

Cave millipede diversity with the description of six new species from Guangxi, China

Weixin Liu¹, J. Judson Wynne²

1 Department of Entomology, College of Agriculture, South China Agricultural University, 483 Wushanlu, Guangzhou 510642, China **2** Department of Biological Sciences, Merriam-Powell Center for Environmental Research, Northern Arizona University, Box 5640, Flagstaff, AZ 86011, USA

Corresponding author: J. Judson Wynne (jut.wynne@nau.edu); Weixin Liu (da2000wei@163.com)

Academic editor: O. Moldovan | Received 19 April 2019 | Accepted 3 June 2019 | Published 02 July 2019

<http://zoobank.org/19205CA6-4680-45D4-A3A0-F1640752D41B>

Citation: Liu WX, Wynne JJ (2019) Cave millipede diversity with the description of six new species from Guangxi, China. *Subterranean Biology* 30: 57–94. <https://doi.org/10.3897/subtbiol.30.35559>

Abstract

We synthesized the current knowledge of cave-dwelling millipede diversity from Guangxi Zhuang Autonomous Region (Guangxi), South China Karst, China and described six new millipede species from four caves from the Guilin area, northeastern Guangxi. Fifty-two cave-dwelling millipedes are known for the region consisting of 38 troglobionts and 14 troglaphiles. Of the troglobionts, 24 are presently considered single-cave endemics. New species described here include *Hyleoglomeris rukouqu* **sp. nov.** and *Hyleoglomeris xuxiakei* **sp. nov.** (Family Glomeridae), *Hylomus yuani* **sp. nov.** (Family Paradoxosomatidae), *Eutrichodesmus jianjia* **sp. nov.** (Family Haplodesmidae), *Trichopeltis liangfengdong* **sp. nov.** (Family Cryptodesmidae), and *Glyphiulus maocun* **sp. nov.** (Family Cambalopsidae). Our work also resulted in range expansions of *Pacidesmus trifidus* Golovatch & Geoffroy, 2014, *Blingulus sinicus* Zhang & Li, 1981 and *Glyphiulus melanoporus* Mauriès & Nguyen Duy-Jacquemin, 1997. As with many hypogean animals in Southeast Asia, intensive human activities threaten the persistence of both cave habitats and species. We provide both assessments on the newly described species' distributions and recommendations for future research and conservation efforts.

Keywords

Single cave endemic, disturbance relict, cave conservation

Introduction

Southeast Asia is considered the most biologically diverse for troglomorphic animals among the well-sampled tropical regions of the globe (Clements et al. 2006). Yet despite research conducted over the past three decades, few areas in Southeast Asia have been sufficiently investigated and knowledge of cave biological diversity and ecological processes is limited (Deharveng and Bedos 2000). The expansive South China Karst represents one of these regions (Clarke 2006, Chen et al. 2001). Among the four administrative units in China where this formation occurs, Guangxi is considered the most taxonomically well-studied region. At least 100 troglomorphic (subterranean-adapted) arthropods have been identified from Guangxi (Wynne, unpublished data). Most have been identified as short-range endemic species (Tian 2011, Deharveng et al. 2008) with more than half (or 58 species) considered single cave endemics (Gao et al. 2018).

Common in cave-arthropod communities, millipedes represent a dominant and widespread group in southern China (Golovatch 2015, Liu et al. 2017a). Approximately 150 cave-dwelling millipedes have been described from China (Golovatch 2015, Liu unpublished data) with 52 species known from Guangxi. Of these, 38 species are troglobionts with 24 identified as single-cave endemics (Table 1). Fig. 1 summarizes millipede diversity by family with Cambalopsidae (14 species), Glomeridae (11) and Paradoxosomatidae (10) being among the most speciose groups.

In the paper, we describe six new species (representing five families, Glomeridae, Paradoxosomatidae, Haplodesmidae, Cryptodesmidae and Cambalopsidae), as well as discuss range expansions of three additional cave-dwelling species. We have also summarized the cave-dwelling millipedes known to Guangxi, their known distributions, and provide recommendations to guide future research and management efforts.

Material and methods

Study area

Located in southwest China, Guangxi encompasses 236,700 km². Once an ancient shallow sea during the middle Cambrian to Late Triassic periods, this region is now largely characterized by a massive karst (limestone) stratum over 10,000 m thick (Cao et al. 2007) with steep-sided mountains called *fenglin* or “tower karst” protruding skyward. As a result of the subtropical climate and rock stratum, Guangxi supports at least 564 known caves (Yuanhai Zhang, pers. comm. 2019).

We sampled four caves in the northeastern most extent of Guangxi within a 30 km radius of the city of Guilin, China (Fig. 2). Caves were selected based upon two criteria – sufficient length to support deep zone conditions, and the availability of a current cave map. Cave deep zones are defined as completely dark region with relatively stable temperature, low to no airflow, and a near water saturated atmosphere with a

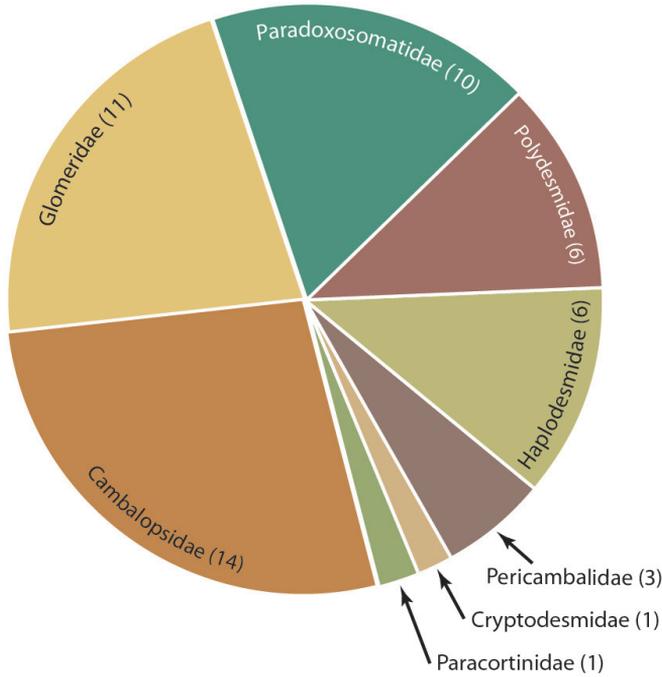


Figure 1. Species richness (total number of species provided in parentheses) for the eight known families of subterranean-dwelling millipedes from Guangxi, China.

negligible evaporation rate (Howarth 1980, 1982). While we recognize other factors may contribute to the occurrence of cave deep zones (e.g., mazy and/or constricted passageways, small or partially rock-fall obstructed entrances, and cave structure in general), we used this criterion because logistics prevented us from selecting study sites based upon site visit evaluations. This work represents the first effort to sample these caves for subterranean-adapted arthropods.

All caves occurred at low elevations within tower karst formations. While extensive agriculture, as well as rural village and suburban habitation characterized the surrounding lowlands, vegetation on the tower karst represented a marginally disturbed combination of native and introduced plant and tree species.

Literature review and synthesis

Based on our knowledge of the South China Karst (SCK) cave-dwelling millipede literature, we summarized the total number of caves sampled and cave-dwelling millipedes detected for Guangxi. For selected species occurring within two or more caves, we determined maximum distances between caves and, in some cases, average distances across all caves using ArcGIS 10.6.1.

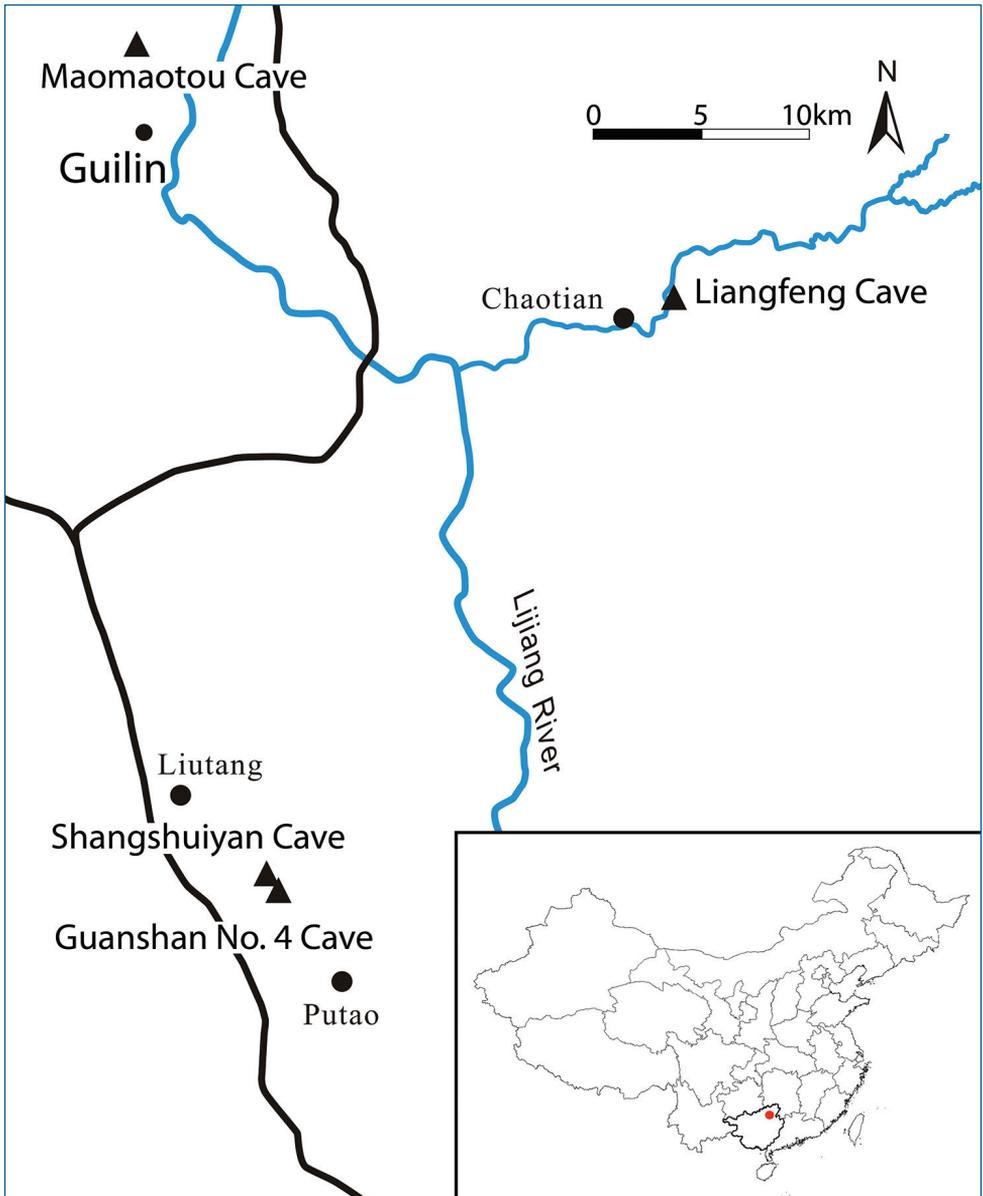


Figure 2. Study area with general locations of the four study caves (black triangles). Locator map depicts the Guilin area (red dot), Guangxi (bold black outline), China.

Field sampling

We hand collected cave-dwelling arthropods at four caves from 15 to 18 November 2016. Approximately eight hours (2 observers at 4 hours per observer) was spent conducting direct intuitive searches within estimated deep zones of each cave. We examined bat guano, dead insects, mud banks and floors, flood detritus, or vegetation

brought in by humans and deposited within the cave. Given the four caves varied in size and the diversity of arthropods encountered, the areal extent sampled varied. We also sampled the vegetation within the entrance of Liangfeng Cave applying a direct intuitive search approach. For all four caves, we also opportunistically collected arthropods as encountered while transiting from entrance to estimated deep zones. Sampling methods were applied *sensu stricto* Wynne et al. (2019).

Analysis and preparation

All specimens examined in this study were collected by the second author in the Guilin area, Guangxi, southern China and preserved in 95% ethanol. Holotypes and paratypes are deposited in the Zoological Collection of the South China Agricultural University, Guangzhou, Guangdong Province, China (SCAU). Detailed examination of characters and dissections were performed using a Leica S8 APO stereo microscope. Line drawings were prepared with a ZEISS Axioskop40 microscope with a camera lucida attached. Photographs were taken using a Keyence VHX-5000 digital microscope, and further edited using Adobe Photoshop CS5.

Cave locations

We recognize standard practice for new species description is to provide sample locality information including geographical data to facilitate future collecting, interpretation and research. Because caves often represent sensitive resources, we provided general geographical information and offset the latitude and longitude coordinates by ~1 km. This level of detail is sufficient for future comparative studies, while protecting the precise location of our study caves.

Terminology

Cave ecosystems typically consist of four zonal environments (Howarth 1980, 1983): (1) *entrance zone* – combination of surface and cave environmental conditions; (2) *twilight zone* – both diminished light conditions and influence of surface environment; (3) *transition zone* – aphotic, yet barometric and diurnal shifts are observed at a significantly diminished rate approaching near stable climatic conditions; and, (4) *deep zone* – complete darkness, high environmental stability, constant temperature, and near water-saturated atmosphere with low to no airflow (typically occurs in the deepest portion of the cave). While there are four primary cave specific functional groups generally recognized, the specimens discussed are *troglophilic* (subterranean-adapted) organisms known as *troglobionts* (Sket 2008). These animals are obligate cave dwellers that require the stable environmental conditions of the deep zone to complete their life cycle and exhibit morphological characteristics indicative of cave adaptation. We also

Table 1. Fifty-two known cave-dwelling millipede species from Guangxi, South China Karst, China. ‘Order: Family: Species’, ‘Functional Group’ (TB=presumed troglobiont, TP=troglophile), number of caves (# Caves) to suggest a level of potential endemism), and main Reference(s) are provided. As troglophiles are expected to have regional distributions, the number of caves where TPs were detected is not included.

Order: Family: Species	Functional group	# Caves	Reference(s)
Glomerida: Glomeridae			
<i>Hyleoglomeris baxian</i> Liu & Tian, 2015	TB	1	Liu and Tian 2015a
<i>Hyleoglomeris curtisulcata</i> Golovatch, Liu & Geoffroy, 2012	TB	1	Golovatch et al. 2012a
<i>Hyleoglomeris grandis</i> Liu & Tian, 2015	TB	1	Liu and Tian 2015a
<i>Hyleoglomeris heshang</i> Golovatch, Liu & Geoffroy, 2012	TB	1	Golovatch et al. 2012a
<i>Hyleoglomeris kunnan</i> Golovatch, Liu & Geoffroy, 2012	TB	1	Golovatch et al. 2012a
<i>Hyleoglomeris lii</i> Golovatch, Liu & Geoffroy, 2012	TP	–	Golovatch et al. 2012a
<i>Hyleoglomeris mashanorum</i> Golovatch, Liu & Geoffroy, 2012	TB	1	Golovatch et al. 2012a
<i>Hyleoglomeris mulunensis</i> Golovatch, Liu & Geoffroy, 2012	TB	1	Golovatch et al. 2012a
<i>Hyleoglomeris rukouqu</i> sp. nov.	TP	–	This study
<i>Hyleoglomeris xueju</i> Golovatch, Liu & Geoffroy, 2012	TB	1	Golovatch et al. 2012a
<i>Hyleoglomeris xuxiakei</i> sp. nov.	TB	1	This study
Polydesmida: Cryptodesmidae			
<i>Trichopeltis liangfengdong</i> sp. nov.	TB	1	This study
Haplodesmidae			
<i>Eutrichodesmus distinctus</i> Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009	TB	1	Golovatch et al. 2009a
<i>Eutrichodesmus jianjia</i> sp. nov.	TB	1	This study
<i>Eutrichodesmus latus</i> Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009	TB	4	Golovatch et al. 2009b
<i>Eutrichodesmus lipsae</i> Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2015	TB	1	Golovatch et al. 2015
<i>Eutrichodesmus planatus</i> Liu & Tian, 2013	TB	1	Liu and Tian 2013
<i>Eutrichodesmus similis</i> Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009	TB	2	Golovatch et al. 2009b
Paradoxosomatidae			
<i>Piccola golovatchi</i> Liu & Tian, 2015	TB	1	Liu and Tian 2015b
<i>Hylomus longispinus</i> (Loksa, 1960)	TB	1	Loksa 1960, Golovatch et al. 2010a, Srisonchai et al. 2018
<i>Hylomus lui</i> (Golovatch, Li, Liu & Geoffroy, 2012)	TB	1	Golovatch et al. 2012b, Srisonchai et al. 2018
<i>Hylomus nodulosus</i> (Liu, Golovatch & Tian, 2014)	TP	–	Liu et al. 2014, Srisonchai et al. 2018
<i>Hylomus phasmoides</i> (Liu, Golovatch & Tian, 2016)	TB	1	Liu et al. 2016, Srisonchai et al. 2018
<i>Hylomus scolopendroides</i> Golovatch, Geoffroy & Mauriès, 2010	TB	4	Golovatch et al. 2010a, Liu et al. 2014, Srisonchai et al. 2018
<i>Hylomus scutigeroideus</i> Golovatch, Geoffroy & Mauriès, 2010	TB	6	Golovatch et al. 2010a, Liu et al. 2014, Srisonchai et al. 2018
<i>Hylomus spinissimus</i> (Golovatch, Li, Liu & Geoffroy, 2012)	TB	1	Golovatch et al. 2012b, Srisonchai et al. 2018
<i>Hylomus variabilis</i> (Liu, Golovatch & Tian, 2016)	TP	–	Liu et al. 2016, Srisonchai et al. 2018
<i>Hylomus yuani</i> sp. nov.	TB	1	This study
Polydesmidae			
<i>Epanerchodus orientalis</i> Attems, 1901	TP	–	Golovatch et al. 2012c
<i>Pacidesmus armatus</i> Golovatch, Geoffroy & Mauriès, 2010	TB	3	Golovatch et al. 2010b
<i>Pacidesmus bedosae</i> Golovatch, Geoffroy & Mauriès, 2010	TB	3	Golovatch et al. 2010b
<i>Pacidesmus bifidus</i> Golovatch & Geoffroy, 2014	TB	1	Golovatch and Geoffroy 2014
<i>Pacidesmus tiani</i> Golovatch, Geoffroy & Mauriès, 2010	TB	2	Golovatch et al. 2010b
<i>Pacidesmus trifidus</i> Golovatch & Geoffroy, 2014	TB	4	Golovatch and Geoffroy 2014, This study

Order: Family: Species	Functional group	# Caves	Reference(s)
Callipodida: Paracortinidae			
<i>Paracortina yinae</i> Liu & Tian, 2015	TP	–	Liu and Tian 2015c
Spirostreptida: Pericambalidae			
<i>Bilingulus sinicus</i> Zhang & Li, 1981	TP	–	Zhang and Li 1981, This study
<i>Parabilingulus aramulus</i> Zhang & Li, 1981	TP	–	Zhang and Li 1981
<i>Parabilingulus simplicius</i> Mauriès & Nguyen Duy-Jacquemin, 1997	TP	–	Mauriès and Nguyen Duy-Jacquemin 1997
Cambalopsidae			
<i>Hypocambala polytricha</i> Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011	TB	1	Golovatch et al. 2011a
<i>Glyphiulus acutus</i> Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011	TB?	2	Golovatch et al. 2011b
<i>Glyphiulus calceus</i> Jiang, Guo, Chen & Xie, 2018	TP	–	Jiang et al. 2018
<i>Glyphiulus difficilis</i> Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011	TB	2	Golovatch et al. 2011b
<i>Glyphiulus echinoides</i> Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011	TP	–	Golovatch et al. 2011c
<i>Glyphiulus foetidus</i> Jiang, Guo, Chen & Xie, 2018	TP	–	Jiang et al. 2018
<i>Glyphiulus impletus</i> Jiang, Guo, Chen & Xie, 2018	TP	–	Jiang et al. 2018
<i>Glyphiulus maocun</i> sp. nov.	TB	1	This study
<i>Glyphiulus melanoporus</i> Mauriès & Nguyen Duy-Jacquemin, 1997	TP	–	Mauriès and Nguyen Duy-Jacquemin 1997, This study
<i>Glyphiulus mulunensis</i> Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011	TB	2	Golovatch et al. 2011b
<i>Glyphiulus paramulunensis</i> Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011	TB	2	Golovatch et al. 2011b
<i>Glyphiulus proximus</i> Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011	TB	2	Golovatch et al. 2011b
<i>Glyphiulus speobius</i> Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011	TB	2	Golovatch et al. 2011b
<i>Glyphiulus tiani</i> Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011	TB	1	Golovatch et al. 2011b

reference *troglophiles* (or *troglophilous* organisms) – non-troglobiontic animals that occur facultatively within caves and complete their life cycles there, but also exist in similar cave-like habitats on the surface (Barr 1967, Howarth 1983, Sket 2008). Terms used for taxonomic descriptions follow Minelli (2015).

Results

Since ~1960, at least 49 caves have been sampled for cave-dwelling millipedes. Of these, nearly half (24 caves) supported single-cave endemic troglobionts, nine caves supported at least two troglobitic millipede species, and three caves (present study; Table 2) contained three troglobionts. For species occurring in two or more caves, maximum distance between caves ranged from 11.22 km for *Glyphiulus speobius* to 137.27 km for *Hylomus scutigeroideus* (Table 3).

A total of nine cave-dwelling millipede species were collected from four caves near Guilin (Table 2). Four millipede species were detected in Liangfeng Cave, the other three caves contained three species each. Of the six undescribed species, four are troglo-

Table 2. Nine cave-dwelling millipedes including both troglotic and potentially relict species from four caves near Guilin, Guangxi, South China Karst, China.

Species	Maomaotou cave	Guanshan No. 4 cave	Shangshuiyan cave	Liangfeng cave
<i>Hyleoglomeris rukouqu</i> sp. nov.	–	–	×	–
<i>Hyleoglomeris xuxiakei</i> sp. nov.	–	×	–	–
<i>Hylomus yuani</i> sp. nov.	–	–	–	×
<i>Eutrichodesmus jianjia</i> sp. nov.	–	×	–	–
<i>Trichopeltis liangfengdong</i> sp. nov.	–	–	–	×
<i>Pacidesmus trifidus</i>	×	×	×	–
<i>Blingulus sinicus</i>	×	–	×	×
<i>Glyphiulus melanoporus</i>	×	–	–	–
<i>Glyphiulus maocun</i> sp. nov.	–	–	–	×

Table 3. Fourteen troglomorphic millipede species detected in more than one cave, Guangxi, South China Karst, China. ‘Order: Family: Species’, number of caves (# Caves) to suggest a level of potential endemism), and maximum distance between caves in kilometers (Max Dist.) are provided. *Indicates coordinate data for all caves was unavailable for that species. ‘?’ denotes maximum distance was indeterminate due to lack of cave coordinate data. ‘Landscape features’ potentially affecting distribution of caves separated by more than 10 km.

Order: Family: Species	# Caves	Max dist. (km)	Landscape features
Polydesmida: Haplodesmidae			
* <i>Eutrichodesmus latus</i>	4	14.32	Maximum distance between two caves provided, the third cave occurs in between the two.
* <i>Eutrichodesmus similis</i>	2	?	
Paradoxosomatida			
<i>Hylomus scolopendroides</i>	4	81.27	Three caves clustered within 21.24 km; one cave separated by Diaojiang, Hongshui and Jincheng Rivers and lowland areas
<i>Hylomus scutigeroideus</i>	6	137.6	One cave separated from others by Hongshui River; others may occur in same formation
Polydesmidae			
* <i>Pacidesmus armatus</i>	3	12.4	Two of three caves separated by lowland areas
* <i>Pacidesmus bedosae</i>	3	2.67	
<i>Pacidesmus tiani</i>	2	1.88	
<i>Pacidesmus trifidus</i>	4	59.7	Separated by lowland areas
Spirostreptida: Cambalopsidae			
<i>Glyphiulus acutus</i>	2	8.85	
<i>Glyphiulus difficilis</i>	2	9.32	
<i>Glyphiulus mulunensis</i>	2	7.77	
<i>Glyphiulus paramulunensis</i>	2	6.67	
<i>Glyphiulus proximus</i>	2	2.67	
<i>Glyphiulus speobius</i>	2	11.22	Separated by lowland areas

morphic and may represent single cave and/or short-range endemics. One undescribed epigeal species, *Hyleoglomeris rukouqu* sp. nov., was identified within cave entrance vegetation, and may represent a ‘disturbance relict’ species (*sensu stricto* Wynne et al. 2014). *Glyphiulus maocun* sp. nov., a troglophile, was detected in one cave, but likely has a more regional distribution. For known troglophiles, *Blingulus sinicus* Zhang & Li, 1981 were more widely distributed occurring in three caves each, while *Glyphiulus melanoporus* Mauriès & Nguyen Duy-Jacquemin, 1997 was detected in one cave.

Class Diplopoda**Order Glomerida Leach, 1814****Family Glomeridae Leach, 1815****Genus *Hyleoglomeris* Verhoeff, 1910**

Type species. *Hyleoglomeris multilineata* Verhoeff, 1910.

Remarks. The genus can be characterized by the telopods, which with frontomesal trichosteles on the prefemur and femur, and the caudomesal femoral process forming a distinct angle to femur proper (Golovatch et al. 2006, Liu and Tian 2015a). It encompasses over 90 species distributed in Eurasia from Japan and Sulawesi to the Balkans (Enghoff et al. 2015). At present, 30 species of this genus occur in China, 25 are subterranean-adapted.

***Hyleoglomeris rukouqu* sp. nov.**

<http://zoobank.org/EFA33915-ECD8-4B25-B874-28D0354B907C>

Figs 3A, 5, 6

Type material. Holotype male (SCAU), China, Guangxi Zhuang Autonomous Region, Yangshou County, Shangshuiyan Cave [24°57'43.6"N, 110°20'37.21"E], 191 m elevation (el.), cave entrance, ferns and other vegetation (refer to habitat section below), direct intuitive search, 17 November 2016, J.J. Wynne leg. Paratype, 1 female (SCAU), same data as holotype.

Etymology. The species name, *rukouqu*, is used as a noun in apposition from the Mandarin phrase, rùkǒu qū (入口区). When translated to English it means “entrance zone” or “entrance area” to denote the area in the cave where this species was collected.

Diagnosis. Adult male of *H. rukouqu* sp. nov. is distinct from other *Hyleoglomeris* species based on the following combination of characters: (1) peculiar color pattern (Fig. 5); (2) telopods with a large, rectangular, central syncoxital lobe (Fig. 6D). This new species is similar to *H. lii* (a troglophile from a cave in Guangxi), but is distinguished by (1) 2+2 dark brown spots on the thoracic shield (Fig. 5B, C) *vs.* 1+1 light grey-yellow spots in *H. lii*; (2) sycoxital lobe of telopods being high, large and rectangle-shaped (Fig. 6D) *vs.* low, linguiform, apically evidently concave in *H. lii*.

Description. Based on type specimens. Length *ca.* 8.0 mm (holotype), 11.0 mm (paratype), width 5.0 mm (holotype), 7.0 mm (paratype). **Coloration:** pattern vivid (Fig. 3A). With the exception of the brown dorsal spots, this species had similar coloration as that of the limestone rock and sediment within the entrance. General coloration in alcohol (Fig. 5) light yellowish with contrastingly dark spots, latter absent on rings 3 and 11. Head only brownish caudal margin, antennae and ommatidia dark-brownish. Collum mostly marbled dark-brown except frontal margin part. Thoracic shield with 2+2 dark brown spots, but lateral ones smaller than middle ones. Terga 4 with 1+1 brownish spots, smaller than the above. Terga 5–7 and pygidium with 1+1 large, oblong, transverse, paramedian, marbled, dark spots. Terga 8–10, these paramedian spots increasingly separated

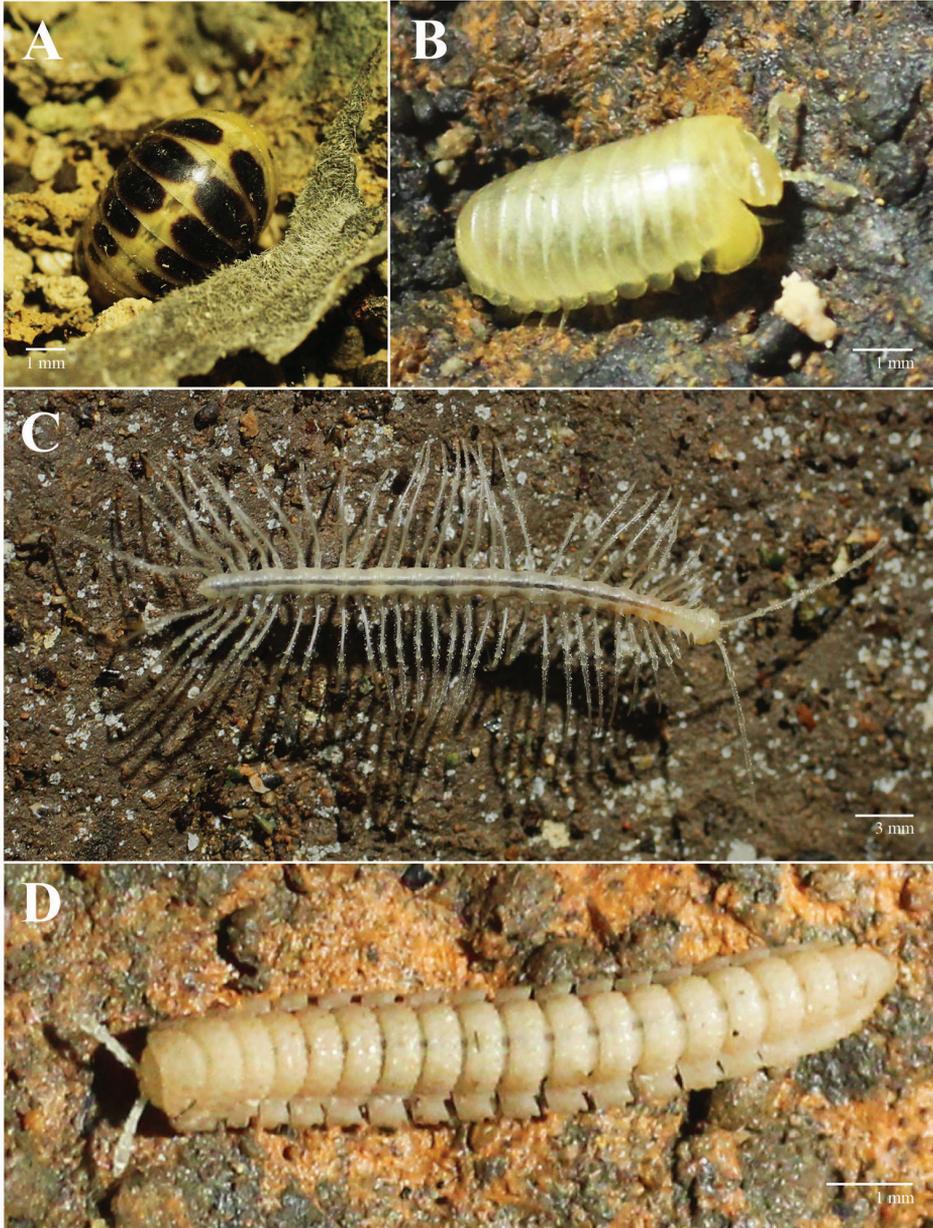


Figure 3. **A** *Hyleoglomeris rukouqu* sp. nov. from Shangshuiyan Cave **B** *Hyleoglomeris xuxiakei* sp. nov. from Guanshan No. 4 Cave **C** *Hylomus yuani* sp. nov. from Liangfeng Cave **D** *Eutrichodesmus jianjia* sp. nov. from Guanshan No. 4 Cave.

into 2+2, but lateral ones smaller than middle ones. Head: Ommatidium at least 7+1, lenses rather convex. Tömösváry's organ transverse-oval, parallel to the body, only slightly wider than *long*. Antennae with four apical *cones*, *ant*ennomere 6 ca 2.5 times as long as

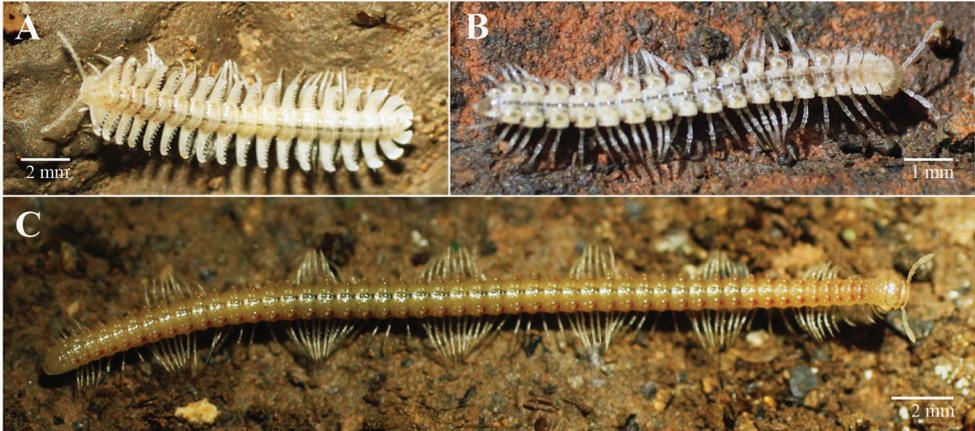


Figure 4. **A** *Trichopeltis liangfengdong* sp. nov. from Liangfeng Cave **B** *Pacidesmus trifidus* Golovatch & Geoffroy, 2014 from Maomaotou Cave **C** *Glyphiulus maocun* sp. nov. from Liangfeng Cave.

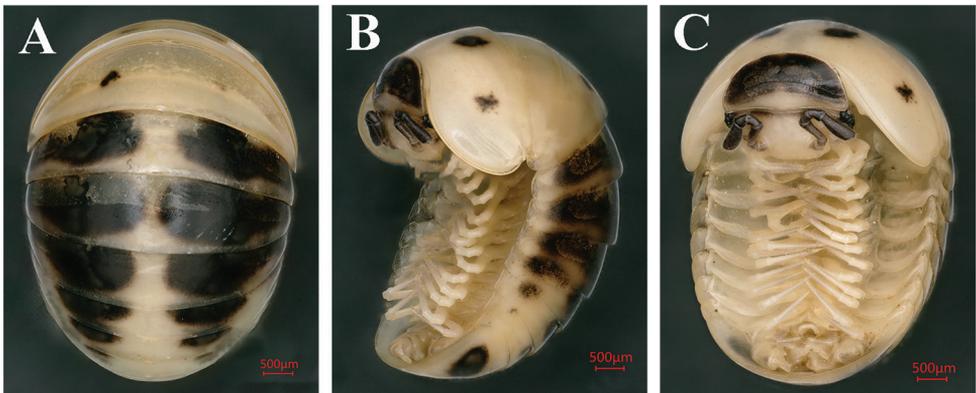


Figure 5. *Hyleoglomeris rukouqu* sp. nov., holotype. **A–C** Habitus, dorsal, lateral and ventral views, respectively.

wide. Exoskeleton: Collum with two transverse striae (Fig. 5C). Thoracic shield (Fig. 5B) with a narrow hyposchism, the latter not reaching behind caudal tergal margin; 7 transverse striae: 3 starting below, 1 level to, 3 above schism; 5 striae (never the first and last from below) crossing the dorsum. Following terga 3–11 with two striae above lateral edge (Fig. 5B). Pygidium (last tergite) of both sexes slightly concave medially at caudal margin. leg 17 with a low, rounded, outer coxal lobe; telopodite 4-segmented (Fig. 6A). leg 18 with a subtriangular *syncoxital* notch; telopodite 4-segmented (Fig. 6B). Telopods: (Fig. 6C–E) with a large, subrectangular, central *syncoxital* lobe flanked by high setose horns, each of the latter with a small lobe on top. Prefemur micropapillate laterally, with a long, digitiform, frontomesal trichostele. Femur with a smaller, digitiform, frontomesal trichostele. Caudomedial femoral process prominent, apically with an evident lobe. Tibia with a frontomesal seta. Caudomesal tibial process evident, recurved; an indistinct, papillate tubercle at base on caudal face. Tarsus strongly sigmoid, narrowly rounded apically.

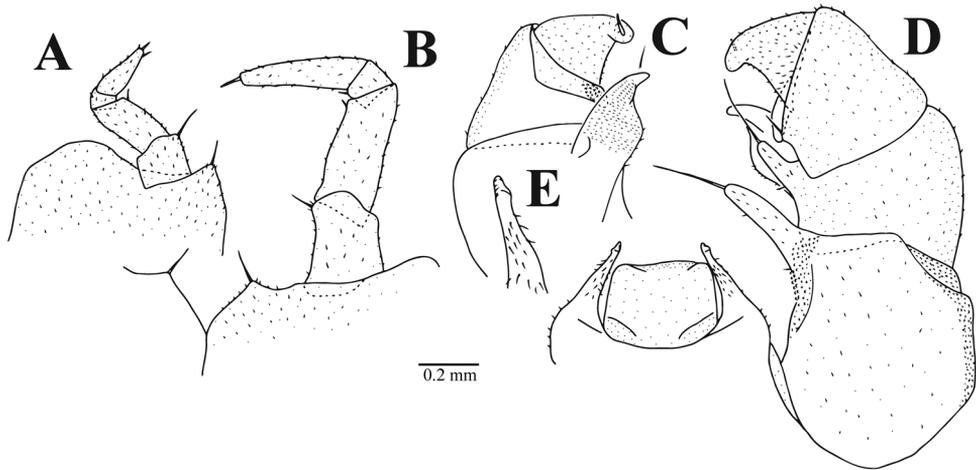


Figure 6. *Hyleoglomeris rukouqu* sp. nov., holotype. **A** leg 17, anterior view **B** leg 18; anterior view **C** right half of telopods, posterior view **D** right half of telopods, anterior views **E** tip of syncoxital horn, anterior view.

Habitat. Specimens were collected within a vegetation association that may be limited to the cave entrance zone and similar geographic features (e.g., sinkholes and fissures in rock). At least three plant species occurred within the entrance including Gesneriaceae sp., *Adiantum* sp., and one other fern species, which cannot be identified without examining the sorii (A. Monro, pers. comm. 2018).

Notes. Based on the vivid color pattern and well-developed ommatidia, as well as the location where it was detected within the cave, this animal represents an epigeal species and may be functioning as an obligate troglophile (*sensu* Peck 1970). While it is likely *H. rukouqu* sp. nov. either occurred or still occurs in similar habitats on the surface, the importance of relict plant species restricted to cave entrances has been discussed for southern China (Monro et al. 2018). Additionally, several arthropod species globally are restricted to cave entrances in Polynesia (Mockford and Wynne 2013, Wynne et al. 2014, Bernard et al. 2015, Taiti and Wynne 2015) and North America (Benedict 1979, Wynne and Shear 2016) due to either extensive surface disturbance and glacial interglacial cycles, respectively. Thus, it is possible this species is a ‘disturbance relict’ restricted to the entrance of Shangshuiyan Cave and potentially other area cave entrances with similar vegetation.

***Hyleoglomeris xuxiakei* sp. nov.**

<http://zoobank.org/D3CA0855-76FD-4683-8A7C-3F0505DC3D8E>

Figs 3B, 7, 8

Type material. Holotype male (SCAU), China, Guangxi Zhuang Autonomous Region, Yangshuo County, Guanshan No. 4 Cave [24°56'58.34"N, 110°20'53.52"E],

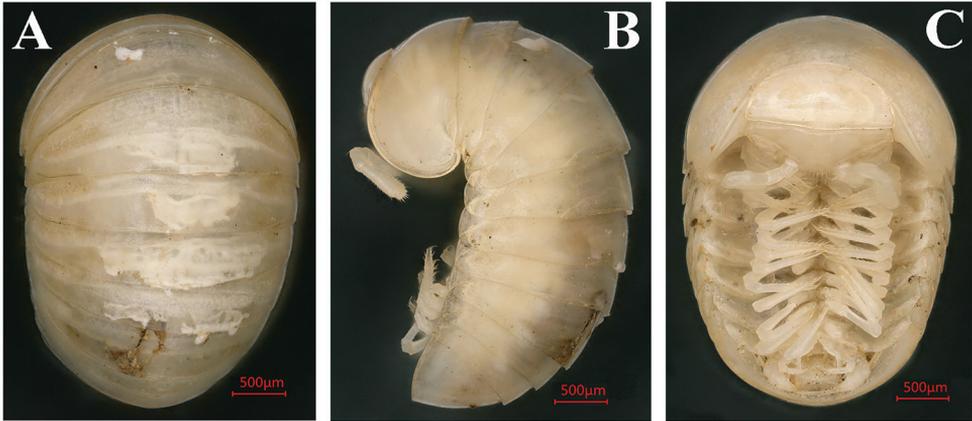


Figure 7. *Hyleoglomeris xuxiakei* sp. nov., holotype. **A–C** Habitus, dorsal, lateral and ventral views, respectively.

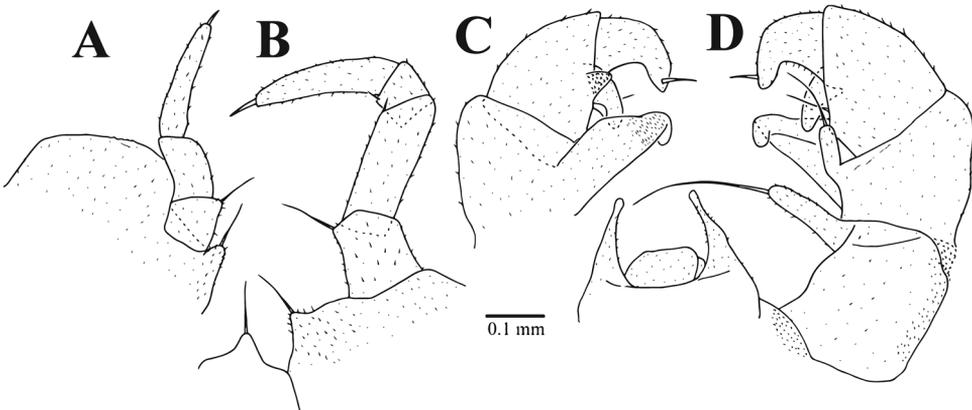


Figure 8. *Hyleoglomeris xuxiakei* sp. nov., holotype. **A** Leg 17, anterior view **B** leg 18; anterior view **C** right half of telopods, posterior view **D** right half of telopods, anterior views.

186 m el., deep zone, direct intuitive search, 16 November 2016, J.J. Wynne leg. Paratype, 1 male (SCAU), same data as holotype. 3 females (SCAU), same data as holotype, but deep zone, slightly muddy flat area.

Etymology. The species name, *xuxiakei*, was Latinized using a combination of the surname and forename of Xu Xiake (徐霞客). Xu was a traveler, explorer, and the first speleologist of China, who studied caves and karst geology during the decline of the Ming Dynasty. He conducted a four-year expedition (1636–1640) across southern China where he examined over 300 caves (including more than 100 from the Guilin area; Sweeting 1995, Ravbar 2016). In his book, *Xu Xiake's Travels* (first published in 1642), he described underground streams and ponds, provided sketch maps of caves, as well as proposed terminology for karst features; many of his speleological terms are still used today (Ravbar 2016).

Diagnosis. Adult male of *H. xuxiakei* sp. nov. is distinct from other *Hyleoglomeris* species based on the following combination of characters: (1) nearly pallid color (Fig. 7); (2) ♂ leg 17 with 3-segmented telopodite (Fig. 8A); (3) telopods with a low, oval-shaped, central syncoxital lobe; (4) horns of syncoxital lobe without any structure on top (Fig. 8D). This new species is clearly distinguished by the depigmented body (Fig. 3B) *vs.* vivid color pattern in *H. rukouqu* sp. nov. (Fig. 3A).

Description. Based on type specimens. Lengths of body *ca* 3.8–4.5 mm, width 2.5–3.0 mm in both sexes. **Coloration:** entirely pallid (Figs 3B, 7). **Head:** Ommatidium at least 5(6) + 1, translucent, barely visible (Fig. 7C). Tömösváry's organ transverse-oval, parallel to the body, only slightly wider than long. Antennae with four apical cones, antennomere 6 *ca* 2.0 (♂) or 1.8 (♀) times as long as wide. **Exoskeleton:** Collum with two transverse striae (Fig. 7C). Thoracic shield with a narrow hyposchism, the latter reaching behind caudal tergal margin; 8–9 transverse striae: 4(5) starting below, one level to, 3(4) above schism; 5 striae (never the first and last from below) crossing the dorsum. Following terga 3–11 with two striae above lateral edge. Pygidium of both sexes regularly rounded at caudal margin. ♂ leg 17 with a low, subrounded, outer coxal lobe; telopodite 3-segmented (Fig. 8A). ♂ leg 18 with an arch-shaped syncoxital notch; telopodite 4-segmented (Fig. 8B). **Telopods:** (Fig. 8C–D) with a rather low, oval-shaped, transverse, central syncoxital lobe flanked by high setose horns, each of the latter without any structure on top. Prefemur micropapillate laterally, with a well-developed frontomesal trichostele. Femur with a smaller frontomesal trichostele. Caudomesal femoral process prominent, apically with an evident lobe strongly curved to frontad. Tibia with a frontomesal seta. Caudomesal tibial process evident, recurved; a distinct, papillate tubercle at base on caudal face. Tarsus strongly sigmoid, narrowly rounded apically.

Habitat. This species was collected from a chamber within the estimated cave deep zone, approximately 50 m from the cave entrance. Cave sediment was compact mud with a small amount of rock breakdown from the ceiling.

Notes. Based on a depigmented habitus and translucent ommatidia, we consider this species is a troglobiont.

Order Polydesmida Leach, 1815

Family Paradoxosomatidae Daday, 1889

Genus *Hylomus* Cook & Loomis, 1924

Type species. *Hylomus draco* Cook & Loomis, 1924.

Remarks. The genus is often referred to as “dragon millipedes” because of the paraterga is antler-like, wing-shaped or spiniform. It can be characterized by the collum and metaterga often with granulate, tuberculate and/or speculate; male femora (5, 6, 7 and/or 9) often humped ventrally; and gonopods mostly suberect, some subfalcated, a shortened solenomere mostly sheathed by a usually condensed, rather simple solenophore

(Liu et al. 2014, 2016). This genus encompasses 33 species distributed from China, Laos, Vietnam and Thailand (Srisonchai et al. 2018). At present, 19 species are known in China and 13 are subterranean-adapted (Liu et al. 2016; Srisonchai et al. 2018).

***Hylomus yuani* sp. nov.**

<http://zoobank.org/89255A98-84A8-4D57-ADF4-F7B4F0BDBE48>

Figs 3C, 9–12

Material examined. Holotype male (SCAU), China, Guangxi Zhuang Autonomous Region, Lingchuan County, Liangfeng Cave [25°12'34.86"N, 110°31'56.8"E], 184 m el., deep zone, direct intuitive search, 18 November 2016, J.J. Wynne leg. Paratypes, 1 male, 3 females (SCAU), same data as holotype.

Etymology. This species is named for Dr. Yuan Daoxian (袁道先), a preeminent and globally recognized Chinese hydrologist. He has made numerous significant contributions in advancing both the science and management of karst and karst waters in southern China since the 1960s.

Diagnosis. Adult males of *H. yuani* sp. nov. are distinct from other *Hylomus* species based on the following combination of characters: (1) paraterga long and spiniform only on collum and rings 2–6, short and coniform thereafter (Figs 9, 10A, B); (2) collum with 8+8 frontal, 3+3 in the middle, 3+3 caudal, setigerous spinules; (3) ♂ femur 6 strongly inflated in distal 1/4 (Fig. 10D); (4) gonopod with a flagelliform solenomere and a strongly condensed solenophore (Figs 9–12). This new species is similar to *H. lui* (a troglobiont from a cave in Guilin), but is distinguished by (1) paraterga long and spiniform on collum and rings 2–6 (Fig. 9) *vs.* on collum and rings 2–5 in *H. lui*; (2) collum and following metaterga with three transverse rows of spinules (Fig. 10A–B) *vs.* two transverse rows of spinules in *H. lui*.

Description. Based on type specimens. Lengths of body *ca* 27–28 (♂), 30–35 mm (♀); width of mid-body pro- and metazonae 1.5–1.6 and 2.0 (♂), 2.0–2.2 and 2.5–2.6 mm (♀). **Coloration:** light brownish to nearly pallid (Figs 3C, 9–10). Antennomere 7 dark brown. **Body:** with 20 rings. In width, head < ring 2 < collum < 4–5 < 3 = 6–7 < 8–9 < 10–13; thereafter body gradually tapered posteriorly towards telson. **Head:** densely setose, but more sparsely on vertex, epicranial suture conspicuous (Fig. 10A). Antennae long and slender, reaching past ring 8 (♂) or 7 (♀) when extended posteriorly. **Exoskeleton:** Collum with 8+8 evident setigerous spinules arranged in a row at front margin, behind it with 3+3 in the middle and 3+3 similarly spinules at posterior margin. Metaterga 2–4 each with 5+5, 3+3 and 5+5(6) similarly setigerous spinules arranged in three transverse rows (Fig. 9A). Following metaterga with same sculpture, but 7–9+7–9 setigerous spinules at posterior margin, 2–4 spinules of them extended to the lateral side (Figs 9C, 10B). Paraterga clearly spiniform, but well-developed only in paraterga 1–6, directed more dorsad than laterad (Fig. 9A). Following paraterga increasingly stout and short, paraterga 7–14 directed dorsolaterad, thereafter directed clearly caudad (Figs 9C, 10A–B). Tegument shining, prozonae delicately microalveolate, metaterga

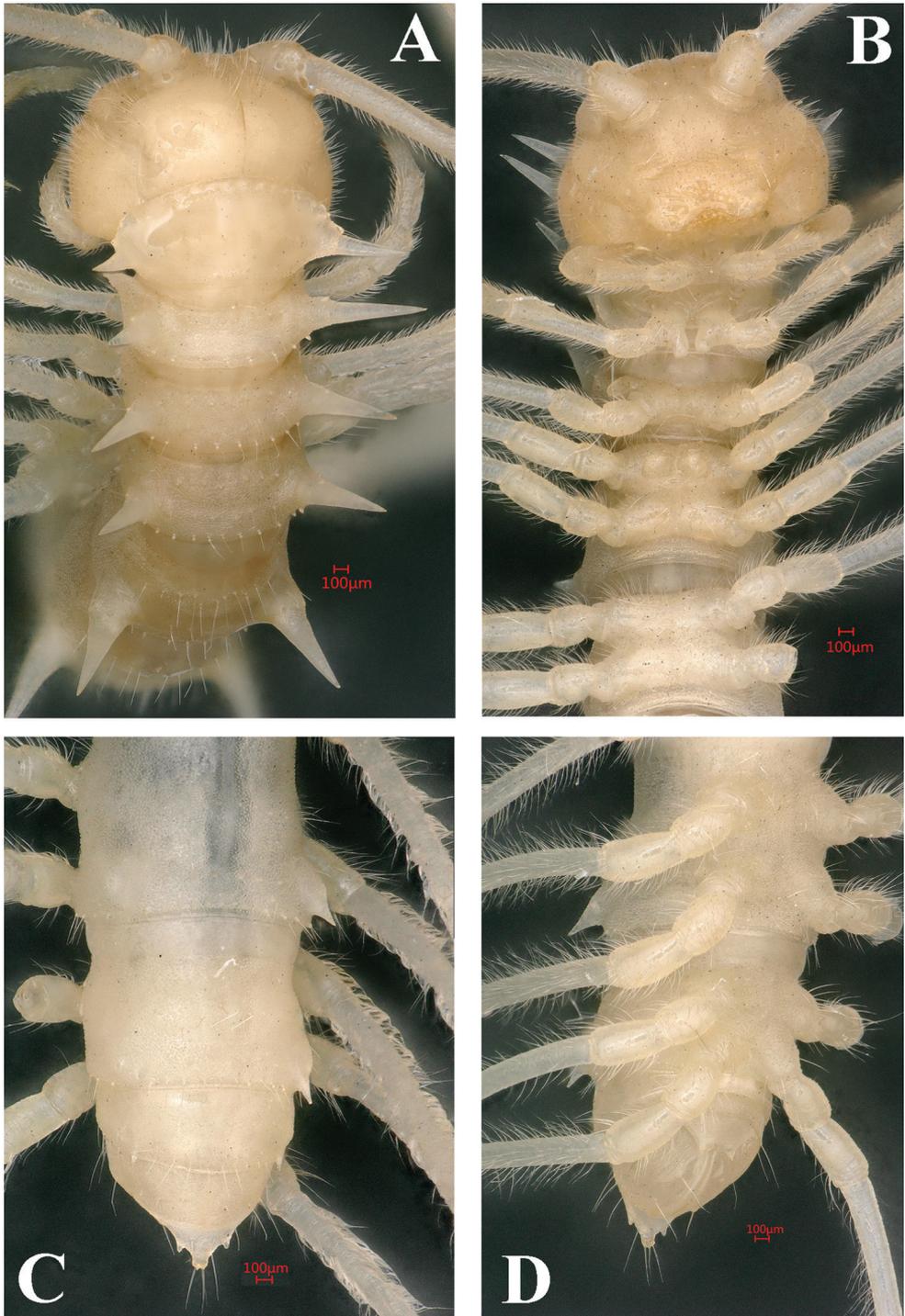


Figure 9. *Hylomus yuani* sp. nov., ♂ paratype. **A** Anterior part of body, dorsal view **B** anterior part of body, ventral view **C** posterior part of body, dorsal view **D** posterior part of body, ventral view.

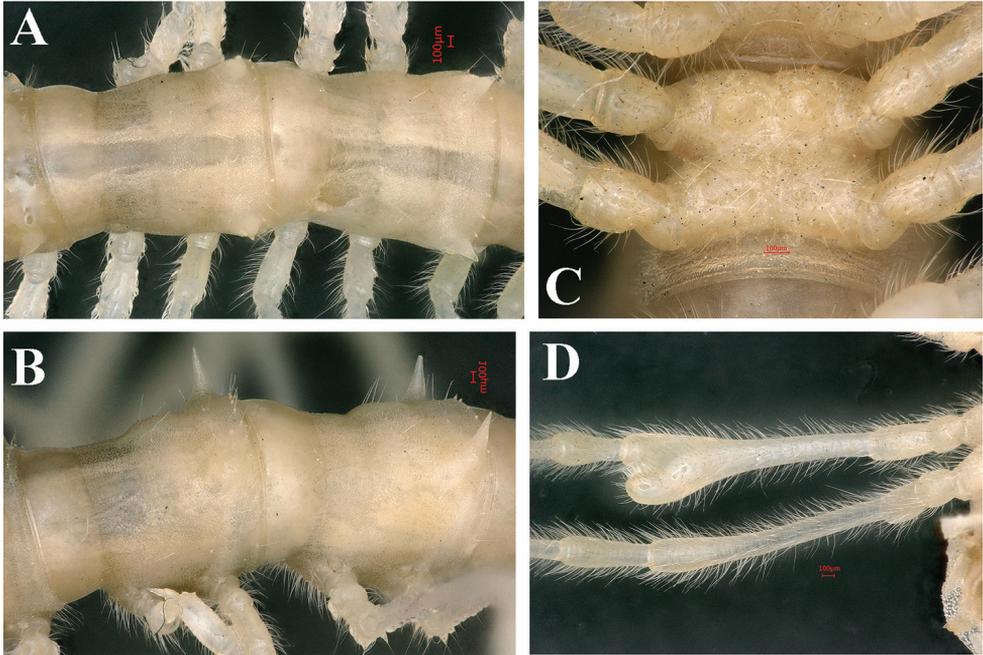


Figure 10. *Hylomus yuani* sp. nov., ♂ paratype. **A** Mid-body rings, dorsal view **B** mid-body rings, lateral views **C** sternite V, ventral view **D** femora 6 and 7, subventral view.

and surface below paraterga finely microgranulate. Constriction between pro- and metazonae broad and shallow (Fig. 10A–B). Pore formula normal; transverse sulcus usually very vague, but traceable in rings 5–19 (Fig. 10A). Ozopores inconspicuous, located near the base on lateral side of pore-bearing paraterga (Fig. 10B). Pleurosternal carinae evident only on rings 2 and 3 in both sexes, absent thereafter. Epiproct simple, lateral pre-apical papillae distinct (Fig. 9C). Hypoproct subtrapeziform, caudal margin emarginate, setigerous cones at caudal edge large, widely separated (Fig. 9D). Sterna sparsely setose, cross-shaped impressions weak. A paramedian pair of short, rounded, independent tubercles between ♂ coxae 4 (Figs 9B, 10C). Legs long and slender, *ca* 5.0 (♂) or 3.5 (♀) times as long as mid-body ring height. ♂ femur 6 strongly inflated ventrally in distal 1/4 (Fig. 10D). **Gonopods:** (Figs 11, 12) Coxite short, subcylindrical, densely setose distodorsally, about 1/3 as long as telopodite. Prefemur densely setose and about half as long as acropodite. Femorite elongate, slightly curved, with seminal groove running entirely on mesal face. Solenophore (**sph**) strongly condensed; solenomere (**sl**) flagelliform, evidently separated at base from solenophore.

Habitat. This species was collected within the estimated cave deep zone, approximately 20 m from the cave entrance. Cave sediment was compact mud and the passageway was swaddled by a slightly visible fog. This species and cave crickets (family Rhaphidophoridae) were among the most abundant species within this portion of cave deep zone.

Notes. Based on the slender elongate antennae and legs, a depigmented cuticle, the species is considered a troglobiont.



Figure 11. *Hylomus yuani* sp. nov., ♂ paratype. **A** Right gonopod, lateral view **B** right gonopod, mesal views.

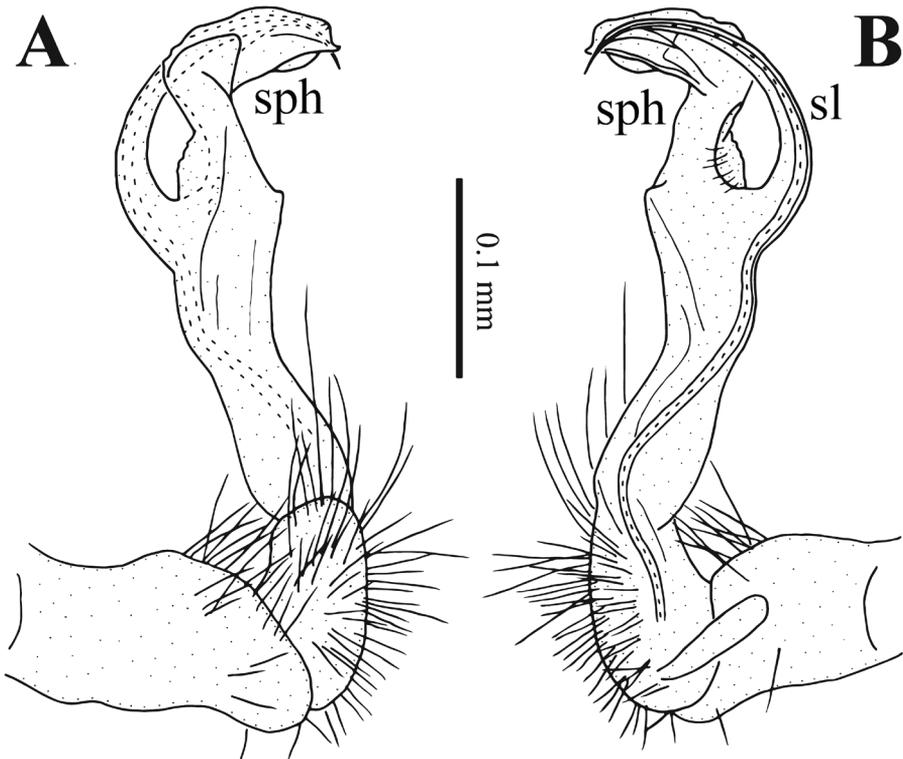


Figure 12. *Hylomus yuani* sp. nov., ♂ paratype. **A** Right gonopod, lateral view **B** right gonopod, mesal views. Designations: sl = solenomere; sph = splenophore.

Family Haplodesmidae Cook, 1895**Genus *Eutrichodesmus* Silvestri, 1910**

Type species. *Eutrichodesmus demangei* Silvestri, 1910.

Remarks. The genus can be characterized by the body often capable of volvation, with or without mid-dorsal projections; paraterga 2 strongly enlarged; and gonopod femorite with a more or less distinct process or outgrowth laterally (Golovatch et al. 2009a, b). It encompasses 53 species distributed from south Japan, southern China, and Southeast Asia to Vanuatu, Melanesia (Enghoff et al. 2015, Liu et al. 2017b). At present, 23 species have been known in continental China, 20 are subterranean-adapted.

***Eutrichodesmus jianjia* sp. nov.**

<http://zoobank.org/403323E4-C776-4DC8-8795-9C53C3B64E02>

Figs 3D, 13, 14

Type material. Holotype male (SCAU), China, Guangxi Zhuang Autonomous Region, Yangshuo County, Guanshan No. 4 Cave [24°56'58.34"N, 110°20'53.52"E], 186 m el., deep zone, direct intuitive search, 16 November 2016, J. J. Wynne leg. Paratypes, 4 females, 1 juv. (SCAU), same data as holotype; 1 male (SCAU), same data as holotype, but collected on mud bank.

Etymology. The species name, *jianjia* (肩甲), is used as a noun in apposition. This phrase was used to denote the well-developed paraterga, which covers the millipede's legs much like the pauldrons of body armor cover the shoulder of the warrior.

Diagnosis. Adult males of *E. jianjia* sp. nov. is distinct from other *Eutrichodesmus* species based on the following combination of characters: (1) collum with five, and metaterga 2–19 with three transverse rows of round microvillose tubercles (Fig. 13). (2) gonopod acropodite with a dorsolateral tooth (t) at midway and apical with a large tube-shaped lobe (l) (Fig. 14). This new species is clearly distinguished from *E. lipsae* (a troglobiont from a cave in Guilin) by (1) metaterga without mid-dorsal projections *vs.* most metaterga with mid-dorsal projections; (2) gonopod acropodite with a triangular, ventral process (p) at about basal 1/3 (Fig. 14) *vs.* without this process in *E. lipsae*.

Description. Based on type specimens. Lengths of adult body *ca* 6.0–7.0 mm, widths of mid-body pro- and metazonae 0.6–1.0 and 1.2–1.3 mm in both sexes. **Coloration:** generally light-yellowish to pallid (Fig. 3D). **Body:** subcylindrical, conglobation complete, adults with 20 rings (Fig. 10A). **Head:** frons densely setose, finely microgranulate on vertex, with a paramedian pair of rounded knobs above antennal sockets. Epicranial suture conspicuous. Antennae short, slightly clavate. **Exoskeleton:** Collum subtrapeziform, slightly broader than head, not covering the latter from above, with five transverse rows of round microvillose tubercles (Fig. 13B). Metaterga 2–19 each with three transverse mixostictic rows of similar tubercles extending onto paraterga, about 6–8+6–8 per row. The middle row of tubercles slightly larger than others. Pre-anal ring short, with four transverse rows of small tubercles (Fig. 13D, E). Paraterga with evident shoulders anteriorly, strongly declivous, broad and usually triobate laterally, evidently

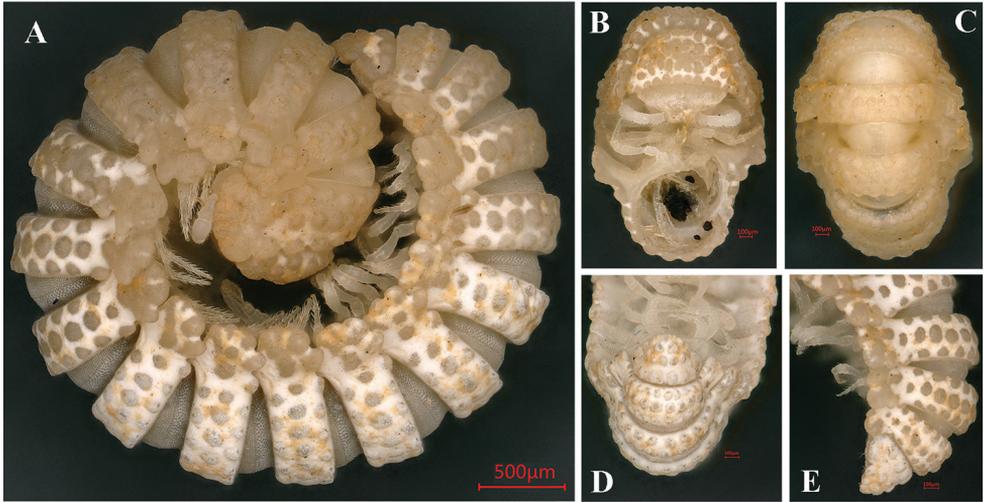


Figure 13. *Eutrichodesmus jianjia* sp. nov., ♂ paratype. **A** Habitus, lateral view **B** anterior part of body, ventral view **C** anterior part of body, dorsal view **D** posterior part of body, ventral view **E** posterior part of body, lateral view.

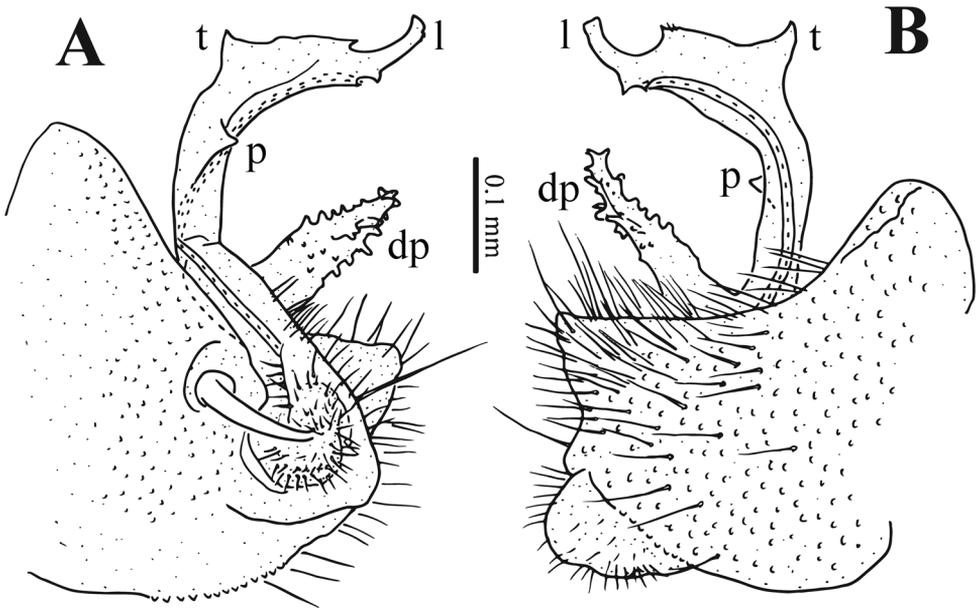


Figure 14. *Eutrichodesmus jianjia* sp. nov., ♂ paratype. **A** Left gonopod, lateral view **B** left gonopod, mesal view. Designations: dp = distofemoral process; l = lobe; p = process; t = tooth.

extending down below level of venter; caudolaterally at base with two distinct lobulations (Fig. 13A). Paraterga 2 strongly enlarged. Tergal setae and ozopores invisible. Ozopores hardly visible. Prozonae finely alveolate; constriction between pro- and metazoan

narrow and shallow. Epiproct apically with four spinnerets. Hypoproct subtrapeziform, with two long setae. Sterna narrow, but much broader between ♂ coxae 6–7 and 9. Gonopod aperture suboval. Legs long and slender, but hardly reaching tips of paraterga. **Gonopods:** (Fig. 14) Coxite large, abundantly setose and micropapillate ventrolaterally. Telopodite subfalcate, distinctly curved ventrad, setose in its basal part, with a prominent, denticulate, lateral, distofemoral process (**dp**) at midway. Acropodite with a triangular, ventral process (**p**) at about basal one-third and a dorsolateral tooth (**t**) at midway; apical with a large tube-shaped lobe (**l**). Seminal groove long, terminating without hair.

Habitat. Specimens were collected in the same general location as *H. xuxiakei* sp. nov. specimens. Thus, refer to the *H. xuxiakei* sp. nov. habitat description.

Notes. Based on the long slender legs and a depigmented cuticle, we consider this species a troglobiont.

Family Cryptodesmidae Karsch, 1880

Genus *Trichopeltis* Pocock, 1894

Type species. *Cryptodesmus bicolor* Pocock, 1894.

Remarks. The genus can be characterized by the metaterga distinctly several transverse rows of tuberculations, usually setose, and gonopod usually foliate, with a tripartite or deeply notched telopodite. It encompasses 12 species distributed from the Himalayas of India, through Bangladesh, Myanmar to southern China, Laos, Vietnam, Cambodia and Indonesia (Likhitrakarn et al. 2017). At present, 5 species have been known in China, 4 are subterranean-adapted.

Trichopeltis liangfengdong sp. nov.

<http://zoobank.org/7E972E70-ADDA-4CA1-924F-3016EF5E3FA7>

Figs 4A, 15–17

Type material. Holotype male (SCAU), China, Guangxi Zhuang Autonomous Region, Lingchuan County, Liangfeng Cave [25°12'34.86"N, 110°31'56.8"E], 184 m el., deep zone, steam bank, direct intuitive search, 18 November 2016, J.J. Wynne leg. Paratypes, 4 females (SCAU), same data as holotype.

Etymology. This species name, *liangfengdong*, is used as a noun in apposition and is the name of the type locality.

Diagnosis. Adult male of *T. liangfengdong* sp. nov. is distinct from other *Trichopeltis* species based on the following combination of characters: (1) metaterga 2–15 with four transverse rows of small, setigerous tubercles (Fig. 15B); (2) gonopod coxae without seta and acropodite with several small subapical lobules (los) (Fig. 17). This new species is similar to *T. reflexus* (a troglobiont from a cave in Hunan), but is distinguished by (1) metaterga 2–15 with four transverse rows of setigerous tubercles *vs.* two transverse rows in *T. reflexus*; (2) tip of acropodite bifid (Fig. 17) *vs.* distorted in *T. reflexus*.

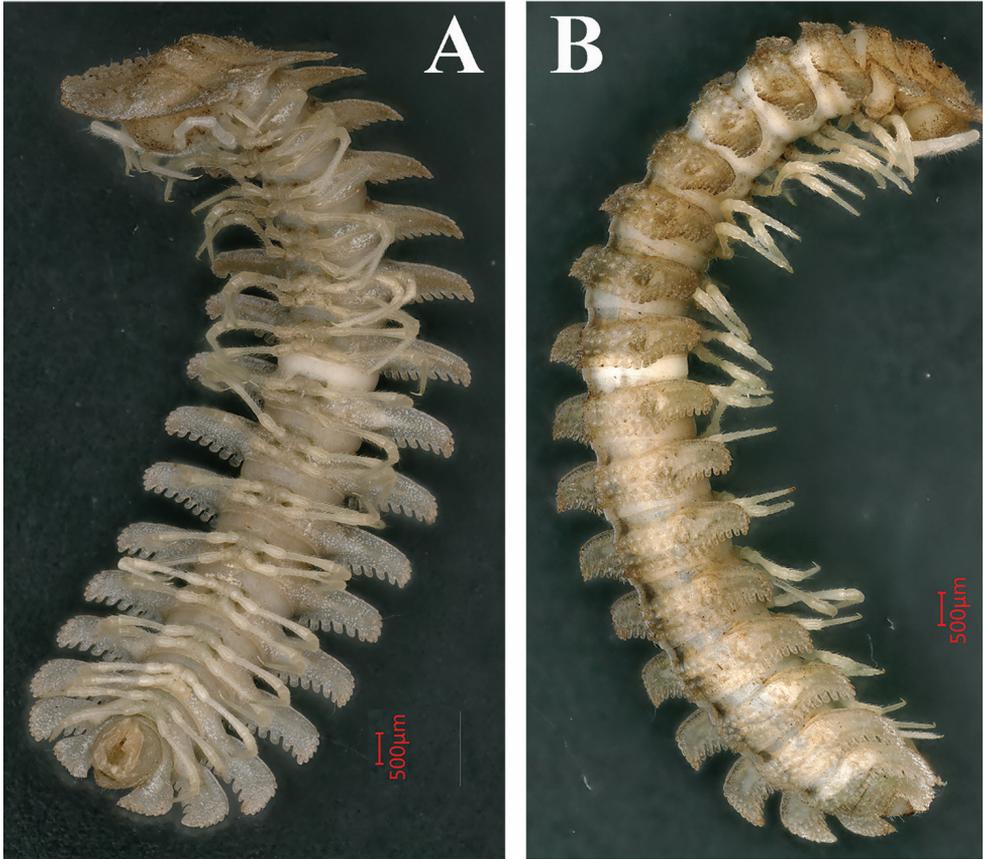


Figure 15. *Trichopeltis liangfengdong* sp. nov. holotype. **A** Habitus, ventral view **B** habitus, sublateral view.

Description. Based on type specimens. Length of both sexes *ca* 14.0–15.0 mm, widths of mid-body pro- and metazonae 1.5–2.0 and 4.8–5.0 mm. **Coloration:** generally pallid (Fig. 4B). **Body:** with 20 rings (Fig. 15). In width, collum < ring 2 < 3 = 4 < 5 < 6 < 7–16; thereafter body gradually tapered posteriorly towards telson. **Head:** densely pilose and microgranulate, epicranial suture present (Fig. 16A). Antennae long, reaching past ring 3 when extended posteriorly; in length, antennomere 6 = 5 > 4 = 3 > 2 > 7 > 1. **Exoskeleton:** Collum fan-shaped (Fig. 15A), covering the head from above, dorsal surface with irregular several small, round, setigerous tubercles. Marginal lobules on collum: 13+13 small, setigerous, rounded anteriorly, 7+7 relative larger, laterally and 5+5 very small caudally. Mid-dorsal regions on rings 2–15 with four more or less regular, transverse rows of similarly small, setigerous tubercles, 4–5 + 4–5 per row (Figs 15B, 16B). Several tubercles extending onto paraterga. Following metaterga with five rows of smaller tubercles, 6–7 + 6–7 per row (Fig. 15B). Paraterga strongly developed, clearly upturned dorsally above the dorsum only on the collum, other paraterga flat. Each with 5–6 small, dentiform, lateral and 7–8 much larger, squarish caudolateral lobules, all evident, setigerous and microvillose (Figs 15, 16A, B). Cau-

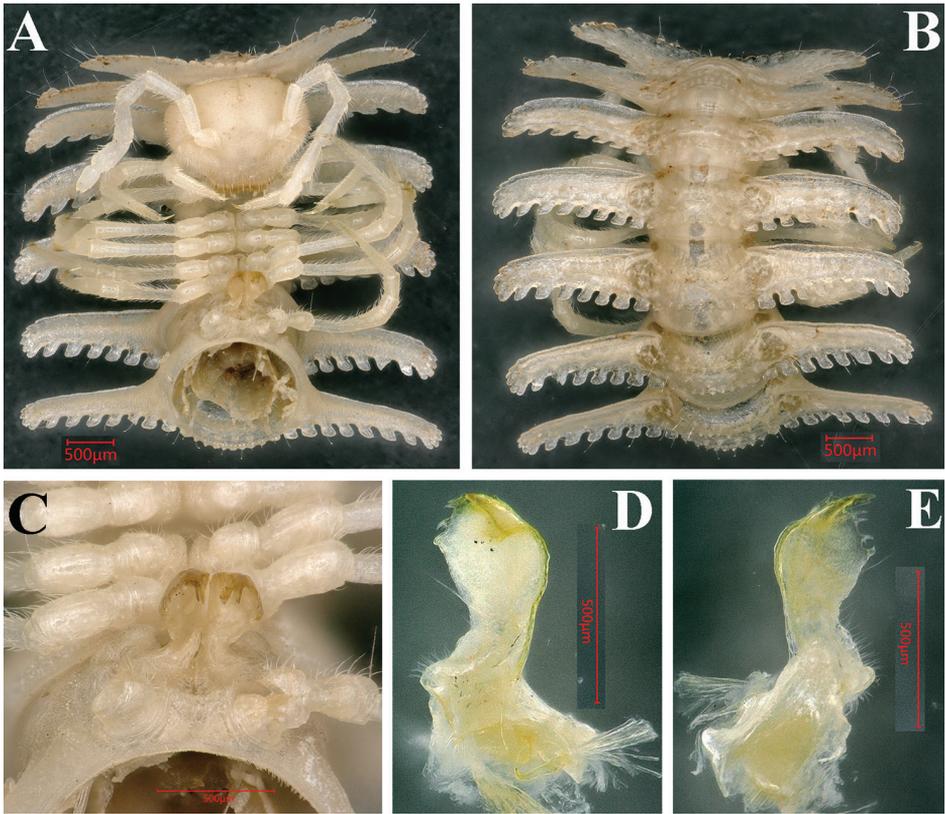


Figure 16. *Trichopeltis liangfengdong* sp. nov., holotype. **A** anterior part of body, ventral view **B** anterior part of body, dorsal view **C** sterna 6 and 7, ventral view **D** right gonopod, mesal view **E** right gonopod, lateral view.

dolateral lobules on paraterga mostly oblong, relatively large, and well separated from one another (Fig. 16A). Caudolateral corner of paraterga projecting behind rear tergal margin on rings 15–19 (Fig. 15). Integument clearly microgranulate throughout, prozonae finely alveolated. Limbus regularly crenulated. Stricture between pro- and metazonae broad, shallow and finely microgranulated. Tergal setae simple and short (Fig. 16A, B). Ozopores invisible, pore formula untraceable. Epiproct short, with four spinnerets apically. Hypoproct subtrapeziform, 1+1 caudal setigerous papillae clearly separated. Pleurosternal carinae present on rings 2 and 3 in both sexes. Sterna modestly setose, cross-shaped impressions moderate, broadened between ♂ coxae 9 (Fig. 16C). Legs long and slender, unmodified, produced beyond paratergal lateral margin (Fig. 15), about 1.8 times as long as mid-body ring height in both sexes. **Gonopods:** (Figs 16D, E, 17) Coxite short and squarish, without seta. Prefemur densely setose and a particularly long setae; nearly half the length of telopodite. Femorite strongly flattened, pie-shaped, with a small lobe (l) ventrally. Acropodite folded, with several small subapical lobules (los), tip bifid. Seminal groove terminating with a hairy pulvillus, forming no distinct solenomere.

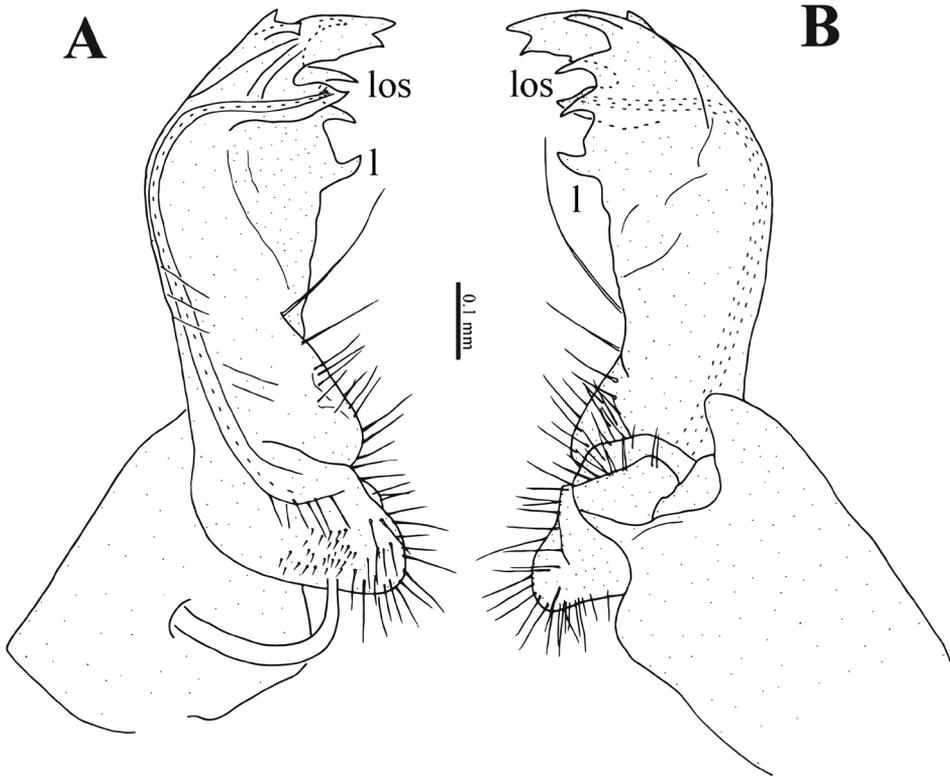


Figure 17. *Trichopeltis liangfengdong* sp. nov., holotype. **A** Left gonopod, mesal view **B** left gonopod, lateral view. Designations: l = lobe; los = lobules.

Habitat. Specimens were collected in the same general location as *H. yuani* sp. nov. specimens. Thus, refer to the *H. yuani* sp. nov. habitat description.

Notes. Based on the long slender antennae and legs and a depigmented cuticle, the species is considered a troglobiont.

Family Polydesmidae Leach, 1815
Genus *Pacidesmus* Golovatch, 1991

Type species. *Pacidesmus shelleyi* Golovatch, 1991

Remarks. The genus can be characterized by metaterga often with three transverse rows of 3+3 sculpture, and gonopod structure showing no prominent clivus to recurve laterad of the seminal groove (Golovatch and Geoffroy 2006). It encompasses 9 species, only the type species from a mountain in Chiangmai, Thailand, all other 8 species have been known from caves in China.

***Pacidesmus trifidus* Golovatch & Geoffroy, 2014**

Fig. 4B

Material examined. 6 males, 3 females (SCAU), China, Guangxi Zhuang Autonomous Region, Yangshuo County, Guanshan No. 4 Cave [24°56'58.34"N, 110°20'53.52"E], 186 m el., deep zone, direct intuitive search, 16 November 2016, J.J. Wynne leg. 1 male, 1 juv. (SCAU), China, Guangxi Zhuang Autonomous Region, Xiufeng District, Maomaotou Cave [25°18'46.12"N, 110°16'12.64"E], 225 m el., deep zone, direct intuitive search, 15 November 2016, J. J. Wynne leg. 2 males, 1 female, 4 juv. (SCAU), China, Guangxi Zhuang Autonomous Region, Yangshou County, Shangshuiyan Cave [24°57'43.6"N, 110°20'37.21"E], 191 m el., deep zone, direct intuitive search, 17 November 2016, J. J. Wynne leg.

Notes. This troglobiont was first found in Skeleton Cave [25°17'13"N, 110°13'26"E], el. 186 m (Golovatch and Geoffroy 2014). We later confirmed *P. trifidus* within three caves with the furthest cave (Guanshan # 4) approximately ~13 km to the south of type locality. The three caves where we detected *P. trifidus* are separated by a distance of ~41 km. The northernmost cave, Maomaotou Cave occurs 39.6 km north from Guanshan No. 4 Cave and Shangshuiyan Cave, which are co-located occurring within 1 km of each other. As it is currently morphologically described as one species, it now has a regional distribution.

Habitat. This species was collected from the estimated deep zones of the three caves. For Maomaotou cave, we collected it within bamboo detritus at mid-cave. In Shangshuiyan Cave, specimens were collected within decomposing detritus and along muddy cave sediment deposits within a sinuous passageway. For Guanshan No. 4 Cave, refer to habitat descriptions of *H. xuxiakei* sp. nov.

Order Spirostreptida Brandt, 1833**Family Pericambalidae Silvestri, 1909****Genus *Bilingulus* Zhang & Li, 1981**

Type species. *Bilingulus sinicus* Zhang & Li, 1981.

Remarks. The genus can be characterized by the lingular lamellae divided into two parts. ♂ legs 1 with a syncoxite carry a pair of long, band-like coxal process; femur with a finger-shaped process at the end protruding posteriorly, tarsus without claw at the end. Anterior gonopod with a very broad coxa; telopodite of posterior gonopod slender, devoid of branch (Zhang and Li 1981).

***Bilingulus sinicus* Zhang & Li, 1981**

Material examined. 3 males, 3 females, 5 juv. (SCAU), China, Guangxi Zhuang Autonomous Region, Yangshou County, Shangshuiyan Cave [24°57'43.6"N, 110°20'37.21"E], 191 m el., deep zone, cartography station #19, direct intuitive

search, 17 November 2016, J.J. Wynne leg. 4 females (SCAU), China, Guangxi Zhuang Autonomous Region, Xiufeng District, Maomaotou Cave [25°18'46.12"N, 110°16'12.64"E], 225 m el., deep zone, direct intuitive search, 15 November 2016, J.J. Wynne leg. 1 juv. (SCAU), China, Guangxi Zhuang Autonomous Region, Lingchuan County, Liangfeng Cave [25°12'34.86"N, 110°31'56.8"E], 184 m el., deep zone, direct intuitive search, 18 November 16, J.J. Wynne leg.

Notes. This species lacked characters suggestive of troglomorphy. It had a pigmented cuticle and ommatidia were present. Thus, *B. sinicus* is considered a troglophile. It was first described by Zhang and Li (1981) from a cave in Guilin; no cave name or coordinate data were provided. While we detected this species in three different Guilin caves, we're unable to determine a distance from the type locality. The caves where we detected *P. trifidus* is separated by an average distance of 34.1 km. Maomaotou Cave occurs to the north-northwest and is 45 km from Liangfeng Cave and 40.4 km to the north of Shangshuiyan Cave. Based upon its epigeal characteristics and that this species is regionally distributed on the landscape, we consider it a troglophile.

Family Cambalopsidae Cook, 1895

Genus *Glyphiulus* Gervais, 1847

Type species. *lulus* (recte: *Julus*) *granulatus* Gervais, 1847.

Remarks. The genus has been divided into two groups, *granulatus*-group and *javanicus*-group. Both groups shared the same gonopods characters as the anterior gonopods usually with a plate-like coxosternum, 1-segmented telopodite. Posterior gonopods highly compressed, showing a plumose, subflagelliform, distal process (Golovatch et al. 2007). It encompasses over 60 species distributed in Southeast Asia and southern China. At present, 42 species have been known in China, 34 are subterranean-adapted. The below two species belong to *granulatus*-group because ♂ legs 1 strongly reduced, sternum devoid of median structures.

Glyphiulus melanoporus Mauriès & Nguyen Duy-Jacquemin, 1997

Material examined. 1 male, 1 female, 1 juv. (SCAU), China, Guangxi Zhuang Autonomous Region, Xiufeng District, Maomaotou Cave, [25°18'46.12"N, 110°16'12.64"E], 225 m el., deep zone, direct intuitive search, 15 November 2016, J. J. Wynne leg.

Notes. *G. melanoporus* is considered a troglophile. The type locality for this species is Skeleton Cave [25°17'13"N, 110°13'26"E] (Mauriès and Nguyen Duy-Jacquemin 1997). We collected this species from Maomaotou Cave, which represents a 21.1 km range expansion to the south of the type locality.

Habitat. For our specimens, we collected them within the deep zone of Maomaotou Cave. Sediment where specimens were collected was compacted and wet.

***Glyphiulus maocun* sp. nov.**

<http://zoobank.org/5CDE1D3A-71A2-48EA-B4BB-F9FDD20D860D>

Figs 4C, 18–20

Type material. Holotype male, China, Guangxi Zhuang Autonomous Region, Lingchuan County, Maocun Village, Liangfeng Cave [25°12'34.86"N, 110°31'56.8"E], 184 m el., deep zone, direct intuitive search, 18 November 2016, J.J. Wynne. Paratypes, 4 females, 4 juv. (SCAU), same data as holotype.

Etymology. The species name, *maocun*, is used as a noun in apposition and is the name of the village nearest to the type locality.

Diagnosis. This new species is similar to *G. melanoporus* (from caves in Guilin) in showing carinotaxy formula of collum I–IV+5c+6a+pc+ma. However, *G. maocun* sp. nov. is distinct from *G. melanoporus* by (1) carinotaxy formula of metaterga 2/2+I/

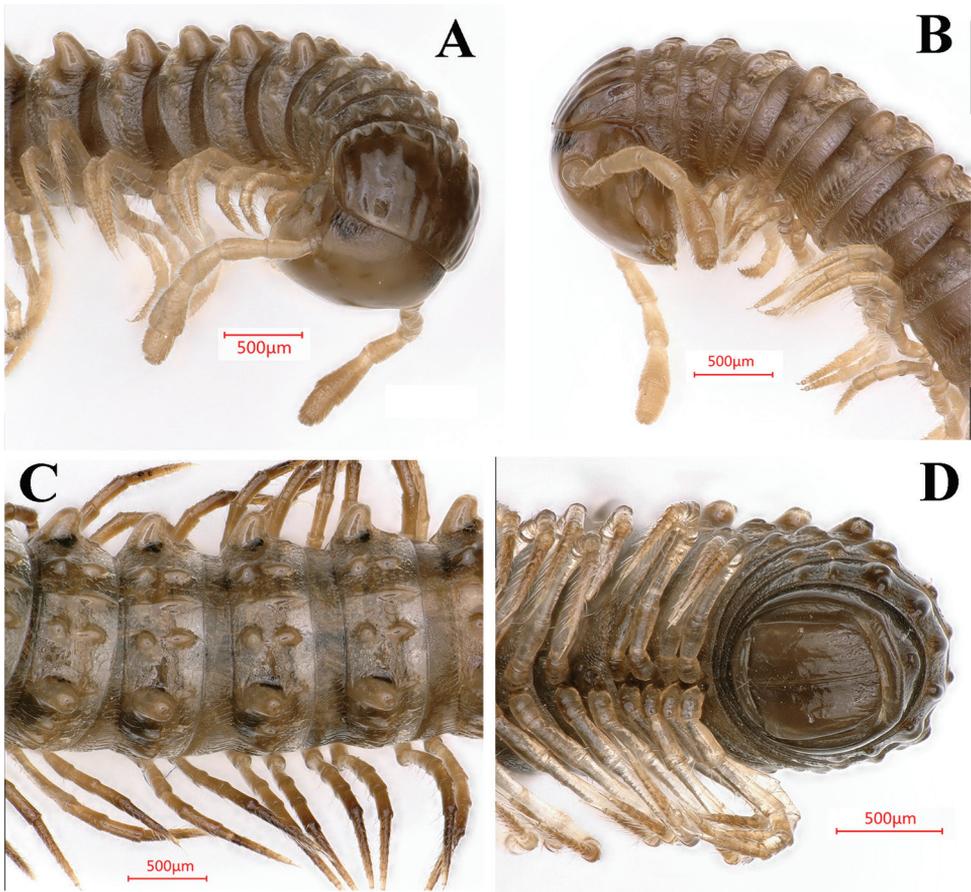


Figure 18. *Glyphiulus maocun* sp. nov., holotype. **A, B** Anterior part of body, sublateral views **C** mid-body rings, dorsal view **D** posterior part of body, ventral view.

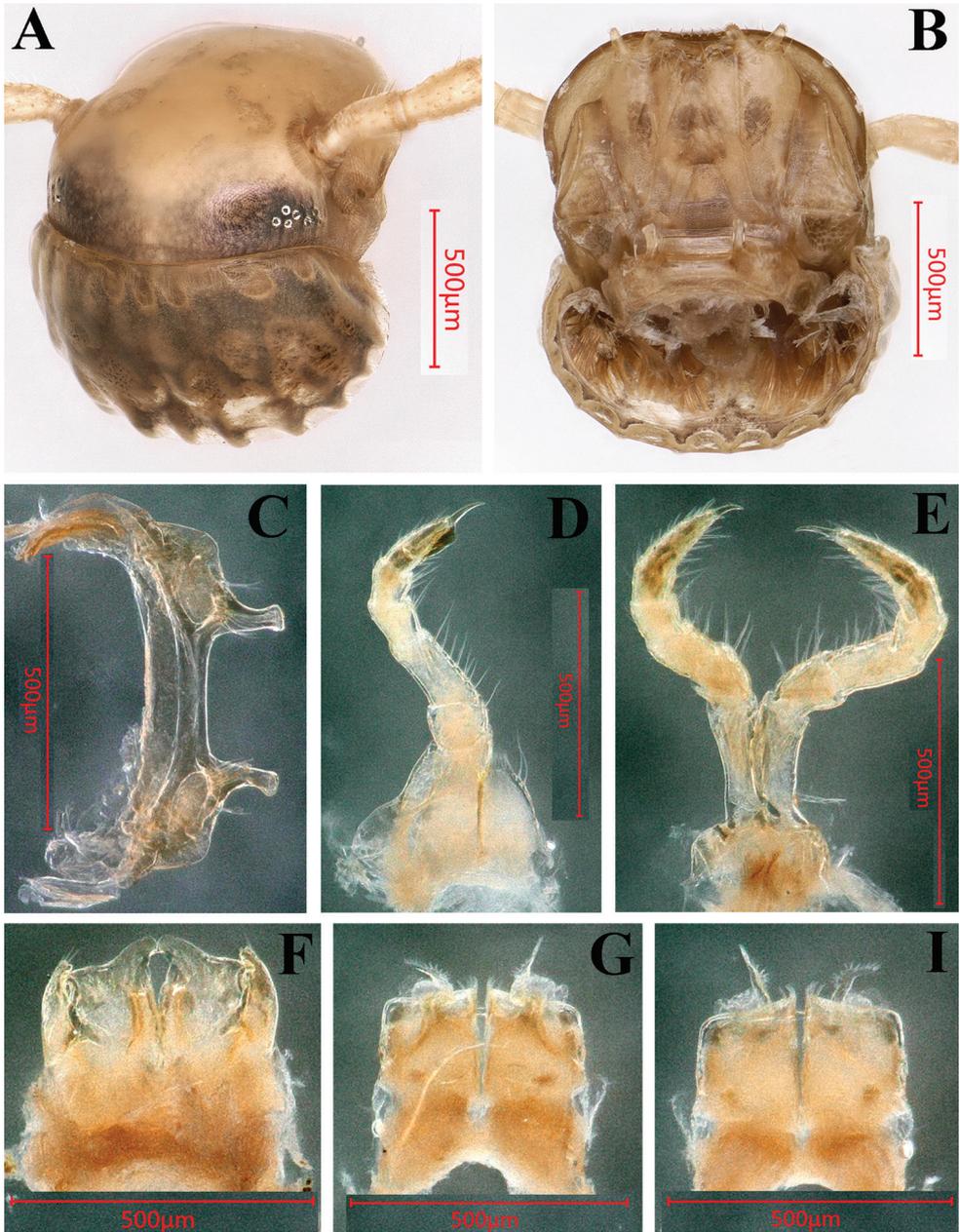


Figure 19. *Glyphiulus maocun* sp. nov., holotype. **A** Head and collum, dorsal view **B** head, collum, and legs 1, ventral view **C** legs 1, anterior view **D** leg 2, caudal view **E** legs 3, frontal view **F** anterior gonopods, caudal view **G** posterior gonopods, anterior view **H** posterior gonopods, caudal view.

i+3/3; (2) anterior gonopod with a conspicuous, high, curved downward process on coxosternum (Figs 19F, 20A); (3) posterior gonopod tip branch plumose flagellum (Figs 19G–I, 20B, C).

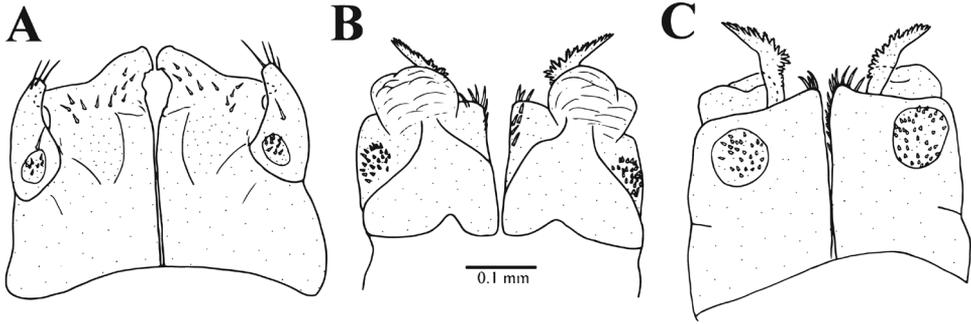


Figure 20. *Glyphiulus maocun* sp. nov., holotype. **A** Anterior gonopods, caudal view **B** posterior gonopods, anterior view **C** posterior gonopods, caudal view.

Description. Based on the type specimens. Lengths of both sexes *ca* 26–32 mm, mid-body rings round in cross-section, their widths and heights similar, 1.2–1.8 mm. **Coloration:** yellow-brown to brownish in alcohol. Ommatidia blackish (Fig. 18A). **Body:** with 46–54 podous rings + 2–1 apodous one(s) + telson. **Head:** clypeus with 4 teeth anteromedially. Each eye patch with about 8–12 ommatidium arranged in three irregular vertical rows (Figs 18A, 19A). Antennae long, antennomere 7 with four short apical cones (Fig. 18A, B). Gnathochilarium usually, with a separate promentum (Fig. 19B). **Exoskeleton:** Carinotaxy formula of collum I–IV+5c+6a+pc+ma, anterior margin crests lower (Fig. 19A). Subsequent metaterga strongly crested, carinotaxy formula 2/2+I/i+3/3. Ozoporiferous tubercles round (Fig. 18). Prozonae delicately alveolate; strictures and metazonae fine longitudinal striations. Rings 2 and 3 with long pleural flaps. Epiproct simple, with a short, low, rounded tubercle medially. Paraprocts rather regularly convex. Hypoproct broadly emarginated (Fig. 18D). ♂ legs 1 very strongly reduced, represented only by a sternum devoid of any median or paramedian structures but carrying 1+1 strongly separated prongs both curved anteriorly and bearing several strong setae (Fig. 18B, C). ♂ legs 2 with large coxae; penes oblong, each with two strong setae distolaterally (Fig. 19D). ♂ legs 3 with slender and elongate coxae (Fig. 19E). Legs slender, about 1.2 times as long as mid-body ring height. Claw simple, without any spine at base. **Anterior gonopods:** (Figs 19F, 20A) with a conspicuous, high, lobe-shaped, curved downward process on coxosternum, which is much higher than telopodite; telopodite slightly coiled, 1-segmented, lateral in position, with 2 or 3 strong apical setae. **Posterior gonopods:** (Figs 19G–I, 20B, C) laterally with a low, lateral lobe carrying a dozen of long setae, tip branch very slender and high, plumose flagellum.

Habitat. Specimens were collected within or at proximity to flood detritus.

Notes. Specimens exhibited no characteristics suggestive of cave adaptation. It had a pigmented cuticle and well-developed blackish ommatidia. We consider this species to be troglophilic within Liangfeng Cave. Subsequently, this species may have a larger, more regional distribution.

Discussion

Our work increased the number of subterranean-adapted millipedes from 34 to 38 species. With 564 known caves in Guangxi (Yuanhai Zhang, pers. comm. 2019), but a fraction (8.7% or 49 caves) of these caves have been examined for troglomorphic millipedes. The identification of six new species of millipedes from four caves in the Guilin area underscores the potential for many additional discoveries. For millipede-specific surveys, direct intuitive searches of selected cave deep zones (*sensu* Wynne et al. 2019) has been identified as the best technique; Mesibov et al. (1995) reported that four weeks of hand collecting during the fall was more efficient than an intensive pitfall trapping effort involving trapping seven days per month for over one year.

Conversely, while advancing our knowledge of regional troglomorphic millipede diversity stands to contribute significantly to the conservation value of the SCK, a more comprehensive understanding (i.e., for all cave-dwelling taxa) of regional diversity, as well as advancing procedures to assessing the vulnerability of cave systems to anthropogenic impact should be considered. Wynne et al. (2018, 2019) provides a systematic framework and guidance for sampling cave-dwelling arthropods using a repeatable framework, which can be modified for application in the SCK. Using such an approach, these data may be then be examined by applying principles similar to the cave vulnerability assessment developed by Tanalgo et al. (2018). Through such an effort, systematic techniques may be used to assemble robust and comparable landscape scale data, and each cave subsequently be evaluated for its vulnerability due to human activities.

Moreover, for conservation biologists and resource managers to best evaluate the importance of SCK cave biological diversity, we will require a more robust understanding of the distributional ranges of troglomorphic species (as well as other subterranean-restricted taxa). Specifically, while nearly 40 percent of troglomorphic millipedes were identified as single cave endemics, 14 troglobionts (including one whose range was expanded from this work) occurred within two or more caves. One species, *P. trifidus*, was confirmed within three caves in the Guilin region (two caves from this work, plus the type locality); the maximum distance between caves for this species was 59.7 km. Three additional subterranean-adapted species occurred in multiple caves with maximum distances ranging from 81.27 and 137.6 km (Table 3). As many troglomorphic arthropods are identified as short-range endemic species, occurring in a single cave or geological formation (Reddell 1994, Culver et al. 2000, Christman et al. 2005, Deharveng et al. 2008, Tian 2011, Harvey and Wynne 2014, Gao et al. 2018, Nitzu et al. 2018) and that rivers and valleys/ lowland areas often result in vicariance (Barr 1985, Faillie et al. 2015, Katz et al. 2018), the genetic relatedness of at least these three species should be further examined using genetic techniques. While these species may be morphological similar, we suggest they may be genetically distinct – potentially representing different subspecies or lineages.

We also reported a possible ‘disturbance relict’, *H. rukouqu* sp. nov., discovered within a cave entrance vegetation community. As similar cave entrance vegetation

communities have been identified as either supporting distinct relict plant communities and/or plant species in southern China (Monro et al. 2018), Easter Island, Chile (Wynne et al. 2014), and west-central New Mexico, USA (Lindsey 1951, Northup and Welbourn 1997, Wynne 2013), their importance in supporting cave-restricted arthropod populations demonstrated (Northup and Welbourn 1997, Wynne 2013, Wynne et al. 2014, Wynne and Shear 2016), and widespread land cover conversion of both lowlands and uplands has occurred in China since 1958, this finding warrants both additional research into this species distribution, as well as a larger scale examination of other potential 'disturbance relict' arthropod species within cave entrance vegetation communities of the SCK.

Although caves are often considered distinct from the surface environment, cave ecosystems are inextricably linked to surface processes. Caves require an allochthonous energy supply, which may include flood detritus, guano deposition from bats, birds and crickets, and dissolved organic materials that percolate from the surface. Thus, when humans adversely change the surface environment, the cave ecosystem may change as well. Deforestation (Trajano 2000, Ferreira and Horta 2001, Clements et al. 2006, Stone and Howarth 2007), intensive agriculture and water diversion (van Beynen and Townsend 2005, Stone and Howarth 2007, Harley et al. 2011), livestock grazing (Stone and Howarth 2007), alien species introductions (Elliott 1992, Reeves 1999, Taylor et al. 2003, Howarth et al. 2007, Price 2016), heavy metals and agrochemicals (Whitten 2009), and global climate change (Chevaldonné and Lejeune 2003, Mamola et al. 2018) have negatively affected both cave organisms and ecological processes.

Despite the impressive biological diversity found in China, there are no government regulations, nor is any government agency responsible for managing and protecting cave resources. Development projects typically progress in caverniferous regions and tourist caves are developed without consideration for subterranean resources and the rich biodiversity they often support (Whitten 2009). While we recognize environmental conditions are improving and environmental regulations have strengthened in China, Whitten (2009) and Cao et al. (2007) identified most of the aforementioned impacts continue to expand and severely stress both epigeal and hypogean ecosystems in southern extent of the country. Thus, we recommend monitoring environmental conditions of the surface and subsurface of caves identified as supporting rare endemic species populations and/or sensitive ecosystems.

This paper revealed that at least 38 troglomorphic millipede species occur in Guangxi. Other examples of SCK's high cave diversity includes at least 19 species of troglomorphic pseudoscorpions (Gao et al. 2018), 29 vascular plant species believed restricted to cave entrances (Monro et al. 2018), and the richest globally diversity of cavefishes with at least 154 species and nearly half of these species considered single cave endemics (Zhao et al. in press). As this work continues, we anticipate the number of subterranean-adapted millipedes, as well as other arthropod species will increase. Through ours and other efforts, we believe the SCK will ultimately emerge as a global hotspot for cave biological diversity.

Acknowledgements

Dr. Wang Jietao at the Wuhan Center, China Geological Survey provided fieldwork and logistical support and developed part of figure 1. We thank International Research Center on Karst in Guilin for additional logistical support. Mr. Zhang Yuanhai provided us with information regarding regional caves while Dr. Qiang Li provided cave coordinates for some of the caves examined in this study. Dr. Wu Zhuoting offered additional assistance with some of the Mandarin names. Dr. Sergei Golovatch provided us with invaluable peer-review comments leading to the improvement of this manuscript. Fieldwork was recognized as an Explorers Club flag expedition. The lead author was sponsored by the National Natural Science Foundation of China (Grant no. 31801956 and Grant no. 41871039) for work related to species' descriptions and manuscript preparation.

References

- Barr Jr TC (1967) Observations on the ecology of caves. *American Naturalist* 101: 475–491. <https://doi.org/10.1086/282512>
- Barr Jr TC (1985) Pattern and process in speciation of trechine beetles in eastern North America (Coleoptera: Carabidae: Trechinae). *Phylogeny and zoogeography of beetles and ants*, Junk, Dordrecht [1985 Sep 30]: 350–407.
- Benedict EM (1979) A new species of *Apochthonius* Chamberlin from Oregon (Pseudoscorpionida, Chthoniidae). *Journal of Arachnology* 7: 79–83.
- Bernard EC, Soto-Adames FN, Wynne JJ (2015) Collembola of Rapa Nui (Easter Island) with descriptions of five endemic cave-restricted species. *Zootaxa* 3949: 239–267. <https://doi.org/10.11646/zootaxa.3949.2.6>
- Cao J, Yang D, Zhang C, Jiang Z (2007) Karst ecosystem of Guangxi Zhuang Autonomous Region Constrained by Geological Setting: Relationship between carbonate rock exposure and vegetation coverage. *International Conference on Karst Hydrogeology and Ecosystems, USA*: 211–218.
- Chen Z, Decu V, Juberthie C, Ueno SI (2001) China. In: Juberthie C, Decu V (Eds) *Encyclopaedia Biospeologica, Part III*, Société Internationale de Biospéologie, Moulis, France, 1763–1781.
- Chevaldonné P, Lejeune C (2003) Regional warming-induced species shift in northwest Mediterranean marine caves. *Ecology Letters* 6: 371–379. <https://doi.org/10.1046/j.1461-0248.2003.00439.x>
- Christman MC, Culver DC, Madden MK, White D (2005) Patterns of endemism of the eastern North American cave fauna. *Journal of Biogeography* 32: 1442–1452. <https://doi.org/10.1111/j.1365-2699.2005.01263.x>
- Clarke AK (2006) Guangxi 2005 cave fauna report (China Caves Project). *YRC Bulletin*, Autumn 2006.
- Clements R, Sodhi NS, Schilthuizen M, Ng PK (2006) Limestone karsts of Southeast Asia: imperiled arks of biodiversity. *Bioscience* 56: 733–742. [https://doi.org/10.1641/0006-3568\(2006\)56\[733:LKOSAI\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)56[733:LKOSAI]2.0.CO;2)

- Culver DC, Master LL, Christman MC, Hobbs HH, III (2000) Obligate cave fauna of the 48 contiguous United States. *Conservation Biology* 14: 386–401. <https://doi.org/10.1046/j.1523-1739.2000.99026.x>
- Deharveng L, Bedos A (2000) The cave fauna of Southeast Asia: origin, evolution and ecology. In: Wilkens H, Culver DC, Humphreys WF (Eds) *Ecosystems of the World 30: Subterranean Ecosystems*, Elsevier, Amsterdam, 603–632.
- Deharveng L, Bréhier F, Bedos A, Tian MY, Li YB, Zhang F, Qin WG, Tan XF (2008) Mulun and surrounding karsts (Guangxi) host the richest cave fauna of China. *Subterranean Biology* 6: 75–79.
- Elliott WR (1992). Fire ants invade Texas caves. *American Caves Winter* 5: 13.
- Enghoff H, Golovatch SI, Short M, Stoev P, Wesener T (2015) Diplopoda – taxonomic overview. In: Minelli A (Ed) *Treatise on Zoology-Anatomy, Taxonomy, Biology. The Myriapoda* 2: 365–457.
- Faille A, Tänzler R, Toussaint EF (2015) On the way to speciation: shedding light on the karstic phylogeography of the microendemic cave beetle *Aphaenops cerberus* in the Pyrenees. *Journal of Heredity* 106: 692–699. <https://doi.org/10.1093/jhered/eshv078>
- Ferreira RL, Horta LCS (2001) Natural and human impacts on invertebrate communities in Brazilian caves. *Revista Brasileira de Biologia* 61: 7–17. <https://doi.org/10.1590/S0034-71082001000100003>
- Gao Z, Wynne JJ, Zhang F (2018) Two new species of cave-adapted pseudoscorpions (Pseudoscorpiones, Neobisiidae, Chthoniidae) from Guangxi, China. *Journal of Arachnology* 46: 345–354. <https://doi.org/10.1636/JoA-S-17-063.1>
- Golovatch SI, Geoffroy JJ (2006) Review of the Southeast Asian millipede genus *Pacidesmus* Golovatch, with the description of a new troglobitic species from southern China (Diplopoda: Polydesmida: Polydesmidae). *Zootaxa* 1325: 363–368. <https://doi.org/10.11646/zootaxa.1325.1.24>
- Golovatch SI, Geoffroy JJ, Mauriès JP (2006) Review of the millipede genus *Hyleoglomeris* Verhoeff, 1910 (Diplopoda, Glomerida, Glomeridae), with descriptions of new species from caves in southeast Asia. *Zoosystema* 28: 887–915.
- Golovatch SI, Geoffroy JJ, Mauriès JP, VandenSpiegel D (2007) 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: 7–49.
- Golovatch SI, Geoffroy JJ, Mauriès JP, VandenSpiegel D (2009a) Review of the millipede genus *Eutrichodesmus* Silvestri, 1910 (Diplopoda, Polydesmida, Haplodesmidae), with descriptions of new species. *ZooKeys* 12: 1–46. <https://doi.org/10.3897/zookeys.12.167>
- Golovatch, SI, Geoffroy, JJ, Mauriès JP, VandenSpiegel D (2009b) Review of the millipede family Haplodesmidae, with descriptions of some new or poorly-known species (Diplopoda, Polydesmida). *ZooKeys* 7: 1–53. <https://doi.org/10.3897/zookeys.7.117>
- Golovatch SI, Geoffroy JJ, Mauriès JP (2010a) Two new species of the millipede genus *Desmoxytes* Chamberlin, 1923 (Diplopoda: Polydesmida: Paradoxosomatidae) from caves in southern China. *Arthropoda Selecta* 19: 57–61. <https://doi.org/10.15298/arthscl.19.2.01>
- Golovatch SI, Geoffroy JJ, Mauriès JP (2010b) Review of the millipede genus *Pacidesmus* Golovatch, 1991, with descriptions of three new species from caves in southern China (Diplopoda: Polydesmida: Polydesmidae). *Tropical Natural History* 10: 159–169.

- Golovatch SI, Geoffroy JJ, Mauriès JP, VandenSpiegel D (2011a) Two new species of the millipede genus *Hypocambala* Silvestri, 1895 from China and Vietnam (Diplopoda: Spirostreptida: Cambalopsidae). *Arthropoda Selecta* 20: 167–174. <https://doi.org/10.15298/arthsel.20.3.03>
- Golovatch SI, Geoffroy JJ, Mauriès JP (2011b) New species of the millipede genus *Glyphiulus* Gervais, 1847 from the *granulatus*-group (Diplopoda, Spirostreptida, Cambalopsidae). *Arthropoda Selecta* 20: 65–114. <https://doi.org/10.15298/arthsel.20.2.01>
- Golovatch SI, Geoffroy JJ, Mauriès JP, VandenSpiegel D (2011c) New species of the millipede genus *Glyphiulus* Gervais, 1847 from the *javanicus*-group (Diplopoda: Spirostreptida: Cambalopsidae). *Arthropoda Selecta* 20: 149–165. <https://doi.org/10.15298/arthsel.20.3.02>
- Golovatch SI, Liu WX, Geoffroy JJ (2012a) Review of the millipede genus *Hyleoglomeris* Verhoeff, 1910 in China, with descriptions of new species (Diplopoda, Glomerida, Glomeridae). *Zootaxa* 3358: 1–27. <https://doi.org/10.11646/zootaxa.3358.1.1>
- Golovatch SI, Li Y, Liu W, Geoffroy JJ (2012b) Three new cavernicolous species of dragon millipedes, genus *Desmoxytes* Chamberlin, 1923, from southern China, with notes on a formal congener from the Philippines (Diplopoda, Polydesmida, Paradoxosomatidae). *ZooKeys* 185: 1–18. <https://doi.org/10.3897/zookeys.185.3082>
- Golovatch SI, Li Y, Liu W, Geoffroy JJ (2012c) One new and two little-known species of the millipede family Polydesmidae from southern China (Diplopoda: Polydesmida). *Arthropoda Selecta* 21: 131–136. <https://doi.org/10.15298/arthsel.21.2.02>
- Golovatch SI, Geoffroy JJ (2014) On some new or poorly-known species of the millipede family Polydesmidae from southern China (Diplopoda: Polydesmida). *Russian Entomological Journal* 23: 91–105. <https://doi.org/10.15298/rusentj.23.2.01>
- 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>
- Golovatch SI, Geoffroy JJ, Mauriès JP, VandenSpiegel D (2015) Review of the millipede genus *Eutrichodesmus* Silvestri, 1910, in China, with descriptions of new cavernicolous species (Diplopoda, Polydesmida, Haplodesmidae). *Zookeys* 505: 1–34. <https://doi.org/10.3897/zookeys.505.9862>
- Harley GL, Polk JS, North LA, Reeder PP (2011) Application of a cave inventory system to stimulate development of management strategies: The case of west-central Florida, USA. *Journal of Environmental Management* 92: 2547–2557. <https://doi.org/10.1016/j.jenvman.2011.05.020>
- Harvey MS, Wynne JJ (2014) Troglomorphic pseudoscorpions (Arachnida: Pseudoscorpiones) of northern Arizona, with descriptions of two new short-range endemic species. *Journal of Arachnology* 42: 205–219. <https://doi.org/10.1636/K14-34.1>
- Howarth FG (1980) The Zoogeography of Specialized Cave Animals: A Bioclimatic Model. *Evolution* 34: 394–406. <https://doi.org/10.1111/j.1558-5646.1980.tb04827.x>
- Howarth FG (1982) Bioclimatic and geological factors governing the evolution and distribution of Hawaiian cave insects. *Entomologia Generalis* 8: 17–26.
- Howarth FG (1983) Ecology of cave arthropods. *Annual Review of Entomology* 28: 365–389. <https://doi.org/10.1146/annurev.en.28.010183.002053>

- Howarth FG, James SA, McDowell W, Preston DJ, Imada CT (2007). Identification of roots in lava tube caves using molecular techniques: Implications for conservation of cave arthropod faunas. *Journal of Insect Conservation* 11: 251–261. <https://doi.org/10.1007/s10841-006-9040-y>
- Jiang X, Guo X, Chen H, Xie Z (2018) Four new species of the *Glyphiulus javanicus* group from southern China (Diplopoda, Spirostreptida, Cambalopsidae). *ZooKeys* 741: 155–179. <https://doi.org/10.3897/zookeys.741.23223>
- Katz AD, Taylor SJ, Davis MA (2018) At the confluence of vicariance and dispersal: Phylogeography of cavernicolous springtails (Collembola: Arrhopalitidae, Tomoceridae) codistributed across a geologically complex karst landscape in Illinois and Missouri. *Ecology and Evolution* 8: 10306–10325. <https://doi.org/10.1002/ece3.4507>
- Lindsey AA (1951) Vegetation and habitats in a southwestern volcanic area. *Ecological Monographs* 21: 227–253. <https://doi.org/10.2307/1943559>
- Likhitrakarn N, Golovatch SI, Srisonchai R, Panha S (2017) A new species of *Trichopeltis* Pocock, 1894 from southern China, with a checklist and a distribution map of *Trichopeltis* species (Diplopoda, Polydesmida, Cryptodesmidae). *ZooKeys* 725: 123–137. <https://doi.org/10.3897/zookeys.725.22014>
- Liu WX, Tian MY (2013) Four new cavernicolous species of the millipede genus *Eutrichodesmus* Silvestri, 1910 from southern China (Diplopoda: Polydesmida: Haplodesmidae). *Zootaxa* 3734: 281–291. <https://doi.org/10.11646/zootaxa.3734.2.11>
- Liu WX, Golovatch SI, Tian MY (2014) A review of the dragon millipede genus *Desmoxytes* Chamberlin, 1923 in China, with descriptions of four new species (Diplopoda: Polydesmida: Paradoxosomatidae). *ZooKeys* 448: 9–26. <https://doi.org/10.3897/zookeys.448.8081>
- Liu WX, Tian MY (2015a) A checklist of millipede genus *Hyleoglomeris* Verhoeff, 1910 in mainland China, with descriptions of seven new species (Diplopoda, Glomerida, Glomeridae). *Zootaxa* 4032: 103–116. <https://doi.org/10.11646/zootaxa.4032.1.5>
- Liu WX, Tian MY (2015b) Occurrence of the millipede genus *Piccola* Attems, 1953 in China (Diplopoda: Polydesmida: Paradoxosomatidae). *Zootaxa* 3904: 403–408. <https://doi.org/10.11646/zootaxa.3904.3.5>
- Liu WX, Tian MY (2015c) Two new cave-dwelling species of the millipede genus *Paracortina* Wang & Zhang, 1993 from southern China (Diplopoda, Callipodida, Paracortinidae). *ZooKeys* 517: 123–140. <https://doi.org/10.3897/zookeys.517.9949>
- Liu WX, Golovatch SI, Tian MY (2016) Six new species of dragon millipedes, genus *Desmoxytes* Chamberlin, 1923, mostly from caves in China (Diplopoda, Polydesmida, Paradoxosomatidae). *ZooKeys* 557: 1–24. <https://doi.org/10.3897/zookeys.557.7825>
- Liu WX, Golovatch SI, Wesener T, Tian MY (2017a) Convergent Evolution of Unique Morphological Adaptations to a Subterranean Environment in Cave Millipedes (Diplopoda). *PLoS One* 12: e0170717. <https://doi.org/10.1371/journal.pone.0170717>
- Liu WX, Golovatch SI, Wesener T (2017b) Four new species of the millipede genus *Eutrichodesmus* Silvestri, 1910 from Laos, including two with reduced ozopores (Diplopoda, Polydesmida, Haplodesmidae). *ZooKeys* 660: 43–65. <https://doi.org/10.3897/zookeys.660.11780>
- Loksa I (1960) Einige neue Diplopoden- und Chilopodenaren aus chinesischen Höhlen. *Acta Zoologica Academiae Scientiarum Hungaricae* 6: 135–148.

- Mauriès JP, Nguyen Duy-Jacquemin M (1997) Nouveaux craspedosomides et glyphiulides cavernicoles de Chine (Diplopoda). *Mémoires de Biospéologie* 24: 49–62.
- Mammola S, Goodacre SL, Isaia M (2018) Climate change may drive cave spiders to extinction. *Ecography* 41: 233–243. <https://doi.org/10.1111/ecog.02902>
- Mesibov R, Taylor RJ, Brereton RN (1995) Relative efficiency of pitfall trapping and hand-collecting from plots for sampling of millipedes. *Biodiversity and Conservation* 4: 429–439. <https://doi.org/10.1007/BF00058426>
- Minelli A (2015) *Treatise on Zoology-Anatomy, Taxonomy, Biology. The Myriapoda 2*. Brill., 482 pp. <https://doi.org/10.1163/9789004188273>
- Mockford EL, Wynne JJ (2013) Genus *Cyptophania* Banks (Psocodea: Lepidopsocidae): Unique features, augmented description of the genotype, and descriptions of three new species. *Zootaxa* 3702: 437–449. <https://doi.org/10.11646/zootaxa.3702.5.3>
- Monro AK, Bystriakova N, Fu L, Wen F, Wei Y, (2018) Discovery of a diverse cave flora in China. *PloS One* 13: e0190801. <https://doi.org/10.1371/journal.pone.0190801>
- Nitzu E, Vlaicu M, Giurginca A, Meleg IN, Popa I, Nae A, Baba Ş (2018) Assessing preservation priorities of caves and karst areas using the frequency of endemic cave-dwelling species. *International Journal of Speleology* 47: 43–52. <https://doi.org/10.5038/1827-806X.47.1.2147>
- Northup DE, Welbourn WC (1997) Life in the twilight zone – Lava tube ecology, natural history of El Malpais National Monument. *New Mexico Bureau of Mines and Mineral Resources Bulletin* 156: 69–82.
- Peck SB (1970) The terrestrial arthropod fauna of Florida caves. *Florida Entomologist* 53: 203–207. <https://doi.org/10.2307/3493189>
- Price L (2016) An introduction to some cave fauna of Malaysia and Thailand. *Acta Carsologica* 33: 311–317. <https://doi.org/10.2307/3493189>
- Ravbar N (2016) The earliest Chinese karstologist Xu Xiake. *Acta Carsologica* 32: 243–254. <https://doi.org/10.3986/ac.v32i1.376>
- Reddell JR (1994) The cave fauna of Texas with special reference to the western Edwards Plateau. In: Elliott WR, Veni G (Eds) *The caves and karst of Texas*. National Speleological Society, Huntsville, 31–50.
- Reeves WK (1999) Exotic species of North American Caves. In: Henderson K (Ed.) *Proceedings of the 1999 National Cave and Karst management symposium, Chattanooga, Tennessee: National Cave & Karst Management Symposia*, 164–166.
- Sket B (2008) Can we agree on an ecological classification of subterranean animals? *Journal of Natural History* 42: 1549–1563. <https://doi.org/10.1080/00222930801995762>
- Srisonchai R, Enghoff H, Likhitrakarn N, Panha S (2018) A revision of dragon millipedes I: genus *Hylomus* Chamberlin, 1923, with the description of eight new species (Diplopoda, Polydesmida, Paradoxosomatidae). *ZooKeys* 761: 1–177. <https://doi.org/10.3897/zookeys.761.24214>
- Stone FD, Howarth FG (2007) Hawaiian cave biology: status of conservation and management. In: *Proceedings of the 2005 National Cave and Karst Management Symposium; Albany, New York [October 31–November 4, 2005]*, 21–26.
- Sweeting MM (1995) *Karst in China. Its geomorphology and environment*. Springer Verlag, New York, 265 pp. <https://doi.org/10.1007/978-3-642-79520-6>

- Taiti S, Wynne JJ (2015) The terrestrial Isopoda (Crustacea, Oniscidea) of Rapa Nui (Easter Island), with descriptions of two new species. *ZooKeys* 515: 27–49. <https://doi.org/10.3897/zookeys.515.9477>
- Tanalgo KC, Tabora JA, Hughes AC (2018) Bat cave vulnerability index (BCVI): A holistic rapid assessment tool to identify priorities for effective cave conservation in the tropics. *Ecological Indicators* 89: 852–860. <https://doi.org/10.1016/j.ecolind.2017.11.064>
- Taylor SJ, Krejca J, Smith JE, Block VR, Hutto F (2003) Investigation of the potential for red imported fire ant (*Solenopsis invicta*) impacts on rare karst invertebrates at Fort Hood, Texas: A field study. In: Illinois Bexar County Karst Invertebrates Draft Recovery Plan Natural History Survey. Center for Biodiversity Technical Report, vol. 28, 1–153.
- Tian MY (2011) A new subgenus and two new species of the troglobitic genus *Dongodytes* Deuve from Guangxi, China (Coleoptera, Carabidae). *Subterranean Biology* 8: 57–64. <https://doi.org/10.3897/subtbiol.8.1232>
- Trajano E (2000) Cave faunas in the Atlantic tropical rain forest: Composition, ecology and conservation. *Biotropica* 32: 882–893. <https://doi.org/10.1111/j.1744-7429.2000.tb00626.x>
- van Beynen P, Townsend K (2005) A disturbance index for karst environments. *Environmental Management* 36: 101–116. <https://doi.org/10.1007/s00267-004-0265-9>
- Whitten T (2009) Applying ecology for cave management in China and neighboring countries. *Journal of Applied Ecology* 46: 520–523. <https://doi.org/10.1111/j.1365-2664.2009.01630.x>
- Wynne JJ (2013) Inventory, conservation and management of lava tube caves at El Malpais National Monument, New Mexico. *Park Science* 30: 45–55.
- Wynne JJ, Shear WA (2016) A new millipede (*Austrotyla awishashola*, n. sp., Diplopoda, Chordeumatida, Conotylidae) from New Mexico, USA, and the importance of cave moss gardens as refugial habitats. *Zootaxa* 4084: 285–292. <https://doi.org/10.11646/zootaxa.4084.2.8>
- Wynne JJ, Bernard EC, Howarth FG, Sommer S, Soto-Adames FN, Taiti S, Mockford EL, Horrocks M, Pakarati L, Pakarati-Hotus V (2014) Disturbance relicts in a rapidly changing World: The Rapa Nui (Easter Island) factor. *BioScience* 64: 711–718. <https://doi.org/10.1093/biosci/biu090>
- Wynne JJ, Sommer S, Howarth FG, Dickson BG, Voyles KD (2018) Capturing arthropod diversity in complex cave systems. *Diversity and Distributions* 24: 1478–1491. <https://doi.org/10.1111/ddi.12772>
- Wynne JJ, Howarth FG, Sommer S, Dickson BG (2019) Fifty years of cave arthropod sampling: techniques and best practices. *International Journal of Speleology* 48: 33–48. <https://doi.org/10.5038/1827-806X.48.1.2231>
- Zhang CZ, Li ZY (1981) Bilinguidae family nov. of Diplopoda in karst landform of south China. *Acta Zootaxonomica Sinica* 6: 373–377. [In Chinese]
- Zhao Y, Gluesenkamp A, Fenolio D, Soares D, Niemiller M, Bichuette M-E, Chakrabarty P (in press) The species diversity and conservation of cavefishes in China. In: Wynne JJ (Ed.) *Cave Ecology: Drivers of Diversity and Speciation*. NOVA Science Publishers, NY.