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### Monograph

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## A mountain of millipedes XI. The trachystreptoform spirostreptids of the Udzungwa Mountains, Tanzania (Diplopoda, Spirostreptida, Spirostreptidae)

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**Abstract.** The “trachystreptoform” species of Spirostreptidae, i.e., species which would formerly have been ascribed to the tribe Trachystreptini, from the Udzungwa Mountains are (re)described, including one new genus and five new species: *Attemsostreptus reflexus* Akkari & Enghoff, 2019, *A. cataractae* Enghoff sp. nov., *A. leptoptilos* Enghoff sp. nov., *A. julostriatus* Enghoff sp. nov., *Lophostreptus tersus* (Cook, 1896) (= *L. ptilostreptoides* Carl, 1909 syn. nov.), *L. magombera* Enghoff sp. nov., and *Udzungwastreptus marianae* Enghoff gen. et sp. nov. The type material of *Lophostreptus regularis* Attems, 1909 (= *L. tersus*) is discussed. The discussion includes paragraphs on the classification and the

Udzungwa fauna of Spirostreptidae, on grouping of the Udzungwa trachystreptoform species in relation to altitude, and on the possibly recent immigration of *A. reflexus* and *L. tersus* into the Udzungwa Mts.

**Keywords.** Taxonomy, new genus, new species, Eastern Arc Mountains, endemic.

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## Introduction

This is the eleventh paper in a series devoted to the millipede fauna of the Udzungwa Mountains in Tanzania. See Enghoff (2022) for a list of previous papers in the series, and see Enghoff (2014) and Scharff *et al.* (2015) for general information on the Udzungwa Mountains. The present contribution is the first in the series to deal with the large family Spirostreptidae Brandt, 1833 and addresses two genera formerly assigned to the tribe Trachystreptini Cook, 1896, as well as a new genus. Some Udzungwan species of Spirostreptidae have recently been treated in papers outside the “A mountain of millipedes” series (Enghoff 2017a; Enghoff & Larsson 2018).

Although the family Spirostreptidae includes the world’s largest millipedes, the taxonomy of the family is very far from being well-resolved, see, e.g., Hoffman (1980), Hoffman *et al.* (2001) and Enghoff (2017a). One of the problems concerns the group of genera which have been classified in the tribe Trachystreptini, originally described as a separate family. These genera are distinguished by strong metazonal sculpture including longitudinal ridges along the entire perimeter of the body. On the other hand, the gonopods of species in these genera are not principally different from gonopods of the other spirostreptids. To add to the confusion, Demange & Mauriès (1975) and Krabbe (1982) mentioned that some genera exist in which the gonopods are very similar between species, but in which some species according to their body sculpture would key out as trachystreptinines, whereas other would not.

Until the relationships between spirostreptid genera have been better clarified, it is preferable to follow the recommendation of Hoffman (1980), viz., not to operate with subfamilies and tribes within Spirostreptidae. As a collective term for the carinate genera which have been brought together in a tribe Trachystreptini, “trachystreptoform spirostreptids” or just “trachystreptoforms” is suggested, thus avoiding any formal nomenclatorial connotations. The genera which include trachystreptoform as well as other species might similarly be referred to as “partim-trachystreptoform” (partially trachystreptoform). Table 1 presents a list of all these genera, with information on how they were recognized in the three most recent major treatments.

## Material and methods

With a few exceptions, the studied specimens are deposited in the zoological collections of the Natural History Museum of Denmark, University of Copenhagen (NHMD, formerly ZMUC). A very large proportion of this material (e.g., Fig. 1) was collected in connection with the Forest Restoration and Climate Experiment (FoRCE). FoRCE is a research project aiming to understand global forest recovery from heavy disturbance, using several indicators of forest recovery and function. The primary indicators used by FoRCE are tree and vine growth – competition between these two plant forms is having a major impact on stalled forest recovery, especially in the tropics (Marshall *et al.* 2020). Millipedes and other detritivores are also used as indicators of forest function, selected for their role in litter decomposition and hence also nutrient and carbon cycling. The FoRCE project operates in four countries, and originated in Tanzania, where the focus is the Udzungwa Mountains, a globally significant region for



**Table 1.** Trachystreptoform genera. In the first column, genera in **boldface** are regarded as valid. The last column only includes genera explicitly discussed in the present work.

Genus ( <b>bold</b> = here regarded as valid)	Demange & Mauriès (1975)	Hoffman (1980)	Krabbe (1982)	present work
<b>Anastreptus</b> Cook, 1896	valid	valid	valid	valid
<b>Attemostreptus</b> Verhoeff, 1941	valid	valid	valid	valid
<b>Bucinogonus</b> Demange & Mauriès, 1975	valid	valid	valid	
<i>Carlostreptus</i> Verhoeff, 1941	syn. of <i>Lophostreptus</i>	syn. of <i>Lophostreptus</i>	syn. of <i>Lophostreptus</i>	valid
<b>Calostreptus</b> Cook, 1896	valid	valid	valid	valid
<b>Cochleostreptus</b> Demange & Mauriès, 1975	valid	valid	valid	
<b>Furcillogonus</b> Demange & Mauriès, 1975	valid	valid	valid	
<i>Givviogonus</i> Demange & Mauriès, 1975	valid	valid	syn. of <i>Humilistreptus</i>	
<i>Krugeroastreptus</i> Demange & Mauriès, 1975	valid	syn. of <i>Synophryostreptus</i>	syn. of <i>Synophryostreptus</i>	
<i>Lemostreptus</i> Cook, 1896	dubious	syn. of <i>Tropiulus</i>	dubious	
<b>Lophostreptus</b> Cook, 1895	valid	valid	valid	valid
<i>Lophogonus</i> Demange & Mauriès, 1975	valid	syn. of <i>Ptilostreptus</i>	syn. of <i>Lophostreptus</i>	syn. of <i>Lophostreptus</i>
<b>Myostreptus</b> Cook, 1896	valid	valid	valid	
<i>Porostreptus</i> Cook, 1896	syn. of <i>Anastreptus</i>	valid	dubious	
<i>Ptilostreptus</i> Cook, 1896	dubious	valid	dubious	syn. of <i>Lophostreptus</i>
<b>Rutabulogonus</b> Demange & Mauriès, 1975	valid	valid	valid	
<b>Streptolus</b> Chamberlin, 1951	–	valid	valid	
<b>Trachystreptus</b> Cook, 1895	valid	valid	valid	
<i>Tropiulus</i> Silvestri, 1896	–	valid	syn. of <i>Lemostreptus</i>	
<i>Tropirachelus</i> Silvestri, 1897	dubious	syn. of <i>Anastreptus</i>	syn. of <i>Anastreptus</i>	valid
<i>Udzungwastreptus</i> gen. nov.	–	–	–	valid
“Partim-trachystreptoform” genera				
<b>Humilistreptus</b> Demange, 1958 (incl. <i>Givviogonus</i> )				
<b>Synophryostreptus</b> Attems, 1926 (incl. <i>Krugeroastreptus</i> )				

biodiversity and species endemism (Burgess *et al.* 2007), and Magombera Nature Reserve, a forest of major importance for conservation of plants, primates and elephants (Marshall 2008) and home to the Magombera chameleon (Menegon *et al.* 2009). All millipedes were collected in leaf litter/loose topsoil, through timed searches within 20×20 m permanent vegetation sample plots, and within 3×3 m quadrats within these. The 20×20 m plots were either (a) subplots within 100×40 m plots for sampling large trees (FoRCE), (b) subplots within 100×20 m plots (half-FoRCE), or (c) stand-alone plots for sampling sapling trees (micro-FoRCE). All samples were collected within moist to wet forest with rainfall >1450 mm/year. We intend to deposit samples of species of which there are duplicate specimens in Tanzania (collection to be decided).

A few additional important samples from the Virginia Museum of Natural History (VMNH), Naturhistorisches Museum Wien (NHMW) and Naturhistoriska Riksmuseet Stockholm (NRMS) were kindly placed at our disposal by the respective curators, either physically or in the form of high-quality images.

Specimens were stored and examined in 70% ethanol under a stereo microscope. Specimens for scanning electron microscopy (SEM) were cleaned with ultrasound, transferred to 96% ethanol, then to acetone, air-dried, mounted on aluminium stubs or on triangles of flexible aluminium tape, in turn mounted on stubs, coated with platinum-palladium and studied in a JEOL JSM-6335F scanning electron microscope.



**Fig. 1.** Example of a millipede sample from the FoRCE experiment. Magombera Nature Park, Half-FoRCE Plot 38, 17 Feb. 2018. A.R. Marshall leg. 1. *Lyodesmus dollfusi* (Cook, 1896) (Oxydesmidae). 2. *Lophostreptus tersus* (Cook, 1896) (Spirostreptidae). 3. *Tropostreptus sigmatospinus* Enghoff, 2017 (Spirostreptidae). Photo: A.R. Marshall.

Images were processed with Photoshop, in some cases involving stacking of multiple images, and plates were composed with Microsoft Publisher. Graphs were made with Microsoft Excel.

### Abbreviations

a.s.l. = above sea level  
 FoRCE = Forest Restoration and Climate Experiment

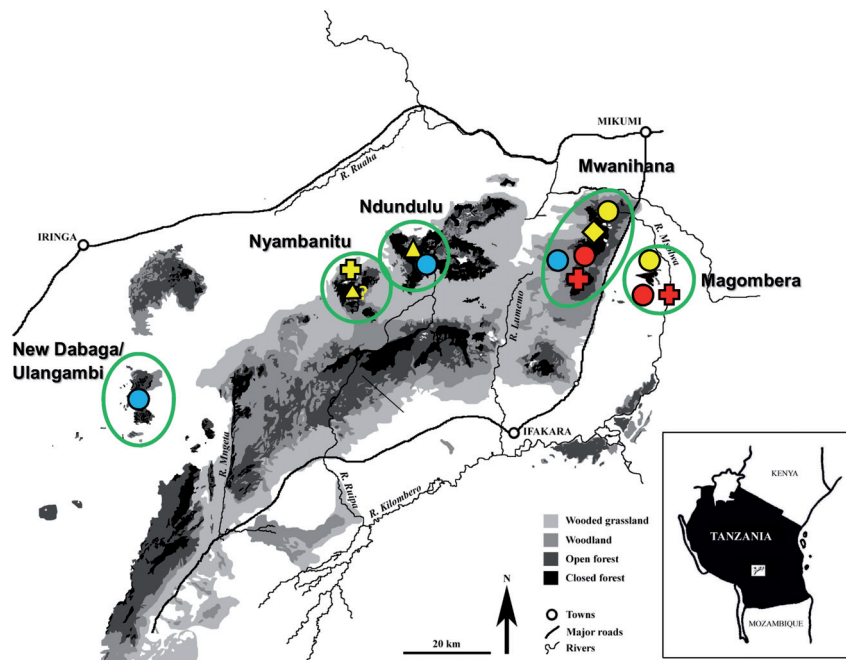
Abbreviations for body parts are explained in the text and in the figure captions. See also Hoffman (2008). The meaning of the terms for body parts are mostly evident from the illustrations, but a few require explanation:

- gonocoel: the cavity formed by the longitudinally folded gonopod coxa. The gonopod telopodite originates at the base of the coxa, runs internally through the length of the gonocoel before it emerges near the tip of the proplica, see, e.g., Krabbe (1982: fig. 3).
- sigilla (plural, singular: sigillum): round, light-coloured spots (“Gelbe Punkte”, i.e., “yellow dots” in the German literature), arranged in one or more rows or in an irregular band along the perimeter of the metaozonites (Hoffman 1971, see also, e.g., Enghoff & Larsson 2018: fig. 2a–b).

### Repositories

NHMD = Natural History Museum of Denmark, University of Copenhagen  
 NHMW = Naturhistorisches Museum Wien  
 NRMS = Naturhistoriska Riksmuseet, Stockholm  
 VMNH = Virginia Museum of Natural History, Martinsville, Virginia

Figure 2 shows the areas in which the seven trachystreptoform species treated here have been collected.



**Fig. 2.** Map of the Udzungwa Mts showing collection areas for trachystreptoform Spirostreptidae Brandt, 1833. Yellow symbols: *Attemsostreptus* spp.; dots: *A. reflexus*, diamond: *A. cataractae* Enghoff sp. nov., cross: *A. leptoptilos* Enghoff sp. nov., triangles; *A. julostratus* Enghoff sp. nov. Red symbols: *Lophostreptus* spp.; dots: *L. tersus*, crosses: *L. magombera* Enghoff sp. nov. Blue dots: *Udzungwastreptus marianae* Enghoff gen. et sp. nov. Based on Marshall *et al.* (2010: fig. 1).

## Results

### Taxonomy

Class Diplopoda de Blainville in Gervais, 1844  
Order Spirostreptida Brandt, 1833  
Family Spirostreptidae Brandt, 1833  
  
Genus *Attemsostreptus* Verhoeff, 1941

*Attemsostreptus* Verhoeff, 1941: 261

### Type species

*Attemsostreptus costatus* Verhoeff, 1941 (Tanzania) by monotypy.

### Other included species

*Attemsostreptus reflexus* Akkari & Enghoff, 2019  
*Attemsostreptus cataractae* Enghoff sp. nov.  
*Attemsostreptus julostratus* Enghoff sp. nov.  
*Attemsostreptus leptoptilos* Enghoff sp. nov.

### Diagnosis

The discovery of three new species in the genus necessitates a revision of the genus diagnosis proposed by Akkari & Enghoff (2019). Species of *Attemsostreptus* differ from other Spirostreptidae by the combination of the following characters: anterior margin of collum unmodified, metazonites with longitudinal ridges (carinae), or at least striae along the entire perimeter of the body (trachystreptoform habitus); prefemoral lobes of first pair of male legs triangular, covered with minute short spines; tip of gonopod coxal metaplica folded back on anterior side, forming a ‘roof’ or canopy over gonocoel; a long to very long pointed lateroapical metaplical process; gonopod telopodite long and slender, with a long to very long, pointed antetorsal process; posttorsal part of telopodite very long and thin, forming loose coils; telopodite ending in two short branches of subequal length, one broad and more or less serrated, the other acuminate.

*Attemsostreptus reflexus* Akkari & Enghoff, 2019  
Figs 2, 3A–B, 4–7

*Attemsostreptus reflexus* Akkari & Enghoff, 2019: 3

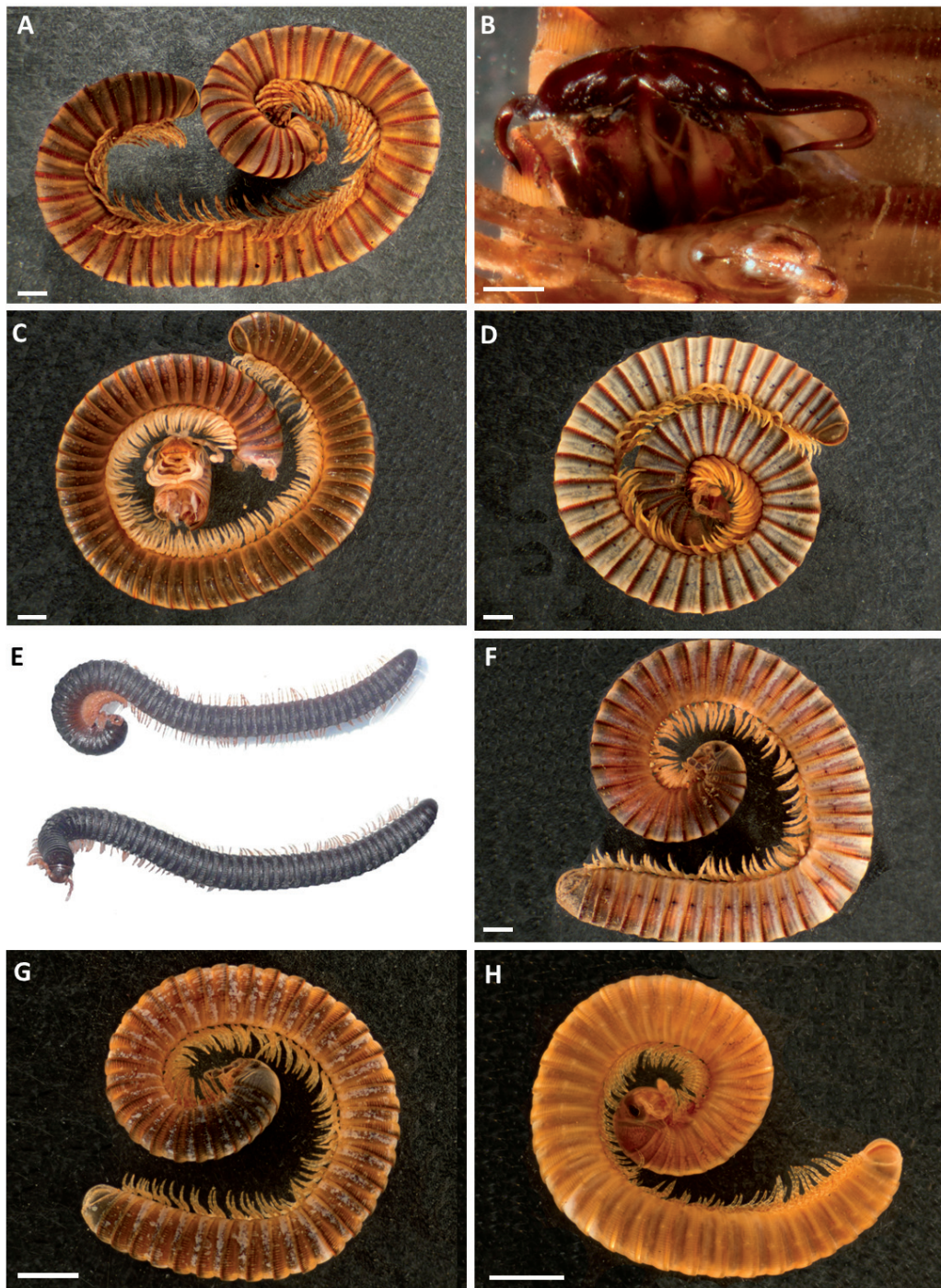
### Diagnosis

Easily distinguishable from congeners by the extremely long lateroapical metaplical process bent in a U-shape (Figs 3B, 7A).

### Material examined (total 25 ♂♂, 33 ♀♀, 78 juvs)

TANZANIA – **Morogoro Region, Kilombero District, Udzungwa Mountains National Park, Mwanihana** • 4 ♂♂, 9 ♀♀, 11 juvs; Njokamoni; 07°50'35.9" S, 36°52'38.6" E; 474 m a.s.l.; 20 Dec. 2021; A. Ngute, R. Malanda, W. Mhagawale, A. Marshall leg.; FoRCE Plot 10, closed canopy; COLL. NHMD - ACC.NO. 2022-EN-003; NHMD 621851 • 1 ♂, 12 juvs; same collection data as for preceding; 07°50'31.9" S, 36°52'47.1" E; 401 m a.s.l.; 21 Dec. 2021; FoRCE Plot 11, open canopy; NHMD 621852 • 1 ♂, 4 ♀♀, 1 juv.; same collection data as for preceding; 07°50'33.2" S, 36°52'54.9" E; 357 m a.s.l.; 22 Dec. 2021; FoRCE Plot 12, open canopy; NHMD 621853 • 1 ♀, 12 juvs; Sonjo; 07°48'22.6" S,

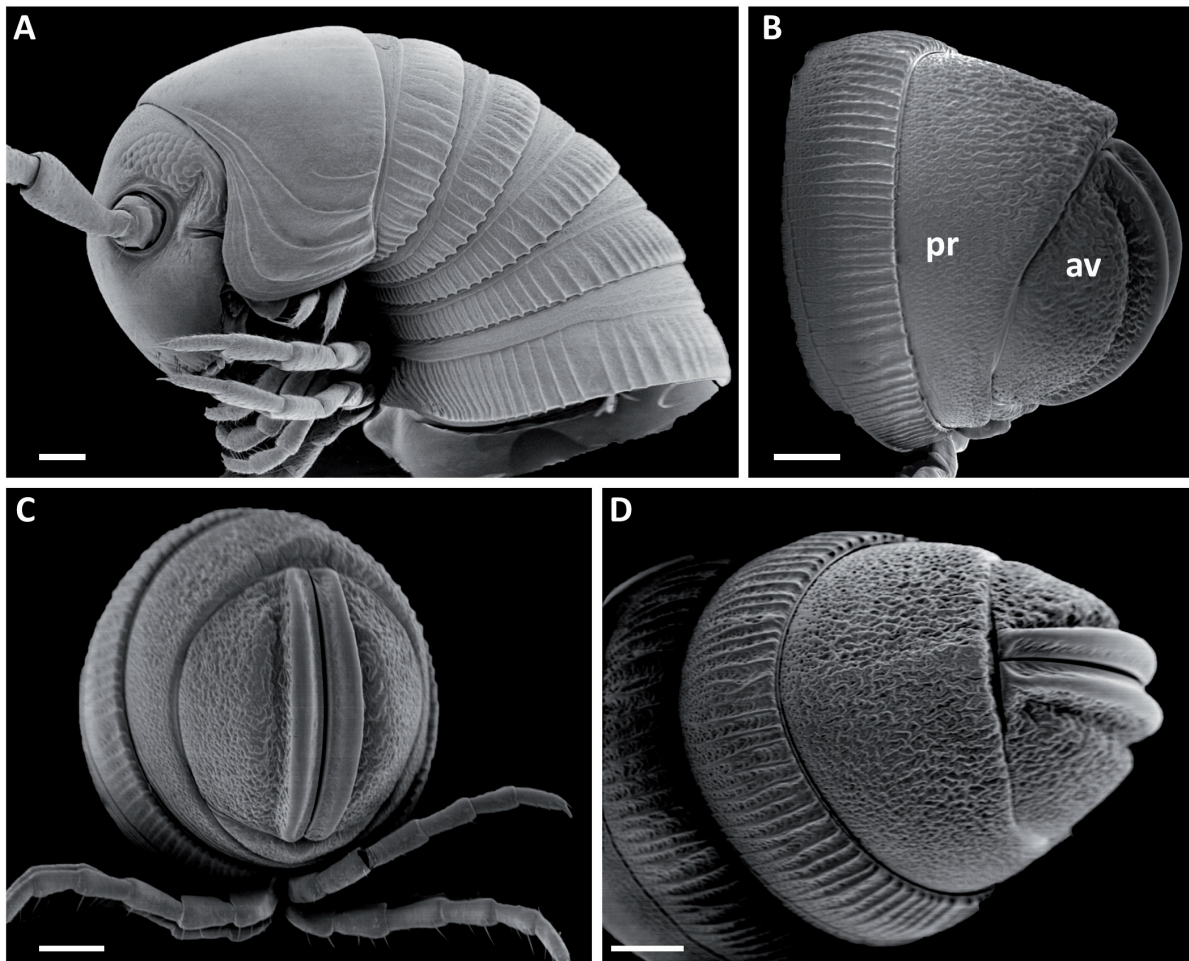




**Fig. 3.** Trachystreptoforms from the Udzungwa Mts. **A.** *Attemsostreptus reflexus* Akkari & Enghoff, 2019, ♂ (Mwanihana, Njokamoni, NHMD 621851). **B.** Same, close-up of gonopod in situ. **C.** *Attemsostreptus julostratus* Enghoff sp. nov., holotype, ♂ (NHMD 621878). **D.** *Attemsostreptus leptoptilos* Enghoff sp. nov., paratype, ♂ (NHMD 621877). **E–F.** *Lophostreptus tersus* (Cook, 1896). **E.** Two living females from Magombera Nature Reserve (NHMD 1184642). **F.** Male from Magombera Nature Reserve (NHMD 1184640). **G.** *Lophostreptus magombera* Enghoff sp. nov., paratype, ♂ (NHMD 621886). **H.** *Udzungwastreptus marianae* gen. et sp. nov., paratype, ♂ (NHMD 621893). Scale bars: A, C–D, F–H = 2 mm; B = 0.5 mm; E not to scale. Photos: S.G. Selvantharan (A–D, F–H), A.R. Marshall (E).

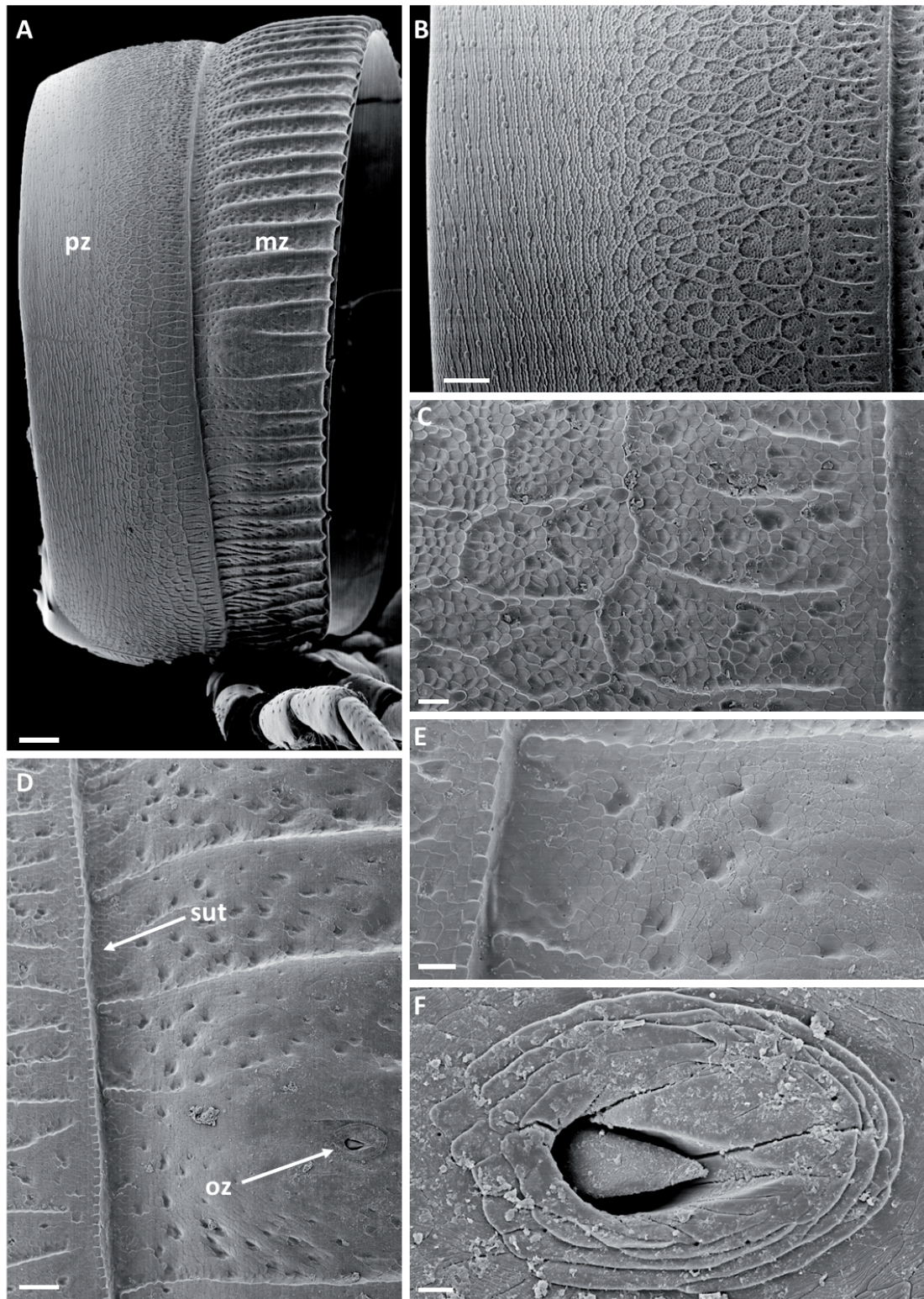


36°52'17.0" E; 579 m a.s.l.; 14 Dec. 2021; A. Ngute, R. Malanda, H. Mnendendo, W. Mhagawale, A. Mpoto, A. Marshall leg.; FoRCE Plot 13, closed canopy; NHMD 621854 • 2 juvs; same collection data as for preceding; 07°48'24.4" S, 36°52'21.7" E; 589 m a.s.l.; 15 Dec. 2021; FoRCE Plot 14, open canopy; NHMD 621855 • 1 juv.; same collection data as for preceding; 07°48'22.3" S, 36°52'32.2" E; 595 m a.s.l.; 17 Dec. 2021; FoRCE Plot 15, open canopy; NHMD 621856 • 3 ♂♂, 2 ♀♀, 1 juv.; Sanje; 07°46'43.4" S, 36°54'04.3" E; 504 m a.s.l.; 26 Feb. 2022; A. Ngute, E. Kivambe, R. Malanda, H. Mnendendo, W. Mhagawale, M. Mpoto, A. Marshall leg.; FoRCE Plot 24, open canopy; NHMD 621857 • 3 ♂♂; same collection data as for preceding; 07°46'47.6" S, 36°54'07.6" E; 495 m a.s.l.; 23 Feb. 2022; FoRCE Plot 25, open canopy; NHMD 621858 • 1 ♀, 2 juvs; same collection data as for preceding; 07°46'52.1" S, 36°54'11.8" E; 421 m a.s.l.; 20 Feb. 2022; A. Ngute, E. Kivambe, R. Malanda, W. Mhagawale, H. Mnendendo, A. Marshall leg.; FoRCE Plot 92, open canopy; NHMD 621859 • 1 ♀; same collection data as for preceding; 07°47'03.0" S, 36°54'05.8" E; 410 m a.s.l.; A. Ngute, E. Kivambe, R. Malanda, W. Mhagawale, H. Mnendendo, A. Marshall leg.; FoRCE Plot 93, open canopy; NHMD 621860. – **Morogoro Region, Kilombero District, Udzungwa Mountains National Park** • 1 ♂, 2 juvs; 07°49'21.7" S, 36°58'57.1" E; 283 m a.s.l.; 30 Jan. 2020; A. Ngute and A.R. Marshall leg.; micro-FoRCE plot 12, closed forest; COLL. NHMD. ACC.NO. 2020-EN-002; NHMD 621861 • 2 ♀♀, 1 juv.; same



**Fig. 4.** *Attemsostreptus reflexus* Akkari & Enghoff, 2019, male from Udzungwa Mts (Mwanihana, Njokamoni, NHMD 621851). **A.** Head, collum and rings 2–6, lateral view. **B–D.** Telson and ultimate ring. **B.** Lateral view. **C.** Posterior view, incl. legs of ultimate ring. **D.** Dorsal view. Abbreviations: *av* = anal valve; *pr* = preanal ring. Scale bars = 0.5 mm.

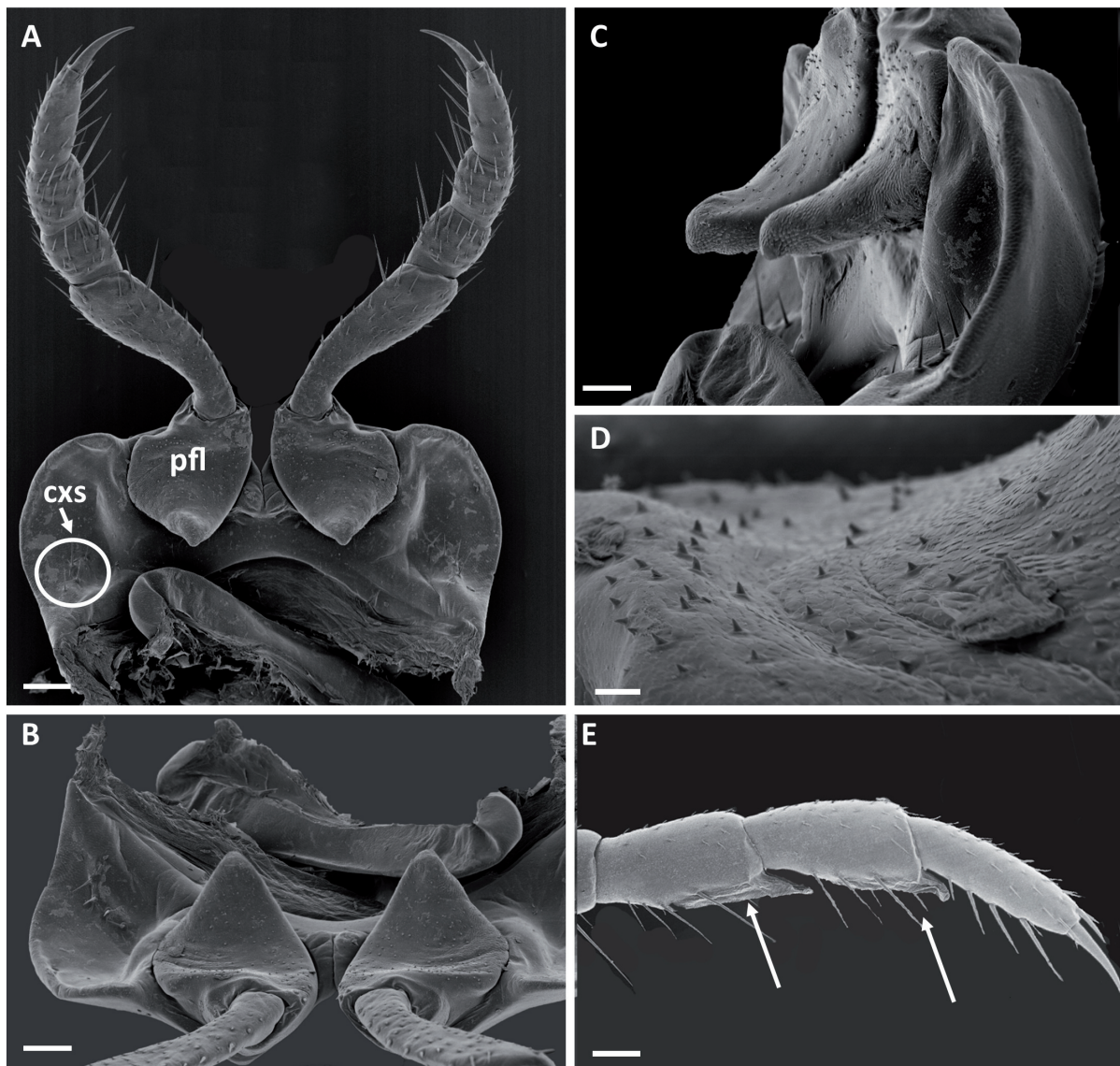




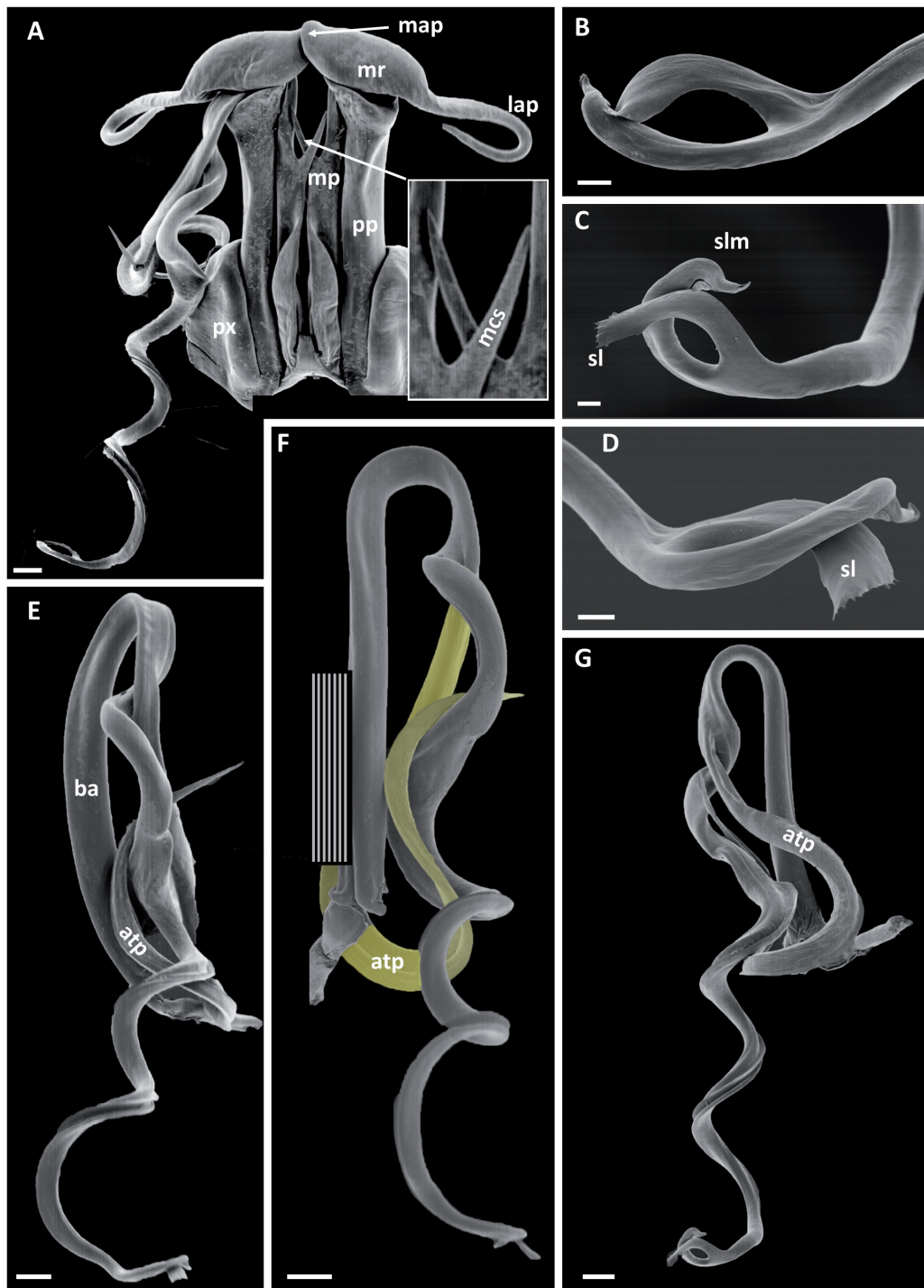
**Fig. 5.** *Attemsostreptus reflexus* Akkari & Enghoff, 2019, male from Udzungwa Mts (Mwanihana, Njokamoni, NHMD 621851), midbody ring. **A.** In toto. **B.** Prozonite, lateral part. **C.** Prozonital sculpture just in front of suture. **D.** Metazonital sculpture just behind suture. **E.** Same, close-up. **F.** Ozopore. Abbreviations: *mz* = metazonite; *oz* = ozopore; *pz* = prozonite; *sut* = suture. Scale bars: A = 0.2 mm; B = 0.1 mm; C, E = 0.02 mm; D = 0.05 mm; F = 0.005 mm.



collection data as for preceding; 07°49'13.2" S, 36°58'57.1" E; 334 m a.s.l.; 25 Feb. 2020; micro-FoRCE plot 17; open forest; NHMD 621862 • 2 ♂♂, 4 juvs; same collection data as for preceding; 07°50'14.5" S, 36°53'07.8" E; 358 m a.s.l.; 13 Feb. 2020; micro-FoRCE plot 18; closed forest; NHMD 621863 • 2 ♀♀; same collection data as for preceding; 07°49'46.5" S, 36°53'27.9" E; 347 m a.s.l.; 27 Feb. 2020; micro-FoRCE plot 20, open forest; NHMD 621864 • 1 juv.; same collection data as for preceding; 07°48'53.2" S, 36°54'13.9" E; 282 m a.s.l.; 5 Mar. 2020; micro-FoRCE plot 22, open forest; NHMD 621865 • 2 ♂♂, 3 ♀♀; same collection data as for preceding; 07°49'03.6" S, 36°57'33.9" E; 280 m a.s.l.; 16 Mar. 2020; micro-FoRCE plot 27, closed forest; NHMD 621866 • 1 ♀, 7 juvs; same collection data as for preceding; 07°47'43.1" S, 36°53'57.6" E; 331 m a.s.l.; 19 Feb. 2020; micro-FoRCE plot 28, open forest; NHMD 621867 • 1 ♂, 4 ♀, 9 juvs; same collection data as for preceding; 07°47'01.1" S, 36°54'13.9" E;



**Fig. 6.** *Attemsostreptus reflexus* Akkari & Enghoff, 2019, male from Udzungwa Mts (Mwanihana, Njokamoni, NHMD 621851). **A–D.** First pair of legs. **A.** Posterior view. **B.** Ventral view. **C.** Sublateral view. **D.** Peglike setae/sensilla from prefemur. **E.** Midbody leg, arrows pointing at soft pads on postfemur and tibia. Abbreviations: *cxs* = coxosternal setae; *pfl* = prefemoral lobe. Scale bars: A–B, E = 0.2 mm; C = 0.1 mm; D = 0.02 mm.



**Fig. 7.** *Attemsostreptus reflexus* Akkari & Enghoff, 2019, male from Udzungwa Mts (Mwanihana, Njokamoni, NHMD 621851). **A.** Gonopods except right telopodite, anterior view; inset: close-up of mesal coxal spines. **B.** Tip of left telopodite. **C–D.** Tip of right telopodite. **E–G.** Right telopodite. **E.** Sublateral view. **F.** anterior view; striped rectangle: area obscured by mounting tape. **G.** Posterior view. Abbreviations: *atp* = antetorsal process (highlighted in yellow in F); *ba* = basomere; *lap* = lateroapical metaplical process; *map* = mesapical metaplical process; *mcs* = mesal coxal spine; *mp* = metaplica; *mr* = metaplical “roof”; *pp* = proplica; *px* = paracoxite; *sl* = serrate lamella; *slm* = solenomere. Scale bars: A, E–G = 0.2 mm; B–D = 0.05 mm.

381 m a.s.l.; 15 Feb. 2020; micro-FoRCE plot 30, closed forest; COLL. NHMD. ACC.NO. 2020-EN-002; NHMD 621868. – **Morogoro Region, Kilombero District, Magombera Nature Reserve** • 1 ♂, 3 ♀, 10 juvs; 07°48'53.0" S, 36°58'29.0" E; 285 m a.s.l.; 5 Mar. 2018; A.R. Marshall leg.; half-FoRCE plot 2, closed forest; COLL. NHMD. ACC.NO. 2020-EN-002; NHMD 621869 • 1 ♂; same collection data as for preceding; 07°48'59.4" S, 36°57'55.6" E; 280 m a.s.l.; 14 Mar. 2018; half-FoRCE plot 3, closed forest; NHMD 621870 • 1 ♂, 1 ♀; same collection data as for preceding; 07°49'03.0" S, 36°57'35.2" E; 284 m a.s.l.; 15 Mar. 2018; half-FoRCE plot 4, closed forest; NHMD 621871 • 1 ♂, 1 ♀, 1 juv.; same collection data as for preceding; 07°48'30.9" S, 36°59'33.1" E; 287 m; 19 Feb. 2018; half-FoRCE plot 37, open forest; NHMD 621872 • 1 juv.; same collection data as for preceding; 07°48'21.5" S, 36°59'47.5" E; 287 m a.s.l.; 17 Feb. 2018; half-FoRCE plot 38, open forest; NHMD 621873 • 2 ♂♂; same collection data as for preceding; 07°48'53.0" S, 36°58'29.0" E; 285 m; 27 Jun. 2019; A. Ngute and A.R. Marshall leg.; half-FoRCE plot 2, closed forest; COLL. NHMD. ACC.NO. 2020-EN-002; NHMD 621874 • 1 ♂, 6 ♀♀, 1 juv.; same collection data as for preceding; 07°49'03.0" S, 36°57'36.2" E; 284 m a.s.l.; half-FoRCE plot 4, closed forest; NHMD 621875.

### Descriptive notes (males)

This species was recently described and illustrated with photographs (Akkari & Enghoff 2019). We here provide descriptive notes based on the new material from the Udzungwa Mountains.

SIZE. Males: vertical diameter 3.6–4.6 mm; 52–54 podous rings, no apodous rings in front of telson.

COLLUM (Fig. 4A). With smooth surface, with 3 strong lateral striae/carinae, above and below these a few indistinct ones, a short stria/carina in each of the spaces between the main ones.

BODY RINGS (Fig. 5). Anterior part of prozonite (*pz*) with fine, dense transverse furrows; central part with an irregular mesh of cells delimited by fine ridges; posterior row of cells longer and more regular; surface of cells pitted; suture (*sut*) between pro- and metazonite delimited by sharp edge, a row of tiny, sub-quadrate cells between edge and posterior row of prozonital cells (Fig. 5E). Metazonite (*mz*) with densely set sharp ridges throughout perimeter, anterior part of ridges with string-of-bead-like sculpture, surface between ridges pitted. Ozopore (Fig. 5D, F) ca  $\frac{1}{3}$  metazonite length behind suture, oval, surrounded by narrow concentric cytoscutes and with a conical sclerotized plug. No sigilla.

TELSON (Fig. 4B–D). Preanal ring (*pr*) with coarsely rugose surface. Anal valves (*av*) with strongly developed submarginal lips; apical and mesal surface of lips smooth, outer surface of lips and rest of valves with coarsely rugose microsculpture.

LEGS (Fig. 6). Male legs with well-developed ventral pads on postfemur and tibia (Fig. 6E). First pair (Fig. 6A–D): coxosternum with lateral groups of a few setae (*cxs*). Prefemoral lobes (*pfl*) in ventral view equilaterally triangular, pointed, covered with minute short spines (Fig. 6D).

GONOPODS (Figs 3B, 7). As described by Akkari & Enghoff (2019). Notable details include 1) coxal metaplica (*mp*) apically folded back on anterior side, forming a “roof” or canopy (*mr*) over gonocoel; 2) distomesal metaplical spine (*mcs*) long, protruding at angles (ca 40°) from mesal metaplical margin; 3) tip of telopodite bifurcate, one branch (*sl*) lamellar, with transverse, slightly serrated tip, the other (solenomere, *slm*) acuminate.

### Descriptive notes (females)

Diameter up to 5.1 mm; 52–55 podous rings, no apodous rings in front of telson.



### Distribution and habitat

In the Udzungwa Mountains, it was found on 25 plots of the FoRCE experiment of which 11 are with open canopy and 14 with closed canopy. The total altitudinal range is 280–595 m a.s.l. Although abundant in the FoRCE material, the species is absent from older collections, maybe an indication that it is a recent immigrant to the Udzungwa Mountains. The only other precise record of the species is from Kimboza Forest Reserve in the Uluguru Mountains, Tanzania (Akkari & Enghoff 2019).

*Attemsostreptus cataractae* Enghoff sp. nov.

urn:lsid:zoobank.org:act:7D1B998B-D832-4821-88FF-B2F7904B3083

Figs 2, 8

### Diagnosis

Differs from congeners, except *A. costatus*, by the very long (>half length of gonopod coxa), only moderately curved and almost straightly laterad lateroapical metapical process (*lap*). Differs from *A. costatus* by a somewhat shorter *lap* and by the lack of a distinct, rounded mesapical metapical process (*map*) – compare Fig. 8D with fig. 1 in Akkari & Enghoff (2019).

### Etymology

A Latin noun in the genitive, meaning ‘of the waterfall’ and referring to the type locality. The name was suggested, but never published, by Richard L. Hoffman (1927–2012), great American myriapodologist.

**Material examined** (total 1 ♂, 1 ♀)

#### Holotype

TANZANIA • ♂; Morogoro Region, Kilombero District, base of Sanje Falls, Mwanihana Forest Reserve; Apr. 1984; K.M. Howell leg.; VMNH 112021.

#### Paratype

TANZANIA • 1 ♀; same collection data as for holotype; VMNH 112022.

### Description (male)

**SIZE.** Length unknown (specimen in several pieces, collum and rings 2–6 missing). Diameter 4.2 mm. 54 podous rings (including 1–6), no apodous rings in front of telson.

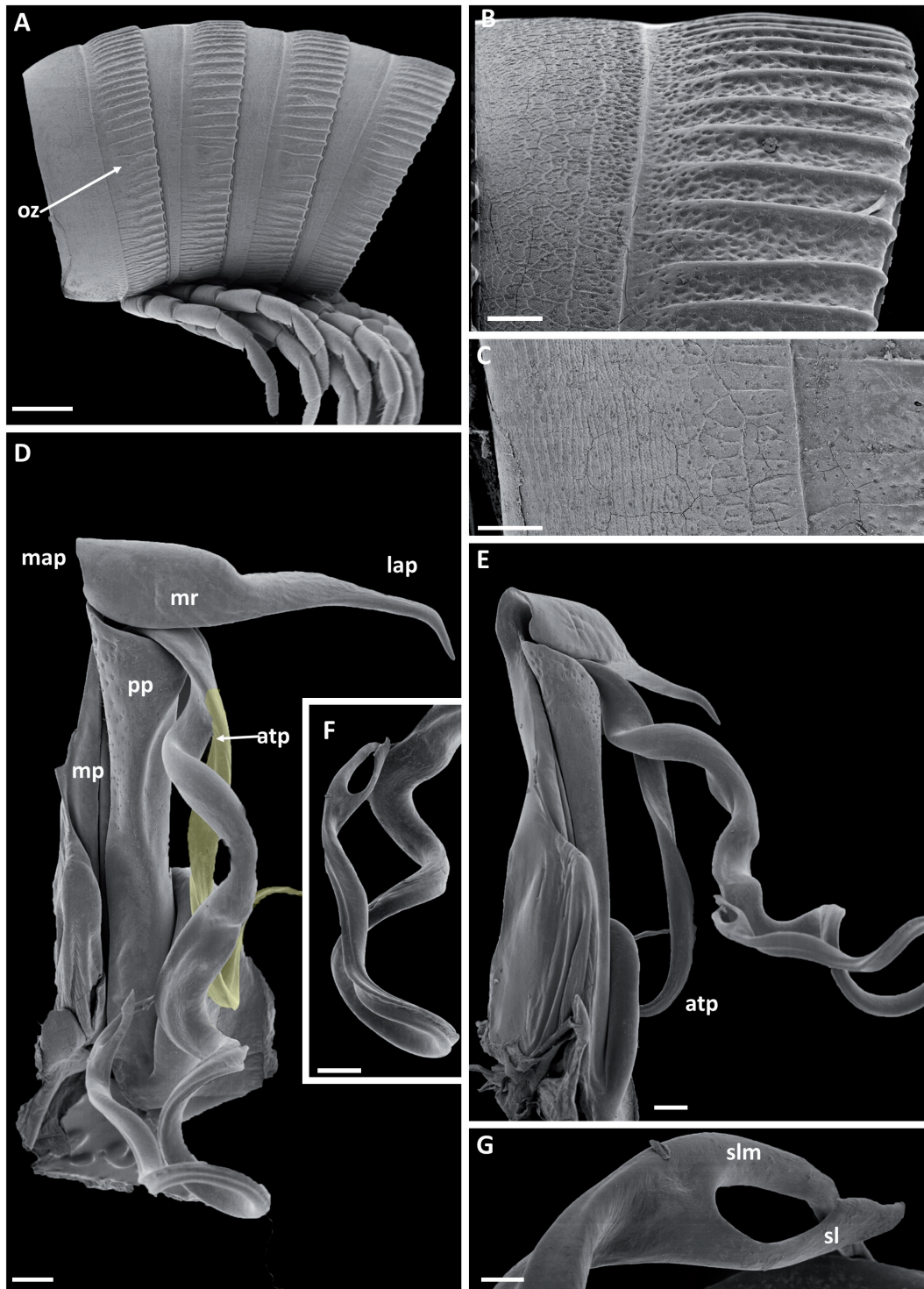
**COLOUR.** After 39 years in alcohol antennae, legs and head below antennae yellowish; head between antennae brown, marbled in upper part. Collum marbled brown, with brown anterior band expanded in middle. Body rings faded to whitish tallow except for amber-coloured posterior ¼ of metazonites.

**HEAD.** Eyes each with ca 30 ommatidia in ca 12 vertical and 5 horizontal rows, extending just mesad of antennal sockets. Antennae (presumably) reaching back to ring 4 when stretched.

**COLLUM.** With three strong complete carinae, otherwise unornamented, resembles Fig. 9A; lateral lobes slightly expanded.

**BODY RINGS** (Fig. 8A–C). Anterior part of prozonites with dense transverse microsculpture which posteriorly gives way to an at first irregular, then regular cell structure; in dorsal part of ring, surface of last cell row coarsely pitted. Metazonites slightly vaulted, carinate throughout; in dorsal part of ring surface between ridges coarsely pitted. Suture between pro- and metazonites simple, straight. Ozopores (*oz*) between two ridges, in middle of metazonite. No sigilla.

**TELSON.** Similar to that of *A. reflexus* (Fig. 4B–D).



**Fig. 8.** *Attemsostreptus cataractae* Enghoff sp. nov., holotype, ♂ (VMNH 112021). **A–C.** Midbody rings. **A.** Four rings with legs. **B.** Close-up of metazonite and posterior part of prozonite. **C.** Close-up of prozonite and anterior part of metazonite. **D–G.** Right gonopod. **D.** Anterior view. **E.** Anterior-mesal view. **F.** Distal part of telopodite. **G.** Tip of telopodite. Abbreviations: *atp* = antetorsal process (highlighted in yellow in D); *lap* = lateroapical metaplical process; *map* = mesapical metaplical process; *mp* = metaplica; *mr* = metaplical “roof”; *oz* = ozopore (hard to see); *pp* = proplica; *px* = paracoxite; *sl* = serrate lamella; *slm* = solenomere. Scale bars: A = 1 mm; B–F = 0.2 mm; G = 0.05 mm.

LEGS (leg-pairs 1–7 missing). Length ca  $0.9 \times$  body diameter. Postfemora and tibiae with ventral pads; pads decreasing in size towards posterior and absent from last pairs of legs.

GONOPOD COXA (Fig. 8D–E). Slender, parallel-sided. Proplica (*pp*) apically punctate and slightly expanded, apical margin oblique, fitting under metapical roof (*mr*), mesally ending in acute-angled process. Metaplica (*mp*) without distomesal spine; apically bent over and forming a ‘roof’ (*mr*) over the gonocoel; mesally slightly produced into poorly defined mesapical process (*map*); laterally forming a very long ( $>$  half length of entire coxa) slender process (*lap*); process directed laterad, almost straight except for ‘downwards’-bent tip.

GONOPOD TELOPODITE (Fig. 8D–G). With a very long, slender, pointed antetorsal process (*atp*) in the shape of a large hook. Post-torsal part of telopodite very slender, directed basad, describing a loose  $360^\circ$  spiral, extending past base of coxa where it makes a  $180^\circ$  turn such that the last part is directed apicad; tip divided into lamellar, slightly serrate process (*sl*) and pointed solenomere (*slm*).

#### Descriptive notes (female)

Length 75 mm. Diameter 5.5 mm, 54 podous rings, no apodous ring in front of telson. Lateral lobes of collum not expanded. Other non-sexual characters as in male.

#### Distribution and habitat

Known only from the type locality; “base of Sanje Falls” could be anywhere between 300 and 500 m a.s.l.

*Attemsostreptus julostriatus* Enghoff sp. nov.

urn:lsid:zoobank.org:act:DD71B6EC-7243-4F22-B13F-E6CA213A0352

Figs 2, 3C, 9–11

#### Diagnosis

Differs from congeners, except *A. leptoptilos* sp. nov., by the relatively short ( $<$  half length of gonopod coxa), pronouncedly basad lateroapical metapical process (*lap*). Differs from *A. leptoptilos* by having more podous rings (58–62 vs 48), by having the metazonites striate as in species of Julidae Leach, 1814, vs carinate as in other trachystreptoform spirostreptids, and by having the mesapical coxal spines (*mcs*) very short and pointing distad vs much longer and pointing distomesad.

#### Etymology

The name refers to the shallow metazonital striation, which reminds more of the sculpture seen in members of the Palaearctic family Julidae than of other trachystreptoform spirostreptids. Adjective.

**Material examined** (total 3 ♂♂, 3 ♀♀)

##### Holotype

TANZANIA • ♂; Iringa Region, Kilolo District, Kilombero Nature Reserve, Ndundulu, Luvalo (“Luala”);  $07^\circ 46' 00.4''$  S,  $36^\circ 29' 32.2''$  E; 1903 m a.s.l.; 26 Oct. 2021; A. Ngute, R. Malanda, W. Mhagawale, A. Mpoto, A. Marshall leg.; FoRCE Plot 70, closed canopy; COLL.NHMD - ACC.NO. 2022-EN-003; NHMD 621878.

##### Paratypes

TANZANIA – Iringa Region • 1 ♂; Udzungwa Mountains, Ndundulu Forest, Waller’s Camp;  $07^\circ 46'$  S,  $36^\circ 29'$  E; 1550 m a.s.l.; 1–12 Jan. 2007; L.A. Hansen and local assistants leg.; tropical semi-evergreen forest; NHMD 621879 • 1 ♂; Mahenge District, West Kilombero Scarp Forest Reserve, Ndundulu



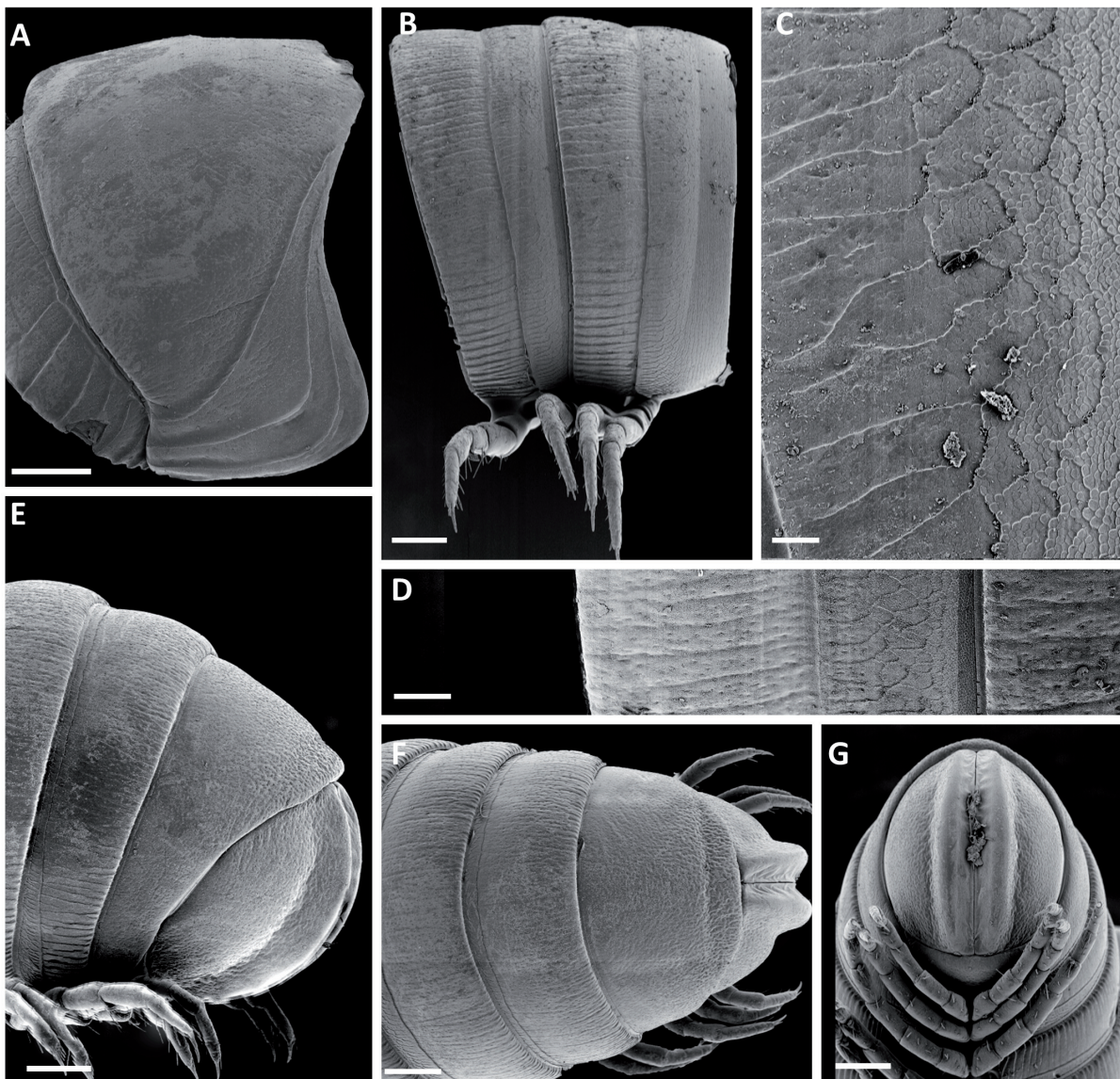
Mountains ESE, Udekwa village; 07°44'37" S, 36°27' E; 1700 m a.s.l.; Mar.–Apr. 1993; L.L. Sørensen leg.; in rotten wood; NHMD 621880.

**Referred material, not types**

TANZANIA – **Iringa region** • 3 ♀♀; Mahenge District, West Kilombero Scarp Forrest Reserve, Nyumbanitu Mountains S, Udekwa village; 07°50'41" S, 36°20' E; 1500 m a.s.l.; Dec. 1993; J.O. Svendsen leg.; NHMD 621881.

**Description (males)**

SIZE. Length 56–64 mm, diameter 3.3–3.5 mm, 58–62 podous rings, no apodous rings in front of telson.



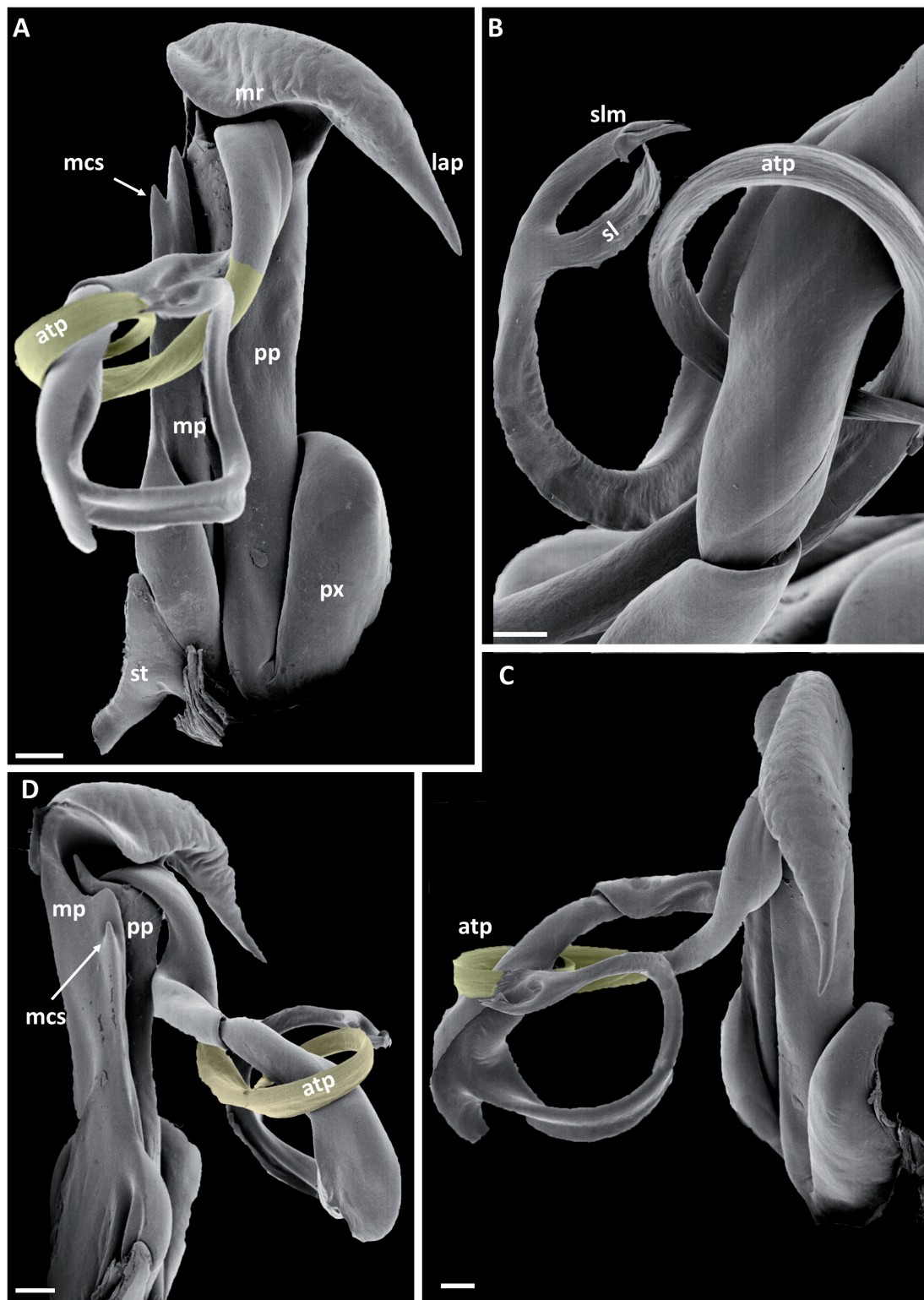
**Fig. 9.** *Attemsostreptus julostratus* Enghoff sp. nov., paratype, ♂ (NHMD 621879). **A.** Collum and part of ring 2, lateral view. **B.** Two midbody rings, lateral view. **C–D.** Midbody ring, details of sculpture. **C.** Posterior part of prozonite, lateral view. **D.** Dorsal view. **E–G.** Telson and last two rings. **E.** Lateral view. **F.** Dorsal view. **G.** Posterior view. Scale bars: A–B, E–G = 0.5 mm; D = 0.2 mm; C = 0.05 mm.





**Fig. 10.** *Attemsostreptus julostratus* Enghoff sp. nov., paratype, ♂ (NHMD 621879), first pair of legs (right leg broken after prefemur). **A.** Sublateral view. **B.** Ventral view. **C.** Posterior view. **D.** Detail of prefemoral lobe. Scale bars: A–C = 0.1 mm; D = 0.05 mm.





**Fig. 11.** *Attemsostreptus julostratus* Enghoff sp. nov., paratype, ♂ (NHMD 621879), right gonopod. **A.** In toto, anterior view. **B.** Detail of telopodite. **C.** Lateroapical view. **D.** Mesanterior view. Abbreviations: *atp* = antetorsal process (highlighted in yellow in A, C and D); *lap* = lateroapical metaplical process; *mcs* = mesal coxal spine; *mp* = metaplica; *mr* = metaplical “roof”; *pp* = proplica; *px* = paracoxite; *sl* = serrate lamella; *slm* = solenomere; *st* = sternum. Scale bars: A, C–D = 0.2 mm; B = 0.1 mm.

COLOUR (Fig. 3C). After 18 months in alcohol overall medium brown, marbled with blackish brown. Head with blackish brown interocular band. Collum with blackish brown margins. Metazonites blackish brown along posterior margin, dorsally with blackish brown zone extending to suture. Telson blackish brown. Legs yellowish brown.

HEAD. Eyes not surpassing antennal sockets medially, with ca 45 ommatidia in 6 horizontal and >10 rather jumbled vertical rows. Antennae reaching back to ring 5–6. Mandibular stipes: distal margin concave.

COLLUM (Fig. 9A) Smooth except for 3 lateral carinae. Lateral lobes slightly expanded.

BODY RINGS (Fig. 9B–D). Anterior part of prozonites with dense transverse microsculpture which posteriorly gives way to a first irregular, later regular cell structure; in dorsal part of ring surface of last cell row coarsely pitted. The cuticular scutes (“cytoscutes”) of the anterior part of the prozonite are remarkable in being rounded rather than polygonal and being arranged in an imbricate pattern (Fig. 9C). Metazonites slightly vaulted, densely striated, but not carinate as in congeners, surface between striae coarsely pitted. Suture between pro- and metazonite simple, straight. Ozopores between two ridges, slightly behind middle of metazonite.

TELSON (Fig. 9E–G). As in *A. reflexus*, *A. cataractae* sp. nov. and *A. leptoptilos* sp. nov.

LEGS. Length ca 0.9 × body diameter. Postfemora and tibiae with ventral pads; pads decreasing in size towards posterior and absent from last pairs of legs. First pair (Fig. 10) similar to those in *A. reflexus*.

GONOPOD COXA (Fig. 11A, D). As in *A. cataractae* sp. nov., with two exceptions: metaplica (*mp*) with very short oblique distomesal spine (*mcs*); lateroapical metaplical process (*lap*) shorter, less than length of coxa, directed basad.

GONOPOD TELOPODITE (Fig. 11). As in *A. cataractae* sp. nov. and *A. leptoptilos* sp. nov. The gonopod telopodite illustrated in Fig. 11 has become somewhat distorted during the preparation for SEM. In alcohol-preserved specimens, the position of the telopodite is as in *A. cataractae* sp. nov. (Fig. 8D).

### **Descriptive notes (females)**

Length unmeasurable, all females broken. Diameter 4.2–4.8 mm. 58–60 podous rings, no apodous rings in front of telson. Lateral lobes of collum not expanded. Other non-sexual characters as in male.

### **Distribution and habitat**

Found at several forested sites in the Ndundulu and Nyambanitu Mountains, 1500–1903 m a.s.l. One specimen collected from rotten wood.

*Attemsostreptus leptoptilos* Enghoff sp. nov.

urn:lsid:zoobank.org:act:34AAD11B-3CA4-44FA-8E21-A13047FC01BC

Figs 2, 3D, 12–13

### **Diagnosis**

Differs from congeners, except *A. julostriatus* sp. nov., by the relatively short (< half length of gonopod coxa), pronouncedly basad lateroapical metaplical process (*lap*). Differs from *A. julostriatus*, by having fewer podous rings (48 vs 58–62), by having the metazonites carinate as in other trachystreptoform spirostreptids, vs striate as in species of Julidae, and by having the mesapical coxal spines (*mcs*) much longer and pointing distomesad, vs very short and pointing distad.

### Etymology

*Leptoptilos* is the name of the genus to which the African marabou stork belongs; here it refers to the somewhat marabou-like profile of the gonopod coxa of the new species. Noun in apposition.

**Material studied** (total 4 ♂♂, 5 ♀♀)

#### Holotype

TANZANIA • ♂; Iringa Region/District, Nyambanitu Mountains, Ukami Forest; 07°42'49" S, 36°25'15" E; Jul.–Nov. 1984; D. Moyer leg.; NHMD 621876.

#### Paratypes

TANZANIA • 3 ♂♂, 5 ♀♀; same collection data as for holotype; NHMD 621877.

### Description (males)

**SIZE.** Length ca 58 mm, diameter 3.7–4.1 mm, 48 podous rings, no apodous rings in front of telson.

**COLOUR.** After 39 years in alcohol head, antennae and collum brown; head becoming yellowish brown towards clypeal margin; collum marbled except for solid brown band along anterior margin, band expanded in the middle. Body rings and telson (faded to?) grey, except for amber-coloured posterior 1/3 of metazonites and brown lips of anal valves. Legs yellowish brown.

**HEAD** (Fig. 12A–B). Eyes each with ca 30 ommatidia in ca 12 vertical and 5 horizontal rows, extending just mesad of antennal sockets. Antennae reaching back to ring 5 when stretched.

**COLLUM** (Fig. 12B). With two deep, complete lateral carinae and short carinae along hind margin along entire perimeter. Lateral lobes slightly expanded.

**BODY RINGS** (Fig. 12D–G). Anterior part of prozonites with dense transverse microsculpture which posteriorly gives way to an at first irregular, later regular cell structure; in dorsal part of ring surface of last cell row coarsely pitted. Cuticular scutes (“cytoscutes”) of anterior part of prozonite remarkable in being rounded rather than polygonal and being arranged in an imbricate pattern (Fig. 12G, left inset). Metazonites vaulted, carinate throughout; anterior part of ridges with fine moniliform sculpture (Fig. 12G, right inset); in dorsal part of ring surface between ridges coarsely pitted. Suture between pro- and metazonite simple, straight. Ozopores between two ridges, slightly behind middle of metazonite. No sigilla.

**TELSON** (Fig. 12C, H–I). As in *A. reflexus* and *A. cataractae* sp. nov.

**LEGS.** Length ca 0.9 × body diameter. Postfemora and tibiae with ventral pads; pads decreasing in size towards posterior and absent from last pairs of legs. First pair (Fig. 13A–B) similar to those of *A. reflexus*, but tip of prefemoral lobes (*pfl*) more rounded.

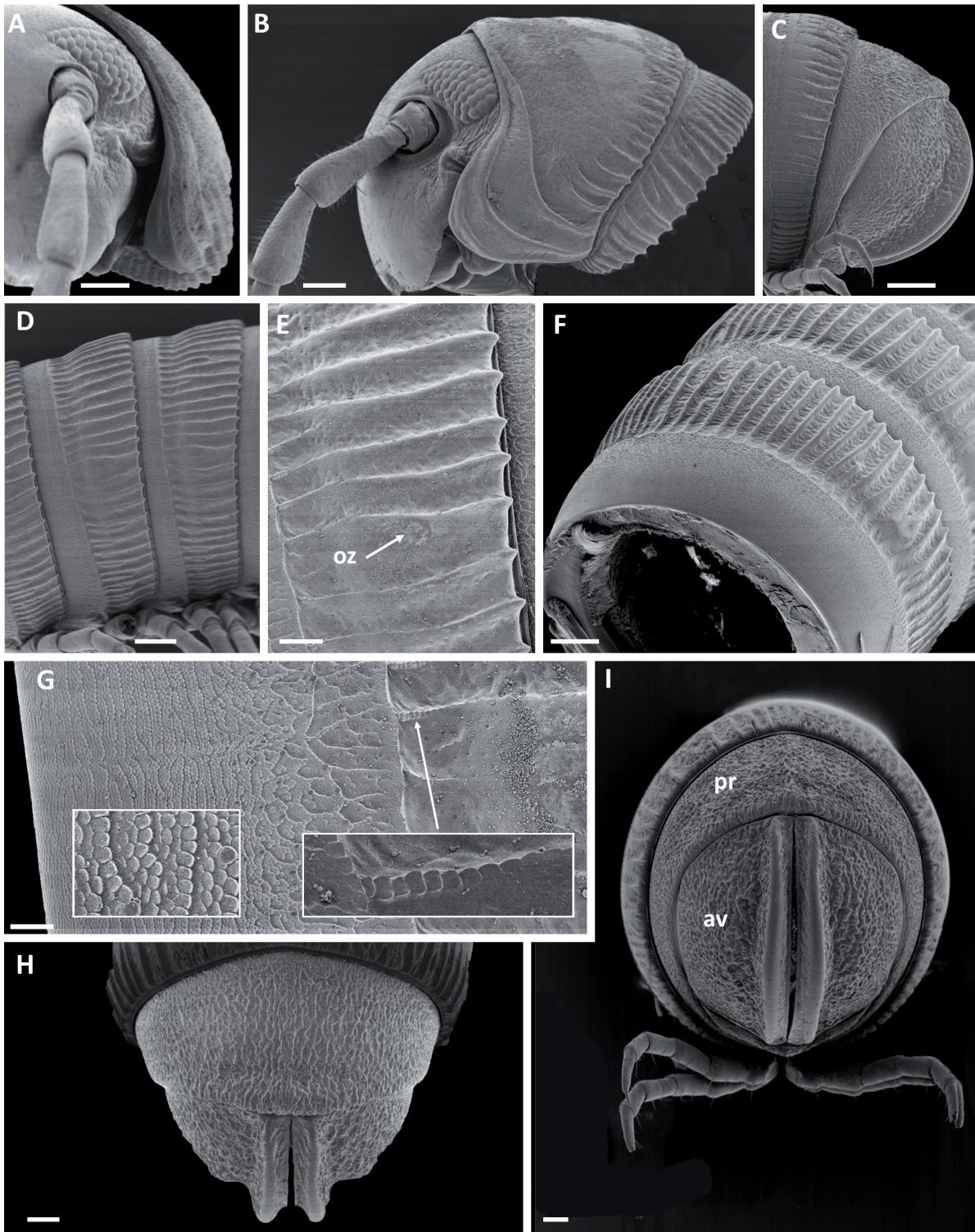
**GONOPOD COXA** (Fig. 13C). As in *A. julostriatu* sp. nov., but distomesal spine (*mcs*) of metaplica long (as in *A. reflexus*).

**GONOPOD TELOPODITE** (Fig. 13D–F). As in *A. cataractae* sp. nov. and *A. julostriatu* sp. nov.

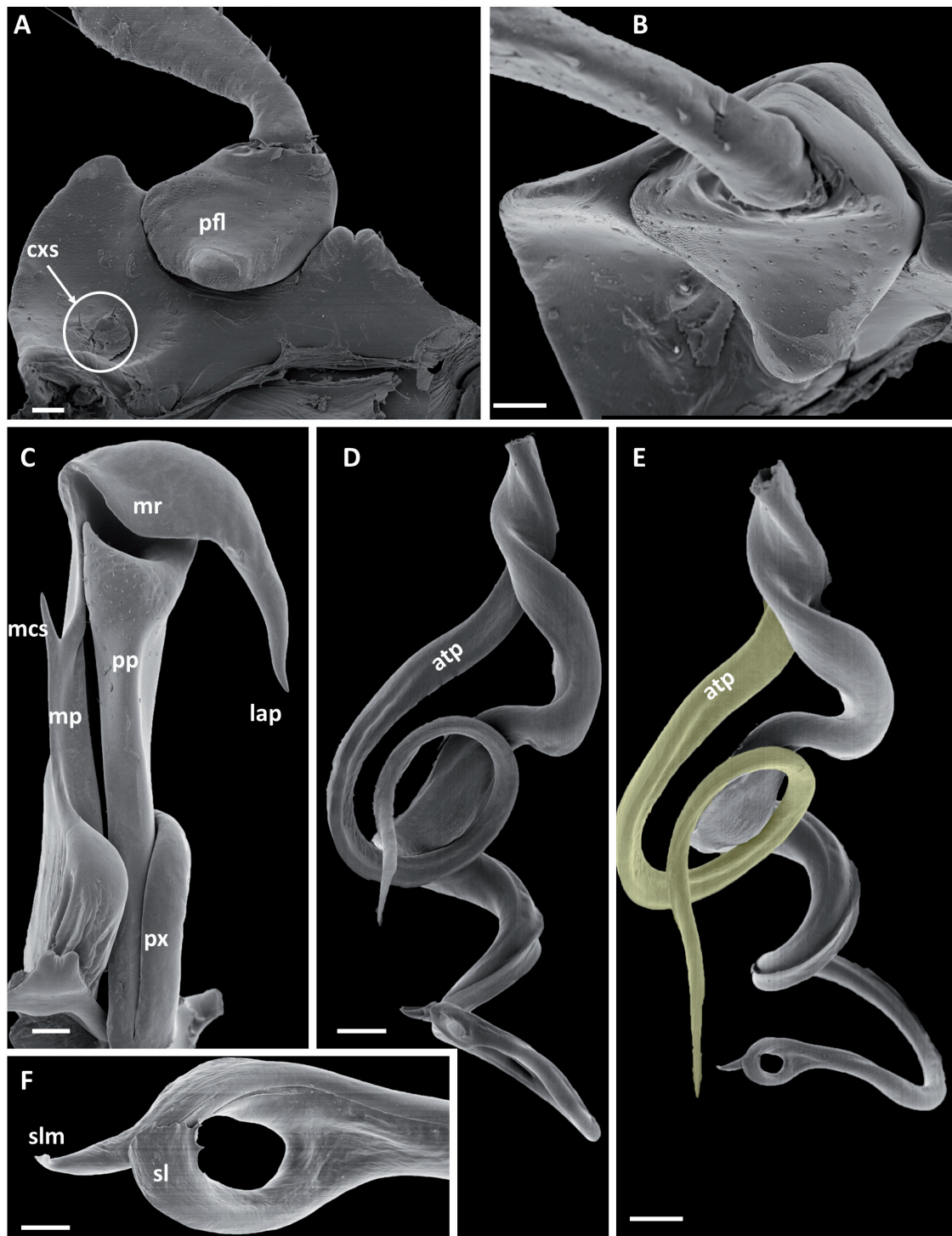
### Descriptive notes (females)

Length unmeasurable, all females broken. Diameter up to 4.8 mm. One specimen with 48 podous rings, no podous rings in front of telson. One subadult specimen (diameter 3.7 mm) with 46 podous + 1 apodous





**Fig. 12.** *Attemsostreptus leptoptilos* Enghoff sp. nov., paratype, ♂ (NHMD 621877). **A.** Head and collum, anterior view. **B.** Head, collum and ring 2, lateral view. **C.** Telson and ultimate ring, lateral view. **D.** Midbody rings, lateral view. **E.** Detail of D. **F.** Midbody rings, oblique dorsolateral view. **G.** Detail of D; left inset: close-up of scalelike microsculpture; right inset: close-up of beaded anterior part of a ridge. **H.** Telson, dorsal view. **I.** Telson and ultimate ring, posterior view. Abbreviations: *av* = anal valve; *oz* = ozopore; *pr* = preanal ring. Scale bars: A–D, F = 0.5 mm; E, H–I = 0.2 mm; G = 0.1 mm.



**Fig. 13.** *Attemsostreptus leptoptilos* Enghoff sp. nov., paratype, ♂ (NHMD 621877). **A–B.** First pair of legs. **A.** Posterior view. **B.** Ventral view. **C.** Right gonopod coxa, anterior view. **D–E.** Right gonopod telopodite (proximal part missing). **D.** Mesal view. **E.** Mesobasal view. **F.** Close-up of telopodite tip. Abbreviations: *atp* = antetorsal process (highlighted in yellow in E); *cxs* = coxosternal setae; *lap* = lateroapical metaplical process; *mcs* = distomesal coxal spine; *mp* = metaplica; *mr* = metaplical “roof”; *pfl* = prefemoral lobe; *pp* = proplica; *px* = paracoxite; *sl* = serrate lamella; *slm* = solenomere. Scale bars: A–B = 0.1 mm; C–E = 0.2 mm; F = 0.05 mm.



ring. Remaining specimens broken. Lateral lobes of collum not expanded. Other non-sexual characters as in male.

### Disribution and habitat

Known only from the type locality. Ukami Forest lies at 1000–1600 m elevation on steep and rocky terrain (Fjeldså *et al.* 2010)

### Key to species of *Attemsostreptus*

1. Lateroapical metaplical process (*lap*) of gonopod coxa extremely long, bent in a U-shape (Figs 3B, 7A) ..... *A. reflexus* Akkari & Enghoff, 2019  
 – Lateroapical metaplical process (*lap*) only moderately curved ..... 2
2. Lateroapical metaplical process (*lap*) more than half as long as gonopod coxa, directed laterad or laterobasad ..... 3  
 – Lateroapical metaplical process (*lap*) less than half as long as gonopod coxa, directed pronouncedly basad ..... 4
3. Lateroapical metaplical process (*lap*) almost as long as coxal height; mesapical metaplical process (*map*) separated from rest of metaplica by rounded incision (Akkari & Enghoff 2019: fig. 1) .....  
 ..... *A. costatus* Verhoeff, 1941  
 – Lateroapical metaplical process (*lap*) only slightly longer than half coxal height; mesapical metaplical process (*map*) poorly delimited from rest of metaplica (Fig. 8D–E) .....  
 ..... *A. cataractae* Enghoff sp. nov.
4. Metazonites not carinate but striate as in species of Julidae (Fig. 9B); 58–62 podous rings; distomesal coxal spine (*mcs*) short, directed apicad (Fig. 11A, D) ..... *A. julostratus* Enghoff sp. nov.  
 – Metazonites with typical trachystreptoform sculpture, i.e., carinate (Fig. 12D–F); 48 podous rings; distomesal coxal spine (*mcs*) long, directed distoapicad (Fig. 13C) .....  
 ..... *A. leptoptilos* Enghoff sp. nov.

### Genus *Lophostreptus* Cook, 1895

*Lophostreptus* Cook, 1895: 5.

*Ptilostreptus* Cook, 1896: 57, synonymized by Attems (1914: 141).

*Carlostreptus* Verhoeff, 1941: 262, synonymized by Demange & Mauriès (1975: 78).

*Lophogonus* Demange & Mauriès, 1975: 78, synonymized with *Ptilostreptus* by Hoffman (1980: 94).

### Type species

*Glyphijulus magnus* Karsch, 1881, by original designation.

### Diagnosis

Modified from Demange & Mauriès (1975) and Krabbe (1982). A trachystreptoform genus with the anterior margin of the collum unmodified, the lateroapical metaplical process (*lap*) of the gonopod coxa inclined or abruptly bent laterad, and the generally slender gonopod telopodite carrying a plate-like post-torsal extension (*sf*) or at least with a marked ‘knee’ (*kn*) at the same place.

### Other included species

*Lophostreptus armatus* Pocock, 1896

*Lophostreptus bicolor* Carl, 1909

*Lophostreptus cameranii* Silvestri, 1896

*Lophostreptus luridus* Attems, 1934  
*Lophostreptus magombera* Enghoff sp. nov.  
*Lophostreptus minimus* Mwabvu & VandenSpiegel, 2009  
*Lophostreptus neglectus* Enghoff & Akkari, 2024  
*Lophostreptus poriger* Verhoeff, 1941  
*Lophostreptus similis* Attems, 1914  
*Lophostreptus tersus* (Cook, 1896)  
*Lophostreptus ulopygus* Attems, 1928

### Remarks

The type species of *Lophostreptus*, *Glyphijulus magnus* Karsch, 1811, is known only in the female sex, and the current concept of the genus is based on *L. armatus* (Demange & Mauriès 1975: 78).

Keys to the species then assigned to *Lophostreptus* were given by Attems (1914: 142; 1928: 360; 1938: 261). These keys, mainly based on non-sexual characters, are outdated and not useful, and to be able to construct a useful key, several species would need re-study. See also remarks under *L. tersus* below.

The identity of *Ptilostreptus* has been the cause of much uncertainty. *Ptilostreptus* was described by Cook (1896), based on a new species, *P. tersus* Cook, 1897, from Mpapua, Tanzania. Like several other genera described by Cook in unillustrated papers, *Ptilostreptus* was largely neglected by subsequent authors. Carl (1909) criticized Cook's trachystreptinine genera, but at the same time suggested that his *Lophostreptus ptilostreptoides* Carl, 1909 "probably is nothing but Cook's undescribed *Ptilostreptus tersus* from Mpapua" (Carl 1909: 317, translated from German). Attems (1914) in his monograph of Spirostreptidae listed *Ptilostreptus* as a synonym of *Lophostreptus* Cook & Collins, 1895.

Sixty-one years after Attems' monograph, the Trachystreptini were reviewed again, this time by Demange & Mauriès (1975). These authors recognized neither *Ptilostreptus* nor its type species, surely because no illustrations were given by Cook of *P. tersus*, and because the gonopods of the type specimen of *P. tersus* were lost, a fact already noted by Attems (1914). Instead they described a new genus, *Lophogonus* Demange & Mauriès, 1975, to accommodate *Lophostreptus ptilostreptoides* (type species) and *Lophostreptus regularis* Attems, 1909.

In Hoffman's (1980) comprehensive classification of the Diplopoda, on the other hand, *Ptilostreptus* was listed as a valid genus, with *Lophogonus* as a junior synonym.

Finally, in the third major review of Trachystreptini in the 20<sup>th</sup> century Krabbe (1982), unaware of Hoffman's synonymization, listed *Ptilostreptus* as an uncertain genus and *Lophogonus* as a synonym of *Lophostreptus*. This synonymy is supported by the discovery of *L. magombera* sp. nov. because this species has a character regarded as characteristic of *Lophogonus* by Demange & Mauriès (1975), viz., the strong laterad flexion of the lateroapical metapical process (*lap*), but on the other hand lacks the large, spoon-shaped telopodital process (*pal*) characteristic of *L. tersus*.

### *Lophostreptus tersus* (Cook, 1896)

Figs 1–2, 3E–F, 14–17

*Ptilostreptus tersus* Cook, 1896: 57.

*Lophostreptus ptilostreptoides* Carl, 1909: 321, **syn. nov.** (tentatively suggested by Carl 1909: 317).

*Lophostreptus regularis* Attems, 1909: 31, synonymized with *L. ptilostreptoides* by Krabbe (1982: 258).

*Lophostreptus malleolus* Kraus, 1958: 12, synonymized with *L. ptilostreptoides* by Demange & Mauriès (1975: 79).

*Lophostreptus tersus* – Attems 1914: 143.

*Lophogonus ptilostreptoides* – Demange & Mauriès 1975: 78.



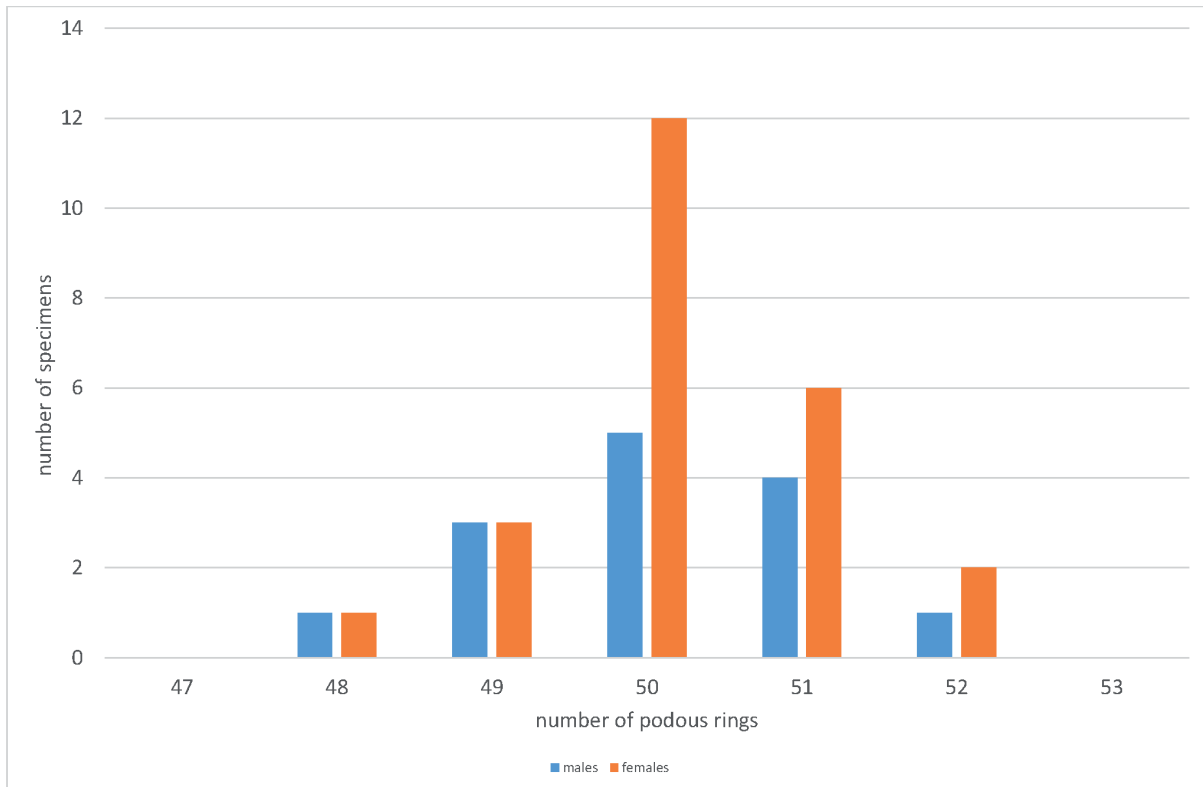
**Diagnosis**

Differs from congeners and all other trachystreptoform spirostreptids by the complex and highly characteristic lateroapical metaplical process (*lap*): sharply bent laterad, in the shape of a long, twisted slipper with a rounded mesal ‘heel’. Very similar to that of the sympatric *L. magombera* sp. nov., but larger (Fig. 17).

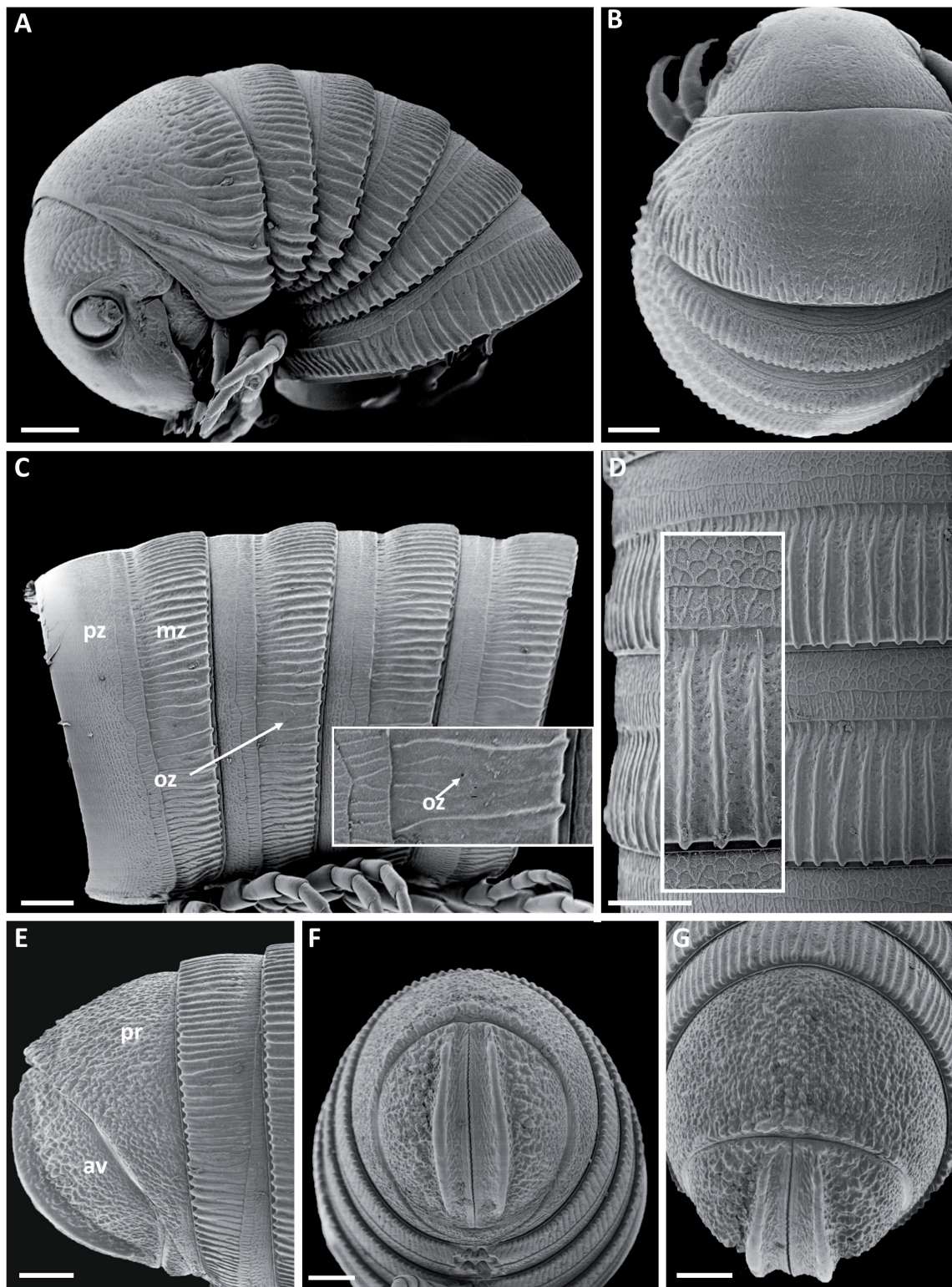
**Material examined**

**Material from Udzungwa Mountains** (total 16 ♂♂, 27 ♀♀, 24 juvs)

TANZANIA – **Morogoro Region, Kilombero District, Magombera Nature Reserve** • 2 ♂♂, 4 ♀♀; 07°49’03.6” S, 36°58’40.0” E; 279 m a.s.l.; 22 Jan. 2020; A. Ngute and A.R. Marshall leg.; micro-FoRCE plot 10, open forest; COLL. NHMD. ACC.NO. 2020-EN-002; NHMD 1184638 • 1 ♀, 1 juv.; same collection data as for preceding; 07°49’21.7” S, 36°58’57.1” E; 283 m a.s.l.; 30 Jan. 2020; A. Ngute and A.R. Marshall leg.; micro-FoRCE plot 12, closed forest; NHMD 1184639 • 3 ♂♂, 5 ♀♀, 2 juvs; same collection data as for preceding; 07°49’28.0” S, 36°58’55.2” E; 271 m a.s.l.; 31 Jan. 2020; micro-FoRCE plot 13, open forest; NHMD 1184640 • 3 ♂♂; Udzungwa Mountains National Park; 07°50’56.4” S, 36°53’00.4” E; 325 m a.s.l.; 2 Mar. 2020; A. Ngute and A.R. Marshall leg.; micro-FoRCE plot 26, open forest; NHMD 1184641 • 2 ♀♀, 1 juv.; same collection data as for preceding; 07°48’30.9” S, 36°50’33.1” E; 287 m a.s.l.; 14 Jul. 2019; A. Ngute and A.R. Marshall leg.; half-FoRCE plot 37, open forest; COLL. NHMD. ACC.NO. 2020-EN-002; NHMD 1184642 • 1 juv. ♂; same collection data as for preceding; Ngulumilo; 07°49’13.2” S, 36°59’10.3” E; 285 m a.s.l.; 23 Aug. 2021; A. Ngute, E. Kivambe, R. Malanda, W. Mhagawale, H. Mnendo, A. Marshall leg.; FoRCE plot 1, closed canopy; COLL. NHMD - ACC.NO. 2022-EN-003; NHMD 1184643. – **Morogoro Region, Kilombero District,**



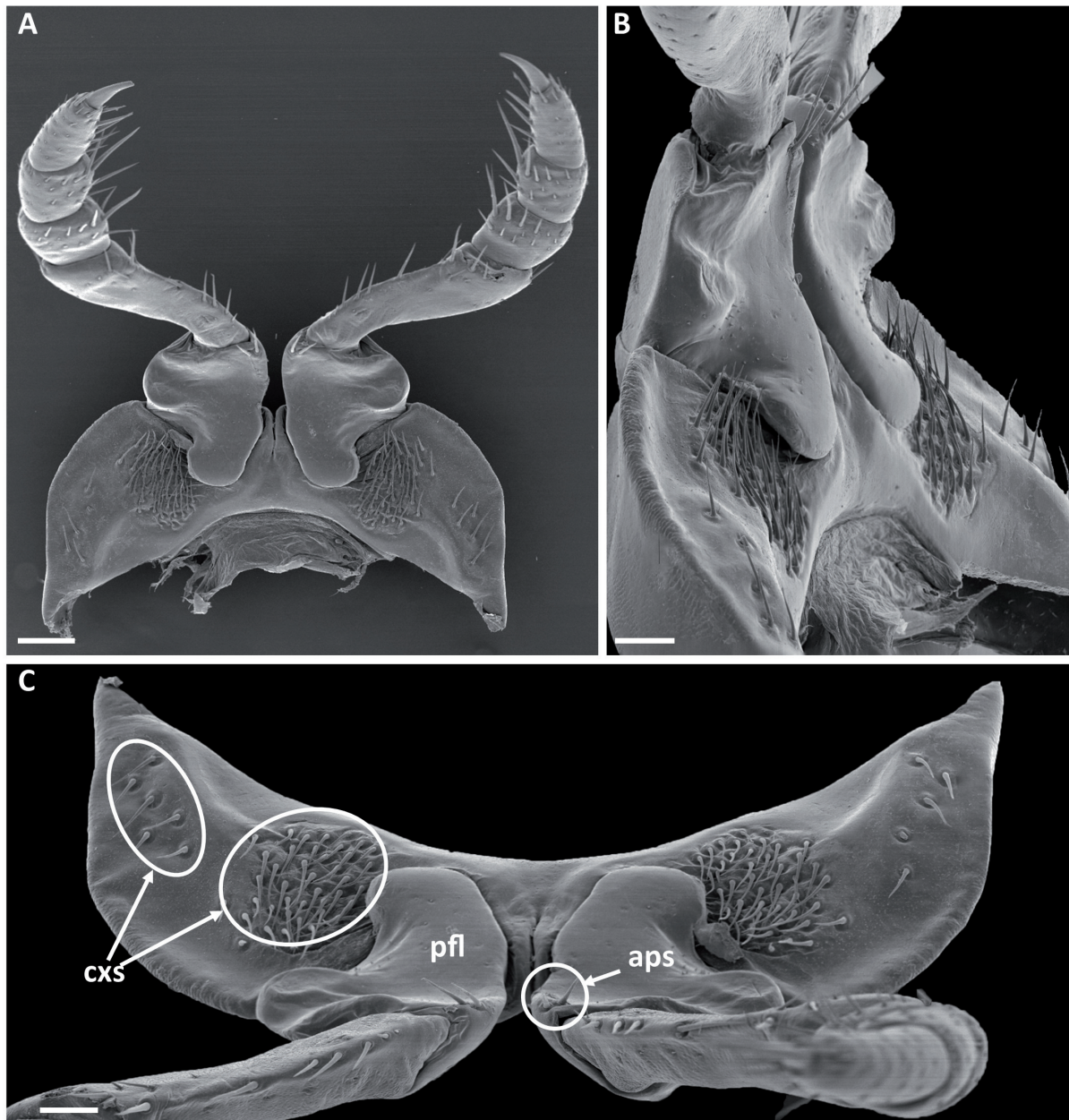
**Fig. 14.** Numbers of body rings in adults and epimorphic juveniles of *Lophostreptus tersus* (Cook, 1896) from the Udzungwa Mountains.



**Fig. 15.** *Lophostreptus tersus* (Cook, 1896), male from Udzungwa Mts National Park (NHMD 1184641). **A–B.** Head, collum and rings 2–6. **A.** Lateral view. **B.** Dorsal view. **C–D.** Midbody rings. **C.** Lateral view; inset: close-up of ozopore. **D.** Dorsal view; inset: close-up. **E–G.** Telson and last rings. **E.** Lateral view. **F.** Posterior view. **G.** Dorsal view. Abbreviations: *av* = anal valve; *mz* = metazonite; *oz* = ozopore; *pr* = preanal ring; *pz* = prozonite. Scale bars = 0.5 mm.



**Udzungwa Mountains National Park, Mwanihana** • 1 ♂, 5 ♀♀, 7 juvs; Njokamoni; 07°50'35.8" S, 36°52'38.5" E; 474 m a.s.l.; 20 Dec. 2021; A. Ngute, R. Malanda, W. Mhagawale, A. Marshall leg.; FoRCE plot 10, closed canopy; COLL.NHMD - ACC.NO. 2022-EN-003; NHMD 1184644 • 2 ♀♀, 2 juvs; same collection data as for preceding; Njokamoni; 07°50'31.9" S, 36°52'47.1" E; 401 m a.s.l.; 21 Dec. 2021; FoRCE plot 11, open canopy; NHMD 1184645 • 1 ♀; same collection data as for preceding; Njokamoni; 07°50'33.1" S, 36°52'54.9" E; 357 m a.s.l.; 22 Dec. 2021; FoRCE plot 12, open canopy; NHMD 1184646 • 1 ♂, 1 ♀, 1 juv.; same collection data as for preceding; Sonjo; 07°48'24.4" S, 36°52'21.7" E; 589 m a.s.l.; 15 Dec. 2021; A. Ngute, R. Malanda, H. Mnendendo, W. Mhagawale, A. Mpoto, A. Marshall leg.; FoRCE plot 14, open canopy; NHMD 1184647 • 1 ♂, 2 ♀♀, 7 juvs; same



**Fig. 16.** *Lophostreptus tersus* (Cook, 1896), male from Udzungwa Mts National Park (NHMD 1184641), first pair of legs. **A.** Posterior view. **B.** Sublateral view. **C.** Ventral view. Abbreviations: *aps* = apicomasal prefemoral setae; *cxs* = coxosternal setae; *pfl* = prefemoral lobes. Scale bars: A = 0.2 mm; B–C = 0.1 mm.

collection data as for preceding; Sonjo; 07°48'22.3" S, 36°52'32.2" E; 595 m a.s.l.; 17 Dec. 2021; FoRCE plot 15, open canopy; NHMD 1184648 • 1 ♀, 1 juv.; same collection data as for preceding; Sonjo; 07°48'22.3" S, 36°52'32.2" E; 541 m a.s.l.; 18 Aug. 2021; A. Ngute, E. Kivambe, W. Mhagawale, H. Mnendendo, A. Mwakisoma, A. Marshall leg.; FoRCE plot 95, open canopy; NHMD 1184649 • 1 ♂, 1 ♀; same collection data as for preceding; Mizimu; 07°48'34.0" S, 36°51'17.0" E; 900 m a.s.l.; 12 Dec. 2021; FoRCE plot 17, open canopy, subplot 1; NHMD 1184650 • 2 ♂♂, 1 ♀; same collection data as for preceding; Sanje; 07°46'47.6" S, 36°54'07.6" E; 495 m a.s.l.; 23 Feb. 2022; A. Ngute, E. Kivambe, R. Malanda, H. Mnendendo, W. Mhagawale, M. Mpoto, A. Marshall leg.; FoRCE plot 25, open canopy; NHMD 1184651 • 1 ♂; same collection data as for preceding; Sanje; 07°46'52.1" S, 36°54'11.8" E; 421 m a.s.l.; 20 Feb. 2022; A. Ngute, E. Kivambe, R. Malanda, W. Mhagawale, H. Mnendendo, A. Marshall leg.; FoRCE plot 92, open canopy; NHMD 1184652 • 1 ♀, 1 juv.; same collection data as for preceding; Sanje; 07°47'03.0" S, 36°54'05.8" E; 410 m a.s.l.; 17 Feb. 2022; A. Ngute, E. Kivambe, W. Mhagawale, H. Mnendendo, M. Mpoto, A. Marshall leg.; FoRCE plot 93, open canopy; NHMD 1184653. – **Morogoro Region, Ecological Monitoring Centre Mang'ula** • 1 ♂; 07°50'44.9" S, 36°53'28.2" E; 339 m a.s.l.; 20 Mar. 2013; T. Pape and N. Scharff leg.; hand-collected; NHMD 1184654.

**Material from other places than Udzungwa Mountains** (total 11 ♂♂, 30 ♀♀, 4 juvs)

TANZANIA • 3 ♂♂, 14 ♀♀; Arusha, Momella; 1300 m a.s.l.; ult. Dec. 1975; L. and T. Nielsen leg.; NHMD 1184655 • 1 ♂; ca 10 km E of Arusha; 1300 m a.s.l.; 19 Jan. 1971; H. Enghoff, O. Lomholdt and O. Martin leg.; NHMD 1184656 • 4 ♂♂; Morogoro Region, Morogoro District, Kimboza Forest Reserve; 07°01' S, 37°48' E; Jan.–Mar. 1994; Frontier Tanzania leg.; NHMD 1184657 • 1 ♂; Morogoro Region, Morogoro District, Mindu Mountains; 06°29' S, 37°21' E; 1200 m a.s.l.; 24 Dec. 1983; J. Kielland leg.; VMNH 112023 • 1 ♂, topotype of *Ptiosstreptus tersus*; Dodoma Region, Mpwapwa District, Wota Forest Reserve; Apr. 1984; J. Kielland leg.; VMNH 112024 • 1 ♂, 6 ♀♀, syntypes of *Lophostreptus regularis*; Kilimandjaro, Kibonoto, Stepp-Kulturzon; 1000–1900 m a.s.l.; Oct. 1905; Y. Sjöstedt leg.; also 1 ♂ of *L. neglectus*; NHRS-TOBI 000005480 • 4 ♀♀, syntypes of *L. regularis*; Kilimandjaro, Kibonoto, Massaistappen; 1000 m a.s.l.; 23 Aug. 19905; Y. Sjöstedt leg.; NHRS-TOBI 000005478 • 1 ♀, syntype of *L. regularis*; Usambara, Tanga; Jun. 1905; Y. Sjöstedt leg.; NHRS-TOBI-000005482 • 4 ♀♀, syntypes of *L. regularis*; Kilimandjaro, Kibonoto; Nov. 1905; Y. Sjöstedt leg.; “under multnande blad i bananfarmerkulturzon” [under decaying leaves in banana farm cultural zone]; NHRS-TOBI-000005476 • 4 ♀♀, syntypes of *L. regularis*; Kilimandjaro, Kibonoto; 1300 m a.s.l.; 1905; Y. Sjöstedt leg.; “I förnan under nedfallna plantanblad” [in förna under fallen plantain leaves]; NHRS-TOBI-000005479 • 1 ♀, syntype of *L. regularis*; Kilimandjaro, Kibonoto; 1905; Y. Sjöstedt leg.; Mischwald-Kulturzone; NHRS-TOBI-000005481 • 4 ♀♀, 4 anamorphic juvs, syntypes of *L. regularis*; Kilimandjaro, Kibonoto; Nov. 1905; Y. Sjöstedt leg.; Kulturzon; NHRS-TOBI-0000077.

**Descriptive notes on males from Udzungwa Mountains**

SIZE. Length 52–58 mm; vertical diameter 3.8–4.5 mm; adults and epimorphic juveniles with 48–52 podous rings (Figs 14, 18), no apodous rings in front of telson.

COLOUR. Live colour (Fig. 3E) overall grey, legs orange yellow. After 2–3 years in alcohol head, antennae, collum, body rings 2–7, telson and dorsal part of remaining body rings blackish brown (head capsule sometimes broadly yellow at labral margin); lateral and ventral part of remaining body rings from well above ozopore level rarely same colour, usually rusty red-brown with contrasting small black spots covering ozopores; posterior edge dark amber; legs medium brown.

HEAD (Fig. 15A–B). Almost smooth below antennae, longitudinally wrinkled near anterior edge, finely punctate between antenna and eyes. Vertex very densely and rather coarsely punctate, with a clearly demarcated parietal furrow. Eyes not reaching mesal of antennal socket, ca 40 ommatidia

in ca 6 horizontal and ca 12 vertical rows. Antennae reaching posterior margin of 2<sup>nd</sup>–3<sup>rd</sup> body ring. Antennomeres 3–5 strongly narrowed at base.

**COLLUM** (Fig. 15A–B). Not modified for accommodation of antennae, densely punctate, finely dorsally, more coarsely towards the sides; along posterior margin a row of quite short, weak furrows and carinae which towards the sides gradually reach further forwards. Lateral lobes much narrower than dorsal part, not expanded, traversed by 3 or 4 anteriorly strongly ascending carinae/furrows of which uppermost is strongest and almost straight, reaching anterior margin above eye level, anterior corner rectangular, posterior corner more rounded, margins straight.

**BODY RINGS** (Fig. 15A, C–D). Prozonites (*pz*) in anterior part (ca half) with very fine ring furrows which further back give place to an irregular cell structure; posterior part (ca 20%) especially dorsally delimited by clear line, with a more regular pattern of larger cells. Suture between pro- and metazonites straight, simple. Metazonites (*mz*) with clear constriction a little behind suture, with numerous simple keels which at least dorsally reach from suture, across constriction and until posterior ring margin; ca 25 keels between dorsal midline and ozopore in a male of 4.3 mm diameter; in larger specimens keels on lateral flanks of anterior segments projecting as short spines beyond posterior metazonital margin (as described by Attems 1914). Ozopores (*oz*) small, a little before middle of metazonite. A row of large sigilla. Sternites transversely striate.

**TELSON** (Fig. 15E–G). Preanal ring (*pr*) regularly and densely grainy-rugose. Anal valves (*av*) overall with same sculpture, strongly vaulted, their mesal margins slightly raised as low rims, smooth, meeting in midline, paralleled more laterally by much higher lips with smooth edge; distance between lips and mesal margin equal to or larger than height of lips; area between mesal margin and keel with weaker sculpture than main part of valve.

**LEGS**. Short, length ca 0.6 × body diameter. No ventral pads. First pair (Fig. 16): coxosternum with lateral groups of a few long setae (*cxls*) and more mesally with large groups of numerous long setae (*cxms*) next to prefemoral lobes. Prefemoral lobes (*pfl*) rounded-rectangular, with a few apicomeral setae (*aps*), otherwise naked.

**GONOPODS** (Fig. 17). As described by Cook (1896), Carl (1909), Attems (1909), Kraus (1958) and Krabbe (1982). Notable features include:

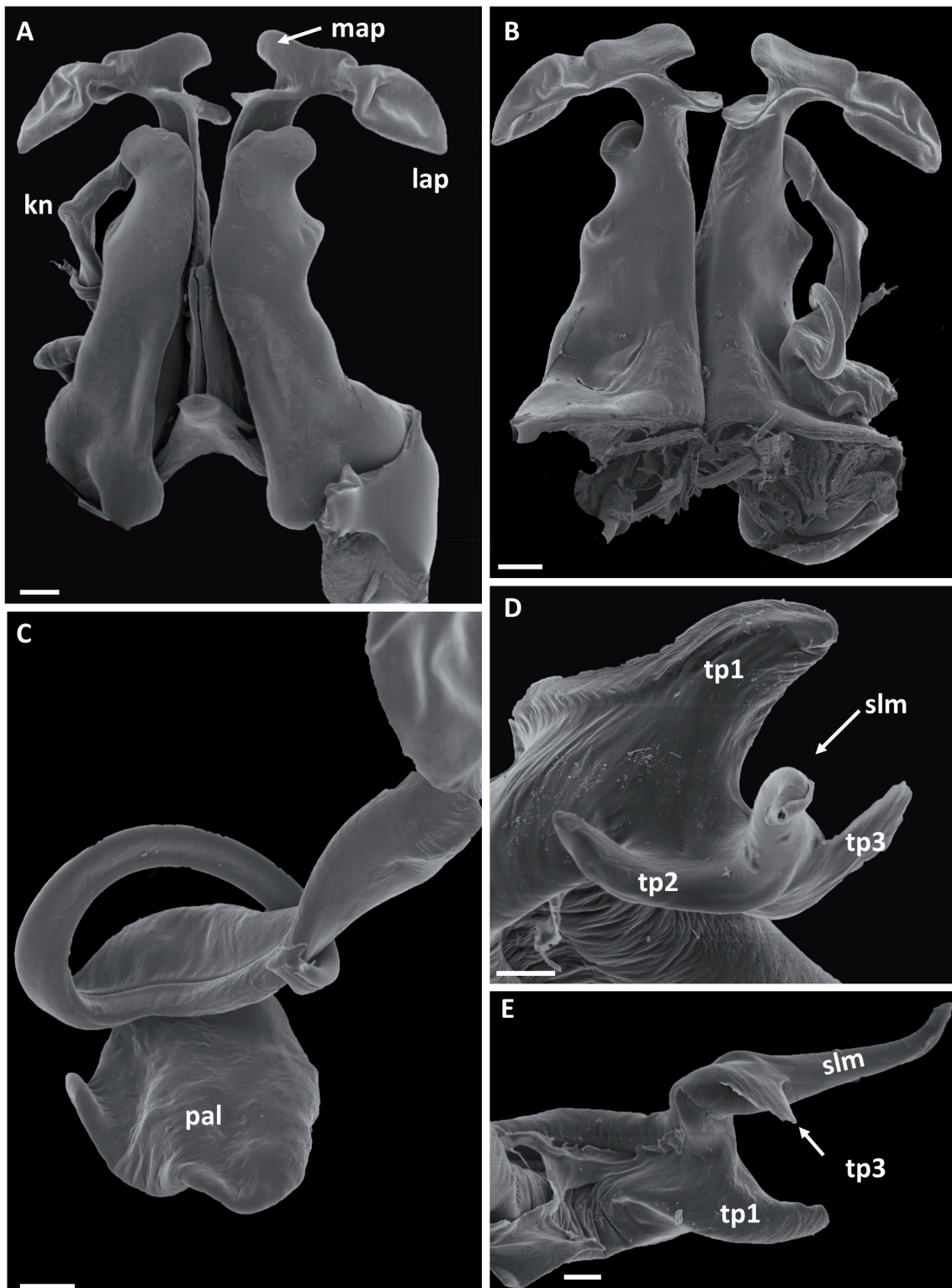
- the very distinctive lateroapical metapical process (*lap*); shaped like an irregular, twisted slipper, somewhat constricted ca at midlength
- the rounded mesapical metapical process (*map*); forming the “heel of the slipper”
- a distinct “knee” (*kn*) on the free part of the telopodite, ca 1/3 from its emergence from the gonocoel
- the very large, palette-shaped appendage (*pal*) at the transition between the middle and the distal 1/3 of the telopodite
- the four-pronged tip of the telopodite, the solenomere (*slm*) being flanked by one tongue-shaped (*tp1*) and two slender processes (*tp2*, *tp3*)

### **Descriptive notes on females from Udzungwa Mountains**

Vertical diameter up to 5.3 mm. Adults and epimorphic juveniles with 48–52 podous rings (Figs 14, 18), no apodous rings in front of telson.

Vulvae quite well sclerotized; operculum small, tongue-shaped; valves transversely wrinkled, meeting in very oblique line, mesal valve much larger than lateral valve, resemble the vulva ascribed to “*Lophostreptus ? regularis*” by Brölemann (1920: fig. 30).





**Fig. 17.** *Lophostreptus tersus* (Cook, 1896), male from Udzungwa Mts National Park (NHMD 1184641), gonopods. **A–B.** Coxae and left telopodite. **A.** Anterior view. **B.** Posterior view. **C.** Right telopodite, distal part. **D–E.** Two views of telopodite tip. Abbreviations: *kn* = knee; *lap* = lateroapical metaplical process; *map* = mesapical metaplical process; *pal* = palette-like appendage; *slm* = solenomere; *tp1*, *tp2*, *tp3* = subapical telopodital processes. Scale bars: A–B = 0.2 mm; C = 0.1 mm; D–E = 0.01 mm.

### Distribution and habitat

Quite widespread in the northern half of Tanzania and in southern Kenya (Enghoff *et al.* 2016, as *L. ptilostreptooides*). In the Udzungwa Mountains, it was found on 16 plots of the FoRCE experiment of which 13 are with open canopy and only three with closed canopy. The total altitudinal range is 271–900 m a.s.l., but 15 of the 16 plots are below 600 m a.s.l. Although abundant in the FoRCE material, the species is absent from older collections, maybe an indication that it is a recent immigrant to the Udzungwa Mountains. Some earlier reports of the species suggest that it is at least in part synanthropic: banana plantation (Carl 1909, as *L. ptilostreptooides*) cultural zone (Attems 1909, as *L. regularis*), botanical garden (Kraus 1958, as *L. malleolus*), around houses (Mwabvu & VandenSpiegel 2009, as *L. ptilostreptooides*).

### Notes on a topotype of *Ptilostreptus tersus* Cook, 1896

The male from Dodoma Region, Mpwapwa District, Wota Forest Reserve (VMNH 112024) can be regarded as a topotype, at least a near-topotype of *Ptilostreptus tersus* – type locality “Mpapua, German East Africa” according to Cook (1896).

Compared side-by-side to a male from the Udzungwa Mountains, the *P. tersus* topotype differs in a few gonopod details:

- the coxa on the whole appears relatively slenderer
- the mesapical metapical process (*map*) forms a small hook at its meso-basal corner
- the part of the telopodite from the torsus until the large palette-like appendage (*pal*) is straighter
- the palette-like appendage (*pal*) is narrower, more than twice as long as broad
- the part of the telopodite distal to the palette-like appendage (*pal*) appears longer

See further under “Remarks” below.

### Notes on type material of *Lophostreptus regularis* Attems, 1909

Syntypical material of this nominal species belonging to NRMS (see Material examined) was studied, and Nesrine Akkari kindly provided detailed information on the syntypes belonging to NHMW, including photos of the specimens and of Attems’ microscope slides. Further syntypes are present in Museum für Naturkunde, Berlin (Moritz & Fischer 1974: 371), but have not been examined.

The syntypes from NRMS include two adult males. One of them lacks its posterior part and has a body diameter of 3.0 mm. Notably, the legs have no traces of ventral pads (contra Attems 1909: 32, fig. 57). One of the males has gonopods exactly like those of *L. tersus*, but the second belongs to *L. neglectus*. This species is also “trachystreptoform” but is much smaller than *Lophostreptus tersus* (= *L. regularis*): 46 podous rings, no apodous rings, vertical diameter 2.4 mm. Also this species lacks ventral pads on the legs.

The syntypes from NHMW include two undissected males which, according to the photos provided by Nesrine Akkari, belong to *L. regularis* (the characteristic process *lap* is clearly visible on the photos). On the other hand, Attems’ original slides are rather confusing: slide “NHMW MY 8871 (ex 4076)”: contains a set of gonopods which clearly belong to *L. tersus*. However, among the slides labelled “NHMW MY 4076”, one contains a set of typical *L. tersus* gonopods (in very poor condition), two contain legs with pads on postfemur and tibia (one of the legs corresponds in all details to Attems’ fig. 57), and one contains a full set of gonopods which obviously belong to *L. neglectus*. Considering that this species, like all examined males of *L. tersus*, lacks postfemoral and tibial pads, the origin of the pad-bearing legs in the slide from the NHMW MY 4076 series remains a mystery. In summary, it seems that the NHMW

syntypes of *L. regularis* represent three species: an unknown species with padded legs, *L. tersus*, and a probably undescribed “trachystreptoform”.

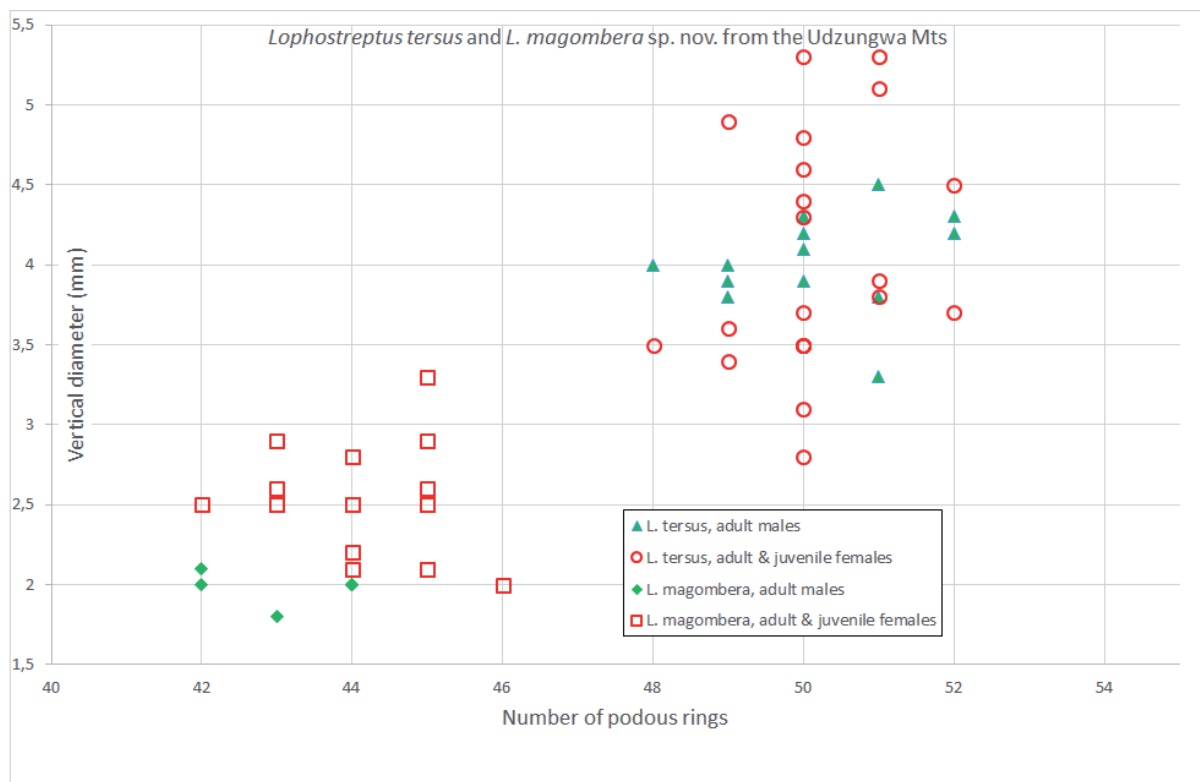
In couplet 5 of the key to species of *Lophostreptus* by Attems (1938), *L. regularis* is separated from *L. tersus* and *L. ptilostreptoides* by having a “femoral” spine on the gonopods, whereas the two latter species have no such spine. This must be a mistake – nothing like a femoral spine is mentioned or illustrated in the original description of *L. regularis*.

### Remarks

In Table 2, the dimensions of *L. tersus* according to previous authors are shown, together with data on examined specimens from various localities.

Mwabvu & VandenSpiegel (2009) recorded *L. ptilostreptoides* from the Taita Hills in S Kenya and presented a drawing of the gonopods, but they gave no further descriptive details.

The colour has been described quite differently, but given the known, variable effect of preservation, already evident after a few years, cf. the description of Udzungwa material, such differences are not regarded significant.



**Fig. 18.** *Lophostreptus tersus* (Cook, 1896), specimens from the Udzungwa Mts, and *L. magombera* Enghoff sp. nov., number of body rings vs midbody vertical diameter. Notice that adult and juvenile epimorphic females have not been distinguished – the symbols in the lower range of the *L. tersus* female “cloud” certainly represent juvenile females.



**Table 2.** Characters of *Lophostreptus tersus* (Cook, 1896) according to previous authors and based on examined specimens.

Nominal species	examined specimens of <i>Lophostreptus tersus</i>									
	<i>Ptilostreptus tersus</i> Cook (1896); Attems (1914)	<i>Lophostreptus ptilostreptoides</i> Carl (1909)	<i>Lophostreptus regularis</i> Attems (1909)	<i>Lophostreptus malleolus</i> Kraus (1958)	specimens from Udzungwa Mountains	syntypes of <i>L. regularis</i> (NHRS-TOBI 000005480, NHRS-TOBI 000005478, NHRS-TOBI 000005476, NHRS-TOBI 000005481, NHRS-TOBI 0000077)	topotype of <i>P. tersus</i> (VMNH 112024)	specimens from Kimboza Reserve (NHMD 1184655)	specimens from Arusha (NHMD 1184655)	specimen from Mindu Mountain (VMNH 112923)
Type locality	Mpapua	Bushland between Kagera and the Mabira camp in S Karagwe	Kilimanjaro: Kibonoto, steppe, cultural zone, mixed forest, 1000–1900 m • Masasai steppe • Usambara: Tanga	Dar es Salaam, botanical garden	–	Kilimanjaro: Kibonoto, steppe, cultural zone, mixed forest, 1000–1900 m • Masasai steppe • Usambara: Tanga	Mpapua (Mpwapwa)	–	–	–
No. of rings	47 (48 segments)	45–48 (46–49 segments)	46–49 (47–50 segments)	49 (50 segments)	48–52	46–48	51	49	48–50	47
Male diameter	4 mm	3 mm	3 mm	3.0 mm	3.8–4.5 mm	3.0 mm	3.7 mm	3.4–3.7 mm	2.5–3.2 mm	3.4 mm
Pads on male legs	no	no	<b>large pads on postfemur and tibia of pregonopodal legs</b>	no	no	<b>no</b>	no	no	no	no

The overall variation in ring number (45–52) is largely covered by Udzungwa specimens (48–52), and this provides no basis for subdividing the material into several species. In terms of body diameter, the variation is considerable (2.5–4.5 mm for adult males), and males from the Udzungwa Mountains (3.8–4.5 mm) are thicker than all others (2.5–3.7 mm), except for the diameter of 4 mm for the type specimen of *P. tersus* published by Attems (1914).

The descriptions and illustrations of the very characteristic gonopods agree as good as completely between the various authors. Some apparent differences may be due to slight differences in the angle of view. For example, in the drawings by Mwabvu & VandenSpiegel (2009) the constriction at midlength of the lateroapical metaplical process (*lap*) is not so obvious, but this may be due to a slightly apical view.

The most deviating specimen is the topotype of *Ptilostreptus tersus* from Mpwapwa District, but with only a single specimen from Mpwapwa District at hand, the significance of these slight differences cannot be properly evaluated, and we hesitate to ascribe this specimen to a separate species.

Similarly, based on the confusing situation regarding *L. regularis* described above, there seems to be no justification for regarding *L. regularis* as a species distinct from *L. tersus*.

***Lophostreptus magombera*** Enghoff sp. nov.

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Figs 2, 3G, 18–20

**Diagnosis**

Differs from congeners, except *L. similis* Attems, 1934, by the distinctive shape of the gonopod coxa, in particular the long, stout, somewhat duck-head-shaped lateroapical process (Fig. 20D–E). In other characters very similar to the co-existing *L. tersus*, but smaller (Fig. 18). Differing from *L. similis* by having a semicircular flange on the gonopod telopodite, by lacking a mesal coxal process, and by lacking an elongate lobe on the gonopod telopodite.

**Etymology**

Named after the Magombera Nature Reserve, see Marshall (2008). Noun in apposition.

**Material examined** (total 6 ♂♂, 21 ♀♀, 1 juv.)

**Holotype**

TANZANIA • ♂; Morogoro Region, Kilombero District, Magombera Nature Reserve; 07°49'21.7" S, 36°58'57.1" E; 283 m a.s.l.; 30 Jan. 2020; A. Ngute and A.R. Marshall leg.; Micro-FoRCE plot 12, closed forest; NHMD 621882.

**Paratypes**

TANZANIA – **Morogoro Region, Kilombero District, Magombera Nature Reserve** • 2 ♀♀; same collection data as for holotype; 07°48'43.4" S, 36°57'22.3" E; 288 m a.s.l.; 6 Mar. 2018; A.R. Marshall leg.; Half-FoRCE plot 32, open forest; NHMD 621883 • 1 ♂, 3 ♀♀; same collection data as for holotype; 07°48'21.5" S, 36°59'47.5" E; 287 m a.s.l.; 17 Feb. 2018; A.R. Marshall leg.; Half-FoRCE plot 38, open forest; NHMD 621884. – **Morogoro Region, Kilombero District, Udzungwa Mountains National Park, Mwanihana** • 7 ♀♀; Sonjo; 07°48'22.6" S, 36°52'17.0" E; 579 m a.s.l.; 14 Dec. 2021; A. Ngute, R. Malanda, H. Mnendo, W. Mhagawale, A. Mpoto, A. Marshall leg.; FoRCE plot 13, closed canopy; NHMD 621885 • 4 ♂♂, 6 ♀♀; same collection data as for preceding; Sonjo; 07°48'24.4" S, 36°52'21.7" E; 589 m a.s.l.; 15 Dec. 2022; A. Ngute, R. Malanda, H. Mnendo, W. Mhagawale, A. Mpoto, A. Marshall leg.; FoRCE plot 14, open canopy; NHMD 621886 • 1 ♀; same collection data as

for preceding; Sonjo; 07°47'57.1" S, 36°52'51.0" E; 540 m a.s.l.; 12 Aug. 2021; A. Ngute, E. Kivambe, W. Mhagawale, H. Mnendendo, A. Marshall leg.; FoRCE plot 94, open canopy; NHMD 621887 • 2 ♀♀; same collection data as for preceding; Sonjo; 07°47'55.6" S, 36°52'43.6" E; 541 m a.s.l.; 18 Aug. 2021; A. Ngute, E. Kivambe, W. Mhagawale, H. Mnendendo, A. Mwakisoma, A. Marshall leg.; FoRCE plot 95, open canopy; NHMD 621888 • 1 juv. ♂; same collection data as for preceding; Gologolo; 07°43'37.2" S, 36°55'03.7" E; 675 m a.s.l.; 16 Sep. 2021; A. Ngute, R. Malanda, W. Mhagawale, A. Mpoto, A. Marshall leg.: FoRCE plot 46, closed canopy; NHMD 621889.

### Description (males)

**SIZE.** Length 27–34 mm; diameter 1.8–2.1 mm; 42–44 podous rings, no apodous rings in front of telson. See Fig. 18.

**COLOUR** (Fig. 3G). After 11 months in alcohol: head, antennae, collum, rings 2–6 and telson blackish; rings 7–8 transitory; from ring 9 light brownish yellow, keels above ozopore level with narrow brown stripe, at hind end of keel more extensively brown, resulting in narrow brown band across dorsal half of each ring. Legs light yellowish.

**HEAD** (Fig. 19A). Vertex very densely and rather coarsely punctate, with a clearly demarcated parietal furrow. Eyes not reaching mesal of antennal socket, ca 35 ommatidia in 5–6 horizontal and ca 10 vertical rows. Antennae reaching 3<sup>rd</sup> body ring. Antennomeres 3–5 strongly narrowed at base.

**COLLUM** (Fig. 19A). Not modified for accommodation of antennae, coarsely punctate; along posterior margin a row of quite short, weak furrows and carinae which towards the sides gradually reach further forwards. Lateral lobes much narrower than dorsal part, not expanded, traversed by 3 or 4 anteriorly strongly ascending carinae/furrows of which uppermost is strongest and almost straight, reaching anterior margin above eye level, anterior corner rectangular, posterior corner more rounded, margins straight.

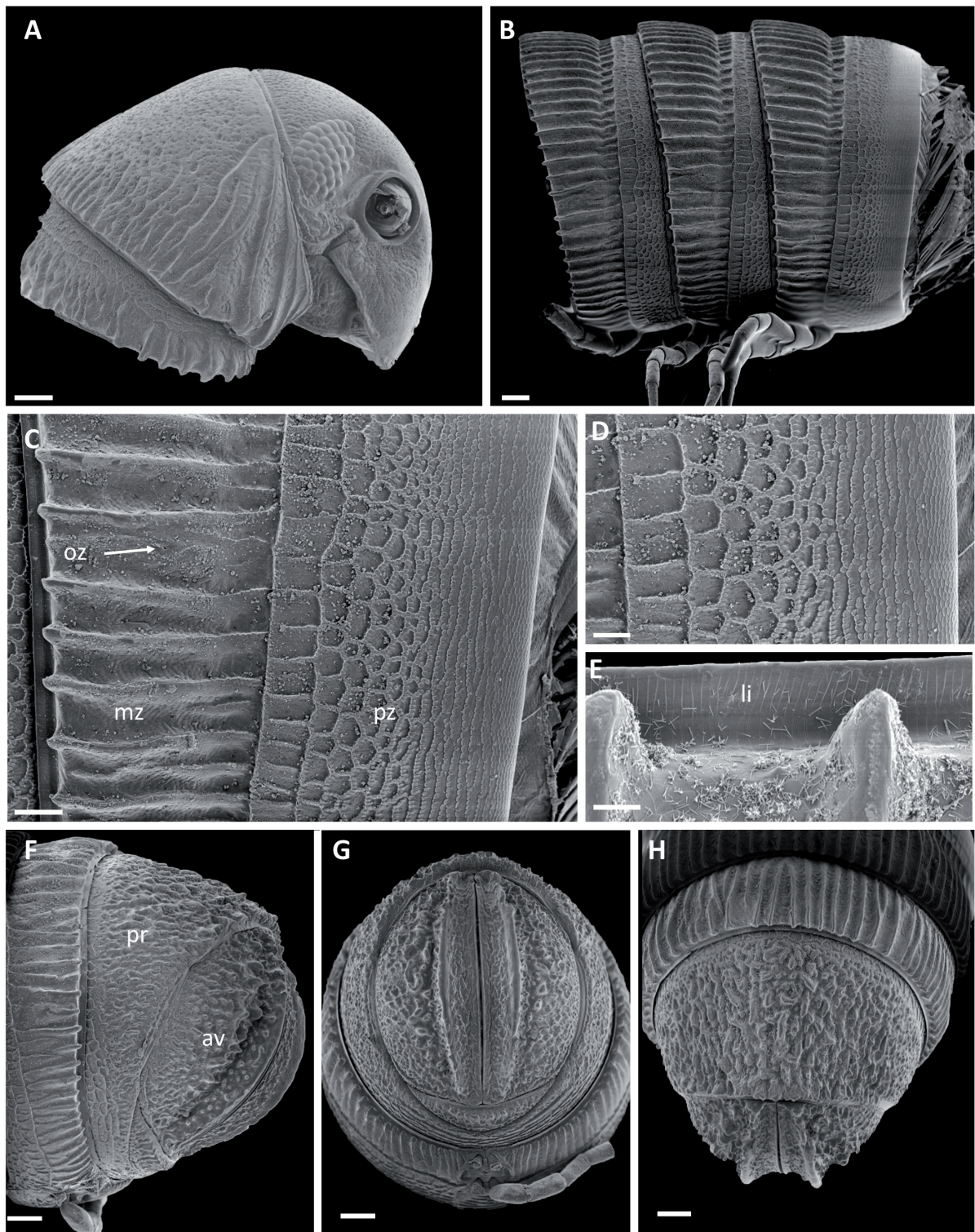
**BODY RINGS** (Fig. 19B–E). Prozonites (*pz*) in anterior part (ca half) with very fine ring furrows which further back give place to a cell structure; posterior part (ca 20%) delimited by clear line, with a regular pattern of larger, rectangular cells. The cuticular scutes (“cytoscutes”) of the anterior part of the prozonite are remarkable in being rounded rather than polygonal and being arranged in an imbricate pattern, as in *Attemsostreptus leptoptilos* sp. nov. (Fig. 12G, left inset). Suture between pro- and metazonites straight, simple. Metazonites (*mz*) with clear constriction a little behind suture, with numerous simple keels which at least dorsally reach from suture, across constriction and until posterior ring margin; ca 15 keels between dorsal midline and ozopore in a male of 2.0 mm diameter. Ozopores (*oz*) small, ca in middle of metazonite. A row of large sigilla.

**TELSON** (Fig. 19F–H). As in *L. tersus*: preanal ring (*pr*) regularly and densely grainy-rugose. Anal valves (*av*) overall with same sculpture, strongly vaulted, their mesal margins slightly raised as low rims, smooth, meeting in midline, paralleled more laterally by much higher lips with smooth edge; distance between lips and mesal margin equal to or larger than height of lips; area between mesal margin and lip with weaker sculpture than main part of valve.

**LEGS.** Short, length ca 0.7 × body diameter. No ventral pads. First pair (Fig. 20A–C): coxosternum with lateral groups of a few long setae (*cxs*) and more mesally with large groups of numerous long setae (*cxs*) next to prefemoral lobes. Prefemoral lobes (*pfl*) rounded-rectangular, with a few apicomeral setae (*aps*) and a diagonal field of long setae (*dps*).

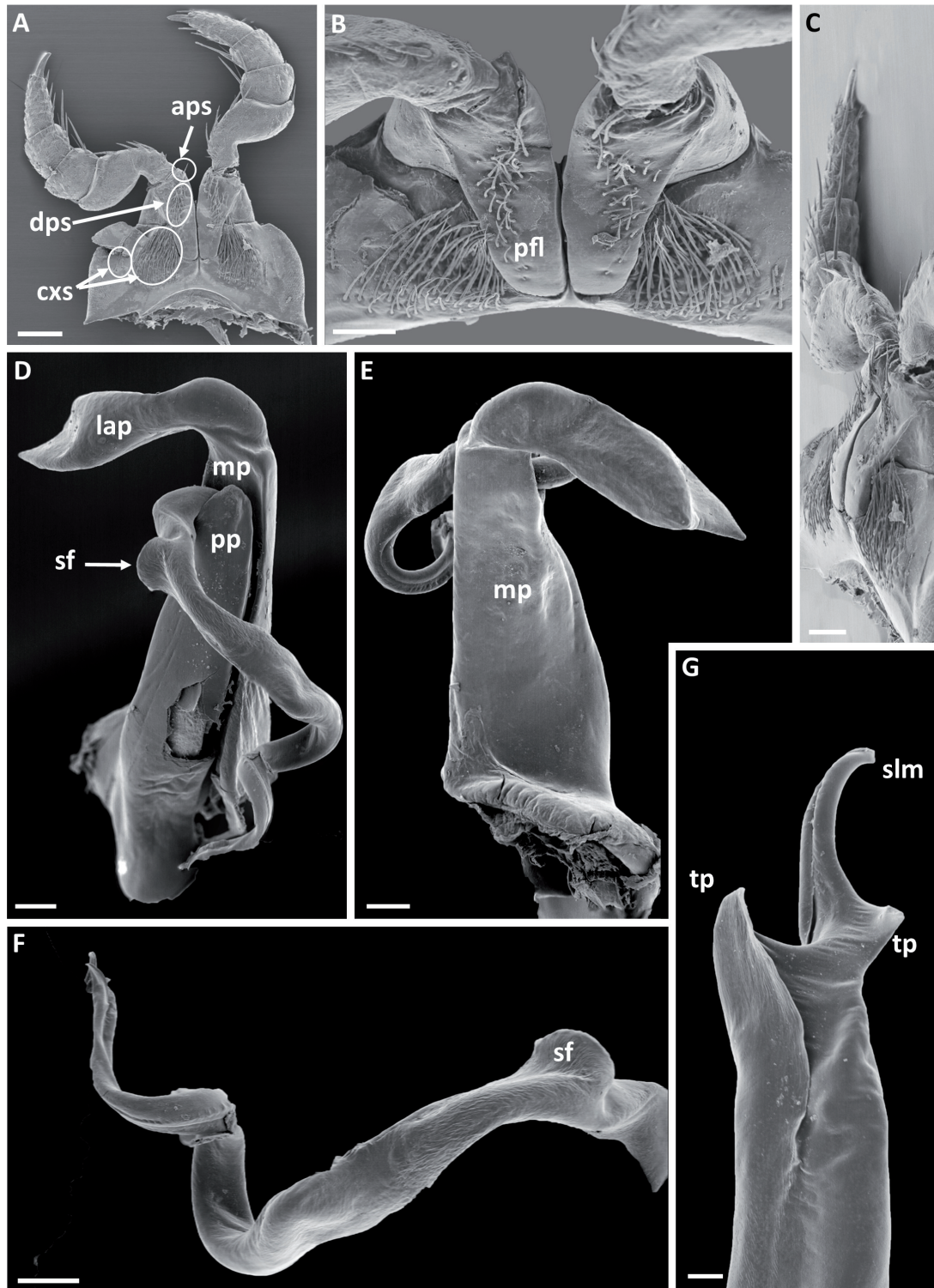
**GONOPOD COXA** (Fig. 20D–E). Proplica (*pp*) parallel-sided, apically rounded. Metaplica (*mp*) with straight mesal margin and oblique lateral margin, hence broadest at base; apically turning smoothly laterad at





**Fig. 19.** *Lophostreptus magombera* Enghoff sp. nov., paratype, ♂ (NHMD 621884). **A.** Head, collum and ring 2. **B.** Three midbody rings. **C.** Lateral part of a ring. **D.** Close-up of prozonital microsculpture. **E.** limbus. **F–H.** Telson and ultimate ring. **F.** Lateral view. **G.** Posterior view. **H.** Dorsal view. Abbreviations: *av* = anal valve; *li* = limbus; *mz* = metazonite; *oz* = ozopore (hard to see); *pr* = preanal ring; *pz* = prozonite. Scale bars: A–B, F–H = 0.2 mm; C = 0.1 mm; D = 0.05 mm; E = 0.02 mm.





**Fig. 20.** *Lophostreptus magombera* Enghoff sp. nov., paratype, ♂ (NHMD 621884). **A–C.** First pair of legs. **A.** Posterior view. **B.** Subventral view. **C.** Sublateral view. **D–G.** Left gonopod. **D.** Anterior view. **E.** Posterior view. **F.** Free part of telopodite. **G.** Tip of telopodite. Abbreviations: *aps* = apicomeral prefemoral setae; *cxs* = coxosternal setae; *dps* = diagonal field of prefemoral setae; *lap* = lateroapical metaplical process; *mp* = metaplica; *pfl* = prefemoral lobe; *pp* = proplica; *sf* = semicircular flange; *slm* = solenomere; *tp* = telopodital processes. Scale bars: A = 0.2 mm; B–F = 0.1 mm; G = 0.01 mm.

right angles and forming a long, stout, somewhat duck-head-shaped lateroapical process (*lap*); no trace of a mesapical process.

GONOPOD TELOPODITE (Fig. 20D–G). Slender, simple, with a semicircular flange (*sf*) shortly after the emergence of the telopodite from the gonocoel. Solenomere (*slm*) flanked by two tongue-shaped processes (*tp*).

#### **Descriptive notes** (females)

Length up to 41 mm, diameter up to 3.3 mm; 42–45 podous rings, no apodous rings in front of telson.

#### **Distribution and habitat**

An Udzungwa endemic, known from the Mwanihana area in Udzungwa Mountains National Park and from Magombera Nature Reserve. There are approximately the same number of samples from plots with open (5) and closed (3) canopy. Altitudinal range 283–675 m a.s.l.

#### **Remarks**

The new species bears a remarkable resemblance to *Lophostreptus similis* Attems, 1934, described from Angola. Not only are the gonopods, including the unusually shaped lateral metapical process, largely identical; the body size of *L. similis* (adult male diameter 2.8 mm, 45 “Segmente”, i.e., 44 podous rings + telson) is only slightly larger than in of *L. magombera* sp. nov. (adult male diameter 1.8–2.1 mm, 42–44 podous rings). Non-gonopodal characters of *L. similis* as described by Attems (1934) are fully compatible with *L. magombera*. However, the new species lacks the small, digitiform mesal coxal process “c” and the elongate telopodite lobe “b” described for *L. similis* by Attems (1938), and the semicircular flange on the gonopod telopodite of *L. magombera* (Fig. 20D, F) is lacking in *L. similis*.

Genus *Udzungwastreptus* Enghoff gen. nov.

urn:lsid:zoobank.org:act:83A888D7-740C-4F3A-AEE0-09B56F6FCA92

#### **Type species**

*Udzungwastreptus marianae* Enghoff gen. et sp. nov.

#### **Other included species**

None.

#### **Diagnosis**

Differs from other trachystreptoform genera by the combination of an unmodified anterior margin of the collum, largely hairless prefemoral lobes of the first pair of male legs, closely appressed to the coxosternum, a ribbon-like free part of the telopodite with a slender accessory lobe branching off ca at midlength, and a simple solenomere originating subapically from the margin of the telopodite.

#### **Etymology**

Named after the Udzungwa Mountains, in recognition of their astonishing biological richness; ‘-streptus’ is a common ending of names of genera of Spirostreptidae, probably derived from the Greek ‘*streptos*’, meaning twisted. Masculine.

#### **Remarks**

*Udzungwastreptus* gen. nov. belongs in group “γ) Télopodite en gouttière ou en bandelette” (telopodite like a gutter or a ribbon) of Demange & Mauriès, 1975. In the key to trachystreptine genera of Demange & Mauriès (1975), *Udzungwastreptus* runs to *Calostreptus* Cook, 1896 with which it shares



**Table 3.** Comparison of *Udzungwastreptus* gen. nov. and *Calostreptus* Cook, 1896.

Character	<i>Udzungwastreptus</i> gen. nov.	<i>Calostreptus</i>
Collum	Anterior margin not modified (Fig. 21A)	Anterior margin strongly expanded laterad, forming trough for accommodation of antenna (Fig. 24A–B)
First pair of legs	Coxosternum with a few lateral setae ( <i>cxs</i> ). Prefemoral lobes without setae (Fig. 22B–D)	Coxosternum with a large field of numerous setae ( <i>cxs</i> ). Prefemoral lobes densely clad with setae (Fig. 24C–E, Krabbe 1982: fig. 179)
Post-torsal gonopod telopodite	With a curved slender lobe detaching from margin ca. at midlength (Fig. 23C, E–F: ltp)	No such lobe (Fig. 24F–G)
Tip of solenomerite	Simple (Fig. 23D–E, G)	With a multi-pronged differentiation (Fig. 24H–I)

the lamellate borders of the posttarsal telopodite and the slender solenomere originating from the margin of the telopodite. Also, the prefemoral lobes of the first pair of legs is similar in the two genera (very flat, closely appressed to coxosternum). The new genus differs from *Calostreptus* as shown in Table 3. See Fig. 24.

*Udzungwastreptus marianae* Enghoff gen. et sp. nov.

urn:lsid:zoobank.org:act:1188266A-4EA1-45D5-8DD1-26244ECCF867

Figs 2, 3H, 21–23

**Diagnosis**

Redundant, genus monospecific.

**Etymology**

Named in fond memory of María Ángeles (Marian) Ramos (1952–2023), Spanish zoologist, close project partner and friend of HE through decades.

**Material examined** (total 15 ♂♂, 11 ♀♀, 24 juvs)

**Holotype**

TANZANIA • ♂; Morogoro Region, Udzungwa Mountains National Park, Kidatu; 07°40'42.1" S, 36°55'06.8" E; 1482 m a.s.l.; 21 Sep. 2014; J. Malumbres-Olarte leg.; Plot 6, pitfall trap; NHMD 621890.

**Paratypes**

TANZANIA – **Morogoro Region, Udzungwa Mountains National Park, Kidatu** • 3 ♂♂, 2 ♀♀; same collection data as for holotype; combined catch from 2 pitfall traps; NHMD 621891 • 5 ♂♂, 1 ♀; same collection data as for holotype; 07°41'06.2" S, 36°54'52.4" E; 1527 m a.s.l.; 23 Oct. 2014; Plot 9, combined catch from 4 pitfall traps; NHMD 621892. – **Iringa region, Udzungwa Mountains, Ndundulu Forest** • 3 ♂♂, 5 ♀♀, 1 juv. ♂; 7°45' S, 36°29' E; 1550 m a.s.l., 1–7 Dec. 2007; L.A. Hansen and local assistants leg.; Waller's camp, tropical semi-evergreen forest; NHMD 621893. – **Iringa Region, Kilolo District, Kilombero Nature Reserve, Ndundulu, Lua-la** • 1 ♂, 1 ♀, 16 anamorphic juvs; 07°45'56.8" S, 36°29'27.0" E; 1949 m a.s.l.; 29 Oct. 2021; A. Ngute, R. Malanda, W. Mhagawale,

A. Mpoto, A. Marshall leg.; Plot 71, open canopy; COLL.NHMD-ACC.NO. 2022-EN-003; NHMD 621926 • 2 ♀♀, 7 anamorphic juvs; same collection data as for preceding; 07°45'51.3" S, 36°29'16.1" E; 2007 m a.s.l.; 1 Nov. 2021; Plot 72, open canopy; NHMD 621927. – **Morogoro Region, Kilombero District, Udzungwa Mountains National Park, Mwanihana** • 1 ♂; Uzungwa Mountains, Mwanihana Forest above Sanje; 1700 m a.s.l.; 15 Aug. 1982; M. Stoltze and N. Scharff leg.; NHMD 621928. – **Iringa Region, Iringa district, New Dabaga/Ulangambi Forest Reserve** • 1 ♂; 08°00'26.6" S, 35°56'06.1" E; 1908 m a.s.l.; 19–26 Oct. 2000; Frontier Tanzania leg.; scrub/thicket/bush, plot FP; NHMD 621929.

### Description (males)

**SIZE.** Length 27–32 mm, diameter 1.8–2.1 mm (the male from Mwanihana Forest, NHMD 621928, is thicker: 2.4 mm); 40–44 podous rings, no apodous rings in front of telson.

**COLOUR** (Fig. 3H). After eight years in alcohol mostly yellowish white; posterior  $\frac{1}{3}$  of metazonites light amber, preceded by narrow reddish-brown band; area between crests in front of band brownish or yellowish white; head above eyes dark brown with small light spots, occipital furrow also light; area between eyes and antennal sockets uniformly dark brown, area below antennal sockets light brown below. Collum dark brown, marbled.

**HEAD** (Fig. 21A). Eyes small, separated by 3 times their diameter, not reaching beyond mesal margin of antennal socket; each eye with 13–20 ommatidia in 3–4 horizontal rows, number of vertical rows indiscernible. Antennae short, reaching back to body ring 5 when stretched; antennomeres 2–6 of subequal length. Mandibular stipes in lateral view ca twice as long as high, ventroanteriorly produced in a rectangular lobe, distal edge of stipes above lobe regularly concave. Gnathochilarium: lateral edge of stipites forming pigmented keel in basal part; mentum with deep, circular concavity.

**COLLUM** (Fig. 21A). Not modified for accommodation of antennae. Not keeled, surface finely wrinkled, laterally with a short marginal carina/furrow, one or two long, strong oblique carinae/furrows and a few short irregular ones above; lateral lobes truncate, with straight margin.

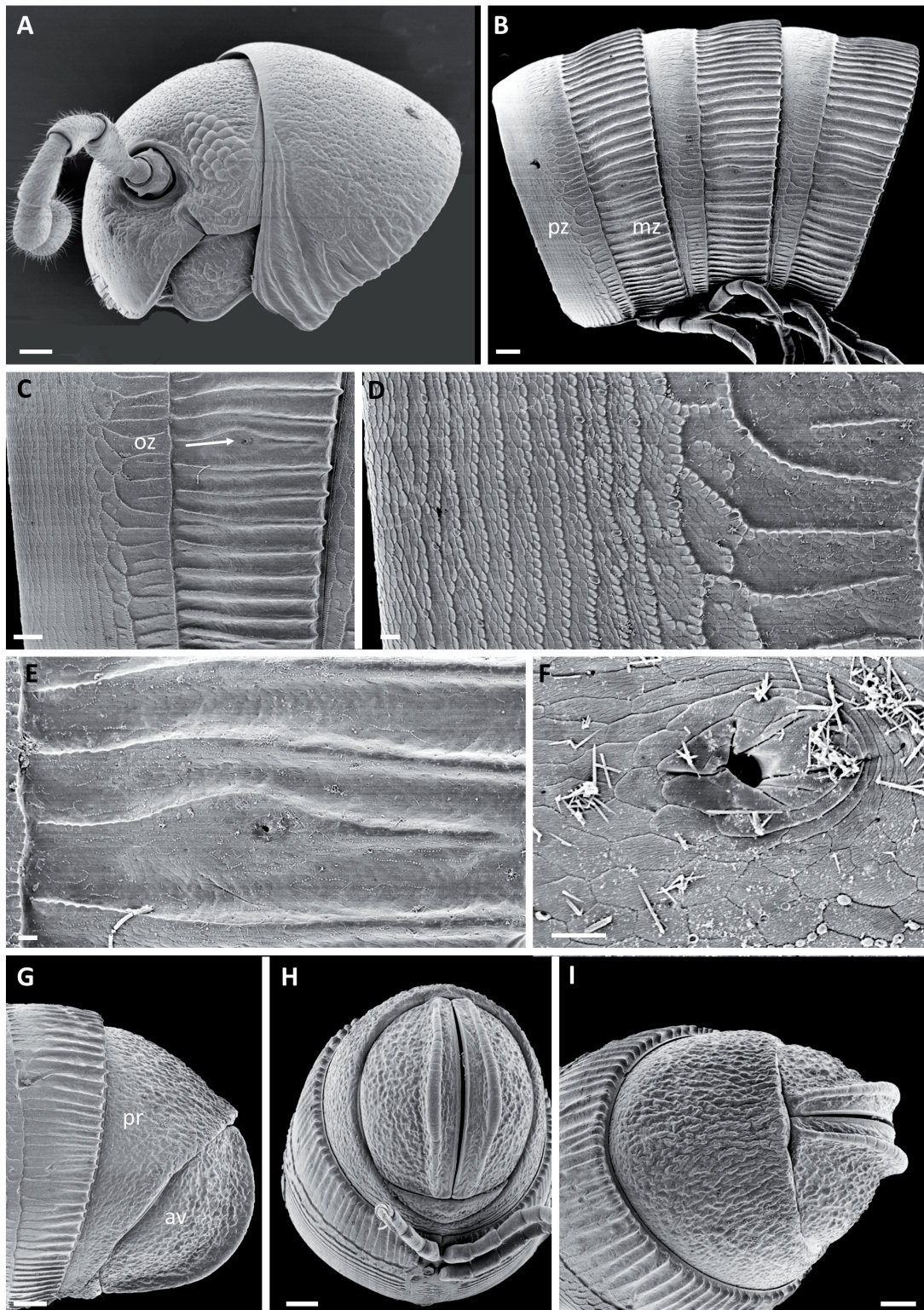
**BODY RINGS** (Fig. 21B–F). Prozonites in anterior  $\frac{2}{3}$  with very fine ring furrows which further back give place to a cell structure; posteriormost row of cells longer and more regular. The cuticular scutes (“cytoscutes”) of the anterior part of the prozonite are remarkable by being rounded rather than polygonal and being arranged in an imbricate pattern, as in *Attemsostreptus leptoptilos* sp. nov. (Fig. 12G, left inset). Metazonites significantly vaulted, imposing a slightly moniliform shape of the body, densely keeled, ca 16 keels per dorsal quarter. Ozopores (*oz*, Fig. 21E–F) slightly in front of middle of metazonite, between two keels. One row of large (not very obvious) sigilla ca in middle of metazonite

**TELSON** (Fig. 21G–I). As in *Lophostreptus tersus* and *L. magombera* sp. nov. Preanal ring (*pr*) regularly and densely grainy-rugose. Anal valves (*av*) overall with same sculpture, strongly vaulted, their mesal margins slightly raised as low rims, smooth, meeting in midline, paralleled more laterally by much higher lips with smooth edge; distance between lips and mesal margin equal to or larger than height of lips; area between mesal margin and lip with weaker sculpture than main part of valve.

**LEGS.** Short, length ca  $0.7 \times$  body diameter. No ventral pads. First pair (Fig. 22B–D): coxosternum with lateral groups of a few long setae (*cx*s). Prefemoral lobes (*pfl*) long triangular, closely appressed to coxosternum, with a few apicomeral setae (*aps*) and scattered minute pegs, otherwise bare.

**GONOPOD COXA** (Figs 22A, 23A–B). Proplica (*pp*) parallel-sided, in distal ca 40% with scattered minute pegs, meso-apically with subrectangular process (*ppp*). Metaplica (*mp*) with almost straight, subparallel margins; apically smoothly rounded, with a slender, sinuous lateral, laterad process (*lap*) and a shorter straight process (*aap*) originating next to *lap* and pointing antieriad.





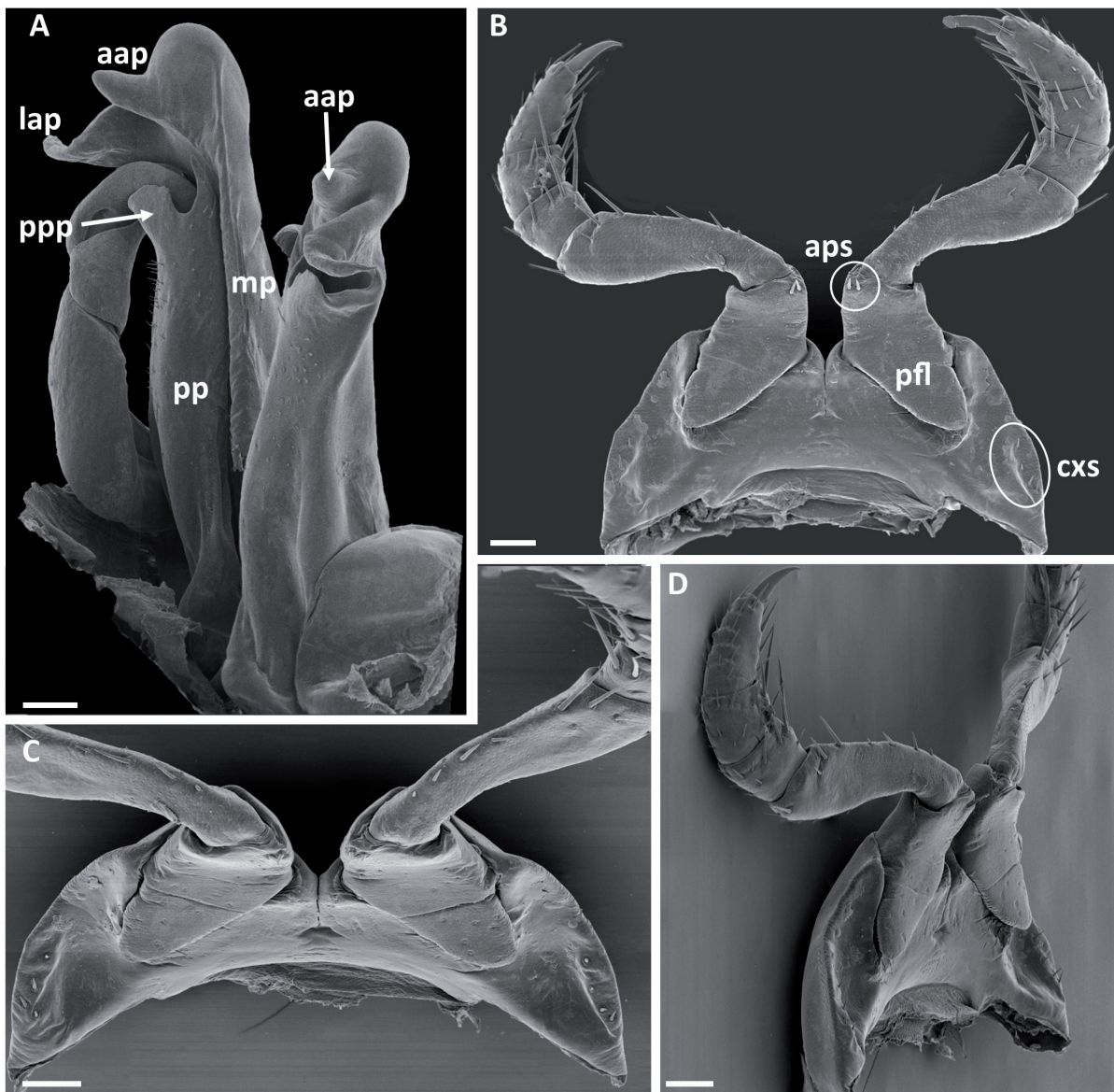
**Fig. 21.** *Udzungwastreptus marianae* gen. et sp. nov., paratype, ♂ (NHMD 621928). **A.** Head and collum, lateral view. **B–E.** Midbody rings. **B.** Three rings. **C.** Sculpture of lateral pro- and metazonite. **D.** Close-up of prozonite. **E.** Close-up of metazonite. **F.** Ozopore. **G–I.** Telson. **G.** Lateral view. **H.** Posterior view. **I.** Dorsal view. Abbreviations: *av* = anal valve; *mz* = metazonite; *oz* = ozopore; *pr* = preanal ring; *pz* = prozonite. Scale bars: A–B, G–I = 0.2 mm; C = 0.1 mm; D–E = 0.02 mm; F = 0.01 mm.



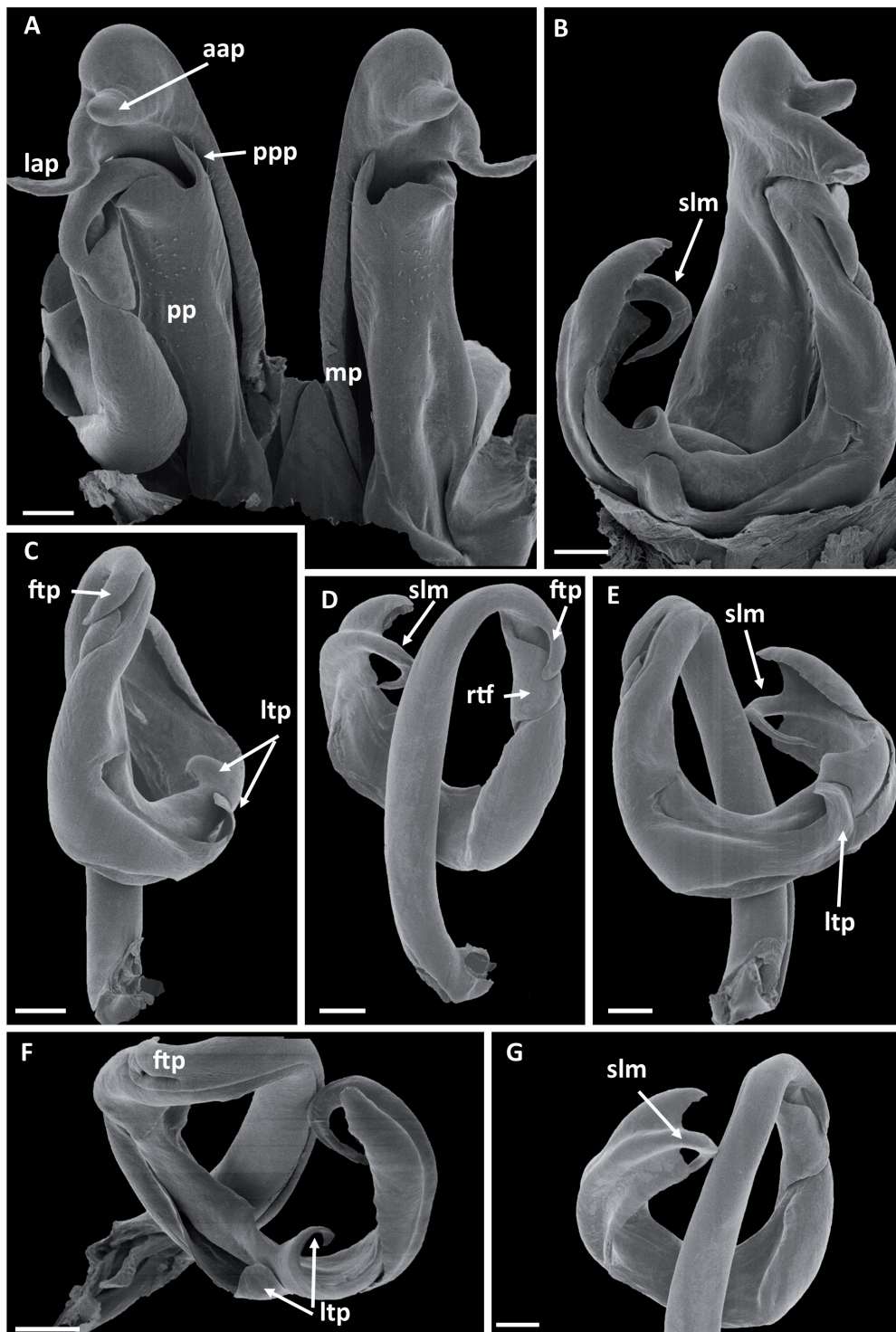
GONOPOD TELOPODITE (Fig. 23). Free part band-shaped, folded longitudinally, shortly after emergence from gonocoel with a finger-shaped process (*ftp*) and a rounded rectangular flap (*rtf*), more distally (ca  $\frac{2}{3}$  after emergence from gonocoel with two neighbouring lamellate processes (*ltp*); apically more open, ending in transverse straight edge from which the simple, slender, tapering and curved solenomere (*slm*) emerges.

**Descriptive notes** (females)

Length up to 38 mm, diameter up to 2.4 mm; 41–43 podous rings, no apodous rings in front of telson.



**Fig. 22.** *Udzungwastreptus marianae* gen. et sp. nov. **A.** Paratype, ♂ (NHMD 621891), gonopods, anterio-lateral view. **B–D.** Paratype, ♂ (NHMD 621928), first pair of legs. **B.** Posterior view. **C.** Subventral view. **D.** Sublateral view. Abbreviations: *aap* = anterior-apical metaplical process; *aps* = apicomasal prefemoral setae; *cxs* = coxosternal setae; *lap* = lateroapical metaplical process; *mp* = metaplica; *pfl* = prefemoral lobe; *pp* = proplica; *ppp* = proplical process. Scale bars = 0.1 mm.



**Fig. 23.** *Udzungwastreptus marianae* gen. et sp. nov., paratype, ♂ (NHMD 621891). **A.** Gonopods, posterior (left gonopod) and latero-posterior (right gonopod) view. **B.** Left gonopod, lateral view. **C–G.** Right gonopod telopodite. **C.** Submesal view. **D.** Subposterior view. **E.** Subanterior view. **F.** Subbasal (dorsal) view. **G.** Subposterior view. Abbreviations: *aap* = antero-apical metaplical process; *ftp* = finger-shaped telopodital process; *lap* = lateroapical metaplical process; *ltp* = lamellate telopodital process; *mp* = metaplica; *pp* = proplica; *ppp* = proplical process; *rtf* = rounded-rectangular telopodital process; *slm* = solenomere. Scale bars = 0.1 mm.

### Distribution and habitat

An Udzungwan endemic. Known from three places, all at high altitudes (1482–2007 m a.s.l.). Habitat notes include “tropical semi-evergreen forest”, “open canopy” and “scrub/thicket/bush”.

### Remarks

A male and a female (NHMD 621892) and another male (NHMD 621929) carry numerous thalli of *Rickia lophophora* Santamaria, Enghoff & Reboleira, a fungus of the order Laboulbeniales. The male from NHMD 621929 was recorded by Santamaria *et al.* (2016), as “Spirostreptida indet.”, as host of *R. lophophora*. A further male, the holotype (NHMD 621890), is host to a different fungus, a so-called “amphoromorph” which is probably a secondary capilliconidium of the genus *Basidiobolus* Eidam (Enghoff & Reboleira 2017).

Genus *Calostreptus* Cook, 1895

*Calostreptus chelys* Cook, 1895

Fig. 24

### Material examined (total 2 ♂♂)

TANZANIA • 1 ♂; Pwani Region, Kisarawe District, Rivu South Forest Reserve; 140 m a.s.l.; date?; Frontier Tanzania leg.; NHMD 84658 • 1 ♂; Kilimanjaro Region, Rombo District, at Lake Chala; 03°18'30" S, 37°41'10" E; 880 m a.s.l.; 1 Dec. 2020; C. Hemp leg.; NHMD 1184659.

This species does not occur in the Udzungwa Mts, but Fig. 24 shows important morphological details of *C. chelys* for comparison with *Udzungwastreptus mariane* Enghoff gen. et sp. nov.

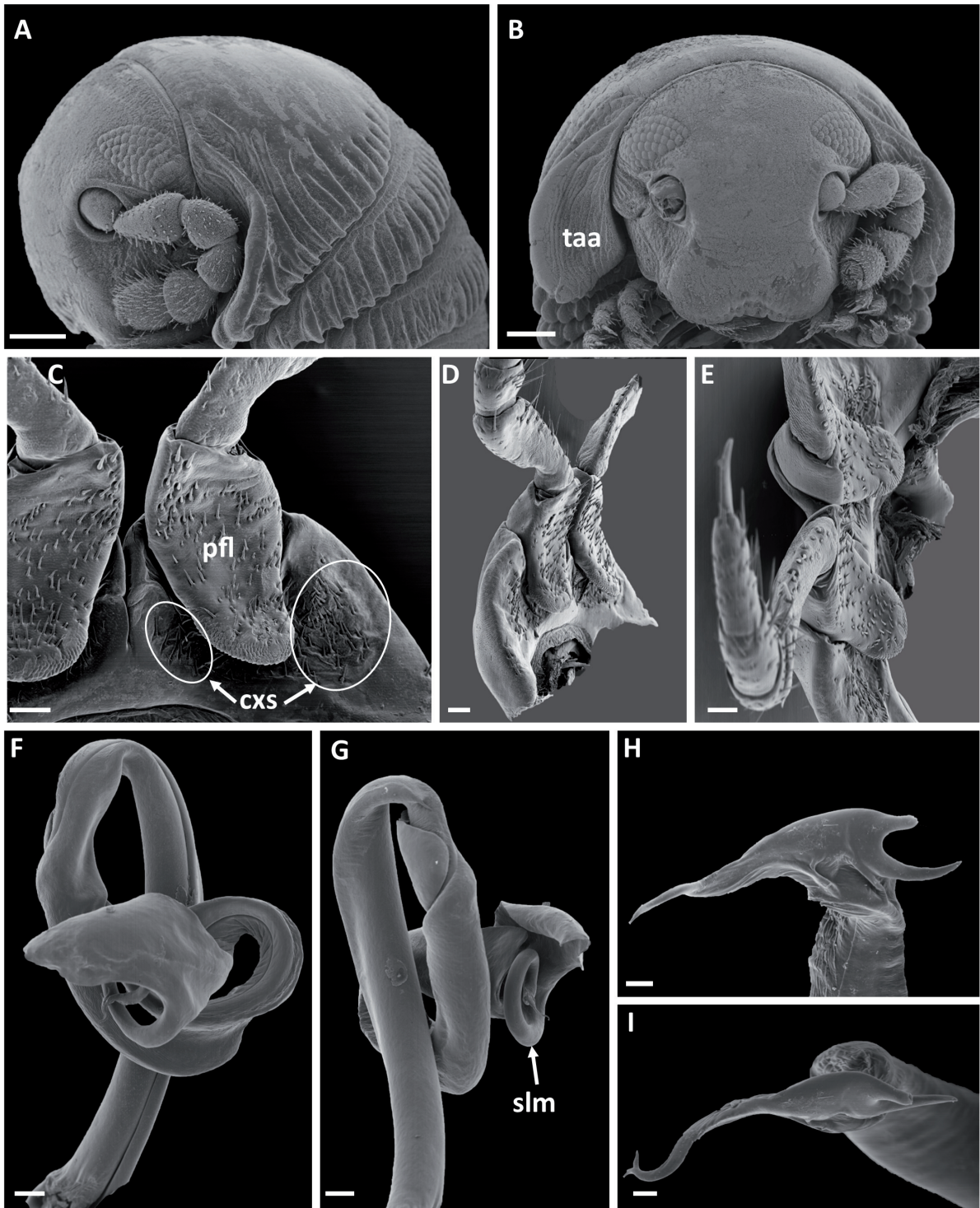
### Unidentified trachystreptoforms

Several samples included females and/or juveniles of unidentifiable small trachystreptoforms with the general habitus of *Lophostreptus magombera* sp. nov. and *Udzungwastreptus marianae* gen. et sp. nov., but differing in body dimensions. It is unclear whether these specimens, which were all collected in the same areas as the identified species (cf. Fig. 2), belong to either of these, or whether they represent one or several additional new species.

### Discussion

When Hoffman *et al.* (2001) established the true identity of the genus *Spirostreptus* Brandt, 1833 as a senior synonym of *Triaenostreptus* Attems, 1914, the tribal name Spirostreptini Brandt, 1833 became a senior synonym of Triaenostreptini Attems, 1914. And just as the numerous species which had been wrongly assigned to *Spirostreptus* by this action became ‘homeless’ (see Enghoff 2017a), the ca 50 genera assigned to Spirostreptini by Krabbe (1982) and earlier authors all of a sudden would need a new tribe to accommodate them. However, Hoffman *et al.* (2001) “consider[ed] it premature to suggest substitute group names for the numerous “non-triaenostreptine” [i.e., “non-spirostreptine” sensu Hoffman *et al.* 2001.] genera listed by Krabbe (1982) under Spirostreptinae”, and although a solution to these problems has recently been provided (Enghoff 2023), Hoffman’s approach has been followed here by adopting the non-formal designation ‘trachystreptoform’ for the genera in question. The classification of Spirostreptidae will certainly need revision, once phylogenetic analyses have been made. Few studies addressing the phylogeny of Spirostreptidae are available (Mwabvu *et al.* 2013, 2015; Hassan & Hassan 2021; VandenSpiegel *et al.* 2021; Nielsen *et al.* 2022) all of which concern at most a few genera – there is obviously a long way to go before a robust phylogenetic hypothesis for Spirostreptidae will be available.





**Fig. 24.** *Calostreptus chelys* Cook, 1895. **A–B.** Male from Rivu South Forest Reserve (NHMD 84658). **A.** Head and collum, lateral view. **B.** Same, anterior view. **C–I.** Male from Rombo District, at Lake Chala (NHMD 1184659). **C–E.** First pair of legs. **C.** Posterior view. **D.** Sublateral view. **E.** Subventral view. **F–I.** Right gonopod telopodite. **F.** Subanterior view. **G.** Subposterior view. **H–I.** Two close-ups of solenomere. Abbreviations: *cxs* = coxosternal setae; *pfl* = prefemoral lobe; *slm* = solenomere; *taa* = trough for accommodation of antenna. Scale bars: A–B = 0.5 mm; C–G = 0.1 mm; H–I = 0.01 mm.

**Table 4.** Species of Spirostreptidae Brandt, 1833 recorded from the Udzungwa Mts. Abbreviation: tr = trachystreptomorph.

Species	tr	Reference(s)
<i>Analocostreptus semilunaris</i> (Peters, 1855)	no	Enghoff <i>et al.</i> (2016), cf. Enghoff (2023)
<i>Archispirostreptus gigas</i> (Peters, 1855)	no	new record (FoRCE material)
<i>Attemsostreptus cataractae</i> Enghoff sp. nov.	yes	present work
<i>Attemsostreptus julostratus</i> Enghoff sp. nov.	yes	present work
<i>Attemsostreptus leptoptilon</i> Enghoff sp. nov.	yes	present work
<i>Attemsostreptus reflexus</i> Akkari & Enghoff, 2019	yes	present work
<i>Dendrostreptus macracanthus</i> (Attems, 1914)	no	Hoffman & Howell (1983)
<i>Haplogonopus inflatannulus</i> Verhoeff, 1941	no	Enghoff <i>et al.</i> (2016)
<i>Lophostreptus magombera</i> Enghoff sp. nov.	yes	present work
<i>Lophostreptus tersus</i> (Cook, 1896)	yes	present work
<i>Macrolenostreptus orestes</i> Hoffman & Howell, 1996	no	Hoffman & Howell (1996)
<i>Pseudotibiozus cerasopus</i> (Attems, 1914)	no	Enghoff <i>et al.</i> (2016), Enghoff & Larsson (2018)
<i>Tropostreptus droides</i> Enghoff, 2017	no	Enghoff (2017), Nielsen <i>et al.</i> (2022)
<i>Tropostreptus hamatus</i> (Demange, 1977)	no	Enghoff <i>et al.</i> (2016), Enghoff (2017), Nielsen <i>et al.</i> (2022)
<i>Tropostreptus microcephalus</i> Enghoff, 2017	no	Enghoff (2017), Nielsen <i>et al.</i> (2022)
<i>Tropostreptus sigmatospinus</i> Enghoff, 2017	no	Enghoff (2017), Nielsen <i>et al.</i> (2022)
<i>Udzungwastreptus marianae</i> Enghoff gen. et sp. nov.	yes	present work

In addition to the species treated here, several non-trachystreptoform species of Spirostreptidae have been identified from the Udzungwa Mountains, see Table 4. Several additional non-trachystreptoform species are present in the NHMD collection but have still not been identified/described.

Two genera stand out: *Attemsostreptus* is represented by four species, viz. three new species and the recently described *A. reflexus*. It is at present not clear whether the three newly described species represent an endemic species swarm. *Tropostreptus* Enghoff, 2017, with four species in the Udzungwas, was analysed by Nielsen *et al.* (2022). The genus is widespread in the Eastern Arc Mountains, and two of the species occurring in the Udzungwas, viz., *T. hamatus* (Demange, 1977) and *T. sigmatospinus* Enghoff, 2017, also occur in other Eastern Arc mountain blocks, the latter even on the island of Zanzibar and on the Rondo Plateau in SE Tanzania. The phylogenetic analysis by Nielsen *et al.* (2022: fig. 4) does not unequivocally suggest speciation within the Udzungwas. The Spirostreptidae thus do not offer any

obvious parallels to the endemic species swarm in the odontopygid genus *Chaleponcus* Attems, 1914 (Enghoff 2014, 2017b).

The species treated here can roughly be divided into two groups according to their altitudinal distribution: *Attemsostreptus julostratus* sp. nov., *A. leptoptilos* sp. nov. and *Udzungwastreptus marianae* gen. et sp. nov. are restricted to altitudes above 1000 m a.s.l., and *Attemsostreptus reflexus*, *Lophostreptus tersus* and *L. magombera* sp. nov., in contrast, populate the lower altitudes: 271–595 m a.s.l., with a single outlier at 900 m a.s.l. (*L. tersus*). *Attemsostreptus cataractae* sp. nov., for which altitudinal information is dubious (300–500 m. a.s.l.?), may also be included in this group. *Attemsostreptus reflexus* and *L. tersus* are very abundant in the material, and it is remarkable that they are completely absent from earlier extensive collections of millipedes from Udzungwa Mountains National Park. Considering that *L. tersus* and *A. reflexus*, unlike the other species, are also known from other places than the Udzungwa Mountains, and that *L. tersus* has previously been recorded from habitats strongly influenced by man, the apparently recent arrival of this species (and *A. reflexus*?) to the Udzungwas may be due to human-mediated dispersal. The prevalence of Udzungwa-endemic species at high altitudes is in line with the pattern seen in the related family Odontopygidae (Enghoff 2018).

Like most of the other papers in the series “A Mountain of millipedes” this one is based on a large number of specimens. Experience from FoRCE fieldwork strengthens the impression that millipedes are notably more abundant in the Udzungwa Mountains than in any other tropical region where we have worked. It is for this reason that millipedes were selected as a representative of leaf litter invertebrates in the FoRCE experiment.

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