

Echiniscidae from the Sierra Nevada de Santa Marta, Colombia, new records and a new species of *Bryodelphax* Thulin, 1928 (Tardigrada)

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Academic editor: Sandra McInnes | Received 4 March 2017 | Accepted 18 August 2017 | Published 27 September 2017

<http://zoobank.org/359F5DC2-4483-402B-BA5F-B86050E89E20>

Citation: Lisi O, Daza A, Londoño R, Quiroga S (2017) Echiniscidae from the Sierra Nevada de Santa Marta, Colombia, new records and a new species of *Bryodelphax* Thulin, 1928 (Tardigrada). ZooKeys 703: 1–14. <https://doi.org/10.3897/zookeys.703.12537>

Abstract

Three species of *Echiniscus* are recorded for the first time from Colombia: *Echiniscus dariae*, *Echiniscus kofordi*, and *Echiniscus perarmatus*. In addition, the description of the new species *Bryodelphax kristenseni* sp. n., is mainly based on the presence of ten paired plus two unpaired granularly sculptured ventral plates, the dorsal plate ornamentation with superficial irregular pores, no spine on the anterior legs, and the hind legs without papillae or dentate collar.

Keywords

Biodiversity, *Bryodelphax kristenseni* sp. n., *Echiniscus*, Heterotardigrada, water bear

Introduction

To date, only ten species of Echiniscidae Thulin, 1928, have been reported from Colombia: *Echiniscus bigranulatus* Richters, 1908a, *Echiniscus blumi* Richters, 1903 *sensu lato*, *Echiniscus madonnae* Michalczyk & Kaczmarek, 2006, *Echiniscus quadrispinosus* Richters, 1902 *sensu lato*, *Echiniscus spiniger* Richters, 1904, *Echiniscus testudo* (Doyère, 1840), *Echiniscus virginicus* Rigglin, 1962, *Echiniscus wendti* Richters, 1903, *Pseudechiniscus novaezeelandiae* (Richters, 1908b) *sensu lato*, and *Pseudechiniscus suillus* (Ehrenberg, 1853) (Meyer 2013, Lisi et al. 2014, Kaczmarek et al. 2015). In the present study, material deposited in the “Centro de Colecciones Biológicas de la Universidad del Magdalena” collected between 2011 and 2012 from different localities in the Sierra Nevada de Santa Marta (Colombia) was examined. In this material new records of *Echiniscus* C.A.S. Schultze, 1840, and a new species of *Bryodelphax* Thulin, 1928, were found which are described in this paper.

Materials and methods

This survey was based on tardigrade specimens deposited in the Centro de Colecciones Biológicas de la Universidad del Magdalena under the catalogue acronym CBUMAG:TAR. The material was collected between 2011 and 2012, from different localities (San Lorenzo, Bella Vista, and Medium basin of Garupal River) in the Sierra Nevada de Santa Marta, Colombia, from 543 and 2,200 m a.s.l. All specimens were preserved on slides in Hoyer's medium.

Tardigrades were examined using a Phase Contrast Microscope (PCM) Zeiss AxioLab A1 with an adapted digital camera Zeiss AxioCam ERc 5s used for the photographic records, and a Differential Interference Contrast Microscope (DIC) Zeiss Axio Scope A1. The measurements were acquired with the software Zeiss AxioVision SE64. The *sc* ratio is the ratio of the length of a given structure to the length of the scapular plate (Fontoura and Morais 2011). The configuration of ventral plates is indicated in accordance with Kaczmarek et al. (2012). Identification was based on morphological characters, using Ramazzotti and Maucci (1983) for species described before 1983, and literature containing the original descriptions of several species: Murray (1907), Schuster and Grigarick (1966), Pilato (1974), Pilato and Lisi (2003), Kaczmarek and Michalczyk (2004), Kaczmarek and Michalczyk (2010), Kristensen et al. (2010), Pilato et al. (2010). We also compared our material with the holotypes of *Echiniscus walteri* Pilato & Lisi, 2003 and *E. kofordi* Schuster & Grigarick, 1966.

For evaluations at genus level regarding *Bryodelphax*, the following material was examined from the Pilato and Binda collection: *Bryodelphax brevidentatus* Kaczmarek, Michalczyk & Degma, 2005 (paratype, slide No. 5386), *Bryodelphax meronensis* Pilato, Lisi & Binda, 2010 (holotype, slide No. 5350 and a paratype, slide No. 5347), *Bryodelphax parvulus* Thulin, 1928 (from Israel, slide No. 5348; from northern Italy, slide Nos. 1288, 1290–91; from Morocco, slide No. 1280; from central Sicily, slide No. 1880, and from Ustica island, about 60 km north of Sicily, slide No. 1296), *Bryodelphax mateusi* (Fontoura, 1982) (holotype, slide No. 5062).

Results

Class: Heterotardigrada Marcus, 1927

Order: Echiniscoidea Richters, 1926

Family: Echiniscidae Thulin, 1928

Genus: *Echiniscus* C.A.S. Schultz, 1840

Echiniscus dariae Kaczmarek & Michalczyk, 2010

Material examined. 21 specimens, CBUMAG:TAR:00068 (1 specimen), 00085 (11 specimens), 00098 (2 specimens), 00099 (2 specimens), 00101 (1 specimen), 00102 (2 specimens), 00103 (2 specimens). Microhabitat: mixture of a moss from the family Meesiaceae and lichens of the genera *Hypotrachyna*, *Usnea*, *Parmotrema*, *Parmelinopsis*, growing on tree trunks. Localities: San Lorenzo, Sierra Nevada de Santa Marta, 11°06'20.0"N, 74°03'54.4"W, 1930 m a.s.l, and Bella Vista Sierra Nevada de Santa Marta, 11°05'47.8"N, 74°05'04.4"W, 2200 m a.s.l.

Remarks. The morphological features of the specimens correspond with the description of *E. dariae* (Kaczmarek & Michalczyk, 2010), a species that has only been reported for the Neotropical region; with the type locality of Costa Rica, and Peru (Kaczmarek and Michalczyk 2010, Kaczmarek et al. 2014).

This is the first record of this species for Colombia.

Echiniscus kofordi Schuster & Grigarick, 1966

Material examined. 11 specimens, CBUMAG:TAR:00143 (5 specimens), 00144 (6 specimens). Microhabitat: lichen from the genus *Parmotrema* growing on a tree trunk. Locality: Medium basin of Garupal River, Sierra Nevada de Santa Marta, 10°13'48.4"N, 073°48'01.5"W, 543 m a.s.l.

Remarks. These specimens were compared with the holotypes of *E. walteri* Pilato & Lisi, 2003 and *E. kofordi* Schuster & Grigarick, 1966 deposited in the Binda and Pilato collection (Catania, Italy), concluding that the specimens corresponded perfectly with *E. kofordi*. This species has a wide distribution; with the type locality Santa Cruz Island (Galápagos Islands, Ecuador), it has been recorded from India (Andaman Islands), United States, Mexico, Costa Rica, and Venezuela (Grigarick et al. 1983, Meyer 2013). Due to the disjunct geographical distribution reported for this species, it is suspected that the Indian record might refer to another similar species.

This identification provides the first record for Colombia.

Echiniscus perarmatus Murray, 1907

Material examined. 21 specimens, CBUMAG:TAR:00098 (7 specimens), 00099 (10 specimens), 00101 (4 specimens). Microhabitat: lichen from the genus *Parmo-*

trema, growing on a tree trunk. Localities: Bella Vista, Sierra Nevada de Santa Marta, 11°05'47.8"N, 74°05'04.4"W, 1930 m a.s.l.

Remarks. The morphological characters of the Colombian specimens agree with the original description of *E. perarmatus* (Murray, 1907). This species, according to the literature, has a tropical and subtropical distribution; with the type locality, Cape Colony (South Africa), it has also been recorded in Indonesia, Hawaii, United States, and Venezuela (McInnes 1994). The apparent wide distribution we suggest indicates *E. perarmatus* might be a species complex. Therefore further work with original material, or specimens from the type locality, would be required to solve this problem.

This is the first record (*sensu lato*) for Colombia.

Genus: *Bryodelphax* Thulin, 1928

Bryodelphax kristenseni sp. n.

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Figs 1–3, Table 1

Material examined. Holotype and 10 paratypes extracted from a sample composed of lichen (*Parmotrema*), liverworts (*Frullania*, *Plagiochila*), and mosses (Calymperaceae, Amblystegiaceae). The sample was collected in 2011 at the medium basin of Garupal River, Sierra Nevada de Santa Marta, 10°13'48.4"N, 073°48'01.5"W, 543 m a.s.l.

Four additional specimens, CBUMAG:TAR:00198 (1 specimen), 00100 (3 specimens), collected in 2012 from Bella Vista, Sierra Nevada de Santa Marta, 11°05'47.8"N, 74°05'04.4"W, 1,930 m a.s.l. The microhabitat was a lichen from the genus *Usnea*.

Type repository: The holotype and paratypes are deposited in the Centro de Colecciones Biológicas de la Universidad del Magdalena (CBUMAG), Santa Marta, Colombia. Slide numbers: Holotype (mature female) CBUMAG:TAR:00143-8; Paratypes: CBUMAG:TAR:00137 (3 specimens: 1 juvenile and 2 mature females), 00138 (5 specimens: 1 larva and 4 mature females), 00143 (1 specimen: mature female), 00144 (1 specimen: juvenile).

Diagnosis. Small *Bryodelphax* with ten paired plus two or three unpaired ventral plates (IX/X:2-(1)-4-4-2-4-2-1-2-1 according to Kaczmarek et al. 2012), often poorly visible, with fine granular sculpture; dorsal plate ornamentation with superficial irregular pores, and deeper dark “dots” (i.e. cuticular pillars); 6 pairs of faint supplementary plates present laterally between paired plates, ventral cuticle between ventral plates smooth; spine on anterior legs and papilla on hind legs absent or not visible in optical microscopy, dentate collar absent.

Description of the holotype. Body colourless, eyespots absent or not visible after mounting. Total body length, 126.5 µm. Scapular and terminal plate not distinctly divided but unsculptured folds indicate the different portions of the plates (Fig. 1B, 2A). In particular on the scapular plate, a pair of lateral longitudinal grooves differentiates clearly the small

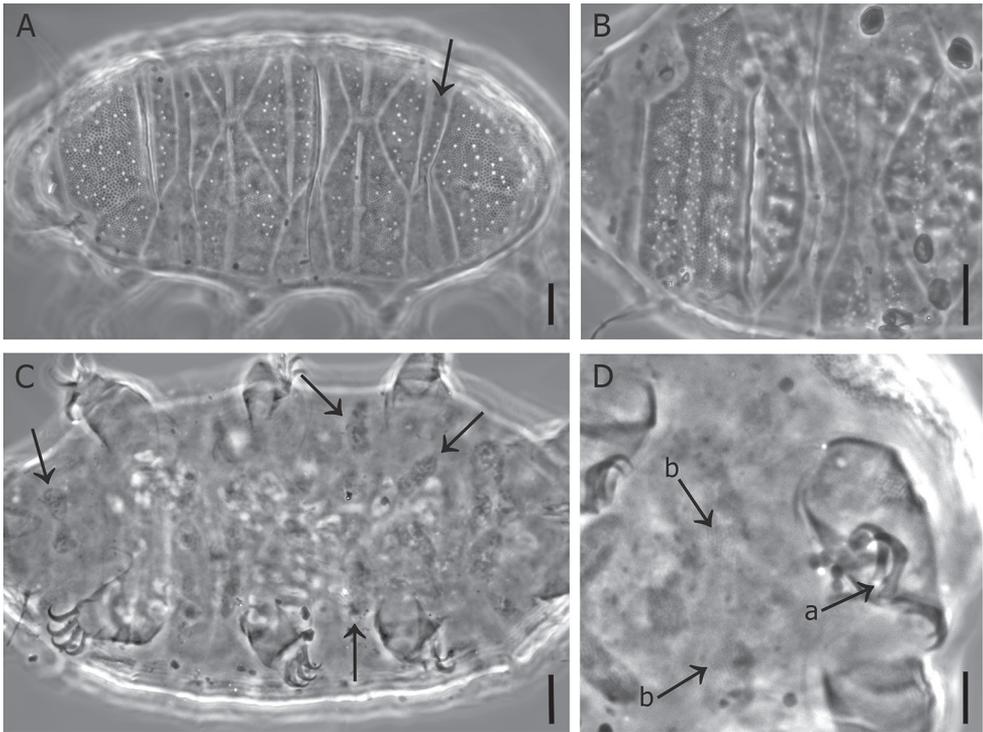


Figure 1. *Bryodelphax kristenseni* sp. n. **A** habitus and dorsal cuticular plates (paratype CBUMAG:TAR:00137-2; the arrow indicates the caudal portion of the third median plate) **B** scapular plate of the holotype, the ornamentation is visible (the specimen is oriented with the head pointing left) **C** ventral surface of the holotype, with several ventral plates visible (arrows indicate those that are better visible) **D** internal claw spurs (arrow **a**), and granular sculpture of the ventral plates (arrows **b**) (paratype CBUMAG:TAR:00144-7). Scale bars: 10 μm (**A–C**); 5 μm (**D**).

lateral portions from the main median, which shows a median longitudinal fold crossed by three less defined transversal bends (Fig. 2A). A median longitudinal fold, not always obvious, is also present in the unpaired plates. The terminal plate has a pair of longitudinal folds (Fig. 2A), which separate the plate into a median and two lateral portions; the former appearing crossed by irregular transversal folds that are not always clearly visible (Fig. 1A, 2A). All three median plates divided, but the posterior portion of the third plate is narrow and rectangular. The first median plate transversally subdivided in two parts by a suture devoid of sculpture, a trapezoid anterior portion, and a triangular posterior section with a rounded caudal edge. The anterior portion of the second median plate is triangular and the posterior section trapezoid; in the posterior area an unsculptured triangular region is visible but, due to its appearance, was not interpreted as a plate. The third median plate is divided, the main anterior plate triangular, with an anterior rounded edge, and a posterior sculptured portion, but sometimes hidden by the terminal plate in contracted specimens. Paired plates also divided into an anterior moderately narrower portion, and a posterior wider portion (Figs 1A, 2A). The shape and arrangement of all plates and their sub-portions is outlined in Fig. 2A.

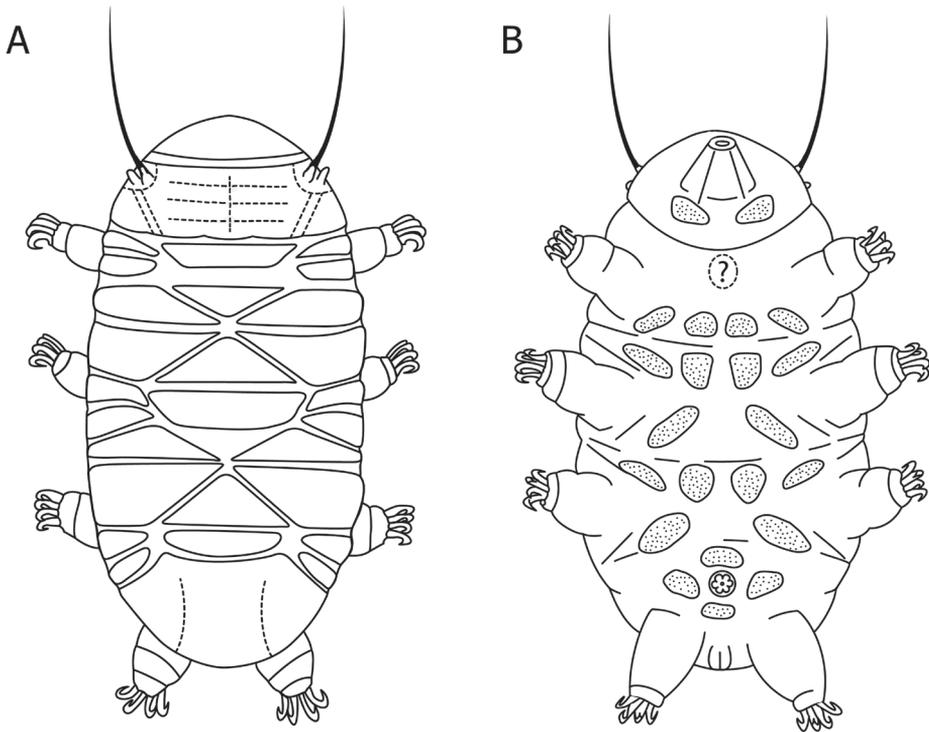


Figure 2. Drawings of the dorsal **A** and ventral **B** plates arrangement of *Bryodelphax kristenseni* sp. n.

All plates show apparent double sculpture: big pores more or less irregular in size and distribution, often fused to one another (Fig. 1A–B) in some cases almost forming patterns, and a lower level of regular “granules” (i.e. cuticular pillars). The pores tend to form three transversal bands on the scapular plate (Fig. 1B), while on the terminal plate they tend to be grouped in areas that are separated by stripes without pores, thus almost outlining “facets”. On the remaining plates, the pores tend to be arranged on each sub-portion of the plate in a more or less defined transversal band (or a single line on the narrowest sub-plates) (Fig. 1), i.e. a band on the anterior and a band on the posterior portions of the paired plates, a band on the anterior and a single line on the narrow posterior portions of the unpaired plates.

The cuticular pillars (Fig. 1A, B) appear regularly distributed, and vary in size between plates and the different part of each plate/sub-plate. The largest (about 1.2 μm) are on the scapular and terminal plates, and the proportion among the granules of the different plates is as follows: scapular = terminal > posterior portions of the paired plates > anterior portions of the paired plates > unpaired plates. In the latter, the “granules” appear not only smaller but also fainter. On each plate or sub-plate, the terminal plate excluded, the “granules” are larger on the median transverse band, and gradually decrease in the more cephalic and caudal portions as well as the very lateral portions,

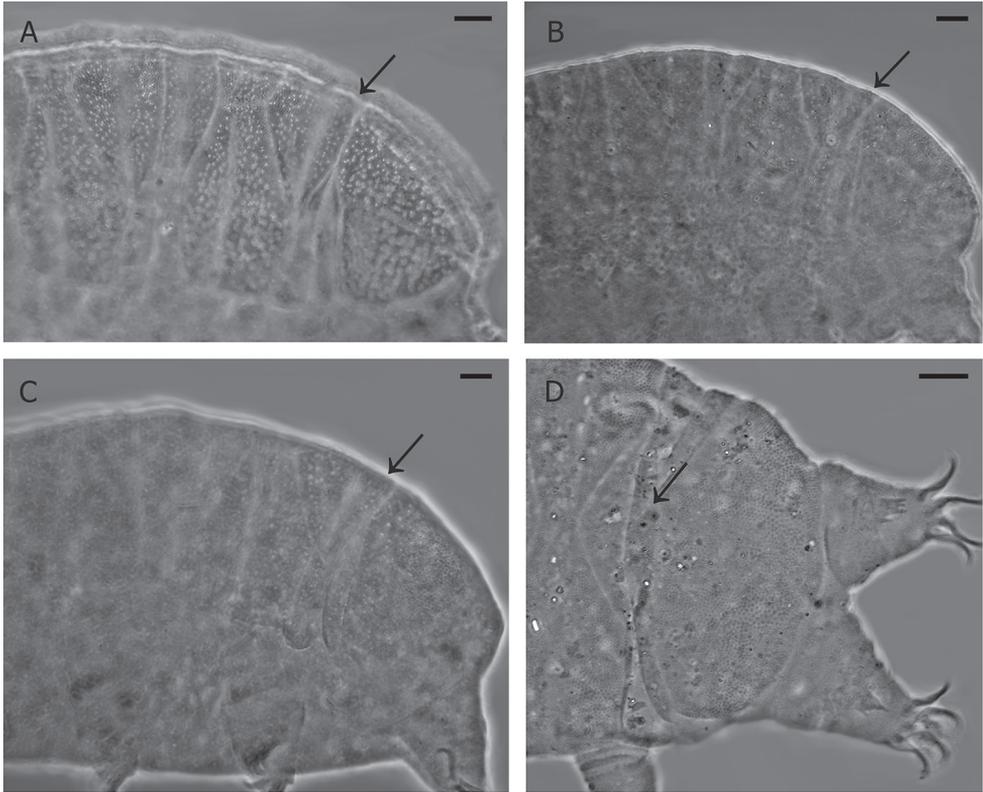


Figure 3. Divided third median plate (arrows indicate its caudal piece) in **A** *Bryodelphax brevidentatus* Kaczmarek, Michalczyk & Degma, 2005 **B** *B. meronensis* Pilato, Lisi & Binda, 2010 **C** *B. parvulus* Thulin, 1928, and **D** *B. weglarskae* (Pilato, 1972). Scale bars 10 μ m.

almost at the borders. On the terminal plate the largest granules lie on a band at about $\frac{3}{4}$ of the length of the plate, gradually decreasing, going to the more cephalic portion and at the very lateral and caudal portions, almost at the borders. Six pairs of lateral supplementary platelets, difficult to see, are present between the paired plates (Fig. 2A).

Ventral plates present, but faint and difficult to observe, consist of ten paired plus two unpaired (IX/X:2-(1)-4-4-2-4-2-1-2-1 according to Kaczmarek et al. 2012), as depicted in Fig. 2B; the brackets in the formula and the question mark in Fig. 2B indicate the difficulty in ascertaining the presence of an unpaired ventral plate at the level of legs I: if that plate is present, then the unpaired plates are three and not only two, and the plate rows are ten instead of nine. All ventral plates show a faint granulation under PCM (Fig. 1C, arrows). The rest of the ventral cuticle is smooth. All legs with a band of small dots.

Apart from the cephalic cirri, only the lateral filament *A* is present (26.5 μ m long = 21.0% of body length and 150.7% of the scapular plate length). Internal cephalic cirrus 8.0 μ m long; external cephalic cirrus 11.5 μ m long; cephalic papilla 4.0 μ m long; clava *c.* 4.7 μ m long (Table 1).

Spines on the first pair of legs absent or not visible under PCM. The dentate collar on the fourth pair of legs absent (but the sculptured platelet of the dentate collar present). No papilla visible on the hind legs under PCM. External claws smooth. Internal claws with spur oriented towards the base (Fig.1D, arrow *a* indicating a spur). Measurements of some structures of the holotype and ranges among the paratypes (larva excluded) are given in Table 1 (Supplementary Data provides all measurements for these specimens). No eggs were found.

Remarks. The paratypes exhibit the same morphology, but with a certain degree of variation with regard to appearance of the bands of the scapular and terminal plates, more visible in less relaxed specimens. The narrow posterior portions of the median plates (especially with regard to the third), are more visible in well-relaxed specimens but can be totally hidden in contracted specimens. In such specimens, the posterior elements of each couple of supplementary platelets, especially the third, could also be hidden. In addition, the orientation of the specimen on the slide meant the supplementary lateral platelets were not always clearly visible. With regard to the ventral plates, these were evident in some specimens, e.g. that chosen as holotype, but were not always easy to see. In general, the ventral plates varied from faint to almost invisible (without clear indication of a link with life stage); it took a very accurate, long observation under both PCM and DIC to identify all the plates and to be certain of the number and arrangement. Such plates show in PCM a faint granulation, which is actually what, in some cases, made them visible; their borders often being unclear. In some of the specimens not even one ventral plate was apparent at first sight, requiring very careful observation to detect at least some of them; thus this character can pass unnoticed. We therefore recommend great care in observing *Bryodelphax* before considering whether a specimen is without ventral plates, and also without supplementary lateral platelets.

Another character, for which considerable individual variability is noted, is the distribution of the cuticular pores, which may be arranged from a relatively regular distribution, as described in the holotype, to a quite random distribution. Additionally, the transversal bands of pores of the sub-portions of the paired and unpaired plates can be reduced to a single, more or less regular row.

Finally, the papilla of the hind legs in most specimens was not visible, but in a couple of individuals, there appeared to be an extremely small, faint papilla. However, the presence of particles in the slides preparation prevented us from being sure that what we observed was a papilla and not some out of focus particle. This character, therefore, needs to be confirmed.

Etymology. The species is named in honour of Professor Reinhardt Møbjerg Kristensen, in particular for his valuable contribution to the taxonomy of Echiniscidae (Kristensen 1987).

Differential diagnosis. According to Kristensen et al. (2010), the new species falls into the *weglarskae* group due to the presence of ventral plates. Within this group the dentate collar is absent from only two species: *Bryodelphax sinensis* (Pilato, 1974) and *B. aaseae*. However, due to the difficulty in observing the ventral plates in some specimens of our new species, we also compare species descriptions where ventral plates were not

Table 1. Measurements (μm) and %bo %osc values of selected morphological structures of the holotype and paratypes of *Bryodetlphax kristenseni* sp. n.

CHARACTER	N	MIN – MAX				MEAN				SD				HOLOTYPE			
		μm	%bo	%osc		μm	%bo	%osc		μm	%bo	%osc		μm	%bo	%osc	
Body length	10	106	–	131		121.1			9.1				126.5				
Scapular plate length	10	16.2	–	21.7	13.9	–	19.4	16.4	1.9	1.5			17.6	13.9			
Lateral appendage A	8	24.8	–	27.2	18.8	–	24.0	21.4	0.8	1.8	129.0		26.5	21.0	150.7		
Clava	5	3.8	–	4.8	3.4	–	4.3	3.7	0.4	0.3	19.0		4.7	3.7	21.0		
Int. cephalic cirrus	9	6.6	–	8.3	5.2	–	7.0	6.3	8.0	0.5	39.0		0.7	8.0	45.5		
Ext. cephalic cirrus	10	9.5	–	13.1	8.5	–	10.6	9.2	11.4	0.7	56.3		1.0	11.5	65.4		
Cephalic papilla	7	3.5	–	4.5	3.1	–	3.8	3.4	4.1	0.2	21.2		0.4	4.0	3.2	22.8	
Ext. claw I	9	5.3	–	6.4	4.7	–	5.6	4.9	6.2	0.3	29.9		0.4	6.0	4.7	33.8	
Int. claw I	8	5.6	–	7.0	5.0	–	5.9	5.3	6.6	0.3	32.2		0.5	6.4	5.0	36.2	
Spur	8	1.0	–	1.3					1.2				0.1	1.1			
Spur/Claw		0.2	–	0.2					0.2				0.0	0.2			
Ext. claw II	7	5.1	–	6.3	4.5	–	5.6	4.7	5.8	0.4	28.7		0.4	5.8	4.6	32.9	
Int. claw II	6	5.5	–	6.6	4.7	–	5.1	5.0	6.0	0.1	26.2		0.5	6.0	4.7	26.9	
Spur	7	0.9	–	1.1					1.1				0.1	1.0			
Spur/Claw		0.1	–	0.2					0.2				0.0	0.2			
Ext. claw III	7	4.4	–	6.3	4.2	–	5.5	4.7	6.0	0.4	28.5		0.7	5.6	4.4	31.7	
Int. claw III	4	5.2	–	6.4	4.7	–	5.7	4.8	6.1	0.5	29.7		0.6	5.9	4.7	33.6	
Spur	4	1.0	–	1.2					1.1				0.1	1.1			
Spur/Claw		0.2	–	0.2					0.2				0.0	0.2			
Ext. claw IV	6	5.2	–	7.2	4.9	–	6.0	5.3	6.5	0.7	31.5		0.7	0.4			
Int. claw IV	3	6.0	–	6.5	5.0	–	5.5	5.3	6.3	0.3	32.3		0.3	0.3			
Spur	2	1.0	–	1.3					1.2				0.2				
Spur/Claw		0.2	–	0.2					0.2								

reported (stressing the fact that especially in early publications the ventral plates may have passed unnoticed or not considered a valuable character). Species with the same type of cuticular ornamentation, and without the dentate collar include: *B. parvulus*, *B. asiaticus* Kaczmarek & Michalczyk, 2004 and *B. ortholineatus* (Bartoš, 1963).

Bryodelphax aaseae (Kristensen, Michalczyk & Kaczmarek, 2010) is the most similar species, sharing with the new species the same ventral plate configuration (if the median unpaired plate at the level of legs I is also present in the new species). These plates were described as smooth by the authors, but in Kristensen et al. (2010 – figs 9–11 and 19), there is the appearance under PCM of granulation, and this might be similar to the new species. Another character we noted was the apparent presence of lateral supplementary platelets between the paired plates in *B. aaseae*, (see: Kristensen et al. 2010 – fig. 7), which was not mentioned by the authors. Despite the similarities, *B. kristenseni* sp. n. differs from *B. aaseae* by: less evident ventral plates; the unpaired ventral plate at the level of the pharyngeal bulb appears absent in *B. kristenseni* sp. n. (present in *B. aaseae*); shorter cirrus A (18.8–24.0% of the body length *vs.* about 24–34% μm in *B. aaseae*); longer clava (3.4–4.3% of the body length *vs.* less than 3% μm in *B. aaseae*); shorter claws (4.2–6.0% of the body length *vs.* about 7.3–7.7% in *B. aaseae*).

Bryodelphax kristenseni sp. n. differs from *B. sinensis* by having supplementary platelets, more numerous ventral plates (IX/X:2-(1)-4-4-2-4-2-1-2-1 *vs.* VII:2-2-2-2-2-2-1 in *B. sinensis*), ventral cuticle smooth (dotted in *B. sinensis*), longer clava (3.4–4.3% of the body length *vs.* about 2.5% in *B. sinensis*).

The diagnosis of *B. parvulus* was revised by Pilato et al. (2010), and this species should lack ventral plates. Moreover, another difference with the new species is the length of the clava: 3.4–4.3% of the body *vs.* about 2.5% of the body in *B. parvulus* (see Pilato et al. 2010, in which a specimen from Poland attributed to *B. parvulus* by Węglarska 1959, and confirmed by Pilato, was measured, slide No. 1476 of Pilato and Binda collection).

Bryodelphax kristenseni sp. n. differs from *B. asiaticus*, which lacks the ventral plates, in having non-granulated ventral cuticle, anterior portions of median plates 1 and 2 markedly larger than the posterior portions (which are almost a stripe), while in *B. asiaticus* the posterior portions of those plates are only slightly smaller.

The new species differs from *B. ortholineatus* in having spurs on internal claws (absent in *B. ortholineatus*), in having supplementary platelets (not mentioned in the original description (Bartoš, 1963) and reported as absent by Fontoura et al. 2008), and the shape of the median plates looks different in Bartoš' original drawing, but it must be stressed that the drawing was very stylised.

Discussion

As mentioned above, in *B. kristenseni* sp. n. the third median plate is divided into an anterior and a posterior portion; this character, until now, has been considered typical of the genus *Brychoerus*, while in *Bryodelphax* the third median plate has been considered undivided.

At first, there were doubts on the identification due to the division of the third median plate, although hidden in some specimens, which led us to *Brychoerius*; on the other hand, there was evident resemblance between these specimens and *Bryodelphax aaseae*, and with other species, e.g., *Bryodelphax weglarskae* (Pilato, 1972). This encouraged careful examination of that species as well as many others congeners, and it was noted that the divided third median plate was also present in *B. aaseae* (figs 7 and 8 in Kristensen et al. 2010), *B. asiaticus* (fig. 6 in Kaczmarek and Michalczyk 2004), *B. parvulus* (Ramazzotti and Maucci 1983, page 221, fig. 70 from Thulin's 1928 original description), and the following material from the Pilato and Binda collection, which was examined: *B. brevidentatus* (paratype, slide No. 5386, Fig. 3 A), *B. meronensis* (holotype, slide No. 5350, Fig. 3 B), *B. parvulus* (from Israel, slide No. 5348, Fig. 3C; from Northern Italy, slide Nos. 1288, 1290–91; from Morocco, slide No. 1280; from central Sicily, slide No. 1880, and from Ustica Island, about 60 km North from Sicily, slide No. 1296). Furthermore, a specimen of *B. weglarskae* also had that piece of plate partially covered by the terminal plate (Fig. 3 D).

The definition of the genus *Bryodelphax* is therefore suggested as follows:

Small Echiniscidae with non-flexible buccal tube with CaCO_3 encrusted stylet supports. No lateral or dorsal appendages present except cirrus A. Median plates all divided, but the caudal portion of the third median plate may be hidden by the terminal plate. Without pseudosegmental plates. Ventral plates may be present.

With respect to Kristensen's (1987) definition, we have preferred not to include the presence of "red granulate eyes" as a character of the genus because the presence or absence of eyes is variable in many genera, and can be lost in the slide mounting process (e.g. *B. kristenseni* sp. n.).

Conclusions

Authors from an earlier period (ca. 1900–1950s) traditionally considered many species to be cosmopolitan, which in tardigrade taxonomy created species-groups. These species-groups, along with past errors and misinterpretations, now require careful analysis in order to amend taxa descriptions and differentiate the sibling species. As taxonomic knowledge has progressed, key characters have been added that were not considered essential in older references. We are left with a legacy of early species descriptions that are often impossible to identify without type material, which in many cases is sadly unavailable. Taking into account the absent or poor state of older type material, and the difficulty in resampling a vaguely described *locus typicus*, the possibility of abolishing or classifying a suspect species as "*species dubia*" should be considered. This would help prevent further confusion created by non-taxonomists or beginners using an apparently simple diagnostic key (e.g., Ramazzotti and Maucci (1983) monograph) to record questionable species.

With our present contribution, based on material in a museum collection, three new records enrich the list of Echiniscidae recorded for Colombia. In addition, a species new to science was discovered, which provided the occasion to make evalu-

ations at a higher taxonomic level. The fact that a relatively limited study provides new and interesting results, in spite of the great efforts from past decades, is evidence of how little is known about tardigrade fauna and biogeography for most regions of the world. It further highlights how much our taxonomic knowledge has grown and can still grow.

Acknowledgements

We are grateful to Prof. Giovanni Pilato for useful suggestions and making available his precious collection, to the Subject Editor Sandra McInnes and the reviewers for having improved the paper. This work was carried out in the framework of the research projects “Composición taxonómica de flora y fauna anhidrobiótica en micro-doseles de la Sierra Nevada de Santa Marta”, supported by Departamento Administrativo de Ciencia, Tecnología e Innovación “COLCIENCIAS” (#0091288) and the Universidad del Magdalena (BIO-659/2014), and “Diversidad de ositos de agua (Tardigrada) asociados a briófitos y líquenes epífitos en cultivos de café de la Sierra Nevada de Santa Marta, con un enfoque innovador para la apropiación social del conocimiento” supported by Fondo Patrimonial para la Investigación “FONCIENCIAS” 2015–2017 de la Universidad de Magdalena.

This is a scientific contribution number 8 from the Centro de Colecciones Biológicas de la Universidad del Magdalena.

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Taxonomy of North European *Lumbricillus* (Clitellata, Enchytraeidae)

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Academic editor: S. James | Received 24 April 2017 | Accepted 29 August 2017 | Published 27 September 2017

<http://zoobank.org/9BAAB4A5-CDE1-493B-8A04-13D8F301E198>

Citation: Klinth MJ, Rota E, Erséus C (2017) Taxonomy of North European *Lumbricillus* (Clitellata, Enchytraeidae). ZooKeys 703: 15–96. <https://doi.org/10.3897/zookeys.703.13385>

Abstract

Lumbricillus is a genus of clitellate worms with about 80 described species that inhabit marine and limnic habitats. This study follows a recent analysis of the phylogeny of the genus based on 24 species of *Lumbricillus* collected mainly in Norway and Sweden. We provide the illustrated taxonomic descriptions of all these species and describe two of them as new; *Lumbricillus latithecatus* **sp. n.** and *L. scandicus* **sp. n.** Using the recent phylogeny, we informally divide *Lumbricillus* into five distinct morphological groups, into which we also tentatively place the *Lumbricillus* species not included in this study. Furthermore, we establish *Claparedrilus* **gen. n.**, with the type species *C. semifuscoides* **sp. n.**, and transfer *Pachydriilus semifuscus* Claparède, 1861 (previously referred to *Lumbricillus*) into said genus.

Keywords

Annelida, Oligochaeta, *Lumbricillus latithecatus* sp. n., *Lumbricillus scandicus* sp. n., *Claparedrilus* gen. n., *Claparedrilus semifuscoides* sp. n., *Claparedrilus semifuscus* (Claparède, 1861) comb. nov.

Introduction

Enchytraeids (Annelida, Clitellata, Enchytraeidae) are small clitellate worms that mainly inhabit terrestrial soils but the family is well represented in the aquatic environment. One of the about 30 genera, *Lumbricillus* Ørsted, 1844, is primarily found in marine and freshwater habitats, but also in humid soils (Nielsen and Christensen 1959). It was established by Ørsted (1844), and *Lumbricus lineatus* Müller, 1774, the first enchytraeid ever described (Michaelsen 1889), was later regarded as its type species (Brinkhurst and Jamieson 1971; Coates and Ellis 1981). Ørsted (1842) had earlier referred *Lumbricus lineatus* to one of three groups constituting the “Lumbricillae”, and specifically to the group distinguished by having short, almost straight chaetae, “resembling stitching awls”, in both upper and lower bundles. He would later (Ørsted 1844) name this group *Lumbricillus*. Today, after several emendations, the genus is conceived as having straight to sigmoid chaetae, nephridia with short anteseptale consisting of nephrostome only, and testes enclosed in lobed peritoneal sacs (testis sacs) which, for most species, are structured as regular bunches (Nielsen and Christensen 1959).

Returning to the 19th Century, Claparède described his *Pachydriulus* Claparède, 1861 as an assemblage of marine littoral species lacking “hair bristles”, but having a single pair of spermathecae in segment V, clitellum covering segments XI–XIII, male pores in XII, and simple vascular and nervous systems. *Pachydriulus* (and its five representatives) shared these basic traits with the terrestrial species then classified in *Enchytraeus* Henle, 1837, but was distinguished by the lack of dorsal pores and by generally possessing red-colored blood. *Pachydriulus* was later redefined by Vejdovský (1879) to include only species with sigmoid chaetae and small nephridial anteseptals and then further restricted by Roule (1888, 1889) and Michaelsen (1888, 1889), with a diagnosis focusing on the possession of multilobed testes, which led to the selection of *P. verrucosus* Claparède, 1861 as the type species. It must be mentioned that the very same species epithet had been used by Ørsted in 1844 for his *Lumbricillus verrucosus*, but due to the lack of an adequate description, it was considered a *nomen nudum* and *incertae sedis* (both Vejdovský 1884:45 and Michaelsen 1900:51 believed it should be placed among Tubificidae). The present study will treat *P. verrucosus* Claparède, 1861 as a valid enchytraeid species.

The name *Pachydriulus* soon became a competitor for *Lumbricillus* in the taxonomic literature. Some scientists favored *Pachydriulus* (Michaelsen 1888, 1889; Ude 1929; Černosvitov 1937), others *Lumbricillus* (Eisen 1904; Southern 1909; Stephenson 1911, 1930). In 1900, Michaelsen attempted to resolve the conflict by accepting the seniority of the name *Lumbricillus* and placing *Pachydriulus verrucosus* within this genus (Michaelsen 1900) and proceeded to use this name in following publications (Michaelsen 1905, 1911). However, he later went back to using *Pachydriulus* instead of *Lumbricillus* (Michaelsen 1925, 1929, 1934, 1935; see Rota et al. 2008). The use of two competing names ended in 1959 when Nielsen and Christensen synonymized *P. verrucosus* with *L. lineatus*, directly rendering *Pachydriulus* a junior synonym of *Lumbricillus*; *P. verrucosus* had previously been suggested as a form of *L. lineatus* by

Ude (1929) and Černosvitov (1937). *Lumbricillus verrucosus* has recently been resurrected as a separate species with molecular support (Klinth et al. 2017) and will be given a more extensive morphological description in this paper. It is important to note that by re-instating *L. verrucosus* as a valid species, we do not change the status of *Pachydrilus* as a junior synonym to *Lumbricillus*, as *L. verrucosus* and *L. lineatus*, using genetic data, have been found to be closely related to each other (Klinth et al. 2017; see also Fig. 1 herein).

In 1885, Saint-Loup described the species *Pachydrilus enchytraeoides* Saint-Loup, 1885 from the Marseille harbor. The rather brief description mentioned pouch-like spermathecae, a simple circulatory system and irregularly lobed testes (Saint-Loup 1885). The combination of these characters, interpreted by Saint-Loup's fellow researcher Roule to be intermediate between *Lumbricillus* and *Enchytraeus*, convinced Roule (1888) to transfer the species to a new genus, which he named *Enchytraeoides* Roule, 1888 in acknowledgement of Saint-Loup's work. However, to avoid tautonymy (i.e., when genus name and species epithet are identical), he also unconventionally changed the species epithet to *marioni* substituting *Pachydrilus enchytraeoides* with *Enchytraeoides marioni*. Furthermore, Roule provided an extensive description of the embryology and development of his species along with over a hundred illustrations (Roule 1889). The male anatomy of *E. marioni* is in many ways reminiscent of some species of *Lumbricillus*, such as *L. arenarius* (Michaelsen, 1889), in lacking the typical regularly lobed testis sacs of most *Lumbricillus* and having sperm funnels several times longer than wide. In fact, *L. arenarius* has been placed in *Enchytraeoides* by some authors (Ude 1929; Knöllner 1935; von Bülow 1957). It is not completely clear if *Pachydrilus enchytraeoides* and *Enchytraeoides marioni* are indeed the same species. Regardless, the descriptions of both species fit within *Lumbricillus*, and thus *Enchytraeoides* should be considered a junior synonym of *Lumbricillus* (Stephenson 1930). A more extensive account on the intricate taxonomical history of *Enchytraeoides* and other genera can be found in Rota et al. (2008).

Among the new species described by Claparède (1861) when he established the genus *Pachydrilus* was *P. semifuscus* Claparède, 1861. This species was noted to have the body colorless anteriorly and brown posteriorly (due to the strongly pigmented chloragogen tissue), conspicuous nephridia, solid unlobed testes and huge penial bulbs. The species was later transferred to *Marionia* (a name soon after replaced by *Marionina*) by Michaelsen (1889) and remained there until Nielsen and Christensen (1959) moved it to *Lumbricillus*. The brief original description was amended partly by Southern (1909) and more extensively by Stephenson (1911), who reported 4 to 5 pairs of pharyngeal glands, along with details of the chaetae, brain, copulatory glands and more. The species was also described from Iceland by Erséus (1976), who observed that the anteseptale of the nephridia might contain more than just a funnel (also a few coils). It has later been noted that this species (as well as others) lack the typical lobes of the testes and thus might not fit in *Lumbricillus* (Kossmagk-Stephan 1983).

The molecular phylogenetic study by Erséus et al. (2010) documented that *Lumbricillus* is a non-monophyletic group, and that a group of species (including

L. arenarius) is sister to *Grania* Southern, 1913 rather than to the remaining *Lumbricillus*. However, the more recent analysis of the North European *Lumbricillus* by Klinth et al. (2017) showed ambiguity as to whether three *Lumbricillus* species (*L. arenarius*, *L. dubius* (Stephenson, 1911) and an unidentified species) comprise the sister group of the remaining *Lumbricillus* or the sister to *Grania*, where they together with *Grania* in turn would be the sister to *Lumbricillus* sensu stricto. The same study also found strong evidence for excluding what they refer to as “*L. semifuscus*” from *Lumbricillus* sensu stricto (Klinth et al. 2017). Lately, with increased taxon sampling that species (which we here describe as *C. semifuscooides* sp. n.) has been found to be more closely related to *Globulidrilus* Christensen & Dózsa-Farkas, 2012 and *Bryodrilus* Ude, 1892 (Martinsson et al. 2017).

The aim of this study is to increase the knowledge of the taxonomy of North European *Lumbricillus*, based on the most recent phylogenetic reconstruction and molecular delimitation of species (Klinth et al. 2017), and herein, by the addition of morphological studies. However, we will not use the morphological characters for any phylogenetic analysis. We will provide illustrated descriptions of all the included species and establish three new species and one new genus and re-describe *L. helgolandicus* (Michaelsen, 1927), in order to clear up parts of the taxonomy of this poorly studied group.

Material and methods

Worms were collected in marine, brackish and limnic habitats, mainly in Norway and Sweden (Appendix 1), by decantation of suspended organic material from bottom substrates and killed and preserved in 80 % ethanol. After sorting under a dissecting microscope, the posterior end of each worm was cut away for DNA analyses (partly published by Klinth et al. 2017) while the anterior end was stained in paracarmine, dehydrated in xylene and mounted in Canada balsam on microscope slides; for a more detailed description of procedures see Erséus (1994). Using a compound microscope, specimens on slides were identified to species using the primary taxonomic literature, and largely adhering to the list of accepted species in Schmelz and Collado (2012), with the following exceptions: *L. aegialites* Stephenson, 1922 and *L. georgiensis* Tynen, 1969, both synonymized with *L. pagenstecheri* (Ratzel, 1868) by Coates & Ellis, 1981, *L. magdalenae* Nurminen, 1965 which we consider a synonym of *L. arenarius* (Michaelsen, 1889), and finally *L. cervisiae* Kossmagk-Stephan, 1983 and *L. christenseni* Tynen, 1966, which we consider separate species from *L. knoellneri* Nielsen & Christensen, 1959 with which they were previously synonymized. In the species descriptions we provided brief chresonymy lists of the references we found most relevant for each species. Morphological characters were drawn using a camera lucida and the images were treated by Gimp 2.8.10 software. All specimens studied are vouchers of DNA sequences (Appendix 1), including the COI-barcodes generated by Klinth et al. (2017) study, which were also used in this study to find matches between our specimens and records in the

Barcoding of Life Database (**BOLD**), to better estimate the geographical ranges of the species. Where available, Barcode Index Numbers or BIN:s have been noted in each species description. These BIN:s refer to clusters of COI-barcodes on BOLD that are considered to comprise specimens of the same species. Finally, the only remaining syntype of *Pachydriulus helgolandicus* Michaelsen, 1927, herein designated as the lectotype, was borrowed from the Zoological Museum in Hamburg (**ZMH**). It has now been mounted and morphologically examined. Types and other voucher specimens are deposited in the Swedish Museum of Natural History (**SMNH**) and the Zoological Museum, University of Bergen (**ZMBN**).

Results

General notes

All descriptions are based on fixed worms mounted on slides. This has some disadvantages for discerning the shape of certain internal organs such as the nephridia, but is not an unusual method for marine worms, and it improves the description of other characters such as chaetae. Nevertheless, morphology can differ from descriptions in the literature based on living specimens. Welch (1914) noted that fixation in alcohol can reduce *Lumbricillus* body length from about 15–19 mm in living specimens, to about 9–14 mm in fixed specimens. Finogenova and Streltsov (1978) noted that the ratio between the length and width of the sperm funnels was similarly reduced in fixed specimens. They reported sperm funnels about 2–4 times longer than wide in living specimens and a ratio of about 1.2–1.5:1 after fixation. Furthermore, Finogenova and Streltsov (1978) as well as Southern (1909) reported the ratio length:width of the sperm funnels to vary in living specimens due to body contractions. Southern (1909) further questioned the importance of the midventral subneural glands (previously referred to as copulatory glands) for separating species, as these glands seem to vary in size and sometimes in segmental distribution between individuals of the same species. We also observed great variation in these features. Lastly, as the colour cannot be distinguished after the staining, remarks on the colour of the worms is based on the notes made by the collector, prior to preservation and mounting.

All specimens in this study are amputated of their posterior segments (used for DNA extraction). Therefore, comparisons of total length and segment number with original descriptions have not been possible. When available, the length of the fifteen first segments as well as the width at the clitellum of the worms has been used to compare the general body size of the species.

In fixed *Lumbricillus* worms the origin of the dorsal vessel can be difficult to establish since vessel expansions are more or less conspicuous according to the peristaltic movement of the blood at the time of fixation. Thus, due to the varying conditions when animals were killed and fixed, the dorsal vessel may appear to originate in different segments.

Abbreviations in the figures

as=anteseptale, b=brain, cl=clitellum, dg=duct glands, e=egg, ed=ectal duct, eg=ectal gland, mu=musculature, nd=nephridial duct, oe=oesophagus, ov=ovaries, pb=penial bulb, pg=pharyngeal glands, ps=postseptale, s=spermatheca, sa=spermathecal ampulla, sf=sperm funnel, sm=sperm mass, sp=spermathecal pore, t=testis, ts=testis sac, vd=vas deferens.

Taxonomy

Lumbricillus Ørsted, 1844

Genus description/diagnosis. Mainly red, pink, orange, yellow or white when alive, sometimes green or black. Living worms ranging from about 5 to 20 (35 in extremes) mm, fixed from 3 to 14 mm (35 mm in *L. maximus* (Michaelsen, 1888) even after fixation; Rota 2001). Prostomium hemispherical. Head pore at 0/1. Epidermis with transverse rows of gland cells. Chaetae usually sigmoid, sometimes straight, without nodulus, upper bundles varying from a dorsolateral to a midlateral position. Oesophageal appendages absent. Pharyngeal glands in three pairs, located in IV–VI, usually converging dorsally, sometimes connected dorsally, usually with ventral lobes, but secondary glands absent. Only nucleated coelomocytes present. Dorsal vessel originating intra- or in a segment posterior to clitellum. Nephridia with anteseptale made up of funnel only. Clitellum covering XII–XIII, sometimes also extending over parts of XI. Testes surrounded by peritoneal sacs; the latter usually made up of large lobes arranged in a regular bunch, in some smaller species forming a compact mass, only slightly and irregularly lobed. Penial bulbs round and compact, in a few species bilobed. Midventral subneural glands usually present in XIII–XV, sometimes further back. Spermathecae in V, sometimes extending further back, attached to and usually communicating with lumen of oesophagus; glands surrounding ectal part of ectal duct, sometimes also along ectal duct. Spermathecae either club-shaped with ampulla distinctly set off from duct or spindle-shaped without clear distinction between ampulla and duct. Spermathecal diverticula absent. Mainly living in the littoral zone of the sea but some species also found in limnic and/or terrestrial habitats.

Type species. *Lumbricus lineatus* Müller, 1774.

Other species. See Table 1 and notes below.

Remarks. Based on the recent phylogenetic analysis of North European *Lumbricillus*, a number of monophyletic groups within the genus were recognized (Klinth et al. 2017). Several of these are distinguished by a combination of morphological characters that we refer to when discussing the taxonomy below. For convenience, we informally divide the species investigated into five groups based on their morphology: the *lineatus* group, the *pagenstecheri* group, the *buelowi* group and the *arenarius* group, all molecularly monophyletic, and the “*tuba*” group, which is molecularly paraphyletic (thence the

Table 1. The informal division of *Lumbricillus* into five morphological groups based on the phylogenies by Klinth et al. (2017), together with comparisons of some morphological characters. Furthermore, the *Lumbricillus* species not included in the present study are listed with tentative placements to one of these groups. Note that it is likely that some of the species not studied could upon closer examination prove to be synonyms to the included species in this study. * *L. latithecatus* sp. n. was referred to as *L. sp. E* in Klinth et al. (2017). ** *L. scandicus* was referred to as *L. cf. belgolandicus* in Klinth et al. (2017).

	Monophyletic (Based solely on Klinth et al. 2017)	Testis sacs	Spermathecal shape	Spermathecal duct glands	Penial bulb	Sperm funnels	Chaetae per bundle	
<i>lineatus</i> group	Yes	Regularly lobed into bunch- shape	Spindle-shaped, indistinct ampulla	No	Round	1-5 times longer than wide	3-6 or more	
<i>pagenstecheri</i> group	Yes	Regularly lobed into bunch- shape	Club-shaped, distinct ampulla	Yes	Round	About twice longer than wide	3-6 or more	
“ <i>tuba</i> ” group	No	Regularly lobed into bunch- shape	Club-shaped, distinct ampulla	No	Round	About as long as wide	3-6	
<i>buelowi</i> group	Yes	Irregularly lobed without bunch- shape	Club-shaped, distinct ampulla	No	Round	About as long as wide	2-3	
<i>arenarius</i> group	Yes	Irregularly lobed without bunch- shape	Pouch-shaped, indistinct ampulla	No	Round or bilobed	3-10 times longer than wide	2-3	
	Species included in the present study	Species not included in the present study, placed on the basis of their descriptions						
<i>lineatus</i> group	<i>L. fennicus</i> Nurminen, 1964 <i>L. kaloensis</i> Nielsen & Christensen, 1959 <i>L. latithecatus</i> sp. n. * <i>L. lineatus</i> (Müller, 1774) <i>L. pumilio</i> Stephenson, 1932a <i>L. rivalis</i> Levensen, 1884 <i>L. rubidus</i> Finogenova & Streltsov, 1978 <i>L. rutilus</i> Welch, 1914 <i>L. verrucosus</i> (Claparède, 1861) <i>L. sp F</i> <i>L. sp G</i>	<i>L. aestuum</i> (Stephenson, 1932b) <i>L. alaricus</i> Shurova, 1974 <i>L. antarcticus</i> Stephenson, 1932b <i>L. americanus</i> (Ude, 1896) <i>L. benhami</i> Stephenson, 1932b <i>L. enteromorphae</i> von Bülow, 1957 <i>L. griseus</i> (Stephenson, 1932b) <i>L. healyae</i> Rodriguez & Rico, 2008 <i>L. incisus</i> Wang & Liang, 1997 <i>L. insularis</i> (Ude, 1896) <i>L. immoderatus</i> Finogenova, 1988 <i>L. macqueriensis</i> Benham, 1905 <i>L. maximus</i> (Michaelson, 1888) <i>L. minimus</i> (Černosvitov, 1929)			<i>L. minutus</i> (Müller, 1776) sensu Michaelson, 1911 <i>L. murmanicus</i> Finogenova & Streltsov, 1978 <i>L. parabolus</i> Shurova, 1978 <i>L. parvus</i> (Ude, 1896) <i>L. pseudominutus</i> Timm, 1988 <i>L. pygmaeus</i> (Michaelson, 1935) <i>L. Rupertensis</i> Coates, 1981 <i>L. sadovskiyi</i> Marcus, 1965 <i>L. santaclarae</i> Eisen, 1904 <i>L. scoticus</i> Elmhirst & Stephenson, 1926 <i>L. werthi</i> (Michaelson, 1905)			
<i>pagenstecheri</i> group	<i>L. pagenstecheri</i> A-D (Ratzel, 1868) <i>L. viridis</i> Stephenson, 1911	<i>L. annulatus</i> Eisen, 1904 <i>L. belli</i> Tynen, 1969 <i>L. corallinae</i> Shurova, 1977 <i>L. curtus</i> Coates, 1981 <i>L. franciscanus</i> Eisen, 1904 <i>L. ignotus</i> Shurova, 1977 <i>L. kalatdlitus</i> Nurminen, 1970 <i>L. kamschatkanus</i> (Michaelson, 1929) <i>L. kurilensis</i> Shurova, 1974 <i>L. maritimus</i> (Ude, 1896) <i>L. merriami</i> Eisen, 1904 <i>L. mirabilis</i> Tynen, 1969			<i>L. nipponicus</i> (Yamaguchi, 1937) <i>L. orientalis</i> Shurova, 1974 <i>L. pinquis</i> Shurova, 1977 <i>L. qualicumensis</i> Tynen, 1969 <i>L. reynoldsoni</i> Backlund, 1948 <i>L. rufulus</i> Shurova, 1974 <i>L. taisiae</i> Shurova, 1978 <i>L. tenuis</i> (Ude, 1896) <i>L. tsimpseanis</i> Coates, 1981 <i>L. sapitus</i> Shurova, 1979 <i>L. similis</i> Shurova, 1977			

	Species included in the present study	Species not included in the present study, placed on the basis of their descriptions	
“tuba” group	<i>L. scandicus</i> sp. n. ** <i>L. tuba</i> Stephenson, 1911 <i>L. helgolandicus</i> (Michaelsen, 1927)	<i>L. balticus</i> von Bülow, 1957 <i>L. charae</i> (Tynen, 1970) <i>L. imakus</i> Nurminen, 1970 <i>L. lentus</i> Shurova, 1978	<i>L. macrothecatus</i> Erséus, 1976 <i>L. niger</i> Southern, 1909 <i>L. ochotensis</i> Shurova, 1979
<i>buelowi</i> group	<i>L. buelowi</i> Nielsen & Christensen, 1959 <i>L. knoellneri</i> Nielsen & Christensen, 1959	<i>L. cervisiae</i> Kossmagk-Stephan, 1983 <i>L. eltoni</i> (Stephenson, 1924) syn. <i>L. knoellneri</i> ? <i>L. mangeri</i> (Michaelsen, 1914)	<i>L. muscicolus</i> (Stephenson, 1924) syn. <i>L. knoellneri</i> ? <i>L. nielseni</i> Nurminen, 1965
<i>arenarius</i> group	<i>L. arenarius</i> (Michaelsen, 1889) <i>L. dubius</i> (Stephenson, 1911) <i>L. sp. H</i>	<i>L. christenseni</i> Tynen, 1966 <i>L. crymodes</i> (Stephenson, 1922) syn. <i>L. arenarius</i> ? <i>L. eudioptus</i> (von Bülow, 1955) <i>L. westheidei</i> Kossmagk-Stephan, 1983	
Species with uncertain placement	<i>L. algensis</i> Erséus, 1977 (seminal vesicles irregularly lobed without bunch-shape but otherwise <i>lineatus</i> -like) <i>L. brunoi</i> Martínez-Ansemil, 1982 (seminal vesicles irregularly lobed without bunch-shape but otherwise <i>lineatus</i> -like) <i>L. colpites</i> (Stephenson, 1932b) (seminal vesicles irregularly lobed without bunch-shape, penial bulb with several lobe-shaped glands) <i>L. horridus</i> Finogenova, 1988 (intricate penial apparatus unlike that of other <i>Lumbricillus</i>) <i>L. intricatus</i> Finogenova, 1977 (spermathecae with ventral openings, nodulate chaetae, but otherwise <i>lineatus</i> -like)		

quotation marks) (see Klinth et al. 2017) (Table 1, Fig. 1). The *lineatus*, *pagenstecheri* and “tuba” groups all have testis sacs with several large lobes in a bunch-like arrangement, characteristic for the majority of *Lumbricillus* species. The testis sacs of the *buelowi* and *arenarius* groups appear as a more or less compact irregular mass, which can still be lobed but not bunch-like. Interestingly, we noted that in the former three groups the upper and lower chaetal bundles are arranged almost symmetrically around the body (as dorsolateral and ventrolateral bundles), whereas in the *buelowi* and *arenarius* groups the upper bundles tend to be closer to the lateral lines (observed by all three authors). The number of chaetae varies within each group and is usually 3–6 in each bundle but can reach 10 or more, except in the *buelowi* and *arenarius* groups where there are rarely more than 2–3 chaetae per bundle. The length/width ratio of the sperm funnels varies within and among the species in each group, but the funnels are usually only a few times longer than wide in all groups except for the *lineatus* and *arenarius* groups, where they can be 5–10 times longer than wide. The penial bulbs are round and compact in all groups except the *arenarius* group where they can also be bilobed. Finally, the spermathecae are spindle-shaped without a clear distinction between the ectal duct and the ampulla in the *lineatus* group; have a clear distinction between ectal duct and ampulla in the *pagenstecheri*, “tuba” and *buelowi* groups, with gland cells also along the duct in the *pagenstecheri* group; or have a gradually widening ectal duct, making the ampulla more or less indistinct in the *arenarius* group (Table 1, Fig. 1). Using these combinations of characters we made a preliminary placement of the remaining *Lumbricillus* species, not studied in this paper, into any of these five groups (Table 1). Note that, as we have not been able to include these species in our molecular phylogeny, we cannot be certain that our species groups would remain monophyletic with the addition of these species.

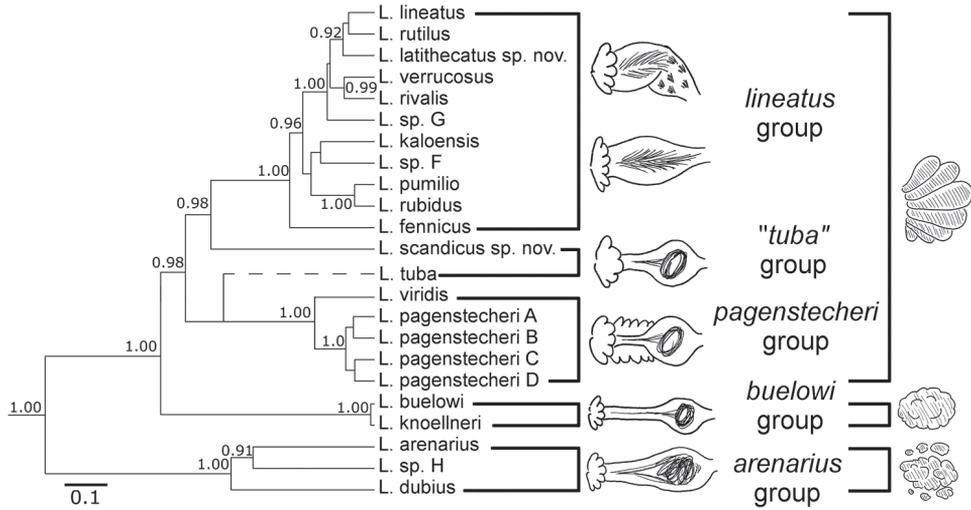


Figure 1. Phylogeny of North European *Lumbricillus*, modified from Klinth et al. (2017). Species tree based on 12S, 16S, COI, 18S, 28S, ITS and H3 genes, estimated using Bayesian inference under the multispecies coalescent model in *BEAST. Posterior probabilities higher than 0.9 shown as support values. Scale shows expected number of changes per site in COI with all other genes relative to it. *Lumbricillus tuba* has been added to the tree at the most probable position given the other gene and species trees from Klinth et al. (2017). The tree depicts the five morpho-groups that are used in the present study to discuss the relationships within *Lumbricillus*. The general morphology of the spermathecae and testes/testis sacs of these groups are also shown.

Preliminary key to species groups (based on species included in study only)

- 1 Chaetae 3–6 (or higher) per bundle, upper bundles located dorsolaterally; testis sacs with lobes in bunch-like arrangement..... **2**
- Chaetae 2–3 (occasionally higher) per bundle, upper bundles located midlaterally, just above the lateral line; testis sacs irregularly lobed, not bunch-like **4**
- 2 Spermathecae with short, indistinct ducts, and spindle-shaped ampullae; sperm funnels about 1–5 times longer than wide **lineatus group**
- Spermathecae club-shaped, with rather long ducts and clearly set-off ampullae; sperm funnels about 1–2 times longer than wide **3**
- 3 Sperm funnels about as long as wide; no glands along each spermathecal duct inside compact gland around duct at spermathecal pore **"tuba" group**
- Sperm funnels about 2 times longer than wide; numerous glands along each spermathecal duct (inside compact gland around duct at spermathecal pore) **pagenstecheri group**
- 4 Sperm funnels about as long as wide; spermathecae club-shaped, with rather long ducts and clearly set-off ampullae **buelowi group**
- Sperm funnels about 3–10 times longer than wide; spermathecae club-shaped, but ducts gradually widening into ampullae **arenarius group**

The *lineatus* group

Characteristics: Testis sacs regularly lobed in bunch-like arrangement. Spermathecae spindle-shaped with short duct which is difficult to distinguish from ampulla, and glands surrounding the ectal pore. Chaetae sigmoid and usually 3–6 or more per bundle; upper bundles located dorsolaterally. Penial bulbs round. Sperm funnel from as long as wide to about 5 times longer than wide.

Lumbricillus lineatus (Müller, 1774)

Figs 2, 3A

Lumbricus lineatus Müller, 1774: p. 29.

Lumbricillus lineatus; Erséus et al. 1999; Erséus et al. 2010; Klinth et al. 2017.

Pachydriilus claparedeanus Ditlevsen, 1904: pp. 431–435, figs 28 a–b.

Lumbricillus agilis Moore, 1905: pp. 395–397, pl. XXXIII, figs 23–28.

Lumbricillus lineatus partim; Michaelsen 1900: p. 80; Welch 1917: pp. 123–130; Nielsen and Christensen 1959: pp. 100–102, figs 109–112.

“*Lumbricillus lineatus* L2”; BOLD (unpublished records)

Non *Pachydriilus lineatus*; sensu Backlund 1947: pp. 3–5, figs 1–2 (see *Lumbricillus latithecatus* sp. n. below).

Type material (neotype). *Lumbricillus lineatus* was described long before reference to types had become common practice and there is no remaining original material (“*Typus amissus*” in *Nomenclatura Oligochaetologica*). We designate SMNH Type-8931 [former SMNH 152751] (CE1894) as a neotype of this species. It is a whole-mounted voucher of a sexually mature and DNA-barcoded worm (COI barcode is KU894040 in NCBI/GenBank; Klinth et al. 2017) from the Baltic Sea, Öland, Mörbylånga, Skärlov fishing harbor, on beach with mixed shelly sand, pebbles and organic material, 56.4241 N, 16.5815 E, collected 10 June 2006 by Lisa Matamoros, Sweden. Our decision to designate this neotype is further discussed in Remarks below.

Other material examined. SMNH 152742 (CE1640), one mature specimen from Sweden; SMNH 152744 (CE1694), one mature avesculate triploid specimen from Spain; ZMBN 107872 (CE12043), ZMBN 107875 (CE21688), ZMBN 107879 (CE22604) & ZMBN 107880 (CE22605), four mature specimens from Norway; ZMBN 107878 (CE21986), one mature avesculate triploid specimen from Norway. For information on collection localities and GenBank accession numbers for COI barcodes see Appendix 1.

Description. Orange, red or pink worms. Length (fixed worms) more than 2.2–5.5 mm (amputated specimens), first 15 segments 2.1–2.8 mm long, width at clitellum 0.45–0.75 mm. More than 14–38 segments. Chaetae sigmoid (Fig. 2A). Upper bundles dorsolateral, with 3–6 chaetae anterior to clitellum, 3–7 chaetae in postclitellar segments. Ventral bundles with 4–8 chaetae anterior to clitellum, 3–7(8) chaetae posteriorly. Each worm’s longest measured chaetae 50–75 µm long, about 3–5 µm wide. Clitellum extending over XII–1/2XIII/XIII. Head pore not observed.

Coelomocytes, in some specimens numerous, 10–20 µm long, round, oval or spindle-shaped, granulated with distinct nucleus. Paired pharyngeal glands present in IV, V and VI; each pair converging dorsally (Fig. 2B). Dorsal vessel originating in XII–XIV. Nephridia observed in VIII–X and XIII–XX, about 85–110 µm long. Anteseptale small, consisting of funnel only. Postseptale oval, tapering into posteroventral efferent duct. Brain with posterior incision.

Male genitalia paired (Fig. 2D). Testes originating in XI, extending forwards into X, sometimes IX, with testis sacs forming regular club-shaped lobes, except in two “avesiculate” specimens (SMNH 152744 and ZMBN 107878) which have atrophic testes. Sperm funnels in XI, 215–420 µm long, 125–185 µm wide, making them about 1.5–2.5 times longer than wide, funnels tapering towards vasa deferentia. Most of vasa irregularly coiled in XII, 15–20 µm wide. Penial bulbs round, 65–140 µm in diameter. Ovaries in XII. One to six mature eggs present at a time.

Spermathecae (Figs 2C, 3A) in V, spindle-shaped, without distinct ampulla. Ectal duct very short, widening into ampulla. Ampulla with constriction midway dividing it into sections, ectal part narrow, ental part wider, sometimes circular, connecting with oesophagus. Sperm in lumen of ectal part of ampulla, heads of spermatozoa embedded in wall of ental part of ampulla, forming aggregates. Spermathecae 220–275 µm long, 60–125 µm wide at widest part of ampulla. Gland cells surrounding ectal duct at pore, forming compact mass, glandular body 80–150 µm in diameter at its widest part. Two midventral subneural glands in XIII–XIV, 60–110 µm and 60–95 µm long, respectively.

Details of neotype. Length 3.3 mm (amputated specimen), first 15 segments 2.4 mm long, width at clitellum 0.45 mm. 20 segments. Dorsal bundles with 4–6 chaetae anterior to clitellum, 3–4 chaetae in postclitellar segments. Ventral bundles with 6–8 chaetae anterior to clitellum, 3–5 chaetae posteriorly. Longest chaetae 50 µm, about 3 µm wide. Clitellum extending over XII–XIII.

Coelomocytes 15 µm long. Dorsal vessel originating in XIII. Nephridia observed in VIII–X and XIII–XX, about 110 µm long.

Testes originating in XI, extending forwards into X. Sperm funnels folded, length and width unclear. Vasa deferentia 15 µm wide. Penial bulbs 115 µm in diameter. No mature eggs observed.

Spermathecae (Fig. 2C) 270 µm long, 120 µm wide at widest part of ampulla. Glandular body at ectal pore 115 µm in diameter at its widest part. No midventral subneural glands observed.

Geographical distribution including BOLD data. Genetically identified from the Netherlands, Norway, Spain and Sweden; also recognized from Canada (BIN-numbers BOLD:AAF9630 & BOLD:ACV7068). This species has historically been widely reported from Europe and North America, and even from the southern hemisphere (Stephenson 1932b).

Remarks. *Lumbricillus lineatus*, possibly the first ever described enchytraeid, has an interesting history and was for a long time poorly defined as a species. It was given the name *Lumbricus lineatus* by Müller (1774) who described it as abundant on the shores of the Baltic Sea. Müller classified the worm under “Setosa”, and gave a brief description of its circulatory system and short protruding chaetae. In the same work, he refers to a worm that

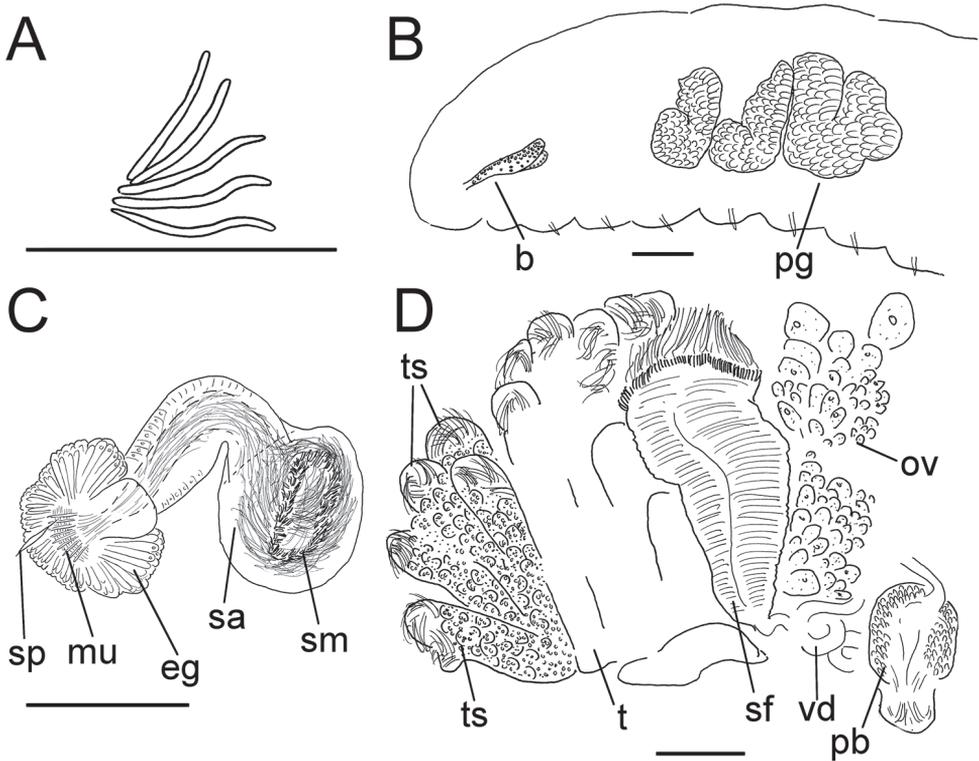


Figure 2. *Lumbricillus lineatus*. **A** Chaetal bundle **B** Anterior body **C** Spermatheca (neotype) **D** Other genitalia. Abbreviations under general notes. Scale bars: 100 μ m.

he previously described (Müller 1771), which he found on sandy shores of the Baltic and particularly among the rotting seaweed by the ramparts of Copenhagen, where he did most of his work. However, he classified that worm in *Gordius*, referred to it as a Faden Wurm (nematode) said to lack any segments or ring, and he failed to mention anything about chaetae. It is therefore difficult to say if Müller simply missed those characters or if the worm from 1771 was something different. Nevertheless, as Müller worked with live material, it is most plausible that the type locality for the first described *Lumbricillus lineatus* is around Copenhagen. Unfortunately, we do not have any specimens from Copenhagen, but we have found that our molecularly defined *L. lineatus* is common throughout the Baltic Sea. For the sake of finally defining the true *L. lineatus* and connecting it to a molecular profile, we decided to designate one of our specimens from Öland in the Baltic Sea as a neotype.

The specimens of *L. lineatus* in this study were smaller than the ones in the re-description by Nielsen and Christensen (1959) and the sperm funnels were shorter in relation to their length. However, the shape of the spermathecae, number of chaetae and segments conformed well with these authors' description. Furthermore, both the vesiculate and avesciculate forms of the species were observed, as has previously been noted to occur in *L. lineatus* (Nielsen and Christensen 1959, Christensen 1961), further supporting the

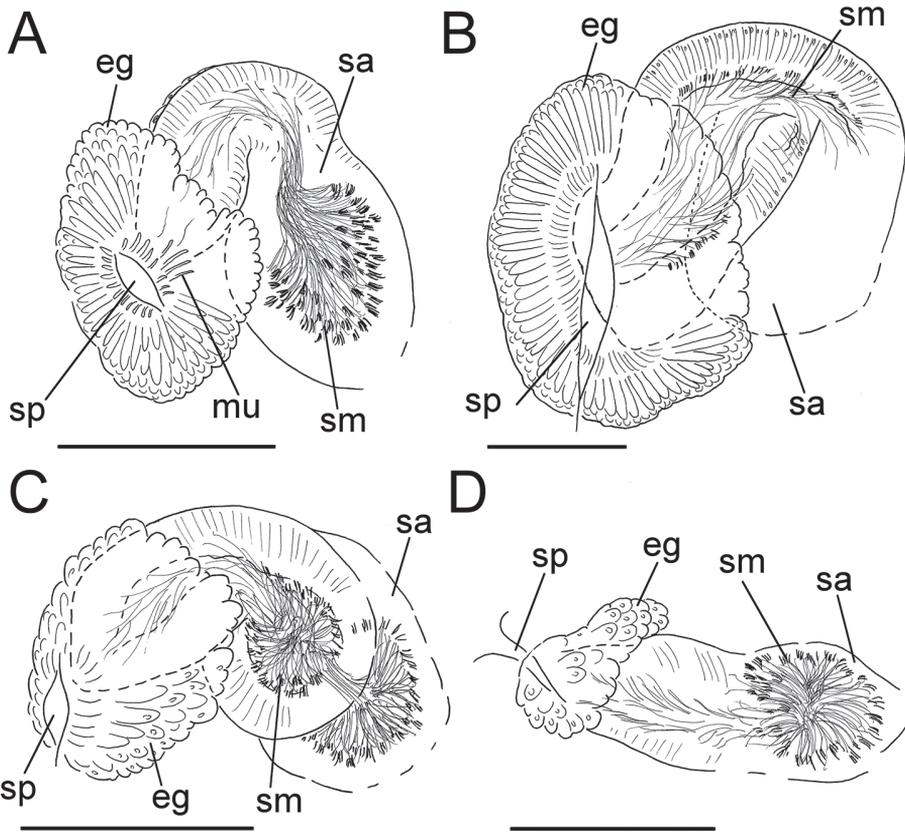


Figure 3. **A** *Lumbricillus lineatus*, spermatheca **B** *Lumbricillus latithecatus* sp. n. (holotype), spermathecae **C** *Lumbricillus verrucosus*, spermatheca **D** *Lumbricillus verrucosus*, spermatheca seen from below. Scale bars: 100 μ m.

designation of a neotype from our material. Christensen and O'Connor (1958) were the first to describe diploid vesiculate and triploid avesticulate forms of *L. lineatus* and their intriguing life histories (see also Christensen 1960). While the diploid form has normal gametogenesis and is amphimictic, the triploid form is dependent on copulation with the diploid form, which acts as sperm donor, to produce offspring. Furthermore, the sperm from the diploid form does merely activate the egg of the triploid individual, without fertilizing it. Instead, oogenesis in the triploid cytotype follows a peculiar pattern of chromosome divisions and mergings that results ultimately in the restoration of triploid nuclei. The relationship between the two forms has been described as an obligatory co-existence (Christensen 1960). To further complicate things, tetra- and pentaploids have also been observed within *L. lineatus*. The tetra- and pentaploids have testis sacs that are smaller than those of diploids but larger than those of triploids. Furthermore, the sperm funnels are smaller in tetra- pentaploids than in di- and triploids. Apparently, the testes sacs of tetra- and pentaploids sometimes produce sperm which can activate the eggs of all polyploid

forms (Christensen et al. 1978). Unfortunately, we did not determine the ploidy level of our sampled specimens, but we did not observe any genetic distinction between the vesiculate and avesciculate forms, neither in COI nor in ITS sequences (Klinth et al. 2017).

Lumbricillus lineatus is morphologically most similar to *L. verrucosus* and *L. latithecatus* sp. n. (compare spermathecae in Fig. 3 and see Remarks for these species), but also superficially similar to the other members of the group we have chosen to call the *linaetus* group. Genetically it is closely related to *L. rutilus* Welch, 1914 and *L. latithecatus* sp. n. (Klinth et al. 2017; where *L. latithecatus* is called *L. sp. E*) (Fig. 1).

***Lumbricillus rutilus* Welch, 1914**

Fig. 4

Lumbricillus rutilus Welch, 1914: 143–151, pl. VIII, fig. 13, pl. IX, figs 14–24; Klinth et al. 2017.

“*Lumbricillus rivalis*”; BOLD (published records; Vivien et al. 2015)

Type material. USNM 25507, 26318, 30863–4 (Nomenclatura Oligochaetologica). Type locality: Chicago Sewage Testing Station, United States (Welch 1914). Not studied.

Material examined. SMNH 152801 (CE1887), SMNH 152802 (CE1903), SMNH 152804 (CE2510), SMNH 152809 (CE2937), SMNH 152811 (CE2939), SMNH 152813 (CE3060), SMNH 152814 (CE3061) & SMNH 152819 (CE9267), eight mature specimens from Sweden; SMNH 152815 (CE3502) & SMNH 152816 (CE3506), two mature specimens from the United Kingdom. For information on specimen collection locality and GenBank accession numbers see Appendix 1.

Description. Orange-reddish worms. Length (fixed worms) more than 2.7–7.2 mm (amputated specimens), first 15 segments 2.4–4.8 mm long, width at clitellum 0.39–0.65 mm. More than 14–30 segments. Chaetae (Fig. 4C) slightly sigmoid. Dorsal bundles with 3–6, rarely 2 or 7, chaetae anterior to clitellum, 2–5 chaetae in postclitellar segments. Ventral bundles with 3–9, usually 4–6, chaetae anterior to clitellum, 2–6 chaetae posteriorly. Each worm’s longest measured chaetae 70–105 µm long, about 3–5 µm wide. Clitellum generally extending over XII–1/2XIII, sometimes including all of XIII. Head pore at 0/1. Epidermis with transverse rows of gland cells.

Coelomocytes in some specimens numerous, 10–25 µm long, round, oval or spindle-shaped, granulated. Paired pharyngeal glands present in IV, V and VI; each pair converging dorsally (Fig. 4B). Third pair larger, occupying most of VI, sometimes extending into VII. Dorsal vessel originating in XIV. Nephridia (Fig. 4D) observed in XV–XXI, about 120–170 µm long. Anteseptale small, consisting of funnel only. Postseptale oval, tapering posteriorly into efferent duct. Brain (Fig. 1B) slightly widening posteriorly, with posterior incision.

Male genitalia paired (Fig. 4F). Testes originating in XI, extending forwards into X, sometimes IX, with testis sacs forming regular club-shaped lobes. Sperm funnels in XI, 295–395 µm long, 145–225 µm wide, making them about 1.5–2.5 times longer

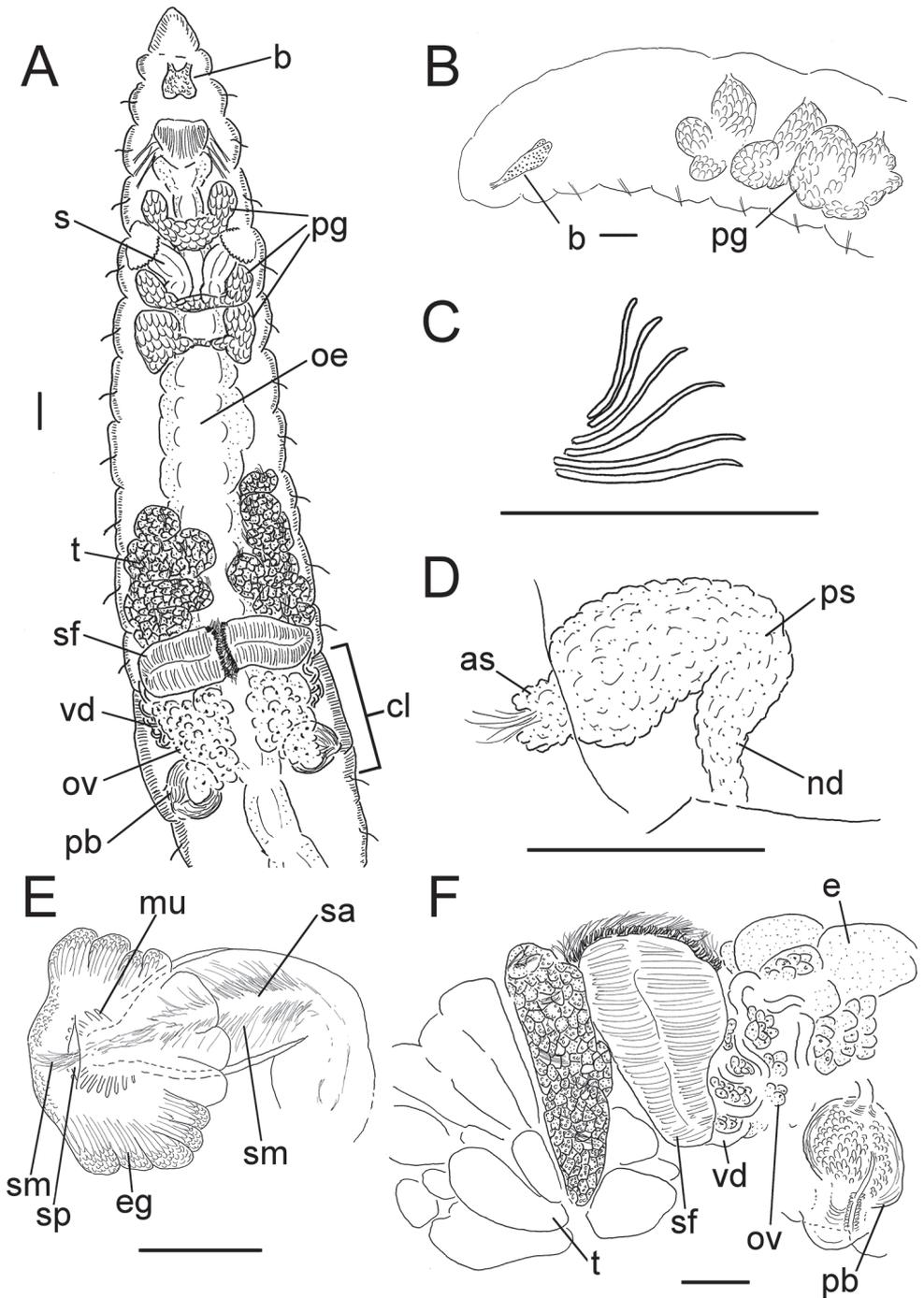


Figure 4. *Lumbricillus rutilus*. **A** Anterior body, seen from above **B** Anterior body **C** Chaetal bundle **D** Nephridium **E** Spermatheca **F** Other genitalia. Abbreviations under general notes. Scale bars: 100 μ m.

than wide, funnels tapering towards vasa deferentia. Most of vasa irregularly coiled in XII, 20–30 µm wide. Penial bulbs round, 110–175 µm in diameter. Ovaries in XII. Two to six mature eggs present at a time.

Spermathecae (Fig. 4D) in V, spindle-shaped, without distinct ampulla. Ectal duct short, muscular, widening into ampulla. Ampulla, after widest part, making sharp bend before entally connecting with oesophagus. Sperm evenly embedded in tissue of ectal duct and ampulla. Spermathecae 215–335 µm long, 70–115 µm wide at widest part of ampulla. Crown of gland cells surrounding ectal pore, lobed, whole glandular body 110–225 µm in diameter at its widest part. Up to four midventral subneural glands in XIII–XVI, 80–325 µm, 55–200 µm, 60–100 µm and 50 µm long, respectively; glands in XIII, XV or XVI not observed in all specimens.

Geographical distribution including BOLD data. Originally described from USA, now genetically identified from Norway, Sweden and United Kingdom; also recognized from Canada and Switzerland (BIN-number: BOLD:ACV8942).

Remarks. Our newly sampled material matches Welch's (1914) description of *Lumbricillus rutilus* well in all characters, except for the sperm funnel shape, where our specimens had funnels less elongate in relation to their width. The material in this study was collected in Sweden and the United Kingdom, whereas this species was originally described from a sewage treatment plant in Chicago, USA. Interestingly, some of our sampled specimens also come from two such plants, in Sweden and the UK, respectively. The species was additionally collected in littoral and freshwater environments in Sweden, and it is likely to be an opportunist that thrives in nutrient-rich habitats. Specimens found in the treatment plants showed increased body size and reduced number of chaetae per bundle, compared to the specimens sampled in the sea, possibly a side effect of living in such rich environments.

Lumbricillus rutilus is genetically most closely related to *L. lineatus* and *L. latithecatus* sp. n. (Fig. 1). However, morphologically it is more similar to *L. rivalis*, particularly in the shape of the spermathecae. *Lumbricillus rutilus* has on average fewer chaetae per bundle compared with *L. rivalis* and sperm funnels that are shorter in relation to their width.

***Lumbricillus latithecatus* sp. n.**

<http://zoobank.org/575B08C8-3F02-4D35-B9FF-814F52DD3573>

Figs 3B, 5

“*Lumbricillus lineatus* L1”; BOLD (unpublished records)

Lumbricillus sp. E; Klinth et al. 2017.

? *Pachydriulus lineatus*; sensu Backlund 1947: pp. 3–5, figs 1–2.

Holotype. ZMBN 107940 (CE12041), a whole-mounted voucher of a sexually mature and DNA-barcoded worm (COI barcode is KU894054 in NCBI/GenBank; Klinth et al. 2017).

Type locality. Norway, Rogaland, Sola, Ölbörhamna, intertidal in decomposing algae, 58.8697N, 5.5654E, collected 15 June 2012 by C. Erséus. Norway.

Paratype. ZMBN 107941 (CE12042), one whole-mounted sexually mature specimen from the type locality.

Other material examined. SMNH 152830 (CE1976) & SMNH 152831 (CE1979), two mature specimens from Sweden. For information on specimen collection localities and GenBank accession numbers see Appendix 1.

Etymology. Named from the Latin *latus* meaning wide and *theca* for spermatheca.

Diagnosis. This species can be distinguished from other *Lumbricillus* species by the shape of the spermathecae, which do not gradually widen from the ectal pore but instead originates from a very wide pore followed by an ectal duct and ampulla of even width throughout. This makes the duct and ampulla of the spermathecae virtually indistinguishable. There is at least a superficial similarity to the spermathecae of *Lumbricillus lineatus* and *L. verrucosus* with a midway constriction or bend and sperm aggregated in the ental part of the ampulla (Fig 3). However, the spermathecae of *L. lineatus* and *L. verrucosus* have ectal pores that are much smaller than the diameter of their ampullae, giving the impression of a rapid widening of the spermathecae after the ectal pore, even though the duct and ampulla are difficult to distinguish also in these species.

Description of all material. Length (fixed worms) more than 2.5–7.8 mm (amputated specimens), first 15 segments 2.5–4.7 mm long, width at clitellum 0.42–0.85 mm. More than 15–27 segments. Chaetae slightly sigmoid (Fig. 5A). Dorsal bundles with (3)4–8(9) chaetae anterior to clitellum, 3–7 chaetae in postclitellar segments. Ventral bundles with 5–10 chaetae anterior to clitellum, 4–9 chaetae posteriorly. Each worm's longest measured chaetae 60–75 μm long, about 4–5 μm wide. Clitellum extending over XII–XIII. Head pore not observed. Epidermis with transverse rows of gland cells.

Coelomocytes numerous, 10–25 μm long, round, oval or spindle-shaped, granulated. Paired pharyngeal glands present in IV, V and VI; each pair converging dorsally (Fig. 5B). Dorsal vessel originating in XIII. Nephridia examined in IX and XIV–XXV, about 75–155 μm long. Anteseptale small, consisting of funnel only. Postseptale oval, tapering posteriorly into efferent duct. Brain with posterior incision.

Male genitalia paired (Fig. 5D). Testes originating in XI, extending forwards into IX, with testis sacs forming regular club-shaped lobes. Sperm funnels in XI, sometimes extending into X or XII, 360–1300 μm long, 155–235 μm wide, making them about 2–6 times longer than wide, funnels tapering towards vasa deferentia. Most of vasa irregularly coiled in XII, 15–30 μm wide. Penial bulbs round, 155–285 μm in diameter, possibly with a small ventral lobe set off from the rest of the bulb. Ovaries in XII. One to four mature eggs present at a time.

Spermathecae (Figs 3B, 5C) in V, pouch-shaped, without distinct ampulla. Ectal duct seemingly indistinguishable from ampulla as the wide pore is followed by a lumen that remains about the same width or possibly widening slightly. Ectal pore surrounded by mass of gland cells forming compact body 140–325 μm in diameter at its widest part. Ampulla, with possible constriction midway dividing it into two sections; ental connection with oesophagus. Sperm filling middle of ectal duct, heads of spermatozoa embedded and forming aggregates mainly in ental part of ampulla. Each spermatheca altogether 220–410 μm long, 65–160 μm wide at widest part of ampulla. Up to three

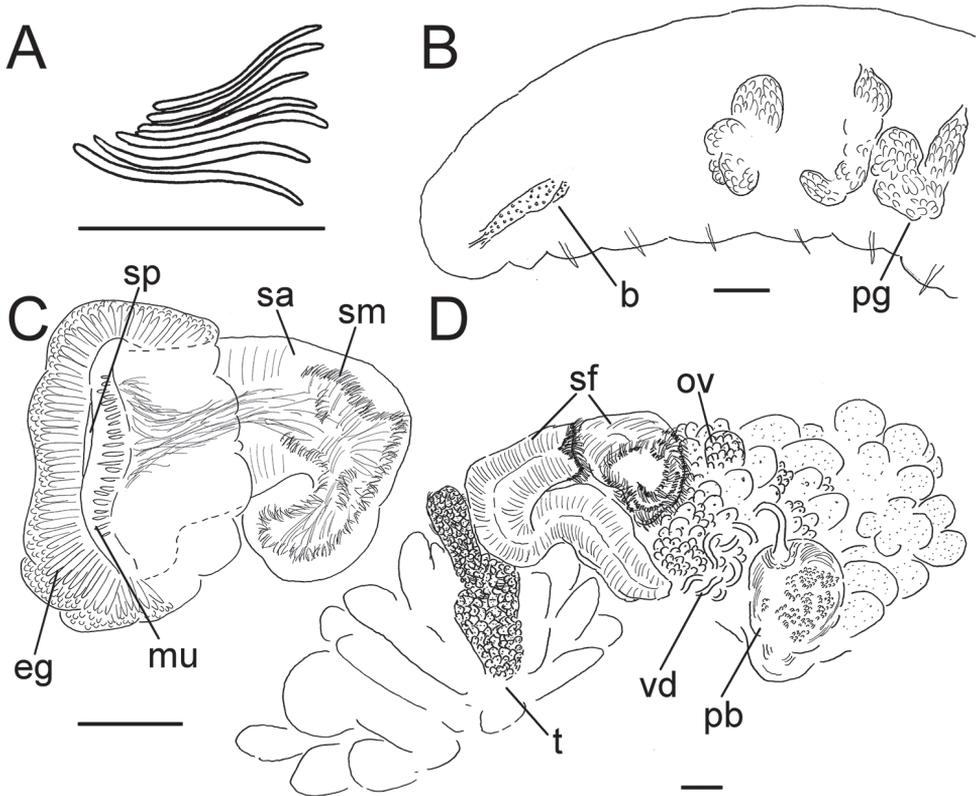


Figure 5. *Lumbricillus latithecatus* sp. n. **A** Chaetal bundle **B** Anterior body **C** Spermatheca **D** Other genitalia. Abbreviations under general notes. Scale bars: 100 μ m.

midventral subneural glands in XIII–XV, 80–200 μ m, 100–250 μ m and 115 μ m long, respectively; glands in XIV and XV not observed in all specimens.

Details of holotype. The largest specimen of the lot. Length 7.8 mm (amputated specimen), first 15 segments 4.7 mm long, width at clitellum 0.85 mm. 27 segments. Dorsal bundles with 5–8 chaetae anterior to clitellum, 4–7 chaetae in postclitellar segments. Ventral bundles with 5–10 chaetae anterior to clitellum, 5–9 chaetae posteriorly. Longest measured chaetae 75 μ m long, about 5 μ m wide. Clitellum extending over XII–1/2XIII.

Coelomocytes 10–25 μ m long. Dorsal vessel originating in XIII. Nephridia observed in IX and XXIII–XXV, about 125–135 μ m long.

Testis sacs extending forwards into IX. Sperm funnels in XI, 1100 μ m long, 210 μ m wide, making them about 5 times longer than wide. Vasa deferentia 30 μ m wide. Penial bulbs 285 μ m in diameter. No mature eggs present.

Spermathecae (Fig. 3B) 335 μ m long, 135 μ m wide at widest part of ampulla. Glandular body at ectal pores 275 μ m in diameter at its widest part. Midventral subneural glands in XIII and XIV, 200 μ m and 150 μ m long, respectively.

Geographical distribution including BOLD data. Genetically identified from Norway and Sweden; also recognized from Denmark (BIN-number BOLD :AAU0294).

Remarks. The measured lengths of the sperm funnels are probably underestimated due to the difficulty of tracing them through the worms and due to folding. The two Swedish specimens were somewhat smaller than the Norwegian ones, and their funnels folded and only measurable for about 360 μm , but the length:width ratio was close to 4–6:1, as noted for the Norwegian specimens.

The description of *Pachydriilus lineatus* by Backlund (1947), from a drainpipe in Southern Sweden, in some ways reminds of our new species. Backlund was uncertain if his species belonged to *P. lineatus* because of the very wide spermathecal duct (which seemed as wide at the pore as in its medial part), the lack of a distinct ampulla and the possession of a large gland around the ectal pore. Furthermore, he described the penial bulbs as bilobed with a larger dorsal and a smaller ventral lobe. The description of the spermathecae sounds like the one of those of *L. latithecatius*, and after having examined the penial bulbs in the whole-mounted specimens of the latter species, it seems as if there could be a small lobe hidden behind the large spherical lobe (when viewed laterally). However, we would need transverse sections to truly compare this character to that which Backlund described. Lastly, Backlund reported small pharyngeal glands without dorsal development, which does not match with what we have observed for our species. Therefore, we are not certain as to the identity of Backlund's *P. lineatus*.

Lumbricillus latithecatius is genetically most closely related to *L. lineatus* and *L. rutilus* (Fig. 1).

***Lumbricillus verrucosus* (Claparède, 1861)**

Figs 3C–D, 6

Pachydriilus verrucosus Claparède, 1861: pp. 82–85, pl. I, figs 1–6;

Lumbricillus verrucosus; Michaelsen 1900: p. 80; Klinth et al. 2017.

Pachydriilus lineatus forma *verrucosus*; Černosvitov 1937: p. 292.

Lumbricillus lineatus partim; Nielsen and Christensen 1959: pp. 100–102, figs 109–112.

Type material. Typus amissus (Nomenclatura Oligochaetologica). Type locality: Sound of Sleat, Isle of Skye, Hebrides, United Kingdom (Claparède, 1861). We did not designate a neotype as we do not have material from the type locality.

Material examined. SMNH 152826 (CE968), one mature specimen from Sweden, ZMBN 107919 (CE21479), ZMBN 107920 (CE21486), ZMBN 107921 (CE21490), ZMBN 107922 (CE21494), ZMBN 107924 (CE21811), ZMBN 107925 (CE21816) & ZMBN 107926 (CE21821), seven mature specimens from Norway. For information on specimen collection localities and GenBank accession numbers see Appendix 1.

Description. White to yellow worms. Length (fixed worms) more than 2.3–5.7 mm (amputated specimens), first 15 segments 2.3–3.4 mm long, width at clitellum 0.42–0.60 mm. More than 18–33 segments. Chaetae slightly sigmoid (Fig. 6A). Dorsal bundles

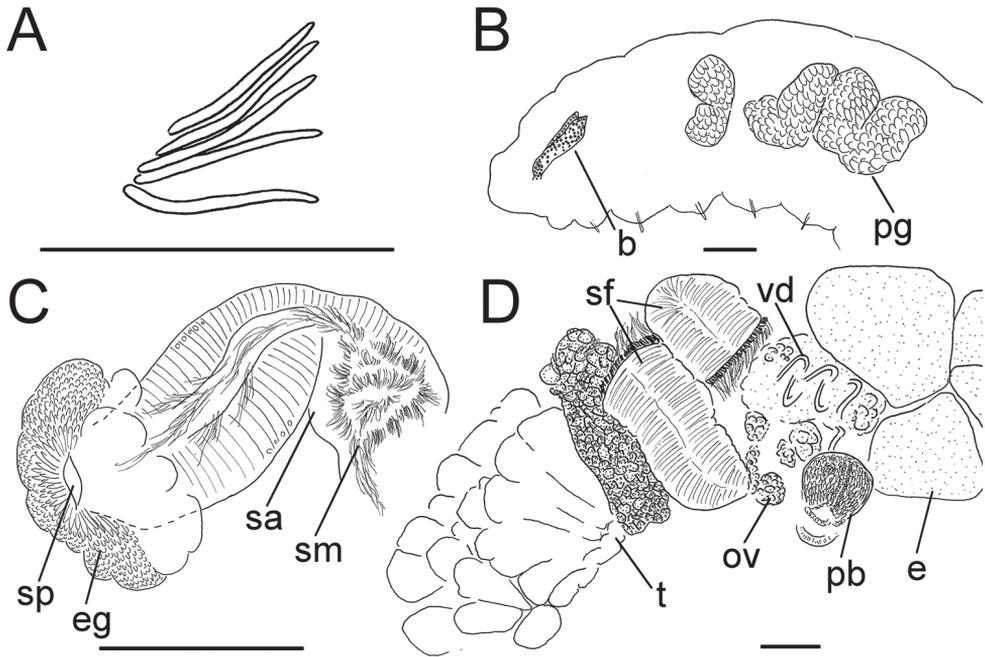


Figure 6. *Lumbricillus verrucosus*. **A** Chaetal bundle **B** Anterior body **C** Spermatheca **D** Other genitalia. Abbreviations under general notes. Scale bars: 100 μ m.

with (2)3–5(6) chaetae anterior to clitellum, 2–4 chaetae in postclitellar segments. Ventral bundles with (2)3–6(7) chaetae anterior to clitellum, (2)3–4(5) chaetae posteriorly. Each worm's longest measured chaetae 45–60 μ m long, about 2.5 μ m wide. Clitellum extending over XII–XIII. Head pore at 0/1. Epidermis with transverse rows of gland cells.

Coelomocytes in some specimens numerous, 10–25 μ m long, round, oval or spindle-shaped, granulated. Paired pharyngeal glands present in IV, V and VI; each pair converging dorsally (Fig. 6B). Dorsal vessel originating in XIII. Nephridia observed in XIV–XXV, 75–120 μ m long. Anteseptale small, consisting of funnel only. Postseptale oval, tapering posteriorly into efferent duct. Brain twice as long as wide, with posterior incision.

Male genitalia paired (Fig. 6D). Testes originating in XI, extending forwards into X, sometimes IX, with testis sacs forming regular club-shaped lobes. Sperm funnels in XI, 230–370 μ m long, 125–175 μ m wide, making them about 1.5–2.5 times longer than wide, funnels tapering towards vasa deferentia. Most of vasa irregularly coiled in XII, 15–20 μ m wide. Penial bulbs round, 105–140 μ m in diameter. Ovaries in XII. One to five mature eggs present at a time.

Spermathecae (Figs 3C–D, 6C) in V, spindle-shaped, without distinct ampulla. Ectal duct short, widening into ampulla. Ampulla with constriction midway to two thirds of the length, dividing it into two sections, the inner one of which connecting with oesophagus. Sperm filling lumen of ectal duct, heads of spermatozoa embedded in inner part of ampulla, sometimes also in outer part, forming aggregates. Spermathecae

180–300 µm long, 65–110 µm wide at widest part of ampulla. Gland cells surrounding ectal pore, forming compact mass, whole glandular body 95–180 µm in diameter at its widest part. One or two midventral subneural glands in XIII–XIV, 90–125 µm and 95–125 µm long, respectively; gland in XIV not observed in all specimens.

Geographical distribution. Originally described from the United Kingdom, now genetically identified from Norway and Sweden. The full extent of this species' distribution is difficult to ascertain since it was previously synonymized with *L. lineatus*, a species distributed worldwide. BIN-number BOLD:ACV7714.

Remarks. *Lumbricillus verrucosus* was originally described by Claparède (1861) and later synonymized with *L. lineatus* by Nielsen and Christensen (1959), probably following Černosvitov (1937) who had downgraded the former to a form of the latter. Specimens from the two species examined in this study are indeed very similar when considering the shape of the spermathecae (Fig. 3) and most body measurements, but they differ in body colour, chaetal number and the proportions of the sperm funnels: indeed *Lumbricillus verrucosus* was described as being pale yellow, having 3–5 chaetae and sperm funnels about three times longer than wide (Claparède 1861), against *L. lineatus* being orange-red, having more chaetae and sperm funnels about five times longer than wide. Furthermore, the spermathecae of *L. verrucosus* seem to have an ampulla that is slightly longer and wider in the part ectal to the constriction, but the importance of this character remains to be proved. Even though the two species may be very difficult to separate morphologically, except perhaps by body colour, they are supported as separate species molecularly and avesciculate specimens have been found by us only in *L. lineatus*, not in *L. verrucosus*.

Interestingly, *Lumbricillus verrucosus* is genetically most closely related to *L. rivalis* (Levinsen, 1883) and not to *L. lineatus* (Fig. 1). However, these three species are well supported as closely related to each other.

***Lumbricillus rivalis* (Levinsen, 1883)**

Fig. 7

Pachydriulus rivalis Levinsen, 1883: p. 231; Ditlevsen 1904: pp. 430–431.

Lumbricillus rivalis; Nielsen and Christensen 1959: pp. 97–98, figs 107–108; Erséus et al. 1999; Erséus et al. 2010; Klinth et al. 2017.

Pachydriulus subterraneus Vejdovsky, 1889: pp. 1–3.

Pachydriulus germanicus Michaelsen, 1886: pp. 43–44.

Lumbricillus evansi Southern, 1909: pp. 151–152, pl. X, figs 10a–f.

Non *Lumbricillus enteromorphae* von Bülow, 1957: pp. 82–84, pl. XXVI, figs 6–10, pl. XXVII, fig. 1, pl. XXX, fig. 16.

Type material. Typus amissus (Nomenclatura Oligochaetologica). Type locality: Langelinie, Denmark (Levinsen, 1883). We did not designate a neotype as we do not have material from the type locality.

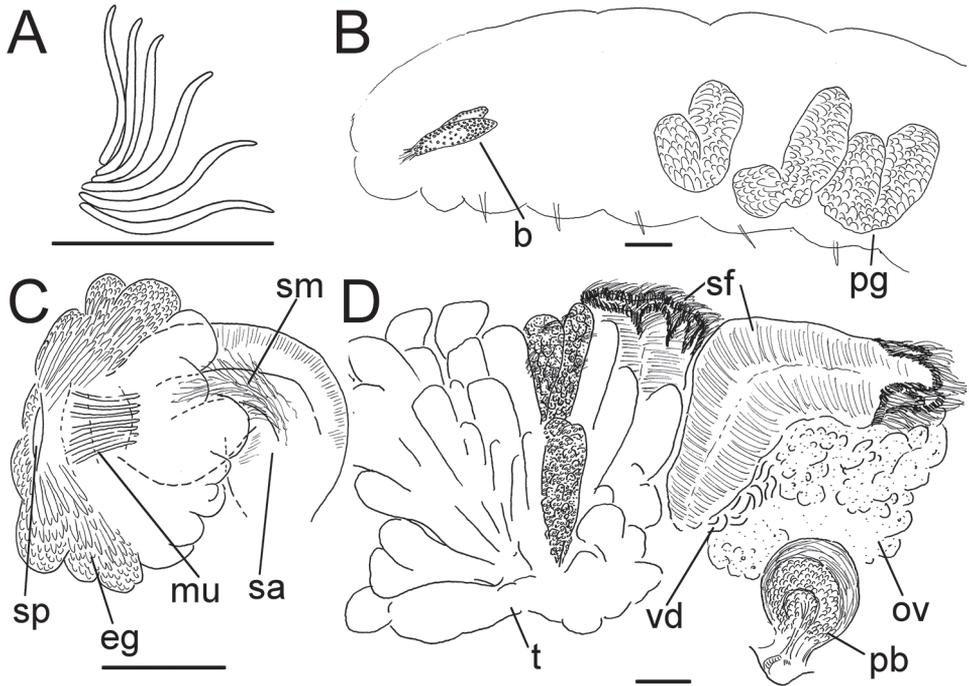


Figure 7. *Lumbricillus rivalis*. **A** Chaetal bundle **B** Anterior body **C** Spermatheca **D** Other genitalia. Abbreviations under general notes. Scale bars: 100 μm .

Material examined. SMNH 152782 (CE1873), SMNH 152783 (CE1874) & SMNH 152785 (CE2503), three mature specimens from Sweden, ZMBN 107897 (CE22596), ZMBN 107898 (CE22600) & ZMBN 107899 (CE22602), three mature specimens from Norway. For information on specimen collection localities and Gen-Bank accession numbers see Appendix 1.

Description. Orange-red worms. Length (fixed worms) more than 3.4–7.6 mm (amputated specimens), first 15 segments 2.6–3.8 mm long, width at clitellum 0.60–0.85 mm. More than 17–44 segments. Chaetae slightly sigmoid (Fig. 7A). Dorsal bundles with 4–8(9) chaetae anterior to clitellum, (3)4–7(8) chaetae in postclitellar segments. Ventral bundles with (4)5–10(11) chaetae anterior to clitellum, (4)5–8(9) chaetae posteriorly. Each worm's longest measured chaetae 85–105 μm long, about 5 μm wide. Clitellum extending over XII–XIII. Head pore at 0/1. Epidermis with transverse rows of gland cells.

Coelomocytes numerous, 15–20 μm long, spindle-shaped, oval, granulated. Paired pharyngeal glands present in IV, V and VI; each pair converging dorsally (Fig. 7B). Dorsal vessel originating in XIV. Nephridia observed in VII–X and XV–XXIII, about 145–170 μm long. Anteseptale small, consisting of funnel only. Postseptale oval, tapering posteriorly into efferent duct. Brain with posterior incision, about as long as wide.

Male genitalia paired (Fig. 7D). Testes originating in XI, extending forwards into X, sometimes IX, with testis sacs forming regular club-shaped lobes. Sperm funnels in XI, 325–685 μm long, 110–295 μm wide, making them about 1.5–4.5 times longer than wide, funnels tapering towards vasa deferentia. Most of vasa irregularly coiled in XII, 25 μm wide. Penial bulbs round, 105–190 μm in diameter. Ovaries in XII. Two mature eggs present in one specimen.

Spermathecae (Fig. 7C) in V, spindle-shaped, without distinct ampulla. Ectal duct short, gradually widening into ampulla. Ampulla with constriction two thirds of the length from pore, dividing it into sections, entally connecting with oesophagus. Sperm evenly embedded in ampulla. Spermathecae 250–360 μm long, 85–140 μm wide at widest part of ampulla. Gland cells surrounding ectal pore forming lobed collar, 140–240 μm in diameter at its widest part. Up to three midventral subneural glands in XIII–XV, 90–130 μm , 80–145 μm and 80–90 μm long, respectively; glands in XV not observed in all specimens.

Geographical distribution. Genetically identified from Greenland, Norway and Sweden; also recognized from Canada (BOLD:AAF9076). This species was originally described from Denmark and is considered well distributed throughout Europe, and North America.

Remarks. *Pachydriilus rivalis* was originally defined by Levinsen (1884) as a species with up to 9 chaetae per bundle, spermatheca formed by a large, red, pear-shaped container (Danish “beholder”), ending ectally with a glandular rosette, but bearing no glands on duct. The nephridial efferent duct originated at the posterior end of postseptale; the postseptals had red spots; the body color was red. Michaelsen (1889, 1900) placed the species in synonymy with *L. lineatus* along with his own *Pachydriilus germanicus* Michaelsen, 1886, but Ditlevsen (1904) reinvestigated Levinsen’s type locality (Langelinie, a pier in the port of Copenhagen) and found that only one species conformed to Levinsen’s short primary diagnosis, a species that was different from *L. lineatus*. He thus expanded the description of *rivalis* by adding the following traits: body length 15–20 mm, copulatory glands in XIII–XV, dorsal vessel from XIV, chaetal number 6–9 dorsally, 8–11 ventrally. Nevertheless, Welch (1917) and Černosvitov (1937) adhered to Michaelsen’s opinion and the species had to await Nielsen and Christensen (1959) to be revalidated.

Our new specimens fit well with the more detailed re-descriptions, particularly in the number of chaetae and the shape of the spermathecae. The only differences concern the body size, where our worms are much smaller than those reported before, and the length/width ratio of the sperm funnels, which Nielsen and Christensen described as up to 10 times longer than wide, compared to our observed 4.5 times. These differences could be explained by our examination of fixed instead of live material.

Lumbricillus rivalis is genetically most closely related to *L. verrucosus* (Fig. 1), but it is morphologically more alike *L. rutilus* (see remarks for that species) and *L. enteromorphae*, although it can be distinguished from the latter by lacking an atrium-like part where the vas deferens meets the penial bulb (see remarks for *L. rubidus*).

***Lumbricillus* sp. G**

Fig. 8

Lumbricillus sp. G; Klinth et al. 2017.

Material examined. Specimen SMNH 152834 (CE2246) & SMNH 152835 (CE2661), one mature and one immature specimen from the United Kingdom, and ZMBN 107942 (CE23373), one immature specimen from Norway. For information on specimen collection localities and GenBank accession numbers see Appendix 1.

Description. Colour of worms unknown. Length (fixed worms) more than 3.3–4.1 mm (amputated specimens), first 15 segments 2–2.8 mm long, width at clitellum 0.42–0.49 mm. More than 17–33 segments. Chaetae slightly sigmoid (Fig. 8A). Dorsal bundles with 2–5 chaetae anterior to clitellum, 3–6 chaetae in postclitellar segments. Ventral bundles with 3–6 chaetae anterior to clitellum, 3–4 chaetae posteriorly. Each worm's longest measured chaetae 55–60 µm long, about 5 µm wide. Clitellum extending over XII–1/2XIII. Head pore at 0/1. Epidermis with transverse rows of gland cells.

Coelomocytes numerous, 15–30 µm long, round, oval or spindle-shaped, granulated with distinct nucleus. Paired pharyngeal glands present in IV, V and VI (Fig. 8B). Dorsal vessel originating in XIII–XV. Nephridia not observed. Brain elongate, further details unknown.

Male genitalia paired (Fig. 8D). Testes originating in XI, extending forwards into IX, with testis sacs forming regular club-shaped lobes. Sperm funnels in XI, extending backwards into XII, 335–430 µm long, 180 µm wide, making them about 1.9–2.4 times longer than wide, funnels tapering towards vasa deferentia. Most of vasa irregularly coiled in XII, 15 µm wide. Penial bulbs pear-shaped, 110 µm in diameter. Ovaries in XII. One mature egg present in the single mature individual.

Spermathecae (Fig. 8C) in V, spindle-shaped, without distinct ampulla. Ectal duct short, widening into ampulla. Ampulla with constriction midway, dividing it into two sections, the inner of which connecting with oesophagus. No sperm observed. Spermathecae 210 µm long, 80 µm wide at widest part of ampulla. Gland cells surrounding ectal pore, forming compact mass, 105 µm in diameter at its widest part. Two midventral subneural glands in XIII–XIV, 70 µm and 90 µm long, respectively.

Geographical distribution. Only known from Norway and the United Kingdom.

Remarks. Unfortunately only one mature specimen was available for this study making it difficult to assign it to a known species. On the other hand, the description of a new species on such limited material would be premature. *Lumbricillus* sp. G is genetically placed within the *lineatus* group (Fig.1).

***Lumbricillus kaloensis* Nielsen & Christensen, 1959**

Fig. 9

Lumbricillus kaloensis Nielsen & Christensen, 1959: p. 100, figs 113–114; Erséus et al. 2010; Klinth et al. 2017.

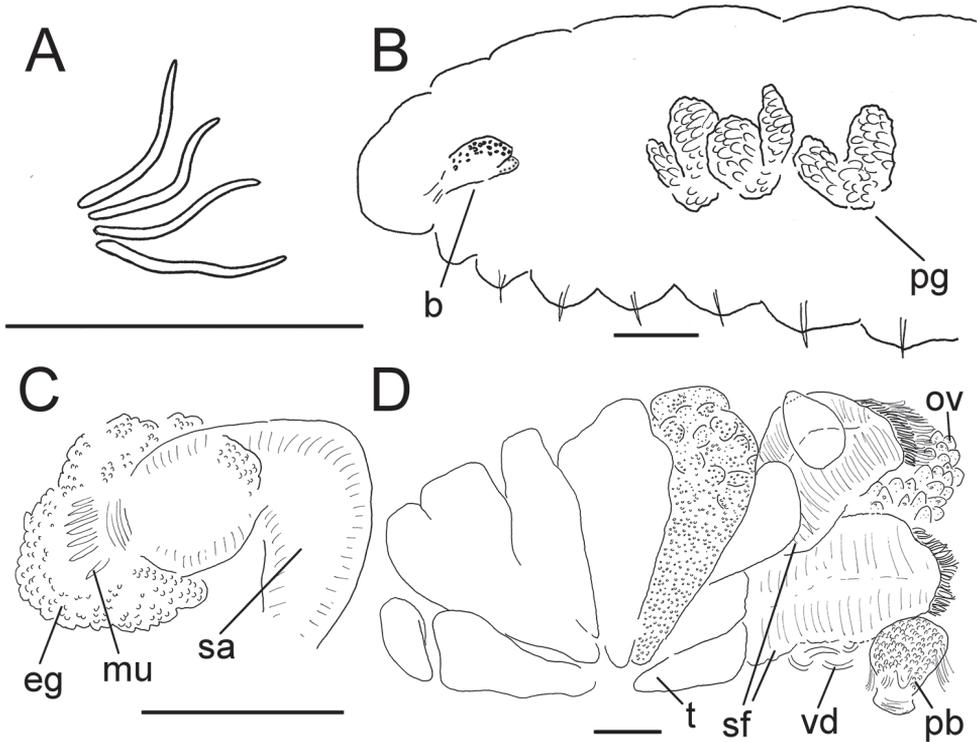


Figure 8. *Lumbricillus* sp. G. **A** Chaetal bundle **B** Anterior body **C** Spermatheca **D** Other genitalia. Abbreviations under general notes. Scale bars: 100 μ m.

Type material. *Typus amissus* (Nomenclatura Oligochaetologica). Type locality: Kalø Vig, Denmark. We did not designate a neotype as we do not have material from the type locality.

Material examined. SMNH 152733 (CE978), one mature specimen from Sweden & ZMBN 107842 (CE5412), one immature specimen from Norway. For information on specimen collection localities and GenBank accession numbers see Appendix 1.

Description. Orange or whitish worms. Length (fixed worms) more than 2.8–3.6 mm (amputated specimens), first 15 segments 2.5–3.1 mm long, width at clitellum 0.32–0.37 mm. More than 18 segments. Chaetae slightly sigmoid (Fig. 9A). Dorsal bundles with 3–5 chaetae anterior to clitellum, 2–3 chaetae in postclitellar segments. Ventral bundles with 3–6 chaetae anterior to clitellum, 2–5 chaetae posteriorly. Each worm's longest measured chaetae 50–60 μ m long, about 3 μ m wide. Clitellum extending over XII–1/2XIII. Head pore at 0/1. Epidermis with transverse rows of gland cells.

Coelomocytes numerous, 15 μ m long, round, oval, granulated. Paired pharyngeal glands present in IV, V and VI; each pair converging dorsally (Fig. 9B). Dorsal vessel originating in XIII. Nephridia observed in IX–X and possibly XIV–XV, about 110 μ m

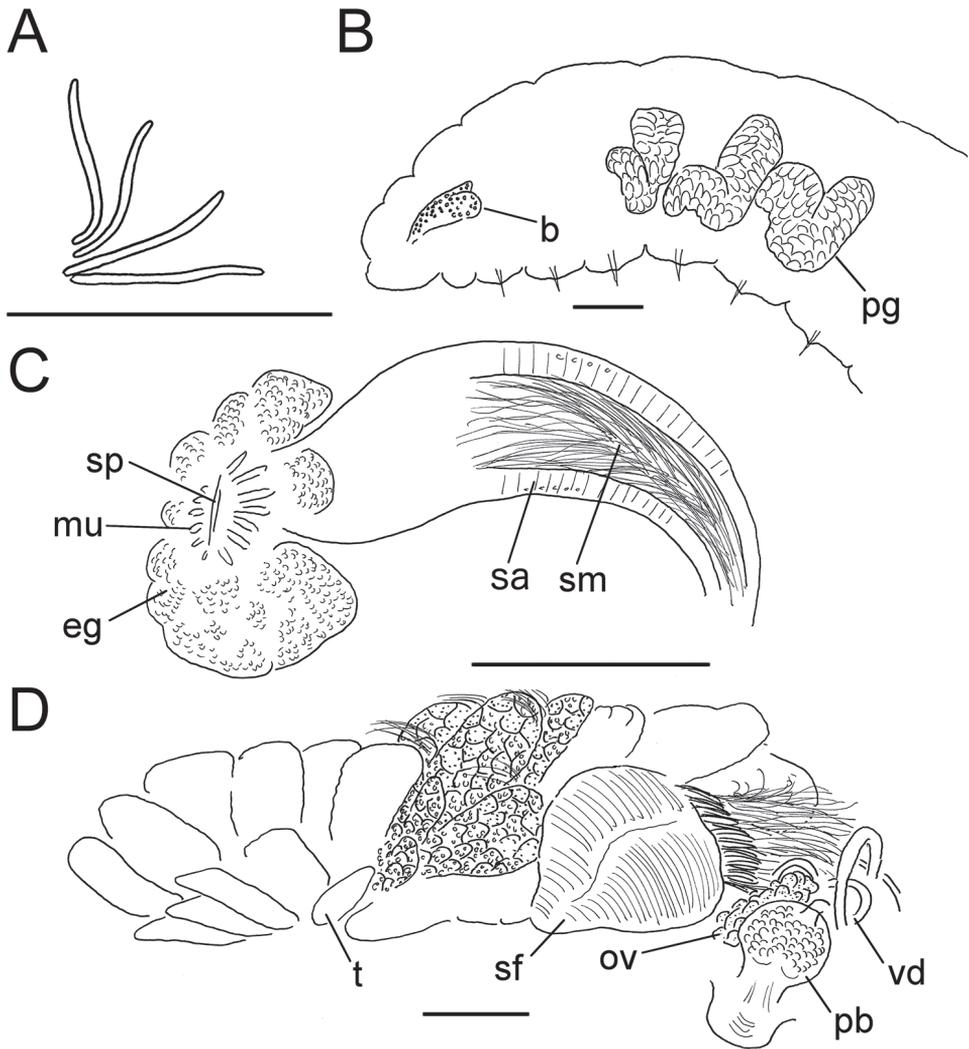


Figure 9. *Lumbricillus kaloensis*. **A** Chaetal bundle **B** Anterior body **C** Spermatheca **D** Other genitalia. Abbreviations under general notes. Scale bars: 100 μm .

long. Anteseptale small, consisting of funnel only. Postseptale oval, tapering posteriorly into efferent duct. Brain with posterior incision.

Male genitalia paired (Fig. 9D). Testes originating in XI, extending forwards into IX, in one specimen also extending backwards into XII, with testis sacs forming regular club-shaped lobes. Sperm funnels in XI, 185 μm long, 155 μm wide, making them slightly longer than wide, funnels tapering towards vasa deferentia. Most of vasa irregularly coiled in XII, 15 μm wide. Penial bulbs round, 80 μm in diameter. Ovaries in XII. No mature eggs observed.

Spermathecae (Fig. 9C) in V, spindle-shaped, without distinct ampulla, gradually widening, entally connecting with oesophagus. Sperm evenly embedded in ampulla. Spermathecae 290 μm long, 65 μm wide at widest part of ampulla. Gland cells surrounding ectal pore divided into at least three somewhat separated lobes, one lobe significantly larger than the others, whole glandular body 120 μm in diameter at its widest part. Two midventral subneural glands in XIII–XIV, 95 μm and 75 μm long, respectively.

Geographical distribution including BOLD data. Originally described from Denmark, now genetically identified from Norway and Sweden. BIN-number: BOLD:AAU0152.

Remarks. The specimens examined in this study match the original description by Nielsen and Christensen (1959) in the majority of the characters. Our worms were smaller than theirs, with slightly fewer chaetae (particularly in postclitellar bundles) and sperm funnels shorter in relation to their width, the latter of which could be explained by the difference between live and mounted material. We also observed two subneural glands which were not originally reported by Nielsen and Christensen. The spermathecae, despite being slightly damaged in our mature specimen, exhibit the typical large asymmetrical ectal gland subdivided into flap-like lobes, one of which is clearly larger than the others. Asymmetrical ectal glands have also been observed in *L. enteromorphae* von Bülow, 1957, and to some extent in *L. rubidus* Finogenova & Streltsov, 1978. The former can be distinguished from *L. kaloensis* by having sperm funnels 8 times longer than wide, and an atrium-like part where the vasa deferentia meet the penial bulbs. *Lumbricillus rubidus*, while having ectal glands on the spermathecae that may appear asymmetrical, does not have the glands subdivided into such clearly asymmetrical flaps as in *L. kaloensis*. Furthermore, *L. rubidus* has a more distinct musculature covering the ectal duct of the spermathecae, sometimes appearing as a muscular bulb; *L. kaloensis* also has a muscular coating of the duct, but it is thinner.

Lumbricillus kaloensis is genetically placed within the *lineatus* group. Its possible sister-group relationship with *Lumbricillus* sp. F (suggested by the tree in Fig. 1) is not statistically supported by the DNA data.

Lumbricillus sp. F

Fig. 10

Lumbricillus sp. F; Klinth et al. 2017.

Material examined. SMNH 152832 (CE2659), one mature specimen from the United Kingdom. For information on specimen collection locality and GenBank accession number see Appendix 1.

Description. Colour of worms unknown. Length (fixed worm) more than 3.1 mm (amputated specimen), first 15 segments 2.2 mm long, width at clitellum 0.35 mm. More than 21 segments. Chaetae slightly sigmoid (Fig. 10A). Dorsal bundles with 3–5 chaetae anterior to clitellum, 3–4 chaetae in postclitellar segments. Ventral

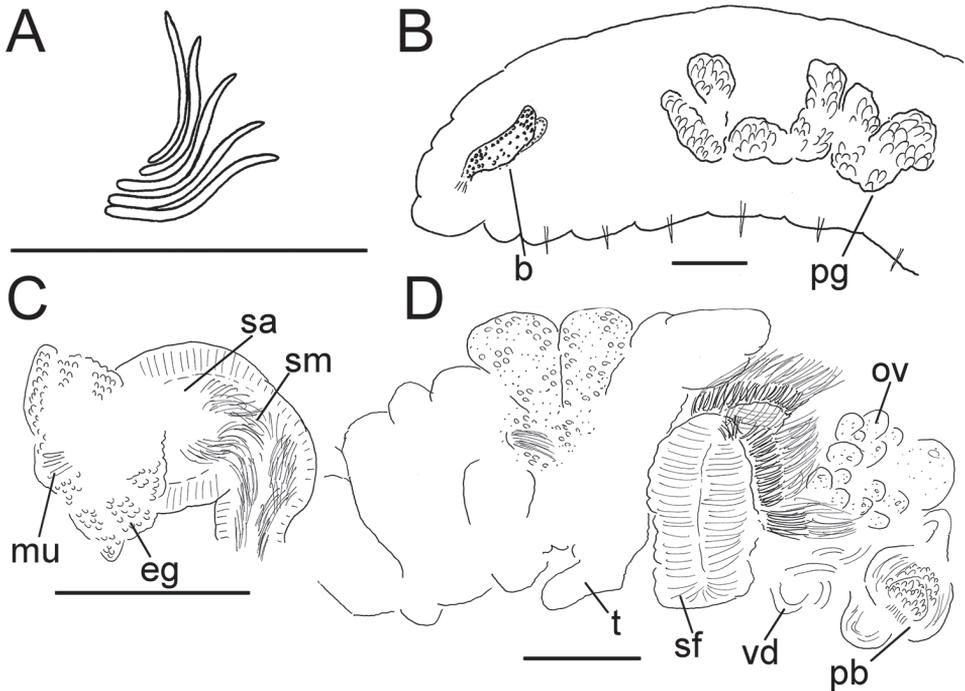


Figure 10. *Lumbricillus* sp. F. **A** Chaetal bundle **B** Anterior body **C** Spermatheca **D** Other genitalia. Abbreviations under general notes. Scale bars: 100 μ m.

bundles with 3–5 chaetae anterior to clitellum, 2–4 chaetae posteriorly. The worm's longest measured chaetae 45 μ m long, about 3 μ m wide. Clitellum extending over XII–1/2XIII. Head pore at 0/1. Epidermis with transverse rows of gland cells.

Coelomocytes numerous, 15 μ m long, round, oval or spindle-shaped, granulated with distinct nucleus. Paired pharyngeal glands present in IV, V and VI (Fig. 10B). Dorsal vessel originating in XIV. Nephridia possibly observed in X, about 95 μ m, shape uncertain. Brain elongate, with posterior incision.

Male genitalia paired (Fig. 10D). Testes originating in XI, extending forwards into X, with testis sacs forming regular club-shaped lobes. Sperm funnels in XI, 175 μ m long, 90 μ m wide, making them about twice as long as wide. Vasa deferentia not observed. Penial bulbs round, 85 μ m in diameter. Ovaries in XII. About two or three mature eggs present.

Spermathecae (Fig. 10C) in V, spindle-shaped, without distinct ampulla. Ectal duct short, widening into ampulla. Ampulla with constriction midway, dividing it into two sections, the inner of which connecting with oesophagus. Sperm concentrated in inner part of ampulla, embedded in wall of ampulla. Spermathecae 210 μ m long, 80 μ m wide at widest part of ampulla. Gland cells surrounding ectal pore, forming compact mass, 110 μ m in diameter at its widest part. Possibly one subneural gland in XIV, 50 μ m long.

Geographical distribution. Only known from the United Kingdom and Norway (unpublished results).

Remarks. Unfortunately only one mature specimen was available for this study, making it difficult to assign it to a known species. On the other hand, the description of a new species on such limited material is not recommended. *Lumbricillus* sp. F is genetically placed within the *lineatus* group; it is possibly phylogenetically close to *L. kaloensis*, but this is not strongly supported (Fig. 1).

***Lumbricillus pumilio* Stephenson, 1932**

Fig. 11

Lumbricillus pumilio Stephenson, 1932a: pp. 902–904, figs 1–3; Nielsen and Christensen 1959: p. 96; Tynen and Nurminen 1969: pp. 151–153; Klinth et al. 2017. *Lumbricillus pumillio* (sic); Erséus 1976: p. 9.

Type material. Typus amissus (Nomenclatura Oligochaetologica). Type locality: Wembury Bay, Plymouth, United Kingdom (Stephenson 1932a). We did not designate a neotype as we do not have material from the type locality.

Material examined. SMNH 152775 (CE3346), SMNH 152776 (CE3347), SMNH 152777 (CE3427), SMNH 152778 (CE3428), SMNH 152779 (CE3430), SMNH 152780 (CE3436) & SMNH 152781 (CE3437), seven mature specimens from the United Kingdom. For information on specimen collection localities and GenBank accession numbers see Appendix 1.

Description. Short and stout worms. Colour unknown. Length (fixed worms) more than 1.7–3.2 mm (amputated specimens), first 15 segments 1.3–2.3 mm long, width at clitellum 0.24–0.38 mm. More than 15–23 segments. Chaetae slightly sigmoid (Fig. 11A). Dorsal bundles with 3–6 chaetae anterior to clitellum, 3–5 chaetae in postclitellar segments. Ventral bundles with 3–6, rarely 2 or 7, chaetae anterior to clitellum, 3–6 chaetae, rarely 2, posteriorly. Each worm's longest measured chaetae 36–48 µm long and about 2.5 µm wide. Clitellum extending over XII–1/2XIII. Head pore not observed. Epidermis with transverse rows of gland cells.

Coelomocytes difficult to identify as such in this species, but small round, oval or spindle-shaped granulated cells about 5–7 µm long were noted in the coelomic cavity. Paired pharyngeal glands present in IV, V and VI; each pair converging dorsally (Fig. 11B). Dorsal vessel originating in XII or XIII. Nephridia observed in IX and XV–XVIII, about 45–50 µm long. Anteseptale small, consisting of funnel only. Postseptale oval, tapering posteriorly into efferent duct. Brain longer than wide, with a marked posterior incision creating two horn-like structures.

Male genitalia paired (Fig. 11D). Testes originating in XI, extending forwards into X, with testis sacs forming regular club-shaped lobes. Sperm funnels in XI, 115–190 µm long, 65–140 µm wide making them about 1.5–2 times longer than wide, funnels tapering towards vasa deferentia. Most of vasa deferentia irregularly coiled in XII together with ovaries, vasa 5–10 µm wide. Penial bulbs round, 55–80 µm in diameter. One or two mature eggs present at a time.

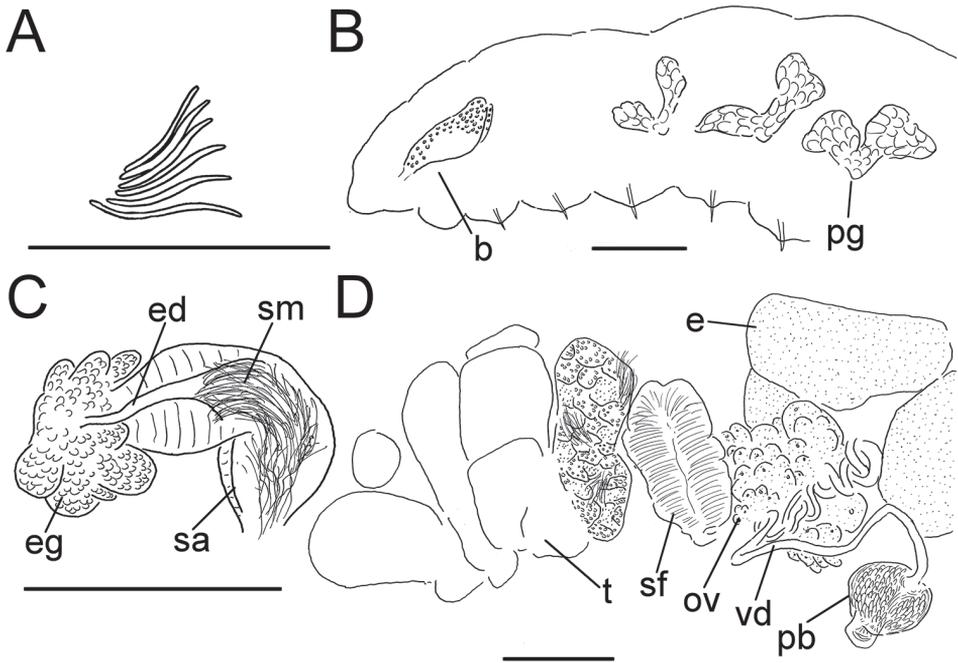


Figure 11. *Lumbricillus pumilio*. **A** Chaetal bundle **B** Anterior body **C** Spermatheca **D** Other genitalia. Abbreviations under general notes. Scale bars: 100 μm .

Spermathecae (Fig. 11C) in V, spindle-shaped. Ectal duct short, ampulla indistinct, lumen of ampulla usually filled with sperm, ental duct connected to oesophagus. Ampulla usually making a sharp bend caudad towards oesophagus at about half its length. Spermathecae 100–150 μm long, 30–50 μm wide at widest part of ampulla. Ectal pore surrounded by compact, roundish mass of gland cells; whole glandular body 45–110 μm in diameter at its widest part. One midventral subneural gland in XIV, 60–90 μm long.

Geographical distribution. Genetically identified from the United Kingdom. Also reported and briefly described from Iceland (Erséus 1976).

Remarks. Our measurements of the coelomic corpuscles (5–7 μm long) contradict the original description where they are described as being 20–28 μm . This could either be due to a high degree of variation in this trait or that we are comparing non-homologous cell types. The smaller subneural gland in XV described by Stephenson could not be distinguished, either because of its small size or because it was absent. Despite a few discrepancies from the original description the small body size of the worms together with the shape of the spermathecae and other reproductive organs supports that the sampled specimens belong to *L. pumilio*.

Lumbricillus pumilio is genetically closely related to *L. rubidus* Finogenova & Streltsov, 1978 (Fig. 1), with which it also shares morphological similarities. However, *L. pumilio* is generally smaller than *L. rubidus*, and it does not have an as distinct muscular covering of the spermathecal ectal duct as that of the latter (compare Figs 11 and 12).

***Lumbricillus rubidus* Finogenova & Streltsov, 1978**

Fig. 12

Lumbricillus rubidus Finogenova & Streltsov, 1978: pp. 17–23, fig. 1; Kossmagk-Stephan 1983: p. 8; Klinth et al. 2017.

Lumbricillus enteromorphae; sensu Kossmagk-Stephan 1985; nec von Bülow, 1957.

Type material. ZIAS 1/42509 (Nomenclatura Oligochaetologica). Type locality: Dal'nii Plyazh in Dal'nie Zelentsy Bay, Murmansk, Russia (Finogenova and Streltsov 1978). Not studied.

Material examined. SMNH 152792 (CE2549), SMNH 152793 (CE2551), SMNH 152794 (CE2553), SMNH 152795 (CE6105), SMNH 152796 (CE6106), SMNH 152797 (CE6107) & SMNH 152798 (CE6108), seven mature specimens from Sweden. For information on specimen collection localities and GenBank accession numbers see Appendix 1.

Description. Pale to pinkish worms. Length (fixed worms) more than 2.2–3.9 mm (amputated specimens), first 15 segments 2.0–3.1 mm long, width at clitellum 0.31–0.68 mm. More than 17–23 segments. Chaetae slightly sigmoid (Fig. 12A). Dorsal bundles with 3–7 chaetae anterior to clitellum, 3–6 chaetae in postclitellar segments. Ventral bundles with 3–8 chaetae anterior to clitellum, 3–8 chaetae posteriorly. Each worm's longest measured chaetae 45–50 µm long and 3–5 µm wide. Clitellum extending over XII–1/2XIII. Head pore not observed. Epidermis with transverse rows of gland cells.

Coelomocytes numerous, 10–20 µm long, round, oval or spindle-shaped. Paired pharyngeal glands present in IV, V and VI; each pair converging dorsally (Fig. 12B). Dorsal vessel originating in XIII. One nephridium observed in X, pear-shaped, about 80 µm long, narrowing posteriorly. Anteseptale small, consisting of funnel only. Efferent duct originating at mid length. Brain widening posteriorly, but exact shape uncertain.

Male genitalia paired (Fig. 12E). Testes originating in XI, extending forwards into X, sometimes IX, with testis sacs forming regular club-shaped lobes. Sperm funnels in XI, 135–265 µm long, 85–170 µm wide making them about 1.5–2 times longer than wide, funnels tapering towards vasa deferentia. Most of vasa irregularly coiled in XII, and 10–20 µm wide. Penial bulbs round, 70–130 µm in diameter. Ovaries in XII. One to five mature eggs present at a time.

Spermathecae (Fig. 12C, D) in V, spindle-shaped, without distinct ampulla. Ectal duct short, about 1/5 of total length of spermatheca, rapidly widening into ampulla. Conspicuous muscle cells encircling duct and connecting it to epidermis. Ampulla making sharp bend inwards and entally connecting with oesophagus. Sperm tightly packed in ectal duct, possibly covered by thin layer of secretion, spermatozoan tails occupying outer part of ampulla, heads aggregating into distinct clusters in inner part, and partly embedded in wall, of ampulla. Spermathecae 120–275 µm long, 60–110 µm wide at widest part of ampulla. Gland cells surrounding ectal pore, forming com-

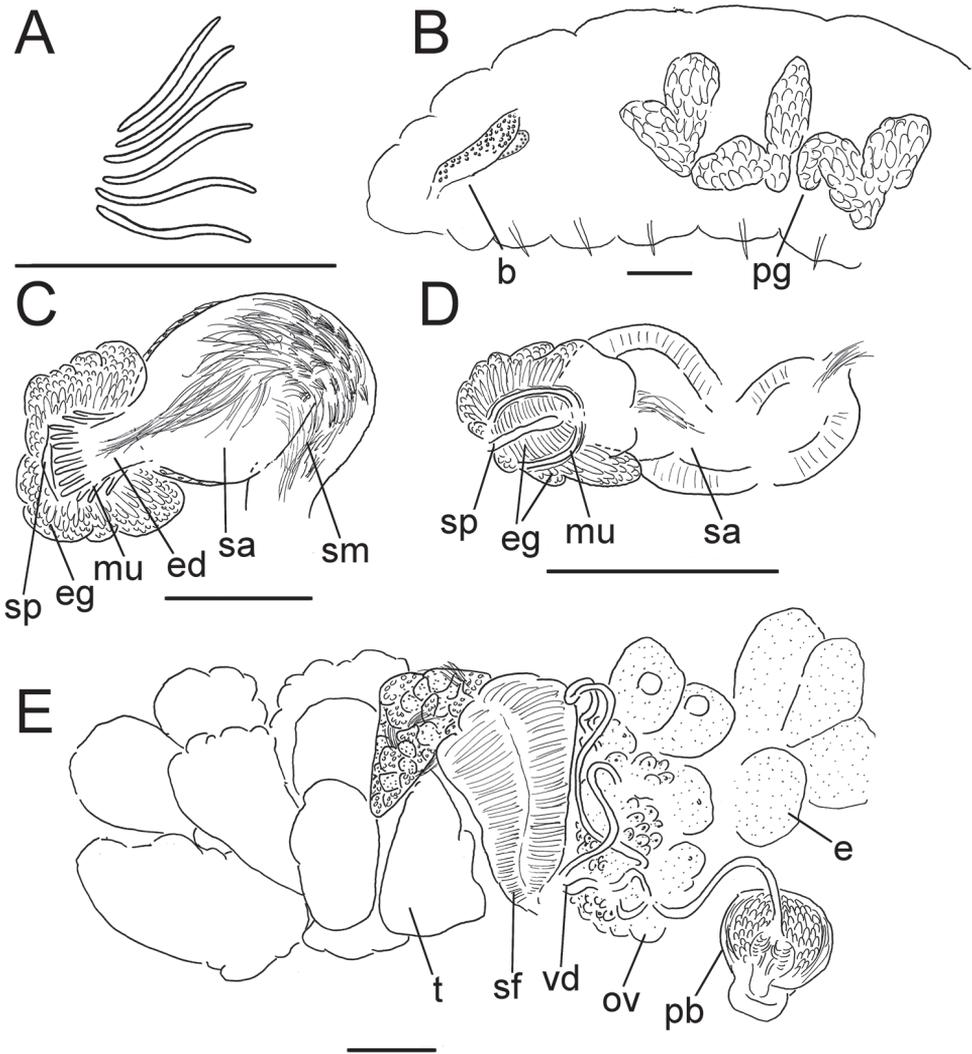


Figure 12. *Lumbricillus rubidus*. **A** Chaetal bundle **B** Anterior body **C**, **D** Spermatheca. **E** Other genitalia. Abbreviations under general notes. Scale bars: 100 μ m.

pact body with few marginal lobes, glandular body 60–135 μ m in diameter at its widest part. One midventral subneural gland in XIV, 60–150 μ m long.

Geographical distribution. Described from Russia and Germany, now genetically identified from Sweden.

Remarks. The specimens in this study match the original description of *L. rubidus* by Finogenova and Streltsov (1978) in most characters such as length, number of chaetae and sperm funnel ratio. It seems that our specimens in general possessed larger internal organs, such as sperm funnels, penial bulbs and spermathecae. Nevertheless, the strong musculature around the ectal pore of the spermathecae, originally described

as a muscular bulb, was found with clear resemblance in our specimens. This muscular sleeve covering the ectal duct of the spermathecae is conspicuous in all specimens. Several separate muscle bundles radiate around the base of the duct connecting to the body wall and may have a function in widening the pore in conjunction with copulation or fertilization of eggs. In one specimen, where one spermatheca was seen from above, the layers of musculature created a circle seemingly dividing the ectal gland in two. A closer examination revealed that the musculature more probably is tightly encircling the gland cells of the ectal gland without dividing them. The muscular bulb, as originally termed by Finogenova and Streltsov, is probably the same ectal part of the ectal gland, separated by the encircling musculature, rather than a compact mass of muscles. Similar muscle structures encircling the ectal pore of the spermathecae have been seen in most species of *Lumbricillus* during this study but they never appeared so conspicuous as in *L. rubidus*.

In 1959, Nielsen and Christensen classified the species *L. enteromorphae* von Bülow, 1957 as a hunger form of *L. rivalis*. Kossmagk-Stephan (1985) rejected this idea and instead synonymized *L. rubidus* with von Bülow's species based on the fact that they both have muscular bulbs. We agree that *L. enteromorphae* should be considered a separate species from *L. rivalis*, because of the asymmetrical ectal glands of the spermathecae and the atrium-like part where the vasa deferentia meets the penial bulbs, observed only in the former species. However, we do not agree that *L. rubidus* is a synonym of *L. enteromorphae*, as the former has sperm funnels that are much shorter in relation to their width (2–4 compared to 8 times longer than wide) and lacks any atrium-like part of the vasa deferentia. It is true that von Bülow described a funnel-like thickening of the spermathecal ectal duct which could be a structure similar to the muscular bulb seen in *L. rubidus*. However, we have observed varied extents of muscular coverings of the ectal ducts in most species belonging to the *lineatus* group, and a true comparison of this character can only be made once we have specimens of von Bülow's species.

Lumbricillus rubidus is genetically closely related to *L. pumilio* (Fig. 1), and shares morphological similarities with both *L. pumilio* and *L. kaloensis* (see remarks for each species respectively).

***Lumbricillus fennicus* Nurminen, 1964**

Fig. 13

Lumbricillus fennicus Nurminen, 1964: pp. 48–51, fig. 2; Graefe and Schmelz 1999: p. 61; Rota and Healy 1999: p. 54; Erséus et al. 1999; Klinth et al. 2017.

Type material. HUZM (Nomenclatura Oligochaetologica). Type locality: Tvärminne, Finland (Nurminen 1964). Not seen.

Material examined. SMNH 152729 (CE2767), SMNH 152730 (CE2768), SMNH 152731 (CE2988) & SMNH 152732 (CE6092), four mature specimens from Sweden. For information on specimen collection localities and GenBank accession numbers see Appendix 1.

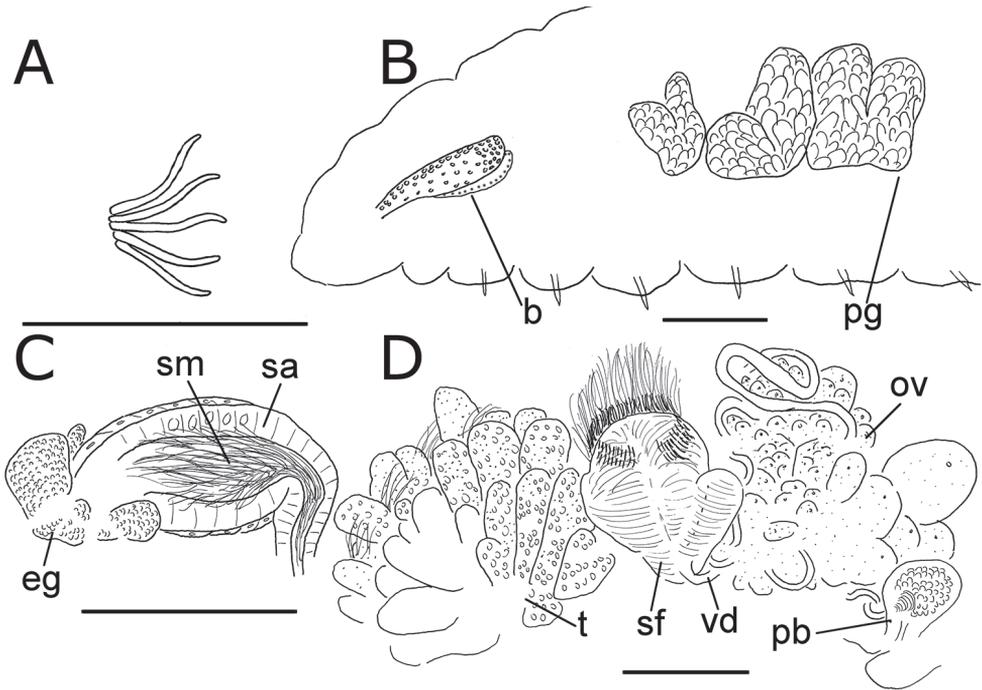


Figure 13. *Lumbricillus fennicus*. **A** Chaetal bundle **B** Anterior body **C** Spermatheca **D** Other genitalia. Abbreviations under general notes. Scale bars: 100 μ m.

Description. Colour of worms unknown. Length (fixed worms) more than 1.8–3.5 mm (amputated specimens), first 15 segments 2.0–2.3 mm long, width at clitellum 0.4–0.48 mm. More than 12–23 segments. Chaetae slightly sigmoid (Fig. 13A). Dorsal bundles with 3–5, rarely 2 or 7, chaetae anterior to clitellum, 2–5 chaetae in postclitellar segments. Ventral bundles with 3–7, usually 4–5, chaetae anterior to clitellum, 4–5 chaetae posteriorly. Each worm's longest measured chaetae 35–50 μ m long and about 2.5 μ m wide. Clitellum extending over XII–1/2XIII, with granulated and hyaline cells irregularly distributed. Head pore not observed. Epidermis with transverse rows of gland cells.

Coelomocytes numerous, 15–25 μ m long, round, oval or spindle-shaped. Paired pharyngeal glands present in IV, V and VI; each pair converging dorsally (Fig. 13B). Dorsal vessel originating in XIII. Nephridia observed in XIII–XVI about 45 μ m long, anteseptale consisting of funnel only, efferent duct originating at mid length of postseptale. Brain widening posteriorly, with posterior incision creating two hornlike structures.

Male genitalia paired (Fig. 13D). Testes originating in XI, extending forwards into X, sometimes IX, with testis sacs forming regular club-shaped lobes. Sperm funnels in XI, 100–125 μ m long, 95–110 μ m wide making them about 1–1.5 times longer than wide. Funnels lobed rather than cylindrical, and abruptly tapering towards vasa deferentia.

Vasa with few irregular coils around ovaries in XII, and about 10 μm wide. Penial bulbs round/pear-shaped 45–50 μm in diameter. Three to four mature eggs present at a time.

Spermathecae (Fig. 13C) in V, spindle-shaped, without distinct ampulla. Ectal duct short, encircled by musculature, and rapidly widening into ampulla. Ampulla after maximum width making sharp bend inwards, entally connecting with oesophagus. Sperm evenly embedded in wall of ampulla, filling but not embedded in ental duct. Spermathecae 170–195 μm long, 45–65 μm wide at widest part of ampulla. Gland cells surrounding ectal pore, forming compact mass, somewhat lobed, whole glandular body 60–75 μm in diameter at its widest part. Midventral subneural glands in XIII, XIV and in one specimen in XV, measuring 45–70 μm , 75–90 μm and 70 μm respectively.

Geographical distribution. Originally described from Finland, but also reported from Denmark, France (Lafont and Vivier 2006), Germany (Giere 1976), Ireland (Healy 2007), Norway and Sweden, now genetically identified from Sweden.

Remarks. The original description of *L. fennicus* matches the specimens of this study in most characters, but there are a few differences. Our specimens measured 2–3.5 mm in length after fixation, but considering that some had been cut directly posterior to the clitellum the length of the complete worms probably was 3–5 mm. This is smaller than the 8 mm reported by Nurminen (1964), but he based his description on living worms. Nurminen described the clitellum as covering 1/2XI–XII while in our specimens, the clitellum extends over XII–1/2XIII. The extension of the clitellum may vary as it develops, but the whole structures does not generally shift in position, and this suggests the possibility of a printing or observation error in the original description.

The lobed, as opposed to cylindrical, sperm funnels are so far (in European species) only reported for *L. fennicus*, and this, together with the matching shape of the spermathecae, allowed confident allocation of the specimens to this species despite some incongruence among the characters mentioned above. The interpretation of the lobes of the sperm funnels probably also differs between living and fixed specimens. Our Swedish specimens were collected in freshwater habitats, but the sites are possibly subjected to brackish water at times, making the range of salinity similar to the original records from the Gulf of Finland. Most other records in Europe are from coastal oligohaline or inland freshwater habitats.

Lumbricillus fennicus is both genetically (Fig. 1) and morphologically placed within the *L. lineatus* group.

The *pagenstecheri* group

Characteristics: Testes with testis sacs regularly lobed in bunch-like arrangement. Spermathecae with distinct ampulla and glands both surrounding the ectal pore and distributed along the duct. Chaetae 3–6 per bundle, or more; upper bundles dorsolateral. Penial bulbs round. Sperm funnels about twice as long as wide.

***Lumbricillus pagenstecheri* (Ratzel, 1869), a species complex**

- Enchytraeus pagenstecheri* Ratzel, 1869: pp. 587–588, pl. XLII, figs 2, 13, 20b & 21.
Pachydriilus pagenstecheri; Vejdovsky 1877: p. 298; Ditlevsen 1904: pp. 433–434, fig. 29, pl. XVIII, fig. 6; Knöllner 1935: p. 436; Černosvitov 1937: p. 292.
Lumbricillus pagenstecheri; Ude 1901: p. 9, pl. I, fig. 14; Southern 1909: p. 153; Stephenson 1925: pp. 1315–1316; von Bülow 1957: pp. 77–78, pl. XXV, figs 1–7; Nielsen and Christensen 1959: pp. 104–105, figs 117–120; Erséus 1976: pp. 9–11, fig. 8.
Lumbricillus henkingi Ude, 1901: pp. 9–10, pl. II, figs 15–18; Stephenson 1925: p. 1315.
Lumbricillus ritteri Eisen, 1904: pp. 84–86, figs 53–54, pl. XIII, figs 5–9; Nielsen and Christensen 1959: p. 97; Erséus 1976: pp. 9–10, fig. 12.
Lumbricillus aegialites Stephenson, 1922: pp. 1126–1130, figs 2–3; Stephenson 1924: p. 211; Stephenson 1925: p. 1314.
Lumbricillus necrophagus Stephenson, 1922: pp. 1130–1133, figs 4–5.
Lumbricillus georgiensis Tynen, 1969: pp. 390–391, figs 1–3.

Type material. Typus amissus (Nomenclatura Oligochaetologica). Type locality: The original material was collected in Rhine River near Karlsruhe, and in ponds around Heidelberg, Germany (Ratzel 1869), but none of these places has yet been specifically designated as the type locality. We did not designate a neotype as we do not have material from any of the original localities, nor do we know which one, if any, of our cryptic species that represent the true nominate species.

Remarks. The molecular studies by Klinth et al. (2017) supported the delimitation of four different species with the morphology of *L. pagenstecheri*, here denoted as cryptic species A–D. Particularly the morphology of the spermathecae characterizes this group. There are two groups of gland cells, one creating the typical mass of glands surrounding the ectal pore, as seen in the other species of *Lumbricillus*, and the other group composed of numerous, rather long, gland cells covering the ectal duct. These two groups of gland cells can be difficult to distinguish from each other, depending on the orientation of the mounted specimens, but they create the impression of a very narrow duct followed by a distinct, almost spherical, thin-walled ampulla. While there seems to be some morphological differences between the four species in this study, such as size and number of chaetae, there are too few sampled specimens to verify that these characters do not overlap.

Lumbricillus pagenstecheri was originally described by Ratzel (1869) from the Rhine River in Germany and has later been re-described by Nielsen and Christensen (1959) as well as others and today includes five synonymized species (listed above). Such synonymies may need reappraisal as there are some differences between the original descriptions concerning size, number of segments and number of chaetae and there is a possibility that some of the synonymized species are present in our material. Moreover, about thirteen described species from the Northwestern Pacific and eight from the Northeastern Pacific have a morphology similar to that of *L. pagenstecheri* (Timm

2005), and a more extensive phylogenetic study focused on this part of the genus will be necessary, to resolve the taxonomy of this complex group.

For this study, we chose to present the morphological measurements only for our cryptic species A, which is the only one with a sufficient sample size, and provide a comparison of some characters with the other three cryptic species in Table 2. In general, species B and D were the largest, species D possessed fewer chaetae per bundle than the others, and for species C we unfortunately had no fully mature specimens. Full information on collection localities and accession numbers of all four species are given in Appendix 1.

***Lumbricillus pagenstecheri* (Ratzel, 1869) Cryptic species A**

Fig. 14, Table 2

Material examined. SMNH 152766 (CE1896), SMNH 152767 (CE1897), SMNH 152768 (CE1899), SMNH 152769 (CE2497), SMNH 152770 (CE2498) & SMNH 152771 (CE2500), six mature specimens from Sweden. For information on specimen collection localities and GenBank accession numbers see Appendix 1.

Description. White to yellow worms. Length (fixed worms) more than 2.8–9.3 mm (amputated specimens), first 15 segments 2.4–4.2 mm long, width at clitellum 0.59–0.75 mm. More than 17–40 segments. Chaetae sigmoid (Fig. 14A). Dorsal bundles with 2–5 chaetae anterior to clitellum, 2–5(6) chaetae in postclitellar segments. Ventral bundles with (2)4–7 chaetae anterior to clitellum, (2)3–6(8) chaetae posteriorly. Each worm's longest measured chaetae 70–95 µm long, about 5–8 µm wide. Clitellum extending over XII–XIII. Head pore at 0/1. Epidermis with transverse rows of gland cells.

Coelomocytes numerous, 15–25 µm long, spindle-shaped, oval, round, granulated with distinct nucleus. Paired pharyngeal glands present in IV, V and VI; two first pairs connected dorsally, third pair with uncertain connection (Fig. 14B). Dorsal vessel originating in XIII. Nephridia observed in VII–X and XII–XXI, 120–130 µm long, anteseptale funnel only, postseptale oval, tapering into posterior efferent duct. Brain with shallow posterior incision.

Male genitalia paired (Fig. 14D). Testes originating in XI, extending forwards into X, sometimes IX, with testis sacs forming regular club-shaped lobes. Sperm funnels in XI, 210–300 µm long, 145–225 µm wide, making them about as long as wide or twice as long as wide, funnels gradually tapering towards vasa deferentia. Most of vasa irregularly coiled in XII, 10–15 µm wide. Penial bulbs round, 135–185 µm in diameter. Ovaries in XII. About two to eight mature eggs present at a time.

Spermathecae (Fig. 14C) in V, club-shaped, with distinct ampulla. Ectal duct narrow, about as long as ampulla, abruptly widening into ampulla. Ampulla round, entally connecting with oesophagus. Sperm arranged in circular masses in ampulla. Spermathecae 140–215 µm long, 75–110 µm wide at widest part of ampulla. Two groups of gland cells, one covering ectal duct, the other surrounding ectal pore. Gland cells surrounding ectal pore forming compact mass, slightly lobed, whole glandular

Table 2. Comparison of selected measured traits from the four possibly cryptic species of *L. pagenstecheri*, as well as their known geographical distribution. As our specimens were amputated for the extraction of DNA we could only compare the size of the first 15 segments.

<i>L. pagenstecheri</i> cryptic species: distribution	Length I–XV (mm) / Width at clitellum (mm)	Chaetae				Length (μm)	Penial bulbs diameter (μm)	Spermathecae		
		Dorsal		Ventral				Length (μm)	Width of ampulla (μm)	Ectal gland diameter (μm)
		Predlit.	Postclit.	Predlit.	Postclit.					
A: Canada, Denmark, Sweden	2.4–4.2 /0.6–0.8	2–5	2–5(6)	(2)4–7	(2)3– 6(8)	70–95	135–185	140– 215	75–110	80–195
B: Norway	4.3–5.3 /0.9–1.8	5–6(7)	3–5	(6)7–8	4–6(7)	125–135	365–390	170– 265	125–225	260–340
C: Canada, Norway, Spain	2.5–2.7 /0.3–0.7	3–5	2–4	4–6	2–7	65–75	130	110	80	105
D: Canada, Norway	2.5–5.0 /0.6–1.0	3–5	2–3(4)	4–6(7)	2–4	95–110	115–245	180– 205	145–170	190–250

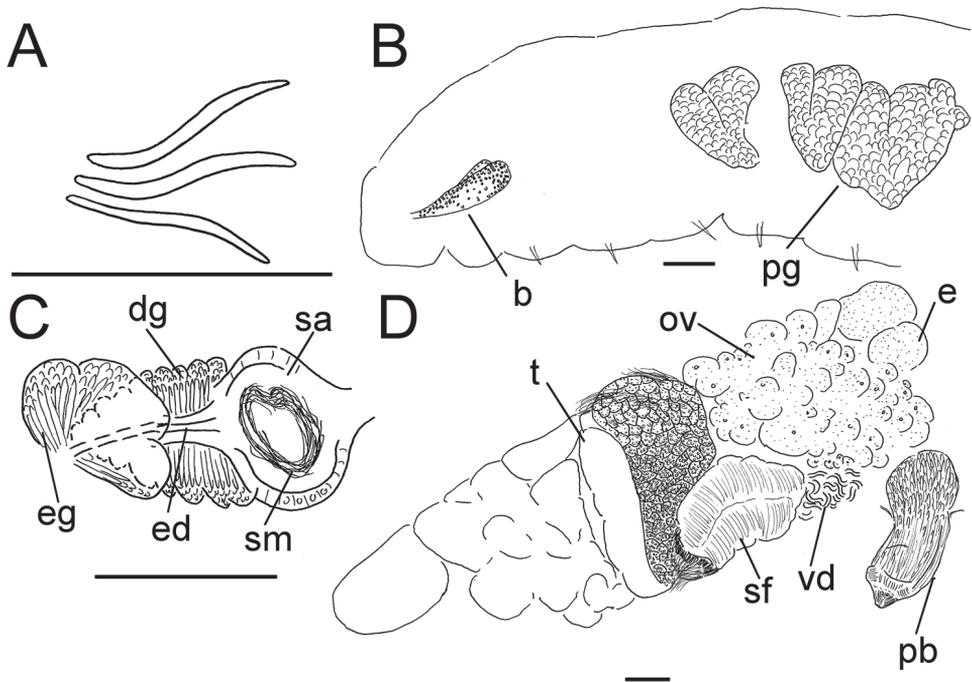


Figure 14. *Lumbricillus pagenstecheri*. **A** Chaetal bundle **B** Anterior body **C** Spermatheca **D** Other genitalia. Abbreviations under general notes. Scale bars: 100 μm .

body 80–195 μm in diameter at its widest part. Two midventral subneural glands in XIII–XIV, 130 μm and 95 μm long, respectively.

Geographical distribution including BOLD data. Genetically identified from Sweden; also recognized from Canada and Denmark (BIN-number: BOLD:AAF9627).

***Lumbricillus viridis* Stephenson, 1911**

Fig. 15

Lumbricillus viridis Stephenson, 1911: pp. 46–50, figs 6a–b & 7a–c; Nielsen and Christensen 1959: pp. 103–104, fig. 116; Klinth et al. 2017.

Pachydriulus orthochaetus Delphy, 1921: pp. 64–82, figs 29–41.

Type material. *Typus amissus* (Nomenclatura Oligochaetologica). Type locality: Firth of Clyde, Wemyss Bay, United Kingdom (Stephenson, 1911). We did not designate a neotype as we do not have material from the type locality.

Material examined. ZMBN 107933 (CE12037), ZMBN 107934 (CE12038), ZMBN 107935 (CE12039) & ZMBN 107938 (CE23255), three mature and one half-mature specimens from Norway. For information on specimen collection localities and GenBank accession numbers see Appendix 1.

Description. Green worms (sometimes yellowish-green). Length (fixed worms) more than 7.9–10.6 mm (amputated specimens), first 15 segments 3.8–6.2 mm long, width at clitellum 0.74–1.05 mm. More than 23–41 segments. Chaetae straight or slightly sigmoid (Fig. 15A). Dorsal bundles with 3–6 chaetae anterior to clitellum, 3–5 chaetae in postclitellar segments. Ventral bundles with 3–6 chaetae anterior to clitellum, 3–5 chaetae posteriorly. Each worm's longest measured chaetae 70–85 µm long, about 5 µm wide. Clitellum extending over XII–XIII. Head pore at 0/1. Epidermis with transverse rows of gland cells.

Coelomocytes numerous, 20–35 µm long, spindle-shaped, oval, round, granulated. Paired pharyngeal glands present in IV, V and VI; each pair converging dorsally (Fig. 15B). Dorsal vessel originating in XIII. Nephridia observed in VIII–X and XV–XIX, about 250 µm long, anteseptale funnel only, postseptale oval, tapering into posterior efferent duct. Brain with posterior incision.

Male genitalia paired (Fig. 15D). Testes originating in XI, extending forwards into X, with testis sacs forming regular club-shaped lobes. Sperm funnels in XI, 620–670 µm long, 320–350 µm wide, making them about twice as long as wide, funnels tapering towards vasa deferentia. Most of vasa irregularly coiled in XII, 25–30 µm wide. Penial bulbs round, 170–180 µm in diameter. Ovaries in XII. About five mature eggs present at a time.

Spermathecae (Fig. 15C) in V, club-shaped, with distinct ampulla. Ectal duct narrow, shorter than ampulla, abruptly widening into ampulla. Ampulla round. Sperm arranged in a compact central sphere in the ampulla as well as embedded in the wall of ampulla, creating a circle around the sphere. Spermathecae 265–320 µm long, 270–310 µm wide at widest part of ampulla. Gland cells surrounding ectal pore, forming compact mass, slightly lobed, whole glandular body 310–325 µm in diameter at its widest part. Gland cells also along the ectal duct. Up to four midventral subneural glands in XIV–XVII, 240–270 µm, 215–245 µm, 190–215 µm and 130 µm long, respectively; glands in XVII not observed in all specimens.

Geographical distribution including BOLD data. Genetically identified from France and Norway. Previously described from Denmark, Norway (Nurminen 1965b) the United Kingdom and Sweden (Erséus 1977). BIN-number: BOLD:AAU1636.

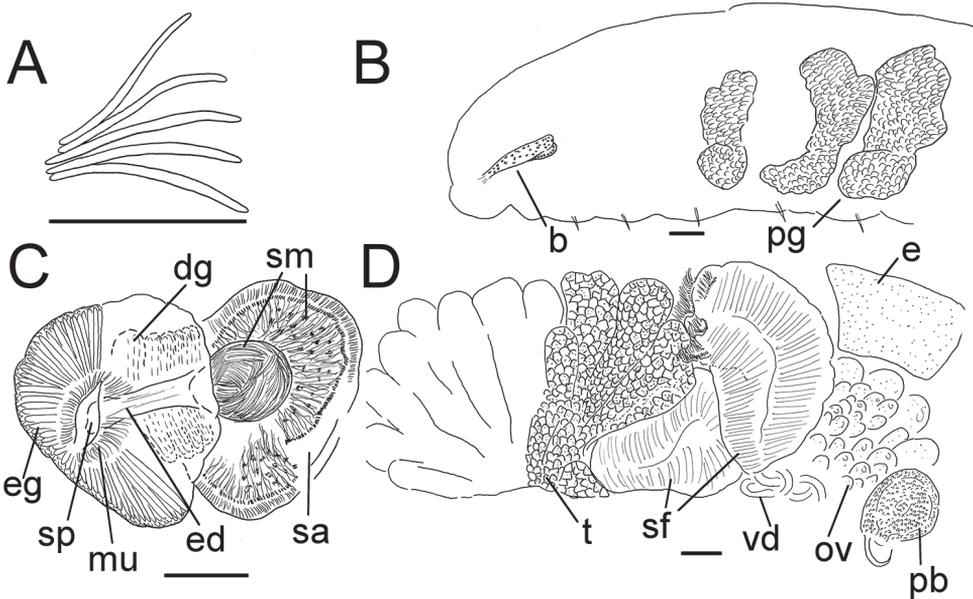


Figure 15. *Lumbricillus viridis*. **A** Chaetal bundle **B** Anterior body **C** Spermatheca **D** Other genitalia. Abbreviations under general notes. Scale bars: 100 μ m.

Remarks. Specimens in this study are smaller and possess somewhat fewer chaetae, than the ones from the original description by Stephenson and the later re-description by Nielsen and Christensen. Furthermore, the observed proportions of the sperm funnels (twice longer than wide) differ greatly from those (7–10:1, or 6–8:1) described by Stephenson and Nielsen and Christensen, respectively. However, folding of these organs may have caused us to underestimate their true length. Nevertheless, the distinct greenish colour of the sampled specimens and the resemblance between their spermathecae and particularly the one described by Nielsen and Christensen confirm these specimens as *Lumbricillus viridis*.

According to our knowledge, the presence of gland cells along the spermathecal ectal duct has not been reported for *L. viridis* before, possibly because of the difficulty of distinguishing these gland cells from the large ones surrounding the ectal pore. In this study, similar duct glands have only been observed in *L. pagenstecheri* sensu lato.

Lumbricillus viridis is genetically most closely related to the *L. pagenstecheri* species complex (Fig. 1: *L. pagenstecheri* A–D).

The “*tuba*” group

Characteristics: Testes with testis sacs regularly lobed in bunch-shaped arrangement. Spermathecae with ampulla distinctly set off from the duct and glands surrounding the

ectal pore. Chaetae usually 3–6 per bundle; upper bundles dorsolateral. Penial bulbs round. Sperm funnels about as long as wide.

Note that this group, containing also *L. scandicus* sp. n., is not monophyletic (Fig. 1); it is based on morphological similarity only.

***Lumbricillus tuba* Stephenson, 1911**

Fig. 16

Lumbricillus tuba Stephenson, 1911: pp. 42–46, figs 5a–b, pl. I, figs 6–8; Nielsen and Christensen 1959: p. 105, fig. 131; Erséus et al. 2010; Klinth et al. 2017.

Type material. Typus amissus (Nomenclatura Oligochaetologica). Type locality: Firth of Clyde, Millport, Island of Cumbrae, United Kingdom (Stephenson 1911). We did not designate a neotype as we do not have material from the type locality.

Material examined. ZMBN 107916 (CE22614), one mature specimen from Norway. For information on specimen collection locality and GenBank accession number see Appendix 1. Note that this specimen is the only sexually mature available for this study, but additional (immature) worms were studied genetically by Klinth et al. (2017).

Description. White to grey worm. Length (fixed worm) more than 4.8 mm (amputated specimen), first 15 segments 2.0 mm long, width at clitellum 0.39 mm. More than 39 segments. Chaetae slightly sigmoid (Fig. 16A). Dorsal bundles with 2–3 chaetae anterior to clitellum, 2–3 chaetae in postclitellar segments. Ventral bundles with 3–4 chaetae anterior to clitellum, 2–3 chaetae posteriorly. The worm's longest measured chaeta 48 μ m long, about 3 μ m wide. Clitellum extending over XII–1/2XIII. Head pore not observed. Epidermis with transverse rows of gland cells.

Coelomocytes numerous, 20 μ m long, spindle-shaped, oval, round, granulated. Paired pharyngeal glands present in IV, V and VI (Fig. 16B). Dorsal vessel originating in XII. Nephridia not observed. Brain longer than wide, further shape unclear.

Male genitalia paired (Fig. 16D). Testes originating in XI, extending forwards into IX, with testis sacs forming regular club-shaped lobes. Sperm funnels in XI, 120 μ m long, 105 μ m wide, making them slightly longer than wide, funnels tapering towards vasa deferentia. Most of vasa irregularly coiled in XII, 10 μ m wide. Penial bulbs round, 85 μ m in diameter. Ovaries in XII. Two mature eggs present.

Spermathecae (Fig. 16C) in V, club-shaped, with distinct ampulla. Ectal duct as long as ampulla, abruptly widening into oval ampulla. Sperm circularly arranged in ampulla. Spermathecae 120 μ m long, 85 μ m wide at widest part of ampulla. Gland cells surrounding ectal pore, forming compact mass, whole glandular body 75 μ m in diameter at its widest part. Three midventral subneural glands in XIII–XV, 85 μ m, 90 μ m and 85 μ m long, respectively.

Geographical distribution including BOLD data. Genetically identified from Norway and Sweden. Also described from Denmark and the United Kingdom. BIN-number: BOLD:ACQ1913.

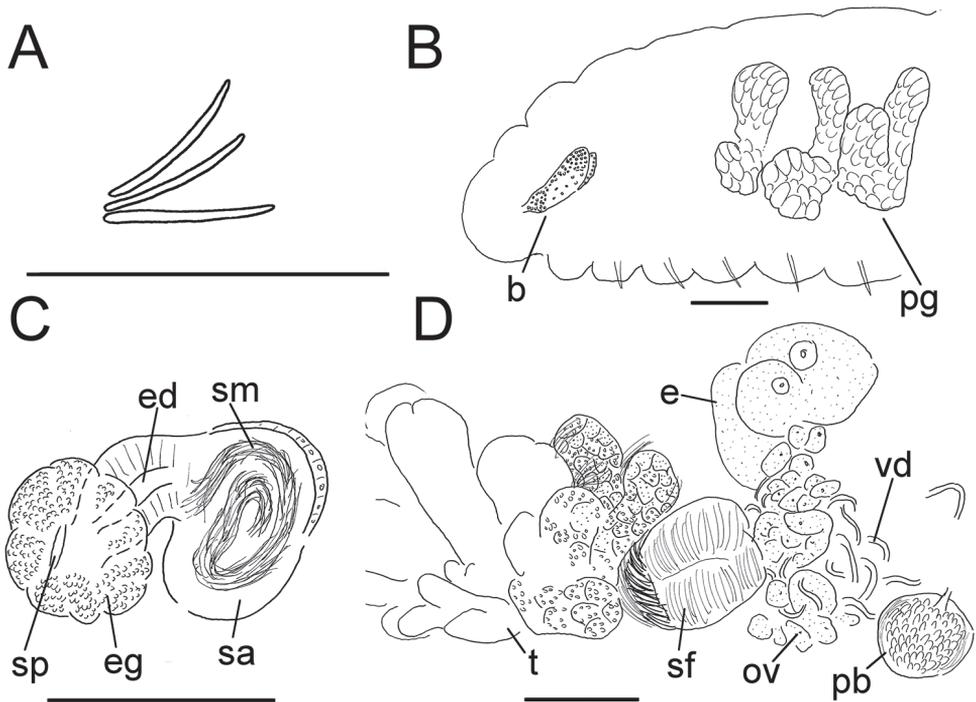


Figure 16. *Lumbricillus tuba*. **A** Chaetal bundle **B** Anterior body **C** Spermatheca **D** Other genitalia. Abbreviations under general notes. Scale bars: 100 μm .

Remarks. Our specimen matches the original description by Stephenson (1911) well in most characters, including the shape of the spermathecae and the proportions of the sperm funnels. However, its body size was smaller and the chaetae per bundle slightly fewer than in the original description.

Lumbricillus tuba is genetically most closely related to the *L. pagenstecheri* group (including *L. viridis*), but it is morphologically most similar to *L. scandicus* sp. n. described below.

***Lumbricillus scandicus* sp. n.**

<http://zoobank.org/A45F3597-1CA9-40D1-96C8-D4034588A6A6>

Fig. 17

Lumbricillus cf. *helgolandicus* Nielsen and Christensen 1959: pp. 102–103, fig. 115;

Finogenova and Timm 1988: 97–99, figs 6–10; Klinth et al. 2017.

Lumbricillus helgolandicus sensu von Bülow 1957: p. 79, pl. XXV, figs 11–12, pl. XXIX, figs 5–6; Tynen and Nurminen 1969: p. 152, fig. 1i.

Non *Pachydriulus helgolandicus* Michaelsen, 1927: p. 12, fig. 11; Michaelsen 1934: pp. 135–141, fig. 1.

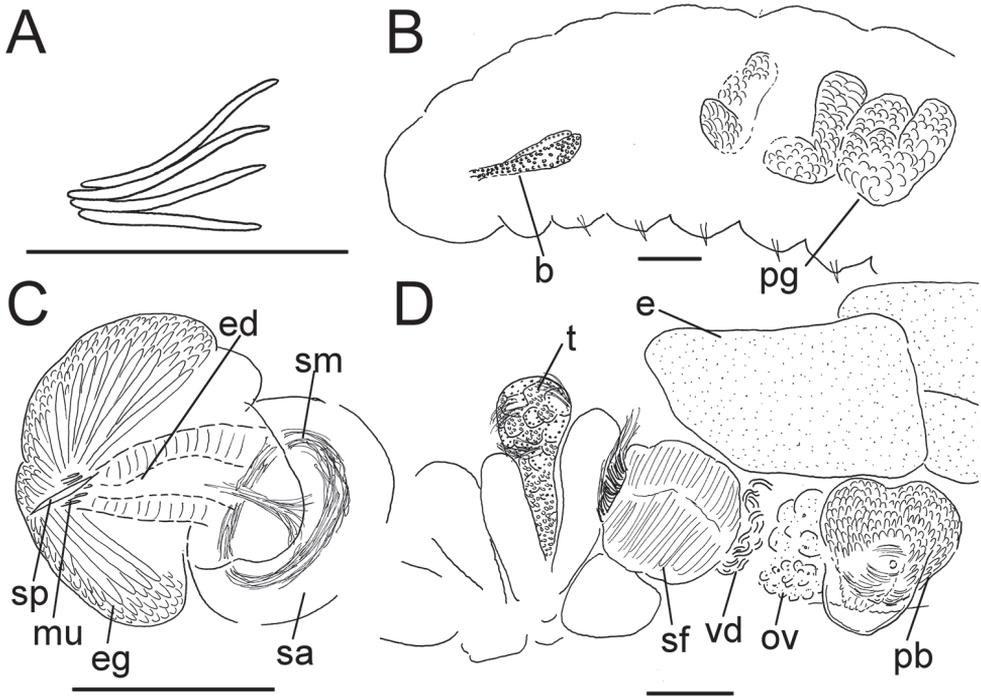


Figure 17. *Lumbricillus scandicus* sp. n. **A** Chaetal bundle. **B** Anterior body **C** Spermatheca **D** Other genitalia. Abbreviations under general notes. Scale bars: 100 μ m.

Holotype. SMNH Type-8923 [former SMNH 152721] (CE1905), a whole-mounted voucher of a sexually mature and DNA-barcoded worm (COI barcode is KU893950 in NCBI/GenBank; Klinth et al. 2017).

Type locality. Sweden, Öland, Borgholm, Neptuni Åkrar, beach with mixed shelly sand, pebbles and organic material, 57.3346 N, 17.0102 E, collected 11 June 2006 by L. Matamoros.

Paratype. SMNH Type-8925 [former SMNH 152722] (CE1907), a whole-mounted sexually mature specimen from the type locality.

Other material examined. SMNH 152720 (CE975), SMNH 152723 (CE1915), SMNH 152724 (CE2548) & SMNH 152725 (CE2552), four mature specimens from Sweden. For information on specimen collection localities and GenBank accession numbers see Appendix 1.

Etymology. Named after Scandinavia where the species has been found.

Diagnosis. This species is morphologically most similar to *L. helgolandicus* and *L. tuba*. It is distinguished from *L. helgolandicus* in having shorter sperm funnels, sperm arranged circularly in the spermathecae and generally possessing more chaetae per bundle. *Lumbricillus scandicus* can be distinguished from *L. tuba* in having spermathecal ectal glands that are larger than the ampulla and generally possessing more chaetae per bundle.

Description of all material. Pale, white to pinkish or orange worms. Length (fixed worms) more than 2.6–3.9 mm (amputated specimens), first 15 segments 2.0–2.9 mm long, width at clitellum 0.3–0.7 mm. More than 18–24 segments. Prostomium hemispherical, sometimes triangular. Chaetae slightly sigmoid (Fig. 17A). Dorsal bundles with 3–6, usually 4–5, chaetae anterior to clitellum, 2–5 chaetae in postclitellar segments. Ventral bundles with 4–7 chaetae anterior to clitellum, 3–6 chaetae posteriorly. Each worm's longest measured chaetae 50–60 μm long and about 2.5 μm wide. Clitellum extending over XII–1/2XIII, with granulated and hyaline cells irregularly distributed. Head pore not observed. Epidermis with transverse rows of gland cells.

Coelomocytes numerous, 15–20 μm long, round or oval. Paired pharyngeal glands present in IV, V and VI; each pair converging dorsally, with large ventral lobes (Fig. 17B). Posteriormost pair sometimes extending into VII. Dorsal vessel originating in either XII or XIII, difficult to distinguish due to presence of mature eggs. One nephridium observed in XIV about 85 μm long, anteseptale consisting of funnel only, duct originating posteroventrally. Brain widening posteriorly, possibly with posterior incision.

Male genitalia paired (Fig. 17D). Testes originating in XI, extending forwards into X, sometimes IX, with testis sacs forming regular club-shaped lobes. Sperm funnels in XI, 95–205 μm long, 90–160 μm wide making them about 1–1.5 times longer than wide. Funnels cylindrical, abruptly tapering towards vasa deferentia. Vasa with few irregular coils around ovaries in XII, and about 7–10 μm wide. Penial bulbs round/pear-shaped 75–145 μm in diameter. Two to six mature eggs present at a time.

Spermathecae (Fig. 17C) in V, club-shaped, with ampulla distinctly set apart from ectal duct. Ectal duct wall with long cylindrical cells. Ampulla sub-spherical, thin-walled, entally communicating with oesophagus. Sperm following duct to ampulla, in ampulla aggregated into central mass haloed by circle of spermatozoa. Spermathecae 90–160 μm long, 65–115 μm wide at widest part of ampulla. Gland cells surrounding ectal pore, forming compact, slightly folded mass, 100–155 μm in diameter at its widest part. Up to three midventral subneural glands in XIII–XV, 85–90 μm , 90–140 μm and 70–100 μm long, respectively; glands in XIII and XIV not observed in all specimens.

Details of holotype. Length 3.5 mm (amputated specimen), first 15 segments 2.7 mm long, width at clitellum 0.5 mm. More than 20 segments. Dorsal bundles with 3–5, chaetae anterior to clitellum, 3–4 chaetae in postclitellar segments. Ventral bundles with 4–7 chaetae anterior to clitellum, 3–5 chaetae posteriorly. Longest chaetae about 60 μm long and about 2.5 μm wide.

Coelomocytes about 20 μm long.

Sperm funnels about 155 μm long and 160 μm . Vasa deferentia about 7 μm wide. Penial bulbs 145 μm in diameter. Four mature eggs present.

Spermathecae (Fig. 17C) 120 μm long, 80 μm wide at widest part of ampulla. Gland cells surrounding ectal pore 155 μm in diameter at its widest part. Three midventral subneural glands in XIII–XV, 85 μm , 105 μm and 85 μm long, respectively.

Geographical distribution. Genetically identified from Norway and Sweden. Also reported from Denmark and Russia (White Sea).

Remarks. The new species corresponds well to the description of *Lumbricillus* cf. *helgolandicus* (Michaelsen, 1927) by Nielsen and Christensen (1959), which is why this name was used in the molecular study by Klinth et al. (2017). However, Nielsen and Christensen noted several differences in the morphology of their specimens in comparison to the extended description of *L. helgolandicus* given later by Michaelsen (1934), the most important being the morphology of the spermathecae and the sperm funnels. The spermathecal ampulla was interpreted by Michaelsen as being filled with an irregular mass of spermatozoa. Von Bülow (1957) instead redrew the spermathecae as having a distinct circle of spermatozoa which also corresponds to the interpretation by Nielsen and Christensen and what we observed in this study. Furthermore, Michaelsen originally described the sperm funnels as 12 times longer than wide. Nielsen and Christensen, on the other hand, found the funnels to be only 2–3 times longer than wide, which corresponds better to the ratio measured in our material. von Bülow, 1957, unfortunately did not comment on the length/width ratio of the funnels.

These circumstances prompted re-examination of the last remaining syntype of *Pachydriilus helgolandicus* from Michaelsen's collection in the Zoological Museum in Hamburg (see description of that material below). We found that the sperm funnels were more than 4 times longer than wide, compared to his reported 12 times. This difference could be explained by Michaelsen having examined live material, whereas the syntype that we studied had been fixed (contracted) in formalin or alcohol, shortening the sperm funnels. Furthermore, we might have underestimated the true length of the sperm funnels due to the difficulties with measuring folded organs in mounted material. Regardless, compared to our material of "*L. cf. helgolandicus*", here described as *L. scandicus* sp. n., the sperm funnels of *L. helgolandicus* sensu stricto clearly have a higher length/width ratio.

The spermathecae of *L. helgolandicus* are similar to those of *L. scandicus* in having a distinct ampulla and a very large ectal gland. However, in *L. helgolandicus*, the spermatheca contains sperm that are arranged in an irregular mass, and it has a very distinct musculature covering the ectal duct (possibly made more apparent by the aging of the material), whereas the spermatheca of *L. scandicus* has sperm arranged in a more circular manner and only weakly defined musculature covering the ectal duct.

Lumbricillus helgolandicus is larger than *L. scandicus* and has generally larger internal organs. It also has fewer chaetae per bundle, no more than 5 in preclitellar, and 2–3 in postclitellar bundles, whereas *L. scandicus* has up to 7 chaetae in preclitellar, and up to 6 in postclitellar bundles.

Nielsen and Christensen (1959) examined specimens that seem to have been larger than ours and closer to *L. helgolandicus* in size. However, like our material, they had sperm funnels that were not much longer than wide, more chaetae per bundle and spermathecae with sperm arranged in a circular manner. Similarly, the material that von Bülow (1957) referred to as *L. helgolandicus* also had more chaetae per bundle than Michaelsen's worm and had spermathecae with sperm arranged in a circular manner.

Based on our assessment of the syntype from Helgoland, we conclude that our Scandinavian material is not conspecific with *L. helgolandicus* (Michaelsen, 1927), and

instead deserves to be treated as a new species (*L. scandicus*). Furthermore, we conclude that *L. helgolandicus* sensu von Bülow 1957 and *L. cf. helgolandicus* sensu Nielsen and Christensen 1959 are identical to *L. scandicus*.

Lumbricillus scandicus was genetically found as sister to the *L. lineatus* group (Fig. 1).

***Lumbricillus helgolandicus* (Michaelsen, 1927)**

Fig. 18

Pachydrilus helgolandicus Michaelsen, 1927: p. 12, fig. 11; Michaelsen 1934: pp. 135–141, fig. 1.

Type material. ZMH V5786 Zoologisches Museum Hamburg (Michaelsen 1927), syntype, now designated as lectotype. Type locality: Helgoland beach.

Description of lectotype. White worm. Length (fixed) 13 mm, 41 segments; first 15 segments 4.9 mm long, width at clitellum 1.1 mm. Prostomium hemispherical. Chaetae straight to slightly sigmoid (Fig. 18A). Dorsal bundles with 3–5, chaetae anterior to clitellum, 2–3 chaetae in postclitellar segments. Ventral bundles with 3–5 chaetae anterior to clitellum, 2–3 chaetae posteriorly. The worm's longest measured chaetae 70 µm long and about 7.5 µm wide. Clitellum extending over XII.

Coelomocytes numerous, about 25 µm long, round or oval. Paired pharyngeal glands present in IV, V and VI; each pair converging dorsally, with large ventral lobes. Nephridia observed in XX, XXVI–XXVII, and possibly VIII–X, about 120–130 µm long, anteseptale consisting of funnel only, duct originating posteroventrally.

Male genitalia paired (Fig. 18C). Testes originating in XI, extending forwards into X, and possibly IX, with testis sacs forming regular club-shaped lobes. Sperm funnels in XI, about 685 µm long, 205 µm wide making them about 3.5 times longer than wide. Funnels cylindrical, gradually tapering towards vasa deferentia. Vasa with irregular coils around ovaries in XII, about 17 µm wide. Penial bulbs round 230 µm in diameter. Several large oocytes but no mature eggs present.

Spermathecae (Fig. 18B) in V, club-shaped, with ampulla distinctly set apart from ectal duct. Ampulla sub-spherical, thin-walled, entally possibly communicating with oesophagus. Sperm in ampulla, aggregated into irregular mass or in circle embedded in wall of ampulla. Spermathecae 290–350 µm long, 180–190 µm wide at widest part of ampulla. Gland cells surrounding ectal pore, forming large compact mass, 235–285 µm in diameter at its widest part. Four midventral subneural glands in XIV–XVII, 225 µm, 205 µm, 145 µm and 115 µm long, respectively.

Geographical distribution. Originally described from Germany.

Remarks. We have mounted and re-examined the only remaining syntype of *L. helgolandicus* from the Zoological Museum in Hamburg and found the worm to correspond well to the descriptions of *L. helgolandicus* by Michaelsen (1927, 1934) and no doubt to represent the attached species name. However, we found some discrepancies

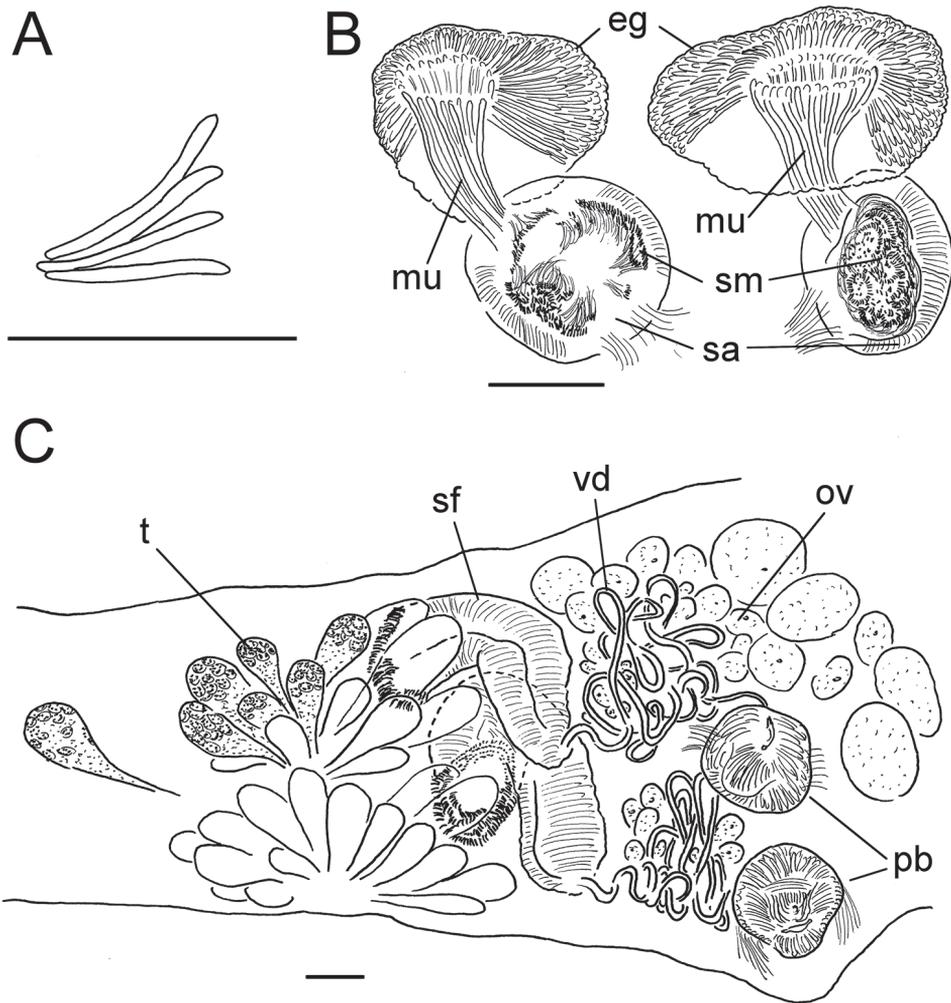


Figure 18. *Lumbricillus helgolandicus*. **A** Chaetal bundle **B** Spermathecae **C** Other genitalia. Abbreviations under general notes. Scale bars: 100 μ m.

with the published measurements of the sperm funnels (also discussed above). As the slide of the mounted specimen is of good quality and since this is the only remaining syntype of the species we designate ZMH V5786 as the lectotype of *L. helgolandicus*.

Based on morphology, *L. helgolandicus* is similar to *L. scandicus* and is probably closely related to this species. In the DNA-based phylogeny, *L. scandicus* is placed close to the *lineatus* group (Fig. 1), and it is likely that *L. helgolandicus* phylogenetically belongs there too. However, for convenience of morphological identification, both taxa are referred to the paraphyletic “*tuba*” group.

The *buelowi* group

Characteristics: Testes with testis sacs irregularly lobed and compact. Spermathecae with long duct distinctly set off from ampulla, and glands surrounding the ectal pore. Chaetae usually 2–3 per bundle; upper bundles midlateral, just above the lateral line. Penial bulbs round. Sperm funnels about as long as wide.

Lumbricillus buelowi Nielsen & Christensen, 1959

Fig. 19

Lumbricillus buelowi Nielsen & Christensen, 1959: pp. 106, figs 121–124 & 129; Erséus et al. 2010; Klinth et al. 2017.

Fridericia bulbosa; sensu von Bülow 1957: pp. 87–88, pl. XXVII, figs 5–11; nec Rosa, 1887.

Type material. Typus amissus (Nomenclatura Oligochaetologica). Type locality not precisely defined; the species was originally described from four different sites (Kalø, Femmøller, Ebeltoft and Avedøre) in Denmark (Nielsen and Christensen 1959). We did not designate a neotype as we do not have material from any of the type localities.

Material examined. SMNH 152719 (CE5224), one mature specimen from Sweden, and ZMBN 107802 (CE22293), ZMBN 107804 (CE23273), ZMBN 107805 (CE23375), ZMBN 107806 (CE23376), ZMBN 107811 (CE24678), ZMBN 107814 (CE24688) & ZMBN 107816 (CE24690), seven mature specimens from Norway. For information on specimen collection localities and GenBank accession numbers see Appendix 1.

Geographical distribution including BOLD data. Genetically identified from Norway and Sweden. Also known from Denmark and Germany. BIN-number: BOLD:ACQ3084.

Description. White to slightly pink or yellow worms. Length (fixed worms) more than 2.4–5.2 mm (amputated specimens), first 15 segments 1.7–2.4 mm long, width at clitellum 0.28–0.49 mm. More than 21–32 segments. Chaetae straight or slightly sigmoid (Fig. 19A). Lateral bundles with 2–3 chaetae anterior to clitellum, 2(3) chaetae in postclitellar segments. Ventral bundles with 2–3(4) chaetae anterior to clitellum, 2(3–4) chaetae posteriorly. Each worm's longest measured chaetae 30–55 µm long, about 5 µm wide. Clitellum extending over XII–1/2XIII. Head pore at 0/1. Epidermis with transverse rows of gland cells.

Coelomocytes numerous, 10–25 µm long, spindle-shaped, oval, round, granulated with distinct nucleus. Paired pharyngeal glands present in IV, V and VI; each pair converging dorsally (Fig. 19B). Dorsal vessel originating in XIV. Nephridia observed in VIII–X and XV–XXVIII, about 95 µm long, anteseptale funnel only, postseptale oval, tapering into posterior efferent duct. Brain slightly longer than wide, with posterior incision.

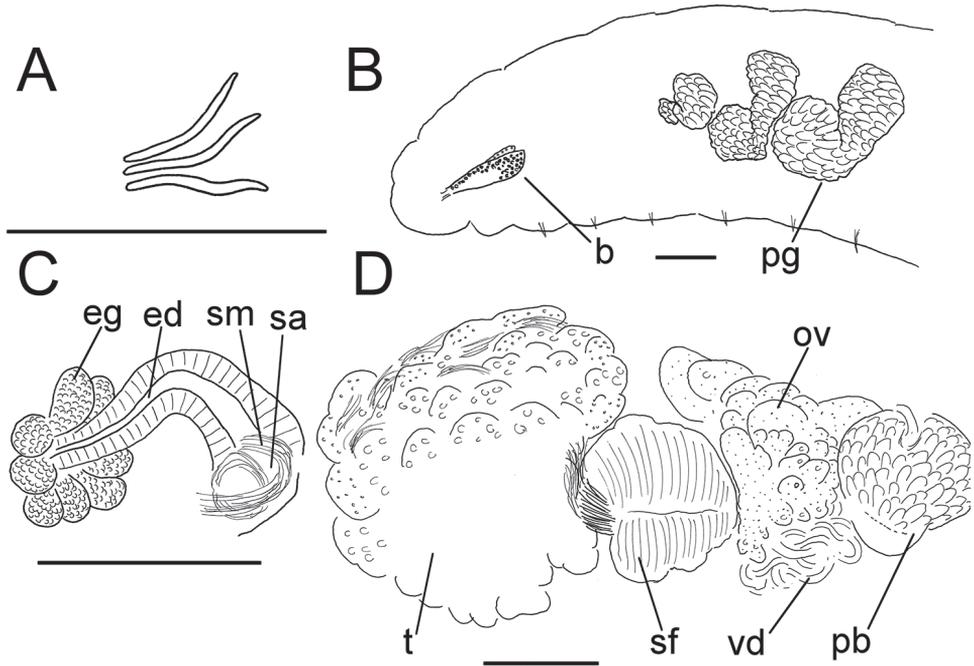


Figure 19. *Lumbricillus buelowi*. **A** Chaetal bundle **B** Anterior body **C** Spermatheca **D** Other genitalia. Abbreviations under general notes. Scale bars: 100 μ m.

Male genitalia paired (Fig. 19D). Testes originating in XI, extending forwards into X, with testis sacs covering compact mass, slightly but not regularly lobed. Sperm funnels in XI, 85–140 μ m long, 100–145 μ m wide, making them about as long as wide, funnels tapering towards vasa deferentia. Most of vasa irregularly coiled in XII, 5–10 μ m wide. Penial bulbs round, 75–110 μ m in diameter, everted in one specimen. Ovaries in XII. One to three mature eggs present at a time.

Spermathecae (Fig. 19C) in V, club-shaped, with distinct ampulla. Ectal duct narrow, more than twice the length of the ampulla, abruptly widening into ampulla. Ampulla round, entally connecting with oesophagus. Sperm in ampulla aggregated into central mass haloed by circle of spermatozoa. Spermathecae 130–160 μ m long, 45–65 μ m wide at widest part of ampulla. Gland cells surrounding ectal pore, folded, glandular body 40–90 μ m in diameter at its widest part. Up to five midventral subneural glands in XIII–XVII, 50–95 μ m, 60–120 μ m, 60–95 μ m, 50–65 μ m and 45 μ m long, respectively; glands in XVI–XVII not observed in all specimens.

Geographical distribution including BOLD data. Genetically identified from Norway and Sweden. Also known from Denmark and Germany. BIN-number: BOLD:ACQ3084.

Remarks. It is clear that the two species here identified as *L. buelowi* and *L. knoe-llneri* Nielsen & Christensen, 1959 are closely related (Klinth et al. 2017) (see also

Fig. 1), and most morphological characters such as the spermathecae, sperm funnels and penial bulbs are virtually identical between them. However, there are some general differences in our studied material: *L. buelowi* is on average larger than *L. knoellneri*, as originally noted by Nielsen and Christensen, although there is overlap between the two. *Lumbricillus buelowi* possesses 2–3 chaetae in the lateral bundles anterior of the clitellum while *L. knoellneri* possesses only 2. In their original description, Nielsen and Christensen also differentiate the two species by colour and size of coelomocytes where *L. buelowi* is red with two types of coelomocytes, one being larger than the chaetae, compared with *L. knoellneri* which is white and have only one type of coelomocytes, shorter than the chaetae. We observed only the smaller coelomocytes in both species, and as we stained the material we only have observations of the live animals; some specimens of *L. buelowi* were noted as being pinkish.

There are a number of species with descriptions similar to the ones of *L. buelowi*, and therefore also of *L. knoellneri*, such as *L. eltoni* (Stephenson, 1924), *L. muscicolus* (Stephenson, 1924) and *L. nielseni* Nurminen, 1965. All these latter three were described from Svalbard where we found specimens of *L. knoellneri* but not *L. buelowi*. Unfortunately, the two species described by Stephenson (1924) were not illustrated and the descriptions are not extensive enough for us to synonymize either of them with *L. knoellneri* (Stephenson's species would in that case hold seniority in name). Also *L. nielseni* was described too briefly (Nurminen 1965a) and the illustrated spermathecae seems slightly different from those of *L. buelowi* and *L. knoellneri*, causing us once again to avoid synonymization.

***Lumbricillus knoellneri* Nielsen & Christensen, 1959**

Fig. 20

Lumbricillus knoellneri Nielsen & Christensen, 1959: pp. 106–107, figs 125–126, 130; Klinth et al. 2017.

Fridericia bulbosa; sensu Knöllner 1935: p. 443; nec Rosa, 1887.

Type material. Typus amissus (Nomenclatura Oligochaetologica). Type locality: Ebeltoft Vig, Denmark (Nielsen and Christensen 1959). We did not designate a neotype as we do not have material from the type locality.

Material examined. SMNH 152734 (CE980) & SMNH 152735 (CE982), two mature specimens from Sweden, and ZMBN 107859 (CE19369), ZMBN 107860 (CE20761), ZMBN 107861 (CE20762), ZMBN 107863 (CE22615), ZMBN 107865 (CE23252) & ZMBN 107866 (CE23253), four mature and two immature specimens from mainland Norway and Svalbard. For information on specimen collection localities and GenBank accession numbers see Appendix 1.

Description. White to yellow worms. Length (fixed worms) more than 2.1–3.6 mm (amputated specimens), first 15 segments 1.6–1.9 mm long, width at clitellum 0.20–0.32 mm. More than 16–32 segments. Chaetae straight or slightly sig-

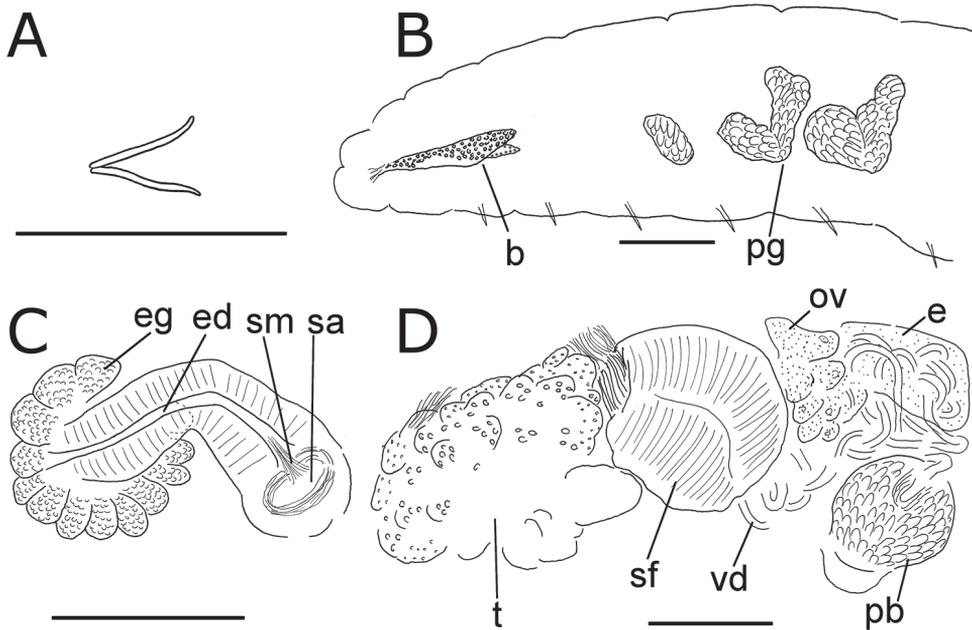


Figure 20. *Lumbricillus knoellneri*. **A** Chaetal bundle **B** Anterior body **C** Spermatheca **D** Other genitalia. Abbreviations under general notes. Scale bars: 100 μm .

moid (Fig. 20A). Lateral bundles with 2 chaetae anterior to clitellum, 2 chaetae in postclitellar segments. Ventral bundles with 2–3 chaetae anterior to clitellum, 2 chaetae posteriorly. Each worm's longest measured chaetae 25–50 μm long, about 3 μm wide. Clitellum extending over XII–1/2XIII. Head pore at 0/1. Epidermis with transverse rows of gland cells.

Coelomocytes numerous, 10–25 μm long, spindle-shaped, oval, round, granulated with distinct nucleus. Paired pharyngeal glands present in IV, V and VI (Fig. 20B). Dorsal vessel originating in XIII–XV. Nephridia observed in VIII–X and XV–XXXII, about 70 μm long, anteseptale funnel only, postseptale oval, tapering into posterior efferent duct. Brain with posterior incision.

Male genitalia paired (Fig. 20D). Testes originating in XI, extending forwards into X, with testis sacs covering compact mass, slightly lobed but not regularly arranged. Sperm funnels in XI, 100–150 μm long, 70–155 μm wide, making them about as long as wide or 1.5 times longer than wide, funnels tapering towards vasa deferentia. Most of vasa irregularly coiled in XII, 5–10 μm wide. Penial bulbs round, 70–115 μm in diameter. Ovaries in XII. One to two mature eggs present at a time.

Spermathecae (Fig. 20C) in V, club-shaped, with distinct ampulla. Ectal duct more than twice the length of the ampulla, abruptly widening into ampulla. Ampulla round, entally connecting with oesophagus. Sperm in ampulla aggregated into central mass haloed by circle of spermatozoa. Spermathecae 145–270 μm

long, 45–65 μm wide at widest part of ampulla. Gland cells surrounding ectal pore, divided in several small lobes, whole glandular body 75–100 μm in diameter at its widest part. Up to four midventral subneural glands in XIII– XVI, 50–65 μm , 35–65 μm , 35–65 μm and 35–60 μm long, respectively; glands in XVI not observed in all specimens.

Geographical distribution including BOLD data. Genetically identified from Norway (mainland and Svalbard) and Sweden. Also known from Denmark and Germany. BIN-number: BOLD:ACM5261.

Remarks. *Lumbricillus knoellneri* is described as having only 2 chaetae throughout the body but the newly studied material suggests that the preclitellar ventral bundles possess 2–3 chaetae. In fact, all of the eight studied specimens had 3 chaetae in at least 2 of the preclitellar ventral bundles, some in as many as 9. We found no pattern of this distribution and for each preclitellar ventral segment bearing chaetae (II–XI), we found representatives with either 2 or 3 chaetae. This shows how variable this trait is and could explain the difference to the description by Nielsen and Christensen. However, it could also mean that our “*L. knoellneri*” is in fact another species. Many of the internal organs of *L. knoellneri* were as long as or even slightly longer than the ones in *L. buelowi*. This in combination with a generally smaller size caused the segments of *L. knoellneri* to appear more contracted. For a further discussion see the Remarks for *L. buelowi* above.

In 1985, Kossmagk-Stephan synonymized *L. cervisiae* (which he himself had described as a new species two years earlier) and *L. christenseni* Tynen, 1966 with *L. knoellneri*. All three species are small, have only two chaetae per bundle (at least according to the original descriptions) and similarly shaped spermathecae. However, *L. christenseni* has a sperm funnel that is 7–8 times longer than wide which is significantly longer than the 1.5 times measured in *L. knoellneri*. The sperm funnel of *L. cervisiae* is 3–4 times longer than wide which is also more than that of *L. knoellneri*. Furthermore, the testis sacs of *L. cervisiae* cover several small scattered lobes and the vasa deferentia extends backwards into XIII. Finally, *L. cervisiae* appears to be more slender than *L. knoellneri* and has significantly smaller internal organs, which we were able to discern by examining the mounted original material of Kossmagk-Stephan. Therefore, we reject the idea of *L. cervisiae* and *L. christenseni* being synonyms of *L. knoellneri* and treat them as separate species.

The *arenarius* group

Characteristics: Testes with testis sacs irregularly lobed. Spermathecae with short gradually widening duct, which is difficult to distinguish from ampulla, and glands surrounding the ectal pore. Chaetae usually 2–3 or more per bundle; upper bundles mid-lateral, just above the lateral line. Penial bulbs round or bilobed. Sperm funnels three to ten times longer than wide.

***Lumbricillus arenarius* (Michaelsen, 1889)**

Fig. 21

Enchytraeus arenarius Michaelsen, 1889: pp. 12–14, figs 5a–d.*Marionina arenaria*; Michaelsen 1900: pp. 74–75.*Enchytraeoides arenarius*; Ude 1929: pp. 62–63; von Bülow 1957: p. 84; Knöllner 1935: pp. 437–438, figs 7–8.*Lumbricillus arenarius*; Nielsen and Christensen 1959: pp. 107–108, figs 127–128; Rota and Healy 1999: pp. 53–54; Erséus et al. 1999; Erséus et al. 2010; Klinth et al. 2017.*Lumbricillus magdalenae* Nurminen, 1965: pp. 6–7, figs 2e–g.

Type material. Typus amissus (Nomenclatura Oligochaetologica). Type locality: Elbe River, Hamburg, Germany (Michaelsen 1889). We did not designate a neotype as we do not have material from the type locality.

Material examined. SMNH 152716 (CE1001), one mature specimen from Sweden, and ZMBN 107784 (CE8474), ZMBN 107787 (CE20748), ZMBN 107788 (CE20749) & ZMBN 107789 (CE20750), four mature specimens from Norway. For information on specimen collection localities and GenBank accession numbers see Appendix 1.

Description. White to yellow worms. Length (fixed worms) more than 5.0–8.6 mm (amputated specimens), first 15 segments 3.5–4.0 mm long, width at clitellum 0.31–0.51 mm. More than 19–35 segments. Chaetae straight or slightly sigmoid (Fig. 21A). Lateral bundles with 2–3 chaetae anterior to clitellum, 2 chaetae in postclitellar segments. Ventral bundles with 2–3(4) chaetae anterior to clitellum, 2–3 chaetae posteriorly. Each worm's longest measured chaetae 40–70 µm long, about 5 µm wide. Clitellum extending over XII–1/2XIII, in some covering all of XIII. Head pore at 0/1. Epidermis with transverse rows of gland cells.

Coelomocytes numerous, 20–50 µm long, spindle-shaped, oval, round, granulated with distinct nucleus, some with distally hooked ends. Paired pharyngeal glands present in IV, V and VI (Fig. 21B). Dorsal vessel originating in XIII. Nephridia observed in XV–XVI and XX–XXV, 105–145 µm long, anteseptale funnel only, postseptale oval, tapering into efferent duct. Brain with posterior incision.

Male genitalia paired (Fig. 21D). Testes originating in XI, extending forwards into X, with testis sacs covering mass of rather large irregularly arranged lobes. Sperm funnels in XI, in some specimens extending back into XII, 375–975 µm long, 55–103 µm wide, making them 6–13 times longer than wide, funnels tapering towards vasa deferentia. Most of vasa irregularly coiled in XII, in one specimen extending back into XIV, 5–10 µm wide. Penial bulbs round, 110–140 µm in diameter. Ovaries in XII. One to six mature eggs present at a time.

Spermathecae (Fig. 21C) in V, pouch-shaped. Ectal duct longer than and gradually widening into ampulla. Ampulla oval or round, entally connecting with oesophagus. Irregular mass of sperm aggregated in ampulla. Spermathecae 100–255 µm long, 50–115 µm wide at widest part of ampulla. Gland cells surrounding ectal

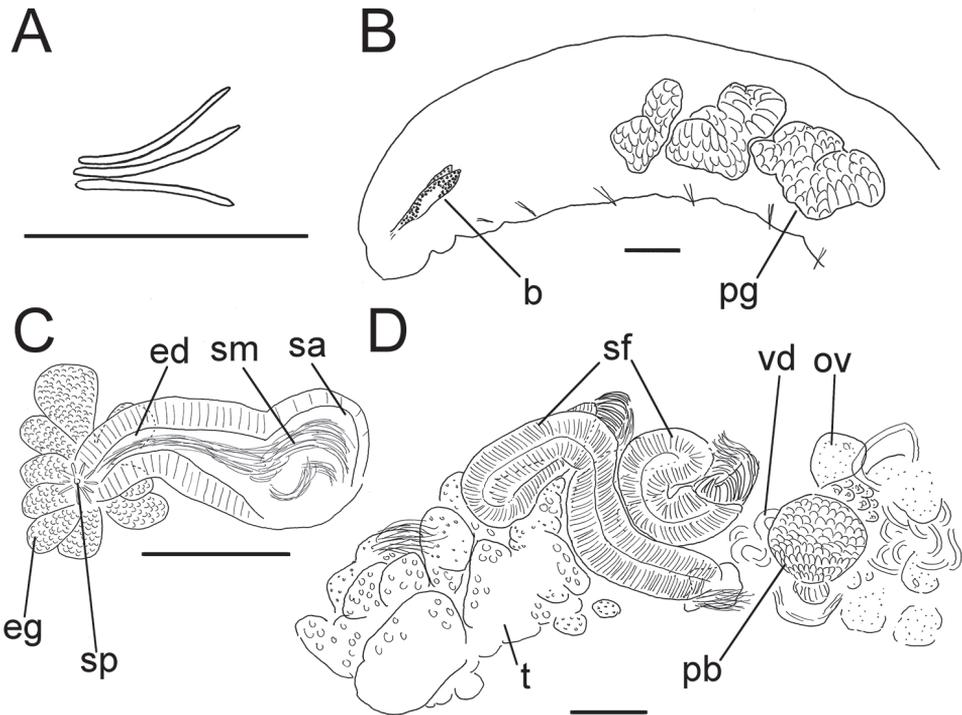


Figure 21. *Lumbricillus arenarius*. **A** Chaetal bundle **B** Anterior body **C** Spermatheca **D** Other genitalia. Abbreviations under general notes. Scale bars: 100 μ m.

pore, divided into several flaps, whole glandular body 75–135 μ m in diameter at its widest part. Up to four midventral subneural glands in XIII–XVI, 75–110 μ m, 90–115 μ m, 75–85 μ m and 95 μ m long, respectively; glands in XVI not observed in all specimens.

Geographical distribution including BOLD data. Genetically identified from Norway (mainland and Svalbard) and Sweden. Also reported from Denmark, Canada, Germany, Greenland, Iceland, Ireland, Wales and North–Western Australia (Rota and Healy 1999). BIN-number: BOLD:AAT8953.

Remarks. The original description by Michaelsen (1889) was later amended by Knöllner (1935) who redrew the shape of the nephridia and spermathecae, also confirmed by Nielsen and Christensen (1959). The newly examined material in this study resembles the original description in most characters but the spermathecae and nephridia are in agreement with the amended descriptions. Coelomic corpuscles were found with hooked ends which seemed to bind to the internal tissue in a way that is described by Michaelsen. The testes seemed to be either an irregular compact mass or divided into separate lobes, encased in testis sacs, but these lobes were not arranged in the bunch-shape seen in the *lineatus*, *pagenstecheri* and “*tuba*” groups.

Lumbricillus arenarius is genetically closely related to *L. sp. H* and *L. dubius* (Fig. 1).

***Lumbricillus* sp. H**

Fig. 22

Lumbricillus sp. H; Klinth et al. 2017.

Material examined. ZMBN 107945 (CE23136), ZMBN 107947 (CE24967) & ZMBN 107948 (CE24968), three half mature specimens from Norway. For information on specimen collection localities and GenBank accession numbers see Appendix 1.

Description. White to orange worms. Length (fixed worms) more than 3.8–5.4 mm (amputated specimens), first 15 segments 2.0–2.8 mm long, width at clitellum 0.40–0.42 mm. More than 31–33 segments. Chaetae straight or slightly sigmoid (Fig. 22A). Lateral bundles with 2–3 chaetae anterior to clitellum, 2 chaetae in postclitellar segments. Ventral bundles with 2–3 chaetae anterior to clitellum, 2 chaetae posteriorly. Each worm's longest measured chaetae 70–75 µm long, about 5 µm wide. Clitellum extending over XII–1/2XIII. Head pore at 0/1. Epidermis with transverse rows of gland cells.

Coelomocytes numerous, 15–20 µm long, spindle-shaped, oval, round, granulated with distinct nucleus. Paired pharyngeal glands present in IV, V and VI, sometimes extending into VII; each pair converging dorsally (Fig. 22B). Dorsal vessel originating in XIII. Nephridia observed in XIII–XXVIII, 100–145 µm long, anteseptale funnel only, postseptale oval, tapering into efferent duct. Brain with posterior incision.

Male genitalia paired. Testes (Fig. 22D) originating in XI, extending forwards into X, in one specimen back into XII, with testis sacs covering mass of irregularly arranged lobes. Sperm funnels in XI, 145–170 µm long, 45–50 µm wide, making them 3–4 times longer than wide, funnels tapering towards vasa deferentia. Most of vasa irregularly coiled in XII, 10 µm wide. Penial bulbs (Fig. 22E) slightly bilobed, 85–120 µm in diameter. Ovaries in XII. Mature eggs not observed.

Spermathecae (Fig. 22C) in V, pouch-shaped. Ectal duct long, gradually widening. Ampulla not clearly set off from duct, entally connecting with oesophagus. No sperm observed. Spermathecae 125–145 µm long, 25–40 µm wide at widest part. Gland cells surrounding ectal pore, divided into several lobes, whole glandular body 35–65 µm in diameter at its widest part. Two midventral subneural glands in XV–XVI, 45–100 µm, 50–65 µm long, respectively.

Geographical distribution. Genetically identified from Norway.

Remarks. Initial comparisons found similarities between this species and *Lumbricillus westheidei* Kossmagk-Stephan, 1983, such as similar shape of spermathecae and slightly bilobed penial bulbs. However, having re-examined Kossmagk-Stephan's type material we found some important differences compared to our specimens. First, *L. westheidei* has only two chaetae per bundle, whereas our specimens have up to three chaetae in the preclitellar segments (the position of the upper bundles is identical in the two species). Second, the three pairs of pharyngeal glands are clearly separated in *L. westheidei* but in our specimens at least the first two pairs appear to have a dorsal connection. Third, the testis sacs of *L. westheidei* are much smaller than the ones we observed in our specimens. Fourth, the vasa deferentia appear to be much longer and form many more coils in segment XII in *L. westheidei* compared to our *L. sp. H*. Finally,

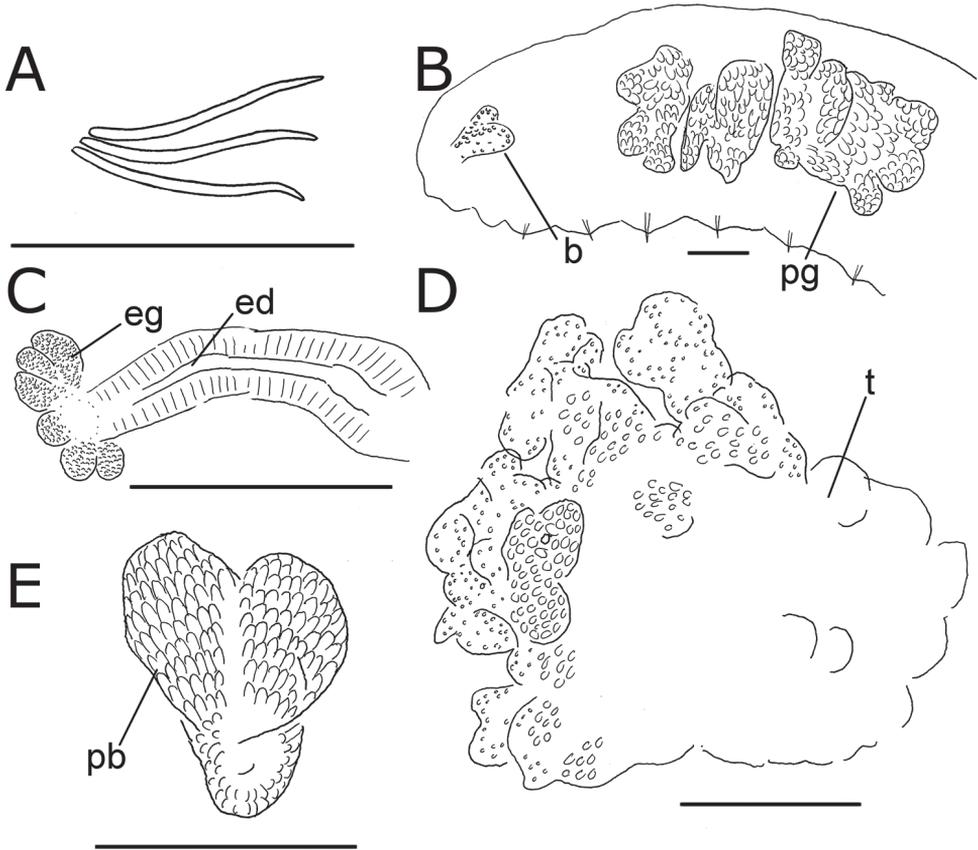


Figure 22. *Lumbricillus* sp. H. **A** Chaetal bundle **B** Anterior body **C** Spermatheca **D** Testis **E** Penial bulb. Abbreviations under general notes. Scale bars: 100 μ m.

the sperm funnels of *L. westheidei* are about 10 times longer than wide, against the 4:1 length:width ratio observed in our specimens. Unfortunately, none of our examined specimens appeared to be fully mature, as sperm were not observed either at the sperm funnels or in the spermathecae, and there were no mature eggs present. This suggests that the sperm funnels and spermathecae were not fully developed and could at maturity resemble those of *L. westheidei* more. Due to this uncertainty we cannot completely rule out that our specimens are of the same species as *L. westheidei*; however, for now we will continue to treat it as an unknown species, simply referred to as *L. sp. H*.

Since *L. westheidei* resembles, in its general morphology, our *L. sp. H*, it is important to add some notes on its generic allocation. Kossmagk-Stephan (1983) questioned the placement in *Lumbricillus* due to the undivided testis sacs. He had also observed this feature in some other “*Lumbricillus*” species, such as *L. arenarius* and *L. semifuscus*, the latter here below transferred to *Claparedrilus* gen. n. Furthermore, he noted a similarity in the morphology of the spermathecae between *L. westheidei*, *L. buelowi*, *L. knoellneri* and *L.*

codensis Lasserre, 1971. In 1985, Coates and Erséus established the new genus *Randidrilus* and designated *Lumbricillus codensis* as its type species. Because of the resemblance to the latter in the bilobed penial bulb, the long spermathecal ectal duct, the long sperm funnels and the undivided testis sac, Kossmagk-Stephan (1985) proposed in his doctoral thesis the new combination, *R. westheidei*, and since then the species was regarded as another member of *Randidrilus* (Coates, 1989; Mackei and Erséus 1997; Schmelz and Colorado 2012). However, we confirm here that, unlike other species of *Randidrilus*, *L. westheidei* has more than a single chaeta per bundle, does not lack chaetae in numerous lateral and ventral bundles and does not have an unpaired sperm sac extending backwards into postclitellar segments. Instead, *L. westheidei* resembles members of the *arenarius* group within *Lumbricillus* by having few chaetae, long sperm funnels, slightly bilobed penial bulbs and paired testis sacs that are not regularly lobed. Therefore, we transfer this species back from *Randidrilus* into *Lumbricillus*, making it *L. westheidei* once again.

Lumbricillus sp. H is genetically closely related to *L. arenarius* and *L. dubius* (Stephenson, 1911) (Fig. 1).

***Lumbricillus dubius* (Stephenson, 1911)**

Fig. 23

Enchytraeus dubius Stephenson, 1911: pp. 54–58, figs 10–12 & pl. II, figs 12–14;
Lumbricillus dubius; Nielsen and Christensen 1959: p. 96; Finogenova and Timm
1988: pp. 92–93, fig. 1; Klinth et al. 2017.

Type material. Typus amissus (Nomenclatura Oligochaetologica). Type locality: Firth of Clyde, Wemyss Bay, United Kingdom (Stephenson 1911). We did not designate a neotype as we do not have material from the type locality.

Material examined. SMNH 152726 (CE5221) & SMNH 152727 (CE5223), two mature specimens from Sweden, and ZMBN 107835 (CE22767), ZMBN 107836 (CE23370), ZMBN 107837 (CE23371), ZMBN 107839 (CE24700), ZMBN 107840 (CE24711) & ZMBN 107841 (CE24726), six mature specimens from Norway. For information on specimen collection localities and GenBank accession numbers see Appendix 1.

Description. White to yellow worms. Length (fixed worms) more than 2.1–6.1 mm (amputated specimens), first 15 segments 1.5–2.5 mm long, width at clitellum 0.32–0.55 mm. More than 20–44 segments. Chaetae straight or slightly sigmoid (Fig. 23A). All observed bundles with two chaetae. Each worm's longest measured chaetae 50–75 µm long, about 5 µm wide. Clitellum extending over XII–1/2XIII. Head pore at 0/1. Epidermis with transverse rows of gland cells.

Coelomocytes numerous, 15–30 µm long, spindle-shaped, oval, round, granulated with distinct nucleus. Paired pharyngeal glands present in IV, V and VI. Each pair converges dorsally, connection, if present at all, indistinct (Fig. 23B). Dorsal vessel originating in XIII. Nephridia observed in XVIII–XXI, 50–65 µm long, anteseptale funnel only, post-septale oval, tapering into efferent duct. Brain longer than wide, with posterior incision.

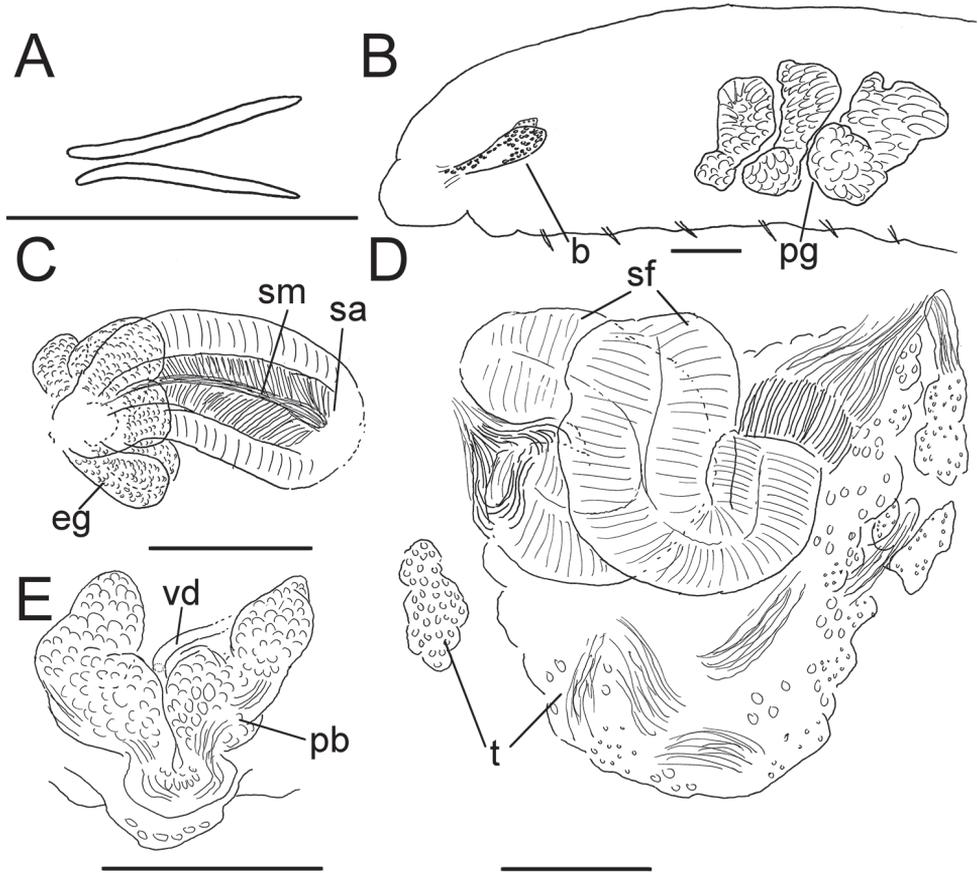


Figure 23. *Lumbricillus dubius*. **A** Chaetal bundle **B** Anterior body **C** Spermatheca **D** Male genitalia **E** Penial bulb. Abbreviations under general notes. Scale bars: 100 μ m.

Male genitalia paired. Testes (Fig. 23D) originating in XI, in some specimens extending forwards into X, with testis sacs covering mass of irregularly arranged lobes and detached fragments, fragments spreading in XI–XII. Sperm funnels (Fig. 23D) in XI, 180–390 μ m long, 70–145 μ m wide, making them 2.5–4 times longer than wide, funnels tapering towards vasa deferentia. Most of vasa irregularly coiled in XI–XII, 5–10 μ m wide. Penial bulbs (Fig. 23E), 110–190 μ m in diameter, divided into two bulbs each with an extending horn. Ovaries in XII. One to five mature eggs present at a time.

Spermathecae (Fig. 23C) in V, pouch-shaped, without distinct ampulla, gradually widening, entally connecting with oesophagus. Sperm completely occupying lumen of duct and ampulla, regularly arranged with spermatozoan heads facing the wall and tails along the duct, forming denser aggregation throughout the centre of the spermathecae. Spermathecae 95–205 μ m long, 40–100 μ m wide at widest part of ampulla. Gland cells surrounding ectal pore, divided into few flaps, whole glandular body 70–120 μ m

in diameter at its widest part. Up to two midventral subneural glands in XIV–XV, 60–80 μm , 60–65 μm long, respectively; glands in XV not observed in all specimens.

Geographical distribution including BOLD data. Genetically identified from Norway, Russia (White Sea), Sweden and the United Kingdom (Klinth et al. 2017). BIN-number: BOLD:AAU0151.

Remarks. The specimens examined match the description of *Lumbricillus dubius* by Stephenson (1911) well, but they are smaller in body size and have testes that seem to form an irregular mass rather than being made up of branches as observed by Stephenson. The clearly divided penial bulbs and the morphology of the spermathecae bear a close resemblance between our specimens and the original description. Stephenson wrote that no sperm were observed in the spermathecae, but his illustrations depicting sections of the same clearly show the unique distribution of spermatozoa with heads regularly arranged perpendicular to the spermathecal wall. It is possible that he did not recognize them as sperm, simply because of this unusual arrangement.

Lumbricillus dubius has irregularly lobed testis sacs and spermathecae that are at least superficially similar to those of *L. arenarius*. The chaetae are straight to slightly sigmoid and few in number, which further supports the close relationship with *L. arenarius* and *L. sp. H*.

Lumbricillus dubius is genetically closely related to *L. sp. H* and *L. arenarius* (Fig. 1).

***Claparedrilus* gen. n.**

<http://zoobank.org/E7A1215B-D41F-4721-89E9-226176994F0C>

Genus description/diagnosis. Prostomium hemispherical. Head pore at 0/1. Epidermis with transverse rows of gland cells. Chaetae straight to sigmoid, without nodulus, grouped into two dorsolateral and two ventrolateral bundles per segment. Oesophageal appendages absent. Pharyngeal glands in four pairs, in IV–VII, converging but not connected dorsally, some with ventral lobes, but without secondary glands. Only nucleated coelomocytes present. Dorsal vessel originating intra or in segments posterior to clitellum. Nephridia with anteseptale made up of funnel on a short stalk. Clitellum more or less covering segments XII–XIII. Testes paired, surrounded by testis sacs; the latter forming compact mass with shallow lobes irregularly arranged. Penial bulbs round and compact. Midventral subneural glands present in XIV–XV. Spermathecae in V, attached to and usually communicating with oesophagus lumen, and with crown of glands surrounding ectal part of ectal duct. Spermathecae club-shaped with ampulla distinctly set off from duct. Spermathecal diverticula absent. Marine, living in the littoral zone.

Type species. *Claparedrilus semifuscoides* sp. n.

Other species. *Claparedrilus semifuscus* (Claparède, 1961) comb. nov.

Etymology. *Clapare-* from Claparède, the original author of the species *C. semifuscus*, a poorly defined species with which the type species for this new genus (*C. semifuscoides*) has been misidentified, and *-drilus* (Latinized Greek) for worm.

Remarks. The need for this new genus arose from the difficulty of placing the type species *C. semifuscoides* (which we previously referred to as *L. semifuscus*) in the phylogeny

of the Enchytraeidae. Molecular data had previously supported that this species was not a member of *Lumbricillus* and instead closer to, but not a member of, *Globulidrilus* and *Bryodrilus* (Klinth et al. 2017; Martinsson et al. 2017). Both these genera share some traits with *Claparedrilus*, such as the shape of the spermathecae and nephridial anteseptale with small part of the nephridial body, but both have only three pairs of pharyngeal glands and are aquatic or terrestrial. The phylogenetic studies lacked representatives from several potential candidate genera of marine enchytraeids. Therefore, we compared the morphology of our species with these candidates (presented in Table 3), after which we still found support for the recognition of the new genus *Claparedrilus*. In particular, the combination of four pairs of pharyngeal glands, nephridia with a stalked funnel in the anteseptale and the presence subneural glands distinguishes this new genus.

***Claparedrilus semifuscoides* sp. n.**

<http://zoobank.org/09A6ACEC-1D21-49AA-A134-6966F14D17C8>

Fig. 24

Marionina semifusca; sensu Stephenson 1911: pp. 35–39, figs 2–3, pl. I, fig. 2.

Lumbricillus semifuscus; sensu Nielsen and Christensen 1959: p. 96; Erséus 1976: pp. 8–9, figs 5–6; Finogenova and Timm 1988: pp. 94–96, figs 2–4; Klinth et al. 2017; Martinsson et al. 2017.

? *Marionina semifusca*; sensu Southern 1907: p. 71; Southern 1909: pp. 148–149, pl. X, figs 9a–c.

? *Lumbricillus semifuscus*; Nurminen 1965a: p. 6.

Non *Pachydriulus semifuscus* Claparède, 1861: pp. 76–79, pl. II, figs 1–5.

Non *Marionina semifusca*; Michaelsen 1889: p. 29.

Non *Marionina semifusca*; Michaelsen 1900: p. 76.

Non *Enchytraeoides semifuscus*; Michaelsen 1927: p. 13, fig. 12; von Bülow 1957: p. 86.

Holotype. SMNH Type-8932 [former SMNH 152823] (CE2249), a whole-mounted voucher of a sexually mature and DNA-barcoded worm (COI barcode is KU893995 in NCBI/GenBank; Klinth et al. 2017).

Type locality. United Kingdom, Wales, Anglesey, Beaumaris, intertidal zone of beach with sand and algae, 53.2623 N, 4.0914 W, collected 15 February 2007 by M. Strand and P. Sundberg.

Paratypes. SMNH Type-8933 [former SMNH 152821] (CE2247), SMNH Type-8934 [former SMNH 152822] (CE2248), SMNH Type-8935 [former SMNH 152825] (CE2252), all whole-mounted sexually mature specimen from the type locality.

Other material examined. ZMBN 107908 (CE23750) & ZMBN 107912 (CE24657), one mature and one half mature specimen from Norway. For information on specimen collection localities and GenBank accession numbers see Appendix 1.

Etymology. Named after its similarity to *Claparedrilus semifuscus*, which it has previously been confused with and misidentified as.

Table 3. A comparison of characters distinguishing *Claparedrilus* gen. n. from other marine enchytraeid taxa. Traits of particular importance highlighted in boldface. *Coded according to Rota et al (2008); see differing interpretation in Schmelz and Collado (2008). ** One species (*Randidrilus quadrithecatus* Coates & Erséus, 1985) with two pairs of spermathecae, and four pairs of pharyngeal glands distributed from IV–VII.

Genus	Chaetal shape Upper bundles	Brain posterior	Pharyngeal glands	Coelomocytes	Gut appendages	Nephridial anteseptal	Blood vessel End/Origin	Testes	Subneural glands	Penial bulb	Spermathecal ampulla
<i>Claparedrilus</i>	Slightly sigmoid dorsolateral	Indented	Dorsally free; With ventral lobes; 4 pairs	Nucleated	No.	Funnel on a short thin stalk	Peristomial/ XIII	Compact With seminal vesicles	Yes	Compact	No diverticula
<i>Christensenidrilus blocki</i> (Dózsa- Farkas & Convey, 1997)	Sigmoid dorsolateral	Slightly indented	Dorsally free; With secondary lobes; 3 pairs	Anucleate	No	Funnel and some coils	?/ XIII	Compact With seminal vesicles	No	Compact	No diverticula
<i>Lumbricillus</i> Ørsted, 1844	Straight to sigmoid Dorso- or Midlateral	Indented	Dorsally free or fused; With ventral lobes; 3 pairs	Nucleated	No	Funnel only	Peristomial/ XIII-XV	Reg. or irreg- lobed With testis sacs	Yes or No	Compact, rarely bilobed	No diverticula
<i>Marionina georgiana</i> (Michaelsen, 1888)	Sigmoid dorsolateral	Indented	Dorsally free; No ventral lobes; 3 pairs	Nucleated	No	Funnel only	Peristomial/ XIII	Compact With seminal vesicles	No*	Small*	No diverticula
<i>Randidrilus</i> Coates & Erséus, 1985	Slightly curved Absent	Deeply indented	Dorsally fused With ventral lobes; 3–4 pairs**	Nucleated	No	Funnel only	Peristomial/ XX-XXIII	Compact With sperm sacs	No	Bilobed	No diverticula
<i>Stephensoniella</i> Černovítov, 1934	Str. or slightly sigmoid Midlateral	Slightly indented	Dorsally fused With ventral lobes; 3 pairs	Nucleated	No	Funnel only	Peristomial/ XII-XXIII	Compact With seminal vesicles	No	Compact	Diverticulate

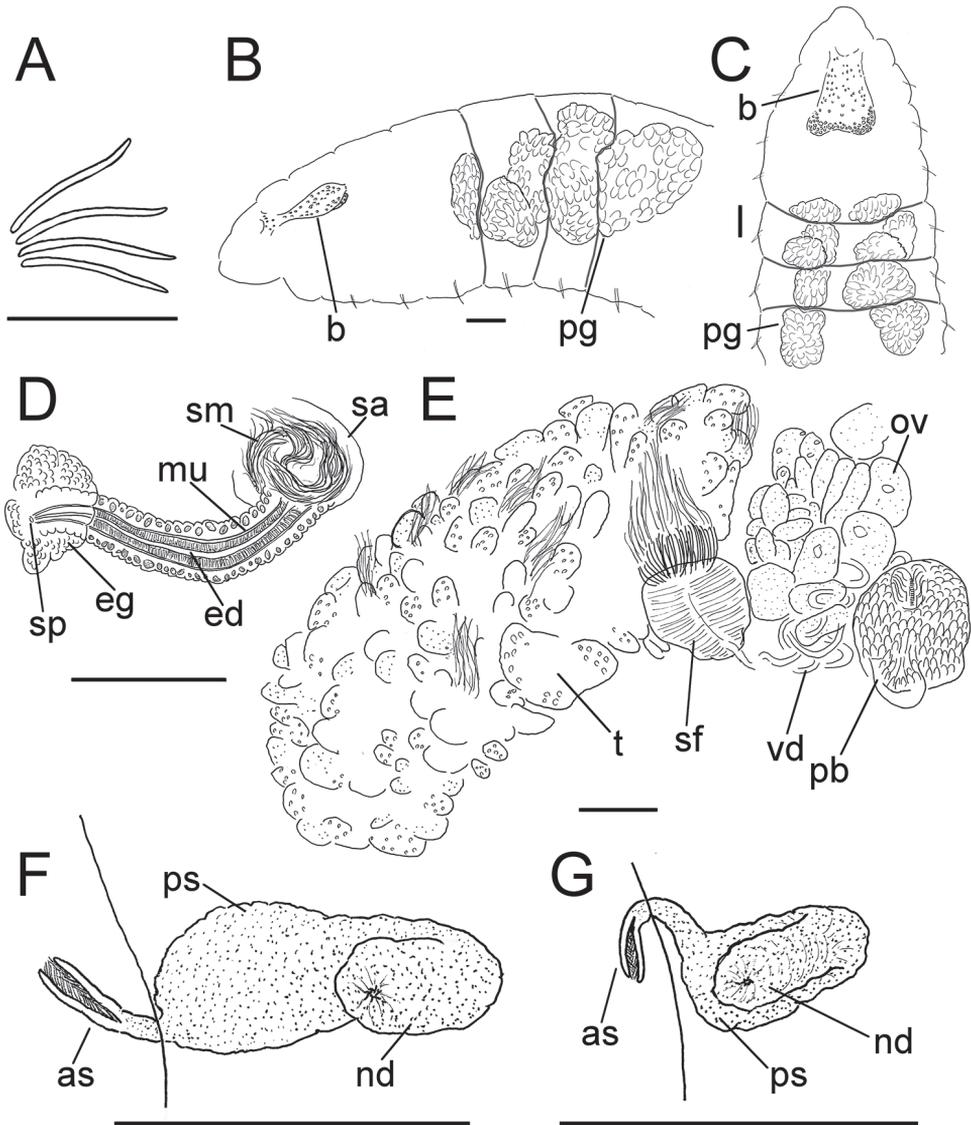


Figure 24. *Claparedrilus semifuscoides* sp. n. **A** Chaetal bundle **B** Anterior body **C** Anterior body dorsal view **D** Spermatheca **E** Other genitalia. **F** Nephridium from XIV **G** Nephridium from XXIX in another individual. Abbreviations under general notes. Scale bars: 100 μ m.

Diagnosis. This species can be distinguished from *C. semifuscus* by the size of the penial bulbs. In *C. semifuscus*, the bulbs are much larger than the sperm funnels, whereas in *C. semifuscoides* they are of about the same size as the funnels or smaller.

Description. White, grey to pinkish worms. Length (fixed worms) more than 4.0–7.3 mm (amputated specimens), first 15 segments 2.1–3.4 mm long, width at

clitellum 0.54–0.69 mm. More than 22–45 segments. Chaetae sigmoid or straight (Fig. 24A). Dorsal bundles with 2–5(6) chaetae anterior to clitellum, 2–5(6) chaetae in postclitellar segments. Ventral bundles with 3–6 chaetae anterior to clitellum, 2–5 chaetae posteriorly. Each worm's longest measured chaetae 85–115 μm long, about 5–8 μm wide. Clitellum extending over XII–1/2XIII, sometimes XIII. Head pore at 0/1. Epidermis with transverse rows of gland cells.

Coelomocytes numerous, 10–20 μm long, spindle-shaped, oval, round, granulated with distinct nucleus. Paired pharyngeal glands 4 pairs, in IV, V, VI and VII, respectively; each pair converging but not connected dorsally (Figs 24B–C), pair in IV with dorsal lobes only, pair in V with both dorsal and ventral lobes, pairs in VI and VII large and compact, but dorsal lobes difficult to distinguish from potential ventral ones. Dorsal vessel originating in XIII. Nephridia (Figs 24F–G) observed in VI–VIII and XIV and onwards, 65–130 μm long, with various shapes, anteseptale with funnel on a thin stalk, postseptale oval, tapering into efferent duct which seems to originate either terminally or from posterior of the midventral of the postseptale (compare Figs 24F–G). Brain with posterior incision.

Male genitalia paired (Fig. 24E). Testes originating in XI, with testis sacs enclosing compact sperm mass with numerous inconspicuous, irregularly arranged lobes, extending forwards into X, in some specimens extending into IX and XII. Sperm funnels in XI, 125–160 μm long, 110–145 μm wide, making them 1–1.5 times longer than wide, funnels tapering towards vasa deferentia. Most of vasa irregularly coiled in XII, 10–15 μm wide. Penial bulbs round, 140–155 μm in diameter. Ovaries in XII. Two to five mature eggs present at a time.

Spermathecae (Fig. 24D) in V, club-shaped, with distinct ampulla. Ectal pore mid-lateral. Ectal duct seemingly divided into two zones by intermediary layer of musculature. The outer zone, or coelomic lining, covering muscular layer, containing large, clearly defined nuclei. The inner zone, which is the epithelium and cuticle, lining muscular layer, appearing to be made up by numerous fine lines (perpendicular to the duct axis); these lines possibly epithelial cells or their nuclei, or microvilli crossing the cuticle. Duct twice as long as ampulla, abruptly widening into ampulla. Ampulla round, entally connecting with oesophagus, and containing irregular mass of sperm in postcopulatory specimens. Spermathecae 240–270 μm long, 60–110 μm wide at widest part (the ampullae). Gland cells surrounding ectal duct near spermathecal pore, forming compact mass, 50–105 μm in diameter at its widest part. Two midventral subneural glands in XIV–XV, 40–100 μm , 70–85 μm long, respectively.

Geographical distribution. Genetically identified from Norway and the United Kingdom. Also known (by morphology) from Iceland (Erséus 1976) and Sweden (Erséus 1977).

Remarks. In 1861, Claparède described *Pachydriilus semifuscus* from the Hebrides in Scotland. Due to its unusual and confusing morphology, this species has been moved around among some enchytraeid genera. It was transferred to *Marionina* (Michaelsen 1900), then to *Enchytraeoides* (Michaelsen 1927), and finally to *Lumbricillus* (Nielsen and Christensen 1959). The original description focused almost entirely on the reproductive organs and noted sperm funnels about 1.5 times longer than wide, spermathecae with

a long thin duct and clearly separated ampulla, nephridia with anteseptales made up of funnels only, and large kidney-shaped penial bulbs. Southern (1909), studying material from Dublin Bay (Ireland) and Edinburgh (Scotland), added that his specimens had 4–5 chaetae per bundle, a concave posterior of the brain, five pairs of pharyngeal glands in IV–VII (two of them in V), but with cylindrical rather than kidney shaped penial bulbs. Stephenson (1911) also recorded this species from Scotland but then increased the number of chaetae to 4–8 per bundle. He agreed with Southern's description of the pharyngeal glands but questioned the shape of the penial bulbs, which he found to be spherical and not unusually large, compared to the descriptions by Claparède and Southern. In 1976, Erséus described the species from Iceland, also with pharyngeal glands in IV–VII, but with fewer chaetae per bundle and with anteseptales of the nephridia made up of a few coils as well as the funnels. Having studied our material, which is partly from Wales, we are confident that we have the same species as the one studied by Stephenson, Erséus, and possibly Southern, but that this (new) species is different from the original *Pachydriilus semifuscus*. Considering the way that it has been misidentified throughout history, we have named it *semifuscoïdes* and, at the same time, established a new genus for it called *Claparedrilus*. However, based on the similarities in the spermathecae and nephridia, we have decided to also transfer *L. semifuscus* into this genus, making it *C. semifuscus* (Claparède, 1861) comb. nov.

Claparedrilus semifuscoïdes can be separated from *C. semifuscus* by the size of the penial bulbs, where the former species have bulbs about the same size as the sperm funnels (about 150 µm in diameter) whereas the latter have bulbs larger than the funnels; they are 400–500 µm long. The nephridium illustrated by Claparède is reminiscent of what we observed (Fig. 24F–G), although our specimens seem to have the septa further back in relation to the funnel, making the funnel appear with a thin stalk, and with the efferent duct originating much further back on the postseptale. Unfortunately, Claparède did not mention the number of chaetae, subneural glands, or pharyngeal glands for his species, which makes its placement into the new genus *Claparedrilus* a bit tentative. This, and the fact that we have no genetic information for *C. semifuscus*, are the reasons why we designated the new taxon, *C. semifuscoïdes*, as the type species of the new genus.

Our specimens of *C. semifuscoïdes* are smaller than the ones described by Stephenson as *M. semifusca*, and they possess fewer chaetae, but we still believe that they belong to the same species. Stephenson remarks that (1) the nephridia can be found from V, (2) the anteseptale is made up of funnel only, and (3) the efferent duct extends backwards towards the pore, not forwards as illustrated by Claparède for *C. semifuscus*. We found nephridia from VI (possibly not finding any in V because they were obscured by the pharyngeal glands) and observed that the anteseptale consists of a funnel on a thin stalk. As this character was difficult to see and because there is no true nephridial tissue anterior to the septa this could still have been interpreted by Stephenson as a funnel only. We found that the efferent duct extended forward towards the pore which is more in agreement with Claparède's illustration of *C. semifuscus* than what Stephenson noted, but the interpretation of this character may differ as the animal extends or contracts. Finally, Stephenson stated that the efferent duct originates well in front of the middle of the postseptale, whereas we observed it originating behind the middle or even from

the posterior end. However, Stephenson also noted that this was not apparent in living specimens and only became clear from sections, which we have not studied.

Our specimens of *C. semifuscoides* also largely agree with Southern's account of *M. semifusca* except for his description of the cylindrical penial bulbs. It is possible that the bulbs he studied were everted (as illustrated for *L. pagenstecheri* A in the present study; Fig. 14), which may have given the impression of them being cylindrical rather than spherical. Unfortunately, Southern did not mention the exact size of the bulbs or their size in relation to that of the sperm funnels, which makes us unable to confidently conclude that his species is the same as ours.

The species reported as *L. semifuscus* from Iceland (Erséus 1976) is probably the same as our *C. semifuscoides*, as Erséus noted the four pairs of pharyngeal glands and an anteseptale with more than just a funnel. From his sectioned material he stated that the anteseptal portion was made up of a few coils of the nephridial canal in addition to the funnel, something we could not make out in our whole-mounted material. Another illustrated nephridium that resembles the one in our species was provided by Finogenova and Timm (1988) who reported *L. semifuscus* from the White Sea (Russia). Their description only differs from that of *C. semifuscoides* in reporting three pairs of pharyngeal glands, with the third pair extending into VII, but this could be a misinterpretation of a fourth pair. As we have not examined their material, we cannot be certain that this is the case, but we find it highly probable that they actually were describing *C. semifuscoides*. Finally, we are not certain about the identity of the species "*Lumbricillus semifuscus*" that Nurminen (1965a) reported from Spitsbergen (Svalbard), as he mentions sperm funnels "considerably longer than 1.5 times the width".

Compared to the species of *Lumbricillus*, i.e., the genus in which we previously placed this species (and erroneously referred to it as *L. semifuscus*), *C. semifuscoides* can be distinguished mainly by its four pairs of pharyngeal glands, the stalked nephridial funnel, and the irregularly lobed testes.

Discussion

General comments on *Lumbricillus* taxonomy

Klinth et al.'s (2017) molecular assessment of *Lumbricillus* was a starting point for the present taxonomic study of the genus, which also has taken the species morphology into account. The *lineatus*, *pagenstecheri*, *buelowi* and *arenarius* species groups, which are monophyletic according to Klinth et al. are also supported by consistencies in the morphological characters (Fig. 1, Table 1). The fifth, but non-monophyletic, "*tuba*" group appears morphologically coherent too. In Table 1, 65 additional species of *Lumbricillus* not studied herein, but with some exceptions regarded as valid by Schmelz and Collado (2012), are tentatively classified into these five groups after considering their original descriptions. It is likely that the placement of many of them will be challenged in the future after molecular and morphological examination, and that some of them will even prove to represent lineages of *Lumbricillus* not covered by our sample of care-

fully studied taxa. Finally, in Table 1, yet five other species with uncertain affinities are listed. The long needed re-assessment of this large genus has just begun.

Diagnosing and delimiting *Lumbricillus* are problematic, as one of its most striking features, the bunch-like arrangement of the lobed testis sacs, is not shared by all species in the genus. This character appears to be a synapomorphy of the *lineatus*, *pagenstecheri* and “*tuba*” groups, which together make up a monophyletic clade, but excludes the *buelowi* and *arenarius* groups, which have unlobed or irregularly lobed testis sacs (Fig. 1). The *buelowi* group has been supported as the sister to the *lineatus*, *pagenstecheri* and “*tuba*” groups, sharing most characters except for the bunch-like arrangement of the testis sacs. The two species in this group studied (*L. buelowi* and *L. knoellneri*) are very small, and it seems that each of their testis sacs comprises a single large lobe, or possibly numerous shallow lobes. However, body size and number of testis lobes do not seem to be functionally correlated because there are other small *Lumbricillus* species, such as *L. pumilio* within the *lineatus* group, which despite their small size have testes with bunch-like arrangement.

Klinth et al. (2017) discussed the possibility of splitting off the *arenarius* group as a separate genus, especially as this group earlier had been suggested as the sister to *Grania* (Erséus et al. 2010). However, the most reliable phylogenetic topology recovered by Klinth et al. (2017) still favored the *arenarius* group as sister to the remaining *Lumbricillus*. Having studied the morphology of the species included in the *arenarius* group we conclude that they resemble *Grania* in some morphological characters, such as non-sigmoid chaetae and few chaetae per bundle. However, in most other characters, first of all the organization of sperm in the spermathecae, *Grania* is clearly different from the *arenarius* group. Furthermore, the *arenarius* group has testes encased in testis sacs, which is only found in *Lumbricillus* and *Enchytraeus* (Stephenson 1930, Tynen et al. 1991), and now also in *Claparedrilus* (present study). Therefore, we propose to keep the three species of the *arenarius* group within *Lumbricillus*, thereby retaining the broad morphological definition of the genus. The different location of the upper chaetal bundles in the *arenarius* and *buelowi* lineages as compared to the other *Lumbricillus* species may simply reflect their adaptation to a mineral, sandy bottom rather than to a loose, water-saturated, organic-rich substrate (for a discussion on this topic see Rota 2001).

Comments on *Enchytraeoides*

Before we came to the conclusion that the *arenarius* group should remain within *Lumbricillus*, we explored the possibility that it could be treated as a separate genus. Searching the taxonomic literature for possible candidate genera we found *Enchytraeoides*, in which *L. arenarius* had previously been placed by some authors (Ude 1929, Knöllner 1935, von Bülow 1957). Due to the similarity in morphology between *Enchytraeoides* and the *arenarius* group, it is important to determine the proper status of *Enchytraeoides* in relation to *Lumbricillus*.

It is difficult to establish whether *Pachydriilus enchytraeoides* Saint-Loup, 1885 is the same species as *Enchytraeoides marioni* Roule, 1888, but through personal communications with Roule, Delphy (1920) was persuaded that the former had studied the same

species, a species that Delphy pointed out should therefore be named *Enchytraeoides enchytraeoides* (more on this in Rota et al. 2008). This taxon, which was described from Marseille, resembles the *arenarius* group in some traits; mainly the irregularly lobed testis sacs, sperm funnels that are several times longer than wide, and spermathecae with what appears to be gradually widening ducts that are difficult to distinguish from the ampulla. However, *E. enchytraeoides* was described as having two to eight chaetae per bundle, which is much more variable than the two to three chaetae per bundle in the *arenarius* group.

Roule described the penial bulbs as situated in segment XI, a trait neither seen in any *Lumbricillus* nor in any other typical enchytraeid in which the bulbs are in XII. Furthermore, there were some discrepancies in Roule's description as to the location of the spermathecae, which were described as located in segment VI, but were illustrated as in segment V. This could be explained by Roule counting the prostomium as a separate segment, but this still does not explain the placement of the penial bulbs which are also illustrated as part of segment XI. If the material was studied live without proper magnification, and the description and illustration were produced later, this might have caused a misinterpretation of the position of the penial bulbs. However, given the extensive descriptions and illustrations based on such large amounts of material this seems unlikely. Therefore, the true phylogenetic placement of *Enchytraeoides* remains uncertain until newly sampled species have been examined and sequenced and for now it should remain as a junior synonym of *Lumbricillus*.

Geographical distribution and habitat

It is difficult to make any conclusions of the full geographical distribution of the species in this study, as most of our samples are from Norway and Sweden, with some also from the United Kingdom and other parts of Northern Europe. When taking into account the BOLD data and the reports by other authors it seems that some species are very common, such as *L. lineatus*, *L. rivalis* and *L. pagenstecheri* sensu lato (e.g. Timm 2005). These taxa have been found throughout Europe and in some cases also in North America and the northern Pacific region. Unfortunately, for most reports we do not have DNA sampled specimens to compare with and we are unable to ensure that it is indeed the same species as ours that have been found at some remote location. Fortunately, we could find matching barcoding sequences in the BOLD database for several species that were also collected in Canada, such as *L. lineatus*, *L. rutilus*, *L. rivalis* and *L. pagenstecheri* sensu lato, showing how widespread these species can be and supporting the idea of a partly Holarctic fauna. There are few reports of *Lumbricillus* from tropical areas (possibly due to poor sampling), but species have been reported from the Southern hemisphere, mainly from islands surrounding Antarctica. It would be interesting to compare the genetic information of these species to see if they are parts of, or lineages separate from, the species occurring in the Northern hemisphere. For the *L. pagenstecheri* complex, in which we found support for four different species, our material as well as the many descriptions of species that are very similar to this species seems to indicate that this group is more diverse in the Arctic than it is further south (see for example Shurova 1974, 1977, 1978, 1979).

As evident from Appendix I and the taxonomic literature on *Lumbricillus*, this genus is mostly associated with seashores and brackish waters, but many species (such as *L. arenarius*, *L. fennicus*, *L. knoellneri*, *L. rutilus* and *L. scandicus*) are commonly encountered also in freshwater habitats.

Future research

Having studied only about one fourth of the 80 or so described species of *Lumbricillus* with a primarily molecular approach, it is clear that a lot of taxonomic and genetic work remains to be done on this genus. Ideally, we would like to be able to link each of the described species to one or more molecular barcodes of COI, and to clearly delimit the species from each other using also nuclear genetic data (as in Klinth et al. 2017). There are several undescribed species left in this genus and we have several unnamed species that could either belong to previously described species or be new to science. A majority of the previously described species identified in our study lack types or other reference material. Thus, a future challenge is to visit type localities of such species, to determine if we truly have the same species or not. Lastly, some groups within *Lumbricillus*, such as *L. pagenstecheri* sensu lato, require some extra attention. For this complex, there are several synonymized names to examine in order to see if they match our specimens. Furthermore, there are many species described from the Pacific coast of Russia (Shurova 1974; 1977; 1978; 1979), and they all seem to share a morphology similar to that of *L. pagenstecheri*, and molecular data will be needed to determine the true number of species in this complex.

Conclusions

Having studied the morphology of the *Lumbricillus* species included in the molecular study by Klinth et al. (2017) we have found that this genus can be divided into at least five informal subgroups with differing morphology, which may become a useful backbone when resolving the taxonomy and phylogeny of other species in *Lumbricillus*. We propose to keep *L. arenarius*, *L. dubius* and *L. sp. H* within *Lumbricillus* despite their somewhat differing morphology, and their uncertain phylogeny vis-à-vis *Grania*. This means that the morphological characters defining *Lumbricillus* remain quite broad. We have described two new species of *Lumbricillus*: *L. latithecatus* sp. n., which is somewhat reminiscent of *L. lineatus*, and *L. scandicus* sp. n., which was previously thought to be the same as *L. helgolandicus*. *Lumbricillus verrucosus*, which was resurrected from junior synonymy with *L. lineatus* by Klinth et al. (2017), has been given a proper morphological re-description. *Lumbricillus lineatus* remains as the type species for the genus and a neotype has been designated. The genera *Pachydrilus* and *Enchytraeoides* remain as junior synonyms to *Lumbricillus*. Lastly, we have established *Claparedrilus* gen. n., with *C. semifuscoides* sp. n. as the type species, and transferred *Pachydrilus semifuscus* Claparède, a former member of *Lumbricillus*, into the same genus.

Acknowledgements

We would like to thank Robert Almstrand, Anna Ansebo, Nicholas Bekkouche, Mike Dempsey, Torbjørn Ekrem, Diego Fontaneto, Ton van Haaren, Karstein Hårsaker, Magnus Johansson, Sebastian Kvist, Svante Martinsson, Lisa Matamoros, Erica Mejlön (=E. Sjölin), Urban Olsson, Belén Reboreda Rivera, Malin Strand, Per Sundberg, David Templeman, Hong-Zhou Wang, Pierre De Wit and Endre Willassen, for assistance in the field and/or collecting or otherwise providing material; to Anna Ansebo, Daniel Gustafsson, Per Hjelmstedt, Magnus Johansson, Emelie Lindqvist, Maria Lindström, Svante Martinsson, Lisa Matamoros, Urban Olsson and Marcus Svensson for lab assistance; and to the Norwegian Barcode of Life (NorBOL), and to The Canadian Center of DNA Barcoding, for COI-barcoding some of our specimens. Financial support was given by The Swedish Research Council (VR), Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS), Swedish Taxonomy Initiative (ArtDatabanken, Uppsala), Norwegian Taxonomy Initiative (Artsdatabanken, Trondheim), Royal Society of Arts and Sciences in Gothenburg and Adlerbert Foundation (also Gothenburg).

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Appendix I

List of specimens used in this study, with specimen identification number, collection data, GPS coordinates (in decimal degrees), GenBank accession numbers for the COI barcode, and voucher numbers. Letters for *Lumbricillus pagenstecheri* refer to barcoding clusters. Country codes: ES=Spain, GL=Greenland, NO=Norway, SE=Sweden and UK=United Kingdom.

Species	ID	Collection locality	Coordinates		Date	Leg	Habitat	Barcode Acc. No.	Voucher No.
			Lat.	Long.					
<i>Claparedrilus semifuscoides</i> sp. n.	CE2247	UK, Wales, Anglesey, Beaumaris	53.2623	-4.0914	15-Feb-2007	M. Strand & P. Sundberg	Intertidal, sand, algae	KU893993	SMNH Type-8933
<i>Claparedrilus semifuscoides</i> sp. n.	CE2248	UK, Wales, Anglesey, Beaumaris	53.2623	-4.0914	15-Feb-2007	M. Strand & P. Sundberg	Intertidal, sand, algae	KU893994	SMNH Type-8934
<i>Claparedrilus semifuscoides</i> sp. n.	CE2249	UK, Wales, Anglesey, Beaumaris	53.2623	-4.0914	15-Feb-2007	M. Strand & P. Sundberg	Intertidal, sand, algae	KU893995	SMNH Type-8932
<i>Claparedrilus semifuscoides</i> sp. n.	CE2252	UK, Wales, Anglesey, Beaumaris	53.2623	-4.0914	15-Feb-2007	M. Strand & P. Sundberg	Intertidal, sand, algae	KU893996	SMNH Type-8935
<i>Claparedrilus semifuscoides</i> sp. n.	CE23750	NO, Nordland, Bognås, Tysfjorden	68.2248	16.0771	17-Aug-2014	C. Erséus	Upper intertidal, seaweeds, stones	KU894097	ZMBN 107908
<i>Claparedrilus semifuscoides</i> sp. n.	CE24657	NO, Nordland, Lofoten, Grimsøystraumen Strait	68.2607	14.2679	10-Sep-2014	C. Erséus & E. Willassen	Upper intertidal, coarse shelly sand	KU893989	ZMBN 107912
<i>Lumbricillus arenarius</i>	CE1001	SE, Bohuslän, Lysekil, Fiskebäckskil, Kristineberg	58.248	11.4458	16 May 2005	A. Ansebo	Intertidal shelly sand and gravel	KU893917	SMNH 152716
<i>L. arenarius</i>	CE8474	NO, Svalbard, Ny-Ålesund, Kongsfjorden	78.973	11.4443	21-Jul-2010	D. Fontaneto	Land-locked lagoon	KU894140	ZMBN 107784
<i>L. arenarius</i>	CE20748	NO, Svalbard, Spitsbergen, Nordfjorden, Tschermak	78.4903	15.3289	27-Jul-2013	K. Hårsaker	Freshwater stream, sand	KU893909	ZMBN 107787
<i>L. arenarius</i>	CE20749	NO, Svalbard, Spitsbergen, Nordfjorden, Tschermak	78.4903	15.3289	27-Jul-2013	K. Hårsaker	Freshwater stream, sand	KU893910	ZMBN 107788
<i>L. arenarius</i>	CE20750	NO, Svalbard, Spitsbergen, Nordfjorden, Tschermak	78.4903	15.3289	27-Jul-2013	K. Hårsaker	Freshwater stream, sand	KU893911	ZMBN 107789
<i>L. bueloui</i>	CE5224	SE, Bohuslän, Strömstad, Tjärnö	58.8754	11.1458	8-Oct-2008	C. Erséus	Upper intertidal, sand	KU893945	SMNH 152719
<i>L. bueloui</i>	CE22293	NO, Sogn og Fjordane, Nerøyfjorden, Bakka	60.9202	6.8674	15-May-2014	C. Erséus & M. Klinth	Lower intertidal, gravel, sand, algae	KU893941	ZMBN 107802
<i>L. bueloui</i>	CE23273	NO, Troms, Tromsø, Tromsø, Lanes	69.629	18.9207	14-Aug-2014	C. Erséus	Intertidal, sand, gravel	KU894284	ZMBN 107804
<i>L. bueloui</i>	CE23375	NO, Troms, Tromsø, Sommarøya, Gurahaugen	69.6321	18.0278	15-Aug-2014	C. Erséus	Lower intertidal, mixed mineral and shell sand	KU893942	ZMBN 107805
<i>L. bueloui</i>	CE23376	NO, Troms, Tromsø, Sommarøya, Gurahaugen	69.6321	18.0278	15-Aug-2014	C. Erséus	Lower intertidal, mixed mineral and shell sand	KU893943	ZMBN 107806
<i>L. bueloui</i>	CE24678	NO, Nordland, Lofoten, Grimsøystraumen Strait	68.2607	14.2679	10-Sep-2014	C. Erséus & E. Willassen	Upper intertidal, coarse shelly sand	KU893946	ZMBN 107811
<i>L. bueloui</i>	CE24688	NO, Nordland, Lofoten, Grimsøystraumen Strait	68.2607	14.2679	10-Sep-2014	C. Erséus & E. Willassen	Upper intertidal, coarse shelly sand	KU894208	ZMBN 107814

Species	ID	Collection locality	Coordinates		Date	Leg	Habitat	Barcode Acc. No.	Voucher No.
			Lat.	Long.					
<i>L. buelovi</i>	CE24690	NO, Nordland, Lofoten, Grimsoystraumen Strait	68.2607	14.2679	10-Sep-2014	C. Erséus & E. Willassen	Upper intertidal, coarse shelly sand	KU893947	ZMBN 107816
<i>L. dubius</i>	CE5221	SE, Bohuslän, Strömstad, Tjörnö	58.8754	11.1458	8-Oct-2008	C. Erséus	Upper intertidal, coarse sand	KU893930	SMNH 152726
<i>L. dubius</i>	CE5223	SE, Bohuslän, Strömstad, Tjörnö	58.8754	11.1458	8-Oct-2008	C. Erséus	Upper intertidal, coarse sand	KU893926	SMNH 152727
<i>L. dubius</i>	CE22767	NO, Finnmark, Mageröya, Skipsfjorden	71.0093	25.8933	12-Aug-2014	C. Erséus	Grass at high water mark, roots and sand	KU893931	ZMBN 107835
<i>L. dubius</i>	CE23370	NO, Troms, Tromsø, Sommaröya, Gurahaugen	69.6321	18.0278	15-Aug-2014	C. Erséus	Lower intertidal, mixed mineral and shell sand	KU893934	ZMBN 107836
<i>L. dubius</i>	CE23371	NO, Troms, Tromsø, Sommaröya, Gurahaugen	69.6321	18.0278	15-Aug-2014	C. Erséus	Lower intertidal, mixed mineral and shell sand	KU893932	ZMBN 107837
<i>L. dubius</i>	CE24700	NO, Nordland, Lofoten, Grimsoystraumen Strait	68.2607	14.2679	10-Sep-2014	C. Erséus & E. Willassen	Upper intertidal, coarse shelly sand	KU893928	ZMBN 107839
<i>L. dubius</i>	CE24711	NO, Nordland, Lofoten, Grimsoystraumen Strait	68.2607	14.2679	10-Sep-2014	C. Erséus & E. Willassen	Upper intertidal, coarse shelly sand	KU893929	ZMBN 107840
<i>L. dubius</i>	CE24726	NO, Nordland, Lofoten, Grimsoystraumen Strait	68.2608	14.2678	10-Sep-2014	C. Erséus & E. Willassen	Mid-intertidal, coarse shelly sand, algae	KU893927	ZMBN 107841
<i>L. fennicus</i>	CE2767	SE, Öland, Borgholm, S of Föra	56.9855	16.8764	12-Jun-2007	A. Ansebo, L. Matamoros & C. Erséus	Stream, muddy clay	KU894132	SMNH 152729
<i>L. fennicus</i>	CE2768	SE, Öland, Borgholm, S of Föra	56.9855	16.8764	12-Jun-2007	A. Ansebo, L. Matamoros & C. Erséus	Stream, muddy clay	KU894003	SMNH 152730
<i>L. fennicus</i>	CE2988	SE, Öland, Borgholm, S of Föra	56.9855	16.8764	12-Jun-2007	A. Ansebo, L. Matamoros & C. Erséus	Stream, muddy clay	KU894125	SMNH 152731
<i>L. fennicus</i>	CE6092	SE, Bohuslän, Lysekil, Färlev, Färlevsfjorden	58.4785	11.5722	27-May-2009	C. Erséus, A. Ansebo & M. Johansson	Sand, fine mud	KU894002	SMNH 152732
<i>L. haloensis</i>	CE978	SE, Torslanda, Lilleby, Sillvik	57.7467	11.755	10-Apr-2005	A. Ansebo	Intertidal sand	KU894128	SMNH 152733
<i>L. haloensis</i>	CE5412	NO, Hordaland, Bergen, Blomsterdalen	60.2689	5.2212	4-Nov-2011	P. De Wit	Intertidal, sand, rocks	KU894149	ZMBN 107842
<i>L. knoellneri</i>	CE980	SE, Västergötland, Göteborg, Fiskebäck	57.6567	11.8483	15-May-2005	A. Ansebo	Intertidal sand	KU894121	SMNH 152734
<i>L. knoellneri</i>	CE982	SE, Västergötland, Göteborg, Fiskebäck	57.6567	11.8483	15-May-2005	A. Ansebo	Intertidal sand	KU894122	SMNH 152735
<i>L. knoellneri</i>	CE19369	NO, Sogn og Fjordane, Luster Nes, Lustrafjorden	61.3864	7.369	12-Aug-2013	C. Erséus	Upper intertidal, sand	KU893940	ZMBN 107859

Species	ID	Collection locality	Coordinates		Date	Leg	Habitat	Barcode Acc. No.	Voucher No.
			Lat.	Long.					
<i>L. knoellneri</i>	CE20761	NO, Svalbard, Spitsbergen, Nordfjorden, Tschermak	78.4903	15.3289	27-Jul-2013	K. Hårsaker	Freshwater stream, sand	KU893938	ZMBN 107860
<i>L. knoellneri</i>	CE20762	NO, Svalbard, Spitsbergen, Nordfjorden, Tschermak	78.4903	15.3289	27-Jul-2013	K. Hårsaker	Freshwater stream, sand	KU893939	ZMBN 107861
<i>L. knoellneri</i>	CE22615	NO, Finnmark, Porsanger, Roddnessjøen	70.0927	25.0739	11-Aug-2014	C. Erséus	Intertidal, algae, rubble	KU893937	ZMBN 107863
<i>L. knoellneri</i>	CE23252	NO, Troms, Tromsø, Tromsø, Lanes	69.6291	18.9205	14-Aug-2014	C. Erséus	Supralittoral, seaweed, herbs growing on top	KU894131	ZMBN 107865
<i>L. knoellneri</i>	CE23253	NO, Troms, Tromsø, Tromsø, Lanes	69.6291	18.9205	14-Aug-2014	C. Erséus	Supralittoral, seaweed, herbs growing on top	KU894106	ZMBN 107866
<i>L. latithecatus</i> sp. n.	CE1976	SE, Skåne, Höganäs, Mölle	56.2576	12.5192	29-Jul-2006	C. Erséus	Decaying algae, sand	KU894053	SMNH 152830
<i>L. latithecatus</i> sp. n.	CE1979	SE, Skåne, Höganäs, Mölle	56.2576	12.5192	29-Jul-2006	C. Erséus	Decaying algae, sand	KU894055	SMNH 152831
<i>L. latithecatus</i> sp. n.	CE12041	NO, Rogaland, Sola, Ölborhamna	58.8697	5.5654	15-Jun-2012	C. Erséus	Intertidal, algae	KU894054	ZMBN 107940
<i>L. latithecatus</i> sp. n.	CE12042	NO, Rogaland, Sola, Ölborhamna	58.8697	5.5654	15-Jun-2012	C. Erséus	Intertidal, algae	KU894127	ZMBN 107941
<i>L. lineatus</i>	CE1640	SE, Bohuslän, Strömstad, Tjärnö	58.8766	11.1456	1-Sep-2004	C. Erséus	Intertidal, sand, gravel	KU894030	SMNH 152742
<i>L. lineatus</i>	CE1694	ES, Galicia, Ponedra, Illa de Arousa	42.56	-8.87	1-Apr-2006	B. Reboreda Rivera	<i>Ulva</i> compost culture	KU894118	SMNH 152744
<i>L. lineatus</i>	CE1894	SE, Öland, Mörbylånga, Skärilöv	56.4241	16.5815	10-Jun-2006	L. Matamoros	Beach, shelly sand, organic material	KU894040	SMNH Type-8931
<i>L. lineatus</i>	CE12043	NO, Rogaland, Sola, Ölborhamna	58.8697	5.5654	15-Jun-2012	C. Erséus	Intertidal, algae	KU894033	ZMBN 107872
<i>L. lineatus</i>	CE21688	NO, Telemark, Kragerø, Gunnarsholmen Island	58.8649	9.4117	12-May-2014	C. Erséus & M. Klinth	Anaerobic, sand, gravel, 0.3-0.5 m depth.	KU894181	ZMBN 107875
<i>L. lineatus</i>	CE21986	NO, Hordaland, Maurangerfjorden, Nedrehus	60.1295	6.3146	14-May-2014	C. Erséus & M. Klinth	High-water mark, grass roots with sand	KU894177	ZMBN 107878
<i>L. lineatus</i>	CE22604	NO, Finnmark, Porsanger, Roddnessjøen	70.0927	25.0739	11-Aug-2014	C. Erséus	Intertidal, algae, rubble	KU894196	ZMBN 107879
<i>L. lineatus</i>	CE22605	NO, Finnmark, Porsanger, Roddnessjøen	70.0927	25.0739	11-Aug-2014	C. Erséus	Intertidal, algae, rubble	KU894029	ZMBN 107880
<i>L. pagenstecheri</i> A	CE1896	SE, Öland, Mörbylånga, Skärilöv	56.4241	16.5815	10-Jun-2006	L. Matamoros	Beach, shelly sand, organic material	KU893986	SMNH 152766

Species	ID	Collection locality	Coordinates		Date	Leg	Habitat	Barcode Acc. No.	Voucher No.
			Lat.	Long.					
<i>L. pagenstecheri A</i>	CE1897	SE, Öland, Mörbylånga, Skärövä	56.4241	16.5815	10-Jun-2006	L. Matamoros	Beach, shelly sand, organic material	KU893987	SMNH 152767
<i>L. pagenstecheri A</i>	CE1899	SE, Öland, Mörbylånga, Skärövä	56.4241	16.5815	10-Jun-2006	L. Matamoros	Beach, shelly sand, organic material	KU893988	SMNH 152768
<i>L. pagenstecheri A</i>	CE2497	SE, St Förö, Västergötland, Göteborg, Stora Förö Island	57.6252	11.8469	2-Jun-2007	C. Erséus	Supralittoral, algae, gravel and pebbles	-	SMNH 152769
<i>L. pagenstecheri A</i>	CE2498	SE, St Förö, Västergötland, Göteborg, Stora Förö Island	57.6252	11.8469	2-Jun-2007	C. Erséus	Supralittoral, algae, gravel and pebbles	KU894141	SMNH 152770
<i>L. pagenstecheri A</i>	CE2500	SE, St Förö, Västergötland, Göteborg, Stora Förö Island	57.62512	11.8469	2-Jun-2007	C. Erséus	Supralittoral, algae, gravel and pebbles	KU893985	SMNH 152771
<i>L. pagenstecheri B</i>	CE22586	NO, Finnmark, Porsanger, Roddnessjøen	70.0927	25.0739	11-Aug-2014	C. Erséus	Intertidal, algae, rubble	KU893983	ZMBN 107890
<i>L. pagenstecheri B</i>	CE22727	NO, Finnmark, Porsanger, Olderfjorden	70.4799	25.209	12-Aug-2014	C. Erséus	Driftline of dead algae	KU893984	ZMBN 107891
<i>L. pagenstecheri C</i>	CE1699	ES, Galicia, Ponevedra, Illa de Arousa	42.56	-8.87	1-Apr-2006	B. Reboveda Rivera	<i>Ulna</i> compost culture	KU893981	SMNH 152772
<i>L. pagenstecheri C</i>	CE20718	NO, Svalbard, Spitsbergen, Wijdefjorden, Gunvorvatn	79.8186	15.6646	21-Jul-2013	K. Hårsaker & T. Ekrem	Decaying seaweed	KU893982	ZMBN 107892
<i>L. pagenstecheri D</i>	CE22728	NO, Finnmark, Porsanger, Olderfjorden	70.4799	25.209	12-Aug-2014	C. Erséus	Driftline of dead algae	KU894110	ZMBN 107893
<i>L. pagenstecheri D</i>	CE22729	NO, Finnmark, Porsanger, Olderfjorden	70.4799	25.209	12-Aug-2014	C. Erséus	Driftline of dead algae	KU894210	ZMBN 107894
<i>L. pagenstecheri D</i>	CE23482	NO, Nordland, Bjerkvik	68.5481	17.5422	15-Aug-2014	C. Erséus	Highwater line, sand	KU893980	ZMBN 107895
<i>L. pagenstecheri D</i>	SM191	GL, Disko Island, Qeqertarsuaq	69.2489	-53.5437	27-Jul-2013	S. Marttinsson	Beach, sand, algae	KU893978	SMNH 152774
<i>L. pumilio</i>	CE3346	UK, Wales, Cardiff, Newport, St. Brides	51.517	-3.000	13-Nov-2007	S. Kivist	Supralittoral peat	KU894205	SMNH 152775
<i>L. pumilio</i>	CE3347	UK, Wales, Cardiff, Newport, St. Brides	51.517	-3.000	13-Nov-2007	S. Kivist	Supralittoral peat	KU894195	SMNH 152776
<i>L. pumilio</i>	CE3427	UK, Wales, Cardiff, Newport, St. Brides	51.517	-3.000	13-Nov-2007	S. Kivist	Supralittoral peat	KU894084	SMNH 152777
<i>L. pumilio</i>	CE3428	UK, Wales, Cardiff, Newport, St. Brides	51.517	-3.000	13-Nov-2007	S. Kivist	Supralittoral peat	KU894085	SMNH 152778
<i>L. pumilio</i>	CE3430	UK, Wales, Cardiff, Newport, St. Brides	51.517	-3.000	13-Nov-2007	S. Kivist	Supralittoral peat	KU894086	SMNH 152779

Species	ID	Collection locality	Coordinates		Date	Leg	Habitat	Barcode Acc. No.	Voucher No.
			Lat.	Long.					
<i>L. pumilio</i>	CE3436	UK, Wales, Cardiff, Newport, St. Brides	51.517	-3.000	13-Nov-2007	S. Kvist	Supralittoral peat	KU894087	SMNH 152780
<i>L. pumilio</i>	CE3437	UK, Wales, Cardiff, Newport, St. Brides	51.517	-3.000	13-Nov-2007	S. Kvist	Supralittoral peat	KU894088	SMNH 152781
<i>L. rivialis</i>	CE1873	SE, Blekinge, Sölvesborg, Norje	56.1413	14.6742	7-Jun-2006	L. Matamoros	Beach, sand, clay	KU894064	SMNH 152782
<i>L. rivialis</i>	CE1874	SE, Blekinge, Karlskrona, Torhamn	56.0726	15.8402	8-Jun-2006	L. Matamoros	Beach, stones, organic material	KU894056	SMNH 152783
<i>L. rivialis</i>	CE2503	SE, St Förö, Västergötland, Göteborg, Stora Förö Island	57.6252	11.8469	2-Jun-2007	C. Erséus	Supralittoral, algae, gravel and pebbles	KU894146	SMNH 152785
<i>L. rivialis</i>	CE22596	NO, Finnmark, Porsanger, Roddnessjøen	70.0927	25.0739	11-Aug-2014	C. Erséus	Intertidal, algae, rubble	KU894103	ZMBN 107897
<i>L. rivialis</i>	CE22600	NO, Finnmark, Porsanger, Roddnessjøen	70.0927	25.0739	11-Aug-2014	C. Erséus	Intertidal, algae, rubble	KU894112	ZMBN 107898
<i>L. rivialis</i>	CE22602	NO, Finnmark, Porsanger, Roddnessjøen	70.0927	25.0739	11-Aug-2014	C. Erséus	Intertidal, algae, rubble	KU894102	ZMBN 107899
<i>L. rubidus</i>	CE2549	SE, Saltholmen, Västergötland, Göteborg, Saltholmen	57.6631	11.8516	7-Jun-2007	C. Erséus	Supralittoral, roots and brown soil	KU894094	SMNH 152792
<i>L. rubidus</i>	CE2551	SE, Saltholmen, Västergötland, Göteborg, Saltholmen	57.6631	11.8516	7-Jun-2007	C. Erséus	Supralittoral, roots and brown soil	KU894153	SMNH 152793
<i>L. rubidus</i>	CE2553	SE, Saltholmen, Västergötland, Göteborg, Saltholmen	57.6631	11.8516	7-Jun-2007	C. Erséus	Supralittoral, roots and brown soil	KU894152	SMNH 152794
<i>L. rubidus</i>	CE6105	SE, Bohuslän, Lysekil, Färlev, Färlevsfjorden	58.4765	11.576	27-May-2009	C. Erséus, A. Ansebo & M. Johansson	Sand and clay	KU894091	SMNH 152795
<i>L. rubidus</i>	CE6106	SE, Bohuslän, Lysekil, Färlev, Färlevsfjorden	58.4765	11.576	27-May-2009	C. Erséus, A. Ansebo & M. Johansson	Sand and clay	KU894092	SMNH 152796
<i>L. rubidus</i>	CE6107	SE, Bohuslän, Lysekil, Färlev, Färlevsfjorden	58.4765	11.576	27-May-2009	C. Erséus, A. Ansebo & M. Johansson	Sand and clay	KU894089	SMNH 152797
<i>L. rubidus</i>	CE6108	SE, Bohuslän, Lysekil, Färlev, Färlevsfjorden	58.4765	11.576	27-May-2009	C. Erséus, A. Ansebo & M. Johansson	Sand and clay	KU894150	SMNH 152798
<i>L. rutilis</i>	CE1887	SE, Blekinge, Karlskrona, Torhamn	56.0723	15.8402	8-Jun-2006	L. Matamoros	Organic sediment	KU894115	SMNH 152801
<i>L. rutilis</i>	CE1903	SE, Öland, Borgholm, Neptuni Åkrar	57.3346	17.0102	11-Jun-2006	L. Matamoros	Sand, shells, org. material	KU894013	SMNH 152802
<i>L. rutilis</i>	CE2510	SE, St Förö, Västergötland, Göteborg, Stora Förö Island	57.6252	11.8469	2-Jun-2007	C. Erséus	Supralittoral, algae, gravel and pebbles	KU894004	SMNH 152804

Species	ID	Collection locality	Coordinates		Date	Leg	Habitat	Barcode Acc. No.	Voucher No.
			Lat.	Long.					
<i>L. rutilus</i>	CE2937	SE, Öland, Mörbylånga, Sandbyborg	56.5536	16.6394	13-Jun-2007	A. Ansebo, L. Matamoros & C. Erséus	Seashore, sand, organic material, 0.1 m deep in sand	KU894203	SMNH 152809
<i>L. rutilus</i>	CE2939	SE, Öland, Mörbylånga, Sandbyborg	56.5536	16.6394	13-Jun-2007	A. Ansebo, L. Matamoros & C. Erséus	Seashore, sand, organic material, 0.1 m deep in sand	KU894011	SMNH 152811
<i>L. rutilus</i>	CE3060	SE, Västergötland, Göteborg, Ryaverket	57.6974	11.8928	15-Aug-2007	R. Almstrand	Sewage treatment plant	KU894006	SMNH 152813
<i>L. rutilus</i>	CE3061	SE, Västergötland, Göteborg, Ryaverket	57.6974	11.8928	15-Aug-2007	R. Almstrand	Sewage treatment plant	KU894007	SMNH 152814
<i>L. rutilus</i>	CE3502	UK, Manchester, Urmston, United Utilities, Davyhulme Wastewater Treatment Works	53.4639	-2.3741	10-Feb-2008	M. Dempsey	Biofilter (indoors)	KU894008	SMNH 152815
<i>L. rutilus</i>	CE3506	UK, Manchester, Urmston, United Utilities, Davyhulme Wastewater Treatment Works	53.4639	-2.3741	10-Feb-2008	M. Dempsey	Biofilter (indoors)	KU894126	SMNH 152816
<i>L. rutilus</i>	CE9267	SE, Gotland, Visby, Palissaderna Park	57.6346	18.284	7-Aug-2010	C. Erséus	Freshwater	KU894142	SMNH 152819
<i>L. scandiicus</i> sp. n.	CE975	SE, Torslanda, Lilleby, Sillvik	57.7467	11.755	10-Apr-2005	A. Ansebo	Intertidal sand	KU893954	SMNH 152720
<i>L. scandiicus</i> sp. n.	CE1905	SE, Öland, Borgholm, Neptuni Åkrar	57.3346	17.0102	11-Jun-2006	L. Matamoros	Sand, shells, org. material	KU893950	SMNH Type-8923
<i>L. scandiicus</i> sp. n.	CE1907	SE, Öland, Borgholm, Neptuni Åkrar	57.3346	17.0102	11-Jun-2006	L. Matamoros	Sand, shells, org. material	KU893951	SMNH Type-8925
<i>L. scandiicus</i> sp. n.	CE1915	SE, Öland, Borgholm, Ölands Norra Udde	57.3681	17.0918	11-Jun-2006	L. Matamoros	Beach, sand, stones	KU893952	SMNH 152723
<i>L. scandiicus</i> sp. n.	CE2548	SE, Saltholmen, Västergötland, Göteborg, Saltholmen	57.6631	11.8516	7-Jun-2007	C. Erséus	Supralittoral, roots and brown soil	KU893953	SMNH 152724
<i>L. scandiicus</i> sp. n.	CE2552	Göteborg, Västergötland, Göteborg, Saltholmen	57.6631	11.8516	7-Jun-2007	C. Erséus	Supralittoral, roots and brown soil	KU893955	SMNH 152725
<i>L. tuba</i>	CE22614	NO, Finnmark, Porsanger, Roddnessjøen	70.0927	25.0739	11-Aug-2014	C. Erséus	Intertidal, algae, rubble	KU894207	ZMBN 107916
<i>L. verrucosus</i>	CE968	SE, Torslanda, Lilleby, Sillvik	57.7467	11.755	10-Apr-2005	A. Ansebo	Intertidal sand	KU894068	SMNH 152826
<i>L. verrucosus</i>	CE21479	NO, Vestfold, Larvik, Jordfallen	59.0427	10.0174	12-May-2014	C. Erséus & M. Klinth	Subtidal, sand, gravel	KU894193	ZMBN 107919

Species	ID	Collection locality	Coordinates		Date	Leg	Habitat	Barcode Acc. No.	Voucher No.
			Lat.	Long.					
<i>L. verrucosus</i>	CE21486	NO, Vestfold, Larvik, Jordfållen	59.0427	10.0174	12-May-2014	C. Erséus & M. Klinth	Subtidal, sand, gravel	KU894186	ZMBN 107920
<i>L. verrucosus</i>	CE21490	NO, Vestfold, Larvik, Jordfållen	59.0427	10.0174	12-May-2014	C. Erséus & M. Klinth	Subtidal, sand, gravel	KU894184	ZMBN 107921
<i>L. verrucosus</i>	CE21494	NO, Vestfold, Larvik, Jordfållen	59.0427	10.0174	12-May-2014	C. Erséus & M. Klinth	Subtidal, sand, gravel	KU894067	ZMBN 107922
<i>L. verrucosus</i>	CE21811	NO, Vest-Agder, Lyngdal, Lene, Lenefjorden	58.1353	7.1817	13-May-2014	C. Erséus & M. Klinth	Subtidal, sulfidic gravel	KU894071	ZMBN 107924
<i>L. verrucosus</i>	CE21816	NO, Vest-Agder, Lyngdal, Lene, Lenefjorden	58.1353	7.1817	13-May-2014	C. Erséus & M. Klinth	Subtidal, sulfidic gravel	KU894114	ZMBN 107925
<i>L. verrucosus</i>	CE21821	NO, Vest-Agder, Lyngdal, Lene, Lenefjorden	58.1353	7.1817	13-May-2014	C. Erséus & M. Klinth	Subtidal, sulfidic gravel	KU894073	ZMBN 107926
<i>L. viridis</i>	CE12037	NO, Rogaland, Sola, Ölbörhamna	58.8697	5.5654	15-Jun-2012	C. Erséus	Intertidal, decomp. algae	KU893969	ZMBN 107933
<i>L. viridis</i>	CE12038	NO, Rogaland, Sola, Ölbörhamna	58.8697	5.5654	15-Jun-2012	C. Erséus	Intertidal, decomp. algae	KU893970	ZMBN 107934
<i>L. viridis</i>	CE12039	NO, Rogaland, Sola, Ölbörhamna	58.8697	5.5654	15-Jun-2012	C. Erséus	Intertidal, decomp. algae	KU893971	ZMBN 107935
<i>L. viridis</i>	CE23255	NO, Troms, Tromsø, Tromsø, Lanes	69.629	18.9207	14-Aug-2014	C. Erséus	Intertidal, sand, gravel	KU893967	ZMBN 107938
<i>L. sp. F</i>	CE2659	UK, Devon, Plymouth, River Plym	50.3757	-4.1082	20-Jul-2007	L. Matamoros	Intertidal, stones, clay	KU893997	SMNH 152832
<i>L. sp. G</i>	CE2246	UK, Wales, Anglesey, Beaumaris	53.2623	-4.0914	15-Feb-2007	M. Strand & P. Sundberg	Intertidal, sand, algae	KU894001	SMNH 152834
<i>L. sp. G</i>	CE2661	UK, Devon, Plymouth, River Plym	50.3757	-4.1082	20-Jul-2007	L. Matamoros	Intertidal, stones, clay	KU893999	SMNH 152835
<i>L. sp. G</i>	CE23373	NO, Troms, Tromsø, Sommarøya, Gurahaugen	69.6321	18.0278	15-Aug-2014	C. Erséus	Lower intertidal, mixed mineral and shell sand	KU894000	ZMBN 107942
<i>L. sp. H</i>	CE23136	NO, Troms, Rotsundselv	69.8001	20.7158	14-Aug-2014	C. Erséus	Upper intertidal, sand	KU893920	ZMBN 107945
<i>L. sp. H</i>	CE24967	NO, Nordland, Gildeskål, Kjøpstad, Holmsundsforden Bay	67.0536	14.2729	11-Sep-2014	C. Erséus & E. Willassen	Upper intertidal, rock pool, gravel, sand	KU893921	ZMBN 107947
<i>L. sp. H</i>	CE24968	NO, Nordland, Gildeskål, Kjøpstad, Holmsundsforden Bay	67.0536	14.2729	11-Sep-2014	C. Erséus & E. Willassen	Upper intertidal, rock pool, gravel, sand	KU893919	ZMBN 107948

A new species of *Tridactylogonus* Jeekel, 1982 from South Australia (Diplopoda, Polydesmida, Paradoxosomatidae)

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Academic editor: S. Golovatch | Received 14 September 2017 | Accepted 16 September 2017 | Published 28 September 2017

<http://zoobank.org/9520AF9A-9F9A-4892-B875-D39D4A4C5B25>

Citation: Mesibov R (2017) A new species of *Tridactylogonus* Jeekel, 1982 from South Australia (Diplopoda, Polydesmida, Paradoxosomatidae). ZooKeys 703: 97–107. <https://doi.org/10.3897/zookeys.703.20986>

Abstract

Tridactylogonus warrenbenensis sp. n. is described from Warrenben Conservation Park at the southern end of the Yorke Peninsula in South Australia. Like *T. obscurus* Jeekel, 1982 and *T. rugosissimus* Jeekel, 2002, the new species has prominent cellular sculpturing on the prozonites and granulose sculpturing on parts of the metazonites. Unlike its congeners and most species in the subfamily Australiosomatinae, the new species lacks a femoral process or tubercle on male leg 1.

Keywords

Diplopoda, Polydesmida, Paradoxosomatidae, South Australia, Australia

Introduction

I collected the new species described here during two recent visits to the lower Yorke Peninsula in South Australia (Fig. 1). It was the only native polydesmidan species I found in the area, much of which has been heavily colonised by the introduced Portuguese millipede *Ommatoiulus moreleti* (Lucas, 1860). It is a remarkably atypical species within the Australian Paradoxosomatidae, as it lacks a femoral process on male leg 1 and has prominent cuticular sculpturing on the prozonites and metazonites.

Materials and methods

All specimens are stored in ethanol in the South Australian Museum (SAM). Body measurements were estimated with a Nikon SMZ800 binocular dissecting microscope using an eyepiece scale. Stacks of colour images were manually generated using a Canon EOS 1000D digital SLR camera mounted on the Nikon SMZ800 fitted with a beam splitter, then focus-stacked with Zerene Stacker 1.04 software. One gonopod was cleared in 80% lactic acid, temporarily mounted in a 1:1 glycerol:water mixture and imaged using an eyepiece video camera mounted on an Amscope binocular microscope. Preliminary drawings were traced from printed copies of the images, then corrected by reference to the actual gonopod. Scanning electron microscope images were acquired digitally using a Hitachi SU-70; body parts were examined after air-drying and sputter-coating with platinum, and later returned to alcohol. Figures were composed using GIMP 2.8 software. Parts of the backgrounds of the colour photomicrographs have been edited to remove distracting highlights and artifacts.

Locality details are given with latitude and longitude in decimal degrees based on the WGS84 datum. The estimated uncertainty for a locality is the radius of a circle around the given position in metres. Abbreviations: SA = South Australia, Australia; SAM = South Australian Museum, South Australia, Australia.

Results

Order Polydesmida Pocock, 1887

Suborder Strongylosomatidea Brölemann, 1916

Family Paradoxosomatidae Daday, 1889

Subfamily Australiosomatinae Brölemann, 1916

Tribe Antichiropodini Brölemann, 1916

Genus *Tridactylogonus* Jeekel, 1982

Tridactylogonus: Jeekel 1982: 128; Shelley et al. 2000: 135; Nguyen and Sierwald 2013: 1160.

Type species. *Tridactylogonus obscurus* Jeekel, 1982, by original designation.

Other assigned species. *T. rugosissimus* Jeekel, 1982, *T. warrenbenensis* sp. n.

Tridactylogonus warrenbenensis sp. n.

<http://zoobank.org/535BAB9A-9AAC-4E74-AFED-6708BC8D301C>

Figs 1 (maps), 2, 3, 4, 5C, 5E

Holotype. Male, Warrenben Conservation Park, SA, -35.1102 137.0222 ±25 m, 30 m a.s.l., 16 August 2017, R. Mesibov and C. Arnold, open she-oak woodland, SAM OM2184.

Paratypes. 3 males, 7 females, details as for holotype, SAM OM2185-OM2194.

Other material. 1 male, 2 females, 1 juvenile, Warrenben Conservation Park, SA, -35.0926 137.0121 ±100 m, 20 m a.s.l., 3 June 2016, R. Mesibov and T. Moule, degraded she-oak woodland, SAM OM2169; 1 juvenile, same details but -35.0922 137.0464 ±100 m, 40 m a.s.l., 4 June 2016, burned she-oak and eucalypt woodland, SAM (not registered); 1 male, 2 juveniles, same locality but -35.1113 137.0184 ±25 m, 30 m a.s.l., 15 August 2017, R. Mesibov, eucalypt and tea tree woodland, SAM OM2195-OM2197; 1 juvenile, same details but -35.1125 137.0152 ±25 m, tea tree copse, SAM OM2198; 1 juvenile, same details but -35.1107 137.0122 ±25 m, degraded she-oak woodland, SAM OM2199.

Diagnosis. Differs from *T. obscurus* in having variably rugose rather than smooth metatergites, and in the anteromedial process of the gonopod telopodite being flattened rather than lanceolate. Differs from *T. rugosissimus* in having one process extending from the base of the solenomere rather than two. Differs from both *T. obscurus* and *T. rugosissimus* in lacking a femoral process or tubercle on male leg 1.

Description. Male/female approximate measurements (all adults): length ca 12/14 mm, maximum midbody width 1.1/1.3 mm. Colour in alcohol (Fig. 2) light to medium brown, lightening ventrally, with yellowish paramedian bands dorsally, the bands on the prozonite closest together at the waist (Fig. 2C). Head yellowish laterally. Antennae brown, legs pale, in both cases darkening distally.

Male with vertex bare, frons sparsely setose, clypeus moderately setose; vertigial sulcus distinct, ending just above level of antennal sockets; post-antennal groove shallow; antennal sockets separated by ca 1 socket diameter. Antennae clavate, reaching dorsally to rear of ring 2; antennomeres with relative lengths $6 > (2=3) > (4=5)$; 6 thickest. Collum (Fig. 2A) half moon-shaped, strongly convex, rear margin straight, corners rounded and slightly upturned. Head slightly wider than collum; collum to ring 18 nearly uniform in width but rings 2 and 3 slightly narrower. Ring 2 paranotum (Fig. 2A) thin, dorsally concave, set lower than collum corner and ring 3 paranotum, extending slightly past posterior ring margin. Paranota on rings 3 and 4 (Fig. 2A) similar but thicker. Paranota on rings 5–18 (Figs 2A–D, 4A) prominent, set at ca 1/2 ring height; in lateral view rounded anteriorly, bluntly pointed posteriorly, extending just past posterior ring margin; dorsally concave medial to thickened lateral margin (Fig. 3A). No pleural keels on anterior rings.

Waist (Figs 2C, 3A) distinct, the zone between suture and anterior metazonite margin longitudinally ridged. Prozonites (Fig. 3) with prominent cellular sculpture dorsally, laterally and ventrally. Metatergites with transverse row of 4 prominent setae anterior to transverse furrow, the setae often abraded; posterior rings (Fig. 2B) with transverse row of setae near rear margin of metatergite. Metazonites laterally and ventrally with very small, irregular ridges (Fig. 4A, E) with flattened tops and rounded edges. Metatergites sometimes also with low, irregular folds, giving metatergite a variably wrinkled appearance (Figs 2D, 3A). Transverse furrow (Figs 2C, 3A) on rings 3–18 at ca 1/2 metatergite length, deeply impressed with some longitudinal ridging. Limbus a short, thin, uniformly wide sheet. Pore formula normal; ozopore (Fig. 4A) round, opening laterally

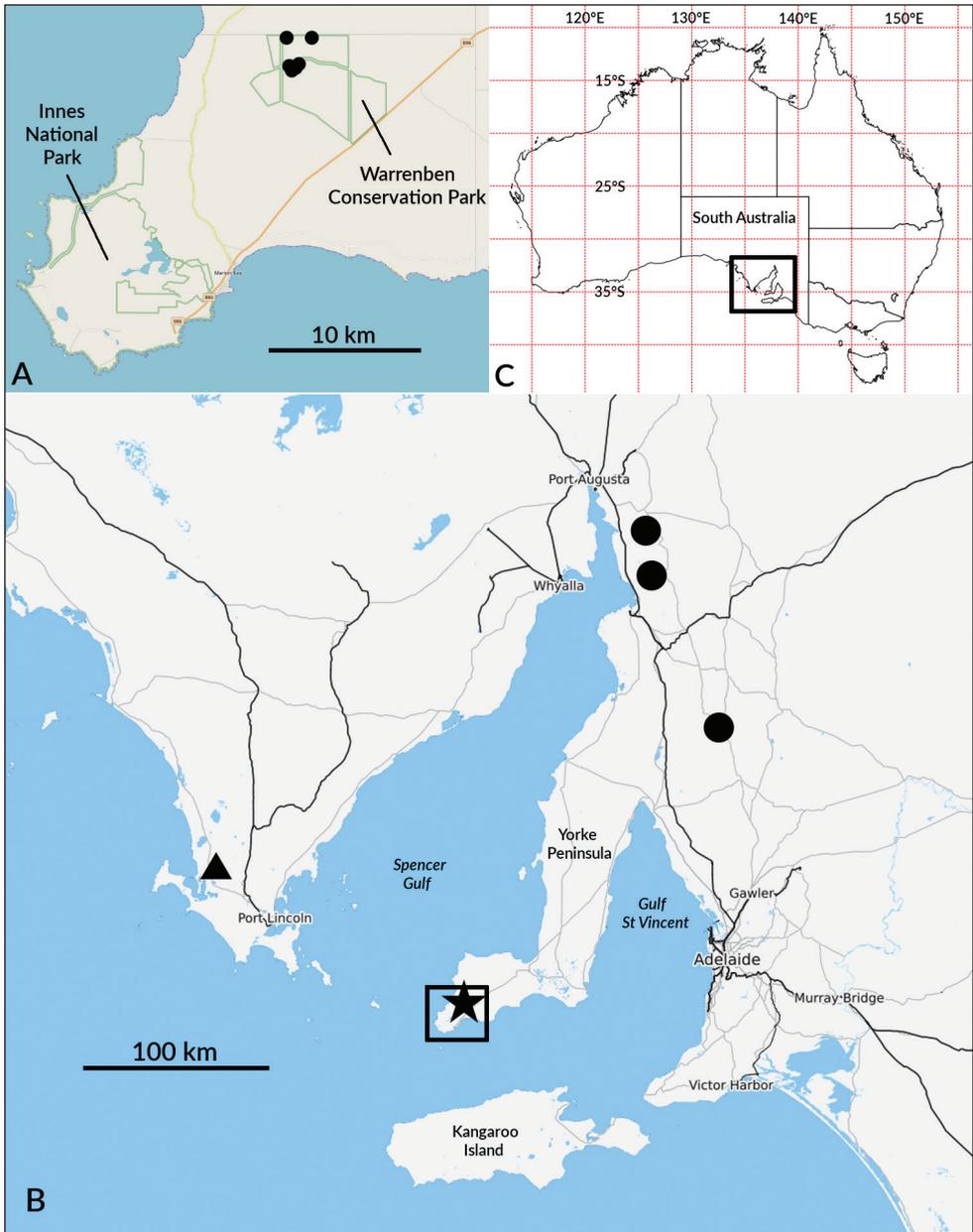


Figure 1. Known distribution of *Tridactylogonus* species as of 1 September 2017. **A** Localities for *T. warrenbenensis* sp. n. (filled circles) in Warrenben Conservation Park **B** Localities for *T. obscurus* Jeekel, 1982 (filled circles), *T. rugosissimus* Jeekel, 2002 (triangle) and *T. warrenbenensis* sp. n. (star); rectangle on Yorke Peninsula shows extent of map **A**. **C** Map of Australia; rectangle in South Australia shows extent of map **B**. Locality data for *T. obscurus* and *T. rugosissimus* from Mesibov (2006–2017); base maps for maps **A** and **B** from Open Street Map project (<https://www.openstreetmap.org>).

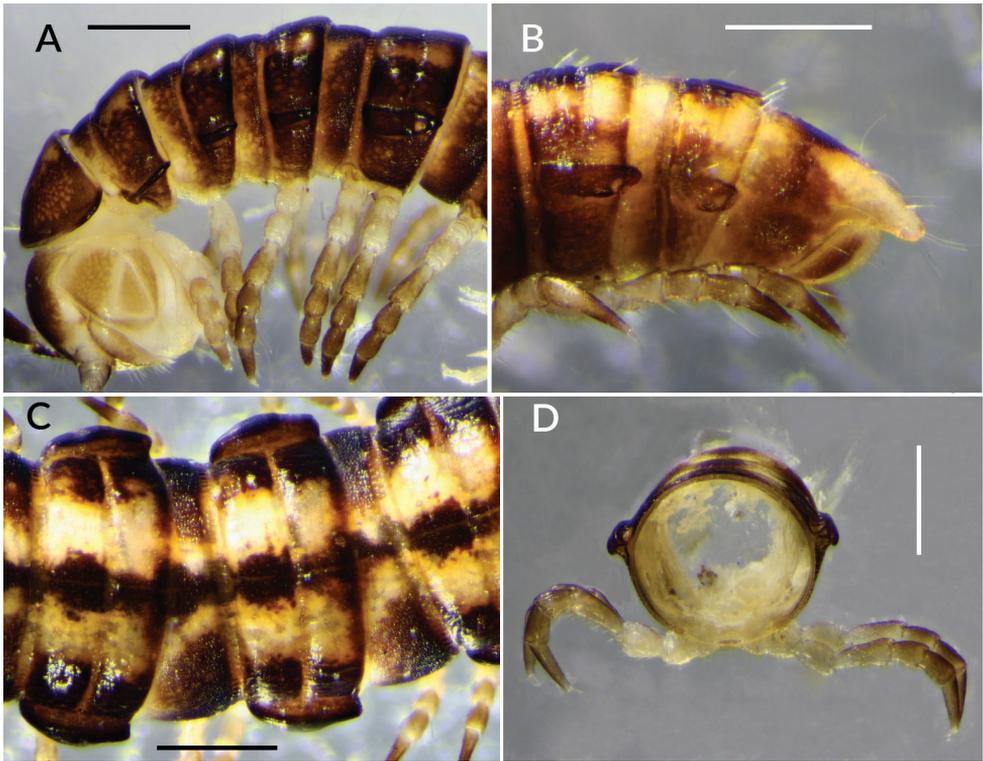


Figure 2. *Tridactylogonus warrenbenensis* sp. n. **A** Holotype (SAM OM2184), anterior end **B** Paratype male (ex SAM OM2185-OM2194), posterior end **C** Paratype female (ex SAM OM2185-OM2194), dorsal view of midbody rings **D** Paratype male (ex SAM OM2185-OM2194), posterior view of isolated midbody ring. Scale bars: 0.5 mm.

at anterior end of narrow, ovoid depression at rear of paranotal margin. Spiracles on diplosegments above and just anterior to leg bases, rims thin; anterior spiracle (Fig. 4D) with rim slightly elevated, filter slightly emergent dorsally, filter elements flattened and with forked tips. Midbody sternites about as long as wide, sparsely and finely setose, cross impressions about equal in depth; no cones or other projections on any sternites. Midbody legs (Fig. 2D) with relative podomere lengths (femur=tarsus)>prefemur>(post femur= tibia). Pre-anal ring (Fig. 2B) with a few long setae; epiproct extending well past anal valves, in dorsal view slightly tapering and truncate, tip ca 1/3 width of pre-anal ring; hypoproct paraboloid. Spinnerets in square array, dorsal setae longer than ventral, each pair set in narrow, shallow, transverse concavity on posterior surface of epiproct.

Leg 1 without ventral femoral process or tubercle (Fig. 4C). Gonopore small, round, opening on slight distomedial bulge of leg 2 coxa. Sternal lamella (Fig. 4B) between legs 5 ca 2/3 as wide as space between leg 5 coxae, short, distally with 2 bluntly rounded, setose projections. Sparse brush setae on leg 2 tarsus only. Anterior leg prefemora not swollen dorsally. Gonopod aperture (Fig. 3B) just wide enough to accommodate gonocoxae,

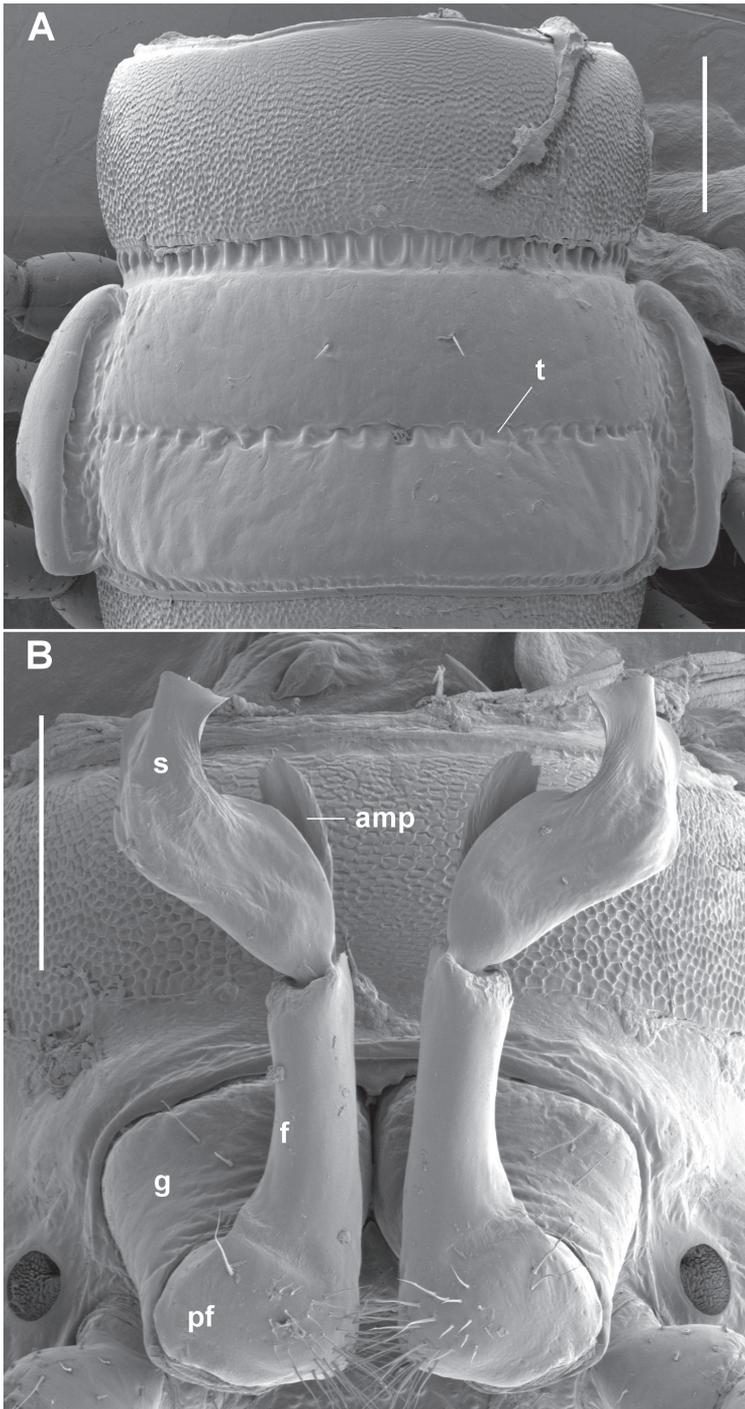


Figure 3. *Tridactylogonus warrenbenensis* sp. n., male (SAM OM2195). **A** Dorsal view of midbody ring; **t** = transverse furrow **B** Ventral view of gonopods in situ; **amp** = anteromedial process, **f** = femoral portion, **g** = gonocoxa, **pf** = prefemoral portion of telopodite, **s** = solenomere. Scale bars: 0.25 mm.

ca 1/2 ring 7 prozonite width. Gonopod telopodites (Figs 3B, 5C, 5E) straight, parallel, reaching leg 6 bases when retracted; sternite between legpairs 6 and 7 slightly excavate. Gonocoxa short, truncate-conical, with a few long setae anterolaterally. Cannula prominent. Telopodite with prefemoral portion moderately setose medially, marked distally by very slight constriction and by obvious reduction in telopodite width. Femoral portion ca 1/2 acropodite length, subcylindrical, ending posteriorly in lip-like extension. Distal half of acropodite with two (not three) processes: broad, laminate, distally rounded-truncate solenomere, slightly concave anteriorly and broadly emarginate medially; and short anteromedial process, ca 1/2 solenomere length, directed slightly distomedially, laminate with rounded, sparsely microdentate distal margin. Prostatic groove prominent, running distally along anteromedial surface of femoral portion, then curving between bases of solenomere and anteromedial process and along anterior surface of solenomere, terminating as short, central projection on distal solenomere margin.

Female more robust than male; epigyne thickened but barely protruding; cyphopods not examined.

Name. For the type locality, Warrenben Conservation Park.

Distribution. Known from six localities over ca 4 km² in Warrenben Conservation Park at the southern end of the Yorke Peninsula, South Australia (Fig. 1A, B). Found in bark litter under dead she-oak trees (*Allocasuarina stricta*) and in *Eucalyptus* sp. bark litter in shrubby, mallee-type vegetation on limestone at 20–30 m elevation. The area has an annual rainfall of ca 440 mm (Bureau of Meteorology 2017).

Remarks. *Taxonomic affinities.* Although its gonopod telopodite is “bidactylous” rather than “tridactylous”, *T. warrenbenensis* sp. n. closely resembles the other two *Tridactylogonus* species in its small size and gonopod form. The genus was thought by Jeekel (1982, p. 128) to “stand rather isolated” within the tribe Antichiropodini, and its discovery “might seem to narrow the taxonomic disjunction between this tribe and the Australiosomatini”. However, as in other Australian Antichiropodini, especially *Aethalosoma* Jeekel, 2006, *Aulacoporus* Verhoeff, 1924, *Brochopeltis* Verhoeff, 1924, *Pseudostrongylosoma* Verhoeff, 1924 and *Walesoma* Verhoeff, 1928, the gonopod telopodite in *Tridactylogonus* has a narrow, straight femoral portion arising from a small, setose prefemoral portion, with the femoral portion clearly demarcated from the solenomere and any other apical processes. Also, as in *Aethalosoma*, *Dicranogonus* Jeekel, 1982, *Notodesmus* Chamberlin, 1920 and *Pogonosternum* Jeekel, 1965 (fig. 2 in Mesibov 2009, fig. 4B in Decker et al. 2017), the spiracular filter elements in the new species are flattened and have forked tips.

Within the genus, *T. warrenbenensis* sp. n. is most similar to *T. rugosissimus* in gonopod form and in metazonite sculpturing (see below), which Jeekel (2002, p. 65) thought could distinguish the latter species “from all other known Australian Paradoxosomatidae”. The new species is remarkable in lacking a femoral process or tubercle on male leg 1, a character almost universally present in Australiosomatinae. Jeekel reported that the leg 1 femur in *T. obscurus* had “the usual ventral tubercle” (Jeekel 1982, p.130), and in *T. rugosissimus* “a small ventral tubercle” (Jeekel 2002, p. 64). Unfortunately I have not been able to examine the type and only known specimen of *T. rugosissimus*; it was not deposited in the South Australian Museum as proposed (Jeekel 2002, p. 60) and has not

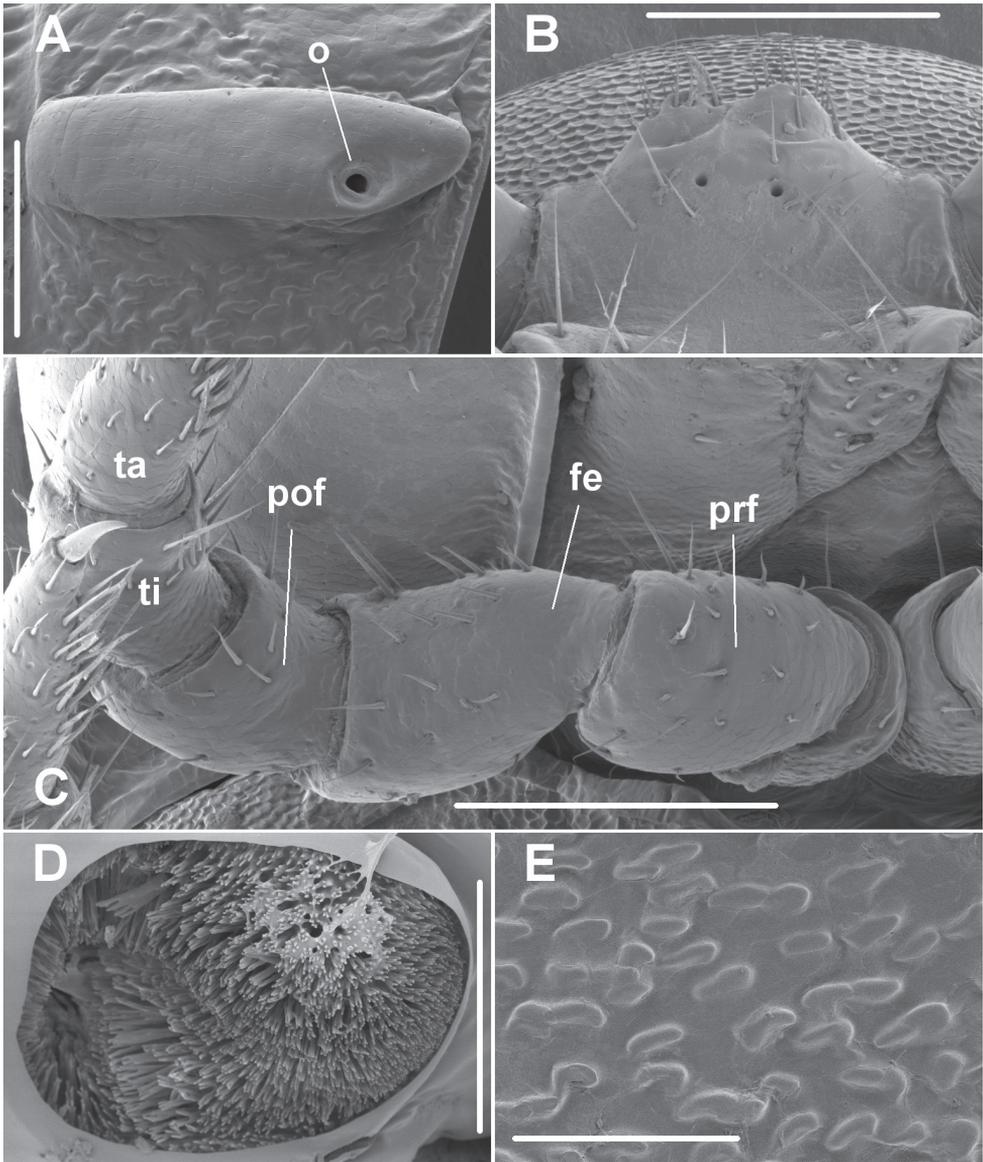


Figure 4. *Tridactylogonus warrenbenensis* sp. n., male (SAM OM2195). **A** Left lateral view of midbody paranotum; **o** = ozopore **B** Posterior view of sternal lamella between legs 5 **C** Posteroventral view of right leg 1; **fe** = femur, **pof** = postfemur, **prf** = prefemur, **ta** = tarsus, **ti** = tibia **D** Left lateral view of anterior spiracle on midbody ring **E** Close-up of microscopic ridges below paranotum in **A**. Scale bars: 0.2 mm (**A, B, C**); 0.05 mm (**D**), 0.1 mm (**E**).

been found among material in the late Dr Jeekel's study collection in the Naturalis Biodiversity Center in Leyden, the Netherlands (K. van Dorp, in litt., 17 September 2014).

Surface sculpture. Jeekel (1982, p. 129) noted “a fine, but quite conspicuous cellular structure” on the prozonites and “subgranulose” sides in *T. obscurus*. In *T. rugosissimus* the

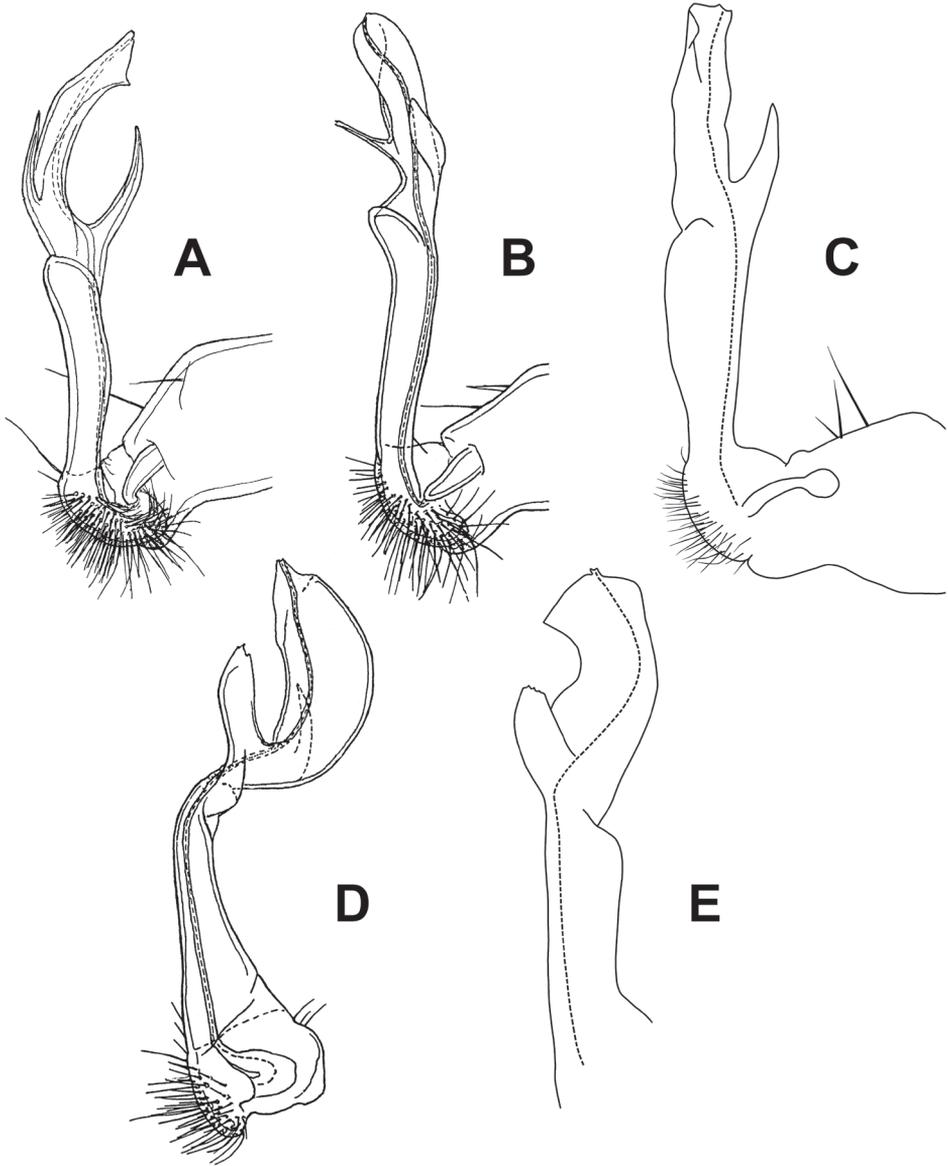


Figure 5. Gonopods of *Tridactylogonus* species. **A** *T. obscurus* holotype (after Jeekel 1982) **B, D** *T. rugosissimus* holotype (after Jeekel 2002) **C, E** *T. warrenbenensis* sp. n. paratype (ex SAM OM2185-OM2194) **A–C** medial views of right gonopod **D, E** anterior and anterior and slightly medial views, respectively **D** originally of left gonopod telopodite, here right-left reversed for comparison with right gonopod in **E**. Dashed line in **C** and **E** marks the prostatic groove. Drawings not to scale.

prozonites were said to have either “pronounced reticulate structure or minute and regular granulation”, while the metatergites were “coarsely and densely rugose, with irregular longitudinal or somewhat oblique or undulate rugae”, and the sides “coarsely granulose to

subrugulose” (Jeekel 2002, p. 63). Cellular prozonite sculpturing seems to be a constant character state in *T. warrenbenensis* sp. n. and closely resembles the prozonite sculpturing in another Australian paradoxosomatid, *Desmoxytoides hasenpuschorum* Mesibov, 2006 (fig. 5A in Mesibov 2009). “Rugose” sculpturing of the metazonites is more variable. It is always present on the sides as irregular microscopic ridges, but is variably prominent on the metatergites as coarse, narrow wrinkles. Each microscopic ridge appears to project from one cuticular scale, but ridges on adjoining scales sometimes appear to be confluent (Fig. 4E), in contrast to the discretely spaced projections seen in some other recently examined Polydesmida (Mesibov 2009, Akkari and Enghoff 2011).

Biogeography and conservation. The three *Tridactylogonus* species occur around Spencer and St Vincent Gulfs in southern South Australia (Fig. 1B) and form an allopatric species mosaic. *T. warrenbenensis* sp. n. is so far known only from Warrenben Conservation Park (Fig. 1A), which covers ca 4000 ha and is managed for nature conservation. Over several days of searching in 2016 and 2017 I was unable to find any native millipedes in the nearby and larger Innes National Park (Fig. 1A), despite the presence there of apparently suitable woodland and scrub habitats. The National Park instead has a dense and almost ubiquitous population of the introduced Portuguese millipede *Ommatoiulus moreleti* (Lucas, 1860). *O. moreleti* is also the most common millipede elsewhere on the Yorke Peninsula in both partly natural and entirely agricultural habitats. If *O. moreleti* has displaced native millipedes in Innes National Park, it may displace *T. warrenbenensis* sp. n. in future in Warrenben CP, which is linked to Innes NP by several large blocks of privately owned bushland. During my 2016 and 2017 visits I saw no *O. moreleti* in Warrenben CP.

Acknowledgements

I am grateful to Kate Sparks and Mark Stevens (South Australian Museum) for help with deposits and registrations, to Karen van Dorp (Naturalis Biodiversity Center) for advice on Jeekel types and to the South Australian Department of Environment, Water and Natural Resources (DEWNR) for issuing and renewing scientific research permit Q-26482-1, which authorised my collections in Innes National Park and Warrenben Conservation Park. I thank my wife, Trina Moule, and Christine Arnold (DEWNR) for patient assistance with fieldwork in 2016 and 2017, respectively. Sandrin Feig (Central Science Laboratory, University of Tasmania) kindly operated the Hitachi SU-70 for me. Nesrine Akkari made very useful suggestions for improving the manuscript.

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Callosa gen. n., a new troglobitic genus from southwest China (Araneae, Linyphiidae)

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Academic editor: *Yuri Marusik* | Received 12 May 2017 | Accepted 8 September 2017 | Published 28 September 2017

<http://zoobank.org/0FF3A9EB-0AC1-45A8-8957-6D3AA945B5C8>

Citation: Zhao Q, Li S (2017) *Callosa* gen. n., a new troglobitic genus from southwest China (Araneae, Linyphiidae). ZooKeys 703: 109–128. <https://doi.org/10.3897/zookeys.703.13641>

Abstract

A new linyphiid genus *Callosa* gen. n., with two new species *Callosa ciliata* sp. n. (♂♀, type species) and *Callosa baiseensis* sp. n. (♂♀), from southwest China are described. Detailed description of genitalic characters and somatic features is provided, as well as light microscopy and SEM micrographs of each species. *Callosa* gen. n. was found in caves in Yunnan and Guangxi, and its copulatory organs are similar to those of *Bathyphantes* and *Porrhomma*, but differ greatly in details. The monophyly and placement of *Callosa* gen. n. are supported by the results of molecular analysis.

Keywords

Asia, cave spider, eyeless, Linyphiinae, morphology, photographs

Introduction

In previous collecting work conducted in caves in southwest China, a considerable number of troglobitic spider species belonging to Nesticidae, Leptonetidae, Telemidae, and Pholcidae were found, but Linyphiidae were seldom encountered. Due to insufficient efforts in taxonomy, no more than 100 linyphiid species have been reported from there, and only one of them was found in caves. Here a new linyphiid genus collected in caves from southwest China is described, whose copulatory organs identify it as a genus of Porrhommini. It has obvious somatic characters of real cave dwellers, indicating its long-term underground

evolutionary history. In order to test its placement in Porrhommini suggested by morphological characters, an additional molecular analysis based on newly sequenced DNA data of the two species and sequences available from GenBank was conducted.

Materials and methods

Specimens were studied using a LEICA M205 C stereomicroscope. Further details were examined under a BX51 compound microscope. Copulatory organs were examined after being dissected from the spiders' bodies. Left male palps were used, except as otherwise indicated. Female epigynes and vulvae were removed and treated in warm potassium hydroxide (KOH) water solution before study. All embolic divisions, epigynes and vulvae were photographed after being embedded in gum arabic. Photos were taken with an Olympus c7070 wide zoom digital camera (7.1 megapixels) mounted on an Olympus BX51 compound microscope. Images from multiple focal planes were combined using Helicon Focus (version 3.10) image stacking software. All measurements are given in millimeters. Eye diameters were measured at their widest extent. Leg measurements are shown as: total length (femur, patella, tibia, metatarsus, tarsus). The terminology of copulatory organs follows Saaristo (1995), Tanasevitch (2014).

SEM images were taken using the FEI Quanta 450 at the Institute of Zoology, Chinese Academy of Sciences. Specimens for SEM examination were critical point dried and sputter coated with gold-palladium. Specimens were mounted on copper pedestals using double-sided adhesive tape.

The tibial spine formula, which expresses the number of dorsal tibial spines on each of legs I to IV, is given for species in which it differs from the type species of the genus. The patellar spine formula is given only if it differs from the most common one (1-1-1-1).

All type specimens are deposited in the Institute of Zoology, Chinese Academy of Sciences in Beijing (**IZCAS**), except as otherwise indicated.

Abbreviations used in the text and figures are given below. References to figures in cited papers are noted in lowercase type (fig.).

Male palp

CV	convector
DSA	distal suprategular apophysis
E	embolus
MM	median membrane
PC	paracymbium
PT	protegulum
ST	subtegulum
T	tegulum

Epigyne

A	atrium
CF	copulatory furrows
CO	copulatory opening
DP	dorsal plate
P	parmula
R	receptacle
SO	socket
VP	ventral plate

Somatic morphology

ALE	anterior lateral eye
ALS	anterior lateral spinneret
AME	anterior median eye
CY	cylindrical gland spigot
PLE	posterior lateral eye
PLS	posterior lateral spinneret
PME	posterior median eye
PMS	posterior median spinneret

Phylogenetic analysis

Analysis conducted here is partially based on the data matrix of Arnedo et al. (2009). A few taxa were taken out, and more taxa of Linyphiinae downloaded from GenBank were added to reconstruct phylogeny. A total of 66 taxa were included for the final test. Partial fragments of the mitochondrial genes cytochrome *c* oxidase subunit I (COI), 16SrRNA (16S) and the nuclear genes Histone 3 (H3), 18SrRNA (18S) were amplified and sequenced for *Callosa ciliata* sp. n. and *C. baiseensis* sp. n. following the procedure in Arnedo et al. (2009). Sequences for each gene were edited in Bioedit (Hall 1999), and aligned in MAFFT (<http://mafft.cbrc.jp/alignment/server/>). Bayesian inference was performed in MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) using parameters selected by jModelTest (Posada 2008). The Markov chains were sampled every 1000 generations for 2 million generations, with the first 25% of sampled trees discarded as burn-in. Taxonomic and sequence information of the used taxa are presented in Table 1.

Bayesian inference based on four genes yielded a similar phylogenetic tree to Arnedo's (Arnedo et al. 2009) and Sun's (Sun et al. 2014). The *Callosa* gen. n. species belong to Porrhommini as indicated by the cladogram (Fig. 10).

Table I. DNA data information of species included in the phylogenetic analysis

Family	Genus	Species	16S	18S	COI	H3
Pimoidae	<i>Pimoida</i>	sp. X131	AY230940	AY230893	AY231025	AY230985
	<i>Agyneta</i>	<i>ramosa</i>	FJ838670	FJ838694	FJ838648	FJ838740
	<i>Anguliphantes</i>	<i>nasus</i>	JN816483	JN816703	JN817115	
	<i>Australolinyphia</i>	<i>remota</i>	FJ838671	FJ838695	FJ838649	FJ838741
	<i>Bathyphantes</i>	<i>floralis</i>	GU338604	GU338465	GU338659	
	<i>Bathyphantes</i>	<i>gracilis</i>	FJ838672	FJ838696	FJ838650	FJ838742
	<i>Bolyphantes</i>	<i>alticeps</i>	AY078660	AY078667	AY078691	AY078700
	<i>Callosa</i> gen. n.	<i>baiseensis</i> sp. n.	MF095861	MF095862	MF095863	MF095864
	<i>Callosa</i> gen. n.	<i>ciliata</i> sp. n.	MF095865		MF095866	MF095867
	<i>Centromerus</i>	<i>trilobus</i>	GU338599	GU338468	GU338656	
	<i>Dicymbium</i>	<i>sinofacetum</i>	GU338614	GU338487	GU338665	
	<i>Diplocentria</i>	<i>bidentata</i>	GU338629	GU338494	GU338688	
	<i>Diplocephalus</i>	<i>cristatus</i>	GU338637	GU338490	GU338696	
	<i>Diplostyla</i>	<i>concolor</i>	FJ838673	FJ838697	FJ838651	FJ838743
	<i>Doenitzius</i>	<i>pruvus</i>	GU338632	GU338474	GU338691	
	<i>Drapetisca</i>	<i>socialis</i>	FJ838674	FJ838698	FJ838652	FJ838744
	<i>Dubiaranea</i>	<i>aysenensis</i>	FJ838675	FJ838699	FJ838653	FJ838745
	<i>Dubiaranea</i>	<i>distincta</i>	GU338624	GU338459	GU338648	
	<i>Dubiaranea</i>	<i>propinqua</i>	GU338627	GU338460	GU338675	
	<i>Erigone</i>	<i>prominens</i>		GU338539	GU338679	
<i>Eskovina</i>	<i>clava</i>	JN816489	JN816710	JN817122		
Linyphiidae	<i>Floronia</i>	<i>bucculenta</i>	FJ838676	FJ838700	FJ838654	FJ838746
	<i>Frontinella</i>	<i>communis</i>	GU338628	GU338517		
	<i>Gnathonarium</i>	<i>dentatum</i>	GU338593	GU338477	GU338651	
	<i>Haplinis</i>	<i>diloris</i>	FJ838680	FJ838704	FJ838657	FJ838750
	<i>Helophora</i>	<i>insignis</i>	FJ838681	FJ838705	FJ838658	FJ838751
	<i>Himalaphantes</i>	<i>azumiensis</i>		GU338522	GU338677	
	<i>Hylyphantes</i>	sp. 'irellus'	GU338618	GU338481	GU338668	
	<i>Kaestneria</i>	<i>pullata</i>	KT003126	KT002937	KT002739	KT002838
	<i>Labulla</i>	<i>thoracica</i>	AY078662	AY078674	AY078694	AY078707
	<i>Laetesia</i>	sp. MAA-20099	FJ838682	FJ838706	FJ838659	FJ838752
	<i>Leptyphantes</i>	sp. 17 SL-2010	GU338610	GU338509	GU338664	
	<i>Linyphia</i>	<i>triangularis</i>	AY078664	AY078668	AY078693	AY078702
	<i>Microlinyphia</i>	<i>dana</i>	AY078665	AY078677	AY078690	
	<i>Microneta</i>	<i>viaria</i>	FJ838684	FJ838708	FJ838661	FJ838754
	<i>Moebelia</i>	<i>rectangula</i>	GU338591	GU338485		
	<i>Nerieni</i>	<i>albolimbata</i>	JN816480	JN816700	JN817112	
	<i>Nerieni</i>	<i>clathrata</i>	JN816478	JN816698	JN817110	
	<i>Nerieni</i>	<i>emphana</i>	JN816474	JN816694	JN817106	
	<i>Nerieni</i>	<i>japonica</i>	GU338633	GU338462	GU338692	
	<i>Nerieni</i>	<i>longipedella</i>	JN816476	JN816696	JN817108	
<i>Nerieni</i>	<i>nigripectoris</i>	JN816481	JN816701	JN817113		
<i>Nerieni</i>	<i>oidedicata</i>	JN816479	JN816699	DQ396860		

Family	Genus	Species	16S	18S	COI	H3
Linyphiidae	<i>Neriene</i>	<i>radiata</i>	AY078710	AY078670	AY078696	AY078709
	<i>Neriene</i>	<i>variabilis</i>	AY078711	AY078669	AY078699	AY078706
	<i>Nippononeta</i>	<i>kantonis</i>	GU338634	GU338471	GU338693	
	<i>Novafroneta</i>	<i>vulgaris</i>	FJ838686	FJ838710	FJ838663	FJ838756
	<i>Oedothorax</i>	<i>apicatus</i>	FJ838687	FJ838711	FJ838664	FJ838757
	<i>Orsonwelles</i>	<i>malus</i>	AY078737	AY078676	AY078697	AY078708
	<i>Orsonwelles</i>	<i>polites</i>	AY078725	AY078671	AY078755	AY078701
	<i>Pacifiphantes</i>	<i>zakharovi</i>	KT003159	KT002971	KT002771	KT002872
	<i>Paikiniana</i>	sp. 8 SL-2010	GU338617	GU338495	GU338647	
	<i>Parameioneta</i>	<i>bilobata</i>	GU338605	GU338503	GU338660	
	<i>Parasisis</i>	sp. 27 SL-2010	GU338592	GU338500	GU338650	
	<i>Pityohyphantes</i>	<i>costatus</i>	AY078666	AY078675	AY078695	
	<i>Pocobletus</i>	sp. MAA-2009	FJ838689	FJ838713	FJ838665	FJ838759
	<i>Porrhomma</i>	<i>montanum</i>	JN816486	JN816706	JN817118	
	<i>Porrhomma</i>	sp. 24 SL-2010	GU338607	GU338466	GU338661	
	<i>Pseudafroneta</i>	<i>incerta</i>	FJ838690	FJ838714	FJ838666	FJ838760
	<i>Sisicottus</i>	<i>montanus</i>	GU338625	GU338479	GU338673	
	<i>Solenysa</i>	sp. 14 SL-2010	GU338616	GU338506	GU338667	
	<i>Sphecozone</i>	<i>bicolor</i>	GU338622	GU338496	GU338671	
	<i>Stemonyphantes</i>	<i>lineatus</i>	FJ838691	FJ838715	FJ838667	FJ838761
<i>Tenuiphantes</i>	<i>tenuis</i>	FJ838693	FJ838716	FJ838669	FJ838763	
<i>Walckenaeria</i>	<i>clavicornis</i>	GU338596	GU338483			
<i>Walckenaeria</i>	<i>keikoae</i>	GU338636	GU338484	GU338695		

Taxonomy

Family Linyphiidae Blackwall, 1859

Genus *Callosa* gen. n.

<http://zoobank.org/4EC11D86-CC7A-4467-8AB6-83356A928616>

Type species. *Callosa ciliata* sp. n.

Etymology. The generic name is an arbitrary combination of letters. Gender is feminine.

Diagnosis. The copulatory organs in this genus clearly resemble those in *Porrhommini*, but differ from the similar genera by: embolus in *Callosa* gen. n. is long and forms one big loop (Figs 1A, 5A), neither a short and curved one as in *Porrhomma* Simon, 1884, *Diplostyla* Emerton, 1882, *Pacifiphantes* Eskov & Marusik, 1994 (Roberts 1987: figs 58a–e, 59a–e; Eskov and Marusik 1994: fig. 42), nor an apically coiled one as in most *Bathyphantes* Menge, 1866 (Roberts 1987: fig. 70a–e); the embolus in *Bathyphantes approximatus* (O. Pickard-Cambridge, 1871) is longer and slimmer, forming more than 2 loops (Ivie 1969: fig. 102); *Microbathyphantes* Helsdingen, 1985 has coiled, whip-like, and fully exposed embolus (Tu and Li 2006: fig. 2C), unlike the one enveloped in a membranous plate of the convector in *Callosa*

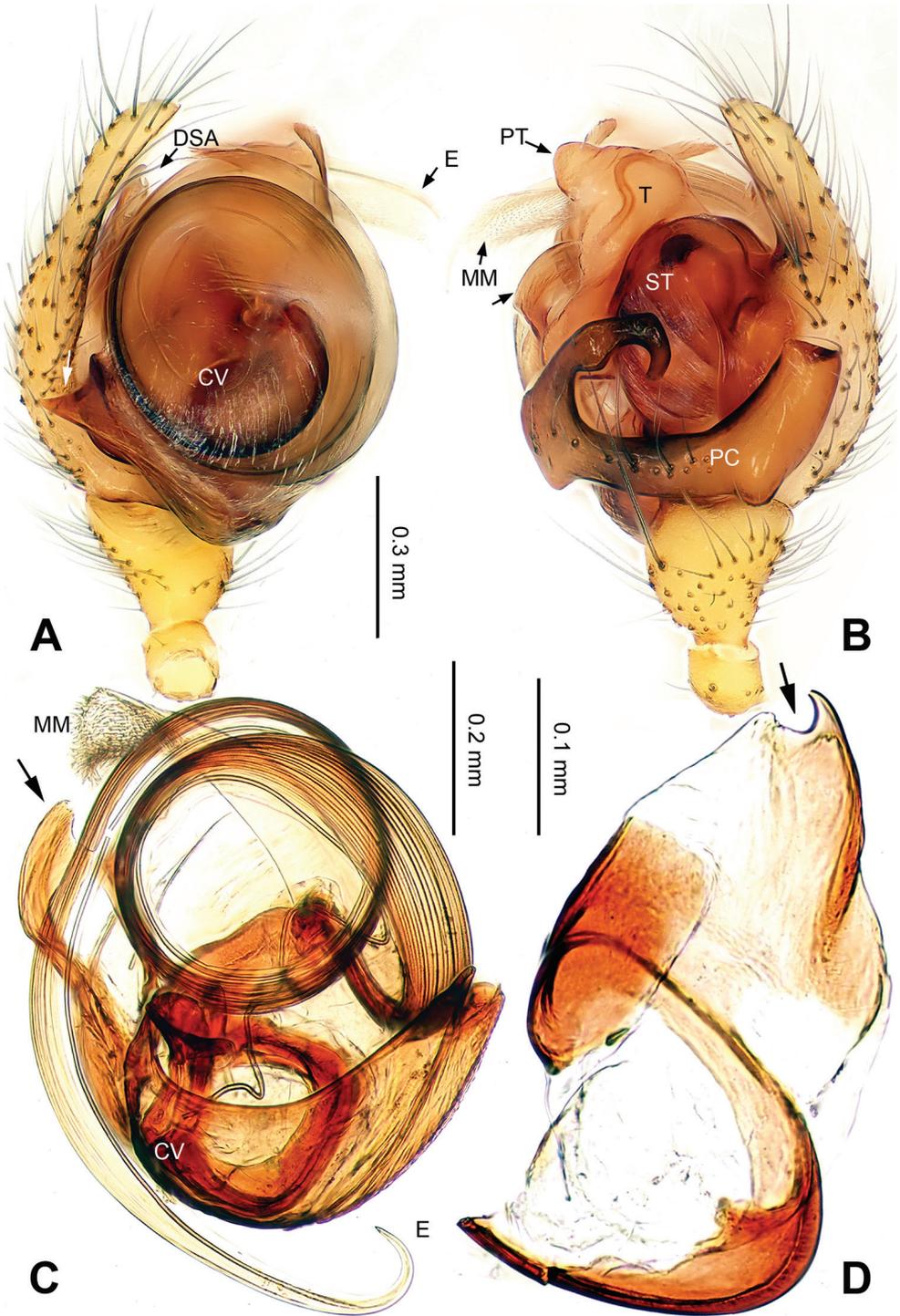


Figure 1. *Callosa ciliata* sp. n., male holotype. **A** Palp, prolateral view **B** Palp, retrolateral view **C** Embolic division, retrolateral view **D** Distal suprategular apophysis, retrolateral view. Scale bars: **B** as **A**.

gen. n. The epigyne in *Callosa* gen. n. is distinguished by its long, spiraling copulatory furrows and the presence of a septum (Figs 3C, 7C); the receptacles are situated farther from atrium in most *Bathyphantes* species, furrows are not in double-helix; *Kaestneria* Wiehle, 1956 and *Pacifyphantes* have shorter copulatory furrows, which fold or curve (Slowik and Blagoev 2012: fig. 6); the copulatory furrows in *Microbathyphantes* make only half a turn.

Description. Median size, 2.5–2.8. Chelicerae with three promarginal, and four retromarginal teeth. AME completely lost, PME reduced to small unpigmented spots, ALE and PLE highly reduced (Figs 2C, 2E, 3D, 3F, 6C, 6E, 7D, 7F); ocular area with several rows of short setae (Figs 2C, 6C). Carapace length/leg I 0.13–0.15. Coxae IV separated by their diameter. Chaetotaxy: 2-2-2-2. TmI 0.15–0.20, TmIV absent. Leg formula I-II-IV-III. Legs yellow without obvious patterns.

Male palp: femur about four times longer than patella; tibia with two trichobothria, one ventral and one retrolateral (Fig. 5B). Cymbium spindle-shaped at dorsal view (Figs 2A, 6A); Paracymbium 'J'-shaped, stout at base, attenuated and curved at apex (Figs 1B, 5B). Bulb with an oblate subtegulum and a protruding prottegulum (Figs 1B, 5B). Convector with a membranous plate enveloping the prolateral side of embolic division (Figs 1A, 5A), and a ribbon-like ventral process (Figs 1B, 2B, 5B, 6B); dorsal projection of convector situated near the base of cymbium in prolateral view (Figs 1A, 5A); distal suprategular apophysis pick-like, broad at base, hooked at apex (Figs 1D, 5D); median membrane with dense membranous short cilia (Figs 4B, 8B); embolus long and belt-like, with a tapering tip, making 1.5 loops along the exterior margin of convector plate (Figs 1A, 5A).

Epigyne: dome-shaped in lateral view, with atrium fully exposed in ventral view (Figs 3A, 4C–D, 7A, 8C–D); septum stretched along the axis of atrium; parmula short with a shallow socket near tip (Figs 4D, 8C); copulatory furrows making a spiral course (Figs 3C, 7C); receptacles oval, with short, tube-like processes (Figs 3C, 7C).

Species composition. Two species, *Callosa ciliata* sp. n. (type species) and *Callosa baiseensis* sp. n.

Distribution. Yunnan Province and Guangxi Zhuang Autonomous Region, China (Fig. 9).

Callosa ciliata sp. n.

<http://zoobank.org/2FF3B2E8-915E-487E-8F79-C5609A12D972>

Figs 1–4, 9

Types. Holotype ♂: CHINA, Yunnan Province: Baoshan City: Tengchong County; Gudong Town; Jiangdong Village; 24°58.103'N, 98°52.104'E, ca 1900 m, Jiangdong Mountain, Luoshui Cave, 26.XI.2013, (Y.C. Li & J.C. Liu). Paratypes: 1♂ 2♀, same data as for holotype.

Etymology. This specific name is taken from the Latin word 'ciliatus', meaning 'with cilia', which refers to the median membrane with cilia; adjective.

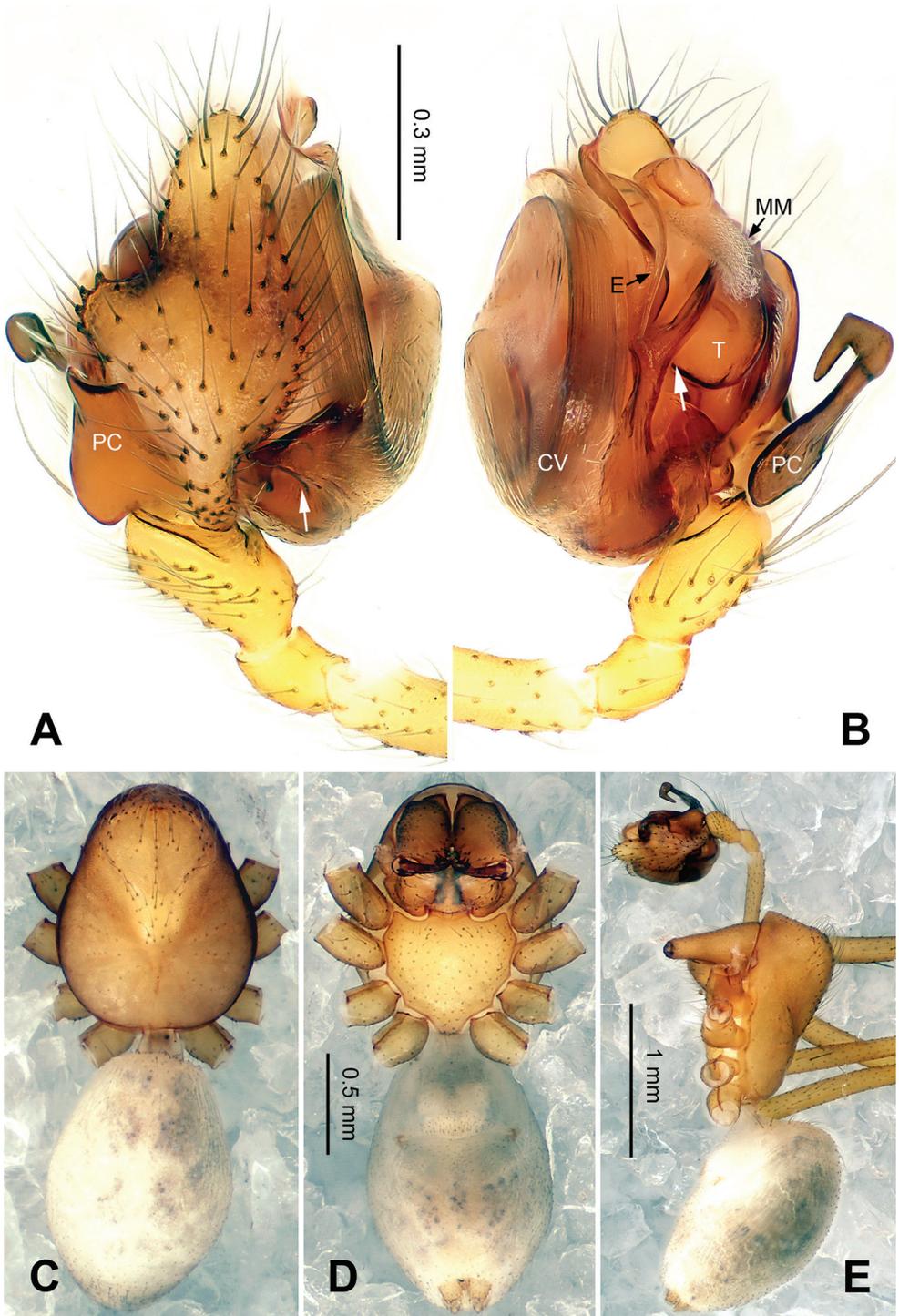


Figure 2. *Callosa ciliata* sp. n., male holotype. **A** Palp, dorsal view **B** Palp, ventral view **C** Habitus, dorsal view **D** Habitus, ventral view **E** Habitus, lateral view. Scale bars: **B** as **A**; **C** as **D**.

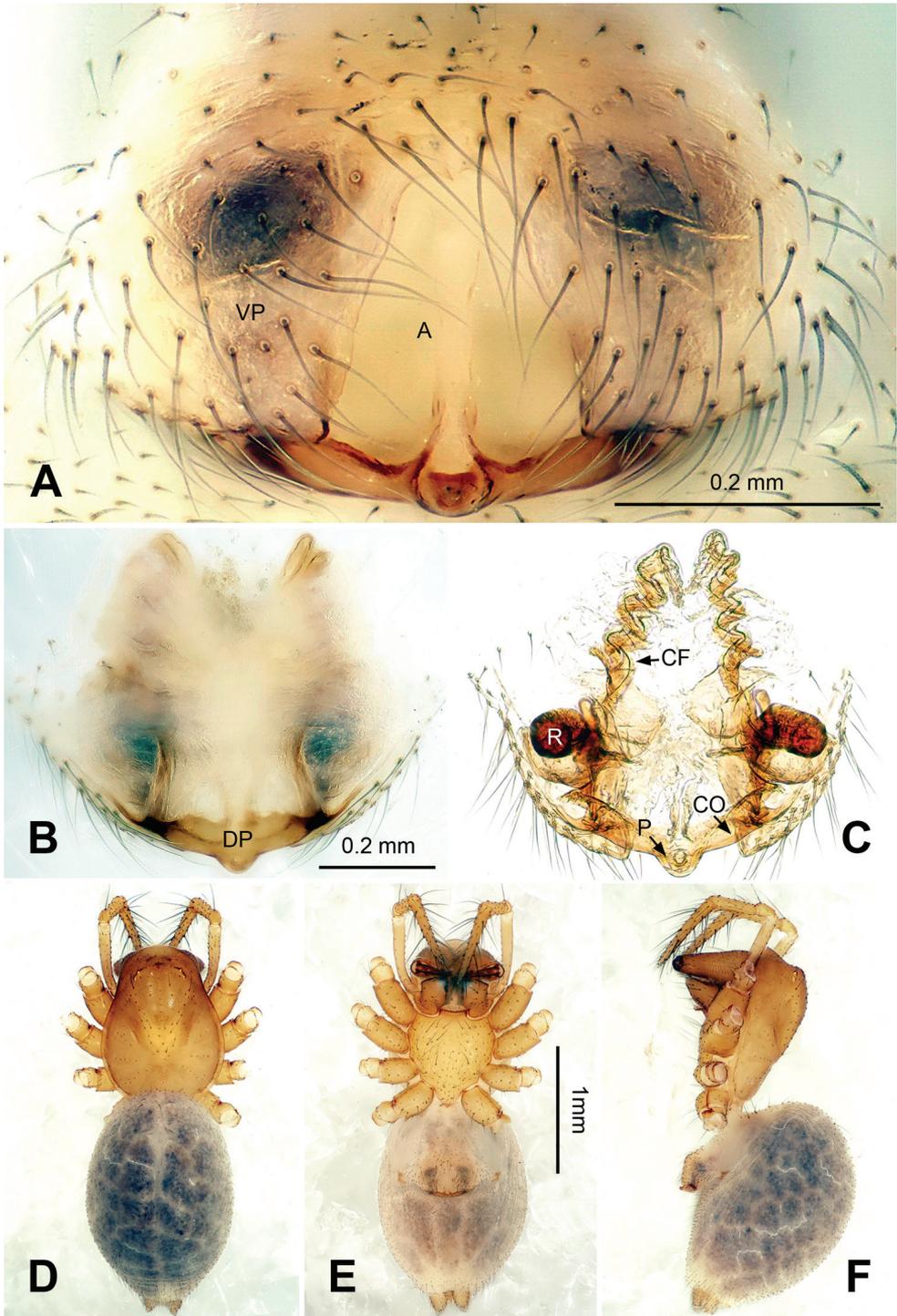


Figure 3. *Callosa ciliata* sp. n., female paratype. **A** Epigyne, ventral view **B** Epigyne, dorsal view **C** Vulva, dorsal view **D** Habitus, dorsal view **E** Habitus, ventral view **F** Habitus lateral view. Scale bars: **C** as **B**; **D**, **F** as **E**.

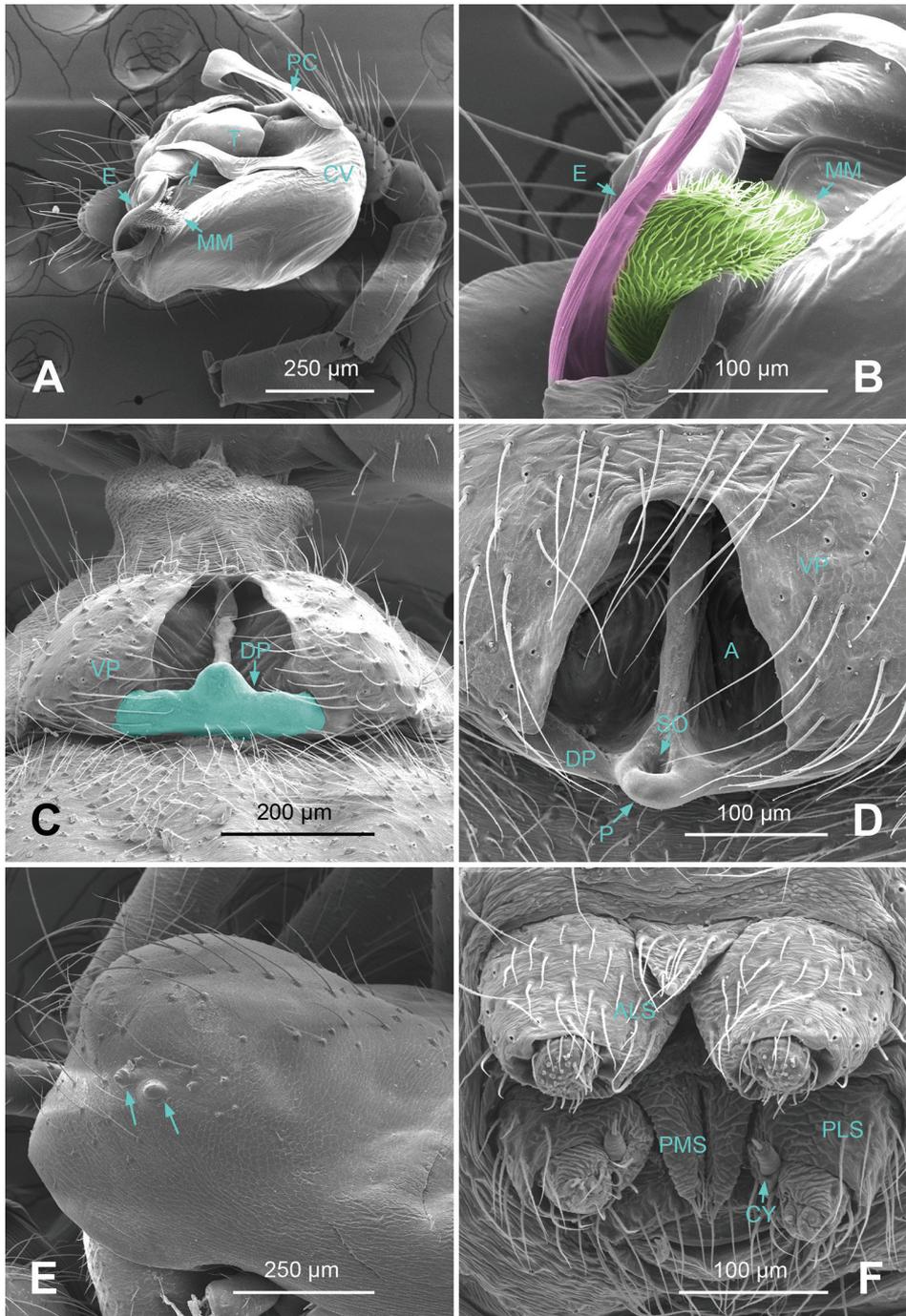


Figure 4. *Callosa ciliata* sp. n., SEM of a male paratype and a female paratype. **A** Palp of male paratype, ventral view **B** Detail showing embolus and embolic membrane of palp **C** Epigyne of female paratype, ventral view **D** Detail showing parmula of epigyne **E** Anterior lateral eye and posterior lateral eye of male paratype **F** Spinnerets of female paratype.

Diagnosis. It is characterised by the subdivided tip of distal suprategular apophysis (Fig. 1D) and in having three coils in copulatory furrows in epigyne (Fig. 3C). *Callosa ciliata* sp. n. also has a narrower atrium and shorter parmula.

Description. *Male (holotype).* Total length: 2.60. Carapace 1.25 long, 0.94 wide, brownish yellow (Fig. 2C, E), AME and PME entirely lost, ALE and PLE strongly reduced (Figs 2E, 4E). Sternum 0.68 long, 0.63 wide. Clypeus 0.50 high. Eye sizes: ALE 0.02, PLE 0.03. Leg length: I 8.06 (2.10, 0.40, 2.38, 2.05, 1.13), II 7.44 (2.00, 0.38, 2.13, 1.88, 1.05), III 5.74 (1.56, 0.30, 1.50, 1.55, 0.83), IV 6.98 (2.03, 0.31, 2.03, 1.75, 0.86). TmI 0.20. Abdomen pale, with irregular dark patterns (Fig. 2C–E). Palp: paracymbium large, with distal end strongly curved inward; tegulum broad at base, protegulum conical, crooked at tip; distal suprategular apophysis with a small indentation at apex (Fig. 1D); convector with a sharp projection at the 8 o'clock position at prolateral view (Fig. 1A); convector's ventral process ribbon-like, with a slightly broadened tip (Fig. 1B); embolus coiling from 4 o'clock position in prolateral view (Fig. 1A).

Female. Total length: 2.80. Carapace 1.25 long, 0.59 wide, same coloration as in male, AME vanished, ALE, PLE and PME reduced to white spots (Fig. 3D, F). Sternum 0.63 long, 0.69 wide. Clypeus 0.34 high. Eye sizes: ALE 0.03, PME 0.02, PLE 0.02. Leg length: I 8.21 (2.25, 0.40, 2.43, 2.00, 1.13), II 7.52 (2.18, 0.40, 2.19, 1.75, 1.00), III 5.79 (1.70, 0.38, 1.55, 1.38, 0.78), IV 7.07 (2.13, 0.35, 2.00, 1.75, 0.84). TmI 0.15. Abdomen with same coloration as in male (Fig. 3D, F). Epigyne: atrium roughly triangular in form, broad at posterior, narrowing towards anterior (Fig. 3A); fovea large, with ridged inner walls; parmula small; receptacles suboval, with digit-like outgrowth, separated by 3 diameters (Fig. 3C); copulatory furrows making 3 coils.

***Callosa baiseensis* sp. n.**

<http://zoobank.org/2433C26A-75D0-4B76-9720-1AA133CA168D>

Figs 5–9

Types. Holotype ♂: CHINA, Guangxi Zhuang Autonomous Region: Baise City; Longlin County; De'e Town; Yakou Village: 24°39.130'N, 105°09.557'E, ca 1500 m, Da Cave, 14–15.XII.2012, (Z.G. Chen & Z. Zhao). Paratypes: 1♂ 2♀, same data as for holotype; 1♀, Yumigan Cave, 24°39.145'N, 105°09.430'E, ca 1549 m, 14–15.XII.2012, (Z.G. Chen & Z. Zhao).

Etymology. This specific name is derived from Chinese Pinyin 'bǎi sè' (百色), referring to its type locality; adjective.

Diagnosis. Non-indented apex of distal suprategular apophysis (Fig. 5D), and the broad tip of convector ventral process in male palp (Figs 5B, 6B); it differs from the type species *C. ciliata* sp. n. by the relatively longer parmula (Figs 7B, 8C) and wider atrium (Fig. 7C).

Description. *Male (holotype).* Total length: 2.60. Carapace 1.20 long, 1.00 wide, beige, ocular area brownish yellow (Fig. 6C), AME completely lost, ALE, PLE and PME strongly reduced (Fig. 6C, E). Sternum 0.68 long, 0.66 wide. Clypeus 0.44 high.

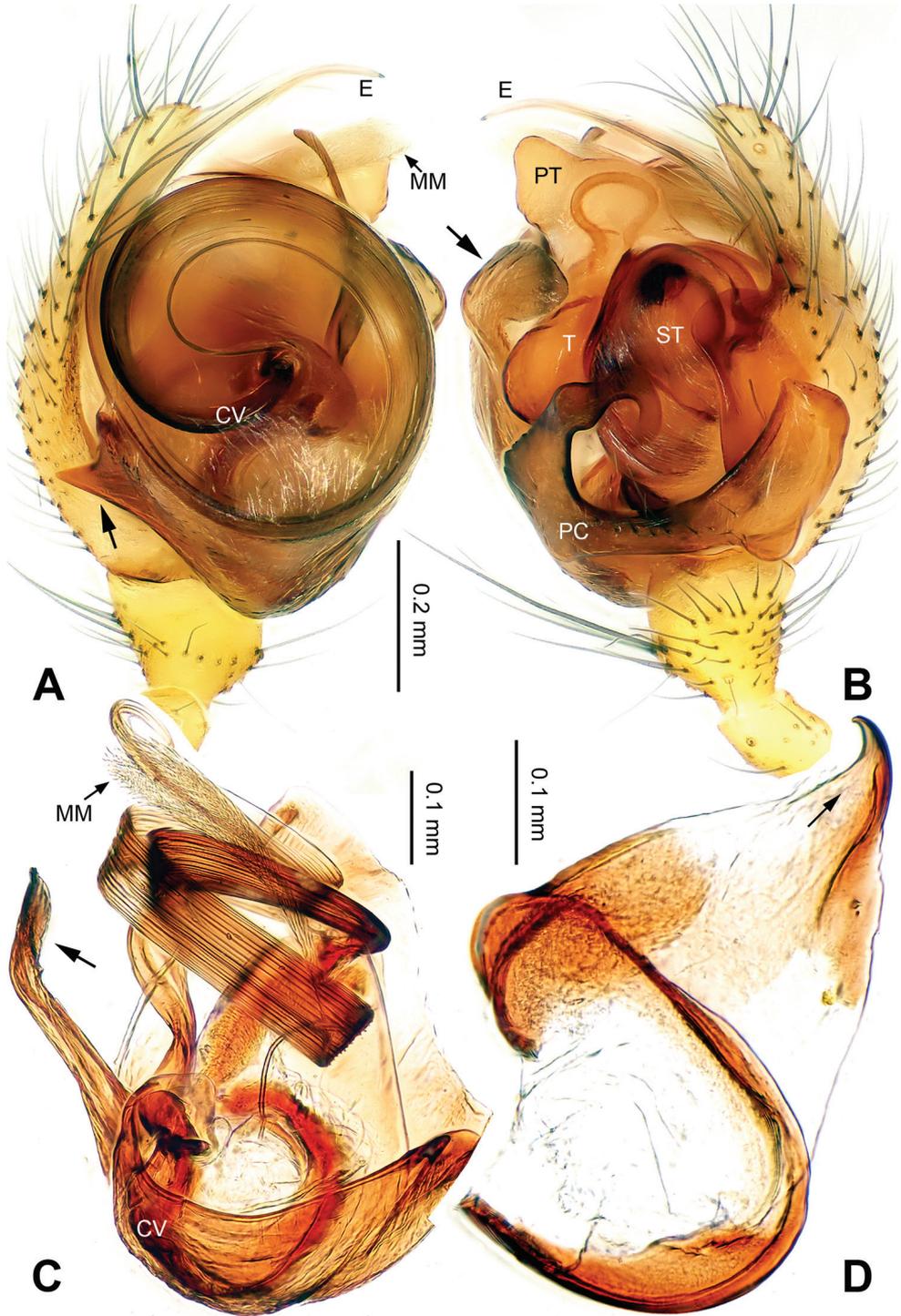


Figure 5. *Callosa baiseensis* sp. n., male holotype. **A** Palp, prolateral view **B** Palp, retrolateral view **C** Embolic division, retrolateral view **D** Distal supratergular apophysis, retrolateral view. Scale bars: **B** as **A**.

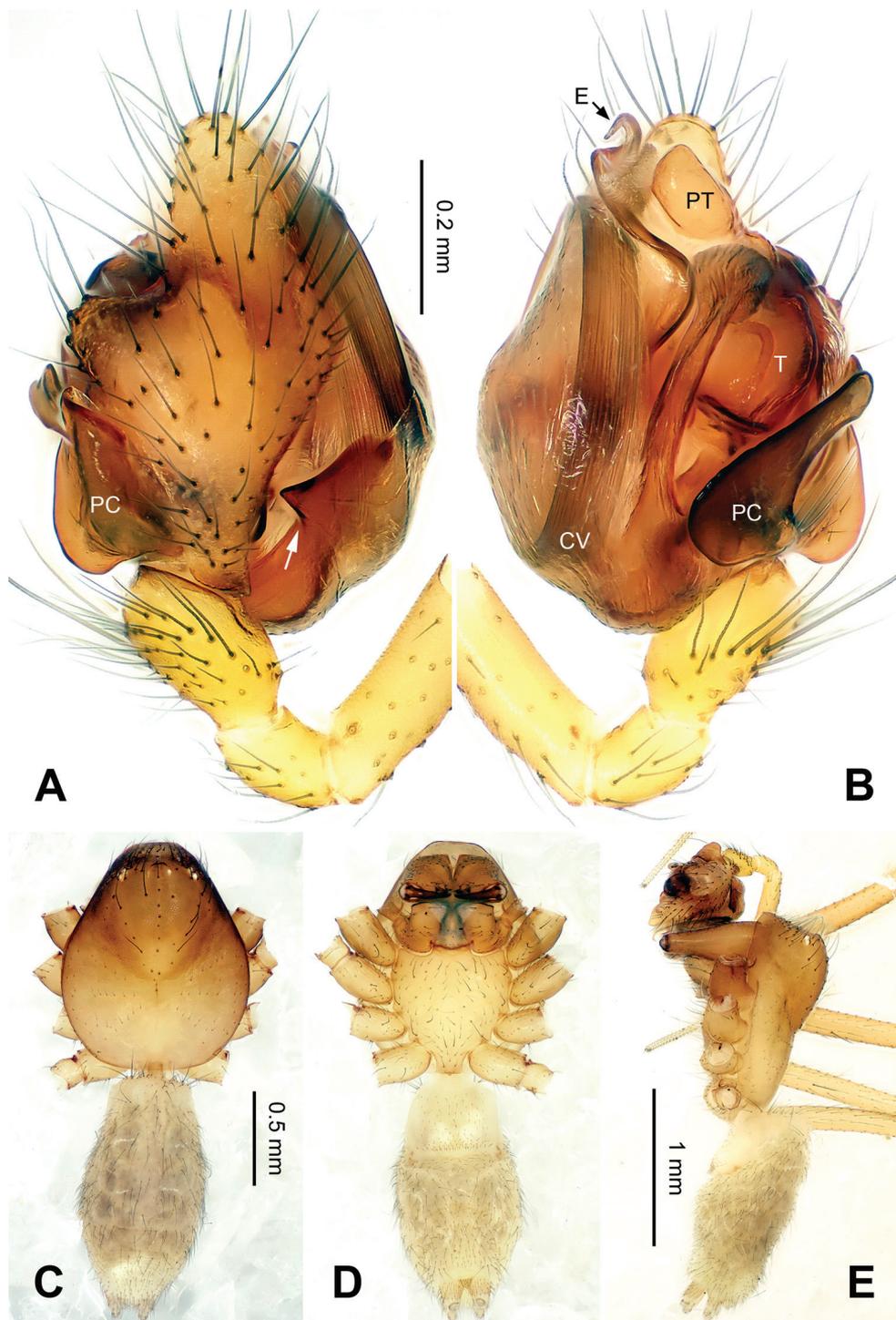


Figure 6. *Callosa baiseensis* sp. n., male holotype. **A** Palp, dorsal view **B** Palp, ventral view **C** Habitus, dorsal view **D** Habitus, ventral view **E** Habitus, lateral view. Scale bars: **B** as **A**; **D** as **C**.

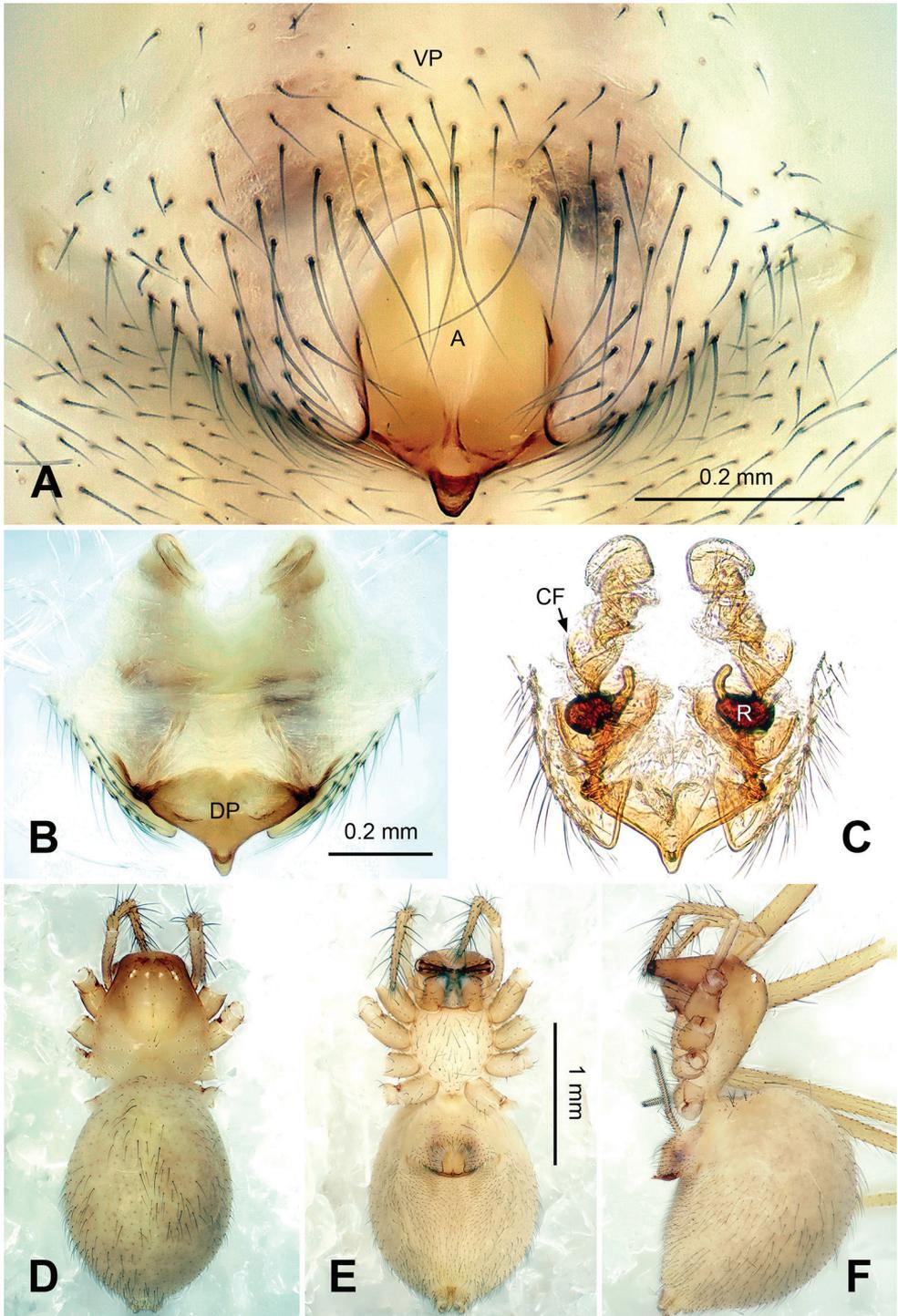


Figure 7. *Callosa baiseensis* sp. n., female paratype. **A** Epigyne, ventral view **B** Epigyne, dorsal view **C** Vulva, dorsal view **D** Habitus, dorsal view **E** Habitus, ventral view **F** Habitus lateral view. Scale bars: **C** as **B**; **D**, **F** as **E**.

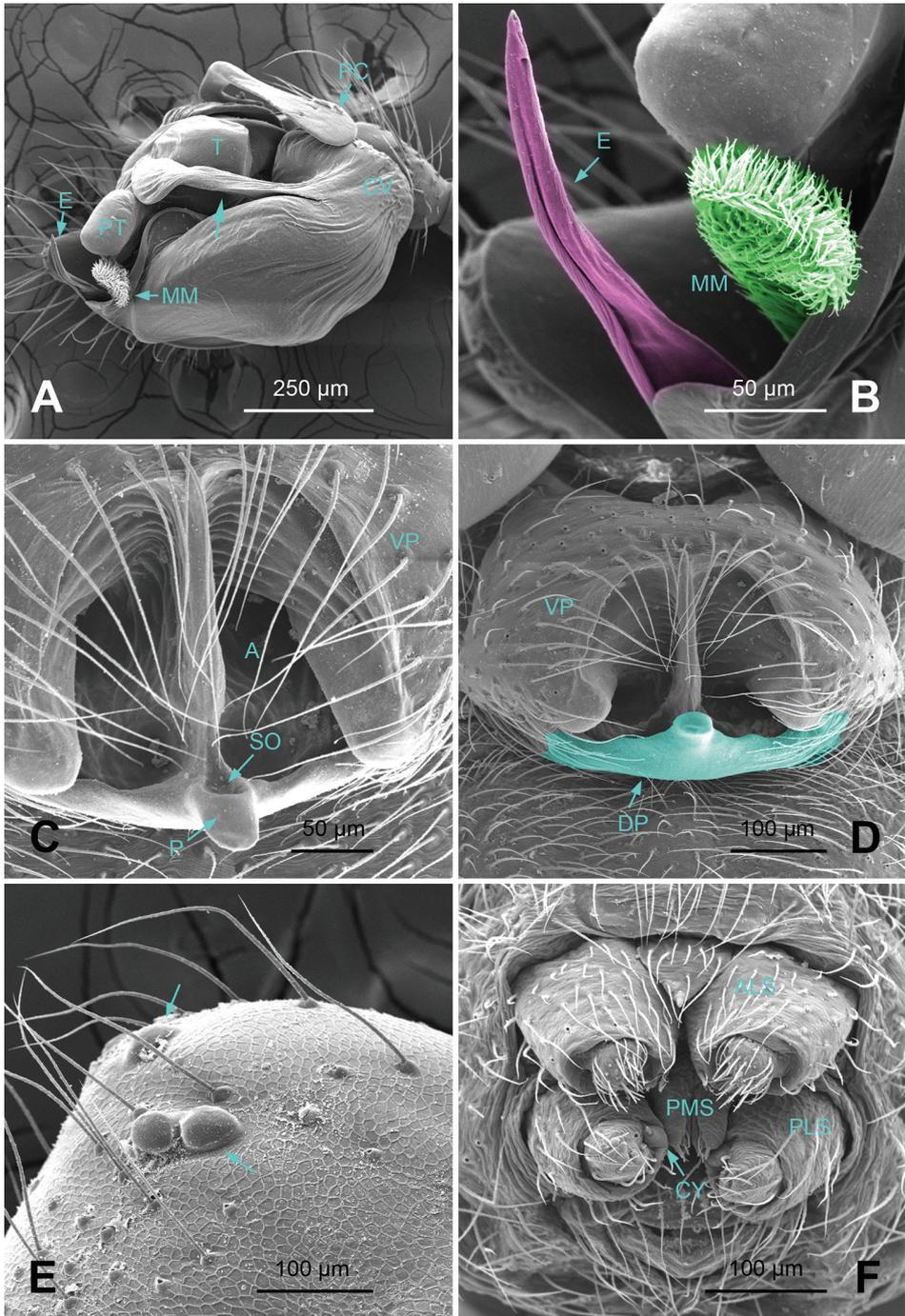


Figure 8. *Callosa baiseensis* sp. n., SEM of a male paratype and a female paratype. **A** Palp of male paratype, ventral view **B** Detail showing embolus and embolic membrane **C** Detail showing scape of epigyne **D** Epigyne of female paratype, ventral view **E** Anterior lateral eye, anterior median eye and posterior lateral eye of male paratype **F** Spinnerets of female paratype.

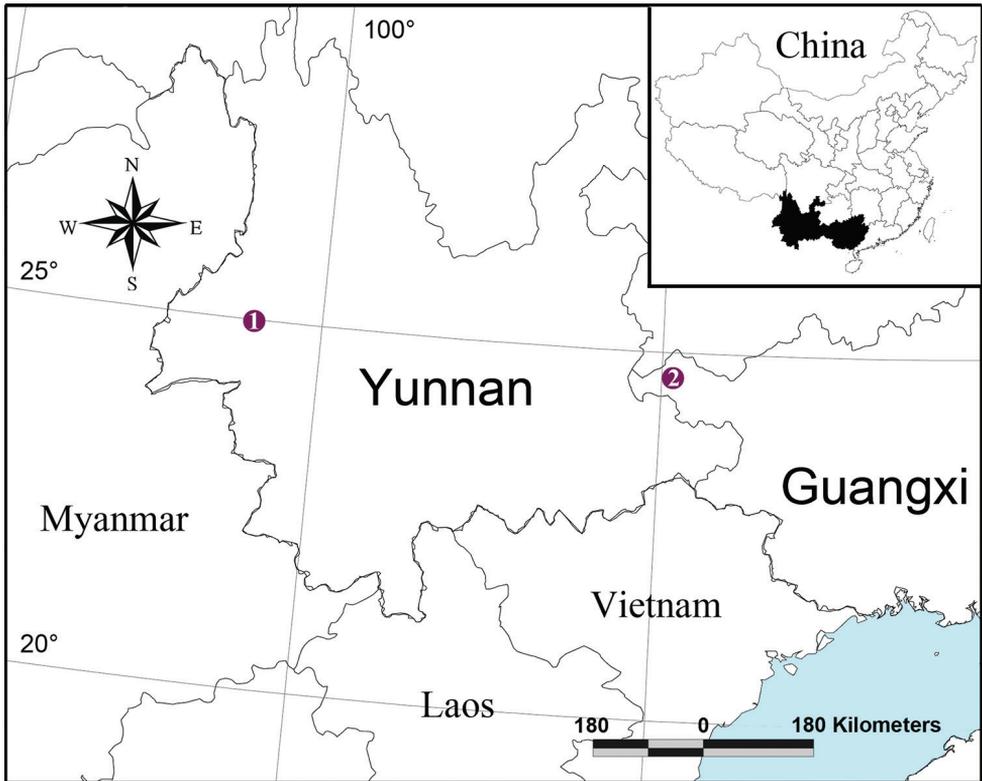


Figure 9. Type localities of new species *Callosa ciliata* sp. n. (1) and *C. baiseensis* sp. n. (2).

Eye sizes: ALE 0.03, PME 0.02, PLE 0.04. Leg length: I 9.25 (2.50, 0.38, 2.80, 2.41, 1.16), II 8.27 (2.28, 0.38, 2.38, 2.23, 1.00), III 6.33 (1.84, 0.40, 1.68, 1.56, 0.85), IV 8.05 (2.38, 0.38, 2.33, 2.03, 0.93). TmI 0.16. Abdomen pale, with dark yellow markings (Fig. 6C–E). Male palp: protégulum medially expanded, then attenuated at tip (Fig. 5B); distal suprategular apophysis with a small, hooked apex (Fig. 5D); embolus coiling from 8 o'clock position in prolateral view (Fig. 5C).

Female. Total length: 2.50. Carapace 1.19 long, 0.94 wide, same coloration as in male. Sternum 0.55 long, 0.63 wide. Clypeus 0.34 high. Eye sizes: ALE 0.05, PME 0.04, PLE 0.05. Leg length I 8.91 (2.48, 0.40, 2.56, 2.34, 1.13), II 8.30 (2.28, 0.40, 2.34, 2.19, 1.09), III 6.29 (1.88, 0.38, 1.63, 1.59, 0.81), IV 7.91 (2.30, 0.38, 2.15, 2.08, 1.00). TmI 0.18. Abdomen with same coloration as in male (Fig. 7D–E). Epigyne: atrium nearly semicircular, partitioned by a septum along the long axis (Fig. 8C–D); copulatory furrows forming 2 coils; receptacles oval separated by 2 diameters, with curved outgrowths (Fig. 7C–D).

Remarks. To confirm the species delimitation, the p-distance of COI sequences of *C. baiseensis* sp. n. and *C. ciliata* sp. n. was calculated using MEGA 6 (Tamura et al.

2013), and the result is 0.12, which falls within the genetic distance interval of 0.07 to 0.16 among *Bathyphantes* species and 0.07 to 0.17 in *Porrhomma* based on data from NCBI (The National Center for Biotechnology Information <https://www.ncbi.nlm.nih.gov/>).

Discussion

Linyphiidae Blackwall, 1859 is not commonly found in caves. In China, in contrast to more than 370 terrestrial linyphiids, only two species have been reported from caves so far (Song and Li 2009), but none of them exhibited traits of cave adaptation, such as depigmentation, reduction or complete loss of eyes, or elongation of legs (Sket 2008). *Callosa* gen. n. is the first true troglobiont linyphiid genus discovered in southwest China, encompassing two new species found in caves almost 600 kilometers apart, and they display apparent characters of true cave dwellers. It is assumed their ancestors were widely distributed in the montane area in southwest China, and almost certainly extrinsic forces (e.g. geological events, climatic changes) drove them to colonize the caves, which are considered to be a relatively stable environment.

Callosa gen. n. belongs to Porrhommini as suggested by both molecular analysis (Fig. 10) and morphological characteristics. It is obviously monophyletic, and its distinctive traits in both body and copulatory organs might be a result of long-term solitary evolution. Despite its morphological similarities to *Bathyphantes* (especially *B. approximatus*), *Callosa* gen. n. is situated relatively farther from *Bathyphantes* in the cladogram (Fig. 10). The taxonomical history of *Bathyphantes* is long and complicated, and several of its subgenera have now been validated as separate genera (e.g. *Kaestneria*, *Diplostyla*, *Pacifiphantes*) based on the conformation of copulatory organs, and some related genera were also established with species transferred from *Bathyphantes* (e.g. *Cresmatoneta* Simon, 1929, *Microbathypantes* Helsdingen, 1985). A better-sampled phylogenetic analysis of Porrhommini was presented by Wang et al. (2015), in which *Bathyphantes* appeared as polyphyletic, with *Pacifiphantes zakharovi* Eskov & Marusik, 1994 grouped with *Bathyphantes eumenis* (L. Koch, 1879). The split between *Porrhomma* + *Diplostyla* and *Bathyphantes* is not well supported. A similar relationship is recovered in our analysis, where *Pacifiphantes zakharovi* is clustered with *Bathyphantes floralis* Tu & Li, 2006 (Fig. 10). It also has been previously pointed out that *Pacifiphantes magnificus* (Chamberlin & Ivie, 1943) could be a misplacement, and probably grouped with *Porrhomma* + *Diplostyla* as indicated by both morphology and DNA barcoding (Slowik and Blagoev 2012). As the type species, *Pacifiphantes zakharovi* was identified with a super short embolus (Eskov and Marusik 1994: fig. 42), the unique trait supposedly distinguishing it from other similar *Bathyphantes*, however, the discrepancy between morphology and molecular analysis results demands a more comprehensive analysis on the delimitation of *Bathyphantes* and its close relatives.

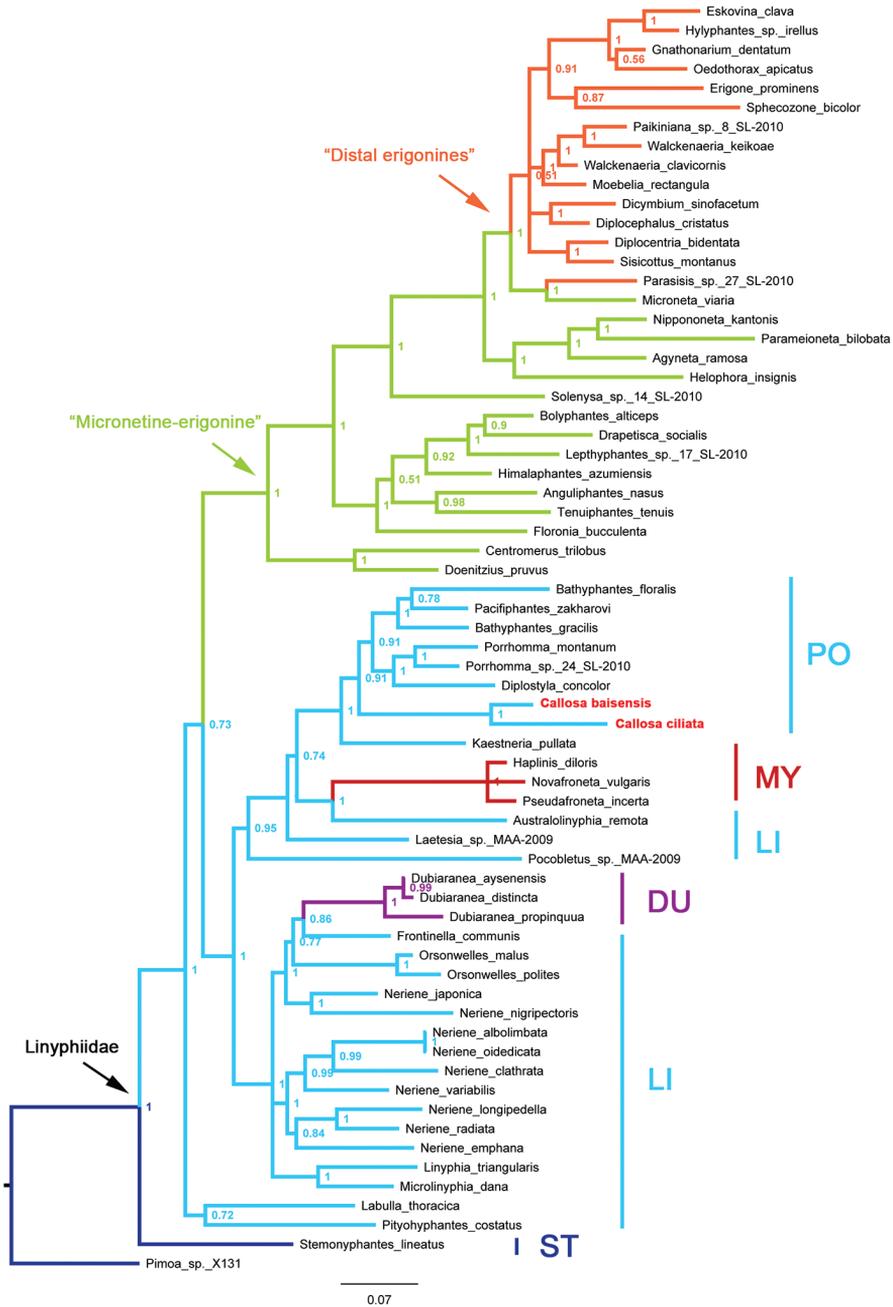


Figure 10. Phylogenetic tree reconstructed using Bayesian inference based on concatenated data. Numbers besides each node are posterior possibilities. Outgroup: *Pimoa* sp. X131 (dark blue) **DU** Dubiaraneinae (purple) **LI** Linyphiinae (blue) **MY** Mynogleninae (red) **PO** Porrhommini (blue) **ST** Stemonyphantinae (dark blue). "Micronetines-erigonines" clade is presented in green, the "distal erigonines" clade is colored in orange. Taxa with sequences downloaded from NCBI are listed at the end of each branch in black accordingly, and *Callosa* gen. n. species are marked in red.

Acknowledgement

The manuscript benefited greatly from comments by Yuri M. Marusik (Magadan, Russia) and Andrei Tanasevitch (Moscow, Russia). Donald J Buckle (Saskatoon, Canada) kindly improved the English. This study was supported by the National Natural Sciences Foundation of China (NSFC-31672260, 31471960) and the Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences (2015CASEABRI005, Y4ZK111B01).

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New records of Sarcophagidae from Turkey (Diptera)

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Academic editor: P. Cerretti | Received 23 February 2017 | Accepted 28 July 2017 | Published 28 September 2017

<http://zoobank.org/DC91518D-5544-4CB1-9120-E08609FDCDFD>

Citation: Verves Y, Barták M, Kubík S, Civelek HS (2017) New records of Sarcophagidae from Turkey (Diptera). ZooKeys 703: 129–158. <https://doi.org/10.3897/zookeys.703.12377>

Abstract

Faunistic records of 68 flesh fly species are presented, and altogether, 22 species are recorded from Turkey for the first time. A further 46 species were recorded for the first time in at least one Turkish province. This paper presents the first locality data for four additional species, which were previously mentioned only generically in catalogues. One new synonym has been established, *Servaisia* (s. str.) *rybaltchenkoi* (Verves, 1977) = *Blaesoxipha ataturkia* Lehrer, 2008, **syn. n.** Two new combinations are proposed: *Helicophagella* (*Parabellieria*) *dreyfusi* (Lehrer, 1994), **comb. n.** and *Helicophagella* (s. str.) *bellae* (Lehrer, 2000), **comb. n.**

Keywords

distribution, flesh flies, new combinations, new records, new synonyms, Turkey

Introduction

Sarcophagidae is a large and important family of Calyptrate section of Muscomorpha comprising almost 3,000 species. Adults reach a body length of 2 mm to 22 mm and their larvae have very diverse feeding habits. Some are schizophagous or predacious (i.e., devour other necro- or coprophagous larvae in substrates). The others are obligate or facultative parasitoids of insects (orthopterans, cicadas, beetles, honeybees, etc.), myriapods, terrestrial snails, predators of earthworms, larvae of soil-inhabiting noctuid caterpillars, and pupae of dendrophilous lepidopterans, kleptoparasites of solitary

wasps, bees and, to a lesser extent, termites. Certain species are known to prey on the eggs of marine turtles and lizards, as well as spider egg cocoons and oothecae of locusts. Larvae of many species can facultatively produce wounds or occasional intestinal myiasis on various vertebrates, including humans. Obligate parasites of vertebrates include larvae of several species of *Wohlfahrtia* Brauer & Bergenstamm and some American specialized species with amphibian hosts. Certain synanthropic species are considered mechanical vectors of various intestinal diseases, including poliomyelitis, leprosy, tuberculosis, and mycosis (Rohdendorf 1937; Pape 1996; Povolný and Verves 1997; Verves 1986a; Verves and Khrokalo 2006a, b, 2015; Verves et al. 2015a).

The first reviews of Turkish Sarcophagidae were prepared by Verves (1986a, b) and Kara and Pape (2002); they listed a total of 85 and 81 species, respectively. Many authors have, through various studies, since brought the number of known Turkish species to 137 (Civelek and Tezcan 2005; Lehrer 2006; Aslan 2006; Hayat et al. 2008; Aslan and Çalişkan 2009; Gözüaçık and Mart 2009; Karaman et al. 2009; Pekbey and Hayat 2010; Xue et al. 2011, 2015; Koçak 2014; Koçak and Kemal 2009, 2012, 2013, 2015; Whitmore 2011; Pekbey and Hayat 2011, 2013a, b, c; Whitmore et al. 2013; Verves & Khrokalo 2015; Verves et al. 2015b; Kemal and Koçak 2015; Pekbey 2011; Pekbey et al. 2011 a, b). Other studies provided detailed data for the species causing obligate myiasis [*Wohlfahrtia magnifica* (Schiner)], and several facultative myiasis-causing species (Kurtpinar 1950; Dinçer 1997; Çiftçioglu et al. 1997; Şaki and Özer 1999a, b; Dinçer et al. 2001; Sevgili et al. 2004; Kökçam and Şaki 2005; Yuca et al., 2005; Ütük 2006; Büyükkurt et al. 2008; Aydenizöz and Dik 2008; Yildirim et al. 2008; Yazgi et al. 2009; İpek et al. 2009; Tuygun et al. 2009; Bayındır et al. 2010; İpek and Şaki 2010; Akduman et al. 2010; Kara and Arslan 2011; Dik et al. 2012; Övet et al. 2012; Kılınç et al. 2013; Ozsoy et al. 2013; Köse et al. 2013; Çevik et al. 2014; Özdemir et al. 2014; Gümüşsoy et al. 2015). The true number of Turkish sarcophagids may range from 175 to 250 species. The main aim of the present paper is to capitalize on the results of several expeditions to Turkey and in such a way to enrich knowledge on the flesh fly fauna of Turkey.

Materials and methods

The material examined in this study originates from southwestern Turkey, mainly from the Muğla province but also, to a minor extent, from the four adjacent provinces of Aydın, Burdur, Denizli, and Antalya and from the Samsun province. Most of the material was obtained during field expeditions of M. Barták and Š. Kubík using Malaise traps (**MT**) and yellow pan traps (**PT**), and by sweeping of vegetation (**SW**). Some specimens were collected by the senior author (**YV**) in southern Turkey in 2010–2011. Most of the specimens were originally preserved in alcohol and later dried and mounted using the method described by Barták (1997).

All specimens were identified by the senior author using numerous published keys, descriptions, and illustrations (Rohdendorf 1955, 1971, 1975, 1988; Verves 1982a, 1982b, 1985, 1989a, 1989b, 1993, 1994, Verves and Khrokalo 2006a, Whitmore

2011, Xue et al. 2011). In this paper, we included only reliably identified species. Specimens with uncertain identity and/or belonging to undescribed species will be published at a later date. We follow the classification scheme of Rohdendorf (1965, 1967) with subsequent additions of Verves (1986), Povolný and Verves (1997), Verves & Khrokalo (2006a, b, 2009, 2015), Verves et al. (2015b), Xue et al. (2011, 2015).

Distributional data of sarcophagids in Turkey were derived from the analysis of all available publications (see reference list). General species distribution was derived from Pape (1996, 2015), Povolný and Verves (1997), Verves & Khrokalo (2006a, b, 2009, 2015), Verves et al. (2015b), Xue et al. (2011, 2015) and other sources (as indicated under several species treated below). Classification of distributional ranges follows Gorodkov (1983, 1984).

Voucher specimens are deposited at **CULSP** (Czech University of Life Sciences, Prague, Czech Republic) and **IEE** (Institute for Evolutionary Ecology, National Academy of Sciences, Kyiv, Ukraine). Other abbreviations are used in text as follows: **DI** distribution, **DIT** distribution in Turkey, **TR** Turkey (species listed in catalogs without specification of locality data). Provinces are abbreviated as follows:

AD (Adana), **AF** (Afyonkarahisar), **AM** (Amasya), **AN** (Ankara), **ANT** (Antalya), **AY** (Aydın), **BT** (Batman), **BY** (Bayburt), **BO** (Bolu), **BU** (Burdur), **CA** (Çanakkale), **DE** (Denizli), **DB** (Diyabakir), **DU** (Düzce), **ED** (Edirne), **EL** (Elazığ), **ER** (Erzincan), **ERZ** (Erzurum), **ES** (Eskişehir), **GA** (Gaziantep), **HA** (Hakkari), **HT** (Hatay), **IG** (İğdır), **IZ** (İzmir), **KM** (Karaman), **KAR** (Kars), **KY** (Kayseri), **KI** (Kırıkkale), **KK** (Kırklareli), **KN** (Konya), **MN** (Manisa), **MR** (Mardin), **ME** (Mersin), **MG** (Muğla), **SA** (Samsun), **SN** (Şanlıurfa), **TO** (Tokat), **TB** (Trabzon), **VA** (Van).

Results

Species newly recorded from Turkey are marked with an asterisk (*), and from individual provinces with two asterisks (**). Localities are listed alphabetically according to province and locality names.

Subfamily Miltogramminae

Tribe Miltogrammini

Subtribe Senotainiina

Senotainia (Arrenopus) albifrons (Rondani, 1859)

Material examined. **AY:** 8 km S of Çine, river bank, SW, 68 m, 37°32'34"N, 28°03'46"E, 28.–30.vi.2015 (Barták & Kubík), 3 ♂, 3 ♀; **MG:** Akyaka, pasture, 4 m, 37°03'09"N, 28°20'17"E, 8.–14.ix.2014 (Barták & Kubík), 1 ♂; *ibid.*, salty meadow, 2 m, PT, 37°01'49"N, 28°20'01"E, 22.vi.–1.vii.2015 (Barták & Kubík), 17 ♂, 17 ♀; *ibid.*, 37°01'62"N, 28°20'00"E, 27.iv.–1.v.2016 (Barták & Kubík), 3 ♀; Dalyan, farm,

MT, 1 m, 36°48'54"N, 28°39'04"E, 8.–20.viii.2015 (Dursun), 1 ♂, 1 ♀ Muğla Univ. campus, SW+PT, 700 m, 37°09'39"N, 28°22'20"E, xi.–iii.2013 (Barták & Kubík), 1 ♀; *ibid.*, 730 m, MT, 37°09'38"N, 28°22'11"E, 5.–19.viii.2015 (H. Kavak), 1 ♂; **SA**: Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 14 ♂, 1 ♀ (CULSP).

DI: Trans-Palaeartic-Afrotropical-Oriental.

DIT: **ANT** (Koçak and Kemal 2009, 2012, 2015; Kara and Pape 2002), **AY****, **MG****, **SA****.

Subtribe *Miltogrammina*

Miltogramma aurifrons Dufour, 1850*

Material examined. **MG**: Muğla University campus, Malaise trap, 700 m, 37°09'42"N, 28°22'21"E (O.Dursun), v.2013, 1 ♂; *ibid.*, SW+PT, 37°09'42"N, 28°22'21"E, 29.iv.–10.v.2013 (Barták & Kubík), 2 ♂; *ibid.*, 730 m, 37°09'38"N, 28°22'11"E, xi.2015–iv.2016 (Barták & Kubík), 2 ♀; Muğla – 13 km NE, pine wood, 1200 m, 37°14'50"N, 28°30'00"E, 23–27.v.2016 (Barták & Kubík), 1 ♀ (CULSP).

DI: Mediterranean.

DIT: **MG****.

Miltogramma brevipila Villeneuve, 1911*

Material examined. **AY**: 8 km S of Çine, river bank, 68 m, 37°32'34"N, 28°03'46"E, 10.–12.ix.2014 (Barták & Kubík), 1 ♀ (CULSP).

DI: West-Central Palaeartic.

DIT: **AY****.

Miltogramma murina Meigen, 1824

Material examined. **MG**: Muğla University campus, MT, 730 m, 37°09'38"N, 28°22'11"E, xi.2015–iv.2016, (Barták & Kubík), 1 ♀ (CULSP).

DI: West Palaeartic.

DIT: **TR** (Povolný and Verves 1997), **MG****.

Miltogramma testaceifrons (Roser, 1840)*

Material examined. **MG**: Muğla University campus, MT, 730 m, 37°09'38"N, 28°22'11"E, xi.2015–iv.2016 (Barták & Kubík), 1 ♀ (CULSP).

DI: West Palaearctic-Oriental.

DIT: MG**.

Miltogramma turkmenora* Rohdendorf, 1930

Material examined. MG: Muğla University campus, 700 m, SW+PT, 37°09'42"N, 28°22'21"E, 29.iv.–10.v.2013 (Barták & Kubík), 4 ♂, 4 ♀ (CULSP).

DI: Western Middle East.

DIT: MG**.

Subtribe Apodacrina

Apodacra dispar* Villeneuve, 1916

Material examined. AY: 8 km S of Çine, river bank, 68 m, 37°32'34"N, 28°03'46"E, 10.–12.ix.2014 (Barták & Kubík), 1 ♂; **MG:** Muğla University campus, 710 m, MT, 37°09'39"N, 28°22'20"E, xi–iii.2013 (Barták & Kubík), 7 ♀; *ibid.*, 730 m, 37°09'38"N, 28°22'11"E, xi.2015–iv.2016 (Barták & Kubík), 6 ♀ (CULSP).

DI: West Palaearctic-Afrotropical.

DIT: AY**, MG**.

Subtribe Craticulinina

Craticulina barbifera* (Pandellé, 1895)

Material examined. MG: Akyaka, salty meadow, 2 m, 37°01'49"N, 28°20'01"E, 22.vi.–1.vii.2015 (Barták & Kubík), 1 ♀; Dalyan, salty meadow, PT, 36°47'49"N, 28°38'55"E, 28.–30.iv.2016 (Barták & Kubík), 1 ♂ 1 ♀ (CULSP).

DI: Mediterranean.

DIT: MG**.

Tribe Metopiaini

Subtribe Metopiaina

***Metopia argyrocephala* (Meigen, 1824)**

Material examined. AY: 8 km S of Çine, river bank, SW, 68 m, 37°32'34"N, 28°03'46"E, 28.–30.vi.2015 (Barták & Kubík), 1 ♂; **MG:** Muğla University campus, SW+PT, 700 m, 37°09'41"N, 28°22'21"E, 29.iv.–10.v.2013 (Barták & Kubík), 3 ♂,

1 ♀; *ibid.*, 720 m, MT, 37°09'42"N, 28°22'13"E, 26.v.–26.vi.2015 (H. Kavak), 1 ♂, 1 ♀; *ibid.*, 26–27.vi.2015 (Barták & Kubík), 1 ♀; **SA**: Samsun, University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 12 ♂, 1 ♀ (CULSP).

DI: Trans Palaearctic-Nearctic-Oriental-Neotropical.

DIT: **TR** (Kara and Pape 2002; Koçak 2014; Koçak and Kemal 2009, 2012, 2015), **AY****, **MG****, **SA****.

Metopia grandii Venturi, 1953*

Material examined. MG: Akyaka, pasture, 4 m, YPWT, 37°03'09"N, 28°20'17"E, 13.–14.ix.2014 (Barták & Kubík), 1 ♂ (CULSP).

DI: Palaearctic.

DIT: **MG****.

Subtribe Taxigrammina

Paragusia elegantula (Zetterstedt, 1844)

Material examined. MG: Muğla University campus, 720 m, MT, 37°09'42"N, 28°22'13"E, iv.2015 (H. Kavak), 1 ♀ (CULSP).

DI: European-Siberian-Mid-Asiatic.

DIT: **TR** (Kara and Pape 2002; Koçak 2014; Koçak and Kemal 2009, 2012, 2013, 2015), **MG****.

Paragusia multipunctata (Rondani, 1859)*

Material examined. MG: Muğla University campus, 710 m, MT, 37°09'39"N, 28°22'20"E, xi.–iii.2013 (Barták & Kubík), 1 ♀; *ibid.*, 720 m, 37°09'42"N, 28°22'13"E, iv.2015 (H. Kavak), 1 ♀ (CULSP).

DI: West Palaearctic-Afrotropical-Oriental.

DIT: **MG****.

Taxigramma heteroneura (Meigen, 1830)

Material examined. AY: 8 km S of Çine river bank, 68 m, 37°32'34"N, 28°03'46"E, 10.–12.ix.2014 (Barták & Kubík), 1 ♂, 1 ♀; *ibid.*, 28.–30.vi.2015 (Barták & Kubík), 2 ♂; **MG**: Muğla University campus, MT, 730 m, 37°09'38"N, 28°22'11"E, xi.2015–iv.2016 (Barták & Kubík), 3 ♂, 4 ♀ (CULSP).

DI: Trans Palaearctic-Nearctic-Oriental.

DIT: TR (Kara and Pape 2002; Koçak 2014; Koçak and Kemal 2009, 2012, 2013, 2015), **AY****, **MG****.

Subtribe Sphenometopiina

Sphenometopa (Xantharaba) steini (Schiner, 1862)

Material examined. MG: Muğla University campus, 700 m, PT, 37°09'42"N, 28°22'21"E (O. Dursun), v.2013, 2 ♀ (CULSP).

DI: Eastern Mediterranean.

DIT: TR (Koçak 2014; Koçak and Kemal 2012), **AN** (Koçak and Kemal 2009, 2013, 2015), **MG****.

Tribe Phyllotelini

Subtribe Arabiscina

Sphecapatodes ornatus Villeneuve, 1912*

Material examined. MG: Toparlar waterfall, 44 m, 36°59'73"N, 28°38'08"E, 30.v.2009 (O. Dursun), 3 ♂, 1 ♀ (CULSP).

DI: East Mediterranean-Midasiatic.

DIT: **MG****.

Subfamily Paramacronychiinae

Tribe Nyctiini

Nyctia halterata (Panzer, 1798)

Material examined. AY: 8 km S of Çine, river bank, 68 m, 37°32'34"N, 28°03'46"E, 10.–12.ix.2014 (Barták & Kubík), 1 ♂; *ibid.*, 28.–30.vi.2015 (Barták & Kubík), 1 ♂; *ibid.*, 29.iv.–1.v.2016 (Barták & Kubík), 2 ♂; **MG:** Akyaka, pasture, YPWT, 37°03'09"N, 28°20'17"E, 4 m, 13.–14.ix.2014 (Barták & Kubík), 1 ♂; *ibid.*, 4 m, 37°03'09"N, 28°20'17"E, 8.–14.ix.2014 (Barták & Kubík), 1 ♂; *ibid.*, salty meadow, 2 m, 37°01'49"N, 28°20'01"E, 22.vi.–1.vii.2015 (Barták & Kubík), 1 ♂, 1 ♀ (CULSP).

DI: West Palaearctic.

DIT: TR (Koçak 2014; Koçak and Kemal 2012), **AM** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015), **AY****, **MG****, **TO** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015).

***Nyctia lugubris* (Macquart, 1843)**

Material examined. MG: Kızılyaka, on flowers, 105 m, 37°01'21"N, 28°26'18"E, 27.iv.–4.v.2016 (Barták & Kubík), 1 ♂, 1 ♀; Akyaka, salty meadow, 2 m, 37°01'49"N, 28°20'01"E, 22.vi.–1.vii.2015 (Barták & Kubík), 5 ♂; *ibid.*, PT, 37°01'62"N, 28°20'00"E, 27.iv.–1.v.2016 (Barták & Kubík), 1 ♂; Dalyan, salty meadow, PT, 36°47'49"N, 28°38'55"E, 28.–30.iv.2016 (Barták & Kubík), 2 ♂ (CULSP).

DI: Mediterranean.

DIT: TR (Koçak 2014; Koçak and Kemal 2012), BU (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015), **MG****, SA (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015).

Tribe Paramacronychiini**Subtribe Wohlfahrtriina*****Sarcophila canaanita* Lehrer, 2007***

Material examined. ANT: Side, 36°47'38"N, 31°22'43"E, 10.–19.viii.2011 (Yu. Verves), 19 ♂♂, 14 ♀♀ (IEE); **AY:** 8 km S of Çine river bank, 68 m, 37°32'34"N, 28°03'46"E, 10.–12.ix.2014 (Barták & Kubík), 1 ♂; *ibid.*, 28.–30.vi.2015 (Barták & Kubík), 1 ♂; **MG:** Muğla University campus, 720 m, MT, 37°09'42"N, 28°22'13"E, iv.2015 (H. Kavak), 1 ♂; Akyaka, salty meadow, 2 m, PT, 37°01'62"N, 28°20'00"E, 27.iv.–1.v.2016 (Barták & Kubík), 1 ♂; 4 km N of Yatağan, flowers, 460 m, 37°22'12"N, 28°09'22"E, 30.vi.2016 (Barták & Kubík), 3 ♂ (CULSP).

DI: East Mediterranean.

DIT: ANT**, AY**, MG**.

***Sarcophila latifrons* (Fallén, 1817)**

Material examined. MG: MuğlaUniv. campus, protein trap, pine wood, 700 m, 37°09'41"N, 28°22'21"E, xi–iii.2013 (Barták & Kubík), 1 ♂; Toparlar, Toparlar waterfall, 44 m, 36°59'73"N, 28°38'08"E, 30.v.2009 (O. Dursun), 1 ♂ (CULSP).

DI: West-Central Palaearctic.

DIT: TR (Aksoy and Bahadıroğlu 2012; Koçak 2014; Koçak and Kemal 2012), AD (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015), ADI (Gözüaçık and Mart 2009), BT (Gözüaçık and Mart 2009), MR (Gözüaçık and Mart 2009), **MG****, SN (Gözüaçık and Mart 2009; Kara and Pape 2002; Koçak and Kemal 2009, 2015).

***Sarcophila meridionalis* Rohdendorf & Verves, 1982**

Material examined. MG: Akyaka, pasture, 6 m, 37°03'19"N, 28°20'07"E, 28.iv–8.v.2013 (Barták & Kubík), 1 ♂; *ibid.* 4 m, 37°03'09"N, 28°20'17"E, 8.–14.ix.2014 (Barták & Kubík), 1 ♂; Muğla University campus, Malaise trap, 700 m, 37°09'42"N, 28°22'21"E (O. Dursun), v.2013, 2 ♂ (CULSP).

DI: West-Central Palaearctic.

DIT: TR (Koçak 2014; Koçak and Kemal 2012), ER (Koçak and Kemal 2015; Pekbey 2011; Pekbey and Hayat 2013b), ERZ (Koçak and Kemal 2013, 2015; Pekbey 2011; Pekbey and Hayat 2010, 2013b), **MG****.

Subfamily Sarcophaginae**Tribe Protodexiini****Subtribe Protodexiina*****Blaesoxipha confusa* Villeneuve, 1912***

Material examined. SN: Birecik, E from Gaziantep, pastures SE from town, 37.00N/38.00E, 24.–25.iv.1997 (Vrabec V.), 1 ♂ (CULSP).

DI: West Palaearctic.

DIT: SN**.

***Blaesoxipha redempta* (Pandellé, 1896)**

Material examined. SA: Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 12 ♂, 1 ♀; **MG:** Toparlar, lowland forest, 8 m, 36°59'27"N, 28°38'50"E, 11.ix. 2014 (Barták & Kubík), 1 ♀ (CULSP).

DI: Transpalaearctic-Afrotropical-Oriental-Australasian/Oceanian (Hawaii, imported: Hardy, 1980).

DIT: TR (Kara and Pape 2002; Koçak 2014; Koçak and Kemal 2009 – as *B. lapidosa*), BY (Pekbey 2011; Pekbey and Hayat 2013c), CA (Calvert 1882), ER (Pekbey 2011; Pekbey and Hayat 2013c), ERZ (Pekbey 2011– as *B. lapidosa*; Pekbey and Hayat 2010, 2013c), **MG****, **SA****.

Comment: Analysis of Pape's (1994) description of *B. lapidosa* and redescriptions of *B. redempta* by Leonide and Leonide (1983) and Pape (1994), our opinion is such: *B. lapidosa* is a synonym of *B. redempta*, because the original descriptions and drawings of ♂ genitalia and ovipositors of both species are very detailed and essentially not differentiated from each other.

***Servaisia* (s. str.) *rybaltschenkoi* (Verves, 1977)**

Blaesoxipha ataturkia Lehrer, 2008a, **syn. n.**

DI: European-Anatolian-Midasiatic.

DIT: TR (Koçak 2014 – as *Blaesoxipha ataturkia*; Koçak and Kemal 2012), **HA** (Kemal and Koçak 2015 – as *Blaesoxipha ataturkia*; Koçak and Kemal 2013– as *Blaesoxipha ataturkia*; Lehrer 2008a).

Taxonomic notes: The original description and drawings of ♂ genitalia of male *Blaesoxipha ataturkia* are very detailed and essentially not differentiated from similar descriptions and drawings of ♂ genitalia of *Blaesoxipha rybaltschenkoi* Verves, 1977. The differences in drawings are very petty and reflected the different styles of painters; they cannot be used as reason for separation *B. ataturkia* from *S. rybaltschenkoi*.

Tribe Johnsoniini**Subtribe Sarcotachinellina*****Sarcotachinella sinuata* (Meigen 1826)**

Material examined. MG: Akyaka, pasture, 6 m, 37°03'19"N, 28°20'07"E, 28.iv.–8.v.2013, YPWT (Barták & Kubík), 5 ♂; *ibid.*, pasture, YPWT, 37°03'09"N, 28°20'17"E, 4 m, 13.–14.ix.2014 (Barták & Kubík), 1 ♂; *ibid.*, salty meadow, 2 m, PT, 37°01'62"N, 28°20'00"E, 27.iv.–1.v.2016 (Barták & Kubík), 1 ♂ (CULSP).

DI: Transpalaeartic-Nearctic [Holarctic].

DIT: TR (Koçak 2014; Koçak and Kemal 2012), **AM** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015), **ER** (Pekbey 2011), **ERZ** (Pekbey 2011), **KY** (Hayat et al. 2008; Koçak and Kemal 2009, 2013, 2015), **MG****, **TO** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015).

Tribe Raviniini**Subtribe Raviniina*****Ravinia pernix* (Harris, 1780)**

Material examined. AY: 8 km S of Çine, river bank, 68 m, 37°32'34"N, 28°03'46"E, 10.–12.ix.2014 (Barták & Kubík), 2 ♂; *ibid.*, 28.–30.vi.2015 (Barták & Kubík), 1 ♂; *ibid.*, 29.iv.–1.v.2016 (Barták & Kubík), 1 ♂; **MG:** Muğla Univ. campus, protein trap, pine wood, 700 m, 37°09'41"N, 28°22'21"E, xi.–iii.2013 (Barták & Kubík), 1 ♂; University campus, SW+PT, 700 m, 37°09'41"N, 28°22'21"E, 29.iv.–10.v.2013 (Barták & Kubík), 1 ♂ (CULSP).

DI: Transpalaeartic-Afrotropical-Oriental.

DIT: **TR** (Koçak 2014; Koçak and Kemal 2012), **AD** (Aslan and Çalışkan 2009; Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015), **AY****, **ER** (Pekbey 2011), **ERZ** (Pekbey 2011; Pekbey and Hayat 2010), **ES** (Aslan and Çalışkan 2009), **KY** (Hayat et al. 2008; Koçak and Kemal 2009, 2013, 2015), **KN** (Aslan 2006; Hayat et al. 2008; Kara and Pape 2002; Koçak and Kemal 2013, 2015), **ME** (Aslan 2006; Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015), **MG****, **SN** (Sevgili et al. 2004), **TO** (Aslan 2006; Hayat et al. 2008; Kara et Pape 2002; Koçak and Kemal 2009, 2013, 2015).

Tribe Sarcophagini

Subtribe Helicophagellina

Helicophagella (Parabellieria) macrura (Rohdendorf, 1937)*

Material examined. **AY:** 9 km S of Çine River bank, 70 m, 37°31'36"N, 28°04'29"E, 2.v.2013 (Barták & Kubík), 1 ♂ (CULSP).

DI: Transpalaeartic subboreal.

DIT: **AY****.

Helicophagella (Parabellieria) melanura (Meigen, 1926)

Material examined. **ANT:** Alanya, Avsallar, 36°36'54"N, 31°46'38"E, ground path in bushes, 4–7.viii.2010, (Yu. Verves), 1 ♀; Antalya, Side, clay loam waste plot of land, 36°47'38"N, 31°22'43"E, 10–19.viii.2011 (Yu. Verves), 6 ♂♂, 7 ♀♀ (IEE); **AY:** 9 km S of Çine river bank, 70 m, 37°31'36"N, 28°04'29"E, 2.v.2013 (Barták & Kubík), 2 ♂; *ibid.*, 68 m, 37°32'34"N, 28°03'46"E, 10.–12.ix.2014 (Barták & Kubík), 5 ♂; *ibid.*, 28.–30.vi.2015 (Barták & Kubík), 2 ♂; **MG:** Akyaka, pasture, 2 m, 37°03'09"N, 28°20'17"E, YPWT, 23–27.ix.2012 (Barták & Kubík), 1 ♀; *ibid.*, 6 m, YPWT, 37°03'19"N, 28°20'07"E, 28.iv.–8.v.2013 (Barták & Kubík), 3 ♂; *ibid.*, salty meadow, SW+PT, 37°02'53"N, 28°19'39"E, 28.iv.–9.v.2013 (Barták & Kubík), 1 ♂; *ibid.*, pasture, YPWT, 37°03'09"N, 28°20'17"E, 4 m, 13.–14.ix.2014 (Barták & Kubík), 3 ♂; *ibid.*, 4 m, 37°03'09"N, 28°20'17"E, 8.–14.ix.2014 (Barták & Kubík), 3 ♂; Dalyan, salty meadow, PT, 36°47'49"N, 28°38'55"E, 28.–30.iv.2016 (Barták & Kubík), 1 ♂; **SA:** Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 3 ♂ (CULSP).

DI: Transpalaeartic-Nearctic-Afrotropical-Oriental.

DIT: **TR** (Kara and Pape 2002; Koçak 2014; Koçak and Kemal 2012): **ANT****, **AY****, **BY** (Pekbey 2011), **ER** (Pekbey 2011), **ERZ** (Pekbey 2011; Pekbey and Hayat 2010), **ES** (Aslan 2006; Aslan and Çalışkan 2009; Koçak and Kemal 2009, 2015), **KY** (Hayat et al. 2008; Kara and Pape 2002; Koçak and Kemal 2009, 2015), **MG****, **SA****, **SN** (Hayat et al. 2008; Koçak and Kemal 2009, 2015), **TO** (Aslan 2006).

Helicophagella* (s. str.) *bellae* (Lehrer, 2000), comb. n.Boettcheriola bellae* Lehrer, 2000

Material examined. MG: Muğla – 13 km NE, pine wood, 1200 m, 37°14'50"N, 28°30'00"E, 23.–27.vi.2015 (Barták & Kubík), 1 ♂ (CULSP).

DI: East Mediterranean.

DIT: **TR** (Koçak 2014; Koçak and Kemal 2012); **ANT** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015), **BU** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015), **KM** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015), **MG****.

***Helicophagella* (s. str.) *crassimargo* (Pandellé, 1896)**

Material examined. AY: 8 km S of Çine river bank, 68 m, 37°32'34"N, 28°03'46"E, 10.–12.ix.2014 (Barták & Kubík), 2 ♂; **MG:** Akyaka, pasture, 6 m, 37°03'19"N, 28°20'07"E, 28.iv.–8.v.2013, YPWT (Barták & Kubík), 6 ♂; *ibid.*, YPWT, 37°03'09"N, 28°20'17"E, 4 m, 13.–14.ix.2014 (Barták & Kubík), 7 ♂; Toparlar, 60 m, lowland wood, SW, 36°58'39"N, 28°39'30"E, 5–7.v.2013 (Barták & Kubík), 1 ♂; *ibid.*, SW+PT, 36°58'39"N, 28°39'30"E, 28.–30.iv.2016 (Barták & Kubík), 2 ♂ (CULSP).

DI: European-Siberian-Midasiatic.

DIT: **TR** (Koçak 2014; Koçak and Kemal 2012), **AM** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015), **AY****, **BY** (Pekbey 2011), **ER** (Pekbey 2011), **ERZ** (Pekbey 2011; Pekbey and Hayat 2010), **KY** (Hayat et al. 2008; Koçak and Kemal 2009, 2013, 2015), **MG****, **TO** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015).

Helicophagella* (s. str.) *novella* (Baranov, 1929)

Material examined. MG: Akyaka, pasture, 4 m, 37°03'09"N, 28°20'17"E, 8.–14.ix.2014 (Barták & Kubík), 2 ♂; Toparlar, pasture, YPWT, 37°03'09"N, 28°20'17"E, 4 m, 13.–14.ix.2014 (Barták & Kubík), 9 ♂; **SA:** Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 14 ♂ (CULSP).

DI: European-Anatolian.

DIT: **MG****, **SA****.

***Helicophagella* (s. str.) *noverca* (Rondani, 1860)**

Material examined. SA: Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 5 ♂ (CULSP).

DI: Mediterranean.

DIT: **ES** (Aslan and Çalışkan 2009), **SA****.

***Helicophagella* (s. str.) *novercoides* (Böttcher, 1913)**

Material examined. MG: Muğla University campus, SW+PT, 700 m, 37°09'41"N, 28°22'21"E, 29.iv.–10.v.2013 (Barták & Kubík), 2 ♂; Akyaka, salty meadow, 2 m, PT, 37°01'52"N, 28°20'00"E, 27.iv.–1.v.2016 (Barták & Kubík), 1 ♂; Muğla – 13 km NE, pine wood + pasture, 1100–1300 m, 37°15'N, 28°30'E, 2–3.v.2016 (Barták & Kubík), 1 ♂ (CULSP).

DI: West Palaearctic.

DIT: TR (Koçak 2014; Koçak and Kemal 2012); **ANT** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015), **ERZ** (Pekbey 2011), **MG****.

***Helicophagella* (*Parabellieria*) *dreyfusi* (Lehrer, 1994), comb. n.**

Ahavanella dreyfusi Lehrer, 1994

DI: West Palaearctic-Oriental.

DIT: TR (Kara and Pape 2002; Koçak 2014; Koçak and Kemal 2012, 2013, 2015).

Subtribe Phytosarcophagina***Phytosarcophaga* (s. str.) *destructor* (Malloch, 1929)**

Material examined. AY: 8 km S of Çine, river bank, 68 m, 37°32'34"N, 28°03'46"E, 28.–30.vi.2015 (Barták & Kubík), 1 ♂; *ibid.*, 29.iv.–1.v.2016 (Barták & Kubík), 1 ♂ (CULSP).

DI: West Palaearctic-Afrotropical.

DIT: TR (Koçak 2014; Koçak and Kemal 2012), **AD** (Kara and Pape 2002), **AY****, **MN** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015), **ME** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015).

Subtribe Heteronychiina***Heteronychia* (*Boettcherella*) *helenae* (Trofimov, 1948)**

Material examined. MG: Akyaka, pasture, YPWT, 37°03'09"N, 28°20'17"E, 4 m, 13.–14.ix.2014 (Barták & Kubík), 5 ♂ (CULSP).

DI: Central Palaearctic.

DIT: TR (Koçak 2014; Koçak and Kemal 2012); **ANT** (Verves and Khrokalo 2015), **ERZ** (Pekbey 2011; Pekbey and Hayat 2011, 2013), **IZ** (Koçak and Kemal 2015; Whitmore 2011), **MG****.

Heteronychia (Boettcherella) setinervis (Rondani, 1860)

Material examined. MG: Akyaka, salty meadow, 2 m, 37°01'49"N, 28°20'01"E, 22.vi.–1.vii.2015 (Barták & Kubík), 4 ♂ (CULSP).

DI: West-Central Palaearctic.

DIT: **TR** (Kara and Pape 2002; Koçak 2014; Koçak and Kemal 2012); **ANT** (Verves and Khrokalo 2015), **DE** (Koçak and Kemal 2015; Lehrer 1977), **ERZ** (Pekbey 2011; Pekbey and Hayat 2011), **GA** (Whitmore 2010), **HT** (Koçak and Kemal 2015; Whitmore 2010), **KY** (Hayat et al. 2008; Koçak and Kemal 2009, 2015), **KN** (Verves and Khrokalo 2015), **ME** (Koçak and Kemal, 2015; Verves and Khrokalo 2015; Whitmore 2010), **MG****, **SN** (Koçak and Kemal 2015), **TO** (Koçak and Kemal 2015; Whitmore 2010).

Heteronychia (Ctenodasypygia) minima (Rondani, 1862)

Leclercqiomys mousseti Lehrer, 1976a: 200.

Material examined. MG: Akyaka, pasture, YPWT, 37°03'09"N, 28°20'17"E, 4 m, 13.–14. ix.2014 (Barták & Kubík), 14 ♂; *ibid.*, salty meadow, SW+PT, 37°02'53"N, 28°19'39"E, 28.iv.–9.v.2013 (Barták & Kubík), 9 ♂; *ibid.*, pasture, 4 m, 37°03'09"N, 28°20'17"E, 8.–14.ix.2014 (Barták & Kubík), 10 ♂; *ibid.*, salty meadow, 2 m, 37°01'49"N, 28°20'01"E, 22.vi.–1.vii.2015 (Barták & Kubík), 19 ♂; *ibid.*, PT, 37°01'62"N, 28°20'00"E, 27.iv.–1.v.2016 (Barták & Kubík), 3 ♂; Dalyan, farm, 1 m, MT, 36°48'54"N, 28°39'04"E, 8.–20.viii.2015 (Dursun), 3 ♂; *ibid.*, salty meadow, PT, 36°47'49"N, 28°38'55"E, 28.–30. iv.2016 (Barták & Kubík), 4 ♂; Muğla University campus, MT, 730 m, 37°09'38"N, 28°22'11"E, 19.xiii.–17.ix.2015 (H. Kavak), 4 ♂ (CULSP).

DI: European-Western Middle East.

DIT: **TR** (Koçak 2014; Koçak and Kemal 2012), **AY** (Koçak and Kemal 2013, 2015), **GA** (Lehrer 1976a), **IZ** (Koçak and Kemal 2013, 2015), **MG****.

Heteronychia (Ctenodasypygia) siciliensis (Böttcher, 1913)

Material examined. SN: Birecik, E from Gaziantep, pastures SE from town, 37.00N/38.00E, 24–25.iv.1997 (Vrabec V.), ♂ (CULSP).

DI: Mediterranean.

DIT: **TR** (Kara and Pape 2002; Koçak 2014; Koçak and Kemal 2009, 2012); **ANT** (Verves & Khrokalo 2015), **AY** (Lehrer 1976a), **IZ** (Koçak & Kemal 2015, Whitmore 2011), **SN****.

Heteronychia (Pandelleola) boettcheri (Villeneuve, 1911)

Pandelleola taurica: Lehrer 2008: 1.

Material examined. **AY:** 8 km S of Çine river bank, 68 m, 37°32'34"N, 28°03'46"E, 10.–12.ix.2014 (Barták & Kubík), 3 ♂; *ibid.*, 28.–30.vi.2015 (Barták & Kubík), 10 ♂; *ibid.*, SW, 29.iv.–1.v.2016 (Barták & Kubík), 3 ♂, **MG:** Akyaka, pasture, YPWT, 37°03'09"N, 28°20'17"E, 4 m, 13.–14.ix.2014 (Barták & Kubík), 1 ♂; *ibid.*, 8.–14.ix.2014 (Barták & Kubík), 3 ♂ (CULSP).

DI: European-Mid Eastern.

DIT: **TR** (Kara and Pape 2002 – as *Sarcophaga (Heteronychia) taurica*; Koçak 2014; Koçak and Kemal 2009 – as *Sarcophaga (Heteronychia) taurica*, 2012); **AM** (Koçak and Kemal 2013, 2015; Whitmore 2011), **ANT** (Verves & Khrokalo 2015), **AY****, **BO** (Lehrer 1977 – as *Heteronychia (Pandelleola) gaspari*), **DU** (Koçak & Kemal 2015), **ER** (Pekbey 2011; Pekbey and Hayat 2011, 2013°), **ERZ** (Pekbey 2011; Pekbey and Hayat 2011, 2013°), **ME** (Koçak and Kemal 2013, 2015; Whitmore 2011), **MG****, **SA** (Koçak and Kemal 2013, 2015; Whitmore 2011), **TO** (Koçak and Kemal 2013, 2015; Whitmore 2011).

Heteronychia (Pandelleola) filia (Rondani, 1860)

Material examined. **AY:** 8 km S of Çine, river bank, 68 m, 37°32'34"N, 28°03'46"E, 10.–12.ix.2014 (Barták & Kubík), 1 ♂; *ibid.*, 28.–30.vi.2015 (Barták & Kubík), 6 ♂; *ibid.*, 29.iv.–1.v.2016 (Barták & Kubík), 3 ♂; **MG:** Akyaka, pasture, YPWT, 37°03'09"N, 28°20'17"E, 4 m, 13.–14.ix.2014 (Barták & Kubík), 6 ♂; *ibid.*, 8.–14.ix.2014 (Barták & Kubík), 1 ♂; *ibid.*, salty meadow, 2 m, PT, 37°01'49"N, 28°20'01"E, 22.vi.–1.vii.2015 (Barták & Kubík), 1 ♂; 4 km N of Yatağan, flowers, 460 m, 37°22'12"N, 28°09'22"E, 30.vi.2016 (Barták & Kubík), 1 ♂; Kızılyaka, on flowers, 105 m, 37°01'21"N, 28°26'18"E, 27.iv.–4.v.2016 (Barták & Kubík), 1 ♂; **SA:** Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 1 ♂ (CULSP).

DI: West Palaearctic.

DIT: **TR** (Koçak 2014; Koçak and Kemal 2012), **AM** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015; Whitmore 2011), **ANT** (Whitmore 2011; Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015; Verves and Khrokalo 2015; Whitmore 2011), **AY****, **BY** (Pekbey 2011; Pekbey and Hayat 2011), **ER** (Pekbey 2011; Pekbey and Hayat 2011), **ERZ** (Pekbey 2011; Pekbey and Hayat 2011), **ES** (Aslan 2006; Aslan and Çalışkan 2009; Koçak and Kemal 2009, 2013, 2015), **KY** (Hayat et al. 2008; Koçak and Kemal 2009, 2015), **MG****, **SA** (Kara and Pape 2002; Koçak and Kemal 2009, 2015), **TO** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015; Whitmore 2011), **TB** (Hayat et al. 2008; Koçak and Kemal 2009, 2013, 2015).

Heteronychia (s. str.) *bulgarica* (Enderlein, 1936)

Material examined. **SA:** Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 1 ♂ (CULSP).

DI: European-Mid Eastern.

DIT: **BY** (Pekbey 2011; Pekbey and Hayat 2011, 2013a), **ER** (Pekbey and Hayat 2011, 2013a), **ERZ** (Pekbey 2011; Pekbey and Hayat 2011, 2013a), **SA****.

***Heteronychia* (s. str.) *haemorrhoides* (Böttcher, 1913)**

Heteronychia wahisi Lehrer, 1976b: 264.

Material examined. **AY:** 8 km S of Çine, river bank, SW, 68 m, 37°32'34"N, 28°03'46"E, 28.–30.vi.2015 (Barták & Kubík), 1 ♂; **MG:** Akyaka, pasture, 6 m, 37°03'19"N, 28°20'07"E, YPWT, 28.iv.–8.v.2013, (Barták & Kubík), 4 ♂; *ibid.*, forest, 30 m, YPWT, 37°03'16"N, 28°19'35"E, 30.iv.–9.v.2013, (Barták & Kubík), 1 ♂; *ibid.*, pasture, YPWT, 37°03'09"N, 28°20'17"E, 4 m, 13.–14.ix.2014 (Barták & Kubík), 5 ♂; **SA:** Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 2 ♂ (CULSP).

DI: European-Middle East-Mid Asiatic.

DIT: **TR** (Kara and Pape 2002; Koçak 2014; Koçak and Kemal 2009, 2012), **AM** (Koçak and Kemal 2013, 2015; Whitmore 2010), **AY****, **ER** (Pekbey 2011; Pekbey and Hayat 2011, 2013°), **ERZ** (Pekbey 2011; Pekbey and Hayat 2011, 2013°), **HT** (Koçak and Kemal 2013, 2015; Lehrer 1976b), **MG****, **SA****, **TO** (Koçak and Kemal 2013, 2015; Whitmore 2010).

Heteronychia* (s. str.) *infixa* (Böttcher, 1913)

Material examined. **SA:** Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 1 ♂ (CULSP).

DI: European-Anatolian.

DIT: **SA****.

***Heteronychia* (s. str.) *kerteszi* (Villeneuve, 1912)**

Material examined. **MG:** Muğla University campus, 700 m, SW+PT, 37°09'41"N, 28°22'21"E, 29.iv.–10.v.2013 (Barták & Kubík), 3 ♂; *ibid.*, 700 m, 37°09'42"N, 28°22'22"E (O.Dursun), iv.–v.2014, 1 ♂; *ibid.*, 720 m, MT, 37°09'42"N, 28°22'13"E, iv.2015 (H. Kavak), 1 ♂; *ibid.*, 26–27.vi.2015 (Barták & Kubík), 2 ♂; Muğla – 13 km NE, pine wood, 1200 m, 37°14'50"N, 28°30'00"E, 23–27.vi.2015 (Barták & Kubík), 1 ♂ (CULSP).

DI: East Mediterranean.

DIT: **TR** (Koçak 2014; Koçak and Kemal 2012), **ANT** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015), **IZ** (Koçak and Kemal 2013, 2015; Whitmore 2011), **MG****.

***Heteronychia* (s. str.) *lacrymans* (Villeneuve, 1912)**

Material examined. MG: Akyaka, pasture, YPWT, 37°03'09"N, 28°20'17"E, 4 m, 13.–14.ix.2014 (Barták & Kubík), 6 ♂ (CULSP).

DI: East Mediterranean.

DIT: TR (Koçak 2014; Koçak and Kemal 2012), AF (Kara and Pape 2002 – as *Sarcophaga* (*Heteronychia*) *zhelochovtzevi*; Koçak and Kemal 2009 – as *Sarcophaga* (*Heteronychia*) *zhelochovtzevi*, 2013, 2015; Whitmore 2011), ER (Pekbey 2011; Pekbey and Hayat 2011, 2013°), ERZ (Pekbey 2011; Pekbey and Hayat 2011, 2013°), MG**.

Heteronychia* (s. str.) *pontica* (Rohdendorf, 1937)

Material examined. SA: Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 13 ♂ (CULSP).

DI: East Mediterranean.

DIT: SA**.

Heteronychia* (s. str.) *porrecta* (Böttcher, 1913)

Material examined. SA: Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 1 ♂ (CULSP).

DI: European-Anatolian.

DIT: SA**.

***Heteronychia* (s. str.) *schineri* (Bezzi, 1891)**

Material examined. SA: Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 1 ♂.

DI: European-Mid Eastern.

DIT: TR (Koçak 2014), AM (Kara and Pape 2002; Koçak and Kemal 2009, 2012, 2013, 2015), BY (Pekbey 2011; Pekbey and Hayat 2011, 2013°), SA**, TO (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015).

Karovia* *hirticrus* (Pandellé, 1896)

Material examined. SA: Samsun University campus, 41°22'N, 36°11'E, 22.vi.–4.vii.2014 (Barták & Kubík), 1 ♂ (CULSP).

DI: West Palaearctic.

DIT: SA**.

Subtribe Phallanthina***Bellieriomima subulata* (Pandellé, 1896)***

Material examined. SA: Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 4 ♂ (CULSP).

DI: European-Siberian-Central Asiatic.

DIT: SA**.

Myorhina* (s. str.) *lunigera* (Böttcher, 1914)

Material examined. SA: Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 1 ♂ (CULSP).

DI: European-Mid Eastern.

DIT: SA**.

***Myorhina* (s. str.) *nigriventris* (Meigen, 1826)**

Material examined. MG: Akyaka, forest, 30 m, 37°03'16"N, 28°19'35"E, 30.iv.–9.v.2013, YPWT (Barták & Kubík), 1 ♂; *ibid.*, pasture, 8 m, 37°03'11"N, 28°20'33"E, 27.iv.2016 (Barták & Kubík), 1 ♂; 4 km N of Yatağan, flowers, 460 m, 37°22'12"N, 28°09'22"E, 30.vi.2016 (Barták & Kubík), 2 ♂; AY: 8 km S of Çine, river bank, SW, 68 m, 37°32'34"N, 28°03'46"E, 28.–30.vi.2015 (Barták & Kubík), 1 ♂; *ibid.*, 28.–30.vi.2015 (Barták & Kubík), 3 ♂; *ibid.*, PT, 37°32'34"N, 28°03'46"E, 29.iv.–1.v.2016 (Barták & Kubík), 1 ♂; SA: Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 8 ♂ (CULSP).

DI: West Palaearctic.

DIT: TR (Koçak 2014; Koçak and Kemal 2012); AM (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015), BY (Pekbey 2011), ER (Pekbey 2011), ERZ (Pekbey 2011; Pekbey and Hayat 2010), MG**, SA**, TO (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015).

Myorhina* (s. str.) *socrus* (Rondani, 1860)

Material examined. MG: Muğla – 13 km NE, pine wood, 1200 m, 37°14'50"N, 28°30'00"E, 23–27.v.i.2016 (Barták & Kubík), 2 ♂, 1 ♀; Toparlar, 8 m, lowland forest, SW+PT, 36°58'39"N, 28°39'30"E, 28.–30.iv.2016 (Barták & Kubík), 1 ♂ (CULSP).

DI: European-Mid Eastern.

DIT: MG**.

***Myorbina* (s. str.) *soror* (Rondani, 1860)**

Material examined. **AY:** 8 km S of Çine, river bank, 68 m, PT, 37°32'34"N, 28°03'46"E, 29.iv.–1.v.2016 (Barták & Kubík), 1 ♂; **MG:** Akyaka, pasture, 6 m, 37°03'19"N, 28°20'07"E, YPWT, 28.iv.–8.v.2013, (Barták & Kubík), 2 ♂; *ibid.*, YPWT, 37°03'09"N, 28°20'17"E, 4 m, 13.–14.ix.2014 (Barták & Kubík), 10 ♂; *ibid.*, 37°03'09"N, 28°20'17"E, 8.–14.ix.2014 (Barták & Kubík), 2 ♂; **SA:** Samsun University campus, 41°22'N, 36°11'E, 22.vi.–4.vii.2014 (Barták & Kubík), 13 ♂ (CULSP).

DI: Westpalaeartic.

DIT: **TR** (Koçak 2014; Koçak and Kemal 2012); **AM** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015), **AY****, **BY** (Pekbey 2011), **ER** (Pekbey 2011), **ERZ** (Pekbey 2011), **MG****, **SA** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015).

***Pandelleana protuberans* (Pandellé, 1896)**

Material examined. **ANT:** Güzelsu nr Akseki, 5.vi.2005 (C. Bystrowski), 1 ♂ (CULSP).

DI: European-Siberian-Centralasiatic.

DIT: **TR** (Koçak 2014; Koçak and Kemal 2012, 2013, 2015, "Anatolia": Rohdendorf 1937), **ANT****, **ERZ** (Pekbey 2011), **ES** (Aslan and Çalışkan 2009).

***Pandelleana tabtaliana* Lehrer, 2004**

Material examined. **MG:** Muğla University campus, SW+PT, 700 m, 37°09'41"N, 28°22'21"E, 29.iv.–10.v.2013 (Barták & Kubík), 1 ♂; Muğla – 13 km NE, pine wood + pasture, 1100–1300 m, 37°15'N, 28°30'E, 2–3.v.2016 (Barták & Kubík), 1 ♂ (CULSP).

DI: Anatolian.

DIT: **KY** (Lehrer 2004), **KN** (Lehrer 2004), **MG****.

***Pseudothyrsocnema spinosa* (Villeneuve, 1912)**

Material examined. **AY:** 8 km S of Çine river bank, 68 m, 37°32'34"N, 28°03'46"E, 10.–12.ix.2014 (Barták & Kubík), 1 ♂; *ibid.*, 28.–30.vi.2015 (Barták & Kubík), 3 ♂; *ibid.*, PT, 37°32'34"N, 28°03'46"E, 29.iv.–1.v.2016 (Barták & Kubík), 1 ♂; **MG:** Akyaka, pasture, 6 m, 37°03'19"N, 28°20'07"E, 28.iv.–8.v.2013, YPWT (Barták & Kubík), 4 ♂; *ibid.*, salty meadow, SW+PT, 37°02'53"N, 28°19'39"E, 28.iv.–9.v.2013 (Barták & Kubík), 1 ♂; *ibid.*, pasture, YPWT, 37°03'09"N, 28°20'17"E, 4 m, 13.–14.ix.2014 (Barták & Kubík), 4 ♂; *ibid.*, pasture, 4 m, 37°03'09"N, 28°20'17"E, 8.–14.ix.2014 (Barták & Kubík), 2 ♂; *ibid.*, salty meadow, 2 m, PT, 37°01'62"N, 28°20'00"E, 27.iv.–1.v.2016 (Barták & Kubík), 1 ♂; Dalyan, farm, MT, 1 m,

36°48'54"N, 28°39'04"E, 8.–20.viii.2015 (Dursun), 1 ♀; *ibid.*, salty meadow, PT, 36°47'49"N, 28°38'55"E, 28.–30.iv.2016 (Barták & Kubík), 3 ♂ (CULSP).

DI: European-Mid Eastern.

DIT: **TR** (Koçak 2014; Koçak and Kemal 2012), **AD** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015), **AY****, **MG****.

Sarina sexpunctata (Fabricius, 1805)

Material examined. **SA:** Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 1 ♂ (CULSP).

DI: Palaearctic.

DIT: **TR** (Koçak 2014; Koçak and Kemal 2012), **BY** (Pekbey 2011), **ERZ** (Pekbey 2011), **SA****, **TO** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015).

Thyrsocnema incisilobata (Pandellé, 1896)

Material examined. **MG:** Muğla – 13 km NE, pine wood, 1200 m, 37°14'50"N, 28°30'00"E, 23–27.v.i.2016 (Barták & Kubík), 1 ♂; Toparlar, 8 m, lowland wood, 36°58'27"N, 28°38'50"E, 22.–24.vi.2015 (Barták & Kubík), 1 ♂; **SA:** Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 3 ♂ (CULSP).

DI: Palaearctic.

DIT: **TR** (Koçak 2014; Koçak and Kemal 2012), **AM** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015), **ERZ** (Pekbey 2011), **MG****, **SA****, **TO** (Kara and Pape 2002; Koçak and Kemal, 2009, 2013, 2015).

Subtribe Parasarcophagina

Bercaea africa (Wiedemann, 1824)

Material examined. **MG:** Akyaka, pasture, 6 m, 37°03'19"N, 28°20'07"E, 28.iv.–8.v.2013, YPWT (Barták & Kubík), 1 ♂; *ibid.*, forest, 30 m, 37°03'16" N, 28°19'35" E, 30.iv.–9.v.2013, YPWT (Barták & Kubík), 1 ♂; Muğla, protein trap, pine wood, 700 m, 37°09'41"N, 28°22'21"E, xi.–iii.2013 (Barták & Kubík), 2 ♂ (CULSP).

DI: Cosmopolitan.

DIT: **TR** (Kara and Pape 2002; Koçak 2014; Koçak and Kemal 2012 – both *Sarcophaga (Bercaea) africa* & *Sarcophaga (Bercaea) cruentata*), **BT** (Koçak and Kemal 2013, 2015 – both *Sarcophaga (Bercaea) africa* & *Sarcophaga (Bercaea) cruentata*), **BY** (Pekbey 2011), **DB** (İpek et al. 2009, 2011 – as *Sarcophaga haemorrhoidalis*), **ED** (Çoban and Beyarslan 2013), **EL** (Şaki and Özer 1999a, b – as *Sarcophaga haemorrhoidalis*), **ERZ** (Pekbey 2011; Pekbey and Hayat 2010), **ES** (Aslan 2006; Aslan and

Çalışkan 2009; Koçak and Kemal 2009, 2013, 2015 – both *Sarcophaga (Bercaea) africa* & *Sarcophaga (Bercaea) cruentata*, **KAR** (Hayat et al. 2008; Koçak and Kemal 2009, 2013, 2015 – both *Sarcophaga (Bercaea) africa* & *Sarcophaga (Bercaea) cruentata*), **KI** (Dik et al. 2012 – as *Sarcophaga haemorrhoidalis*), **KN** (Dik et al. 2012 – as *Sarcophaga haemorrhoidalis*), **ME** (Aslan 2006; Kara and Pape 2002), **MG****, **SN** (Sevgili et al. 2004), **TO** (Aslan 2006; Kara and Pape 2002), **VA** (Koçak and Kemal 2015 2015 – both *Sarcophaga (Bercaea) africa* & *Sarcophaga (Bercaea) cruentata*; Özdal and Değer 2005 – as *Sarcophaga haemorrhoidalis*).

Liopygia (Engelisca) surcoufi* (Villeneuve, 1913)

Material examined. **SA:** Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 1 ♂ (CULSP).

DI: Mediterranean.

DIT: SA**.

***Liosarcophaga (Curranea) tibialis* (Macquart, 1851)**

Material examined. **AY:** 8 km S of Çine river bank, 68 m, 37°32'34"N, 28°03'06"E, 10.–12.ix.2014 (Barták & Kubík), 1 ♂; **MG:** Akyaka, pasture, 6 m, 37°03'19"N, 28°20'07"E, 28.iv.–8.v.2013, YPWT (Barták & Kubík), 3 ♂; *ibid.*, YPWT, 37°03'09"N, 28°20'17"E, 4 m, 13.–14.ix.2014 (Barták & Kubík), 3 ♂; *ibid.*, salty meadow, 2 m, 37°01'49"N, 28°20'01"E, 22.vi.–1.vii.2015 (Barták & Kubík), 1 ♂; Muğla University campus, 720 m, MT, 37°09'42"N, 28°22'13"E, 26–27.vi.2015 (Barták & Kubík), 1 ♂; *ibid.*, protein trap, pine wood, 700 m, 37°09'41"N, 28°22'21"E, xi.–iii.2013 (Barták & Kubík), 2 ♂; Dalyan, salty meadow, PT, 36°47'49"N, 28°38'55"E, 28.–30.iv.2016 (Dursun), 1 ♂; **SA:** Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 1 ♂ (CULSP).

DI: West Palaearctic-Afrotropical-Oriental-Australasian/Oceanian.

DIT: AN (Açikgöz et al., 2011), **AY****, **MG****, **SA****, **SN** (Sevgili et al. 2004).

***Liosarcophaga (Pandelleisca) similis* (Meade, 1876)**

Material examined. **AY:** 8 km S of Çine river bank, 68 m, 37°32'34"N, 28°03'46"E, 10.–12.ix.2014 (Barták & Kubík), 1 ♂; **MG:** Akyaka, pasture, 6 m, 37°03'19"N, 28°20'07"E, 28.iv.–8.v.2013, YPWT (Barták & Kubík), 1 ♂; Toparlar, lowland wood, 8 m, 36°59'27"N, 28°38'50"E, 22.–24.vi.2015 (Barták & Kubík), 1 ♂ (CULSP).

DI: Transpalaearctic-Oriental.

DIT: **TR** (Koçak 2014; Koçak and Kemal 2012), **AY****, **MG****, **TB** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015).

***Liosarcophaga* (s. str.) *emdeni* (Rohdendorf, 1969)**

Material examined. SA: Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 9 ♂ (CULSP).

DI: European-Siberian-Central Asiatic.

DIT: **TR** (Koçak 2014; Koçak and Kemal 2012), **AM** (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015), **ER** (Pekbey 2011), **ERZ** (Pekbey 2011), **SA****.

***Liosarcophaga* (s. str.) *jacobsoni* (Rohdednorf, 1937)**

Material examined. MG: Akyaka, pasture, YPWT, 37°03'19"N, 28°20'07"E, 6 m, 28.iv.–8.v.2013 (Barták & Kubík), 1 ♂; *ibid.*, salty meadow, SW+PT, 37°02'53"N, 28°19'39"E, 28.iv.–9.v.2013 (Barták & Kubík), 2 ♂; *ibid.*, pasture, YPWT, 37°03'09"N, 28°20'17"E, 4 m, 13.–14.ix.2014 (Barták & Kubík), 1 ♂; *ibid.*, salty meadow, 2 m, 37°01'49"N, 28°20'01"E, 22.vi.–1.vii.2015 (Barták & Kubík), 4 ♂; *ibid.*, PT, 37°01'52"N, 28°20'00"E, 27.iv.–1.v.2016 (Barták & Kubík), 2 ♂ (CULSP).

DI: Transpalaeartic subboreal.

DIT: **ERZ** (Pekbey 2011; Pekbey and Hayat 2010), **ES** (Aslan, 2006; Aslan and Çalışkan 2009), **MG****.

***Liosarcophaga* (s. str.) *portschinskyi* (Rohdendorf, 1937)**

Material examined. SA: Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 3 ♂ (CULSP).

Distribution: Transpalaeartic-Oriental.

DIT: **TR** (Kara and Pape 2002; Koçak 2014; Koçak and Kemal 2009, 2012, 2015), **ERZ** (Pekbey 2011), **ES** (Aslan and Çalışkan 2009), **SA****.

***Parasarcophaga* (s. str.) *albiceps* (Meigen, 1826)**

Material examined. SA: Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 1 ♂ (CULSP).

DI: Transpalaeartic- Oriental-Australasian/Oceanian.

DIT: **TR** (Kara and Pape 2002; Koçak 2014; Koçak and Kemal 2009, 2012, 2015), **ERZ** (Pekbey 2011), **SA****.

Subtribe Boettcheriscina***Rosellea aratrix* (Pandellé, 1896)**

Material examined. SA: Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 2 ♂ (CULSP).

DI: Transpalaeartic-Nearctic-Oriental.

DIT: TR (Koçak 2014; Koçak and Kemal 2012), BU (Kara and Pape 2002; Koçak and Kemal 2009, 2013, 2015), SA**.

Rosellea beckiana* Lehrer, 1996

Material examined. AY: 8 km S of Çine, river bank, SW, 68 m, 37°32'34"N, 28°03'46"E, 28.–30.vi.2015 (Barták & Kubík), 1 ♂; *ibid.*, 29.iv.–1.v.2016 (Barták & Kubík), 1 ♂; MG: Akyaka, pasture, YPWT, 37°03'09"N, 28°20'17"E, 4 m, 13.–14.ix.2014 (Barták & Kubík), 2 ♂; Muğla, protein trap, pine wood, 700 m, 37°09'41"N, 28°22'21"E, xi.–iii.2013 (Barták & Kubík), 1 ♂; Toparlar, lowland wood, 8 m, 36°59'27"N, 28°38'50"E, 22.–24.vi.2015 (Barták & Kubík), 2 ♂; *ibid.*, SW+PT, 36°58'39"N, 28°39'30"E, 28.–30.iv.2016 (Barták & Kubík), 1 ♂ (CULSP).

DI: East Mediterranean.

DIT: AY**, MG**.

Subtribe Sarcophagina***Sarcophaga lehmanni* Müller, 1922**

Material examined. AY: 8 km S of Çine, river bank, SW, 68 m, 37°32'34"N, 28°03'46"E, 28.–30.vi.2015 (Barták & Kubík), 2 ♂; HA: 25 km E of Gözeldere, 37°32'N, 43°49'E, 930 m, 22.vi.2010 (Mi. Halada), 1 ♂; MG: Akyaka, forest, 30 m, 37°03'16"N, 28°19'35"E, 30.iv.–9.v.2013, YPWT (Barták & Kubík), 1 ♂; *ibid.*, pasture, 4 m, 37°03'09"N, 28°20'17"E, 8.–14.ix.2014 (Barták & Kubík), 2 ♂; Muğla University campus, SW+PT, 700 m, 37°09'41"N, 28°22'21"E, 29.iv.–10.v.2013 (Barták & Kubík), 1 ♂; *ibid.*, 37°09'42"N, 28°22'22"E (O.Dursun), iv.–v.2014, 1 ♂; *ibid.*, MT, 730 m, 37°09'38"N, 28°22'11"E, 19.viii.–17.ix.2015 (H. Kavak), 1 ♂; Dalyan, farm, MT, 1 m, 36°48'54"N, 28°39'04"E, 8.–20.viii.2015 (Dursun), 1 ♂; *ibid.*, salty meadow, PT, 36°47'49"N, 28°38'55"E, 28.–30.iv.2016 (Barták & Kubík), 1 ♂; SA: Samsun University campus, 41°22'N, 36°11'E, 22vi.–4.vii.2014 (Barták & Kubík), 3 ♂ (CULSP).

DI: West-Central Palaearctic.

DIT: **TR** (Kara and Pape 2002; Koçak 2014; Koçak and Kemal 2012 – as *Sarcophaga* (s. str.) *lasiostyla*), **AM** (Aslan 2006), **AY****, **BY** (Pekbey 2011), **ER** (Pekbey 2011), **ERZ** (Pekbey 2011; Pekbey and Hayat 2010), **ES** (Aslan, 2006; Aslan and Çalışkan 2009; Koçak and Kemal 2009 – as *Sarcophaga* (s. str.) *lasiostyla*, 2013, 2015 – as *Sarcophaga* (s. str.) *lasiostyla*), **HA****, **IG** (Hayat et al. 2008; Koçak and Kemal 2009 – as *Sarcophaga* (s. str.) *lasiostyla*, 2013, 2015 – as *Sarcophaga* (s. str.) *lasiostyla*), **IZ** (Civelek and Tezcan 2005; Koçak and Kemal 2009 – as *Sarcophaga* (s. str.) *lasiostyla*, 2013, 2015 – as *Sarcophaga* (s. str.) *lasiostyla*), **KAR** (Hayat et al. 2008; Koçak and Kemal 2009 – as *Sarcophaga* (s. str.) *lasiostyla*, 2013, 2015 – as *Sarcophaga* (s. str.) *lasiostyla*), **KY** (Hayat et al. 2008; Koçak and Kemal 2009 – as *Sarcophaga* (s. str.) *lasiostyla*, 2013, 2015 – as *Sarcophaga* (s. str.) *lasiostyla*), **MN** (Civelek and Tezcan 2005; Koçak and Kemal 2009 – as *Sarcophaga* (s. str.) *lasiostyla*, 2013, 2015 – as *Sarcophaga* (s. str.) *lasiostyla*), **MG****, **SA****.

Discussion

This paper presents the results of an intensive collecting effort by two of the authors (MB and SK) in Turkey between 2011 and 2016. It adds new faunistic records for 68 species. The following 22 species newly recorded for Turkey are presented: *Apodacra dispar*, *Bellieriomima subulata*, *Blaesoxipha confusa*, *Craticulina barbifera*, *Helicophagella macrura*, *H. novella*, *Heteronychia infixata*, *H. pontica*, *H. porrecta*, *Karovia hirticrus*, *Liopygia surcoufi*, *Metopia grandii*, *Miltogramma aurifrons*, *M. brevipila*, *M. testaceifrons*, *M. turkmenora*, *Myorhina lunigera*, *M. socrus*, *Paragusia multipunctata*, *Rosellea beckiana*, *Sarcophila canaanita*, and *Sphecatodes ornatus*. A further 46 species are recorded for the first time from at least one Turkish province.

Previously, 132 species of Sarcophagidae were listed from Turkey (Hayat et al. 2008; Kara and Pape 2002; Koçak 2014; Koçak and Kemal 2009, 2012, 2013, 2015; Pape et al. 2015; Pekbey 2011; Pekbey and Hayat 2011; Whitmore, 2011; Whitmore et al. 2013). Our findings increase this number to 154. This relatively large number of faunistic novelties indicates that there is a low degree of faunistic research on this family in Turkey.

Acknowledgements

This paper was supported by S grant of MSMT (Ministry of Education, Sports and Youth). We thank Prof. A. Koçak (Centre for Entomological Studies, Ankara) for sending necessary publications about Turkish flies. We would also like to thank Mr. Brian Kavalir for checking English. Our special thanks are due to anonymous reviewers for improving earlier versions of this manuscript.

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