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Further morphological characters for a phylogenetic classification of the Noctuidae (Lepidoptera)

With 13 figures

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Abstract

The authors describe seven characters which provide useful information for phylogenetic analyses in the family Noctuidae and which had not been sufficiently evaluated by previous authors. These characters include (1) the microscopic and submicroscopic structure of the tip of the proboscis, (2) the structure of the male subcostal retinaculum, (3) the position of the male genitalic muscle 4, (4) development of the dorsal phragma on the second abdominal segment, (5) presence of sclerotized ridges on the abdominal tergites and sternites, (6) the presence of pre-abdominal brush-organs, and (7) certain modifications of the internal female genitalia. Using these characters, the authors provide arguments for the monophyly of the camptolomine-chloephorine-sarrothripine-noline lineage, and for the probable monophyly of a complex consisting of the so-called "trifine" noctuids, including the Bryophilinae and possibly the Acronictinae and Pantheinae.

Zusammenfassung

Die Autoren diskutieren sieben Merkmale, die sie bei phylogenetischen Analysen in der Familie Noctuidae für nützlich erachten und die im Schrifttum bislang vernachlässigt wurden. Diese Merkmale sind (1.) die mikroskopische und submikroskopische Struktur der Rüsselspitze, (2.) die Struktur des männlichen subcostalen Retinaculum, (3.) der Verlauf des männlichen Genitalmuskels 4, (4.) die Ausprägung des dorsalen Phragma am zweiten Abdominalsegment, (5.) das Vorhandensein von sklerotisierten Leisten auf den abdominalen Tergiten und Sterniten, (6.) das Vorkommen von praeabdominalen Pinsel-Organen sowie (7.) Modifikationen der inneren weiblichen Genitalien. Mit Hilfe dieser Merkmale werden Argumente für die Monophylie der Camptolominae + Chloephorinae + Sarrothripinae + Nolinae und für die Monophylie einer Gruppe, die aus den sog. "trifinen" Noctuiden, den Bryophilinae und möglicherweise auch den Acronictinae und Pantheinae besteht, vorgetragen.

1. Introduction

The Noctuidae is the largest family of the Lepidoptera; currently about 25,000 species are recognized (HEPPNER, 1991), although many new species are probably still undescribed, especially from the tropical regions. The higher classification of this huge family has gained considerable attention over

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the last 150 years. KITCHING (1984) presented a historical review of the major changes in the classification of the Noctuidae during that period, but from a phylogenetic point of view the basic phyletic patterns of the family remain unresolved (KITCHING, 1984), and some recently proposed classifications are still typological (BECK, 1989, 1992).
It appears to be very difficult to find convincing autapomorphies for some of the subfamilies and for taxa above the subfamily level. Only one monophylum, consisting of the Euteliinae and the Stictopterinae, has so far been established and appears to be well-founded (HOLLOWAY, 1985, KITCHING, 1987).
Therefore, at this stage it seems to be impossible to arrive at a better understanding of the phylogenetic relationships within the Noctuidae without using "new" characters, i.e. characters that may have been used for quite some time within single groups for diagnostic purposes, but which have not yet been evaluated on a larger scale to identify monophyla within the family.
Such characters should be sufficiently complex to reduce the risk of overlooking homoplasy. The few complex organs known in the Noctuidae so far (such as the structure of the tympanal organ, male and female external genitalia) either exhibit too little variation or just the opposite, i.e. they are too diverse to enable one to discover common developments within larger groups of the family.
We have identified a few characters that appear to be of sufficient complexity and variation within the Noctuidae and these characters might contribute to the identification of larger monophyla. This appears to be necessary because one of the currently accepted major taxonomic subdivisions of the Noctuidae, the "Quadrifinae" has been known for quite some time to represent a polyphyletic entity (KITCHING, 1984), which cannot be placed in a consequently developed cladistic system and has to be replaced by monophyla. Other para- or polyphyletic units have, at least, to be identified as such and efforts need to be made to resolve them.
We propose that the following characters are used for further analysis of the phylogenetic history of the Noctuidae:

1. The ultra-structure of the surface of the proboscis.
2. The structure of the male retinaculum.
3. The arrangement of the muscle m4 in the male genitalia.
4. The dorsal phragma of the second abdominal segment.
5. Sclerotized ridges on the abdominal tergites and sternites.
6. Anterior abdominal hair-pencils or brush-organs (coremata).
7. The morphology of the internal female genitalia.

2. Material and methods

Dried adults representing all subfamilies and many of the named tribes of the Noctuidae (about 150 species) were used to examine the male retinaculum (3.2), the dorsal phragma (3.4), the sclerotized ridges (3.5), the brush organs (3.6) and the internal female genitalia (3.7). The abdomens were dissected after 15 min maceration in hot 10% KOH. The preparations were stained with Chlorazol Black. Techniques for the preparation of the internal female genitalia have been described in detail by HÄUSER (1990) and have been adopted for this study.
Specimens of *Asota caricae* (FABRICIUS, 1775) (Aganainae), *Camptoloma interiorata* (WALKER, 1865) (Camptolominae), *Maurilia iconica* (WALKER, 1858) (Chloephorinae) and *Blenina* sp. (Sarrothripinae) were fixed in aqueous Picric acid for preparations of the male genitalic muscles (3.3). The genitalia were stained with Evan's Blue in aqueous solution.
Imagines of *Catocala nupta* (LINNAEUS, 1767), *Scoliopteryx libatrix* (LINNAEUS, 1758) (Catocalinae), *Cryphia raptricula* ([DENIS & SCHIFFERMÜLLER], 1775) and *Noctua pronuba* (LINNAEUS, 1758) were used for examination of the surface of the proboscis (3.1). The galeae were removed, then fixed on double-sided adhesive tape and examined by SEM after coating with gold.

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3. The characters

3.1. The ultra-structure of the surface of the proboscis

Two types surface structures on the proboscis are known within the Noctuidae (BÖRNER, 1932, 1939, 1949): the first has broad ribs which normally cover the entire proboscis, the second has slender ribs which are replaced by a granulated sculpture towards the tip of the proboscis. BÖRNER used these characters to separate two groups of Noctuidae, corresponding roughly to the formerly accepted "quadrifine" and "trifine" noctuids. Subsequent authors have not used these characters for the higher classification, apparently because it is too difficult to check them as an initial step in the formation of a dichotomous grouping of subfamilies. Nevertheless, our preliminary studies suggest that this character may be useful for phylogenetic considerations. Using ultrastructure (SEM) techniques, it is no problem at all to investigate and describe the structure of the proboscis, even when new taxa are described. We cannot yet give a clear polarity in the transformation of this character as our investigations are in an initial phase, especially with regard to the situation in the outgroups.

We illustrate the broadly ribbed character state of the proboscis for two Catocalinae species: *Catocala nupta* (LINNAEUS, 1767) (fig. 1) and *Scoliopteryx libatrix* (LINNAEUS, 1758) (fig. 2). Apart from the figures given here and by BÖRNER, there are, as far as we know, only a few illustrations of the ultrastructure of the galea in Noctuidae, nearly all of which concern the specialised proboscis of "fruit-piercers" or lachryphagous moths. SRIVASTAVA & BOGAWAT (1969) figured the tip of the proboscis of *Elygea* [Othreis] *materna* (LINNAEUS, 1767) (Catocalinae), BÄNZIGER (1973) depicted the same of *Calyptra* [Calpe] *eustrigata* (HAMPSON, 1926) (Catocalinae) and the plusiine *Chrysodeixis chalcites* (ESPER, 1789), WU & CHOU (1985) provided scanning electron micrographs (SEM) of the tip of the proboscis of various Catocalinae: *Eudocima* [Maenas] *salaminia* (CRAMER, 1777), *Plusiodonta coelonota* (KOLLAR, 1844), *Adris tyrannus* (GUENÉE, 1852), *Othreis fullonia* (CLERCK, 1764), *Anomis flava* (FABRICIUS, 1775), *Ophisma* [Parallelia] *gravata* GUENÉE, 1852, *Ophiusa* [Anua] *coronata* (FABRICIUS, 1775), *Spirama* [Speiredonia] *retorta* (CLERCK, 1759), *Dysgonia* [Parallelia] *stuposa* (FABRICIUS, 1794) and *Erebus crepuscularis* (LINNAEUS, 1758). KITCHING (1987) figured SEM micrographs of the proboscis of the plusiine *Autographa bractea* ([DENIS & SCHIFFERMÜLLER, 1775]). It is easy to identify and to confirm the presence of broad ribs at the proboscis tip from these published sources.

SEM micrographs clearly show that the unribbed surface of the tip of the proboscis, termed "granulated" by BÖRNER, is very complicated. There are small plate-like nodules scattered on the surface which has no ribs at all. The structure in the bryophiline *Cryphia raptricula* ([DENIS & SCHIFFERMÜLLER], 1775) (fig. 3) agrees quite well with the situation found in the noctuine *Noctua pronuba* (LINNAEUS, 1758) (fig. 4). Therefore, we consider the Bryophilinae to be best placed with the higher ("trifine") Noctuidae. Figures of tip of the proboscis of the hadenine *Pseudaletia* [Mythimna] *unipuncta* (HAWORTH, 1809) (BÄNZIGER, 1990), the noctuine *Peridroma saucia* (HÜBNER, 1808) (MILLER, 1991), the cuculliines *Cucullia umbratica* (LINNAEUS, 1758) and *Oncocnemis confusa* (FREYER, 1840) (KITCHING, 1987), agree well with BÖRNER's description of the granulated proboscis tip of the "trifine" Noctuidae.

We found that those species which have a distally unribbed proboscis possess acute microprojections between the ribs in the basal part of the proboscis. These were not found in species with a ribbed distal galeal surface. These cuticular dents have also been identified in a SEM micrograph of *Mamestra brassicae* (LINNAEUS, 1758) published by KRENN (1990).

SEM micrographs of the proboscises of two euteliine species (KITCHING, 1987: 210, 211, figs. 109, 115, 118, 119 (*Anuga constricta* GUENÉE, 1852), fig. 114, 116 (*Paectes cristatrix* (GUENÉE, 1852) and of the stictopterine *Stictoptera cucullioides* GUENÉE, 1852 (KITCHING, 1987, fig. 113) show apical nodules similar to those found in the above-mentioned trifine species. Moreover, *Anuga constricta* and *Stictoptera cucullioides* have identical microprojections on the basal ribs of the probos-

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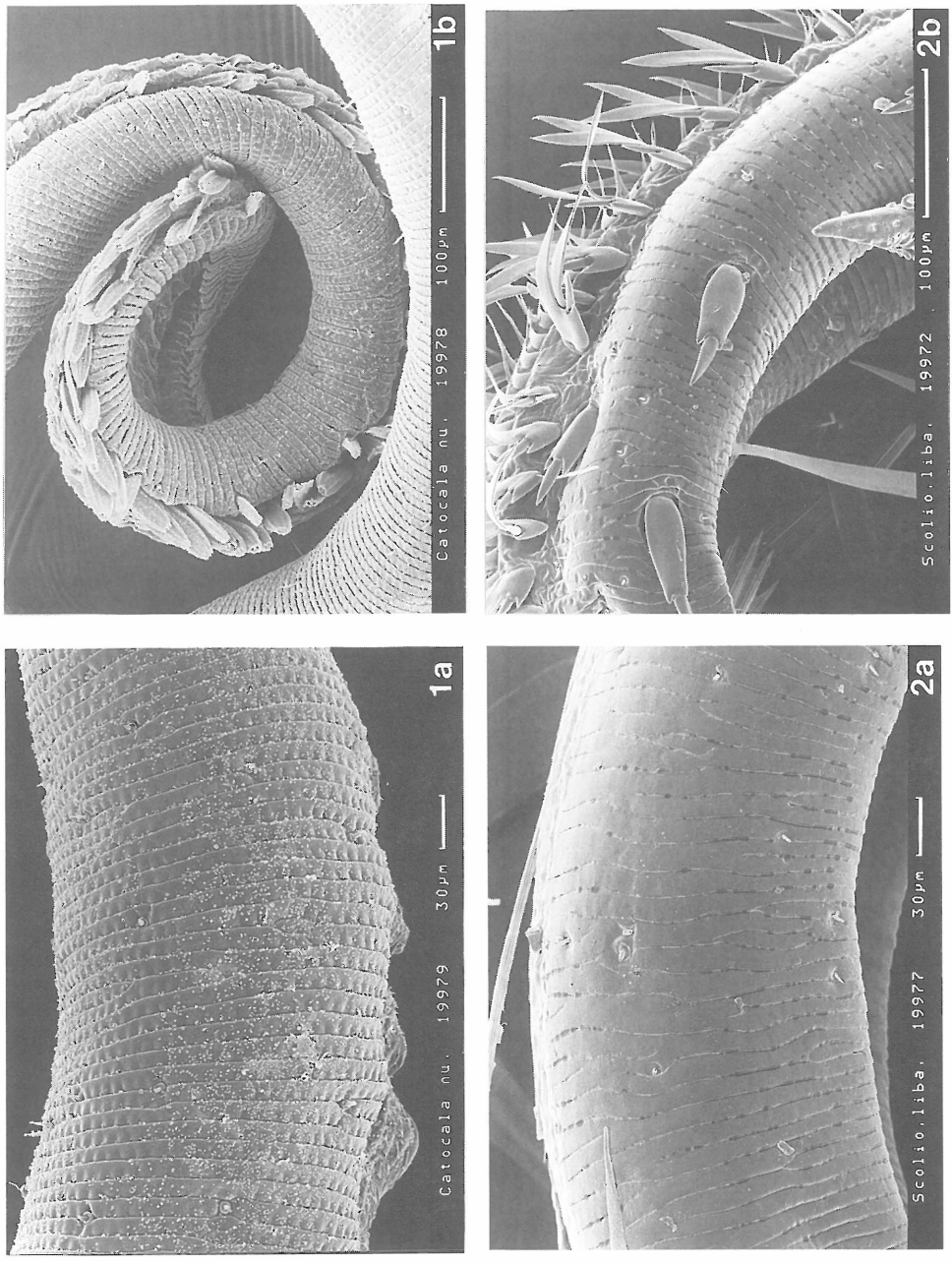

Fig. 1: SEM micrographs of the proboscis of *Catocala nupta* (LINNAEUS, 1767). **a.** basal part, **b.** distal part. - **Fig. 2:** SEM micrographs of the proboscis of *Scoliopteryx libatrix* (LINNAEUS, 1758). **a.** basal part, **b.** distal part.

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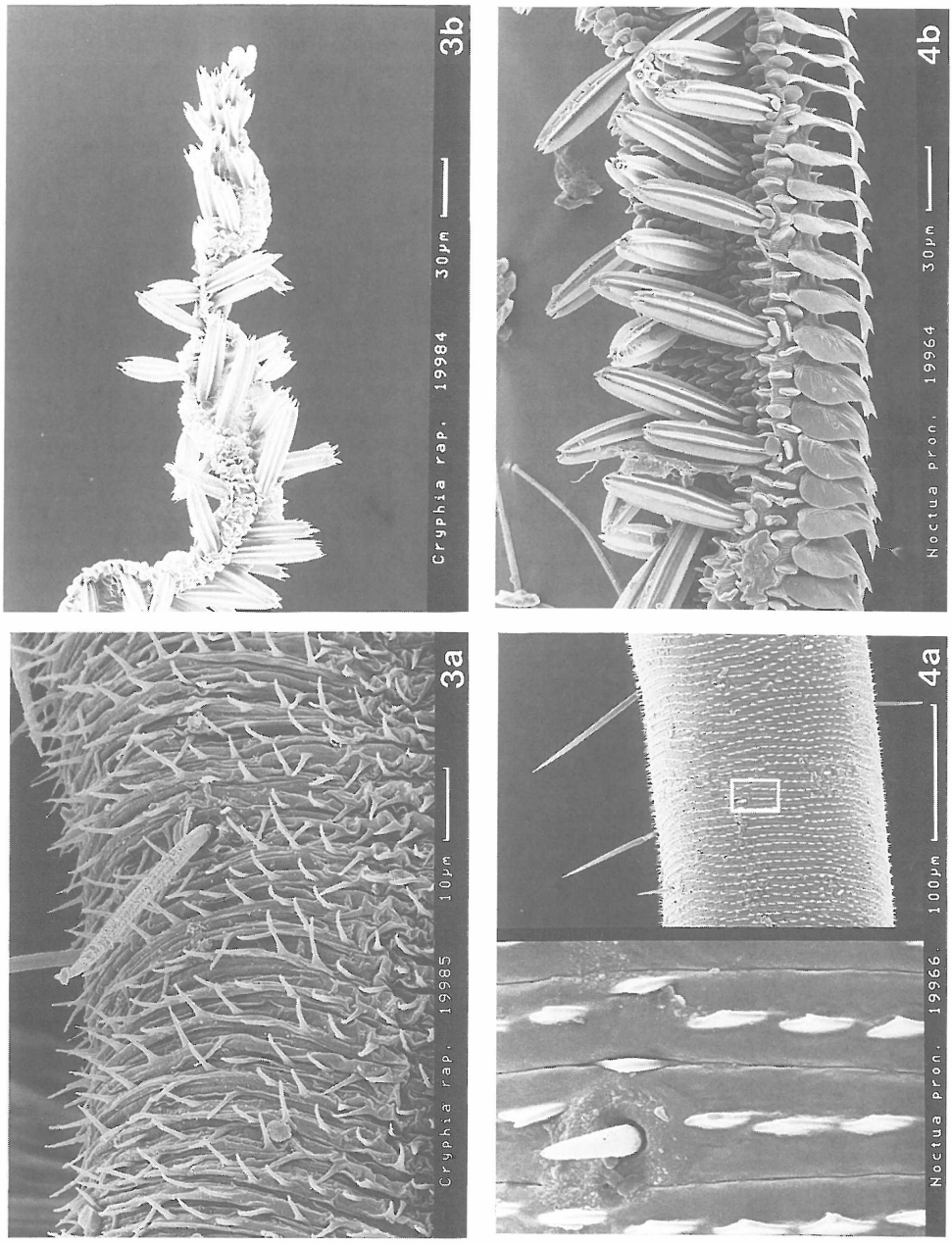

Fig. 3: SEM micrographs of the proboscis of *Cryphia raptricula* ([DENIS & SCHIFFERMÜLLER], 1775). **a.** basal part, **b.** distal part. - **Fig. 4:** SEM micrographs of the proboscis of *Noctua pronuba* (LINNAEUS, 1758). **a.** basal part, **b.** distal part.

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cis like those in the trifine species mentioned above. The acronictine *Acronicta americana* (HARRIS, 1841) (MILLER, 1991), the noline *Nola pustulata* (WALKER, 1865) (MILLER, 1991) and all Chloephorinae (BÖRNER, 1949, light microscopical observations which we have confirmed in *Maurilia iconica* (WALKER, 1858)) also possess distal nodules on the proboscis, but their galeal structures have not yet been sufficiently analysed. The tribe Toxocampini was defined by BÖRNER (1932) as follows: "end of proboscis without ribs, granulated, papillae [= sensillae] of proboscis with lateral appendices. Larva feeding on Papilionaceae [= Fabaceae]". At present this tribe includes the genera Lygephila BILLBERG, 1820, Autophila HÜBNER, 1823, Apopestes HÜBNER, 1813, and Tathorhynchus HAMPSON, 1894.

The fact that the tip of the proboscis is granulated in these quadrifine taxa may indicate that they also belong to the higher noctuids. This is partly in agreement with the views of BECK (1992) who removed *Apopestes* from the Catocalinae-complex and placed it in the subfamily Cuculliinae. This mainly trifine subfamily, as defined by BECK (1992), appears to be at least a paraphyletic group. BECK's main argument is the position of the spiracular line on the anal segment of the larva which ends at the angle between the anal prolegs and the anal plate. According to BECK (1992) this character situation is also found in some Hypeninae and Notodontidae. Thus it probably represents the plesiomorphic character state and therefore cannot be used as an argument to place Apopestes with the higher noctuids. In any case, the Toxocampini show a remarkable tendency towards the higher ("trifine") Noctuidae. The position of two components of the Toxocampini, *Apopestes* and *Autophila*, was the object of a long debate. Both genera were placed by BOURSIN, once the leading taxonomist on Palaearctic "trifine" Noctuidae, with the "trifine" subfamily Amphipyrinae, but most of the more recent authors (SUGI, in INOUE et al., 1982, FIBIGER & HACKER, 1990) have placed them back into the Catocalinae or Ophiderinae, close to Lygephila. This also reflects the difficulties involved when defining the appropriate place of this tribe.

The ultra-structure of the proboscis tip in the outgroups is known in the arctiid moth *Amerila* [Rhodogastria] *bubo* (WALKER, 1855) (ALTNER & ALTNER, 1986), several Notodontidae (*Peridea angulosa* (SMITH, 1797), *Nadata gibbosa* (SMITH, 1797), *Gluphisia septentrionis* WALKER, 1855, *Hippia packardii* (MORRISON, 1875), *Schizura biedermani* BARNES & MCDUNNOUGH, 1911, *Lochmaeus bilineata* (PACKARD, 1864), *Lirimiris truncata* (HERRICH-SCHÄFFER, 1856), *Zunacetha annulata* (GUÉRIN-MÉNEVILLE, 1844), *Odontosia elegans* STRECKER, 1885) and the Lymantriidae (*Dasychira obliquata* (GROTE & ROBINSON, 1866)) (MILLER, 1991). In some of these species the distal proboscis also shows plate-like nodular projections similar to those in the higher noctuids. However, these projections are larger and densely cover the surface of the galea. Therefore it cannot be decided whether it is ribbed in the same way as that described above for the Catocalinae.

"Comparative morphology of notodontid proboscises provided a wealth of phylogenetic information" (MILLER, 1991). The same applies to the Noctuidae. As mentioned above, it is still very difficult to determine the polarity in the transformation of these galeal characters within the Noctuidae.

An extensive comparative SEM investigation of the ultrastructure of the noctuid proboscis tip, covering also the outgroups, is under way. At present we only want to point out that the Pantheinae and Acronictinae also possess the unribbed condition of the proboscis tip (BÖRNER (1949)). This may indicate that these taxa should also be placed with the higher noctuids.

3.2. The structure of the male retinaculum

Most male Noctuidae have a quite simple, lobate subcostal retinaculum (fig. 5a of *Catocala* SCHRANK, 1802). Only in a few noctuid subfamilies is the male subcostal retinaculum elongate (bar-shaped). This structure has been widely used to characterize the Chloephorinae and Sarrothripinae, and is also known to be present in the Camptolominae (HOLLOWAY, 1988) and the Nolinae (e.g. SUGI, 1990) and it certainly represents a synapomorphy of these subfamilies. "The bar-shaped subcostal retinaculum in the male is the character to separate the noline-chloephorine-sarrothripine

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lineage from others in the Noctuidae" (SUGI, 1990) (figs. 5c-f). Intermediate development of the male retinacula is rarely found, e.g. in *Xanthodes* GUENÉE, 1825 (compare the situation found in *Xan-*

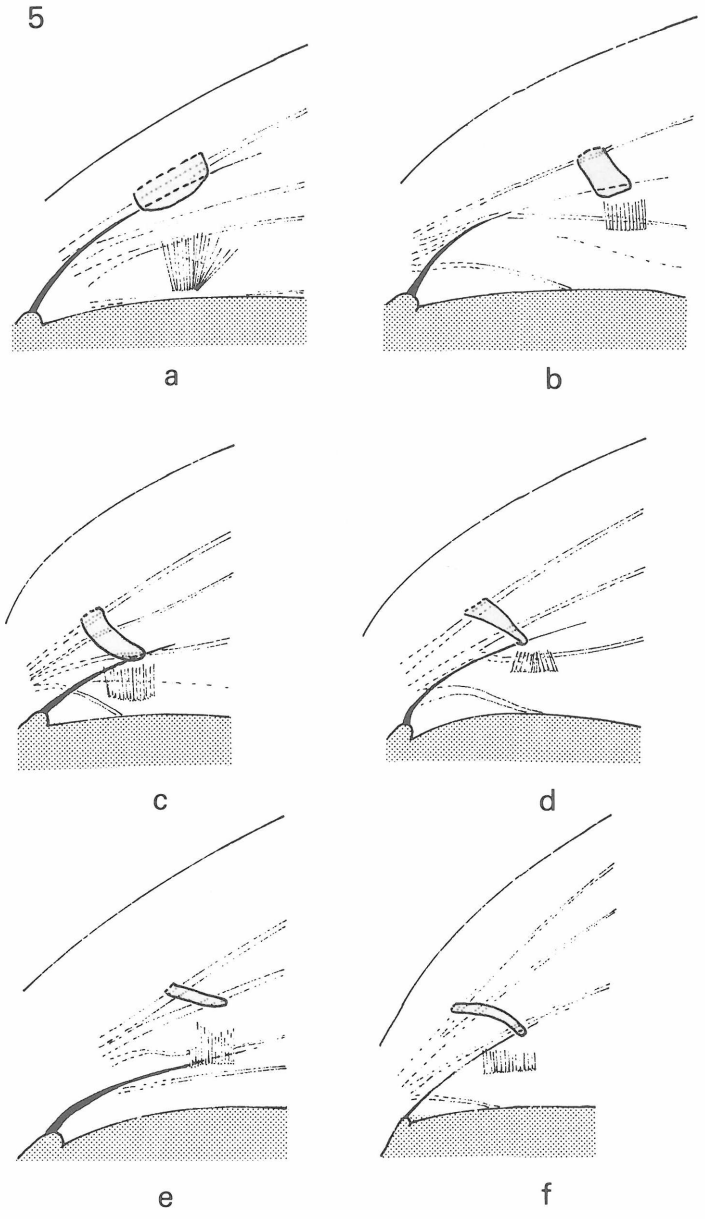

Fig. 5: Wing bases and coupling mechanisms in Noctuidae **a.** *Catocala nupta* (LINNAEUS, 1767); **b.** *Xanthodes albago* (FABRICIUS, 1794); **c.** *Camptoloma tigrinus* (HAMPSON, 1894); **d.** *Nolathripa lactaria* (GRAESER, 1892); **e.** *Iscadia inexacta* (WALKER, 1858); **f.** *Nola cucullatella* (LINNAEUS, 1758).

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thodes albago (FABRICIUS, 1794), fig. 5b), but probably this genus does not belong to the Chloephorinae (MELL, 1943). The male subcostal retinaculum is very often completely reduced in subfamilies such as the Chloephorinae, Sarrothripinae and Nolinae. This is easily explained by the fact that in these subfamilies the frenulum is approximated to the setaceous retinaculum which has no function in the wing-coupling of the males of other noctuid groups. In the males of *Iscadia inexacta* (WALKER, 1858) (fig. 5 e), the frenulum is inserted in the setaceous retinaculum and the subcostal retinaculum must be considered to be rudimentary; in many others it is completely lost. The functionof this reduced or lost male subcostal retinaculum is taken over by the setaceous retinaculum. Thus it is understandable that only about half of the chloephorine species, less than half of the Sarrothripinae and only a few Nolinae, have an elongate retinaculum. So far, only the Camptolominae are known not to contain a species with a reduced subcostal male retinaculum. The complete loss of the subcostal retinaculum in *Narangodes* HAMPSON, 1910 is not highly exceptional, as stated by SUGI (1990), and is a normal character state found in many species of the Chloephorinae, Sarrothripinae and Nolinae.

An elongate retinaculum is also present in some Arctiidae: we found it to be very distinctive in *Amerila omissa* (ROTHSCHILD, 1910) but less distinctive in *Axiopoena maura* (EICHWALD, 1839). The male retinaculum is also distinctly elongate in the Aganainae, in which subfamily we found it in *Asota caricae* (FABRICIUS, 1775). If the current classification of the Arctiidae as a separate family, based mainly on the structure of the tympanal organs, i.e. recognizing them as an independent monophylum, is correct, this situation may indicate homoplasy. The Aganainae and Arctiidae do not have the specialized situation of the male genitalic muscle m4 (see 3.3) and we therefore propose to exclude them from the camptolomine-chloephorine-sarrothripine-noline lineage.

3.3. The arrangement of the muscle *m4* in the male genitalia

The male genitalia and their muscles provide further synapomorphies which enable us to identify the Camptolominae, Chloephorinae, Sarrothripinae and Nolinae as a well-founded monophylum within the Noctuidae (FÄNGER, SPEIDEL & NAUMANN in prep.).

Here we give a short review of the male genitalia muscles, using the system of FORBES (1939) and BIRKET-SMITH (1974). TIKHOMIROV (1979b) described the male genitalic muscles of many noctuid species belonging to various subfamilies. A schematic presentation of two different types of musculature in the male genitalia of Noctuidae is shown in fig. 6; the illustration is restricted to the tegumen, the vinculum and the muscle *m4*.

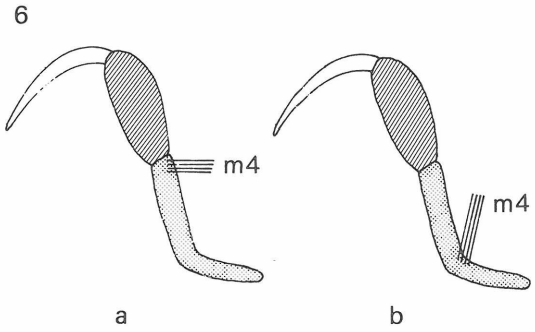

Fig. 6: Schematic lateral view of the male genitalia with the muscle m4. Striped: tegumen; stipped: vinculum.; **a.** Plusiinae, Acontiinae, Heliothinae, Noctuinae (incl. Hadeninae, Amphipyrinae, Cuculliinae), Acronictinae, Hypeninae, Rivulinae, Catocalinae, Herminiinae, Aganainae. **b.** Camptolominae, Sarrothripinae, Chloephorinae, Nolinae. [This figure is based on that of TIKHOMIROV (1979b) and our own results (FÄNGER; SPEIDEL & NAUMANN, in prep.].

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A major synapomorphy of the Camptolominae, Chloephorinae, Sarrothripinae and Nolinae is the situation of the genitalic muscle *m4*: it is inserted in the basal processes of the valva (transtilla) and the central part of the vinculum (fig. 6b). In all other noctuid groups and in the outgroups studied (e.g. Arctiidae), this muscle inserts in the dorsal part of the vinculum (fig. 6a). This does not mean a simple shifting of the insertion: the muscle is directed dorso-ventrally in the Chloephorinae lineage and horizontal in the other noctuids.

In his phylogenetic diagram TIKHOMIROV (1979b) placed the Nolidae as a separate family that branches off at the base of the noctuid lineage, whereas the Sarrothripinae (including the Chloephorinae) only branch off within the Noctuidae, thus indicating that he gave plesiomorphic status to the condition where m4 inserts in the middle of the vinculum. TIKHOMIROV's interpretation conflicts with the outgroup situation in the Arctiidae (TIKHOMIROV, 1979a) and Notodontidae (TIKHOMIROV, 1979c), where muscle m4 is in a horizontal position. Therefore, in contrast to TIKHOMIROV (1979b), we regard the situation found in the Camptolominae, Chloephorinae, Sarrothripinae and Nolinae to represent the apomorphic character state. A monophylum consisting of the Camptolominae + Sarrothipinae + Chloephorinae + Nolinae is also supported by the elongate retinaculum (see above).

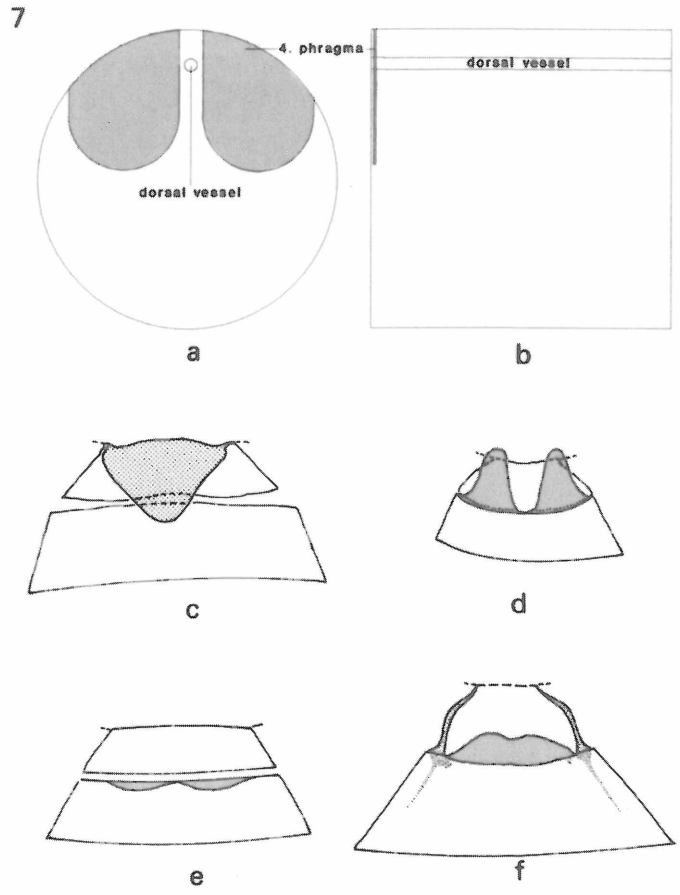

Fig. 7: Scheme of second abdominal segment to show position of phragma 4. **a.** cross-section; **b.** lateral view with anterior margin on the left. Abdominal tergites 1 and 2 of **c.** *Litoprosopus* GROTE, 1869, **d.** *Rivula* GUENÉE, 1845, **e.** *Cymatophoropsis* HAMPSON, 1894, **f.** *Meganola* DYAR, 1898.

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3.4. The dorsal phragma of the second abdominal segment

The basal part of the abdomen exhibits highly interesting structures: the second abdominal tergite bears the 4th phragma (HESSEL, 1969), which possesses lobular ventral extensions. This structure has also been cited by KITCHING (1988) as an "inflected flange". Such large extensions are observed in the outgroups (Geometroidea and most Noctuoidea, e.g. Lymantriidae, Notodontidae) and only a part of the Noctuidae. Normally, they consist of two large and separate phragma lobes on the anterior margin of the second abdominal tergite (fig. 7b) (HESSEL, 1969 and pers. obs.); we consider this to represent the plesiomorphic character state. These lobes are reduced in all higher Noctuidae, but are present in most "quadrifine" noctuids. An exception is found in the genus Litoprosopus GROTE, 1869 (Catocalinae), which instead has reduced phragma lobes and an unpaired lobe on the anterior margin of the first tergite just behind the tympanal organs (fig. 7a).
We have found large phragma lobes (fig. 7b) to be present in the Aganainae (*Asota* HÜBNER, 1819), Hypeninae (*Hypena* SCHRANK, 1802), Rivulinae (*Rivula* GUENÉE, 1845) and in most Catocalinae (*Chrysorithrum* BUTLER, 1878, *Colobochyla* HÜBNER, 1825, *Cyligramma* BOISDUVAL, 1833, *Eulepidotis* HÜBNER, 1823, *Ischyja* HÜBNER, 1823, *Lygephila* BILLBERG, 1820, *Melipotis* HÜBNER, 1818, *Parachalciope* HAMPSON, 1913, *Parascotia* HÜBNER, 1825, *Spirama* GUENÉE, 1852, *Tinolius* WALKER, 1855, *Zethes* RAMBUR, 1833).
Smaller or somewhat reduced phragma lobes (fig. 7c) were observed in some Plusiinae (*Abrostola* OCHSENHEIMER, 1816), Acronictinae (*Cymatophoropsis* HAMPSON, 1894, *Euromoia* STAUDINGER, 1892) and Stictopterinae (*Stictoptera* GUENÉE, 1852).
The phragma lobes in the catocaline *Litoprosopus* GROTE, 1869 (fig. 7a), the sarrothripine *Nycteola* HÜBNER, 1822, the chloephorine *Earias* HÜBNER, 1825, Camptolominae (*Camptoloma* FELDER, 1874), the pantheine *Colocasia* OCHSENHEIMER, 1816, Dilobinae (*Diloba* BOISDUVAL, 1840), Bryophilinae (*Chytobrya* DRAUDT, 1950 and *Cryphia* HÜBNER, 1818) and in the "trifine" subfamilies Noctuinae, Hadeninae, Amphipyrinae and Cuculliinae, are strongly reduced or absent. Fused phragmata (fig. 7d) are typical for those Nolinae that have been studied (*Meganola* DYAR, 1898, *Nola* LEACH, 1815).

3.5. The presence of sclerotized ridges on the abdominal tergites and sternites

Some Noctuidae possess strongly developed sclerotized ridges on the anterior part of the abdominal tergites and sometimes also on the sternites. In the Notodontidae and Lymantriidae these ridges are present on both the tergites and sternites, but here they are weakly developed. These structures have also been observed in the Aganainae (*Asota* HÜBNER, 1819), Herminiinae (*Paracolax* HÜBNER, 1825), Hypeninae (*Hypena* SCHRANK, 1802), Rivulinae (*Rivula* GUENÉE, 1845), Camptolominae (*Camptoloma* FELDER, 1874) and many Catocalinae (*Catocala* SCHRANK, 1802, *Chrysorithrum* BUTLER, 1878 (fig. 8a), *Cyligramma* BOISDUVAL, 1833, *Dinumma* WALKER, 1858, *Ischyja* HÜBNER, 1823, *Melipotis* HÜBNER, 1818, *Spirama* GUENÉE, 1852, *Zethes* RAMBUR, 1833). We regard this character state to be plesiomorphic. The ridges are reduced on the sternites, but not on the tergites (fig. 8b) in many other Catocalinae (*Callistege* HÜBNER, 1823, *Colobochyla* HÜBNER, 1825, *Cortyta* WALKER, 1858, *Drasteria* HÜBNER, 1818, *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, *Thyas* HÜBNER, 1824, *Tyta* BILLBERG, 1820 (tergite-ridge weak)), Acontiinae (*Deltote* REICHENBACH, 1817, *Protodeltote* UEDA, 1984), Sarrothripinae (*Eligma* HÜBNER, 1819, *Risoba* MOORE, 1881, *Nycteola* HÜBNER, 1822), Agaristinae (*Episteme* HÜBNER, 1820, *Eudryas* BOISDUVAL, 1836, *Metagarista* WALKER, 1854), Stictopterinae (*Stictoptera* GUENÉE, 1852) and Plusiinae (*Autographa* HÜBNER, 1821). All "trifine" genera that have been examined have reduced sternal ridges. No sternal ridge and only a weak tergal ridge is found in some Chloephorinae (Earias HÜBNER, 1825,

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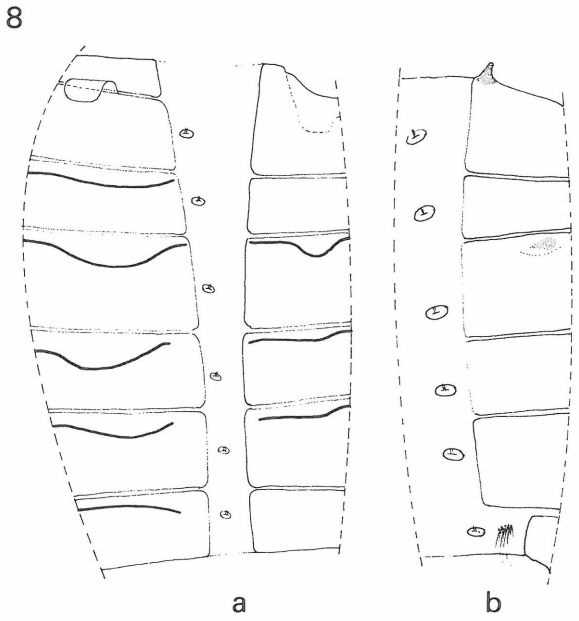

Fig. 8: Abdomen, lateral view to show sclerite ridges. **a.** *Chrysorithrum* BUTLER, 1878 *[amata* (BREMER & GREY, 1853)], **b.** *Thyas* HÜBNER, 1824 [*juno* (DALMAN, 1823)].

Pseudoips HÜBNER, 1822), Pantheinae (*Colocasia* OCHSENHEIMER, 1816), Dilobinae (*Diloba* BOISDUVAL, 1840), Acronictinae (*Acronicta* OCHSENHEIMER, 1816, *Belciades* KOZHANTSHIKOV, 1950, *Craniophora* SNELLEN, 1867, *Cymatophoropsis* HAMPSON, 1894, *Euromoia* STAUDINGER, 1892) and Bryophilinae (*Chytobrya* DRAUDT, 1950, *Cryphia* HÜBNER, 1818).
No examples have been found where the ridges are present on the sternites and absent on the tergites.
More or less reduced ridges on both tergites and sternites occur in some Catocalinae (*Corgatha* WALKER, 1859, *Parascotia* HÜBNER, 1825), Chloephorinae (*Bena* BILLBERG, 1820), Euteliinae (*Eutelia* HÜBNER, 1823) and Nolinae (*Meganola* DYAR, 1898, *Nola* LEACH, 1815).
The "subfamily" Catocalinae displays a great variety of different situations with regard to the presence or absence of ridges on the abdominal segments. This character distribution seems to reflect the heterogeneous nature of this subfamily.

3.6. Anterior abdominal hair-pencils or brush-organs (coremata)

Quite a lot of information is available on pre-abdominal brush-organs in noctuid moths. The most important primary reference is that of BIRCH (1972) and a summary is provided by BIRCH & POPPY (1990). Pre-abdominal brush-organs are apparently widely distributed within the family and are known from 7 conventionally defined subfamilies: Noctuinae, Hadeninae, Cuculliinae, Amphipyrinae (BIRCH, 1972), Acontiinae (KOBAYASHI, 1977), Agaristinae (HAASE, 1887, EDGAR et al., 1979, HOLLOWAY, 1989) and Heliothinae (HOLLOWAY, 1989). According to HAASE (1887), pre-abdominal brush-organs are also found in the Cocytiidae. The usefulness of these brush-organs as a single character for systematic purposes is quite doubtful, because they may be absent or present even in closely related species or species-groups. BIRCH (1972) considered this organ to be confined to the "trifine" noctuids, but this appears not to be correct as it is also found in "quadrifine" noctuids, viz.

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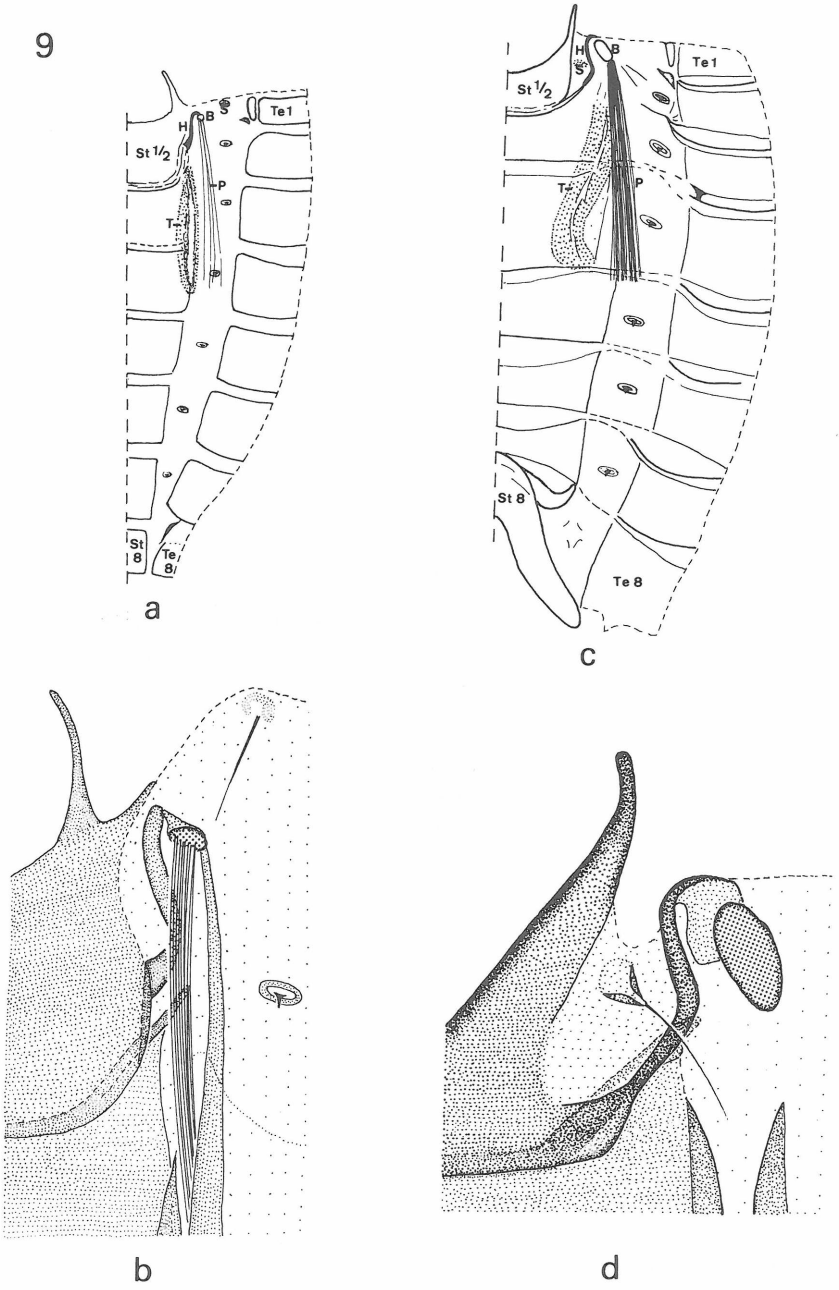

Fig. 9: Pre-abdominal brush organs. **a, c.** Abdomen in lateral view; **b, d** details in higher magnification. Abbreviations: B = basal plate, H = lever, P = brush, S = Stobbe's gland, St = sternite, T = pocket, Te = tergite. - **a, b** Acontiinae (*Pseudeustrotia candidula* ([DENIS & SCHIFFERMÜLLER], 1775)), **c, d.** Agaristinae (*Episteme lectrix* (LINNAEUS, 1764)).

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most Agaristinae and the acontiine *Pseudeustrotia candidula* ([DENIS & SCHIFFERMÜLLER], 1775) (fig. 9). Closer studies may reveal its presence in even more "quadrifine" genera.
The anterior abdominal coremata are highly complicated and possess a specialized "lever-mechanism" consisting of a sclerotized arm, attached by its base to the posterior angle of abdominal sternite 2, which can be moved away from the abdomen by the contraction of specialized muscles. The brush-hairs are fanned out by contraction of a muscle across the basal plate of each brush. A special gland ("Stobbe's gland": STOBBE, 1912, VARLEY, 1962) at the base of the abdomen, consisting of a group of hairs with deeply invaginated secretory bases, produces secretions. The secretions are stored in a cuticular pocket where they are received by a hair-brush and then released when the brush is everted.
The internal construction of the pre-abdominal brush-organs in the subfamilies Acontiinae and Agaristinae was hitherto unknown. It can be shown here that it agrees well with the situation found in the "trifine" noctuids, therefore homology appears to be very likely (fig. 9a to d). The relationship of the Agaristinae and the "trifine" Noctuidae had already been recognized by JORDAN (1912) and HOLLOWAY (1989). BECK (1992) even placed that particular section of the Acontiinae containing Pseudeustrotia with the "trifine" cuculliines, stressing that the larval morphology was a reason for doing so.
The pre-abdominal brush-organ of the Cocytiidae is only known from the description of HAASE (1887). The internal construction is still unknown and so homology remains doubtful. The cocytiides are also candidates for "trifine" relations.

3.7. The morphology of the internal female genitalia

The internal female genitalia have been shown to provide very useful information for the definition of monophyletic groups in a number of Lepidoptera, e.g. Zygaenidae (NAUMANN, 1988), Nymphalidae (SCHADE & NAUMANN, 1990, HÄUSER, 1990). PETERSEN (1900) presented the first comparative study of the internal female genitalia of the Lepidoptera; in the present work the terminology used by HÄUSER (1990) has been adopted. A comparative study of the internal female genitalia, based on the examination of 47 noctuid species, has been published by ROSE & SINGH (1984), and another 150 species have been studied for the present paper. The basic situation of the Ditrysia is not modified in the Noctuidae, but the organs proved to be extremely diverse structurally and may be very useful for defining smaller units within the Noctuidae, such as the Euclidiini (SPEIDEL & NAUMANN, in press), for example.
We illustrate an extreme case of modification in order to show the diversity of the internal female genitalia of the Noctuidae: in the sarrothripine genus *Nycteola* HÜBNER, 1822 (fig. 10) the corpus bursae is almost entirely reduced. Instead there is a huge dilation of the ductus seminalis. Other Sarrothripinae that have been studied do not show this reduction of the corpus bursae.
The Agaristinae, however, have a weak, frequently coiled ductus bursae, a situation which is considered here to represent an autapomorphy of the subfamily. In the Asian species *Episteme lectrix* (LINNAEUS, 1764) (fig. 11), the ductus bursae is narrower than the ductus seminalis, in the African species *Metagarista maenas* (HERRICH-SCHÄFFER, 1853) (fig. 12) it has about the same diameter as the ductus seminalis, and in the American species *Eudryas grata* (FABRICIUS, 1793) (fig. 13) it is comparatively broad, but strongly coiled. The Agaristinae were already known to be a well-defined monophylum by the following more or less convincing synapomorphies: counter-tympanum several times the size of the tympanal membrane, hood very reduced or absent, usually clubbed antennae (KITCHING, 1984). Further evidence for the monophyly of the Agaristinae is the fact that the larvae feed almost exclusively on Vitaceae and Onagraceae (KITCHING, 1984, RABENSTEIN & SPEIDEL, in prep.). The newly discovered autapomorphy augments the arguments for an agaristine monophyly and may be useful in doubtful cases.

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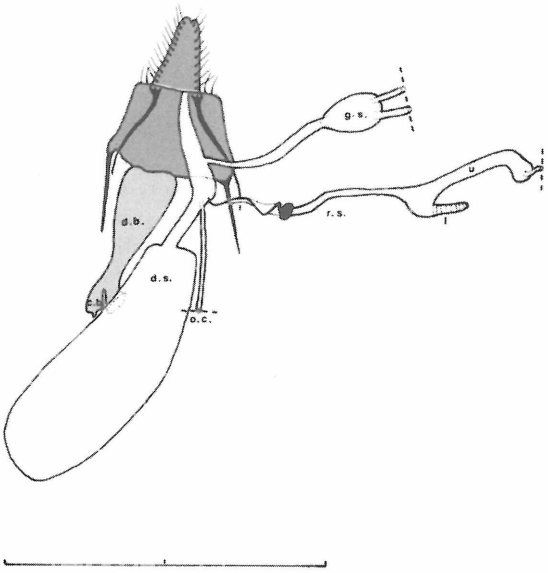

Fig. 10: Female internal genitalia of *Nycteola revayana* (SCOPOLI, 1772). Scale: 2 mm. Abbrev.: b. s. = bulla seminalis, c. b. = corpus bursae, d. b. = ductus bursae, d. s. = ductus seminalis, g. s. = glandulae sebaceae, l = lagena, o. c. = oviductus communis, r. = rectum, r. s. = receptaculum seminis, s. r. = saccus rectalis, u = utriculus

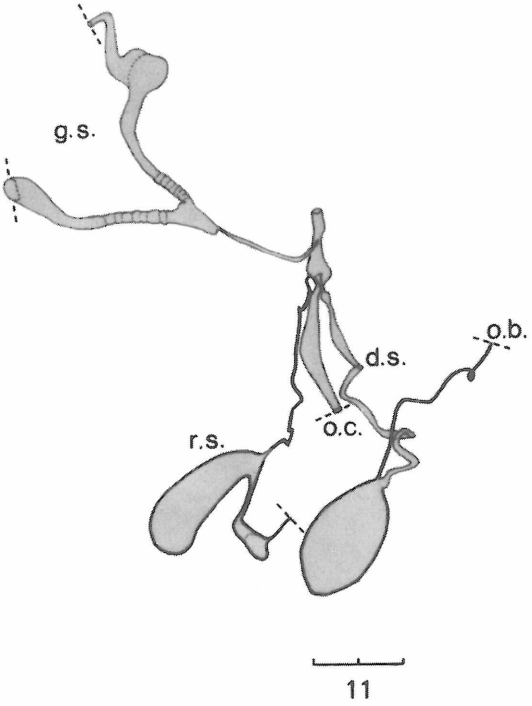

Fig. 11: Female internal genitalia of *Episteme lectrix* (LINNAEUS, 1764). Scale: 2 mm. Abbreviations: c. b. = corpus bursae, d. b. = ductus bursae, d. s. = ductus seminalis, g. s. = glandulae sebaceae, o. b. = ostium bursae, o. c. = oviductus communis, r. s. = receptaculum seminis.

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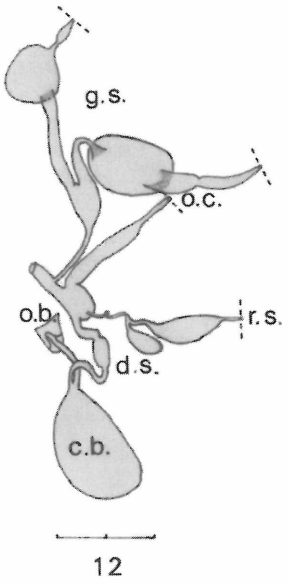

Fig. 12: Female internal genitalia of *Metagarista maenas* (HERRICH-SCHÄFFER, 1853). Scale: 2 mm. Abbreviations: c. b. = corpus bursae, d. s. = ductus seminalis, g. s. = glandulae sebaceae, o. b. = ostium bursae, o. c. = oviductus communis, r. s. = receptaculum seminis.

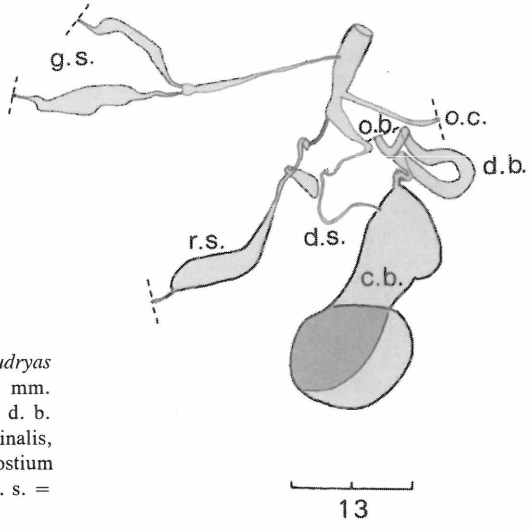

Fig. 13: Female internal genitalia of *Eudryas grata* (FABRICIUS, 1793). Scale: 2 mm. Abbreviations: c. b. = corpus bursae, d. b. = ductus bursae, d. s. = ductus seminalis, g. s. = glandulae sebaceae, o. b. = ostium bursae, o. c. = oviductus communis, r. s. = receptaculum seminis.

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4. Conclusions

The following contribution towards a new classification is proposed, based on the evidence presented above.

(1) The Camptolominae, Chloephorinae, Sarrothripinae and Nolinae form a monophyletic group. The Camptolominae have to be considered as an independent subfamily which may form the sister-group of the remaining three taxa.

(2) The Bryophilinae form part of the higher noctuids ("trifine" Noctuidae) because of the identical submicroscopical structure of the proboscis tip. The Acronictinae and Pantheinae also belong here (BÖRNER, 1949). This hypothesis remains to be verified in a broader study.

(3) It has been confirmed that the Agaristinae represent a monophylum and are correctly associated with the "trifine" Noctuidae, with which they share the presence of a pre-abdominal brush-organ.

(4) The monophyly of the Acontiinae cannot be confirmed. The section containing Pseudeustrotia can also be associated with the higher "trifine" Noctuidae, with which it shares an identical condition of the pre-abdominal brush-organ. The group founded on the primary presence of a pre-abdominal brush-organ, though certainly monophyletic, cannot be defined exactly, as pre-abdominal brush-organs have very often been reduced (homoplasy). Therefore, further autapomorphic characters are needed in order to define a more comprehensive group, including the "trifine" noctuids, the Agaristinae and parts of the Acontiinae.

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