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The phylogeny of the Noctuidae (Lepidoptera)

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Abstract. A new phylogenetic system of the Noctuidae is proposed. The system should, however, be regarded as provisional because it is primarily based on only two character complexes: the male genitalia and the tympanal region. The presence of preabdominal brush-organs and the length of tibial spurs in the adult male, the presence of a ventral cervical gland and the lack of the SV 2 setae on the first abdominal segment of the larvae are considered. The results confirm the monophyly of the Noctuidae. The Herminiinae are considered to represent the sister-group of all other Noctuidae. Remaining noctuid subfamilies are grouped in a series of clades for which the corresponding autapomorphies are given. Some formerly accepted subfamilies, such as the Acontiinae, prove to be polyphyletic. Accordingly, these subfamilies are subdivided into separate lineages. A sister-group relationship between the Noctuidae and the Aganaidae is supported. These two families may be united with the Arctiidae to form a still broader clade.

Introduction

Seven moth families, the Oenosandridae, Doidae, Notodontidae, Lymantriidae, Arctiidae, Aganaidae and Noctuidae, are currently recognized in the large superfamily Noctuoidea (Miller, 1991), comprising some 40 000 described species (Heppner, 1991). Monophyly of the Noctuoidea is based on the presence of a metathoracic tympanal organ (Miller, 1991). With almost 25 000 included species, the Noctuidae form the largest family within the superfamily, and within the order Lepidoptera as a whole (Heppner, 1991). Nevertheless, our understanding of the phylogenetic affinities of the Noctuidae to other noctuoid families, as well as interrelations among the various noctuid subfamilies, is still in its infancy.

Holloway (1988) noted that the Aganaidae and Noctuidae share a similar number of thoracic subventral setae in the larvae, and both have an orbicular stigma in the forewing cell. On these grounds he relegated the Aganaidae to a subfamily of the Noctuidae. However, there is homoplasy in the distribution of the subventral setae among the families under consideration. We prefer to retain family rank for the Aganaidae, because this corresponds better with the historical development of noctuoid classification, and because the sister-group relationship is still weakly supported.

Kitching (1984) published an historical review of noctuid subfamily relationships. His synopsis shows that current ideas on the higher classification of the Noctuidae are based on superficial resemblance and vaguely defined characters, rather than on rigorous application of cladistic principles.

In an attempt to progress beyond the age of traditional noctuid taxonomy we started a morphological investigation, based on a set of characters, which we considered particularly useful in elucidating the basic relationships of the noctuid subfamilies.

The tympanal region was chosen because it was demonstrated by Eggers (1919) to be structurally heterogeneous within the Noctuidae. Richards (1932) proposed a noctuid classification based on a comparative study of the tympanal region. Unfortunately, Richard's system relies exclusively on intuitive character interpretation; characters or character states to delimit subfamily groups were not provided.

The male genitalia and their associated muscles were considered because they are thought to evolve quickly (Eberhard, 1985), and may thus provide considerable information. Tikhomirov (1979a,b,c), in a series of valuable papers, has demonstrated that some noctuid subfamilies share the unique presence of an additional (novel) male genitalic muscle.

The males of most 'higher' Noctuidae are characterized by the presence of a paired brush-organ, situated on the second abdominal segment, that is presumably responsible for the dissemination of male sexual pheromones (reviewed in Birch *et al.*, 1990). We investigated the distribution of this character in order to find the point at which it evolved within the family.

During our studies we suspected that the spurs of noctuid species might be relatively long. We therefore compared spur length of the Noctuidae with that of outgroups.

The presence of a ventral cervical gland in noctuid larvae has been known for quite a long time (e.g. Gardner, 1941;

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Peterson, 1962). Curiously, the precise distribution of this character within Noctuoidea has never been investigated. We therefore decided to include this character in our analysis.

The absence of seta SV 2 on the first abdominal segment of the larva has been considered to represent an apomorphic character for the higher Noctuidae (Poole, 1995). We also included this important character.

Material and methods

For the study of cuticular structures, the specimens were cleared in hot aqueous KOH (10%) for about 10 min. In some cases the specimens were later stained in an aqueous solution of Evan's Blue in order to clearly visualize delicate membraneous structures.

Specimens to be studied by scanning electron microscopy (SEM) were either macerated in KOH, or fixed in an aqueous solution of picric acid. In both cases they were dehydrated through a graded series of ethanol before being transferred to hexamethyldisilazan. Specimens were then air-dried and sputter-coated with gold prior to SEM examination.

For the investigation of genitalic muscles, male moths were stored in a saturated aqueous solution of picric acid until dissection. Penetration of the aqueous solution into the specimens was greatly facilitated by first soaking them briefly in 70% ethanol. Prolonged storage in picric acid stains the muscles a bright yellow colour, while they simultaneously remain soft and flexible. During dissection, which was carried out in 70% ethanol, specimens were occasionally dipped in a diluted alcoholic solution of Evan's Blue in order to obtain enhanced contrast.

We obtained fixed male specimens from the noctuoid families Oenosandridae, Notodontidae, Lymantriidae, Arctiidae, Aganaidae and from most subfamilies of the Noctuidae (Table 1a). Unfortunately, we were unable to obtain fixed male specimens of the Doidae, a small family confined to the Americas.

A list of the species examined for the other characters is given on Table 1(b–d).

Results

At the outset, the phylogenetic system we propose as a result of our morphological investigations will be briefly introduced. Family relationships between the Arctiidae, Aganaidae and Noctuidae, and the principal noctuid subfamily arrangements, are depicted in Fig. 1. For each taxon the approximate number of species has been added in parentheses, mainly following Heppner (1991). Information concerning the monophyly and composition of individual noctuid subfamilies is presented later in the discussion. The cladogram is accompanied by a list of the presumed autapomorphies for each of the ten clades indicated (Table 2). In the following pages the apomorphies in Table 2 are detailed through successive treatment of the five character systems examined.

Character system 1: the tympanal region

General description

The term tympanal region is used here in a rather broad sense. It refers to the area around the waist-like cleft separating the thorax and abdomen, commonly known in the Noctuoidea as the tympanal cavity (Figs 2 and 3). Thus, the tympanal region includes the tympanal organ proper as well as functionally related structural modifications of the metathorax and first abdominal segment. Sexual dimorphism in tympanal morphology is probably restricted to species with wingless females, e.g. the lymantriid genus *Orgyia* (Eggers, 1919). The sex of the specimens investigated is therefore not noted.

We focus on external structures of the tympanal region. An overview of structures and morphological terms is presented in Fig. 2, showing the metathorax and the first two abdominal segments of a higher noctuid species, *Agrotis exclamationis* (Noctuinae). The following structures are of particular interest:

1 *Hood structures of the A1 pleuron*

The presence of a metathoracic tympanum has influenced the structure of the pleural region of the first abdominal segment (A1). The anterior parts of A1, forming the posterior wall of the tympanal cavity, are often prominently expanded. There are three principal configurations. A prespiracular hood, i.e. a pleural evagination situated anterior to the A1 spiracle, is present in the Oenosandridae, Lymantriidae, Arctiidae and in a strongly reduced form in the Aganaidae (Fig. 4). The Herminiinae are the only noctuids possessing this configuration (Fig. 5). A postspiracular hood originating immediately behind the A1 spiracle is typical for the remaining Noctuidae (Figs 2, 6, 7). Reduction of the hood to simple dorsal remnants occurs in the Nolinae (Fig. 8). Finally, a perispiracular cup on the A1 pleura is typical for all Notodontidae (Fig. 9). In some cases the cup has shifted anterad to such an extent that it bears superficial resemblance to a postspiracular hood, and may even be mistaken for that structure.

In addition, the pleural region posterior to the A1 hood is, at least in the Noctuidae, provided with a lateral sclerotization (Figs 5–7). This lateral A1 sclerotization should not be confused with the hood itself. This sclerotization may be an autapomorphy of the Noctuidae + Aganaidae (Minet, 1986; character a), but has not been studied here in detail.

2 *The alula*

The alula, the posterobasal lobe of the wing, forms a thin membraneous flap covering the dorsal part of the tympanal region. Its tubular posterior margin (axillary cord) is continued into the scutellar arm, connecting the hindwing with the metanotum (Fig. 14). Generally, the insect metanotum houses a pulsatile wing-heart that is responsible for sucking haemolymph out of the hindwings along the scutellar arm (e.g. Krenn & Pass, 1994, 1995). Because of its large size the alula

Table 1 List of families and species investigated.

(a) For the survey of the muscles in the male genitalia*

Oenosandridae
  - *Oenosandra boisduvalii* Newman, 1856

Notodontidae
  - *Cerura vinula* (Linnaeus, 1758)
  - *Phalera bucephala* (Linnaeus, 1758)
  - *Thaumatopoea solitaria* (Freyer, 1838)
  - *Traumatocampa pityocampa* ([Denis & Schiffermüller], 1775)

Lymantriidae
  - *Calliteara pudibunda* (Linnaeus, 1758)
  - *Lymantria dispar* (Linnaeus, 1758)

Arctiidae
  - *Eilema complana* (Linnaeus, 1758)
  - *Euplagia quadripunctaria* (Poda, 1761)

Aganaidae
  - *Asota caricae* (Fabricius, 1775)

Noctuidae
  - *Herminia grisealis* ([Denis & Schiffermüller], 1775) (Herminiinae)
  - *Hydrillodes moloalis* (Walker, 1859) (Herminiinae?)
  - *Rivula sericealis* (Scopoli, 1763) (Rivulinae)
  - *Hypena proboscidalis* (Linnaeus, 1758) (Hypeninae)
  - *Penicillaria simplex* (Walker, 1865) (Euteliinae)
  - *Stictoptera cucullioides* Guenée, 1852 (Stictopterinae)
  - *Catocala fraxini* (Linnaeus, 1758) (Catocalinae)
  - *Oxyodes scrobiculata* (Fabricius, 1775) (Catocalinae?)
  - *Panthea coenobita* (Esper, 1785) (Pantheinae)
  - *Colocasia coryli* (Linnaeus, 1758) (Pantheinae)
  - *Diloba caeruleocephala* (Linnaeus, 1758) (Pantheinae)
  - *Camptoloma interiorata* (Walker, 1865) (Camptolominae)
  - *Maurilia iconica* (Walker, 1858) (Chloephorinae)
  - *Pseudoips prasinana* (Linnaeus, 1758) [= *fagana* (Fabricius, 1781)] (Chloephorinae)
  - *Blenina lucretia* (Dalman, 1823) [= *accipiens* Walker, [1858]] (Sarrothripinae)
  - *Blenina quinaria* Moore, 1882 (Sarrothripinae)
  - *Meganola albula* ([Denis & Schiffermüller], 1775) (Nolinae)
  - *Meganola strigula* ([Denis & Schiffermüller], 1775) (Nolinae)
  - *Abrostola triplasia* (Linnaeus, 1758) [= *trigemina* (Werneburg, 1864)] (Plusiinae)
  - *Autographa gamma* (Linnaeus, 1758) (Plusiinae)
  - *Acronicta rumicis* (Linnaeus, 1758) (Acronictinae)
  - *Cryphia algae* (Fabricius, 1775) (Bryophilinae)
  - *Sarbanissa* sp. (Agaristinae)
  - *Heliothis virescens* (Fabricius, 1777) (Heliothinae)
  - *Noctua pronuba* Linnaeus, 1758 (Noctuinae)
  - *Hecatera bicolorata* (Hufnagel, 1766) (Hadeninae)

(b) For the survey of the presence of a ventral cervical gland in the larvae

Notodontidae
  - *Phalera bucephala* (Linnaeus, 1758)
  - *Pheosia gnoma* (Fabricius, 1776)
  - *Stauropus fagi* (Linnaeus, 1758)

Lymantriidae
  - *Lymantria dispar* (Linnaeus, 1758)
  - *Orgyia* sp.

Arctiidae
  - *Arctia caja* (Linnaeus, 1758)
  - *Divarctia diva* (Staudinger, 1887)
  - *Eilema caniola* (Hübner, [1808])
  - *Phragmatobia fuliginosa* (Linnaeus, 1758)
  - *Spilosoma lubricipeda* (Linnaeus, 1758)

Aganaidae
  - *Asota plana* Walker, 1854

Table 1 *Continued.*

- Noctuidae
  - *Herminia tarsicrinalis* (Knoch, 1782) (Herminiinae)
  - *Pechipogo strigilata* Linnaeus, 1758 (Herminiinae)
  - *Rivula sericealis* (Scopoli, 1763) (Rivulinae)
  - *Schrankia taenialis* (Hübner, [1809]) (Hypenodinae)
  - *Schrankia costaestrigalis* (Stephens, 1834) (Hypenodinae)
  - *Hypena proboscidalis* (Linnaeus, 1758) (Hypeninae)
  - *Hypena rostralis* (Linnaeus, 1758) (Hypeninae)
  - *Eutelia adulatrix* (Hübner, [1813]) (Euteliinae)
  - *Calyptra thalictri* (Borkhausen, 1790) (Catocalinae)
  - *Catocala promissa* ([Denis & Schiffermüller], 1775) (Catocalinae)
  - *Dysgonia algira* (Linnaeus, 1767) (Catocalinae)
  - *Colocasia coryli* (Linnaeus, 1758) (Pantheinae)
  - *Diloba caeruleocephala* (Linnaeus, 1758) (Pantheinae)
  - *Pseudoips prasinana* (Linnaeus, 1758) (Chloephorinae)
  - *Nycteola revayana* (Scopoli, 1772) (Sarrothripinae)
  - *Eligma narcissus* (Cramer, 1776) (Sarrothripinae)
  - *Autographa gamma* (Linnaeus, 1758) (Plusiinae)
  - *Protodeltote pygarga* (Hufnagel, 1766) (Eustrotiinae)
  - *Eublemma minutata* (Fabricius, 1794) (Acontiinae?)
  - *Phlogophora meticulosa* (Linnaeus, 1758) (Amphipyrinae)
  - *Omphaloscelis lunosa* (Haworth, 1809) (Amphipyrinae)
  - *Discestra trifolii* (Hufnagel, 1766) (Hadeninae)

(c) For the survey of the tympanal region

- Oenosandridae
  - *Oenosandra boisduvalii* Newman, 1856
- Notodontidae
  - *Cerura vinula* (Linnaeus, 1758)
  - *Drymonia obliterata* (Esper, 1785)
  - *Leucodonta bicoloria* ([Denis & Schiffermüller], 1775)
  - *Phalera bucephala* (Linnaeus, 1758)
  - *Pheosia gnoma* (Fabricius, 1776)
  - *Thaumatopoea solitaria* (Freyer, 1838)
- Lymantriidae
  - *Calliteara pudibunda* (Linnaeus, 1758)
  - *Lymantria dispar* (Linnaeus, 1758)
- Arctiidae
  - *Creatonotus transiens* (Walker, 1855)
  - *Dysauxes ancilla* (Linnaeus, 1767)
  - *Eilema complana* (Linnaeus, 1758)
  - *Euplagia quadripunctaria* (Poda, 1761)
  - *Miltochrista miniata* (Forster, 1771)
  - *Tyria jacobeae* (Linnaeus, 1758)
- Aganaidae
  - *Asota caricae* (Fabricius, 1775)
  - *Asota egens* (Walker, 1854)
  - *Digama hearseyana* Moore, [1860]
- Noctuidae
  - *Adrapsa ablualis* (Walker, [1859]) (Herminiinae)
  - *Herminia grisealis* ([Denis & Schiffermüller], 1775) (Herminiinae)
  - *Herminia ryukyuensis* Owada, 1982 (Herminiinae)
  - *Herminia tarsicrinalis* (Knoch, 1782) (Herminiinae)
  - *Hydrillodes moloalis* (Walker, 1859) (Herminiinae?)
  - *Nodaria tristis* (Butler, 1879) (Herminiinae)
  - *Simplicia caeneusalis* (Walker, [1859]) (Herminiinae)
  - *Trisateles emortualis* ([Denis & Schiffermüller], 1775) (Herminiinae)
  - *Zanclognatha yakushimalis* Sugi, 1959 (Herminiinae)
  - *Rivula sericealis* (Scopoli, 1763) (Rivulinae)
  - *Anoratha costalis* Moore, 1867 (Hypeninae)
  - *Hypena crassalis* (Fabricius, 1787) (Hypeninae)

Table 1 *Continued.*

Hypena proboscidalis (Linnaeus, 1758) (Hypeninae)
Eutelia adulatrix (Hübner, [1813]) (Euteliinae)
Penicillaria simplex (Walker, 1865) (Euteliinae)
Stictoptera cucullioides Guenée, 1852 (Stictopterinae)
Blasticorhinus sp. (Catocalinae)
Catephia alchymista ([Denis & Schiffermüller], 1775) (Catocalinae)
Catocala fraxini (Linnaeus, 1758) (Catocalinae)
Lygephila craccae ([Denis & Schiffermüller], 1775) (Catocalinae)
Lygephila pastinum (Treitschke, 1826) (Catocalinae)
Oxyodes scrobiculata (Fabricius, 1775) (Catocalinae?)
Scoliopteryx libatrix (Linnaeus, 1758) (Catocalinae)
Ulotrichopus macula (Hampson, 1891) (Catocalinae)
Panthea coenobita (Esper, 1785) (Pantheinae)
Colocasia coryli (Linnaeus, 1758) (Pantheinae)
Diloba caeruleocephala (Linnaeus, 1758) (Pantheinae)
Euromoia subpulchra (Alpheraky, 1897) (Pantheinae?)
Raphia frater Grote, 1864 (Pantheinae)
Moma alpium (Osbeck, 1778) (Pantheinae)
Trichosea ludifica (Linnaeus, 1758) (Pantheinae)
Camptoloma interiorata (Walker, 1865) (Camptolominae)
Maurilia iconica (Walker, 1858) (Chloephorinae)
Bena bicolorana (Fuessli, 1775) (Chloephorinae)
Pseudoips prasinana (Linnaeus, 1758) [= *fagana* (Fabricius, 1781)] (Chloephorinae)
Eligma narcissus (Cramer, 1776) (Sarrothripinae)
Nycteola revayana (Scopoli, 1772) (Sarrothripinae)
Risoba prominens Moore, 1881 (Sarrothripinae)
Meganola albula ([Denis & Schiffermüller], 1775) (Nolinae)
Meganola strigula ([Denis & Schiffermüller], 1775) (Nolinae)
Nola cucullatella (Linnaeus, 1758) (Nolinae)
Armada panaceorum (Ménétriés, 1849) (Eustrotiinae?)
Protodeltote pygarga (Hufnagel, 1766) (Eustrotiinae)
Abrostola triplasia (Linnaeus, 1758) [= *trigemina* (Werneburg, 1864)] (Plusiinae)
Autographa gamma (Linnaeus, 1758) (Plusiinae)
Diachrysia chrysitis (Linnaeus, 1758) (Plusiinae)
Acontia lucida (Hufnagel, 1766) (Acontiinae)
Emmelia trabealis (Scopoli, 1763) (Acontiinae)
Aedia funesta (Esper, 1786) (Aediinae)
Tyta luctuosa ([Denis & Schiffermüller], 1775) (Tytinae)
Aegle koekeritziana (Hübner, 1799) (Stiriinae)
Panemeria tenebrata (Scopoli, 1763) (Stiriinae?)
Acronicta leporina (Linnaeus, 1758) (Acronictinae)
Acronicta rumicis (Linnaeus, 1758) (Acronictinae)
Nacna malachitis (Oberthür, 1880) [= *splendens* (Moore, 1888)] (Acronictinae)
Cryphia algae (Fabricius, 1775) (Bryophilinae)
Sinocharis korbae Püngeler, 1912 (Sinocharinae)
Pseudeustrotia candidula ([Denis & Schiffermüller], 1775) (Pseudeustrotiinae)
Sarbanissa sp. (Agaristinae)
Heliothis virescens (Fabricius, 1777) (Heliothinae)
Agrotis exclamationis (Linnaeus, 1758) (Noctuinae)
Agrotis segetum ([Denis & Schiffermüller], 1775) (Noctuinae)
Noctua janthina ([Denis & Schiffermüller], 1775) (Noctuinae)
Cucullia umbratica (Linnaeus, 1758) (Cuculliinae)
Shargacucullia scrophulariae ([Denis & Schiffermüller], 1775) (Cuculliinae)
Hecatera bicolorata (Hufnagel, 1766) (Hadeninae)
Mythimna impura (Hübner, [1808]) (Hadeninae)
Agrochola helvola (Linnaeus, 1758) (Amphipyrinae)
Amphipyra pyramidea (Linnaeus, 1758 (Amphipyrinae)
Conistra erythrocephala ([Denis & Schiffermüller], 1775) (Amphipyrinae)
Cosmia trapezina (Linnaeus, 1758) (Amphipyrinae)
Hoplodrina ambigua ([Denis & Schiffermüller], 1775) (Amphipyrinae)
Mesoligia furuncula ([Denis & Schiffermüller], 1775) (Amphipyrinae)

Table 1 *Continued.*

- *Omphaloscelis lunosa* (Haworth, 1809) (Amphipyrinae)
- *Paradrina clavipalpis* (Scopoli, 1763) (Amphipyrinae)
- *Polymixis argillaceago* (Hübner, [1822]) (Amphipyrinae)

(d) For the survey of the relative spur length

- Geometridae
  - *Operophthera brumata* (Linnaeus, 1758)
- Hesperiidae
  - *Thymelicus sylvestris* (Poda, 1761)
- Pieridae
  - *Pieris napi* (Linnaeus, 1758)
- Lasiocampidae
  - *Eriogaster lanestris* (Linnaeus, 1758)
  - *Malacosoma castrense* (Linnaeus, 1758)
- Saturniidae
  - *Aglia tau* (Linnaeus, 1758)
  - *Saturnia pyri* ([Denis & Schiffermüller], 1775)
- Sphingidae
  - *Mimas tiliae* (Linnaeus, 1758)
  - *Deilephila porcellus* (Linnaeus, 1758)
- Oenosandridae
  - *Oenosandra boisduvalii* Newman, 1856
- Notodontidae
  - *Clostera anachoreta* ([Denis & Schiffermüller], 1775)
  - *Thaumatopoea solitaria* (Freyer, 1838)
- Lymantriidae
  - *Arctornis l-nigrum* (Müller, 1764)
  - *Dasychira dudgeoni* Swinhoe, 1907
  - *Lymantria dispar* (Linnaeus, 1758)
- Arctiidae
  - *Lithosia quadra* (Linnaeus, 1758)
  - *Euplagia quadripunctaria* (Poda, 1761)
  - *Phragmatobia fuliginosa* (Linnaeus, 1758)
  - *Spilosoma lubricipedum* (Linnaeus, 1758)
  - *Amata phegea* (Linnaeus, 1758)
- Aganaidae
  - *Agape chloropyga* (Walker, 1854)
  - *Asota caricae* (Fabricius, 1775)
  - *Asota heliconia* (Linnaeus, 1758)
  - *Digama hearseyana* Moore, [1860]
- Noctuidae
  - *Zanclognatha tarsipennalis* (Treitschke, 1835) (Herminiinae)
  - *Rivula sericealis* (Scopoli, 1763) (Rivulinae)
  - *Hypena crassalis* (Fabricius, 1787) (Hypeninae
  - *Eutelia adulatrix* (Hübner, [1813]) (Euteliinae)
  - *Stictoptera semialba* (Walker, 1864) (Stictopterinae)
  - *Catocala nupta* (Linnaeus, 1767) (Catocalinae)
  - *Euclidia mi* (Clerck, 1759) (Catocalinae)
  - *Lygephila pastinum* (Treitschke, 1826) (Catocalinae)
  - *Oxyodes scrobiculata* (Fabricius, 1775) (Catocalinae)
  - *Colocasia coryli* (Linnaeus, 1758) (Pantheinae)
  - *Diloba caeruleocephala* (Linnaeus, 1758) (Pantheinae)
  - *Euromoia subpulchra* (Alphéraky, 1897) (Pantheinae)
  - *Moma alpium* (Osbeck, 1778) (Pantheinae)
  - *Panthea coenobita* (Esper, 1785) (Pantheinae)
  - *Raphia frater* (Grote, 1864) (Pantheinae)
  - *Camptoloma interiorata* (Walker, 1865) (Camptolominae)
  - *Maurilia iconica* (Walker, [1858]) (Chloephorinae)
  - *Meganola albula* ([Denis & Schiffermüller], 1775) (Nolinae)
  - *Protodeltote pygarga* (Hufnagel, 1766) (Eustrotiinae)
  - *Xanthodes albago* (Fabricius, 1794) (Bagisarinae)

Table 1 *Continued.*

Abrostola tripartita (Hufnagel, 1766) [triplasia *sensu* auct.] (Plusiinae)
Autographa gamma (Linnaeus, 1758) (Plusiinae)
Acontia lucida (Hufnagel, 1766) (Acontiinae)
Aedia leucomelas (Linnaeus, 1758) (Aediinae)
Tyta luctuosa ([Denis & Schiffermüller], 1775) (Tytinae)
Aegle koekeritziana (Hübner, 1799) (Stiriinae)
Acronicta rumicis (Linnaeus, 1758) (Acronictinae)
Cryphia algae (Fabricius, 1775) (Bryophilinae)
Sarbanissa sp. (Agaristinae)
Helicoverpa armigera (Hübner, [1809]) (Heliothinae)
Heliothis virescens (Fabricius, 1777) (Heliothinae)
Pyrrhia umbra (Hufnagel, 1766) (Heliothinae)
Agrotis trux (Hübner, [1824]) (Noctuinae)
Noctua janthina ([Denis & Schiffermüller], 1775) (Noctuinae)
Ochropleura plecta (Linnaeus, 1761) (Noctuinae)
Peridroma saucia (Hübner, [1808]) (Noctuinae)
Xestia xanthographa ([Denis & Schiffermüller], 1775) (Noctuinae)
Shargacucullia scrophulariae ([Denis & Schiffermüller], 1775) (Cuculliinae)
Discestra trifolii (Hufnagel, 1766) (Hadeninae)
Amphipyra pyramidea (Linnaeus, 1758) (Amphipyrinae)
Omphaloscelis lunosa (Haworth, 1809) (Amphipyrinae)
Phlogophora meticulosa (Linnaeus, 1758) (Amphipyrinae)

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*Many male genitalia of dried specimens belonging to various species of Noctuoidea have been dissected. These species are not included in the present list as the exact muscle situation remains unknown to us.

was usually removed prior to the study of the tympanal region (e.g. in Figs 4–6, 8, 9).

3 *The membraneous conjunctiva*

The membraneous conjunctiva (Fig. 2, co) forms the enlarged posterior continuation of the metathoracic pleural membrane. Normally, this membrane is not involved in sound perception, but in some species it has been modified into an accessory tympanal membrane, e.g. in the plusiine *Autographa gamma* (Eggers, 1919).

4 *The tympanal bar*

The tympanal bar separates the conjunctiva from the adjacent tympanum. The structure of the tympanal bar is subject to modifications. Being entirely absent only in the Notodontidae and the Doidae (Richards, 1932), it takes the form of an elongate shallow groove in the remaining noctuoid families (Fig. 10). Because it is membraneous, the tympanal bar is relatively inconspicuous. Within the Noctuidae, however, it is generally sclerotized. The term ‘tympanal sclerite’ is proposed for a sclerotized tympanal bar. A third type of tympanal bar, the epaulette (ep) of Eggers (1919), is clearly restricted to a subset of the Noctuidae where the structure has been modified into an elevated ridge subdivided into a series of closely adjoining individual lobes. The number and form of these irregularly folded lobes are subject to considerable interspecific variation (e.g. compare Figs 11 and 12). An SEM of a typical noctuid epaulette is shown by Ghiradella (1971).

In some acronictine, amphipyrine and hadenine species the epaulette is a bizarre structure with acute projections (Fig. 13). This type of ctenoid epaulette has been assumed to serve as a physical barrier to prevent access of the moth ear mite *Myrmonyssus phalaenodectes* Treat, 1954 (Treat, 1957).

A structure similar to the true epaulette has been found in the catocaline noctuid *Oxyodes scrobiculata* and in the chloephorine *Bena bicolorana*. However, in contrast to the epaulette of higher Noctuidae the surface of this pseudepaulette is smooth.

Still another modification resembling the epaulette was observed in some Pantheinae. A narrow strip of the conjunctiva in front of the tympanum is irregularly folded, but not distinctively elevated.

5 *The tympanum*

The smooth transparent tympanum (= tympanal membrane) is usually hidden within the tympanal cavity, but may be readily seen in some species. In Notodontidae, the tympanum is almost always concealed within a deep invagination of the metepimeron, the epimeral concavity. The notodontid tympanum occupies a dorsal position within the epimeral concavity in a more or less horizontal, roof-like manner.

Internally the distal strand of an auditory chordotonal organ is attached to the delicate tympanal membrane, normally in its centre (Eggers, 1919; Ghiradella, 1971). Around the point of attachment of the chordotonal strand a milky white halo can be seen within the tympanal membrane.

More detailed examination of the tympanal region is possible

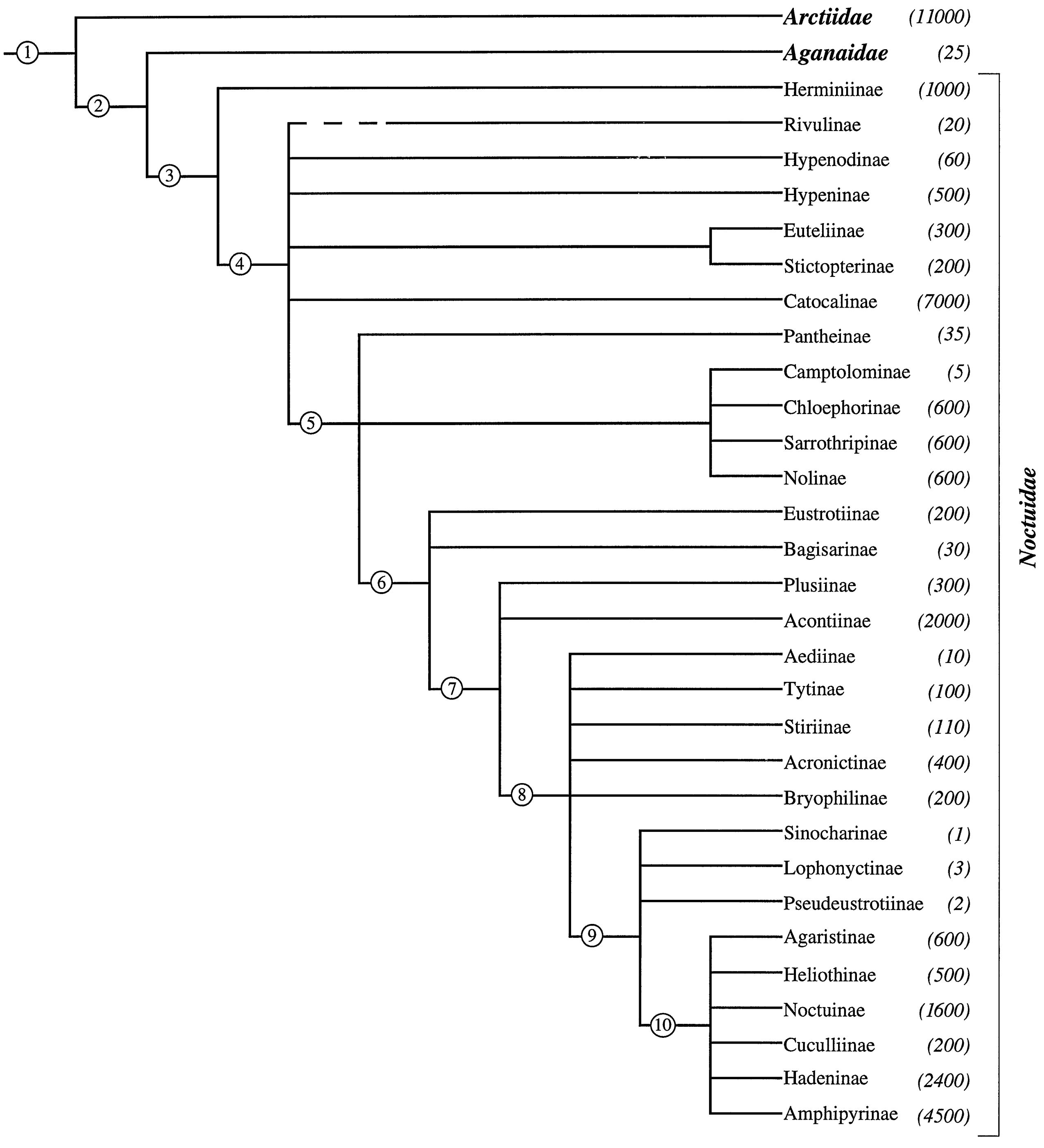


Fig. 1. Cladogram showing proposed phylogenetic relationships. For each taxon the approximate number of species has been added in parentheses.

after careful removal of the abdomen. The thorax can then be observed in posterior view (Fig. 14; see also Fig. 2 in Eggers, 1943). The conjunctiva, the tympanal sclerite (ts) and the tympanum (ty) are recognizable. In addition, a collar-like posterior prolongation (cp) that curves around the oval-shaped thoraco-abdominal opening (tao) becomes visible (please refer additionally to Fig. 20 for orientation). The prolongation is elaborated dorsally to form a small cavity above the thoraco-abdominal opening. The anterior wall of this cavity is tightly fused with the hind wall of the metathoracic scutellum for most of its length. The posterior boundary of the tergal cavity is demarcated by a thin tergal phragma (tp). This somewhat complex morphology may best be observed in a medio-sagittal section through the thoraco-abdominal region (Fig. 3).

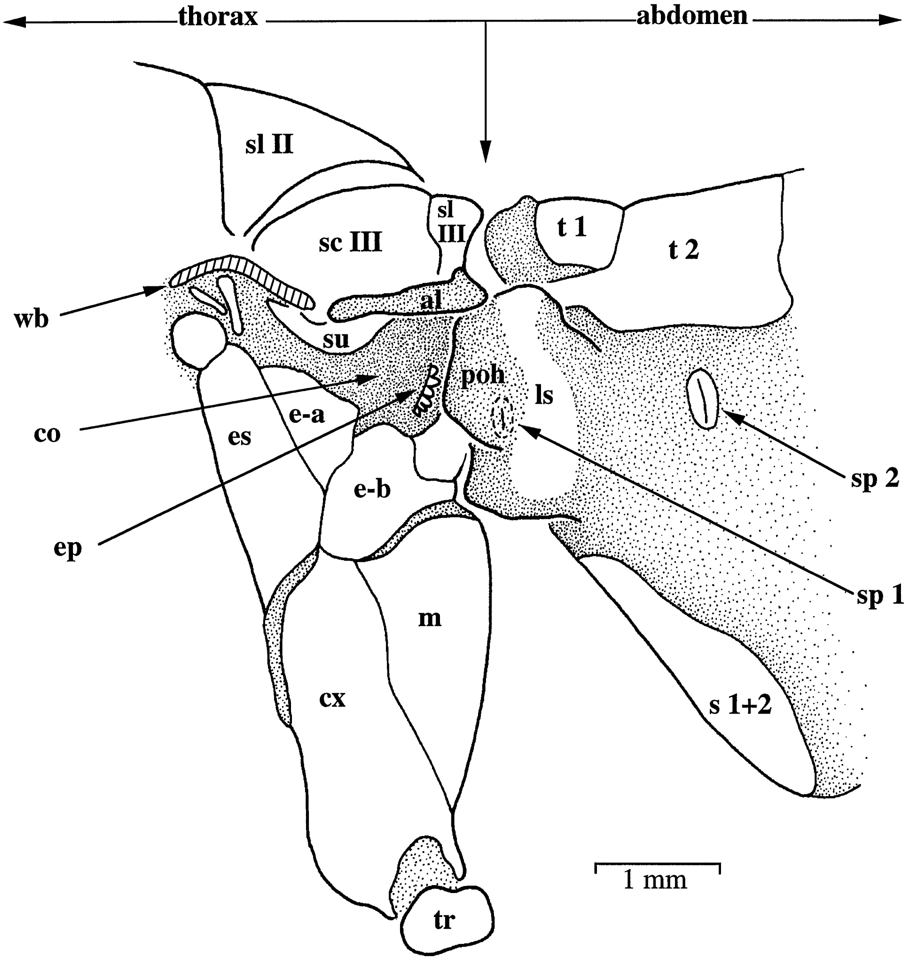


Fig. 2. Drawing of the tympanal region of *Agrotis exclamationiz* (Linnaeus) (Noctuidae, Noctuinae) in lateral view. Abbreviations used: al: alula; co: conjunctiva; cx: eucoxa; e (a, b): metepimeron (a, b); ep: epaulette; es: metepisternum; ls: lateral sclerotization of pleura A 1; m: metameron; poh: postspiracular hood; s 1 + 2: abdominal sternum 1 + 2; sc (II, III): scutum (mesonotal, metanotal); sl (II, III): scutellum (mesonotal, metanotal); sp. 1, 2: abdominal spiracles 1, 2; su: subalare; t 1, 2: abdominal terga 1, 2; tr: trochanter; wb: hindwing base.

Table 2. List of synapomorphies.

Clade number	Corresponding autapomorphies (no.)
1	Bulbus ejaculatorius elongate (1)
2	Uncus elongate (2)
3	Tibial spurs elongate (3a)
	Ventral cervical gland present (larva) (3b)
4	Postspiracular hood present (4)
5	Male genitalic muscle m.4 split (5)
6	Counter–tympanal cavities fused medially (6)
7	SV 2 setae on A 1 absent (larva) (7)
8	Tympanal bar of epaulette type (8)
9	A 2 brush organ present (9)
10	Corona present on valva (10)

However, the phragma remains incomplete leaving an (often ovoid) central opening to the tergal cavity (tpo). The lateral walls of the tergal cavity are invaginated medially to form a pair of deep cavities. Within the Noctuidae, the size and shape of these, commonly known as the counter-tympanal cavities, are subject to considerable variation. In some noctuid subfamilies (Herminiinae, Rivulinae, Hypenodinae, Hypeninae, Euteliinae, Stictopterinae, Catocalinae, Pantheinae, Camptolominae, Chloephorinae, Sarrothripinae, Nolinae) they are relatively small and are similar to those in the outgroup families (Figs 14, 16). In the remaining noctuid subfamilies they meet medially (Figs 17–20). Here, the counter-tympanal cavities are moderately sized (Bagisarinae, Plusiinae, Acontiinae, Stiriinae, Sinocharinae, Cuculliinae) (Fig. 17), or are extraordinarily large, thereby partly obliterating the thoraco-abdominal opening (Eustrotiinae, Aediinae, Tytinae, Acronictinae, Bryophilinae, Lophonyctinae, Pseudeustrotiinae, Agaristinae, Heliothinae, Noctuinae, Hadeninae, Amphipyrinae) (Figs 18–20).

Another pair of smooth membranes, the counter-tympana (= counter-tympanal membranes), are situated medio-dorsally to the tympanum proper in the metathoracic wall. However, the counter-tympanum (ct) normally remains almost entirely concealed behind the counter-tympanal cavities (Fig. 14).

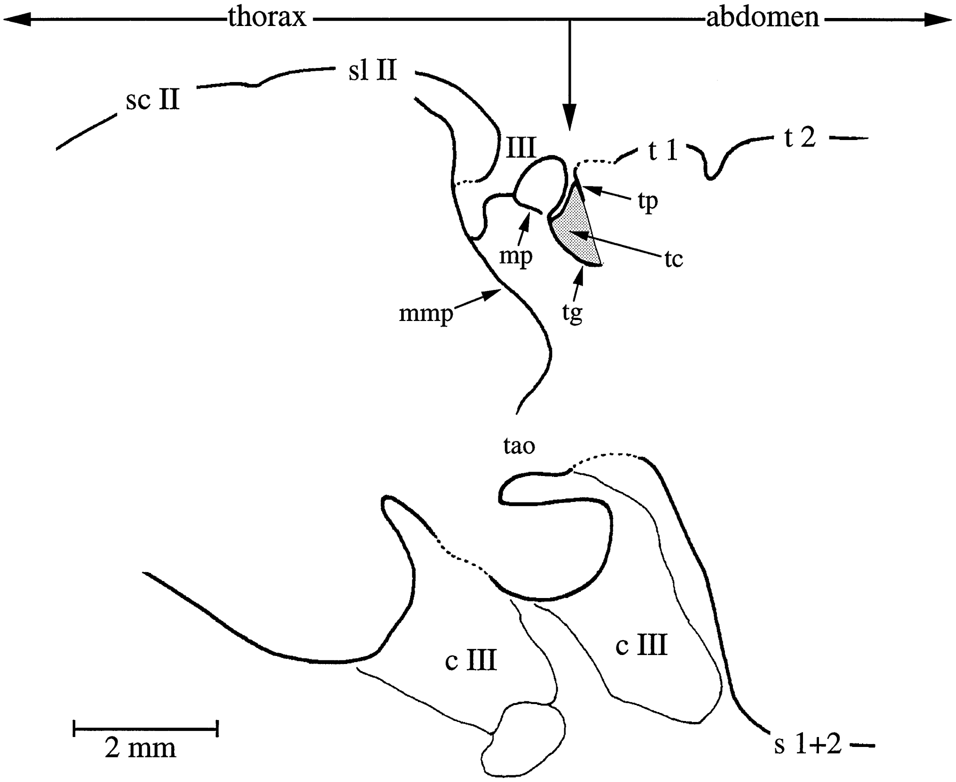


Fig. 3. Diagrammatic representation of a medio-sagittal section through the thoraco-abdominal region of an adult male of *Catocala fraxini* (Linnaeus). The various phragmata and the tergal cavity of the first abdominal segment are indicated. tp: tergal phragma of T 1; c (II, III): coxa II, III; tc: tergal cavity; mmp: meso-metanotal phragma; mp: metanotal phragma; tao: thoraco-abdominal opening; tg: tergal ground. Further abbreviations are given in Fig. 2.

The distribution of postspiracular hood and epaulette in the examined species is given in Table 3.

Unfortunately, different terms have been used by various authors for corresponding tympanal structures. Table 4 lists the synonymic terms of various authors, and may be useful for reference to the original papers on tympanal morphology.

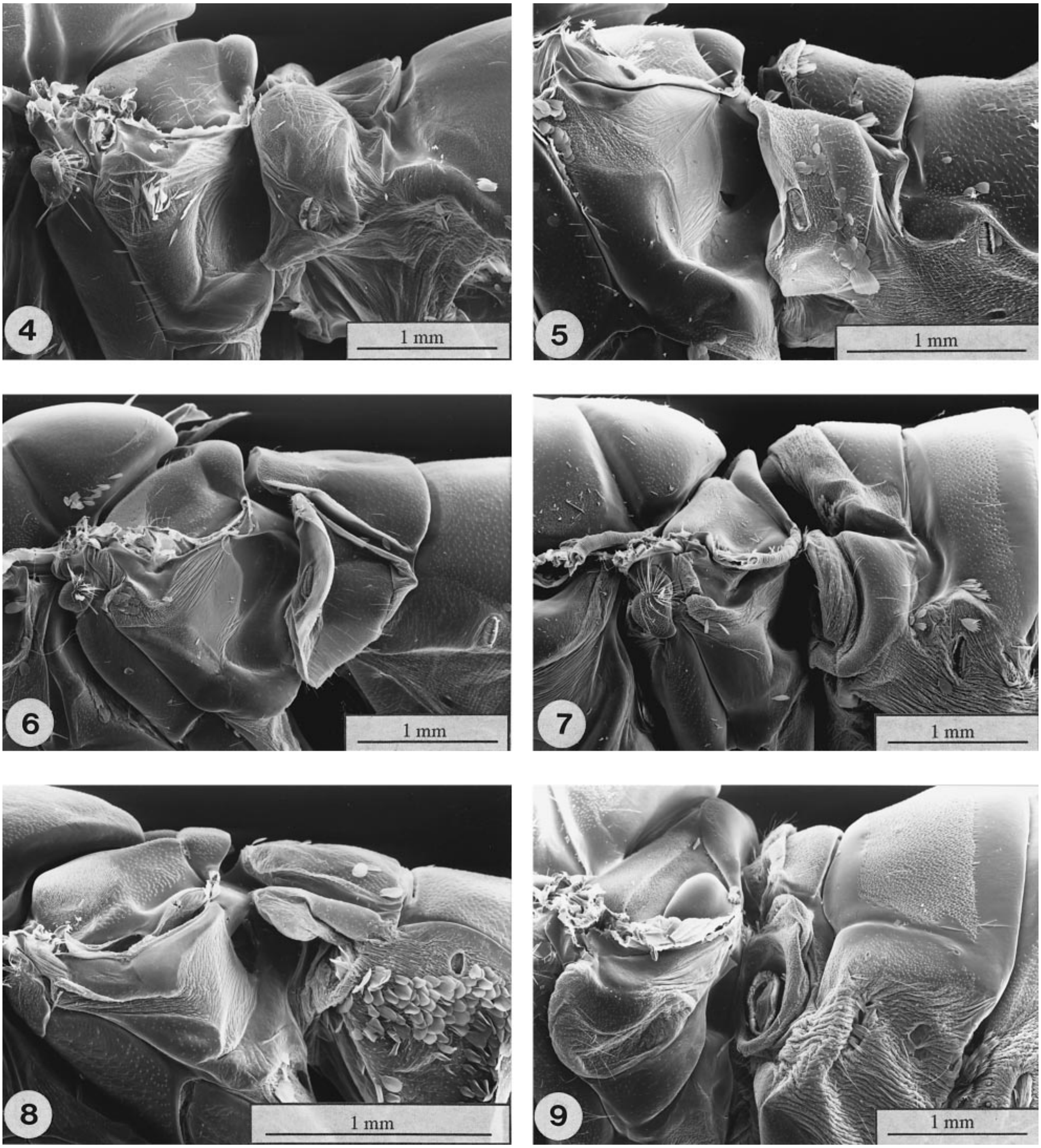
Phylogenetic considerations

Comparative morphological study of the noctuoid tympanal region revealed at least three potentially useful autapomorphies for reconstruction of phylogenetic relationships within the Noctuidae.

Autapomorphy 4. The presence of a prespiracular hood may be considered to represent the ancestral condition within the Noctuoidea. Lack of a prespiracular hood in the Doidae and Notodontidae is possibly due to loss (see Miller, 1991; for detailed discussion). Within the Noctuidae the prespiracular hood is found only in the Herminiinae. Consequently, the presence of a postspiracular hood is considered to represent a convincing autapomorphy for the Noctuidae excluding the Herminiinae (Kitching, 1984). The postspiracular hood is retained in most noctuid subfamilies and genera. However, it has been reduced to a dorsal remnant in almost all members of the Camptolominae–Chloephorinae–Sarrothripinae–Nolinae subfamily group. A convergent reduction has probably occurred in at least some heliothine species. For example, in *Heliothis virescens* no trace of a postspiracular hood has been found.

Autapomorphy 6. The counter-tympanal cavities of the outgroup families and of the basal noctuid subfamilies are usually small to medium-sized, and widely separated from each other. In contrast, there is a general tendency towards enlargement of these structures within the higher Noctuidae. However, differences in size proved to be continuous rather than discrete. Consequently, we face difficulties in assigning a clear-cut autapomorphy.

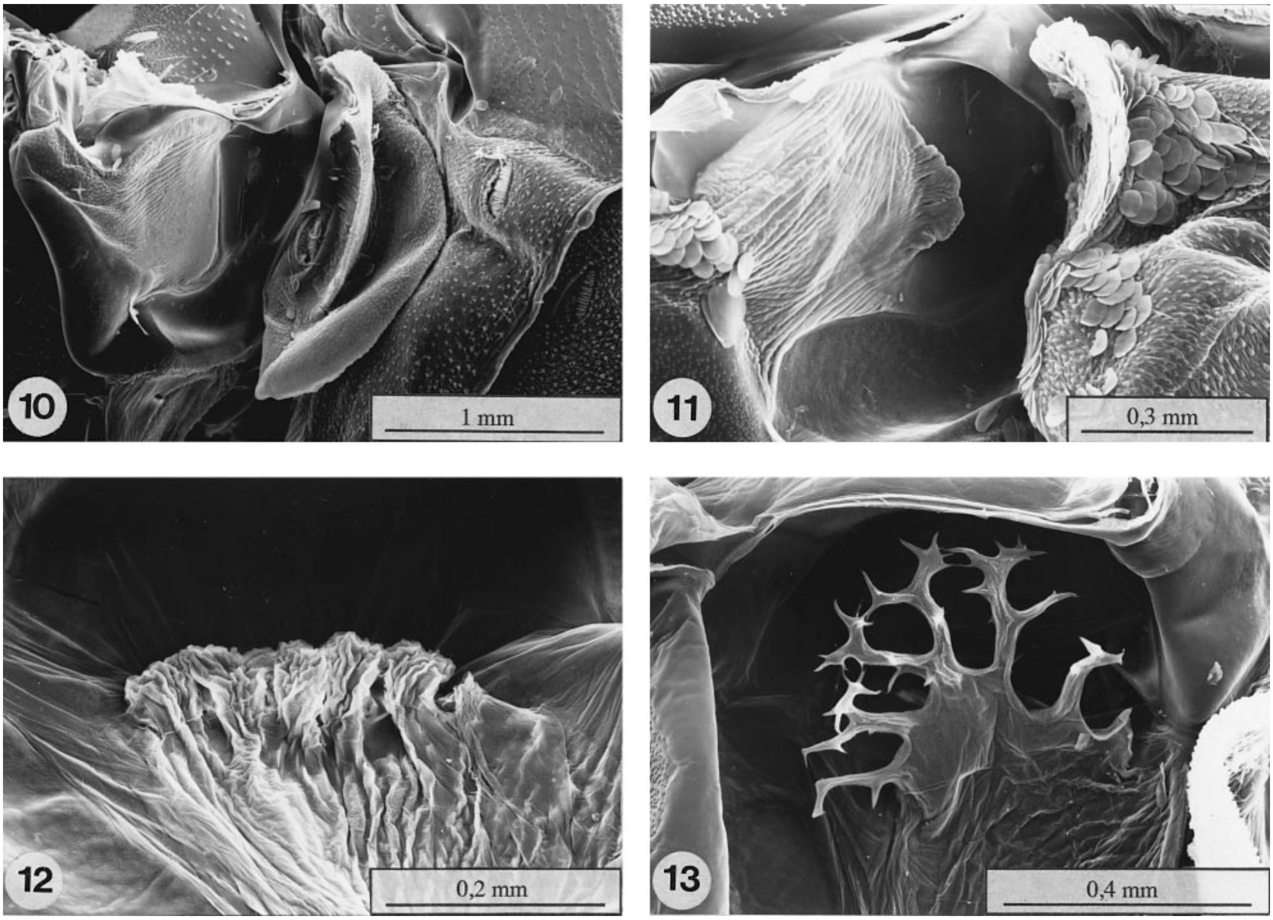
Minet (1986) assumed the enlarged counter-tympanal cavity an autapomorphy of the Noctuidae + Aganaidae. However, we felt that the most appropriate solution was to recognize a division above the camptolomine–chloephorine–sarrothripine–noline clade (Fig. 1). Beyond this clade, the counter-tympanal cavities are not only larger, but are also intimately fused medially. Rather small counter-tympanal cavities which are fused medially exist in the subfamilies Bagisarinae, Plusiinae, Acontiinae, Stiriinae, Sinocharinae and Cuculliinae. Enlargement of the counter-tympanal cavities evolved independently in part of the Catocalinae (e.g. in *Oxyodes scrobiculata*) and also within the Scranciini of the notodontid subfamily Dudusinae (Miller, 1991).



Figs 4–9. Noctuoid tympanal regions in lateral aspects (SEM). Orientations are as in Figs 2 & 3. Fig. 4. *Lymantria dispar* (Linnaeus), Lymantriidae. Fig. 5. *Nodaria tristis* (Butler), Noctuidae, Herminiinae. Fig. 6. *Anoratha costalis* Moore, Noctuidae, Hypeninae. Fig. 7. *Diloba caeruleocephala* (Linnaeus), Noctuidae, Pantheinae. Fig. 8. *Meganola strigula* ([Denis & Schiffermüller)], Noctuidae, Nolinae. Fig. 9. *Pheosia gnoma* (Fabricius), Notodontidae.

Autapomorphy 8. The tympanal bar is a shallow membraneous groove in the plesiomorphic state. Varying degrees of sclerotization, sometimes quite indistinct, can be observed around the tympanal groove in basal lineages of the Noctuidae. The epaulette type of tympanal bar may be considered an apomorphy uniting the subfamilies in clade 8 (Fig. 1).

Usually it is quite easy to decide whether an epaulette is present or not, but doubts concerning the homology of tympanal bar modifications may arise. For example the epaulette of the



Figs 10–13. Tympanal bars in the Noctuidae (SEM). Fig. 10. Tympanal sclerite of *Penicillaria simplex* (Walker), Euteliinae. Fig. 11. Epaulette of *Mesoligia furuncula* ([Denis & Schiffermüller)], Amphipyrinae. Fig. 12. Epaulette of *Heliothis virescens* (Fabricius), Heliothinae. Fig. 13. Specialized epaulette of *Nacna malachitis* (Oberthür), Acronictinae.

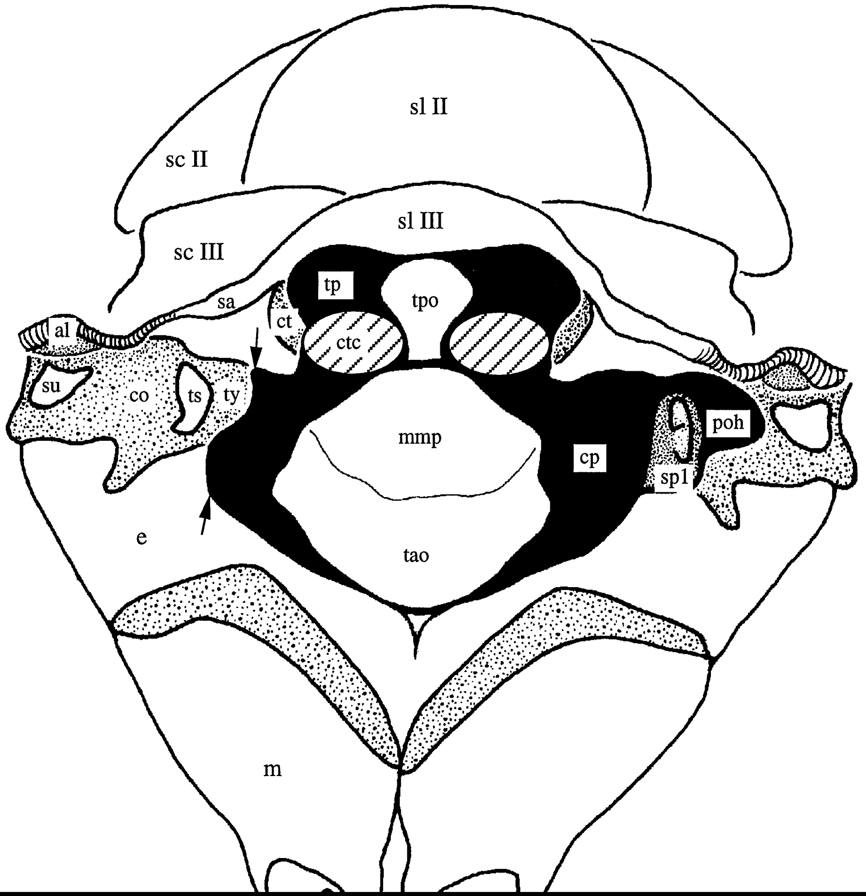
cuculliine *Shargacucullia scrophulariae* is extremely low and not at all ridge-like (Eggers, 1919), but the corrugated surface structure bears resemblance to the typical epaulette. The ctenoid modification of the tympanal bar present in a few members of the Acronictinae, Hadeninae and Amphipyrinae is still another example of a derived type of epaulette (Treat, 1957).

As already noted above, a smooth pseudepaulette that probably evolved independently from the higher noctuid epaulette is present in the catocaline noctuid *Oxyodes scrobiculata*. Most interestingly, in this same species a corresponding enlargement of the counter-tympanal cavities, again probably representing independent evolution, has occurred. The correlated occurrence of these structures (i.e. epaulette and enlarged counter-tympanal cavities), observed within the Noctuidae, might indicate functional inter-relationship.

Character system 2: the male genitalia

General description

The structure of the male genitalia and associated muscles (m.1–8) of the superfamily Noctuoidea are depicted diagrammatically in Fig. 21. The genital segment (i.e. abdominal segment IX) takes the form of a narrow ring that is divided into a dorsal and a ventral semicircle. The dorsal sclerite is termed the tegumen, the ventral one the vinculum (Klots, 1970). Medioventrally the vinculum is prolonged into a hollow apodeme of variable size, the saccus. The movable valvae, a large pair of hollow appendages, are attached to the lateral margins of the vinculum. The supposed remnant of tergum X, the uncus, is dorso-posteriorly connected with the tegumen. The tube-like phallus protrudes backwards between the arms of the vinculum. Normally, the phallus is strongly sclerotized for most of its length. Dorso-anteriorly, the phallus bears a membraneous appendage, the bulbus ejaculatorius (Fig. 22). The bulbus ejaculatorius has been described repeatedly (e.g. Oiticica, 1946; Callahan, 1960; Mitter, 1988), but has not been widely used as a morphological character. In fact it is almost universally mistaken for the ductus ejaculatorius. The bulbus, horseshoe-shaped in cross-section, is attached to the phallus either anteriorly, antero-dorsally, or dorsally. It consists of two intimately approximated contiguous layers (Oiticica, 1946). Apically, the bulbus regularly forms some kind of a cap or hood. The structure of the bulbus ejaculatorius is subject to the same degree of variation as any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