

A review of the higher classification of the Noctuoidea (Lepidoptera) with special reference to the Holarctic fauna

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Abstract

The higher classification of the Noctuoidea (Oenosandridae, Doidae, Notodontidae, Strepsimanidae, Nolidae, Lymantriidae, Arctiidae, Erebiidae, Micronoctuidae, and Noctuidae) is reviewed from the perspective of the classification proposed by KITCHING and RAWLINS (1998). Several taxa are reinstated, described as new, synonymised, or redescribed. Some characters that have been inadequately described, poorly understood, or misinterpreted, are redescribed and discussed. One family, two subfamilies, four tribes, and three subtribes are proposed as new. Available family-group names of Noctuoidea are listed in an appendix.

Introduction

Since 1991 the authors have worked towards a trans-Atlantic / trans-Beringian understanding or agreement between the two sometimes quite incongruent classifications of the Noctuidae used in North America and Eurasia. The necessity to push this work forward and publish our results to date has been precipitated by the need for a new European check list, for the book series Noctuidae Europaeae, and for use in fascicles in the "Moths of North America (MONA)" book series in North America. When Hermann HACKER and the senior author decided to publish a new systematic list for the Noctuoidea in Europe, we agreed to write this review paper as a supplement to the European list so that changes in the higher classification of the Noctuidae, both published and unpublished could be incorporated into the new list.

The main reasons for both this paper and a new European list for the Noctuoidea are the many and dramatic changes in the classification of the Noctuoidea that have been proposed for the superfamily by POOLE (1995), KITCHING and RAWLINS (1998), BECK (1999–2000), fascicles in the MONA series, and in Noctuidae Europaeae, and because of the major differences in classification between the current North American check list (FRANCLEMONT and TODD, 1983) and European check lists (FIBIGER and HACKER, 1991; BECK, 1999; and FIBIGER and SKULE, 2004). The development of a more congruent classification on a holarctic level with more defensible monophyletic groupings is aided by the more standardised use of genitalic structures including everted vesicae and expanded corpus bursae, intensified larval studies, new characters of the adult morphology (e.g., JACOBSEN and WELLER, 2002), and molecular studies (MITCHELL et al., 1997, 2000).

Although we know that this will not be the final word in the higher classification of the Noctuoidea, we present this contribution in order to synthesise our results with earlier morphological data and current molecular data to help alleviate the current state of confusion and in this way to contribute to a consensus classification between Eurasia and North America. A full study of the fauna from the southern hemisphere will undoubtedly result in new higher taxa being added and inserted into this classification.

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Historical perspective

Our starting point for this review is the reclassification of the Noctuoidea by KITCHING and RAWLINS (1998), which for the first time made extensive use of character systems of both the adults and immature stages in presenting the most thoroughly defended and comprehensive reclassification of the superfamily since HAMPSON'S world catalogue (1898–1913). The main departures from other classifications (in particular from the subfamilies and tribes defined by POOLE, 1995) for the trifold noctuids, were: 1) the moving of the Lymantriidae, Nolidae, and Arctiidae to a position after the Noctuidae, thus removing them widely from the quadrifid noctuids (e.g., Catocalinae *sensu lato*) with which they share numerous characters (discussed below); 2) the removal of the Nolinae, Sarrothripinae, Chloephorinae, and Eariadinae from the Noctuidae and treating them as subfamilies of the family Nolidae, which was associated with the Arctiidae; 3) the removal of the Pantheinae from the Noctuidae and treating them as the family Pantheidae, which was associated with the Lymantriidae; 4) the splitting of the Calpinae from the Catocalinae; 5) the raising of the tribes Raphini, Ufeini, and Glottulini to subfamily status; 6) the removal of POOLE'S (1995) tribes Grotellini, Nocloini, and Azenini from the Psaphidinae and treating them as tribes of the Stiriinae, and the Triocnemidini from the Psaphidinae and synonymising it with the Oncocnemidinae, which was treated as a tribe of the Cuculliinae rather than as a separate subfamily; 7) a major new concept of the subfamily Hadeninae by combining the subfamilies Hadeninae (except the Glottulinae), the Amphipyriinae (*sensu* FRANCLEMONT and TODD, 1983) (except *Amphipyra*, the Condicinae, and the Stiriinae), the Ipimorphinae (*sensu* FIBIGER and HACKER, 1991), the Xylenini (from the Cuculliinae), the subfamily Eriopinae (*sensu* POOLE, *op. cit.*) and tribe Phosphilini (which POOLE included as a tribe of his redefined Amphipyriinae); and 8) the reinstatement of a restricted Noctuinae *sensu stricto*, which was treated as distinct from the Hadeninae.

We have followed the majority of the changes in classification and many of the sequences of the subfamilies and tribes proposed by KITCHING and RAWLINS (1998) except for the following:

- 1 we place the arctiid group of families (Nolidae, Arctiidae, and Lymantriidae) in front of the upgraded family Erebidae so that their close relationship with the "quadrifids" is better reflected;
- 2 we move the Lymantriidae from a position in front of the Nolidae to a position after the Arctiidae to reflect the close association of the arctiids and lymantriids following MITCHELL *et al.* (1997, 2000);
- 3 we treat the quadrifid subfamilies (Hermiinae, Hypenodinae, Hypeninae, Catocalinae, Calpinae, Hypeninae, Stictopterinae, and Euteliinae) as subfamilies of the reestablished family Erebidae and as the sister group to the arctiid families and reinstate the subfamily Rivulinae following FIBIGER and HACKER (1991), SPEIDEL *et al.* (1996a), and BECK (1999–2000), the subfamilies Boletobiinae and Phytometrinae following BECK (1999–2000), and the subfamilies Scolecocampinae and Erebininae on the basis of data presented below; the Hypenodinae is reinstated for *Hypenodes* DOUBLEDAY and its relatives, and the name Strepsimaninae is treated as the family Strepsimanidae;
- 4 we revise the classification of the subfamilies Catocalinae, Calpinae, and Erebininae on the basis of GOATER *et al.* (2003) and new information presented below, move the Armadini and Aediini from the Catocalinae to the Acontiinae, and move the Tytini from the Catocalinae into the subfamily Metoponiinae of the Noctuidae;
- 5 following FIBIGER and HACKER (2002, 2004) we remove the tribe Eublemini from the Eustrotiinae and treat it as a primitive subfamily of the Erebidae;
- 6 Araeopteroninae FIBIGER is proposed as a new subfamily of the Erebidae;
- 7 a new family, Micronoctuidae FIBIGER is proposed.
- 8 we reinstate the Pantheinae as a subfamily of the Noctuidae near the Acronictinae on the basis of molecular research by MITCHELL *et al.* (1997, 2000) and YELA and KITCHING (1999);
- 9 we remove the tribe Eriopini from Hadeninae (*s. l.*) and treat it as a subfamily of the Noctuidae;
- 10 we remove the tribe Phosphilini from the Hadeninae (*s. l.*) and move it to the Psaphidinae next to the Nocloini;
- 11 we revise the classification of the Hadeninae *sensu* KITCHING and RAWLINS (1998) into subfamilies, tribes and subtribes;
- 12 we review the classification of the Noctuinae on the basis of LAFONTAINE and FIBIGER (2004) and review the subtribes of the Noctuiini.

The changes from KITCHING and RAWLINS (1998) and SPEIDEL and NAUMANN (2005) and newly introduced changes discussed below are reflected in the new European check list of Noctuoidea (FIBIGER and HACKER, 2005, this volume of *Esperiana*). Groups where no changes in higher classification are proposed are not discussed further, but for reference a list of all recognised families, subfamilies, and tribes is given below. The authorship of the new taxa varies.

Classification of Noctuoidea

The list of families, subfamilies, and tribes is taken from KITCHING and RAWLINS (1998) with our proposed modifications to the classification of the Noctuoidea. Taxa found in Europe are denoted with an asterisk*; those occurring in North America are shown with two asterisks**.

Cladograms depicting the possible relationships of the Noctuoidea, Erebidae, and Noctuidae discussed in the text are given on pages 14 and 15.

Superfamily **Noctuoidea** LATREILLE, 1809 * **

Family **Oenosandridae** MILLER, 1991

Family **Doidae** DONAHUE and BROWN, 1987 **

Family **Notodontidae** STEPHENS, 1829 * **

Subfamily **Thaumetopeinae** AURIVILLIUS, 1889 *

Subfamily **Pygaerinae** DUPONCHEL, [1845] * **

Subfamily **Platychasmatinae** NAKAMURA, 1956 *

Subfamily **Notodontinae** STEPHENS, 1829 * **

Tribe **Notodontini** STEPHENS, 1829 * **

Tribe **Dicranurini** DUPONCHEL, [1845] * **

Subfamily **Phalerinae** BUTLER, 1886 * **

Subfamily **Dudusiinae** MATSUMURA, 1925 **

Tribe **Dudusiini** MATSUMURA, 1925 **

Tribe **Scranciini** MILLER, 1991

Subfamily **Hemiceratinae** GUENÉE, 1852 **

Subfamily **Heterocampinae** NEUMOGEN and DYAR, 1894 * **

Subfamily **Nystaleinae** FORBES, 1948 **

Subfamily **Dioptinae** WALKER, 1862 **

Family **Nolidae** BRUAND, 1846 * **

Subfamily **Nolinae** BRUAND, 1846 * **

Subfamily **Chloephorinae** STANTON, 1859 * **

Tribe **Chloephorini** STANTON, 1859 *

Tribe **Sarrothripini** HAMPSON, 1894 * **

Tribe **Camptolomini** MELL, 1943

Tribe **Careini** MOORE, 1883

Tribe **Ariolicini** MELL, 1943

Subfamily **Westermanniinae** HAMPSON, 1918

Subfamily **Eariadinae** HAMPSON, 1912 *

Subfamily **Bleninae** MELL, 1943

Subfamily **Risobinae** MELL, 1943 **

Subfamily **Collomeninae** KITCHING and RAWLINS, 1998 **

Subfamily **Afridinae** KITCHING and RAWLINS, 1998 **

Subfamily **Eligminae** MELL, 1943

Family **Strepsimanidae** MEYRICK, 1930, **stat rev.**

Family **Arctiidae** LEACH, [1815] * **

Subfamily **Lithosiinae** BILLBERG, 1820 * **

Tribe **Phryganopterygini** BENDIB and MINET, 1999

Tribe **Acsalini** BENDIB and MINET, 1999 **

Tribe **Eudesmiini** BENDIB and MINET, 1999 **

Tribe **Cisthenini** BENDIB and MINET, 1999 **

Tribe **Nudariini** BÖRNER, 1920

Tribe **Endrosini** BÖRNER, 1932

Tribe **Lithosiini** BILLBERG, 1820 * **

Subfamily **Syntominae** HERRICH-SCHÄFFER, [1846] *

Tribe **Syntomini** HERRICH-SCHÄFFER, [1846] *

Tribe **Thyretini** BUTLER, 1876 *

Subfamily **Arctiinae** LEACH, [1815] * **

Tribe **Arctiini** LEACH, [1815] * **

Tribe **Callimorphini** WALKER, [1865] * **

Tribe **Phaegopterini** KIRBY, 1892 **

Tribe **Pericopini** WALKER, [1865] **

Tribe **Ctenuchini** KIRBY, 1837 **

Tribe **Euchromiini** BUTLER, 1876 **

Family **Lymantriidae** HAMPSON, [1893] * **

Subfamily **Lymantriinae** HAMPSON, [1893] * **

Tribe **Lymantriini** HAMPSON, [1893] * **

Tribe **Orgyiini** WALLENGREN, 1861 * **

Tribe **Arctornithini** HOLLOWAY, 1999

Tribe **Leucomini** GROTE, 1895 * **

Tribe **Nygmiiini** HOLLOWAY, 1999

Family **Erebidae** LEACH, [1815] * ** **stat. rev.**

Subfamily **Rivulinae** GROTE, 1895 * ** **stat. rev.**

Subfamily **Boletobiinae** GROTE, 1895 * ** **stat. rev.**

Subfamily **Hyenodinae** FORBES, 1954 * ** **stat. rev.**

Subfamily **Araeopteroninae** FIBIGER, 2005 * ** **subfam. nov.**

Subfamily **Eublemminae** FORBES, 1954 * ** **stat. rev.**

Tribe **Eublemmini** FORBES, 1954 * ** **stat. rev.**

Tribe **Pangraptini** GROTE, 1882 * ** **stat. rev.**

Subfamily **Herminiinae** LEACH, [1815] * **

Subfamily **Scolecocampinae** GROTE, 1883 * ** **stat. rev.**

Subfamily **Hypeninae** HERRICH-SCHÄFFER, [1851] * **

Subfamily **Phytometrinae** HAMPSON, 1913 * ** **stat. rev.**

Subfamily **Aventiinae** TUTT, 1896 * **stat. rev.**

Subfamily **Erebinae** LEACH, [1815] * ** **stat. rev.**

Tribe **Erebini** LEACH, [1815] * ** **stat. rev.**

Tribe **Arcteiini** BERIO, 1992 **stat. rev.**

Subfamily **Calpinae** BOISDUVAL, 1840 * **

Tribe **Anomini** GROTE, 1882 * **

Tribe **Calpini** BOISDUVAL, 1840 * **

Tribe **Scoliopterygini** HERRICH-SCHÄFFER, [1852] * ** **stat. rev.**

Tribe **Anobini** WILTSHIRE, 1990 (**nomen nudum**, needs validation)

Subfamily **Catocalinae** BOISDUVAL, [1828] * **

Tribe **Toxocampini** GUENÉE, 1852 * ** **stat. rev.**

Tribe **Acantholipini** FIBIGER and LAFONTAINE, 2005 * **tribe nov.**
(nomen nov. for Acantholipini GOATER, RONKAY and FIBIGER, 2003, unavailable, not explicitly validated). (= **Acantholipini** WILTSHIRE, [1977], **nomen nudum**)

Tribe **Arytrurini** FIBIGER and LAFONTAINE, 2005 * **tribe nov.**
(nomen nov. for Arytrurini GOATER, RONKAY and FIBIGER, 2003, unavailable, not explicitly validated)

Tribe **Hypocalini** GUENÉE, 1852 * ** **stat. rev.**

Tribe **Melipotini** GROTE, 1895 * ** **stat. rev.**
 (= **Synedini** FORBES, 1954, **syn. nov.**)

Tribe **Euclidiini** GUENÉE, 1852 * ** **stat. rev.**
 (= **Ectypini** GOATER, RONKAY and FIBIGER, 2003, **unavailable**)

Tribe **Panopodini** FORBES, 1954 * ** **stat. rev.**

Tribe **Ophiusini** GUENÉE, 1837 * **
 (= **Omopterini** BOISDUVAL, 1833, **syn. nov.** (suppr. senior syn.))

Tribe **Catocalini** BOISDUVAL, [1828] * ** **stat. rev.**

Subfamily **Aganainae** BOISDUVAL, 1833

Subfamily **Cocytinae** BOISDUVAL, 1874

Subfamily **Stictopterinae** HAMPSON, 1894 * **

Subfamily **Euteliinae** GROTE, 1882 * **

Family **Micronoctuidae** FIBIGER, 2005 * **fam. nov.**

Family **Noctuidae** LATREILLE, 1809 * **

Subfamily **Plusiinae** BOISDUVAL, [1828] * **

Tribe **Abrostolini** EICHLIN and CUNNINGHAM, 1978 * **

Tribe **Argyrogrammatini** EICHLIN and CUNNINGHAM, 1978 * **

Tribe **Plusiini** BOISDUVAL, [1828] * **

Subtribe **Autoplusiina** KITCHING, 1987 * **

Subtribe **Euchalcina** CHOU and LU, 1979 * **

Subtribe **Plusiina** BOISDUVAL, [1828] * **

Subfamily **Eustrotiinae** GROTE, 1882 * **

Subfamily **Bagisarinae** CRUMB, 1956 * **

Tribe **Bagisarini** CRUMB, 1956 * **

Tribe **Cydosiini** KITCHING and RAWLINS, 1998 ** **stat. rev.**

Subfamily **Acontiinae** GUENÉE, 1841 * **

Tribe **Hypercalymniini** FIBIGER and LAFONTAINE, 2005 **tribe nov.**

Tribe **Acontiini** GUENÉE, 1841 * **

Tribe **Armadini** WILTSHIRE, 1961 * **stat. rev.**

Tribe **Aediini** BECK, 1960 * **stat. rev.**

Subfamily **Pantheinae** SMITH, 1898 * **

Subfamily **Dilobinae** AURIVILLIUS, 1889 *

Subfamily **Diphtherinae** FIBIGER and LAFONTAINE, 2005 ** **subfam. nov.**

Subfamily **Raphiinae** BECK, 1996 * **

Subfamily **Acronictinae** HEINEMANN, 1859 * **

Subfamily **Metoponiinae** HERRICH-SCHÄFFER, [1851] *

Subfamily **Sinocharinae** SPEIDEL, FÄNGER, and NAUMANN, 1996

Subfamily **Lophonyctinae** SPEIDEL, FÄNGER, and NAUMANN, 1996

Subfamily **Agaristinae** HERRICH-SCHÄFFER, [1858] **

Subfamily **Eucocytiinae** HAMPSON, 1918

Subfamily **Cuculliinae** HERRICH-SCHÄFFER, [1850] * **

Subfamily **Oncocnemidinae** FORBES and FRANCLEMONT, 1954 * **

Subfamily **Amphipyridae** GUENÉE, 1837 * **

Subfamily **Psaphidinae** GROTE, 1896 * **

Tribe **Psaphidini** GROTE, 1896 * **

Tribe **Feraliini** POOLE, 1995 * **

Tribe **Noclouini** POOLE, 1995 **

Tribe **Phosphilini** POOLE, 1995 ** **stat. rev.**

Tribe **Triocnemidini** POOLE, 1995 **

Subfamily **Stiriinae** GROTE, 1882 **

Tribe **Stiriini** GROTE, 1882 **

Tribe **Grotellini** POOLE, 1995 **

Tribe **Azenini** POOLE, 1995 **

Subfamily **Heliolithinae** BOISDUVAL, [1828] * **

Subfamily **Condicinae** POOLE, 1995 * **

Tribe **Condicini** POOLE, 1995 * **

Tribe **Leuconyctini** POOLE, 1995 **

Subfamily **Eriopinae** HERRICH-SCHÄFFER, [1851] * ** **stat. rev.**

Subfamily **Bryophilinae** GUENÉE, 1852 * **

Subfamily **Xyleninae** GUENÉE, 1837 * **

Tribe **Balsini** GROTE, 1896 **

Tribe **Pseudeustrotiini** BECK, 1996 * **

Tribe **Prodeniini** FORBES, 1954 * **

Tribe **Elaphriini** BECK, 1996 * **

Tribe **Caradrinini** BOISDUVAL, 1840 * **

Subtribe **Caradrinina** BOISDUVAL, 1840 * **

Subtribe **Athetina** FIBIGER and LAFONTAINE, 2005 * ** **subtribe nov.**

Tribe **Cosmiini** GUENÉE, 1852 * **

Tribe **Dypterygiini** FORBES, 1954 * **

Tribe **Actinotiini** BECK, 1996

- Tribe **Phlogophorini** HAMPSON, 1918 * **
- Tribe **Apameini** GUENÉE, 1841 * **
 - (= Nonagriini GUENÉE, 1837, **suppressed senior syn.**)
 - Subtribe **Oxytrypiina** GOZMANY, 1970 *
 - Subtribe **Apameina** GUENÉE, 1841 * **
 - Subtribe **Sesamiina** FIBIGER and GOLDSTEIN, 2005 * **subtribe nov.**
 - Subtribe **Arzamina** GROTE, 1883 **
- Tribe **Episemini** GUENÉE, 1852 *
- Tribe **Xylenini** GUENÉE, 1837 * **
 - Subtribe **Xylenina** GUENÉE, 1837 * **
 - Subtribe **Antitypina** FORBES and FRANCLEMONT, 1954 * **
- Subfamily **Ufeinae** CRUMB, 1956 **
- Subfamily **Hadeninae** GUENÉE, 1837 * **
 - Tribe **Orthosiini** GUENÉE, 1837 * **
 - Tribe **Tholerini** BECK, 1996 * ** **stat. rev.**
 - Tribe **Hadenini** GUENÉE, 1837 * **
 - Tribe **Leucaniini** GUENÉE, 1837 * **
 - Tribe **Eriopygini** FIBIGER and LAFONTAINE, 2005 * ** **tribe nov.**
 - Tribe **Glottulini** GUENÉE, 1852 * **
- Subfamily **Noctuinae** RAMBUR, 1848 * **
 - Tribe **Agrotini** RAMBUR, 1848 * **
 - Subtribe **Austrandesina** ANGULO and OLIVARES, 1990 * **
 - Subtribe **Agrotina** RAMBUR, 1848 * **
 - Tribe **Noctuini** LATREILLE, 1809
 - Subtribe **Axyliina** FIBIGER and LAFONTAINE, 2005 * ** **subtribe nov.**
 - Subtribe **Noctuina** LATREILLE, 1809 * **

Description of Principal Characters

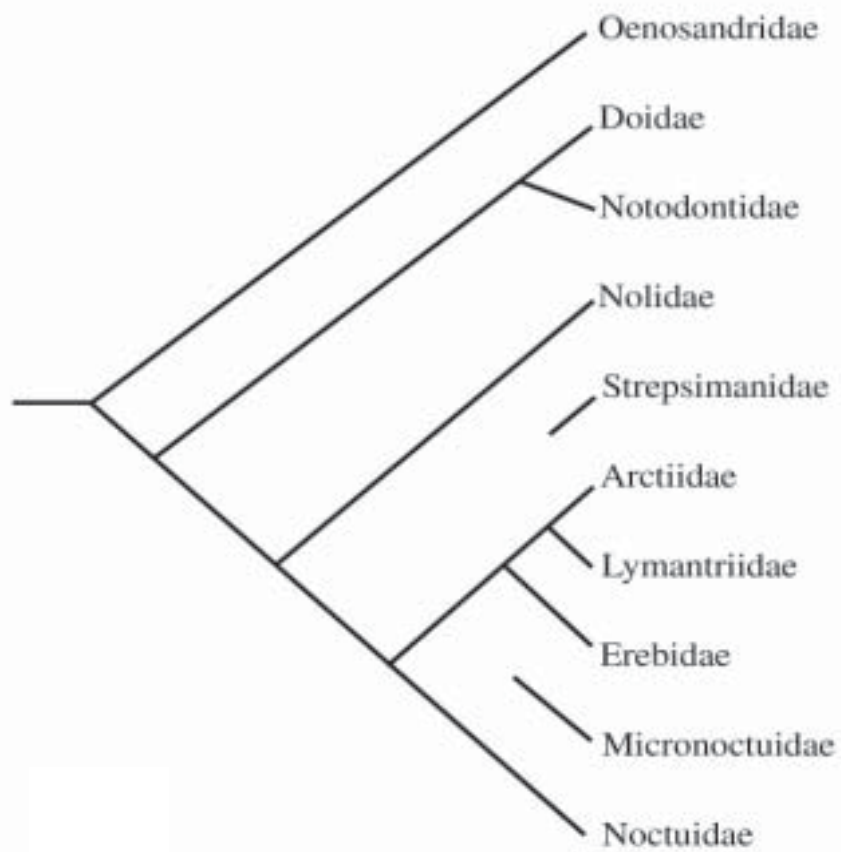
Many of the structural characters presented here and used in classification of the Noctuoidea at the family, subfamily, and tribal level are not commonly used by Lepidopterist's because they are not the type of characters commonly used for identification (e.g., wing shape or pattern, antennal structure, eye size, etc.).

The purpose of this and other classifications are to group species into progressively larger, natural units so that the classification is a predictive hypothesis of relationship, distribution of structural characters, and biological attributes. Generating a classification is not the same process as generating identification aids, so it is not incongruent that a tribe could be defined on the basis of larval characteristics and a closely related tribe be defined on the basis of female genitalia.

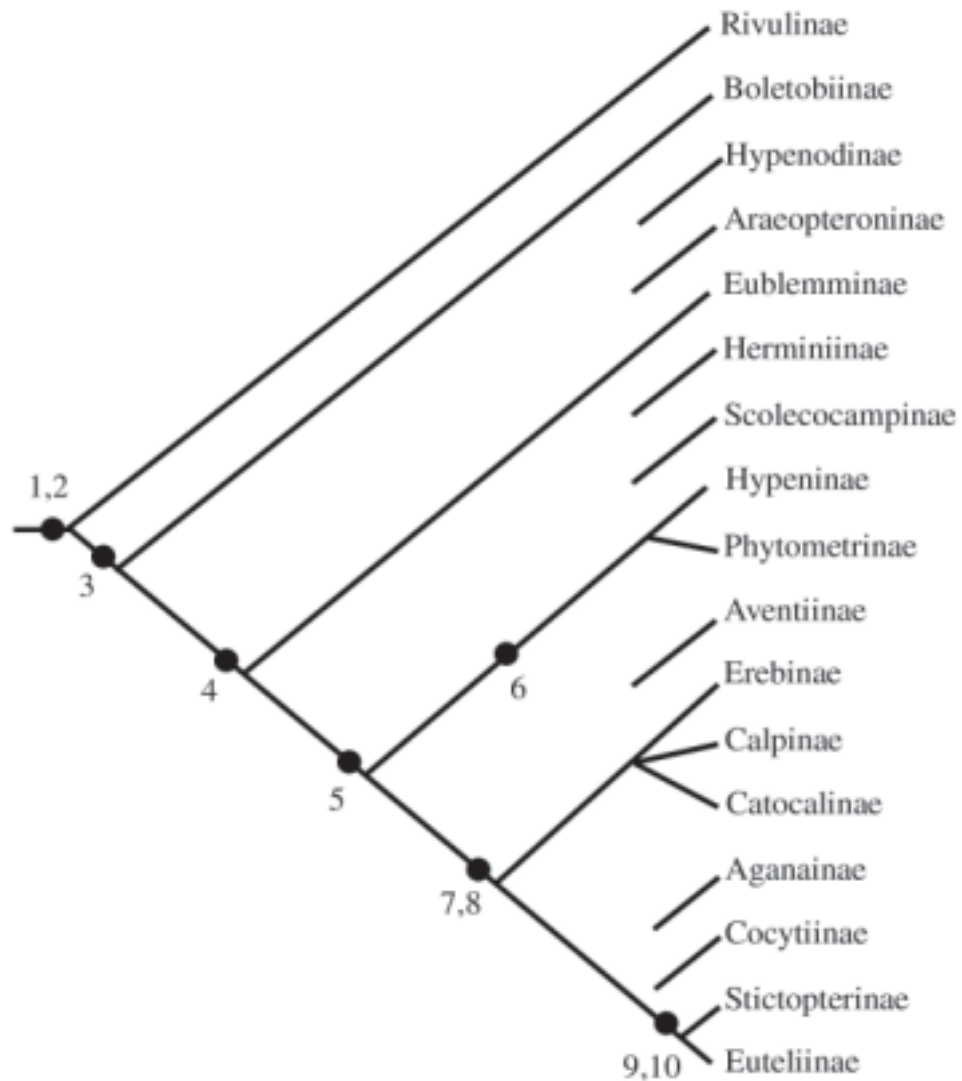
Many characters are useful for identification but are too scattered in their distribution to be of significance for higher classification. For example, a tuberculate frons in a wide array of forms develops in many groups associated with xeric habitats. Similarly, variations in antennal form are widespread, such as broadly bipectinate antennae, which are particularly widespread among genera with adults that fly in cold conditions such as in the early spring or late fall, or on high mountains.

Many of the character systems that we have used may be unfamiliar, some are interpreted in different ways in different works, and some have not previously been used, so we briefly describe some of the more complex characters that we use.

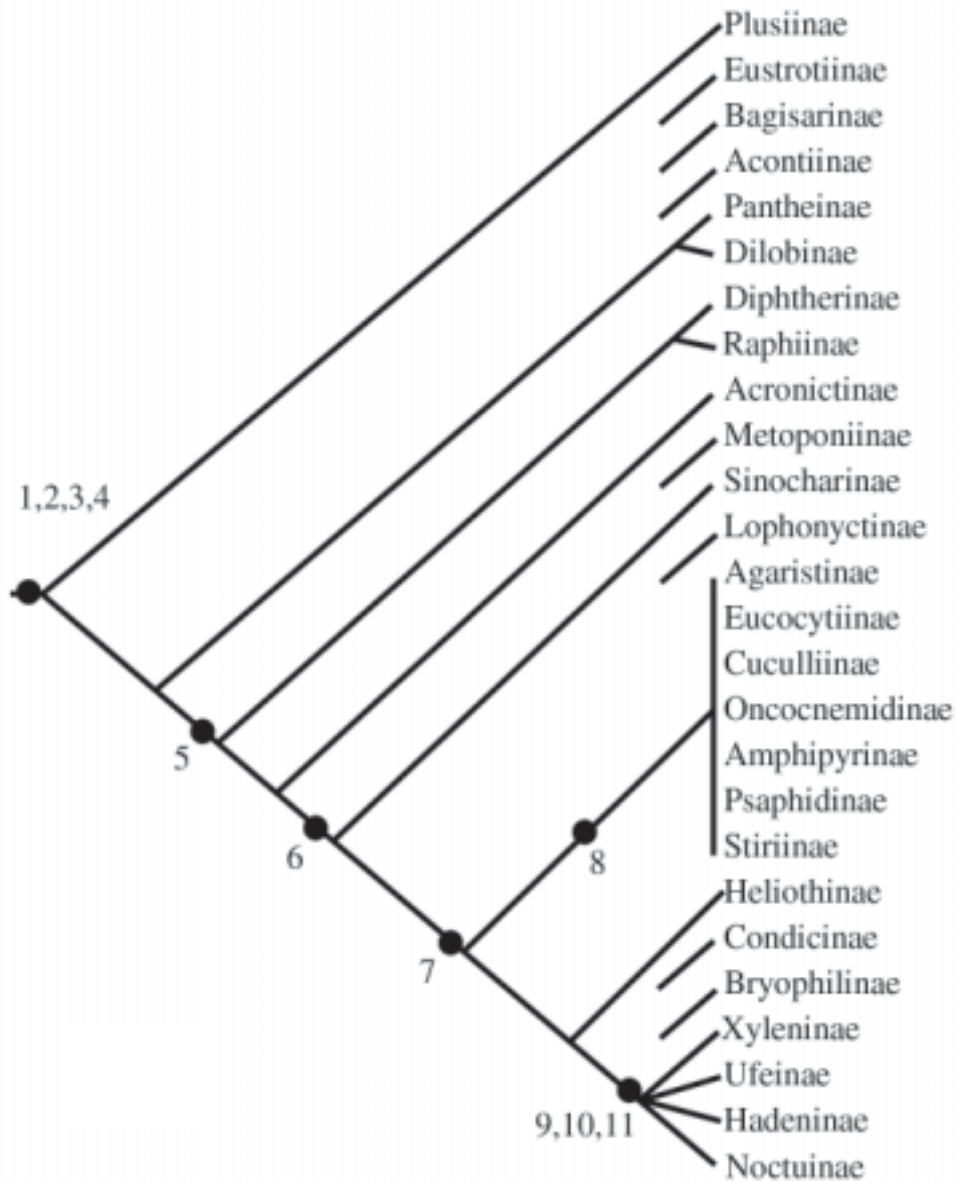
The terms "**quadrifid noctuids**" (or "quadrifids") and "**trifid noctuids**" (or "trifids") have a long history in the literature to refer to those noctuid subfamilies that have either a quadrifid hindwing venation, (i.e., the Catocalinae and their relatives in which vein M2 in the hindwing is strong and is positioned in the lower part of the cell so that the cubital vein appears to have four branches), or a trifid hindwing venation in which vein M2 is reduced or absent. We are proposing to use the family group name Erebidae for the subfamilies generally called "quadrifid noctuids" and restrict the family Noctuidae to the trifids, so we use the terms Noctuidae, noctuids, and "trifid noctuids" to refer to the redefined family Noctuidae *sensu stricto*, and the terms Erebidae, erebids, and "quadrifids" for the group of subfamilies that now constitute the family Erebidae, recognising that the term "quadrifid hindwing" can also include members of the families Nolidae, Strepsimanidae, Arctiidae, and Lymantriidae, most of which also have a quadrifid hindwing venation. A list of character states that define the two families is given below.



Cladogram 1. Cladogram of the families of the Noctuoidea.



Cladogram 2. Cladogram of the subfamilies of the Erebidae. Numbers refer to character systems of major clades discussed in text (characteristics of subfamilies are given in text): 1, spinneret with apical flaps; 2, scaphium sclerotised; 3, larvae mainly on fungi (except Araeopteroninae and Eublemininae); 4, lower frons bare; 5, larvae on vascular plants; 6, palpi beak or snout-like; 7, pleurite fused to tegumen, 8, vein M2 adjacent to M3; 9, double tympanal hood; 10, female frenulum to single seta.



Cladogram 3. Cladogram of the subfamilies of the Noctuidae. Numbers refer to character systems of major clades discussed in text (characteristics of subfamilies are given in text): 1, bullae fused (reversed in Pantheinae and Diphtherinae); 2, scaphium generally membranous (sometimes with lateral bars); subscaphium sclerotised; 3, HW with M2 reduced; 4, post. apophyses with broader pre-apical plate; 5, tympanum with raised nodular sclerite; 6, basal abdominal brushes and pockets (frequently lost); 7, valve with corona (frequently lost); 8, larvae with lateral line bordering anal plate; 9, larval spinneret flattened; 10, larval seta SD1 on A9 hairlike; 11, clasper in center of valve connected to apex of sacculus by rod.

Ocelli

Ocelli is the small eye above the compound eyes and next to the base of the antennae. Its presence and absence is of significant importance in systematics throughout the lepidoptera. In the Noctuoidea they are generally present, but absent in Lymantriidae and in the erebid subfamily Hyphenodinae. We have studied this character and found that several genera, species-groups and species, which had been thought to lack ocelli, actually have ocelli – though only small or vestigial, resulting in more confident placement of several taxa. These are mentioned in the text.

Further it seems that the position of the ocelli (i.e., close to the base of the antennae, or some distance from the antennae) may be an important character with systematic information, but the variation was noticed too late to be considered here.

Wing venation

The trifold forewing configuration of the notodontid group of families, versus the quadrifid forewing of the arctiid-noctuid group of families is described fully by KITCHING and RAWLINS (1998) and will not be discussed further.

The quadrifid versus trifold hindwing configuration, however, has been the subject of much discussion and much confusion. The common but incorrect assumption is that in all quadrifids (Catocalinae, Hypheninae, Herminiinae, etc.) vein M2 is similar in thickness to the other veins and arises in the lower part of the cell close to the branch of veins M3 and CuA1 (and distal to CuA2) so that the cubital stem appears to have four branches and thus appears “quadrifid” (Fig. 2); whereas in trifold noctuids vein M2 arises at the middle of the cell and is usually reduced or absent so that the cubital stem appears to have only three branches and thus appears “trifold.”

We have examined wing preparations of more than 140 genera of erebids and noctuids and find that most “trifolds” have vein M2 in the “quadrifid” position in that the vein is near the middle of the cell on the wing margin but bends downward as it approaches the cell so that the vein meets the cell 2/3 of the way down the cell toward vein M3; however, it is reduced (Fig. 9) in most groups of “trifolds,” but in some groups it is almost as thick as M3 (e.g., *Panthea*, Fig. 8) and sometimes vestigial or absent (e.g., *Peridroma*, Fig. 10). In fact the reported variation in the position of M2 in the Noctuidae s.s. is not nearly as great as the literature would suggest. We have found that the position of vein M2 is fairly constant in the Noctuidae s.s. with most variation being in its thickness. What appears to be the vestiges of vein M2 near the middle of the cell in most trifolds is a fold in the hindwing membrane, but vein M2 meets the cell well below the middle. Frequently it is visible only by clearing the hindwing and staining it. In this interpretation, the “slightly quadrifid hindwing” (vein M2 meeting the cell about 1/3 of the way up the cell) is a derived condition of the entire arctiid-erebid-noctuid lineage (but plesiomorphic within the lineage) with a reduction in vein M2 being characteristic (a further derived character state) of the Noctuidae sensu stricto. The so-called anomalous “quadrifid” hindwing venation in “trifold” groups such as the Plusiinae, Pantheinae, Stiriinae, and some Acontiinae is not the result of a change in the position of the vein as much as its strength (although it is near the lower margin of the cell in some Pantheinae and Raphiinae). In these groups the vein is only slightly reduced, creating the “quadrifid” impression but the vein is reduced compared with the thickness of M3 in almost all groups (the genus *Grotella* HARVEY (Stiriinae) and *Aon* NEUMOEGEN (Raphiinae) are exceptions). The relative thickness of M2 in basal groups of Noctuidae, such as the Plusiinae and Pantheinae, might be a primitive configuration of the veins, whereas a stronger M2 in the Stiriinae and Condicinae is probably a reversal. The presence of M2 in the middle of the cell and continuous with the vestigial vein in the cell, such as in the Agaristinae and Heliothinae, is also probably a reversal. The most variable group of trifolds in terms of the hindwing venation is the subfamily Eustrotiinae (see below under the Eustrotiinae), but this probably is a reflection of the polyphyletic composition of the subfamily.

The more primitive erebid (“quadrifid”) subfamilies (Rivulinae, Hyphenodinae, Herminiinae, Eubleminae, Hypheninae) have the same configuration (Fig. 1) as most noctuids (“trifolds”) in that vein M2 arises about 2/3 of the way down the cell but it differs from the noctuids in that vein M2 is as thick as vein M3, not reduced as in the noctuids. In these groups vein M2 is parallel to M3 for most of its length. Seven subfamilies (Erebinae, Calpinae, Catocalinae, Aganainae, Coccytiinae, Stictopterinae, and Euteliinae) depart from this pattern in that vein M2 bends down towards M3 much more sharply and meets the cell 80–90 % of the distance down the cell (Fig. 2) so that the “quadrifid” appearance is much more pronounced. This modification of vein M2 is taken even further in the arctiid families (Arctiidae and Lymantriidae) where vein M2 bends down to meet M3 at the base of the cell, or even fuses with the base of M3 (Fig. 3), suggesting the possibility that the arctiid line is not a “primitive” clade but could be a highly specialised lineage derived from within the Erebidae much like the butterflies are a highly modified group of Macrolepidoptera. If this interpretation is validated then the Erebidae would be paraphyletic with respect to the arctiid clade and either the Erebidae would have to be divided into several families to render

them monophyletic, or they would have to be treated as subfamilies of an expanded Arctiidae. The transverse vein defining the outer edge of the hindwing cell (often reduced or vestigial) is straight (or close to straight) in the Erebiidae and Noctuidae, but it is angled 90°–110° in the Strepsimanidae (Fig. 6), Arctiidae (Fig. 3), and Lymantriidae.

The new family Micronoctuidae has a highly reduced venation in fore- and hindwings with the hindwing being “bifid” (Fig. 7) (see under Micronoctuidae). A somewhat similar hindwing venation is in some Lithosiinae where veins M2 and M3 are stalked (Fig. 4).

Leg structure

Leg structure has long been used to define groups in the Noctuoidea, especially in the Noctuidae and Erebiidae. The main structures can be grouped into four categories: **1**, the relative length of the tibial spurs; **2**, the presence of brushes and other similar sexually associated modifications to the legs; **3**, modifications to the apex of the foretibia; and **4**, sclerotised spine-like (spiniform) setae on the tibiae and additional rows of spiniform setae on the tarsi.

The forelegs in the Herminiinae are highly modified with the lengths of segments unusually long or short, with eversible tufts of setae on various of the segments and often with the apex of the foretibia enlarged and forming a hood over the reduced tarsal segments and associated brushes of scales (Fig. 11).

SPEIDEL et al. (1996a) used the relatively long **tibial spurs** as a character of the Noctuidae; however, the tibial spur length of the Nolidae examined placed them in the Noctuidae, and the Lymantriidae were intermediate between the short spurs of the Notodontidae and Arctiidae and the longer spurs of the Noctuidae. Overlap in some taxa, and the relatively small sample size of Notodontidae, Arctiidae, and Nolidae measured, limit the value that can be placed on this character.

The many and varied forms of **foreleg brushes** that occur in males of the Herminiinae have already been mentioned. Tufts of specialised setae occur on the legs of many genera of the Noctuoidea, but generally do not define large groupings of genera. A notable exception to this is the tibial brush found on males of the Erebid subfamily Catocalinae (tribes Panopodini, Ophiusini, and Catocalini). In these groups there is a groove on the outer-upper margin of the middle tibia that contains a brush (usually of long, yellow or pale brown hair-like scales that are as long as the tibia itself) that is usually concealed within the groove when the brush is withdrawn) (Fig. 14); (HAMPSON (1913) used this character to define a group of the Ophiusini). The groove, which may be accentuated by an overhanging ridge on the upper margin, is usually covered by a layer of round, white, semitransparent scales that contrast with the normal elongate grey or brown scales of the leg. The groove and brush is lost in some *Catocala* SCHRANK species, and in *Zale* HÜBNER a brush is on the forefemur rather than on the tibia (but it is otherwise similar in form).

The **apex of the foretibia** is lengthened in males of the Herminiinae to form a hood over the reduced tarsal segments and often contains a brush. Many other genera of Noctuoidea have the apex lengthened, usually on one side of the tibia, to produce a spine-like process (e.g., Arctiidae: *Spilosoma* CURTIS; Noctuidae: *Cucullia* SCHRANK (Fig. 12)). POOLE (1995) in his revision of the Cuculliinae refers to several subfamilies as having a “foretibial claw” but morphologically this is a spine in *Cucullia*, but an enlarged apical seta in the Oncocnemididae and Psaphidinae, the latter set into a sclerotised apical extension of the tibia. In the Stiriinae it is a group of fused setae (Fig. 13). Other unrelated genera (e.g., *Mamestra* OCHSENHEIMER; *Lomilysis* FRANCLEMONT) also have a “foretibial claw” derived from an apical seta, so the presence of an enlarged foretibial seta (or its secondary loss) is of limited value for defining family-group taxa.

Spiniform tibial setae occur in many subfamilies but their presence is best known in the Erebiidae: Catocalinae, and in the Noctuidae: Plusiinae, Heliiothinae, and Noctuinae, where the presence and distribution of setae is used to define groupings. In the Catocalinae (mainly the tribes Euclidiini, Ophiusini, and Catocalini) and many Plusiinae the setae are most frequently found on the middle and hind tarsus, usually low down on the tibia near the level of the tibial spurs (Fig. 15). If setae are present on the foretibia they are similar to those on the other tibiae. In most Heliiothinae, Stiriinae: Grotellini, and many Noctuinae (sequentially lost in many genera of the subtribe Noctuina), setae are on all three tibiae and those on the foretibia are stouter than those on the middle and hind tibiae, with the apical setae even stouter and modified into “claws” to aid the adult in digging out of their subterranean pupal cell. In the subtribe Noctuina the setae are lost progressively: first from base to apex on the outer margin, then from base to apex on the inner margin, and finally from the middle tibia. Most Heliiothinae have setal patterns similar to those of the Noctuinae but some genera (e.g., *Pyrrhia* HÜBNER) have lost the spiniform setae. The Ufeinae, many genera in the Xyleninae (especially Xylenini: Antitypina), some Hadeninae (especially some Eriopygini), and some Oncocnemidinae have setae on the middle and hind tibiae. Occasionally

genera in other subfamilies and tribes have some spiniform setae on the hind tibia only (e.g., some species of *Apamea* OCHSENHEIMER). In the Erebidae: Catocalinae the spiniform setae are lost from the hind tibia before they are from the middle tibia, unlike the pattern of loss in the Noctuidae.

The scattered distribution of spiniform tibial setae in the Noctuoidea suggests that this character has developed independently many times, yet its limited distribution, and widespread presence in large lineages, makes it a useful character for identification and classification; although it must be used with great caution and only in concert with other characters.

The presence of extra spiniform setae on the tarsus occurs in several forms. A lateral, partial fourth row of setae on the outer edge of the basal segment of the middle and hind tarsi is confined to the Noctuidae (Fig. 16); although within the Noctuidae it is secondarily lost in genera showing a general reduction of tibial setae. The tarsi normally have three ventral rows of setae, often with the middle row doubled on the apical (fifth) segment. In most genera of the Xyleninae (especially Apameini and Xylenini), Hadeninae (Orthosiini), Psaphidinae, and some genera of the Noctuidae, the central row is irregularly doubled on segments 2–4 (Fig. 17). Generally crowded tarsal setae are most common in species living in cold conditions where the legs tend to be shorter and stouter than those in other groups. The outer row of setae on the basal segment of the foretarsus is greatly enlarged in some genera (e.g., Xyleninae: *Copitarsia* HAMPSON, *Epiglaea* GROTE and related genera; Hadeninae: *Trichoclea* GROTE).

Tympanal structure

The comparative morphology of the noctuid (s.l.) tympanum has been the subject of a number of studies (e.g., RICHARDS, 1933 and SPEIDEL et al., 1996a) summarised by KITCHING and RAWLINS (1998). The principal structures used in classification and phylogenetic interpretation are: 1) the size and shape of the four pockets that surround the tympanic membrane; 2) the form of the sclerite in the tympanic membrane; 3) the size of the alula (a sclerotised flap derived from the metathoracic scutellum that forms a narrow hood over the ear; 4) the size and position of the hood posterior to the ear which is derived from the anterior margin of the abdomen; and 5) the relative size and degree of fusion of the counter-tympanal cavities, which are two air pockets that project into the anterior end of the abdomen

The fundamental differences between the tympanum of the Notodontidae and the arctiid/noctuid families was discussed fully by KITCHING and RAWLINS (1998).

The four **pockets** that surround the ear (Fig. 18) show various degrees of enlargement and fusion but pocket IV seems to have the most phylogenetic information. Pocket IV is frequently described as being “divided” (an open V-shaped structure found in the quadrifids, Fig. 18) or “single” (a U-shaped pocket enclosed and continuous ventrally (Figs. 19, 20)) found in the trifold noctuids, some Nolidae, and some quadrifids). The interpretation provided by RICHARDS (1933), however, describes a much more complex and dynamic situation. RICHARDS described the more primitive subfamilies (herein called Rivulinae, Boletobiinae, Hyphenodinae, Eubleminae, Herminiinae, and Hypheninae) as having a double pocket IV in which each side of the V-shaped brace is a separate narrow pocket and the two overlap slightly at the bottom of the “V.” Pocket IV closes over and fuses into a single pocket at least four times independently: in the Nolidae, Erebidae (Eubleminae: Pangraptini, Scolecocampinae, and Eutelinae + Stictopterinae), and in the Noctuidae s.s. (trifold noctuids). The “double” pocket of the Erebinae + Calpinae + Catocalinae clade is a secondary division involving a re-splitting of pocket IV, which according to RICHARDS (1933: 16) is similar but not homologous with the double pocket IV of the primitive subfamilies.

The **tympanal sclerite** of SPEIDEL et al. (1996a) (= nodular sclerite of RICHARDS, 1933) (Figs. 18, 21, 22) is restricted to the noctuid families with a quadrifid forewing (i.e., absent from the Doidae and Notodontidae). In its most primitive form it is an elongate flat sclerite (Figs. 18, 21), as in the Arctiidae, Nolidae, Erebidae, and in the primitive subfamilies of the Noctuidae (Plusiinae, Eustrotiinae, Bagisarinae, and Pantheinae). It is modified into an elevated ridge of sclerotised nodules (Fig. 22) in the other subfamilies of the Noctuidae.

The anterior part of the abdomen is lobed and forms a flap, or hood, that partially covers the ear. The **tympanal hood** on the first abdominal segment may be in front of the spiracle, a prespiracular hood (Figs. 23, 24) or it may be behind the spiracle, a postspiracular hood (Fig. 25). A prespiracular hood is said to be present in the arctiid group of families, and in the Erebidae: Herminiinae, whereas the hood is postspiracular in the remaining erebids and noctuids. This has been used to suggest that the Herminiinae are the sister group to the Noctuidae and remaining Erebidae and has been used to support the raising of the Herminiinae to family status (KITCHING, 1984). As pointed out by RICHARDS (1933) and more recently by KITCHING and RAWLINS (1998), the spiracle in the herminiines is on the ventral edge of the hood, or even below it, and the shift from postspiracular to a prespiracular position is minor, so the “prespiracular” hood of the arctiid families is not considered to be homologous to the

form of hood in the Herminiinae (KITCHING and RAWLINS (1998: 372).

There are two **bullae**, or air-sacs in the dorso-anterior part of the abdomen that act as resonators for the ear. In the Nolidae, Arctiidae, Lymantriidae, and Erebidae the two lobes are relatively small and separated mesially from each other (Fig. 26). In the Noctuidae the sacs are enlarged and medially fused (Fig. 27); however, in some groups of erebids (e.g., some genera of the Euclidiini) the sacs are moderately large. In all noctuids the bullae are large, but in Diphtherinae they are separated (as much as the width of one bulla), as are Raphiinae (separated by the width of $\frac{1}{2}$ of a bulla), and some Acronyctinae are separated by the width of $\frac{1}{6}$ of a bulla. In some Pantheinae (*Panthea* (HÜBNER) but not *Colocasia* OCHSENHEIMER), Bagisarinae, and Acontiinae the sacs are anteriorly separated but fused ventroposteriorly. In Dilobinae and the rest of the Noctuidae the bullae are fused. So this character is very useful, but not absolutely definitive for all the Noctuidae.

Abdominal coremata

The abdominal coremata are complex character systems made up of levers, apodemes, brushes, pockets and Stobbe's gland located ventrally on the anterior part of the abdomen. If the brushes are concealed in their associated pockets, their presence or absence can be difficult to determine. Where a sclerotised scaphium is characteristic of the Erebidae (and occur independently in a few Noctuidae), the basal abdominal coremata are only in the Noctuidae and are secondarily lost here and there throughout the subfamilies and genera – even between sister-species, e.g. *Apamea maillardi* (GEYER) and *Apamea zeta* (TREITSCHKE) in Europe, and *Anicla lubricans* (GUENÉE) (Fig. 28) and *Anicla sullivani* LAFONTAINE (Fig. 29) in North America. The secondary loss of the basal abdominal coremata happens in a definite sequence with the brushes reduced then lost, then the levers, apodemes, and lastly the pockets are reduced and finally lost.

Atypical resting pockets for the brushes are in some *Leucania* OCHSENHEIMER species, e.g., *L. comma* (LINNAEUS) (BIRCH, 1972, 1989), where the third sternite has a moderately large, deep medioanterior fold for the brushes. Alberto ZILLI (1997) described a folding-complex (Fig. 30) in the *Mythimna* OCHSENHEIMER complex (subgenus *Hypoptericidia* WARREN), where the folds in the sternite extend between sternites 3 and 4 (as separate folds) with each sternite flap connected with the next flap. Brushes, levers and pockets are lost in the Noctuidae except for *Peridroma* HÜBNER and other mainly Neotropical genera of the subtribe Austrandesiina, but in some African Noctuidae (subtribe Axylina), we have found another type of sternal pocket where the normal lateral pockets are replaced by a single, large, ventral pouch or pocket next to the third sternite (Fig. 31); this receives the large brushes that arise from the pleural area next to the third sternite. Levers and apodemes are absent, so this structure appears to be derived independently and is not homologous with the typical noctuid basal abdominal structure.

Coremata no doubt are important in the mating process, but their exact function, and the reasons for their frequent loss, are not yet fully understood.

Male genitalia

Several characters in the male genitalia are particularly useful in the higher classification of the Noctuoidea.

The **anal tube** (Figs. 32, 33) posterior to the diaphragm has not previously been used as a character in classification. We have found it most useful as a character which provides a distinction between the Erebidae and the Noctuidae. The **scaphium** is the dorsal sheath for the anal tube located near the tegumen below the uncus. In some groups the degree of sclerotisation of the scaphium is difficult to determine if it has been heavily stained, so it is best to observe the sclerotisation of the scaphium before staining, or in non-stained genital preparations. The Erebidae (Fig. 32) have a plate-like, more or less heavily sclerotised scaphium (the dorsal wall of the anal tube) and a less sclerotised or membranous **subscaphium** (the ventral wall of the anal tube; e.g., see in GOATER et al., 2003). Often there is a flexible membranous pocket posterior to the sclerotised scaphium which receives the pointed tip of the uncus (GOATER et al., 2003). In the Noctuidae (sensu stricto) the scaphium is membranous and the subscaphium is sclerotised (Fig. 33). The sclerotised subscaphium of the Noctuidae is divided into two elongate triangular plates in a few groups. Some genera and two subfamilies are atypical of the Noctuidae: the Eriopinae, Ampiphyrinae, and the north American genus *Magusa* (WALKER) in Xyleninae, have a scaphium which is heavily sclerotised, either streaked (Eriopinae) or with two dorsolateral bars; they all have the normal noctuid sclerotised subscaphium and other noctuid characteristics (e.g., tympanal and larval structures), so the scaphium is not homologous with that in the Erebidae.

The presence of a **pleural sclerite** (or **pleurite**), and the presence of muscle M.3 (or M4a?), which were taken as apomorphies of the trifold Noctuidae by POOLE (1995), SPEIDEL et al. (1996a) and KITCHING and RAWLINS, (1998),

are not consistent with our own observations and the pleurite is plesiomorphic for the families of the Noctuoidea with a quadrifid forewing, if not to the Noctuoidea as a whole. The apomorphic state is the loss of muscle M.3 and the fusion of the pleural sclerite to the tegumen in the Notodontidae and in the Arctiidae + Lymantriidae clade and the derived part of the Erebidae clade (Calpinae, Erebiniae, Catocalinae, Stictopterinae, and Euteliinae) (Fig. 35), which provides an additional synapomorphy of the erebid clade characterised by a fully quadrifid hindwing.

The primitive form of the pleural sclerite is a spur-like extension from the lateral-anterior margin of the vinculum that projects dorsally with a slight twist and extends along the inner-anterior margin of the lower part of the tegumen, but is separated from the tegumen by a narrow membranous band (Fig. 34). There is also a smaller, thinner process from the lower edge of the tegumen that extends to the inner-posterior margin of the vinculum. By tracking the point of muscle attachment, ТИХОМИРОВ (1979a, 1979b) has determined that the apparent loss of the pleural sclerite in the Arctiidae and many groups of Erebidae is the result of its fusion with the tegumen, coupled with the development of a membranous suture between the sclerite and the vinculum resulting in a simple elbow-like point of articulation between the tegumen and vinculum. The fusion of the pleural sclerite with the tegumen, with the resulting direct articulation between the tegumen and vinculum (Fig. 35), occurs a number of times but generally defines rather large clades. It is characteristic of:

- 1 the Nolidae: Nolinae;
- 2 the Arctiidae + Lymantriidae clade (with the pleurite retained in a few primitive genera in the Lithosiinae and Arctiinae, especially in some Callimorphini and Syntomini (ТИХОМИРОВ, 1979a);
- 3 the Erebiniae + Calpinae + Catocalinae + Euteliinae + Stictopterinae clade; although a pleural sclerite is retained in a few primitive genera (e.g., *Litoprosopus* GROTE, *Phyprosopus* GROTE);
- 4 Noctuidae: Bagisarinae;
- 5 Noctuidae: Condicinae;
- 6 Noctuidae: Eriopinae.

A modification of the pleural sclerite is characteristic of a clade that include some groups in the Xyleninae and Hadeninae. In the Xyleninae: Apameini and Phlogophorini, and Hadeninae: some Hadenini, the pleurite is enlarged and coiled and the apical area towards the tegumen is divided so there are two attachment points with the tegumen (Fig. 36). Also the other more posterior strap-like extension of the vinculum is enlarged and coiled, so the two connecting sclerites between the vinculum and tegumen form a double helix. A further modification in most Apameini is a large central plate on the pleurite for the muscle attachment (Fig. 36).

The musculature of the pleural region has an interesting configuration, but it is difficult to interpret. Muscle M.3 (M.2 of ТИХОМИРОВ, 1979a, 1979b), which connects the tegumen with the dorsal base of the valve (close to the transtilla), is present in other superfamilies of the Lepidoptera, but in the Noctuoidea it is present only in the Oenosandridae (the sister group to the remainder of the Noctuoidea), the Nolidae (except *Meganola* DYAR), and the Noctuidae s.s. (the trifids). This leads to two possibilities.

- 1 The unusual distribution of the occurrence of this muscle, being absent from the Notodontidae, Lymantriidae, Arctiidae, and Erebidae, and its apparent reappearance in the Noctuidae s.s., led SPEIDEL et al. (1996a) to interpreted the muscle as being present in the form of M.3 only in Oenosandridae, and the apparent M.3 muscle in the Nolidae and Noctuidae interpreted as an independent derivation of the muscle originating as a dorsal branch of muscle M.4. The Nolidae subfamilies were included in the trifold noctuids (Noctuidae s.s. in our classification) by SPEIDEL et al. (1996a), but we treat the Nolidae as a primitive lineage of the clade of the Noctuoidea with a quadrifid forewing venation.
- 2 The alternative interpretation of KITCHING and RAWLINS (1998) in which the Nolidae are a basal lineage in the arctiid group of families and not closely related to the trifold noctuids throws doubt into the interpretation of this muscle being a uniquely derived branch of M.4 in the nolid + trifold clade. It suggests that an interpretation of this muscle being M.3, as in other superfamilies, and being secondarily lost in the Notodontidae and again in the Arctiidae/Lymantriidae/Erebidae clade, is equally plausible.

A second pleural muscle (M.4) is also phylogenetically significant. In most Noctuoidea it extends from the dorsal base of the valve (by the fused transtilla), as does M.3 (M.4a of SPEIDEL et al., 1996), to the base of the tegumen, or to the pleural sclerite in those groups in which the pleural sclerite is separated from the tegumen. The main departure from this position of attachment is in the Nolidae (including at least the subfamilies Nolinae, Chloephorinae, and Eariadinae), where M.4 attaches to the middle of the vinculum.

The “**clasper**” (discussed in detail by FORBES, 1934, 1939) is a sclerotised plate on the inner surface of the valve to which the main valve flexor muscle is attached. Within the Noctuidae (s. s.) there is rarely any doubt as to which sclerite is the clasper, but in the Erebidae there may be several sclerotised plates and processes arising from the costal and ventral margins of the valve, and in the absence of studies of genital musculature, it is not

always possible to determine which sclerite is the clasper. Some groups (e.g., Rivulinae, Hyphenodinae: *Hyphenodes* DOUBLEDAY) have very simple valves without an obvious indication of a clasper sclerite but in most primitive groups (e.g., Herminiinae, Hypheninae, Araeopteroninae) the lower margin of the valve is more heavily sclerotised and in some groups (e.g., Calpinae, Catocalinae: Toxocampini) the clasper is more differentiated on the ventral margin of the valve, often with the apex free from the surface of the valve and sometimes with an ampulla-like process from the dorsal margin of the clasper. Other groups of Erebidae add processes to this basic structure, and often the costal margin is also sclerotised with associated processes as well. The most complicated structures completing these trends are in those tribes of the subfamily Catocalinae that correspond to the clade of the Catocalinae that have setose tibiae (i.e., tribes Euclidini, Ophiusini, and Catocalini). In the most derived of these tribes, the Catocalini, the clasper has moved into the centre of the valve in a similar position to that of the noctuid clade Xyleninae + Hadeninae + Noctuinae. In the most primitive subfamilies of the Noctuidae (e.g. Plusiinae, Acronictinae) the clasper is also a long sclerotised process on the ventral margin, but it is usually differentiated from the sacculus by a lightly sclerotised suture and the ampulla is well differentiated and projects dorsally near the apical 1/3 of the clasper. This basic form of the clasper occurs in the Plusiinae, Raphiinae, Acronictinae, Bryophilinae, Agaristinae, Eucocytiinae, Cuculliinae, Oncocnemidinae, Amphipyriinae, Psaphidinae, Stiriinae, and Heliiothinae. In some groups the ampulla becomes enlarged and tear-drop shaped (Oncocnemidinae) or spine-like (Cuculliinae) but the basic ground plan is similar. In the “higher” noctuids (Xyleninae, Hadeninae, Noctuinae) the clasper moves to the middle of the inner surface of the valve, but its origins can be traced because in almost every genus there is a narrow sclerite that extends from the anteroventral corner of the clasper down to the lower margin of the valve at the apex of the sacculus. In many genera in these subfamilies the ampulla becomes very large and either continues to project dorsally from the dorsal margin of the clasper (e.g., *Euxoa* HÜBNER), or rotates to project posteriorly along the middle of the inner surface of the valve (e.g., *Agrotis* OCHSENHEIMER). Some genera need special study to determine the homology of the clasper, ampulla, or saccular extension. The posterior end of the clasper might be fused to the inner surface of the valve, but extended into a process (a pollex) projecting from the ventral margin of the valve (e.g., *Eugnorisma* BOURSIN, *Xestia* HÜBNER).

Systematics

This discussion builds on that of KITCHING and RAWLINS (1998) and deals for the rest of this paper only with newly proposed changes to the classification. Changes include new taxa as well as differences in rank, composition, and sequence of taxa. We also provide additional character states to support the ranking of taxa.

Family Strepsimanidae MEYRICK, stat. rev.

The family Strepsimanidae, based in the Indian genus *Strepsimanes* MEYRICK, was originally proposed as a family in the Gelechioidea and defined by vein 4 on the forewing extending to the costa rather than to the outer margin as in other Lepidoptera. It was transferred to the Noctuoidea by HODGES (1978) because of the presence of thoracic ears and later associated with the genus *Hyphenodes* DOUBLEDAY by MINET (1986: 305). On the basis of forewing vein R4 extending to the forewing costa in both *Strepsimanes* and *Hyphenodes*, the name Strepsimaninae was used as a senior synonym of the Hyphenodinae by KITCHING and RAWLINS (1998). We restore the Strepsimanidae to unresolved family status within the Noctuoidea because its position within the superfamily will not be resolved until the tympanal structure and larval morphology have been studied. *Strepsimanes* has ocelli, unlike the Hyphenodinae, and the presence or absence of the two derived larval character states for the Hyphenodinae (see below) is unknown. The forewing venation of *Strepsimanes* is unique and not at all like that of *Hyphenodes*. MEYRICK (1930: 10) states that the family Strepsimanidae is unique within Lepidoptera because “vein 4” extends to the forewing costa; however, MEYRICK was using the HAMPSON system of venation nomenclature that starts from the bottom of the wing rather than the top, so “vein 4” of MEYRICK is actually vein M3 of our current system of venation nomenclature. In *Strepsimanes* the radial and cubital veins bend upwards so that all of the radial veins, as well as M2 and M3, extend to the forewing costa (Fig. 5). This is a unique configuration, and very different from that of the Hyphenodinae. The forewing and hindwing of *Strepsimanes* have a quadrid venation; in the hindwing vein M2 meets the cell adjacent to M3, as in the arctiid-lymantriid clade and the erebine-calpinea-catocalinae-euteliinae clade. In the Hyphenodinae, as in other related subfamilies (Rivulinae, Boletobiinae, Hypheninae, Herminiinae, etc.) vein M2 is parallel to M3 and meets the cell about 1/3 of the way up the outer margin of the cell. Also vein M2 of the hindwing is strong through the middle of the cell between the wing base and the outer wall of the cell; distal to the cell M2 is displaced posteriorly so that it arises from the lower part of the cell wall adjacent to M3. The hindwing cross-vein at the apex of the cell is angled medially, which also removes the Strepsimanidae from the Erebidae and associates it with the Arctiidae-Lymantriidae clade. In addition to the

unique forewing venation, another unique character state of *Strepsimanus* is the presence of a pair of coremata on the fourth abdominal sternite in males.

The arctiid families (Lymantriidae, Nolidae, Strepsimanidae, and Arctiidae)

Three of these families (Lymantriidae, Nolidae, and Arctiidae) were listed after the family Noctuidae (sensu lato) by KITCHING and RAWLINS (1998), presumably because of the distinctive derived character states that define them, especially the dorsal glands in the larvae of Lymantriidae, the boat-shaped cocoon with a vertical exit slit in the Nolidae, the thoracic metepisternal microtymbals in the Arctiidae, and the paired eversible pheromone glands at the base of the anal papillae dorsally in arctiid females. Several characters discussed by KITCHING and RAWLINS (1998) are shared by these families and the Erebidae: quadrifid hindwing venation; use of polyenic hydrocarbons as the base for the female pheromones; and the attachment of muscle M4 to the tegumen rather than to a pleural sclerite in the male genitalia (treated as plesiomorphic), are considered by KITCHING and RAWLINS to be convergent character states between the two groups (erebids and the three arctiid families). These character states, however, in combination with the lack of any consistent character state to define the family Noctuidae (sensu lato), suggest that the Erebidae are more closely related to the "arctiid" families than they are to the Noctuidae sensu stricto. This conclusion is strongly supported by the findings of MITCHELL et al. (1997, 2000) in the reconstructed phylogeny of the Noctuoidea using two nuclear genes, elongation factor-1" (EF-1") and dopa decarboxylase (DDC), both of which supported an association of the "quadrifid noctuids" [Erebidae] and the "arctiid families." These data support an overall association of the erebids with the arctiid families as a clade distinct from the redefined Noctuidae, although some of the branches within this erebid + arctiid clade are weakly supported by the molecular data. For example, support for the inclusion of the Nolidae and the Euteliinae + Stictopterinae within the clade was not nearly as high as support for the clade that includes the other erebid subfamilies plus the arctiids and lymantriids.

On the basis of these results we move the families Nolidae, Arctiidae, and Lymantriidae from a position after the family Noctuidae (as in KITCHING and RAWLINS, 1998) to a position before the family Noctuidae sensu lato, to reflect their close association with the "quadrifids" [Erebidae]. We treat the "quadrifid subfamilies" (discussed below) as the family Erebidae in order to associate them more closely with the nolids, arctiids, and lymantriids than with the "trifid noctuids." We redefine the Noctuidae to include only the subfamilies generally described as "trifid noctuids" (see below).

Arctiidae, subfamily Lithosiinae

This subfamily was arranged into two tribes by KITCHING and RAWLINS (1998), the Lithosiini and Acsalini. Since the publication of their work, however, the subfamily classification of the Lithosiinae was revised by BENDIB and MINET (1999) and we follow their classification herein. JACOBSEN and WELLER (2002) was in press when the BENDIB and MINET paper was published so they were not able to assess the validity of the additional subfamilies proposed by BENDIB and MINET (op. cit.).

Family Erebidae, stat. rev.

On the basis of the data reviewed above under "the arctiid families" and that of MITCHELL et al. (1997, 2000) the subfamilies Herminiinae, Hypeninae, Calpinae, Catocalinae, Stictopterinae, and Euteliinae are united into the family Erebidae and treated as the sister group to the arctiid families. In addition, the Rivulinae, Boletobiinae, Hyphenodinae, Phytometrinae, Scolecocampinae, and Erebininae are reinstated as subfamilies of the Erebidae. Eublemininae is transferred from the Noctuidae (s.s.) and treated as a subfamily of the Erebidae.

The need to recognise the Erebidae as a separate family from the Noctuidae began in the 1990's when the results from molecular research provided increasingly strong support for a close relationship between the Arctiidae and the quadrifid subfamilies of the Noctuidae (WELLER et al., 1994.; MITCHELL et al., 1997, 2000), indicating that the Noctuidae (s.l.) are paraphyletic with respect to the Arctiidae and Lymantriidae. The publication of a new European check list (FIBIGER and HACKER, 2005) has precipitated the need to have these family level changes in classification formally recognised.

KÜHNE and SPEIDEL (2004: 174) proposed conserving the subfamily name Catocalinae over the rarely used name Erebininae on the basis of ICZN Article 23.9.1. This article requires that a name has not been used since 1899; KÜHNE and SPEIDEL argue that Erebininae has not been used as a senior synonym of Catocalinae since 1899, however, since it has been used as a subfamily in conjunction with the subfamily Catocalinae (e.g., RICHARDS,

1933, 1935, 1936, 1939; FORBES, 1954) it is still available and takes priority over Catocalinae. We are proposing the use of the family name Erebidae for the “quadrid noctuids” which includes both the subfamily Catocalinae and the subfamily Erebiinae. The Erebiinae correspond to a small part of the “Calpinae” as defined in GOATER et al. (2003) where relatively few genera are listed, compared with the genera of the World. NYE (1975: 11) writes: “Those genera without mid tibial spines [those with spines he called Catocalinae] are retained as Ophiderinae. An immense amount of research is required into this large and uncatalogued subfamily of over 1100 genera which must be reclassified particularly where they merge into the following two subfamilies. The Hypeninae and Herminiinae ...”

We restrict the Calpinae to the fruit-piercing moths as defined by KITCHING and RAWLINS (1998). The family-group name Herminiidae has equal priority to the Erebidae (and also has priority over the Catocalidae) but since the Herminiinae is a long recognised group of genera currently recognised as a subfamily, and was treated as a family by KITCHING (1984), we felt that there would be less confusion in using the name Erebidae for this newly composed family. The family-group name Erebidae was last used as a subfamily by FORBES (1954).

Three groups of genera have been particularly problematic in their placement within the quadrid subfamilies. They are the *Parascotia* HÜBNER group (Boletobiinae GROTE), the *Phytometra* HAWORTH group (Phytometrinae HAMPSON), and the *Pangrapta* HÜBNER group (Eublemininae, tribe Pangraptini GROTE). The Pangraptini was used for *Zethes* RAMBUR by BECK (1999–2000) but *Zethes* is in the Catocalinae: Ophiusini (GOATER et al., 2003) and only superficially resembles the genera of the Pangraptini. In the most recent North American list (FRANCLEMONT and TODD, 1983) these three groups were placed in the Rivulinae, Hypeninae, and Catocalinae respectively, following the work of RICHARDS (1933) on the progressive development of the tympanum. In Europe the first two groups were included in the Rivulinae by FIBIGER and HACKER (1991) but were moved to the Catocalinae by BECK (1999–2000). All three groups have a primitive hindwing venation (vein M2 about 1/3 up the cell parallel to M3), like the Rivulinae, Hypenodinae, Herminiinae, and Hypeninae, and differ from the Erebiinae + Calpinae + Catocalinae, which have vein M2 converging toward M3 and adjacent to it at the cell; however, they lack the diagnostic larval characteristics of the Rivulinae, Hypenodinae, Herminiinae, and Hypeninae described by BECK (1999–2000), so we follow BECK and use the names Boletobiinae and Phytometrinae, but as subfamilies of the Erebidae, not as tribes of the Catocalinae; and finally we treat the Pangraptini as a tribe of the Eublemininae.

The family Erebidae is characterised by the following character states (**apomorphic character states are in bold**):

- 1 larvae with only primary setae;
- 2 larvae with three SV setae on A1. Three SV setae on A1 has generally been assumed to be the primitive condition with the loss of seta SV2 to make the SV group bisetose being the derived condition (e.g., LAFONTAINE and POOLE, 1991); however, KITCHING and RAWLINS raised the possibility that a trisetose SV group on A1 could be derived independently (or reversed) in some Noctuidae s.s. because the condition in the Erebiinae does not appear to be homologous to the trisetose condition when it appears in the Noctuidae in the Condidinae, Eustrotiinae, and the Plusiinae (KITCHING and RAWLINS, 1998: 370);
- 3 **silk pore of the larval spinneret concealed by an apical depression margined laterally by flaps** (illustrated in CRUMB, 1956, and BECK, 2000) (silk pore open in the Noctuidae and secondarily open in some Erebidae);
- 4 adults with vein M2 in the hindwing as thick as M3 (a character state shared with some groups of primitive Noctuidae sensu stricto (some Eustrotiinae, Pantheinae, and Raphiinae)*;
- 5 **the erbid subfamilies Erebiinae, Calpinae, Catocalinae, Euteliinae, and Stictopterinae (and the Arctiidae and Lymantriidae) have vein M2 in the hindwing arising in the lower part of the cell adjacent to the M3-CuA1 stem;**
- 6 **scales on the ventral half of the frons deciduous, quickly falling off to leave the area bare in most specimens** (Fig. 37). This latter character is an easy way to recognise the moths of most species in the family, however, the frons is scaled in the more primitive subfamilies (Rivulinae, Boletobiinae, Hypenodinae, and Araeopteroninae) (Fig. 38), so the bare frons is likely a derived condition of the clade formed by the Eublemininae, Herminiinae, Hypeninae, Erebiinae, Calpinae, Catocalinae, Stictopterinae, and Euteliinae.
- 7 **the erbid subfamilies Erebiinae, Calpinae, Catocalinae, Euteliinae, and Stictopterinae (and the Arctiidae and Lymantriidae) have a direct articulation between the tegumen and vinculum** (i.e. pleural sclerite fused to anteroventral margin of tegumen, unlike most Noctuidae);
- 8 the Erebidae have no basal abdominal brushes (and associated levers and pockets) which is a derived

* The quadrid condition of the hindwing occurs in several forms; these are discussed under “Description of Principal Characters”.

- character found in most of the subfamilies of the Noctuidae (absent from the basal lineages of the Noctuidae and lost secondarily many times);
- 9 in the tympanal area pocket 4 is open (V-shaped), as in the Arctiidae, not closed (with a small opening at the top) as in the Noctuidae; a closed pocket interpreted as an independent modification is in some Nolidae and in some Erebidae (i.e., Eublemminae: Pangraptini, Scolecocampinae, and Stictopterinae) (RICHARDS, 1933);
 - 10 the sclerite defining the posterior margin of the tympanum proper is a bar or flat plate in the Erebidae (a non-sclerotised fold in the Arctiidae; an epaulette with raised, rounded nodules (= nodular sclerite) in most Noctuidae) (SPEIDEL et al., 1996a);
 - 11 the two counter tympanal bullae are small and separated in the Erebidae (large and fused medially in the Noctuidae) (see also under “Description of Principal Characters”);
 - 12 **the Erebidae have a heavily sclerotised scaphium, and often also a less heavily sclerotised subscaphium** (Noctuidae have a membranous scaphium and a more or less sclerotised subscaphium) (see above under scaphium in the chapter “Description of Principal Characters”); and
 - 13 posterior apophysis of females of Erebidae stick-like (Fig. 39), often expanded where it fuses with base of anal papillae (Fig. 40) (lacking the elongated or diamond-shaped preapical sclerite near the base of the anal papillae in Noctuidae (Fig. 41)).

Erebidae, subfamily Rivulinae

The subfamily Rivulinae was included in the Hypeninae by KITCHING and RAWLINS (1998) but it shares no derived character states with the Hypeninae, so we recognise it as a separate subfamily on the basis of several apomorphic character states. BECK (1960, 1999–2000) lists many of the peculiar larval features. The most conspicuous of these are (**apomorphic in bold**) :

- 1 **the long barbed setae (like those of arctiids and acronictines);**
- 2 **the dorsolateral movement of the SV3 seta on A1 and A2 to share a common pinaculum with L3 (giving the SV-group a bisetose appearance);**
- 3 the unreduced prolegs on abdominal segments 3 to 6; and
- 4 the larva of *Rivula* GUENÉE lacks the ventral prothoracic adenosma, as do those of the Arctiidae and Lymantriidae, a character known elsewhere in the Erebidae only in *Hypena rostralis* (LINNAEUS) (SPEIDEL et al., 1996a) and in the Noctuidae only in some genera of Pantheinae (KITCHING and RAWLINS, 1998); and The adults of the Rivulinae are characterised by:
 - 1 **a unique proboscis microsculpturing unknown elsewhere in the Erebidae or Noctuidae** (SPEIDEL et al., 1996a, b).

Based on the rudimentary pockets of the tympanum, RICHARDS (1933: 12) treats *Rivula* as the most primitive genus of his Rivulinae, and as the most primitive genus of the Noctuidae. In his phylogeny (RICHARDS, op. cit., plate 20) shows *Rivula* as being basal to a branch leading to the remaining Rivulinae (and on to the Erebiniae) and another branch leading to the Herminiinae. His concept of the Rivulinae therefore is a paraphyletic grade group leading to the structurally more complex Erebiniae. We restrict the Rivulinae to *Rivula* (and possibly to *Zebeeba* KIRBY, which shares the unique proboscis structure of *Rivula* (SPEIDEL et al. 1996a, b)) and remove the other genera that were associated with the Rivulinae by RICHARDS (and in the most recent North American list by FRANCLEMONT and TODD, 1983) to the Boletobiinae. Proboscis structure has been studied in relatively few taxa and the immature stages of *Zebeeba* are unknown, so the association of *Zebeeba* with the Rivulinae is tentative pending molecular data or the discovery of the larvae. The members of the Rivulinae, like the next three subfamilies (Boletobiinae, Hypenodinae, and Araeopteroninae), have a fully scaled frons, so we follow RICHARDS (1933) in recognising the species in these three subfamilies (treated as a single tribe by RICHARDS) as more primitive lineages than the Herminiinae, which is associated with the remaining subfamilies of the Erebidae by the deciduous scales on the lower part of the frons. Rivuline larvae feed on living plants.

Erebidae, subfamily Boletobiinae, stat. rev.

This subfamily corresponds to the Rivulinae of FRANCLEMONT and TODD, 1983, after the removal of *Rivula*, *Colobochyla* HÜBNER and *Melanomma* GROTE. The Boletobiinae are defined by:

- 1 the relatively primitive tympanal structure described by RICHARDS (1933);
- 2 the broad-winged geometrid-like appearance of the adults; and
- 3 the long, thin, roughly-scaled labial palpi (lacking the blade-like palpi of the herminiines, hypenines, etc.).

- 4 the frons is fully scaled (like the Rivulinae);
- 5 the larvae feed on fungi on decaying plant material.
- 6 the larvae have reduced prolegs and three normally positioned SV setae on A1 and A2 (unlike the Rivulinae);

There are two groups of genera included in the subfamily, one containing *Oxycilla* GROTE and *Zelicodes* GROTE (both North American), and one containing *Parascotia* HÜBNER (Eurasian, introduced into North America), and the North American genera, *Mycterophora* HULST and *Prosoparia* GROTE.

Erebidae, subfamily Hypenodinae

KITCHING and RAWLINS (1998) used the subfamily name Strepsimaninae for this group of genera, but we exclude *Strepsimanus* from the Hypenodinae (see discussion of Strepsimanidae above). The Hypenodinae was originally based on genera that have lost the ocelli (*Hypenodes* DOUBLEDAY, *Parahypenodes* BARNES and McDUNNOUGH, and *Schrankia* HÜBNER), but the group was expanded in FRANCLEMONT and TODD (1983) and KITCHING and RAWLINS (1998) to include genera in which the ocelli are present (*Abablemma* NYE, *Dasyblemma* DYAR, *Dyspyralis* WARREN, *Nigetia* WALKER, *Phobolosia* DYAR), but we place these genera elsewhere. BECK (1999–2000) characterises the subfamily on the basis of two derived character states: the loss of one of the SV setae on A2 of the larvae giving the SV group a unique 3–2 count on the first two segments, and the first four abdominal segments are swollen, being 1–2 X as wide as the thoracic segments. The two European genera were included by BECK, however, the larval characteristics have not been studied in the North American genera, so we do not know if these are characteristics of the subfamily or a group of genera within the subfamily. The frons is evenly scaled.

Erebidae, subfamily Araeopteroninae FIBIGER, subfamily nov.

Type genus: *Araeopteron* HAMPSON, 1893

The autapomorphic character states defining the Araeopteroninae are described in detail by FIBIGER and HACKER (2001). The most conspicuous ones are tegumen shape, uncus articulation, and the shape of the signum in the corpus bursae.

The tribe is characterised by the following character states (**apomorphic characters in bold**):

- 1 **species very small (wingspan 9–18 mm) with hindwing much shorter than forewing;**
- 2 concavity under apex of hindwing shallow;
- 3 reniform spot black;
- 4 frons scaled;
- 5 **a small raised membranous or lightly sclerotised patch or low cone covered with long hair-like setae between posterior ends of anal papillae;**
- 6 **signum in corpus bursae cone-like or hat-like with a rounded top fringed basally with spines; signum sometimes a relatively large, flat plate;**
- 7 **sacculus heavily sclerotised, narrow (bar-like), forming longest part of valve;**
- 8 **apex of sacculus spatulate or club shaped;**
- 9 **costa of valve and cucullus membranous;**
- 10 **tegumen short, broad, heavily sclerotised, twisted medially;**
- 11 vinculum short and broad;
- 12 **uncus very long, broad basally with a hinge point between base of uncus and tegumen;**

The ring formed by the saccus, vinculum, tegumen, and uncus has three moveable connections: one between the vinculum and tegumen (i.e., pleurite absent), one medially on the tegumen, and one between the tegumen and uncus which allows the uncus to move up to a maximum of 120 degrees. In other erebids and noctuids the uncus usually can bend only 30–45 degrees.

The tribe includes more than 150 species and is cosmopolitan in distribution. Only a small portion of these species (less than 30) are described but a revision by FIBIGER is in preparation. The New World genera *Sigela* HULST, 1896 (= *Quandara* NYE, 1975, **syn nov.**, = *Lycaugesia* HAMPSON, 1912) and *Abablemma* NYE belong to the Araeopteroninae. In the tribe the ocelli sometimes reduced but present; the sacculus as long as the valve; the ampulla is absent; the ventral part of tegumen is short and coiled; the uncus is relatively short and stout; and the apex of the aedeagus is pointed.

Erebidae, subfamily Eublemminae

This group, generally treated as a tribe of the Acontiinae or Eustrotiinae, is moved to the Erebidae mainly on the basis of six characters:

- 1 the tympanum has the open V-shaped pocket IV typical of the Erebidae, not the enclosed pouch-shaped pocket characteristic of the Noctuidae;
- 2 the scales on the lower half of the clypeofrons are deciduous;
- 3 the palpi of the adults are beak-like;
- 4 a free pleural sclerite is absent (fused to tegumen);
- 5 the larva has 3 SV setae on A1; and
- 6 the body of the larva is thickest near the middle (A5 and A6) and tapered to each end.

The Eublemminae is defined by the following character states (**apomorphic characters in bold**) (most character states are illustrated in FIBIGER and HACKER, 2002, 2004):

- 1 **juxta balloon-like, heavily fused to the saccular base of the valve;**
- 2 valve broadest mesially;
- 3 cucullus membranous;
- 4 clasper and digitus mostly fused to the inner surface of the valve
- 5 aedeagus almost straight, with a long coecum;
- 6 **ostium/antrum and the posterior part of the ductus bursae sclerotised with a membranous band between them;**
- 7 **basal part of corpus bursae and appendix bursae curling.**

Erebidae, Eublemminae, tribe Eublemmini

The tribe includes *Eublemma* HÜBNER, one of the largest and most complicated genera in the Erebidae with a world wide distribution. The tribe includes many other genera (e.g., *Metachrostis* HÜBNER in the Old World, and *Metalectra* HÜBNER in the New World).

It is characterised by (**apomorphic characters in bold**):

- 1 **larva with MD1 and MSD2 setae enlarged on the abdomen** (at present only confirmed in *Eublemma* HÜBNER and *Odice* HÜBNER; absent in *Metachrostis* HÜBNER and *Calymna* HÜBNER; BECK, 1999);
- 2 small to very small often colourful species with slender bodies and a wingspan 9–22 mm;
- 3 both fore- and hindwing broad, and almost equally long;
- 4 lower half of frons bare (scales deciduous);
- 5 valve broadest medially at position of clasper-digitus complex;
- 6 **ampulla of clasper and digitus short and broad, similar in length, overlapping and fused basally;**
- 7 **cucullus of valve (distal to ampulla and digitus) entirely membranous, setose, apically rounded, unarmed;** and
- 8 corpus bursae oval, often much longer than wide.

Erebidae Eublemminae, tribe Pangraptini, stat. rev.

This tribe, like the other Eublemminae, has vein M2 in the hindwing about 1/3 of the way up the cell. The tribe includes the genera *Pangraptia* HÜBNER and *Ledaea* DRUCE in North America and an unknown number of genera elsewhere. We include Pangraptini here on the basis of the male and female genitalia. In the male the uncus is medially globular and setose; the valve is tapered with the sacculus as long as the valve (like Araeopteroninae); the juxta is cone-like with a window at the top; the aedeagus is broadest at the ductus ejaculatorius; the vesica has two large spine-like cornuti. In the female genitalia the antrum is short and heavily sclerotised with a long membranous area of ductus bursae posterior to a part of the ductus bursae with spined sclerites (flat, unbroken, heavy sclerites in Eublemmini); the appendix bursae and basal part of corpus bursae are coiled; the corpus bursae is oval with a few sclerotised plates/signa.

Erebidae, subfamily Herminiinae

This subfamily is well characterised by KITCHING and RAWLINS (1998); it is hereby transferred from the Noctuidae to the Erebidae. Generally all four prolegs are present in the larvae, although some species of *Idia* HÜBNER have

some proleg reduction. On the basis of the discussion under “tympanic structure,” we interpret the prespiracular hood of the herminiines as a derived character of the group, not a primitive character as have been suggested by some authors. The larvae of most herminiines feed on fungi in dead and decaying plant material, but a few genera (e.g., *Palthis* HÜBNER) feed on living plants; some feed on dead insects and vertebrate dung (KITCHING and RAWLINS (1998).

Erebidae, subfamily Scolecocampinae, stat. rev.

This is a distinctive group of the genera related to *Scolecocampa* GUENÉE and includes *Arigusa* WALKER, *Gabara* WALKER, *Hormoschista* MÖSCHLER, *Isogona* GUENÉE, *Nigetia* WALKER, *Nychioptera* FRANCLEMONT, *Phobolusia* DYAR, and *Pseudorgyia* HARVEY. It was characterised by RICHARDS (1933: 16) by the enclosed tympanal pocket IV, which he treated as a convergently similar but not homologous to the closed pocket in the Noctuidae (s.s.). In addition to the tympanal character, which distinguishes the subfamily from other Erebidae but has resulted in some genera being associated with the Ereastriinae, the subfamily is also characterized by the bifurcate valve with a long heavily sclerotised costa and a long more membranous sacculus/cucullus which are usually not differentiated. The larvae feed on fungi in decaying vegetation.

The subfamily is defined by the following character states (**apomorphic characters in bold**):

- 1 **tympanum with pocket 4 closed, sac-like;**
- 2 hindwing venation of the primitive form, with the well developed M2 parallel with M3;
- 3 bullae small, well separated;
- 4 uncus and tegumen prominent, long; tegumen slightly longer than vinculum;
- 5 pleurite absent;
- 6 **valve usually split with costa extended dorsoapically into a long, free process (shorter in eastern North American species of *Gabara*);**
- 7 **sacculus slender, equally prominent, reaching to or beyond tip of costa;**
- 8 juxta large, wide (similar in shape to some Catocalinae, but hindwing venation and position of the ostium exclude this group from Catocalinae);
- 9 vesica with multiple diverticula;
- 10 ovipositor apically quadrangular;
- 11 apophyses rod-shaped;
- 12 ostium bursae at posterior end of abdominal segment eight;
- 13 antrum heavily sclerotised;
- 14 **corpus bursae ovoid, membranous, with a band of prominent spines medially;**
- 15 appendix bursae coiling around posterior end of corpus bursae.

The genera included in the subfamily are superficially very different – not a rare situation in the Erebidae, so we include a diagnosis for three exemplar genera to help characterise the subfamily.

***Scolecocampa* GUENÉE, based on the type-species: *S. liburna* (GEYER)**

Bullae separated. Male: uncus strong, narrow; scaphium sclerotised; subscaphium membranous; vinculum bent dorsally; pleurite absent; juxta ventrally catocaline-shaped (an inverted Y), with a deep dorsal cleft; anellus membranous (in Catocalinae sclerotised and fused with juxta); costa separated from valve near middle of valve and forms a long, narrow, spine-like process; aedeagus long, narrow, straight; vesica with multiple small diverticula, some with a small apical cornutus. Female: seventh abdominal sternite (antevaginal plate) overlapping ostium (ostium 8,2 as described in GOATER et al., 2003); ductus bursae heavily sclerotised, long, cylindrical; corpus bursae posteriorly with short sclerites merging into sclerotised area with a 60° bend where a belt of about 70 prominent spines dominate the area posterior to the otherwise membranous corpus bursae; appendix bursae lightly twisted around posterior end of corpus bursae.

***Arigusa* WALKER, based on *A. latiorella* (WALKER)**

Bullae separated. Male: uncus thick, widest subapically, with a short, stout, apical spine; scaphium sclerotised; subscaphium membranous; vinculum dorsally straight; pleurite absent; juxta very large, wider than long, laterally heavily fused with sacculus (though valves not difficult to open); anellus membranous; sacculus and valve with processes; aedeagus short, broad, bent; vesica with small diverticula, some with spinules. Female: seventh abdominal sternite (antevaginal plate) triangular, slightly overlapping ostium (ostium 8,1 as described in GOATER et al., 2003); antrum sclerotised, triangular; ductus bursae with sclerites; corpus bursae ovoid, medially with a band of about 70 prominent spines; otherwise membranous (with tiny spicules); appendix bursae arising posteriorly

and coiled around posterior end of corpus bursae.

Gabara WALKER, based on the type-species *G. subnivosella* WALKER

Bullae separated. Male: uncus strong, subapically widest, apically with a short stout spine; scaphium sclerotised; subscaaphium membranous; vinculum dorsally bent; pleurite absent; juxta quadrangular, widest medially; anellus membranous; sacculus and valve with processes; aedeagus short, broad; vesica with small diverticula, three with a small cornuti apically. Female: seventh abdominal sternite (antevaginal plate) overlapping ostium (ostium 8,2 as described in GOATER et al., 2003); antrum sclerotised, short, cylindrical; ductus bursae with sclerites; corpus bursae ovoid, subapically with two small sclerotised plates; medially with a band of approx. 130 small spines; appendix bursae arising basally, lightly coiled.

Erebidae, subfamily Hypeninae

The subfamily Hypeninae is restricted to a group of genera closely related to *Hypena* SCHRANK that share a unique set of larval characteristics described by BECK (1999–2000), especially the lateral movement of SV3 on A1 and A2 so that the seta is as close to L3 as to SV1, or closer (i.e., the SV group of setae appears to have two rather than three setae). A second group of genera included in the Hypeninae by FRANCLEMONT and TODD (1983) that lacks these larval characteristics is moved to the Phytometrinae. KITCHING and RAWLINS (1998) refer to a spinulose cuff at the apex of the aedeagus as a possible synapomorphy of the Hypeninae (based on LÖDL, 1993). We have not been able to confirm such a structure and suspect that this might have been a torn part of the manica and not a part of the aedeagus.

Erebidae, subfamily Phytometrinae, stat. rev.

This subfamily is based on RICHARDS (1933: 14) "Hypeninae Group 3" and like the Hypeninae, vein M2 in the hindwing is about 1/3 of the way up the cell. The group has traditionally been included in the Hypeninae (e.g., FRANCLEMONT and TODD, 1983; FIBIGER and HACKER, 1991), mainly because of the beak-like labial palpi and the oblique transverse line on the forewing. We remove it from the Hypeninae and treat it as a separate subfamily so that each group can be defined on derived character states. The male valves are entire with the clasper near the centre of the valve and often with sclerotised processes on the dorsal and ventral margins of the valve. Valve structure is most similar to species in the Hypeninae. Like the Hypeninae, Calpinae, Erebininae, and Catocalinae, the larvae feed on living vascular plant foliage, not on fungi as in Boletobiinae, Hypenodinae, Herminiinae, and Scolecocampinae.

Genera included in the Phytometrinae are *Antharchea* HÜBNER, *Colobochyla* HÜBNER, *Hemeroplanis* HÜBNER, *Glympis* WALKER, *Janseodes* VIETTE, *Melanomma* GROTE, *Mursa* WALKER, *Myana* SWINHOE, *Nimasia* WILTSHIRE, *Ommatochila* BUTLER, *Phytometra* HAWORTH, and *Raparna* MOORE.

The Phytometrinae was originally proposed by HAMPSON for the subfamily now known as the Plusiinae because of an incorrect type species designation for *Phytometra*.

The subfamily is characterised by the following character states (**apomorphic characters in bold**):

- 1 relatively small species with a wingspan between 10 and 25 mm;
- 2 bullae separated, small;
- 3 valve broadest submedially; valve entire, not bifurcate;
- 4 pleurite absent;
- 5 **sacculus with a process free from ventral margin of valve;**
- 6 **clasper displaced to ventral edge of valve;**
- 7 ampulla prominent, bent, most often upturned;
- 8 **juxta large, plate-like, laterodorsal margins heavily sclerotised, converging dorsad, like an inverted V;**
- 9 **some genera with two circular invaginations adjacent to ostium bursae** (probably significant during mating);
- 10 ductus bursae heavily sclerotised; and
- 11 **corpus bursae membranous with spicules on inner surface of bursa concentrated near middle of bursa to form vague signa.**

Erebidae, subfamily Aventiinae, stat. rev.

This tribe, which contains only the genus *Laspeyria* GERMAR, was included in the Catocalinae as a subtribe of the Catocalini by GOATER et al. (2003) and is fully diagnosed there. We move it out of the Catocalinae because a reexamination of the genitalia reveals that the position of the ostium is at base of the 8th abdominal segment, and that the juxta is subdivided into a dorsal more heavily sclerotised part, resembling an inverted Y, and a ventral part, which is a less sclerotised, semi-lunar-shaped plate. Thus the tribe cannot be included in Catocalinae. Also, vein M2 in the hindwing is in the primitive condition about 1/3 up the cell, not adjacent to M3 as in the Catocalinae. We place it tentatively here until molecular data are available to classify it more precisely.

Erebidae, subfamily Erebininae, stat. rev.

This subfamily is reestablished in order to further diminish the Calpinae (s.l.) as diagnosed by GOATER et al. (2003: 11). The removal of the monophyletic Calpinae (s.s.) leaves a large (over 1000 genera) para- or polyphyletic subfamily Erebininae that is in need of revision; however such a revision will be a major undertaking because there are so many genera in the tropics and many of these are poorly known and inadequately diagnosed. A revision is beyond the scope of this review but the list of genera of Erebininae in GOATER et al. (2003) could serve as a starting point.

The character states that define this subfamily are all plesiomorphic. The reason for this is that the subfamily includes a large number of tropical genera whose relationships have not been established and may be related to various subfamilies (Calpinae, Hypeninae, etc.). Until the tropical genera relegated to the Erebininae are studied, and this will also involve larval and molecular research, the monophyly of the lineages remaining in the Erebininae will not be resolved. The characters defining the Erebininae are:

- 1 scaphium more or less sclerotised, subscaphium more lightly sclerotised;
- 2 tegumen longer than vinculum (except in a few genera, e.g., *Tamba* WALKER and *Brevipecten* HAMPSON);
- 3 juxta not fused with a heavily sclerotised anellus;
- 4 juxta occurring in many shapes (but not like an inverted Y, as in the Catocalinae);
- 5 antevaginal plate inconspicuous;
- 6 postvaginal plate membranous or lightly sclerotised;
- 7 ostium positioned in the sclerotised 8th abdominal segment, close to the membrane to the 7th segment (see difference to Catocalinae);
- 8 antrum with sclerites (not a heavily sclerotised cylinder, nor two plates, as in the Catocalinae);
- 9 ductus bursae rarely sclerotised; and
- 10 vein M2 in the hind wing located near the bottom of the cell adjacent to veins M3, Cu1, and Cu2. This character state is an apomorphy of the Erebininae + Calpinae + Catocalinae + Stictopterinae + Euteliinae clade, but is plesiomorphic in the Erebininae within this clade.

No species of this mainly tropical subfamily occurs in Europe. Typical members of the Erebininae that occur in North America are the genera *Ascalapha* HÜBNER, *Hemeroblemma* HÜBNER, *Latebraria* GUENÉE, and *Thysania* DALMAN. In the Old World the genera *Dasypodia* GUENÉE, *Donuca* WALKER, *Erebus* LATREILLE, and *Spirama* GUENÉE are included in this core group. Other genera that will probably be relegated to tribes other than the Erebinini are: *Antiblemma* HÜBNER, *Athyrra* HÜBNER, and *Eulepidotis* HÜBNER. The tribe **Arcteini** BERIO, 1992, was erected for the genus *Arcte* KOLLAR, 1844 (see GOATER et al., 2003). The members of Arcteini are wide spread, especially in the Old Worlds tropics.

Erebidae, subfamily Calpinae

When the majority of the genera of the subfamily Calpinae as defined in GOATER et al. (2003) are transferred to the subfamily Erebininae, the Calpinae become monophyletic again (as in KITCHING and RAWLINS, 1998). It includes three tribes: Calpini, Anomini, and Scoliopterygini (= Gonopterini). It is defined by the autapomorphic, highly specialised, fruit-piercing (a few are skin-piercing) proboscis described in SPEIDEL et al. (1996b), and KITCHING and RAWLINS (1998). The tribal name Anobini WILTSHIRE, 1990 (nomen nudum) was erected for the genus *Anoba* WALKER, 1858, but without a description. It should be validated as a tribe of the Calpinae but a review of the classification of the tropical lineages of the Calpinae is beyond the scope of this paper. The members in this 'tribe' Anobini are wide spread, especially in the Old Worlds tropics.

Erebidae, Calpinae, tribe Anomini

KITCHING and RAWLINS (1998) mention only the genus *Anomis* HÜBNER in this tribe but the North American genus *Alabama* GROTE can be added on the basis of the distinctive tympanal structure, especially the enlarged alula (RICHARDS, 1933). The larvae of the Anomini and Scoliopterygini are unique in having an extra seta below D2 on abdominal segments 1–7 (CRUMB, 1956: 269). Many additional genera occur in tropical regions.

Erebidae, Calpinae, tribe Calpini

KITCHING and RAWLINS (1998) mention the genera *Calyptra* OCHSENHEIMER, *Gonodonta* HÜBNER, and *Eudocima* BILLBERG as occurring in this tribe, all of which have ranges that extend into North America; of these only *Calyptra* (*C. thalictri* (BORKHAUSEN), the type species) occurs in Europe. Additional genera that occur in North America (some also in the Old World) are *Checharismena* MÖSCHLER, *Goniapteryx* PERTY, *Hypsoropha* HÜBNER, *Pharga* WALKER, *Phyprosopus* GROTE, *Plusiodonta* GUENÉE (almost world wide in tropical areas), *Psammathodoxa* DYAR, and *Radara* WALKER. Most of these additional genera (except *Plusiodonta*) lack the piercing modifications to the proboscis but are included here because of characteristics of the palpi, genitalia, and larvae. Undoubtedly, many additional tropical genera will be added to the tribe as revisions of the Erebidae continue.

Erebidae, Calpinae, tribe Scoliopterygini

The tribal name Gonopterini was used by KITCHING and RAWLINS (1998), and GOATER et al. (2003). The name was proposed by HERRICH-SCHÄFFER, [1850] but was replaced with Scoliopterygini by HERRICH-SCHÄFFER, [1852] and according to ICZN Code Article 40.2 a family-group name replaced before 1961 remains replaced if the substitute name is in prevailing usage. Neither name has had extensive usage; no prevailing usage case could be made to preserve Gonopterini, so KÜHNE and SPEIDEL (2004) and SPEIDEL and NAUMANN (2005) use the name Scoliopterygini. The tribe includes the genus *Scoliopteryx* GERMAR, which occurs in both North America and Eurasia, and the genus *Litoprosopus* GROTE. The latter genus lacks the piercing proboscis but is included here because of the following combination of characters: 1) bullae separated; 2) scaphium sclerotised, subscaphium lightly sclerotised; 3) juxta triangular with a small ventromedial cleft; 4) vesica projects dorsally; 5) female with an extremely long ductus bursae (disproportional to the length of the aedeagus and vesica). *Litoprosopus* differs from *Scoliopteryx* in having a large, curved, strap-like pleural sclerite.

Erebidae, subfamily Catocalinae

In order to make this subfamily monophyletic, two “catocaline” tribes and one subtribe diagnosed in Noctuidae Europaeae, vol. 10 (GOATER et al., 2003), Armadini and Aediina are hereby transferred to the subfamily Acontiinae and the Tytini to the subfamily Metoponiinae of the Noctuidae. The character states defining the Catocalinae (sensu stricto) are listed and described by GOATER et al. (2003: 20). This large tropical and subtropical subfamily, consists of many as yet unrecognised tribes (e.g., the African *Marcipa* WALKER genus-group, PELLETIER, 1978) is in urgent need of examination and classification. After the removal of the above tribes, the seven Holarctic tribes that we recognise (in a revised new sequence) are: Toxocampini, Acantholipini, Arytrurini, Melipotini (= Synedini), Euclidini (= Ectypini, **unavail.**, **syn. nov.**), Ophiusini (= Omopterini, **syn. nov.**), and Catocalini.

A tribal classification for the North American Catocalinae (sensu stricto) has not been formally proposed but FORBES (1954) arranged the Eastern North American fauna into four groups with the statement “on genitalic characters our genera divide rather well into four groups” (FORBES, 1954: 309). These four groups are centred on *Catocala* SCHRANK, *Parallelia* HÜBNER, *Euclidia* OCHSENHEIMER, and *Zale* HÜBNER, representing the tribes Catocalini, Ophiusini, Euclidiini, and Omopterini, respectively. We depart from the classification of FORBES (op. cit.) by moving the Melipotini, Panopodini, and genera associated with the Toxocampini (e.g., *Tathorhynchus* HAMPSON) from the Erebiinae where FORBES placed them because of the lack of tibial setae, into the Catocalinae following GOATER et al., (2003). Also we combine the Omopterini with the Ophiusini (see discussion under Ophiusini) and as a result arrange the North American Catocalinae into six tribes (Toxocampini, Melipotini, Euclidini, Panopodini, Ophiusini, and Catocalini).

The Catocalinae was defined by GOATER et al. (2003) on the basis of three characters: the first, the black patch on the wing margin near the cubital vein is also present in some species in Hypeninae and Acontiinae; the second, the stick-like posterior apophyses is listed above as a synapomorphic character for the Erebidae; and the third character, which is a unique combination of several character states is still useful for defining groups of Catocalinae, but they are not uniquely derived character states that would define strictly monophyletic groups.

With the removal of the Tytini, Armadini and Aediini, the Catocalinae (described as Catocalini by GOATER et al., 2003) become monophyletic.

The Catocalinae share the following two autapomorphies:

- 1 the juxta is shaped like an inverted Y; the anterior (ventral) ends are heavily fused with sacculus; and
- 2 ostium bursae (the round entrance to the always heavily sclerotised antrum) is positioned variably but the opening has moved anteriorly onto the 7th abdominal segment rather than between the 7th and 8th segments and there is partial fusion between segments 7 and 8.

For other characteristics of the subfamily, and for illustrations of structural characters, see GOATER et al. (op cit.).

The sequence of tribes is based mainly on the increasing complexity of the male genitalia. This sequence begins with the primitive form of valve and clasper of the Toxocampini, which is similar to that of the primitive subfamilies of the Noctuidae. Following this are two highly autapomorphic tribes (Acantholipini and Arytrurini) with single genera and with uncertain affinities. The tribe Melipotini has a highly complex valve structure that associates it with the tribes Euclidiini, Ophiusini, and Catocalini. These latter three tribes all have sclerotised setae on the middle and usually the hind tibia. Although this character is not always reliable in that it is occasionally lost and is known in other lineages, including the Noctuidae, it is still a very useful character in associating most of the genera with this clade. BERIO (1959) pointed out many of the pitfalls of the use of the tibial setae as a character by demonstrating the progressive loss of setae, first from the foretibia, and then from the hind tibia, similar to the progressive loss of setae among the genera of the Noctuidae: Noctuini. Males in the tribes Panopodini, Ophiusini, and Catocalini have a dorsal groove on the tibia that contains a brush or specialised scales (lost in some Catocalini).

Erebidae, Catocalinae, tribe Toxocampini

We depart from the classification of the Toxocampini in GOATER et al (2003) only in reinstating *Tathorhynchus* HAMPSON to the status of full genus rather than as a subgenus of *Lygephila* BILLBERG on the basis of the differences in the larvae (e.g., *Tathorhynchus* larvae have lost the first pair of prolegs and the second pair are vestigial, whereas in *Lygephila* larvae all prolegs are present).

Erebidae, Catocalinae, tribes Acantholipini and Arytrurini

The subtribal names Acantholipina and Arytrurina were described by GOATER et al. (2003) but without indication that these names were new. It was thought that these names were valid from WILTSHIRE [1977] and so were accompanied only by the notation "stat. rev." but were never validly proposed by WILTSHIRE (SPEIDEL and NAUMANN, 2005). According to ICZN Code Article 16.1 "Every new name published after 1999, including new replacement names (nomina nova), must be explicitly indicated as intentionally new." Accordingly, we propose the following two new tribal names:

Tribe **Acantholipini** FIBIGER and LAFONTAINE, **nomen nov.** for **Acantholipina** GOATER, RONKAY and FIBIGER, 2003: 29. **Type genus:** *Acantholipes* LEDERER, 1857.

Tribe **Arytrurini** FIBIGER and LAFONTAINE, **nomen nov.** for **Arytrurina** GOATER, RONKAY and FIBIGER, 2003: 29. **Type genus:** *Arytrura* JOHN, 1912.

Both tribes are restricted to the Old World.

Erebidae, Catocalinae, tribe Hypocalini

The Hypocalini, containing at present only *Hypocala* GUENÉE, 1852. *Hypocala* was included in the Melipotini by RICHARDS (1933) on the basis of tympanal structure, especially the "shape of nodular sclerite, pouched pocket 1, and flanged pocket 4" (RICHARDS, 1933: 17) but later he removed it from the Melipotini because of the very different genitalia in both sexes (RICHARDS, 1936). In the female genitalia the ductus bursae is short and heavily sclerotised, about as long as abdominal segment 8, but the posterior half of the corpus bursae is very long and slender and resembles the ductus bursae and was described as such by RICHARDS, but the position of the ductus seminalis at the posterior end and its constricted and twisted junction with the ductus bursae associates it with the anterior swollen part of the corpus bursae, which has a long, broad, spiny signum. In the male genitalia (illustrated by RICHARDS, 1936: 373) the valves are rounded with the surface structures broad and appearing

deformed or aborted; the uncus is highly modified with setose processes that are species specific for the genus.

Erebidae, Catocalinae, tribe Melipotini, stat. rev.

This tribe (as Synedini) was diagnosed in detail by GOATER et al., (2003). The 12 North American genera that belong to the tribe are based on RICHARD'S (1936) generic revision of the group; they are: *Boryzops* RICHARDS, *Bulia* WALKER, *Cissusa* WALKER, *Drasteria* HÜBNER (= *Synedoïda* Hy. EDWARDS), *Forsebia* RICHARDS, *Ianius* RICHARDS, *Litocala* HARVEY, *Melipotis* HÜBNER, *Orodesma* HERRICH-SCHÄFFER, *Panula* GUENÉE, and *Phoberia* HÜBNER. RICHARDS (1933, 1936) states that this tribe is the best defined group in the Catocalinae in terms of tympanal structure, especially the shape of the tympanum, and the broad, somewhat C-shaped nodular sclerite. CRUMB (1956: 269) separates the group from other Catocalinae by the short labial palpi of the larvae; these are about half as long as the spinneret, or less, in the Melipotini, but are as long as the spinneret, or longer, in other catocalines. Melipotini GROTE, 1895, has not been used since the 19th century, but there are too few usages of the name Synedini FORBES, 1954, during the 20th century to conserve the name Synedini.

Erebidae, Catocalinae, tribe Euclidiini, stat. rev.

The subtribal name **Ectypina** was used in GOATER et al. (2003) for the taxon that we are treating as the tribe Euclidiini. Ectypina is an unavailable name because it was not specifically described as new in GOATER et al., 2003 (ICZN Code Article 16.1). The older name Euclidiini GUENÉE, 1852, is available for this taxon.

In addition to the European genera included in the tribe by GOATER et al., (2003), the New World genera *Caenurgina* WALKER, *Caenurgina* McDUNNOUGH, *Mocis* HÜBNER, *Celiptera* GUENÉE, *Cutina* WALKER, *Focillidia* HAMPSON, *Ptichodes* HÜBNER, *Argyrostromis* HÜBNER, and *Doryodes* GUENÉE can be added.

The larvae are unusual for erebids in having the SD1 seta on A9 hairlike rather than setose. CRUMB (1956: 269) characterises the larvae by the short, stout (conical in some genera) V1 seta on A1, A2, and A7.

Erebidae, Catocalinae, tribe Panopodini, stat. rev.

The tribe Panopodini is a New World tribe that shares the same distinctive mid-tibial groove and brush as the Ophiusini and could be combined with the Ophiusini, except that sternum seven is unmodified in females with the opening to the ostium bursae on the posterior margin of the seventh sternite (except in *Epidromia* GUENÉE). As in the Ophiusini, tympanal pocket IV is distinctly flanged (RICHARDS, 1933: 18). The genera in the Panopodini usually have large triangular forewings, frequently with a slightly falcate apex, and the hindwing is relatively small. The genera in the Panopodini that occur in North America are: *Anticarsia* HÜBNER, *Azeta* GUENÉE, *Ephyrodes* GUENÉE, *Epidromia* GUENÉE, *Epitausa* WALKER, *Gonicarsia* HAMPSON, *Herminiocala* HAMPSON, *Manbuta* WALKER, *Massala* WALKER, *Metallata* MÖSCHLER, *Obrima* WALKER, *Panopoda* GUENÉE, *Renodes* GUENÉE, and *Syllectra* HÜBNER.

Erebidae, Catocalinae, tribe Ophiusini

We retain the tribal name Ophiusini in place of Omopterini, **syn. nov.** (based on the genus *Omoptera* GUÉRIN-MÉNEVILLE, [1832], a junior synonym of *Zale* HÜBNER). The tribal name Omopterini BOISDUVAL, 1833 has priority over the name Ophiusini GUENÉE, 1837 but we treat Omopterini as an older but junior synonym of Ophiusini because Omopterini has not been used since the eighteenth century and Ophiusini has been widely used in Europe during the past 50 years, including GOATER et al., 2003. In North America the tribe includes *Acidogramma* FRANCLEMONT, *Allotria* HÜBNER, *Bendisodes* HAMPSON, *Coenipeta* HÜBNER, *Coxina* GUENÉE, *Dysgonia* HÜBNER, *Eubolina* HARVEY, *Euclystis* HÜBNER, *Euparthenos* GROTE, *Helia* HÜBNER, *Heteronassa* SMITH, *Itomia* HÜBNER, *Kakopoda* SMITH, *Lesmone* HÜBNER, *Matigramma* GROTE, *Metria* HÜBNER, *Mimophisma* HAMPSON, *Ophisma* GUENÉE, *Parallelia* HÜBNER, *Pseudanthracia* GROTE, *Selenisa* HAYWARD, *Toxonprucha* MÖSCHLER, *Tyrissa* WALKER, *Zale* HÜBNER, and *Zaleops* HAMPSON.

Females in the tribe are characterised by the autapomorphic bulbous sclerotised lodix, a modified seventh sternum, which forms a plate over the ostium bursae (GOATER et al., 2003). Males are characterised by the presence of a longitudinal groove along the upper side of the middle tibia, which in most groups contains a long hair-pencil, specialised rounded scales, or a cluster of both (see discussion under "Description of Principal Characters"). A similar groove with associated brush and specialised scales is also found in the tribes Panopodini and Catocalini.

Family *Micronoctuidae* FIBIGER, 2005, family nov.

Type genus: *Micronoctua* FIBIGER, 1997

This new family is tentatively placed here. Its relationships with other taxa of the Noctuoidea will probably only be resolved when the immatures have been studied in all instars and through molecular research.

The character states that define this new established family are given in detail in FIBIGER (1997b); a revision is in preparation; **apomorphic character states are in bold**:

- 1 clypeofrons fully and smoothly scaled;
- 2 extremely small size (the smallest *Macrolepidoptera* in the world, as small as 5.7 mm, excluding fringes; the largest measures 13 mm);
- 3 **cubital vein two-branched (bifid hindwing)** (Fig. 7); (not found in the *Erebidae* nor in the *Noctuidae*, except in a somewhat similar form in some *Eustrotiinae*);
- 3 **reniform spot pure yellow or whitish-yellow, outlined in black or brown** (Figs. 43–45 (present in some *Microlepidoptera*);
- 4 orbicular spot absent;
- 5 male genitalia (Fig. 42) and female genitalia asymmetrical in all species (found occasionally elsewhere, especially in the *Erebidae*: *Catocalinae*, but not as extreme as in *Micronoctuidae*);
- 6 **uncus lost** (occurs in some *Nolinae* and in subtribe *Athetina* (*Noctuidae*: *Xyleninae*: *Caradrinini*);
- 7 **the fultura superior has been transformed into bizarre configurations in the majority of species, apparently as compensation for the lost uncus** (not found elsewhere in the *Noctuoidea*);
- 8 **cucullus absent** (not found elsewhere in the *Noctuoidea*);
- 9 **clasper-bar at a right angle (or almost so) to the valve margins** (not found elsewhere in *Noctuoidea*);
- 10 **ampulla plate-like** (misinterpreted by FIBIGER (1997a) as *cucullus*) (not found elsewhere in the *Noctuoidea*);
- 11 *juxta-anellus* fused (present also in *Erebidae*: *Catocalinae*);
- 12 posterior apophyses stick-like (similar to those of the *Erebidae*);
- 13 **signum single, crossbar-shaped** (not found elsewhere in the *Noctuoidea*);
- 14 larvae semi-loopers in all known instars (1st–3rd);
- 15 **seta D1 absent on mesothorax** (Matti AHOLA, pers. comm); and
- 16 **L2 seta on meso- and metathorax strongly reduced** (Matti AHOLA, pers. comm).

All known larvae are fungus feeders. Preliminary interpretation of DNA studies are in progress (Felix SPERLING and Andrew MITCHELL, pers. comm.). More than 300 species are known, all from the Old World tropics and subtropics; a revision is in preparation by FIBIGER. One species of *Micronoctuidae* occurs in Europe, *Micronoctua karsholti* FIBIGER, 1997.

The highly autapomorphic *Micronoctuidae* lack the defining characteristics of both the *Erebidae* and the *Noctuidae*. They appear to be closest morphologically to the arctiid families + *Erebidae* clade and so they are placed here as a family between this clade and the *Noctuidae* pending molecular studies and more data from the immatures. A preliminary unpublished classification of the family indicates that the 300+ species known will be arranged in about 40 genera and several subfamilies.

Family *Noctuidae*

The family *Noctuidae* as restricted here consists of the group traditionally and informally known as the “trifid noctuids.”

The family is characterised by the following character states (**apomorphic states in bold**):

- 1 **hindwing trifid with vein M2 reduced so that the cubital vein appears three-branched** (see “Discussion of Principal Characters: wing venation”);
- 2 **abdominal scent brushes on A1 in males** (a synapomorphy of most of the subfamilies of the *Noctuidae* but secondarily lost in many genera and some subfamilies so the clade that this character defines is tentative (see above under the ‘Description of Principal Characters’);
- 3 **bullae fused** (exceptions discussed in ‘Description of Principal Characters’);
- 3 **scaphium membranous** (but in *Eriopinae* it is sclerotised but streaked; in *Amphypirinae* and the genus *Magusa* (WALKER) of *Xyleninae* it is sclerotised, but divided into two elongate bars); **subscaphium sclerotised** (sometimes divided into two elongated plates);
- 4 pleural sclerite between the tegumen and vinculum (secondarily lost in the *Condicinae*, *Eriopinae*, and

- many Eustrotiinae);
- 5 **larvae with two SV setae on A1** (with a reversal or an independent convergent condition in Bagisarinae, Condicinae, and some Plusiinae and Eustrotiinae);
 - 6 **a muscle is present between the tegumen and the transtilla.** This muscle is called M.2 by ТИХОМИРОВ (1979a, b) and considered a division of M.4 by SPEIDEL et al. (1996a). This character was discussed by KITCHING and RAWLINS (1998: 369) and was considered to be an apomorphic character of the trifold noctuids but convergently derived in the Acronictinae. This hypothesis was required because the Acronictinae and their relatives, mainly with larvae with verrucae and abundant secondary setae were treated as the most primitive group of the Noctuidae and separated from the trifold noctuids by the quadrifid groups. With the removal of the “quadrifids” from the Noctuidae to the Erebidae and associated with the arctiid families, the Acronictinae are reunited with the trifids in the redefined Noctuidae so the presence of muscle M2 becomes a derived character state of the Noctuidae;
 - 7 the juxta is usually surrounded by the membranous diaphragm so it is free from the sacculus; in the Erebidae the juxta is more or less fused to the inner saccular fold (which makes it very difficult or impossible to open the valves to 180°, without breaking the juxta);
 - 8 **the posterior end of each posterior apophysis (adjacent to the anal papillae) is expanded into a pre-apical rectangular or diamond-shape plate** (the posterior apophyses are rod-like or evenly expanded posteriorly in the Erebidae and Micronoctuidae).

The placement of the basal lineages of the Noctuidae *sensu stricto* is supported by molecular results (MITCHELL et al., 1997, 2000). Morphologically there are few characters to provide any branching sequence, and thus the relative sequence of these subfamilies requires further studies. Generally the Plusiinae, Eustrotiinae, Bagisarinae, and Acontiinae have been placed at the base because of the quadrifid hindwing venation, the widespread presence of three SV setae on A1 of the larvae (as in the quadrifid lineages), and the loss of prolegs on A3 and A4 (also widespread in the quadrifids). The loss of prolegs, however, appears to have happened independently many times, probably a reflection of the widespread tendency for many trifold lineages to have looping larvae and reduction in prolegs in the early instars. The “quadrifid hindwing,” is only the result of less reduction of vein M2 than in the other trifids and not a change in the position of vein M2. The presence of three SV setae on A1 is a primitive character shared with the quadrifid subfamilies and suggests a basal position for these subfamilies.

KITCHING and RAWLINS (1998: 367) discuss the highly autapomorphic character of basal abdominal coremata with associated levers and pockets as a character that supports a clade consisting of all trifold noctuids (Noctuidae s. s.) except Plusiinae, Eustrotiinae, Acontiinae, Bagisarinae, Condicinae, Acronictinae, and Bryophilinae, but this character is secondarily lost in the Condicinae, judging from their phylogenetic position in trifold phylogeny. Until more character states are discovered to resolve the relative position of the basal subfamilies, or molecular research has been done on more taxa using more genes, the relative sequence of the basal subfamilies will remain tentative.

We suggest the following sequence: Plusiinae, Eustrotiinae, Bagisarinae, Acontiinae, Pantheinae, Dilobinae, Raphiinae, and Acronictinae, which best reflects a synthesis of current classification and the distribution of derived character states. We have not found any evidence to support the association of the Bryophilinae with the Acronictinae so we move it to a position near the Xyleninae, a position supported by the molecular results of MITCHELL et al. (1997, 2000). The characters to support this sequence are discussed under the individual subfamilies.

Noctuidae, subfamily Eustrotiinae

The only recent major revisionary works at the generic level in the subfamily in the Eustrotiinae are those of UEDA (1984, 1987). The more typical genera of eustrotiines, such as *Deltote* R. L. (= *Lithacodia* HÜBNER) have vein M2 slightly reduced when compared with M3 and it meets the cell at about 3/4 of the way down the cell. Other genera, such as *Cobubatha* WALKER and *Metaponpneumata* MÖSCHLER have no trace of the M2 vein. In *Cerma* HÜBNER M2 is 2/3 of the way down the cell like most other trifids but in *Capis* GROTE M2 is 4/5 of the way down the cell and only very slightly thinner than M3. The genus *Hyperstrotia* HAMPSON has M2 almost touching the base of M3 and is as thick as M3, supporting the view of RICHARDS (1933: 14–15) who placed this genus in the quadrifids (Erebidae) based on tympanal morphology. The polyphyletic nature of the Erastrinae is further supported by the fact that various “erastrine” genera have recently been relegated to the Plusiinae, e.g. *Exyra* GROTE (LAFONTAINE and POOLE, 1991), the Stiriinae, e.g., *Grotellaforma* BARNES and BENJAMIN and *Homogloa* BARNES and McDUNNOUGH (POOLE, 1995), and the Condicinae, e.g., *Leuconycta* HAMPSON and *Diastema* GROTE (POOLE, 1995). Some eustrotiines lack a free pleural sclerite, including the African genera *Androlymnia* HAMPSON, *Elyptron*

SAALMÜLLER, *Ethiopica* HAMPSON, *Ethioterpia* HAMPSON, *Matapo* DISTANT, and *Phoperigea* VIETTE. The larvae of most eustrotiines retain seta SV2 on the first abdominal segment.

Noctuidae, subfamily Bagisarinae

We follow KITCHING and RAWLINS (1998) in treating the Bagisarinae as a subfamily closely related to the Eustrotiinae, but we transfer their tribe Cydosiini from the Acontiinae to the Bagisarinae. The Cydosiini possess none of the apomorphic character states listed below for the Acontiinae, but have the bases of the valves fused together so that they can not be separated without breaking them as in other bagisarines. The tympanal structure of the Cydosiini is also like that of the bagisarines and not as in the Acontiinae (described below).

Noctuidae, subfamily Acontiinae

Traditionally the Acontiinae has been a varied and polyphyletic collection of trifold noctuids characterised mainly by small size and scaly body vestiture. KITCHING and RAWLINS (1998) followed CRUMB (1956) in arranging the group in three subfamilies, Acontiinae, Eustrotiinae and Bagisarinae. They included (with some doubt) the North American genus *Cydosia* WESTWOOD in the Acontiinae as the tribe Cydosiini FRANCLEMONT and TODD, 1983, a nomen nudum, and validated the tribal name as Cydosiini KITCHING and RAWLINS, 1998.

The tribe Acontiini is being revised by HACKER, LEGRAIN, and FIBIGER. In addition to the tympanal character discussed by RICHARDS (1933), KITCHING and RAWLINS (1998), and SPEIDEL et al. (1996a), the tribes Acontiini, Armadini, and the African tribe Hypercalymniini share two newly discovered apomorphic character states, namely, the sacculus has a heavily sclerotised, asymmetrical, dorsal crest, and the scaphium has a patch or lobe with long setae on each side. The dorsal crest on the sacculus takes on various often asymmetrical shapes (e.g., straight, curved, thorn-shaped, club-shaped).

In addition to the genera typically associated with the Acontiinae, we transfer the tribes Armadini and Aediini to the Acontiinae; these were included in the Catocalinae in GOATER et al. (2003). We transfer the tribe Cydosiini out of the Acontiinae and treat it as a tribe of the Bagisarinae. The reasons for these transfers are given in the tribal discussions. We also describe a new tribe of African Acontiinae.

The Acontiinae are characterised by the following character states (apomorphic states in bold)

- 1 moths relatively small;
- 2 **scaphium membranous, with one or two areas of hair-like setae** (not in Aediini);
- 3 valves broadest medially or subapically;
- 4 sacculus, and processes of sacculus, more or less asymmetrical;
- 5 sacculus most often with a sclerotised dorsal crest or lobe (all Acontiini and in many other Acontiinae);
- 6 clasper asymmetrical;
- 7 ampulla asymmetrical;
- 8 medial part of transtilla short;
- 9 aedeagus short with ductus ejaculatorius wide
- 10 **tympanum with alula enlarged and forming a flap partially covering tympanic opening;**
- 11 **tympanum with hood reduced or absent;**
- 12 larvae with 2 SV setae on A1 (unlike Eustrotiinae and Bagisarinae).

Noctuidae, Acontiinae, tribe Hypercalymniini FIBIGER and LAFONTAINE, tribe nov.

Type genus: *Hypercalymnia* HAMPSON, 1910

This new tribe of five genera includes splendidly and distinctly patterned and colourful moths from tropical Africa. The tribe is a true member of the Acontiinae, sharing the distinctive hairy area on the scaphium, but these hairs are scattered on the scaphium in the Hypercalymniini, but form a pair of patches in the Acontiini and Armadini. We include the genera *Hypercalymnia* HAMPSON, *Paracaroides* KENRICK, 1917, *Procrateria* HAMPSON, 1905, *Pseudelaeodes* VIETTE, 1965, and *Eutelephia* HAMPSON, 1926 in the tribe (additional genera could be added in the future).

The tribe Hypercalymniini is characterised by the following character states (**apomorphies are in bold**):

- 1 forewings boldly patterned and colourful;
- 2 **scaphium membranous, clothed with a few to many hair-like setae** (in Acontiini and Amardini they are separated into two patches);

3 antrum ventrally with a sclerotised plate with a V-shaped cleft (weakly defined in some species).

Noctuidae, Acontiinae, tribe Acontiini

CRUMB (1956) defined the tribe (as Acontiinae) by the stout posteriorly projecting D2 setae on A9 which form an anal fork. Also the sacculus has a heavily sclerotised dorsal crest, often with a spine-like process or a lobe, and the sacculi are asymmetrical.

Noctuidae, Acontiinae, tribe Armadini

The Armadini comprises 40 species found exclusively in the Old World. The tribe was revised by WILTSHIRE (1979), but no autapomorphies were given and a systematic position for the tribe was not suggested. The Armadini have traditionally been treated as a tribe of the Catocalinae because the hindwing venation is quadrid and the hind wing pattern is catocaline-like, although LAFONTAINE (1981) discussed a series of characteristics that suggested an association with the trifold subfamilies. The apomorphic character states of the Armadini were first listed by GOATER et al., 2003. The male genitalia are typical of the acontiine-oncognemidine form of clasper in which the clasper is positioned along the ventral margin of the valve and the ampulla is located toward the valve apex (most obvious in the genera *Epharmottomena* JOHN and *Drasteriodes* HAMPSON). Also, the male genitalia have a free pleural sclerite, some species of *Epharmottomena* have an apical corona on the valve, and species in the genus *Metopistis* WARREN have a well developed digitus, all supporting an association with the trifold noctuids. The genitalia and tympanum of *Drasteriodes* was described by RICHARDS (1935), mainly to show that the genus "differs from this group [the *Melipotis-Drasteria* group which he was revising] in practically every genitalic and tympanal structure" (RICHARDS, 1935: 131). A comparison of RICHARD's description and figures of the tympanum of *Drasteriodes* with those of the Erastrinae, which he divided into the tribes Erastriini [= Erastrinae] and Tarachini [= Acontiinae], show how similar these structures are, including a vestigial hood. The presence of the saccular crest (though less prominent compared with the Acontiini), and the paired setose patches on the scaphium in the Armadini, clearly associates the Armadini with the Acontiinae.

Noctuidae, Acontiinae, tribe Aediini

We include the Aediini as a tribe of the Acontiinae. GOATER et al. (2003) included the Aediini in the Catocalinae based on two characters: the black patch by the hindwing fringe, and the two ventral lobes on the juxta. The former character is discussed above, and although useful it is too variable to make it fully reliable. The latter character, however, is difficult to interpret because the juxta is autapomorphic, being W-shaped and expanded, a character state not seen elsewhere in the Erebidae or the Noctuidae, and thus it must be excluded from the monophyletic Catocalinae (s.s.), which has an inverted Y-shaped juxta. Also, the juxta of the Aediini are surrounded by membrane and the valve has a corona, both characteristic of the Noctuidae. The position of ostium on the 8th abdominal segment also excludes the Aediini from the Catocalinae.

Because of the presence of a raised epaulette type of tympanal sclerite on the tympanal membrane, the tribe was removed from an association with the Acontiinae and treated as a subfamily of the higher trifold Noctuidae by SPEIDEL et al. (1996a). The tympanal sclerite, while raised, is long and bar-like and not lobed or nodular so we consider it to not be homologous to the nodular sclerite (epaulette) of the higher noctuids. The ear of the Aedini has an enlarged alula and a reduced tympanal hood, and the sacculus has a dorsal lobe or "crest," all characteristics of the Acontiinae. The scaphium is membranous and wrinkled basally, but the setae characteristic of other acontiine groups are absent. The subscaaphium is sclerotised.

Noctuidae, subfamilies Pantheinae, Dilobinae, Raphiinae, Acronictinae, and Bryophilinae

KITCHING and RAWLINS (1998) placed Acronictinae, Bryophilinae, and Raphiinae in "group 1" at the beginning of the Noctuidae (s.l.), apparently treating them as the most primitive lineage of the family, probably because of the arctiid-like verrucae in the larvae. In spite of the larval verrucae, other characters such as two SV-setae on A1, the free pleural sclerite and the hindwing venation, associate them with the trifold noctuids (Noctuidae s. s.). The Pantheinae were put with the "quadrid" subfamilies and were associated with the Lymantriidae by KITCHING and RAWLINS (op. cit.), mainly on the basis of the presence of verrucae rather than only primary setae in the first instar larvae. Other similarities to the Lymantriidae that they list were stated to have exceptions in that the same state occurred in at least some Acronictinae, leaving its association with the Lymantriidae somewhat tentative. We follow YELA and KITCHING (1999) in placing the Pantheinae back with the trifold noctuids. Molecular work by MITCHELL

et al. (1997, 2000) and more recent work (MITCHELL, pers. comm.) has also shown that the Pantheinae belong with the Noctuidae. As yet no close association between the Pantheinae and the Acronictinae has been demonstrated. The Dilobinae were associated with the Psaphidinae by KITCHING and RAWLINS (1998) on the basis of tegulae shape but *Diloba* lacks the diagnostic psaphidine characters of the adult tibia and the pupa. We reinstate the association of the Dilobinae and Acronictinae on the basis of the two L setae on the prolegs. We transfer the Bryophilinae to a position near the Xyleninae on the basis the molecular research of MITCHELL et al. (1997, 2000); and we have not found any characters to support the traditional association of the Bryophilinae with the Acronictinae.

Noctuidae, subfamily Diphtherinae FIBIGER and LAFONTAINE, subfamily nov.

Type genus: *Diphthera* HÜBNER, [1820]

This new subfamily includes only the highly anomalous monotypic genus *Diphthera*, which we transfer from the quadrifid group of subfamilies (herein the Erebidae) because of the quadrifid hindwing, and move it to the Noctuidae near the Pantheinae and Raphiinae on the basis of the character states discussed below. The larva was described by CRUMB (1956) in the appendix of the book because no relationships to other were groups were suggested by the curious combination of characters. The larvae are described as being closest to the Acronictine-Cuculline series of subfamilies on the basis of an open apex of the spinneret, 2 SV setae on A1, and 10th abdominal segment free (larvae confluentae of CRUMB).

The character states that define the subfamily are (**apomorphies in bold**):

- 1 eye smooth;
- 2 forewing apically rounded;
- 3 M2 in hindwing curving down to meet cell wall about 4/5 of distance down cell and similar in thickness to M3 (similar to Pantheinae and Raphiinae);
- 4 **tympanum with pocket 3 absent** (reduced or absent in Pantheinae; absent in Raphiinae);
- 5 **tympanum with hood and alula reduced** (as in Pantheinae and Raphiinae);
- 6 bullae large, mostly separated but partially fused ventrally (intermediate between the typical erebid type of bullae and noctuid bullae (also separated in many Pantheinae and Raphiinae);
- 7 **scaphium membranous except for a very narrow sclerotised band along dorsal margin**;
- 8 subscaphium sclerotised;
- 9 pleurite essentially absent; a narrow band mainly fused to the anteroventral margin of the tegumen;
- 10 **valves asymmetrical; right valve narrow basally with a small sacculus but outer part of valve greatly enlarged and rounded apically with a large pollex-like process subapically; left valve only slightly wider apically than basally and without pollex-like process**;
- 11 **sacculus asymmetrical with a heavily sclerotised dorsal crest** (like Acontiinae);
- 12 clasper not evident, fused to inner surface of valve;
- 13 **bases of valves fused** (similar to Bagisarinae);
- 14 **juxta very short, much wider than long**;
- 15 **transtilla short, heavily sclerotised, two parts meeting dorsal to juxta**;
- 16 **vesica about twice as long as aedeagus with many short diverticula and two sclerotised structures, a raised triangular plate near base and an elongated cylindrical cornutus near apex**;
- 17 ovipositor anteriorly heavily sclerotised;
- 18 **posterior apophyses short but broad and plate-like**;
- 19 **anterior apophysis fused into a sclerotised lobe on anterolateral margin of 8th abdominal segment**;
- 20 **ostium with a heavily sclerotised, quadrangular postvaginal plate conspicuously displaced to left** (otherwise known only in Erebidae: Catocalinae);
- 21 **corpus bursae with posterior half sclerotised and extended into tapered appendix bursae which crosses axis of ductus bursae ventrally; anterior half of corpus bursae with interior walls densely covered with short spines.**

Noctuidae, subfamily Raphiinae

In KITCHING and RAWLINS (1998) the subfamily Raphiinae was placed next to the Acronictinae and well removed from the Pantheinae, which was treated as a family related to the Lymantriidae. Raphiinae shares many structural characteristics with the Pantheinae, while having other character states similar to those of the Acronictinae, indicating a progressive relationship among these three subfamilies. We treat the North American *Aon noctuiformis* NEUMOEGER as a raphiine. *Aon noctuiformis* is an enigmatic species that was first described as a cossid in the

Microlepidoptera, later moved to the Lymantriidae, and finally moved to the Noctuidae, where it has been classified in various subfamilies. Most recently it was moved from the Euteliinae to the Catocalinae by KITCHING and RAWLINS (1998) more to define the Euteliinae as a monophyletic group than on the basis of any catocaline characters.

Aon shares the following character states with Pantheinae and Raphiinae:

- 1 aedeagus very short and stout;
- 2 hindwing quadrifid (like Lymantriidae and Erebidae) with vein M2 strong and moved well down cell (a more extreme quadrifid configuration occurs in *Raphia* and *Aon* than in Pantheinae);
- 3 first abdominal spiracle inside ear (i.e., postspiracular hood, like all Erebidae and Noctuidae) (Lymantriidae and Arctiidae with spiracle behind hood);
- 4 pocket 4 in ear complete (pocket 4 an open V-shaped brace in Lymantriidae, Arctiidae, and most Erebidae);
- 5 tympanum with pocket 3 reduced or absent (large in Lymantriidae; normal size in other Noctuidae, Erebidae, and Arctiidae);
- 6 pocket 3 absent (some Pantheinae, Raphiinae, *Aon*, Diphtherinae);
- 7 hood (on first abdominal segment) reduced (also in Lymantriidae);
- 8 ocelli present but reduced (ocelli absent in Lymantriidae).

Aon and *Raphia* share:

- 1 eyes smooth (like Acronictinae; hairy in Pantheinae)
- 2 ear with nodular sclerite (like Acronictinae, not in Pantheinae)
- 3 tympanal bullae large and fused (exclusively a noctuid character; smaller and separated in Lymantriidae, Erebidae, and most Pantheinae).

Other characters of *Aon* are:

- 1 anal tube entirely membranous (as in Lymantriidae; unlike other Noctuidae and Erebidae);
- 2 clasper and ampulla absent (occasional elsewhere);
- 3 pleurite lost (like Lymantriidae and many Erebidae; pleurite a strap-like extension of the vinculum in Pantheinae, free in Acronictinae);
- 4 transtilla entirely membranous;
- 5 a large spine coiled clock-wise around apex of aedeagus;
- 6 antrum of bursa copulatrix with a sclerotised band ventrally, but ductus and corpus bursae entirely membranous.

Noctuidae, subfamily Acronictinae

We include the North American genus *Miracavira* FRANCLEMONT in the Acronictinae; it was classified in the Amphipyriinae, tribe Apameini in FRANCLEMONT and TODD (1983).

Noctuidae, subfamily Metoponiinae

The Metoponiinae have recently been segregated from the Acontiinae and were associated with the New World subfamily Stiriinae by MATTHEWS (1991), this supported mainly by the scale-like spinneret in the larva; however, a short scale-like spinneret is also found in the Acontiinae and Condicinae, and the Metoponiinae lack the diagnostic leg and genital characteristics that define the Stiriinae (POOLE, 1995). BECK (1999–2000) also used the name Stiriini for this group of genera and placed it next to the Acontiini. The name Metoponiinae is based on *Metoponia flavida* (OCHSENHEIMER), a junior synonym of *Aegle kaekeritziana* (HÜBNER). Also included in the Metoponiinae are six western Palaearctic genera (*Aegle* HÜBNER, *Apaustis* HÜBNER, *Metaegle* HAMPSON, *Mycteroplus* HERRICH-SCHÄFFER, *Megalodes* GUENÉE, *Synthymia* HÜBNER, and *Panemeria* HÜBNER) and three southern African genera (*Dipinacia* DOGNIN, *Ectolopha* HAMPSON, and *Ochrocalama* HAMPSON).

The Metoponiinae differs from the Acontiinae in having fully developed prolegs in the larvae (first two pairs lost in Acontiinae), a raised nodular sclerite (epaulette) on the tympanic membrane, and lacks the principal characteristics of the Acontiinae (enlarged alula and reduced hood of the ear, dorsal saccular crests, setose scaphium). In the larvae the pale spiracular lines extends down the hind proleg, not along the margin of the anal shield as in the cuculline group of subfamilies.

Tyta luctuosa ([DENIS and SCHIFFERMÜLLER]) has traditionally been included in the Acontiinae because of small size and similar habitus to *Acontia lucida* (HUFNAGEL). It was moved to the Catocalinae by GOATER et al. (2003) mainly because of the catocaline-like dark patch on the outer margin of the hindwing opposite veins M3 and Cu1. The other characters given argued for *Tyta* not being a member of the subfamily Catocalinae. *Tyta* (as the

subfamily Tytinae) was removed from the Acontiinae by SPEIDEL et al. (1996a) and treated as a subfamily next to the Metoponiinae (as the Stiriinae), but the only difference between the Tytinae and the Metoponiinae is that the first two pairs of prolegs in the larva are reduced in the first instar in *Tyta* but not in the other Metoponiinae.

Noctuidae, subfamily Sinocharinae

This subfamily, based on the genus *Sinocharis* PÜNGLER, was segregated from the Acontiinae and treated as distinct subfamily by SPEIDEL et al. (1996a). The male genitalia of *Sinocharis* are similar to those of the Bagisarinae in that the bases of the valves are fused together, the tegumen articulates directly with the vinculum (i.e., pleurite absent), the costa of the valve and the sacculus are extended as spine-like processes, and the ampulla is spine-like. The male genitalia are illustrated by SUGI (1970). In the female genitalia the ostium/antrum and the ductus bursae are membranous until just before the corpus bursae where the ductus bursae and posterior part of the corpus bursae and appendix bursae are lightly sclerotised.

In spite of the similarities of the genital characters, we follow SPEIDEL et al. (1996a) and place the Sinocharinae with the higher noctuids and not with the Bagisarinae on the basis of the presence of basal abdominal coremata in *Sinocharis*.

Noctuidae, subfamily Lophonyctinae

This subfamily, like the East Palaearctic Sinocharinae, was elevated to subfamily status from an association with the Acronictinae by SPEIDEL et al. (1996a) because of the presence of basal abdominal brushes and pockets and on this basis we retain it as a subfamily of unknown affinities. The valves are peculiar in that they are asymmetrical and each is deeply cleft into two lobes. In the female genitalia the anterior apophyses are membranous and inconspicuous, the ductus bursae is very short, and the ductus and corpus bursae are entirely membranous.

Noctuidae, subfamilies Cuculliinae, Amphipyriinae, Psaphidinae, and Stiriinae

These four subfamilies of KITCHING and RAWLINS (1998) are treated by BECK (1999–2000) (with the addition of the Acontiinae) as tribes of the subfamily Cuculliinae. POOLE (1995) also recognised these subfamilies, but with a very different composition from that of KITCHING and RAWLINS, and also recognised the Oncocnemidinae as a separate subfamily. Molecular data suggest that the Agaristinae, Acronictinae, and possibly the Pantheinae also belong to this clade (MITCHELL et al., 1997, 2000). Four subfamilies in this clade (Cuculliinae, Oncocnemidinae, Amphipyriinae, and Psaphidinae) are characterised by the position of the lateral line in the larva, which extends along the margin of the anal plate. In other subfamilies in the clade (Pantheinae, Acronictinae, Agaristinae), and in many species of *Cucullia*, the larval pattern is blotchy, without a distinct lateral line. In most other subfamilies, including the Heliiothinae, Condicinae, Xyleninae, Hadeninae, and Noctuinae, the lateral line extends down the hind proleg.

Noctuidae, subfamily Cuculliinae

The subfamily Cuculliinae was defined by KITCHING and RAWLINS (1998) to include POOLE'S (1995) subfamily Oncocnemidinae (as tribe Oncocnemidini) and POOLE'S Psaphidinae: tribe Triocnemidini was included in the tribe Oncocnemidini. The inclusion of the Oncocnemidini (and Triocnemidini) in the Cuculliinae was based on the biordinal crochets of the larvae (KITCHING and RAWLINS, 1998: 380); however, the crochets in the larvae of Oncocnemidinae are at best weakly biordinal and are uniordinal in most genera.

The Cuculliinae are characterised by five character states:

- 1 **proboscis of the adult elongated (also expressed in the pupa)**, which allows the moths to feed while hovering over the flower like sphingids or hummingbirds, rather than having to land on the flower to feed;
- 2 **prothoracic collar enlarged** (projects anteriorly like a cape or process when the moth is at rest to give the moth a cryptic stick-like appearance);
- 3 **vesica with two or three cornuti at the apices of subbasal diverticuli, otherwise unarmed**;
- 4 larva with biordinal crochets (also in Oncocnemidinae, Plusiinae, Heliiothinae, and a few genera of Xyleninae); and
- 5 apical seta on labial palpus short (about as long as the second segment).

Other characteristics, such as the lateral stripe in the larva continuing along the anal plate rather than down the hind proleg is also in the Oncocnemidinae, Amphipyrinae, and Psaphidinae. The “foretibial claw,” which characterises several species groups of *Cucullia*, is a spine formed from and extension of the foretibia, whereas in other subfamilies (e.g., Psaphidinae, Oncocnemidinae, Stiriinae), the foretibial claw is an enlarged seta at the apex of the foretibia.

Noctuidae, subfamily Oncocnemidinae

This subfamily was treated as a tribe of the Cuculliinae because of the biordinal larval crochets, but as discussed under the Cuculliinae, the association based on this character is weak. For this reason, and because molecular data based on two nuclear genes fail to recover the Cuculliinae and Oncocnemidinae as sister groups (MITCHELL et al., 2000), we prefer to follow POOLE (1995) in treating the Oncocnemidinae as a subfamily. The Oncocnemidinae are characterised by the long vesica with an elongated field of spines on the apical half of the vesica. The spinneret is long and tubular (unlike the Stiriinae) and the apical seta on the labial palpus is usually long (unlike the Cuculliinae).

Noctuidae, subfamily Amphipyrinae

On the basis of the unique structures of the male and female genitalia the taxon was treated as a subfamily by FIBIGER and HACKER (1991), SPEIDEL et al. (1996a), and BECK (1996). Previously, BECK (1960) had demonstrated through larval characteristics that the genus *Amphipyra* OCHSENHEIMER was more closely related to the Cuculliinae (sensu lato) than to the xylenine genera with which it had been associated since HAMPSON's time.

POOLE (1995) added the primarily Neotropical tribe Phosphilini to the Amphipyrinae, mainly because of the very simplified valve structure in both groups, but the latter tribe was reunited with the xylenine tribes (in the Hadeninae sensu lato) in their redefinition of the Amphipyrinae (KITCHING and RAWLINS, 1998: 380); we return the Phosphilini to the cuculliine group of subfamilies in the Psaphidinae (below).

The Amphipyrinae are defined by the uniordinal larval crochets combined with the lack of the psaphidine pupal characteristics, the lack of a recognisable clasper on the male valve, the vesica has many long spines, the juxta is very large, and the scaphium is heavily sclerotised as two lateral rods with the subscaphium only sclerotised posteriorly. The female genitalia have a heavily sclerotised postvaginal plate.

Noctuidae subfamily Psaphidinae

KITCHING and RAWLINS (1998) restricted the Psaphidinae to a group of genera with deep dorsal pits on the pupa anterior to the cremaster, and with larvae that feed on tree foliage. This restriction led to the removal of four of POOLE's (1995) tribes (Triocnemidini, Nocloini, Grotellini, and Azeniini) to other subfamilies.

POOLE (1995: 162–163) provides a series of synapomorphies to support the inclusion of the Feraliini, Triocnemidini, and Nocloini in the Psaphidinae and the lack of the derived characteristics of the pupa of the Psaphidini and Feraliini do not negate a subfamily grouping based on the characters listed by POOLE so we return the Triocnemidini and Nocloini to the Psaphidinae. We follow KITCHING and RAWLINS (1998) in including the Grotellini and Azeniini in the Stiriinae because POOLE provides no character states to support an association with the Psaphidinae and the short scale-like spinneret of the Grotellini associates it with the Stiriinae.

Noctuidae, Psaphidinae, tribe Phosphilini, stat. rev.

This mainly Neotropical group of genera was treated as a tribe of the Amphipyrinae by POOLE (1995), mainly on the basis of the simple valve of the male genitalia. The group was included in the Hadeninae s.l. by KITCHING and RAWLINS (1998) without explanation, although they do describe it as problematic in the Hadeninae. Although the genitalia of *Phosphila* HÜBNER has a very simple valve (similar to *Amphipyra* OCHSENHEIMER), other related genera (e.g., *Apsaphida* FRANCLEMONT, *Cropia* WALKER, *Heterochroma* GUENÉE, *Paratrachea* HAMPSON, *Speocropia* HAMPSON) have species with the clasper on the ventral margin of the valve articulating with the sacculus as in most cuculliine subfamilies, and the larva of *Apsaphida* (illustrated by FRANCLEMONT, 1973: 173, fig. 3) clearly associates it with the cuculliine subfamilies in which the lateral line extends along the anal shield rather than down the hind proleg. We include the group next to the Nocloini because of FRANCLEMONT's comments on the close relationship of *Apsaphida* with *Paratrachia viridescens* (as “*Paramiana*”) and other *Paramiana* species. The genitalia of two species of *Paratrachea* were illustrated by LALANNE-CASSOU and POGUE (2003). The larvae of *Phosphila* is boldly

patterned with pale blotches and is more reminiscent of a *Cucullia* than a psaphidine; they feed on members of the catbrier family (Smilacaceae). The larvae of *Apsaphida eremna* FRANCLEMONT were reared on oak *Quercus* spp. The New World genera *Phuphena* WALKER and *Acherdoa* WALKER are tentatively associated with the tribe on the basis of the simple valve and spiny vesica.

Noctuidae, subfamily Stiriinae

We follow the classification proposed by KITCHING and RAWLINS (1998), except for following POOLE (1995) in including the Nocloini in the Psaphidinae. The molecular results of MITCHELL et al. (2000) give strong support for the inclusion of the Nocloini in the Psaphidinae rather than in the Stiriinae.

The Stiriinae are defined by the scale-like larval spinneret, a feature found convergently in the Condicinae and Acontinae. Also the vesica has many very large cornuti distributed either throughout the vesica or arranged in one or two large patches, and the foretibial "claw" is a cluster of several fused setae. Similar patches of spines, but relatively smaller, occur convergently in the Xyleninae and Hadeninae. The larvae of Stiriinae feed on the seeds of Asteraceae.

MATTHEWS (1991) included five Palearctic genera in the Stiriinae, however, these lack the foretibial "claw," the fields of enlarged cornuti in the vesica, and the larvae do not specialise on seeds of Asteraceae. We remove these five genera to the subfamily Metoponinae.

Noctuidae, subfamily Eriopinae, stat. rev.

This is a highly enigmatic group consisting of the genus *Callopietria* HÜBNER and a few African genera (e.g., *Megalonycta* VIETTE, *Megeochaeta* VIETTE, and *Tanocryx* VIETTE). It was treated as a separate trifold subfamily by POOLE (1995) and BECK (1999–2000) but KITCHING and RAWLINS (1998) put it in the Hadeninae *sensu lato*, presumably on the basis of the hairlike SD1 seta on A9 of the larva, and the mesial position of the clasper on the valve.

Several characteristics of the Eriopinae, such as the highly modified valve and clasper, the presence of a basal brush on the abdomen that appears to be independent in origin from that of other noctuids, and the aedeagus is heavily sclerotised only apically and ventrally with the sides and dorsum very lightly sclerotised, shed little light on the relationships of the group.

Some characters are peculiar but not definitive. For example there are eversible coremata on the sacculus. Similar but probably independently derived coremata occur in some Xyleninae (e.g., *Spodoptera*), Hadeninae (e.g., *Eriopyga*), and some Erebidae (e.g., Catocalinae: Ophiusini and Melipotini). The spinneret has an apical pair of flaps that cover the opening of the spinneret (BECK, 1999, figs. 598a, 599a), a character normally associated with the Erebidae (CRUMB, 1956: 6), however, similar spinneret flaps also occur in some Eustroitiinae and in the Nolidae (tribe Sarrothripini), and the flaps often consist of four lobes in the Erebidae, suggesting that the character has arisen several times (see illustrations in BECK, 1999, vol 2).

Characters that suggest affinities with the Erebidae are the rod-like posterior apophyses (without the posterior rectangular or diamond-shaped plates characteristic of the Noctuidae), absence of a free pleural sclerite in the male genitalia, enlarged apical setae on the tarsi of the larvae, and the scaphium is heavily sclerotised; however, the sclerotisation of the scaphium is broken into streaks like planks in a floor. The subscaphium is sclerotised as in other Noctuidae.

Contrasting with these erebid characters are ones that suggest affinities with the Noctuidae, such as: 2 versus 3 SV setae on A1 in the larva; larva cylindrical (not tapered posteriorly as in most Erebidae); trifold noctuid tympanal structure; bullae large and medially fused; reduced vein M2 in the hindwing; and fully scaled frons. The most conclusive characters, however, are 1) SD1 seta on A9 of the larva is hair-like and in an enlarged sclerotised pocket, and 2) the spinneret has a dorsal groove. These are characteristics of a group of subfamilies that includes Condicinae, Xyleninae, Ufeinae, Hadeninae, and Noctuinae. The Eriopinae differ from these subfamilies in that the pale lateral line extends across the posterior part of the abdomen (but not the anal shield as in the Cuculliinae s. l.) rather than extending down the hind proleg.

On the basis of this peculiar mix of shared and unique character states we follow POOLE (1995) and BECK (1960, 1999–2000) in treating the Eriopinae as a distinct subfamily. The cladograms of MITCHELL et al. (1997, 2000) place the Eriopinae (*Callopietria*) well within the trifold noctuids as the sister group to the Xyleninae + Hadeninae + Noctuinae clade.

Callopietria larvae feed on ferns, a very rare choice of host plants for the Noctuoidea.

Noctuidae, subfamily Xyleninae, stat. rev.

The subfamily Xyleninae is resurrected in order to define monophyletic units within the large para- or polyphyletic Hadeninae *sensu lato* of KITCHING and RAWLINS (1998), and to treat the restricted subfamily Hadeninae as a possible sister group to the subfamily Noctuidae. The subfamily Xyleninae may be paraphyletic with respect to the Hadeninae (and possibly the Noctuidae), being defined mainly by plesiomorphic character states, but we have attempted to define monophyletic tribes and subtribes within the Xyleninae. The relationship of these tribes will probably only be resolved through molecular research but to date this has been inconclusive. Character states of the Xyleninae are:

- 1 the valve is more or less constricted below the cucullus at the distal end of the clasper (not the ampulla) (a character state shared with most Hadeninae);
- 2 the cucullus tends to be expanded and bears a corona of stout setae (lost in a few groups) (also a character state shared with most Hadeninae);
- 3 the ampulla is small and usually finger-like (except in the subtribe Xylenina, where the ampulla often bent midway and extends above the costal margin of the valve);
- 4 the dorsal surface of the sacculus is usually irregular toward the base (the clavus area), often with an area of dense setae or raised spine-like processes (as in many Hadeninae; see genitalia illustrations in HACKER et al., 2002);
- 5 the vesica is often short and tube-like or triangular, rarely longer than the aedeagus;
- 6 the vesica has a few basal cornuti (1–3) and an elongate patch of spines on the apical half of the vesica (as in many Hadeninae: Hadenini);
- 7 the ante- and post-vaginal plates are both often heavily sclerotised
- 8 the ductus bursae is short and heavily sclerotised;
- 9 the appendix bursae is small and inconspicuous, or absent.

The oldest available family-group names for this subfamily are the Nonagriinae GUENÉE, 1837 and the Xyleninae GUENÉE, 1837. We use the name Xyleninae for the subfamily because the name has been in common usage, whereas Nonagriinae has not been used since the 19th century.

Noctuidae, Xyleninae, tribe Balsini

The genus *Balsa* WALKER has relatively simple valve structure in the males; although the remnants of the normal xylenine structures (clasper, digitus) are evident in some species. The tribe includes only the genus *Balsa* with three North American and one East Asian species. We revive GROTE's tribal name for the group because of the uncertain affinities within the Xyleninae, particularly because of the simple valve structure and the reduction of the first pair of prolegs in the mature larva, a character more reminiscent of the Eustrotiinae than the Xyleninae.

Noctuidae, Xyleninae, tribe Pseudeustrotiini

The two species of *Pseudeustrotia* WARREN placed in this subfamily have traditionally been classified in the Eustrotiinae as close relatives of *Deltote* R. L. species. BECK (1996) proposed a new tribe for the European *Pseudeustrotia candidula* ([DENIS and SCHIFFERMÜLLER]) in his inclusive definition of the subfamily Noctuidae because the larva has a full complement of prolegs, two SV setae on A1, and SV1 on A9 is hairlike, all characteristics of the Xyleninae-Hadeninae-Noctuidae clade, and not of the Eustrotiinae. A position for the genus in the “higher” trifids was confirmed by SPEIDEL et al. (1996a) because of the raised nodular sclerite (epaulette) on the tympanal membrane (Fig. 20), and the presence of fully developed basal abdominal brushes and pockets in the male. SPEIDEL et al. raised the group to subfamily status and treated it as one of several unresolved sister groups to the Cuculliinae s. l. + Noctuidae s. l. clade because of the absence of a corona on the male valve. The North American species *Pseudeustrotia carneola* (GUENÉE), however, does have a corona so the position of the group within this clade is confirmed. A position within the Xyleninae-Hadeninae-Noctuidae clade is further demonstrated by the medial position of the clasper on the valve in the male genitalia, and the hairlike SD1 seta on A9 of the larvae; a position near the base of the Xyleninae is based on the lack of the derived characters of the Hadeninae and Noctuidae (flattened spinneret with fringed apex; hairy eyes; setose tibiae), or the higher Xyleninae (spine patch on vesica subapically; raised spiny dorsal surface of the sacculus), so we place the Pseudeustrotiini at the base of the Xyleninae next to the Balsini. We also include *Anterastria* SUGI in the Pseudeustrotiinae which also has been associated with the Bryophilinae and Eustrotiinae, but like *Pseudeustrotia*, the form of the male genitalia, the presence of a raised nodular sclerite, and basal abdominal coremata and pockets, associates it with the “higher” noctuids. The male genitalia are similar to those of *Pseudeustrotia*.

Noctuidae, Xyleninae, tribe Prodeniini

The genus *Spodoptera* GUENÉE (*Prodenia* GUENÉE is a synonym) has such a highly modified genital structure that it is difficult to relate them to those of other genera and establish relationships with any degree of certainty (POGUE, 2002). The genera *Galgula* GUENÉE and *Elaphria* HÜBNER have traditionally been treated as members of the tribe, but the characters that might support such an association are not stated. The distinctive characteristics that allow *Galgula* and *Elaphria* to be associated with each other are absent from the Prodeniini; similarly the peculiarities of the genitalia of the Prodeniini are absent from the *Galgula/Elaphria* clade, so we treat these two clades as separate tribes. The three genera form a clade in MITCHELL et al. (2000, fig. 3) but the bootstrap values are low. The spinneret of *Spodoptera* species is short and dorsoventrally flattened with a few apical spinules near the centre; this is possibly the reason for BECK (1999–2000) placing the Prodeniini immediately before the Hadeninae (his tribe Hadenini). The structural characteristics of the Prodeniini are fully described and illustrated by POGUE (2002).

Noctuidae, Xyleninae, tribe Elaphriini

The association of *Galgula* and *Elaphria* is much easier to support than one with the Prodeniini because of several unique character states: in both genera the sacculus is divided into two parts which are separated by a membranous suture with the apical part more heavily sclerotised; the costal margin of the valve has an unsclerotised band which in *Elaphria* results in the apical part of the valve bending quite freely with the respect to the basal half when being dissected, and in *Galgula* it is the point where the cucullus bends 180 degrees back on the valve to look like an apical flap. The larva has a very unusual shape, appearing humped anteriorly, with segments T2, T3, A1, and A2 swollen (compare figures 263 and 314 in BECK, 2000, volume 3). In addition to *Galgula* and *Elaphria* the mainly Neotropical genera *Bryolymnia* HAMPSON, *Gonodes* DRUCE, and *Hampsonodes* NYE are included in the tribe.

The genus *Elaphria* and the tribe Elaphriini have sometimes been associated with the Eustrotiinae because of the superficial eustrotiine-like appearance of the only European species, *Elaphria venustula* (HÜBNER).

Noctuidae, Xyleninae, tribe Caradrinini, stat rev.

The tribe Caradrinini is best defined by the larva, which has a very long spinneret, about 6X as long as the width near the middle and more than 2X longer than the labial palpi. This character unites two otherwise dissimilar groups of genera, which are arranged in two subtribes.

Noctuidae, Xyleninae, Caradrinini, subtribe Caradrinina

A large part of the Caradrinina (the *Caradrina* complex) were recently revised by HACKER (2004), however, he and FIBIGER only revised the *Caradrina*-genus group itself and did not actually define the tribe (or subtribe) to which the genus complex belongs, nor did they list all the included genera. They included four genera in the *Caradrina* OCHSENHEIMER complex (*Caradrina*, *Hoploadrina* BOURSIN, *Stygiodrina* BOURSIN, and *Stenodrina* BOURSIN). The subtribe is characterised by the heavily sclerotised extension to the sacculus that projects along the inner surface of the valve, the digitus forms the apex of the valve in most genera, and there is a posteroventral extension of the clasper that forms a true pollex (as opposed to a pollex-like structure derived from the digitus or the cucullus). On the basis of these characters, and the larval characters that define the tribe Caradrinini, the tribe can be expanded to include *Charanyca* BILLBERG, *Pseudoxestia* BOURSIN, and *Rusina* STEPHENS.

Noctuidae, Xyleninae, Caradrinini, subtribe Athetina FIBIGER and LAFONTAINE, tribe nov.

Type genus: *Athetis* HÜBNER, [1821]

This subtribe is established for a large World wide group of genera of which the largest genus is *Athetis* HÜBNER; although "*Athetis*" probably includes a number of unrecognised genera and is in need of revision. As many as 250 species can be associated with the Athetina. The most obvious synapomorphy is the form of the uncus, which is vestigial or absent in all species. This character state otherwise occurs only in some Nolidae (Nolinae: *Nola* LEACH), and in all Micronoctuidae. The subtribe includes *Anorthodes* SMITH, *Athetis*, and *Proxenus* HERRICH-SCHÄFFER.

Noctuidae, Xyleninae, tribe Cosmiini, stat rev.

The larvae of the tribe Cosmiini, like those of the Xylenini, feed on woody plants, but the adults, unlike those of the Xylenini, usually fly in mid- and late summer. Most cosmiines have even postmedial lines on the forewing rather than dentate ones, and the antemedial and postmedial lines often form a V-shape when they converge towards to posterior margin of the wing. In the male genitalia the pleurite is two overlapping straps, the ampulla is long, the clavus is heavily sclerotised, the transtilla is sclerotised, and there are two or more spine-fields in the vesica. In the female genitalia the ovipositor is ovoid. The larvae are a translucent green, often with faint white lines, and feed on the foliage of trees where they tie several leaves together to form a feeding shelter. The most frequent host plants for cosmiine larvae are poplar (*Populus* spp.) and willow (*Salix* spp.) (e.g., *Energia* HÜBNER and *Ipimorpha* HÜBNER), but *Cosmia* OCHSENHEIMER and *Dicycla* GUENÉE are associated with oak (*Quercus* spp.). The larvae of some *Cosmia* species are cannibalistic on other larvae, especially those of Geometridae. One species group of *Cosmia* (the *epipaschia* group) in North America feeds on conifers (LAFONTAINE and TROUBRIDGE, 2003). The larvae of *Zotheca* GROTE, a close relative of *Cosmia*, feeds on elderberry (*Sambucus* spp.).

Noctuidae, Xyleninae, tribe Actinotiini, stat rev.

This tribe is best characterised by the larvae, which have a plusiine-like raduloid on the side of the hypopharynx; the normal row of about 10–15 wedge-shaped spines is replaced by a row of 30–40 narrow peglike spines that form a comb on the side of the hypopharynx. Five genera are included in the tribe: *Actinotia* HÜBNER, *Chloantha* BOISDUVAL, RAMBUR and GRASLIN, *Nedra* CLARKE, *Iodopepla* FRANCLEMONT, and *Alastria* LAFONTAINE and TROUBRIDGE. These genera also can be characterised by the male genitalia (illustrated in part by LAFONTAINE and TROUBRIDGE, 2004, and FIBIGER, 1990):

- 1 juxta with a paired of posterior processes;
- 2 clasper and digitus shape in which a posteroventral extension of the clasper extends along the ventral margin of the digitus making it appear as though the clasper and digitus are fused;
- 3 simple articulation between the tegumen and vinculum with pleural sclerite a simple straplike extension of vinculum extending along ventroanterior margin of tegumen and overlapping tegumen.

Where known the larval host plants are members of the St. John's-wort family (Hypericaceae), usually species of *Hypericum* LINNAEUS.

The distinctive “neck” on the cucullus gives the genitalia of this group a very hadenine-like appearance and we would have been tempted to treat it as a non-hairy eyed hadenine were it not also for the lack of a spinulose fringe on the larval spinneret.

The genus *Auchmis* HÜBNER is superficially similar to these genera in the male genitalia, but differs in clasper and juxtal shape and has a double helix pleurite; the larva lacks the raduloid-like structure characteristic of the Actinotiini, has a large serrate plate on the inner surface of the mandible rather than a small triangular tooth, and is not associated with the Hypericaceae for a host plant. On the basis of pleurite structure, and the lack of critical *Actinotia* characteristics, we exclude *Auchmis* from the Actinotiini and tentatively associate it with the Phlogophorini.

Noctuidae, Xyleninae, tribe Dypterygiini, stat rev.

FORBES (1954) erected this tribe for genera that were characterised by a diffuse corona, broad, flat digitus; oblique clasper; tapered pleurite; and surface feeding, cryptically patterned larvae. We redefine the tribe for a seemingly heterogeneous assemblage of genera with their diversity centred in the tropics with isolated species and genera extending into the Holarctic region. The group may be paraphyletic or polyphyletic but until the tropical xylenine fauna is better studied, we propose this interim classification. Included in the tribe are the genera: *Andobana* VIETTE, *Anthracia* HÜBNER, *Callymna* GUENÉE, *Dypterygia* STEPHENS, *Feliniopsis* ROEPKE, *Heterophysa* BOURSIN, *Karana* MOORE, *Madegalatha* VIETTE, *Mormo* OCHSENHEIMER, *Phoebophilus* STAUDINGER, *Polyphaenis* BOISDUVAL, *Prototrachea* VIETTE, and *Trachea* OCHSENHEIMER. The tribe is held together by the following character states (apomorphies in bold):

- 1 pleural sclerite straight or evenly curved along posterior margin of tegumen;
- 2 valve without a strong subapical constriction (no neck);
- 3 dorsal margin of clavus smooth and rounded (no spines or processes);
- 4 digitus absent or fused into wall of valve (tip rarely free);
- 5 transtilla sclerotised;

- 6 juxta triangular, tapered dorsally;
- 7 **ovipositor quadrangular with posterior margin often slightly concave** (rather than rounded or tapered);
- 8 ductus bursae heavily sclerotised;
- 9 **ventral wall of ostium slightly extended posteriorly (towards ovipositor).**

Noctuidae, Xyleninae, tribe Phlogophorini, stat. rev.

The tribe in its restricted sense includes only three genera: *Euplexia* STEPHENS, *Conservula* GROTE, and *Phlogophora* TREITSCHKE. The tribe was characterised by FORBES (1954) mainly by the peculiar longitudinal folds in the forewings that give the wings a crumpled look when the moth is at rest. Most of the other characters given below are not in all genera. The larvae are polyphagous cutworms on low plants, unlike the Cosmiini and Xylenini. The tribe is characterised by the following character states (**apomorphic states in bold**):

- 1 **forewing folded longitudinally;**
- 2 transtilla sclerotised;
- 3 double helix coiled pleural sclerite;
- 4 digitus prominent;
- 5 sacculus heavily sclerotised dorsally;
- 6 juxta shield-like;
- 7 ampulla long;
- 8 corona a single row of setae;
- 9 **ductus bursae longitudinally sclerotised on one side and with separated sclerites on the other.**

We tentatively expand the definition of the tribe to include other genera that have a double helix pleural sclerite, like the Apameini, but lack the other essential characteristics of the Apameini in ovipositor shape and structure, and in lacking the enlarged plate for muscle attachment on the pleurite. Additional genera included are: *Auchmis* HÜBNER, *Magusa* WALKER, and *Pseudenargia* BOURSIN. The tribe occurs world wide in temperate, subtropical, and tropical regions.

Noctuidae, Xyleninae, tribe Apameini, stat. rev., nomen conservandum

The family-group name Nonagriini GUENÉE, 1837 has priority over the name Apameini GUENÉE, 1841 and refers to the same tribe as the Apameini. We apply ICZN Article 40.2 to preserve the junior synonym Apameini for the tribe because it has come into common usage in the past 50 years and the family-group name Nonagridi has not been used since the 19th century.

The tribe Apameini is best known for its diversity of borers, though the larvae of the genus *Apamea* OCHSENHEIMER are cutworms. The tribe was defined by FORBES (1954) as having: a double helix pleural sclerite which has an enlarged central plate for the muscle attachment; a well-differentiated cucullus (usually with the cucullus separated from the rest of the valve by a narrower “neck” and often by a raised, partly sclerotized ridge; a large usually transverse digitus; and usually a prominent penicillus at the base of the tegumen. FORBES treated the Apameini as two tribes (Septidini and Apameini) separating the genera with cutworm larvae (mainly *Apamea*) from those with larvae that bore in the host plant, almost exclusively monocotyledonous hosts. The larvae are characterised by having a row of tonofibrillary platelets between setae XD2 and D2 on cervical shield; these platelets form a ring (open or fleck-filled) in most Apameini larvae (Matti AHOLA, pers. comm.). The monophyly of the Apameini is supported by the following character states (**apomorphic character states in bold**):

- 1 **ovipositor lobes heavily sclerotised, flattened dorsoventrally in subtribe Apameina (flattened cones in a few species), conical in Sesamiina and Oxytrypiina (extended and only sclerotised medially in Oxytrypiina), vertical in Arzamina with posterior margin rounded and heavily sclerotised, blade-like;** (the hadenine tribe Leucaniini also have heavily sclerotised ovipositor lobes, but these are laterally flattened);
- 2 the ovipositor can be seen in many genera without dissection because they protrude from the end of the abdomen and in many genera of Apameina they are strongly bent ventrally; the cone-like ovipositor of Sesamiina and Oxytrypiina are directed posteriorly;
- 3 **ovipositor lobes with two narrow, heavily sclerotised, rod-like structures between them;** these sclerites are very narrow, stick-like in Sesamiina, and even lost in a few species (e.g., a few species of *Apamea* in SE Asia (L. RONKAY, pers. comm.); and
- 4 **pleural sclerite double and shaped like a double helix (like DNA) with an enlarged plate on one**

**strand for the muscle attachment (occasionally reduced in some genera); and
5 larvae associated with monocotyledons as host plants.**

The tribe comprises approximately 1000 species, mainly distributed in the north temperate and northern subtropical zones (although a few species are known from the tropics and the arctic). Three subtribes are included: Apameina GUENÉE, Sesamiina FIBIGER and GOLDSTEIN, **new subtribe**, and Arzamina GROTE. All three subtribes are under revision (FIBIGER and GOLDSTEIN for the Old World in Noctuidae Europaeae; GOLDSTEIN, QUINTER, and FIBIGER for the New World in the North American MONA series). The larvae of all three subtribes, and the closely related Episimeini, are closely associated with monocotyledonous hosts.

Noctuidae, Xyleninae, Apameini, subtribe Apameina, stat. nov.

The subtribe Apameina includes the great majority of the genera in the tribe. The tribe is defined by one prominent autapomorphy:

1 ovipositor lobes heavily sclerotised, flattened dorsoventrally (flattened cones in a few species)
(see above).

The North American genera referable to the Apameina are the 30 genera listed in FRANCLEMONT and TODD (1983) from *Apamea* OCHSENHEIMER (page 137) to *Peraniana* STRAND (p. 139) with the exception of *Parastichtis* HÜBNER (Xyleninae: Xylenini), and "*Oligia*" *marina* (GROTE), "*O.*" *mactata* (GUENÉE), and "*O.*" *illocata* (WALKER) (Xyleninae: Caradrinini).

Noctuidae, Xyleninae, Apameini, subtribe Sesamiina FIBIGER and GOLDSTEIN, 2005, subtribe nov.

Type genus: *Sesamia* GUENÉE

The subtribe circumscribes a large monophyletic unit of relatively few genera but numerous species. The species are stem-borers, and the majority are pests of significant economical importance. The subtribe is distributed primarily in the Old World tropics and subtropics. Because of the larval habits and importance, diagnoses for the genera and their possible control have been well studied and described (e. g., TAMS and BOWDEN, 1953, BOWDEN, 1956, NYE, 1960, CARTER, 1984, LAPORTE, 1984, and HOLLOWAY, 1989, and pers. comm.). The Sesamiina comprises 201 species distributed in 10 nominal genera (which probably should be reduced): *Sesamia* GUENÉE (59 species); *Acrapex* HAMPSON (89 species); *Busseola* THURAU (16 species); *Manga* BOWDEN (2 species); *Conicofrontia* HAMPSON (3 species); *Carelis* BOWDEN (2 species); *Poecopa* BOWDEN (1 species); *Poconoma* TAMS and BOWDEN (7 species); *Sciomesa* TAMS and BOWDEN (20 species); and *Tridentifrons* WARREN (2 species).

We define Sesamiina by the following character states (**autapomorphies in bold**):

- 1 forewing pattern straw-coloured or greyish (including the veins, which excludes the Leucaniini), and often with a few longitudinal streaks, but with no transverse lines and almost always without stigmata;**
- 2 basal half of valve costa heavily sclerotised, concave, short and broad, often ending in a broad free process; remainder of valve membranous** (except sacculus, clasper and digitus);
- 3 cucullus membranous, without subapical constriction or corona;
- 4 clasper, ampulla (if present), and digitus (if present) located on distal portion of valve;
- 5 anellus heavily sclerotised, clothed with small spines;
- 6 aedeagus with caecum very long; ductus ejaculatorius near middle of aedeagus;
- 7 carina of aedeagus often with one or more spines;
- 8 vesica globular, with one or more sclerotised patches or cornuti;
- 9 ovipositor conical, acute or rounded, with many short setae, these often larger ventrally and directed anteriorly (i.e., towards base of ovipositor);**
- 10 ovipositor directed posteriorly** (similarly to Oxytrypiina and not like Apameina where they bend ventrally; and
- 11 rod-like bars between ovipositor lobes very narrow or absent** (those of Apameina are relatively broad, rod-like; those of Oxytrypiina are weak).

Noctuidae, Xyleninae, Apameini, tribe Oxytrypiina, stat. rev.

The systematic position of the widely distributed but rarely collected *Oxytrypia orbiculosa* (ESPER) has long been debated. STAUDINGER, who described the genus (1871) placed it between *Valeria* STEPHENS (Psaphidinae, Psaphidini) and *Luperina* BOISDUVAL (Apameini, Apameina). NYE (1975) place it in Noctuidae. GOZMANY (1970) described a new monotypic subfamily Oxytypiinae for the species and placed it next to Plusiinae, Colocasiinae, Pantheinae and Dilobinae. HACKER (1989) incorporated it provisionally in the Heliiothinae. SUGI (1982), FIBIGER and HACKER (1991), VIVES MORENO (1994), RAKOSY (1996), and LERAUT (1997) placed it among *Trachea* OCHSENHEIMER, *Heterophysa* BOURSIN, and *Thalpophila* HÜBNER (all in Xyleninae, Dypterygini). BECK (1999) placed it as a subtribe of Apameini, between Dasypliina and Apameina. After reexamination of its morphology, we confirm the latter position in Apameini (although not associated with *Dasypliina* GUENÉE, which belongs in the Psaphidinae).

The subtribe is defined by the following character states (including tribal characteristics to support the placement of the Oxytrypiina in the Apameini) (**apomorphic states in bold**):

- 1 larvae borers (Apameini);
- 2 uncus short, broad, high (some Apameini);
- 3 pleurite helicoidal (Apameini);
- 4 **cucullus finger-like, without subapical constriction nor corona** (similar to Sesamiina);
- 5 clavus heavily sclerotised, triangular, with short spines (cf., Apameina, *Mesapamea* HEINICKE);
- 6 digitus and ampulla prominent, stout, short (ampulla similar to some Asian Apameina, digitus typical Apameini);
- 7 aedeagus long and narrow, with a short, plate-like, triangular carina (similar to some *Apamea*);
- 8 vesica a narrow tube (as in Apameina), projecting laterally to right with a posterior bend (as in Xylenini);
- 9 vesica shorter than aedeagus and with subapical spicules (as in Xylenini);
- 10 **ovipositor heavily sclerotised, narrow and pointed** (though still slightly dorsoventrally flattened, as in Apameina);
- 11 **rod-like plates between ovipositor lobes absent** (though irregular sclerites present);
- 12 postvaginal plate (including antrum) with spinules (as in Apameina);
- 13 antrum heavily sclerotised ventrally, slightly wider than long (as in many Noctuidae);
- 14 **ductus bursae basally with a circular pouch** (somewhat similar subbasal pouches present in some species of *Luperina* BOISDUVAL and *Mesapamea* (Apameina)).

Noctuidae, Xyleninae, Apameini, subtribe Arzamina

The Arzamina lack the characteristic ovipositor lobes of other Apameini but are included here on the basis of the larval characters given by CRUMB (1956, group 8). The larva, like most Apameini other than *Apamea*, are borers. The Arzamina bore in the stems of aquatic and semi-aquatic monocots and the larvae are able to swim (snake-like) between plants. The posterior pair of spiracles are modified to point backwards to enable the larva to breathe while almost completely submerged in water.

The subtribe is characterised by the structurally reduced, compact, male genital capsule: the tegumen is short and thick, abruptly expanded posteriorly into a pencillus lobe; the valve is short and rounded with the clasper and broad ampulla near the apex of the valve; there is no digitus or modified cucullus. The rounded, blade-like, outer margin of the ovipositor lobes are adapted to cutting the plant tissue to insert the eggs into the aquatic monocots on which the larvae feed. The subtribe includes only the genus *Bellura* WALKER (*Arzama* WALKER on which the subtribal name is based is a synonym).

Noctuidae, Xyleninae, tribe Episemini

The tribe Episemini needs revision to determine its composition and position in the Noctuidae. The tribe was treated in detail by RONKAY et al. (2001) and we accept their treatment of the group pending molecular data that may shed more light on its composition and placement.

The tribe includes two groups of genera that are only tentatively associated, seven genera related to *Episema* OCHSENHEIMER, and three groups related to *Ulochlaena* LEDERER. In both groups the valve is simplified with the only armature being the stout C-shaped clasper that projects over the dorsal margin of the valve. The apex of the vesica has one or two apical patches of cornuti, a common feature of most Xylenini and Hadenini. In the female genitalia the ovipositor lobes are generally short and truncated, not at all like those of the Apameini (although those of *Cleoceris* BOISDUVAL are similar to some Apameini). We place the Episemini after the Apameini because the form of mandible and spinneret are similar to those of Apameini, the cervical shield has a similar

patch of tonofibrillary platelets between setae XD2 and D2, and the larvae bore in the bulbs of Liliaceae. The second group of genera are grass feeders, also a common host group of members of the Apameini.

Noctuidae, Xyleninae, tribe Xylenini

The tribe Xylenini corresponds to the Cuculliinae of HAMPSON (1906) after the cuculline group of subfamilies are removed. HAMPSON defined the group on the basis of the long hair-like lashes hanging over the eye from both behind the eye and especially from in front of the eye at the base of the antenna. While this character is useful for associating moths with the Xyleninae, it is associated with the overwintering habits of the adults and is less prominent (or absent) in non-overwintering genera.

The male genitalia are characterised by the very large digitus which forms a sclerotised area along the costal margin of the valve and is often partially or completely fused with the apical portion of the valve.

Two behavioural characteristics of the members of the tribe are the fall flight of the adults, with many species in the subtribe Xylenina overwintering as adults and flying again in the spring, and the use of woody host plants by the larvae.

Noctuidae, Xyleninae, tribe Xylenini, subtribe Xylenina

The male genitalia of the Xylenina are characterised by the long, twisting ampulla of the clasper that extends well beyond the dorsal margin of the valve; the ampulla usually has one or more abrupt angles (not straight or evenly curved like most other groups). The digitus forms a sclerotised area along the costal margin of the valve, often extending over the dorsal part of the cucullus (covering the entire cucullus in *Xylena* OCHSENHEIMER). The long plate-like digitus often has one or more ventral extensions towards the ventral margin of the valve and may form a pollex-like process, or extend over the end of the cucullus to form an apical spine-like process.

The larva has a narrow tubular spinneret that is usually about as long as the labial palpi (much longer in some species of *Lithophane* and *Conistra*); also the apical seta on the labial palpus is usually longer than the basal segment.

The European genera in the subtribe are listed in FIBIGER and HACKER (2005). The North American genera referable to the Xylenina are the 20 genera listed in FRANCLEMONT and TODD (1983) from *Xylina* OCHSENHEIMER (page 144) to *Hillia* GROTE (p. 145), and the genera *Brachylomia* HAMPSON, *Parastichtis* HÜBNER, *Lomilysis* FRANCLEMONT, and *Epidemas* SMITH.

Noctuidae, Xyleninae, tribe Xylenini, subtribe Antitypina

The genera associated with the subtribe Antitypina differ from those in the Xylenina in having a short ampulla on the clasper, this usually not extending over the costal margin of the valve.

The larva has a short, broad spinneret with a distinct dorsal groove. As in the Xylenina the apical seta on the labial palpus is usually longer than the basal segment.

The European genera in the subtribe are listed in FIBIGER and HACKER (2005). North American genera are: *Andropolia* GROTE, *Dryotype* HAMPSON, *Fishia* GROTE, *Mniotype* FRANCLEMONT, *Pachypolia* GROTE, *Platypolia* GROTE, *Pseudohadena* ALPHÉRAKY, *Rhizagrotis* SMITH, *Sutyna* TODD, and *Xylotype* HAMPSON.

Noctuidae, subfamily Ufeinae

We have placed the subfamily Ufeinae after the Xyleninae on the suggestion of Andrew MITCHELL (pers. comm.) to better reflect changes in classification that are resulting from ongoing molecular research. The subfamily has traditionally been associated with the Noctuidae on the basis of the spiniform setae on the tibiae, but this character state is not reliable in reflecting relationships because similar setose tibiae also occur in some genera of Hadeninae: Eriopinae, Xyleninae: Xylenini: Antitypina, Heliiothinae, and Stiriinae: Grotellini. The adults of the Ufeinae overwinter and the larvae feed on wood plants, as in many genera in the Xylenini.

Noctuidae, subfamily Hadeninae, stat. rev.

We reinstate the subfamily Hadeninae in its traditional more restricted usage partly to emphasise that the six

tribes it contains probably represent a monophyletic group, and partly because of the uncertainty of the relationships among the Xyleninae, Hadeninae, and Noctuidae.

The subfamily has traditionally been defined as trifold noctuids with hairy eyes (hairs projecting from the surface of the eye between the facets). The presence of hair on the eyes of other Noctuidae (e.g., Pantheinae and some Noctuidae: some northern *Feltia* and *Xestia* species) led KITCHING and RAWLINS (1998) to combine the Hadeninae with most of the former catch-all subfamily "Amphipyriinae" (after *Amphipyra* had been removed) and a portion of the Cuculliinae (the tribe Xylenini). While hairy eyes occur occasionally in other noctuids and are occasionally lost in some hadenines (e.g., some species of *Protorthodes* McDUNNOUGH, *Trichocerapoda* BENJAMIN, and *Escaria* GROTE), this character is still immensely useful in associating the vast majority of Hadeninae. The Hadeninae, however, are characterised by more than hairy eyes and these characters suggest a possible relationship with the Noctuidae. CRUMB (1956) was unable to separate the subfamilies Hadeninae (s.s.) and Noctuidae in his larval key, because in both subfamilies the spinneret is dorsoventrally flattened with the opening a narrow transverse slit. In addition, the opening of the spinneret is fringed in both subfamilies; in the Hadeninae this varies from minute serrations on the dorsal margin of the spinneret (tribes Hadenini and Orthosiini), to deeply lacerate fringes on both margins (tribe Leucaniini). These larval characteristics contrast with two male genitalia character states that suggest a relationship with the Xyleninae. In most genera of both the Hadeninae and Xyleninae there is a patch or field of spines on the apical half of the vesica, and the dorsal margin of the sacculus is irregular towards the base, often with a roughened area of hairy or spiny processes.

In addition to the characters shared by the Xylenini and Hadeninae described above, the tribe Orthosiini share some characteristics with the Xylenini in that digitus is enlarged and fused with the apical portion of the valve, and the larvae in both groups feed on woody plants. By contrast, the habits of the adults differ with those of the Xylenini flying in the fall (sometimes overwintering and flying again in the spring), whereas those of the Orthosiini fly in the spring. The shared character states between the Xylenini and Hadeninae, and more particularly between the Xylenini and Orthosiini (described above), may suggest a point of derivation for the Hadeninae from within the Xyleninae. For this reason we place the Orthosiini at the base of the Hadeninae so that they follow the Xylenini in the sequence of taxa.

We arrange the Hadeninae in six tribes.

Noctuidae, Hadeninae, tribe Orthosiini

Most orthosiines overwinter as fully developed adults in the pupa and emerge very early in the spring. The hairy body vestiture are adaptations for this early season emergence.

The members of the tribe Orthosiini are best characterised by the structure of the larval hypopharynx. The hypopharynx is divided by a deep transverse groove, as in the Hadenini and Leucaniini, but the spines on the anterior lobe are mainly confined the posterior portion of the lobe and are coarse, stout, triangular spines, not minute spinules or thin spines as in other tribes. Also the spinneret is short, usually about as long as wide, or less. Other characters are similar to the Hadenini (e.g., hypopharynx with median transverse cleft; mandible with one or two prominent teeth on the inner surface; spinneret with a minute fringe in the middle of the upper margin). The larvae feed on the woody plants. The adults and genitalia of the European fauna are described and illustrated by RONKAY et al. (2001).

Noctuidae, Hadeninae, tribe Tholerini, stat. rev.

The North American genus *Nephelodes* GUENÉE, and the Holarctic genera *Tholera* HÜBNER and *Cerapteryx* CURTIS (introduced into North America) were listed at the end of the *Orthosia* group of genera by both FRANCLEMONT and TODD (1983) and BECK (1999–2000); although the latter two genera were placed in the subtribe *Tholerina* by BECK. These three genera share a number of peculiar features that preclude their placement in any other tribe. Although the larva and habitus of the adult are most similar to those of species in the Orthosiini, they differ from the Orthosiini in having an undivided hypopharynx, the first inner ridge of the mandible is modified into a thickened rounded basal process, the larvae feed on herbaceous plants rather than woody plants, and the adults fly in late summer and early autumn rather than the early spring. On the basis of these characters we include these three genera in the tribe Tholerini.

Noctuidae, Hadeninae, tribe Hadenini

The larvae of the Hadenini are characterised by the presence of a transverse cleft on the hypopharynx (reduced

in the North American genus *Trichordestra* McCABE); apical lobe of hypopharynx covered with short fine spines, usually to the base of the labial palpi; mandible with one or two teeth on the inner surface (sometimes reduced to swellings on the first or second ridge; absent in some species of *Anarta* and *Hadena*); spinneret usually about 1–2 X as long as wide with a minute fringe in the middle of the upper margin. The tribe was diagnosed and the European fauna illustrated by HACKER et al. (2002).

Noctuidae, Hadeninae, tribe Leucaniini

The tribe Leucaniini (= Mythimnini) are easily defined with derived character states. In the larva the apical lobe of the hypopharynx is densely clothed with long hairlike spines forming an apical “brush;” the mandible is adapted to crushing silica in the grasses on which the larvae feed with the normal ridges on the inner surface replaced by a heavily sclerotised molar area, and the row of apical teeth are replaced by a thick, rounded crushing surface; the spinneret is deeply lacerated on both the upper and lower margins. The larvae have the cryptic longitudinally striped pattern typical of many grass-feeders. The ovipositor lobes are unique in shape (heavily sclerotised, laterally compressed, blade-like) and usually visible ventrally when the moth is in a resting position. The diversity of the male genitalia, are illustrated in HACKER et al. (2002). The adults can generally be recognised by the fine longitudinal streaking of the forewing but a similar pattern occurs convergently in other grass-feeding groups of noctuids as well.

Noctuidae, Hadeninae, tribe Eriopygini FIBIGER and LAFONTAINE, tribe nov.

Type genus: *Eriopyga* GUENÉE, 1852

The name Eriopygini was first proposed as a tribe of the Hadeninae by FRANCLEMONT and TODD (1983) in a North American check list, but like other new tribal names proposed in this list, the name is a nomen nudum.

The Eriopygini is best defined by larval characters:

- 1 the hypopharynx is undivided, without the distinctive transverse groove separating the basal and distal lobes in other Hadeninae;
- 2 the mandible lacks an inner tooth (rarely lost in other Hadeninae);
- 3 the spinneret is long and narrow, usually 2–3 X as long as wide;
- 4 the fringe at the apex is confined to a small area at the end of the narrow dorsal groove.

The adults of Eriopygini do not have diagnostic tribal characters like the larvae, but a number of characters are found in many genera and these are helpful for associating adults with the tribe. Many genera (e.g., *Trichorthosia* GROTE, *Mimobarathra* BARNES and McDUNNOUGH, *Trichofeltia* McDUNNOUGH, and *Trichagrotis* McDUNNOUGH) have spiniform setae on the middle and hind tibiae and the species were originally classified as hairy-eyed Noctuidae by HAMPSON (1903) and McDUNNOUGH (1929). In most genera the vesica is long and tubular, usually about 2–3 X as long as the aedeagus; the vesica usually has one to several tight subbasal coils and more open coils towards the apex. In many genera there is a series of long peg-like cornuti that form a straight row in the basal area of the vesica. The genus *Eriopyga* has an amazing amount of structural variation between species; the type species *E. punctulum* GUENÉE has the costal part of the valve and the tegumen greatly enlarged.

The Eriopygini is most diverse in South America but at least 26 genera occur as far north as the United States and 10 as far as Canada. Traditionally the genera *Lasionycta* AURIVILLIUS and *Lacinipolia* McDUNNOUGH have been associated with the Hadenini near *Hadena* SCHRANK, but the larvae (described and illustrated by GODFREY, 1972) show that they are members of the Eriopygini.

In Eurasia the tribe is represented only by *Lasionycta* AURIVILLIUS (= *Eriopygodes* HAMPSON, 1905; = *Anartomima* BOURSIN, 1952; = *Lasionhada* BERIO, 1981). Curiously, *Lasionycta* and its generic synonyms were treated as full genera and were widely scattered among the tribes Apameini, Ipimorphini, and Hadenini by BECK (1999-2000). *Clemathada calberlai* (STAUDINGER) has sometimes been put in the genus *Lasionycta* and is the basis of the subtribal name Clemathadina BECK; however, it belongs in the Hadenini on the basis of the strongly divided hypopharynx and the large inner tooth on the mandible.

In North America we add the genera *Lasionycta*, *Lacinipolia*, and *Trichocerapoda* to the genera listed in the Eriopygini by FRANCLEMONT and TODD (1983).

Noctuidae, Hadeninae, tribe Glottulini

This tribe was raised to a subfamily by KITCHING and RAWLINS (1998), mainly on the basis of the two SV setae on T2 and T3, and the pale waxy bloom on the pupa, both characters normally associated with the Catocalinae in the Erebiidae and in the Arctiidae. All other characters, however, suggest an association with the trifold noctuids and the tribe was moved back into the Hadeninae by YELA and KITCHING (1999). Since the larval spinneret is short, flat, and apically fringed, we include the Glottulini as a tribe of the Hadeninae.

Noctuidae, subfamily Noctuinae

We arrange the genera of the Noctuinae into two tribes and each tribe into two subtribes. Of the two tribes we list the tribe Agrotini first because it includes the subtribe Austrandesiina, the most primitive group of genera in the subfamily. Many previous lists have placed the Agrotini last with *Agrotis* at the end, seemingly based on a misconception that the relative simple valve structure of *Agrotis* and that of members of the subfamily Heliothinae were related and that *Agrotis* was the lineage from which the Heliothinae were derived. The genus *Peridroma* HÜBNER has the most basic male genitalia of any genus in the Noctuinae and could serve as a structural prototype for basal lineages in both the Hadeninae and Xyleninae. *Peridroma* and its South American relatives are the only genera in the Noctuinae that retain fully developed and functional basal abdominal brushes, pockets, and levers like those of other trifold subfamilies. We have found that one lineage of African Noctuini has a highly autapomorphic basal abdominal coremata that lies in a single ventral pocket on the second sternite, and is not homologous to the brush organs that occur widely through the trifold noctuids (see “abdominal coremata” above under “Description of Principal Characters”); a superficially similar brush and pocket in some species of *Leucania* OCHSENHEIMER is very different in its details (three double-flaps on the sternites 2, 3 and 4) and is obviously independently derived.

The subfamily Noctuinae was defined by HAMPSON (1903) [under the name Agrotinae] as trifold noctuids with spines (actually heavily sclerotised setae) on the tibiae. Over the past century this definition has continued to be the basis of the subfamily with the caveat “except those groups which are related to genera with unspined tibia.” This has resulted in HAMPSONIAN noctuine genera being removed from the Noctuinae and placed in the Hadeninae: Eriopygini (e.g., *Trichorthosia*, *Trichagrotis*, *Mimobarathra*), the Cuculliinae: Oncochemidini (e.g. *Adita* GROTE), the Xyleninae: Apameini (e.g., *Apamea niveivenosa* (GROTE), formerly in *Protagrotis* HAMPSON because of the presence of a few tibial setae), the Xyleninae: Xylenini (e.g., *Sutya* TODD, *Mesogona*), the Heliothinae, and the Ufeinae. KITCHING and RAWLINS (1998) redefined the Noctuinae on the basis of the distinctive wing folding mechanism of the adults in which the wings are held flat over the back and overlap broadly so that the costa of the two forewings are largely parallel to each other and to the sides of the body. Most other noctuids hold the wings roof-like over the body with the posterior margins of the forewings parallel so that the outline of the moth at rest is an elongated triangle. In terms of larvae the subfamily is mainly characterised by the relatively short, flat spinneret with the upper apical margin (occasionally the lower also) fringed or lacerate.

The subfamily Noctuinae was revised for Europe by FIBIGER (1990, 1993 and 1997a), and for North America by LAFONTAINE (1987, 1998, 2004).

Noctuidae, Noctuinae, tribe Agrotini

The classification of the tribe Agrotini and its two subtribes, the Austrandesiina and Agrotina, was discussed in detail by us recently (LAFONTAINE and FIBIGER, 2004) and the characters defining the tribe and the two subtribes and its South American origin will not be repeated here.

Noctuidae, Noctuinae, Agrotini, subtribe Austrandesiina

The subtribe Austrandesiina is found mainly in South America where 25 genera occur. Five of these genera occur as far north as Mexico, three as far as the United States, and one species, *Peridroma saucia* (HÜBNER), has become almost worldwide in distribution, partly because of its migratory habitats and probably also with the assistance of man. In most of its range, including Eurasia, it is the only representative of the Austrandesiina. The presence of basal abdominal brushes in males, often thought to be found in the Noctuinae only in *Peridroma saucia*, are actually widely distributed within the Austrandesiina.

Noctuidae, Noctuinae, Agrotini, subtribe Agrotina

The subtribe Agrotina is almost worldwide in distribution, mainly because of the wide distribution of *Agrotis* itself. All of the genera of the Agrotina are listed below. Taxa found in Europe are denoted with an asterisk*. Taxa occurring in North America are shown with two asterisks**.

- Subtribe **Agrotina** RAMBUR, 1848 * **
- Striacosta** LAFONTAINE, 2004 **
- Actebia** STEPHENS, 1829 * **
 - Subgenus **Actebia** STEPHENS, 1829 * **
 - Subgenus **Protexarnis** McDUNNOUGH, 1929 * **
 - Subgenus **Parexarnis** BOURSIN, 1946 *
 - Subgenus **Hemiexarnis** STEPHENS, 1829
 - Subgenus **Perissandria** WARREN, 1909
 - Subgenus **Ledereragrotis** VARGA, 1991 *
- Dichagyris** LEDERER, 1857 * **
 - Subgenus **Albocosta** FIBIGER and LAFONTAINE, 1997 *
(= *Basistriga* FIBIGER and LAFONTAINE, 1997)
 - Subgenus **Stenosomides** STRAND, 1942 *
 - Subgenus **Dichagyris** LEDERER, 1857 *
(= *Yigoga* NYE, 1975; = *Phleboeis* CHRISTOPH, 1887)
 - Subgenus **Loxagrotis** McDUNNOUGH, 1929 **
 - Subgenus **Pseudorichia** LAFONTAINE, 2004 **
 - Subgenus **Pseudorthosia** GROTE, 1874 **
 - Subgenus **Mesembragrotis** BENJAMIN, 1927 **
- Eucrotopocnemis** GROTE, 1874 * **
 - Subgenus **Eucrotopocnemis** GROTE, 1874 **
 - Subgenus **Cladocerotis** HAMPSON, 1903 *
(= *Pachyagrotis* BOURSIN, 1953)
 - Subgenus **Manruta** SMITH, 1903 **
 - Subgenus **Desertica** LAFONTAINE, 2004 **
- Richia** GROTE, 1887 **
- Copablepharon** HARVEY, 1878 **
- Protogygia** McDUNNOUGH, [1929] **
- Euxoa** HÜBNER, [1821] * **
 - Subgenus **Crassivesica** HARDWICK, 1970 **
 - Subgenus **Chorizagrotis** SMITH, 1890 * **
 - Subgenus **Palaeoeuxoa** LAFONTAINE, 1987 **
 - Subgenus **Heteroeuxoa** LAFONTAINE, 1987 **
 - Subgenus **Longivesica** HARDWICK, 1970 **
 - Subgenus **Pleonectopoda** GROTE, 1873 * **
 - Subgenus **Euxoa** HÜBNER, [1821] * **
 - Subgenus **Orosagrotis** HAMPSON, 1903 * **
- Feltia** WALKER, 1856 * **
 - Subgenus **Feltia** WALKER, 1856 **
 - Subgenus **Trichosilia** HAMPSON, 1918 * **
- Agrotis** OCHSENHEIMER, 1816 * **
(= *Lycophorus* STAUDINGER, 1901; = *Powellinia* OBERTHÜR, 1912).

Noctuidae, Noctuinae, tribe Noctuini

The primitive genera of the Agrotini are found in South America, whereas, those of the Noctuini occur in southern Africa. The classification of the Noctuini was reviewed by LAFONTAINE (1998) and the African genera of the tribe were considered basal lineages associated either with *Ochropleura* HÜBNER or with *Diarsia* HÜBNER, the latter association based mainly on the deeply excavated ventral margin of the valve below the cucullus. We now include all of the sub-Saharan genera of the Noctuini in the subtribe Axyliina.

Noctuidae, Noctuinae, Noctuini, subtribe Axyliina FIBIGER and LAFONTAINE, **subtribe nov.**

Type genus: *Axylia* HÜBNER, [1821]

The subtribal name Axyliina was first proposed by BECK (1996) in a check list with a footnote that says "this subtribe is justified on the basis of the habitus of the adult and the pattern of the larva (BECK, 1960)" (translated from BECK, 1996:19); the type is listed as "*Axylia putris* (LINNAEUS)." This cannot be accepted as a description because no diagnostic characters are given to define the tribe. The reference to the 1960 description of the larva of *Axylia putris* is also insufficient to validate the taxon because no suprageneric characters are given or discussed in the 1960 larval description that would have defined and supported the 1996 proposal of the name. BECK (1999) diagnosed the subtribe as "characterised by the wing pattern and wing-folding of the adult, the genital structure, and the specific pattern of the larva and dorsal warts on S1, S2, and S8" (BECK, 1999: 654). Again, this is a list of structural features that may contain diagnostic features but none is given. As a result, we validate the name Axyliina here and use BECK's (1996) unavailable name in order to retain Axyliina for this large African group of genera.

The subtribe Axyliina is defined here by the following character states (**apomorphies in bold**):

- 1 forewing pattern surprisingly consistent: reniform and often orbicular prominent, or with a contrasting black patch between them;
- 2 uncus prominent; some genera with **dorsal processes and apex upturned** (an upturned apex also occurs in some genera in the South American subtribe Austrandesiina);
- 3 valve usually broadest medially (illustrated in BAYER, 1964) and BERIO, 1972);
- 4 corona present (pleisiomorphic) (lost in most Noctuini);
- 5 clavus absent;
- 6 ampulla prominent, oblique, directed posterodorsally;
- 7 pollex often prominent (easily misinterpreted as an extension of the sacculus);
- 8 digitus often present;
- 9 **vesica long (much longer than aedeagus) and projecting posteriorly from aedeagus (appearing as a continuation of the aedeagus)**;
- 10 **vesica with a large, dorsal, pouch-like diverticulum subbasally, which has a cornutus on top, or is covered with spinules** (illustrated in FIBIGER, 1997a, and LAFONTAINE, 1998);
- 11 appendix bursae often arising posteriorly on corpus bursae.

The genera of the Axyliina listed below can be arranged in three groups (some more generic taxa occur in Africa):

Ochropleura group

Ochropleura HÜBNER
Mentaxya GEYER
Euneophlebia BERIO
(= *Euxootera* FLETCHER)¹
(= *Pseudelyptron* BERIO)
Episcotia BERIO
Efracilis BERIO

Amazonides group

Amazonides FLETCHER
(= *Stilbotis* BERIO)
Micraxylia BERIO
(= *Hyperfrontia* BERIO)
Brachytegma BERIO
Mabilleana FLETCHER

Axylia group

Axylia HÜBNER
(= *Micragrotis* HAMPSON)
Psectraxylia FLETCHER

¹ These genera were synonymised in LAFONTAINE (1998) but *Euxootera* was listed as the senior synonym in error (Albert LEGRAIN, pers. comm.).

The *Ochropleura* group is characterised by the presence of a clavus which is fused to the base of the sacculus, and by apical modifications of the uncus. The *Micragrotis* group usually has four rows of tarsal setae (an extra outer row on the middle and hind basitarsi); the frons is bulging or tuberculate in *Micragrotis* and *Amazonides*; the valve is deeply excavated ventrally below the cucullus with the ventral margin of the cucullus produced into a pollex-like extension in *Mabileana* and *Amazonides*. In the *Axyliia* group there is usually a complete row of sclerotised setae on the inner and outer margins of the foretibia, and the ampulla of the clasper is represented by a small setose knob.

The subtribe Axyliina is represented in Europe by two species of *Ochropleura* and one species of *Axyliia*. One species of *Ochropleura* occurs in the eastern Palaearctic, and a few undescribed species of *Axyliia* and *Ochropleura* occur in Southeast Asia, the Oriental Region, and the Indo-Australian Region.

It is represented in the New World by one species of *Ochropleura*. It is not yet clear whether records of *Ochropleura plecta* from Ecuador represent an introduction or are mislabelled European specimens.

Noctuidae, Noctuinae, Noctuini, subtribe Noctuina

The subtribe Noctuina is characterised mainly by losses of character states. Most genera have lost the fourth row of tarsal setae; there is a progressive loss of foretibial setae (first the outer row of setae, then the inner row); the digitus and corona are lost in most genera; the cucullus is reduced to a rounded apex and in many genera it becomes tapered or even pointed; in the bursa copulatrix the sclerotised ventral plates on the ostium bursae and ductus bursae are separated by an unsclerotised band. The larvae are also characterised by their lack of the derived character states (e.g., smooth skin, frontal punctures located below the frontal setae; mandible with tooth on inner surface) compared with the Agrotini (e.g., granular skin in more derived genera, frontal punctures between the frontal setae; mandible without a tooth on the inner surface). The sequence of genera for the Noctuina used in the check list (FIBIGER and HACKER, this volume) follows that of the North American genera in LAFONTAINE (1998).

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Appendix

Family group names of Noctuoidea

This list of valid family group names is based on SPEIDEL and NAUMANN (2005) and is arranged in alphabetical order by family, subfamily, and tribe. Many of the names proposed by BECK (1996) as foot notes in his European check list of Noctuidae are nomen nuda in that no diagnostic characters are given; the names are based almost entirely on European taxa without considering the fauna of the whole Palaearctic Region, or that of other parts of the world. Many of the taxa proposed in 1996 are not validated until BECK (1999).

ARCTIIDAE

Arctiinae

Arctiini

- Arctiidae** LEACH, [1815], type genus: *Arctia* SCHRANK, 1802
- Cosciniini** BÖRNER, 1925, type genus: *Coscinia* HÜBNER, [1819]
- Deilemerinae** SWINHOE, 1904, type genus: *Deilemera* HÜBNER, [1820]
- Micrarctiinae** SEITZ, 1910, type genus: *Micrarctia* SEITZ, 1910
- Rhodogastrinae** KIRIAKOFF, 1950, type genus: *Rhodogastria* HÜBNER, [1819]
- Spilosominae** SEITZ, 1910, type genus: *Spilosoma* CURTIS, 1825

Callimorphini

- Callimorphidae** WALKER, [1865], type genus: *Callimorpha* LATREILLE, 1809
- Eucheliinae** TUTT, 1896, type genus: *Euchelia* BOISDUVAL, 1828
- Euplagiini** AGENJO, 1946, type genus: *Euplagia* HÜBNER, [1820]
- Nyctemeridae** WALKER, [1865], type genus: *Nyctemera* HÜBNER [1820]
- Utetheisini** FORBES, 1960, type genus: *Utetheisa* HÜBNER, [1819]

Ctenuchini

- Antichlorinae** BUTLER, 1876, type genus: *Antichloris* HÜBNER, 1818
- Belemniini** FORBES 1939, type genus: *Belemnia* WALKER, 1854
- Ctenuchidae** KIRBY, 1837, type genus: *Ctenucha* KIRBY, 1837
- Eunomiinae** BUTLER, 1876, type genus: *Eunomia* HÜBNER, 1818

Euchromiini

- Euchromiinae** BUTLER, 1876, type genus: *Euchromia* HÜBNER, [1819]

Pericopini

- Hypocritidae** DYAR, 1897, type genus: *Hypocrita* HÜBNER, [1807]
- Pericopidae** WALKER, [1865], type genus: *Pericopis* HÜBNER, [1819]

Phaegopterini

- Phaegopterinae** KIRBY, 1892, type genus: *Phaegoptera* HERRICH-SCHÄFFER, [1853]

Lithosiinae

Acsalini

- Acsalini** BENDIB and MINET, 1999, type genus: *Acsala* BENJAMIN, 1935

Cisthenini

- Cisthenini** BENDIB and MINET, 1999, type genus: *Cisthene* WALKER, 1854
- Clemensiti** BENDIB and MINET, 1999, type genus: *Clemensia* PACKARD, 1864

Endrosini

- Endrosinae** BÖRNER, 1932, type genus: *Endrosa* HÜBNER, [1819]

Eudesmiini

- Eudesmiini** BENDIB and MINET, 1999, type genus: *Eudesmia* HÜBNER, [1823]

Lithosiini

- Eileminia** BIRKET-SMITH, 1965, type genus: *Eilema* HÜBNER, [1819]
- Lithosides** BILLBERG, 1820, type genus: *Lithosis* BILLBERG, 1820

Nudariini

- Nudariidae** WALKER, [1865], type genus: *Nudaria* HAWORTH, [1809]

Phryganopterygini

- Phryganopterygini** BENDIB and MINET, 1999, type genus: *Phryganopteryx* SAALMÜLLER, 1884

Syntomiinae

Syntomini

- Amatidae** JANSE, 1917, type genus: *Amata* Fabricius, 1807
- Syntomides** HERRICH-SCHÄFFER, [1846], type genus: *Syntomis* OCHSENHEIMER, 1808

Thyretini

- Automolidae** AURIVILLIUS, 1892, type genus: *Automolis* HÜBNER, [1819]
- Hexaneuridae** WALLENGREN, 1865, type genus: *Hexaneura* WALLENGREN, 1860
- Thyretinae** BUTLER, 1876, type genus: *Thyretes* BOISDUVAL, 1847

DOIDAE

- Doidae** DONAHUE and BROWN, 1987, type genus: *Doa* NEUMOEGEN and DYAR, 1894

EREBIDAE

Araeopteroninae

- Araeopteroninae** FIBIGER, 2005, type genus: *Araeopteron* HAMPSON, 1893

Aganainae

- Aganaidae** BOISDUVAL, 1833, type genus: *Aganais* BOISDUVAL, 1832
- Asotinae** TURNER, 1904, type genus: *Asota* HÜBNER, [1819]
- Hypsidae** WALKER, [1865], type genus: *Hypsa* HÜBNER, [1919]

Aventiinae

- Aventiidae** TUTT, 1896, type genus: *Aventia* DUPONCHEL, 1829

Boletobinae

- Boletobidae** GUENÉE, [1858], type genus: *Boletobia* BOISDUVAL, 1840

Calpinae (s.l.)

Anomini

- Anomiinae** GROTE, 1882, type genus: *Anomis* HÜBNER, [1821]

Calpini

- Calpides** BOISDUVAL, 1840, type genus: *Calpe* TREITSCKE, 1825
- Ophideridae** GUENÉE, 1852, type genus: *Ophideres* BOISDUVAL, 1832
- Othreinae** BERIO, 1955, type genus: *Othreis* HÜBNER, [1823]
- Phyllodini** GUENÉE, 1852, type genus: *Phyllodes* BOISDUVAL, 1832

Scoliopterygini

- Litoprosopinae** GROTE, 1882, type genus: *Litoprosopus* GROTE, 1869
- Scoliopteryges** HERRICH-SCHÄFFER, [1852], type genus: *Scoliopteryx* GERMAR, 1810
= Gonopterini HERRICH-SCHÄFFER, [1850] [unavailable, permanently replaced by Scoliopteryges
HERRICH-SCHÄFFER, [1852]

Anobini

- Anobini** WILTSHIRE, 1990 (nomen nudum, needs validation)

Acantholipini

- Acantholipini** FIBIGER and LAFONTAINE, 2005, type genus: *Acantholipes* LEDERER, 1857
= Acantholipini GOATER, RONKAY and FIBIGER, 2003, unavailable, not explicitly validated

Arytrurini

- Arytrurini** FIBIGER and LAFONTAINE, 2005, type genus: *Arytrura* JOHN, 1912
= Arytrurini GOATER, RONKAY and FIBIGER, 2003, unavailable, not explicitly validated

Catocalini

- Audeini** WILTSHIRE, 1990, type genus: *Audea* WALKER, [1858]
- Catocalidi** BOISDUVAL, [1828] 1829, type genus: *Catocala* SCHRANK, 1802

Euclidiini

- Euclididae** GUENÉE, 1852, type genus: *Euclidia* OCHSENHEIMER, 1816
- Mocisini** BERIO, 1992, type genus: *Mocis* HÜBNER, [1823]
- Poaphilidae** GUENÉE, 1852, type genus: *Poaphila* GUENÉE, 1852
- Remigiidae** GUENÉE, 1852, type genus: *Remigia* GUENÉE, 1852

Hypocalini

- Hypocalini** GUENÉE, 1852, type genus: *Hypocala* GUENÉE, 1852

Melipotini

- Melipotini** GROTE, 1895, type genus: *Melipotis* HÜBNER, 1818
- Synedini** FORBES, 1954, type genus: *Syneda* GUENÉE, 1852

Ophiusini

- Achaeini** WILTSHIRE, [1977], type genus: *Achaea* HÜBNER, [1823]
- Anuini** WILTSHIRE, [1977], type genus: *Anua* WALKER, 1858
- Bendidae** GUENÉE, 1852, type genus: *Bendis* HÜBNER, [1823]
- Catephidae** GUENÉE, 1852, type genus: *Catephia* OCHSENHEIMER, 1816

- Dysgoniidae** MOORE, [1885], type genus: *Dysgonia* HÜBNER, [1823]
Focillidae GUENÉE, 1852, type genus: *Focilla* GUENÉE, 1852
Lagopteridae KIRBY, 1897, type genus: *Lagoptera* GUENÉE, 1852
Omopterini BOISDUVAL, 1833, type genus: *Omoptera* GUÉRIN-MÉNEVILLE, [1832] [an unused suppressed senior synonym of Ophiusidi GUENÉE, 1837]
Ophiusidi GUENÉE, 1837, type genus: *Ophiusa* OCHSENHEIMER, 1816
Pericymatini WILTSHIRE, [1977], type genus: *Pericyma* HERRICH-SCHÄFFER, [1851]
Phaeocymini GROTE, 1890, type genus: *Phaeocyma* HÜBNER, 1818
- Panopodini**
Panopodini FORBES, 1954, type genus: *Panopoda* GUENÉE, 1852
- Toxocampini**
Anumetini WILTSHIRE, [1977], type genus: *Anumeta* WALKER, 1858
Apopestini BECK, 1996, type genus: *Apopestes* HÜBNER, [1823], **syn. nov.**
Exophylini BECK, 1996, type genus: *Exophyla* GUENÉE, 1841, **syn. nov.**
Lygephilini WILTSHIRE, [1977], type genus: *Lygephila* BILLBERG, 1820
Scodionygini WILTSHIRE, [1977], type genus: *Scodionyx* STAUDINGER, 1899, **syn. nov.**
Toxocampidae GUENÉE, 1852, type genus: *Toxocampa* GUENÉE, 1841
- [Catocalinae/Erebinae Unplaced]**
Amphigoniidae GUENÉE, 1852, type genus: *Amphigonia* GUENÉE, 1852 [Catocalinae]
Anydrophilini WILTSHIRE, [1977], type genus: *Anydrophila* JOHN, 1909
Ctenusini BERIO, 1992, type genus: *Ctenusa* HAMPSON, 1910
Ercheiini BERIO, 1992, type genus: *Ercheia* WALKER, [1858] [Catocalinae]
Hulodides GUENÉE, 1852, type genus: *Hulodes* GUENÉE, 1852 [Catocalinae]
Hypogrammidae GUENÉE, 1852, type genus: *Hypogramma* GUENÉE, 1852 [Catocalinae]
Hypopyridae GUENÉE, 1852, type genus: *Hypopyra* GUENÉE, 1852 [Catocalinae]
Ommatophoridae GUENÉE, 1852, type genus: *Ommatophora* GUENÉE, 1852 [Catocalinae]
Speiredoniinae SWINHOE, 1900, type genus: *Speiredonia* HÜBNER, [1823] [Catocalinae]
Tachosini BERIO, 1992, type genus: *Tachosa* WALKER, 1869
Tinoliidae MOORE, [1885], type genus: *Tinolius* WALKER, 1855 [Catocalinae]
Yriidae GUENÉE, 1852, type genus: *Yrias* GUENÉE, 1852
- Coccytiinae**
Coccytides BOISDUVAL, 1874, type genus: *Coccytia* BOISDUVAL, 1828
- Erebinae s. s.**
Dyopsidae GUENÉE, 1852, type genus: *Dyops* GUENÉE, 1852
Erebida LEACH, [1815], type genus: *Erebus* LATREILLE, 1910
Thermesidae GUENÉE, 1852, type genus: *Thermesia* HÜBNER, 1823
Thysaniini GROTE, 1895, type genus: *Thysania* DALMAN, 1824
- Erebinae s. l.**
Eulepidotini GROTE, 1895, type genus: *Eulepidotis* HÜBNER, 1823
= Palindidae GUENÉE, 1852, [unavailable, permanently replaced by Eulepidotini GROTE, 1895]
Arcteini BERIO, 1992 **stat. rev.**
- Eublemminae**
Eublemmini
Eublemmini FORBES, 1954, type genus: *Eublemma* HÜBNER, [1821]
Metachrostini BECK, 1996, type genus: *Metachrostis* HÜBNER, [1820], **syn. nov.**
- Pangraptini**
Pangraptinae GROTE, 1882, type genus: *Pangrapta* HÜBNER, 1818
- Euteliinae**
Euteliinae GROTE, 1882, type genus: *Eutelia* HÜBNER, [1823]
= Eurhipidae HERRICH-SCHÄFFER, [1851] [unavailable, permanently replaced by Euteliinae GROTE, 1882]
Ingurinae GROTE, 1882, type genus: *Ingura* GUENÉE, 1852
- Herminiinae**
Herminida LEACH, [1815], type genus: *Herminia* LATREILLE, 1802
Polypogoninae HAMPSON, 1918, type genus: *Polypogon* SCHRANK, 1802
Trisatelini BECK, 1999, type genus: *Trisateles* TAMS, 1939, **syn. nov.**
- Hypeninae**
Hypenidae HERRICH-SCHÄFFER, [1851], type genus: *Hypena* SCHRANK, 1802

- Hyphenodinae**
Hyphenodinae FORBES, 1954, type genus: *Hyphenodes* DOUBLEDAY, 1850
- Phytometrinae**
Phytometrinae HAMPSON, 1913, type genus: *Phytometra* HAWORTH, 1809
- Rivulinae**
Rivulini GROTE, 1895, type genus: *Rivula* GUENÉE, [1845]
- Scolecocampinae**
Scolecocampinae GROTE, 1883, type genus: *Scolecocampa* GUENÉE, 1852
- Stictopterinae**
Odontodinae HAMPSON, 1918, type genus: *Odontodes* GUENÉE, 1852
Stictopterinae HAMPSON, 1894, type genus: *Stictoptera* GUENÉE, 1852
- LYMANTRIIDAE**
- Arctornithini**
Arctornithini HOLLOWAY, 1999, type genus: *Arctornis* GERMAR, 1810
- Leucomini**
Leucomidae GROTE, 1895, type genus: *Leucoma* HÜBNER, 1822
- Lymantriini**
Lymantriidae HAMPSON, [1893], type genus: *Lymantria* HÜBNER, [1819]
Ocneriadae MEYRICK, 1895, type genus: *Ocneria* HÜBNER, [1819]
- Nygmiini**
Nygmiini HOLLOWAY, 1999, type genus: *Nygmia* HÜBNER, [1820]
- Orgyiini**
Dasychirae PACKARD, 1864, type genus: *Dasychira* HÜBNER, [1809]
Orgyides WALLENGREN, 1861, type genus: *Orgyia* OCHSENHEIMER, 1810
- MICRONOCTUIDAE**
Micronoctuidae FIBIGER, 2005, type genus: *Micronoctua* FIBIGER, 1997
- NOCTUIDAE**
- Acontiinae**
- Acontiini**
Acontidi GUENÉE, 1841, type genus: *Acontia* OCHSENHEIMER, 1816
Agrophilidae DUPONCHEL, [1845], type genus: *Agrophila* BOISDUVAL, 1840
Emmelidi STEPHENS, 1850, type genus: *Emmelia* HÜBNER, [1821]
Tarachini GROTE, 1890, type genus: *Tarache* HÜBNER, [1823]
- Aediini**
Aediinae BECK, 1960, type genus: *Aedia* HÜBNER, [1823]
- Armadini**
Armadini WILTSHIRE, 1961, type genus: *Armada* STAUDINGER, 1884
- Hypercalymniini**
Hypercalymniini FIBIGER and LAFONTAINE, 2005, type genus: *Hypercalymnia* HAMPSON, 1910
- Acronictinae**
Acronictidae HEINEMANN, 1859, type genus: *Acronycta* TREITSCHKE, 1825
Craniophorini BECK, 1996, type genus: *Craniophora* SNELLEN, 1867, **syn. nov.**
Maniidae HERRICH-SCHÄFFER, [1851], type genus: *Mania* TREITSCHKE, 1825
Mominae HAMPSON, 1902, type genus: *Moma* HÜBNER, [1820]
- Agaristinae**
Agaristoidea HERRICH-SCHÄFFER, [1858], type genus: *Agarista* LEACH, 1814
Eudryini FORBES, 1954, type genus: *Eudryas* BOISDUVAL, 1836
Pemphigostolinae STRAND, 1909, type genus: *Pemphigostola* STRAND, 1909
Phalaenoididae HAMPSON, 1918, type genus: *Phalaenoides* LEWIN, 1805
- Amphipyridae**
Amphipyridae GUENÉE, 1837, type genus: *Amphipyra* OCHSENHEIMER, 1816
Adpyramidcampina BECK, 1996, type genus: *Adpyramidcampa* BECK, 1991, **syn. nov.**
Pyramidcampina BECK, 1996, type genus: *Pyramidcampa* BECK, 1991, **syn. nov.**
Pyroina BECK, 1996, type genus: *Pyrois* HÜBNER, [1820], **syn. nov.**
- Bagisarinae**
Bagisarinae CRUMB, 1956, type genus: *Bagisara* WALKER, 1858

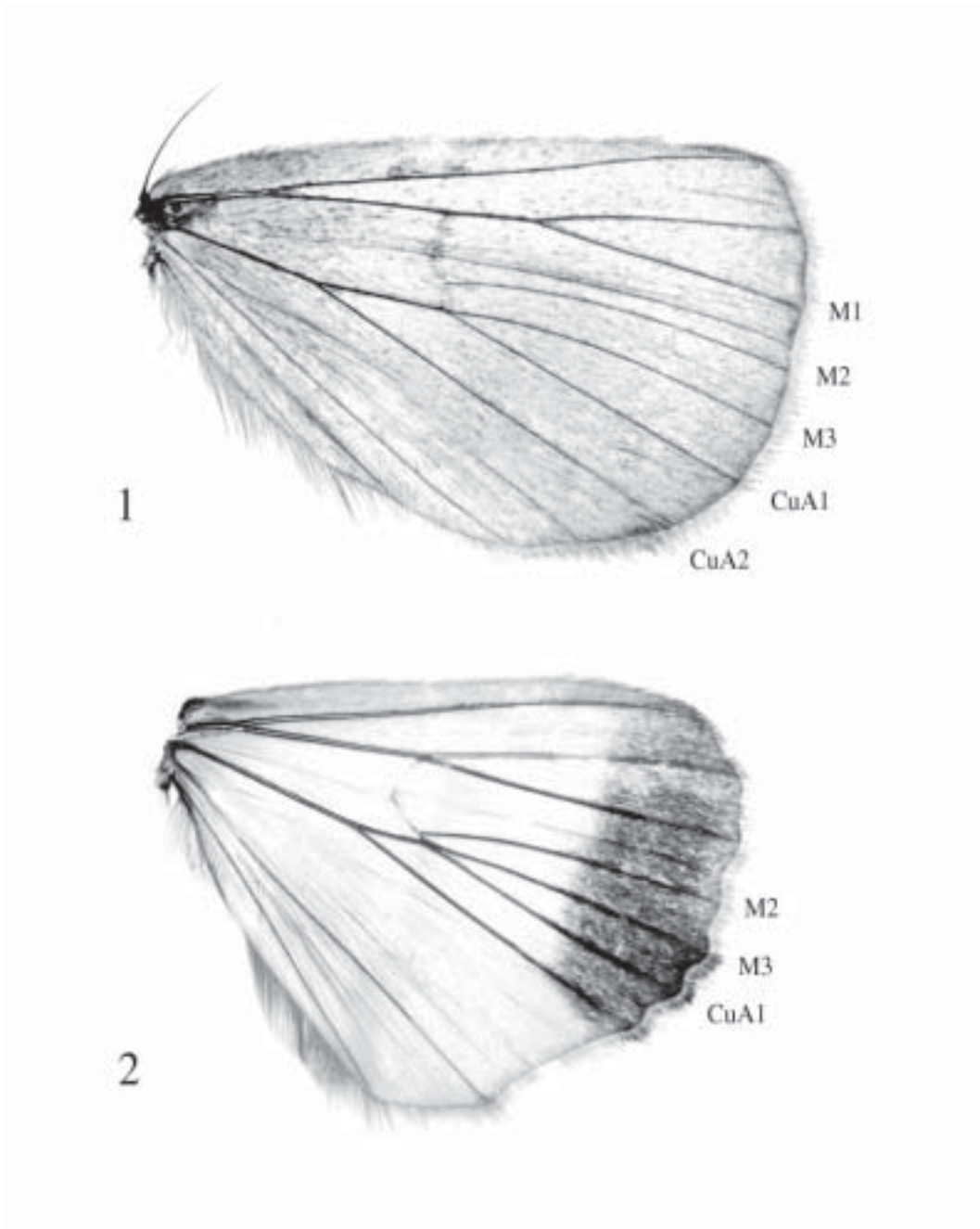
- Bryophilinae** **Cydosiini** KITCHING and RAWLINS, [1998], type genus: *Cydosia* DUNCAN, 1841
- Bryoleucini** BECK, 1996, type genus: *Bryoleuca* HAMPSON, 1908, **syn. nov.**
- Bryophilidae** GUENÉE, 1852, type genus: *Bryophila* TREITSCHKE, 1825
- Cryphiinae** INOUE and SUGI, 1958, type genus: *Cryphia* HÜBNER, 1818
- Jaspidiinae** AUBERT, 1952, type genus: *Jaspidia* HÜBNER, 1822
- Condicinae**
- Condicini**
- Acosmetiina** BECK, 1999, type genus: *Acosmetia* STEPHENS, 1829, **syn. nov.**
- Condicinae** POOLE, 1995, type genus: *Condica* WALKER, 1856
- Leuconyctini**
- Leuconyctini** POOLE, 1995, type genus: *Leuconycta* HAMPSON, 1908
- Cuculliinae**
- Cucullidae** HERRICH-SCHÄFFER, [1850], type genus: *Cucullia* SCHRANK, 1802
- Dilobinae**
- Dilobinae** AURIVILLIUS, 1889, type genus: *Diloba* BOISDUVAL, 1840
- Diphtherinae**
- Diphtherinae** FIBIGER and LAFONTAINE, 2005, type genus: *Diphthera* HÜBNER, [1820]
- Eriopinae**
- Eriopidae** HERRICH-SCHÄFFER, [1851], type genus: *Eriopus* TREITSCHKE, 1825
- Eucocytiinae**
- Eucocytidae** HAMPSON, 1918, type genus: *Eucocytia* ROTHSCHILD and JORDAN, 1905
- Eustrotiinae**
- Cerathosiini** GROTE, 1890, type genus: *Cerathosia* SMITH, 1887
- Eustrotiinae** GROTE, 1882, type genus: *Eustrotia* HÜBNER, [1821]
- Lithacodiinae** CRUMB, 1956, type genus: *Lithacodia* HÜBNER, 1818
- Hadeninae**
- Eriopygini**
- Eriopygini** FIBIGER and LAFONTAINE, 2005, type genus: *Eriopyga* GUENÉE, 1852
- Glottulini**
- Glottulidae** GUENÉE, 1852, type genus: *Glottula* GUENÉE, 1837
- Xanthopastinae** BIEZANKO and SOUZA GUERRA, 1971, type genus: *Xanthopastis* HÜBNER, [1821]
- Hadenini**
- Anartidae** HEINEMANN, 1859, type genus: *Anarta* OCHSENHEIMER, 1816
- Clemathadina** BECK, 1996, type genus: *Clemathada* BECK, 1991, **syn. nov.**
- Conisaniina** BECK, 1996, type genus: *Conisania* HAMPSON, 1905, **syn. nov.**
- Coranartina** BECK, 1996, type genus: *Coranarta* BECK, 1991, **syn. nov.**
- Discestrina** BECK, 1996, type genus: *Discestra* HAMPSON, 1905, **syn. nov.**
- Hadenidi** GUENÉE, 1837, type genus: *Hadena* SCHRANK, 1802
- Hadina** BECK, 1996, type genus: *Hada* BILLBERG, 1820, **syn. nov.**
- Mamestrinae** HAMPSON, 1902, type genus: *Mamestra* OCHSENHEIMER, 1816
- Melanchrides** MEYRICK, 1912, type genus: *Melanchra* HÜBNER, [1820]
- Pachetrina** BECK, 1996, type genus: *Pachetra* GUENÉE, 1841, **syn. nov.**
- Polianae** HAMPSON, 1902, type genus: *Polia* OCHSENHEIMER, 1816,
 = *Poliina* BECK, 1996, type genus: *Polia* OCHSENHEIMER, 1816, **syn. nov.**
- Leucaniini**
- Leucanidi** GUENÉE, 1837, type genus: *Leucania* OCHSENHEIMER, 1816
- Mythimnini** RUNGS, 1956, type genus: *Mythimna* OCHSENHEIMER, 1816
- Orthosiini**
- Orthosides** GUENÉE, 1837, type genus: *Orthosia* OCHSENHEIMER, 1816
- Perigraphina** BECK, 1996, type genus: *Perigrapha* LEDERER, 1857, **syn. nov.**
- Taeniocampinae** GROTE, 1882, type genus: *Taeniocampa* GUENÉE, 1839
- Tholerini**
- Tholerina** BECK, 1996, type genus: *Tholera* HÜBNER, [1821]
- Heliothinae**
- Heliothinae** BOISDUVAL, [1828], type genus: *Heliothis* OCHSENHEIMER, 1816
- Melicleptriinae** WARREN, 1911, type genus: *Melicleptria* HÜBNER, [1823]
- Pyrrhiini** FORBES, 1954, type genus: *Pyrrhia* HÜBNER, [1821]

- Lophonyctinae**
Lophonyctinae SPEIDEL, FÄNGER and NAUMANN, 1996, type genus: *Lophonycta* SUGI, 1970
- Metoponinae**
Metoponidae HERRICH-SCHÄFFER, [1851], type genus: *Metoponia* DUPONCHEL, [1845]
Tytina BECK, 1999, type genus: *Tyta* BILLBERG, 1820. (a nomen nudum in BECK, 1996)
- Noctuinae**
Agrotini
Agrotina RAMBUR, 1848, type genus: *Agrotis* OCHSENHEIMER, 1816 (**subtribe**)
Dichagyryna BECK, 1996, type genus: *Dichagyris* LEDERER, 1857, **syn. nov.**
Euxoinae WARREN, 1909, type genus: *Euxoa* HÜBNER, [1821]
Austrandesiiina ANGULO and OLIVARES, 1990, type genus *Austrandesia* KÖHLER, 1967 (**subtribe**)
Boursinidini ANGULO, 1993, type genus *Boursinidia* KÖHLER, 1953
Peridromina BECK, 1996, type genus: *Peridroma* HÜBNER, [1821], **syn. nov.**
- Noctuini** LATREILLE, 1809, type genus: *Noctua* LINNAEUS, 1758
Axyliina FIBIGER and LAFONTAINE, 2005, type genus: *Axyliia* HÜBNER, [1821] (**subtribe**)
Noctuina LATREILLE, 1809, type genus: *Noctua* LINNAEUS, 1758 (**subtribe**)
Anaplectoidina BECK, 1996, type genus: *Anaplectoides* McDUNNOUGH, [1929], **syn. nov.**
Archanartina BECK, 1996, type genus: *Archanarta* BARNES and BENJAMIN, 1929, **syn. nov.**
Cerastina BECK, 1996, type genus: *Cerastis* OCHSENHEIMER, 1816, **syn. nov.**
Chersotina BECK, 1996, type genus: *Chersotis* BOISDUVAL, 1840, **syn. nov.**
Coenophilina BECK, 1996, type genus: *Coenophila* STEPHENS, 1850, **syn. nov.**
Diarsiina BECK, 1996, type genus: *Diarsia* HÜBNER, [1821], **syn. nov.**
Eugnorismina BECK, 1996, type genus: *Eugnorisma* BOURSIN, 1946, **syn. nov.**
Eugraphina BECK, 1996, type genus: *Eugraphe* HÜBNER, [1821], **syn. nov.**
Euroina BECK, 1996, type genus: *Eurois* HÜBNER, [1821], **syn. nov.**
Lycophotiina BECK, 1996, type genus: *Lycophotia* HÜBNER, [1821], **syn. nov.**
Naeniina BECK, 1996, type genus: *Naenia* STEPHENS, 1827, **syn. nov.**
Netrocercorina BECK, 1996, type genus: *Netrocercora* BARTEL, 1902, **syn. nov.**
Noctuidae LATREILLE, 1809, type genus: *Noctua* LINNAEUS, 1758
Opigenina BECK, 1996, type genus: *Opigena* BOISDUVAL, 1840, **syn. nov.**
Rhyaciina BECK, 1996, type genus: *Rhyacia* HÜBNER, [1821], **syn. nov.**
Standfussianina BECK, 1996, type genus: *Standfussiana* BOURSIN, 1946, **syn. nov.**
Xestiina BECK, 1996, type genus: *Xestia* HÜBNER, 1818, **syn. nov.**
- Oncocnemidinae**
Calophasiina BECK, 1996, type genus: *Calophasia* STEPHENS, 1829, **syn. nov.**
Cleophanidae HEINEMANN, 1859, type genus: *Cleophana* BOISDUVAL, RAMBUR and GRASLIN, 1832
[*Calophasia*]
Metopocera BECK, 1996, type genus: *Metopoceras* GUENÉE, 1850, **syn. nov.**
Omiini BECK, 1996, type genus: *Omia* HÜBNER, [1821], **syn. nov.**
Omphalophanina BECK, 1996, type genus: *Omphalophana* HAMPSON, 1906, **syn. nov.**
Oncocnemidini FORBES and FRANCLEMONT, 1954, type genus: *Oncocnemis* LEDERER, 1853
Recorophina BECK, 1996, type genus: *Recoropha* NYE, 1975, **syn. nov.**
Stilbidae GUENÉE, 1852, type genus: *Stilbia* STEPHENS, 1829
Sympistina BECK, 1996, type genus: *Sympistis* HÜBNER, [1823], **syn. nov.**
Xylocampidi TUTT, 1896, type genus: *Xylocampa* GUENÉE, 1837
- Pantheinae**
Pantheini SMITH, 1898, type genus: *Panthea* HÜBNER, [1820]
Trichoseini KOBES, 1992, type genus: *Trichosea* GROTE, 1875
- Plusiinae**
Abrostolini
Abrostolini EICHLIN and CUNNINGHAM, 1978, type genus: *Abrostola* OCHSENHEIMER, 1816
Argyrogrammini
Argyrogrammini EICHLIN and CUNNINGHAM, 1978, type genus: *Argyrogramma* HÜBNER, 1823
Omorphinini
Omorphinini CHOU and LU, 1979, type genus: *Omorphina* ALPHÉRAKY, 1892
Plusiini
Autoplusiina
Autoplusiina KITCHING, 1987, type genus: *Autoplusiia* McDUNNOUGH, 1944

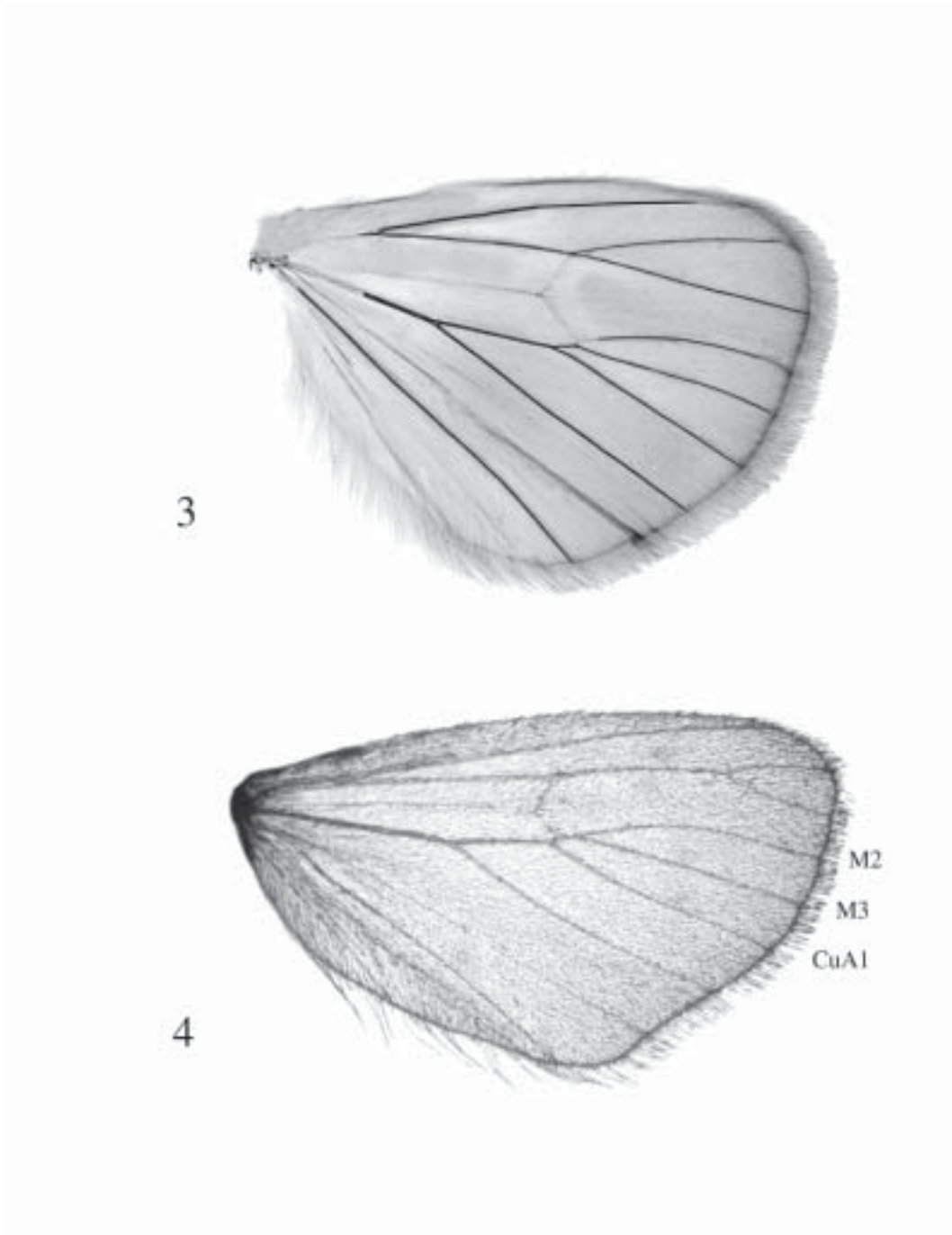
- Diachrysiina** BECK, 1996, type genus: *Diachrysia* HÜBNER, [1821], **syn. nov.**
- Euchalciina**
- Euchalciini** CHOU and LU, 1979, type genus: *Euchalcia* HÜBNER, [1821]
- Panchrysiina** BECK, 1996, type genus: *Panchrysia* HÜBNER, [1821], **syn. nov.**
- Plusidiina** BECK, 1996, type genus: *Plusidia* BUTLER, 1879, **syn. nov.**
- Polychrysiina** KLJUTSHKO, 1985, type genus: *Polychrysia* HÜBNER, [1821], **syn. nov.**
- Plusiina**
- Autographini** EICHLIN and CUNNINGHAM, 1978, type genus: *Autographa* HÜBNER, [1821]
- Caloplusiini** CHOU and LU, 1979, type genus: *Caloplusia* SMITH, 1884
- Plusiinae** BOISDUVAL, [1828], type genus: *Plusia* OCHSENHEIMER, 1816
- Psaphidinae**
- Feraliini**
- Feraliini** POOLE, 1995, type genus: *Feralia* GROTE, 1874
- Nocloini**
- Nocloini** POOLE, 1995, type genus: *Nocloa* SMITH, 1906
- Phosphilini**
- Phosphilini** POOLE, 1995, type genus: *Phosphila* HÜBNER, 1818
- Psaphidini**
- Allophyini** BECK, 1996, type genus: *Allophyes* TAMS, 1942, **syn. nov.**
- Asteroscopinae** TUTT, 1896, type genus: *Asteroscopus* BOISDUVAL, 1828
- Psaphidini** GROTE, 1896, type genus: *Psaphida* WALKER, 1865
- Triocnemidini**
- Triocnemidini** POOLE, 1995, type genus: *Triocnemis* GROTE, 1881
- Raphiinae**
- Raphiinae** BECK, 1996, type genus: *Raphia* HÜBNER, [1821]
- Sinocharinae**
- Sinocharinae** SPEIDEL, FÄNGER and NAUMANN, 1996, type genus: *Sinocharis* PÜNGELER, 1912
- Stiriinae**
- Azeniini** POOLE, 1995, type genus: *Azenia* GROTE, 1882
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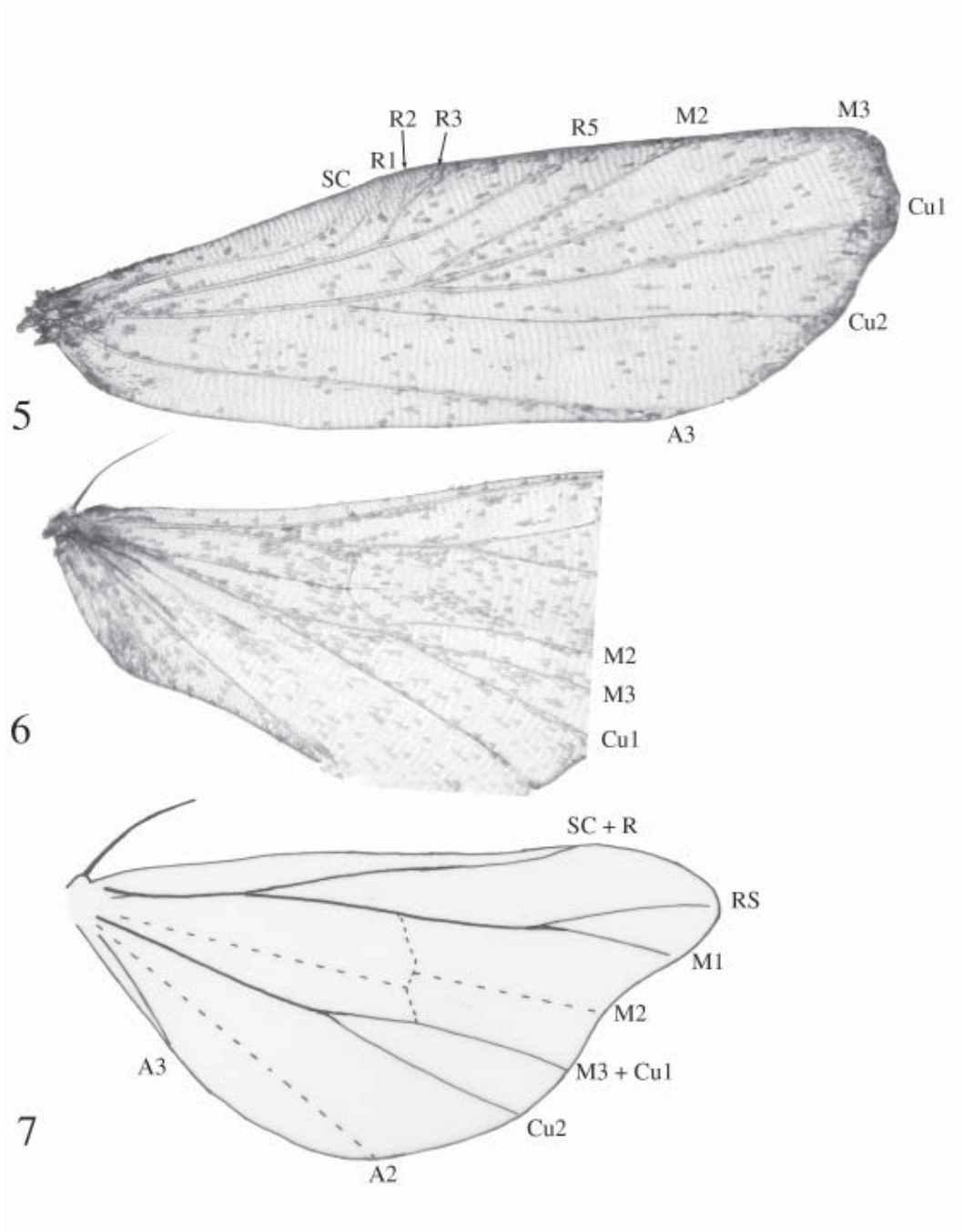
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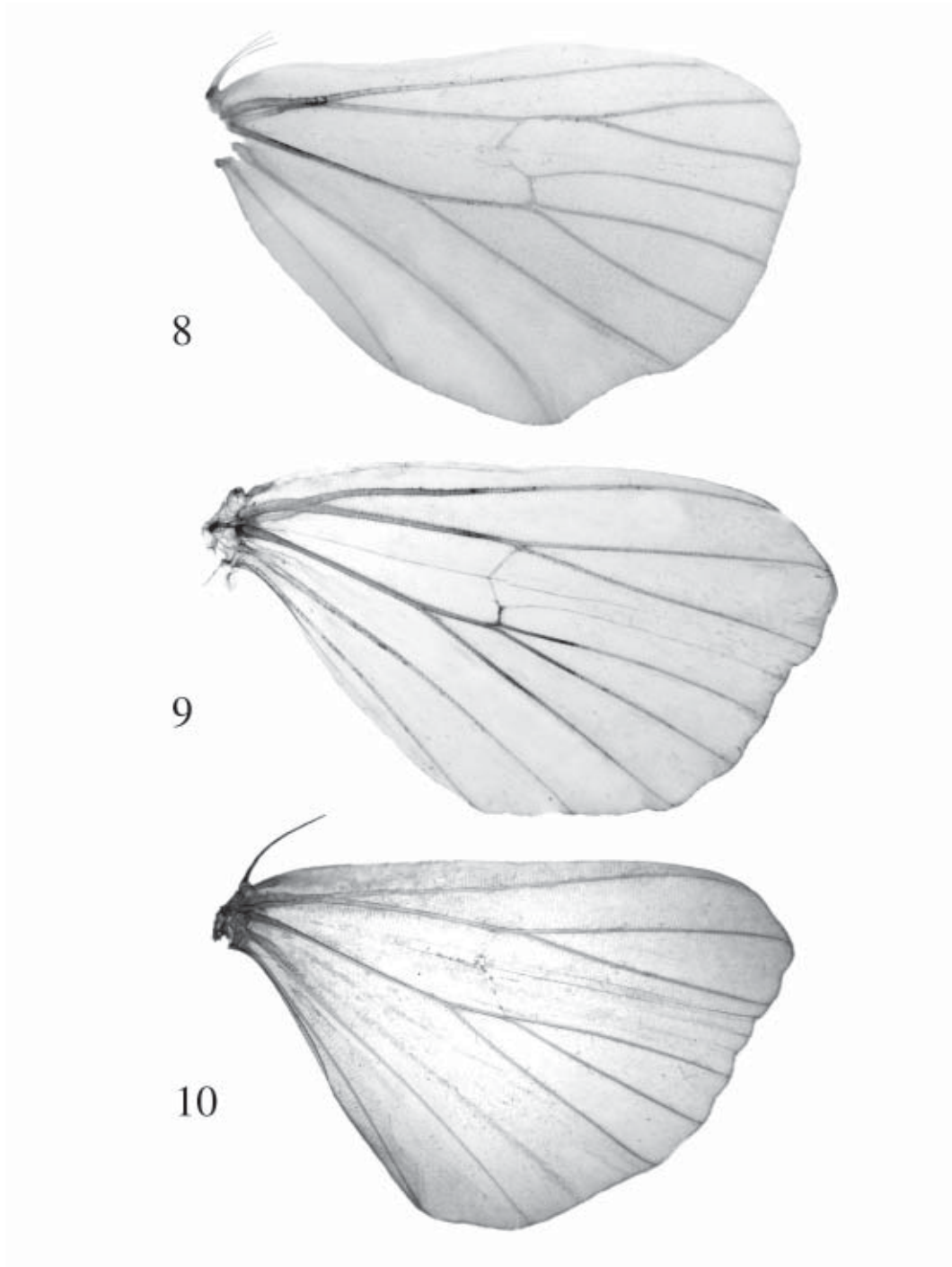
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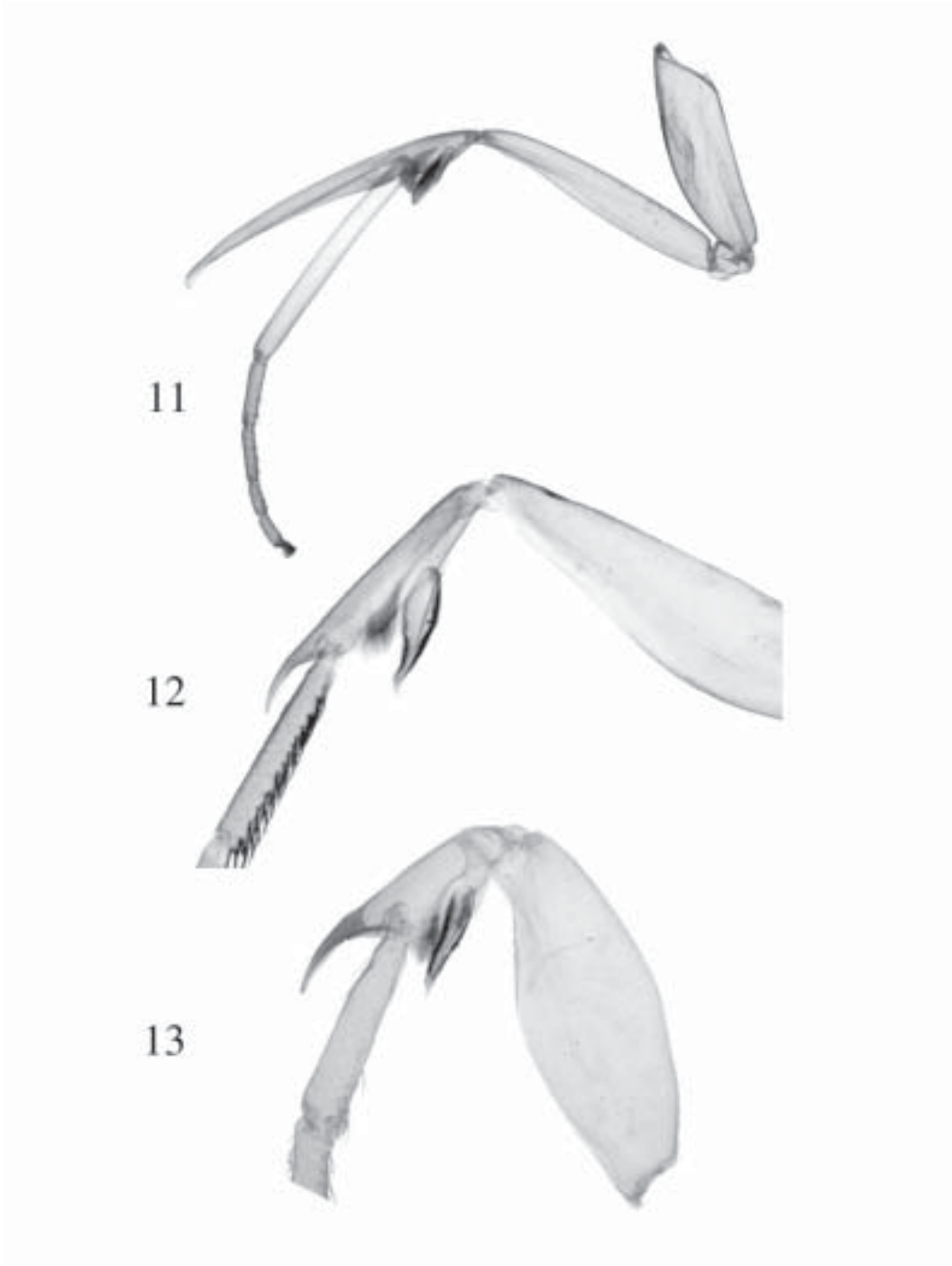
Figs. 3–4. Hindwing venation of Arctiidae.
3. “Quadrifid” venation showing base of M2 close to M3 (Arctiidae: Arctiinae: *Spilosoma*); 4. “Quadrifid” venation with M2 and M3 on common stalk (Arctiidae: Lithosiinae: *Acsala*).



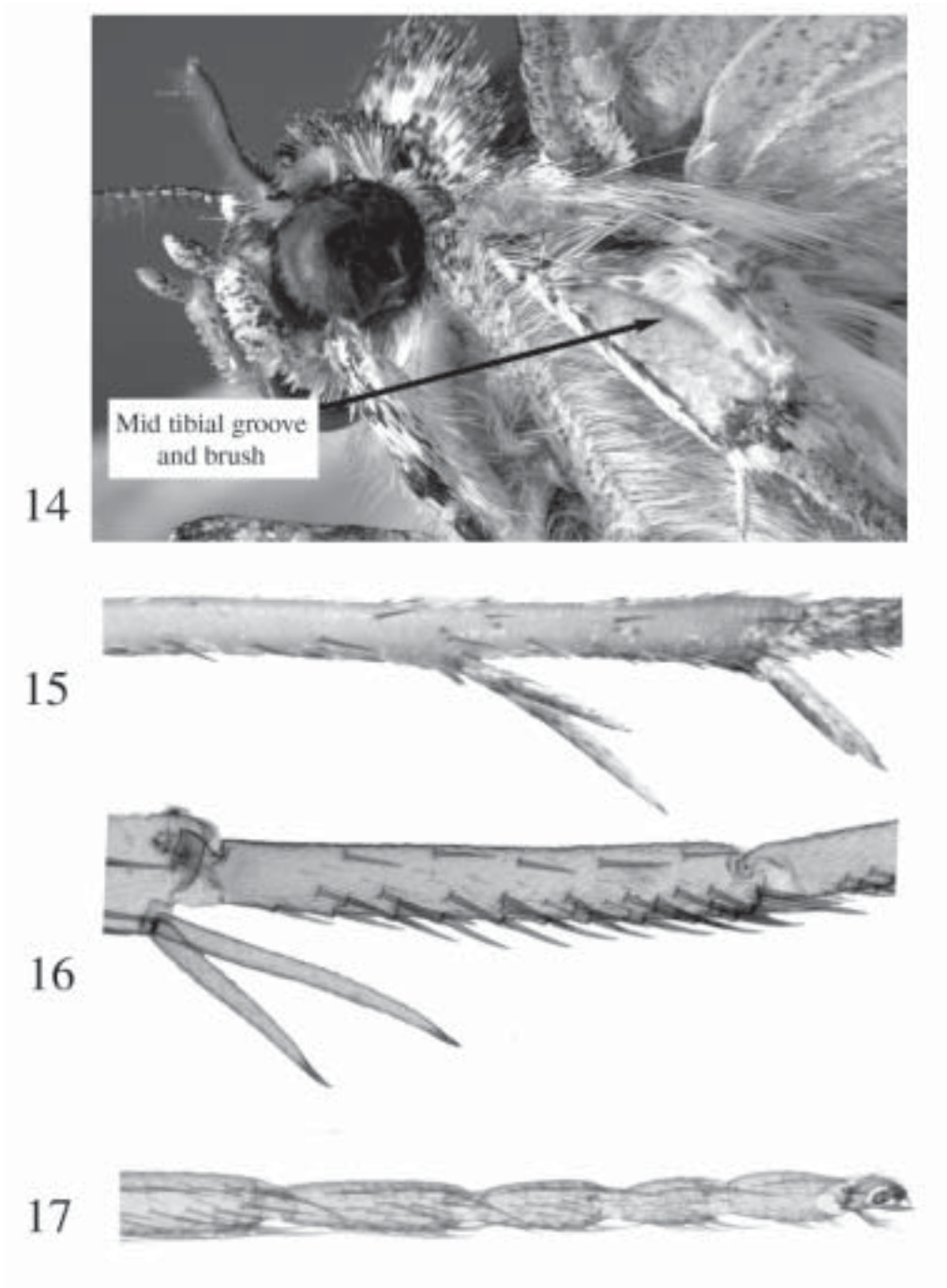
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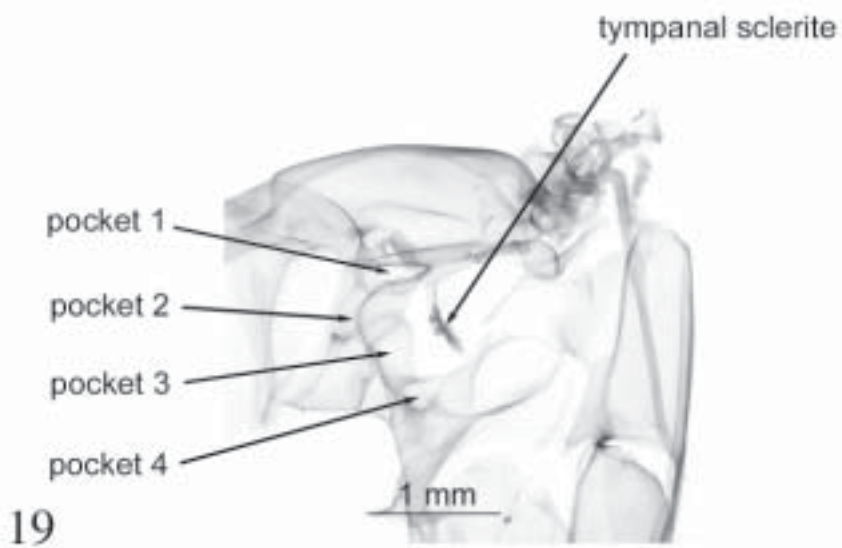
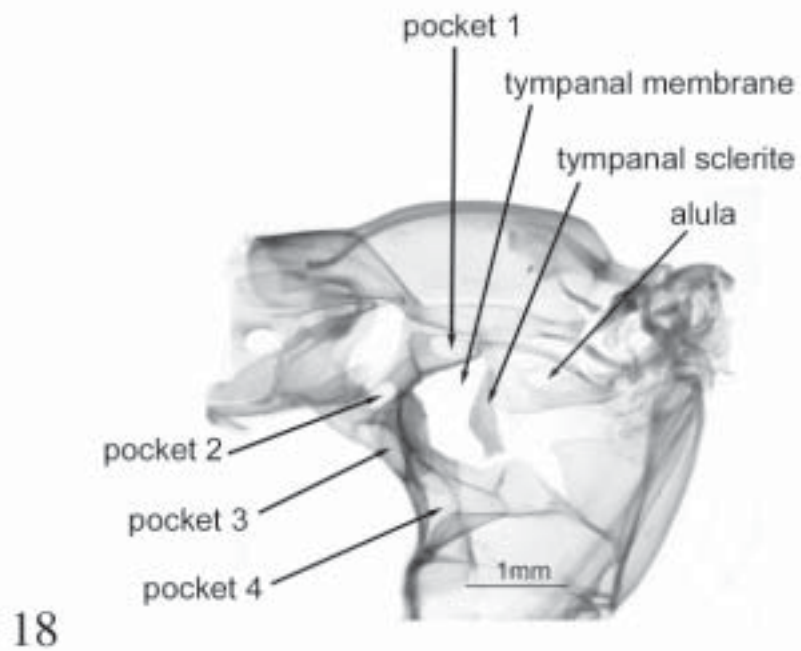
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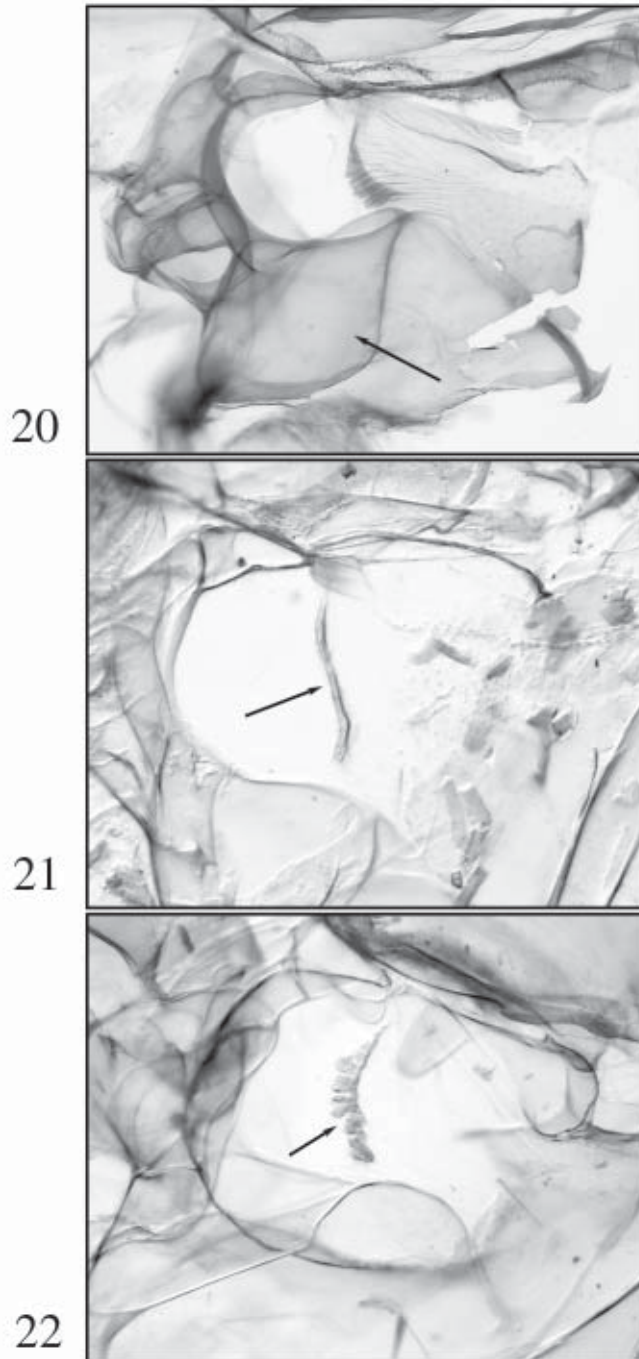
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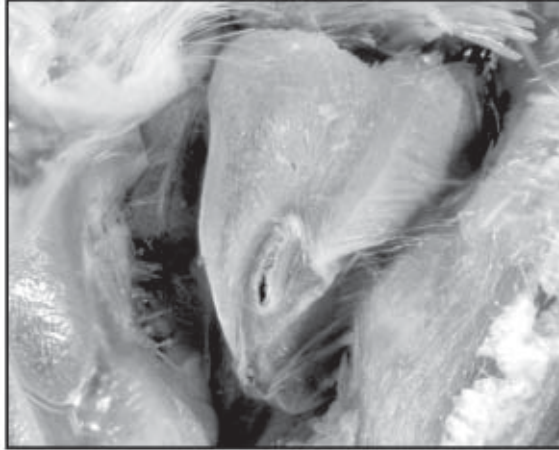


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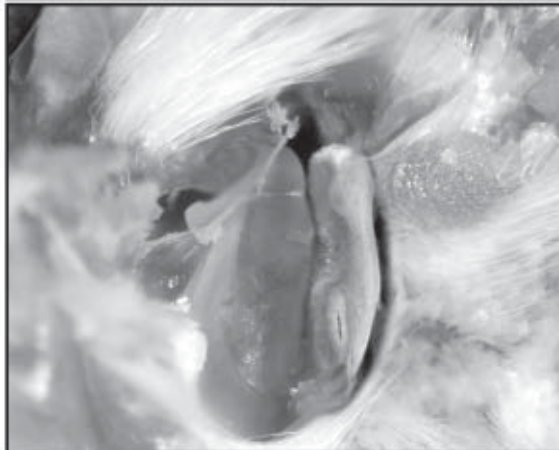
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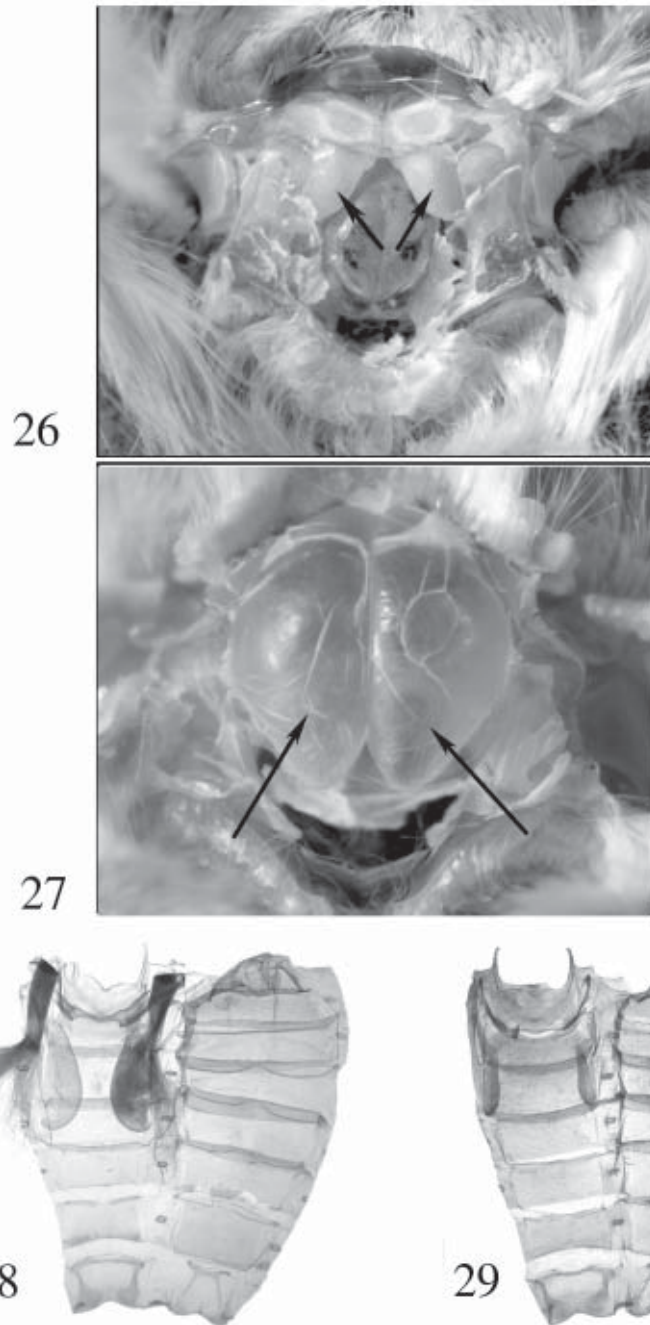
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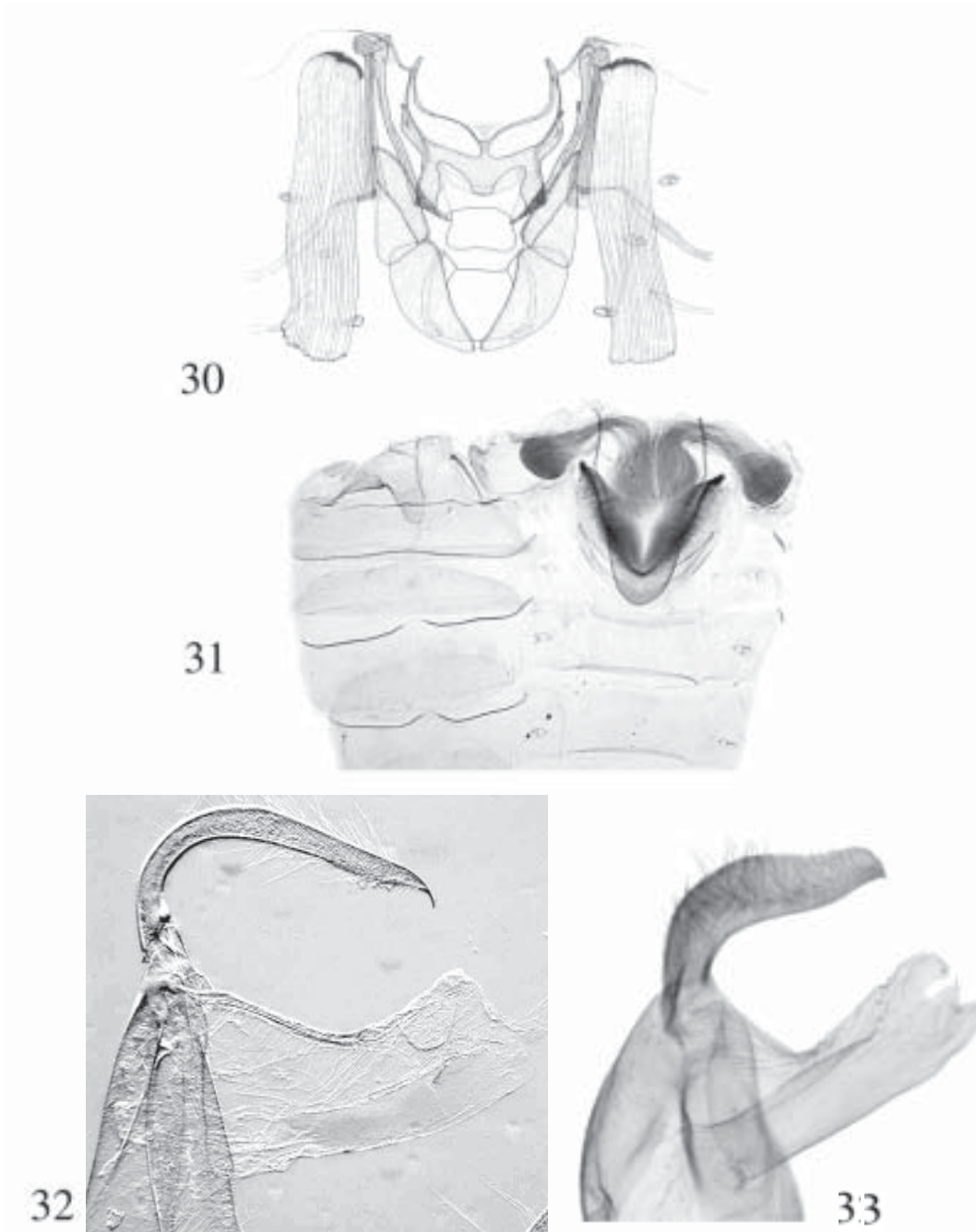
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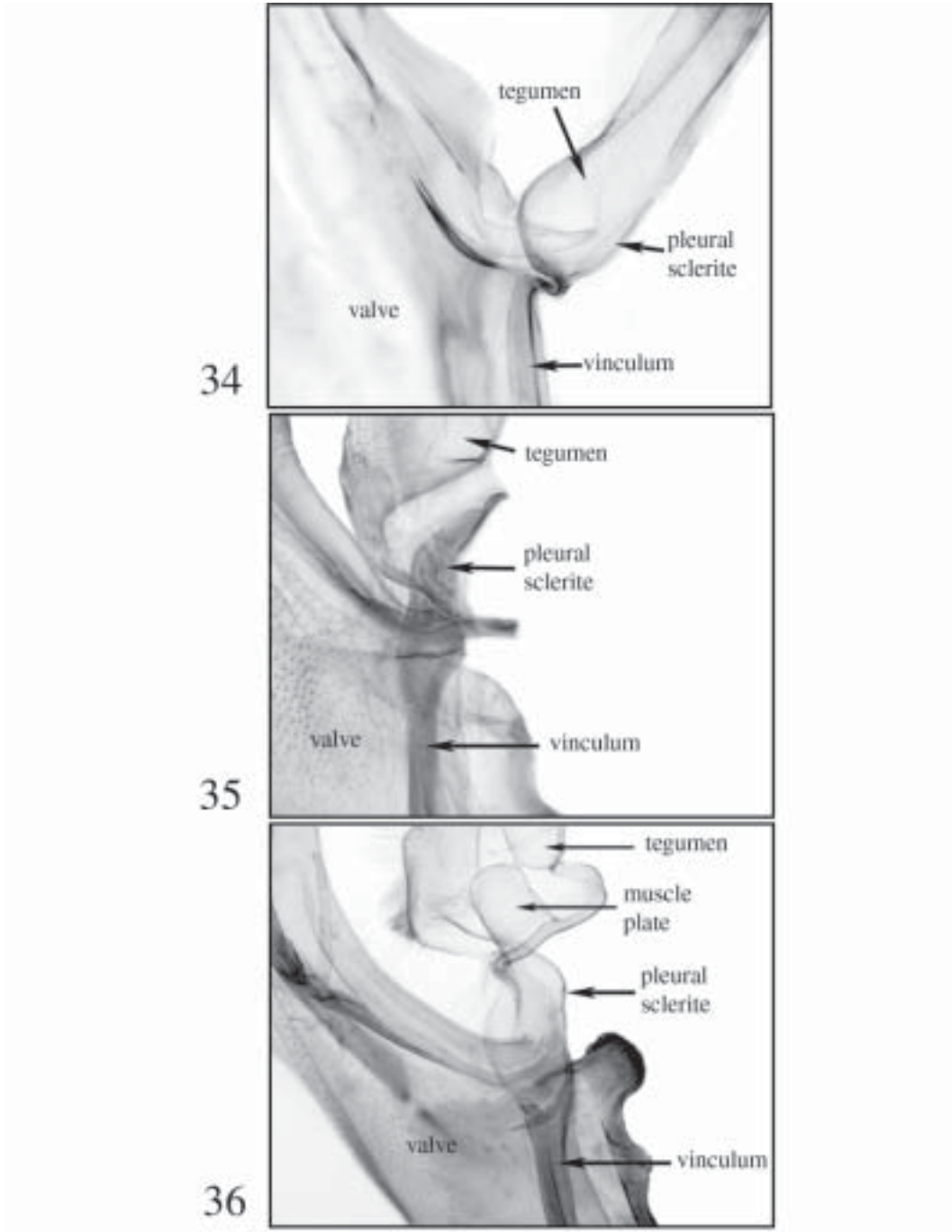
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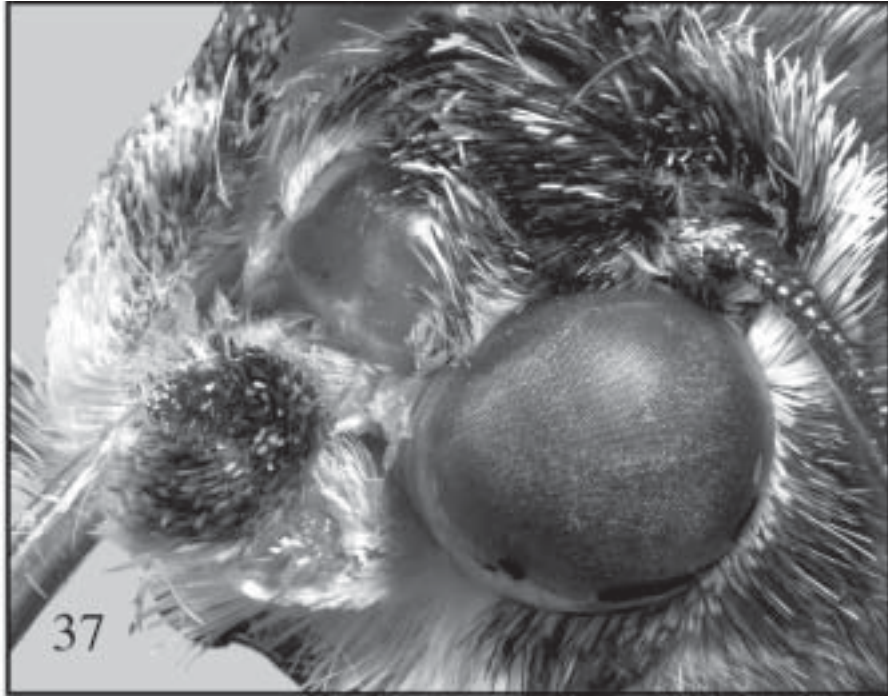
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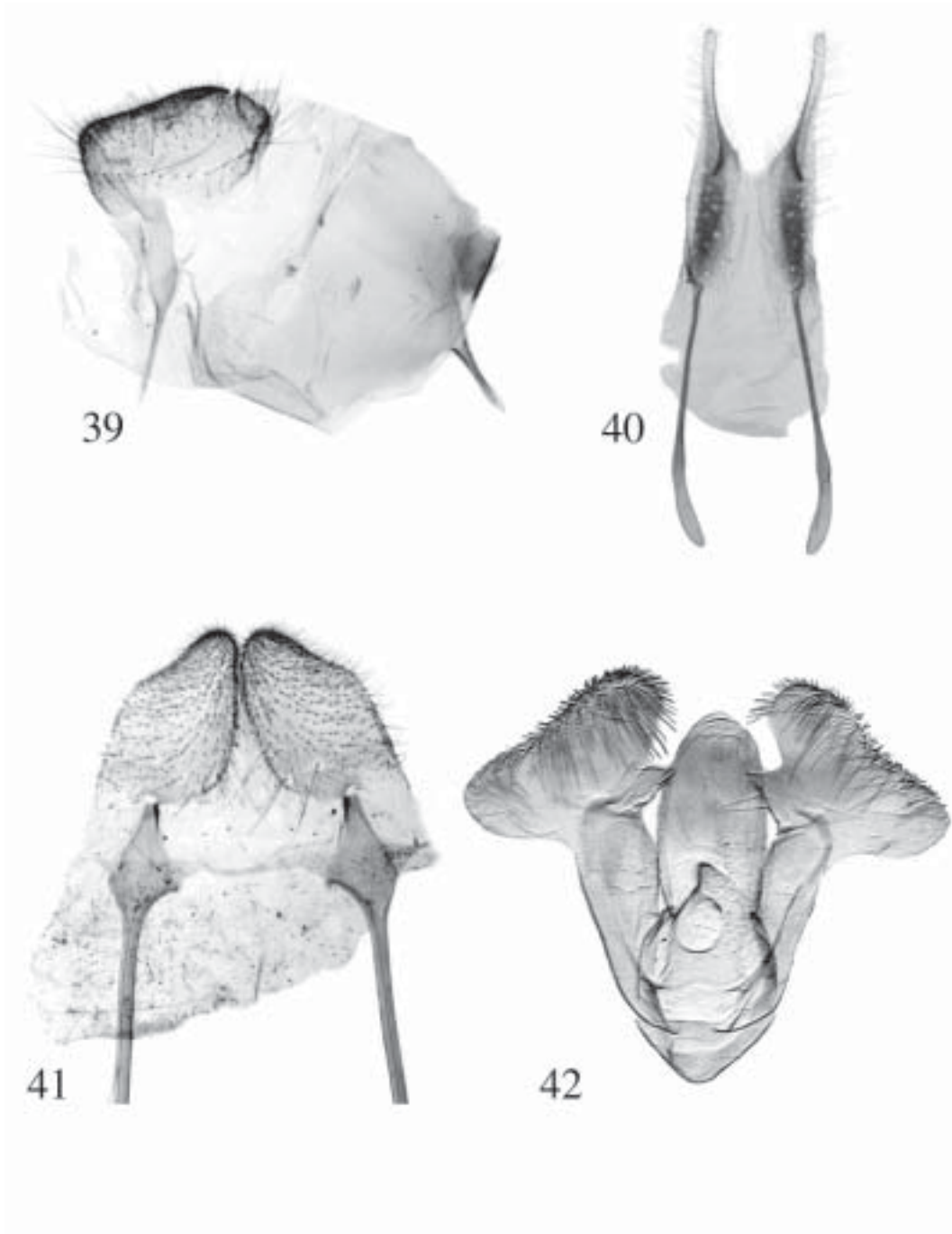
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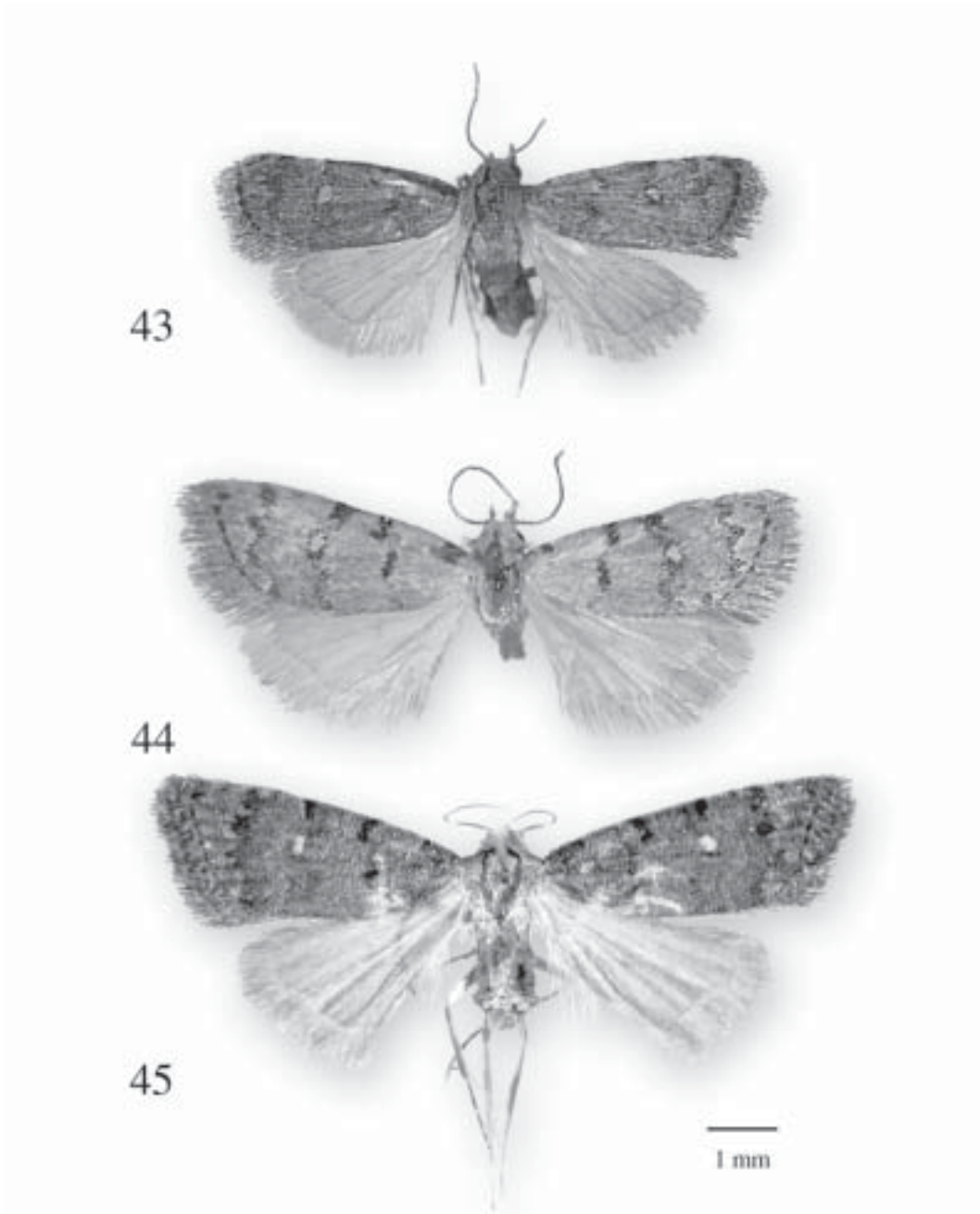
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Figs. 37–38. Scaling on frons. 37. Lower frons bare (scales deciduous) (Erebidae: Catocalinae: *Catocala*).
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Figs. 39–42. Figs. 39–41, posterior apophyses. 39. Apophyses stick-like, expanded posteriorly (Erebidae: Calpinae: *Scoliopteryx*). 40. Apophyses narrow posteriorly (Erebidae: Catocalinae: *Catocala*). 41. Apophyses with diamond-shaped preapical sclerite (Noctuidae: Noctuinae: *Euxoa*). **Fig. 42. Male genitalia of *Micronoctuidae* (*Micronoctua karsholti* FIBIGER).**



Figs. 43–45. Adults of Micronoctuidae. 43. Species. 1 (FIBIGER, in litt.), Java, Indonesia (8 mm). 44. Species. 2 (FIBIGER, in litt.), Namibia (9 mm). 45. Species. 3 (FIBIGER, in litt.), Cameroon (10 mm).

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