Revised higher classification of the Noctuoidea (Lepidoptera)

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Abstract—The higher classification of the families of the Noctuoidea with a quadrifid forewing (Nolidae, Strepsimanidae, Arctiidae, Lymantriidae, Erebidae, and Noctuidae) is reviewed from the perspective of recent classifications and the distribution of derived character states. On the basis of recent morphological and molecular studies, we propose a more inclusive definition of the family Noctuidae that adds the subfamilies Nolinae, Strepsimaninae, Arctiinae, Lymantriinae, and Erebinae to the subfamilies more traditionally included in the Noctuidae. Consequently, the superfamily Noctuoidea comprises the families Oenosandridae, Doidae, Notodontidae, Micronoctuidae, and Noctuidae. The tribe Cosmiini, currently in the subfamily Xyleninae, is downgraded to the status of subtribe Cosmiina and placed in the tribe Xylenini. The tribe Balsini, currently in the subfamily Xyleninae, is elevated to the status of subfamily Balsinae. The tribe Phosphilini is transferred from the subfamily Psaphidinae to the Xyleninae.

Résumé—Nous révisons la classification supérieure des familles de Noctuoidea possédant une aile antérieure quadrifide (Nolidae, Strepsimanidae, Arctiidae, Lymantriidae, Erebidae et Noctuidae) à la lumière de classifications récentes et des répartitions actuelles des états dérivés des caractères. D'après des études morphologiques et moléculaires récentes, nous proposons une définition plus compréhensive de la famille des Noctuidae qui ajoute les sous-familles Nolinae, Strepsimaninae, Arctiinae, Lymantriinae et Erebinae à celles qui sont plus traditionnellement incluses dans les Noctuidae. La superfamille des Noctuoidea comprend donc les familles Oenosandridae, Doidae, Notodontidae, Micronoctuidae et Noctuidae. La tribu des Cosmiini, présentement dans la sous-famille des Xyleninae, est réduite au niveau de sous-tribu des Cosmiina et placée dans la tribu des Xylenini. La tribu des Balsini, couramment placée dans la sous-famille des Xyleninae, est élevée au rang de sous-famille des Balsinae. La tribu Phosphilini est transférée de la sous-famille des Psaphidinae à Xyleninae.

[Traduit par la Rédaction]

Introduction

After almost 100 years of relative stability, Hampson's (1898–1913) classification of the family Noctuidae (Lepidoptera) has undergone radical revision and modification in the past 10 years (Fibiger and Hacker 1991; Poole 1995; Speidel *et al.* 1996; Mitchell *et al.* 1997, 2000, 2006; Kitching and Rawlins 1998; Beck 1999–2000; Fibiger and Lafontaine 2005). Hampson's classification had long been known to contain large unnatural subfamilies, especially the Catocalinae in the quadrifine noctuids and the Acronyctinae in the trifine noctuids. These two subfamilies, the largest in the family, were defined by the absence of the characteristics of the other subfamilies and as a result they became assemblages of related and unrelated genera that did not fit elsewhere. Other subfamilies, such as the Cuculliinae *sensu* Hampson that was based on the presence of lashes (long hairlike scales) around the eye, included large groups of genera that were shown by Crumb (1956) and Beck

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(1960) to be in conflict with larval characteristics, but the arrangement of genera based on the adults prevailed. The relatively sudden flurry of new classifications is due to a combination of factors: the use of cladistic methodology to define monophyletic groups based on shared, derived character states; the discovery of additional morphological characters, especially in the genitalia, combined with surveys of these characters in larger numbers of taxa; the integration of characters of adults and immatures to identify natural groupings; and the entry of molecular data into the realm of noctuoid classification. The most recent and most comprehensive morphological classification (Figs. 25–27, based on Fibiger and Lafontaine 2005), which included both adult and immature characters, is surprisingly concordant with the most recent and most comprehensive molecular classification (Figs. 23, 24, based on Mitchell *et al.* 2006), the main difference being the rankings given to various subfamilies and tribes. The similarities and conflicts between these two different approaches were presented in the Noctuoidea Workshop during the Societas Europaeae Lepidopterologica Congress in Rome, September 2005. We indicated that there were two most probable solutions: either to accept the quadrifid Noctuoidea as 22 weakly defined families or to lump them into one large, well-defined family. Here we defend the latter proposal. We examine former classifications, with emphasis on the two most recent ones, and propose a new classification that we believe best reflects the data from all sources.

Materials and methods

Our discussion of morphological characters and their distribution in the Noctuoidea is based on our examination of material in the Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Ontario, Canada (CNC), the Natural History Museum, London, United Kingdom (BMNH), the National Museum of Natural History, Washington, D.C., United States of America (USNM), and the personal collection of Michael Fibiger, Sorø, Denmark, and on data contained in the cited papers. Discussion of molecular data is based on Mitchell *et al.* (2006).

Dissection methodology and the terminology used for structural characters of adults follow Lafontaine (2004). Terminology for larval characters follows Godfrey (1987) and Beck (1999–2000). Descriptions and discussions of most of the morphological characters used are in Fibiger and Lafontaine (2005).

Definitions

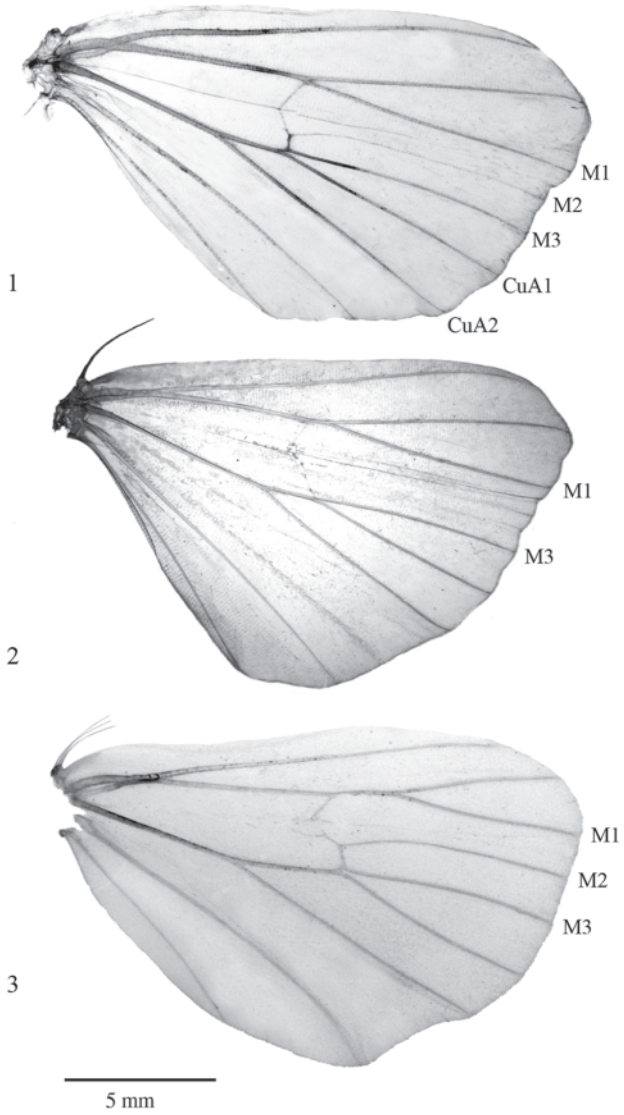
We define the following terms for use in the discussion of the higher classification of the Noctuoidea:

- **trifid Noctuoidea** are groups of the Noctuoidea (*i.e.*, Oenosandridae, Notodontidae, and Doidae) that have vein M2 near the middle of the cell of the **forewing** so that the cubital vein appears to branch into three veins;
- **quadrifid Noctuoidea** are groups (*i.e.*, Nolidae, Strepsimanidae, Arctiidae, Lymantriidae, Erebidae, and Noctuidae) in which vein M2 is in the lower part of the cell of the **forewing** so that the cubital vein appears to branch into four veins;
- **trifine Noctuidae** refers to a large clade of subfamilies of the Noctuidae in which vein M2 in the **hind wing** is usually vestigial or absent so that the cubital vein appears to branch into three veins; vein M2 is in the lower third of the cell but is usually reduced (Fig. 1) or absent (Fig. 2) but can occasionally be as strong as vein M3 (Fig. 3);
- **quadrifine Noctuidae** refers to subfamilies in which vein M2 in the **hind wing** is in the lower third of the cell and is as strong as vein M3, so the cubital vein appears to have four branches; in primitive groups of quadrifine Noctuidae, vein M2 is in the same position as it is in the trifine noctuids (Fig. 4), whereas in derived groups the vein is adjacent to vein M3 (Fig. 5) and we refer to these as having a **true quadrifine hind wing**; the families Nolidae, Strepsimanidae, Arctiidae, and Lymantriidae also have a true quadrifine hind wing (Fig. 6);
- **Noctuidae *sensu stricto* (*s.s.*)** are the trifine subfamilies as defined by both Fibiger and Lafontaine (2005) and Mitchell *et al.* (2006);
- **Erebidae** are the "quadrifine" subfamilies formerly included in the Noctuidae but segregated as a separate family by Fibiger and Lafontaine (2005);
- "**L.A.Q. clade**", defined by Mitchell *et al.* (2006), is a clade containing the Lymantriidae, Arctiidae, and part of the quadrifine Noctuidae (*i.e.*, Hypeninae, Aganainae, Herminiinae, Calpinae, Catocalinae, Scolecocampinae [as Strepsimaninae (*Phobolosia*

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Figs. 1–3. Hind wing venation of trifine Noctuidae: 1, *Mamestra configurata* (Walker) (Hadeninae), showing reduced vein M2; 2, *Peridroma saucia* (Hübner) (Noctuinae) with vein M2 lost; 3, *Panthea pallescens* McD. (Pantheinae), showing strong vein M2.



Dyar) in Mitchell *et al.* 2006], Boletobiinae [as Rivulinae (*Mycterophora* Hulst) in Mitchell *et al.* 2006], Eublemminae [as Eublemmini in Mitchell *et al.* 2006], and Rivulinae (*s.s.*));

- **Noctuinae *sensu lato* (*s.l.*)** are the trifine subfamilies Xyleninae, Hadeinae, and Noctuinae in Fibiger and Lafontaine (2005) and in this analysis; these three subfamilies are combined into a single subfamily in Mitchell *et al.* (2006) following the usage of Poole (1995).

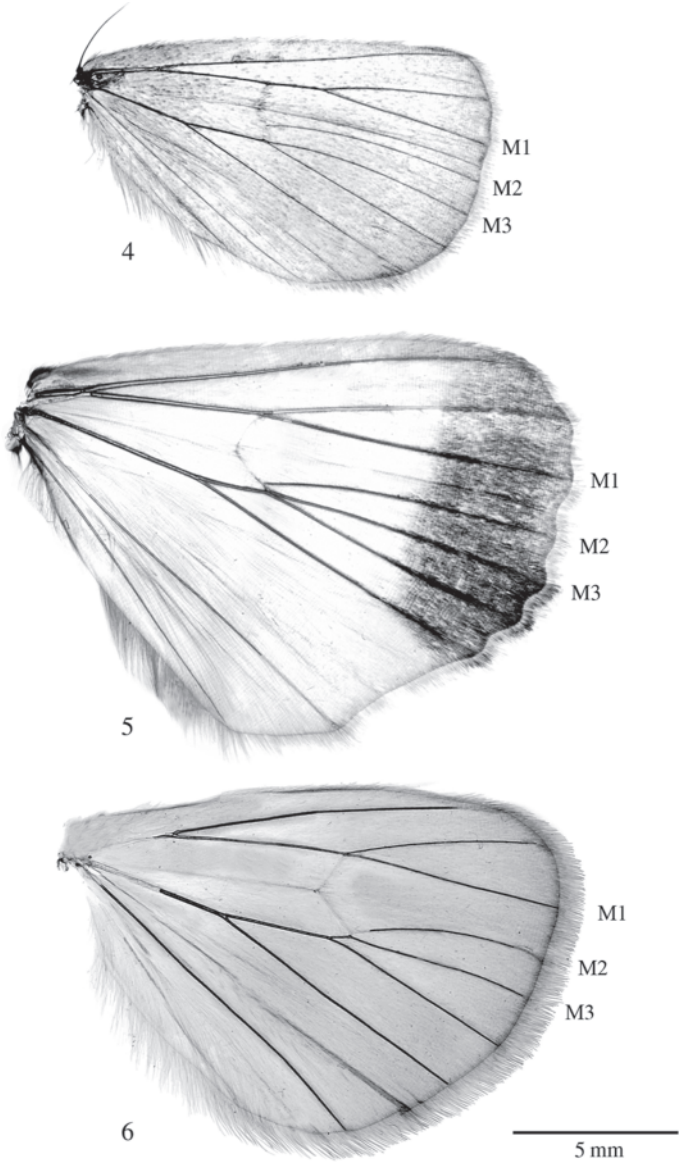
Recent changes in noctuoid classification

We begin our review of recent changes in the classification of the Noctuoidea with Poole (1995) (Fig. 20). Although Poole's classification was limited to the trifine Noctuidae (= Noctuidae *s.s.* of Fibiger and Lafontaine 2005), it has provided a basis for discussion of trifine noctuid classification. It departs from the classification used in the most recent North

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Figs. 4–6. Hind wing venation of quadrifine Noctuidae: 4, *Chytolita morbidalis* (Guenée) (Herminiinae), showing position of vein M2; 5, *Melipotis jucunda* (Hübner) (Catocalinae) with vein M2 in fully quadrifine position; 6, *Spilosoma virginica* (Fabricius) (Arctiinae) with vein M2 in fully quadrifine position.



American checklist (Franclemont and Todd 1983) in several key areas:

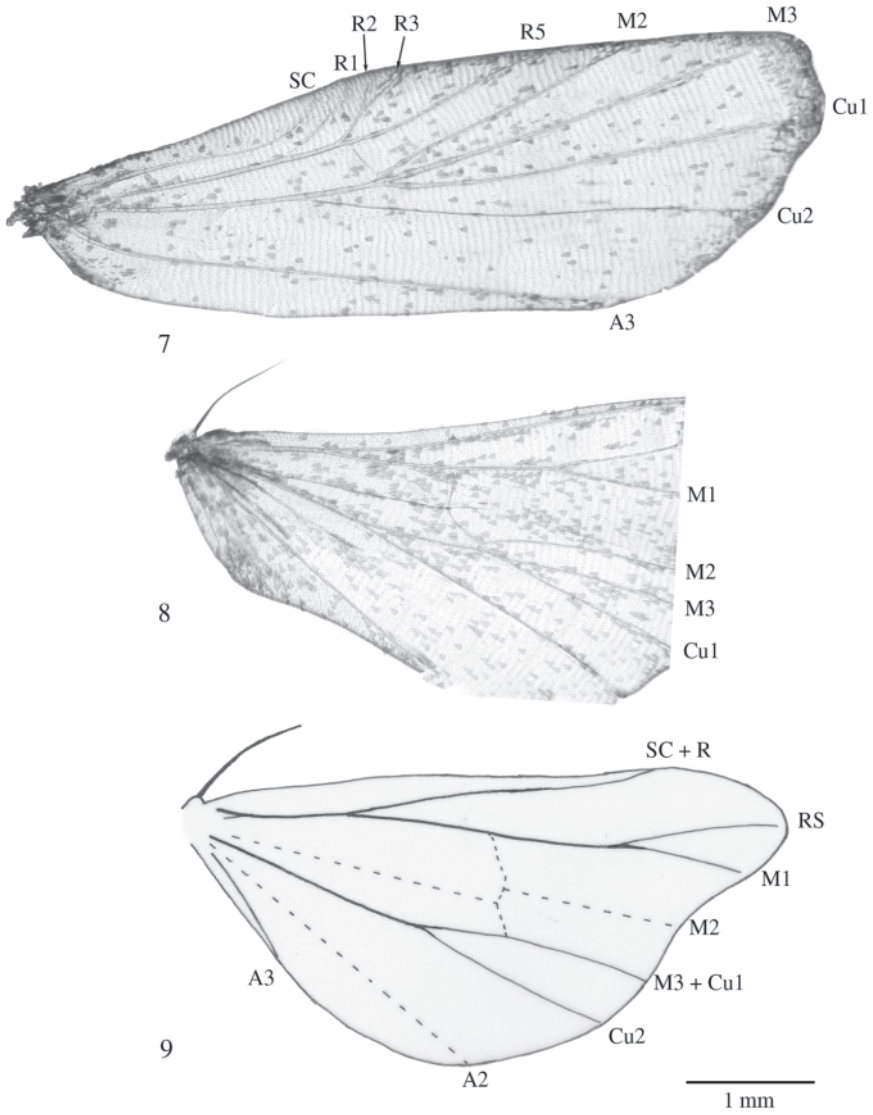
(1) the subfamily Condicinae was proposed for an assortment of genera collected from the Acontiinae and the "unassociated genera" of the Amphipyrinae of Franclemont and Todd (*op. cit.*); it was treated as a basal subfamily by Poole because of the presence of three SV setae on the first abdominal segment (A1) of the larva and the pleural sclerite being fused to the tegumen, both features being mainly characteristic of quadrifine noctuids;

(2) the subfamily Psaphidinae was expanded to include the Feraliini and Grotellini as tribes, and many genera from the "unassociated genera" of the Amphipyrinae of Franclemont and Todd (*op. cit.*) were arranged in three new tribes: Nocloini, Triocnemidini, and Azenini;

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Figs. 7–9. Wing venation: 7, forewing venation of *Strepsimanes* Meyrick (Noctuidae: Strepsimaninae); 8, hind-wing venation of *Strepsimanes* Meyrick (Noctuidae: Strepsimaninae); 9, hind wing venation of *Micronoctua* Fibiger (Micronoctuidae).



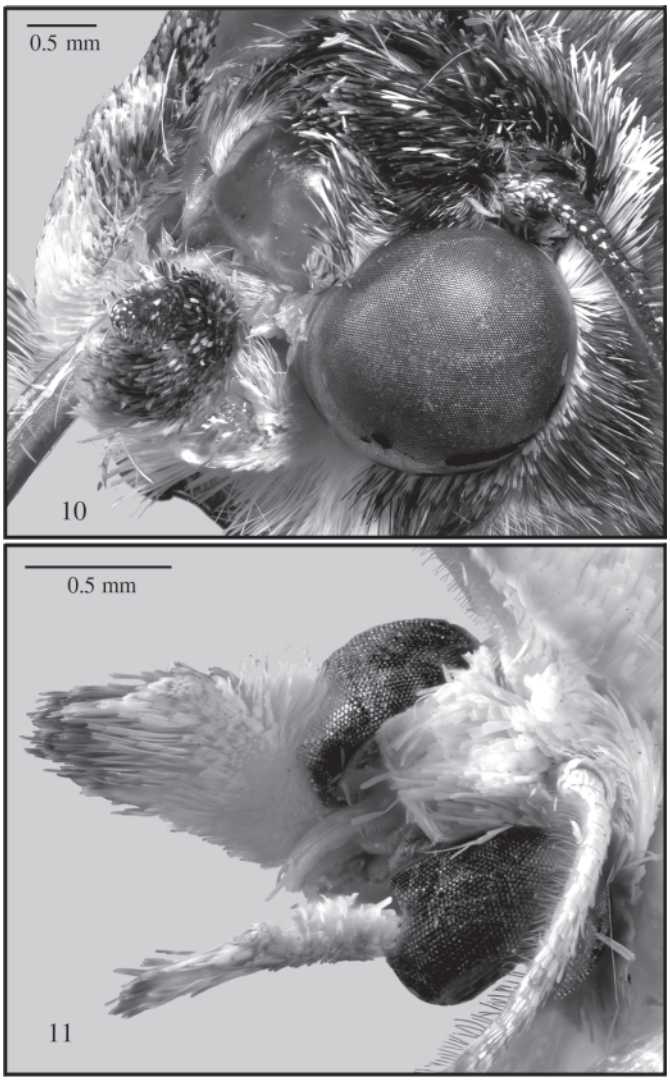
(3) the Oncocnemidinae were treated as a subfamily separate from the Cuculliinae, the latter restricted to *Cucullia* Schrank and a few closely related genera;
(4) the Amphipyrinae were restricted to *Amphipyra* Ochsenheimer and the genus *Phosphila* Hübner (included as the tribe Phosphilini), and the subfamily Amphipyrinae was treated as the sister group to both the cuculliine *s.l.* and the noctuine *s.l.* groups of subfamilies on the basis of the simplified valves (no corona, no digitus, and a reduced clasper);
(5) the Noctuinae was used in its more inclusive sense, like that of Beck (1960), hereafter referred to as Noctuinae *s.l.*, and included the subfamilies Noctuinae *s.s.* and Hadeninae, most of the former Amphipyrinae, and major parts of the subfamily Cuculliinae.

The main features of the classification of Speidel *et al.* (1996) (Fig. 21) follow:

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Figs. 10–11. Scaling of frons of Noctuidae: 10, bare, descaled lower frons (Catocalinae: *Catocala* Schrank); 11, fully scaled frons (Rivulinae: *Rivula* Guenée).



(1) the family Noctuidae was characterized by the presence of an adenosma (a tube-like ventral prothoracic gland) in the larva, this structure being absent from the two families basal to the Noctuidae in their phylogeny, namely the Arctiidae and Aganaidae; the absence of the gland in the Rivulinae and in one species of Hypeninae were treated as secondary losses;
(2) the Aganaidae were treated as the sister group to the Noctuidae on the basis of the two families sharing an elongated uncus;
(3) the remainder of the classification was similar to that of Franclemont and Todd (1983) and Fibiger and Hacker (1991), with the Herminiinae treated as basal because of the prespiracular hood (similar to that of the Arctiidae (Fig. 14) and Aganaidae);
(4) the noline–chloephorine–sarrothripine clade was included in the Noctuidae next to the Eustrotiinae;
(5) the Amphipyrinae were retained as a mixture of cuculliine *s.l.* and noctuine *s.l.* genera resembling previous lists;
(6) on the basis of the nodular form of the tympanal sclerite (Fig. 13), the genera *Aedia* Hübner and *Tyta* Billberg were moved from the quadrifine noctuids to form

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two subfamilies near the Acontiinae, in which the tympanal sclerite is a flat plate or is bar-like as in the quadrifine Noctuidae (Fig. 12) and the more primitive subfamilies of the trifine Noctuidae;

(7) on the basis of the presence of basal abdominal brushes and associated structures (Fig. 15), the genera *Pseudeustrotia* Warren, *Sinocharis* Püngeler, and *Lophonycta* Sugi were moved from the Acontiinae *s.l.* and placed as monobasic subfamilies next to the higher trifine subfamilies (the cuculliine *s.l.* and noctuine *s.l.* groups of subfamilies).

The classification of the Noctuoidea by Kitching and Rawlins (1998) (an interpreted cladogram is shown in Fig. 22) made extensive use of character systems of both adults and immatures. The main departures from previous classifications were the following:

(1) the Nolinae, Sarrothripinae, Chloephorinae, and Eariadinae were removed from the Noctuidae and treated as subfamilies of the family Nolidae;

(2) the Nolidae were associated with the Arctiidae on the basis of the elongate, bar-shaped retinaculum of the male and other characters;

(3) the Pantheinae were removed from the Noctuidae and treated as the family Pantheidae, which was closely associated with the Lymantriidae;

(4) the Calpinae were segregated as a subfamily separate from the Catocalinae;

(5) a group of quadrifine subfamilies (Herminiinae, Catocalinae, Calpinae, Hypeninae, Aganainae, Cocytiinae, Strepsimaninae, Euteliinae, and Stictopterinae) were associated on the basis of the bare lower frons (Fig. 10);

(6) the tribes Raphiini, Ufeini, and Glottulini were raised to subfamily status;

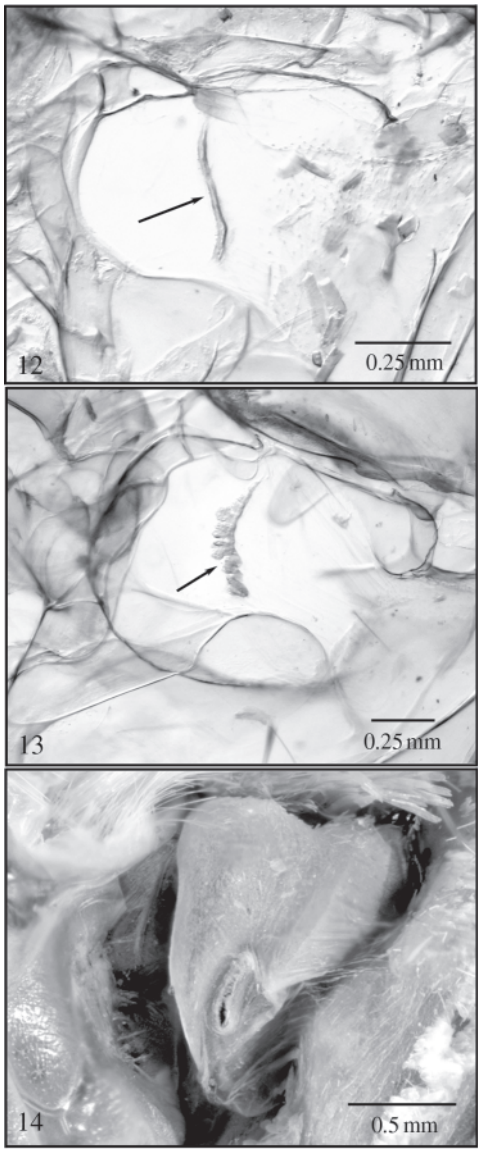
(7) Poole's (1995) tribes Grotellini, Nocloini, and Azenini were removed from the Psaphidinae and treated as tribes of the Stiriinae;

(8) the Triocnemidini were removed from the Psaphidinae and placed in the Oncocnemidinae;

(9) the Oncocnemidinae were treated as a tribe of the Cuculliinae rather than as a separate subfamily; and

(10) the subfamily Hadeninae was expanded to include most of the genera placed in the Noctuinae *s.l.* by Poole (1995) and Beck (1960) except for those in the Noctuinae *s.s.*, which were excluded from the expanded Hadeninae and retained as the subfamily Noctuinae *s.s.*

Figs. 12–14. Tympanal structures of Noctuidae: 12, bar-like tympanal sclerite (Eublemminae: *Pangrapta* Hübner); 13, nodular tympanal sclerite (Noctuinae: *Xestia* Hübner); 14, prespiracular hood (spiracle on outer (posterior) surface of tympanal hood) (Arctiinae: *Spilosoma* Curtis).

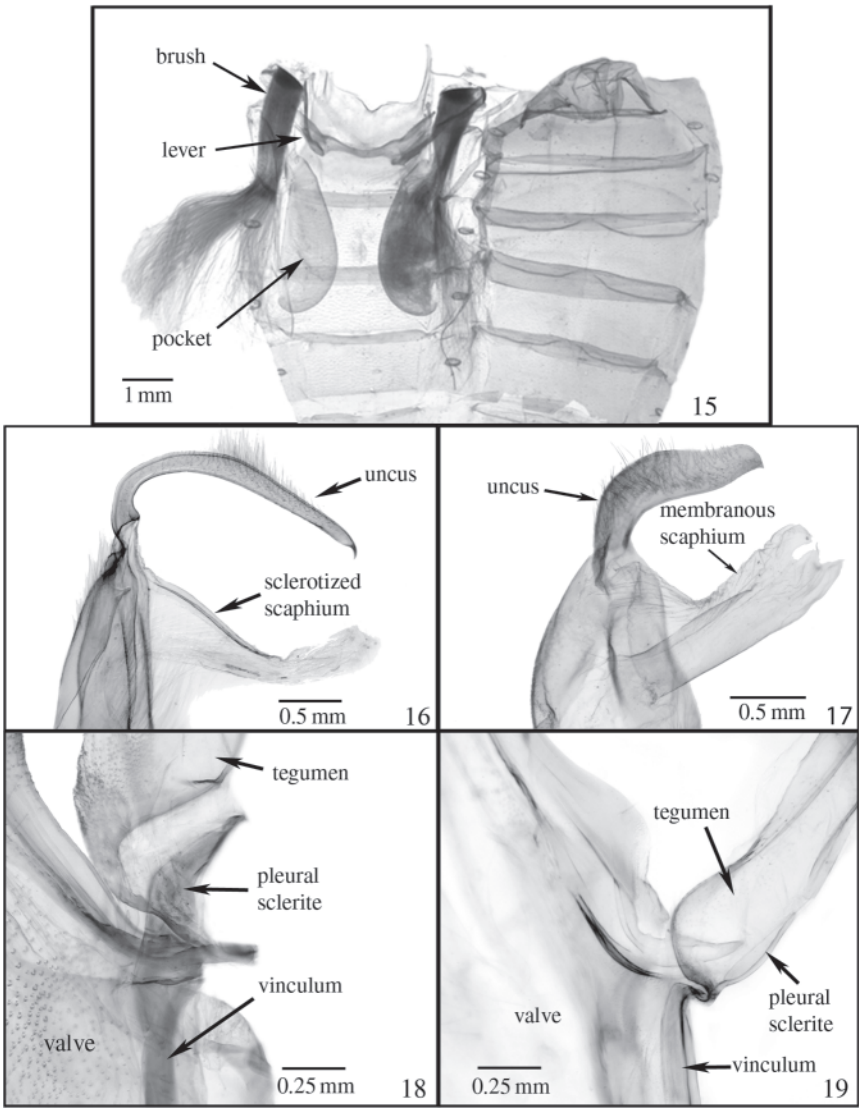


The classification of Beck (1999–2000) split the Noctuidae into a large number of tribes, subtribes, and genera, which were grouped into a relatively small number of subfamilies. The classification, based almost exclusively on

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Figs. 15–19. Abdominal structures of Noctuidae: 15, basal abdominal brushes and pockets (Noctuinae: *Anicla* Grote); 16, scaphium sclerotized dorsally and ventrally (Catocalinae); 17, scaphium membranous dorsally, sclerotized ventrally (Xyleninae: *Cosmia* Ochsenheimer); 18, free pleural sclerite between tegumen and vinculum (Xyleninae: *Actinotia* Hübner); 19, pleural sclerite fused with tegumen (Catocalinae: *Argyrostrotis* Hübner).



larval characters, included a very large number of family-group names, of which 68 were proposed by Beck either in this work or in a previous checklist (Beck 1996). These family-group names were diagnosed but not defined in a hierarchical classification on the basis of derived character states.

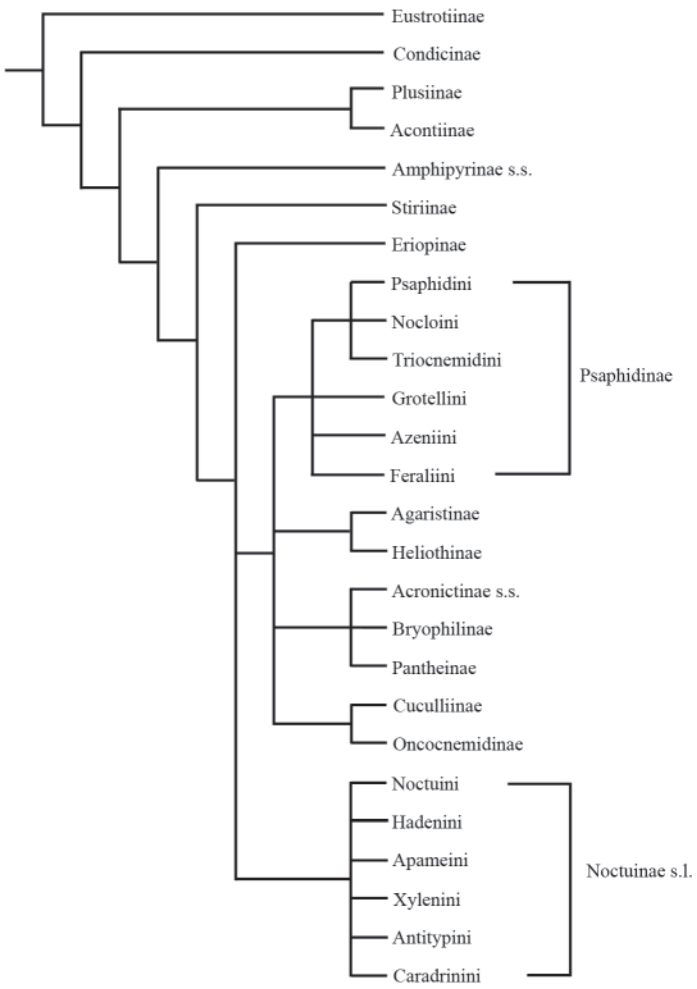
The classification of Mitchell *et al.* (2006) (Figs. 23, 24) is the latest of three studies of the Noctuoidea based on nuclear genes (*i.e.*, Mitchell *et al.* 1997, 2000), but the 2006 study included twice as many taxa (146 species), with an emphasis on trifines, so the authors gave a more definitive interpretation of the results in terms of proposing changes in classification than they had in the two previous studies. The major findings of the study were

(1) the close relationship between a clade comprising the Arctiidae and Lymantriidae and one containing five subfamilies of

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Fig. 20. Phylogeny of trifine Noctuidae, adapted from Poole (1995, Fig. 1).



quadrifine Noctuidae (*i.e.*, Calpinae, Catocalinae, Strepsimaninae [on the basis of *Phobolosia anfracta* (Hy. Edwards), which is in Scolecocampinae in Fibiger and Lafontaine 2005], Rivulinae [on the basis of *Mycterophora* Hulst, which is in Boletobiinae in Fibiger and Lafontaine 2005], and Eublemmini [Eublemminae in Fibiger and Lafontaine 2005]);

(2) placement of the Rivulinae *s.s.* between the Lymantriidae and the Arctiidae as the sister group to the Arctiidae in the strict consensus tree (Fig. 2 in Mitchell *et al.*), although this position is unstable because the Rivulinae are the sister group to the Lymantriidae and Arctiidae in the maximum-likelihood tree (Fig. 4 in Mitchell *et al.*);

(3) placement of the Nolidae as the sister group to the rest of the quadrifine Noctuidae (including the Arctiidae and Lymantriidae); and

(4) placement of a clade grouping the Eutelliinae and Stictopterinae above the Nolidae as sister group to the remainder of the quadrifine noctuids.

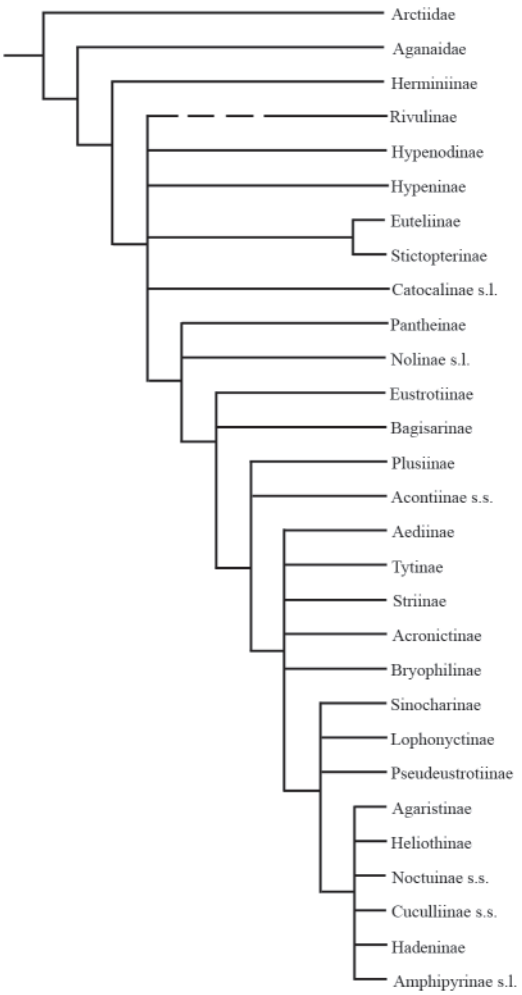
Most of the subfamilies among the quadrifine noctuids had high bootstrap support, but most of the groupings of subfamilies showed weak support, with three exceptions:

(1) a large clade that included the Hypeninae, Aganainae, Herminiinae, Calpinae, Catocalinae, "Strepsimaninae" [Scolecocampinae], "Rivilinae" [Boletobiinae], Eublemminae, Lymantriidae, Rivulinae, and

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Fig. 21. Phylogeny of Noctuoidea, adapted from Speidel *et al.* (1996, Fig. 1).



Arctiidae, termed the "L.A.Q. clade" (*i.e.*, lymantriids, arctiids, quadrifine noctuids) by Mitchell *et al.*;

(2) a clade supporting the "L.A.Q. clade" plus the eutelliine–stictopterine clade (55%–66% support); and

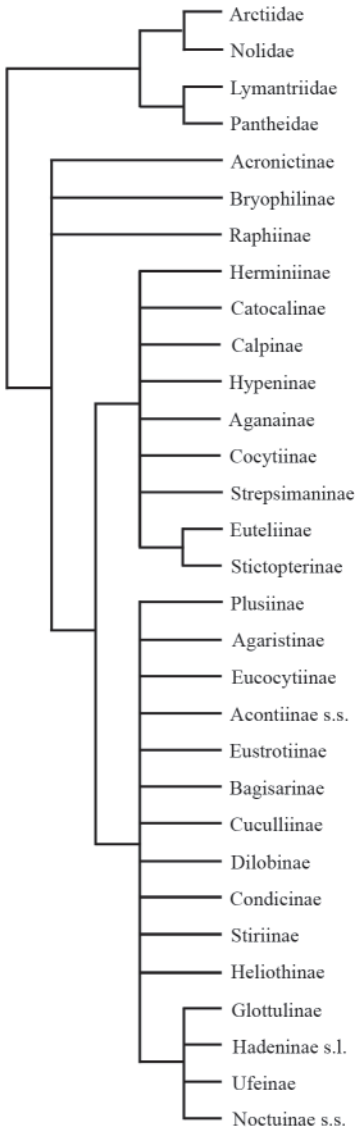
(3) a clade grouping the Eutelliinae with the Stictopterinae (99% support).

The trifine noctuids were treated by Mitchell *et al.* (2006) as a series of four major clades:

(1) the Plusiinae;

(2) the cuculliine group of subfamilies (Dilobinae, Raphiinae, Cuculliinae, Pantheinae, Oncocnemidinae, Agaristinae, Stiriinae, Amphipyrinae, Psaphidinae, Grotellinae, Azeninae, and Acronictinae);

Fig. 22. Phylogeny of Noctuoidea from Kitching and Rawlins (1998) (adapted from Mitchell *et al.* 2006, Fig. 1C).



(3) the Eustrotiinae, "Old World Stiriinae", and Acontiinae; and

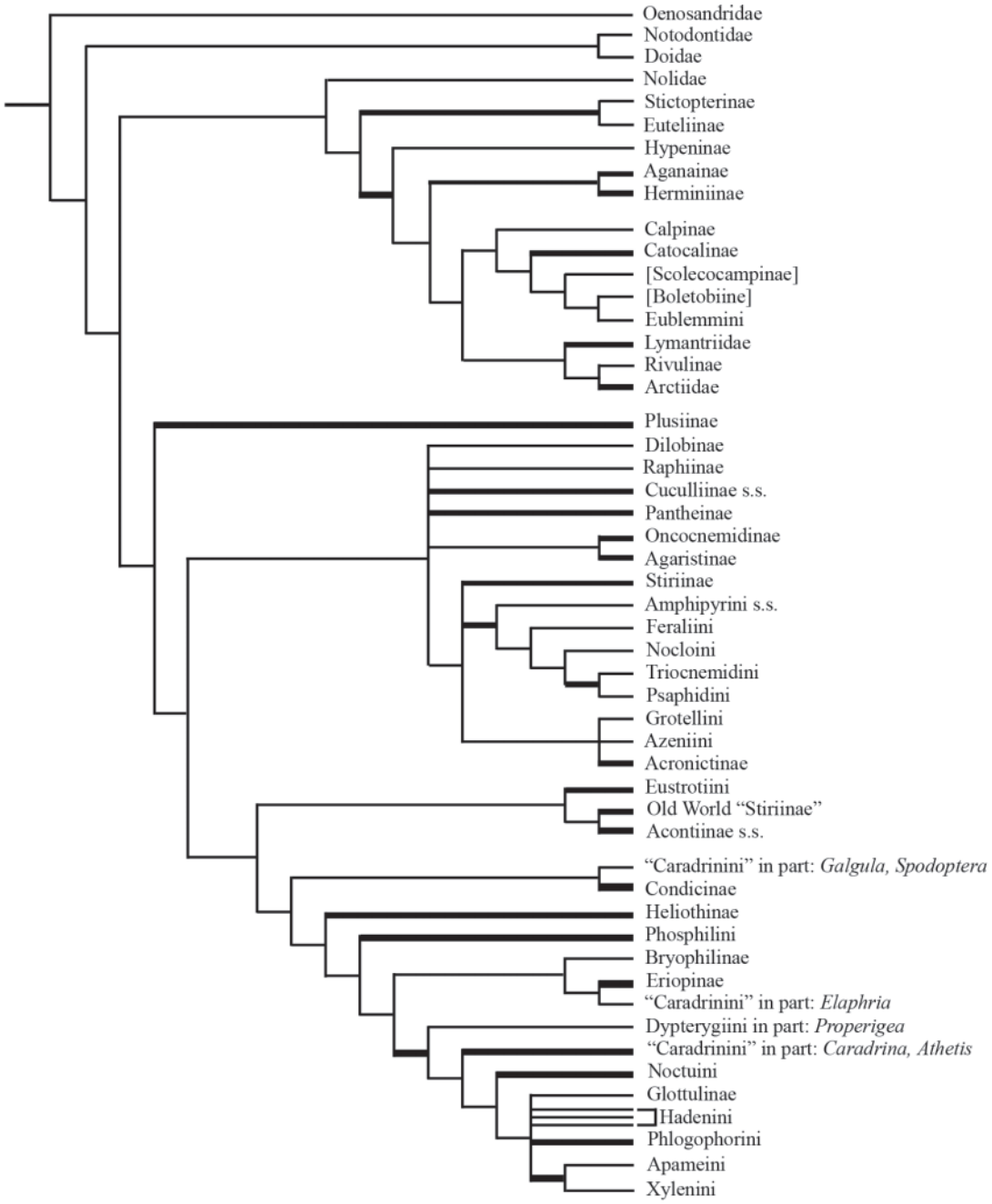
(4) a higher clade termed the "pest clade", comprising the Heliothinae, Condicinae, Eriopinae, Bryophilinae, and Noctuinae *s.l.* of Poole (1995).

Most of the subfamilies within the basal three clades had high bootstrap support, generally 90% or more, but the groupings of subfamilies that form these clades and those within these clades had low bootstrap values, with only the association of the Amphipyrinae +

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Fig. 23. Phylogeny of Noctuoidea, adapted from Mitchell *et al.* (2006, Fig. 5).

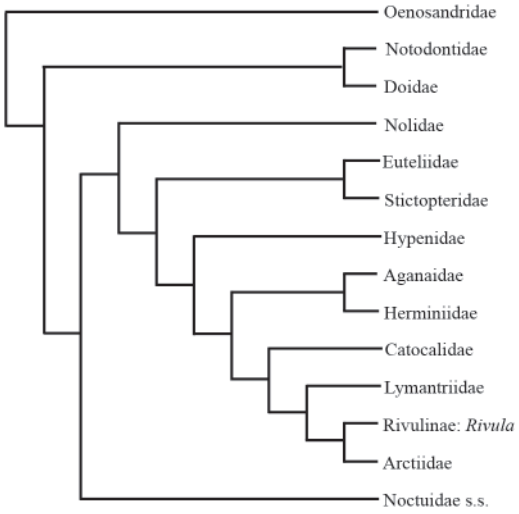


Psaphidinae *sensu* Poole (1995) showing high support (89%). The Pantheinae and Acronictinae were both grouped with the cuculliine *s.l.* clade of subfamilies, but support was weak. Curiously, the larvae of species in the Acronictinae that have a lateral line (*e.g.*, *Acronicta radcliffei* (Harvey)) have the line extending to the anal plate, suggesting an association with the cuculliine group of subfamilies. In the "pest clade" the genera *Spodoptera* Guenée and *Galgula* Guenée, previously associated with the Noctuinae *s.l.*, are associated

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Fig. 24. Phylogeny of families of Noctuoidea, adapted from Mitchell *et al.* (2006, Table 2 and Fig. 5).

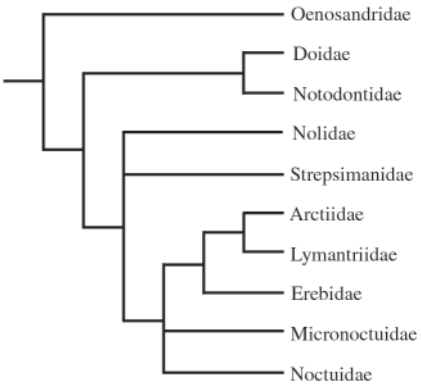


with the Condicinae in the strict consensus tree (Fig. 2 in Mitchell *et al.*), but their position is unstable, as they are the sister group to a clade consisting of Phosphilini + Eriopinae + Noctuinae *s.l.* in the maximum-likelihood tree (Fig. 4 in Mitchell *et al.*). Similarly, support is weak for an association of the Elaphriinae with the Eriopinae in the strict consensus tree; the Elaphriinae are associated with *Galgula* and *Spodoptera* in the maximum-likelihood tree. Another surprising suggestion was that within a well-supported Noctuinae *s.l.*, the genus *Properigea* Barnes and Benjamin and the tribe Caradrinini *s.s.* formed two sister groups to the remainder of the Noctuinae *s.l.* The Noctuinae *s.s.* (= Noctuini in Mitchell *et al.* 2006) appear monophyletic and are the sister group to the Hadenini + Apameini + Xylenini. The Hadenini are shown as paraphyletic, with the clade Apameini + Xylenini derived from within the Hadenini.

In order to retain the Lymantriidae and Arctiidae as families, Mitchell *et al.* (2006) raised six subfamilies to family status (Stictopteridae, Euteliidae, Aganaidae, Herminiidae, Hypenidae, and Catocalidae) and restricted the family Noctuidae to the trifine noctuids.

The classification of Fibiger and Lafontaine (2005) (Figs. 25–27) was based on larval, pupal, and adult morphological characters and was built mainly on the framework of the Kitching and Rawlins (1998) classification, but the following changes were proposed:

Fig. 25. Phylogeny of Noctuoidea, adapted from Fibiger and Lafontaine (2005, cladogram 1).



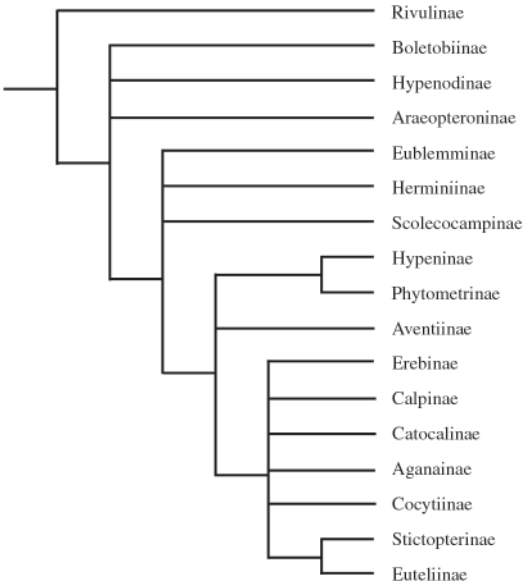
(1) the arctiid group of families (Nolidae, Arctiidae, and Lymantriidae) was moved to a position in front of the upgraded family Erebidae, so the close relationship with the quadrifine noctuids was better reflected;
(2) the Lymantriidae were moved from a position in front of the Nolidae to a position after the Arctiidae to reflect the close association of the arctiids and lymantriids;
(3) the quadrifine noctuid subfamilies (Herminiinae, Hypenodinae, Hypeninae, Catocaslinae, Calpinae, Hypeninae, Stictopterinae, and Euteliinae) were treated as subfamilies of the re-established family Erebidae and as the sister group to the Arctiidae and Lymantriidae;
(4) the subfamilies Rivulinae, Boletobiinae, Phytometrinae, Scolecocampinae, Erebinae, and Hypenodinae were reinstated;
(5) the subfamily Strepsimaninae was treated as the family Strepsimanidae and placed between the Nolidae and the Arctiidae;
(6) the classification of the subfamilies Catocalinae, Calpinae, and Erebinae was revised, and the Armadini and Aediini were transferred from the Catocalinae to the Acontiinae, and the Tytini from the Catocalinae to the subfamily Metoponiinae of the Noctuidae;
(7) the tribe Eublemmini was removed from the Eustrotiinae in the Noctuidae *s.s.* and treated as a primitive subfamily of the Erebidae;
(8) Araeopteroninae Fibiger was proposed as a new subfamily in the Erebidae;
(9) Micronoctuidae Fibiger was proposed as a new family for a large number of undes-

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cribed genera and species occurring mainly in Africa and Southeast Asia;
(10) the family Noctuidae was redefined and restricted to the group of subfamilies generally referred to as the "trifine" subfamilies;
(11) the Pantheinae were reinstated as a subfamily of the Noctuidae near the Acronictinae;
(12) the tribe Eriopini was removed from the Hadeninae (*s.l.*) and treated as a subfamily of the Noctuidae;
(13) the tribe Phosphilini was removed from the Hadeninae (*s.l.*) and included in the Psaphidinae next to the Nocloini;
(14) the classification of the Hadeninae *sensu* Kitching and Rawlins (1998) was revised into subfamilies, tribes, and subtribes; and
(15) the classification of the Noctuinae was reviewed on the basis of Lafontaine and Fibiger (2004), and the subtribe Axyliina was proposed in the Noctuini.

Fig. 26. Phylogeny of Erebidae, adapted from Fibiger and Lafontaine (2005, cladogram 2).



Discussion

This discussion deals primarily with the results of Mitchell *et al.* (2006) and Fibiger and Lafontaine (2005), so we omit the repeated references to 2006 and 2005, respectively, in this section.

We find the results of these two studies encouragingly similar in reconstructing the higher classification of the Noctuidae, differing mainly in ranking. Our goal is to assess the similarities and differences between these two classifications and derive a revised classification by combining the morphological and molecular results.

One problem in making direct comparisons between the two classifications is the differing names for the same groups of genera. In order to compare effectively the two classifications, we list the taxon used in the Mitchell *et al.* classification and then give the equivalent taxon in the classification of Fibiger and Lafontaine.

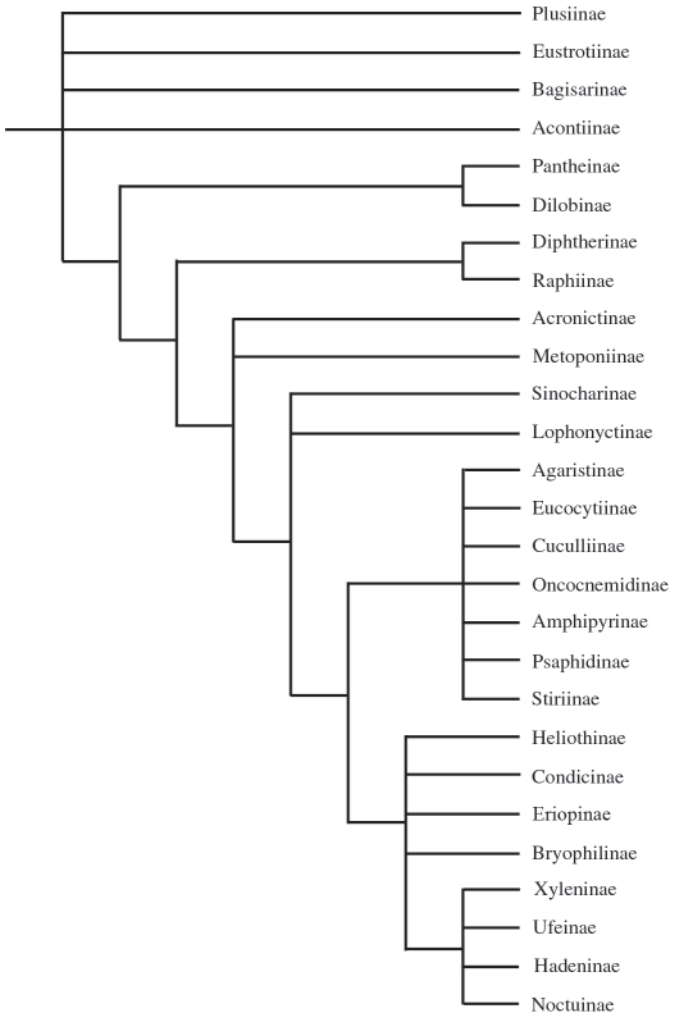
Most of the taxonomic differences between the two classifications (shown in Tables 1 and 2) result from different family and subfamily rankings and are resolved through the changes in the rankings proposed below.

There are two main difficulties in converting the consensus trees generated by Mitchell *et al.* (2006, Figs. 2–5) into a classification. Firstly, it can be difficult to treat nuclear gene sequences as uniquely derived character states. Secondly, the trees are based on only 146 species and these are strongly biased towards the trifine Noctuidae (= Noctuidae *s.s.*) and especially towards the Noctuinae *s.l.* (Xyleninae, Hadeninae, and Noctuinae *s.s.*). The subfamilies and tribes of the quadrifine noctuids and those of the other families of the quadrifid noctuoids (72 taxa in Fibiger and Lafontaine 2005) are represented by only 30 species from 20 family-group taxa and only 9 of these represent the type species for the taxon, so some subfamilies and tribes are represented by genera not closely related to the type species. As a result, Mitchell *et al.* generally did not attempt to change the names of higher taxa on the basis of so few exemplars, but listed these taxa in their current status. For this reason, a genus or tribe could be treated as the sister group to a subfamily. For example, *Properigea* Barnes and Benjamin was shown as the sister group to the remainder of the Noctuinae *s.l.* Similarly, the Eublemmini were shown as the sister group to the Rivulinae (part: *Mycterophora* Hulst). In order to preserve the family status of the Arctiidae and Lymantriidae, Mitchell *et al.* departed from this use of "traditional" rather than revised categories for family-group names and raised the basal six subfamilies of the quadrifine Noctuidae to family status (*i.e.*, Stictopteridae, Euteliidae, Aganaidae, Herminiidae, Hypenidae, and Catocalidae) (Table 2). Three tribes used in Kitching and Rawlins (1998) (*i.e.*, Eublemmini, Eustrotiini, and Oncocnemidini) were raised to

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Fig. 27. Phylogeny of Noctuidae *s.s.*, adapted from Fibiger and Lafontaine (2005, cladogram 3).



subfamilies, and the subfamily Ufeinae was reduced to a genus (*Ufeus* Grote) of the tribe Xylenini. The definition of the Noctuinae was left unresolved, with genera of the Caradrinini left in the Noctuinae *s.l.* (*sensu* Beck 1960 and Poole 1995) and the Noctuinae *s.s.* and Hadeninae *s.l.* essentially following the usage of Kitching and Rawlins (1998).

In terms of the positions of taxa, we see seven principal areas where the classification of Fibiger and Lafontaine (2005) differs from that of Mitchell *et al.* (2006): (1) the Arctiidae–Lymantriidae clade; (2) the Aganainae; (3) the Nolidae; (4) the Stictopterinae–Euteliinae clade; (5) the Rivulinae; (6) the Phosphilini; and (7) the Noctuinae *s.l.* (*sensu* Beck 1960 and Poole 1995). These seven issues are discussed below.

(1) The Arctiidae–Lymantriidae clade in the classification of Mitchell *et al.* is nested within a large clade comprising the noctuid subfamilies Hypeninae, Aganainae, Herminiinae, Calpinae, Catocalinae, Scolecocampinae (as Strepsimaninae), Boletobiinae (as Rivulinae), Eublemminae, and Rivulinae (*s.s.*). This clade is strongly supported by the molecular results of Mitchell *et al.* and is referred to as the "L.A.Q. clade" (Lymantriidae, Arctiidae, quadrifine Noctuidae clade). Within the "L.A.Q. clade" the relationships among subfamilies are weakly supported, with the exception of a well-supported clade uniting the Aganainae and the Herminiinae. In the classification of Fibiger and Lafontaine, the Arctiidae–Lymantriidae clade is the sister group to the Erebidae (= quadrifine Noctuidae). The monophyly of the Erebidae,

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Table 1. Taxonomic comparison between Mitchell *et al.* (2006, Table 1) and Fibiger and Lafontaine (2005).

Mitchell *et al.*	Fibiger and Lafontaine
Catocalinae: Tytini	Noctuidae: Metoponiinae (*Tyta*)
Catocalinae: Armadini	Noctuidae: Acontiinae: Armadini
Catocalinae: Catocalini: Catocalina	Catocalinae: Catocalini
Catocalinae: Catocalini: Ectypina	Catocalinae: Euclidiini
Calpinae: Gonopterini	Calpinae: Scoliopterygini
Strepsimaninae [*s.s.*]	Strepsimanidae
Strepsimaninae (incl. Hypenodinae)	Hypenodinae
Strepsimaninae (*Phobolosia*)	Scolecocampinae (*Phobolosia*)
Rivulinae (*Mycterophora*)	Boletobiinae (*Mycterophora*)
Rivulinae (*Rivula* Guenée)	Rivulinae
Acontiinae: Cydosiini	Bagisarinae: Cydosiini
Noctuidae: Eustrotiinae: Eublemmini	Erebidae: Eublemminae
Stiriinae *s.l.* (Old World species)	Metoponiinae
Amphipyrinae: Phosphilini	Psaphidinae: Phosphilini
Psaphidinae: Grotellini	Stiriinae: Grotellini
Psaphidinae: Azenini	Stiriinae: Azenini
Noctuinae *s.l.*	Xyleninae, Hadeninae, and Noctuinae
Noctuinae: Noctuini: Noctuina	Noctuinae: Noctuini
Noctuinae: Noctuini: Agrotina	Noctuinae: Agrotini: Agrotina
Noctuinae: Noctuini: Aniclina	Noctuinae: Agrotini: Austrandesiina
Noctuinae: Hadenini: Hadenina	Hadeninae: Hadenini
Noctuinae: Hadenini: Eriopygina	Hadeninae: Eriopygini
Noctuinae: Caradrinini	Xyleninae: Caradrinini
Noctuinae: Dypterygiini	Xyleninae: Dypterygiini
Noctuinae: Phlogophorini	Xyleninae: Phlogophorini
Noctuinae: Apameini	Xyleninae: Apameini
Noctuinae: Xylenini *s.s.*	Xyleninae: Xylenini
Noctuinae: Xylenini *s.s.*: *Lithophane* Hübner	Xyleninae: Xylenini: Xylenina
Noctuinae: Xylenini *s.l.*: Antitypini	Xyleninae: Xylenini: Antitypina
Noctuinae: Xylenini *s.l.*: Cleocerini *s.s.*	Xyleninae: Episemini
Noctuinae: Xylenini *s.l.*: Cleocerini *s.l.* (*Epidemas* Smith)	Xyleninae: Xylenini: Xylenina
Glottulinae	Hadeninae: Glottulini

however, was based on the smooth, dorsally sclerotized scaphium (Fig. 16) and the apical flaps on the larval spinneret; both characters are secondarily lost in some lineages of the Erebidae, creating the possibility that the arctiid–lymantriid clade might be derived from within the Erebidae (the dorsal surface of the scaphium is membranous in the arctiid–lymantriid clade and in the trifine Noctuidae (Fig. 17)). The possibility that the arctiid–lymantriid clade might be derived from within the Erebidae is further strengthened by two derived character states shared by the arctiid–lymantriid clade with only part of the Erebidae, namely a clade consisting of the Erebinae, Calpinae, Catocalinae, Aganainae, Cocytiinae, Stictopterinae, and Euteliinae (the erebine–euteliine clade). These characters are the fully quadrifine hind wing venation, where vein M2 in the hind wing has moved to the lower part of the cell adjacent to or fused with the base of M3 and CuA1 (Figs. 5, 6), and the fusion of the pleural sclerite with the posterior margin of the tegumen that creates a simple elbow-like articulation between the tegumen and the vinculum (Fig. 19). These two character states, shared by most subfamilies of the quadrifine Noctuidae and the arctiid–lymantriid clade, were treated as convergent by

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Table 2. Taxonomic comparison between Mitchell *et al.* (2006, Table 2) and Fibiger and Lafontaine (2005).

Mitchell *et al.*	Fibiger and Lafontaine
Stictopteridae	Erebidae: Stictopterinae
Euteliidae	Erebidae: Euteliinae
Aganaidae	Erebidae: Aganainae
Herminiidae	Erebidae: Herminiinae
Hypenidae	Erebidae: Hypeninae
Catocalidae	Erebidae (in part)
Catocalidae: Catocalinae	Erebidae: Catocalinae
Catocalidae: Calpinae	Erebidae: Calpinae
Catocalidae: Strepsimaninae	Erebidae: Hypenodinae
Catocalidae: Rivulinae	Erebidae: Rivulinae
Catocalidae: Eublemminae	Erebidae: Eublemminae
Noctuidae *s.s.*	Noctuidae *s.s.*
Noctuinae *s.s.*	Noctuinae
Noctuinae *s.l.*: Caradrinini	Xyleninae: Caradrinini
Hadeninae *s.s.*	Hadeninae
Hadeninae *s.l.*: Phlogophorini, Xylenini, Apameini, + unassociated genera	Xyleninae: Phlogophorini, Xylenini, Apameini, + 8 other tribes

Kitching and Rawlins (1998), but their presence in these two clades, in combination with the lack of any consistent character state to define the family Noctuidae (*sensu lato*), suggests that the Erebidae are more closely related to the arctiid–lymantriid clade than to the Noctuidae *s.s*. This interpretation led Fibiger and Lafontaine to treat the quadrifine noctuids as the family Erebidae and as more closely related to the arctiid–lymantriid clade than to the trifine noctuids (Noctuidae *s.s.*). The difficulty with this classification, however, is that the derived character states that the arctiid–lymantriid clade shares with the Erebidae are in only part of the Erebidae, namely the erebine–euteliine clade (defined above). The possibility that the Erebidae could be paraphyletic with respect to the arctiid–lymantriid clade was discussed by Fibiger and Lafontaine (2005, pp. 16–17), with the implications this would have for classification. These morphological characters, in combination with the well-supported "L.A.Q. clade" from the molecular results of Mitchell *et al.*, lead us to accept that the Erebidae as defined by Fibiger and Lafontaine is a paraphyletic group and that a new classification is needed to reflect this; such a classification is proposed below. The adults of Arctiidae and Lymantriidae have a fully scaled frons, unlike other members of the erebine–euteliine clade, whereas the frons is denuded in genera of the Lymantriidae with larger labial palpi (*e.g.*, *Dasychira* Hübner and *Leucoma* Stephens), suggesting that the general lack of a denuded area on the lower part of the frons in the arctiid–lymantriid clade may be related to the smaller size of the labial palpi because this close correlation indicates that it is the long, upturned labial palpi that are denuding the frons.

(2) The Aganainae have been, and continue to be, an enigmatic group that has both noctuid and arctiid characteristics. In addition to the aposematic arctiid-like form of the adults, the aganaines share three character states with the Arctiidae: a bar-like retinaculum in males, a prespiracular tympanal hood, and the loss of the adenosma (ventral prothoracic gland) in the larvae. The Aganainae lack the two derived character states of the Arctiidae (the metathoracic microtymbal organs and the dorsal eversible pheromone glands associated with the anal papillae) used by Kitching and Rawlins (1998) to define the Arctiidae, but the absence of these two arctiid synapomorphies does not exclude the possibility that the Aganainae are the sister group of the Arctiidae, with the association supported by the three character states listed above. The quadrifine noctuid characteristics of the Aganainae (bare lower frons, long pointed uncus, dorsally sclerotized scaphium, one SV seta on T2 and T3 in the larva, larvae with primary setae only) are all plesiomorphic character

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states of the "L.A.Q. clade" and are not relevant to a possible association of the Aganainae with the Arctiidae. In Mitchell *et al.* the Aganainae are associated with the Herminiinae with strong (>90%) support but, as stated above, such an association is not supported by the morphological characters; therefore, an association of the Aganainae with the Herminiinae must await confirmation by other means, such as molecular studies using more nuclear genes, longer gene sequences, and more taxa (two genera of aganaines and two of herminiines were included in Mitchell *et al.* 2006). The Aganainae have a prespiracular tympanal hood, a character state shared with the Herminiinae (and the Arctiidae), but the bar-like retinaculum in males, the loss of the adenosma, and the fully quadrifine hind wing venation all suggest a closer association of the Aganainae with the Arctiidae than with the Herminiinae.

(3) The Nolidae combine character states of the trifine Noctuidae and the Arctiidae. The tympanal structure of the Nolidae is similar to that of the trifine noctuids, especially the Eustrotiinae, whereas the bar-like retinaculum of the Nolidae is similar to that of the Arctiidae. Also, the larvae of the Chloephorinae and Risobinae have only primary setae and two SV setae on A1, as in the trifine Noctuidae, whereas the larvae of the Nolinae have secondary setae on verrucae, as in the Arctiidae. The family was treated as the sister group to the remainder of the quadrifid Noctuoidea (*i.e.*, Strepsimanidae, Arctiidae, Lymantriidae, Erebidae, Micronoctuidae, and Noctuidae) by Fibiger and Lafontaine. In Mitchell *et al.* the Nolidae are the sister group to a large clade consisting of the euteliine–stictopterine clade plus the "L.A.Q. clade", with only weak molecular support. The best-known derived morphological character state of the Nolidae is the boat-shaped cocoon with a vertical exit slit. Holloway (2003) gave seven additional characters to support the monophyly of the Nolidae, but most have not been surveyed throughout the Nolidae, and the derived *versus* primitive condition of many has not been determined. The Nolidae have a bar-like retinaculum in males, like the Arctiidae, and this, in association with the fully quadrifine hind wing plus the fused pleural sclerite, suggests a placement of the Nolidae within the "L.A.Q. clade" near the Arctiidae in spite of the basal position of the family in Mitchell *et al.*, where it is far removed from the "L.A.Q. clade". As in the Arctiidae, the scaphium is unsclerotized and the frons is fully scaled in most groups, although some genera with larger labial palpi (*e.g.*, *Iscadia* Walker) have a bare lower frons. The Nolidae share a derived character state with the Arctiidae that is not in the Lymantriidae, namely the bar-like retinaculum in males. The isolation of some highly divergent long-branch groups, and the relatively few taxa of quadrifine noctuids (17 species) included in the molecular study, might contribute to taxa such as the Nolidae being misplaced in the phenogram in Mitchell *et al.*

(4) We believe that the stictopterine–euteliine clade is also misplaced in the Mitchell *et al.* classification, where it is treated as the sister group to the entire "L.A.Q. clade" of subfamilies. The subfamilies Stictopterinae and Euteliine are part of a smaller clade (*i.e.*, Erebinae, Calpinae, Catocalinae, Aganainae, Cocytiinae, Stictopterinae, and Euteliinae) that has a fully quadrifine hind wing (Fig. 5) and a fused pleural sclerite (Fig. 19). The arctiid–lymantriid clade also has these last two character states but has lost the denuding of the frons characteristic of a larger clade (Eublemminae, Herminiinae, Scolecocampinae, Hypeninae, Phytometrinae, Aventiinae, Erebinae, Calpinae, Catocalinae, Aganainae, Cocytiinae, Stictopterinae, and Euteliinae), although it is retained in some genera of Lymantriidae. It is possible that the arctiid–lymantriid clade is more closely related to the erebine–calpine–catocaline–aganainae–cocytiine part of the clade than is the stictopterine–euteliine part of the clade. This in part may explain the divergence of the stictopterine–euteliine clade in Mitchell *et al.*

(5) The Rivulinae *s.s.* were shown as the sister group to the Arctiidae (Fig. 2 in Mitchell *et al.*) or the Arctiidae + Lymantriidae (Fig. 4 in Mitchell *et al.*), but with weak molecular support. The instability in the placement of the Rivulinae was probably why they were not raised to family status in Mitchell *et al.* In Fibiger and Lafontaine, the Rivulinae were treated as the most primitive subfamily of the Erebidae because of the primitive tympanal structure, the fully scaled frons (Fig. 11), the partially quadrifine hind wing in the adult, and the lack of a ventral prothoracic adenosma in the larva. This latter character might suggest an association with the Arctiidae; however, the free pleural sclerite and the lack of a fully quadrifine hind wing (similar to that shown in Fig. 4) suggest a basal position of the Rivulinae within the quadrifine Noctuidae rather than a

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position within the erebine–euteliine clade. A free pleural sclerite is typical of the trifine Noctuidae (Fig. 18) but also is present in the more primitive subfamilies of the quadrifine Noctuidae (*e.g.*, Rivulinae, Boletobiinae, Hypenodinae, Araeopteroninae, Eublemminae, Herminiinae, Scolecocampinae, Hypeninae, Phytometrinae, and Aventiinae). The long, barbed setae in the larvae gives them an arctiid look, but the hairy appearance is based on the unusual length of the setae rather than on multiple setae; as for the barbs, all noctuid setae are minutely barbed but the barbs are conspicuous in the Rivulinae because of the enlarged size of the setae.

(6) In Mitchell *et al.* the Phosphilini are placed at the base of the "pest clade" between the Heliothinae and the Bryophilinae. The tribe was included in the subfamily Psaphidinae in Fibiger and Lafontaine because the larvae of other seemingly related genera, as judged by genital structure, have a tubular spinneret and a lateral line extending along the anal plate, which associates them with the Psaphidinae and Amphipyrinae. The larvae of the genus *Phosphila* have now been examined and have a dorsally grooved spinneret and a hairlike SD1 seta on A9, characters that associate *Phosphila* with the Xyleninae–Hadeninae–Noctuinae clade. *Phosphila*, together with the genera *Acherdoa* Walker, *Phuphena* Walker, and *Speocropia* Hampson, all of which have simple valves without a clasper plate and a spinose vesica, are treated as the tribe Phosphilini and tentatively placed in the Xyleninae. The genera in which the larva has a tubular spinneret, a setose SD1 seta on A9, a lateral line extending along the anal plate, a male valve with a ventral clasper, and long spines in the vesica (*i.e.*, *Apsaphida* Franclemont, *Cropia* Walker, *Heterochroma* Guenée, *Paratrachea* Hampson, and *Viridemas* Smith) are transferred to the subfamily Amphipyrinae. Like other Amphipyrinae, the larvae have a dorsal hump on A8.

(7) The Noctuinae *s.l.*, originally proposed by Beck (1960), was re-established by Poole (1995) to unite the large assemblage of cutworm genera formerly placed in the subfamilies Noctuinae, Hadeninae, and Amphipyrinae (in part: Apameini, Xylenini, Antitypini, Phlogophorini, Caradrinini, Dypterygiini, and Cleocerini). Most workers support the monophyly of this group based mainly on the dorsally grooved spinneret in the larvae and the mesially positioned clasper in the male genitalia. Whether or not this very large group should be further subdivided is the main issue in terms of classification. Kitching and Rawlins (1998) retained the Noctuinae *s.s.* as a subfamily but united the other groups into the enlarged and redefined subfamily Hadeninae. Mitchell *et al.* seemed to follow Poole's system more closely in most areas but used the arrangement of Kitching and Rawlins in their final classification (see Table 2 in Mitchell *et al*. 2006). Fibiger and Lafontaine arranged these genera in three subfamilies, the Noctuinae, the Hadeninae, and the Xyleninae. The Noctuinae and Hadeninae are probably monophyletic groups and may be sister groups, based on the short, apically fringed spinneret in the larvae. The Xyleninae could be paraphyletic, or even polyphyletic (the Caradrinini, Elaphriini, and Prodeniini are placed as sister groups to the Xylenini + Hadenini + Noctuini clade in Fig. 5 of Mitchell *et al.*). Fibiger and Lafontaine retained the Xyleninae to accommodate 12 tribes of uncertain affinity rather than try to justify more subfamily names or lose the resolution of the Hadeninae and Noctuinae that results from amalgamating all three subfamilies. Morphological characters are few and seemingly unreliable. Molecular data on more taxa of the Noctuinae *s.l.* are much needed.

Other taxa in the classification remain unresolved. The family Strepsimanidae is based on a few specimens of *Strepsimanes scieropis* Meyrick that have a fully quadrifine hind wing venation (Fig. 8) similar to that of the Nolinae–Aganainae–Arctiinae–Lymantriinae–Erebinae–Calpinae–Catocalinae–Cocytiinae–Stictopterinae–Euteliinae clade. The forewing is quadrifid in venation, but the venation is highly modified, with most veins bending up to the forewing costa (Fig. 7). The former association of the Strepsimanidae with the Hypenodinae was based on a mistaken association of the venation, as discussed by Fibiger and Lafontaine: the system of venation nomenclature that Meyrick used numbered the veins from the bottom of the wing rather than the top. The positions of the Cocytiinae, Eucocytiinae, Sinocharinae, Lophonyctinae, and Micronoctuidae as classified in Fibiger and Lafontaine will likely remain unresolved until the immature stages are studied or molecular analyses include representatives of these groups. The position of the Australian family Oenosandridae is also in need of further study. At present, this family is treated as the sister group to the remainder of the Noctuoidea,

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following Kitching and Rawlins (1998), based on the presence of only a single MD seta on the third thoracic segment of the larva; the remainder of the Noctuoidea have two. The Oenosandridae have a tympanal structure similar to that of the Arctiidae and Noctuidae in having a posteriorly oriented tympanum, a tympanal sclerite, and a counter-tympanal hood. By contrast, the other two trifid noctuoid families, the Notodontidae and Doidae, have a posteroventrally oriented tympanum and the tympanal sclerite and counter-tympanal hood are both absent. The Oenosandridae might be the sister group to the rest of the Noctuoidea, with the tympanal apparatus dramatically altered in the Notodontidae and Doidae, or the tympanal structure might be a uniquely derived characteristic of the Oenosandridae and the quadrifid noctuoid families, with the second MD seta having been secondarily lost on T3 of the larva of Oenosandridae. Hopefully, future molecular research or the discovery of new characters will shed light on the position of the Oenosandridae.

Revised classification

On the basis of the discussion above, we modify our classification (Fibiger and Lafontaine 2005) in the following ways.

(1) We retain Micronoctuidae as a family because the forewing venation is intermediate between the trifid and the quadrifid position (vein M2 in the forewing is two-thirds of the way down the cell). Also, the hind wing venation is bifid (Fig. 9) rather than trifid or quadrifid, there is no tympanal sclerite in the ear, and the cucullus of the valve is absent. The group could be a highly modified lineage from a eustrotiine-like ancestor or a primitive quadrifine noctuid, but until the larvae are better known (besides the two characters listed in Fibiger and Lafontaine 2005) or molecular data shed light on its phylogenetic position in the Noctuoidea, we prefer to retain it as a family of uncertain affinity.
(2) We move the Arctiidae and Lymantriidae into the Erebidae (*sensu* Fibiger and Lafontaine 2005) and treat them as subfamilies and the sister groups to the erebine–calpine–catocaline–cocytiine clade.
(3) We treat the Aganainae as a plesiomorphic sister group to the redefined Arctiinae.
(4) We move the Nolidae into the quadrifine Noctuidae and treat it as a subfamily and as the sister group to the arctiine–aganaine clade.
(5) We include the stictopterine–euteliine clade within the larger "L.A.Q. clade" in the subgroup with a fully quadrifine hind wing and a fused pleural sclerite and treat it as a highly derived sister group to the clade consisting of the Erebinae, Calpinae, Catocalinae, Cocytiinae, Nolinae, Aganainae, Arctiinae, and Lymantriinae.
(6) We tentatively retain the three subfamilies (Xyleninae, Hadeninae, Noctuinae) used in Fibiger and Lafontaine (2005) until the classification of the genera of the Noctuinae *s.l.* is better resolved.
(7) We move the subtribe Arzamina from the Apameini (Xyleninae) and treat it as a tribe of the Xyleninae on the basis of molecular work and morphological characters in Goldstein and Fibiger (2005).
(8) We move the Ufeinae into the Xylenini (Xyleninae) as the subtribe Ufeina on the basis of the molecular data of Mitchell *et al.* (2006).
(9) We move the tribe Cosmiini as defined by Fibiger and Lafontaine (2005) into Xylenini (Xyleninae) on the basis of molecular data and treat it as subtribe Cosmiina; like other groups in the Xylenini, the larvae feed on woody plants.
(10) We move the tribe Balsini from the Xyleninae and treat it as the subfamily Balsinae, and we tentatively place it between the Raphinae and the Acronictinae. The larvae, now available for study, have a normal setose SD1 seta on A9 and a tubular spinneret; these characters exclude the group from the xylenine–hadenine–noctuine clade.
(11) We move the tribe Phosphilini from the Psaphidinae to the Xyleninae.

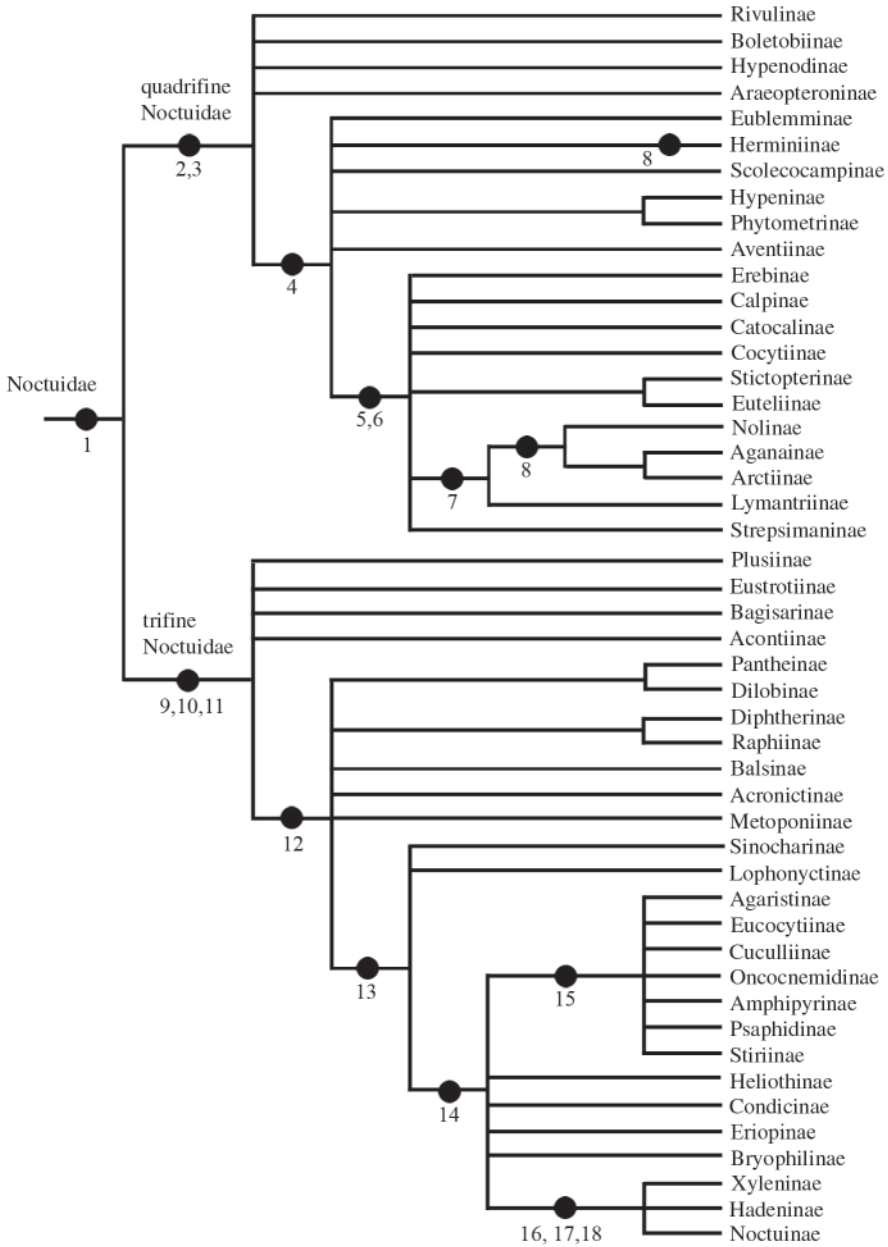
The series of phylogenetic transfers above creates a conflict with the current classification of the quadrifid Noctuoidea. This can be resolved in one of four ways.

First, the number of families could be increased to retain the family status of the Arctiidae and Lymantriidae. This approach was used by Mitchell *et al.* (2006): six noctuid subfamilies were raised to family status as Stictopteridae, Euteliidae, Aganaidae, Herminiidae, Hypenidae, and Catocalidae. If the larger, more comprehensive classification proposed herein (Fig. 28) is considered, 22 families would be needed to preserve the use of the

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Fig. 28. Revised classification of Noctuidae *s.l.* Numbers refer to principal derived character states: 1, forewing venation quadrifid (bases of M2 and M3 approximate); 2, scaphium sclerotized dorsally; 3, vesica globular and multi-pouched; 4, lower frons denuded of scales; 5, hind wing fully quadrifid (bases of M2 and M3 approximate); 6, pleural sclerite fused to tegumen; 7, tympanal hood prespiracular (spiracle below hood in Nolinae); 8, retinaculum 2 times as long as wide (bar-like); 9, hind wing vein M2 reduced or vestigial; 10, bullae fused mesially; 11, posterior apophyses with diamond-shaped plate subapically; 12, tympanum with nodular sclerite; 13, abdomen with basal brushes and pockets; 14, valve with apical corona; 15, larva with lateral line bordering anal plate; 16, larval spinneret flattened; 17, larval seta SD1 on A9 hairlike; 18, clasper in center of valve connected by rod to ventral apex of sacculus.



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names Arctiidae and Lymantriidae and undoubtedly additional families would be needed as more tropical lineages are studied. Not only is such a proliferation of families problematic, but most of these families would be poorly defined, only a small fraction of the tropical fauna would be assigned to a family, and many of these families would be based on characters of only one sex or of the larvae. Some family-group names (*e.g.*, Boletobiinae, Phytometrinae, Scolecocampinae, and Erebinae) are weakly defined and if these groups are shown to be paraphyletic or polyphyletic, further rearrangements of the families of the Noctuoidea would be necessary. We believe that families, like genera, are primary categories in classification and should be better defined, more easily identified, and more stable than sub-primary categories such as subfamilies and subgenera.

The second way to resolve the classification of the quadrifid Noctuoidea would be to treat the group as two families by retaining the name Noctuidae for the trifine noctuids, as was done by Fibiger and Lafontaine (2005) and Mitchell *et al.* (2006), and break the quadrifine subfamilies (Erebidae of Fibiger and Lafontaine 2005) into a series of families. Unfortunately, this approach has the same series of shortcomings as the first approach.

The third approach would be to arrange the quadrifid Noctuoidea in two families, using the Noctuidae *s.s.* for the trifine noctuids and either the Erebidae or the Arctiidae (they have equal priority, both proposed in Leach [1815]) for the remainder of the quadrifid noctuoids by combining the Nolidae, Strepsimanidae, Arctiidae, Lymantriidae, and quadrifine Noctuidae into a single family. However, there are no characters unique to this clade because of secondary losses in some subfamily groups, so the family would be recognized only by a combination of characters that are sometimes only in one sex or in the larva.

The fourth and, to us, the most practical approach would be to treat all of the quadrifid Noctuoidea as the family Noctuidae and reduce the families Nolidae, Strepsimanidae, Arctiidae, and Lymantriidae to subfamilies within the Noctuidae. There are several advantages to this approach: the family Noctuidae would be easily defined and monophyletic, the apparent anomalies of the arctiid–lymantriid clade sharing derived character states with a subset of the quadrifine Noctuidae would be resolved, and the curious mix of noctuid and arctiid characters of the Aganainae and Nolinae would be resolved by the Aganainae and Nolinae being plesiomorphic sister groups of the Arctiinae (*sensu novo*) in the redefined Noctuidae.

The downgrading of the families Nolidae, Arctiidae, and Lymantriidae may seem a difficult transition for some but the proper placement of highly derived groups in a phylogenetic context is important for stability and the predictability of a classification. Most workers currently accept that the Agaristidae are a derived group of trifine noctuids, the Ctenuchidae are a derived group of arctiids, the Satyridae are a derived group of nymphalids, and the Megathymidae are a derived group of hesperiids, and this is just another example of classifying a group in a phylogenetic context.

Of the above four choices, we believe the last option will produce the most stability and we present it in the classification below.

Classification of Noctuoidea

Our synthesis of the molecular work by Mitchell *et al.* (1997, 2000, 2006) and our largely morphological work (Fibiger and Lafontaine 2005) results in the following classification of the Noctuoidea. The list of families, subfamilies, and tribes is taken from Fibiger and Lafontaine (2005). The Nolidae, Arctiidae, and Lymantriidae are downgraded to subfamilies within the Noctuidae. The Noctuidae: Catocalinae *s.l.* were revised for the fauna of Borneo by Holloway (2005). Based on this work, we add 11 names (indicated below with asterisks).

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

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Tribe **Notodontini** Stephens, 1829
Tribe **Dicranurini** Duponchel, [1845]
Subfamily **Phalerinae** Butler, 1886
Subfamily **Dudusinae** 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 **Micronoctuidae** Fibiger, 2005
Family **Noctuidae** Latreille, 1809
Subfamily **Rivulinae** Grote, 1895
Subfamily **Boletobiinae** Grote, 1895
Subfamily **Hypenodinae** Forbes, 1954
Subfamily **Araeopteroninae** Fibiger, 2005
Subfamily **Eublemminae** Forbes, 1954
Tribe **Eublemmini** Forbes, 1954
Tribe **Pangraptini** Grote, 1882
Subfamily **Herminiinae** Leach, [1815]
Subfamily **Scolecocampinae** Grote, 1883
Subfamily **Hypeninae** Herrich-Schäffer, [1851]
Subfamily **Phytometrinae** Hampson, 1913
Subfamily **Aventiinae** Tutt, 1896
Subfamily **Erebinae** Leach, [1815]
Subfamily **Calpinae** Boisduval, 1840
Tribe **Anomini** Grote, 1882
Tribe **Calpini** Boisduval, 1840
*Tribe **Phyllodini** Guenée, 1852
Tribe **Scoliopterygini** Herrich-Schäffer, [1852]
Subfamily **Catocalinae** Boisduval, [1828]
Tribe **Toxocampini** Guenée, 1852
Tribe **Acantholipini** Fibiger and Lafontaine, 2005
Tribe **Arytrurini** Fibiger and Lafontaine, 2005
Tribe **Melipotini** Grote, 1895
Tribe **Euclidiini** Guenée, 1852
Tribe **Panopodini** Forbes, 1954
Tribe **Ophiusini** Guenée, 1837 (= **Omopterini** Boisduval, 1833 (suppressed senior syn.)
Tribe **Catocalini** Boisduval, [1828]
*Tribe **Anobini** Holloway, 2005 (= **Anobini** Wiltshire, 1990, nomen nudum)
*Tribe **Sypnini** Holloway, 2005
*Tribe **Hypopyrini** Guenée, 1852
*Tribe **Tinolini** Moore, [1885]
*Tribe **Hulodini** Guenée, 1852 (= **Speiredoniinae** Swinhoe, 1900)
*Tribe **Ommatophorini** Guenée, 1852
*Tribe **Pericymini** Wiltshire, 1976
*Tribe **Pandesmini** Wiltshire, 1990, nomen nudum
*Tribe **Catephiini** Guenée, 1852
*Tribe **Ercheini** Berio, 1992
Subfamily **Cocytiinae** Boisduval, 1874
Subfamily **Stictopterinae** Hampson, 1894
Subfamily **Euteliinae** Grote, 1882
Subfamily **Nolinae** Bruand, 1846, **stat rev.**
Tribe **Nolini** Bruand, 1846, **stat rev.**

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Tribe **Chloephorini** Stainton, 1859, **stat rev.**
Subtribe **Chloephorina** Stainton, 1859, **stat rev.**
Subtribe **Sarrothripina** Hampson, 1894, **stat rev.**
Subtribe **Camptolomina** Mell, 1943, **stat rev.**
Subtribe **Careina** Moore, 1883, **stat rev.**
Subtribe **Ariolicina** Mell, 1943, **stat rev.**
Tribe **Westermanniini** Hampson, 1918, **stat rev.**
Tribe **Eariadini** Hampson, 1912, **stat rev.**
Tribe **Blenini** Mell, 1943, **stat rev.**
Tribe **Risobini** Mell, 1943, **stat rev.**
Tribe **Collomenini** Kitching and Rawlins, 1998, **stat rev.**
Tribe **Afridini** Kitching and Rawlins, 1998, **stat rev.**
Tribe **Eligmini** Mell, 1943, **stat rev.**
Subfamily **Aganainae** Boisduval, 1833
Subfamily **Arctiinae** Leach, [1815], **stat. nov.**
Tribe **Lithosiini** Billberg, 1820, **stat. rev.**
Subtribe **Phryganopterygina** Bendib and Minet, 1999, **stat. rev.**
Subtribe **Acsalina** Bendib and Minet, 1999, **stat. rev.**
Subtribe **Eudesmiina** Bendib and Minet, 1999, **stat. rev.**
Subtribe **Cisthenina** Bendib and Minet, 1999, **stat. rev.**
Subtribe **Nudariina** Börner, 1920, **stat. rev.**
Subtribe **Endrosina** Börner, 1932, **stat. rev.**
Subtribe **Lithosiina** Billberg, 1820, **stat. rev.**
Tribe **Syntomini** Herrich-Schäffer, [1846], **stat. rev.**
Subtribe **Syntomina** Herrich-Schäffer, [1846], **stat. rev.**
Subtribe **Thyretina** Butler, 1876, **stat. rev.**
Tribe **Arctiini** Leach, [1815], **stat. rev.**
Subtribe **Arctiina** Leach, [1815], **stat. rev.**
Subtribe **Callimorphina** Walker, [1865], **stat. rev.**
Subtribe **Pericopina** Walker, [1865], **stat. rev.**
Subtribe **Phaegopterina** Kirby, 1892, **stat. rev.**
Subtribe **Ctenuchina** Kirby, 1837, **stat. rev.**
Subtribe **Euchromiina** Butler, 1876, **stat. rev.**
Subfamily **Lymantriinae** Hampson, [1893], **stat. nov.**
Tribe **Lymantriini** Hampson, [1893], **stat. rev.**
Tribe **Orgyiini** Wallengren, 1861, **stat. rev.**
Tribe **Arctornithini** Holloway, 1999, **stat. rev.**
Tribe **Leucomini** Grote, 1895, **stat. rev.**
Tribe **Nygmiini** Holloway, 1999, **stat. rev.**
Subfamily **Strepsimaninae** Meyrick, 1930, **stat rev.**
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 **Euchaciina** 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
Subfamily **Acontiinae** Guenée, 1841
Tribe **Hypercalymniini** Fibiger and Lafontaine, 2005
Tribe **Acontiini** Guenée, 1841

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Tribe **Armadini** Wiltshire, 1961
Tribe **Aediini** Beck, 1960
Subfamily **Pantheinae** Smith, 1898
Subfamily **Diphtherinae** Fibiger and Lafontaine, 2005
Subfamily **Dilobinae** Aurivillius, 1889
Subfamily **Raphiinae** Beck, 1996
Subfamily **Balsinae** Grote, 1896, **stat. rev.**
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 **Amphipyrinae** Guenée, 1837
Subfamily **Psaphidinae** Grote, 1896
Tribe **Psaphidini** Grote, 1896
Tribe **Feraliini** Poole, 1995
Tribe **Nocloini** Poole, 1995
Tribe **Triocnemidini** Poole, 1995
Subfamily **Stiriinae** Grote, 1882
Tribe **Stiriini** Grote, 1882
Tribe **Grotellini** Poole, 1995
Tribe **Azenini** Poole, 1995
Subfamily **Heliothinae** Boisduval, [1828]
Subfamily **Condicinae** Poole, 1995
Tribe **Condicini** Poole, 1995
Tribe **Leuconyctini** Poole, 1995
Subfamily **Eriopinae** Herrich-Schäffer, [1851]
Subfamily **Bryophilinae** Guenée, 1852
Subfamily **Xyleninae** Guenée, 1837
Tribe **Pseudeustrotiini** Beck, 1996
Tribe **Phosphilini** Poole, 1995, **stat. rev.**
Tribe **Prodeniini** Forbes, 1954
Tribe **Elaphriini** Beck, 1996
Tribe **Caradrinini** Boisduval, 1840
Subtribe **Caradrinina** Boisduval, 1840
Subtribe **Athetina** Fibiger and Lafontaine, 2005
Tribe **Dypterygiini** Forbes, 1954
Tribe **Actinotiini** Beck, 1996
Tribe **Phlogophorini** Hampson, 1918
Tribe **Apameini** Guenée, 1841 (= **Nonagriini** Guenée, 1837, suppressed senior syn.)
Subtribe **Oxytripiina** Gozmány, 1970
Subtribe **Apameina** Guenée, 1841
Subtribe **Sesamiina** Fibiger and Goldstein, 2005
Tribe **Arzamini** Grote, 1883
Tribe **Episemini** Guenée, 1852
Tribe **Xylenini** Guenée, 1837
Subtribe **Xylenina** Guenée, 1837
Subtribe **Cosmiina** Guenée, 1852, **stat. rev.**
Subtribe **Antitypina** Forbes and Franclemont, 1954
Subtribe **Ufeina** Crumb, 1956
Subfamily **Hadeninae** Guenée, 1837

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Tribe **Orthosiini** Guenée, 1837
Tribe **Tholerini** Beck, 1996
Tribe **Hadenini** Guenée, 1837
Tribe **Leucaniini** Guenée, 1837
Tribe **Eriopygini** Fibiger and Lafontaine, 2005
Tribe **Glottulini** Guenée, 1852
Subfamily **Noctuinae** Latreille, 1809
Tribe **Agrotini** Rambur, 1848
Subtribe **Austrandesiina** Angulo and Olivares, 1990
Subtribe **Agrotina** Rambur, 1848
Tribe **Noctuini** Latreille, 1809
Subtribe **Axyliina** Fibiger and Lafontaine, 2005
Subtribe **Noctuina** Latreille, 1809

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