

New view of the higher classification of the Noctuidae (Lepidoptera)

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Summary

Several examples are given to demonstrate that the current higher classification of the Noctuidae has resulted from a predarwinistic thinking. A generally acknowledged system can only be achieved by applying the principles of phylogenetic systematics. The evolution of the Noctuidae is seen as a multi-phasic progressive process, the more advanced evolutionary phases presenting a mosaic of derived and more primitive characters. Stability in the system can only be achieved by an intensive collaboration between larval and imaginal systematists ; our knowledge of larval systematics has so far hardly been used in noctuid classification. The Cuculliinae are redefined based on certain larval and imaginal (valvae) characters. This and closely related subfamilies are collectively termed the Cuculliinae complex.

Taxonomic changes

Of the original 56 Cuculliinae genera recognised by HARTIG & HEINICKE (1973), 20 are retained in this subfamily. A further 21 genera are transferred to the Cuculliinae from the 'Amphipyridae' sensu BOURSIN (11), Heliethinae (1) and Acontiinae (9). Thirty-eight genera are removed from the Cuculliinae and transferred to the Noctuinae, Hadapameini **trib.n.** (the numbers of the genera are not exactly comparable because larval material is not available for all genera, and some of the traditional genera, e.g. *Polymixis* HÜBNER and *Xanthia* OCHSENHEIMER, have since been split). The name 'Amphipyridae' is obsolete because of the transfer of *Amphipyra* OCHSENHEIMER to the Cuculliinae (PIERCE, 1909 ; BECK, 1960, 1989 ; MERZHEEVSKAYA, 1967). The residue of these 'Amphipyridae' is combined with the Hadenini (BECK, 1960) in the new tribe Hadapameini. The subfamily Acontiinae is obsolete ; the remnants not transferred to the Cuculliinae (i.e. the tribe Eublemmini) are to be found in the upgraded subfamily Eublemminae, **stat.n.**, (Typus : *Eublemma* HÜBNER, 1821). *Apopestes* HÜBNER is removed from the Catocalinae (DUFAY, 1975) and put to its former position, close to *Amphipyra*, now within the Cuculliinae.

Résumé

L'auteur fournit plusieurs exemples pour démontrer que la classification courante des genres de Noctuidae en sous-familles résulte d'une pensée prédar-

winienne. Or un système généralement accepté ne peut être établi qu'en appliquant les principes de la systématique phylogénétique. L'évolution des Noctuidae doit donc être considérée comme un processus «multiphasique». Les phases les plus avancées de l'évolution présentent une mosaïque de caractères dérivés et de caractères plus primitifs. Nous ne parviendrons à un système stable que si nous arrivons à les reconnaître et à découvrir quels taxons partagent quels caractères dérivés. A cet effet, une collaboration étroite et active entre systématiciens tant des stades larvaires que des adultes est indispensable. Nos connaissances en matière de systématique larvaire n'ont pour le moment guère été utilisées dans la classification des Noctuidae.

Changements taxonomiques

Sur les 56 genres de Cuculliinae reconnus par HARTIG & HEINICKE (1973), 20 restent dans cette sous-famille. 21 autres genres lui sont incorporés : 11 en provenance des «Amphipyridae» sensu BOURSIN, 1 des Heliothinae et 9 des Acontiinae. 38 genres sont retirés des Cuculliinae et transférés aux Noctuidae, Hadapameini **trib.n.** Les nombres de genres ne sont pas exactement comparables parce que quelques-uns des genres traditionnels tels que *Polymixis* HÜBNER et *Xanthia* OCHSENHEIMER ont été entre temps divisés. Le nom d'«Amphipyridae» n'est plus valable à cause du transfert d'*Amphipyra* OCHSENHEIMER aux Cuculliinae (PIERCE, 1909 ; BECK, 1960 ; MERZHEEVSKAYA, 1967). Le reste de ces «Amphipyridae» est combiné, avec la tribu des Hadenini (BECK, 1960), dans la nouvelle tribu des Hadapameini. La sous-famille des Acontiinae n'est plus valable. Ses restes non transférés aux Cuculliinae (la tribu des Eublemmini) doivent être placés dans la sous-famille des Eublemminae **stat.n.** (Type : *Eublemma* HÜBNER, 1821). *Apopestes* HÜBNER est retiré des Catocalinae (DUFAY, 1975) et replacé dans sa position antérieure, près du genre *Amphipyra*, actuellement dans les Cuculliinae.

Zusammenfassung

An mehreren Beispielen wird gezeigt, daß die Hauptursache für die unbefriedigende höhere Klassifizierung der Noctuidae der Denk- und Arbeitsweise der vordarwinistischen Zeit zuzuschreiben ist. Im Gegensatz dazu kann ein stabileres System nur durch die Anwendung der Prinzipien einer phylogenetischen Systematik erzielt werden. Die phylogenetische Systematik ist wesentlich komplexer als die bisherige Anwendung oft fragwürdiger (Syn-) Apomorphien zeigt. Bei der Evolution der Noctuidae handelt es sich um einen mehrphasigen Progressivtyp. Die häufigen und fortwährenden Umstellungen im System dieser Familie sind durch die Nichtbeachtung dieses Evolutionstyps bedingt. Erschwerend für eine Einordnung im System ist, wenn von älteren zu phylogenetisch jüngeren Phasen ursprünglichere Merkmale weitergeleitet werden, die dann neben moderneren Merkmalen auftreten. Je nach Höherbewertung, entweder der ursprünglicheren oder der moderneren Merkmale, können solche Taxa einer phylogenetisch älteren oder jüngeren Gruppe zugeordnet werden. Nur wenn bei der Klassifizierung solcher Taxa gewichtigen

progressiven Merkmalen der Vorrang vor ursprünglichen eingeräumt wird, wie es gemäß des Evolutionsprinzips sinnvoll ist, kann eine größere Stabilität des Systems erreicht werden. Dazu ist eine enge Zusammenarbeit zwischen Larval- und Imaginalsystematik erforderlich. Die bisherigen larvalsystematischen Erkenntnisse wurden von der Imaginalsystematik bis heute ignoriert. Die Cuculliinae werden auf der Basis von larvalen und imaginalen (Valvae !) Merkmalen neu definiert. Zusammen mit verwandten Unterfamilien werden sie als der Cuculliinae-Komplex herausgestellt.

Taxonomische Veränderungen

Von 56 Gattungen der Cuculliinae, gemäß des Verzeichnisses von HARTIG & HEINICKE (1973), verbleiben 20 Gattungen in dieser Unterfamilie. 21 Gattungen werden den Cuculliinae zugefügt. Sie stammen von den 'Amphipyridae' (11), von den Heliethinae (1) und von den Acontiinae (9 Gattungen). 38 Gattungen wechseln von den Cuculliinae zu den Noctuidae, Hadapameini **trib.n.** Die Zahlen für die Anzahl der Genera sind nicht exakt vergleichbar, da nicht von allen bei HARTIG & HEINICKE aufgeführten Gattungen larvales Material für eine Überprüfung zur Verfügung stand; ferner sind einige traditionelle Gattungen inzwischen weiter unterteilt worden, so u.a. *Polymixis* HÜBNER und *Xanthia* OCHSENHEIMER. Der Name 'Amphipyridae' ist aufgrund des Transfers von *Amphipyra* OCHSENHEIMER zu den Cuculliinae hinfällig (PIERCE, 1909, BECK, 1960, 1989, MERZHEEVSKAYA, 1967). Der Rest dieser 'Amphipyridae' wird, mit den Hadenini (s. BECK, 1960), zur neuen Tribus Hadapameini vereinigt. Die Unterfamilie Acontiinae wird völlig aufgelöst; die nicht zu den Cuculliinae transferierten Reste, die Tribus Eublemmini, werden zur Unterfamilie Eublemminae **stat.n.** aufgewertet (Typus *Eublemma* HÜBNER, 1821). *Apopestes* HÜBNER wird von den Catocalinae (DUFAY, 1975) wieder in die Nähe von *Amphipyra* (der nach BOURSIN, 1964, innegehabten Position), also zu den Cuculliinae gestellt.

Difficulties of imaginal higher classification of the Noctuidae

The detailed study by KITCHING (1984) on the historical development of the Noctuidae, from LINNAEUS until now, concludes in a cladogram (Fig. 1). Apart from positions 1-3 (Arctiidae to Herminiidae) this exactly reproduces the partition of GUENÉE (quadrifine subfamilies — positions 5 to 21 and trifine subfamilies — positions 22 to 33). All 'classical' subfamilies, sometimes divided into tribes, are clearly separated. This suggests that KITCHING is still largely following the system of HAMPSON (1898-1913) (and his predecessors), even though he repeatedly rejects the characterization of certain subfamilies of that author. HAMPSON's system was not influenced by the ideas of evolution, but was arranged according to the principles of LINNAEUS, by using diagnostic features; evolutionary ideas can only be seen in his phylo-

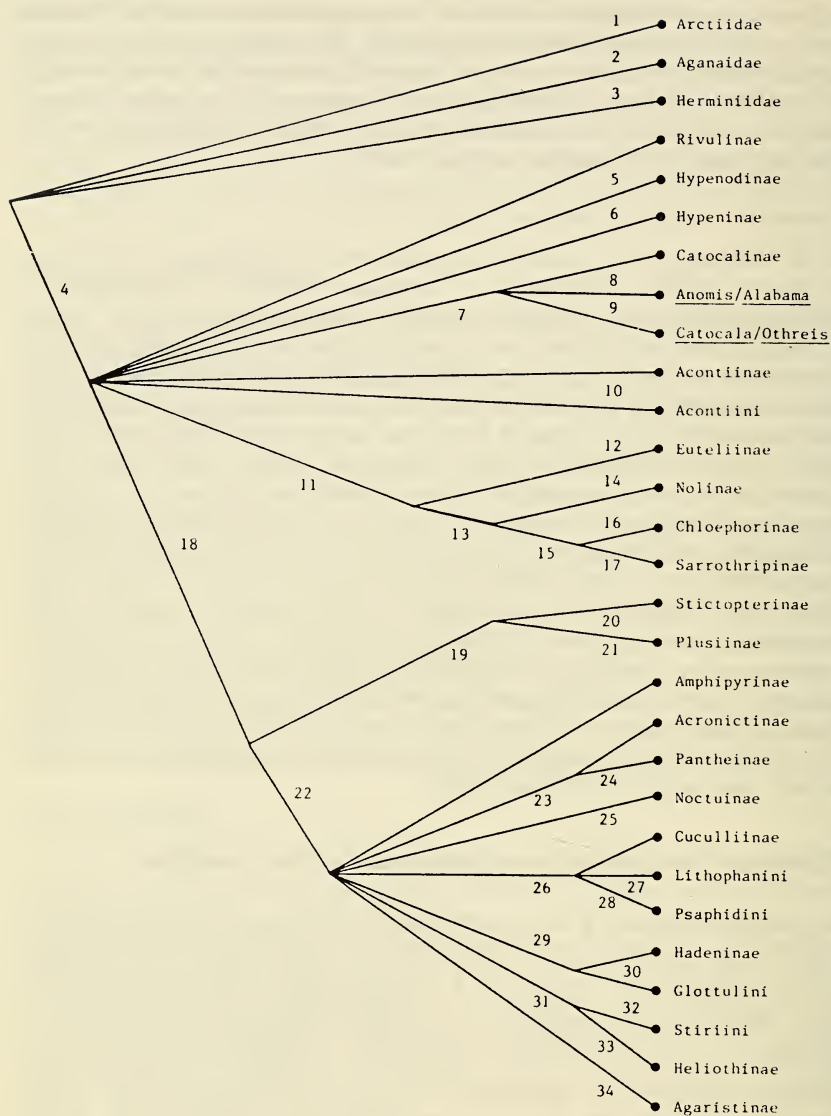


Fig. 1. Cladogram from KITCHING (1984), illustrating the relationships between the various noctuid subgroups.

geny of higher Lepidoptera classification (HAMPSON, 1893-1895) (Fig. 2), where the trifine Noctuidae preceed the quadrifine. The points of view used for the system as it stands today therefore come from the time before DARWIN published his ideas on evolution in 1859. Essentially, the system of the Noctuidae used today has arisen from a horizontal comparison of the recent taxa based on few characters (e.g. HAMPSON characterized subfamilies according to hairy eyes or spined tibiae etc.), whereas studies combining several character sets have been lacking.

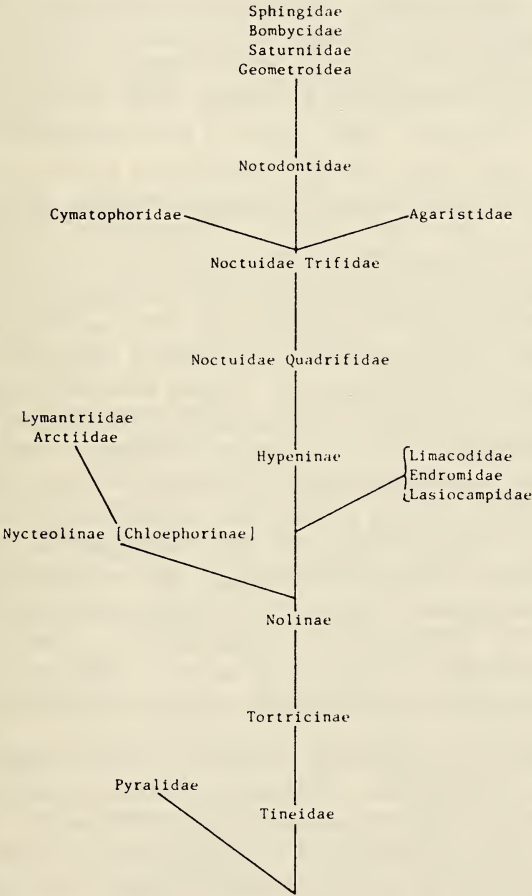


Fig. 2. Phylogeny of the higher Lepidoptera, with particular reference to the Noctuidae, proposed by HAMPSON (1893-5). Taken from KITCHING (1984).

In his historical review, KITCHING did not refer to the larval (BECK, 1960) and imaginal (PIERCE, 1909) parallels within the system of the Noctuidae (see below). Meanwhile, these have been detailed and further developed by BECK (1989). The investigations of complex organs (wing venation, genital structure, tympanum, scent brushes and hair pencils, etc.) could not shake the system of HAMPSON. These investigations led to superspecialization on individual organs and thus to a one-sided systematics (KITCHING, 1987, tries to overcome this dilemma in his detailed investigation of the Plusiinae).

Importance of larval investigations

The so-called naked noctuid larvae show as a rule plenty of ornamental and morphological (both external and internal) characters which can easily be examined. An evaluation of these characters can give important hints to a fundamental research of the noctuid system based on the adults. KITCHING, 1984, writes of larval research: "Generally, classifications based upon noctuid larvae have proved to be at least partially incongruent with the Hampsonian system, while the degree of conformity with the newer arrangement exemplified by FRANCLEMONT & TODD (1983) remains to be seen. Larvae have proved to be potentially very useful in elucidating the higher classification of nymphalid butterflies (DE VRIES, KITCHING & VANE-WRIGHT, in prep. ; KITCHING, 1983) where previous systems based upon adult characters have been shown to be incorrect by varying amounts. It seems likely, therefore, that no satisfactory arrangement of the noctuid genera into tribes and subfamilies can be achieved without reference to the immature stages and much work still remains to be carried out in this field." By these remarks of KITCHING a good deal of responsibility for developing a natural system (of the Noctuidae) is given to larval research. Of course larval systematics may also err by placing too much weight on the taxonomic value of a particular character. Ideally, all characters, i.e. the 'holomorph' of a taxon (HENNIG, 1984 ; NAUMANN, 1985) should be used, but practically as many characters as possible, of all stages of the insect, including the biology, must be studied.

GHILAROV (1965) has discussed in detail the importance of larval investigations for systematics: "The embryological method which also includes the use of characters of postembryological development has been taken by Ernst Haeckel for his phylogenetical trees. Only this method formed the base of his biogenetical law. But Haeckel was of the opinion that not all characters of embryos and larval instars are essential to solve phylogenetical problems ... Haeckel did not think

the adaptive characters of the larval instars to be important for solving phylogenetical problems. For him they were so-called 'Caenogenese', which falsifies the phylogenesis of organisms ! As all characters of insect larvae are to be considered as caenogenesis, one thought for a long time that the study of the larvae of insects would be useless for the solution of phylogenetical problems." GHILAROV continues: "The organism is always a unit during the whole ontogenesis and the characters of the adults are of no more importance for the phylogenetical and systematical studies than those of any former stage." For the importance of larval systematics STAMMER (1961), who had initiated a series of larval systematical investigations at the Zoological Institute of Erlangen-Nürnberg-University, says: "With regard to a natural, phylogenetic system in insects we are at the very beginning." and "An immense part of our present system of the insects suffers from having examined only a very small number of characters on their systematical value and significance."

Uncertainties and disparity between imaginal and larval classifications

MAYR (1969/1975 : 122) writes: "Bei Gruppen mit vollständiger Metamorphose entwickeln sich völlig verschiedene Merkmalsgarnituren bei Larven und Adulti. Larval- und Adultmerkmale sind sichtbare Manifestationen desselben Genotypus. Natürlich wird es unterschiedliche Bestimmungsschlüssel für Larven und Adulti geben müssen, aber für eine bestimmte Organismengruppe ist nur eine Klassifikation möglich." The aim of larval systematics is not to produce an exclusively larval system, but by comparison with the corresponding imaginal system to find a definitive natural, phylogenetic system. Various degrees of agreement or disagreement may be observed. HENNIG (1948-1950) discerns four possible cases: Congruence, analogy, analogy that is to be corrected and incongruence. While real congruence has seldom been observed, the case of analogy that is to be corrected between imaginal and larval systems is not rare. The well known discrepancy between the imaginal and larval systems of the Chironomidae (Diptera) could be put down to the insufficient analysis of adult characters (FITTKAU, 1960). According to STAMMER each case of disagreement between larval and imaginal systems is the consequence of misinterpretation of the phylogenetic relations. This is also confirmed by studies on Coleoptera (GHILAROV, 1965). The examples of FITTKAU and GHILAROV may be due to the fact that a large number of imaginal and larval characters could be easily examined. KITCHING (1984) pointed out the difficulties of imaginal investigations of Lepidoptera. This may be one of the

reasons for the disagreements between imaginal and larval investigations in the Lepidoptera.

There are however arguments against the classical opinion of these zoologists (GHILAROV, HENNIG, MAYR, STAMMER, et al.), i.e. that there has to be perfect agreement between imaginal and larval systematics.

Firstly : As the phenotype is the result of the reaction of the genotype with its environment and because the genotype is normally exposed longer to environmental conditions during larval development than in the adult stage, the pressure of selection is heavier on the larva and character changes can occur more quickly in the larva than in the adult. Thus the larva of an imaginally less advanced species may be ornamentally modern (see the example of *Apopestes* HÜBNER below). Secondly : In spite of identical DNA throughout the development of a holometamorphic insect, the differentiated expression of the genetic material at different stages may lead to a limited evolution of the larvae and adults in divergent directions. Thirdly : The biogenetic rule of HAECKEL may be explained by an embryological interval-activation of latent genetic material. Fourthly : Postembryological 'modern larvae' can possess one or several 'original' characters due to the regulation of activity of normally suppressed 'original' genes.

All these points imply the possibility of apparently correct, but conflicting imaginal and larval classifications.

Inconsistencies in the present Noctuidae classification

During my larval investigations of the so-called trifine subfamilies of the Noctuidae at Erlangen-Nürnberg-University I referred to the system of BOURSIN (1953), a successor of that of HAMPSON. It was totally impossible to find congruent features in the larvae to parallel the imaginal order of subfamilies. It proved that the subfamily diagnosis for the Noctuinae, Hadeninae, Cuculliinae and Amphipyrrinae was unsuitable (compare KITCHING, 1984). The characteristic feature of the Noctuinae, spined tibiae, can also be found in the Heliothinae, Catocalinae and in some plusiine genera (KITCHING, 1987 : 220). The fact that these subfamilies are not closely related would suggest that this character evolved convergently. Despite the presence of spined tibiae, some genera of the Noctuinae have been put in the Amphipyrrinae auct. (e.g. *Auchmis* HÜBNER, *Actinotia* HÜBNER), Heliothinae (*Axylia* HÜBNER) or Cuculliinae (*Ammoconia* LEDERER, *Ammopolia* BOURSIN, *Blepharita amica* TREITSCHKE). BOURSIN (1952) based these changes on genitalic characters. Consequently, due to the presence of the spined

tibiae, GOMEZ-BUSTILLO, 1980 concluded a special relationship between the Noctuinae and Heliothinae.

Similarly, the characteristic feature of the Hadeninae, hairy eyes, is also to be found in some genera of the Acronictinae, ? Pantheini (*Panthea* HÜBNER, *Colocasia* HÜBNER and *Trichosea* GROTE) (BECK, 1960) and *Trichosilia* HAMPSON (Noctuinae) (LAFONTAINE, 1986). Further, *Enterpia laudeti* BOISDUVAL is put in the Hadeninae, despite the lack of hairy eyes(*). It is therefore clear that these characters have little systematic value. A comparison of the genera of the Cuculliinae recognised by BOURSIN (1953) and BECK (1960, with additional unpublished observations made since 1972) demonstrates the differences (Tab. 1). The adults of the Cuculliinae are characterized by lashed eyes and spineless tibiae. The first feature can only be recognised in a fresh state and even then only with difficulty (WARREN in SEITZ, 1914). At the subfamily level, larvae can be expected to share some striking morphological and ornamental features (MAYR, 1969). No such features could be found in the Cuculliinae sensu BOURSIN. A useful character proved to be the position of the spiracular line (stigmatale) on the anal segment (S10) (Figs 3a,b). Normally, this line runs down the anal prolegs, the caudal edge touching setae L1 and L2, but in the Cuculliinae sensu BECK this line runs to the ventrolateral side of the anal shield. The larvae of *Amphipyra* OCHSENHEIMER also show this feature (synapomorph). On this basis a good morphological character could be found: Seta SD1 on S9 (Fig. 4a) is always bristle-like (Fig. 4b) in the Cuculliinae s. BECK whereas this seta is hair-like (Fig. 4c) in the Noctuinae, Hadeninae and 'Amphipyrinae' (without *Amphipyra* and *Pyrois* HÜBNER). A further morphological feature is the shape of the spinneret, which is always tube-like in the Cuculliinae, whereas in the Noctuinae, Hadeninae and 'Amphipyrinae' it is dorso-ventrally flattened, and apically fringed in the Noctuinae and part of the Hadeninae (Figs 5a,b). There are however also characters which are shared (possibly parallel developments) between the Noctuinae, Hadeninae and 'Amphipyrinae', thus a sharp separation and characterization of these three subfamilies (according to MAYR) is not possible. I therefore reduced these subfamilies to tribes (BECK, 1960).

(*) For this study, a magnification of 12x was used, which would normally be sufficient to detect this character. On rechecking recently at 37.5x, a few scattered hairs could be seen, thereby confirming the observation of BOURSIN (1940). KOBES (in litt.) has also noted hairs at large magnification in *Amphipyra tragopoginis* (CLERCK), which again questions the systematic value of this good diagnostic character.

Tab. 1. Synopsis of the genera of the Cuculliinae s. BOURSIN, 1953 and BECK, 1960. '+' denotes genera belonging imaginally (male genitalia) and larvally (ornamentation and morphology) to the Cuculliinae. '-' denotes genera to be eliminated from the Cuculliinae. 'not examined' means that there has been no morphological investigation to date, the decision taken being based on the larval markings only.

BOURSIN, 1953	BECK, 1960
<i>Cucullia</i> SCHRANK, 1802	+
<i>Calophasia</i> STEPHENS, 1829	+
<i>Calliergis</i> HÜBNER, 1821	+
<i>Brachionycta</i> HÜBNER, 1821	+
<i>Bombycia</i> STEPHENS, 1829	- not examined
<i>Derthisa</i> WALKER, 1857	- not examined
<i>Aporophila</i> GUENÉE, 1841	-
<i>Lithophane</i> HÜBNER, 1821	-
<i>Lithomoia</i> HÜBNER, 1821	-
<i>Xylina</i> OCHSENHEIMER, 1816	-
<i>Xylocampa</i> GUENÉE, 1837	+
<i>Dryobota</i> LEDERER, 1857	- not examined
<i>Allophytes</i> TAMS, 1939	+
<i>Synvaleria</i> BUTLER, 1890	+ not examined
<i>Griposia</i> TAMS, 1939	-
<i>Dryobotodes</i> WARREN, 1911	- not examined
<i>Blepharita</i> HAMPSON, 1907	-
<i>Lamprosticta</i> HÜBNER, 1820	+ not examined
<i>Antitype</i> HÜBNER, 1821	-
<i>Ammoconia</i> LEDERER, 1857	-
<i>Rhizotype</i> HAMPSON, 1906 (= <i>Trigonophora</i> Hb.)	- not examined
<i>Eupsilia</i> HÜBNER, 1821	-
<i>Xanthia</i> HÜBNER, 1809-13 (= <i>Jodia</i> Hb.)	- not examined
<i>Conistra</i> HÜBNER, 1821	-
<i>Agrochola</i> HÜBNER, 1821	-
<i>Parastichtis</i> HÜBNER, 1821	- not examined
<i>Spudaea</i> SNELL, 1867	- not examined
<i>Aethmia</i> HÜBNER, 1821	- not examined
<i>Cirrha</i> HÜBNER, 1821 (= <i>Xanthia</i> O.)	-

It is astonishing that we can also find the same, or slightly modified, characteristic features of the Cuculliinae larvae in the Heliiothinae, Plusiinae and, less pronounced, in the Bryophilinae. A spiracular line, ending at the angle between the anal prolegs and the anal shield can also be found in some Hypeninae. Outside the Noctuidae, it is to be found in some Notodontidae (?convergence) (e.g. *Paradrymonia vittata* STAUDINGER ; DEUTSCH & BRUER, 1989).

Consequences to the system of the Noctuidae

There was little echo after my 1960 paper, except for confirmation of the results by MERZHEEVSKAYA (1967). I therefore started to look

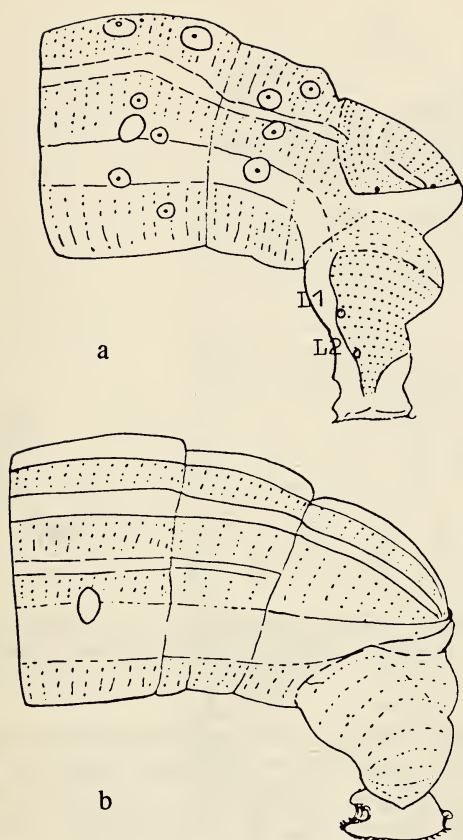


Fig. 3. Course of the spiracular line on anal segment (S10). a - Ending on the anal proleg, the caudal edge touching setae L1 and L2 (Noctuinae); b - Ending on the ventrolateral side of the anal shield (Cuculliinae).

at adult morphology myself, though at first I was retained by the following remarks of BOURSIN (1952): "This (he writes about *Blepharita amica* TREITSCHKE) is by the way not the only case that Cuculliinae have been put erroneously into the subfamily Agrotinae [=Noctuinae] ... because of spined tibiae and under complete neglect of the general habitus of the species and especially of the structure of the genitalia, the examination of which would have shown their natural relationship." From this statement of BOURSIN it is a riddle how to characterize a Cuculliinae s. BOURSIN by the genitalia. However, if one compares the genitalia of the Cuculliinae s. BECK (Fig. 6A), it is possible to recognise a trend in the valva form which can also be seen in the

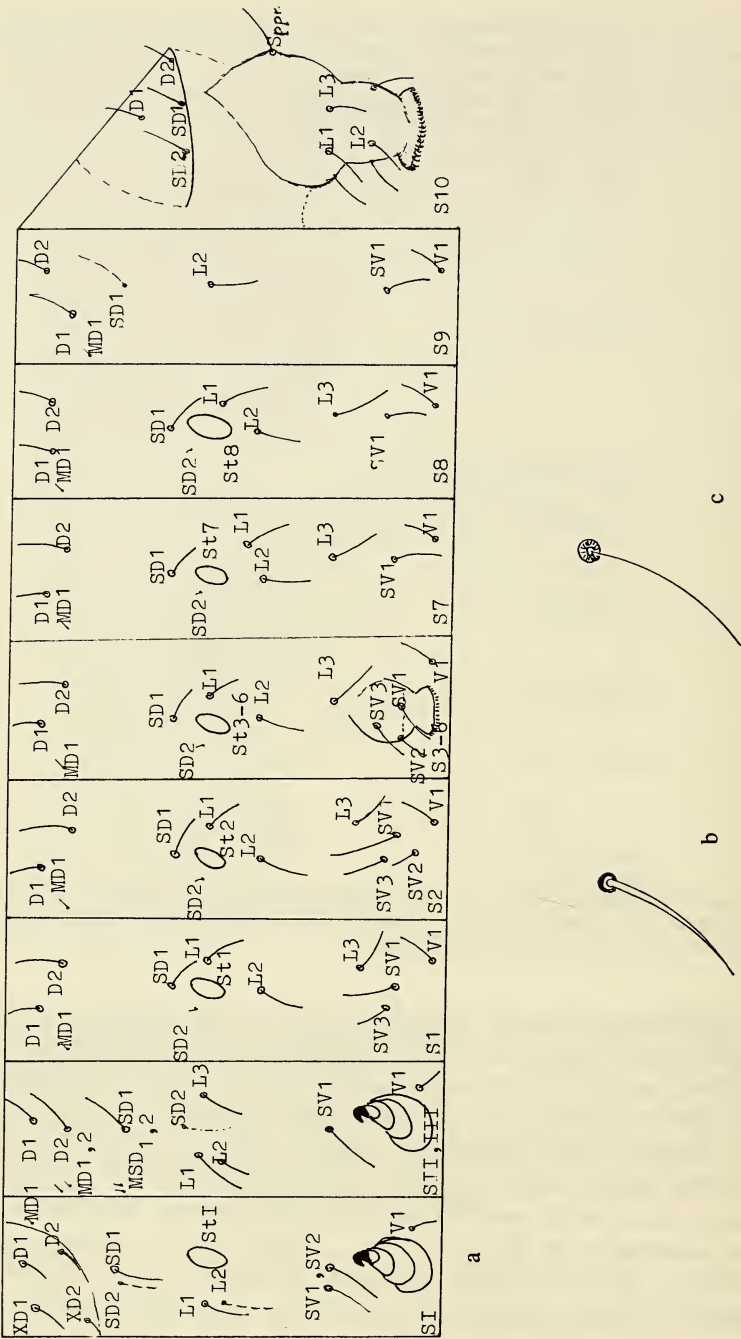


Fig. 4. a - Order and form of setae on the thoracic (SI-III) and abdominal segments (S1-10) ; b - Bristle-like seta ; c - Hair-like seta.

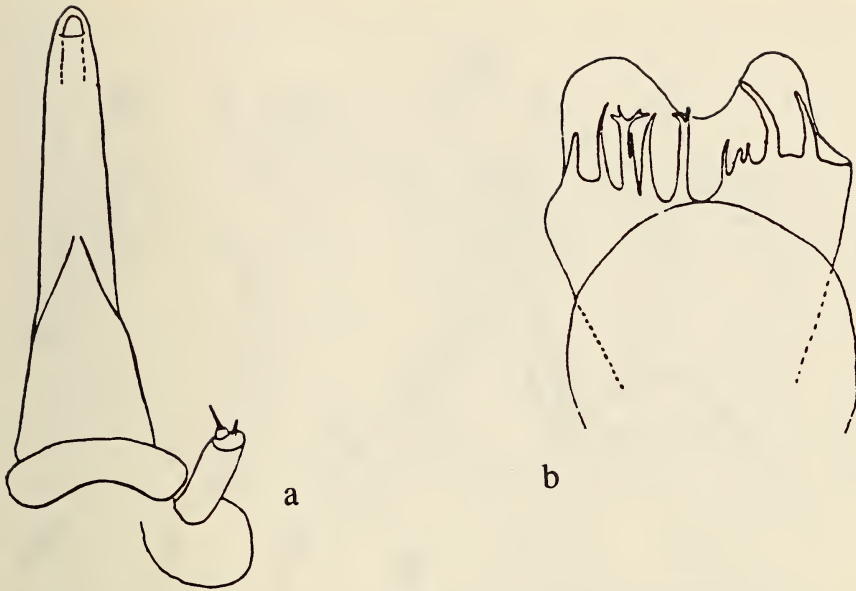
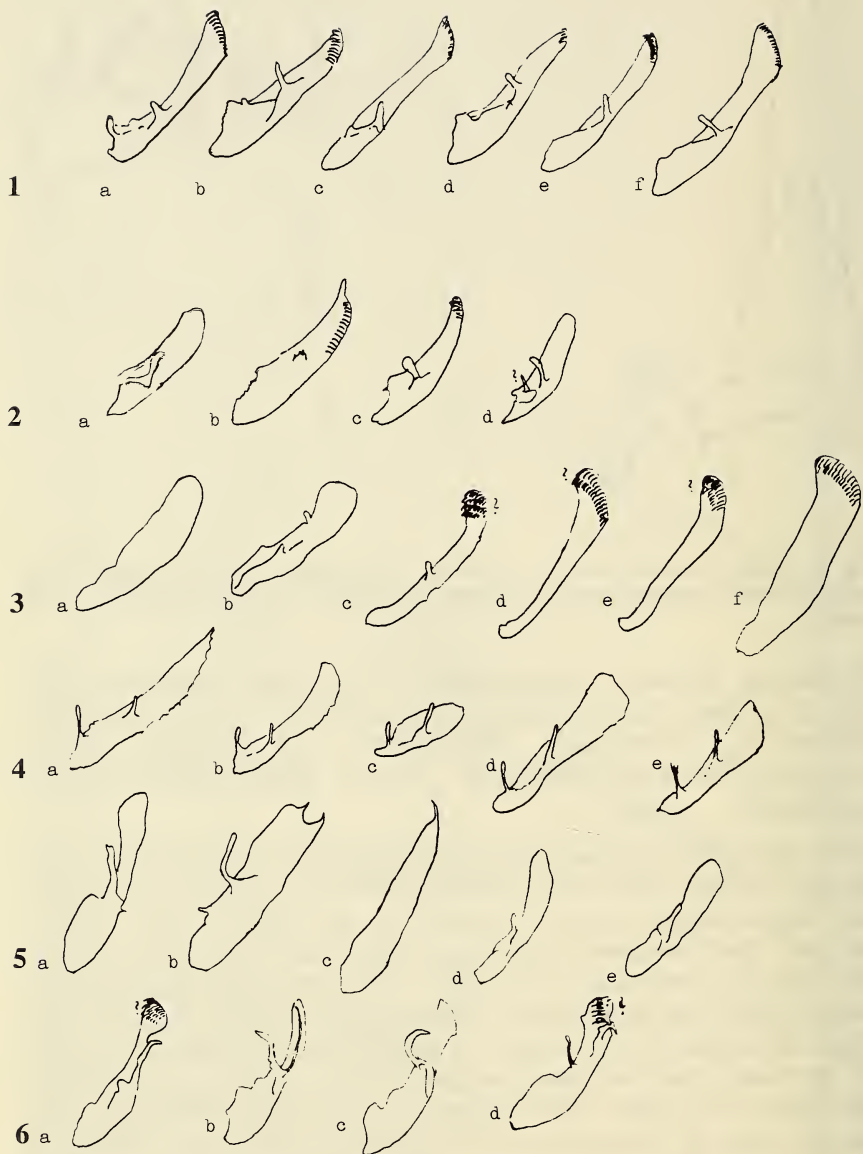


Fig. 5. Form of the spinneret. a - Tube-like (Cuculliinae), *Cucullia verbasci* L. ; b - dorsoventrally flattened, upper lip fringed (Noctuinae : Noctuini, Hadenini), *Axylia putris* L.

Heliothinae, Plusiinae, Bryophilinae and the genus *Amphipyra* (Fig. 6A). It is likely that the Acronictinae (with the tribes Acronictini, Dilobini and ?Pantheini), Chloephorinae (e.g. *Pseudoips fagana* FABRICIUS) and the Eublemminae are also closely related with the Cuculliinae.

In the ideal case (e.g. *Cucullia praecana* EVERSMAAN) the valva is long, straight and slim. The harpe (clasper of Pierce) is close to the equally slim finger-shaped process (=clavis) of the more or less reduced sacculus. Both processes, clavis and harpe, stand up erect from the valva and are connected by a stronger chitinous, oblique ridge directed to the caudal rim of the valva. The corona is oblique (30-45°) to the longitudinal axis of the valva ; it is generally longer than the breadth of the latter, but may also be completely reduced, e.g. in valvae narrowing to a point. The tendency to reduction within the same original form of the valva is to be observed in the same manner in the corresponding representatives of the Heliothinae (except for in *Pyrria umbra* HUFNAGEL, the clavis and harpe have been lost due to the strongly reduced slender basal part of the valva). The situation in the Plusiinae needs no commentary, the finger-shaped slender



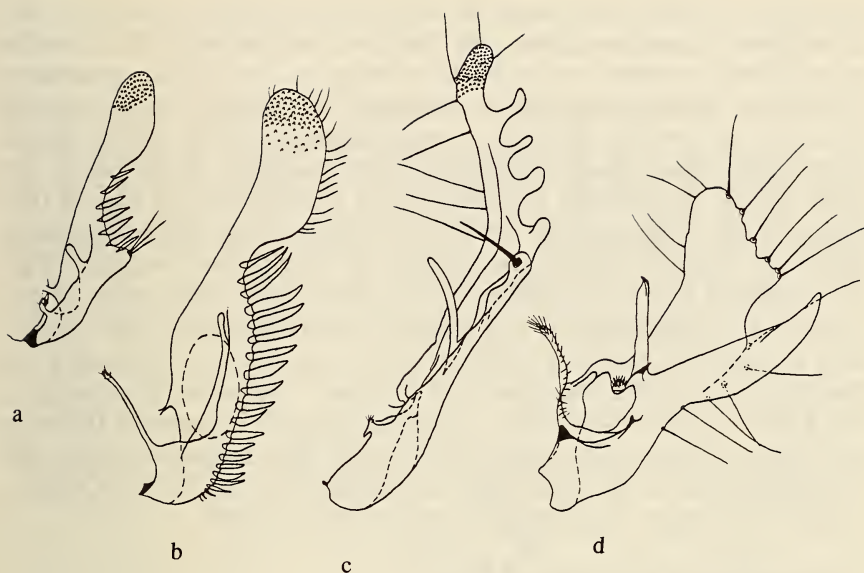


Fig. 6B. Left valves, considerably deviating from the cuculliine type according to PIERCE (1909) and BECK (1989), taken from KITCHING (1987 : 241,243) : a - *Plusiotricha livida* HOLLAND ; b - *Ctenoplusia limbirena* GUENÉE ; c - *Stigmoplusia chalcoides* DUFAY ; d - *Macdunnoughia confusa* STEPHENS.



Fig. 6A. Valvae (simplified line drawings after PIERCE, 1909, except the Bryophilinae, which are from FORSTER & WOHLFAHRT, 1971).

1st row : a - *Cucullia chamomillae* D. & S. ; b - *C. gnaphalii* HB. ; c - *C. absinthii* L. ; d - *C. verbasci* L. ; e - *C. scrophulariae* D. & S. ; f - *C. lychnitis* RBR.

2nd row : a - *Asteroscopus sphinx* HFN. ; b - *Brachionycha nubeculosa* ESP. ; c - *Meganephria bimaculosa* L. ; d - *Valeria oleagina* D. & S.

3rd row : a - *Amphipyra pyramidea* L. ; b - *A. tragopoginis* CL. ; c - *Pyrrhia umbra* HFN. ; d - *Heliothis peltigera* D. & S. ; e - *H. viriplaca* D. & S. ; f - *Helicoverpa armigera* HBN.

4th row : a - *Diachrysia chrysitis* HBN. ; b - *Plusia festucae* L. ; c - *Polychrysia moneta* F. ; d - *Autographa jota* L. ; e - *A. gamma* L.

5th row : a - *Bryopsis muralis* FORST. ; b - *Cryphia fraudatricula* HBN. ; c - *Euthales algae* F. ; d - *Bryoleuca raptricula* D. & S. ; e - *B. ravula* HBN.

6th row : a - *Axylia putris* L. (deviating from the Heliothinae type) ; examples from genera placed in the Cuculliinae by BOURSIN, but their valvae deviate from the *Cucullia* type : b - *Lithophane lamda* F. (*zinckenii* in PIERCE) ; c - *Xylena vetusta* HBN. ; d - *Blepharita adusta* ESP. (nomenclature from LERAUT, 1980).

processes of clavis and harpe in *Polychrysis moneta* FABRICIUS are in relation to position, form and direction identical with the *Cucullia* type. These processes are however missing in *Amphipyra pyramidea* LINNAEUS, whereas they can be recognised in *Amphipyra tragopoginis* CLERCK. In the Bryophilinae, corresponding parallels can be found in *Euthales algae* FABRICIUS and *Cryphia fraudatricula* HÜBNER : In these species the cucullus (corona absent) is extended into one or two points. This synapomorphy within the male genitalia defines a distinct group of noctuid subfamilies, termed the Cuculliinae complex (Fig. 7 : cuculliid phase of evolution of the Noctuidae). The system of the Noctuidae is now weighted very differently and the division into a trifine and a quadrifine series of subfamilies becomes more questionable by the delegation of the Plusiinae to the 'trifine' Noctuidae. Equivalently, the hitherto 'trifine' Noctuidae *Autophila* HÜBNER, *Apopestes* HÜBNER and *Tathorhynchus* HAMPSON have already been transferred from the 'Amphipyridae' to the quadrifine Catocalinae (DUFAY, 1975, as Ophideriinae). The case of *Apopestes* is treated in detail below.

Confirmation of the results of Pierce

PIERCE based his corresponding noctuid classification on a study of the male genitalia. He writes (1909 : 72) : ".....The following genera require a good deal of re-arranging, and I believe the genitalia will prove an important help in the sequence. There is a certain amount of connection between the groups, which in the present classification, has unfortunately been interrupted, by interspersing several little odd genera among natural relatives. The Cucullias, with their narrow coronated harpes [=valva] and simple clasper [=harpa], lead to the Heliethidae, from which should be excluded *Anarta* and *Heliaca* [= *Panemeria* HÜBNER]. The harpe of the Heliethias, being very closely allied to the Cucullias, except that the clasper is lost. *Asteroscopus* [= *Brachionycha* HUFNAGEL] , including *Valeria oleagina* and *Miselia bimaculosa* again form another connecting link, and continue the sequence to the Plusidae, which may be followed by *Habrostola* [*Abrostola* OCHSENHEIMER] and made to include, or at any rate be followed by the Amphipyridae."

If PIERCE had included in his investigations species of the Plusiinae *Macdunnoughia* KOSTROWICKI or the tropical *Ctenoplusia* DUFAY (BEHOUNEK & RONKAY, 1989) and other 'aberrant' plusiine taxa (KITCHING, 1987 : 240-247), which have valvae differing strongly from the 'Plusia' or 'Cucullia' type described above (Fig. 6B), he would have had difficulties in believing a relationship existed between the Plusiinae

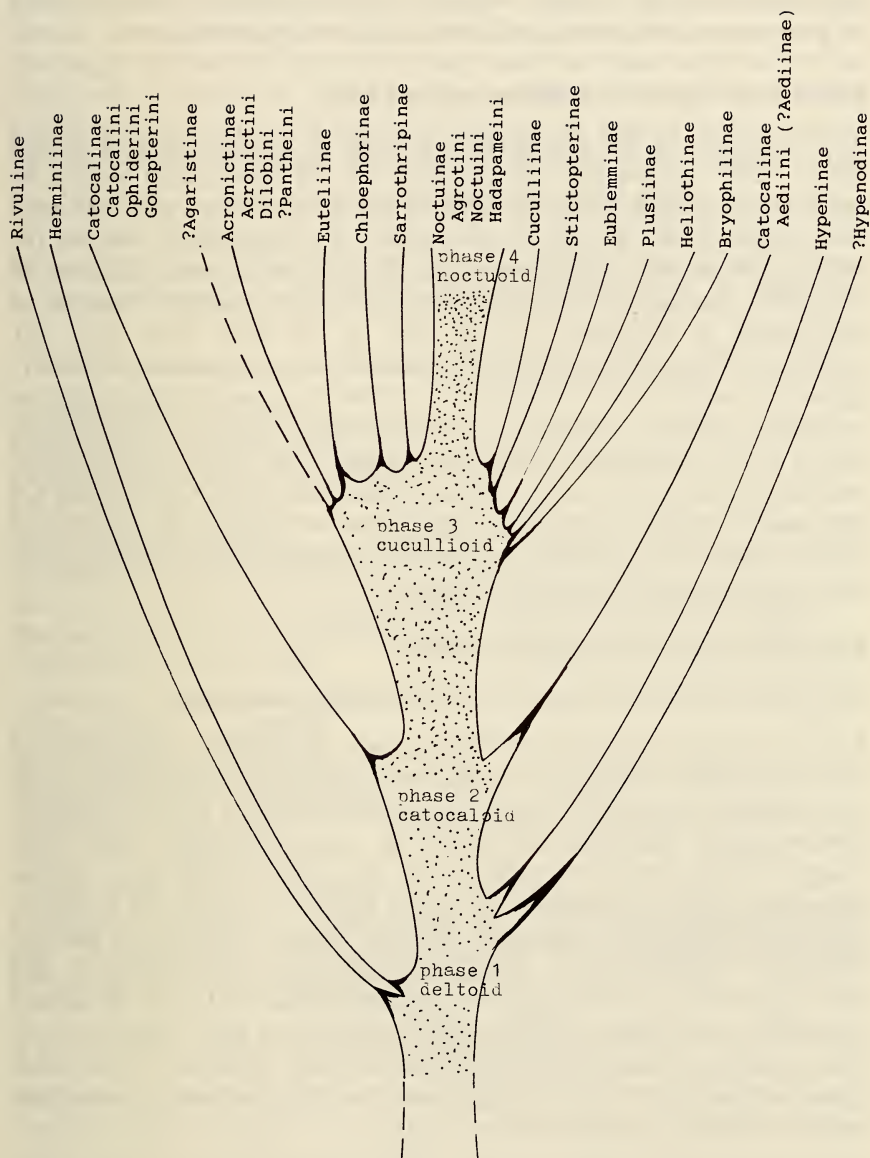


Fig. 7. A diagram to illustrate the multiphasic evolution of the Noctuidae. For clarity, the specialised higher taxa are shown to stem from the centre of each phase. The several branches off phases 1 and 3 are not equivalent to the successions of a cladogram. Branches can also be multiphasic, but these are not shown.

and the Cuculliinae. Further evidence for this relationship can be found in wing shape and pattern, and larval size and ornamentation.

Difficulties with the Cuculliinae concept s.str.

The extension of the Cuculliinae concept to further noctuid genera (BECK, 1991) shows that the diagnosis of the Cuculliinae cannot be maintained in this form. Exceptions to the definition of 1960 have been found in all characters: the course of the spiracular line on the lateral side of the anal shield (Fig. 3b), bristle-like seta SD1 on S9 (Fig. 4b), the long tube-like spinneret (Fig. 5a) and the number of macrosetae in SV-group: on S1 two, on S2 three setae (Fig. 4a). *Calliergis* HÜBNER, for instance, possesses three macrosetae in the SV-group as well on S1 as on S2 - a hitherto 'typical' catocaloid or 'quadrifine' feature. According to this primitive feature *Calliergis* should be put in the 'quadrifine' Noctuidae, but the more advanced characters, including those of the adult, indicate placement in the Cuculliinae. On the basis of further material (a new larval collection was initiated in 1972) it proved not possible to develop a natural system by using only one or a few larval or adult characters.

Present concept of Cuculliinae s. BECK

Very rich in form and pattern, both in the larva and adult.

LARVAL CHARACTERIZATION: Body stout to slender; prolegs on S3 and S4 possibly missing (as in the first instar mostly obligatory), little or completely developed. Spinneret tube-like and long, rarely shortened, dorsoventrally flattened and lower lip notched apically, lips never fringed. SV-group on S1 mostly with two, rarely with three macrosetae (the latter condition in *Epimecia* GUENÉE, *Apopestes* HÜBNER, *Phyllophila* GUENÉE, *Alvaradoia* AGENJO, *Apaustis* HÜBNER, *Calliergis* HÜBNER, *Tyta* BILLBERG, *Mesotrosta* LEDERER, *Omia* HÜBNER and *Recoropha* NYE), on S2 always three macrosetae; SD1 on S9 always bristle-like, sometimes a little weaker than D1 or D2; SD2 on S1 to SIII sometimes bristle-like. Integument of body smooth or with small grana, seldom with thin or rough spines (the latter, heliothine condition, only in *Cucullia artemisiae* HUFNAGEL)

ORNAMENTATION: Head usually with reticulation fields darker than background, sometimes unicolourous in greenish larvae. Middorsal line as broad as or broader than subdorsal line or (seldom) longitudinally bisected; middorsal line sometimes missing, then subdorsal line conspicuous and the greenish zones without elements; epistigmatal line

seldom present, in some species distinct only on SI ; spiracular line usually running along the side of anal shield, sometimes running to the angle formed by the anal prolegs and the anal shield or to the anal prolegs, behind or, rarely, in front of and touching setae L1 and L2. Zones in green, yellowish or whitish larvae always of one colour, but occasionally with large black spots both between and around setae.

The European genera currently placed in the Cuculliinae (according to the list of HARTIG & HEINICKE, 1973) are partitioned below according to the above subfamily concept (there are interesting parallels to the former system of STAUDINGER & REBEL ; sic HACKER, 1990) :

1. Genera remaining in the subfamily Cuculliinae (list 1)

Cucullia SCHRANK, 1802
Calophasia STEPHENS, 1829
Omphalophana HAMPSON, 1906
Omia HÜBNER, [1821]
Recoropha NYE, 1975
Sympistis HÜBNER, [1823]
Asteroscopus BOISDUVAL, 1828 (Typus : *sphinx* HUFNAGEL, 1766)
Brachionycha HÜBNER, [1819] (Typus : *nubeculosa* ESPER, [1785])
Dasypolia GUENÉE, 1852
Lophoterges HAMPSON, 1906
Calliergis HÜBNER, [1821]
Xylocampa GUENÉE, 1837
Meganephria HÜBNER, [1820]
Allophyes TAMS, 1942
Valeria STEPHENS, 1829
Lamprosticta HÜBNER, [1820]
Copiphana HAMPSON, *Metopoceras* GUENÉE, *Amephana* HAMPSON and *Cleonymia* BERIO probably belong to the Cuculliinae, according to figures of larvae in SPULER, 1908.

2. Genera to be added to the Cuculliinae (list 2)

Apopestes HÜBNER, [1823]
Pyrois HÜBNER, [1820]
Amphipyra OCHSENHEIMER, 1816
Mesotrosta LEDERER, 1857
Stilbia STEPHENS, 1829
Stilbina STAUDINGER, 1892
Epimecia GUENÉE, 1839
Synthymia HÜBNER, [1823]

Aegle HÜBNER, [1823]
Elaphria HÜBNER, [1818] (= *Hapalotis* HÜBNER)
Panemeria HÜBNER, [1823]
Apaustis HÜBNER, [1823]
Phyllophila GUENÉE, 1852
Alvaradoia AGENJO, 1984 (Typus : *numerica* BOISDUVAL, 1840)
Protodeliote UEDA, 1984 (Typus : *pygarga* HUFNAGEL, 1766)
Deltote REICHENBACH 1817 (Typus : *argentula* HÜBNER, [1787])
Pseudeustrotia WARREN, 1913 (Typus : *candidula* D. & S., 1775)
Lithacodia HÜBNER, [1818] (Typus : *bellicula* HÜBNER, [1818])
Acontia OCHSENHEIMER, 1816
?Tyta BILLBERG, 1820
Emmelia HÜBNER, [1821]

3. Genera to be removed from the Cuculliinae (list 3)

Brachylomia HAMPSON, 1916
Episema OCHSENHEIMER, 1816 (Typus : *glaucina* ESPER, [1789])
Cleoceris BOISDUVAL, [1836] (Typus : *scoriacea* ESPER, [1789])
Leucochlaena HAMPSON, 1906
Aporophila GUENÉE, 1841
Lithomoia HÜBNER, [1821]
Scotochrosta LEDERER, 1857
Lithophane HÜBNER, [1821])
Prolitha BERIO, 1980
Xylena OCHSENHEIMER, 1816
Rileyiana MOUCHA & CHVALA, 1963
Dichonia HÜBNER, [1821]
Dryobota LEDERER, 1857
Dryobotodes WARREN, 1910
Blepharita HAMPSON, 1907 (Typus : *amica* TREITSCHKE, 1825)
Mniotype FRANCLEMONT, 1941 (Typus : *ducta* GROTE, 1878)
Trigonophora HÜBNER, [1821]
Polymixis HÜBNER, [1820] (Typus : *polymita* LINNAEUS, 1761)
Myxinia BERIO, 1985 (Typus *rufocincta* GEYER, [1828])
Propolymixis BERIO, 1980 (Typus : *argillaceago* HÜBNER, [1822])
Simplitype BERIO, 1980 (Typus : *dubia* DUPONCHEL, [1838])
Crypsedra WARREN, 1910 (Typus : *gemmea* TREITSCHKE, 1825)
Antitype HÜBNER, [1821]
Ammoconia LEDERER, 1857
Ammopolia BOURSIN, 1955
Eumichtis HÜBNER, [1821]
Eupsilia HÜBNER, [1821]

Jodia HÜBNER, [1818]
Conistra HÜBNER, [1821]
Dasycampa GUENÉE, 1837
Agrochola HÜBNER, [1821]
Omphaloscelis HAMPSON, 1906
Parastichtis HÜBNER, [1821]
Spudaea SNELLEN, 1867
Atethmia HÜBNER, [1821]
Xanthia OCHSENHEIMER, 1816 (Typus : *flavago* FABRICIUS, 1787)
Cirrha HÜBNER, [1821] (Typus : *icteritia* HUFNAGEL, 1766)
Tiliacea TUTT, 1896 (Typus : *citrago* LINNAEUS, 1758)

Note : Generic types are only listed when the original genera have been split in recent years or in the case of holarctic genera established by North-American authors and unknown in Europe hitherto.

The position of *Apopestes* HÜBNER (1823)

Because of some affinities to *Amphipyra*, BOURSIN (after DUFAY, 1975) put *Apopestes* in the 'Amphipyrinae' near *Amphipyra*. DUFAY, 1975, himself placed *Apopestes*, together with *Tathorhynchus* HAMPSON and *Autophila* HÜBNER in the subfamily 'Ophiderinae', because of 'absolute identity' of the male genitalia with those of *Lygephila* BILLBERG. Here *Apopestes* is returned to the neighbourhood of *Amphipyra*, now within the Cuculliinae. *Apopestes* shows features of both the Ophiderini and the Cuculliinae. The male genitalia are equally comparable with *Lygephila* BILLBERG spp. as with those of *Calophasia* STEPHENS. Wing size and pattern resembles some Ophiderini. The larva of *Apopestes* is compared below with those of the Ophiderini *Minucia lunaris* DENIS & SCHIFFERMÜLLER and *Lygephila cracca* DENIS & SCHIFFERMÜLLER.

MORPHOLOGY : Trunk moderately stout ; size of head equally cuculline as ophiderine, shape of frons typically ophiderine, P1 on a transverse line through AF2 or a little (about one diameter of setaepoint P1) behind it, cuculline (although also in *Lygephila*) ; ridge of teeth of mandible ophiderine ; hypopharynx laterally ophiderine and cuculline, without ridge of teeth ; spinneret cuculline ; labial palpus, segment 1 cuculline and ophiderine ; segment 2 of antenna short, cuculline ; inside tibia of thoracic legs with ophiderine arrangement of setae ; abdomen, S1 : D1 nearly on longitudinal line through D2 (D1-D1 4/5-5/6 D2-D2), ophiderine ; longitudinal distance between transversal lines through D1 and D2 about 1/2 D1-D1, cuculline ; arrangement

of setae around stigma (SD1, L1, L2) cuculline ; SV group with three macro-setae (on S1), ophiderine ; prolegs : shape and size, especially size of planta and the arrangement of the uniordinal crotchets on it, typically ophiderine.

On the whole there are numerically more ophiderine morphological features ; many of these characters are also to be found variously within several genera of the Cuculliinae s.l. BECK. Typically cuculline are the characters of the spinneret, of the antenna, of the distance between the transversal lines through D1 and D2 on S1 and the arrangement of setae around the spiraculum of S1.

ORNAMENTATION : The well-known, richly ornamented larva (figured in SPULER, 1908) has a pure yellow spiracular line running directly to the common base of the anal shield and the anal prolegs ; middorsal line pale yellow running through, width on S1 $1/3$ D1-D1 (to $2/5$), edges sharp and straight ; subdorsal line similar, width $1/6$ D1-D1, S1 ; epistigmatal line as subdorsal, width $1/12$ - $1/18$ D1-D1 ; spiracular line running through, width on S1 about 1 SD1-L2, dorsal edge displaced dorsally, interrupted by large black spots of the ventral subdorsal zone ; a basal and subventral line follows, each more or less interrupted by the SV seta group and with one dorsal bow (from SV group to the next SV group), ventral zone plain whitish-grey. Head of the larva whitish-grey with large black spots around the setae (setae on the trunk, within the ventral subdorsal zone and within the pleural zone, also with large black basal spots, each edged narrowly with ground colour).

SUMMARY : The characters of the dorsal, subdorsal and spiracular lines cannot be found in any larva of the Ophiderini or Catocalinae (in *Lygephila limosa* TREITSCHKE, only the subdorsal and the spiracular line are somewhat comparable ; the latter extends dorsally only to L1 and ends on the anal prolegs) ; I do not know any 'quadrifine' larva with a pure, broad, straight and sharp-edged middorsal line and I know no quadrifine larva with large, black, round spots (one/seta point) on the head and/or the body. These ornamentation characters in the larva of *Apopestes spectrum* are modern (compared to the mostly conservative morphological features) and thus the evolutionary advanced ornamentation recommends its position to the Cuculliinae. This decision is the same as that of placing *Archaeopteryx* to the root of the class Aves, in spite of many reptilian features. At the same time we recognise in *Apopestes* a transitional state between the Catocalinae (Ophiderini) and the Cuculliinae.

Importance of the subfamily Cuculliinae, effects to Noctuidae classification as a whole, nomenclatural changes

From the above discussion, it follows that the subfamily Cuculliinae is a transition between the Catocalinae-Ophiderini and the Noctuinae, s. BECK (1960) (compare also the view of HAMPSON, Fig. 2). We can find many catocaline-ophiderine (but also some noctuine) features within this subfamily and it is sometimes difficult and arbitrary to decide about the position of such a problematical taxon.

Most of the recent subfamilies and tribes are not to be seen as direct descendants of the (recent) 'quadrifine' Noctuidae, but as a mixture of modern forms and representatives of former phases of a multiphasic progressive evolution (Fig. 7). Within the central 'stream' each phase retains some characters of preceeding phase(s) in addition to those newly acquired.

Several specialised and clearly definable subfamilies stem from the cucullioid phase. Thus this phase takes a position similar to that of the former subfamily groups 'Trifinae' and 'Quadrifinae', nomenclaturally invalid names. Instead of these terms I take for the multiphasic-progressive type of evolution of the Noctuidae the terms used for the centres of this development: the deltoid (Hypeninae, Herminiinae, etc. subfamilies), the catocaloid, the cucullioid and the noctuoid phases.

These centres, with the exception of the most recent, the noctuoid, are marked on the one side by the emergence of several more or less highly specialised and therefore relatively clearly definable subfamilies, on the other side there are the centres themselves, mostly difficult to define because of the beginning of differentiation into tribes and subtribes. Contrary to current opinions (KITCHING, 1984, FRANCLEMONT & TODD, 1983, et al.) it is impossible to maintain an order of equivalent subfamilies on a horizontal level. At least the 'subfamilies' of the most recent phase of noctuoid evolution, the so-called 'Amphipyrrinae', the Hadeninae and the Noctuinae, do not merit the rank of subfamilies (BECK, 1960); compare also the comment of KITCHING (1984: 204): "Franclemont also recognises the very close similarity between trifine subfamilies and would possibly advocate their amalgamation into a single subfamily, the Noctuinae."

For the "Amphipyrrinae" remaining in the Noctuinae (*Amphipyra* having been transferred to the Cuculliinae), the name Apameini (FRANCLEMONT & TODD, 1983) is unsuitable. Because of a continuous transition between the Hadenini (BECK, 1960: Hadeninae) and the Apameini both larvally (BECK, 1960) and imaginally (within the male

genitalia, VARGA, pers. comm., 1989) I propose the combined name Hadapameini **trib.n.** for the fusion of these tribes (as a tribe within the Noctuinae); further tribes of the Noctuinae are the Agrotini and the Noctuini.

It is also proposed to upgrade the tribe Eublemmini (FORBES, 1954 and FRANCEMONT & TODD, 1983) to subfamily: Eublemminae **stat.n.**, type *Eublemma respersa* HÜBNER. The reasoning behind this decision is on the one hand the delegation of the acontiine genera *Phyllophila* *Acontia* *Tyta* (see list 2) to the Cuculliinae and on the other a residue of unique genera within the Noctuidae with similar biology and larval morphology (for adult diagnosis see KITCHING (after FORBES), 1984 : 219). A preliminary larval diagnosis follows : medium-sized to very small species, mode of life tortricoid, body stout, fusiform, prolegs missing on S3 and S4 ; setae long, about half of the transverse diameter of the trunk at S6, strong ; chaetotaxy unique (MD1 and SD2 on S1-S8 macrosetous, position of MD1 !), S1 and S2 each with three macro-setae in SV group.

Acknowledgements

I would like to express my thanks to Mr. S. Whitebread for editing and improving the English of this article, to Mr. E. de Bros for translating the summary into French and to an anonymous referee for helpful comments and suggestions.

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Jahr/Year: 1992

Band/Volume: [15](#)

Autor(en)/Author(s): Beck Herbert

Artikel/Article: [New view of the higher classification of the Noctuidae \(Lepidoptera\) 3-28](#)