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A mountain of millipedes III: A new genus for three new species from the Udzungwa Mountains and surroundings, Tanzania, as well as several 'orphaned' species previously assigned to *Odontopyge* Brandt, 1841 (Diplopoda, Spirostreptida, Odontopygidae)

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Abstract. The new genus *Geotypodon* gen. nov. is described. It includes two species from the Udzungwa Mountains: *G. millemanus* gen. et sp. nov. (type species) and *G. submontanus* gen. et sp. nov., one species from nearby Iringa: *G. iringensis* gen. et sp. nov., and 18 previously described species hitherto incorrectly assigned to *Odontopyge* Brandt, 1841.

Keywords. Eastern Arc, taxonomy, new species.

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Introduction

This is the third in a series of articles about the millipedes, especially the endemic Afrotropical family Odontopygidae, of the Udzungwa Mountains, Tanzania. For general information on the Odontopygidae and the Udzungwa Mountains see the first article in the series (Enghoff 2014); see also Enghoff & Frederiksen (2015).

In the present article three further new odontopygid species are described from the Udzungwa Mountains and their immediate surroundings (Fig. 1). The new species resemble several species which were assigned to the genus *Odontopyge* Brandt, 1841 by Kraus (1960) and authors before him. However, Hoffman (1991) showed that *Odontopyge* had been misinterpreted by virtually everybody dealing with the genus after its original description and that *Odontopyge* is the correct name for a genus until then known as *Omopyge* Manfredi, 1941. Hoffman (1991) rectified the situation and formally synonymized *Omopyge* under *Odontopyge*, but by this action he left a large number of species originally described in or subsequently transferred to *Odontopyge* 'orphaned', i.e., without a valid genus name. Some of these have been transferred to other genera by Hoffman & Howell (1981, 2012), Hoffman (2000, 2002) and Frederiksen & Enghoff (2015), but very many remain orphaned.

Kraus (1960) was aware of the situation and therefore accepted Attems' (1909) designation of *Odontopyge kilimandjaronus* Attems, 1909, as type species of *Odontopyge*, mentioning that the ICZN would be asked to make Attems' designation valid. This, however, has not happened, and Attems' type designation remains invalid, as does that of Silvestri (1896: *Julus bicuspidatus* Brandt, 1841) (Jeekel 1970).

Table 1 lists all species assigned to *Odontopyge* by Kraus (1960) and subsequent authors, with an indication of their subsequent re-classification. Part 2 of the table includes the dubious species of '*Odontopyge*' listed by Kraus (1960) – many of these names were based on female specimens and may never be resolvable.

To accommodate the new species described here, a new genus is established to which several of the orphaned species can be assigned as well.

Material and methods

The material for this article comes from the zoological collections of the Natural History Museum of Denmark, University of Copenhagen (ZMUC). The specimens were partly collected during field trips

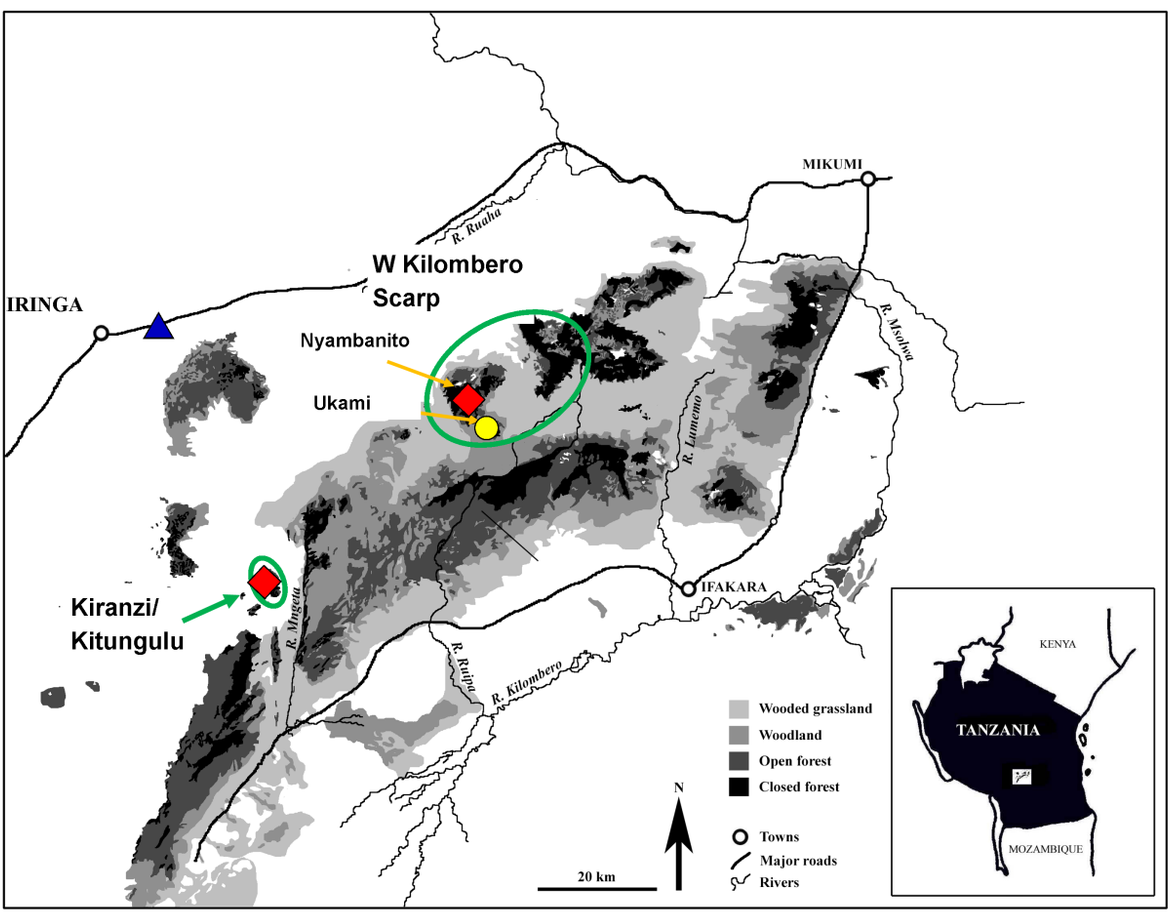

Fig. 1. Map of the Udzungwa Mountains, showing the collecting sites for the three new *Geotypodon* species, as well as names of the Forest Reserves in question and names of individual mountains in West Kilombero FR. Red diamonds = *G. millemanus* gen. et sp. nov., yellow dot: *G. submontanus* gen. et sp. nov., blue triangle: *G. iringensis* gen. et sp. nov. Based on fig. 1 in Marshall *et al.* (2010) and information in Doody *et al.* (2001).

Table 1. Species of *Odontopyge* sensu auctorum *nec* Brandt, 1841. The table is based on Kraus (1960), with updates as indicated. Part 1 of the list contains species placed by Kraus and subsequent authors in *Odontopyge.* Part 2 contains the "*nomina dubia*" listed by Kraus (1960). Numerous additional species originally described in *Odontopyge* and transferred to other genera by Kraus and his predecessors are not listed.

Part 1. Species assigned to '*Odontopyge* sensu auctorum' by Kraus and subsequent authors.

	Species	Current placement	Reference
Odontopyge	*angolana* Kraus, 1958	*Geotypodon* **comb. nov.**	
Odontopyge	*antrophila* Attems, 1951	'orphaned'	
Odontopyge	*arrogans* (Attems, 1935)	'orphaned'	
Odontopyge	*astragalus* (Attems, 1912)	'orphaned'	
Odontopyge	*bayoni* Silvestri, 1910	*Geotypodon* **comb. nov.**	
Odontopyge	*carli* Kraus, 1960	*Geotypodon* **comb. nov.**	
Odontopyge	*citernii* Silvestri, 1910	'orphaned'	
Odontopyge	*delitescens* Attems, 1935	'orphaned'	
Odontopyge	*dewittei* Kraus, 1958	'orphaned'	
Odontopyge	*difficilis* Silvestri, 1895	'orphaned'	
Odontopyge	*dispersa* Carl, 1909	*Geotypodon* **comb. nov.**	
Odontopyge	*dorsalis* Carl, 1909	*Calyptomastix*	Hoffman (2012)
Odontopyge	*errata* Kraus, 1960	*Geotypodon* **comb. nov.**	
Odontopyge	*francosudanica* Attems, 1914	'orphaned'	
Odontopyge	*gracilitarsus* Kraus, 1958	*Geotypodon* **comb. nov.**	
Odontopyge	*heteromodesta* Kraus, 1960	*Geotypodon* **comb. nov.**	
Odontopyge	*indecisus* Pierrard, 1970	*Geotypodon* **comb. nov.**	Pierrard (1970)
Odontopyge	*intermedia* Carl, 1909	*Geotypodon* **comb. nov.**	
Odontopyge	*kakandae* Kraus, 1958	*Calyptomastix*	Hoffman (2012)
Odontopyge	*kandti kandti* Carl, 1909	'orphaned'	
Odontopyge	*kandti denticulata* Attems, 1937	'orphaned'	
Odontopyge	*kilembeensis* Demange, 1990	'orphaned'	Demange (1990)
Odontopyge	*kilimanjarona* Attems, 1909	*Rhamphidarpoides*	Frederiksen & Enghoff (2015)
Odontopyge	*latifolia* (Attems, 1914)	*Callistodontopyge*	Hoffman & Howell (1981)
Odontopyge	*leviceps* (Attems, 1909)	*Calyptomastix*	Hoffman (2012)
Odontopyge	*medjensis* (Chamberlin, 1927)	'orphaned'	
Odontopyge	*meneliki* Attems, 1927	'orphaned'	
Odontopyge	*multianulata* Attems, 1914	*Geotypodon* **comb. nov.**	
Odontopyge	*ollieri* Silvestri, 1907	*Geotypodon* **comb. nov.**	
Odontopyge	*paludosa* (Attems, 1953)	'orphaned'	
Odontopyge	*pardalis* (Gerstäcker, 1873)	*Calyptomastix*	Hoffman (2012)
Odontopyge	*picea* Attems, 1938	*Geotypodon* **comb. nov.**	
Odontopyge	*procera* Attems, 1914	*Geotypodon* **comb. nov.**	
Odontopyge	*procerula* Kraus, 1960	*Geotypodon* **comb. nov.**	
Odontopyge	*punctulata* Attems, 1912	*Geotypodon* **comb. nov.**	
Odontopyge	*scaphula* Attems, 1912	'orphaned'	
Odontopyge	*sennae* Brölemann, 1903	*Geotypodon* **comb. nov.**	
Odontopyge	*severini* Silvestri, 1897	'orphaned'	
Odontopyge	*simplex* (Chamberlin, 1927)	'orphaned'	

Odontopyge	*specularis* Attems, 1927	*Geotypodon* **comb. nov.**
Odontopyge	*stenotarsa* Attems, 1938	*Geotypodon* **comb. nov.**
Odontopyge	*terebrum* Ribaut, 1907	'orphaned'
Odontopyge	*tumidens* Karsch, 1881	'orphaned'
Odontopyge	*uvirensis* Kraus, 1960	'orphaned'
Odontopyge (?)	*vanutellii* Silvestri, 1898	'orphaned'

Part 2. *Nomina dubia* listed by Kraus (1960).

Original genus (subgenus)	**Species**	**Current placement**	**Reference**
Spirostreptus (Odontopyge)	*acutus* Karsch, 1881		
Spirostreptus (Odontopyge)	*aequalis* Porath, 1982		
Odontopyge	*amaura* Brolemann, 1926		
Odontopyge	*angolensis* Karsch, 1881		
Odontopyge	*anomala* Silvestri, 1896		
Odontopyge	*attenuata* Silvestri, 1895		
Odontopyge	*bicolor* Silvestri, 1897		
Iulus (Spirostreptus)	*bicuspidatus* Brandt, 1841		
Spirostreptus	*binodifer* Voges, 1878		
Ctenoiulus	*chatelainei* Cook, 1893	*Ctenoiulus*	Hoffman (1980)
Odontopyge	*dilatata* Brölemann, 1905		
Odontopyge	*dimidiatiformis* Porat, 1893		
Odontopyge	*diversicolor* Silvestri, 1895		
Odontopyge	*diversifacies* Silvestri, 1898		
Odontopyge	*doriae* Silvestri, 1896		
Odontopyge	*ecarinata* Porat, 1894		
Odontopyge	*exquisita* Silvestri, 1896		
Iulus (Spirostreptus)	*flavotaeniatus* Brandt, 1841		
Spirostreptus (Odontopyge)	*foveolatus* Porath, 1872		
Spirostreptus (Odontopyge)	*furcatus* Karsch, 1881	= *Ctenoiulus chatelainei* Cook, 1893	Hoffman (1980)
Odontopyge	*gestrii* Silvestri, 1896		
Iulus (Spirostreptus)	*gracilicornis* Brandt, 1841		
Odontopyge	*jallae* Silvestri, 1896		
Iulus (Spirostreptus)	*kollarii* Brandt, 1841	*Odontopyge*	Hoffman (1991)
Odontopyge	*litoranea* Silvestri, 1897		

Spirostreptus (Odontopyge)	*maculatus* Karsch, 1881	*Callistodontopyge*	Hoffman & Howell (1981)
Spirostreptus (Odontopyge)	*mitellatus* Karsch, 1881	*Callistodontopyge*	Hoffman (2002)
Spirostreptus (Odontopyge)	*praetextus* Porath, 1872		
Odontopyge	*puerilla* Daday, 1889		
Spirostreptus (Odontopyge)	*puncticaudis* Porath, 1872		
Odontopyge	*rubripes* Silvestri, 1895		
Odontopyge	*ruspolii* Silvestri, 1896		
Spirostreptus	*scaliger* Gerstäcker, 1873		
Odontopyge	*trivialis* var. *strigulosa* Porat, 1891		
Odontopyge	*subelegans* Silvestri, 1897		
Spirostreptus	*sugillatus* Gerstäcker, 1873	*Callistodontopyge*	Hoffman & Howell (1981)
Odontopyge	*trivialis* Porat, 1894		
Odontopyge	*uebicola* Silvestri, 1896		

by ZMUC staff and students, partly by the NGO Frontier Tanzania (see Marshall *et al.* 2001). A total of seven male specimens was examined. All are kept in 70% alcohol.

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

See Enghoff (2014) for the description standards used.

Abbreviations for morphological terms used in the descriptions and on illustrations

atl = anterior distal lobe of telomere
bl = basal lamella of telomere
cx = coxa
itl = intermediate distal lamella of telomere
lc = lateral concavity of coxa
lfl = longitudinally folded lamella
ll = longitudinal lamella
mf = anteriad metaplical flange
mla = metaplical lamella
mp = metaplica
msp = metaplical spine-like process
pn = posttorsal narrowing
pp = proplica
ptl = posterior distal lobe of telomere
pts = proximal telomeral spine

slm = solenomere
tl = terminal lobe of telomere
tt = torsotope

Abbreviations used in the text, other than the above

asl = above sea level
FR = Forest Reserve
ZMUC = Natural History Museum of Denmark (Zoological Museum)

Results

Taxonomy

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

Geotypodon gen. nov.
urn:lsid:zoobank.org:act:54706BDE-AF06-42BC-A2B3-F2D23A097B28

Type species

G. millemanus gen. et sp. nov.

Diagnosis

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 posttorsal narrowing without spines, a division of the telopodite into solenomere and telomere immediately distal to posttorsal narrowing, a spine emerging from the base of the telomere and curving more or less parallel to the basal parts of the solenomere, a slender, whip-like, smooth solenomere without any outgrowths or appendages (except sometimes a *tiny* subapical spine), a highly three-dimensional telomere consisting of various lobes and lamellae with largely smooth margins.

Etymology

An anagram of *Odontopyge*. To be regarded as masculine in analogy with other names ending in –odon.

Other species included:

G. angolanus (Kraus, 1958) (**comb. nov.** ex *Odontopyge*)
G. bayoni (Silvestri, 1910) (**comb. nov.** ex *Odontopyge*)
G. carli (Kraus, 1960) (**comb. nov.** ex *Odontopyge*)
G. dispersus (Carl, 1909) (**comb. nov.** ex *Odontopyge*)
G. erratus (Kraus, 1960) (**comb. nov.** ex *Odontopyge*)
G. gracilitarsus (Kraus, 1958) (**comb. nov.** ex *Odontopyge*)
G. heteromodestus (Kraus, 1960) (**comb. nov.** ex *Odontopyge*)
G. indecisus (Pierrard, 1970) (**comb. nov.** ex *Odontopyge*)
G. intermedius (Carl, 1909) (**comb. nov.** ex *Odontopyge*)
G. iringensis **gen. et sp. nov.**
G. multianulatus (Attems, 1914) (**comb. nov.** ex *Odontopyge*)
G. ollieri (Silvestri, 1907) (**comb. nov.** ex *Odontopyge*)

G. piceus (Attems, 1938) (**comb. nov.** ex *Odontopyge*)
G. procerus (Attems, 1914) (**comb. nov.** ex *Odontopyge*)
G. procerulus (Kraus, 1960) (**comb. nov.** ex *Odontopyge*)
G. punctulatus (Attems, 1912) (**comb. nov.** ex *Odontopyge*)
G. sennae (Brölemann, 1903) (**comb. nov.** ex *Odontopyge*)
G. specularis (Attems, 1927) (**comb. nov.** ex *Odontopyge*)
G. stenotarsus (Attems, 1938) (**comb. nov.** ex *Odontopyge*)
G. submontanus **gen. et sp. nov.**

Descriptive notes

Species of *Geotypodon* gen. nov. have a typical odontopygid habitus (Fig. 2) and are mostly medium-sized by odontopygid standards (cf. Kraus 1966). Published numbers of podous rings range from 49 (*G. ollieri*) to 72 (*G. multianulatus*) (one has been subtracted from the published numbers because these include the telson), and published male body diameters range from 1.7 mm (*G. sennae*) to 5.5 mm (*G. specularis*). The majority of species have 54–66 podous rings and a diameter of 4.3–5.5 mm, but there is a group of smaller species (*G. angolanus*, *G. erratus*, *G. heteromodestus*, *G. ollieri*) with 49–54 podous rings and a diameter of 2.2–3.2 mm. *G. sennae* is a particularly slender species: 66–68 podous rings and 1.7 mm diameter, and *G. multianulatus*, true to its name (at least as misspelled by Kraus (1960): *multiannulatus*), stands out with 72 podous rings and 4.8 mm diameter. Of the new species described here, *G. millemanus* gen. et sp. nov. falls neatly in the main group, *G. submontanus* gen. et sp. nov. is slightly more slender than the main group, whereas *G. iringensis* gen. et sp. nov. has a larger body diameter than any other described congener (Fig. 3).

Several of the species assigned to *Geotypodon* gen. nov. have the same type of limbus (with hand-like lobes) as the type species; this is true of *G. angolanus*, *G. carli*, *G. erratus*, *G. gracilitarsus*, *G. procerulus* and *G. punctulatus* (Attems 1912; Kraus 1958, 1960) as well as *G. submontanus* gen. et sp. nov. Other species have other types of limbus: *G. heteromodestus*, *G. indecisus*, *G. multianulatus*, *G. piceus*, *G. sennae*, *G. specularis* and *G. stenotarsus* (Attems 1914, 1927, 1938, 1953 [*G. heteromodestus*, as *Haplothysanus modestus*]; Brölemann 1903; Pierrard, 1970), as well as *G. iringensis* gen. et sp. nov. The limbus of *procerus* somewhat but not quite resembles that of *G. millemanus* gen. et sp. nov. (Attems 1914), and no information is available about this character in *G. bayoni*, *G. dispersus* or *G. intermedius*. On the other hand, several species outside *Geotypodon* gen. nov. as here defined have the same type of limbus as *G. millemanus* gen. et sp. nov.. This is, for example, the case for several species of *Rhamphidarpoides* Kraus, 1960, including *R. kilimandjarona* (Attems, 1909), *R. ruandensis* Kraus, 1960, and *R. regina* (Carl, 1909) (Attems 1914; Kraus 1960; Frederiksen & Enghoff 2015), *Helicochetus* spp. (e.g., Kraus 1966: figs 83–87), *Solenozophyllum kazibaense* Kraus, 1958 and '*Odontopyge*' *dewittei* Kraus, 1958.

Remarks

Although *Geotypodon* gen. nov. is proposed to accommodate several species of *Odontopyge* sensu Kraus (1960), its diagnosis and circumscription are narrower. Species of *Odontopyge* sensu Kraus (1960), may thus lack a long basad metaplical spine on the anterior side of the coxa (present in *Geoptypodon*), may have spines in the torsal region (absent in *Geotypodon* gen. nov.), and may lack a spine emerging from the base of the telomere and curving more or less parallel to the basal parts of the solenomere (present in *Geotypodon* gen. nov.).

None of the characters listed in the diagnosis are exclusive to *Geotypodon* gen. nov.: Notably, the conspicuous coxal metaplical anterior spine is also found in, e.g., several species of *Rhamphidarpoides* and *Raduliverpa* Frederiksen & Enghoff, 2015 (Frederiksen & Enghoff 2015) as well as *Spinotarsus* Attems, 1909 (Kraus 1960, 1966), but the species in question differ from *Geotypodon* gen. nov. by

either having the solenomere with spines or fluting (*Rhamphidarpoides*, *Raduliverpa*) or by having characteristic structures on the telomere ("Basallamelle" and/or "Bogenlamelle" sensu Kraus 1960) (*Spinotarsus*).

A spine emerging from the base of the telomere is also found in several other '*Odontopyge'* species, e.g., *citernii* Silvestri, 1898, *difficilis* Silvestri, 1895, and *severini*, Silvestri, 1897 – see Kraus (1960), where this spine is called "Tibialdorn". It is also found in *Rhamphidarpoides* species (Frederiksen & Enghoff 2015), in *Calyptomastix kakandae* (Kraus, 1958), as well as several *Spinotarsus* species, etc. In the *Chaleponcus dabagaensis*-group there is a spine at almost the same place, but emerging from the base of the solenomere instead of the base of the telomere (Enghoff 2014).

Considering the notorious mosaic-like distribution of morphological characters throughout the family, the genus *Geotypodon* gen. nov. as defined here is quite possibly not a monophyletic group, cf. the Discussion section (see below). Until a more satisfactory analysis of relationships within Odontopygidae becomes available, the new genus can, however, serve as a 'home' for several (but not all) 'orphaned' species hitherto classified in *Odontopyge*.

Geotypodon millemanus gen. et sp. nov.
urn:lsid:zoobank.org:act:D65889F9-1063-4FBB-AEBB-A594052220B1
Figs 1–4

Diagnosis

A species of *Geotypodon* gen. nov. in which the gonopod coxal metaplica is produced mesad in a thin lamella, a small longitudinal lamella, perpendicular to the other, is present on the anterior part of the

Fig. 2. *Geotypodon millemanus* gen. et sp. nov., paratype from West Kilombero Scarp FR after nine years in alcohol. Photograph by N. Ioannou.

metaplica, the telomere is apically divided into two lobes of approximately equal size, and the limbus lobes are multi-cusped, hand-like. It shares these characters with *G. submontanus* gen. et sp. nov., but differs from that species in larger size, straight mesal margin of metaplical lamella and absence of a spine-like process on the posterior apical telomeral lobe.

Etymology

The name is a Latin noun in apposition, meaning "a thousand hands" and referring to the hand-like limbus lobes. A specimen with a diameter of 5 mm will have a body perimeter of approximately 15 mm. Assuming that the limbus covers only 10 mm, and taking into account that each "hand" occupies about 10 microns of the perimeter, each body ring will carry about a thousand "hands", and a specimen with 60 body rings will therefore have roughly 60,000 "hands".

Material studied (total: 4 ♂♂)

Holotype

TANZANIA: ♂, Iringa Region, Iringa District, Udzungwa Mts, West Kilombero Scarp FR, 07°50'38.4"S, 36°22'17.6" E, montane forest, 1390–1410 m asl, Plot Paradiso, casual, 18 Nov. 2000, Frontier Tanzania leg. (ZMUC00040350).

Paratypes

TANZANIA: 2 ♂♂, same data as holotype (ZMUC100969, ZMUC00040345); 1 ♂, Iringa Region, Iringa District, Udzungwa Mts, Kiranzi-Kitungulu FR, 08°09' S, 35°05' E, forest, 1500 m asl, Jan. 1996, M. Andersen, P. Gravlund & A. Jakobsen leg. (ZMUC00046991).

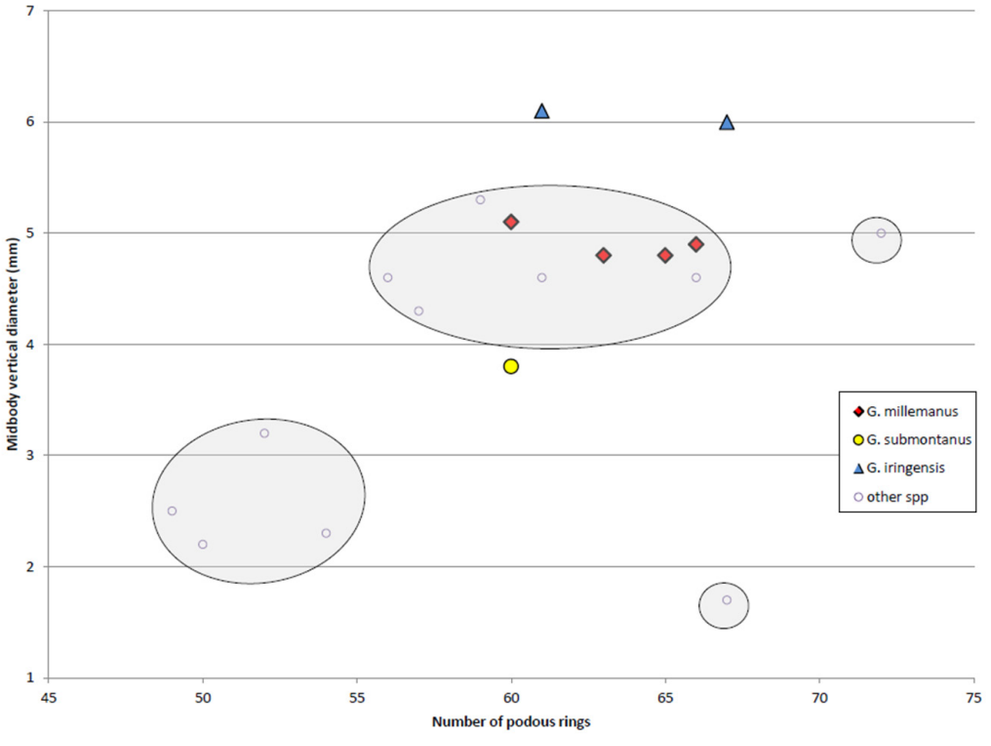

Fig. 3. Body size of males of *Geotypodon* spp. Bold symbols indicate numbers of podous rings and midbody vertical diameter of the new species described here. Small circles and shaded areas indicate published measurements for other *Geotypodon* species.

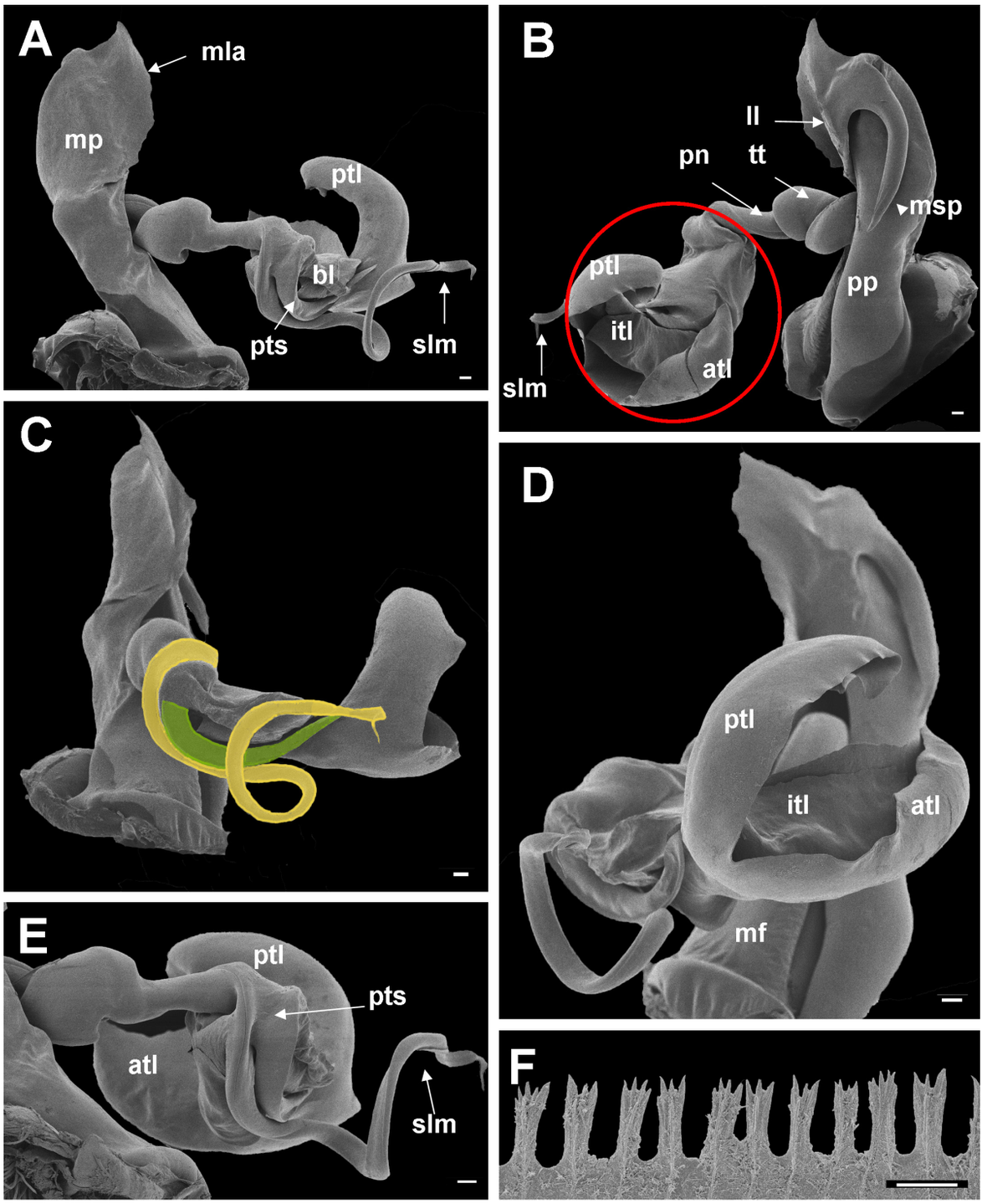

Fig 4. *Geotypodon millemanus* gen. et sp. nov., paratype from Kiranzi-Kitungulu FR. **A–E**: Right gonopod. **A**. Posterior view. **B**. Anterior view, telomere in red oval. **C**. (Posterior-)mesal view, solenomere (yellow) and proximal telomeral spine (green) coloured. **D**. (Anterior-)mesal view. **E**. Telomere (part of coxa at lower left), basal (dorsal) view. **F**. Limbus. Abbreviations: *atl* = anterior distal lobe of telomere; *bl* = basal lamella of telomere; *itl* = intermediate distal lamella of telomere; *ll* = longitudinal lamella; *mf* = anteriad metaplical flange; *mla* = metaplical lamella; *mp* = metaplica; *msp* = metaplical spine-like process; *pn* = posttorsal narrowing; *pp* = proplica; *ptl* = posterior distal lobe of telomere; *pts* = proximal telomeral spine; *slm* = solenomere; *tt* = torsotope. Scales: A–E = 0.1 mm, F = 0.01 mm.

Type locality

TANZANIA, Iringa Region, Iringa District, Udzungwa Mts, West Kilombero Scarp FR, 07°50'38.4" S, 36°22'17.6" E, montane forest, 1390–1410 m asl, cf. Marshall *et al*. (2001).

Description

Size. Length ca. 9 cm. Diameter 4.8–5.1 mm. 60–66 podous rings, no apodous rings in front of telson.

Colour. After 15 years in alcohol somewhat faded, but pattern still evident. Upper part of head blackish, lower part yellowish. Overall colour of body ventrally and laterally yellowish. Posterior ca. 40% of metazona amber, in front of amber zone a blackish zone; blackish zone narrow laterally, becoming wider dorsally where extending onto posterior ¼–⅓ of prozona; resulting mid-dorsal dark band becoming narrower towards head. Telson blackish with yellowish margins, legs yellowish.

Head. Without peculiarities.

Collum. With a marginal and a submarginal furrow.

Body rings. Almost perfect cylinders, not vaulted; suture straight; ozopores ca. three diameters behind suture.

Limbus (Fig. 4). Consisting of isolated hand-like lobes of ca. 10 microns' length, each with 3–6 'fingers' and each with a ridge running along its length.

Anal valves. Each with a well-developed dorsal spine and a smaller, yet distinctive ventral one; margin raised, with 3 setae not borne on tubercles.

Male legs. From 5th pair with postfemoral and tibial pads on all legs, except last four pairs; tibial pads absent from several pairs in front of these.

Gonopod coxa (Fig. 4). Slender, slightly sigmoid. Proplica (*pp*) ending in small proplical lobe hidden behind anterior edge of metaplical lamella (*mla*), on Fig. 4B. Metaplica (*mp*) with poorly developed basal anteriad flange (*mf*), disto-mesally expanded into thin lamella (*mla*), with a straight mesal margin, tip of metaplica formed by blunt-triangular extension of *mla*; a second smaller longitudinal lamella (*ll*) on anterior surface of metaplica partly covering proplical lobe; metaplica at level of proplical lobe, with a long, slightly curved spine-like process (*msp*) directed toward base of coxa on its anterior side.

Gonopod telopodite (Fig. 4). Arculus 90°. Torsotope (*tt*) simple, compact, without processes (Fig. 4B). Posttorsal narrowing (*pn*) pronounced, very slender, without processes or spines (Fig. 4B). Telopodite just distal to posttorsal narrowing dividing into slender, whip-like solenomere and complicated telomere. Solenomere (*slm*) curved in 3 dimensions (at least on preserved specimens), apically pointed, without any outgrowths (Fig. 4A, C, E). Efferent groove continuing from posttorsal narrowing onto solenomere and running all the way to its tip. Telomere with long, stout basal spine (*pts*), spine first curving in parallel with solenomere, but then becoming straight and directed mesad (Fig. 4A, C). Telomere close to *pts* with a basal lamella (*bl*) (Fig. 4A), followed by several complicated lamellar parts; basal part of telomere partly sheathing base of solenomere, distal part divided into two equally-sized thin lobes (*atl* and *ptl*), which initially diverge at ca. 90° but then curve towards each other (Fig. 4B, D–E). An intermediate lamella (*itl*) lodged in the space between *atl* and *plm* (Fig. 4D). Surfaces of *atl* and *ptl* facing each other, concave, margins of each lobe subparallel, smooth; telomere entirely without denticles or spines.

Distribution and habitat

Known from West Kilombero FR and Kiranza-Kitungulu FR. Altitudinal range: 1145–1500 m asl. Haibtat: (montane) forest.

Coexisting species

In Kiranza-Kitungulu FR *G. millemanus* gen. et sp. nov. was found in the same sample as *Chaleponcus dabagaensis* Kraus, 1958 and *C. gracilior* Enghoff, 2014. In West Kilombero FR no other odontopygids were found in the same sample as *G. millemanus* gen. et sp. nov., but *G. submontanus* gen. et sp. nov., *Chaleponcus basiliscus* Enghoff, 2014, *C. circumvallatus* Enghoff, 2014, *C. gracilior*, *C. ibis* Enghoff, 2014, *C. netus* Enghoff, 2014, *C. tintin* Enghoff, 2015, *Aquattuor longipala* Enghoff 2015 and *A. udzungwensis* Enghoff, 2015 also occur in West Kilombero FR.

Geotypodon submontanus gen. et sp. nov.

urn:lsid:zoobank.org:act:02DBFF6A-56A1-4EB3-9001-AF063F22C1B6

Figs 1, 3, 5

Diagnosis

A species of *Geotypodon* gen. nov. in which the gonopod coxal metaplica is produced mesad in a thin lamella, a small longitudinal lamella, perpendicular to the other, is present on the anterior part of the metaplica, the telomere is apically divided into two lobes of approximately equal size, and the limbus lobes are multi-cusped, hand-like. Shares these characters with *G. millemanus* gen. et sp. nov., but differs from that species in smaller size, bicuspid mesal margin of metaplical lamella and presence of a spine-like process on the posterior apical telomeral lobe.

Etymology

The name is a Latin adjective referring to the habitat.

Material studied (total: 1 ♂)

Holotype

TANZANIA: ♂, Iringa Region, Iringa District, Udzungwa Mts, West Kilombero Scarp FR, 07°53'19.5" S, 36°23'11.6" E, submontane forest, 1145 m asl, trapsite Ukami, casual, Nov. 2000, Frontier Tanzania leg. (ZMUC00046992).

Type locality

TANZANIA, Iringa Region, Iringa District, Udzungwa Mts, West Kilombero Scarp FR, 07°53'19.5" S, 36°23'11.6" E, submontane forest, 1145 m asl, cf. Marshall *et al*. (2001).

Description

Size. Length ca. 7 cm. Diameter 3.8 mm. 60 podous rings, no apodous rings in front of telson.

Other characters. As in *G. millemanus* gen. et sp. nov., with the following exceptions:
- telson (after 15 years in alcohol) yellowish,
- postfemoral and tibial pads on male legs smaller,
- metaplical lamella (*mla*) produced mesad, with two sharp angles (Fig. 5A–B),
- posterior distal lobe of telomere (*ptl*) apically with a dark, spine-like process (Fig. 5E).

Distribution and habitat

Known only from West Kilombero FR. Altitude: 1145 m asl. Habitat: submontane forest.

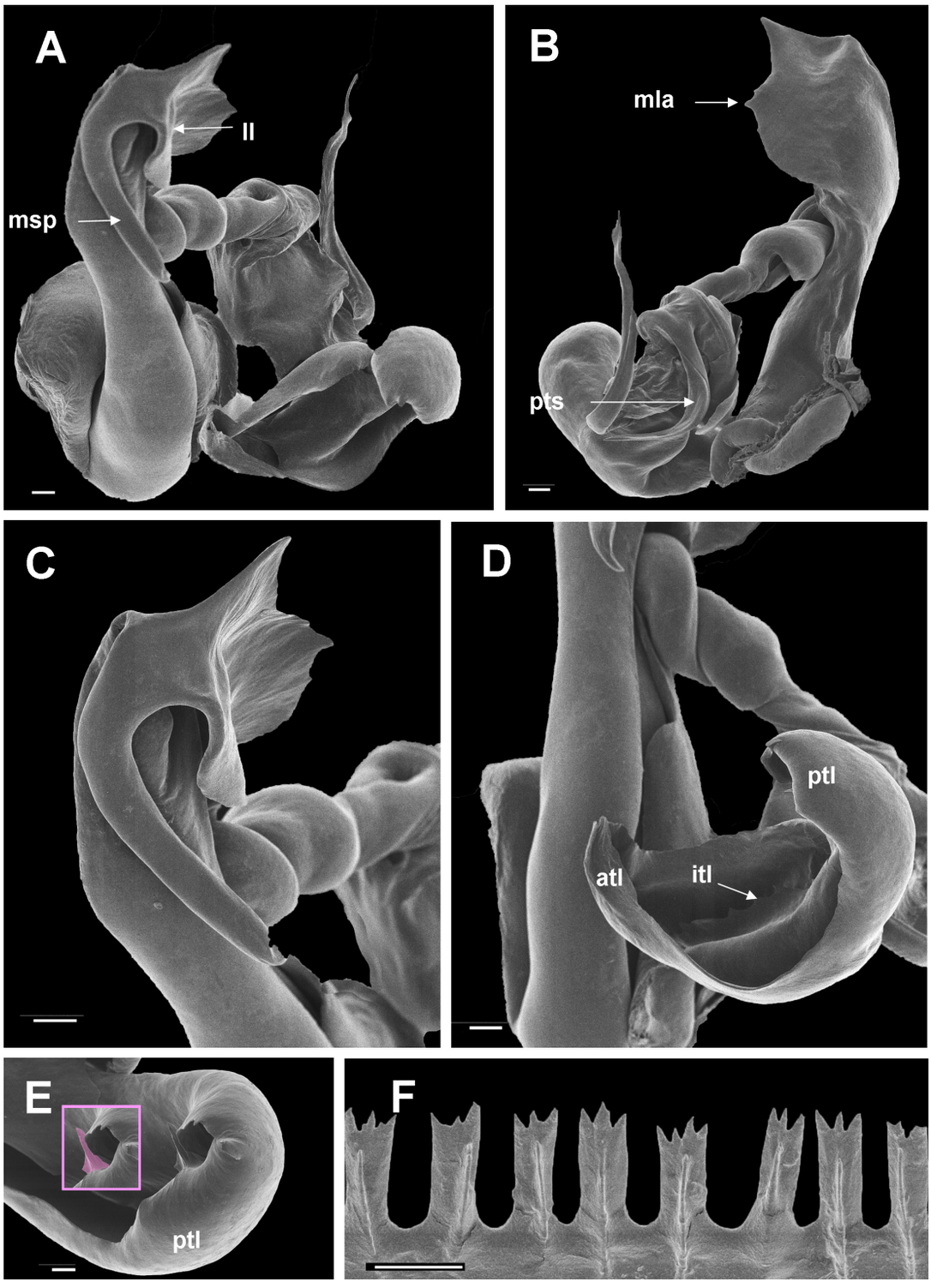

Fig. 5. *Geotypodon submontanus* gen. et sp. nov., holotype. **A–E**. Left gonopod. **A**. Anterior view. **B**. Posterior view. **C**. Apical part of coxa and proximal part of telopodite, anterior view. **D**. (Anterior-) mesal view. **E**. Posterior distal lobe of telomere; insertion highlights spine-like process. **F**. Limbus. Abbreviations: *atl* = anterior distal lobe of telomere; *itl* = intermediate distal lamella of telomere; *ll* = longitudinal lamella; *mla* = metaplical lamella; *msp* = metaplical spine-like process; *ptl* = posterior distal lobe of telomere; *pts* = proximal telomeral spine. Scales: A–D = 0.1 mm, E = 0.05 mm, F = 0.01 mm.

Coexisting species

No other odontopygids were found in the same sample as *G. submontanus* gen. et sp. nov., but *G. millimanus* gen. et sp. nov., *Chaleponcus basiliscus* Enghoff, 2014, *C. circumvallatus* Enghoff, 2014, *C. gracilior*, *C. ibis* Enghoff, 2014, *C. netus* Enghoff, 2014, *C. tintin* Enghoff, 2015, *Aquattuor longipala* Enghoff, 2015 and *A. udzungwensis* Enghoff, 2015 also occur in West Kilombero FR.

Geotypodon iringensis gen. et sp. nov.
urn:lsid:zoobank.org:act:0171D40F-1E0D-4194-8D1B-045D46F92095
Figs 1, 3, 6

Diagnosis

A species of *Geotypodon* gen. nov. in which the gonopod coxal metaplica is apically rounded, the telomere is apically divided into a small posterior lobe and a large anterior lobe, which gives rise to a strongly curved terminal lobe, and the limbus lobes are pointed triangular.

Etymology

The species is named after the type locality.

Material studied (total: 2 ♂♂)

Holotype

TANZANIA: ♂, Iringa Region, 10 km E of Iringa city, 7°46' S, 35°42' E, Mar.–Apr. 1996, L.L. Sørensen leg. (ZMUC00046993).

Paratype

TANZANIA: 1 ♂, same data as holotype (ZMUC00046994).

Type locality

TANZANIA: Iringa Region, 10 km east of Iringa city, 7°46' S, 35°42' E.

Description

Size. Length ca. 9 cm. Diameter 6.0–6.1 mm. 61–67 podous rings, no apodous rings in front of telson.

Colour. After 19 years in alcohol uniform greyish; posterior part of metazona amber, legs and antennae dark brownish.

Head. Without peculiarities.

Collum. With a marginal and a submarginal furrow.

Body rings. Almost perfect cylinders, not vaulted; suture straight; ozopores *ca*. three diameters behind suture.

Limbus (Fig. 6). With sharply pointed lobes.

Anal valves. Each with a well-developed dorsal spine and a smaller, yet distinctive ventral one, margin raised, with 3 setae not borne on tubercles.

Male legs. From 4th pair with postfemoral and tibial pads on all legs, except last few pairs where only postfemoral pads are present.

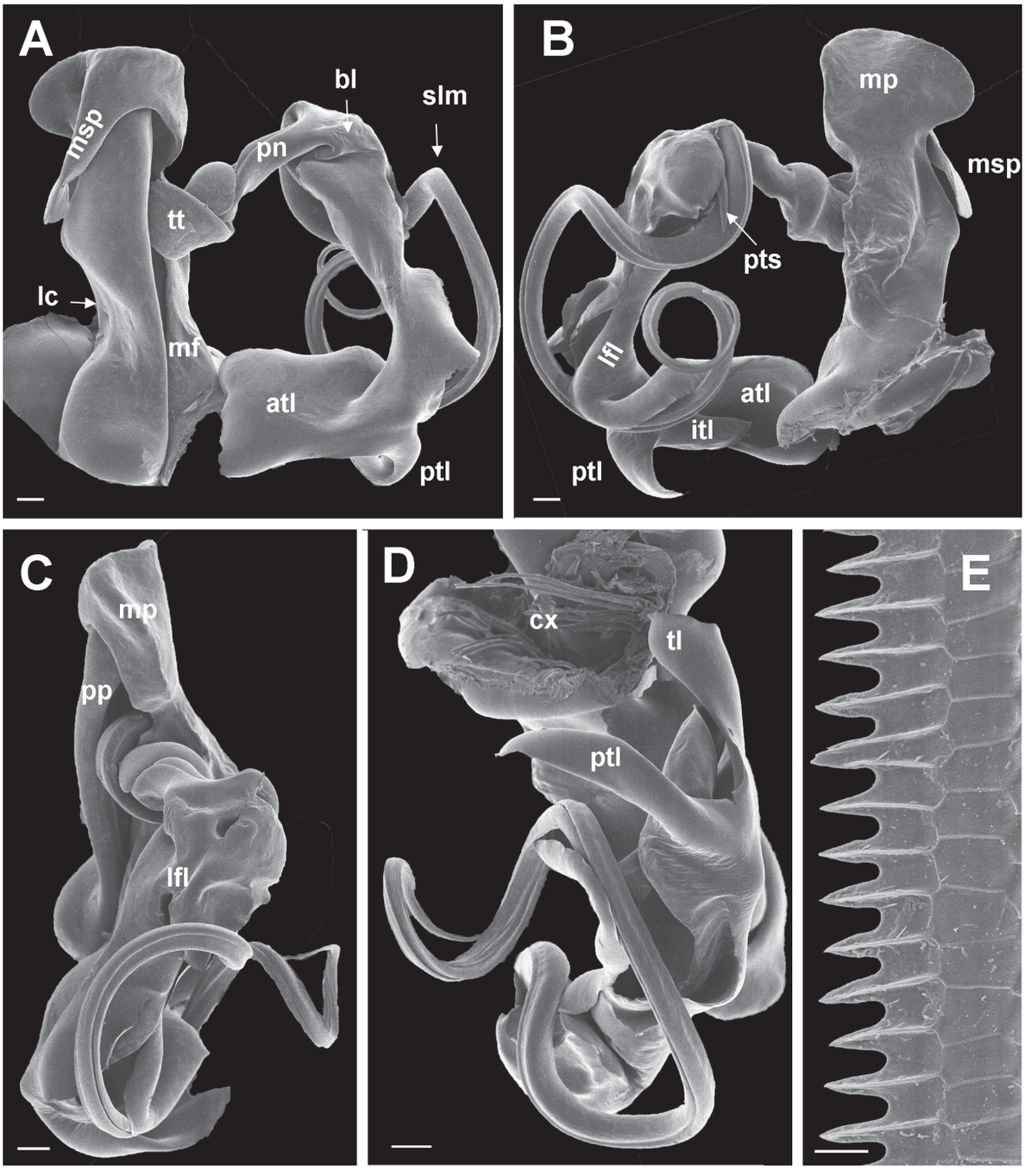

Fig. 6. *Geotypodon iringensis* gen. et sp. nov. **A–D**. Holotype, left gonopod. **A**. Anterior view. **B**. Posterior view. **C**. Mesal-ventral view. **D**. Telomere and solenomere, basal (dorsal) view. — **E**. Paratype, limbus. Abbreviations: *atl* = anterior distal lobe of telomere, *bl* = basal lamella of telomere, *cx* = coxa (seen from the basis, with remains of muscles); *itl* = intermediate distal lamella of telomere; *lc* = lateral concavity of coxa; *lfl* = longitudinally folded lamella; *mf* = anteriad metaplical flange; *mp* = metaplica; *msp* = metaplical spine-like process; *pn* = posttorsal narrowing; *pp* = proplica; *ptl* = posterior distal lobe of telomere; *pts* = proximal telomeral spine; *slm* = solenomere; *tl* = terminal lobe of telomere; *tt* = torsotope. Scales: A–D = 0.2 mm, E = 0.01 mm.

Gonopod coxa (Fig. 6). Basally parallel-sided, with antero-lateral concavity (*lc*) (Fig. 6A). Proplica ending in small proplical lobe (hidden behind anterior edge of metaplica on Fig. 6A). Metaplica with poorly developed basal anteriad flange (*mf*) (Fig. 6A), distally regularly rounded and projecting laterad as semicircular lobe; metaplica at level of proplical lobe, with a long, latero-basad process (*msp*) on anterior side of coxa (Fig. 6A–B); process straight and slender in anterior view, slightly curved and broader in lateral view.

Gonopod telopodite (Fig. 6). Arculus 90°. Torsotope (*tt*) simple, compact, without processes (Fig. 6A). Posttorsal narrowing (*pn*) pronounced, very slender, without processes or spines (Fig. 6A). Telopodite just distal to posttorsal narrowing dividing into slender, whip-like solenomere and complicated telomere. Solenomere (*slm*) curved in 3 dimensions (at least on preserved specimens), apically pointed, without any outgrowths (Fig. 6A–D). Efferent groove continuing from posttorsal narrowing onto solenomere and running all the way to its tip. Telomere with short, dark basal spine (*pts*) (Fig. 6B) and a basal lamella (*bl*) (Fig. 6A), followed by a slender part formed by a longitudinally folded lamella (*lfl*) with irregular edges (Fig. 6B–C); distal part divided into a slender posterior lobe (*ptl*) and a large, broad anterior lobe (*atl*) (Fig. 6A–B, D), the latter terminally giving rise to a slender, strongly curved terminal lobe (*tl*, curvature not visible on Fig. 6D). An intermediate lamella (*itl*) lodged in the space between *atl* and *plm* (Fig. 6B).

Distribution and habitat

Known only from the environs of Iringa city. The altitude of the type locality will be at *ca*. 1600 m asl.

Coexisting species

No other odontopygid species were found together with *G. iringensis* gen. et sp. nov.

Notes

Geotypodon iringensis gen. et sp. nov. is very similar to *G. multianulatus* from Kenya, but there are differences, including that in *G. multianulatus* the gonopod coxa has a much larger, narrower and less rounded lateral lobe, and the solenomere has a small subdistal spine (cf. Discussion section).

Discussion

Of the three species described here, *G. millemanus* gen. et sp. nov. and *G. submontanus* gen. et sp. nov., both from the Udzungwa Mountains proper, are particularly similar, notably sharing the lamellar structure of the mesal part of the coxal metaplica and the apically divided telomere with an intermediate lamella (*itl*) between the apical and posterior distal lobes (*atl* and *ptl*). *G. iringensis* gen. et sp. nov. does not have the metaplical lamella, but its telomere has the same distal elements (*atl*, *itl*, *ptl*) as the two other species. In most other species of *Geotypodon* gen. nov. as here defined, the telomere does not show a similar apical subdivision. Exceptions are *G. multianulatus*, *G. sennae* and *G. specularis,* where the telomere is divided into two large lobes (Attems 1914, 1927; Brölemann 1903).

The unsatisfactory state of odontopygid taxonomy was characterized as follows by Hoffman & Howell (2012): “That classification of odontopygid millipeds remains in a highly unsettled condition is due both to the inherent complexity of the male genitalia and the traditional reliance on a few obvious key-characters (*a priori* definition) instead of groupings made on the basis of overall similarity of the appendages. Either approach is further complicated by frequent contradictory states of characters as expressed in coxal or telopodital regions. Almost identical coxal forms may recur randomly amongst taxa defined on the basis of the telopodite and thought to be not closely related. Body form tends to be of monotonous similarity throughout the group, and female genitalia have so far provided very few insights into relationships.” Hoffman & Howell went on to speculate that “The impression is thus gained

of a group of organisms which have stabilized their general Gestalt whilst expressing innate genetic variability dominantly in permutations of male reproductive structures. A young evolutionary status is implied by the paucity of strong discontinuities in character systems and typical spectral expression of traits." Anybody who has tried to refer odontopygid specimens to a genus will agree that this is not easy. Whereas the gonopods of each species are often highly characteristic, when it comes to grouping the species, the problems are massive.

As an illustrative example, one may mention the record of *Odontopyge* cf. *picea* by Dieudonné (2014). The record is illustrated with a very nice optical photo of the gonopods, and they do indeed look very much like *Geotypodon picea* gen. et comb. nov. Examination of several specimens from among the material recorded by Dieudonné, kindly put at my disposal by Didier VandenSpiegel (Royal Museum for Central Africa, Tervuren, Belgium), did, however, reveal that whereas the specimens in most respects agree with the definition of *Geotypodon* gen. nov. given above, they differ in a striking detail: just distal to the posttorsal narrowing where the solenomere and the telomere begin, there is a peculiar sclerite protruding from the main telopodite axis. The basal telomeral spine sometimes curves *between* this sclerite and the main axis. Such a sclerite is absent from the true *G. picea* (Attems 1938: fig. 32). Furthermore, the solenomere of these specimens has a tiny spine-like side branch near the tip, whereas the solenomere tip is not visible on Attems' figure and is not mentioned in the description. (As noted above, one of the few differences between *G. iringensis* gen. et sp. nov. and *G. multianulatus* is that the latter species has a similar small subapical spine.)

An alternative approach to odontopygid classification is clearly needed, and molecular characters are the obvious choice. This will, however, require a huge effort. A search for "Odontopygidae" in GenBank yields no results whatsoever, so there is scope for large-scale sampling and sequencing of well-vouchered odontopygids.

This way, a more satisfactory classification may one day be obtained, but until then, in order to be able to handle the amazing diversity of odontopygids, several existing genera need to be revised and probably split into several smaller genera. This approach might seem to be at variance with the ideas expressed by Hoffman & Howell (2012), i.e., "traditional reliance on a few obvious key-characters (*a priori* definition) instead of groupings made on the basis of overall similarity", but at least as a temporary solution such a splitting approach will be useful. Taking the monographic work of Kraus (1960, 1966) as the starting point, several such splits have already been made by Demange (1981), Frederiksen & Enghoff (2015), Hoffman (2002) and Hoffman & Howell (2012). One further split is proposed in the present paper.

Around 400 species of Odontopygidae have been described (Enghoff 2014), but virtually every new collection of millipedes from the Afrotropical region contains undescribed species. The number of described odontopygid species can therefore potentially be multiplied by an unknown factor (5? 10?), and the number of genera will – at least temporarily – also need to be multiplied, hopefully to a somewhat smaller degree.

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