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The classification of the Sarrothripinae, Chloephorinae, Camptolominae and Nolinae as the Nolidae (Lepidoptera: Noctuoidea).

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Abstract

The morphology of adults and early stages of a wide selection of genera in the **Nolinae**, **Sarrothripinae**, **Chloephorine** and **Camptolominae** is reviewed in order to answer three questions: whether the group as a whole is monophyletic; its relationship with other groups within the Noctuoidea; resolution of classificatory structure within the group. The second and third questions proceed from a positive answer to the first, which is supported by characters of the cocoon, pupa, adult thorax and male retinaculum and genitalia. Particular note is made of the wide occurrences of tymbal organs in males within the group, mostly at the base of the abdomen, but also in the hindwing and genitalia. Within this new, monophyletic concept of the **Nolidae**, subfamily and tribal groupings are identified. Some groups traditionally included in the complex are examined and several excluded, with particular reference to a complex of genera that are better placed in the Bagisarinae. Placement of the genus *Eligma* HÜBNER [1819] 1816 is still not resolved and requires further study, as does the relationship of the Nolidae to other noctuoid families. Current hypotheses group them with the Arctiidae and Lymantriidae, or with the Noctuidae.

Zusammenfassung

Die Morphologie einer repräsentativen Zahl von Gattungen der Unterfamilien **Nolinae**, **Sarrothripinae**, **Chloephorinae** und **Camptolominae** wird untersucht um folgende Fragestellungen zu beantworten: 1. Sind die genannten Unterfamilien als monophyletische Einheiten zu betrachten ? 2. Wie ist die Verwandtschaft zu anderen Gruppen der Noctuoidea ? 3. Welche für die Klassifikation relevanten Strukturen innerhalb der Gruppe können erkannt werden ? Aus der Beantwortung der zweiten und dritten Frage ergibt sich die positive Beantwortung der ersten, basierend vor allem auf Merkmalen der Puppe und des Kokons, des adulten Thorax und des männlichen Retinaculums, sowie der Genitalarmaturen. Die weite Verbreitung von Tymbal Organen (Abdomenbasis, Hinterflügel, Genitalia) innerhalb der Gruppe wird besonders herausgearbeitet. Das neue monophyletische Konzept der **Familie Nolidae** wird ergänzt durch eine entsprechende Unterteilung in Unterfamilien und Triben. Einige Gruppen werden exkludiert und besonders die Überführung in die Bagisarinae näher erläutert. Die Gattung *Eligma* HÜBNER [1819] 1816 kann derzeit nicht befriedigend eingeordnet werden und bedarf ebenso einer weiterführenderen Untersuchung wie die Klärung der verwandtschaftlichen Stellung der Nolidae innerhalb der Noctuoidea. Eine Hypothese stellt die Nolidae in die Nähe der Arctiidae und Lymantriidae, eine andere in die unmittelbare Nähe der Noctuidae.

Key words: Noctuidae; Noctuoidea; Nolidae; Sarrothripinae; Chloephorinae; Camptolominae; Bagisarinae; *Eligma*; phylogeny; classification; morphology; tymbal organs; early stages.

Introduction

This paper is the culmination of a long gestatory process that commenced at the beginning of the decade and has benefitted from periodic interaction with several colleagues, particularly I.J. Kitching, S.E. Miller and J.E. Rawlins. Some observations on the Nolinae s. str. have already been published (HOLLOWAY & MILLER, 1995), and an early draft of this paper has been cited as HOLLOWAY (in prep) in the Noctuoidea chapter for the „Handbuch der Zoologie“ volumes on the Lepidoptera (KITCHING & RAWLINS, 1998). Some of the observations made in that earlier draft and here have been made independently by SPEIDEL, FÄNGER & NAUMANN (1996), who have also contributed additional findings that help resolve the questions addressed here.

Due to the significant number of cited taxa genera and species normally are cited without the year of description.

The principal question is whether the **Nolinae**, **Sarrothripinae**, **Chloephorinae** and **Camptolominae** form a **monophyletic group**. Kitching, in his review of the higher classification of the Noctuidae (KITCHING, 1984) grouped together the Sarrothripinae, Chloephorinae and Nolinae because they are "united by the common possession of a boat-shaped cocoon with a vertical exit slit". This character was reiterated by KITCHING & RAWLINS (1998) and by SPEIDEL et al. (1996), who noted three other characters that are shared by the group: in the male genitalic musculature; in the form of the transtilla; and in the elongation of the male retinaculum. These will be reviewed further here.

A second question that follows from affirmation of monophyly concerns the relationships of the group within the Noctuoidea. Here there is some disagreement between SPEIDEL et al. (1996), who placed the group within the Noctuidae in a sister-relationship to the higher (mainly trifine) subfamilies, with most of the other quadrifine groups branching off earlier in the basal part of their phylogeny, and KITCHING & RAWLINS (1998), who placed the group as a family distinct from their concept of the Noctuidae. Their Noctuidae included both quadrifine and trifine groups, and the Aganainae, treated as a good family by SPEIDEL et al. KITCHING & RAWLINS grouped the Nolidae with the Arctiidae, Lymantriidae and Pantheidae. Treatment of the Pantheidae as a distinct family is another point of disagreement with SPEIDEL et al. (1996) who placed the group within the Noctuidae as Pantheinae in an unresolved trichotomy with the nolid complex and the 'higher' noctuids. KITCHING & RAWLINS suggested the pantheids were probably paraphyletic, but might, in part, be sister-group to the Lymantriidae.

Resolution of these questions is relevant to the title and scope of this new Journal: if the classification of KITCHING & RAWLINS is proved to be correct, this may be the first and last paper on the nolid complex to appear in it.

A third question concerns classificatory structure within the group if monophyly is supported. MELL (1943) had already suggested a relationship between the Chloephorinae and Sarrothripinae. He erected a number of family-group names at the tribal level within this broad concept of the Sarrothripinae. The validity of his tribal concepts needs to be assessed, as does the position relative to the main grouping of such taxa as his Eligmini.

Most of this essay will be concerned with the first and third questions. The status of the group as a whole within the Noctuoidea will be reviewed in a final section.

The majority of sarrothripines, chloephorines and nolines are found in the Old World tropics, and the camptolomines are Oriental only (HOLLOWAY 1988). Hence this study will concentrate on type species of exemplar genera from the Oriental tropical centre of diversity of the groups, though genera from Africa and the New World have also been examined. The Nolinae have already been considered in some detail by HOLLOWAY & MILLER (1995). Details of the genera and their type species may be found in NYE (1975) and POOLE (1989). The latter work presents an accurate portrayal of the state of noctuid classification at the time of writing, including as new synonyms and combinations unpublished curatorial decisions in The Natural History Museum, London (= BMNH) collection and elsewhere. Any criticism of Poole's catalogue is therefore directed at the classification rather than the author! An account of the Sumatran Chloephorinae fauna as in the old classification has recently been published by KOBES (1997).

Not all the taxa studied here have been reared, so information on early stage morphology is less comprehensive than that for adult morphology. Therefore, though the cocoon character, and indeed the means of cocoon construction, provides a strong apomorphic feature for the complex, supportive features from the adult stage will be essential to enable membership of the group as a whole to be assessed.

Therefore the first section reviews charactistics of adults, pupae (including the cocoon) and larvae. Conclusions on the monophyly of the group are then presented, followed by a commentary on the family-group names available and their priority. A tentative system of classification within the group is suggested, and the status of a number of groups that have wholly or partially been associated in the past is assessed, before a final commentary on the position of the group within the Noctuoidea.

Characters of the adult

Head

No definitive features were located on the head, though presence of scaling on the lower part of the clypeofrons is used by KITCHING & RAWLINS (1998) to distinguish the group from other noctuoids with an elongate male retinaculum. Ocelli are present in all taxa except the Nolinae (including the *Barasa* Walker group of genera).

The labial palps have the third segment extremely variable in length, but usually much shorter than the second segment. It is long only in *Iscadia* WALKER, *Ptisciana* WALKER, *Labanda* WALKER and *Eligma* HÜBNER, but moderate and slender in some other taxa such as the *Westermannia* group of genera (p. 267) and *Lasiolopha* TURNER.

Male antennae are generally filiform, ciliate, exceptions being in the Nolinae (excluding *Barasa* and allies, and some *Nola* LEACH) and the *Gelastocera* BUTLER group of genera (p. 267) where they are bipectinate.

The tongue is normal in the majority of genera, but is small, vestigial or absent (HAMPSON 1912) in *Titulcia* WALKER, *Chandica* MOORE, *Cossedia* WALKER, *Gabala* WALKER, and most *Iscadia* taxa (normal in typical *Gadirtha* WALKER). It is vestigial in *Eligma*.

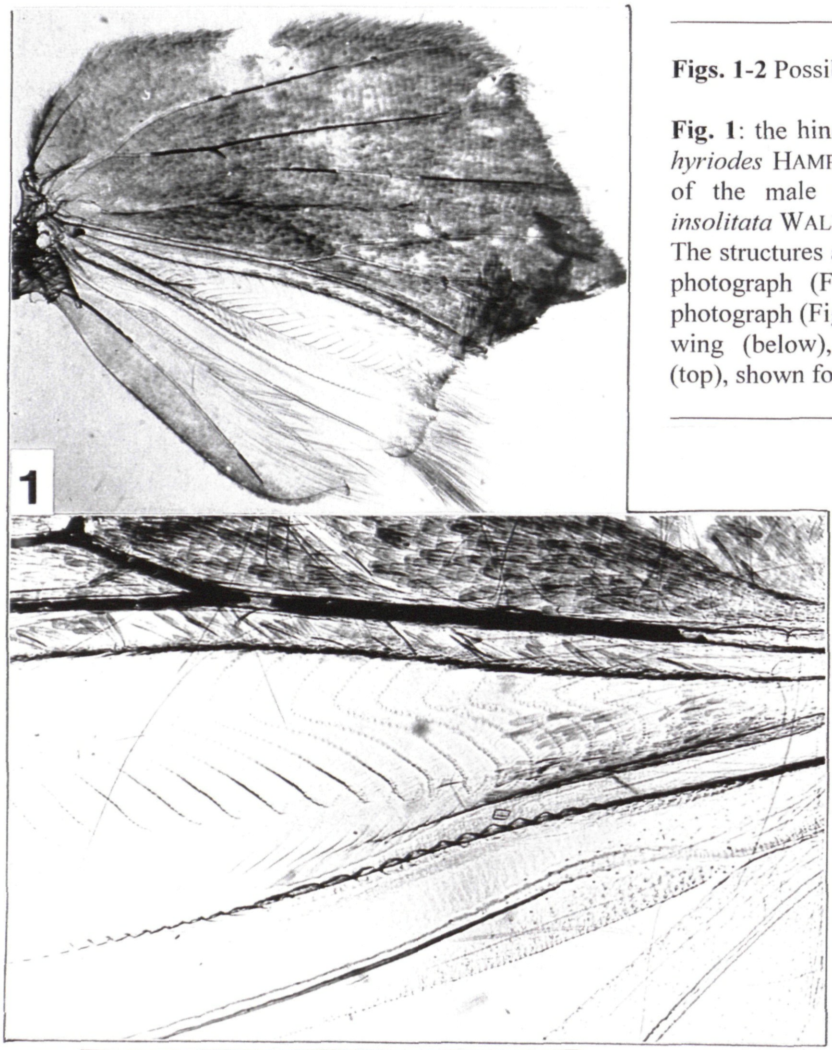
Thorax

A feature noted in the course of setting numerous Sarrothripinae and Chloephorinae from relaxed dried material was the facility with which patagia and sometimes tegulae became detached when the thorax was compressed with "wings up/wings down" to stretch or fracture the wing muscles and render the insect more malleable. This has not been observed in other noctuid groups. The morphological basis of this feature is unclear, and a full survey of taxa has not been undertaken for this study.

Characters of the legs have not been investigated, but SPEIDEL et al. (1996) noted that the tibial spurs of the group were relatively long, a feature that they regarded as one of two apomorphies for their concept of the Noctuidae.

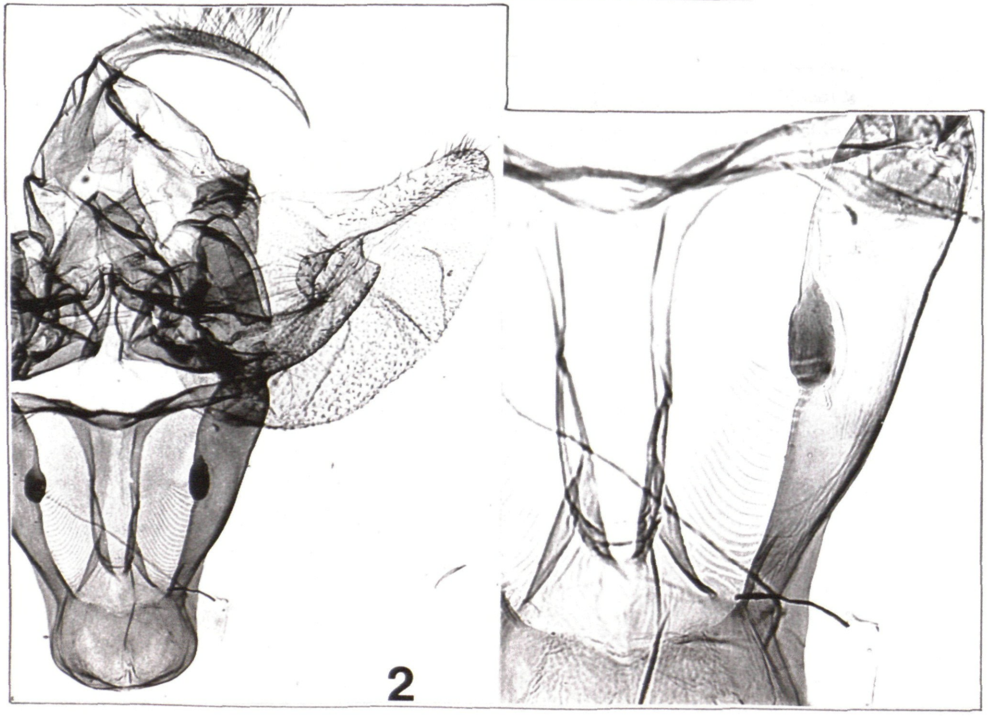
A feature often associated with this complex is an elongate, bar-shaped retinaculum on the male forewing. This is seen in most taxa of the complex. The retinaculum (though not the frenulum) is absent in *Bena* BILLBERG, *Tyana* WALKER, *Parasinna* KOBES, *Gabala* and *Earias* HÜBNER. It is moderate in *Chloriola* HAMPSON and *Cacyparis* WALKER, and short in *Calathusa* WALKER, *Macrobarasa* HAMPSON, and *Xanthodes* GUENÉE. The last three taxa will be discussed further below as dubious members of the group. SPEIDEL et al. (1996) also observed that this feature was not universal to the group. MELL (1943) included *Cymatophoropsis* HAMPSON in his tribe Cymatophoropsini within his concept of the Sarrothripinae: the retinaculum is not bar-shaped, and the genus is currently placed (POOLE 1989) in the Ophiderinae. The genus *Lasiolopha* is characterised by an extremely large (both broad and deep) retinaculum that must be regarded as an extreme modification.

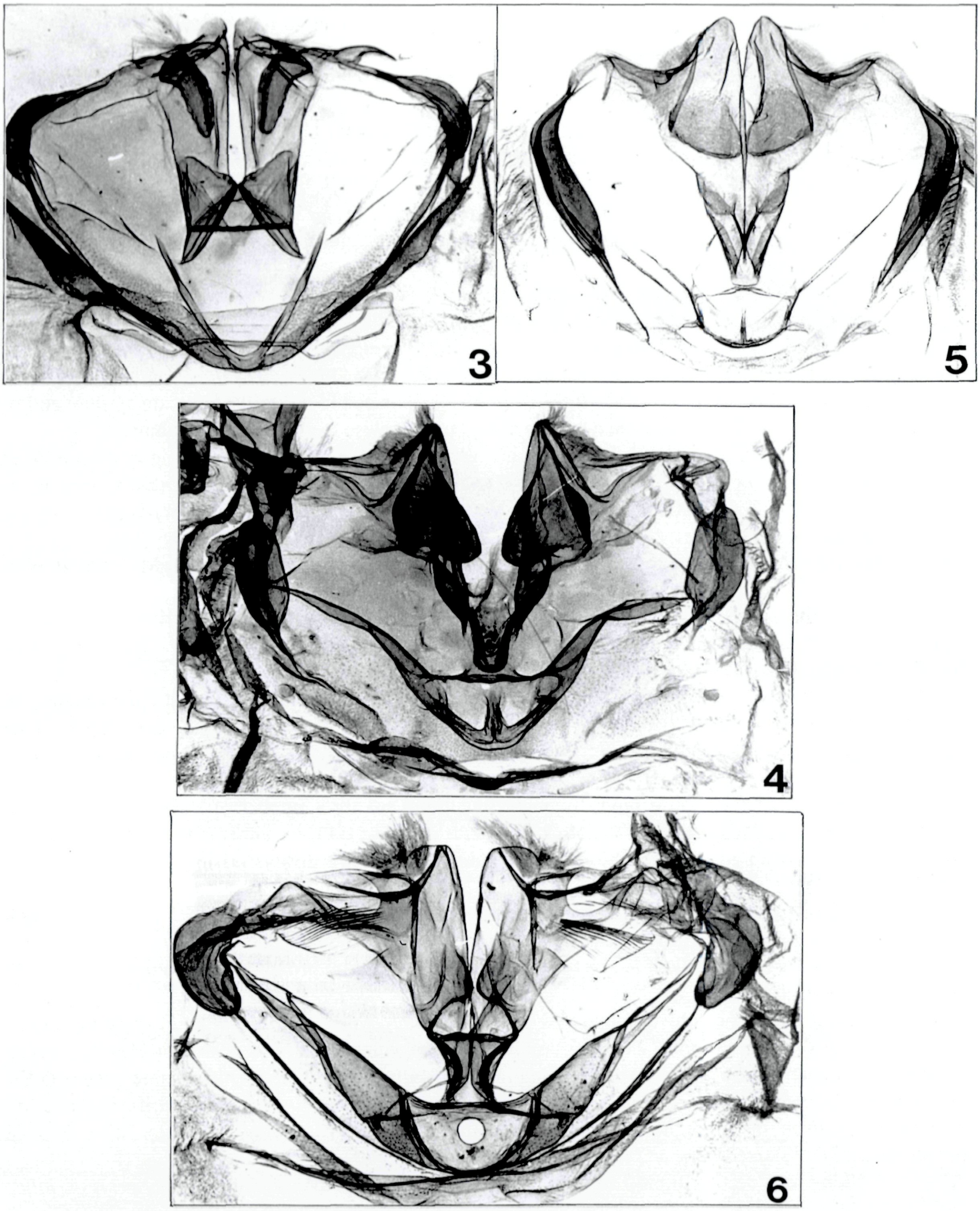
The forewings in many taxa have raised scales on the upper surface. This feature is seen particularly in the Nolinae and in many genera of the Sarrothripinae (as recognised by POOLE (1989)). It is widespread but not ubiquitous in the *Nycteola* HÜBNER group of genera (p. 262), in *Iscadia* and allies and in *Blenina* WALKER.



Figs. 1-2 Possible tymbal organs on:

Fig. 1: the hindwing of male *Cossedia hyriodes* HAMPSON.- **Fig. 2**: the saccus of the male genitalia of *Cacyparis insolitata* WALKER.
The structures are enlarged in the lower photograph (Fig. 1) or in the right photograph (Fig. 2), with that of the left wing (below), rather than the right (top), shown for *C. hyriodes*.





Figs. 3-6 Tymbal organs on the basal abdominal sternites of male Chloephorini:

Fig. 3: *Tyana callichlora* WALKER.- **Fig. 4**: *Pseudoips fagana* FABRICIUS.- **Fig. 5**: *Tympanistes pallida* MOORE.- **Fig. 6**: *Clethrophora distincta* LEECH.

The forewing venation shows modification on a frequent noctuid pattern where R1 arises direct from the cell, and R2, R3+R4 and R5 form an areole and arise more or less symmetrically from it. Many taxa show this typical pattern, such as *Characoma* HAMPSON and *Garella* WALKER in the *Nycteola* complex.

The *Nycteola* complex also exhibits the two most frequently observed variants from this theme. In *Apothripa* HAMPSON, *Nanaguna* WALKER and *Etanna* WALKER, the areole is very small or absent, and the venation is of the formula (HOLLOWAY 1987, 1988) R1,(R2((R3,R4)R5)), with R5 arising more distally than R2 from Rs. R2 sometimes arises from the small areole. Other genera with this type of venation are *Selepa* MOORE, *Calathusa*, *Gyrtothripa* HAMPSON, and most species currently placed in *Giaura* WALKER (POOLE 1989).

Typical *Giaura*, *Symitha* WALKER, *Dilophothripa* HAMPSON and *Chloethripa* HAMPSON represent the opposite extreme condition with R5 'split back' to arise directly from the cell: R1,(R2(R3,R4)),R5. This condition is also seen in *Plagiograpta* HAMPSON, *Negeta* WALKER, *Tortriciforma* HAMPSON, *Parasinna*, *Pseudoips* HÜBNER, *Bena* BILLBERG, *Erizada* WALKER, *Siglophora* BUTLER, *Gabala* and *Ariolica* WALKER. In *Titulcia* R2-4 is reduced to a distally bifurcate system, and in *Chandica* and *Cossedia* R2 arises from a small areole, but otherwise the venation is as above.

An intermediate condition has R5 arising from Rs but more basally than R2, either from a small areole (*Tathothripa* HAMPSON, *Tympanistes* MOORE, *Gelastocera* and *Beara* WALKER (areole is elongate), *Chloriola*, *Sinna* WALKER and *Maceda* WALKER) or directly from Rs (*Chloroplaga* HAMPSON, *Tyana*, *Hylophilodes* HAMPSON, *Clethrophora* HAMPSON, and *Camptoloma* FELDER).

The *Carea* complex of genera (p. 265) has typical areolate venation, but with M1 connate with the areole or arising basally from it.

More unusual venation is seen in *Arachnognatha* HAMPSON, where R2-5 all rise independently from the areole, *Earias*, with R1,R2((R3,R4)R5), and *Erizada semifervens* WALKER, with R1,(R2(R3,R4)),(R5,M1). *Xanthodes* is also atypical as discussed on p. 270.

In the Nolinae, the *Barasa* group has the typical areolate condition but the rest have venation as in *Chloroplaga* above: R1,((R2(R3,R4))R5). Amongst noline taxa with trifine hindwing venation (see below and HOLLOWAY & MILLER (1995)) there is a trend for the radial branches from Rs to be more distal and reduced in number.

The hindwing venation is typically quadrifine, but there are a number of instances of reduction to a trifine condition. This occurs in the Nolinae where M3 and CuA1 are either stalked (plesiomorphic condition) or totally fused (apomorphic, trifine condition), with M2 always arising from the cell well anterior from its posterior angle.

In the rest of the group it is often less clear whether the trifine condition has arisen through fusion of veins or loss of a vein.

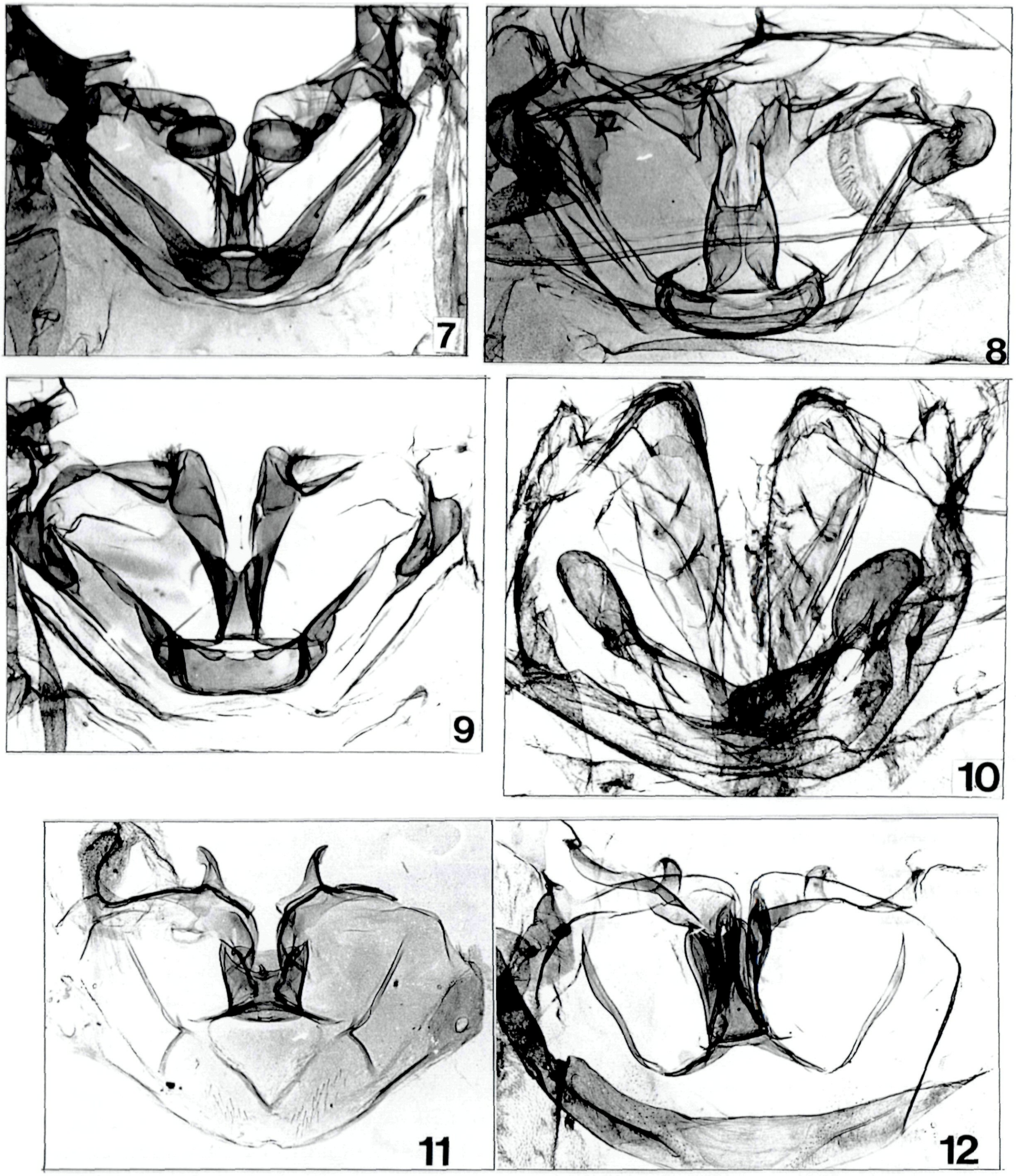
M3 and CuA1 are stalked in most genera of the Chloephorini group (p. 265), otherwise M2, M3 and CuA1 are closely connate.

Tyana is trifine, possibly through loss of M2. *Camptoloma* is quadrifine with all veins separate.

In the *Nycteola* complex there is a stalked pair of veins in all genera except *Symitha*, which exhibits a trifine condition with all veins arising independently from the cell. Other trifine genera in the group are *Characoma*, *Garella*, *Etanna*, *Pardasena* Walker, and *Dilophothripa*. In quadrifine genera M2 is connate or even on a slight stalk with M3+CuA1, so the trifine condition may arise through lengthening of this stalked zone and fusion of M3 and CuA1.

Stalking also occurs in most of the current (POOLE 1989) Chloephorinae, with *Earias*, *Ariolica* and *Titulcia* trifine and the rest quadrifine. Stalking of M3 and CuA1 is weak in most of the Careini, with them being merely connate in some instances within a genus. They are connate in *Sinna*, *Orthocraspis* HAMPSON, *Paracrama* MOORE, *Plectothripa* HAMPSON, *Chloriola* and the *Westermannia* group, and connate to weakly stalked in *Asinduma* WALKER.

More typical quadrifine venation, though sometimes with M3 and CuA1 connate, is seen in *Arachnognatha*, *Cacyparis*, *Selepa*, *Iscadia*, *Lamprothripa*, *Calathusa*, *Labanda*, *Tathothripa (*slightly stalked), *Blenina*, *Risoba* MOORE, *Macrobarasa* and *Beana* WALKER. In *Ptisciana* and *Timorodes* MEYRICK, M2 and M3 are connate at the posterior angle of the cell, rather than M3 and CuA1, and in *Phaeothripa* HAMPSON they are connate or stalked.



Figs. 7-12 Tymbal organs on the basal abdominal sternites of male Chloephorini (Figs. 7-9), Camptolomini (Fig. 10) and Ariolicini (Figs. 11-12):

Fig. 7: *Tortriciforma viridipuncta* HAMPSON.- **Fig. 8**: *Chloroplaga nygmia* SWINHOE.- **Fig. 9**: *Hylophilodes orientalis* HAMPSON.- **Fig. 10**: *Camptoloma mirabilis* ROEPKE.- **Fig. 11**: *Ariolica lineolata* WALKER.- **Fig. 12**: *Ariolica superba* MOORE.

KOBES (1988: 88, fig. 26) described an unusual modification to the hindwing in *Gabala* that he called Tarmann's organ. It appears to be unique to the genus.

Tympanal organs

RICHARDS (1932), reviewed by KITCHING (1984), made detailed studies of noctuid tympanal structures and concluded that the Sarrothripinae and Chloephorinae were very similar and had affinities with the Acontiinae. He also associated the trifine subfamilies with the Acontiinae, together with the Nolinae. This arrangement is similar to the system of SPEIDEL et al. (1996). The counter-tympanal hood is only strong dorsally. Ventral to it is a groove running obliquely from the first abdominal spiracle ventrad, caudad. SPEIDEL et al. (1996) noted the dorsal counter-tympanal hood is not present in *Camptoloma* but does occur in *Eligma*. They interpreted this dorsal condition as a reduction from the typical noctuid postspiracular condition.

POOLE (1995) noted that nolines have an individual and almost enclosed pocket IV in the internal tympanic structure, a derived feature otherwise seen in the Plusiinae and trifine noctuid groups. The sarrothripine and chloephorine assemblages do not show this feature.

Sound-producing organs

Sound-producing organs occur widely in male adults of the group, mostly associated with the basal abdominal sclerites. Sound production is also a widespread feature of the pupal stage (see below). There are two exceptions to this: *Cossedia* has an elongate, corrugate, scaleless zone associated with the fold representing vein CuP on the hindwing (**Fig 1**); *Cacyparis* has an enlarged saccus to the genitalia with what appear to be tymbal structures within it (**Fig 2**).

No such structures have been observed in the Nolinae (including *Barasa* and allies), the Westermanniini group of genera (p. 267) and the *Gelastocera* group of genera (p. 267), though the last tends to have the apodemes in both sexes broad and rather bulbous. Tymbal structures are lacking in *Earias*, and in *Selepa*, *Iscadia*, *Lamprothripa*, *Ptisciana*, *Phaeothripa*, *Risoba* MOORE, *Timorodes*, *Calathusa*, *Macrobarasa*, *Beana*, *Blenina*, *Plectothripa* and *Labanda* amongst the Sarrothripinae outside the *Nycteola* group.

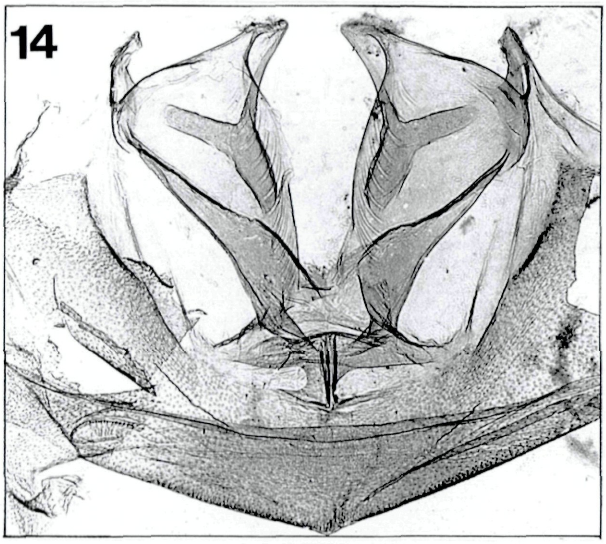
Tymbal structures are present in some taxa of the *Nycteola* group, in the Careini, the Chloephorini, the Camptolomini and in the genera *Maurilia* MÖSCHLER (possibly a careine), *Sinna*, *Gabala*, *Asinduma*, *Ariolica* and *Titulcia*. They occur in a number of different forms, and can provide a guide to generic groupings.

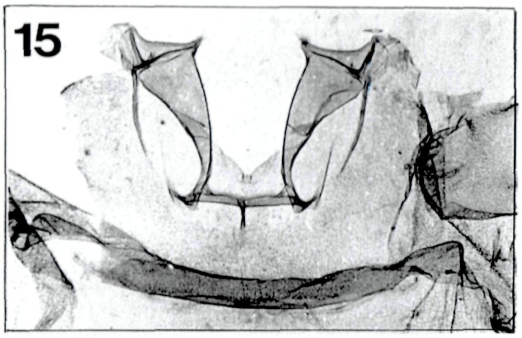
They reach their greatest complexity in the Chloephorini and Camptolomini. It is within the first group that records of actual sound production have been located in the literature. The male of *Pseudoips fagana* FABRICIUS was stated by LORIMER (in HEATH & EMMET 1983) to have 'often been heard to stridulate in flight, the sound being described as 'crackling'; although presumably sexual in nature, there is no record of any response being noted'. Sound production has also been recorded in *Tympanistes* MOORE (MOORE 1867; HOLLOWAY 1976: 27, 1988: 75) as clicking or as a regular, high-pitched squeak.

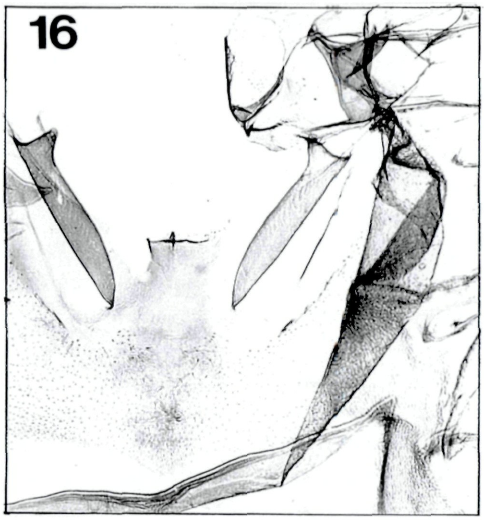
Features that appear to be unique to tymbal structures in genera of the Chloephorini are: a lateral, pouch-like structure; a posterior chamber; a tongue-pad-like structure associated with the interior element; no marked zone of corrugation associated with the structure. These features are indicated in **Figs 3-9**. In *Camptoloma*, illustrated by HOLLOWAY (1988: fig 70) and in **Fig 10**, the corrugations are present but reduced to three or four in number, the chloephorine features are lacking, and there is a massive ligulate structure in each tymbal, arising posteriorly.

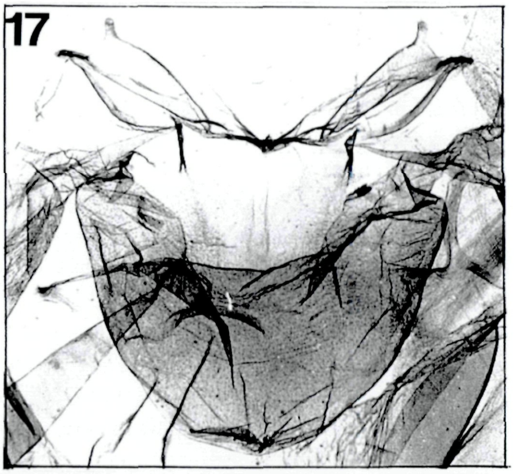
In *Ariolica* and *Titulcia* the corrugate zone is missing as in the Chloephorini, but the chloephorine features are lacking. The structure in these two genera is very similar (**Figs 11, 12**), indicating a close relationship.

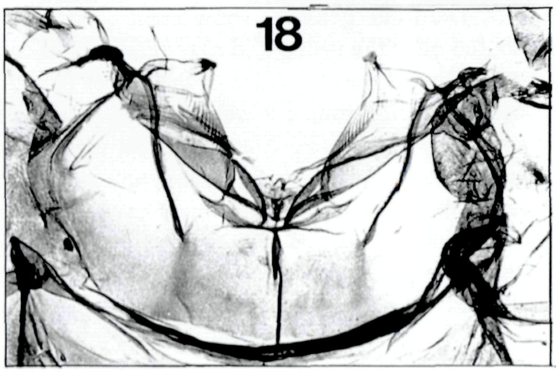
The Careini have the tymbal structures strongly associated with the apodemes of the basal sclerite, set somewhat obliquely, diverging from each other, with a zone of fine corrugation set dorsally on the interior, oblique face of the organ (**Figs 13-20**, and see also KOBES (1988: fig 36C)). The structure is small in *Didigua* WALKER and *Bessara* WALKER but still has a corrugate zone (**Fig 16**). In *Calymera*











Figs. 13-18 Tymbal organs on the basal abdominal sternites of male Careini:

Fig. 13: *Pseudelydna rufoflava* WALKER.- **Fig. 14**: *Calymera picta* MOORE.- **Fig. 15**: *Xenochroa erectilinea* PROUT.- **Fig. 16**: *Didigua* sp. (Borneo).- **Fig. 17**: *Aiteta musculina* WALKER.- **Fig. 18**: *Carea varipes* WALKER.

MOORE (**Fig 14**) the structure tends towards the Chloephorini state with a weak posterior double chamber, and a tongue-like thickening associated with the main tymbal. The association with the apodemes is less evident, the main tymbals less oblique, but still with a definite zone of corrugation. *Xenochroa* FELDER (**Fig 15**) is somewhat intermediate between this condition and the more typical careine state, but with corrugations not evident.

In *Maurilia* (**Fig 20**) the structures are more ovoid in shape with some indications of a chloephorine-like lateral pouch but with a corrugate zone and without a posterior chamber. Lateral to the tymbal structures on each side are coremata, bearing hair-like scales. Rather different corematous glandular structures are seen in a slightly more posterior lateral position in *Gabala* (**Fig 21**), where the tymbal structures are more as in the final group but with a small, centrally divided posterior chamber, and more robust thickenings as distinct from corrugations on the interior side of the only weakly separated, parallel tymbals. This type of thickening is seen in *Camptoloma* also, but in *Gabala* there are about nine thickenings rather than three or four. *Parasinna* also has such thickenings, reduced as in *Camptoloma*, but with general structure somewhat similar to that in the Chloephorini (see KOBES 1988: 86, fig 25).

In *Sinna* and *Asinduma* the tymbals are rather oblong, narrow, parallel and well separate, with a transverse thickening linking them posteriorly. Corrugations are numerous along the interior side of the tymbals (**Figs 22, 23**).

This last type of tymbal is seen in a few members of the *Nycteola* group such as *Garella* (**Fig 24**) and *Lophothripa* (**Fig 25**) and also in *Gyrtothripa semiplumbea* WARREN (**Fig 26**) though not in typical *Gyrtothripa* (**Fig 28**) and in some Oriental species of *Giaura* such as *G. rebeli* TAMS (**Fig 31**). Tymbal structures of unusual form are seen in *Mniothripa* HAMPSON (**Fig 29**) and *Characoma* (**Fig 30**), and some sexual dimorphism is observed in many other genera in the group: *Giaura* (**Fig 28**) with glandular structures associated with the apodemes), *Apothripa*, *Etanna*, *Gyrtothripa* and very weakly in *Pardasena*. In most of these cases there is a vestige of the transverse thickening that links the tymbal structures posteriorly (**Figs 27, 28**). These genera contain some of the smallest species in the sarrothripine/chloephorine complex and so this condition may represent reduction and loss rather than a primitive state of the character.

The male abdomen

The eighth segment is usually modified in taxa of the complex, a feature by no means unique to it within the Noctuidae. The modification is usually in the form of a pair of apodemes on both sternite and tergite. These are variable in form, but the pair on the tergite is usually stronger. The feature is not seen in *Eligma* or *Earias*.

Abdominal coremata and scent pencils are rare. Those at the base of the abdomen in *Maurilia* and other genera have been mentioned in the previous section. Coremata and other modifications are seen in typical *Giaura* on segments 4 and 5 as well as in association with the apodemes of segment 8. *Nanaguna* also has a series of lateral coremata between the segments as does *Etanna* between 4 and 5, and 5 and 6. In *Dilophothripa* and *Clethrophora* there is a pair between segments 7 and 8. Coremata are also sometimes seen on the genitalia, as discussed below.

Ariola WALKER has a pair of sclerotised lateral grooves running from the base of the abdomen to the distal corners of the tergites on segment 4.

The male genitalia show great variety in structure but have two features that are very widely distributed over the group and may therefore be autapomorphies. The first, elongation and apical fusion or connection of the transtillae of the valves (**Fig 32**), is less general than the second and may also occur in other noctuoid groups: it was noted as an autapomorphy for the group by SPEIDEL et al. (1996), who referred to it as a U-like transformation that protruded far into the interior of the body, except in the Nolinae. The second, a flanged structure in the position of the juxta that appears to be formed from interior extensions of the dorsal margins of the valve sacculi fusing with the juxta, appears to be unique. It is illustrated in **Fig 32**. It occurs in most noline taxa and in almost all representatives of all major groupings of genera in the complex. It is sometimes small or obscure, so its lack cannot always be determined with confidence (extreme modification of the genitalia can also make it difficult to recognise), but it appears definitely absent from *Eligma*, *Xanthodes*, *Calathusa* and *Macrobarasa*, taxa that may prove best excluded from the complex on other grounds as well (see p. 271 et seq.).

The tegumen is often rather elongate, the ventral portions on each side often expanded, invested with long, hair-like setae and frequently with prominent setal bases, e.g. in **Fig 32** (*Calymera*), **Fig 33** (*Characoma*) and **Fig 34** (*Arachnognatha*).

The uncus is simple, sometimes apically hooked, in most genera, often small, but is vestigial to absent in *Nola* Leach (HOLLOWAY & MILLER, 1995) and in another group of genera that may be related to each other: *Iscadia*, *Lamprothripa*, *Timorodes*, *Ptisciana* and *Phaeothripa*. It is also vestigial in *Selepa*.

In the *Nycteola* group the uncus is frequently modified in shape, usually small, and also in genera suggested to be associated with *Labanda* on p. 267. It is strikingly modified into a dorsoventral pincer-like structure embracing a cordate pad in *Beana* (HOLLOWAY 1976: fig 138). In *Earias* it is bifid. In *Macrobarasa* the uncus bears a single ventral socius-like structure. The scaphium is modified in several instances. In the Nolinae, including the *Barasa* group, there are lateral setose lobes or patches, though these are lost in *Nola* (HOLLOWAY & MILLER 1995). In *Beana* there is a pair of distinctive setose, elbowed processes reinforcing the scaphium laterally, resembling a gnathus. In *Mniothripa* there is a structure consisting of two sclerotised arms, apically fused resembling a gnathus even more, and something similar is seen in *Tyana*. In *Garella* there is a balloon-like, membranous structure supported on bands arising laterally from the tegumen, with a pair of finely setose discs on the 'balloon'.

A more frequent scaphial modification is typified in *Labanda* where it is strengthened in bands that arise laterally at the base, to converge shortly ventrally, and then the fused bands extend subscaphially as a single band over a considerable length. This feature is seen in *Tathothripa*, *Plagiograpta*, *Arachnognatha* (**Fig 34**), more weakly in *Gyrtothripa*, *Maceda*, *Asinduma*, *Chloriola*, *Orthocraspis* and *Paracrama*. In the Careini a similar condition is seen in most genera, closest to *Labanda* in *Xenochroa*, but with a more rhomboidal subscaphial sclerotisation in *Calymera*.

The scaphium is also modified in many of the taxa such as *Iscadia* and allies where the uncus has been lost, often having lateral setal patches. In *Blenina* there is general sclerotisation, and also in *Bena* and *Clethrophora*.

Coremata are present arising from the basal exterior of the valves in the *Gelastocera* group of genera and *Siglophora*, at the base of the tegumen in *Blenina*, at the base of the valves in association with the sacculus in *Triorbis* HAMPSON (in *Iscadia*), broadly over the whole exterior of the valve in *Plectrothripa* and as part of an extension of the saccus containing a tuft of black hair scales in *Phaeothripa*.

An extensive pencil of hair-like setae arises from the expanded base of the sacculus in *Pseudoips*, *Tympanistes*, *Parasinna*, *Tortriciforma*, *Didigua*, *Ariolica*, *Titulcia*, *Chandica*, *Plagiograpta* and *Sinna*. There is an uniquely convolute structure in the same position in *Miaromima* MEYRICK of the Westermanniini.

The valve of the genitalia has a number of features that occur widely within the complex, though excluding the Nolinae. These are mostly present in *Arachnognatha* (**Fig 34**) and include: a costa thickened over the basal half only, though often with a band of thickening extending into the circular, paddle-shaped distal part of the valve; a process arising dorsally from the costal thickening prior to the broadening of the valve, or often associated with an angular process from the dorsal edge of the valve lamina; a field of basally directed setae on the interior of the dorsal distal sector of the valve lamina; a bilobed valve apex, with the saccular portion narrower, often separated from the rest by a thickening or fold, and with fine setal bases increasing in number towards the apex.

These features are mostly all present in the Careini, *Maurilia*, *Paracrama*, *Orthocraspis*, *Maceda* and *Asinduma*. Several are seen in *Tyana* of the Chloephorini, but other members lack all (*Tympanistes*, *Pseudoips*) or most of them. Other taxa mostly exhibit a few of the features, but they are absent from *Eligma*, *Xanthodes*, *Titulcia*, *Cacyparis*, *Plectothripa*, *Beana*, *Macrobarasa*, *Selepa*, *Ptisciana*, *Siglophora*, *Chandica*, *Cossedia* and *Chloethripa*. Several of these are questionable members of the complex or should be excluded from it as discussed later. The presence or not of these features will be discussed further when subgroups of the complex are considered.

About half the genera of the *Nycteola* group (*Characoma*, *Garella*, *Apothripa*, *Nanaguna*, *Giaura*, *Etanna*, *Pardasena*) share possession of a distinctive, slender scaled process arising subbasally and dorsally on the valve (**Figs 33, 35**). The structure of the valve in this complex is usually so modified that it is unclear whether this process is homologous with the more generally distributed costal process mentioned above. It serves to mark its possessors as forming a probable monophyletic group.

A number of genera have fields of short, peg-like setae or setal bases on the dorsal half of the distal part of the valve (**Figs 36-39**). Their potential homology is not clear. This type of feature is seen in *Lophothripa* and *Mniothripa* of the *Nycteola* group, in *Ariola*, *Lasiolopha*, *Chandica*, *Siglophora*, *Cossedia*, *Labanda*, *Tathothripa* and *Plagiograpta*.

The Nolinae (including *Barasa* and allies) generally have a simple valve with a typically noctuid saccular harpe. A similar harpe is seen in *Macrobarasa*.

The aedeagus does not appear to offer any useful features. The vesica can be elongate to globular, usually with a scattering of cornuti or groups of cornuti.

SPEIDEL et al. (1996), extending the observations of Tikhomirov, noted that the state of muscle m.4 of the genitalia is split between the tegumen and vinculum as in the higher Noctuidae, though the dorsal part of this split (m.4a) is lost in most Nolinae. The ventral part (m.4b) is displaced ventrally towards the saccus in all members of the complex that they assessed, another potential autapomorphy.

The female abdomen

Features of interest appear to be restricted to the ovipositor lobes, bursa copulatrix and ductus bursae.

The ovipositor lobes are usually quadrate to rounded and moderately setose. In many of the *Nycteola* group they are narrow and acute. All the genera with the process on the male genitalia discussed above exhibit this condition, as do *Nycteola*, *Mniothripa* and *Gyrtothripa*. The lobes are narrow but apically rounded in *Dilophothripa*. In *Lophothripa* and *Chloethripa* they are quadrate with a ring-like array of setae. This last condition is also seen in the Chloephorini, where the lobes are densely setose, and also in the Westermanniini, the *Gelastocera* group of genera, and the genera *Ariolica*, *Titulcia*, *Ariola*, *Chandica*, *Siglophora*, and *Cossedia*. In the Careini the lobes tend to be rounded. In *Maurilia* they are markedly elongated and acute.

The ductus bursae is very variable in length, extremes of length being seen within the *Nycteola* group. The ductus is very long in *Garella*, *Nanaguna*, *Giaura*, *Etanna*, *Pardasena*, *Dilophothripa* and *Gyrtothripa* and very short in *Nycteola*, *Lophothripa* and *Chloethripa*. The bursa in this group is generally scobinate or immaculate except in *Garella* where there is a single small signum, and *Dilophothripa* where scobination occurs in a band and patch. In most other groups and genera the bursa is either generally scobinate in varying degrees of intensity or immaculate. Localised coarse scobination is seen in *Ariolica*, *Titulcia*, *Chandica* and *Cossedia*. In the Careini the bursa is either immaculate or with a signum: a single round sclerotisation adorned with a spine, nipple or ridge.

Diversity is seen in the Westermanniini: the bursa is finely corrugate and scobinate throughout in *Pterogonia* SWINHOE; it is immaculate in *Negeta* WALKER; it has a central scobinate disc in *Miaromima* and *Urbona* WALKER; it contains two pairs of scobinate bands in *Westermannia* HÜBNER.

In the *Iscadia* group of genera there is a distinct type of signum consisting of two adjacent bands of coarse scobination, the point of the spines directed outwards. This is seen in *Iscadia*, *Lamprothripa*, *Timorodes* and *Ptisciana* (two pairs of bands). In *Phaeothripa*, also possibly in this group, the signum is a narrow, longitudinal, lenticular, spiny, sclerotised band that may represent the fusion of a double band.

Selepa has a single, central, small, scobinate, umbonate signum. *Labanda* has central cluster of slender spines directed basad. *Austrocarea* Holloway has opposed stellate clusters of spines, but with male genitalia similar to those of *Paracrama* (HOLLOWAY 1977). *Risoba* has general scobination with corrugation that is intensified in a longitudinal zone. *Earias* has a very narrow, long ductus and an elliptical bursa that is finely scobinate and with unusual, acute, longitudinal fluting. *Macrobarasa* has a long ductus that enters the bursa distally with a single spiral: the bursa contains a weak, narrow, longitudinal, scobinate band.

The more plesiomorphic Nolinae have double scobinate bands in the bursa, very diffuse in *Barasa* and allies. More advanced taxa have single or paired blade-like, thorn-like or umbonate invaginate signa (HOLLOWAY & MILLER 1995).

Characters of the cocoon and pupa

The boat-shaped cocoon with a vertical, anterior exit slit has already been mentioned as a major, unifying feature for the group. It undoubtedly owes its form to its mode of construction. This was described by MCFARLAND (1978) for the noline genus *Uraba* WALKER, but a similar mode of construction has been described for other taxa in the group by T.R.D. BELL (unpublished manuscripts in BMNH). The cocoon is elongate, spindle-shaped. It is started by building up both sides, boat-like, with silk, often incorporating particles of chewed bark or epidermis and being built up into small peaks or projections on the exterior surface. The walls eventually meet in the middle, often with the construction of a prominent anterior peak, below which the junction of the walls is presumably left weak to provide the vertical exit slit.

Possession of this type of cocoon serves to unite the major groupings of the complex and to bring in rather morphologically isolated taxa such as *Earias*, *Selepa*, the *Iscadia* group, *Blenina* and probably *Risoba*. It serves to exclude *Xanthodes* and probably *Eligma*, but there is no information on the early stages of *Cacyparis*, *Macrobarasa* or *Plectothripa*. *Beana* pupates in a spindle-shaped cell of leaves lined with silk (T.R.D. BELL, MS).

Two features of the pupa are noteworthy. It lacks a cremaster, the terminal segment being domed or bluntly conical (GARDNER 1948b). This feature is only seen otherwise in the Noctuidae in subfamily Euteliinae, sister-group to the Stictopterinae where there is a strong and distinctive cremaster (HOLLOWAY 1985; KITCHING 1987). A cremaster is present in *Xanthodes* and indicates the genus to be misplaced in the Chloephorinae (see p. 270).

The second feature is beading or a series of longitudinal ridges on the anterior margin of the terminal abdominal segment. This has been noted (mostly by HINTON (1948) after T.R.D. BELL (MS) but also by GARDNER (1948b)) in the *Nycteola* group (*Nanaguna*, *Giaura* (Oriental taxa), *Lophothripa*, *Nycteola*, *Symitha*, *Dilophothripa*), in *Blenina*, *Labanda*, *Plagiograpta*, in *Paracrama*, and *Risoba* (a wrinkled zone at the junction rather than ridges), in the Westermanniini (*Westermannia*, *Pterogonia*), in the Chloephorini (*Bena*), in the *Iscadia* group (*Triorbis*, *Ptisciana*), in *Earias* and in *Selepa*. It is also observed in *Eligma* (HINTON 1948; SUGI 1987; see also p. 272), a possible homoplasy.

It is probably a stridulatory mechanism with a defensive function (HINTON), as a number of taxa with the features have been observed to produce a rustling sound from the cocoon by 'shivering' (T.R.D. BELL, MS) when disturbed. These include *Eligma* (SUGI 1987), *Risoba*, *Triorbis*, *Ptisciana*, and the Westermanniini (T.R.D. BELL, MS). Hinton noted it for *Bena* (as *Pseudoips*).

Hinton also observed that some, but by no means all, of these taxa had corresponding ridges constructed on the inner wall of the cocoon, particularly *Selepa*, *Iscadia* (sensu lato) and *Eligma*. Hinton indicated that such taxa had a more plesiomorphic cocoon construction relative to other sarrothripines, chloephorines and careines. Beadings or carinae are not seen in the Euteliinae apart from the genus *Phalga* MOORE where there is a circular patch of longitudinal carinae at the posterior extremity (GARDNER 1948b).

Characters of the larva

The larvae of the nolines are distinguished from those of the rest of the complex by two features: presence of verrucae with secondary setae; absence of a proleg on abdominal segment A3, with that on A4 fully developed. Some genera exhibit the peculiarity of retaining cast head capsules stacked in a horn-like structure on the thorax (HOLLOWAY & MILLER 1995). *Beana* has prolegs on A3 reduced and was placed by GARDNER (1947) in his group BIVa with catocaline and ophiderine taxa: it was stated to have an unique pygidial horn. Loss of prolegs also occurs in *Xanthodes*: its affinities and unusual appendiculate crochets are discussed on p. 270.

GARDNER (1941, 1946a, b, 1947, 1948a) discussed the classification of Noctuidae on larval characters (reviewed by KITCHING (1984)). He used GERASIMOV's (1935) system of setal nomenclature, translated here to that of HINTON (1946: table 5). He segregated *Selepa* and *Earias* with *Eligma* in his Group D on the grounds that they were bisetose subventrally on the thorax as in arctiids, rather than unisetose as in other noctuids. The Camptolomini are also bisetose (see p. 272 for discussion of *Eligma*): however, the subventral group is bisetose on abdominal segments as in noctuids rather than trisetose as in arctiids (see below). *Selepa docilis* BUTLER differs from the type species, *S. celtis* MOORE, in having a verruca in the L1 position on abdominal segments (GARDNER 1941). SPEIDEL et al. (1996) regarded double versus single SV setae on the thoracic segments as homoplastic.

The majority of members of the complex was placed by GARDNER (1947) in his Division C, exceptions being *Plagiograpta* in Group AII (usually Amphipyrinae) and Careini with *Maurilia* in their own group AV. Division C also included Euteliinae, Stictopterinae and some Ophiderinae.

Gardner did not consider his groupings to be much more than a convenient but artificial means of dividing up the noctuids, as they were based on features such as loss of prolegs that were suspected to be homoplastic.

He recognised a major dichotomy in the Noctuidae based on whether the subventral setal group is bisetose or trisetose on the first abdominal segment. The sarrothripine complex falls within the bisetose section with the trifine subfamilies, most of the Euteliinae and Stictopterinae and part of the Plusiinae. The Plusiinae are shown to be a natural group by KITCHING (1987), and the stictopterine genera *Lophoptera* GUENÉE and *Odontodes* GUENÉE, segregated in Gardner's two sections, are probably sister-genera within the subfamily (HOLLOWAY 1985; KITCHING 1987). This dichotomy trangresses Gardner's divisional groupings, but much of the bisetose section parallels the grouping on the basis of adult tympanal organs by Richards mentioned earlier. SPEIDEL et al. (1996) regarded the bisetose condition as apomorphic.

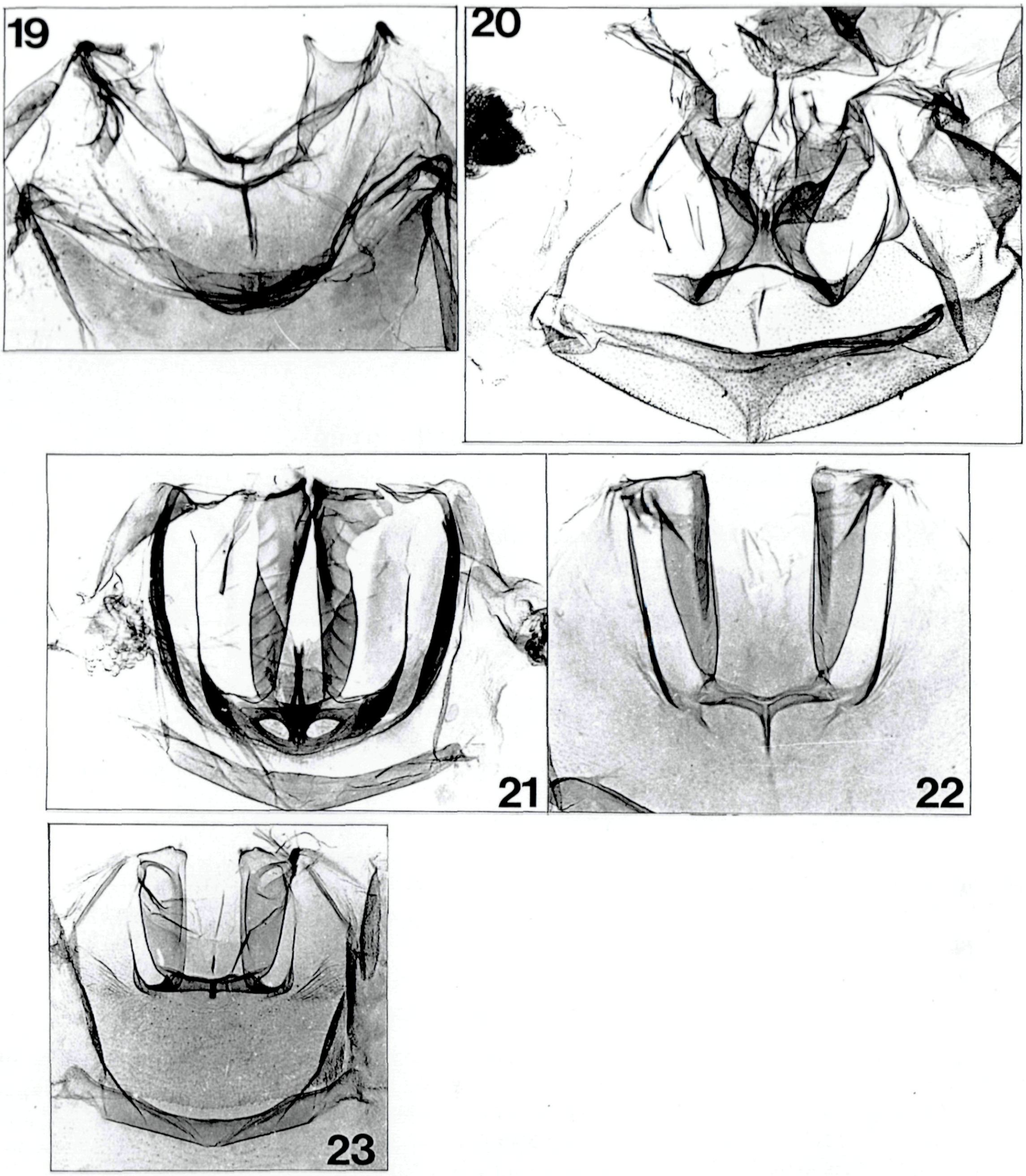
Gardner's Division C includes genera where all prolegs are present. Seta SD1 on A8 is usually anterior to the spiracle; if vertically above, then the SV group on A1 is trisetose. This trisetose condition is the characteristic of the second noctuid section mentioned above, but all of the sarrothripine complex have SD1 more or less anterior to the spiracle. *Labanda* has it approaching the vertical position and might therefore be placed alternatively in Group A (see below).

Within Division C, the *Nycteola* (*Sarrothripus*) group is segregated as a unit (represented by *Garella* (probably including *ruficirra* HAMPSON, referred to *Characoma*), *Nycteola*, *Symitha* and *Giaura sceptica* SWINHOE). The principal features given are the position of the frontal setae in the head, well above the level of the frontal pores, sometimes half way up the frons, and the position of ocellus 2 about half way between 1 and 3.

The Careini are placed in Group A as SD1 on A8 is well above the spiracle usually vertically so, yet the SV group on A1 is bisetose (GARDNER, 1946b). They are segregated in their own group AV on the grounds of moderate to strong tumidity of the thorax, sometimes described as 'berry-like'. This is strong in *Carea* WALKER, *Aiteta* WALKER and *Pseudelydna* HAMPSON, only moderate in *Maurilia*. The thorax is also berry-like in *Calymera* and *Lasiolopha*, the latter not a careine.

Plagiograpta, in group AII, is exceptional, but occurs there through the position of SD1 on A8. *Labanda* could be grouped with it on this feature. Comparison of features given by GARDNER (1948a) reveals other similarities. Ocelli 1 and 2 are very close or contiguous. The mandible is more strongly toothed, with several teeth, than in other genera of the group discussed by Gardner.

GROTE (1895) pointed out (from the work of Dyar) similarities in chaetotaxy between *Nycteola* and the Palaearctic chloephorine genus *Bena*.



Figs. 19-23 Tymbal organs on the basal abdominal sternites of male Careini (Figs. 19-20) and Ariolicini (Figs. 21-23):

Fig. 19: *Diehlea tumida* HAMPSON.- **Fig. 20**: *Maurilia* sp. (Seram).- **Fig. 21**: *Gabala polyspilalis* WALKER.- **Fig. 22**: *Sinna calospila* WALKER.- **Fig. 23**: *Asinduma exscripta* WALKER.

Figs. 24-31 Tymbal organs and other structures on the basal abdominal sternites of male Sarrothripini (next page):

Fig. 24: *Garella rotundipennis* WALKER.- **Fig. 25**: *Lophothripa vitea* SWINHOE.- **Fig. 26**: *Gyrtothripa semiplumbea* WARREN.- **Fig. 27**: *Gyrtothripa pusilla* MOORE.- **Fig. 28**: *Giaura repletana* WALKER.- **Fig. 29**: *Mniothripa bradleyi* FLETCHER.- **Fig. 30**: *Characoma metalophota* HAMPSON.- **Fig. 31**: *Giaura rebeli* TAMS.

Monophyly of the group

Monophyly of the group is strongly supported by the following characteristics:

- Possession of a boat-shaped cocoon with a vertical exit slit and a two-walled method of construction;
- Detachment of patagia and tegulae;
- Absence of a pupal cremaster coupled with, in more plesiomorphic taxa, beading or a row of carinae along the anterior margin of A10;
- Presence of a complex flanged structure between the sacculi of the male genitalia;
- Extension of the valve transtillae, with apical fusion, into the interior of the body;
- Ventral position of genitalic muscle m.4b;
- An elongate, bar-shaped male retinaculum in conjunction with scaling of the lower part of the clypeofrons.

Loss of a cremaster is seen in euteliine noctuids and Arctiidae, and a bar-shaped retinaculum is present in the Arctiidae, Aganainae and *Eligma* (KITCHING & RAWLINS 1998). The presence of raised scales on the forewing is not universal, but may be a ground-plan feature of the group, like pupal beading.

Proposed classification within the group

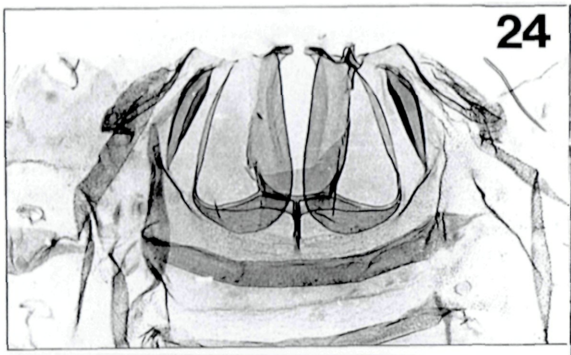
A number of groupings within the complex can be recognised with varying degrees of confidence. Where family-group names are already available, these are given tribal status, pending a more detailed review of the group. KITCHING & RAWLINS (1998), in according the group family status as the Nolidae, recognised a number of subfamilies with it, based on the findings presented here. These are indicated in brackets in the heading for each group in the text following.

Family-group names involved

Before attempting to provide a more satisfactory classification of the complex, it is necessary to review the nomenclatural position, as a number of names at the family-group level are available.

Nolinae was not formally associated with the group as a whole until the classification of KITCHING & RAWLINS (1998), though KITCHING (1984) pointed to the relationship of the Nolinae, Sarrothripinae and Chloephorinae but proposed no nomenclatural changes. The name dates from the Nolites of BRUAND (1846).

Nycteolidae of HERRICH-SCHÄFFER (1845 [1851]) was applied conceptually by that author to several of the genera included here (*Chloephora*, *Earias*, *Sarrothripus*), but based on *Nycteola* HERRICH-SCHÄFFER, a junior homonym of *Nycteola* HÜBNER. The type species of the former is an acontiine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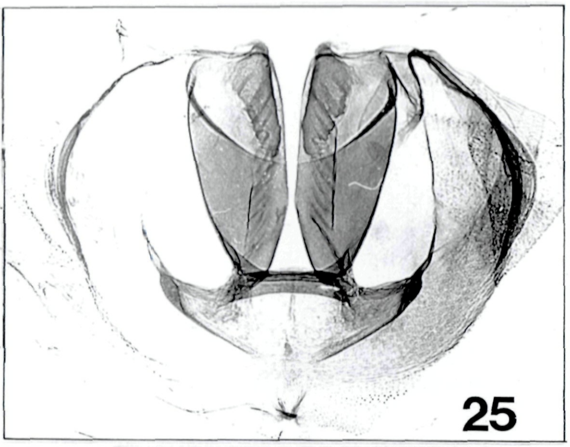
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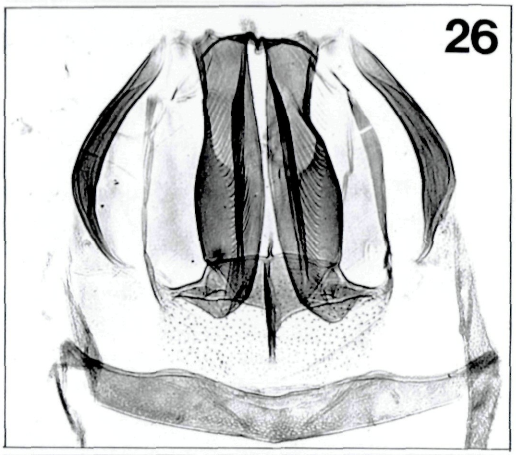
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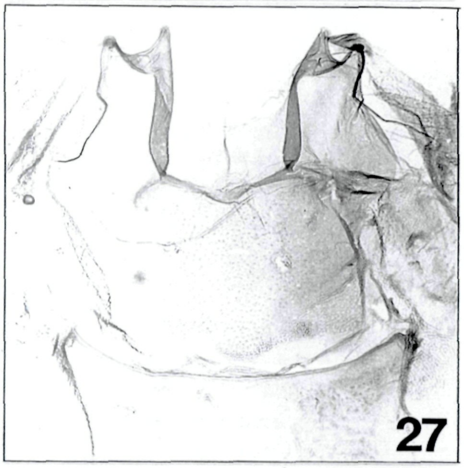
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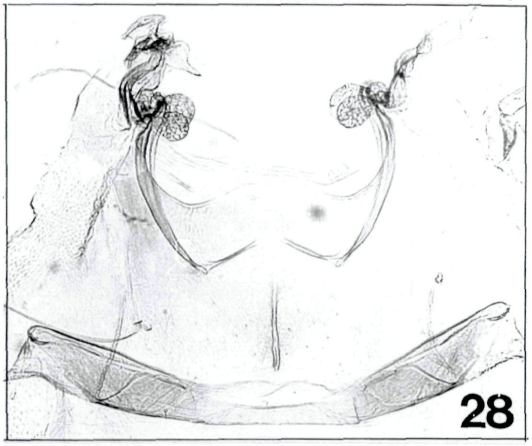
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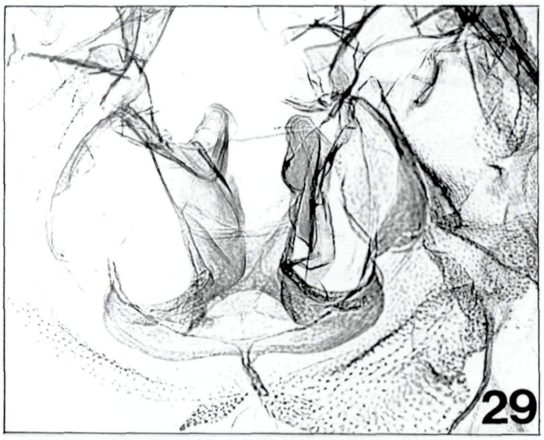
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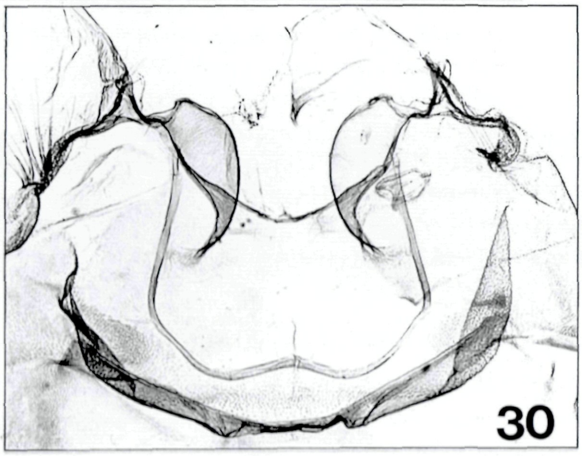
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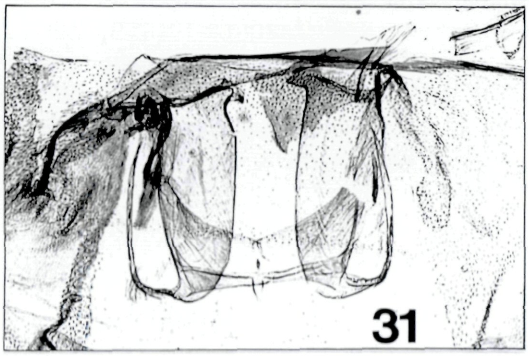
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(POOLE 1980), now located in *Zebeeba* KIRBY, a replacement name for the junior homonym (NYE 1975). Therefore, Nycteolidae is not an available family-group name and also postdates Nolinae.

Chloephorinae, dating from 1859 (STEPHENS), has priority over other names based on generic synonyms (Pseudoipsidae, Hylophilini), or related genera (Beninae), and was therefore preferred by NYE (1975), followed by POOLE (1989).

Eariasinae is a name mentioned in passing by HAMPSON (1912: 456) and referred to also by KITCHING (1984: 184) but was never formally presented with included taxa. The correct derivation is Eariadinae as for the butterfly subfamily Coliadinae, and as used by KITCHING & RAWLINS (1998).

MELL (1943) gave precedence to Sarrothripinae over Chloephorinae, placed Camptolominae with equal rank and erected a number of new tribes. His Hylophilini is a synonym of Chloephorini, but Ariolicini, Blenini, Careini, Cymatophoropsini, Eligmini and Risobini are all available, though Cymatophoropsini and Eligmini fall outside the group (see p. 272).

The Nolini (Nolinae)

The classification of the Nolini is discussed by HOLLOWAY & MILLER (1995). The group is most clearly defined on larval characteristics: loss of the first pair of abdominal prolegs and presence of verrucae. All except *Barasa* and related genera have strongly bipectinate male antennae, though this feature is secondarily lost in many *Nola* species. Lateral setose patches on the scaphium of the male genitalia are general to the group, but lost in *Nola*. The male genitalia have a rather basic, noctuid harpe arising from the sacculus.

The genus *Beana* may be a plesiomorphic member of the Nolini. The larva shows reduction of the first pair of abdominal prolegs but lacks verrucae. Elbowed, setose lateral sclerotisations to the scaphium may be homologous to those mentioned above. In the male genitalia, the valves are unusually modified but there is a bicornute structure distally on the sacculus that may represent the harpe. Unlike the Nolini, the pupa is carinate, and the adult has ocelli.

The genera *Barasa* WALKER, *Aquis* WALKER and *Hypolochma* FELDER, referred to in earlier sections as the *Barasa* group, have many noline features such as loss of ocelli, modification of the scaphium, a simple valve with a noctuid-type harpe, and noline larval characters, so are best placed here rather than in their old association with the sarrothripines. The group is probably relatively basal within the nolines, having an areole in the forewing venation, quadrifine hindwing venation and unmodified signa. The male antennae are bipectinate rather than filiform, though bipectinate antennae are seen in some *Nola*.

A preliminary survey of many noline genera was conducted to provide a context for HOLLOWAY & MILLER (1995). Three features may be useful in indicating relationships within the subfamily: development of trifine hindwing venation; modification of the signa in the bursa as described on p. 258-259 stacking of head capsules in the larva. Almost all genera with trifine venation have modified signa.

Most taxa exhibiting larval head capsule stacking have quadrifine hindwing venation, the exception being the E. Palaearctic *Evonima mandschuriana* (OBERTHUR), but the signa are of the modified type. The occurrence of this feature was reviewed by MCFARLAND (1978 [1980]) and HOLLOWAY & MILLER (1995) with particular reference to the Australian genus *Uraba* WALKER. Further references to this habit have been found for *Proneca fola* SWINHOE (SEVASTOPULO 1938), *Sarbena lignifera* WALKER (GARDNER 1943; BIGGER 1988), a species in the *Acatapaustus* BETHUNE-BAKER and *Eurynola* HAMPSON complex (BIGGER 1988) and further quadrifine taxa currently placed in *Meganola* DYAR by POOLE (1989). These last are *togatulalis* HÜBNER, *nitida* HAMPSON (MCFARLAND 1978 [1980]), *gigas* BUTLER and *mikabo* INOUE (SUGI 1987).

Included genera: see HOLLOWAY & MILLER (1995) and POOLE (1989).

Groups with tymbal organs at the base of the abdomen (Chloephorinae)

This new concept of the Chloephorinae is very different from the old Hampsonian concept of the group. The latter was most recently followed for reason of convenience by KOBES (1997), who was aware that changes to the classification were both necessary and imminent, and therefore refrained from embarking on such revisional work himself. The reader will find considerable structural information, further illustrations of male genitalia and illustrations of habitus for all known Sumatran species in Kobes' monograph.

The Sarrothripini

This tribe consists of the *Nycteola* group of genera first referred to on p. 249. Full tymbal organs are not universal amongst constituent genera, but many show some sexual dimorphism in the basal abdominal sclerite. Features that characterise the group include: the position of the frontal setae on the larval head; generally acute, narrow ovipositor lobes. In many instances the saccus of the male is long, particularly in those taxa that have an unusual scaled process to the valves. Several genera have coremata in the male abdomen.

The species are mostly small in size, and many genera show reduction of the hindwing venation to a trifine condition. When present, the tymbal usually has the pouches parallel, proximate with many corrugations. The tribe is the only one with tymbal organs where taxa have raised scales on the forewing and, with some genera tentatively placed in the Ariolicini, where pupae with beading have been noted. Several genera show a type of forewing venation unusual in the Nolidae (p. 252).

Included genera: *Apothripa*, *Characoma*, *Etanna*, *Garella*, *Giaura*, *Nanaguna*, *Pardasena*, (all with a setose process on valve); *Chloethripa*, *Dilophothripa*, *Gyrtothripa*, *Lophothripa*, *Mniothripa*, *Nycteola*, *Symitha*.

The Chloephorini

The Chloephorini are distinguished by the complexity of tymbal features described on p. 254. They include the only genera where actual production of sound has been noted. The forewing venation either has R5 split back to arise independently from the cell, or with it arising relatively basally from Rs or an areole. M3 and CuA1 in the hindwing are usually stalked. Some genera have a hair pencil on the expanded base of the sacculus in the male genitalia, a feature also seen in some Ariolicini. The ovipositor lobes are highly setose distally, this setal zone often forming a ring. The species usually appear robust, broad of thorax.

Included genera: *Bena*, *Chloroplaga*, *Clethrophora*, *Hylophilodes*, *Pseudoips*, *Tortriciforma*, *Tyana*, *Tympanistes* and possibly *Parasinna*. This enlarges MELL's (1943) concept of his Hylophilini but excludes the genus *Earias*.

The Camptolomini

This tribe is monobasic (HOLLOWAY 1988), also having rather elaborate tymbal structures, though these possess thickened ridges (p. 254). The male genitalia have a number of characteristic chloephorine features such as a paddle-shaped valve with a costal spur and reversed distal setae. The seventh abdominal segment of the female is expanded, membranous, densely invested with fine scales. The larva has two subventral setae on the meso- and metathoracic segments.

Included genus: *Camptoloma*.

The Careini

The principal unifying feature of this tribe is the 'berry-like' swelling to the larval thoracic segments (though also seen in *Lasiolopha* of the Ariolicini). But also the tymbal organs tend to be oblique, strongly associated with the apodemes, and M1 is connate with the areole or arises basally from it in the forewing. Ornamentation of the bursa copulatrix, when present, is with a small signum bearing a single projection. The group exhibits most of the unusual features of the male genitalia listed on p. 257.

In addition to the berry-like form of the larval thorax, the Careini differ from all except two members of the Ariolicini in having SD1 on A8 well above the spiracle, usually vertically so, rather than anterior to it (p. 260).

Included genera: *Aiteta*, *Bessara*, *Calymera*, *Carea*, *Chora*, *Didigua*, *Diehlea*, *Maurilia*, *Pseudelydna*, *Xenochroa*; *Maurilia* is atypical and may prove to be sister group to the rest.

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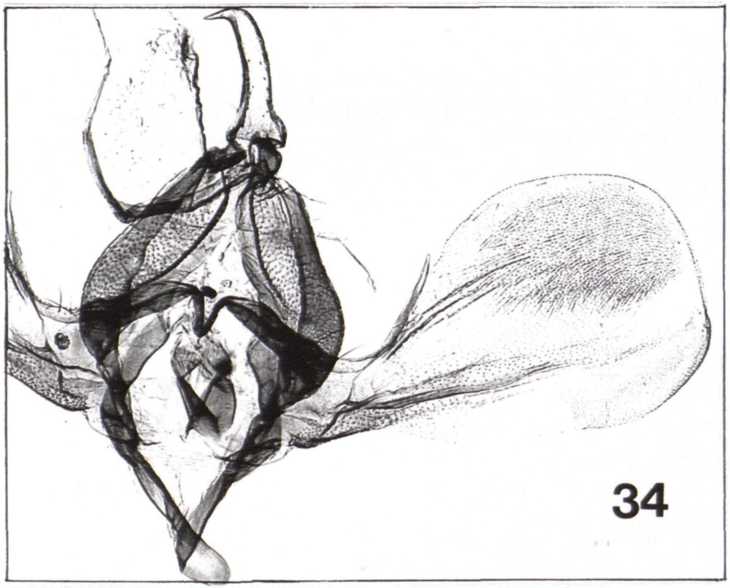

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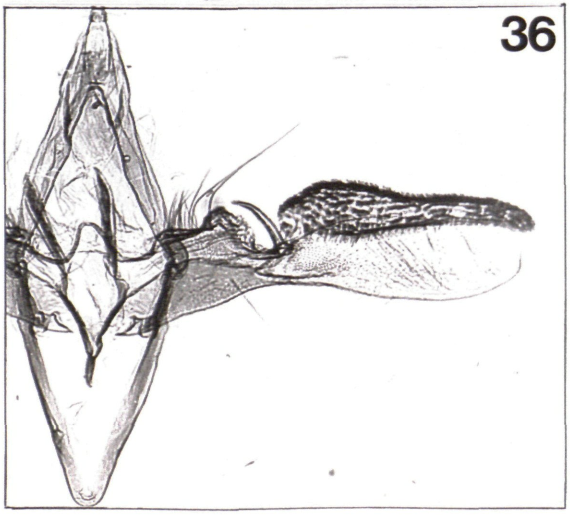

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Figs. 32-36 Male genitalia of:

Fig. 32: *Calymera picta* MOORE (Careini) (part only, showing elongate transtillae (t) and saccular flange (s)).- **Fig. 33**: *Characoma metalophota* HAMPSON (Sarrothripini).- **Fig. 34**: *Arachnognatha metascotia* HAMPSON (Ariolicini).- **Fig. 35**: *Giaura niveidisca* HAMPSON (Sarrothripini).- **Fig. 36**: *Lophothripa vitea* SWINHOE (Sarrothripini).

The Ariolicini

This tribe contains a rather heterogeneous assemblage of genera with a number of features shared amongst some, but not all of them. Several have tymbal organs of the parallel Sarrothripini type (*Sinna*, *Gabala*, *Asinduma*), but *Ariolica* and *Titulcia* have rather unusual ones, broad and lacking a corrugate zone, suggesting a trend towards the Chloephorini. There is little information on the early stages, though *Paracrama* and *Labanda* have a beaded pupa, and *Labanda* and *Tathothripa* larvae resemble the Carcini in setal characters of A8. *Cossedia* has a possible tymbal organ on the hindwing (p. 254; **Fig 1**). All lack raised scales on the forewing.

Other features serving to bring at least some members of the group together, albeit rather unsatisfactorily, are: the *Labanda* type of scaphial reinforcement (p. 257); a high proportion of typical structural features of the valve. Several taxa have the apodemes of the male eighth tergite, and sometimes the sternite, significantly longer than is normal for the group (*Labanda, Tathothripa, Plagiograpta, Sinna, Ariola, Chandica, Siglophora, Arachnognatha*).

Tentatively included genera: *Arachnognatha, Ariola, Ariolica, Asinduma, Chandica, Chloriola, Cossedia, Gabala, Labanda, Lasiolopha, Maceda, Orthocraspis, Paracrama, Plagiograpta, Siglophora, Sinna, Tathothripa, Titulcia.*

Groups without tymbal organs at the base of the abdomen

The *Gelastocera* group of genera (unplaced by KITCHING & RAWLINS)

Members of this group share possession of strongly bipectinate antennae in the male. The valves of the male genitalia bear large coremata at their base, and are themselves usually simple, unornamented. The ovipositor lobes are ring-like, highly setose. The apodemes of the basal abdominal sternite in the male are usually rather bulbous in both sexes (**Figs 40, 41**). There are no raised scales on the forewing, and the only reared genus (*Beara*) has not got pupal beading or carinae (HINTON 1948; T.R.D. BELL MS).

Included genera: *Beara*, *Erizada*, *Gelastocera* (*Arrhapa* WALKER may be closely related), *Ptyonota.*

The Westermanniini (Westermanniinae)

Species often have a highly satiny appearance to their forewings, sometimes with silver patches or bands. There are no raised scales evident. The basal sternite is not modified into a tymbal organ (**Fig 42**). The pupa has beading and is noted to shiver in the cocoon. The ovipositor lobes are ring-like, highly setose.

The group is best defined on features of the male genitalia. The tegumen is long relative to the vinculum. The scaphium has a narrow dorsal band of sclerotisation. The uncus is highly setose with a terminal hook, though the complete structure is lost in *Pterogonia.* The distal part of the valve is rounded, the margin with a thick fringe of basally directed setae on its interior surface. Ornamentation of the bursa copulatrix is diverse (p. 258).

Included genera: *Miaromima, Negeta, Pterogonia, Urbona, Westermannia.*

The genus *Cacyparis* (unplaced by KITCHING & RAWLINS)

This genus has the unusual feature of what appears to be a paired tymbal structure in the saccus of the male genitalia (**Fig 2**). The build of the moth is rather slender, the forewings apically rounded, without raised scales of the normal sort following dark fasciae, but with an oval patch of longer, dark scales in the centre of the dorsum that is domed and protrudes over the hindwing. The forewings have a scattering of iridescent, silvery scales and a diagnostic subapical ocellate mark. The basal and distal segments of the male abdomen are highly modified, the former rather elongate, though without tymbal structures. The female genitalia have the ostium bursae displaced well anteriorly onto the seventh segment.


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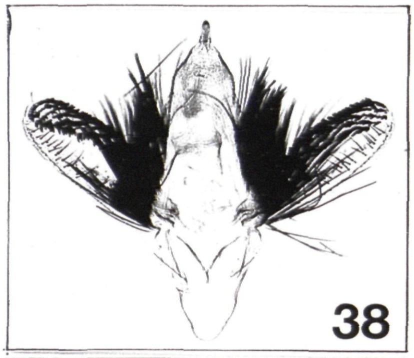
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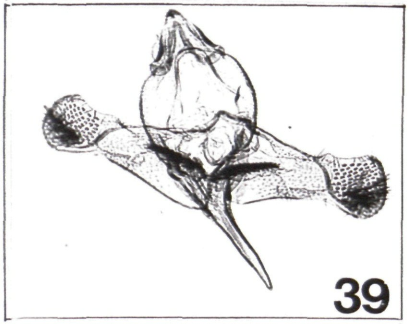
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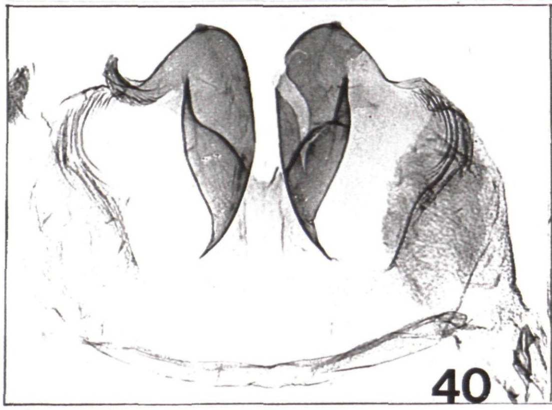
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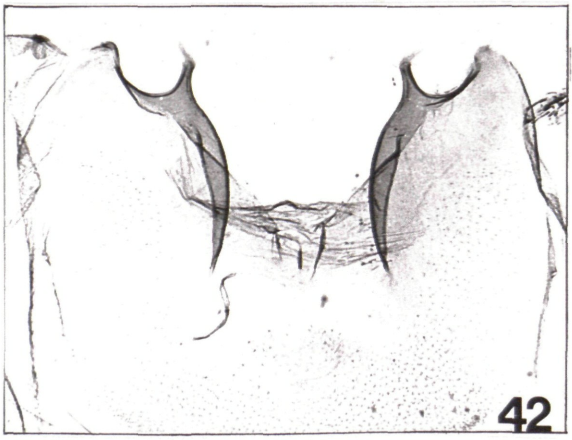
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Figs. 37-42 Male genitalia of species of Sarrothripini (Fig. 39) and Ariolicini (Figs. 37-38) with fields of short, peg-like setae on the valves and structures on the male basal abdominal sternites (Fig. 40-42) of:

Fig. 37: *Chandica quadripennis* MOORE.- **Fig. 38**: *Cossedia hyriodes* HAMPSON.- **Fig. 39**: *Mniothripa bradleyi* FLETCHER.- **Fig. 40**: *Gelastocera exusta* BUTLER (*Gelastocera*-group).- **Fig. 41**: *Ptyonota formosa* HAMPSON (*Gelastocera*-group).- **Fig. 42**: *Westermannia superba* HÜBNER (Westermanniini).

The genus *Earias* (Eariadinae)

Species of *Earias* lack raised scales on the forewing and have reduced, trifine hindwing venation. The frenulum and retinaculum are absent. The larva has some arctiid features (p. 260) and lacks the cervical gland (KITCHING & RAWLINS, 1998) noted as a noctuid apomorphy by SPEIDEL et al. (1996). The bifid uncus and distal spine to the valve in the male genitalia, and the fluting of the bursa copulatrix in the female are also distinctive features.

The genus *Selepa* (unplaced by KITCHING & RAWLINS)

This is a large genus consisting mainly of small species, many with a characteristic looped postmedial pattern to the forewing: some raised scales are present. In the male genitalia the uncus has been lost. The sacculus has a typical harpe, sometimes very long and modified, and there are weak coremata at the base of the valve. The bursa copulatrix has a central and scobinate signum, slightly invaginated.

The larva has arctiid thoracic setation (p. 260) as in *Earias*, and a verruca is present in some species. The pupa is beaded and shivers in the cocoon on alarm.

The features are thus mainly plesiomorphic.

The genus *Iscadia* and allies (Collomeninae - see below)

Iscadia was considered by Poole to include the Oriental genera *Gadirtha* and *Triorbis*. All these have the forewing reniform enlarged, with a central patch of raised scales. Most have the tongue reduced or vestigial. Poole's concept of *Iscadia* includes both Neotropical and Indo-Australian taxa.

Features such as loss of the uncus and presence of a strong costal arm or process to the valve in the male genitalia, and presence of a signum consisting of a pair of parallel sclerotised bands (fused in *Phaeothripa*) with outwardly directed spines are shared by a few other genera. MELL's (1943) concept of the Eligmini included some of these with *Selepa* and *Eligma*.

Where known, the pupa has beading and shivers in the cocoon.

Included genera: *Iscadia*, *Lamprothripa*, *Phaeothripa*, *Ptisciana*, *Timorodes*.

The Blenini (Bleninae)

This Mell tribe is monobasic, consisting of the large, Palaeotropical genus *Blenina*. It is a rather plesiomorphic member of the Nolinae, distinguished by unusual features of the male genitalia: coremata arising from the tegumen and unusual bird's head shaped structures arising from the sacculus. There are weak hair pencils laterally on segment 7 of the male abdomen. The forewing pattern is cryptic, but the hindwing pattern often involves yellow bands or areas, possibly flash coloration.

The Risobini (Risobinae)

This tribe consists of the large, Palaeotropical genus *Risoba* and, according to FORBES (1954), the American genus *Baileya* GROTE.

Risoba species usually have a rather striking forewing pattern in greens, browns and blacks, and a pale hindwing with a broad dark border. The male genitalia are distinctive, with a slender sinuous uncus, a deep saccus, and valves with prominent subbasal processes on the costa. The sacculus bears a harpe that sometimes shows bilateral asymmetry, and the distal margin of the valve has a zone of basally directed setae.

Raised scales are not evident in *Risoba* or *Baileya*. Valves of American species of the latter were illustrated by Forbes. A harpe is present, and also a prominent costal process.

Taxa probably misplaced in the Nolidae

Comments on the classification of *Xanthodes* and *Eligma* merit sections of their own, following this, but a number of other taxa have been identified as potentially misplaced in any revised concept of the Nolidae.

The Collomenini of FRANCLEMONT & TODD, discussed by KITCHING (1984: 219), were erected without explanation as a tribe within the Sarrothripinae. The tribe consists of the New World genera *Motya* WALKER and *Collomena* MÖSCHLER. These have highly modified male genitalia that nevertheless lack nolid features. The retinaculum is elongate, not bar-shaped, and there are no raised scales on the forewing. No information on the early stages has been located. However, KITCHING & RAWLINS (1998) place Collomeninae as a subfamily of the Nolidae and include the *Iscadia* group in it (see above).

KITCHING & RAWLINS (1998) also tentatively refer the New World subfamily Afridinae to the Nolidae. These lack ocelli as in the Nolinae. It was suggested by KITCHING & RAWLINS that they may be nolids of uncertain affinity, but no strong justification of this placement was presented. The group was not examined here.

The predominantly Australasian genus *Calathusa* WALKER (HOLLOWAY 1979) also lacks noline features. The male genitalia do not exhibit the fused saccular structure. The retinaculum is curled round the frenulum, bar-shaped according to HAMPSON (1912), but this is debatable as it is very much broader than in typical Nolidae. The male antennae are bipectinate. There are no raised scales on the forewings. The counter-tympanal hood is not typical, more ear-like and extending for the depth of the tympanum. A few species have been reared from *Casuarina*, but no information on cocoon structure or the state of the pupal cremaster has been located.

The monobasic genus *Plectothripa* HAMPSON lacks raised scales and a bar-shaped retinaculum. The male genitalia lack the fused saccular structure. The valves are laminate with a subapical interior spur and massive coremata that extend over the whole of the exterior surface. The uncus suspends a single gnathus structure with an acute, upturned apex. There is some sexual dimorphism in the basal sternite of the abdomen, the apodemes of the male being associated with shallow pockets and an interior triangular flap.

Macrobarasa HAMPSON contains two Oriental species. Again, the retinaculum is only weakly bar-shaped, and raised scales are absent. In the male genitalia the valves are simple with a typical noctuid harpe. The uncus subtends a sinuous ventral structure in a pincer-like manner. The transtillae are reduced, not fused together apically, and the juxta is simple with no saccular component. In both the male and the female basal sternite, the zone between the apodemes consists of an oblong plate flanked by declivities. The female genitalia are described on p. 258.

Confirmation that these taxa should be excluded from the Nolinae must await study of the cocoon structure and state of the pupal cremaster.

Xanthodes GUENÉE (including *Pardoxia* VIVES & GONZALES).

This genus is undoubtedly misplaced in the Chloephorinae (assignment by POOLE (1989) and in the BMNH collections). The retinaculum is only slightly elongated, and none of the distinctive genitalic features present. The cocoon is loosely spun in the soil, and the pupa is attached to it by a distinct hooked cremaster. Host plants are in the Malvaceae (*Abutilon*, *Kydia*, *Urena*, *Hibiscus*, *Decaschista*, *Thespesia*, *Gossypium*).

The larva has the prolegs on A3 and A4 vestigial. In the Nolidae they are strong, though lost completely on A3 in the Nolinae. The larva is a semi-looper more typical of the 'lower' trifines (HOLLOWAY 1989) and the quadrifines, and the genus was grouped with several of these by GARDNER (1946a) in Group B1. A particular feature of this group is the presence, on the fully developed prolegs, of 'appendiculate' crochets: with a large, additional subapical tooth.

Other taxa included by GARDNER (1946a, 1947, 1948a) were as follows:

Chasmina WALKER. This genus was reviewed by HOLLOWAY (1989). The host-plants noted for it were *Hibiscus* (Malvaceae), *Helicteres* (Sterculiaceae) and *Grewia* (Tiliaceae).

"*Bocula*" sp. near *megastigmata* HAMPSON. This combination in the Ophiderinae is also found in POOLE (1989), but *megastigmata* is close to, or synonymous with, *Allocosmia sugii* KOBES and should be transferred to that small Oriental amphipyrine genus as *Allocosmia megastigmata* **comb.n.** The Chinese taxon *apicalis* LEECH, combined with *Oglasa* WALKER by POOLE (1989), is probably also a member of this group. The host-plant of *megastigmata* was *Sterculia* (Sterculiaceae);

Oglasa separata WALKER (on *Sterculia*) and *O. hypenoides* MOORE (on *Grewia*) in the Ophiderinae;

Androlymnia emarginata HAMPSON (on *Grewia*) and *Elydna transversa* WALKER (on *Schleichera* of the Sterculiaceae) of the Amphipyrinae. *Elydna* is currently (POOLE 1989; HOLLOWAY 1989) a synonym of *Athetis* HÜBNER, but this needs re-examination.

Amyna leucostriga HAMPSON (a herbaceous feeder, unspecified) in the Acontiinae.

With the exception of *Chasmina* and *Amyna*, these taxa tend to have angled, pale postmedial fasciae to the forewing, often with a well defined dark brown patch on the costa immediately distal to it. The antemedial and often medial fasciae are clearly defined, and the reniform and orbicular stigmata are often large. A second costal brown patch is sometimes associated with the reniform. Some *Chasmina* species that are not pure white have similar brown costal patches. The forewing fasciation in some *Xanthodes* species is also consistent.

The forewing venation of these taxa is of the typical areolate formation, except for *Xanthodes* where R2 and R3 are independently stalked from R4 and R5, leading to two independent bifurcate systems arising from the cell. This feature is also seen in the Afrotropical genus *Leocyma* Guenée, where the species are of similar coloration and, in some cases, facies to *Xanthodes*. *Leocyma* larvae also have the first two pairs of prolegs vestigial, and pupate in a loose cocoon in the soil. The crochets on blown larval material in BMNH appear to be appendiculate, but are mostly obscured by glue. There are unpublished host records (identification at BMNH) for *L. camilla* DRUCE from *Hibiscus* in E. Africa.

GARDNER (1947) also noted appendiculate crochets in the catocaline genera *Anomis* HÜBNER (not all species) and *Marcillada* WALKER, but these taxa have the prolegs of A4 well developed and so are probably not related to the other taxa. *Anomis*, however, is strongly associated with the Order Malvales in its larval host preferences, an Order that contains the families Malvaceae, Tiliaceae, Sterculiaceae, Bombacaceae and Elaeocarpaceae (MABBERLEY 1987). The genera mentioned above, with the exception of the acontiine *Amyna*, are recorded only from these families.

It is possible that most of these taxa (excepting *Amyna*) form a natural grouping. *Dyrzela* WALKER (HOLLOWAY 1989), with a larva lacking prolegs on A3 and A4, *Grewia* as a host-plant, pupation in a loose silken cocoon in soil and forewing facies features similar to those of *Allocosmia*, may also be related. The Amphipyrinae involved have vein M2 of the hindwing present but weak, and it tends to be weaker than the other veins in the Ophiderinae. GARDNER (1948b) noted pupal similarities also: the caudal extremity is rounded, with a pair of straight cremastral setae.

Such a natural grouping could be referred to the Bagisarinae of CRUMB (1956), recognised as a subfamily by POOLE (1989). Crumb defined the subfamily effectively on possession of appendiculate crochets, and drew attention to the similarity of the New World *Bagisara* WALKER to *Xanthodes*. *Bagisara* larvae have been recorded from the malvaceous *Hibiscus* and *Malvaciscus*. The broadened concept of the subfamily is supported by KITCHING & RAWLINS (1998).

HOLLOWAY (1989) suggested that the genus *Mudaria* MOORE, with larvae boring in the pods and fruits of Bombacaceae, was related to *Chasmina*. However, examination of larval skins from cocoons of *Mudaria variabilis* ROEPKE from Thailand revealed a full four pairs of prolegs bearing normal crochets.

The enigma of *Eligma* HÜBNER

The genus *Eligma* HÜBNER consists of a number of large, brightly coloured moths from the tropics and subtropics of Africa, Madagascar, Asia and Australasia. It is the type genus for the tribe Eligmini of MELL (1943). Mell also included *Gadirtha*, *Triorbis*, *Selepa* and *Lamprothripa*: all these genera have the uncus vestigial or absent in the male genitalia (see p. 257). POOLE (1989) placed *Gadirtha* and *Triorbis* in synonymy with *Iscadia* Walker. He assigned *Eligma* to the Chloephorinae and all the rest to the Sarrothripinae.

UEDA & SAIGUSA (1982) hand-paired *Eligma narcissus* CRAMER and discovered an unusual copulatory mechanism that appears to be unique with the Noctuidae, involving divergence of the valves against ridge-like structures flanking the female ostium, an action that holds the sexes together during copulation and opens the ostium. Features noted, apart from the absence of uncus structures, were: fusion of valves and vinculum; absence of the juxta; peculiarities of genital musculature.

The male eighth sternite in *narcissus* is vestigial, the tergite semicircular. In the female, the ductus bursae is very long. The bursa is pyriform, generally corrugate and scobinate, with a more heavily sclerotised lateral cleft more or less centrally. A striking feature is the presence of a pair of glands, possibly pheromone glands, on the dorsal membrane just anterior to the ovipositor lobes, resembling those noted widely in the Arctiidae by HOLLOWAY (1988). None of the Nolidae complex shows this feature.

The retinaculum of the forewing is bar-shaped, the venation typically noctuoid with an areole, though R5 arises from Rs just distal from it rather than from the areole itself. There is no pronounced counter-tympanal hood.

The third segment of the labial palps is long and slender as in many Ophiderinae and in the Aganainae (see HOLLOWAY 1988: 77). No tymbal organ has been located.

GARDNER (1941, 1947) placed *Eligma* in his group D on larval features, together with *Selepa*, *Earias* and the hadenine genus *Brithys* HÜBNER. The principal feature is the presence of the arctiid bisetose (compared with unisetose in the Noctuidae including Aganainae) condition of the subventral primary setae of the thorax. However, these taxa differ from Arctiidae in having this group bisetose rather than trisetose on abdominal segments. The Camptolomini (see above (p.260) and HOLLOWAY (1988)) also have the bisetose thoracic condition. *Eligma* has primary setae only, but these are long, set on chalazae. In the Aganainae (e.g. *Asota* HÜBNER), the thoracic subventral condition is unisetose as in Noctuidae (GARDNER 1941).

The pupa lacks a cremaster but has fine longitudinal ridges on the margins of the terminal segments which it uses to stridulate against ridges on the interior of the cocoon when alarmed, as in many of the Nolidae group (HINTON 1948; SUGI 1987).

The systematic position of the Eligmini, which must be restricted to *Eligma* itself, is therefore unclear, but association with the Arctiidae may, on balance, be preferable to association with the Nolidae as suggested as a provisional placement by SPEIDEL et al. (1996). Larval and genitalic characters are atypical of the latter, and the glands associated with the ovipositor lobes are an arctiid feature.

The type species appears to be restricted to *Ailanthus* (Simaroubaceae) as a larval host plant.

The position of the Nolidae in the Noctuoidea

The morphological survey described here has thrown up no new pointers to the classificatory position of the Nolidae within the Noctuoidea. There are three possibilities that require further investigation: subfamily status within the Noctuidae; subfamily status within the Arctiidae; full family status.

Evidence from tympanal and larval features reviewed above suggests association with the Acontiinae and trifine subfamilies (HOLLOWAY 1989) of the Noctuidae; arctiid features in some larvae would then be homoplastic, as would noline features of the pupa in *Eligma*.

The evidence surveyed by KITCHING (1984) weighed in favour of placement within the Noctuidae. MILLER's (1991) cladistic analysis of the higher classification of the Notodontidae, generally regarded as the sister-group to the rest of the Noctuoidea, used as an outgroup a selection of taxa from the

Noctuidae, Arctiidae and Lymantriidae, including both *Nola* and *Nycteola*. The consensus classification (MILLER 1991: fig 99) from an analysis of 174 unweighted characters from both adults (100) and final instar larvae (74) placed *Nycteola* and *Nola* as sister-taxa within a 'noctuid' clade that also included *Acronicta*, *Peridroma* HÜBNER, *Alypia* HÜBNER, *Diloba* BOISDUVAL and *Panthea* HÜBNER. However, it is dangerous to place much weight on cladistic structure amongst taxa selected as outgroups.

SPEIDEL et al. (1996) grouped the complex with their concept of the Noctuidae because of the following shared features that they considered apomorphic to all or part of the Noctuidae: long tibial spurs in the adult legs; a ventral cervical gland present in the larva; a postspiracular counter-tympanal hood, albeit reduced; splitting of the male genitalic muscle m.4. They also included an elongate uncus as a noctuid character, but this is extremely variable in the nolid complex, and is generally relatively short, sometimes absent. A larval cervical gland is present in the Notodontidae and in the butterflies (KITCHING & RAWLINS 1998), hence the polarity of this character is debatable.

KITCHING & RAWLINS (1998) group the Nolidae as a family with the Lymantriidae, Arctiidae and Pantheidae on the grounds of presence in the larvae of secondary setae on the body restricted to verrucae at primary setal localities, though this feature also occurs sporadically in other families including the Noctuidae, and is reversed to the primary setal state in some nolids and arctiids.

The numerous instances of sound production in nolid pupae and presumed sound production in adults as indicated by the abdominal tymbal structures offer a tenuous connection with the Arctiidae and Lymantriidae where tymbal structures are frequently found in the adults, on the thorax and on the abdomen (4th sternite) respectively. Some Lymantriidae also exhibit pupal stridulation (HINTON 1948). KITCHING & RAWLINS (1998) proposed that, whilst these features may be autapomorphic for each family, their general structure may be serially homologous. This is seen even within the nolid group, with structures in the wings and male genitalic saccus as well as at the base of the abdomen.

KITCHING & RAWLINS suggested that there were several apomorphies that support a sister-relationship between Arctiidae and at least part of the Nolidae, such as presence of two SV setae on T2 and heteroideous crochets in the larvae of some lineages of each family, but indicated that the Nolidae might be paraphyletic. The groups discussed on pp. 271–272, such as *Eligma*, may belong to this paraphyletic tail. The pupae of nolines within the Nolidae have the larval D1 and D2 verrucae fused as in Arctiidae, and another common feature is the presence of short secondary setae around the scars of the larval verrucae in the pupa (KITCHING & RAWLINS).

The unisetose/bisetose condition of thoracic larval segments appears to be hightly homoplastic throughout the Noctuoidea and provides no reliable pointers to the affinities of the nolid complex. The occurrence of secondary setae on verrucae also presents ambiguities within the noctuoids, but perhaps offers another indication of relationship to the Arctiidae.

Similarly the bisetose versus trisetose states of the subventral setae on abdominal segments A1-6 may also be homoplastic, and the polarity is debated: SPEIDEL et al. (1996) consider the bisetose condition (SV2 absent) as apomorphic and KITCHING & RAWLINS (1998) consider the trisetose condition thus.

The Nolidae lack the paired dorsal pheromone glands that characterise the female genitalia of the Arctiidae (HOLLOWAY 1988) except for *Eligma*, but KITCHING & RAWLINS (1998) cite work in preparation that indicates these are not homologous.

In conclusion, there is still no clear answer to the second question posed in the introduction. The position of the nolid complex remains enigmatic as does the relationship of *Eligma*. Treatment of the complex as a distinct family, the Nolidae, is probably the most pragmatic solution until more evidence is available from a broader sample of early stage material, or perhaps from molecular studies.

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