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East African giant millipedes of the tribe Pachybolini (Diplopoda, Spirobolida, Pachybolidae)

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Abstract

The East African species of the millipede tribe Pachybolini are revised. Three new genera are described: *Crurifarcimen* **n. gen.** (monotypic, type species: *C. vagans* **n. sp.**, Tanzania), *Hyperbolus* **n. gen.** (type species: *H. apicomplexus* **n. sp.**, Tanzania and Uganda; further species: *H. morogoroensis* Kraus, 1958, Tanzania, transferred from *Pachybolus), Parabolus* **n. gen.** (type species: *Trigoniulus dimorphus* Carl, 1909, Tanzania, transferred from *Pachybolus*, further species: *P. calceus* **n. sp.**, Kenya). *Hadrobolus* Cook, 1897 and its only species, *H. crassicollis* (Peters, 1855), Mozambique, are redescribed. *Epibolus bravensis* (Silvestri, 1897) and *E. mossabicensis* Lawrence, 1967, are both synonymised under *E. pulchripes* (Gerstäcker, 1873), Somalia to Mozambique, rendering *Epibolus* Cook, 1897, monotypic. *Pachybolus* Cook, 1897, is restricted to its poorly known type species, *P. tectus* Cook, 1897, Zanzibar. A cladistic analysis of Pachybolini (W Africa, E Africa, Madagascar) does not support monophyly of the East African genera, but does support a clade consisting of *Crurifarcimen+Hyperbolus+Parabolus*, as well as monophyly of the two latter genera.

Key words: New genera, new species, *Crurifarcimen, Hyperbolus, Parabolus, Pachybolus, Hadrobolus, Epibolus*, Tanzania, Kenya, Uganda, Eastern Arc Mountains

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Introduction

The tribe Pachybolini was defined by Wesener *et al.* (2008) to include five genera of large to gigantic Afrotropical millipedes, and a sixth genus was added by Enghoff (2008). The Pachybolini are distributed in West Africa (*Pelmatojulus*, *Gabolus*), East Africa (*Pachybolus*, *Hadrobolus*, *Epibolus*) and Madagascar (*Madabolus*). The latter genus was described and treated in detail by Wesener *et al.* (2008). The present paper deals with the East African genera of Pachybolini.

The genera of Pachybolini described from East Africa so far are:

Pachybolus Cook, 1897. Currently included species: *P. tectus* Cook, 1897 (type species), *P. dimorphus* (Carl, 1909)—transferred to *Pachybolus* by Hoffman (1965), *P. morogoroensis* Kraus, 1958.
Hadrobolus Cook, 1897. Currently included species: *H. crassicollis* (Peters, 1855) (type species) —transferred to *Hadrobolus* by Cook (1897).
Epibolus Cook, 1897. Currently included species: *E. pulchripes* (Gerstäcker, 1873), *E. bravensis* (Silvestri, 1897), *E. mossambicensis* (Lawrence, 1967) —all three transferred to *Epibolus* by Enghoff (1977).

As is obvious from the above, the American myriapodologist O.F. Cook played a dominant role in the development of the taxonomy of East African Pachybolini. Although his names date from 1897, where they first appeared briefly, it is his paper from 1899 which forms the real basis.

Unfortunately, the type and only known specimens of *Pachybolus tectus* seem to be lost, so all we know about the type species of *Pachybolus* is the description and drawings by Cook (1899). Several West African species referred to *Pachybolus* have been transferred to *Pelmatojulus* (Wesener *et al.* 2008). *Hadrobolus* seems to be a well-founded genus; although it remains known only from the unique type specimen of the type species, and although the taxonomically important gonopods of that specimen are lost, unpublished drawings of these gonopods exist to supplement the original description of the type species and the subsequent description and drawings by Cook (1899). *Epibolus* in contrast is well-defined, having being revised relatively recently (Enghoff 1977).

Although the identity of *Pachybolus*, even in a restricted sense, remains questionable, the two non-type East African species referred to *Pachybolus*, i.e., *P. dimorphus* and *P. morogoroensis*, clearly belong in other, so far undescribed genera. Finally, material of three new species, neither of which fits into a described genus, has accumulated over the last decades.

The purpose of the present paper is to define the genera of East African Pachybolini and to (re)describe their constituent species.

Material and methods

Specimens were examined from the following collections (curators in parentheses):

CAS	California Academy of Sciences (C. Griswold)
MFN	Museum für Naturkunde, Berlin (J. Dunlop)
MHNG	Muséum d'Histoire Naturelle, Genève (P. Schwendinger)
MSNF	Museo di Storia Naturale, Firenze (L. Bartolozzi)
NHML	Natural History Museum, London (J. Beccaloni)
MND	Museum für Naturkunde, Dresden (C. Schmidt)
SMNG	Senckenberg Museum für Naturkunde, Görlitz (P. Decker, K. Voigtländer)
SNM	Forschungsinstitut und Naturmuseum Senckenberg (M. Grasshoff)
UMB	Überseemuseum Bremen (P.-R. Becker)
VMNH	Virginia Museum of Natural History (R.L. Hoffman)
ZMUH	Zoologisches Museum, Universität Hamburg (H. Dastych)
ZMUC	Zoological Museum, Natural History Museum of Denmark, University of Copenhagen

FIGURE 1. *Crurifarcimen vagans* **n.gen.**, **n. sp.**, male paratype from East Usambara Mts., Amani. Length of specimen 16 cm. G. Brovad phot.

All studied specimens were stored in ca. 70% ethanol. Counts of body rings and rows of ocelli, and measurements of body diameter, were made on entire and unequivocally reconstructable specimens. Vulvae and gonopods of several species were examined with a JEOL JSM-6335F scanning electron microscope.

Georeferences, when not included in original label data, were found using a combination of Google Earth and Google.

The cladistic analysis was done by Piyatida Pimvichai using Mesquite (Maddison & Maddison 2009) for the data matrix, and TNT (Goloboff *et al.* 2008) for data analyses, and for tracing character changes.

In terms of presentation, the species treated first (*Crurifarcimen vagans*) is described in great detail, whereas for the following species, many characters are only mentioned if their state differs from that seen in *C. vagans*.

The East African Pachybolini

Monophyly of the tribe Pachybolini, and relationships within the tribe, were discussed by Wesener *et al.* (2008) and Enghoff (2008). The latter author very tentatively placed the West African genus *Gabolus* as the sister-group of the remaining tribe members. Among these, the likewise West African genus *Pelmatojulus* is characterized by a clearly apomorphic increase in the number of apical antennal sensilla. The remaining genera occur in East Africa and Madagascar and constitute a provisionally monophyletic subgroup, characterized by the apomorphic condition of having more than two setae on each lamella lingualis of the gnathochilarium.

Six genera of East African Pachybolini are recognised here. The genera are defined mainly on characters of the gonopods, especially the posterior gonopods, see Table 4. Some might argue that the characters here regarded as diagnostic at the genus level do not warrant separation at that level. A taxonomic lumper might choose to retain most of the species treated here in the genus *Pachybolus* but such an approach would run into at least two difficulties. Firstly, the type species of *Pachybolus* remains very poorly known. Secondly, the already named genera *Epibolus, Hadrobolus* and *Madabolus* appear no more deviating than *Pachybolus,* and the new genera proposed here would therefore have to be included in an 'extended *Pachybolus*' of which the other three named genera would then be synonyms. Realizing that splitting versus lumping to a large degree remains a matter of personal taste, I have chosen the former approach.

Table 1 gives an overview of the genera and species of East African Pachybolini.

TABLE 1. Genera and species of East African Pachybolini as recognised in this paper. See Wesener *et al.* (2008) and Enghoff (2008) for Malagasy and West African Pachybolini.

Pachybolus Cook, 1897	*P. tectus* Cook, 1897
Hadrobolus Cook, 1897	*H. crassicollis* (Peters, 1855)
Epibolus Cook, 1897	*E. pulchripes* (Gerstäcker, 1873)
Crurifarcimen **n.gen.**	*C. vagans* **n. sp.**
Hyperbolus **n.gen.**	*H. morogoroensis* (Kraus, 1958), **n.comb.** *H. apicomplexus* **n. sp.**
Parabolus **n.gen.**	*P. dimorphus* (Carl, 1909), **n.comb.** *P. calceus* **n. sp.**

Notes on selected characters

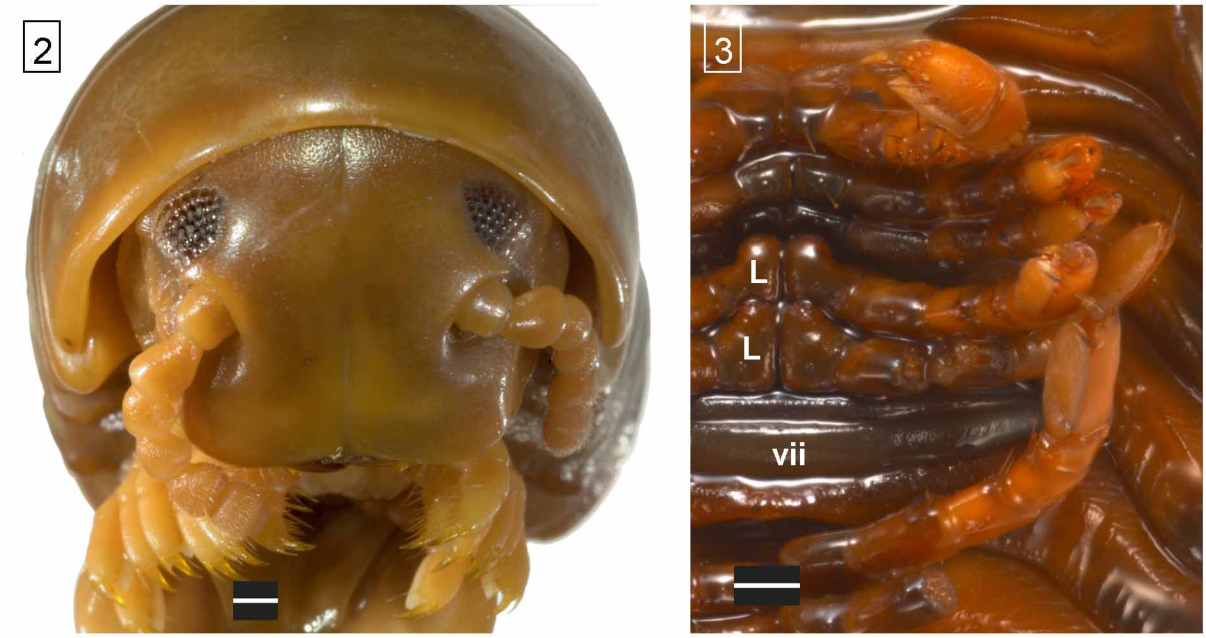
Male legs. Like many other Spirobolida, males of many Pachybolini have some of the pregonopodal leg coxae lobed (Fig. 3). Distinct, anteriad lobes on coxae 6 and 7 occur in *Crurifarcimen, Hyperbolus, Parabolus* and *Madabolus* but are absent in *Epibolus, Hadrobolus* and the W African genera *Pelmatojulus* and *Gabolus*.

All genera have strongly developed soft tarsal pads from leg 3 onward (Figs 4 –8). In most genera, each tarsus from leg 5 onward has one pair of strong apicoventral macrosetae (Figs 4, 5, 7, 60, 71), legs 3–4 have 2 (–3) pairs. The exception is *Epibolus* where the legs from leg 5 onward have 3 (2–5) pairs of ventral tarsal macrosetae (Fig. 6).

The 'sperm canal' . Spirobolidan posterior gonopods mostly have a canal or groove extending from the base of the telopodite to a point near its tip. This structure, the function of which is unknown, has variously been called 'seminal groove' (e.g., Hoffman 1962, Dhaenens & VandenSpiegel 2006), 'sperm canal' (e.g., Wesener *et al.* 2008, Enghoff 2008), and 'prostatic groove' (e.g., Hoffman & Mahsberg 1996). Whatever its function, it is a conspicuous structure, and its course is usually mapped in taxonomic descriptions. The neutral term 'efferent groove' will be used here. In those species studied with SEM, the efferent groove appears as a groove between two closely appressed cuticular sheets (e.g., Fig. 20). When a free solenomerite is present (*Crurifarcimen, Hyperbolus*), the efferent groove continues to the tip of the solenomerite which is formed by a thin sheet rolled up somewhat like a paper cone with overlapping margins (Figs 22, 23, 34, 35). Sometimes the efferent groove appears to be particularly well-sclerotized, but in an opened posterior gonopod of *Epibolus pulchripes* the sclerotized structure was found to be solid (Figs 9–10) and therefore is neither a groove nor a canal.

Female second leg-pair and vulvae. The second pair of legs have strong lateral extensions of the coxosterna; the distal margin of the extensions is usually angled (Fig. 11) but is smoothly rounded in *Epibolus* (Fig. 12).

The vulvae (or cyphopods) are placed in pouches behind the second pair of legs. Descriptions of pachyboline vulvae are available for the genera *Pelmatojulus* (Demange 1961: Figs 60–61), *Gabolus* (Enghoff 2008), *Epibolus* (Enghoff 1977) and *Madabolus* (Wesener *et al.* 2008), only *Epibolus* being among the genera treated here. The genera *Pachybolus* and *Hadrobolus* remain unknown in the female sex.



FIGURES 2–3. *Crurifarcimen vagans* **n.gen.**, **n. sp.**, male paratypes. 2: Head, collum and anterior legs. G. Brovad phot. 3: Body rings 5–7, ventral view, showing coxal lobes on leg-pairs 6–7. N. Ioannou phot. Scales 1 cm. L: lobes, vii: smooth 'shelf' of ventrally fused bodyring seven.

A pachyboline vulva (Figs 24–25, 36–37, 43, 51–53, 79–80) consists of a basal small, oval to subrectangular **operculum** which is usually poorly sclerotized, and two large, heavily sclerotized **valves**, one oral, one aboral. The valves are quite diverse in shape and provide good taxonomic characters. Between the valves, an irregular structure, the **crest**, is sometimes seen. In some genera, the oral valve has a large, poorly sclerotized **apical appendix**. The valves carry numerous short setae on the parts closest to their free margins and the operculum.

Wesener *et al.* (2008) listed a protruding crest as one of the autapomorphies of Pachybolini, but this appears to have been an over-generalisation. Whereas the crest in *Epibolus* is indeed strongly protruding (Fig. 80), this is much less evident in other genera, and in some, the crest does not protrude at all, e.g., *Parabolus calceus* (Fig. 51). Enghoff (2008) noted the absence of a protruding crest in *Gabolus* and regarded this as a potential plesiomorphy vis-a-vis other Pachybolini. In the light of the present findings, this interpretation is dubious, and the phylogenetic and taxonomic significance of the protruding crest appears uncertain.

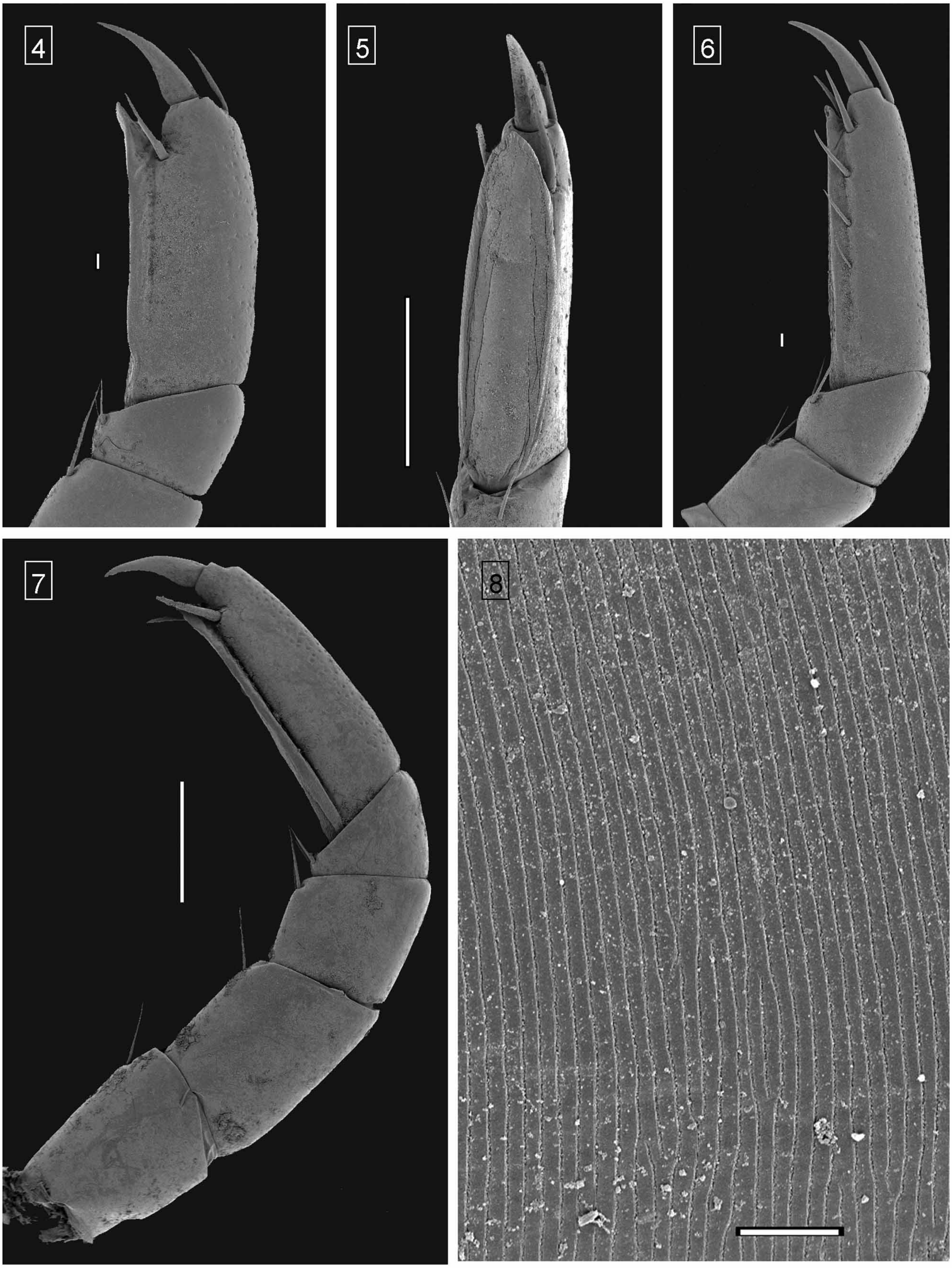
Postembryonic development. Dhaenens & VandenSpiegel (2006) studied postembryonic development of *Epibolus pulchripes*. New data are given here on *Crurifarcimen vagans* (Tables 2–3).

Ecology. With the exception of *Epibolus pulchripes*, as good as nothing is known about the habits of the East African Pachybolini. The available information about *E. pulchripes* is summarised under this species, and small bits of information are given under some of the other species. Pachybolini can play important ecological roles, see under *E. pulchripes*, and see Mahsberg (1997) on a species of *Pelmatojulus*.

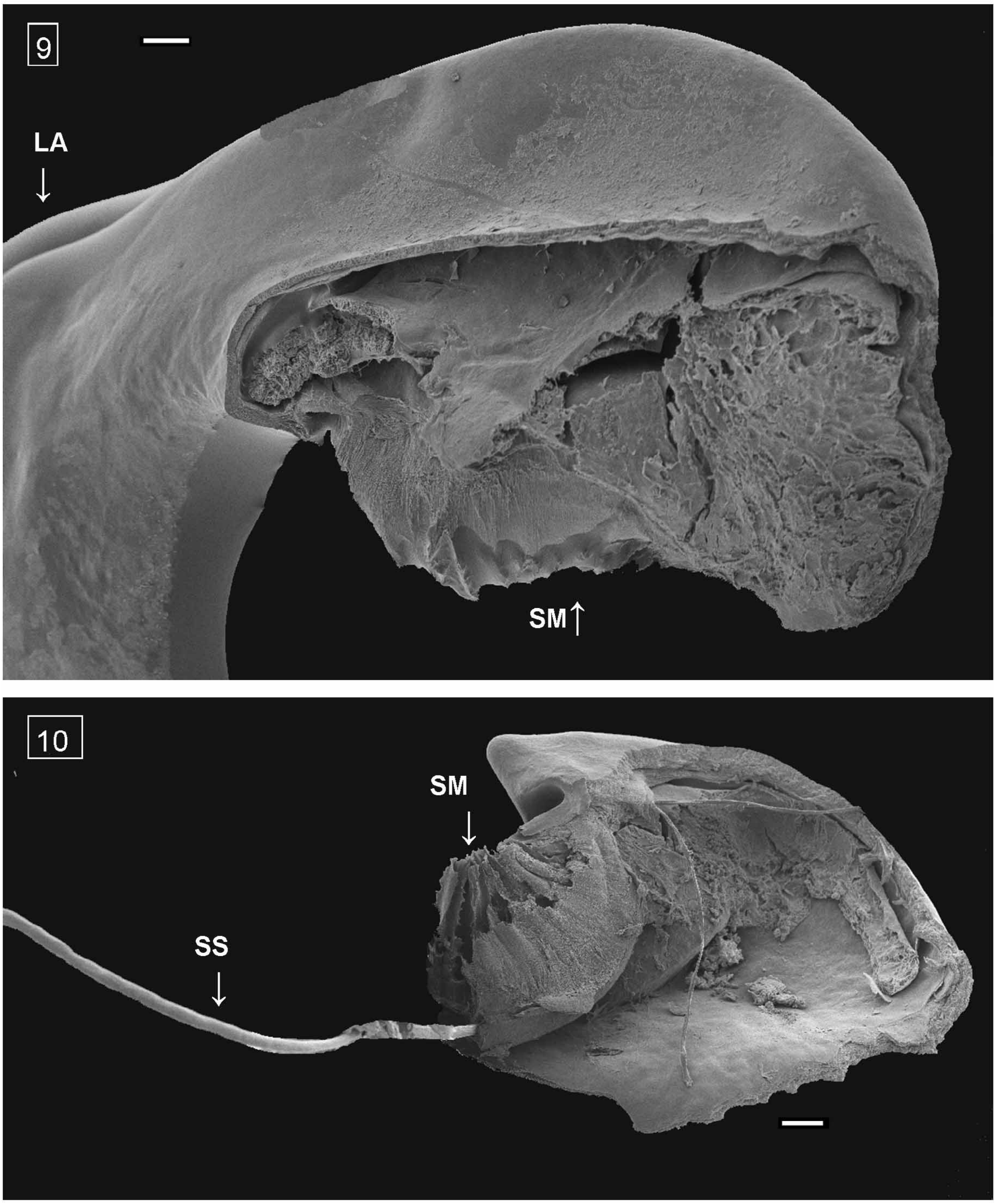
Key to the genera of Pachybolini

Except for the first two couplets, the key requires examination of the male gonopods.

1. Fifteen or more apical sensilla on antenna (W Africa) . . . . *Pelmatojulus*
1a. Four apical sensilla on antenna 2
2. Two apical setae on lamella lingualis of gnathochilarium (Gabon) . . . . *Gabolus*
2a. Three or more apical setae on lamella lingualis of gnathochilarium . . . . 3.
3. Posterior gonopod with a lateral, moveable appendix (E. Africa) . . . . *Epibolus*
3a. Posterior gonopod without a moveable appendix . . . . 4.
4. Posterior gonopod with a distinct mesal process ca. at midlength . . . . 5.
4a. Posterior gonopod without a distinct mesal process ca. at midlength . . . . 6.

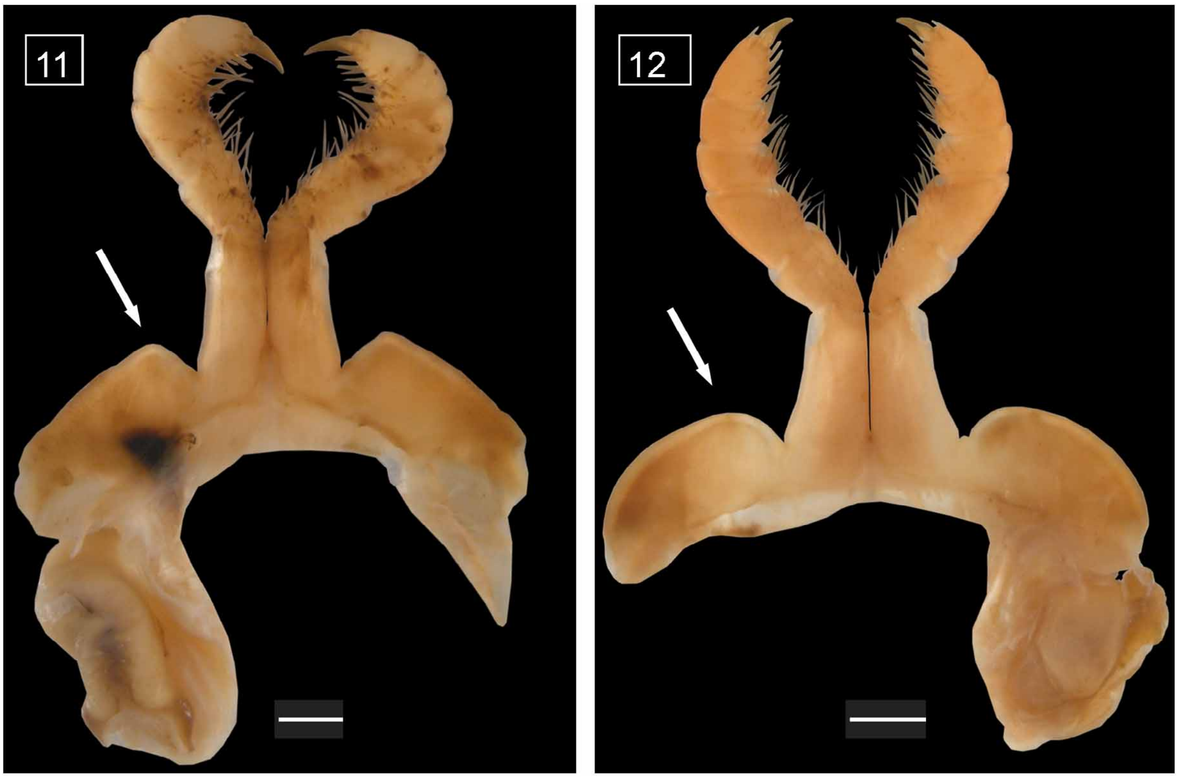


FIGURES 4–8. Male legs, SEM. 4: *Crurifarcimen vagans* **n.gen.**, **n. sp.**, paratype, tarsus, lateral view. 5: *C. vagans*, paratype, tarsus, ventral view. 6: *Epibolus pulchripes*, tarsus, lateral view. 7: *Hadrobolus crassicollis*, holotype, ventral-lateral view. 8: *C. vagans*, paratype, surface structure of ventral pad. Scales 1 mm (5, 7), 0.1 mm (4, 6), 0.01 mm (8).



FIGURES 9–10. *Epibolus pulchripes*, left posterior gonopod, SEM pictures. 9: tip of gonopod, anterior view, part of anterior surface removed. 10: removed part, seen from the inside (posterior view). LA: lateral appendix, SM: striated membranous lamellae, SS: sclerotized structure (’sperm canal’). Scales 0.1 mm.

5. Posterior gonopod with striated lamellae at tip (Madagascar) . . . . *Madabolus*
5a. Posterior gonopod without striated lamellae at tip (Mozambique) . . . . *Hadrobolus*
6. Posterior gonopod with a free solenomerite 7
6a. Posterior gonopod without a free solenomerite 8
7. Posterior gonopod apically with a complex of parallel ridges; anterior gonopod telopodites with mesal, overlapping lobes (Tanzania, Uganda) . . . . *Hyperbolus*
7a. Posterior gonopod without an apical complex of parallel ridges; anterior gonopod telopodites without overlapping lobes (Tanzania) . . . . *Crurifarcimen*
8. Anterior gonopod coxite with a long, mesal process (Kenya, Tanzania) . . . . *Parabolus*
8.a Anterior gonopod coxite without a long, mesal process (Zanzibar) . . . . *Pachybolus*



FIGURES 11–12. Female second pair of legs with one vulva attached, anterior view. 11: *Crurifarcimen vagans*, 12: *Epibolus pulchripes*. The arrows point to the distal margin of the lateral extensions of the coxosternum. Scales 1 cm. P. Pimvichai phot.

Crurifarcimen new genus

Type species: *Crurifarcimen vagans* **n. sp.**

Included species. *Crurifarcimen vagans* **n. sp.**

Etymology. From Latin crus (foot) and farcimen (sausage), i.e. "foot-sausage"

Diagnosis. A genus of East African Pachybolini characterized by

- coxal lobes on male legs 6 and 7
- one pair of ventral macrosetae on male legs from pair 5 onward
- a free solenomerite on posterior gonopod

  no distal complex of parallel ridges, no moveable appendix, no striated membranous lamellae, no mesal process on posterior gonopod
- no long meso-distal process on anterior gonopod coxite
- no distinct overlapping mesal lobes on anterior gonopod telopodites
- apical margin of winglike expansions of second female coxae angled
- no apical appendix on oral vulval valve.

Crurifarcimen vagans n. sp.

Figs 1–5, 8, 11, 13–27, 84

Pachybolus **n. sp.** II. Enghoff & Enghoff 1976

HOLOTYPE: ♂ TANZANIA, Tanga Region, E. Usambara Mts., Amani 5°06'S 38°38'E, forest clearing at Kwankoro road, ca. 1000 m, on the ground, 1.viii.1974, I. B. Enghoff & H. Enghoff leg. (ZMUC 00100972).

PARATYPES from TANZANIA, Tanga Region, East Usambara Mts., Amani 5°06'S 38°38'E: 1 ♀, 2 juveniles, data as holotype (ZMUC 00100973-100974). – 3 ♂♂, 1 juvenile data as holotype, but 2. – 7.viii.1974

(ZMUC 00100982, 00100983, 00100975). – 1 ♀, forest house, secondary rainforest, ca. 1000 m, in rotten wood, 29.vii.1974, I. B. Enghoff & H. Enghoff leg. (ZMUC 00100978). – 1 ♂, 1 ♀ , Bomole, ca. 1000 m, 5.viii.1974, I. B. Enghoff & H. Enghoff leg. (ZMUC 00100979-00100980). – 1 ♂ TANZANIA, Monga, ca. 1000 m, 6.ii.1977, H. Enghoff, O. Lomholdt, O. Martin leg. (ZMUC 00100984). – 1 ♂, 2 ♀♀, ca. 1000 m, 26.i. –1.ii.1977, H. Enghoff, O. Lomholdt, O. Martin leg. (ZMUC 00100985, 00100987). – 1 ♂ 1 ♀, Kwamkoro, 25.i.1977, H. Enghoff, O. Lomholdt, O. Martin leg. (ZMUC 00100992). - 2 ♀♀, 3 juveniles, ca. 1000 m. 1–5.viii.1979, M. Stoltze leg. (ZMUC 00100988, 00100990). – 1 ♂ ca. 1000 m, 24.vi.1970, R. Jacobsen leg. (ZMUC 00100991). – 7 ♂♂, 1 ♀, 1 subad. ♂ TANZANIA, ca. 1000 m, 27.x. – 9.xi. 1995, C. Griswold, N. Scharff & D. Ubick leg. (CAS).

PARATYPES from TANZANIA, Tanga Region, West Usambara Mts., Mazumbai, 4°49'S 38°30'E: 1 ♂, 3 juv. 1600 m, in trunk, 1.viii.1980, M. Stoltze & N. Scharff leg. (ZMUC 00100995). – 1 ♂, 1550 m, 15.xi. 1974, I. Jakobsen leg. (ZMUC 00100996). – 2 ♀♀ , 1600 m, 7.xii.1978, J.B. Rasmussen leg. (ZMUC 00100997). – 1 ♂, 2 ♀♀, montane forest, 1600– 1800 m, 10. – 20.xi.1995, C. Griswold, N. Scharff & D. Ubick leg. (CAS).

ADDITIONAL MATERIAL from TANZANIA, Tanga Region, East Usambara Mts., Amani 5°06'S 38°38'E: 3 juv. Monga, ca. 1000 m, on the ground, 5.viii.1974, I. B. Enghoff & H. Enghoff leg. (ZMUC 00100976). – 1 subadult ♀, ca. 1000m, arable land, 6.viii.1974, I. B. Enghoff & H. Enghoff leg. (ZMUC 00100977). – 1 ♀, 9 juveniles, cultivation in rain forest, ca. 1000 m, on the ground, 26.vii.1974, I. B. Enghoff & H. Enghoff leg. (ZMUC 00100981). – 2 eggs, 1 small juv., lab-reared from parents from Amani (ZMUC 00100993). – 3 juveniles ca. 1000 m, 24.i.1977, in rotten wood, H. Enghoff, O. Lomholdt, O. Martin leg. (ZMUC 00100986). – 1 juvenile, ca. 1000 m. 14.vii.1979, M. Stoltze leg. (ZMUC 00100989).

ADDITIONAL MATERIAL from TANZANIA, Tanga Region, East Usambara Mts: 5 ♂♂, 1 ♀, Muheza + Korogwe District, East Usambara Mts. 4°56'32"S 38°39'38.5"E, 940 masl, trapsite 8 plot 59A, 31.i.2001, Frontier Tanzania leg. (ZMUC 00101001). – 1 ♀, 1 juvenile Nilo Forest Reserve 4°54'16"S, 38°39'45"E, date?, Frontier Tanzania leg. (ZMUC 00101000). – 1 ♂, 1 ♀, 1 subad. ♀ Muheza District, Magrotto Estate, 5°07 S, 38°45' E, 2000–3000 ft asl, iii.1981, S.N.Stuart leg. (VMNH.)

ADDITIONAL MATERIAL from TANZANIA, Tanga Region, Lushoto District, West Usambara Mts., Mazumbai, 4°49'S 38°30'E: 16 juveniles 1600 m, in trunk, 1.viii.1980, M. Stoltze & N. Scharff leg. (ZMUC 00100998). – 3 juveniles TANZANIA, 19. – 29.ix.1992, M. Andersen leg. (ZMUC 00100999). – 1 ♂, 17.vi.1980, S. Mandia leg. (VMNH). – 22 ♂♂, 10 ♀♀, 2 juveniles, S. Mandia leg. (VMNH). – 3 ♂♂, 1 ♀, i.1981, K. M. Howell leg. (VMNH).

ADDITIONAL MATERIAL from TANZANIA, Tanga Region, West Usambara Mts : 1 ♂, 1 subadult ♂, Lushoto District, Mahezangulu Forest Reserve 4° 57' S, 38° 31' E, rain forest, 3000–3500 ft asl, 14–16.iii.1982, S.N. Stuart leg (VMNH). – 5 ♂♂ Korogwe District, Ambangulu Estate Rain Forest, 5° 4'51" S, 38° 25'54" E, 2–11.iv.1980, S.N. Stuart & J. Simkin leg. (VMNH). — 3 ♂♂ Lushoto District, Balangai Forest Reserve, 4° 55'55" S, 38° 37'07" E, 11– 13.iii.1981, S.N. Stuart leg. (VMNH).

Etymology. Latin vagans (wandering, itinerant). The full species name thus means "the itinerant sausage with feet", and this species is indeed the most sausagelike millipede I have seen.

Diagnosis. See that of genus.

Description. Adults with 56 podous rings (exceptionally 54, 55 or 57), no apodous rings. Length 14–16 cm. Width of specimens from East Usambara Mts.: 14.2–16.2 mm (♂♂) / 14.4–16.1 mm (♀♀). Width of specimens from West Usambara Mts.: 13.5–14.2 mm (♂♂) / 14.9–15.4 (♀♀).

Colour: overall impression light brown, occasionally darker brown; head, collum, antennae, legs and telson brownish yellow; legs occasionally dark caramel; prozona of body rings yellow, mesozona greyish brown, metazona reddish brown (Fig. 1).

Head capsule (Fig. 2) punctate above eye level, otherwise smooth; occipital furrow extending down between but not beyond eyes; clypeal furrow reaching level of antennal sockets. Area below antennal socket and eyes impressed, forming part of antennal furrow. 2+2 or 3+3 low, broad labral teeth. A row of labral setae present or missing (abraded?). Supralabral setae absent in adults (abraded?), one subadult ♀ with 1+1 tiny setae. Eyes small, largest diameter 43–47% of interocular space in frontal view; ocelli usually arranged in neat rows, adults with 9–10 RO (see chapter on postembryonic development), 5 horizontal series, 30–39 ocelli per eye. Antennae short, not reaching past collum when stretched back, accommodated in shallow furrow composed of a horizontal segment in the head capsule and a vertical segment in the mandibular cardo and stipes, lateral margins of head capsule also shallowly concave adjacent to mandibular segment of antennal furrow. Antennomeres 1, 3 and 4 as long as broad, 2 longer, 5 and 6 broader, 7 very short, almost contained within subspherical antennomere 6; antennomeres 1–2 glabrous, 3–4 with a few ventral setae, 5–6 densely setose and each with a dorsodistal field of small sensilla; four apical sensilla partly separated by outgrowths from the wall of antennomere 7. Mandibles in part visible in frontal view; cardo and stipes excavated for accomodation of antenna. Cardo with vertical ridge ca. 1/3 from anterior margin. Stipes ventrally excavated in mesal half for accommodation of gnathochilarium. Gnathal lobe (terminology of Enghoff 1979): external tooth with single, subrectangular lobe; internal tooth with four shallow cusps plus an isolated, triangular cusp dorsally; Four pectinate lamellae, plus a short fifth row and a few isolated teeth basal to fifth row; a narrow strip ("fringe") of small spines ventral to pectinate lamellae; a soft, smooth-edged ridge between pectinate lamellae and mola, ridge dorsally with a row of small spines; molar plate with six transverse ridges decreasing in size towards base. Gnathochilarium similar to those of *Pelmatojulus tigrinus* Hoffman & Mahsberg, 1996, and *Madabolus maximus* Wesener *et al.*, 2008. Mentum transversely wrinkled. Stipites wrinkled parallel to mento-stipital suture, each with 3–5 distal setae. Lamellae linguales each with 3–6 setae arranged in a transverse, distal row or group.

Collum (Fig. 2) entirely smooth, or with faint short striae along lowermost part of anterior margin, somtimes a weak marginal furrow along lateral parts of anterior margin; lateral lobes rounded/triangular, not extending as far ventrad as body ring 2.

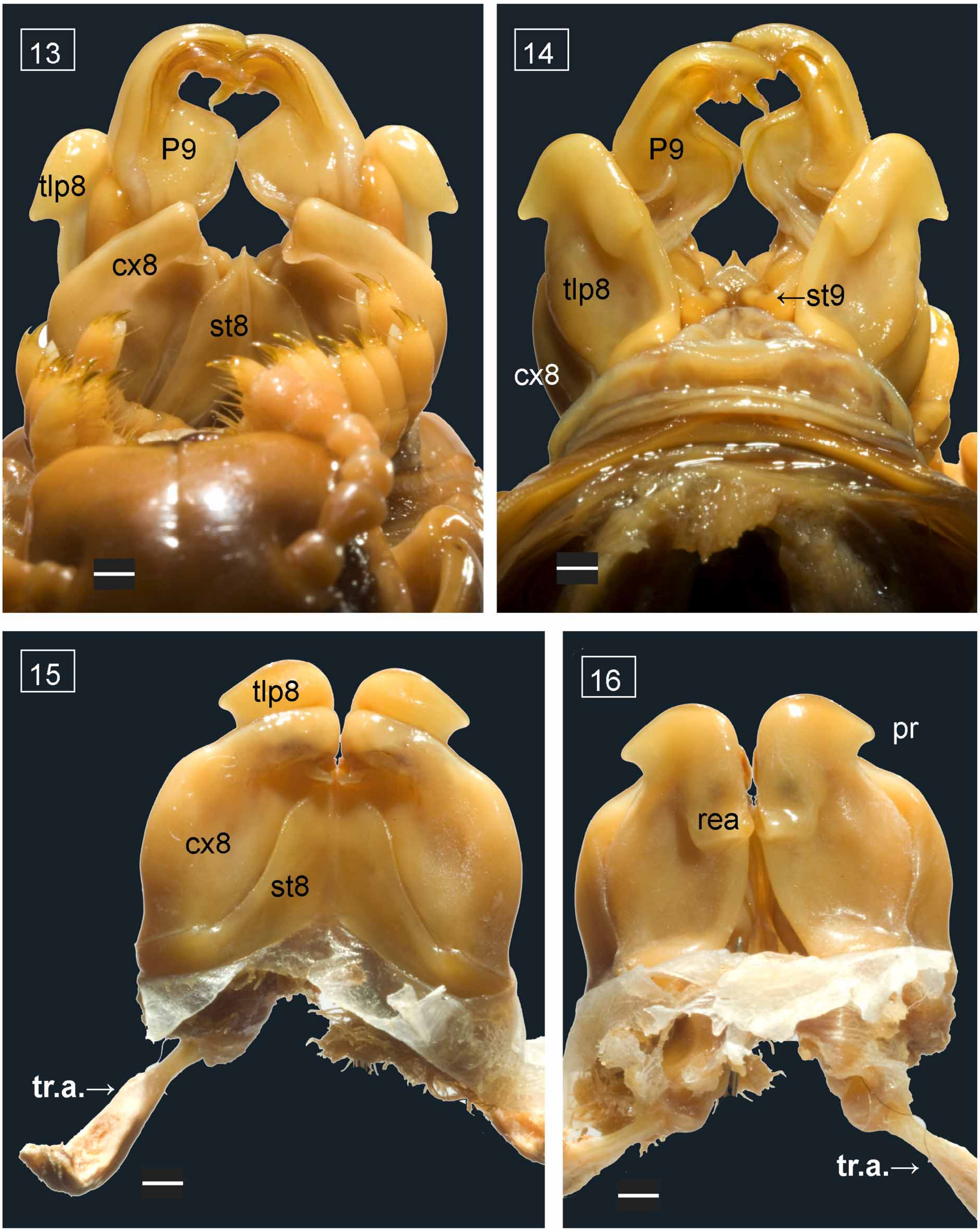
Body rings two to five/six ventrally concave, hence with distinct ventrolateral "corners". Body rings very smooth, dorsal profile linear. "Tergo-pleural" suture visible on pro- and mesozona. Prozona with very fine chagrination. Mesozona ventrally with fine oblique striae, gradually changing into fine punctation laterally and dorsally. Metazona ventrally with fine longitudinal striae, otherwise smooth in ♂♂, finely punctate to coriaceous in ♀♀. "Pleural" parts of rings with fine oblique striae. Sterna transversely striate. Ozopores from ring 6, situated in mesozona, ca. 1½ pore diameter in front of metazona. Sutures between pro-, meso- and metazona fine but distinct; horizontal suture sometimes distinct on pro- and mesozona, less so on metazona. Posterior margin of body rings with numerous very short longitudinal impressions, giving a crenulate impression; margin itself straight, however; no limbus.

Telson very shallowly punctate, appearing smooth. Preanal ring with slightly concave dorsal profile. Anal valves slightly impressed submarginally; margins hence slightly protruding, liplike. Subanal scale broadly triangular.

Legs: Length of midbody legs 62% of body diameter in ♂, 51% of body width in ♀. Coxa dorsally angled; prefemur basally constricted; tarsus longer than other podomeres. First and second legs with numerous (35–40) ventral setae, third and following pairs with much fewer setae, numbers of setae reaching constancy from pair 5 or 6, each leg with 1 coxal, 1–2 prefemoral, 1–2 femoral, 2 postfemoral, and 2 tibial setae. Tarsi in ♂♂ with 2 ventral apical and one dorsal apical seta (Figs 4–5), ♀♀ with 2+2 ventral and one dorsal apical seta, the basal ventral pair smaller than the others.

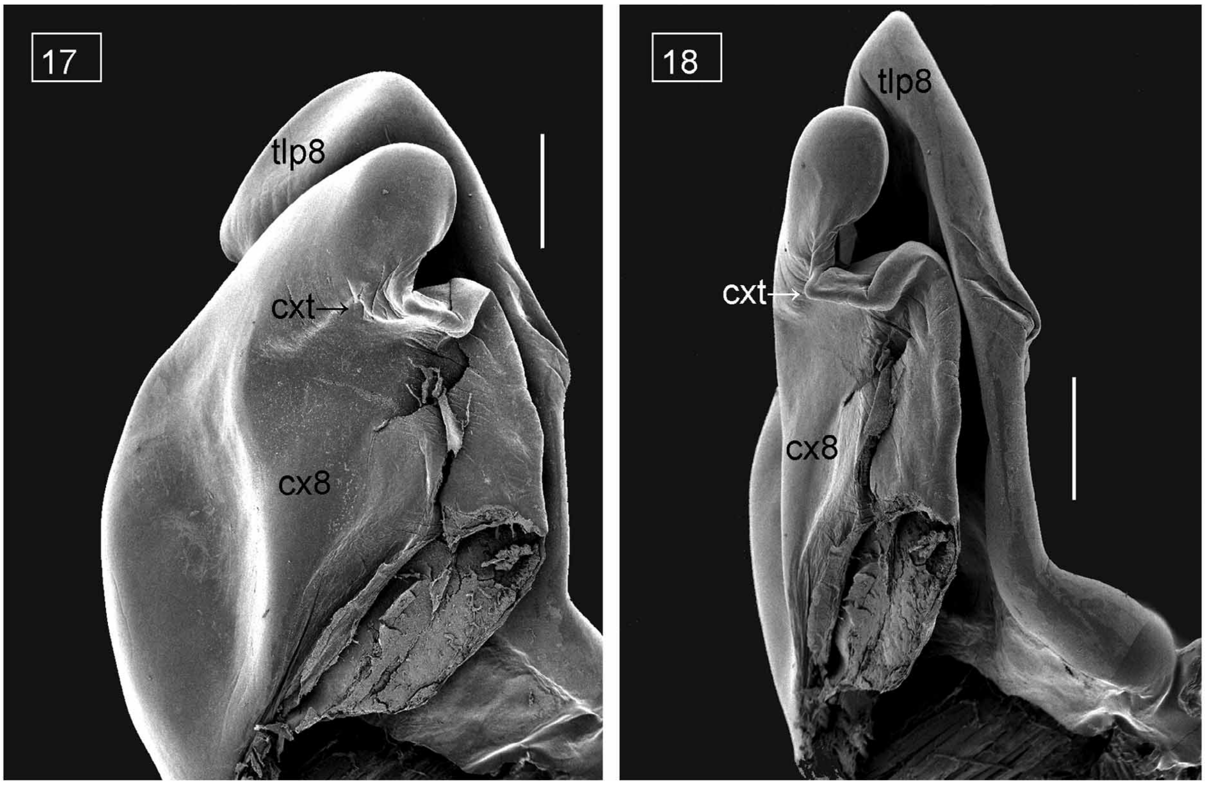
Male sexual characters. Body more shining than in females, due to absence of punctation on metazona. Tarsus of all legs from third to last pair with large ventral soft pad occupying entire ventral surface (Figs 4–5). Coxae of fifth and sixth pair of legs with anterior, rounded lobes, slightly larger on fifth (Fig. 3). Body ring seven (Fig. 3) entirely fused ventrally, no trace of a suture. Anterior part ventrally clearly delimited as smooth "shelf", contrasting with sculptured areas posteriorly and laterally. Gonopods (Figs 13–23) entirely concealed within body ring seven at rest.

Anterior gonopod sternum concave on oral face, with high, broad, bell-shaped mesal process reaching ca. 3/4 the height of the coxae; right and left halves of process meeting under blunt angle in midline, sometimes forming a midline ridge; tip of process more or less pointed; sternum laterally continuing as narrow band around side of gonopod, reaching well along base of coxa on aboral side, articulating with a narrow sclerite at base of telopodite, the "bride trachéenne” of Demange (1967) (Fig. 19). Coxae in oral view with apical margins oblique, set off from parallel lateral margins by blunt angle somewhat apical to mid-height of coxa; opposing coxae meeting in midline distal to sternum; here with small tooth (*cxt* on Figs 17, 18) projecting basad-mesad over tip of sternum, sometimes with an impression delimited by a small vertical ridge just distal of *cxt*; oral surface of coxa slightly concave, i.e., due to rounded lateral ridge occupying ca. half of coxal width; aboral surface of coxa (hidden from view in undissected specimens) broadly swollen mesally, swelling apically connecting with basad-mesad tooth on oral surface. Coxae extending to aboral side of gonopod where they appear as narrow lateral bands. Telopodites (Figs 14–19) extending well beyond coxal tips, overall shape ovoid; *in situ* meeting in midline; posterior face of telopodite with rectangular elevated area, the basal-mesal corner of which meets that of opposite telopodite; opposite corners usually slightly asymmetrical (one telopodite forming short process fitting into concavity on the other); lateral margin of telopodite with sub-semicircular incision, delimiting a subapical lateral rounded-triangular projection.



FIGURES 13–16. *Crurifarcimen vagans* **n.gen.**, **n. sp.** paratypes. 13: everted gonopods in situ, anterior view. 14: do., posterior view. 15: anterior gonopods, anterior view. 16: do., posterior view. cx8: anterior gonopod coxa, P9:posterior gonopod, pr: lateral projection of anterior gonopod telopodite, rea: rectangular elevated area of anterior gonopod telopodite, st8: anterior gonopod sternum, st9: rounded-triangular sclerite of posterior gonopod sternum, tlp8: anterior gonopod telopodite, tr.a.: tracheal apodeme of posterior gonopod. Scales 1 cm. G. Brovad phot.

Posterior gonopods (Figs 13–14, 20–23) *in situ* completely hidden within anterior ones, connected by median sternal remnant consisting of mesal membranous region flanked by a pair of rounded-triangular sclerites (Fig. 14). Gonopods oriented with larger surfaces facing aboral-lateral and oral-mesal, respectively, for simplicity these faces are termed aboral and oral below. Each posterior gonopod clearly divisible into four parts:



FIGURES 17–18. *Crurifarcimen vagans* **n.gen.**, **n. sp.**, paratype, left anterior gonopod coxa and telopodite. 17: oral view, 18: mesal view. cx8: anterior gonopod coxa, cxt: mesal coxal tooth, tlp8: anterior gonopod telopodite. Scales 1 mm. SEM.

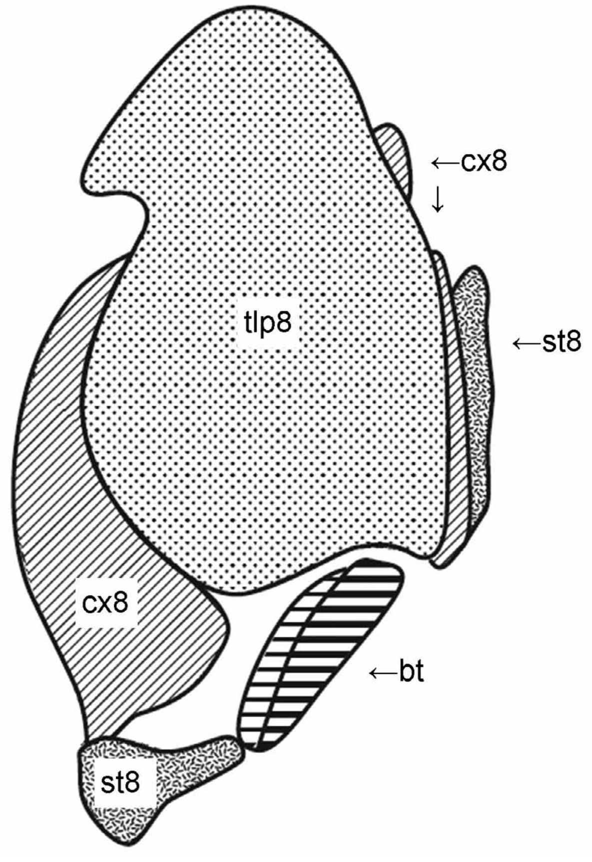
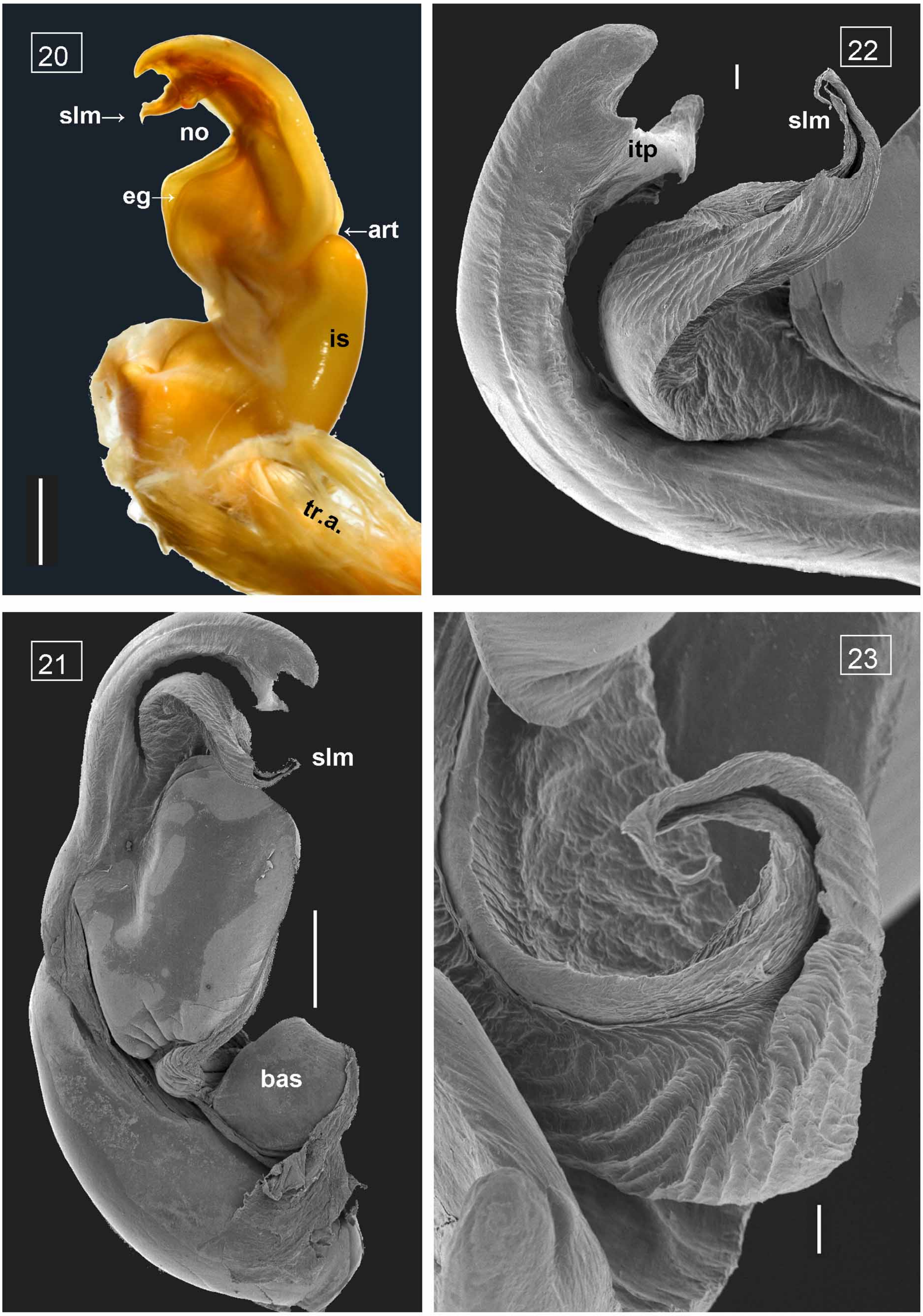


FIGURE 19. *Crurifarcimen vagans* **n.gen.**, **n. sp.**, paratype, semidiagrammatic drawing based on right anterior gonopod macerated with trypsin. bt: ’bride trachéenne’(lighter horizontal stippling indicates a part of the ’bride trachéenne’ embedded in membrane), cx8: coxa, st8: anterior gonopod sternum (cut in midline, to the right in the drawing), tlp8: anterior gonopod telopodite.



FIGURES 20–23. *Crurifarcimen vagans* paratype, left posterior gonopod. 20: anterior view, G. Brovad phot. 21: posterior view, SEM, 22: tip, posterior view, SEM, 23: solenomerite, SEM. Scales 1 mm (20–21), 0.1 mm (22–23). art: articulation between intermediate and terminal segment, bas: basal, aboral sclerite, eg:efferent groove, is: intermediate segment, itp: irregular triangular process, no: notch, slm: solenomerite, tr.a.: tracheal apodeme (hidden in muscle).

1. a long, slender, almost straight *tracheal apodeme* (Figs 15–16, 20), flattened towards its end,
2. a *basal, aboral sclerite* (Fig. 21) which articulates with the tracheal apodeme, is roughly pentagonal in outline and has a distinct notch on its distal margin, next to articulation with median sternal sclerite,
3. a smooth, stout, sausagelike *intermediate segment* delimited against terminal segment by very distinct articulation across lateral margin (Fig. 20, *art*), by membranes on oral and aboral faces, membrane most extensive on latter face,
4. a complicated *terminal segment* with smoothly convex lateral margin, this margin with longitudinal concavity next to basal articulation against intermediate segment. Basal part of terminal segment roughly quadrate in outline, extensively covered by membrane on lateral face. Distal part of terminal segment abruptly set off by rectangular notch. Aboral face of terminal segment with longitudinal groove parallel to lateral margin; distalmost part of groove covered by large irregular, ±triangular process; this process forming part of slightly concave apical-mesal margin of gonopod, corners of concavity blunt, slightly protruding. Apical-mesal margin overreached by conspicuous solenomerite emerging from oral face of gonopod, lamellate, longitudinally striate, sinuous, attenuated, ending as curved tip pointing in a mesal-basal direction. Efferent groove only visible on terminal segment of gonopod, running along mesal edge of broad basal part, moving to lateral surface and there running subparallel to distal margin of basal part, further along mesal edge of distal part (where accompanied by narrow, transparent, striate membrane) and onto solenomerite where it ends as an open furrow near the tip.

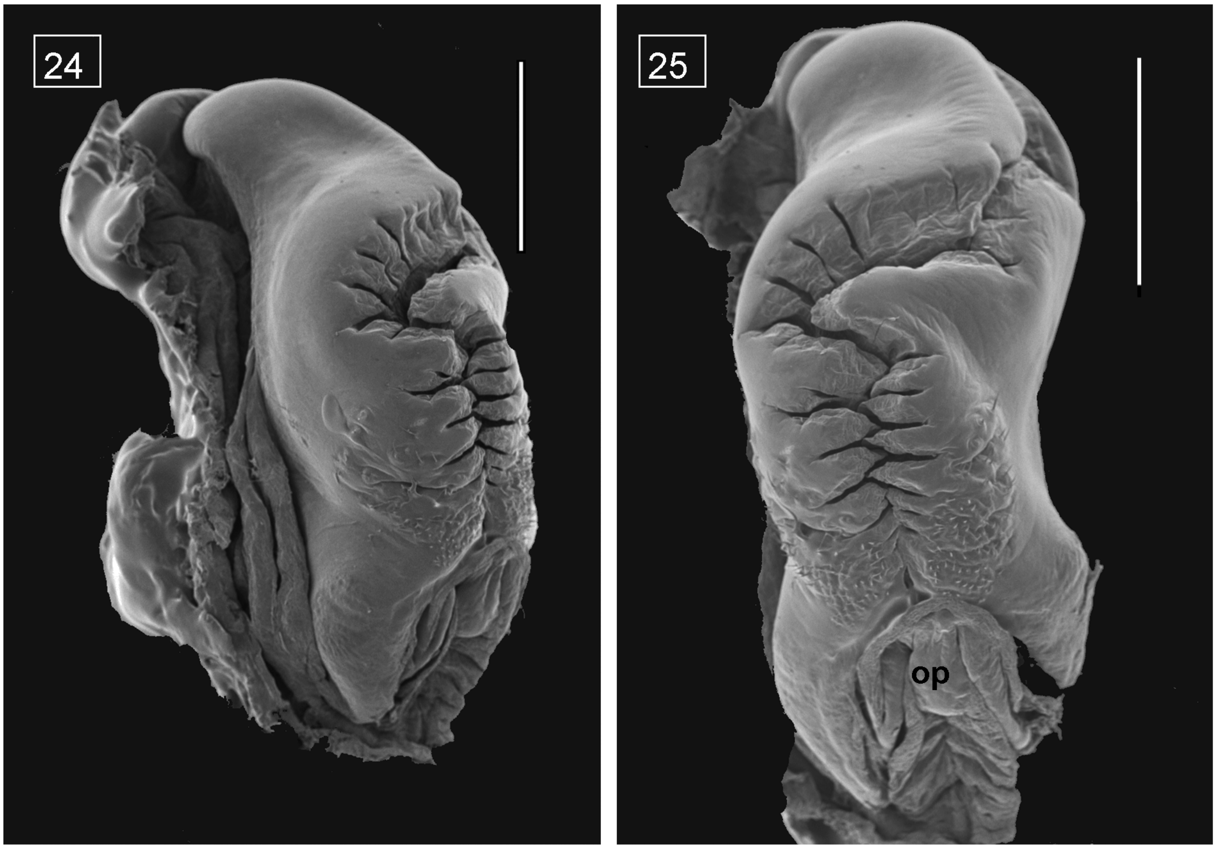
Female sexual characters. Distal margin of lateral coxosternal extensions projecting as right-angled lobe (Fig. 11). Vulva (Figs 11, 24–25) in posterior view sausage-shaped. Valves very elongated, slightly curved (their bases concave), quite asymmetrical and variable in details, margins lobed except distally, lobes interlocked, basally in a coarse zig-zag pattern. No apical appendix. Crest not protruding.

Postembryonic development. Eggs and first stadium juveniles were obtained in culture (offspring of a female collected in Amani, E Usambaras, in 1974). Stadia II-X were collected in the field (cumulative material from E and W Usambaras, 1970–1995). The stadium numbers can be read by counting rows of ocelli (RO). Stadium I has one row, II has two etc. (cf. Enghoff *et al.* 1993).

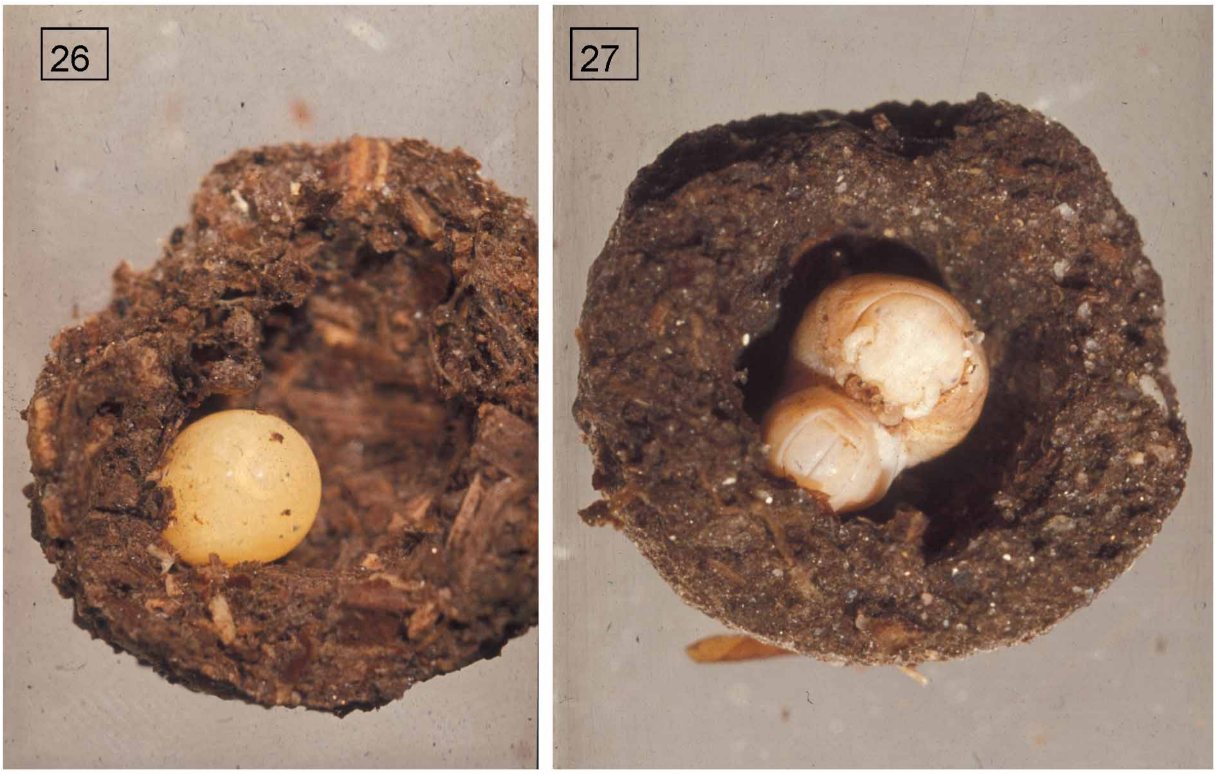
The eggs are placed individually in spherical earthen capsules manufactured by the female (Fig. 26), as in *Epibolus pulchripes* (Dhaenens & VandenSpiegel 2006). The stadium I juveniles (Fig. 27) remain inside the capsules. The body ring formulae of the studied specimens are shown in Table 2. Out of 91 specimens, 82 follow the principal pathway. Whereas not observed formulae can be inferred with some confidence from the preceding stadium (e.g., 54+3+T in stadium VIII can be inferred from 49+5+T in stadium VII), it is more difficult to infer a not observed formula preceding an observed one, e.g., 49+5+T in stadium VII could have resulted from 43+6+T or 42+7+T in stadium VI. The course of anamorphosis in *C. vagans* is almost identical to that observed in two species of the West African pachybolinine genus *Pelmatojulus* (Enghoff *et al.* 1993), whereas in *Epibolus pulchripes*, stud-

TABLE 2. Postembryonic development of *Crurifarcimen vagans* based on all examined entire specimens. Entries are body ring formulae sensu Enghoff *et al.* (1993), i.e., (number of podous rings) + (number of apodous rings) + T [=telson]. Stadium numbers are inferred from counts of rows of ocelli, see further in text. Numbers of specimens in each stadium and with each body ring formula are given in (parentheses) after the formula. Inferred formulae which were not observed, are given in [square brackets]. The single stadium I juvenile was not dissected; it has 6 body rings, a long zone of not fully formed segments, and a telson; the formula 4+2+T is given in analogy with what is known for other pachybolids (*Pelmatojulus* spp., Enghoff *et al.* 1993). The principal pathway of postembryonic development is indicated with **bold** types.

Stadium I			**4+2+T** (1)	
Stadium II			**6+18+T** (1)	
Stadium III			**24+6+T** (2)	
Stadium IV			**30+6+T** (8)	
Stadium V			**36+6+T** (2)	
Stadium VI			**42+6+T** (4)	
Stadium VII			**48+5+T** (9)	49+5+T (2)
Stadium VIII		52+3+T (2)	**53+3+T** (8)	[54+3+T]
Stadium IX	54+0+T(2)	55+0+T(1)	**56+0+T** (33)	57+0+T(1)
Stadium X		55+0+T (1)	**56+0+T** (14)	
[Stadium XI]			[56+0+T]	



FIGURES 24–25. *Crurifarcimen vagans*, paratype, right vulva, SEM. 24: posterior-lateral view, 25: lateral view. Scales 1 mm. op: operculum.



FIGURES 26–27. *Crurifarcimen vagans*, early stadia, from female from Anami, collected in terrarium. 26: egg in earthen capsule, 27: stadium I juvenile in earthen capsule. Diameter of earthen capsules ca. 8 mm. G. Brovad phot.

TABLE 3. *Crurifarcimen vagans*, comparison of adults and immatures. Entries are horizontal diameters in mm, followed by no. of observed specimens (in parentheses). In each cell, the upper line refers to specimens from the E Usambaras, the lower line to the slightly smaller specimens from the W Usambaras.

Stadium	Diameter of ad. males	Diameter of juv. males	Diameter of ad. females	Diameter of juv. females
IX	14.3–16.2 (14) 13.5–14.2 (7)	12.2–13.9 (3) 11.8–11.9 (2)	14.7–16.0 (5) 14.9–15.4 (3)	12.8 (1) 12.2 (1)
X	14.2–15.2 (6) -	- -	14.4–16.1 (7) 14.9–15.3 (2)	12.2 (1) -

ied by Dhaenens & VandenSpiegel (2006), the numbers of podous rings in each stadium are somewhat smaller, corresponding with the generally lower number of podous rings (50–53) in adults.

Sexes are separable from stadium IV inclusive. The observed adults belong to stadia IX and X. Immature specimens were observed belonging to both stadium IX and X. However, several stadium X specimens had the tenth row of ocelli represented only by a single ocellus, sometimes even only on one side of the head. Thus, some specimens assigned to stadium IX may in fact belong to stadium X. Likewise, the hypothetical stadium XI may be "cryptically" represented in the sample. Immatures were consistenly slenderer than adults in the same stadium, see Table 3.

Habitat. Montane forest, most often found in decaying wood.

Distribution. E and W Usambara Mts., from 940 to 1600–1800 m altitude (Fig. 84).

Hyperbolus new genus

Type species: *Hyperbolus apicomplexus* **n. sp.**

Inlcluded species. *Hyperbolus apicomplexus* **n. sp.**, *Hyperbolus morogoroensis* (Kraus, 1958), n. comb..

Etymology. Name formed in analogy with many other names in the order Spirobolida, masculine.

Diagnosis. A genus of East African Pachybolini characterized by

- coxal lobes on male legs 6 and 7
- one pair of ventral macrosetae on male legs from pair 5 onward
- a distal complex of parallel ridges on posterior gonopod
- a free solenomerite on posterior gonopod
- distinct overlapping mesal lobes on anterior gonopod telopodites
- no moveable appendix, no striated membranous lamellae, no mesal process on posterior gonopod
- no long meso-distal process on anterior gonopod coxite
- apical margin of winglike expansions of second female coxae angled
- an apical appendix on oral vulval valve

Hyperbolus apicomplexus n. sp.

Figs 28–37, 84

Pachybolus **n. sp.** 1 (prope *morogoroensis* Kraus, 1958): Enghoff & Enghoff 1976
PACHYBOLIDAE Gen. & sp. nov.: Doggart *et al.* 1999: 75
Pachybolus aff. *morogoroensis*: Wesener *et al.* 2008

HOLOTYPE: ♂ TANZANIA, Tanga Region, East Usambara Mts., Amani 5°06'S 38°38'E, at Sigi River, 500m, under fallen leaves of *Dillenia indica*, 5.ii.1977, H. Enghoff, O. Lomholdt, O. Martin leg. (ZMUC 00101067).

PARATYPES from TANZANIA: 2 ♂♂, 4 ♀♀, 1 subadult ♀, data as holotype (ZMUC 00101068-00101074). – 2 ♂♂, 1 subadult ♂, same data but 30.vii. –9.viii.1977, I.B. &H. Enghoff leg. (ZMUC 00101077-001010078). – 1 ♂, 2 ♀♀ Tanga Region, Muheza district, East Usambara Mts., Kwamgumi Forest Reserve, 4°57'S 38°44'E, 170–

220 m, 15.vii.1995, L. Sørensen leg. (ZMUC 00101079). – 1 ♂, 1 subadult ♀ Tanga region, Muheza district, Handeni Hill Forest Reserve, 5°27'S 38°03'E, 790– 1040 m, i–iii.1993, Frontier Tanzania leg. (VMNH). – 1 ♂, 1 ♀ Tanga Region, Muheza district, East Usambara Mts., Manga Forest Reserve, 5°01'S 38°46'E, 120–360m, viii.1997, Frontier Tanzania leg. (VMNH). – 3 ♂♂ Lindi Region, Rufiji District, Mchungo Forest Reserve, 7°42'S 39°16'E, viii.1990, Frontier Tanzania leg. (VMNH). – 1 ♂ Tanga Region, Muheza District, Tongwe Forest Reserve, Mount Tongwe, 5°18'S 38°44'E, 300–600 m ASL, i–ii.1992, Frontier Tanzani leg. (VMNH).

ADDITIONAL MATERIAL FROM TANZANIA: 3 juveniles Tanga Region, East Usambara Mts., Amani 5°06'S 38°38'E, at Sigi River, 500m, under fallen leaves on rock, 7.ii.1977, H. Enghoff, O. Lomholdt, O. Martin leg. (ZMUC 00101075). – 1 ♀ Tanga Region, East Usambara Mts., Amani 5°06'S 38°38'E, 900 m, 1.ix.1981, M. Stoltze & N. Scharff leg. (ZMUC). – 1 ♀ Usambara Mts., Amani, 1935, L.S. Venables leg. (NMHL). – 2 ♂♂, 1 (subadult) ♀ Rubeho Mts., forest 5 km SW of Madizini, 7°12'S 36°47'E, 900 masl, 10–24.ix.1993, M. Andersen leg. (ZMUC 00101088, 00101089, 00101089). – 1 ♀ Morogoro Region, Morogoro District, Nguru Mts., Divue River gorge, 6°9'S 37°33'E, 1200m, date? D. Emmrich leg. (VMNH).

ADDITIONAL MATERIAL FROM UGANDA: 1 ♂, 1 subadult ♂ Mt. Elgon 1°11'N 34°25'E, 1998, E. Fischer leg. (MND)

Etymology. The specific epithet is a Latin noun referring to the complex posterior gonopod apex.

Diagnosis. A species of *Hyperbolus* in which the anterior gonopod coxite has two mesal processes, the anterior gonopod telopodite has a long, finger-shaped mesal process directed straight mesad, the posterior gonopod solenomerite is smooth, and the apical, multi-ridged structure of the posterior gonopod telopodite is mushroom-like and covered with parallel, strongly sclerotized ridges almost to the tip.

Description. Adults usually with 56 (19 out of 24 entire specimens), rarely with 55 (4 specimens) or 57 (1 specimen) podous rings, no apodous rings. Length 12–14 cm. Width 11.0–2.9 mm (♂♂) / 13.1–14.5 mm (♀♀).

Colour: overall impression blackish brown, slightly lighter in ♀♀. Pro- and mesozona light brown, preserved specimens hence appearing annulated. Head, antennae, collum and legs reddish brown in ♂♂, yellowish brown in ♀♀; telson light brown.

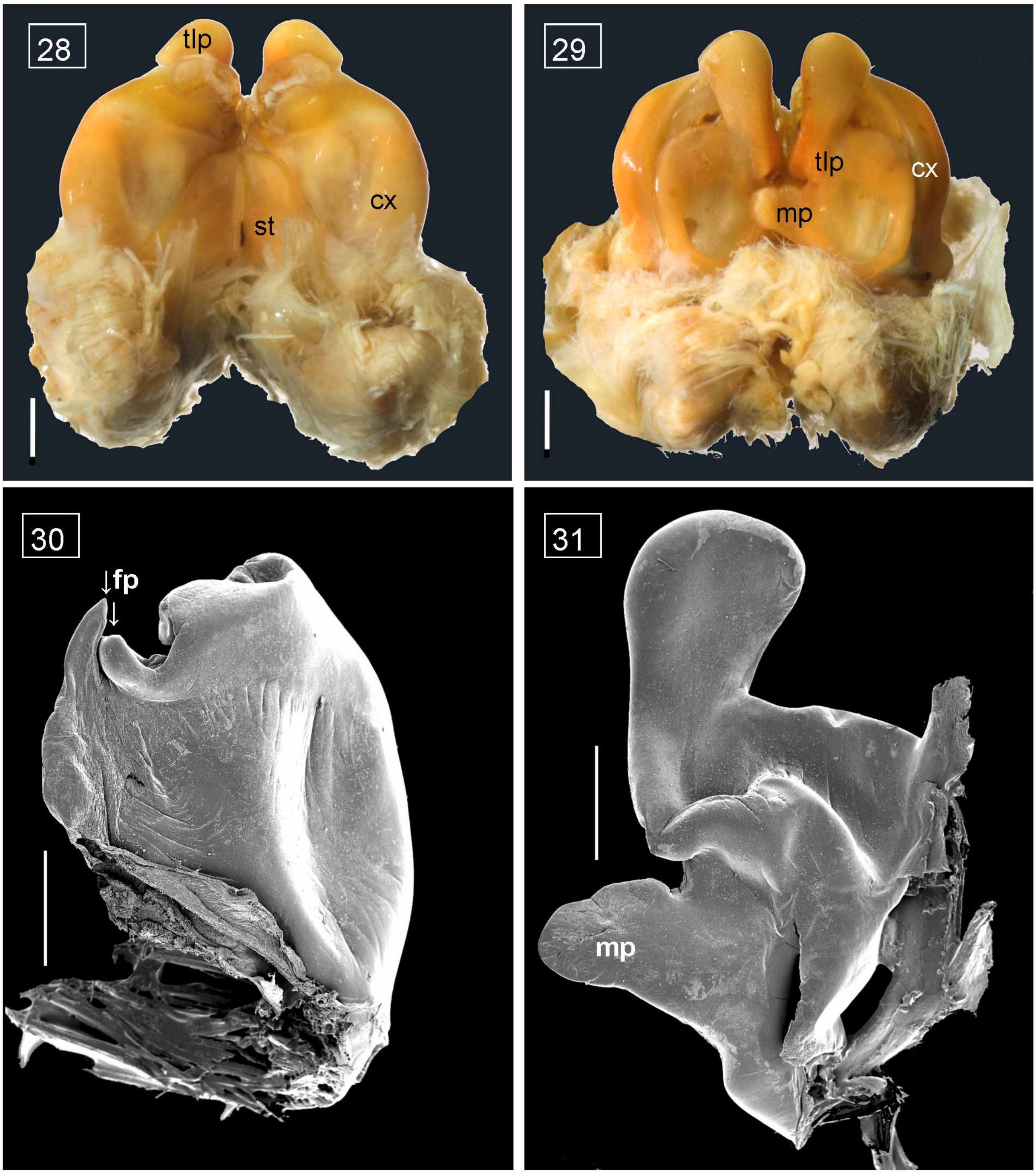
Head capsule smooth, except above eyes, where it is punctate: occipital furrow reaching down between eyes; clypeal furrow at most reaching level of antennal sockets. Clypeal and labral setae missing but some specimens with 1+0 or 1+1 pits which are probably setal sockets; 2+2 partly abraded labral teeth. Eyes small, largest diameter 51–52% (♂♂) / 38–46% (♀) of interocular space in frontal view; adults with 10(–11) RO, 5 horizontal series, 33–39 ocelli per eye. Antennae at most reaching hind margin of collum when stretched back; antennomeres and antennal furrow as in *Crurifarcimen vagans*. Mandibles with 4–6 pectinate lamellae plus a variable number of teeth in a jumbled group basally; a sclerotized smooth-edged ridge between pectinate lamellae and mola, ridge dorsally with a row of small spines; 5 molar ridges; mandibles otherwise as in *Crurifarcimen vagans*. Gnathochilarium as in *Crurifarcimen vagans*, each stipes with 3 distal setae, each lamella lingualis with 4–7 distal setae.

Collum as in *Crurifarcimen vagans*. Body rings as in *Crurifarcimen vagans*, but ozopores no more than 1 diameter in front of meso-metazonal suture. No appreciable difference in surface fine sculpture between male and female. Telson as in *Crurifarcimen vagans*.

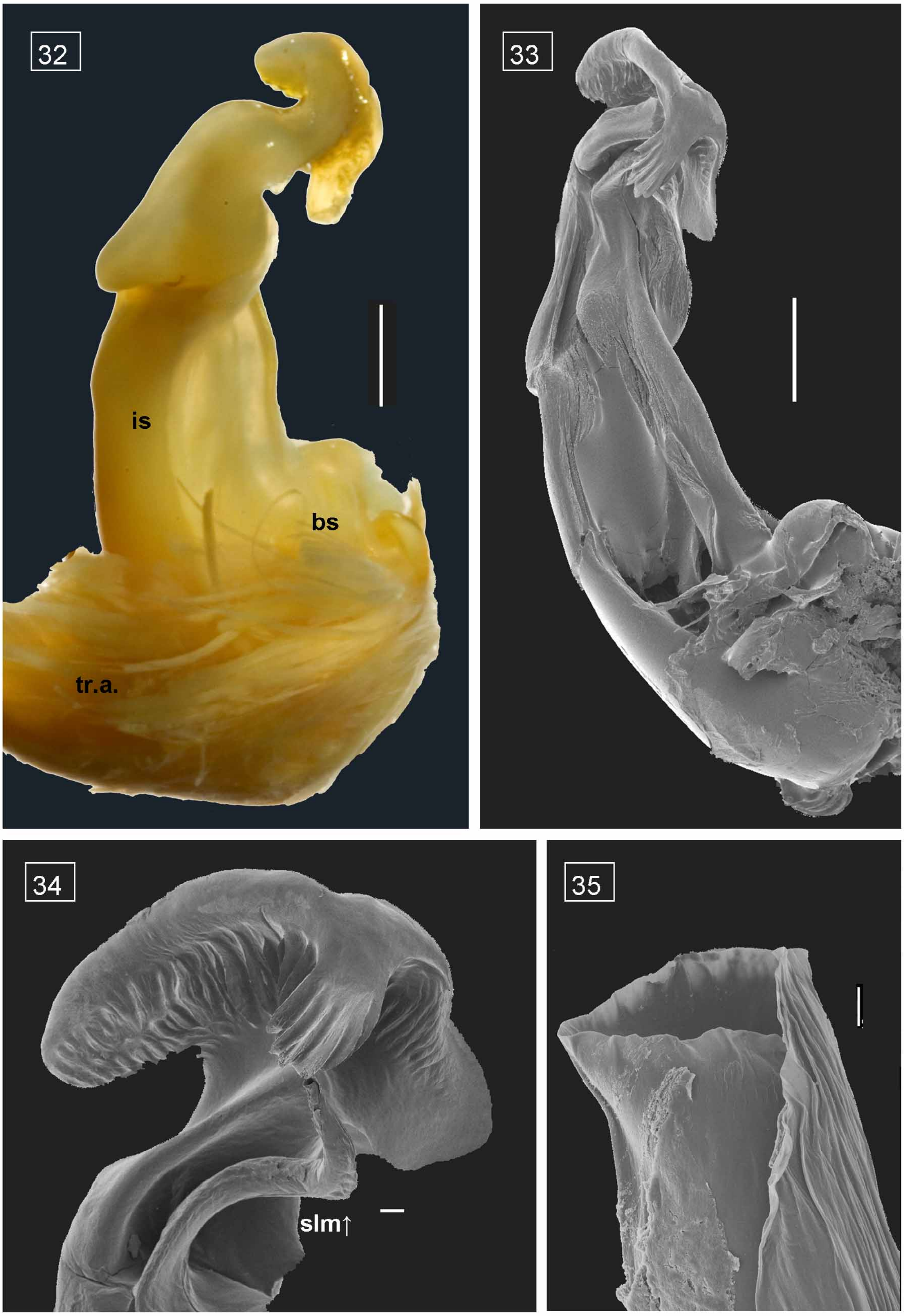
Legs as in *Crurifarcimen vagans*; length of midbody legs 53–61% of body diameter in ♂♂, 40% of body width in ♀♀.

Male sexual characters. Ring VII and leg modifications as in *Crurifarcimen vagans*. Gonopods (Figs 28–35) entirely concealed within ring VII at rest.

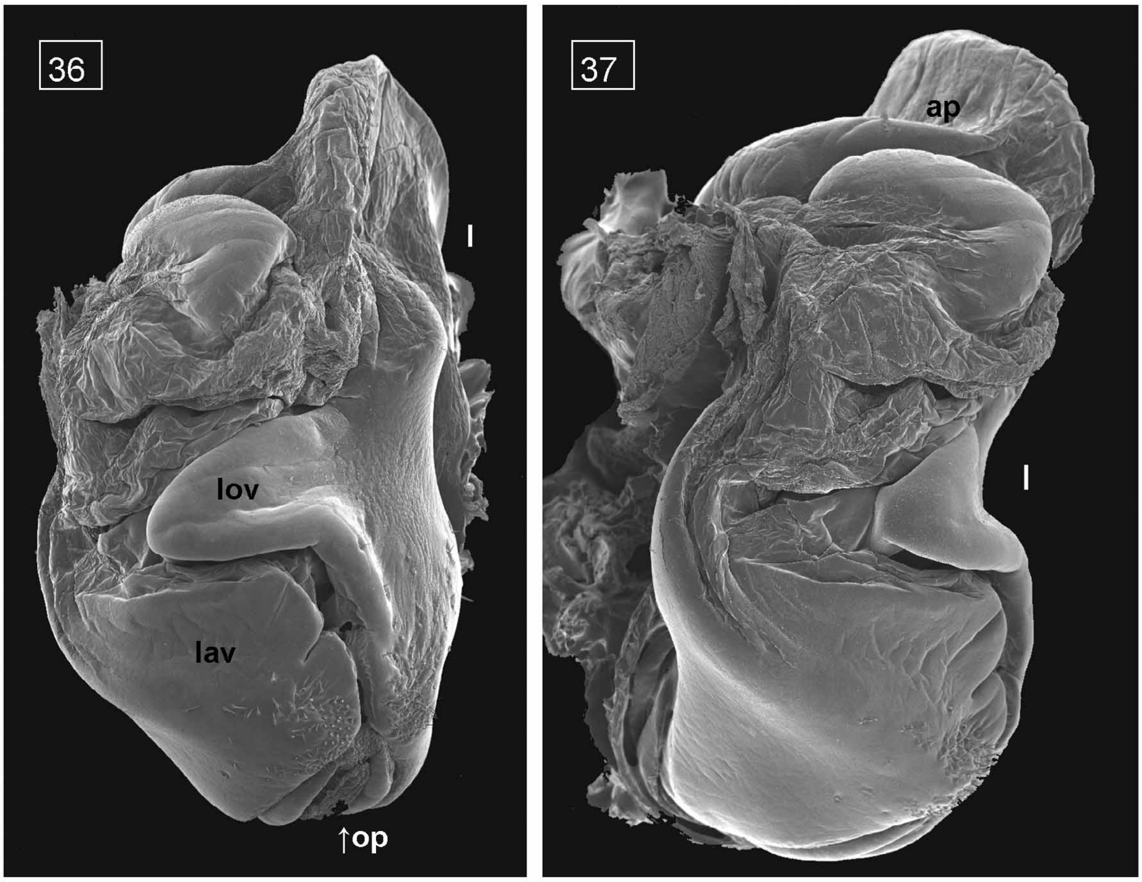
Anterior gonopods (Figs 28–31) concave on oral face: sternum with high, broad, rounded-triangular mesal process reaching just beyond midheight of coxae; right and left halves of process meeting under blunt angle in midline; sternum laterally continuing as narrow band around side of gonopod, reaching well along base of coxa on aboral side, articulating with a narrow sclerite ("bride trachéenne") at base of telopodite (as in *Crurifarcimen vagans*). Coxa in oral view with convex, lateral margin, overreached by tip of telopodite and by the visible tip of posterior gonopod; opposing coxae almost meeting in midline distal to sternum; here with two finger-shaped processes, one projecting distad-mesad, the other projecting straight distad (Fig. 30); apical margin of coxa sloping, with concavity for accommodation of posterior gonopod tip; oral surface of coxa shallowly concave; aboral surface (hidden from view in undissected specimens) broadly swollen mesally, swelling laterally delimited by sharp ridge, apically connecting with distad-mesad process on oral surface; coxae extending to aboral side of gonopod where they appear as crescent-shaped lateral structures. Telopodite (Figs 29, 31) consisting of a broad basal part abruptly set off against much narrower, clubshaped apical part; basal part of mesal margin with very large, rounded, irregularly lobed, somewhat thumb-like process overlapping with opposite lobe under strong asymmetry (left lobe visible from aboral side); right lobe same shape and size as left.



FIGURES 28–31. *Hyperbolus apicomplexus*, paratype, gonopods. 28: gonopod block, anterior view, G. Brovad phot., 29: do., posterior view, G. Brovad phot., 30: right anterior gonopod coxa, anterior view, SEM, 31: right anterior gonopod telopodite, anterior view (i.e., from inside of anterior gonopod cavity), SEM. Scales 1 mm. cx: coxa, fp: finger-shaped processes, mp: mesal, thumb-like process of telopodite, st: sternum, tlp: telopodite.



FIGURES 32–35. *Hyperbolus apicomplexus*, paratype. 32: right posterior gonopod, aboral view, G. Brovad phot., 33: left posterior gonopod, oral view, SEM, 34: do., detail, showing mushroom-shaped terminal segment and solenomerite, SEM, 35: left posterior gonopod, oral view, tip of solenomerite, SEM. Scales 1 cm (32–33), 0.1 mm (34), 0.01 mm (35). bs: basal sclerite. is: intermediate segment, slm: solenomerite, tr.a.: tracheal apodeme (hidden in muscle).



FIGURES 36–37. *Hyperbolus apicomplexus*, paratype, right vulva, SEM. 36: posterio-lateral view, 37: lateral view. Scales 0.1 mm. ap: apical appendix, lav: subrectangular lobe of aboral valve, lov: subtriangular lobe of oral valve, op: operculum. SEM.

Posterior gonopods (Figs 32–35) with tips partly visible in situ (not obvious in Fig. 28, however), connected by median sternal remnant similar to that seen in *Crurifarcimen vagans*. Orientation and divisions of gonopods following same scheme as in *Crurifarcimen vagans*. Each posterior gonopod consisting of:

1. a long, slender, almost straight tracheal apodeme, flattened towards its end
2. a basal, aboral sclerite which articulates with the tracheal apodeme, is roughly pentagonal in outline and has a distinct notch on its distal margin, next to articulation with median sternal sclerite
3. a slender intermediate segment (much longer in relation to terminal segment than in *C. vagans*), delimited vis-a-vis basal sclerite across lateral half-width by shallow groove (no proper suture), across mesal half the limit appears as a limit between the sclerotized basal sclerite and a large membraneous area on the intermediate segment. Intermediate segment broadly sclerotized laterally, membranous orally and aborally, and again narrowly sclerotized along mesal margin; limit against terminal segment a very distinct, deep groove laterally.
4. a complicated terminal segment roughly with the profile of a twisted mushroom, i.e. with a basal "bulb", a "stalk" and a distal "hat" with basal and distal, rounded lobes; a small triangular tooth at base of "stalk"; "hat" on oral side with a field of densely set, strongly sclerotized ridges; towards both ends this field detaches itself from the surface, producing strongly striate lobes. Efferent groove running along mesal margin of intermediate segment, along narrow sclerotized strip, at base of mushroom stalk of terminal segment running onto slender, sigmoid solenomerite; solenomerite mostly without denticles (denticles present in ♂ from Rubeho Mts.), ending near serrate edge of basal striate lobe.

Female sexual characters. Distal margin of lateral coxosternal extensions projecting as right-angled lobe. Vulva (Figs 36–37) less elongated than in *Crurifarcimen vagans*, valves highly irregular in shape, with large interlocking lobes along free margins, including a large, subrectangular lobe on aboral valve just distal to operculum, distal margin of this lobe fitting against large, subtriangular lobe of oral valve; oral valve much longer than aboral valve, with large, rounded-subpyramidal apical appendix *in situ* lying close to lateral coxosternal extension. Crest not protruding.

Postembryonic development. Only five immature individuals were seen. One 6RO specimen has 43 podous and 6 apodous rings, i.e., one podous ring more than the studied 6RO specimens of *C. vagans*. Two 8RO specimens with 53 podous and 3 apodous rings agree with stadium 8RO in *Crurifarcimen vagans*. Two subadults, one ♂ and one ♀, had 10RO, 56 podous and no apodous rings.

All mature specimens have 10RO, except one questionable 11RO (this is the single known specimen with 57 podous rings). The existence of 10RO subadults, cf. above, however requires that some mature specimens are at least 11RO. In a few of the 10RO specimens, the tenth row consists on only 1–2 ocelli, cf. discussion under *Crurifarcimen vagans*.

Habitat. Montane forest, collected under leaf litter.

Distribution. Quite widespread in NE Tanzania (Fig. 84). Most finds are from the East Usambara Mountains, but *H. apicomplexus* has also been collected on Mt. Tongwe, a southern outlier of the East Usambara mountains, on Handeni Hill slightly more to the SW, in the Rubeho and Nguru mountains. Surprisingly, it has also been found in coastal forest at sea level in Mchungo Forest Reserve more than 250 km S and on Mt. Elgon in Uganda some 750 km NW of the Usambaras. Altogether, the known distribution area spans more than 1000 km in a SE-NW direction. Most records are from 500 masl or below, but the one from Handeni Hill is from 790–1040 masl, the one from Rubeho Mts is from 900 masl, and the one from Nguru Mts from 1200 masl.

Hyperbolus morogoroensis (Kraus, 1958), n. comb.

Figs 38–43, 84

Pachybolus morogoroensis Kraus, 1958
'*Pachybolous' morogoroensis*: Wesener *et al.* 2008

HOLOTYPE ♂, TANZANIA, Morogoro District, Uluguru Mountains, between Kimboza and Kibungu, 7°02'S 37°44'E, 500 m, in rain forest under leaf litter and in rotten wood, 16.vii.1952, H. Knipper leg. (UMB). – PARATYPE 1 ♀, same data (SNF).

NEW MATERIAL from TANZANIA, Morogoro region, Morogoro district, N. Doggart, Uluguru Mountains Biodiversity Conservation Project, leg.: 1 ♂, 1 ♀, 1 juvenile ♀ Kasanga Forest Reserve, 7°10'S 37°45'E, leaf litter and rotting logs, 27.vii. –2.viii.2000, (ZMUC 00101080). – 2 ♂♂, 1 ♀ Mkungwe Forest Reserve, 6°52'30''S 37°53'30''E, lowland submontane forest, 400–1000 masl, viii.2000, (ZMUC 00101082). – 1 ♂, 1 ♀ Ruvu Forest Reserve, 7°00'S 37°51'E, 200 masl, 2000 (ZMUC 00101083). - 1 ♂, 1 ♀ Ngambaula L.A. Forest Reserve, 6°59'S 37°45'E, 250 masl, 2000 (ZMUC 00101084). – 1 ♀ Chamanyani Forest Reserve, Mvuha, lowland forest, 7°10'30''S 37°49'E, 140–400 masl, ix. 2000 (ZMUC 00101086).

MORE NEW MATERIAL from TANZANIA: 2 ♂♂, Uluguru Mountains, Vituri, 7°10'S 37°45'E, 30.x.1926, A. Loveridge leg. (MCZ no. 67914). – 1 ♀ Uluguru Mountains, Kikosi near Bagilo. 6°55'S 37°40'E, 9.ix.1926, A. Loveridge leg. (MCZ no. 43311). – 1 ♀ Morogoro Region, Uluguru South Forest Reserve, forest above Ukwama Village, 7°11'S 36°42'E, 1500–1600 masl, x.1993, L. Sørensen leg. (ZMUC 00101085). – 1 ♀ Uluguru Mountains, Kimboza Forest, 7°02'S 36°47'E, 250 masl, 18.vii.1981, M. Stoltze & N. Scharff leg. (ZMUC 00101087).

Diagnosis. A species of *Hyperbolus* in which the anterior gonopod coxite has a single mesal process, the anterior gonopod telopodite has an approximately semicircular mesal process directed straight mesad, and the apical lobe of the multiridged 'mushroom-like' structure of the posterior gonopod telopodite drawn out in to a smooth hook.

Description. Adults mostly with 56 (9 out of 15 entire specimens), sometimes with 55 (3 specimens) or 57 (3 specimens) podous rings, no apodous rings. Length 12–13 cm. Width: 11.3–12.2 mm (♂♂) / 11.9–13.9 mm (♀♀). Head, including eyes, antennae, mandibles, and gnathochilarium as in *H. apicomplexus*. Each gnathochilarial stipes with 3 apical setae; each lamella lingualis with 4 apical setae.

Collum, body rings, telson and legs as in *H. apicomplexus*.

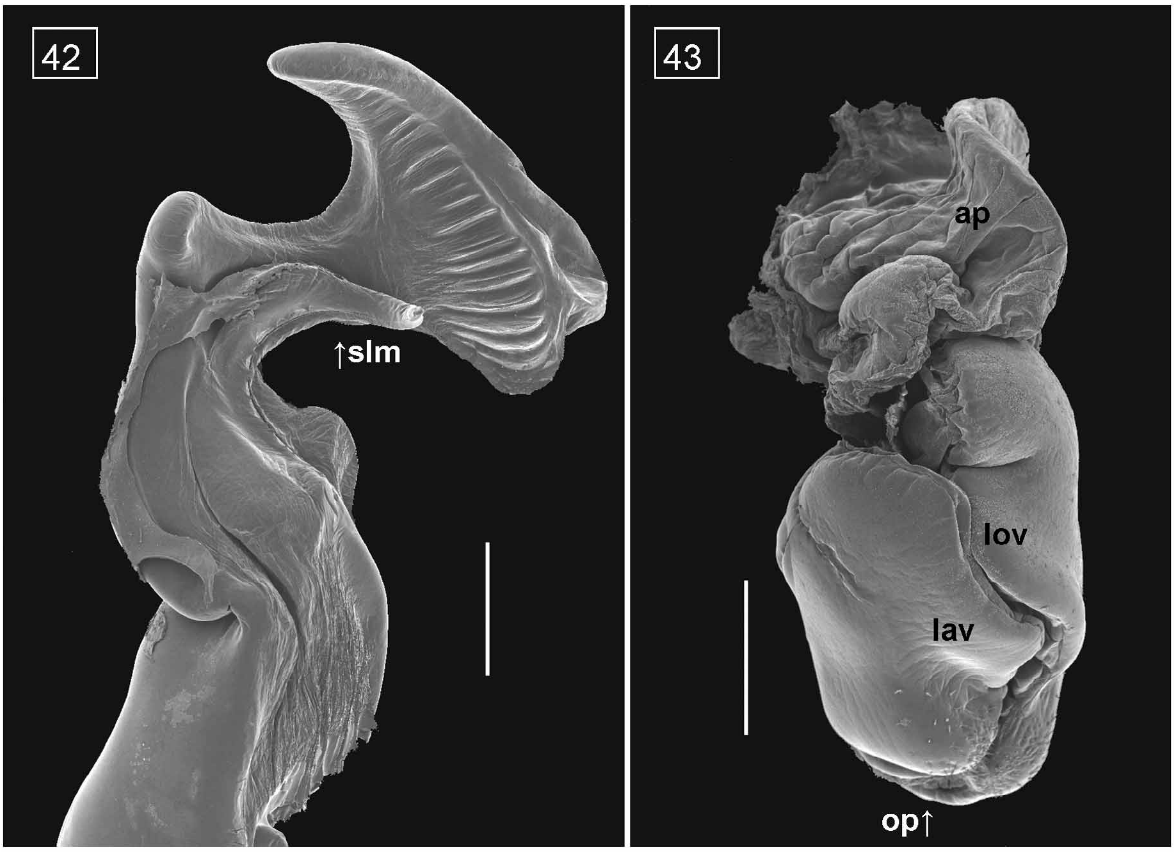
Male sexual characters. Ring VII and leg modifications as in *Crurifarcimen vagans*.

Gonopods (Figs 38–42) as in *H. apicomplexus*, with the following exceptions:

- Anterior gonopod coxa (Figs 38, 40) with apical margin not sloping, almost straight, and with one rounded-triangular process at mesal margin just distal to sternum (*versus* two finger-shaped processes in *H. apicomplexus*)
- Overlapping lobes of anterior gonopod telopodites much smaller, sub-semicircular (Fig. 39)

- Terminal segment of posterior gonopods (Fig. 42) less mushroom-like; distal lobe of “hat” drawn out into slender hook; oral side of “hat” with parallel, strongly sclerotized ridges; field of ridges detached from surface basally and hiding basal lobe of “hat” from view; ridges diminishing in size and eventually disappearing towards tip of distal lobe.

FIGURES 38–41. 38: *Hyperbolus morogoroensis*, male from Ngambaula L.A. Forest Reserve, gonopod block, anterior view, G. Brovad phot., 39: do., posterior view, G. Brovad phot.s, 40: do., right anterior gonopod coxa, anterior view, SEM, 41: right anterior gonopod telopodite, anterior view (i.e., from inside of anterior gonopod cavity), SEM. Scales 1 cm. cx: coxa, fp: finger-shaped process, mp: mesal, thumb-like process of telopodite, st: sternum, tlp: telopodite.



FIGURES 42–43. *Hyperbolus morogoroensis.* 42: male from Mkungwe Forest Reserve, tip of left posterior gonopod, oral view. 43: female from Mkungwe Forest Reserve, left vulva, posterior-lateral view. Scales 1 mm. ap: apical appendix, lav: subrectangular lobe of aboral valve, lov: subtriangular lobe of oral valve, op: operculum, slm: solenomerite.

In some specimens, the posterior gonopod solonomerite has a row of small denticles.

Female sexual characters. Distal margin of lateral coxosternal extensions projecting as right-angled lobe. Vulva (Fig.43) similar to those of *H. apicomplexus* but differing in having the subrectangular lobe on the aboral valve and the subtriangular lobe on the oral valve much less developed.

Habitat. Lowland forest and lowland submontane forest, found in litter and rotten logs.

Distribution. Only known from the Uluguru Mountains (Fig. 84) where it occurs from 250 (possibly 140) to 1500–1600 masl.

Parabolus new genus

Type species: *Trigoniulus dimorphus* Carl, 1909.

Included species. *Parabolus dimorphus* (Carl, 1909), n. comb., *Parabolus calceus* **n. sp.**

Etymology. Name formed in analogy with many other names in the order Spirobolida, masculine.

Diagnosis. A genus of East African Pachybolini characterized by

- coxal lobes on male legs 6 and 7
- one pair of ventral macrosetae on male legs from pair 5 onward
- a very long meso-distal process on anterior gonopod coxite
- a small laterobasal stout spine on terminal gonopod segment
- no moveable appendix, no striated membranous lamellae, no mesal process, no free solenomerite, no distal complex of parallel ridges on posterior gonopod
- no distinct overlapping lobes on anterior gonopod telopodites
- apical margin of winglike expansions of second female coxae angled
- an apical appendix on oral vulval valve

Parabolus dimorphus **(Carl, 1909), n.comb.**
(Figs 44–53, 84)

Trigoniulus dimorphus Carl, 1909
Pachybolus dimorphus: Hoffman (1965)

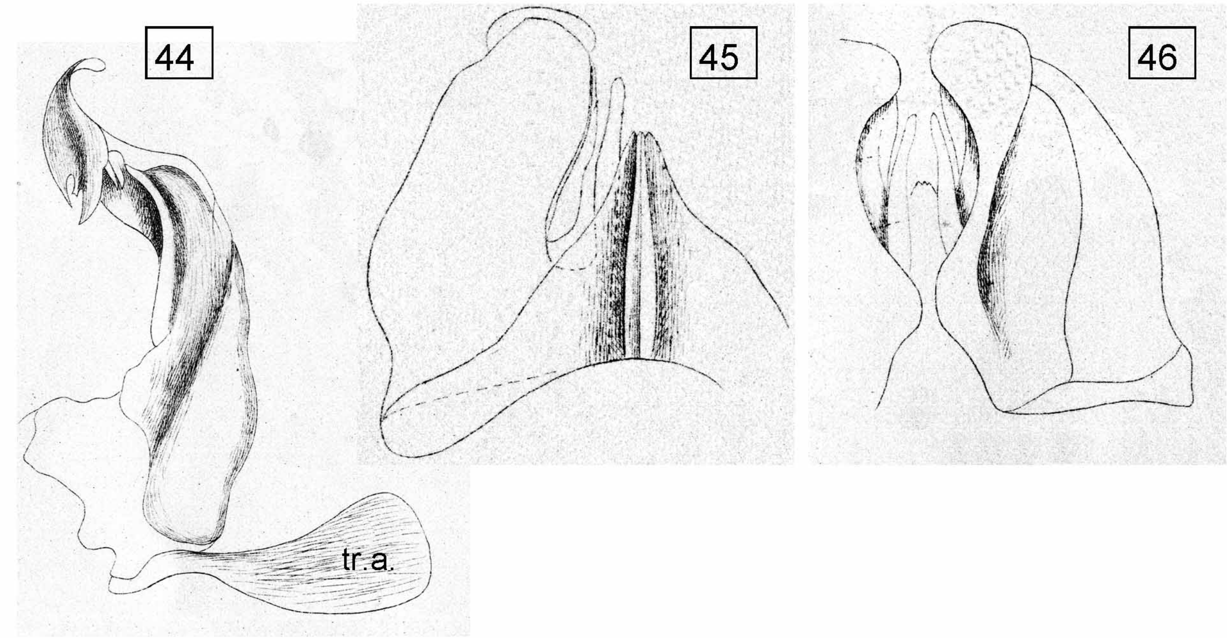
SYNTYPES: 2 ♂♂, 1 ♀ TANZANIA, Dar-es-Salaam, 6°50'S 39°20'E, J. Carl leg. (MHNG).

ADDITIONAL MATERIAL: 1 ♀, 1 subadult ♀ TANZANIA, Dar-es-Salaam (ZMUH). – 1 ♂ "Deutsch Ost-Afrika" 1903, F. Eichelbaum leg., R.L. Hoffman det., 1964 (ZMUH). – 1 ♂ "Ost-Afrika", plantations and roads in vicinity of Dar-es-Salaam, 1929, H. Brinkmann leg, R.L. Hoffman det., 1964 (ZMUH).

Notes to the material. The type series (MHNG) contains two ♂♂ and one ♀. Since they were all in the same container, and the gonopods of both ♂♂ had been dissected, it was not possible to associate the two sets of gonopods (one of which lacks one of the posterior gonopods) with the two male bodies. The latter could be reconstructed based on Carl's information about body ring number ("57 Segmente"). Each of the three individuals has now been placed in a separate container, and the two sets of gonopods in two further, separate containers. The two ♂♂ are obviously conspecific, and given the uncertainty about which gonopods belong to which body, I have not selected a lectotype. The female and subadult female from Dar-es-Salaam (ZMUH) are labelled as paratypes and listed as "Paratypoid" by Weidner (1960), but it is uncertain if they belong to the material studied by Carl (1909) who did not indicate how many specimens he had studied; the hand-writing on the label is different from that on the type-vial label.

Diagnosis. A species of *Parabolus* in which the anterior gonopod coxa has no distinct distolateral shoulder and the terminal segment of the posterior gonopod has a coarsely serrated mesobasal lobe and a slender, curved, blunt apical process

Descriptive notes. Carl's original description is quite good. In particular, his illustrations are fine and are reproduced here as Figs 44–46.



FIGURES 44–46. *Parabolus dimorphus*, original drawings from Carl (1909), original labelling removed. 44: right posterior gonopod, anterior view, 45: left anterior gonopod + anterior gonopod sternum, anterior view, 46: anterior gonopods, posterior view. tr.a.: tracheal apodeme.

As *Crurifarcimen vagans* except:

- Adults with 56 podous rings, no apodous rings. Length ca. 12 cm. Width: 11.9–12.4 mm (♂♂) / 11.9–12.2 mm (♀). Ten rows of ocelli in 5–6 horizontal series.
- 2+2 labral teeth, one ♂ with ca. 10+10 labral setae in bight above labral teeth, other specimens without setae.

- Mandibles with 4 pectinate lamellae plus a variable number of teeth in a jumbled group basally; ventral margin of gnathal lobe pectinate area not concave; a sclerotized smooth-edged ridge between pectinate lamellae and mola, ridge dorsally with a row of small spines; 5 molar ridges.
- Gnathohilarium with 3+3 distal stipital and 4–5+4–5 distal lingual lamellar setae in transverse row.
- Collum smooth, no striae, with more or less marked marginal furrow at anterior margin.
- Body rings: tergo-pleural suture visible on pro-, meso- and metazonite.
- Terga smooth, except for fine oblique striae ventrally on mesozona and fine, dense longitudinal striae on metazona.
- Ozopores 1 diameter in front of suture.
- Telson as in *Crurifarcimen v.* but dorsal profile straight.
- Legs. Length 63% of body width.

Male sexual characters. Leg modifications as in *C. vagans*. The coxal lobes on legs 6–7 were not mentioned by Carl (1909). In the two males of the type series, these legs are badly damaged, but in the males from ZMUH, the lobes are evident.

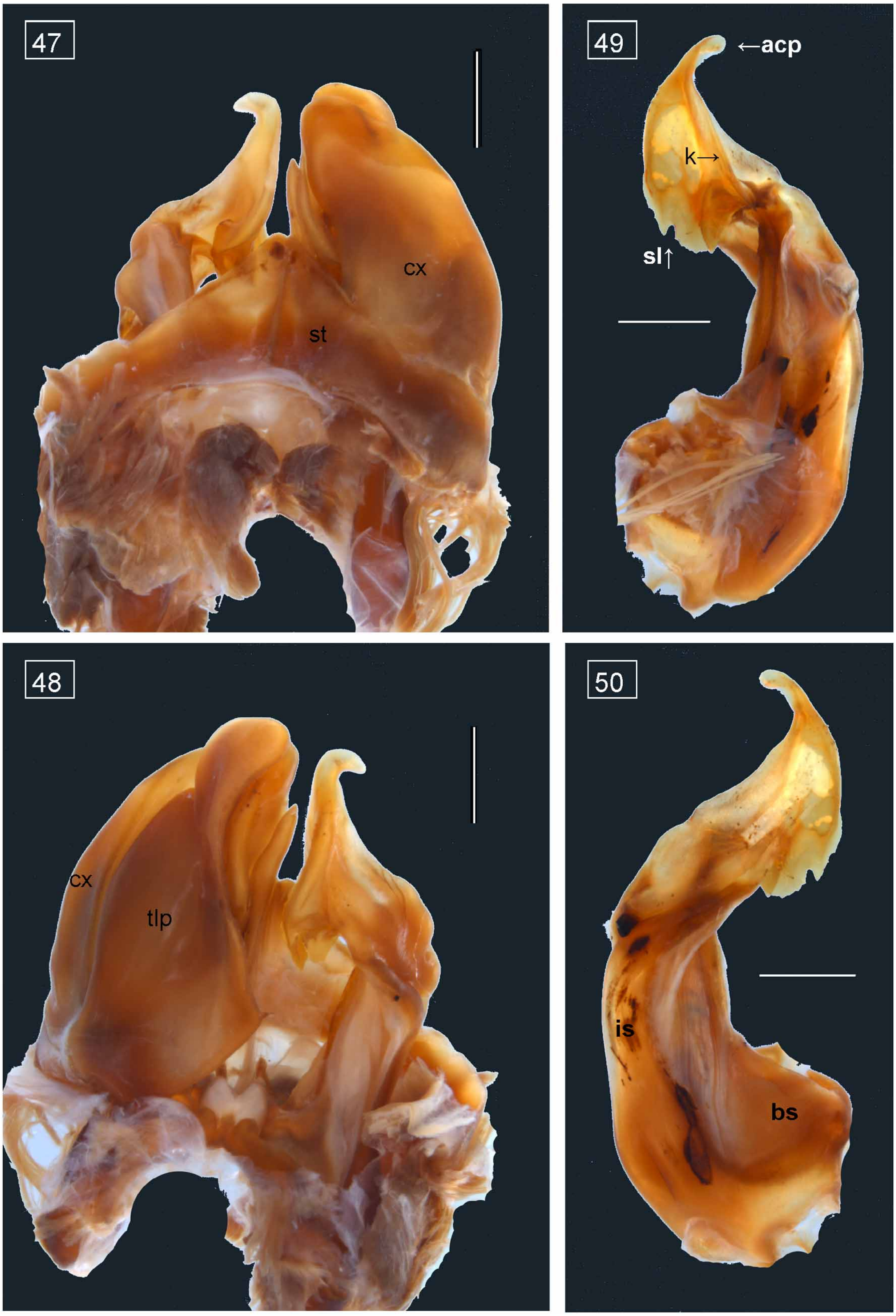
Anterior gonopods (Figs 45–48): sternum concave on oral face, with high, broad, triangular mesal process reaching ca. 2/3 the height of the coxae; two halves of process meeting under blunt angle in midline, forming a midline ridge; tip of process with small median indentation; sternum laterally continuing as narrow band around side of gonopod, reaching well along base of coxa on aboral side, articulating with a narrow sclerite at base of telopodite (“ bride-trachéenne” of Demange 1967). Coxa in oral view kidney- to sausage-shaped, lateral margins evenly convex, mesally with very big slender process directed distad parallel to mesal margin of main part of coxa; internal surface of coxa (hidden from view in undissected specimens) with ridge at base of mesal process. Coxa extending to aboral side of gonopod where it appears as a narrow lateral band. Telopodite (Fig 48) extending slightly beyond coxal tip, with a distolateral incision and a shallow impression running from incision to base of low mesal process which very slightly overlaps that of opposite telopodite; tip of telopodite distally broadly rounded; oral surface of telopodite (hidden from view in undissected specimens) with strong, oblique ridge delimiting a narrow furrow.

Posterior gonopods (Figs 44, 49–50) *in situ* supported by ridge at base of mesal coxal process and oblique ridge on oral surface of telopodite of anterior gonopod; visible in oral and aboral view as narrow bands along mesal margin of coxa and telopodite, respectively, connected by median sternal remnant consisting of mesal membranous region flanked by a pair of rounded-triangular sclerites. Each posterior gonopod clearly divisible into four parts:

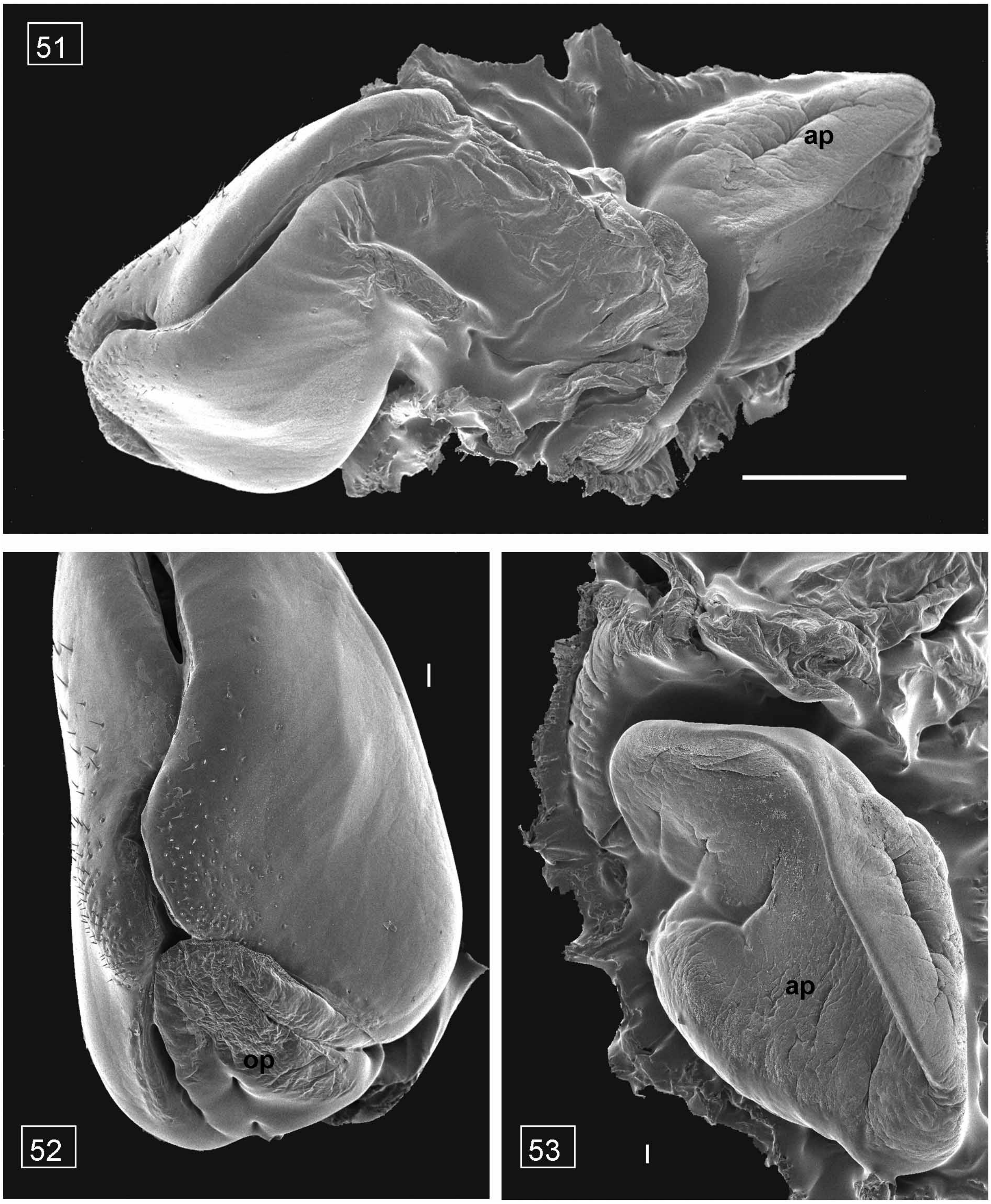
1. a long, slender, almost straight *tracheal apodeme*, flattened towards its end,
2. a *basal sclerite* which articulates with the tracheal apodeme, is roughly pentagonal in outline and has a distinct notch on its distal margin, next to articulation with median sternal sclerite,
3. an *intermediate segment* originating from lateral half of basal sclerite, parallel-sided, with extensive membranous areas, especially on mesal part of aboral surface,
4. a *terminal segment* separated from intermediate segment by distinct impression across lateral and aboral surface. Overall shape of terminal segment triangular (or like the profile of a hadrosaur head); with a small laterobasal, stout spine at articulation with intermediate segment, a coarsely serrate mesobasal lobe resting (*in situ*) on convex ridge at base of mesal coxal process and a slender, curved, apically clublike rounded process; aboral surface smooth, oral surface with a longitudinal keel running from base to tip. Efferent groove running along mesal edge of intermediate segment, then making an abrupt turn and terminating behind longitudinal keel of terminal segment.

Female sexual characters. Distal margin of lateral coxosternal extensions projecting as right-angled lobe. Vulva (Figs 51–53) less elongate than in *Crurifarcimen vagans*, valves quite regularly sub-ovoid in shape, with free margins only very shallowly sinuous, oral valve much longer than aboral valve, with large, rounded-subpyramidal apical appendix (Fig. 53) *in situ* lying close to lateral coxosternal extension. Crest not protruding.

Distribution. Only known from Dar-es-Salaam, Tanzania (Fig. 84).



FIGURES 47–50. *Parabolus dimorphus*. 47: male from the vicinity of Dar-es-Salaam, Brinkmann leg., gonopods (without left anterior gonopod coxa and telopodite), anterior view, 48: do., posterior view, 49: male from ”Deutsch Ost-Afrika”, Eichelbaum leg., right posterior gonopod, anterior view, 50: do., posterior view. Scales 2 cm. acp: apical clublike process, bs: basal sclerite, cx: coxa, is: intermedite segment, k: keel, sl: serrate lobe, st: sternum, tlp: telopodite.



FIGURES 51–53. *Parabolus dimorphus*, female from the vicinity of Dar-es-Salaam, Brinkmann leg., right vulva. 51: posterio-lateral view, 52: basis of vulva with operculum; 53, apical appendix. Scales: 1 mm (51), 0.1 mm (52–53). ap: apical appendix, op: operculum. SEM.

***Parabolus calceus* n. sp.**

Figs 54–57, 84

HOLOTYPE ♂ KENYA, Gede, 3°28'S, 39°18E, 29.iv.1981, CIE A13123 (NHML). – PARATYPES: 2 ♂♂, 3 ♀♀, strongly fragmented, KENYA, Changamwe 4 miles W of Mombasa, 4°01'30''S, 39°37'45''E, 21–30.iii.(?) 1909, E.A. Mearns leg. (USNM, ZMUC).

Etymology. The specific epithet is a Latin noun in apposition meaning "shoe" and refers to the tip of the posterior gonopod which somewhat resembles a (rather distorted) shoe.

Diagnosis. A species of *Parabolus* in which the anterior gonopod coxa has a distinct distolateral shoulder, and the terminal segment of the posterior gonopod has a faintly serrate mesobasal ridge, a strongly concave distolateral profile and no slender apical process.

Descriptive notes (mainly based on holotype): As *Crurifarcimen vagans* except as noted:

57 podous rings, no apodous rings. L 14 cm, B 13.4 mm. 10–11 rows of ocelli in six horizontal series, 41–44 ocelli per eye. 2+2 labral teeth, labral setae not visible. Lamellae linguales each with 5–6 distal setae. Collum smooth, no striae, with marginal furrow at anterior margin. Body rings: tergo-pleural suture visible on pro-, meso- and metazonite. Terga smooth, except for fine oblique striae ventrally on mesozona and fine, dense longitudinal striae on metazona. Ozopores 1 diameter in front of suture. Legs: length 51% of body width (markedly shorter than in *P. dimorphus*). Telson as in *Crurifarcimen v.* but dorsal profile straight.

Male sexual characters. Anterior gonopods (Figs 54–55) as in *P. dimorphus*, except that the coxa has a marked distolateral 'shoulder', is apically truncate and lacks the internal ridge at the base of the mesal process
Posterior gonopods (Figs 56–57) as in *P. dimorphus*, except for shape of terminal segment which has a low, faintly serrate mesobasal ridge (instead of the coarsely serrate lobe of *P. dimorphus*), a strongly concave distolateral profile, concavity basally delimited by strong triangular tooth; distolateral surface deeply hollowed, forming a long, curved trough; oral wall of trough with a low subtriangular lobe.

Female sexual characters as in *P. dimorphus.*

Distribution. Only known from two sites in SE Kenya. (Fig. 84) This is the only species of Pachybolini known from Kenya, excepting the widespread *Epibolus pulchripes.*

Genus *Pachybolus* Cook, 1897

Type species: *Pachybolus tectus* Cook, 1897.

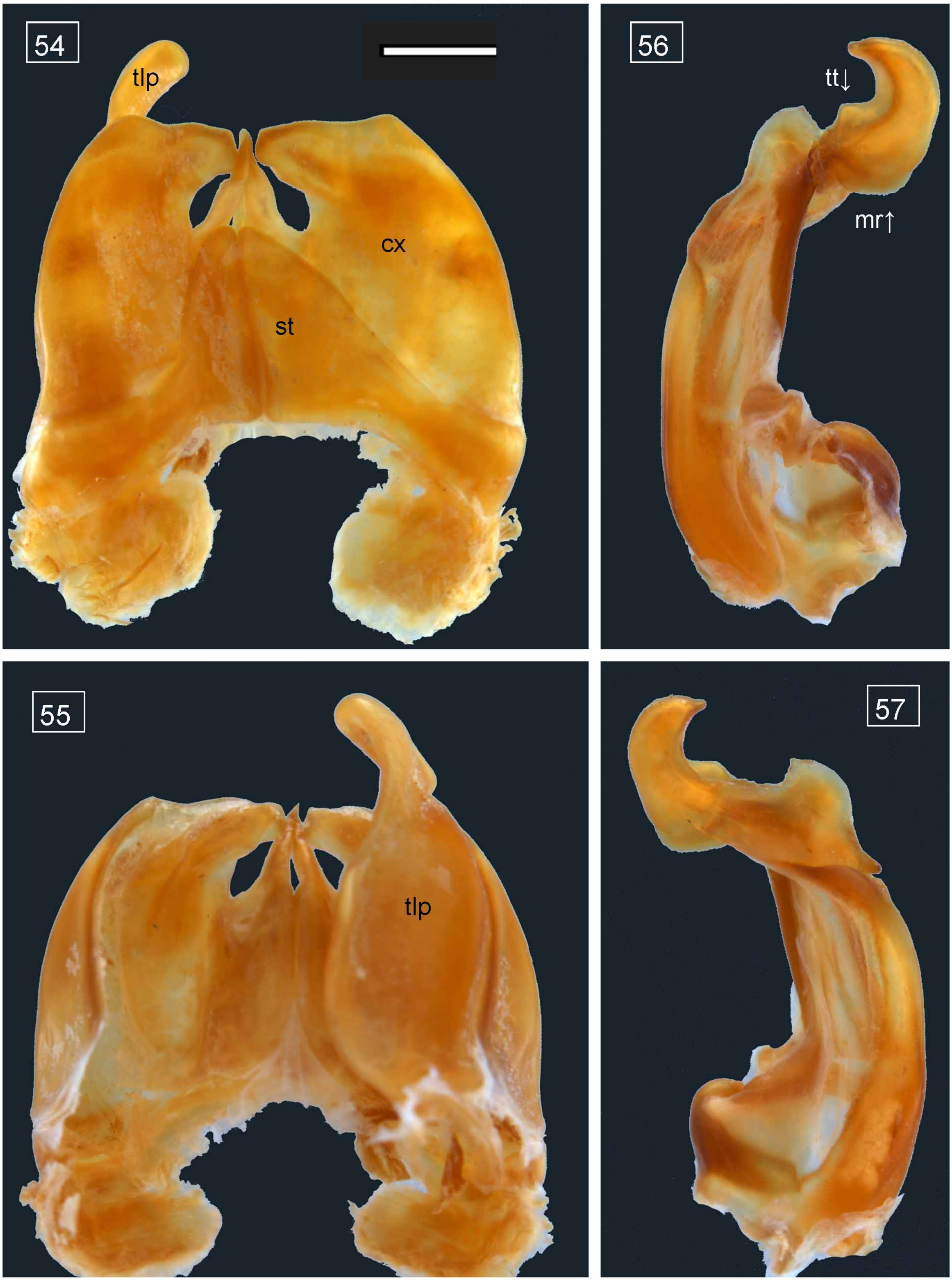
Included species. *Pachybolus tectus* Cook, 1897.
Diagnosis. A genus of East African Pachybolini characterized by

- no moveable appendix, no striated membranous lamellae, no mesal process, no free solenomerite, no distal complex of parallel ridges on posterior gonopod
- no long meso-distal process on anterior gonopod coxite
- no distinct overlapping lobes on anterior gonopod telopodites

(chartacters of vulvae and male legs unknown)

Note. A number of species in addition to the type species have been assigned to *Pachybolus*. Most of these are now classified in the West African genus *Pelmatojulus* de Saussure, 1860 (see Wesener *et al.*, 2008). In the present paper, I transfer *Trigoniulus dimorphus* Carl, 1909—reallocated to *Pachybolus* by Hoffman (1965)—to the new genus *Parabolus*, and *Pachybolus morogoroensis* Kraus, 1958, to the new genus *Hyperbolus*. *Pachybolus* is thereby rendered monotypic.

Pachybolus in this restricted sense remains known only from the original description of its type species. The diagnostic number of setae on the lamellae linguales is unknown, and *Pachybolus* is assigned to the group of genera here referred to as East African Pachybolini on purely geographical grounds.



FIGURES 54–57. *Parabolus calceus*, paratypes. 54: anterior gonopods, without right telopodite, anterior view, 55: do., posterior view, 56: left posterior gonopod, anterior view, 57: do, posterior view. Scale for all: 2 cm. cx: coxa, mr: mesobasal ridge, st: sternum, tlp: telopodite, tt: triangular tooth.

Pachybolus tectus Cook, 1897

Figs 58–65, 84

Material examined: none, and none is known to exist. Cook (1899) gave the type repository as "Hamburg Museum" from where the specimen, however, is missing (Weidner 1960). All we have therefore is Cook's original description and illustrations (reproduced here as Figs 58–65). According to Cook, the *P. tectus* male is ca. 150 mm long, ca. 15 mm in diameter and has 55 'segments' (which presumably means a body ring formula 54+0+T). The anterior gonopods (Figs 61–63) have a tall sternal projection, the coxites seem to be smoothly rounded, the telopodites overlap but have no distinct mesal process; distally they are narrowed and form a rounded process somewhat similar to that seen in *Hyperbolus* species. The posterior gonopod (Figs 64–65) seems to have a basal laminate process and is otherwise quite slender, without distinct processes, lamellae etc. The female is unknown.

Distribution. Only known from Zanzibar (Fig. 84)

Genus *Hadrobolus* Cook, 1897

Type species: *Spirobolus crassicollis* Peters, 1855

Included species. *Hadrobolus crassicollis* (Peters, 1855)
Diagnosis. A genus of East African Pachybolini characterized by

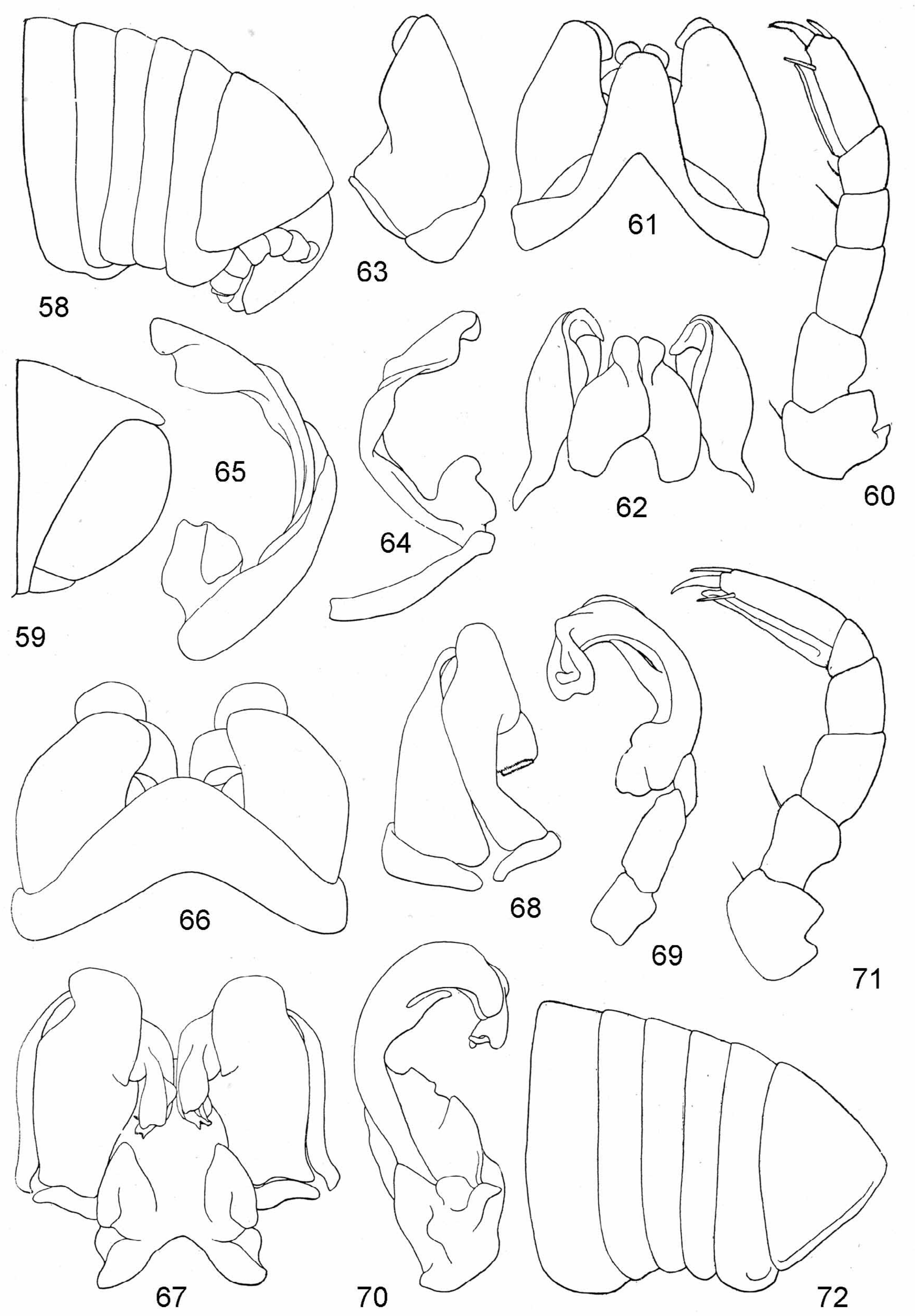
- no coxal lobes on male legs 6 and 7
- one pair of ventral macrosetae on male legs from pair 5 onward
- a distinct mesal process ca. at midlength of posterior gonopod
- no striated membranous lamellae at tip of posterior gonopod
- no mesal process, no free solenomerite, no distal complex of parallel ridges on posterior gonopod
- no long meso-distal process on anterior gonopod coxite
- no overlapping lobes on anterior gonopod telopodites

(female characters unknown)

Cook (1899) listed a number of characters separating *Hadrobolus* from his "*Pachybolus*" (which also included species now classified in *Pelmatojulus*). In addition to the characteristic mesal process of the posterior gonopod, these are:

- sternum of anterior gonopods very broad and short, being scarcely produced in the middle
- telopodites of anterior gonopods widely separated ("in *Pachybolus* they are crowded mesad by the flagella [= posterior gonopods]...")
- the last podomere (tarsus) of male legs greatly elongated in comparison with the penultimate podomere (tibia) (Fig. 71)
- the ventral pad of the male tarsus oblong and extending the whole length of the podomere, the subterminal setae being farther apart
- the ventral pad "fleshy throughout, the sides being scarcely chitinized and the surface being convex or irregularly shrunken" as opposed to the condition in *Pachybolus* sensu Cook where "the sides of the pad are much more prominent, strongly chitinized, and dark coloured, while the surface is also of firm texture and always uniformly and strongly concave.

In the light of the variability seen between the genera recognised here, the two gonopodal characters listed by Cook (1899) are insignificant. The tarsus of *Hadrobolus crassicollis* (Figs 7, 71) is indeed quite long (and the tibia ventrally quite short), but not strikingly different from what is seen in the other genera (Figs 4–6, 60). The ventral pad in *H. crassicollis* is slightly, but not dramatically longer than that of *Pelmatojulus, Gabolus, Crurifarcimen, Hyperbolus, Parabolus, Madabolus* and *Epibolus*. The drawing of the pads in *Pachybolus tectus* by Cook (1899) (Fig. 60) shows a much shorter pad, so maybe it is *Pachybolus* s.s. that differs markedly here. The ventral surface of the pad in *H. crassicollis* is indeed particularly soft and convex, where in the other genera this surface is concave and delimited by a sharp rim, the difference is, however, not at all obvious in the scanning electron microscope (Figs 4–8). The significance of these differences cannot be properly evaluated until fresh material of *Hadrobolus* and *Pachybolus* s.s. can be studied.



FIGURES 58–72. Plate LII from Cook (1899), relabelled. 58–65. *Pachybolus tectus*. 58: head and first six body rings, lateral view, 59: telson: lateral view, 60: male leg, 61: gonopods, anterior view, 62: do: posterior view, 63: do: lateral view, 64: posterior gonopod, posterior-lateral view, 65: do., anterior-mesal view. 66–72. *Hadrobolus crassicollis*. 66: gonopods, anterior view, 67: do., posterior view, 68: do., lateral view, 69: posterior gonopods, anterior-lateral view, 70: do., posterior-mesal view, 71: male leg, 72: first six body rings.

Hadrobolus crassicollis (Peters, 1855)

Figs 66–77

Spirobolus crassicollis Peters, 1855
Hadrobolus crassicollis: Cook, 1897

HOLOTYPE ♂ MOÇAMBIQUE (MFN)

Notes on material. Peters (1855) mentioned two specimens, but Cook (1899) referred to "the type specimen at Berlin", and Mortiz & Fischer (1978) listed only one specimen ("♂ sicc., Syntypus). The available specimen is in alcohol but carries the same number (ZMB 528) as the one listed by Mortiz & Fischer; it lacks the gonopods. R.L. Hoffman has studied the type specimen of *H. crassicollis* in MFN and made drawings of the gonopods, but the gonopods have since then become lost or separated from the rest of the Berlin specimen. Dr. Hoffman has very kindly placed his original drawings at my disposal, and they are reproduced here as Figs 73–77. The original drawings by Cook (1899) are also shown (Figs 66–72).

Diagnosis. see that of genus.

Descriptive notes. (based on the studied specimen): As *Crurifarcimen vagans* except as noted:

56 podous rings, no apodous rings. L ca. 13 cm, B 12.5 mm. 11 rows of ocelli in seven horizontal series, 11th row consisting of four tiny ocelli. 49–51 oceli per eye (Peters [1855] counted 45, he probably overlooked the 11th row). 2+2 labral teeth, labral setae not visible. Lamellae linguales each with 5-6 distal setae. Collum smooth, no striae, with marginal furrow at anterior margin. Ozopores 1 diameter in front of suture. Legs: length ca. 63% of body width. Telson as in *Crurifarcimen v.* but dorsal profile straight.

Colour, according to Peters (1855): "Color faciei rufus, versus partem superiorem in nigraofuscum transiens. Cingulorum pars posterior nigra, anterior aurantiaca. Pedes supra rubri, subtus aurantiaci. Margo prominens squamaeum analium lateralium ruber." (Colour of face red, becoming blackish brown towards upper part. Posterior part of body rings black, anterior part orange. Legs red above, orange below. Protruding margin of anal valvs red.)

Male coxae 6–7 unmodified.

Gonopods (based on Cook 1899 and R.L. Hoffman's drawings, Figs 66–70, 73–77):

Anterior gonopod sternum with relatively low, broadly rounded mesal protrusion reaching little more than ½ the height of the coxae. Coxae in oral view kidney-shaped, apically broadly rounded, widely separated from each other, extending to aboral side of gonopod where they appear as narrow lateral bands. Telopodites extending well beyond coxal tips, widely separated in midline, apically broadly rounded, mesal margin with large rounded lobe ca. at mid-length.

Posterior gonopods with a tracheal apodeme, a stout basal part, a small lateral sclerite (possibly homologous with the intermediate segment in *Crutifarcimen vagans*), and a slender, arched terminal segment. Terminal segment medio-basally expanded, with several low cusps, ca. at mid-length with large process arising from concave mesal side, process lying close to and following apical curvature of mesal margin. 'Head' of terminal part in anterior-lateral view with a serrated keel, distal margin of 'head' with fine fringe.

Female unknown.

Distribution. Only known from the type locality. Peters (1855) did not give a locality (although he did so for the other species described in the same paper). Cook (1899) gave "Island of Mozambique", Moritz & Fischer (1978) "Mossambique". The studied specimen has no original label attached to it. "Island of Mozambique" is a small island situated at 15°02'30''S, 40°43'50''E. It is now entirely urbanized, so the chances of ever collecting topotypes of *H. crassicollis* are minimal.

Genus *Epibolus* Cook, 1897

Type species: *Spirobolus pulchripes* Gerstäcker, 1873

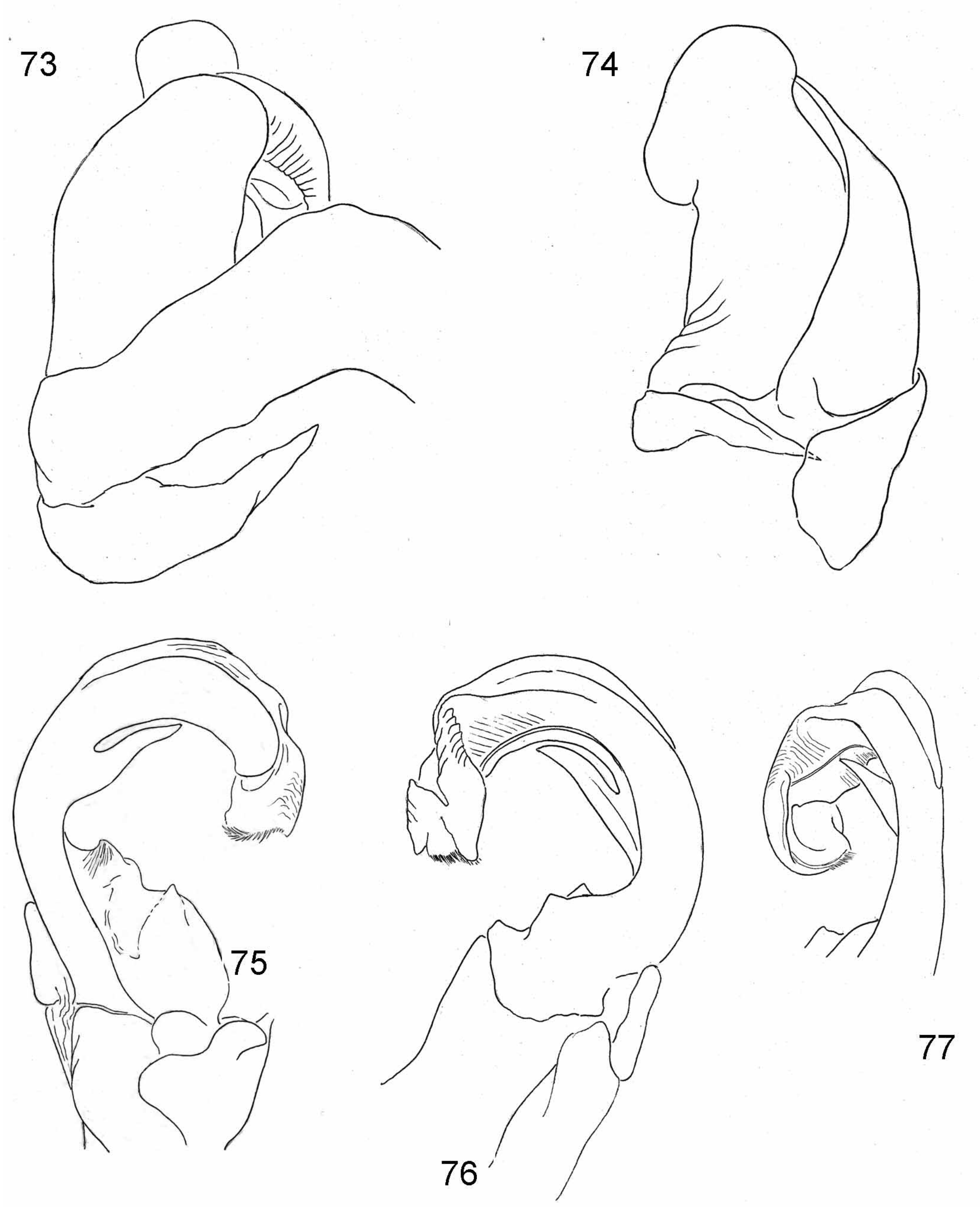
Included species. *E. pulchripes* (Gerstäcker, 1873); *E. mossambicensis* (Lawrence, 1967)

Diagnosis. A genus of East African Pachybolini characterized by

- no coxal lobes on male legs 6 and 7
- three (two to five) pairs of ventral macrosetae on male legs from pair 5 onward (Fig. 6).

- a moveable lateral appendix on the posterior gonopods
- striated membranous lamellae at tip of posterior gonopod
- no mesal process, no free solenomerite, no distal complex of parallel ridges on posterior gonopod
- no long meso-distal process on anterior gonopod coxite
- no overlapping lobes on anterior gonopod telopodites
- apical margin of winglike expansions of second female coxae regularly rounded (Fig. 12)
- an apical appendix on oral vulval valve

Enghoff (1977) recognised three species of this genus: the widespread *E. pulchripes* (Kenya and Tanzania), *E. bravensis* from Somalia and *E. mossambicensis* from Mozambique. The morphological characters distinguishing the two “geographical satellite” species from *E. pulchripes* were subtle, and in the case of *E. bravensis* drawn exclusively from the original description (Silvestri, 1897) because these characters could not be seen on the male holotype. See further under *E. pulchripes.*



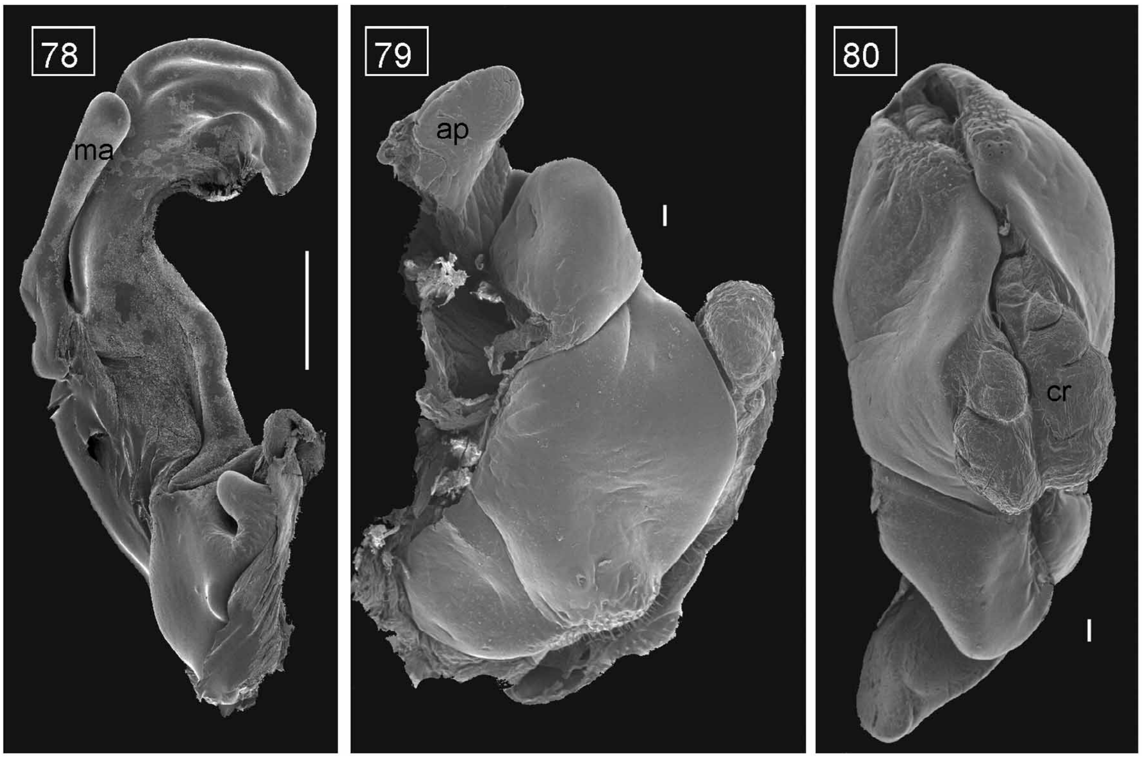
FIGURES 73–77. *Hadrobolus crassicollis,* original drawings by R.L. Hoffman, from type specimen. 73: anterior gonopod sternum, left coxite, and left telopodite, anterior view, 74: right anterior gonopod, posterior view, 75–77: posterior gonopod, different views.

Epibolus pulchripes (Gerstäcker, 1873)

(Figs 6, 9–10, 12, 78–82)

Spirobolus pulchripes Gerstäcker, 1873
Spirobolus proporus Attems, 1896, synonymized by Enghoff (1977)
Trigoniulus ruspolii Silvestri, 1896, synonymized by Enghoff (1977)
Epibolus pulchripes: Cook (1897)
Trigoniulus bravensis Silvestri, 1897, **new synonym**
Metiche bravensis: Attems (1909)
Metioche attemsi Kraus, 1958, synonymized by Enghoff (1977)
Metiche tanganyicense Kraus, 1958, synonymized by Enghoff (1977)
Callipodolus pulchripes: Hoffman & Keeton (1960)
Metiche mossambicense Lawrence, 1967, **new synonym**
Epibolus bravensis: Enghoff (1977)
Epibolus mossambicensis: Enghoff (1977)
Metiche tanganyciense [sic!]: Banerjee (1980)
Epibolus pulchripes bravensis: Cecchi & Chelazzi (1984).

Material examined (numerous specimens from Kenya and Tanzania not listed): 5 ♂♂ Somalia, (Gelib) Alessandra, July 1937, F. Bigi leg. (MSNF).



FIGURES 78–80. *Epibolus pulchripes*. 78: male from Tanzania, E Usambara Mts., Mgambo Forest Reserve, right posterior gonopod posterior view, #79: female from Kenya, Tiwi, left vulva, anterior view, 80: do., right vulva, lateral view. Scales 1 mm (78), 0.1 mm (79-80). ap: apical appendix, cr: protruding crest, ma: lateral moveable appendix. SEM.

Diagnosis. See that of genus.

Descriptive notes. Usually 52 podous rings (27 out of 43 specimens studied by Enghoff 1977), exceptionally 50, 51 or 53 podous rings, no apodous rings. Dhaenens & VandenSpiegel (2006) observed only 52 podous rings in the population they studied.

Male sexual characters. Male coxae 6–7 unmodified. Posterior gonopods unmistakable because of the moveable lateral appendix (Figs 78, 81–82). See, e.g., Kraus (1958), Hoffman (1962), Enghoff (1977) and Dhaenens & VandenSpiegel (2006) for descriptions of *E. pulchripes* gonopods.

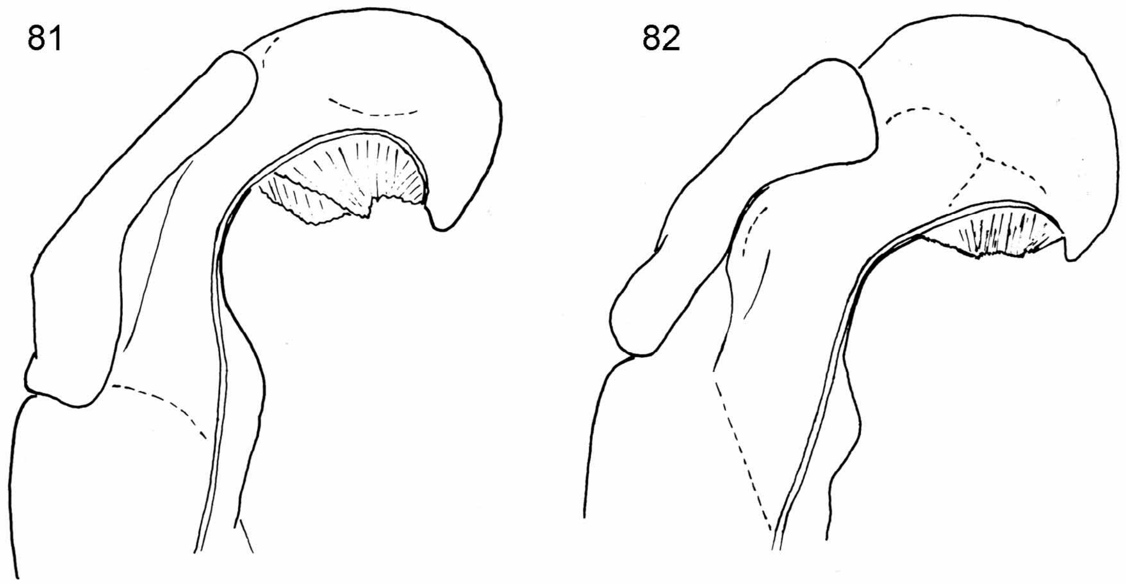
Female sexual characters. Distal margin of lateral coxosternal extensions projecting as smoothly rounded, subhemicircular lobe (Fig. 12). Vulvae (Figs 79–80) complicated; operculum particularly poorly sclerotized; oral valve divided into two sclerites and in addition with a hood-shaped appendix; aboral valve constricted ca. at same level as subdivision of oral valve. Crest strongly protruding. (Enghoff (1977) described and illustrated the vulva of

E. pulchripes but mistook the apical appendix for the operculum and translated the French term 'cimier' as 'ridge', whereas I use 'crest' here.)

Notes to the new synonyms. Enghoff (1977) provisionally upheld *E. bravensis* and *E. mossambicensis* as distinct species, but there is little justification for this.

E. bravensis was distinguished from *E. pulchripes* by 1) the number of ocelli per eye: ca. 35 in *bravensis* (Silvestri 1897), *vs.*, 38–57 in male *E. pulchripes*, 2) the shape of the anterior gonopod sternum which in *bravensis* has a deep, acute incision of the basal margin (Silvestri 1987: fig. 6). The studied specimens from Alessandra, Somalia are perfectly normal *E. pulchripes* in all characters, including the number of ocelli. They do have a pronounced basal incision in the anterior gonopod sternum but so do other specimens from Tanzania which I have studied after 1977. The purported differences between *pulchripes* and *bravensis* can therefore be dismissed as either intraspecific variation (the gonopod character) or a possible inaccuracy of observation by Silvestri (number of ocelli). Alessandra is now known as Labadaad and lies at 0°30' N, 42°45' E, quite close to (160 km) the type locality of *E. bravensis*, Brava, now known as Bawaawe and lying at 1°6'N, 44°2'E. Cecchi & Chelazzi (1984) took a step in the direction of synonymizing *bravensis* under *pulchripes* by treating it as a subspecies (without any argumentation for doing so).

E. mossambicensis was kept separate exclusively on the basis of its very slender posterior gonopod finger-formed process. Although no additional specimens from Mozambique have come to hand, and although no specimen with an equally slender process has been found anywhere, the variability in shape of the finger-shaped process observed in Tanzanian specimen (Figs 78, 81–82, Dhaenens & VandenSpiegel 2006: fig. 3) is so great that separate status of *mossambicensis* cannot be maintained.



FIGURES 81–82. *Epibolus pulchripes*, right posterior gonopods, posterior view. 81: male from Kenya, Mombasa, 82: lectotype, from Tanzania, Zanzibar. From Enghoff (1977).

Distribution. *E. pulchripes* including its new synonyms *bravensis* and *mossambicensis*, is widely distributed in eastern Africa: from Bawaawe, Somalia, in the north to Island of Mocambique in the south although the vast majority of finds are from Kenya and Tanzania. Most, but not all occurrences are close to the Indian Ocean coast. See map in Enghoff (1977).

Further notes. *Epibolus pulchripes* is by far the best studied among the species treated here and is subject of several non-taxonomic papers. Thus Wood *et al.* (1975) studied the defensive secretion of *E. pulchripes* (reporting that it can be sprayed by the animal as far as 40 cm), Banerjee (1980) studied population characteristics of the species, Cecchi & Chelazzi (1984) described its internal genital organs and spermatogenesis, and Dhaenens & VandenSpiegel (2006) provided information on post-embryonic development and reproduction.

According to United Nations Environment Programme (1998: 42), *E. pulchripes* is common on the East African coast and "very seldom damages living plants, but instead is a very valuable agent in humus formation". In this publication, *E. pulchripes* is in this respect contrasted with the giant spirostreptid *Archispirostreptus gigas* (Peters, 1855) with which it often coexists: "Like many other giant millipedes, *A. gigas* can cause serious localized seasonal damage to crops and small forestry seedlings. In dry conditions, millipedes turn to living plants as a source of food and they burrow down and seek shelter in crevices. On the other hand, under wet conditions their populations appear to increase explosively but they seem to confine their diet to leaf litter and other dead plant matter.”

In an account of a reforestation project at Bamburi Nature Trail near Mombasa, Kenya, *E. pulchripes* was recorded to play an important role, as shown by the following quote from http://www.cosy.sbg.ac.at/~zzspri/travels/BANweb/bantrail.html (accessed 25 September 2009): “*Casuarina* and *Conocarpus* are evergreen trees that constantly drop and renew "needles" and leaves. Thus the dropping foliage was covering the rocky ground at a steady pace. However, the break down of foliage's by micro-organism was prolonged because of the high content of tannin in *Casuarinas* "needles". The process of releasing the confined nutrients to other organisms was slowed down and the establishment of subsequent plant species was delayed thus. A lucky incident solved this problem when the red legged **Mombasa trains** (*Epibolus pulchripes*) happily started feeding on dry *Casuarina* "needles". The compost bacteria in millipedes' dropping converted needles into the needed humus. These useful animals were collected from coastal bushes and there was an instant success as the millipedes multiplied fast in the young forest. The leaf litter was slowly reduced and a layer of humus thickened underneath. The millipedes had found a land of milk and honey having the forest floor for them only but this happy state of affairs did not last long. Soon they became part of the food chain too as white tailed mongooses and civet cats started eating millipedes as they came in the forest on their own.” See also http://blog.earthshope.org/wp-content/uploads/2009/02/jp-morgan-2008-jl-essay.pdf and http://www.iaphworldports.org/HoustonPresentations/IAPH2007-Kahumbu.pdf (both accessed 25 September 2009).

E. pulchripes is a popular pet millipede (e.g., Decker & Pfeifle 2008) and has received a variety of common names, e.g. Mombasa train, Tanzanian red-legged millipede, and giant red-legged millipede in English, Afrikanischer Lackschnurfüßer and Rotbeiniger Schnurfüsser or Rotfuss-Schnurfüsser in German. In Kenya it is eaten by the elephant shrew *Rhynchocyon chrysopygus*, but is avoided by the dwarf mongoose *Helogale parvula* although this mongoose will readily eat *Archispirostreptus gigas* (unpublished obervations reported by Wood *et al.* (1975)).

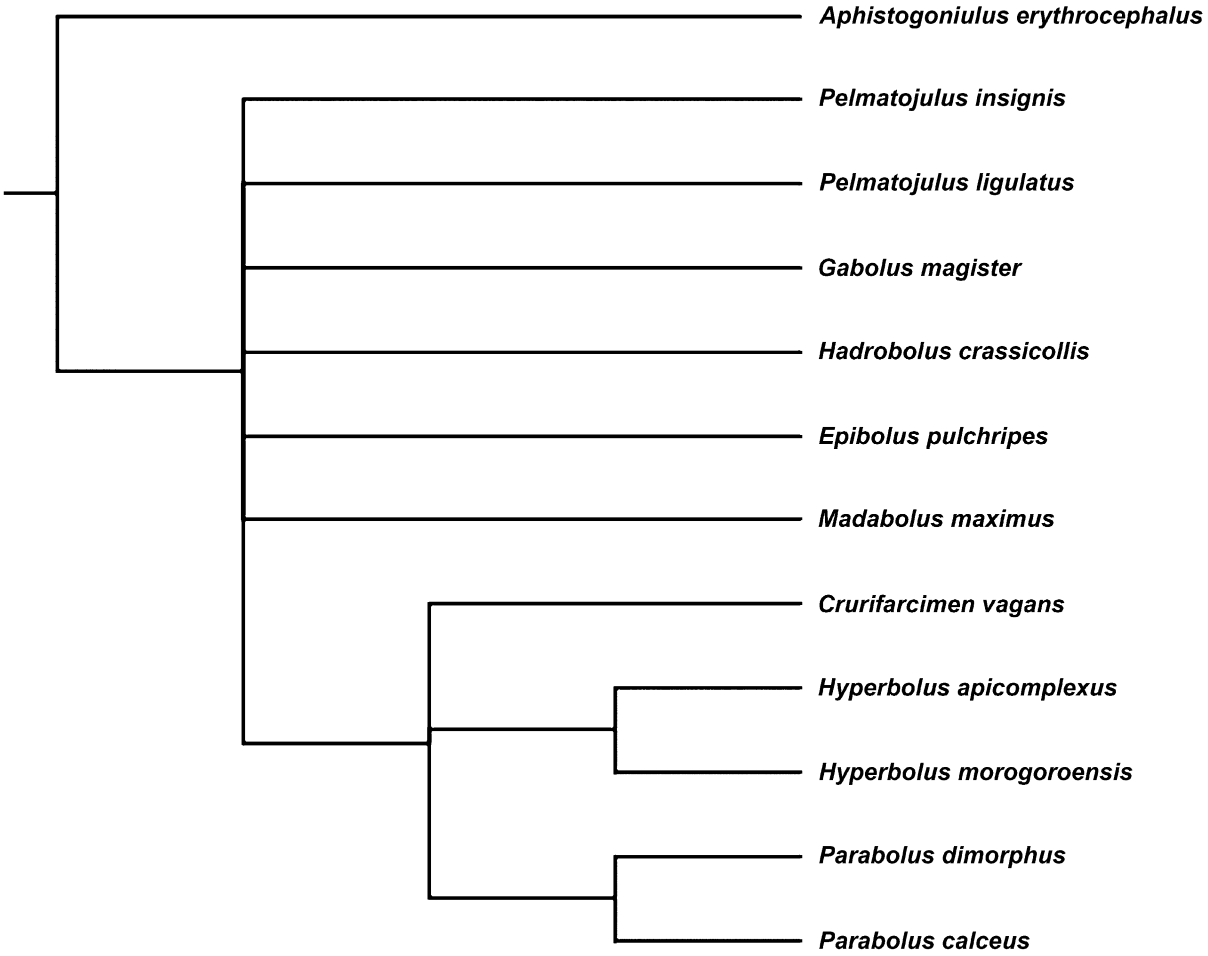


FIGURE 83. Relationships in Pachybolini as indicated by a cladistic analysis. Strict consensus of 12 most parsimonious trees under equal character weights.

Pachybolini indet.

Fig. 84

Material examined. 1 subadult ♂, 1 ♀ TANZANIA: Kilimandjaro, 2008 (from pet trade) (SMNG). The subadult gonopods of the male look similar, but not identical, to the gonopods of a subadult *Hyperbolus apicomplexus* **n. sp.** Until an adult male can be studied, the identity of this species remains uncertain.

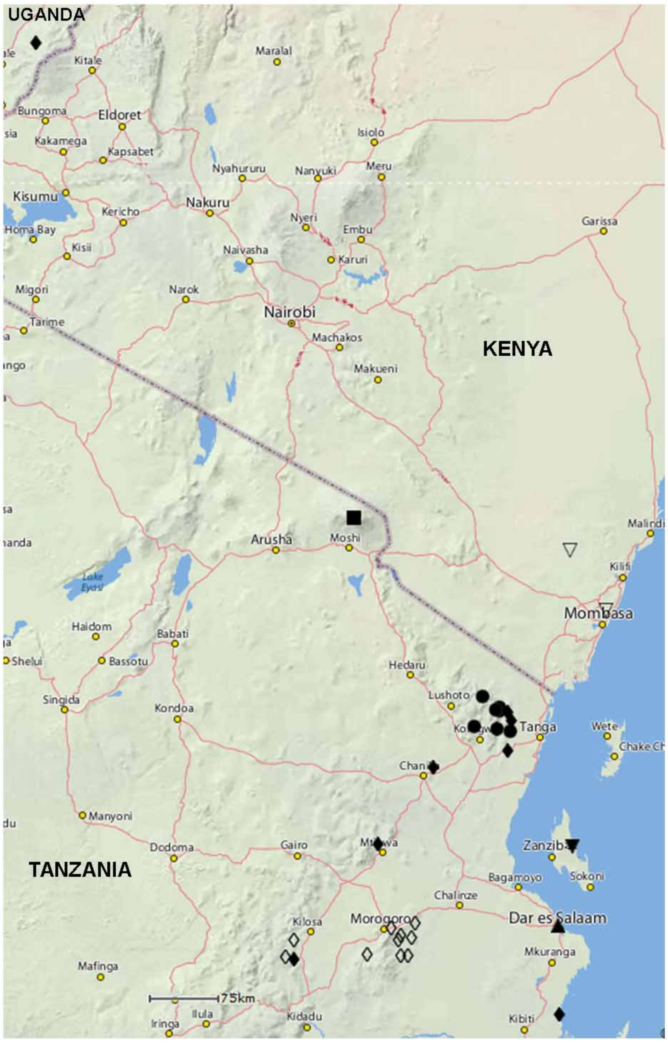


FIGURE 84. Known distribution of East African Pachybolini, except *Hadrobolus crassicollis* and *Epibolus pulchripes*. dots (●): *Crurifarcimen vagans*, filled diamonds (♦): *Hyperbolus apicomplexus*, open diamonds (◊): *Hyperbolus morogoroensis*, filled triangle (▲): *Parabolus dimorphus*, inverted open triangle(▽): *Parabolus calceus*, inverted filled triangle (▼): *Pachybolus tectus*, , filled square(■): Pachybolini indet. Based on Yahoo maps.

Relationships

Wesener *et al.* (2008) argued for monophyly of Pachybolini, based on a phylogenetic analysis. Their analysis included representatives of the genera *Pelmatojulus* (2 species), *Crurifarcimen* (“Gen. et sp. nov. [Tanzania]”), *Hyperbolus* (“”*P.*” sp. aff. *morogoroensis*”), *Epibolus* (*E. pulchripes*), *Madabolus* (*M. maximus*) and *Hadrobolus* (*H. crassicollis*), as well as numerous other pachybolids. Pitz & Sierwald (2010) included only one species of Pachybolini in their phylogenetic analysis of the order Spirobolida, viz., *Pelmatoiulus ligulatus* (Voges, 1878) (misnamed as *Pachybolus l.*). Their analysis therefore is uninformative about relationships with in Pachybolini (but unambiguously supports monophyly of the family Pachybolidae). The work presented here has revealed a number of new characters of potential use for analysing intratribal relationships, and a new analysis is therefore in order.

Wesener *et al.*'s cladogram included a 13-fold polytomy with one of the branches leading to Pachybolini. One of the other branches lead to *Aphistogoniulus erythrocephalus* (Pocock, 1893) which is chosen as outgroup for the present analysis because of its size which matches that of the Pachybolini (the new female characters were taken from *A. cowani* (Butler, 1882) because a female *A. erythrocephalus* was not available). Possible size effects on characters are therefore eliminated. The charaters include those among Wesener *et al.*'s characters found to vary within Pachybolini + *A. erythrocephalus*, in addition to the new characters (Table 4).

TABLE 4. Characters used for the phylogenetic analysis. For discussion of characters, see also Wesener *et al.* (2008) whose character numbers have been used when possible. Unrepresented states have been removed, remaining states renumbered accordingly and in some cases re-coded assigning state 0 to the outgroup. Characters 28 and 29 of Wesener *et al.* have been merged into one character. Character 31 (anal valve lips absent/present) was scored identically for all the taxa included here by Wesener *et al.* (2008), except for *Pelmatojulus ligulatus*; re-examination of the two included *Pelmatojulus* species revealed no difference between them, and this character has therefore been omitted. Character 35 (vulval ridge/crest) has been omitted, cf. discussion of this character in text.

(4) Incisura lateralis: open (0); closed (1).
(6) Number and position of setae on each lamella lingualis: two setae, behind each other (0); two setae on distal edge (1); more than two setae on distal edge (2).
(9) Mandible, internal tooth, no. of cusps: four (0); two-three (1).
(10) Mandible, no. of complete rows of pectinate lamellae: 6 or more (0); five or fewer (1)
(11) Apical cones on each antenna: four (0); more than four (1).
(20) Posterior gonopods: telopodite, long mesal process ~halfway, absent (0); present (1).
(21) Posterior gonopods: telopodite, striated and membranous lamellae on tip, absent (0); present (1).
(28+29) Male 6th and 7th pairs of legs, coxae: non-modified (0); with processes (1)
(33) Vulva: simple, bivalve-like (0); kidney- or crescent-shaped (1). (Only slightly kidney-shaped in *Parabolus* spp.)
(34) Vulva: both valves meet in a straight, regular fissure (0); strongly sinuous fissure (1). (The fissure is only slightly sinuous in *Pelmatojulus ligulatus* and *Parabolus* spp.)
(A) Male tarsal ventral macrosetae: 1 pair (0); 3 (2-5) pairs: (1)
(B) Posterior gonopods: telopodite without a moveable appendix (0); with a moveable appendix (1)
(C) Posterior gonopods: telopodite without a free solenomerite (0); with a free solenomerite (1)
(D) Posterior gonopods: telopodite distally without a complex of parallel ridges (0); with a complex of parallel ridges (1)
(E) Anterior gonopods: coxite without a very big slender process directed distad parallel to mesal margin of main part of coxa (0), with such a process (1)
(F) Anterior gonopods: telopodites without mesal overlapping processes (0); with mesally overlapping processes (1)
(G) Second female legs: lateral coxosternal extension distal margin angled (0); rounded (1)
(H) Vulvae: oral valve without an apical appendix (0); with an apical appendix (1)

Cladistic analysis. The character matrix constructed from the data in Table 4 is shown in Table 5. The matrix was analysed by Piyatyida Pimvichai. The analysis was run with equal weight and resulted in 12 shortest trees, the strict consensus of which is shown in Fig. 83. Resolution is low (as is the number of informative characters), the only clades in the consensus tree being:

- the ingroup (Pachybolini)
- a clade consisting of the genera *Crurifarcimen*, *Hyperbolus* and *Parabolus*
- the genus *Hyperbolus* (two species)
- the genus *Parabolus* (two species)

In the following discussion, character and state numbers refer to Table 4, and state changes are indicated as ([original state number]→[new state number]).

Thus, in all 12 shortest trees:

- The ingroup is nonhomoplasiously supported by characters 4 (0→1), 6 (0→1 **or** 2), 10 (0→1), 33 (0→1) and 34 (0→1).
- (*Crurifarcimen* + *Hyperbolus* + *Parabolus*) is supported by character 28+29 (0→1), parallelled in *Madabolus*
- *Hyperbolus* is nonhomoplasiously supported by character D (0→1) and character F (0→1)
- *Parabolus* is nonhomoplasiously supported by character E (0→1)

A number of clades which do not occur in all 12 shortest trees deserve comment:

- *Pelmatojulus* (two species included) is nonhomoplasiously supported by character 11 (0→1) in 11 trees
- (*Pelmatojulus* + *Gabolus*) is supported by character 6 (2→1) in 9 trees. The clade occurs in one further tree, but without support. In the last two trees, the clade does not occur, and character 6 (1→2) supports a clade consisting of *Madabolus*, *Hadrobolus*, *Epibolus*, *Parabolus*, *Crurifarcimen* and *Hyperbolus*, i.e., all the East African (incl. Madagascar) Pachybolini. The latter clade also occurs in the tree in which the *Pelmatojulus*+*Gabolus* clade is present but unsupported.
- Within (*Crurifarcimen* + *Hyperbolus* + *Parabolus*), *Crurifarcimen* + *Hyperbolus* is supported nonhomoplasiously by character D (0→1) in 8 trees. In the remaining 4 trees, *Hyperbolus* + *Parabolus* is supported by character H (0→1), parallelled in *Epibolus*.
- *Madabolus* + *Hadrobolus* is nonhomoplasiously supported by character 20 (0→1) in 6 trees. In the remaining 6 trees, *Madabolus* + *Epibolus* is nonhomoplasiously supported by character 21 (0→1). A clade consisting of *Madabolus*, *Hadrobolus* and *Epibolus* occurs in 4 trees, but without support. The cladistic analysis of Wesener *et al.* (2008) did result in a poorly supported *Madabolus*+*Hadrobolus* clade, but these authors regarded *Epibolus* as an equally likely sister-group to their new genus *Madabolus.*

TABLE 5. Character matrix based on the character states in Table. 4.

character no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
character no(s) in Table 4	4	6	9	10	11	20	21	28+29	33	34	A	B	C	D	E	F	G	H
Aphistogoniulus erythrocephalus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pelmatojulus insignis	1	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0
Pelmatojulus ligulatus	1	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0
Gabolus magister	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Crurifarcimen vagans	1	2	0	1	0	0	0	1	1	1	0	0	1	0	0	0	0	0
Hyperbolus apicomplexus	1	2	0	1	0	0	0	1	1	1	0	0	1	1	0	1	0	1
Hyperbolus morogoroensis	1	2	0	1	0	0	0	1	1	1	0	0	1	1	0	1	0	1
Parabolus dimorphus	1	2	0	1	0	0	0	1	1	1	0	0	0	0	1	0	0	1
Parabolus calceus	1	2	0	1	0	0	0	1	1	1	0	0	0	0	1	0	0	1
Hadrobolus crassicollis	1	2	?	1	0	1	0	0	?	?	0	0	0	0	0	0	?	?
Epibolus pulchripes	1	2	1	1	0	0	1	0	1	1	1	1	0	0	0	0	1	1
Madabolus maximus	1	2	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0

Biogeography

In the absence of a robust phylogenetic hypothesis about relationships within the East African Pachybolini, nothing sensible can be said about possible historical biogeographical scenarios. It may, however, be noticed that the Eastern Arc Mountains seem to play an important role for this group of millipedes (Fig. 84): *Crurifarcimen* is endemic to the Usambara Mountains and *Hyperbolus* (sister-group to *Crurifarcimen* in 8 out of 12 shortest trees) is nearly endemic to the Eastern Arc Mountain group as a whole. The Pachybolini thus join the long list of animals and plants that contribute to making the Eastern Arc Mountains a crucial center of biodiversity (e.g., Burgess *et al.* 1998, 2007, Fjeldså & Bowie 2008).

Acknowledgements

This study has been on my agenda since 1974, when my wife Inge Bødker Enghoff and I collected the first *Crurifarcimen vagans* and *Hyperbolus apicomplexus*. Inge's help and support then and ever since has been of immense importance. Thank you, Inge! My thanks are also due to the curators mentioned in the material and methods section for lending specimens under their care, and further to Geert Brovad, Nicolas Ioannou, Christian Lange, Jan Pedersen, Knud and Andreas Rosenlund, and Birgitte Rubæk (all ZMUC), to Thomas Wesener (Chicago), Peter Decker (Görlitz), Nesrine Akkari (Tunis), and Piyatida Pimvichai (Bangkok) for help with providing specimens, illustrations and doing phylogenetic analysis. Special thanks are due to Richard L. Hoffman for inspiration and advice over several decades, and for placing his unpublished drawings of *Hadrobolus crassicollis* at my disposal. The careful review of the manuscript by Thomas Wesener is much appreciated.

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