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THE MILLIPED GENUS *PHALLORTHUS* REVALIDATED: ANOTHER FACET OF A TAXONOMIC ENIGMA (SPIROSTREPTIDA: PSEUDONANNOLENIDAE)

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ABSTRACT

Phallorthus mauriesi is described from specimens taken in Valle Province, southwestern Colombia, providing the opportunity to revive *Phallorthus* from synonymy under *Orthoporus* and determine that the genus is closely related to *Physiostreptus* and *Holopodostreptus*, now placed in the family Pseudonannolenidae (of which Phallorthidae thus becomes a junior synonym). The name *Epinannolene lorenzonus* (Chamberlin, 1923) is referred to *Phallorthus* (comb. nov.!). The occurrence of two gnathochilarial patterns within the Pseudonannolenidae is noted.

INTRODUCTION

Classification of the Diplopoda has more than its share of problems, both taxonomic and nomenclatorial, but few are more intractable than that of relationships amongst the so-called juloid-cambaloid-spirostreptoid groups. And few are more basically comprehensive, since the recognition and definition of taxa at the level of order is at stake.

By way of providing a brief historical account of the situation, it may be said that an entity embracing these forms was first established in 1895 by O. F. Cook, whose order Diplocheta encompassed the suborders Cambaloidea, Iuloidea, Spirostreptoidea, and Siphoniuloidea. Of these, the cambaloids were rather poorly-known, and the siphoniulids even more so (their placement in Diplocheta being an act of intuition rather than of direct knowledge). Nonetheless, at the time there was little reason to doubt the distinctness of the other two, on the basis of both gnathochilarial and genitalic structure.

Almost immediately, however, fragments of a continuum between cambaloids and spirostreptoids began to appear, chiefly in the Neotropical region: such genera as *Pseudonannolene* (Silvestri, 1895), *Epinannolene* (Brolemann, 1903), *Physiostreptus* (Silvestri, 1903), *Holopodostreptus* (Carl, 1913), and *Choctella* (Chamberlin, 1918). These shared a dramatic reduction or loss of the "posterior gonopods" just as occurs in all spirostreptoids. Other characters, such as gnathochilarial sclerites, varied substantially from one genus to another, usually not congruent with gonopodal structure or general habitus.

More or less concurrently, it was realized that in both body form and gonopod structure, some of the generalized juloid taxa (such as Nemasomatidae) closely approximate some of the generalized cambaloids (such as *Cambala* itself). In fact, about the only substantial point of difference occurs in arrangement of the gnathochilarial sclerites. Finally, it is likewise being perceived (e.g. by Hoffman, 1972, and Jeekel, 1985) that some Australian species, traditionally referred to the "cambaloids", show tendencies in gonopod structure toward the highly derived condition of spirostreptoids.

All of these revelations have cast considerable doubt about the actual interrelationships of the three major groups mentioned, and in recent years three differing points of view have been exposed (Hoffman, 1980, Mauriès, 1983, Jeekel, 1985), calling in question the traditional status of existing families, suborders, and orders. The accumulation of more information must preceed any kind of consensus on this subject.

Extensive collections of diplopods from west-central Colombia, assembled by the second author included a curious "cambaloid" obviously congeneric with the enigmatic taxon published by R. V. Chamberlin (1952) under the name *Phallorthus colombianus*. As the status of this creature has long been uncertain, the opportunity to present some observations and illustrations of important anatomical features is taken with much satisfaction, not only for the intrinsic pleasure of solving a small puzzle, but also for the exposure of another element in the cambaloid-spirostreptoid continuum.

SYSTEMATICS

Family Pseudonannolenidae

Pseudonannolenidae Silvestri, 1895, Ann. Mus. civ. stor. nat. Genova, 34: 774. —Jeekel, 1985, Bijdr. Dierk., 55: 101.–Mauriès, 1987, Bull. Mus. natn. Hist. nat. Paris, (4) 9 (A 1): 169.

Physiostreptidae Silvestri, 1903, Boll. Mus. Torino, 18 (433): 14.–Hoffman, 1980, Classification of the Diplopoda, p. 91.—Mauriès, 1983, Bull. Mus., nat. Hist. natur. Paris, (4) 5 (A 1): 250.

Phallorthidae Chamberlin, 1952, Gt Basin Natur., 12: 20.

Apparently generalized spirostreptoid millipeds in which the coxae of the first legs of males are similar to those of Spirostreptoidea (flattened and broadened laterally and prefemora are provided with retrorse basal lobes on anterior side) and posterior legs of the 7th segment are similarly suppressed in the adult male; the anterior legs of that segment (gonopods) are composed of two (possibly 3) immovably coalesced podomeres. the basalmost of which (coxa) lacks a flagellum on posterior side but may contain a deep pit on median side, merging into a prominent internal duct (+ chamber) extending distad but not carried out onto a solenomere or equivalent structure.

The original, very succinct, diagnosis of the group Phallorthidae, stated that the family "apparently" differed from the Spirostreptidae "in having the posterior as well as the anterior legs of the seventh segment modified and functioning as gonopods instead of having the posterior pair missing." The verbal account of the type species *P. colombianus* was reasonably detailed, but the two gonopod drawings offered little to substantiate the statement about retention of posterior gonopods in both the familial and generic diagnoses. Nor was a word of contrast with the local family Pseudonannolenidae provided. In considering the status of this group when compiling the 1980 "Classification", the first author over-reacted to a long sensitivity to Chamberlinian excesses, and placed Phallorthidae as a synonym of

Spirostreptidae without a word of comment (at the time being convinced that Chamberlin had based his new names upon an immature male of some local species of *Orthoporus).*

Owing to the shortcomings of its original description (and possibly acceptance of its unjustified synonymization), *Phallorthus* did not figure in the papers by Jeekel and Mauriès. With access to material of a species obviously congeneric with *P. colombianus,* we are able to restore generic validity to this taxon and refer it to the Pseudonannolenidae as a close relative of both *Physiostreptus* and *Holopodostreptus.* Perhaps more species must be discovered before we can distinguish which characters used to discriminate these three taxa are generic, and which only specific in value. For the present no harm is done by maintaining the separate identity of *Phallorthus.*

The same constraint applies to the question, whether such taxa as Physiostreptidae, Choctellidae, and Epinannolenidae are valid families or better subsumed under the older name Pseudonannolenidae (as suggested by Jeekel, 1985, and Mauriès, 1987). Resolution of this point is not easy to achieve since the traditional taxonomic characters vary in a kind of mosaic, dispersed randomly and without obvious concurrence. However, there has been within the past decade a tendency to minimize the relative systematic importance of, e. g., gnathochilarium structure, when it contradicts indications from male genitalia, as in the case of the animals under consideration. We believe that the initiative of Jeekel and Mauriès is essentially correct and are glad to endorse it at this point.

In such character systems as the first pair of male legs and gonopods of "physiostreptids", there is such evident similarity with comparable features in *Pseudonannolene* that the most striking remaining difference between them — the medially divided promentum of *Pseudonannolene* — seems no longer defensible as a family level character.

The Pseudonannolenidae as now conceived thus appears to contain forms which, as noted by Hoffman in 1980, ". . . suggest to one what a possible protospirostreptid might have looked like" at least in terms of gnathochilarium and first legs of males, as well as some in which the gnathochilarium shows distinctly "cambalid" facies. Perhaps two subfamilial taxa will reflect this difference as a matter of practical convenience, although their cladistic rationale remains to be justified.

Subfamily Pseudonannoleninae Silvestri

The essential structural congruence of the nominal genera *Pseudonannolene, Epinannolene,* and *Cambalomma* implies that the divided promentum of the first-named, and duplomentum of the third, are autapomorphies of individual genera and that a suprageneric taxon including all three must be defined on the basis of some derived character they share in common. Perhaps the fact that the lingual lamellae are largely separated by the apex of the mentum (or promentum) fulfills the requirement (although the polarity of the condition has not been determined).

Subfamily Physiostreptinae Silvestri

Aside from their sympatric occurrence in the northern Andes, the three genera referred to this taxon share the "spirostreptidan" gnathochilarium pattern, in which the lingual lamellae are in contact for their entire length.

Key to genera of Physiostreptinae

1. First pair of legs of male reduced to coxa and a monarticular telopodite; coxae broadly in

contact along entire mesal surface; oral surface of coxa without field of long dense setae; telopodite of gonopod relatively long, slender, and simple, without internal chamber . . . . . *Physiostreptus*

— First pair of legs of male with five normal podomeres distad of coxa; coxae not in contact medially; oral surface of latter with profuse setation; telopodite of gonopod relatively short and broad, with prominent globose chamber at end of internal duct 2

2. Stipes of gnathochilarium extending proximad below level of base of mentum, latter broader than long; mandible with 10 full rows of pectinate lamellae + several incomplete rows; prefemur of first pair of legs of male with prominent fringe of setae on anteromedian surface; coxae broad, extended lateral well beyond apex of femora, not separated by distal extension of sternum; telopodite of gonopod short, about as broad as long, distally membranous and setulose, with a prominent marginal fringe of specialized plumose setae, internal prostatic chamber subglobose . . . . . *Phallorthus*

— Stipes of gnathochilarium not extended proximad below base of mentum, latter longer than broad; mandible with 7-8 rows of pectinate lamellae; prefemur of first pair of male legs without anteromedial tuft of setae, coxae narrow, distally not extended lateral beyond midlength of femora; telopodite of gonopod twice as long as basal width, distally (apparently) without marginal fringe of plumose setae, internal prostatic chamber long and slender, prolonged apically as a spiniform sleeve . . . . . *Holopodostreptus*

Phallorthus

Phallorthus Chamberlin, 1952, Gt Basin Nat., 12: 20. Proposed with a new species. Type species: *Phallorthus colombianus* Chamberlin, 1952, by monotypy and original designation.

Orthoporus (nec Silvestri, 1897) Hoffman, 1980, Classification of the Diplopoda, p. 94 (incorrect synonymization of *Phallorthus* under this name).

Diagnosis: Distinguished from *Physiostreptus* by the form of the first pair of male legs, and from *Holopodostreptus* by the structure of the gonopod telopodite (other differences are stipulated in the foregoing key to genera).

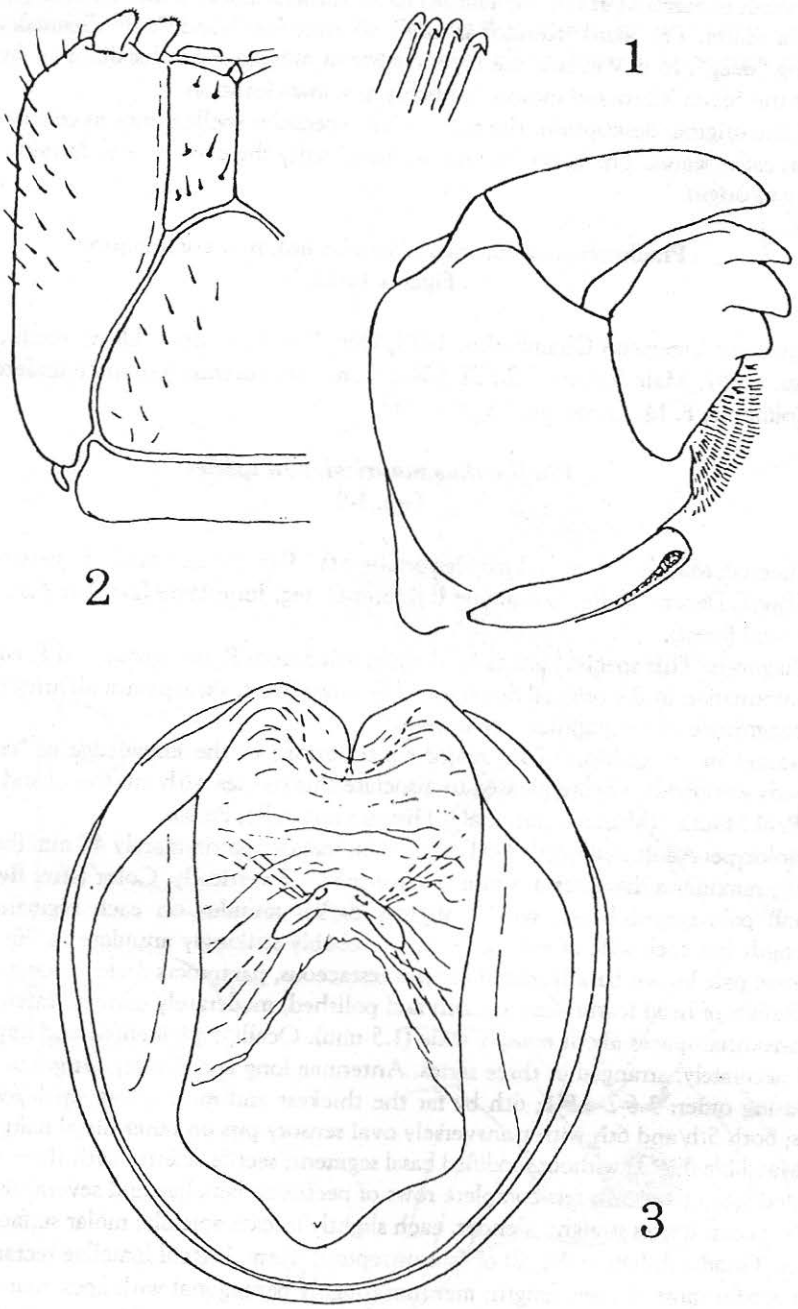
Range: Southwestern and northern Colombia (provinces of Valle and Magdalena).

Species: Three nominal species are referred to this genus. Judged from very schematic published drawings and proximity of type localities, two of them (*lorenzonus* and *colombianus*) are possibly synonyms. Without a study of the relevant type material it is impossible to address this problem, nor construct a key for their separation. However, since the species inhabit widely separated parts of Colombia, where local endemicism millipeds is the rule, it seems likely to us that validity will be confirmed. For the present we provide the essential bibliographic information about the two named species.

Phallorthus colombianus Chamberlin
Figures 10-11

Phallorthus columbianus [sic] Chamberlin, 1952, Gt Basin Nat., 12: 20, figs. 10, 11. Male holotype (Field Museum) from "vicinity of Santa Marta and Manzanaris on River Kondo", Magdalena Prov., Colombia, H. W. Howland leg. 6 August 1902.

According to the most detailed map at hand (produced by the Instituto Geographico



Figs. 1-3. *Phallorthus mauriesi*, structural details. 1. Mandible, with four units of a pectinate lamellae shown (upper center) highly magnified. 2. Right side of gnathochilarium, all setae shown. 3. Seventh segment, anterior aspect, showing sternal remnant in situ on intersegmental membrane at center.

Militar y Catastral, Republica de Colombia, 1950, scale 1:2,500,000) Manzanaris is about 50 km south of Santa Marta on the railroad to Fundacion. There is also a Manzanares River at Santa Marta. The word "Kondo" is surely an error for "hondo", the Spanish adjective meaning "deep". In any event, the type locality of *colombianus* is localized at the western base of the Santa Marta mountains, probably at a low elevation.

In the original description, the name of the species is spelled once as *columbianus* and twice as *colombianus*. The latter version is undoubtedly the correct one, deriving from the country of origin.

Phallorthus lorenzonus (Chamberlin), new combination
Figures 12-13

Epinannolene lorenzonus Chamberlin, 1923, Occ. Pap. Mus. Zool. Univ. Mich., 133: 16, figs. 65-67. Male holotype (MCZ 5066) from San Lorenzo (province undetermined), Colombia, F. M. Gaige leg. 16 July 1913.

Phallorthus mauriesi, new species
Figs. 1-9

Material: Male holotype and female partatype (VMNH) from Vereda El Janeiro, 23 km SE of Buga, Depart. Valle, Colombia; E. Florez D. leg. June 1989 (2000 m ASL in humid subtropical forest).

Diagnosis: This species cannot be distinguished from *P. lorenzonus* and *P. colombianus* from information in the original descriptions of those two taxa; separate identity is assumed from magnitude of geographical separation.

Name: In recognition of his major contributions to the knowledge of "cambaloid" millipeds worldwide, we are pleased to associate this species with our friend and colleague Jean-Paul Mauriès (Muséum national d'Histoire naturelle, Paris).

Holotype: Adult male with 64(1) segments, length approximately 48 mm (broken and curled), maximum diameter 3.5 mm transversely, 3.7 vertically. Color (after five years in alcohol) pale greyish-beige, with a slightly darker annulus on each segment near its midlength (on each side of sulcus), animal probably strikingly annulate in life. Legs and antennae pale brown basally, distal articles testaceous, paraprocts darker brown.

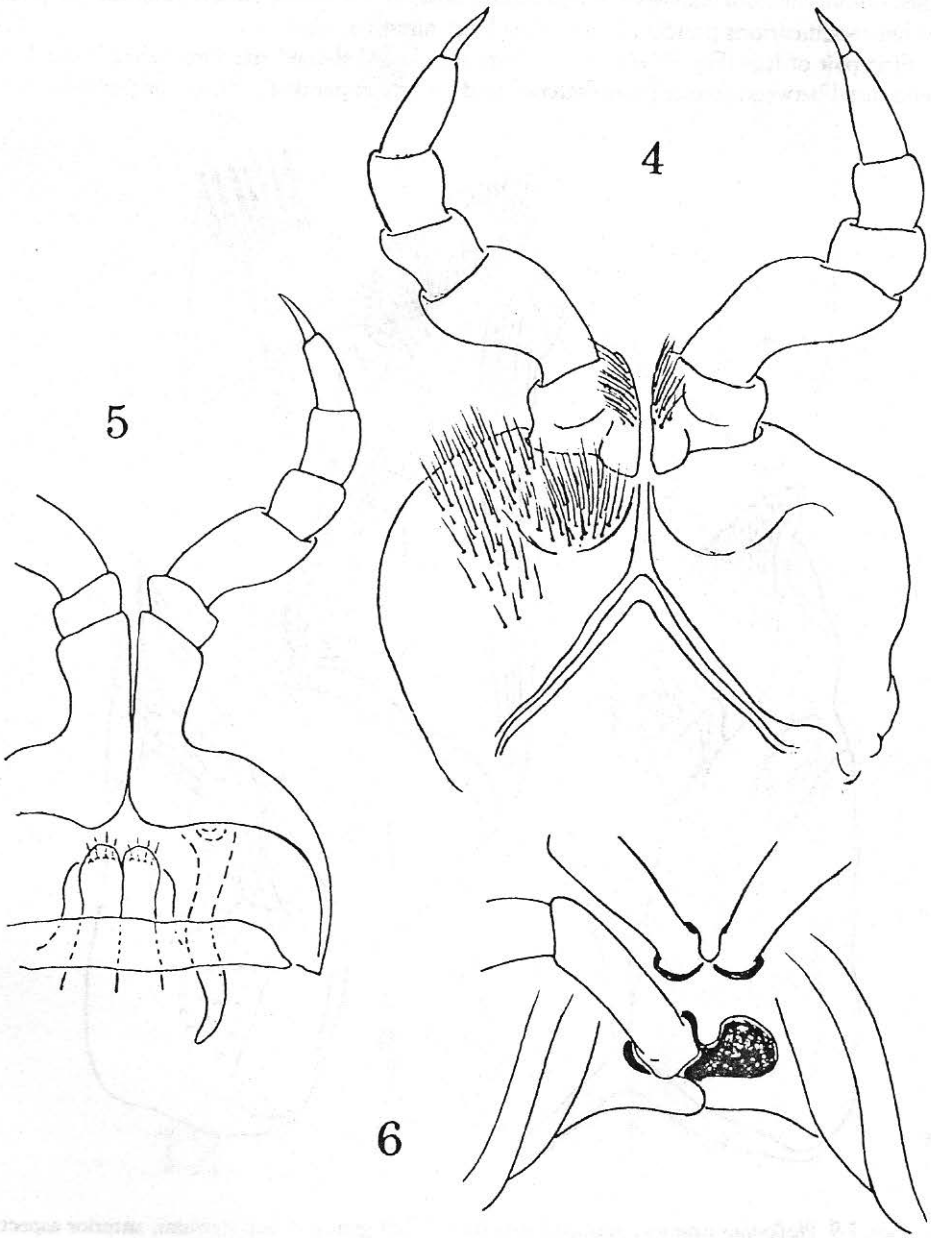
Surface of head featureless, smooth and polished, moderately convex, interocular and interantennal spaces about equally wide (1.5 mm). Ocelli depigmented and impossible to count accurately, arranged in three series. Antennae long and slender, length of articles in decreasing order: 3-6-2-4-5-1; 6th by far the thickest and most setose, with four sensory cones; both 5th and 6th with transversely oval sensory pits on outer distal margin.

Mandible (Fig. 1) without modified basal segment; sectile sclerite with three prominent rounded lobes ("teeth"); ten complete rows of pectinate lamellae and several shorter rows basally, pectinomeres straight, slender, each slightly uncate apically; molar surface medially convex. Gnathochilarium (Fig. 2) of "spirostreptoid" form: lingual lamellae rectangular and in cntact for most of their length; mentum roughly pentagonal with apex rounded; stipes sparsely setose disolaterally, with a slightly larger setae near base of inner palp, in position of stipital spur typical of Spirostreptoidea. Basal sclerite of gnathochilarium not modified for accomodation of prefemoral lobes of 1st pair of legs.

Anterolateral edge of collum unmodified or lobed; surface with about four curved striae visible in lateral aspect, others are present ventromesad.

Segments smooth and polished, without trace of setae, impunctate, surface texture (high

magnification) of minute isodiameteric meshwork; posterior edge of metazona grading into a broad, clear limbus without modified free edge. Anterior end of prozona only very slightly reduced and telescoping of segments thus minimal; annular sulcus evident but not prominent; ozopores located in metazona but touching sulcus; lower sides of segments with

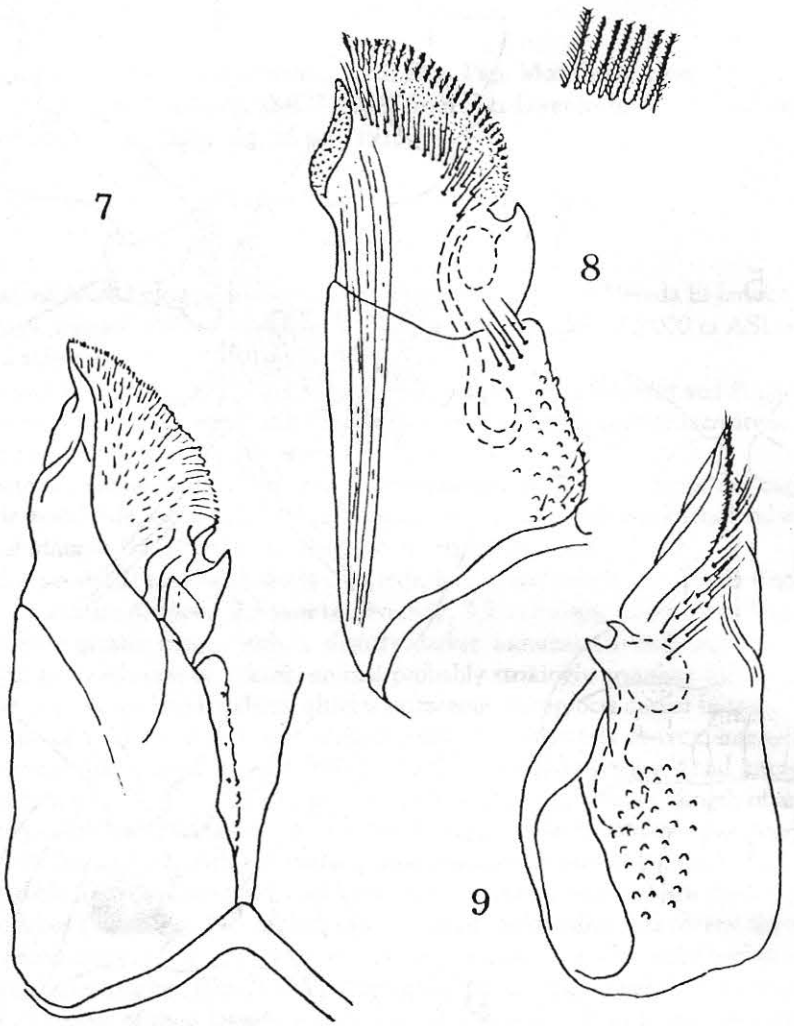


Figs. 4-6. *Phallorthus mauriesi*, structural details. 4. First pair of legs of male, anterior aspect with setation shown on left side. 5. Second pair of legs of male, posterior view showing penial apices. 6. Sternum of midbody segment showing "closed" coxal cavities (one leg removed).

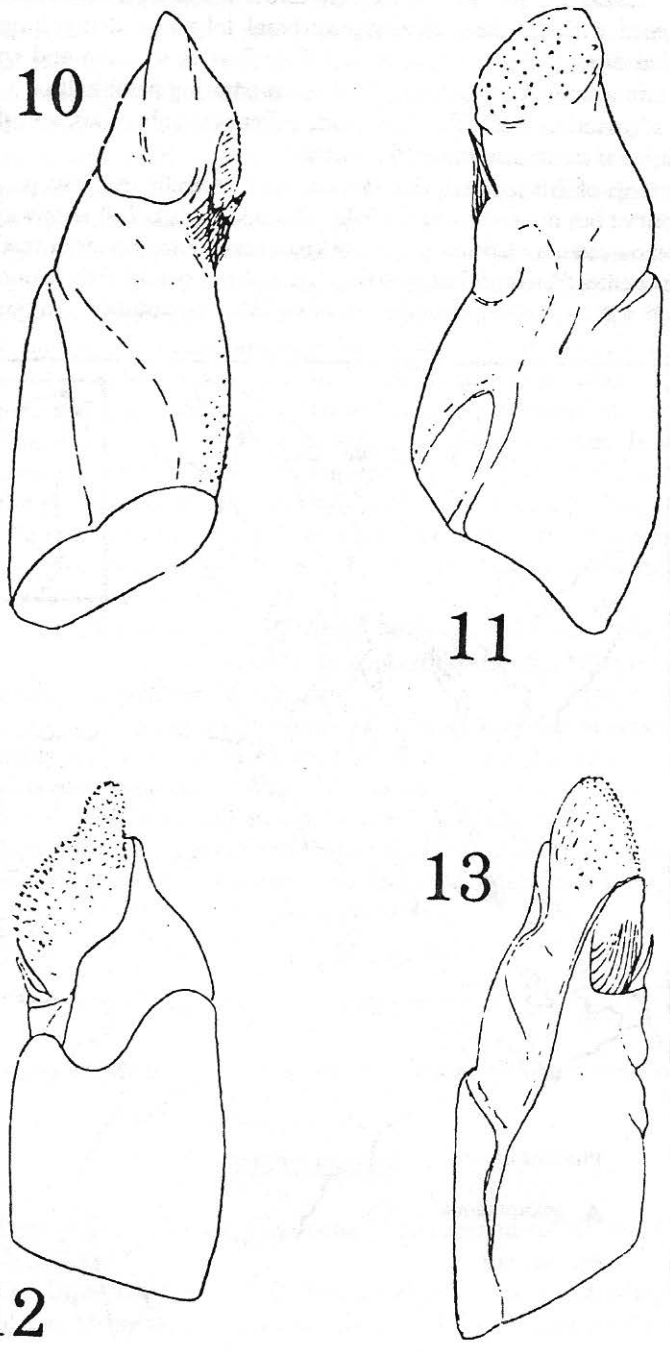
about 10-12 poorly defined longitudinal striae which extend upward less than one-third distance to ozopore. Epiproct not produced medially, paraprocts moderately convex, distal edges with moderately thickened rim; hypoproct transversely triangular.

Sterna (Fig. 6) relatively elongated, smooth and polished, each with a small median lobe separating coxal bases, metasterna closed behind posterior coxal sockets. Legs short, apices of tarsi not visible from above when legs extend laterad; podomeres almost glabrous; no pads or other modifications present. Tarsal claw long, almost straight.

First pair of legs (Fig. 4) with small, very slender, V-shaped sternum, which does not extend distal between coxae; latter flattened and broadly expanded as in spirostreptoids, not



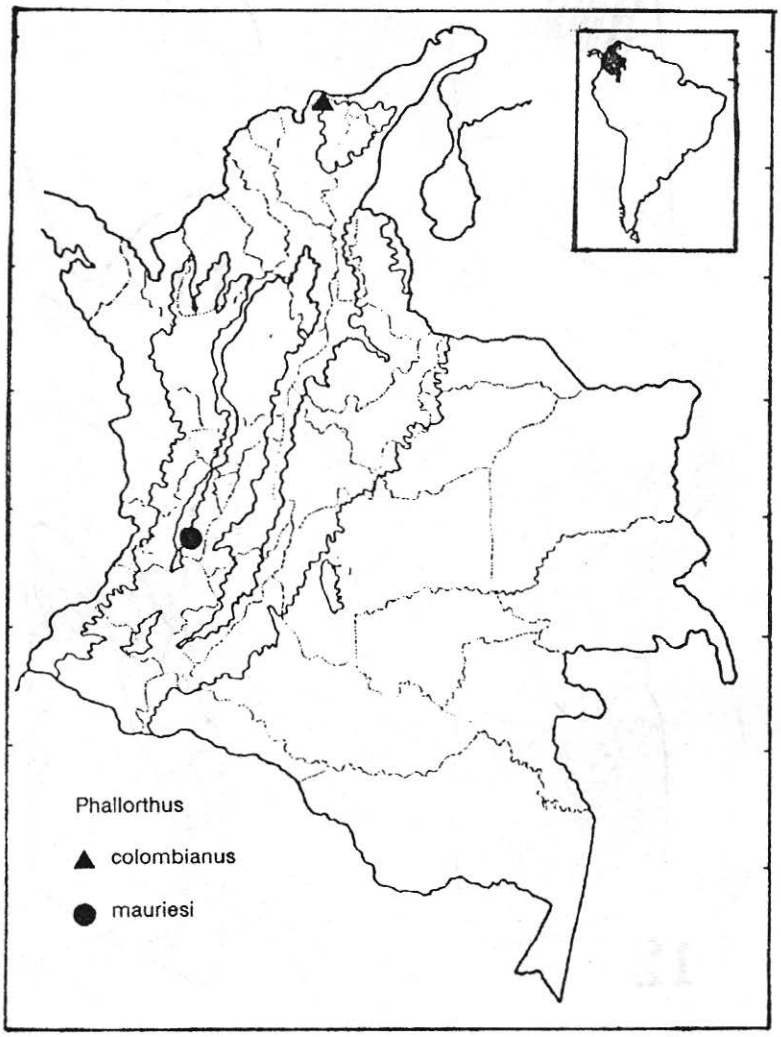
Figs. 7-9. *Phallorthus mauriesi*, gonopod structure. 7. left gonopod and sternum, anterior aspect. 8. right gonopod, posterior aspect, showing segmentation, internal prostatic (?) duct and its apical chamber, vestigial muscle into distal podomere, and distal fringe of plumose laciniae. The latter shown enlarged at upper right. 9. Left gonopod, mesal aspect, showing large basal cavity and internal duct into which it merges.



Figs. 10-11. *Phallorthus lorenzonus* (Chamberlin). 10. Gonopod, ?mesal aspect. 11. Gonopod, ?posterior aspect (both figures from Chamberlin, 1923). Fig. 12-13. *Phallorthus colombianus* Chamberlin. 12. Gonopod, anterior aspect. Fig. 13. Gonopod, posterior aspect (both figures from Chamberlin, 1952).

in contact medially, each with a densely setose distomedial convexity; prefemora not enlarged, each with retrorse subtriangular basal lobe and dense fringe of setae along anteromedial surface. Second pair of legs (Fig. 5) with sternum and coxae more or less coalesced into a single transparent sclerite incorporating basal half of tracheal apodemes, opening of stigmata not traceable with accuracy. Penes membranous, apically rounded, each with subterminal transverse row of four setae.

Pleuroterga of 7th segment (Fig. 3) produced ventrally into two paramedian rounded lobes, in contact but not coalesced medially. Gonopods (Figs. 7-9) relatively short and stout, a small, narrow sterum encircling bases of coxae except for posterior median interruption. Tracheal apodemes damaged during dissection and not describable. Gonopod composed of two elements separated to different degrees of visibility on anterior and posterior sides: basal



Map 1. Colombia, showing distribution of two species of *Phallorthus*. The locality for *P. lorenzonus* cannot be located at this time with certainty.

podomere (coxa) relatively short (nearly as broad as long), with field of papilliform tubercles on posteromedian surface, and with a prominent deep fossa on median side merging into a rounded internal chamber at the base of an internal duct leading to a cylindrical cavity at base of second podomere (telopodite). Latter short and broad, compressed, with a large apical membranous lobe beset with microsetulae and fringed by plumose laciniae.

Vestibular membrane of 7th segment behind gonopods with small but well-sclerotized sternum of 9th pair of legs (Fig. 3, St9), with spatulate sternal apodemes and distinct stigmal openings, but without trace of appendicular remnants.

Remarks: One of the paraprocts of the holotype bears a curious circular marking on its dorsal half, closely similar to the "formations anales" first discussed by Demange (1961: 8) in harpagophorids but illustrated by him a year earlier (1960: figs. 22, 38). Although apparently of common occurrence amongst harpagophorids, it is rarely seen in other spirostreptidans and even less frequently in such satellite taxa as pseudonannolenids. Is it possibly a symptom of some condition peculiar to "spirostreptomorph" millipeds?

Carl's drawing (1917, fig. 3) of the gonopod in *Holopodostreptus braueri* shows a prominent telopodite retractor muscle occupying a large part of the coxal interior. Treatment of the gonopod of *P. mauriesi* with lactic acid revealed a much smaller and obviously different muscle originating at lateral base of the coxa and inserting not on the telopodite base, but closer to the distal lateral lobe. Possibly it is a vestigial motor unit of a third podomere no longer evident.

The curious distal fringe of the telopodite (Fig. 8, enlargement) is not composed of plumose setae, but of slender projections from a membranous edge. The function of this laciniate production evades our understanding.

The mechanism involved in sperm transfer is likewise recondite at present. The type specimen has a partly dissolved spermatophore attached at the distal aperture of the internal duct, suggesting its placement there rather than in the deep coxal fossa. If, from analogy with other diplopods, the "prostatic groove" is involved with delivery of a lysing agent produced by a coxal (or coelomic) gland, the reason for a coxal fossa is not apparent. Insights could be gained from dissection of some large species of *Pseudonannolene,* concerning location and discharge site of a prostatic gland or its duct.

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