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On the identity of further two millipede species (Diplopoda) from the environs of Manaus, Central Amazonia, Brazil

by

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Abstract

The millipede genus *Pycnotropis* CARL, 1914 is shown to be represented in the floodplains near Manaus by a single, highly variable and obviously eurytopic species which occurs also in secondary upland forest: *P. epiclysmus* HOFFMAN, 1996 (Polydesmida: Platyrhacidae). To facilitate recognition, especially so vis-a-vis a number of its nominal and by far more poorly known congeners, some of which are possibly its senior synonyms, the variation range of this species is briefly outlined. In addition, a direct, side-by-side re-examination of topotypes of *Epinannolene arborea* HOFFMAN, 1984 (Spirostreptida: Pseudonannolene exilio BRÖLEMANN, 1904, all from Manaus, results in a new formal synonymy and combination: *Epinannolene exilio* (BRÖLEMANN, 1904), syn. n., comb. n.

Keywords: Diplopoda, Pycnotropis. Epinannolene, Manaus.

Resumo

Mostra-se que nos diplópodos o gênero *Pycnotropis* CARL, 1914, nas áreas alagáveis de Manaus, é representado somente por uma espécie, altamente variável e aparentemente euritópica, a qual ocorre também em floresta secundária de terra firme: *P. epiclysmus* HOFFMAN, 1996 (Polydesmida: Platyrhacidae). Para facilitar seu reconhecimento, especialmente em comparação aos seus congêneres, muito menos conhecidos e alguns deles provavelmente representando o seu sinônimo senior, o grau de variação nesta espècie é brevemente detalhado. Além disso, uma reexaminação direta, lado-à-lado, de topotipos de *Epinannolene arhorea* HOFFMAN, 1984 (Spirostreptida: Pseudonannolenidae) e do holótipo de *Pseudonannolene exilio* (BRÖLEMANN, 1904), todos provenientes de Manaus, resultou em uma nova sinonímia formal e combinação: *Epinannolene exilio* (BRÖLEMANN, 1904), syn. n., comb. n.

Introduction

This paper continues our studies on the millipede fauna of the Manaus region, Central Amazonia, Brazil, and is devoted to the identities of further two species. One of these, *Pycnotropis epiclysmus* HOFFMAN, 1995 (Polydesmida: Platyrhacidae), appears to be eurytopic and highly variable, thus casting some doubts about the attribution of its numerous populations from near Manaus alone to a single species and even about the identity of several nominal congeners. The second species is *Epinannolene arborea* HOFFMAN, 1984 (Spirostreptida: Pseudonannolenidae), which, upon reexamination of all pertinent material and also with consideration of its provenance and ecology, is formally synonymized under *Pseudonannolene exilio* BRÖLEMANN, 1904, this resulting in a new synonymy and combination: *Epinannolene exilio* (BRÖLE-MANN, 1904), syn. n., comb. n.

Taxonomic part

Pycnotropis epiclysmus HOFFMAN, 1995 (Figs. 1-3, 8-13)

Material: Several hundred adult males and females from INPA Campus and ASSINPA at Manaus (nonflooded secondary upland forests); Lago Janauacá (03'28'S, 60'17'W), Paraná de Capitarí (IC) and BR-319 Road km 10 near Ilha do Careiro (whitewater inundation forests at the Solimões-Amazon River); Lago Janauarí (LJ) and AM-070 Road km 15 near Lago Iranduba (mixedwater inundation forests between the Solimões-Amazon River and Negro River). Only the latter sample contained a few specimens (4 males and 1 female) while the others at least a few dozen, all collected in the environs of Manaus, Amazonas, Brazil (see map) by J. ADIS & K. VOHLAND.

Remarks: As outlined and redefined recently by HOFFMAN (1995), the Neotropical genus *Pycnotropis* CARL, 1914 currently comprises 11 described species (three each in Colombia, Peru and Brazil, two in Ecuador) as well as several further, still undescribed congeners in Ecuador and Colombia. The identity of some of them is still to be clarified, but what seems particularly important for the on-going research on the ecology and survival strategies of various arthropod groups/species in the conditions of inundated vs. noninundated selva, conducted by J. ADIS and his collaborators, there appears only a single, yet highly variable and eurytopic *Pycnotropis* species in the floodplains of the entire Manaus region: *P. epiclysmus* HOFFMAN, 1996. Below are some additional, purely morphological arguments in support to such an opinion. They happen to be nicely consistent with the preliminary results of genetic analyses (BACH-MANN et al. 1997; TOMIUK et al. 1996) and lob cross breeding of various populations (INPA vs. LJ vs. IC; ADIS & VOHLAND unpubl.), which also demonstrate that individuals from different habitats belong to populations of a single species.

Two main patterns of body shape can be distinguished in the samples at hand. One is closer to the typical *epiclysmus*, yet with the paraterga in the bulk of the specimens broadly to narrowly rounded (Figs. 1, 8 & 9), not pointed, as described in the *epiclysmus* holotype. The other displays the peritremata more or less strongly swollen, "humped", in dorsal view (Figs. 2, 10 & 11). However, all possible intermediates can be observed even within a single sample. In addition, the distal part of the gonopod tibiotarsus varies from broader to flagelliform (usually subflagelliform), the dorsocaudal tergal denticulations from (almost) missing to strongly developed (usually relatively well-developed), the middorsal pale (sometimes up to dark reddish, but usually yellow and vaguely delimited) spot/band well-expressed to almost totally wanting, either merging with a pallid background or disappearing at all (usually present), body width ranges between 5 and 7 mm (usually closer to 5.8-6.0 mm), the hypoproct with or without a rear midmarginal knob (usually without), the polygons on the metaterga from sublateral in position to covering the

(almost) entire dorsal surface (usually sublateral), the caudal corners of midbody paraterga from broadly rounded to (almost) pointed, often with a "hump" in front of the ozopore (usually rather narrowly rounded, as in Figs. 1 & 8), and finally, the epiproct is almost always longer, parallel-sided next to throughout, broadly rounded only terminally (that is, typically *epiclysmus*-like, as in Figs. 3, 12 & 13), yet a few specimens showed it quite close to the *tida*-type, that is, almost not parallel-sided but shorter and more gently rounded (see also below).

None of the above variations seems to be sex-linked, nor do they appear correlated with one another.

The above striking intraspecific variability casts doubts concerning the status of *epiclysmus* vis-a-vis some older names available in the nomenclature. Based on gonopod structure, one such name is *subareatus* JEEKEL. 1963, from Amapá State, Brazil, downstream the Amazon River from Manaus. However, judged from the original description (JEEKEL 1963), this form is somewhat larger, 8.2-9.5 mm in width, with a completely dark epiproct, and the metaterga apparently devoid of a pale middorsal spot/band. Another taxon particularly closely related to *epiclysmus* seems to be *P. tida* (CHAMBERLIN, 1941), a form rather widely distributed in northern Peru, all along the Maranón River, that is, definitely Andean. The only character that defines *tida* as opposed to the bulk of the above *epiclysmus* samples appears to be the shape of the epiproct. The latter is shorter, with sides slightly converging caudad in *tida* but generally longer, parallel-sided in *epiclysmus* (Fig. 3). As HOFFMAN (1995) has already emphasized, with such inconspicuous differences observed, both *epiclysmus* and *tida* might well be regarded only as subspecies. In any event, in this case no formal synonymy is advanced herewith.

Pycnotropis acuticollis (ATTEMS), a species described from São Paulo de Olivença, upstream the Amazon River from Manaus (not far from the common border of Brazil, Peru and Colombia), was at first considered as a possible member of the *tida*-group. However, examination of the holotype of this species (Naturhist. Mus. Wien), shows *acuticollis* to be a quite different species, larger than *tida*, with the paranota wider and nearly horizontal, and with three transverse rows of distinct areolations. Also, the tibiotarsal element of the gonopods shows a more sigmoid curvature, with a prominent "heel" at about the midlength. The presence of this species along the Amazon River above Manaus is of interest in adding another facet to the already known diversity in this region, reaffirmed also by numerous fresh samples of further two species taken early this year by two of us (JA and AM) in the vicinity of Iquitos, Peru.

We suggest that the genus *Pycnotropis* originated in the Andes, where most of the known species now occur. Variation in body structures of its species, in particular of *epiclysmus*, may be associated with the relatively recent occupation of new areas and biotopes, probably by migrants (see below). In Peruvian Amazonia, channel changes of meandering rivers are a common phenomenon (cf. SALO et al. 1986). This may have been one of the reasons that populations of *epiclysmus* inhabiting upland forest sites had to cope with the transformation of their biotope into a floodplain forest and vice versa within a relatively short time period. In the process of adaptation to the new environments, the "pioneers" changed their external structure more quickly than the gonopods. Subsequent downstream colonization along the Solimões-Amazon River and adaptation to new niches removed the old genetic constraints, but the conservative gonopods did not keep pace and still show a common, quite restricted pattern. Classical examples of this are the xystodesmid genus *Rhysodesmus* COOK in Mexico, with dozens of species looking quite different but sharing a uniform gonopod pattern and the even more extreme case of *Coromus* GERVAIS from West Africa (HOFFMAN 1990).

According to HOFFMAN (1990), the diversification of external body form with little modification of gonopod structures in Polydesmida seems "associated with those taxa (usually genera) which seem to have recently occupied a new area or biotope independently of close relatives, and are indulging in a burst of adaptive radiation unimpeded by sibling competition. It is presumed that after an initial period of great diversification some selection of successful lineages would occur, during which time body form types, stabilized by adaptational factors, would tend to remain rather constant henceforth whilst generic variability might be expressed much more rapidly in structures such as genitalia less directly influenced by environmental constraints. Thus a period would ensue in which these speciesgroups (or genera) would consist of species readily distinguishable by highly distinctive gonopods. Such a stasis would endure for a long time unless it were again possible for a fragment of a group (probably migrant populations of one or two

species) to escape into a new area or new ecological niche and begin the cycle anew. This situation seems to be different from the punctual evolution of new clades in that two basically different characters-systems alternate in phase with the chronological status of the organisms in "new" and "old" territory, and would thus underscore the principle that phylogeny cannot be adequately interpreted outside the context of biogeography."

Our new insights derived from the local *Pycnotropis* situation tend to lend credence to the foregoing, purely inferential, postulations. A good local example of a taxon in the "stable body - variable gonopod" stage is provided by the chelodesmid genus *Camptomorphy* SILVESTRI which likewise is species-rich in the Andes.

It would be highly desirable to examine larger topotypic samples of *P. acuticollis*, *P. subareata* and *P. tida* for intra- or interspecific variability and to make cross-breeding experiments with *P. epiclysmus*. Only after the phenotopic plasticity (morphological, physiological and ecological states in response to environmental conditions, according to WEST-EBERHARD, 1989) has been studied in more detail it becomes possible to resolve whether the Amazonian fauna supports either only a few or a whole guild of (sub)species, some of which definitely variable and eurytopic.

Epinannolene exilio (BRÖLEMANN, 1904), comb. n. (Figs. 4-7)

Pseudonannolene exilio BRÖLEMANN, 1904: 78.

Epinannolene arborea HOFFMAN, 1984: 92, Figs. 1-5; syn. n.

Material: 1 female (holotype of *Pseudonannolene exilio*, Museu de Zoologia, Universidade de São Paulo; courtesy of Prof. J.L. Moreira Leme), "Manaos, Bicego leg.". - 1 male and numerous females (topotypes of *Epinannolene arborea*, INPA and ADIS' collections), Brazil, Amazonas, environs of Manaus, Rio Tarumã Mirím, blackwater inundation forest, tree trunks, 2.09.1976; leg. J. ADIS.

Remarks: A direct, side-by-side comparison of both samples has revealed no differences whatever between both taxa, hence the new synonymy and combination. As one can see, the pattern of striation of the collum (Figs. 4, 5) and the outline of the telson (Figs. 6, 7) are virtually identical. The segment counts suggest the *exilio* holotype may actually belong to (one of) the latest developmental stages, because 61 body segments (excluding the paraprocts, or anal valves) seems the maximum. Only very few females among the topotypes at hand are with 60 or 61 body segments (the maximum is 64 segments), whereas the bulk are only with 49, 50, 51, 52, 54, 56 or 57 segments. HOFFMAN (1984) specified 52 body segments in the holotype of *arborea*.

We have compared the gnathochilaria, too, more superficially and without dissection in the *exilio* holotype for fear of destruction, but they all turned out to be the same as well. We have decided not to dissect the holotype of *exilio* to investigate the structural details of its vulvae, thinking this might hardly be rewarding.

In addition, we have been able to confirm HOFFMAN's (1984) opinion that the somewhat reduced (5-6 vs. 10-15 per podomere) number of modified, spatulate setae on the anterior male postfemora and tibiae of *exilio*, not the gonopod conformation, holds as the sole character distinguishing this species from *E. alticola* (SILVESTRI, 1898), the latter taxon originating from high elevations in Colombia (cf. CARL 1914). From a zoogeographical standpoint, such a highly peculiar relationship as the one displayed by *alticola* and *exilio* (Colombian high mountains and Amazonian lowlands respectively) has already been discussed elsewhere (HOFFMAN 1984).

As another piece of evidence supporting the above synonymy may serve the fact that the Manaus faunule contains at least two more terricolous, not arboricolous, congeners (secondary upland forest at Rio Tarumā Mirim and primary upland forest at Reserva Florestal A. Ducke) which could not be identified because of the absence of adult males in the small samples in hand. Yet at least their collar striation pattern and paraproct outline are quite different from those observed in *exilio*. Indeed, it seems difficult to imagine that any other congener but *exilio* could have been taken by a causal collector at Manaus at the end of the last century.

Acknowledgments

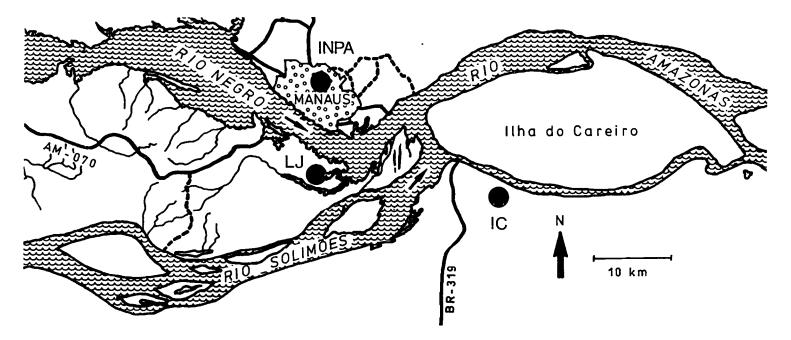
One of us (SG) wishes to again extend his cordial thanks to the Max-Planck-Society for awarding a grant for his work for a few weeks in 1996 and 1997 at the Max-Planck-Institute for Limnology, Tropical Ecology Working Group, Plön, Germany. Prof. Dr. José Luiz Moreira Leme (São Paulo, Brazil) kindly loaned the holotype of *Pseudonannolene exilio* BRÖLEMANN, 1904 under his care. Dr. Jürgen Gruber (Vienna, Austria) is thanked for access to the type specimen of *Pycnotropis acuticollis*.

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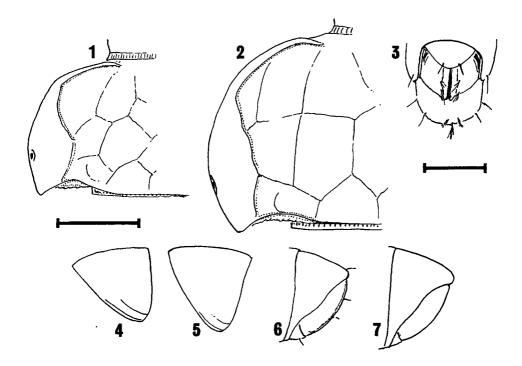
Resumen

Entre los diplópodos, el género Pycnotropis CARL 1914, en las áreas inundables de Manaus, está representado solamente por una especie altamente variable y aparentemente euritópica, la cual también se la puede hallar en bosque secundario de tierra firme (no inundable): *P. epiclysmus* HOFFMAN 1996 (Polydesmida: Platyrhacidae). Para facilitar su reconocimiento, especialmente en comparación con sus congéneres mucho menos conocidos y alguno de ellos probablemente representa su sinónimo senior, el grado de variación en esta especie es detallado brevemente. Además de esto, un reexamen directo - lado-a-lado - de topotipos de *Epinannolene arborea* HOFFMAN 1984 (Spirostreptida: Pseudonannolenidae) y del holotipo de *Pseudonannolene exilio* BRÖLEMANN 1904, todos provenientes de Manaus, resultó en una nueva sinonimia formal y combinación: *Epinannolene exilio* (BRÖLEMANN 1904), syn. n., comb. n.



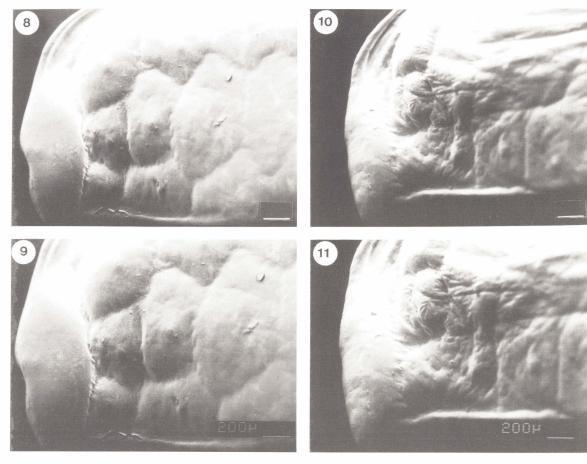
Map:

Location of the main sampling sites. INPA = non-flooded secondary upland forest on the Campus of the National Institute for Amazonian Research at Manaus (03'08'S, 60'1'W); LJ= mixedwater inundation forest at Lago Janauarí (03'29'S, 60'17'W); IC = whitewater inundation forest near Ilha de Careiro (03'17'S, 59'0'W). See text for other sampling sites.

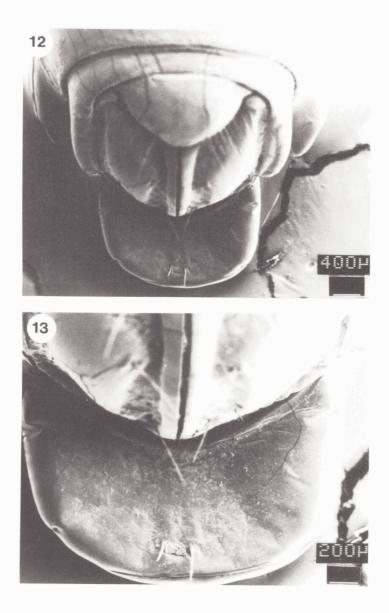


Figs. 1-7:

Pycnotropis epiclysmus HOFFMAN, 1996 (1-3) and Epinannolene exilio BRÖLEMANN, 1904 (4-7).
1: segment 10, left side, dorsal view (male from INPA Campus); 2: same (female from ASSINPA);
3: telson, ventral view (same female from ASSINPA); 4: collum, lateral view (topotype of arborea);
5: same (holotype of exilio); 6: telson, lateral view (topotype of arborea); 7: same (holotype of exilio).
Scale bars: 1.0 mm (1, 2, 4-7) and 2.0 mm (3).



Figs. 8-11:
Pycnotropis epiclysmus HOFFMAN, 1996.
8 & 9: segment 10, left side dorsal view (SEM; female I from INPA Campus);
10 & 11: same (SEM; female II from INPA Campus). Scale bar in figures 8 & 11: 300 μm.



Figs. 12 & 13: Pycnotropis epiclysmus HOFFMAN, 1996. Telson, ventral view (SEM; male from INPA).

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