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Research article

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A mountain of millipedes VIII. The genus *Aquattuor* Frederiksen, 2013 revisited – a new species from the Udzungwa Mts, Tanzania, another from the Nguru Mts, and introduction of the first pair of male legs as a source of taxonomic characters (Diplopoda, Spirostreptida, Odontopygidae)

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Abstract. A large, newly collected material of the genus *Aquattuor* from the Udzungwa Mts, Tanzania, has been studied. Two new species are described, viz., *A. mollilobus* sp. nov. from the Udzungwa Mts and *A. nguruensis* sp. nov. from the Nguru Mts, Tanzania. *Aquattuor claudiahempae* Enghoff & Frederiksen, 2015, is recorded as new for the Udzungwa fauna. Characters from the first pair of male legs are illustrated for all *Aquattuor* species and are shown to be useful for species discrimination. A new gonopodal difference between *A. submajor* Enghoff, 2015 and *A. udzungwensis* Enghoff, 2015 is described and illustrated. Intrageneric relationships and distribution patterns are discussed. A distribution map and a key to all *Aquattuor* species are presented.

Keywords. Eastern Arc, taxonomy, new species, identification key.

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Introduction

The genus *Aquattuor* was described by Frederiksen (2013) for a new species from the East Usambaras in the Eastern Arc Mts of Tanzania. Enghoff & Frederiksen (2015) reviewed the genus and added five new species from the Udzungwa Mts and one new species from Mt Kilimanjaro. Still another species, *A. fasciatus* (Attems, 1896), was re-allocated into *Aquattuor* by Enghoff (2016b). The genus thus currently includes eight species. Subsequently, a very large collection of *Aquattuor* spp. from the Udzungwa Mts has become available. The study of this material has clarified some problems of species delimitation; also, an additional new species from the Udzungwa Mts is described here. Additionally, a male from the Nguru Mts is here described as the tenth species of *Aquattuor*; this is probably conspecific with the female mentioned as “*Aquattuor* sp.” in Enghoff & Frederiksen (2015: 21). During the examination of

the new material, several characters of the first pair of male legs have been found to exhibit significant inter-specific variation, see below.

The present contribution is the eighth in a series of papers devoted to the millipede fauna of the Udzungwa Mts Numbers 1–6 in the series (Enghoff 2014, 2016a, 2016b, 2016c, 2018a; Enghoff & Frederiksen 2015) deal with Odontopygidae Attems, 1909, like the present one, while number 7 (Enghoff 2018b) is devoted to a genus of the family Paradoxosomatidae Daday, 1889.

In adult males of Odontopygidae the first pair of legs is modified; notably, the prefemur is enlarged and carries a large lobe on its anterior side. Similar lobes also occur in the related family Spirostreptidae Brandt, 1833 where details of their structure have been recognized as sometimes furnishing useful taxonomic characters (Krabbe 1979, 1982). In the Odontopygidae, however, variations in the first pair of male legs have not been explored, although several authors have described modification of these legs in certain species; see Mauriès (1997) who examined about 80 odontopygid species, found prefemoral lobes in them all, but did not describe the variation. The published drawings, however, suggest some interspecific variation, and this has been corroborated by a preliminary examination of several odontopygid species, not the least in the genus under consideration here. Therefore, characters from the first pair of legs are here described for all species of *Aquattuor*.

Material and methods

The vast majority of material comes from the zoological collections of the Natural History Museum of Denmark, University of Copenhagen (NHMD, formerly ZMUC). Almost all specimens were collected in pitfall traps by Jagoba Malumbres-Olarte. The holotype of the new species from the Nguru Mts derives from the Virginia Museum of Natural History (VMNH), where the very large collection of Tanzanian millipedes accumulated by Richard L. Hoffman (1927–2012) is housed.

Fig. 1 shows the collecting sites for *Aquattuor* spp. in the Udzungwa (sometimes spelled Uzungwa) Mts.

A total of 364 male specimens were examined, of which 305 belonged to one species, *A. udzungwensis* Enghoff, 2015. Some females have tentatively been referred to a species although in odontopygids, particularly in *Aquattuor*, only adult males can be identified to species level with any degree of certainty. All samples are kept in 70% alcohol.

Specimens were stored and examined in 70% ethanol under a stereo microscope. Specimens for scanning electron microscopy (SEM) were cleaned with ultrasound, transferred to 96% ethanol, then to acetone, air-dried, mounted on aluminium stubs or on triangles of flexible aluminium tape, in turn mounted on stubs, coated with platinum/palladium and studied in a JEOL JSM-6335F scanning electron microscope. Images were processed in Photoshop (in some cases this included stacking of multiple images) and plates were composed in Microsoft Publisher.

The diagnoses and descriptions, including the measurements, apply to adult males, unless otherwise specified. Terminology and abbreviations as far as possible follow Enghoff & Frederiksen (2015).

Abbreviations for morphological terms used in descriptions and illustrations

- btl* = basal telomer lamella
- dpl* = distal prefemoral lobe
- li* = lateral incision
- mbL* = meso-basal lobe of palette
- mi* = mesal incision
- mpl* = meso-posterior telomer lamella

- pa* = palette
pdf = prefemoral depression
pfp = prefemoral process of first pair of legs.
pp = proplica
slm = solenomere
spl = spinose lid-like flap
tm = telomere

Other abbreviations used in the text

- a.s.l. = above sea level
 FR = Forest Reserve
 Mts = Mountains
 HMNH = Hungarian Museum of Natural History, Budapest, Hungary
 NHMD = Natural History Museum of Denmark, Copenhagen, Denmark
 VMNH = Virginia Museum of Natural History, Martinsville, VA, USA

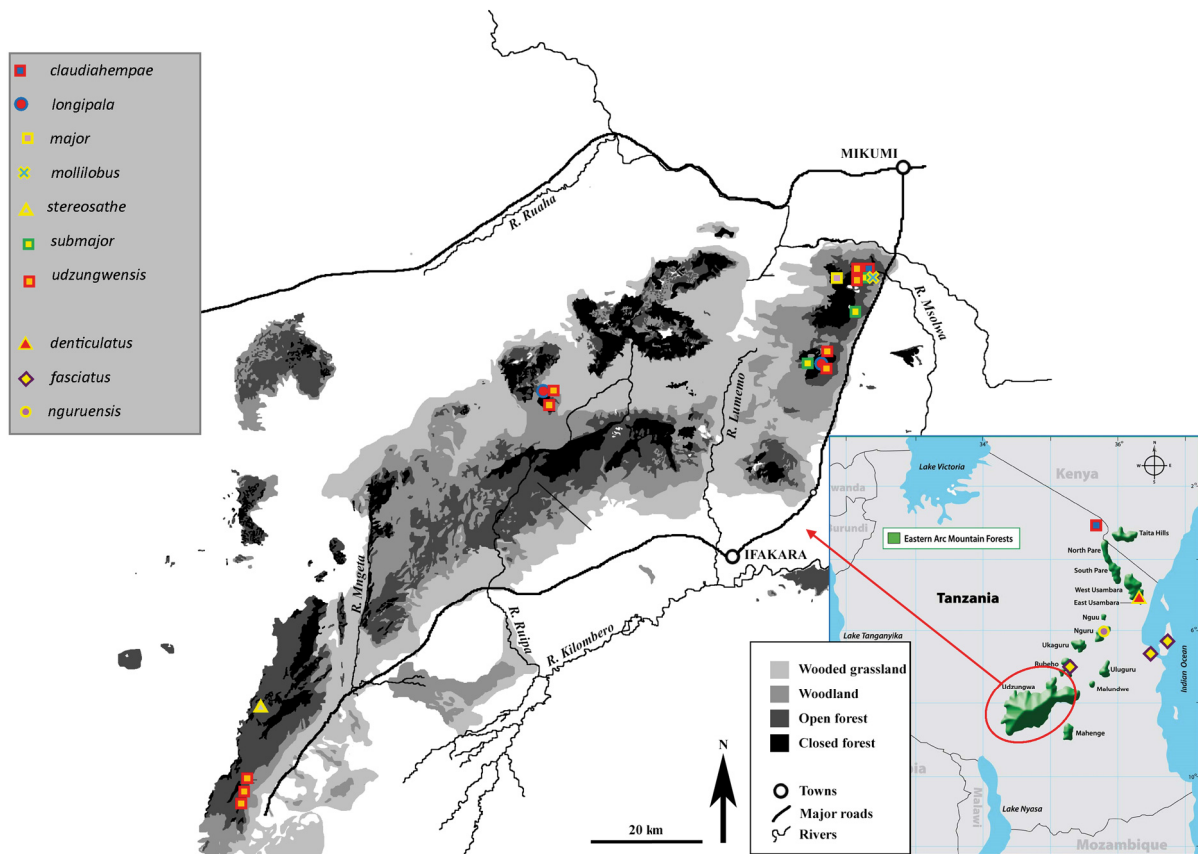


Fig. 1. Collecting sites for *Aquattuor* spp. in the Udzungwa Mts. Based on Marshall *et al.* (2010: fig. 1); inset by permission of the Eastern Arc Mountains Conservation Endowment Fund.

Results

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

Diagnosis (modified after Enghoff & Frederiksen 2015)

Differs from all other Odontopygidae by the structure of the limbus, which consists of large, rectangular, easily detachable flaps. Gonopods of the Prionopetalini type, i.e., basomere of telopodite with a torsate flexible zone followed by a posttarsal narrowing; solenomere elongated. Gonopodal proplica apically expanded into a distal palette; metaplica with an oblique flange; solenomere simple, thin and whip-like; telomere terminating in a long, curved, gutter-like to tubular part.

Descriptive notes

For characters not mentioned here, see Enghoff & Frederiksen (2015).

Mandibular stipes (Fig. 2): in males, but not in females with a disto-ventral expansion.

First pair of male legs: in the genus *Aquattuor* the first pair of legs is remarkably diverse. Figs 3–7 illustrate the first pair of legs in all known species of the genus, with a focus on the prefemur. In all of them, the prefemur carries a more or less finger-shaped process (*pdf*) which projects orad from the

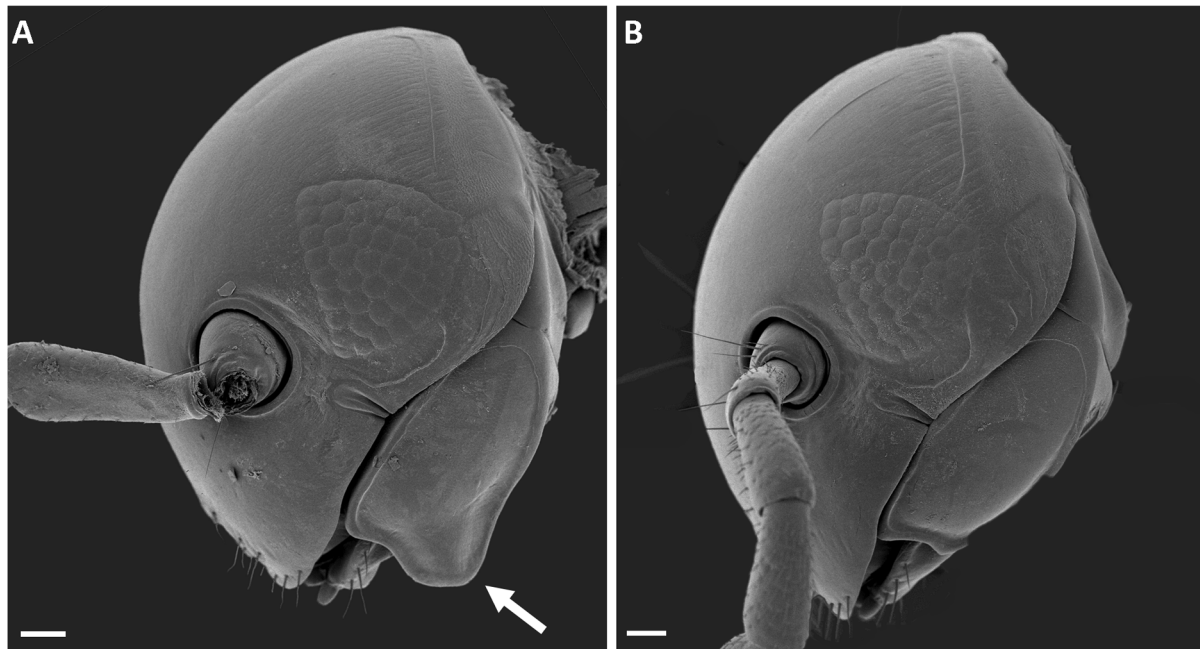


Fig. 2. *Aquattuor udzungwensis* Enghoff, 2015, specimens from Chita, heads, lateral view. **A.** Male (NHMD 621667). **B.** Female (NHMD 621667). Scale bars = 0.1 mm. The arrow points at the disto-ventral stipital expansion lobe in the male.

anterior surface of the prefemur (Figs 3–7). The distal (ventral) surface of the process is smooth, the basal (dorsal) surface is more or less scaly-rugose. The shape of the process varies from slender finger-shaped to relatively broad/triangular, and in one species (*A. nguruensis* sp. nov.) there is a clearly delimited depression (*pdf*) on the distal surface of the process (Fig. 4A–C). In *A. major* Enghoff, 2015, *A. longipala* Enghoff, 2015 and *A. mollilobus* sp. nov. there is in addition a second, more distal, more irregularly shaped prefemoral lobe (*dpl*, Figs 5–6).

Another type of variation is seen in the setation of the telopodites of the first pair of legs (Fig. 8). Here, *A. mollilobus* sp. nov. (Fig. 8C) stands out by having very short setae on all podomeres. *Aquattuor major* and *A. longipala* have long setae on the tarsus, but very short ones on the femur (Fig. 8B). The remaining species have long setae (same length as on the following leg-pairs) on all podomeres (Fig. 8A). These differences in setation do not seem to reflect the setation of normal walking legs.

In one species (*A. udzungwensis*), the podomeres distal to the prefemur of the first leg pair seem to be invariably missing (several specimens examined) (Fig. 7D–E).

Adhesive pads on walking legs are absent.

Included species (alphabetically)

Aquattuor claudiahempae Enghoff & Frederiksen, 2015

A. denticulatus Frederiksen, 2013 (type species)

A. fasciatus (Attems, 1896)

A. longipala Enghoff, 2015

A. major Enghoff, 2015

A. mollilobus sp. nov.

A. nguruensis sp. nov.

A. stereosathe Enghoff, 2015

A. submajor Enghoff, 2015

A. udzungwensis Enghoff, 2015

Aquattuor claudiahempae Enghoff & Frederiksen, 2015

Figs 1, 3D–I, 9–10

Aquattuor claudiahempae Enghoff & Frederiksen, 2015: 17.

Diagnosis

Diameter 1.41–1.58 mm, 50–53 podous rings (Fig. 9). Shares a short (as broad as long, or slightly longer) gonopodal palette with *A. denticulatus*, *A. fasciatus*, *A. stereosathe*, *A. submajor*, and *A. udzungwensis*. Differs from these species, except *A. fasciatus*, by the combination of fully developed telopodites on the first pair of male legs, the gonopodal telomere describing a ca 270° curve, curving almost in one plane only, by lacking a spinose lid-like flap on the basal telomer lamella, and by having a distinct meso-basal lobe of the gonopod palette. Very similar to, and perhaps not distinct from *A. fasciatus*, differs by being mostly smaller (male diameter < 1.7 mm) and by having the prefemoral processes of the first pair of male legs more slender, finger-shaped.

Material studied (total: 25 ♂♂, 29 ♀♀)

TANZANIA • 1 ♂, paratype; Kilimanjaro Region, Mt Kilimanjaro, Hai District; 03°13'59.37" S, 37°16'09.28" E; 1345 m a.s.l.; 20 Nov. 2013; S.B. Frederiksen leg.; coffee plantation, plot 2; NHMD 621638 • 24 ♂♂, 29 ♀♀; Morogoro Region, Udzungwa Mts National Park, Kidatu, Plot 2; 07°41'14.9" S,

36°56'24.7" E; 650 m a.s.l.; 24 Oct. 2014; J. Malumbres-Olarte leg.; pitfall trapping (summed catch from eight traps); NHMD 621639.

Descriptive notes

The specimens from Udzungwa Mts National Park very much resemble those from Mt Kilimanjaro (type locality of *A. claudiahempae*), in size (Fig. 9) as well as in gonopod structure (Fig. 10, cf. Enghoff & Frederiksen 2015: fig. 10). In particular, the two samples agree in having the distal part of the telomere compressed, i.e., instead of forming a gutter, the lamella constituting the telomere is folded flat such that the inside of the gutter becomes invisible; the outside is strongly microspinose on one side and the free margin of the other side is characteristically wavy-spinose (Fig. 10D, Enghoff & Frederiksen 2015: fig. 10d).

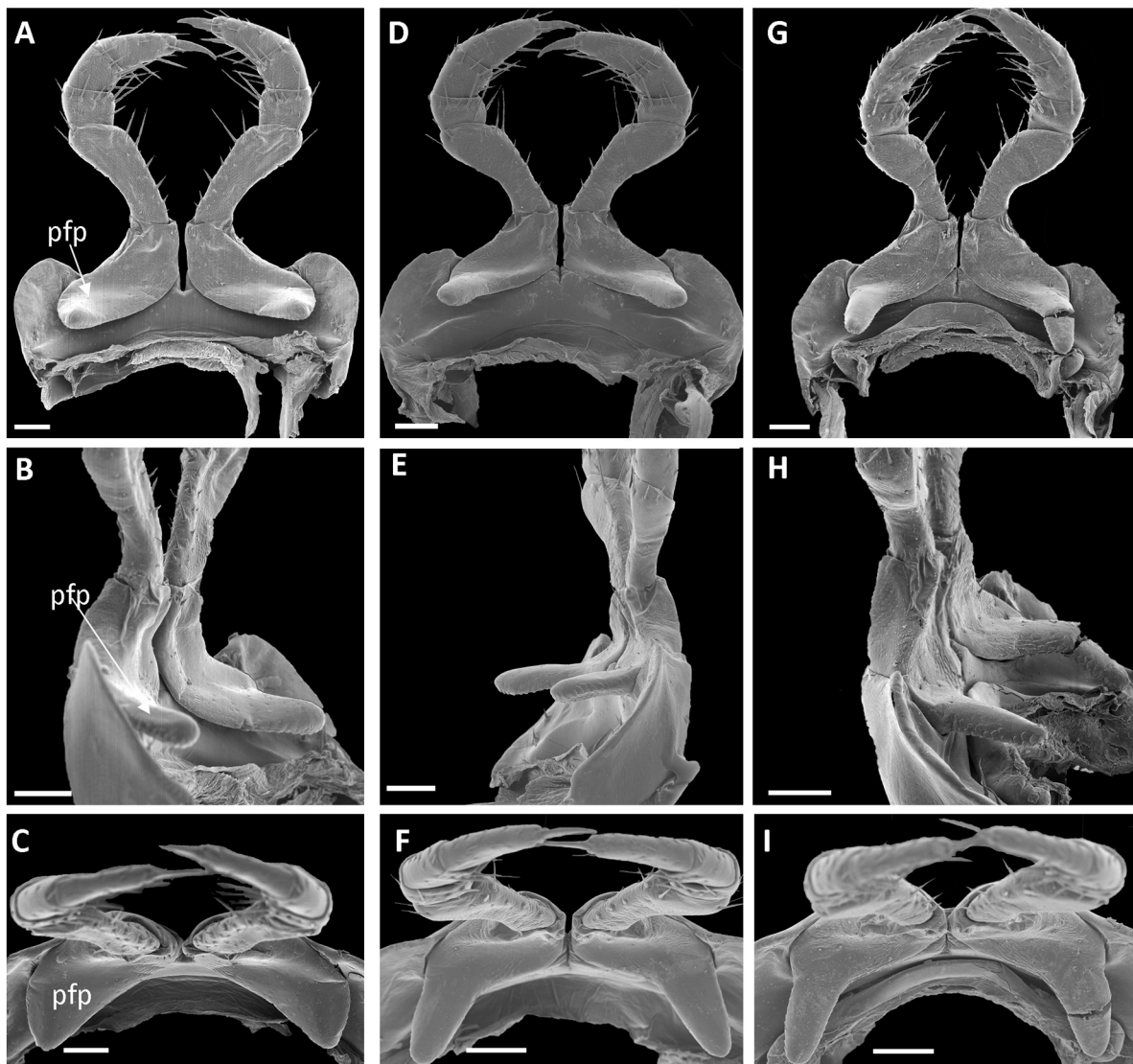


Fig. 3. *Aquattuor* spp., first pair of male legs. **A–C.** *A. fasciatus* (Attems, 1896), non-type male from Zanzibar (NHMD 621641). **D–F.** *A. claudiahempae* Enghoff & Frederiksen, 2015, paratype from Kilimanjaro (NHMD 621638). **G–I.** *A. claudiahempae*, specimen from Udzungwa Mts (NHMD 621639). **A, D, G.** Anterior view. **B, E, H.** Sublateral view. **C, F, I.** Ventral view. Abbreviation: *pfp* = prefemoral process. Scale bars = 0.1 mm.

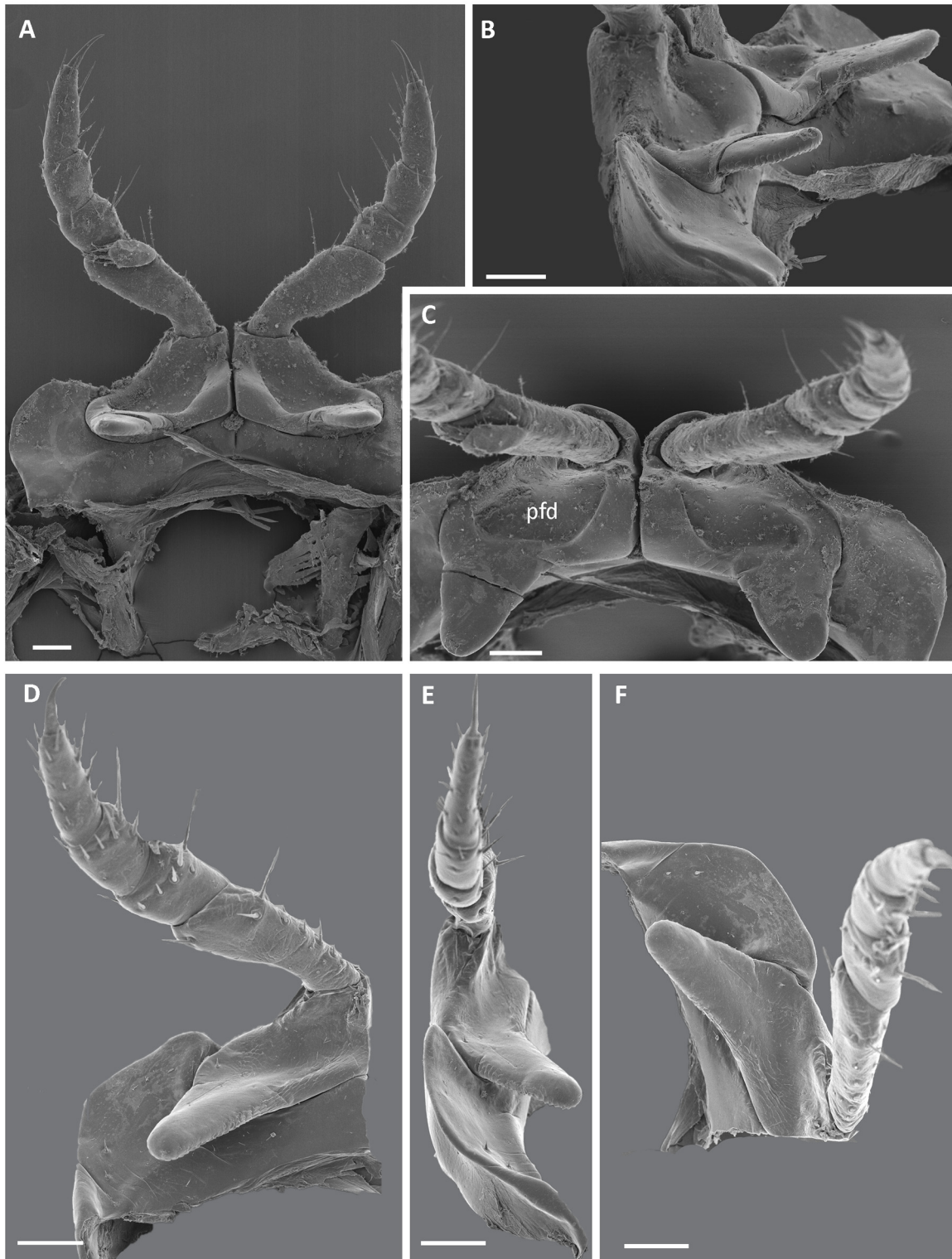


Fig. 4. A–C. *Aquattuor nguruensis* sp. nov., holotype, ♂ (VMNH110617), first pair of legs. Notice mite larva (“hypopus”) on left femur. D–F. *A. denticulatus* Frederiksen, 2013, paratype, ♂ (NHMD 621640), left leg of first pair. A, D. Anterior view. B, E. Sublateral view. C, F. Sub-ventral view. Abbreviation: *pfd* = prefemoral depression. Scale bars = 0.1 mm.

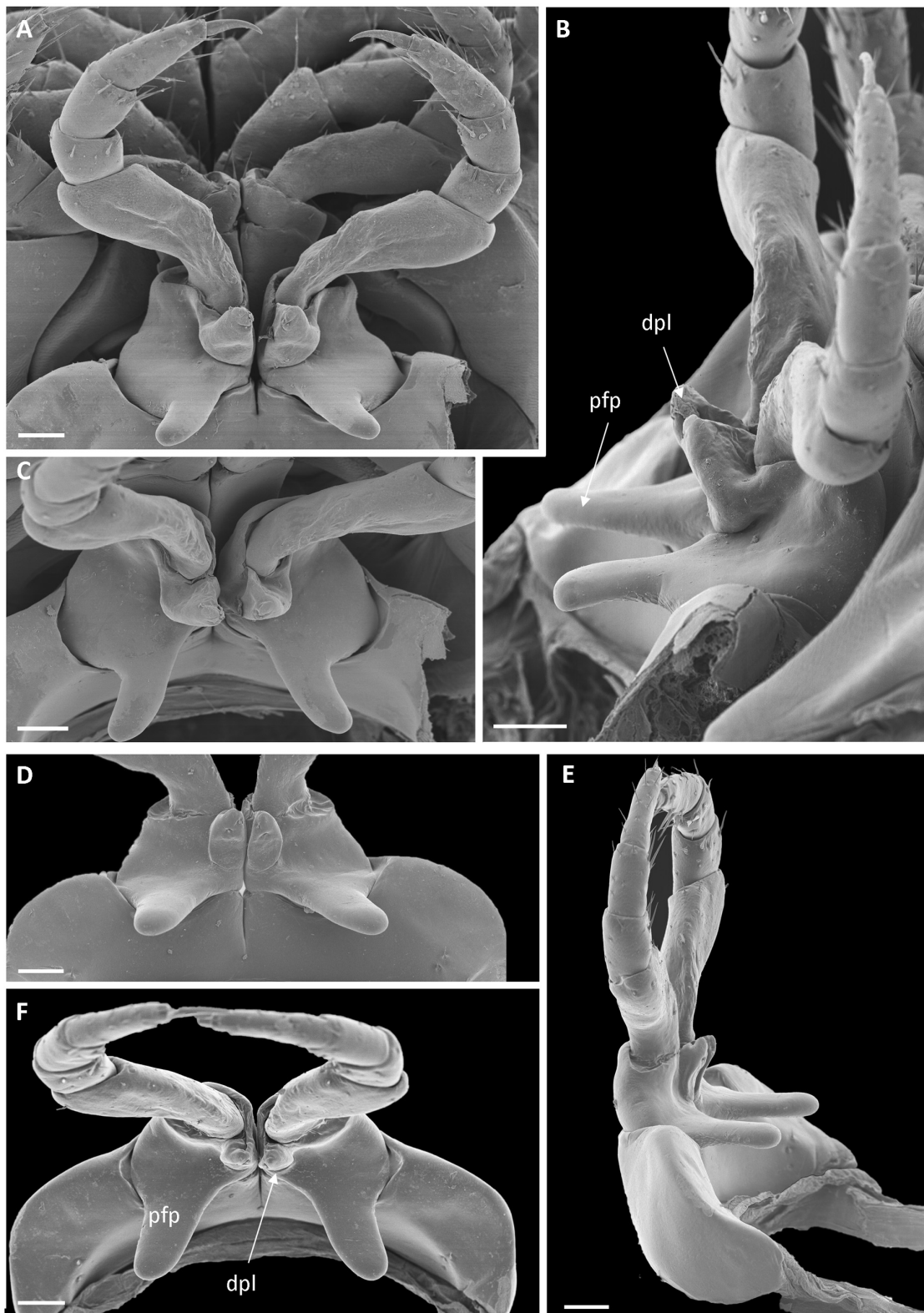


Fig. 5. *Aquattuor* spp., first pair of male legs. **A–C.** *A. major* Enghoff, 2015, paratype, ♂ (NHMD 621644), first pair of legs *in situ*. **D–F.** *A. longipala* Enghoff, 2015, male from Udzungwa Mts National Park, Mito Mitatu (NHMD 621642). **A, D.** Anterior view. **B, E.** Sublateral view. **C, F.** Sub-ventral view. Abbreviations: *dpl* = distal prefemoral lobe; *pfp* = prefemoral process. Scale bars = 0.1 mm.

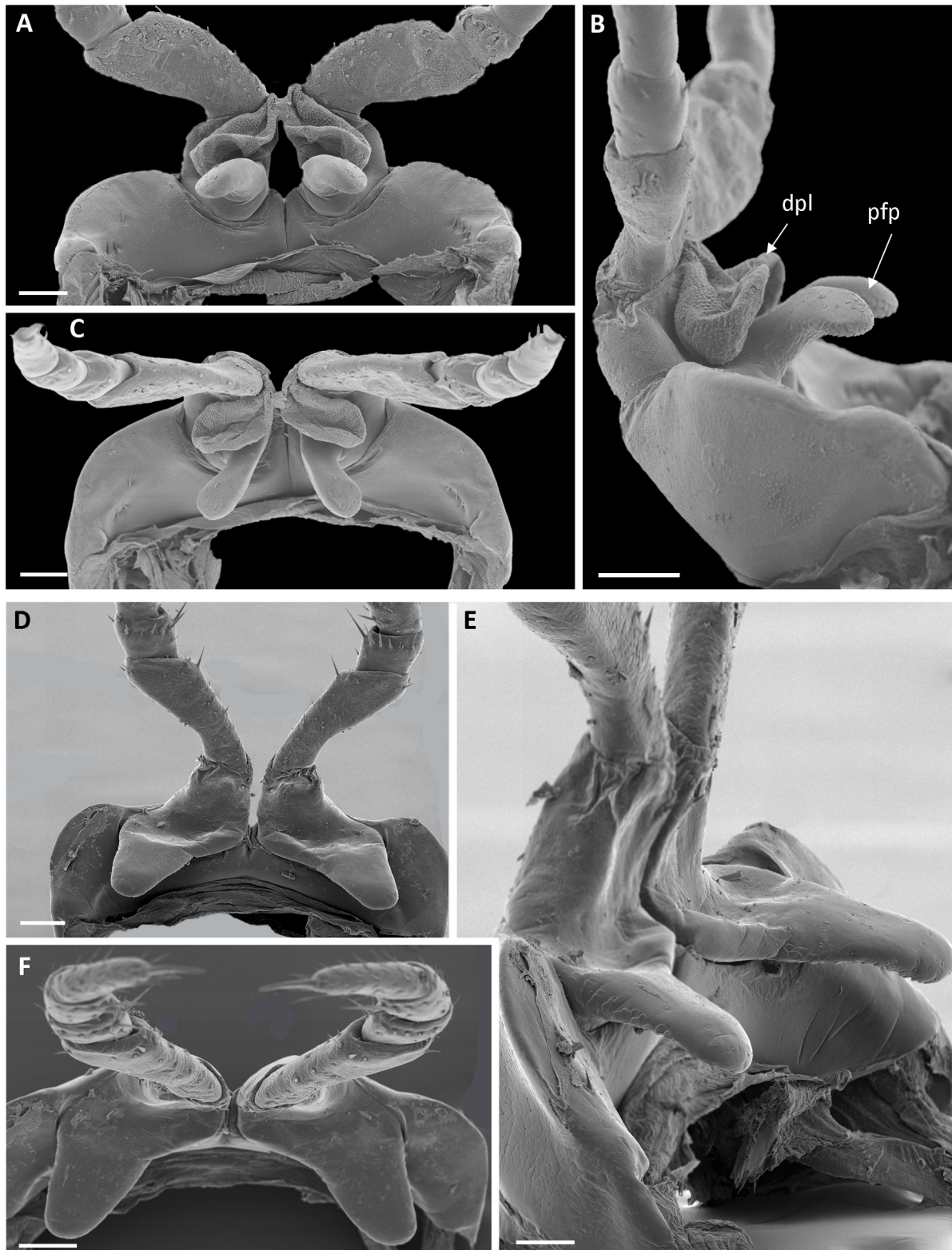


Fig. 6. *Aquattuor* spp., first pair of male legs. **A–C.** *A. mollilobus* sp. nov., paratype, ♂ (NHMD 621647). **D–F.** *A. stereosathe* Enghoff, 2015, paratype, ♂ (NHMD 621650). **A, D.** Anterior view. **B, E.** (Sub)lateral view. **C, F.** (Sub)ventral view. Abbreviations: *dpl* = distal prefemoral lobe; *pfp* = prefemoral process. Scale bars = 0.1 mm.

First pair of male legs (Fig. 3D–I) each with a single, finger-shaped prefemoral process; prefemoral processes more slender than those of the otherwise very similar *A. fasciatus* (Fig. 3A–C); setae of telopodite distal to prefemur similar in length to those of normal walking legs.

Distribution

Described from Mt Kilimanjaro (1169–1345 m a.s.l., in habitats disturbed by human activities; Enghoff & Frederiksen 2015); now also known from one site at 650 m a.s.l. in the Udzungwa Mts (Fig. 1).

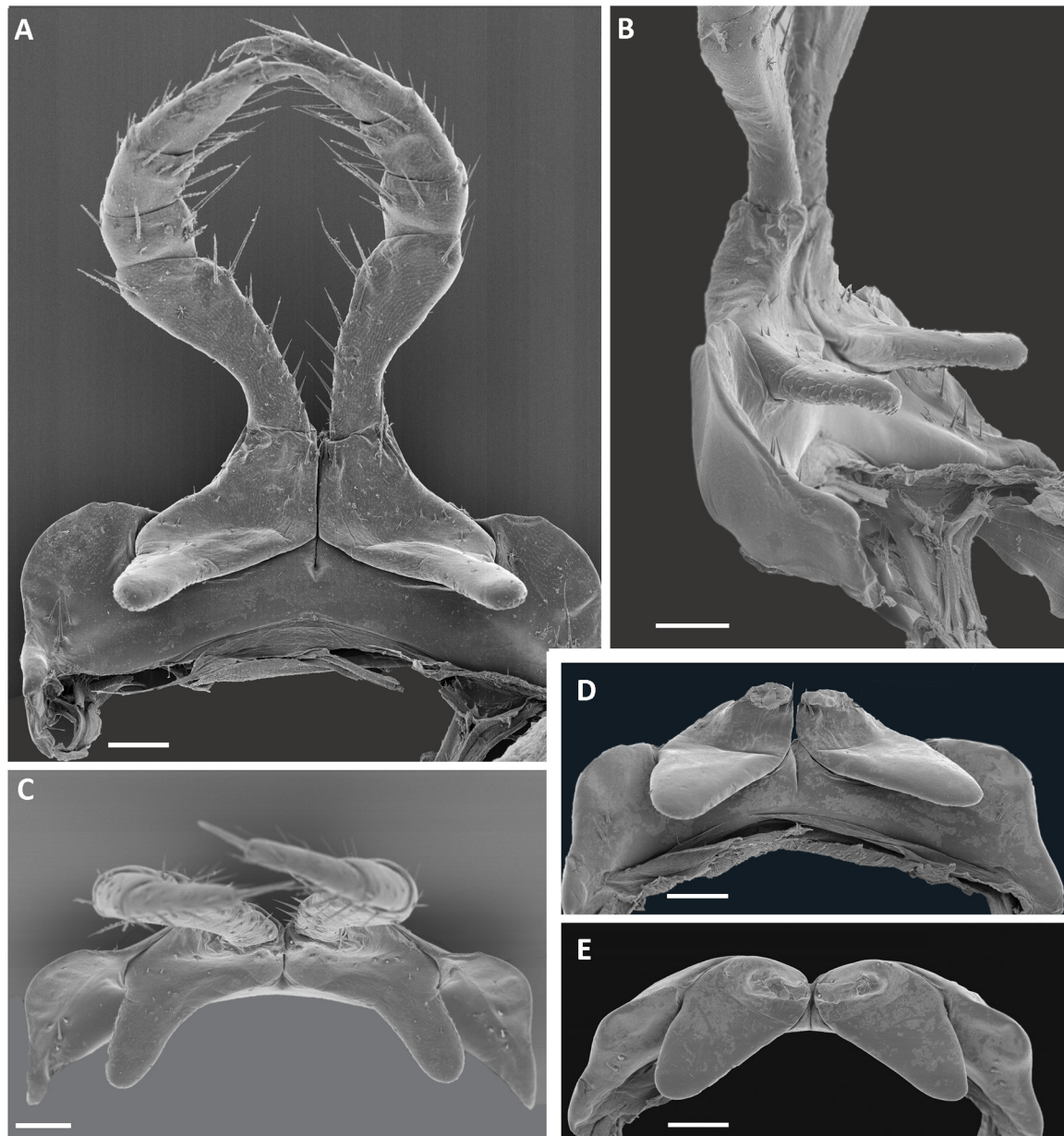


Fig. 7. *Aquattuor* spp., first pair of male legs. **A–C.** *A. submajor* Enghoff, 2015, paratype, ♂ (NHMD 621651). **A.** Anterior view. **B.** Sublateral view. **C.** Ventral view. **D–E.** *A. udzungwensis* Enghoff, 2015, male from Udzungwa Mts National Park, Kidatu (NHMD 621662). **D.** Anterior view. **E.** Ventral view. Scale bars = 0.1 mm.

Remarks

Enghoff (2016b) discussed *A. fasciatus* (Attems, 1896) (see below), emphasizing its great similarity with *A. claudiahempae* and suggesting that the latter might be a synonym of *A. fasciatus*. The similarity between both nominal species also extends to the compressed distal part of the telomere (Enghoff 2016b: fig. 7c, f). The only differences between the two seem to be size (cf. the identification key below, couplet 9) and the shape of the prefemoral process of the first pair of legs (Fig. 3). The new specimens of *A. claudiahempae* from Kidatu, Udzungwa Mts are of the same size as *A. claudiahempae* from Mt Kilimanjaro (Fig. 9), and their prefemoral processes strongly resemble those of Kilimanjaro specimens. *Aquattuor claudiahempae* and *A. fasciatus* are, for the time being, upheld as separate species.

***Aquattuor denticulatus* Frederiksen, 2013**

Figs 1, 4D–F

Aquattuor denticulatus Frederiksen, 2013: 64.**Diagnosis**

Diameter 1.58–1.77 mm, 50–52 podous rings. Shares a short (as broad as long, or slightly longer) gonopodal palette with *A. claudiahempae*, *A. fasciatus*, *A. stereosathe*, *A. submajor* and *A. udzungwensis*. Differs from these species by having the subdistal part of the gonopodal telomere almost straight, parallel to the coxa, the telomere tip being bent abruptly laterad.

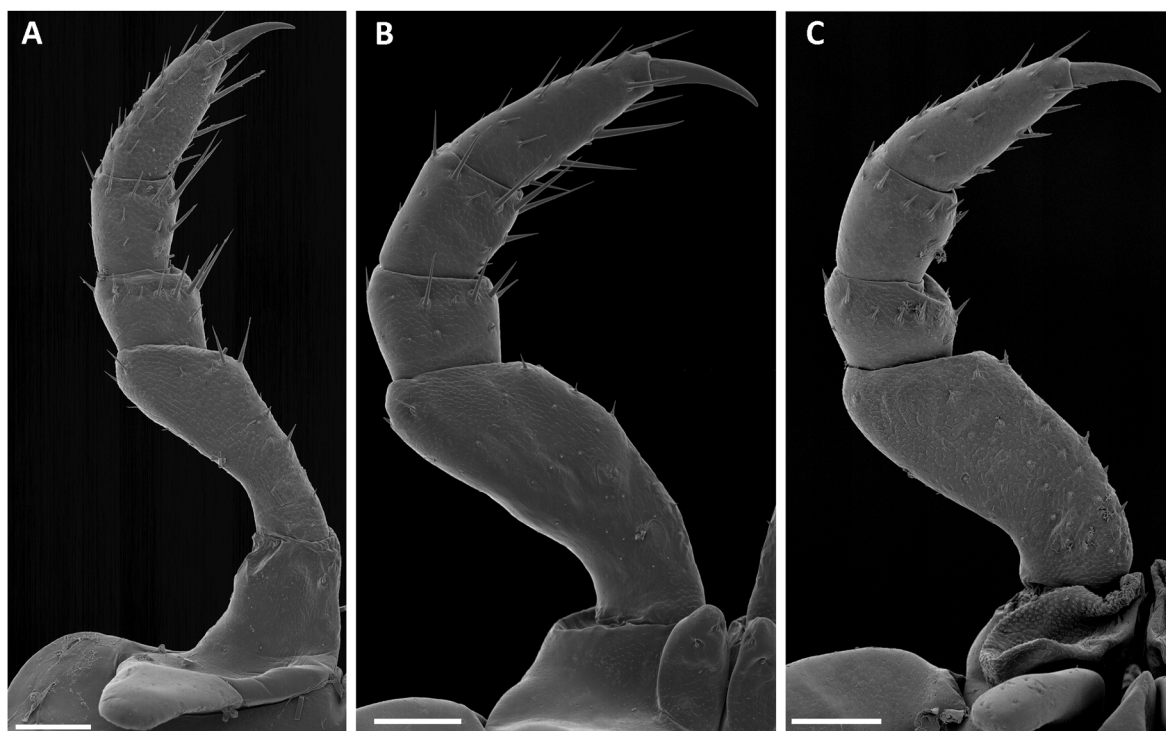


Fig. 8. *Aquattuor* spp., males, left leg of first pair. **A.** *A. stereosathe* Enghoff, 2015, paratype, ♂ (NHMD 621650): setae same length as in normal walking legs. **B.** *A. longipala* Enghoff, 2015, specimen from Udzungwa Mts National Park, Mito Mitatu (NHMD 621642): setae of femur shortened. **C.** *A. mollilobus* sp. nov., paratype, ♂ (NHMD 621646): all setae shortened. Scale bars = 0.1 mm.

Material studied (total: 1 ♂)

TANZANIA • 1 ♂, paratype; Tanga Region, Muheza District, East Usambara Mts, Amani, at Sigi River; 500 m a.s.l.; 7 Feb. 1977; H. Enghoff, O. Lomhodt and O. Martin leg.; NHMD 621640 [=ZMUC 00020528].

Descriptive notes

First pair of male legs (Fig. 4D–F) each with a single, finger-shaped prefemoral process; setae of telopodite distal to prefemur similar in length to those of normal walking legs.

Distribution

Known only from the type locality, Tanga Region, Muheza District, E Usambara Mts, Amani. Altitudinal range: 500–1000 m a.s.l. (Frederiksen 2013).

Aquattuor fasciatus (Attems, 1896)

Figs 1, 3A–C

Odontopyge fasciata Attems, 1896: 40.

Prionopetalum fasciatum – Attems 1914: 210. — Brolemann 1920: 123. — Kraus 1960: 86. — VandenSpiegel & Pierrard 2009: 152. — Enghoff *et al.* 2016: 69.

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

Aquattuor fasciatus – Enghoff 2016b: 14.

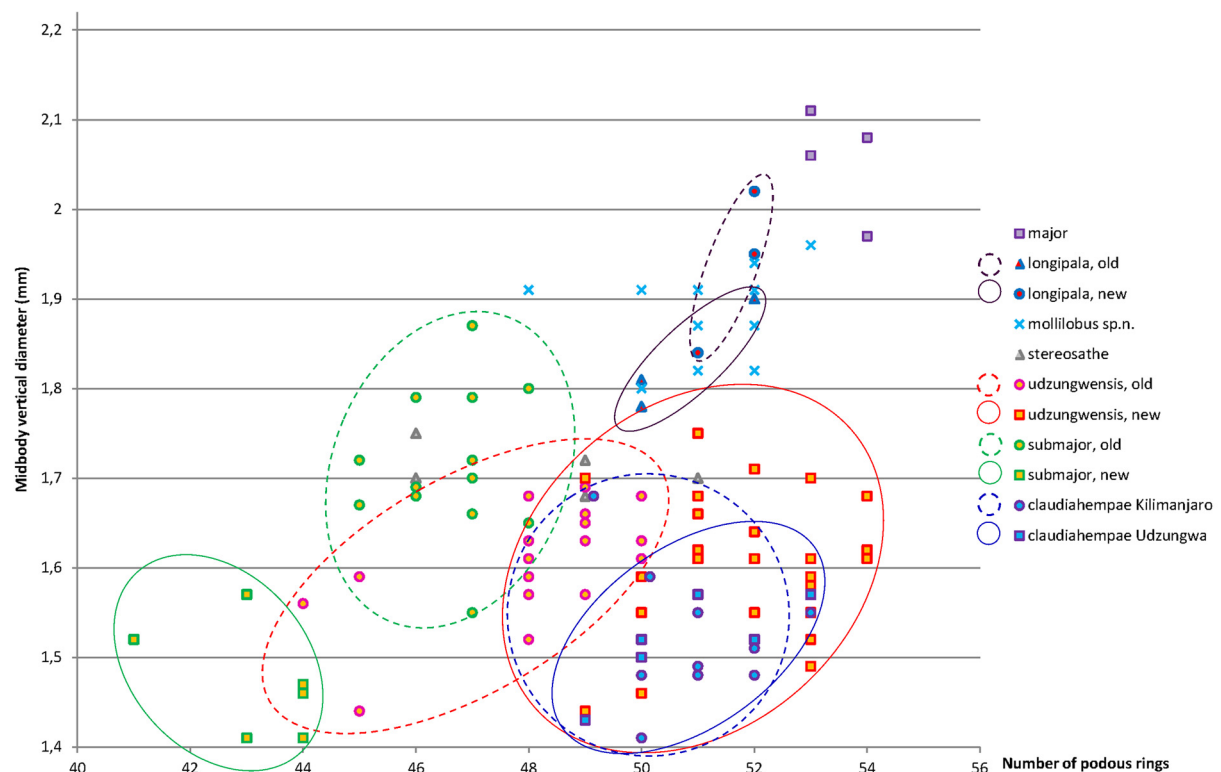


Fig. 9. *Aquattuor* spp. Body size (number of podous rings and midbody vertical diameter) in males of *Aquattuor* species from the Udzungwa Mts, and of *A. claudiahempae* Enghoff & Frederiksen, 2015 from Mt Kilimanjaro. In case of (almost) coinciding values, symbols have been slightly displaced horizontally.

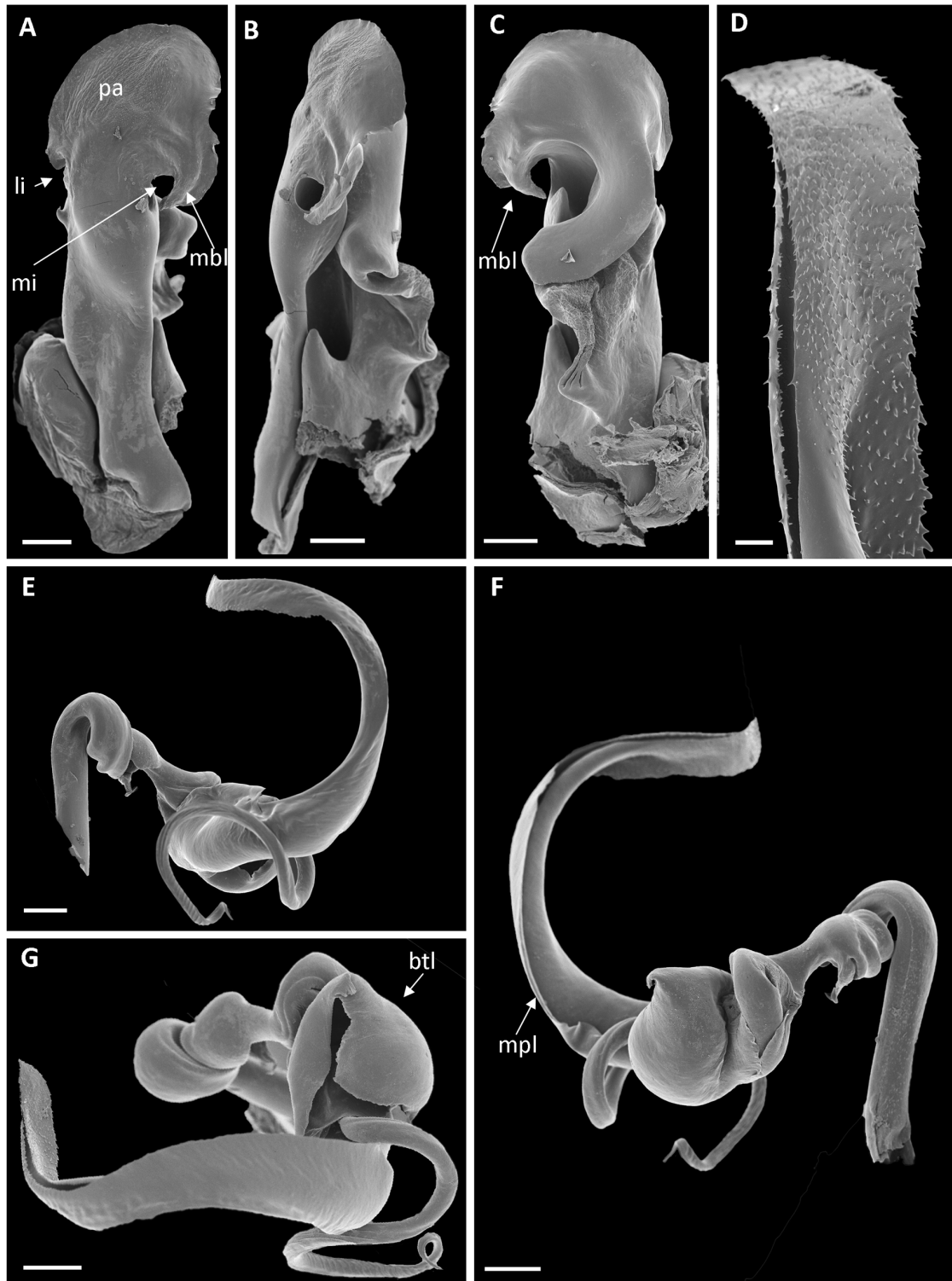


Fig. 10. *Aquattuor claudiahempae* Enghoff & Frederiksen, 2015, male, specimen from the Udzungwa Mts (NHMD 621639), left gonopod. **A–C.** Coxa. **A.** Anterior view. **B.** Mesal view. **C.** Posterior view. **D–G.** Telopodite. **D.** Tip of telomere. **E.** Anterior view. **F.** Posterior view. **G.** Mesal view. Abbreviations: *btl* = basal telomer lamella; *li* = lateral incision; *mbl* = meso-basal lobe of palette; *mi* = mesal incision; *mpl* = mesal-posterior telomer lamella; *pa* = palette. Scale bars: A–C, E–G = 0.1 mm; D = 0.02 mm.

Diagnosis

Diameter 1.55–1.91 mm, 51–53 (55?) podous rings. Shares a short (as broad as long, or slightly longer) gonopodal palette with *A. claudiahempae*, *A. fasciatus*, *A. stereosathe*, *A. submajor* and *A. udzungwensis*. Differs from these species, except *A. claudiahempae*, by the combination of fully developed telopodites on the first pair of male legs, the gonopodal telomere describing a ca 270° curve, curving almost in one plane only, by lacking a spinose lid-like flap on the basal telomer lamella, and by having a distinct meso-basal lobe of the gonopod palette. Very similar to, and perhaps not distinct from *A. claudiahempae*, differs by being mostly larger (male diameter > 1.5 mm) and by having the prefemoral processes of the first pair of male legs stouter, subtriangular.

Material studied (total: 1 ♂)

TANZANIA • 1 ♂; Zanzibar, the sultan's palace; 16 Jun. 1979; M. Stoltze leg.; NHMD 621641.

Descriptive notes

First pair of male legs (Fig. 3A–C) each with a single, relatively stout, triangular prefemoral process; prefemoral processes stouter than those of the otherwise very similar *A. claudiahempae*; setae of telopodite distal to prefemur similar in length to those of normal walking legs.

See remarks under *A. claudiahempae*.

Distribution

Recorded from Zanzibar (type locality), Pwani Region, Bagamoyo Distr., Vula Mountain, Pongwe (VandenSpiegel & Pierrard, 2009, as *Prionopetalum fasciatum*) and from Morogoro Region, Kilosa District, Rubeho Mts, 900 m a.s.l. (Enghoff & Frederiksen 2015, as *A. aff. claudiahempae*).

Aquattuor longipala Enghoff, 2015

Figs 1, 5D–F, 8B, 9, 11

Aquattuor longipala Enghoff, in Enghoff & Frederiksen, 2015: 12.

Diagnosis

Diameter 1.78–2.02 mm, 50–52 podous rings (Fig. 9). Differs from congeners, except *A. longipala* and *A. major*, by having the gonopodal palette considerably longer than broad, and by having a distal prefemoral lobe on the first pair of male legs, in addition to the normal prefemoral process. Differs from *A. mollilobus* sp. nov. by having distinct lateral and mesal incisions on the gonopod coxa and by having the tarsal setae of the first pair of male legs of normal length; differs from *A. major* in lacking a triangular tooth on the anterior margin of the gonopod telomere.

Material studied (total: 3 ♂♂, 3 ♀♀, 3 juvs)

TANZANIA • 2 ♂♂, 3 ♀♀, 3 juvs; Morogoro Region, Udzungwa Mts National Park, Mito Mitatu, Plot 15; 07°49'39.8" S, 36°50'26.0" E; 1552 m a.s.l.; 27 Oct. 2014; J. Malumbres-Olarte leg.; pitfall trapping (summed catch from two traps); NHMD 621642 • 1 ♂; Morogoro Region, Udzungwa Mts National Park, Mito Mitatu; 07°50'14.3" S, 36°50'46.8" E; 1207 m a.s.l.; 25 Nov. 2013; T. Pape and N. Scharff leg.; pitfall trapping; NHMD 621643.

Descriptive notes

The new specimens perfectly fit the original description of *A. longipala*, except that they are marginally larger (51–52 podous rings, diameter 1.84–2.02 mm, vs 50–52 podous rings, diameter 1.78–1.90 mm for type specimens) (Fig. 9).

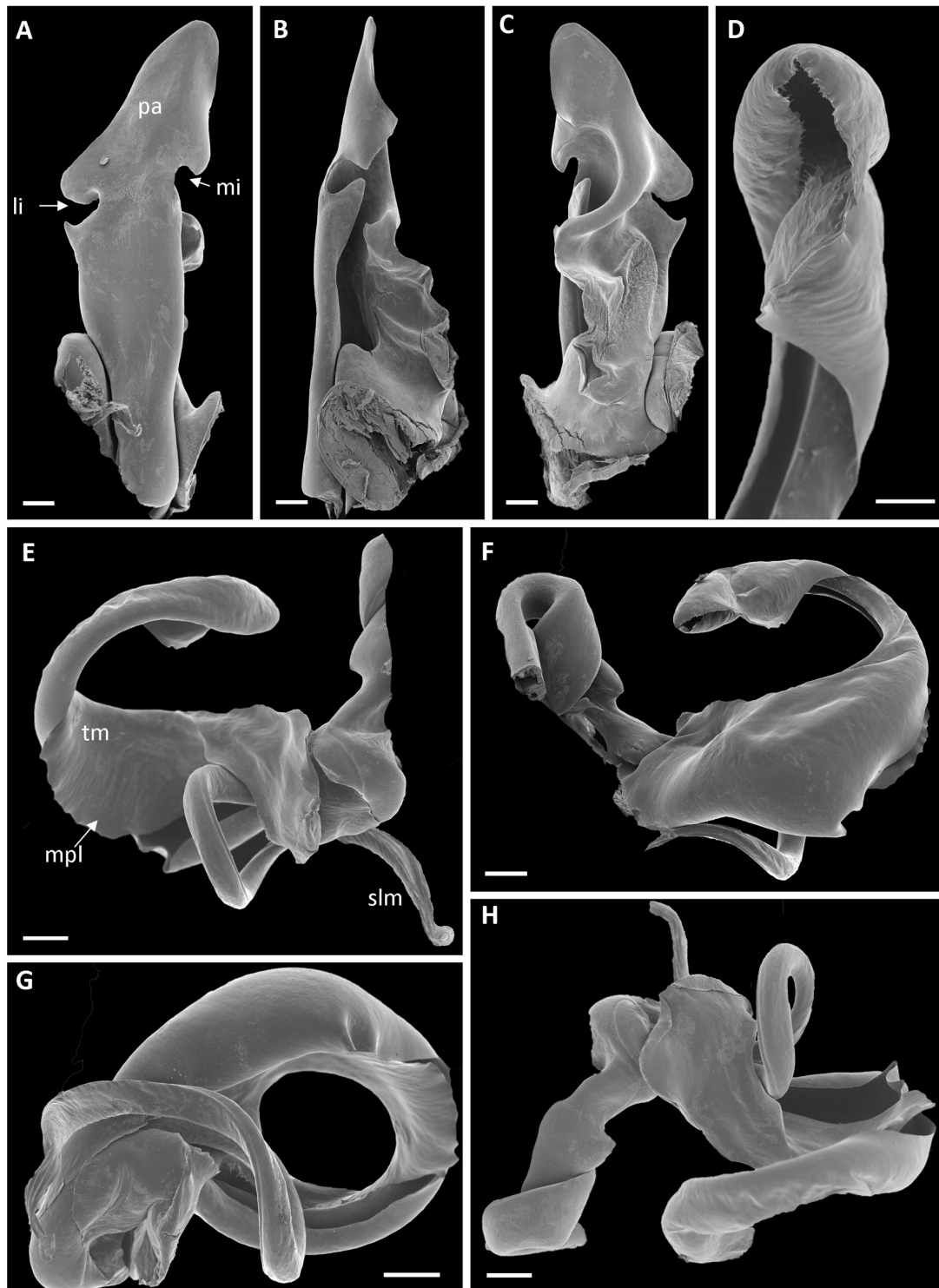


Fig. 11. *Aquattuor longipala* Enghoff, 2015, male, specimen from Udzungwa Mts National Park, Mito Mitatu (NHMD 621642), left gonopod. **A–C.** Coxa. **A.** Anterior view. **B.** Mesal view. **C.** Posterior view. **D–H.** Telopodite. **D.** Tip of telomere. **E.** Posterior view. **F.** Anterior view. **G.** Posterior-ventral view. **H.** Distal (ventral) view. Abbreviations: *li* = lateral incision; *mi* = mesal incision; *mpl* = mesal-posterior telomeral lamella; *pa* = palette; *slm* = solenomere; *tm* = telomere. Scale bars: A–C, E–H = 0.1 mm; D = 0.05 mm.

First pair of male legs (Fig. 5D–F) each with a single slender, finger-shaped prefemoral process (*pfp*); in addition, each prefemur has a smaller, irregular lobe (*dpl*) on the oral side of the distal margin; setae of femur much shorter than corresponding setae on normal walking legs (Fig. 8B).

Fig. 11 shows a gonopod of one of the newly collected specimens.

Aquattuor longipala is very similar to *A. major* (see Discussion).

Distribution

Known from two sites in the Udzungwa Mts, viz., West Kilombero FR and Mito Mitatu in Udzungwa Mts National Park (Fig. 1). Altitudinal range: 1207–1552 m a.s.l.

Aquattuor major Enghoff, 2015
Figs 1, 5A–C, 9

Aquattuor major Enghoff, in Enghoff & Frederiksen, 2015: 10.

Diagnosis

Diameter 1.97–2.11 mm, 53–54 podous rings (Fig. 9). Differs from congeners, except *A. longipala* and *A. mollilobus* sp. nov., by having the gonopodal palette considerably longer than broad, and by having a distal prefemoral lobe on the first pair of male legs, in addition to the normal prefemoral process. Differs from *A. longipala* and *A. mollilobus* sp. nov. by having a triangular tooth on the anterior margin of the gonopod telomere, from *A. mollilobus* sp. nov. further by having distinct lateral and mesal incisions on the gonopod coxa and by having the tarsal setae of the first pair of male legs of normal length.

Material studied (total: 1 ♂)

TANZANIA • 1 ♂, paratype; Morogoro Region, Udzungwa Mts, Mwanihana FR, above Sanje; 1650 m a.s.l.; 18 Aug. 1982; M. Stoltze and N. Scharff leg.; pitfall trap; NHMD 621644.

Descriptive notes

First pair of male legs (Fig. 5A–C) each with a single, finger-shaped prefemoral process (*pfp*); in addition each prefemur has a smaller, irregular lobe (*dpl*) on the oral side of the distal margin; setae of femur much shorter than corresponding setae on normal walking legs, as in *A. longipala* (see Fig. 8B).

Aquattuor major is very similar to *A. longipala* (see Discussion).

Distribution

Known only from Mwanihana FR in the Udzungwa Mts. Altitudinal range: 1650–1850 m a.s.l.

Aquattuor mollilobus sp. nov.
[urn:lsid:zoobank.org:act:A453CBE6-5FF7-4327-9B45-FA0C6A9AE84F](https://doi.org/10.21203/rs.3.rs-1000000/v1)
Figs 1, 6A–C, 8C, 9, 12–13

Diagnosis

Diameter 1.80–1.96 mm, 48–53 podous rings (Fig. 9). Differs from congeners, except *A. longipala* and *A. major*, by having the gonopodal palette considerably longer than broad, and by having a distal prefemoral lobe on the first pair of male legs, in addition to the normal prefemoral process. Differs from *A. longipala* and *A. major* by having the lateral and mesal incisions of the gonopod coxa indistinct, and by having the tarsal setae of the first pair of male legs much shorter than tarsal setae of normal walking legs.

Etymology

The name is an adjective meaning soft (Latin: mollis) lobe and refers to the distal modification of the first male prefemora.

Material studied (total: 21 ♂♂, 11 ♀♀, 1 juv.)

Holotype

TANZANIA • ♂; Morogoro Region, Udzungwa Mts National Park, Kidatu, Plot 6; 07°40'42.1" S, 36°55'06.8" E; 1482 m a.s.l.; 21 Oct. 2014; J. Malumbres-Olarte leg.; pitfall trapping; NHMD 621645.

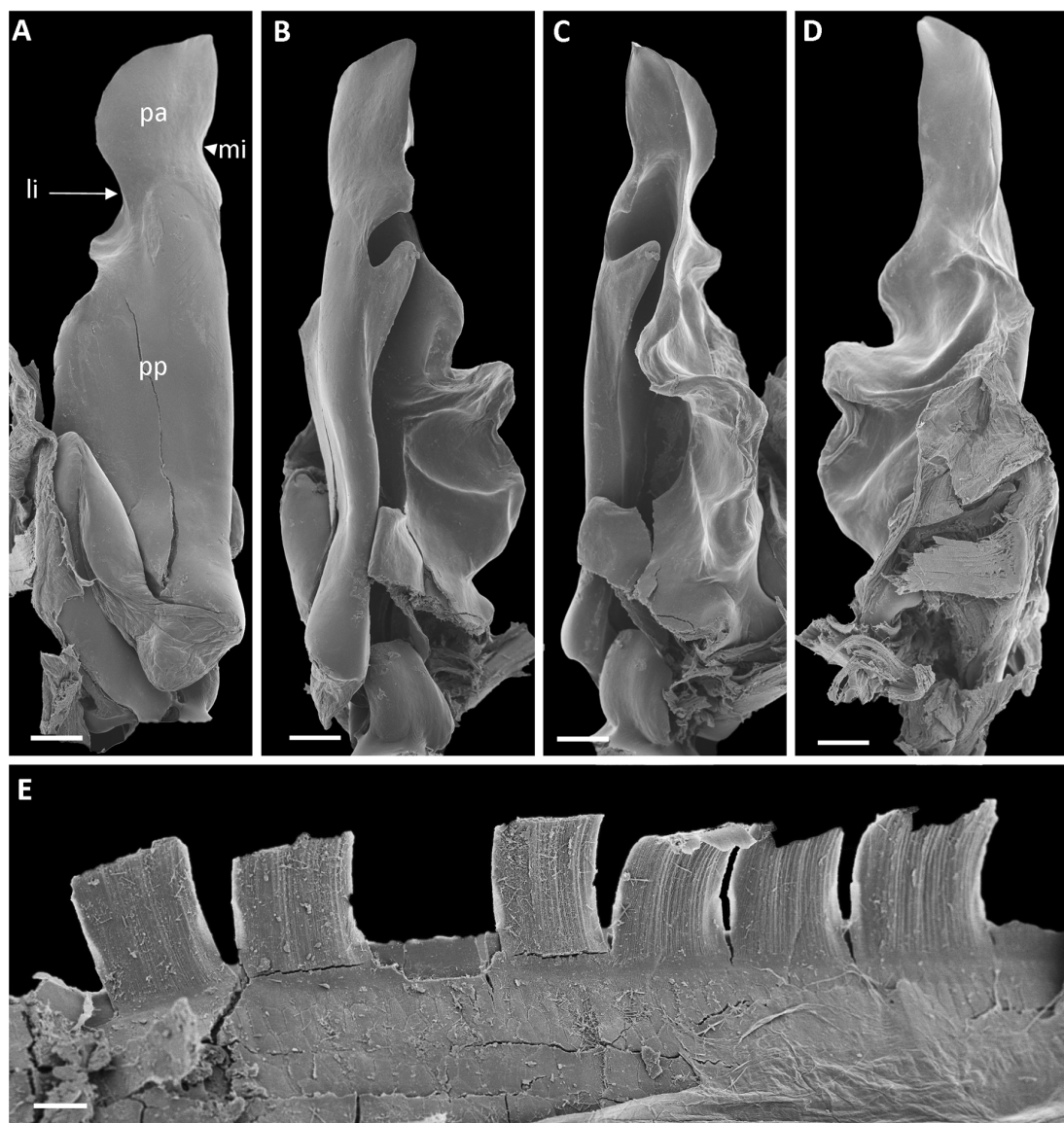


Fig. 12. *Aquattuor mollilobus* sp. nov., paratype, ♂ (NHMD 621648). **A–D.** Left gonopod coxa. **A.** Anterior view. **B.** Anterior-mesal view. **C.** Mesal view. **D.** Posterior-lateral view. **E.** Midbody dorsal limbus. Abbreviations: *li* = lateral incision; *mi* = mesal incision; *pa* = palette; *pp* = proplica. Scale bars: A–D = 0.1 mm; E = 0.02 mm.

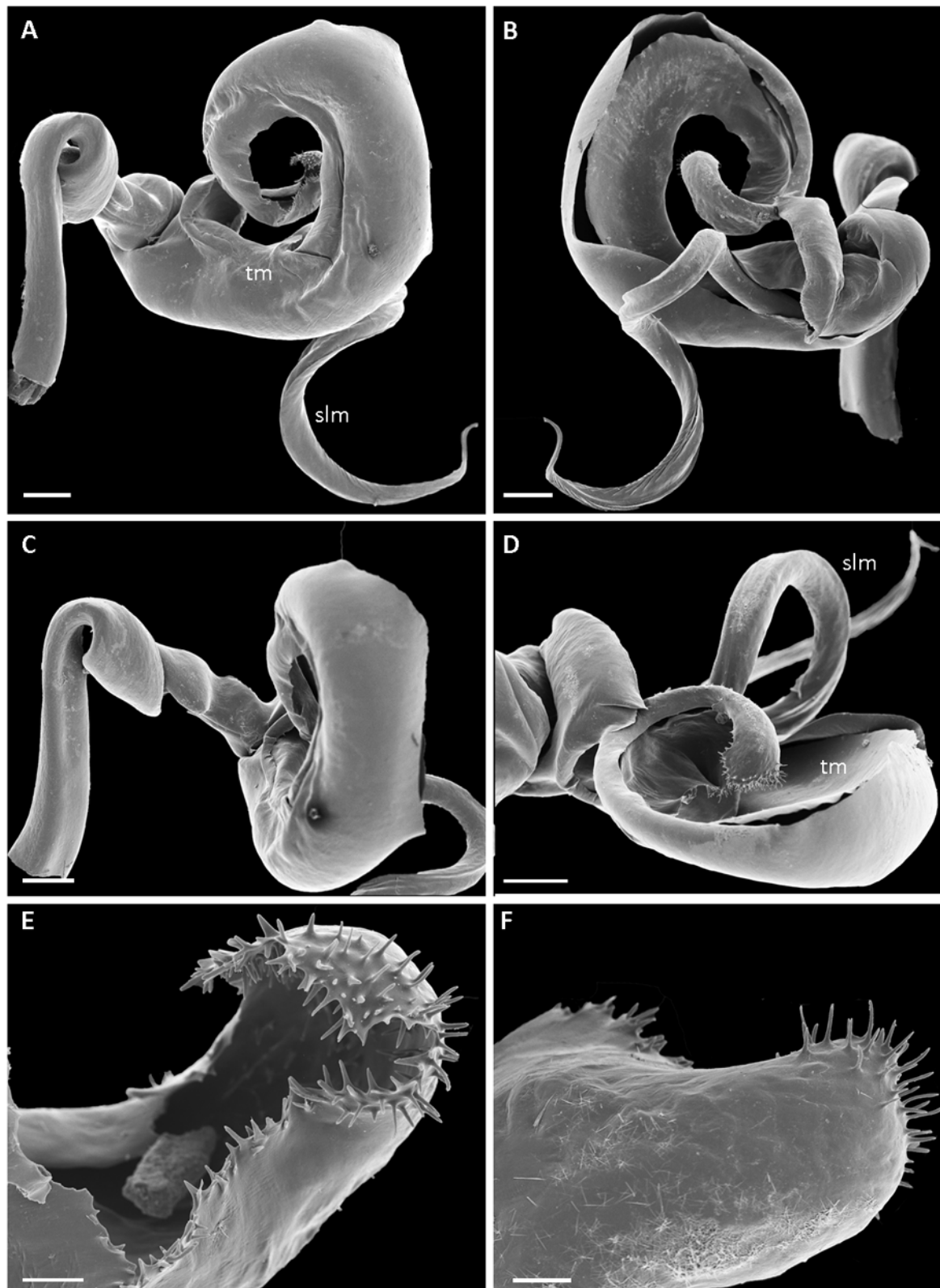


Fig. 13. *Aquattuor mollilobus* sp. nov., paratype, ♂ (NHMD 621648). Left gonopod telopodite. **A.** Anterior view. **B.** Posterior view. **C.** Submesal view. **D.** Distal (ventral) view. **E–F.** Tip of telomere. Abbreviations: *slm* = solenomere; *tm* = telomere. Scale bars: A–D = 0.1 mm; E–F = 0.02 mm.

Paratypes

TANZANIA • 8 ♂♂; Morogoro Region, Udzungwa Mts National Park, Kidatu, Plot 5; 07°40'45.5" S, 36°55'06.9" E; 1448 m a.s.l.; 21 Oct. 2014; J. Malumbres-Olarte leg.; pitfall trapping (summed catch from three traps); NHMD 621646 • 7 ♂♂; Morogoro Region, Udzungwa Mts National Park, Kidatu, Plot 6; 07°40'42.1" S, 36°55'06.8" E; 1482 m a.s.l.; 21 Oct. 2014; J. Malumbres-Olarte leg.; pitfall trapping (summed catch from six traps); NHMD 621647 • 5 ♂♂; Morogoro Region, Udzungwa Mts National Park, Kidatu, Plot 9; 07°41'06.2" S, 36°55'06.8" E, 1527 m a.s.l.; 23 Oct. 2014; J. Malumbres-Olarte leg.; pitfall trapping (summed catch from three traps); NHMD 621648.

Referred non-type material

TANZANIA • 11 ♀♀, 1 juv.; same collection data as for paratypes (plots 5, 6, 9); NHMD.

Description (male)

MEASUREMENTS. Body length 28–31 mm; vertical diameter 1.82–1.91 mm; 48–53 podous rings, no apodous rings in front of telson.

COLOUR. Similar to that of *A. claudiahempae* (Enghoff & Frederiksen 2015: fig. 1). A light mid-dorsal stripe present.

LIMBUS (Fig. 12E). With rectangular, detachable flaps, as typical of the genus.

FIRST PAIR OF MALE LEGS (Figs 6A–C, 8C). Prefemoral processes (*ppf*) of first pair of legs slender, finger-shaped, slightly curved laterad; in addition an irregular, rugose lobe (*dpl*) on oral-distal margin of prefemur; setae of all podomeres much shorter than femoral setae of normal walking legs.

GONOPOD COXA (Fig. 12A–D). In anterior or posterior view ca 3½ × as long as broad. Margins of proplica (*pp*) parallel in basal ca ⅔. Mesal (*mi*) and lateral (*li*) incisions shallow and poorly developed; apical palette (*pa*) narrower than basal part of proplica, lateral margin regularly rounded, mesal margin straight.

GONOPOD TELOPODITE (FIG. 13). Solenomere (*slm*) thin, whiplike. Main part of telomere (*tm*) a rather broad gutter describing a 270° curve in almost one plane; tip of telomere broad rounded, densely beset with minute spicules on external surface.

In all other characters conforming to the general description of *Aquattuor* in Enghoff & Frederiksen (2015).

Distribution

Known only from a single site in Udzungwa Mts National Park (Fig. 1). Altitudinal range: 1448–1527 m a.s.l.

Aquattuor nguruensis sp. nov.

[urn:lsid:zoobank.org:act:B691ECD6-3E7E-4731-AD33-1DD9D39381DB](https://zoobank.org/urn:lsid:zoobank.org:act:B691ECD6-3E7E-4731-AD33-1DD9D39381DB)

Figs 1, 4A–C, 14–15

Aquattuor sp. – Enghoff & Frederiksen 2015: 21 (?).

Diagnosis

Diameter 2.0 mm. Differs from congeners by lacking lateral and mesal incisions on the gonopod coxa and by having the telomere tip flattened and smooth. Differs from *A. mollilobus* sp. nov., in which the lateral and mesal incisions are indistinct, by lacking a distal prefemoral lobe on the first pair of male legs.

Etymology

The name is an adjective referring to the type locality.

Material studied (total: 1 ♂, 2 ♀♀)

Holotype

TANZANIA • ♂; Morogoro Region and District, west side of Nguru Mountains, near Maskati mission, 20 km W of Turisani; 1900 m a.s.l.; unknown date; Jan Kielland leg.; moist evergreen forest; VMNH110617.

Referred non-type material

TANZANIA • 1 ♀; same collection data as for holotype; VMNH110618 • 1 ♀; Nguru Mts, Mhonda Mission at Turiani; Oct. 1992; M. Andersen leg.; NHMD 621649.

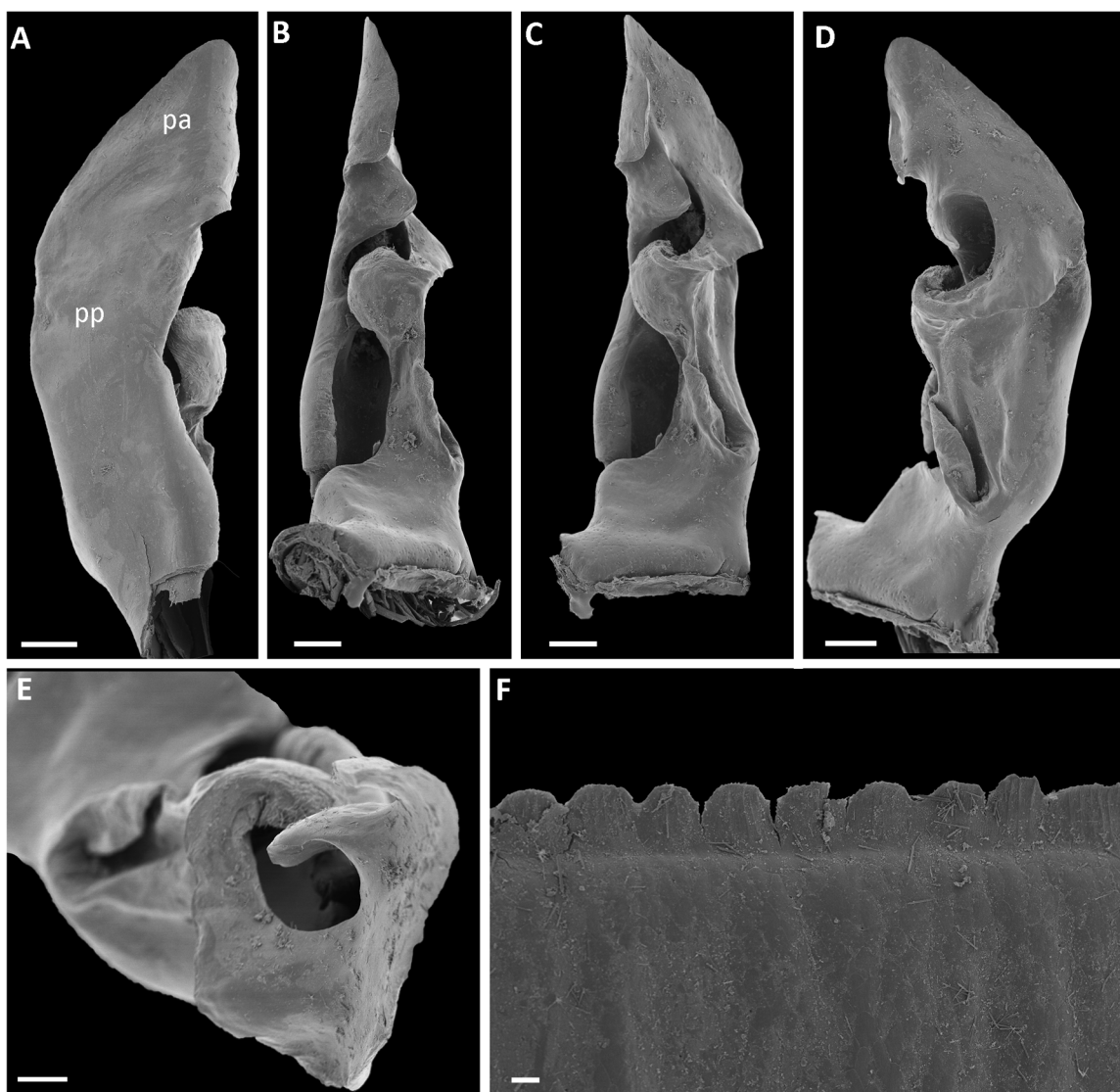


Fig. 14. *Aquattuor nguruensis* sp. nov., holotype, ♂ (VMNH110617). **A–E.** Left gonopod coxa. **A.** Anterior view. **B.** Mesal view. **C.** Meso-posterior view. **D.** Posterior view. **E.** Apical view. **F.** Midbody dorsal limbus. Abbreviations: *pa* = palette; *pp* = proplica. Scale bars: A–D = 0.1 mm; E = 0.05 mm; F = 0.01 mm.

Description (male)

MEASUREMENTS. Vertical diameter 2.0 mm; posterior part of body missing.

COLOUR. Faded, but apparently similar to that of *A. claudiahempae* (Enghoff & Frederiksen 2015: fig. 1). Traces of a light mid-dorsal stripe present.

LIMBUS (Fig. 14 F). Quite worn, but still shows rectangular, detachable flaps as typical of the genus.

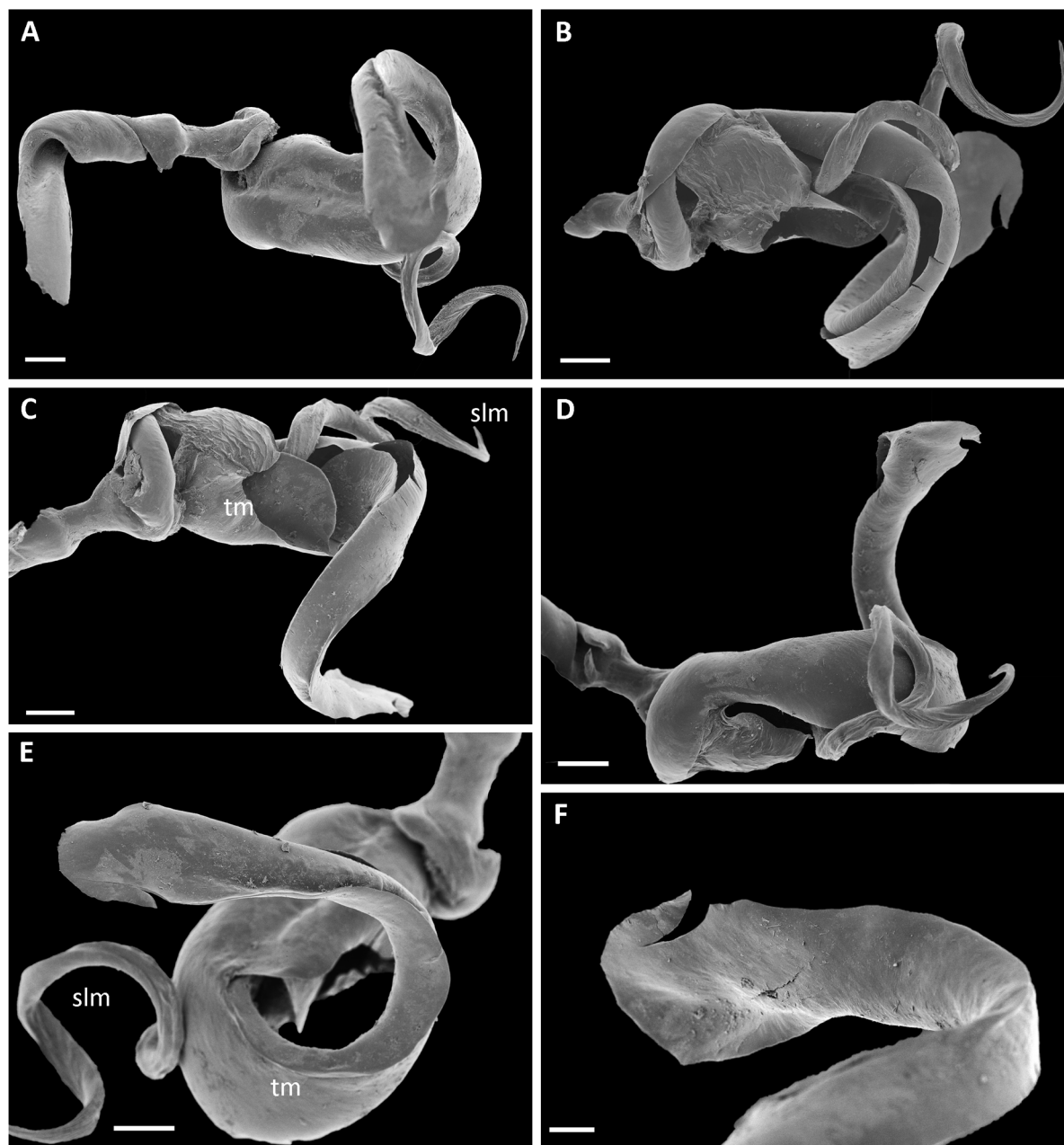


Fig. 15. *Aquattuor nguruensis* sp. nov., holotype, ♂ (VMNH110617), left gonopod telopodite. **A.** Anterior view. **B.** Posterior view. **C.** Distal (ventral) view. **D.** Basal (dorsal) view. **E.** Mesal view. **F.** Tip of telomere (damaged). Abbreviations: *slm* = solenomere; *tm* = telomere. Scale bars: A–E = 0.1 mm; F = 0.05 mm.

FIRST PAIR OF MALE LEGS (Figs 4A–C). Prefemoral processes relatively stout, triangular; distal (ventral) surface of processes with a large, sharply delimited depression (*pdf*); setae of telopodite distal to prefemur same length as setae of normal walking legs.

GONOPOD COXA (FIG. 14). In anterior or posterior view ca 3 × as long as broad. Margins of proplica subparallel, but lateral margin regularly convex, mesal margin correspondingly concave. No mesal and lateral incisions, apical palette (*pa*) hence poorly delimited, triangular.

GONOPOD TELOPODITE (Fig. 15). Solenomere (*slm*) thin, whip-like. Main part of telomere a rather broad gutter describing a 270° curve in almost one plane; tip of telomere flattened, smooth.

In all other characters conforming to the general description of *Aquattuor* in Enghoff & Frederiksen (2015).

Distribution

Known only from one, possibly two sites in the Nguru Mts. Altitude: 1900 m a.s.l.

Aquattuor stereosathe Enghoff, 2015
Figs 1, 6D–F, 8A, 9

Aquattuor stereosathe Enghoff, in Enghoff & Frederiksen, 2015: 15.

Diagnosis

Diameter 1.68–1.75 mm, 46–51 podous rings (Fig. 9). Shares a short (as broad as long, or slightly longer) gonopodal palette with *A. claudiahempae*, *A. denticulatus*, *A. fasciatus*, *A. submajor* and *A. udzungwensis*. Differs from these species by having the gonopodal telomere describing a ca 360° curve, curving in three dimensions, and by having the telomere tip with coarsely laciniate margins and a surface that is not microspiculate.

Material studied (total: 1 ♂)

TANZANIA • 1 ♂, paratype; Iringa Region, Udzungwa Mts, Udzungwa Scarp FR, above Chita Village; 1050 m a.s.l.; 26–29 Oct. 1984; N. Scharff leg.; pitfall trap in intermediate rain forest; NHMD 621650.

Descriptive notes

First pair of male legs (Figs 6D–F): prefemoral processes relatively stout, triangular; setae of telopodite distal to prefemur same length as setae of normal walking legs.

Distribution

Known only from the Udzungwa Scarp FR in the Udzungwa Mts. Altitudinal range: 900–1500 m a.s.l.

Aquattuor submajor Enghoff, 2015
Figs 1, 7A–C, 9, 16, 18

Aquattuor submajor Enghoff, in Enghoff & Frederiksen, 2015: 7.

Diagnosis

Diameter 1.41–1.87 mm, 41–48 podous rings (Fig. 9). Shares a short (as broad as long, or slightly longer) gonopodal palette with *A. claudiahempae*, *A. denticulatus*, *A. fasciatus*, *A. stereosathe* and

A. udzungwensis. Differs from these species by the combination of fully developed telopodites on the first pair of male legs, the gonopodal telomere describing a ca 270° curve, curving almost in one plane only, by lacking a spinose lid-like flap on the basal telomerical lamella and by lacking a distinct meso-basal lobe of the gonopod palette.

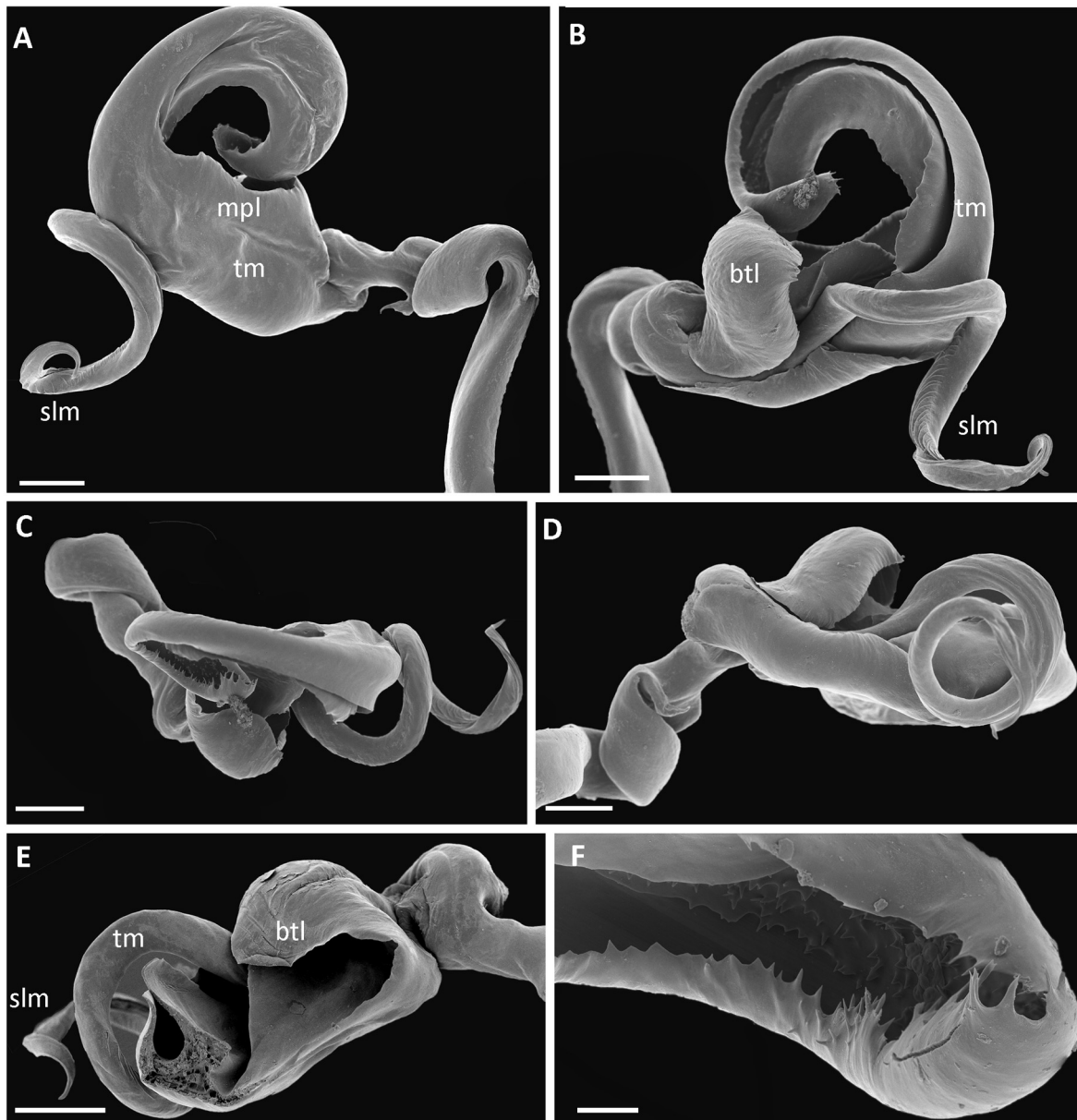


Fig.16. *Aquattuor submajor* Enghoff, 2015. **A–D.** Male from Udzungwa Mts National Park, Kidatu (NHMD 621653), left gonopod telopodite. **A.** Posterior view. **B.** Anterior view. **C.** Distal (ventral) view. **D.** Basal (dorsal) view. **E–F.** Male from Udzungwa Mts National Park, Kidatu (NHMD 621654), right gonopod telopodite, broken into two pieces. **E.** Basal part. **F.** Tip of telomere. Abbreviations: *btl* = basal telomerical lamella; *mpl* = meso-posterior telomerical lamella; *slm* = solenomere; *tm* = telomere. Scale bars: A–E = 0.1 mm; F = 0.02 mm.

Table 1. Comparison of *Aquattuor submajor* Enghoff, 2015 (males) from Mwanihana and Kidatu.

	podous rings	midbody vertical diameter (mm)
Mwanihana (1000–1100 m a.s.l.), data from Enghoff & Frederiksen (2015)	45–48	1.55–1.87
Kidatu (1448–1552 m a.s.l.), new material	41–44	1.41–1.57

Material studied (total: 8 ♂♂)

TANZANIA • 1 ♂, paratype; Udzungwa Mts, Mwanihana Forest above Sanje; 1000 m a.s.l.; 1 Aug. 1981; N. Scharff leg.; pitfall trap; NHMD 261651 • 1 ♂; Morogoro Region, Udzungwa Mts National Park, Kidatu, Plot 5; 07°40'45.5" S, 36°55'06.9" E; 1448 m a.s.l.; 21 Oct. 2014; J. Malumbres-Olarte leg.; pitfall trapping; NHMD 621652 • 1 ♂; Morogoro Region, Udzungwa Mts National Park, Kidatu, Plot 6; 07°40'42.1" S, 36°55'06.8" E; 1482 m a.s.l.; 21 Oct. 2014; J. Malumbres-Olarte leg.; pitfall trapping; NHMD 621653 • 4 ♂♂; Morogoro Region, Udzungwa Mts National Park, Kidatu, Plot 9; 07°41'06.2" S, 36°54'52.4" E; 1527 m a.s.l.; 23 Oct. 2014; J. Malumbres-Olarte leg.; pitfall trapping (summed catch from four traps); NHMD 621654 • 1 ♂; Morogoro Region, Udzungwa Mts National Park, Mito Mitatu, Plot 15; 07°49'39.8" S, 36°50'26.9" E; 1552 m a.s.l.; 27 Oct. 2014; J. Malumbres-Olarte leg.; pitfall trapping; NHMD 621655.

Descriptive notes

The newly studied specimens from Kidatu are considerably smaller than those from Mwanihana FR; see Table 1.

First pair of male legs (Figs 7A–C): prefemoral processes finger-shaped; setae of telopodite distal to prefemur same length as setae of normal walking legs.

Gonopod telopodite (Fig. 16): basal telomer lamella (*btl*) forming a subspherical chamber but without a spinose lid-like flap, cf. *A. udzungwensis*. In the specimen illustrated in Fig. 16 the tip has remarkably long marginal laciniae, approaching the condition typical of *A. stereosathe* (Enghoff & Frederiksen 2015: fig. 9c).

Remarks

The distinction between *A. submajor* and *A. udzungwensis* is discussed under the latter species.

Distribution

Known from Mwanihana FR and Kidatu in Udzungwa Mts National Park. Altitudinal range: 1000–1552 m a.s.l.

Aquattuor udzungwensis Enghoff, 2015

Figs 1, 2, 7D–E, 9, 17–18

Aquattuor udzungwensis Enghoff, in Enghoff & Frederiksen, 2015: 13.

Diagnosis

Diameter 1.44–1.75 mm, 44–54 podous rings (Fig. 9). Shares a short (as broad as long, or slightly longer) gonopodal palette with *A. claudiahempae*, *A. denticulatus*, *A. fasciatus*, *A. stereosathe* and *A. submajor*. Differs from these species by having the telopodite of the first pair of male legs represented by the prefemur only, and by having the basal telomer lamella forming a subspherical chamber with a spinose, lid-like flap.

Material studied (total: 302 ♂♂, 120 ♀♀)

TANZANIA • 4 ♂♂, paratypes; Iringa Region, Udzungwa Mts, Udzungwa Scarp FR, above Chita Village; 730 m a.s.l.; 25–29 Oct. 1984; N. Scharff leg.; pitfall traps in lowland rain forest; NHMD 621656 • 16 ♂♂, 13 ♀♀; Morogoro Region, Udzungwa Mts National Park, Kidatu, Plot 1; 07°41'13.5" S, 36°56'28.6" E; 650 m a.s.l.; 24 Oct. 2014; J. Malumbres-Olarte leg.; pitfall trapping (summed catch from seven traps); NHMD 621657 • 1 ♂, 4 ♀♀; Morogoro Region, Udzungwa Mts National Park, Kidatu, Plot 2; 07°41'14.9" S, 36°56'24.7" E; 650 m a.s.l.; 24 Oct. 2014; J. Malumbres-Olarte leg.; pitfall trapping; NHMD 621658 • 45 ♂♂, 12 ♀♀; Morogoro Region, Udzungwa Mts National Park, Kidatu, Plot 3; 07°41'02.4" S, 36°55'49.3" E; 1005 m a.s.l.; 14 Oct. 2014; J. Malumbres-Olarte leg.; pitfall trapping (summed catch from twelve traps); NHMD 621659 • 24 ♂♂, 2 ♀♀; Morogoro Region, Udzungwa Mts National Park, Kidatu, Plot 4; 07°41'05.2" S, 36°55'48.4" E; 993 m a.s.l.; 15 Sep. 2014; J. Malumbres-Olarte leg.; pitfall trapping (summed catch from eight traps); NHMD 621660 • 8 ♂♂, 5 ♀♀; Morogoro Region, Udzungwa Mts National Park, Kidatu, Plot 7; 07°41'23.4" S, 36°56'00.7" E; 708 m a.s.l.; 24 Oct. 2014; J. Malumbres-Olarte leg.; pitfall trapping (summed catch from six traps); NHMD 621661 • 167 ♂♂, 68 ♀♀; Morogoro Region, Udzungwa Mts National Park, Kidatu, Plot 8; 07°41'12.9" S, 36°55'39.2" E; 978 m a.s.l.; 14 Oct. 2014; J. Malumbres-Olarte leg.; pitfall trapping (summed catch from eleven traps); NHMD 621662 • 2 ♂♂; Morogoro Region, Udzungwa Mts National Park, Mito Mitatu, Plot 13; 07°50'29.6" S, 36°52'01.3" E; 674 m a.s.l.; 26 Oct. 2014; J. Malumbres-Olarte leg.; pitfall trapping (summed catch from two traps); NHMD 621663 • 5 ♂♂, 2 ♀♀; Morogoro Region, Udzungwa Mts National Park, Mito Mitatu, Plot 14; 07°50'26.1" S, 36°51'33.0" E; 1006 m a.s.l.; 26 Oct. 2014; J. Malumbres-Olarte leg.; pitfall trapping (summed catch from four traps); NHMD 621664 • 1 ♂; Morogoro Region, Udzungwa Mts National Park, Mito Mitatu, Plot MM2; 07°50'15.1" S, 36°50'49.9" E; 1109 m a.s.l.; T. Pape and N. Scharff leg.; pitfall trapping; NHMD 621665 • 13 ♂♂, 4 ♀♀; Morogoro Region, Udzungwa Scarp Catchment Forest Reserve, Chita, Plot 16; 08°30'13.4" S, 35°55'08.9" E; 659 m a.s.l.; 31 Oct. 2014; J. Malumbres-Olarte leg.; pitfall trapping (summed catch from seven traps); NHMD 621666 • 19 ♂♂, 10 ♀♀; Morogoro Region, Udzungwa Scarp Catchment Forest Reserve, Chita, Plot 17; 08°29'58.1" S, 35°54'59.5" E; 908 m a.s.l.; 30 Oct. 2014; J. Malumbres-Olarte leg.; pitfall trapping (summed catch from six traps); NHMD 621667.

Descriptive notes

The newly studied specimens on average have more podous rings than those studied by Enghoff & Frederiksen (2015) (Fig. 9). In particular, the specimens from Kidatu and Mito Mitatu have more podous rings (49–54, most specimens 53), whereas the new specimens from Chita (49–51 podous rings) overlap with the previously studied ones; see also Discussion.

First pair of male legs (Fig. 7D–E): prefemoral processes finger-shaped to triangular; telopodital podomeres distal to prefemur missing in all studied specimens; see Discussion.

Gonopod telopodite (Fig. 17): basal telomer lamella (*btl*) forming a subspherical chamber with a spinose, lid-like flap, cf. *A. submajor* and remarks below.

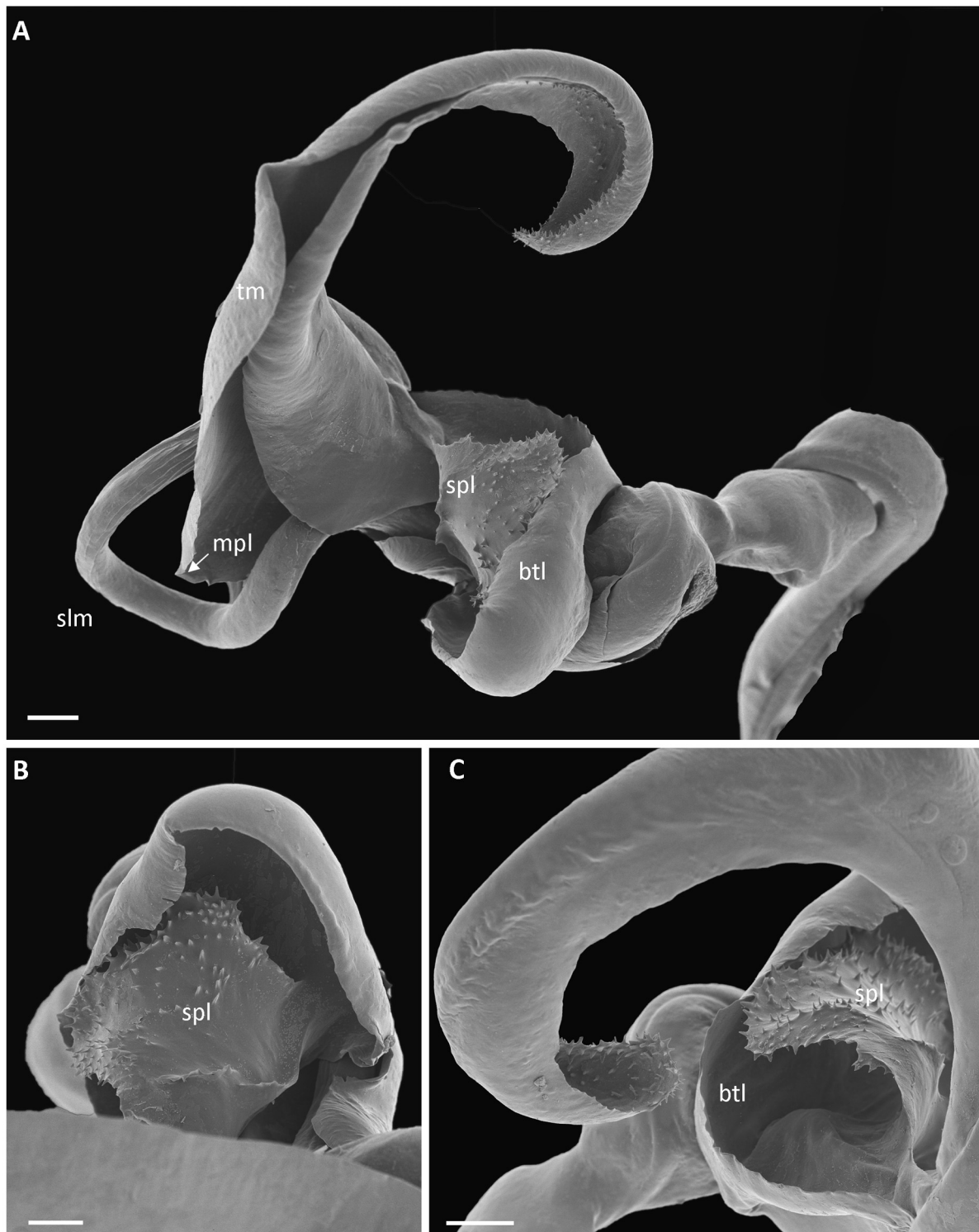


Fig. 17. *Aquattuor udzungwensis* Enghoff, 2015, male from Udzungwa Mts National Park, Kidatu (NHMD 621659), left gonopod telopodite. **A.** (Meso-)posterior view. **B.** Basal telomeral lamella, distal (ventral) view. **C.** Telomere, sublateral view. Abbreviations: *btl* = basal telomeral lamella; *mpl* = meso-posterior telomeral lamella, the arrow points to the diagnostic angle; *slm* = solenomere; *spl* = spinose lid-like flap; *tm* = telomere. Scale bars = 0.05 mm.

Remarks – The distinction between *A. submajor* and *A. udzungwensis*

The distinction between *A. udzungwensis* and *A. submajor* according to Enghoff & Frederiksen (2015) is quite subtle. The newly studied material has contributed to a better understanding of the differences between these two species. Among the differences stated by Enghoff & Frederiksen (2015), the shape of the meso-posterior lamella of the telomere seems to be the only reliable one (Figs 16–17). The meso-posterior lamella is high and basally angled in *A. udzungwensis*, and towards the tip of the telomere, the lamella narrows gradually. In *A. submajor*, the lamella is lower, not angled, and not narrowing so strongly towards the tip.

However, two new clear differences can now be added:

- The basal telomeral lamella (*btl*) in *A. udzungwensis* has a small, spinose, lid-like flap (*spl*) (Fig. 17); such a flap is absent in *A. submajor* (Fig. 16).
- In all dissected males of *A. udzungwensis* (> 10), collected in several parts of the Udzungwa Mts, the telopodites of the first leg-pair are strongly reduced distal to the prefemur (Fig. 7D–E). Only tiny, somewhat irregular and darkened remnants are present, suggesting that their absence may be due to some physical damage inflicted on the male. In all examined males of *A. submajor*, the telopodites are normal (Fig. 7A–C).

For both species, the newly studied material considerably widens their size range: newly studied specimens of *A. submajor* have fewer podous rings and a smaller body diameter than those studied by Enghoff & Frederiksen (2015); in *A. udzungwensis* the newly studied specimens tend to have more podous rings than those previously studied, while there is a marked difference in diameter. These differences may, at least in part, be correlated with altitude: both species show a clear decrease of numbers of podous rings with increasing altitude from mostly > 50 podous rings at 600–900 m altitude to < 46 rings at 1400–1550 m altitude (Fig. 18).

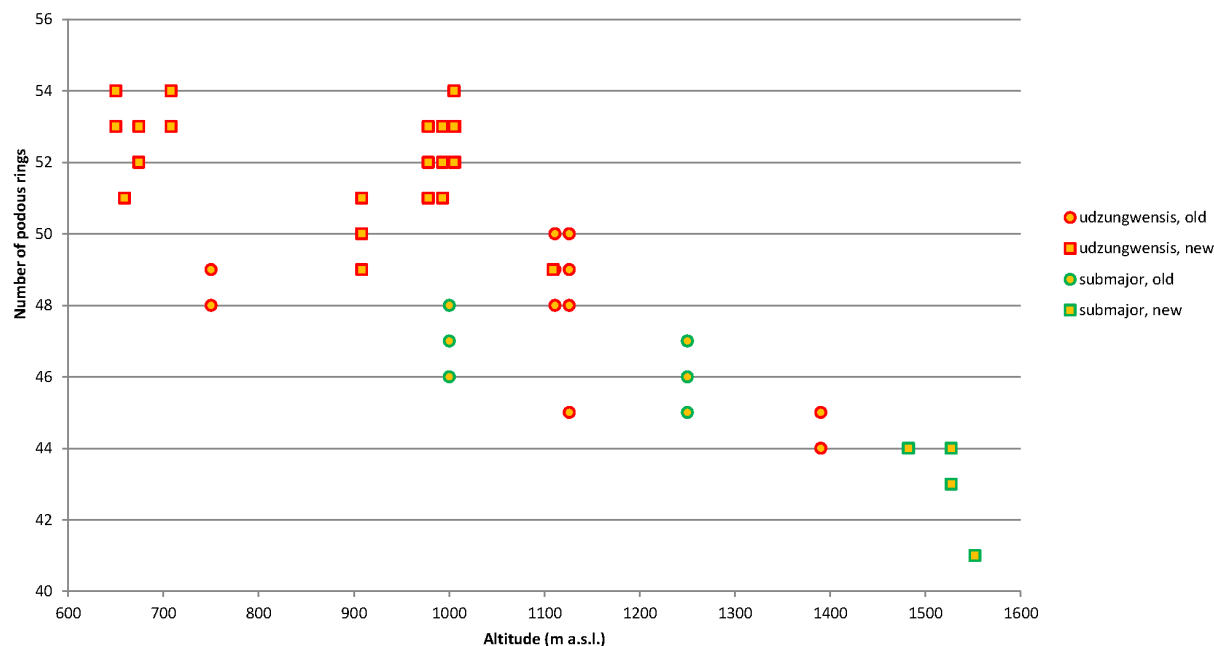


Fig. 18. *Aquattuor submajor* Enghoff, 2015 and *A. udzungwensis* Enghoff, 2015; numbers of podous rings as a function of altitude.

Distribution

Known from several localities in the Udzungwa Mts (Fig. 1). Altitudinal range: 650–1410 m a.s.l.

Aquattuor sp.

Material studied

TANZANIA • Several ♀♀/juveniles; Morogoro, Sokoine University Campus, NORAD guest house; 28 Mar. 1989; Zicsi leg.; HMNH.

Remarks

These specimens represent a range extension of the genus *Aquattuor*, but a closer identification is not possible.

Key to the species of *Aquattuor* (males)

1. Palette (*pa*) of gonopods elongate, considerably to much longer than broad (Figs 11–12; Enghoff & Frederiksen 2015: figs 6–7); first pair of legs with a distal prefemoral lobe (Figs 5, 6A–C); 48+ podous rings, diameter > 1.7 mm 2
 - Palette as long as broad or slightly longer; first pair of legs without a distal prefemoral lobe (as in Fig. 3); diameter < 1.9 mm 4
2. Palette (*pa*) not clearly delimited by lateral (*li*) and mesal (*mi*) incisions (Fig. 12A); tarsal setae of first pair of legs much shorter than tarsal setae of normal walking legs (Fig. 8C) *A. mollilobus* sp. nov. (Udzungwa)
 - Palette delimited by lateral and mesal incisions (e.g., Fig. 11A); tarsal setae of first pair of legs ca of same length as tarsal setae of normal walking legs (Fig. 8B) 3
3. 53–54 podous rings, diameter > 1.9 mm; anterior margin of telomere with a triangular tooth (Enghoff & Frederiksen 2015: fig. 6A, *tt*) *A. major* Enghoff, 2015 (Udzungwa)
 - 50–52 podous rings; anterior margin of telomere without a triangular tooth *A. longipala* Enghoff, 2015 (Udzungwa)
4. Subdistal part of telomere almost straight, parallel to coxa; telomere tip bent abruptly laterad (Enghoff & Frederiksen 2015: fig. 11); 50–52 podous rings, diameter 1.6–1.8 mm *A. denticulatus* Frederiksen, 2013 (E Usambara)
 - Telomere describing a more complex curve 5
5. Gonopod coxa without lateral and mesal incisions; telomere tip flattened, smooth (Figs 14–15) *A. nguruensis* sp. nov. (Nguru)
 - Gonopod coxa with lateral (*li*) and mesal (*mi*) incisions; telomere tip microspiculate or with serrated margins 6
6. Telomere describing a ca 360° curve, curving in three dimensions; telomere tip with coarsely lacinate margins, but surface not microspiculate (Enghoff & Frederiksen 2015: fig. 9) *A. stereosathe* Enghoff, 2015 (Udzungwa)
 - Telomere describing a ca 270° curve, curving almost in one plane only; telomere tip more or less microspiculate 7

7. Telopodites of first pair of legs only represented by prefemur; basal telomer lamella (*btl*) forming a subspherical chamber with a spinose, lid-like flap (Fig. 17)
 *A. udzungwensis* Enghoff, 2015 (Udzungwa)
 – Telopodites of first pair of legs fully developed; basal telomer lamella without a spinose, lid-like flap 8
8. < 49 podous rings; meso-basal lobe of gonopod palette indistinct (Enghoff & Frederiksen 2015: fig. 5)..... *A. submajor* Enghoff, 2015 (Udzungwa)
 – > 48 podous rings; meso-basal lobe (*mbt*) of gonopod palette well-developed (Enghoff & Frederiksen 2015: fig. 10; Enghoff 2016: fig. 7) 9
9. Diameter > 1.5 mm. Prefemoral processes of first pair of legs subtriangular (Fig. 3A-C)
 *A. fasciatus* (Attems, 1896) (Zanzibar, Rubeho Mts, Mt Vula)
 – Diameter < 1.7 mm. Prefemoral processes of first pair of legs finger-shaped (Fig. 3D–I)
 *A. claudiahempae* Enghoff & Frederiksen, 2015 (Udzungwa, Kilimanjaro)

Discussion

Intragenetic relationships

A preliminary study of relationships between eight *Aquattuor* species (*A. denticulatus* and *A. mollilobus* sp. nov. were not included), based on the CO1 gene and partly on the 16S gene, was made by Sara Frederiksen. The results indicate a close relationship between, and a short genetic distance between each of the pairs *A. major/longipala*, *A. claudiahempae/fasciatus* and *A. udzungwensis* (West Kilombero Scarp FR)/*udzungwensis* (Udzungwa Scarp FR), but are otherwise inconclusive. These findings seem to agree with morphological evidence: *A. major* and *A. longipala*, together with *A. mollilobus* sp. nov. share an elongate gonocoxal palette, a distal prefemoral lobe and shortened telopodital setae of the first pair of legs; *A. claudiahempae* and *A. fasciatus* are extremely similar, and their separate species status may even be questioned.

Distribution patterns

Out of the ten currently known species of *Aquattuor*, seven occur, six of them as endemics, in the Udzungwa Mts, which thus is clearly a ‘center of diversity’ for this genus. The seventh Udzungwa species, *A. claudiahempae*, is also known from disturbed habitats on Mt Kilimanjaro. Two species, *A. denticulatus* and *A. nguruensis* sp. nov., are endemic to the East Usambara and Nguru Mts, respectively, and the tenth species, *A. fasciatus*, is known from coastal Tanzania and the Rubeho Mts.

Within the Udzungwa Mts there is a strong concentration of species in the NE part (Udzungwa Mts National Park, the former Mwanihana FR, see Fig. 1). *Aquattuor major*, *A. mollilobus* sp. nov. and *A. submajor* are known only from this area; *A. longipala* is also known from the former West Kilombero FR further west, and *A. udzungwensis* is widespread in the Udzungwas from NE to SW. The SW of the Udzungwas (Udzungwa Scarp FR) harbor one endemic species, *A. stereosathe*.

In the absence of a phylogenetic hypothesis little can be said about this distribution pattern. It may, however, be noticed that the one species shared between the Udzungwas and elsewhere, viz., *A. claudiahempae*, in the Udzungwas has been collected only at a relatively low altitude (650 m a.s.l.). This is in agreement with the altitudinal pattern of Udzungwa odontopygids found by Enghoff (2018a), viz., that the few non-endemic Udzungwas, except one, have been collected at the lowest-lying sites. On Mt Kilimanjaro, *A. claudiahempae* occurs in disturbed habitats, and accidental transport by humans may well have played a role in the dispersal of this species, as may also be the case with *A. fasciatus* (the status of this species vis-à-vis *A. claudiahempae* is even dubious).

Altitudinal differences in ring numbers

Two species known from several sites in the Udzungwa Mts, viz., *A. submajor* and *A. udzungwensis*, show a negative correlation between altitude and numbers of podous rings (Fig. 18). Such a decrease is, however, not a general trend in millipedes. Thus, in the European *Ommatoiulus sabulosus* (Linnaeus, 1758) (Julida: Julidae), according to studies by F. Sahli synthesized by Enghoff *et al.* (1993), specimens of a high-altitude population grew to having more podous rings than those in a low-altitude population.

The first pair of male legs

As mentioned in the introduction, the first pair of odontopygid male legs has not been described systematically in the literature. Published drawings, e.g., Attems (1909: fig. 51; 1953: fig. 180), Brolemann (1920: fig. xxx), Hoffman & Howell (1981: fig. 2) and Schubart (1966: figs 105, 108, 113, 117, 121, 126, 132) do suggest some differences between taxa, and the present study confirms that the first pair of legs should receive more attention.

Within *Aquattuor* alone, the shape of the prefemoral processes varies (finger-shaped or triangular, straight or curved); an additional distal prefemoral lobe may be present or absent; the setae of the telopodite may be reduced in length to varying degrees, the telopodital podomeres distal to the prefemur may be absent. The last-mentioned condition is puzzling. In all examined males of *A. udzungwensis*, the telopodite seems to have been broken off between prefemur and femur, rather than not having been formed from the beginning. Such damage may have been inflicted during copulation, in analogy with the situation in *Julus scandinavicus* Latzel, 1884 (Julida: Julidae) where males are very often found with the long coxal processes of the second pair of legs broken (Schubart 1934; pers. obs.) – during mating, females ‘lick’ an attractive substance from these processes (Haacker 1969), and while doing so may break them. In Spirostreptidae, the first pair of legs plays a role in the ‘fixation’ of the female during copulation (Krabbe 1982); there is no reason to believe that this is different in their close relatives the odontopygids, and the lack of the distal telopodital podomeres in *A. udzungwensis* might be due to ?accidental bites from the females.

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References

- Attems C.G. 1896. Beschreibung der von Dr. Stuhlmann in Ost-Afrika gesammelten Myriopoden. *Jahrbuch der hamburgischen wissenschaftlichen Anstalten* 13, Suppl.: 23–42. Available from: <https://biodiversitylibrary.org/page/28745426> [accessed 1 Oct. 2019].
- Attems C. 1909. Myriopoda. In: Sjöstedt Y. (ed.) *Wissenschaftliche Ergebnisse der schwedischen zoologischen Expedition nach dem Kilimandjaro, dem Meru und den umgebenden Massaistepfen Deutsch-Ostafrikas 1905–1906, unter Leitung von Prof. Dr. Yngve Sjöstedt* 3 (19): 1–64. Available from: <https://biodiversitylibrary.org/page/1410223> [accessed 1 Oct. 2019].
- Attems C.G. 1914. Afrikanische Spirostreptiden nebst Überblick über die Spirostreptiden orbis terrarum. *Zoologica Stuttgart* 65–66: 1–233.

- Attems C. 1953. Neue Myriopoden des belgischen Congo. *Annales du Musée royal du Congo Belge, Série 8°, Sciences Zoologiques* 18: 1–139.
- Brolemann H.W. 1920. Myriapodes. In: Allaud Ch. (ed.) *Voyage de Ch. Alluaud et R. Jeannel en Afrique Orientale 1911–1912. Résultats Scientifiques*, Myriapoda 3: 49–298. A. Schultz, Paris.
- Enghoff H. 2014. A mountain of millipedes I: An endemic species-group of the genus *Chaleponcus* Attems, 1914, from the Udzungwa Mountains, Tanzania (Diplopoda, Spirostreptida, Odontopygidae). *European Journal of Taxonomy* 100: 1–75. <https://doi.org/10.5852/ejt.2014.100>
- Enghoff H. 2016a. 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). *European Journal of Taxonomy* 177: 1–19. <https://doi.org/10.5852/ejt.2016.177>
- Enghoff H. 2016b. 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). *European Journal of Taxonomy* 215: 1–23. <https://doi.org/10.5852/ejt.2016.215>
- Enghoff H. 2016c. A mountain of millipedes V: Three new genera of Odontopygidae from the Udzungwa Mountains, Tanzania. (Diplopoda, Spirostreptida, Odontopygidae). *European Journal of Taxonomy* 221: 1–17. <https://doi.org/10.5852/ejt.2016.221>
- Enghoff H. 2018a. 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). *European Journal of Taxonomy* 394: 1–29. <https://doi.org/10.5852/ejt.2018.394>
- Enghoff H. 2018b. A mountain of millipedes VII. The genus *Eviulisoma* Silvestri, 1910, in the Udzungwa Mountains, Tanzania, and related species from other Eastern Arc mountains. With notes on *Eoseviulisoma* Brolemann, 1920, and *Suohelisoma* Hoffman, 1963 (Diplopoda, Polydesmida, Paradoxosomatidae). *European Journal of Taxonomy* 445: 1–90. <https://doi.org/10.5852/ejt.2018.445>
- Enghoff H. & Frederiksen S.B. 2015. A mountain of millipedes II: The genus *Aquattuor* Frederiksen, 2013 – five new species from the Udzungwa Mountains and one from Mt. Kilimanjaro, Tanzania (Diplopoda, Spirostreptida, Odontopygidae). *European Journal of Taxonomy* 150: 1–25. <https://doi.org/10.5852/ejt.2015.150>
- Enghoff H., Dohle W. & Blower J.G. 1993. Anamorphosis in millipedes (Diplopoda) – the present state of knowledge with some developmental and phylogenetic considerations. *Zoological Journal of the Linnean Society* 109: 103–234. <https://doi.org/10.1111/j.1096-3642.1993.tb00305.x>
- Enghoff H., Hoffman R.L. & Howell K.M. 2016. Checklist of the millipedes (Diplopoda) of Tanzania. *Journal of East African Natural History* 105 (1): 51–113. <https://doi.org/10.2982/028.105.0103>
- Frederiksen S.B. 2013. East African odontopygid millipedes 3: Two new genera, *Lamelloramus* and *Aquattuor* proposed to contain three new species (Diplopoda, Spirostreptida, Odontopygidae). *Zootaxa* 3694: 59–66. <https://doi.org/10.11646/zootaxa.3694.1.4>
- Haacker U. 1969. An attractive secretion in the mating behaviour of a millipede. *Zeitschrift für Tierpsychologie* 26: 988–990. <https://doi.org/10.1111/j.1439-0310.1969.tb01986.x>
- Hoffman R.L. & Howell K.M. 1981. A new genus, composed of brightly colored East African species, in the diplopod family Odontopygidae. *Revue de Zoologie africaine* 95 (3): 687–696.
- Krabbe E. 1979. The first pair of legs in male Spirostreptidae: their function and taxonomic importance. In: Camatini M. (ed.) *Myriapod Biology*: 59–72. Academic Press. London.

- Krabbe E. 1982. Systematik der Spirostreptidae (Diplopoda, Spirostreptomorpha). *Abhandlungen des naturwissenschaftlichen Vereins in Hamburg (NF)* 24: 1–476.
- Kraus O. 1960. Äthiopische Diplopoden I. Monographie der Odontopygidae-Odontopyginae (Diplopoda, Spirostreptoidea). *Annalen van het Koninklijk Museum van Belgisch-Congo* 82: 1–207.
- Marshall A.R., Jørgensbye H.I.O., Rovero F., Platts P.L., White P.C.L. & Lovett J.C. 2010. The species-area relationship and confounding variables in a threatened monkey community. *American Journal of Primatology* 72: 325–336. <https://doi.org/10.1002/ajp.20787>
- Mauriès J.-P. 1997. Is the family Atopogestidae based on a case of teratology or a periodomorphic stage? (Diplopoda, Spirostreptida: Odontopygoidea). *Entomologica Scandinavica Supplement* 51: 139–147.
- Schubart O. 1934. Tausendfüßler oder Myriapoda I: Diplopoda. *Die Tierwelt Deutschlands* 28: i–vii + 1–318.
- Schubart O. 1966. Diplopoda III. Pselaphognatha, Opisthospermophora, Colobognatha. *South African Animal Life* 12: 9–227.
- VandenSpiegel D. & Pierrard G. 2009. Révision du genre *Prionopetalum* (Odontopygidae, Diplopoda) et descriptions de nouvelles espèces d’Afrique de l’Est. *Journal of Afrotropical Zoology* 5: 149–163.

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