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A review of the milliped genus *Haplogonopus* with commentary on the so-called "Charactopygus-Bildung" modification of spirostreptid paraprocts (Diplopoda: Spirostreptidae)

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Abstract

The status of the monotypic taxon *Haplogonopus* (Verhoeff, 1941), proposed for a disjunct Tanzanian spirostreptoid, is reviewed in light of two additional species, which despite different peripheral appearances, are referable to this genus on the basis of genitalic features. *Haplogonopus inflatannulus* Verhoeff is redescribed from topotypic material, the nominal species *Charactopygus jeanneli* (Brolemann, 1920) is relocated in *Haplogonopus* (**n. comb**.), and the **new species *H. cingulatus*** is described from the Rondo Plateau in southeastern Tanzania. A terminology for the modified paraproct structure ("Charactopygus-Bildung") of spirostreptids is proposed.

Key words: Spirostreptidae, *Haplogonopinae*, *Haplogonopus*, paraprocts, Tanzania, Kenya

Introduction

Haplogonopus, proposed by Verhoeff in 1941 to accommodate a single species from east central Tanzania, has spent the past six decades in the obscurity not uncommon for monotypic genera of tropical millipeds. As implied by the name, this nominal taxon was based largely upon the "simple" form of the gonotelopodite, by which Verhoeff was so impressed that he justified a new subfamily Haplogonopinae [*sic!*] with the statement "*Ausgezeichnet vor allen anderen Spirostreptiden sowohl durch die völlig einfachen Exospermiten, welche weder tibiale noch tarsale Erweiterungen, noch Dornfortsätze besitzen.*"

Subsequent references to *Haplogonopus* have been few and unsympathetic. Attems (1950: 186) considered it to be a synonym of *Eumekius*, without expressing an opinion on the status of the type species *H. inflatannulus.* Demange (1970: 381) provisionally admitted *Haplogonopus* to his category *"Télopodite flagelliformes sans différenciations tibiotarsales"*; he felt that the original description did not offer adequate information on which to make any judgement aside from disagreement with Attems' placement under *Eumekius.* My "Classification" (1980: 93) listed the name provisionally, stating "Status of this genus and number of species uncertain" and, without comment, relegating the subfamily name to the limbo of synonymy under Spirostreptidae. Taking a more draconian stance, Krabbe (1982: 196) disposed of *Haplogonopus* as a junior synonym of her broadly-defined *Spirostreptus.*

Quite some years ago, it was my good fortune to receive a number of collections from the type locality of *H. inflatannulus*, thus having the opportunity to examine Verhoeff's assertions about its taxonomic status. Despite concluding that the genus was defensible, and using the name in my discussion of millipeds in the "Eastern Arc" mountains of Tanzania (1993: 106), I failed to publish any explication of my views, and so *Haplogonopus* languished for an additional decade.

While any small contribution to the taxonomy of tropical millipeds needs no apology, a primary rationale for consideration of this genus is the position it assumes in the broader context of spirostreptid classification, namely, the primacy of telopodite structure over unusual peripheral features in framing generic definitions.

It is reminded that the genus called *Spirostreptus* as defined by Attems and Krabbe was extremely heterogenenous, and with the recent fixation of the name *Spirostreptus, sensu* Brandt, 1833, to the taxon previously known as

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Triaenostreptus (Hoffman *et al.*, 2001), the name can no longer be associated with any of the species referred to it prior to that time. These must now be distributed among a number of generic groups defined more stringently, and with consideration of character systems other than gonopods. *Haplogonopus* must be one of such taxa, and is here considered in the role of a "test case."

Taxonomy

Family Spirostreptidae

Haplogonopus Verhoeff 1941.

Haplogonopus Verhoeff, 1941, Jenaische Zeitschr. Naturw., 73: 265. Proposed for a new species.
Type species: *H. inflatannulus* Verhoeff, by monotypy.
Haplogonopus: Hoffman, 1980, Classification of the Diplopoda, p. 93.

Definition. Moderate-sized spirostreptids, length 50–120 mm. Gonopod structure generalized; a median sternal sclerite present in various forms but basically small and transverse; coxal folds of simple form, not closely applied resulting in an open gonoschisma with telopodite partly visible in anterior aspect, metaplica produced laterad as an acuminate projection, proplica slightly broadened distally, produced distomesad, the mesal edge bearing a slender aciculate apical process (Figs.6–8, *a*). Telopodite long and slender, carried on the anterior side of coxal folds, torsal region distinctly distad of arculus, elongated and gradual, an antetorsal process present in one species, posttorsal telopodite attenuated, without marginal processes, cingulate in one species, a minute apical lobe present.

Remarks. Spirostreptids are generally so conservative in terms of peripheral characters that almost any modification is conspicuous and invites utilization in the definition of new taxa. One of the features thus noted by Verhoeff and memorialized in the species name *inflatannulus* is the greater diameter of the metazona and their ornamentation with elongate shallow depressions (cf. Fig. 5). When taken in combination with the gonopod structure, such modification rather justifies Verhoeff's decision to propose a new genus and subfamily for this one taxon..

However, a definition of the genus on the basis of gonopod structure only, as here proposed, results in the inclusion of two additional species with isoplanar metaterga and modified paraprocts, implying that the "inflatannulus" condition reflects differentiation at the species level only. Comparison of the drawings here provided leaves no doubt that the gonopods of these three forms are very similar, implying a close degree of relationship. The form and location of proplical process *a* is a convincing shared apomorphy. Perhaps some unusual environmental condition in the Uluguru Mountains evoked disjunct peripheral modifications in one of the three species.

If the peripheral features of *H. inflatannulus* are considered to be of specific importance only, a search for possible related taxa may be directed towards other regional genera having similar genitalic structure. Some reasonable candidates would include the nominal genera *Macrolenostreptus* and *Elkestreptus*, both with species in eastern Tanzania. Attention is also directed to the similarity of gonopod structure between *H. cingulatus* and the Madagascar species "*Spirostreptus" micromelas* Saussure & Zehntner, 1897, in particular the subspecies *croceipes* Brolemann 1923. If this similarity is not merely a case of random homoplasy in a number of traits, a case might be made for inclusion of *micromelas* in *Haplogonopus*.

Comparison of specimens should, of course, precede any formalized generic placement.

Range. Higher elevations in central Kenya and southeastern Tanzania (Fig. 12).

Species. Three.

Key to species

1. Metazona convex, of a distinctly greater diameter than prozona, imparting an annulate aspect to the body profile, each with about 10–12 elongate, shallow depressions; ozopore located at the anterior end of a thin shallow groove (Fig. 5); paraprocts convex, virtually immarginate, the edges in contact . . . . . *inflatannulus.*
- Metazonal diameter not notably greater than prozonal, body profile essentially parallel-sided; surface of metazona without elongate depressions; ozopore not at anterior end of distinct elongate groove; paraprocts diastemmate. . . . . 2.

2. Telopodite with a prominent, acuminate, antetorsal process, posttorsal region evenly curved in one plane; body uniformly black; metazona middorsally smooth; paraprocts not fossate, the diastemma narrow . . . . . *jeanneli*

- Telopodite without trace of antetorsal process, posttorsal region with prominent reflexed cingulum (Fig. 9); body annulate; the metazona piceous to black, prozona light gray; metazona with middorsal belt of fine but distinct longitudinal ridges; paraprocts distinctly fossate . . . . . *..cingulatus.*

Haplogonopus inflatannulus Verhoeff

Figures 1–6

Haplogonopus inflatannulus Verhoeff, 1941, Jenaische Zeitschr. Naturw., 73: 265, figs. 45–47. Male holotype (Zoologisches Staatssammlung München) from "...dem Gebirge bei Morogoro am Tanganyikasee..." [=North Uluguru Mountains, Morogoro Region and District, Tanzania], W. V. Harris leg.

Spirostreptus nebularius Kraus, 1958, Veröff. Überseemus. Bremen, A, 3: 10, text fig. 2, pl. 3, figs. 27–29. Male holotype (Überseemuseum Bremen) from Lukwangule Peak, Uluguru Mountains, Morogoro Region and District, Tanzania, H. Knipper leg. 2 July 1952. **New synonymy.**

Spirostreptus inflatannulus: Krabbe, 1982, Abh. Naturw. Ver. Hamburg, NF 24: 204.

Spirostreptus nebularius: Krabbe, 1982, Abh. Naturw. Ver. Hamburg, NF 24: 207.

Haplogonopus inflatannulus: Hoffman, 1993, in: *Biogeography and Ecology of the Rain Forests of Eastern Africa,* p. 106.

Material. TANZANIA: Morogoro Region and District: *Northern Uluguru Mountains*: Lupanga Peak West, 1800 m, 1 July 1981, Nikolaj Scharff and Michael Stoltze, 6 ♂, 2 ♀ (ZMUC); north slope of Lupanga, 11 January 1980, S. N. Stuart & T. van der Willigen, 1♀ (VMNH); in forest near Morningside, 23 December 1973, K. M. Howell et al., 5 ♂ (VMNH); Morningside, 27 April 1980, K. M. Howell, 1♂ (VMNH). *Southern Uluguru Mountains:* Hululu Falls, Mgeta River valley south of Bunduki, 6000 ft asl, 16 November 1979, W. A. Rodgers & K. Bulstrode, 1♂ (VMNH), also 1♂, 1♀, date and collector not specified (VMNH); Bondwa Mountain, Uluguru Forest Reserve, 24 April 1980, J. Kielland, 1♂ (VMNH); 2 February 1982, Kielland, 1♀ (VMNH).

Diagnosis. Distinguished from the two known congeneric species (and other Tanzanian spirostreptids) by its larger size, elevated, orange-red metazona, and unmodified paraprocts.

Descriptive notes. Male diameter to 6.5 mm, female to 9 mm, female length to about 110 mm. Front of head smooth and convex, unmodified, ocellaria elongate-triangular, about as long as interocellarial space. Mandibular basomere with distal projection (Fig. 2).. Elevated part of metazona orange to light brown, prozona grayish, in preserved specimens, legs yellow. Postfemoral and tibial pads of male small, diminishing posterior to gonopods, scarcely evident posterior to legs of 25th segement. Sigilla small, generally bacilliform but highly variable, dispersed as an irregular belt over anterior two-thirds of pigmented metazonal surface. Paraprocts strongly convex, the caudal edges virtually immarginate, no trace of fossae or diastemma. Hypoproct short, transversely elongated.

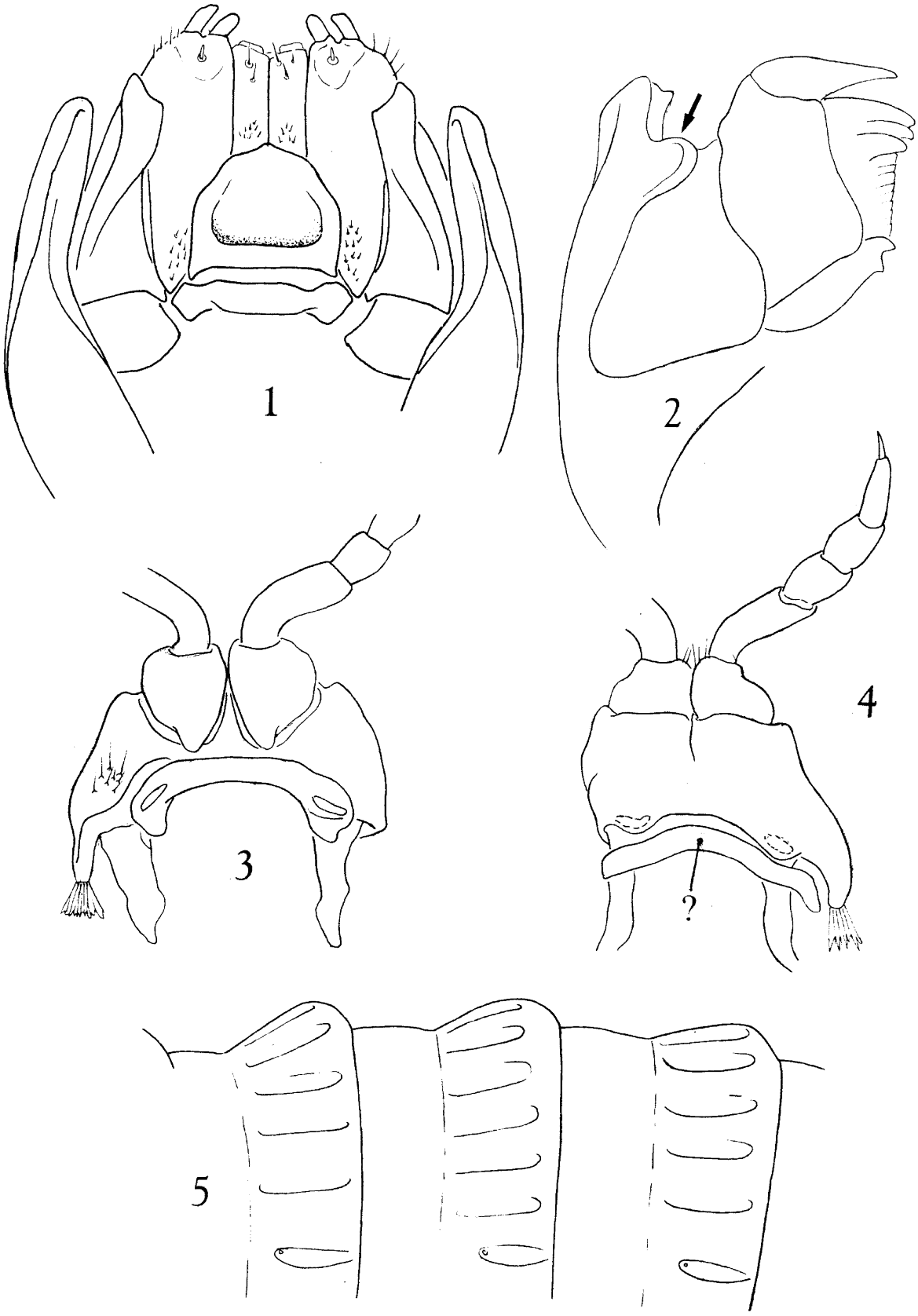
Coxae of 1st pair of legs medially coalesced with only a trace of suture line on posterior side, this syncoxa only slightly prolonged laterad beyond base of prefemora. Sternum of these legs with distinct stigmata .

Remarks. Although I have not examined the type material of either *inflatannulus* or *nebularius*, the original accounts of these names leave no doubt of their actual identity, as further substantiated by the study of topotypic specimens.

The legs of the first pair are of the conventional spirostreptid form, prefemoral lobes relatively small and subtriangular, but of interest by the presence of a transverse sclerite (Fig. 4, ?) subtending the syncoxon on the posterior side.. Whether this is merely the detatched continuation of the sternum or an intercalary element between the 1st and 2nd leg pairs could not be established with the material at my disposal.

General uniformly within the several samples available for study suggest that apparently the Uluguru Mountains are not extensive or fragmented enough to have engendered any local diversification (although only a few specimens originated in the southern component of the range). Segment counts (including collum but not the epiproct) range between 47 and 51 (avg. 48.7) in 14 males, and 48–51 (avg. 50.2) in five females. Gonopods show what appears to be only minor individual variation.

The gonopods of *inflatannulus* are so similar to those of *jeanneli* that I initially suspected that the latter was a synonym based on specimens transported from the Ulugurus into Kenya in plant material although the virtual absence of commerce between Kenya and Tanganyika in the early colonial period seemed to militate against such an option. My colleague J.-P. Mauriès examined the type specimen of *jeanneli* and reported that the metazona are



FIGURES 1–5. *Haplogonopus inflatannulus* Verhoeff., structural features. 1. Gnathochilarium and adjacent parts of mandibles and collum. 2. Right mandible, posterior aspect, with distal lobe of basomere indicated by the ←. 3. First pair of legs of male, syncoxa, sternum, and basal podomeres, anterior aspect. 4. The same, posterior aspect, sclerite of uncertain identity indicated by the **?** 5. Dorsal half of three midbody segments, lateral aspect, showing convex metazona with ovoid depressions.

absolutely flat and smooth, confirming the status of *jeanneli* as a valid species, as do additional characters mentioned in the following accounts. This, with another "smooth-bodied" species discovered in southern Tanzania, gives the impression of a fragmented generic range resulting from late Tertiary climatic changes, and the evolution of singular peripheral characters in the Uluguru isolate. Such a scenario evokes the possibility, even liklihood, that additional highly localized species may yet be discovered in, e.g., the Usambara or Nguru mountains.

Haplogonopus jeanneli (Brolemann), new combination

Figure 7

Charactopygus jeanneli Brolemann, 1920, in: Res. Sci. Voy. Alluaud & Jeannel en Afr. orient., 3: 95, text figs. xvii–xx, pl. VII, figs. 34, 35. Male holotype (Museum.national d'Histoire naturelle, Paris) from *"Pays Kikuyu. . .forêt de Nairobi, district de Kyambu"* [Kenya], Exped. Alluaud-Jeannel leg. 29 December 1911.
Spirostreptus jeannelli [sic]: Attems, 1950, Ann. Naturh. Mus. Wien, 57: 188.
Charactopygus (?) jeanelli [sic]: Krabbe, 1982, Abh. Naturw. Ver. Hamburg, NF 24: 425.

Diagnosis. This species is distinguished from *H. cingulatus* by the presence of a prominent, acuminate, antetorsal process on the gonotelopodite, which also lacks a posttorsal cingulum. The body is uniformly shiny black, with legs and antennae yellow. Diastemmal width not greater than the thickness of a labium, the latter not basally fossate.

Remarks. The generic placement of this species was equivocal from the beginning. Brolemann himself remarked that "*Ces deux especes ne sont pas typique*" in contrasting his new forms *C. jeanneli* and *C. lucifugus* against the more characteristic members of the genus inhabiting various islands in the Indian Ocean. The so-called "*Charactopygus-Bildung"* of the paraprocts (in which the thickened marginal rims are separated by a small basal flange on the inner edge, see "Commentary" below), is now generally considered to have only specific value in classification, Krabbe (1982: 135) having defined *Charactopygus* on the basis of gonopod structure instead. The modification seems to have been Brolemann's rationale in assigning his Kenyan species to *Charactopygus*.

The similarity of *jeanneli* to *inflatannulus* in gonopod structure is noted under that species, and is evident from Brolemann's two figures of the gonopods, one reproduced as figure 7. That the telopodite is shown as nearly straight is probably the result of the gonopod having been macerated in a caustic solution.

Distribution. Known only from the type locality, despite a modicum of general collecting in Kenya in recent decades. It is not certain if this patch of forest has survived the burgeoning population growth and rampant forest clearing around Nairobi, and it is possible that *jeanneli* is extinct.

Haplogonopus cingulatus, new species

Figures 8–9

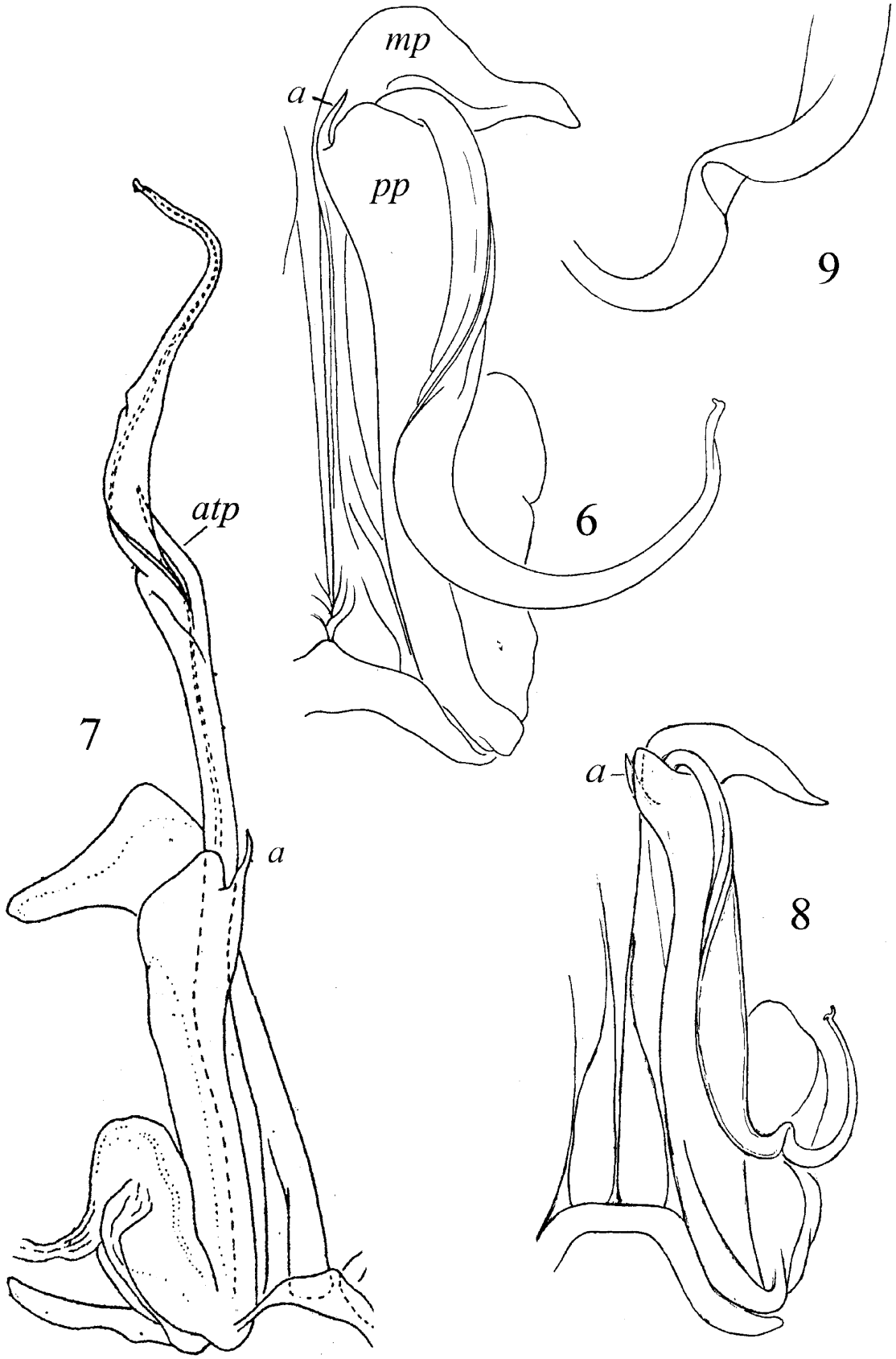
Diagnosis. Telopodite of gonopod without antetorsal process, its posttorsal region with distinct abrupt flexure (Fig. 9); paraprocts fossate and diastemmate; prementum without deep paramedian pits; metazona with a median belt of indistinct fine ridges

Material. Male holotype (Virginia Museum of Natural History Martinsville) from the Rondo Plateau (10º10'S, 39º10'E), 800 m. ASL, ca. 60 km WSW of Lindi, Lindi Region, Tanzania; Jan Kielland leg. 1 April 1986 ("in thick forest"). Male and female paratype (VMNH) from the Litipo Forest Reserve (10º02'S, 39º29'E), ca. 200 m ASL, Lindi District and Region, Tanzania; "Frontier Tanzania" group, July–September 1993.

Holotype: Body with 48 segments. Broken into fragments; maximum diameter at midbody, 8.0 mm.

Coloration annulate: prozona and front half of mesozona yellowish-gray, metazona black (restricted to posterior margin on lower sides); legs and antennae yellow, probably lemon yellow in life.

Head convex, smooth, surface undmodified. Ocellaria large, subtriangular-reniform, 2.2 mm long, and close-set, twice the interocellarial width of 1.1 mm. Gnathochilarium similar to that of *inflatannulus,* proportionately a little wider and with much deeper mental cavity; basilar sclerite intact, shallowly indented on each side of middle but not distinctly fossate. Basomere of mandible without medially directed apical process.



FIGURES 6–9. *Haplogonopus*, gonopod structure of three species. 6. *H. inflatannulus*, right gonopod, anterior aspect. 7. *H. jeanneli*, left gonopod, anterior aspect (adapted from Brolemann, 1920). 8. *H.cingulatus*, right gonopod, anterior aspect. 9. Midlength section of posttorsal telopodite, enlarged, to show form of cingulum. Abbreviations: *a*, apicomedial process of proplica; *atp*, antetorsal process of telopodite, *mp*, distal end of metaplica.

Prozona and mesozona smooth, without concentric striations. Metazona somewhat coriaceous, with a middorsal belt of fine, parallel longitudinal ridges (most evident on dried surface). Sides of segment below ozopores with fine striations, larger and more prominent on segments 2–8, where projecting beyond edge of metazona as small prominent knobs. Ozopores very small, placed on metazona at about midlength, not associated with a longitudinal groove. Distal margins of paraprocts diastemmate (Figs.10d, ll). Legs long (7.6 at midbody) and slender, three podomeres visible from above when extended. Tibial pads present back to legs of 36th segment; postfemoral pads smaller, visible only to 30th segment. Posterior coxal cavities closed, with median projection. Anterior sternum smooth, posterior with median carina. Procoxae and metacoxae slightly dissimilar, the latter somewhat thicker and more produced caudally. Sigilla small, rounded, in a single row placed at midlength of pigmented belt of metazona.

First legs similar to those of *H. inflatannulus* (Fig. 3). projecting directly anteriad and actually longer than suggested by the posterior aspect drawing in which they are foreshortened.

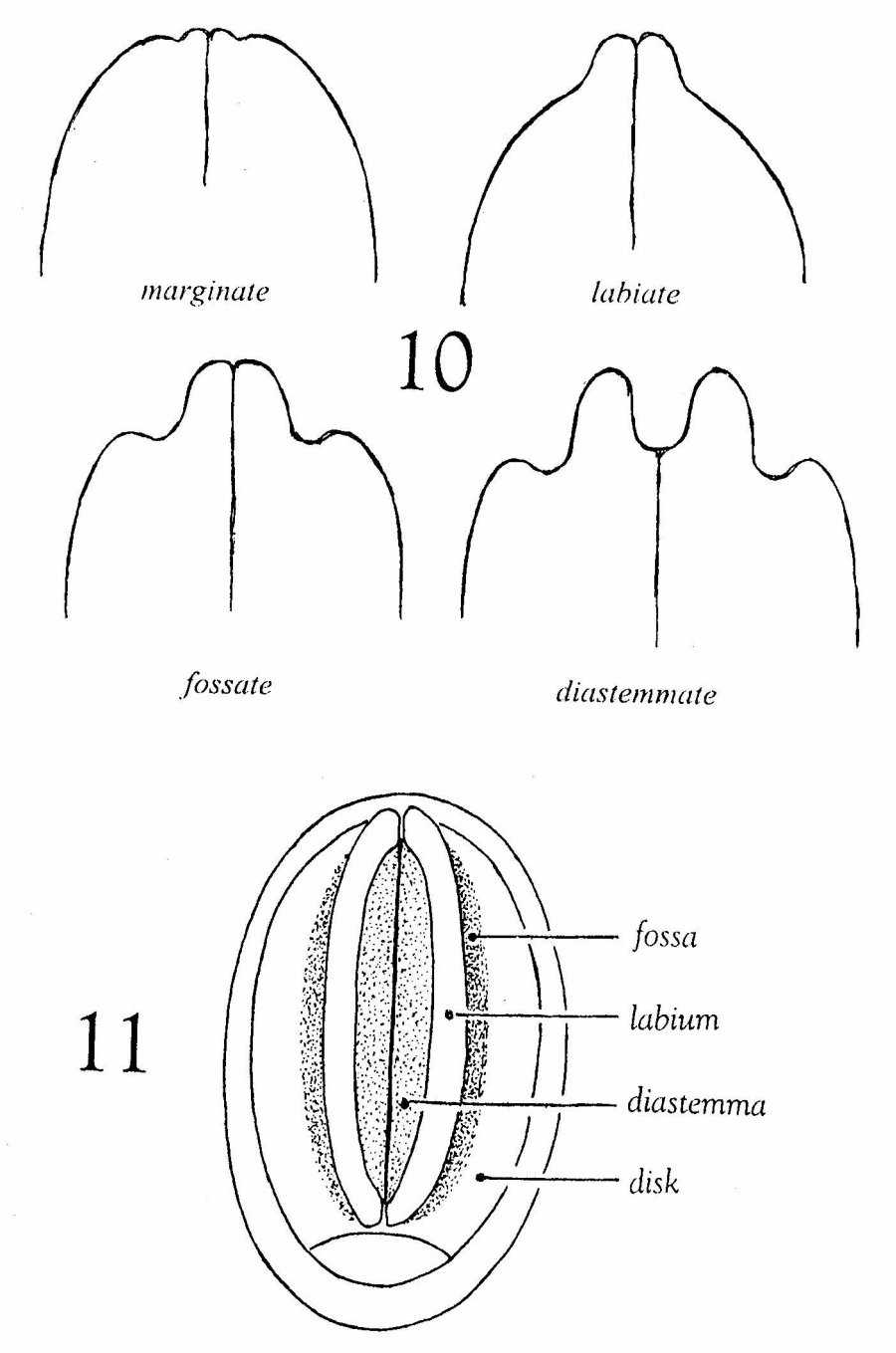


FIGURE 10. Diagrammatic cross-sections representing four modifications of paraproct structure.
FIGURE 11. Schematic representation of "diastemmate" modification of paraprocts, posterior aspect.

Gonopods (Figs.8, 9) similar to those of *inflatannulus*, but mesal edge of the proplica slightly incurved distally, partly obscuring the apical process *a*. Telopodite with extended torsion region, no antetorsal process present, posttorsal region with distinct cingulum at about midlength.

Name. Refers to the reflexed modification (cingulum) of the posttorsal region of the gonotelopodite.

Distribution. While known so far only from two localities on the Rondo Plateau, this species may occur southward into adjacent Mozambique (Fig.12).

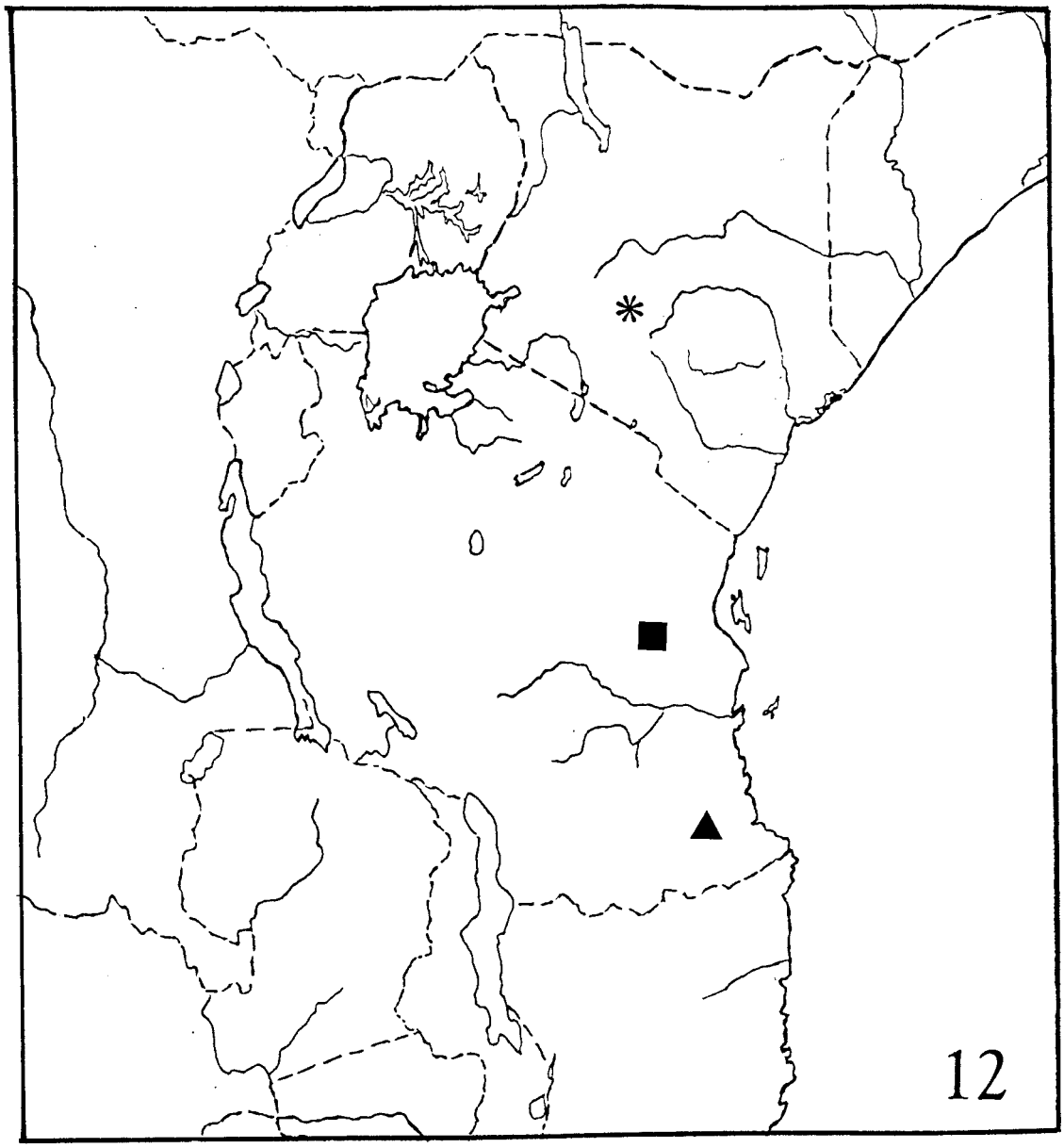


FIGURE 12. Tanzania and adjacent countries, showing known localities of the three species of *Haplogonopus*. Star, *H. jeanneli*; square, *H. inflatannulus*; triangle, *H. cingulatus*.

Observations on the "*Charactopygus*-Bildung" character

The form of the paraprocts (*olim* "anal valves", "analklappen", "valves anales") has been used as a character in the taxonomy of spirostreptoid millipeds for a long time (at least since Karsch, 1881) but not in a systematic way prior to the great monograph on the millipeds of Madagascar by DeSaussure & Zehntner (1897, 1902). In a discussion of variable external characters in this group (1902: 184) these authors concluded that *"C'est seulement dans le forme des valves anales que nous avons pu trouver des caracteres permittant d'etablir une coupure distincte dans le genre"* and "*On peut ensuite etablir des sous-divisions d'apres la forme exterieure des valves"*.

Such a possibility found expression in the new taxon *Charactopygus*, proposed as a subgenus in the body of a key to the Malagasy species of *Spirostreptus* to accommodate 11 species with notably modified paraprocts, none of which was indicated as the type. Attems (1914: 99) recognized *Charactopygus* as a valid genus with 18 species, mostly from Madagascar, but one as far removed as Morocco. But no type species was selected until Brolemann (1923: 74) chose ("*pourra etre*") *Spirostreptus atratus* Karsch. Although *atratus* was not one of the originally included species, Brolemann cited as its junior synonym the name *S. sepia* DeSaussure & Zehntner, which was, and so *sepia* became type through the back door, so to say.

Charactopygus persisted as a valid generic concept through the publications of Count Attems as late as 1938, subsequent to which his support waned and the name was informally subordinated to the synonymy of *Spirostreptus* in his last review of the Spirostreptidae (Attems, 1950). Although *Charactopygus* was not mentioned by name, most of the species assigned to it by Brolemann and Attems himself were included in a key to species of *Spirostreptus*, where taken out in couplet 9: "*Analklappen mit Charaktopygus-Bildung*." This precedent was adopted in the encyclopaedic catalog of Spirostreptidae by Dr. Krabbe (1982: 135) who concluded that "*Die Charactopygus-bildung mag allenfalls ein Artmerkmal liefern.*"

The weight of recent opinion, including the information presented in the foregoing pages, is that the modified paraprocts reflect differentiation at the species level only. Although DeSaussure & Zehntner very carefully described the various ways in which these sclerites are modified (1902: 185), and provided illustrations of three variations, there exists so far no descriptive terminology. To facilitate description of paraproct modifications in the definition of species, I suggest here a provisional nomenclature intended to replace the awkward vernacular names applied in previous accounts. The four categories are very likely stages in a transformation series, and intermediate expressions may certainly be expected.

The condition, in which the distal (posterior) edges of the paraprocts are in close contact, is so prevalent in diplopods generally that it can only be considered to be a plesiomorphic expression in the Spirostreptidae. Other modifications, such as enlargement of the margins and their internal separation from the line of contact, may reasonably be considered as derived. The only descriptive term known to me that refers of this formation is Attem's term "Charactopygus-Bildung" that apparently dates from his initial use in "Afrikanischen Spirostreptiden" (1914: 103).

1. *Marginate*. The paraprocts are evenly convex, their posterior edge set off by a low narrow *rim* and simply meet at a plane surface (like the appressed two halves of any spherical object cut into two halves). This is a common condition among most groups of diplopods (Fig. 10a). Notably, in *H. inflatannulus* the paraprocts are minimally modified, with a scarcely evident rim on the posterior edge , in strong contrast to the other two species referred to this genus which embody the opposite extreme.

2. *Labiate:* The posterior margin of the paraprocts is compressed and set off from the convex discal surface as a discrete "lip" lying directly in contact with that of the opposed valve. (Fig. 10b). This is perhaps the most common expression of paraproct modification amongst spirostreptoids. Brolemann's term for it was "bourrelet" (flange, in English).

3. *Fossate:* (*fossa*, Lat., a moat or ditch at the base of a wall).The paraprocts are labiate, and the compressed labia are separated from the discal surface by a basal groove of varying depth (Fig. 10c).

4. *Diastemmate:* The condition in which the contact between the posterior edges of the two valves is withdrawn between the labia, the internal bases of which are separated by a flat interlabial space (diastemma) of varying width (Fig. 10d). This is the relationship usually implied by the term "Charactopygus-Bildung". It is not the same as what O. F. Cook described as "reentrant" in species of the spiroboloid family Atopetholidae, in which the paraprocts are convex but not labiate and their commissure is simply withdrawn inward.

Commentary. The situation documented in the foregoing pages represents an issue of interest in the practice of character weighting. Conventional wisdom over the past century has assigned primacy to gonopod structure in the definition of taxonomic categories. But, pragmatically, must gonopods represent an arbitrary taxonomic Absolute to which all structural modifications of body form must be subordinated? If the generic status of some taxon reflects a greater level of its derivation. do peripheral character systems (even if more subject to random environmental selection influences) have no importance in such an assessment? Could not significant peripheral modifications of disjunct species outweigh the overall similarity of gonopod structure?

Selecting this more flexible option would mandate separate generic status for *jeanneli* and *cingulatus*, which although very similar in anatomical characters do not occupy a coherent biogeographic distribution.

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