



# A tarsal spinning organ in glomeridesmid millipedes (Diplopoda: Pentazonia: Glomeridesmida)

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## Abstract

The production of sticky threads from spinnerets is known from various myriapod groups including some representatives of the millipedes (Diplopoda). In Diplopoda the thread-producing glands are mostly seta-like and positioned terminally on the telson, and the secretion product is typically used to build molting chambers or egg sacs. So far, no such secretions or organs have been documented for the subgroup Pentazonia. Here we describe thread-producing glands from the species-poor Glomeridesmida. These putative spinning organs are single circular fields of small pores (spinning fields) positioned on the outer side of the tarsi of all walking legs of mature and juvenile individuals of both sexes. These pores are the openings of cuticular tubuli (conducting canals), which extend from the tarsus to an aggregation of cells, a putative gland, within the femur. In several specimens thin threads were observed to be extruded from the pores. The tarsal spinning fields are present in all 21 investigated Glomeridesmida morphospecies, including Termitodesmidae and Glomeridesmidae from South East Asia, the Indian subcontinent, Oceania, and South and Central America. These organs might constitute an apomorphic character of the Glomeridesmida, as similar organs are absent in other Myriapoda. The function of the extruded threads in Glomeridesmida remains speculative, because observations of living specimens of the group are almost non-existing. We suggest that the secretion might be used for defense, to build molting chambers or to secure tunnels burrowed in the substrate.

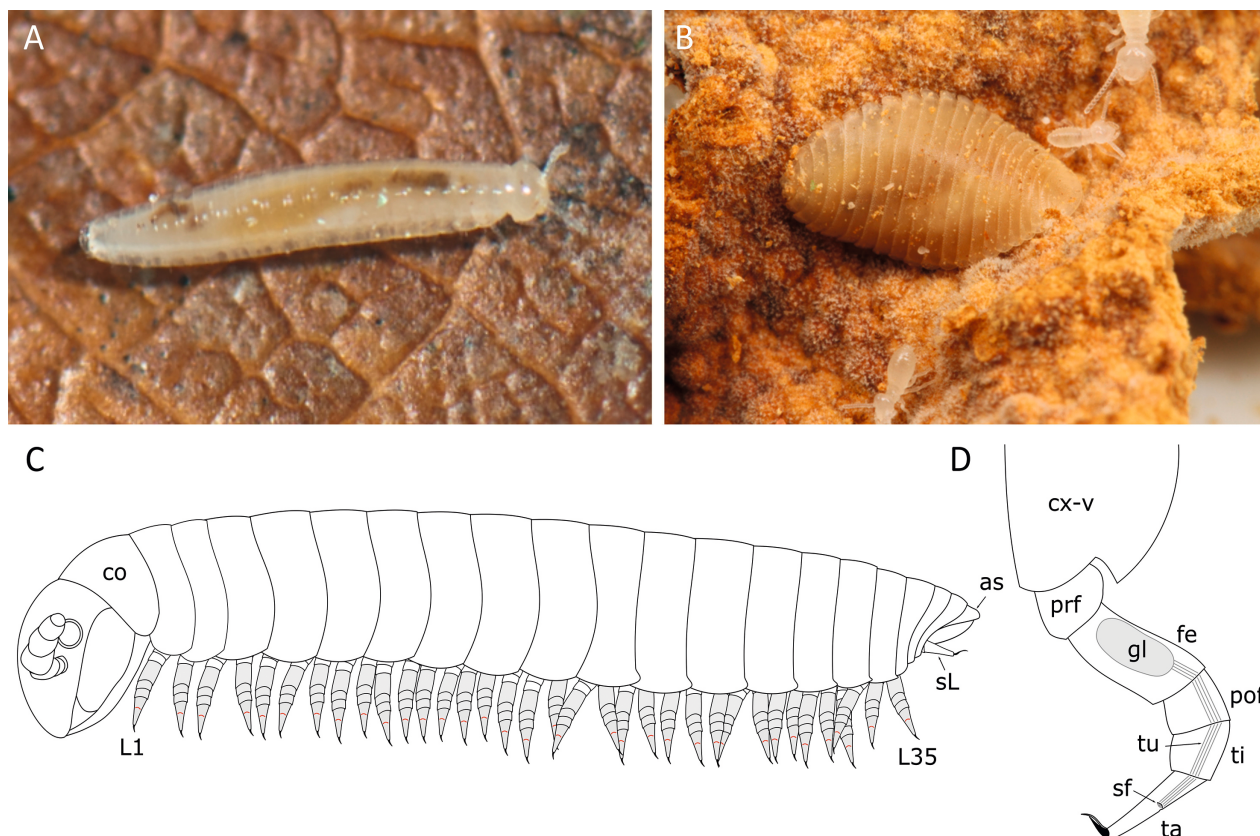
## Keywords

exocrine gland, *Glomeridesmus*, leg, Limacomorpha, scanning electron microscopy, silk, spinnerets, *Termitodesmus*

## 1. Introduction

Exocrine glands, which produce superficially silk-like threads and are often referred to as spinning organs or spinnerets, can be found in several Myriapoda taxa, including millipedes (Diplopoda), and differ in their

structure and position on the body. Spinning glands are not known for Pauropoda but are present in Symphyla, where they open on appendages of the preanal segment (spinnerets) (Verhoeff 1934; Szucsich and Scheller



**Figure 1.** Glomeridesmida and the distribution of the tarsal spinning organ. **A:** Glomeridesmidae (*Glomeridesmus* cf. *javanicus*), photograph of living specimen in Indonesia by Jan-Philip Oeyen. **B:** Termitodesmidae (*Termitodesmus* sp.) in a termite nest in Malaysia, photograph of living specimen by Munetoshi Maruyama and Taisuke Kanao. **C:** Habitus of adult female with 35+1 legs, schematic drawing, each walking leg is equipped with a spinning organ. **D:** Schematic representation of the spinning organ in a walking leg. **Abbreviations:** as = anal shield, co = collum, cx = coxa, fe = femur, gl = glandular cells, L1 = walking leg 1, L35 = walking leg 35, pof = postfemur, prf = prefemur, sf = spinning field, sL = sensory leg, ta = tarsus, ti = tibia, tu = tubuli, v = stigmatic plate.

2011). In Symphyla the secreted threads can be attached to the ground and used for abseiling, and as defense by blocking the passage for predators in narrow crevices (Verhoeff 1934; Dunger 1983; Betz and Kölsch 2004). Lithobiomorph centipedes (Chilopoda, Lithobiomorpha) produce long sticky fibers, which are used for defense and predation, from telopodal pores on the four distal podomeres of the posterior leg pairs 12–15 (Blower 1952; Rosenberg and Müller 2009; Kenning et al. 2019). When disturbed, many Lithobiomorpha raise their ultimate legs and release a milky secretion, which hardens immediately and can entangle predators as well as prey (Verhoeff 1925; Attems 1926; von Byern et al. 2017; Kenning et al. 2019). Within Diplopoda, exocrine glands which release threads can be found in the Polyxenida, Polydesmida, Nematophora, and potentially in the Siphoniulida and Siphonophorida. Some male pincushion millipedes (Polyxenida, Polyxenidae) possess coxal spinning glands on their 2<sup>nd</sup> leg pair associated with their gonopores (penes), which secrete threads for the placement of sperm (Schömann 1956; Huynh and Veenstra 2016). Furthermore, male Polyxenidae produce guide threads from glands on leg-pairs 8 and 9 to help females find fresh spermatophores (Schömann and Schaller 1954; Schömann 1956). Polydesmida and Nematophora (Callicopida, Chordeumatida, Stemmiulida) share terminal

fiber-producing glands or spinnerets, which are located on the epiproct of the telson, and largely resemble setae (Verhoeff 1928; Adis et al. 2000; Shear 2008; Enghoff and Akkari 2011; Enghoff and Reboleira 2013; Blanke and Wesener 2014; Iniesta and Ferreira 2015; Fiemapong et al. 2017). A detailed overview of these spinnerets in Polydesmida and Nematophora was provided by Shear (2008). In the Polydesmida and Nematophora the (silk-like) threads produced by the spinnerets are used to build molting chambers or in some cases egg-sacs (Adis et al. 2000; Shear 2008; Enghoff and Akkari 2011). Similar telsonian spinnerets can also be found in the enigmatic Siphoniulida (Sierwald et al. 2003; Liu et al. 2017), although the homology of these terminal spinning organs among the orders remains unknown (Sierwald et al. 2003; Shear 2008). Furthermore, tergal setae, which extrude a silk-like substance, might be present in the Siphonophorida (Marek and Bond 2006; Read and Enghoff 2009; Marek et al. 2012, 2016). The internal morphology of these glands and the chemical composition of the secreted threads in millipedes is largely unknown, but staining experiments show, that it is not true silk (i.e. made of fibrous protein) but consists of mucopolysaccharides in the Polydesmida (Adis et al. 2000).

For the Pentazonia, which include large and conspicuous animals like the Holarctic pill millipedes (*Glomerida*)

and the giant pill-millipedes (Sphaerotheriida), as well as the small and poorly known glomeridesmid millipedes (Glomeridesmida) (Enghoff et al. 2015), no spinning organs or spinning activity have been reported so far. Silvestri (1902, 1903) probably misinterpreted the tips of the sensory legs in Glomeridesmida as cylindrical spinning organs opening on the preanal tergite. The taxon Glomeridesmida is among the least-diverse and least-studied millipede orders, and its members are thought to be particularly similar to the chilognathan ground-plan (Enghoff 1990). Glomeridesmida comprises 36 described species from South-East Asia, India, and South and Central America (undescribed species are also known from Oceania: Shelley 2011), classified in two families, Glomeridesmidae (Fig. 1A) and Termitodesmidae (Fig. 1B) (Jeekel 2003; Enghoff et al. 2015; Wesener et al. 2021). Most of the few described species are only known from their type series, the majority of them collected more than 100 years ago (Jeekel 2003). Unlike Helminthomorpha and Glomerida, which possess defense secretions (Shear et al. 2011; Shear 2015), or the strongly sclerotized Glomerida and Sphaerotheriida, which can roll into a ball (Blanke and Wesener 2014; Enghoff et al. 2015), the weakly sclerotized Glomeridesmida appear to be relatively defenseless against predation. Observations of living specimens and therefore information on the behavior and ecology of this group are rare and mostly anecdotal (Escherich 1911; Hirst 1913; Wesener et al. 2021). Observations show that *Glomeridesmus spelaeus* Iniesta & Wesener, 2012 is able to dig tunnels into compact substrate (Iniesta et al. 2012), and that *Termitodesmus* Silvestri, 1911 (Escherich 1911; Hirst 1913) and *Glomeridesmus* Gervais, 1844 (Wesener et al. 2021) are capable of (relatively) fast and swift movements, showing great flexibility of the body.

Here we present first evidence for the presence of tarsal thread-producing organs (putative spinning organs) in the Glomeridesmida combining scanning electron microscopy, histology, and light microscopy.

## 2. Methods

### 2.1. Abbreviations

**FMNH** – Field Museum of Natural History, Chicago, USA; **ISLA** – Subterranean Invertebrate Collection of Lavras, Center for Studies on Subterranean Biology, Federal University of Lavras, Brazil; **LM** – Light microscopy; **MHNG** – Muséum d'histoire naturelle de la ville de Genève, Geneva, Switzerland; **NHMD** – Natural History Museum of Denmark, University of Copenhagen, Denmark; **SEM** – Scanning electron microscopy; **SMNG** – Senckenberg Museum für Naturkunde Görlitz, Germany; **VMNH** – Virginia Museum of Natural History, Martinsville, USA; **ZCSWU** – Zoological Collection of Srinakharinwirot University, Bangkok, Thailand; **ZFMK** – Zoological Research Museum A. Koenig, Leibniz Institute for Animal Biodiversity, Bonn, Germany.

### 2.2. Material examined

19 morphospecies of the family Glomeridesmidae from South East Asia, the Indian subcontinent, Oceania, and South and Central America, spanning the known geographical distribution of the family, and two morphospecies of the family Termitodesmidae from Vietnam and Malaysia were studied. Investigated specimens included mature females (20 tergites (T) + anal shield (AS)) and males (19 tergites + anal shield) and immatures/juveniles (9–19 tergites + anal shield) (tergite number including collum). All material, including mostly undescribed species, is deposited in the collections of different museums (Table 1) and had initially been fixed and stored in ethanol (70% or 96%). Additional images are provided as supplementary files (Figs S1–S5; <https://doi.org/10.3897/asp.79.e70002.suppl1>).

### 2.3. Scanning electron microscopy (SEM)

To study the external morphology and structure of the putative spinning organs SEM was used. SEM data was obtained for three *Glomeridesmus* and one *Termitodesmus* morphospecies (Table 1). Specimens were dehydrated in an ascending ethanol series and dried overnight. The dried samples were sputtered with gold (ca 35 nm) using a Cressington 108 auto sputter coater (TESCAN GmbH, Dortmund, Germany). Images were obtained using a Zeiss Sigma 300 VP SEM (Carl Zeiss AG, Oberkochen, Germany) at the ZFMK. Furthermore, SEM images previously obtained for *Glomeridesmus* spp. (Philippines, Ecuador) and *Termitodesmus* sp. (Malaysia) by TW and for *Glomeridesmus* sp. (Ecuador) by William A. Shear, were checked for the absence or presence of the described structure.

### 2.4. Light microscopy (LM) and histology

The legs were examined microscopically with transmitted light to check for the presence of the putative spinning organs and to investigate their internal morphology. Legs, unstained or stained (Table 1) for 3–4 minutes with 1% Toluidine blue (PanReac AppliChem, ITW Reagents (Chicago, USA), A3842.0010) to enhance contrast, and subsequently washed with ethanol, were temporarily mounted onto microscopic slides, and investigated with an Olympus BX51 light microscope (Olympus, Shinjuku, Tokyo, Japan).

Histological sections were obtained for mid-body legs of a female *Glomeridesmus* cf. *sumatranus* Pocock, 1894 (SUM06/08 01). Legs were embedded in epoxy resin (Araldite CY212, Agar Scientific Ltd (Stansted, UK), R1030) and semi-thin sections with a thickness of 0.5 µm were obtained with a Leica HistoCore NANOCUT R microtome (Leica Biosystems, Wetzlar, Germany) with a DiATOME histo Jumbo diamond blade (Diatome Ltd,



**Table 1.** Material examined. **Abbreviations:** H = histology, LM = light microscopy without Toluidine, LMT = light microscopy with Toluidine, SEM = scanning electron microscopy, <sup>TW</sup> = SEM images obtained previously by TW, <sup>WS</sup> = SEM images obtained previously by William A. Shear.

Species	Locality	Method
<i>Glomeridesmus siamensis</i> Wesener, Wongthamwanich & Moritz, 2021	THAILAND • 1 ♂, 1 ♀, 2 juv (19T+AS); Krabi Province, N. of Krabi Town, western aspect of Tiger Cave temple (Wat Tham Suea); 08°07'23.8"N, 098°55'18.9"E; 27.VII.2018; Wesener, Wongthamwanich, Nawaneti Wong, Moritz leg.; overgrown rocks next to rubber plantation; ZCSWU-MyrD000011, ZFMK-MYR10302, ZFMK-MYR10301; ZFMK-MYR10304	SEM + LM
<i>Glomeridesmus spelaus</i> Iniesta & Wesener, 2012	BRAZIL • 1 ♀; Pará, Curionópolis, iron cave SL 31; E 0650189m, N 9339714m; R.A. Zampaulo, leg.; in bat guano pile far from entrance; ISLA MII GEM 176150	LMT
<i>Glomeridesmus</i> cf. <i>sumatranus</i> Pocock, 1894	INDONESIA • 1 ♂, 1 ♀, 2 juv (19+AS; 15+AS); Sumatra, West Sumatra Province, Mt. Merapi, ca. 15 km SE of Bukittinggi; 0°23'32"S, 100°26'54"E; 1650–1700 m a.s.l.; 4.VI.2006; A. Schulz leg.; hill forest; MHNG SUM06/08 01	SEM + LMT + H
<i>Glomeridesmus</i> sp.	INDONESIA • 1 ♂, 1 ♀, 1 juv (19T+AS); Sumatra, West Sumatra Province, Mt. Merapi, ca. 15 km SE of Bukittinggi; 0°23'32"S, 100°26'54"E; 1650–1700 m a.s.l.; 4.VI.2006; A. Schulz leg.; hill forest; MHNG SUM06/08 02	SEM + LMT
<i>Glomeridesmus</i> cf. <i>javanicus</i> Attems, 1907	INDONESIA • 1 ♀; Java, Jawa Barat, Cikaniki Research Station, Erstes Bachthal von der Station aus (HAL92); 6°44'54"S, 106°32'21"E; 1082 m a.s.l.; 19.IV.2016; Myriapoda Team leg.; Winklerextraktion; ZFMK-MYR07870	LMT
<i>Glomeridesmus</i> sp.	MALAYSIA • 1 juv (19T+AS); Pahang, Cameron Highlands, “Orang Asli vill.” env. Gunung Perdah [Mt.]; 4°29.2N, 101°22.1E; 1575 m a.s.l.; 2–14.V.2009; Petr Baňar leg.; Sifting leaf litter in shallow ravine; NHMD	LMT
<i>Glomeridesmus</i> sp.	THAILAND • 1 juv (9T+AS, 8 leg-pairs); Doi Sutep; 1150 m a.s.l.; 29.IX.1958; B. Degerbøl leg.; Lok 3a; Zool. Mus. Kbh. 1/7 59; NHMD	LM
<i>Glomeridesmus</i> sp.	PAPUA NEW GUINEA • 1 ♀; New Britain, Valoka; 12.V.1962; Noona Dan Exp. 61–62 leg.; NHMD	LM
<i>Glomeridesmus</i> sp.	FIJI • 1 juv (19T+AS); Colo-i-Surva Forest Park; 29.III.–6.IV.199?; van Harten A. leg.; NHMD Fiji 580	LM
<i>Glomeridesmus</i> sp.	FIJI • 1 juv (15T+AS); Colo-i-Surva Forest Park; 9.II.1997; van Harten A. leg.; NHMD glomeridesmids553	LM
<i>Glomeridesmus</i> sp.	PHILIPPINES • 1 ♀; Panay, Sibaliw; 11°49'37"N, 121°56'21"E; 220 m a. s. l.; 2007; leg. Prof. Curio leg.; SMNG	SEM <sup>TW</sup>
<i>Glomeridesmus</i> sp.	INDIA • 1 ♀, 1 juv (10T+AS, 13 leg-pairs); Chennai (Madras), Anamalai Hills, au-dessus d'Aliyar Dam; 1150 m a.s.l.; 18.XI.1972; C. Besuchet & I. Löbl leg.; tamis-ages en foret, au pied d'un groupe d'arbras envahis par les lianes; MHNG Inida34	LMT
<i>Glomeridesmus</i> sp.	INDIA • 1 ♀; Meghalaya, Khasi Hills: en-dessous de Cherapunjee; 1200 m a.s.l.; 26.X.1978; C. Besuchet & I. Löbl leg.; MHNG India28	LMT
<i>Glomeridesmus</i> sp.	SRI LANKA • 1 ♂; Sinharaja; 400 m a.s.l.; 2.XII.1979; V. Mahler leg.; NHMD	LM
<i>Glomeridesmus</i> sp.	PANAMA • 1 juv (19T+AS); Gamboa; 01.XI.1983; W. Netwig leg.; NHMD; PR4 B	
<i>Glomeridesmus</i> sp.	ECUADOR • VMNH	SEM <sup>WS</sup>
<i>Glomeridesmus</i> sp.	ECUADOR • 1 ♀; Pichincha, Río Palenque Station, 47 km S Santo Domingo; 700 ft; 18.V.1975; S. B. Peck & J. Kukalova-Peck leg.; FMNH INS 0000 011 916	SEM <sup>TW</sup>
<i>Glomeridesmus</i> sp.	COLOMBIA • 1 ♂; Nevada del Ruiz; 3700–3800 m a.s.l.; 10.X.1978; H. Sturm leg. (78/94); under Calamagrostis; NHMD Colombia78/94	LM
<i>Glomeridesmus</i> sp.	BRAZIL • 1 juv (18T+AS); Taperinka, Santarém; 3./11.70, Pr. 9–10 Myriapoda, S.I. Tuxen & O. Densen; NHMD	LM
<i>Termitodesmus calvus</i> Attems, 1938	VIETNAM • 1 ♀; Cat Tien; 16.I.2012; Semenyuk leg.; termite nest; ZFMK	SEM + LM
<i>Termitodesmus</i> sp.	MALAYSIA • 1 ♀; 06.VI.2012; M. Maruyama leg.; <i>Odontotermes</i> termite nest; ZFMK MYR596	SEM <sup>TW</sup>

Nidau, Switzerland). Semi-thin sections were stained with 1% Toluidine blue for 2 minutes. The mounted legs and histological sections were photographed with a Zeiss AxioCam HRc camera mounted to a Zeiss Imager.Z2m light microscope (Carl Zeiss AG, Oberkochen, Germany). The histological sections are deposited at the ZFMK (ZFMK-HIST00001).

## 2.5. Terminology

The terminology for the podomeres of the walking legs follows Iniesta et al. (2012) and Wesener et al. (2014) with a basal coxa fused to a ventral sclerite (stigmatic plate) followed by prefemur, femur, postfemur, tibia and tarsus. Terminology for the musculature follows Manton (1961).



### 3. Results

#### 3.1. External morphology

The investigated mature males, mature females, and juveniles of the 19 *Glomeridesmidae* morphospecies and two *Termitodesmidae* morphospecies (Table 1, Figs S1–S5) carried a single circular field of pores, hereafter referred to as a spinning field, on the tarsi of all walking legs (Figs 1C, 2, 3). A spinning field was absent on the modified posterior legs of mature individuals (telopods in males; sensory legs in males and females). Already in the earliest stadium studied, a juvenile from Thailand (NHMD 1/7 59) with 9 tergites + anal shield, 8 leg pairs and ca. 1 mm in length, the tarsal spinning fields were present on all walking legs (Fig. S1). Each spinning field was located on the dorsal/outer side of the tarsus. In the studied *Glomeridesmidae* it was located ca at mid-length of the tarsus distally of a faint suture and the most apical setae (Fig. 2B). In *Termitodesmidae*, where the podomeres were generally shorter and thicker (Fig. 3A), the spinning field was located in the distal third of the tarsus, distally of the most apical setae (Fig. 3B).

The tarsal spinning fields were 3–5 µm in diameter, slightly recessed into the tarsal cuticle, and comprised of 20–30 pores, which faced distally. Each pore had a diameter of ca 0.35 µm in the studied specimens (Figs 2C, 3C). In *Glomeridesmus* sp. (SUM06/08 02) from Sumatra the field of pores appeared clean on the SEM images and only in few pores small buds (the tips of threads) could be seen (Figs 2C, S2A, B). In *Glomeridesmus* cf. *sumatranus* (SUM06/08 01), from the same locality as the previous species, thin threads with a regular diameter of ca 0.35 µm were extruded from the pores of some legs. The threads coiled up separately (Figs 2D, S2C, D) or unified distally to a larger mass (Fig. 2E). In some cases small particles stuck to the threads (Fig. 2D). In *Glomeridesmus siamensis* Wesener, Wongthamwanich & Moritz, 2021 (Fig. S3) and *Glomeridesmus* spp. from Ecuador (Fig. S4A–C) and the Philippines (Fig. S4D) the separate pores could not be identified on the SEM images, as these were obscured, but a depression was present at the corresponding position.

#### 3.2. Internal morphology

In the 16 *Glomeridesmidae* and the single *Termitodesmidae* species studied with light microscopy (Table 1), thin cuticular tubuli (conducting canals), which arose internally from the pores of the spinning field, were visible through the translucent cuticle (Figs 3D, 4A, B, S5). These tubuli ran in a bundle proximally within the tarsus (Figs 3D, 4B). In the stained mounts of the whole legs, the femur appeared to be filled by a granular mass between well-defined muscular strands in *Glomeridesmidae* (Fig. 4A) and *Termitodesmidae*. The histological sections show suboptimal preservation of soft tissue and a clear or reliable identification of glandular tissue is not pos-

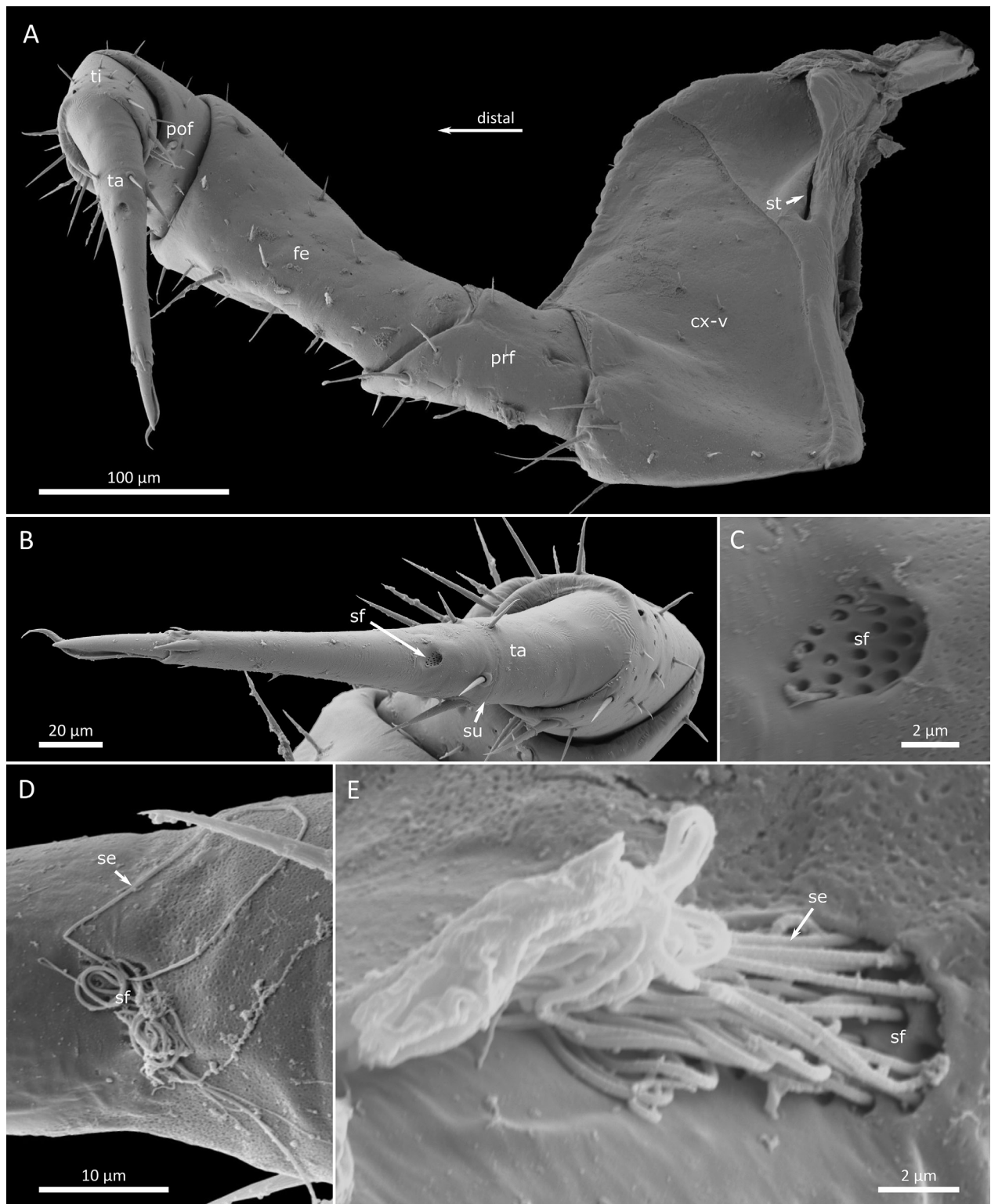
sible. Nevertheless, the cuticular tubuli arising from the sieve plate can be discerned. The cuticular tubuli run as a bundle from the tarsal sieve plate (Fig. 4C, D) through the tibia (Fig. 4E) and postfemur into the femur, where they lead to an accumulation of tissue (Figs 1D, 4F, G), probably the secretory cells of the gland.

### 4. Discussion

#### 4.1. A tarsal spinning gland in *Glomeridesmida*

We suggest that *Glomeridesmida* possess tarsal spinning organs in the form of exocrine glands, which release threads through a field of pores on their walking legs' tarsi. Such threads are thin filaments of unknown composition and were observed to be extruded from the pores on some legs (Fig. 2D, E). The buds observed in some of the pores (Fig. 2C) are the tips of these filaments. Furthermore, in the figures of Iniesta et al. (2012; fig. 2A, C), the first publication of photos of a living *Glomeridesmida* specimen, threads can be observed on the substrate close to *Glomeridesmus spelaeus* Iniesta & Wesener, 2012, although it is not clear if these threads have been produced by the glomeridesmid. The putative tarsal spinning organs could be observed in all 21 *Glomeridesmida* morphospecies studied here, which span the whole biogeographic distribution of the group, and include *Glomeridesmidae* as well as *Termitodesmidae* (Table 1). Therefore, we suggest that *Glomeridesmida* in general possess tarsal thread-producing organs, although the recently described genus *Glomeridesmoides* Mauriès, 2020 needs to be studied in this respect. Although the legs of some *Glomeridesmidae* have been studied and depicted before (e.g. Silvestri 1903; Carl 1942; Iniesta et al. 2012; Wesener et al. 2014; Mauriès 2020) and Carl (1942) described glandular tissue within the syncoxite of the first leg-pair of a female, this spinning organ has not been reported. This is mainly due to the small size of the external structure (3–5 µm in diameter) and its position in a depression on the outer side of the tarsus, as it is not clearly visible in anterior or posterior views, which are typically depicted in taxonomic description. We initially discovered the sieve plate only by means of SEM and it is only visible at certain angles (Fig. 2). Only then we were able to also locate the organ using transmitted light microscopy of whole legs (Figs 3D, 4A, B, S5). Furthermore, the sieve plates are often obscured by dirt, the secretion, or setae.

The spinning organ of the *Glomeridesmida* is an aggregated gland with several secretory units; cells are clustered within the femur, but open via separate tubuli (conducting canals), which run through the podomeres to the tarsus (Figs 1D, 4C–G). To understand the detailed structure of these glandular units, ultrastructural investigations are needed. Aggregated glands are known from various myriapods, like the defense glands of millipedes

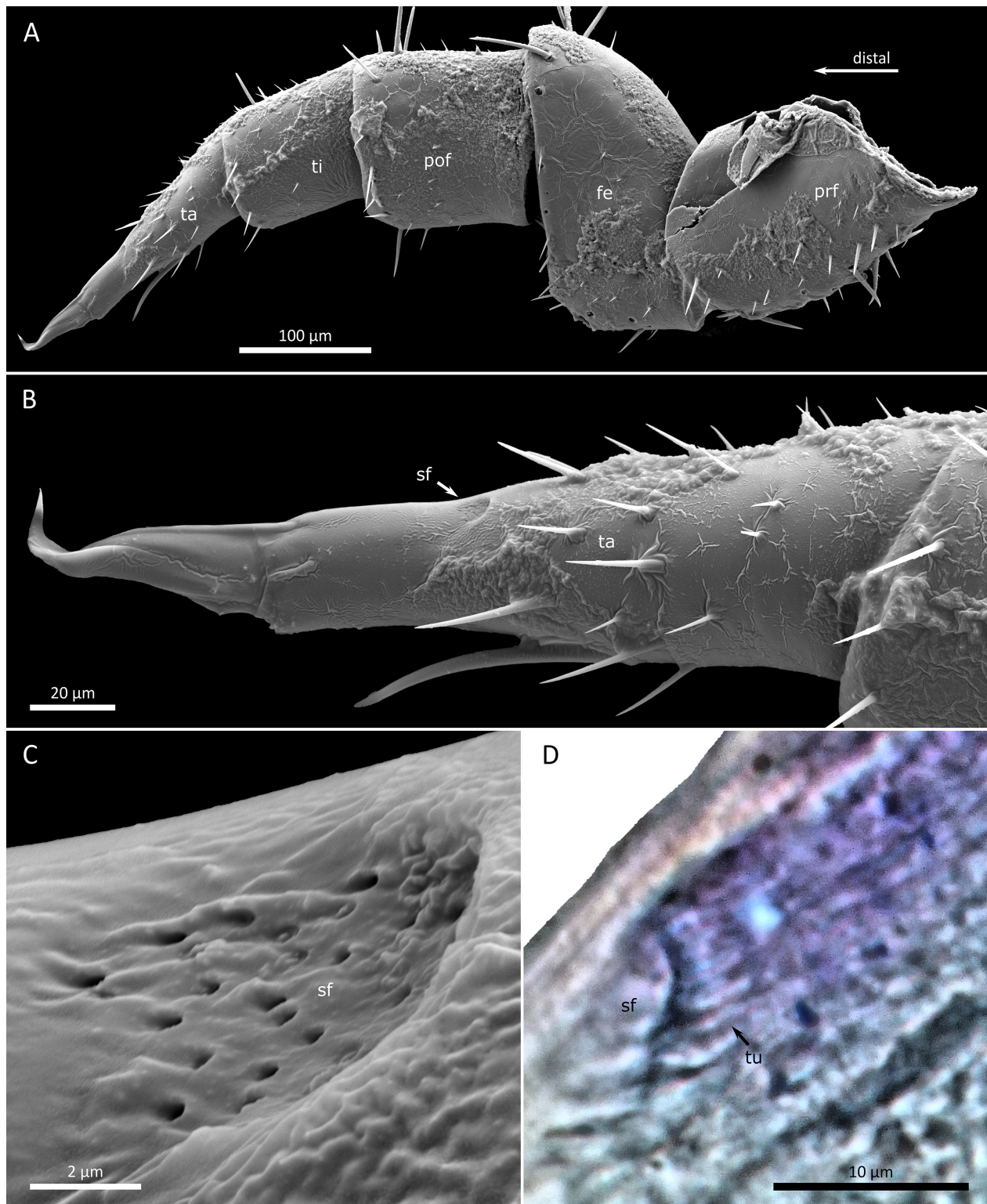


**Figure 2.** The putative spinning organ in the Glomeridesmidae, external morphology, SEM. **A–C:** *Glomeridesmus* sp. (SUM06/08 02), female, mid-body leg. **A:** Overview of leg. **B:** Detail of tarsus. **C:** Detail of spinning field. **D, E:** *Glomeridesmus* cf. *sumatranus* (SUM06/08 01), female, spinning fields on tarsi of leg pair 2 with extruded threads/secretion. **Abbreviations:** cx = coxa, fe = femur, pof = postfemur, prf = prefemur, se = secretion, sf = spinning field, st = stigmata, su = suture, ta = tarsus, ti = tibia, v = stigmatic plate.

(Weatherston and Percy 1969). The various aggregated glands of centipedes have been summarized by Rosenberg et al. (2011), and include the vesicular glands (Hilken and Rosenberg 2009), the maxillary organ gland (Hilken et al. 2003), the epidermal maxilla II-gland (Hilken et al. 2005) and the poison gland (Rosenberg and Hilken

2006), as well as the sternal glands of Geophilomorpha (Turcato and Minelli 1990) and the telopodal glands of Lithobiomorpha (Keil 1975). In the latter two the conducting canals open directly to the outside and not into a common duct or lumen, as is also the case in the spinning organs of the Glomeridesmida.



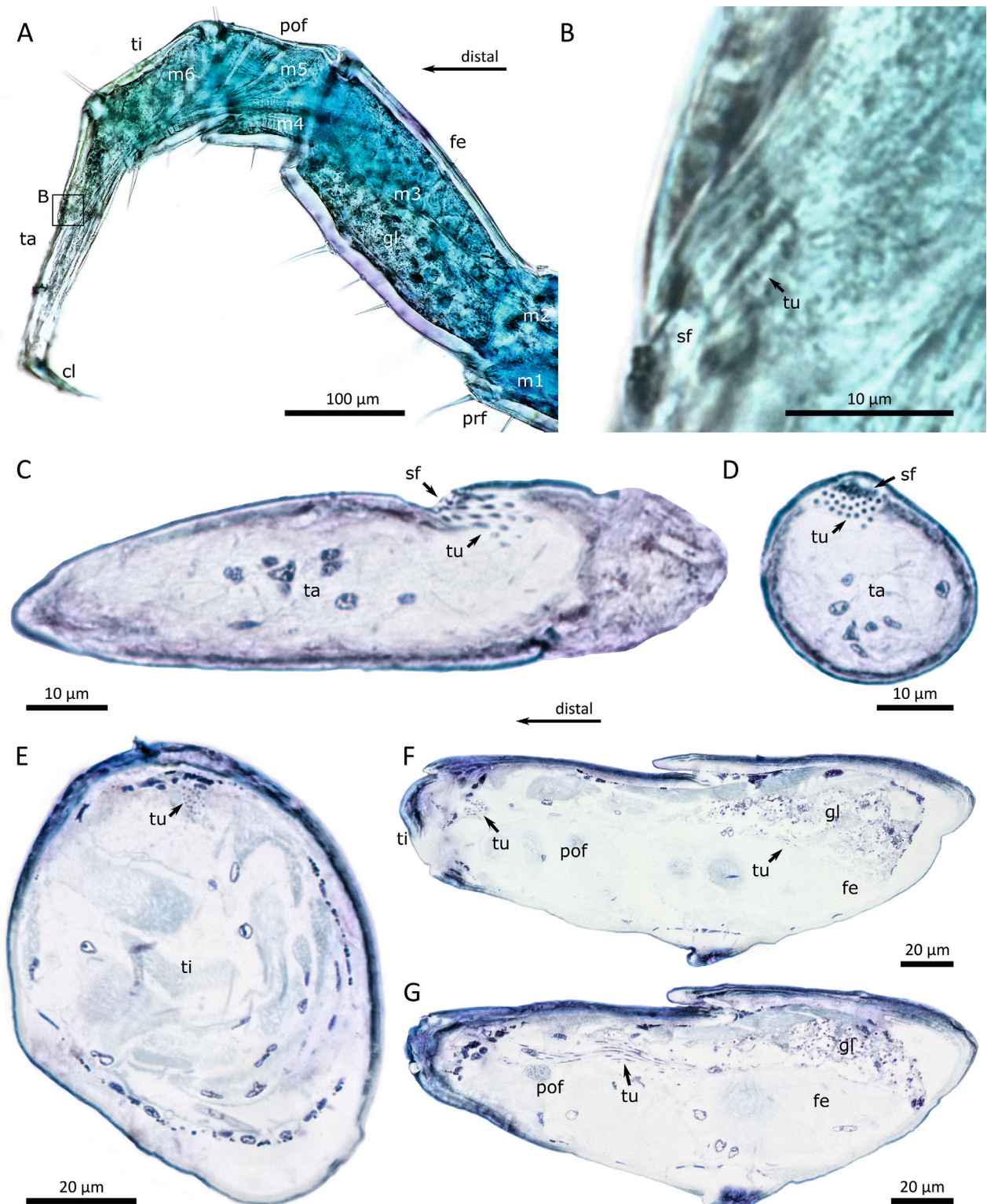


**Figure 3.** The putative spinning organ in the Termitodesmidae, mid-body leg of *Termitodesmus calvus* Attems, 1938, female. **A–C:** External morphology, SEM. **A:** Overview of leg. **B:** Detail of tarsus. **C:** Detail of spinning field. **D:** Detail of the spinning field with the underlying tubuli, mid-body leg stained with Toluidine blue, light microscopy. **Abbreviations:** fe = femur, pof = postfemur, prf = prefemur, sf = spinning field, ta = tarsus, ti = tibia, tu = tubuli.

Exocrine glands positioned on the legs are known from several millipede taxa but are typically restricted to males and differ in their position (i.e. on which legs and/or podomeres) from those in Glomeridesmida, in which pores are present in both sexes and in juveniles on the tarsi of all walking legs (Fig. 1C). Thus, pores can be

found on the coxae of leg-pairs 7 and 9 in male Chordeumatida (Verhoeff 1928), leg-pairs 8 and 9 in male Polyxenida (Schömann and Schaller 1954; Schömann 1956) and on the posterior gonopods in male Julida. In the latter, these glands release long and viscose threads (zähe Sekretfäden sensu Verhoeff 1928). Furthermore, exo-





**Figure 4.** The putative spinning organ of the Glomeridesmidae, internal morphology of a mid-body leg of *Glomeridesmus* cf. *sumatranus* (SUM06/08 01), female, light microscopy. **A, B:** Mid-body leg stained with Toluidine blue. **A:** Overview, terminology for the musculature follows Manton (1961). **B:** Detail of the spinning field with the underlying tubuli, as indicated in **A**. **C–G:** Histological sections. **C:** Sagittal section through tarsus. **D:** Cross section through tarsus. **E:** Cross section through tibia. **F, G:** Sagittal sections through postfemur and femur. **Abbreviations:** cl = claw, fe = femur, gl = putative glandular tissue, m1 = depressor femoris, m2 = flexor femoris, m3 = flexor postfemoris, m4 = flexor tibiae, m5 = flexor tarsi, m6 = flexor unguiculi, pof = postfemur, prf = prefemur, sf = spinning field, ta = tarsus, ti = tibia, tu = tubuli.

crine glands open on the inner side of the femur of single or several walking legs of some male Polydesmida and Julida and might be related to mating (Verhoeff 1928).

Although spinning organs are reported from various millipede (Diplopoda) taxa, these differ largely in their location and structure from the putative spinning organs

found in Glomeridesmida. In Glomeridesmida these are porous fields on the tarsi (Fig. 2B, C), while Polydesmida (Adis et al. 2000; Shear 2008), Nematophora (Shear 2008; Enghoff and Akkari 2011; Enghoff and Reboleira 2013; Blanke and Wesener 2014; Iniesta and Ferreira 2015; Fiemapong et al. 2017) and possibly Siphoniulida (Sierwald et al. 2003) carry terminal seta-like spinnerets on their epiproct, Siphonophorida carry potential seta-like spinning organs on their tergites (Marek and Bond 2006; Read and Enghoff 2009; Marek et al. 2012, 2016), and polyxenid millipedes have ‘silk-producing coxal glands’ (Schömann and Schaller 1954; Schömann 1956; Huynh and Veenstra 2016). The internal structure of these spinning glands in millipedes remains largely unknown.

In addition to the structure of the putative spinning organ, the structure of the threads observed in Glomeridesmida differs from that found in other millipede taxa with spinning abilities. Thus, the threads released from telsonian spinnerets are rather flattened in Chordeumatida (Enghoff and Reboleira 2013) or can have regular swellings in some Chordeumatida (Verhoeff 1928: p. 1061, figs 601–603), Callipodida (Enghoff and Akkari 2011) and Polydesmida (Adis et al. 2000; Shear 2008), while the threads in Glomeridesmida are of a uniform circular diameter (Fig. 2D, E).

From the other pentazonian taxa Glomerida and Sphaerotheriida, which are comparatively well-studied, including SEM images of the legs (e.g. Wesener and VandenSpiegel 2009; Wesener 2012; Oeyen and Wesener 2015; Wesener 2016; Wesener 2018), similar structures are unknown. Therefore, we suggest that the putative spinning organ of the Glomeridesmida constitutes an apomorphy of the group and supports the monophyly of Glomeridesmida (Glomeridesmidae + Termitodesmidae). Other characters supporting the monophyly of Glomeridesmida are a strongly elongated membranous fringe on the mandible molar plate, the presence of 20 tergites, and modifications of the penultimate and ultimate leg pairs in females (Oeyen and Wesener 2018). Apart from these characters, the Glomeridesmida are mainly characterized by reductive or supposedly plesiomorphic traits (Enghoff 1990; Iniesta et al. 2012).

## 4.2. Function of the putative tarsal spinning organ

The actual function of the extruded threads in the Glomeridesmida remains speculative because the biochemical composition of the threads (as for most millipedes) is unknown, and no spinning activity or spinning product has been observed so far in living specimens. For Polydesmida, it has been shown by staining experiments that the threads are not true silk (i.e. made of fibrous protein) but consist of mucopolysaccharides (Adis et al. 2000), while the threads in lithobiomorph centipedes are apparently a lipid-protein complex or mixture (Blower 1952). Because small particles adhere to some threads in the studied Glomeridesmida (Fig. 2D), we suggest that the threads are adhesive. As tarsal spinning organs were not

only found in mature male and female Glomeridesmida, but also in the smallest juveniles studied here (Fig. S1), we suggest that the threads are not primarily used for mating or brood care (although they might additionally play a role in it), but are rather used to build molting chambers, as is the case in Polydesmida and Nematophora (Adis et al. 2000; Shear 2008; Enghoff and Akkari 2011), or as defense against predation as in Symphyla (Dunger 1983) and Chilopoda-Lithobiomorpha (Rosenberg and Müller 2009; Kenning et al. 2019). Glomeridesmida neither possess defensive glands as present in Glomerida and Helminthomorpha (Blanke and Wesener 2014; Enghoff et al. 2015; Shear 2015), nor can they roll up into a tight ball like Glomerida and Sphaerotheriida (Blanke and Wesener 2014; Enghoff et al. 2015) to ward off predators.

In insects thread-producing or spinning organs can be found on the apical podomeres of several taxa, like web-spinners (Embioptera), dance flies (Diptera: Empididae), and some ants (Hymenoptera: Formicidae). In these insects the secretions serve to build tunnels as in Embioptera (Mukerji 1927; Büsse et al. 2015) and potentially in some ants (Billen and Peeters 2020), or to wrap nuptial gifts, as in dance flies (Young and Merritt 2003; Sutherland et al. 2007). Furthermore, thread-producing organs opening on apical podomeres are also known from some marine crustaceans, like the corophioid amphipod *Crassikorophium bonellii* (Kronenberg et al. 2012) and the order Tanaidacea (Kakui and Hiruta 2014; Kaji et al. 2016), in which the secreted threads (i.e. silk) are involved in tunneling and building tubes. Similar to the Glomeridesmida, the glands of these crustaceans are located in proximal podomeres or within the body, and ducts lead to the distal podomere.

To clarify the function of the spinning product in Glomeridesmida, behavioral observations of living specimens are needed. Until now such observations of living specimens are rare and mostly anecdotal (Escherich 1911; Hirst 1913; Wesener et al. 2021) and spinning activity has not been reported. *Glomeridesmus spelaesus* Iniesta & Wesener, 2012 specimens have been observed to dig small tunnels into compact guano substrate, despite their delicate appearance, and to shelter themselves in these small passages (Iniesta et al. 2012). Possibly the spinning product is used to secure the walls of these tunnels, as might be the case in some tunneling ants, which have similar exocrine glands and pores (the so called Delage-Darchen gland in *Melissotarsus* Emery, 1877) on the basitarsi of their walking legs (Delage-Darchen 1972; Billen 2009; Hölldobler et al. 2014; Billen and Peeters 2020). In these ants, solid ‘toothpaste like’ threads are excreted through the pores (Billen 2009; Hölldobler et al. 2014; Billen and Peeters 2020) and rubbed along the walls and roof of the ant’s tunnels, which are made of silk (from a cephalic gland) and wood fragments (Delage-Darchen 1972; Billen and Peeters 2020). As the thread-producing organs found on the basitarsi of ants and on the tarsi of the Glomeridesmida are superficially similar in their position and structure, they might be used in a similar manner in Glomeridesmidae; i.e. the threads secreted serve in stabilizing the walls of their molting chambers or even tun-



nels. However, the latter function would not explain their presence in the termitophilous Termitodesmidae, which exclusively inhabit termite mounds (Silvestri 1911; Hirst 1911, 1913; Enghoff et al. 2015), in which tunnels are maintained by the termites, thus making tunneling and (if they are involved in this) the putative spinning glands obsolete. Therefore, a defensive function either during molting or against predation seems to be most plausible at the moment, although it might have multiple (e.g. tunneling and brood care) rather than a single function.

### 4.3. No terminal spinnerets in Glomeridesmida

For Glomeridesmida Silvestri (1902, 1903) reported paired cylindrical glands that open on the preanal tergite, and interpreted these as mucus glands (ghandole mucipare sensu Silvestri 1902), which are possibly homologous to the spinnerets of Callipodida and Chordeumatida. We could not identify any such organs in the studied specimens using SEM or light microscopy. We suggest that Silvestri (1902, 1903) interpreted the apical podomeres of the ultimate legs, which are modified into sensory legs (Fig. 1C), as gland openings. The apical podomeres of the sensory legs are cylindrical, equipped with a terminal spine, and protrude (visible in dorsal view) from underneath the preanal tergite (tergite 19/20) beyond the anal shield, while its basal podomeres remain hidden (Iniesta et al. 2012; Enghoff et al. 2015; Mauriès 2020; Wesener et al. 2021), thus appearing superficially similar to telsonian spinnerets of other millipedes. Therefore, we conclude that such preanal glands are absent in Glomeridesmida.

### 4.4. Outlook

For this study we only had access to material from museum collections, which has been initially fixed and subsequently stored over a long period in ethanol (70% or 96% EtOH), resulting in the suboptimal preservation of soft tissue and in artefacts, as visible in the histological sections (Fig. 4). Therefore, the histological data presented here have to be taken with caution. To better understand the structure and function of the putative spinning glands in Glomeridesmida, future studies should focus on ultrastructure using transmission electron microscopy (TEM), as has been done for the cephalic glands and nephridia of several millipede taxa (e.g. El-Hifnawi and Seifert 1971, 1972; El-Hifnawi 1973, 1974) and epidermal glands in centipedes (e.g. Sombke and Müller 2021). A more complete series of postembryonic stadia might shed light on the first appearance and changes within the organ during development. In this study the earliest stadium has 9 tergites + anal shield and 8 leg pairs. Furthermore, the biochemical composition of the secretion should be analyzed, and, most importantly, the behavior of living specimens should be observed to better understand the function of the organ and the extruded threads.

## 5. Conclusion

Glomeridesmida possess exocrine glands in their walking legs, which open through a field of pores (spinning field) on their tarsi and extrude threads. These putative spinning glands, are present in both major groups of the Glomeridesmida, the Glomeridesmidae and Termitodesmidae, and are probably an apomorphic character of the group. The function of these threads remains speculative, but we suggest that the threads serve for a defensive function against predation and during molting, or that they are involved in tunneling. To clarify the structure and function of the glands and their excretion ultrastructural examination and behavioral observations of living specimens are needed.

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## 7. References

- Adis J, Hansen B, Wilck L, Adis I, Hirschel K (2000). A spinning apparatus documented in Polydesmida for the first time. In: Wytwer J, Golovatch SI (eds) Progress in Studies on Myriapoda and Onychophora. Fragmenta Faunistica 42: 139–148.
- Attems CMT (1907) Javanische Myriopoden, gesammelt von Direktor K. Kraepelin im Jahre 1903. Mitteilungen aus dem Naturhistorischen Museum in Hamburg 24: 77–142.



- Attems CMT (1926) Chilopoda. In: Kükenthal W (ed.) Handbuch der Zoologie. Walter de Gruyter, Berlin, 239–402.
- Attems CMT (1938) Die von Dr. C. Dawydoff in französisch Indochina gesammelten Myriapoden. Mémoires du Muséum National d'Histoire Naturelle 6: 187–353.
- Betz O, Kölsch G (2004) The role of adhesion in prey capture and predator defence in arthropods. Arthropod Structure & Development 33(1): 3–30.
- Billen J (2009) Occurrence and structural organization of the exocrine glands in the legs of ants. Arthropod Structure & Development 38(1): 2–15. <https://doi.org/10.1016/j.asd.2008.08.002>
- Billen J, Peeters C (2020) Glandular innovations for a tunnelling life: Silk and associated leg glands in *Melissotarsus* and *Rhopalomas-tix* queen and worker ants. Arthropod Structure & Development 59: 100979. <https://doi.org/10.1016/j.asd.2020.100979>
- 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>
- Blower G (1952) Epidermal glands in centipedes. Nature 4317: 166–167. <https://doi.org/10.1038/170166b0>
- Büsse S, Hörschemeyer T, Hohn K, McMillan D, Edgerly JS (2015) The spinning apparatus of web-spinners – functional-morphology, morphometrics and spinning behaviour. Scientific Reports 5: 1–9. <https://doi.org/10.1038/srep09986>
- von Byern J, Müller C, Voigtländer K, Dorner V, Marchetti-Dechmann M, Flammang P, Mayer G (2017) Examples of bioadhesives for defence and predation. In: Gorb S, Gorb E (eds) Functional Surfaces in Biology III. Biologically-Inspired Systems, vol 10. Springer, Cham, 141–191. [https://doi.org/10.1007/978-3-319-74144-4\\_7](https://doi.org/10.1007/978-3-319-74144-4_7)
- Carl J (1942) Contribution à la connaissance des Limacomorpha. Essai de morphologie comparée. Revue Suisse de Zoologie 49: 133–167.
- Delage-Darchen B (1972) Une fourmi de Côte-d'Ivoire: *Melissotarsus titubans* Del., n. sp. Insectes Sociaux 19(3): 213–226.
- Dunger W (1983). Tiere im Boden. Neue Brehm-Bücherei, Magdeburg, 280 pp.
- El-Hifnawi ES (1973) Die Speicheldrüsen der Diplopoden, I. Topographie und Histologie der Speicheldrüsen von *Polyxenus lagurus*, *Craspedosoma rawlinsii* und *Schizophyllum sabulosum*. Zeitschrift für Morphologie und Ökologie der Tiere 74: 323–348.
- El-Hifnawi ES (1974) Die Speicheldrüsen der Diplopoden, II. Ultrastruktur der sekretbildenden Zellen. Zeitschrift für Morphologie und Ökologie der Tiere 75: 297–314.
- El-Hifnawi ES, Seifert G (1971) Über den Feinbau der Maxillarnephridien von *Polyxenus lagurus* (L.) (Diplopoda, Penicillata). Zeitschrift für Zellforschung und Mikroskopische Anatomie 112: 518–530.
- El-Hifnawi ES, Seifert G (1972) Die Ultrastruktur des Gabschen Organs von *Schizophyllum sabulosum* L. (Diplopoda, Iuliformia). Zeitschrift für Zellforschung und Mikroskopische Anatomie 132: 273–285.
- Emery C (1877) Catalogo delle formiche esistenti nelle collezioni del Museo Civico di Genova. Parte prima. Formiche provenienti dal Viaggio dei signori Antinori, Beccari e Issel nel Mar Rosso e nel paese dei Bogos. Annali del Museo Civico di Storia Naturale di Genova 9: 363–381.
- Enghoff H (1990) The ground-plan of chilognathan millipedes (external morphology). In: Minelli A (ed.) Proceedings of the 7<sup>th</sup> International Congress of Myriapodology. Brill, Leiden, 1–21.
- Enghoff H, Akkari N (2011) A callipodidan cocoon (Diplopoda, Callipodida, Schizopetalidae). International Journal of Myriapodology 5: 49–53. <https://doi.org/10.3897/ijm.5.1995>
- Enghoff H, Golovatch S, Short M, Stoev P, Wesener T (2015) Diplopoda – taxonomic overview. In: Minelli A (ed.) Treatise on Zoology – Anatomy, Taxonomy, Biology. The Myriapoda, Volume 2. Brill, Leiden, 363–453. [https://doi.org/10.1163/9789004188273\\_017](https://doi.org/10.1163/9789004188273_017)
- Enghoff H, Reboleira ASPs (2013) A new cave-dwelling millipede of the genus *Scutigona* from central Portugal (Diplopoda, Chordeumatida, Chamaesomatidae). Zootaxa 3736(2): 175–186. <http://dx.doi.org/10.11646/zootaxa.3736.2.5>
- Escherich K (1911) Termitenleben auf Ceylon, Neue Studien zur Soziologie der Tiere, zugleich ein Kapitel kolonialer Forstentomologie. Verlag von Gustav Fischer, Jena.
- Fiemapong ARN, Masse PSM, Tamesse JL, Golovatch SI, Vanden-Spiegel D (2017) The millipede genus *Stemmiulus* Gervais, 1844 in Cameroon, with descriptions of three new species (Diplopoda, Stemmiulida, Stemmiulidae). ZooKeys 708: 11–23. <https://doi.org/10.3897/zookeys.708.14072>
- Gervais P, Goudot J (1844). [Without title]. Annales de la Société Entomologique de France, 2e série 1: 27–29.
- Hilken G, Brockmann C, Rosenberg J (2003) The maxillary organ gland: description of a new head gland in *Scutigera coleoptrata* (Chilopoda, Notostigmophora). African Invertebrates 44(1): 175–184.
- Hilken G, Rosenberg J (2009) Ultrastructural investigation of the vesicular glands in *Scutigera coleoptrata* (Chilopoda, Notostigmophora). Journal of Morphology 270(4): 451–458. <https://doi.org/10.1002/jmor.10700>
- Hilken G, Rosenberg J, Brockmann C (2005) Ultrastructure of the epidermal maxilla II-gland of *Scutigera coleoptrata* (Chilopoda, Notostigmophora) and the ground pattern of epidermal gland organs in Myriapoda. Journal of Morphology 264(1): 53–61. <https://doi.org/10.1002/jmor.10317>
- Hirst S (1911) A new termitophilus millipede from Bengal. The Annals and Magazine of Natural History 8(8): 256–257.
- Hirst S (1913) On a second Indian species of the genus *Termitodesmus* (*T. fletcheri*, sp. n.). The Annals and Magazine of Natural History 11(8): 481–482.
- Hölldobler B, Obermayer M, Plowes NJ, Fisher BL (2014) New exocrine glands in ants: the hypostomal gland and basitarsal gland in the genus *Melissotarsus* (Hymenoptera: Formicidae). Naturwissenschaften 101(7): 527–532. <https://doi.org/10.1007/s00114-014-1186-y>
- Huynh C, Veenstra AA (2016) Reproduction, egg morphology and development observed in two Australian penicillate millipedes, *Lophoturus queenslandicus* (Lophoproctidae) and *Phryssonotus novaehollandiae* (Synxenidae) (Diplopoda). Australian Journal of Zoology 64(2): 138–150. <https://doi.org/10.1071/ZO16035>
- Iniesta LFM, Ferreira RL (2015) *Stemmiulus brasiliensis* n. sp., a new species of millipede from Brazilian iron ore caves (Diplopoda: Stemmiulida: Stemmiulidae). Zootaxa 3964(5): 546–552. <http://dx.doi.org/10.11646/zootaxa.3964.5.4>
- Iniesta LFM, Ferreira RL, Wesener T (2012) The first troglobitic *Glomeridesmus* from Brazil, and a template for a modern taxonomic description of *Glomeridesmida* (Diplopoda). Zootaxa 3550(1): 26–42. <https://doi.org/10.11646/zootaxa.3550.1.2>
- Jeckel CAW (2003) A bibliographic catalogue of the order Glomeridesmida (Diplopoda). Myriapod Memoranda 6: 102–109.
- Kaji T, Kakui K, Miyazaki N, Murata K, Palmer AR (2016) Mesoscale morphology at nanoscale resolution: serial block-face scanning electron microscopy reveals fine 3D detail of a novel silk spinneret system in a tube-building tanaid crustacean. Frontiers in Zoology 13(1): 1–9. <https://doi.org/10.1186/s12983-016-0146-0>

- Kakui K, Hiruta C (2014) Diverse pereopodal secretory systems implicated in thread production in an apseudomorph tanaidacean crustacean. *Journal of Morphology* 275(9): 1041–1052. <https://doi.org/10.1002/jmor.20281>
- Keil T (1975) Die Antennensinnes- und Hautdrüsenorgane von *Lithobius forficatus* L. Eine licht- und elektronenmikroskopische Untersuchung. Dissertation, FU Berlin, 1–61.
- Kenning M, Schendel V, Müller CH, Sombke A (2019) Comparative morphology of ultimate and walking legs in the centipede *Lithobius forficatus* (Myriapoda) with functional implications. *Zoological letters* 5(1): 1–18. <https://doi.org/10.1186/s40851-018-0115-x>
- Kronenberger K, Dicko C, Vollrath F (2012) A novel marine silk. *Naturwissenschaften* 99(1): 3–10. <https://doi.org/10.1007/s00114-011-0853-5>
- Liu W, Rühr PT, Wesener T (2017) A look with  $\mu$ CT technology into a treasure trove of fossils: The first two fossils of the millipede order Siphoniulida discovered in Cretaceous Burmese amber (Myriapoda, Diplopoda). *Cretaceous Research* 74: 100–108. <https://doi.org/10.1016/j.cretres.2017.01.009>
- Manton SM (1961) The evolution of arthropodan locomotory mechanisms. Part 7. Functional requirements and body design in Colobognatha (Diplopoda), together with a comparative account of Diplopoda burrowing techniques, trunk musculature and segmentation. *The Journal of the Linnean Society of London* 44(299): 383–461. <https://doi.org/10.1111/j.1096-3642.1961.tb01622.x>
- Marek PE, Bond JE (2006) Rediscovery of the world's leggiest animal. *Nature* 441(7094): 707–707. <https://doi.org/10.1038/441707a>
- Marek PE, Shear WA, Bond JE (2012) A redescription of the leggiest animal, the millipede *Illacme plenipes*, with notes on its natural history and biogeography (Diplopoda, Siphonophorida, Siphonorhinidae). *ZooKeys* 241: 77–112. <https://doi.org/10.3897/zookeys.241.3831>
- Marek PE, Krejca JK, Shear WA (2016) A new species of *Illacme* Cook & Loomis, 1928 from Sequoia National Park, California, with a world catalog of the Siphonorhinidae (Diplopoda, Siphonophorida). *ZooKeys* 626: 1–43. <https://doi.org/10.3897/zookeys.626.9681>
- Mauriès JP (2020) Les premiers Glomeridesmida découverts dans le département français de Guyane: nouvelles données sur leur ontogenèse et descriptions de nouveaux taxa: *Glomeridesmoides* n. g., et trois espèces nouvelles, dont une termitophile (Diplopoda, Glomeridesmida). *Bulletin de la Société d'Histoire Naturelle de Toulouse* 155: 47–64.
- Mukerji S (1927) On the morphology and bionomics of *Embia minor*, sp. nov. with special reference to its spinning organ. A contribution to our knowledge of the Indian Embioptera. *Records of the Indian Museum* 29: 253–284.
- Oeyen JP, Wesener T (2015) Steps towards a phylogeny of the pill millipedes: non-monophyly of the family Protoglomeridae, with an integrative redescription of *Eupeyerimhoffia archimedis* (Diplopoda, Glomerida). *ZooKeys* 510: 49–64. <https://doi.org/10.3897/zookeys.510.8675>
- Oeyen JP, Wesener T (2018) A first phylogenetic analysis of the pill millipedes of the order Glomerida, with a special assessment of mandible characters (Myriapoda, Diplopoda, Pentazonia). *Arthropod Structure & Development* 47: 214–228. <https://doi.org/10.1016/j.asd.2018.02.005>
- Pocock RI (1894) Contributions to our knowledge of the arthropod fauna of the West Indies. Part III. Diplopoda and Malacopoda, with a supplement on the Arachnida of the class Pedipalpi. *Journal of the Linnean Society of London* 24(157): 473–519.
- Read HJ, Enghoff H (2009) The order Siphonophorida – a taxonomist's nightmare? Lessons from a Brazilian collection. *Soil Organisms* 81(3): 543–556.
- Rosenberg J, Hilken G (2006) Fine structural organization of the poison gland of *Lithobius forficatus* (Chilopoda, Lithobiomorpha). *Norwegian Journal of Entomology* 53(2): 119–127.
- Rosenberg J, Müller C (2009) Morphology in Chilopoda – a survey. *Soil Organisms* 81(3): 1–55.
- Rosenberg J, Müller C, Hilken G (2011) Chilopoda – integument and associated organs. In: Minelli A (ed.) *Treatise on Zoology – Anatomy, Taxonomy, Biology. The Myriapoda, Volume 1*. Brill, Leiden, 67–111.
- Schömann K (1956) Zur Biologie von *Polyxenus lagurus* L. 1758. *G. Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere* 84: 196–256.
- Schömann K, Schaller F (1954). Das „Paarungs“-Verhalten von *Polyxenus lagurus* L. (Diplopoda). *Naturwissenschaften* 41(13): 310–310.
- Shear WA (2008) Spinnerets in the milliped order Polydesmida, and the phylogenetic significance of spinnerets in millipeds (Diplopoda). *International Journal of Myriapodology* 1(2): 123–146. <https://doi.org/10.1163/187525408X395904>
- Shear WA (2015) The chemical defenses of millipedes (Diplopoda): biochemistry, physiology and ecology. *Biochemical Systematics and Ecology* 61: 78–117. <https://doi.org/10.1016/j.bse.2015.04.033>
- Shear WA, Jones TH, Wesener T (2011) Glomerin and homoglomerin from the North American pill millipede *Onomeris sinuata* (Loomis, 1943) (Diplopoda, Pentazonia, Glomeridae). *International Journal of Myriapodology* 4: 1–10. <https://doi.org/10.3897/ijm.4.1105>
- Shelley RM (2011) The milliped order Glomeridesmida (Diplopoda: Pentazonia: Limacomorpha) in Oceania, the East Indies, and south-eastern Asia; first records from Palau, the Philippines, Vanuatu, New Britain, the Island of New Guinea, Cambodia, Thailand, Borneo and Sulawesi, Indonesia. *Insecta Mundi* 0196: 1–11.
- Sierwald P, Shear WA, Shelley RM, Bond JE (2003) Millipede phylogeny revisited in the light of the enigmatic order Siphoniulida. *Journal of Zoological Systematics and Evolutionary Research* 41(2): 87–99. <https://doi.org/10.1046/j.1439-0469.2003.00202.x>
- Silvestri F (1902) Note preliminari sulla morfologia dei Diplopodi e Chilopodi. *Rivista di Patologia Vegetale* 10: 179–184.
- Silvestri F (1903) *Classis Diplopoda*. Vol. 1, Anatome. Pars 1a, Segmenta, Tegumentum, Musculi. Della Torre, Portici, 272 pp.
- Silvestri F (1911) Beschreibung der von K. Escherich auf Ceylon gesammelten termitophilen Thysanuren, Myriapoden, sowie einer unbekannten mimetischen, termitophilen Coleopterenlarve. In: Escherich K (ed.) *Termitenleben auf Ceylon, Neue Studien zur Soziologie der Tiere, zugleich ein Kapitel kolonialer Forstentomologie*. Verlag von Gustav Fischer, Jena, 239–247.
- Sombke A, Müller CH (2021) When SEM becomes a deceptive tool of analysis: the unexpected discovery of epidermal glands with stalked ducts on the ultimate legs of geophilomorph centipedes. *Frontiers in Zoology* 18(1): 1–19.
- Sutherland TD, Young JH, Sriskantha A, Weisman S, Okada S, Haritos VS (2007) An independently evolved dipteran silk with features common to Lepidopteran silks. *Insect Biochemistry and Molecular Biology* 37(10): 1036–1043. <https://doi.org/10.1016/j.ibmb.2007.05.016>
- Szucsich N, Scheller U (2011) Symphyla. In: Minelli A (ed.) *The Myriapoda, Volume 1*. Brill, Leiden, 445–466. [https://doi.org/10.1163/9789004188266\\_021](https://doi.org/10.1163/9789004188266_021)

- Turcato A, Minelli A. (1990) Fine structure of the ventral glands of *Pleurogeophilus mediterraneus* (Meinert) (Chilopoda, Geophilomorpha). In: Minelli A (ed.) Proceedings of the 7<sup>th</sup> International Congress of Myriapodology. Brill, Leiden, 165–173.
- Verhoeff KW (1925) Klasse Chilopoda. In Bronn HG (ed.) Klassen und Ordnungen des Tierreichs 5. Band, 2. Abteilung, Gliederfüßler, Arthropoda. Akademische Verlagsgesellschaft, Leipzig, 1–725.
- Verhoeff KW (1928) Klasse Diplopoda, 1. Teil. In: Bronn HG (ed.) Klassen und Ordnungen des Tierreichs, 5. Band, 2. Abteilung, Gliederfüßler, Arthropoda. Akademische Verlagsgesellschaft, Leipzig, 1–1071.
- Verhoeff KW (1934) Symphyla und Pauropoda. In: Bronn HG (ed.) Klassen und Ordnungen des Tierreichs 5. Band, 2. Abteilung, Gliederfüßler, Arthropoda. Akademische Verlagsgesellschaft, Leipzig, 1–119.
- Weatherston J, Percy JE (1969) Studies of physiologically active arthropod secretions. III. Chemical, morphological, and histological studies of the defence mechanism of *Uroblaniulus canadensis* (Say) (Diplopoda: Julida). Canadian Journal of Zoology 47(6): 1389–1394.
- Wesener T (2012) *Nearctomeris*, a new genus of pill millipedes from North America, with a comparison of genetic distances of American pill millipede genera (Glomerida, Glomeridae). Zootaxa 3258(1): 58–68. <https://doi.org/10.11646/zootaxa.3258.1.5>
- 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 (2018) An integrative and citizen science based approach to the rediscovery and redescription of the only known high-altitude endemic pill millipede, *Glomeris aurita* Koch (Diplopoda, Glomerida). PeerJ 6: e5569. <https://doi.org/10.7717/peerj.5569>
- Wesener T, Sierwald P, Wägele JW (2014) Sternites and spiracles – the unclear homology of ventral sclerites in the basal millipede order Glomeridesmida (Myriapoda, Diplopoda). Arthropod Structure & Development 43(1): 87–95. <https://doi.org/10.1016/j.asd.2013.11.003>
- Wesener T, VandenSpiegel 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(6): 545–573. <https://doi.org/10.1111/j.1096-0031.2009.00267.x>
- Wesener T, Wongthamwanich N, Moritz L (2021) Description of the first species of Glomeridesmida from Thailand (Diplopoda, Glomeridesmida, Glomeridesmidae). Zookeys 1024: 137–156. <https://doi.org/10.3897/zookeys.1024.63678>
- Young JH, Merritt DJ (2003) The ultrastructure and function of the silk-producing basitarsus in the Hilarini (Diptera: Empididae). Arthropod Structure & Development 32(2–3): 157–165. [https://doi.org/10.1016/S1467-8039\(03\)00006-9](https://doi.org/10.1016/S1467-8039(03)00006-9)

## Supplementary material 1

### Figures S1–S5

**Authors:** Moritz and Wesener (2021)

**Data type:** .pdf

**Explanation note:** Figures S1–S5 including legends.

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