ON THE CLASSIFICATION OF THE FAMILY BRACHYPAUROPODIDAE (MYRIAPODA; PAUROPODA)

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ABSTRACT

The taxonomic history of the Brachypauropodidae and the characters of the family are discussed briefly. The current diagnosis is too narrow and the delimitation towards other families is unsatisfactory.

Some generic characters are considered. The tubelike extensions on the temporal organs, thought to be peculiar to Brachypauropodes and one species in Hansenauropus, occur in at least four more genera and do not provide a good criterion on the generic level. Another character to be used with great caution is the number of tergal head setae. On the other hand, some antennal characters seem to be important.

A preliminary family diagnosis and a subfamilial classification are proposed, and an updated key to the genera and a synopsis of the genera are given.

It is shown that the genus Colinauropus has more features in common with genera of the Pauropodidae than with those of the Brachypauropodidae; it is transferred to the former family in a new subfamily Colinauropodinae close to the Scleropauropodinae.

INTRODUCTION

The family Brachypauropodidae (8 genera, 22 species) seems to have an almost worldwide distribution but it is never a conspicuous part of the soil fauna. The fact that the representatives are seldom collected and the species often poorly investigated has led to an unsatisfactory classification. Moreover, there exists a great heterogeneity in many external morphological features. The family diagnosis built up through the years does not work and the delimitation towards other families is partly unclear.

The purpose of this paper is to draw attention to this problem, to pinpoint invalid diagnostic characters on the family and generic levels and to introduce some new and probably more important ones. Furthermore, a review of the genera which now have to be included is given and a key and a revised classification is presented.

TAXONOMIC HISTORY

Latzel (1884) arranged the three pauropod genera known at his time in the groups "Pauropoda agilia" and "Pauropoda tardigrada", the latter including the genus Brachypauropus. This first system was improved by Kenyon (1895) who erected the families Pauropodidae and Eurypauropodidae for the species with 6 tergites, viz. Pauropus and Eurypauropus, and separated the third genus, Brachypauropus, with 10 tergites (dorsal plates), as a group of uncertain position. For the latter Silvestri (1902: 63) set up the family Brachypauropodidae which since has been accepted. Like Hansen in the same year (1902: 407-408), Silvestri (1902: 67) also compiled a more detailed diagnosis of the family, in reality consisting of the characters separating Brachypauropus from Eurypauropus.

Attems (1926: 27) narrowed the diagnosis by adding further Brachypauropus characters. The latter diagnosis was quoted by Verhoeff (1934: 87) and was followed by Remy for more than 30 years.

The family was treated also in Bagnall’s classification (1935) in which the pauropods were divided into the suborders Ectomorpha and Endomorpha, the former including the superfamilies Brachypauropodoidea with the two families Brachypauropodidae and Scleropauropodidae.

The diagnosis used by these early authors was extended by MacSwain & Lanham (1948) to include also forms with only 8 pairs of legs in the adult stage.
Since then many new taxa have been described. A review of these shows that the family has become very heterogeneous as to the following characters: the number of both undivided tergites and smaller sclerites and the degree of their sclerotization, the shape and distribution of the tergal setae on the head as well as on the trunk, the shape of the temporal organs on the head and the number of leg segments.

Actually, of all the characters proposed and used as characteristic features of the family not a single one exclusively pertains to the Brachypauropodidae. As the family now appears, it stands out, at least partly, as a resort for those taxa not readily fitting into other families.

SOME GENERIC CHARACTERS

A character of particular interest is the shape of the temporal organs of the head. In diagnosing the genus Brachypauropoides (genotype B. pistillifer) Remy (1952: 175-176) attached great importance to a feature not earlier observed in pauropods: three tubelike extensions ("digitations saillantes") protruding in different directions from the temporal organs. Actually they were the only unique character of the genus. However, the six species described later have only one extension. Similar structures were described also in Hansenaurobus abrasus Remy from Madagascar and Brachypauropus strebeli Hüther from Europe and I have found such (fig. 1) in the European B. hamiger Latzel and B. superbus Hansen (in B. occultus Rafalski they occur too, Dr. Jan Rafalski, in litt.) and in the North American Aletopauropus lentus, Zygopaurobus hesperius, Deltopauropus luteus and D. magnus, all described by MacSwain & Lanham. The structure is known also in my ?Aletopauropus tridens (Pauropodidae) from tropical Africa. Tubelike extensions on the temporal organs have now been found in six out of eight genera in the Brachypauropodidae and can no longer be used as a criterion for defining Brachypauropoides.

Another character which has to be used with great caution is the number of tergal head setae. It is often difficult to establish which setae are tergal and which are lateral. Sometimes they are thin or transparent and difficult to see. Moreover, the number often varies between the species of a single genus.

On the other hand, the shape of the setae of the tergites is most valuable in distinguishing genera. In all the species of Brachypauropus, Aletopauropus and Zygopaurobus they are hastate and bent posteriorly near the base, in Brachypauropoides they are strongly clavate or spatulate, in Deltopauropus, Panamaurobus and Hansenaurobus they are very strongly modified in various directions.

The shape of the anal plate is of similar importance. It characterizes all genera with the exception of Panamaurobus. The "brachypauropodid" plate is posteriorly pointed with two subposterior, submedian, clavate append-
ages protruding in posterior direction. In Panamauropus, deviating in other characters too, there is a posteromedian incision and two large submedian and two short lateral appendages protruding posteriorly.

From studies in other families it is known that the antennae yield many characters which serve well in distinguishing genera. In the Brachypauropodidae particularly the sternal branch and its globulus seem to be both taxonomically important and practically convenient. In the key to the genera below they have been of help in distinguishing Hansenauropus and Panamauropus (fig. 2).

At the present state of knowledge the number of usable characters for compiling a family diagnosis is low and the classification presented below is merely an attempt to sum up what is known about the family.

![Fig. 2. Sternal antennal branch, sternal view (flagella and seta q omitted): a, Hansenauropus abrassus Remy, right side; b, H. gratus Remy, left side; c, Panamauropus williamsi Remy, left side; d, P. eucharis Remy, right side. (After Remy 1954a, 1954b, 1956b, 1958; slightly simplified and transferred to about equal size.]

3. antennal globulus subglobular (not in Afrauropodidae and subfam. Polypauropodinae in Pauropodidae),
4. setae on tergites modified (not in Afrauropodidae, generally not in Pauropodidae),
5. trunk oval (not in Afrauropodidae, generally not in Pauropodidae).

Notes. — Though all brachypauropodid genera fitting into this diagnosis have 5-segmented legs I hesitate to use that character because the number of leg segments is varying in both Pauropodidae and Eurypauropodidae. Likewise the tubelike extensions of the temporal organs have been disregarded because they have not been described in all species. Divided tergites occur often, but a few species have entire tergites. Therefore, sclerite patterns have not been used in the family diagnosis. Moreover, these patterns are sometimes incompletely known.

Even after the removal of Colinauropus (see below), the morphological heterogeneity is considerable and the family seems not to be clearly delimited from the Pauropodidae. However, the short-legged, oval, often flattened brachypauropodids are usually easily distinguished from the fusiform, generally more long-legged pauropodids.

CLASSIFICATION

No attempt towards a subfamilial classification has been published and the following division into two subfamilies is to be regarded as preliminary.

Subfam. Brachypauropodinae Silvestri

Diagnosis. — A brachypauropodid subfamily with 6 entire tergites or 1-2 entire tergites combined with tergites split up longitudinally-transversally or only longitudinally; the pygidial sternum lacks the setae b₂ (exception Brachypauropoides).

Type-genus. — Brachypauropus.

Genera. — Brachypauropus, Aletopauropus, Zygopauropus, Deltopauropus, Brachypauropoides.
Notes. — The first four genera may form a natural group. They show considerable intergeneric similarity e.g. as to shape, pattern, chaetotaxy and sclerotization of the tergites, leg segmentation, shape of the trichobothria and the temporal organs. The gaps between them are much smaller than the one separating them from Brachypauropoides which is heterogeneous as to the tergite pattern (1, 2 or 6 tergites are entire) and the degree of sclerotization of the tergites.

Subfam. Hansenauropodinae Remy

Diagnosis. — A brachypauropodid subfamily with 2 or 3 entire tergites (1 + 6 or 1 + 5 + 6), those interposed divided transversally; the pygidial sternum has the setae $b_2$.

Type-genus. — Hansenauropus.

Genera. — Hansenauropus, Panamauropus.

Notes. — After having described Hansenauropus gratus, Remy (1954a) placed it in a new subfamily, Hansenauropinae, in the Eurypauropodidae, which was referred later to the Brachypauropodidae. The two genera show features which justify a separate position, but, unfortunately, the present knowledge of their taxonomic characters makes them unamenable to a critical study.

The taxonomic position of Colinauropus Remy, 1956

A genus of great interest is Colinauropus because it does not fit well into the family. It was created by Remy for a species from Réunion, later found also on Mauritius. Remy (1956a) based its reference to the Brachypauropodidae mainly on the occurrence of fragmented tergites and on the shape of the anal plate. Other characters of value were not critically analyzed, neither in the original description nor later.

However, the following features must be considered too: the tegmental head setae are subcylindrical, blunt, arranged in four transversal rows; evidently no appendages on the temporal organs; the $F_2$ is much shorter than the $F_3$; the chaetotaxy of the tergites is $4 + 4$ setae on tergite 1, $6 + 6$ on tergites 2-5 and $4 + 2$ on tergite 6; the legs are 5-segmented in the first and last pairs, 6-segmented in those interposed.

All these characters indicate a close affinity to the Pauropodidae. The pygidial chaetotaxy points in the same direction and the anal plate can be pauropodid as well as brachypauropodid. The conclusion must be that there seems to be no doubt about the pauropodid nature of Colinauropus. It has to be placed in the Pauropodidae in a new subfamily, Colinauropodinae, close to the Scleropaupodinae.

Colinauropodinae n. subfam.

Diagnosis. — Sternal antennal branch with 2 flagella, 1 seta $q$ and 1 globulus; mediointergal plate of head lacking; tergites split up into distinctly sclerotized plates, partly of irregular shape.

The above revision leads to the following classification of the Pauropodidae and Brachypauropodidae:

Pauropodidae Lubbock

Pauropodinae Lubbock

Allopauropus Silvestri, Cauvetauropus Remy, Hemi-pauropus Silvestri, Monodauropus Remy, Pauropus Lubbock, Rabaudauropus Remy, Stylopauropoides Remy, Stylopauropus Cook

Scleropaupodinae Bagnall

Scleropaupus Silvestri

Colinauropodinae n. subfam.

Colinauropus

Polyopaupodinae Verhoeff

Fagepauropus Remy, Polyopaupoides Remy, Polypauropus Remy

Brachypauropodidae Silvestri

Brachypauropodinae Silvestri

Aletopauropus, Brachypauropoides, Brachypauropus, Delto-pauropus, Zygopaupus

Hansenauropodinae Remy

Hansenauropus, Panamauropus

A SYNOPSIS OF THE GENERA

Brachypauropus Latzel, 1884

Type-species. — Brachypauropus hamiger

Latzel, 1884.
Distribution. — Middle and southern Europe; eastern U.S.A.

Head free; temporal organs seem to have one tubelike extension. Distal part of sternal antennal branch posteriorly truncate; stalk of antennal globulus about as long as the globulus. Trunk oblong-oval. Tergites sclerotized; the 1st entire or 2-4-parted, the 2nd-5th divided into 3-4 central sclerites and 2 lateral ones, 6th tergite divided into 1-2 central sclerites and 2 lateral ones. Setae on tergites generally tapering or lanceolate, pointed, most often distinctly curved at the base. At most 9 pairs of legs, all 5-segmented. Pygidial sternum has setae $b_1$ and $b_3$. (Five species. Bagnall’s only partly described $B. lubbocki$ from 1914 not included.)

Aletopauponus MacSwain & Lanham, 1948

Type-species. — *Aletopauponus lentus* MacSwain & Lanham, 1948.

Distribution. — Western U.S.A. and Canada.

Head free; central setae lanceolate; temporal organs have three tubelike extensions. Stalk of antennal globulus fairly long. Trunk narrowly oval. Tergites entire or 2-8-parted, sclerotized, the ground sculpture consists of small rounded tubercles; 1st-4th tergites have two longitudinal rows of larger tubercles, the last of each row appearing as large scales beyond margin of plate; small sclerites are near bases of some trichobothria. Setae on tergites bristle-shaped to slightly hastate, partly bent posteriorly near base. At most 8 pairs of legs, all 5-segmented. Pygidial sternum has setae $b_1$ and $b_3$. (One species.)

Deltopauropus MacSwain & Lanham, 1948

Type-species. — *Deltopauropus luteus* MacSwain & Lanham, 1948.

Distribution. — U.S.A.

Head free; central setae Y-shaped or hastate; temporal organs with extensions. Stalk of antennal globulus thin, long. Trunk broadly oval. Tergites entire or 3-4-parted, weakly sclerotized; anterior trichobothria associated with lateral sclerites. Setae on sclerites consisting of large triangular to almost circular scales with surface ornamented with conspicuous network of cuticular thickenings. At most 9 pairs of legs, all 5-segmented. Pygidial sternum has setae $b_1$ and $b_3$. (Three species.)

Brachypauropoides Remy, 1952

Type-species. — *Brachypauropoides pistillifer* Remy, 1952.

Distribution. — Madagascar and New Zealand.

Head free; central setae clavate, arranged in four rows; nine pairs of tergal setae; temporal organs have at most three tubelike extensions. Distal part of sternal antennal branch anteriorly truncate; its two flagella subequal in length. Trunk oval. Tergites entire or 2- or 4-parted; anterior tergites have 6 pairs of irregularly inserted clavate setae. At most 9 pairs of legs, all
5-segmented. Pygidial sternum has setae $b_1$, $b_2$ and $b_3$. (Seven species. Remy's incompletely described ?Brachypauropoides moselleus of 1960 not included as it belongs more likely to the Pauropodidae.)

Hansenauroorus Remy, 1954a

Type-species. — Hansenauroorus gratus Remy, 1954a.

Distribution. — Madagascar and New Zealand.

Head (always?) covered by 1st tergite. Sternal antennal branch widest in its distal part, about as truncate posteriorly as anteriorly; antennal globulus long-stalked, its diameter half the width of the branch. Trunk oval, doroventrally flattened. Tergites sclerotized; 1st, 5th and 6th simple, 2nd-4th divided transversally, together 9 tergal plates. Setae on head and tergal plates modified, small, fungiform or with a collar. At most 9 pairs of legs, all short, 5-segmented. Pygidial sternum has setae $b_1$, $b_2$ and $b_3$. (Two species.)

Panamauroorus Remy, 1954b

Type-species. — Panamauroorus williamsi Remy, 1954b.

Distribution. — Panama and Jamaica.

Head free. Sternal antennal branch widest at the middle, anteriorly distinctly truncate. Antennal globulus short-stalked, its diameter about as long as greatest width of the branch. Trunk oval. Tergites sclerotized; 1st and 6th simple, 2nd-5th divided transversally, together 10 tergal plates. Setae on head and tergites modified: small, fungiform, irregularly inserted (subgenus Panamauroorus s. str.); large, scalelike, symmetrically inserted (subgenus Antillauropus Remy). At most 9 pairs of legs, all short, 5-segmented. Pygidial sternum has setae $b_1$ and $b_2$. (Two species.)

UPDATED KEY TO THE GENERA

In 1948 MacSwain & Lanham published a key including the four genera known at that time, but so far nobody has made any attempt to extend it to include all the presently known genera. The reason may be that it has been impossible to set up a meaningful system for the many patterns into which the tergites have split up, and that earlier authors were not aware of the taxonomic value of certain characters, which therefore were not described. Obviously another reason has been the great uncertainty whether the adult stage in some genera and species is reached at 8 or 9 pairs of legs because in some taxa specimens with the maximum number of legs have not been found. Together with well-developed penes already in the 8-legged stadium, which sometimes has been stated, it may indicate that the development was arrested at the close of the 4th instar. Since the number of trunk segments, tergites and/or sclerites changes throughout development, it has been difficult to tell the definite numbers.

Thus, in constructing a key it was necessary to concentrate on the characters of the head, antennae, anterior tergites/sclerites and on the pygidium, all of which scarcely change from 1st instar larva to adult stage.

1. Pygidial sternum with setae $b_2$.......................... 2
   — Pygidial sternum without setae $b_2$.......................... 4
2. Tergite 2 entire or 4-parted.................. Brachypauropoides
   — Tergite 2 2-parted ............................................... 3
3. Nine tergal plates; tergite 1 covering (?) the head; sternal antennal branch broadest in distal part and its greatest width at least twice longer than the diameter of its globulus............................ Hansenauroorus
   — Ten tergal plates; tergite 1 not covering the head; sternal antennal branch broadest at the middle and its greatest width only slightly longer than the diameter of its globulus ........................................ Panamauroorus
4. Setae on tergites strongly modified, scutellate, triangular to almost circular, with surface ornamented with conspicuous thickenings in mesh patterns........
   — Setae on tergites bristle-shaped to slightly hastate..... 5
5. Temporal organs with at most one anterior tubelike extension .......................... Brachypauropus
   — Temporal organs with anterior, median and posterior tubelike extensions .................................. 6
6. Tergite 4 is 2-parted, tergite 5 is entire.... Aletopauropus
   — Tergite 4 is 4-parted, tergite 5 is 2-parted. Zygepauropus

Type and Allotype (subgenus Deltopauropus)

Type and Allotype (subgenus Deltopauropus)

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ACKNOWLEDGEMENTS

I am very grateful to Drs. W. J. Pulawski, California Academy of Sciences, San Francisco, E. Tremblay, Istituto di Entomologia Agraria, Portici, and F. R. Wanless, British Museum (Natural History), London, for the loan of type-specimens, and to Dr. Jan Rafalski, Instytut Biologii, Poznan, who kindly gave me access to his drawings of Brachypauropus species.

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