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Research article

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A mountain of millipedes XII. The Chelodesmidae of the Udzungwa Mountains, Tanzania (Diplopoda, Polydesmida)

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Abstract. The species of the millipede family Chelodesmidae from the Udzungwa Mountains are (re)described, including one new genus and six new species: *Morogorius divisus* Enghoff sp. nov., *M. louishanseni* Enghoff sp. nov., *M. pugio* Enghoff sp. nov., *M. kitugulu* Enghoff sp. nov., *M. cochlear* Enghoff sp. nov., *Tanzaniella howelli* Hoffman, 1977, *Dionaeadesmus force* Enghoff gen. et sp. nov., and *Callistocilla dolorotrix* Hoffman, 2005. *Tanzaniella howelli* is also recorded from Magombera Nature Reserve. The discussion includes comments on paranotal microsculpture, globular structures flanking the spinnerets, a gonopodal coxal process, altitudinal distribution, and the possible recent immigration of *T. howelli* into the Udzungwa Mts.

Keywords. Taxonomy, new genus, new species, Eastern Arc Mountains, surface microstructure.

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Introduction

This is the twelfth paper in a series devoted to the millipede fauna of the Udzungwa Mountains in Tanzania. See Enghoff (2022) and Enghoff *et al.* (2024) 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. It is the second in the series which is partly based on material collected in connection with FoRCE project, see the section Material and methods. The present contribution deals with the large family Chelodesmidae Cook, 1895. As in Enghoff *et al.* (2024) records from the neighbouring Magombera Nature Reserve are included.

Chelodesmidae is one of the largest millipede families. A decade ago, Enghoff *et al.* (2015) gave the number of about 800 species, and many new taxa have been added since then, e.g., by VandenSpiegel *et al.* (2016), Bouzan *et al.* (2021, 2022, 2024) and Means *et al.* (2023). Disturbingly, a clear diagnosis of Chelodesmidae is not available. For example, under "Family CHELODESMIDAE Cook, 1895" Enghoff *et al.* (2015: 394) summarized morphological diversity within the family but did not provide diagnostic characters vis-à-vis other families. The family has traditionally been subdivided into two subfamilies, viz., Chelodesminae Cook, 1895 for the Neotropical taxa, and Prepodesminae Cook, 1896 for the Afrotropical (and European) taxa. Satisfactory diagnoses of the two subfamilies are not available either which is perhaps not so strange, because "It is indeed not unlikely that continued investigation will mandate abolition of these two traditional major groups, with subfamily lines drawn in quite different ways" (Hoffman & Reid 1990: 32).

In order to gain clarity about chelodesmid monophyly and relationships (external as well as internal), phylogenetic analyses are much needed. So far, only a few morphology-based analysis of a few genera are available (Pena-Barbosa *et al.* 2013; Bouzan *et al*. 2019, 2021). Regarding the monophyly and external relationships of the family, the situation is not better. Thus, the two chelodesmid species included in the molecular analysis by Benavides *et al.* (2023) do not form their own clade.

Material and methods

The studied specimens are deposited in the zoological collections of the Natural History Museum of Denmark, University of Copenhagen (NHMD, formerly ZMUC). A large proportion of this material was collected in connection with the Forest Restoration and Climate Experiment (FoRCE, www.force-experiment.com). FoRCE is a research project aiming to understand global and regional 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 disturbed, warm tropical forests (Marshall *et al.* 2020; Ngute *et al.* 2024a). Millipedes and other detritivores are also used by FoRCE 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 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 m × 20 m permanent vegetation sample plots, and within 3 m × 3 m quadrats within these. The 20 m × 20 m plots were either (a) subplots within 100 m × 40 m plots for sampling large trees (FoRCE, see Ngute *et al.* 2024b), (b) subplots within 100 m × 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).

In addition to FoRCE material, many specimens collected earlier by staff and students of NHMD were included.

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 Zeiss Gemini 360VP scanning electron microscope in NHMD, a few specimens were studied in a JEOL JSM-6610LV scanning electron microscope (Natural History Museum of Vienna).

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

For coordinates, decimal degrees were converted to degrees, minutes and second using the service at https://www.fcc.gov/media/radio/dms-decimal.

The descriptions are based on males whenever possible. Females are generally a bit larger than conspecific males and have relatively shorter appendages.

Gonopod orientation and terminology

For orientation of the gonopod, each gonopod is understood as emerging perpendicularly from the gonopod aperture and then making a 90° anteriad bend resulting in the gonopod telopodite pointing anteriad (see Fig. 5C). For the different parts of the gonopods we use a modified version of the terminology used by Verhoeff (1941) in the original description of *Morogorius* Verhoeff, 1941 and *M. pallidus* Verhoeff, 1941. See Table 1.

Abbreviations for body parts in text and in figure captions

as = seta(e) on anterior surface of gonopod coxa
asp = anterior spiracle
ca = cannula
ci = cingulum
cx = coxa
cxp = coxal process
ds = dorsal seta on anal valve
eg = epicranial groove
ep = epiproct
fx = flexed edge of solenomere
gs = globular swelling
hp = subanal scale (hypoproct)
lg = labrogenal offset
ls = lateral coxal setae
msp = marginal spikes of prefemoral process
mvs = meso-ventral setae

Table 1. Terminology for gonopods of *Morogorius* Verhoeff, 1941.

Present paper	Verhoeff (1941)	Hoffman (1977)
acropodite	(including Femur, *fe*)	–
cingulum (*ci*)	–	–
coxa (*cx*)	Coxit (*ct*)	coxa
cannula (*ca*)	Coxalhorn (*coa*)	–
prefemoral part (*prf*)	Präfemur (*prf*)	–
coxal process (*cxp*)	Fortsatz [des Coxits] (*pr*)	conical apophysis [of coxa] (*fp*)
efferent canal	–	prostatic groove
prefemoral process (*prp*)	Tibiotarsus (*tt*)	process apparently originating from prefemur (*tt*)
solenomere (*slm*)	Solänomerit (*sl*)	solenomerite (*s*)
parasolenomere (*ps*)	Parsolänomerit (*z* and *ps*)	spiniform lobes

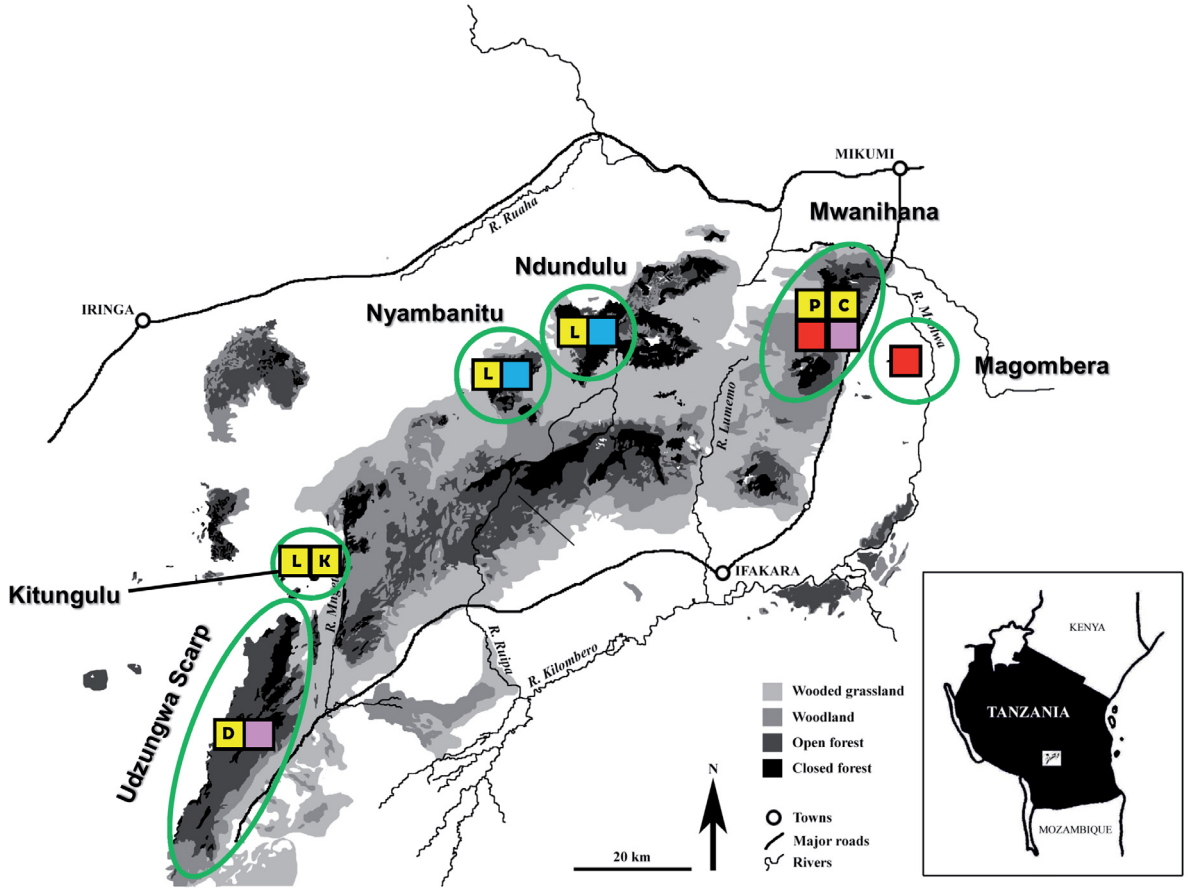

Fig. 1. Map of the Udzungwa Mts showing collecting areas for Chelodesmidae Cook, 1895. Yellow squares: *Morogorius* spp. **D**: *M. divisus* Enghoff sp. nov., **L**: *M. louishanseni* Enghoff sp. nov., **P**: *M. pugio* Enghoff sp. nov. **K**: *M. kitungulu* Enghoff sp. nov., **C**: *M. cochlear* Enghoff sp. nov. Red squares: *Tanzaniella howelli* Hoffman, 1977. Blue squares *Dionaeadesmus force* Enghoff gen. et sp. nov. Purple squares: *Callistocilla dolorotrix* Hoffman, 2005. The position of the squares within the green circles/ovoids does not indicate exact location. Based on Marshall *et al.* (2010: fig. 1).

nb = needlelike side branch of parasolenomere
pe = peritrema
pop = posterior spiracle
pp = anal valve (paraproct)
prf = prefemoral part
prp = prefemoral process
prt = prefemoral tooth
ps = parasolenomere
psp = process of parasolenomere
slm = solenomere
sph = solenophore
spr = spiked ridge of prefemoral process
sr = serrate ridge of solenomere
sslm = solenomere s. str.
tr = triangular canopy of prefemoral process.
ts = transverse sulcus
vs = ventral seta on anal valve

Other abbreviations

a.s.l. = above sea level
FoRCE = Forest Restoration and Climate Experiment
NHMD = Natural History Museum of Denmark, University of Copenhagen

Fig. 1 shows the areas in which the eight chelodesmid species treated here have been collected.

Results

Taxonomy

Class Diplopoda de Blainville in Gervais, 1844
Order Polydesmida Leach, 1815
Family Chelodesmidae Cook, 1895
Subfamily Prepodesminae Cook, 1896

Genus ***Morogorius*** Verhoeff, 1941

Morogorius Verhoeff, 1941: 249.

Type species

Morogorius pallidus Verhoeff, 1941 (Tanzania) by monotypy.

Other included species

Morogorius divisus Enghoff sp. nov.
Morogorius louishanseni Enghoff sp. nov.
Morogorius pugio Enghoff sp. nov.
Morogorius kitungulu Enghoff sp. nov.
Morogorius cochlear Enghoff sp. nov.

Table 2. Comparison of chelodesmid genera occurring in Tanzania.

Character	***Morogorius***	***Tanzaniella***	***Dionaeadesmus*** gen. nov.	***Callistocilla***	***Morphotelus***[1]	***Mesodesmus***[2]
Paranotal microsculpture	Cytoscutes narrow, more or less irregular, not microspiculate	Cytoscutes narrow, more or less irregular, not microspiculate	Cytoscutes narrow, more or less irregular, not microspiculate	Cytoscutes isodiametric, densely microspiculate	?	?
Gonopod coxa	With a conical process distally on the anterior side (exception: *M. divisus* sp. nov.)	With a conical process distally on the anterior side	With a conical process distally on the anterior side	No such process	No such process	No such process
Prefemoral process / "solenophore"	In close contact with solenomere, without rows of spikes	In close contact with solenomere, very slender, without rows of spikes	In close contact with solenomere, with rows of strong spikes	Not in contact with solenomere	"solenophore"very broad, with several lobes, "surrounding" solenomere	"solenophore"apparently very large, "surrounding" other processes
Solenomere	Not much broader than prefemoral process	Very broad, much broader than prefemoral process	Complicated, narrower than prefemoral process	Not very broad	Simple, slender	?

[1] fide Carl (1909), Chamberlin (1952)
[2] fide Carl (1909), Silvestri (1909)

History and diagnosis

The history of *Morogorius* is brief. In the original description, it was placed in subfamily Cordyloporinae Brölemann, 1916 (now: Prepodesminae) and was diagnosed as follows (translated from Verhoeff 1941: 249): "This genus is based on the absence of dorsal processes, on lack of denticulation on the paranota as well as on the hind margin of the diplosomites between paranota and sterna, and on characters of the gonopods" and "Different from the related genera *Cordyloporus*, *Paracordyloporus*, *Scolopopleura* and *Graphidochirus* in the gonopods, in part also in body characters" (Verhoeff 1941: 249–250). Chamberlin (1952) didn't mention *Morogorius*, nor did Demange & Mauriès (1975). Hoffman (1977) restudied and re-drew the gonopods of the type species and compared it to his *Tanzaniella howelli* Hoffman, 1977. That's all.

A useful differential diagnosis of *Morogorius* is thus not available, as is the case for very many millipede genera. Considering the very large number of genera in Chelodesmidae, in combination with the lack of useful diagnoses of the family Chelodesmidae and the subfamily Prepodesminae, such a diagnosis cannot be presented here. However, *Morogorius* differs from other Tanzanian genera of Chelodesmidae in the characters presented in Table 2. The homology of the largest gonopodal process in *Morphotelus* and *Mesodesmus* is uncertain, therefore the process may preliminary be termed "solenophore".

General description of *Morogorius* (males)

Size. Length 21–31 mm, max. width 3.6–5.7 mm. Collum wider than head but narrower than ring 2, roughly parallel-sided from ring 3 to midbody, thereafter moderately tapering.

Colour. Overall colour (reddish) brown, in part (species-specific) with some or all paranota contrastingly pale (Fig. 2A–B).

Head (Fig. 3A–B). Densely setose below and between antennal sockets, labrogenal offset not very pronounced, epicranial groove distinct, interantennal space narrow, 0.5–0.6 × length of antennomere 2. Antennae reaching back to ring 6 when stretched.

Collum (Fig. 3A, C). In the shape of an isosceles curved trapezoid with the longer margin anteriorly, lateral corners smoothly rounded, surface granular, especially laterally. A row of 2–4 setae close to anterior margin.

Body rings (Figs 3C–H, 7, 10B–F). Prozonites smooth, with simple, cellular microsculpture (Fig. 3D). Metazonites flat, granular dorsally and laterally, 1.4–1.8 × as broad as prozonites, with 1+1 small, thin setae anteriorly (setae apparently absent in *M. pugio* Enghoff sp. nov.) and a prominent transverse sulcus on rings 5–18. Paranota horizontal, those of rings 2–3 very slightly projecting forwards, following paranota rectangular but from some point (ring 5–15 according to species) with posterior corners increasingly projecting backward. Paranotal microsculpture (Fig. 10D) formed by longitudinally stretched, narrow cytoscutes of more or less irregular shape. Ozopore formula normal (5, 7, 9–10, 12–13, 15–19), ozopores circular, delimited by smooth ring in peritremata on edge of paranota, ca midway between anterior and posterior margin. Sterna (Fig. 4E) broad, with a transverse impression and a row of fine setae near anterior margin. Spiracles (only studied in *M. divisus* Enghoff sp. nov.): anterior spiracle on each diploring pear-shaped, posterior spiracle subcircular, both with plugs showing a very pronounced cellular pattern (Fig. 3G). Limbus (Fig. 4F) with straight margin, consisting of a densely, finely striate marginal zone preceded by a row of rectangular cells.

Legs (Figs 4C–D, 10F). Slender, without modifications, length 1.2–1.6 × maximum body width, length not increasing towards hind end,

Fig. 2. Chelodesmids from the Udzungwa Mts. **A**. *Morogorius divisus* Enghoff sp. nov., paratype, ♀ (NHMD 1184699). **B**. *Morogorius louishanseni* Enghoff sp. nov., paratype, ♂ (NHMD 1184563). **C–D**. *Tanzaniella howelli* Hoffman, 1977. **C**. Freshly preserved specimen (uncatalogued). **D**. Female from Mwanihana (NHMD 1184730). **E**. *Dionaeadesmus force* Enghoff gen. et sp. nov., paratype, ♀ (NHMD 1184572), rings 11–13 missing. **F**. *Callistocilla dolorotrix* Hoffman, 2005, male from Udzungwa Scarp Nature Reserve (NHMD 1184742). Scale bars: A–B, D–F = 2 mm; C not to scale. Photos: S.G. Selvantharan (A–B, D–F), A.R. Marshall (C).

Telson (Fig. 4A–B). Preanal ring with several setae along dorsal part of posterior margin; epiproct large, with prominent lateral setiferous tubercles; spinnerets arranged in an almost quadratic trapezoid on a smooth terminal swelling, simple, flanked by 1+1 globular, sometimes partly collapsed structures. Anal valves (paraprocts, *pp*) unmodified, each with 2 setae, dorsal seta (*ds*) on marginal rim, ventral seta (*vs*) more lateral, Subanal scale (hypoproct, *hp*) semicircular, unmodified, with 1+1 marginal setae.

Gonapophyses. Short, triangular.

Gonopod aperture. Transversely oval, more than twice as broad as long, rim simple.

Gonopods (Figs 5–6, 8–9, 11–12). No sternal remnant. Coxa (*cx*) cylindrical, short, length ≈ diameter (perhaps slightly longer in *M. pallidus*), with a conical process (*cxp*) distally on the anterior side (absent to barely discernible in *M. divisus* sp. nov.); two long setae on anterior surface basal to process, a field of up to ca a dozen setae (*ls*) on lateral surface (except in *M. louishanseni* sp. nov. and perhaps *M. pallidus*) and numerous setae on meso-posterior surface. Cannula (*ca*) stout. Prefemoral part (*prf*) bent at right angles relative to *cx*, cylindrical: length 2–2½ × diameter (maybe slightly less in *M. pallidus*), numerous long setae on ventral surface. Efferent canal running straight on meso-dorsal side of *prf*, at level of base of parasolenomere bending laterad into solenomere; prefemoral process (*prp*) originating dorso-laterally from main body of *prf*, at least as long as solenomere and parasolenomere, basally slender, apically more or less expanded, of species-specific shape and curving over solenomere and parasolenomere; *prf* distally delimited by cingulum (*ci*), cingulum very distinct on ventral side of gonopod (except in *M. kitungulu* Enghoff sp. nov. where it is less distinct). Acropodite: main body strongly reduced, indiscernible, giving rise to solenomere and parasolenomere. Solenomere (*slm*) slightly shorter than *prp* (apparently same length in *M. pallidus* according to the original decription of that species), several times as long as broad, of species-specific shape, either regularly tapering or abruptly narrowing at ⅔ of its length. Parasolenomere (*ps*) originating mesal to *slm*, of species-specific shape, more or less shorter than *slm*, sometimes simple, sometimes deeply divided into two branches.

The following descriptions of individual species of *Morogorius* focus on species-specific characteristics. For body parts which are not mentioned, the general description of genus *Morogorius* applies.

Morogorius divisus Enghoff sp. nov.
urn:lsid:zoobank.org:act:48AFBD40-57E0-4F1B-9F58-ABF792FFE13E
Figs 1, 2A, 3–6

Diagnosis

Differs from other species of *Morogorius* by the deep division of the parasolenomere (*ps*) into two long, subequal lobes (Fig. 6A) and by the very poorly developed coxal process (Fig. 5C).

Etymology

Named after the deeply divided parasolenomere. Adjective.

Material examined (total 11 ♂♂, 11 ♀♀)

Holotype

TANZANIA • ♂; Iringa Region, Kilolo District, Udzungwa Scarp Nature Reserve, Uhafiwa; 8°31′58.404″ S, 35°51′28.368″ E; 1375 m a.s.l.; 25 Jan. 2022. A. Ngute, R. Malanda, W. Mhagawale, H. Mnendendo, A. Mpoto and A. Marshall leg.; FoRCE Plot 106, open canopy; COLL.NHMD - ACC. NO. 2022-EN-003; NHMD 1184703.

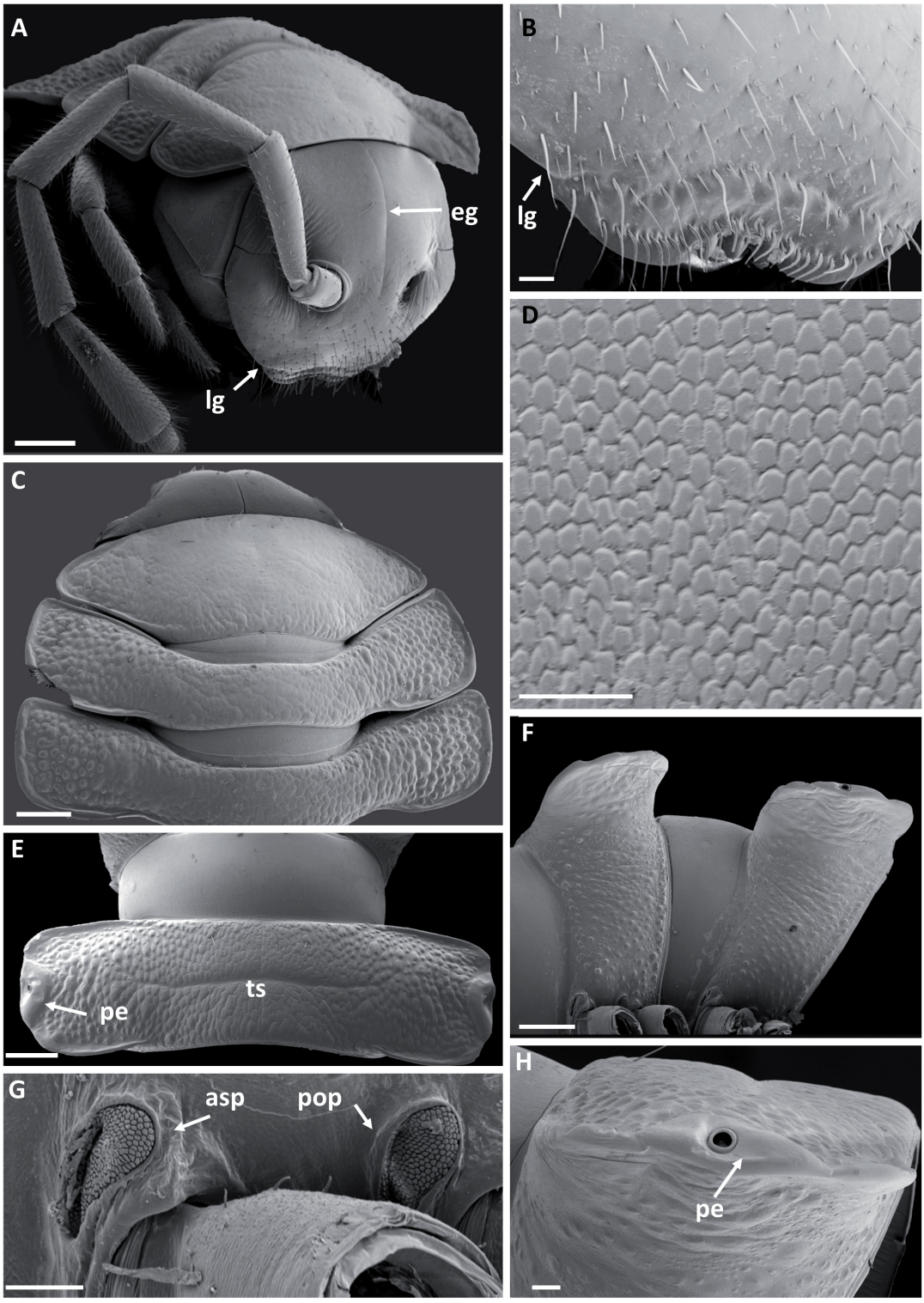

Fig. 3. *Morogorius divisus* Enghoff sp. nov., paratype, ♂ (NHMD 1184702). **A**. Head, right antenna, collum and rings 2–3, oblique view. **B**. Clypeus and labrum. **C**. Head, collum and rings 2–3, dorsal view. **D**. Microsculpture of prozonite, ring 9. **E**. Ring 9, dorsal view. **F**. Rings 8–9, lateral view. **G**. Stigmata of ring 8, lateral view. **H**. Left paranotum and ozopore of ring 9, lateral view. Abbreviations: *asp* = anterior spiracle; *eg* = epicranial groove; *lg* = labrogenal offset; *pe* = peritreme with ozopore; *pop* = posterior spiracle; *ts* = transverse sulcus. Scale bars: A, C, E–F = 0.5 mm; B, G–H = 0.1 mm; D = 0.05 mm.

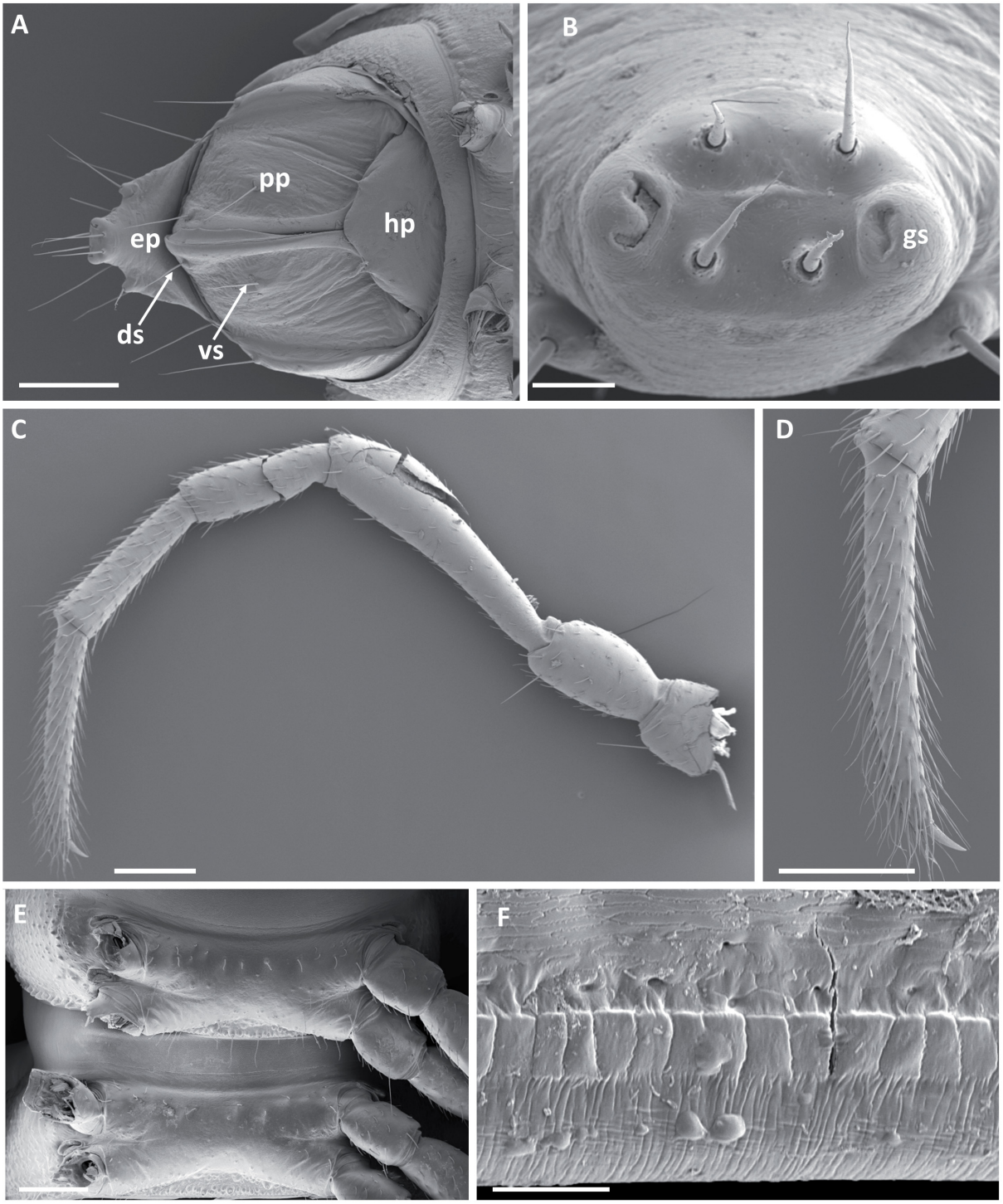

Fig. 4. *Morogorius divisus* Enghoff sp. nov., paratype, ♂ (NHMD 1184702). **A**. Telson, ventral view. **B**. Tip of preanal process (epiproct) with spinnerets, posterior view. **C–D**. Right leg 10, anterior views. **E**. Sterna 11–12. **F**. Midbody dorsal limbus. Abbreviations: *ds* = dorsal seta on anal valve; *ep* = epiproct; *gs* = globular swelling; *hp* = subanal scale (hypoproct); *pp* = anal valve (paraproct); *vs* = ventral seta on anal valve. Scale bars: A, C–E = 0.5 mm; B = 0.05 mm; F = 0.02 mm.

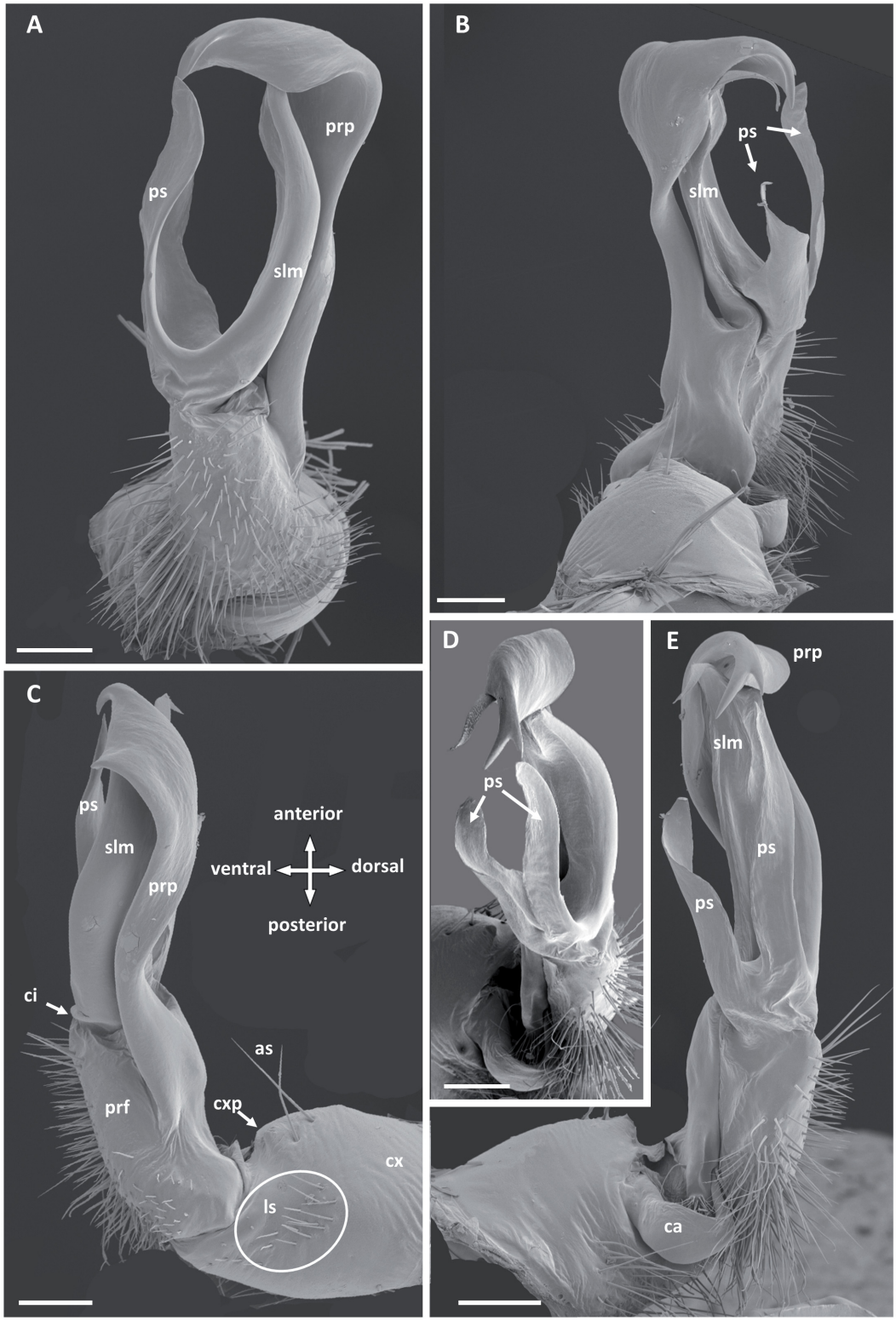

Fig. 5. *Morogorius divisus* Enghoff sp. nov., paratype, ♂ (NHMD 1184699), left gonopod, **A**. Ventral view. **B**. Dorsal view. **C**. Lateral view with directions indicated. **D**. Submesal view. **E**. Mesal view. Abbreviations: *as* = anterior coxal setae; *ca* = cannula; *ci* = cingulum; *cx* = coxa; *ls* = lateral coxal setae; *prf* = prefemoral part; *prp* = prefemoral process; *ps* = parasolenomere; *slm* = solenomere. Scale bars = 0.2 mm.

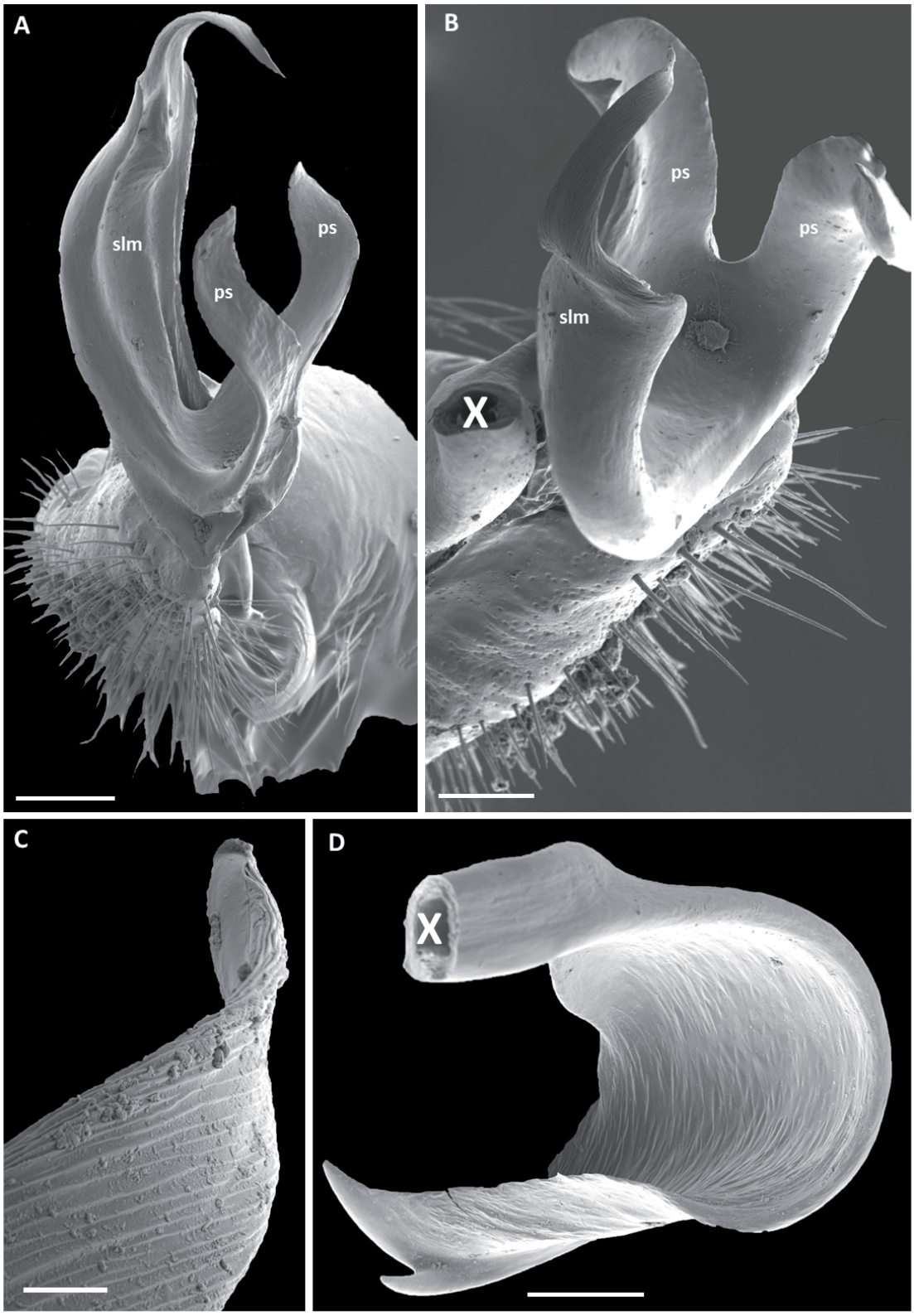

Fig. 6. *Morogorius divisus* Enghoff sp. nov., paratype, ♂ (NHMD 1184701), right gonopod, prefemoral process cut at X. **A**. Meso-ventral view. **B**. Sub-anterior view. **C**. Tip of solenomere. **D**. Separated prefemoral process. Abbreviations: *ps* = parasolenomere; *slm* = solenomere. Scale bars. A = 0.2 mm; B, D = 0.1 mm; C = 0.01 mm.

Paratypes

TANZANIA – **Iringa Region, Kilolo District, Udzungwa Scarp Nature Reserve** • 8 ♂♂, 7 ♀♀; same data as for holotype; NHMD 1184699, NHMD 1184701, NHMD 1184702 • 2 ♂♂, 2 ♀♀; same data as for holotype; Uhafiwa; 8°31′49.296″ S, 35°51′20.772″ E; 1354 m a.s.l.; 24 Jan. 2022; FoRCE Plot 107, open canopy; NHMD 1184704 to NHMD 1184706 • 2 ♀♀; Chita Juu; 8°32′23.388″ S, 35°51′36″ E; 1387 m a.s.l.; 1 Feb. 2022; A. Ngute, R. Malanda, W. Mhagawale, H. Mnendendo, A. Mpoto and A. Marshall leg.; FoRCE Plot 109, open canopy; COLL.NHMD - ACC.NO. 2022-EN-003; NHMD 1184708, NHMD 1184709.

Description (males)

Size. Length 24–27 mm, max. width 4.4–4.8 mm.

Colour (Fig. 2A). After 2 years in alcohol head, collum and most of dorsum reddish-brown. Paranota of rings 2, 5, 7, 9–10, 12–15 and 15–19 contrastingly white, like epiproct and paraprocts. Antennae, venter and legs light brown; antennomeres 1 and 5–7 whitish.

Collum (Fig. 3A, C) with a row of 4 setae close to anterior margin.

Body rings (Fig. 3C, E–H). Metazonites 1.7–1.8 × as broad as prozonites, with 1+1 small, thin setae anteriorly and a prominent transverse sulcus from ring until ring 17 or 18, granulation regular also behind sulcus. Paranota rectangular until ring 13 or 14, thereafter posterior corners projecting increasingly backwards, triangular, those of rings 16–18 with a few denticles at base of mesal margin. Anterior spiracle (*asp*) on each body ring pear-shaped, posterior spiracle (*pop*) subcircular, both with plugs showing a very pronounced cellular pattern (Fig. 3G). Ozopores (Fig. 3E, H) in smooth peritremata (*pe*) on edge of paranota, ca midway between anterior and posterior margin. Sides of rings with a row of slightly larger tubercles along posterior margin.

Legs (Fig. 4C–D). Length 1.3 × maximum body width.

Gonopods (Figs 5–6). Coxa (*cx*) with a barely discernible apical process (*cxp*), with two long setae (*as*) a on anterior surface field of ca a dozen setae (*ls*) on lateral surface. Prefemoral part (*prf*) ca 2 × as long as broad. Prefemoral process (*prp*) closely appressed to and distally curving over solenomere; *prp* slender in basal ²/₃, distally expanded and ending in two tines. Solenomere (*slm*) long, slender, taeniate with parallel margins, at ca ⁴/₅ of its length abruptly narrowed from ventral side; apical ¹/₅ thin, tapering. Parasolenomere (*ps*) deeply divided into two branches; ventral branch ca ³/₄ as long as solenomere, slender; dorsal branch slightly shorter and broader, apically strongly tapering.

Distribution and habitat

Only known from three sites in the Udzungwa Scarp Nature Reserve (Fig. 1). Collected under open canopy at 1354–1387 m a.s.l.

Morogorius louishanseni Enghoff sp. nov.
urn:lsid:zoobank.org:act:4F551606-55DA-40F7-818B-C21F9BA84545
Figs 1, 2B, 7–8

Diagnosis

Differs from other species of *Morogorius* by the shape of the parasolenomere: broad base, lateral shoulder and tapering apical part (Fig. 8C–D).

Etymology

Named after Louis Hansen, collector of many new millipede species in the Udzungwa Mts. Noun in genitive.

Material examined (total 31 ♂♂, 10 ♀♀)

Holotype

TANZANIA • ♂; Iringa Region, Mahenge Distr., West Kilombero Scarp Forest Reserve, Nyumbanitu Mts, S Udekwa Village; 07°48′ S, 36°21′ E; 1500 m a.s.l.; Dec. 1993; J.O. Svendsen leg.; NHMD 1184745.

Paratypes

TANZANIA • 9 ♂♂, 5 ♀♀; same data as for holotype; NHMD 1184713 • 4 ♂♂, 2 ♀♀; same data as for holotype; 1700 m a.s.l.; NHMD 1184577 • 1 ♂, 2 ♀♀; Iringa Region, Udzungwa Mts, Ndundulu Forest, Waller's camp; 07°46′ S, 36°29′ E; 1550 m a.s.l.; Dec. 2006; L.A. Hansen and local assistants leg.; tropical semi-evergreen forest; NHMD 1184700 • 2 ♂♂, 1 ♀; same data as for preceding; 1–12 Jan. 2007; NHMD 1184712 • 14 ♂♂; Udzungwa Mts, Kitungulu Forest Reserve; 08°09′ S, 36°05′ E; 1500 m a.s.l.; Jan. 1996; M. Andersen, P. Gravlund and A. Jakobsen leg.; NHMD 1184563.

Description (males)

Size. Length 29–30 mm, max. width 3.6–3.8 mm.

Colour (Fig. 2B). After 17–28 years in alcohol head light brown, collum light brown with broad whitish margin. Dorsal side of rings with posterior half of each ring whitish to very light brown, anterior half of each ring brownish; paranota whitish, no difference between poriferous and non-poriferous rings. Antennae, legs, venter and telson very light brown to whitish.

Collum. With a row of 4 setae close to anterior margin.

Body rings (Fig. 7). Metazonites 1.4–1.6 × as broad as prozonites, with 1+1 small, thin setae anteriorly and a prominent transverse sulcus on rings 5–17, granulation irregular, with a tendency to longitudinal striolation behind sulcus. Paranota already from ring 5 with posterior corners projecting increasingly backwards, first as rounded lobes, further back as pointed triangles, those of ring 16 with a few denticles at base of mesal margin. Ozopores in smooth peritremata on edge of paranota, ca midway between

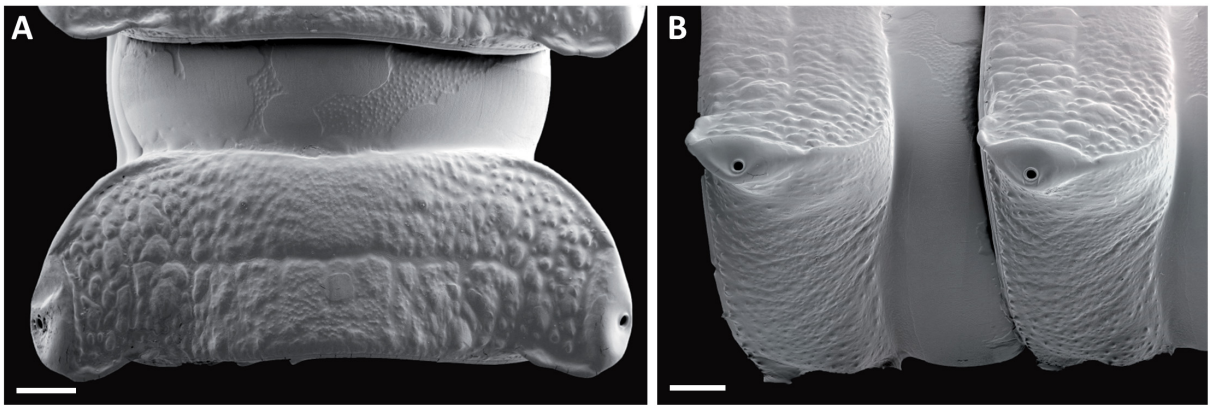

Fig. 7. *Morogorius louishanseni* Enghoff sp. nov., paratype, ♂ (NHMD 1184713). **A**. Ring 12, dorsal view. **B**. Rings 11–12, lateral view. Scale bars = 0.4 mm.

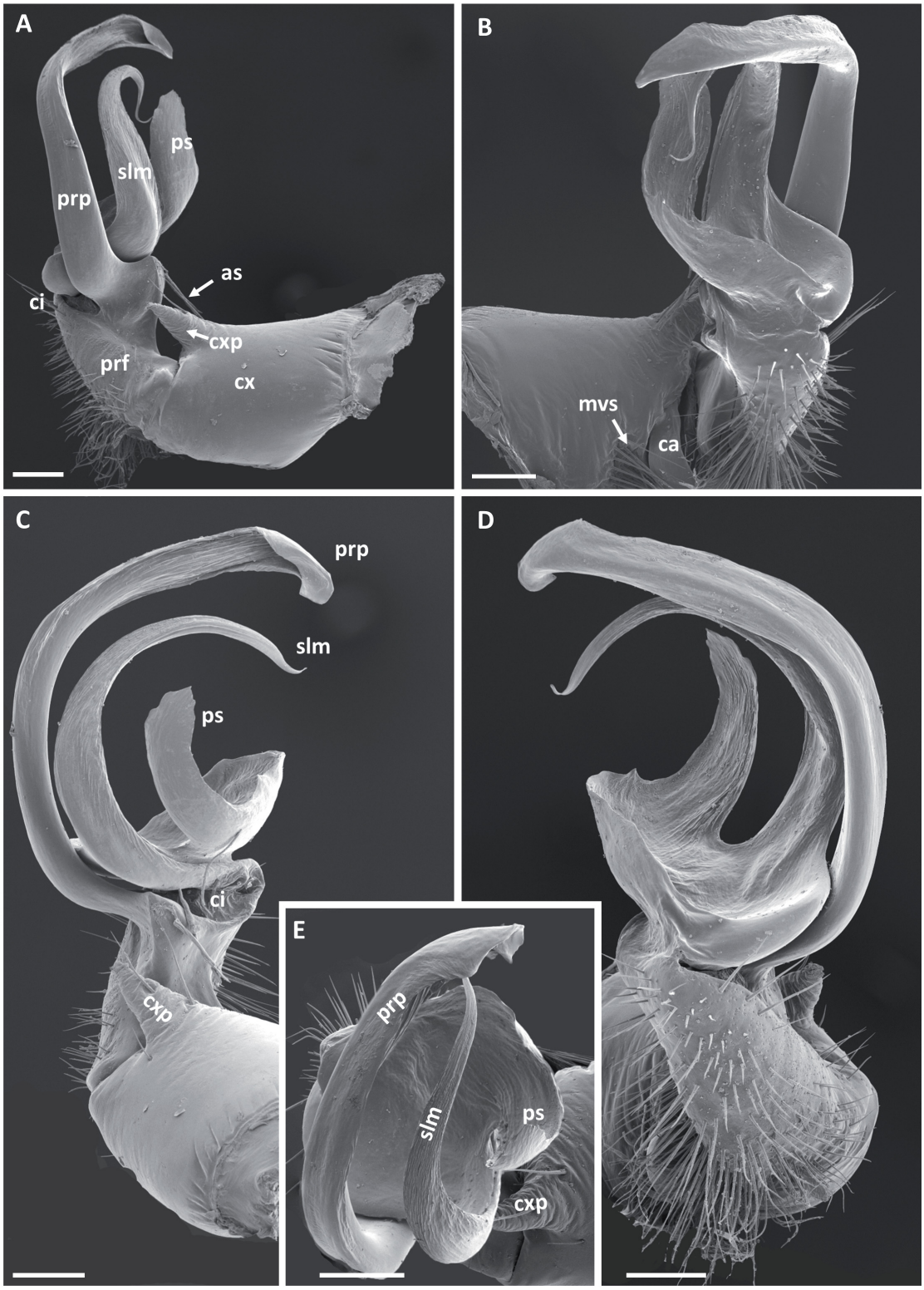

Fig. 8. *Morogorius louishanseni* Enghoff sp. nov., paratype, ♂ (NHMD 1184653), left gonopod. **A**. Lateral view. **B**. Submesal view. **C**. Dorsal view. **D**. Ventral view. **E**. Anterior view. Abbreviations: *as* = anterior coxal setae; *ca* = cannula; *ci* = cingulum; *cx* = coxa; *cxp* = coxal process; *mvs* = mesoventral setae; *prf* = prefemoral part; *prp* = prefemoral process; *ps* =parasolenomere; *slm* = solenomere. Scale bars = 0.2 mm.

anterior and posterior margin. Sides of rings with a row of slightly larger tubercles along posterior margin.

Legs. Length 1.5–1.6 × maximum body width.

Gonopods (Fig. 8). Coxa (*cx*) with a stout cone-shaped apical process (*cxp*), two long setae (*as*) at base of process, no setae on lateral surface. Prefemoral part (*prf*) ca 2 × as long as broad. Prefemoral process (*prp*) closely appressed to and distally curving over solenomere, *prp* at base with triangular expansion, distally expanding, its tip curved back on itself. Solenomere (*slm*) long, slender, regularly tapering. Parasolenomere (*ps*) slightly shorter than solenomere, lamellate, basal part broad, lateral margin with marked 'shoulder', *ps* thereafter more or less regularly tapering.

Distribution and habitat

Known from three sites in the Udzungwa Mountains: Nyumbanitu Mountains, Ndundulu Forest and Kitungulu Forest Reserve (Fig. 1). Collected in tropical semi-evergreen forest at 1500–1550 m a.s.l.

Morogorius pugio Enghoff sp. nov.
urn:lsid:zoobank.org:act:66768505-0FD5-4E1B-AC6F-D763ADD4639E
Figs 1, 9

Diagnosis

Differs from other species of *Morogorius* by the simple thin, straight, pointed parasolenomere with a small needlelike side branch (Fig. 9D–E).

Etymology

Named after the parasolenomere which reminds of a dagger (Latin '*pugio*'). Noun in apposition.

Material examined (total 1 ♂)

Holotype

TANZANIA • ♂; Morogoro Region, Udzungwa Mts Natl. Park, Kidatu; 07°40′42.1″ S, 36°55′06.8″ E; 1482 m a.s.l.; 21 Apr. 2014; J. Malumbres-Olarte leg.; Plot 6, pitfall trap, sample code 6 PT8; NHMD 1184710.

Description (male)

Size. Length ca 31 mm, max. width 5.7 mm.

Colour. After 10 years in alcohol head medium brown, collum and dorsal side of body rings dark; paranota 2, 3, 5, 7, 9–10, 12–13 and 15–19 contrastingly whitish, paranota 4, 6 and 8 of a slightly lighter hue than main part of dorsum, sides of body rings medium brown; telson light brown, epiproct whitish; antennae and venter light brown; legs whitish brown.

Collum. With pair of setae close to anterior margin.

Body rings. Metazonites 1.4 × as broad as prozonites, apparently without setae; with a prominent transverse sulcus on rings 5–17. Granulation irregular, but with a tendency to longitudinal striolation behind sulcus. Paranota from ring with 7 posterior corners projecting slightly backwards, first as rounded lobes, further back more triangular. Sides of rings with uniform tuberculation, no larger tubercles along posterior margin.

Legs. Length 1.2 × maximum body width.

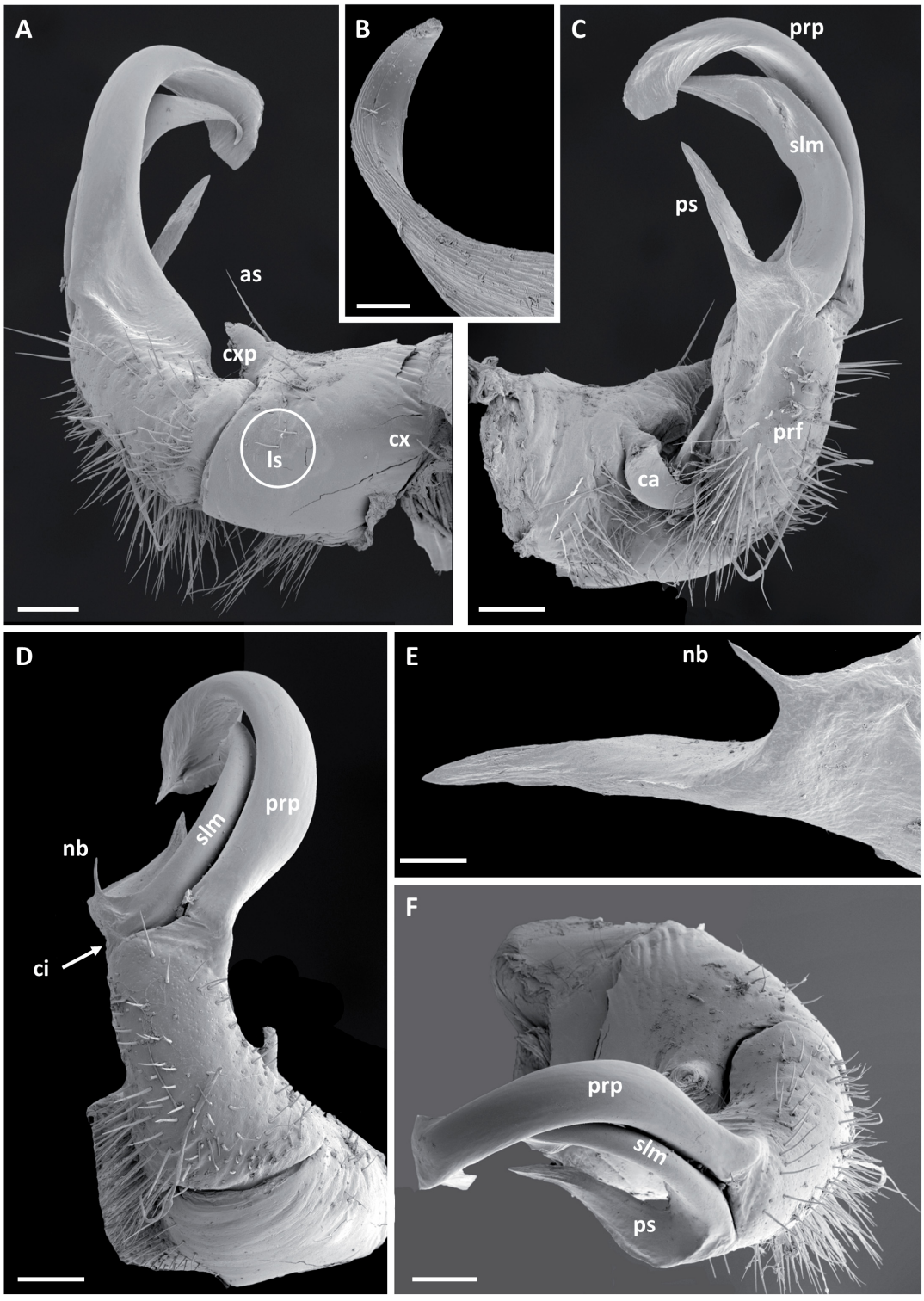

Fig. 9. *Morogorius pugio* Enghoff sp. nov., holotype, ♂ (NHMD 1184710), left gonopod. **A**. Lateral view. **B**. Tip of solenomere. **C**. Mesal view. **D**. Ventral view (most prefemoral setae trimmed). **E**. Parasolenomere, isolated. **F**. Anterior view. Abbreviations: *as* = anterior coxal seta; *ca* = cannula; *ci* = cingulum; *cx* = coxa; *cxp* = coxal process; *ls* = lateral coxal setae; *nb* = needlelike side branch; *prf* = prefemoral part; *prp* = prefemoral process; *ps* = parasolenomere; *slm* = solenomere. Scale bars: A, C–D, F = 0.2 mm; B = 0.02 mm; E = 0.1 mm.

Gonopods (Fig. 9). Coxa (*cx*) with a strong conical apical process (*cxp*), one long seta (*as*) on anterior surface basal to process, a field of setae (*ls*) on lateral surface. Prefemoral part (*prf*) ca 2 × as long as broad. Prefemoral process (*prp*) closely appressed to and distally curving over solenomere. Solenomere (*slm*) long, slender, taeniate, pointed. Parasolenomere (*ps*) much shorter than solenomere, thin, straight, pointed, with small needlelike side branch (*nb*) basally.

Distribution and habitat

Known only from one site in the Udzungwa Mountains National Park (Fig. 1). Collected in a pitfall trap at 1482 m a.s.l.

Morogorius kitungulu Enghoff sp. nov.
urn:lsid:zoobank.org:act:052AECF5-0923-403F-AEC2-F2E1F918DB22
Figs 1, 10–11

Diagnosis

Differs from other species of *Morogorius*, except *M. cochlear* sp. nov., by the short, compact parasolenomere. Differs from *M. cochlear* by the pointed shape of the parasolenomere, the slenderer prefemoral process and the larger coxal process (Fig. 11, compare with Fig. 12).

Etymology

Named after the type locality. Noun in apposition.

Material examined (total 1 ♂)

Holotype

TANZANIA • ♂; Udzungwa Mts, Kitungulu Forest Reserve; 08°09′ S, 36°05′ E; 1500 m a.s.l.; Jan. 1996; M. Andersen, P. Gravlund and A. Jakobsen leg.; NHMD 1184573.

Description (male)

Size. Length ca 27 mm, max. width 4.6 mm.

Colour. After 28 years in alcohol head brownish; dorsal side of all rings including collum brownish with contrasting whitish paranota on all rings, post-sulcus area of rings also whitish; telson anteriorly brownish, posteriorly whitish; antennae, legs and ventral side light brown.

Collum. With two setae close to anterior margin.

Body rings (Fig. 10A–C). Metazonites ca 1.6 times as broad as prozonites, with 1+1 small, thin setae anteriorly, a prominent transverse sulcus on rings 5–18, granulated with irregular shallow, longitudinal striae behind transverse sulcus. Paranota rectangular until ring 14, thereafter posterior corners projecting increasingly backwards, triangular. Ozopores in smooth peritremata on edge of paranota, ca midway between anterior and posterior margin (Fig. 10B–C). Sides of rings with uniform tuberculation, no larger tubercles along posterior margin.

Legs (Fig. 10F). Length 1.2 × maximum body width.

Gonopods (Fig. 11). Coxa (*cx*) with a long, stout, conical apical process (*cxp*) on anterior side, two long setae (*as*) on anterior surface basal to process, a field of ca a dozen setae (*ls*) on lateral surface. Prefemoral part (*prf*) ca 2½ × as long as broad, distally delimited by distinct cingulum (*ci*) on ventral side. Efferent duct running straight on meso-dorsal side of prefemoral part, at level of base of parasolenomere bending laterad into hollowed side of acropodite. Prefemoral process (*prp*) with slender club-shaped outline,

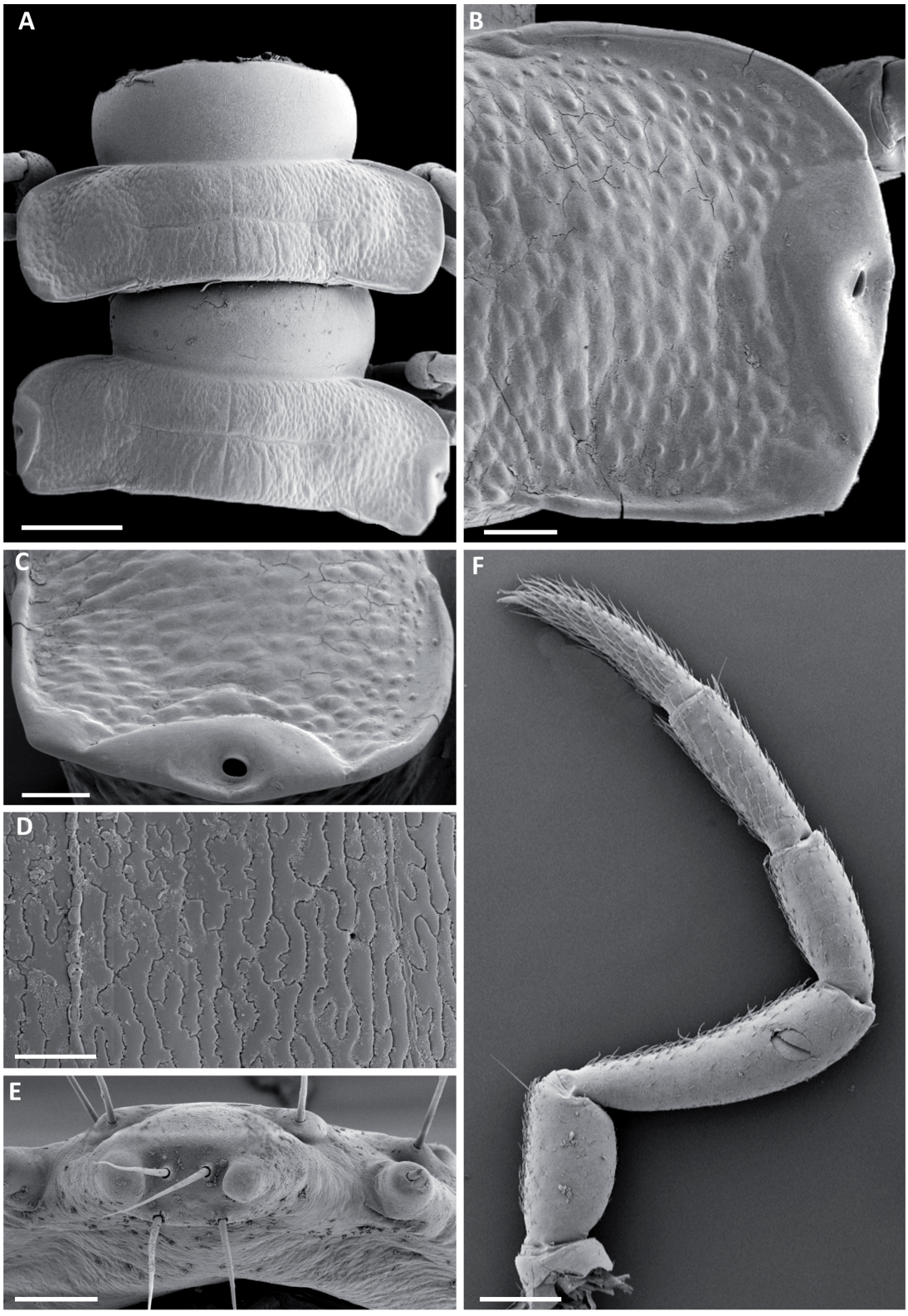

Fig. 10. *Morogorius kitungulu* Enghoff sp. nov., holotype, ♂ (NHMD 1184573). **A**. Rings 11–12, dorsal view. **B**. Ring 12, right paranotum, dorsal view. **C**. Ring 12, right paranotum, lateral view. **D**. Paranotal dorsal microsculpture. **E**. Tip of epiproct, with spinnerets and lateral knobs. **F**. Midbody leg. Scale bars: A = 1 mm; B–C = 0.2 mm; D = 0.01 mm; E = 0.1 mm; F = 0.4 mm.

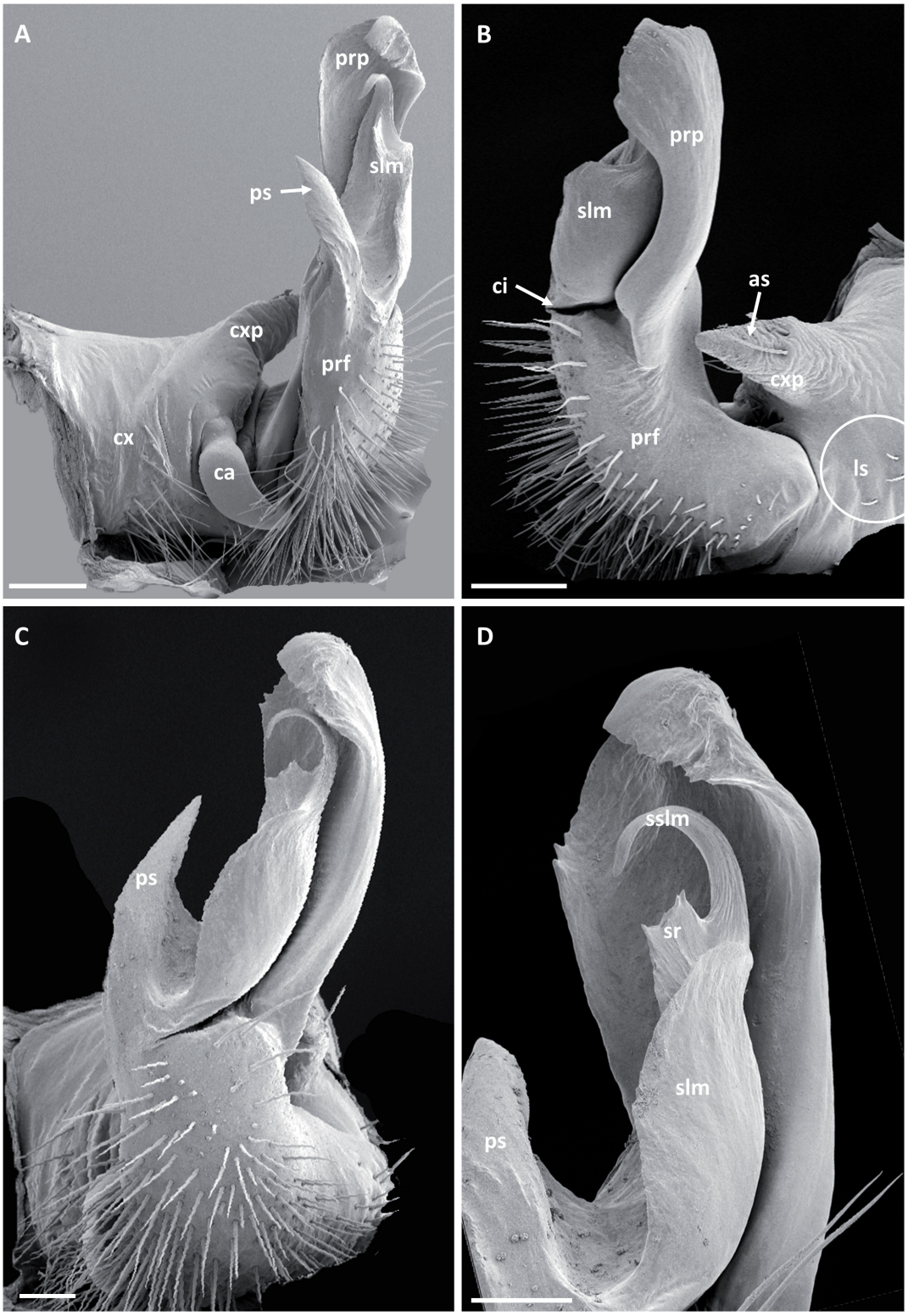

Fig. 11. *Morogorius kitungulu* Enghoff sp. nov., holotype , ♂ (NHMD 1184573), left gonopod. **A**. Mesal view. **B**. (Dorso)lateral view. **C**. Ventrolateral view. **D**. Acropodite, meso-ventral view. Abbreviations: *as* = anterior coxal setae; *ca* = cannula; *ci* = cingulum; *cx* = coxa; *cxp* = coxal process; *ls* = lateral coxal setae; *prf* = prefemoral part; *prp* = prefemoral process; *ps* = parasolenomere; *slm* = solenomere; *sr* = serrate ridge of solenomere; *sslm* = solenomere s. str. Scale bars: A–B = 0.2 mm; C–D = 0.1 mm.

apical part sub-rhomboid, dorsal surface concave (accommodating solenomere), apically forming hood over tip of solenomere; a few denticles on distal margin and subdistally on dorsal margin. Solenomere (*slm*) shorter (ca 0.8 ×) than *prp*, stout and slightly tapering in basal ⅔, then abruptly narrower, forming slender hook, the solenomere s. str. (*sslm*); a slightly serrate high, short ridge (s*r*) facing concave side of *sslm.* Parasolenomere (*ps*) originating mesal to *slm*, much shorter than *slm*, stout, pointed.

Distribution and habitat

Known only from one site in the Kitungulu Forest Reserve, Udzungwa Mountains (Fig. 1). Collected at 1300 m a.s.l.

Morogorius cochlear Enghoff sp. nov.
urn:lsid:zoobank.org:act:5E6446F3-AF09-4A1F-8716-E117ECC2D99A
Figs 1, 12

Diagnosis

Differs from other species of *Morogorius*, except *M. kitungulu* sp. nov., by the short, compact parasolenomere. Differs from *M. kitungulu* by the rounded shape of the parasolenomere, which has a retrose pointed process, the broader, spoonlike prefemoral process and the smaller coxal process (Fig. 12, compare with Fig. 11).

Etymology

Named after the prefemoral process which is in the shape of a spoon (Latin '*cochlear*'). Noun in apposition.

Material examined (total 1 ♂)

Holotype
TANZANIA • ♂; Morogoro Region, Udzungwa Mountains National Park, Kidatu; 07°41′06.2″ S, 36°54′52.4″ E; 1527 m a.s.l.; 23 Oct. 2014; J. Malumbres-Olarte leg.; Plot 9, pitfall trap; NHMD 1184574.

Description (male)

Size. Length ca 25 mm, max. width 5.0 mm.

Colour. After 10 years in alcohol head brownish; dorsal side of all rings including collum brownish with whitish paranota on all rings; antennae light brown; telson, legs and ventral side whitish.

Collum. With three setae close to anterior margin (a fourth setae has probably been present, too).

Body rings. Ca 1.6 times as broad as prozonites, with 1+1 small, thin setae anteriorly, a prominent transverse sulcus on rings 5–18, granulated with irregular shallow, longitudinal striae behind transverse sulcus. Paranota rectangular until ring 13, thereafter posterior corners projecting increasingly backwards, triangular. Ozopores in smooth peritremata on edge of paranota, ca midway between anterior and posterior margin. Sides of rings with uniform tuberculation, no larger tubercles along posterior margin.

Legs. Length ≈ 1.3 × maximum body width.

Gonopods (Fig. 12). Coxa (*cx*) with a pointed, slightly curved apical process (*cxp*), two long setae (*as*) on anterior surface basal to process, and a field of ca a dozen setae (*ls*) on lateral surface. Prefemoral part (*prf*) ca 2½× as long as broad, distally delimited by distinct cingulum (*ci*) on ventral side. Prefemoral process (*prp*) with club-shaped outline, apical part almost circular, dorsal surface concave

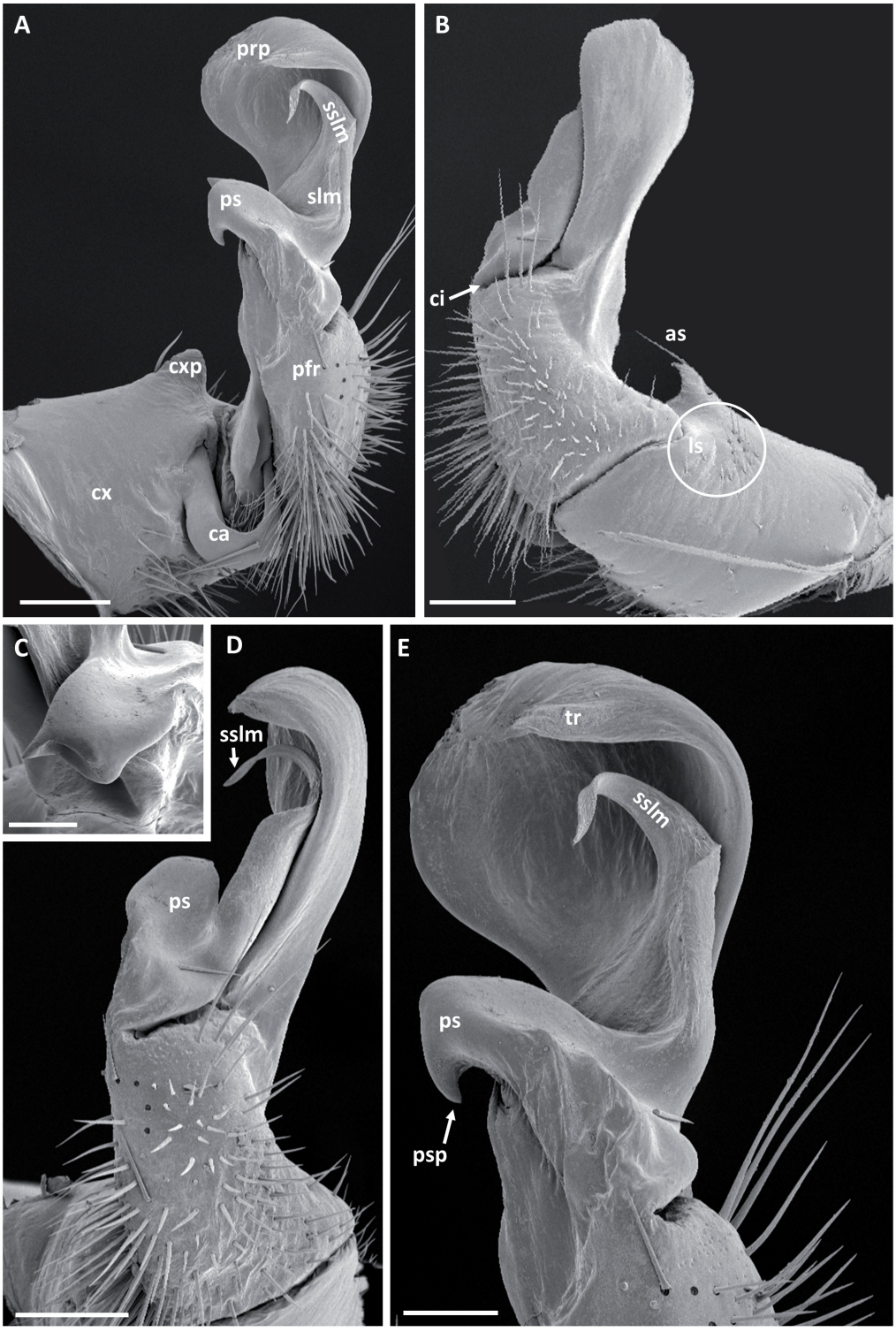

Fig. 12. *Morogorius cochlear* Enghoff sp. nov., holotype, ♂ (NHMD 1184574), left gonopod. **A**. Mesal view. **B**. Lateral view. **C**. Close-up of parasolenomere. **D**. Ventral view. **E**. Acropodite, mesal view. Abbreviations: *as* = anterior coxal setae; *ca* = cannula; *ci* = cingulum; *cx* = coxa; *cxp* = coxal process; *ls* = lateral coxal setae; *prf* = prefemoral part; *prp* = prefemoral process; *ps* = parasolenomere; *psp* = process of parasolenomere; *slm* = solenomere; *sslm* = solenomere s. str.; *tr* = triangular canopy of prefemoral process. Scale bars: A–B, D = 0.2 mm; C, E = 0.1 mm.

(accommodating solenomere), apically forming hood over tip of solenomere; distal margin with stout, triangular, dorsad canopy (*tr*). Solenomere (*slm*) shorter (ca 0.8 ×) than *prp*, stout and slightly tapering in basal ⅔, then abruptly narrower, forming slender hook, the solenomere s. str. (*sslm*). Parasolenomere (*ps*) originating mesal to *slm*, much shorter than *slm*, stout, subrectangular, with short, pointed retrorse process (*psp*) dorsally.

Remarks

Very similar to *M. kitungulu* sp. nov., sharing, i.a., the general shape of the solenomere and the short, stout parasolenomere. Differs from *M. kitungulu* in the detailed shape of all three processes.

Distribution and habitat

Known only from one site in the Udzungwa Mountains National Park (Fig. 1). Collected in a pitfall trap at 1527 m a.s.l.

Morogorius pallidus Verhoeff, 1941

Diagnosis

Differs from other species of *Morogorius* by the deep division of the parasolenomere into a long slender branch and a considerably shorter daggerlike branch, in combination with a well-developed 'shoulder' of the solenomere (Verhoeff 1941: fig. 21; Hoffman 1977: fig. 11).

Material examined (total 1 ♀)

Paratype

TANZANIA • 1 ♀; "Tanganyika"; "1123"; ZMB 2696.

Descriptive notes

Body length ca 23 mm; max. width 3.0 mm. 20 'segments', i.e., 18 podous + 1 apodous ring + telson.

A side-by side comparison with a female of *Morogorius divisus* Enghoff sp. nov. shows the following differences:

- the posterior margin of the collum is straight, not 'trapezoid' (cp. Fig. 3C);
- the peritremata are clearly, not indistinctly set off from the lateral margin of the paranota (cp. Fig. 3E).

Details of spinnerets not visible (no SEM).

Remarks

Maybe this female is not conspecific with the holotype male and maybe even belong to another genus?

In any case, there is no doubt that the gonopods of *M. pallidus* as described by Verhoeff (1941) and Hoffman (1977) are 'congeneric' with those of the new species of *Morogorius* described above.

Genus ***Tanzaniella*** Hoffman, 1977

Tanzaniella Hoffman, 1977: 77.

Type species

Tanzaniella howelli Hoffman, 1977 (Tanzania) by monotypy.

Diagnosis

Tanzaniella differs from other Tanzanian genera of Chelodesmidae as shown in Table 2, notably by the solenomere which is very much broader than and by far more conspicuous than the other terminal telopodital process.

Other included species

None.

Remarks

Hoffman (1977) compared the type and only species of *Tanzaniella* with the type (and then only) species of *Morogorius*, viz., *M. pallidus* Verhoeff, 1941. He noticed several specific similarities including a broadened solenomere and realized that "eventual annectant forms may be found that connect the two nominal genera" (Hoffman 1977: 76). Although five additional species of *Morogorius* have been described here, *T. howelli* still stands out by the extreme development of the solenomere, compared with a very thin prefemoral process (tibiotarsus of Hoffman 1977). For the time being the two genera are therefore kept separate.

Tanzaniella howelli Hoffman, 1977
Figs 1, 2C–D, 13–14

Tanzaniella howelli Hoffman, 1977: 79.

Diagnosis

Redundant, genus monotypic.

Material examined (total 34 ♂♂, 42 ♀♀, 13 juv.)

TANZANIA – **Morogoro Region, Kilombero District, Magombera Nature Reserve** • 1 ♀, 1 juv.; 7°48′46.332″ S, 36°58′32.2314″ E; 273 m a.s.l.; 26 Dec. 2019; A. Ngute and A.R. Marshall leg.; open forest, Micro-FoRCE plot 2; COLL. NHMD. ACC.NO. 2020-EN-002; NHMD 1184714 • 1 ♀; 7°48′53.946″ S, 36°59′20.025″ E; 267 m a.s.l.; 13 Jan. 2019; A. Ngute and A.R. Marshall leg.; open forest, Micro-FoRCE plot 7; NHMD 1184715 • 3 ♂♂, 2 ♀♀; 7°49′28.0344″ S, 36°58′55.236″ E; 271 m a.s.l.; 31 Jan. 2020; A. Ngute and A.R. Marshall leg.; open forest, Micro-FoRCE plot 13; NHMD 1184716 • 2 ♂♂, 4 ♀♀; 7°48′53.154″ S, 36°58′2.7948″ E; 282 m a.s.l.; 5 Mar. 2020; A. Ngute and A.R. Marshall leg.; open forest, Micro-FoRCE plot 22; NHMD 1184717 • 3 ♂♂, 7 ♀♀; 7°49′3.6114″ S, 36°57′33.8754″ E; 280 m a.s.l.; 16 Mar. 2020; A. Ngute and A.R. Marshall leg.; closed forest, Micro-FoRCE plot 27; NHMD 1184698 • 1 ♂, 2 ♀♀, 4 juvs; 7°48′45.8634″ S, 36°58′38.4954″ E; 274 m a.s.l.; 27 Feb. 2018; A R. Marshall leg.; open forest, Half-FoRCE plot 33; NHMD 1184718 • 1 ♂, 1 juv.; 7°48′34.0554″ E, 36°59′4.4514″ E; 281 m a.s.l.; 2 Feb. 2018; A.R. Marshall leg.; open forest, Half-FoRCE plot 36; NHMD 1184719. – **Morogoro Region, Kilombero District, Udzungwa Mountains National Park, Mwanihana** • 1 ♀; Njokamoni; 7°50′31.8474″ S, 36°52′47.1354″ E; 401 m a.s.l.; 21 Dec. 2021; A. Ngute, R. Malanda, W. Mhagawale and A. Marshall leg.; open canopy, ForCE Plot 11; COLL. NHMD - ACC.NO. 2022-EN-003; NHMD 1184720 • 1 ♂, 2 ♀♀, 1 juv.; same data as for preceding; 7°50′33.1434″ S, 36°52′54.912″ E; 357 m a.s.l.; 22 Dec. 2021; open canopy, ForCE Plot 12; NHMD 1184721 • 1 ♂, 1 ♀; Sanje Kati camp and plot; 7°45′47.6″ S, 36°53′10.4″ E; 850 m a.s.l.; 20–23 Jan. 2014; T. Pape and N. Scharff leg.; in copula, hand-collected; NHMD 1184730 • 1 ♂; Sanje Chini camp; 7°46′24.6″ S, 36°53′47.7″ E; 598 m a.s.l.; 17–19 Jan. 2014; T. Pape and N. Scharff leg.; hand-collected; NHMD 1184731 • 1 ♂, 3 ♀♀, 5 juvs; Sanje; 7°46′43.3914″ S, 36°54′4.32″ E; 504 m a.s.l.; 26 Feb. 2022; A. Ngute, E. Kivambe, R. Malanda, H. Mnendendo, W. Mhagawale, M. Mpoto and A. Marshall leg.; open canopy, ForCE Plot 24; COLL.NHMD - ACC.NO. 2022-EN-003; NHMD 1184722 • 4 ♂♂, 1 ♀;

Sanje; 7°46′52.14″ S, 36°54′11.7714″ E; 421 m a.s.l.; 20 Feb. 2022; A. Ngute, E. Kivambe, R. Malanda, W. Mhagawale, H. Mnendendo and A. Marshall leg.; open canopy. ForCE Plot 92: COLL.NHMD - ACC.NO. 2022-EN-003; NHMD 1184661. – **Morogoro Region, Kilombero District, Udzungwa Mountains National Park** • 8 ♂♂, 11 ♀♀, 1 juv.; 7°49′13.2198″ S, 36°53′33.4608″ E; 334 m a.s.l.; 25 Feb. 2020; A. Ngute and A.R. Marshall leg.; open forest, Micro-FoRCE plot 17; COLL. NHMD. ACC.NO. 2020-EN-002; NHMD 1184723 • 1 ♂; 7°50′14.5314″ S, 36°53′7.7634″ E; 358 m a.s.l.; 13 Feb. 2020; A. Ngute and A.R. Marshall leg.; closed forest, Micro-FoRCE plot 18; COLL. NHMD. ACC.NO. 2020-EN-002; NHMD 1184724 • 5 ♂♂; 7°49′30.8424″ S, 36°53′29.1798″ E; 340 m a.s.l.; 21 Feb. 2020; A. Ngute and A.R. Marshall leg.; open forest, Micro-FoRCE plot 19; COLL. NHMD. ACC.NO. 2020-EN-002; NHMD 1184725 • 1 ♂; 7°49′46.5348″ S, 36°53′27.873″ E; 347 m a.s.l.; 27 Feb. 2020; A. Ngute and A.R. Marshall leg.; open forest, Micro-FoRCE plot 20; COLL. NHMD. ACC.NO. 2020-EN-002; NHMD 1184726 • 2 ♀♀; 7°47′24.216″ S, 36°54′7.128″ E; 334 m a.s.l.; 17 Feb. 2020; A. Ngute and A.R. Marshall leg.; open forest Micro-FoRCE plot 25; COLL. NHMD. ACC.NO. 2020-EN-002; NHMD 1184727 • 1 ♂, 1 ♀; 7°47′43.1088″ S, 36°53′57.6132″ E; 331 m a.s.l.; 19 Feb. 2020; A. Ngute and A.R. Marshall leg.; open forest, Micro-FoRCE plot 28; COLL. NHMD. ACC.NO. 2020-EN-002; NHMD 1184728 • 3 ♀♀, 1 juv.; 7°47′1.1394″ S, 36°54′13.8594″ E; 381 m a.s.l.; 15 Feb. 2020; A. Ngute and A.R. Marshall leg.; closed forest, Micro-FoRCE plot 30; COLL. NHMD. ACC.NO. 2020-EN-002; NHMD 1184729.

Descriptive notes

The original description of *T. howelli*, including the accompanying drawings (Hoffman 1977), are fully satisfactory for recognizing the species. Study of the abundant material from the Udzungwa Mts allows, however, some additions to the description.

Size. Max. body width of males 4.3–4.7 mm (Hoffman 1977: 4.6 mm).

Colour (Fig. 2C–D). Overall colour of freshly preserved specimens (Fig. 2C) reddish brown, with contrasting yellowish paraterga. After four years in alcohol as described by Hoffman (1977), except that the colour of "middorsum of metaterga, most of prozona, and sides of metazona" is dark piceous brown in males, and medium brown in females, rather than "piceous black".

Collum (Fig. 13A). Same shape as in *Morogorius* spp.: an isosceles curved trapezoid with the longer margin anteriorly. A few setae close to anterior margin.

Body rings (Fig. 13B–D). Metazonites regularly granulotuberculate dorsally. Microsculpture of paranota (Fig. 13C) as in *Morogorius* spp.: formed by longitudinally stretched, narrow cytoscutes of more or less irregular shape. Limbus (Fig. 13D) as in *Morogorius* spp.

Telson (Fig. 13E). Spinnerets arranged in an almost quadratic trapezoid on a smooth terminal swelling of the epiproct, simple, flanked by 1+1 globular, sometimes partly collapsed swellings.

Gonopods (Fig. 14) (interpreted in the light of *Morogorius* spp.). Prefemoral part (*prf*) longer than in *Morogorius* spp. Prefemoral process (*prp*) ("tibiotarsus" of Hoffman 1977) a narrow band curving over convex surface of solenomere, apically with two small tines. Solenomere (*slm*) (solenomerite and acropodite of Hoffman 1977) a very large and broad sheet, dorsally deeply concave. Parasolenomere (*ps*) a thin, straight rod.

Distribution and habitat

The type locality is "Kisaware, 6.63° S, 39.05° E, near Dar es Salaam.". This is probably a typo for Kisarawe, a district in Tanzania's Pwani Region. Also known from the Magombera Nature Reserve and

from several sites in the Udzungwa Mountains National Park. Collected in open and closed forest at 267–504 m a.s.l., and a single outlier at 850 m a.s.l.

Remarks

The relatively high abundance of *T. howelli* in the Udzungwa Mts contrasts with the situation at the type locality near Dar es Salaam where, according to Hoffman (1977: 81), "The species does not appear to

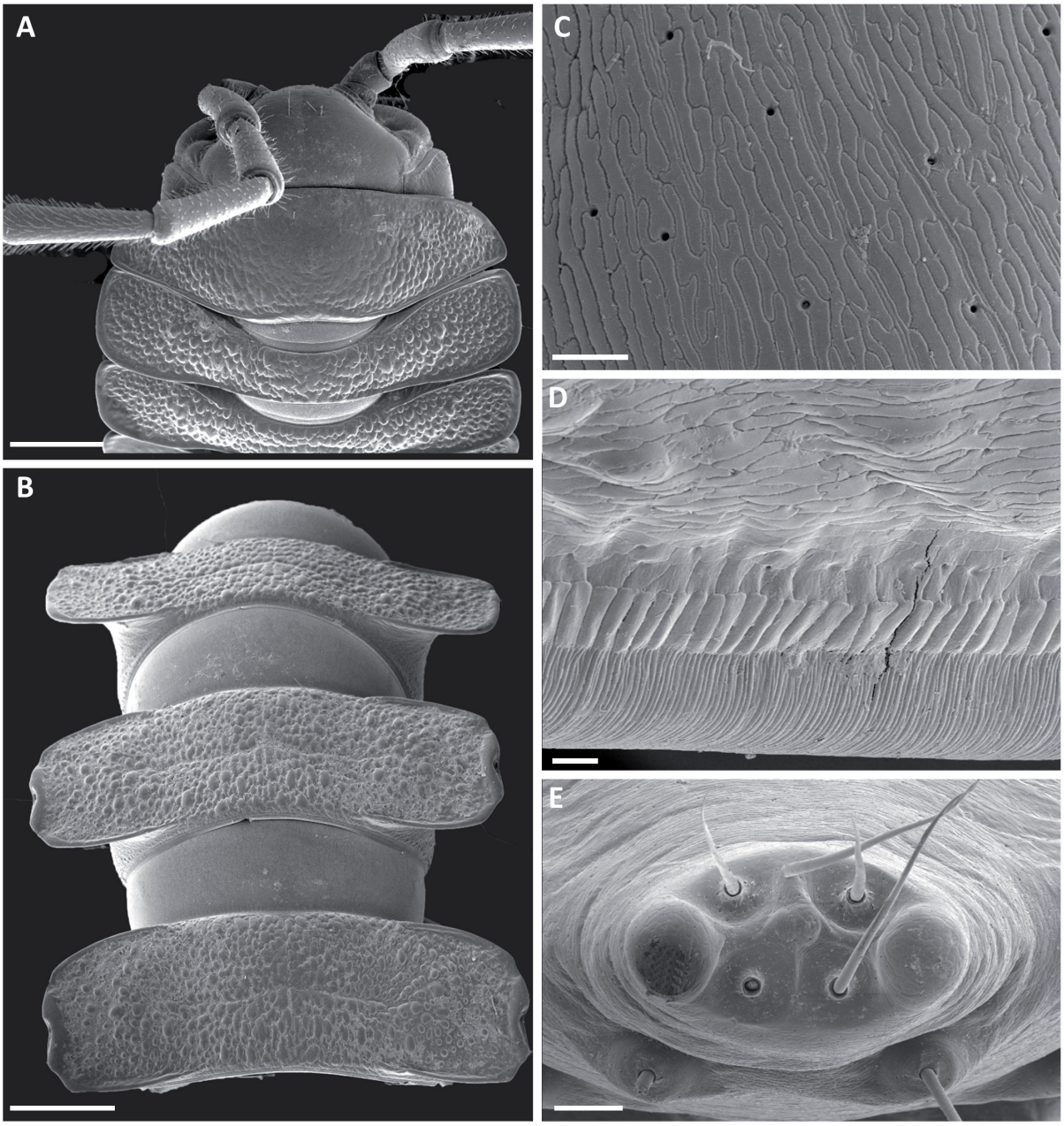

Fig. 13. *Tanzaniella howelli* Hoffman, 1977, male from Udzungwa Mountains National Park (NHMD 1184661). **A**. Head, collum and rings 2–3, dorsal view. **B**. Three midbody rings, dorsal view. **C**. Paranotal microsculpture. **D**. Limbus. **E**. Tip of epiproct, with four spinnerets (one broken and lying loose) and globular swellings, posterior view. Scale bars: A–B = 1 mm; C = 0.05 mm; D = 0.01 mm; E = 0.03 mm.

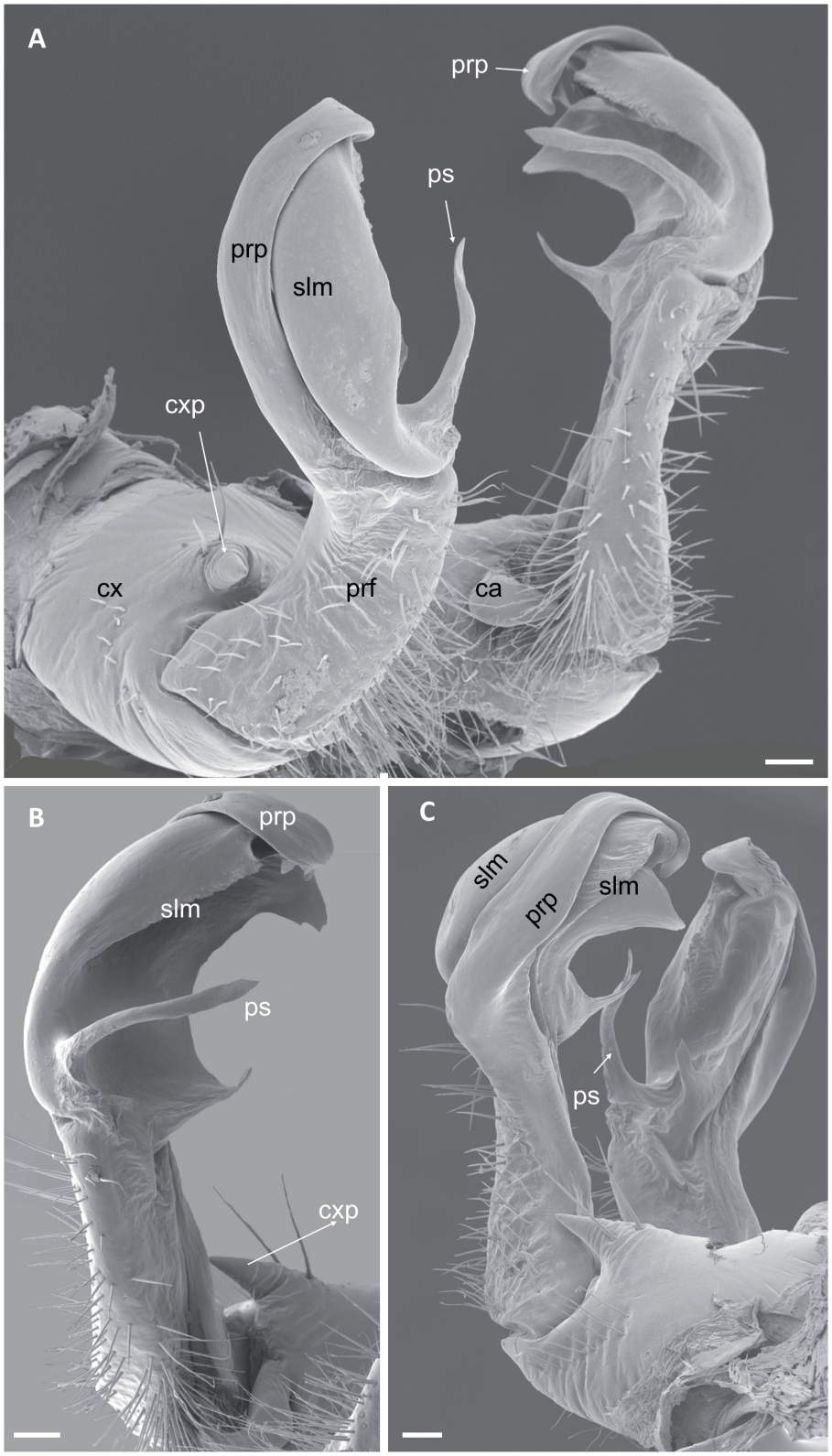

Fig. 14. *Tanzaniella howelli* Hoffman, 1977, male from Udzungwa Mountains National Park (NHMD 1184661), gonopods. **A**. Oblique ventral view. **B**. Right gonopod, mesal view. **C**. Oblique dorsal view. Abbreviations: *ca* = cannula; *cx* = coxa; *cxp* = coxal process; *prf* = prefemoral part; *prp* = prefemoral process; *ps* = parasolenomere; *slm* = solenomere. Scale bars = 0.1 mm.

be abundant (or conspicuous), as two specimens only have been found by Dr Howell over a period of "several years of collecting in the region of Dar es Salaam". See also Discussion below.

Genus ***Dionaeadesmus*** Enghoff gen. nov.
urn:lsid:zoobank.org:act:2F0BBC98-DA48-46A0-80FA-A5C375507E14

Type species

Dionaeadesmus force Enghoff gen. et sp. nov.

Diagnosis

Dionaeadesmus gen. nov. differs from other Tanzanian genera of Chelodesmidae as shown in Table 2, notably by the large spiky postfemoral process (*prp*, Figs 16E–F, 17A–D).

Etymology

Named after the Venus fly-trap *Dionaea muscipula* J.Ellis because the pair of heavily spiked gonopod prefemoral processes may remind of the spike-edged leaves of this carnivorous plant.

Other included species

None.

Dionaeadesmus force Enghoff gen. et sp. nov.
urn:lsid:zoobank.org:act:EDE39835-BCF3-4A30-A5EC-3FF129D9CB29
Figs 1, 2E, 15–17

Diagnosis

Redundant, genus monotypic.

Etymology

Named after the FoRCE project (see Material and methods). Noun in apposition.

Material examined (total 6 ♂♂, 9 ♀♀)

Holotype

TANZANIA • ♂; Iringa Region, Kilolo District, Kilombero Nature Reserve, Ndundulu, Luala; 7°46′00.4″ S, 36°29′33.2″ E; 1903 m a.s.l.; 26 Oct. 2021; A. Ngute, R. Malanda, W. Mhagawale, A. Mpoto and A. Marshall leg.; FoRCE Plot 70, closed canopy, litter sifting; COLL.NHMD – ACC.NO. 2022-EN-003; NHMD 1184575.

Paratypes

TANZANIA • 2 ♂♂, 4 ♀♀; same data as for holotype; Ndundulu, Chawemba; 7°44′54.4″ S, 36°29′02.0″ E; 2256 m a.s.l.; 8 Nov. 2021; FoRCE Plot 81, open canopy; NHMD 1184562 • 1 ♂, 1 ♀; Iringa Region, Mahenge District, West Kilombero Scarp Forest Reserve, Nyumbanitu Mts, S Udekwa Village; 07°48′ S, 36°21′ E; 2300 m a.s.l.; Dec. 1993; J.O. Svendsen leg.; NHMD 1184576 • 2 ♂♂, 4 ♀♀; same data as for preceding; 1700 m a.s.l.; L.L. Sørensen and J.O. Svendsen leg.; NHMD 1184572.

Specimens from Luala are very fragile.

Description (males)

Size. Length 22–25 mm, max. width 4.6 mm.

Colour. Specimens from Luala after 3 years in alcohol completely bleached, whitish. Specimens from Nyumbanitu Mts (Fig. 2E) after 31 years in alcohol: head and dorsum medium brown, lateral lobes of collum narrowly whitish, paranota of rings 2–3 and of poriferous rings broadly whitish, paranota of non-poriferous rings same colour as rest of ring; antennae, venter, legs and telson light brownish.

Head (Fig. 15A–B). Labrogenal offset distinct, otherwise as *Morogorius*. Antennae reaching back to ring 5 when stretched.

Collum (Fig. 15B). As in *Morogorius*: an isosceles curved trapezoid with the longer margin anteriorly, lateral corners smoothly rounded, surface granular, especially laterally. Two setae close to anterior margin.

Body rings (Fig. 15C–E). Prozonites smooth, with simple, cellular microsculpture. Metazonites flat, granular dorsally and laterally, ~1.4 × as broad as prozonites, apparently without setae, with a prominent transverse sulcus on rings 5–17. Paranota horizontal, those of rings 2–3 slightly projecting forwards, rectangular until ring 12–14, thereafter posterior corners projecting increasingly backwards, triangular. Paranotal microsculpture (Fig. 16C) formed by cytoscutes of irregular shape, narrow or amoeba-like branched. Ozopore formula normal (5, 7, 9–10, 12–3, 15–19), ozopores circular, delimited by smooth ring in smooth peritremata on edge of paranota, ca midway between anterior and posterior margin; peritremata protruding from lateral margin of paranota. Sterna broad, with a transverse impression interrupted in the middle and extensive setation along anterior and posterior margins. Sides of body rings (Fig. 15D) with a row of small tubercles along posterior margin. Limbus (Fig. 16D) with straight margin, consisting of a row of rectangular cells with a dense fringe of threadlike ridges ending in free processes.

Legs (Fig. 15G). Rather stout, without modifications, length ~1.3 × maximum body width, length not increasing towards hind end, relative (percentual) length of podomeres (coxa-claw): 8 / 14 / 23 / 14 / 14 / 24 / 2.

Telson (Fig. 16A–B). Preanal ring with several setae along dorsal part of posterior margin; epiproct large, with prominent lateral setiferous tubercles; spinnerets arranged in a trapezoid on a smooth terminal swelling, simple, flanked by 1+1 globular, swellings. Anal valves (paraprocts) unmodified, each with 2 setae, dorsalmost seta on marginal rim, ventralmost seta more lateral, Subanal scale (hypoproct) semicircular, unmodified, with 1+1 marginal setae.

Gonapophyses. Unconspicuous.

Gonopod aperture. Transversely oval, more than twice as broad as long, rim simple.

Gonopods (Figs 16E–F, 17). No sternal remnant. Coxa (*cx*) cylindrical, length slightly > diameter, with a strong conical process (*cxp*) distally on the anterior side; two long setae (as) on anterior surface basal to process, a few setae on lateral surface, and a field of ~15–20 setae on meso-posterior surface. Cannula (*ca*) stout. Prefemoral part (*prf*) continuing in same axis as *cx*, conical, short, length > 1½ × basal diameter, with numerous long setae on ventral and mesal surfaces and a small tooth (*prt*) disto-mesally. Efferent canal running on meso-dorsal side of *prf*, at level of prefemoral tooth (*prt*) bending laterad into solenomere. A huge prefemoral process (*prp*) originating dorso-laterally from *prf*, together with solenomere (*slm*) forming right angles with main body of *prf*, longer than solenomere (*slm*) and accommodating *slm* in mesal concavity; overall shape of *prp* like a twisted spoon with a stout shaft, apically bending mesad over tip of *slm* and ending in a point; dorsal margin of *prp* with numerous (~20) spikelike processes (*msp*); mesal surface with a spiked ridge (*spr*) and additional scattered spikes. Solenomere (*slm*) in the shape of a ribbon with rolled-in edges, apically dividing into a slender, pointed,

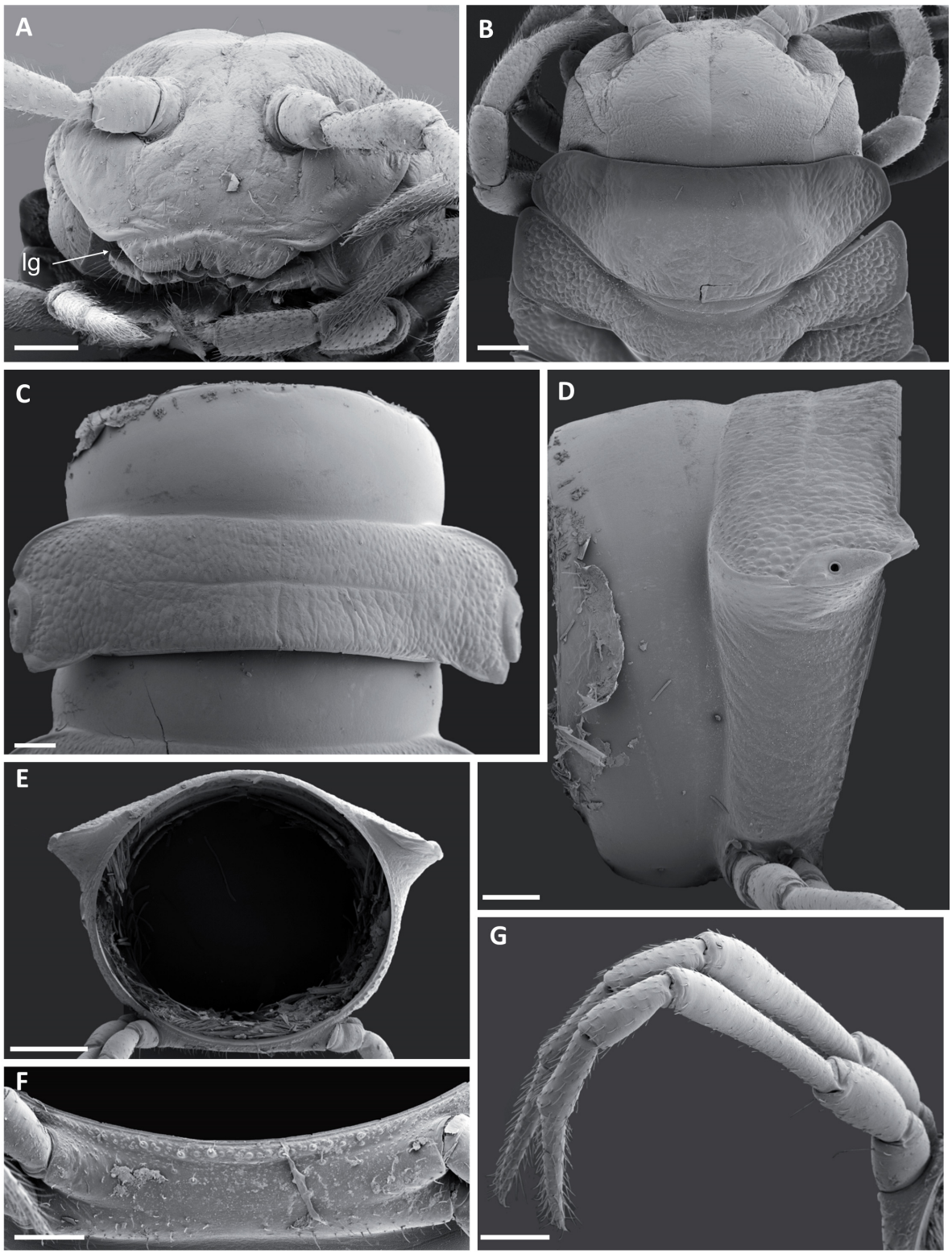

Fig. 15. *Dionaeadesmus force* Enghoff gen. et sp. nov. **A–B**. Paratype, ♂ from Ndundulu (NHMD 1184562). **C–G**. Paratype, ♂ from Nyumbanito Mts (NHMD 1184572). **A**. Head, anterior view. **B**. Head, collum and ring 2, dorsal view. **C**. Ring 13, dorsal view. **D**. Ring 13, lateral view. **E**. Ring 12, posterior view. **F**. Sternum of ring 12. **G**. Legs from ring 12. Abbreviation: *lg* = labrogenal offset. Scale bars = A–D, F–G = 0.4 mm; E = 1 mm.

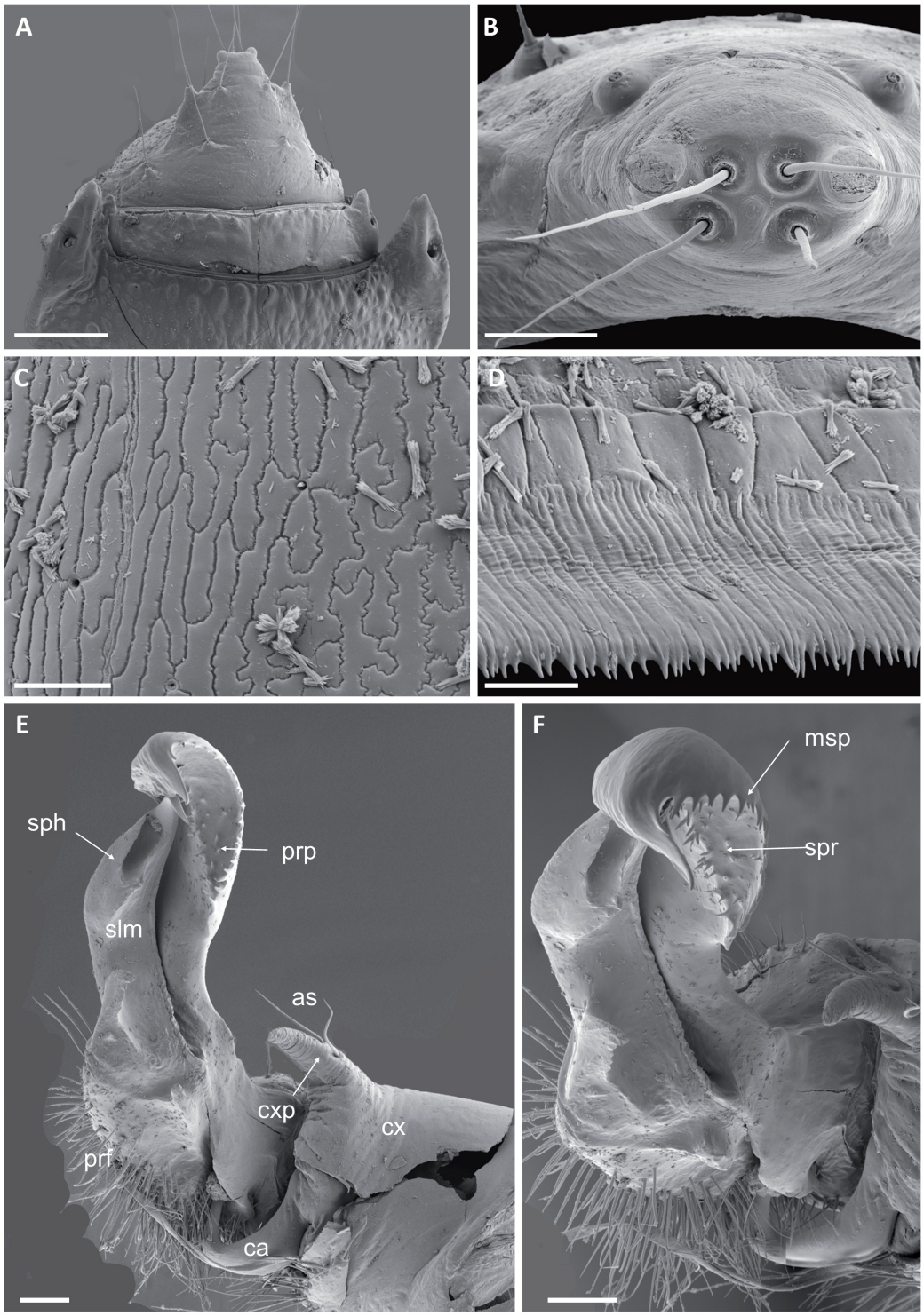

Fig. 16. *Dionaeadesmus force* Enghoff gen. et sp. nov. **A, E–F**. Paratype, ♂ from Ndundulu (NHMD 1184562). **B–D**. Paratype, ♂ from Nyumbanito Mts (NHMD 1184572). **A**. Rings 18–19 and telson, dorsal view. **B**. Tip of epiproct, with four spinnerets and globular swellings, posterior view. **C**. Paranotal microsculpture. **D**. Limbus. **E**. Right gonopod, submesal view. **F**. Right gonopod, anterio-mesal view. Abbreviations: *as* = anterior coxal setae; *ca* = cannula; *cx* = coxa; *cxp* = coxal process; *msp* = marginal spikes; *prf* = prefemoral part; *prp* = prefemoral process; *slm* = solenomere; *sph* = solenophore(?); *spr* = spiked ridge. Scale bars: A = 0.4 mm; B, E–F = 0.1 mm; C–D = 0.01 mm.

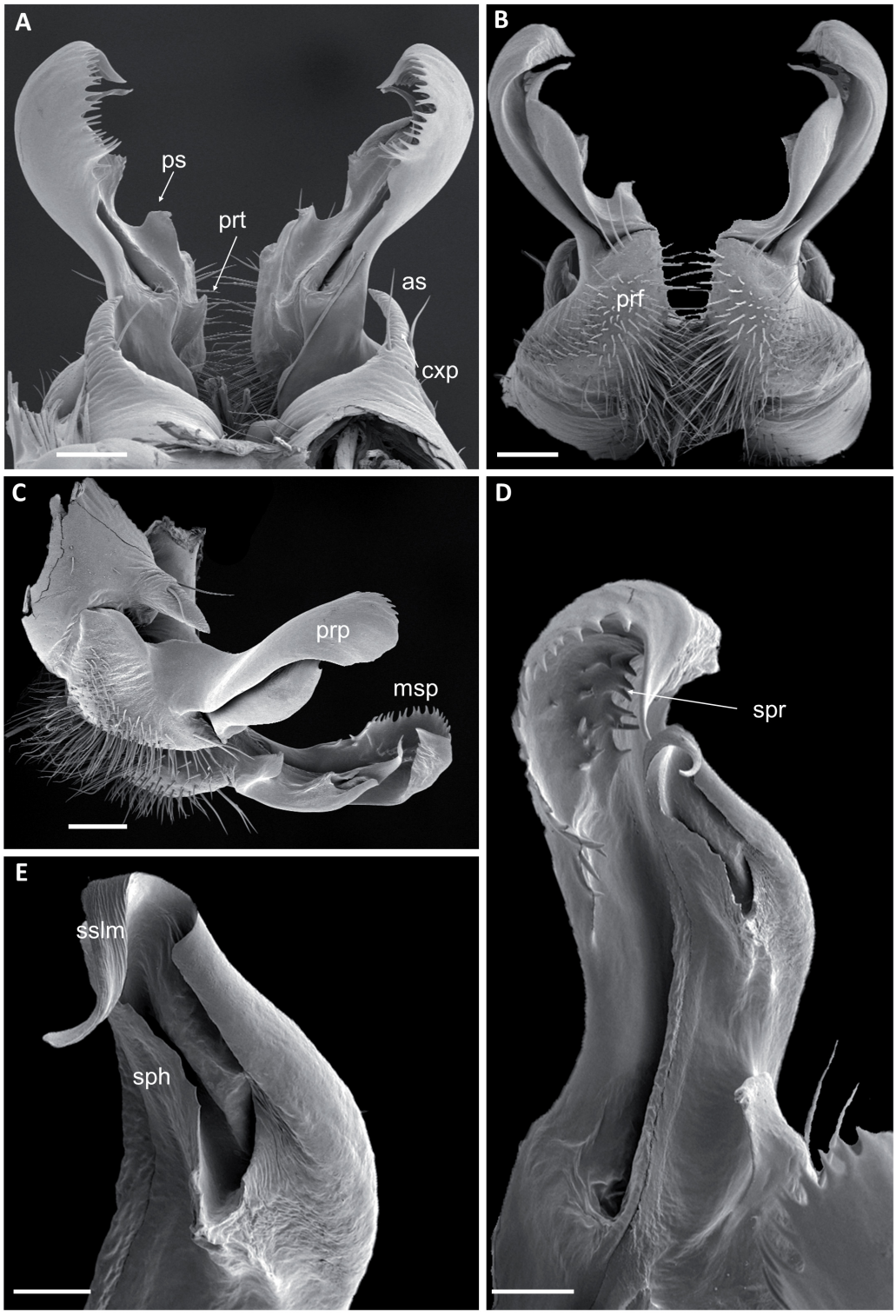

Fig. 17. *Dionaeadesmus force* Enghoff gen. et sp. nov., paratype, ♂ from Nyumbanito Mts (NHMD 1184572), gonopods. **A**. Dorsal view. **B**. Ventral view. **C**. Sublateral (right) view. **D**. Left telopodite. **E**. Left solenomere. Abbreviations: *as* = anterior coxal setae; *cxp* = coxal process; *msp* = marginal spikes; *prf* = prefemoral part; *prp* = prefemoral process; *prt* = prefemoral tooth; *ps* = parasolenomere; *sph* = solenophore(?); *spr* = spiked ridge; *sslm* = solenomere s. str. Scale bars: A–C = 0.2 mm; D = 0.1 mm; E = 0.05 mm.

curved, ridged branch (the solenomere s. str., *sslm*) and a broader, simple, pointed branch which may be regarded as a solenophore (*sph*). A small rectangular process near the base of *slm* may be regarded as a parasolenomere (*ps*).

Distribution and habitat

Only known from two sites in the Udzungwa Mountains: Nyumbanitu Mountains and Ndundulu Forest (Fig. 1). Collected at 1700–2300 m a.s.l.

Remarks

A structure similar to the complicated prefemoral process (*prp*) of *Dionaeadesmus force* gen. et sp. nov. occurs in *Prepodesmus laciniosus* (Attems, 1937), of uncertain generic affiliation (Demange & Mauriès 1975) from Congo. This species, however, differs markedly from *D. force* in having a very short, simple, pointed solenomere (Attems 1937: "Rinnenast") and a two-branched solenophore (Attems 1937: "Tibiotarsus"), and the two taxa are probably not closely related. See also Chamberlin (1952) (as *Morphotelus l.*).

Genus ***Callistocilla*** Hoffman, 1977

Callistocilla Hoffman, 1977: 70. Type species *Callistocilla beatrix* Hoffman, 1977, by original designation.

Type species

Callistocilla beatrix Hoffman, 1977. KENYA, Tiwi S of Mombasa.

Other included species

Callistocilla cingulata Hoffman, 2005. TANZANIA. East Usambara Mts.
Callistocilla dolorotrix Hoffman, 2005. TANZANIA. Udzungwa Mts.
Callistocilla cf. *dolorotrix.* TANZANIA. Pugu Forest Reserve.

Remarks

Hoffman (1977: 71) wrote "This genus is based upon one of the most disjunct and interesting chelodesmoids so far known to me" and "Actually, had the specimen been labelled with a Brasilian locality I should have experienced less difficulty in reconciling it with existing group". These words, coming from the all-time number one authority on the huge family Chelodesmidae, testify to the isolated position of *Callistocilla*. As in so many other millipede groups, a phylogenetic analysis including molecular data is loudly called for. Here, the genus as such will not be discussed further, but notes on the Udzungwan species *C. dolorotrix* are given. The gonopod terminology of Hoffman (2005) will be employed.

Callistocilla dolorotrix Hoffman, 2005
Figs 1, 2F, 18–19, 20A–B

Callistocilla dolorotrix Hoffman, 2005: 52

Diagnosis

Differing from congeners by the presence of ozopores on body rings 5, 7, 9–10, 12–13 and 15–19, i.e., the by far commonest 'pore formula' in Polydesmida (vs ozopores absent in congeners), as well as by the spatulate shape of the gonopodal prefemoral process and the reflexed distal part of the parasolenomere (vs prefemoral process differently shaped and parasolenomere not reflexed in congeners).

Material examined (total 12 ♂♂, 9 ♀♀, 2 juv.)

TANZANIA – **Morogoro Region, Kilombero District, Udzungwa Mountains National Park** • 1 ♀; Njokamoni; 7°50′31.9″ S, 36°52′471″ E; 401 m a.s.l.; 21 Dec. 2021; A. Ngute, R. Malanda, W. Mhagawale and A. Marshall leg.; FoRCE Plot 11, closed canopy; COLL.NHMD - ACC.NO. 2022-EN-003; NHMD 1184735 • 1 ♂, 1 ♀; Sanje; 7°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 and A. Marshall leg.; FoRCE Plot 24, open canopy; COLL.NHMD - ACC.NO. 2022-EN-003; NHMD 1184736 • 3 ♂♂, 1 ♀; same data as for preceding; 7°46′47.6″ S, 36°54′07.6″ E; 495 m a.s.l.; 23 Feb. 2022; FoRCE Plot 25, open canopy; NHMD 1184737 • 2 ♀♀; same data as for preceding; 7°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 and A. Marshall leg.; FoRCE Plot 92, open canopy; NHMD 1184738 • 2 ♂♂, 1 ♀, 1 juv.; same data as for preceding; Sanje; 7°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 and A. Marshall leg.; FoRCE plot 93, open canopy; NHMD 1184739 • 1 subad. ♀; 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; COLL. NHMD. ACC.NO. 2020-EN-002; NHMD 1184740. – **Iringa Region, Kilolo District, Udzungwa Scarp Nature Reserve** • 2 ♂♂; Uhafiwa; 8°31′58.4″ S, 35°51′28.4″ E; 1375 m a.s.l.; 25 Jan. 2022; A. Ngute, R. Malanda, W. Mhagawale, H. Mnendendo, A. Mpoto and A. Marshall leg.; FoRCE Plot 106, open canopy; COLL.NHMD - ACC.NO. 2022-EN-003; NHMD 1184741 • 3 ♂♂, 3 ♀♀; Chita Juu; 8°32′23.4″ S, 35°51′36.0″ E; 1387 m a.s.l.; 1 Feb. 2022; A. Ngute, R. Malanda, W. Mhagawale, H. Mnendendo, A. Mpoto and A. Marshall leg.; FoRCE Plot 109, open canopy, COLL.NHMD - ACC. NO. 2022-EN-003; NHMD 1184742 • 1 ♂; 11 km SE of Masisiwe, Kihanga Stream, 8°22′5.7″ S, 35°58′41.6″ E, 1800 m a.s.l.; 17–27 May 1997; E. Milungu leg.; understorey, NHMD 1184743.

Distribution and habitat

Known from two sites in the Udzungwa Mountains National Park (Fig. 1) – collected at 325–504 m a.s.l., and three sites in the Udzungwa Scarp Nature Reserve – collected at 1373–1800 m a.s.l.

Remarks

The examined specimens agree with the description by Hoffman (2005). However, there are a few differences between specimens from Udzungwa Mountains National Park (topotypes and near topotypes) and specimens from Udzungwa Scarp Nature Reserve, see Table 3 and Figs 18–20). The specimens from the latter place were collected at much higher altitudes than those from the former.

The microsculpture of the paranota (Fig. 18E) is remarkable: the cuticular microscutes ("cytoscutes") are rounded-hexagonal, ca 0.01 mm in diameter, and densely beset with tiny denticles, not only along one edge, as is very common in myriapods, but all over the surface; 74–83 denticles on each of the three central scutes on Fig. 18E. Similar microsculpture was also seen in *C. beatrix* Hoffman, 1977 (Fig. 20F) and in an undescribed congener from Kanga Montauns (Fig. 20E). See Discussion.

The spinnerets were not described by Hoffman (2005). The four simple, setiform sensilla are placed in a quadrat at the tip of the epiproct. On Fig. 18C there is what looks somewhat, but not quite like the socket of a fifth spinneret; this structure was seen only on one of two specimens studied with scanning electron microscopy and may be insignificant. Unlike the other Udzungwa chelodesmids, *C. dolorotrix* has no globular swelling lateral to the spinnerets.

The gonopods (Figs 19, 20B) fully agree with Hoffman's description and drawings. In males from Udzungwa Mountains National Park, the proximal edge of the solenomere is flexed at right angles with main plane of the solenomere (Fig. 20B).

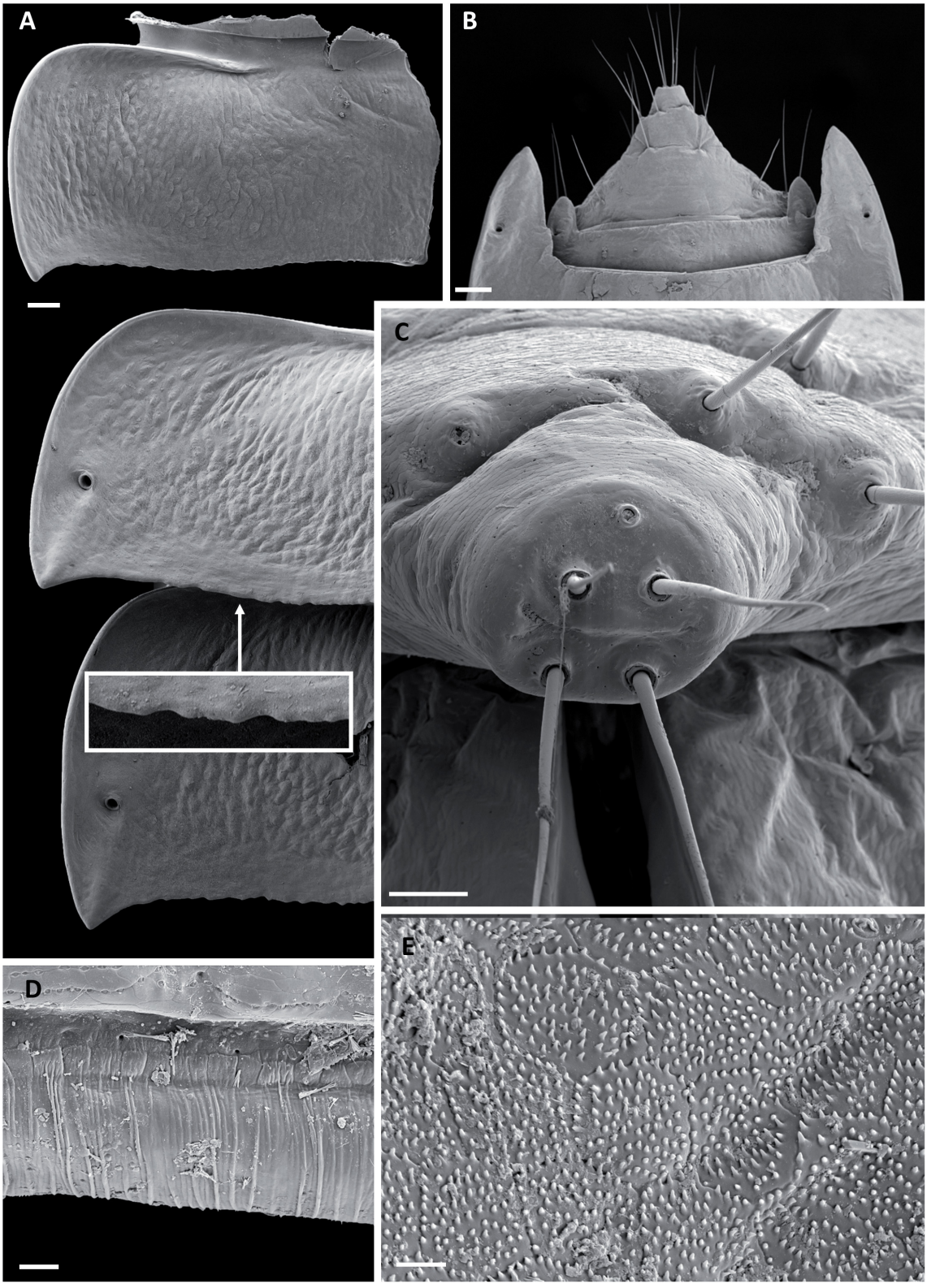

Fig. 18. *Callistocilla dolorotrix* Hoffman, 2005, male from Udzungwa Scarp Nature Reserve (NHMD 1184742). **A**. Rings 11–13, dorsal view; inset: close-up of crenulation. **B**. Telson and rings 18–19, dorsal view. **C**. Epiproct and spinnerets, posterior view. **D**. Limbus from ring 11. **E**. Microsculpture of paranotum 11. Scale bars: A–B = 0.2 mm; C = 0.05 mm; D = 0.01 mm; E = 0.005 mm.

Fig. 19. *Callistocilla dolorotrix* Hoffman, 2005, male from Udzungwa Scarp Nature Reserve (NHMD 1184742), right gonopod. **A**. Lateral view. **B**. Mesal view. **C**. Dorsal view. **D**. Ventral view. **E**. Solenomere and process of parasolenomeree. Abbreviations: *cx* = coxa; *prp* = prefemoral process; *ps* = parasolenomere; *slm* = solenomere. Scale bars: A–C = 0.2 mm; D–E = 0.1 mm.

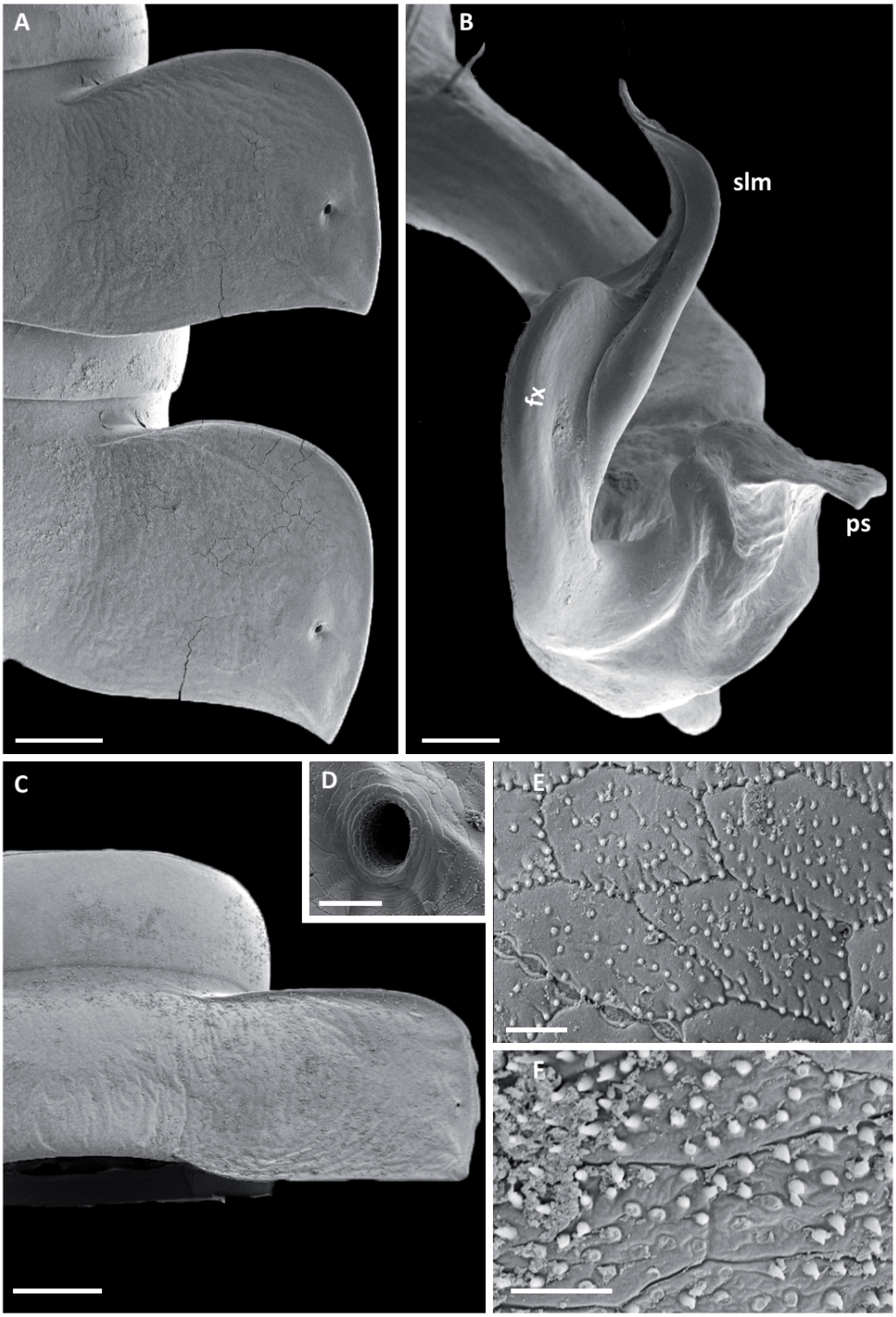

Fig. 20. *Callistocilla* spp. **A–B**. *C. dolorotrix* Hoffman, 2005, male from Udzungwa Mountains National Park (NHMD 1184737). **A**. Rings 12–13, right paranota. **B**. Right gonopod, apical part. **C–E**. *Callistocilla* sp. 1, male from Kanga Mountains (NHMD 1184571), ring 12. **C**. Dorsal view. **D**. Right ozopore. **E**. Microsculpture of paranotum. **F**. *C. beatrix* Hoffman, 1977, holotype, ♂ (ZMUC 00101515), microsculpture of paranotum 13. Abbreviations: *fx* = flexed edge of solenomere; *ps* = parasolenomere; *slm* = solenomere. Scale bars: A, C = 0.5 mm; B = 0.05 mm; D = 0.02 mm; E–F = 0.005 mm.

Table 3. Differences between two populations of *Callistocilla dolorotrix* Hoffman, 2005.

	Specimens from Udzungwa Mountains National Park, (near) topotypes	**Specimens from Udzungwa Scarp Nature Reserve**
Width across metazonite 10	Males: 4.8–5.5 mm Females: 5.0–5.8 mm	Males: 5.6–7.8 mm Females: 5.7–6.6 mm
Posterior margin of paraterga	Not at all crenulate (Fig. 20A, C)	Faintly crenulate from ring 7–12 (ring 7 in very large male only) (Fig. 18A)
Solenomere	Proximal edge of solenomere flexed at right angles with main plane of the solenomere (Fig. 20B)	Proximal edge of solenomere not flexed (Fig. 19D–E)

Callistocilla beatrix Hoffman, 1977
Fig. 20F

Callistocilla beatrix Hoffman, 1977: 73

Material examined (total 1 ♂)

Holotype
KENYA • ♂; Tiwi S of Mombasa; 18 May 1968; Schiøtz leg.; ZMUC 00101515.

Remarks

A small piece of one body ring was removed from the unique holotype and mounted for SEM. The paranotal microsculpture (Fig. 20F) is similar to that seeen in *C. dolotrotrix* (Fig. 18E)

Callistocilla sp. 1
Fig. 20C–E

Material examined (total 1 ♂, 2 ♀♀)

TANZANIA • 1 ♂, 2 ♀♀; Morogoro Region, Kanga Mts, Kanga Forest Reserve; 400–500 m a.s.l.; 22–25 Nov. 1984; N. Scharff leg.; lowland rain forest; NHMD 1184571.

Remarks

These specimens agree closely with the original description of *C. beatrix* (Hoffman 1977), except for the presence of very small ozopores (Fig. 20C–D) and tiny small gonopod details. This species, too, shares the peculiar paranotal microsculpture seen in *C. dolorotrix* and *C. beatrix* (Fig. 20E).

Identification of Chelodesmidae from the Udzungwa Mountains

As mentioned in the introduction, no useful diagnosis of the family Chelodesmidae is available. For identification of chelodesmids from the Udzungwa Mts it is therefore necessary to single out differences between this family and each other polydesmidan family occurring in the Udzungwas. Table 4 provides this information.

Table 4. Differences between Udzungwa species of Chelodesmidae Cook, 1895 and species of other polydesmidan families known from the Udzungwa Mts.

Family	Occurrence in the Udzungwa Mts	Differences from Chelodesmidae	vs condition in Chelodesmidae
Oxydesmidae	Several species, unrevised	Body length often > 30 mm, often with strong dorsal sculpture, always with a row or field of "parantennal setae" just dorsomesal to each antennal socket (Hoffman 1990: figs 2–7)	Body length 21–31 mm, no strong dorsal sculpture, never with a row or fields of "parantennal setae" (e.g., Figs 3A, 15A)
Gomphodesmidae	Several species (Olsen *et al.* 2020)	Body length often > 30 mm, body rings strongly vaulted, smooth and glabrous, metazonites without transverse sulcus (e.g., Olsen *et al* 2020: fig. 1)	Body length 21–31 mm, body rings not strongly vaulted, metazonites not glabrous, often with a transverse sulcus (e.g., Figs 3E, 7A, 10A, 13B, 15C)
Paradoxosomatidae	Many genera and species, only one genus revised (Enghoff 2018)	Very variable; the two setae of the anal valve placed at same distance from rim	Dorsal seta of anal valve placed on rim, ventral seta placed at some distance from rim (Fig. 4A)
Trichopolydesmidae	Several species, unrevised	Body length < 10 mm, delicate, smooth body	Body length 21–31 mm
Cryptodesmidae	One species (Enghoff 2022)	Body length < 15 mm, body rings with strong sculpture, covered in dark secretion (Enghoff 2022: fig. 12)	Body length 21–31 mm, no strong sculpture, no cover of dark secretion
Pyrgodesmidae	Three species (probably more) (Enghoff 2022)	Body length < 15 mm, body rings with strong sculpture (e.g., Enghoff 2022: fig. 1)	Body length 21–31 mm, no strong sculpture
Ammodesmidae	a few unrevised species	body length < 10 mm, body capable of rolling up into a sphere	body length 21–31 mm, body not rollable

Key to Chelodesmidae from the Udzungwa Mountains (based on gonopodal characters)

1. Prefemoral process (*prp*) not in contact with solenomere (Fig. 19); coxa (*cx*) without a conical process distally on anterior side ..... ***Callistocilla dolorotrix*** Hoffman, 2005
– Prefemoral process in close contact with solenomere; coxa usually with a conical process (*cxp*) distally on anterior side 2

2. Prefemoral process (Figs 16–17, *prp*) elaborate, with several rows of strong spikes .... ***Dionaeadesmus force*** Enghoff gen. et sp. nov.
– Prefemoral process not so elaborate, without rows of strong spikes 3

3. Solenomere (*slm*) very broad, much broader than prefemoral process (Fig. 14) .... ***Tanzaniella howelli*** Hoffman, 1977
– Solenomere not much broader than prefemoral process (*Morogorius* spp.) 4

4. Parasolenomere (*ps*) deeply divided into two subequal lobes; coxal process (*cxp*) very poorly developed (Figs 5–6) ..... ***Morogorius divisus*** Enghoff sp. nov.
– Parasolenomere not divided into subequal lobes 5

5. Parasolenomere (*ps*) slender, straight, pointed with a tiny needlelike side branch (*nb*) (Fig. 9) .... ***Morogorius pugio*** Enghoff sp. nov.
– Parasolenomere different 6

6. Parasolenomere (*ps*) short, stout (Figs 11–12) 7
– Parasolenomere (*ps*) larger, consisting of a broad basal part and a tapering apical part (Fig. 8) .... ***Morogorius louishanseni*** Enghoff sp. nov.

7. Parasolenomere (*ps*) rounded, with a basal retrorse process; prefemoral process very broad, almost circular (Fig. 12) ..... ***Morogorius cochlear*** Enghoff sp. nov.
– Parasolenomere (*ps*) pointed; prefemoral process not so broad (Fig. 11) .... ***Morogorius kitungulu*** Enghoff sp. nov.

Discussion

The present study reaffirms the richness of the Udzungwa millipede fauna. Since the beginning of the "A mountain of millipedes" series (Enghoff 2014), 83 species have been added to the previous, very short list of Udzungwa millipedes; 74 of these have been described as new, and several additional species from several families still await description. During the study of Udzungwa chelodesmids, some observations of a more general interest have been made, and the present contribution is no exception:

Paranotal microsculpture

After use of SEM has become common in studies of millipedes, surface microsculpture has proven to show an astounding multitude of characters (e.g., Mesibov 2009; Akkari & Enghoff 2011; Enghoff *et al.* 2024).

The microsculpture of the paranota of species of *Callistocilla*, with the entire surface of each microscute covered with numerous denticles, is remarkable and seems to be unique among Diplopoda. The microscutes of the arthropodan cuticle, which are regarded each to have been secreted by an epidermal cell (Fusco *et al.* 2000), are most often of hexagonal shape and in myriapods frequently have a row of denticles along one edge (e.g., Fusco *et al.* 2000: fig. 7; Reboleira & Enghoff 2015: fig. 3c; Enghoff & Larsson 2018: fig. 3c); similar patterns also occur in some Crustacea Brünnich, 1773 (Seidl *et al.* 2021: figs 1f, 2e). However, an extensive cover of denticles like that in *Callistocilla* has to our knowledge not been described from any other arthropod. In the other chelodesmids described in the present paper, the paranotal microsculpture is completely different, with the microscutes being strongly elongated in a longitudinal direction (Figs 10D, 13C, 16). More species of Chelodesmidae and related families obviously need to be studied with SEM in order to map the distribution of these characters and their potential phylogenetic significance.

Globular structures flanking spinnerets

Species of *Morogorius*, *Tanzaniella* and *Dionaeadesmus* gen. nov. share an unusual character: a pair of globular swellings flanking the group of four spinnerets on the telson (Figs 4B, 10E, 13E, 16B). *Callistocilla dolorotrix* does not have these swelling, but they were also seen in the West African species *Prepodesmus tigrinus* Cook, 1896 (pers. obs.). On the other hand, swellings are absent in the deviating European chelodesmid *Cantabrodesmus lorioli* Mauriès, 1971 (Gilgado *et al.* 2020: fig. 5f), in the Neotropical *Chelodesmus* sp. (= *Eurydesmus* sp.) (Shear 2008: fig. 18), and in the Brazilian *Tupadesmus muyrakata* Bouzan *et al.*, 2024 (Bouzan *et al.* 2024: fig. 2f). They also seem to be absent in *Leiodesmus carcani* Silvestri, 1902 according to the drawings by Silvestri (1903: fig. 201). On the other hand, swellings identical to those seen in *Morogorius*, *Tanzaniella* and *Dionaeadesmus* were illustrated for the xystodesmid *Gyalostethus monticolens* (Chamberlin, 1951) by Shear (2008: fig. 22) who

referred to them as "knoblike extensions of the epiproct". In this connection it is interesting that in the phylogenetic analysis of Benavides *et al.* (2023) one of the two included chelodesmids (*Chondrodesmus cairoensis* Loomis, 1972, misspelled as *Chondromorpha c.*) forms a clade with three xystodesmids and a sphaeriodesmid. More species of Chelodesmidae and related families obviously need to be studied with SEM in order to map the distribution of this character and its potential phylogenetic significance.

Coxal gonopodal process

In *Morogorius* (except *M. divisus* sp. nov.), *Tanzaniella* and *Dionaeadesmus* gen. nov., the gonopod coxa carries a conical coxal process (*cxp*) distally on the anterior side (Hoffman 1977: "on the dorsal side with an acute conical apophysis"). Hoffman (1977: 76) continues: "a development which occurs in relatively few prepodesmids, chiefly in the southernmost part of the family range". I have been able to verify the presence of a disto-anterior coxal apophysis in the genera *Anisodesmus* Cook, 1895 (Kraus 1958a: figs 20–21) and *Pimodesmus* Chamberlin, 1927 (Kraus 1958b: fig. 17). Whether such a process has arisen once or more times remains an open question – the presence of a somewhat similar process in some Neotropical genera, including *Atlantodesmus* Hoffman, 2000 (Hoffman 2000: fig. 7) and *Odontopeltis* Pocock, 1894 (Pena-Barbosa *et al.* 2013: fig. 67) supports the idea of multiple origins.

Altitudinal distribution

The Udzungwan chelodesmids show different altitudinal preferences: *Morogorius* spp. are restricted to 1300–1500 m a.s.l., *Dionaeadesmus force* Enghoff gen. et sp. nov. to even higher altitudes: 1700–2300 m a.s.l. In contrast, *Tanzaniella howelli* occurs at low altitudes: 267–504 m a.s.l., with a single 'highjumper' at 850 m a.s.l. Interestingly, the two populations of *Callistocilla dolorotrix* (which also show slight morphological differences, see Table 3) differ in altitudinal preference: in Udzungwa Mountains National Park, *C. dolorotrix* is a lowland species: 325–504 m a.s.l., whereas in Udzungwa Scarp Nature Reserve it lives at 1375–1800 m a.s.l.

A recent arrival?

Tanzaniella howelli is the only Udzungwan chelodesmid which is also known from elsewhere (Kisarawe near Das es Salaam), and although it is a lowland species and is abundant in the FoRCE material, it is absent from older collections from the Uzungwas. In these respects it reminds of the two spirostreptids *Attemsostreptus reflexus* Akkari & Enghoff, 2019, and *Lophosteptus tersus* (Cook, 1896) (Enghoff *et al.* 2024), and one may suspect that like these species, *T. howelli* is a recent, human-aided immigrant to the Udzungwa Mountains.

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