MYRIAPODOLOGICA

Virginia Museum of Natural History

Vol. 8, No. 1 ISSN 0163-5395 April 15, 2004

A synopsis of *Phaeodesmus*, an East African genus of paradoxosomatid millipeds (Diplopoda: Polydesmida)

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ABSTRACT

Phaeodesmus is defined on the basis of gonopod structure to include the established species *aculeatus* Peters, *alatus* Attems, *flavocinctus* Pocock, and the new species *orestes*, described from the Nyika Plateau. Malawi. The genus extends from Mozambique to southeastern Kenya with one disjunct locality in upland Malawi; the very few records even in well-collected areas suggest a contracting, relictual stage in the generic history. Within the tribe Cnemodesmini, *Pheodesmus* is clearly most closely related to *Podochresimus*, although the two taxa are at present separated by the entire width of South Africa.

INTRODUCTION

Like most genera of tropical millipeds, *Phaeodesmus* has undergone the usual progression from monotypy into polytypic heterogeneity and finally into preliminary revision and clarification of its status *vis-à-vis* related taxa. It is now possible to advance our knowledge of this genus of strikingly colored animals with the description of a new species from Malawi and the assignment hereto of a poorly-known congener from Kenya. These taxa extend the known range of the genus appreciably northward from Mozambique, and the availability of fresh material provides the opportunity for a detailed account of gonopod structure.

HISTORICAL SUMMARY

The first species definitely referable to this genus was named *Strongylosoma aculeatum* by Peters in 1855, from a female specimen he collected in southern Mozambique. In 1896, Attems described *Orthomorpha longipes* from a nearby

locality in Mozambique and in the same year, Pocock published the name *Tetracentrosternus flavocinctus* for specimens from southeast Kenya. Several years later, O. F. Cook (1898) redescribed *longipes* from type material and set up the genus *Phaeodesmus* for it, but like Attems before him, failed to provide drawings of the gonopods. This omission was finally corrected in the same year by Attems in the first part of his "System der Polydesmiden" but unfortunately the illustration was made from a distorted microscopic preparation and gave a very misleading impression of the structure. In the "Nachtrag" to this work, Attems (1899: 175) mentioned Cook's paper, but rejected the genus *Phaeodesmus* and continued to refer *longipes* to *Orthomorpha*.

Not long afterward, however, Attems changed his opinion about Cook's proposal, and in 1914 listed *Phaeodesmus* amongst the 35 genera recognized in his family "Strongylosomidae". Moreover he greatly enlarged the scope of the genus by adding five more African species to it: an unfortunate action since none of the five is congeneric either with *longipes* or each other. *Podochresimus alatus*, described by Attems in 1928 from Mozambique, actually is congeneric with *longipes*, but *Phaeodesmus niger*, named in the same paper, is not, despite their respective generic placements. In 1934 Attems named *Phaeodesmus miles* and *P. neglectus* from Angola. In his 1937 synopsis of the Strongylosomidae, Attems recognized five species in the genus, adding *Cnemodesmus thysanopus* and relocating several of the 1914 members. One year later he defined still another new species, *Phaeodesmus convolutus*, from material taken in Zaire.

More recently, Schubart (1956) named *Phaeodesmus cataractae* from Victoria Falls, and Lawrence (1966) described *P. subtropicus* from the Kruger National Park, Transvaal.

As shown by the foregoing account, *Phaeodesmus* acquired over the years a very unsatisfactory composition, notable for its heterogeneity. Coincidentally, two papers appeared in 1968 that essentially imposed a rational taxonomic context on the genus, one of them being Jeekel's classification of the Paradoxosomatidae (the correct name for the erstwhile Strongylosomidae), the other a brief synopsis of South African genera of that family by the author of the present account.

Both of these papers admitted the species *longipes* and *alatus* to *Phaeodesmus*, and excluded the species *cataractae* as referable to *Congolina (=Ectodesmus)*. Jeekel, however, also recognized Pocock's enigmatic species *T. flavocinctus*, and expressed the view that *subtropicus* was probably a true *Phaeodesmus* related to *alatus*. Both authors restored *Cnemodesmus* to generic rank, with *C. thysanopus* as its type species, and recognized *Campsogon* (Chamberlin, 1951) as a valid genus containing the nominal species *laquifer* Chamb., *iugans* Chamb., *miles* Attems, and *convolutus* Attems.

Lastly, having studied the male characters of *P. neglectus*, Hoffman (1982) established the new genus *Anaclastopus* to accomodate this single disjunct species.

The genus is here considered to contain four nominal species, two of which (*flavocinctus* and *aculeatus*) are probably subspecifically related

ACKNOWLEDGMENTS

The material upon which the following account is based was made available by my colleagues Manfred Moritz (Zoologisches Museum des Humboldt Universitäts, Berlin), Rudy Jocque (Museum Royal de l'Afrique Central, Tervuren), Gisela Rack (Zoologisches Museum, Universität Hamburg), and Paul Hillyard (British Museum - Natural History, London), to whom I express my thanks.

SYSTEMATICS

FAMILY PARADOXOSOMATIDAE

Tribe Cnemodesmini

Cnemodesmini Jeekel, 1968, Paradoxosomatidae, p. 104. – Hoffman, 1980, Classification of the Diplopoda, p. 168.

Phaeodesmus

Phaeodesmus Cook, 1898, Proc. U. S. Nat. Mus. **20**: 706. Type species, *Orthomorpha longipes* Attems, 1896, by original designation and monotypy.--Attems, 1937, Tierreich **68:**. 218. – Jeekel, 1968, Paradoxosomatidae, p. 105. – Hoffman, 1968, Wasmann Jnl Biol. **26**: 218.

DIAGNOSIS: A cnemodesmine genus characterized by a row of 3-6 setae along inner margin of antennal sockets; presence of parantennal organ; moderately well developed paranota; very long and slender legs with tarsi longer than femora and, on anterior legs, provided with a ventral brush of modified setae; femora of 3rd-5th legs of males provided with a ventrodistal adenostyle (one exception); sternum of 5th segment of males with prominent transverse process; and sternum of 6th segment with a median macroseta or cluster of hairs between both pairs of legs.

Coxa of gonopods long, cylindrical, moderately constricted at distal third, with small field of short setae on dorsal side; femur set off from prefemur by distinct cingulum visible on lateral side, median surface of femur with central membranous area bounded on its dorsal edge by a prominent laminate process; distal part of femur prolonged on dorsal side into a large, long, falcate process curved parallel to the arcuate tibiotarsal region; postfemur set off basally by an indistinct cingulum on lateral side, merging gradually into tibiotarsus which extends mesad as an intricately folded, apically expanded blade enveloping solenomere for most of its length; postfemur with a large digitiform medially directed process (e) from its ventral surface.

RELATIONSHIPS: Insofar as can be determined with insufficient reference material and often inadequate published illustrations, I believe that the nearest relative of *Phaeodesmus* must be *Podochresimus,* a view already expressed (Hoffman, 1968). In addition to the synapomorphy of femoral adenostyles on the 3-5th legs of males, the gonopods of these nominal taxa are very similar, distinguished only by the presence of an additional tibiotarsal process (labeled "c" on Attems' drawings) in the

species of *Podochresimus*. The broad geographic separation of these adelphotaxa on the east and west coasts of South Africa is quite likely due to the "relatively recent desiccation of South-West Africa" invoked by Jeekel (1968: 138).

DISTRIBUTION: East Africa, from southern Mozambique (Inhambane) north to eastern Kenya; with one exception (in northern Malawi) the species occur in coastal lowlands and are thus largely allopatric with those of the related cnemodesmine genus *Aklerobunus* (see map, Fig. 12).

SPECIES: Four, one of them new, separable as follows:

1. Femora of anterior legs of males without apicoventral adenostyle; tibiotarsus of gonopod only slightly curved, with a small acicular basal spine on mesal side ..... *orestes*
- Femora of legs 4-6 of males with small acute apicoventral adenostyle 2

2. Apex of tibiotarsus strongly recurved dorsad, with several small marginal denticulations ..... *alatus*
- Apex of tibiotarsus recurved ventrad then laterad 3

3. Subapical lobe of tibiotarsus (ventral aspect) relatively small; postfemoral process *e* without a rounded lobe at midlength (Fig. 9); adenostyle of 3rd leg of male (Fig. 3) ..... *aculeatus*
- Subapical lobe of tibiotarsus relatively large; postfemoral process *e* conspicuously broadened at midlength (Fig. 11); adenostyle of 3rd leg of male (Fig. 4) ..... *flavocinctus*

Phaeodesmus aculeatus (Peters), new combination
(Figs. 3, 7, 8, 9)

Strongylosoma aculeatum Peters, 1855, Monatsber. Akad. Berlin: 81. Female holotype (Zool. Mus. Berlin) from "Terra borror, 18° lat. aust.", Mozambique (W. C. H. Peters).

Strongylosoma aculeatum: Peters, 1862, Reise nach Mossambique, Zool., 5: 532, pl. 33, fig. 7.

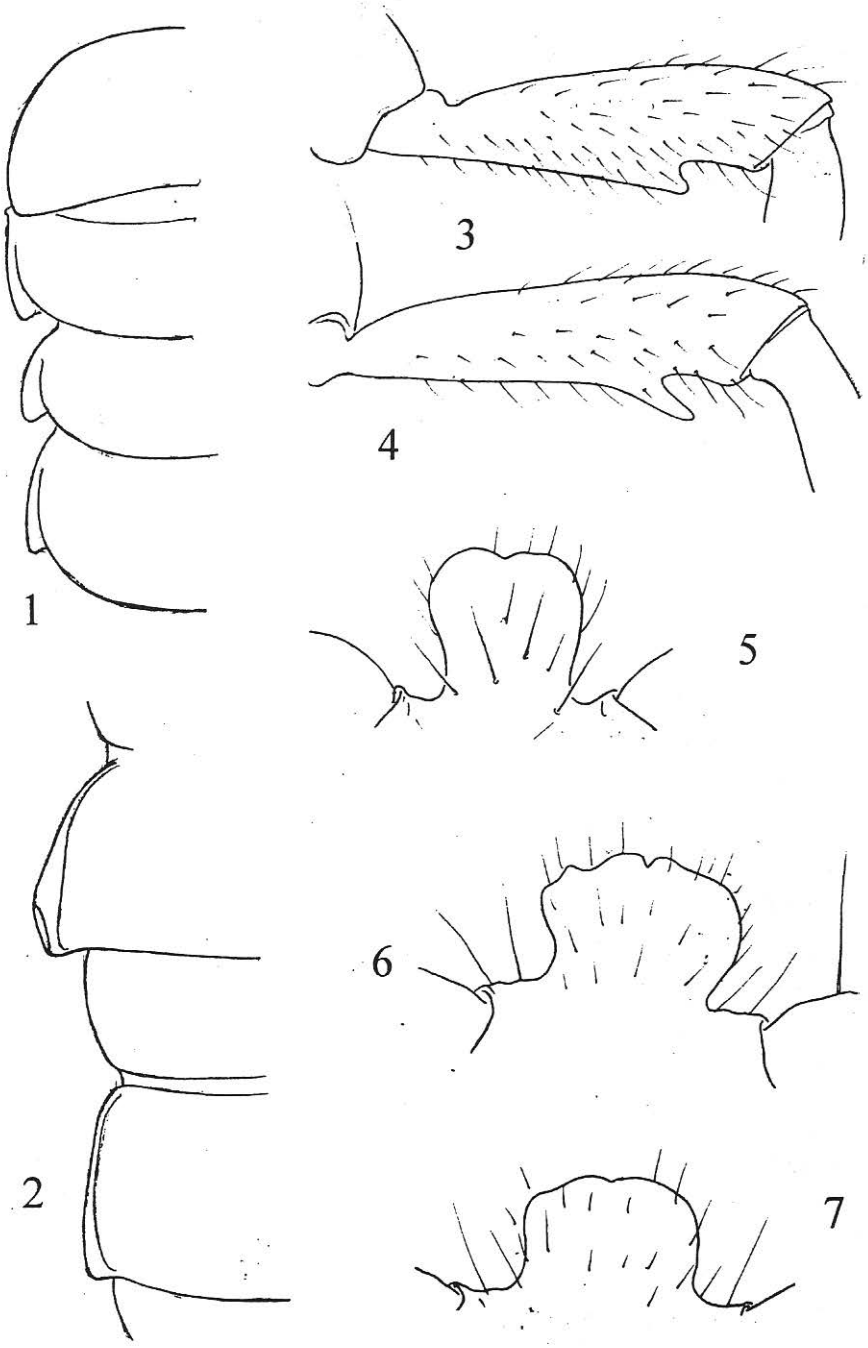
Habrodesmus aculeatus: Cook, 1896, Proc. U. S. Nat. Mus., 18: 98, pl. 5, figs. 6, 7.

Orthomorpha longipes Attems, 1896, Mitt. Naturh. Mus. Hamburg **13**: 25. Male and female syntypes (Zool. Mus. Hamburg) from Quelimane, Mozambique (Franz Stuhlmann).– Attems, 1898, Denks. Akad.Wien **67**: 332, figs. 87, 88. **New Synonymy!**

Phaeodesmus longipes: Cook, 1898, Proc. U. S. Nat. Mus. **20**: 707.--Attems, 1928, Ann. S. Afr. Mus. **26**: 249.– Attems, 1937, Das Tierreich **68**: 219. – Jeekel, 1968, Paradoxosomatidae, p. 105.

Cnemodesmus longipes: Hoffman, 1953, Proc. Biol. Soc. Washington, 66: 81.

MATERIAL: Female holotype of *aculeatum*; male and female syntypes of *longipes*.



Figs. 1-7. *Phaeodesmus* species, structural features. 1. *P. orestes*, left side of segments 1-4, dorsal aspect. 2. P. *orestes*, left side of segments 10 and 11, dorsal aspect. 3. *P. aculeatus*, femur of 3rd leg of male. 4. *P. flavocinctus*, femur of 3rd leg of male. 5. Sternal process of 5th segment, *P. orestes*. 6. The same, *P. flavocinctus*. 7. The same, *P. aculeatus*.

As already remarked by Cook (1898: 704) it is highly probable that Peters' earlier name *aculeatum* is a senior synonym of *longipes* even though the species was based upon a female. There is close agreement in all external details, and the type localities are only 80 km (48 miles) apart (details on the identity and location of "Borror" from Bauer et al, 1995).

Attems' illustration of the gonopod in his "System der Polydesmiden" is inaccurate, drawn from a distorted slide preparation. In 1937 he gave a much better drawing which shows *longipes* to be very similar to *flavocinctus* in gonopod structure, but with the dorsal femoral process shorter and deltoidally expanded apically. Examination of Attems' type series gave the opportunity to make more precise drawings (Figs. 8 and 9) of gonopod structure which show the characters of *longipes* more clearly and permit comparison with other members of the genus.

Cook's 1898 account of *longipes* contained an inadvertent contradiction: in the generic diagnosis he alluded to ventral processes from the femora of the 5th and 6th pairs of legs, whereas in the specific description the 4th and 5th legpairs are correctly so specified. I provide here (Fig. 3) a drawing of the 5th femur of a lectoparatype for comparison with the same structure in *flavocinctus*.

Phaeodesmus flavocinctus (Pocock)
(Figs. 4, 6, 10, 11)

Tetracentrosternus flavocinctus Pocock, 1896, Ann. &. Mag. Nat. Hist. (6) **17**: 438, fig. 5. Male holotype (Brit. Mus. Nat. Hist.1893.11.9.44) labeled "Leikipia and Ngatana" [Kenya] (J. W. Gregory).

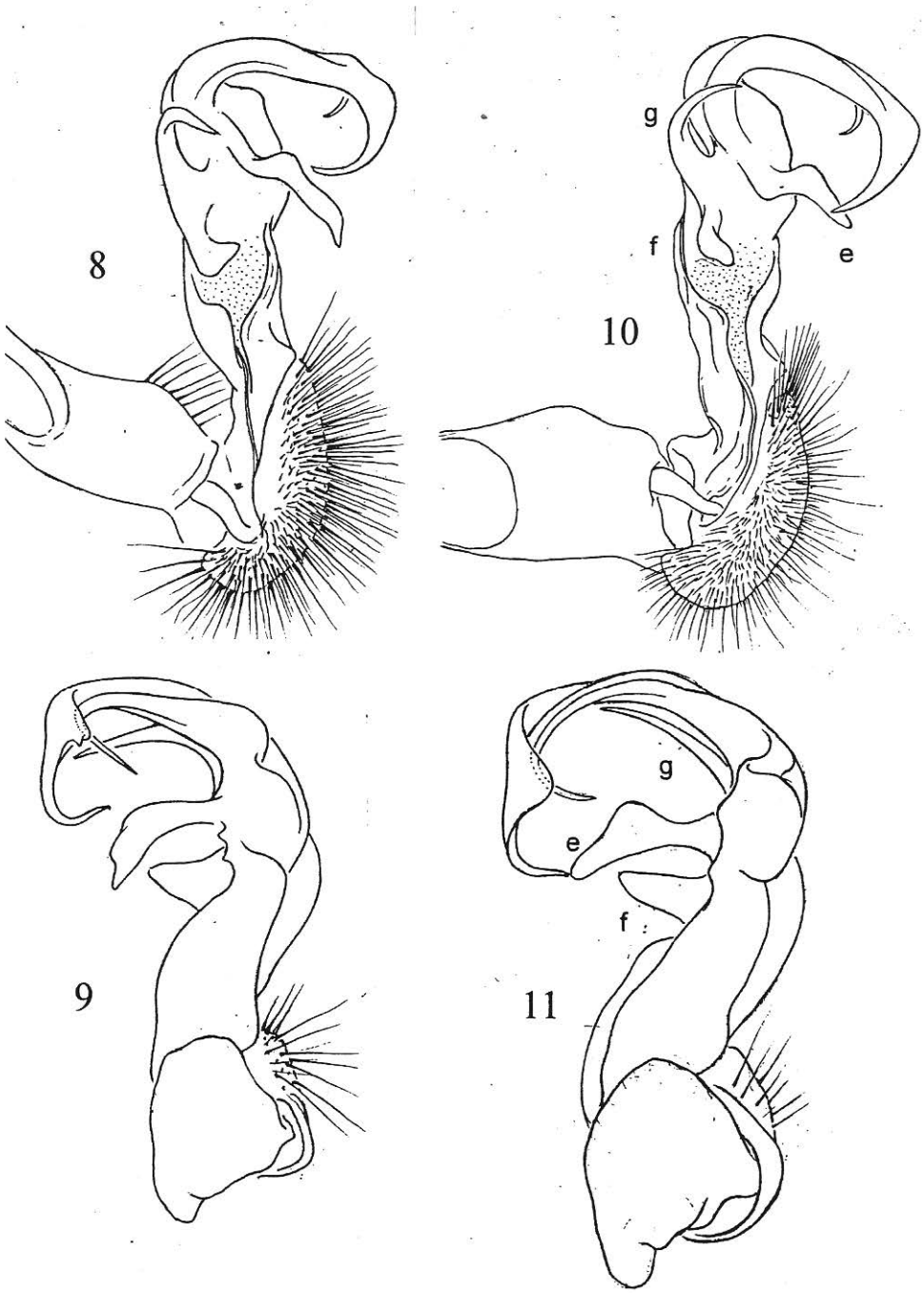
Habrodesmus flavocinctus: Cook, 1898, Proc. U. S. Nat. Mus. **20**: 702.--Attems, 1937, Tierreich **68**: 182.

Phaeodesmus flavocinctus: Jeekel, 1968, Paradoxosomatidae: 105.

MATERIAL: The holotype (BMNH); also **Tanzania**: *Rufiji District*: Mafia Island, evergreen forest on coral, near Mrora village , W. A. Rodgers and J. B. Hall leg. 19-20 February 1983 (VMNH 1♂, 3♀♀).

Pocock's illustration of a gonopod from his type specimen was made from the appendage *in situ,* and despite its small size is quite accurate. It is curious that neither Cook nor Attems, working later with material of *"longipes"* and *alatus*, did not compare their specimens from the same orientation, a measure which would have surely revealed the close structural similarity.

Inspection of the drawings (Figs. 10-11) made from the holotype will show that despite its somewhat distant geographic position, *flavocinctus* is closely related to *aculeatus*. It seems entirely possible that these nominal taxa are only geographic races of a single species. But so long as they remain known only from very widely separated localities - with the implication of effectual reproductive isolation - a conservative non-judgmental posture seems warranted. The fact that only one collection of *flavocinctus* has been made in coastal Tanzania despite extensive collecting in recent decades is noteworthy, and may reflect a declining, fragmentary range.



Figs. 8-11. Gonopod structure of *Phaeodesmus* species. 8. *P. aculeatus*, mesal aspect. 9. *P. aculeatus*, ventral aspect. 10. *P. flavocinctus*, mesal aspect. 11. *P. flavocinctus*, ventral aspect. f, g: dorsal femoral processes; e, postfemoral process.

Phaeodesmus orestes, new species
(Figs. 1, 2, 5, 12-14)

MATERIAL: Male holotype (MRAC) from **Malawi**: Nyika Plateau: Chelinda, 2300 m. ASL, 7 December 1981, R. Jocque leg.

NAME: The Greek word for "mountaineer", in reference to the upland habitat of the species.

DIAGNOSIS: Distinct by the absence of adenostyles on the 5th male legs, by the shorter, less curved, gonopod telopodite, with a basal spine on the tibiotarsus, and by the more proximal placement of femoral process *f* + *g*.

HOLOTYPE: Adult male, length not measureable owing to fragmentation, but about 22 mm, width over most of body 2.1 mm. Color almost entirely bleached by preservative, but appearing to have been dark brown with legs, antennae, paranota, and a broad transverse band on each metatergum yellow.

Head without modifications, supra-antennal organ small; antennae long (4.3 mm) and slender, reaching back to 5th segment, articles 2-6 about equal in length, 6th slightly clavate distally; 7th truncate-conic, about as long as its diameter.

Segments smooth dorsally, metaterga with transverse sulcus evident on segments 4-12, thereafter more obscure, no rows of setae visible; prozona telescoped about half their length at midbody, stricture without evident costulation or striation. Anterior segments convex, with paranota set low on sides, largest on segment 2 where both anterior and posterior corners are acutely produced; thereafter anterior corner replaced by an even curve (Fig. 1). Paranota placed progressively higher on sides, dorsum at midbody thus nearly horizontal, generally only large enough to accomodate ozopores, latter placed near posterior end (Fig. 2). Epiproct conical, the apex not divided or bituberculate, sides without enlarged tubercles.

Legs long and slender, nearly glabrous, attached to low, unmodified podosterna, about as wide at midbody as adjacent prefemora; lengths of podomeres 3=6>5>4>2>1, 2-5 each slightly clavate distally, 6th gradually attenuated, with sparse setation especially ventrally. Entire length of tarsi with brush of dense setae bck to legs of 9th segment; tibiae with ventro-apical tuft of setae back to 7th segment. Femora of anterior legs without adenostyle.

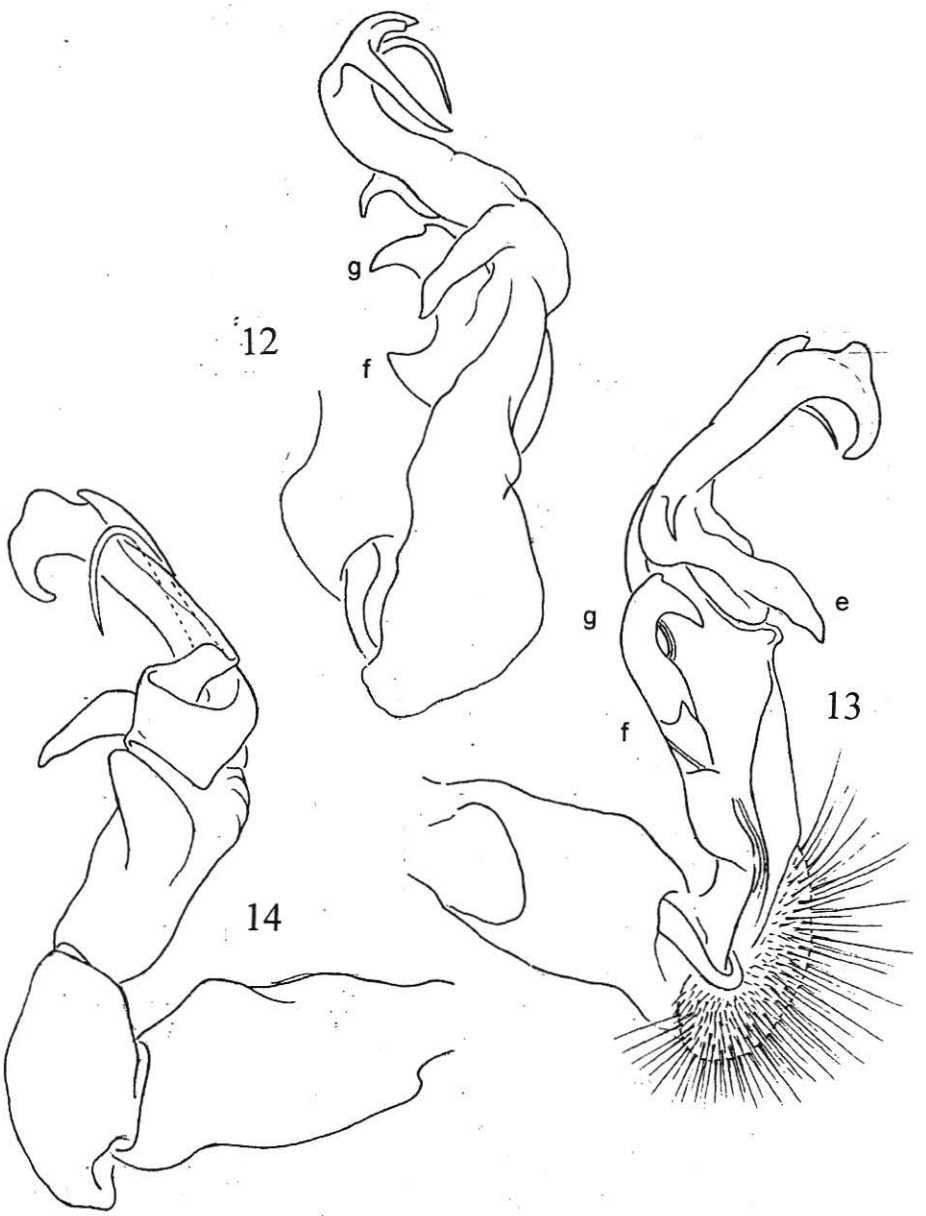
Sternum of 5th segment with median sternal process between anterior pair of legs (Fig. 5), slightly longer than wide, slightly emarginate mediodistally.

Gonopods similar to those of other species, distinctive in the shorter, less arcuate tibiotarsal region with a small spiniform basal process on median side. Femoral process *f*+*g* more proximal: *g* basal to *e* (mesal aspect!) rather than distal to it.

Phaeodesmus alatus (Attems)

Podochresimus alatus Attems, 1928, Ann. South African Mus., **26**: 244, figs. 513-515. Type material (S. Afr. Mus., Naturh. Mus. Wien) from Inhambane, Mozambique..

Phaeodesmus alatus: Attems, 1937, Tierreich **68**: 220, fig. 277. – Jeekel, 1968, Paradoxosomatidae, p. 105.



Figs. 12-14. *Phaeodesmus orestes*, n. sp. left gonopod of holotype. 12. Ventral aspect, "in situ". 13. Mesal aspect. 14. Lateral aspect. Abbreviations as for Figs. 10 and 11.

Cnemodesmus alatus: Hoffman, 1953, Proc. Biol. Soc. Washington, 66: 81.

Phaeodesmus subtropicus Lawrence, 1966, Zool. Africana, 2(2): 244, figs. 5a-5f. Male holotype (NMP 8988) from confluence of the Levubu and Limpopo rivers, west of Pafuri, Northern Province, South Africa (R. F. Lawrence). **New Synonymy!**

SYNONYMY: Comparison of the published information shows a remarkable similarity in the descriptions and drawings for *alatus* and *subtropicus*, as was indeed admitted by Lawrence when describing the latter. His distinction involving the position of the solenomere (his "tibial process") is clearly illusory, as that structure as shown in Attems' drawing (1928: fig. 513) was obviously dislodged from its natural position, a common condition in specimens through this family. In fact the major feature cited to separate the two was the greatly elongated sternal process of the 5th segment shown in Attems' drawing (1928: fig. 515) for *alatus*. I am convinced this drawing is inaccurate, firstly because the shape of this process is so uniform in other members of the genus, secondly because Attems' drawing shows the process as bipartite with a transverse, sinuous, subabasal line: if the part distad to that line be removed, the proximal remnant has exactly the size and shape seen in other species including "*subtropicus*" Lastly, the type localities are only 500 km apart, in this genus not a significant distance considering the more than 1500 km spanned by the range of *aculeatus-flavocinctus*.

Lawrence illustrated the gonopod of *subtropicus* from a lateral aspect, against the standard mesal aspect employed by Attems for *alatus*, making comparison of structures difficult. The drawings of neither author clearly indicated the several subdivisions of the telopodite.

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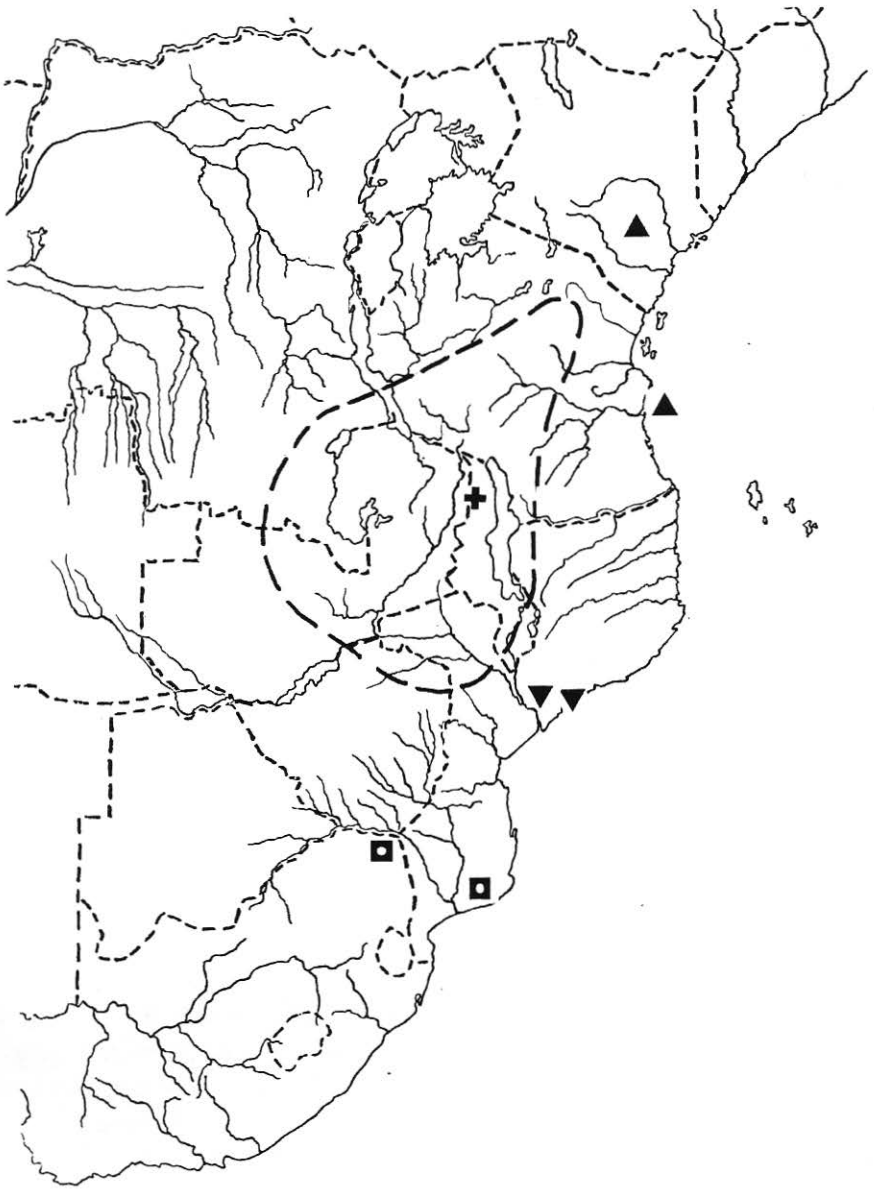

Fig. 12. Distribution of the four species of *Phaeodesmus* in East Africa. Triangles, *P. flavocinctus;* cross, *P. orestes*; inverted triangles, *P. aculeatus*; squares, *P. alatus*. The currently known range of the related genus *Aklerobunus* is indicated by the heavy dashed line.

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