

Review of the millipede subfamily Amphininae (Diplopoda, Polydesmida, Aphelidesmidae) with remarks on phylogeny and the description of some new South American genera and species

by

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Abstract

A review of the millipede subfamily Amphininae (Diplopoda, Polydesmida, Aphelidesmidae) is presented. The genera *Meridiurus*, *Tribrachiorus*, *Coleocacamus*, *Kallistopeltis*, *Sculptoteles* and *Pastazina* are erected as new. Description of the new species *Polylepiscus hirmerae* n.sp., *Meridiurus venitus* n.sp., *Tribrachiorus suarezi* n.sp., *T. huila* n.sp., *Coleocacamus depressus* n.sp., *C. labialveus* n.sp., *Thrinoxethus juani* n.sp., *T. junini* n.sp., *T. siolii* n.sp. and *Pastazina crassa* n.sp. are given. *Tribrachiorus polygonatus* (GERVAIS, 1847), *Kallistopeltis kalonota* (ATTEMS, 1899), and *Sculptoteles braueri* (CARL, 1918) are redescribed. An analysis is attempted to elucidate the phylogenetic and, to some extent, biogeographical relationships of the genera as they are conceived of at the present.

Keywords: Diplopoda, Polydesmida, Aphelidesmidae, Amphininae, taxonomy, systematics, phylogeny, biogeography.

Resumo

Apresenta-se uma revisão da subfamília Amphininae (Aphelidesmidae, Polydesmida, Diplopoda). Os gêneros *Meridiurus*, *Tribrachiorus*, *Coleocacamus*, *Kallistopeltis*, *Sculptoteles* e *Pastazina* são estabelecidos. As espécies novas *Polylepiscus hirmerae* n.sp., *Meridiurus venitus* n.sp., *Tribrachiorus suarezi* n.sp., *T. huila* n.sp., *Coleocacamus depressus* n.sp., *C. labialveus* n.sp., *Thrinoxethus juani* n.sp., *T. junini* n.sp., *T. siolii* n.sp. e *Pastazina crassa* n.sp. estão descritas. As espécies *Tribrachiorus polygonatus* (GERVAIS, 1847), *Kallistopeltis kalonota* (ATTEMS, 1899) e *Sculptoteles braueri* (CARL, 1918) são redescritas. Uma análise tenta elucidar as relações filogenéticas e biogeográficas dos gêneros atualmente arranjados.

Introduction

The millipede superfamily Platyrrhacoidea has long been considered as including the single family Platyrrhacidae (41 genera and over 250 species) confined to tropical America and the Indo-Australian Region. Yet several subfamilies and tribes have been established within the Platyrrhacidae. Among these, the Neotropical tribe Amplinini has hitherto been known to encompass nine valid genera (cf. HOFFMAN 1980).

The present paper follows and continues the recently proposed reclassification of this family inferring its division into the Aphelidesmidae and Platyrrhacidae, with removing the Euryuridae into the superfamily Xystodesmoidea (cf. HOFFMAN 1998). Eventually, this is a revision of the erstwhile tribe Amplinini, currently subfamily Amplininae, with descriptions and/or redefinitions of several new South American taxa. In addition, an analysis is attempted here to elucidate the phylogenetic and, to some extent, biogeographical relationships between the genera as they are conceived of at the present.

The old literature pertaining to the scope of this communication is scattered over several, often miscellaneous, publications (GERVAIS 1847; PETERS 1864; SILVESTRI 1898; ATTEMS 1899; POCOCK 1909; CARL 1914, 1918; VERHOEFF 1941). CHAMBERLIN (1925, 1933, 1941, 1952) was particularly active in having described many new genera and species of Amplinini, yet, like most of his predecessors and contemporaries, his descriptions were often too superficial, and the drawings if any lacked the necessary detail. As a result, the group became highly confused taxonomically. Even against this background, KRAUS (1956, 1959) added a few more new species from Peru.

Revisionary work began with the works of HOFFMAN (1951, 1954), who then considered the Amplininae as belonging to the Euryuridae. However, a real milestone in clearing up much of the confusion and bringing the Amplininae (also treated then within the family Euryuridae) to a kind of order came with the work of JEEKEL (1963). Yet, when surveying *Amplinus*, this author did not accept the concave shape of the hypoproct as a generic character. Hence, he merged under *Amplinus* several species, some of them with a convex hypoproct as e.g. *Pycnotropis* as well as species with a truncated hypoproct, as *Amplinus*.

This has since been corrected and, according to HOFFMAN (1980), the Amplinini (currently Amplininae; cf. HOFFMAN 1998) comprised *Amplinus*, and its junior synonym *Pseudamplinus* HOFFMAN, 1954 (about 30 species in Central America + ? Venezuela; cf. HOFFMAN 1983); *Exallosthetus* HOFFMAN, 1976 (one species in Mexico); *Polylepiscus* POCOCK, 1909 and its junior synonyms *Euplinus* CHAMBERLIN, 1952 (seven species from Central America); *Pycnotropis* CARL, 1914 and its junior synonyms *Seminelloxon* CHAMBERLIN, 1914, *Phinotropis* CHAMBERLIN, 1941, *Amydrinus* CHAMBERLIN, 1941, *Ptyxogon* CHAMBERLIN, 1941 and *Sigmogonotropis* HOFFMAN, 1951 (about 15 species in Central and northwestern South America) (cf. GOLOVATCH et al. 1998); *Colomborus* CHAMBERLIN, 1952 (one species from Colombia); *Thrinoxethus* CHAMBERLIN, 1941 and its junior synonym *Cyclotropis* VERHOEFF, 1941 (about six species in Peru); *Protaphelidesmus* BROLEMANN, 1915 (one species from Venezuela) and *Varyomus* HOFFMAN, 1954 (one species each in Venezuela and Trinidad).

Material

Material serving as the basis for the present paper mainly derives from the collection of the Virginia Museum of Natural History (VMNH), Martinsville, U.S.A., with some samples coming from the Museo Nacional de Historia Natural (MHNL), Lima, Peru; the Muséum National d'Histoire Naturelle (MHNP), Paris, France; Forschungsinstitut und Naturmuseum Senckenberg (SMF), Frankfurt, Germany; Naturkunde Museum der Humboldt-Universität (ZMB), Berlin, Germany; and Zoologisches Institut der Universität Hamburg (ZIM), Hamburg, Germany. A few subsamples have been deposited in the Zoological Museum of the Moscow University (ZMUM), Russia.

General characteristics of the Amplininae

Adults have 20 body segments with lateral keels (= paraterga), and sternites, pleurites and tergites merged to a single body ring, which clasifies them as belonging to the Polydesmida. Adults of amplinine genera range in body length from 40 to 70 mm. Most of them are dark brown with contrastingly yellow or at least lighter paratergal tips. A feature distinguishing Aphelidesmidae from the other polydesmidan families, which they share with the Platyrrhacidae, is the spatula-like epiproct combined with the presence of tufted setae on the head and terminal body segment (HOFFMAN 1995, 1998). However, in contrast to the Platyrrhacidae which possesses a very rough body surface, that of the Aphelidesmidae is smooth to very finely wrinkled/leathery, and the polygonal areation both is restricted mostly to the lateral parts of the metazonites and is less prominent. The prozonites are always entirely smooth, the metazonites are finely granulated ventrally. The ventral granulation is extending from the collum at least to body segment 3. The setigerous tubercles on the paraproct and hypoproct are relatively small to totally missing. The ozopore openings consist of a ring which lies in "a crater-like structure" (JEEKEL 1963). The ozopores open laterally on the paraterga in thickened peritremata. The surface behind the stout antennae is finely striated, and beneath each antenna there is an ovoid bulge.

The Aphelidesmidae consists of two subfamilies which differ in their gonopod structure. In the Aphelidesminae, the solenomerite originates from the prefemur separately from the 360° torsate tibiotarsus and is sheathed by it. In the Amplininae, the acropodite branches are narrower connected at base. With the exception of *Amplinus*, a suture separates the setigerous part of the prefemur from the smoother distal part supporting the seminal groove. Such somatic characters as the shape of the epiproct and of tubercles on the sternites have been shown to be unsuitable as they vary within a single genus, same as e.g. the degree of metatergal areation even within a single species (GOLOVATCH et al. 1997).

The Amplininae ranges from Mexico in the north down to Brazil and Peru in the south. Most specimens have been found in and/or under logs and there is no indication of any litter-dwelling species.

Descriptive part

Amplinus ATTEMS, 1898 (Figs. 1-6)

Mexico, Guatemala, Costa Riva, ?Venezuela.

Amplinus ATTEMS, 1899: 264.

Amplinus, POCOCK 1909: 147; HOFFMAN 1980: 164.

Pseudamplinus HOFFMAN, 1954: 49, Synonymized by HOFFMAN, 1980.

Type species: *Amplinus (Polydesmus) klugii* BRANDT, 1839, by subsequent designation of ATTEMS (1938). Redescribed by HOFFMAN (1983).

Diagnosis: Hypoproct concave (Fig. 5), with two setigerous tubercles. Ventral surface of paraterga totally granulated (Fig. 4). Dorsal surface totally areated (Figs. 2, 3). Gonopods cylindrical, without sulcus between prefemur and acropodite (Fig. 1).

Remarks: ATTEMS (1898) introduced the name *Amplinus* (also misspelt as *Amphinus*) as a subgenus of *Pachyurus* for those American species in which the collum was as large as the second segment, while in species of "*Pachyurus*" from the Sunda Islands, the collum was much narrower than the second segment. *Pachyurus kalonotus* ATTEMS, 1899, was invalidly chosen as type species of *Amplinus* by POCOCK (1909), so the true typification is to be ascribed to ATTEMS (1938) who selected *Polydesmus klugii* BRANDT, 1839, as type species (cf. HOFFMAN 1976, 1983). HOFFMAN (1980) synonymized *Pseudamplinus* with *Amplinus* and excluded such genera as *Seminellogon* and *Pycnotropis* which JEEKEL (1963) had sunk under *Amplinus*.

Species of this genus have never been revised since JEEKEL (1963), LOOMIS (1968) and HOFFMAN (1983), though a generic revision is badly needed. Hence no list of *Amplinus* species is attempted here.

***Polylepiscus* POCOCK, 1909 (Fig. 7-10)**

Mexico, Guatemala.

Polylepiscus POCOCK, 1909: 147.

Polylepiscus, CAUSEY 1954: 55; HOFFMAN 1954: 49; HOFFMAN 1962: 135.

Type species: *Polylepiscus stollii* POCOCK, 1909, by original designation.

Diagnosis: Acropodite divided in three slender branches (Fig. 7).

Remarks: POCOCK (1909) created *Polylepiscus* as a new genus distinct from *Amplinus* because of the convex outline of the hypoproct as opposed to the concave one in *Amplinus*. In addition to the type species, *Pachyurus heterosculptus* CARL, 1902 was also included there.

The following species are currently recognized within *Polylepiscus*:

heterosculptus heterosculptus (CARL, 1902) (Guatemala), originally described in *Pachyurus*;

actaeon POCOCK, 1909 (Guatemala);

furcifer POCOCK, 1909 (= *Euplinus volcanicola* CHAMBERLIN, 1952, synonymized by HOFFMAN (1954) (Guatemala, Volcano Tajumulco);

stollii POCOCK, 1909 (Guatemala, Cholhuitz);

major (CHAMBERLIN, 1952) (Guatemala), originally described in *Aphelidesmus*;

burgeri CAUSEY, 1954 (Mexico, Chiapas, Simojoval);

heterosculptus pococki HOFFMAN, 1954 (Mexico, Chiapas, Tumbala);

trimaculatus HOFFMAN, 1954 (Guatemala, Pancajche & Trez Aguas);

campanulae HOFFMAN, 1962 (Mexico, Chiapas, San Christobal de las Casas);

vomeri SHEAR, 1977 (Mexico, Chiapas);

hirmerae n.sp. (Mexico, Chiapas, Huixtla).

Species of this genus are highly variable in size and surface structure. The caudal tips of the paraterga are very acute. All species have in common the very characteristic gonopods which consist of three acute branches above a setose prefemur (no setae in *P. burgeri*). The solenomerite is the shortest branch, the longer tibiotarsal branches are similar. At the base of the branches there is a wide whitish field. The epicranial suture is shortly bifurcated between the antennal sockets. The subtransverse genal convexities are relatively flat. The openings of the ozopores are invisible from above. At the broadened anterior margin of the paraterga, there is a field of spinules (Figs. 8, 9), termed strigilis by HOFFMAN (1962). The caudal

margins of the paraterga are serrate.

***Polylepiscus hirmerae* n.sp. (Figs. 7-10)**

Holotype (VMNH), Mexico, Chiapas, 54 km N of Huixtla, 1,829 m a.s.l., 27.02.1966, leg. G.E. BALL & D.R. WHITEHEAD.

Name: Named after German ethnographer Andrea HIRMER for her encouraging women in science.

Diagnosis: A small species of *Polylepiscus* with a relatively strongly sculptured body surface. Gonopods very similar to those of *P. campanulae*, only the tibiotarsal branches differing in orientation.

Description: Holotype 40 mm long, width of midbody metazonites 5.0 mm, of prozonites 3.0 mm. Colour chocolate brown, legs and labrum lighter brown, antennae lighter distad, paraterga and epiproct yellowish. Epicranial suture distinct. Width of collum = segments 2-4 > subsequent segments. Paraterga positioned in upper 1/3 of metaterga, horizontal (Fig. 10). Segments 3-18 very strongly sculptured (Figs. 8-10), collum and segments 2 and 19 much more weakly so. Hypoproct semicircular, sides of epiproct subparallel, tapering caudad. Gonopod aperture thickened laterally. Solenomerite at base slightly hidden by a small shield-like structure of the prefemur (Fig. 7).

***Exallostethus* HOFFMAN, 1975 (Figs. 11-15)**

Mexico (Chiapas).

Exallostethus HOFFMAN, 1975: 221.

Type species: *Exallostethus thrinax* HOFFMAN, 1975, by original designation.

Diagnosis: Very prominent median processes on sterna of segments 4 and 5 in males and on segment 4 in females.

Remarks: The only species included is *thrinax* HOFFMAN, 1975.

This monotypic genus was erected because of "the singular form of the gonopods and the enormous median processes on the sterna of segments 4 and 5 in males and 4 in females" (HOFFMAN 1975). Anterior paratergal edges are strigilate (Figs. 12-14) as in *Polylepiscus*. All metazonite are roughly granulated ventrally (Fig. 14). The relatively small gonopod aperture is slightly thickened caudally. There is no sternum between the gonopods. The acropodite consists of a slender and long solenomerite, an apically broadened and falcate postfemoral process, and an apically divided tibiotarsus (Fig. 11).

***Seminellogon* CHAMBERLIN, 1933 (Fig. 16)**

Costa Rica, Panama.

Seminellogon CHAMBERLIN, 1933: 11.

Sigmogonotropis HOFFMAN, 1951: 235.

Seminellogon HOFFMAN, 1954: 49.

Type species: *Seminellogon chitarianus* CHAMBERLIN, 1933, by original designation.

Diagnosis: Hypoproct convex, prefemur without conspicuous longer setae, acropodite without vesicle-like structure, two-branched (Fig. 16).

Remarks: The following species are assigned to this genus:

panamicus (CHAMBERLIN, 1925) (Panama, near headwater Rio Chinilla), originally described in *Aphelidesmus*;

chitarianus CHAMBERLIN, 1933 (Costa Rica, Chitaria);

serratus (HOFFMAN, 1951) (Panama, Cana), originally described in *Sigmogonotropis*;

cerroazulensis HOFFMAN, 1954 (Panama, Chiriqui, Cero Azul);
magnus LOOMIS, 1964 (Panama, Coclé);
bituberculosus (LOOMIS, 1973) (Costa Rica, San Vito, Finca las Cruces), originally described in *Amplinus*.

The generic characteristics were very broadly formulated, mainly mentioning a free solenomerite and a semicircular hypoproct. Overlooking *Seminelloxon* in ATTEMS (1938), HOFFMAN (1951) erected a new genus, *Sigmogonotropis*, to incorporate a new species, *serratus*, and maintained this combination in his second study of the group (1954). JEEKEL (1963) synonymized *Sigmogonotropis* and *Seminelloxon* with some other genera under *Amplinus*. For this reason, LOOMIS (1973) placed his new species of *Seminelloxon* in *Amplinus*, apparently being not totally content with its definition. HOFFMAN (1980) separated *Amplinus* from *Seminelloxon*, but he merged *Seminelloxon* and *Sigmogonotropis* under *Pycnotropis*. But in the redefinition of *Pycnotropis* (HOFFMAN, 1995), he did not mention these Central American species. As the vesicle is missing I took *Seminelloxon* out again and compiled the species list by declaration of HOFFMAN (HOFFMAN, pers. comm., 1998).

Remarks: The solenomerite and tibiotarsus of the gonopod are coalesced, forming a broad ridge at their base and leaving nearly no trunk between the ridge and the prefemur. The margins of the gonopod aperture are elevated or at least thickened caudally and laterally. The ozopores on segments 18 and 19 open ventrally. The second tergite is wider than the third one and all paraterga are less strongly acute caudally than in other genera.

***Protaphelidesmus* BROLEMANN, 1915 (Figs. 17-24)**

Venezuela.

Type species: *Platyrrhacus ligula* BROLEMANN, 1898, by original designation.

Diagnosis: Gonopod prefemur elongated and cylindrical (Figs. 17, 18), solenomerite sheathed by a broadened tibiotarsus. Ventral surface of paraterga less strongly granulated than in *Amplinus* (Fig. 21).

Remarks: The genus comprises only one species:

ligula (BROLEMANN, 1898) (Venezuela, Colonie Tovar), originally described in *Platyrrhacus* C.L. KOCH, 1847, later listed in *Pachyurus* (cf. ATTEMS 1899).

***Protaphelidesmus ligula* BROLEMANN, 1898 (Figs. 17-24)**

Material: 2 ♂♂, 2 ♀♀ (MHNP), Venezuela, Colonia Tovar, 1888, leg. E. SIMON.

Redescription: Length about 37 mm, width of midbody metazonites about 5 mm, of prozonites about 3 mm. Colour faded, live probably dark brown with lighter legs, antennae and caudal corners of paraterga. Epicranial suture deep, collum subtrapezoid (Fig. 24), segment 2 slightly wider than collum and subsequent segments. Paraterga relatively small, only slightly protruding caudad (Figs. 19, 20). Hypoproct broadly rounded, paraprocts with small setigerous tubercles, margin of epiproct undulated (Fig. 22). Midbody paraterga set at upper 1/3 of metazonite, slightly ascending caudad (Fig. 21). Collum and metazonite strongly sculptured dorsally, with mostly three rows of tubercles/areations. Ventrally, paraterga 2-9 microgranulated, in subsequent segments slightly rough, without projections. Ozopores not visible from above. Sterna with distinct crossimpressions. Legs sparsely setose. Gonopod aperture with an elevated ridge.

Gonopod prefemur long and slender, acropodite flat in ventral view, solenomerite sheathed by a broadened tibiotarsus (Figs. 17, 18).

***Varyomus* HOFFMAN, 1954 (Figs. 25-29)**

Northern Venezuela, Trinidad, Ecuador.

Varyomus HOFFMAN, 1954: 49.

Type species: *Aphelidesmus confluens* CHAMBERLIN, 1950, by original designation.

Diagnosis: Solenomerite long and slender, "tibiotarsus broadly laminate, complicated by secondary processes, the end truncate or widely rounded. Solenomerite arising from the medial side of the femoral portion, its end sometimes concealed by the lamellae of the tibiotarsus" (JEEKEL 1963) (Fig. 25).

Remarks: As stated in the original description, *Varyomus* differs from all other Amphininae in the complicated laminate tibiotarsus. It is certainly not related to *Aphelidesmus*, though this genus is also characterized by a laminate tibiotarsus (HOFFMAN, 1998) as it does not have a torsate tibiotarsus and the seminal groove is running directly onto the solenomerite (JEEKEL 1963). JEEKEL (1963) placed other two species, *devillei* (SILVESTRI, 1898) and *levigatus* (ATTEMS, 1944), in this genus.

The following species are currently attributable to *Varyomus*:

devillei (SILVESTRI, 1898) (Ecuador), originally described in *Euryurus*;

roreri (CHAMBERLIN, 1918) (Trinidad, Mt Tucutche), originally described in *Polylepiscus*;

levigatus (ATTEMS, 1944) (Venezuela), originally described in *Protaphelidesmus*;

confluens (CHAMBERLIN, 1950) (northern Venezuela, Rancho Grande), originally described in *Aphelidesmus*.

***Colomborus* CHAMBERLIN, 1952 (Figs. 30-33)**

Colombia.

Colomborus CHAMBERLIN, 1952: 587.

Colomborus HOFFMAN, 1954: 49.

Type species: *Colomborus martanus* CHAMBERLIN, 1952, by original designation.

Diagnosis: Gonopod acropodite spherical as the "solenomerite and tibiotarsus both abruptly bent cephalad at their base and both are curving more or less semicircularly distad and caudad" (JEEKEL 1963) (Figs. 30-32). Tergite 2 wider than third one.

Remarks: HOFFMAN (1954) synonymized *Pycnotropis colombiensis* CHAMBERLIN, 1923, with *Colomborus martanus* CHAMBERLIN, 1952.

The single species currently included in this genus:

colombiensis (CHAMBERLIN, 1923) (Colombia, San Lorenzo, Cincinnati Coffee Plantation), originally described in *Pycnotropis*.

***Meridiurus* n.gen. (Figs. 34-38)**

Type species: *Meridiurus venitus* sp.n.

Name: Emphasizes the "Cordillera de Merida" as the place of origin.

Diagnosis: Gonopod tibiotarsus bent toward solenomerite, causing vesicle-like structure lying between acropodite branches instead of below them (Fig. 34).

***Meridiurus venitus* n.sp. (Figs. 34-38)**

Holotype ♂ (VMNH), Venezuela, Edo Mérida, Cueva de Venito, 100 m inside from entrance, no date, leg. P.J. CHAPMAN.

Name: Referring to the name of the cave.

Description: Holotype 50 mm long, width of metazonites 5.0 mm, of prozonites 3.0 mm. Colour mostly faded, live animal supposedly dark brown. Epicranial suture distinct. Collum gently rounded, dorsolaterally with areations, subsequent segments with polygonal fields with small knobs scattered all over metazonites, but distinctly less expressed middorsally than dorsolaterally. Paraterga 2 slightly wider than collum and subsequent segments. Paraterga broadly thickened and slightly declivent, caudal paratergal corner mostly gently rounded (Figs. 35, 36), only in segments 17-19 acutely pointed (Fig. 39). Ozopores visible in dorsal view, only in segment 19 situated clearly ventrally. Sternite 2 laterally with two small projections. Paraterga with tiny cones ventrocaudally. Epiproct broadly spatula-like, with two caudal setae on very small tubercles (Fig. 38). Legs sparsely setose. Aperture of gonopods thickened laterally, with a small groove on each side for accommodation of coxa 9.

Solenomerite bending at base away from tibiotarsus and curving with the tip directed toward apical end of tibiotarsus. A small projection at base of solenomerite (Fig. 34).

***Tibrachiorus* n.gen. (Figs. 39-49)**

Colombia.

Type species: *Tibrachiorus suarezi* n.sp.

Name: (Greek: Tri- = three, brachion- = branch). Emphasizing the three-branched gonopods.

Diagnosis: Segment 2 wider than collum and subsequent segments. Ventral surface of metazonite divided by a slight fold/groove running from between legs toward lateral margin, on both sides accompanied by a small projection near stigma. Male legs densely setose ventrally, relatively strong setae clearly visible under stereoscope. Margins of epiproct undulated, epiproct bearing two setae dorsally.

Gonopod acropodite strongly expanded and divided into three branches: solenomerite curved, semicircular; tibiotarsus shield-like with processes; and a sigmoid, slightly enlarged, generally slender branch.

Remarks: The species included are:

polygonatus (GERVAIS, 1847) (Colombia), originally described in *Polydesmus*;

huila n.sp. (Colombia, Huila);

suarezi n.sp. (Colombia, Rio Suarez).

In a short redescription of *polygonatus*, CARL (1914) classified it under *Pycnotropis*. To avoid too many monotypic genera, JEEKEL (1963) assigned this species under *Colomborus*, as this was the most similar genus known at that time. The gonopod structure of the newly collected specimens is very similar to that of *T. polygonatus*, yet it is different from that of *Colomborus*. This seems sufficient to justify the introduction of an additional new genus to incorporate *T. polygonatus*.

***Tibrachiorus polygonatus* (GERVAIS, 1847)**

Material: 1 ♂ (MHNP), Colombia, leg. M. GOUDOT.

Diagnosis: A small processes in the middle of shield-like part of gonopod tibiotarsus.

Redescription: Length 67 mm, width of metazonites 9.0 mm, of prozonites 6.0 mm. Epicranial suture very superficial, lateral flaps of collum obtusangular. Segment 2 slightly broader than collum and subsequent segments. Paraterga slightly declivent, ascending caudad. Caudal corner of paraterga 14 slightly protruding, of subsequent segments increasingly protruding and acuminate. Ventral surface of paraterga 2-4 granulose, on subsequent segments slightly rugose with stout cones ventrocaudally, caudal paratergal margin slightly serrate. Polygonal areation restricted to paraterga, peritremata slightly incrossate, ozopores visible from above. Sterna of segment 4 separated by a groove, sterna of segments 5 and 6 with tubercles, subsequent sterna slightly prominent. Hypoproct semicircular to obtusangular, epiproct undulated. Legs setose ventrally. Gonopod aperture elevated laterally, forming a ridge.

Remarks: The colour of the live millipede was described as grey-violet (GERVAIS 1847), and even

alcohol material is dark blue, with lighter venter, sterna and peritremata. CARL (1914) described it as black-brown dorsally, red-brown laterally, and the paraterga yellow.

***Tribrachiorus suarezi* n.sp. (Figs. 39-43)**

Holotype ♂ (VMNH), Colombia, Santander, Rio Suarezi (Jaurez?), 800-1,000 m a.s.l., date and collector unknown.

Name: Emphasizing the type locality.

Diagnosis: Well-developed cones on sterna even in front of gonopod aperture (Fig. 43).

Description: Length 75 mm, width of midbody metazonites 10.1, of prozonites 6.0 mm. Colour of alcohol material faded, apparently paraterga lighter than rest of metazonite. Epicranial suture deep and not bifurcated. Collum anteromedially with a slight inlet surrounded by a small bulge. Paraterga dorsolaterally with polygonal fields surmounted by very small knobs (Figs. 40, 41). Ventral surface of metazonites 2-5 microgranulated, caudad restricted to lateral edges, but granules produced into spines/small cones and present until segment 18 (Fig. 42). Ventral body surface slightly shagreened. Sterna with projections: in segment 4 with two small caudal cones, in segment 5 with four cones separated by notches, in segment 6 only with cones on anterior part, in segment 7 with cones behind gonopod aperture, in segment 8 with four cones, the cones decreasing in size to nearly totally disappear toward caudal end of body. Coxae distally surrounded by some slightly sclerotized rings/bulges. Entire dorsal surface of metazonite covered with polygonal fields with small knobs. Paraterga horizontal to ascending, protruding caudad, caudal corner droplike to acute. Margins of epiproct sinuate.

Solenomerite curved toward a slender tibiotarsal branch. Shield-like branch divided into a broader shield and a smaller, furcated process (Fig. 39).

***Tribrachiorus huila* n.sp. (Figs. 44-49)**

Holotype ♂ (VMNH), Colombia, Huila, San Augustin, 1.09.1969, leg. D. MESSERSMITH. - Paratype: 1 ♀ (VMNH), Colombia, Huila, Finca Merenberg, 100 km east of Popoyan en route La Plata, 2,300 m a.s.l., Feb. 1983, leg. C. MURCIA.

Name: Emphasizing the type locality.

Diagnosis: With a longitudinal suture on collum (Fig. 49). In comparison with *T. suarezi*, paraterga thicker (Fig. 46), sterna unmodified and a shield-like tibiotarsus not divided but with a serrate end in the holotype (Fig. 43), a smooth one in the paratype.

Description: Length of holotype 65 mm, of paratype 55 mm, width of metazonites 9.1 mm, of prozonites 4.4 mm. Head yellow-beige, with a brown frons. Colour dark brown, collum and paraterga finely and narrowly bordered whitish. Legs and antennae yellowish. Collum subangular, rounded, bordered with a small bulge/circumference, areated laterally, with a longitudinal suture (Fig. 49). First four segments bordered laterally with a small circumference. Segments dorsally nearly totally areated, with small knobs in polygonal fields. Paraterga slightly declivent, not protruding caudally, slightly swollen (Figs. 45, 46). Paraterga with strong spines ventrocaudally (Fig. 47). Pore-bearing paraterga with small projections on ventral surface. Sterna slightly elevated in anterior part of body but in general flat and unmodified. Epiproct undulated (Fig. 47).

Gonopods relatively stout, solenomerite running between a divided tibiotarsus, a shield-like branch with protuberances at distal end and a slender branch (Fig. 44). Sternum between gonopods well-developed.

***Coleocacamus* n.gen. (Figs. 50-53)**

Colombia.

Type species: *Coleocacamus depressus* n.sp.

Name: (Latin: Coleus = sheath, cacamus = apical tip). Referring to the solenomerite tip covered by the broader tibiotarsus.

Diagnosis: Medium-sized amphinine millipede. Metazonites slightly undulated ventrally, caudal paratergal margin not serrate but nearly smooth. Gonopod coxite subtriangular, prefemur ovoid and setose, femorite stout, with a membranous structure (= vesicle) at base of solenomerite. Solenomerite strongly sigmoid, curved, tip covered by a broader flexible shield of tibiotarsus.

Remarks: The following species are attributable to this new genus:

depressus n.sp. (Colombia, Mpio de Burga);

labialveus n.sp. (Colombia, Farralones).

***Coleocacamus depressus* n.sp. (Figs. 50-53)**

Holotype ♂ (VMNH), Colombia, Valle Varedo El Janeiro, Mpio de Burga, 2,000 m a.s.l., subtropical humid forest, under trunk, June 1989, leg. E. FLOREZ. - Paratypes: 3 ♂♂, 1 ♀ (VMNH), same place, date and collector.

Name: Emphasizing the depression behind the anterior paratergal margin.

Diagnosis: Gonopod tibiotarsus divided distally into two lobes covering the solenomerite (Fig. 50).

Description: Holotype 55 mm long, width of midbody metazonites 8.7 mm, of prozonites 5.1 mm. Colour brown, probably darker in live specimens. Paraterga and end of epiproct yellowish, same as vertex, being lighter than frons and collum. Antennae yellowish, infuscated distad. Epicranial suture distinct. Collum subtriangular and broadly rounded, subsequent segments subangulate, anterior paratergal margin with a distinct ridge, caudal paratergal margin slightly indentated, caudal paratergal tip slightly protruding, more or less rounded (Figs. 51-53), only in segments 17-20 more acute. On midbody metazonite, a flat groove running distodorsally (Fig. 53). Dorsal surface slightly areated laterally, some areated fields with a small knob. Ventral surface of segments 1-6 granulated, subsequent segments with small cones ventrocaudally. Epiproct relatively long, undulated, hypoproct subtrapezoid. Gonopod aperture laterally with a prominent ridge decreasing in height caudad.

Tibiotarsus divided distally into two lobes covering the solenomerite (Fig. 50).

***Coleocacamus labialveus* n.sp. (Fig. 54)**

Holotype ♂ (VMNH), Colombia, Valle P.N. Farralones, Quebrahonda, humid premontane forest, inside trunk, 1,800 m a.s.l., May 1989, leg. E. FLOREZ. - Paratype: 1 ♀ (VMNH), same place, day and collector.

Name: Emphasizing a groove running between the labium and the clypeus.

Diagnosis: Gonopod tibiotarsus with a single broadened tip covering the solenomerite (Fig. 54).

Description: Holotype 65 mm long, width of midbody metazonites 8.0 mm, of prozonites 5.0 mm. Colour faded. Surface smooth without polygonal areation. All somatic characters as in *C. depressus* except as follows: A distinct groove running between labium and clypeus. Lateral ridges less well-expressed than in *C. depressus*. Tips of caudal corners of paratergum 19 very sharp and elevated.

Gonopod tibiotarsus with a single broadened tip covering the solenomerite (Fig. 54).

***Kallistopeltis* n.gen. (Figs. 55-61)**

Ecuador (Pastaza, Cushueme), Peru (Iquitos, Loreto), Brazil (Amazonia).

Name: (GK: kallistos = beautiful, peltis = shield). Alluding to the beautiful dorsal pattern.

Type species: *Pachyurus kalonotus* ATTEMS, 1899.

Diagnosis: Spines on the ventral surface of the paraterga are absent (Fig. 60). The solenomerite is much longer than the widely broadened tibiotarsus (Figs. 55-57). In lateral view, the solenomerite is lateral instead of mesal.

Remarks: A single species can be attributed to this new genus:

kalonota (ATTEMS, 1899) (Brazil: São Paulo de Olivença (former Peru)), originally described in *Pachyurus*.

Originally, ATTEMS (1899) described this species in the genus *Pachyurus*. POCOCK (1909) chose *kalonotus* as type species of *Amplinus*, but this action was invalid (see above). HOFFMAN (1951) classified *kalonota* under *Phinotropis* as he regarded it to be congeneric with *P. tida*. Three years later, HOFFMAN (1954) synonymized *Phinotropis* under *Amplinus* (which was misspelt as *Amphinus*) and maintained *kalonotus* as type species of *Amplinus*, followed by JEEKEL (1963). Hence *Amplinus* was meant in the scope of the nowadays *Pycnotropis*. To group the Central American species which still were included in POCOCK's *Amplinus* concept, HOFFMAN (1954) proposed the name *Pseudamplinus* (the type species: *Amplinus orphinus* CHAMBERLIN (1922)). In his classification, HOFFMAN (1980) got rid of *Pseudamplinus* and placed the Central American species with a concave hypoproct in *Amplinus*. In his latest redefinition of *Pycnotropis*, however, HOFFMAN (1995) synonymized *Phinotropis* under *Pycnotropis*, though mentioning no *kalonota* as its constituent member.

***Kallistopeltis kalonota* (ATTEMS, 1899) (Figs. 55-61)**

Material: 1 ♂, 1 ♀ (VMNH), Peru, Loreto, Yagua Indian village, headwaters Rio Loreto-Yacu, 21.04.-01.05.1970, leg. B. MALKIN; 1 ♂ (VMNH), Ecuador, Dept. Pastaza-Napo, Cushueme, Rio Cushueme, 320 m a.s.l., ca. 150 km SE of Puyo, 15.-28.05.1971, leg. B. MALKIN; 1 ♂, 1 ♀ (SMF) Peru, Depto. Loreto, 21 road-km S of Iquitos on road to Nauta, Allpahuayo Experimental Station (IAP) (3°53'S, 73°20'W), terra firme, rotten wood, 04.-05.1997, leg. A. MÁRMOL; 2 ♂♂ (ZMUM), 1 ♂, 1 ♀ (MHNL), same place, in pitfall traps with fish bait, December 1997, leg. A. MÁRMOL; 3 ♂♂, 2 ♀♀ (MHNL), same place and collector, November 1997.

Redescription: Length (male) about 52 mm, width of midbody metazonites 7.7-8.2 mm (female 9.3-9.7 mm), of prozonites 3.5-3.7 mm (female 5.3-5.5 mm). Colour dark brown, legs and labrum slightly lighter, gonopods yellowish, tips of antennae white. Dorsum with continuous yellowish spots centrally, broader on metazonite than on prozonite. Epicranial suture very deep and slightly bifurcated between antennae. Collum narrowly rounded laterally, distinctly bordered. Width of collum < segment 2 > segment 3 > segment 4-18 > segment 19 > segment 20. Paraterga lying level to midbody metaterga, horizontal, directed dorsocaudally. Paraterga finely granulated ventrally, segments 5+6 granulated ventrocaudally, subsequent segments ventrally smooth to rugulose, segments 15-18 with a small, ellipsoid projection ventrally. Dorsum totally areated, peritremata thick, ozopores visible from above (Figs. 58, 59). Caudal paratergal margin serrate. Hypoproct semicircular, each paraproct with a setigerous tubercle, epiproct broadly spatula-like (Figs. 61). Sterna 4+5 with small tubercles, subsequent sterna relatively deeply cut in. Legs sparsely setose. Gonopod aperture surrounded by a prominent ridge, ventrally so higher than anteriorly or caudally.

Gonopod prefemur long, tibiotarsus blade-like, solenomerite lanceolate and strongly curved (Figs. 55-57). Sternum between gonopods absent.

Remarks: The species seems to be quite widespread in the upper Amazon region, ranging from Ecuador and Peru down to Brazil along the Amazon River (São Paulo de Olivença).

Thrinoxethus CHAMBERLIN, 1941 (Figs. 62-82)

Peru.

Thrinoxethus CHAMBERLIN, 1941: 498.

Cyclotropis VERHOEFF, 1941: 37.

Type species: *Thrinoxethus hermosus* CHAMBERLIN, 1941, by original designation.

Diagnosis: Solenomerite with a subapical projection, longer than tibiotarsus. Tibiotarsus slender and acute distally. Vesicle-like structure larger on distolateral side than mesally.

Remarks: CHAMBERLIN (1941) proposed eight new species in *Thrinoxethus*, five of the descriptions were based on female material only. VERHOEFF (1941) erected the monotypic subgenus *Cyclotropis* within the genus *Pycnotropis*. As the name *Cyclotropis* was preoccupied, CHAMBERLIN's name *Thrinoxethus* has been accepted.

T. paucartambus (KRAUS, 1956), *T. verhoeffi* (KRAUS, 1956) and *T. pichitaensis* (KRAUS, 1959) fit into the concept of *Thrinoxethus* as their solenomerite is bifurcate and longer than the tibiotarsus.

The following species are assigned to this genus:

peruanus (VERHOEFF, 1941) (South Peru, near Sivia), originally described in *Cyclotropis*;

bombonus CHAMBERLIN, 1941 (Peru, Rio Bombo, Alto Tapiche);

cainarachus CHAMBERLIN, 1941 (Peru, Rio Cainarachi) (only female);

hermosus CHAMBERLIN, 1941 (Peru, Pampa hermosa, Rio Ucayali);

iquitos CHAMBERLIN, 1941 (Peru, Iquitos) (only female);

lamprus CHAMBERLIN, 1941 (Peru, Moyobamba, Balsapuerto Trail);

nitens CHAMBERLIN, 1941 (Peru, Rio Bombo, Alto Tapiche) (only female);

phanotypus CHAMBERLIN, 1941 (Peru, Loreto, Pongo de Manseriche) (only female);

ucayalus CHAMBERLIN, 1941 (Peru, Suhuaya, Ucayali) (only female);

paucartambus (KRAUS, 1956) (Peru, Cusco, Rio Paucartambo, San Luis Shuaro); originally described in *Pycnotropis*;

verhoeffi (KRAUS, 1956) (Peru, Loreto, San Alejandro), originally described in *Pycnotropis*;

pichitaensis (KRAUS, 1959) (Peru, Rio Chanchamayo: Rio Casca), originally described in *Pycnotropis*;

juani n.sp. (Peru, San Martin, near Pongo);

junini n.sp. (Peru, Junini);

siolii n.sp. (Peru, Loreto and San Martin).

Thrinoxethus siolii n.sp. (Figs. 61-62)

Holotype ♂ (MHNL), Peru, Loreto, Yurimaguas, Exp. Station "Rio Shanusi" (6°56'S, 76°6'W), 23.08.1996, leg. K. VOHLAND. - Paratypes: 1 ♂ (SMF), same place, date and collector; 1 ♀ (MHNL), Peru, San Martin, road Pongo-Terapoto, (6°27'S, 76°17'W), 1,000 m a.s.l. 16.08.1996, leg. K. VOHLAND.

Name: Honours H. SIOLI, the prominent German limnologist who emphasizes the special character of the aquatic and terrestrial reaches of Amazonia and threats to the region due to human activities.

Diagnosis: Tibiotarsus with a very short process. Colour brown with lighter paraterga.

Description: Male: Length 60 mm, width of metazonites 9.0 mm, of prozonites 4.7 mm. Colour dark brown, paraterga, legs and antennae whitish-yellow, except for an infuscated antennomere 7. Labrum, venter and gonopods light brown, margins of gonopod aperture darker. Epicranial suture distinct, collum subtrapezoid, width of head << collum < segment 2 > segment 3 > segment 4-18 > segment 19 > segment 20. Paraterga subangulate, caudal edge of segment 13 and of subsequent segments slightly protruding, tip rounded. Caudal margin of paraterga serrate. Paraterga 2-4 granulated ventrally, subsequent paraterga rugose and granulated ventrocaudally. Sterna of segments 5 and 6 with small projections. Epiproct broadly rounded, paraprocts with projections, hypoproct semicircular. Legs sparsely setose. Gonopod aperture

caudally with a distinct rim.

Gonopod coxite and prefemur cylindrical, cingulum with a membranous structure, both branches lanceolate, solenomerite longer, bifurcated distally (Figs. 62, 63).

Remarks: Colour pattern very similar to that of *T. cainarachus* CHAMBERLIN, 1941, differing in the darker epiproct and stronger caudoventral granulation. However, CHAMBERLIN's species was based on a female holotype only, so I cannot consider the association to be correct only because of the congruence of the colour pattern.

***Thrinoxethus verhoeffi* (KRAUS, 1956) (Figs. 63-70)**

Material: Holotype ♂ (SMF-2533), Peru, Depto., Loreto, San Alejandro, 300 m a.s.l., 30.07.1955, leg. W. WEYRAUCH, 1 ♂ (MHNL), Peru, Rio Ucayali, P.N.A. von Humboldt, 06.10.1982, leg. A. VIVANCO, R. SEGOVIA, S. CRUZ, F. PERALTA.

Remarks: This species probably shows a plesiomorphic state in some characters. In particular, each of the gonopod coxae supports as many as 12 macrosetae (Figs. 64-66). The presence of numerous setae on coxae might be evidence of ancestral traits rather than an autapomorphy. Similarly, the projections on the anterior sterna in *T. verhoeffi* might be regarded as symplesiomorphies shared with some other genera (e.g. *Exallostethus*, *Pastazina*).

Some characters seem to be variable within this species: The specimen from Ucayali is larger than the holotype, is sculptured less heavily and the tip of the tibiotarsus is less strongly broadened, with a longer tip. However, the presence of the high number of large setae on the gonopod coxae in both males seems to allow to group them under a single species.

***Thrinoxethus pichitaensis* (KRAUS, 1959)**

Material: Holotype ♂ (SMF), Central Peru, eastern slope of Eastern Andes, Mina Pichita Caluga, 2,200 m a.s.l., Rio Casca, affluent of Rio Chanchamayo, cloud forest, 25.02.1957, leg. W. WEYRAUCH.

***Thrinoxethus paucartambus* (KRAUS, 1959)**

Material: Holotype ♂ (SMF), Peru, Dept. Cusco, Eastern Andes, Rio Paucartambo, San Luis Shuaro, 900 m a.s.l., montaneous rain forest, 19.03.1955, leg. KOEPCKE.

Remarks: Close to *T. verhoeffi*, as the gonopod coxa also bears as many as 12 macrosetae, the tibiotarsus is elongated and strongly curved and the solenomerite is slightly bent. However, the colour pattern is very different, this species having a uniform brown dorsum with yellow paraterga and epiproct.

***Thrinoxethus juani* n.sp. (Figs. 72-76)**

Name: In honour of the hospitality and support received from some members of the Peruvian Amazonian University, Iquitos, Peru.

Holotype ♂ (MHNL), Peru, San Martin, road Pongo-Terapoto (6°27'S, 76°18'W), 1,000 m a.s.l., leg. K. VOHLAND. - Paratypes: 2 ♀♀ (MHNL), together with holotype; 2 ♀♀ (SMF), ca. 2 km west on same road, 800 m a.s.l., same date and collector.

Diagnosis: Colour and somatic characteristics very similar to those of *T. peruanus*, but gonopod tibiotarsus less strongly curved (Fig. 72). Colour pattern striped transversely.

Description: Holotype 60 mm long, width of midbody metazonites 7.8 mm, of prozonites 4.9 mm.

Colour of head and prozonites dark brown, collum, metazonites, venter, labrum and gnathochilarium light brown, paraterga, legs, antennae and epiproct yellowish. Epicranial groove deep. Collum triangular, relatively narrowly rounded, with a broad margin anteriorly, collum and subsequent segments subequal in width, paraterga horizontal, caudal paratergal corner of segment 9 slightly protruding, in subsequent segments increasingly protruding and acute (Figs. 73-75). Paraterga 2-4 ventrally granulated, subsequent paraterga ventrocaudally with small cones. Dorsal surface with conspicuous areation. Epiproct subangulate, slightly undulated (Fig. 76), hypoproct semicircular. Margins of gonopod aperture laterally and caudally slightly elevated and with a thin rim.

Gonopod prefemur ellipsoid, cingulum with a membranous structure, both branches lanceolate, tibiotarsus shorter than solenomerite, latter with a process at distal end (Fig. 72).

Thrinoxethus junini n.sp. (Figs. 77-82)

Name: Emphasizing place of collection.

Holotype ♂ (MHNL), Peru, Junini, 1-3 km SW Mina Pichito 2,100 m a.s.l., 20.08.1988, leg. I. SEVILLANO. - Paratype: 1 ♀ (MHNL), same place, date and collector.

Diagnosis: Compact dark species with knobs on slightly areated metazonite (Figs. 79-82).

Description: Holotype 42 mm long, width of midbody metazonites 8.2 mm, of prozonites 5.1 mm. Paratype 50 mm long, width of midbody metazonites 7.9 mm, of prozonites 4.7 mm. Colour dark castaneous brown, paraterga contrastingly yellow, collum and segment 2-4 bordered dark. Antennae dark brown, antennomere 7 and legs slightly lighter. Collum broadly rounded, segment 2 slightly wider, paraterga set slightly above half-height of segment, very slightly declivent. Caudal corner in segments 2-13 subrectangular, in segment 14 and subsequent segments increasingly protruding. Surface below paraterga 2-4 granulated ventrally, subsequent paraterga ventrocaudally with very small cones (Fig. 81). Dorsal surface smooth with traces of areation, best expressed on segments of anterior body part, increasingly numerous bosses with a small knob each toward caudal segments because of gradual obliteration of areation. Epiproct of male with a very slight horizontal ridge (Fig. 82), latter in female even less expressed. Sterna unmodified. Gonopod aperture laterally and caudally slightly elevated and with a thin rim.

Each gonopod coxa with a seta, both branches of telopodite relatively long and slender, tibiotarsus slightly shorter (Fig. 77).

Remarks: Colour pattern close to *T. bombonus* CHAMBERLIN, 1941, but differs in position of gonopods, degree of metatergal areation and shape of paratergal tips.

Sculptoteles n.gen. (Figs. 83-87)

Ecuador (Pastaza).

Name: Emphasizing the strongly sculptured dorsum.

Polylepiscus, CARL, 1918: 419.

Phinotropis, HOFFMAN, 1951: 235.

Amplinus, JEEKEL, 1963: 62.

Pycnotropis, HOFFMAN, 1995: 283.

Type species: *Polylepiscus braueri* CARL, 1918.

Diagnosis: Differs in the very strongly sculptured dorsal surface (Figs. 84-87). Gonopods very similar to those of *Pycnotropis*, except for the more strongly curved seminal groove and the lower position of the vesicle (Fig. 83). In overall habitus resembling *Polylepiscus*.

Remarks: In spite of the major differences from the known species of *Polylepiscus*, CARL (1918) placed *braueri* in this genus where two of the four described species were based on female material only. HOFFMAN (1951) joined *braueri* together with some nowadays *Kallistopeltis* and *Pycnotropis* species

under *Phinotropis* CHAMBERLIN, 1941, because of the two-branched acropodite and South American origins. Using his extensive *Amplinus* concept, JEEKEL (1963) assigned *braueri* to this genus. HOFFMAN (1995) referred *braueri* to *Pycnotropis* because of the vesicle-like structure at the base of the solenomerite.

A single species can be attributed to this new genus:

braueri (CARL, 1918) (Acuador, Santa Inez), originally described in *Polylepiscus*.

***Sculptoteles braueri* (CARL, 1918) (Figs. 83-87)**

Material: 1 ♂ (VMNH), Ecuador, Pastaza Province, 2-8 miles N of Puye, leg. E.I. SCHLINGER & E.S. ROSS. 1 ♂ (ZMB-8195), Ecuador, Santa Inez, 09.12.1899, leg. R. HAENSCH.

Redescription: Length about 65 mm, width of metazonites 8.5 mm, of prozonites 3.9 mm. Colour very dark red-brown, antennae, tips of legs and dorsal fosses slightly lighter. Epicranial suture distinct. Collum subtriangular, narrowly rounded, segments 2-6 subangulate, caudal paratergal corner of subsequent segments increasingly protruding and beak-like, slightly uplifted (Figs. 84-86). Ozopores visible from above, peritremata thick (Fig. 86). Paraterga 2-5 granulated ventrally, in segments 6-9 granules ventrocaudally and near coxae, in segments 10-18 small spines ventrocaudally, caudal paratergal margin serrate. Dorsal surface very strongly sculptured/areated. Sterna of segment 5 with cone-like projections, of segment 6 with conspicuous cones. Epiproct broadly rounded, slightly undulated (Fig. 87), hypoproct oblong semicircular. Legs with long setae ventrally. Gonopod aperture laterally and caudally with a prominent ridge.

Gonopod prefemur ovoid, socket distinct, a small membranous structure at base of cingulum, both branches tapering distad, solenomerite shorter than a gently curved tibiotarsus (Fig. 83).

***Pycnotropis* CARL, 1914**

See review by GOLOVATCH et al. (1998).

Peru, Ecuador, Colombia, Brazil.

Pycnotropis CARL, 1914: 419.

Amydrinus, CHAMBERLIN, 1941: 498.

Phinotropis CHAMBERLIN, 1941: 498.

Ptyxogon CHAMBERLIN, 1941: 498.

Type species: *Pycnotropis taenia* CARL, 1914, by original designation.

Diagnosis: Paraterga thick, small ridge in caudad view missing and united broadly with body trunk. Caudal corners becoming more acute only in paraterga 16 to 19. Polygonal areation weak and often restricted to lateral edges of paraterga or missing completely.

Remarks: CARL (1914) erected the new genus with *P. taenia* as type species because he judged the species from South America was different from the North American counterparts (nowadays Euryuridae). He emphasized the thick paraterga. CHAMBERLIN (1941) created several new genera, two based on virtually the same species described twice under two different generic names. Because of the great similarity between *P. tida* and *P. epiclysmus*, HOFFMAN (1995) hesitated to describe the latter as new, which nowadays is considered to be only one, although highly variable species (GOLOVATCH et al. 1997). A similar problem actually concerns *P. ponga*. It is indeed so very similar to *P. tida* that HOFFMAN (1995) formally synonymized both. However, since the holotype of *Amydrinus pongus* is somewhat smaller and completely faded, the above synonymy ought to be revised based on new, strictly topotypic material.

The following species are currently recognized within *Pycnotropis*:

taenia (PETERS, 1864) (Bolivia, Bogotá), originally described in *Polydesmus*;

flavocarinata (SILVESTRI, 1898) (Colombia, Villavicencio, Monteredondo-Buenavista), originally described in *Euryurus*;

melanostigma (SILVESTRI, 1898) (Colombia, Villavicencio, Monteredondo-Buenavista), originally described in *Euryurus*;

acuticollis (ATTEMS, 1899) (Brazil: São Paulo de Olivença (formerly in Peru)), originally described in *Pachyurus*;

haenschi CARL, 1918 (Ecuador, Santa Inez);

latzeli ATTEMS, 1931 (Panama, eventually a wrong label);

inca (CHAMBERLIN, 1941) (Peru, Loreto, Iquitos), originally described in *Ptyxogon*;

tida (CHAMBERLIN, 1941) (Peru, Loreto, Iquitos), originally described in *Phinotropis* (= *epiclysmus* HOFFMAN, 1995) (Brazil, Amazonia, Manaus City, Lago Janauari and a few other localities near Manaus); *Amydrinus ponga* CHAMBERLIN, 1941 (Peru, Loreto, Pongo de Manseriche), synonymized by HOFFMAN 1995);

achiraensis KRAUS, 1959 (Peru, Achira, trail Sokota-San Andres);

mammata (ATTEMS, 1931) (Ecuador, Sabanilla), originally described in *Amplinus*;

nitida KRAUS, 1959 (Peru, Cueva de San Andres, 30 km NE of Cutervo);

subareata (JEEKEL, 1963) (Brazil, Amapá, Carsevenne), originally described in *Amplinus*;

carli GOLOVATCH, VOHLAND & HOFFMAN, 1998 (Ecuador, Pastaza, Cushueme);

curvata GOLOVATCH, VOHLAND & HOFFMAN, 1998 (Peru, Loreto, headwaters of Rio Loreto-Yacu);

falcata GOLOVATCH, VOHLAND & HOFFMAN, 1998 (Peru, Loreto, Rio Nanay, Padre Cocha);

goeldii GOLOVATCH, VOHLAND & HOFFMAN, 1998 (Brazil, Amapa, Serra do Navio);

jeekeli GOLOVATCH, VOHLAND & HOFFMAN, 1998 (Peru, Loreto, 21 km S of Iquitos);

madeira GOLOVATCH, VOHLAND & HOFFMAN, 1998 (Brazil, Rondonia, Rio Madeira, Porto Velho);

pallidicornis GOLOVATCH, VOHLAND & HOFFMAN, 1998 (Peru, Loreto, 21 km S of Iquitos);

sigma GOLOVATCH, VOHLAND & HOFFMAN, 1998 (Brazil, Amazonia, 20 km N of Manaus);

similis GOLOVATCH, VOHLAND & HOFFMAN, 1998 (Peru, Rio Yubinetto, St. Rita);

subfalcata GOLOVATCH, VOHLAND & HOFFMAN, 1998 (Peru, Loreto);

torresi GOLOVATCH, VOHLAND & HOFFMAN, 1998 (Peru, Loreto, 21 km S of Iquitos);

unapi GOLOVATCH, VOHLAND & HOFFMAN, 1998 (Peru, Loreto, Rio Nanay, Padre Cocha);

urucu GOLOVATCH, VOHLAND & HOFFMAN, 1998 (Brazil, Amazonia, Rio Urucu);

zumbii GOLOVATCH, VOHLAND & HOFFMAN, 1998 (Peru, Loreto, Indiana).

***Pastazina* n.gen. (Figs. 88-92)**

Ecuador (Pastaza: Cushueme).

Name: Emphasizing the Pastaza Province in Ecuador, provenance of a lot of material treated here.

Type species: *Pastazina crassa* n.sp.

Diagnosis: In habitus, very similar to *Pycnotropis*, with a smooth, weakly areated dorsum, a laterally widened and grooved gonopod aperture, and a two-branched gonopod with a small vesicle at base of the solenomerite. Yet the position of the gonopod branches is different, with the extraordinarily thick tibiotarsus (Fig. 88) which, in ventral view, is hiding the solenomerite (Fig. 89). Each seta on the hypoproct surmounts a very small projection. The paraterga are strongly declivent, the peritremata are set low.

***Pastazina crassa* n.sp. (Figs. 88-92)**

Name: Emphasizing the thick tibiotarsus (Latin: crassus = thick).

Holotype ♂ (VMNH), Ecuador, Dept. Pastaza-Napo, Cushueme, Rio Cushueme, 320 m a.s.l., ca. 150 km SE of Puyo, 15.-28.05.1971, leg. B. MALKIN. - Paratypes: 3 ♂♂, 5 ♀♀ (VMNH), same place, date and collector.

Description: Males 54-57 mm long, width of metazonites 8.0-9.0 mm, of prozonites 4.5-5.0 mm. Females 56-58 mm long, 7.5-9.0 and 5.0 mm wide, respectively. Colour reddish-brown, probably darker when live. Antennae brown with a light tip, legs from brown to yellow, gonopods yellowish, paraterga yellow. Epicranial groove well-expressed, ten labral and four supralabral setae. Collum with relatively narrow lateral flaps, segment 2 > collum and subsequent segments. Sometimes a very slight polygonal areation pattern on metaterga and prozonites present, visible in the faded specimens as colour pattern. Paraterga 2 and 3 subangulate, subsequent paraterga slightly serrate and indentated caudally, all slightly declivent (Fig. 92), caudal corners increasingly protruding and acute (Figs. 90, 91), sharpest in segments 15-18. Ozopores invisible from above. Sterna of segment 5 with small projections, subsequent sterna more or less flat. Epiproct broadly spatula-like, hypoproct rounded to subtrapezoid, with setae located on very small projections. Body surface smooth, with polygonal areation restricted to lateral margins of metaterga. Metaterga 2-4 ventrally with microgranulation, on subsequent segments granulation only at caudal margin, increasing in size up to spinules. Legs very sparsely setose. Gonopod aperture with a distinct ridge caudally.

Gonopod prefemur ovoid, setose. Vesicle at base of a sickle-shaped solenomerite, tibiotarsus strongly widened distad, trapezoid, thick (Figs. 88, 89).

Key to genera of Amplininae based on gonopod characters:

1. - Acropodite of gonopods divided into two more or less slender branches
(Figs. 1, 16, 34, 50, 55) 2
- Acropodite divided into three or more branches or shield-like appendages
(Figs. 7, 11, 18, 30, 44) 9
2. - Tibiotarsus covering solenomerite distally; caudal paratergal margin not
serrate but nearly smooth (Figs. 50, 54) *Coleocacamus*
- Solenomerite terminating free 3
3. - Solenomerite longer than tibiotarsus (Figs. 56, 62, 66) 4
- Solenomerite shorter than tibiotarsus (Figs. 1,81) 5
4. - Tibiotarsus shield-like, solenomerite long and strongly curved, without subapical projection;
body black with conspicuous light spots on dorsum (Figs. 55-57) *Kallistopeltis*
- Tibiotarsus slender, solenomerite with a subapical projection (Figs. 62, 66);
colour uniform or transversely striped pattern *Thrinoxethus*
5. - Hypoproct concave to truncate (Fig. 5) *Amplinus*
- Hypoproct convex (Fig. 22) 6
6. - Tibiotarsus very thick (Fig. 88) *Pastazina*
- Tibiotarsus long and slender or falcate 7
7. - Acropodite without a vesicle, prefemur without prominent setae,
solenomerite set lower than tibiotarsus (Fig. 16) *Seminellogon*
- Acropodite with a vesicle, prefemur with longer setae 8
8. - Vesicle basal on acropodite; dorsum very strongly sculptured (Fig. 83) *Sculptoteles*
- Vesicle more blister-like at base of solenomerite *Pycnotropis*
9. - Tibiotarsus consisting of two slender branches, the acropodite thus appearing tripartite;
spines at anterior paratergal margin (Fig. 7) *Polylepiscus*
- Tibiotarsus lobed at least to some extent 10
10. - Solenomerite free 11
- Solenomerite sheathed by tibiotarsus at least partly 12

- 11. - Acropodite abruptly deflexed (Figs. 30-32) *Colomborus*
 - Acropodite generally straight, apically not recurved proximad; tibiotarsus divided into
 a cylindrical branch and a lobe-like structure (Figs. 39, 44) *Tibrachiorus*
- 12. - Tip of solenomerite not covered by tibiotarsus; spines at anterior
 paratergal margin (Fig. 11) *Exallostethus*
 - Tip of solenomerite covered by tibiotarsus 13
- 13. - Solenomerite sigmoid, curved away from tibiotarsus (Fig. 34) *Meridiurus*
 - Solenomerite embed in lobes of tibiotarsus 14
- 14. - Acropodite broadened apically (Fig. 25), areation of paraterga only lateral *Varyomus*
 - Whole acropodite cylindrical, paraterga totally areated (Figs. 17, 18) *Protaphelidesmus*

Discussion

The purpose of this paper is not only to present a classification of the Amplininae but also to elucidate the phylogenetic relationships of the constituent genera (Fig. 93) and their geographical patterns (Fig. 94).

The genera *Amplinus*, *Exallostethus* and *Polylepiscus* share the trait that all paraterga are strongly granulated ventrally, while in the other genera ventral granulation is very weak (*Protaphelidesmus*) or restricted to the first few segments only (Fig. 93). *Amplinus* is probably monophyletic in having a concave to subtruncate hypoproct. In addition, only *Amplinus* and *Protaphelidesmus* show no sulcus demarcating the gonopod prefemur from the acropodite. *Polylepiscus* and the monotypic *Exallostethus* share a field of spinules, termed "strigilis" by HOFFMAN (1962), at the broadened anterior edge of the paraterga. All other genera concerned are considered as the sister group to *Amplinus*, *Exallostethus* and *Polylepiscus* as the paraterga 4 and subsequent paraterga are smooth or wrinkled ventrally, but not completely granulated. *Varyomus* and *Protaphelidesmus* as the next genera excluded from this branch show a continuous transition between the gonopod acropodite and prefemur, with the tibiotarsus bearing processes. All other genera have in common a distinctly separated gonopod prefemur and acropodite as evidence for their closer relationship. Only in case the acropodite represents true podomeres, a distinct separation of them is plesiomorphic (ENGHOFF, pers. comm.), and this would be a paraphyletic group only.

For *Seminello*, no apomorphic feature has been identified. It is similar to *Pycnotropis* but has neither conspicuous long setae on the prefemur of the gonopods nor a less heavily sclerotized structure on the acropodite, i.e. the vesicle regarded as characteristic of *Pycnotropis* alone by HOFFMAN (1995). All further genera in the cladogram have this vesicle-like structure in common. In *Pycnotropis*, *Sculptoteles* and *Pastazina*, the vesicle is smaller and located closer to the base of the solenomerite compared to that of *Thrinoxethus*, *Meridiurus*, *Coleocacamus*, *Tibrachiorus*, and *Kallistopeltis*. Eventually, in *Pycnotropis* this structure is more vesicle-like and restricted to a smaller area than in all other genera mentioned before. The tibiotarsus is surrounded by this structure, this area is less heavily sclerotized and this possibly allows the tibiotarsus to move. The existence of a vesicle is possibly an apomorphic feature, while its size reduction, especially in *Pycnotropis*, is perhaps an even more derived condition.

Meridiurus, *Colomborus*, *Coleocacamus*, and *Tibrachiorus* are joined into one group, since the gonopod acropodite stems directly from the prefemur, while in *Kallistopeltis*, *Pastazina*, *Pycnotropis*, *Sculptoteles* and *Thrinoxethus* the acropodite is based

on a short trunk.

Both *Coleocacamus* and *Tribrachiorus* have the tibiotarsus oriented in the same way. The paraterga have small grooves ventromedially. In *Colomborus* this cannot be seen, but it shares with *Tribrachiorus* an enlarged acropodite and cones on the sterna.

As already mentioned, the generic position of *Kallistopeltis kalonota* was not unequivocal. The new genus has been erected here because of the inverse situation of the solenomerite and tibiotarsus, and the absence of ventrocaudal cones from the paraterga. The very differently positioned gonopods of *K. kalonota* could have been caused by a simple torsion of the distal part of the gonopod. Following this assumption, superficially this species looks closer to *Thrinoxethus*, as it fits into the usual pattern of a long solenomerite and a shorter tibiotarsal branch. However, despite the opposite proportions of the gonopod tibiotarsus and solenomerite, *K. kalonota* seems also to be closely related to *Pycnotropis* in sharing not only such a somatic character as the shape of the paraterga but also the basically same orientation of both distal gonopod branches (also suggesting torsion).

Pastazina, *Pycnotropis*, *Sculptoteles* and *Thrinoxethus* have prominent gonopod apertures forming a ridge laterally with a small groove for accommodation of coxae 9. The gonopods consist of two branches, more or less lanceolate, and the tibiotarsal branch is sometimes enlarged. The solenomerite and tibiotarsus junction is U-shaped, placed upon a short trunk.

Pastazina and *Pycnotropis* share the thick swollen paraterga and a small sacciform vesicle at base of the solenomerite as possible evidence of their monophyly.

Caudal paratergal corners in *Sculptoteles* and *Thrinoxethus* are prolonged and strongly acute. In addition, this couple of genera have stiff setae on their legs, hence they are considered as sister groups.

This cladogram is further supported by the distribution patterns (Fig. 94). The center of generic radiation seems to have lain in the northern part of South America (Colombia). Some members of the subfamily, namely *Amplinus*, *Polylepisus*, *Exallostethus* and *Seminellogon*, could have invaded Central America up to Mexico in the north. So far as known, *Varyomus* and *Meridiurus* seem to be restricted to Venezuela, with only one species in Ecuador. All other genera concerned are currently distributed in the Andean region and the Amazon Basin. There is no record of species in more southern countries, perhaps indicating the present limit of dispersal (if not a collecting bias).

It seems safe to surmise that speciation and distributions are related to the geological development and structure of the Andes as well as to the courses of rivers. Members of two genera invaded the Amazon Basin. *Kallistopeltis kalonotus* has been found in the headwater region of a tributary of the Amazon as well as near Iquitos, Peru and further down the Amazon at São Paulo de Olivença, Brazil, indicating fluvial distribution. The same phenomenon is observed in *Pycnotropis tida*, with a distribution pattern ranging from Rio Marañon, Peru at least down to Manaus, Brazil (cf. GOLOVATCH et al. 1998).

Meridiurus, *Coleocacamus*, *Tribrachiorus* and *Colomborus* are restricted to higher elevated areas, with *M. venitus* collected in a cave. In contrast to the previous groups, their gonopods seem to be much more derived. For example, they have more numerous and conspicuous processes. This may be due to the stronger geographical barriers formed by the mountains. The unusual forms may be caused by random gene drift, while the species distributed in the lower Andean region tend to comprise larger

population sizes.

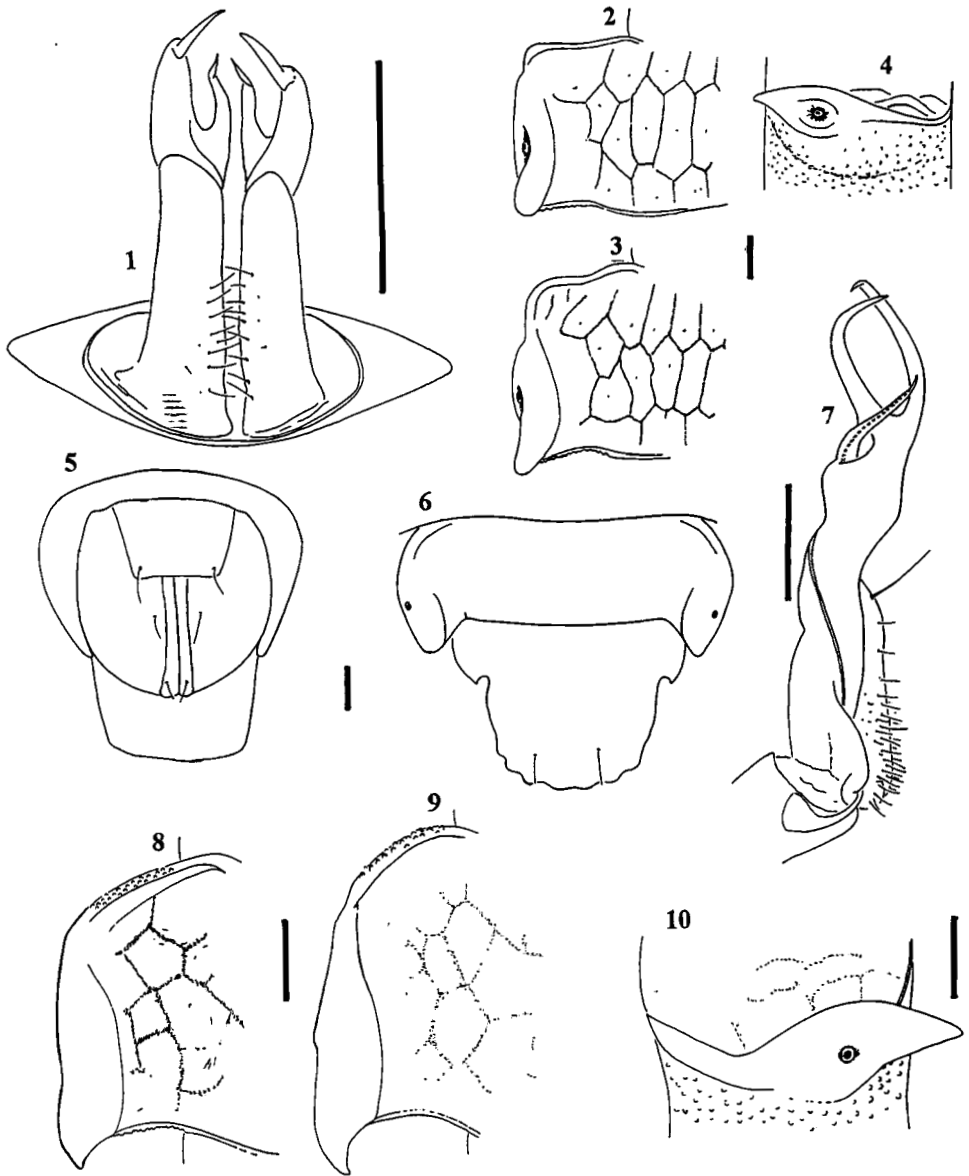
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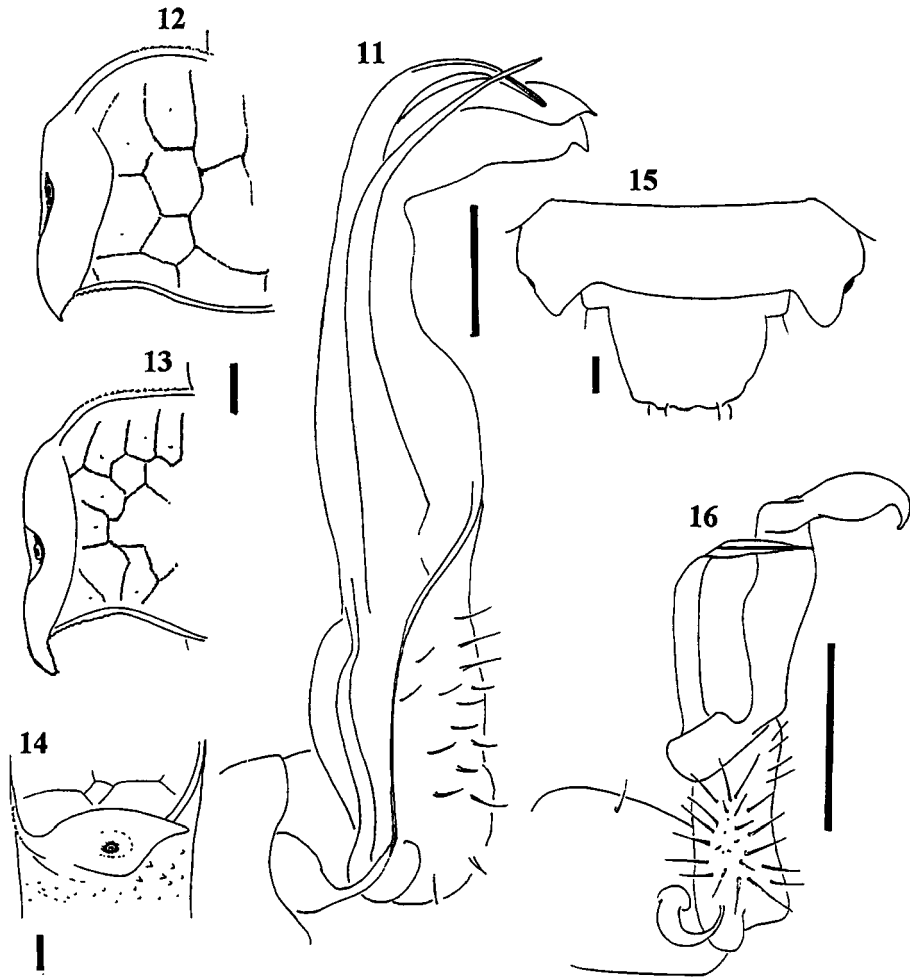
Figs. 1-10:

Amplinus sp. ATTEMS, 1898, male.

1: Gonopods, ventral view. 2: Paratergum 10, dorsal view. 3: Paratergum 16, dorsal view. 4: Paratergum 10, lateral view. 5: Hypoproct, paraproct and epicproct, ventral view. 6: Segment 19 and epicproct, dorsal view.

Polylepiscus hirmærae n.sp., holotype.

7: Left gonopod, mesal view. 8: Paratergum 10, dorsal view. 9: Paratergum 16, dorsal view, with "spiculae". 10: Paratergum 10, dorsal view.



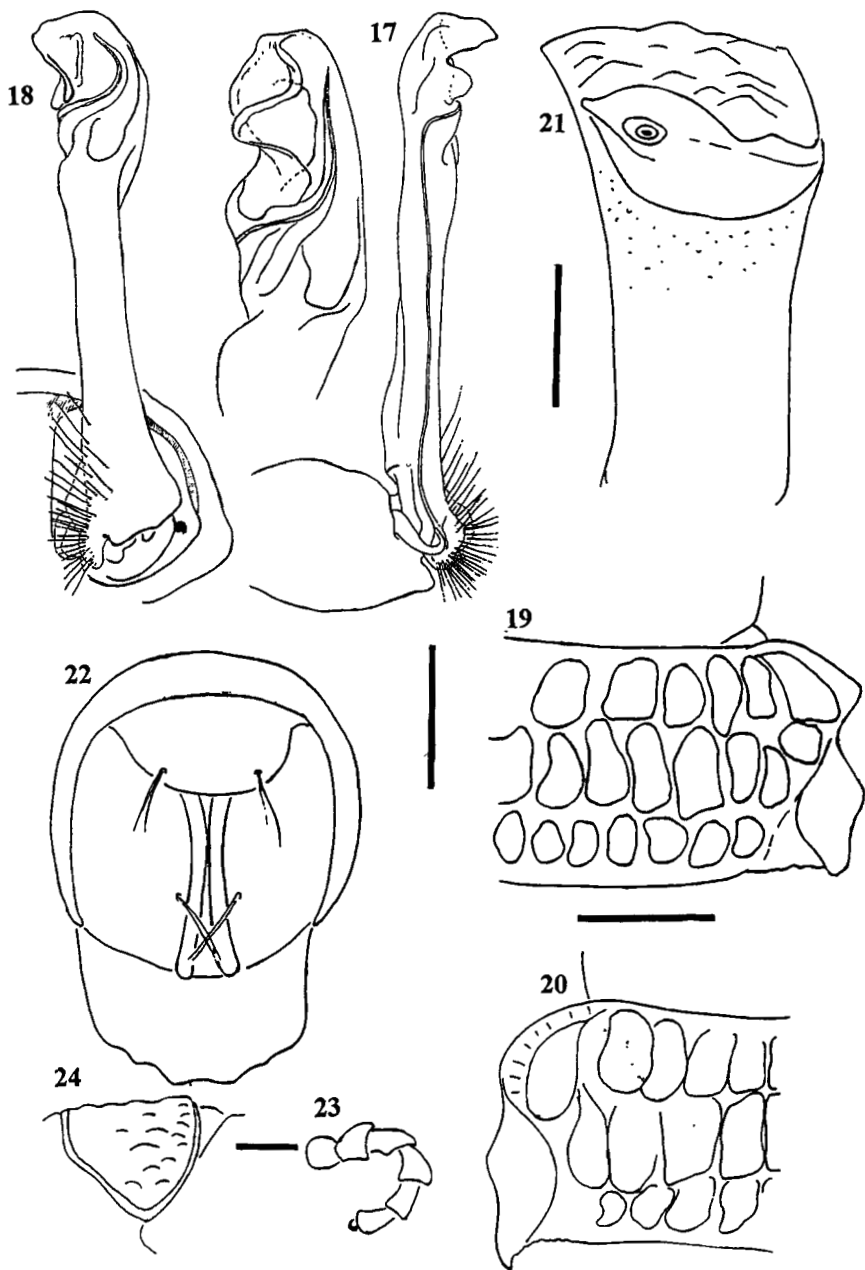
Figs. 11-16:

Exallostethus thrinax HOFFMAN, 1975, male.

11: Left gonopod, mesal view. 12: Paratergum 10, dorsal view. 13: Paratergum 16, dorsal view. 14: Paratergum 10, lateral view. 15: Segment 19 and epiproct, dorsal view.

Seminellogon bituberculosis (LOOMIS, 1973), male.

16: Left gonopod, mesal view.

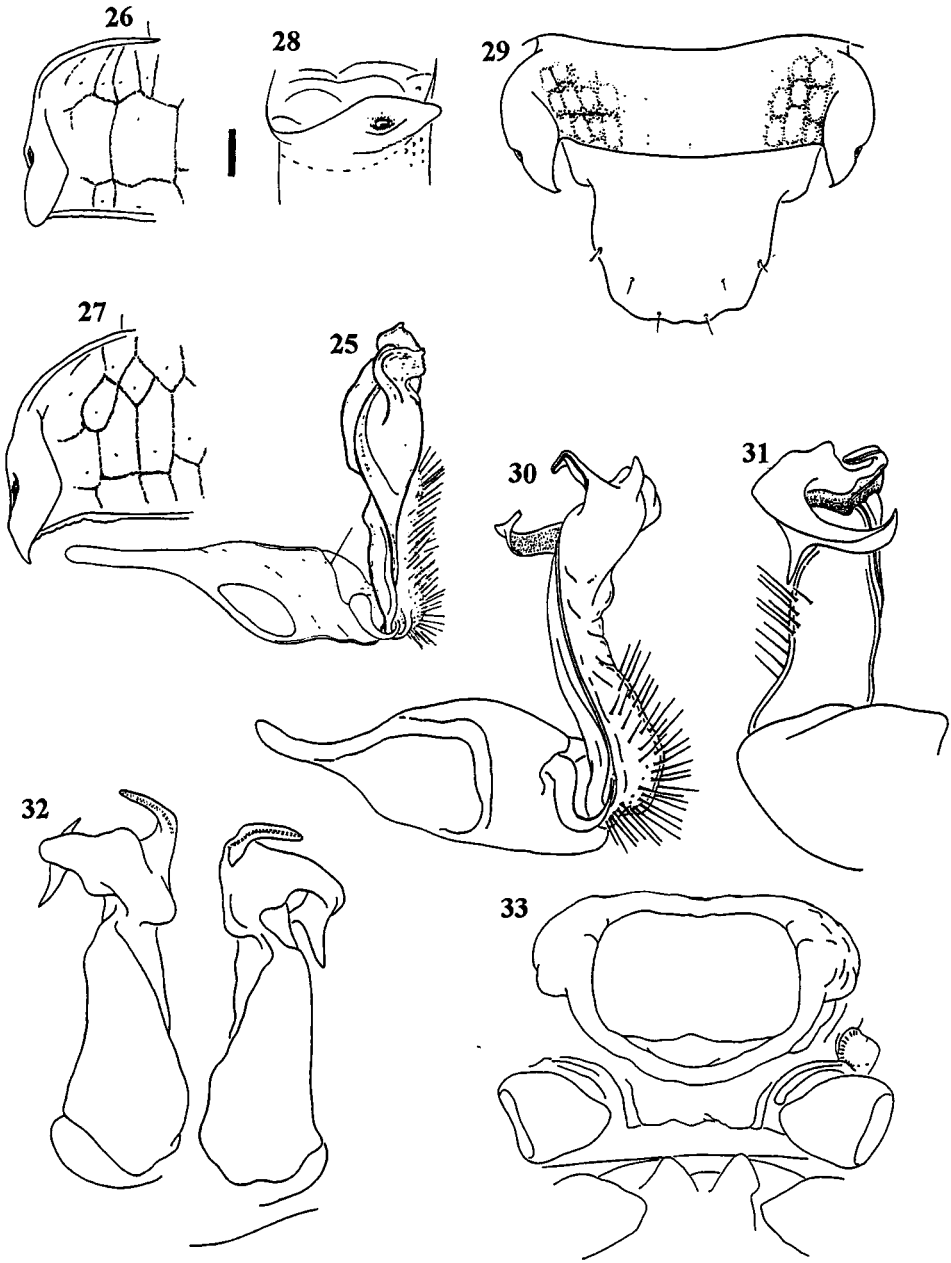


Figs. 17-24:

Protaphelidesmus ligula (BROLEMANN, 1898) male.

17: Left gonopod, mesal view. 18: Left gonopod, lateral view. 19: Paratergum 10, dorsal view.

20: Paratergum 16, dorsal view. 21: Segment 10, lateral view. 22: Hypoproct, paraprocts and epiproct, ventral view. 23: Antennae. 24: Collum, lateral view.



Figs. 25-33:

Varyomus confluens CHAMBERLIN, 1950, male.

25: Left gonopod, mesal view (from HOFFMAN 1954).

Varyomus roreri (CHAMBERLIN, 1918), female.

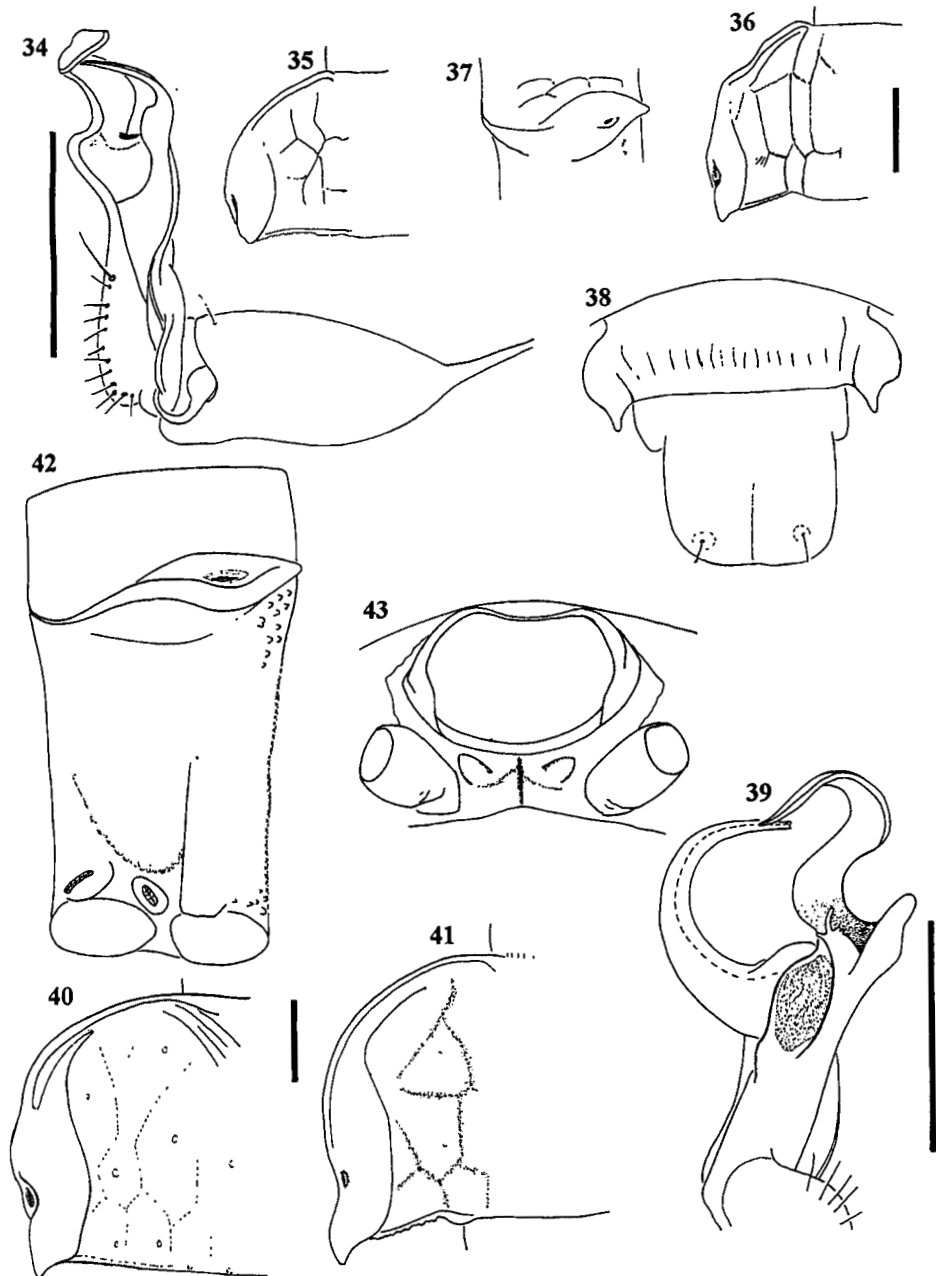
26: Paratergum 10, dorsal view. 27: Paratergum 16, dorsal view. 28: Paratergum 10, lateral view. 29:

Segment 19 and epiproct, dorsal view. Scale bars: 1.0 mm.

Colomborus colombiensis (CHAMBERLIN, 1952), male.

30: Left gonopod, mesal view. 31: Left gonopod, lateral view. 32: Left gonopod, ventral view. 33:

Gonopod aperture and cones on segment 9. All drawings supplied by R. HOFFMAN.



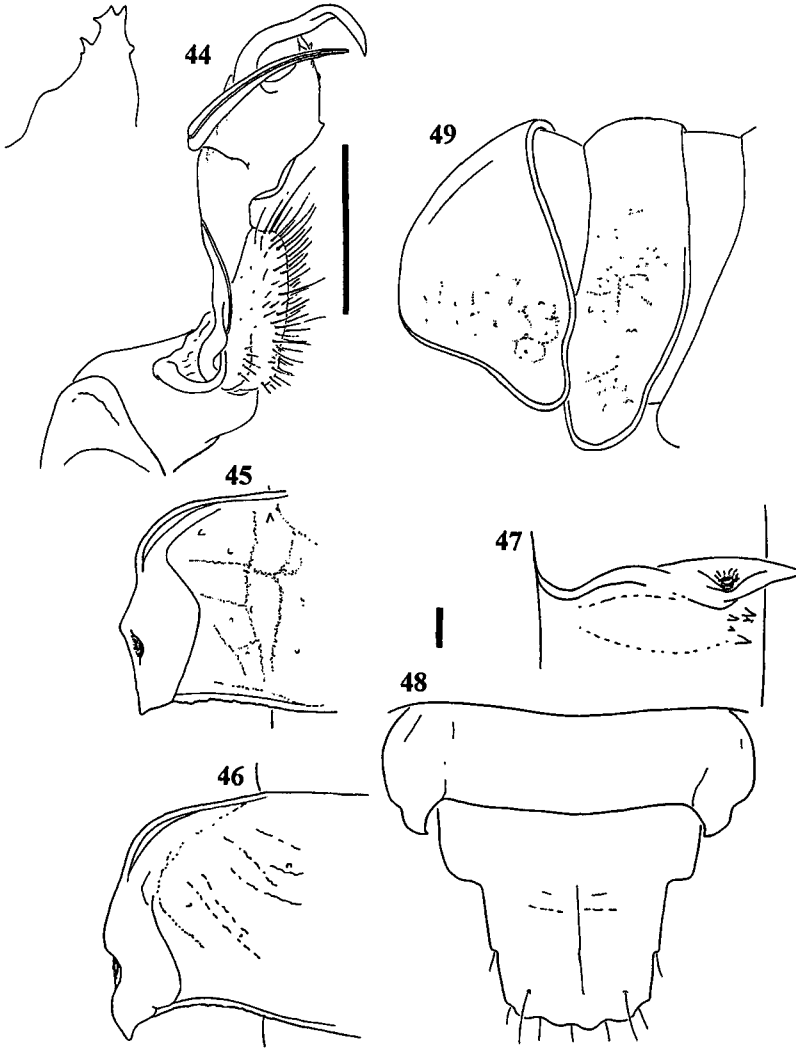
Figs. 34-43:

Meridiurus venitus n.sp., holotype.

34: Right gonopod, mesal view. 35: Paratergum 10, dorsal view. 36: Paratergum 16, dorsal view.
37: Paratergum 10, lateral view. 38: Segment 19 and epiproct, dorsal view.

Tribrachiorus suarezi n.sp., holotype.

39: Left gonopod, mesal view. 40: Paratergum 10, dorsal view. 41: Paratergum 16, dorsal view.
42: Segment 10, lateral view. 43: Gonopod aperture, ventral view. Scale bars: 1.0 mm.

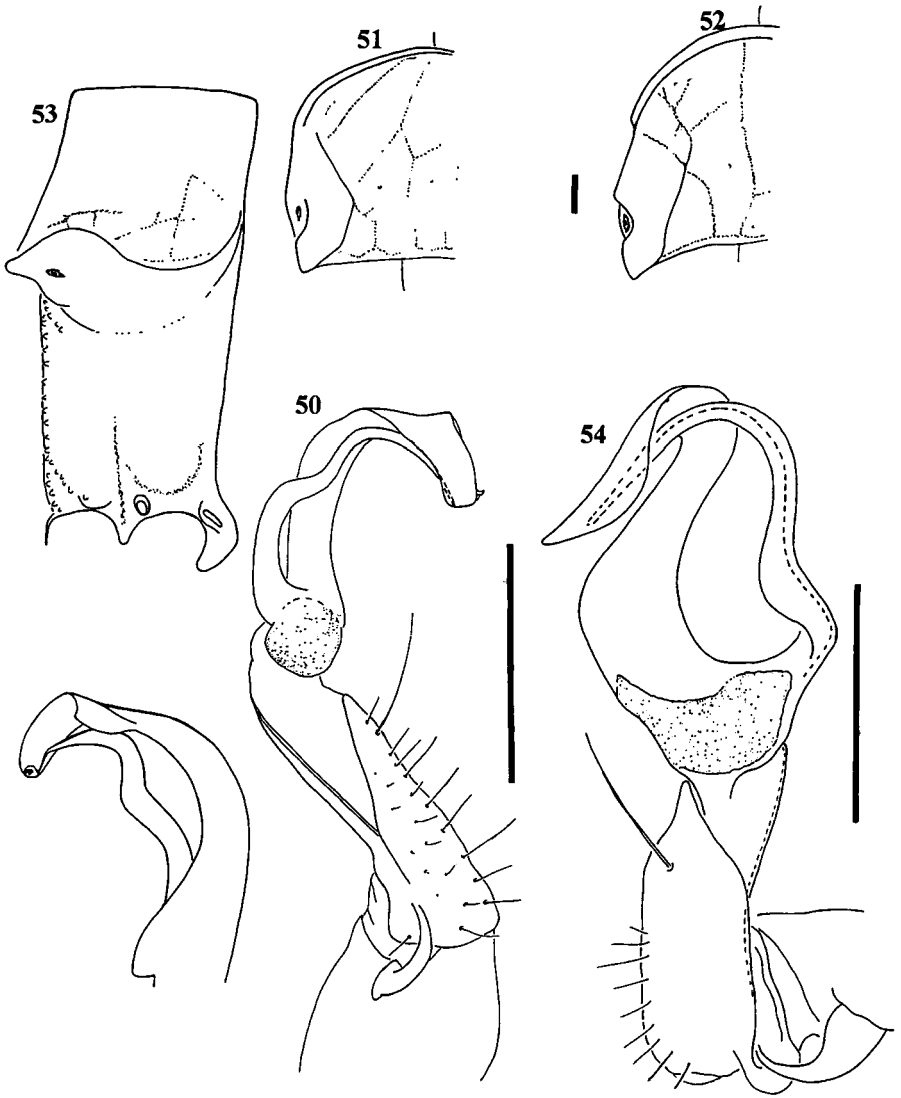


Figs. 44-49:

Tribrachiorus huila n.sp., holotype.

44: Left gonopod, mesal view. 45: Paratergum 10, dorsal view. 46: Paratergum 16, dorsal view.

47: Paratergum 10, lateral view. 48: Segment 19 and epiproct, dorsal view. 49: Collum and segment 2, dorso-lateral view. Scale bars: 1.0 mm.



Figs. 50-54:

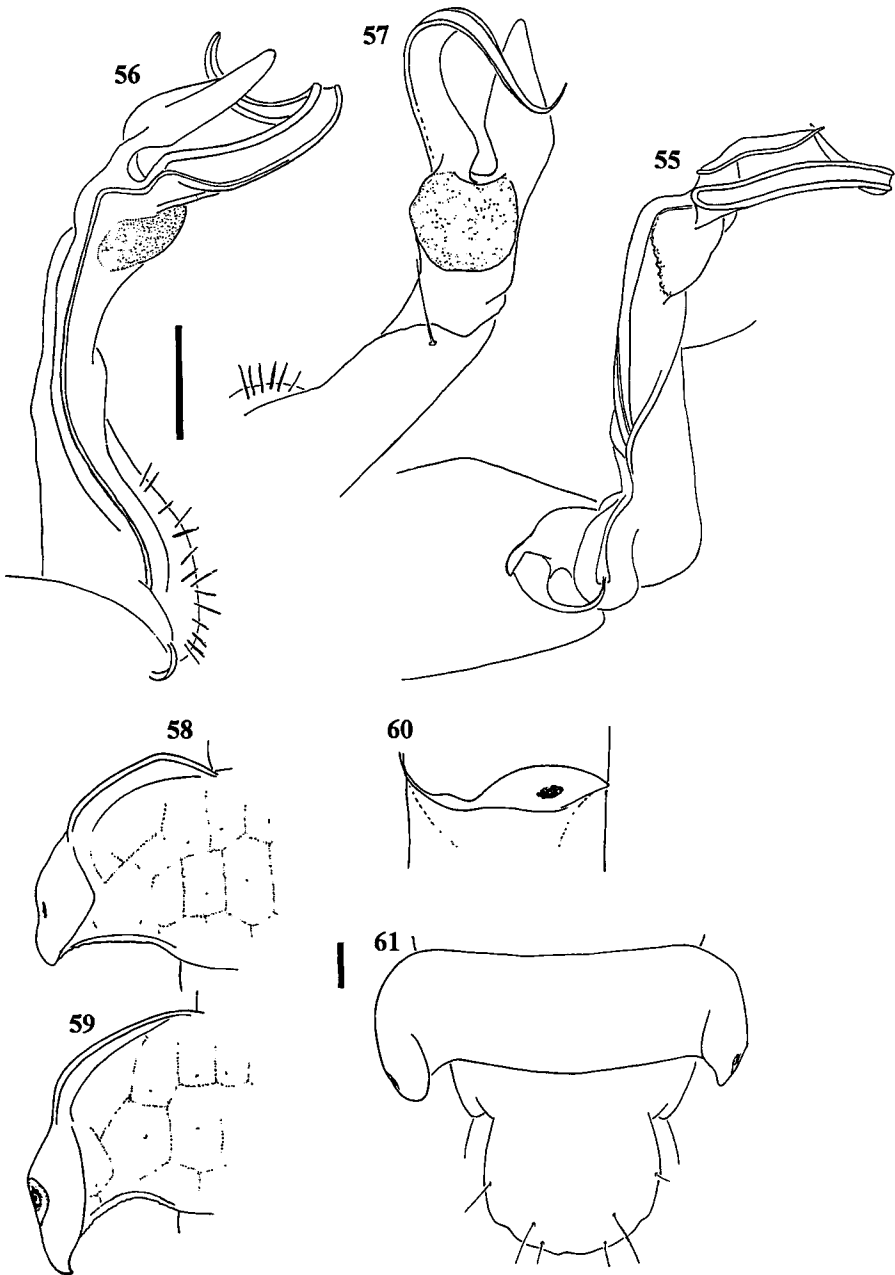
Coleocacamus depressus n.sp., holotype.

50: Left gonopod, mesal view. **51:** Paratergum 10, dorsal view. **52:** Paratergum 16, dorsal view.

53: Segment 10, ventral view.

Coleocacamus labialveus n.sp., holotype.

54: Left gonopod, mesal view. Scale bars: 1.0 mm.



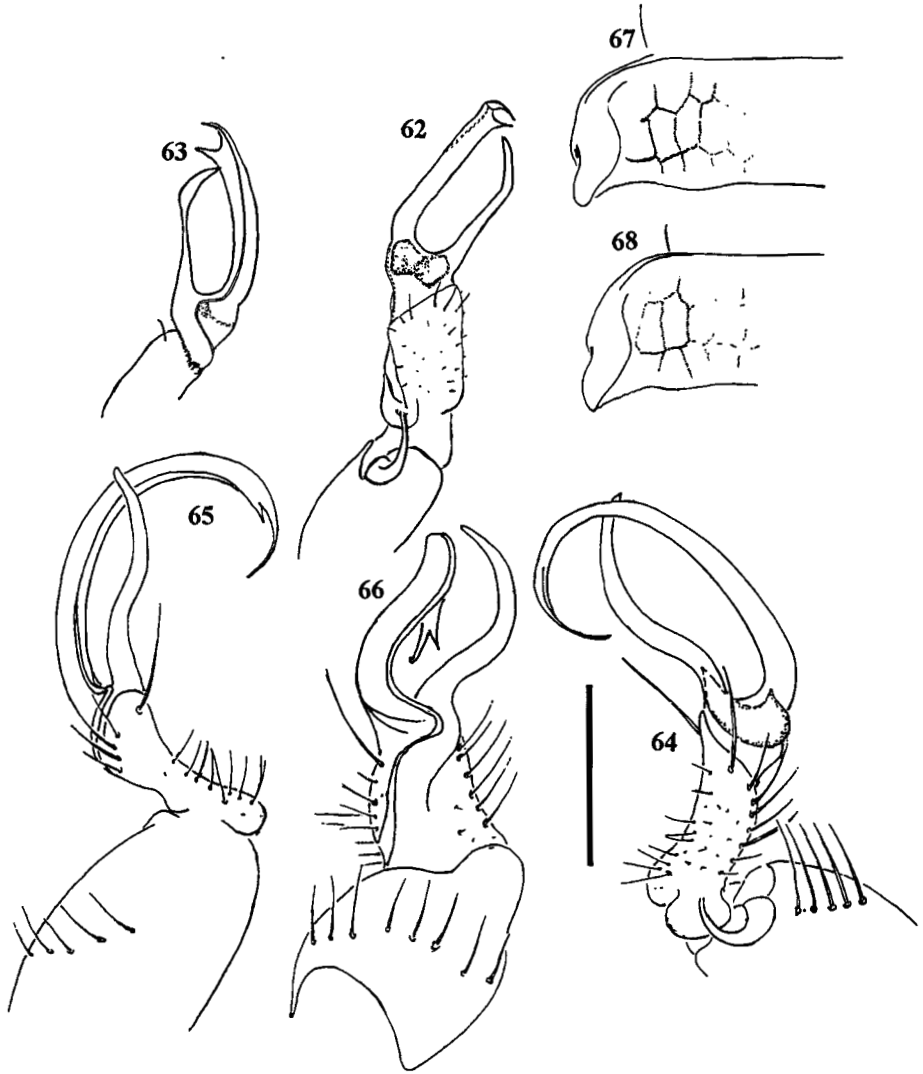
Figs. 55-61:

Kallistopeltis kalonota (ATTEMS, 1899), male.

55: Left gonopod, mesal view. 56: Left gonopod, from behind. 57: Left gonopod, sternal view.

58: Paratergum 10, dorsal view. 59: Paratergum 16, dorsal view. 60: Paratergum 10, lateral view.

61: Segment 19 and epiproct, dorsal view. Scale bars: 1.0 mm.



Figs. 62-68:

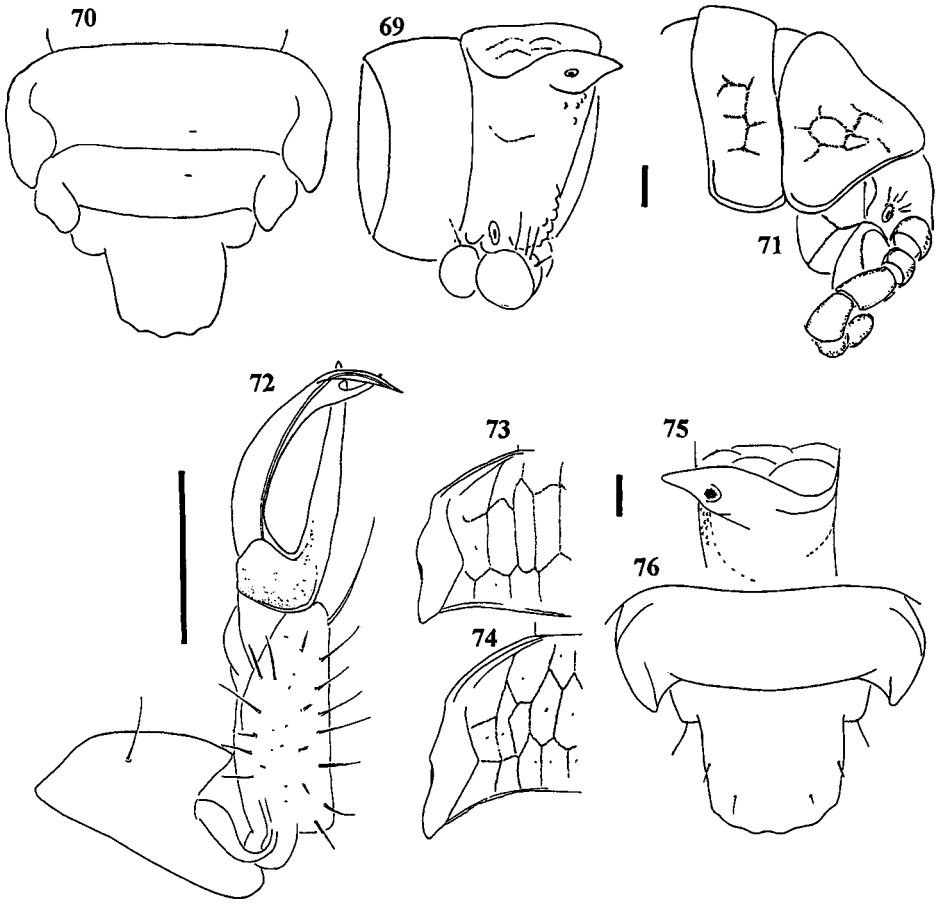
Thrinoxethus siolii n.sp., paratype.

62: Left gonopod, mesal view. 63: Left gonopod, sternal view.

Thrinoxethus verhoeffi (KRAUS, 1956), male.

64: Left gonopod, mesal view. 65: Left gonopod, lateral view. 66: Left gonopod, sternal view.

67: Paratergum 10, dorsal view. 68: Paratergum 16, dorsal view. Scale bars: 1.0 mm.



Figs. 69-76:

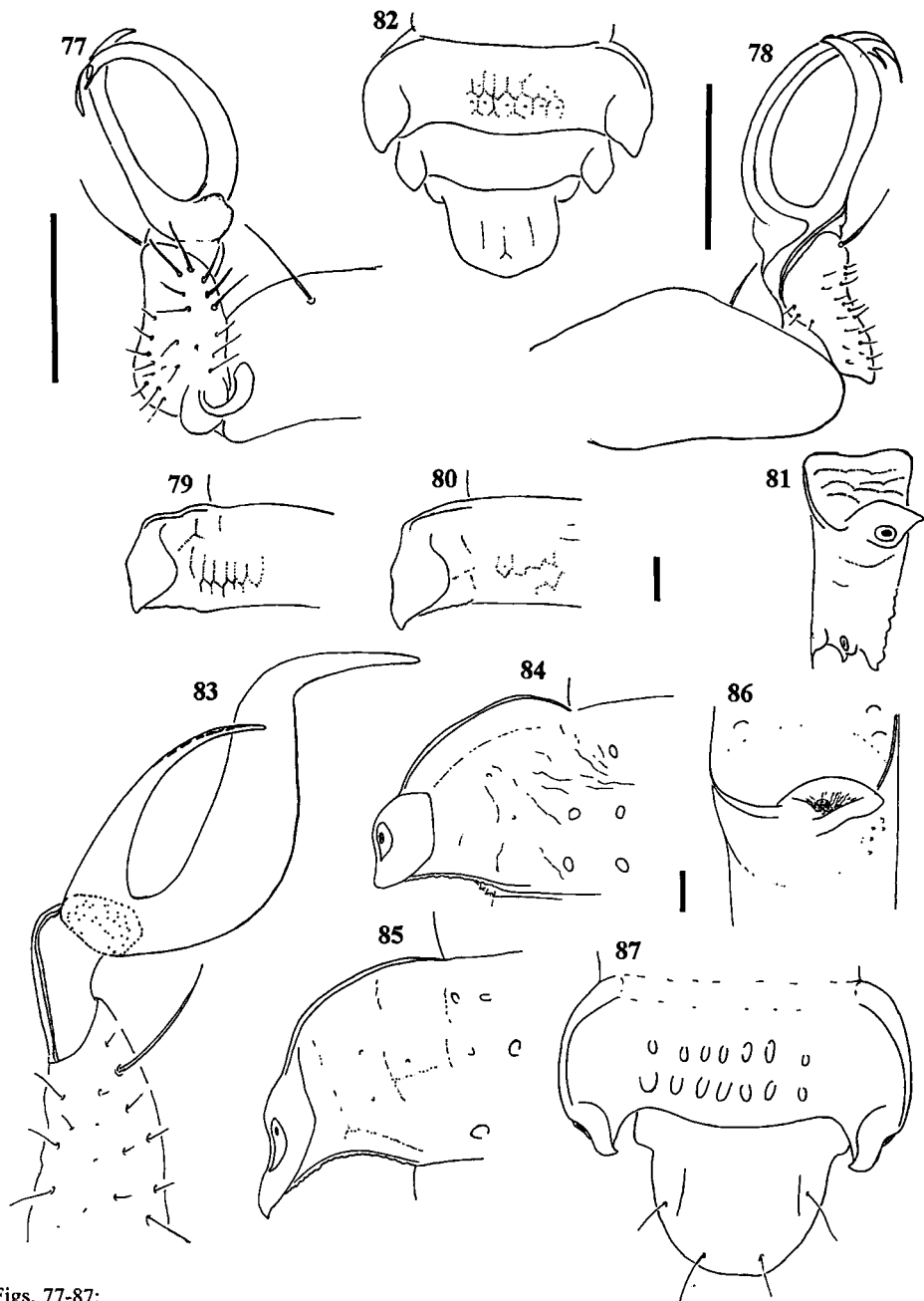
Thrinoxethus verhoeffi (KRAUS, 1956), male.

69: Paratergum 10, lateral view. 70: Segment 18-19 and epiproct, dorsal view. 71: Head, collum and segment 2, lateral view.

Thrinoxethus juani n.sp., holotype.

72: Left gonopod, mesal view. 73: Paratergum 10, dorsal view. 74: Paratergum 16, dorsal view.

75: Paratergum 10, lateral view. 76: Segment 19 and epiproct, dorsal view. Scale bars: 1.0 mm.



Figs. 77-87:

Thrinoxethus junini n.sp., holotype.

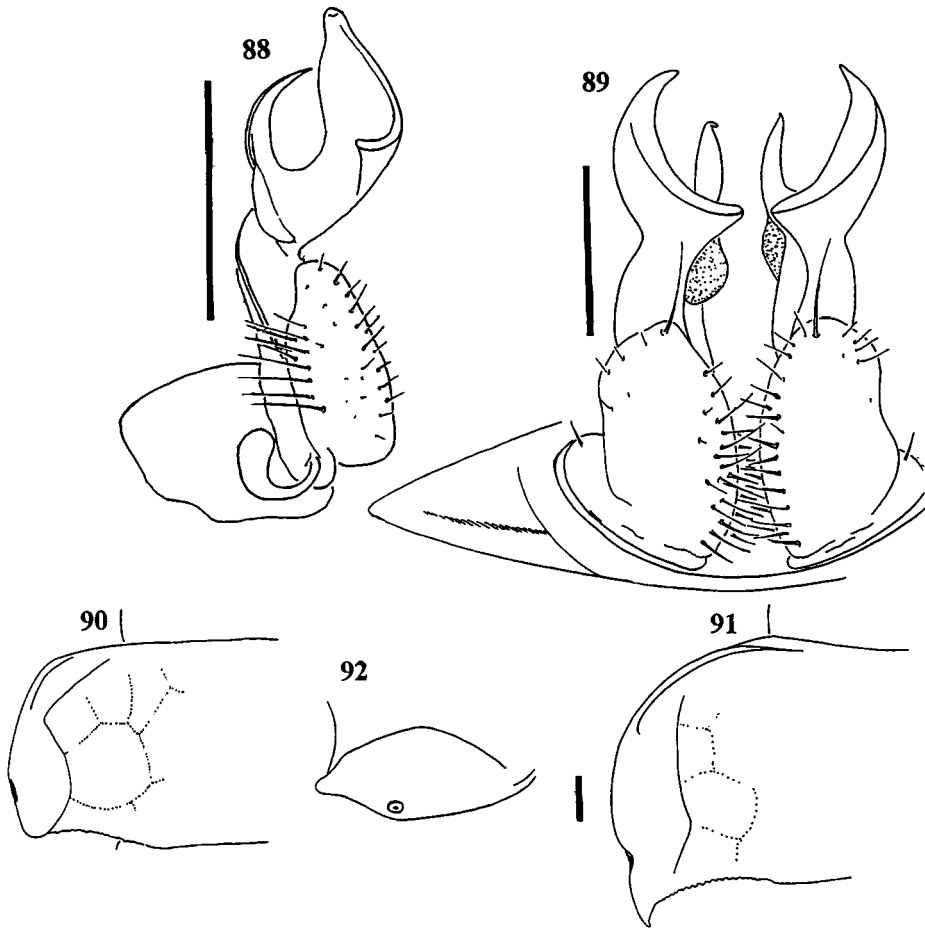
77: Left gonopod, mesal view. 78: Left gonopod, lateral view. 79: Paratergum 10, dorsal view.

80: Paratergum 16, dorsal view. 81: Paratergum 10, lateral view. 82: Segment 18-19 and epiproct, dorsal view.

Sculptoteles braueri (CARL, 1918), male.

83: Left gonopod, mesal view. 84: Paratergum 10, dorsal view. 85: Paratergum 16, dorsal view.

86: Paratergum 10, lateral view. 87: Segment 19 and epiproct, dorsal view. Scale bars: 1.0 mm.



Figs. 88-92:

Pastazina crassa n.sp., holotype.

88: Left gonopod, mesal view. 89: Gonopods, ventral view. 90: Paratergum 10, dorsal view.

91: Paratergum 16, dorsal view. 92: Paratergum 10, lateral view. Scale bars: 1.0 mm.

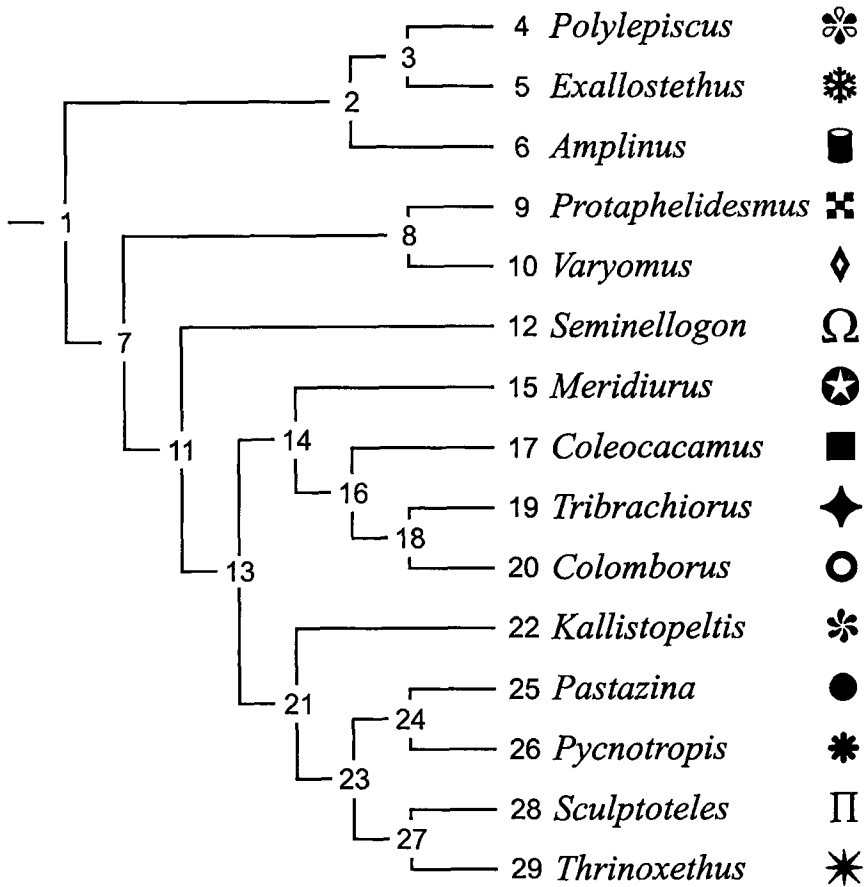


Fig. 93:

Cladogram based on probably monophyletic characters. Numbers refer to branching in the cladogram (? = no character found):

1) Plesiomorphic characters of Amphininae as tufted setae, spatula like epiproct, ozopores laterally, smooth and sometimes areated dorsal surface. 2) Ventral surface of paraterga granulated (perhaps plesiomorphic). 3) Spines at anterior paratergal margin. 4) Gonopod tibiotarsus divided; longer setae on prefemur. 5) Large cones laterally on anterior sterna. 6) Concave hypoproct. 7) Paraterga 4/5 and subsequent paraterga ventrally smooth or only very slightly granulated. 8) Gonopod tibiotarsus enlarged. 9) Collum and metazonites strongly sculptured dorsally (perhaps plesiomorphic). 10) Gonopod tibiotarsus with processes. 11) Gonopod prefemur and acropodite clearly separated. 12) ? 13) Vesicle-like structure on gonopod acropodite, conspicuous long setae on prefemur. 14) ? 15) Setigerous projections on epiproct. 16) Ventral surface of metazonites divided by a slight groove; tibiotarsus oriented in same direction. 17) Caudal paratergal margin not serrate but nearly smooth. 18) Cones on sterna, gonopod acropodite enlarged. 19) Processes on gonopod tibiotarsus. 20) Gonopod acropodite bent cephalad. 21) Gonopod acropodite based on a small trunk. 22) Gonopod tibiotarsus and solenomerite inversely situated, absence of ventrocaudal cones on paraterga. 23) Margins of gonopod aperture thickened laterally, 24) Vesicle small and placed at base of solenomerite; paraterga thick. 25) Very thick tibiotarsus. 26) Ozopores open caudoventrally. 27) Paraterga prolonged and relatively acute caudally; stiff setae on legs. 28) Dorsum strongly sculptured/-areated. 29) Solenomerite with a process.

Fig. 94:
Distribution of amphinine genera in South and Central America. Symbols refer to genera.

