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Phylogenetic aspects in the higher classification of the subfamily Catocalinae (Lepidoptera, Noctuidae)

With 5 figures

WOLFGANG SPEIDEL¹ & CLAS M. NAUMANN

Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn

Abstract

The subfamily Catocalinae is shown to be based on a typological concept. A re-evaluation of the subfamily as a whole is not yet possible. Thus, it appears appropriate to define smaller monophyletic units within the subfamily. Based on the shape of the internal female genitalia (ductus receptaculi), it is shown that the Euclidiini form a monophylum. We do not think that it is advisable to incorporate the Melipotini and Eulepidotini in that monophylum, as we could not find any synapomorphies for these tribes, which proved to be rather different structurally.

Zusammenfassung

Die Abgrenzung der Unterfamilie Catocalinae beruht auf einem typologischen Konzept. Eine Neubewertung der gesamten Unterfamilie ist noch nicht möglich. Daher scheint es angebracht, kleinere monophyletische Einheiten innerhalb der Unterfamilie zu definieren. Aufgrund der Ausbildung der inneren weiblichen Genitalien (ductus receptaculi) wird gezeigt, daß die Euclidiini ein Monophylum darstellen. Wir halten es nicht für ratsam, die Melipotini und Eulepidotini in dieses Monophylum einzuschließen, da wir keine Synapomorphien dieser drei Tribus finden konnten, die sich als strukturell ziemlich verschieden erwiesen.

1. Introduction

At present, the phylogeny of the Noctuidae is only imperfectly resolved. The monophyly of many of the subfamilies is weakly supported or even uncertain, as most of them are defined on a typological basis only. The relationships between the different subfamilies are, in most cases, completely unknown or highly speculative (KITCHING, 1984). The present paper deals with parts of the Catocalinae, which represent the least defined and largest subfamily of the "Quadrifinae". European readers may question the importance of the Catocalinae, because only a few species occur in Europe. The subfamily is represented here by one large genus, *Catocala* SCHRANK, 1802, and only a few species of other genera. However, the situation is entirely different in other biogeographic regions. In the tropics the Catocalinae are the most diverse of all subfamilies and have the highest number of species. In order to compare the species density of the different subfamilies of the Noctuidae we have selected two areas of about equal size (fig. 1) viz. Borneo and central Europe; in both the fauna is

¹Anschrift der Verfasser: Dr. WOLFGANG SPEIDEL & Prof. Dr. CLAS M. NAUMANN, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 160, D-53113 Bonn

comparatively well known. The figure amply illustrates the fact that the number of species within the traditionally defined subfamilies differs considerably in the palaetotropics and in Europe. In fact the number of catocaline species represented in Borneo may be even higher than illustrated, because the Bornean catocaline fauna has not been revised since the work of HOLLOWAY (1976). Nevertheless, the Catocalinae contain by far more species (about 200) than any other subfamily on this island. About 2,500 species of Catocalinae occur in the Neotropical region (HEPPNER, 1991), representing more than half of the species of the entire subfamily.

There are no autapomorphic characters defining the Catocalinae (KITCHING, 1984). At present, the subfamily is defined - basically according to the classification of HAMPSON (comprehensively shown in its finite form by HAMPSON, 1902) - as the part of the "quadrifid" noctuids remaining after the removal of the following groups (with the exception of the Acontiinae they are well supported monophyla): 1. Herminiinae and Hypeninae (M2 of hindwing parallel to M3), 2. Euteliinae and Stictopterinae (female frenulum consisting of one bristle only), 3. Plusiinae (lashed eyes), 4. Acontiinae (M2 of hindwing weakly sclerotized and originating more remotely from the lower angle of the discal cell), 5. Camptolominae + Chloephorinae + Sarrothripinae + Nolinae (bar-shaped male retinaculum, if not reduced). Thus, the Catocalinae form an artificial taxon defined by the exclusion of other taxa from the so called "Quadrifinae". In traditional classifications (e.g. the classification of HAMPSON, 1902) the Catocalinae as defined above are treated as two distinct subfamilies, viz. the Catocalinae s.str., characterized by the midtibiae being covered with spines; and the Ophiderinae, which lack such tibial spines. All credit should go to BERIO (1959) who recognized that closely related groups exist in the Catocalinae s.str. and the Ophiderinae, these groups consisting of genera either with or without such tibial spines. This indicates that the spines were lost convergently several times. Therefore BERIO proposed that both subfamilies, Catocalinae and Ophiderinae, should be combined. However, the monophyly of this new "subfamily" has also not yet been demonstrated, and it is to be expected that the group represents either a poly- or a paraphyletic "waste-paper basket" taxon.

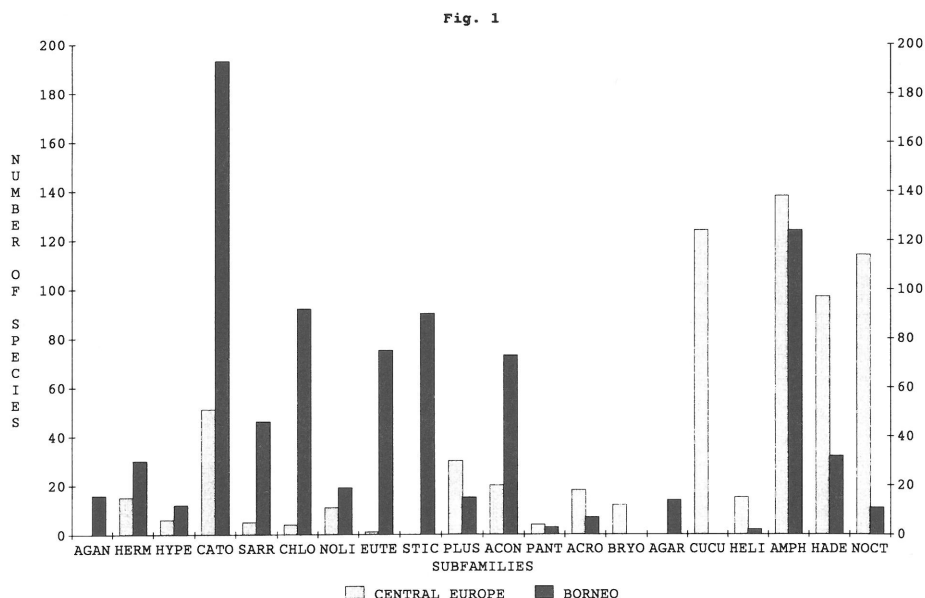


Fig. 1: Species-representation of the different subfamilies of the Noctuidae in Borneo and Central Europe

2. The Present Situation

From the above-mentioned definition of the Catocalinae it is apparent that the monophyly of the subfamily is highly doubtful. The heterogeneity of the taxon and the high number of species included further complicate comparative studies. Therefore it appears reasonable first to define monophyletic groups within the complex and next to establish the phylogenetic relations of these monophyla. Hardly any modern classification of the Catocalinae agrees as far as the definition and composition of the subfamily is concerned. In some recent revisions, the Scoliopteryginae, Aediinae, Ophideriinae, Rivulinae, Hyphenodinae, or even only some of them have been removed from the Catocalinae (FORBES, 1954, BECK, 1960, FRANCLEMONT & TODD, in HODGES, 1983, BUSZKO, 1983, FIBIGER & HACKER, 1991). For the moment, we prefer to retain these groups within the catocaline complex, as there are no characters to define the remaining Catocalinae after the removal of these subfamilies (or a part of them). It appears insufficient to recognize monophyletic units in the Catocalinae and to remove them from the subfamily. From a phylogenetic point of view it appears more important to avoid poly- or paraphyletic remains, which can neither be defined on typological nor on phylogenetic principles, because closer relations might exist between the removed monophyla and parts of the remainder.

The number of tribes presently accepted by various authors is very high, though most of them have no clear definition and almost none of them has been defined by autapomorphies. The Catocalinae s.l. as presented in the introduction include about 70 family-group names which have to be considered and might be used, when the subfamily is split.

3. The first step: the monophylum Euclidiini

3.1. Generalities

As a phylogenetic system for the whole subfamily cannot yet be presented, we begin with the definition of monophyletic units within the Catocaline complex. For the sake of convenience we propose to give these units tribal rank, which would be consistent with the historical development of the Noctuid system.

In this paper, we present arguments for a monophylum "Euclidiini" based on derived characters of the internal female genitalia. The Euclidiini represent just a small part of the very large subfamily, but three of the existing family-group names (Euclididae GUENÉE, 1852, Synedini FORBES, 1954, Drasteriini WILTSHIRE, 1976) are referable to it, and include a most unusual genus which is often even not recognized as belonging to the Noctuidae (*Tinolius* WALKER, 1855).

The Euclidiini share the possession of a very long spirally twisted ductus receptaculi (ductus spermathecae). Inside the ductus there is a thread-like sclerotization which MITTER (1988) termed "fertilization canal". This sclerotization is often coiled to stabilize the lumen of the ductus. These coils do not correspond to the coils of the ductus receptaculi itself. We have verified the presence of a long and coiled ductus receptaculi in *Tinolius*, *Euclidia* and *Drasteria* (see figs. 2, 3, 4 and descriptions below).

With regard to nearly all other tribes of the Catocalinae, all other subfamilies of the Noctuidae and representatives of the outgroups Lymantriidae, Arctiidae and Notodontidae, it appears that the character situation found in the Euclidiini represents a uniquely derived, i.e. an autapomorphic state, supporting the monophyly of the Euclidiini.

Since we have only been able to study a few selected genera of the subfamily, one has to assume that the Euclidiini will have to be increased by a considerable number of further genera. If BERIO (1959) is correct in placing *Cerocala* BOISDUVAL, 1829 and *Drasteria* HÜBNER, 1818 (= *Leucanitis*) into a common group, then *Cerocala* has to be placed in the Euclidiini as well. Due to the lack of material we have not yet been able to verify this proposal.

3.2. Internal female genitalia

1. *Drasteria* HÜBNER, 1818

The female genitalia of *Drasteria cailino* (LEFEBVRE, 1827) (fig. 2) have been illustrated together with the ovipositor, in order to show the relative situation of the various elements. The ductus seminalis originates from the upper part of the corpus bursae; it begins very thinly and thickens towards the oviductus communis. The ductus receptaculi is twisted spirally and forms a very large coil.

The concepts of *Drasteria* proposed by RICHARDS (1939) for the Nearctis, and by JOHN (1910) for the Palearctis do not correspond completely. It appears desirable to revise *Drasteria* and closely related genera in a Holarctic context, because apparently closely related species occur in both regions.

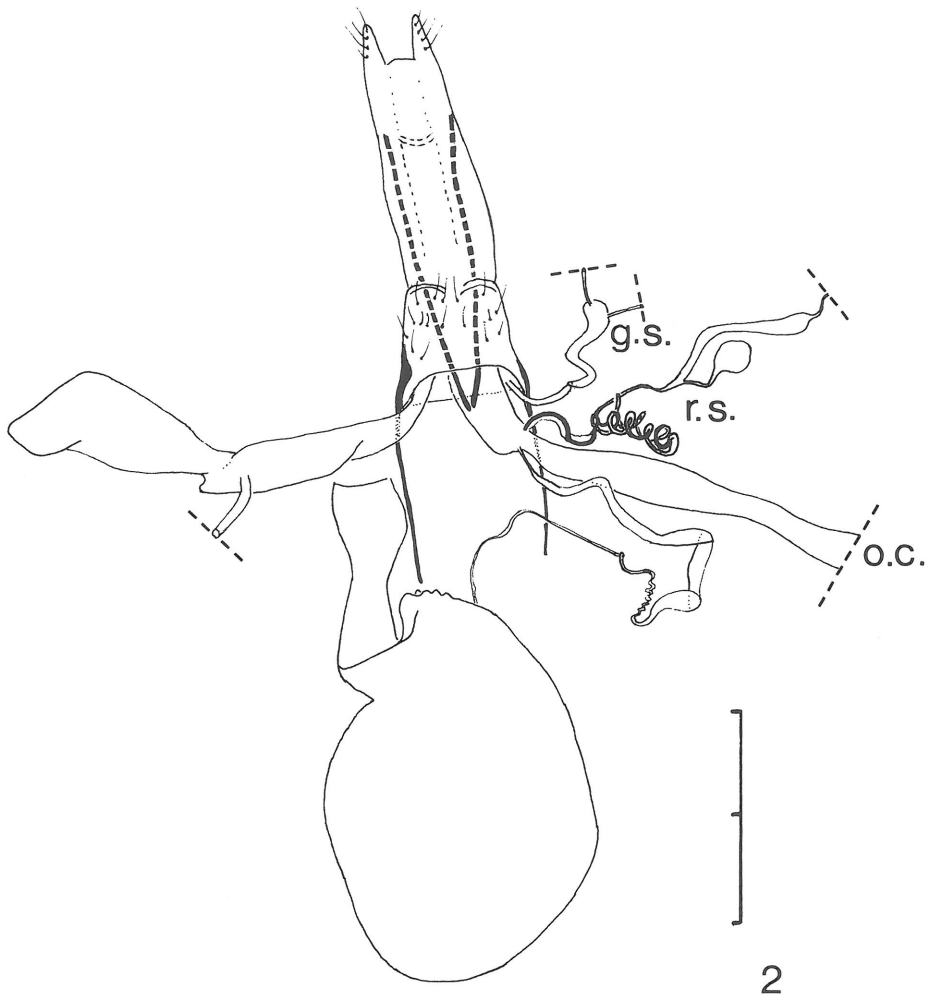


Fig. 2: Internal female genitalia of *Drasteria cailino*

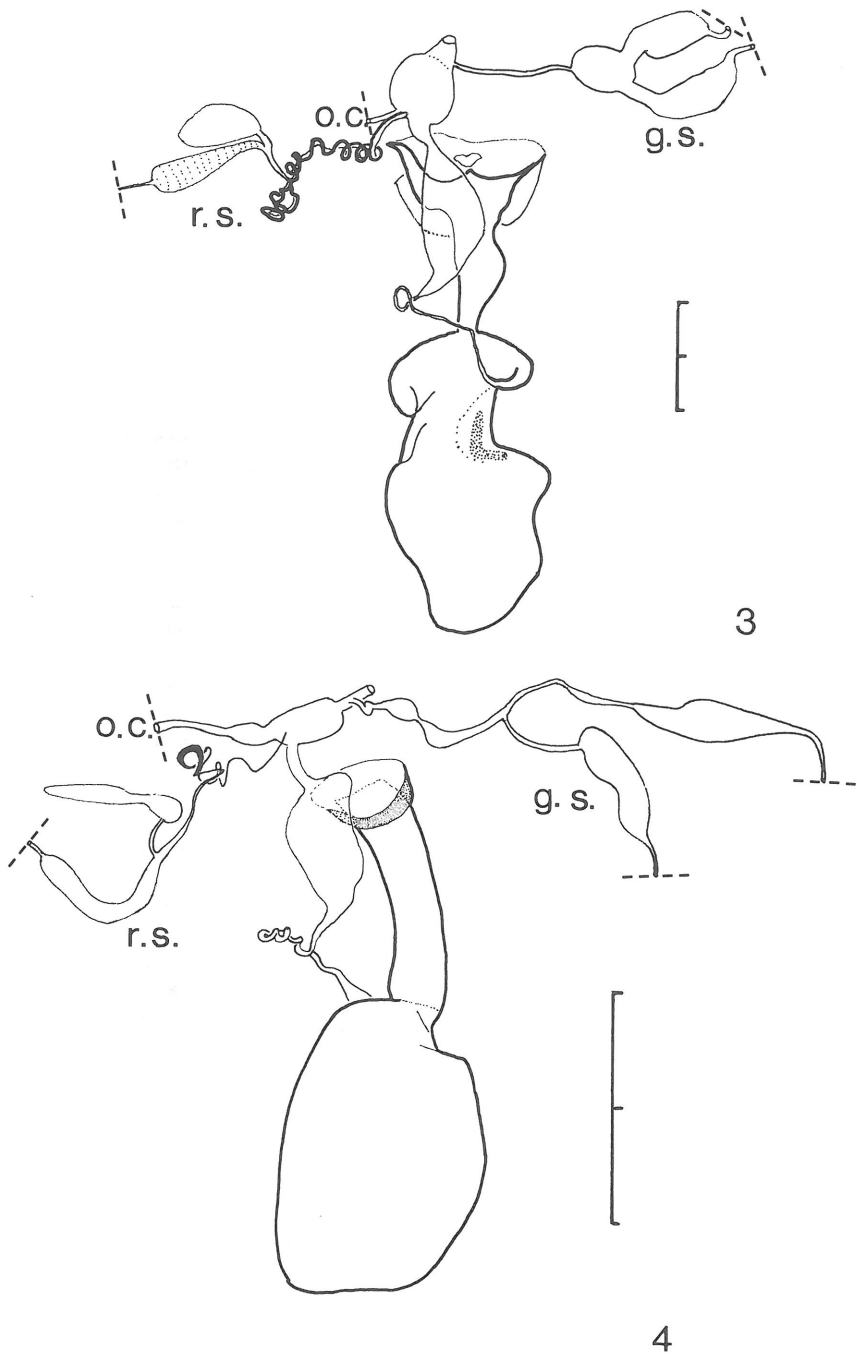


Fig. 3: Internal female genitalia of *Tinolius hypsana*. - Fig. 4: Internal female genitalia of *Callistege mi*

2. *Tinolius* WALKER, 1855

In *Tinolius hypsana* SWINHOE, 1889 (fig. 3), the ductus seminalis also originates from the corpus bursae. It starts thinly at the bursa and broadens considerably towards the oviductus communis. The ductus receptaculi is extremely long and spiralled, though forming only a small coil.

3. *Callistege* HÜBNER, 1823

In *Callistege mi* (CLERCK, 1759) (fig. 4) the ductus seminalis also originates from the corpus bursae. Again it is slender at the bursa and broadens considerably towards the oviductus. The ductus receptaculi is not as long as in the preceding species, less spiralled, but again with the characteristic coil. The structure of the ductus receptaculi is very similar to that in *Euclidia glyphica* (LINNAEUS, 1758) (not figured).

3.3. Eye structures

Some of the genera included in the Euclidiini have highly specialized eye-structures: the compound eye is surrounded by an unfaceted area, as illustrated in fig. 5 for *Euclidia glyphica* (LINNAEUS, 1758). This situation is found in the predominantly day-flying genera *Euclidia* OCHSENHEIMER,

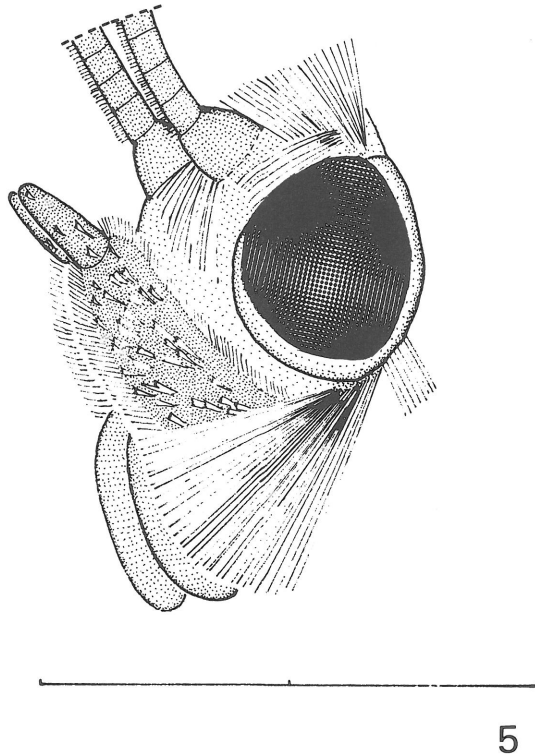


Fig. 5: Head of *Euclidia glyphica* Scale 2 mm Abbreviations: g. s. = glandulae sebaceae; o. c. = oviductus communis; r. c. = receptaculum seminis

1816, *Callistege* HÜBNER, 1823, *Gonospileia* HÜBNER, 1823 and *Euclidiana* RAKOSY, 1985. It may be questioned whether the splitting of this group into four genera is justified, as each of these genera consists of only very few species and none of them is supported by an autapomorphy. If four genera are accepted, the species *fortalitium* TAUSCHER, 1809, currently placed in *Euclidia*, may also deserve generic status, as it seems to be morphologically (antennae, habitus) more divergent from the recognized genera than the latter are between themselves. It appears to be a better taxonomic solution to unite all these genera as they seem to form a monophylum defined by the autapomorphic eye-structure.

We do not consider it advisable to base a more restricted concept of the Euclidiini on the autapomorphic situation of the compound eye, as it is more important to work towards establishing larger monophyletic units in such a rich subfamily.

Similar compound eyes, however, are also found in other day-flying noctuids, which are certainly not closer related to the present genera, viz. in the Plusiinae and Heliethinae. "The prominent rim around the eyes has been convergently gained in *Omorphina* and *Syngrapha* + *Caloplusia* (Plusiinae). This character ... has been functionally correlated with a diurnal habit" (KITCHING, 1987: 126). Especially the eyes of *Pyrocleptria cora* (EVERSMANN, 1837) and *P. copiosa* (LEECH, 1900) (Heliethinae) are very similar to the *Euclidia*-group. "The typical noctuid eye is of a superposition type. In the genus *Anarta*, which has reduced eyes, however, the eye has structurally altered so that it is essentially of the apposition type... Presumably the eye of other exclusively diurnal noctuids has undergone a similar change. Why the eye, in transforming from a type forming images by superposition, to one forming images by apposition, should undergo a corollary reduction in the number of ommatidia and in its external area is not known" (HARDWICK, 1970: 15).

Euclidiine adults possess no ridges on the anterior edge of the abdominal sternites, except in *Drasteria* where there is a straight sclerite just at the anterior border of the third sternite. The same character state (loss of sternal ridges) is also found in other Catocaline tribes (e.g. those containing the genera *Colobochyla* HÜBNER, 1825, *Cortyta* WALKER, 1858, *Hypocala* GUENÉE, 1852, *Laspeyria* GERMAR, 1810, *Litoprosopus* GROTE, 1869, *Lygephila* BILLBERG, 1820, *Minucia* MOORE, 1885, *Othreis* HÜBNER, 1823, *Oxyodes* GUENÉE, 1852, *Scoliopteryx* GERMAR, 1810, *Tinolius* WALKER, 1855, and *Thyas* HÜBNER, 1824). This character state strongly contrasts to the situation found in other tribes of the Catocalinae, which have strong ridges on the anterior part of the abdominal sternites (e.g. genera *Catocala* SCHRANK, 1802, *Chrysorithrum* BUTLER, 1878, *Cyligramma* BOISDUVAL, 1833, *Dinumma* WALKER, 1858, *Ischyja* HÜBNER, 1823, *Melipotis* HÜBNER, 1818, *Spirama* GUENÉE, 1852, and *Zethes* RAMBUR, 1833). Abdominal ridges are also found in the out-groups, therefore they seem to represent the primitive situation. - The 4th phragmata of all Euclidiini checked have two lobes. For a more detailed description of these characters see SPEIDEL & NAUMANN (1995).

4. Phylogenetic relationships of the Euclidiini

It appears quite likely that an adelphotaxon relationship exists between the genera *Anumeta* WALKER, 1858 (= *Palpangula* STAUDINGER, 1877) and *Heteropalpia* BERIO, 1939. For the first genus the family-group name Anumetini WILTSHIRE, 1976 is available.

The internal female genitalia of *Anumeta* have been figured by JOHN (1909), who illustrated the species *A. henkei* (STAUDINGER, 1877), *A. cestina* (STAUDINGER, 1884), *A. fractistrigata* (ALPHERAKY, 1882), *A. cestis* (MÉNÉTRIÉS, 1848), *A. dentistrigata* (ALPHERAKY, 1883), *A. fricta* (CHRISTOPH, 1893), and *A. straminea* (BANG-HAAS, 1906). In all species figured, the ductus seminalis, originating from the corpus bursae, has an elongated bulbous expansion (bullae seminalis) near its centre. *A. straminea* exhibits an extremely long and spiralled ductus receptaculi, though a typically twisted coil is not present. Other species also possess a spiralled ductus receptaculi, but this is less pronounced, especially in *A. cestis*.

In *Heteropalpia acrosticta* (PÜNGELER, 1904) the ductus seminalis is very similar, with the characteristic elongated bulbous expansion near its middle.

We assume that *Heteropalpia* and *Anumeta* are closely related to each other, as the morphological situation of the bulla seminalis described above is unlikely to have evolved independently. WILTSHIRE (1976) placed *Heteropalpia* with *Pericyma* HERRICH-SCHÄFFER, 1851 in a common tribe which he named Pericymatini WILTSHIRE, 1976. In *Pericyma*, however, the bulla seminalis seems to be lacking (ROSE & SINGH, 1984). The genera *Polydesma* BOISDUVAL, 1833 (BERIO, 1959) and *Zale* HÜBNER, 1818 (= *Phaeocyma* HÜBNER, 1818, = *Omoptera* GUÉRIN-MÉNEVILLE, 1832, = *Homoptera* BOISDUVAL, 1833) may possibly also be related to the present group and are type genera of the family-group taxa Polydesmidae GUENÉE, 1852, Homopterides BOISDUVAL, 1833, and Pheocymini GROTE, 1890 (see nomenclatural remarks). As soon as the structure of the internal female genitalia is known, these taxa or some of them may fall into synonymy and the tribal name may have to be changed.

In the Anumetini the ductus receptaculi is less strongly twisted and the ductus seminalis has a bulbous expansion in its central region. Due to the long, spiralled ductus receptaculi there are affinities to the Euclidiini and both tribes may represent sister-groups.

JOHN (1909) also figured the internal female genitalia of the following species of *Anydrophila* JOHN, 1909: *mirifica* (ERSCHOV, 1874), *simiola* (PÜNGELER, 1900) and *imitatrix* (CHRISTOPH, 1887). In all these species the ductus seminalis appears to be thin and to originate from the corpus bursae. There is a small bulla in the ductus seminalis near the aperture which could indicate affinities to the Anumetini which have an extremely elongated and rather broad bulla. JOHN's drawings of *Anumeta* and *Anydrophila* are certainly not too accurate, but the general situation of the organs figured is quite good and there is no reason to believe that the long spiralled ductus receptaculi is purely imaginative. Thus, the Anydrophilini WILTSHIRE, 1976 may also be provisionally grouped with the Anumetini, even though the bulla in the ductus seminalis is much less developed.

FORBES (1954) included *Melipotis* HÜBNER, 1818 and *Eulepidotis* HÜBNER, 1823 in the Synedini, a tribe which he created to accommodate *Drasteria* HÜBNER, 1818 (= *Syneda* GUENÉE, 1852). The genera *Melipotis*, *Lyncestis* WALKER, 1857 and *Eulepidotis* do not show the specialized character situation found in the genera dealt with here and are thus better kept separated. The genera thus excluded are type genera of four family-group names: *Melipotis* and *Lyncestis* are type genera of the Melipotini GROTE, 1895 and Lyncestini WILTSHIRE, 1990, respectively. Both tribes are certainly synonymous: *Lyncestis* and *Melipotis* are sometimes not even separated at generic level (FRANCLEMONT & TODD, in HODGES, 1983). *Eulepidotis*, including the junior synonym *Palindia* GUENÉE, 1852 (FRANCLEMONT & TODD, in HODGES, 1983), are type genera of the *Palindidae* GUENÉE, 1852 and *Eulepidotinae* GROTE, 1895.

We propose to use *Melipotini* and *Eulepidotini* as tribal names (see nomenclatural remarks). Both tribes do not share the autapomorphy described for the Euclidiini. No synapomorphies could be found for *Melipotini* and *Eulepidotini* and any further relationships therefore remain unresolved.

In both tribes abdominal sternal ridges are present. The ridges on the 4th sternite show two characteristic excavations which can be traced in most taxa with abdominal ridges. In *Eulepidotis* the sternal ridges are weak. The two lobes of the 4th phragma are large. The ductus receptaculi is long, but weakly spiralled and forms no coil. In *Melipotis* sternal ridges are strong and the two lobes of the 4th phragma are also large. The ductus receptaculi is comparatively short, with only two turns in those species that have been checked and therefore forms no coil.

5. Nomenclatural remarks

We suggest that the newly proposed monophylum dealt with here should be named "Euclidiini" and that this tribe remains within the subfamily Catocalinae for the moment. The following synonymy is established:

Euclidiini GUENÉE, 1852

Euclididae GUENÉE, 1852

Synedini FORBES, 1954 Syn. n.

Drasteriini WILTSHIRE, 1976 Syn. n.

The names Goniatidae DUPONCHEL, 1844 and Bolinidae GUENÉE, 1852 are unavailable, the first name not being based on an included genus, the second being based on a generic name which is a junior homonym (NYE, 1975).

The case of the family-group name Polydesmidae GUENÉE, 1852 has to be referred to the International Commission on Zoological Nomenclature according to Art. 55 (b) ICZN, as there is a family Polydesmidae LEACH, 1815 in the Myriapoda, Diplopoda which is based on a similar generic name (*Polydesmus* LATREILLE, [1802]). The family-group name Homopterides BOISDUVAL, 1833 has to be corrected to the tribal name Omopterini according to Art. 35 (d) ICZN, and Pheocymini GROTE, 1890 has to be corrected to Phaeocymini according to the same article.

The following tribal synonymies are established:

Melipotini GROTE, 1895

Lyncestini WILTSHIRE, 1990 Syn. n.

Eulepidotini GROTE, 1895 (1852)

Palindidae GUENÉE, 1852

Eulepidotinae GROTE, 1895

If the synonymy of the type genera is accepted, both tribal names are certainly synonymous, but the younger name can possibly be retained according to Art. 40 (b) ICZN.

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