundesanstalt für Landeskunde, Remagen/Bad Godesberg. 9 issues in 8 books, actualized map 1:1.000.000 (1960).
- Meinwald YC, Meinwald J, Eisner T (1966) 1,2-Dialkyl-4 (3H)-quinzolinones in the defensive secretion of a millipede (*Glomeris marginata*). Science (Washington DC) 154(3747): 390–391. <https://doi.org/10.1126/science.154.3747.390>
- Minelli A, Fusco G (2013) Arthropod Post-embryonic Development. In: Minelli (Ed) Arthropod Biology and Evolution, 91–122. [https://doi.org/10.1007/978-3-662-45798-6\\_5](https://doi.org/10.1007/978-3-662-45798-6_5)
- Minelli A (2015) Diplopoda - development. In: Minelli A (Ed) Treatise on zoology - anatomy, taxonomy, biology. The Myriapoda 2(1): 267–302. [https://doi.org/10.1163/9789004188273\\_012](https://doi.org/10.1163/9789004188273_012)

- Müller CHG, Sombke A (2015) Diplopoda - sense organs. In: Minelli A (Ed.) Treatise on zoology - anatomy, taxonomy, biology. The Myriapoda 2(9): 181–236.
- Nicholson PB, Bocock KL, Heal OW (1966) Studies on the decomposition of the faecal pellets of a millipede [*Glomeris marginata* (Villers)]. *Journal of Ecology* 54: 755–766. <https://doi.org/10.2307/2257815>
- Olivier AG (1792) Encyclopédie méthodique. Dictionnaire des Insectes, vol. 7. Paris, 827 pp.
- Panzer W (1793–1813) *Faunae Insectorum Germaniae initia*. Nürnberg, Vol. 2, issue 9.
- Prpic NM, Tautz D (2003) The expression of the proximodistal axis patterning genes *Distal-less* and *dachshund* in the appendages of *Glomeris marginata* (Myriapoda: Diplopoda) suggests a special role of these genes in patterning the head appendages. *Developmental Biology* 260: 97–112. [https://doi.org/10.1016/S0012-1606\(03\)00217-3](https://doi.org/10.1016/S0012-1606(03)00217-3)
- Prpic NM (2004) Homologs of wingless and decapentaplegic display a complex and dynamic expression profile during appendage development in the millipede *Glomeris marginata* (Myriapoda: Diplopoda). *Frontiers in Zoology* 1(6): 1–12.
- Prpic NM (2005) Duplicated Pax6 genes in *Glomeris marginata* (Myriapoda: Diplopoda), an arthropod with simple lateral eyes. *Zoology (Jena)* 108(1): 47–53. <https://doi.org/10.1016/j.zool.2004.11.003>
- Prpic NM, Janssen R, Damen WGM, Tautz D (2005) Evolution of dorsal-ventral axis formation in arthropod appendages: H15 and optomotor-blind/bifid-type T-box genes in the millipede *Glomeris marginata* (Myriapoda: Diplopoda). *Evolution and Development* 7(1): 51–57. <https://doi.org/10.1111/j.1525-142X.2005.05006.x>
- Rawlins AJ, Bull ID, Poirier N, Ineson P, Evershed RP (2006) The biochemical transformation of oak (*Quercus robur*) leaf litter consumed by the pill millipede (*Glomeris marginata*). *Soil Biology & Biochemistry* 38: 1063–1076. <https://doi.org/10.1016/j.soilbio.2005.09.005>
- Regier JC, Shultz JW (2001) A phylogenetic analysis of Myriapoda (Arthropoda) using two nuclear protein-encoding genes. *Zoological Journal of the Linnean Society* 132(4): 469–486. <https://doi.org/10.1111/j.1096-3642.2001.tb02471.x>
- Regier JC, Wilson HM, Shultz JW (2005) Phylogenetic analysis of Myriapoda using three nuclear protein-coding genes. *Molecular phylogenetics and evolution* 34(1): 147–158. <https://doi.org/10.1016/j.ympev.2004.09.005>
- Reip HS, Spelda J, Voigtländer K, Decker P, Lindner EN (2016) Rote Liste und Gesamtartenliste der Doppelfüßer (Myriapoda: Diplopoda) Deutschlands. In: Gruttke H, Binot-Hafke M, Balzer S, Haupt H, Hofbauer N, Ludwig G, Matzke-Hajek G, Ries M (Eds) *Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands, Band 4: Wirbellose Tiere (Teil 2)*. Landwirtschaftsverlag, Münster. *Naturschutz und Biologische Vielfalt* 70(4): 301–324.
- Roberts N (2014) *The Holocene: An Environmental History*, Wiley-Blackwell, Hoboken, 376 pp.
- Sahli F (1966) Contribution à l'étude de la périodomorphose et du système neurosécréteur des Diplopodes Iulides. Thèse Doctoral Sciences, Université de Bourgogne, Dijon 94, 226 pp.
- Seifert G (1966) Das stomatogastrische Nervensystem der Diplopoden. *Zoologische Jahrbücher / Abteilung für Anatomie und Ontogenie der Tiere* 83: 449–492.

- Schildknecht H, Wenneis WF, Weis KH, Maschwitz U (1966) Glomerin, ein neues Arthropoden-Alkaloid. Zeitschrift für Naturforschung 21 B(2): 121–127. <https://doi.org/10.1515/znb-1966-0206>
- Schildknecht H, Maschwitz U, Wenneis WF (1967) Über Arthropoden-Abwehrstoffe XXIV. Neue Stoffe aus dem Wehrsekret der Diplopodengattung *Glomeris*. Naturwissenschaften 54: 196–197. <https://doi.org/10.1007/BF00594514>
- Schildknecht H, Wenneis WF (1967) Über Arthropoden-Abwehrstoffe XX. Strukturaufklärung des Glomerins. Zeitschrift für Naturforschung C 21: 552–556.
- Schlüter U (1980) Die Feinstruktur der Pylorusdrüsen von *Polydesmus angustus* Latzel und *Glomeris marginata* Villers (Diplopoda). Zoomorphology 94: 307–319. <https://doi.org/10.1007/BF00998207>
- Schubart O (1934) Tausendfüßler oder Myriapoda. I: Diplopoda. In: Dahl F (Ed.) Die Tierwelt Deutschlands und der angrenzenden Meeresteile, vol. 28, 318 pp.
- Spelda J, Reip HS, Oliveira-Biener U, Melzer RR (2011) Barcoding Fauna Bavarica: Myriapoda - a contribution to DNA sequence-based identifications of centipedes and millipedes (Chilopoda, Diplopoda). ZooKeys 156: 123–139. <https://doi.org/10.3897/zookeys.156.2176>
- Charles S (1802) Elements of Natural History. Volume II, London, 491 pp.
- Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0. Molecular Biology and Evolution 30: 2725–2729. <https://doi.org/10.1093/molbev/mst197>
- Tavaré S (1986) Some Probabilistic and Statistical Problems in the Analysis of DNA Sequences. Lectures on Mathematics in the Life Sciences (American Mathematical Society) 17: 57–86.
- Van der Drift J (1975) The significance of the millipede *Glomeris marginata* (Villers) for oaklitter decomposition and an approach of its part in energy flow. In: Vanek J (Ed.) Progress in soil zoology. Junk, The Hague, 293–298. [https://doi.org/10.1007/978-94-010-1933-0\\_32](https://doi.org/10.1007/978-94-010-1933-0_32)
- Verhoeff KW (1895) Ein Beitrag zur Kenntnis der Glomeriden. Verhandlungen des naturhistorischen Vereins der Preußischen Rheinlande, Westfalens und des Regierungsbezirks Osnabrück 52: 221–234.
- Verhoeff KW (1906) Über Diplopoden. 4. (24.) Aufsatz: Zur Kenntnis der Glomeriden (zugleich Vorläufer einer *Glomeris*-Monographie) (Beiträge zur Systematik, Geographie, Entwicklung, vergleichenden Morphologie und Biologie). Archiv für Naturgeschichte 72(1): 107–226.
- Verhoeff KW (1911) Ueber Diplopoden. 20. (40.) Aufsatz: Neuer Beitrag zur Kenntnis der Gattung *Glomeris*. Jahreshfte des Vereins für vaterländische Naturkunde in Württemberg 67: 78–147.
- Villers CJ de (1789) Caroli Linnaei Entomologia, faunae Suecicae descriptionibus aucta Scopoli, Geoffroy, de Geer, Fabricii, Schrank. Volume 4, Aptera. Lugduni, 556 pp.
- Voigtländer K (2011) Preferences of common Central European millipedes for different biotope types (Myriapoda, Diplopoda) in Saxony-Anhalt (Germany). International Journal of Myriapodology 6: 61–83. <https://doi.org/10.3897/ijm.6.2172>
- Voigtländer K, Reip HS, Decker P, Spelda J (2011) Critical reflections on German Red Lists of endangered myriapod species (Chilopoda, Diplopoda) (with species list for Germany). International Journal of Myriapodology 6: 85–105. <https://doi.org/10.3897/ijm.6.2175>



- Vrieze SI (2012) Model selection and psychological theory: A discussion of the differences between the Akaike information criterion (AIC) and the Bayesian information criterion (BIC). *Psychological Methods* 17(2): 228–243. <https://doi.org/10.1037/a0027127>
- Wernitzsch W (1910) Beiträge zur Kenntnis von *Craspedosoma simile* und des Tracheensystems der Diplopoden. *Jenaische Zeitschrift für Naturwissenschaft* 39: 225–228.
- Wesener T (2015a) No millipede endemics north of the Alps? DNA-Barcoding reveals *Glomeris malmivaga* Verhoeff, 1912 as a synonym of *G. ornata* Koch, 1847 (Diplopoda, Glomerida, Glomeridae). *Zootaxa* 3999(4): 571–580. <https://doi.org/10.11646/zootaxa.3999.4.7>
- Wesener T (2015b) Integrative redescription of a forgotten Italian pill millipede endemic to the Apuan Alps - *Glomeris apuana* Verhoeff, 1911 (Diplopoda, Glomerida, Glomeridae). *Zootaxa* 4039(2): 391–400. <https://doi.org/10.11646/zootaxa.4039.2.11>
- Wesener T, Conrad C (2016) Local Hotspots of Endemism or Artifacts of Incorrect Taxonomy? The Status of Microendemic Pill Millipede Species of the Genus *Glomeris* in Northern Italy (Diplopoda, Glomerida). *PLoS ONE* 11(9): 1–22, e0162284. <https://doi.org/10.1371/journal.pone.0162284>
- Wesener T, Raupach MJ, Sierwald P (2010) The origins of the giant pill-millipedes from Madagascar (Diplopoda: Sphaerotheriida: Arthrosphaeridae). *Molecular phylogenetics and evolution* 57(3): 1184–1193. <https://doi.org/10.1016/j.ympev.2010.08.023>
- Wesener T, Voigtländer K, Decker P, Oeyen JP, Spelda J (2015) Barcoding of Central European *Cryptops* centipedes reveals large interspecific distances with ghost lineages and new species records from Germany and Austria (Chilopoda, Scolopendromorpha). *ZooKeys* 564: 21–46. <https://doi.org/10.3897/zookeys.564.7535>

## Supplementary material 1

### Complete sequences dataset

Authors: Hans S. Reip, Thomas Wesener

Data type: FASTA format.

Explanation note: Complete sequences dataset of all specimens of this study in format FASTA.

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Link: <https://doi.org/10.3897/zookeys.741.21917.suppl1>

## Supplementary material 2

### P-distance matrix

Authors: Hans S. Reip, Thomas Wesener

Data type: Microsoft Excel Worksheet (.xls).

Explanation note: P-distance matrix over all specimens as EXCEL-file. Export from MEGA7.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.741.21917.suppl2>

## Supplementary material 3

### P-distance – geographical distance

Authors: Hans S. Reip, Thomas Wesener

Data type: Microsoft Excel Worksheet (.xls).

Explanation note: P-distance – geographical distance table of all *G. marginata* specimens as EXCEL-file.

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Link: <https://doi.org/10.3897/zookeys.741.21917.suppl3>

## **Supplementary material 4**

### **POPART-data**

Authors: Hans S. Reip, Thomas Wesener

Data type: NEXUS format.

Explanation note: POPART-data file of haplotypes in format NEXUS.

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Link: <https://doi.org/10.3897/zookeys.741.21917.suppl4>

## **Supplementary material 5**

### **ESTIMATES-data**

Authors: Hans S. Reip, Thomas Wesener

Data type: Text Document (.txt).

Explanation note: ESTIMATES-data file of haplotypes as text file.

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Link: <https://doi.org/10.3897/zookeys.741.21917.suppl5>



# Two new *Lophoturus* species (Diplopoda, Polyxenida, Lophoproctidae) from Queensland, Australia

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Academic editor: P. Stoev | Received 23 October 2017 | Accepted 28 November 2017 | Published 7 March 2018

<http://zoobank.org/A3B9317A-69D9-4803-A2DF-D07736193677>

**Citation:** Huynh C, Veenstra AA (2018) Two new *Lophoturus* species (Diplopoda, Polyxenida, Lophoproctidae) from Queensland, Australia. In: Stoev P, Edgecombe GD (Eds) Proceedings of the 17<sup>th</sup> International Congress of Myriapodology, Krabi, Thailand. ZooKeys 741: 133–154. <https://doi.org/10.3897/zookeys.741.21814>

## Abstract

*Lophoturus queenslandicus* Verhoeff, 1924 was the first penicillate millipede in the family Lophoproctidae collected from Cairns, a tropical region in Queensland, Australia, to be formally described. Specimens collected from this region in a recent study had the morphological characters known to define this genus. However, their body form and length, as well as dorsal colouration proved to be different, suggesting the possibility of more than one *Lophoturus* species. This assertion was supported by the results of a phylogenetic analysis of DNA extracted and sequenced using 18S and COI regions from *L. queenslandicus* and two undescribed species from this genus. Specimens preserved in ethanol can prove difficult to confidently identify to species level because their colour gradually fades. Examination of live specimens with their body colour visible, together with morphological characters and DNA analysis is the most reliable way of correctly distinguishing between these three species. Two new species, *L. boondallus* **sp. n.** and *L. molloyensis* **sp. n.** collected in Queensland, Australia are described.

## Keywords

Millipedes, morphological characters, body length, colouration, phylogenetic analysis

## Introduction

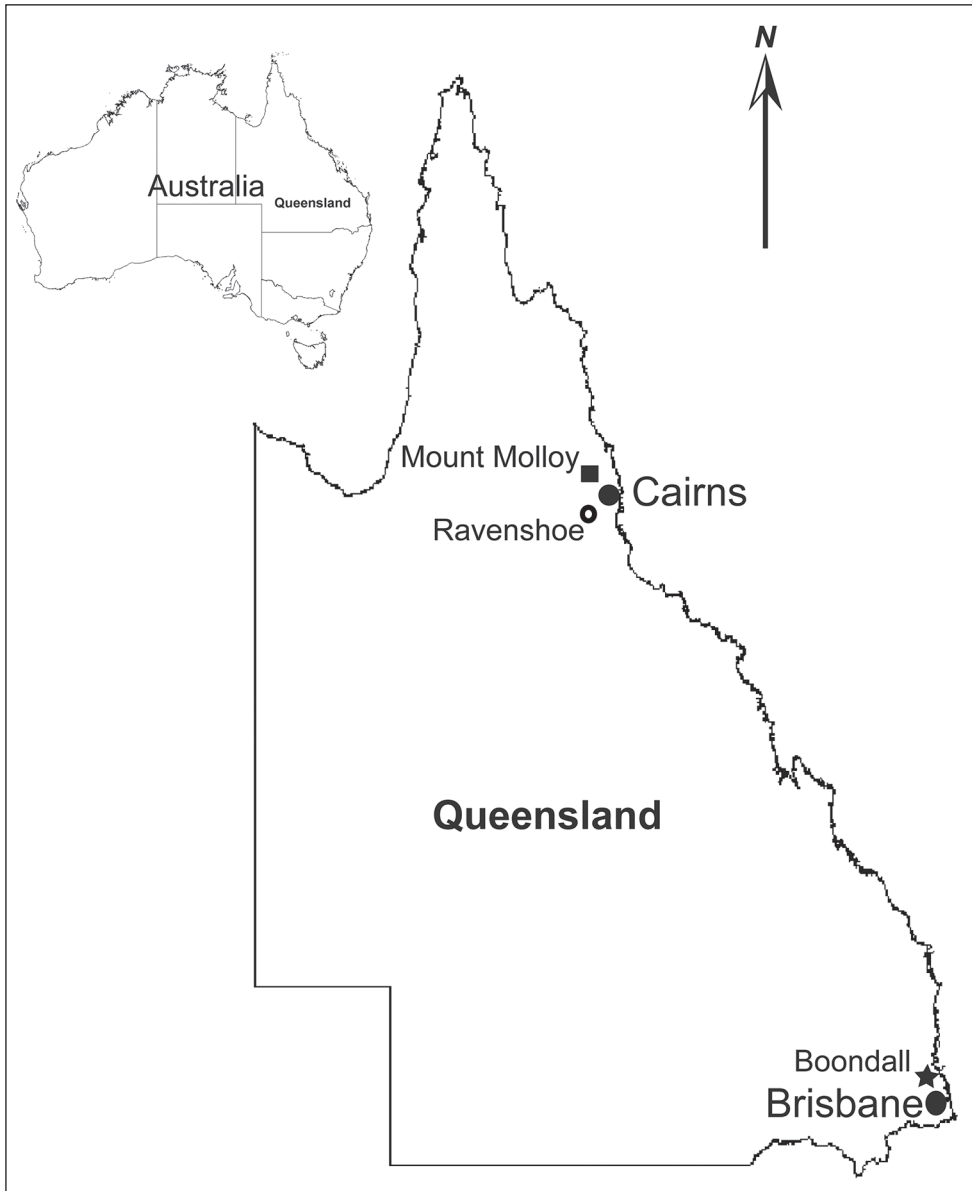
Penicillate millipedes from family Lophoproctidae Silvestri, 1897 are characterised as lacking ommatidia, having 13 pairs of legs (except *Lophoturus madecassus* Marquet & Condé, 1950 having only 11 pairs of legs), a gnathochilarium with medial palp



only; the 7<sup>th</sup> and 8<sup>th</sup> antennal articles are equal in length and reduced sensory cones, coxal glands absent in male, and simple claw structure. These millipedes are commonly found in low light environments such as deep leaf litter or cave habitats. The similarity in their morphological characters proves to be difficult with the classification to genus or species. Ishii et al. (1999) provided a key to the 5 genera in the Lophoproctidae based on the labrum structure and the number of sensilla on the 6<sup>th</sup> antennal article. These genera are *Alloproctoides* Marquet & Condé, 1950; *Ancistroxenus* Schubart, 1947; *Lophoproctinus* Silvestri, 1948; *Lophoproctus* Pocock, 1894 and *Lophoturus* Brölemann, 1931. Genus *Lophoturus* Brölemann, 1931 is defined by the following characteristics: 0 to 4 pairs of linguiform processes on each side of median cleft of labrum and the 6<sup>th</sup> antennal article with 3 thick sensilla. There were 27 described species in genus *Lophoturus* worldwide (Nguyen Duy-Jacquemin and Geoffroy 2003). *L. jianshuiensis* (Ishii & Yin, 2000) from China and two species: *L. speophilus* and *L. humphreysi* (Nguyen Duy-Jacquemin, 2014) from Christmas Island, Australia were recently added to the species list that totals 30 species to date. *Lophoturus queenslandicus* Verhoeff, 1924 was the first lophoproctid penicillate millipede collected from Cairns, a tropical region in far north Queensland, Australia, formally described (Condé 1979). In this study, penicillate millipedes collected from this region had morphological characters known to define the genus *Lophoturus*. However, their body form and length, as well as dorsal colouration proved to be different, suggesting the possibility of more than one species. The region, where the holotype of *L. queenslandicus* was first found, was visited and fresh specimens collected for comparison with two new *Lophoturus* species collected in Queensland, Australia are described below.

## Materials and methods

*Lophoturus* specimens (Lophoproctidae) were collected from the Cairns region, in tropical far north Queensland and Boondall Wetlands Park in Boondall, a northern suburb of Brisbane, Queensland, Australia (Fig. 1). Specimens of *Lophoturus queenslandicus* were collected from Millstream Falls, Ravenshoe, Tableland region, Queensland for comparison; 17°37'26.56"S, 145°28'42.89"E, elevation 886 m; 15 November 2014 (25 specimens collected: 4 male and 10 female adults, stadium VIII, 13 leg pairs; and 11 sub-adults with 4 males, 5 females in stadium VII, with 12 leg pairs; and 2 males in stadium VI, with 10 leg pairs). From Lake Eacham, Cairns region, Queensland; 17°16'59.90"S, 145°36'46.92"E, elevation 756 m; 5 December 2013 (eight specimens were collected: 3 males and 5 females (adults)). From a roadside of Gillies Highway, 8.5 km SE Goldsborough, Cairns region, Queensland; 17°13'1.98"S, 145°41'55.55"E, elevation 965 m, 6 December 2013 (8 specimens collected: 3 males, 4 females (adults) and one male (12 leg pairs)). *Lophoturus boondallus* sp. n. were collected from Boondall Wetlands Park; 27°20'25.85"S, 153°4'36.94"E, elevation 9 m, 10 November 2015 (12 specimens collected: 2 males and 10 females, all were adult stage). *Lophoturus molloyensis* sp. n. were collected from Mount Molloy (Bakers Road, 3 Km NW from the town of Mount Molloy,



**Figure 1.** Map of state of Queensland with a map of Australia, indicating type localities of *Lophoturus queenslandicus* Verhoeff, 1924 (○) and other two new *Lophoturus* species: *L. boondallus* sp. n. found in Boondall (★), Brisbane and *L. molloyensis* sp. n. found in Mount Molloy (■), Cairns region, Queensland, Australia. (Not in scale)

along Mulligan Highway), Cairns region, Queensland;  $16^{\circ}41'10.50''\text{S}$ ,  $145^{\circ}19'49.43''\text{E}$ , elevation 396 m, 8 December 2016. Seven specimens collected: 2 males and 4 females (adult – stadium VIII), and 1 with 12 leg pairs (subadult – stadium VII).

## Morphometric study

**Light microscopy.** *Lophoturus* specimens were examined and measured using a SMZ 800 stereoscope with an Infinity I camera and an Olympus CX 41 compound microscope with an image capture DP21 digital camera (a reticule with calibration of 0.1 mm stage micrometer and the Infinity I camera program were used for all measurements). Specimens were measured from head to telson, excluding the caudal bundle of trichomes. The sex of the specimens was identified by the presence of reproductive organs on the coxal plates of the 2nd pair of legs.

**Taxonomic drawings** Prepared slides (method described below) were used to complete drawings of the body trichomes using a Nikon drawing tube YID-T attached to a Nikon Eclipse E200 compound microscope.

**Scanning Electron Microscopy (SEM).** Whole specimens were preserved in 80% ethanol and dehydrated by passing through a graded series of ethanol, 80%, 90% and 100%, bathed in acetone for 2 minutes then air dried for a further 2 minutes. Specimens were subsequently mounted on a stub for gold coating using a Fisons sputter coater (0.02 mbar, 18 mA, 2 nm/min), then examined using a JEOL (JSM-IT300 Scanning Electron Microscope). Digital SEM images of the specimens were obtained.

**Morphometric and genetic studies.** The specimen preparation technique of Short and Huynh (2010) was used with modification to permit extraction of DNA for genetic studies. *Lophoturus* specimens were transferred from 80% ethanol onto a slide with a drop of 100% ethanol. Trichomes from the body and caudal bundle were stripped in the presence of ethanol. A resultant slide was then dried for 5 minutes before a drop of DPX was added to mount the slide. This slide was then used to depict the caudal trichomes. Individual stripped specimens were placed in 1.7 mL Eppendorf tubes with the initial extraction buffer solution (Invisorb Spin Forensic Kit (STRATEC Molecular GmbH, D-13125 Berlin, Germany)), left at room temperature for 12 hours then heated for 1 hour at 56 °C before DNA was extracted following manufacturer's instructions. The extracted DNA was put aside for the genomic DNA study. Cuticles of the same specimens used for DNA extraction were then cleared, dehydrated, stained 1% Fast Green and mounted with DPX mounting medium for microscopic examination following the method of Short and Huynh (2010).

Two common gene markers were used in this study: the small subunit ribosomal RNAs (SSU18S rRNAs) and the mitochondrial cytochrome c oxidase subunit I gene (COI). Both have been used as universal primers for highly conserved gene regions and are common molecular markers used for species detection and identification. The 18S gene marker has been used to elucidate relationships among arthropod groups including crustaceans, insects and myriapods (Turbeville et al. 1991; Luan et al. 2005, Wesener et al. 2010; 2016) This region has also been used to separate penicillate millipede species from genus *Monographis* with similar morphological characters (Huynh and Veenstra 2013; 2015). The COI region was also used because it is used in Barcode of Life (2010–2017) for species identification.

The quality of the DNA extracted from individual specimens of *L. queenslandicus*, *L. boondallus* sp. n. and *L. molloyensis* sp. n. were determined by using a NanoDrop

1000 Spectrophotometer (ND 1000V3.60 software) following manufacturer's instructions. The primers used for amplification and sequencing of COI were dgLCO1490 and dgHCO2198 (Meyer 2003) obtained from Sigma-Aldrich Co; 18S rDNA were SSUnRNA 1F, SSUnRNA 5R (White et al. 1990) obtained from GeneWorks Pty Ltd. Two microliters of the extracted DNA were sufficient for one Polymerase Chain Reaction (PCR) with 23  $\mu$ L master mix: 2.5  $\mu$ L PCR buffer 10x Reaction Buffer plus 15 mM MgCl<sub>2</sub>, 2.5  $\mu$ L 25 mM MgCl<sub>2</sub>, 2.5  $\mu$ L 2mM dNTP, 2.5  $\mu$ L BSA (Bovine Serum Albumin, 10% solution), 1  $\mu$ L forward primer, 1 $\mu$ L reverse primer, 0.1  $\mu$ L *Taq* (Thermo Fisher Scientific), and 10.9  $\mu$ L double distilled water. There after the method described by Huynh and Veenstra (2013; 2015) was used.

Representative sequences of *L. queenslandicus*, *L. boondallus* sp. n. and *L. molloyensis* sp. n. were used in a phylogenetic analysis. Partial genomic sequences from these species obtained using the molecular markers SSU18S rRNAs (18S) and the mitochondrial cytochrome c oxidase subunit I gene (COI), were deposited in GenBank: For 18S, the GenBank accession numbers are MG210573 for *L. boondallus* sp. n., MG210574 for *L. molloyensis* sp. n. and MG210575 for *L. queenslandicus*. For COI, the GenBank accession numbers are MG204535 for *L. queenslandicus*; MG204536 for *L. boondallus* sp. n. and MG204537 for *L. molloyensis* sp. n.

18S: The consensus 18S sequences from *L. queenslandicus*, *L. boondallus* sp. n. and *L. molloyensis* sp. n. were used in a BLAST search (<http://www.ncbi.nlm.nih.gov>) to identify sequences of closely related species. To explore relationships between these species, an entire sequence from *Monographis* sp. collected in China (GenBank accession number AY596371), partial sequences from *M. queenslandicus* (KF147166), *M. dongnaiensis* (KP255446), *Polyxenus lagurus* (EU368619), *Polyxenus fasciculatus* (AF173235), *Propolyxenus australis* (MF592753), *Unixenus mjobergi* (MF592755), *Lophoproctus coecus* (MF592760), *Chilexenus rosendinus* (MF592765), *Lophoturus madecassus* (MF592767), *Alloproctoides* sp. (MF592759), and two species of pill millipedes (Sphaerotheriida): *Sphaeromimus musicus* (FJ409961) and *Procyliosoma leae* (FJ409955) as an outgroup, were aligned with sequences from *Lophoturus* species using BioEdit (Hall 2010); MEGA7 (Kumar et al. 2016) was used to calculate with maximum composition likelihood method for distance analysis of the nucleotides and a phylogenetic tree was generated using PAUP\*4.0b10 (Swofford 2002). A rooted consensus tree of *Lophoturus* species was generated by the bootstrap test with 1000 repetitions.

COI: Sequences of *L. queenslandicus*, *L. boondallus* sp. n. and *L. molloyensis* sp. n. were aligned with the following sequences from related species available on GenBank using a BLAST search (<http://www.ncbi.nlm.nih.gov>): *Polyxenus lagurus* (HQ966144), *Propolyxenus trivittatus* (MF592724), *Chilexenus rosendinus* (MF592731), *Lophoproctus coecus* (MF592729), *Alloproctoides* sp. (MF592725), *Eudigraphis* sp. (LC010908), a pill millipede *Glomeridella minima* (JN271878) (Sphaerotheriida) and *Pogonsternum* sp. (KU745274) (Polydesmida) as outgroups. Phylogenetic analysis of these species was performed as described above for 18S. The maximum likelihood method was used for pairwise distance analysis of nucleotide composition between these *Lophoturus*.

## Results

### Order Polyxenida Lucas, 1840

### Family Lophoproctidae Silvestri, 1897

### Genus *Lophoturus* Brölemann, 1931

**Type species.** *Lophoturus obscurus* Brölemann, 1931.

*Lophoturus*, is a synonym of *Alloproctinus* Jeekel, 1963 and it was replaced by *Alloproctus* Silvestri, 1948; reassessed by Condé and Nguyen Duy-Jacquemin (1977). It is characterized by 0 to 4 pairs of linguiform processes on each side of median cleft of labrum and antennal article VI with 3 thick sensilla (Ishii et al. 1999: 252, key).

### *Lophoturus queenslandicus* Verhoeff, 1924 (Condé 1979)

**Note.** *Lophoturus queenslandicus* Verhoeff, 1924 was the first lophoproctid penicillate millipede collected from Ravenshoe, Australia (Condé 1979). Ravenshoe is a town in north-east Queensland previously known as Cedar Creek, where the type specimen of *L. queenslandicus* was collected.

*L. queenslandicus* has 13 pairs of legs, 10 segments and a telson; 9 pleural projections; body covered with barbate trichomes; tergal trichomes form 2 latero-posterior groups with a few trichomes extending anteriorly and these groups are separated by a gap; Chaetotaxy with pubescent oval setae; simple claw; the ornamental trichomes with 8*a*, 1*b* and 2*c* (*c*1 and *c*3); labrum with setose surface and 0 to 1 pairs of linguiform processes; the 6<sup>th</sup> antennal article with 3 thick sensilla (Condé 1979).

### *Lophoturus boondallus* sp. n.

<http://zoobank.org/9FF56672-4164-42F2-84E2-37721098D16E>

**Holotype.** Adult male, stadium VIII – 13 leg pairs stage, collected from Boondall Wetlands Park, Boondall, Brisbane, Queensland; 27°20'25.85"S, 153°4'36.94"E, elevation 9 m. The species was collected from leaf litter near the main entrance of the park on 10 November 2015 by author (CH).

**Paratypes.** One male and 9 females were collected in the same location and date as holotype. (1 male and 2 females were used for SEM imaging in this study).

**Etymology.** The species is named *Lophoturus boondallus* sp. n. as they were first found in Boondall Wetlands Park, Boondall, Queensland, Australia.

**Diagnosis.** *L. boondallus* has the following morphological characteristics: 3 sensilla on the 6<sup>th</sup> antennal article and labrum with two linguiform processes. These features are typical characteristics of *Lophoturus*. Live specimens from this species are light or-



ange in colour with a round arc-shaped body form in cross section. Adults body length range from 1.6–2.2 mm.

**Description.** *Measurements:* Holotype male body length 1.9 mm, females (paratypes) ( $n = 8$ ) range from 1.9–2.2 mm. Caudal bundle of the male is slightly narrower in width with 0.6 mm in length than that of the female (0.5 mm) (Fig. 6A–B)

**Colouration.** Head light orange and dark reddish-brown laterally; body light orange, contrasting with their white pleural trichomes and lighter coloured caudal bundle (Figure 2B).

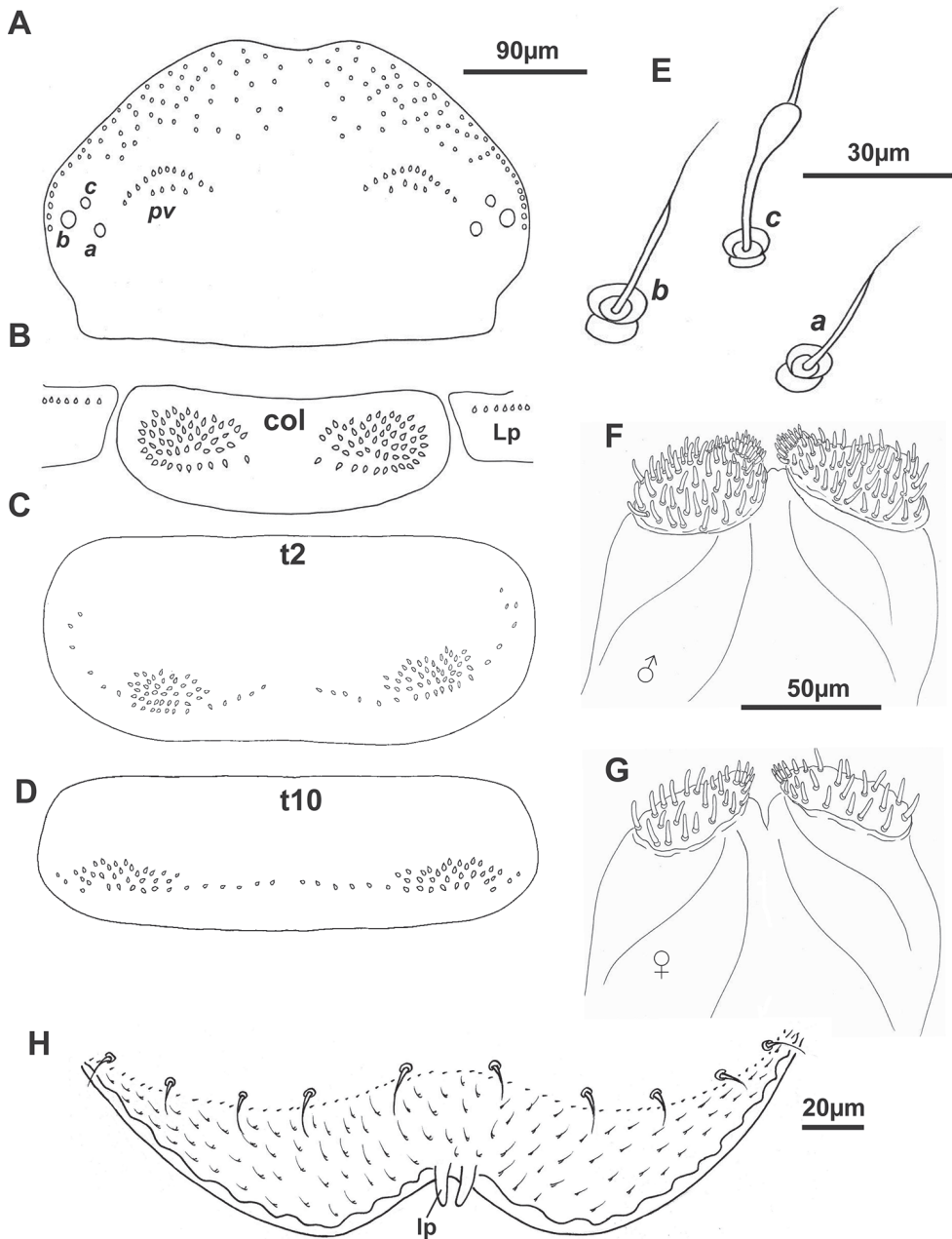
**Head.** Ommatidia absent. Vertex with two posterior trichome groups, a large gap presents between them. Each group consists of 2 rows, the anterior, oblique row has similar sized trichome sockets. Posterior row has fewer trichome sockets with a narrow space between the anterior and posterior rows. Holotype male has 12 + 12 trichome sockets in anterior rows and 4 + 4 trichome sockets in posterior rows (Fig. 3A); paratypes indicate that variation is common in this species, ranging from 12–15 (anterior rows) and 3–7 (posterior rows) (Fig. 6C). Trichobothria: trichobothrium *a*, located in posterior position with a medium socket; trichobothrium *b*, lateral position with largest socket; and trichobothrium *c*, anterior position with smallest socket. Trichobothria *a* and *b* have typically thin sensory hairs with narrow cylindrical funicles compared to trichobothrium *c*, with a claviform funicle. Trichobothrium sockets (*a*, *b* and *c*) arranged unevenly between *ab* and *bc*, as trichobothria *a* and *c* located more inward (Figs 3E, 6D).

**Antennae.** 8 articles (4 tiny, reduced sensory cones), 7<sup>th</sup> and 8<sup>th</sup> antennal articles are equal in length (Fig. 4A), which is characteristic of Lophoproctidae. The 6<sup>th</sup> antennal article has 3 thick bacilliform sensilla (T) of differing lengths: medium sensillum posteriorly (Tp); the longest and thicker intermediate sensillum (Ti); a short sensillum anteriorly (Ta) with its socket located distally; and a conical sensillum posteriorly (c) (Figs 4C, 6F). The 7<sup>th</sup> antennal article has 2 thick bacilliform sensilla (T), the anterior Ta shorter than Tp located posteriorly, with one setiform sensillum (s) between them plus a conical sensillum (c) located in the posterior position (Figs 4B, 6E). This pattern of sensilla on the 7<sup>th</sup> article is common to all *Lophoturus* species.

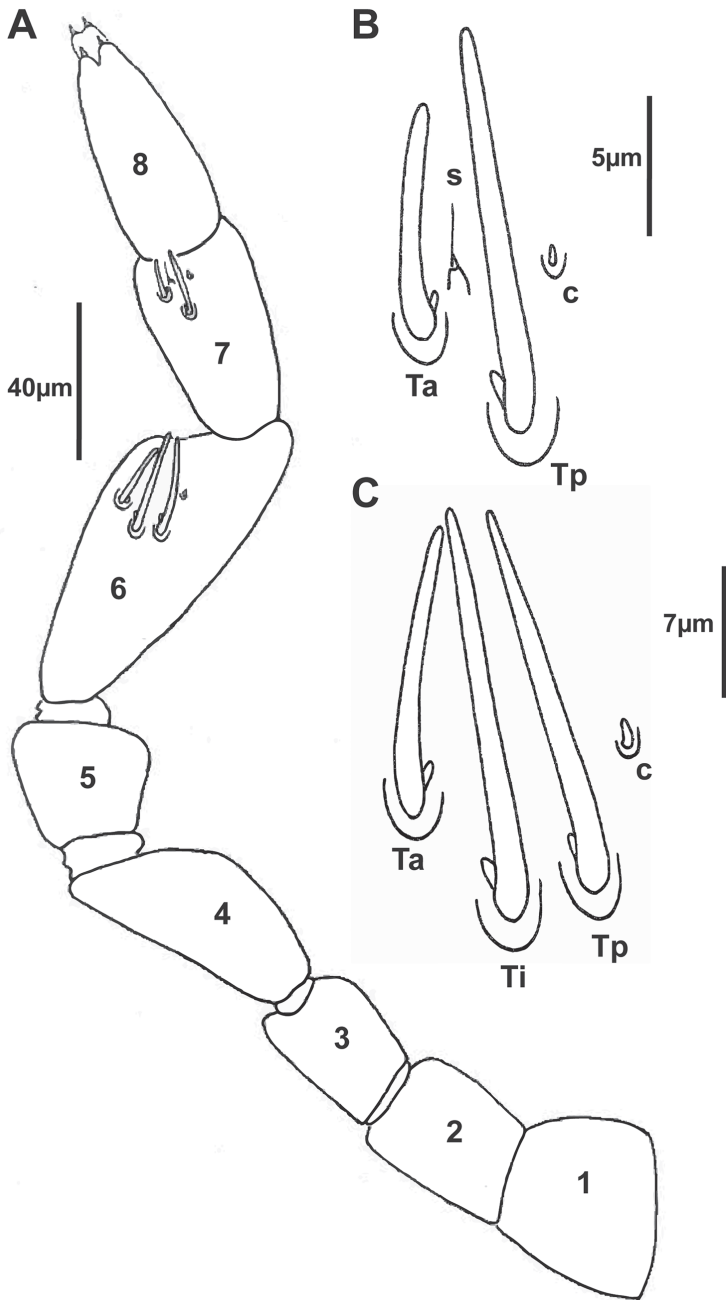
**Clypeo-labrum:** Holotype has 10 setae, all half the width of the labrum. Setae on paratypes ranged from 10–12. Labrum surface setose, with tiny, backward facing hairs.



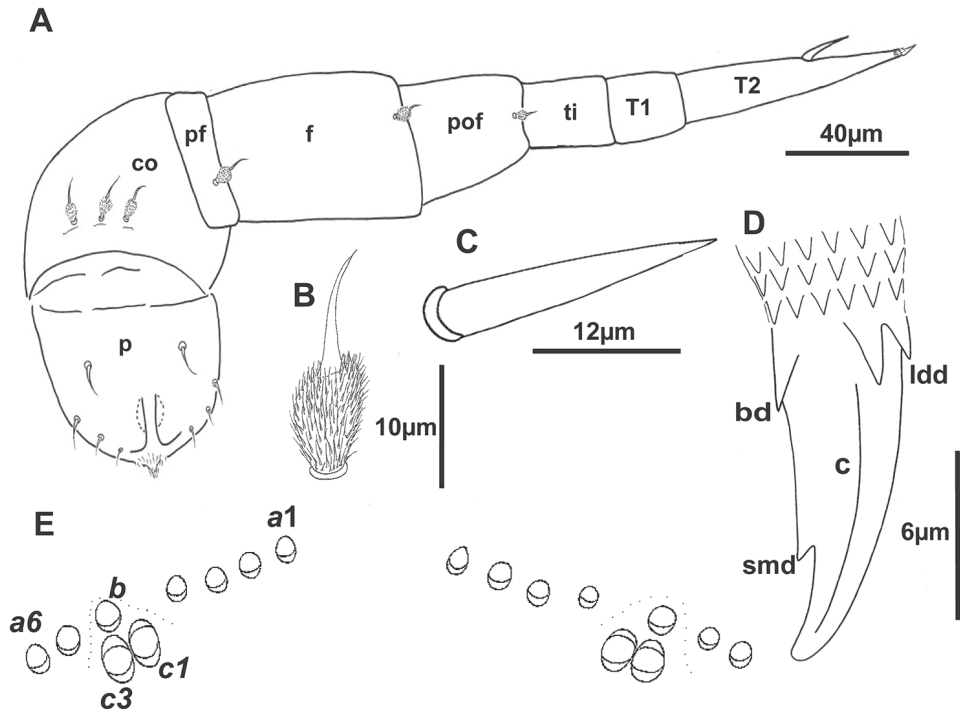
**Figure 2.** Three *Lophoturus* species were found in state of Queensland, Australia. **A** *L. queenslandicus* Verhoeff, 1924 **B** *L. boondallus* sp. n. and **C** *L. molloyensis* sp. n. These *Lophoturus* species showed differences in body lengths and colour.



**Figure 3.** The depiction of holotype of *Lophoturus boondallus* sp. n. **A** A head capsule showed the posterior vertex trichome sockets (pv) and trichobothria **B, C, D** Collum (col) with the lateral protuberances (Lp), tergite 2 (t2) and tergite 10 (t10), with trichome socket patterns **E** Trichobothria: Trichobothrium **a** (located posteriorly with medium socket), trichobothrium **b** (located laterally with largest socket) are typical thin sensory hairs and trichobothrium **c** with a claviform funicle (located anteriorly with smallest socket) **F** Gnathochilaria of male and **G** Gnathochilaria from female (paratype) **H** Labrum displayed two lingiform processes (lp) and setose surface.



**Figure 4.** Antennal articles of the holotype *Lophoturus boondallus* sp. n. **A** Antenna with eight articles and the arrangement of sensilla on the 6<sup>th</sup> and 7<sup>th</sup> articles; articles 7<sup>th</sup> and 8<sup>th</sup> were equal in length; the arrangement of sensilla on the 6<sup>th</sup> and 7<sup>th</sup> antennal articles **B** Sensilla on the 7<sup>th</sup> antennal article; a conical sensillum (c), a long thick sensillum located posteriorly (Tp) and a short thick sensillum located anteriorly (Ta) with a setiform sensillum (s) located between these sensilla **C** Sensilla on the 6<sup>th</sup> antennal article; a conical sensillum (c), a medium length thick sensillum (Tp), a long thick sensillum (Ti) and the short thick sensillum (Ta).



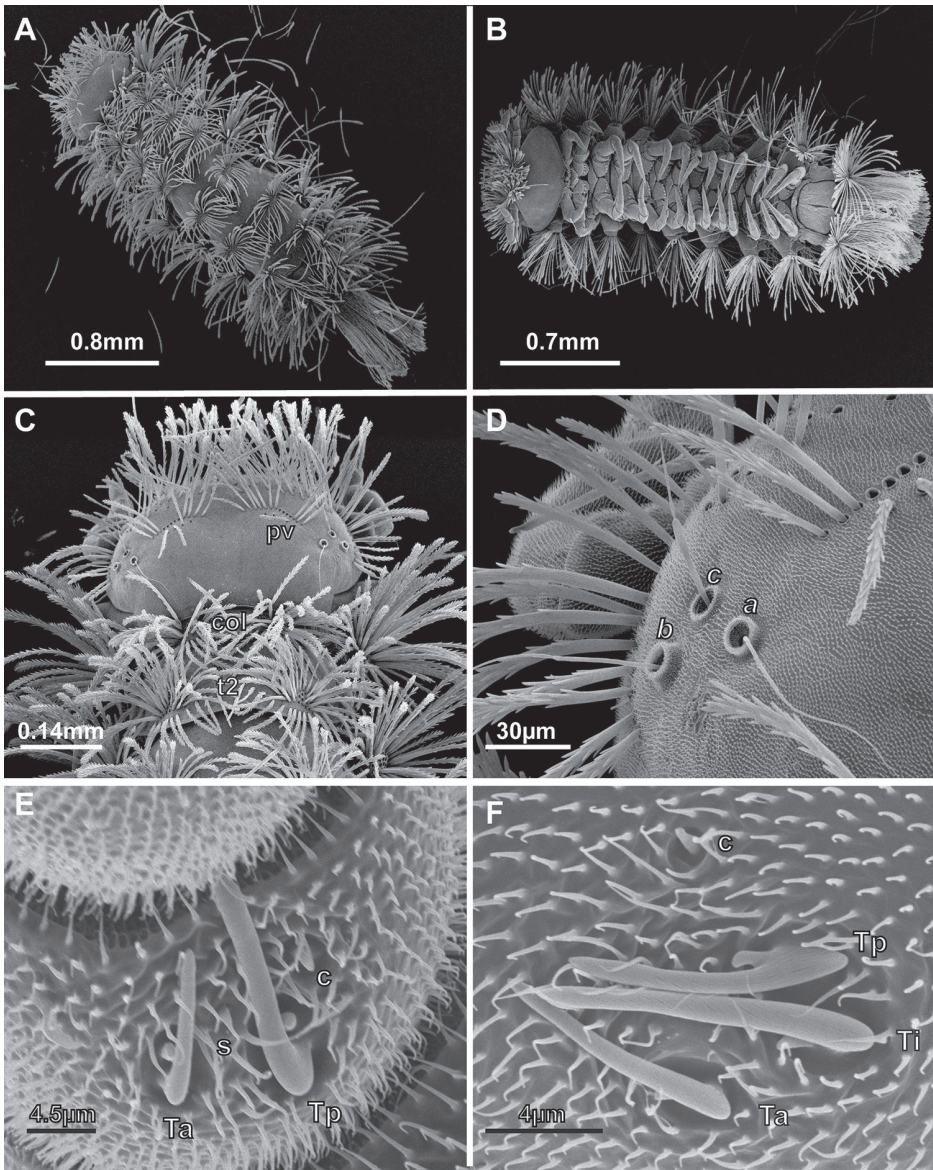
**Figure 5.** Holotype of *Lophoturus boondallus* sp. n. **A** The second left leg showing a penis (**p**), seven leg segments (**co** coxa, **pf** pre-femur, **f** femur, **pof**: post-femur, **ti** tibia, **T1** tarsus 1, **T2** tarsus 2 and a spine), a claw and its chaetotaxy (setae on the leg segments) **B** a pubescent oval seta **C** a spine on tarsus 2 **D** A simple claw structure with two latero-dorsal denticles (**ldd**), claw (**c**), a basal denticle (**bd**) and small denticle (**smd**) **E** The ornamental trichome sockets, located dorsally on the caudal bundle structure, with six trichomes **a**, one trichome **b** and two trichomes **c** (**c1** and **c3**).

Anterior margin of labrum with two whole lamellae, and a linguiform process present on each side of median cleft of labrum (Figs 3H, 7A).

**Gnathochilaria.** Medial palps only, 58 sensilla on the palp of holotype (male) and 18–22 sensilla on paratypes (females) (Fig. 3F–G).

**Trunk.** Comprised of 10 segments, 9 pleural projections, excluding the telson and caudal bundle; 13 pairs of legs. Collum – tergite 1 (smallest tergite) with trichome sockets arranged in 2 oval shapes laterally, connected by posterior curved rows of trichome sockets with a large gap in the middle. The collum is the only tergite with lateral protuberances bearing a small number of trichome sockets. In holotype, the collum has 52 (Left: L), 52 (Right: R) trichome sockets and the lateral protuberances with 7 trichome sockets on each side (Fig. 3B). Numbers varied in paratype females within a range of 46–58 trichome sockets in the collum and the number of lateral protuberances trichome sockets range 6–8. Tergites 2 to 10, have a pair of pleural projections located antero-laterally. The arrangement of tergal trichome sockets from tergites 2 to 10 typically have 2 latero-posterior oval groups with a few sockets extended on both ends with these groups separated by a

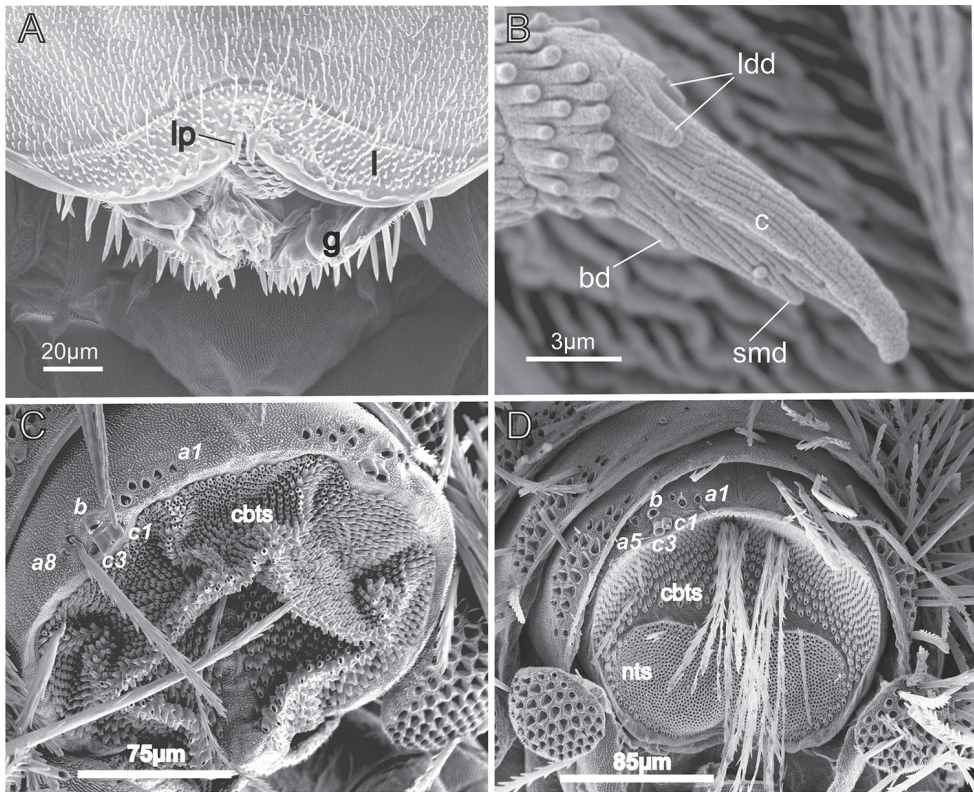




**Figure 6.** SEM (Scanning Electron Microscopy) images of *Lophoturus boondallus* sp. n. **A** A dorsal view of whole body showing the body trichome arrangements and the caudal bundle **B** A ventral view of whole body showed 13 pairs of legs **C** A head capsule displaying two posterior vertex trichome groups (pv), a colium (col) and tergite 2 (t2) **D** Trichobothria **a** (a), **b** (b) and **c** (c) showing different sizes in trichobothrium sockets **E** and **F** Antennal articles 6 and 7 with sensilla (Ta: thick sensillum located anteriorly, Ti: intermediate thick sensillum, Tp: posterior thick sensillum, setiform sensillum (s) and a conical sensillum (c)).

large medial gap. Trichome sockets of tergite 2 in the holotype has 54 (L) and 54 (R) (Figs 3C, 6C), tergite 10 has 38 on both sides (Fig. 3D). In contrast, the trichome sockets of tergite 2 in paratypes ranged 54–66 and tergite 10 ranged 34–46 trichome sockets.





**Figure 7.** SEM images of *Lophoturus boondallus* sp. n. **A** Mouth part showed setose labrum (l) with typical two linguiform processes (lp) and sensilla from the gnathochilarium (g) **B** Simple claw with lateral dorsal denticles (ldd), claw (c), small denticle (smd) and basal denticle (bd) **C** Male caudal bundle showed an ornamental trichome sockets (a, b and c) and the uniform caudal bundle trichome sockets (cbts); **D** Female caudal bundle structure displaying ornamental trichome sockets and two main parts: caudal bundle trichome sockets dorsally (cbts) and two nest trichome sockets (nts) ventrally.

**Legs.** Leg segments are named following Manton (1956). Legs 1 and 2 without trochanter; leg 1 also lacks tarsus 1. Chaetotaxy as follows: coxa 1: 2 pubescent oval setae, coxa 2: 3 pubescent oval setae, coxae 3–13: 0–4 pubescent oval setae; pre-femur, femur and post-femur with 1 pubescent oval seta (Fig. 5A–B), tarsus 2 with a spine (Fig. 5C). Posterior edge of last sternite has 0–4 pubescent oval setae similar to those present on the coxa and the number of these pubescent oval setae varies: 2 on the holotype and 0–4 on the paratypes. Sex organs in male: A pair of penes on the 2<sup>nd</sup> coxa and coxal glands absent.

**Telotarsus–Claw.** slender with two latero-dorsal denticles (ldd) equal in length, a basal denticle (bd) and a small denticle (smd) present near the tip of the claw (Figs 5D, 7B).

**Telson.** Dorsal ornamental trichome sockets symmetrically arranged on each side, with 6 sockets of trichome **a** in the holotype; paratype females have 6–8 sockets of trichome **a**, a single trichome **b** and two large protruding base sockets of trichome **c**: c1 and c3 (The absence of c2 is characteristic of lophoproctid species) (Fig. 5E).

**Caudal bundles.** In the holotype male, the caudal bundle is formed by a single group of trichome sockets of uniform sizes; this structure is split ventrally with trichome socket-free tissue present and extending with a small gap dorsally toward the centre. 3 rows of the largest size barbate trichome sockets present, forming slightly uneven lateral rows that extend toward the centre of the caudal structure (Fig. 7C). In paratype females, the caudal bundle structure differed from the male, with two distinguishing structures apparent: the main dorsal structure, was similar to the male, and 2 latero-sternal structures with finer nest trichome sockets. These finer sockets located on the interior and were surrounded by 2 rows of caudal trichome sockets on exterior surface. A trichome socket-free area is present ventrally, extending with a small gap and connecting with central bare tissue with few barbate trichome sockets present. Caudal and nest trichome sockets are clearly separated. These structures gradually form a single caudal bundle structure (Fig. 7D). The structure of *L. boondallus* caudal bundles and their caudal trichomes is similar to those of *Monographis* (Polyxenidae) (Huynh and Veenstra 2013, 2015) and classified as Type II by Condé and Nguyen Duy-Jacquemin (2008).

**Remarks.** *L. boondallus* differs from *L. queenslandicus* in being shorter in length, in having light orange colouration, a round arc-shaped body form when viewed in cross section. Furthermore, it also differs genetically from the other *Lophoturus* species. In contrast, *L. queenslandicus* is rusty brown with a yellowish light green median band dorsally and two darker brown strips laterally; body 2.4–2.8 mm long, with a flattened arc shape (Fig. 2).

***Lophoturus molloyensis* sp. n.**

<http://zoobank.org/79421543-DA49-454F-AA29-904170B24D9B>

**Holotype.** Adult male, stadium VIII – stage 13 leg pairs, was collected from Mount Molloy, Cairns region, Queensland; 16°41'10.50"S, 145°19'49.43"E, elevation 396 m, 8 December 2016.

**Paratypes.** 1 male, 4 females and one 12 leg pairs (subadult), collected with holotype.

**Etymology.** *Lophoturus molloyensis* sp. n. is named after the collection location, Mount Molloy in the Cairns region of far north Queensland, Australia.

**Diagnosis.** *L. molloyensis*, has 3 sensilla on the 6<sup>th</sup> antennal article, and labrum has two linguiform processes. These features are typical of *Lophoturus*. In live, this species is white in colour with rounded body shape, covered with shorter trichomes. Body length of adults ranges from 1.4–1.8 mm, which distinguishes it from the longer *Lophoturus* species.

**Description.** *Measurements:* Holotype male body length 1.4 mm; females (paratypes) ( $n = 4$ ) range from 1.6–1.8 mm. Caudal bundle of male is slightly narrower in width and 0.2 mm in length than that of the female with 0.3 mm (Fig. 11A–B).

**Colouration.** Head white and dark reddish brown in eye area; body yellowish-white with dull white pleural trichomes and bright white in caudal bundle (Fig. 2C).

**Head.** Ommatidia absent. Vertex with two posterior trichome groups, a large gap presents between them. Each group consists of 2 rows, the anterior, oblique row has similar sized trichomes. Posterior row has fewer trichome sockets with a narrow space between the anterior and posterior rows (Figs 8A, 11C). Holotype male has 10 + 10 trichome sockets in anterior rows and 4 + 4 trichome sockets in posterior rows; paratypes indicate that variation is common in this species, ranging from 9–11 (anterior rows) and 3–6 (posterior rows). Trichobothria: This species has the same structure and arrangement of trichobothria as seen all *Lophoturus* species: Trichobothria **a** and **b** are typically thin sensory hairs with narrow cylindrical funicles compared to trichobothrium **c**, with a claviform funicle. (Figs 8F, 11D).

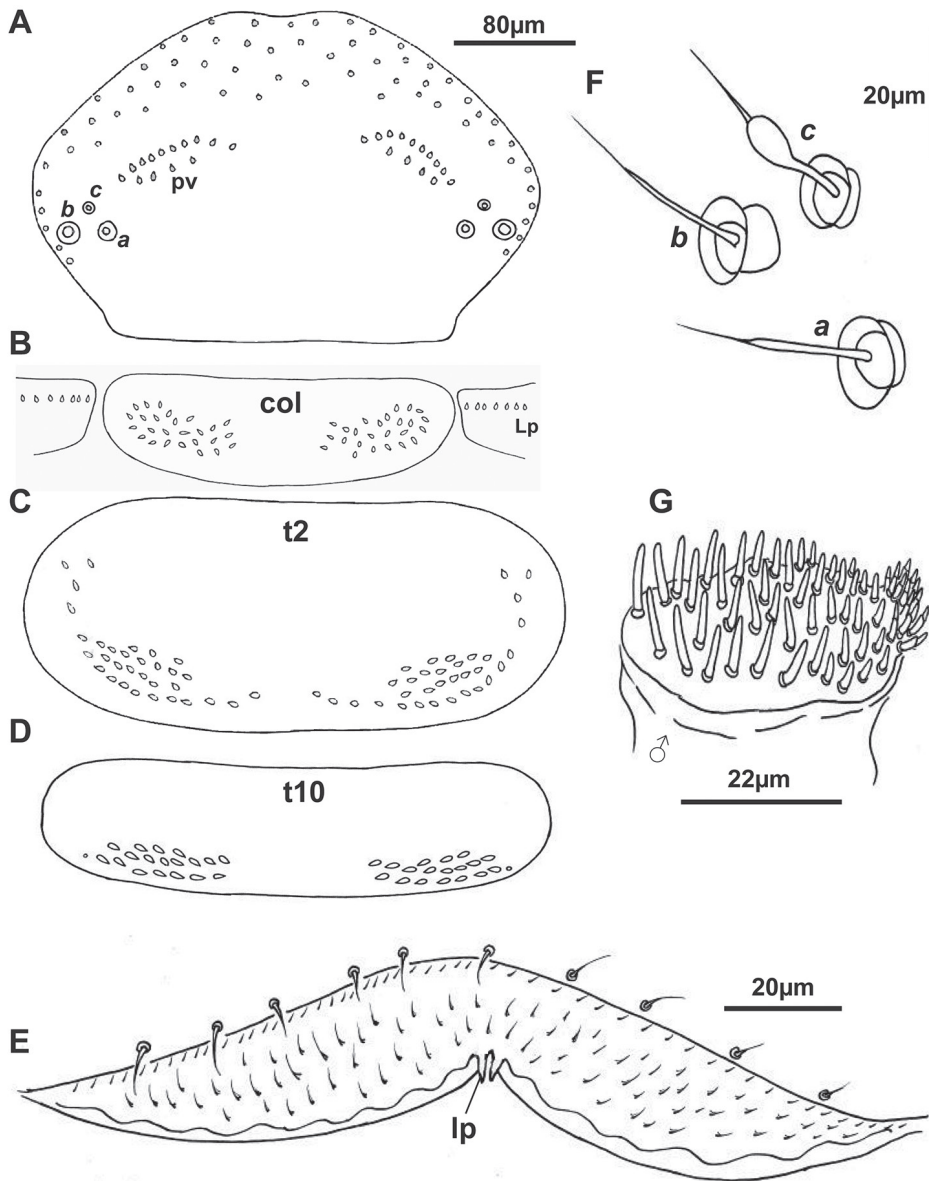
**Antennae.** 8 articles, 7<sup>th</sup> and 8<sup>th</sup> antennal articles are equal in length (Fig. 9C). The 6<sup>th</sup> antennal article has 3 thick bacilliform sensilla (T): Medium sensillum posteriorly (Tp), the longest, thicker intermediate sensillum (Ti), a short sensillum anteriorly (Ta) with its socket distal to other, and a conical sensillum posteriorly (c) (Figs 9B, 11E). The 7<sup>th</sup> antennal article has 2 thick bacilliform sensilla (T), the anterior one (Ta) shorter than (Tp) located posteriorly, with one setiform sensillum (s) between them and a conical sensillum (c) in the posterior position (Figs 9A, 11E).

**Clypeo-labrum.** Holotype has 10 setae, all shorter than half the width of the labrum. Setae on the paratypes ranged from 10–12. Labrum surface setose, with tiny, backward facing hairs. Anterior margin of labrum has two whole lamellae, and a linguiform process present on each side of median cleft of labrum (Figs 8E, 11F).

**Gnathochilaria.** Medial palps only, 58 sensilla on the palp of holotype (male) and 18–22 sensilla on paratypes (females) (Fig. 8G).

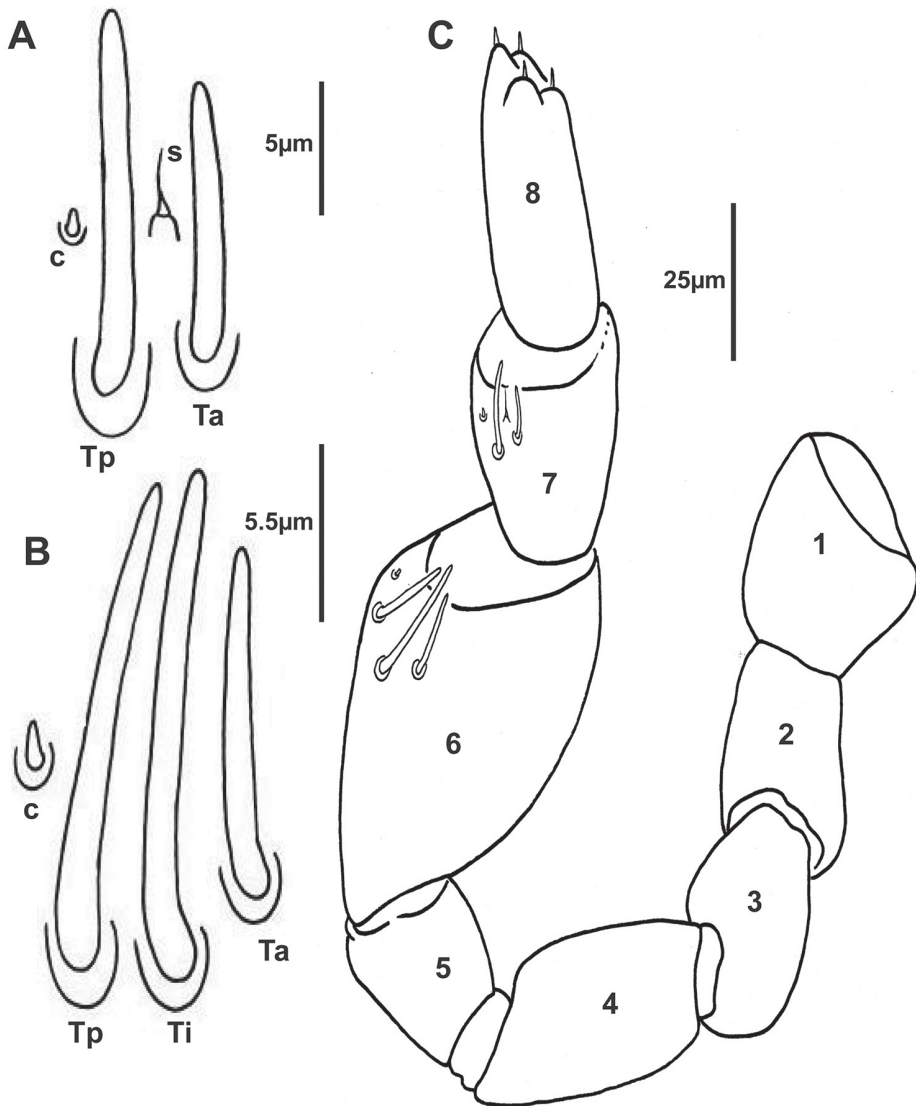
**Trunk.** Comprised of 10 segments, 9 pleural projections, excluding the telson and caudal bundle; 13 pairs of legs. Collum with trichome sockets arranged in 2 oval shapes laterally, connected by a posterior row of trichome sockets forming a line with a large gap in the middle. Lateral protuberances have a small number of trichome sockets. In holotype, the collum has 26 trichome sockets on both sides and the lateral protuberances have 7 trichome sockets on each side (Figs 8B, 11C). Numbers varied in paratype females within a range of 26–29 trichome sockets in the collum and the number of lateral protuberances trichome sockets range 4–6. All other tergites, from tergites 2 to 10, have a pair of pleural projections located antero-laterally. The arrangement of tergal trichome sockets from tergites 2 to 9 typically have 2 latero-posterior oval groups with a few sockets extending on both ends with these groups separated by a large gap. Trichome sockets of tergite 2 in the holotype have 33 on each side (Figs 8C, 11C), tergite 10 has two groups of 18 sockets both sides without any extended sockets, (Fig. 8D). In contrast, the trichome sockets of tergite 2 in paratypes ranged 30–34 and tergite 10 range was 16–19 trichome sockets.

**Legs.** Leg segments are named following Manton (1956). Legs 1 and 2 are without trochanter, leg 1 also lacks tarsus 1. Chaetotaxy as follows: coxa 1: 2 pubescent oval setae, coxa 2: 3 pubescent oval setae, coxae 3–13: 0–4 pubescent oval setae; pre-femur, femur



**Figure 8.** Holotype of *Lophoturus molloyensis* sp. n. **A** Head capsule, absence of ommatidia indicated, two posterior vertex trichome sockets (**pv**) and trichobothria **a**, **b** and **c** with the sockets only **B** the column (**col**) and two lateral protuberances (**Lp**) **C** Tergite 2 (**t2**) and **D** The last tergite 10 (**t10**), showing the arrangement of trichome sockets **F** Trichobothria: **a** (the medium base socket located posteriorly) and **b** (the largest base socket located laterally) are typical thin sensory hairs, **c** with with a claviform funicle (the smallest base socket located anteriorly) **G** The male, right gnathochilarium showing numerous sensilla (ranged 56 – 58 sensilla in male) **E** Labrum showing a pair of linguiform processes (**lp**) and setose surface.

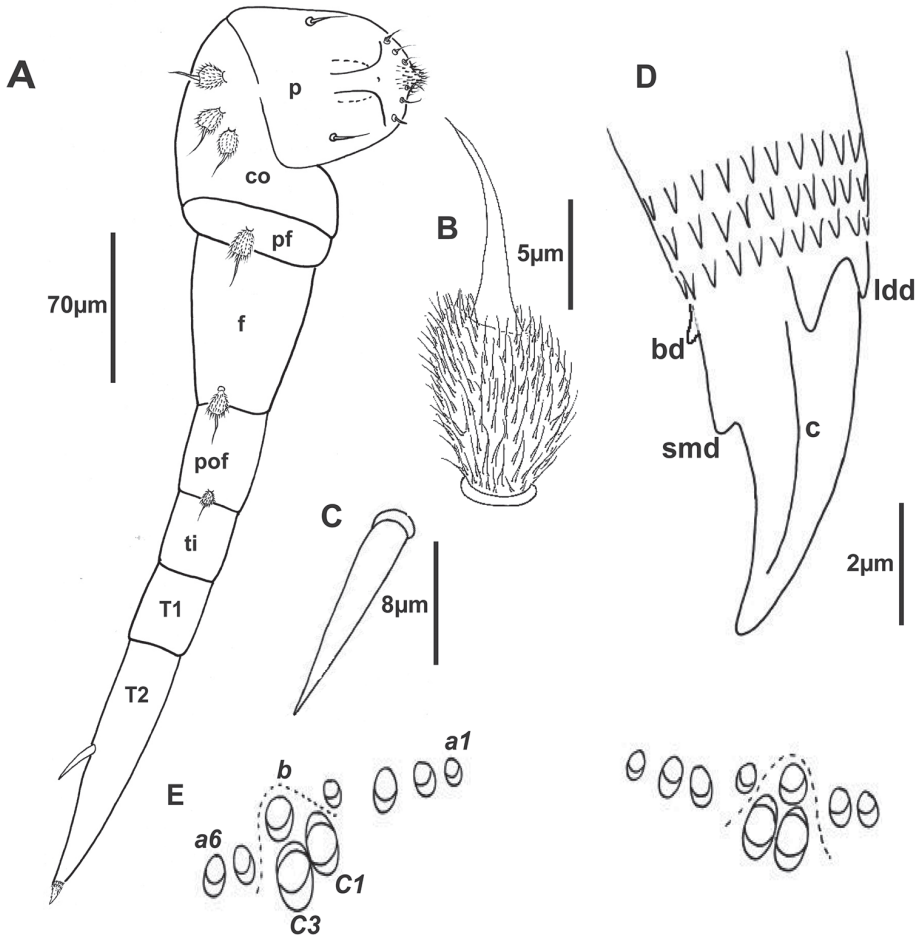




**Figure 9.** Holotype of *Lophoturus molloyensis* sp. n. **A** The arrangement of sensilla on the 7<sup>th</sup> antennal article: A conical sensillum (c), a long thick sensillum located posteriorly (Tp) and a short thick sensillum located anteriorly (Ta) with a setiform sensillum (s) located between these sensilla **B** Sensilla on the 6<sup>th</sup> antennal article: a conical sensillum (c), a medium length thick sensillum located posteriorly (Tp) and a long thick sensillum located intermediately (Ti) followed the short thick sensillum (Ta) **C** The left antenna with eight articles and the arrangement of sensilla on the 6<sup>th</sup> and 7<sup>th</sup> articles.

and post-femur with 1 pubescent oval seta (Fig. 10A–B), tarsus 2 with a spine (Fig. 10C). Posterior edge of last sternite has 0–4 pubescent oval setae, similar those present on the coxa and the number of these pubescent oval setae varies: 4 on the holotype and 0–4 on the paratypes. Sex organs in male: A pair of penes on the 2<sup>nd</sup> coxa and coxal glands absent.





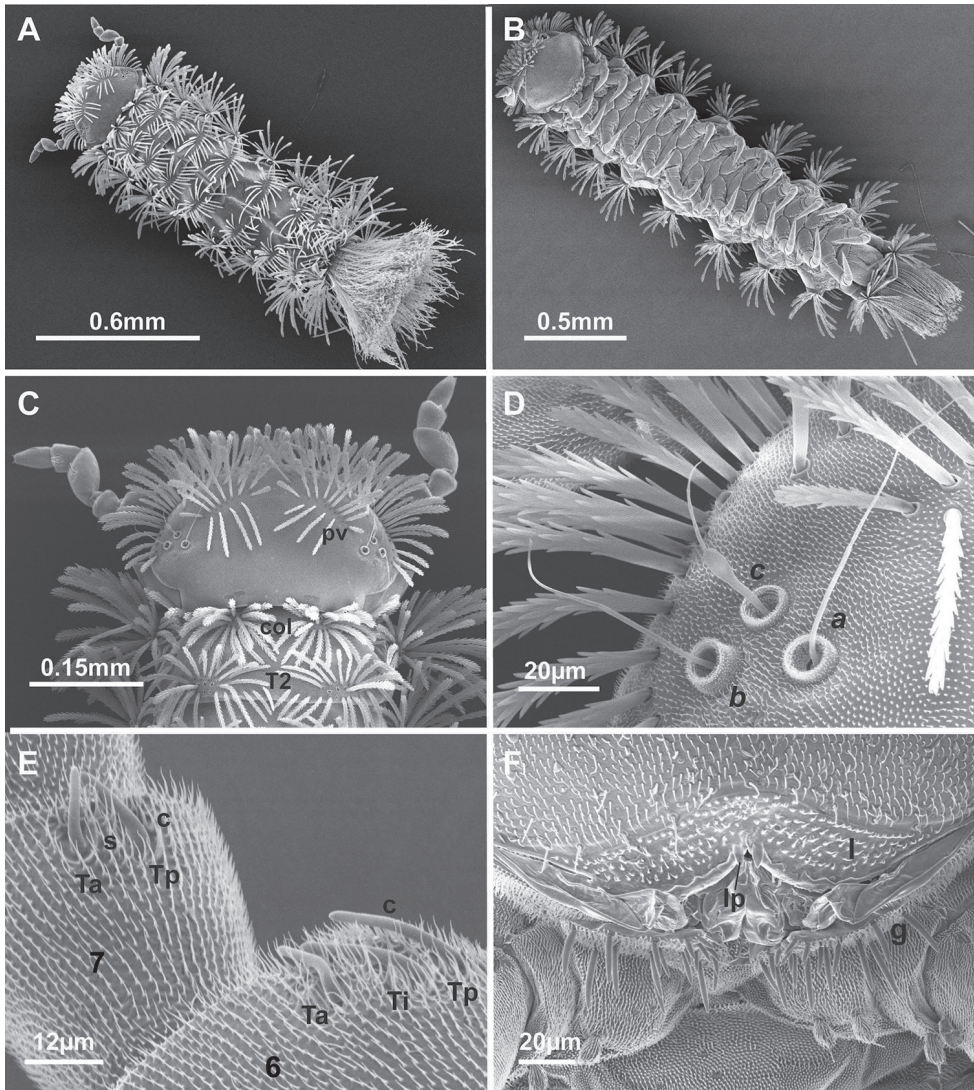
**Figure 10.** Holotype of *Lophoturus molloyensis* sp. n. **A** The second right leg with a penis (**p**), seven leg segments (**c** coxa, **pf** pre-femur, **f** femur, **pof** post-femur, **ti** tibia, **T1** tarsus 1, **T2** tarsus 2 and a spine), a claw and its chaetotaxy (setae on the leg segments) **B** A pubescent oval seta **C** A spine on tarsus 2 **D** A simple claw structure showing two latero-dorsal denticles (**ldd**), claw (**c**), a basal denticle (**bd**) and a small denticle (**smd**) **E** The ornamental trichome sockets, which located dorsally above the caudal bundle structure, with six trichomes **a**, one trichome **b** and two trichomes **c** (**c1** and **c3**).

**Telotarsus - Claw:** robust with two latero-dorsal denticles (**ldd**) equal length, a basal denticle (**bd**) and a small denticle (**smd**) present near the middle of the claw (Fig. 10D).

**Telson.** Dorsal ornamental trichome sockets symmetrically arranged on each side, with 6 sockets of trichome **a** in the holotype; paratype females have 4–6 sockets of trichome **a**, a single trichome **b** and two large protruding base sockets of trichome **c**: **c1** and **c3** (Fig. 10E).

**Caudal bundles.** These caudal structures similar in both sexes and like those of *L. boondallus* described above.

**Remark.** *L. molloyensis* differs from both *L. queenslandicus* and *L. boondallus* in size, body length (about 1.6 mm), form and colouration. Body trichomes are short. The 12



**Figure 11.** SEM images of *Lophoturus molloyensis* sp. n. **A** A dorsal view of whole body showing the body trichome arrangements and the caudal bundle **B** A ventral view of whole body showing 13 pairs of legs **C** A head capsule displaying two posterior vertex trichome groups (**pv**), a collum (**col**) and tergite 2 (**T2**) **D** The trichobothria: **a**, **b** and **c**, showing different sizes in trichobothrium sockets **E** Antennal articles 6 and 7 with their sensilla (**Ta**: thick sensillum located anteriorly, **Ti**: intermediate thick sensillum, **Tp**: posterior thick sensillum, setiform sensillum (**s**) and a conical sensillum (**c**) **F** Mouth parts with setose labrum (**l**) with typical two linguiform processes (**lp**) and the gnathochilarium (**g**).

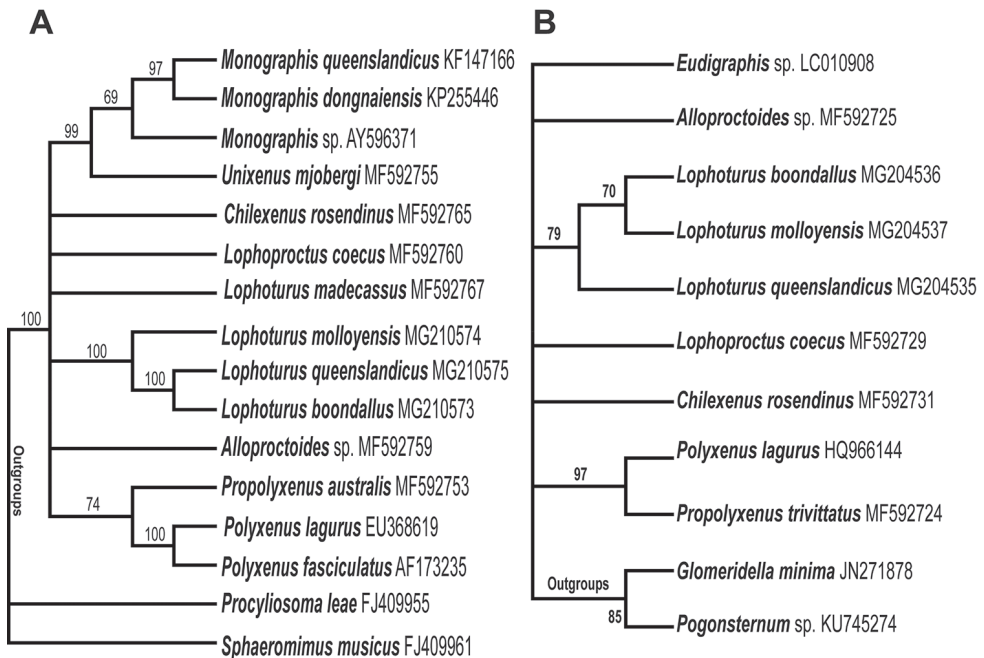
leg pairs stage of this species may initially be confused with *L. madecassus* Marquet & Condé, 1950 as they have the same body length and appearance. Both have 8 pleural projections, but *L. molloyensis* has 12 leg pairs in subadult stage compared to *L. madecassus* which has 11 leg pairs in the adult stage.

## Genetic analysis

The 18S maximum likelihood tree was generated by 1000 bootstrap replications yielded a strongly supported phylogenetic tree. The 18S region of the 3 sequences from studied *Lophoturus* species formed a statistically supported clade with all sequences of *Lophoturus* species. Phylogenetic analysis indicated that these species belong in the same genus *Lophoturus* (Fig. 12A).

Another bootstrap maximum likelihood tree based on comparison of the COI region of three *Lophoturus* species also yielded a strongly supported phylogenetic tree with the bootstrap value (>50%, shown on the nodes of the clade of three species) that these *Lophoturus* species are sufficiently distinct to warrant separation into 3 species (Fig. 12B).

Pairwise distances of the genomic DNA among *Lophoturus* species were analysed based on the maximum likelihood method to estimate of the evolutionary divergence between sequences. The genomic sequences based on the COI molecular marker showed significant percentage difference in the genetic distance between these *Lophoturus* spp.: *L. queenslandicus* was 16% genetic distance to *L. boondallus* sp. n. and 14% genetic distance to *L. molloyensis*. *L. boondallus* sp. n. and 14% genetic distance to *L. molloyensis* (Table 1).



**Figure 12.** The molecular phylogenetic analysis by maximum likelihood method. **A** A consensus tree of sequences from 18S marker generated by the bootstrap test (1000 replications and the support values >50% shown on the nodes) yielded a strongly supported phylogenetic tree **B** The maximum likelihood test of sequences from COI marker provided the molecular phylogenetic tree of evolutionary history between each species. Again, this tree supported all *Lophoturus* species in the same clade as in the result of 18S.

**Table 1.** Pairwise distances of the sequences from three *Lophoturus* species were analysed based on the estimate of the evolutionary divergence between sequences from 18S and COI.

Species		Pairwise distance 18S		Pairwise distance COI	
<i>Lophoturus queenslandicus</i>	MG204535				
<i>Lophoturus boondallus</i>	MG204536	0.02		0.16	
<i>Lophoturus molloyensis</i>	MG204537	0.04	0.04	0.14	0.14

## Discussion

*L. queenslandicus* Verhoeff, 1924, *L. boondallus* sp. n. and *L. molloyensis* sp. n. all exhibit many similar morphological characteristics i.e. labrum with setose surface and a pair of linguiform processes, 3 thick sensilla (thick sensilla: located in anterior position (Ta), intermediate position (Ti) and posterior position (Tp)) on the 6<sup>th</sup> antennal article, which are typical characteristics of genus *Lophoturus*. In preserved specimens where their colouration has gradually faded and trichomes damaged or lost, it is difficult to identify to species level. In live specimens, these species appear quite different based on body colouration and form: *L. queenslandicus* is rusty brown colour with a yellowish light green median band dorsally with two darker brown strips laterally; body length ranged 2.4–2.8 mm and it has a flattened arc body shape. *L. boondallus* is different in colour, being light orange with a rounded arc body shape, the adult body lengths often ranged from 1.6–2.2 mm. In contrast, *L. molloyensis* differs from the other two species having the shortest body length of about 1.6 mm and being white colour with round body shape (Fig. 2). However, there is an alternative way to identify these species, especially with the advances in molecular technology, by using genetic analysis. The molecular markers such as 18S and COI can help to confirm species identification.

## Acknowledgements

Special thanks to Megan Short who reviewed an earlier version of this manuscript; also to Dr Nick Porch who produced the beautiful pictures of the specimens for Figure 2.

## References

- Barcode of Life (2010–2017) Available from URL: <http://www.barcodeoflife.org> [Accessed 10 May 2017]
- Brölemann HW (1931) Myriapodes recueillis par Madame Pruvot en Nouvelle-Calédonie et aux Loyalty. Archives de Zoologie Expérimentale et Générale 72: 275–316.
- Condé B, Nguyen Duy-Jacquemin M (1977) De l'utilisation nouvelle du nom de genre *Lophoturus* Brölemann (Diplopodes, Pénicillates). Bulletin du Muséum national d'histoire naturelle, 3e série, Zoologie, 334(477): 909–915.



- Condé B (1979) Caractères et affinités de *Lophoproctus queenslandicus* Verhoeff (Diplopodes Pénicillates). *Revue Suisse de Zoologie* 86(3): 605–609. <https://doi.org/10.5962/bhl.part.82323>
- Condé B, Nguyen Duy-Jacquemin M (2008) Classification actuelle des Diplopodes Pénicillates (Myriapodes) avec nouvelles définition des taxa. *Bulletin de la Société Zoologique de France*, 133(4): 291–302.
- GenBank (2017) GenBank website: <http://www.ncbi.nlm.nih.gov> [Accessed 13 November 2017]
- Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Window 95/98/NT. *Nucleic Acid Symposium Series* 41: 95–98.
- Huynh C, Veenstra AA (2013) Taxonomy and biology of a new species of Pincushion Millipede of the genus *Monographis* (Diplopoda: Polyxenida) from Australia. 367 *Zootaxa* 3721(6): 573–588. <https://doi.org/10.11646/zootaxa.3721.6.4>
- Huynh C, Veenstra AA (2015) Description of a new species of Penicillate Millipede from the genus *Monographis* (Diplopoda: Polyxenidae) found in Vietnam. *Zootaxa* 3964(4): 460–474. <https://doi.org/10.11646/zootaxa.3964.4.5>
- Ishii K, Nguyen Duy-Jacquemin M, Condé B (1999) The first penicillate millipedes from the vicinity of Manaus, Central Amazonia, Brazil (Diplopoda: Polyxenida). *Amazoniana*, 15(3–4): 239–267.
- Ishii K, Yin Wen-ying (2000) New species of Penicilata (Diplopoda) from Yunnan, Southwest China. In: Aoki J, Yin WY, Imadate G (Eds) *Taxonomical studies on the soil fauna of Yunnan Province in Southwest China*. Tokai University Press, 91–116.
- Jeekel CAW (1963) *Alloproctinus* nom. nov. (Diplopoda, Polyxenida). *Entomologische Berichten* (Amsterdam) 23(8): 156.
- Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular Evolutionary Genetics 379 Analysis Version 7.0 for Bigger Datasets. *Molecular Biology Evolution* 33(7): 1870–4. <https://doi.org/10.1093/molbev/msw054>
- Luan YX, Mallatt JM, Xie RD, Yang YM, Yin WY (2005) The phylogenetic positions of three basal-hexapod groups (Protura, Diplura, and Collembola) based on ribosomal RNA gene sequences. *Molecular Biology and Evolution* 22: 1579–1592. <https://doi.org/10.1093/molbev/msi148>
- Manton SM (1956) The Evolution of Arthropodan Locomotory Mechanisms Part 5: The Structure, Habits and Evolution of the Pselaphognatha (Diplopoda). *Journal of the Linnean Society London* 43: 153–187. <https://doi.org/10.1111/j.1096-3642.1957.tb02516.x>
- Marquet ML, Condé B (1950) Contribution à la connaissance des Diplopodes Pénicillates d'Afrique et de la région madécasse. *Mémoires de l'Institut Scientifique de Madagascar, série A*, 4: 113–134.
- Meyer CP (2003) Molecular systematics of cowries (Gastropoda: Cypraeidae) and diversification patterns in the tropics. *Biological Journal of the Linnean Society* 79: 401–459. <https://doi.org/10.1046/j.1095-8312.2003.00197.x>
- Nguyen Duy-Jacquemin M, Geoffroy JJ (2003) A revised comprehensive checklist, relational database, and taxonomic system of reference for the bristly millipedes of the world (Diplopoda, Polyxenida). *African Invertebrates* 44(1): 89–101.
- Nguyen Duy-Jacquemin M (2014) Two new species of *Lophoturus* (Diplopoda, Penicillata, Lophoproctidae) from caves in Christmas Island, Australia, including the second troglomorphic in Penicillata. *Zoosystema* 36(1): 29–39. <https://doi.org/10.5252/z2014n1a2>



- Pocock RI (1894) *Res ligusticae*. XXI. Contributions to the knowledge of the Diplopoda of Liguria. *Annali del Museo Civico di Storia Naturale di Genova*, serie 2(14): 505–525.
- Schubart O (1947) Os Diplopoda da viagem do naturalista Antenor Leitão de Carvalho aos Rios Araguaia e Amazonas em 1939 e 1940. *Bol Mus Nac Rio de Janeiro Nova sér Zoologia* 82: 1–74.
- Short M, Huynh C (2010) A technique for examination of disagnostic characters of penicillate millipedes. *Memoirs of Queensland Museum, Nature* 55(1): 231–234.
- Silvestri F (1897) *Systema Diplopodum*. *Annali del Museo Civico di Storia Naturale di Genova*, serie 2(18): 644–651.
- Silvestri F (1948) Tavola sinottica dei generi dei Diplopoda Penicillata. *Boll Lab Entomol Agr Portici* 8: 214–220.
- Swofford DL (2002) PAUP\* Phylogenetic Analysis Using Parsimony (\*and other 427 methods), Version 4. Sinauer Associates, Sunderland, MA.
- Turbeville JM, Pfeifer DM, Field KG, Raff RA (1991) The phylogenetic status of arthropods, as inferred from 18S rRNA sequences. *Mol Biol Evol* 8: 669–686.
- Verhoeff KW (1924) Results of Dr. E. Mjöberg's scientific expeditions to Australia 1910–1913. 34. Myriapoda: Diplopoda. *Arkiv för Zoologi* 16(5): 1–142. [pls 1–5]
- Wesener T, Raupach MJ, Sierwald P (2010) The origins of the giant pill-millipedes from Madagascar (Diplopoda: Sphaerotheriida: Arthrosphaeridae). *Molecular Phylogenetics and Evolution* 57: 1184–1193. <https://doi.org/10.1016/j.ympev.2010.08.023>
- Wesener T, Voigtländer K, Decker P, Oeyen JP, Spelda J (2016) Barcoding of Central European Cryptops centipedes reveals large interspecific distances with ghost lineages and new species records from Germany and Austria (Chilopoda, Scolopendromorpha). *ZooKeys* 564: 21–46. <https://doi.org/10.3897/zookeys.564.7535>
- White TJ, Bruns T, Lee S, Taylor JW (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (Eds) *PCR Protocols: A Guide to Methods and Applications*. Academic Press, Inc., New York, 315–322. <https://doi.org/10.1016/B978-0-12-372180-8.50042-1>

# Four new species of the *Glyphiulus javanicus* group from southern China (Diplopoda, Spirostreptida, Cambalopsidae)

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Academic editor: P. Stoev | Received 24 December 2017 | Accepted 21 February 2018 | Published 7 March 2018

<http://zoobank.org/B4832805-14EF-406E-A31E-C6F8D99B7C4B>

**Citation:** Jiang X, Guo X, Chen H, Xie Z (2018) Four new species of the *Glyphiulus javanicus* group from southern China (Diplopoda, Spirostreptida, Cambalopsidae). In: Stoev P, Edgecombe GD (Eds) Proceedings of the 17<sup>th</sup> International Congress of Myriapodology, Krabi, Thailand. ZooKeys 741: 155–179. <https://doi.org/10.3897/zookeys.741.23223>

## Abstract

Hitherto, 24 species of the *Glyphiulus javanicus* group have been recorded, all endemic to Southeast Asia, including 14 in China. Nevertheless, this species group needs further exploration. In this context, four new species of this group are described, all collected from limestone caves in Southern China: *G. calceus* sp. n., *G. foetidus* sp. n., *G. guangnanensis* sp. n., and *G. impletus* sp. n. They can be separated easily from each other and other congeners by their carinotaxic formulae, the structures of male legs I, and the gonopods. Due to the absence of any troglomorphic traits in our specimens, they may be troglophilic only.

## Keywords

Cave, China, *Glyphiulus*, millipede, new species, taxonomy

## Introduction

Since Golovatch et al. (2007b) established and revised the *javanicus*-group, one of two groups of the species-rich millipede genus *Glyphiulus* Gervais, 1847, 25 valid species have been recorded up to date. They are endemic to southeast Asia, distributed from

southern China, across Vietnam, Laos, and Thailand, to Java, Indonesia (Golovatch et al. 2007b, Jiang et al. 2017, Likhitrakarn et al. 2017). Among them, fourteen species occur in China, with most of them being cavernicolous:

- G. echinoides* Golovatch et al., 2011: from a cave in Fushui County, Guangxi Zhuang Autonomous Region;
- G. formosus* (Pocock, 1895): from Hong Kong, known only from female material;
- G. intermedius* Golovatch et al., 2007: from a cave in Chengdu County (possibly Chengdu City), Sichuan Province;
- G. latus* Jiang et al., 2017: from a cave in Muchuan County, Sichuan Province;
- G. liangshanensis* Jiang et al., 2017: from two caves in Liangshan Yi Autonomous Prefecture, Sichuan Province;
- G. oblitteratoides* Golovatch et al., 2007: from three caves in Anshun County, Guizhou Province;
- G. oblitteratus* Golovatch et al., 2007: from a cave in Mile County, Yunnan Province;
- G. paracostulifer* Golovatch et al., 2007: from a cave in Qianlin County, Guizhou Province;
- G. paroblitteratus* Golovatch et al., 2007: from two caves in Suiyang County, Guizhou Province;
- G. pulcher* (Loksa, 1960): from a cave in Fulong Town, Daxin County, Guangxi Zhuang Autonomous Region;
- G. reticulatus* Zhang & Li, 1982: from Qingyuan County, Zhejiang Province;
- G. sinensis* (Meng & Zhang, 1993): from a cave in Guanling County, Guizhou Province;
- G. suboblitteratus* Golovatch et al., 2007: from a cave in Shilin County, Yunnan Province;
- G. zorzini* Mauriès & Nguyen Duy-Jacquemin, 1997: from a cave in Shuicheng County, Guizhou Province.

Recently, several taxonomical surveys of cave millipedes in southern China were carried out. As a result of these investigations, several species of *Glyphiulus* were identified, of which four new species of the *javanicus*-group are described here. Due to the absence of any troglomorphic traits in our specimens, they are thought to be troglophilic. Our findings confirm the hypothesis that southern China harbours an extremely high level of *Glyphiulus* diversity (Golovatch 2015).

## Materials and methods

Live specimens were collected by hand from localities in southern China. Type specimens are deposited in the Institute of Biology, Guizhou Academy of Sciences, Guiyang, China (IBGAS).

Live animals were first observed and photographed with a Canon EOS 5D Mark III camera with a Canon EF 100mm macro lens. All specimens were then preserved in 75 % ethanol. In the lab, some mature specimens were carefully picked out for examina-

tion, illustration, photography, and measuring using a Leica M205C stereomicroscope equipped with a Leica DFC450 Camera and LAS software (Version 4.1). Scanning electron micrographs (SEM) were taken with a Hitachi S-4800 field emission scanning electron microscope. Their geographical distributions were sketched with ArcGIS software (Ver. 10.2). All images were edited with Adobe Photoshop CC 2015 Software.

Terminology used in this paper follows the descriptions by Golovatch et al. (2007a, b, 2011) and Jiang et al. (2017).

## Taxonomy

### Order Spirostreptida Brandt, 1833

### Family Cambalidae Cook, 1895

### Genus *Glyphiulus* Gervais, 1847

#### *Glyphiulus foetidus* sp. n.

<http://zoobank.org/C306F018-1EAF-40C8-AC73-2208DF00FDA9>

Figs 1A, 2–6

**Type material.** **Holotype** male, China: Guangxi Zhuang Autonomous Region, Xilin County, Zhoubang Village, Zhoubang Cave, 24°33.201'N, 105°06.634'E, alt. 820 m, 9 Jan. 2017, X.K. Jiang, H.M. Chen & X. Guo leg. (IBGAS). **Paratypes:** 61 males, 87 females and 12 juveniles, same date and locality as holotype (IBGAS).

**Other material.** One male, Yunnan Province, Guangnan County, Bamei Town, Ake Village, Miaopu Cave, 24°14.767'N, 105°05.384'E, alt. 690 m, 8 Jan. 2017, X.K. Jiang, H.M. Chen & X. Guo leg. (IBGAS).

**Etymology.** This specific name is derived from the Latin word *foetidus*, meaning 'smelly' and refers to the extremely strong and unpleasant smell of the animals.

**Diagnosis.** The new species can be diagnosed by the following combination of morphological characteristics: (1) all crests on collum complete and fully developed, carinotaxic formula I–III + P + M; (2) telopodite of male legs I strongly degenerated, bi-segmented, as high as coxal process; (3) coxosternal mesal process of anterior gonopod prolonged and subtriangular; (4) flagellum of posterior gonopod short, with multiple branches at inner margin. See also Key below.

**Description.** *Body* segments with 53–67p + 1–2a + T (holotype 67p + 1a + T). Body size of ca. 45–63 mm long and 2.3–3.0 mm wide (holotype 62 and 2.7 mm, respectively).

*Colouration.* Brown to dark brown *in vivo* (Fig. 1A). In fixed condition, head red-brown with yellow dapples; collum yellow-brown, anterior and posterior margins and the crests red-brown; midbody red-brown, lateral crests, ozoporiferous tubercles and anterior rows of metatergal crests light yellow; antennae and legs pale to light yellow (Fig. 2).

*Head.* Each eye patch with 30–45 pigmented ocelli arranged in five irregular vertical rows (Fig. 2A, B). Antennae slender, 2.88–3.35 mm long. Terminal part of antennomeres V expanded (Fig. 2B). Gnathochilarium with a separate promentum, polytrichous (Fig. 3A).



**Figure 1.** Living animals. **A** *Glyphiulus foetidus* sp. n. from Zhubang Cave **B** *Glyphiulus calceus* sp. n. from Xianren Cave **C** *Glyphiulus guangnanensis* sp. n. from Miaopu Cave **D** *Glyphiulus impletus* sp. n. from Guanyin Cave.

*Collum.* All crests on collum complete and fully developed, carinotaxic formula I–III + P + M (Fig. 2A, B).

*Body segments.* Postcollum constriction modest (Fig. 2A). Metatergal crests well-developed (Fig. 2A–E). Crests divided into two transverse rows of tubercles, carinotaxic formula 2/2+I/i+3/3+I/i+2/2. Anterior tubercle (except ozoporiferous one) small and round, posterior one strip-shaped (Fig. 2A–E). Ozoporiferous tubercles round, wider than high, obviously larger than other tubercles (Fig. 3E). Location of the tubercle behind ozopore relatively medial, set off from ozoporiferous tubercle (Figs 2C–E, 3E). Lateral crests rather small (Fig. 15). Midbody rings round in cross-section (Fig. 3E), 2.02–2.44 mm high (vertical diameter) and 2.15–2.56 mm wide (horizontal diameter), the ratio of height to width 0.92–0.97.

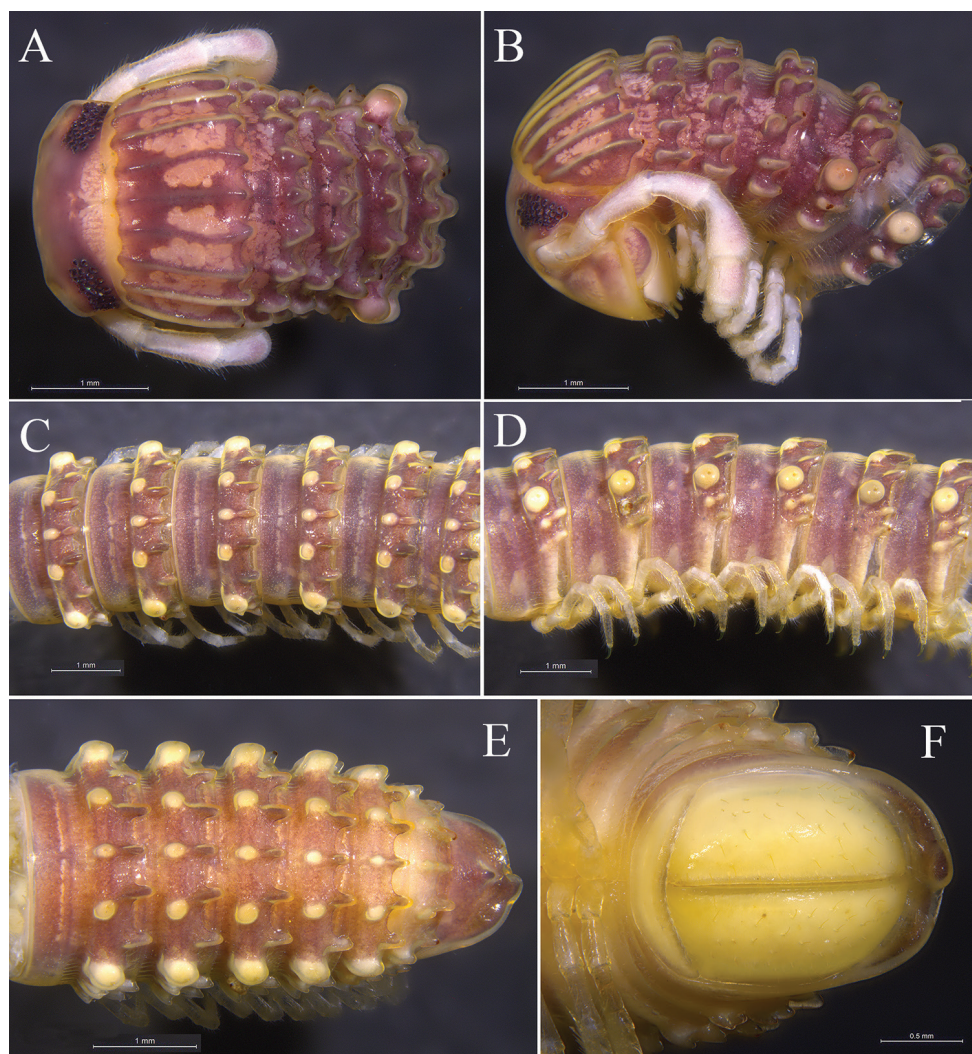
*Telson.* Epiproct simple, with a rounded caudal ridge and a strong dorsal tooth (Fig. 2E). Paraprocts convex, polytrichous. Hypoproct crescent-shaped (Fig. 2F).

*Walking legs.* Slender, 2.71–3.15 mm long, obviously longer than body width (Fig. 3E, F).

*Male sexual characters.* Male legs I strongly degenerated, with a pair of bi-segmented telopodites and a pair of large, subdigitiform, coxal processes. Coxal processes contiguous medially and curved forward, with clusters of long and robust setae at base (Fig. 3B). Male legs II normal. Penes trapeziform and small, each possessing three robust distolateral setae (Fig. 3C). Male legs III modified, with coxa especially slender and elongated (Fig. 3D). Femora VI and VII normal, not inflated.

*Anterior gonopods.* Coxosterna shield-like, sunken medially. Coxosternal mesal processes prolonged, obviously higher than telopodites. Telopodites one-segmented,





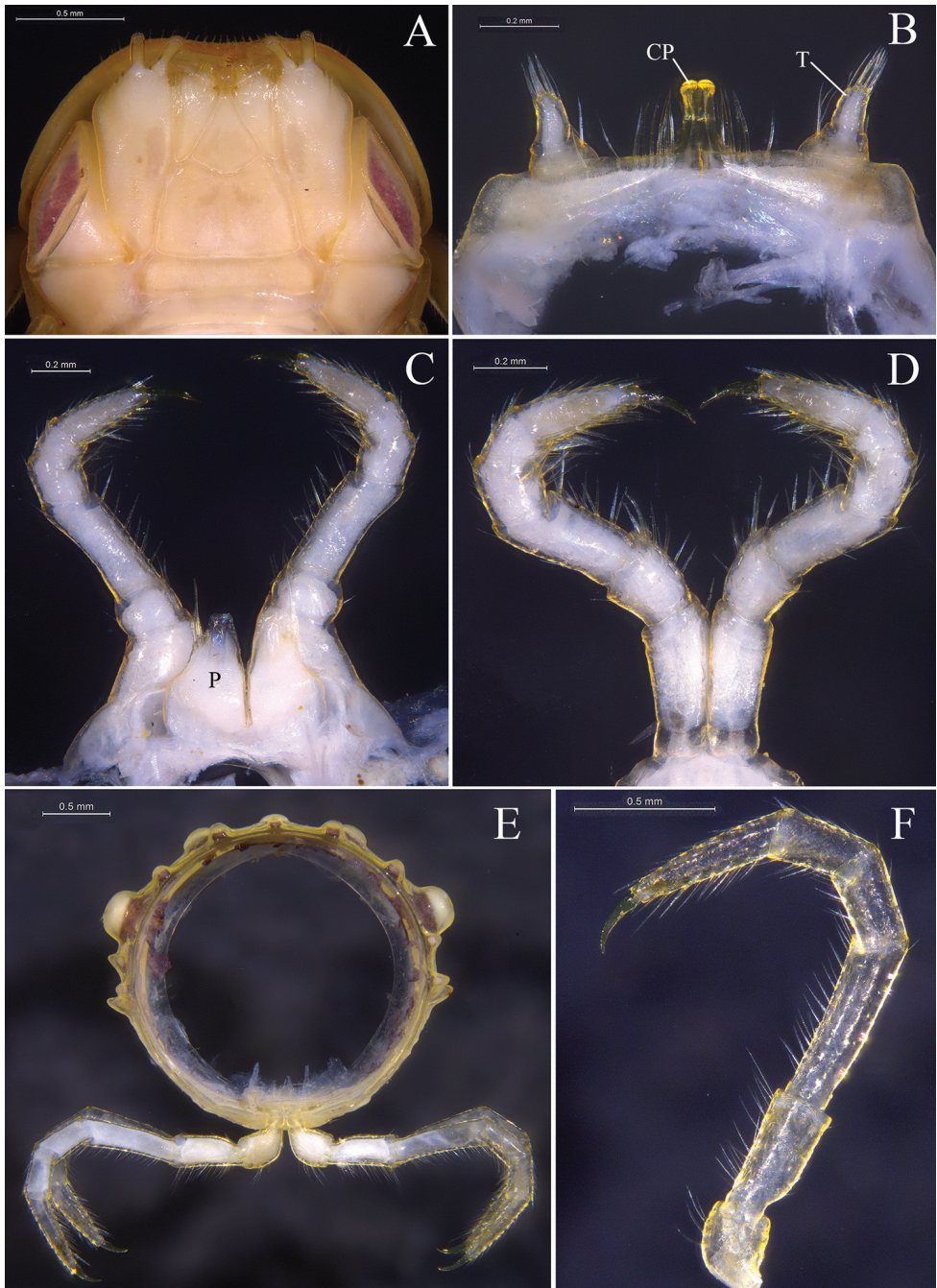
**Figure 2.** *Glyphiulus foetidus* sp. n., holotype. **A** anterior part of body, dorsal view **B** same, lateral view **C** mid-body segments, dorsal view **D** same, lateral view **E** posterior part of body, dorsal view **F** same, ventral view.

placed laterally, curved and moveable, with several distal setae and a field of microsetae at base (Figs 4A, 5A, 6A).

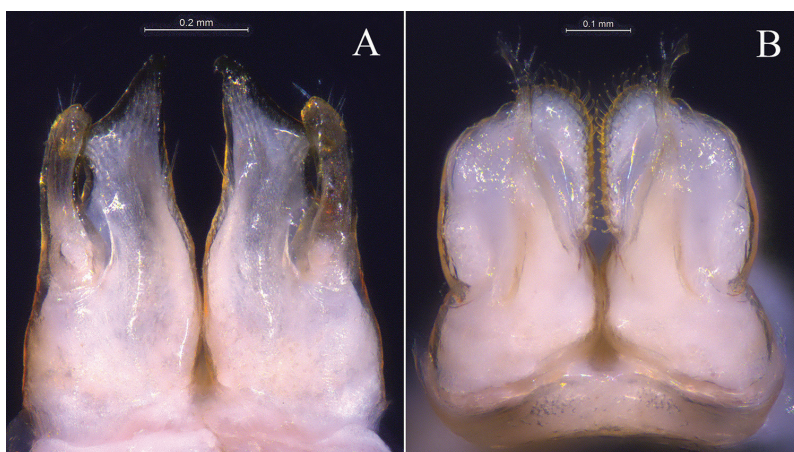
**Posterior gonopods.** Compact (Figs 4B, 5B, 6B). Coxite with a medial lamelliform lobe and two rows of strong and curved setae at mediolateral margin. Flagella short with multiple branches at inner margin (Fig. 5C). Lateral margin with a field of microsetae (Fig. 5D).

**Distribution.** Known only from the type locality, a cave in Xilin County, Guangxi, and another cave in Guangan County, Yunnan. The two caves are ca. 35 kilometres apart.

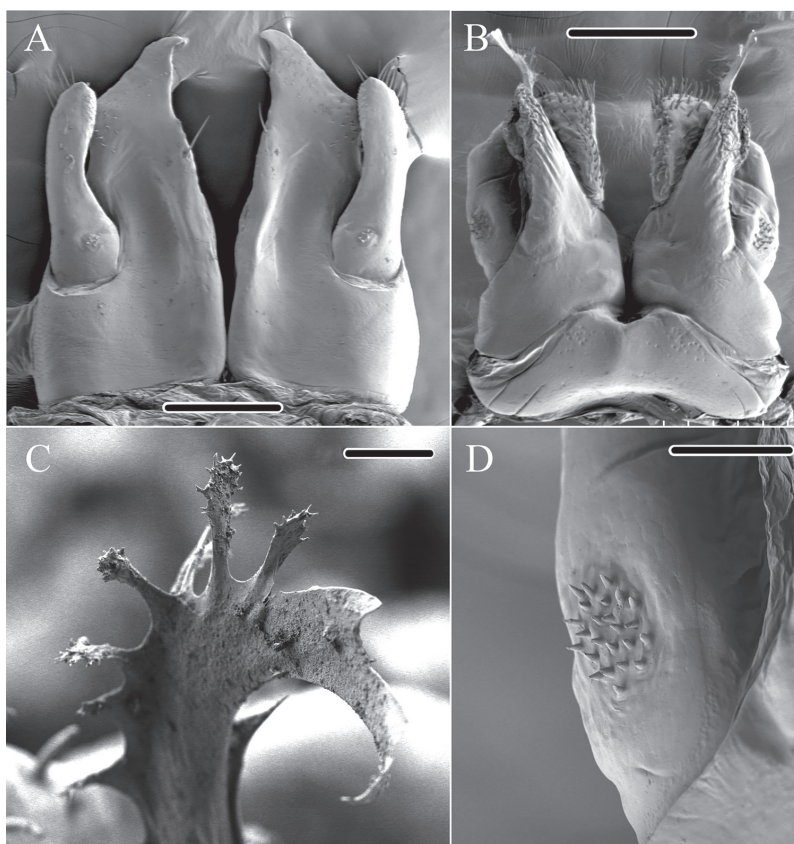




**Figure 3.** *Glyphiulus foetidus* sp. n., holotype. **A** gnathochilarium, ventral view **B** legs I, anterior view **C** legs II, caudal view **D** legs III, caudal view **E** cross-section of a midbody segment, caudal view **F** midbody leg, anterior view. Abbreviations: CP = coxal process; P = penes; T = telopodite.

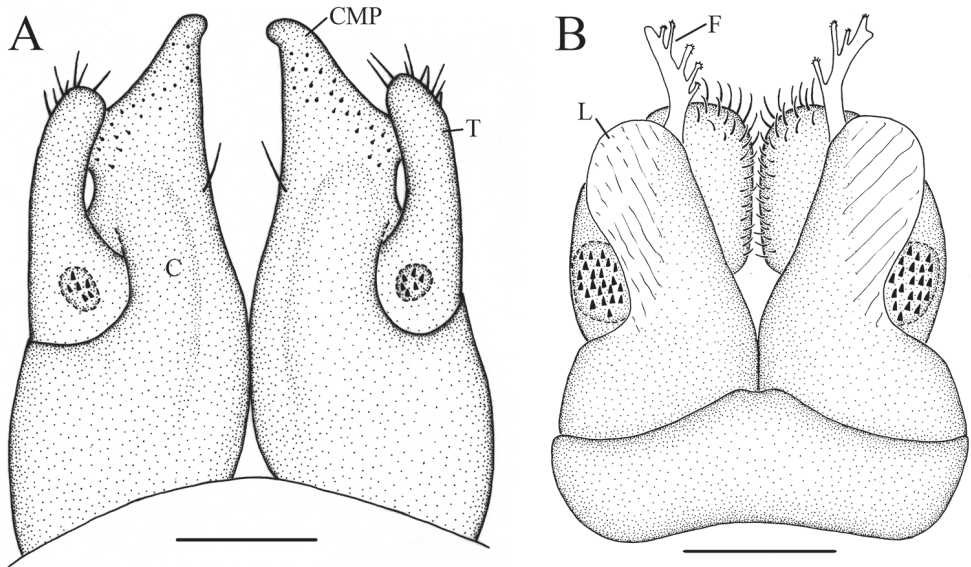


**Figure 4.** *Glyphiulus foetidus* sp. n., holotype. **A** anterior gonopods, caudal view **B** posterior gonopods, caudal view.



**Figure 5.** *Glyphiulus foetidus* sp. n., paratype. **A** anterior gonopods, caudal view **B** posterior gonopods, caudal view **C** flagellum of posterior gonopods **D** microsetae at lateral margin of posterior gonopods. Scale bars: **A, B** 0.2 mm **C, D** 0.02 mm.





**Figure 6.** *Glyphiulus foetidus* sp. n., holotype. **A** anterior gonopods, caudal view **B** posterior gonopods, caudal view. Abbreviations: C = coxosternum; CMP = coxosternal mesal process; F = flagellum; L = lamelliform lobe; T = telopodite. Scale bars: **A, B** 0.2 mm.

***Glyphiulus calceus* sp. n.**

<http://zoobank.org/39980A3D-3D10-4EFB-991D-A58E7AC13B54>

Figs 1B, 7–11

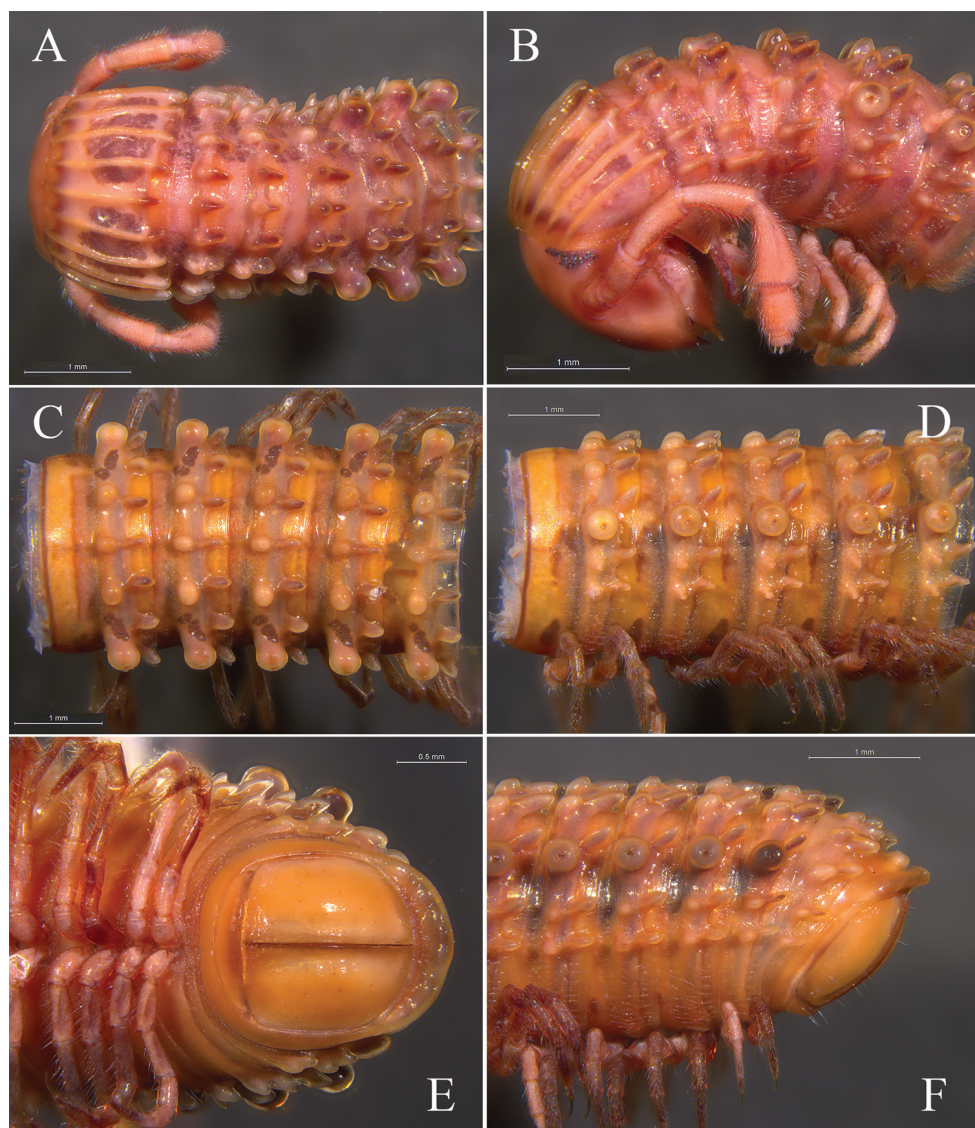
**Type material.** **Holotype** male, China: Guangxi Zhuang Autonomous Region, Tian'e County, Bala Town, Madong Village, Hanyatun, Xianren Cave 24°47.117'N, 107°04.851'E, alt. 900 m, 2 Jan. 2017, X.K. Jiang, H.M. Chen & X. Guo leg. (IB-GAS). **Paratypes:** Thirteen males, 11 females and 1 juvenile, same date and locality as holotype (IBGAS).

**Etymology.** This specific name is derived from the Latin word *calceus*, meaning 'shoe' and refers to the shape of the coxosternal mesal process of the anterior gonopod.

**Diagnosis.** The new species can be diagnosed by the following combination of morphological characteristics: (1) all crests on collum complete and fully developed, carinotaxic formula I–III + P + M; (2) telopodite of male legs I bi-segmented, obviously shorter than coxal process; (3) coxosternal mesal process of anterior gonopod prolonged and shoe-shaped; (4) flagellum of posterior gonopod short and zigzag-shaped. See also Key below.

**Description.** *Body* segments with 58–67p + 1–2a + T (holotype with 67p + 1a + T). Body size of ca. 45–63 mm long and 2.6–3.1 mm wide (holotype 58 and 2.9 mm, respectively).

**Colouration.** Brown to yellow brown *in vivo* (Fig. 1B); brown to red-brown in fixed condition (Fig. 7A–F).



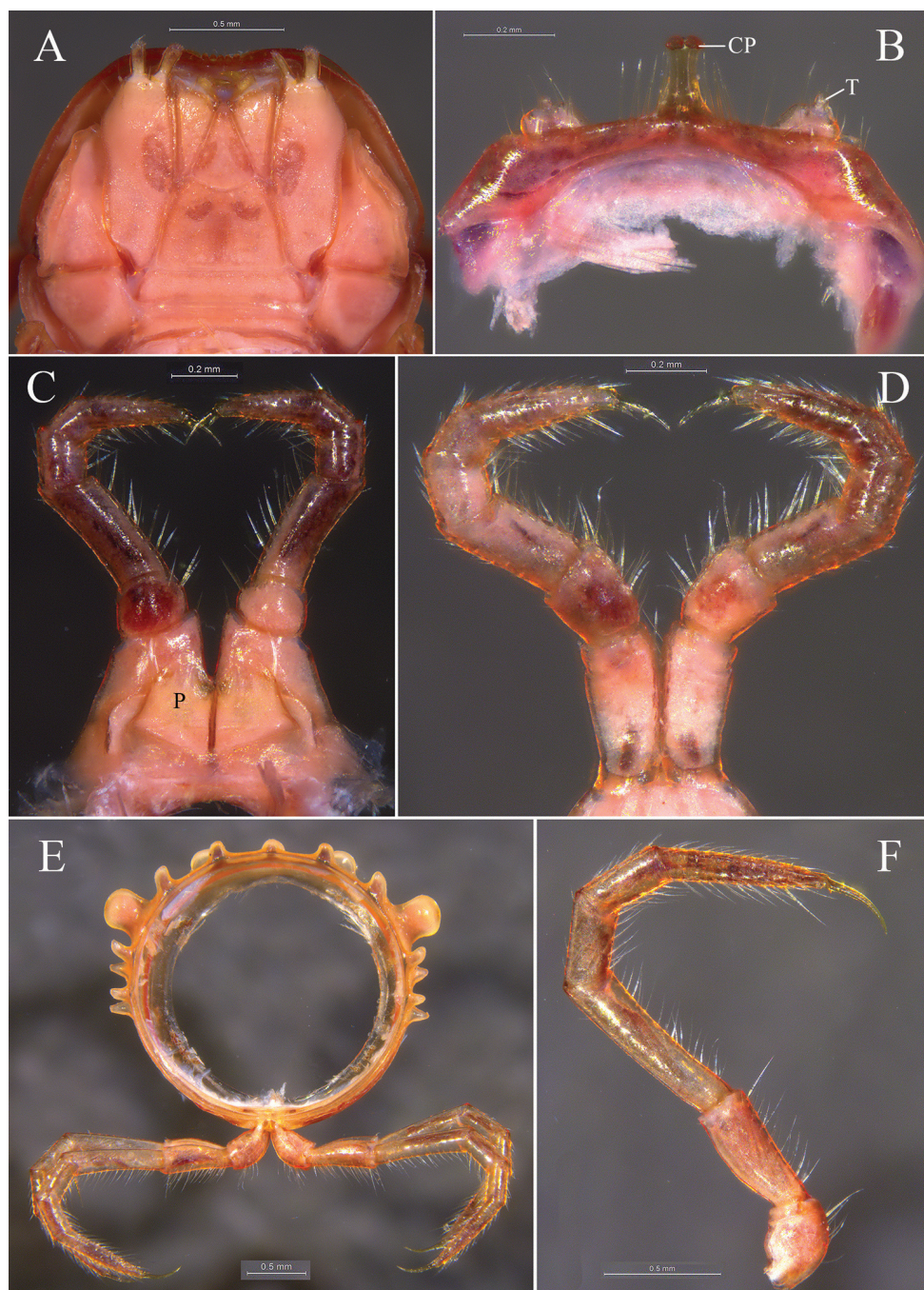
**Figure 7.** *Glyphiulus calceus* sp. n., holotype. **A** anterior part of body, dorsal view **B** same, lateral view **C** mid-body segments, dorsal view **D** same, lateral view **E** posterior part of body, ventral view **F** same, lateral view.

*Head.* Each eye patch with 8–15 pigmented ocelli, arranged in two irregular vertical rows (Fig. 7B). Antennae slender, 2.90–3.28 mm long. Terminal part of antennomeres V expanded (Fig. 7B). Gnathochilarium with a separate promentum, polytrichous (Fig. 8A).

*Collum.* All crests complete and obvious, carinotaxic formula I–III + P + M (Fig. 7A, B).

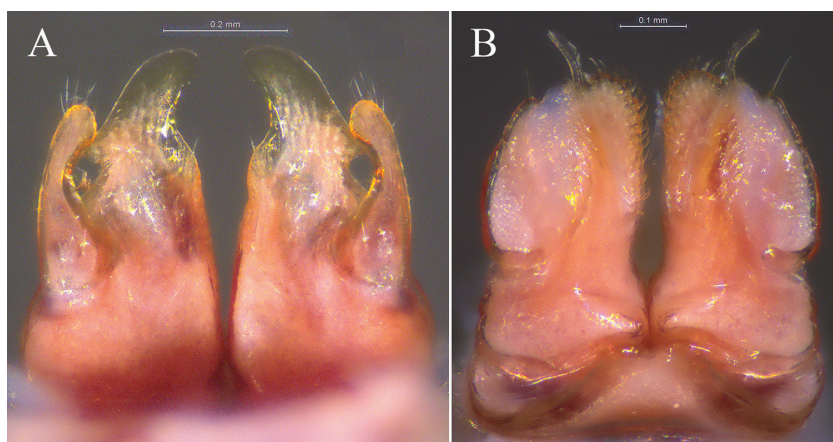
*Body segments.* Postcollum constriction obvious (Fig. 7A). Metaterga strongly crested (Fig. 7A–F). Crests with two transverse rows of tubercles, carinotaxic for-



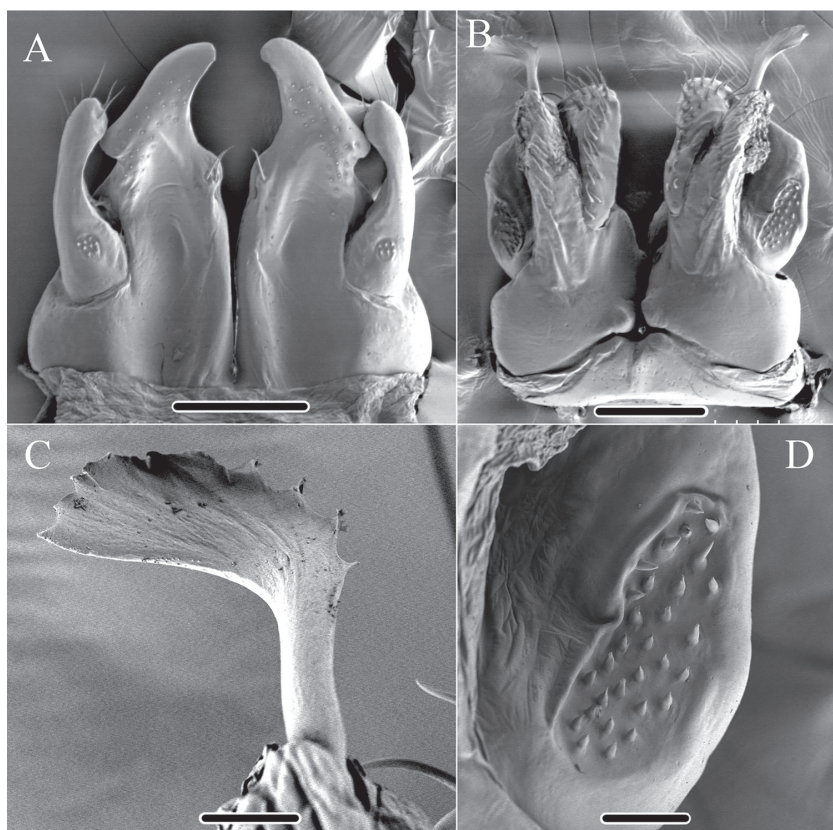


**Figure 8.** *Glyphiulus calceus* sp. n., holotype. **A** gnathochilarium, ventral view **B** legs I, anterior view **C** legs II, caudal view **D** legs III, caudal view **E** cross-section of a midbody segment, caudal view **F** midbody leg, anterior view. Abbreviations: CP = coxal process; P = penes; T = telopodite.

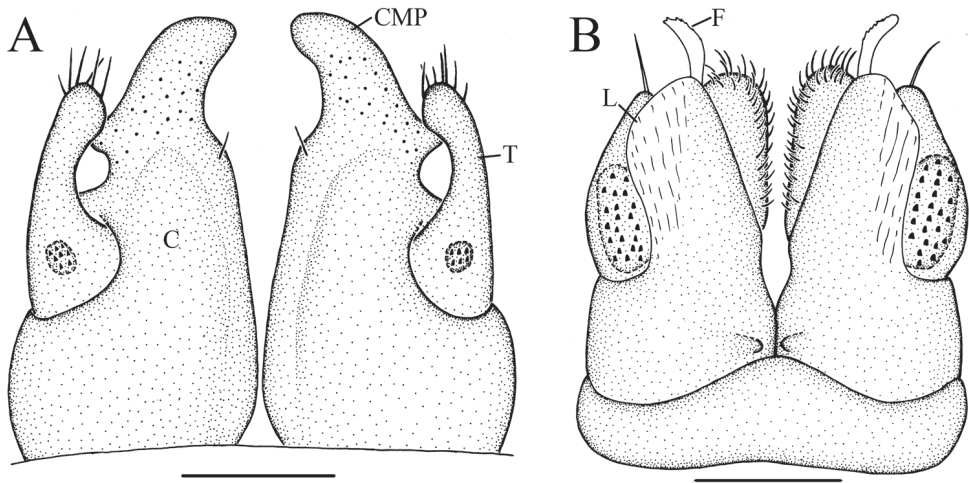




**Figure 9.** *Glyphiulus calceus* sp. n., holotype. **A** anterior gonopods, caudal view **B** posterior gonopods, caudal view.



**Figure 10.** *Glyphiulus calceus* sp. n., paratype. **A** anterior gonopods, caudal view **B** posterior gonopods, caudal view **C** flagellum of posterior gonopods **D** microsetae at lateral margin of posterior gonopods. Scale bars: **A** 0.2 mm **B** 0.15 mm **C** 0.025 mm **D** 0.03 mm.



**Figure 11.** *Glyphiulus calceus* sp. n., holotype. **A** anterior gonopods, caudal view **B** posterior gonopods, caudal view. Abbreviations: C = coxosternum; CMP = coxosternal mesal process; F = flagellum; L = lamelliform lobe; T = telopodite. Scale bars: **A, B** 0.2 mm.

mula 2/2+I/i+3/3+I/i+2/2. Anterior tubercle (except ozoporiferous one) small and upright, posterior one directed caudally, both with sharp tips (Fig. 7A–F). Ozoporiferous tubercle round, higher than broad, obviously larger than other tubercles (Fig. 8E). Location of the tubercle behind ozopore relatively medial, set off from ozoporiferous tubercle in caudal view (Figs 7C, D, 8E). Lateral crests rather small. Midbody rings round in cross-section (Fig. 8E), 2.10–2.48 mm high (vertical diameter) and 2.19–2.59 mm wide (horizontal diameter), the ratio of height to width 0.95–0.98.

**Telson.** Epiproct simple, with a rounded caudal ridge and a strong dorsal tooth. Paraprocts convex. Hypoproct crescent-shaped (Fig. 7E, F).

**Walking legs.** 3.17–3.67 mm long, obviously longer than body width (Fig. 8E, F).

**Male sexual characters.** Telopodite of male legs I strongly degenerated, bi-segmented. Coxal processes obviously longer than telopodites (Fig. 8B). Penes broad, tongue-shaped (Fig. 8C). Male legs III with slender and elongated coxa (Fig. 8D). Femora VI and VII normal, not inflated.

**Anterior gonopods.** Coxosternum shield-like, sunken medially. Coxosternal mesal processes of anterior gonopods elongated and shoe-shaped, obviously higher than telopodites. Telopodite one-segmented, curved and moveable, with round tip and a field of microsetae at base (Figs 9A, 10A, 11A).

**Posterior gonopods.** Mediolateral margins of coxite brush-like. Flagella short and zigzag-shaped (Fig. 10C). A long seta at anterolateral margin (Figs 9B, 11B). Lateral margin with a field of microsetae (Fig. 10D).

**Distribution.** Known only from the type locality, a cave in Tian'e County, Guangxi Zhuang Autonomous Region.



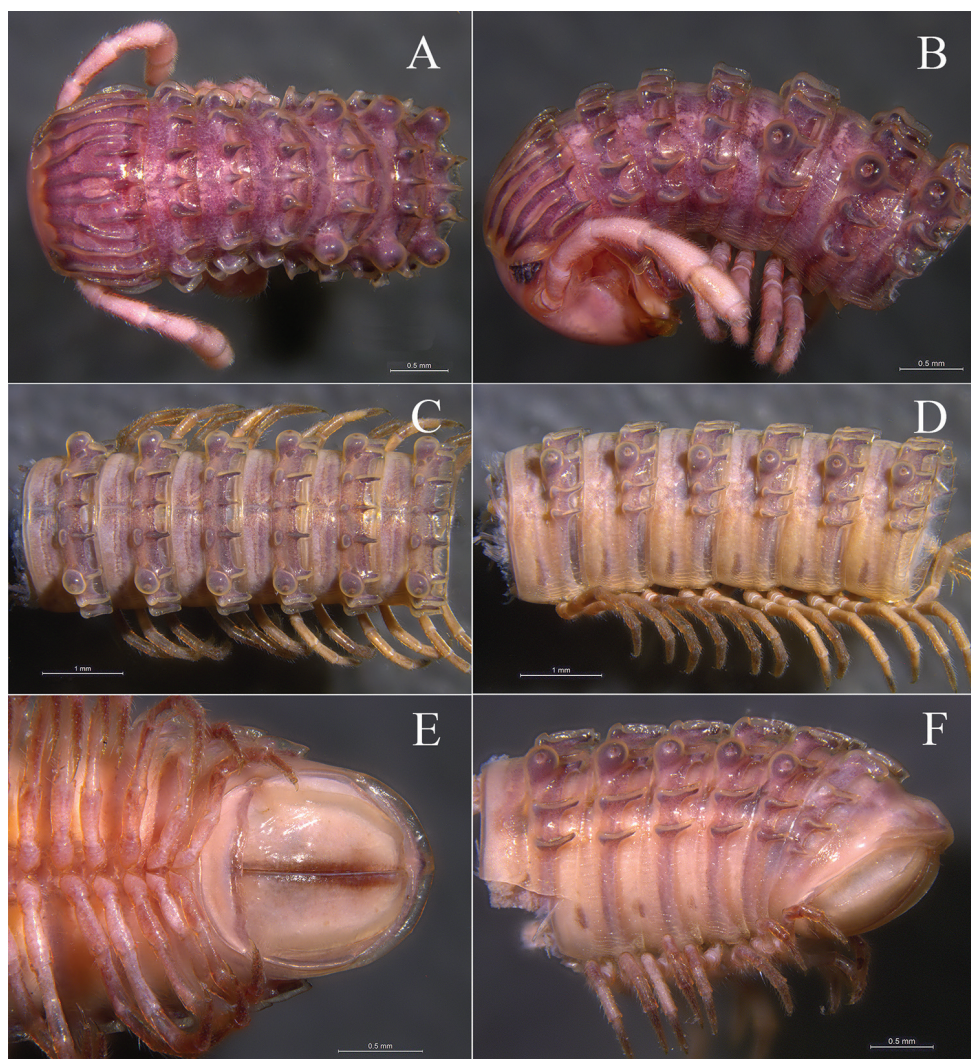
***Glyphiulus guangnanensis* sp. n.**

<http://zoobank.org/EDB6ECE1-6518-443A-8E64-882573FA9B9F>

Figs 1C, 12–16

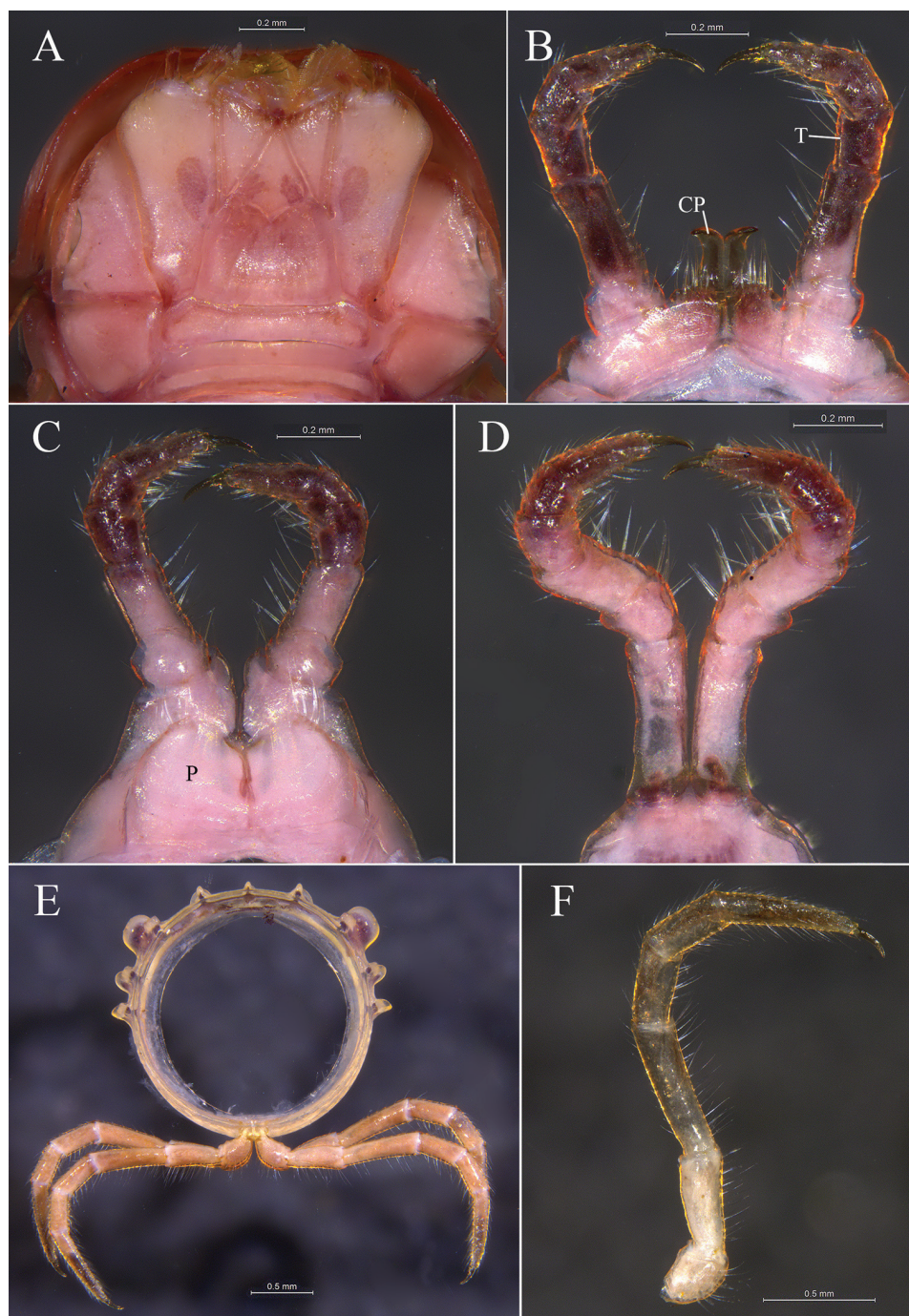
**Type material.** **Holotype** male, China: Yunnan Province, Guangnan County, Bamei Town, Ake Village, Miaopu Cave, 24°14.767'N, 105°05.384'E, alt. 690 m, 8 Jan. 2017, X.K. Jiang, H.M. Chen & X. Guo leg. (IBGAS). **Paratypes:** 9 males, 12 females and 9 juveniles, same date and locality as holotype (IBGAS).

**Etymology.** This specific name is derived from the type locality.



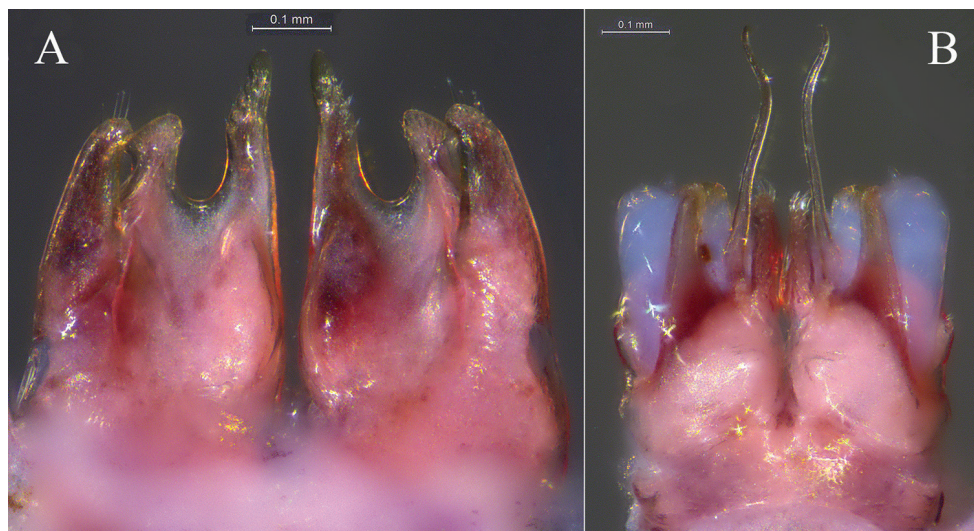
**Figure 12.** *Glyphiulus guangnanensis* sp. n., holotype. **A** anterior part of body, dorsal view **B** same, lateral view **C** midbody segments, dorsal view **D** same, lateral view **E** posterior part of body, ventral view **F** same, lateral view.



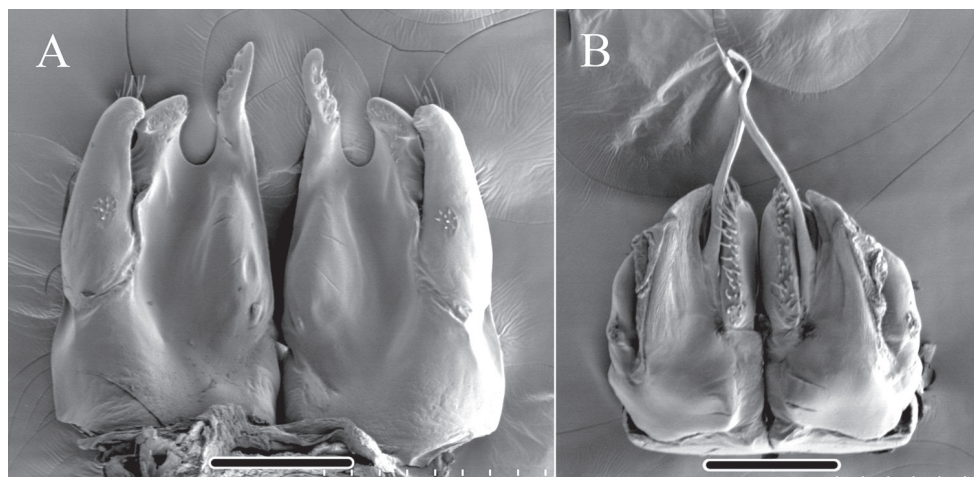


**Figure 13.** *Glyphiulus guangnanensis* sp. n., holotype. **A** gnathochilarium, ventral view **B** legs I, anterior view **C** legs II, caudal view **D** legs III, caudal view **E** cross-section of a midbody segment, caudal view **F** midbody leg, anterior view. Abbreviations: CP = coxal process; P = penes; T = telopodite.



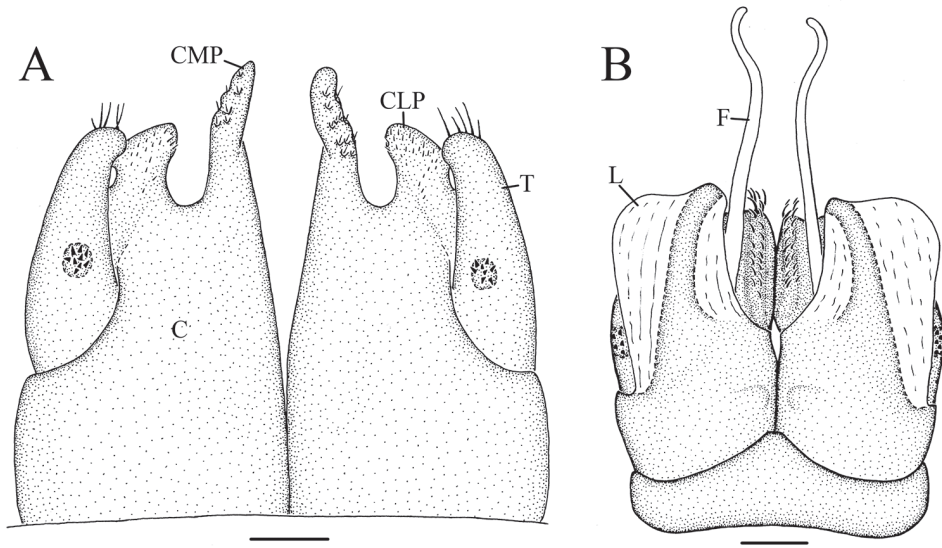


**Figure 14.** *Glyphiulus guangnanensis* sp. n., holotype. **A** anterior gonopods, caudal view **B** posterior gonopods, caudal view.



**Figure 15.** *Glyphiulus guangnanensis* sp. n., paratype. **A** anterior gonopods, caudal view **B** posterior gonopods, caudal view. Scale bars: **A, B** 0.2 mm.

**Diagnosis.** The new species can be diagnosed by the following combination of morphological characteristics: (1) all crests on collum fully developed, carinotaxic formula  $1a+2c+III-IV+5c+6a+pc+ma+pc+6a+5c+IV-III+2c+1a$ ; (2) metatergal crests not divided, carinotaxic formula  $2+I/i+3+I/i+2$  (3) telopodite of male legs I complete, not degenerated, five-segmented; (4) anterior gonopod possessing a coxosternal mesal process and a coxosternal lateral process, coxosternal mesal process with



**Figure 16.** *Glyphiulus guangnanensis* sp. n., holotype. **A** anterior gonopods, caudal view **B** posterior gonopods, caudal view. Abbreviations: C = coxosternum; CLP = coxosternal lateral process; CMP = coxosternal mesal process; F = flagellum; L = lamelliform lobe; T = telopodite. Scale bars: **A, B** 0.1 mm.

a long and sharp tip, coxosternal lateral process with a blunt tip; (5) flagellum of posterior gonopod extremely long and smooth, slightly curved. See also Key below.

**Description.** *Body segments* with 56–73p + 1a + T (holotype 73p + 1a + T). Body size of ca. 38–55 mm long and 2.0–2.3 mm wide (holotype 54 and 2.3 mm, respectively).

*Colouration.* Brown to dark brown *in vivo* (Fig. 1C); taupe to red-brown in fixed condition (Fig. 12A–F).

*Head.* Each eye patch with 9–12 pigmented ocelli arranged in 2–3 irregular vertical rows (Fig. 12B). Antennae slender, 2.20–2.38 mm long. Terminal part of antenno-meres V slightly expanded (Fig. 12B). Gnathochilarium with a separate promentum, polytrichous (Fig. 13A).

*Collum.* All crests developed, carinotaxic formula 1a+2c+III–IV+5c+6a+pc+ma+pc+6a+5c+IV–III+2c+1a (Fig. 12A, B).

*Body segments.* Postcollum constriction modest (Fig. 12A). Metaterga strongly crested (Fig. 12A–F). All metatergal crests undivided (Fig. 12A–D, F), carinotaxic formula 2+I/i+3+I/i+2. Anterior part of crest round and broad, posterior part strip-shaped. Ozo-poriferous tubercles large and round, as high as broad. Lateral crests fully developed. Midbody rings round in cross-section (Fig. 13E), 1.70–2.01 mm high (vertical diameter) and 1.74–2.08 mm wide (horizontal diameter), the ratio of height to width 0.96–0.99.

*Telson.* Epiproct with a rounded caudal ridge and an evident, axial, dorsal rib (Fig. 12F). Paraproct convex, with an evident depression near caudal edge, polytrichous. Hypoproct crescent-shaped (Fig. 12E, F).

*Walking legs.* 2.64–2.80 mm long, obviously longer than body width (Fig. 13E, F).

**Male sexual characters.** Telopodite of male legs I complete, five-segmented (Fig. 13B). Penes rather broad and round (Fig. 13C). Male legs II and III modified as usual (Fig. 13C, D). Femora VI and VII normal, not inflated.

**Anterior gonopods.** Coxosternum shield-like, sunken medially. Distal part of coxosternum with a deep indentation, the latter separating a mesal process and a lateral process. Coxosternal mesal process digitiform, obviously higher than telopodite. Coxosternal lateral process broad, with a blunt tip, nearly as high as telopodite. Telopodite short, one-segmented with thin and round tip and a field of microsetae at base (Figs 14A, 15A, 16A).

**Posterior gonopods.** Mediolateral margins of coxite brush-like. Flagella smooth, curved and extremely long. Lateral margin with a field of microsetae (Figs 14B, 15B, 16B).

**Distribution.** Known only from the type locality, a cave in Guangnan County, Yunnan Province.

**Notes.** Since the definitions of *Glyphiulus* and *Hypocambala* are still uncertain, this new species may be a member of *Hypocambala*. Mauriès (1977) considered that the two genera are distinguished only by the absence (*Hypocambala*) and presence (*Glyphiulus*) of transverse crests on body. Golovatch et al. (2011) dealt with the crests as a species-level character, and transferred *Glyphiulus vietnamicus* Mauriès, 1977 to *Hypocambala* based on the complete male legs I. However, this arrangement didn't fully resolve this problem. In the genus *Glyphiulus*, there are still several species which present the same feature of male legs I and were not transferred to *Hypocambala*, for example *G. costulifer*, *G. intermedius*, *G. parobliteratus*, *G. percostulifer*, *G. pulcher*, and *G. semicostulifer*. A serious revision of the two genera is definitely needed but until then, this new species is assigned to *Glyphiulus*.

Usually, one cave supports one species of Cambalopsidae (Likhitrakarn et al. 2017). However, in our investigations, it was found that two species (*G. guangnanensis* sp. n. and *G. foetidus* sp. n.) could coexist in one place (Miaopu Cave), possibly due to the fact that they are troglophilic. Besides this, sympatry is also true for *G. semigranulatus* (likely troglophilic) and *G. obliteratus* (presumably troglobitic) which coexist in another cave (Bailong Cave).

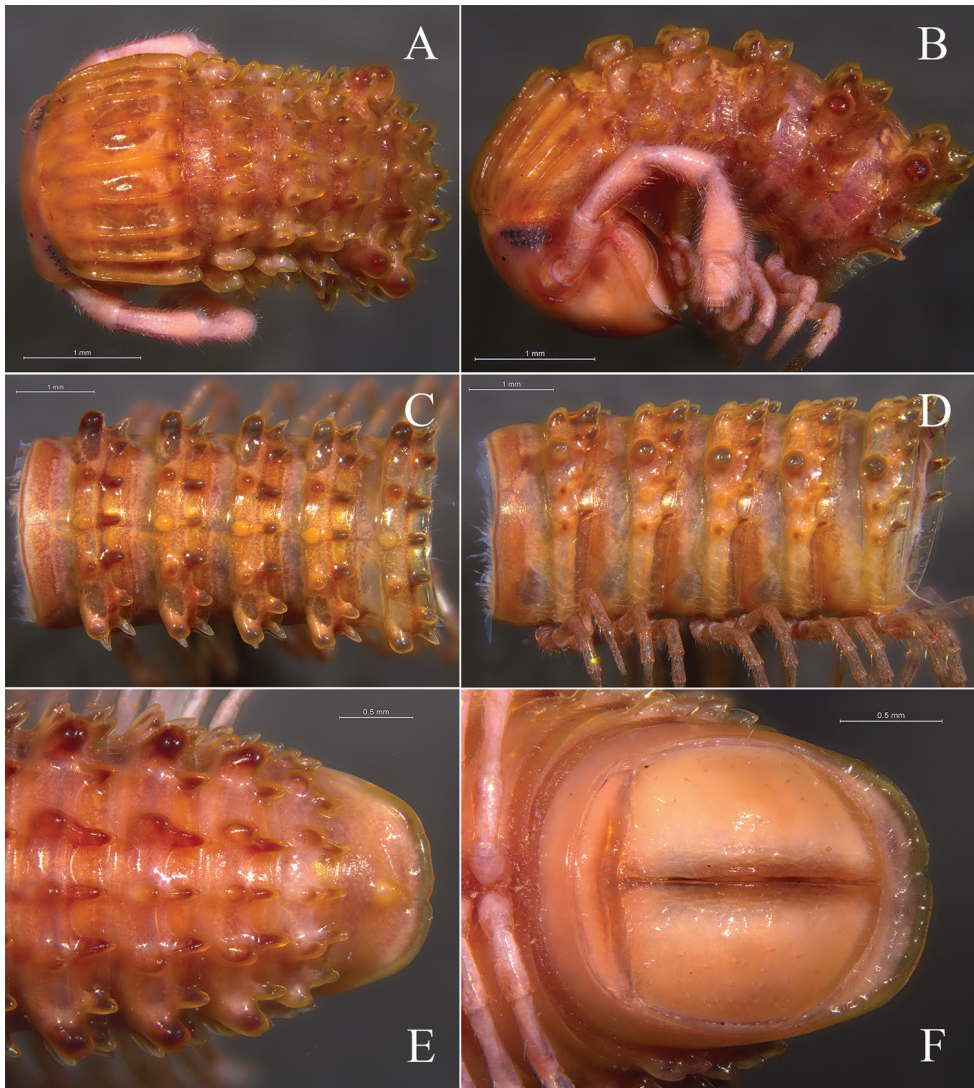
***Glyphiulus impletus* sp. n.**

<http://zoobank.org/F02E3546-7C94-4C0E-8091-88D4999003B4>

Figs 1D, 17–21

**Type material.** **Holotype** male, China: Guangxi Zhuang Autonomous Region, Lingyun County, Luolou Town, Geding Village, Longcitun, Guanyin Cave 24°24.700'N, 106°49.517'E, alt. 830 m, 4 Jan. 2017, X.K. Jiang, H.M. Chen & X. Guo leg. (IBGAS). **Paratypes:** 22 males, 26 females and 9 juveniles, same date and locality as holotype (IBGAS); 17 males, 14 females and 43 juveniles, Lingyun County, Luolou Town, Geding Village, Longweitun, Paifang Cave 24°24.884'N, 106°48.900'E, alt. 830 m, 4 Jan. 2017, X.K. Jiang, H.M. Chen & X. Guo leg. (IBGAS).

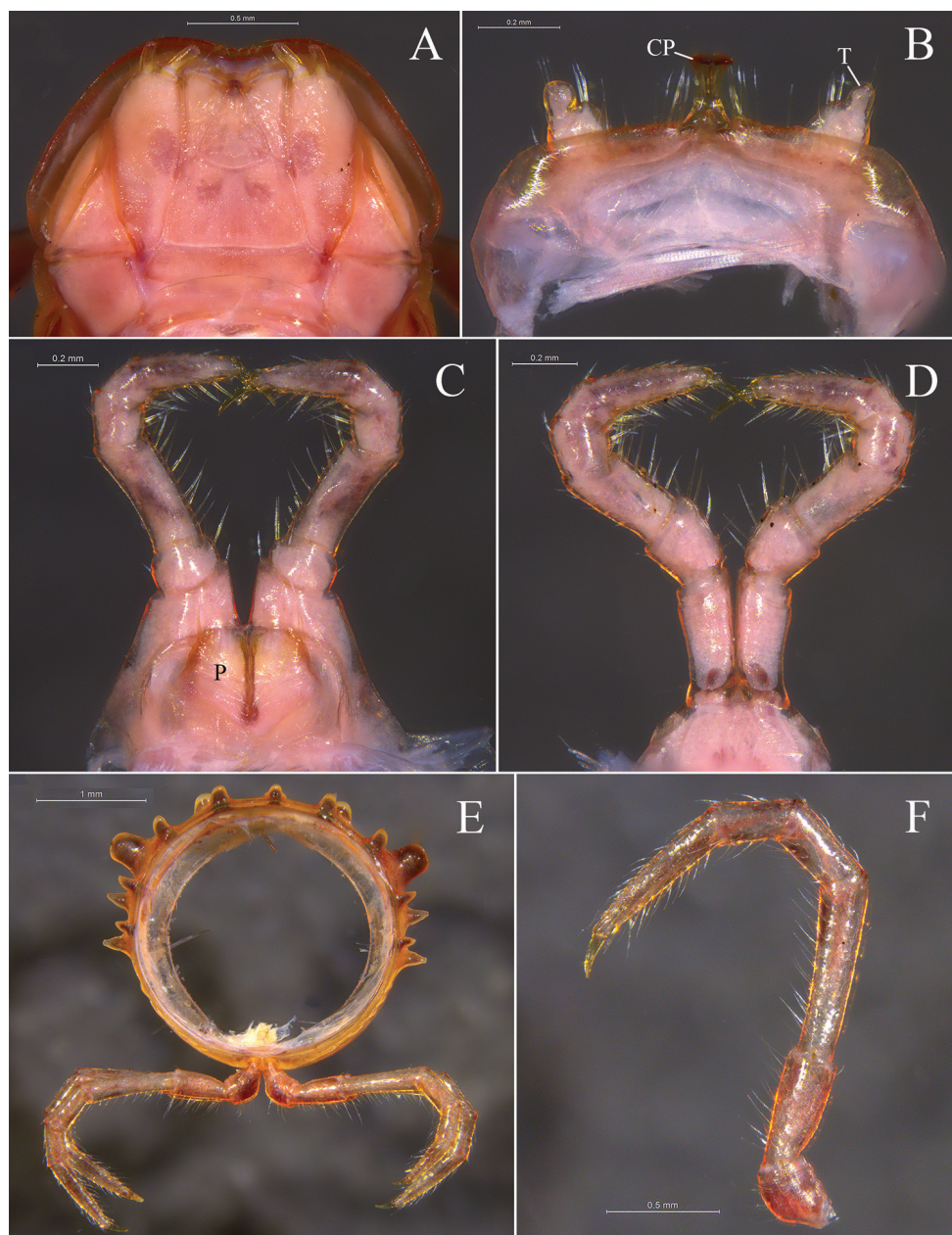




**Figure 17.** *Glyphiulus impletus* sp. n., holotype. **A** anterior part of body, dorsal view **B** same, lateral view **C** midbody segments, dorsal view **D** same, lateral view **E** posterior part of body, dorsal view **F** same, ventral view.

**Other material examined.** Seven males, 6 females and 4 juveniles, Lingyun County, Sicheng Town, Shuiyuan Cave 24°21.992'N, 106°34.670'E, alt. 450 m, 3 Jan. 2011, H.M. Chen leg. (IBGAS); 17 males and 14 females, Lingyun County, Sicheng Town, Naling Cave 24°21.926'N, 106°33.911'E, alt. 500 m, 4 Jan. 2011, H.M. Chen leg. (IBGAS); 3 males and 1 female, Fengshan County, Yuanyang Cave 24°32.518'N, 107°03.768'E, alt. 640 m, 3 Jan. 2017, X.K. Jiang, H.M. Chen & X. Guo leg. (IBGAS); 1 male, 2 females and 1 juvenile, Nandan County, Bachuan Cave 25°03.966'N, 107°37.392'E, 31

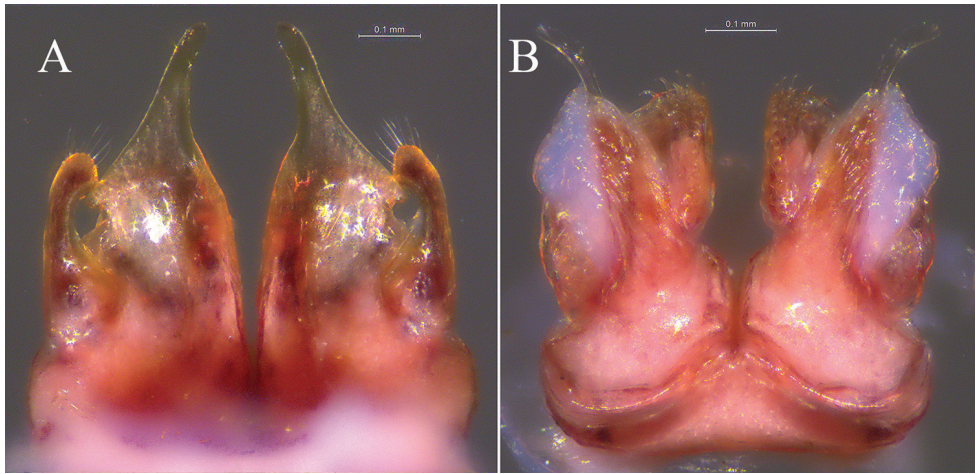




**Figure 18.** *Glyphiulus impletus* sp. n., holotype. **A** gnathochilarium, ventral view **B** legs I, anterior view **C** legs II, caudal view **D** legs III, caudal view **E** cross-section of a midbody segment, caudal view **F** midbody leg, anterior view. Abbreviations: CP = coxal process; P = penes; T = telopodite.

Jan. 2017, H.M. Chen & C. Chen leg. (IBGAS); 17 males, 24 females and 24 juveniles, Donglan County, Xinyan Village, Qiumotun, Ganma Cave 24°26.784'N, 107°20.584'E, alt. 320 m, 2 Feb. 2017, H.M. Chen & C. Chen leg. (IBGAS).





**Figure 19.** *Glyphiulus impletus* sp. n., holotype. **A** anterior gonopods, caudal view **B** posterior gonopods, caudal view.

**Etymology.** This specific name is derived from the Latin word *impletus*, meaning ‘plentiful’, referring to the large number of specimens of the new species in our collections.

**Diagnosis.** The new species can be diagnosed by the following combination of morphological characteristics: (1) all crests on collum complete and fully developed, carinotaxic formula I–III + P + M; (2) telopodite of male leg I bi-segmented, shorter than coxal process; (3) coxosternal mesal process of anterior gonopod slender and strongly prolonged; (4) flagellum of posterior gonopod short and zigzag-shaped. See also Key below.

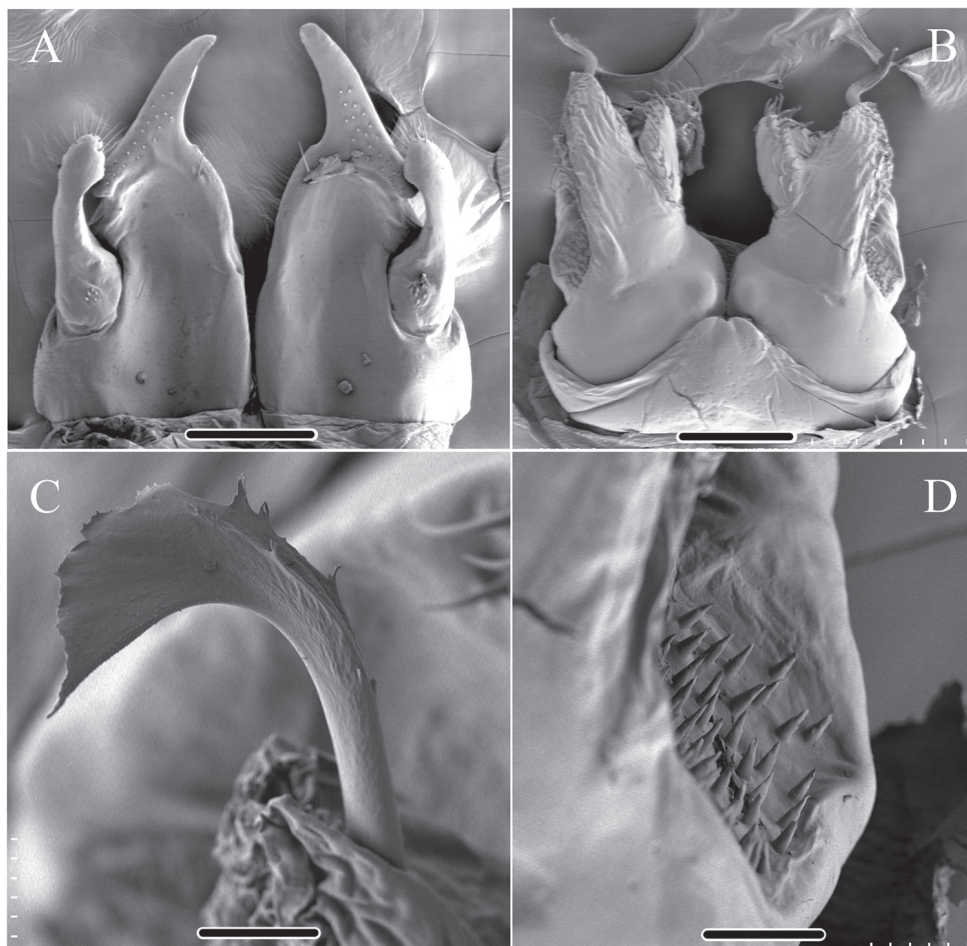
**Description.** *Body segments* with 71–82p + 1a + T (holotype 73p + 1a + T). Body ca. 51–66 mm long and 2.3–3.2 mm wide (holotype 64 mm and 3.0 mm, respectively).

*Colouration.* Brown to dark brown *in vivo* (Fig. 1D). In fixed condition, yellow-brown to red-brown, tergal crests dark red-brown to castaneous brown (Fig. 17A–F).

*Head.* Each eye patch with 7–20 pigmented ocelli arranged in 1–3 irregular vertical rows (Fig. 17A, B). Antennae slender, 2.34–3.31 mm long. Terminal part of antennomeres V obviously expanded (Fig. 17B). Gnathochilarium with a separate promentum, polytrichous (Fig. 18A).

*Collum.* All crests on collum complete and fully developed, carinotaxic formula I–III + P + M (Fig. 17A, B).

*Body segments.* Postcollum constriction modest (Fig. 17A). Metaterga strongly crested (Fig. 17A–E). Metatergal crests divided into two transverse rows of tubercles, carinotaxic formula 2/2+I/i+3/3+I/i+2/2. Anterior tubercle (except ozoporiferous one) small and upright, posterior one directed caudally, both tubercles with sharp tips (Fig. 17A–E). Ozoporiferous tubercle round, higher than broad, obviously larger than



**Figure 20.** *Glyphiulus impletus* sp. n., paratype. **A** anterior gonopods, caudal view **B** posterior gonopods, caudal view **C** flagellum of posterior gonopods **D** microsetae at lateral margin of posterior gonopods. Scale bars: **A** 0.2 mm **B** 0.15 mm **C, D** 0.3 mm.

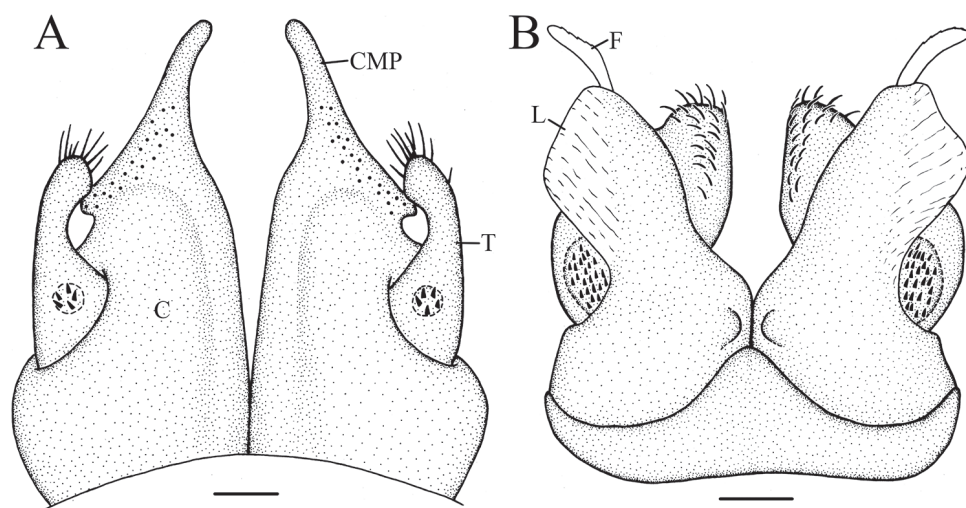
other tubercles (Fig. 18E). Location of the tubercle behind ozopore relatively medial, set off from ozoporiferous tubercle in caudal view (Figs 17B–E, 18E). Lateral crests well developed. Midbody rings round in cross-section (Fig. 18E), 1.88–2.42 mm high (vertical diameter) and 1.91–2.42 mm wide (horizontal diameter), the ratio of height to width 0.95–1.00.

*Telson.* Epiproct simple, with a rounded caudal ridge and a strong dorsal tooth. Paraprocts convex, polytrichous. Hypoproct crescent-shaped (Fig. 17E, F).

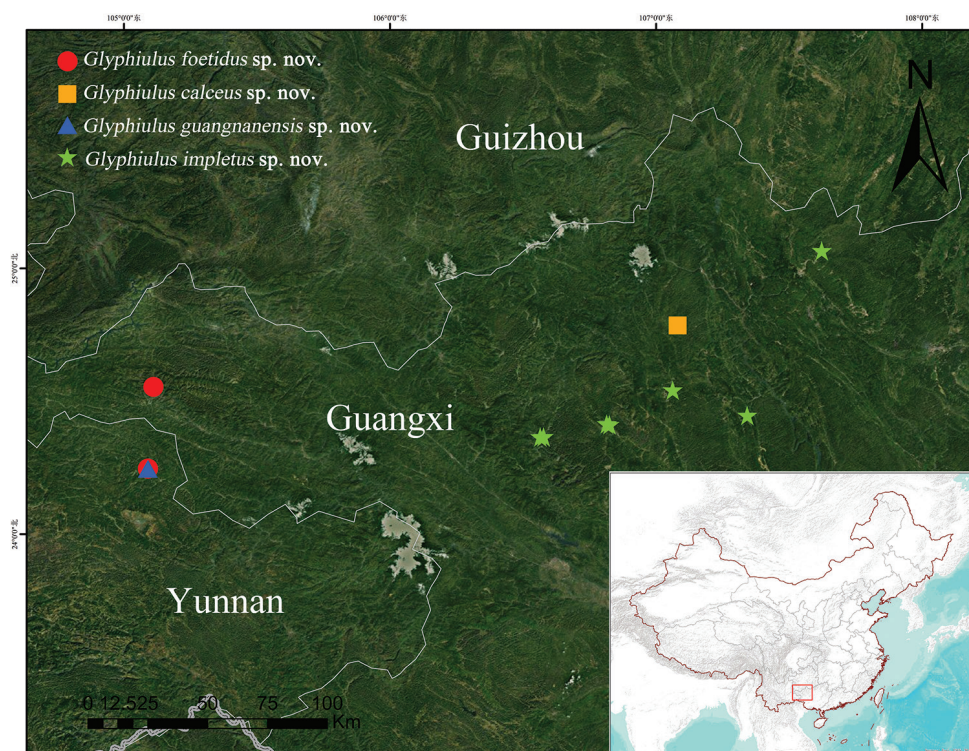
*Walking legs.* Slender, 2.52–3.41 mm long, longer than body width (Fig. 18E, F).

*Male sexual characters.* Telopodite of male legs I strongly degraded, bi-segmented (Fig. 18B). Penes rather small and oval (Fig. 18C). Male legs II and III modified as usual (Fig. 18C, D). Femora VI and VII normal, not inflated.





**Figure 21.** *Glyphiulus impletus* sp. n., holotype. **A** anterior gonopods, caudal view **B** posterior gonopods, caudal view. Abbreviations: C = coxosternum; CMP = coxosternal mesal process; F = flagellum; L = lamelliform lobe; T = telopodite. Scale bars: **A, B** 0.1 mm.



**Figure 22.** Distributions of *Glyphiulus foetidus* sp. n., *Glyphiulus calceus* sp. n., *Glyphiulus guangnanensis* sp. n. and *Glyphiulus impletus* sp. n.

*Anterior gonopods.* Coxosternum shield-like, sunken medially. Coxosternal mesal process slender and strongly prolonged. Telopodite thin, curved with a rounded tip, and a field of microsetae at base (Figs 19A, 20A, 21A).

*Posterior gonopods.* Mediolateral margins of coxite brush-like. Flagella short and zigzag-shaped. Lateral margin with a field of microsetae (Figs 19B, 20B, 21B).

**Distribution.** Known from the type locality and several caves scattered in north-western Guangxi.

**A key to species of the *Glyphiulus javanicus* group currently known from China (except *G. formosus*), based mainly on male characters**

- 1 Crests on collum fully developed (Figs 2A, 7A, 12A, 17A).....2
- At least some crests on collum more or less obliterated.....12
- 2 All crests on collum complete, carinotaxic formula of collum I–III + P + M (Figs 2A, 7A, 17A); epiproct with a strong dorsal tooth (Figs 2E, 7E, 17E); paraprocts convex (Figs 2F, 7E, 17F); telopodites of male legs I strongly reduced, 1–3-segmented (Figs 3B, 8B, 18B); flagella of posterior gonopods short (Figs 4B, 9B, 19B) ..... 3
- Not all crests on collum complete (Fig. 12A); epiproct with an axial dorsal rib (Fig. 12F); paraproct convex, with an evident depression near caudal edge (Fig. 12E); telopodites of male legs I normal or slightly reduced in size, 4–5-segmented (Fig. 13B); flagella of posterior gonopods long (Fig. 14B) ..... 8
- 3 Coxosternal mesal processes of anterior gonopods elongated, obviously higher than telopodites (Figs 4A, 9A, 19A) .....4
- Coxosternal mesal processes of anterior gonopods short.....6
- 4 Flagella of posterior gonopods with multiple branches (Fig. 5C).....  
..... *G. foetidus* sp. n.
- Flagella of posterior gonopods zigzag-shaped (Figs 10C, 20C) .....5
- 5 Coxosternal mesal processes of anterior gonopods shoe-shaped (Figs 9A, 10A, 11A)..... *G. calceus* sp. n.
- Coxosternal mesal processes of anterior gonopods thin and strongly elongated (Figs 19A, 20A, 21A) ..... *G. impletus* sp. n.
- 6 Male femora VI and VII inflated..... *G. recticollis*
- Male femora VI and VII normal, not inflated .....7
- 7 Telopodites of male legs I one-segmented; anterior gonopod coxosternum lower than telopodites..... *G. pulcher*
- Telopodites of male legs I bi-segmented; anterior gonopod coxosternum higher than telopodites ..... *G. echinoides*
- 8 Carinotaxic formula of collum 1a+2c+III–IV+5c+6a+pc+ma (Fig. 12A, B)...  
..... *G. guangnanensis* sp. n.
- Carinotaxic formula of collum not as above.....9



9	Carinotaxic formula of collum I–III+4c+5a+pc+ma.....	10
–	Carinotaxic formula of collum I+2c+III–IV+5c+6a+pc+ma .....	11
10	Carinotaxic formula of midbody segments 2/2+I/i+3/3+I/i+2/2; coxosternal mesal processes of anterior gonopods broad .....	<i>G. latus</i>
–	Carinotaxic formula of midbody segments 2+I/i+3+I/i+2; coxosternal mesal processes of anterior gonopods slender.....	<i>G. paracostulifer</i>
11	Telopodites of male legs I normal, five-segmented; coxosternal mesal processes of anterior gonopods elongated and strong; lamelliform lobes of posterior gonopods obviously elongated .....	<i>G. intermedius</i>
–	Telopodites of male legs I reduced in size, five-segmented; coxosternal mesal processes of anterior gonopods slender; lamelliform lobes of posterior gonopods short.....	<i>G. liangshanensis</i>
12	Telopodites of male legs I normal; coxosternal mesal processes of anterior gonopods elongated; flagella of posterior gonopods long.....	<i>G. parobliteratus</i>
–	Telopodites of male legs I reduced in size, 4–5-segmented; coxosternal mesal processes of anterior gonopods not elongated; flagella of posterior gonopods absent .....	13
13	Collum not completely smooth, only medial crests obliterated .....	<i>G. zorzini</i>
–	Collum smooth, without apparent longitudinal crests.....	14
14	Coxosternal mesal processes of anterior gonopods folded.....	<i>G. oblitteratoides</i>
–	Coxosternal mesal processes of anterior gonopods not folded.....	15
15	Carinotaxic formula of midbody segments 1/1+I/i+3+I/i+1/1; telopodites of male legs I with a claw .....	<i>G. obliteratus</i>
–	Carinotaxic formula of midbody segments 2/2+I/i+3/3+I/i+2/2; telopodites of male legs I without claw.....	16
16	Lamelliform lobes of posterior gonopods elongated .....	<i>G. sinensis</i>
–	Lamelliform lobes of posterior gonopods short .....	<i>G. subobliteratus</i>

## Acknowledgements

Thanks are given to our colleagues, Mr. Hanwu Long and Fujun Zhang (IBGAS), for their assistance during the field work and Mr. Jingcai Lv (IBGAS) for providing the distribution map. We also thank Dr. Peter Decker (Senckenberg Museum of Natural History, Germany) for his assistance with references. The manuscript benefited greatly from comments by Dr. Sergei Golovatch (Russian Academy of Sciences, Russia), Dr. Piyatida Pimvichai (Mahasarakham University, Thailand), and Dr. Pavel Stoev (National Museum of Natural History, Bulgaria). This research was jointly supported by the Talents Introduction Foundation of the Guizhou Academy of Sciences (2009-2), and the Foundation of Biologic Resource and Environment Big Data ([2015] 4013).

## References

- Golovatch SI, Geoffroy J-J, Mauriès J-P, VandenSpiegel D (2007a) Review of the millipede genus *Glyphiulus* Gervais, 1847, with descriptions of new species from Southeast Asia (Diplopoda, Spirostreptida, Cambalopsidae). Part 1. The *granulatus*-group. *Zoosystema* 29(1): 7–49.
- Golovatch SI, Geoffroy J-J, Mauriès J-P, VandenSpiegel D (2007b) Review of the millipede genus *Glyphiulus* Gervais, 1847, with descriptions of new species from Southeast Asia (Diplopoda, Spirostreptida, Cambalopsidae). Part 2. The *javanicus*-group. *Zoosystema* 29(3): 417–456.
- Golovatch SI, Geoffroy J-J, Mauriès J-P, VandenSpiegel D (2011) New species of the millipede genus *Glyphiulus* Gervais, 1847 from the *javanicus*-group (Diplopoda: Spirostreptida: Cambalopsidae). *Arthropoda Selecta* 20(3): 149–165.
- Golovatch SI (2015) Cave Diplopoda of southern China with reference to millipede diversity in Southeast Asia. *ZooKeys* 510: 79–94. <https://doi.org/10.3897/zookeys.510.8640>
- Jiang XK, Lv JC, Guo X, Yu ZG, Chen HM (2017) Two new species of the millipede genus *Glyphiulus* Gervais, 1847 from Southwest China (Diplopoda: Spirostreptida: Cambalopsidae). *Zootaxa* 4323(2): 197–208. <https://doi.org/10.11646/zootaxa.4323.2.3>
- Likhitrakarn N, Golovatch SI, Inkhavilay K, Sutcharit C, Srisonchai R, Panha S (2017) Two new species of the millipede genus *Glyphiulus* Gervais, 1847 from Laos (Diplopoda, Spirostreptida, Cambalopsidae). *ZooKeys* 722: 1–18. <https://doi.org/10.3897/zookeys.722.21192>
- Loksa I (1960) Einige neue Diplopoden- und Chilopodenarten aus chinesischen Höhlen. *Acta Zoologica Academiae Scientiarum Hungaricae* 6: 135–148.
- Mauriès J-P (1977) Le genre *Glyphiulus* Gervais, 1847, et sa place dans la classification des Cambalides, à propos de la description d'une nouvelle espèce du Viêt-Nam (Diplopoda, Iulida, Cambalidea). *Bulletin du Muséum national d'Histoire naturelle 3e série* 431 (Zoologie 301): 243–250.
- Mauriès J-P, Nguyen Duy-Jacquemin M (1997) Nouveaux Craspedosomides et Glyphiulides cavernicoles de Chine (Diplopoda). *Mémoires de Biospéologie* 24: 49–62.
- Meng WX, Zhang CZ (1993) A new troglobitic millipede, *Podoglyphiulus sinensis*, sp. nov. from Guizhou Province (Diplopoda, Spirostreptida, Cambalopsidae). *Proceedings of the 11<sup>th</sup> International Congress of Speleology, August 2003, Beijing*, 130–131.
- Pocock RI (1895) Report upon the Chilopoda and Diplopoda obtained by P. W. Bassett-Smith Esq. Surgeon R. N. and J. J. Walker Esq. R. N. during the cruise in the Chinese seas of H. M. S. "Penguin" Commander W. U. Moore commanding. *Annals and Magazine of Natural History* (6) 15: 121–142.
- Zhang CZ, Li ZY (1982) Die Gattung *Glyphiulus* (Diplopoda: Cambalidea) von China. *Sinozoologia* 2: 85–93.



# *Lithobius (Monotarsobius) meifengensis*, a new species of centipede from high altitude forest in central Taiwan (Chilopoda, Lithobiomorpha, Lithobiidae)

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Academic editor: G. Edgecombe | Received 16 September 2017 | Accepted 10 November 2017 | Published 7 March 2018

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<http://zoobank.org/73E7AAF2-91F5-4248-B150-8E0C9412E77A>

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**Citation:** Chao J-L, Lee K-S, Chang H-S (2018) *Lithobius (Monotarsobius) meifengensis*, a new species of centipede from high altitude forest in central Taiwan (Chilopoda, Lithobiomorpha, Lithobiidae). In: Stoev P, Edgecombe GD (Eds) Proceedings of the 17<sup>th</sup> International Congress of Myriapodology, Krabi, Thailand. ZooKeys 741: 181–192. <https://doi.org/10.3897/zookeys.741.21036>

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## Abstract

*Lithobius (Monotarsobius) meifengensis* **sp. n.** occurring at Mei-Feng Farm, Highland Experimental Farm of National Taiwan University, Nantou, Taiwan, is characterised by a male secondary sexual character on leg 15, a very large ventral swelling occupying almost 50% of the ventral surface of the femur; the gently curved apical region bearing approximately 20 short setae and numerous very small pores of flexo-canal epidermal glands. This male secondary sexual character is described for the first time in the genus *Lithobius*.

## Keywords

*Lithobius*, male secondary sexual character, taxonomy

## Introduction

In some male *Lithobius* species, there are secondary sexual characters on the dorsal surface of the femur or tibia of legs 14 and 15 (Lewis, 1981). In *Lithobius calcaratus* C. L. Koch, 1844, leg 15 has a dorsal wart-like projection on the inner end of the femur (Carballo et al. 1992). For four species described from East Asia: a characteristic



crest with long setae as a Chasen-bamboo whisk at the distal end of the tibia of anal legs is present in *Lithobius (Monotarsobius) tuberculatus* (Murakami, 1965); a small oval region densely covered with small pores of epidermal glands and long setae at the dorsal tibia of legs 15 in *Lithobius (Monotarsobius) sasanus* (Murakami, 1965); a dorsal wart-like projection is present on the femur of legs 15 in *Lithobius (Monotarsobius) dziadoszi* Matic, 1970, and a dorsal wart-like projection on the tibia of legs 15 in *Lithobius (Monotarsobius) riedeli* Matic, 1970. Eason (1973) described the male secondary sexual characters of six species originally assigned to *Lithobius*, mostly from Central America. a shallow excavation bearing a tuft of setae on the dorsal surface of 14<sup>th</sup> tibia, and a small wart-like outgrowth projection from the dorsal excavation on the 15<sup>th</sup> tibia in *Vulcanbius godmani* (Pocock, 1895); a dorsal shallow excavation on the 14<sup>th</sup> tibia in *Vulcanbius salvini* (Pocock, 1895); a crest rises from the dorsal excavation on 15<sup>th</sup> tibia in *Vulcanbius vulcani* (Pocock, 1895); a dorsal wart-like projection on 15<sup>th</sup> tibia in both *Guerrobis pontifex* (Pocock, 1895) and *Guerrobis humberti* (Pocock, 1895); a dorsal wart-like projection on 15<sup>th</sup> femur in *Lithobius obscurus* (Meinert, 1872).

The subgenus *Lithobius (Monotarsobius)* is among the poorly studied taxa of East Asia (Takakuwa 1941a, b; Wang 1955, 1956, 1957, 1959, 1963; Murakami 1965; Matic 1970; Pei et al. 2011; Ma et al. 2009, 2012, 2014). Three species of *Lithobius (Monotarsobius)*: *Lithobius (Monotarsobius) holstii* (Pocock, 1895), *Lithobius (Monotarsobius) obtusus* (Takakuwa, 1941), and *Lithobius (Monotarsobius) ramulosus* (Takakuwa, 1941), were recorded from Taiwan by Takakuwa (1941a, b) and Wang (1955, 1956, 1957, 1959, 1963). However, Takakuwa's specimens were destroyed in an air attack during the war in 1945, and we could not locate Wang's specimens in Taiwan. We studied specimens of centipedes collected from Taiwan, deposited at the National Museum of Natural Science (NMNS) and here describe a new lithobiid.

## Materials and methods

Forty-nine specimens of both sexes of the new species treated below were collected from Mei-Feng Farm, Highland Experimental Farm of National Taiwan University, Nantou, Taiwan. The material was studied using stereo-microscope and SEM. Type specimens are preserved in 75% alcohol and deposited in the department of Zoology, National Museum of Natural Science, Taichung, Taiwan. Terminology for external anatomy follows Bonato et al. (2010). The following abbreviations are used in the text and tables:

<b>T, TT</b>	tergite, tergites;	<b>a</b>	anterior,
<b>F</b>	femur,	<b>t</b>	trochanter,
<b>S, SS</b>	sternite, sternites;	<b>m</b>	median,
<b>Ti</b>	tibia;	<b>P</b>	prefemur,
<b>C</b>	coxa,	<b>p</b>	posterior.

## Taxonomy

### *Lithobius (Monotarsobius) meifengensis* sp. n.

<http://zoobank.org/C7382703-E3CE-445D-8166-6A3C34416C04>

Figures 1–7

**Type material.** **Holotype** ♂ (NMNS7634-073): Taiwan, Nantou County, Mei-Feng Farm, apple orchard, 24°05'N, 121°10'E, 2080 m, 19 Feb 2002, leg. Sheng-Hai Wu.

**Paratypes:** 1♂ (NMNS7634-072), grassland; 1♂ (NMNS7634-074), plum orchard; 1♂ (NMNS7634-075); 1♀ (NMNS7634-068), pear orchard; 2♀ (NMNS7634-071), waste land; 1♂1♀ (NMNS7634-070), grassland; same data as holotype.

**Other material.** 1♀ (NMNS7634-096), pear orchard; 3♀ (NMNS7634-098), plum orchard; 1♂1♀ (NMNS7634-099), plum orchard; 1♂ (NMNS7634-100), pear orchard; 1♂4♀ (NMNS7843-006), grassland; 2♂1♀ (NMNS7843-007), grassland; 1♂2♀ (NMNS7843-003), grassland; 2♂5♀ (NMNS7843-004), plum orchard; 2♀ (NMNS7843-005), pear orchard; 2♀ (NMNS7843-002), grassland; 1♂ (NMNS7843-001), pear orchard; 2♂5♀ (NMNS7843-009), grassland; 2♂1♀ (NMNS7843-008), pear orchard; same locality as holotype, 15 Apr 2002, leg. Sheng-Hai Wu.

**Etymology.** Refers to the type locality.

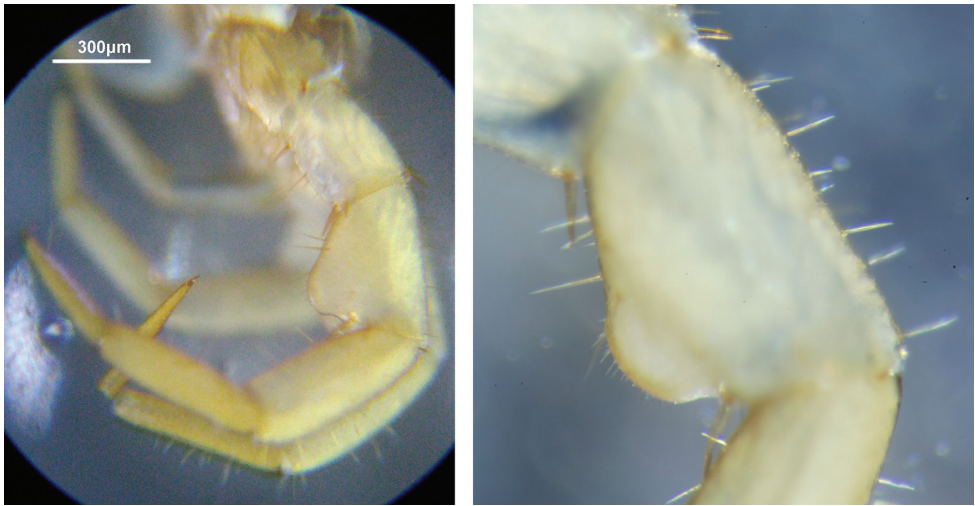
**Diagnosis.** A species of the genus *Lithobius* Leach, 1814, subgenus *Monotarsobius* Verhoeff, 1905, normally with 19+19 elongate antennal articles, body length approximately 9 mm; cephalic plate 0.8–0.9 times as long as wide; six ocelli [one posterior and three dorsal, two ventral] on each side, posterior ocellus comparatively large; Tömösváry's organ moderately small, slightly larger than adjacent ocelli; 2+2 coxosternal teeth; porodonts moderately slender, posterolateral to the outer tooth; posterior angles of all tergites lacking triangular projections; tarsi fused on legs 1–13; male secondary sexual characters on legs 15, a large ventral domed swelling on femur (Figure 1), and a dorsal shallow excavation on tarsus 2; coxal pores round, 3333 in males, 3443 or 3444 in females; female gonopods with 2+2 sharp coniform spurs, claw undivided.

**Description.** Body length: 7.0–9.8 mm. Body colour (in alcohol): yellowish with dark patches.

*Antennae* with 19 articles (Figure 2A); basal three articles typically wider than long, following articles markedly longer than wide; distal article much longer than wide, up to 2.8 times as long as wide; abundant setae on antennal surface, less so on basal articles, gradual increase in density to around fourth article, then more or less constant in number.

*Cephalic plate* smooth, convex, 0.8–0.9 times as long as wide; posterior marginal ridge moderately broader and weakly concave (Figure 2B); small pores of flexo-canal epidermal glands (gp), large pores of recto-canal epidermal glands (gp\*) and setae scattered sparsely over the whole surface (Figure 2C) (Müller, 2009).

Six *ocelli* on each side, one posterior and three dorsal, two ventral, arranged in two irregular row (Figure 3A); the posterior ocellus comparatively large; ocelli domed, translucent, usually darkly pigmented.



**Figure 1.** *Lithobius (Monotarsobius) meifengensis* sp. n., **A** ♂ (NMNS7843-004), lateral view of male 15<sup>th</sup> legs **B** ♂ (NMNS7634-074), lateral view of male 15<sup>th</sup> femur.

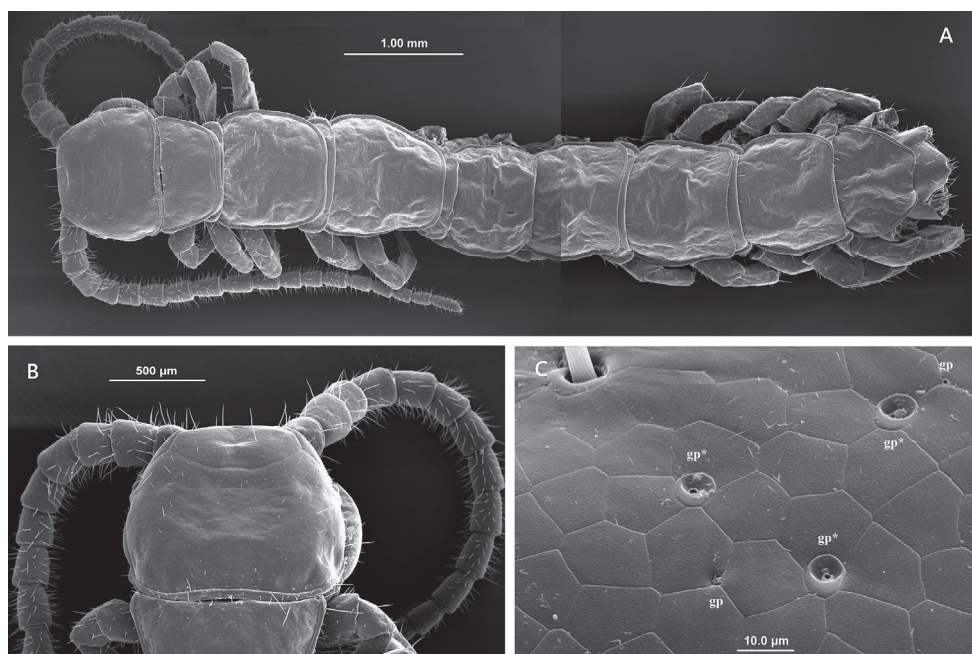
*Tömösváry's organ* comparatively small, nearly rounded; situated at anterolateral margin of cephalic plate, slightly bigger than the adjoining ocelli (Figure 3B).

*Forcipular coxosternite* sub-trapezoidal, anterior margin narrow, external side lightly longer than internal side; median longitudinal cleft moderately deep (Figure 4A); anterior border with 2+2 large triangular coxosternal teeth, inner tooth slightly larger than outer one; porodonts moderately slender, setiform, posterolateral to the outer tooth (Figure 4B); some scattered setae on the ventral side of coxosternite.

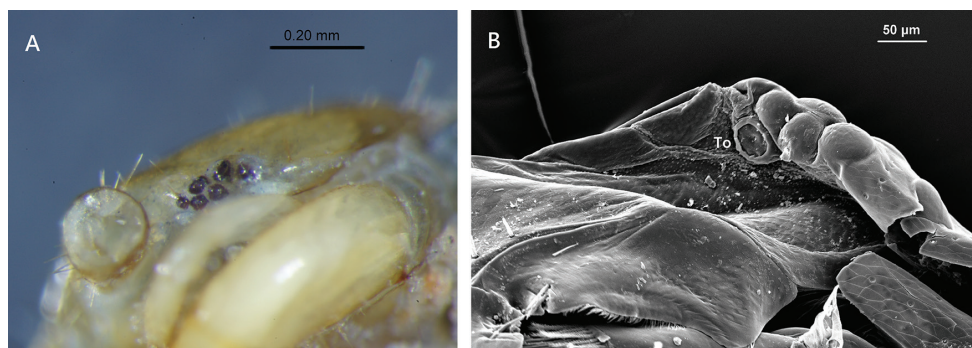
*Tergites* smooth, without wrinkles, backside slightly hunched; T1 generally trapeziform, posterior margin narrower than anterior margin, narrower than T3 and the cephalic plate; T3 slightly narrower than the cephalic plate; posterior margin of TT1, 3, 5, 8, 10 and 12 weakly concave; TT1, 3 and 5 with continuous lateral and posterior marginal ridges, other tergites with discontinuous posterior marginal ridges; posterior angles of all tergites lacking triangular projections (Figure 2A); tiny setae scattered very sparsely over the surface.

*Sternites* narrower posteriorly, generally trapeziform, comparatively smooth, setae emerging from pores scattered very sparsely over the surface.

*Legs*: tarsi fused on legs 1–13 (Figure 5A), well-defined on legs 14–15; all legs with fairly long claws, curved ventrally; anterior and posterior accessory spines on legs 1–14, the anterior one moderately slender, the posterior spine short and thick (Figure 5B); legs 15 lack anterior accessory spines; legs 14–15 with numerous large pores (9.1–11.1 µm) of the telopodal glands on the inner surfaces of femur, tibia, tarsus 1 and tarsus 2 (Figure 5C), the pores each opening into the centre of a bell-shaped cavity (3.5–3.9 µm) (Figure 5C), some small pores (1.4–1.6 µm) of flexo-canal epidermal glands sparsely distributed along the border of the epidermal cells (Figure 5D). Male 15<sup>th</sup> legs with secondary sexual character; female legs 15 and other legs without secondary sexual characters on femur or tibia (Figure 7A). Leg plectrotaxy as in Table 1.



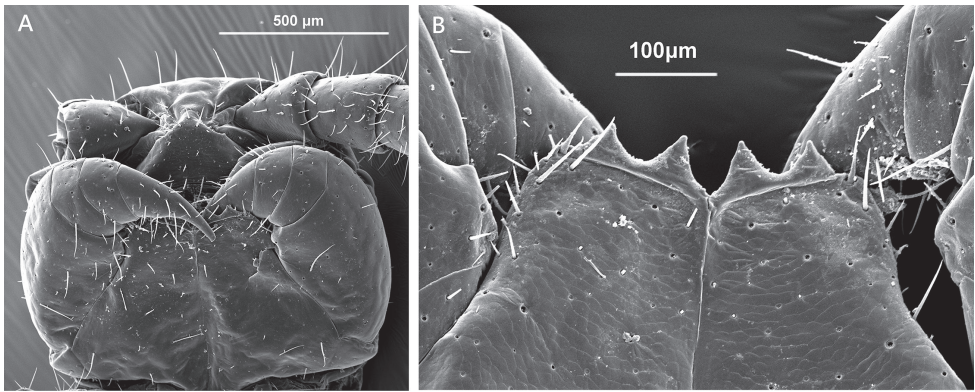
**Figure 2.** *Lithobius (Monotarsobius) meifengensis* sp. n. ♂ (NMNS7843-007), **A** habitus, dorsal view **B** cephalic plate **C** small pores of flexo-canal epidermal glands (gp) and large pores of recto-canal epidermal glands (gp\*) on the cephalic plate.



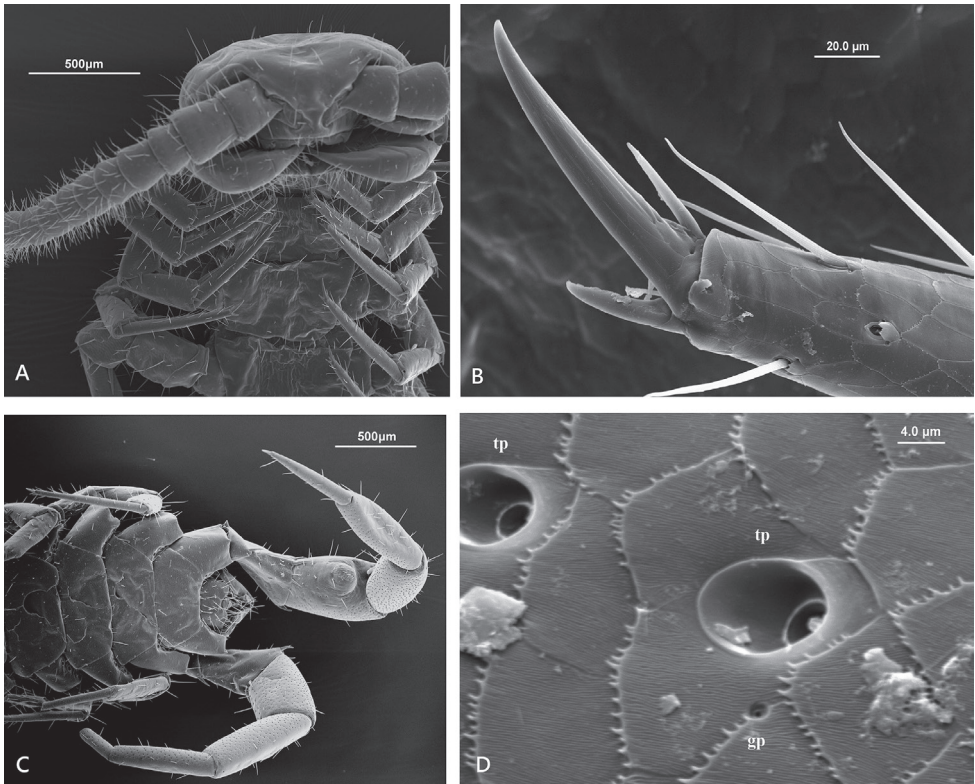
**Figure 3.** *Lithobius (Monotarsobius) meifengensis* sp. n. **A** ♂ (NMNS7843-004), six ocelli on right side **B** ♂ (NMNS7843-008), Tömösváry's organ (To).

Male secondary sexual character on leg 15: a large domed swelling on the ventral surface of femur, covering almost 50% (Figure 1, 6A); the surface of femoral swelling lacks the large pores of the telopodal glands (Figure 6B); the gently curved apical region bears approximately 20 short setae, and numerous very small pores (0.8–1.0 µm) of flexo-canal epidermal glands densely distributed (Figure 6C); a dorsal shallow excavation on the tarsus 2 (Figure 5C).

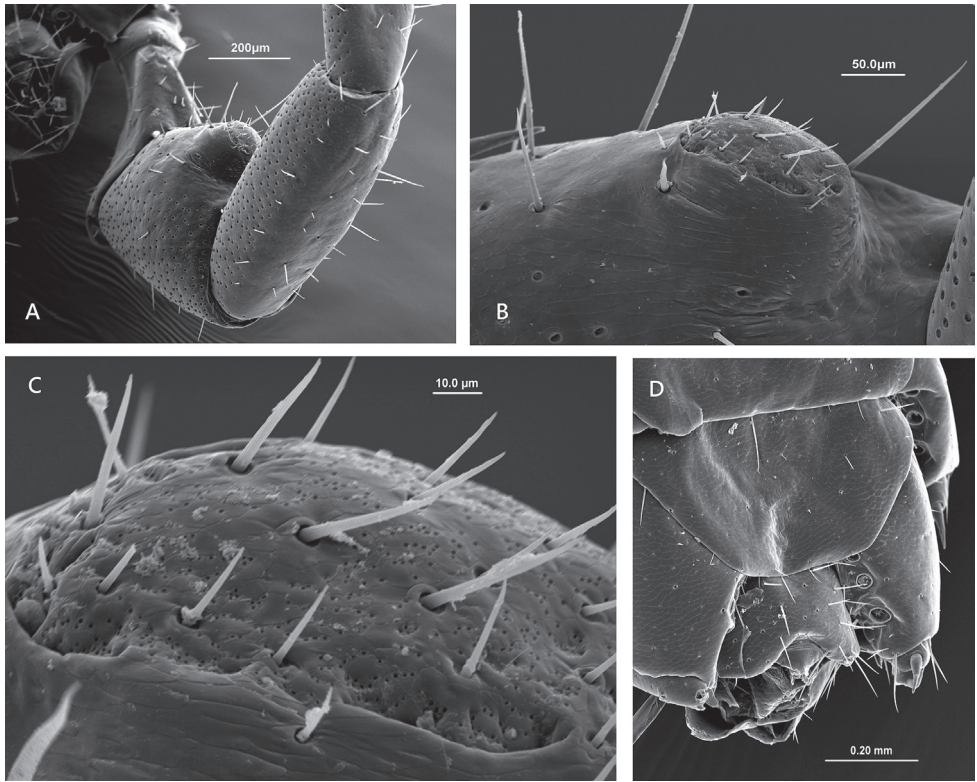




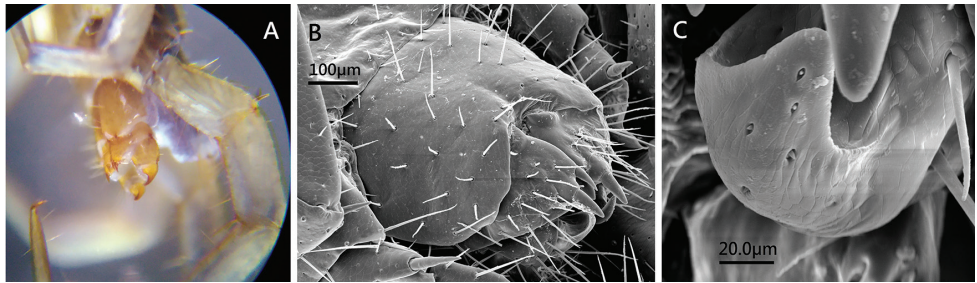
**Figure 4.** *Lithobius (Monotarsobius) meifengensis* sp. n., **A** ♂ (NMNS7634-070), ventral view of the head **B** ♂ (NMNS7843-008), coxosternal teeth and prodonts.



**Figure 5.** *Lithobius (Monotarsobius) meifengensis* sp. n. **A, B**, ♀NMNS7843-009: **A** the 1<sup>st</sup> to 4<sup>th</sup> leg-bearing segments, ventral view **B** the claw of 4<sup>th</sup> leg **C, D** ♂ NMNS7634-070): **C** left 15<sup>th</sup> leg and right 14<sup>th</sup> leg, lateral-ventral view **D** large pores of the telopodal glands (tp) and small pore of flexo-canal epidermal gland (gp) on the 15<sup>th</sup> leg.



**Figure 6.** *Lithobius (Monotarsobius) meifengensis* sp. n. **A–C** ♂ NMNS7634-070): **A** the femur and tibia of male 15<sup>th</sup> leg, ventral view **B** a large domed swelling on the ventral surface of male 15<sup>th</sup> femur **C** apical region of the swelling on the male 15<sup>th</sup> femur **D** ♂ NMNS7843-008, male genital sternite and 15<sup>th</sup> sternite.



**Figure 7.** *Lithobius (Monotarsobius) meifengensis* sp. n. **A** (♀ NMNS7843-005): 15<sup>th</sup> leg and female gonopod; **B, C** (♀ NMNS7843-009): **B** female genital sternite **C** terminal claw of female gonopod.

**Table 1.** Leg plectrotaxy of *Lithobius (Monotarsobius) meifengensis* sp. n.

leg	Ventral					Dorsal				
	C	t	P	F	Ti	C	t	P	F	Ti
1	–	–	–	am	m	–	–	p	ap	a
2	–	–	–	am	m	–	–	p	ap	a
3	–	–	–	am	m	–	–	p	ap	a
4	–	–	–	am	m	–	–	p	ap	a
5	–	–	–	am	m	–	–	p	ap	a
6	–	–	–	am	m	–	–	p	ap	ap
7	–	–	–	am	m	–	–	p	ap	ap
8	–	–	m	am	m	–	–	ap	ap	ap
9	–	–	m	am	m	–	–	ap	ap	ap
10	–	–	m	am	am	–	–	ap	ap	ap
11	–	–	mp	amp	am	–	–	ap	ap	ap
12	–	m	mp	amp	am	–	–	amp	ap	ap
13	–	m	mp	amp	am	–	–	amp	p	ap
14	–	m	mp	am	–	–	–	amp	–	–
15	–	m	amp	am	–	–	–	amp	–	–

*Coxal pores:* 3333 in males, 3443 or 3444 in females, round, coxal pore field set in a relatively shallow groove, margin of coxal pore-field with slightly eminence.

*Male sternite 15:* trapeziform, posterolaterally narrower than anterolaterally, posterior margin straight, long setae scattered sparsely over the surface.

Male first genital sternite: wider than long, usually well chitinised; posterior margin quite deeply concave between the gonopods, without a medial bulge (Figure 6D); comparatively long setae evenly scattered on the ventral surface; gonopods short and small, with 2–3 long setae, apically slightly chitinized.

*Female sternite 15:* generally trapeziform, anterolaterally broader than posterolaterally, posterior margin straight, long setae scattered sparsely over the surface; the sternite of genital segment well chitinised, wider than long; posterior margin of genital sternite deeply concave (Figure 7B); short to long setae sparsely scattered over the ventral surface of the genital segment.

*Female gonopod:* first article fairly broad, bearing 11–13 long setae, arranged in three irregular rows; 2+2 sharp coniform spurs, inner spur smaller (Figure 7A, B); second article with 7–9 rather long setae arranged in two irregular rows on its ventral side; third article usually with 2–3 long setae on its ventral surface; terminal claw undivided, bearing a few thick sensilla coeloconica on its dorsodistal and ventral surface (Figure 7C).

**Remarks**

Some *Lithobius* species, all from Russia, also have distinct sexual characters on male leg 15: the proximal part of male 15<sup>th</sup> tibia of *Lithobius (Monotarsobius) kurchaevae*



described by Zaleskaja (1978) has a large swelling bearing a tuft of long bristles, and a longitudinal deep excavation on the dorsal surface; the dorsal surface of the male 15<sup>th</sup> tibia of *Lithobius (Monotarsobius) evsyukovi* (Zuev 2017) a large, flat, ovoid wart supporting a few short setae at apex; the dorsal surface of 15<sup>th</sup> tibia *Lithobius (Monotarsobius) ferganensis* (Trotzina, 1894) a small cylindrical wart supporting a few short setae at apex; while the male 15<sup>th</sup> tibia of *Lithobius (Chinobius) yuchernovi* (Farzalieva et al. 2017) is characterized by a tubercle supporting a cluster of curved and long setae on the ventral surface. *Lithobius (Monotarsobius) meifengensis* sp. n. differs from those by its unique male secondary sexual character on the ventral surface of 15<sup>th</sup> femur, a large swelling with approximately 20 short setae and numerous very small pores, not found in any of those congeners.

Records of the species of *Lithobius (Monotarsobius)* from Taiwan by Takakuwa and Wang are listed as follows: locality: old name = new name; place name ??: unknown.

*Lithobius (Monotarsobius) ramulosus* (Takakuwa, 1941)

- [1] *Monotarsobius ramulosus* Takakuwa, 1941a – Trans. Nat. Hist. Soc. Formosa 31 (213): 294-295; fig. 5, 6 (original description, key) (locality: Keisyu = Xizhou)  
*Monotarsobius ramulosus*: Takakuwa, 1941b – Fauna Nippon. 9(8-3): 74; fig. 84; (description, key) (locality: Keisyu = Xizhou)  
*Monotarsobius ramulosus*: Takakuwa, 1942 – Trans. Nat. Hist. Soc. Formosa 32(231): 360 (locality: Keisyu = Xizhou)  
*Monotarsobius ramulosus*: Wang 1955 – Quar. J. Taiwan Mus. 8(1): 16 (locality: Taipei)  
*Monotarsobius ramulosus*: Wang 1956 – Quar. J. Taiwan Mus. 9(2): 159 (locality: Hualien)

*Lithobius (Monotarsobius) obtusus* (Takakuwa, 1941)

- [1] *Monotarsobius obtusus* Takakuwa, 1941a – Trans. Nat. Hist. Soc. Formosa 31 (213): 293-294; fig. 2 (original description, key) (locality: Keisyu = Xizhou, Shaka = Shalu, Tikunan = Zhunan)  
*Monotarsobius obtusus*: Takakuwa 1941b – Fauna Nippon. 9(8-3): 75; fig. 85; (description, key) (locality: Keisyu = Xizhou, Shaka = Shalu)  
*Monotarsobius obtusus*: Wang 1955 – Quar. J. Taiwan Mus. 8(1): 16 (locality: Shin-Tien = Hsintien)  
*Monotarsobius obtusus*: Wang 1956 – Quar. J. Taiwan Mus. 9(2): 159 (locality: Hualien)  
*Monotarsobius obtusus*: Wang 1957 – Quar. J. Taiwan Mus. 10(1): 28 (locality: Kao Yung ??)  
*Monotarsobius obtusus*: Wang 1959 – Quar. J. Taiwan Mus. 12(3, 4): 198 (locality: Taipei, Kao Yung ??)  
*Monotarsobius obtusus*: Wang 1963 – Quar. J. Taiwan Mus. 16(1, 2): 95 (locality: Rai Wu ??)



*Lithobius (Monotarsobius) holstii* (Pocock, 1895)

- [1] *Monotarsobius crassipes holstii* (+*M. takakuwai*): Takakuwa 1941a – Trans. Nat. Hist. Soc. Formosa 31 (213): 292–293; fig. 1 (description, key)  
*Monotarsobius crassipes holstii* (+*M. takakuwai*): Takakuwa 1941b – Fauna Nippon. 9 (8–3): 78–79; fig. 90–91; (description, key) (locality: Puli, Taipei)
- [2] *Monotarsobius crassipes*: Wang 1959 – Quar. J. Taiwan Mus. 12 (3, 4): 198 (locality: Nantou, Taipei)  
*Monotarsobius crassipes*: Wang 1963 – Quar. J. Taiwan Mus. 16 (1, 2): 95 (locality: Shao Tso Kiang ??)

Chamberlin and Wang (1952) recorded two species of *Monotarsobius* from three specimens allegedly collected by Takakuwa in 1933 from Taiwan: *Monotarsobius rhyus* Attems, 1934 and *Monotarsobius argaeensis* Attems, 1934. However, Takakuwa never came to Taiwan, and never reported these two species in any of his publications. Wang came to Taiwan and studied Taiwanese chilopods since 1953, and he did not record these two species again. We consider that the record of the two species is questionable.

*Lithobius (Monotarsobius) meifengensis* sp. n. is morphologically close to *Lithobius (Monotarsobius) ramulosus* (Takakuwa, 1941), *Lithobius (Monotarsobius) obtusus* (Takakuwa, 1941) and *Lithobius (Monotarsobius) holstii* (Pocock, 1895), with which it shares the following characters: antennae composed of 19–20 articles, six ocelli on each side of cephalic plate, 2+2 coxosternal teeth. It can however be distinguished using the following key.

**Key to the Taiwanese species of *Lithobius (Monotarsobius)***

- |   |  |  |
|---|--|--|
| 1 | 2222 coxal pores; terminal claw of female gonopod divided, biapiculate.....  | <b><i>L. (M.) obtusus</i> Takakuwa, 1941</b>   |
| – | 3–5 coxal pores; terminal claw of female gonopod undivided .....   | <b>2</b>                                       |
| 2 | 5555 coxal pores; a small sharp tooth on the base of terminal claw of female gonopod .....   | <b><i>L. (M.) ramulosus</i> Takakuwa, 1941</b> |
| – | 3–4 coxal pores; base of terminal claw of female gonopod without sharp tooth.....  | <b>3</b>                                       |
| 3 | Male legs 15 with secondary sexual characters, a large ventral swelling on the femur, a dorsal shallow excavation on the tarsus 2 (Figure 5C); terminal claw of female gonopod with smooth lateral margin, without ridge ..... | <b><i>L. (M.) meifengensis</i> sp. n</b>       |
| – | Male legs 15 without secondary sexual characters; terminal claw of female gonopod with irregular internal and external ridges .....  | <b><i>L. (M.) holstii</i> (Pocock, 1895)</b>   |

## Acknowledgements

We are grateful to Dr. J. G. E. Lewis and Dr. Gregory D. Edgecombe for valued help during our study. Thanks to Dr. Sheng-Hai Wu for his specimens. Thanks to Mr. Shih-Chen Chang, who translated the Japanese literature for us. We are indebted to Prof. Hsi-Te Shih, Prof. Huiqin Ma, and Prof. Pavel Stoev for providing us with valuable literature.

## References

- Bonato L, Edgecombe GD, Lewis JGE, Minelli A, Pereira LA, Shelley RM, Zapparoli M (2010) A common terminology for the external anatomy of centipedes (Chilopoda). *ZooKeys* 69: 17–51. <https://doi.org/10.3897/zookeys.69.737>
- Carballo JL, Escot C, Estacio FJ, Carmona MP (1992) Sobre la presencia de *Lithobius calcarius* C. Koch, 1844 y *Lithobius pilicornis* Newport, 1844 en el sur de la Península Ibérica. *Aquivos do Museu Bocage* 2(9): 149–153.
- Chamberlin RV, Wang YHM (1952) Some records and descriptions of chilopods from Japan and other oriental areas. *Proceedings of the Biological Society of Washington* 65: 177–187.
- Eason EH (1973) The type specimens and identity of the species described in the genus *Lithobius* by R. I. Pocock from 1890 to 1901. *Bulletin of the British Museum (Natural History)* Zoology 25(2): 39–83.
- Ernst A, Rosenberg J (2003) Structure and distribution of sensilla coeloconica on the maxillipedes of Chilopoda. *African Invertebrates* 44(1): 155–168.
- Farzalieva SG, Nefediev PS, Tuf IH (2017) *Lithobius (Chinobius) yuchernovi*, a new lithobiid species from northeastern Siberia and the Kamchatka Peninsula, Russia (Chilopoda, Lithobiomorpha). *ZooKeys* 693: 95–108. <https://doi.org/10.3897/zookeys.693.14769>
- Lewis JGE (1981) *The Biology of Centipedes*. Cambridge University Press, Cambridge, 272–275. <https://doi.org/10.1017/CBO9780511565649>
- Ma H, Pei S, Hou X, Zhu T (2014) *Lithobius (Monotarsobius) zhangii* sp. n., a new species from Eastern China (Chilopoda, Lithobiomorpha, Lithobiidae). *ZooKeys* 459: 1–10. <https://doi.org/10.3897/zookeys.459.8169>
- Ma H, Pei S, Wu DGai Y (2012) *Lithobius (Monotarsobius) monoforaminis* sp. n., a new species of lithobiid centipede from central China (Chilopoda, Lithobiomorpha, Lithobiidae). *ZooKeys* 193: 79–87. <https://doi.org/10.3897/zookeys.193.2802>
- Ma H, Pei S, Zhu M, Zhang G, Liu L (2009) A new species of *Lithobius (Monotarsobius)* Verhoeff, 1905 (Lithobiomorpha: Lithobiidae) from China. *Entomological News* 120(3): 313–318. <https://doi.org/10.3157/021.120.0310>
- Matic Z (1970) Contribution à la connaissance des Lithobiides (Chilopoda, Lithobiomorpha) de Corée. *Annales Zoologici Warszawa* 28: 55–63.
- Müller CHG, Rosenberg J, Hilken G (2009) Fine structure and phylogenetic significance of ‘flexo-canal epidermal glands’ in Chilopoda. *Soil Organisms* 81(3): 269–294.
- Murakami Y (1965) Postembryonic development of the common Myriapoda of Japan XIX. Two species of *Monotarsobius* (Chilopoda: Lithobiidae). *Zoological Magazine* 74: 69–75.

- Pei S, Ma H, Shi B, Wu D, Zhou W (2011) A new species of *Lithobius* (*Monotarsobius*) Verhoeff, 1905 (Lithobiomorpha, Lithobiidae) from China. *ZooKeys* 82: 59–66. <https://doi.org/10.3897/zookeys.82.823>
- Takakuwa Y (1941a) Über Einige Japanische Lithobiiden. *Transaction of Natural History Society Formosa* 31(213): 292–297.
- Takakuwa Y (1941b) Class Chilopoda, Epimorpha, Lithobiomorpha. *Fauna Nipponica* Vol. 9 Fas. 8 No. (3). Sanseido Book Store, Tokyo, 73–79. [In Japanese]
- Takakuwa Y (1942) Die Myriopoden aus Formosa, Philippinen U. S. W. *Transaction of Natural History Society Formosa* 32 (231): 359–367.
- Wang YHM (1955) Serica 1a: Records of myriapods on Formosa with description of new species. *Quarterly Journal of the Taiwan Museum* 8: 13–16.
- Wang YHM (1956) Serica 1e: Records of myriapods on Formosa with description of new species (2). *Quarterly Journal of the Taiwan Museum* 9: 155–159.
- Wang YHM (1957) Serica 1f: Records of myriapods on Taiwan Islands (3) – Pescadore Islets, Kao-Yung, Pingtung, Changhua and Taipei. *Quarterly Journal of the Taiwan Museum* 10: 23–29.
- Wang YHM (1959) Serica 1j: On Chilopoda from Taiwan with a new Lithobid. *Quarterly Journal of the Taiwan Museum* 12: 195–199.
- Wang YHM (1963) Serica 1q: Millipedes and Chilopoda of Quemoy, Fukien Province and Taiwan Island, Botel Tobago (Lan Yu), Taiwan province and of Singapore. *Quarterly Journal of the Taiwan Museum* 16: 89–96.
- Zalesskaja NT (1978) Identification book of the lithobiomorph centipedes of the USSR (Chilopoda: Lithobiomorpha). Nauka Publ. House, Moscow, 154–157. [In Russian]
- Zuev RV (2017) Two new species of lithobiid centipedes (Chilopoda: Lithobiomorpha) from the northern Caucasus, Russia. *Arthropoda Selecta* 26(1): 15–24.

# *Hessebius luculentus*, a new species of the genus *Hessebius* Verhoeff, 1941 from China (Lithobiomorpha, Lithobiidae)

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Academic editor: G. Edgecombe | Received 6 August 2017 | Accepted 15 October 2017 | Published 7 March 2018

<http://zoobank.org/A4C7E928-B4F5-4B14-9772-80531806BC6E>

**Citation:** Ma H, Lu Y, Liu H, Hou X, Pei S (2018) *Hessebius luculentus*, a new species of the genus *Hessebius* Verhoeff, 1941 from China (Lithobiomorpha, Lithobiidae). In: Stoev P, Edgecombe GD (Eds) Proceedings of the 17<sup>th</sup> International Congress of Myriapodology, Krabi, Thailand. ZooKeys 741: 193–202. <https://doi.org/10.3897/zookeys.741.20061>

## Abstract

*Hessebius luculentus* sp. n. (Lithobiomorpha: Lithobiidae), recently discovered from Shandan County, Zhangye City, Province Gansu, Qinghai-Tibet Plateau, China, is described. Morphologically it resembles *H. jangtseanus* (Verhoeff, 1942), but can be easily distinguished from the latter by size of Tömösváry's organ's, the morphological characters of a protuberance on the dorsal end of the second article of the female gonopods; and obvious differences in the dorsal plectrotaxy of both the 14<sup>th</sup> and 15<sup>th</sup> legs. The main morphological characters and a key to the known Chinese species of genus *Hessebius* based on adult specimens are presented.

## Keywords

China, *Hessebius luculentus* sp. n., Lithobiidae, Qinghai-Tibet Plateau

## Introduction

*Hessebius* was originally proposed as a genus in the family Lithobiidae by Verhoeff (1941) to accommodate the species *H. kosswigi* Verhoeff, 1941 and *H. tauricus* Verhoeff, 1941 described from Turkey. The latter species was reassigned to the genus



*Lithobius* Leach, 1814 by Zapparoli (1999). Zaleskaja (1978), Eason (1981), Pei et al. (2010) and Bonato et al. (2011) debated the taxonomic status of *Hessebius* and considered it at generic rank and selected *H. kosswigi* Verhoeff, 1941, from Turkey, as type species by subsequent designation (Verhoeff 1941, Zaleskaja 1978, and Eason 1981). Presently, the genus comprises 12 species (Zapparoli 2016), characterized by the following traits: antennae generally with 20 articles, 13–15 ocelli, forcipular coxosternal teeth 2+2; tergites without posterior triangular projections; legs 14 and 15 thicker than the anterior legs in females, both thicker in males; coxal pores 4–7; the first article of the female gonopods with 2+2 spurs, the second article with a massive expansion and projection on the dorsolateral ridge, and a long claw sometimes with a stout lateral tooth at its base. *Hessebius* has a distribution that extends from Mongolia and south-east China through central Asia (Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan), the southern Urals, south-west Russia (Kalmykia and adjacent areas), westwards up to the Middle East (Iran, Armenia) and eastern Mediterranean basin (south-west Turkey, Rhodes, Cyprus, Syria, Palestine, Israel, Jordan, north Egypt, Cyrenaica) (Pei et al. 2010).

The myriapod fauna of China is still poorly known and very little attention has been paid to the study of Lithobiomorpha, with only 74 species/subspecies hitherto known from the country (Ma et al. 2014a, b, 2015; Pei et al. 2010, 2014, 2015, 2016; Qin et al. 2014), among which are three species of *Hessebius* viz., *H. jangtseanus* (Verhoeff, 1942), *H. longispinipes* Ma, Pei & Zhu, 2009 and *H. multiforaminis* Pei, Ma, Zapparoli & Zhu, 2010. In the present study another new species of *Hessebius* from Gansu Province, Qinghai-Tibet Plateau, China, is described and illustrated. The main morphological characters and key to the known Chinese species of genus *Hessebius* are presented.

## Materials and methods

All specimens were hand-collected under leaf litter or stones. The material was examined with the aid of Nikon SMZ-1500 stereomicroscope. The colour description is based on specimens in 75% ethanol, body length is measured from the anterior margin of the cephalic plate to the posterior end of the postpedal tergite. Type specimens are deposited in the School of Life Sciences, Hengshui University, Hengshui, China. Terminology applied to external anatomy follows Bonato et al. (2010).

The following abbreviations are used in the text and tables:

<b>a</b>	anterior;	<b>P</b>	prefemur;
<b>C</b>	coxa;	<b>S, SS</b>	sternite, sternites;
<b>F</b>	femur;	<b>T, TT</b>	tergite, tergites;
<b>m</b>	median;	<b>Tr</b>	trochanter;
<b>p</b>	posterior;	<b>Ti</b>	tibia.

## Taxonomy

### Lithobiidae Newport, 1844

### *Hessebius* Verhoeff, 1941

#### *Hessebius luculentus* sp. n.

<http://zoobank.org/CAA43A06-280A-4127-8BE6-C71C5E7A705A>

Figs 1–8

**Material examined. Holotype:** ♀ (Fig. 1), body length 19.9 mm, cephalic plate 1.7 mm long, 1.9 mm broad, from the Mountain Yanzhi, Shandan County, Zhangye City, Gansu Province, 38°35'N, 101°41'E, 1395 m, 28 July 2007, leg. Z. Di, deposited in the School of Life Sciences, Hengshui University, Hengshui, China. **Paratypes:** 4 ♀♀, 4 ♂♂, same data as holotype.

**Etymology.** the specific name *luculentus* refers to the moderately transparent protuberance on the dorsal terminal part of the second article of the female gonopods.

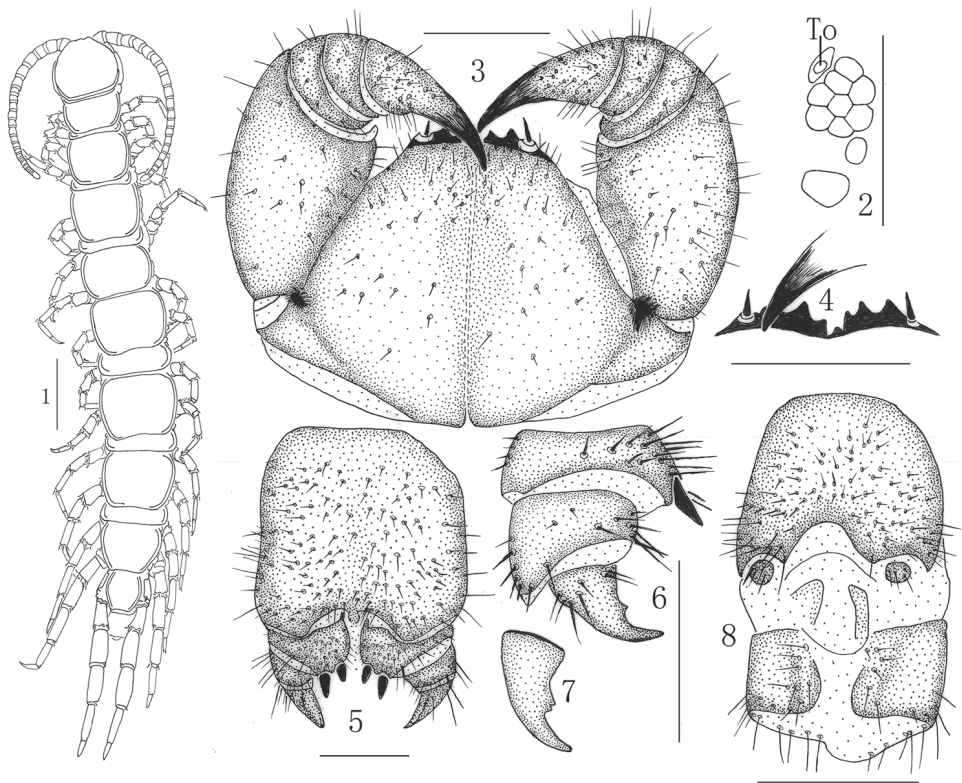
**Diagnosis.** *Hessebius* with body length 15.8–19.9 mm, antennae composed of 20 articles; 9–10 ocelli on each side, arranged in 3 irregular rows, terminal ocellus comparatively large; Tömösváry's organ smaller than the adjacent ocelli; 2+2 coxosternal teeth; porodonts moderately thick, posterolateral to the lateralmost tooth; posterior angles of all tergites without triangular projections; tarsal articulation well defined on legs 1–15; coxal pores 3–6, oval to round, arranged in one row; female gonopods with 2+2 moderately large, coniform spurs; dorsal terminal claw of the third article of the female gonopods simple, but with a small dentation in base; male gonopods short and small, with 3–4 long setae on the terminal segment.

**Description.** body length: 15.8–19.9 mm, cephalic plate 1.4–1.7 mm long, 1.5–1.9 mm wide; colour: antennal articles yellow-brown; cephalic plate and tergites yellow-brown with a reddish hue, edge of tergites lighter; pleural region and all sternites pale yellow-brown; all legs pale yellow-brown with greyish hue; distal part of forcipules brownish black, basal and proximal parts of forcipules, forcipular coxosternite and TT 14 and 15 darker.

*Antennae:* 20+20 articles, one specimen with 20+22 articles; basal article slightly longer than wide, the second one markedly longer than wide, following articles gradually shortening, distal article up to 4.0 times as long as wide; abundant setae on the antennal surface, less so on the basal articles, gradually increase in density of setae to about sixth article, then more or less constant.

*Cephalic plate* smooth, convex, longer than wide; tiny setae emerging from pores scattered very sparsely over the whole surface; frontal marginal ridge with shallow anterior median furrow; short to long setae scattered along the marginal ridge of the cephalic plate; lateral marginal ridge discontinuous, posterior margin continuous, straight (Fig. 1).

Nine–ten oval to rounded *ocelli* on each side (Fig. 2), most of them rounded, domed, translucent, usually darkly pigmented, situated in three irregular rows; the



**Figures 1–8.** *Hessebius luculentus* sp. n., 1–3 and 8 holotype, male: 1 habitus, dorsal view 2 ocelli and Tömösváry's organ (To), lateral view 3 forcipular coxosternite, ventral view 4–7 paratype, female: 4 anterior margin of forcipular coxosternite, ventral view 5 posterior segments and gonopods, ventral view 6 gonopods, transparent protuberance in dorsolateral view 7 claw of female gonopod, lateral view 8 posterior segments and gonopods, ventral view. Scale bars: 500  $\mu$ m (2, 3, 5–8), 2 mm (1); 1 mm (4).

posterior ones comparatively large; the adjoining ventral ocelli slightly smaller and the adjoining dorsal ones slightly larger.

*Tömösváry's organ* situated at the anterolateral margin of the cephalic plate, moderately smaller than the adjoining ocelli and lying well apart from them (Fig. 2–To).

*Coxosternite* subtrapezoidal (Fig. 3), anterior margin narrow, lateral margins slightly longer than medial margins; median diastema moderately shallow, broad V-shaped; anterior margin with 2+2 subtriangular small sharp teeth; porodonts slender, lying posterolateral to and separated from the lateralmost tooth (Fig. 3), with slight bulge at base; scattered short setae on the ventral side of coxosternite, longer setae near the dental margin, more longer setae near the porodonts.

All *tergites* smooth, without wrinkles, dorsum slightly convex, tiny setae emerging from pores scattered sparsely over the entire surface, near the margin with few long setae; T 1 narrower posterolaterally than anterolaterally, generally trapezoidal, narrower

than the cephalic plate and T 3, obviously longer than T 3, the cephalic plate slightly wider than T 3. Lateral marginal ridges of all tergites continuous. Posterior marginal ridges of TT 1 and 3 straight, continuous; posterior marginal ridges of TT 5, 7 and 8 slightly concave, discontinuous; posterior marginal ridges of TT 10, 12 and 14 concave, discontinuous. Posterior angles of tergites generally rounded, without triangular projections. Miniscule setae scattered sparsely over the surface, more numerous setae on anterior and posterior angles of each tergite, with 2–5 long setae on anterior angles and posterior angles of each tergite.

Posterior side of *sternites* narrower than anterior, generally trapezoidal, smooth; setae emerging from sparsely scattered pores on the surface and lateral margin, few long setae; a pair of longer setae approximately symmetrical on the surface of the anterior part of each sternite; 1–2 long setae on the surfaces both of the middle part and posterior part of each sternite.

*Legs* robust, tarsal articulation defined on legs 1–15, tarsus 1 longer than tarsus 2. All legs with fairly long curved claws. Legs 1–14 with anterior and posterior accessory spurs; anterior accessory spurs moderately long and slender, forming a moderately small angle with the claw, posterior accessory spurs slightly more robust, forming a comparatively large angle with the claw; leg 15 lacking accessory spurs; short to long setae sparsely scattered over the surface of prefemur, femur and tibia of legs 1–13, more setae on the tarsus, thicker setae scattered evenly over the tarsal surface, one row of thicker setae regularly arranged on the medial ventral side of tibia of legs 1–13, with setae significantly reduced on legs 14 and 15, no thicker setae regularly arranged in one row on the medial ventral side of tibia; legs 14 and 15 slightly thicker than the anterior pairs in the both female and male, especially in male; tarsus 1 5.1–5.3 times as long as wide. Leg plectrotaxy as in table 1.

*Coxal pores* 3–6, round, variable in size, arranged in a row; usually 4(5)6(5)6(5)6(5) in males and 3(4)554(4) in females. Coxal pore field set in a relatively shallow groove, the coxal pore-field fringe with prominence. Prominence with short to moderately long setae sparsely scattered over the surface.

**Table 1.** Leg plectrotaxy of *Hessebius luculentus* sp. n.

Legs	Ventral					Dorsal				
	C	Tr	P	F	Ti	C	Tr	P	F	Ti
1			mp	amp	am			ap	ap	a
2–8			mp	amp	am			ap	ap	ap
9			mp	amp	am			a(m)p	ap	ap
10–11			mp	amp	am			amp	ap	ap
12			mp	amp	am	(m)		amp	ap	ap
13		(m)	amp	amp	am	m		amp	ap	ap
14		m	amp	amp	am	m		amp	p	p
15		m	amp	am	a	m		amp	p	

Letters in brackets indicate variable spines.



**Female** S 15 with anterior margin broader than posterior, generally trapezoidal, posteromedially straight. Short to long sparse setae evenly scattered on surface. Surface of the lateral sternal margin of genital segment well chitinized, posterior margin of genital sternite deeply concave between condyles of gonopods, except for a small, median tongue-shape bulge. Relatively long setae scattered over ventral surface of the genital segment, few setae near S 15. Gonopods: first article fairly broad, bearing many short to moderately long setae about evenly scattered; with 2+2 moderately long and slender, coniform spurs, inner spur slightly smaller than the outer (Fig. 5); with 6 robust spines arranged in one irregular row dorsally on the posterior part of the external margin. Second article with approximately ten long setae, arranged in two irregular rows, with nine robust spines lying dorsally on the posterior part of the external margin, 6 of them arranged in an irregular longitudinal row, three of them arranged in an irregular transversal row; the dorsal terminal part extending backwards and forming a moderately transparent protuberance. Third article with 2–3 long setae ventrally, and two short, robust spines lying dorsally on the posterior part of the external margin (Fig. 6). Third article with a simple apical claw, and with a very small subtriangular denticle on inner margin (Fig. 7).

**Male** S 15 posterior margin narrower than anterior, posteromedially straight; density of setae on the surface of SS 13 and 14 in the male significantly increased, the S 15 is more significant, and the posterior more than the anterior; sternite of genital segment obviously smaller than the female, usually well sclerotized; posterior margin deeply concave between the gonopods, without medial bulge. Long setae scattered on the ventral surface of the genital segment, fewer setae near S 15, fringed with longer setae along the posterior margin; more than the female. Gonopods short, appearing as a small finger-shaped bulge, with 3–4 long setae, apically slightly sclerotized (Fig. 8).

**Remarks.** The new species resembles *H. jangtseanus* (Verhoeff, 1942) from Sichuan Province, Central China, in having 9–10 ocelli on each side of the cephalic plate, 3–6 coxal pores, 2+2 spurs on the first article of the female gonopods, leg pair 15 lacking accessory spurs; but can be easily distinguished from *H. jangtseanus* by Tömösváry's organ moderately smaller than the adjoining ocelli versus slightly larger than the adjoining ocelli or as large as the closest ocelli in *H. jangtseanus*; the dorsal end on the second article of the female gonopods forming a moderately transparent short protuberance instead of forming a long terminal spur pointing backwards as in *H. jangtseanus*; 15<sup>th</sup> accessory spur absent versus present in *H. jangtseanus*; and both the 14<sup>th</sup> and 15<sup>th</sup> legs' dorsal plectrotaxy obviously different: 10311 on legs 14 and 10310 on legs 15 compared to 10322 on legs 14 and 10320 on legs 15 in *H. jangtseanus*.

**Habitat.** *Larix* forest at about 1400 m above sea level, in moderately moist habitats under roadside stones and litter of the forest floor.

To assist in the identification of the Chinese species of *Hessebius*, the following main morphological characters (table 2) and key to the known Chinese species of the genus based on adult specimens is presented.

**Table 2.** Main morphological characters of the known Chinese species of genus *Hessebius* Verhoeff, 1941 based on adult specimens.

	<i>luculentus</i> sp. n.	<i>jangtseanus</i>	<i>longispinipes</i>	<i>multiforaminis</i>
Sources	this paper	Verhoeff 1942; Pei et al. 2010	Ma et al. 2009	Pei et al. 2010
Distribution	China SW (Gansu)	China SE (Sichuan)	China NW (Xinjiang Uygur)	China SW (Tibet)
Body length (mm)	15.8–19.9	6.9 – 14.0	10.7 – 12.6	18.9 – 22.9
Number of antennal articles	20+20	19+19 – 22+22, commonly 20+20	17+17 – 19+19, commonly 18+18	20+20
Number, arrangement and shape of the ocelli	9 – 10 in 3 irregular rows, oval to rounded, commonly rounded	9–12, oval to round, in 3 rows	1+3, 2, oval to rounded, commonly oval, in 2 irregular rows	13 (1+5,4,3)–15 oval to rounded, commonly rounded, in 3 irregular rows
Posterior ocellus	oval, small	oval to round, comparatively large	oval, larger than the seriate ocelli	bigger than the seriate ocelli
Seriate ocelli	the adjoining ventral ocelli slightly smaller, the adjoining dorsal ocelli slightly larger	moderately small, approximately equal in size	moderately small, approximately equal in size; posterosuperior ocellus of the same size or slightly larger than other seriate ocelli	moderately small, approximately equal in size except the posterosuperior ocellus comparatively larger than other seriate ocelli
Tömösváry's organ	moderately smaller than the adjoining ocelli	moderately large, rounded, slightly bigger than the adjoining ocelli or as big as the closest ocelli	moderately small, nearly rounded, about same size as the adjoining ocelli	very small, rounded; comparatively close to the adjoining ocelli
Number and arrangement of coxosternal teeth	2+2, triangular	2+2, moderately sharp	2+2, triangular, terminal part of each tooth slightly blunt	2+2, comparatively sharp, terminal part of each tooth approximately blunt
Porodont	porodonts slender, lying posterolateral to the lateralmost, apart from the tooth	moderately thickset	moderately stout, just posterolateral to the lateral tooth, without bulge near the base	moderately stout, just posterolateral and moderately far from the lateral tooth, without bulge near their base
Tergites	smooth	smooth	moderately smooth, without wrinkles	moderately rough, with some wrinkles
Number of coxal pores	usually 4(5)6(5)6(5)6(5) in males and 3(4)554(4) in females.	4454 (Verhoeff, 1942); or 4–6	2–5: usually 2343 (male); 3444, 2444 (female)	4–7: usually 6766, 7777, 5666, 5666 (male); 5676, 5564, 4554, 66(7)6(5) (female)
Shape of coxal pores	round	ovate to round	round or slightly ovate, small to moderately large	round or slightly ovate, small to moderately large
Tarsus 1–tarsus 2 articulation on legs 1–13	well–defined	not well–defined	not well–defined	not well–defined

	<i>luculentus</i> sp. n.	<i>jangtseanus</i>	<i>longispinipes</i>	<i>multiforaminis</i>
Male 14 <sup>th</sup> leg	slightly thicker than 1–13 legs	thicker than 1–13 legs	moderately thicker and stronger than 1–13 legs, more thicker and stronger than female	markedly thicker and stronger than 1–13 legs,
Male 15 <sup>th</sup> leg	slightly thicker than 1–13 legs	thicker than 1–13 legs	moderately thicker and stronger than 1–13 legs; more thicker and stronger than in female	markedly thicker and stronger than in 1–13 legs
Dorsal sulci on male 14 <sup>th</sup> and 15 <sup>th</sup> legs	absent	absent	a comparatively obvious dorsal furrow on the tibia of legs 14 and 15	two comparatively obvious shallow dorsal furrow on the tibia of legs 14 and 15
DaC spine	on (12 <sup>th</sup> ) 13 <sup>th</sup> –15 <sup>th</sup> legs	on 13 <sup>th</sup> –15 <sup>th</sup> legs	on 9 <sup>th</sup> –15 <sup>th</sup> legs	on 12 <sup>th</sup> –15 <sup>th</sup> legs
14 <sup>th</sup> accessory spur	present on both anterior and posterior side of the claw	present on both anterior and posterior side of the claw	absent	present on both anterior and posterior side of the claw
15 <sup>th</sup> accessory spur	absent	present	absent	absent
Number and shape of spurs on female gonopods	2+2 moderately long and slender, bullet-shaped	2+2, thick, bullet-shaped	2+2, moderately long, bullet-shaped, the inner slightly smaller and more anterior than the outer	2+2, moderately long, bullet-shaped
Shape of dorsal terminal thorn on 2 <sup>nd</sup> article of female gonopods	extending backwards and forming a moderately transparent protuberance	moderately feeble long terminal spur pointing backwards	strongly extending backwards and forming a thick and long terminal thorn	strongly extending backwards and forming a thick terminal protuberance
Apical claw of female gonopods (and lateral denticles)	simple, with a very small subtriangular denticle on inner margin	simple, only with one small ventral triangular denticle	simple, slender and sharp, with moderately small protuberance on both ventral and dorsal sides, the dorsal one more anterior; usually 3 moderately long setae	simple and broad
Male gonopods	short, appearing as a small fingered bulge, with 3–4 long setae, apically slightly sclerotized	short and small, only a small hemispherical bulge, with 1–2 long setae on the surface, tip slightly sclerotised	short and small, only a small hemispherical bulge, with 2 long setae on surface, terminal slightly sclerotised	short and small, only a small hemispherical bulge, with 6–8 long setae on surface, terminal slightly sclerotised

## Key to the Chinese species of genus *Hessebius*

- 1 Four ocelli on each side of the cephalic plate, the dorsal terminal part of second article of the female gonopods strongly extending backwards and forming a thick and long terminal thorn ..... *H. longispinipes*
- At least 9 ocelli on each side of cephalic plate, the dorsal terminal part of second article of the female gonopods not strongly extending backwards nor forming a thick and long terminal thorn..... **2**
- 2 At least 13 ocelli on each side of the cephalic plate..... *H. multiforminis*
- At most 12 ocelli on each side of the cephalic plate..... **3**
- 3 Dorsal plectrotaxy on leg 15 is 10320 ..... *H. jangtseanus*
- Dorsal plectrotaxy on leg 15 is 10310 ..... *H. luculentus* sp. n.

## Acknowledgements

This study was supported by the National Natural Science Foundation of China (NSFC grant No. 31572239). We are grateful to Dr. Gregory D. Edgecombe, London, U. K., Dr. Pavel Stoev, Sofia, Bulgaria, and Dr. Marzio Zapparoli, Viterbo, Italy, for their hospitality and help during our research, respectively. We thank Dr. Rowland M. Shelley, North Carolina, USA, and Dr. His-Te Shih, Taichung, China, for providing us with invaluable literature.

## References

- Bonato L, Edgecombe GD, Lewis JGE, Minelli A, Pereira LA, Shelley RM, Zapparoli M (2010) A common terminology for the external anatomy of centipedes (Chilopoda). *ZooKeys* 69: 17–51. <http://dx.doi.org/10.3897/zookeys.69.737>
- Eason EH (1981) On some new and little-known southern Asiatic species of Lithobiidae (Chilopoda: Lithobiomorpha). *Insect Systematics & Evolution* 12: 327–338. <https://doi.org/10.1163/187631281794709755>
- Ma HQ, Pei SJ, Hou XJ, Zhu TG (2014a) *Lithobius* (*Monotarsobius*) *zhangi* sp. n., a new species from Eastern China (Chilopoda, Lithobiomorpha, Lithobiidae). *ZooKeys* 459: 1–10. <http://dx.doi.org/10.3897/zookeys.459.8169>
- Ma HQ, Pei SJ, Hou XJ, Zhu TG, Gai YH (2015) *Lithobius* (*Ezembius*) *anabilineatus* sp. nov., a new species (Lithobiomorpha: Lithobiidae) from Eastern China. *Oriental Insects* 49(3–4): 256–263. <http://dx.doi.org/10.1080/00305316.2015.1081647>
- Ma HQ, Pei SJ, Hou XJ, Zhu TG, Wu DY, Gai YH (2014b) An annotated checklist of Lithobiomorpha of China. *Zootaxa* 3847(3): 333–358. <http://dx.doi.org/10.11646/zootaxa.3847.3.2>



- Ma HQ, Pei SJ, Zhu MS (2009) A new species of the Genus *Hessebius* Verhoeff, 1941 (Lithobiomorpha: Lithobiidae). Entomological News 20: 195–200. <https://doi.org/10.3157/021.120.0211>
- Pei SJ, Lu YM, Liu HP, Hou XJ, Ma HQ, Zapparoli M (2016) *Lithobius (Ezembius) multispinipes* n. sp., a new species of centipede from Northwest China (Lithobiomorpha: Lithobiidae). Zootaxa 2: 390–400. <https://doi.org/10.11646/zootaxa.4169.2.12>
- Pei SJ, Ma HQ, Hou XJ, Zhu TG, Gai YH (2015) *Lithobius (Ezembius) laevidentata* sp. n., a new species (Chilopoda: Lithobiomorpha: Lithobiidae) from the Northwest region of China. Biologia 70(8): 1113–1117.
- Pei SJ, Ma HQ, Zapparoli M, Zhu MS (2010) A review of the Chinese species of *Hessebius* Verhoeff, 1941 (Chilopoda: Lithobiomorpha: Lithobiidae). Zootaxa 2631: 51–61.
- Pei SJ, Ma HQ, Zhu TG, Gai YH (2014) A new species of *Lithobius (Ezembius)* Chamberlin (Lithobiomorpha: Lithobiidae) from China. Oriental Insects 48(1–2): 102–107. <http://dx.doi.org/10.1080/00305316.2014.959787>
- Qin W, Lin GH, Zhao XX, Li B, Xie JX, Ma HQ, Su JP, Zhang TZ (2014) A new species of *Australobius* (Lithobiomorpha: Lithobiidae) from the Qinghai-Tibet Plateau, China. Biologia 11: 1601–1605. <http://dx.doi.org/10.2478/s11756-014-0459-4>
- Verhoeff KW (1941) Asyanin zoogeografiyasi ve hayvan sistematige hakkinda. Asiatische Beiträge. II. Türkische Chilopoden – Istanbul Universitesi Orman Fakültesi Dergisi 6 B: 85–117.
- Verhoeff KW (1942) Chilopoden aus innerasiatischen Hochgebirgen. Zoologischer Anzeiger 137: 35–52.
- Zalesskaja NT (1978) Identification book of the lithobiomorph centipedes of the USSR (Chilopoda: Lithobiomorpha). Nauka Publ House, Moscow, 212 pp. [In Russian]
- Zapparoli M (1999) The present knowledge on the centipede fauna of Anatolia (Chilopoda). Biogeographia, Lavori della Società Italiana di Biogeografia, Nuova Serie 20: 105–177. <https://doi.org/10.21426/B6110130>
- Zapparoli M (2016) Lithobiidae. In: Bonato L, Chagas Junior A, Edgecombe GD, Lewis JGE, Minelli A, Pereira LA, Shelley RM, Stoev P, Zapparoli M (Eds) ChiloBase 2.0 – A World Catalogue of Centipedes (Chilopoda). Available at <http://chilobase.biologia.unipd.it>
- Zapparoli M, Edgecombe G (2011) Chilopoda – Taxonomic overview. Order Lithobiomorpha. In: Minelli A (Ed.) Treatise on Zoology – Anatomy, Taxonomy, Biology. The Myriapoda I. Brill, Leiden, 371–389.

# *Lithobius (Ezembius) tetraspinus*, a new species of centipede from northwest China (Lithobiomorpha, Lithobiidae)

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Academic editor: G. Edgecombe | Received 6 August 2017 | Accepted 15 October 2017 | Published 7 March 2018

<http://zoobank.org/399C7789-2C1A-410F-A32D-B540DCAD2C35>

**Citation:** Pei S, Lu Y, Liu H, Hou X, Ma H (2018) *Lithobius (Ezembius) tetraspinus*, a new species of centipede from northwest China (Lithobiomorpha, Lithobiidae). In: Stoev P, Edgecombe GD (Eds) Proceedings of the 17<sup>th</sup> International Congress of Myriapodology, Krabi, Thailand. ZooKeys 741: 203–217. <https://doi.org/10.3897/zookeys.741.19980>

## Abstract

*Lithobius (Ezembius) tetraspinus* **sp. n.** (Lithobiomorpha: Lithobiidae), recently discovered from Hami City, Xinjiang Autonomous Region, NW China, is described. Morphologically this species resembles *L. (E.) sibiricus*, Gersfeldt, 1858, but is distinguishable by a different coxal pore formula, absence of accessory spurs on leg 15, morphology of the second article of the female gonopod, and legs 14 plectrotaxy. A table of the main morphological characters of Chinese *Lithobius (Ezembius)* species is presented.

## Keywords

Chilopoda, *Lithobius (Ezembius)*, NW China, Xinjiang Autonomous Region

## Introduction

The centipede subgenus *Lithobius (Ezembius)* Chamberlin, 1919 accommodates a group of 58 species/subspecies mostly known from Asia, with little extension into north-western North America. Known species colonize a wide range of habitats, from arctic and sub-arctic to tropical and sub-tropical forests, to steppe and overgrazed stony areas of central Asia, to Himalayan montane forests, from sea shore up to 5500 m (Himalayas) (Zapparoli and Edgecombe 2011). Although the subgenus was formally proposed as new

and described in 1923 (Chamberlin 1923), according to Jeekel (2005) its name had been already validated in 1919 (Chamberlin 1919). *Ezembius* is characterized by antennae with ca 20 articles; ocelli 1+4–1+20; forcipular coxosternal teeth usually 2+2; porodonts generally setiform, sometimes stout. Tergites are generally without posterior triangular projections; tarsal articulation of legs 1–13 is distinct. Female gonopods are with uni-, bi- or tridentate claw, and 2+2–3+3 (rarely 4+4) spurs (Zapparoli and Edgecombe 2011).

The myriapod fauna of China is still poorly known and very little attention has been paid to the study of Lithobiomorpha, with only 74 species/subspecies hitherto known from the country (Ma et al. 2014a, b, 2015; Minelli et al. 2016; Pei et al. 2014, 2015, 2016; Qin et al. 2014). Xinjiang Autonomous Region is among the poorly studied regions of China with only eight species at present registered from its territory (Ma et al. 2014 b; Pei et al. 2015, 2016). Altogether, 18 species of *Lithobius* (*Ezembius*) have been recorded from China, only three of them from Xinjiang Autonomous Region. Here with a new species recently found in Balikun County is described.

## Materials and methods

All specimens were hand-collected under leaf litter or stones. The material was examined with the aid of a Motic-C microscope (Xiamen, China). The colour description is based on specimens in 75% ethanol, and the body length is measured from the anterior margin of the cephalic plate to the posterior margin of the postpedal tergite. Type specimens are preserved in 75% ethanol and deposited in the School of Life Sciences, Hengshui University, Hengshui, China (HUSLS). The terminology of the external anatomy follows Bonato et al. (2010). The following abbreviations are used throughout:

<b>T, TT</b>	tergite, tergites;	<b>F</b>	femur,
<b>S, SS</b>	sternite, sternites;	<b>Ti</b>	tibia,
<b>C</b>	coxa,	<b>a</b>	anterior,
<b>Tr</b>	trochanter,	<b>m</b>	median,
<b>P</b>	prefemur,	<b>p</b>	posterior.

## Taxonomic part

### Lithobiidae Newport, 1844

#### *Lithobius* (*Ezembius*) *tetraspinus* sp. n.

<http://zoobank.org/846D108B-D41F-4C20-9161-DA2137A17977>

Figs 1–7

**Material examined. Holotype:** ♂ (Fig. 1), body length 11.7 mm, cephalic plate 1.10 mm long, 1.17 mm broad, Balikun County, Hami City, Xinjiang Autonomous

Region, 43°06'N, 93°00'E, 968 m, a.s.l., 25 July 2006, leg. H. Ma, F. Zhang, S. Liu (HUSLS). **Paratypes:** 8 ♀♀, 1 ♂, same data as holotype (HUSLS).

**Etymology.** The specific name refers to the second article of the female gonopods with four short, robust spines lying dorsally on the posterior part of the external margin.

**Diagnosis.** A *Lithobius* (*Ezembius*) species with body length 9.6–13.3 mm, antennae composed of 19–22 articles, commonly 20+20; 8–10 ocelli on each side, arranged in 3 irregular rows, posterior two ocelli comparatively large; Tömösváry's organ small, subequal in size to the adjoining ocelli; 2+2 coxosternal teeth; porodonts moderately thick, posterolateral to the lateralmost tooth; posterior angles of all tergites without triangular projections; coxal pores 2–5, oval to round; female gonopods commonly with 3+3 moderately large, coniform spurs; second article of female gonopods with four short, robust spines lying dorsally on the posterior part of the external margin; gonopods with a simple terminal article; male gonopods short and small, with 1–2 long setae on the terminal segment.

**Description.** Body length 9.6–13.3 mm, cephalic plate 1.03–1.24 mm long, 1.06–1.31 mm wide.

**Colour:** basal antennal articles chocolate, distal articles gradually lighter, distalmost article yellow-brown. Tergites yellow-brown, TT 1 and 14 more darker. Cephalic plate and T 15 chocolate. Pleural region pale grey. Sternites pale yellow-brown. Distal part of forcipules red-brown, with basal and proximal parts of forcipules and forcipular coxosternite and sternite 15 yellow-brown. Legs 1–13 pale yellow-brown with greyish hue, legs 14 and 15 red-brown, tarsi of legs yellow-brown.

**Antennae:** 19–22 articles, commonly 20+20 (Fig. 1), only one specimen 20+25 articles; basal article longer than wide, second article markedly longer than wide, with following articles gradually shortening distally. Distalmost article 2.0–2.4 times as long as wide. Abundant setae on antennal surface, gradual increase in density of setae basally to distally to approx. 3–4<sup>th</sup> article.

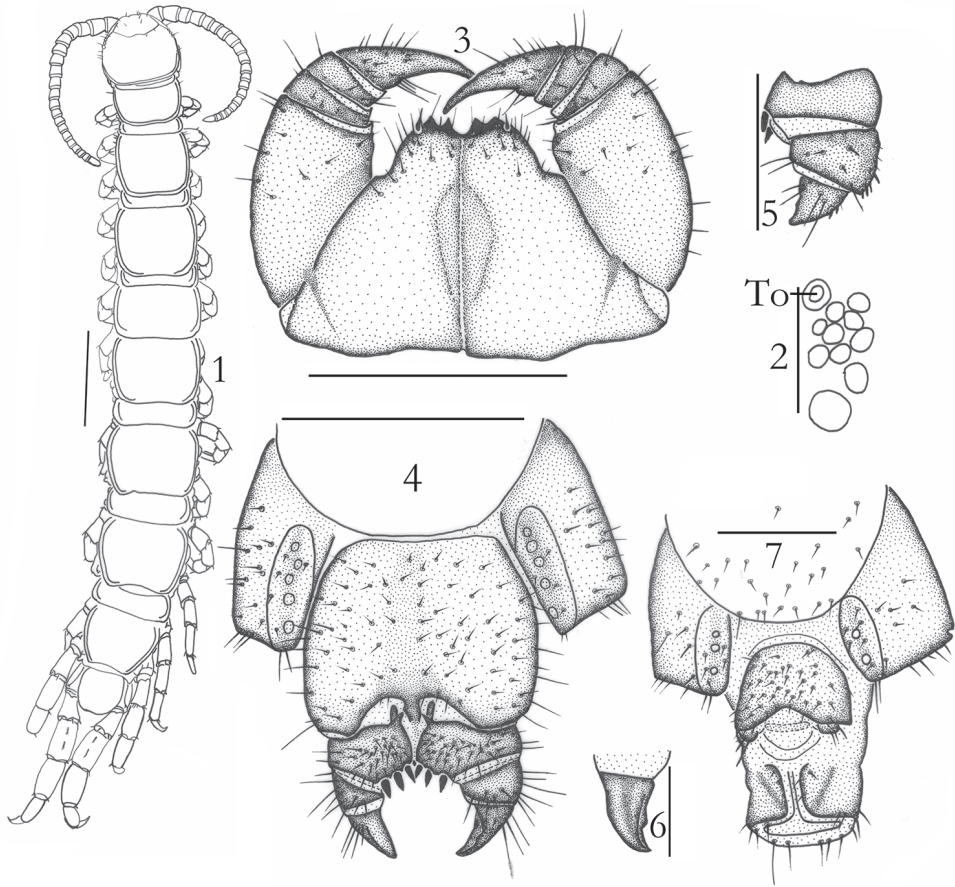
**Cephalic plate** smooth, convex, tiny setae emerging from pores scattered sparsely over the entire surface. Frontal marginal ridge of head with shallow anterior median furrow. Setae of various lengths scattered along the marginal ridge of the cephalic plate. Lateral marginal ridge discontinuous. Posterior margin continuous, straight (Fig. 1).

Eight to ten oval to rounded *ocelli* on each side (Fig. 2), arranged in three irregular rows; posterior two ocelli large; ocelli adjacent to the Tömösváry organ slightly small. Seriate ocelli domed, translucent, usually darkly pigmented.

**Tömösváry organ** at anterolateral margin of the cephalic plate, moderately smaller, subequal in size to the adjacent ocelli (Fig. 2-To).

**Coxosternite** subtrapezoidal (Fig. 3), anterior margin narrow, lateral margins of the coxosternite slightly longer than medial margins. Median diastema moderately deep, V-shaped; anterior margin with 2+2 subtriangular slightly acute teeth. Porodont thick and strong, just posterolateral and separated from the lateral tooth, hardly bulged at base (Fig. 3). Scattered short setae on the ventral side of coxosternite, longer setae near the dental margin, more longer setae near the porodont. Forcipules and forcipular coxosternite without obvious special modifications.





**Figures 1–7.** *Lithobius (Ezembius) tetraspinus* sp. n., 1–3 and 7 paratype, male: **1** habitus, dorsal view, scale bar 1 mm **2** ocelli and Tömösváry's organ (To), lateral view, scale bar 250 µm **3** forcipular segment, ventral view, scale bar 500 µm **4–6** holotype, female: posterior segments and gonopods, ventral view, scale bar 500 µm **5** posterior segments and gonopods, ventral view, scale bar 500 µm **6** posterior part of the external margin of second article of gonopods, ventral view, scale bar 250 µm **7** terminal claw of right gonopod, dorsal view, scale bar 250 µm.

All *tergites* smooth, without wrinkles, dorsum slightly convex, tiny setae emerging from pores scattered sparsely over the entire surface, near the margin with few long setae; T 1 narrower posterolaterally than anterolaterally, generally trapezoidal, narrower than the cephalic plate and T 3, cephalic plate slightly wider than T 3. Lateral marginal ridges of all tergites continuous. Posterior marginal ridges of TT 1 and 3 slightly concave, continuous, posterior marginal ridges of TT 5, 8, 10, 12 and 14 shallow concave, discontinuous. Posterior angles of tergites generally rounded, without triangular projections. Miniscule setae scattered sparsely over the surface, more numerous setae on anterior and posterior angles of each tergite, with 2–4 long setae on anterior angles and 2–3 long setae on posterior angles of each tergite.

*Sternites* smooth, trapezoidal, posterior side narrower than anterior. Setae emerging from sparsely scattered pores on the surface, a pair of approximate symmetrically arranged long setae on both anterior part and posterior part of each sternite. The setae obviously increase in number on S 15, scattered evenly over the surface.

*Legs* robust, tarsal articulation ill-defined on legs 1–13, well defined on legs 14–15. All legs with fairly long curved claws. Legs 1–14 with anterior and posterior accessory spurs; anterior accessory spurs moderately long and slender, forming a moderately small angle with the claw, posterior accessory spurs slightly more robust, forming a comparatively large angle with the claw. Dense glandular pore on the surface of prefemur, femur, tibia, and tarsi of legs 14 and 15. Leg pair 15 lacking accessory spurs. Long setae sparsely scattered over the surface of prefemur, femur, tibia, and tarsi of legs 1–13; more setae on the tarsal surface, many thicker setae scattered evenly over the tarsal surface, setae arranged in one row on the ventral surface of tarsi of legs 1–13, with setae significantly reduced on legs 14 and 15, no thicker setae and setae arranged in one row on the ventral surface of tarsi present. Legs 14 and 15 slightly thicker than the anterior pairs in the female, tarsus 1 3.7–4.7 times as long as wide in legs 15. Legs 15 significantly thicker and stronger than the anterior pairs in the male, with a central longitudinal discontinuous shallow groove on the dorsal of femur, and a black vertical line at the bottom; tarsus 1 3.8–4.3 times as long as wide in legs 15. Leg plectrotaxy as in table 1.

*Coxal pores* 2–5, round or slightly oval, variable in sizes, arranged in a row; usually 4555, 4554, rarely 3454, 3455, 3343 in females and 2332, 2333 in males. Coxal pore field set in a relatively shallow groove, the coxal pore-field fringe with prominence. Prominence with short to moderately long setae sparsely scattered over the surface.

**Male.** S 15 posterior margin narrower than anterior, posteromedially slightly convex, sparsely covered with long setae, more than the anterior; sternite of genital segment obviously smaller than the female, usually well sclerotized; posterior margin deeply concave between the gonopods, without medial bulge. Long setae scattered on the ventral surface of the genital segment, fewer setae near S 15, fringed with longer setae along the posterior margin. Gonopods short, appearing as a small hemispherical bulge, with 1–2 long setae, apically slightly sclerotized (Fig. 7).

**Table 1.** Leg plectrotaxy of *L. (E.) tetraspinus* sp. n.

Legs	Ventral					Dorsal				
	C	Tr	P	F	Ti	C	Tr	P	F	Ti
1			p	am	m			p	ap	a
2			mp	amp	m			(a)p	ap	ap
3			mp	amp	am			(a)p	ap	ap
4-10			mp	amp	am			ap	ap	ap
11			mp	amp	am			amp	ap	ap
12			amp	amp	am	m		amp	p	ap
13			amp	amp	am	m		amp	p	p
14		m	amp	am	a	m		amp	p	p
15		m	amp	am	a	m		amp	p	

Letters in brackets indicate variable spines.

**Table 2-1.** The main morphological characters of the known Chinese species of subgenus *Lithobius* (*Ezembius*) Chamberlin, 1919.

Characters	<i>anabilineatus</i>	<i>anasulcifemorialis</i>	<i>bidens</i>	<i>bilineatus</i>	<i>chekitanus</i>	<i>gantoensis</i>	<i>giganteus</i>	<i>insolitus</i>	<i>irregularis</i>
Sources	Ma et al., 2015	Ma, et al.2013	Takakuwa, 1939	Pei et al., 2014	Chamberlin & Wang, 1952	Takakuwa & Takashima, 1949	Eason, 1986	Eason, 1993	Takakuwa & Takashima, 1949
Distribution	China S (Guangxi)	China S (Guangxi)	China S (Taiwan)	China S (Guangxi)	China S (Zhengjiang and Taiwan)	China NW (Shanxi)	China N (Inner Mongolia Autonomous region)	China S (Hongkong)	China W (Shanxi)
Body length (mm)	11.9–12.1	10.1–12.3	15.0	9.0–9.1	16.0	9.0	15.0–50.0	10.0–11.5	12.0
Number of antennal articles	23+23 articles in female, unknown in male	19+19–24+24, commonly 20+20	20–21	two specimens with 20+21, one specimen with 20+23	20+20	20–23	20+20	18+18–19+19	20+20
Number, arrangement and shape of the ocelli	5 – 6, in 2 rows	6, in 3 rows	7	5–6, in 2 rows	5, in 3 rows	6	6–10, in 2–3 rows	6–8, in 2 rows	7, in 2 rows
Posterior ocellus	round, large	oval to round, large	comparatively large	oval to rounded	oval to round, comparatively large	oval to round, comparatively large	oval to round, comparatively large	oval to round, comparatively large	round, comparatively large
Seriate ocelli	subequal, all ocelli domed, translucent, usually darkly pigmented.	the one near ventral margin moderately small, others almost equal	not reported	subequal, all ocelli domed, translucent, usually darkly pigmented	not reported	comparatively large	not reported	not reported	subequal
Tömös-váry's organ	round, smaller than the adjoining ocelli	moderately large, rounded, slightly larger than the adjoining ocelli	at most same size as one ocellus	slightly larger than the adjoining ocelli	not reported	subequal in size to the adjoining medium large ocelli	slightly smaller than the adjoining ocelli	slightly smaller than the adjoining ocelli	same size as largest ocellus
Number and arrangement of coxosternal teeth	2+2, subtriangular	2+2, moderately blunt	2+2	2+2, slightly triangular	2+2	2+2, approximately sharp	2+2	2+2, approximately sharp	2+2, small

Characters	<i>anabilineatus</i>	<i>anasulcifemorialis</i>	<i>bidens</i>	<i>bilineatus</i>	<i>chekianus</i>	<i>gantoensis</i>	<i>giganteus</i>	<i>insolitus</i>	<i>irregularis</i>
Porodont	long, lying posterolateral to the most lateral teeth	slender, lying posterolateral to the lateral most tooth, their basal moderately bulged	moderately long	thick and long, lying posterolateral to the lateral most tooth	not reported	not reported	not reported	slender, lying posterolateral to the lateral tooth, their basal slightly bulged	long, their basal slightly bulged
Tergites	smooth, backside slightly hunched	smooth	not reported	smooth, slightly hunched behind	not reported	smooth, without wrinkles	smooth, with slightly wrinkles	T1 smooth, other with wrinkles	smooth
Number of coxal pores	3–5, female 4454, 3554; male 4443, 4453	3–6, usually 4663, 5654, 5553, 5563 and 5565	5(6)555	usually females 4554, 5565; males 4553, 4454	6655 or 7665	3333	3333, 4554, 4555, 4565, 5565 or 5566	3–6, male 3443; female 4454, 4555, 5555, 5565	3–10, female 3–6 in 12 <sup>th</sup> leg, 4–6 in 13 <sup>th</sup> leg, 7–10 in 14 <sup>th</sup> and 15 <sup>th</sup> leg
Shape of coxal pores	round or slightly ovate	round or slightly ovate	round	ovate	not reported	round	round	round	round
Tarsus 1–tarsus 2 articulation on legs 1–13	not well-defined	not well-defined	well-defined	not well-defined	not reported	not reported	well-defined	not defined	well-defined
Male 14 <sup>th</sup> leg	obvious thicker and stronger than other legs	markedly thicker and stronger than 1–13 legs, more thicker and stronger than female	not reported	distinctly thick and strong	not reported	not reported	not reported	distinctly thick and strong	not reported
Male 15 <sup>th</sup> leg	obvious thicker and stronger than other legs	markedly thicker and stronger than 1–13 legs, more thicker and stronger than female	not reported	distinctly thick and strong	not reported	not reported	not reported	distinctly thick and strong, with dark zones on dorsal of tibia	not reported
Dorsal sulci on male 14 <sup>th</sup> legs	absent	absent	not reported	with two, shallow longitudinal sulci	not reported	not reported	not reported	absent	not reported

Characters	<i>anabilineatus</i>	<i>anasulcifemorialis</i>	<i>bidens</i>	<i>bilineatus</i>	<i>chekianus</i>	<i>gantoensis</i>	<i>giganteus</i>	<i>insolitus</i>	<i>irregularis</i>
Dorsal sulci on male 15 <sup>th</sup> legs	two distinct, shallow, dorsal sulci on the femur and tibia	with a distinct, shallow, dorsal sulci on the tibia	not reported	with two, shallow longitudinal sulci	not reported	not reported	not reported	absent	not reported
DaC spine	on 14 <sup>th</sup> –15 <sup>th</sup> legs	on 14 <sup>th</sup> –15 <sup>th</sup> legs	absent	on 4 <sup>th</sup> –15 <sup>th</sup> legs	on 14 <sup>th</sup> –15 <sup>th</sup> legs	absent	on 12 <sup>th</sup> –15 <sup>th</sup> legs (on 11 <sup>th</sup> and 12 <sup>th</sup> legs sometimes present)	absent	on 13 <sup>th</sup> –15 <sup>th</sup> legs
14 <sup>th</sup> accessory spur	anterior accessory spur reduced in size, only half the length of the posterior accessory spur	absent	not reported	anterior accessory spur absent	present	present	present	not reported	not reported
15 <sup>th</sup> accessory spur	absent	absent	not reported	anterior accessory spur absent	present	present	absent	absent	not reported
Number and shape of spurs on female gonopods	2+2 moderately small, blunt, coniform spurs, inner spur slightly smaller than the outer	2+2 moderately blunt, with conical spurs, inner spur slightly smaller	3+3 or 4+4, sharp	2+2 moderately small, blunt, coniform spurs, inner spur slightly smaller than the outer one	not reported	1+1, conical spurs	2+2	3+3, coniform spurs	2+2 or 2+3, moderately small, blunt, coniform spurs
Dorsal side of the second article of female gonopods	with one spine lying dorsally on its external margin	no striking features	not reported	with three short, robust setae lying dorsally on its external margin	not reported	not reported	with eight spines in two irregular rows lying dorsally on its external margin	not reported	not reported
Apical claw of female gonopods (and lateral denticles)	simple, there a small subtriangular teeth in the inner	apical claw dimidiolate	simple, there a small sharply teeth in the inner	apical claw bipartite, and its inner aspect broader	not reported	simple	simple	simple	simple and broad
Male gonopods	short and small bulge, with one to two long setae, apically slightly sclerotised	with a small bulge, without setae and apically less sclerotised	hemispherical, with two long setae	short and small bulge, having a long seta, apically slightly sclerotised	not reported	not reported	not reported	not reported	not reported



**Table 2-2.** Range and main morphological characters of the known Chinese species of subgenus *Lithobius* (*Ezembius*) Chamberlin, 1919.

Characters	<i>laevidentata</i>	<i>lineatus</i>	<i>mandschurensis</i>	<i>multispinipes</i>	<i>parvicornis</i>	<i>rhysus</i>	<i>sulcipes</i>	<i>sulcifemorialis</i>	<i>zhui</i>	<i>tetraspinus</i>
Sources	Pei et al., 2015	Takakuwa, 1939	Takakuwa, 1940	Pei et al., 2016	Zapparoli 1991	Attems, 1934	Attems, 1927	Takakuwa & Takashima, 1949	Pei et al., 2011	This paper
Distribution	China NW (Xinjiang Uygur)	China S (Taiwan)	China (Taiwan, Sichuan, Jiangsu, Heilongjiang, Jilin, Liaoning)	China NW (Xinjiang Uygur)	China S (Taiwan)	China S (Fujian and Taiwan)	China S (Taiwan)	China W (Shanxi)	China NW (Xinjiang Uygur)	China NW (Xinjiang Uygur)
Body length (mm)	9.6–13.3	18.0	22.0–23.0	11.6–22.6	16.0	15.0	Not reported	12.0	8.1–15.0	9.6–13.3
Number of antennal articles	19+19–21+21 commonly 20+20	19+19–21+21	20–28	commonly 20+20, (three specimens with 20+21, one specimen with 20+26 of 134 specimens)	20+20, 21+21	20+20 in female, 20+21 in male	19–22	20+20	20–24, commonly 20	19–22, commonly 20
Number, arrangement and shape of the ocelli	8–10, in 3 rows	8–11, in 3 rows	9–13, in 3 rows	8, in 3 rows	3–4, in 1 or 2 rows	8, in 4 rows	7, in 2 rows	6	10–13, in 3–4 rows	8–10, in 3 rows
Posterior ocellus	posterior two ocelli bigger than the seriate ocelli	comparatively small	comparatively large	two ocelli large, oval to rounded	comparatively large	comparatively large	comparatively large	all ocelli same size	comparatively large	two ocelli comparatively large
Seriate ocelli	other seriate ocelli slightly larger than the ocelli adjoining to the ventral	not reported	same size of wath	the two near ventral margin moderately small, others almost equal	not reported	not reported	not reported	same size of wath	dorsal ones moderately large, those near ventral margin of ocellar field moderately small, others of moderate size	the adjoining Tömösváry organ slightly small

Characters	<i>laevidentata</i>	<i>lineatus</i>	<i>mandschurensis</i>	<i>multispinipes</i>	<i>parvicornis</i>	<i>rhysus</i>	<i>sulcipes</i>	<i>sulcifemorialis</i>	<i>zbui</i>	<i>tetraspinus</i>
Tömösváry's organ	subequal in size to the adjoining ocelli	same size as the adjoining ocelli	larger than the adjoining ocelli	slightly smaller than the adjoining ocelli	not reported	not reported	not reported	same size as ocelli	slightly larger than the adjoining ocelli	subequal in size to the adjoining ocelli
Number and arrangement of coxosternal teeth	2+2, approximately blunt	2+2, comparatively large	2+2, small and sharp	3+3, slightly triangular	2+2	2+2	2+2	2+2, small and sharp	2+2 moderately pointed	2+2 subtriangular slightly acute
Porodont	thick and long, lying posterolateral to the most lateral teeth	long and strong	lying posterolateral to the lateral most tooth	thick and long, lying posterolateral to the lateral most tooth	lying posterolateral to the most lateral teeth	not obvious	not reported	slender and long	moderately thick in basal, moderately pointed, just posterolateral to the lateral tooth	Porodons thick and strong, just posterolateral and separated from the lateral tooth,
Tergites	smooth, without wrinkles, backside slightly hunched	smooth	smooth, without wrinkles	smooth, without wrinkles and slightly hunched behind	smooth	With shallow wrinkles	Smooth, posterior angles slightly triangular in T1/4	not reported	smooth, without wrinkles, backside slightly hunched	smooth, without wrinkles, dorsum slightly convex
Number of coxal pores	2–5, female commonly 4555, 4554, sometime 3454, 3455, 3343. male commonly 2332, 2333, sometime 3444, 3333	6–7, usually 66(7)6	776(7)5(6)	3–5, 4555, 5555, 4444, 4455 (females) and 4444, 3344 (males)	3334	6554	4554	5555	2–4, 3444, 3344, 3443, 3333 in female, and 3443, 2343, 2433, 2333 in male.	usually 4555, 4554, rarely 3454, 3455, 3343 in females and usually 2332, 2333, rarely 3444, 3333 in males
Shape of coxal pores	round or slightly ovate	round to ovate	round or ovate	round to ovate	not reported	round	round	round	round or slightly ovate	round or slightly oval
Tarsus 1–tarsus 2 articulation on legs 1–13	not well-defined	well-defined	well-defined	well-defined	not reported	not reported	well-defined	well-defined	well-defined	ill-defined

Characters	<i>laevidentata</i>	<i>lineatus</i>	<i>mandschurensis</i>	<i>multispinipes</i>	<i>parvicornis</i>	<i>rhyus</i>	<i>sulcipes</i>	<i>sulcifemorialis</i>	<i>zbui</i>	<i>tetraspinus</i>
Male 14 <sup>th</sup> leg	remarkably thicker and stronger than 1–13 legs,	not reported	thick and strong	not reported	not reported	not reported	not reported	thick and strong	moderately thicker and stronger	significantly thicker and stronger
Male 15 <sup>th</sup> leg	markedly thicker and stronger than in 1–13 legs	not reported	thick and strong	thick and strong	not reported	femur and tibia thicker	femur and tibia thicker	thick and strong	thicker and stronger, with a circular protuberance on distal end of tibia	significantly thicker and stronger
Dorsal sulci on male 14 <sup>th</sup> legs	absent	absent	not reported	absent	not reported	not reported	present on the femur	present on the femur and tibia	absent	absent
Dorsal sulci on male 15 <sup>th</sup> legs	with a distinct, shallow, dorsal sulci on the tibia	not reported	absent	absent	not reported	not reported	present on the femur and tibia	present on the femur and tibia	absent	present on the femur
DaC spine	on 12 <sup>th</sup> –15 <sup>th</sup> legs	on 14 <sup>th</sup> –15 <sup>th</sup> legs	on 12 <sup>th</sup> –15 <sup>th</sup> legs	on 11 <sup>th</sup> –15 <sup>th</sup> legs, 9 <sup>th</sup> –10 <sup>th</sup> sometimes present	not reported	on 15 <sup>th</sup> legs present	on 15 <sup>th</sup> legs present	absent	on 13 <sup>th</sup> –15 <sup>th</sup> legs, 12 <sup>th</sup> sometimes present	on 12 <sup>th</sup> –15 <sup>th</sup> legs
14 <sup>th</sup> accessory spur	present	present	not reported	present	not reported	not reported	not reported	not reported	present	present
15 <sup>th</sup> accessory spur	anterior absent	present	not reported	absent	not reported	absent	not reported	not reported	absent	absent
Number and shape of spurs on female gonopods	3+4, or 4+4 small, blunt, coniform spurs, commonly with 3+3, inner spur smaller than the outer one	3+3 moderately sharp, slender conical spurs	3+3, same size	2+2, blunt, coniform spurs, with inner spur smaller than the outer one	2+2	2+2, slender	2+2, thick spurs	2+2, strong, long and sharp	2♂ 2 moderately long, coniform spurs, inner spur slightly smaller and more anterior than outer	3+3, few 3+4, only one 4+4 coniform spurs

Characters	<i>laevidentata</i>	<i>lineatus</i>	<i>mandschurensis</i>	<i>multispinipes</i>	<i>parvicornis</i>	<i>rhysus</i>	<i>sulcipes</i>	<i>sulcifemorialis</i>	<i>zbui</i>	<i>terraspinus</i>
dorsal side of the second article of female gonopods	with three long setae lying dorsally on its anterior external margin	not reported	not reported	with 3–4 long setae and 5–6 spines lying dorsally on its external margin	not reported	not reported	not reported	not reported	three spurs arranged in one irregular row on the dorsal terminal part	3 long setae and four short, robust spines lying dorsally on the posterior part of the external margin
Apical claw of female gonopods (and lateral denticles)	simple and broad	simple	simple	simple	simple	simple	dimidiate	simple	broad, and tridentate	simple, with a very small subtriangular blunt denticle on inner margin
Male gonopods	small bulge, with one to two long setae apically slightly sclerotised	hemispherical bulge,	without setae	hemispherical bulge, having a long seta, and apically slightly sclerotised	not reported	not reported	not reported	not reported	small bulge, with 1–2 long setae on surface, and terminal slightly sclerotised	small hemispherical bulge, with 1–2 long setae

**Female.** S 15 anterior margin broader than posterior, generally trapezoidal, posteromedially slightly convex. Short to long setae sparsely scattered on S 15 surface. Surface of the lateral sternal margin of genital segment well chitinized, posterior margin of genital sternite deeply concave between condyles of gonopods, except for a small, median linguliform bulge. Relatively long setae scattered over ventral surface of the genital segment, few setae near S 15. Gonopods: first article fairly broad, bearing 23–30 short to moderately long setae, arranged in four irregular rows; with 3+3, few 3+4, only one 4+4 moderately long and slender, coniform spurs, inner spur slightly smaller than the outer (Fig. 4); second article with 8–12 long setae, arranged in three irregular rows, with three long setae and four short, robust spines lying dorsally on the posterior part of the external margin; third article with 4–6 long posteroventral setae, and two short, robust spines lying dorsally on the posterior part of the external margin (Fig. 5). Third article of female gonopods with a simple apical claw with a very small subtriangular blunt denticle on the inner margin (Fig. 6).

**Remarks.** The new species with 2+2 coxosternal teeth, 9–10 ocelli on each side of head, female gonopods with 3–4 moderately large, coniform spurs, and leg pair 15 lacking accessory spurs, is morphologically similar to *Lithobius (Ezembius) sibiricus* Gerstfeldt, 1858 from Mongolia and Russia, but is readily distinguished by having coxal pores arranged in a 2–5-formula in contrast to *L. (E.) sibiricus* with a coxal pore formula 5–8; the second article of the female gonopods with four short, robust spines lying dorsally on the posterior part of the external margin versus with eight short, robust spines lying dorsally on the posterior part of the external margin; lacking accessory spurs on legs 15<sup>th</sup> versus having small accessory spurs on legs 15<sup>th</sup>; moreover, leg 14 plectrotaxy is distinctly different, 10311 (dorsal) and 01321 (ventral) compared to 10311 (dorsal) and 01332 (ventral).

**Habitat.** The specimens were collected in a *Larix* forest at 950–1000 m alt. It inhabits moderately moist habitats under roadside stones and litter of the forest floor.

To assist in the identification of the Chinese species of *Lithobius (Ezembius)*, the range and main morphological characters of the known species of the subgenus in the area is presented (table 2). These characters are specific only to adults of the taxa occurring in China.

## Acknowledgements

This study was supported by the National Natural Science Foundation of China (NSFC grant No. 31572239). We are grateful to Dr. Gregory D. Edgecombe, London, U. K., Dr. Pavel Stoev, Sofia, Bulgaria, and Dr. Marzio Zapparoli, Viterbo, Italy, for their hospitality and help during our research, respectively. We thank Dr. Rowland M. Shelley, North Carolina, USA, and Dr. His-Te Shih, Taichung, China, for providing us with invaluable literature. Thanks must go to Dr. Zi-Zhong Yang and Dr. Zhi-Sheng Zhang for their help in preparing the paper.



## References

- Attems C (1927) Neue Chilopoden. Zoologischer Anzeiger 72: 291–305.
- Attems C (1934) Einige neue Geophiliden und Lithobiiden des Hamburger Museums. Zoologischer Anzeiger 107: 310–317.
- Bonato L, Edgecombe GD, Lewis JGE, Minelli A, Pereira LA, Shelley RM, Zapparoli M (2010) A common terminology for the external anatomy of centipedes (Chilopoda). ZooKeys 69: 17–51. <https://doi.org/10.3897/zookeys.69.737>
- Chamberlin RV (1919) The Chilopoda collected by the Canadian Arctic Expedition, 1913–1918. In: Report of the Canadian Arctic Expedition, 1913–1918. Volume III: Insects. Part H: Spiders, Mites and Myriapods, 15–22.
- Chamberlin RV (1923) Chilopods of the Pribilof Islands. North American Fauna 46: 240–244.
- Chamberlin RV, Wang YX (1952) Some records and descriptions of Chilopods from Japan and other oriental areas. Proceeding of the Biological Society of Washington 65: 177–188.
- Eason EH (1993) Descriptions of four new species of *Lithobius* from the oriental region and a redescription of *Australobius palnis* (Eason 1973) from Sri Lanka (Chilopoda: Lithobiomorpha) – Bollettino del Museo Civico di Storia Naturale di Verona 17: 181–199.
- Eason EH (1986) On the synonymy of *Lithobius giganteus* Sselivanoff 1881 and the taxonomic status of *Porobius* Attems 1926 (Chilopoda) – Annalen des Naturhistorischen Museums, Wien 87 B: 181–192.
- Jeekel CAW (2005) Nomenclator generum et familiarum Chilopodorum: a list of the genus and family-group names in the class Chilopoda from the 10th edition of Linnaeus, 1758, to the end of 1957. Myriapod Memoranda Supplement 1: 1–130.
- Ma HQ, Pei SJ, Hou XJ, Zhu TG (2014a) *Lithobius (Monotarsobius) zhangii* sp. n., a new species from Eastern China (Chilopoda, Lithobiomorpha, Lithobiidae). ZooKeys 459: 1–10. <https://doi.org/10.3897/zookeys.459.8169>
- Ma HQ, Pei SJ, Hou XJ, Zhu TG, Gai YH (2015) *Lithobius (Ezembius) anabilineatus* sp. nov., a new species (Lithobiomorpha: Lithobiidae) from Eastern China. Oriental Insects 49(3–4): 256–263. <https://doi.org/10.1080/00305316.2015.1081647>
- Ma HQ, Pei SJ, Hou XJ, Zhu TG, Wu DY, Gai YH (2014b) An annotated checklist of Lithobiomorpha of China. Zootaxa 3847(3): 333–358. <https://doi.org/10.11646/zootaxa.3847.3.2>
- Ma HQ, Pei SJ, Wu DY, Gai YH (2013) A new lithobiid centipede of *Lithobius (Ezembius)* (Lithobiomorpha) from China, Oriental Insects 47(1): 1–6. <https://doi.org/10.1080/00305316.2012.753763>
- Minelli A, Pereira LA, Shelley RM, Stoev P, Zapparoli M (2016) ChiloBase 2.0. A World Catalogue of Centipedes (Chilopoda). <http://chilobase.biologia.unipd.it>
- Pei SJ, Lu YM, Liu HP, Hou XJ, Ma HQ, Zapparoli M (2016) *Lithobius (Ezembius) multispinipes* n. sp. a new species of centipede from North West China (Lithobiomorpha: Lithobiidae). Zootaxa 4169(2): 390–400. <https://doi.org/10.11646/zootaxa.4169.2.12>
- Pei SJ, Ma HQ, Zhu TG, Gai YH (2014) A new species of *Lithobius (Ezembius)* Chamberlin (Lithobiomorpha: Lithobiidae) from China. Oriental Insects 48(1–2): 102–107. <https://doi.org/10.1080/00305316.2014.959787>

- Pei SJ, Ma HQ, Hou XJ, Zhu TG, Gai YH (2015) *Lithobius (Ezembius) laevidentata* sp. n., a new species (Chilopoda: Lithobiomorpha: Lithobiidae) from the Northwest region of China. *Biologia* 70(8): 1113–1117.
- Qin W, Lin GH, Zhao XX, Li B, Xie JX, Ma HQ, Su JP, Zhang TZ (2014) A new species of *Australobius* (Lithobiomorpha: Lithobiidae) from the Qinghai-Tibet Plateau, China. *Biologia* 69(11): 1601–1605. <https://doi.org/10.2478/s11756-014-0459-4>
- Takakuwa Y (1939) Über Japanische *Lithobius*-Arten - Transactions of the Sapporo Natural History Society 16: 28–37.
- Takakuwa Y (1940) Class Chilopoda, Epimorpha, Lithobiomorpha. *Fauna Nipponica* Vol. 9 Fas. 8 No. (3). Sanseido Book Store, Tokyo, 104 pp.
- Takakuwa Y, Takashima H (1949) Myriapods collected in Shansi, North China. *Acta Arachnologica* 11: 51–69. <https://doi.org/10.2476/asjaa.11.51>
- Wang YM (1955) Serica 1b. A preliminary report on the Myriapoda and Arachnida of Lan Yu Islets (Botel Tobago) China - *Quarterly Journal of the Taiwan Museum* 8: 195–201.
- Zapparoli M, Edgecombe G (2011) Lithobiomorpha. In: Minelli A (Ed.) *Treatise on Zoology. Anatomy, Taxonomy, Biology. The Myriapoda, Volume 1*. Jordaen Luchtmans, Brill, 538 pp.
- Zapparoli M (1991) Note su alcune specie di chilopodi della regione palestinese. *Fragmenta Entomologica* 23: 15–33.



# Millipede and centipede assemblages on the northern and southern slopes of the lowland Altai, southwestern Siberia, Russia (Diplopoda, Chilopoda)

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Academic editor: P. Stoev | Received 30 October 2017 | Accepted 29 November 2017 | Published 7 March 2018

<http://zoobank.org/8581A1B1-1CBA-44C0-8B04-1D6CDCD03827>

**Citation:** Nefediev PS, Farzalieva GS, Tuf IH, Nedoev KK, Niyazov ST (2018) Millipede and centipede assemblages on the northern and southern slopes of the lowland Altai, southwestern Siberia, Russia (Diplopoda, Chilopoda). In: Stoev P, Edgecombe GD (Eds) Proceedings of the 17<sup>th</sup> International Congress of Myriapodology, Krabi, Thailand. ZooKeys 741: 219–254. <https://doi.org/10.3897/zookeys.741.21936>

## Abstract

The total species richness in the myriapod assemblages of the lowland Altai near Charyshskoe Village, Altai Province, southwestern Siberia, Russia is estimated to be at least 19 species from ten genera, eight families, five orders, and two classes. The following species are new to SW Siberia: *Lithobius (Ezembius) ostiacorum* Stuxberg, 1876, *L. vagabundus* Stuxberg, 1876, and *L. (Monotarsobius) nordenskiöldii* Stuxberg, 1876, while *L. (E.) proximus* Sseliwanooff, 1880 and *L. (M.) insolens* Dányi & Tuf, 2012 are recorded for the first time from the Altai Province of Russia. A species of *Strigamia* which is morphologically similar to *Strigamia* cf. *transilvanica* (Verhoeff, 1928) has been found in the study area but its true specific identity is yet to be determined. The seasonal dynamics of myriapod assemblages in terms of the species diversity, density, sex-age structure, and vertical distribution along the soil profile have been studied with regard to the different slope exposures.

## Keywords

Altai, millipedes, centipedes, distribution, ecology, lowland, new records, Siberia

## Introduction

Despite the recent increased interest in the myriapod fauna of southwestern Siberia (Mikhaljova et al. 2007, 2008, 2014, 2015, Mikhaljova 2009, 2013, 2016, 2017, Nefediev et al. 2013, 2014a, b, c, 2016a, b, c, 2017a, b, Nefedieva et al. 2014, 2015, Nefediev 2016), the biodiversity and ecological characteristics of myriapods in the study area of the lowland Altai, a transition zone from the plains of the southwestern Siberia to the mountains of southern Siberia have not been studied to date.

## Materials and methods

The present study is based on fresh samples collected in the lowlands of the Charysh District, Altai Province, SW Siberia. The area has a continental climate, with cold and snowy winters, and hot and dry summers: mid-temperature in January is  $-17^{\circ}\text{C}$  and in July  $+18.5^{\circ}\text{C}$ ; annual amount of precipitation is about 600 mm. Material from the environs of the Altai State University Student Field Station, titled “Goluboi Utios” (= “Blue Rock” in English), situated ca. 4.5 km SE of Charyshskoye Village (Figure 1) was collected. The vast majority of study material was obtained from two types of habitat. Two sites were sampled in each habitat:

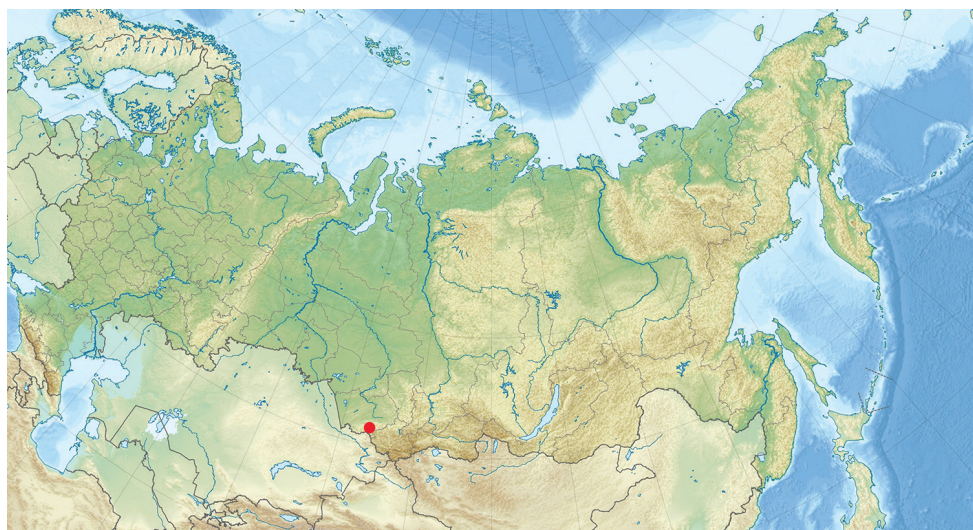
(1) rocky xeromorphic steppe with bushes of Siberian peashrub (*Caragana arborescens*), Tartarian honeysuckle (*Lonicera tatarica*) and germander meadowsweet (*Spiraea chamaedryfolia*) located on the southern slope (Figures 2, 3): site 1 on S slope ( $51^{\circ}21'20.3''\text{N}$ ,  $83^{\circ}37'36.5''\text{E}$ , 480 m a.s.l.) and site 2 on S slope ( $51^{\circ}21'14.5''\text{N}$ ,  $83^{\circ}38'03.8''\text{E}$ , 530 m a.s.l.);

(2) rocky forested sites with silver birch (*Betula pendula*), Scots pine (*Pinus sylvestris*), germander meadowsweet (*S. chamaedryfolia*) and Korean elephant-ear, or badan (*Bergenia crassifolia*) on the northern slope (Figures 4, 5): site 1 on N slope ( $51^{\circ}21'44.3''\text{N}$ ,  $83^{\circ}37'42.6''\text{E}$ , 620 m a.s.l.) and site 2 on N slope ( $51^{\circ}21'38.0''\text{N}$ ,  $83^{\circ}38'02.7''\text{E}$ , 630 m a.s.l.).

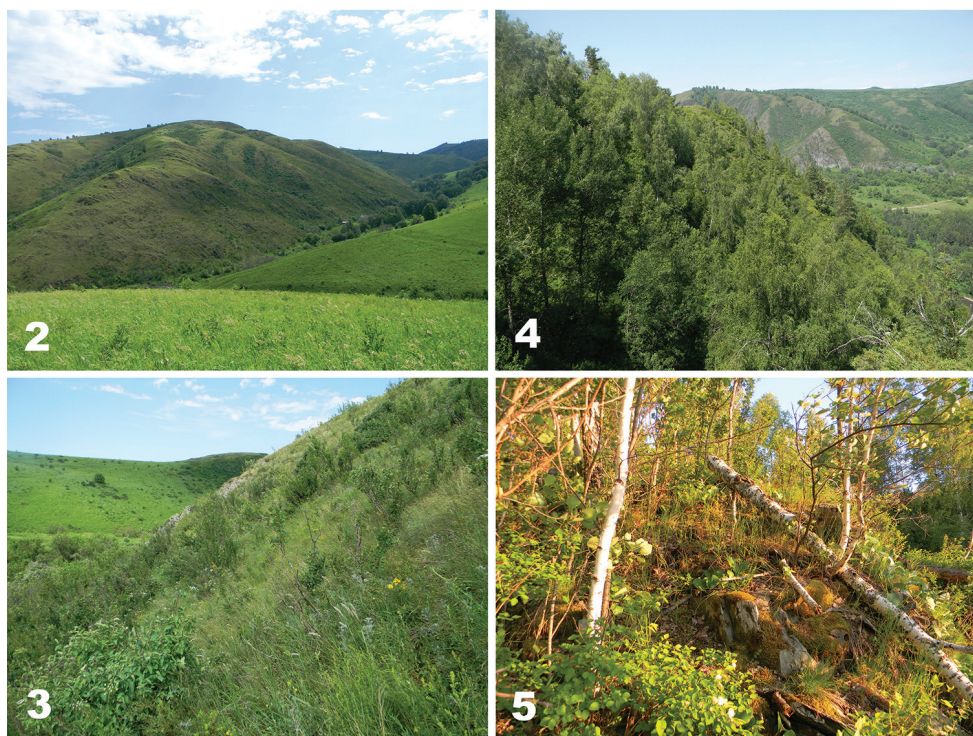
The material was collected using the standard soil fauna sampling techniques practiced in Russia (Ghilarov 1987) by taking 5 soil samples per study site, hand-sorting each 10 cm layer down to 30 cm until fauna penetration, with the sample area totaling  $\frac{1}{4} \text{ m}^2$ . Soil samples were taken three times during summer 2016, starting at the beginning of summer (31 May–2 June), through mid-summer (12–13 July) to late summer (22–23 August). Also we collected additional faunistic material in nearby localities by hand sampling in the summers of 2015–2017. The total number of studied millipedes and centipedes was 684 and 666 specimens, respectively.

The distribution of recorded species in soil samples was analyzed using CANOCO for Windows 4.5 (ter Braak and Šmilauer 1998). Following lengths of gradient in species data we selected Redundancy analyses (RDA) using environmental variables, i.e. exposure (south/north), month, depth of soil sample and sample ID. The significance of models was evaluated using Monte Carlo tests with 499 permutations. For the





**Figure 1.** Map of study locality (shown by the red spot).



**Figures 2–5.** Two types of study habitats. **2–3** rocky xeromorphic steppe with bushes on the southern slope **4–5** rocky forested sites on the northern slope (**2–3** taken in mid-July 2017, **5** taken at the end of May 2016; all by P.N.).

evaluation of significance and effect of tested environmental variables forward selection was applied. The effect of selected significant environmental variables (month, depth) for predicting the distribution of individual species was tested using Generalized linear models (GLM) with evaluation of AIC.

The material treated here was collected by A.M. Alenov (A.A.), E.V. Andreeva (E.A.), Kh.Kh. Nedoev (Kh.N.), P.S. Nefediev (P.N.), S.T. Niyazov (S.N.), V.Yu. Slatina (V.S.), and T.A. Zakirov (T.Z.) (all from Barnaul). These samples have been deposited mainly in the collection of the Altai State University, Barnaul, Russia (ASU), and shared also with the collection of the Perm State University, Perm, Russia (PSU) and Zoological Museum of the Moscow Lomonosov State University, Moscow, Russia (ZMMU), as indicated in the text. The species names documented in the literature references include those from southwestern Siberia (Asian Russia) only.

## Taxonomic part

**Class Diplopoda de Blainville in Gervais, 1844**

**Order Julida Brandt, 1833**

**Family Julidae Leach, 1814**

**Genus *Leptoiulus* Verhoeff, 1894**

***Leptoiulus tigirek* Mikhajlova, Nefediev, Nefedieva & Dyachkov, 2015**

Figure 6

Julidae gen. sp. – Dyachkov 2014: 41.

undescribed species of Julidae – Nefediev et al. 2014a: 63.

*Leptoiulus tigirek* Mikhajlova, Nefediev, Nefedieva & Dyachkov 2015: 268, 269–273: figs.

*Leptoiulus tigirek* – Nefediev 2016: 30; Mikhajlova 2017: 77, 78: figs, insets 733–740, 789, 790, 90: map; Nefediev et al. 2017c: 13.

**Material examined** (all from Russia, southwestern Siberia, Altai Province, Charysh District, ca. 4.5 km SE of Charyshskoye Village). 1 ♀ (ASU), site 2 on N slope, soil sample 1 (10–20 cm deep), 2.06.2016; 1 ♀ (ASU), site 2 on N slope, soil sample 3 (litter), 2.06.2016, all leg. P.N., Kh.N., S.N., V.S.; 1 ♀ (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., pitfall traps, 12–14.07.2016, leg. P.N.; 1 ♂ (ASU), site 2 on N slope, soil sample 3 (0–10 cm deep), 13.07.2016; 1 ♂ (ZMMU), 1 ♂, 1 juv. (ASU), site 2 on N slope, hand sampling, 13.07.2016, all leg. Kh.N., S.N., V.S.; 1 ♀ (ASU), site 2 on N slope, hand sampling, 23.08.2016, all leg. P.N., Kh.N., S.N., V.S.; 1 ♀ (ZMMU), 5 ♀♀, 1 juv. (ASU), site 2 on N slope, hand sampling, 23.06.2017, leg. P.N., Kh.N., A.A., E.A.

**Distribution.** Being an Altai endemic, the species has been recorded only in the Altai Province in southwestern Siberia (Mikhajlova et al. 2015; Nefediev 2016).





**Figure 6–7.** Range limits of some millipede species in the study area. **6** Distribution of *Leptoiulus tigirek* (diamond) **7** Distribution of *Sibirius latuspremum* (triangle). The new localities are shown in red.

**Remarks.** The julid *L. tigirek* has been collected outside its *terra typica* for the first time. The above records on the northern slope show the species preference for more humid habitats.

### Genus *Megaphyllum* Verhoeff, 1894

#### *Megaphyllum sjaelandicum* (Meinert, 1868)

*Megaphyllum sjaelandicum* (Meinert, 1868) – Mikhajlova et al. 2007: 62, fig; Nefediev and Nefedieva 2007b: 162; 2008b: 62; Babenko et al. 2009: 183; Mikhajlova 2013: 9; 2016: 7; 2017: 97, 98; figs, 56: map; Nefediev et al. 2014a: 63; 2017c: 13.

**Material examined** (all from Russia, southwestern Siberia, Altai Province, Charysh District, ca. 4.5 km SE of Charyshskoye Village). 16 juv. (ASU), site 1 on S slope, 13.07.2015; 1 ♂, 1 ♀, 1 juv. (ZMMU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., 14.07.2015, all leg. P.N.; 3 juv. (ASU), foot of S slope of mountain, *Padus avium* and *Populus tremula* stand near brook, hand sampling, 31.05.2016; 12 juv. (ASU), site 1 on S slope, soil sample 1 (0–10 cm deep), 31.05.2016; 2 juv. (ASU), site 1 on S slope, soil sample 2 (0–10 cm deep), 31.05.2016; 2 juv. (ASU), site 1 on S slope, soil sample 3 (0–10 cm deep), 31.05.2016; 5 juv. (ASU), site 1 on S slope, soil sample 4 (0–10 cm deep), 1.06.2016; 5 juv. (ASU), site 1 on S slope, soil sample 5 (0–10 cm deep), 1.06.2016; 1 juv. (ASU), S slope between site 1 and site 2, broad gully with *Padus avium*, hand sampling, 1.06.2016; 43 juv. (ASU), site 1 on S slope, hand sampling, 1.06.2016; 9 juv. (ASU), site 2 on S slope, soil sample 1 (0–10 cm deep), 1.06.2016; 11 juv.

(ASU), site 2 on S slope, soil sample 2 (0–10 cm deep), 1.06.2016; 4 juv. (ASU), site 2 on S slope, soil sample 3 (0–10 cm deep), 1.06.2016; 2 juv. (ASU), site 2 on S slope, soil sample 4 (0–10 cm deep), 1.06.2016; 3 juv. (ASU), site 2 on S slope, soil sample 5 (0–10 cm deep), 1.06.2016; 4 juv. (ASU), site 2 on S slope, hand sampling, 1.06.2016; 3 juv. (ASU), site 2 on N slope, soil sample 2 (0–10 cm deep), 2.06.2016; 3 juv. (ASU), site 2 on N slope, hand sampling, 2.06.2016, all leg. P.N., Kh.N., S.N., V.S.; 1 ♀ (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., 12.07.2016, leg. P.N.; 1 ♂, 6 juv., 1 fragm. (ASU), site 1 on S slope, soil sample 1 (0–10 cm deep), 12.07.2016; 2 juv., 1 fragm. (ASU), site 1 on S slope, soil sample 1 (10–20 cm deep), 12.07.2016; 3 juv. (ASU), site 1 on S slope, soil sample 2 (0–10 cm deep), 12.07.2016; 1 ♂, 1 ♀ (ASU), site 1 on S slope, soil sample 2 (10–20 cm deep), 12.07.2016; 1 ♀, 3 juv. (ASU), site 1 on S slope, soil sample 3 (0–10 cm deep), 12.07.2016; 1 ♀, 2 juv. (ASU), site 1 on S slope, soil sample 3 (10–20 cm deep), 12.07.2016; 3 ♀♀, 8 juv. (ASU), site 1 on S slope, soil sample 5 (0–10 cm deep), 12.07.2016; 11 juv. (ASU), site 1 on S slope, hand sampling, 12.07.2016; 1 ♀, 1 juv. (ASU), site 2 on S slope, soil sample 2 (0–10 cm deep), 12.07.2016; 1 juv. (ASU), site 2 on S slope, soil sample 4 (0–10 cm deep), 12.07.2016; 1 ♂, 1 ♀ (ASU), site 2 on S slope, soil sample 5 (0–10 cm deep), 12.07.2016; 1 ♂, 1 fragm. (ASU), site 2 on N slope, soil sample 1 (0–10 cm deep), 13.07.2016; 1 juv. (ASU), site 2 on N slope, soil sample 1 (10–20 cm deep), 13.07.2016; 1 ♂ (ASU), site 2 on N slope, soil sample 2 (litter), 13.07.2016; 1 ♀, 2 juv. (ASU), site 2 on N slope, soil sample 2 (0–10 cm deep), 13.07.2016; 2 juv. (ASU), site 2 on N slope, soil sample 3 (0–10 cm deep), 13.07.2016; 1 ♂ (ASU), site 2 on N slope, soil sample 4 (litter), 13.07.2016; 1 juv. (ASU), site 2 on N slope, soil sample 4 (0–10 cm deep), 13.07.2016, all leg. Kh.N., S.N., V.S.; 2 juv. (ASU), site 1 on S slope, soil sample 1 (0–10 cm deep), 22.08.2016; 2 juv. (ASU), site 1 on S slope, soil sample 2 (0–10 cm deep), 22.08.2016; 2 juv. (ASU), site 1 on S slope, soil sample 3 (0–10 cm deep), 22.08.2016; 2 ♀♀, 3 juv. (ASU), site 1 on S slope, soil sample 4 (0–10 cm deep), 22.08.2016; 4 juv. (ASU), site 1 on S slope, soil sample 5 (0–10 cm deep), 22.08.2016; 1 ♂, 2 ♀♀, 3 juv. (ASU), site 2 on S slope, soil sample 2 (0–10 cm deep), 22.08.2016; 1 ♂, 1 ♀, 5 juv. (ASU), site 2 on S slope, soil sample 3 (0–10 cm deep), 22.08.2016; 2 ♀♀ (ASU), site 2 on S slope, soil sample 4 (0–10 cm deep), 23.08.2016; 1 ♀, 1 juv. (ASU), site 2 on S slope, soil sample 5 (0–10 cm deep), 23.08.2016; 1 ♀, 1 juv. (ASU), site 2 on N slope, soil sample 1 (0–10 cm deep), 23.08.2016; 1 juv., 1 fragm. (ASU), site 2 on N slope, soil sample 4 (0–10 cm deep), 23.08.2016; 1 ♂ (ASU), site 2 on N slope, soil sample 5 (0–10 cm deep), 23.08.2016; 1 ♀ (ASU), site 2 on N slope, hand sampling, 23.08.2016, all leg. P.N., Kh.N., S.N., V.S.; 1 ♀, 1 fragm. (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., hand sampling, 20.06.2017; 1 juv. (ASU), site 2 on S slope, hand sampling, 24.06.2017, all leg. P.N.

**Distribution.** European–Western Siberian temperate range: this species appears to be widespread from northern and central Europe (Scandinavia, Finland, the Baltics,

Germany, Poland, Belarus) through European Russia and the Urals to East Kazakhstan and SW Siberia (Altai Province, Republic of Altai and Novosibirsk Area).

**Remarks.** In the study area, *M. sjaelandicum* dominates habitats on the southern slope, where its abundance reaches up to 22 ind./m<sup>2</sup>.

## Genus *Sibiriulus* Gulička, 1963

### *Sibiriulus latisupremus* Mikhajlova, Nefediev & Nefedieva, 2014

Figure 7

*Sibiriulus multiradicatus* pro parte – Mikhajlova and Nefediev 2003: 85, figs 1–3; Mikhajlova et al. 2007: 60, 61: figs 12–14, 18.

*Sibiriulus latisupremus* Mikhajlova, Nefediev & Nefedieva, 2014: 35, 36–38: figs, 51: map.

*Sibiriulus latisupremus* – Mikhajlova 2017: 90, 91: figs, insets 741, 743, 748, 752, 753, 785, 786, 92: map; Nefediev et al. 2017c: 13.

**Material examined** (all from Russia, southwestern Siberia, Altai Province, Charysh District, ca. 4.5 km SE of Charyshskoye Village). 1 ♂, 3 ♀♀, 1 juv. (ASU), site 1 on S slope, 13.07.2015; 3 ♀♀ (ASU), site 1 on S slope, 13.07.2015, all leg. P.N.; 1 ♂ (ASU), foot of S slope of mountain, *Padus avium* and *Populus tremula* stand near brook, hand sampling, 31.05.2016; 4 ♀♀ (ASU), site 1 on S slope, soil sample 1 (0–10 cm deep), 31.05.2016; 2 ♂♂, 2 ♀♀, 2 juv. (ASU), site 1 on S slope, soil sample 2 (0–10 cm deep), 31.05.2016; 2 ♀♀, 1 fragm. (ASU), site 1 on S slope, soil sample 3 (0–10 cm deep), 31.05.2016; 1 ♀, 1 fragm. (ASU), site 1 on S slope, soil sample 3 (10–20 cm deep), 31.05.2016; 3 ♂♂, 2 ♀♀, 1 juv. (ASU), site 1 on S slope, soil sample 4 (0–10 cm deep), 1.06.2016; 2 ♂♂, 1 ♀ (ASU), site 1 on S slope, soil sample 4 (10–20 cm deep), 1.06.2016; 3 ♀♀, 2 juv., 1 fragm. (ASU), site 1 on S slope, soil sample 5 (0–10 cm deep), 1.06.2016; 6 ♂♂, 9 ♀♀, 3 juv. (ASU), site 1 on S slope, hand sampling, 1.06.2016; 2 juv. (ASU), site 2 on S slope, soil sample 1 (0–10 cm deep), 1.06.2016; 1 ♀ (ASU), site 2 on S slope, soil sample 2 (0–10 cm deep), 1.06.2016; 1 juv. (ASU), site 2 on S slope, soil sample 3 (0–10 cm deep), 1.06.2016; 1 ♂, 6 ♀♀, 2 juv. (ASU), site 2 on S slope, soil sample 4 (0–10 cm deep), 1.06.2016; 3 ♀♀, 1 juv. (ASU), site 2 on S slope, hand sampling, 1.06.2016; 1 ♀, 1 juv., 1 fragm. (ASU), site 1 on N slope, soil sample 1 (litter), 2.06.2016; 1 ♂, 4 ♀♀, 4 juv. (ASU), site 1 on N slope, soil sample 1 (0–10 cm deep), 2.06.2016; 1 fragm. (ASU), site 1 on N slope, soil sample 2 (litter), 2.06.2016; 2 ♂♂, 3 ♀♀, 3 juv., 1 fragm. (ASU), site 1 on N slope, soil sample 2 (0–10 cm deep), 2.06.2016; 2 ♀♀ (ASU), site 1 on N slope, soil sample 3 (litter), 2.06.2016; 1 juv. (ASU), site 1 on N slope, soil sample 3 (0–10 cm deep), 2.06.2016; 1 ♀, 1 juv. (ASU), site 1 on N slope, soil sample 4 (litter), 2.06.2016; 1 ♀, 1 fragm. (ASU), site 1 on N slope, soil sample 4 (0–10 cm deep), 2.06.2016; 1 juv. (ASU), site 1 on N slope, soil sample 4



(10–20 cm deep), 2.06.2016; 1 juv. (ASU), site 1 on N slope, soil sample 5 (litter), 2.06.2016; 2 ♀♀, 2 juv. (ASU), site 1 on N slope, soil sample 5 (0–10 cm deep), 2.06.2016; 1 ♂, 12 ♀♀ (ASU), site 1 on N slope, hand sampling, 2.06.2016; 1 ♀, 2 juv. (ASU), site 2 on N slope, soil sample 1 (0–10 cm deep), 2.06.2016; 1 ♀ (ASU), site 2 on N slope, soil sample 4 (litter), 2.06.2016; 1 juv. (ASU), site 2 on N slope, soil sample 4 (0–10 cm deep), 2.06.2016, all leg. P.N., Kh.N., S.N., V.S.; 8 ♂♂, 5 ♀♀ (ASU), site 1 on N slope, hand sampling, 22.06.2016, leg. Kh.N.; 2 juv. (ASU), site 1 on S slope, soil sample 1 (0–10 cm deep), 12.07.2016; 1 juv. (ASU), site 1 on S slope, soil sample 1 (10–20 cm deep), 12.07.2016; 1 ♀, 3 juv. (ASU), site 1 on S slope, soil sample 2 (0–10 cm deep), 12.07.2016; 2 juv. (ASU), site 1 on S slope, soil sample 2 (10–20 cm deep), 12.07.2016; 1 juv. (ASU), site 1 on S slope, soil sample 3 (0–10 cm deep), 12.07.2016; 4 juv. (ASU), site 1 on S slope, soil sample 4 (0–10 cm deep), 12.07.2016; 1 ♀, 1 juv. (ASU), site 1 on S slope, soil sample 4 (10–20 cm deep), 12.07.2016; 1 ♂, 1 ♀, 3 juv. (ASU), site 1 on S slope, soil sample 5 (0–10 cm deep), 12.07.2016; 2 ♂♂ (ASU), site 2 on S slope, soil sample 2 (0–10 cm deep), 12.07.2016; 1 ♀ (ASU), site 2 on S slope, soil sample 2 (10–20 cm deep), 12.07.2016; 3 juv. (ASU), site 2 on S slope, soil sample 3 (0–10 cm deep), 12.07.2016; 2 juv. (ASU), site 2 on S slope, soil sample 4 (0–10 cm deep), 12.07.2016; 2 ♂♂, 6 juv. (ASU), site 1 on N slope, soil sample 1 (0–10 cm deep), 13.06.2016; 1 juv. (ASU), site 1 on N slope, soil sample 1 (10–20 cm deep), 13.06.2016; 1 ♂, 4 ♀♀, 2 juv. (ASU), site 1 on N slope, soil sample 2 (0–10 cm deep), 13.06.2016; 2 ♀♀, 1 juv. (ASU), site 1 on N slope, soil sample 3 (0–10 cm deep), 13.06.2016; 1 juv. (ASU), site 1 on N slope, soil sample 4 (0–10 cm deep), 13.06.2016; 1 ♂ (ASU), site 1 on N slope, soil sample 5 (0–10 cm deep), 13.06.2016; 2 ♀♀, 1 juv. (ASU), site 1 on N slope, hand sampling, 13.06.2016; 1 juv. (ASU), site 2 on N slope, soil sample 5 (0–10 cm deep), 13.06.2016, all leg. Kh.N., S.N., V.S.; 2 ♀♀, 1 juv. (ASU), site 1 on S slope, soil sample 1 (0–10 cm deep), 22.08.2016; 1 juv. (ASU), site 1 on S slope, soil sample 2 (0–10 cm deep), 22.08.2016; 3 juv. (ASU), site 1 on S slope, soil sample 3 (0–10 cm deep), 22.08.2016; 2 ♂♂ (ASU), site 1 on S slope, soil sample 3 (10–20 cm deep), 23.08.2016; 1 ♀, 1 juv. (ASU), site 1 on S slope, soil sample 5 (0–10 cm deep), 23.08.2016; 1 ♀ (ASU), site 1 on S slope, soil sample 5 (10–20 cm deep), 23.08.2016; 2 ♀♀, 1 juv., 1 fragm. (ASU), site 1 on N slope, soil sample 1 (0–10 cm deep), 23.08.2016; 2 ♀♀, 1 juv. (ASU), site 1 on N slope, soil sample 2 (0–10 cm deep), 23.08.2016; 2 ♀♀ (ASU), site 1 on N slope, soil sample 5 (0–10 cm deep), 23.08.2016; 1 ♂, 4 ♀♀ (ASU), site 2 on N slope, soil sample 2 (0–10 cm deep), 23.08.2016; 1 ♀ (ASU), site 2 on N slope, hand sampling, 23.08.2016, all leg. P.N., Kh.N., S.N., V.S.; 3 ♂♂, 5 ♀♀, 1 juv. (ZMMU), site 1 on N slope, hand sampling, 23.06.2017, leg. P.N., Kh.N., A.A., E.A.; 1 juv. (ASU), site 2 on S slope, hand sampling, 24.06.2017, leg. P.N.

**Distribution.** Being an endemic of SW Siberia, *S. latuspremus* has previously been recorded in a few localities in SE part of the Altai Province and NW part of the Republic of Altai (Mikhaljova et al. 2014).

**Remarks.** The above records of the julid *S. latisupremus* are the southwesternmost for the species. In the study localities, the species demonstrates no preference between investigated habitats as regards different slope exposures.

**Family Nemasomatidae Bollman, 1893**

**Genus *Orinisobates* Lohmander, 1933**

***Orinisobates sibiricus* (Gulička, 1963)**

*Isobates sibiricus* Gulička, 1963: 522: figs.

*Isobates sibiricus* – Byzova and Chadaeva 1965: 337.

*Isobates (Orinisobates) sibiricus* – Gulička 1972: 45: figs; Nefediev and Nefedieva 2008a: 117; Babenko et al. 2009: 182.

*Orinisobates sibiricus* – Enghoff 1985: 53, 54: figs; Mikhajlova 1993: 16; 2002: 206; 2004: 96: figs, 94: map; 2017: 120, 121: figs, 122: map; Mikhajlova and Golovatch 2001: 107; Mikhajlova and Nefediev 2003: 83; Nefediev and Nefedieva 2006: 98; 2007a: 139; 2007b: 160; 2008a: 117; 2008b: 62; 2013: 87; Nefedieva and Nefediev 2008: 123; Nefediev et al. 2014a: 63; 2017c: 13; Nefedieva et al. 2014: 65; 2015: 147.

**Material examined** (all from Russia, southwestern Siberia, Altai Province, Charysh District, ca. 4.5 km SE of Charyshskoye Village). 1 ♀ (ASU), site 1 on S slope, 13.07.2015, leg. P.N.; 1 ♀ (ASU), site 2 on S slope, soil sample 1 (0–10 cm deep), 1.06.2016; 1 ♂, 1 ♀, 1 juv. (ASU), site 2 on S slope, soil sample 4 (0–10 cm deep), 1.06.2016; 1 ♂ (ASU), site 1 on N slope, soil sample 1 (litter), 2.06.2016; 3 ♂♂, 1 juv. (ASU), site 1 on N slope, soil sample 1 (0–10 cm deep), 2.06.2016; 1 ♀ (ASU), site 1 on N slope, soil sample 2 (0–10 cm deep), 2.06.2016; 6 ♀♀ (ASU), site 1 on N slope, hand sampling, 2.06.2016, all leg. P.N., Kh.N., S.N., V.S.; 2 ♀♀ (ASU), site 1 on N slope, hand sampling, 22.06.2016, leg. Kh.N.; 1 ♂, 1 ♀, 4 juv. (ASU), site 2 on S slope, soil sample 2 (0–10 cm deep), 12.07.2016; 1 ♀, 1 juv., 1 fragm. (ASU), site 2 on S slope, soil sample 2 (10–20 cm deep), 12.07.2016; 1 ♂, 1 ♀ (ZMMU), 2 ♂♂, 3 juv. (ASU), site 1 on N slope, soil sample 1 (0–10 cm deep), 13.07.2016; 2 ♂♂, 1 ♀, 1 juv. (ASU), site 2 on N slope, soil sample 1 (0–10 cm deep), 13.07.2016, all leg. Kh.N., S.N., V.S.; 1 ♂ (ASU), site 2 on S slope, soil sample 1 (0–10 cm deep), 22.08.2016, leg. P.N., Kh.N., S.N., V.S.

**Distribution.** Being a Central Palaearctic species, *O. sibiricus* is very widespread in southern Siberia, Russia as far as the Zabaikalskii Province, Republic of Tyva, southern part of the Krasnoyarsk Province, Republic of Khakassia, Republic of Altai, Altai Province and Kemerovo Area; also known from Eastern Kazakhstan and Kyrgyzstan.

**Remarks.** This species shows no significant difference in its abundance between two studied slope exposures.

**Order Chordeumatida C. L. Koch, 1847****Family Diplomaragnidae Attems, 1907****Genus *Altajosoma* Gulička, 1972*****Altajosoma* sp.**

**Material examined** (all from Russia, southwestern Siberia, Altai Province, Charysh District, ca. 4.5 km SE of Charyshskoye Village). 1 ♂, 1 ♀ (ASU), site 1 on N slope, 13.07.2015; 2 juv. (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., 14.07.2015, all leg. P.N.; 1 juv. (ASU), site 1 on S slope, soil sample 5 (0–10 cm deep), 1.06.2016; 1 juv. (ASU), site 1 on N slope, soil sample 1 (litter), 2.06.2016; 1 juv. (ASU), site 1 on N slope, soil sample 2 (litter), 2.06.2016; 1 juv. (ASU), site 1 on N slope, soil sample 4 (litter), 2.06.2016; 1 juv. (ASU), site 1 on N slope, hand sampling, 2.06.2016, all leg. P.N., Kh.N., S.N., V.S.; 2 juv. (ASU), site 1 on N slope, hand sampling, 22.06.2016, leg. Kh.N.; 1 ♂, 1 ♀ (ASU), site 1 on S slope, soil sample 2 (0–10 cm deep), 12.07.2016; 1 ♀ (ASU), site 1 on S slope, soil sample 4 (0–10 cm deep), 12.07.2016; 1 ♀ (ASU), site 1 on S slope, soil sample 4 (10–20 cm deep), 12.07.2016; 1 ♀ (ASU), site 1 on N slope, soil sample 2 (0–10 cm deep), 13.07.2016; 1 ♀, 1 juv. (ASU), site 2 on N slope, soil sample 5 (0–10 cm deep), 13.07.2016, all leg. Kh.N., S.N., V.S.; 1 juv. (ASU), site 2 on S slope, soil sample 2 (litter), 22.07.2016; 1 ♂ (ASU), site 1 on N slope, soil sample 2 (0–10 cm deep), 23.08.2016; 1 juv. (ASU), site 2 on N slope, soil sample 5 (0–10 cm deep), 23.08.2016, all leg. P.N., Kh.N., S.N., V.S.; 4 juv. (ASU), site 1 on N slope, hand sampling, 23.06.2017, leg. P.N., Kh.N., A.A., E.A.

**Distribution.** This species is currently known only from the study area.

**Remarks.** The above recorded specimens of *Altajosoma* sp. are most similar to *Altajosoma bakurovi bakurovi* (Shear, 1990) in some details of gonopod structure, i.e. in the shape of colpocoxites of the posterior gonopods and in particular in their distal parts, but the colpocoxites are a little bit narrower in the newly found species compared to *A. bakurovi bakurovi*. These specimens also differ significantly in the shape of the large posterior angiocoxal processes.

**Order Polydesmida Leach, 1815****Family Polydesmidae Leach, 1815****Genus *Schizoturanius* Verhoeff, 1931*****Schizoturanius clavatipes* (Stuxberg, 1876)**

*Polydesmus clavatipes* – Nefediev and Nefedieva 2008a: 117.

*Schizoturanius clavatipes* – Mikhajlova 1993: 31, 32: figs; 2002: 206; 2004: 238, 239: figs, 228: map; 2013: 9; 2016: 24; 2017: 288, 289: figs, 290: map; Nefediev 2001: 85; 2002a: 30; 2002b: 139; Mikhajlova and Golovatch 2001: 116; Mikhajlova and Nefediev 2003: 81; Nefediev and Nefedieva 2005: 178; 2006: 98; 2007a: 139;

2007b: 161; 2007c: 99; 2008b: 62; 2011: 100; 2012a: 51; 2012b: 47; 2013: 87; Nefedieva and Nefediev 2008: 123; Nefediev et al. 2014a: 63; 2017c: 13; Nefedieva et al. 2014: 65; 2015: 152.

**Material examined** (all from Russia, southwestern Siberia, Altai Province, Charysh District, ca. 4.5 km SE of Charyshskoye Village). 2 juv. (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., 14.07.2015, leg. P.N.; 4 juv. (ASU), site 1 on S slope, soil sample 3 (0–10 cm deep), 1.06.2016; 2 ♀♀, 9 juv. (ASU), site 1 on S slope, soil sample 4 (0–10 cm deep), 1.06.2016; 1 juv. (ASU), site 1 on S slope, soil sample 5 (0–10 cm deep), 1.06.2016; 2 ♂♂, 1 ♀, 2 juv. (ASU), foot of S slope of mountain, *Padus avium* and *Populus tremula* stand near brook, hand sampling, 1.06.2016; 2 ♂♂, 2 ♀♀ (ASU), site 1 on N slope, hand sampling, 2.06.2016, all leg. P.N., Kh.N., S.N., V.S.; 2 juv. (ASU), site 1 on S slope, soil sample 1 (0–10 cm deep), 12.07.2016; 1 juv. (ASU), site 1 on S slope, soil sample 3 (0–10 cm deep), 12.07.2016; 3 juv. (ASU), site 1 on S slope, soil sample 3 (10–20 cm deep), 12.07.2016; 2 juv. (ASU), site 1 on S slope, soil sample 5 (0–10 cm deep), 12.07.2016; 1 juv. (ASU), site 1 on N slope, soil sample 1 (0–10 cm deep), 13.07.2016; 1 juv. (ASU), site 1 on N slope, hand sampling, 13.07.2016; 1 juv. (ASU), site 2 on N slope, soil sample 3 (0–10 cm deep), 13.07.2016; 1 juv. (ASU), near Komendantka Village, hand sampling, 14.07.2016, all leg. Kh.N., S.N., V.S.; 1 ♂ (ASU), site 1 on S slope, soil sample 2 (10–20 cm deep), 22.08.2016; 1 ♂ (ASU), site 1 on S slope, soil sample 4 (0–10 cm deep), 23.08.2016; 1 ♂, 1 ♀ (ZMMU), 1 ♀ (ASU), site 1 on S slope, soil sample 5 (0–10 cm deep), 23.08.2016; 1 ♂ (ASU), site 2 on S slope, soil sample 2 (0–10 cm deep), 22.08.2016; 1 juv. (ASU), site 2 on S slope, soil sample 4 (0–10 cm deep), 22.08.2016; 1 ♂ (ASU), site 2 on N slope, soil sample 2 (0–10 cm deep), 23.08.2016; 1 ♀ (ASU), site 2 on N slope, soil sample 4 (litter), 23.08.2016, all leg. P.N., Kh.N., S.N., V.S.

**Distribution.** Being a Western-Central Siberian species, *S. clavatipes* appears to be very widespread in southwestern Siberia, Russia, inhabiting Tomsk, Novosibirsk, and Kemerovo areas, Altai Province, Republic of Altai, Republic of Khakassia, and also along the Yenisei River in the Krasnoyarsk Province, central Siberia, Russia.

**Remarks.** The results of this study suggest that *S. clavatipes* prefers the southern slope, in spite of its highly ecological valence.

**Class Chilopoda Latreille, 1817**

**Order Lithobiomorpha Pocock, 1895**

**Family Lithobiidae Newport, 1844**

**Genus *Lithobius* Leach, 1814**

***Lithobius (Ezembius) ostiacorum* Stuxberg, 1876**

*Lithobius (Ezembius) ostiacorum* – Nefediev et al. 2017c: 13; 2017d: 218: map.

**Material examined** (all from Russia, southwestern Siberia, Altai Province, Charysh District, ca. 4.5 km SE of Charyshskoye Village). 1 ♀ (ZMMU), foot of S slope of mountain, *Padus avium* and *Populus tremula* stand near brook, hand sampling, 31.05.2016; 1 ♀ (ASU), site 1 on N slope, soil sample 1 (0–10 cm deep), 2.06.2016; 1 juv. (ASU), site 1 on N slope, soil sample 2 (0–10 cm deep), 2.06.2016; 1 ♂ (ASU), site 1 on N slope, soil sample 3 (litter), 2.06.2016; 1 ♀, 1 juv. (ASU), site 1 on N slope, soil sample 5 (0–10 cm deep), 2.06.2016, all leg. P.N., Kh.N., S.N., V.S.; 1 ♀ (ASU), site 1 on S slope, soil sample 3 (0–10 cm deep), 12.07.2016; 2 ♀♀, 1 juv. (ASU), site 1 on N slope, soil sample 2 (0–10 cm deep), 12.07.2016; 1 ♂, 1 juv. (ASU), site 1 on N slope, soil sample 5 (0–10 cm deep), 12.07.2016; 1 juv. (ASU), site 2 on N slope, soil sample 2 (0–10 cm deep), 13.07.2016; 1 ♀ (ASU), site 2 on N slope, soil sample 4 (10–20 cm deep), 13.07.2016, all leg. Kh.N., S.N., V.S.; 2 juv. (ASU), site 1 on S slope, soil sample 5 (0–10 cm deep), 22.08.2016; 1 juv. (ASU), site 2 on N slope, soil sample 2 (0–10 cm deep), 23.08.2016; 2 juv. (ASU), site 2 on N slope, soil sample 3 (0–10 cm deep), 23.08.2016, all leg. P.N., Kh.N., S.N., V.S.; 1 ♂ (PSU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., hand sampling, 20.06.2017, leg. P.N.

**Distribution.** Southern Siberian boreal range with isolated Yenisei population: this species has previously been recorded in the Yenisei River area, Krasnoyarsk Province and Irkutsk Area (central and eastern Siberia, respectively) (Zalesskaja 1978), also recently found in northern Mongolia (Poloczek et al. 2016), Altai Province (Nefediev et al. 2017c) and Republic of Altai (Nefediev et al. 2017d).

**Remarks.** The above record of *L. ostiacorum*, recently announced at the 17th International Congress of Myriapodology (Nefediev et al. 2017c), can be considered as the first formal find of the species in SW Siberia. In the study localities, the species was found more frequently on N facing habitats.

### *Lithobius (Ezembius) proximus* Sseliwanoff, 1880

*Lithobius proximus* – Zalesskaja 1978: 125–126; Striganova and Poryadina 2005: 226; Bukhkalov and Sergeeva 2012: 61; Sergeeva 2013: 530–532; Bukhkalov et al. 2014: 71–72;

*Lithobius (Ezembius) proximus* – Nefediev et al. 2017b: 116, 117: map; 2017c: 13; 2017d: 218: map.

**Material examined** (all from Russia, southwestern Siberia, Altai Province, Charysh District, ca. 4.5 km SE of Charyshskoye Village). 2 ♂♂ (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., 14.07.2015, leg. P.N.; 4 ♂♂ (ASU), same locality, 15.07.2015, leg. P.N., T.Z.; 1 ♂ (ASU), S slope between site 1 and site 2, broad gully with *Padus avium*, hand sampling, 31.05.2016, leg. P.N., Kh.N., S.N., V.S.; 1 subadult ♂ (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., 12.07.2016; 2 ♂♂, 1 ♀ (ASU), same locality, pitfall traps, 12–14.07.2016, all leg. P.N.; 1 ♂ (ASU), site 2 on S



slope, soil sample 1 (0–10 cm deep), 12.07.2016, leg. Kh.N., S.N., V.S.; 2 juv. (ASU), site 1 on N slope, soil sample 2 (0–10 cm deep), 23.08.2016; 1 ♂ (ASU), site 2 on N slope, soil sample 4 (litter), 23.08.2016; 1 ♀ (ASU), site 2 on N slope, hand sampling, 23.08.2016, all leg. P.N., Kh.N., S.N., V.S.; 1 ♂ (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., hand sampling, 20.06.2017, leg. P.N.

**Distribution.** Eastern European-transSiberian temperate range: this species is widespread from the eastern Russian Plain (republics of Mari El and Tatarstan, Kirov and Samara areas) in the west through Siberia to the Russian Far East (Maritime Province, Sakhalin and the Kuriles) (Zalesskaja 1978; Farzalieva and Esysunin 2008; Farzalieva 2009; Farzalieva and Tselishcheva 2009).

**Remarks.** The above find of the species, recently announced at the 17th International Congress of Myriapodology (Nefediev et al. 2017c), can be considered as the first formal record of it in the Altai Province, SW Siberia. In the investigated area, *L. proximus* is very rare and shows no significant differences in its distribution between slopes.

### *Lithobius (Ezembius) sibiricus* Gerstfeldt, 1858

*Lithobius sibiricus* – Nefediev 2001: 85.

*Lithobius (Ezembius) sibiricus* – Nefediev et al. 2016d: 263; 2017c: 13; 2017d: 219, 218: map.

**Material examined** (all from Russia, southwestern Siberia, Altai Province, Charysh District, ca. 4.5 km SE of Charyshskoye Village). 2 ♂♂, 1 ♀, 2 juv. (ASU), site 1 on S slope, 13.07.2015; 1 ♂, 1 ♀, 2 subadult ♀♀ (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., 14.07.2015, all leg. P.N.; 1 ♂, 1 subadult ♀, 2 juv. (ZMMU), foot of S slope of mountain, *Padus avium* and *Populus tremula* stand near brook, hand sampling, 31.05.2016; 1 ♂, 1 ♀, 1 juv. (PSU), site 1 on S slope, hand sampling, 31.05.2016; 2 ♂♂, 8 ♀♀ (ASU), S slope between site 1 and site 2, broad gully with *Padus avium*, hand sampling, 1.06.2016; 1 ♂ (ASU), site 1 on S slope, soil sample 3 (10–20 cm deep), 1.06.2016; 2 juv. (ASU), site 1 on N slope, soil sample 2 (0–10 cm deep), 2.06.2016; 7 ♂♂, 1 ♀, 3 juv. (ASU), site 1 on N slope, soil sample 3 (litter), 2.06.2016; 1 ♂ (ASU), site 1 on N slope, soil sample 3 (10–20 cm deep), 1.06.2016; 1 ♀ (ASU), site 1 on N slope, soil sample 4 (0–10 cm deep), 2.06.2016; 2 ♂♂, 1 ♀ (ASU), site 1 on N slope, hand sampling, 2.06.2016; 1 ♂, 1 subadult ♂, 4 ♀♀, 1 subadult ♀ (ASU), site 2 on N slope, hand sampling, 2.06.2016; 1 juv. (ASU), site 2 on N slope, soil sample 1 (0–10 cm deep), 2.06.2016; 1 juv. (ASU), site 2 on N slope, soil sample 1 (10–20 cm deep), 2.06.2016, all leg. P.N., Kh.N., S.N., V.S.; 4 ♂♂, 1 ♀ (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., pitfall traps, 12–14.07.2016, leg. P.N.; 1 ♀ (ASU), site 1 on S slope, soil sample 1 (10–20 cm deep), 12.07.2016; 1 ♂, 3 juv. (ASU), site 2 on S slope, soil sample 1 (0–10 cm deep), 12.07.2016; 1 ♂, 2 ♀♀, 1 juv. (ASU), site 2 on S slope, soil sample

1 (10–20 cm deep), 12.07.2016; 1 ♀ (ASU), site 2 on S slope, soil sample 2 (10–20 cm deep), 12.07.2016; 1 ♂ (ASU), site 1 on N slope, soil sample 1 (10–20 cm deep), 13.07.2016; 2 ♂♂, 1 ♀, 1 juv. (ASU), site 1 on N slope, soil sample 2 (0–10 cm deep), 13.07.2016; 1 juv. (ASU), site 1 on N slope, soil sample 5 (0–10 cm deep); 1 ♂ (ASU), site 2 on N slope, hand sampling, 13.07.2016; 1 ♂ (ASU), site 2 on N slope, soil sample 1 (0–10 cm deep), 13.07.2016; 1 ♂, 1 ♀ (ASU), site 2 on N slope, soil sample 3 (0–10 cm deep), 13.07.2016; 1 ♀ (ASU), site 2 on N slope, soil sample 4 (litter), 13.07.2016; 1 ♂, 1 fragm. (ASU), site 2 on N slope, soil sample 4 (0–10 cm deep), 13.07.2016; 1 ♂ (ASU), near Komendantka Village, hand sampling, 14.07.2016, all leg. Kh.N., S.N., V.S.; 1 juv. (ASU), site 1 on S slope, soil sample 4 (0–10 cm deep), 23.08.2016; 1 ♀, 1 juv. (ASU), site 1 on S slope, soil sample 5 (0–10 cm deep), 23.08.2016; 1 ♂, 1 ♀ (ASU), site 1 on N slope, soil sample 1 (0–10 cm deep), 23.08.2016; 1 ♂, 1 juv., 1 fragm. (ASU), site 1 on N slope, soil sample 2 (0–10 cm deep), 23.08.2016; 1 juv. (ASU), site 1 on N slope, soil sample 3 (0–10 cm deep), 23.08.2016; 1 ♂ (ASU), site 1 on N slope, soil sample 4 (0–10 cm deep), 23.08.2016; 1 ♀ (ASU), site 2 on N slope, soil sample 2 (0–10 cm deep), 23.08.2016; 1 ♀ (ASU), site 2 on N slope, soil sample 3 (0–10 cm deep), 23.08.2016; 3 ♂♂, 1 juv. (ASU), site 2 on N slope, soil sample 4 (0–10 cm deep), 23.08.2016; 1 ♂ (ASU), site 2 on N slope, soil sample 5 (litter), 23.08.2016; 2 ♂♂, 1 ♀, 1 juv. (ASU), site 2 on N slope, soil sample 5 (0–10 cm deep), 23.08.2016; 2 ♂♂, 2 ♀♀, 1 juv. (ASU), site 2 on N slope, soil sample, hand sampling, 23.08.2016, all leg. P.N., Kh.N., S.N., V.S.; 1 ♀, 1 juv. (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., hand sampling, 20.06.2017, leg. P.N.; 2 ♂♂, 3 ♀♀ (ASU), site 1 on N slope, hand sampling, 23.06.2017; 1 ♂ (ASU), site 2 on N slope, hand sampling, 23.06.2017, all leg. P.N., Kh.N., A.A., E.A.

**Distribution.** Trans-Siberian temperate range: *L. sibiricus* is one of the most widely spread lithobiomorph centipedes in the Asian part of Russia, having been reported from southwestern Siberia (Tomsk Area, Altai Province and Republic of Altai), central and eastern Siberia (Krasnoyarsk Province, Irkutsk Area, Zabaikalskii Province and the republics of Buryatia and Sakha) and the Russian Far East (Amur Area, Maritime Province and Sakhalin Island); also recorded in northern Mongolia (Nefediev et al. 2016, 2017c, d).

**Remarks.** In the study localities, *L. sibiricus* shows a higher abundance on the northern slope.

### ***Lithobius (Monotarsobius) curtipes* C.L. Koch, 1847**

*Lithobius curtipes* – Striganova and Poryadina 2005: 226; Bukhkalo and Sergeeva 2012: 61; Sergeeva 2013: 530–532.

*Lithobius (Monotarsobius) curtipes* – Nefediev et al. 2016d: 263, 260: map; 2017b: 116, 117: map; 2017c: 13; 2017d: 219, 218: map.

**Material examined** (all from Russia, southwestern Siberia, Altai Province, Charysh District, ca. 4.5 km SE of Charyshskoye Village). 1 subadult ♀ (ASU), site 1 on S slope, 13.07.2015,

leg. P.N.; 1 ♀ (ZMMU), foot of S slope, *Padus avium* and *Populus tremula* stand near brook, hand sampling, 31.05.2016; 1 ♂ (ASU), site 1 on S slope, soil sample 5 (0–10 cm deep), 1.06.2016; 1 ♂ (ASU), site 1 on N slope, soil sample 4 (litter), 2.06.2016; 1 ♂, 1 juv. (ASU), site 1 on N slope, soil sample 5 (litter), 2.06.2016; 2 ♂♂, 1 juv. (ASU), site 1 on N slope, soil sample 5 (0–10 cm deep), 2.06.2016; 1 ♂, 1 juv. (ASU), site 2 on N slope, soil sample 1 (0–10 cm deep), 2.06.2016; 1 ♂, 2 ♀♀, 2 juv. (ASU), site 2 on N slope, soil sample 2 (0–10 cm deep), 2.06.2016; 1 ♀ (ASU), site 2 on N slope, soil sample 3 (litter), 2.06.2016; 1 ♀, 2 juv. (ASU), site 2 on N slope, soil sample 3 (0–10 cm deep), 2.06.2016, all leg. P.N., Kh.N., S.N., V.S.; 1 ♂, 2 ♀♀ (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., 12.07.2016, leg. P.N.; 2 ♂♂ (ASU), site 1 on N slope, soil sample 3 (litter), 13.07.2016; 1 ♂ (ASU), site 1 on N slope, soil sample 3 (0–10 cm deep), 13.07.2016; 1 ♂, 1 ♀ (ASU), site 1 on N slope, soil sample 4 (0–10 cm deep), 13.07.2016; 2 ♂♂ (ASU), site 1 on N slope, soil sample 5 (0–10 cm deep), 13.07.2016; 1 ♀ (ASU), site 2 on N slope, soil sample 1 (0–10 cm deep), 13.07.2016; 2 ♂♂ (ASU), site 2 on N slope, soil sample 2 (litter), 13.07.2016; 1 ♂, 4 ♀♀, 2 juv. (ASU), site 2 on N slope, soil sample 3 (0–10 cm deep), 13.07.2016; 1 juv. (ASU), site 2 on N slope, soil sample 4 (litter), 13.07.2016; 1 ♂, 1 ♀ (ASU), site 2 on N slope, soil sample 4 (0–10 cm deep), 13.07.2016, all leg. Kh.N., S.N., V.S.; 2 ♂♂, 2 ♀♀, 1 juv. (ASU), site 2 on N slope, soil sample 1 (0–10 cm deep), 23.08.2016; 1 ♀ (ASU), site 2 on N slope, soil sample 2 (0–10 cm deep), 23.08.2016; 1 ♂, 5 ♀♀ (ASU), site 2 on N slope, soil sample 3 (0–10 cm deep), 23.08.2016; 1 ♀ (ASU), site 2 on N slope, soil sample 3 (10–20 cm deep), 23.08.2016; 1 juv. (ASU), site 2 on N slope, soil sample 4 (litter), 23.08.2016; 2 ♂♂, 2 ♀♀ (ASU), site 2 on N slope, soil sample 4 (0–10 cm deep), 23.08.2016; 6 ♂♂, 2 juv. (ASU), site 2 on N slope, soil sample 5 (0–10 cm deep), 23.08.2016, all leg. P.N., Kh.N., S.N., V.S.; 4 ♂♂, 3 ♀♀ (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., hand sampling, 20.06.2017, leg. P.N.; 1 subadult ♀ (ASU), site 2 on N slope, hand sampling, 23.06.2017, leg. P.N., Kh.N., A.A., E.A.

**Distribution.** Trans-Palaearctic: the species displays extremely wide distribution in Europe, Asian Russia, the Near East and the Arabian Peninsula, also in northern Mongolia. In Siberia *L. curtipes* has been reported from the Novosibirsk, Omsk, Tyumen and Tomsk areas, the Altai and Krasnoyarsk provinces and the Republic of Altai (Nefediev et al. 2016d, 2017b, c).

**Remarks.** Despite a wide geographical range, and its high ecological valence, in the study area, the species inhabits mainly the northern slope.

### *Lithobius (Monotarsobius) insolens* Dányi & Tuf, 2012

*Lithobius (Monotarsobius) insolens* – Nefediev et al. 2017b: 116, 117: map; 2017c: 13; 2017d: 221, 220: map.

**Material examined** (all from Russia, southwestern Siberia, Altai Province, Charysh District, ca. 4.5 km SE of Charyshskoye Village). 1 ♀ (ASU), site 1 on S slope, 13.07.2015;

5 ♂♂, 4 ♀♀, 2 juv. (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., 14.07.2015, all leg. P.N.; 10 ♂♂, 7 ♀♀, 3 subadult ♀♀, 1 juv. (PSU), site 1 on S slope, hand sampling, 31.05.2016; 1 juv. (ASU), site 1 on S slope, soil sample 1 (10–20 cm deep), 31.05.2016; 1 juv. (ASU), site 1 on S slope, soil sample 2 (0–10 cm deep), 31.05.2016; 2 ♂♂, 1 ♀, 2 juv. (ASU), site 1 on S slope, soil sample 4 (0–10 cm deep), 1.06.2016; 1 ♂, 2 ♀♀ (ASU), site 1 on S slope, soil sample 5 (0–10 cm deep), 1.06.2016; 1 ♂ (ASU), S slope between site 1 and site 2, broad gully with *Padus avium*, hand sampling, 1.06.2016; 1 ♀ (ASU), site 2 on S slope, soil sample 2 (0–10 cm deep), 1.06.2016; 2 ♂♂, 1 ♀, 1 juv. (ASU), site 2 on S slope, soil sample 4 (0–10 cm deep), 1.06.2016; 2 ♀♀ (ASU), site 2 on S slope, soil sample 5 (0–10 cm deep), 1.06.2016; 1 ♂, 2 ♀♀, (ASU), site 2 on S slope, hand sampling, 1.06.2016; 1 ♀ (ASU), site 1 on N slope, soil sample 1 (0–10 cm deep), 2.06.2016; 1 ♂ (ASU), site 1 on N slope, soil sample 2 (0–10 cm deep), 2.06.2016; 1 ♂, 1 ♀ (ASU), site 1 on N slope, soil sample 5 (litter), 2.06.2016; 1 ♂ (ASU), site 1 on N slope, soil sample 5 (0–10 cm deep), 2.06.2016; 3 ♂♂ (ASU), site 1 on N slope, hand sampling, 2.06.2016; 1 ♀ (ASU), site 2 on N slope, soil sample 1 (0–10 cm deep), 2.06.2016; 1 ♀ (ASU), site 2 on N slope, soil sample 4 (litter), 2.06.2016, all leg. P.N., Kh.N., S.N., V.S.; 3 ♂♂, 1 subadult ♂ (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., 12.07.2016; 1 ♂ (ASU), same locality, pitfall traps, 12–14.07.2016, all leg. P.N.; 1 ♂, 4 ♀♀, 8 juv. (ASU), site 1 on S slope, soil sample 1 (0–10 cm deep), 12.07.2016; 1 ♂, 1 juv. (ASU), site 1 on S slope, soil sample 1 (10–20 cm deep), 12.07.2016; 1 juv. (ASU), site 1 on S slope, soil sample 1 (20–30 cm deep), 12.07.2016; 2 juv. (ASU), site 1 on S slope, soil sample 2 (0–10 cm deep), 12.07.2016; 1 ♀ (ASU), site 1 on S slope, soil sample 3 (0–10 cm deep), 12.07.2016; 3 ♂♂, 2 ♀♀ (ASU), site 1 on S slope, soil sample 4 (0–10 cm deep), 12.07.2016; 2 ♂♂, 1 ♀ (ASU), site 1 on S slope, soil sample 5 (0–10 cm deep), 12.07.2016; 1 ♀, 1 juv. (ASU), site 1 on S slope, hand sampling, 12.07.2016; 2 juv. (ASU), site 2 on S slope, soil sample 2 (0–10 cm deep), 12.07.2016; 2 juv. (ASU), site 2 on S slope, soil sample 5 (0–10 cm deep), 12.07.2016; 2 ♂♂, 1 ♀, 1 juv. (ASU), site 1 on N slope, soil sample 1 (0–10 cm deep), 13.07.2016; 1 ♂, 1 ♀, 2 juv. (ASU), site 1 on N slope, soil sample 3 (0–10 cm deep), 13.07.2016; 2 juv. (ASU), site 1 on N slope, soil sample 4 (0–10 cm deep), 13.07.2016; 1 ♂, 1 juv. (ASU), site 1 on N slope, soil sample 5 (0–10 cm deep), 13.07.2016; 1 ♂, 1 ♀, 2 juv. (ASU), site 2 on N slope, soil sample 1 (0–10 cm deep), 13.07.2016, all leg. Kh.N., S.N., V.S.; 1 ♂, 3 ♀♀, 1 juv. (ASU), site 1 on S slope, soil sample 1 (0–10 cm deep), 22.08.2016; 2 ♂♂, 6 ♀♀, 6 juv., 1 fragm. (ASU), site 1 on S slope, soil sample 2 (0–10 cm deep), 22.08.2016; 1 ♂, 1 ♀, 1 juv. (ASU), site 1 on S slope, soil sample 3 (0–10 cm deep), 22.08.2016; 4 ♀♀, 5 juv., 1 fragm. (ASU), site 1 on S slope, soil sample 4 (0–10 cm deep), 23.08.2016; 2 ♂♂, 4 juv. (ASU), site 1 on S slope, soil sample 5 (0–10 cm deep), 23.08.2016; 1 ♂ (ASU), site 2 on S slope, soil sample 2 (litter), 22.08.2016; 1 ♀, 1 juv. (ASU), site 2 on S slope, soil sample 2 (0–10 cm deep), 22.08.2016; 2 juv. (ASU), site 2 on S slope, soil sample 4 (0–10 cm deep), 22.08.2016; 1 juv. (ASU), site 2 on S slope, soil sample 5 (litter), 22.08.2016; 1 juv. (ASU), site 1 on N slope, soil sample 1 (0–10 cm deep), 23.08.2016; 1 ♂, 1 juv. (ASU), site 1 on N slope, soil sample 3 (litter), 23.08.2016; 2 ♂♂, 1 ♀, 2 juv. (ASU), site 1 on

N slope, soil sample 3 (0–10 cm deep), 23.08.2016; 1 ♂ (ASU), site 1 on N slope, hand sampling, 23.08.2016; 2 ♂♂, 3 ♀♀, 1 juv. (ASU), site 2 on N slope, soil sample 1 (0–10 cm deep), 23.08.2016; 1 juv. (ASU), site 2 on N slope, soil sample 4 (0–10 cm deep), 23.08.2016; 1 juv. (ASU), site 2 on N slope, soil sample 5 (litter), 23.08.2016, all leg. P.N., Kh.N., S.N., V.S.; 1 subadult ♂ (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., hand sampling, 20.06.2017, leg. P.N.; 1 ♀, 1 subadult ♀, 1 juv. (ASU), site 1 on N slope, hand sampling, 23.06.2017, leg. P.N., Kh.N., A.A., E.A.

**Distribution.** Central-Palaearctic temperate range: a central Asian species, *L. insolens* has very recently been found in the Omsk Area, Altai Province, and Republic of Altai (Nefediev et al. 2017b, c, d).

**Remarks.** The above record of *L. insolens*, recently announced at the 17th International Congress of Myriapodology (Nefediev et al. 2017c), can be considered as the first formal record of the species in the Altai Province, SW Siberia. In the study area, the species has significant preference for the southern slope. A single ♂ with aberrant numbers of antennomeres (22+24 vs. 20+20 in original description) was found.

### *Lithobius (Monotarsobius) nordenskiöldii* Stuxberg, 1876

*Lithobius (Monotarsobius) nordenskiöldii* – Nefediev et al. 2017c: 13; 2017d: 221, 220: map.

**Material examined.** 1 juv. (ASU), Russia, southwestern Siberia, Altai Province, Charysh District, ca. 4.5 air-km SE of Charyshskoye Village, site 1 on N slope, soil sample 3 (0–10 cm deep), 13.07.2016, leg. Kh.N., S.N., V.S.

**Distribution and remarks.** Until recently this species was been known only from its *terra typica* in the Krasnoyarsk Province, central Siberia, Russia. New records of *L. nordenskiöldii* in the Altai Province, as announced at the 17th International Congress of Myriapodology (Nefediev et al. 2017c), and in the Republic of Altai (Nefediev et al. 2017d) seems to indicate the low level of species abundance in the Altai region.

### *Lithobius (Monotarsobius) sp.*

**Material examined** (all from Russia, southwestern Siberia, Altai Province, Charysh District, ca 4.5 km SE of Charyshskoye Village). 1 juv. (ASU), site 1 on N slope, soil sample 4 (litter), 2.06.2016; 1 ♂ (ASU), site 1 on N slope, soil sample 5 (litter), 2.06.2016; 1 ♂, 2 subadult ♂♂ (ASU), site 1 on N slope, hand sampling, 2.06.2016, all leg. P.N., Kh.N., S.N., V.S.

**Remarks.** The species identity of this new record is delayed pending an examination of additional material of specimens with similar diagnostic characters from the Republic of Altai.



***Lithobius vagabundus* Stuxberg, 1876**

*Lithobius vagabundus* – Nefediev et al. 2017c: 13; 2017d: 219, 218: map.

**Material examined** (all from Russia, southwestern Siberia, Altai Province, Charysh District, ca. 4.5 km SE of Charyshskoye Village). 1 ♂, 1 subadult ♂ (PSU), foot of S slope of mountain, *Padus avium* and *Populus tremula* stand near brook, hand sampling, 31.05.2016; 1 ♀ (PSU), site 2 on S slope, soil sample 1 (0–10 cm deep), 12.07.2016, leg. Kh.N., S.N., V.S.; 1 ♂, 1 ♀ (PSU), site 1 on N slope, hand sampling, 23.06.2017; 1 ♂ (PSU), site 2 on N slope, hand sampling, 23.06.2017, all leg. P.N., Kh.N., A.A., E.A.

**Distribution.** Originally described from the Yenisei River basin, Krasnoyarsk Province, central Siberia (Zalesskaja 1978), the species has been found recently in the Altai Province and Republic of Altai (Nefediev et al. 2017c, d), both SW Siberia, Russia.

**Remarks.** The above finding of *L. vagabundus*, recently announced at the 17th International Congress Myriapodology (Nefediev et al. 2017c), can be considered as the first formal record of the species in southwestern Siberia. In the study region, the species was very rare in all biotopes.

***Lithobius* sp.**

**Material examined** (all from Russia, southwestern Siberia, Altai Province, Charysh District, ca. 4.5 km SE of Charyshskoye Village). 1 juv. (ASU), site 1 on N slope, soil sample 2 (litter), 2.06.2016; 1 ♂ (ASU), site 1 on N slope, soil sample 3 (10–20 cm deep), 2.06.2016, all leg. P.N., Kh.N., S.N., V.S.; 1 juv. (ASU), site 1 on S slope, soil sample 3 (0–10 cm deep), 12.07.2016, leg. Kh.N., S.N., V.S.; 2 juv. (ASU), site 1 on N slope, hand sampling, 23.06.2017, all leg. P.N., Kh.N., A.A., E.A.

**Remarks.** The identification of the above recorded specimens to the species level is impossible due to their early instars or lack of legs.

**Order Geophilomorpha Pocock, 1895****Family Geophilidae Cook, 1895****Genus *Arctogeophilus* Attems, 1909*****Arctogeophilus macrocephalus* Folkmanová & Dobroruka, 1960**

? *Arctogeophilus* sp. – Byzova and Chadaeva 1965: 337.

*Arctogeophilus macrocephalus* – Zalesskaja et al. 1982: 189; Nefediev et al. 2017a: 8, 10: map; 2017c: 13; 2017d: 221, 222: map.

**Material examined** (all from Russia, southwestern Siberia, Altai Province, Charysh District, ca. 4.5 km SE of Charyshskoye Village). 1 juv. (ASU), site 1 on S slope, soil

sample 1 (10–20 cm deep), 31.05.2016; 1 juv. (ASU), site 1 on S slope, soil sample 2 (10–20 cm deep), 31.05.2016; 1 juv. (ASU), site 1 on S slope, soil sample 4 (0–10 cm deep), 1.06.2016; 1 juv. (ASU), site 2 on S slope, soil sample 2 (0–10 cm deep), 1.06.2016; 1 juv. (ASU), site 2 on S slope, soil sample 3 (0–10 cm deep), 1.06.2016; 1 juv. (ASU), site 2 on S slope, soil sample 4 (0–10 cm deep), 1.06.2016; 1 juv. (ASU), site 2 on S slope, soil sample 5 (0–10 cm deep), 1.06.2016; 1 ♀ (ASU), site 1 on N slope, hand sampling, 2.06.2016, all leg. P.N., Kh.N., S.N., V.S.; 1 juv. (ASU), site 2 on N slope, soil sample 1 0–10 cm deep), 13.07.2016, leg. Kh.N., S.N., V.S.; 1 ♂, 1 ♀ (ASU), site 1 on S slope, soil sample 1 (0–10 cm deep), 22.08.2016; 1 ♀ (ASU), site 1 on S slope, soil sample 2 (0–10 cm deep), 22.08.2016; 1 juv. (ASU), site 1 on S slope, soil sample 4 (0–10 cm deep), 23.08.2016, all leg. P.N., Kh.N., S.N., V.S.; 2 ♂♂, 1 ♀ (ZMMU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., hand sampling, 20.06.2017, leg. P.N.

**Distribution.** Trans-Eurasian temperate range: this species is very widely distributed, ranging from European Russia through Siberia to the Far East of Russian (Zalesskaja et al. 1982). In southwestern Siberia *A. macrocephalus* has been recorded in the Kemerovo and Tomsk areas, Republic of Altai and Altai Province (Byzova and Chadaeva 1965; Zalesskaja et al. 1982; Nefediev et al. 2017a, c, d).

**Remarks.** Apparently a very euryoecious species, *A. macrocephalus* has currently been recorded mainly from habitats on the southern slope.

## Family Linotaeniidae Cook, 1904

### Genus *Strigamia* Gray, 1843

#### *Strigamia pusilla* (Sseliwanoff, 1884)

*Strigamia pusilla* – Nefediev et al. 2017c: 13; 2017d: 223, 222: map.

**Material examined** (all from Russia, southwestern Siberia, Altai Province, Charysh District, ca. 4.5 km SE of Charyshskoye Village). 1 ♂, 1 juv. (ZMMU), 1 ♂ (ASU), site 1 on N slope, soil sample 5 (0–10 cm deep), 2.06.2016; 1 ♀ (ASU), site 1 on N slope, soil sample 1 (0–10 cm deep), 23.08.2016; 1 juv. (ASU), site 2 on N slope, soil sample 1 (0–10 cm deep), 23.08.2016, all leg. P.N., Kh.N., S.N., V.S.

**Distribution.** Central-Palearctic temperate range: widespread from Central Europe and the Caucasus, *S. pusilla* is found in the Urals, SW and central Siberia and N Mongolia (Bonato et al. 2012; Poloczec et al. 2016; Nefediev et al. 2017c, d).

**Remarks.** In the study area, the species was found rarely and on the northern slope only.

#### *Strigamia* cf. *transsilvanica* (Verhoeff, 1928)

*Strigamia* sp. – Nefediev et al. 2017c: 13.

**Material examined** (all from Russia, southwestern Siberia, Altai Province, Charysh District, ca. 4.5 km SE of Charyshskoye Village). 1 ♂ (ASU), *Betula pendula* and *Populus tremula* stand, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., hand sampling, 14.07.2015, leg. P.N.; 1 ♂ (ASU), site 2 on S slope, soil sample 5 (0–10 cm deep), 2.06.2016, leg. P.N., Kh.N., S.N., V.S.

**Distribution.** A central-eastern European species, *S. transsilvanica* appears to be quite widespread in continental Europe from the Alps to the Carpathians and from the Baltic states to mainland Greece. It has been doubtfully reported from Sakhalin (Russia), Japan and Taiwan (Bonato et al. 2012) and recently found in the Rostov-on-Don Area, south of European Russia (Zuev and Evsyukov 2016).

**Remarks.** Although both specimens resemble *S. transsilvanica*, the study area is far from the known distribution of the species. Aside from the possibility of human introduction of this species in the Charysh District, the presence of a possible undescribed species similar in morphology to *S. transsilvanica* could be tested by molecular methods in the future.

## Family Schendylidae Cook, 1896

### Genus *Escaryus* Cook & Collins, 1891

#### *Escaryus koreanus* Takakuwa, 1937

*Escaryus koreanus* – Titova 1972a: 112; 1972b: 135; Pereira and Hoffman 1993: 9; Nefediev et al. 2017a: 11, 12: map; 2017c: 13; 2017d: 222: map.

**Material examined** (all from Russia, southwestern Siberia, Altai Province, Charysh District, ca. 4.5 km SE of Charyshskoye Village). 1 ♂, 1 ♀ (ZMMU), 5 ♀♀, 5 juv. (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., 14.07.2015; 1 juv. (ASU), *Lonicera tatarica* on E slope, 51°21'24.9"N, 83°37'24.4"E, 493 m a.s.l., 16.07.2015, all leg. P.N.; 1 ♂, 3 ♀♀ (ASU), foot of S slope of mountain, *Padus avium* and *Populus tremula* stand near brook, hand sampling, 31.05.2016; 1 ♀ (ASU), site 1 on S slope, soil sample 3 (10–20 cm deep), 31.05.2016; 2 juv. (ASU), site 1 on N slope, soil sample 3 (litter), 2.06.2016; 2 juv. (ASU), site 1 on N slope, soil sample 3 (10–20 cm deep), 2.06.2016; 1 ♂ (ASU), site 1 on N slope, soil sample 5 (0–10 cm deep), 2.06.2016; 2 ♂♂ (ASU), site 1 on N slope, hand sampling, 2.06.2016; 2 juv. (ASU), site 2 on N slope, soil sample 1 (0–10 cm deep), 2.06.2016; 2 juv. (ASU), site 2 on N slope, soil sample 2 (0–10 cm deep), 2.06.2016; 1 juv. (ASU), site 2 on N slope, soil sample 3 (litter), 2.06.2016; 2 juv. (ASU), site 2 on N slope, soil sample 3 (0–10 cm deep), 2.06.2016; 1 ♂ (ASU), site 2 on N slope, soil sample 5 (litter), 2.06.2016; 1 juv. (ASU), site 2 on N slope, soil sample 5 (0–10 cm deep), 2.06.2016, all leg. P.N., Kh.N., S.N., V.S.; 1 ♂, 1 ♀, 3 juv. (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., 12.07.2016, leg. P.N.; 1 ♀ (ASU), site 1 on N slope, soil sample 1 (0–10 cm

deep), 13.07.2016; 2 ♂♂ (ASU), site 1 on N slope, soil sample 2 (0–10 cm deep), 13.07.2016; 1 ♂ (ASU), site 1 on N slope, hand sampling, 13.07.2016; 1 ♀, 2 juv. (ASU), site 2 on N slope, soil sample 1 (0–10 cm deep), 13.07.2016; 1 ♀ (ASU), site 2 on N slope, soil sample 4 (0–10 cm deep), 13.07.2016; 1 ♀ (ASU), site 2 on N slope, soil sample 5 (0–10 cm deep), 13.07.2016, all leg. Kh.N., S.N., V.S.; 1 juv. (ASU), site 1 on N slope, soil sample 1 (0–10 cm deep), 23.08.2016; 1 ♂ (ASU), site 1 on N slope, soil sample 2 (0–10 cm deep), 23.08.2016; 2 ♀♀, 13 juv. (ASU), site 1 on N slope, soil sample 3 (0–10 cm deep), 23.08.2016; 1 juv., 1 fragm. (ASU), site 2 on N slope, soil sample 1 (0–10 cm deep), 23.08.2016; 1 ♀ (ASU), site 2 on N slope, soil sample 2 (0–10 cm deep), 23.08.2016; 1 juv., 1 fragm. (ASU), site 2 on N slope, soil sample 4 (0–10 cm deep), 23.08.2016; 1 ♂ (ASU), site 2 on N slope, soil sample 5 (0–10 cm deep), 23.08.2016; 2 ♂♂, 2 ♀♀, 1 juv. (ASU), site 2 on N slope, hand sampling, 23.08.2016, all leg. P.N., Kh.N., S.N., V.S.; 1 subadult ♂, 4 ♀♀, 1 juv. (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., hand sampling, 20.06.2017, leg. P.N.

**Distribution.** Trans-Palaearctic: originally described from Korea, the species is widespread throughout Asian Russia; also known from Armenia, Azerbaijan, Kazakhstan, Tadzhikistan, Turkmenistan and Uzbekistan (Bonato et al 2016); in SW Siberia *E. koreanus* was formally recorded in the Kemerovo and Tomsk areas, Altai Province and Republic of Altai (Titova 1972a, b; Nefediev et al. 2017a, c, d).

**Remarks.** In the study region, *E. koreanus* appears to be found mainly on the northern slope.

### *Escaryus retusidens* Attems, 1904

*Escaryus retusidens* – Titova 1972a: 110; 1972b: 135; Pereira and Hoffman 1993: 9; Volkova 2016: 675; Nefediev et al. 2017a: 11, 13; map; 2017c: 13; 2017d: 222; map.

**Material examined** (all from Russia, southwestern Siberia, Altai Province, Charysh District, ca. 4.5 km SE of Charyshskoye Village). 1 ♂, 1 ♀ (ZMMU), 2 ♂♂, 4 juv. (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., 14.07.2015, leg. P.N.; 1 ♂ (ASU), foot of S slope of mountain, *Padus avium* and *Populus tremula* stand near brook, hand sampling, 31.05.2016; 2 ♀♀, 3 juv. (ASU), site 1 on S slope, hand sampling, 31.05.2016; 2 juv. (ASU), site 1 on S slope, soil sample 1 (10–20 cm deep), 31.05.2016; 1 ♀ (ASU), site 1 on S slope, soil sample 1 (20–30 cm deep), 31.05.2016; 3 ♀♀ (ASU), site 1 on S slope, soil sample 3 (10–20 cm deep), 31.05.2016; 1 ♀, 3 juv. (ASU), site 1 on S slope, soil sample 3 (20–30 cm deep), 31.05.2016; 1 juv. (ASU), site 1 on S slope, soil sample 4 (20–30 cm deep), 1.06.2016; 1 juv. (ASU), site 1 on S slope, soil sample 5 (0–10 cm deep), 1.06.2016; 3 juv. (ASU), site 1 on S slope, soil sample 5 (10–20 cm deep), 1.06.2016; 1 ♂, 1 juv. (ASU), site 1 on S slope, soil sample 5 (20–30 cm deep), 1.06.2016; 1 ♂ (ASU), S slope between site 1 and site 2, broad

gully with *Padus avium*, hand sampling, 1.06.2016; 1 juv. (ASU), site 2 on S slope, soil sample 1 (0–10 cm deep), 1.06.2016; 1 fragm. (ASU), site 2 on S slope, soil sample 1 (10–20 cm deep), 1.06.2016; 2 juv. (ASU), site 2 on S slope, soil sample 2 (0–10 cm deep), 1.06.2016; 1 juv. (ASU), site 2 on S slope, soil sample 2 (10–20 cm deep), 1.06.2016; 1 juv. (ASU), site 2 on S slope, soil sample 3 (0–10 cm deep), 1.06.2016; 1 juv. (ASU), site 2 on S slope, soil sample 5 (0–10 cm deep), 1.06.2016; 1 juv. (ASU), site 2 on S slope, hand sampling, 1.06.2016; 2 juv. (ASU), site 1 on N slope, soil sample 1 (0–10 cm deep), 2.06.2016; 2 ♀♀, 1 juv. (ASU), site 1 on N slope, soil sample 2 (0–10 cm deep), 2.06.2016; 2 juv. (ASU), site 1 on N slope, soil sample 2 (10–20 cm deep), 2.06.2016; 2 ♂♂, 2 ♀♀, 2 juv. (ASU), site 1 on N slope, soil sample 3 (0–10 cm deep), 2.06.2016; 1 ♂, 1 juv. (ASU), site 1 on N slope, soil sample 3 (10–20 cm deep), 2.06.2016; 1 ♀, 2 juv. (ASU), site 1 on N slope, soil sample 4 (0–10 cm deep), 2.06.2016; 1 ♂ (ASU), site 1 on N slope, soil sample 4 (10–20 cm deep), 2.06.2016; 1 ♂, 3 ♀♀ (ASU), site 1 on N slope, soil sample 5 (0–10 cm deep), 2.06.2016; 1 ♀ (ASU), site 1 on N slope, hand sampling, 2.06.2016; 1 ♀, 1 juv. (ASU), site 2 on N slope, soil sample 1 (0–10 cm deep), 2.06.2016; 3 juv. (ASU), site 2 on N slope, soil sample 2 (0–10 cm deep), 2.06.2016; 2 ♂♂, 2 ♀♀, 1 juv. (ASU), site 2 on N slope, soil sample 3 (0–10 cm deep), 2.06.2016; 1 ♀, 3 juv. (ASU), site 2 on N slope, soil sample 4 (0–10 cm deep), 2.06.2016; 1 juv. (ASU), site 2 on N slope, soil sample 4 (10–20 cm deep), 2.06.2016, all leg. P.N., Kh.N., S.N., V.S.; 1 ♀ (ASU), site 1 on N slope, hand sampling, 22.06.2016, leg. Kh.N.; 1 adult specimen (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., 12.07.2016, leg. P.N.; 1 juv. (ASU), site 1 on S slope, soil sample 1 (0–10 cm deep), 12.07.2016; 2 juv. (ASU), site 1 on S slope, soil sample 5 (10–20 cm deep), 12.07.2016; 1 ♂, 2 juv. (ASU), site 1 on N slope, soil sample 1 (10–20 cm deep), 13.07.2016; 1 fragm. (ASU), site 1 on N slope, soil sample 3 (0–10 cm deep), 13.07.2016; 2 ♀♀ (ASU), site 2 on N slope, soil sample 1 (0–10 cm deep), 13.07.2016; 1 juv. (ASU), site 2 on N slope, soil sample 2 (0–10 cm deep), 13.07.2016; 1 ♀, 1 juv. (ASU), site 2 on N slope, soil sample 4 (0–10 cm deep), 13.07.2016; 2 ♀♀ (ASU), site 2 on N slope, soil sample 4 (10–20 cm deep), 13.07.2016, all leg. Kh.N., S.N., V.S.; 1 juv., 2 fragm. (ASU), site 1 on S slope, soil sample 1 (10–20 cm deep), 22.08.2016; 1 fragm. (ASU), site 1 on S slope, soil sample 2 (10–20 cm deep), 22.08.2016; 1 ♀, 2 juv., 1 fragm. (ASU), site 1 on S slope, soil sample 4 (0–10 cm deep), 23.08.2016; 1 ♂ (ASU), site 2 on S slope, soil sample 5 (0–10 cm deep), 22.08.2016; 1 ♂, 2 ♀♀, 2 juv. (ASU), site 1 on N slope, soil sample 2 (0–10 cm deep), 23.08.2016; 1 juv. (ASU), site 1 on N slope, soil sample 4 (0–10 cm deep), 23.08.2016; 2 ♀♀, 1 juv. (ASU), site 1 on N slope, soil sample 5 (0–10 cm deep), 23.08.2016; 3 ♂♂, 1 ♀, 1 juv. (ASU), site 2 on N slope, soil sample 1 (0–10 cm deep), 23.08.2016; 1 ♀ (ASU), site 2 on N slope, soil sample 2 (0–10 cm deep), 23.08.2016; 2 ♀♀, 1 juv. (ASU), site 2 on N slope, soil sample 3 (0–10 cm deep), 23.08.2016; 1 ♀, 1 juv., 2 fragm. (ASU), site 2 on N slope, soil sample 3 (10–20 cm deep), 23.08.2016; 2 ♂♂, 1 ♀, 1 juv. (ASU), site 2 on N slope, soil sample 5 (0–10 cm deep), 23.08.2016; 1 ♀ (ASU), site 2 on N slope, hand



sampling, 23.08.2016, all leg. P.N., Kh.N., S.N., V.S.; 3 ♂♂, 4 ♀♀, 3 juv. (ASU), *Betula pendula* and *Populus tremula* stand on N slope, 51°21'33.8"N, 83°37'23.2"E, 518 m a.s.l., 20.06.2017, leg. P.N.; 1 ♂ (ASU), site 1 on N slope, hand sampling, 23.06.2017, leg. P.N., Kh.N., A.A., E.A.

**Distribution.** Central-Eastern-Palaearctic subboreal range: originally described from Kyrgyzstan, the species is widely distributed in Eurasia, spanning from the Black Sea region in the west through eastern Kazakhstan to Cisamuria in the east (Titova 1972b). In Siberia *E. retusidens* has been known from the Kemerovo Area, Altai Province, and Republic of Altai (Nefediev et al. 2017a, c, d).

**Remarks.** In the study area, *E. retusidens* inhabits both slopes, and is one of the most dominant species.

## Results and discussion

The myriapod fauna of the study area comprises at least 19 species from 10 genera, 8 families, 5 orders and two classes (Diplopoda and Chilopoda).

The species richness in the millipede assemblages was found to be very low and similar on both slopes ( $I_j = 0.83$ ). Thus, 5 diplopod species are known to occur on both slopes (*Megaphyllum sjelandicum*, *Sibiriulus latisupremus*, *Orinisobates sibiricus*, *Schizoturanius clavatipes* and *Altajosoma* sp.), whereas *Leptoiulus tigirek* inhabits the northern slope only (Table 1).

The total species richness in the centipede assemblages is twice as high compared to the millipede one, with 10 and 12 species recorded on the southern and northern slopes, respectively. Most Chilopoda species are common to both slopes, namely, *Lithobius (Ezembius) ostiacorum*, *L. (E.) proximus*, *L. (E.) sibiricus*, *L. (Monotarsobius) curtipes*, *L. (M.) insolens*, *L. vagabundus*, *Arctogeophilus macrocephalus*, *Escaryus koreanus* and *E. retusidens*. However, the similarity in species composition between the study slopes is weak ( $I_j = 0.69$ ). Thus, a single species was recorded only on the southern slope (*Strigamia* cf. *transilvanica*) while three species dwell only on the northern slope (*L. (M.) nordenskiöldii*, *L. (M.)* sp. and *Strigamia pusilla*) (Table 1).

The julid *L. tigirek*, which has recently been included in the Red Data Book of the Altai Province (Nefediev 2016), has been collected outside its *terra typica* for the first time, thus also expanding the eastern range limit of the species (Figure 6). The julid *S. latisupremus* has previously been known from the Smolenskoe and Altaiskoe districts in the Altai Province and from the Shebalino District in the Republic of Altai (Mikhaljova et al. 2014). The current record of the species is the westernmost known to date (Figure 7). The species identity of *Altajosoma* sp. is delayed pending a revision of the variation in *Altajosoma bakurovi bakurovi* (Shear, 1990), which the currently recorded diplomaragnid is close to in the shape of colpocoxites of posterior gonopods and in their distal parts, but differs significantly in the large posterior angiocoxal processes.

Five lithobiids, *L. (E.) proximus*, *L. (M.) insolens*, *L. (E.) ostiacorum*, *L. vagabundus* and *L. (M.) nordenskiöldii*, are new to the Altai Province, while the three latter are also

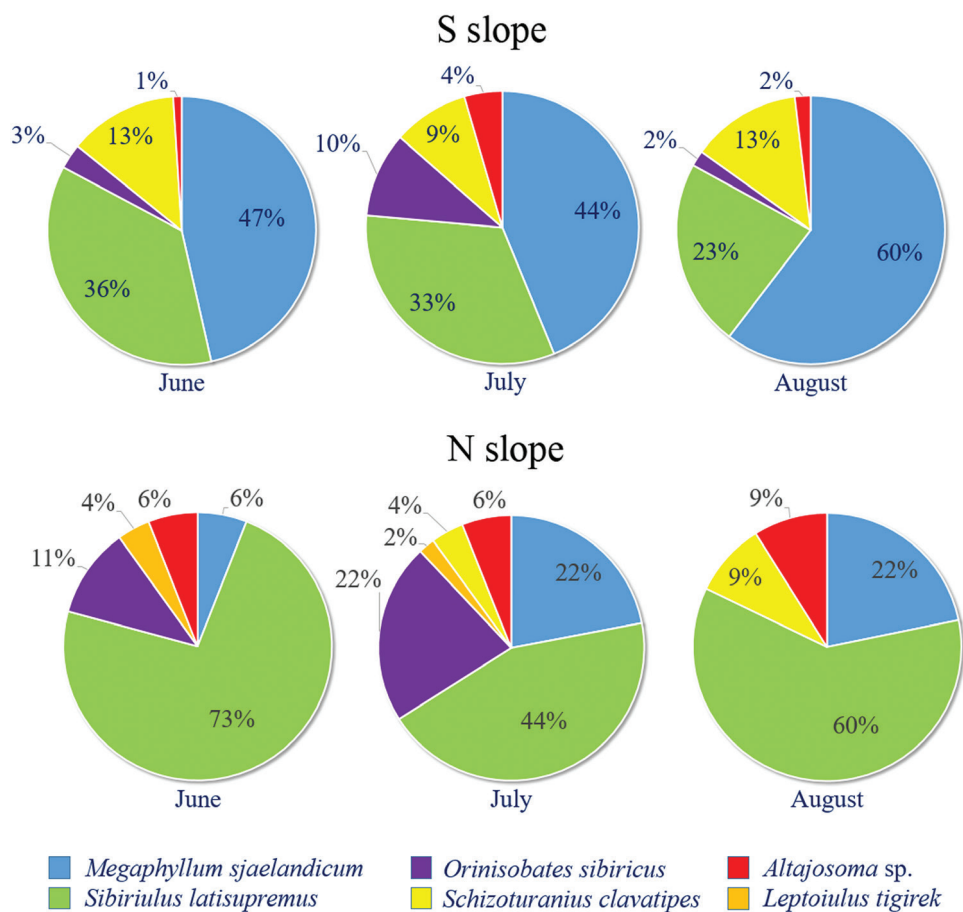
**Table 1.** Species composition and species richness in Chilopoda and Diplopoda assemblages in the study area.

Species	S slope		N slope	
	site 1	site 2	site 1	site 2
<i>Megaphyllum sjaelandicum</i> (Meinert, 1868)	+	+	—	+
<i>Sibiriulus latisupremus</i> Mikhajlova, Nefediev & Nefedieva, 2014	+	+	+	+
<i>Orinisobates sibiricus</i> (Gulička, 1963)	+	+	+	+
<i>Leptoiulus tigirek</i> Mikhajlova, Nefediev, Nefedieva & Dyachkov, 2015	—	—	+	+
<i>Schizoturanius clavipes</i> (Stuxberg, 1876)	+	+	+	+
<i>Altajosoma</i> sp.	+	+	+	+
<i>Lithobius</i> ( <i>Ezembius</i> ) <i>ostiacorum</i> Stuxberg, 1876	+	—	+	+
<i>Lithobius</i> ( <i>Ezembius</i> ) <i>proximus</i> Sseliwanoff, 1880	—	+	+	+
<i>Lithobius</i> ( <i>Ezembius</i> ) <i>sibiricus</i> Gerstfeldt, 1858	+	+	+	+
<i>Lithobius</i> ( <i>Monotarsobius</i> ) <i>curtipes</i> C.L. Koch, 1847	+	+	+	+
<i>Lithobius</i> ( <i>Monotarsobius</i> ) <i>insolens</i> Dányi & Tuf, 2012	+	+	+	+
<i>Lithobius</i> ( <i>Monotarsobius</i> ) <i>nordenskioeldii</i> Stuxberg, 1876	—	—	+	—
<i>Lithobius</i> ( <i>Monotarsobius</i> ) sp.	—	—	+	—
<i>Lithobius vagabundus</i> Stuxberg, 1876	—	+	+	+
<i>Arctogeophilus macrocephalus</i> Folkmanová & Dobroruka, 1960	+	+	+	+
<i>Strigamia pusilla</i> (Sseliwanoff, 1884)	—	—	+	+
<i>Strigamia</i> cf. <i>transsilvanica</i> (Verhoeff, 1928)	—	+	—	—
<i>Escaryus koreanus</i> Takakuwa, 1937	+	—	+	+
<i>Escaryus retusidens</i> Attems, 1904	+	+	+	+
Species richness in each site	12	13	17	16
Species richness on each slope	15		17	
Total species richness on both slopes	19			

recorded in southwestern Siberia for the first time; the linotaeniid *Strigamia* cf. *transsilvanica* is reported from Asian Russia for the first time too.

The species diversity of Diplopoda is very low on both slopes. The julid *M. sjaelandicum* predominates on the dry southern slope, ranging from 44 to 60 % of the total millipede abundance, whereas *S. latisupremus* tends to dominate on the more humid northern slope, ranging from 44 to 73 % of the total diplopod abundance (Figure 8). The latter species may also be considered as a codominant species on the southern slope (23–36 % of the total millipede abundance), while the rest of the millipede species are rare or very rare on the southern slope. Codominants of the northern slope appear to be *M. sjaelandicum* and *O. sibiricus* with 22 % of the diplopod abundance. The RDA model also reveals the pattern of millipede distribution (Figure 9) explaining 20.3 % of the variability in species data. Of the tested environmental variables, slope exposure (south/north) and time of sampling (month) are significant ( $F = 9.88$ ,  $p = 0.002$  and  $F = 3.42$ ,  $p = 0.018$ , respectively). Of the recorded species, *M. sjaelandicum* and *S. clavipes* predominate on the southern slope.

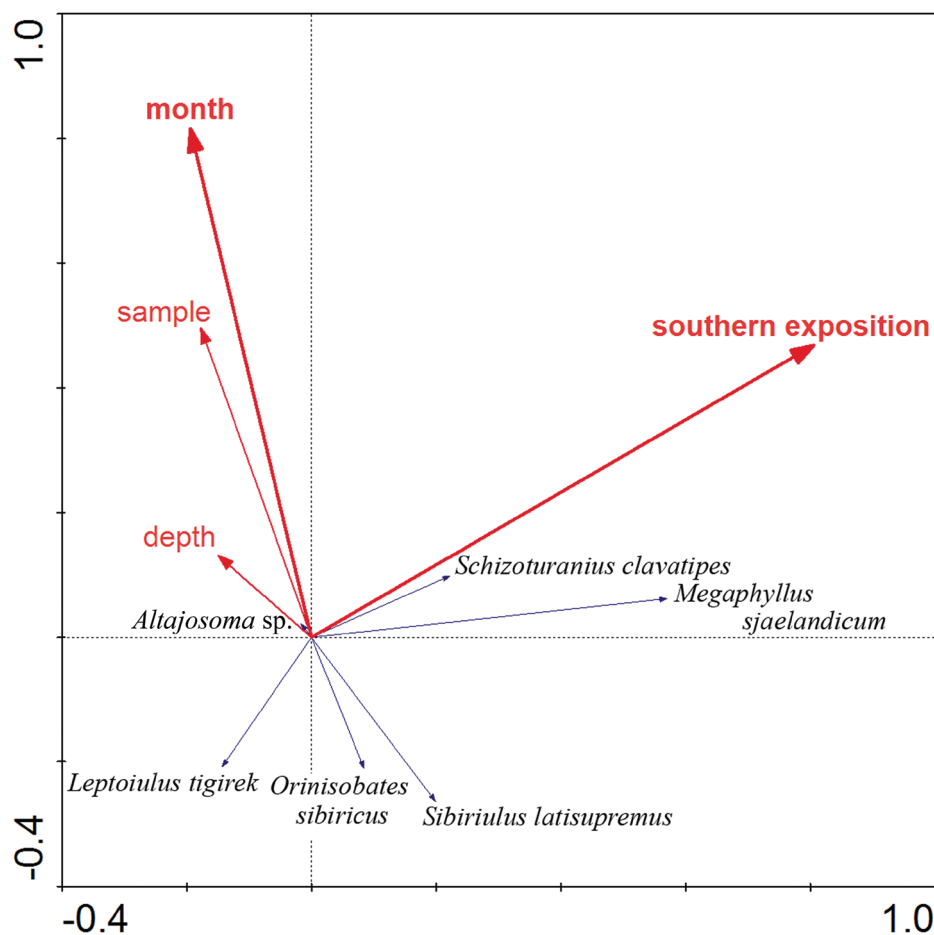
Species diversity of Chilopoda is low on the southern slope: two species predominate, in particular, *L. (M.) insolens*, ranging from 34 to 72 % of the total chilopod



**Figure 8.** The species diversity of millipedes on the southern and northern slopes.

abundance, and *E. retusidens* with 45 % of the total centipede abundance in June, likewise *L. (E.) sibiricus* codominating there (21 % in July); the rest of the centipede species are rare or very rare on the southern slope (Figure 10). On the northern slope, the centipede community is more similar to that on the southern slope: five dominant or codominant species – *E. retusidens*, *E. koreanus*, *L. (E.) sibiricus*, *L. (M.) curtipes* and *L. (M.) insolens* – inhabit the northern slope. The RDA model confirms this pattern of centipede distribution (Figure 11) explaining 15.2 % of variability in its distribution. Of the tested environmental variables, slope exposure (south/north), depth of soil sample and time of sampling (month) are significant ( $F = 7.28$ ,  $p = 0.002$ ;  $F = 5.54$ ,  $p = 0.002$ ; and  $F = 2.55$ ,  $p = 0.032$ , respectively). Of the recorded species, *A. macrocephalus* and *L. (M.) insolens* predominate on the southern slope, whereas several of the above mentioned species predominate on the northern one.

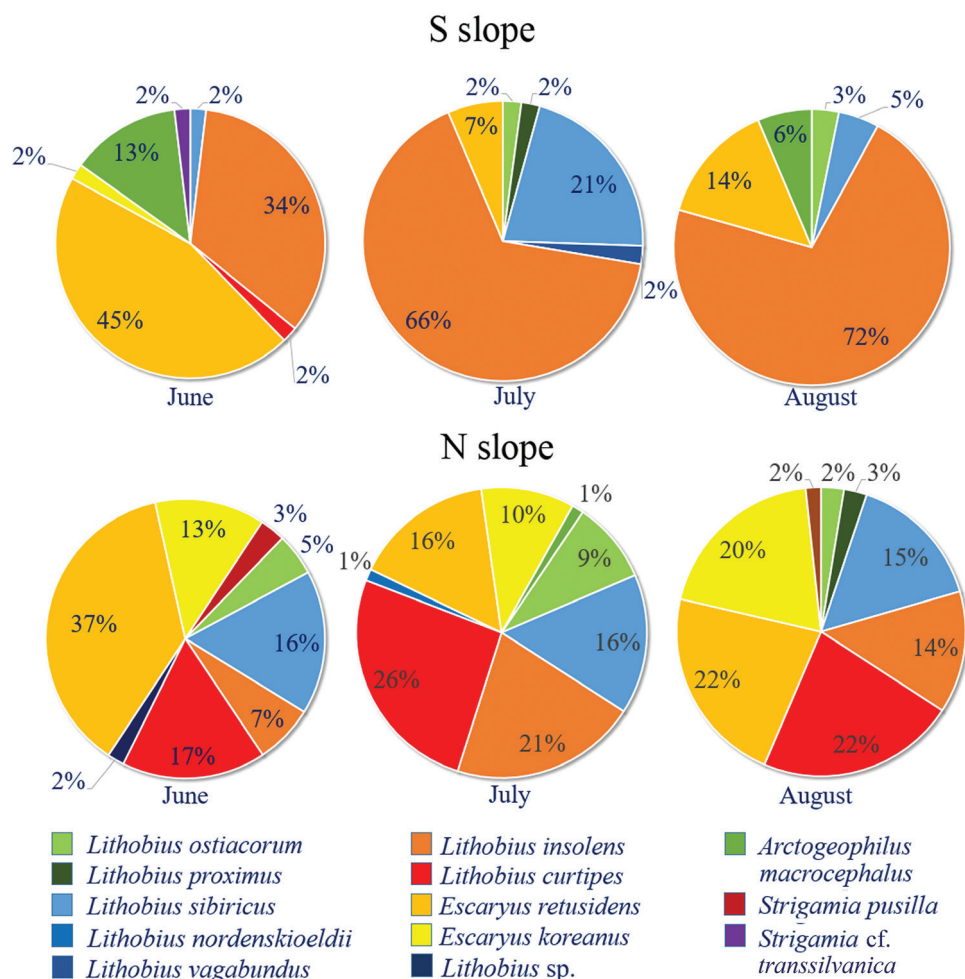
The density of millipedes on the southern slope is twice as high compared to the northern slope. The seasonal dynamics of diplopod numbers range from  $21 \pm 4.4$  to



**Figure 9.** RDA ordination biplot of the distribution patterns of millipedes in soil samples on the study slopes. Environmental variables significantly contributing to the prediction are in bold. The whole model is statistically significant ( $F = 4.73$ ,  $p = 0.002$ ) and explains 20.3 % of variability of species data, the X-axis explains 16.5 %.

$48 \pm 10.8$  ind./m<sup>2</sup> on the southern slope, and from  $9 \pm 1.2$  to  $22 \pm 13.6$  ind./m<sup>2</sup> on the northern one, gradually declining from June to August in both habitat types (Figure 12). Of the recorded species, abundance of the only julid, *S. latusupremus*, are significantly affected by the time of sampling as the population decreases from June to August (GLM:  $F = 6.92$ ,  $p = 0.010$ ). The numbers of centipedes on the northern slope are twice as high compared to the southern one. The seasonal dynamics of Chilopoda density ranges from  $20 \pm 6.8$  to  $27 \pm 19.6$  ind./m<sup>2</sup> on the southern slope, and from  $31 \pm 0.0$  to  $47 \pm 11.6$  ind./m<sup>2</sup> on the northern one, the highest being in June and August and the lowest in July in both habitat types (Figure 13).

The age structure will be considered here, using the dominant species as an example. Thus, in the age structure of the julid *M. sjaelandicum* population on the southern

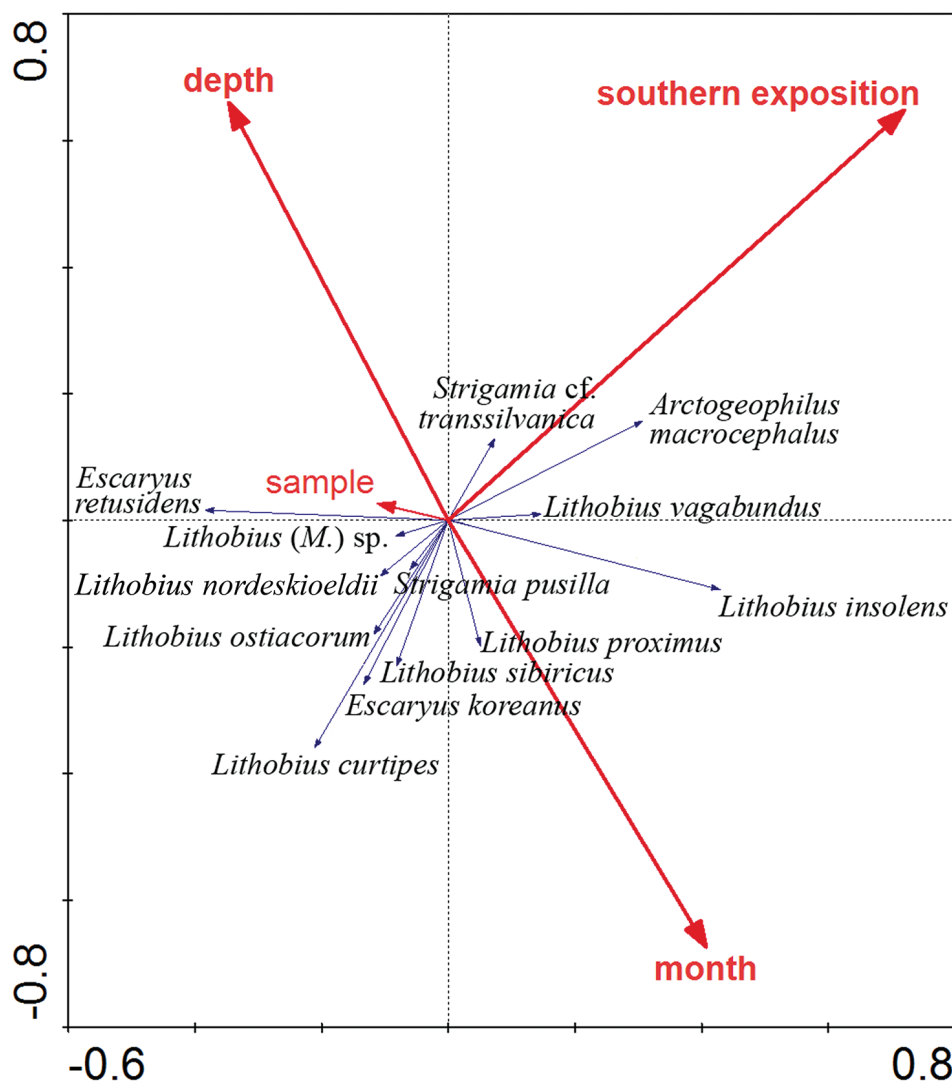


**Figure 10.** The species diversity of centipedes on the southern and northern slopes.

slope, juveniles predominated during the summer, and their abundance varied from 100 % of the population in June to 70 % in July and August. In contrast, in the julid *S. latisupremus*, overwintering adults predominated at the beginning of summer (with 75 % of the population), producing juveniles, which started to prevail in the middle of summer (with 76 % of the population).

The age structure in the population of the lithobiid *L. (M.) insolens* is as follows: adults predominate at the beginning of summer on both slopes, ranging from 70 to 100 % of the population, while young individuals emerge in the middle of summer in amounts equal to the total numbers of males and females, and this ratio is maintained until the late summer. The sex ratio is close to 50:50 during summer on both slopes, but on the southern slope only females exceed males twice over by the end of summer. In the -age structure of *E. retusidens* on the southern slope, the abundance of juveniles

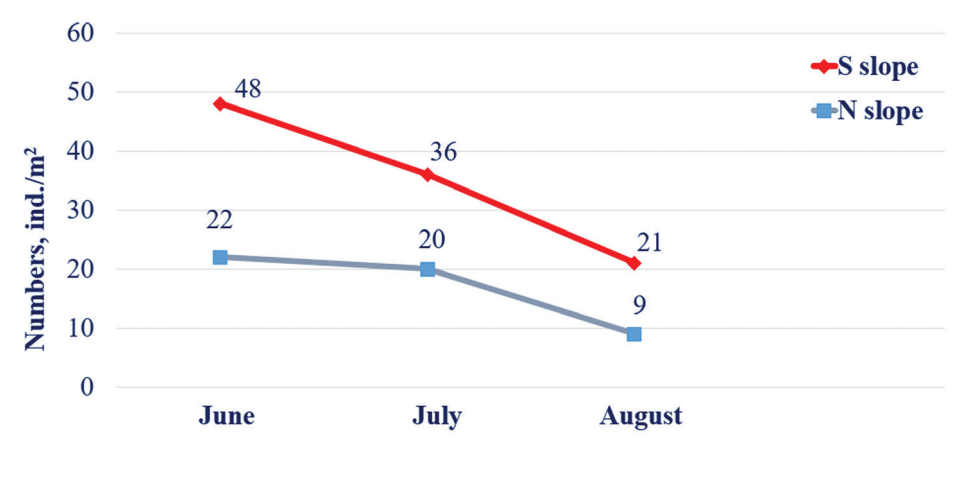




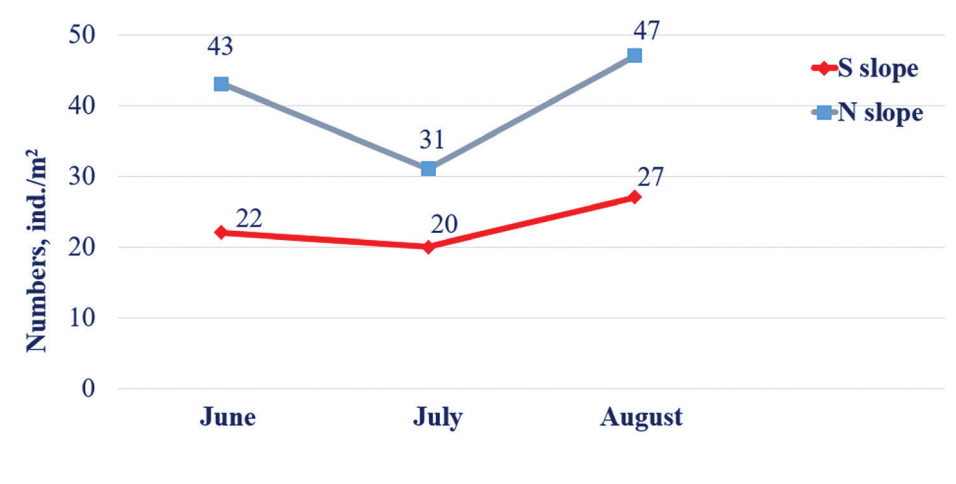
**Figure 11.** RDA ordination biplot of the distribution patterns of centipedes in soil samples on the study slopes. Environmental variables significantly contributing to the prediction are in bold. The whole model is statistically significant ( $F = 4.12$ ,  $p = 0.002$ ) and explains 15.2 % of variability of species data, the X-axis explains 10.3 %.

is 3 times higher than in adults. On the northern slope, the ratio of adults and juveniles is equal at the beginning of summer, while in the middle and late summer adults start to prevail to become twice as abundant. For adults, the females steady prevailed, outnumbering males from 2 to 5 times throughout the season in both habitats.

Regarding the vertical distribution in the soil profile, more than 80 % of millipedes prefer the upper soil layer to a depth of 10 cm on both slopes. Diplopods are very rare in the litter, especially on the dry southern slope (where they numbered less than 1 %),

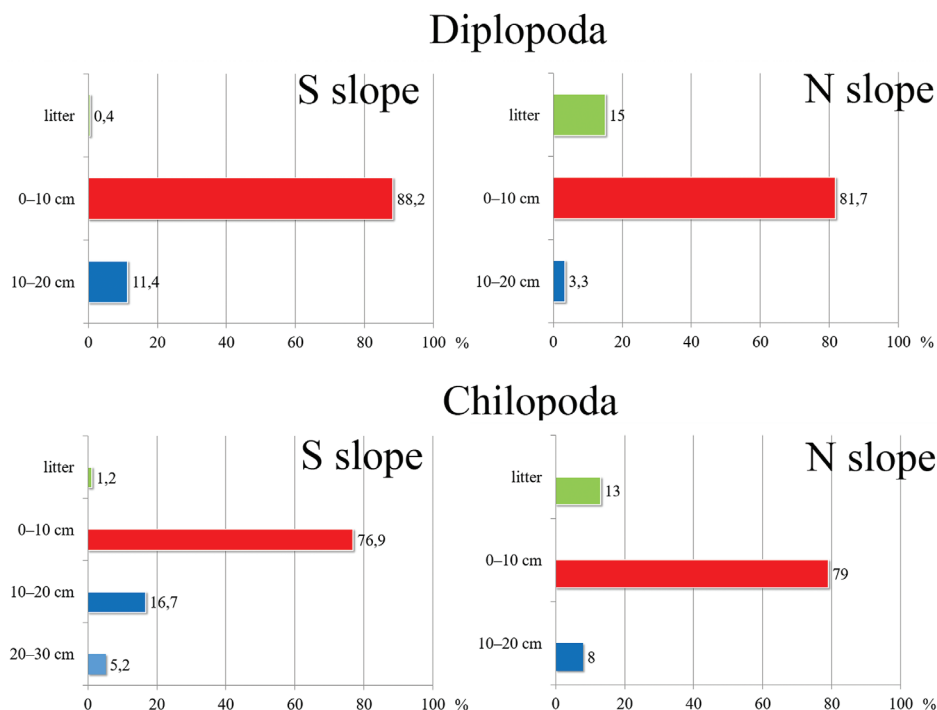


**Figure 12.** The seasonal dynamics of Diplopoda density on study slopes.



**Figure 13.** The seasonal dynamics of Chilopoda density on study slopes.

but the numbers are about 15 % more on the humid northern slope, with maximum penetration in depth to no more than 20 cm (Figure 14). With regard to the vertical distribution in the soil profile in centipedes, we observe the preference of chilopods to the upper soil layer. Thus, approximately 80 % of centipedes of the total chilopod abundance has been reported from the top 10 cm layer on both study slopes, with the maximum penetration in depth to no more than 30 cm. Centipedes are very rare in the litter, accounting for about 1 % on the dry southern slope and about 13 % on the more humid northern one (Figure 14). As the depth of the sample is a significant variable for RDA model, we tested its power to predict the distribution of individual species.



**Figure 14.** The distribution of myriapods along soil profile on both slopes.

Abundances of the geophilomorph *E. retusidens* and the lithobiomorph *L. (M.) curtipes* are the only species significantly affected by depth of sample. The geophilomorph prefers deeper soil layers and the lithobiomorph prioritizes the surface and upper soil layers (GLM:  $F = 6.41$ ,  $p = 0.013$  and  $F = 4.01$ ,  $p = 0.048$ , respectively). This is not surprising, as the preference for the upper layers of soil by *L. (M.) curtipes* is well known (Tuf 2002, 2015). The ability of geophilomorphs to penetrate to deeper soil layers is documented and also recorded, using subterranean pitfall traps, too (Tuf et al. 2017).

## Conclusions

1. The species richness of millipedes is found to be very low in both habitat types studied, on the northern and southern slopes, whereas the centipede species richness is assessed as twice as high. The total richness comprises at least 19 species, belonging to ten genera, eight families, five orders, and two classes.
2. The new faunistic records for two millipede species, *Megaphyllum sjaelandicum* and *Sibirius latisupremus*, clarify their distribution areas. Two lithobiid species, *Lithobius (Ezembius) proximus* and *L. (Monotarsobius) insolens*, are new to the Altai Province, while *L. (E.) ostiacorum*, *L. vagabundus* and *L. (M.) nordenskiöldii* are recorded here in southwestern Siberia for the first time. A species of *Strigamia*

which is morphologically similar to *S. transsilvanica* was found in the study area. Two species from two genera, *Altajosoma* and *Lithobius*, are likely to be new to science, but their descriptions are delayed pending further information.

3. Two species predominate on the southern slope (*M. sjaelandicum* and *L. (M.) insolens*), and six species are dominant or codominant on the northern one (*S. latisupremus*, *Escaryus retusidens*, *E. koreanus*, *L. (E.) sibiricus*, *L. (M.) curtipes* and *L. (M.) insolens*). Thus, species diversity of millipedes is very low on both slopes, while in centipedes it is low only on the southern slope.
4. The density of millipedes on the southern slope is twice as high compared to the northern one, gradually declining from June to August in both habitat types. In contrast in centipedes, the numbers on the northern slope are twice as high compared to the southern one, with the minimum in mid-summer on both slopes.
5. The age structure of the dominant species is as follows: in *M. sjaelandicum*, juveniles predominated during summer; in *S. latisupremus*, overwintered adults predominate at the beginning of summer (with 75 % of total species abundance), juveniles start to prevail in the middle of summer (with 76 % of total species abundance); in *L. (M.) insolens* the sex ratio is 50:50; adults predominate in June, while juveniles emerge in the middle of summer in amounts equal to adults; in *E. retusidens* females outnumber males 2–5 times during the whole season in both habitat types.
6. The distribution of myriapods in the soil profile shows that millipedes and centipedes prefer the upper soil layer to 10 cm deep (about 80 % of total myriapod abundance) with the litter more populated on the northern slope, containing from 13 to 15 % of the fauna, and the maximum penetration in depth to no more than 20 cm in millipedes and 30 cm in centipedes. The only geophilomorph centipede, *E. retusidens*, prefers deeper soil layers.

## Acknowledgements

We are most grateful to H.J. Read (Farnham Common, UK) who kindly checked the English of an advanced draft. We are also much obliged to V.Yu. Slatina, an ASU Masters student, for her collecting efforts. We are very thankful to L. Bonato (University of Padova, Italy) for his confirmation of *Strigamia* cf. *transsilvanica* identification. We are also deeply grateful to M. Zapparoli (Viterbo, Italy), P. Stoev (Sofia, Bulgaria), and an anonymous reviewer for their critical remarks on this paper. The results were obtained within the framework of the state task No. 6.2884.2017/4.6 Ministry of Education and Science of the Russian Federation.

## References

- Babenko AS, Nefediev PS, Nefedieva JS (2009) [The fauna and population dynamics of millipedes (Diplopoda) in Salair chern taiga]. *Vestnik Tomskogo gosudarstvennogo universiteta, Seriya biologiya* 319: 182–185. [in Russian]

- Bonato L, Chagas Junior A, Edgecombe GD, Lewis JGE, Minelli A, Pereira LA, Shelley RM, Stoev P, Zapparoli M (2016) ChiloBase 2.0 – A World Catalogue of Centipedes (Chilopoda). Available at <http://chilobase.biologia.unipd.it> [accessed 20 June 2017]
- Bonato L, Dányi L, Socci AA, Minelli A (2012) Species diversity of *Strigamia* Gray, 1843 (Chilopoda: Linotaeniidae): a preliminary synthesis. *Zootaxa* 3593: 1–39.
- Bukhkalov SP, Galitch DE, Sergeeva EV, Vazhenina NV (2014) [Synopsis of the invertebrate fauna of the southern taiga in western Siberia (basin of the Lower Irtysh)]. KMK Scientific Press, Ltd., Moscow, 189 pp. [in Russian]
- Bukhkalov SP, Sergeeva EV (2012) [Interannual dynamics of composition and structure of soil invertebrate communities in the root terrace of the Irtysh]. Belgorod State University Scientific Bulletin. Natural sciences 15(20): 59–64. [In Russian]
- Byzova YuB, Chadaeva ZV (1965) [Comparative characteristics of soil fauna of various associations in an *Abies sibirica* forest (Kemerovo Area)]. *Zoologicheskii Zhurnal* 44(3): 331–339. [in Russian, with English summary]
- Dyachkov YuV (2014) [Biodiversity and ecological peculiarities of millipedes in the Tigirek State Nature Reserve (Diplopoda)]. Lecture abstracts of XIX International ecological student conference “Ecology of Russia and adjacent territories”. Novosibirsk, 41. [in Russian]
- Enghoff H (1985) The millipede family Nemasomatidae with the description of a new genus and a revision of *Orinisobates* (Diplopoda, Julida). *Entomologica Scandinavica* 16: 27–67. <https://doi.org/10.1163/187631285X00045>
- Farzaliyeva GSh (2009) [To the knowledge of the fauna of Myriapoda in the Kirov Area]. Scientific research as a basis for the protection of natural complexes in nature reserves and wildlife preserves. Proceedings of All-Russian Scientific and Practical Conference. Staraya Vyatka Publ., Kirov, 152–155. [in Russian]
- Farzaliyeva GSh, Eshyulin SL (2008) A review of the centipede (Lithobiomorpha, Henicopidae, Lithobiidae) fauna of the Urals and Cis-Ural Area. *Entomological Review* 88(5): 598–623. <https://doi.org/10.1134/S0013873808050102>
- Farzaliyeva GSh, Tselishcheva LG (2009) [Population of Myriapoda of some biocenoses in the Nurgush Nature Reserve]. Scientific research as a basis for the protection of natural complexes in nature reserves and wildlife preserves. Proceedings of All-Russian Scientific and Practical Conference. Staraya Vyatka Publ., Kirov, 155–159. [in Russian]
- Ghilarov MS (1987) [Censuses of larger invertebrates (mesofauna)]. Quantitative methods in soil zoology. Nauka Publ., Moscow, 9–26. [in Russian]
- Gulička J (1963) [New millipedes (Diplopoda) from the USSR. Part 1]. *Zoologicheskii Zhurnal* 42(4): 518–524. [in Russian, with English summary]
- Gulička J (1972) [New millipedes (Diplopoda) from the USSR. Part 2]. *Zoologicheskii Zhurnal* 51 (1): 36–45. [in Russian, with English summary]
- Mikhailova EV (1993) The millipedes (Diplopoda) of Siberia and the Far East of Russia. *Arthropoda Selecta* 2(2): 3–36.
- Mikhailova EV (2002) On some poorly-known millipedes from Siberia (Diplopoda). *Arthropoda Selecta* 10(3): 201–207. [for 2001]
- Mikhailova EV (2004) The millipedes (Diplopoda) of the Asian part of Russia. Pensoft Publishers, Sofia-Moscow, Series Faunistica 39, 292 pp.



- Mikhailjova EV (2009) New species of the family Julidae Leach, 1814 from Altai, Russia (Diplopoda, Julida). *Zootaxa* 2235: 59–68.
- Mikhailjova EV (2013) New data on the millipede fauna (Diplopoda) of Altai, Russia. *Far Eastern Entomologist* 265: 1–10.
- Mikhailjova EV (2016) New species and new records of millipedes (Diplopoda) from the Asian part of Russia. *Far Eastern Entomologist* 316: 1–25.
- Mikhailjova EV (2017) [The millipede fauna (Diplopoda) of the Asian part of Russia]. *Dal'nauka Publ., Vladivostok*, 336 pp. [in Russian, with English summary]
- Mikhailjova EV, Golovatch SI (2001) A review of the millipede fauna of Siberia (Diplopoda). *Arthropoda Selecta* 9(2): 103–118. [for 2000]
- Mikhailjova EV, Nefediev PS (2003) A contribution to the millipede fauna of Siberia (Diplopoda). *Arthropoda Selecta* 11(1): 81–87. [for 2002]
- Mikhailjova EV, Nefediev PS, Nefedieva JS (2007) New data on millipedes of the family Julidae (Diplopoda, Julida) from Altai, Siberia. *Zootaxa* 1541: 57–63.
- Mikhailjova EV, Nefediev PS, Nefedieva JS (2008) A new species and new records of millipedes of the family Diplomaragnidae (Diplopoda, Chordeumatida) from Altai. *Zootaxa* 1931: 49–56.
- Mikhailjova EV, Nefediev PS, Nefedieva JS, Dyachkov YuV (2015) Genus *Leptoiulus* Verhoeff, 1894 new to the fauna of the Asian part of Russia, with description of a new species from the Altai and its comparison with the European *Leptoiulus trilineatus* (C.L. Koch, 1847) (Diplopoda, Julida, Julidae). *Zootaxa* 3974(2): 267–276. <https://doi.org/10.11646/zootaxa.3974.2.10>
- Mikhailjova EV, Nefediev PS, Nefedieva JS, Sakhnevich MB, Dyachkov YuV (2014) Review of the millipede genus *Sibiriulus* Gulička, 1972, with descriptions of three new species from Altai, Siberia, Russia (Diplopoda, Julida, Julidae). *Zootaxa* 3866(1): 30–52. <https://doi.org/10.11646/zootaxa.3866.1.2>
- Nefediev PS (2001) [On the fauna and ecology of myriapods (Myriapoda) in the environs of the village of Smolenskoe, Altai Province]. *Landscapes of Western Siberia: Investigation problems, ecology and rational use. Proceedings of 7th International Conference, devoting to the International Day of the Earth. Biysk Pedagogical State University Publ., Biysk*, 84–86. [in Russian]
- Nefediev PS (2002a) On the Diplopoda fauna of South-West Siberia. 12th International Congress of Myriapodology. Book of Abstracts. Pietermaritzburg, 30 pp.
- Nefediev PS (2002b) [Populations and some ecological peculiarities of myriapods of gray forest soils in the southern of the Tomsk Area]. *Biology, a Science of the XXI Century. Abstracts of 6th School Conference of Young Researchers. Pushchino Scientific Centre RAS Publ., Pushchino-on-Oka*, 138–139. [in Russian]
- Nefediev PS (2016) [*Leptoyulus tigirekskii* (*Leptoiulus tigirek*)]. *Red Data Book of the Altai Province. Volume 2. Rare and endangered species of animals. Altai State University Publ., Barnaul*, 30–31. [in Russian]
- Nefediev PS, Dyachkov YuV, Nefedieva JS (2014a) Fauna and ecology of millipedes (Diplopoda) in the Tigirek State Nature Reserve, Russian Altai. In: Tuf IH, Tajovský K (Eds) 16th International Congress of Myriapodology. Book of Abstracts. Institute of Soil Biology, BC ASCR & Faculty of Science, Palacký University, Olomouc, 63 pp.

- Nefediev PS, Farzalieva GSh, Tuf IH (2017d) A preliminary review of the centipede fauna of the Altai State Nature Biosphere Reserve, southwestern Siberia, Russia (Chilopoda: Lithobiomorpha, Geophilomorpha). *Arthropoda Selecta* 26(3): 217–224.
- Nefediev PS, Farzalieva GSh, Tuf IH, Nedoev HKh, Niyazov ST (2017c) Millipede and centipede assemblages on the northern and southern slopes of the lowland Altai, southwestern Siberia, Russia (Diplopoda, Chilopoda). *Tropical Natural History. Suppl.* 5. Book of Abstracts. 17th International Congress of Myriapodology, Krabi, Thailand, 13.
- Nefediev PS, Knyazev SYu, Farzalieva GSh, Tuf IH (2017b) A contribution to the myriapod fauna of the Omsk Area, Siberia, Russia (Myriapoda: Diplopoda, Chilopoda). *Arthropoda Selecta* 26(2): 113–118.
- Nefediev PS, Kocourek P, Nefedieva JS (2016a) The first record of *Polydesmus inconstans* Latzel, 1884 (Diplopoda: Polydesmida: Polydesmidae) in the Asian part of Russia. *Arthropoda Selecta* 25(1): 19–21.
- Nefediev PS, Nefedieva JS (2005) [Seasonal fluctuations of diplopod density in some forests of Western Siberia]. Ecological diversity of soil biota and biological productivity of soils. Proceedings of IV (XIV) All-Russian Conference of Soil Zoology. Tyumen State University Publ., Tyumen, 177–178. [in Russian]
- Nefediev PS, Nefedieva JS (2006) [Regional peculiarities of millipede fauna (Diplopoda) in the south-east of Western Siberia]. Ecology of South Siberia and adjacent territories. Proceedings of X International School Conference of Students and Young Researchers. Khakassian State University Publ., Abakan 1: 98. [in Russian]
- Nefediev PS, Nefedieva JS (2007a) A brief analysis of the biotopic distribution of millipedes (Diplopoda) in the south-east of Western Siberia. Forest Soils: Research Results, Problems and Future Outlook. Abstracts of International Conference. Institute of Biology, Komi Scientific Center, Ural Division of RAS Publ., Syktyvkar, 139–140. [in Russian and in English]
- Nefediev PS, Nefedieva JS (2007b) [Biogeographical characteristic of millipede fauna in the south-east of Western Siberia]. Biodiversity of invertebrate animals. Proceedings of II All-Russian School Conference «Conceptual and applied aspects of scientific investigations and education in invertebrate zoology». Deltaplan Publ., Tomsk, 159–164. [in Russian]
- Nefediev PS, Nefedieva JS (2007c) [Seasonal dynamics of locomotor activity of millipedes (Diplopoda) in forests of Western Siberia]. Ecological problems of unique natural and anthropogenic landscapes. Proceedings of All-Russian Conference. Yaroslavl State University, Yaroslavl, 98–103. [in Russian]
- Nefediev PS, Nefedieva JS (2008a) [A historical review of faunistic investigations of millipedes (Diplopoda) in Western Siberia]. Altai: ecology and environmental management. Proceedings of VII Russian-Mongolian Conference of Students and Young Researchers. Biysk Pedagogical State University Publ., Biysk 1: 117–120. [in Russian]
- Nefediev PS, Nefedieva JS (2008b) Zoogeographical analysis of the millipede fauna (Diplopoda) in the south-east of Western Siberia. Myriapoda and Onychophora of the World Diversity, Biology and Importance. Abstracts of 14th International Congress of Myriapodology. Staatliches Museum für Naturkunde, Görlitz. Peckiana 6: 62.
- Nefediev PS, Nefedieva JS (2011) [Millipedes (Diplopoda) of green plantations of Tomsk City and its suburbs]. Conceptual and applied aspects of scientific investigations in inverte-

- brate zoology. Proceedings of III All-Russian School Conference. Agraf-Press Publ., Tomsk, 100–102. [in Russian]
- Nefediev PS, Nefedieva JS (2012a) [Some peculiarities of distribution of millipedes (Diplopoda) along the soil profile in the south-taiga and small-leaved forests of Western Siberia]. *Izvestia Altaiskogo gosudarstvennogo universiteta, Biologicheskie nauki* 3(75)1: 49–54. [in Russian]
- Nefediev PS, Nefedieva JS (2012b) [Some peculiarities of seasonal dynamics of sex-age structure of millipede populations (Diplopoda) in the southern taiga and small-leaved forests of Western Siberia]. *Izvestia Altaiskogo gosudarstvennogo universiteta, Biologicheskie nauki* 3(75)2: 46–48. [in Russian]
- Nefediev PS, Nefedieva JS (2013) [Biodiversity and ecology of millipedes in the environs of Lake Teletskoe (Diplopoda)]. *Izvestia Altaiskogo gosudarstvennogo universiteta, Biologicheskie nauki* 3(79)1: 86–87. [in Russian]
- Nefediev PS, Nefedieva JS, Dyachkov YuV (2013) Review of the millipede genus *Cylindroiulus* Verhoeff, 1894 in the Asian part of Russia (Diplopoda: Julida: Julidae). *Arthropoda Selecta* 22(4): 339–342.
- Nefediev PS, Nefedieva JS, Dyachkov YuV (2014b) A review of the anthrochore fauna of Asian Russia, with new records from the Altai Province, Siberia (Diplopoda). In: Tuf IH, Tajovský K (Eds) 16th International Congress of Myriapodology. Book of Abstracts. Institute of Soil Biology, BC ASCR & Faculty of Science, Palacký University, Olomouc, 64 pp.
- Nefediev PS, Nefedieva JS, Dyachkov YuV (2014c) A review of the anthrochore fauna of Asian Russia, with new records from the Altai Province, Siberia (Diplopoda). *Arthropoda Selecta* 23(4): 337–345.
- Nefediev PS, Tuf IH, Dyachkov YuV (2016c) First record of *Cryptops* (*Cryptops*) *hortensis* (Dobson, 1810) in southwestern Siberia, Russia (Chilopoda: Scolopendromorpha: Cryptopidae). *Biological Bulletin of Bogdan Chmel'nikovskiy Melitopol State Pedagogical University* 6(2): 107–109. <https://doi.org/10.15421/201642>
- Nefediev PS, Tuf IH, Dyachkov YuV, Efimov DA (2016b) First records of *Scutigera coleoptrata* (Linnaeus, 1758) in the south of western Siberia, Russia (Chilopoda: Scutigeroidea: Scutigeridae). *Biological Bulletin of Bogdan Chmel'nikovskiy Melitopol State Pedagogical University* 6(1): 428–432. <https://doi.org/10.15421/201626>
- Nefediev PS, Tuf IH, Farzalieva GSh (2016d) Centipedes from urban areas in southwestern Siberia, Russia (Chilopoda). Part 1. Lithobiomorpha. *Arthropoda Selecta* 25(3): 257–266.
- Nefediev PS, Tuf IH, Farzalieva GSh (2017a) Centipedes from urban areas in southwestern Siberia, Russia (Chilopoda). Part 2. Geophilomorpha. *Arthropoda Selecta* 26(1): 8–14.
- Nefedieva JS, Nefediev PS (2008) Ecofaunistic investigations of millipedes (Diplopoda) in the environs of Lake Teletskoe. Myriapoda and Onychophora of the World Diversity, Biology and Importance. Abstracts of 14th International Congress of Myriapodology. Staatliches Museum für Naturkunde, Göttingen. Peckiana 6: 123–124.
- Nefedieva JS, Nefediev PS, Sakhnevich MB, Dyachkov YuV (2014) Distribution of millipedes (Diplopoda) along an altitudinal gradient in the south of Lake Teletskoye, Altai Mts. In: Tuf IH, Tajovský K (Eds) 16<sup>th</sup> International Congress of Myriapodology. Book of Abstracts. Institute of Soil Biology, BC ASCR & Faculty of Science, Palacký University, Olomouc, 65 pp.

- Nefedieva JS, Nefediev PS, Sakhnevich MB, Dyachkov YV (2015) Distribution of millipedes along an altitudinal gradient in the south of Lake Teletskoye, Altai Mts, Russia (Diplopoda). In: Tuf IH, Tajovský K (Eds) Proceedings of the 16th International Congress of Myriapodology, Olomouc, Czech Republic. ZooKeys 510: 141–161. <https://doi.org/10.3897/zookeys.510.8855>
- Pereira LA, Hoffman RL (1993) The American species of *Escaryus*, a genus of Holarctic centipeds (Geophilomorpha: Schendylidae). Jeffersoniana 3: 1–72.
- Poloczek A, Pfeiffer M, Schneider R, Mühlenberg M (2016) The Chilopoda (Myriapoda) of the Khentey-Mountain Range, Northern Mongolia. Communities of different forest-types under a varying fire regime. European Journal of Soil Biology 74: 114–120. <https://doi.org/10.1016/j.ejsobi.2016.04.004>
- Sergeeva EV (2013) [Biotopic distribution and number of centipedes (Chilopoda) in Irtysh valley of West Siberia, Russia]. Euroasian Entomological Journal 12(6): 529–533. [In Russian, with English summary]
- Striganova BR, Poryadina NM (2005) [Soil animal population in boreal forests of the West Siberian Plain]. KMK Scientific Press Ltd., Moscow, 234 pp. [in Russian]
- ter Braak CJE, Šmilauer P (1998) CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4). Microcomputer Power, Ithaca, 352 pp.
- Titova LP (1972a) [New species of the genus *Escaryus* Cook et Collins (Schendylidae, Chilopoda)]. In: Ghilarov MS (Ed.) Ecology of soil invertebrates. Nauka Publ., Moscow, 94–119. [in Russian]
- Titova LP (1972b) [Pattern of the distribution of the genus *Escaryus* (Chilopoda) in the USSR]. In: Ghilarov MS (Ed.) Problems of soil zoology. Proceedings of IV All-Union Conference, Baku, 1972. Nauka Publ., Moscow, 135–136. [in Russian]
- Tuf IH (2002) Contribution to the knowledge of vertical distribution of soil macrofauna (Chilopoda, Oniscidea). In: Tajovský K, Balík V, Pižl V (Eds) Studies on Soil Fauna in Central Europe. Institute of Soil Biology, Czech Academy Science, České Budějovice, 241–246.
- Tuf IH (2015) Different collecting methods reveal different ecological groups of centipedes. Zoologia (Curitiba) 32(5): 345–350. <https://doi.org/10.1590/S1984-46702015000500003>
- Tuf IH, Kopecký O, Mikula J (2017) Can montane and cave centipedes inhabit soil? Turkish Journal of Zoology 41: 375–378. <https://doi.org/10.3906/zoo-1508-34>
- Volkova YuS (2016) [An annotated catalogue of geophilomorph centipedes (Chilopoda, Geophilomorpha) from the European part of Russia]. Zoologicheskii Zhurnal 95(6): 669–678. <https://doi.org/10.7868/S0044513416060179> [In Russian, with English summary]
- Zalesskaja NT (1978) [Identification book of the lithobiomorph centipedes of the USSR]. Nauka Publ., Moscow, 212 pp. [In Russian]
- Zalesskaja NT, Titova LP, Golovatch SI (1982) [The myriapod fauna of the Moscow Region]. In: Ghilarov MS (Ed.) Soil invertebrates of the Moscow Area. Nauka Publ., Moscow, 179–200. [In Russian]
- Zuev RV, Evsyukov AP (2016) Centipedes (Chilopoda) from the Rostov-on-Don Region, southern Russia. Russian Entomological Journal 25(4): 417–426.

# Why be red listed? Threatened Myriapoda species in Brazil with implications for their conservation

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Academic editor: P. Stoev | Received 31 October 2017 | Accepted 14 December 2017 | Published 7 March 2018

<http://zoobank.org/C5E704DD-A333-4EBD-955D-AF21B05BD12A>

**Citation:** Karam-Gemael M, Izzo TJ, Chagas-Jr A (2018) Why be red listed? Threatened Myriapoda species in Brazil with implications for their conservation. In: Stoev P, Edgecombe GD (Eds) Proceedings of the 17<sup>th</sup> International Congress of Myriapodology, Krabi, Thailand. ZooKeys 741: 255–269. <https://doi.org/10.3897/zookeys.741.21971>

## Abstract

The biodiversity crisis we live in, marked by high extinction rates, requires well-planned conservation efforts. To overcome this issue, red lists of threatened species are recognized as the main objective approach for evaluating the conservation status of species and therefore guiding conservation priorities. This work focuses on the Myriapoda (Chilopoda and Diplopoda) species listed in the Brazilian red list of fauna to enable discussion of the practical implications of red lists for conservation. Almost all myriapods assessed are endemic to Brazil (99 %) and 73 % are known from subterranean habitats only. Despite of 33 % being recorded from protected areas (PAs), downgrading, degazettement or downsizing of PAs and intense and unregulated ecotourism represent great threats. The PAs network in Brazil tends to fail in conserving myriapod species. The number of data deficient species (42 %) states the need of investing in ecological and taxonomic studies about the group, in order to fill in important knowledge gaps in species assessments nationally and globally. In this work we show that there is a lack of communication between national and global agencies concerning red lists, which results in a significant loss for science and for conservation. Despite investing in national and state red lists, individual countries must take the final step of submitting its data to IUCN global database, as significant international funding is available for IUCN red listed species conservation. Being one of the most diverse countries in the world, and facing the biggest cuts ever on national science funding, losing these important funding opportunities is a huge loss for Brazilian bio-



diversity conservation and for science. This study raises awareness on subterranean habitats conservation, due to its high endemism and fragility. Since the first edition of the Brazilian Red List in 1968, centipedes are now included for the first time, and millipedes for the second time. The presence of these myriapods in the list brings attention to the group, which usually receives little or no attention in conservation programs and environmental impact assessments. Rather than a specific case for Myriapoda and for Brazil, the points discussed here can be related to arthropods and the tropics, as the most biodiverse countries are emerging economies facing similar challenges in PAs network management, species extinction risks and science funding.

### Keywords

caves, centipedes, conservation management, ecotourism, extinction risk, IUCN, millipedes, protected areas, public policies, tropical region

## Introduction

Species extinction has always been part of biodiversity history. But recent extinction rates are 100 to 1000 times their pre-human levels in well-known and taxonomically diverse groups from widely different environments (Pimm et al. 1995). The overarching driver of species extinction is human population growth and increasing per capita consumption. How long these trends continue, where and at what rate, will dominate the scenarios of species extinction and challenge efforts to protect biodiversity (Pimm et al. 2014).

To understand and prevent human-driven extinction processes in progress, it is reasonable to know current living species diversity and distribution, in order to evaluate their probability of extinction. The red lists of threatened species are recognized as the most objective approach for evaluating the conservation status of species (IUCN 2013), and they represent the primary source of information to establish a species conservation status following defined protocols (Lewinsohn et al. 2005, Mallon and Jackson 2017). Red lists gather essential scientific evidence required to guide strategic and financial biodiversity conservation planning, the formulation of environmental public policies and conservation priorities and trends. Red lists are also indicators of data gaps in taxonomic groups or regions, orientating new biodiversity research. For example, a high number of species classified as Data Deficient shows that there is not enough knowledge about a given taxonomic group. Although inclusion in a red list is an indication of actual threat, absence of an entire taxonomic group from the list should be treated with circumspection because its omission could result from a lack of information rather than the absence of threat (Lewinsohn et al. 2005).

Given the growing concern about environment conservation, governments and/or environmental NGOs have been working in local conservation initiatives. Individual countries' red lists are constructed in regional or national levels and may inform local to global conservation decisions (Byrne and Fitzpatrick 2009). Red lists are implemented officially throughout environmental public policies at national and state levels across the countries. Usually they are funded by state or national governments, and co-

ordinated by its environmental agencies. In Brazil, the process of the list construction involves an extensive literature review by specialists, followed by workshops to discuss and validate each species assessments details and criteria.

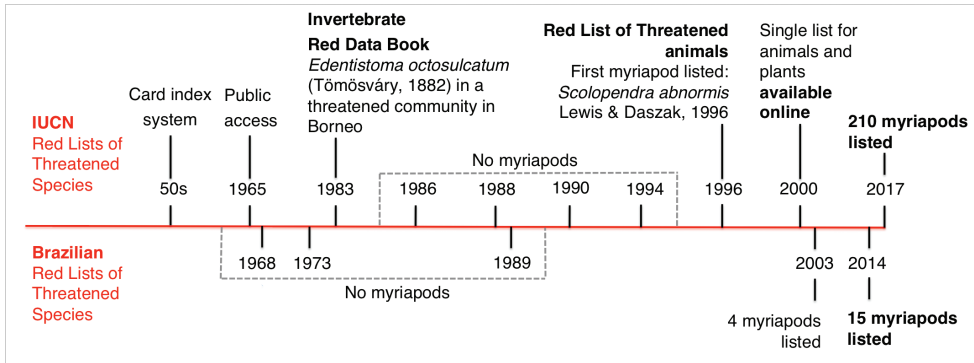
On the other hand, the IUCN (International Union for Conservation of Nature) Red List is considered the international authority for assessing species' extinction risk, informing global to local conservation decisions (Ocampo-Peñuela 2016). The list construction is based on a protocol that classifies species into different categories of risk using a formal set of objective and standard criteria (IUCN 2017a). The process regularly updates species status, and all the associated data are publicly accessible. Certainly, individual countries make their own decisions and may set management policies based on the IUCN assessments (Ocampo-Peñuela 2016). Both national lists and IUCN global assessments are primary information sources and may be complementary to each other on conservation programs.

### Threatened myriapods in red lists

Despite their relevant ecosystem services and functions, in general arthropods are poorly represented in conservation assessments (Lewinsohn et al. 2005, Diniz-Filho et al. 2010, Cardoso et al. 2011), which hinder an in-depth analysis of their conservation status (Lewinsohn et al. 2005). However, comprehensive biodiversity studies need to include as many taxa as possible (Oliveira et al. 2017). Considering invertebrates' high abundance and diversity worldwide, studies extending its knowledge and helping to fill in its scientific gaps are really necessary to its conservation and, therefore, to ecosystems services conservation in the long run.

The Myriapoda includes four classes: Chilopoda, Diplopoda, Pauropoda, and Symphyla. The myriapod fauna known for Brazil encompasses mainly Chilopoda (134 described species (Chagas-Jr 2017)) and Diplopoda (536 described species (Pena-Barbosa 2017)). It is estimated that there are around 400 Chilopoda species and 5,000 Diplopoda species only in the Amazon Forest (Adis and Harvey 2000). Pauropoda and Symphyla are almost unknown to science, and estimates indicate that there are fewer than 200 species of Pauropoda and fewer than 20 species of Symphyla in the Amazon Forest (Adis and Harvey 2000). Myriapods are widely distributed in Brazil and can be easily found in urban areas. Scolopendromorphs are most responsible for accidents with humans and their venom has been studied due to its medical interest, the novelty of its protein and peptide composition (Undheim et al. 2015) and potential for pharmacology (Harvey 2014; Hakim et al. 2015; Undheim et al. 2016). In China centipedes are one of the crucial venomous arthropods that have been used in traditional medicine for hundreds of years (Hakim et al. 2015).

Invertebrate animals were not initially included in red lists. The early beginnings for the IUCN Red List started in the 1950s with a card index system documenting data on threatened mammals and birds (Figure 1). In 1965 the first most comprehensive lists of threatened mammals and birds were published – enabling public ac-



**Figure 1.** Myriapoda in the IUCN and Brazilian red lists. Timeline of Myriapoda species included in the IUCN Red Lists of Threatened Species (above the red line), and in the Brazilian Red Lists of Threatened Species (below the red line), highlighting the first myriapods listed and the current number of species listed.

cess to the data for the first time. Since then, IUCN published several versions of its red lists encompassing mammals, birds, amphibians, reptiles, fishes, and several lists focused also on plant species. Invertebrates were first evaluated for the IUCN Red List in 1983, when The IUCN Invertebrate Red Data Book was published. Although this list presents all four classes of Myriapoda (Chilopoda, Diplopoda, Symphyla, and Pauropoda), and mention its scientific interest and threats to survival, the species were not yet assessed individually at that time. The IUCN Invertebrate Red Data Book also assessed some biological communities as a whole, where entire sets of invertebrates were in need of conservation. In Gunung Mulu National Park, in Borneo, the bizarre and rare centipede *Edentistoma octosulcatum* (Tömösváry, 1882) is listed in a threatened community. The first myriapod specifically assessed and listed in the IUCN Red List, according to the historical publications available at the institution website, was *Scolopendra abnormis* Lewis & Daszak, 1996, classified as vulnerable with a very small population. Since 2000 the IUCN Red List is available online (<http://www.iucnredlist.org/>) and nowadays it includes 200 millipede and ten centipede species.

In Brazil, the first national red list was published in 1968 (Figure 1), but it was only in the 2000 decade that the Brazilian lists adopted international standards of species assessments, using IUCN method, criteria and categories. Invertebrate assessments have been included in Brazilian red lists recently (Figure 1). The first myriapods included in a Brazilian red list were four millipede species in the 2003 list (*Leodesmus yporangae* (Schubart, 1946), *Peridontodesmella alba* Schubart, 1957, *Yporangiella stygius* Schubart, 1946, and *Rhinocricus padbergi* Verhoeff, 1938). The current Brazilian red list was published in 2014 and it includes 15 myriapod species (12 millipedes and three centipedes) (MMA 2014).

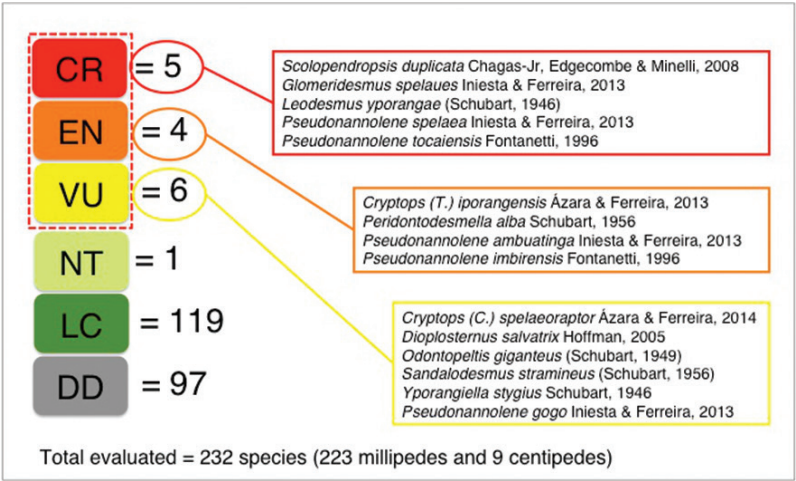
Given the continental size and great biodiversity of Brazil, it is unsurprising that sampling coverage is very unequal among biomes and taxonomic groups (Lewinsohn et al. 2005). Both in the IUCN Red List and in the Brazilian lists, invertebrate animal

assessments have always been uneven to vertebrate animals. For example, the 2017 IUCN Red List (version 2017-1) evaluated 1 % of invertebrates and 66 % of vertebrates of all described species. Even taking into account that the number of described species explains part of this unevenness (1.3 million for invertebrates and 68,000 for vertebrates (IUCN 2017b)), the number of species evaluated emphasizes invertebrate negligence (19,000 for invertebrates and 45,000 for vertebrates). Similarly, the current Brazilian Red List (2014) evaluated 3 % of invertebrates and 99 % of vertebrates described (3,000 invertebrate and 9,000 vertebrate species). However, this quantitative similarity between invertebrate and vertebrate proportions in Brazilian and IUCN red lists may hide an important qualitative mismatch between the lists, which can be a product of the lack of communication between national and international agencies. A focus on the implications of 2014 Brazilian Red List data for myriapods (Chilopoda and Diplopoda) conservation in Brazil allows a discussion of the current context and the relative effectiveness of the red lists of threatened species for biodiversity conservation in Brazil. Additionally, the implication of the discrepancies between the Brazilian red list and the IUCN list and the effectiveness of protected areas (PAs) Brazilian network in conserving threatened myriapods is discussed.

## **Materials and methods**

The current Brazilian red list of threatened species of fauna was constructed through specialists workshops held by ICMBio (Chico Mendes Institute of Biodiversity Conservation, a national agency of the Brazilian Ministry of Environment) and it was published as a legal act in December 17, 2014 (MMA 2014). In 2016, ICMBio also published the Executive Summary of the Brazil Red Book of Threatened Species of Fauna, which includes more information about the threatened species listed in 2014 (MMA 2016). The assessments workshops followed IUCN methods, categories and criteria to assess species, which classifies the extinction risk as Critically endangered (CR), Endangered (EN), Vulnerable (VU), Near threatened (NT), Least concern (LC), and Data deficient (DD). The categories CR, EN and VU are considered the threatened ones.

This study focused on the Myriapoda species in the 2014 Brazilian red list (Figure 2) and its related data available on the Executive Summary published in 2016. The analysis consisted of a qualitative comparison between the species listed in the 2014 Brazilian red list and those listed in the IUCN Red List (version 2017-1, <http://www.iucnredlist.org/>). The software QGIS (version 2.18.7) was used to create the map using Brazilian biomes and protected areas shape files, besides Myriapoda threatened species distribution data. Both biomes and protected areas shape files were downloaded from the Brazilian Environment Ministry website (<http://mapas.mma.gov.br/i3geo/datadownload.htm>) in June 2017. Myriapoda threatened species geographic coordinates were compiled from the original descriptions' publications (See Suppl. material 1: Myriapoda threatened species geographic coordinates).



**Figure 2.** Myriapoda species assessment by the current Brazilian Red List. Myriapoda threatened species according to the 2014 Brazilian Red List, which follows IUCN classification categories (CR = Critically endangered, EN = Endangered, VU = Vulnerable, NT = Near threatened, LC = Least concern, DD = Data deficient). Dashed red line indicates threatened categories.

Results

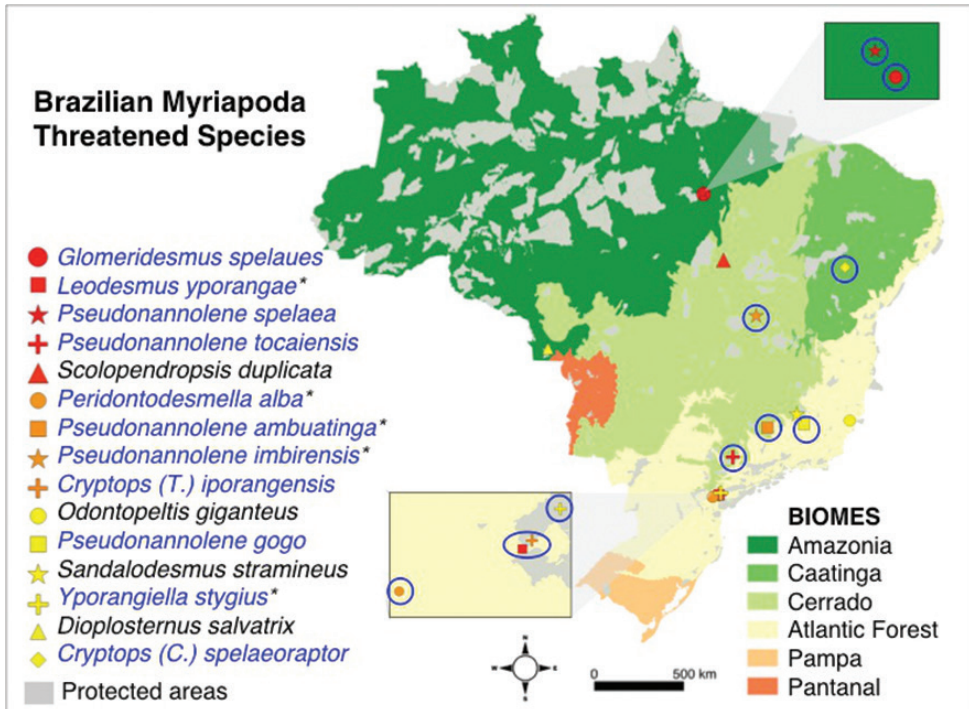
The Brazilian red list encompasses more Myriapoda families and genera than IUCN red list, especially for Diplopoda species (Table 1). Comparing the families, four Diplopoda families (Paradoxosomatidae, Pyrgodesmidae, Siphonophoridae, Spirostreptidae), and two Chilopoda families (Ballophilidae and Scolopendridae) are shared between the two lists. Concerning the genera, only one of each class is included in both the IUCN and the Brazilian lists: *Rhinocricus* (Diplopoda), and *Ityphilus* (Chilopoda). There are no shared myriapod species between the IUCN and the Brazilian red lists.

Almost all myriapods species assessed for the Brazilian red list are endemic to Brazil (99 %), and so are all of those classified as threatened (100 %). Among the species categorized as threatened, 73 % are only known for subterranean habitats (Figure 3), and just 33 % occurs inside PAs. Concerning the Brazilian biomes, 40 % of threatened myriapod species are in Atlantic Forest, 33 % in Cerrado, 20 % in Amazonia, and 7 % in Caatinga (Figure 3).

**Table 1.** Myriapoda diversity in IUCN Red List (2017) and in Brazil Red List (2014), including all extinction risk categories: Critically endangered, Endangered, Vulnerable, Near threatened, Least concern, and Data deficient.

Reference	Diplopoda			Chilopoda		
	Families	Genera	Species	Families	Genera	Species
IUCN Red List	12	35	200	5	5	10
Brazil Red List	17	76	223	6	7	9
Shared taxa	4	1	0	2	1	0





**Figure 3.** Distribution of the Brazilian Myriapoda threatened species. The color of the legend represents the IUCN threatened category: red (Critically endangered – CR), orange (Endangered – EN), and yellow (Vulnerable – VU). Species in blue are only known from subterranean habitats. Species with an asterisk (\*) occur inside PAs.

**Table 2.** Myriapoda orders represented among Data Deficient (DD) species and cave species in the 2014 Brazilian Red List of Threatened Species.

Class	Order	DD species	Cave species
Diplopoda	Polydesmida	51 %	27 %
	Spirobolida	25 %	0 %
	Spirostreptida	21 %	46 %
	Siphonophorida	1 %	0 %
	Glomeridesmida	0 %	9 %
Chilopoda	Scolopendromorpha	2 %	18 %
	Geophilomorpha	0 %	0 %
	Scutigermomorpha	0 %	0 %
	Lithobiomorpha	0 %	0 %

Concerning the species classified as Data Deficient (DD), 98 % refers to Diplopoda and just 2 % refers to Chilopoda (Table 2). Among Diplopoda, the order Polydesmida encompasses the highest number of DD species in Brazil. Concerning the subterranean myriapod fauna, Spirostreptida is the order more frequently recorded (Table 2).

## Discussion

### What is the importance of a species being included in a red list?

There are some implications of a species being included in a red list. First, the assessment data itself have an intrinsic value of knowing biodiversity status in a given period of history and its associated extinction risks (Dijkstra 2017). At each update of the list, new species are assessed, compiled, and summarized and, thus, more knowledge is generated about the group itself. This kind of data also allows temporal assessment of the species populations (Schachat et al. 2015, Cruickshank et al. 2016). Second, when a species is included in a red list it gets attention and becomes among the priorities for conservation efforts, once red lists gather scientific evidence required to guide biodiversity conservation planning, the formulation of public policies and conservation priorities and trends (Mallon and Jackson 2017). Conservation science being an applied discipline, red lists operate like the first step to the management of species. Third, but not less important, the inclusion of a species in a red list increases the possibility of raising funds to study the species (but on the other hand, bureaucratic obstacles also increase).

Science funding in Brazil has been suffering huge cuts at federal and state levels in recent years, which have paralyzed research (Gibney 2015). From electric and cleaning expenses to laboratories working and field research and meetings, science and research institutions do not have enough funds to pay the basics, and face one of the worst science funding crisis to strike Brazil in decades (Escobar 2015). Besides paralyzing research in Brazil, after a decade of economic boom and its investments resulting in high quality science (Gibney 2015), Brazil is also facing the loss of scientists that have opportunity to live and work abroad; Brazilian science is bankrupt (Escobar 2015).

Once conservation efforts are limited and priorities must be set, in practice red lists work as a priority indicator for conservation investments. In Brazil there are calls for biodiversity conservation directed specifically to threatened species, i.e. Fundação O Boticário (<http://www.fundacaogrupoboticario.org.br>). For those, the presence of a given species in the Brazilian red list is the main criteria for funding eligibility. Similarly, there are international calls directed to fund research and conservation programs of species assessed for the IUCN Red List. There are several small grants provided by scientific associations that potentially fund postgraduate research, i.e. Whitley Fund for Nature (<https://whitleyaward.org/>), The Rufford Foundation (<https://www.rufford.org/rsg/>), Saving Species (<http://www.savingspecies.org/>), People's Trust for Endangered Species (<https://ptes.org/>). There are also bigger agencies providing grants to entire conservation programs. For example, SOS – Save Our Species (<http://www.saveourspecies.org/>) is a joint initiative of the IUCN, the Global Environment Facility, and the World Bank. Its objective is to ensure the long-term survival of threatened species and their habitats, supporting direct action on species conservation priorities informed by the IUCN Red List of Threatened Species, among other criteria. Between 2010 and 2016, the SOS initiative allocated US\$ 10 million to species conservation, encompassing 250 threatened species in more than 50 countries (including Brazil in

a critically endangered bird project in 2010). Another example is The Mohamed bin Zayed Species Conservation Fund (<https://www.speciesconservation.org/>), a private institution that invested US\$ 15.5 million in the last nine years in conservation programs across the planet. Brazilian projects received US\$ 750,000 from that amount (3 %), distributed across 79 projects encompassing mammals (53 %), birds (18 %), reptiles (12 %), plants (7 %), amphibians (5 %), fishes (4 %), invertebrates (1 %), and fungi (0,004 %). The Fund uses the IUCN Red List as the primary guide to the conservation status of a given species. Taken altogether, these two funding opportunities directed more than US\$ 25 million in the last decade specifically to fund the conservation of red listed species assessed in the IUCN. Being one of the most diverse countries in the world, and facing the biggest cuts ever on national science funding (Gibney 2015), why are Brazilian myriapod species, and probably many others, not eligible for international conservation grants?

Despite the IUCN being listed among the supporters of the 2014 Executive Summary of Brazil Red Book, the species listed in Brazil were not submitted to the IUCN global database. The Brazilian government invests in the elaboration of the national lists based on IUCN method and categories, but not taking this final step of submitting its assessments to the IUCN prevents international funding from being directed to Brazilian species. If a given species is classified as threatened in Brazil, but it is not listed in the IUCN Red List, it is not eligible for considerable international funding. Losing these important opportunities is a huge loss for Brazilian biodiversity conservation and for science, especially when investments are so scarce.

Fine scale red lists (i.e., country and state) are mandatory to know biodiversity and to plan short and mid-term conservation actions. However, consolidating those smaller pictures in a global database is also essential, because of their intrinsic value to science. For example, all the Myriapoda species assessed for the IUCN Red List are from Africa (98 %) and Southeast Asia (1 %). But myriapods are globally distributed, which suggests that there is a huge geographic gap in Myriapoda assessed data in the IUCN. As the endemic Brazilian myriapods were already assessed according to IUCN criteria but the data have not been yet sent to IUCN, analyzing the IUCN Red List alone could led to an erroneous conclusion that myriapods are only threatened in Africa and Southeast Asia. Besides that, Brazilian data have a significant impact on the knowledge of threatened Myriapoda considering also the diversity of the group, as the Brazilian Red List encompasses more families and genera than the IUCN Red List, especially for Diplopoda species. Then, adding national data to IUCN global database increases scientific knowledge of a given group, as it gathers scattered information into a single source. Second (and in a more applied sense), consolidating those smaller pictures in a global database is important to concentrate efforts for biodiversity conservation allowing priorities to be set at a global scale – which, in the red list case, would include countries' red lists information which is not yet encompassed by IUCN global database. Besides that, it also allows endemic threatened species to be eligible for international funding. Then, countries that elaborate their national red lists based on IUCN methods (guidelines are available at its website) must take the final step of submitting their data to the

IUCN staff for validation and inclusion in the red list. Submitting national red lists data to IUCN allows countries to achieve international funding and also helps to fill in the gaps in biodiversity knowledge and in the IUCN global database.

### **Myriapoda threatened species in Brazilian protected areas**

The myriapod species in the Brazilian Red List are not widely distributed across Brazil. Our results show that there are more threatened species in threatened habitats. Among threatened myriapods, 40 % are in the Atlantic Forest, and 33 % in the Cerrado – the biomes with the lowest proportion of remaining vegetation in Brazil: 8.5 % (MMA 2017) and 45 % (Coura et al. 2011), respectively. Oliveira et al. (2017) found that most species of vertebrates, arthropods (including millipedes) and angiosperms in their dataset had less than 30 % of their geographical distribution within Brazilian PAs. Our results, which include centipedes, and exclude non-myriapod groups, are consistent with theirs, as only 33 % of species among the threatened Brazilian Myriapoda occur inside PAs. Added to these low percentages there are PADDD events (downgrading, degazettement or downsizing of PAs) and intense and unregulated tourism representing great threats to biodiversity conservation within PAs in Brazil. In fact, there is an urgent call to designate new PAs in the Atlantic Forest and the Cerrado to prevent species loss due to the potential impact of the human population growth and agricultural expansion (Junk et al. 2006, Overbeck et al. 2015). The Cerrado, particularly, is the most coveted biome for agribusiness expansion (Overbeck et al. 2015, Strassburg et al. 2017). Even though invertebrates play essential ecological roles in ecosystem functioning, the pollination function developed by bees is probably the most common argument for conserving invertebrates. In Brazil, there are two cases of PAs created for invertebrate's conservation (the velvet worm *Epiperipatus acacioi* (Marcus and Marcus 1955) and dragonfly communities), both PAs in Brazil Southeast. However, these are clearly exceptions in the Brazilian conservation agenda. Unfortunately, without the creation of PAs and protection of the threatened myriapod species, their extinction becomes more probable.

Additionally, the majority of threatened Myriapoda species is only known for subterranean habitats, considered as fragile environments with a high degree of endemism and morphological, ecological, and behavioral specialization among its communities (Bichuette and Trajano 2010). Among many aspects of nature that have a great potential for tourism, caves stand out due to their unique features, both scientific and esthetic, resulting in a high degree of attractiveness (Lobo et al. 2013). However, excessive human visitation is pointed as one of the major causes of impact for subterranean faunas, as a result of the considerable development of speleology as sport and adventure, overcrowding many caves (Bichuette and Trajano 2010). Being at the same time fragile and attractive, cave conservation turns to be a huge challenge concerning whole endemic invertebrate communities. The IUCN (1992) lists tourism as the sec-

and major threat to protected areas (after exotic fauna). Globally, terrestrial PAs receive approximately 8 billion visits per year (Balmford et al. 2015). On the other hand, Brazil's national parks received 6.5 million visits in 2014 (Castro et al. 2015). Tourism related to nature or wildlife is a rapidly growing economic activity, especially in developing countries, which are more biodiverse and where it can generate income for local communities and governments (Curtin and Kragh 2014). Then, the lack of management plans in PAs represents a barrier to the development of ecotourism (Tortato and Izzo 2017). If carefully planned, managed and controlled, ecotourism in caves can minimize or even avoid most negative effects (Gossling 1999), and generate economic opportunities for local communities. For example, the economic benefits accrued from jaguar observation tourism far outweighed the costs of cattle losses in private ranches in Brazil, where local people still engage in the persecution and killing of large cats (Tortato et al. 2017). So, even if controversial, cave ecotourism can contribute to safeguard biodiversity and ecosystem functions in developing countries, even though meeting the requirements for ecotourism is extremely difficult (Gossling 1999).

The whole picture of PAs in Brazil, considering both the PADDD events and unregulated tourism, suggests that the PAs network in Brazil tends to fail in conserving biodiversity and needs to be strengthened to achieve conservation goals in the long run. However, the political scenario in Brazil is not optimistic. Ironically, politicians defending the agriculture industry, hydropower system and mineral extraction expansion have a strong influence on environmental political decisions in Brazil, and frequently succeed in getting polemic decisions quickly approved without public and technical consultations (Fearnside 2015). It seems that mineral extraction pressure will not cool down in the near future in Brazil, considering national government's recent proposition of attracting private investments to explore minerals in the Amazon, among other measures of the Brazilian Mineral Industry Revitalization Program (DNPM 2017). Then, our analysis suggests that Myriapoda species extinction risks are likely to be worse than those stated in the 2014 Brazilian Red List, once the high number of Data Deficient species (42 %) may hide a significant number of species in threatened conditions. Besides, this scene may be similar, or worse, when considering other invertebrate groups. The total number of myriapods assessed for the 2014 Brazilian Red List represents 35% of all species registered from Brazil of its two major classes (Chilopoda and Diplopoda). The proportion of other invertebrate groups assessed was much smaller, such as Lepidoptera (3 %), Hymenoptera (3 %), Arachnida (2 %), and Coleoptera (0.005%). These important data gaps in scientific knowledge probably hide a significant number of terrestrial invertebrate species not being protected by the Brazilian PAs system. The current PA system fails to protect the majority of endemic species in Brazil (Oliveira et al. 2017) and here it also fails when considering Myriapoda endemic species in Brazil, and likely other terrestrial invertebrate groups.

Then, rather than a specific case for Myriapoda and for Brazil, the points discussed here can be related to arthropods (Lewinsohn et al. 2005, Diniz-Filho et al. 2010, Cardoso et al. 2011) and for the tropics, as most diverse countries are mainly emerging



economies facing similar challenges in assessing species extinction risks, PAs network management, and science funding. Therefore, we recommend:

- Investing in taxonomic and ecological studies concerning myriapods and other arthropods in the tropics;
- Investing in biodiversity inventories within PAs networks in the tropics;
- Stimulating individual countries to submit their national red lists data to the IUCN.

## Acknowledgements

MKG's PhD scholarship is funded by the Fundação de Amparo à Pesquisa do Estado de Mato Grosso (FAPEMAT). The authors thank Carlos Alberto Martínez Muñoz, Shirley Daniella Martínez-Torres and an anonymous reviewer for their comments on the manuscript.

## References

- Adis J, Harvey MS (2000) How many Arachnida and Myriapoda are there world-wide and in Amazonia? *Studies on Neotropical Fauna and Environment* 35: 139–141. [https://doi.org/10.1076/0165-0521\(200008\)35:2;1-9;FT139](https://doi.org/10.1076/0165-0521(200008)35:2;1-9;FT139)
- Balmford A, Green JMH, Anderson M, Beresford J, Huang C, Naidoo R, Walpole M, Manica A (2015) Walk on the wild side: estimating the global magnitude of visits to protected areas. *Plos Biology* 13: e1002074. <https://doi.org/10.1371/journal.pbio.1002074>
- Bichuette ME, Trajano E (2010) Conservation of subterranean fishes. In: Trajano E, Bichuette ME, Kapoor BG (Eds) *Biology of subterranean fishes*. Science Publishers, Enfield, 65–80. <https://doi.org/10.1201/EBK1578086702-c3>
- Byrne A, Fitzpatrick U (2009) Bee conservation policy at the global, regional and national levels. *Apidologie* 40(3): 194–210. <https://doi.org/10.1051/apido/2009017>
- Cardoso P, Erwin TL, Borges PAV, New TR (2011) The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation* 144: 2647–2655. <https://doi.org/10.1016/j.biocon.2011.07.024>
- Castro EV, Souza TB, Thapa B (2015) Determinants of tourism attractiveness in the national parks of Brazil. *Parks* 21: 51–62. <https://doi.org/10.2305/IUCN.CH.2014.PARKS-21-2EVDC.en>
- Chagas-Jr A (2017) Chilopoda in Catálogo Taxonômico da Fauna do Brasil. PNUD. <http://fauna.jbrj.gov.br/fauna/faunadobrasil/35> [accessed November 2017]
- Chardonnet PH, des Clers B, Fischer J, Gerhold R, Jori F, Lamarque F (2002) The value of wildlife. *Revue Scientifique et Technique* 21(1): 15–51. <https://doi.org/10.20506/rst.21.1.1323>
- Coura SMC, Lima A, Shimabukuro YE (2011) Status da conservação de remanescentes de vegetação natural de distintos biomas do Brasil. In: Epiphânio JCN, Galvão LS (Eds)

- Anais XV Simpósio Brasileiro de Sensoriamento Remoto – INPE, Curitiba (Brazil), May 2011. INPE, São Paulo, 3197–3204. <http://marte.sid.inpe.br/col/dpi.inpe.br/marte/2011/09.28.16.42/doc/@sumario.htm>
- Cruickshank SS, Ozgul A, Zumbach S, Schmidt BR (2016) Quantifying population declines based on presence-only records for red-list assessments. *Conservation Biology* 30(5): 1–10. <https://doi.org/10.1111/cobi.12688>
- Curtin S, Kragh G (2014) Wildlife tourism: reconnecting people with nature. *Human Dimensions of Wildlife* 19(6): 545–554. <https://doi.org/10.1080/10871209.2014.921957>
- Dijkstra KDB (2017) Taxonomy: use the Red List as a registry. *Nature* 546: 599–600. <https://www.nature.com/nature/journal/v546/n7660/pdf/546599d.pdf>
- Diniz-Filho JAF, De Marco PJ, Hawkins B (2010) Defying the curse of ignorance: perspectives in insect macroecology and conservation biogeography. *Insect Conservation and Diversity* 3(3): 157–245. <https://doi.org/10.1111/j.1752-4598.2010.00091.x>
- DNPM – Departamento Nacional de Produção Mineral (2017) Criada a Agência Nacional de Mineração. <http://www.dnpm.gov.br/criada-a-agencia-nacional-de-mineracao-2013-anm> [accessed October 2017]
- Escobar H (2015) Fiscal crisis has Brazilian scientists scrambling. *Science* 349(6251): 909–910. <https://doi.org/10.1126/science.349.6251.909>
- Fearnside PM (2015) Amazon dams and waterways: Brazil's Tapajós Basin plans. *Ambio* 44(5): 426–439. <https://doi.org/10.1007/s13280-015-0642-z>
- Gibney E (2015) Brazilian science paralysed by economic slump. *Nature* 526: 16–17. <https://doi.org/10.1038/526016a>
- Gossling S (1999) Ecotourism: a means to safeguard biodiversity and ecosystem functions? *Ecological Economics* 29(2): 303–320. [https://doi.org/10.1016/S0921-8009\(99\)00012-9](https://doi.org/10.1016/S0921-8009(99)00012-9)
- Hakim MA, Yang S, Lai R (2015) Centipede Venoms and Their Components: Resources for Potential Therapeutic Applications. *Toxins* 7: 4832–4851. <https://doi.org/10.3390/toxins7114832>
- Harvey AL (2014) Toxins and drug discovery. *Toxicon* 92: 193–200. <https://doi.org/10.1016/j.toxicon.2014.10.020>
- IUCN (1992) World Heritage Twenty Years Later. IUCN, Gland, 191 pp.
- IUCN (2013) The IUCN Red List of Threatened Species. <http://www.redlist.org> [accessed January 2013]
- IUCN (2017a) The IUCN Red List of Threatened Species. Version 2017-2. <http://www.iucn-redlist.org/about/overview> [accessed September 2017]
- IUCN (2017b) The IUCN Red List of Threatened Species. Version 2017-1. Table 1. [http://www.iucnredlist.org/about/summary-statistics#Tables\\_1\\_2](http://www.iucnredlist.org/about/summary-statistics#Tables_1_2) [accessed September 2017]
- Junk WJ, Cunha CN, Wantzen KM, Petermann P, Strussmann C, Marques MI, Adis J (2006) Biodiversity and its conservation in the Pantanal of Mato Grosso. *Aquatic Sciences* 68: 278–309. <https://doi.org/10.1007/s00027-006-0851-4>
- Lewinsohn TM, Freitas AVL, Prado PI (2005) Conservation of terrestrial invertebrates and their habitats in Brazil. *Conservation Biology* 19(3): 640–645. <https://doi.org/10.1111/j.1523-1739.2005.00682.x>
- Lobo HAS, Trajano E, Marinho MA, Bichuette ME, Scaleante JAB, Scaleante OAF, Rocha BN, Laterza FV (2013) Projection of tourist scenarios onto fragility maps: Framework for

- determination of provisional tourist carrying capacity in a Brazilian show cave. *Tourism Management* 35: 234–243. <https://doi.org/10.1016/j.tourman.2012.07.008>
- Mallon DP, Jackson RM (2017) A downlist is not a demotion: Red List status and reality. *Oryx* 51(4): 605–609. <https://doi.org/10.1017/S0030605317000606>
- MMA – Ministério do Meio Ambiente (2014) Portaria nº 444, de 17 de dezembro de 2014. Lista Nacional Oficial de Espécies da Fauna Ameaçadas de Extinção. *Diário Oficial da União* 245(1): 121–126. Online source: [http://www.icmbio.gov.br/portal/images/stories/biodiversidade/fauna-brasileira/avaliacao-do-risco/PORTARIA\\_N%C2%BA\\_444\\_DE\\_17\\_DE\\_DEZEMBRO\\_DE\\_2014.pdf](http://www.icmbio.gov.br/portal/images/stories/biodiversidade/fauna-brasileira/avaliacao-do-risco/PORTARIA_N%C2%BA_444_DE_17_DE_DEZEMBRO_DE_2014.pdf)
- MMA – Ministério do Meio Ambiente (2016) Executive Summary of Brazil Red Book of Threatened Species of Fauna. MMA, Brasília, 75 pp. [http://www.icmbio.gov.br/portal/images/stories/comunicacao/publicacoes/publicacoes-diversas/dcom\\_sumario\\_executivo\\_livro\\_vermelho\\_ed\\_2016.pdf](http://www.icmbio.gov.br/portal/images/stories/comunicacao/publicacoes/publicacoes-diversas/dcom_sumario_executivo_livro_vermelho_ed_2016.pdf)
- MMA – Ministério do Meio Ambiente (2017) Mata Atlântica. <http://www.mma.gov.br/biomas/mata-atlantica> [accessed August 2017]
- Ocampo-Peñuela N, Jenkins CN, Vijay V, Li BV, Pimm SL (2016) Incorporating explicit geo-spatial data shows more species at risk of extinction than the current Red List. *Science Advances* 2: e1601367. <https://doi.org/10.1126/sciadv.1601367>
- Oliveira U, Soares-Filho BS, Paglia AP, Brescovit AD, de Carvalho CJB, Silva DP, Rezende DT, Leite FSE, Batista JAN, Barbosa JPPP, Stehmann JR, Ascher JS, de Vasconcelos MF, De Marco P, Löwenberg-Neto P, Ferro VG, Santos AJ (2017) Biodiversity conservation gaps in the Brazilian protected areas. *Nature* 7: 9141. <https://doi.org/10.1038/s41598-017-08707-2>
- Overbeck GE, Vélez-Martin E, Scarano FR, Lewinsohn TM, Fonseca CR, Meyer ST, Müller SC, Ceotto P, Dadalt L, Durigan G, Ganade G, Gossner MM, Guadagnin DL, Lorenzen K, Jacobi CM, Weisser WW, Pillar VD (2015) Conservation in Brazil needs to include non-forest ecosystems. *Diversity and Distributions* 21: 1455–1460. <https://doi.org/10.1111/ddi.12380>
- Pack SM, Ferreira MN, Krithivasan R, Murrow J, Bernard E, Mascia MB (2016) Protected area downgrading, downsizing, and degazettement (PADDD) in the Amazon. *Biological Conservation* 197: 32–39. doi: [10.1016/j.biocon.2016.02.004](https://doi.org/10.1016/j.biocon.2016.02.004)
- Pena-Barbosa JPP (2017) Diplopoda in Catálogo Taxonômico da Fauna do Brasil. PNUD. <http://fauna.jbrj.gov.br/fauna/faunadobrasil/42> [accessed November 2017]
- Pimm SL, Russell GJ, Gittleman JL, Brooks TM (1995) The future of biodiversity. *Science* 269: 347–350. [https://doi.org/10.1016/0006-3207\(96\)85981-7](https://doi.org/10.1016/0006-3207(96)85981-7)
- Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, Raven PH, Roberts CM, Sexton JO (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344: 1246752. <https://doi.org/10.1126/science.1246752>
- Sarmento WM, Berger J (2017) Human visitation limits the utility of protected areas as ecological baselines. *Biological Conservation* 212(A): 316–326. <https://doi.org/10.1016/j.biocon.2017.06.032>
- Schachat SR, Mulcahy DG, Mendelson JR (2015) Conservation threats and the phylogenetic utility of IUCN Red List rankings in *Incilius* toads. *Conservation Biology* 30(1): 72–81. <https://doi.org/10.1111/cobi.12567>

- Strassburg BBN, Brooks T, Feltran-Barbieri R, Iribarrem A, Crouzeilles R, Loyola R, Latawiec AE, Oliveira Filho FJB, Scaramuzza CAM, Scarano FR, Soares-Filho B, Balmford A (2017) Moment of truth for the Cerrado hotspot. *Nature Ecology and Evolution* 1: 99. <https://doi.org/10.1038/s41559-017-0099>
- Tortato FR, Izzo TJ (2017) Advances and barriers to the development of jaguar-tourism in the Brazilian Pantanal. *Perspectives in Ecology and Conservation* 15(1): 61–63. <https://doi.org/10.1016/j.pecon.2017.02.003>
- Tortato FR, Izzo TJ, Hoogesteijn R, Peres CA (2017) The numbers of the beast: Valuation of jaguar (*Panthera onca*) tourism and cattle depredation in the Brazilian Pantanal. *Global Ecology and Conservation* 11: 106–114. <https://doi.org/10.1016/j.gecco.2017.05.003>
- Undheim EAB, Fry BG, King GF (2015) Centipede Venom: Recent Discoveries and Current State of Knowledge. *Toxins* 7(3): 679–704. <https://doi.org/10.3390/toxins7030679>
- Undheim EAB, Jenner RA, King GF (2016) Centipede venoms as a source of drug leads. *Expert Opinion on Drug Discovery* 11(12): 1139–1149. <https://dx.doi.org/10.1080/17460441.2016.1235155>

## Supplementary material I

### Myriapoda threatened species geographic coordinates

Authors: Manoela Karam-Gemael, Thiago Junqueira Izzo, Amazonas Chagas-Jr

Data type: occurrence

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Link: <https://doi.org/10.3897/zookeys.741.21971.suppl1>





# VIRMISCO – The Virtual Microscope Slide Collection

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Academic editor: *P. Stoev* | Received 15 November 2017 | Accepted 8 February 2018 | Published 7 March 2018

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<http://zoobank.org/C83B0146-1BDA-496B-ABCF-AAC7C3465E4F>

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**Citation:** Decker P, Christian A, Xylander WER (2018) VIRMISCO – The Virtual Microscope Slide Collection. In: Stoev P, Edgecombe GD (Eds) *Proceedings of the 17th International Congress of Myriapodology*, Krabi, Thailand. ZooKeys 741: 271–282. <https://doi.org/10.3897/zookeys.741.22284>

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## Abstract

Digitisation allows scientists rapid access to research objects. For transparent to semi-transparent three-dimensional microscopic objects, such as microinvertebrates or small body parts of organisms, available databases are scarce. Most mounting media used for permanent microscope slides deteriorate after some years or decades, eventually leading to total damage and loss of the object. However, restoration is labour-intensive, and often the composition of the mounting media is not known. A digital preservation of important material, especially types, is important and an urgent need. The Virtual Microscope Slide Collection – VIRMISCO project has developed recommendations for taking microscopic image stacks of three-dimensional objects, depositing and presenting such series of digital image files or z-stacks as an online platform. The core of VIRMISCO is an online viewer, which enables the user to virtually focus through an object online as if using a real microscope. Additionally, VIRMISCO offers features such as search, rotating, zooming, measuring, changing brightness or contrast, taking snapshots, leaving feedback as well as downloading complete z-stacks as jpeg files or video file. The open source system can be installed by any institution and can be linked to common database or images can be sent to the Senckenberg Museum of Natural History Görlitz. The benefits of VIRMISCO are the preservation of important or fragile material, to avoid loan, to act as a digital archive for image files and to allow determination by experts from the distance, as well as providing reference libraries for taxonomic research or education and providing image series as online supplementary material for publications or digital vouchers of specimens of molecular investigations are relevant applications for VIRMISCO.

## Keywords

Database, digitisation, morphology, museum collection, soil invertebrates, type material, visualisation

## Introduction

Recent advantages in digitisation facilitate use, processing, duplication, distribution, archiving, and playback on common media devices, and improved applications for inquiries and comparison. Furthermore, digital copies protect the originals or serve as documentation in case of loss or damage. There are many strategic initiatives to digitise collection material from natural history museums, such as ultra-high resolution images of e.g., insect boxes, labels or three-dimensional scans (e.g., skulls, taxidermy mounts) (Mantle et al. 2012, Blagoderov et al. 2012, Holovachov et al. 2014, Copes et al. 2016, Short et al. 2018). While projects on virtual microscopy in biology or micropalaeontology are rare, in medical applications virtual microscopy and virtual (histological) slide collections are well known and acknowledged as beneficial e.g., for documentation, teaching, diagnoses, and research (Kumar et al. 2004, Gu and Ogilvie 2005, Helin et al. 2005, Krippendorf and Lough 2005, Goldberg and Dintzis 2007, Mikula et al. 2007, Dee 2009, Weinstein et al. 2009). However, these are mostly restricted to two-dimensional histological slices or cell biology, are not open source, are not accessible publicly online, restricted to a specific manufacturer or do not comply with the needs of a soil zoological collection.

Permanent microslides in collections often lose their quality due to ageing and physico-chemical alterations of the mounting media. Whereas some mounting media like Canada balsam, Euparal and glycerol-paraffin sealed with Glyceel show proper quality even after 50 to more than 150 years, others darken or deteriorate by dehydration, contraction, oxidation, or crystallisation of the media (Brown 1997, Brown and De Boise 2006, Allington and Sherlock 2007, Neuhaus et al. 2017). Additionally, the former collection owners may have used several different mounting media or the composition was changed by the producers or manufacturers in the course of time. Thus, the mounting media are not known for all slides. Cleaning, re-mounting and restoration is very labour-intensive or even impossible for some mounting media. Furthermore, the object may be damaged during the re-mounting process (Upton 1993, Brown and De Boise 2006, Neuhaus et al. 2017). In practice, objects are already irretrievably damaged or partly destroyed when alterations are noticed by the curator. Several microscope slide collections have already been lost or will be lost within the next decades (Upton 1993, Jersabek et al. 2010, Lillo et al. 2010, Neuhaus et al. 2017).

Unfortunately, most institutions and collections do not have staff with experience on microscope slide restoration and no financial resources for this time-consuming task. Often the general storage and conservation conditions of the collection (e.g., temperature, humidity, light exposure, volatiles) require replacement or new investments (e.g., cabinets).

To rescue at least the relevant information of the valuable collection specimens an equivalent digital documentation, especially of type material, is crucial. However, digital images can never replace the original specimen and restoration of a microscope slide collection should be the first goal of a curator or institution.

In this publication we introduce the open source system “the Virtual Microscope Slide Collection – VIRMISCO” to present digital microscope images of different focal planes. General recommendations for digitisation of three-dimensional collection objects on permanent microscope slides of soil fauna and other small organisms are also provided.

## Objectives

The **Virtual Microscope Slide Collection** – VIRMISCO project at the Senckenberg Museum of Natural History Görlitz aims to develop recommendations for methods and procedures for digitisation of three-dimensional microscope objects and to make their information accessible online for free public use (open access database). Such an (almost) complete documentation with digital images of microscopic objects guarantees the permanent conservation at least of the relevant taxonomic information of most of the objects. Within VIRMISCO recommendations for light microscopic documentation of slide mounts were developed and a wide range of microscopic methods (e.g., phase contrast, differential interference contrast, confocal microscopy, digital microscopy) were tested in order to receive optimal results. Digital image files are made available by an online database via an open access internet platform. Metadata of specimens, collections, localities, sampling and the production of image sets are provided to optimise search and retrieval of the data in the internet.

Specimens, types or voucher for which molecular data are available, e.g., via Barcode of Life Data Systems (BOLD) or/and GenBank, documented with digital images may be deposited on the VIRMISCO platform. Such correlation of morphological and genetic information fulfils the demands of integrative taxonomy. Within the last three years, specimens or permanent microscope slides (including type material from more than 400 species) of various taxa of soil fauna (Acari, Collembola, Protura, Myriapoda, Plathelminthes, Tardigrada, Nematoda) from the collections of the Senckenberg Museum of Natural History Görlitz (SMNG) have been digitised (Table 1).

**Table 1.** Number of digitised specimens, taxa and types available online in VIRMISCO (1 February 2018).

	Taxa	Specimens	Types
Gamasina	87	215	198
Uropodina	34	116	116
Oribatida	5	15	1
Collembola	23	58	21
Tardigrada	2	2	0
Protura	3	4	0
Diptera	1	1	0
Myriapoda	21	100	18
Nematoda	1	2	0
Plathelminthes	5	11	0

The open source internet platform comprises a viewer and the digitised material may be employed for a wide range of applications: (1) Digital preservation of important or fragile material, especially of type material, to avoid loss or damage e.g., during loan; (2) archival of digital image files from collections or project data to verify taxonomic information; (3) determination from the digital images by experts; (4) creation of a reference library for taxonomic research or education; (5) provision of image series of type specimens (digitypes) or supplementary information for publication (e.g., series of specimens); (6) provision of image series of voucher specimens (or type material) for which molecular data is available.

The VIRMISCO system offers features such as interface to link it to other databases, search functions, rotating, zooming, measuring (two- or three-dimensional), changing brightness or contrast, taking snapshots, leaving feedback, downloading complete z-stacks as jpeg files or video file as well as a wide range of metadata fields on the collection object and the technical data (e.g., used camera, microscope, settings).

## **Implementation**

The open source system VIRMISCO can be set up individually by any institution on a server. It can be linked to or integrated in an already existing system of databases or data warehouses using the featured interfaces. Other modifications, adaptations or upgrading according to the individual needs are possible.

## **Search engine**

A search engine provides a full-text search. Advanced searches are also possible, e.g., hierarchical availability for locality (country, province, region, place), filtering of a taxon with hierarchical order (higher taxon, genus, species) and date or period of sampling.

Image stacks that meet the criteria specified by the query are grouped by objects (Fig. 2). General information about the selected object is displayed. An (animated) preview of the image stack video is visible and (if available) an overview image with a marking of the digitised part of the object the image stack refers to. The selected objects to be shown in the viewer can be sorted or removed.

## **Viewer**

The core of the viewer (Fig. 3) is the image display, where an image or image series are presented (OGG/Theora file). The display area can be moved by dragging. On a thumbnail, the current display area of the image display is indicated in the total image with a snap frame.

## Search for digital photomicrographs

### Full-text search

Enter keywords

Enter one or multiple words to gain results matching as many of them as possible.

### Advanced search

Country	<input type="text" value="Germany"/>	Quick-filter	<input type="text" value="gamasina"/>
Province	<input type="text" value="Saxony"/>	Filter the list "Higher taxon" below by entering some initial letters of any taxon monomial above the genus rank. This does not affect the actual search result when hitting the "Search" button.	
Region	<input type="text" value="(not specified)"/>	Higher taxon	<input type="text" value="Gamasina Laelapidae"/>
Place	<input type="text" value="(all)"/>	Genus	<input type="text" value="Hypoaspis"/>
Date on or after	<input type="text"/>	Species	<input type="text" value="(all)"/>
and before	<input type="text"/>	<input type="button" value="Search"/>	

**Figure 1.** Screenshot of the VIRMISCO “Search” page.

## virmisco | Select digital photomicrographs

### 1. Select a photomicrograph

Acetomommonemoralis\_f\_thorax\_III\_A15-89-3\_2017-07-11  
 Acrochordoposthia\_vandeputae\_cirrus\_451\_2017-05-04  
 Afrodacarellus\_unospiniae  
 Afrogamasellus\_unospiniae\_HT\_f\_chelicerae\_and\_tectum  
 Afrogamasellus\_unospiniae\_HT\_f\_gnathosoma\_90\_32297\_03  
 Afrogamasellus\_unospiniae\_HT\_f\_leg\_I\_II\_90\_32297\_03  
 Afrogamasellus\_unospiniae\_HT\_f\_leg\_I\_II\_90\_32297\_03  
 Afrogamasellus\_unospiniae\_HT\_f\_leg\_I\_tarsus\_90\_32297\_03  
 Afrogamasellus\_unospiniae\_HT\_f\_leg\_II\_tarsus\_90\_32297\_03  
 Afrogamasellus\_unospiniae\_HT\_f\_leg\_III\_90\_32297\_03  
 Afrogamasellus\_unospiniae\_HT\_f\_leg\_III\_tarsus\_90\_32297\_03  
 Afrogamasellus\_unospiniae\_HT\_f\_leg\_III\_tarsus\_90\_32297\_03  
 Afrogamasellus\_unospiniae\_HT\_f\_leg\_IV\_90\_32297\_03  
 Afrogamasellus\_unospiniae\_HT\_f\_leg\_IV\_tarsus\_90\_32297\_03  
 Afrogamasellus\_unospiniae\_HT\_f\_palps\_90\_32297\_03  
 Afrogamasellus\_unospiniae\_HT\_f\_slide\_label\_001\_2015-04-01  
 Afrogamasellus\_unospiniae\_HT\_f\_slide\_label\_002\_2015-04-01  
 Alloparsitus\_pratensis  
 Alloparsitus\_pratensis\_PT\_f\_chelicerae\_04\_46019\_20\_05  
 Alloparsitus\_pratensis\_PT\_f\_gnathosoma\_04\_46019\_20\_05  
 Alloparsitus\_pratensis\_PT\_f\_gnathosoma\_04\_46019\_20\_05

### 2. Drag the preview image down to the selection box

Afrogamasellus\_unospiniae\_HT\_f\_chelicerae\_and\_tectum\_90\_32297\_03.02.2016

Higher taxa: [Animalia](#) » [Arthropoda](#) » [Chelicerata](#) » [Arachnida](#) » [Acari](#) » [Anactinotrichida](#) » [Mesostigmata](#) » [Germansysina](#) » [Rhodacaridae](#) » [Rhodacaridae](#)

Original name: Afrogamasellus unospiniae Karg, 2003

Valid name: Afrodacarellus unospiniae (Karg, 2003)

Properties matching search criteria

Select

### 3. Reorder items or drag them to the trash bin

Afrogamasellus\_u  
 nospiniae\_HT\_f  
 gnathosoma\_90\_32  
 297\_03.02.2016

Afrogamasellus\_u  
 nospiniae\_HT\_f  
 gnathosoma\_90\_32  
 297\_03.02.2016

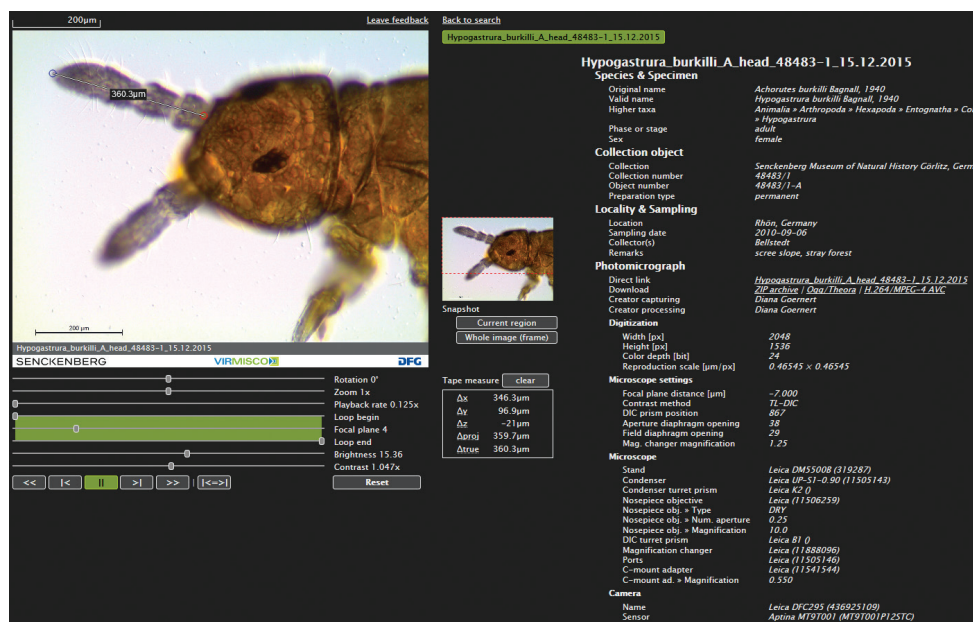
Afrogamasellus\_u  
 nospiniae\_HT\_f  
 gnathosoma\_90\_32  
 297\_03.02.2016

**Figure 2.** Screenshot of the VIRMISCO “Results” page.

**Functions:** Several functions and features are available to control and modify the image video file, e.g., rotation, zoom, playback rate, brightness and contrast (the latter two only when paused). The user can choose any focal plane or set the start and end of the playback loop. Common media control buttons are available, e.g., pause, play forward/backward, skip to start/end, and endless loop.

Body parts or regions, e.g., tarsus or chaeta, can be measured when the magnification scale of the image or series is available. By choosing any two points on





**Figure 3.** Screenshot of the VIRMISCO “Viewer”.

one or two different focal planes, the distances between the different axes (vertical = X, horizontal = Y, height = Z) and/or the distance ( $\Delta_{\text{true}}$ ) between two points is indicated in the viewer. Snapshots of the currently displayed modified or whole image (the video frame) can be saved in a new frame.

**Download images/videos:** Image stacks as ZIP archive (JPEG) or in two video formats (OGG/Theora or H.264/MPEG-4 AVC).

**Metadata:** Information and metadata on the digitised object, image, and the equipment used is provided, e.g., taxon, collection, locality, sampling, microscope slide, settings, microscope, and camera used.

**Feedback:** Visitors can leave a message or feedback with reference to an actually viewed image stack using a contact form.

## Editor

Input of data and image stacks is done via an input form. Authorised users can import their biological and technical metadata offline and upload them later. This may be done manually or by using the import function.

**Metadata fields:** More than 20 information fields are currently available for each object (e.g., species, specimen, collection object, locality, sampling) and more than 80 values for each photograph (digitisation, microscope settings, microscope, camera, exposure settings, and histogram adjustments). According to the needs fields can be added or renamed.

**Import:** Technical metadata from a microscopes slide object are imported on a local server via a web-based form or by uploading the LAS files generated by Leica microscopic camera systems (image stack and technical metadata).

Alternatively cooperation with the Senckenberg Museum of Natural History Görlitz can be considered to upload image stacks with the associated metadata of specimens to the Görlitz VIRMISCO system. The provider of the image files and data may choose a Creative Common (CC) license that condition the terms of use.

**Conversion of images routine:** TIFF-files are used as master file in VIRMISCO. The TIFF-files are automatically converted to JPEG and subsequently converted to final derivatives by an implemented conversion routine: ZIP archive with JPEG files, OGG/Theora and H.264/MPEG-4 AVC. In the JPEG files a footer with relevant information (e.g., direct link, species, collection number, institution logo) on the object is included. The conversion routine is scheduled for one time per day (midnight). Thus, derivatives are available one day later.

## **Inventory of digitised objects at SMNG**

VIRMISCO currently (1 February 2018) provides more than 4,700 image stacks of about 180 taxa and more than 350 types, basically from collection material of the Senckenberg Museum of Natural History Görlitz (Tab. 1).

## **Time required for digitisation**

Once familiar with the microscoping technique and the VIRMISCO user interface it takes approximately one hour to take a 15 z-stack series of one specimen of Acari and import it into VIRMISCO. However, time depends on investigated taxa and used microscope systems. Storage space of all files amounts currently 1.1 TB, including original TIFFS, derivatives (videos), and total views.

## **Recommendations for digitisation**

The authors experiences in digitizing SMNG collection material, the comparison of different light microscopy types and feedback from colleagues of various institutions and different fields of biology or physics add up to general recommendations to be considered when digitizing or planning digitisation projects of permanent microscope slide mount collections of three-dimensional objects, especially soil organisms.

The photographic and microscopic equipment used depends on the fitting, needs and budget of the institution and the specific imaging demanded for certain taxa or characters. Generally, good results can be achieved with bright-field microscopy. Differential interference contrast microscopy (DIC) shows very good results regarding

lateral contrast. To capture three-dimensionality of an object a series of images at different focal planes should be taken. If available a digital motor-focus or macro-rail should be used to define the focus distances between the single images. Auto-montage images or focus stacks bear the risk of incorrect software calculations sometimes producing erroneous final montage-images or artefacts when applied to transparent or semi-transparent objects or using DIC microscopy (Neuhaus et al. 2017).

Non-compressed image files, e.g., TIFF format, are recommended as a common master image file. For subsequent size comparison or measurements a scale bar with the used linear measure labelled should be embedded into each image. Metadata on the taxon, specimen, collection, inventory number, type status, sex, and other label information (locality, sampling) must be provided for each image series. Furthermore, information on the documented part (e.g., body region), if not using a total view only, and the view of the object (e.g., ventral, lateral) is indispensable. Technical information like the microscope, camera and microscope settings used are helpful for documentation and data re-usability. An overview image of the object and/or the complete microscope slide documents and correlates original label information and gives a quick impression of the condition of the object or microscope slide. The expertise of an experienced taxonomist for the group investigated is crucial to select the characters of taxonomic relevance for documentation for digitisation. A single total view is usually not useful to document and preserve the information of the taxonomic characters of an object or type specimen.

## Outlook

The Senckenberg Museum of Natural History will continue to digitise important material (especially type material of soil organisms) and import existing series or image files (e.g., whole slide photographs). Other institutions are invited for a wide range of cooperation, e.g., to modify or upgrade VIRMISCO or to present their images on the VIRMISCO system of the SMNG. Updated versions will be available online on GitHub.

## Project Information

**Project title:** Development of standards for the photographic documentation of permanent microscope slide mounts in precarious mounting media. The photographs are available on the internet platform “VIRMISCO – The Virtual Microscope Slide Collection”.

**Funding:** The project was funded by the DFG (XY 12/6-1) from May 2014 to December 2017.

**Personnel:** The project was conducted at the Senckenberg Museum of Natural History under the supervision of Willi Xylander and Axel Christian. Eberhard Wurst

(2014–2016) and Peter Decker (2016–2017) were involved as project managers. Diana Goernert (2014–2017) and Kerstin Franke (2014–present) provided technical assistance.

**Design and Software:** SednaSoft A. Schaffhirt and A. Wünsche GbR, Biesnitzer Straße 8, 02826 Görlitz, Germany and Senckenberg Museum of Natural History Görlitz.

**Email address:** [virmisco@senckenberg.de](mailto:virmisco@senckenberg.de)

**Suggested citation of VIRMISCO:** Christian, A., Decker, P., Wurst, E. and W.E.R. Xyländer: VIRMISCO – The Virtual Microscope Slide Collection. [www.virmisco.org](http://www.virmisco.org).

**Microscope equipment used at SMNG:** Leica DM5500B DIC microscope and Leica M165C stereomicroscope, both with Leica DFC295 camera.

**Integration to other databases:** All available digitised objects in the GBIF database on soil zoology, “Edaphobase” (<http://www.edaphobase.org>, see Burkhardt et al. 2014) are linked to the respective images series in the SMNG VIRMISCO.

## Manual

A manual for the VIRMISCO Search, Results, and Viewer pages is available online <http://cms.virmisco.org/index.php/manual.html>

## Web location (URIs)

**Homepage:** [http:// www.virmisco.org](http://www.virmisco.org)

**Project description SMNG:** [http://www.senckenberg.de/root/index.php?page\\_id=18729](http://www.senckenberg.de/root/index.php?page_id=18729)

**Project description DFG:** <http://gepris.dfg.de/gepris/projekt/248331536?language=en>

## Repository

**Repository Type:** GitHub.

**Browse URI:** <https://github.com/virmisco/virmisco>

Source code: CC0 1.0 Universal (CC0 1.0) Public Domain Dedication.

## Terminal equipment

**Display:** All control elements are accessible and all represented information is visible from 1,000 pixel width and 660 pixel height.

**Browser:** VIRMISCO can be used with almost every common computer browser, but had been optimised for Mozilla Firefox (v. 44/45.2), Microsoft Internet Explorer (v. 8), and Microsoft Edge (v. 38).

**System Requirements:** Fast internet connection and a mass storage are required.

**Programming languages:** JavaScript, HTML, PHP, shell script, SQL.

**Utility software:** Apache HTTP Server, Redis, MariaDB.

**External frameworks:** Behat (v. 2.5.5), Behat MinkExtension (v. 1.3.3), Behat MinkGoutteDriver (v. 1.1.0), Fabpot Goutte (v. 1.\*), PHP Markdown (v. 1.6.0), Predis (v. 1.0.1). Composer file for automatically installing frameworks available in the GitHub repository <https://github.com/virmisco/virmisco>.

## Application programming interface

The data collected in the database are accessible as XML documents at any time. For this purpose, an HTTP-based data provider is used as the OAI-PMH, which uses METS as a container format. DarwinCore (including expedient extensions) is also to be used as a metadata format.

## Acknowledgements

Sincere thanks to Diana Goernert and Kerstin Franke for their valuable technical assistance. For the help in providing material and giving instructions about photographed characters we would like to thank Birgit Balkenhol, Ulrich Burkhardt, Karin Hohberg, Astrid König, Ricarda Lehmitz, Hans-Jürgen Schulz, Meike Schuppenhauer, Karin Voigtländer, Raphael Weniger, and Cornelia Wiesner. Christian Düker, Sebastian Rick, and Stephan Lesch gave useful suggestions on the draft manuscript. Birger Neuhäus, Robert Mesibov, and Sarah Faulwetter gave many comments that improved the quality of the work presented here.

This project was funded by the German Science Foundation (DFG XY 12/6-1).

## References

- Allington L, Sherlock E (2007) Choosing a microscope slide sealant: a review of cleaning characteristics and the development of a new test, using low oxygen environments. *Natural Sciences Collections Association News* 12: 4–14.
- Blagoderov V, Kitching I, Livermore L, Simonsen T, Smith V (2012) No specimen left behind: industrial scale digitization of natural history collections. *ZooKeys* 209: 133–146. <https://doi.org/10.3897/zookeys.209.3178>
- Brown PA (1997) A review of techniques used in the preparation, curation and conservation of microscope slides at the Natural History Museum, London. *The Biology Curator* 10(Supplement): 1–33.
- Brown PA, De Boise E (2006) Procedures for the preparation of whole insects as permanent microscope slides and for the remounting of deteriorating aphid slides. *Natural Sciences Collections Association* 8: 15–19.



- Burkhardt U, Russell DJ, Decker P, Döhler M, Höfer H, Römbke J, Trog C, Vorwald J, Wurst E, Xylander WER (2014) The Edaphobase project of GBIF-Germany – A new online soil-organism zoological data warehouse. *Applied Soil Ecology* 83: 3–12. <https://doi.org/10.1016/j.apsoil.2014.03.021>
- Copes LE, Lucas LM, Thostenson JO, Hoekstra HE, Boyer DM (2016) A collection of non-human primate computed tomography scans housed in MorphoSource, a repository for 3D data. *Scientific Data* 3: 160001. <https://doi.org/10.1038/sdata.2016.1>
- Dee FR (2009) Virtual microscopy in pathology education. *Human Pathology* 40 (8): 1112–1121. <https://doi.org/10.1016/j.humpath.2009.04.010>
- Goldberg HR, Dintzis R (2007) The positive impact of team-based virtual microscopy on student learning in physiology and histology. *Advances in Physiology Education* 31 (3): 261–265. <https://doi.org/10.1152/advan.00125.2006>
- Gu J, Ogilvie RW (2005) Virtual microscopy and virtual slides in teaching, diagnosis, and research. Taylor and Francis, Boca Raton, 356 pp. <https://doi.org/10.1201/9781420039306>
- Holovachov O, Zatushevsky A, Shydlovsky I (2014) Whole-Drawer Imaging of entomological collections: benefits, limitations and alternative applications. *Journal of Conservation and Museum Studies* 12 (1): 1–13. <https://doi.org/10.5334/jcms.1021218>
- Helin H, Lundin M, Martikainen P, Tammela T, Helin H, Kwast T van der (2005) Web-based virtual microscopy in teaching and standardizing Gleason grading. *Human Pathology* 36 (4): 381–386. <https://doi.org/10.1016/j.humpath.2005.01.020>
- Jersabek CD, Bolortsetseg E, Taylor HL (2010) Mongolian rotifers on microscope slides: Instructions to permanent specimen mounts from expedition material. *Mongolian Journal of Biological Sciences* 8: 51–57. <https://doi.org/10.22353/mjbs.2010.08.06>
- Krippendorf BB, Lough J (2005) Complete and rapid switch from light microscopy to virtual microscopy for teaching medical histology. *The Anatomical Record* 285B (1): 19–25. <https://doi.org/10.1002/ar.b.20066>
- Kumar RK, Velan GM, Korell SO, Kandara M, Dee FR, Wakefield D (2004) Virtual microscopy for learning and assessment in pathology. *The Journal of Pathology* 204: 613–618. <https://doi.org/10.1002/path.1658>
- Lillo E de, Craemer C, Amrine JW, Nuzzaci G (2010) Recommended procedures and techniques for morphological studies of Eriophyoidea (Acari: Prostigmata). *Experimental and Applied Acarology* 51: 283–307. <https://doi.org/10.1007/s10493-009-9311-x>
- Mantle BL, Salle JL, Fisher N (2012) Whole-drawer imaging for digital management and curation of a large entomological collection. *ZooKeys* 209: 147–163. <https://doi.org/10.3897/zookeys.209.3169>
- Mikula S, Trotts I, Stone JM, Jones EG (2007) Internet-enabled high-resolution brain mapping and virtual microscopy. *NeuroImage* 35 (1): 9–15. <https://doi.org/10.1016/j.neuroimage.2006.11.053>
- Neuhaus B, Schmid T, Riedel J (2017) Collection management and study of microscope slides: Storage, profiling, deterioration, restoration procedures, and general recommendations. *Zootaxa* 4322 (1): 1–173. <https://doi.org/10.11646/zootaxa.4322.1.1>
- Short AEZ, Dikow T, Moreau CS (2018) Entomological Collections in the Age of Big Data. *Annual Review of Entomology* 63: 513–530. <https://doi.org/10.1146/annurev-ento-031616-035536>

- Upton MS (1993) Aqueous gum-chloral slide mounting media: an historical review. *Bulletin of Entomological Research* 83: 267–274. <https://doi.org/10.1017/S0007485300034763>
- Weinstein RS, Graham AR, Richter LC, Barker GP, Krupinski EA, Lopez AM, Erps KA, Bhattacharyya AK, Yagi Y, Gilbertson JR (2009) Overview of telepathology, virtual microscopy, and whole slide imaging: prospects for the future. *Human Pathology* 40 (8): 1057–1069. <https://doi.org/10.1016/j.humpath.2009.04.006>