



Research article

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A mountain of millipedes IV: Species of *Prionopetalum* Attems, 1909, from the Udzungwa Mountains, Tanzania. With notes on “*P.*” *fasciatum* (Attems, 1896) and a revised species key (Diplopoda, Spirostreptida, Odontopygidae)

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Abstract. Two species of the genus *Prionopetalum* Attems, 1909, are recorded from the Udzungwa Mountains: *P. asperginis* sp. nov. and *P. kraepelini* (Attems, 1896). *Prionopetalum stuhlmanni* Attems, 1914, is synonymized under *P. kraepelini*. *Odontopyge fasciata* Attems, 1896, is transferred from *Prionopetalum* to *Aquattuor* Frederiksen, 2013, and new illustrations are given. A new illustrated key to species of *Prionopetalum* is provided.

Keywords. Eastern Arc, taxonomy, new species.

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Introduction

This is the fourth 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 and Enghoff 2016).

Unlike many other genera of Odontopygidae, *Prionopetalum* Attems, 1909, is well-defined and easily recognized since the monumental work of Kraus (1960). It is also one of the few odontopygid genera which have been subject of a subsequent comprehensive review (VandenSpiegel & Pierrard 2009). In both of these treatments, a key to species is included, in German and French, respectively. Considering that the vast majority of species of *Prionopetalum* live in East Africa, where English is much more widely understood than German and French, a key in English is provided here.

Two species of *Prionopetalum*, one of them new, have been collected in the Udzungwa Mountains and are (re)described here. *Prionopetalum stuhlmanni* Attems, 1914, is shown to be the same species as *P. kraepelini* (Attems, 1896). Furthermore, *Odontopyge fasciata* Attems, 1896, which had been included, with some doubts, in *Prionopetalum* by previous authors, is shown to belong in the genus *Aquattuor* Frederiksen, 2013. With these adjustments, *Prionopetalum* now contains 23 described species.

Material and methods

The bulk of the material for this article comes from the zoological collections of the Natural History Museum of Denmark, University of Copenhagen (ZMUC). These specimens were collected during field trips by ZMUC staff and students. Additional specimens from other institutions (see below) were also examined. All specimens 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.

As in previous articles in this series, only adult males are considered. A total of 22 adult males of the two Udzungwa species were examined. Figure 1 shows the Udzungwa localities where *Prionopetalum* specimens were collected.

See Enghoff (2014) for the description standards used.

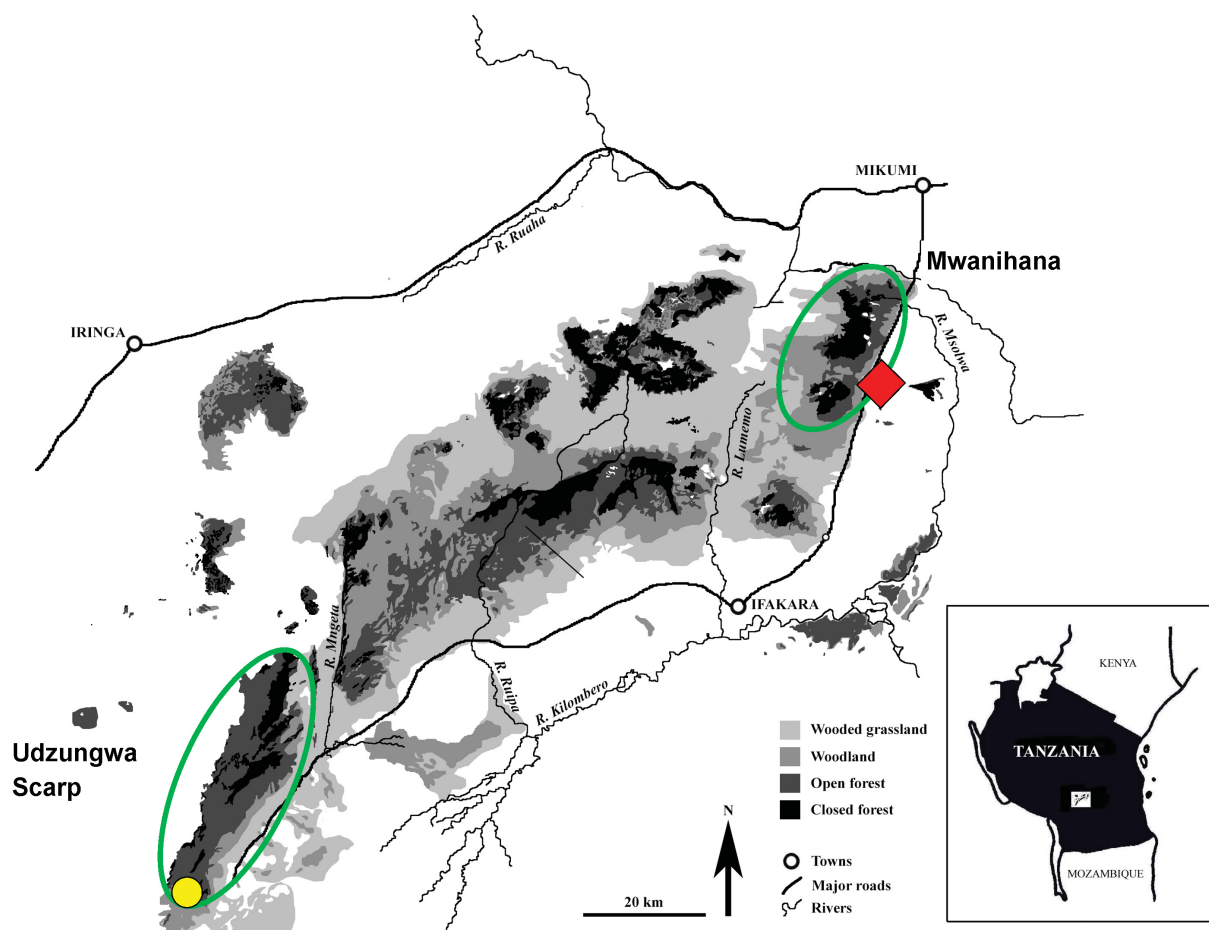


Fig. 1. Map of the Udzungwa Mountains, showing the collecting localities for *Prionopetalum asperginis* sp. nov. (yellow dot) at the southern extremity of the Udzungwa Scarp Forest Reserve and for *P. kraepelini* (Attems, 1896) (red diamond) at the eastern edge of the Mwanihana Forest Reserve. Based on fig. 1 in Marshall *et al.* (2010).

Abbreviations for morphological terms used in the descriptions and on illustrations

<i>amp</i>	=	anterior metapical process
<i>ba</i>	=	basomere
<i>eg</i>	=	efferent groove
<i>ic</i>	=	internal canal
<i>lt</i>	=	lateral coxal tubercle
<i>mbl</i>	=	mesobasal lobe of coxal palette
<i>mlf</i>	=	metapical longitudinal flange
<i>mml</i>	=	metapical mesad lobe
<i>mmp</i>	=	distomesal metapical process
<i>mof</i>	=	metapical oblique/horizontal flange
<i>pa</i>	=	apical palette of coxa
<i>prl</i>	=	propical lobe
<i>pts</i>	=	post-torsal spine
<i>pxl</i>	=	proximal lobe of telomere
<i>ra</i>	=	rough area on telomere
<i>slm</i>	=	solenomere
<i>tdp</i>	=	telomeral distal process
<i>tpa</i>	=	telomeral proximal process

Other abbreviations used in the text

asl	=	above sea level
NHMW	=	Naturhistorisches Museum, Vienna
VMNH	=	Virginia Museum of Natural History
ZMUC	=	Natural History Museum of Denmark (Zoological Museum)
ZMUH	=	Zoologisches Museum der Universität Hamburg

Results

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

 Genus *Prionopetalum* Attems, 1909

Prionopetalum Attems, 1909: 51.

Type species: *Prionopetalum serratum* Attems, 1909, by original designation.

Unlike many other genera of Odontopygidae, *Prionopetalum* is well-defined and quite homogeneous, not only in non-sexual characters, but also in gonopod structure.

Diagnosis

(Modified after Kraus 1960 and VandenSpiegel & Pierrard 2009, excluding some non-gonopodal characters which were mentioned by these authors but which are of no diagnostic value.)

Prionopetalini in which the anal valves have a raised rim, a well-developed dorsal spine and sometimes a smaller ventral one; limb with simple, pointed denticles (true of all species after removal of

Table 1. Numbers of podous rings and body diameter of adult males of species of *Prionopetalum*. One has been subtracted from published “segment” numbers because these include the telson. None of the species are known to have apodous rings between the last podous ring and the telson.

	No. of podous rings	Diameter (mm)	Source
<i>P. aculeatum</i>	66	5	Attems 1914
<i>P. asperginis</i> sp. nov.	60–65	4.4–4.9	this study
<i>P. bifidum</i>	68–71	5.6–6.8	VandenSpiegel & Pierrard 2009
<i>P. clarum</i>	“nearly forty-three”	5.5	Chamberlin 1927
<i>P. cornutum</i>	63	3	Kraus 1958
<i>P. coronatum</i>	58	3.7	Kraus 1958
<i>P. dentigerum</i>	65	6.0	this study ¹
<i>P. etiennei</i>	60	2.5	this study ²
<i>P. exaratum</i>	57	2.5	Attems 1938
<i>P. frundsbergi</i>	72	7.6	this study ³
<i>P. fryeri</i>	65	6	Turk 1956
<i>P. glomeratum</i>	58	2.5	Attems 1935
<i>P. kraepelini</i>	61–65	3.2–3.6	Attems 1896; this study
<i>P. lindi</i>	58–59	3.3–3.8	VandenSpiegel & Pierrard 2009
<i>P. megalacanthum</i>	62	4.3	Attems 1912
<i>P. ndelei</i>	61–63	4.2	VandenSpiegel & Pierrard 2009
<i>P. pulchellum</i>	64	3.0	Kraus 1960
<i>P. serratum</i>	62–66	5.6	Attems 1909
<i>P. suave</i>	62	5	Attems 1896
<i>P. tanganjikum</i>	92	?	Verhoeff 1941
<i>P. tricuspis</i>	65	5.5	Brolemann 1920
<i>P. urbicolum</i>	61–64	4.5	Carl 1909
<i>P. xerophilum</i>	c. 60	4.5	Carl 1909

¹*P. dentigerum*: diameter not provided by Verhoeff (1941). Values based on ♂ from Tanzania, Pwani Region, Kisarawe District, Ruvu South Forest Reserve, 140 m asl, 6°57'27" S, 38°50'51" E, date unknown, leg. Frontier Tanzania, det. H. Enghoff (ZMUC).

²*P. etiennei*: diameter not provided by Demange (1982). Values based on ♂ from Guinée-Bissau, Buba, 9–11 Jun. 1989, leg. A. van Harten & M. Neves., det. H. Enghoff (ZMUC).

³*P. frundsbergi*: no published information. Values based on ♂ from Kenya, Bushwackers near Kibwezi, 30 Dec. 1982, leg. C.C. Kinze *et al.*, det. H. Enghoff (ZMUC).

“*P.*” *fasciatum*, see below). Male legs with ventral soft pads on postfemur and tibia, except on anteriormost and posteriormost legs (true of all species after removal of “*P.*” *fasciatum*, see below).

GONOPODS. Coxal metaplica on its basal part with a large longitudinal mesad flange (*mlf*), separated by a deep sinus from an oblique-horizontal sub-semicircular mesad flange (*mof*). Telopodite with a post-torsal (“femoral”) spine (*pts*), but without a (“tibial”) spine near the origin of the solenomere, divided into solenomere and telomere shortly after post-torsal narrowing. Solenomere (*slm*) simple, whip-like, without outgrowths (exception: *P. fryeri* (Turk, 1956) with a short accessory branch at c. $\frac{2}{3}$ of the

solenomere's length). Telomere with two characteristic processes: a variously shaped, often species-specific proximal process (*tpp*) which projects at \pm right angles from the main telomere axis, and a long, slender distal process (*tdp*) which is armed with a row of spines or thorns. (In the terminology of Kraus (1960), *tpp* is "eine hornartige Spitze oder auch eine entsprechende, schalige Lamelle", and *tdp* is "der meist auffallende schlankere Distalabschnitt gezackt oder bezahnt". For VandenSpiegel & Pierrard (2009), *tpp* is a "processus basal du tarse".)

Body size

Published body diameters for adult males range from 2.5 mm (*P. exaratum*, *P. glomeratum*) to 6.8 mm (*P. bifidum*), but a male of *P. frundsbergi* in the ZMUC collection has a diameter of 7.6 mm. Published numbers of podous rings range from 57 (*P. exaratum*) to 71 (*P. bifidum*), but the above-mentioned male of *P. frundsbergi* has 72 podous rings. Table 1 and Fig. 2 summarise the size information and give detailed information for the two Udzungwa species. One has been subtracted from published "segment" numbers because these have traditionally included the telson. Two records have been omitted: "nearly forty-three" for *P. clarum* (Chamberlin, 1927) and 93 for *P. tanganjikum* Verhoeff, 1941 – the latter number is probably a *lapsus calami*.

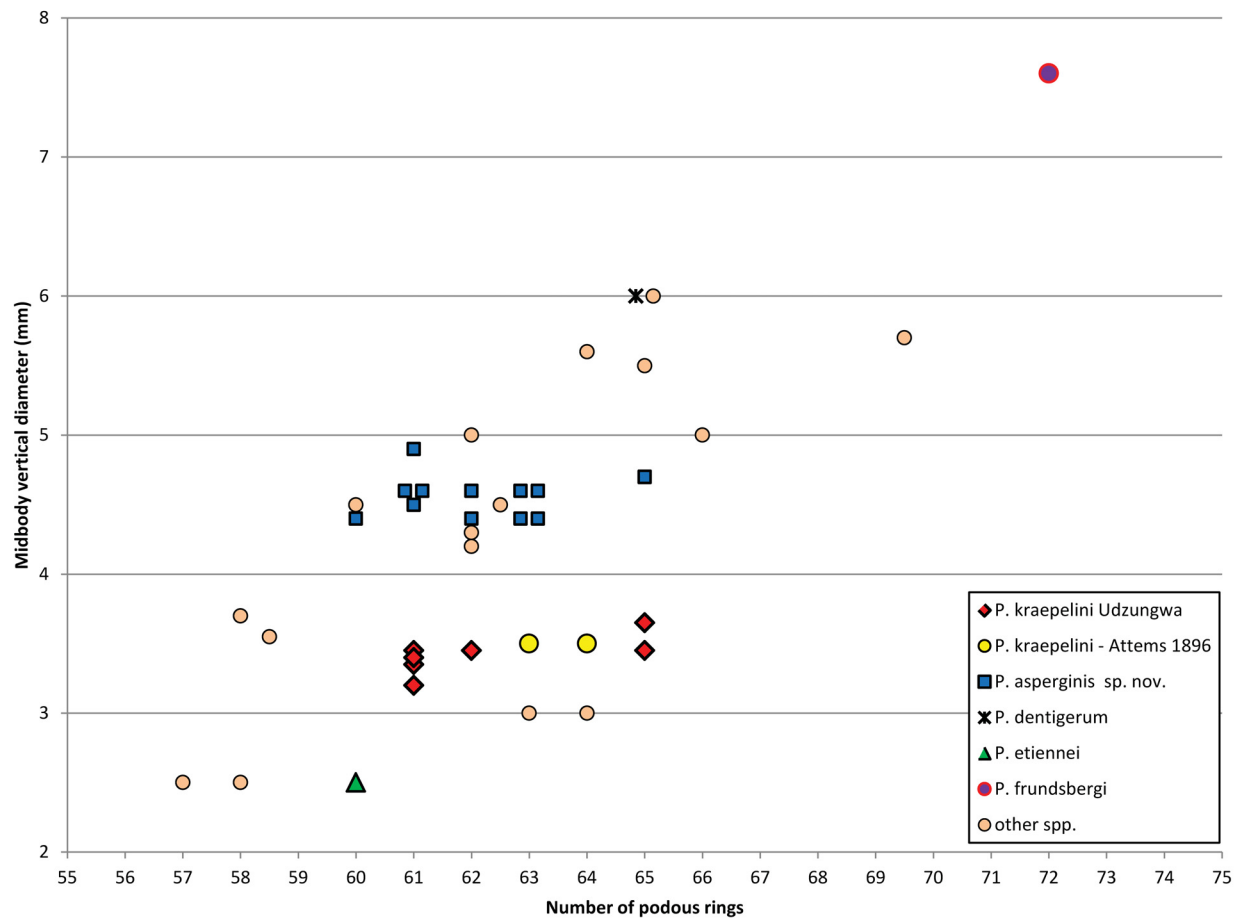


Fig. 2. Body size (body diameter / number of podous rings) of ♂♂ of *Prionopetalum* spp. Based on original measurements and data from the literature (see Table 1). For "other spp." the entries are median values of the intervals in Table 1. The report of "93 (1) Rumpfringen" (corresponding to 92 podous rings) for *P. tanganjikum* by Verhoeff (1941) has been omitted, as has Chamberlin's (1927) "nearly forty-three" segments for *P. clarum*; both are regarded as quite unlikely and are probably erroneous.

Included species

P. aculeatum Attems, 1914 – Somalia, Kenya
P. asperginis sp. nov. – Tanzania
P. bifidum VandenSpiegel & Pierrard, 2009 – Tanzania
P. clarum (Chamberlin, 1927) – D.R. Congo
P. cornutum Kraus, 1958 – D.R. Congo
P. coronatum Kraus, 1958 – D.R. Congo
P. dentigerum Verhoeff, 1941 – Tanzania, Rwanda
P. etiennei Demange, 1982 – Gambia, Guinée-Bissau, Sénégal
P. exaratum (Attems, 1938) – D.R. Congo
P. frundsbergi (Attems, 1927) – Kenya, Tanzania
P. fryeri (Turk, 1956) – Malawi, Zambia
P. glomeratum Attems, 1935 – D.R. Congo
P. kraepelini (Attems, 1896) – Tanzania
P. lindi VandenSpiegel & Pierrard, 2009 – Tanzania
P. megalacanthum Attems, 1912 – D.R. Congo, Rwanda
P. ndelei VandenSpiegel & Pierrard, 2009 – Central African Republic
P. pulchellum Kraus, 1960 – Mozambique
P. serratum Attems, 1909 – Kenya, Tanzania
P. suave (Gerstäcker, 1873) – Tanzania
P. tanganjikum Verhoeff, 1941 – Tanzania
P. tricuspis Brolemann, 1920 – Kenya
P. urbicum (Carl, 1909) – Tanzania
P. xerophilum (Carl, 1909) – Rwanda, Tanzania

Prionopetalum asperginis sp. nov.

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Figs 3–4, 9W, 10D, 11K

Diagnosis

Differs from congeners by the combination of a laterally smooth gonopod coxa, a pointed apical mesad metapical process subtended by a rounded mesad lobe, a simple, fingerlike proximal telomere process and a simple distal telomere process without secondary branches.

Etymology

The species is named after the recently discovered Kihansi spray toad, *Nectophrynoides asperginis* Poynton, Howell, Clarke & Lovett, 1999; see “Distribution and habitat”.

Material studied (total: 15 ♂♂)

Holotype

TANZANIA: ♂ Udzungwa Mts, Kihansi, 8°24' S, 36°21' E, “forest site”, Jun.–Aug. 1997, I. Zilihona leg. (ZMUC).

Paratypes

TANZANIA: 12 ♂♂, same data as holotype (ZMUC); 1 ♂ Iringa Region, Mufindi District, Udzungwa Scarp Forest Reserve, 8°31.58' S, 35°53.91' E, 750 m asl, 5–12 Mar. 1996, GUV28-2, Proj. S.H. McKamey *et al.* leg. (ZMUC); 1 ♂ Morogoro Region, Kilombero District, Lower Kihansi Project, Udagaji Gorge, 7 Nov. 1997, Jan Kielland leg. (VMNH).

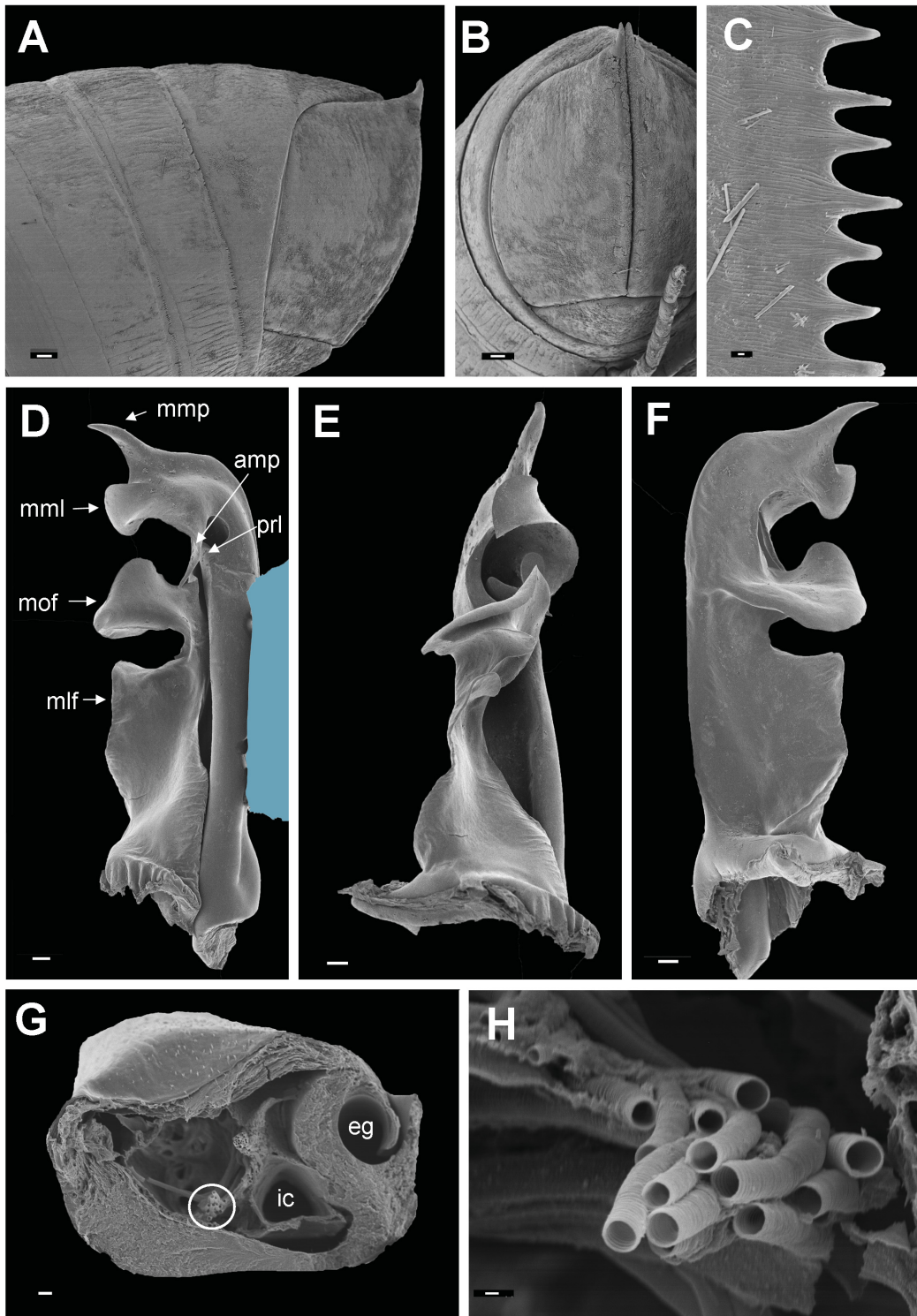


Fig. 3. *Prionopetalum asperginis* sp. nov., paratype from Kihansi, “forest site”. **A–B.** Hind end. **A.** Lateral view. **B.** Posterior view. **C.** Limbus. **D–F.** Right gonopod coxa. **D.** Anterior view (light blue: mounting tape). **E.** Mesal view. **F.** Posterior view. **G.** Transverse section of right gonopod basomere (circle: bundle of tracheae). **H.** Cluster of tracheae next to internal canal. Abbreviations: *amp* = anterior metapical process; *eg* = efferent groove; *ic* = internal canal; *mlf* = metapical longitudinal flange; *mml* = metapical mesad lobe; *mmp* = distomesal metapical process; *mof* = metapical oblique/horizontal flange; *prl* = propical lobe. Scale bars: **A, B, D–F** = 0.1 mm; **C, H** = 0.001 mm; **G** = 0.01 mm.

Type locality

TANZANIA: Udzungwa Mts, Kihansi, 8°24' S, 36°21' E.

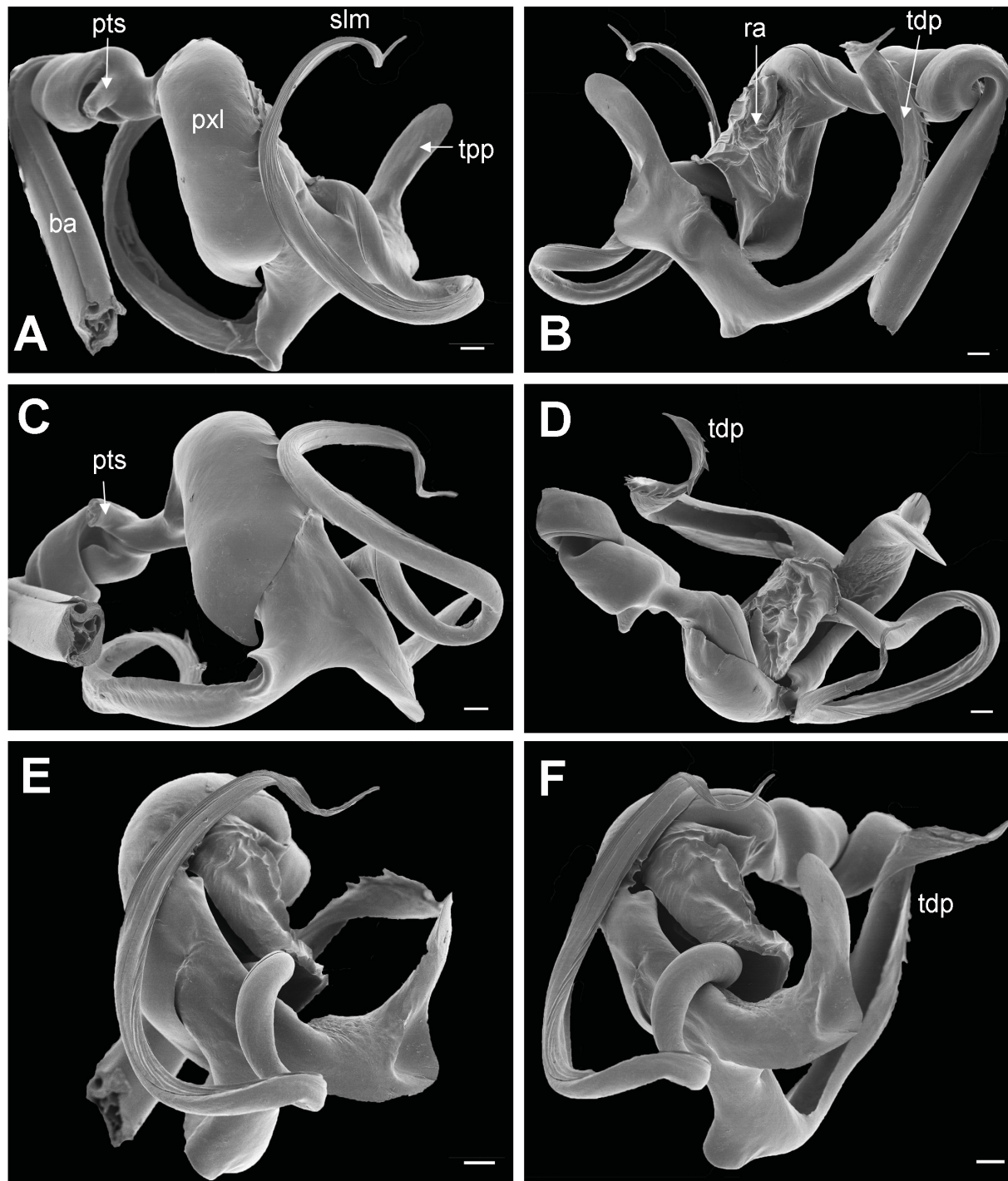


Fig. 4. *Prionopetalum asperginis* sp. nov., paratype from Kihansi, “forest site”, right gonopod telopodite. **A.** Anterior and slightly mesal view. **B.** Posterior view. **C.** Basal view. **D.** Apical view. **E.** Apical-mesal view. **F.** Mesal and slightly posterior view. Abbreviations: *ba* = basomere; *pts* = post-torsal spine (broken); *pxl* = proximal lobe of telomere; *ra* = rough area of telomere; *slm* = solenomere; *tdp* = distal process of telomere; *tpp* = proximal process of telomere. Scale bars = 0.1 mm.

Description

SIZE. Length *c.* 6½ cm, diameter 4.4–4.9 mm, 60–65 podous rings, no apodous rings in front of telson.

COLOUR. After 18 years in alcohol almost uniform light brown. No lighter dorsal markings.

ANAL VALVES (Fig. 3A–B). Each with a long, pointed dorsal spine, no ventral spine, marginal rim raised, with 3 setae on very poorly demarcated tubercles.

LIMBUS (Fig. 3C). With triangular, almost equilateral, pointed lobes, external surface of lobes densely striate.

MALE LEGS. Postfemora and tibiae with large, soft pads, except on first four to five and several posteriormost leg pairs.

GONOPOD COXA (Fig. 3D–F). Lateral margin almost straight, entirely smooth. Mesal margin of proplica straight, proplical lobe (*prl*) in anterior view almost hidden behind apical expansion of metaplica. Basal part of metaplica with large longitudinal mesad flange (*mlf*), separated by a deep sinus from an oblique-horizontal, sub-semicircular mesad flange (*mof*), apical part of metaplica expanded anteriorly, forming a pointed process (*amp*) covering proplical lobe, a rounded mesad lobe (*mml*) and a slender disto-mesad process (*mmp*).

GONOPOD TELOPODITE (Fig. 4). A well-developed post-torsal spine (“femoral spine”, *pts*) just before post-torsal narrowing (broken on illustrated specimen). Solenomere (*slm*) simple, slender. Telomere with a large, proximal lobe (*pxl*) and a rough area (*ra*) on apical surface, further distally divided into two processes. Proximal telomere process (*tpp*) parallel-sided, apically rounded. Distal telomere process (*tdp*) only slightly broader than solenomere, apically with one margin denticulate (Fig. 4F).

Distribution and habitat

Known only from the southern part of the Udzungwa Mts, Udzungwa Scarp Forest Reserve and the Kihansi area. The latter area has become famous because of the Kihansi spray toad, *Nectophrynoides asperginis* Poynton, Howell, Clarke & Lovett, 1999, which occurred in the Kihansi area but is now regarded as extinct in the wild although a reintroduction programme was started in 2013 (IUCN SSC Amphibian Specialist Group 2015). Zilihona *et al.* (1998) described in detail the area where I. Zilihona collected her specimens. Altitudinal range 550–750 m asl (cf. Zilihona *et al.* 1998).

Coexisting species

The sample collected by I. Zilihona also contains another, much smaller odontopygid which will be described in a forthcoming paper.

Remarks

Fig. 3G shows a transverse section (= break) of the basal part (basomere, *ba*) of the gonopod telopodite. The picture clearly shows how the canal (*eg*) that continues to the tip of the solenomere is formed as a groove near the surface. This canal has been supposed to be a sperm canal (“Samenrinne” of Kraus 1966, e.g., his figs 28–29), but considering that nothing is known about its function, the neutral term “efferent groove” is preferable (cf. Enghoff 2011). There is also what looks like an entirely internal canal (*ic*) which is accompanied by dense bundles of tubuli, probably tracheae (Fig. 3H), similar to those recently described by Reboleira *et al.* (2015) from the base of the vulva of a cambalid millipede. The extent and function of this canal is unknown.

Prionopetalum kraepelini (Attems, 1896)

Figs 5–6, 9R, 11I

Odontopyge kraepelini Attems, 1896: 37.

Prionopetalum stuhlmanni Attems, 1914: 210. **New synonymy**

Odontopyge pardalis – Attems 1896: 39.

Prionopetalum pardalis – Attems 1909: 52.

Prionopetalum kraepelini – Attems 1914: 210.

Not *Spirostreptus pardalis* Gerstäcker, 1873.

Diagnosis

Differs from all congeners by the multi-cusped proximal telomere process (Fig. 6F).

Material studied (total: 9 ♂♂)

Syntypes

TANZANIA: 1 ♂, 1 ♀, Mhonda (Unguru), 6 Sep. 1888, F. Stuhlmann leg. (ZMUH).

Other material

TANZANIA: 1 ♂, Lewa (Usambara), 26 Apr. 1888, F. Stuhlmann leg., holotype of *Prionopetalum stuhlmanni* (ZMUH); 3 ♂♂, Morogoro Region, Mang'ula, at Udzungwa Ecological Monitoring Centre, 300 m, 7°50'56" S, 36°53'17" E, 28–31 Sep. 2012, T. Pape leg. (ZMUC); 4 ♂♂, Morogoro Region, Udzungwa Mts, Udzungwa Ecological Monitoring Centre, Mang'ula, 07°50'44.9" S, 36°53'28.2" E, 339 m, 18–20 Jan. 2014, T. Pape & N. Scharff leg. (ZMUC).

Type locality

TANZANIA: Tanga Region, Lushoto District, Usambara Mts, Lewa.

Description (male)

SIZE. Length *c.* 5 cm, diameter 3.2–3.6 mm, 61–65 podous rings, no apodous rings in front of telson.

COLOUR. After 1–3 years in alcohol head amber below antennae, blackish above; antennae blackish brown; collum blackish brown with light margins; body rings light brown below ozopores and immediately above, dorsally blackish brown with broad middorsal light spot; telson and legs medium brown.

ANAL VALVES. Each with a long, pointed dorsal spine and a much smaller ventral one, marginal rim raised, with 3 setae on very poorly demarcated tubercles.

LIMBUS (Fig. 5F). With triangular, almost equilateral, pointed lobes, external surface of lobes densely striate.

MALE LEGS. Postfemora and tibiae with large soft pads, except on first four to five and several posteriormost leg pairs.

GONOPOD COXA (Fig. 5A–E). Lateral margin almost straight, entirely smooth or with a tiny tubercle (*lt*) at *c.* $\frac{2}{3}$ height. Mesal margin of proplica straight, proplical lobe (*prl*) in anterior view hidden behind apical expansion of metaplica. Basal part of metaplica with large, longitudinal mesad flange (*mlf*), separated by a deep sinus from an oblique-horizontal, two-lobed mesad flange (*mof*), apical part of metaplica expanded anteriorly to form a process (*amp*) covering proplical lobe and produced disto-mesad into slender, apically bifid process (*mmp*).

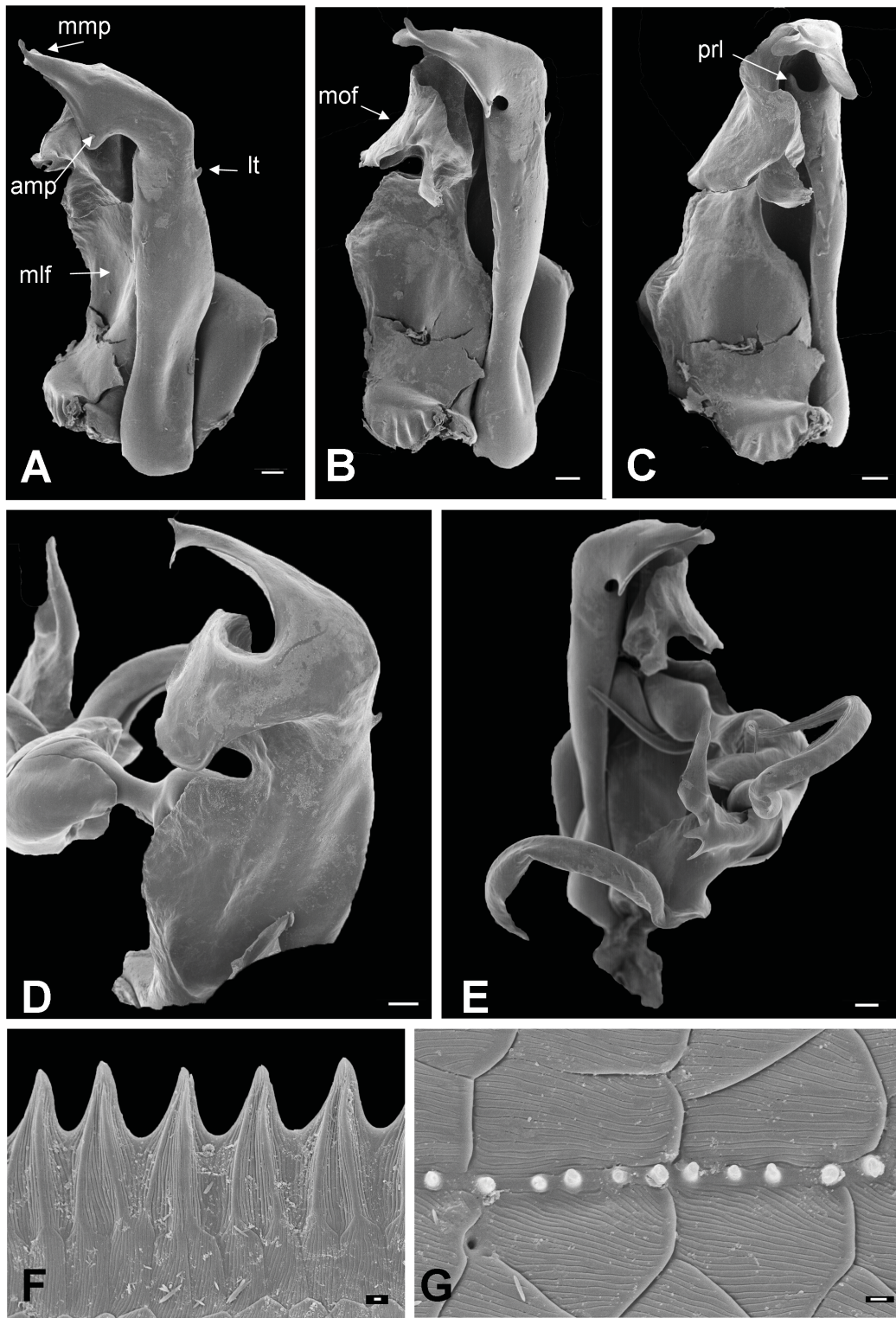


Fig. 5. *Prionopetalum kraepelini* (Attems, 1896), specimen from Mang'ula, 339 m asl. **A–C.** Right gonopod coxa. **A.** Anterior view. **B.** Anterior-mesal view. **C.** Mesal view. **D–E.** Left gonopod. **D.** Posterior view. **E.** Anterior-mesal view. **F.** Midbody-dorsal limbus. **G.** Row of intercalary microscutes with knobs, from midbody metazona. Abbreviations: *amp* = anterior metaplical process; *lt* = lateral coxal tubercle; *mlf* = metaplical longitudinal flange; *mmp* = distomesal metaplical process; *mof* = metaplical oblique/horizontal flange; *prl* = propical lobe. Scale bars: A–E = 0.1 mm; F–G = 0.001 mm.

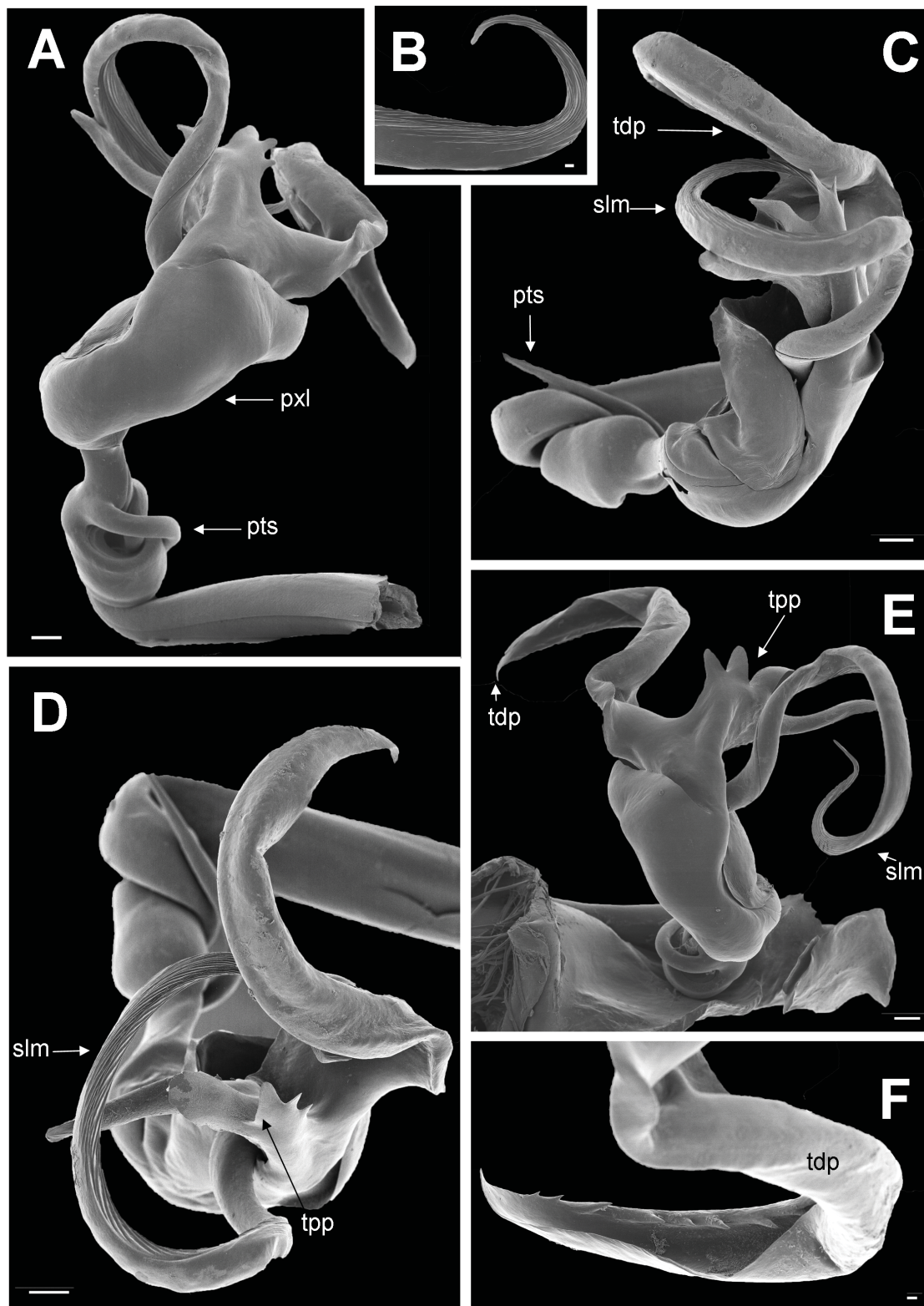


Fig. 6. *Prionopetalum kraepelini* (Attems, 1896), specimen from Mang'ula, 339 m asl. Gonopod telopodite. **A, C–D, F.** Right gonopod telopodite. **A.** Posterior view. **C.** Apical (ventral) view. **D.** Anterior view. **F.** Telomere distal process. **B.** Tip of left solenomere. **E.** Left gonopod, (posterior-) mesal view. Abbreviations: *pts* = post-torsal spine; *pxl* = proximal lobe of telomere; *slm* = solenomere; *tdp* = telomeral distal process; *tpp* = telomeral proximal process. Scale bars: **A, C–D, E** = 0.1 mm; **B, F** = 0.2 mm.

GONOPOD TELOPODITE (Figs 5D–E, 6). A well-developed post-torsal spine (“femoral spine”, *pts*) inserted just before post-torsal narrowing. Solenomere (*slm*) simple, slender. Telomere with a large, proximal lobe (*pxl*). Proximal telomere process (*tpp*) elaborate, with a longitudinal 3–5-dentate flange and a slender apical process, in certain views (Fig. 5E) recalling the head profile of cartoon character Woody Woodpecker. Distal telomere process (*tdp*) only slightly broader than solenomere, apically with one margin denticulate (Fig. 6F).

Distribution and habitat

In addition to the newly collected material from the Udzungwa Mts, Udzungwa Ecological Monitoring Centre, Mang’ula (<http://www.udzungwacentre.org/>) at 300–339 m asl, *O. kraepelini* has been recorded from several other sites, all in Tanzania: Morogoro Region, Mhonda (Nguru) (type locality); Tanga Region, Lushoto Distr. Usambara Mts, Lewa (type locality of *P. stuhlmanni*); Arusha Region, Arusha District, near Lake Babati; Dar es Salaam (the latter two records by VandenSpiegel & Pierrard 2009).

Coexisting species

At Mang’ula, *P. kraepelini* was collected together with another odontopygid species which will be described in a forthcoming article.

Remarks

Two of the four species of *Odontopyge* (re)described by Attems (1896) distinguished themselves by the possession of a peculiar, multi-cusped process on the gonopod telopodite. This process, labelled *c* on Attems’ figures, corresponds to the proximal telomere process (*tpp*) in the sense of the present paper. The two species in question were *O. kraepelini*, described as new, and a species which Attems identified as *O. pardalis* (Gerstäcker). He later (Attems 1914) realised that this was not the real *pardalis* Gerstäcker and offered the replacement name *Prionopetalum stuhlmanni* Attems, 1914 (*pardalis* has subsequently been transferred to the genus *Calyptomastix* Hoffman & Howell, 2012).

The two species, *kraepelini* and *stuhlmanni*, are very similar indeed according to the descriptions and illustrations offered by Attems (1896). The only substantial apparent difference concerns the profile of the gonopod coxa. Attems (1896) provided two gonopod drawings of *stuhlmanni* (as *pardalis*), and one of *kraepelini*. The three drawings are all quite different regarding the gonopod coxa profiles, but this is due to the fact that two of them, the one of *kraepelini* (Attems’ fig. 1) and one of those of *stuhlmanni* (Attems’ fig. 8), are based on gonopods macerated in KOH, whereas his fig. 7 (of *stuhlmanni*) is based on unmacerated gonopods. Attems’ fig. 7 is fully compatible with the present illustrations (Figs 5–6) of specimens from Mang’ula, and side-by-side comparisons of the body and gonopods of Mang’ula specimens with the holotype of *stuhlmanni* reveal no differences (see Fig. 2 for agreement in body size). The male syntype of *kraepelini* is devoid of its gonopods, and these are not retrievable elsewhere. I interpret the apparent differences between macerated gonopods of *kraepelini* (Attems 1896: fig. 1) and *stuhlmanni* (Attems 1896: fig. 8) as being artificial and possibly due to different durations of the KOH maceration, and I therefore synonymize the two names.

Knob-like intercalary cuticular micro-scutes were observed in this species (Fig. 5G), cf. Enghoff (2014).

Under the name *Prionopetalum stuhlmanni* this species is a popular pet millipede; see, e.g., Sigling (2010) and <http://www.diplopoda.de/index.php> (accessed 29 February 2016).

The status of “*Prionopetalum*” *fasciatum* (Attems, 1896)

Attems (1896) described *Odontopyge fasciata* from Zanzibar, but later (1914) transferred the species to *Prionopetalum* without further comment. Brolemann (1920) redescribed the species based on new

material from Zanzibar and expressed doubts about the genus-level classification of it, suggesting that it might belong in a separate subgenus of *Prionopetalum*. Kraus (1960), however, accepted the inclusion of *fasciata* in *Prionopetalum*. In the most recent treatment of *Prionopetalum* VandenSpiegel & Pierrard (2009) discussed *fasciata*, noticing that it differs from other species of *Prionopetalum* in several characters: the limbus is almost straight, not serrate; there are no ventral tibial pads on male legs; and the proximal telomeral process (*tpp*) is a simple, rounded lobe. The latter authors reported further new material from Zanzibar as well as from Bagamoyo District, Vula Mountain, Pongwe, on the Tanzanian mainland.

After having examined several specimens from Zanzibar I can now offer a re-classification of this species:

Aquattuor fasciatus (Attems, 1896) comb. nov.
Figs 7–8

Odontopyge fasciata Attems, 1896: 40.

Prionopetalum fasciatum – Attems 1914: 210. — Brolemann 1920: 123. — Kraus 1960: 86. — VandenSpiegel & Pierrard 2009: 152. — Enghoff *et al.* 2016.

Aquattuor aff. *claudiahempae* – Enghoff & Frederiksen 2015: 19.

Material studied

Syntypes

TANZANIA: 1 ♂ (+ one extra set of gonopods), 6 ♀♀/juvs, Zanzibar, Kibueni (ZMUH).

Other material

TANZANIA: 3 ♂♂, Zanzibar, Kizimkazi, at foot of mango tree, 17 Jun. 1979, M. Stoltze leg. (ZMUC); 1 ♂, Zanzibar, the sultan's palace, 16 Jun. 1979, M. Stoltze leg. (ZMUC).

In addition, Dr. Nesrine Akkari has kindly examined syntypes of *O. fasciata* in NHMW and has placed information and images at my disposal.

Remarks

The single intact male among the examined syntypes has 53 podous rings (no apodous rings in front of the telson) and a diameter of 1.91 mm. A syntype at NHMW has the same number of rings and a diameter of 1.86 mm. The specimens from Kizimkazi are all broken, the males have maximum body diameters of 1.55–1.62 mm. The male from the sultan's palace has 51 podous rings (no apodous rings in front of the telson) and a diameter of 1.86 mm.

The limbus (Fig. 7A) consists of large, rectangular, easily detached flaps, characteristic of the genus *Aquattuor*.

The gonopods (Figs 7B–F, 8) are indistinguishable from those of *Aquattuor claudiahempae* Enghoff & Frederiksen, 2015 (cf. their fig. 15). Noticeable special similarities include the profile of the apical palette (*pa*), the well-developed mesobasal lobe (*mbl*) of the coxal palette, and the partly micro-serrate margin of the telomere (Fig. 7 E, arrow).

The characteristic limbus was not noted by previous authors. Attems (1896) and Brolemann (1920) did not mention the limbus at all. VandenSpiegel & Pierrard (2009: fig. 1b) illustrated the limbus, but their SEM micrograph only showed an irregularly wavy margin. The large limbus lobes were probably all broken off in the specimens examined by these authors (compare the left part of Fig. 7A with fig 1b

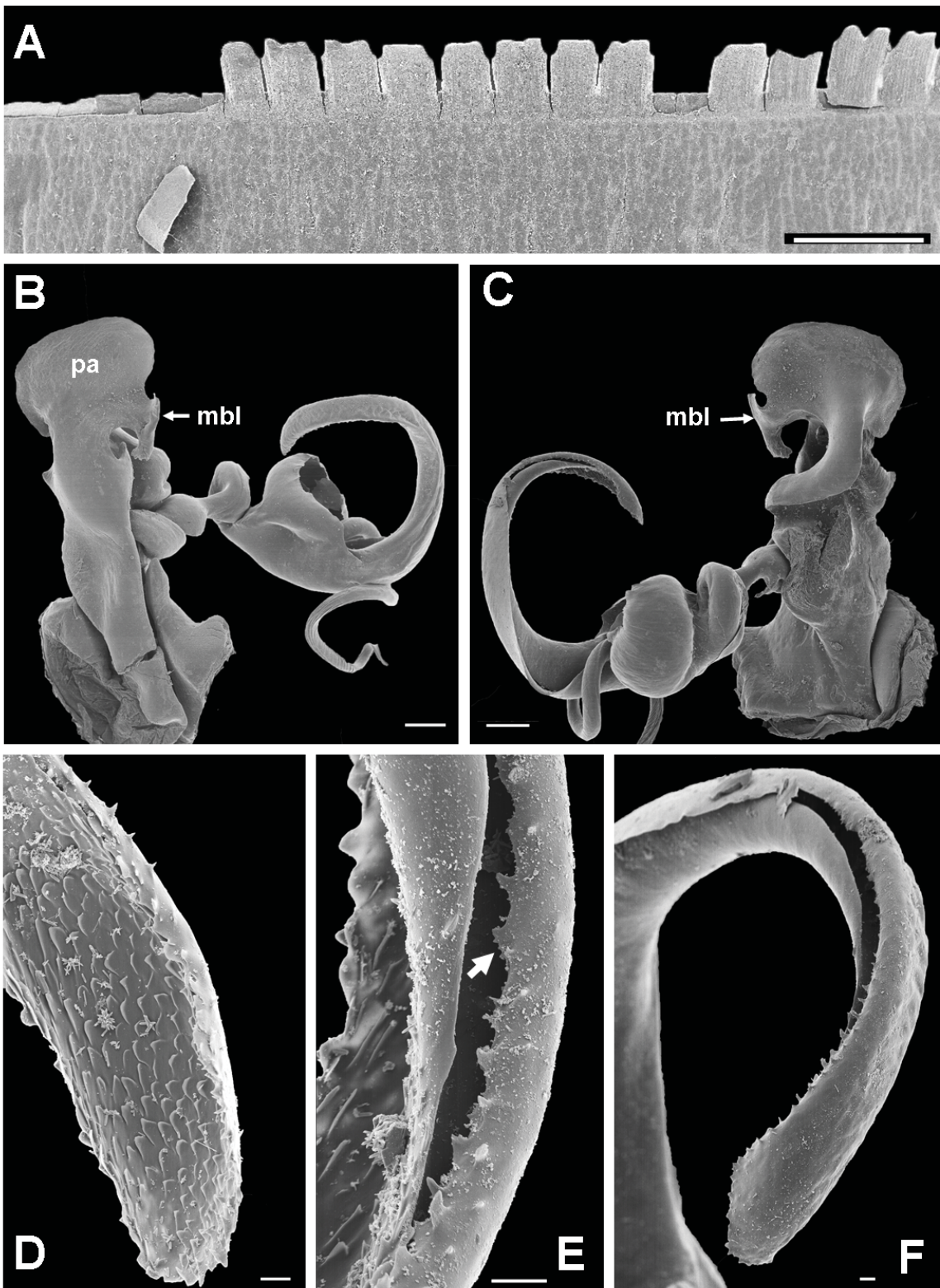


Fig. 7. *Aquattuor fasciatus* (Attems, 1896) comb. nov., specimen from Zanzibar, Kirimkazi. **A.** Limbus. **B–C.** Left gonopod. **B.** Anterior view. **C.** Posterior view. **D–F.** Left telomere. **D.** Tip, basal-anterior view. **E.** Subdistal part, posterior view (bold arrow points to a micro serrate lobe on the margin). **F.** Tip, apical-posterior view. Abbreviations: *mbl* = mesobasal lobe of coxal palette; *pa* = apical palette of coxa. Scale bars: A–C = 0.1 mm; D–F = 0.01 mm.

in VandenSpiegel & Pierrard 2009). In the syntypes from ZMUH the limbus seems to be completely worn off. However, Dr. Nesrine Akkari has kindly provided images based on the syntypes of *O. fasciata* in NHMW which clearly show the *Aquattuor* type of limbus, as well as confirm the great similarity in gonopod structure between this species and *A. claudiahempae* (Fig. 8). The gonopods of the intact male syntype (now dissected by me) closely agree with the illustrations in Figs 7–8. The extra set of gonopods among the syntypes very much resembles fig. 6 in Attems (1896), which is based on macerated gonopods, and they were most probably the model for this drawing.

The syntypes of *fasciatus* as well as the Zanzibar specimens collected by M. Stoltze are very similar to *A. claudiahempae* Enghoff & Frederiksen (2015), and it is possible that the latter name should be regarded as a junior synonym of *A. fasciatus*. However, the body diameter of the specimens from Kizimkazi is at the high end, and partly larger, compared to *A. claudiahempae* from Mt. Kilimanjaro. The two intact specimens from Zanzibar examined here, viz., the intact syntype and the male from the sultan's palace, are definitely much larger. The latter specimens are more similar in size to *A. cf. claudiahempae*, recorded from the Morogoro Region, Kilosa District, Rubeho Mts by Enghoff & Frederiksen (2015). Attems (1896) gave the (horizontal) diameter of *A. fasciatus* as 2 mm. Brolemann (1920) gave 55 podous rings (= “56 segments ... 1 segment apode”) and a diameter of 1.70 mm for an adult male. Whereas “2 mm” is much more than any other specimen in this complex, Brolemann's values would fit *A. claudiahempae* by extrapolation.

The situation is obviously complicated, and for the time being, *A. fasciatus* and *A. claudiahempae* are kept as separate species.

A key to the species of *Prionopetalum*

This key builds extensively on previous keys provided by Kraus (1960) and VandenSpiegel & Pierrard (2009). The new species described here is included, but *Aquattuor fasciatus* is excluded, and *P. stuhlmanni* is treated as a synonym of *P. kraepelini* (cf. above). I follow VandenSpiegel & Pierrard (2009) in not

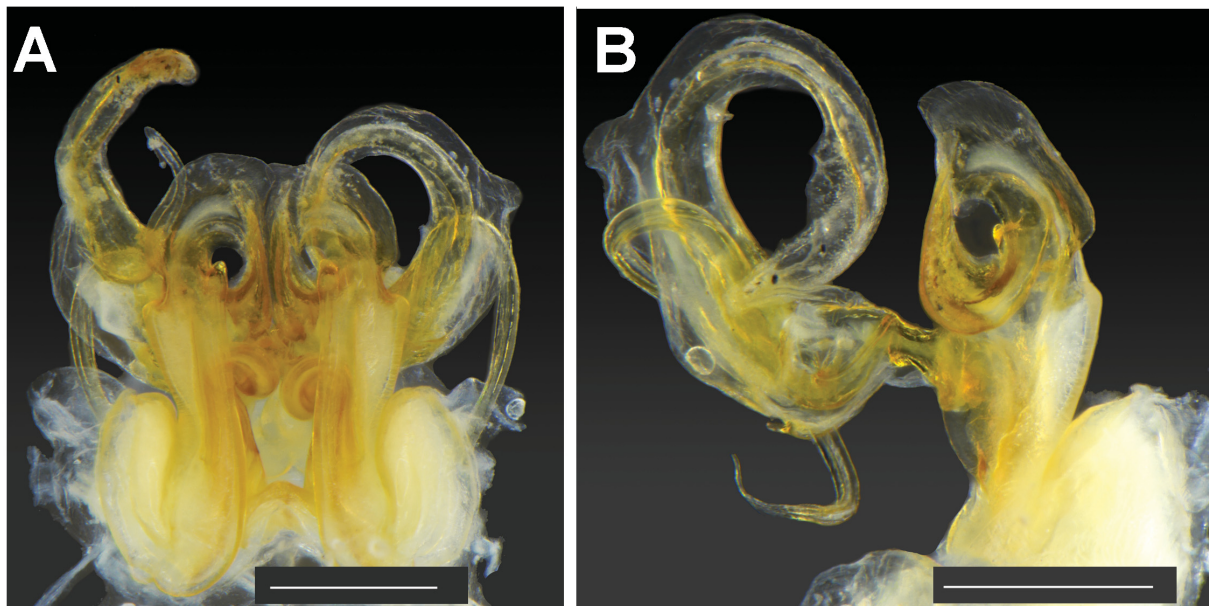


Fig. 8. *Aquattuor fasciatus* (Attems, 1896) comb. nov., syntype of *Odontopyge fasciata* (NHMW 2672). **A.** Gonopods, anterior view. **B.** Left gonopod, posterior view. Scale bars = 0.5 mm. Photographs: N. Akkari.

considering *Spinotarsus weneri* Attems, 1910 as a species of *Prionopetalum*, although Kraus (1960) suggested such a relationship (but still listed *S. weneri* under "species *incertae sedis*").

1. Coxa with a straight, mostly long lateral spine pointing basad, laterobasad or laterad (Fig. 9A–L)2
 – Coxa different, sometimes with another type of lateral process, but not a straight basad, laterobasad or laterad spine13
2. Lateral coxal spine directed laterad, set off by right angles from main coxal margin (Fig. 9A)
*P. megalacanthum* Attems, 1912
 – Lateral coxal spine different3
3. Lateral coxal spine directed basad, in part overlying main body of coxa (Fig. 9B)
*P. frundsbergi* (Attems, 1927)
 – Lateral coxal spine different4
4. Tip of distal telomere process (*tdp*) divided into two equal branches (Fig. 10A). Gonopod coxa profile as Fig. 9C
*P. bifidum* VandenSpiegel & Pierrard, 2009
 – Tip of distal telomere process not divided into two equal branches, but one or two small subapical processes may be present5
5. Distal telomere process (*tdp*) ending in three dark spines (Fig. 10B). Gonopod coxa profile as Fig. 9D
*P. tricuspis* Brolemann, 1920
 – Tip of distal telomere process at most with a single accessory process/spine6
6. Proximal telomere process (*tpp*) distally expanded, asymmetrically club-shaped (Fig. 11A–F)7
 – Proximal telomere process not strongly expanded distally (Fig. 11G–K)12
7. Distal telomere process (*tdp*) with a small accessory process (Fig. 10C)8
 – Distal telomere process without accessory process (like Fig. 10D)9
8. Lateral coxal spine relatively short, directed almost basad (Fig. 9E). Proximal telomere process (*tpp*) moderately asymmetrical (Fig. 11A)
*P. aculeatum* Attems, 1914
 – Lateral coxal spine directed almost laterad (Fig. 8F). Proximal telomere process strongly asymmetrical (Fig. 11B)
*P. ndelei* VandenSpiegel & Pierrard, 2009
9. Coxa mesapically rounded (Fig. 9G). Proximal telomere process as in Fig. 11C
*P. serratum* Attems, 1909
 – Coxa mesapically with a spinous projection (Fig. 9H–J, arrows)10
10. Distal margins of proximal telomere process (*tpp*) smooth (Fig. 10D). Gonopod coxa profile as Fig. 9H
*P. dentigerum* Verhoeff, 1941
 – Distal margin of proximal telomere process wavy or with a denticle (Fig. 11E–F)11
11. Distal margin of proximal telomere process (*tpp*) wavy (Fig. 11E). Gonopod coxa profile as Fig. 9I
*P. tanganjikum* Verhoeff, 1941
 – Distal margin of proximal telomere process with a single denticle (Fig. 11F, arrow). Gonopod coxa profile as Fig. 9J
*P. xerophilum* (Carl, 1909)

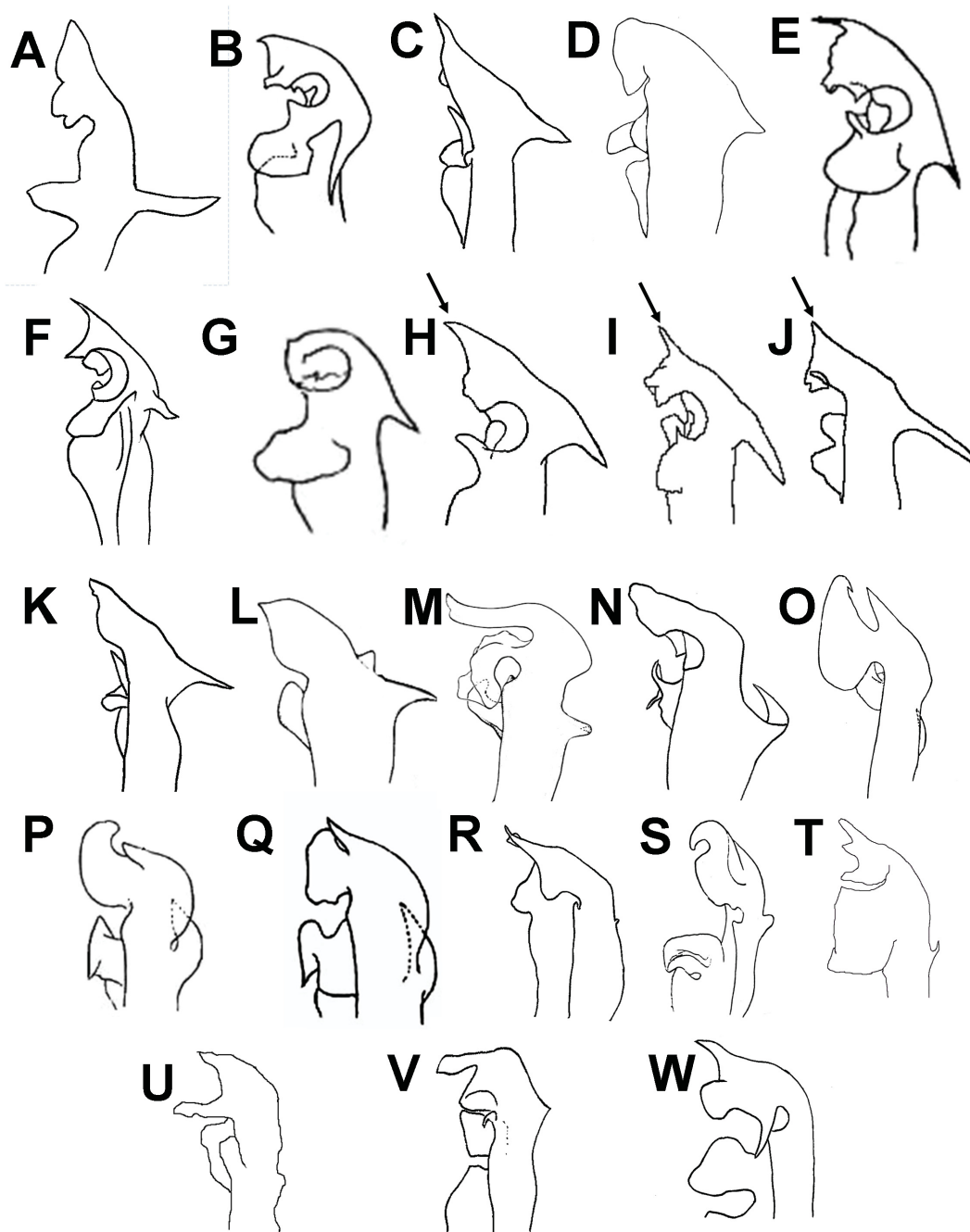


Fig. 9. *Prionopetalum* spp., outlines of distal part of gonopod coxa. The species appear in the sequence in which they key out in the identification key. **A.** *P. megalacanthum* (after a specimen in NHMW). **B.** *P. frundsbergi* (based on Kraus 1960). **C.** *P. bifidum* (based on VandenSpiegel & Pierrard 2009). **D.** *P. tricuspis* (based on Brolemann 1920). **E.** *P. aculeatum* (based on Kraus 1960). **F.** *P. ndelei* (based on VandenSpiegel & Pierrard 2009). **G.** *P. serratum* (based on Kraus 1960). **H.** *P. dentigerum* (based on Kraus 1960). **I.** *P. tanganjikum* (based on Kraus 1960). **J.** *P. xerophilum* (based on Kraus 1960). **K.** *P. clarum* (based on Kraus 1960). **L.** *P. pulchellum* (based on Kraus 1960). **M.** *P. etiennei* (based on Demange 1982). **N.** *P. lindi* (based on VandenSpiegel & Pierrard 2009). **O.** *P. coronatum* (based on Kraus 1958). **P.** *P. exaratum* (based on Kraus 1960). **Q.** *P. cornutum* (based on Kraus 1960). **R.** *P. kraepelini* (orig.). **S.** *P. glomeratum* (based on Attems 1935). **T.** *P. urbiculum* (based on Kraus 1960). **U.** *P. suave* (based on Kraus 1960). **V.** *P. fryeri* (based on Kraus 1960). **W.** *P. asperginis* sp. nov. (orig). Not to scale.

12. Proximal telomere process (*tpp*) straight, apically rounded (Fig. 11G). Body diameter 5.5 mm. Gonopod coxa profile as Fig. 9K *P. clarum* (Chamberlin, 1927)
 – Proximal telomere process slightly curved, pointed (Fig. 11H). Body diameter 3 mm. Gonopod coxa profile as Fig. 9L *P. pulchellum* Kraus, 1960
13. Coxa with a strongly curved lateral spine (Fig. 9M–N)14
 – Lateral coxal spine, if present, not strongly curved15
14. Gonopod coxa profile as Fig. 9M. Body diameter 2.5 mm *P. etiennei* Damange, 1982
 – Gonopod coxa profile as Fig. 9N. Body diameter 3.3–3.8 mm
 *P. lindi* VandenSpiegel & Pierrard, 2009
15. Lateral coxal spine sizeable, directed apicad and partly overlying main body of coxa. Coxa apically bifid (Fig. 9O–Q)16
 – Coxa at most with a tiny lateral spine or bump (Fig. 9R–W)18
16. Both apical branches of coxa pointed, the mesal branch hook-like (Fig. 9O)
 *P. coronatum* Kraus, 1958
 – Mesal-apical branch of coxa not pointed (Fig. 9P–Q)17
17. Gonopod coxa profile as Fig. 9P *P. exaratum* (Attems, 1938)
 – Gonopod coxa profile as Fig. 9Q *P. cornutum* Kraus, 1958
18. Proximal telomere process (*tpp*) with several lobes along one side (Fig. 11I). Gonopod coxa profile as Fig. 9R *P. kraepelini* (Attems, 1896)
 – Proximal telomere process at most with a single lateral lobe (Fig. 11J–K)19
19. Coxal apex hook-like (Fig. 9S). Body diameter 2.5 mm *P. glomeratum* Attems, 1935
 – Coxal apex not hook-like (Fig. 9T–W). Body diameter 4.4–5 mm20
20. Coxal apex with three mesad processes (Fig. 9T) *P. urbicolum* (Carl, 1909)
 – Coxal apex with two mesad processes (Fig. 9U–W)21

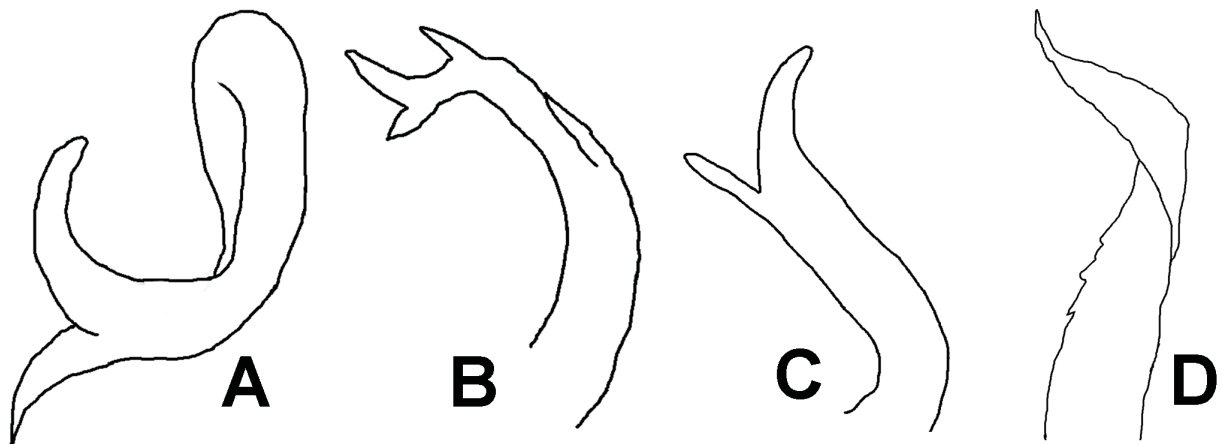


Fig. 10. *Prionopetalum* spp., outlines of distal telomere process (*tdp*). **A.** *P. bifidum* (based on VandenSpiegel & Pierrard 2009). **B.** *P. tricuspis* (based on VandenSpiegel & Pierrard 2009). **C.** *P. aculeatum* (based on Attems 1914). **D.** *P. asperginis* sp. nov. (orig.). Not to scale.

21. Both mesad processes of coxal apex pointed (Fig. 9U) *P. suave* (Gerstäcker, 1873)
 – Subapical mesad process of coxal apex rounded (Fig. 9V–W) 22
22. Gonopod coxa profile as Fig. 8V. Solenomere with a short accessory branch at *c.* $\frac{2}{3}$ of its length. Proximal telomere process as Fig. 11J. *P. fryeri* (Turk, 1956)
 – Gonopod coxa profile as Fig. 8W. Solenomere without an accessory branch. Proximal telomere process as Fig. 11K *P. asperginis* sp. nov.

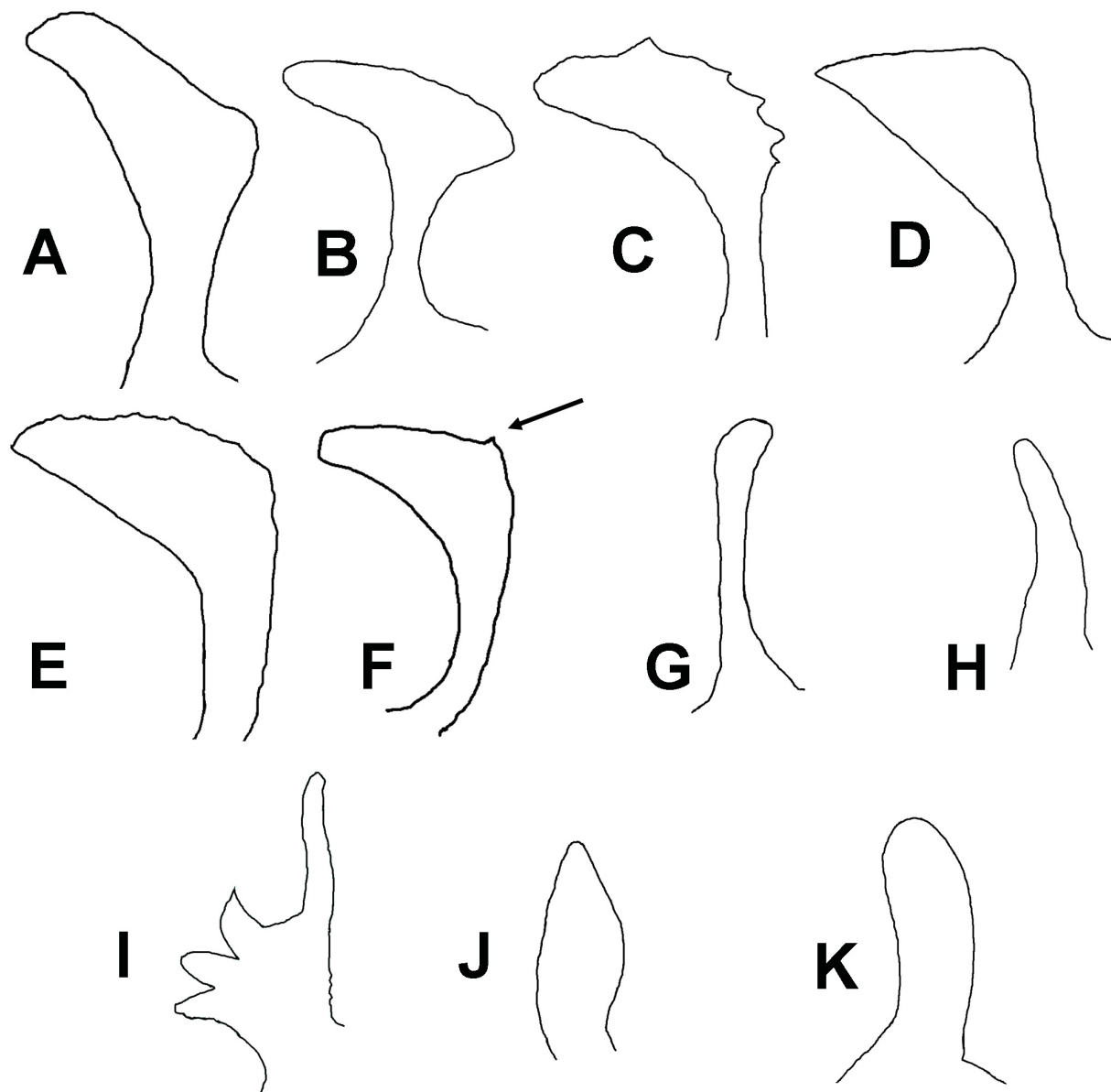


Fig. 11. *Prionopetalum* spp., outlines of proximal telomere process (*tpp*). **A.** *P. aculeatum* (based on Attems 1914). **B.** *P. ndelei* (based on VandenSpiegel & Pierrard 2009). **C.** *P. serratum* (based on Attems 1909). **D.** *P. dentigerum* (based on Kraus 1960). **E.** *P. tanganjikum* (based on Kraus 1960). **F.** *P. xerophilum* (based on Kraus 1960). **G.** *P. clarum* (based on Kraus 1960). **H.** *P. pulchellum* (based on Kraus 1960). **I.** *P. kraepelini* (orig.). **J.** *P. fryeri* (based on Kraus 1960). **K.** *P. asperginis* sp. nov. (orig.). Not to scale.

Discussion

Among the Odontopygidae from the Udzungwa Mts studied so far, species of *Prionopetalum* occur at the lowest altitudes: 300–339 m asl for *P. kraepelini* and 550–750 m asl for *P. asperginis* sp. nov. In comparison, the altitudinal span of the Udzungwa endemic *Chaleponcus dabagaensis* group is 1390–2100 m asl (Enghoff 2014), of Udzungwa *Aquattuor* species 750–1800 (1850) m asl (Enghoff & Frederiksen 2015), and of Udzungwa *Geotypodon* species 1145–1500 m asl (Enghoff 2016). This is in line with the general tendency of *Prionopetalum* species to occur in savanna-like habitats where some of them even have synanthropic tendencies: *P. urbicolum*, true to its name, has often been found in Dar-es-Salaam, and *P. frundbergi* has been collected in Mombasa and Tanga in Kenya (Enghoff *et al.* 2016). Some *Prionopetalum* species are even known as pests on various crops, including *P. etiennei* on potato, African eggplant and okra in Senegal (Demange 1982; Etienne *et al.* 1992) and *Prionopetalum* sp. (possibly *P. xerophilum*) on sweet potato in Uganda (Ebregt *et al.* 2005).

It is worth noting that *P. kraepelini*, the most ‘lowlandish’ Udzungwa odontopygid known so far, is the only species among the Udzungwa odontopygids which (according to present knowledge) is not endemic to this mountain range.

Acknowledgements

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Correction to Enghoff (2016)

On p. 17 of the previous article in the “A mountain of millipedes” series (Enghoff 2016), the reference to Dieudonné (2016) should instead be to Ntashavu (2016).

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