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A mountain of millipedes VI. New records, new species, a new genus and a general discussion of Odontopygidae from the Udzungwa Mts, Tanzania (Diplopoda, Spirostreptida, Odontopygidae)

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Abstract. *Damacornu* gen. nov. (type species: *D. transversum* gen. et sp. nov.), *Geotypodon papei* sp. nov. and *Spinotarsus fortehamatus* sp. nov. are described, and *Helicochetus dimidiatus* (Peters, 1855), *H. mutaba* Kraus, 1960 and *Hoffmanides dissutus* (Hoffman, 1963) are recorded from the Udzungwa Mts, Tanzania. A complete overview of the 39 odontopygid species now known from the Udzungwa Mts is given, including notes on endemism, biogeographical relationships and altitudinal distribution patterns.

Keywords. Eastern Arc, taxonomy, endemism, altitudinal distribution.

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Introduction

The very rich fauna of odontopygid millipedes from the Udzungwa Mts has been the subject of five recent papers (Enghoff 2014, 2016a, 2016b, 2016c; Enghoff & Frederiksen 2015). The present contribution deals with the remaining Udzungwa odontopygids in the very large collections of Tanzanian millipedes in the Natural History Museum of Denmark and the Virginia Museum of Natural History (but see note on the genus *Aquattuor* Frederiksen, 2013). Three new species are described, one of them belonging to a new genus, and three previously described species are recorded for the first time from the Udzungwa Mountains. The collecting sites for the treated species are shown in Fig. 1. A list of the known odontopygid fauna of the Udzungwa Mountains, now comprising 39 species, is included, as well as notes on distribution and endemism.

Material and methods

The material described in this paper derives from the zoological collections of the Natural History Museum of Denmark, University of Copenhagen (ZMUC) and the Virginia Museum of Natural History (VMNH). Methods of study are as in the previous papers in this series, as detailed by Enghoff (2014).

Abbreviations for morphological terms used in the descriptions and on illustrations

<i>ap</i>	= angular process of metaplica
<i>bla</i>	= basal lamella of telomere
<i>bp</i>	= apical basad process of coxa
<i>btl</i>	= basal lamella of telomere
<i>cu</i>	= cucullus
<i>el1, el2</i>	= smooth telomeral lamellae
<i>kn</i>	= knob-like turn of solenomere
<i>ld</i>	= lateral denticle of coxa
<i>mf</i>	= metaplical flange
<i>mlp</i>	= metaplical lamellar process
<i>mmf</i>	= mesal metaplical flange
<i>mp</i>	= metaplica
<i>mr1, mr2</i>	= metaplical ridges
<i>ms</i>	= metaplical shelf
<i>msp</i>	= metaplical spine-like process

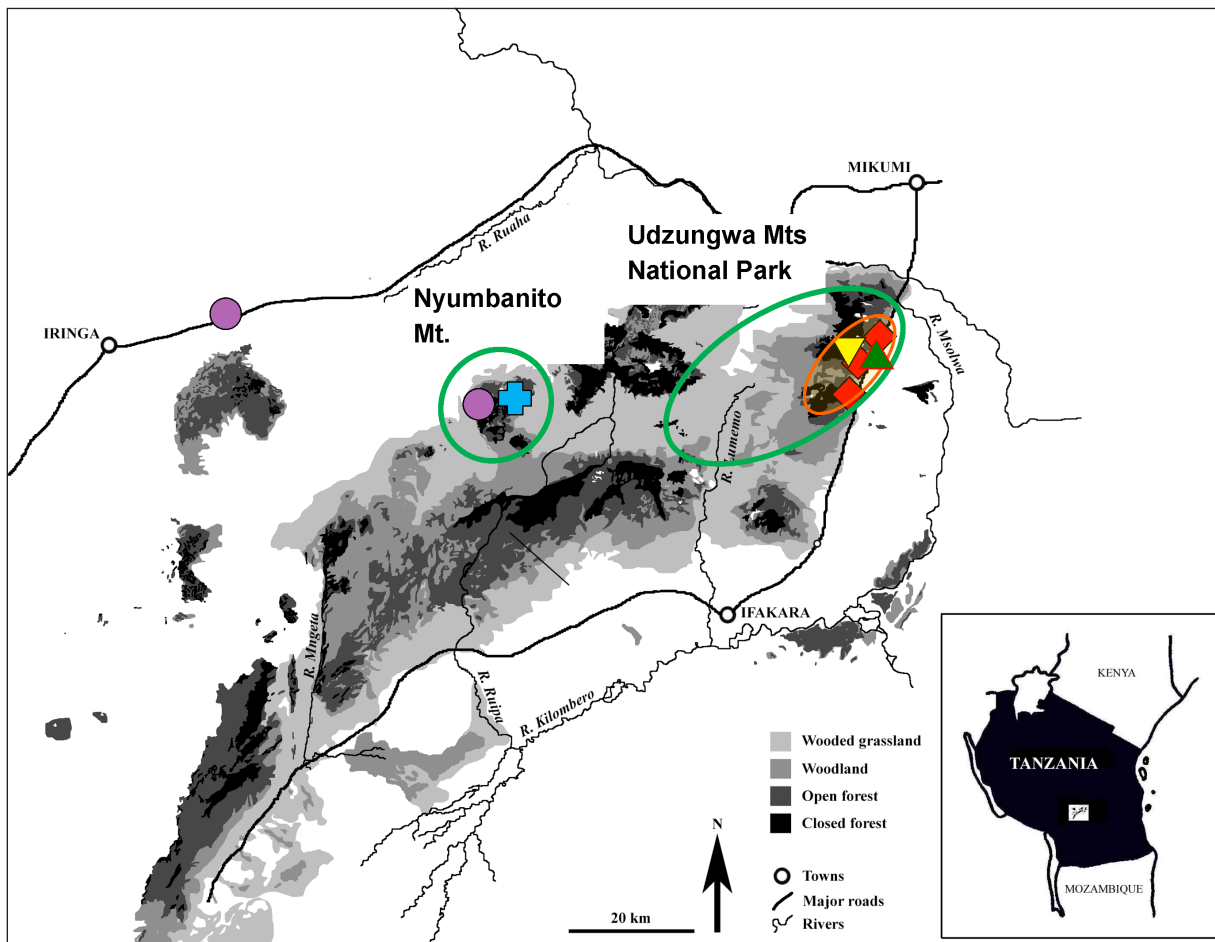


Fig. 1. Map of the Udzungwa Mts, showing the collecting sites for the treated species. Blue cross = *Damacornu transversum* gen. et sp. nov.; red diamonds = *Geotypodon papei* sp. nov.; yellow triangle = *Helicochetus dimidiatus* (Peters, 1855); purple dots = *H. mutaba* Kraus, 1960; orange oval = *Hoffmanides dissutus* (Hoffman, 1963) (approximate location); green triangle = *Spinotarsus fortehamatus* sp. nov. Based on Marshall *et al.* (2010: fig. 1).

pn = post-torsal narrowing
pp = proplica
ppl = proplical lobe
ps = proximal solenomeral spine
pst = proximal spine of telomere
pts = post-torsal spine
rhp = rhomboidal plate
shl = shovel-like flange
slm = solenomere
sp = prostatic stylet
ssb = spine-like side branch from solenomere
stu = setiferous tubercle
td = telomeral denticles
thp = thumb-like solenomeral process
tlh = hook-shaped telomeral process
tll = telomeral lobe
tlt = telomeral teeth
tm = telomere
tsp = terminal spine of metaplica
tt = torsotope

Other abbreviations used in the text

a.s.l. = above sea-level
KMH = Kim M. Howell collection code
VMNH = Virginia Museum of Natural History
ZMUC = Natural History Museum of Denmark (Zoological Museum)

Taxonomy

Class Diplopoda de Blainville in Gervais, 1844
Order Spirostreptida Brandt, 1833
Family Odontopygidae Attems, 1909
Subfamily Archepyginae Manfredi, 1939
Tribe Prionopetalini Hoffman, 1991

Genus *Aquattuor* Frederiksen, 2013

Aquattuor Frederiksen, 2013: 64.

A considerable new collection of *Aquattuor* spp. from the Udzungwa Mts has recently been acquired by the ZMUC, the treatment of which awaits a renewed study of the genus by Sara Frederiksen.

Genus *Damacornu* gen. nov.
[urn:lsid:zoobank.org:act:6D078904-52C2-43CF-9930-050C487442DA](https://doi.org/10.3897/zoobank.org/act:6D078904-52C2-43CF-9930-050C487442DA)

Type species

Damacornu transversum gen. et sp. nov., by original designation.

Other included species

None.

Diagnosis

A genus of Odontopygidae–Prionopetalini characterized by the following combination of characters: gonopod coxa with a mesal spineless metapical shelf, without a basad metapical spine; telopodital torsotope with a long spine; solenomere whip-like, with a basal spine but otherwise without outgrowths, apically fluted and spiraled; telomere a longitudinally folded lamella; distal half of telomere bent at right angles in relation to basal half, with a row of teeth on internal surface.

Etymology

A composite noun, from *Dama* (fallow deer) and *cornu* (horn, antler), referring to the (slight) resemblance between the gonopod telomere and an antler from the fallow deer, *Dama dama* (Linnaeus, 1758). Gender neuter.

Remarks

In the key to genera of “Odontopyginae” by Kraus (1966), *Damacornu transversum* gen. et sp. nov. keys out to the genus *Odontopyge*, and in the key to species of “*Odontopyge*” by Kraus (1960) it keys out in couplet 11 (“*O.*” *citernii* Silvestri, 1898 and “*O.*” *difficilis* Silvestri, 1895). The new species is, however, clearly different from these two species in which there is no metapical shelf and the proximal solenomeral spine (*ps*) (“Tibialdorn”) is rudimentary. None of the “orphaned” species assigned to *Odontopyge* by earlier authors (see Enghoff 2016a) can be adopted by *Damacornu* gen. nov., which for the time being remains monotypic.

Damacornu transversum gen. et sp. nov.

[urn:lsid:zoobank.org:act:4B0BC420-38E0-492E-85DC-0879E83BCDA7](https://zoobank.org/act:4B0BC420-38E0-492E-85DC-0879E83BCDA7)

Fig. 2

Diagnosis

See generic diagnosis (genus monotypic).

Etymology

The name is a Latin adjective and refers to the transverse yellow markings on the body rings.

Material studied (total: 1 ♂)

Holotype

TANZANIA: ♂, Iringa Region and District, Ndekwa village, Mt Nyumbenito, Udzungwa Mountains, 1400 m a.s.l., 4 Apr. 1982, Jan Kielland leg. (VMNH).

Description

Male

SIZE. Length ? (broken). Body diameter 6.4 mm. 60 podous body rings, no apodous rings in front of telson.

COLOUR. After 35 years in alcohol blackish, anterior part of head and posterior part of metazona amber; a transverse yellow band on prozona extending from midline ca. halfway down to ozopores; legs yellow.

HEAD. Without peculiarities. Four supralabral setae.

COLLUM. With a marginal furrow, followed by two abbreviated and one complete submarginal furrow.

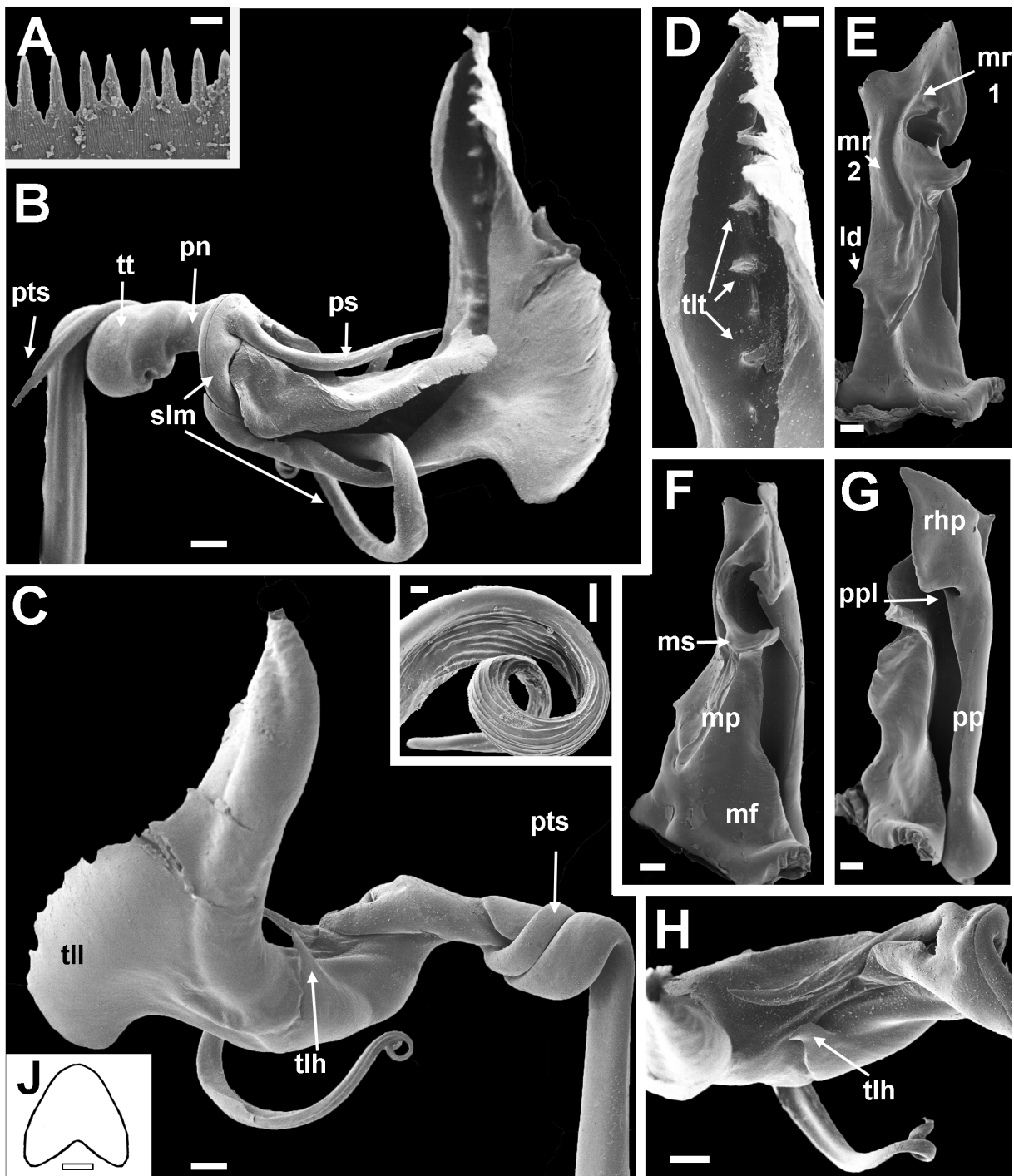


Fig. 2. *Damacornu transversum* gen. et sp. nov., holotype. **A.** Limbus. **B–I.** Right gonopod. **B.** Telopodite, posterior view. **C.** Telopodite, anterior view. **D.** Terminal process of telomer lamella, posterior view. **E.** Coxa, posterior view. **F.** Coxa, mesal view. **G.** Coxa, anterior, slightly mesal view. **H.** Basal part of telomere, ventral view. **I.** Tip of solenomere. **J.** Sternum of rudimentary ninth leg-pair. Abbreviations: *ld* = lateral denticle of coxa; *mf* = metapical flange; *mp* = metaplica; *mr1*, *mr2* = metapical ridges; *ms* = metapical shelf; *pn* = post-torsal narrowing; *pp* = proplica; *ppl* = proplical lobe; *ps* = proximal solenomeral spine; *pts* = post-torsal spine; *rhp* = rhomboidal plate; *slm* = solenomere; *tlh* = hook-shaped telomer process; *tll* = telomer lobe; *tlt* = telomer teeth; *tt* = torsotope. Scale bars: A = 0.01 mm; B–C, E–H = 0.2 mm; D = 0.1 mm; I = 0.02 mm; J = 0.5 mm.

BODY RINGS. Almost perfect cylinders, not vaulted; suture straight; ozopores starting from ring 6, placed ca $\frac{1}{3}$ of metazona length behind suture. 18–22 metazonital striae reaching up to ca one metazonite length below ozopore.

ANAL VALVES. With a well-developed dorsal tooth and a small ventral one; margin barely raised, setiferous tubercles inconspicuous.

LIMBUS (Fig. 2A). Divided into simple, pointed teeth, each tooth > 3 times longer than broad.

MALE LEGS. With adhesive pads on postfemur and tibia.

GONOPOD COXA (Fig. 2E–G). Proplica (*pp*) (Fig. 2G) narrow, parallel-sided, ending in a small proplical lobe (*ppl*), distal to *ppl* continuing as a large, irregularly rhomboidal plate (*rhp*); disto-mesal corner of *rhp* drawn out into blunt triangular process. Metaplica (*mp*) with large metaplica flange (*mf*) covering base of proplica in mesal view (Fig. 2F), with bowl-shaped shelf (*ms*) slightly basal to level of proplical lobe, distal margin of shelf continuing distad as longitudinal ridge (*mr1*); another longitudinal ridge (*mr2*) parallel to *mr1*, close to lateral margin of coxa; a small denticle (*ld*) on lateral margin ca $\frac{1}{3}$ from base (Fig. 2E); lateral surface of coxa concave.

GONOPOD TELOPODITE (Fig. 2B–D, H–I). Arculus 90° . Torsotope (*tt*) simple, compact, with a long spine (*pts*, “Femoraldorn” *sensu* Kraus 1960, “Praefemoraldorn” *sensu* Kraus 1966) (Fig. 2B–C). Post-torsal narrowing (*pn*) pronounced, without processes or spines (Fig. 2B). Telopodite just distal to post-torsal narrowing dividing into slender, whip-like solenomere and lamellate telomere. Solenomere (*slm*) (Fig. 2B) with a long, straight basal spine (*ps*), otherwise without any outgrowths, apically fluted and spiraled (Fig. 2I). Telomere consisting of a single, longitudinally folded lamella. Proximal half of telomere roughly parallel-sided, continuing in same direction as torsotope and post-torsal narrowing; a small hook-shaped process (*tlh*) (Fig. 2C, H) originating from anterior external surface; distal half of telomere set off by 90° angle, posterior margin of distal half first forming large rounded lobe (*tl*) (Fig. 2C), in distal part irregularly serrate; a row of coarse teeth (*tlt*) on internal surface of terminal process of telomeral lamella (Fig. 2D).

STERNUM OF RUDIMENTARY NINTH LEG-PAIR (Fig. 2J). Heart-shaped.

Female

Unknown.

Distribution

Known only from Mt. Nyambanito (Nyumbenito), 1400 m a.s.l.

Genus *Geotypodon* Enghoff, 2016

Geotypodon Enghoff, 2016a: 6.

Type species

Geotypodon millemanus Enghoff, 2016, by original designation.

Other included species

Geotypodon papei sp. nov. and 20 further species, see Enghoff (2016a).

Diagnosis

(From Enghoff 2016a, slightly modified.) A genus of Odontopygidae–Prionopetalini characterized by: a long basad metaplical spine on the anterior side of the coxa; a compact torsotope; lack of pretorsal or

torsal spines/processes; a pronounced post-torsal narrowing without spines; a division of the telopodite into solenomere and telomere immediately distal to post-torsal narrowing; a spine emerging from the base of the telomere; a slender, whip-like, smooth solenomere without any outgrowths or appendages (except sometimes a tiny subapical spine); a telomere consisting of various lobes and lamellae with largely smooth margins.

Geotypodon papei sp. nov.

[urn:lsid:zoobank.org:act:3D36FD3A-B534-422E-8354-D0EDCAB2A748](https://doi.org/10.3896/BI.2015.3D36FD3A-B534-422E-8354-D0EDCAB2A748)

Fig. 3

Diagnosis

Differs from all other species of *Geotypodon*, except *G. carli* (Kraus, 1960), by the combination of a very long, slender metapical spine and a relatively simple telomere mainly consisting of a longitudinally folded sheet. Differs from *G. carli* by the shape of the basad, metapical, spine-like process (spine strongly expanded in basal part in *G. papei* sp. nov., not so in *G. carli*). See also Table 1.

Etymology

The name honours Thomas Pape, collector of the holotype and a leading figure in the Eastern Arc program of the Natural History Museum of Denmark.

Material studied (total: 3 ♂♂)

Holotype

TANZANIA: ♂, Morogoro Region, Udzungwa Mountains National Park, Sanje Chini Camp, 07°46'24.6" S, 36°53'47.7" E, 598 m a.s.l., 17–19 Jan. 2014, T. Pape leg. (ZMUC).

Paratypes

TANZANIA: 1 ♂, Morogoro Region, Udzungwa Ecological Monitoring Centre, Mang'ula, 07°50'44.9" S, 36°53'28.2" E, 339 m a.s.l., 18–20 Jan. 2014, T. Pape and N. Scharff leg. (ZMUC); 1 ♂, Morogoro Region, Udzungwa Mountains National Park, Kidatu, Plot 1, 07°41'13.8" S, 36°56'28.6" E, 650 m a.s.l., 24 Oct. 2014, pitfall trap. J. Malumbres-Olarte leg. (ZMUC).

Description

Male

SIZE. Length 5–6 cm, diameter 4.5–4.6 mm, 53–55 podous rings, no apodous rings in front of telson.

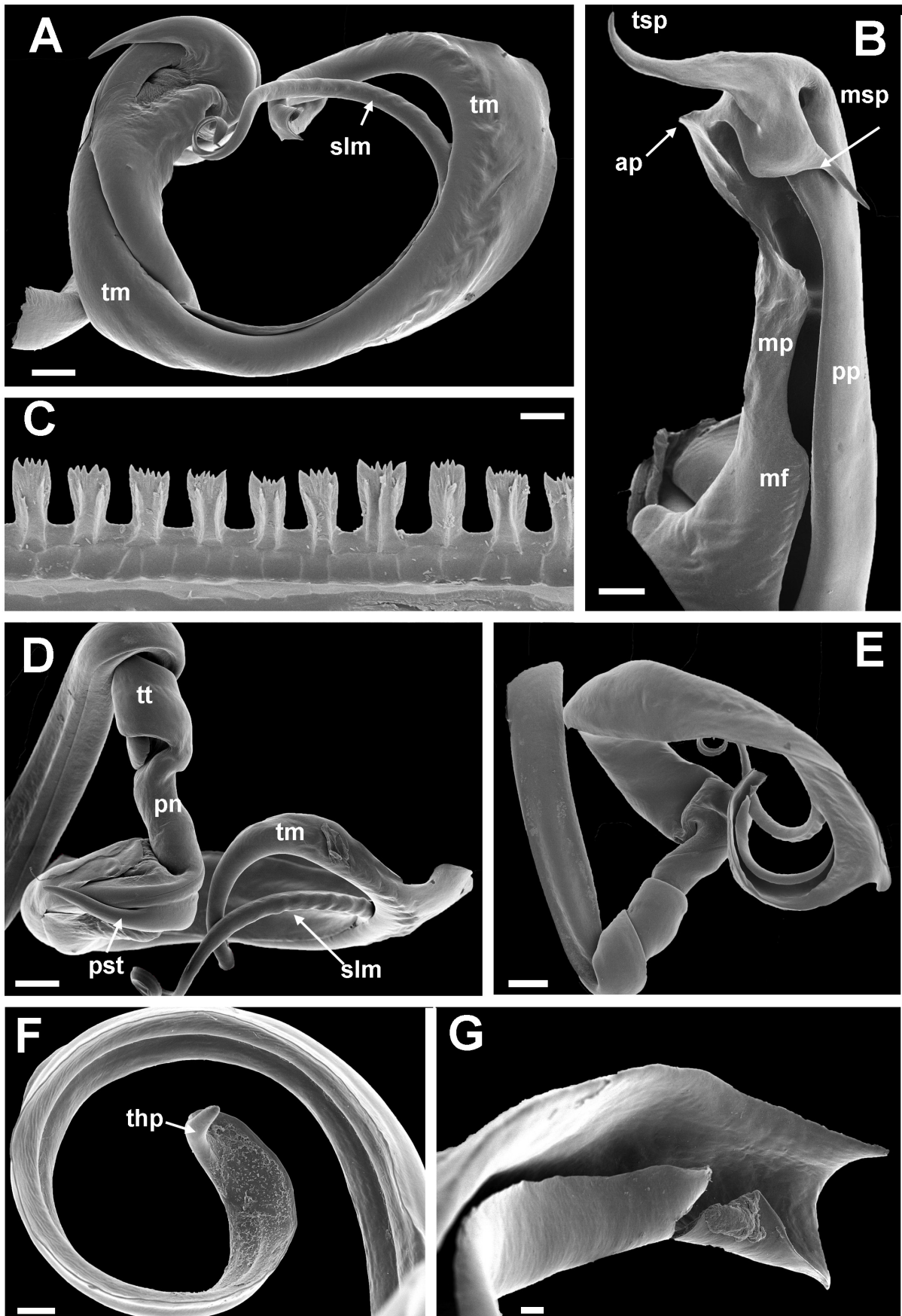
COLOUR. After 3 years in alcohol, head reddish brown to dark brown, antennae dark brown, collum, body rings and telson dark grey without contrasting markings, posterior ¼ of metazona amber, legs reddish brown.

HEAD. Without peculiarities. Seven or eight supralabral setae.

COLLUM. With a marginal and two submarginal furrows.

BODY RINGS. Almost perfect cylinders, not vaulted; suture straight; ozopores starting from ring 6, placed midway between suture and limbus. 13–15 metazonital striae, reaching up to ca one metazonite length below ozopore.

ANAL VALVES. Each with a stout dorsal spine; ventrally slightly angular; margins raised; each valve with three marginal setae not borne on tubercles.



LIMBUS (Fig. 3C). Consisting of isolated hand-like lobes with a length of ca 10 μm , each with 5–9 ‘fingers’ and each with two ridges running along its length.

MALE LEGS. With tiny postfemoral ventral pads from leg-pair 3–5, from leg-pair 6 postfemoral pads large, covering entire podomere, but gradually smaller posteriorly before disappearing completely shortly before posterior end. Tibiae with tiny ventral pads from leg-pair 3 until somewhere between gonopods and mid-body.

GONOPOD COXA (Fig. 3B). Slender, almost parallel-sided. Proplica (*pp*) simple, ending in small proplical lobe hidden from view by metaplical spinelike process (*m_{sp}*). Metaplica (*mp*) with small, basal, anteriad flange (*mf*); subdistally with angular process (*ap*); distally terminating in very long, slender, sigmoid spine (*tsp*); on anterior side with long, pointed, basally expanded, basad spine-like process (*m_{sp}*).

GONOPOD TELOPODITE (Fig. 3A, D–G). Arculus 90°. Torsotope (*tt*) simple, without processes (Fig. 2D). Post-torsal narrowing (*pn*) not very pronounced, yet distinct (Fig. 2D). Telopodite just distal to post-torsal narrowing dividing into simple, slender solenomere and equally long, narrow, almost parallel-sided telomere. Solenomere (*slm*) resting in curvature of telomere (Fig. 3A, D), terminally taeniate, with thumb-like process (*thp*) at very tip (Fig. 3F). Telomere (*tm*) with stout, curved proximal spine (*pst*) (Fig. 2D); main body of telomere a long, parallel-sided sheet, folded longitudinally and then curved in almost complete circle, abruptly narrower at ca $\frac{2}{3}$ of its length (Fig. 3D–E, G).

Female

Unknown.

Remarks

In the genus key of Kraus (1966), *Geotypodon papei* sp. nov. easily keys out in the last couplet (33), where the choice is between *Patinatius* Attems, 1928 and *Odontopyge* Brandt, 1841. In the couplet, the two genera are distinguished by *Patinatius* having the “Lateralblatt” prolonged into a cone or extended into a long spine vs *Odontopyge* not having such modifications. Couplet 33 in Kraus (1966) is copied from couplet 33 in Kraus (1960) with the difference that in the 1960 version, this couplet separates *Odontopygista* Kraus, 1960 from *Odontopyge*. Kraus (1966) synonymised *Odontopygista* with *Patinatius*. In both versions of couplet 33, Kraus made an error because the part of the gonopod coxa that has a cone- or spine-like outgrowth is the metaplica, which in Kraus’ terminology is the “Medialblatt” (as also used in his genus and species descriptions). This aside, one might argue that the long, sigmoid terminal spine (*tsp*) could be the homologue of such a “long spine”, but *Geotypodon papei* sp. nov. disagrees with the definition of *Patinatius* in several respects, including the limbus (spatulate and multicusped in *Geotypodon papei* sp. nov., rounded lobes in *Patinatius*), the internal surface of the telomere (smooth in *Geotypodon papei* sp. nov., with a row of denticles in *Patinatius*) and the tip of the solenomere (“thumb and lamella” in *Geotypodon papei* sp. nov., simply pointed in *Patinatius*). *Geotypodon papei* sp. nov. therefore keys out to *Odontopyge* in Kraus’ keys, and as explained by Enghoff (2016a) this generic name is not available for other than a small group of species very different from *Geotypodon papei* sp. nov. In the key to species of “*Odontopyge*” in Kraus (1960), *Geotypodon papei*

Fig. 3 (page 8). *Geotypodon papei* sp. nov., holotype. **A–B, D–G**. Right gonopod. **A**. Telopodite, mesal view. **B**. Coxa, anterior view. **D**. Telopodite, posterior view. **E**. Telopodite, anterior view. **F**. Tip of solenomere. **G**. Tip of telomere. **C**. Limbus. Abbreviations: *ap* = angular process of metaplica; *mf* = metaplical flange; *mp* = metaplica; *m_{sp}* = metaplical spine-like process; *pn* = post-torsal narrowing; *pp* = proplica; *pst* = proximal telomeral spine; *slm* = solenomere; *thp* = thumb-like solenomeral process; *tm* = telomere; *tsp* = terminal spine of metaplica; *tt* = torsotope. Scale bars: A–B, D–E = 0.2 mm; C = 0.01 mm; F–G = 0.02 mm.

Table 1. Comparison of *Geotypodon papei* sp. nov. with *G. carli* (Kraus, 1960).

	<i>G. papei</i>	<i>G. carli</i> (data from Kraus 1960)
Podous body rings	53–55	61 (“62 Segmente”)
Diameter	4.5–4.6 mm	4.6 mm
Supralabral setae	7–8	4
Metazonital striae	13–16	≈6
Metapical spine-like process	with a large mesad lobe at base	without a basal lobe
Telomere	abruptly narrower at ca ⅓ of length	gradually a little narrower towards end
Solenomere	tip apparently with “finger”, as in Fig. 3F, but difficult to see	simple, according to drawing
Provenance	Tanzania: Udzungwa Mountains National Park, 339–650 m a.s.l.	Democratic Republic of the Congo: Kivi, Kabare, Fizi M’Boko, 800 m a.s.l.

sp. nov. smoothly keys out to *carli* Kraus, 1960, one of the species that was transferred to *Geotypodon* by Enghoff (2016a), and the two species are indeed very similar. There are, however, enough differences to regard them as separate species, cf. Table 1.

Distribution

Known from three sites in the northeastern part of the Udzungwa Mts, at moderate altitudes (339–650 m a.s.l.).

Genus *Helicochetus* Attems, 1909

Helicochetus Attems, 1909a: 158.

Type species

Spirostreptus dimidiatus Peters, 1855, by original designation. See further below.

Other included species

Helicochetus aberrans Kraus, 1966 (Zambia), *H. digitarsus* Kraus, 1957 (Democratic Republic of the Congo, Tanzania), *H. electricus* Kraus, 1958 (Democratic Republic of the Congo), *H. gregorii* (Pocock, 1896) (Kenya), *H. inversus* Kraus, 1958 (Democratic Republic of the Congo), *H. involutus* Attems, 1935 (Democratic Republic of the Congo), *H. laciniatus* Attems, 1935 (Democratic Republic of the Congo), *H. levifolius* Attems, 1914 (“Sambesi”, Mozambique), *H. monodon* Kraus, 1960 (Zambia), *H. mutaba* Kraus, 1960 (Democratic Republic of the Congo), *H. pococki* (Carl, 1909) (Tanzania), *H. rarus* Kraus, 1958 (Democratic Republic of the Congo).

Kraus (1960) provided an identification key to the species, except *H. aberrans*.

Remarks

The material from the Udzungwa Mts includes specimens of two species of *Helicochetus*. Separate descriptive notes are given for each species, but two characters shared by both species may prove to be genus-characteristic and are therefore commented on here.

LIMBUS (Fig. 4A, C, E). Kraus (1960) characterized the limbus of *Helicochetus* (translated from German): “Limbus divided by rounded indentations into processes which each carry three to six nail-like points. Limbus very broad, ca. 10 × as broad as the processes, with a silky sheen due to the characteristic surface

sculpture (exception *H. laciniatus*)". The limbus of the two studied species, especially *H. mutaba*, is indeed very broad (Fig. 4A, C), and the processes and nail-like points agree fully with Kraus' description. It is not clear from his publications (Kraus 1960, 1966) what he meant by the "characteristic surface structure". The SEM images (Fig. 4A, C, E) provide no clue. There is, however, another remarkable detail, visible in Fig. 4E: under the limbus proper, there is a "sub-limbus" consisting of rounded, almost semicircular lobes.

CYTOSCUTE DENTICLES (Fig. 4B, D, F). The "cytoscutes", i.e., cuticular "cells" each corresponding to a hypodermis cell (Fusco *et al.* 2000) very often carry a row of tiny denticles along one edge. In both studied species of *Helicochetus*, these denticles are much larger than normal and point away from the cuticular surface rather than lying parallel to it.

***Helicochetus dimidiatus* (Peters, 1855)**

Figs 4A–B, 5

Spirostreptus dimidiatus Peters, 1855: 79.

Helicochetus dimidiatus – Attems (1909a): 158.

Material studied (total: 1 ♂)

TANZANIA: 1 ♂, Morogoro Region, Udzungwa Ecological Monitoring Centre, Mang'ula, 07°50'44.9" S, 36°53'28.2" E, 339 m a.s.l., 20 Mar. 2013, T. Pape and N. Scharff leg. (ZMUC).

Description

Male

Based on studied specimen. Details from previous descriptions in parentheses.

SIZE. Diameter 5.4 mm, 59 podous rings, no apodous rings in front of telson. (Peters 1855: length 65–60 mm; diameter 5–5.5 mm; 62 "annuli"; Peters 1862: length 60–70 mm; diameter 5 mm; 66 body rings; Verhoeff 1901, ♂, as *Odontopyge attemsi* Verhoeff, 1901: length 62½ mm; 61 body segments.)

COLOUR. After 4 years in alcohol greyish; head, antennae, legs, and posterior ca 40% of metazonites yellowish.

HEAD. Without peculiarities. Supralabral setae not countable due to damage. (Peters 1855, 1862: 6–7; Verhoeff 1901: 5; Attems 1914: 6.)

COLLUM. With two complete furrows on each side, none of them marginal. (Peters 1855: a marginal and two further striae; Verhoeff 1901: four striae; Attems 1914: a marginal ridge, then an incomplete, and then two complete striae.)

BODY RINGS. Almost perfect cylinders, not vaulted; suture straight; ozopores starting from ring 6, placed ca ⅓ of metazonite length between suture and limbus. Ca 13 metazonital striae reaching almost up to ozopore. Surface microsculpture (Fig. 4B), see Remarks for genus.

ANAL VALVES. Each with a moderate dorsal spine; margins raised; each valve with three marginal setae not borne on tubercles.

LIMBUS (Fig. 4A). See Remarks for genus.

MALE LEGS. With postfemoral ventral pads from first post-gonopodal leg-pair 3–5 until ca midbody; anteriormost and posteriormost pads small, intermediate ones covering entire ventral side of postfemur.

GONOPOD COXA (Fig. 5A–D). As typical for the genus, including small, distal basad process (*bp*) (Fig. 5B, D). Prostatic stylet (*sp*) visible in coxal cavity (Fig. 5B–C).

GONOPOD TELOPODITE (Fig. 5E–H). Tip of solenomere (*slm*) tightly spiraled (like a corkscrew) (Fig. 5H); no processes visible in spiral. Telomere (*tm*) ending in long, slender process with a terminal brush of long fringes (Fig. 5F–G).

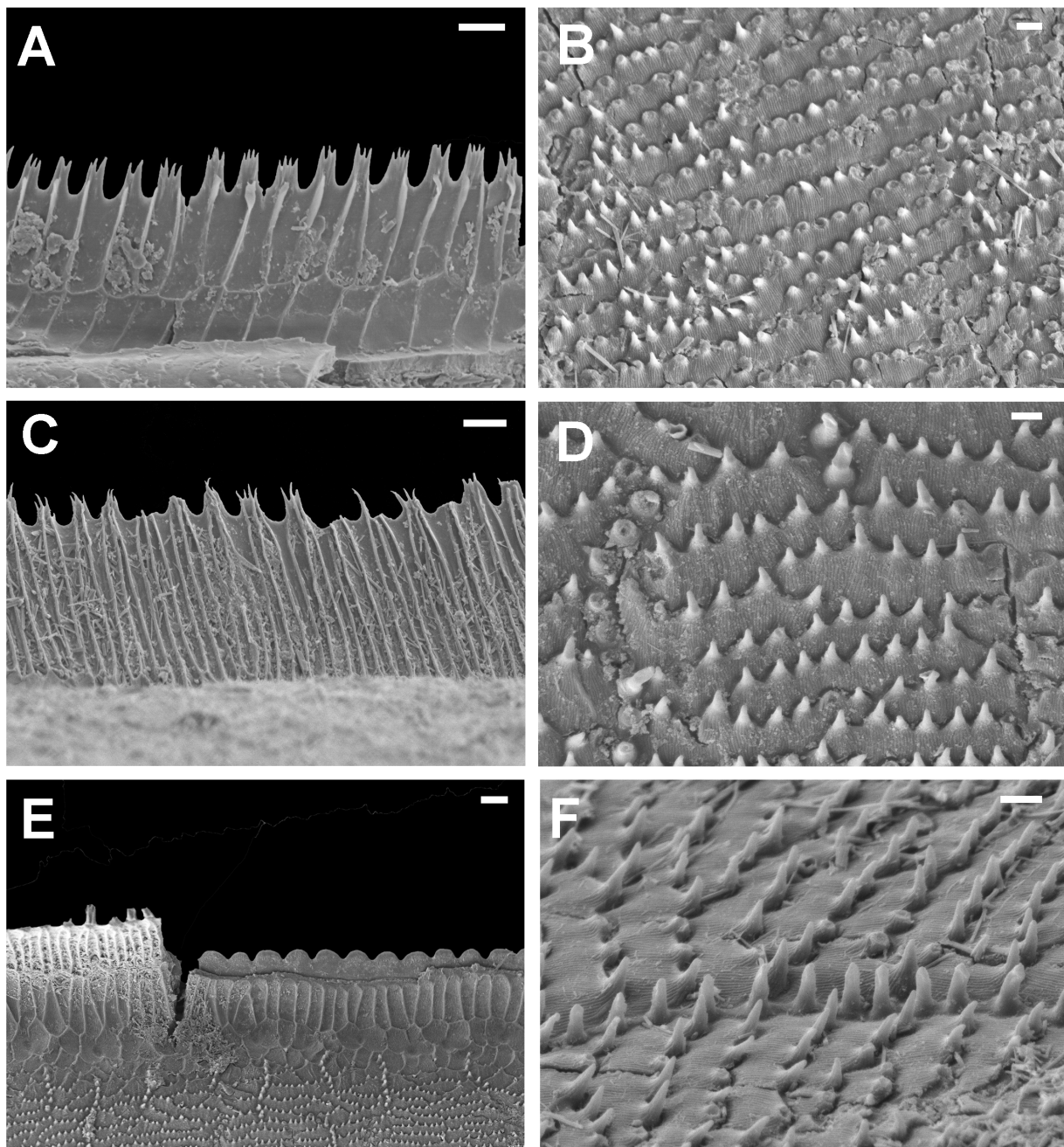


Fig. 4. *Helicochetus* spp., ♂♂, from Udzungwa Mts. **A–B.** *H. dimidiatus* (Peters, 1855). **C–F.** *H. mutaba* Kraus, 1960. **A, C, E.** Limbus; in E the limbus proper is damaged (remains are seen to the left), so the round-lobed “sublimbus” becomes visible. **B, D, F.** Surface microsculpture of limbus. Scale bars: A, C, E = 0.01 mm; B, D, F = 0.002 mm.

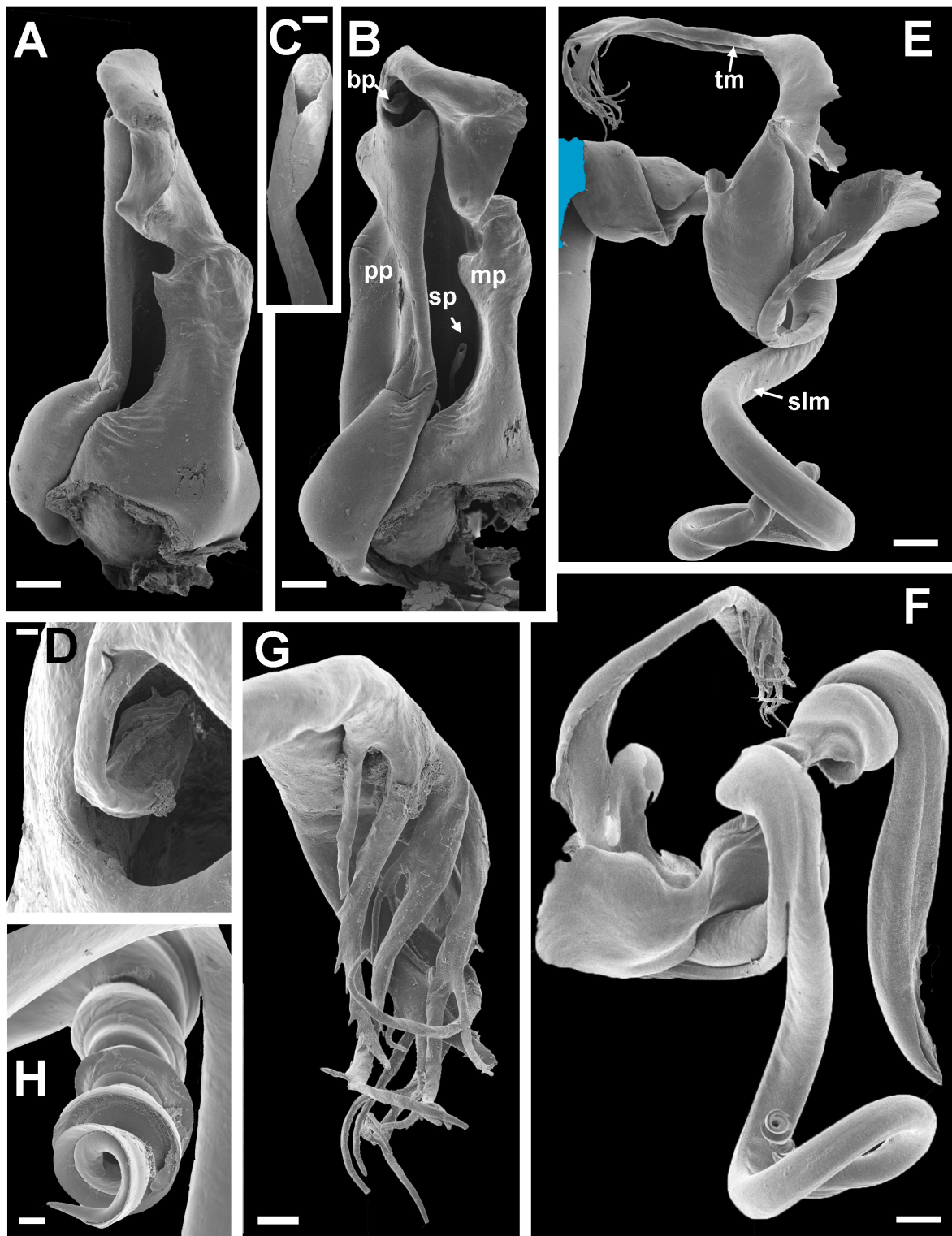


Fig. 5. *Helicochetus dimidiatus* (Peters, 1855), ♂, from Udzungwa Mts. Left gonopod. **A–D.** Coxa. **A.** Mesal view. **B.** Anterior view. **C.** Prostatic stylet. **D.** Apical basad process. **E–H.** Telopodite. **E.** Anterior view (the area marked with blue is covered by the mounting tape). **F.** Posterior view. **G.** Tip of telomere. **H.** Tip of solenomere. Abbreviations: *bp* = apical basad process of coxa; *mp* = metaplica; *pp* = proplica; *slm* = solenomere; *sp* = prostatic stylet; *tm* = telomere. Scale bars: A–B, E–F = 0.2 mm; C–D, H = 0.02 mm; G = 0.05 mm.

Female

Unknown.

Distribution and habitat

Known from several localities in Mozambique and Tanzania (Enghoff *et al.* 2016).

Verhoeff (1901) quoted a report on *H. dimidiatus* (as *Odontopyge attemsi* Verhoeff, 1901) from the small island of Kwale (off the southern Tanzanian coast) where this species appeared in very large numbers, destroyed the islander's crops and forced them to move their agricultural activities to the mainland.

Helicochetus dimidiatus is sometimes kept in terraria, see, e.g., www.diplopoda.de/html/species/hdimidiatus/_helico.php (accessed 19 Apr. 2007).

Remarks

The prostatic stylet (“stylet prostatique” *sensu* Brolemann 1920) is rarely seen, but seems to be a general feature of odontopygid and spirostreptid gonopods (Brölemann 1917; Brolemann 1920; Kraus 1966). This structure has been regarded as homologous with the cannula of Polydesmida and the flagella of many Julida, Cambalidea and Chordeumatida, in which case it would constitute a synapomorphy of subterclass Eugnatha *sensu* Enghoff *et al.* (2015); see discussions by Brolemann (1932), Demange (1967) and Enghoff (1984).

Helicochetus mutaba Kraus, 1960 Figs 4C–F, 6

Helicochetus mutaba Kraus, 1960: 40.

Diagnosis

Resembles *H. digititarsus* Kraus, 1957, *H. gregorii* (Pocock, 1896) and *H. monodon* Kraus, 1960 in the combination of a broad, shovel-like process (“Tibialdorn”) at the level of the post-torsal narrowing; absence of ventral pads on male tibiae; presence of a basal lamella (“Grundblatt”) on the telomere; tip of telomere not drawn out into long process, with several short to moderately long spine-like outgrowths from the margin. Differs from these species in the shape of the basal lamella: slender, pointed and curved (with a few denticles on the concave margin in the new specimens).

Material studied (total: 2 ♂♂)

TANZANIA: 1 ♂, KMH 2097, Nyumbenito Mt, forest near Udekwa, Uzungwa Mountains, 2000–3000 m a.s.l., date?, W.A. Rodgers leg. (VMNH); 1 ♂, Iringa Region and District, Mazombo, 20 km NE of Iringa, 1700 m a.s.l., Jan. 1984, Jan Kielland leg. (ZMUC).

Description

Male

Based on studied specimens. Details from original description (Kraus 1960) in parentheses. Both of the new specimens are strongly fragmented and completely faded.

SIZE. Diameter 4.1–4.7 mm (4.0 mm), specimen from Mazombo with ca 64 podous rings, no apodous rings in front of telson, specimen from Nyumbenito Mt probably incomplete (48 podous rings present, no apodous rings in front of telson).

HEAD. Without peculiarities. Five supralabral setae (6).

COLLUM. With two complete furrows on each side, none of them marginal (two distinct furrows, marginal furrow less distinct).

BODY RINGS. Almost perfect cylinders, not vaulted; suture straight; ozopores starting from ring 6, placed ca $\frac{1}{3}$ of metazonite length between suture and limbus. Ca 14 metazonital striae, reaching almost up to ozopore (10–11 striae, not at all reaching ozopore level). Surface microsculpture (Fig. 4D, F), see Remarks for genus.

ANAL VALVES. Dorsally drawn out into pointed triangular process, ventrally with small protruding knob; mesal margin raised, setiferous tubercles not detectable.

LIMBUS (Fig. 4C, E). See Remarks for genus.

MALE LEGS. With postfemoral ventral pads from first post-gonopodal leg-pair 3–5 until ca midbody.

GONOPOD COXA (Fig. 6A–B). Lateral margin convex in basal half. Proplica (*pp*) simple, with straight mesal margin, ending in small propical lobe (*ppl*). Metaplica (*mp*) higher than proplica, apically regularly rounded, subapically with low mesal flange (*mmf*), mesal margin of flange shallowly concave; distal, basad process (*bp*) slender.

GONOPOD TELOPODITE (Fig. 6C–G). Basomere including torsotope without spines, arculus 90°. A large, shovel-like flange (*shl*) (“Tibialdorn”) present at level of post-torsal narrowing (Fig. 6F). A long, slender, curved spine (*ps*) at base of solenomere (Fig. 6E–F). Solenomere (*slm*) slender, round in transverse section, as long as telomere (*tm*), apically wound up in tight, corkscrew-like spiral; spiraled part basally delimited by tight, knob-like turn (*kn*) (“knotige Drehung”) of solenomere shaft (Fig. 6G). Telomere basically a moderately narrow band curved in almost complete circle; with a curved, pointed basal lamella (*btl*) (“Grundblatt”) pointing into main telomere curvature and with 1–2 small denticles on concave side (Fig. 6C, E) (no denticles); tip of telomere on specimen from Mazombo with several long, thin, spinelike processes from margin (Fig. 6D), in specimen from Nyumbenito Mt more shallowly serrate.

Female

Unknown.

Distribution

Hitherto known only from the type locality, Mutaba in the vicinity of Kirungu (= Baudoinville), in the Democratic Republic of the Congo. The two records from Tanzania, Nyumbenito Mt in the Udzungwa Range and Mazombo N of the Udzungwas, thus represent a considerable range extension. See, however, Remarks below.

Remarks

Helicochetus mutaba belongs to a group of very similar nominal species characterized by the following combination of key characters: a shovel-like lamella (“Tibialdorn”) at the level of the post-torsal narrowing; no ventral pads on male tibiae; telomere with a basal lamella (“Grundblatt”); tip of telomere not drawn out into a long process, with several short to moderately long, spine-like outgrowths from the margin. This group consists of *H. digititarsus* Kraus, 1957 (Democratic Republic of the Congo), *H. gregorii* (Pocock, 1896) (Kenya), *H. monodon* (Kraus, 1960) (Zambia) and *H. mutaba* (Democratic Republic of the Congo, Tanzania). Table 2 shows the differences between these four species. The outline of the basal lamella of the telomere differs between the species, but it is not unlikely that future collections will bridge the small morphological gaps and that some or all of the four species will have to be synonymized.

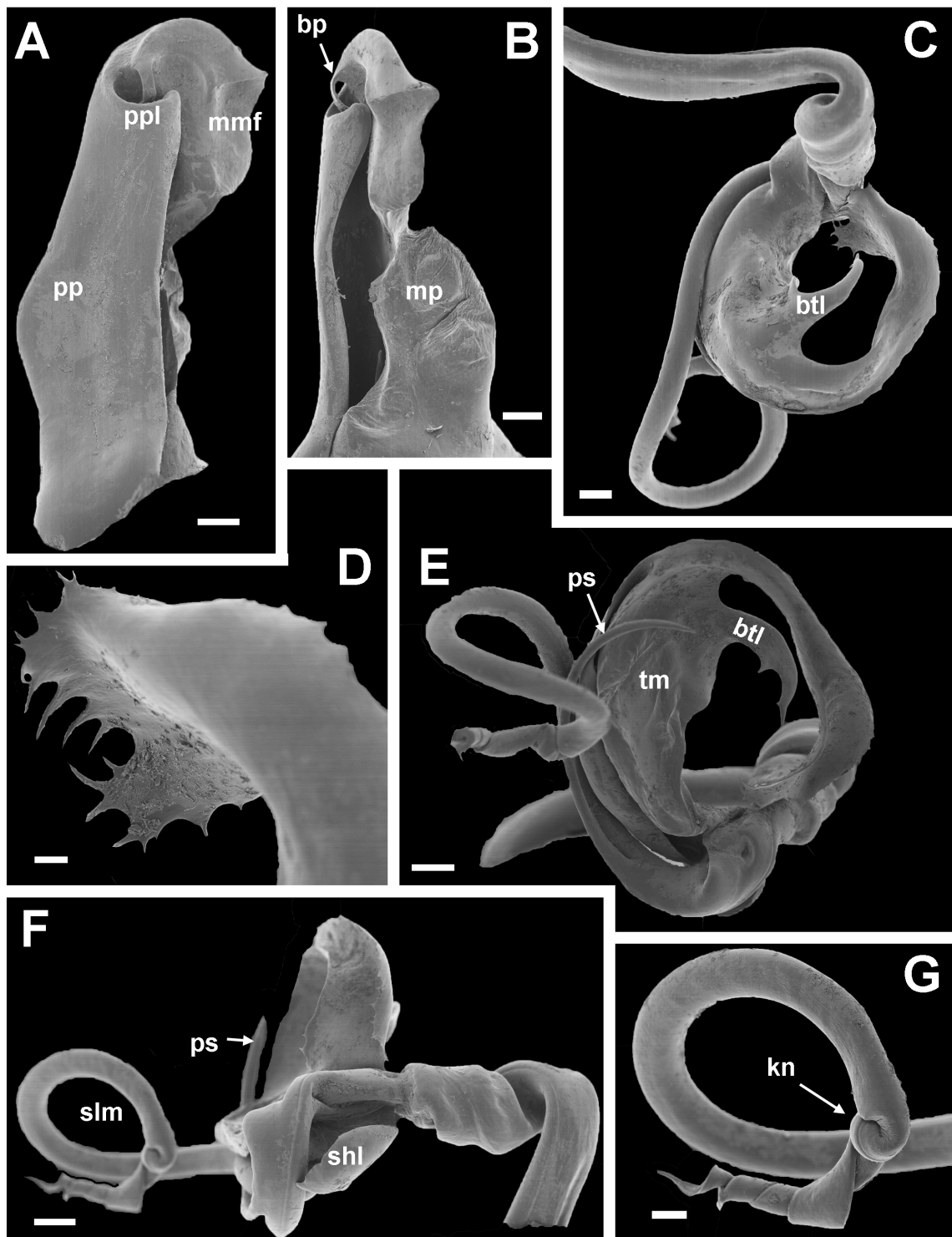


Fig. 6. *Helicochetus mutaba* Kraus, 1960, ♂, from Mazombo. Left gonopod. **A–B.** Coxa. **A.** Anterior view. **B.** Mesal view. **C–G.** Telopodite. **C.** Anterior-lateral view. **D.** Detail of **C** (tip of telomere). **E.** Mesal-posterior view. **F.** Anterior-ventral view. **G.** Detail of **F** (tip of solenomere). Abbreviations: *bp* = apical basad process of coxa; *btl* = basal lamella of telomere; *kn* = knob-like turn of solenomere; *mmf* = mesal metaplical flange; *mp* = metaplica; *pp* = proplica; *ppl* = proplical lobe; *ps* = proximal solenomeral spine; *shl* = shovel-like flange; *slm* = solenomere; *tm* = telomere. Scale bars: **A–C**, **E–F** = 0.2 mm; **D** = 0.05 mm; **G** = 0.1 mm.

Table 2. Comparison of four species of *Helicochetus* Attems, 1909.

	<i>H. mutaba</i> Tanzania	<i>H. mutaba</i> D.R. of the Congo (from Kraus 1960)	<i>H. digitarsus</i> (from Kraus 1960)	<i>H. gregorii</i> (from Pocock 1896 and Kraus 1960)	<i>H. monodon</i> (from Kraus 1960)
No. of body rings	ca 64	?	60	71–72	64
Body diameter (♂)	4.1–4.7 mm	4.0	3.7	?	3.5
Distal, basad process (<i>bp</i>) on coxa	long	long	long	short	long
Mesal margin of distal part of coxa	very shallowly concave	shallowly concave	with a deep sinus	shallowly concave	shallowly concave
Basal lamella of telomere (<i>btl</i>)	slender, pointed, curved, with a few denticles on concave margin	slender, pointed, curved, smooth	very slender, pointed, smooth	broad, subrectangular, smooth	slender, margin in part serrate
Tip of telomere	margin with short or long, slender denticles	margin with short denticles	margin with short denticles	with many short and long denticles, apparently not only on margin	margin with short denticles
Solenomere with a 'knot' (<i>kn</i>) at base of terminal spiral	yes	yes	yes	no	yes
Terminal spiral of solenomere with an accessory spine	yes	yes	yes	no	yes

Enghoff *et al.* (2016) recorded *H. digitarsus* from two Tanzanian localities: 1) Mara Region, Serengeti District, Seronera, Serengeti National Park; 2) Tabora Region, Nzega District, Nzega City. In light of the above discussion, it cannot be excluded that these specimens are conspecific with the one recorded here as *H. mutaba*.

The vial containing the male from Mazombo also contained a microvial with a mite which was presumably collected in association with the millipede. The mite was infested with numerous thalli of the fungus *Rickia* sp. (Ascomycota, Laboulbeniales). Several species of mites are known to be closely associated with millipedes (Farfan & Klompen 2012), and several species of *Rickia* Cavara are known to use mites as their host (Tavares 1985; Seeman & Nahrung 2000), but this seems to be the first known instance of a *Rickia*–mite–millipede association.

Genus *Hoffmanides* Kraus, 1968

Hoffmanides Kraus, 1966: 134.

Type species

Spinotarsus dissutus Hoffman, 1963, by original designation and monotypy.

Remarks

This genus, remarkable for its widely open gonopod coxa, was erected by Kraus for a species originally placed in the large, mainly southern African genus *Spinotarsus* Attems, 1909. By doing so, Kraus deprived Tanzania of the genus *Spinotarsus*, an action neutralized by the description below of a new Tanzanian species of *Spinotarsus*.

Hoffmanides dissutus (Hoffman, 1963)
Figs 7–8

Spinotarsus dissutus Hoffman, 1963: 1.

Hoffmanides dissutus – Kraus (1966): 135.

Material studied (total: 6 ♂♂)

TANZANIA: 6 ♂♂, Iringa–Morogoro Regions, Udzungwa National Park, 350 m a.s.l., 8 Dec. 1995, Steven Liselli leg. (VMNH; 1 ♂, ZMUC).

Description

Male

Based on studied specimens. Details from previous descriptions (Hoffman 1963; Kraus 1966) in parentheses. Considering that two detailed descriptions of *H. dissutus* are thus available, and that the studied specimens agree completely with both of them, only a few details are highlighted here.

SIZE. Diameter 3.5–3.9 mm (3.7 mm); 61–64 podous rings, no apodous rings in front of telson (“56 Segmente”).

HEAD. Without peculiarities. Five supralabral setae (6).

COLOUR. After 22 years in alcohol, overall yellowish (Fig. 7); prozonites from ozopore level up to ca $\frac{2}{3}$ of distance to midline blackish; also a thin blackish midline, i.e., dorsum with two paramedian yellow bands.



Fig. 7. *Hoffmanides dissutus* (Hoffman, 1963), ♂, from Udzungwa Mts National Park. Photograph by A. Illum. Scale bar = 5 mm.

ANAL VALVES (Fig. 8A–B). Dorsally drawn out into pointed, triangular, spine-like process, ventrally with small protruding knob; mesal margin raised, setiferous tubercles, especially middle one (*stu*) on pronounced “ravelins”.

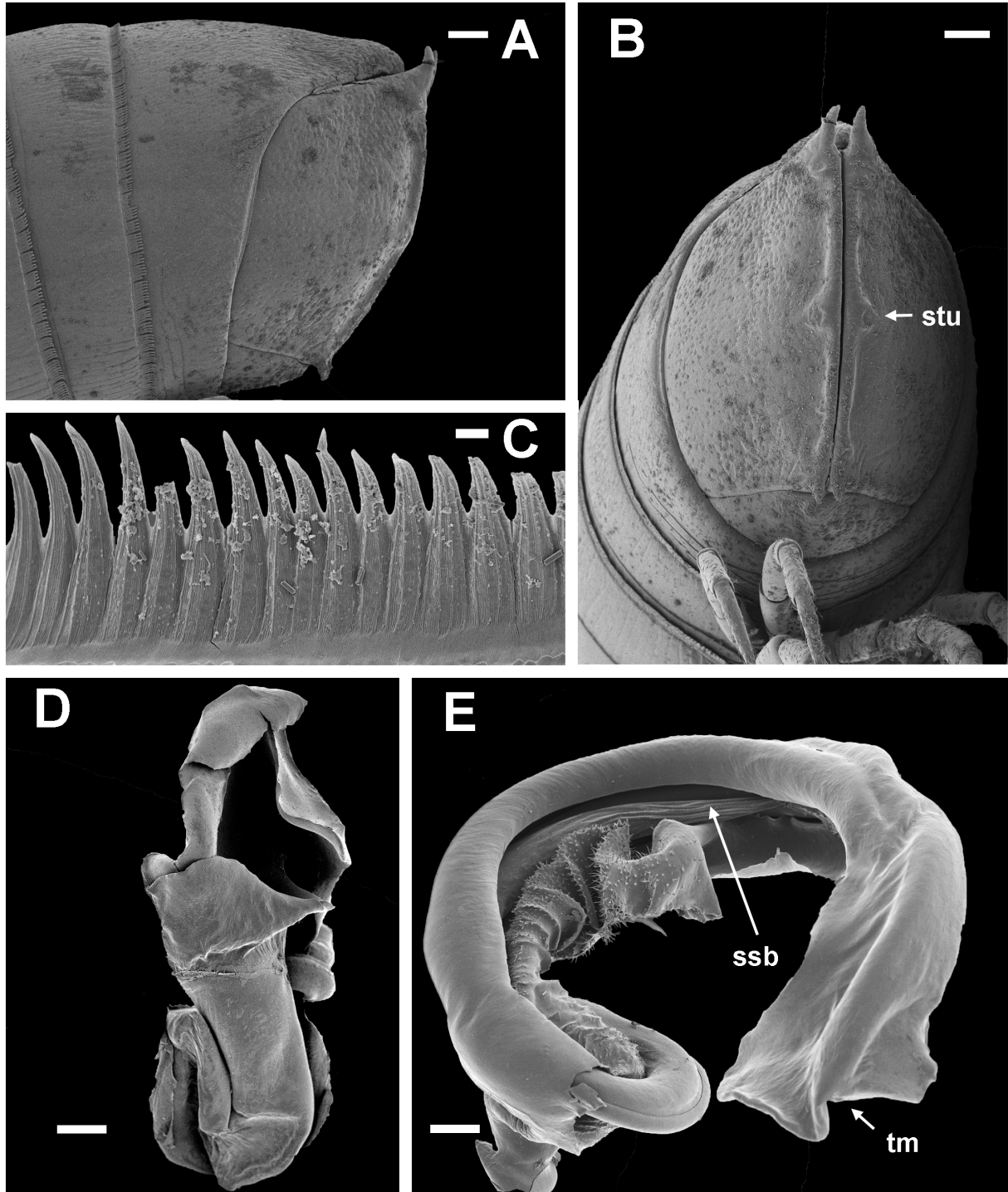


Fig. 8. *Hoffmannides dissutus* (Hoffman, 1963), ♂, from Udzungwa Mts National Park. A–B. Telson. A. Lateral view. B. Posterior view. C. Limbus. D. Gonopod coxa, anterior view. E. Gonopod telopodite, posterior-mesal view. Abbreviations: *ssb* = spine-like side branch of solenomere, nested in cavity of telomere; *stu* = middle setiferous tubercle on “ravelin”; *tm* = tip of telomere. Scale bars: A–B, D = 0.2 mm; C = 0.001 mm; E = 0.1 mm.

LIMBUS (Fig. 8C). With long, spine-like lobes.

GONOPOD COXA (Fig. 8D). As illustrated by Hoffman (1963) and Kraus (1966).

GONOPOD TELOPODITE (Fig. 8E). As illustrated by Kraus (1966). In some specimens the solenomere is hidden within the telomere (Fig. 8E), but in others the solenomere has come free (due to preservation?), and the long, spine-like branch (*ssb*) arising from it, overlooked by Hoffman (1963) but illustrated by Kraus (1966: fig. 358), is obvious.

Female

Unknown.

Distribution

Helicochetus dissutus was described from “Morogoro” (Hoffman 1963); this does not necessarily refer to the city of Morogoro, ca 150 km NE of Udzungwa National Park, but possibly to anywhere in the Morogoro Region. Enghoff *et al.* (2016) also recorded the species from the Morogoro Region, Uluguru Mts, Morningside.

Genus *Spinotarsus* Attems, 1909

Spinotarsus Attems, 1909b: 46.

Type species

Spinotarsus xanthonotus Attems, 1909.

Other included species

Almost one hundred; see Kraus (1960, 1966).

Remarks

The vast majority of species of *Spinotarsus* occur in southern Africa; only two, viz, *S. serrulatus* Kraus, 1958 and *S. terrestris* (Attems, 1935), are from the Democratic Republic of the Congo. Two species described from other parts of the Afrotropical region have subsequently been transferred to other genera: *S. caboverdus* Pierrard, 1987 (Cape Verde Islands) was transferred to the genus *Bandeirenica* Kraus, 1960 by Hoffman (2000); *S. dissutus* Hoffman, 1963 (Tanzania), was made type of the genus *Hoffmanides* by Kraus (1966), see above. The new species described below is thus the first true *Spinotarsus* from Tanzania.

Spinotarsus fortehamatus sp. nov.

[urn:lsid:zoobank.org:act:B9ACE322-7B35-4879-9DC4-B5F08E666121](https://doi.org/10.21203/rs.3.rs-1111111/v1)

Fig. 9

Diagnosis

A species of *Spinotarsus* characterized by the very large, regularly curving lateral metapical spine, in combination with the presence of a spine at the base of the solenomere and a row of denticles on the terminal part of the telomere.

Etymology

The name is a composite Latin adjective, meaning “with a strong hook” and referring to the strong lateral, hook-shaped spine of the gonopod coxa.

Material studied (total: 1 ♂)

Holotype

TANZANIA: ♂, Morogoro Region, Udzungwa Mountains National Park, Sanje Kati camp and plot, 07°45'47.6" S, 36°53'10.4" E, 850 m a.s.l., 7 Feb. 2014, J. Malumbres-Olarte leg. (ZMUC).

Description

Male

SIZE. Length ca 6 cm, diameter 5.0 mm, 59 podous rings, no apodous rings in front of telson.

COLOUR. Apparently quite well-preserved after 3 years in alcohol: head below antennae yellowish; head above antennae blackish, parietal and interocular furrows contrastingly yellow; antennae brown, collum blackish with lighter margins; body rings light grey, metazona with black sputtering, posterior $\frac{1}{3}$ of metazona amber; a yellow dorsal longitudinal stripe on posterior $\frac{1}{4}$ of body; legs yellow; preanal ring grey, dorsally yellow; anal valves blackish with lighter margin; subanal scale yellow.

HEAD. Parietal and interocular furrows present; 7 supralabral setae. Antennae reaching to ring 6 when folded back. Eyes reaching to median tangent to antennal socket, each with nine rows of ommatidia, 7 horizontal rows, and a total of ca 38 ommatidia each.

COLLUM. Lateral lobes subrectangular, each with two furrows.

BODY RINGS. Unvaulted; metazona and posterior part of prosoma with numerous short very fine longitudinal furrows; ozopores ca $\frac{1}{3}$ of metazona length behind straight suture.

OZOPORES. Missing from rings 31 (left side), 47 (both sides), 56 (right), 58 (left) and 59 (both).

ANAL VALVES. Each with a stout dorsal spine and a tiny ventral knob-like spine; mesal margin slightly raised, setiferous tubercles indistinct, not on ravelins.

LIMBUS (Fig. 9G). With long (more than twice as long as broad), pointed lobes.

GONOPOD COXA (Fig. 9F). Slightly more than twice as long as broad. Proplica ending in small proplical lobe (*ppl*). Metaplica longer than proplica, apically forming a "cucullus" (*cu*). Mesal margin of metaplica with a curved lamellar process (*mlp*) just distal to exit point of telopodite ("arculus"). Metaplica laterally with a very large spine (*msp*) curving distad in a latero-posterior plane. Proplical lobe, lateral metaplical spine and a stripe parallel to lateral metaplical margin from spine to tip of cucullus black (not visible on SEM image).

GONOPOD TELOPODITE (Fig. 9A–E). Arculus 90°. A very long post-torsal spine (*pts*) making almost $1\frac{1}{2}$ turns around torsotope (*tt*) (Fig. 9C–D). Solenomere (*slm*) as long as telomere, thin, simple, without outgrowths, apically with oblique-longitudinal fluting. A long spine (*ps*) originating at base of solenomere and projecting at right angles to it (Fig. 9A). Telomere (*tm*) curving in an almost complete circle, basally with large spinose lamella (*bla*) projecting into space delimited by telomere curvature, followed by two smooth lamellae (*el1*, *el2*) projecting from outside of curvature (Fig. 9A); distal part of telomere slender, longitudinally folded, one margin with a series of black denticles (*td*, colour not visible on SEM image; Fig. 9D).

Female

Unknown.

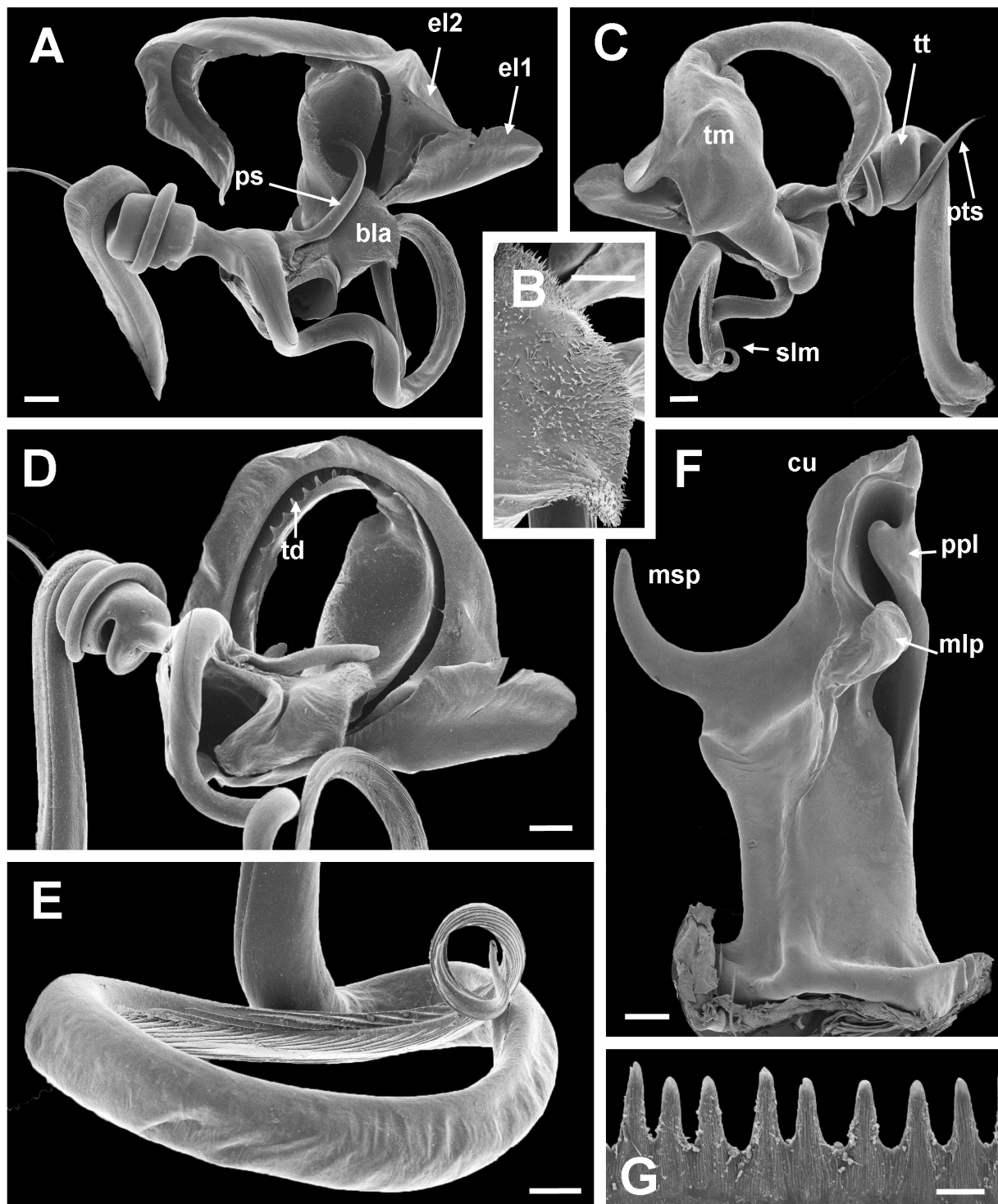


Fig. 9. *Spinotarsus fortehamatus* sp. nov., holotype. **A–E.** Right gonopod telopodite. **A.** Posterior view. **B.** Basal lamella of telomere, enlarged. **C.** Anterior view. **D.** Posterior-mesal view. **E.** Distal part of solenomere. **F.** Right gonopod coxa, posterior and slightly mesal view. **G.** Limbus. Abbreviations: *bla* = basal lamella of telomere; *cu* = cucullus; *el1*, *el2* = smooth telomeral lamellae; *mlp* = metaplical lamellar process; *msp* = metaplical spine-like process; *ppl* = proplical lobe; *ps* = proximal solenomeral spine; *pts* = post-torsal spine; *slm* = solenomere; *td* = telomeral denticles; *tm* = telomere; *tt* = torsotope. Scale bars: A, C–D, F = 0.2 mm; B, E = 0.1 mm; G = 0.01 mm.

Remarks

The basal spinose lamella of the telomere (*bla*) is a key character for *Spinotarsus* (the name actually refers to the lamella – the telomere was formerly referred to as the tarsus). Many species of *Spinotarsus* possess an additional apomorphy, namely a darkly sclerotized ridge on the posterior surface of the telomere, but such a ridge is absent in *S. fortehamatus* sp. nov. In the most recent key to species of *Spinotarsus* (Kraus 1966: 110–113), the new species keys out without problems to couplet 60, as follows (couplet texts translated from German and adapted to current terminology, characters of *S. fortehamatus* sp. nov. in bold): couplet 1: Gonopodal metaplica with **one** or several dark sclerotized lateral spines which stand clearly out in strict oral view → couplet 38: **One** or more spine(s) (“Postfemoraldorn”) at base of solenomere present → couplet 59: **One** spine at base of solenomere → couplet 60. “Couplet” 60 is, however, deficient in the key, which can be seen by comparison with the older key by Kraus (1960: 122, “couplet” 42). The “couplet” in question is actually a “triplet”, but the third option is lacking in the 1966 key. In translation, “triplet” 60 in Kraus (1966) should run:

60. Metaplica distally coarsely serrate*denticulatus*
 – Metaplica distally ending in a slender, spine-like process with a blackened tip; this process inserting apico-mesally61
 – **Tip of metaplica different**65

Continuing in couplet 65, the new species fulfils the second alternative: Lateral metaplical spine directed ± **apicad** → couplet 68: Metaplica apically **without a process** or just with a delicate hyaline, spoon-shaped appendage → couplet 81: Terminal lamella of telomere with spiny margin and **1–2** longitudinal **rows** of denticles on the internal surface (→ couplet 82) vs Terminal lamella of telomere **completely smooth**, internal surface of telomere without obvious spine rows (→ couplet 84). The new species has a smooth margin of the terminal part of the telomere, but it also has a very obvious row of spines on the internal surface of the telomere. It thus fits one criterium of each alternative. In addition to its unique combination of key characters, it also differs from congeners in the shape of the lateral metaplical spine: none of the almost one hundred described species of *Spinotarsus* have an equally large, equally smoothly curved lateral metaplical spine. Those which come closest in this character, i.e., *S. demotus* Kraus, 1966 (Angola), *S. kruegeri* Kraus, 1966 (South Africa), *S. lanceolatus* Kraus, 1966 (Zimbabwe) and *S. pusillus* Kraus, 1966 (South Africa), differ clearly in other characters.

The lack of ozopores on one or both sides of certain body rings is a highly unusual trait. In juliformian millipedes, ozopores are normally present in an uninterrupted series usually starting on body ring 6, rarely on ring 5, exceptionally on ring 3, and continuing to include the last podous ring. Up to now, the only exception to this rule is constituted by two species of the family Mongoliulidae, in which ozoporeless body rings occur in a regular pattern along the body (Enghoff *et al.* 2017).

Discussion

The Odontopygidae of the Udzungwa Mountains

Thirty-nine species of Odontopygidae (Table 3) are now known from the Udzungwa Mts as a result of the series of studies entitled “A mountain of millipedes” (Enghoff 2014, 2016a, 2016b, 2016c; Enghoff & Frederiksen 2015; this paper). Previously, just one species (*Chaleponcus dabagaensis* Kraus, 1958) was known. Based on the examination of a huge collection of millipedes from the Udzungwas, Odontopygidae is clearly the most species-rich millipede family in these mountains. Paradoxosomatidae are also represented by many species, whereas such families as Spirostreptidae, Oxydesmidae, Gomphodesmidae, Chelodesmidae, several families of “micropolydesmoids” and Stemmiulidae seem to have no more than one or two handfuls of species each.

Table 3. Species of Odontopygidae known from the Udzungwa Mts. Endemic = endemic to the Udzungwa Mts.

Species	Distribution	Altitudinal range in the Udzungwa Mts (m a.s.l.)
1. <i>Aquattuor longipala</i> Enghoff, 2015	endemic	1390–1410
2. <i>A. major</i> Enghoff, 2015	endemic	1650–1850
3. <i>A. stereosathe</i> Enghoff, 2015	endemic	900–1500
4. <i>A. submajor</i> Enghoff, 2015	endemic	1000–1250
5. <i>A. udzungwensis</i> Enghoff, 2015	endemic	750–1410
6. <i>Casuariverpa scarpa</i> Enghoff, 2016	endemic	1050
7. <i>Chaleponcus basiliscus</i> Enghoff, 2014	endemic	?
8. <i>C. circumvallatus</i> Enghoff, 2014	endemic	1390–1650
9. <i>C. dabagaensis</i> Kraus, 1958	endemic	1700–1955
10. <i>C. gracilior</i> Enghoff, 2014	endemic	1500–2100
11. <i>C. hamerae</i> Enghoff, 2014	endemic	1600–1800
12. <i>C. howelli</i> Enghoff, 2014	endemic	1700–1900
13. <i>C. ibis</i> Enghoff, 2014	endemic	?
14. <i>C. krai</i> Enghoff, 2014	endemic	1900–2100
15. <i>C. malleolus</i> Enghoff, 2014	endemic	1904–1944
16. <i>C. mwabvui</i> Enghoff, 2014	endemic	1800–1955
17. <i>C. mwanihanensis</i> Enghoff, 2014	endemic	1800–1850
18. <i>C. nectarinia</i> Enghoff, 2014	endemic	1930–1955
19. <i>C. netus</i> Enghoff, 2014	endemic	1390–1963
20. <i>C. nikolajscharffi</i> Enghoff, 2014	endemic	1400–1800
21. <i>C. quasimodo</i> Enghoff, 2014	endemic	1700–1900
22. <i>C. scopus</i> Enghoff, 2014	endemic	1700–1900
23. <i>C. teres</i> Enghoff, 2014	endemic	1930–1950
24. <i>C. termini</i> Enghoff, 2014	endemic	1800–1955
25. <i>C. tintin</i> Enghoff, 2014	endemic	2100
26. <i>C. vandenspiegelii</i> Enghoff, 2014	endemic	1800–1900
27. <i>C. vilici</i> Enghoff, 2014	endemic	1908–1955
28. <i>Damacornu transversum</i> gen. et sp. nov.	endemic	1400
29. <i>Geotypodon millemanus</i> Enghoff, 2016	endemic	1145–1500
30. <i>G. submontanus</i> Enghoff, 2016	endemic	1145
31. <i>G. papei</i> sp. nov.	endemic	339–650
32. <i>Helicochetus dimidiatus</i> (Peters, 1855)	Tanzania, widespread; Mozambique (Enghoff <i>et al.</i> 2016)	339
33. <i>H. mutaba</i> Kraus, 1960	Tanzania, D.R. of the Congo	1700–3000
34. <i>Hoffmanides dissutus</i> (Hoffman, 1963)	Tanzania	350
35. <i>Prionopetalum asperginis</i> Enghoff, 2016	endemic	550–750
36. <i>P. kraepelini</i> (Attems, 1896)	Tanzania, widespread (Enghoff 2016b)	300–339
37. <i>Spinotarsus fortehamatus</i> sp. nov.	endemic	850
38. <i>Utiliverpa decapsulatrix</i> Enghoff, 2016	endemic	?
39. <i>Yia geminispina</i> Enghoff, 2016	endemic	1100

Out of the 39 odontopygid species, no less than 35 are known only from the Udzungwa Mts and should be regarded as Udzungwa endemics. No phylogenetic analyses are available for any Udzungwan odontopygid, but nevertheless some preliminary geographical patterns may be inferred (Fig. 10):

- The endemic *Chaleponcus dabagaensis* group seems to be most closely related to *C. altirungwensis* Enghoff, 2017 from Mt Rungwe, SW of the Udzungwas, see Enghoff (2017a, 2017b).

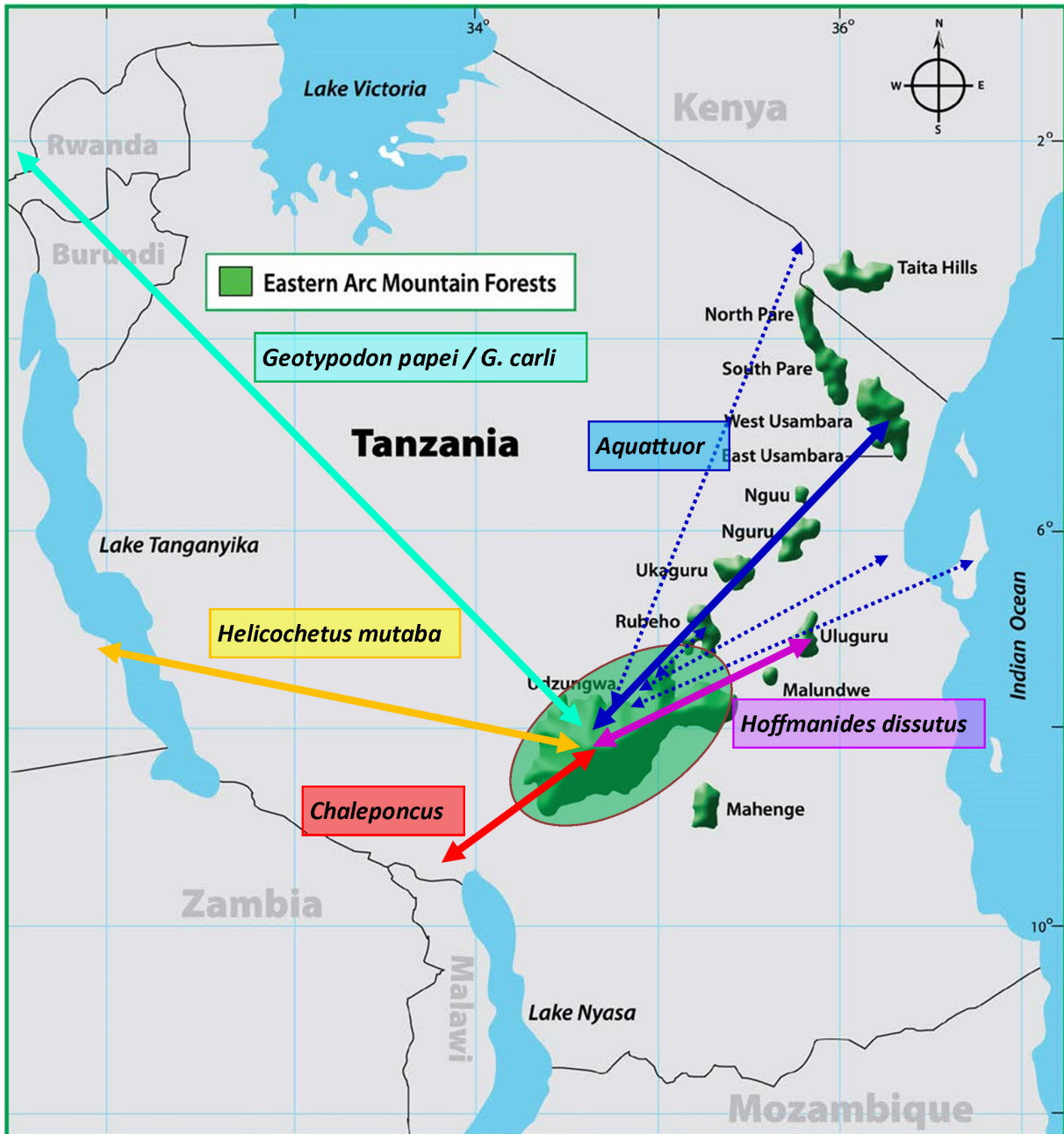


Fig. 10. Geographical relationships of the Odontopygidae of the Udzungwa Mts. See main text for explanation. No relationships are shown for the three endemic genera (*Casuariverpa* Enghoff, 2016, *Utiliverpa* Enghoff, 2016 and *Yia* Enghoff, 2016), nor for the Udzungwa species of the large genus *Spinotarsus* Attems, 1909, nor for the widespread species *Helicochetus dimidiatus* (Peters, 1855) and *Prionopetalum kraepelini* (Attems, 1896). Base map by permission of the Eastern Arc Mountains Conservation Endowment Fund.

- The genus *Aquattuor* (five endemic species in the Udzungwas) has a further species endemic to the E Usambara Mts, and still one (or two?) species recorded from several sites in NE Tanzania, where they may have arrived by means of human transportation (Enghoff 2016b; Enghoff & Frederiksen 2015).
- *Hoffmanides dissutus* (Hoffman, 1963) is also known from the Uluguru Mts.
- *Geotypodon papei* sp. nov. is very similar to and presumably closely related to *G. carli* Kraus, 1960 (Democratic Republic of the Congo).
- *Helicochetus mutaba* is also known from the eastern Democratic Republic of the Congo.

Odontopygid “tracks” thus connect the Udzungwa Mts with other mountain blocks in the (extended) Eastern Arc (*Aquattuor*, *Chaleponcus* and *Hoffmanides dissutus*, but surprisingly also with areas in the Democratic Republic of the Congo further west.

The altitudinal distribution of the odontopygids (Fig. 11) shows a striking pattern: the endemic species swarm constituted by the *Chaleponcus dabagaensis* group (Enghoff 2014) occupies high altitudes (species medians ranging from 1520 (*C. circumvallatus* Enghoff, 2014) to 2100 m a.s.l. (*C. tintin* Enghoff, 2014). Other endemic species occur at lower altitudes (medians: 400–1799 m a.s.l.), whereas three out of four non-endemic species all occur at low altitudes (medians: 300–399 m), as might be expected.

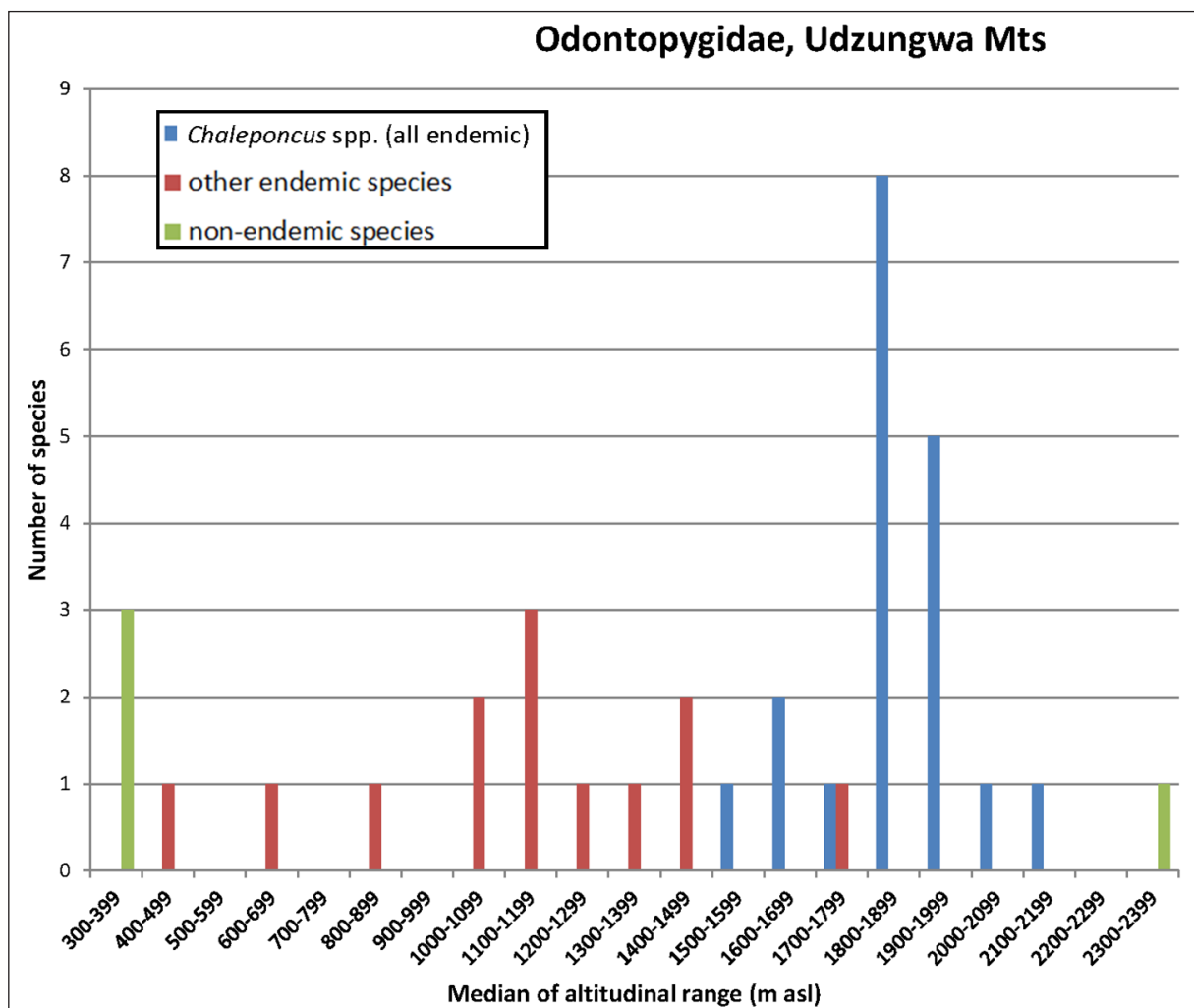


Fig. 11. Odontopygidae of the Udzungwa Mts, altitudinal distribution. Based on medians of the altitudinal ranges shown in Table 3.

The striking exception is *Helicochetus mutaba* with a median occurrence altitude in the Udzungwas of 2350 m a.s.l. It seems highly unlikely that this species, described from the Democratic Republic of the Congo (the altitude of the type locality, Mutaba, is unknown, but the town of Kirungu in the territory of which Mutaba was stated to be situated, is at an altitude of 400 m a.s.l.), should occur naturally at 2000–3000 m a.s.l. in the Udzungwas (as well as at 1700 m a.s.l. at Mazombo), another hint that the current species-level taxonomy of *Helicochetus* is in need of further scrutiny.

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