A phylogenetic study on Cossidae (Lepidoptera: Ditrysia) based on external adult morphology

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Key words: Lepidoptera; Cossidae; carpenter moths; phylogeny; host-plants; historical biogeography.

A revised classification of the Cossidae is provided. Five cossid subfamilies, of which Chilecomadiinae is new, are recognized. The external adult morphology of many genera and species is described with special attention paid to the thoracic sclerites, including wing bases. Cladograms of the genera are proposed. In total 95 genera are recognized, of which the following 27 are new: *Mirocossus, Hirtocossus, Alcterogystia, Planctogystia, Paracossulus, Brachygystia, Eogystia, Mormogystia, Semagystia, Eburgemellus, Relluna, Aramos, Voousia, Alophonotus, Bergaris, Rapdalus, Rugigegat, Pseudozeuzera, Paralophonotus, Hermophyllon, Cecryphalus, Tarsozeuzera, Brypoctia, Panau, Skeletophyllon, Trismelasmos* and *Aethalopteryx*. Thirteen new generic synonymies and six new specific ones are established. *Planctogystia gaedei* is proposed as the objective replacement name for *Cossus fuscibasis* Gaede. Six new synonymies are proposed for species. Keys to the genera of the larger subfamilies and a check-list of all the genera included are given. Many genera previously placed in the family are excluded. The possible relationships of the Cossidae with other taxa are discussed.

The author postulates that the subfamily Zeuzerinae was distributed over Gondwanaland in the Early Cretaceous. Migrations across Beringia and from South to North America or vice versa at various times, including the Early Tertiary, are discussed. Some zeuzerine distribution patterns as well as other data suggest a former forest connection across Peninsular Arabia. Turkestan is regarded to have been a main refugium during the Glacial Periods for the species of several cossine genera. Distribution patterns probably related to one or both Melanesian arcs are pointed out. The ranges of several species suggest a close relation between the (northern) Vogelkop and midnorth New Guinea.

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Contents

Introduction

The Cossidae Leach, 1815 [1830] is a cosmopolitan moth family with roughly seven hundred described species. The English vernacular name for the family is Carpenter Moths, because of the larval habit of boring in plants, particularly trees. The family has generally been recognized by a combination of characteristics. The only autapomorphy the author could find for the Cossidae is a rather high (cossoid) mesepimeron, but this structure is, however, often secondarily lowered and occasionally heightened. In this study five subfamilies are recognized, one of which is new. The author distinguishes 94 genera, 26 of which are introduced as new in this paper.

Nearly all species live as a larva in plants. Most species bore in the trunk or branches of trees or shrubs, but several are known to live in the roots of herbs, and one in the stem of Reed. Only the larva of *Endoxyla leucomochla* Turner, 1915 is known to feed externally on the roots of certain trees (see Common, 1970: 798). A number of species have a very wide host range. Several species are known to cause serious damage to plants of economic importance, such as Ground-nuts, Sugar-cane, Cocoa, Coffee, Tea, Kapok, Cotton, Wattle and timber of various kinds (a.o. Arora, 1976; Carter & Deeming, 1980: 399; Dammerman, 1919: 63-63, 1929: 70-72). There is also a record of mining in bonsais (Ulenberg et al., 1986: 34). The larva of *Cossus cossus* (Linnaeus, 1758) is known to live for three or four years before emerging from the plant and making a cocoon on the bark or in the upper layer of the ground (e.g., Daniel, 1956a: 258-262). The larvae of certain other species are presumed to live for two to three years (Skinner, 1985: 70-71). Of certain species it is known that pupation takes place in the larval gallery in the plant (Common, 1970: 798; Skinner, 1985).

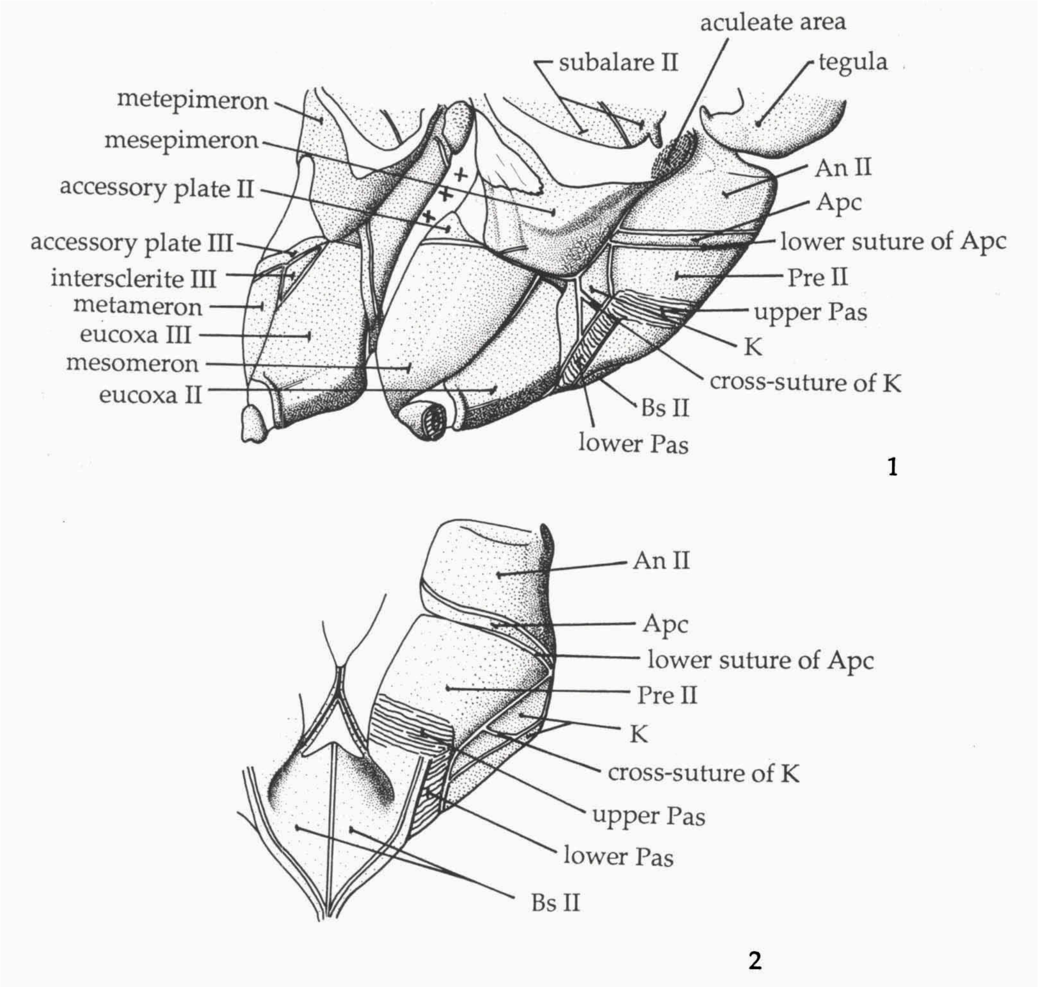
The larval structure, especially the head, has been modified probably in relation to the boring habit (see Fracker, 1915: 177). Descriptions of the larva are provided by e.g. Fracker (1915: 177-178), Schierbeek (1917: 56-59) and Hinton (1946). The mandibular glands of the larvae of at least *C. cossus* and *Zeuzera pyrina* (Linnaeus, 1767) produce smelly secretions, which are mixtures of certain acetates and function

Plate 1. Habitus of various Cossidae. A, *Catopta albonubilus*, U.S.S.R., Alexander Mts.; B, *Cossus modestus*, U.S.S.R., Kulja; C, *Holcocerus gloriosus*, Iran, Dshidak; D, *Stygia australis*, Spain, Gallia; E, *Eremocossus faedus*, Pakistan, Karachi; F, *Semagystia agilis*, U.S.S.R., Ashkhabad; G, *Zeuzeropecten combustus*, Madagascar, near Moramanga; H, *Bergaris lutescens* ssp. *lutescens*, Indonesia, Singkep; I, *Chalcidica minea* ssp. *hyphinoe*, Indonesia, Ambon; J, *Langsdorfia franckii*, Serra da Alto.

perhaps as defense substances (Pavan & Valcurone Dazzini, 1976; Trave et al., 1960). The larva of *C. cossus* has a goat-like smell and is therefore called the Goat Moth.

Natural enemies of the larvae are according to Dammerman (1919: 64, 1929: 71-72): Woodpeckers, parasitic Diptera (e.g. tachinids), parasitic Hymenoptera (e.g. the braconid *Zeuzerilia tricolor* van Achterberg) (van Achterberg, 1989: 88), and Fungi. Two larvae of *Z. pyrina* were found in the stomach of a Great Spotted Woodpecker, *Dendrocopos major* (Linnaeus) (Barrett, 1895: 145-146). The larvae of one or more Australian species were and/or are relished by the local people, and those of *C. cossus* were eaten as a delicacy by the Romans (McCoy, 1879: 49). The larvae of a species of *Holcocerus* Staudinger, 1884 are used commercially as food for pets (W. Hogenes, pers. comm.).

Eggs of Cossinae are of the upright type and, those of Zeuzerinae Boisduval,



Figs. 1-2, unidentified *Rhizocossus* species (a), Chile, Valle Lago Blanco. 1, lower section of meso- and metathorax, lateral view; 2, sternopleural region; An = anepisternum; Apc = anapleural cleft; Bs = basisternum; K = katepisternum; Pas = parepisternal suture; Pre = pre-episternum.

[1828] 1829 are of the flat type (Forbes, 1923: 517). The number of eggs deposited by a single female belonging to a species of *Endoxyla* Herrich-Schäffer, [1853] exceeded 18.000 (Common, 1970: 797). The eggs of this species are covered by a glutinous secretion according to Common (1970). The eggs of *Zeuzera pyrina* are laid singly or in small batches on the foodplant (Skinner, 1985: 71).

The adults of most species are nocturnal. There are few records of activity by certain species during the day (Korb, 1910: 26; Daniel, 1955: 63; Bruce, 1883: 190). Several authors record the attraction of the adults of C. *cossus* by sugar or a sweet liquid (e.g., Dobson, 1876: 183; Barrett, 1895: 149-150).

The types of habitat in which the adults have been caught vary considerably; e.g., tropical rain forest, parks, steppes and desert. Cossidae are known from Africa (including Madagascar), Europe, Asia, Australia, and North- and South-America.

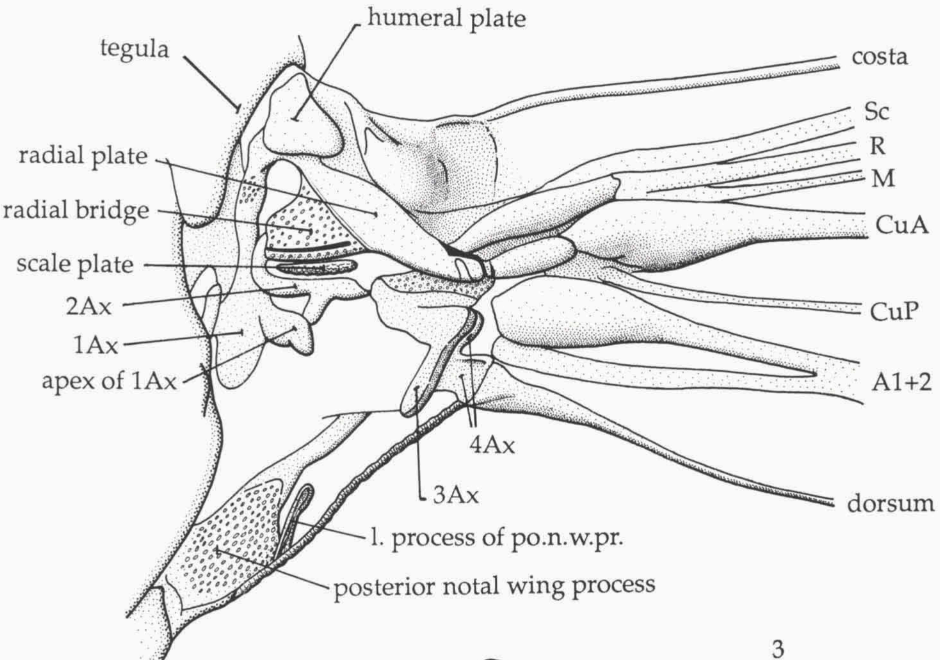
The outward appearance of the adults varies considerably (see also pl. 1). A number of species superficially resemble psychids. The wing-span varies amongst the species from approximately 15 to 220 mm. Particularly in Australia there are many species of which the representatives are large with a heavy abdomen. In many species the females are generally larger and have broader wings than the males. In most genera the female antenna has shorter rami than the male one, or is unilobed or prismatic. In a few genera there is considerable sexual dimorphism in colour pattern.

The probably earliest descriptions of cossid species are those of *Phalaena cossus* and *Phalaena* (*Noctua*) *strix* by Linnaeus in 1758. Most species were described in the last half of the previous century and the first half of this century. A few authors in the second half of this century provide descriptions of genitalia: e.g., Roepke (1955; 1957), Arora (1976) and Holloway (1986). The genitalia of the Cossidae appear to be mostly of a generalized primitive apoditrysian type with few or no special characteristics. Most genera have few or no diagnostic characteristics in colour pattern or wing venation. A growing number of new genera and species distinguished on the basis of head-appendages, colour pattern and wing venation has resulted in considerable confusion, and some genera have become large and heterogeneous groups.

The most important taxonomic revisions of Cossidae are by Barnes & McDunnough (1911), Seitz (1912), Gaede (1930; 1933), Dyar (1940), Turner (1945), Roepke (1955; 1957), Daniel (1955-1965), Arora (1976), and Gentili (1985). They are mainly faunistic works covering restricted regions and have not disentangled the taxonomic confusion of all motley genera, such as *Zeuzera* Latreille, 1804 and *Xyleutes* Hübner, [1820] 1816. Only Turner (1918) and Arora (1976) tried to discover relationships amongst the genera, but they dealt with a restricted number only. Catalogues of species and genera were provided by Kirby (1892) and von Dalla Torre (1923). A checklist of neotropical species is in press (Donahue, in press).

The aim of this study is to describe the external morphology of the Cossidae and to propose a well-founded classification and phylogeny on the basis of morphological data. Originally the intention was to discuss the phylogeny of each subfamily as far as generic level. It appeared that the taxonomic confusion and the structural variation is so great within the Zeuzerinae Barnes & McDunnough, that in several instances the phylogeny is treated to the level of species.

Judging by earlier revisions, it appears that the classical characters of the external morphology, such as venation and head-appendages, and the genitalia characters provide inadequate evidence for a phylogenetic classification of the genera.



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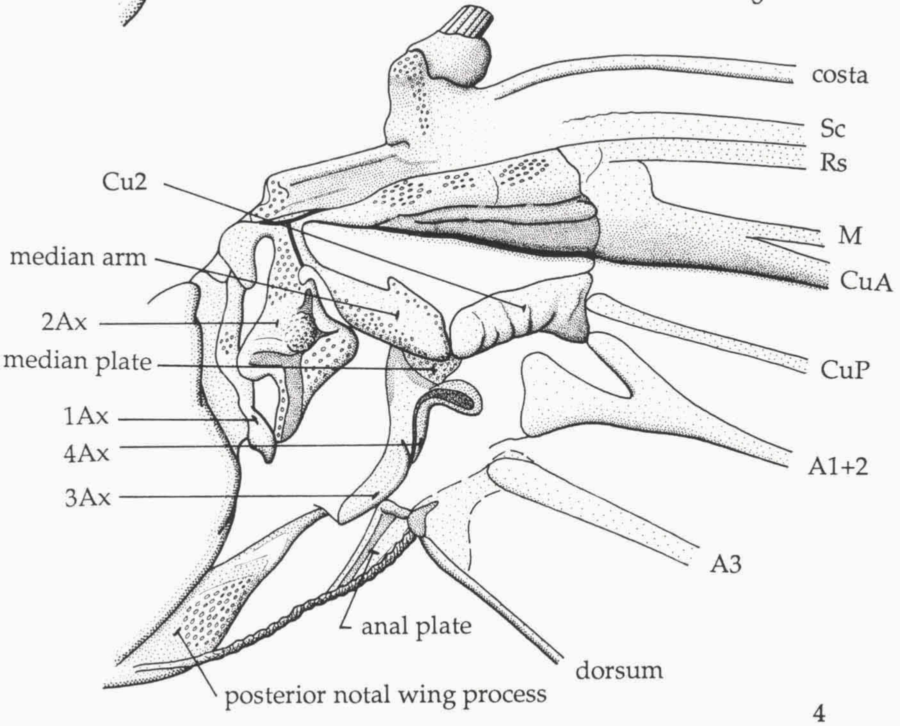

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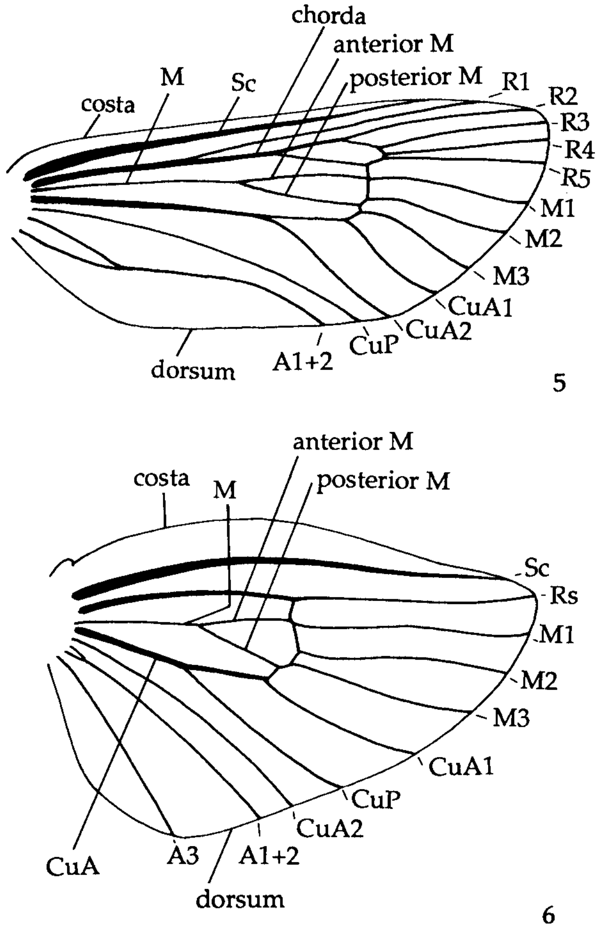
Figs. 3-4, *Zeuzera pyrina*, Germany, Herkulesbad (see also fig. 65). 3, forewing base; 4, hindwing base; Ax = axillary slerite; Cu = cubital plate; l. process of po.n.w.pr. = lateral process of posterior notal wing process.



Figs. 5-6, venation of a hypothetical cossid species with a plesiomorphic pattern. 5, forewing; 6, hindwing.

Therefore the author has investigated the usefulness of other characters of the external morphology. The characters of the thoracic sides and wing bases had previously hardly been studied amongst the Lepidoptera, but are used in this paper. Weber (1924) discusses the thoracic sclerites of a series of Lepidoptera and compares them with those in certain Neuroptera and Trichoptera. Brock (1971) points out characteristics of the thoracic sides amongst a series of ditrysian families (including Cossidae), of which he examined material of one or few species. Sharplin (1963b and 1963c) studied the wing bases of one or two representatives of a series of Ditrysian families, including the Cossidae. In the present study the thoracic sclerites have been studied in more detail and in many more species. It turned out that the characteristics of the thorax are very useful to distinguish genera or groups of genera. With the data of both these "new" character suites in combination with the classical ones it was possible to propose a phylogeny of each subfamily down to generic level. Investigation of thoracic sclerites seemingly provides more useful data for a phylogenetic study of the Cossidae at generic level than that of genitalia, and it consumes considerably less time. However, in the Hypoptinae Neumoegen & Dyar there seems to be considerable variation in the states of the genitalia characters, which will probably be useful to improve the cladogram.

The present paper provides information on important characters of the external morphology for a great number of species. For information on colour patterns of species reference can be made to the original descriptions and the revisions cited above. Nearly all genera are redefined in this paper. Under most genera a list of species and the material examined is given. Many cladograms are presented and in the accompanying paragraphs the character-states considered apomorphies are mentioned. A list of plesiomorphic character-states is given before the taxonomic treatment of the family.

Methods

During a nine months stay in London the collection of Cossidae in the British Museum (Natural History) was investigated. Thereafter the material of the main collections in The Netherlands has been studied. The collection of the Natural History Museum in Paris has also been investigated. Loans from various other institutions offered the opportunity to examine material of taxa not available in the institutions visited.

Of many genera, material of as many species as possible has been studied, and when possible a series of specimens of these. Of several large genera only the material of a seemingly sufficient number of species has been studied to assess one or more characters defining each genus and to give an impression of interspecific variation. Of several American and Australian genera little or no material was available. Material of a total number of approximately 480 species, of which more than fifty are undescribed, from 116 genera has been examined.

Sclerites of thorax and wing bases were studied in situ on the dried specimens after removal of vestiture by use of a fine brush. Wing bases were studied in dorsal view. When only a few specimens of a species were available, only sections of thorax and/or wing bases were examined in order not to inappropriately damage precious material. In the case that enough material of a species was available, usually at least two specimens were extensively examined. Wing venation was studied in situ with the help of toluene.

The cladograms were produced by the method of "out-group comparison" as explained by e.g. De Jong (1980) and Wiley (1981) and on the principle of parsimony. The ground-plan character-states of the family were assessed by considering the distribution of the character-states within the Cossidae and by comparison of these with those in the Metarbelidae Strand and several "primitive" Ditrysian taxa (see chapter on supposed plesiomorphies). The cladograms have been produced by hand, without the help of a computer. In the process of producing cladograms characters were often weighted. More weight has been given to novelties than to (general) reductions. The results of a pilot study have been used to give more weight to reductions which seemingly occurred one or a few times than to those which seemingly occurred within several subfamilies and within these subfamilies several times. The reduction of structures, such as mesothoracic anepisternum, mesepimeron, arolium, paronychia, frenulum structures, fringes, and venation seemingly happened many times within the Cossidae. The author realizes that alternative cladograms are possible. The classification in this paper is a phylogenetic one. Reference can be made to Wiley (1981) for an explanation and discussion of phylogenetics. The use of sections in the classification is just for convenience, and these sections donot have any taxonomic status.

At the base of a cladogram the autapomorphies of the concerning group as a whole are repeated but with numbers differing from those in the preceding, connecting one. An arrow in a cladogram indicates that the concerning taxa are grouped together for biogeographical reasons. An exclamation mark in the cladograms indicates a development which is seemingly rare within the Cossidae. An asterisk in the cladograms denotes a presumable reversal. An asterisk in a list of apomorphies means that a reversal of that development occurs higher in the cladogram.

Publications cited but not seen by the present author are denoted in square brackets in the list of references. Dates of references in square brackets means that they are taken from a source other than the original publication, notably from Horn & Schenkling (1928-1929). For information on type designations for genera, reference should be made to Fletcher & Nye (1982). In the lists of species for each genus the specific name is given in combination with the genus in which the species was established, and both names are spelled as originally published.

The genera are treated in the sequence as they are presented in the cladograms from the top downwards or left to right. The zeuzerine species are listed in the sequence of the cladograms, but the sequence of species from other subfamilies is indiscriminate. For most zeuzerine genera, a list of species with the names and combinations as originally published is provided. The usual sequence in the generic descriptions is the taxonomic history and/or diagnosis followed by a further description of the morphology. Most plesiomorphies are neglected in the generic descriptions, since these are given in a separate paragraph. The states of the vertex and/or humeral plate are known only in those species for which these structures are described. "An" means the anepisternum of the mesothorax when not indicated otherwise. Indications of the height of An and length of the lower suture of "Apc" concern these structures in lateral view. The relative width of the mesomeron has been estimated halfway along its length. In the descriptions of structures "rather" means slightly more (longer, higher, shorter) than "moderately". Descriptions and illustrations of wing bases refer to and depict dorsal views. Unless otherwise stated 1Ax and 4Ax refer to the forewing. Descriptions of the median plate concern the one of the hindwing. The terminology for the thoracic sclerites conforms mainly with Common (1970), Matsuda (1970) and Brock (1971). The author couldnot find names for the plates next to the mes- and metepimeron and has tentatively named them accessory plates. The sclerite between the eucoxa III and metameron is provisionally named intersclerite III. The terminology for the sclerites of wing bases follows mostly Sharplin (1963a and b). The author is unaware of a common name for the (ovate) plate posterior to the radial bridge and has tentatively named it the scale plate. Illustrations of thoracic sections with the described parts named are provided (figs.

1-6). In the cases of type-material and specimens of unidentified or undescribed species, the complete label data are provided under "Material", whereas of other material the dates, names of collectors and the numbers of preparations are omitted. Geographical names are spelled according to "The Times Atlas of the World" (seventh Comprehensive Edition, 1985), when possible.

Illustrations were made by freehand drawing and are on various scales. In the pencil drawings, membranous areas are indicated by small dots, and bending cuticle by larger, open dots. Crosses indicate cavities.

Abbreviations of institutions from which material was used are explained below.

BMH — Bishop Museum, Honolulu, Hawaii, U.S.A.
BMNH — The Natural History Museum (formerly British Museum (Natural History)), London, U.K.
CMNH — Carnegie Museum of Natural History, Pittsburgh, U.S.A.
IPCN — Instituto Patagónico de Ciencias Naturales, San Martín de los Andes, Argentina.
ITZ — Instituut voor Taxonomisch Zoölogie, Universiteit van Amsterdam, Amsterdam, The Netherlands.
LNK — Landessammlungen für Naturkunde, Karlsruhe, West Germany.
MNHN — Muséum National d'Histoire Naturelle, Paris, France.
MHUB — Museum für Naturkunde der Humboldt-Universität, Berlin, East Germany.
MRAC — Musée Royal de l'Afrique Centrale, Tervuren, Belgium.
NHMA — Natural History Museum of Los Angeles County, Los Angeles, U.S.A.
NMW — Naturhistorisches Museum Wien, Wien, Austria.
RMNH — Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands.
USNM — United States National Museum of Natural History (Smithsonian Institution), Washington D.C., U.S.A.
ZMUC — Zoologisk Museum, København, Denmark.

Abbreviations

A — anal vein
An — anepisternum
Apc — anapleural cleft
approx. — approximately
Ax — axillary sclerite
Bs — basisternum
c. — central
Cu — cubital plate
CuA — anterior cubital vein
CuP — posterior cubital vein
e. — eastern
K — katepisternum
M — median vein
n. — northern

Pa	— parepisternum
Pas	— parepisternal suture
Pos	— postinterocellar suture
Pre	— pre- episternum
R	— radial vein
s.	— southern
Sc	— subcostal vein
undescr. gen.	— undescribed genus
undescr. sp.	— undescribed species
w.	— western

Taxonomic history

Cossid genera were for long placed in the Bombycines (Bombycidae Latreille, [1802]). The name Cossida was introduced by Leach ([1815] 1830) for a group of species including *Cossus cossus* (Linnaeus). Boisduval (1829: 51-52) places *Cossus* Fabricius, 1793, *Zeuzera* Latreille, 1804, *Stygia* Latreille, [1802] and *Hepialus* Fabricius, 1775 in the "tribus" Zeuzeridi. Boisduval (1834) adds *Endagria* to this series of genera and names the tribe Zeuzerides. Newman (1832: 67-68) notes Cossi as a natural order and distinguishes Stygiidae, Zeuzeridae and Cossidae. Meyrick (1895: 445-446, 559) distinguishes Zeuzeridae, including *Zeuzera* and *Phragmataecia* Newman, 1850, and Trypanidae for *Trypanus* Rambur, 1866, an unnecessary objective replacement name for *Cossus*. Hampson (1920: 267) establishes the family Engyophlebidae (for *Engyophlebus* Karsch, 1900), which was synonymized with the Cossidae by Handlirsch (1925). Meyrick (1928: 479) uses only the name Zeuzeridae and includes *Trypanus*. Essig (1951, according to Arora, 1976) also distinguishes Cossidae and Zeuzeridae, and combines them as Cossoidea. Most authors, past and present, distinguish only one family, the Cossidae.

The Cossidae were placed in various superfamilies by different authors. Stainton (1857) includes the Zeuzeridae in the Bombycina. Meyrick (1928) places the Zeuzeridae in the Psychina (Psychidae Boisduval, 1840). Forbes (1923: 375-376) includes the Cossidae with the Tortricidae Latreille, [1802] in the Tortricoidea. Handlirsch (1925) treats the Cossidae in the Tineoidea. Turner (1946: 338) places the Cossidae with the Arbelidae Hampson, [1893] 1892 (junior synonym of Metarbelidae Strand, 1909) in the Cossoidea. Best-argued of the present classifications is that by Brock (1971), who includes the Cossidae, Ratardidae Hampson, 1898, Metarbelidae, Megalopygidae Herrich-Schäffer, 1855, Dalceridae Dyar, 1898, Limacodidae Duponchel, [1845] 1844 and Chrysopolomidae Aurivillius, 1895 in the Cossoidea (see chapter on the supposed close relationships of the Cossidae).

Neumoegen & Dyar (1894: 160-163) distinguish the following subfamilies: Zeuzerinae, Cossinae and Hypoptinae. They include *Hypopta* Hübner, 1818 and *Cossula* Bailey, 1882 in the Hypoptinae. This classification of subfamilies has been followed by most authors.

Handlirsch (1925) treats the Cossidae sensu Neumoegen & Dyar as a subfamily and adds Argyrotypinae, Metarbelinae, and Ratardidae (with a question-mark) as new subfamilies to the Cossidae. Handlirsch distinguishes the following new tribes of

Cossinae: Cossini, Zeuzerini, Engyophlebini, and Stygiini.
Zerny & Beier (1936: 1695-1696) distinguish the following subfamilies of Cossidae: Cossinae, Eulophonotinae (Engyophlebinae), Argyrotypinae and Metarbelinae.
Berger (1957) excludes *Dudgeonea* Hampson, 1900 from the Cossidae and proposes a new family Dudgeonidae. He further distinguishes in his key the subfamilies Eulophonotinae and Cossinae.
Clench (1959c: 223-230) synonymizes *Parazeuzera* Bethune-Baker, 1904 with *Pseudarbela* Sauber, 1902, and places this genus, *Casana* Walker, 1865 and *Linggana* Roepke, 1957, which had originally been included in the Cossidae, in the new family Pseudarbelidae.
Hodges (1983: 31) introduces the subfamily Cossulinae for *Cossula*.
Heppner (1984: 99) proposes the subfamily Pseudocossinae, in which he includes *Pseudocossus* Kenrick, 1913, *Chilecomadia* Dyar, 1940 and *Rhizocossus* Clench, 1957.
Minet (1986: 298-299) includes again the Metarbelidae as a subfamily in the Cossidae, because of similar types of pronotum.

Notes on taxonomic history

A problem of most classifications indicated above is that the authors do not indicate one or more (relatively) derived character-states in support of them. Only Brock (1971) and Minet (1986: 299) point out such character-states to justify their classifications of resp. Cossoidea and Cossidae.

Minet (1986: 299) notes an apomorphy of the subfamilies which he includes in the Cossidae, and he refers to Schultz (1914: fig. 8). This apomorphy concerns the type of pronotum; the parapatagia are well-developed, approaching one another, and more or less projecting in the sagittal plane. In most Cossidae and at least certain Metarbelidae the parapatagia are approx. as high as the patagium. A low(ered) patagium or pronotum is known in only a few cossid genera and is seemingly secondary. A high patagium and pronotum are probably ground-plan character-states of the Cossidae. A moderately high pronotum is known in several *Cossula* species and *Culama* Walker, 1856. These two genera are excluded from the Cossoidea for several reasons (see below and chapter on excluded and obscure taxa). It is thus not only important that the parapatagia are well-developed but more that they are approximately as high as the patagium. Judging the figures provided by Schultz (1914), it seems that a high pronotum is also found in the Tineidae Latreille, 1810, Yponomeutidae Stephens, 1829, Zygaenidae Latreille, 1809, Sphingidae Latreille, [1802] and Bombycidae Latreille, [1802]. It is not known which types of pronotum are present in cossoid families other than Cossidae and Metarbelidae.

Minet (1986: 299) includes also the Metarbelidae as a subfamily of the Cossidae, apparently because of the type of pronotum. It is not yet certain if in all other Cossoidea the pronotum is hardly developed or distinctly lower than the patagium. The shape of the parapatagia is perhaps a synapomorphy of the Metarbelidae and Cossidae, but this does not imply that the Metarbelidae should be included in the Cossidae as a subfamily; the Metarbelidae may be the sister-family of the Cossidae sensu Neumoegen & Dyar (1894). The present author believes that it is easier to fit the Metarbelidae in as the sister-group of the Cossidae than somewhere within the family Cossidae. The taxon Metarbelidae is therefore tentatively regarded here as a separate family, pending an extensive study of this group (see also chapter on excluded and obscure taxa).

Minet (1986: 298-299) includes the Cossulinae in the Cossidae, as Hodges (1983: 31) did. At least in certain *Cossula* species the pronotum is high, but the patagium is low or only moderately high. As Minet (1986: 298) notes, the Cossulinae do not show the typical type of mesepimeron of the Cossoidea (see Brock, 1971: 52). Minet records that this type of mesepimeron is absent in several other taxa, which have been included in the Cossidae or Cossoidea, and does not regard it as a good diagnostic characteristic of the Cossoidea. In contrast to what Minet notes, this characteristic is present in at least certain Dalceridae and Chrysopolomidae; it is found in *Dalcerina* Dyar, 1898 (see fig.125) and *Achrocerides* Hering, 1937. In the Pseudocossinae it is present too, although indistinctly in *Pseudocossus*. The absence of this characteristic in certain genera of Cossinae, such as *Dyspessa* Hübner, 1816 is seemingly secondary. The mesepimeron does not have a membranous band, as Brock (1971: 52) notes, but a band of another type of sclerotization, which is normally paler than the rest of the mesepimeron. In this study it is regarded as a good diagnostic characteristic of the Cossoidea. *Cossula* further differs from (other) Cossidae in that the crochets of the larvae are arranged in two transverse bands instead of a complete circle (Fracker, 1915: 77). Because of different types of mesepimeron, patagium and crochets in *Cossula*, the Cossulinae are here excluded from the Cossidae and Cossoidea.

The present author distinguishes the following subfamilies: Cossinae, Zeuzerinae, Hypoptinae, Pseudocossinae, and a new one for *Rhizocossus* and *Chilecomadia*.

Fossils

There are some records of fossils which have been ascribed to the Cossidae on the basis of the forewing venation.

Palaeocossus jurassicus and *Phragmatoecites damesi*, which were described by Oppenheim (1885: 332-333), have been transferred to the Homoptera.

Gurnetia durranti was proposed by Cockerell (1921: 472-473) and based on a forewing fragment from Oligocene deposits from the Isle of Wight (Great Britain). All radials are separate in *durranti*, while the inner cell is wanting according to Cockerell's figure. CuA2 of the forewing branches off very distally, a feature unknown in the Cossidae. The present author does not believe that *Gurnetia* is a cossid.

Cockerell (1926: 16-17) described *Adelopsyche frustrans* from a fossil from Miocene deposits from Colorado (U.S.A.). Cockerell's figure of the fossil shows a species with a very ovate forewing. The type of venation is most unusual for the Cossidae. R1 branches off before the areole but very distally, while R4 and R5 are connate and M in the cell is proximally close to CuA. The description of *frustrans* does not convince the present author that it is a cossid.

Xyleutites miocenicus was described by Koshantschikov (1957: 675-677, fig. 2) from a fossil from Miocene deposits in the Caucasus. The type of venation of *miocenicus* is not typical of a cossid, since R4 is more stalked with R3 than with R5. This state is occasionally found in certain species of Cossinae, but in the Cossinae R3 and R4 are sinuate and R3 and R4 of *miocenicus* are figured as nearly straight. *X. miocenicus* should probably be placed in another family.

It is generally very difficult to tell from the venation of a fossil if that specimen belongs to the Cossidae, since there are also other taxa with a similar type of venation. The author is not aware of any convincing record of a cossid fossil.

Supposed plesiomorphies of Cossidae

The supposed ground-plan character-states of the Cossidae are listed below. The family Metarbelidae is possibly the sistergroup of the Cossidae, if the type of pronotum is indeed a synapomorphy of the two families (see also chapter with notes on the taxonomic history, and the one on excluded and obscure taxa). A problem is that the phylogeny of the Metarbelidae is obscure. The plesiomorphic states of the Cossidae have been assessed by considering the distribution of the character-states amongst the cossid taxa, by comparison of these states with those in several species of Metarbelidae, and by comparison of the states in the Cossidae and these Metarbelidae with those in non-cossoid taxa, such as *Gelechia turpella* Denis & Schiffermüller, 1775, *Anacampsis populella* Clerck (Gelechiidae Stainton, 1854), *Yponomeuta cagnagella* Hübner, 1810-13 (Yponomeutidae), many Tortricidae, *Pseudurgis* Meyrick, 1908, *Meharia* Chrétien, 1915, *Aeonoxena* Meyrick, 1928, *Nomima* Durrant, 1916, *Culama*, *Idioses* Turner, 1927, *Cossula* and closely related genera, *Ptilomacra* Walker, 1855, *Archaeoses* Turner, 1932, *Dudgeonea* and *Acritocera* Butler, 1886. The metarbelid species examined are *Cossodes lyonetii* White, 1841, *Saalmulleria stumpfii* (Saalmüller, 1884), *Lebedodes wichgrafi* Grünberg, 1910, *Melisomimas metallica* (Hampson, 1914), and *Squamura acutistriata* Mell, 1923.

The list thus functions as a working hypothesis for the elucidation of the phylogeny of the Cossidae in this paper. The states are listed in the sequence as used further in this paper.

Head. Vertex moderately long, more or less flat, with pair of small protuberances anteriorly; Pos (sensu Kristensen & Nielsen, 1979: 75) nearly straight or slightly sinuate, at approx. 0.5 or 0.6 times length of vertex; ocelli present; chaetosemata absent. Eyes moderately large. Marginal sclerites of eyes and vertex narrow. Plesiomorphic state of antenna in the family not certain. In the new subfamily Chilecomadiinae perhaps a completely prismatic antenna plesiomorphic. The plesiomorphic state of antenna in the Cossinae and Hypoptinae most probably completely bipectinate in both sexes, up to rather strongly, gradually tapering distally, and with approx. two rows of moderately long hairs on inner side of rami. In the Zeuzerinae antenna proximally bipectinate for approx. 0.7 times its length, up to rather strongly, and further shortly prismatic; rami with approx. two rows of moderately long hairs on inner side. Flagellum with scales irregularly distributed on dorsal side of flagellomeres and not in one or two rows. Frons moderately narrow. Frontal tuft probably ventrally very short and gradually lengthening up to moderately short dorsally; scales two- or multipointed. Clypeus moderately narrow and simple. Labrum small and simple, without pilifers. Tentorial pits moderately small and more or less rounded. Maxillary palpi short and two-segmented. Labial palpi three-segmented, approx. twice length of eye-diameter, moderately thick, upturned; second segment distinctly longer than first and third one; third segment more or less ovate; vestiture ventrally mainly short or moderately short mixed with fewer moderately long scales. Galeae separate and short or very short; often longer in female than in male.

Thorax. Patagium a paired structure and membranous; flaps very high, more or less swollen and curved. Pronotum consisting of pair of very high flaps (parapatagia sensu Schultz, 1914), membranous and often slightly swollen. Mesoscutum long. Mesoscutellum moderately long, posteriorly rounded. Metascutum moderately narrow and not invaginated. Metascutellum moderately wide, posteriorly rounded, and gradually narrowing laterally. Bs I moderately small. Lateral cervical sclerites well-developed, approaching one another. Tegula ventro-posteriorly distinctly upturned and distinctly pointed. An (II) high. Apc approx. narrow; lower suture reaching nearly or approx. complete length of An, terminating on or just dorsally to K; lower suture approx. parallel to upper one. Pre II moderately long and with more or less rounded antero-dorsal corner. Upper Pas at approx. 0.4 or 0.5 times length of Pre plus Pa. Lower Pas approx. moderately long. Pa short. K long, with a longitudinal suture and a cross-suture. Bs II rather large, moderately ovate, more or less vaulted, and gradually tapering posteriorly; anterior arms moderately long and moderately wide; median suture more or less sunk; Bs-Pa more or less invaginated; Bs deeply grooved along most of length of Bs-Pa; latero-posterior margins narrow. Subalare-process II approx. moderately short and moderately thick. Aculeate area at mesepimeron well-developed. Mesepimeron rather high, rather squared in outline of ventral half, with more or less rounded upper margin, and medio-posteriorly with a band of a different type of (paler) sclerotization. Accessory plate II moderately long and wide. Mesomeron halfway along its length approx. as wide as eucoxa II. An III ovate and moderately large. Pre III moderately narrow. Bs III moderately large and lateral arms moderately wide. Metepimeron approx. moderately high. Accessory plate III narrow or very narrow. Intersclerite III moderately large and triangular. Metameron moderately narrow, distinctly narrower than eucoxa III.

Legs stout. Vestiture on tibiae at least dorsally long. I-epiphysis ovate, moderately wide, based at approx. one-third length of tibia, reaching distinctly short of tibia-apex, and similar in both sexes. Midleg with one pair of spurs and this pair at apex. Hindleg with two pairs of spurs; midtibial spurs distinctly beyond half length of tibia; other pair apically. Tibial spurs in pairs of unequal length; long and rather long. Tibia and first tarsomere of hindleg partly swollen. Vestiture of tarsi long but shortening over tarsi apically; vestiture medially brown or fuscous, and whitish at base and apex of each tarsomere. Tarsomeres distinctly widened apically and narrowed at bases; with many moderately long, dark brown and stout spines, but on fifth tarsomere spines fewer and shorter; fifth tarsomere approx. as long as fourth; scales on tarsomeres dorsally ovate and ventrally narrow and more or less stiff. Paronychia moderately short, moderately narrow, and finely haired. Tarsal claws moderately long, moderately thick and distinctly widened at bases. Arolium moderately long, moderately wide, and distally widened.

Forewing moderately long, narrower than hindwing, and not specially widened at approx. one-third wing-length. Fringes long, consisting of approx. three layers of scales, and these scales bi- or multipointed. Folds of forewing along Rs and CuA. Folds of hindwing along Rs, proximally along CuA and distally along CuP, and further along anal veins. Male retinaculum well-developed and broadly triangular, with moderately long base, and against Sc. Male frenulum spine well-developed, long.

Female retinaculum inconspicuous, consisting of somewhat longer scales on wingfold along CuA. Female frenulum bristles long and three to five in number. Costal region of hindwing proximally rather wide, gradually narrowing distally from approx. 0.6 or 0.7 times wing-length onwards. Dorsum of hindwing weakly or not invaginated. Anal region of hindwing moderately wide and not elongate.

Venation: R1 branching off at approx. 0.3 or 0.4 times wing-length; areole moderately long and moderately wide; R2 branching off at approx. 0.6 times length of areole; R3, R4 and R5 all separately from distal margin of areole; all radial veins approx. straight or slightly arcuate; chorda and anterior M terminating at distinct distance from each other; M approx. median in cell; M1 from tip of areole or posterior to areole; inner cell moderately large; posterior M in cell terminating more or less posterior to M2; CuA2 branching off at approx. 0.8 times length of CuA; CuP and A1+2 completely separate from each other; furcation of A1+2 moderately or rather long; cross-vein Sc-Rs (hindwing) absent; Rs-M1 approx. moderately long; M approx. median in cell; M2 and M3 separate; A1+2 furcate at very base; A3 and A1+2 terminating at distinctly wider distance from each other than A1+2 and CuP.

Forewing base. Humeral plate approx. 1.5 times size of radial bridge. Radial plate moderately long, more or less trapezium-like in shape, and with moderately slender apex. Radial bridge moderately large and consisting mainly or completely of bending cuticle. Scale plate shorter than radial bridge, moderately wide, and ovate. 1Ax apically moderately small and gradually tapering. 3Ax and 4Ax fused, but posteriorly partly separate and here 3Ax dorsal to 4Ax; distal plate of 4Ax well-developed. Lateral process of posterior notal wing process appearing (nearly) mainly separate.

Hindwing base. Median arm rather long, approx. moderately narrow, and without (distinct) invagination proximo-anteriorly. 1Ax apically moderately small. 2Ax moderately long, slightly longer than wide, with moderately short and moderately narrow apodeme, and without special bulbed and scaled area. Median plate moderately narrow, and more or less quadrangular. Cu2 proximally rather wide, and distally widened. 3Ax and 4Ax much fused and bar-like. Posterior notal wing process moderately wide. Anal plate rather long.

Abdomen shorter than or nearly as long as hindwing, with rather long anal tufts, but without other, special tufts; its vestiture mainly moderately long. Female abdomen not specially narrowed or elongate apically. Ovipositor hardly or not protuberant. Tergite I sclerotized for approx. proximal one-fourth and further membranous.

Table 1. Apomorphies in fig. 7 (subfamilies of Cossidae).

1.	An reduced in height; at most moderately high.
2.	Mesomeron wider than eucoxa II, at least approx. 1.3 times as wide.
3.	First tarsomere and normally also tibia of hindleg not swollen; first tarsomere of hindleg approx. as thick as second one of this leg.
4.	Ocelli wanting.
5.	Mesomeron approx. 1.5 times width of eucoxa II.
6.	Tibial spurs at most moderately long and moderately short.
7.	Paronychia distinctly reduced to/or wanting.
8.	Labial palpi: third segment conical (instead of ovate).

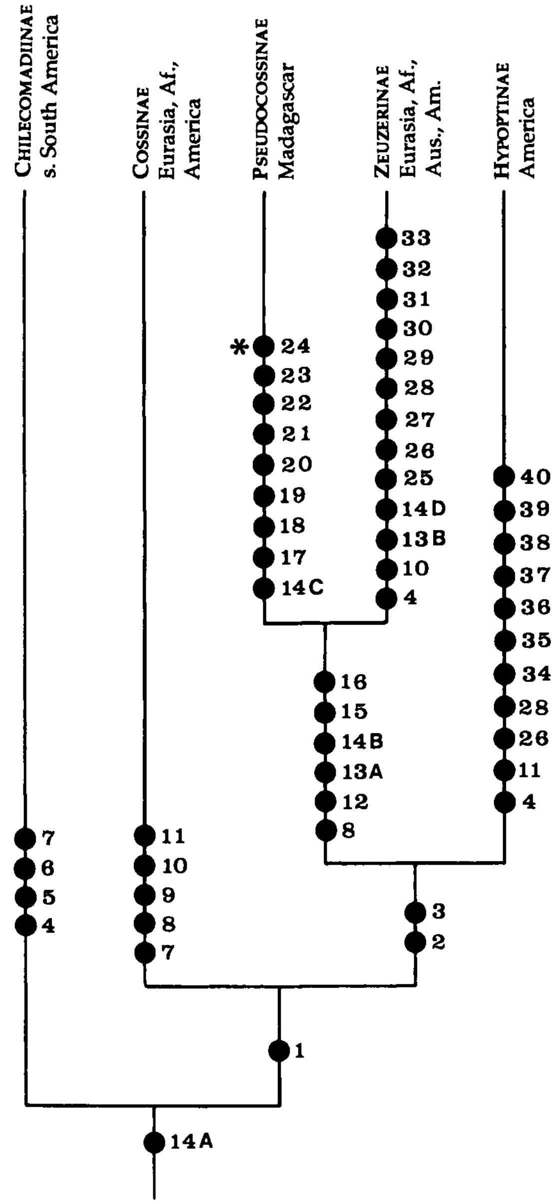


Fig. 7, cladogram of the cossid subfamilies.

9. R3 and R4 sinuate.
10. R4 (normally) stalked with R5.
11. Anal plate moderately long.
12. Mesoscutellum posteriorly elongate, and more or less pointed apically but sometimes or often indistinctly so.

13a. Pre II antero-dorsally elongate (fig. 53).
b. Pre II with distinct process antero-dorsally (figs. 57-58 and 82-83).
14a. Mesepimeron rather high. (*)
b. Mesepimeron reduced in height (at most moderately high).
c. Mesepimeron moderately high.
d. Mesepimeron moderately low, and with sinuate upper margin.

15. Male retinaculum with long base.
16. Median arm moderately long and moderately wide.
17. Pronotum low.
18. An low.
19. Tergite I mainly sclerotized.
20. I-epiphysis finely toothed.
21. Inner cell of forewing indistinct to/or wanting.
22. CuA1 and CuA2 of forewing very close or connate.
23. 1Ax of forewing apically rather large.
24. Posterior notal wing process of forewing: lateral process separate from main structure for approx. one-third its length.
25. Antenna proximally bipectinate and distally prismatic.
26. Frontal tuft moderately or rather long.
27. Apc rather wide and its lower suture reaching up to approx. one-third length of An.
28. Upper Pas situated in extremely ventral postion (see figs. 57-58, 82-83 and 99-100).
29. Accessory plate III wide.
30. Midtibial spurs (of hindleg) wanting.
31. Apical spurs of tibiae II and III (very) short.
32. Areole very long (and moderately wide).
33. R1 from areole and at approx. half wing-length.
34. Vestiture on second segment of labial palpi approx. moderately long. (*)
35. Tegula bluntly pointed and moderately upturned or gradually tapering.
36. M of forewing close to CuA.
37. CuP and A1+2 of forewing normally distally linked by a cross-vein or more or less coalescent.
38. Sc and Rs of hindwing linked by a cross-vein, which is usually rather long to long. (*)
39. M of hindwing close to CuA.
40. 3Ax and 4Ax of hindwing mainly separate and 4Ax approx. as dorsal as 3Ax along most of its length; they are only anteriorly fused.

Key to the subfamilies of Cossidae

1\. Tibia and first tarsomere of the hindleg partly swollen 2

\- Tibia and first tarsomere of the hindleg not swollen; first tarsomere approx. as thick as second one of the hindleg 3

2\. R3 and R4 nearly straight (fig. 27) .... **Chilecomadiinae**

\- R4 and R5 sinuate (figs. 28-30) .... **Cossinae**

3\. Distinct ocelli present. Midtibial spurs (of the hindleg) present. Posterior notal wing process of the forewing: lateral process separate from the main process for only approx. one-third its length (fig. 54) .... **Pseudocossinae**

- Ocelli wanting, but sometimes small protuberances present. Midtibial spurs (of the hindleg) in most species wanting. Posterior notal wing process of the forewing: lateral process mainly separate from the main process (figs. 8, 20-21, 31, 59, 65, and 74) 4

4. Male antenna bipectinate or bilobed along its whole length. CuP and A1+2 of the forewing normally distally linked by a cross-vein or more or less coalescent. 3Ax and 4Ax of the hindwing mainly separate and only anteriorly fused. Strictly American .... **Hypoptinae**

- Male antenna in most species proximally bipectinate and distally prismatic. CuP and A1+2 of the forewing in most species separate. 3Ax and 4Ax of the hindwing fused along considerable part of their length and not only anteriorly (figs. 59 and 65). Cosmopolitan .... **Zeuzerinae**

Systematic section

Family **Cossidae**

Cossidae Leach, [1815] 1830: 131 (as Cossida).
Type genus: *Cossus* Fabricius, 1793: [1].
Contaminatae Hübner, [1820] 1816: 194. [Unavailable name].
Crassae Hübner, [1820] 1816: 195. [Unavailable name].
Graciles Hübner, [1820] 1816: 196. [Unavailable name].
Zeuzeridae Boisduval, [1828] 1829: 51 (as Tribus Zeuzeridi).
Type genus: *Zeuzera* Latreille, 1804: 186.
Trypanidae Meyrick, 1895: 559. [Unavailable name].
Engyophlebidae Hampson, 1920: 267.
Type genus: *Engyophlebus* Karsch, 1900: 3.

Subfamily **Chilecomadiinae** subfam. nov.

Type genus: *Chilecomadia* Dyar, 1940: 1274.

The new subfamily Chilecomadiinae is introduced for *Chilecomadia* and *Rhizocossus*. These two genera share the following apomorphies: ocelli wanting, mesomeron approx. 1.5 times width of eucoxa II, tibial spurs at most moderately long and moderately short, and paronychia very small or wanting. In *Chilecomadia* An is still high, which is unique within the Cossidae. In *Chilecomadia* the anal plate is still nearly or actually rather long. In *Rhizocossus* An is moderately high and the anal plate is rather or moderately long. In *Chilecomadia* the ♂ antenna is moderately shortly unilobed and in *Rhizocossus* prismatic. The ♀ antenna is prismatic in both genera.

It seems that *Chilecomadia* and *Rhizocossus* form a separate monophyletic taxon, which takes the first branch in the cladogram of the Cossidae (fig. 7). Therefore a new subfamily is introduced for the two genera. It is difficult to characterize this subfamily. A widened mesomeron is also found in the other subfamilies. Within the Cossidae ocelli are also known in *Pseudocossus* Kenrick (Pseudocossinae) and *Catopta* Staudinger, 1899 (Cossinae). Reduction in length of the tibial spurs and of the paronychia is a general trend within the Cossidae. A high An is a plesiomorphy which is known only in *Chilecomadia* within the Cossidae. However, the presumed position of *Chilecomadia* and *Rhizocossus* in the cladogram (fig. 7) justifies a subfamily of their own.

Chilecomadia, Rhizocossus and *Pseudocossus* were erroneously included in the Dudgeoneidae by Munroe (1982: 630), who believed that paired tympanic organs are present in these genera, probably misinterpreting the publication by Clench (1959b). Munroe (1988: 79) corrects this view by including only one genus in the Dudgeoneidae (thus *Dudgeonea*).

Chilecomadia and *Rhizocossus* had been included in the Pseudocossinae by Heppner (1984: 99). The type genus of the Pseudocossinae is *Pseudocossus* Kenrick. The only significant characteristics which Heppner notes for the three genera are a filiform antenna, the abdomen with proto-tympanic organ as a lateroventral invagination on anterior sternite, and a slightly bifid uncus.

The ♂ antenna is prismatic in *Pseudocossus*. Females of the *Pseudocossus* species are unknown. In *Chilecomadia* and *Rhizocossus* the ♂ and ♀ antenna are not filiform but unilobed or prismatic.

In *Pseudocossus, Chilecomadia* and *Rhizocossus* the abdominal base has latero-ventrally depressed areas, which are sometimes/often thinner or partly membranous and partly scaleless. Clench (1957: 123; 1959b: 46) interpretates these areas as respectively a rudimentary abdominal tympanum and a prototympanum. Heppner (1984: 99) apparently follows Clench in his interpretation of these areas. Such depressed areas are also known in e.g. *Catopta* and (outside the Cossidae) *Meharia*. An actual tympanum is not found in the Cossidae. This form of the abdominal base is here considered plesiomorphic for the Cossidae and not related to an actual tympanum.

A bifid uncus seems to be special within the Cossidae. It is also known in certain species of *Holcocerus, Bifiduncus* Chou & Hua, 1988, and several ones of Hypoptinae. In probably most other Cossidae the uncus is more or less pointed. Outside the Cossidae a bifid state is known in *Acritocera negligens* Butler, 1886 and occur perhaps in other genera. Perhaps a bifid uncus is a groundplan character-state of the family Cossidae.

Because *Pseudocossus* differs profoundly from *Rhizocossus* and *Chilecomadia* (see under *Pseudocossus*), is seemingly the sister-group of the Zeuzerinae (see fig. 7) and is the type genus of the Pseudocossinae, *Chilecomadia* and *Rhizocossus* are excluded from the Pseudocossinae.

Genus **Chilecomadia** Dyar, 1940

Chilecomadia Dyar, 1940: 1274.

Type species: *Langsdorfia moorei* Silva Figueroa, 1915: 53-55, fig. 14 (female and male), fig. 15 (fringe scale).

Diarthrosia Bryk, 1945: 24-25. [Synonymized by Ureta, 1957: 129, 139].

Type species: *Diarthrosia zeuzerina* Bryk, 1945: 24-25, pl. 2: fig. 19 (female). [Synonymized with *Langsdorfia moorei* Silva Figueroa by Ureta, 1957: 129, 139].

Allocossus Bryk, 1945: 25-26. [Synonymized by Ureta, 1957: 129, 136].

Type species: *Allocossus discoclathratus* Bryk, 1945: 25-26, pl. 2: fig. 18 (female). [Synonymized with *Cossus valdiviana* Philippi, 1859 by Ureta, 1957: 129, 136].

Dyar (1940: 1274) includes both *moorei* and *valdiviana* in *Chilecomadia*. Ureta (1957: 129, 136, 139) synonymizes *Diarthrosia zeuzerina* Bryk with *moorei* and *Allocossus discoclathratus* Bryk with *valdiviana*. Gentili (1985: 51) synonymizes *Rhizocossus* with *Chilecomadia*. In this study *Rhizocossus* is resurrected (see below). In this paper *moorei* and *valdiviana* are the only species included in *Chilecomadia*. The ♂ antenna of *valdiviana* and *moorei* is moderately shortly unilobed. The lobes are apically rounded and have many short or moderately long hairs on the proximal side. The ♀ antenna is shortly prismatic. The ♀ antenna of *valdiviana* is nearly unilobed and that of *moorei* is slightly flattened. The antennal segments have many short hairs ventrally and laterally. Ocelli are wanting. The frontal tuft is moderately or rather long. The third segment of the labial palpi is ovate. The upper Pas of *valdiviana* is against Pa and that of *moorei* is at approx. half length of Pre II plus Pa. The tibial spurs are moderately long and moderately short. Paronychia are wanting. The scale plate is slightly shorter than the radial bridge, which is considered a plesiomorphy. In *Chilecomadia* An is still high. In *Rhizocossus* An is moderately high. The mesepimeron is rather high in *valdiviana* and high in *moorei*. The accessory plate II varies from moderately wide to moderately narrow in *valdiviana*. In both species the mesomeron is approx. 1.5 times width of the eucoxa II. The anal plate is moderately long. Other character-states in the two species seem to be plesiomorphic.

Vertex has a slightly ridged Pos; Pos of *valdiviana* at approx. 0.8 times length of vertex and that of *moorei* at approx. 0.8 length. Vertex probably lacks at least sometimes anterior protuberances. K lacks a cross-suture in examined specimens. Vestiture on tibia of midleg is moderately long on dorsal side. I-epiphysis reaches distinctly short of tibia-apex, and is ovate and apically blunt. Tibia and first tarsomere (partly) of hindleg are distinctly swollen. Fringes are long. Male frenulum spine and retinaculum are well-developed. Number of ♀ frenulum bristles amounts approx. four in at least *moorei* and these are long. Venation: areole moderately small; R4, R5 separate; Rs-M1 moderately long. Humeral plate is slightly larger than radial bridge in at least *moorei*. Median arm is rather long and moderately narrow. Anal plate is nearly or approx. rather long.

C. moorei is distributed from La Serena to Punta Arenas in Chile (Ureta, 1957: 140), and is further known from Argentina (Neuquén, Río Negro, Chubut) (Gentili, 1985: 58). *C. valdiviana* is represented from Coquimba to Magallanes in Chile (Ureta, 1957: 138), and is also known from Argentina (Neuquén, Río Negro, Santa Cruz) (Gentili, 1985: 65). Information on the types of habitats and hosts of both species is provided by Gentili (1985: 57-58, 64-65). Both species live in forest with one or more species of *Nothofagus* Blume, at altitudes up to 1800 m. Hosts of *moorei* are at least Quince and Palto. Hosts of *valdiviana* are *Nothofagus antarctica* Oerst., *N. pumilio* Reiche, *Weinmannia trichosperma* Cav., Quince, Apple, Pear, Olive, Palto, and Willow.

Material:

moorei —(all ZMUC)—1♂, CHILE: Valdivia, near Valdivia, Rincon de la Piedra, 180 m.; 6♂♂, 1♀, ARGENTINA: Río Negro, near Bariloche, La Querencia.

valdiviana —(all ZMUC) —1♀, CHILE: Valdivia, near Valdivia, Rincon de la Piedra, 180 m.; 1♂, 1♀, ARGENTINA: Neuquén, near los Andes, Piedra Trampul, 1000 m.; 7♀♀, ARGENTINA: Río Negro, near Bariloche, Colonia Suize, 800-810 m.

Genus **Rhizocossus** Clench, 1957

Rhizocossus Clench, 1957: 124-125, 128-130.
Type species: *Rhizocossus munroei* Clench, 1957: 130-131, pl. 4: fig. 3 (male genitalia), pl. 5: fig. 1a-c (resp. venation, head profile and antennal segments).

So far only *munroei* has been included in *Rhizocossus*. Gentili (1985: 51, 54, 67) synonymizes *Rhizocossus* with *Chilecomadia*, and *Acossus comadioides* Ureta, 1957 with *munroei*. Gentili (1985) recognizes only one species of *Rhizocossus*, but in the present study two more are known. The present author prefers to keep the two genera separate and resurrects *Rhizocossus*. The three species of *Rhizocossus* differ especially from those of *Chilecomadia* in that the pronotum is distinctly lower than the patagium.

In the BMNH there are three unidentified specimens representing two closely resembling species which should be placed in *Rhizocossus*. The two male specimens of the undescribed species from Patagonia have a bifid uncus, which is characteristic of *Chilecomadia*, *Rhizocossus* and *Pseudocossus*. The three specimens have a prismatic antenna, which seems to be proximally simple, as in *munroei*. Ocelli are wanting, whereas these are present in *Pseudocossus*. The mesomeron of the undescribed species is also widened.

The ♂ and ♀ antenna seem to be proximally flattened and simple, since there is hardly any space between the lobes of the segments. More distally the antenna is more distinctly prismatic. The segments have ventrally and laterally many short hairs. In undescribed species (b) the ventral lobes each have one stout sensillum, which is lacking in *munroei*. The Pos is at 0.5 to 0.7 times length of vertex. Ocelli are wanting. The frontal tuft is moderately or rather long. The pronotum is slightly or considerably lower than the patagium. An is moderately high. The upper Pas is slightly lower than half length of Pre II plus Pa. The species share with those of *Chilecomadia* that the mesomeron is approx. 1.5 times width of the eucoxa II. The midtibial spurs of *munroei* are moderately long and slightly unequal in length and the apical ones are moderately short and also slightly unequal. The midtibial spurs of undescribed species (a) are moderately short and slightly unequal in length and the apical ones short and also slightly unequal. R5 is shortly stalked with R4 in the undescribed species (b) (fig. 26). The humeral plate is approx. as large as the radial bridge (fig. 8). The radial bridge is large.

Vertex of *munroei* lacks anterior protuberances in the two examined specimens. Pos of *munroei* is at approx. half length of vertex and slightly sinuate. Vertex of undescribed species (a) lacks anterior protuberances in the two examined specimens and has anteriorly small, ring-like markings (fig. 13). Pos of undescribed species (a) is at approx. half length of vertex and slightly sinuate, and has subterminally a very small protuberance and a small pit. Vertex of undescribed species (b) has in the examined specimen a pair of protuberances at approx. half length of vertex and little anteriorly to these a pair of smaller ones and a pair of ring-like markings (fig. 14). Pos of undescribed species (b) is moderately arcuate up to approx. 0.7 times length of vertex and has subterminally small, shallow pits. Labial palpi of female are approx. 3 times length of eye-diameter and those of male approx. twice as long. Third segment of labial palpi is ovate, which is presumably a plesiomorphy in this case. Pronotum is

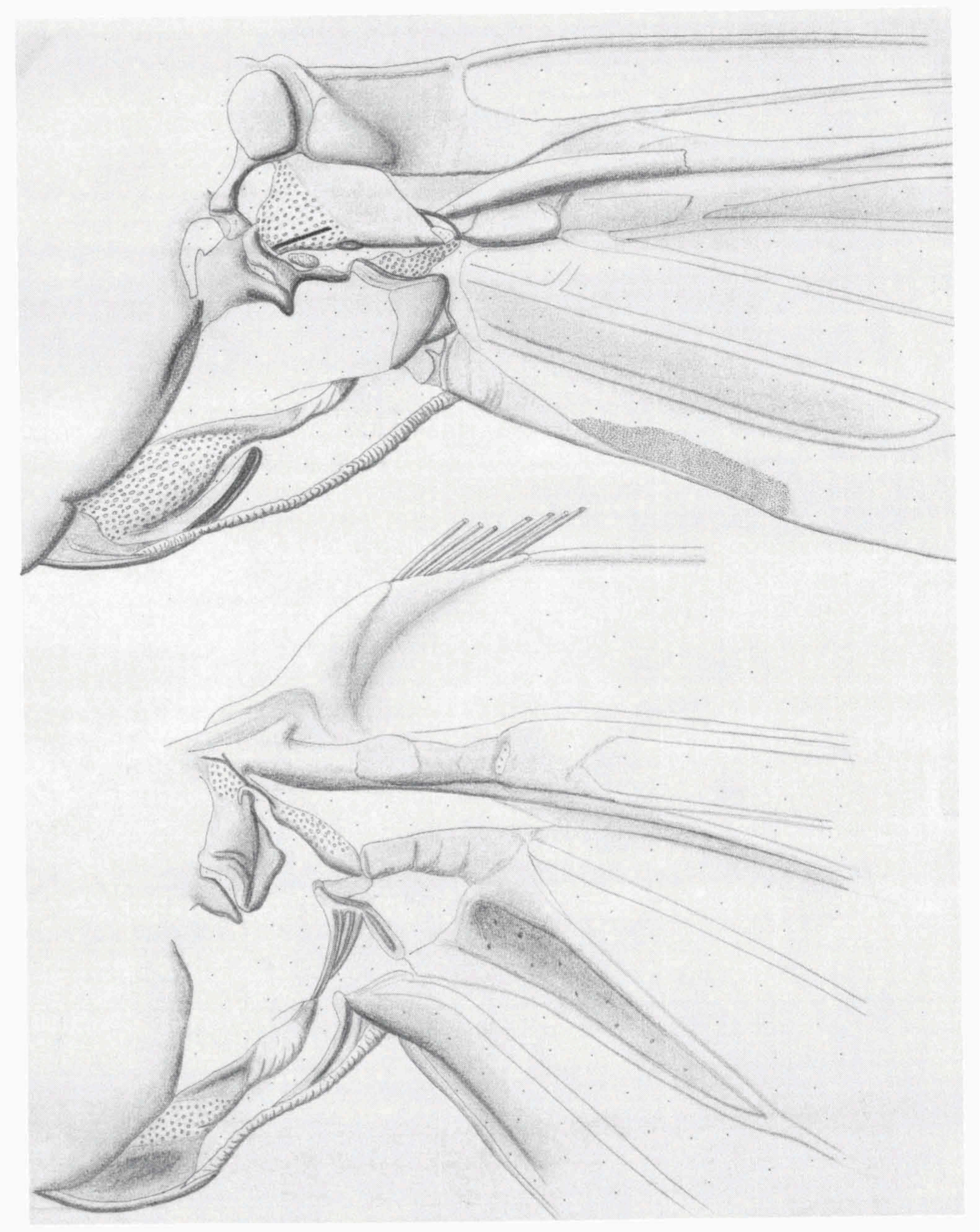


Fig. 8, wing bases of unidentified *Rhizocossus* species (b), Chile.

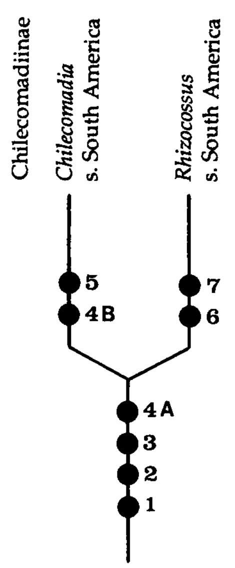


Fig. 9, cladogram of the Chilecomadiinae.

slightly lower than patagium in *munroei*, but distinctly lower in the other two species. Sections of the thorax of the undescribed species (b) are shown in figs. 1-2 and 20. K lacks a cross-suture in the examined specimens of *munroei* and undescribed species (b). Mesepimeron is rather high in undescribed species (b) and moderately high in the other two species. Intersclerite III is moderately large in *munroei* and moderately small in the undescribed species. I-epiphysis reaches distinctly short of tibia-apex and is blunt. Tibia and first tarsomere of hindleg are more or less swollen. Tarsal claws are moderately slender in the undescribed species. Paronychia are minute, and are at least often wanting in *munroei*. Fringes are long. Male frenulum spine and retinaculum are well-developed, and base of retinaculum is rather long in undescribed species (a) and moderately long in *munroei*. Number of ♀ frenulum bristles amounts approx. seven in undescribed species (b) and these are rather long. Venation (see fig. 27): areole moderately small; R4 shortly stalked with R5 in undescribed species (b), but separate in the other two species; R5 from tip of areole; M1 posterior to areole; inner cell rather long and moderately wide; Rs-M1 moderately long and at tip of inner cell; in the specimen of undescribed species (b) an extra cross-vein Rs-M1 present more distally. Wing bases of undescribed species (b) are shown in fig. 8. Scale plate is approx. as long as radial bridge in *munroei*, and shorter than in the undescribed species. Median arm of *munroei* is rather long and moderately narrow. Median arm of the undescribed species is rather long and moderately wide. Anal plate of *munroei* is approx. moderately long and that of the undescribed species approx. rather long.

R. munroei is known from Chile (Clench, 1957: 131) and Argentina (Neuquén, Río Negro, Chubut) (Gentili, 1985: 71). The undescribed species are from Chile.

R. munroei occurs in forest, especially those with *Nothofagus antarctica* and *N. pumilio*, at altitudes between 600 and 1925 m. (Gentili, 1985: 70). A host of *munroei* is *N. pumilio* (Gentili, 1985: 70).

Material:

munroei —(all ARGENTINA and ZMUC) —9 (♂, ♀), Río Negro, near Bariloche, Colonia Suiza, 800 m.; 9 (♂, ♀), Neuquén, near los Andes, Cerro Chapelso; 1♂, Río Negro, El Bolson, Cerro Piltriqutron.

Undescribed species (a) —2♂♂, CHILE: Patagonia, Andes, Chubut, Valle Lago Blanco (BMNH).

Undescribed species (b) —1♀, CHILE (ex coll. Druce and Schaus) (BMNH).

Table 2. Apomorphies in fig. 9 (*Chilecomadia* and *Rhizocossus*).

1.	Ocelli wanting.
2.	Mesomeron approx. 1.5 times width of eucoxa II.
3.	Tibial spurs at most moderately long and moderately short.
4a.	Paronychia minute to/or wanting.
b.	Paronychia only wanting.
5.	Anal plate approx. moderately long.
6.	Pronotum slightly or considerably lower than patagium.
7.	An (at most) moderately high.

Subfamily **Cossinae** Leach, [1815] 1830

Cossinae Leach, [1815] 1830: 131 (as Cossida).
Type genus: *Cossus* Fabricius, 1793: [1].
Cossinae sensu Neumoegen & Dyar, 1894: 160-161.

The subfamily Cossinae shares with the subfamilies Pseudocossinae, Zeuzerinae and Hypoptinae the apomorphy of An being at most moderately high. The subfamily Cossinae has the following autapomorphies: third segment of labial palpi conical (few reversals), R3 and R4 sinuate, R4 and R5 more or less stalked, and anal plate at most moderately long. In all Cossinae, except species of *Catopta*, ocelli and paronychia are wanting and the anal plate is moderately short. In *Catopta* the paronychia are small. In most species of Cossinae Pos is distinctly arcuate reaching far posteriorly. A ground-plan characteristic of the Cossinae is a bipectinate antenna. The presence of a row of hairs on the outer margin of the antennal rami is probably also a ground-plan characteristic. In many species R3 is very shortly stalked with R4 and R5. In nearly all Cossinae the tibia and first tarsomere of the hindleg are partly more or less swollen, which is also found in the Chilecomadiinae.

The subfamily Cossinae is represented in Asia east to Japan and New Guinea, Europe, Africa, and North and South America. Most genera have representatives in the Palaearctic, and the greatest number of species is found in Palaearctic Asia.

A revision of most Palaearctic species is provided by Daniel (1955-1965), who provides illustrations of most species discussed and of the antennae of several species.

Genus **Catopta** Staudinger, 1899

Catopta Staudinger, 1899: 157-159.
Type species: *Catopta albimacula* Staudinger, 1899: 157-159. [Synonymized with *Cossus albonubilus* Graeser, 1888 by Seitz, 1912: 425].
Newelskoia Grum-Grshimailo, 1900: 466. [Synonymized by Seitz, 1912: 425].
Type species: *Cossus albonubilus* Graeser, 1888: 119.
Sinicossus Clench, 1958: 82-84. **Syn. nov.**
Type species: *Sinicossus danieli* Clench, 1958: 84-85, pl. 3: figs. 1-3 (resp. male and holotype, head and venation, and male genitalia).

Staudinger (1899: 157-159) notes a few characteristics of *Catopta albonubilus* (fig. pl.1 fig.: A), of which only the bipectinate antenna and the forward-directed frontal tuft are helpful in recognizing the genus. Daniel (1961) includes a series of species in *Catopta* with the criterion that the ♂ antenna is strongly bipectinate and the ♀ one is simple or bilobed. Many of these species are here excluded; see also under *Paracossulus* and *Semagystia* (new genera).

Material of *C. albonubilus*, *Cossus cashmirensis* Moore, 1879 and an unidentified species from Burma has been examined, and these species form a distinctive group. Judging from the figures given by Daniel (1961: pls. 16-17), it seems that *Catopta griseotincta* Daniel, 1940, *C. rocharva* Sheljuzhko, 1943, an unidentified species (from Karakorum), *C. kendevanensis* Daniel, 1937, and *C. brandti* Bryk, 1947 should remain in this genus. Perhaps more species which Daniel (1961; 1964b; 1965c) places in *Catopta* should be included indeed. Arora (1976: 27-30) points out that *Brachylia acronyctoides* Moore, 1879, which Daniel included in *Catopta*, does not belong to this genus. *Cossus sikkimensis* Arora, 1965 was included in *Catopta* by Arora (1976: 22), which seems to be correct. *Sinicossus danieli* is also included in *Catopta* (see below). Reference can be made to Daniel (1961: 177-183) for the systematics of the subspecies of *albonubilus*.

The four species included have minute paronychia and a moderately long anal plate. In other cossine genera paronychia are wanting and the anal plate is approx. moderately short. In probably most *Catopta* species ocelli are present; in *danieli* these are wanting. Within the Cossidae actual ocelli are further known only in *Pseudocossus* (Pseudocossinae). In *Catopta* the ♂ antenna is moderately or rather strongly bipectinate. The rami are rod-like or moderately flattened, and have moderately long hairs in approx. two rows on the inner margin and approx. one row of hairs on the outer one. The female antenna of *albonubilus* is shortly bilobed, with many short hairs on the proximal side, with one or two moderately long stout sensilla on the outer margin, and with two or three stout sensilla at their apex. In at least *albonubilus* the patagium is slightly higher than the pronotum. The tuft on the vertex of at least *albonubilus* and *danieli* is long and forward-directed. The median arm is nearly long. The species are medium-sized.

So far only *danieli* has been placed in *Sinicossus*. Clench (1958: 82-84) does not make any distinction between *Sinicossus* and other genera. Clench notes a forward-directed tuft on the vertex, which is a characteristic of *Catopta*. *S. danieli* differs from most or all other *Catopta* species in that ocelli are wanting, the ♂ antenna is only moderately bipectinate, and the median arm is moderately wide. Ocelli may be present or absent within a genus, a feature of *Pseudurgis*. The width of the median arm varies interspecifically within many cossinid genera. *S. danieli* has paronychia and a moderately long anal plate and this is further known only in *Catopta* within the Cossinae. *S. danieli* most closely resembles superficially *cashmirensis*. The noted differences are considered insufficient to distinguish *Sinicossus* as a separate genus, and therefore *Sinicossus* is synonymized with *Catopta*.

Vertex in most species has (moderately) small ocelli, but in *danieli* terminations of Pos form slightly sunk areas. Vertex of *albonubilus* has a nearly straight Pos at approx. half its length (fig. 15). Male antenna in probably most species is rather strongly bipectinate, but in *danieli* only moderately bipectinate. An (II) is moderately high. K lacks usually/normally a cross-suture. Mesepimeron is rather high. Accessory plate

II of *albonubilus* varies from wide to moderately narrow. Intersclerite III is moderately large. Tibial spurs vary from long and rather long in *albonubilus* to rather and moderately long or moderately long and moderately short in *cashmirensis*. Arolium is moderately short in *albonubilus* and moderately long in *cashmirensis*. Fringes are long. Male frenulum spine and retinaculum are well-developed. Number of ♀ frenulum bristles in *albonubilus* amounts approx. three, and these are rather long. Venation (see fig. 27): areole moderately large; R3 separate from R4+5; R4+5 very shortly to shortly stalked; Rs-M1 short to connate. Humeral plate is approx. 1.8 times size of radial bridge. Scale plate of at least *albonubilus* and *danieli* is shorter than radial bridge. 4Ax may be distally partly very thin. Median arm is rather long or nearly long and narrow or moderately narrow, but moderately wide in *danieli*.

C. albonubilus has a wide distribution from south U.S.S.R. (e.g. Issyk-Kul) through central Asia to Burma, Korea and east U.S.S.R. (Vladivostok). *C. cashmirensis* occurs in India and China (Daniel, 1961: 188-189), and *danieli* is known from west China. Reference should be made to Daniel (1961) for data of other species which probably belong to *Catopta*.

Material:

albonubilus —long series of both sexes from various localities (BMNH); 1♂, U.S.S.R.: Alexander Mts. (RMNH); 1♂, CHINA: north Tibet (RMNH); 1♂, ? U.S.S.R.: Tyan-Shan', Juldus Mts. (ITZ); 1♂, CHINA: Kuku Noor (ITZ).

cashmirensis —4 ♂♂, INDIA: northwest Himalaya, Dalhousi (BMNH); 2♂♂, YAMMU AND KASHMIR: Kashmir, Srinagar, 1600 m. (MNHN).

danieli —1♂ (holotype), CHINA: west China, Sichuan, Omei-Shan, 31.vii.1935 (coll. Avinoff) (CMNH).

Unidentified species —series, upper BURMA (BMNH).

Genus **Paropta** Staudinger, 1899

Paropta Staudinger, 1899: 159.

Type species: *Cossus paradoxus* Herrich-Schäffer, [1851] 1845: pl. Hepialides & Cossides 2: fig 9.

Staudinger (1899: 159) notes as characteristics of *Paropta* a rather strongly bipectinate ♂ antenna and a shortly bipectinate ♀ one. The fringes and the vestiture of thorax and abdomen would be shorter than in *Catopta*. Later *Paropta johannes* Staudinger, 1899 was described. Seitz (1912: 425) includes also *Cossus henleyi* Warren & Rothschild, 1905 in *Paropta* and synonymizes *Cossus niloticus* Joannis, 1910 and *Paropta pharaonis* Bang-Haas, 1910 with *henleyi*. Gaede (1933a: 243) notices that the figure of *henleyi* given by Seitz (1912: pl. 55: fig. row 1) actually concerns *niloticus*. In his revision of *Paropta*, Daniel (1964a) treats *niloticus* and *pharaonis* as synonyms of *Cossus l-nigrum* Bethune-Baker, 1894 and *henleyi* as a subspecies of the latter. Daniel (1959: 144) synonymizes *Paropta confusa* Rothschild, 1912 with *Holcocerus strioliger* Alphéraky, 1893. The ♂ and ♀ antenna of *confusa* is prismatic. Daniel (1964a) points out that in *Paropta* the ♂ as well as ♀ antenna are bipectinate. Gaede (1933a: 242) and Daniel (1964a: 232-234) include *Cossus frater* Warnecke, 1929 in *Paropta*, although the ♀ antenna is unknown. According to Daniel, Warnecke wrote him that the type-material of *frater* has been destroyed during the war. Daniel (1964a: 235-236) notes that the inclusion of *johannes* in *Paropta* is tentative, since the ♀ antenna is unknown.

The ♂ and ♀ antenna of *paradoxus* are bipectinate, up to nearly rather strongly. The rami have approx. two rows of moderately long hairs on the inner margin and approx. one row of moderately long hairs on the outer margin.

The syntypes of *henleyi* are all males from Sudan (Nakheila). The ♂ antenna of *henleyi* has slightly flattened rami with many short hairs on the proximal side. Therefore *henleyi* is excluded from *Paropta*. *C. henleyi* should probably be placed in *Brachylia* Felder, 1874 (section 3 of Cossinae).

The ♂ antenna of *l-nigrum* and *niloticus* closely resembles that of *henleyi*, and *l-nigrum* and *niloticus* are therefore also excluded from *Paropta*. These two species are placed in a new genus of section 3 of Cossinae.

The identity of *pharaonis* is uncertain. The type-locality of the latter is Cairo, as that of *niloticus*. It may be that *pharaonis* is synonymous with *niloticus*.

No material of *frater* was available. Since the ♀ antenna of *frater* and the type of bipectinate ♂ antenna is obscure, its place in *Paropta* is uncertain and tentative.

In *johannes* the vestiture on the labial palpi is ventrally short and dorsally moderately long. Because of this characteristic *johannes* should perhaps be excluded and placed at a higher branch in the cladogram (fig. 10).

It is obscure if *Catopta rungsi* Daniel & Witt, 1974 should be included in *Paropta*. It differs from *paradoxus* in that: vestiture on labial palpi is moderately short, third segment of labial palpi is moderately ovate, fringes are very long, and median arm is narrow.

In the BMNH there are some specimens of a certain species placed under the name *Paropta buchani* Rothschild, which is seemingly unpublished. The ♂ and ♀ antenna of this material lack seemingly the dorsal row of hairs on the rami. It is obscure if this species should also be included.

A very greyish, unidentified species from Cyprus and Lebanon should probably be included. This species shares with *paradoxus* that the median arm is moderately wide, arolium and paronychia are wanting and a cross-vein Sc-Rs is sometimes present. It differs from *paradoxus* in the following characteristics: mesepimeron varying from rather to moderately high, mesomeron is 1.3 times width of eucoxa II, I-epiphysis reaches nearly as far as tibia-apex, and fringes are only moderately long. In *paradoxus* the mesepimeron is rather high, the mesomeron is as wide as the eucoxa II, the I-epiphysis reaches distinctly short of the tibia-apex and the fringes are rather long.

It is difficult to define *Paropta*, since *paradoxus* seemingly has mostly plesiomorphic character-states and it is uncertain which other species should be included. The bipectinate state of the ♂ and ♀ antenna with approx. two rows of moderately long hairs on the inner margin and one such row on the outer margin seems to be a good characteristic of the genus. A further study of the genus is necessary.

Number of ♀ frenulum bristles is approx. six and these are moderately long. Venation: areole moderately small; R3, R4+5 very shortly separate to very shortly stalked; R4+5 (very) shortly stalked; a cross-vein Sc-Rs sometimes present; Rs-M1 (moderately) shortly separate.

P. paradoxus is distributed from Asia Minor over Syria to Egypt (Seitz, 1912: 425) and Saudi Arabia (Kiriakoff, 1960: 12). *P. johannes* is known from Israel (Dead Sea and En Gedi) and perhaps from Jordan. The type-locality of *frater* is Sanáa (2365 m.) (probably San'a, Yemen), and Wiltshire (1986: 265) records the species also from Yemen.

Host-plants of *paradoxus* are *Ficus carica* L., *F. pseudosycomorus* Decne, *Albizia lebbeck* (L.) Benth., and *Vitis vinifera* L. (Daniel, 1964a: 225-226).

Material (uncertain whether the following species are congeneric):
paradoxus —1♂, ISRAEL: En Gedi (BMNH); 1♂, Jordan Valley (BMNH).
Unidentified species —3♂♂, CYPRUS (BMNH); 1♂, LEBANON (BMNH).
johannes —2♂♂, ISRAEL: En Gedi (BMNH); 1♂, Jordan (BMNH); 1♂, Palestina (MNHN); 2♂♂, ? (MNHN).

Genus **Rethona** Walker, 1855

Rethona Walker, 1855: 1042-1043.
Type species: *Rethona strigosa* Walker, 1855: 1043.

Rethona has been established for two species. Kirby (1892: 865) designated *strigosa* as type species. Gaede (1930: 550) notes that the second species, *Rethona albicans* Walker, 1855, is a notodontid. There is now only one species in this cossid genus. This species has mostly plesiomorphic character-states. The few apomorphies are: vestiture on labial palpi moderately long and fine, tarsal claws moderately slender, arolium wanting and ♂ retinaculum of holotype rudimentary. It seems impossible to elucidate the exact position of this genus in a cladogram based on the external morphology (see also fig. 10). It seems that the genus comes close to *Paropta* and a series of genera with a widened mesomeron, such as *Macrocossus* Aurivillius, 1900 and *Arctiocossus* Felder, 1874. In *Paropta paradoxus* the rami of the antenna have a row of hairs on the outer margin and the median arm is moderately wide.

Male antenna is rather strongly bipectinate. Rami have moderately long hairs in approx. two rows on inner side. Female is unknown. Tibial spurs are moderately long and slightly unequal in length. Fringes are long. Male frenulum spine is rather long. Venation: areole moderately large; R3, R4+5 very shortly stalked; R4+5 shortly stalked; inner cell moderately small; Rs-M1 moderately long. 4Ax of holotype is distally well-developed.

Material:
strigosa —1♂ (holotype), s. Africa [SOUTH AFRICA] (BMNH).

Table 3. Apomorphies in fig. 10 (Cossinae).

1. Labial Palpi: third segment conical, instead of ovate. (*)
2. R3 and R4 sinuate.
3. R4 (normally) more or less stalked with R5.
4a. Anal plate moderately long.
b. Anal plate moderately short.
5. Ocelli wanting.
6. Paronychia wanting.
7. Scale plate approx. as long as radial bridge. N.B. Not examined in several genera.
8. Arolium wanting.
9. Median arm moderately wide.
10. Tarsal claws moderately slender.

11. Male retinaculum rudimentary.
12. Mesomeron approx. 1.3 or 1.5 times width of eucoxa II.
13. Vestiture on second and third segment of labial palpi ventrally only short and dorsally moderately long.
14. Antenna: rami more or less flattened and with hairs only on proximal side. (*)

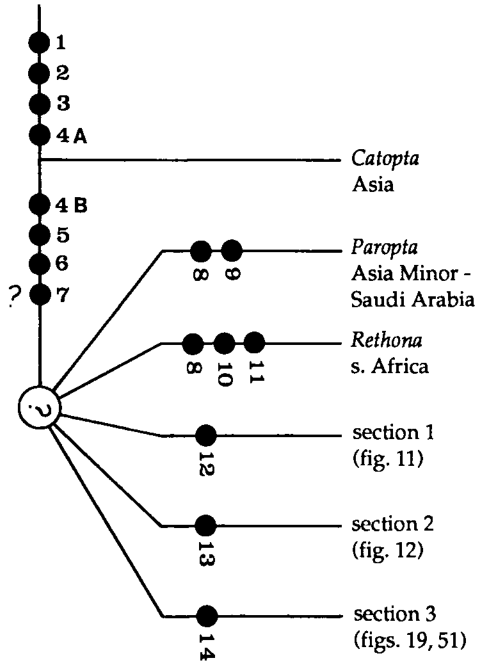


Fig. 10, cladogram of the Cossinae.

Section 1

Section 1 consists of a number of genera in which the species have a distinctly wider mesepimeron than the eucoxa II.

Genus **Arctiocossus** Felder, 1874

Arctiocossus Felder, 1874: pl. 82: fig. 10.
Type species: *Arctiocossus antargyreus* Felder, 1874: pl. 82: fig. 10.

Arctiocossus has been established only for *antargyreus*. Gaede (1930: 543) includes additionally two new species, *punctifera* and *strigulata*, in this genus, although he notes certain differences between the species. Clench (1959a) discusses *Arctiocossus* and notes *Pecticossus* Gaede, 1930 tentatively as a synonym of the former. He includes *Pecticossus castaneus* Gaede, 1930 and *P. gaerdesi* Daniel, 1956, although he did not examine the type of *castaneus*. Clench (1959a) notes that *Pecticossus* is probably a valid genus, separable on the male genitalia, and that his new species *poliopterus* should probably be placed in a new genus. Because he had not examined certain material, he treats *Arctiocossus* tentatively in a broader sense. Clench (1959a) describes three new species and includes these in *Arctiocossus*.

In this study only *A. strigulatus* was available and has been examined. This species shares with *Cossus aries* Püngeler, 1902 the following apomorphies: An moderately low, mesomeron distinctly wider than eucoxa II, I-epiphysis wanting, arolium wanting, tarsal claws moderately slender, and a cross-vein Sc-Rs present. In the only available specimen of *strigulatus* the I-epiphysis is seemingly wanting. In *aries* the fringes are slightly shorter, the mesomeron a slightly narrower and the median arm wider than in *strigulatus*. Furthermore, in *aries* the 1 frenulum spine and retinaculum are wanting. These differences between the two species seem to be of less importance than the similarities and therefore the two are considered congeneric. Perhaps *strigulatus* and *aries* should be placed in a new genus, but as long it is unknown if *antargyreus* has a similar set of apomorphies *aries* is tentatively included in *Arctiocossus*. Considering the close resemblance in colour pattern, which is special for the Cossinae, between *aries* and *Cossus striolatus* Rothschild, 1912, it seems that the latter should probably also be placed in *Arctiocossus*. *A. strigulatus* and *aries* share with the species of the following five genera that the mesomeron is wider than the eucoxa II. Since it is uncertain if *strigulatus* and *aries* should be regarded as congeneric with *antargyreus*, *Arctiocossus* is tentatively placed with a question-mark next to the following five genera in the cladogram (fig. 11). A further investigation of the genus is needed.

Viette (1952: 555) synonymizes *Cossus tahlai* Dumont, 1932 and *C. bongiovanni* Krüger, 1939 with *aries*. Daniel (1956a) includes *aries*, *striolatus* and *Cossus turatii* Krüger, 1934 in *Lamellocossus* Daniel, 1956. Daniel (1956a: 287-288) synonymizes *Cossus pulcher* Rungs, 1942 with *turatii*. Daniel (1965: 88-93) regards these species as a complex of one species, and treats *Cossus aegyptiaca* Hampson, 1910 and *C. cheesmani* Tams, 1925 as subspecies of *aries* and *turatii* as a synonym of *aries*. It is obscure if *striolatus* is not also a subspecies of *aries*.

C. aries is excluded from *Lamellocossus*, since the type species of the latter is quite different. In *Lamellocossus terebra* (Schiffermüller & Denis, 1776) the rami of the ♂ antenna have two rows of moderately short hairs on the inner margin and many very short hairs on the outer margin, An is moderately high, the I-epiphysis is present, the fifth tarsomere is longer than fourth, the fringes are moderately long or moderately short, and Sc-Rs is wanting. *C. striolatus* should probably also be excluded from *Lamellocossus*.

Male antenna is bipectinate, up to nearly rather strongly. Female antenna of *aries* closely resembles that of male, but hairs on inner margin of rami are slightly shorter. Mesomeron is approx. 2 times width of eucoxa II in *strigulatus* and 1.5 times width in *aries*. Tibial spurs are approx. rather and moderately long in *strigulatus*, and moderately long and moderately short in *aries*. Fringes are long in *strigulatus* and rather long in *aries*. Male frenulum spine is approx. rather long and retinaculum is a short flap in *strigulatus*. In *aries* ♂ frenulum spine and retinaculum are wanting and ♀ frenulum bristles are probably absent too. Venation: areole moderately small; R3 separate to very shortly stalked; R4+5 (very) shortly stalked; M1 approx. from tip of areole; Sc-Rs proximal to Rs-M1 and moderately or rather long, sometimes long and occasionally wanting; Rs-M1 moderately long to shortly stalked.

A. antargyreus is known from South Africa (Gaede, 1930: 543). *A. strigulatus* is recorded from southwest Africa, and *punctiferus* from east Africa (Gaede, 1930: 543). *A. aries* is known from Spain, further from Mauritania to Israel, Saudi Arabia (Kiriakoff, 1960: 11), and Bahrain (Daniel, 1964a; 1965c). *C. striolatus*, which should probably be included in *Arctiocossus*, is known from Magnesia.

Material:

strigulatus —1♂ (holotype), TANZANIA: Spitzkjojoe (MHUB).

aries —1♂ (holotype of *tahlai*), TUNISIA: Bled Tahla, forest of Gernonier, 2.iv.1928 (MNHN); 1♂ (holotype of *pulcher*), MAURITANIA: Ft. Trinquet, 2.ix.1942 (Rungs) (MNHN); 1♂ (holotype of *cheesmani*), 1♀ (paratype), SAUDI ARABIA: Jabrin, 200 miles s.s.w. of Hufuf, 23.ii.1924 (Cheesman) (BMNH); 1♂ (holotype of *aegyptiaca*), EGYPT: Suez (Walker) (BMNH); 4♂♂, ALGERIA: Tilghemt (BMNH); 1♂, ALGERIA: south of Biskra, Kef el Dahr (BMNH); 1♂, 1♀, ALGERIA: Mzab Country, Oued Nça (BMNH); 1♂, ALGERIA: Colomb-Bechar (MNHN); 1♀, ALGERIA:

Hassi Bahbah (BMNH); 1♀, Sebdou (MNHN).

Genus **Mirocossus** gen. nov.

Type species: *Brachylia badiala* Fletcher, 1968: 328.

Etymology: "mirus" (Latin) means freak + genus-name *Cossus*. Gender: masculine.

Mirocossus is established for *badialus*, which has erroneously been described as a species of *Brachylia* Felder, 1874. The ♂ antenna of *badialus* is rather strongly bipectinate with rod-like rami, which have approx. two rows of moderately long hairs on the inner margin. In *Brachylia* the rami of the ♂ antenna are distinctly flattened and have short hairs on the proximal side. *Brachylia* is therefore treated as a genus of section 3. Since *badialus* does not fit in one of the known genera, a new genus is here established for it.

M. badialus shares with *Macrocossus*, *Lamellocossus*, *Acossus* Dyar, 1905 and *Prionoxystus* Grote, 1882 the following apomorphies: mesomeron 1.3 to 1.5 times width of eucoxa II, ♂ frenulum spine reduced, ♂ retinaculum rudimentary or wanting, and median arm at least moderately wide. *M. badialus* differs from species of mentioned genera in that An is low and the I-epiphysis reaches nearly as far as the tibia-apex. Among these genera only the I-epiphysis of *Macrocossus toluminus* (Druce, 1887) is known to be also that long. See also fig. 11. The female is unknown.

In the examined specimens of *badialus*, Apc terminates just dorsally to K and K has a cross-suture. Tibial spurs are moderately long and moderately short. Arolium is well-developed. Fringes are long. Male frenulum spine is moderately short. Venation: areole small to minute; R3, R4+5 shortly stalked; R4+5 shortly stalked up to approx. 0.3 times their length; Rs-M1 connate to shortly stalked. Humeral plate has not been examined. Median arm is moderately wide.

Material:
badialus —1♂ (holotype), 1♂, UGANDA: Ruwenzori Range, Mahoma River, 6700 ft. (BMNH); 1♂, UGANDA: Namwamba Valley, 6500 ft. (BMNH).

Genus **Macrocossus** Aurivillius, 1900

Macrocossus Aurivillius, 1900: 1054.
Type species: *Macrocossus rudis* Aurivillius, 1900: 1054. [Synonymized with *Trypanus toluminus* Druce, 1887 by Clench (1959a: 3-4)].

Clench (1959a) redefines the genus, synonymizes *rudis* with *toluminus*, and describes two new species, *coelebs* and *caducus*. Clench's definition of *Macrocossus* does not help very much to distinguish the genus from the many other ones of which the species have a more or less strongly bipectinate ♂ antenna. Clench notes that the presence of a cross-vein Sc-Rs, which Gaede (1930: 540) uses as a diagnostic character, is more specific than characteristic of the genus. *M. toluminus* is a large species and easily recognizable, but *caducus* and *coelebs* are much smaller and not so easily recognizable. No material of *caducus* and *coelebs* was available. Judging the figures given by Clench (1959a: pl. 1: figs. 3-4), the author doubts that *caducus* and *coelebs* actually belong to *Macrocossus*. The genus is defined below after the characters found in *toluminus*.

The ♂ as well as ♀ antenna of *toluminus* is rather strongly bipectinate. The rami of at least the ♂ antenna have many minute hairs on the outer margin. The vertex is distinctly bulbed. The mesepimeron is moderately high. *M. toluminus* shares with species of *Lamellocossus* Daniel, *Acossus* Dyar and *Prionoxystus* Grote the following apomorphies: antennal rami of at least male with moderately short hairs on the inner margin and hairs on the outer one, mesomeron wider than eucoxa II, fifth tarsomere longer than fourth, arolium wanting, fringes at most moderately long, ♂ retinaculum rudimentary or wanting, and median arm at least moderately wide. In *toluminus* the I-epiphysis reaches at least as far as the tibia-apex, whereas in the other genera distinctly short of. Species of *Acossus* and *Prionoxystus*, which occur in America, differ from *toluminus* in that ♂ retinaculum is wanting, An is moderately low and Sc-Rs is normally present. In *toluminus* Sc-Rs is sometimes present. The fringes of *toluminus* are moderately short. The number of ♀ frenulum bristles amounts approx. ten, and these are moderately short. See also fig. 11.

Vertex has an arcuate Pos up to approx. 0.8 times its length. Antenna is blackish. K lacks a cross-suture in the examined specimens. Mesomeron is twice width of eucoxa II. Tibial spurs are moderately short and in pairs of slightly unequal length. Fifth tarsomere is approx. 1.5 times length of fourth. Male frenulum spine is moderately short and retinaculum is rudimentary. Venation: areole small to very small; R3, R4+5 very shortly stalked; R4+5 shortly stalked; M2, M3 approx. connate; Sc-Rs sometimes present; Rs-M1 very short to very shortly stalked. Humeral plate is approx. twice size of radial bridge. 1Ax is apically rather large. 4Ax is distally partly membranous. Median arm is approx. moderately long, rather wide, slightly wider than Cu2, and has a slight anterior invagination up to approx. 1/3 its length.

M. toluminus is known from Ivory Coast to Malawi (Clench, 1959a: 5) and Namibia (Gaede, 1930: 541).

Material:
toluminus —1♂ (holotype of *toluminus*), THE GAMBIA (Moloney) (BMNH); 1♂, IVORY COAST: Bouaflé (RMNH); 1♂, south NIGERIA (RMNH); 1♀, SIERRA LEONE (BMNH); 1♂, CAMEROON (BMNH); 1♂, KENYA: Mombasa (BMNH); 1♂, ? (BMNH).

Genus **Lamellocossus** Daniel, 1956

Lamellocossus Daniel, 1956a: 278-279.
Type species: *Bombyx terebra* Schiffermüller & Denis, 1776: 60.

Daniel (1956a: 278-279) includes in his new genus: *terebrus*, *Cossus colossus* Staudinger, 1887, *C. aries* Püngeler, *C. turatii* Krüger and *C. striolatus* Rothschild. Daniel (1965c: 93) synonymizes *turatii* with *aries*. In this study *aries* is tentatively included in *Arctiocossus*. Considering the resemblance in colour pattern, it seems that *striolatus* should also be tentatively placed in *Arctiocossus*. See also under the latter. Of *colossus* only a damaged ♀ specimen has been partially examined. In this specimen the I-epiphysis is present. It is here not certain if this species fits in *Lamellocossus*. The genus is redefined here below after the characters of *terebrus*.

Male antenna of *terebrus* is dark fuscous and rather strongly bipectinate. Rami have moderately short hairs on inner margin, and a moderate number of very short hairs and few moderately short, stouter hairs on outer margin. Female antenna is moderately bilobed. Lobes have short hairs on the proximal side and one or two stout sensilla at apex and one on outer margin. Vertex has Pos up to approx. half its length. *L. terebrus* shares with *Acossus* and *Prionoxystus* (see fig. 11) the following apomorphies: antennal rami of (at least) male with moderately short hairs on inner margin and many short or very short hairs on outer one, mesomeron widened, fifth tarsomere longer than fourth, arolium wanting, fringes at most moderately long, ♂ frenulum spine wanting, ♂ retinaculum rudimentary or wanting, and median arm at least moderately wide. Apc terminates dorsally to K in the specimens examined, and K lacks a cross-suture. Upper Pas is slightly above half length of Pre plus Pa. Mesepimeron is moderately high. Mesomeron is approx. 1.3 times width of eucoxa II. Female I-epiphysis is short, shorter than ♂ one, and nearly tooth-like. Fifth tarsomere is 1.5 times length of fourth. Fringes are moderately long or moderately short. Male retinaculum is rudimentary. Female frenulum bristles are wanting. Venation: areole rather to moderately small; R3 distinctly sinuate and approx. connate with R4+5; R4+5 shortly stalked; Rs-M1 short to very short. Humeral plate is approx. twice size of radial bridge. 4Ax is distally more or less membranous. Median arm is moderately wide. Anal plate varies from moderately short to short.

L. terebrus occurs locally in Europe, north to southern Finland and south to south Tirol (Daniel, 1956a). Grönvall (1950: 781, fig. 1) provides a map of the distribution in Europe, western U.S.S.R., Turkey and Iran. Grönvall also notes that the species is distributed from Siberia to Amur. Seitz (1912) records the species from eastern Siberia. Daniel (1956a: 280) gives some additional localities, such as south Tirol and Manchuria (Habrin). De Laever (1960: 52-53) records *terebrus* from two localities in the Pyrénées. *C. colossus*, which may belong to *Lamellocossus*, is known from south U.S.S.R.

Material:
terebrus —series of both sexes, south U.S.S.R. (RMNH); 1♂, 1♀, U.S.S.R.: Armenia (ITZ); few, WEST GERMANY: Bayern (RMNH); 2♂♂, FRANCE: Basses Alpes, Colmars-les-Alpes (ITZ); 2, FINLAND (RMNH).

Genus **Acossus** Dyar, 1905

Acossus Dyar, 1905: 178.
Type species: *Cossus undosus* Lintner, 1878: 243-244.

Dyar (1905: 178) includes in *Acossus*: *undosus*, *Cossus centerensis* Lintner, 1877 and *C. populi* Walker, 1856. Dyar and von Dalla Torre (1923) note certain synonyms of *undosus* and Dyar also notes forms of *populi*. Hodges (1983: 31) gives synonyms of *populi* and *undosus*. *Acossus connectus* Barnes & McDunnough, 1916 should probably be included in *Fania* (see under *Fania*). Ureta (1957: 142-143) describes *Acossus comadioides* from Chile. Gentili (1985: 54, 67) synonymizes *A. comadioides* with *Rhizocossus* *munroei* and includes this species in *Chilecomadia*.

In this study only males of *undosus, centerensis* and an unidentified species from Canada have been examined. An of *undosus, centerensis* and probably also the other species is moderately low, as in *Prionoxystus*. *Acossus* appears to differ from *Prionoxystus* in that the frons is only moderately wide, the radial plate is not elongate or narrowed, and there is little sexual dimorphism. The two genera share with *Lamellocossus* that the antennal rami have many short or very short hairs irregularly distributed (scattered) on the outer margin, and the ♂ frenulum spine is wanting. The three genera share with *Macrocossus* the following apomorphies: antennal rami of at least male with moderately short hairs on the inner margin, mesomeron wider than eucoxa II, fifth tarsomere longer than fourth, arolium wanting, fringes at most moderately long, ♂ retinaculum rudimentary or wanting, and median arm moderately or rather wide. The mesepimeron is moderately high as in the species of the other genera, except *Prionoxystus macmurtrei* Guérin-Méneville, 1829 (and perhaps certain others).

Vertex is more or less bulbed anteriorly, and has an arcuate and more or less ridged Pos up to 0.8 or 0.9 times its length. Female antenna of *centerensis* is moderately bipectinate, has short hairs on dorsal side of rami, and has 1 stout sensillum at apex of rami. Patagia are in at least *undosus* widely curved, looking like very swollen. Tegula of *undosus* and perhaps the other species is ventro-posteriorly bluntly pointed. Mesomeron is 1.5 times width of eucoxa II. Tibial spurs are moderately short or short and in pairs of slightly unequal or nearly equal length. Fifth tarsomere is 1.5 times length of fourth. Fringes are moderately long in *undosus* and the unidentified species, and moderately short in *centerensis*. Venation: areole moderately large or moderately small; R3, R4+5 approx. connate; R4+5 shortly stalked; Sc-Rs long; Rs-M1 connate in *centerensis* and shortly stalked in the other two species. 4Ax is distally more or less membranous. Median arm is up to rather wide in *undosus* and moderately wide in the other two species.

All species are distributed in the U.S.A. and several also in Canada.

Material:
undosus —11♂♂, U.S.A.: Oregon (ITZ); 4♂♂, CANADA: Princeton (ITZ).
centerensis —6♂♂, 1♀, U.S.A. (BMNH); 1♂, CANADA: Alberta (ITZ).
Unidentified species —1♂, CANADA: Princeton (ITZ); 1♂, CANADA: Alberta (ITZ).

Genus **Prionoxystus** Grote, 1882

Prionoxystus Grote, 1882: 21, 63.
Type species: *Cossus robiniae* Peck, 1818: 72.
Xystus Grote, 1874: 262. [Junior homonym of *Xystus* Hartig, 1840].
Type species: *Cossus robiniae* Peck, 1818: 72.

In *Prionoxystus* the following species are at least included: *robiniae, Cossus macmurtrei* Guérin-Méneville, 1829, and *Xyleutes piger* Grote, [1866]. Dyar (1940: 1277) notes some synonyms and many forms of *robiniae*, and *Cossus querciperda* Fitch, 1859 as a synonym of *macmurtrei*. Hodges (1983) synonymizes *P. baccharides* Clarke, 1952 with *piger*. Schaus (1905: 342) describes *P. duplex* from South America. Dyar (1940:

1281) places *duplex* in *Psychogena* Schaus, 1911 (Hypoptinae), which appears to be correct.

The three species included show distinct sexual dimorphism. The males are distinctly smaller and have a somewhat different colour pattern than the females. The male of *robiniae* and occasionally also the female have yellow areas on the hindwing (Dyar, 1940: 1277). The male of *macmurtrei* is small and has mainly semi-transparent wings. The radial plate of the three species is slightly elongate and apically rather slender (see fig. 32). The mesomeron of *robiniae* and probably also the other two species is twice width of the eucoxa II. The frons is moderately widened to rather wide. The fringes of the males of *macmurtrei* and *piger* are short and those of *robiniae* are very short. The fringes of the females of *robiniae* are moderately long and those of *macmurtrei* approx. short. In the males of *Acossus* the fringes are moderately long or moderately short. The scale plate of at least *robiniae* is distinctly shorter than the radial bridge. In at least *robiniae* and certain species of *Acossus* An is moderately low. The author supposes that the presence of a cross-vein Sc-Rs is a synapomorphy of *Acossus* and *Prionoxystus*, although it may be (sometimes) wanting in certain species. These two American genera share with *Lamellocossus*, which is represented in Eurasia, that the antennal rami of at least the male have many short or very short hairs irregularly distributed (scattered) on the outer margin, and the ♂ frenulum spine is wanting. The three genera share with *Macrocossus* the following apomorphies: antennal rami of at least male with moderately short hairs on the inner margin and hairs on outer one, mesepimeron moderately high, mesomeron widened, fifth tarsomere is 1.3 or 1.5 times length of fourth, arolium wanting, fringes at most moderately long, ♂ retinaculum rudimentary or wanting, and median arm moderately or rather wide.

Material of *P. macmurtrei* and *piger* has been partially examined. Vertex of *robiniae* is bulbed, and has an arcuate and more or less ridged Pos up to approx. 0.8 its length. Male antenna of *robiniae* is dark fuscous and moderately strongly bipectinate. Male antenna of *macmurtrei* is dark fuscous and moderately bipectinate; rami are slightly flattened. Female antenna of *robiniae* is moderately shortly bipectinate; rami are slightly thickened apically and have approx. one stout sensillum at their apex. Patagia are in at least *robiniae* widely curved, looking like very much swollen. Sternopleural region of thorax of *robiniae* is shown in fig. 34. Bs II of at least *robiniae* is posteriorly shortened. K terminates sometimes dorsally to K in *robiniae*, and lacks often/usually a cross-suture. Mesepimeron is moderately high in *robiniae* and rather high in *macmurtrei*. The plesiomorphic state of the mesepimeron in the latter is most probably a reversal, since the mesepimeron is so far known moderately high in the genera considered to be most closely related. Tibial spurs are short or moderately short and in pairs of slightly unequal length. Vestiture on tibiae of *robiniae* is short. First tarsomere of hindleg is not really or only slightly swollen in at least *robiniae*.

Female frenulum bristles are wanting. This is perhaps an apomorphy shared with *Acossus*, but it couldnot be checked in the latter. Venation: areole moderately large or moderately small; R3, R4+5 shortly stalked; R4+5 shortly stalked; Sc-Rs long, but wanting in the examined specimen of *piger*; Rs-M1 moderately short to shortly stalked. Humeral plate of *robiniae* is 2.5 to 3 times size of radial bridge. Humeral plate has not been examined in the other species. Median arm of *piger* is moderately wide and that of the other two species rather wide.

The genus is represented all over the U.S.A. and in Canada. Fracker (1915: 78) notes Locust-tree as a host-plant of *robiniae*, and Dyar (1940: 1277) notes that the larvae of this species live in different trees.

Material:
robiniae —long series of both sexes, U.S.A. (BMNH); 2♂♂, 2♀♀, U.S.A.: Nebrasca, Missouri and California (ITZ); 1♂, U.S.A.: Texas (RMNH); 3♀♀, CANADA: Alberta (ITZ).
macmurtrei —1♂, U.S.A. (BMNH); 1♀, ? (BMNH).
piger —1♂ (paratype of *baccharidis*), U.S.A.: Florida, Dade Co., 30.iii.1951 (BMNH).

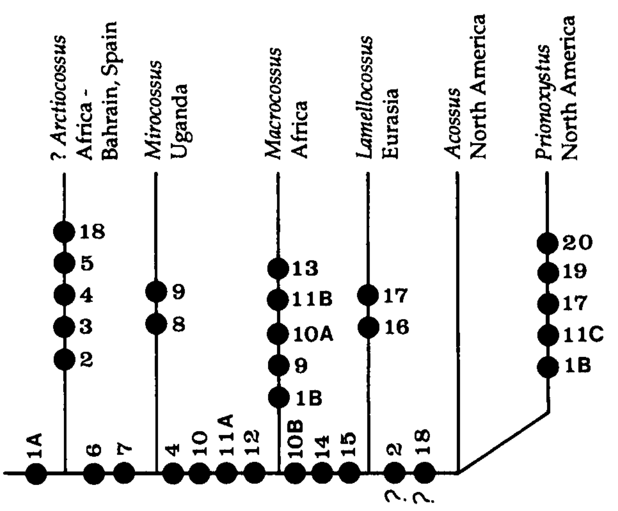


Fig. 11, cladogram of section 1 (Cossinae).

Table 4. Apomorphies in fig. 11 (*Arctiocossus* genus-group).

1a. Mesomeron approx. 1.3 or 1.5 times width of eucoxa II.
b. Mesomeron approx. twice width of eucoxa II.
2. An moderately low.
3. I-epiphysis wanting.
4. Arolium wanting.
5. Tarsal claws moderately slender.
6. Male retinaculum rudimentary to/or wanting.
7. Median arm moderately or rather wide.
8. An low.
9. I-epiphysis reaching nearly as far as tibia-apex.
10. Male antenna: rami with approx. two rows of moderately short hairs on inner margin and furthermore hairs on outer one.
10a. Rami with approx. one row of moderately short hairs on outer margin.
b. Rami with many short or very short hairs irregularly distributed (scattered) on outer margin.
11a. Fringes at most moderately long.
b. Fringes moderately short.
c. Male fringes short.
12. Fifth tarsomere approx. 1.3 or 1.5 times length of fourth.
13. Vertex much swollen.
14. Mesepimeron moderately high.
15. Male frenulum spine wanting.
16. Female I-epiphysis short and tooth-like.
17. Female frenulum bristles wanting.
18. Cross-vein Sc-Rs present.
19. Frons moderately widened.
20. Radial plate slightly elongate and apically slender (fig. 32).

Section 2

Within the genera of section2, the vestiture on the second and third segments of the labial palpi is ventrally short and dorsally moderately long. This is also found within a number of genera within section 3A (*Isocossus, Alcterogystia, Planctogystia, Dyspessacossus*, and partly *Cossulus*). Most species from section 3 have a different type of antenna (rami flattened and with hairs only on their proximal sides).

Genus **Fania** Barnes & McDunnough, 1911

Fania Barnes & McDunnough, 1911: 8 (key), 25.
Type species: *Cossus nanus* Strecker, 1876: 151.

So far only *nana* has been placed in *Fania*. Kirby (1892: 867) places *nana* in *Prionoxystus*. Dyar (1940: 1275) neglects *Fania* and includes *nana* under *Hypopta* Hübner, 1818, the type genus of the Hypoptinae.

Barnes & McDunnough (1911: 25) note as characteristics of the female that the antenna is simple and that M2 and M3 of the hindwing are more or less stalked. The male was unknown to them. In this study only males have been examined. The present author doubts that a stalked M2 and M3 is a good characteristic, since this seems to be too variable. The connate state of M2 and M3 in the hindwing also occurs in at least *Toronia perplexa* Neumoegen & Dyar, 1893 and *Psychidocossus infantilis* (Schaus, 1911). The male antenna is moderately strongly bipectinate. The rami are slightly flattened and have approx. two rows of moderately long hairs on the inner margin and one row of hairs on the outer margin. Since the vestiture on the labial palpi is ventrally short and dorsally moderately long, the genus is placed at a higher branch in the cladogram (fig. 12) next to *Toronia* Barnes & McDunnough, 1911, *Psychidocossus* Fletcher, 1982 and *Miacora* Dyar, 1905. The four genera, all restricted to America, share the following apomorphies: antennal rami of male with hairs on outer margin (not certain of *Psychidocossus*), mesepimeron moderately high, frenulum structures reduced in size, and median arm moderately wide. *F. nana* shows furthermore the following characteristics: pronotum distinctly lower than patagium, accessory plate II varying from moderately wide to moderately narrow, I-epiphysis reaching nearly as far as tibia-apex and slightly pointed, and arolium wanting.

Barnes & McDunnough (1916: 34, pl. 1: fig. 5) introduce a new species *connectus* and include it provisionally in *Acossus*. They state that *connectus* greatly resembles *nana*, but that the former has a slightly different colour pattern and a different hindwing venation than the latter. Judging from their figure, *connectus* shows great similarity in colour pattern with *nana*, much more than with a species of *Acossus*. Barnes & McDunnough note that *connectus* differs from *nana* in that Rs and M1 are well stalked and M2 and M3 are connate. It appears that Rs and M1 are sometimes/often also more or less stalked in *nana*. The present author regards the differences between stalked and connate states of Rs and M1 insignificant. Furthermore the size of *connectus* (30 mm.) is more similar to that of *nana* than of *Acossus* species. Therefore *connectus* should probably be included in *Fania*. It may well be that *connectus* is synonymous with *nana*; the male of *nana* was probably still unknown to Barnes and

McDunnough in 1916.

Vertex has an arcuate Pos, which reaches far posteriorly. An is moderately high. Apc terminates sometimes or usually dorsally to K. K appears to lack often/usually a cross-suture. Upper Pas is a slightly below or at half length of Pre II plus Pa. Tibial spurs are moderately long. Fringes are rather long. Male frenulum spine is moderately long and retinaculum is rudimentary or wanting. Venation: areole moderately small; R3, R4+5 approx. connate; R4+5 shortly stalked; Rs-M1 connate to shortly stalked; M2 and M3 at least sometimes stalked.

The species is known from Texas and Arizona in the U.S.A.

Material:
nana —long series of males, U.S.A.: Arizona (BMNH).

Genus **Toronia** Barnes & McDunnough, 1911

Toronia Barnes & McDunnough, 1911: 8 (key), 24.
Type species: *Trypanus perplexus* Neumoegen & Dyar, 1893: 31.

Barnes & McDunnough (1911: 24) include in addition to *perplexa* also *Cossus luzena* Barnes, 1905 in *Toronia*, because the venation of the two species is very similar. They note that the ♂ antenna of *perplexa* is strongly bipectinate. Dyar (1940: 1274) includes the two species under *Miacora* Dyar. The type species of *Miacora* has a prismatic laminate ♂ antenna and is otherwise quite different. Dyar includes *Miacora subtropicalis* Dyar, 1912, and *Acossus leucegchytes* Dyar, 1912 in *Miacora*, although these species have a bipectinate ♂ antenna. No material of these two species was available and it is uncertain if these also belong to *Toronia*. *Toronia adolescens* Dyar, 1914 was later placed by Dyar (1940: 1274) in *Miacora* and is here tentatively left in the latter.

The male antenna of *perplexa* is moderately bipectinate and its rami have a row of hairs on the outer margin. The ♀ antenna of *perplexa* is moderately shortly bipectinate and that of *luzena* shortly. The lobes of both species have one stout sensillum at their apex and short hairs on the outer margin. Furthermore, the two species share together and with *Fania nana*, *Psychidocossus infantilis* and *Miacora tropicalis*, which are also restricted to America, the following apomorphies: antennal rami of male with hairs on outer margin (not certain of *infantilis*), mesepimeron moderately high, frenulum structures reduced in size, and median arm moderately wide. In both *luzena* and *perplexa* arolium is wanting. The vestiture of the labial palpi is in *luzena* moderately short mixed with moderately long. The species should therefore be placed at a lower branch in the cladogram (fig. 10), but it could however be due to a reversal. In *perplexa* the vestiture is ventrally short and dorsally moderately long. Because the ♀ antenna of *luzena* closely resembles that of *perplexa* and the species share several apomorphies, the former is tentatively left in *Toronia*. Accessory plate II is moderately wide or moderately narrow in the specimens examined of *perplexa* and *luzena*. *Fania* differs from *Toronia* in that the ♀ antenna is simple. It seems impossible to give more diagnostic characteristics of the external morphology of this genus. Labial palpi in the examined ♀ specimen of *perplexa* is two-segmented. An is moderately high in *luzena*. Accessory plate II is in the examined specimens of *luzena* moderately narrow. I-epiphysis is wanting in *perplexa*. Tibial spurs are moderately short or short. Fringes are rather long. Male frenulum spine is approx. moderately long in *perplexa*. Male retinaculum is a short flap in *perplexa*. Number of ♀ frenulum bristles is approx. five to seven, and these are moderately long. Venation: areole moderately large to moderately small; R3, R4+5 separate to connate; R4+5 shortly stalked; inner cell small to moderately large; cross-vein Sc-Rs sometimes/often present in *perplexa*; Rs-M1 very short to shortly stalked; M2, M3 sometimes/usually connate in at least *perplexa*. Tip of ♀ abdomen is moderately elongate.

T. perplexa is known from Colorado, Arizona and California (Donahue, pers. comm.). *T. luzena* is known from Arizona.

Material:

perplexa —1♀, U.S.A.: south Arizona (BMNH); 1♂, 1♀, U.S.A.: California, Los Angeles Co., San Gabriel Mts., 4800 ft. (NHMA).

luzena —1♀, U.S.A.: Arizona, Pima Co., Bahaquivera Mts. (BMNH); 1♀, U.S.A.: Kny-Scheerer Co. (BMNH).

Genus **Psychidocossus** Fletcher, 1982

Psychidocossus Fletcher, in Fletcher & Nye, 1982: 138. [Objective replacement name of *Psychopsis* Dyar, 1940].

Type species: *Cossus infantilis* Schaus, 1911: 632.

Psychopsis Dyar, 1940: 1265 (key), 1274. [Junior homonym of *Psychopsis* Newman, 1842].

So far *Psychidocossus* has been monotypic. Dyar (1940: 1274) describes *infantilis* as small, black, with triangular wings, and resembling a psychid. The figure provided by Seitz (1940: pl. 182: fig. row g) corresponds with Dyar's description. Dr. J.P. Donahue (NHMA) kindly lent me a ♂ specimen of *infantilis*, identified and compared to the the type of this species (USNM) by him. This specimen is rather small (wingspan approx. 25 mm), but not blackish. It has brownish, rounded wings with a fuscous, striate pattern. It thus seems that Dyar made a mistake when he produced the original description. The specimen figured by Seitz does not look like a cossid. The redefinition of the genus hereafter is from the specimen from the collection of the NHMA.

P. infantilis shares with *Fania*, *Toronia* and *Miacora tropicalis* the following apomorphies: mesepimeron moderately high, frenulum structures (at least in male) reduced in size, and median arm moderately wide. In the examined specimen of *infantilis* there seems to be no hairs on the outer margin of the antennal rami of the male, which may be due to damage or a reversal. *P. infantilis* seemingly shares with *Fania* and *Toronia* that the accessory plate II is at most moderately wide. In the other genera mentioned the arolium is wanting, whereas it varies from moderately long to short in *infantilis*. In *infantilis*, as in *Miacora tropicalis*, the mesomeron is approx. 1.5 times width of the eucoxa II. In the specimen examined of *infantilis* the midtibial spurs are wanting. In the specimen examined most of the vestiture on the ventral side of the labial palpi is worn off. The author supposes that this vestiture is also ventrally short, as in e.g. *Fania* and *Toronia*, and tentatively places *Psychidocossus* next to these two genera. However, it could well be that *Miacora* is more closely related to *Fania* and *Toronia* than *Psychidocossus* is.

Fringes are rather long. Male frenulum spine is approx. rather long and retinaculum is a short flap. Venation (1 ex.): R3, R4+5 shortly stalked; R4+5 stalked for approx. 0.6 times their length; inner cell small; Rs-M1 connate; M2 and M3 connate.

P. infantilis is known only from Costa Rica.

Material:
infantilis —1♂, COSTA RICA: Prov. Guanacaste, Santa Rosa National Park (NHMA).

Genus Miacora Dyar, 1905

Miacora Dyar, 1905: 177.
Type species: *Cossus tropicalis* Schaus, 1904: 142.

Originally only *tropicalis* was included in *Miacora*. Dyar (1940: 1274) (later) neglects *Toronia* and includes in *Miacora* a series of species of which some have a simple ♂ antenna and others a bipectinate one. Certain of these had earlier been included in *Toronia*. The type species of *Miacora* has a prismatic ♂ antenna, whereas that of *Toronia* a bipectinate one. *M. tropicalis* further differs from *Toronia perplexa* and *luzena* by the following apomorphies: mesomeron 1.5 times width of eucoxa II, fringes moderately short, Sc-Rs present (sometimes partially), and probably An moderately low (not examined in *perplexa*). Therefore *Toronia* is here kept separate, although it is uncertain if these apomorphies are also found in other species which should be included in *Miacora*. Dyar (1940) notes that *Miacora diffidens* Dyar, 1910 has also a simple ♂ antenna and *Toronia adolescens* a serrated one. No material of these two species has been examined. Perhaps a serrated ♂ antenna is a transitional stage in between a bipectinate and a prismatic one. The present author supposes that a prismatic and/or serrated ♂ antenna is characteristic of *Miacora*.

At least *tropicalis* shares with *Fania nana*, *Toronia* and *Psychidocossus infantilis* the following apomorphies: antennal rami with hairs on outer margin (not certain of *infantilis*), mesepimeron moderately high, frenulum structures reduced in size, and median arm moderately wide. Arolium is wanting in at least *tropicalis*. Investigation of *diffidens* and *adolescens* is needed to be able to define the genus. *Miacora subtropicalis* and *Acossus leucegchytes*, which have a bipectinate ♂ antenna, should probably be excluded and may belong to *Toronia*.

Here below some other characteristics of *tropicalis* follow. Flagellum has dorsally many minute hairs. K lacks a cross-suture in the examined specimens. Tibial spurs are moderately short and in pairs of slightly unequal length. Male frenulum spine is moderately long. Male retinaculum is rudimentary. Venation: areole moderately small to small; R3, R4+5 very shortly stalked; R4+5 shortly stalked; Rs-M1 connate.

M. tropicalis is known from Guyana (Dyar, 1940: 1274), and from Brazil, Peru and Mexico. *M. diffidens* is known from Mexico and *adolescens* from Panama (Dyar, 1940: 1274).

Material:
tropicalis —1♂, MEXICO: State of Oaxacea (BMNH); 4♂♂, PERU: San Gaban, 2500 ft. (BMNH); 1♂, PERU: Yohuarmayo, 1200 ft. (BMNH); 1♂, PERU: Pumayaca (USNM); 1♂, BRAZIL: Espirito Santo (USNM).

Genus **Paracossus** Hampson, 1904

Paracossus Hampson, 1904b: 152.
Type species: *Paracossus furcata* Hampson, 1904b: 152, pl. D: fig. 30.

Paracossus was noted in the legend to the figure of *furcatus* given by Hampson (1904b: 152, pl. D: fig. 30). A diagnosis of the genus and a description of *furcatus* was provided the following year (Hampson, 1905: 194-195) and then a second species, *P. parva* Hampson, 1905, was included.

Of *furcatus* from Burma only one female is known, while of *parvus* only a few males are known. The ♂ antenna of *parvus* is shortly bipectinate in proximal half. The rami are moderately flattened, and have moderately long hairs in approx. two rows on the inner margin and one row of hairs on the outer margin. More distally the antenna becomes two-pointed unilobed, then rounded unilobed, and in distal fourth prismatic with moderately short hairs ventrally. The ♀ antenna of *furcatus* is in proximal half indistinctly prismatic and rounded, has short hairs on the sides, and is in distal half more distinctly prismatic. The vestiture on the labial palpi is in both species ventrally short and dorsally moderately long. The mesepimeron is moderately high. The I-epiphysis reaches nearly as far as the tibia-apex. The tarsi have partly rather long vestiture, which shortens apically. The arolium is minute and membranous. The male retinaculum of *parvus* is rudimentary. The number of ♀ frenulum bristles of *furcatus* amounts approx. five and these are moderately long. The areole is sometimes/often wanting. The inner cell is wanting in both the fore- and hindwing. The scale plate is distinctly smaller than the radial bridge. The median arm is moderately wide. For the rest the two species seemingly show plesiomorphies.

There are more species from southeast Asia of which the ♂ antenna is more or less unilobed or prismatic. The labial palpi of these species have similar vestiture as in *parvus* and *furcatus*. The mesepimeron is also moderately high in these species. The I-epiphysis of these species reaches nearly or approx. as far as the tibia-apex too. Most of these species have a moderately low An, short vestiture on the tarsi, a well-developed ♂ retinaculum, and a scale plate as long as the radial bridge. These species have previously been included in *Cossus* Fabricius, 1793. Certain of these, such as *C. celebensis* Roepke, 1957, *C. javanus* Roepke, 1957 and *C. subfuscus* Snellen, 1895, have an unilobed ♂ antenna, which looks similar to that of *Cossus*. Of at least *subfuscus* and *javanus* the ♀ antenna is prismatic, whereas in *Cossus* species it is also unilobed. Of the other species mentioned the female is unknown. In *C. chloratus* Swinhoe, 1892, which closely resembles superficially *celebensis* and *subfuscus*, the ♂ antenna is mainly unilobed but the apex is often prismatic. In *C. speideli* Holloway, 1986 the ♂ antenna is in proximal half unilobed and distally prismatic. In *Cossus greeni* Arora, 1976 from Sri Lanka and a few unidentified/undescribed species from resp. Sri Lanka, Sulawesi and Irian Jaya the ♂ antenna is two-pointed unilobed. It seems that a rounded unilobed ♂ antenna is one developmental stage further than a two-pointed unilobed one. The author presumes that an unilobed antenna has developed from the state in which the antenna is distally unilobed or prismatic and proximally bipectinate or bilobed. The latter state is found in *Brachylia acronyctoides*, *C. seria* Holloway, 1986, *C. retak* Holloway, 1986, *C. telisai* Holloway, 1986 and *C. cinereus* Roepke, 1957.

It is most parsimonious to place species such as *acronyctoides* and *seria* in one group with *parvus* and *furcatus* with the criterion that the ♂ antenna is proximally bipectinate or bilobed and distally unilobed or prismatic. Such an antenna would have developed from a state in which the antenna is completely bipectinate by fusion and shortening of the rami distally. It could however be that the unilobed state has developed from the bipectinate state with more or less flattened rami and with many hairs on the proximal side of the rami. In section 3 there are two (new) genera in which the ♂ antenna shows the latter state, the vestiture of the labial palpi is similar, and the ♀ antenna is prismatic in certain species. These two genera are represented in Africa. They presumably form the sister-group of *Isocossus* Roepke, 1957, which is represented in southeast Asia. The possibility that the southeast Asian species with an unilobed ♂ antenna and a prismatic ♀ antenna form the sister-group of one of the African genera or of *Isocossus* cannot be ruled out. In *Isocossus* and the African genera the ♂ retinaculum is distinctly reduced in size, whereas in the Asian group well-developed. In *cinereus* from Indonesia, in which the ♂ antenna is partly prismatic, the ♂ retinaculum is also well-developed. Therefore the Asian group with an unilobed ♂ antenna is tentatively included in *Paracossus*. A completely bipectinate ♂ antenna is found in C. *rufipecten* Holloway, 1986 from Sarawak. It is here uncertain if *rufipecten* and perhaps more of such species should be included. Of the only known specimen of C. *cruciatus* Holloway, 1986 the tips of the antennae are broken off and missing. It is obscure if this species should also be included. Of C. *pusillus* Roepke, 1957 only the female is known. Because the ♀ antenna of *pusillus* is prismatic and the species closely resembles superficially *chloratus*, the former is tentatively included too.

All the species included share that the mesepimeron is moderately high and that the I-epiphysis reaches nearly or approx. as far as the tibia-apex. In most of these the median arm is still moderately narrow. In *javanus* and *chloratus* the fifth tarsomere is 1.3 or 1.5 times length of fourth. In *javanus, chloratus, speideli, subfuscus, celebensis,* and a few unidentified species the scales distally in between the veins on the upper-and/or underside of the forewing are distinctly smaller than those on the veins. The number of ♀ frenulum bristles amounts approx. six or seven in several species, except *furcatus,* and these are moderately long. A reduced forewing inner cell and a reduced hindwing inner cell are probably apomorphies of *Paracossus*. In several of these species the inner cell of the hindwing is sometimes wanting. Venation: areole moderately small to very small, but often/usually wanting in *parvus* and *furcatus;* R3, R4+5 separate to shortly stalked; R4+5 (usually) shortly stalked; inner cell small to minute, and sometimes/usually wanting in *parvus* and *furcatus;* Rs-M1 short to shortly stalked; inner cell (hindwing) small to wanting.

A host of *acronyctoides* is *Tamarix articulata* Vahl. (Beeson, 1961: 440).

The genus in the wider sense is represented from India to New Guinea.

Material:

furcatus —1♀ (holotype), BURMA: Magaree, Gen. slide Cossidae no. 1961-158 (BMNH).

parvus —1♂ (holotype), SRI LANKA: Matale, Gen. slide Cossidae no. 145 (BMNH); 2♂♂, SRI LANKA (BMNH).

acronyctoides —1♂ (holotype), INDIA: Bombay, Gen. slide Cossidae no. 125 (BMNH); 1♂, 1♀, INDIA: Bombay (BMNH).

seria —1♂ (holotype), BRUNEI: Seria, 3 m., 28.xii.1978 (Allen), Gen. slide Cossidae no. 127 (BMNH).

retak —1♂ (holotype), BRUNEI: Bukit Retak, 1619 m., 14.ix.1979 (Allen), Gen. slide Cossidae no. 131 (BMNH).

telisai —1♂ (holotype), BRUNEI: Telisai, 15 m., 8.i.1980 (Fairclough), Gen. slide Cossidae no. 153 (BMNH).

cinereus —(all INDONESIA) —1♂ (holotype), n.e. Kalimantan, Pesafoprin (ITZ); 1♂, e. Kalimantan (BMNH); 1♂, 1♀, s.e. Kalimantan, s. Mentawir (RMNH); 1♂, Sumatra, Deli (RMNH).

Undescribed species (a) —(all SRI LANKA and BMNH) —1♂, Haputale; 1♀, Kandy; 1♀, Galagedeia.

Undescribed species (b) —1♂, INDONESIA: n. Sulawesi, Minahassa (van den Bergh) (RMNH).

Undescribed species (c) —1♂, INDONESIA: Irian Jaya, Uskwar, 24.ix.1936 (coll. van Groenendael) (ITZ).

speideli —1♂ (holotype), MALAYSIA: w. Pahang, Genting Tea Estate, 11.v.1978 (Barlow), Gen. slide Cossidae no. 137 (BMNH).

subfuscus —long series (most ♂, 3♀♀), INDONESIA: Medan, Buitenzorg and Radjamandala (RMNH).

Undescribed species (d) —1♂, INDONESIA: w. Flores, Rhese, 400 m., 2.vi.1953 (coll. van Groenendael) (ITZ); 2♂♂, INDONESIA: e. Flores, Sukutukang (coll. van Groenendael) (ITZ).

celebensis —1♂ (holotype), INDONESIA: n. Sulawesi, Minahassa, Bolaong Mongondow (van den Bergh) (RMNH); series of males, INDONESIA: Sulawesi, various localities (RMNH); long series of males, INDONESIA: Minahassa (ITZ); series of males, INDONESIA: s.w. Sulawesi, Pangean (ITZ); 1♂, INDONESIA: s.w. Sulawesi, Bonthain (ITZ); 1♂, INDONESIA: w. Sulawesi, Palu, Mt. Rangkunau (ITZ); 1♂, PHILIPPINES: Camarines Sur, Mt. Isarog, 750-850 m. (BMH).

javanus —(all INDONESIA and RMNH) —1♂ (holotype), w. Java (Walsh); 1♀ (paratype), w. Java, Radjamandala, 350 m., xii.1940 (Olthof); 2♂♂, Perbawah.

chloratus —(all INDONESIA and RMNH) —1♂, Kepulauan Banggai, Sambiut; 2♂♂, e. Kalimantan, Kariorang.

Undescribed species (e) —(all INDONESIA and RMNH) —1♂, Sumatra, Dolok Ilir, 25.ii.1936 (Uil); 1♂, w. Java, Buitenzorg, 1894.

pusillus —1♀ (holotype), 1♀ (paratype), INDONESIA: [w. Java], Garut, viii.1926, ex "Batang Kesemek" (Soekardjo) (RMNH).

Unknown genus/genera

There is a series of species from Africa of which the males have a more or less strongly bipectinate antenna and of which the vestiture on the labial palpi is ventrally short and dorsally moderately long. These species have previously been placed in *Cossus*, which has been restricted to species of which both the ♂ and ♀ antenna are unilobed (Daniel, 1956a). These species with a bipectinate ♂ antenna do not fit in any available genus and should be be placed in a new genus. Only a few of these have been briefly examined. There seem to be several undescribed species amongst the unidentified material in the BMNH. It will be difficult to give a diagnosis of this genus or these genera, since most characters seemingly are in a plesiomorphic state. Only one special group of two species from Madagascar has been distinguished and is described here below. The description of a new genus for the other material is left to a more detailed and extensive study.

Genus **Hirtocossus** gen. nov.

Type species: *Cossus cirrilator* Le Cerf, 1919c: 107-108.

Etymology: "hirtus" (Latin) means hairy + genus-name *Cossus*. Gender: masculine.

Hirtocossus is introduced for *Cossus cirrilator* and *C. crucis* Kenrick, 1914, both from Madagascar. The ♂ antenna of these species is bipectinate, up to nearly rather strongly. *Cossus* has been restricted to species with an unilobed ♂ and ♀ antenna (Daniel, 1956a). The rami of *cirrilator* and *crucis* have approx. two rows of moderately short hairs on the inner margin and short or very short hairs on the outer margin. This type of ♂ antenna is also known in *Macrocossus, Lamellocossus, Prionoxystus* and *Acossus*. In *Hirtocossus* the vestiture on the labial palpi is ventrally short and dorsally moderately long. See also fig. 12. *H. cirrilator* and *crucis* share furthermore the following apomorphies: mesomeron 1.3 or 1.5 times width of eucoxa II, I-epiphysis reaching nearly as far as tibia-apex, and ♂ frenulum spine and retinaculum reduced. Females are unknown.

An is moderately low in *cirrilator* and moderately high in *crucis*. K is at least sometimes without a cross-suture. Mesepimeron is moderately high in *cirrilator* and rather high in *crucis*. Mesomeron is approx. 1.3 times width of eucoxa II in *cirrilator*, and approx. 1.5 times width in *crucis*. Accessory plate II varies from wide to moderately narrow in at least *crucis*. Intersclerite III is probably wanting. Paronychia are wanting. Arolium is moderately long and moderately wide. Tibial spurs are moderately long and moderately short, or moderately long and slightly unequal in length, and apical ones of hindleg may be moderately short and short in *crucis*. Fringes of *cirrilator* are moderately long and those of *crucis* have not been examined. Male frenulum spine is moderately or rather long and retinaculum is a short flap or rudimentary. Venation: areole moderately small to small; R3, R4+5 (very) shortly stalked; R4+5 shortly stalked; M1 posterior to or from tip of areole; Rs-M1 short to very shortly stalked. Humeral plate of at least *crucis* is approx. 1.5 times size of radial bridge. 4Ax is more or less membranous. Median arm of *cirrilator* is moderately wide and that of *crucis* moderately narrow but nearly moderately wide.

Material: (all MADAGASCAR)

cirrilator —1♂ (holotype), ? (ex coll. Oberthür), Gen. slide no. Viette ♂ 912 (MNHN); long series of males, central Madagascar and Station Périnet (BMNH).

crucis —1♂ (holotype), central Madagascar, 2500 ft., i-iii.1911 (Pratt) (BMNH); series of males (BMNH); long series of males (MNHN).

Undescribed genus

There is an undescribed species from Africa with a similar type of ♂ antenna as in the Zeuzerinae. The proximal two-fifths of the antenna is rather strongly bipectinate and more distally it is prismatic. Unique is that the flagellum has dorsally many short hairs on each segment. In other Cossidae as far known the flagellum has only approx. one dorsal hair per segment, or the antenna is prismatic and the flagellum has dorsally many minute hairs (*Miacora* and *Holcocerus*). The state with the many short hairs distinguishes this species from those of *Paracossus* of which the ♂ antenna is also proximally bipectinate and distally prismatic. The female is unknown. The species does not fit in an available genus. The naming of a new genus is left to a more detailed study, including the genitalia and the naming of the species.

Vestiture of the labial palpi is ventrally short and dorsally moderately long. Mesepimeron is moderately high. First tarsomere of the hindleg has many long scales and second one has a few. Arolium is well-developed. Male retinaculum is rudimentary and frenulum spine is moderately long. Venation (1 ex.): areole moderately small; R3, R4+5 shortly stalked; R4+5 shortly stalked; inner cell very small; Rs-M1 very shortly separate. Humeral plate is 3 times size of radial bridge. Median arm is moderately wide.

Material:
Undescribed species —1♂, ZAIRE: Equateur, Ikela, Loile River (BMNH).

Genus **Cossus** Fabricius, 1793

Cossus Fabricius, 1793: [1].
Type species: *Phalaena cossus* Linnaeus, 1758: 504.
Teredo Hübner, 1805/1806: [1]. [Not available].
Lyonetus Rafinesque, 1815: 129. [Unnecessary objective replacement name].
Trypanus Rambur, 1866: 326. [Unnecessary objective replacement name].

Cossus is one of the oldest and best known genera of Cossidae. There exists extensive literature on *C. cossus*, the Goat Moth. Many species from various continents had previously been included in *Cossus*. The genus became a heterogeneous group of species with many different types of antenna. Daniel (1956a) redefines the genus and restricts it to a series of species of which both the ♂ and ♀ antenna are unilobed. He includes the following species: *cossus* with several forms and subspecies, *C. balcanicus* Lederer, 1863, (tentatively) *Holcocerus nigrescens* Rothschild, 1912, *Trypanus funkei* Röber, 1896, *C. araraticus* Teich, 1896, *C. mokanshanesis* Daniel, 1945, *C. bohatschi* Püngeler, 1898, *C. divisa* Rothschild, 1912, *C. hunanensis* Daniel, 1940, *C. tapinus* Püngeler, 1898, *C. aksuensis* Daniel, 1953, *C. modestus* Staudinger, 1887 (plate 1: fig. B), *C. irani* Daniel, 1937 and (tentatively) *C. sareptensis* Rothschild, 1912. Daniel (1965c) gives extra information on certain species. Hua (1986a) raises *Cossus cossus chinensis* Rothschild, 1912 to the species level. *Cossus ligniperda* Fabricius, 1794, which is often found in the literature, is a junior subjective synonym of *C. cossus*.

In this study only material of *cossus*, *bohatschi* and *modestus* has been examined. Only of *cossus* females were available. The ♀ antenna of *cossus* is slightly more shortly unilobed than the ♂ one. The lobes have many very short hairs on the proximal and lateral sides. The three species share the following apomorphies: vestiture on labial palpi ventrally short and dorsally moderately long, I-epiphysis reaching nearly as far as tibia-apex, arolium wanting, and 4Ax more or less reduced. In *cossus* the mesepimeron is moderately high, whereas in the other two species still rather high. The accessory plate II is in *modestus* (1 ex.) moderately narrow, and in *cossus* wide. The mesomeron is in *cossus* 1.5 times width of the eucoxa II, but in *modestus* as wide as. The tibial spurs are moderately short and slightly unequal in *modestus*, and are moderately short and short in *cossus* and *bohatschi*. The tarsal claws of *cossus* are moderately slender. The male retinaculum of *cossus* is a short flap, whereas well-developed in the other two species. The scale plate of *modestus* is distinctly shorter than the radial bridge. The median arm of *cossus* is rather wide. There is probably more diversity amongst the characters of the other species Daniel included. The unilobed antenna of the male as well as female is probably in combination with the long I-epiphysis the only significant characteristic of the genus.

A completely unilobed antenna is also known in the males of certain species which have tentatively been included in *Paracossus*. In several of these *Paracossus* species the lobes of the antenna are two-pointed. The ♀ antenna of *Paracossus* species is as far known prismatic. The species of *Paracossus* occur in southeast Asia, while those of *Cossus* as far known in the Palaearctic.

In *Parahypopta* Daniel the ♂ and ♀ antenna are unilobed too. *Parahypopta caestra* (Hübner) is the only species of this genus of which the female is known. In this species the ♀ antenna is as strongly unilobed as the ♂ one and has laterally approx. two pairs of stout sensilla. In *Cossus* the ♀ antenna is less strongly unilobed than the ♂ one and has only short hairs. The vestiture on the labial palpi is at least in *caestra* and *Parahypopta sheljuzhkoi* (Zukowsky, 1936) longer than in the examined specimens of *Cossus* species. *Parahypopta* is tentatively placed in section 3.

C. *irani* is excluded from *Cossus*, because the ♀ antenna of this species is simple (Daniel, 1956: 277), the lobes of the ♂ antenna are two-pointed, and the vestiture of the labial palpi is short mixed moderately long. It is uncertain in which genus this species should be placed. Daniel (1956: 277) notes that *irani* closely resembles superficially *Cossulus herzi* (Alphéraky, 1893). Perhaps *irani* should be included in *Cossulus* Staudinger, 1887. It differs from (other) species of *Cossulus* in that the ♂ antenna is two-pointed unilobed and An is moderately high.

Vertex of *cossus* has an arcuate and slightly ridged Pos; Pos variable, up to from 0.6 to 0.8 times length of vertex. Antenna has minute or short hairs on the proximal side of lobes. Vestiture of labial palpi is ventrally short and dorsally moderately long. Sternopleural region of thorax of *cossus* is shown in fig. 33. Bs II is posteriorly shortened and rounded. Intersclerite III is wanting. Male I-epiphysis reaching approx. as far as tibia-apex, and female one reaching little short of tibia-apex in *cossus*. Fringes are long. Male frenulum spine is well-developed in *modestus*, but moderately short in *cossus*. Number of ♀ frenulum bristles of *cossus* is more than five. Venation: areole moderately small; R3, R4+5 connate to very shortly stalked; R4+5 (very) shortly stalked; inner cell of *modestus* very small; Rs-M1 moderately short to shortly stalked. Humeral plate has been examined in *cossus* and in this species it is approx. 2.5 times size of radial bridge.

It is here not quite certain in which section of Cossinae *Cossus* should be placed in a cladogram. The author presumes that the unilobed antenna evolved from the bipectinate state. It seems that a similar but independent development happened within *Paracossus*. It is however obscure wich type of rami have reduced. In section 3 a similar type of vestiture on the labial palpi is also known in *Isocossus*, two new genera, *Dyspessacossus* Daniel, 1953 and certain species of *Cossulus* Staudinger, 1887. In *Isocossus*, *Dyspessacossus* and *Cossulus* the ♂ antenna is partly unilobed. It thus might be that *Cossus* should be placed in section 3.

Several species occur in southern U.S.S.R., Iran and/or Iraq. Approx. two species are distributed in Turkey. Two or three species are known from China. C. *cossus* has the widest distribution; the species is represented throughout Europe, and from Turkey to Lebanon, and is further recorded from Morocco, southern U.S.S.R., Iraq, Afghanistan, China (Manchuria), east Siberia, Korea, and Japan (see Daniel, 1956a:

245-257). It is however not certain whether all subspecies which Daniel distinguishes and includes actually belong to *cossus*. Hua (1986a) examined the genitalia of *chinensis* and *cossus* and separates them as species. Daniel did not examine material from Japan. *C. cossus* has been recorded from Norway north to approx. 69°N (Opheim & Fjeldså, 1983: 18-19). Skinner (1985: 73) provides a map of the distribution in Great Britain and Ireland.

Hackray et al. (1985: 35) note the following hosts of *C. cossus cossus*: *Cydonia* Mill., *Betula* L., *Fraxinus* L., *Malus* Mill., *Pirus* L., *Populus* L., *Alnus* Mill., *Salix* L., *Sorbus* L., *Quercus* L., *Ulmus* L., and particularly *Sambucus* L. Griep (1918: 83) believes that *C. cossus uralicus* Seitz is monophagous in willow. Daniel (1956a: 257) records that *cossus* lives particularly in "Pyramidenpappel", a poplar, in the environment of Marasch. A description of the life-history of *cossus* is provided by Daniel (1956a: 258-262).

Material:

cossus —very long series of both sexes from many localities in Europe (BMNH); long series of both sexes, NETHERLANDS (ITZ, RMNH).

modestus —(all U.S.S.R.) —long series of males, Transcaspia (BMNH); 1♂, Kulja (RMNH); 1♂, Turkmeniya (RMNH).

bohatschi —1♂, U.S.S.R.: Issyk-Kul (RMNH).

Genus **Holcocerus** Staudinger, 1884

Holcocerus Staudinger, 1884: 139-140. [Established as a subgenus of *Cossus* Fabricius].
Type species: *Cossus (Holcocerus) nobilis* Staudinger, 1884: 139-140, pl. 9: fig. 1.
? *Holcoceroides* Strand, 1913: 35.
Type species: *Holcoceroides ferrugineotincta* Strand, 1913: 36.

Holcocerus has been established for a few species of which both the ♂ and ♀ antenna is prismatic, but looking like filiform. Daniel (1959) revises the Palaearctic section of *Holcocerus*. He includes approx. thirty-five species with as criterion the prismatic antenna. Reference should be made to Daniel (1959) for the names of these species and their forms and subspecies. *Holcocerus strigillata* Rothschild, 1912 is here excluded and placed in *Cossulus*. Perhaps more species of which Daniel did not examine material should be excluded. Daniel (1965c: 93-99) gives some extra information on certain species and adds *Cossus lucifer* Grum-Grshimailo, 1891 and *C. rufidorsia* Hampson, 1905 to *Holcocerus*. Hua (1986a) describes three new species from China and places these in *Holcocerus*.

Only *ferrugineotincta* has so far been included in *Holcoceroides*. Strand (1912: 36) notes that *Holcoceroides* is easily distinguished from *Holcocerus* by the very short labial palpi and the shorter antennae. Gaede (1930: 543) does not give any difference for this genus from *Holcocerus*, except a more southern distribution (Equatorial Guinea). No type-material was available. Two specimens in the BMNH identified as *ferrugineotincta* differ from examined material of *Holcocerus* species in that the ♂ retinaculum is wanting, the arolium is well-developed, and the tarsal claws are moderately thick. The labial palpi are approx. 1.3 times length of the eye-diameter and thus not that short. In several species included in *Holcocerus* the labial palpi are only slightly longer. The length of the antenna varies amongst the species of *Holcocerus*. The noted differences are here considered insufficient to regard *Holcoceroides* as a separate genus. The only significant difference seems to be the bifid uncus of *ferrugineotincta* (Heppner, 1959: 45), but a bifid uncus has also been found in a specimen of an unidentified species, which appears to be a good *Holcocerus* species. Therefore *Holcoceroides* is here tentatively placed as a synonym of *Holcocerus*.

The most important characteristic of *Holcocerus* is the prismatic antenna in both sexes. The antenna may look like filiform, since there is little or hardly any space in between the ventral lobes. According to Daniel (1959), the ♀ antenna is in certain species thinner than the ♂ one. The antenna is proximally more or less rounded, becoming more flattened distally. The segments of the antenna have many very short hairs. The flagellum has dorsally many very short or minute hairs. In the female of *H. inspersus* Christoph, 1887 and perhaps more species the hairs on the antenna are concentrated near and along the apexes of the segments. The vestiture of the labial palpi is in all material examined, except that of *inspersus*, ventrally short and dorsally moderately long. In *inspersus* the vestiture on the labial palpi is ventrally short with fewer moderately long and hair-like scales in between. In all the material examined the tarsal claws are moderately slender and the I-epiphysis reaches distinctly short of or (nearly) as far as the tibia-apex. Bs II is posteriorly shortened and rounded in at least *H. arenicola* (Staudinger, 1897), *H. inspersus* and *Cossus verbeeki* Roepke, 1957. Too few species have been examined to give an accurate diagnosis of the whole genus.

Vertex of *inspersus* has a slightly arcuate Pos up to approx. 0.8 times length of vertex. Thoracic sclerites have been examined in *inspersus*, *H. strioliger* Alphéraky, 1893 and *H. gloriosus* (Erschoff, 1874). An is moderately low in *gloriosus* and *strioliger*, and low in *inspersus*. Accessory plate II varies from wide to moderately narrow in *inspersus*. Intersclerite III is wanting. Tibial spurs vary amongst the species from rather and moderately long to equal in length and moderately short. Arolium varies amongst the species from well-developed to wanting. Fringes are in most species rather long or long, but in *arenicola* these are moderately long. Male frenulum spine varies amongst the species from nearly long to moderately long and retinaculum from well-developed to rudimentary. Number of ♀ frenulum bristles amounts approx. six to eight and these are moderately long or moderately short. Venation: areole moderately large to moderately small; R3, R4+5 very short to very shortly stalked; R4+5 shortly stalked; Sc-Rs sometimes partly present in at least *inspersus*; Rs-M1 short to very shortly stalked. Humeral plate has been examined in *inspersus*, *gloriosus* and *H. sericeus* Grum-Grshimailo, 1890. This plate is in these species approx. as large as or slightly larger than radial bridge. 4Ax is distally more or less reduced. Median arm is in most species moderately wide, but in *gloriosus* moderately narrow and in *inspersus* narrow.

There is an unidentified/undescribed species known from Ivory Coast, which should probably also be included in *Holcocerus*. There are only ♂ specimens of this species available, so that the ♀ antenna couldnot be checked. In the three males examined there are small, ocelli-like protuberances present, which is probably due to a reversal. An is moderately low. The accessory plate II varies from moderately wide to very narrow. The tarsal claws are moderately thick, whereas these are moderately slender in other *Holcocerus* species. The fringes are moderately long. The areole is small. R4 and R5 are variably stalked from 0.3 up to 0.6 times their length. This species is tentatively included in *Holcocerus*, pending an investigation of the ♀ antenna.

There are three species in southeast Asia of which at least the ♂ antenna is prismatic. These species are: *Cossus kinabaluensis* Gaede, 1933, *C. verbeeki* and an undescribed species from Flores. The figure of the female of *kinabaluensis* given by Seitz (1934: pl. 93: fig. row i) shows a simple or prismatic antenna. The ♀ antenna of *verbeeki* is similar to the ♂ one. Of the undescribed species no females were available. These three species share the following apomorphies: vestiture of labial palpi ventrally short and dorsally moderately long, An moderately low, mesepimeron moderately high, I-epiphysis reaching nearly or approx. as far as tibia-apex and more or less pointed, and fringes moderately short (*kinabaluensis*) or moderately long. In *verbeeki* and *kinabaluensis* the humeral plate has been examined and this plate is in these species 3 times size of radial bridge. In *kinabaluensis* and the undescribed species the mesomeron is 1.5 times width of eucoxa II and the fifth tarsomere is 1.3 to 1.5 times length of fourth. In all three species the tarsal claws are moderately thick.

It seems that these three species differ especially from examined material of *Holcocerus* species by a larger humeral plate and thicker tarsal claws. It is obscure if the three species form a monophyletic group and if their prismatic antenna evolved independently from the one in *Holcocerus*. Perhaps they should be placed in a new genus, but this is here too uncertain. Therefore these three species are tentatively included in *Holcocerus*.

It is uncertain whether the type of antenna in *Holcocerus* evolved independently from that in *Cossus*, which is unilobed. The type of vestiture of labial palpi in *inspersus* is presumably a reversal. Since in both *Cossus* and *Holcocerus* the antenna is not bipectinate and Bs II is posteriorly shortened, the two genera are placed together in the cladogram (fig. 12). However the possibility that *Holcocerus* should be placed in section 3 cannot be ruled out. See also under *Cossus*.

Most species of *Holcocerus* occur in the U.S.S.R., a few in Japan, and some more in China (e.g. Manchuria). Daniel (1965b: 99) records several species from Mongolia. Some representatives are distributed in Iran, Iraq or the Middle East. *H. arenicola* is known from south U.S.S.R. (e.g., Armenia, Caucasus and Turkmeniya), Afghanistan, Pakistan, China, and India (Great Nicobar Islands) (Arora, 1976: 42). *H. rufidorsius* is known from North India (Assam and Sikkim) (Arora, 1976: 46). *Cossus (Holcocerus) holosericeus* Staudinger occurs also in northern Africa. *H. ferrugineotinctus* occurs in Equatorial Guinea and Nigeria. The unidentified/undescribed species is known from Ivory Coast. Three species, which are tentatively included, occur in Malaysia and/or Indonesia. See also Daniel (1959; 1965c) for records of the species.

A host-plant of *verbeeki* is *Acacia tomentosa* Willd. (Roepke, 1957: 9).

Material:

nobilis —1♂, U.S.S.R.: Mary (RMNH).

volgensis Christoph, 1893 —1♂, U.S.S.R.: Sarepta (RMNH).

consobrinus Püngeler, 1898 —1♂, CHINA: Aksu (ITZ); 1♂, Asia (ITZ).

pulverulentus Püngeler, 1898 —1♂, CHINA: north Tibet (RMNH).

gloriosus (plate 1: fig.C)—1♂, U.S.S.R.: Dortkuju (BMNH); 1♂, U.S.S.R.: Mary (RMNH); 1♂, IRAN: Dshidak (RMNH).

holosericeus —1♂, U.S.S.R.: Mary (RMNH); 1♂, U.S.S.R.: Turkmeniya (RMNH); 1♂, U.S.S.R.: Mary

(ITZ); 1♂, Asia (ITZ).

sericeus —3♂♂, IRAN (RMNH).

inspersus —4♂♂ (syntypes), U.S.S.R.: Ashkhabad (coll. Cristoph) (BMNH); 15♂♂, U.S.S.R.: Ashkhabad, Mary, Repetek and Dortkuju (BMNH); 1♀, U.S.S.R.: Bukhara (BMNH); 1♂, U.S.S.R.: Issyk-Kul (ITZ); 3♂♂, AFGHANISTAN: Ruschke (BMNH); 1♂, ? (RMNH).

strioliger (identified as *Paropta confusa* Rothschild) —1♂, south of Sarymat, Serafschan, 8000 ft. (coll. Rothschild) (BMNH).

arenicola —2♂♂ (syntypes of ssp. *transcaucasicus* Zukowsky), U.S.S.R.: Armenia, Dschulfa, Daratshitshag, 2000 m., vi (ex coll. Bang-Haas) (ITZ); 1♂, U.S.S.R.: Mary (ITZ); 1♂, Asia (ITZ); 2♂♂, U.S.S.R.: Turkmeniya (RMNH); 1♂, U.S.S.R.: Kopet-Dag (BMNH).

rufidorsius —1♂ (holotype), INDIA: Sikkim (Dudgeon), Gen. slide cossid no. 136 ♂ (BMNH).

ferrugineotinctus —1♂, EQUATORIAL GUINEA: near Macenta, Soundedou, 1600 ft. (BMNH); 1♂, NIGERIA (BMNH).

Unidentified/undescribed species —2♂♂, IVORY COAST: Bouïtha, 15 km e. of Bouaflé, Begbézéré (Schouten & Buijsen) (RMNH); 1♂, IVORY COAST: 20 km e. of Bouaflé, Titekro (Schouten & Buijsen) (RMNH).

verbeeki —(all INDONESIA: Java, RMNH) —1♂ (holotype), Telawa, 23.ix.1936 (Kalshoven); 1♀ (paratype), Rembang, Tepu Lamp (Verbeek); series of both sexes, Rembang.

kinabaluensis —1♂, MALAYSIA: Selangor, Bukit Kutu (BMNH); 1♀, MALAYSIA: Sarawak, Bidi (BMNH); 1♂, INDONESIA: w. Sumatra, Lebong Tandai (BMNH); 1♂, INDONESIA: w. Java, Tjikadjang, Bandjarwangi, 800-900 m. (RMNH); 1♂, INDONESIA: Sumatra, Bonan Dolok, Sibolga, 500 m. (RMNH).

Undescribed species —1♂, INDONESIA: m. Flores, Maunri (ITZ).

Table 5. Apomorphies in fig. 12 (Fania genus-group).

1. Vestiture on second and third segment of labial palpi ventrally only short and dorsally moderately long.
2. Male antenna bipectinate for approx. 0.4 times its length and further prismatic.
3. Flagellum of at least ♂ antenna with many short hairs dorsally.
4. Male frenulum spine reduced in length; moderately or rather long.
5. Male retinaculum reduced in size; short flap, rudimentary ridge or wanting.
6. Humeral plate approx. 3 times size of radial bridge.
7. Male antenna: Rami with approx. two rows of moderately short hairs on inner margin and many short or very short hairs irregularly distributed (scattered) on outer margin.
8. I-epiphysis reaching nearly or approx. as far as tibia-apex.
9. Male antenna: rami with approx. one row of approx. moderately long hairs on outer margin.
10. Mesepimeron moderately high.
11. Median arm moderately wide.
12. Accessory plate II varying from moderately wide to moderately narrow.
13a. Arolium distinctly reduced to wanting.
b. Arolium only wanting.
c. Arolium moderately long to reduced in length.
14. Mesomeron approx. 1.5 times width of eucoxa II.
15. Male antenna prismatic.
16. Antenna not bipectinate.
16a. Male and female antenna unilobed.
b. Male and female antenna prismatic.
17. Bs II posteriorly shortened and rounded. N.B. Only examined in *Cossus cossus*, *Holcocerus arenicola*, *H. inspersus* and *H. verbeeki* within *Cossus* and *Holcocerus*.
18. Fringes reduced (at most rather long).

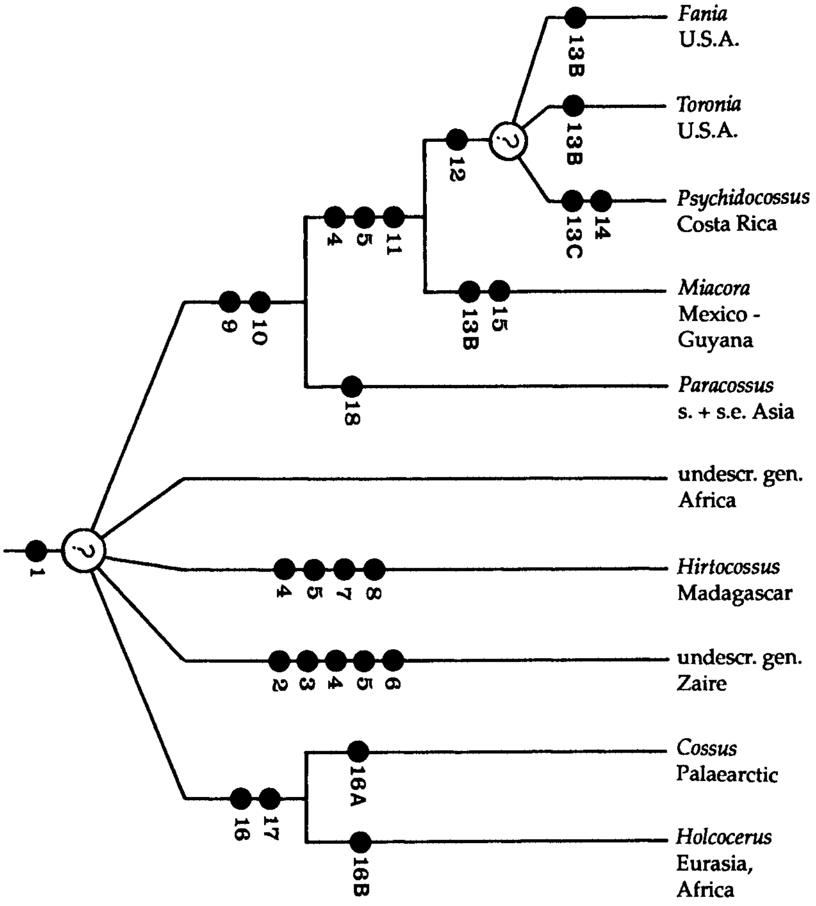


Fig. 12, cladogram of section 2 (Cossinae).

Section 3

Most species of section 3 have flattened antennal rami with hairs on their proximal side. For convenience, section 3 is split into two parts: 3A and 3B (see figs. 19 and 51).

Section 3A

Genus **Neostygia** Wiltshire, 1980

Neostygia Wiltshire, 1980: 190.

Type species: *Neostygia postaurantia* Wiltshire, 1980: 190, pl.: fig. 1 (♀, holotype).

So far only *postaurantia* from Oman has been placed in *Neostygia*. *N. postaurantia* is a rather small species. The forewing is mainly dark fuscous with white stripes. The hindwing of the female is mainly yellow-orange and mixed dark fuscous at its margins, and its fringe is dark fuscous. The male is unknown. The species closely resembles superficially *Stygia australis* Latreille, 1804, of which the ♂ hindwing has also a large yellowish area. The author supposes that the ♂ antenna of *postaurantia* has hairs only on the proximal side of the rami, as in *Stygia* Latreille, 1802. The two genera share the following apomorphies: mesomeron approx. 1.5 times width of eucoxa II, I-epiphysis wanting, tarsal claws moderately slender, and humeral plate at least 2.5 times size of radial bridge. *N. postaurantia* differs especially from *Stygia* species in that the mesepimeron is still rather high, whereas it is moderately high in *Stygia*. The present author prefers to keep the two genera tentatively apart, although the two seemingly form a monophyletic group and could easily be synonymized.

N. postaurantia has been partially examined, since only the holotype was available. Female antenna is moderately strongly, equally bipectinate; the rami are much flattened and rounded, and have short hairs on proximal side. Frontal tuft is ventrally short and more dorsally rather long. Eyes of female are moderately reduced in size and frons is distinctly widened. Labial palpi are porrect in S-shape and approx. 2.5 times length of eye-diameter. State of tegula is unknown. An is moderately high. K has a cross-suture. Intersclerite III is wanting. Arolium and paronychia are wanting. Fringes are long. Number of ♀ frenulum bristles amounts four, and these are rather long. Venation: R3, R4+5 connate; R4+5 shortly stalked; inner cell moderately large; Rs-M1 short; inner cell (hindwing) very small. Humeral plate is approx. 2.5 times size of radial bridge.

Material:
postaurantia —1♀ (holotype), OMAN: Dhofar, 44 km from Salalah, Burg Road, 2000 ft., 25.ix.1977 (Guichard) (BMNH).

Genus **Stygia** Latreille, [1802]

Stygia Latreille, [1802]: 403.
Type species: *Stygia australis* Latreille, 1804: 185.
Cryphia Meigen, 1830: 190. [Unnecessarily objective replacement name, and junior homonym of *Cryphia* Hübner].
Hyalida Sodoffsky, 1837: 83. [Unnecessarily objective replacement name].

Stygia has been revised by Daniel (1955), who includes *S. australis* (plate 1: fig.D) and *S. hades* Le Cerf, 1924. Daniel excludes many species described under *Stygia* and places certain ones of these in a new genus (see under *Stygioides* Bruand, 1853). Daniel (1965c: 80-81) describes a third species, *Stygia mosulensis*.

Stygia shares with *Neostygia* the following apomorphies: mesomeron approx. 1.5 times width of eucoxa II, I-epihysis wanting, tarsal claws moderately slender, and humeral plate at least 2.5 times size of radial bridge. *Stygia* has also the following apomorphies: tegula ventro-posteriorly only little and nearly bluntly pointed, upper Pas below half length of Pre II plus Pa, mesepimeron only moderately high, arolium more or less reduced in size and membranous, inner cell of forewing partly indistinct to wanting, and humeral plate more than three times size of radial bridge. The three species are moderately small.

Only of *australis* males were available. Vertex of *mosulensis* has an arcuate Pos up to approx. 0.6 or 0.7 times its length (see fig. 16). Vertex of *australis* has a sinuate Pos up to approx. 0.8 times its length (see fig. 17). Male antenna of *australis* is rather strongly and unequally bipectinate; rami broad and much flattened, sometimes asymmetrical, with very short hairs on proximal side and small scales on outer margin, and with one stout sensillum at apex. Female antenna of *mosulensis* is moderately strongly bipectinate; rami rather broad and bluntly pointed, with very short hairs on proximal side, with small scales on outer margin, and with one stout sensillum at apex. Female antenna of *hades* is similar to that in *mosulensis,* but rami slightly narrower and without stout sensillum at apex. Female antenna of *australis* is moderately bipectinate; rami broad, broader than in male, rounded, with short hairs on proximal side and scales on outer margin, and with one or two stout sensilla at apex. Eyes in *hades* and *australis* moderately or much reduced in size, and frons moderately widened. Tegula is ventro-posteriorly moderately upturned. An is moderately high. Sternopleural region of *australis* is shown in fig. 22. Apc terminates in *australis* (usually ?) dorsally to K. Accessory plate II is moderately narrow in *australis* and at least sometimes in *hades*. Intersclerite III is wanting. Arolium is short and membranous in *hades* and *australis,* and is wanting in *mosulensis*. Paronychia are wanting. Number of ♀ frenulum bristles is three or four in *mosulensis* and *hades,* and is five or six in *australis;* these hairs are long in *australis,* and moderately to rather long in the other two species. Male frenulum spine and retinaculum is well-developed in *australis*. Fringes are long. Dorsum of hindwing is slightly invaginated at CuP. Venation (see also fig. 28): areole moderately small in *hades* and *australis,* and open in *mosulensis* (6 ex.); R3, R4+5 short to connate; R4+5 shortly stalked; inner cell sometimes present but minute in *mosulensis,* and in the other two species absent; Rs-M1 in *mosulensis* mostly short and sometimes very shortly stalked; Rs-M1 in *australis* connate to shortly stalked, and in *hades* (1 ex.) very shortly stalked; posterior M in cell (hindwing) in *mosulensis* mostly wanting and in *australis* usually wanting. Radial bridge is small, narrow and nearly quadrangular (see fig. 24). Radial plate is wide and distally rather broad. Scale plate of *australis* is sometimes/often distinctly shorter than radial bridge. 4Ax is sometimes slightly reduced distally. Median arm is moderately long. Median arm is in *mosulensis* moderately wide. Median arm of *hades* varies from moderately narrow to moderately wide, and in *australis* it is narrow.

S. hades and *australis* appear to be (also) diurnal (see Daniel, 1955), while *mosulensis* was caught at night (E.P. Wiltshire, pers. comm.). The latter was collected in the Mosul Desert in Iraq. It is a pale species in contrast to the other two species. It seems that the colour pattern of *mosulensis* is adapted to certain desert conditions. In the other two species the wings are mainly dark fuscous and in *australis* the ♂ hindwing is mainly yellowish.

S. mosulensis is known from Iraq, *hades* occurs in Morocco, and*australis* is found in Spain, France and northern Italy.

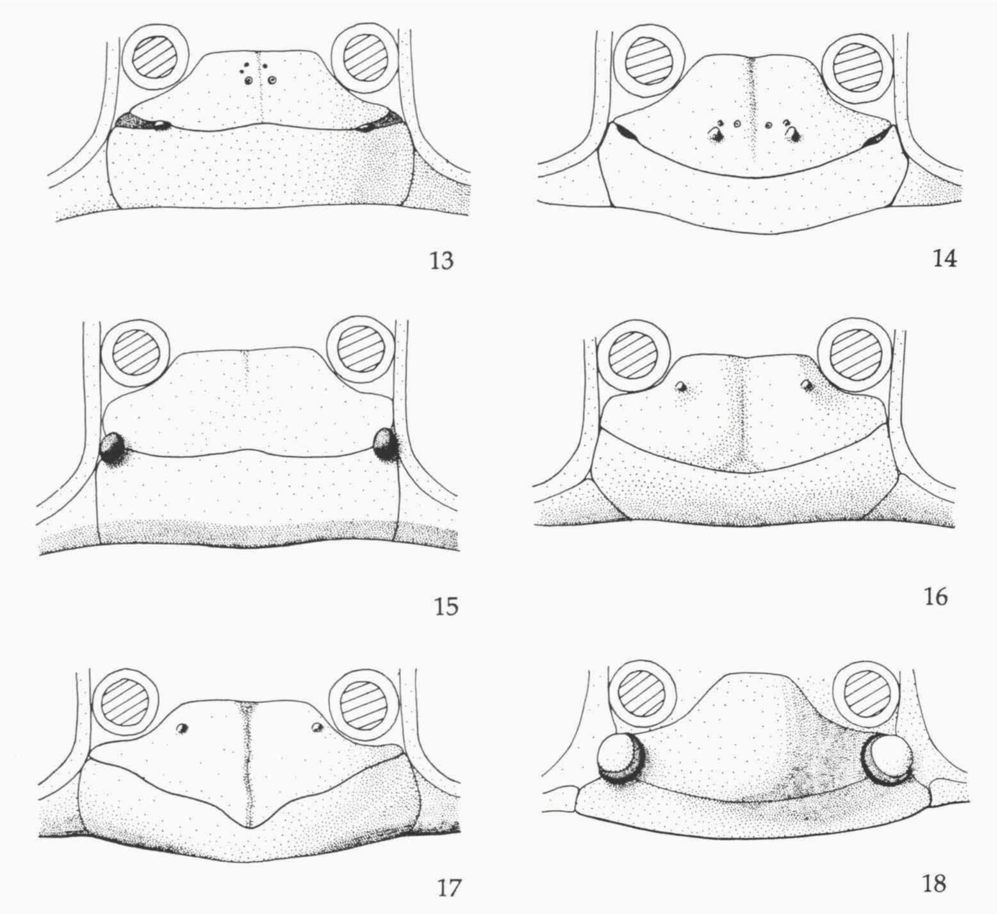
The larva of *australis* lives in the roots of a species of *Echium* L. (Korb, 1910: 26-27; Seitz, 1912: 428).

Material:

mosulensis —1♀ (holotype), 1♀ (paratype), 4♀♀, IRAQ: Mosul Desert, vi.1935 (Wiltshire) (BMNH).

hades —(all MNHN) —1♀ (holotype), MOROCCO: Itzer, 21.vii.1924 (Ungemach); 11♀♀, MOROCCO: Ifrane, Mn-Atlas, 1650 m.; 2♀♀ (probably conspecific), MOROCCO.

australis —long series of both sexes from Spain and south and central France (BMNH); series of both sexes from Spain and France (RMNH and ITZ).



Figs. 13-18, vertices of cossid species. 13, unidentified *Rhizocossus* species (a); 14, unidentified *Rhizocossus* species (b); 15, *Catopta albonubilus*; 16, *Stygia mosulensis*; 17, *Stygia australis*; 18, *Pseudocossus uliginosus*.

Genus **Isocossus** Roepke, 1957

Isocossus Roepke, 1957: 11.

Type species: *Isocossus vandeldeni* Roepke, 1957: 11-12, pl. 1: fig. 8 (male, holotype), pl. 7-figs. 1-1a (male genitalia).

So far only *vandeldeni* has been placed in *Isocossus*. The ♂ antenna of this species is proximally moderately bipectinate for approx. one-third its length and more distally moderately shortly unilobed. A distally unilobed ♂ antenna is known in *Paracossus* and an undescribed genus of section 2, but in these genera the rami have approx. two rows of moderately long hairs on their inner margin. In *vandeldeni* the rami are distinctly flattened and have moderately long hairs on their proximal side. The vestiture of the labial palpi is ventrally short and dorsally longer. In section 3 this type of vestiture is also found in *Dyspessacossus*, in certain species of *Cossulus*, and in the following two genera. In *Dyspessacossus* and *Cossulus* the ♂ antenna is proximally unilobed. See also fig. 19. The following two (new) genera seem to form the sister-group of *Isocossus*. These two genera differ from *Isocossus* in that e.g. the ♂ antenna is completely bipectinate and the ♂ retinaculum is a short flap, a rudimentary ridge or wanting.

Female of *vandeldeni* is unknown. Vertex is medially swollen, has an arcuate Pos up to nearly its dorso-posterior margin, and has small protuberances at terminations of Pos. Tibial spurs are moderately long and moderately short. Lateral side of thorax has not been examined. Fringes are moderately long. Male frenulum spine is approx. rather long. Venation: areole small; R3, R4+5 (very) shortly stalked; R4+5 variably stalked up to for 0.6 times their length; M1 often/usually from areole; inner cell very small; Rs-M1 very short to shortly stalked; inner cell (normally ?) wanting. Humeral plate has not been examined. 4Ax is distally more or less membranous. Median arm is rather long and approx. moderately narrow.

I. vandeldeni is known from Malaysia and Sumatra (Roepke, 1957: 12).

Material:
vandeldeni —5♂♂ (paratypes), MALAYSIA: Bukit Kutu, 3300 ft. (Sanderson) (BMNH).

Genus **Alcterogystia** gen. nov.

Type species: *Cossus l-nigrum* Bethune-Baker, 1894: 36, pl. 1: fig. 3.

Etymology: "alcter" (Greek) means protector + "gystia" is an anagram of the genus-name *Stygia*. Gender: feminine.

C. l-nigrum, *Cossus niloticus* Joannis, 1910 and *C. cadambae* Moore, 1865 share the following apomorphies: female antenna not bipectinate, vestiture on labial palpi ventrally short and dorsally moderately long, arolium very small or wanting, paronychia wanting, ♂ frenulum spine approx. rather long, ♂ retinaculum distinctly reduced or wanting, and median arm moderately wide. In the three species the ♂ antenna is bipectinate, up to nearly rather strongly. The rami are moderately flattened and have short hairs on the proximal side. The ♀ antenna of *nilotica* and *l-nigra* is prismatic and that of *cadambae* is unilobed. *Cossus* has been restricted to species of which both the ♂ and ♀ antenna is unilobed (Daniel, 1956a). The three species mentioned should thus be placed in another genus. In section 3 a similar type of vestiture on the labial palpi is also found in *Isocossus*, the following (new) genus, *Cossulus* and *Dyspessacossus*. In *Cossulus* and *Dyspessacossus* the ♂ antenna is proximally unilobed. These two genera are placed for several reasons at lower branches in the cladogram (see fig. 19). *Isocossus vandeldeni* differs from *Alcterogystia* species in that the ♂ antenna is distally unilobed, the ♂ retinaculum is well-developed, and the median arm is moderately narrow. In the following new genus the ♀ antenna varies from moderately strongly bipectinate to prismatic and the median arm varies from moderately narrow to moderately wide. In the genus treated below probably all species have a moderately low or low An, a moderately high mesepimeron, and a well-developed arolium. The species of the following genus all occur on Madagascar. In *cadambae* An is still moderately high, and in *nilotica* and *l-nigra* the mesepimeron is still rather high.

The three species seem to form a monophyletic group which differs from *Isocossus* and the following (new) genus but is most closely related to the latter. Therefore a new genus is introduced for the three.

Gaede (1933a: 243) notes that the figure of *Cossus henleyi* given by Seitz (1912: pl. 55: fig. row l) actually concerns *nilotica*. Daniel (1964a) places *l-nigra* in *Paropta* in his revision of the latter. He treats *nilotica, Paropta pharaonis* and *Cossus henleyi* as synonyms of *l-nigra*. See also under *Paropta*. Daniel notices that the ♀ antenna of *l-nigra* is bipectinate. However, Daniel appears to have confused several species with *l-nigra*. A ♀ specimen of *l-nigra* from Hadramaut has a prismatic antenna. Perhaps the ♀ antenna of *henleyi* is bipectinate. The latter has a shorter I-epiphysis than *l-nigra*. It is obscure if *henleyi* should be included in *Alcterogystia* or *Brachylia*. In *nilotica* the I-epiphysis is shorter and the fringes are slightly longer than in *l-nigra*. Besides the mesomeron of material in the BMNH identified as *nilotica* is wider than in *l-nigra*. Therefore, *nilotica* and *l-nigra* are regarded as separate species in this study.

No material of *pharaonis* was available. The type-locality of *pharaonis* is Cairo, as that of *nilotica*. Perhaps *pharaonis* is synonymous with *nilotica*.

Antennal segments have many very short hairs ventrally and laterally, and further ventrally approx. one stout sensillum in *nilotica* and one to three stout sensilla in *l-nigra*. Lobes of ♀ antenna in *cadambae* are slightly thickened apically and have many very short hairs on proximal side and one stout sensillum apically. An is moderately low in *nilotica* and *l-nigra*. Mesepimeron of *cadambae* is moderately high. Mesomeron of *nilotica* is approx. 1.5 times width of eucoxa II. I-epiphysis of *l-nigra* and *cadambae* reaches little short of or approx. as far as tibia-apex and is little pointed. In *nilotica* I-epiphysis reaches distinctly short of tibia-apex. Fringes are rather long in *l-nigra* and *cadambae*. Number of ♀ frenulum bristles amounts approx. five or six in *nilotica* and *l-nigra*, and varies from approx. five to nine in *cadambae*. These bristles are moderately long. Venation: areole moderately large in *nilotica* and moderately small in the other two species, sometimes open in *cadambae*; R3, R4+5 very shortly separate to shortly stalked; R4+5 shortly stalked; M1 posterior to areole, but sometimes from tip of areole in *cadambae*; Rs-M1 short to very shortly stalked. Humeral plate has not been examined. 4Ax is well-developed or more or less membranous.

Hosts of *cadambae* are *Ficus* L., *Nauclea cadamba* Roxb. and *Tectonia grandis* L. (Beeson, 1961: 440; Arora, 1976).

Material:

nilotica —1♂ (holotype), 1♀, EGYPT: Cairo [in *Acacia nilotica*] (MNHN); 1♂, 3♀♀, EGYPT: Cairo (BMNH).

l-nigra —1♂ (holotype), EGYPT: Alexandria (Marsden) (coll. Bethune-Baker) (BMNH); 2♂♂, 1♀,

SOUTH YEMEN: n. Hadramaut, south of Zamakh (BMNH).
cadambae —1♀, INDIA: Calcutta (coll. Moore), Gen. slide no. 1961-167 (BMNH).

Genus **Planctogystia** gen. nov.

Type species: *Cossus breviculus* Mabille, 1879: 344.

Etymology: "plazo" (Greek) means wanderer + "gystia" is an anagram of the genus-name *Stygia*. Gender: feminine.

There is a group of species from Madagascar which have a moderately or nearly rather strongly bipectinate ♂ antenna and slightly to moderately flattened rami with short hairs on the proximal side. The ♀ antenna varies interspecifically from moderately strongly bipectinate to prismatic. These species have been formerly placed in *Cossus*. *Cossus* has been restricted to species of which the ♂ and ♀ antenna is unilobed (Daniel, 1956a). The species from Madagascar should thus be placed in another genus.

In all the species the vestiture of the labial palpi is ventrally short and dorsally moderately long. In section 3 this is also known in *Isocossus*, *Alcterogystia*, *Dyspessacossus* and certain *Cossulus* species. See also fig. 19 and under *Isocossus* for differences. In *Alcterogystia* the ♀ antenna is prismatic or unilobed, the arolium is very small or wanting, and the median arm is moderately wide. In the species from Madagascar the arolium is well-developed and in many of them the median arm is still moderately narrow. In all Madagascaran material of which thoracic sclerites have been examined An is moderately low or low and the mesepimeron is moderately high. In *Alcterogystia* An is not always moderately low and the mesepimeron is rather high in two species. In probably all species from Madagascar the tarsomeres of the hindleg, particularly the first one, have dorsally longer vestiture than ventrally. The new genus *Planctogystia* is introduced for these species from Madagascar.

There is a group of unidentified species among the Madagascaran ones of which the I-epiphysis is seemingly wanting. Perhaps *brevicula*, *Cossus pavidus* Butler, 1882 and *C. sakalava* Viette, 1957 also lack the I-epiphysis and thus belong to this subgroup. In at least *Cossus fulvosparsus* Butler, 1882 the I-epiphysis reaches approx. as far as the tibia-apex and is bluntly pointed. *P. fulvosparsa* is special, since its forewings and body have orange markings. This species shares with *Cossus fuscibasis* Gaede, 1930 that the mesomeron is 1.3 to 1.5 times as wide as eucoxa II and the median arm is moderately wide. The female antenna of *fulvosparsa* is moderately strongly or moderately shortly prismatic. In *fuscibasis* the ♀ antenna is bipectinate, up to moderately strongly. In the other material of which the mesomeron has been examined this structure is approx. as wide as the eucoxa II. In *brevicula*, *Cossus crassilineatus* Gaede, 1930 and at least two unidentified species the median arm is also moderately wide. In *crassilineata* and at least one unidentified species (MNHN) the ♀ antenna is moderately strongly bipectinate. In an unidentified species (MNHN) the ♀ antenna is moderately shortly bipectinate, and in another one (MNHN) it is bilobed. K is without a cross-suture in examined specimens of *sakalava* and an unidentified species. The accessory plate II varies interspecifically; e.g., moderately wide in examined specimens of *crassilineata* and moderately narrow or narrow in examined specimens of *sakalava*. The tibial spurs are in many species moderately long and moderately short. In a few unidentified species the midtibial spurs are moderately long and slightly unequal in length and the apical ones of the hindleg moderately short. In another species the midtibial spurs are moderately short and slightly unequal and the apical ones of the hindleg moderately short and short. The fringes are long or rather long. The number of ♀ frenulum bristles varies amongst the species from approx. five to eight. These bristles are usually moderately long. Venation: areole varying from moderately large to small; in holotype of *brevicula* R2 stalked with R3, R4 and R5; R3, R4+5 separate to very shortly stalked; in holotype of *sakalava* R4 and R5 connate and R3 and R4 shortly coalescent approx. halfway along their length; M1 usually posterior to areole, but in *fulvosparsa* from areole; Rs-M1 from short to shortly stalked. The humeral plate is twice size of the radial bridge in at least one unidentified species. 4Ax is usually/normally more or less membranous distally.

It seems that there are five to ten undescribed species represented amongst the unidentified material in the MNHN. Amongst the unidentified material in the BMNH there are probably a few undescribed species, of which one or two are different from those in the MNHN.

Perhaps more described species, such as *Endagria locuples* Mabille, 1879, should be included. It is not clear if *Cossus parvulus* Kenrick, 1914 and *C. senex* Butler, 1882, both from Madagascar, should also be included in *Planctogystia* or perhaps placed in *Hirtocossus*.

Gaede (1930: 541-542) records *Cossus brunneofasciatus* Gaede, 1930 from Madagascar, but on the label of the holotype (BMNH) Ghana is noted.

Cossus fuscibasis Gaede, 1930 is a junior homonym of *Cossus fuscibasis* Hampson, 1895. Therefore *Planctogystia gaedei* is here proposed as replacement name for *C. fuscibasis* Gaede.

Material of named species: (all MADAGASCAR)
brevicula —1♂ (holotype), Mar?tag (ex musaeo Mabille) (MNHN).
sakalava —1♂ (holotype), 2♂♂ (paratypes), Ampijoroa, Ankarafamtsika, 120 m., viii-ix.1956 (Griveaud) (MNHN).
crassilineata —long series of both sexes, Diego Suarez (many "det. Gaede") (BMNH).
gaedei (replacement name for *fuscibasis* Gaede) —1♀ (holotype), 3♀♀, Diego Suarez (Melou) (MNHN).
fulvosparsa —long series (most ♂, 3♀♀), many localities (MNHN).

Genus **Brachylia** Felder, 1874

Brachylia Felder, 1874: pl. 82: fig. 7.
Type species: *Brachylia terebroides* Felder, 1874: pl. 82: fig. 7.

Brachylia has been established for *terebroides* from South Africa.

Kirby (1892: 864-865) includes many species originally described as *Cossus* species. Most of these species included should be placed in other genera (see also under *Catopta*, *Alcterogystia* and *Planctogystia*). It is here uncertain if *Cossus incanescens* Butler, 1875 from Natal should be indeed included in *Brachylia*.

Hampson (1892: 305) synonymizes *Brachylia* with *Cossus*, and von Dalla Torre

(1923: 5) follows Hampson.

Druce (1911: 290) describes two new species, *Brachylia inconspicua* and *B. dentilinea*. These two species occur in South America and should most probably be placed in another genus, probably a hypoptine one.

Gaede (1930: 541) includes *terebroides* under *Cossus* and treats several species as forms of *terebroides*.

Clench (1959a: 16) resurrects *Brachylia*, gives a diagnosis of the genus and descriptions of *terebroides* and of a new species *eutelia* from Namibia. Clench synonymizes only *Cossus windhoekensis* Strand, 1913 with *terebroides*. The only diagnostic characteristics Clench gives for the genus is the bipectinate antenna and the acuminate apical hook of the uncus. However, a bipectinate antenna of many different types is known in many genera and a small well-sclerotized apical hook of the uncus is shown by Roepke (1957) for various, very different Cossinae.

Fletcher (1968: 328) describes a new species *badiala* and includes it in *Brachylia*. *B. badiala* is here excluded from *Brachylia*, since it has a very different type of ♂ antenna and a widened mesomeron.

Only *terebroides* has been examined. This species shows the following apomorphies (see also fig. 19): An moderately low, I-epiphysis reaching nearly as far as tibia-apex, arolium reduced in length, fringes rather long, ♂ retinaculum rudimentary, and median arm moderately wide. It shares furthermore with *Coryphodema tristis* (Drury, 1782) that the ♀ antenna is unilobed. A cross-vein Sc-Rs is sometimes or rarily present in *terebroides*. Although the type species of *Brachylia* and *Coryphodema* Felder, 1874 differ only a little from each other, the two genera are tentatively kept apart. In *Coryphodema* an arolium and a ♂ retinaculum is wanting and An is low. In *Alcterogystia* the ♂ antenna is similar to that in *terebroides* and *tristis* and the ♀ antenna is unilobed or prismatic. In *Alcterogystia* the vestiture on the labial palpi is ventrally short and dorsally moderately long.

Male antenna is rather strongly bipectinate; rami are distinctly flattened and apically rounded, and have short hairs on proximal side. Female antenna is very shortly unilobed; each of its segments has ventrally a short stout sensillum. Male frenulum spine is moderately long and retinaculum is rudimentary. Number of ♀ frenulum bristles is approx. six and these are rather long. Venation: areole moderately small; R3, R4+5 very shortly stalked to stalked for 0.4 times their length; R4, R5 separate to shortly stalked; inner cell moderately small; Rs-M1 short to very shortly stalked. Humeral plate has not been examined. 4Ax is distally well-developed or more or less membranous.

Material:
terebroides —3♂♂, 1♀, SOUTH AFRICA: Natal (BMNH).

Genus **Coryphodema** Felder, 1874

Coryphodema Felder, 1874: pl. 82: fig. 8.

Type species: *Coryphodema capensis* Felder, 1874: pl. 82: fig. 8. [According to Fletcher & Nye (1982: 44), a junior synonym of *Phalaena tristis* Drury, 1782: 27, pl. 21: fig. 1].

Coryphodema has been established for *capensis*. Gaede (1930: 543) erroneously synonymizes *Cossus punctulatus* Walker, 1850 with *capensis*, and treats *Coryphodema albifasciata* Hampson, 1910 and a new species *ochracea* under *Coryphodema*. Material of the new species was not available. *Cossus punctulatus* and *Coryphodema albifasciata* differ significantly from *tristis* in the following characteristics: An moderately high, upper Pas at approx. two-thirds length of Pre plus Pa in *albifasciata* (not examined in *punctulatus*), mesomeron approx. 1.5 times width of eucoxa II, I-epiphysis probably wanting, and tarsal claws moderately slender. These two species are therefore here excluded from *Coryphodema*. It is most probable that they should be placed together in a new genus, but the description of such a genus is here left to a more detailed study, including the genitalia.

Coryphodema is here presumed to be the sister-group of *Brachylia* (see under the latter). Although the two genera differ only a little, they are tentatively placed apart. C. *tristis* has the following apomorphies: An low, and arolium and ♂ retinaculum wanting. See further fig. 19.

Male antenna of *tristis* is moderately strongly bipectinate; rami are distinctly flattened and apically rounded, with very short hairs on proximal side. Female antenna is completely unilobed, without stout sensilla ventrally. Apc terminates sometimes/often dorsally to K. K is (usually ?) without a cross-suture. Tergite I sclerotized for approx. half its length. Male frenulum spine is moderately long. Number of ♀ frenulum bristles is approx. six and these are moderately long to moderately short. Venation: areole moderately small to small; R3, R4+5 (very) shortly stalked; R4+5 shortly stalked; Rs-M1 shortly stalked. 4Ax is at least sometimes distally well-developed. Median arm is moderately long and rather wide.

Material:
tristis —(all BMNH) —1♀ (holotype of *capensis*), 1♂, x.1864 (coll. Felder); 3♂♂, 2♀♀, SOUTH AFRICA: Natal, Durban; 1♂, 1♀, SOUTH AFRICA: Cape; 1♀, SOUTH AFRICA: Stellenbosch, Elsenburg.

Genus **Paracossulus** gen. nov.

Type species: *Bombyces thrips* Hübner, 1818: fig. 265.

Etymology: "para" (Greek) means near + genus-name *Cossulus*. Gender: masculine.

Although *thrips* shows only few significant characteristics, a new genus is here established for this easily recognizable species. This species does not fit in *Brachylia* or *Coryphodema*, since the ♀ antenna is filiform, with many minute hairs and few stout sensilla. Since the ♂ antenna is bipectinate along its whole length, the species does not fit in *Parahypopta* Daniel, 1961 and *Cossulus*. It shares with *Cossulus* and *Parahypopta* the following apomorphies: An at most moderately low, I-epiphysis reaching little short of or approx. as far as tibia-apex, and median arm at least moderately wide. Daniel (1961: 207-208) places *thrips* in *Catopta* with many other very different species. In this study *Catopta* is restricted to a few species with paronychia and a moderately long anal plate (see also fig. 10). Besides in *Catopta* the rami of ♂ antenna have approx. two rows of hairs on the inner margin, and the ♀ antenna is bilobed or shortly bipectinate. In *thrips* the rami of the ♂ antenna are broad and rounded, with very short hairs on the proximal side. The anal plate is moderately short and paronychia are wanting.

The labial palpi of *thrips* have long and dense vestiture. The male retinaculum is wanting. The mesepimeron is moderately high. The species is moderately small. Its forewings are normally sandy brown with few little darker striae and a dark median spot.

Vertex has an arcuate and slightly ridged Pos up to approx. 0.8 times its length. An is moderately low. K has (usually ?) a cross-suture. Accessory plate II varies from moderately wide to moderately narrow. I-epiphysis is finely toothed. Tibial spurs are moderately and rather long. Male frenulum spine is rather long. Number of ♀ frenulum bristles amounts more than five and these are moderately long. Fringes are very long. Venation: areole moderately long and moderately narrow to narrow, sometimes open; R3, R4+5 (nearly) connate to very shortly stalked; R4+5 shortly stalked; Rs-M1 very short to connate. Humeral plate is approx. 3 times size of radial bridge. Radial bridge is rather small and nearly triangular. 4Ax is distally complete or more or less membranous. Median arm is moderately long and rather wide, although sligthly narrower than Cu2. Female ovipositor is usually distinctly protruberant.

The species is distributed from south Poland (near Przemyśl) eastward to Armeniya and the margin of Siberia (Seitz, 1912: 424; Daniel, 1961: 208).

Material:
thrips —long series of both sexes from various localities in U.S.S.R. (BMNH); series from U.S.S.R. (RMNH and ITZ).

Genus **Cossulus** Staudinger, 1887

Cossulus Staudinger, 1887: 91.
Type species: *Cossulus argentatus* Staudinger, 1887: 90.
Cossulinus Kirby, 1892: 860. [Erroneous replacement name].

Seitz (1912: 424) uses the name *Cossulinus* and erroneously treats *Hypopta lignosus* Brandt, 1938 as *argentatus* (see Daniel, 1960: 95). Daniel (1960: 94-105) gives a short description of *Cossulinus*, and places the following species in this genus: *C. argentatus, Cossus intractus* Staudinger, 1887, *Hypopta lignosus, Cossus stertzi* Püngeler, 1899, *Hypopta herzi* Alphéraky, 1893, and *Hypopta turcomanica* Christoph, 1893. Daniel (1960: 103) synonymizes *Holcocerus bolshoji* Zukowsky, 1936 with *herzi*, but the present author doubts this synonymy. Daniel (1965a) describes *Cossulinus kabulense*. Daniel (1965c) gives some extra information on *herzi* and *turcomanicus*.

The only significant characteristic of the genus which Daniel gives is the shape of the antenna. The ♂ antenna is proximally shortly unilobed along a short length and further bipectinate, sometimes apically unilobed again. According to Daniel (1960: 94; 1964b: 3), the ♀ antenna is filiform. In *Dyspessacossus* the ♂ antenna is also proximally unilobed, but in this genus the mesomeron is 1.5 times as wide as the eucoxa II (see also fig. 19). In certain species of *Cossulus* the mesomeron is only slightly wider than the eucoxa II. *Cossulus* shares with *Parahypopta* the apomorphies no.'s 1-2, 6b, 16b, 18-19, 20a and 21 in fig. 19, of which the most important are: An moderately low to low, and I-epiphysis reaching little short of or nearly as far as tibia-apex.

In this study the following species of *Cossulus* have been examined: *argentatus* (partially), *intractus, turcomanicus, herzi, Holcocerus bolshoji,* and *Holcocerus strigillata.* Daniel (1960: 103) treats *bolshoji* as subspecies of *herzi*, but in *bolshoji* the apex of the ♂ antenna is unilobed whereas in *herzi* bipectinate. Here *strigillatus* is added to the genus.

Cossus irani Daniel, 1956 should perhaps also be included in *Cossulus*. The ♂ antenna of *irani* is unilobed and the lobes are two-pointed. This type of ♂ antenna may have evolved by further fusion of the rami of more segments. *C. irani* differs from the (other) species of *Cossulus* in that An is moderately high, whereas it is moderately low in the specimens examined of the other species. Daniel (1956: 277) notes that *irani* closely resembles superficially *herzi*. This type of antenna is also known in species which are tentatively placed in *Paracossus*, which is thought to belong to section 2 (see fig. 12). The ♀ antenna of *irani* is simple (Daniel, 1956: 277), whereas that of *Paracossus* species so far known prismatic.

No females were available. Male antenna is proximally (approx. 10 segments) unilobed, gradually becoming bipectinate more distally; rami more or less fused at inner margins (see fig. 49), but in *argentatus* rami separate along certain length of antenna; lobes and rami distinctly flattened, with very short hairs on proximal side; rami moderately broad or moderately narrow. Vestiture on labial palpi is moderately short mixed moderately long or ventrally short and dorsally moderately long. An is moderately low in most species, but low in *bolshoji*. K is without a cross-suture. Upper Pas appears to be little over half length of Pre II plus Pa in *herzi* and *bolshoji*. Mesepimeron is in most species moderately high, but it varies to rather high in *strigillatus*. Mesomeron is only slightly wider than eucoxa II in *herzi* and perhaps in a few more species, but as wide as in *strigillatus* and *turcomanicus*. Intersclerite III appears to be normally wanting. I-epiphysis is apically finely or bluntly pointed. Tarsal claws are (moderately) slender. Arolium is wanting. In *herzi* the fifth tarsomere has few stout spines and many finer ones. Fringes are long in most species, but rather long in *intractus* and *turcomanicus*. Male frenulum spine is moderately or rather long and in *herzi* moderately short. Male retinaculum is more or less reduced in size and in *intractus* at least sometimes wanting. Venation: areole varying from moderately large in *argentatus* to small in *strigillatus*; R3, R4+5 approx. connate; R4+5 shortly stalked; Rs-M1 short to shortly stalked. Humeral plate is in *turcomanicus* and *bolshoji* approx. twice size of radial bridge; in the others not examined. 4Ax is distally more or less membranous. Median arm is rather long and moderately wide. The species are moderately small.

Most species are known from southern U.S.S.R. *C. herzi* is also recorded from Iran and Afghanistan, and *turcomanicus* from Afghanistan (Daniel, 1965c: 100-101). *C. strigillatus* and *kabulense* occur in Afghanistan and in Iran.

Material:
argentatus —1♂ (holotype), U.S.S.R.: Caucasus (MHUB).
herzi —long series of males, U.S.S.R.: Samarkand (BMNH); 1♂, U.S.S.R.: Samarkand (RMNH).
bolshoji —3♂♂ (syntypes), ? U.S.S.R.: Tyan-Shan', Tshimgan, 1500 m., 11/12.viii.1934 (Sheljuzhko) (ex coll. Bang-Haas) (ITZ).
turcomanicus —long series of males, U.S.S.R.: Repetek, Dortkuju (BMNH).
intractus —1♂, U.S.S.R.: Samarkand (BMNH).

strigillatus —1♂ (holotype), 7♂♂, AFGHANISTAN: Kuliab (BMNH).

Genus **Parahypopta** Daniel, 1961

Parahypopta Daniel, 1961: 160-161.
Type species: *Bombyx caestrum* Hübner, 1804: 151, pl. 49: fig. 199.

The type species of *Parahypopta* was erroneously regarded as the type of *Hypopta* by Kirby (1892: 863). *Hypopta* belongs to the subfamily Hypoptinae and is restricted to America. Daniel (1961) introduces *Parahypopta* for *caestrum* and includes further: *Hypopta issycus* Gaede, 1933, *Holcocerus putridus* Christoph, 1887 and *Hypopta sheljuzhkoi* Zukowsky, 1936. Fang & Chen (1989) ascribe a new species *choui* also to *Parahypopta*. It is uncertain if this is correct, since the ♀ antenna in *choui* differs considerably from that in *caestra*.

Of all the species Daniel included the ♂ antenna is completely unilobed. The lobes have laterally a pair of stout sensilla. Only of *caestra* the female is known. The ♀ antenna of *caestra* is as strongly unilobed as the ♂ one. The lobes have laterally two pairs of stout sensilla. In both sexes the lobes have short hairs on the proximal side.

In *Cossus* the ♀ antenna is less strongly unilobed than the ♂ one and lacks the stout sensilla laterally. In *Paracossus* the ♂ antenna of certain species is also unilobed, but the ♀ antenna is as far known prismatic. The ♀ antenna of *choui*, which may belong to *Parahypopta*, is very shortly bipectinate (Fang & Chen, 1989). In *Cossus* and *Paracossus* the vestiture of the labial palpi is ventrally short and dorsally moderately long. The labial palpi of at least *caestra* and *sheljuzhkoi* have ventrally also moderately long scales.

In this study only *caestra* and *sheljuzhkoi* have been examined. *Parahypopta* appears to share with *Cossulus* the following apomorphies: male antenna at least partly unilobed, An at most moderately low, I-epiphysis reaching nearly or approx. as far as tibia-apex, arolium wanting, tarsal claws moderately slender, and median arm moderately or rather wide. Most or all species of *Cossulus* differ from *Parahypopta* species in that the ♂ antenna is partly bipectinate. Considering the partly unilobed antenna in *Cossulus*, the state of the ♂ antenna in *Parahypopta* seems to have evolved by further fusion of the rami. However, the possibility that *Parahypopta* should be placed in another section cannot be ruled out.

Vertex of *caestra* has an arcuate Pos up to far posteriorly. An is moderately low. K in *caestra* lacks sometimes/usually a cross-suture. Mesepimeron is high in *caestra* and moderately high in *sheljuzhkoi*. I-epiphysis reaches as far as tibia-apex and is apically little pointed. Arolium is wanting. Fringes are very long. Male frenulum spine is rather long in *caestra* and moderately short in *sheljuzhkoi*. In both species ♂ retinaculum is a short flap. Number of ♀ frenulum bristles is in *caestra* approx. five and these are moderately short. Venation: areole moderately short to short and narrow; R3, R4+5 connate; R4+5 shortly stalked; inner cell moderately small; a long cross-vein Sc-Rs sometimes present in *caestra*; Rs-M1 connate to shortly stalked. Humeral plate is approx. twice size of radial bridge, and perhaps sometimes/often 1.5 times in *caestra*. Median arm is moderately long, and moderately narrow in *sheljuzhkoi* but moderately wide in *caestra*. Cu2 is moderately narrow in *caestra*. Tip of ♀ abdomen is elongate and ovipositor is little protruberant.

P. caestra is locally distributed in southern and eastern Europe; from Spain to Poland and Greece, and also on Sicily and Crete (Daniel, 1961: 166-168). The species is further known from southern U.S.S.R. (Caucasus, Armenia, and southern Ural region), Turkey, Syria, Lebanon, and Israel (Daniel, 1961: 166-168). *P. issyca* and *putrida* have been recorded from south U.S.S.R. (Daniel, 1961: 169-171). *P. sheljuzhkoi* is known from Tyan-Shan' (see material examined). The species *choui*, which may belong to *Parahypopta*, is known from Altai in Xinjiang (China) (Fang & Chen, 1989).

P. caestra is known to mine the roots of *Asparagus officinalis* L. in the neighbourhood of Istanbul (Poujade, 1884: cvii), and is known from *Asparagus* L. in Cannes (see material examined).

Material:

caestra —long series of both sexes from many localities in Europe, including Sicily, and south U.S.S.R. (BMNH); series of both sexes from Hungary, Austria and south France (RMNH); long series of both sexes from south U.S.S.R. (Ural'sk), Greece, Austria and Italy, including Sicily (ITZ); 1♂ (lectotype of var. *radoti* Homberg), FRANCE: Cannes, 1.vii.1910, in *Asparagus* (MNHN).

sheljuzhkoi —2♂♂ (paralectotypes), U.S.S.R.: Tyan-Shan', Bolshoj Tschimgan, 2000 m., 26.vii.1934 (Sheljuzhko) (ex coll. Bang-Haas) (ITZ).

Table 6. Apomorphies in fig. 19 (section 3A).

1. Rami of antenna more or less flattened and with hairs only on proximal side. (*)
2. Female frenulum bristles more or less reduced in length.
3a. Mesomeron approx. 1.5 times width of eucoxa II.
b. Mesomeron approx. 1.3 to 1.5 times width of eucoxa II.
4. I-epiphysis wanting.
5. Humeral plate at least 2.5 times size of radial bridge.
6a. Arolium wanting.
b. Arolium more or less reduced in size or wanting.
7. Tegula ventro-posteriorly only slightly pointed to nearly rounded.
8. Mesepimeron moderately high.
9. Vestiture on second and third segment of labial palpi ventrally only short and dorsally moderately long.
10. Male frenulum spine moderately or rather long.
11. Fringes moderately long.
12. Inner cell of forewing very small.
13. Inner cell of hindwing wanting.
14a. Male retinaculum more or less reduced, varying from short flap to wanting.
b. Male retinaculum only wanting.
15a. Female antenna unilobed or prismatic.
b. Female antenna unilobed.
c. Female antenna filiform.
16a. Median arm moderately wide.
b. Median arm moderately or rather wide. (*) N.B. In *Parahypopta sheljuzhkoi* median arm is moderately narrow, which is considered a reversal.
17. An moderately low.
18. An at most moderately low.
19. I-epiphysis reaching slightly short of or approx. as far as tibia-apex.
20. Tarsal claws moderately slender.
21a. Male antenna partly unilobed.
b. Male antenna completely unilobed.

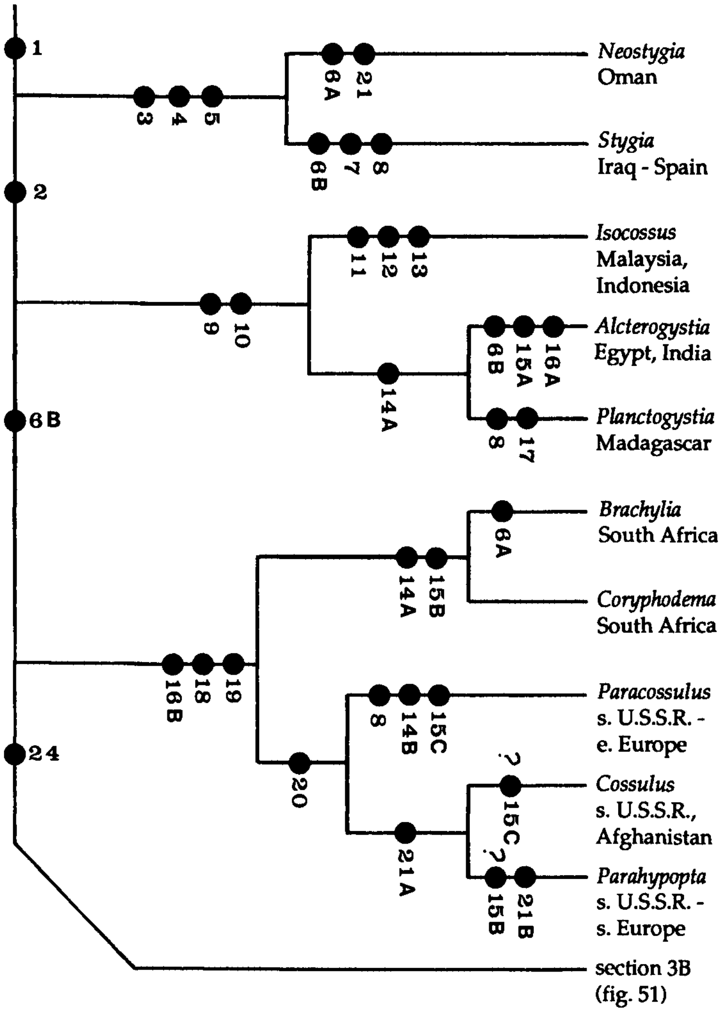


Fig. 19, cladogram of section 3A (Cossinae).

Section 3B

This is the continuation of section 3A.

Genus **Dyspessacossus** Daniel, 1953

Dyspessacossus Daniel, 1953: 258.
Type species: *Dyspessacossus hadjinensis* Daniel, 1953: 258-259.

Daniel (1953; 1960) places *hadjinensis* and *Cossus fereidun* Grum-Grshimailo, 1895 in the new genus *Dyspessacossus*. Daniel (1960: 108-109) treats *Cossus osthelderi* Daniel, 1932 as subspecies of *fereidun*. In this study *osthelderi* is considered a separate species, since it has shorter fringes, a slightly higher mesepimeron and a slightly wider median arm than *fereidun*.

The ♂ antenna of these species closely resembles that in *Cossulus*. The antenna is proximally (approx. 5 segments) unilobed, gradually becoming bipectinate more distally, but the rami are fused at the inner margins for 0.3 to 0.6 times their length. The ♀ antenna of at least *fereidun* is unilobed, more shortly than in *Cossus* (Daniel, 1965a: 141; 1965c: 101). In *fereidun*, *osthelderi* and probably also *hadjinensis* the mesomeron is 1.5 times width of the eucoxa II. Amongst *Cossulus* species only of *herzi* it is known that the mesomeron is widened, but in this species it is only 1.3 times width of the eucoxa II. This widening seems to be an independent development. Material of *Dyspessacossus* species is larger (medium-sized) than that of *Cossulus* species. In at least *fereidun* the I-epiphysis reaches distinctly short of the tibia-apex. The two genera are further very similar. It seems impossible to give more diagnostic characteristics of *Dyspessacossus*.

Only male specimens of *fereidun* and *osthelderi* have been examined. Vertex of *fereidun* has an arcuate and ridged Pos up to approx. 0.8 times its length. Vestiture of labial palpi is ventrally short and dorsally moderately long. An varies from moderately high to moderately low in *osthelderi*, and is moderately low in *fereidun*. K of examined specimens of *fereidun* is without a cross-suture. Mesepimeron is moderately high in *fereidun* and rather high in *osthelderi*. I-epiphysis is apically distinctly pointed in at least *fereidun*. Tibial spurs are moderately long and moderately short. Arolium is wanting. Fringes are moderately long in *fereidun* and rather long in *osthelderi*. Male frenulum spine is moderately long. Male retinaculum is a rudimentary ridge in *osthelderi* and a short flap in *fereidun*. Venation: areole moderately large in *fereidun*, and small in *osthelderi*; R3, R4+5 connate to very shortly stalked; R4+5 shortly stalked, sometimes connate; cross-vein Sc-Rs sometimes/often partly to completely present in *osthelderi*; Rs-M1 short to shortly stalked. 4Ax is distally more or less membranous. Median arm is rather long, moderately wide in *osthelderi*, and rather wide in *fereidun*.

The genus is represented in Iraq, Iran, south U.S.S.R. (Armenia) and Asia Minor (Hadjin) (Daniel, 1960: 106-110; 1965c: 101). The species seem to live in rather high altitudinal ranges.

Material:

fereidun —1♂ (holotype of ssp. *ahmadi* Wiltshire), 2♂♂ (paratypes), IRAQ: Kurdistan, Shaqlawa, 2500 ft., v-vi.1953 (Wiltshire) (BMNH); long series of males, IRAQ: Kurdistan (BMNH).

osthelderi —(all BMNH) —4♂♂, IRAN: Damāvand, Haschtar, more than 2500 m.; 3♂♂, IRAN: Damāvand, Faschem; 1♂, U.S.S.R.: Armenia, Mt. Alibek, 2000 m.; 2♂♂, IRAQ: Kurdistan, Rayak.

Genus **Brachygystia** gen. nov.

Type species: *Cossus mauretanicus* Lucas, 1907: 343.

Etymology: "brachys" (Greek) means short + "gystia" is an anagram of the genus-name *Stygia*. Gender: feminine.

The type species, *mauretanica*, was tentatively placed in *Catopta* by Daniel (1961: 210-212), but he notes that it should probably be placed in a new genus. Daniel uses the criterion of the shape of antenna. Daniel (1961: 212) synonymizes *Holcocerus powelli* Oberthür, 1911 with *mauretanica*. *Catopta minor* Rungs, 1972 is here synonymized with *mauretanica*.

In this study *Catopta* is restricted to cossine species with paronychia and a moderately long anal plate. Since *mauretanica* has flattened rami with short hairs on the proximal side, a widened mesomeron and still a moderately high An, it comes seemingly next to *Dyspessacossus* in the cladogram (figs. 19 and 51). In the latter genus the shape of the ♂ antenna is quite different; the antenna is proximally unilobed and the rami are more or less fused at their inner margins. The species of *Dyspessacossus* are much larger than the rather small *mauretanica*. Therefore *mauretanica* is placed in a new genus.

Both ♂ and ♀ antenna of *mauretanica* are moderately strongly bipectinate. Male rami have a short stout sensillum at apex. Third segment of labial palpi is shortly ovate. I-epiphysis reaches little short of tibia-apex. Tarsal claws are moderately slender. Arolium is minute and membranous or wanting. Tibial spurs are moderately and rather long. Fringes are nearly very long. Male frenulum spine and retinaculum are well-developed. Number of ♀ frenulum bristles varies from four to six, and these are long or rather long. Venation: areole moderately small or wanting; R3, R4+5 very short; R4+5 shortly stalked; Rs-M1 moderately short to shortly stalked. 4Ax is distally partly thin. Median arm varies from moderately wide to moderately narrow. Ovipositor is hardly protruberant.

The species is known from Tunisia, Algeria and Mauritania.

Material:

mauretanica —1♀ (type of *mauretanicus*), TUNISIA: Kebili, x.1907 (Tanidie) (MNHN); 1♂ (holotype of *powelli*), 1♀ (paratype), ALGERIA: near Géryville, South Oranais, viii.1910 (Powell & David) (MNHN); 1♂ (holotype of *minor*), 3♀♀ (paratypes), MAURITANIA: west Baten, Yagrel, Toverga and Adrar, iv/v.1953 (Boniface) (MNHN); long series of both sexes, ALGERIA: Guelt-el-Stehl (BMNH).

Genus **Eogystia** gen. nov.

Type species: *Hypopta sibirica* Alphéraky, 1895: 185-186.

Etymology: "eos" (Greek) means eastern + "gystia" is an anagram of the genus-name *Stygia*. Gender: feminine.

Daniel (1960: 118; 1965c: 101) places *sibirica* in *Isoceras* Turati, 1924, since the ♀ antenna is as strongly bipectinate as the ♂ one. He had not examined any material of *sibirica*. There are differences in the antenna between *Isoceras* species and *sibirica*. In the latter most rami are in pairs at a distinctly obtuse angle from each other (see fig. 40), whereas in *Isoceras* at an acute angle. In *sibirica* the hairs on the rami of the ♂ antenna are moderately long, whereas in *Isoceras* they are short. Daniel (1960: 111) figures the ♀ antenna of *Isoceras bipunctatum* (Staudinger, 1887) with only a moderate number of sensilla on the outer margin and on the apex. The ♀ antenna of *sibirica* has many moderately short hairs on the proximal side of rami and approx. four stout sensilla near and at apex of rami. Most rami of the ♂ antenna of *sibirica* have a stout sensillum at apex. The ♂ antenna is apically (approx. last 10 segments) shortly bipectinate. In *sibirica* Bs II has still deep lateral grooves for approx. two-thirds length of Bs-Pa. In *Isoceras* these grooves are short and shallow. In *Isoceras* the ♂ frenulum spine and retinaculum are wanting, whereas in *sibirica* the frenulum spine is long and the retinaculum is small. *Isoceras* species are generally a little smaller than *sibirica*. The latter is a pale species with silvery white and sandy brown on the forewing. Because of these differences and since *sibirica* takes a separate place in the cladogram (fig. 51), *sibirica* is excluded from *Isoceras* and a new genus is introduced for this species.

Rami of antenna are distinctly flattened; rami in male bluntly pointed and with one stout sensillum at apex (fig. 40a); rami in female more or less rounded apically (fig. 40b). Tegula is at least sometimes ventro-posteriorly finely toothed. An is moderately low. Apc is very narrow and terminates on dorsal apex of or dorsally to K. K lacks a cross-suture in at least one specimen. Subalare-process II is short and rather slender. Mesepimeron varies from rather to moderately high. Intersclerite III is wanting. I-epiphysis reaches as far as or little farther than tibia-apex and is apically finely toothed. Tibial spurs are in pairs of approx. equal length or little unequal, moderately long to moderately short. Fringes are long. Number of ♀ frenulum bristles is four to six and these are moderately long and stout. Venation: areole small; R3, R4+5 apart to connate; R4+5 shortly stalked; inner cell well-developed; Rs-M1 connate. Humeral plate is approx. as large as radial bridge. Radial bridge is moderately large and rather wide. Radial plate is apically moderately wide. 4Ax is distally more or less membranous. Median arm is rather long and moderately narrow. Tip of ♀ abdomen is moderately elongate and ovipositor is moderately protruberant. The species is medium-sized.

The species occurs in east and northeast U.S.S.R., Mongolia (Daniel, 1965b: 99), and north China.

Material:
sibirica —(all BMNH) —1♀, U.S.S.R.: Vladivostok, Sutschanski-Rudnik; 2♂♂, 3♀♀, CHINA: s. Manchuria, Kinchu; 1♂, ? CHINA: Wei-hei-wei.

Genus **Eremocossus** Hampson, 1892

Eremocossus Hampson, 1892: 313-314.
Type species: *Phragmataecia faeda* Swinhoe, 1884: 515, pl. 47: fig. 1. [Cited as *foedus*, a mandatory change].

Eremocossus has been established for *faedus* (plate 1: fig.E) from Pakistan.

Hampson described a second species in this genus, *proleuca*, which is a junior synonym of *Cossus reibellii* Oberthür, 1876. *Eremocossus senegalensis* Le Cerf was synonymized with *Hypopta vaulogeri* Staudinger, 1897 by Daniel (1962b: 15). Daniel treats the latter and its many subspecies/forms under *Dyspessa* Hübner, [1820] 1816. In the present paper *vaulogeri* is included in *Eremocossus*.

C. reibellii is here excluded from *Eremocossus*, for it has many fine spines on the fifth tarsomere and it has a different type of antenna (see also fig. 51). The former is placed in a new genus, which is described below. In *faedus* and *vaulogeri* the rami of the ♂ antenna have only very short hairs on their lateral margins, and have one stout sensillum at their apex (see figs. 41-42a). The female of *faedus* is unknown. The ♀ antenna of *vaulogeri* is filiform. *E. faedus* resembles superficially most closely *vaulogeri* specimens from Algeria and Palestina. Daniel (1962: 18-19) notes a form or subspecies of *vaulogeri* from Pakistan, which is most probably *faedus*. *E. vaulogeri* and *faedus* share the folowing apomorphies: Bs II with shallow lateral grooves, mesomeron at least 1.5 times width of eucoxa II, I-epiphysis reaching little short of tibia-apex, arolium wanting, and humeral plate approx. 1.5 times size of radial bridge.

Vertex has an arcuate Pos up to approx. 0.7 times its length. Rami of ♂ antenna are rather broad or broad, distinctly flattened, and have very short hairs on lateral margins and one stout sensillum at apex. In *faedus* the ♂ rami are in pairs at a distinctly obtuse angle (see fig. 41), and they are slightly longer and narrower than in *vaulogeri* (see fig. 42a). Female antenna of *vaulogeri* is rounded filiform, and has many minute hairs ventrally and laterally and a series of stout sensilla near apexes of segments (see fig. 42b). Pronotum reaches higher than patagium in at least *vaulogeri*. An varies from moderately low to low in *faedus*, and from low to very low in *vaulogeri*. Bs II is rather flat and has moderately long to moderately short, shallow grooves laterally. K is variable in shape and has sometimes/often a cross-suture. Subalare-process II is short. Mesepimeron is high and seemingly lacks a paler band medio-posteriorly. Accessory plate II varies from rather wide to narrow in *faedus*, and from moderately narrow to narrow in *vaulogeri*. Intersclerite III is wanting. Fringes are long. Male frenulum spine is rather long and retinaculum is wanting. Number of ♀ frenulum bristles varies from three to five, and these vary from moderately long to moderately short. Venation: areole small; R3, R4+5 (usually ?) more or less separate; R4+5 shortly stalked; inner cell small; Rs-M1 connate to stalked for 0.4 times their length in *vaulogeri*, and stalked for approx. half their in *faedus*; inner cell (hindwing) moderately small. 4Ax is distally more or less thin or membranous. Median arm is rather long and narrow. Tip of ♀ abdomen is moderately elongate and ovipositor is usually moderately protruberant.

E. vaulogeri is known from Spain (Alicante), from Senegal eastward to U.S.S.R. (Turkmeniya) (Daniel, 1962: 5-21), from Saudi Arabia (Kiriakoff, 1960: 12) and Bahrain. *E. faedus* is known only from Pakistan. Kiriakoff (1960: 11) records *faedus* from Saudi Arabia with a question-mark, but this probably concerns the female of *vaulogeri*.

Material:
faedus —(all PAKISTAN) —2♂♂ (syntypes), Karachi (BMNH); 1♂, Karachi (BMNH); 1♂, Karachi (RMNH).

vaulogeri —1♂ (holotype of var. *meirleirei* Rungs, 1951), 1♀ (paratype), MOROCCO: Sidi Shrir (Meirleire) (MNHN); 1♂ (holotype of *Cossus saharae* Lucas, 1910-11), TUNISIA: Zarcine, Kebili, 1906 (MNHN); 1♂ (holotype of *E. senegalensis* Le Cerf, 1919), SENEGAL: Dakar, 1907 (Waterlot), Gen. slide no. Viette ♂ 2574 (MNHN); 1♂, ALGERIA: Hassi Bahbah (ITZ); long series of both sexes, ALGERIA (BMNH); 12♂♂, 1♀, BAHRAIN (BMNH); 4♂♂ (ssp. *jordana*), Palestina (BMNH); 1♂, OMAN: Sharjan (BMNH).

Genus **Comadia** Barnes & McDunnough, 1911

Comadia Barnes & McDunnough, 1911: 26-27.
Type species: *Hypopta bertholdi* Grote, 1880: 45-46.
Heterocoma Barnes & McDunnough, 1918: 179. [Synonymized by Brown, 1975: 191].
Type species: *Heterocoma albistriga* Barnes & McDunnough, 1918: 179, pl. 20: figs. 16-17 (resp. male, paratype, and female, type).

Comadia has been described for a series of species which had formerly been included under *Hypopta* Hübner, the type genus of the Hypoptinae. Barnes & McDunnough (1911) include the following species: *H. bertholdi*, *H. edwardi* Neumoegen & Dyar, 1893, *H. henrici* Grote, 1882 and *H. manfredi* Neumoegen, 1884. Barnes & Benjamin later described *C. stabilis* Barnes & Benjamin, 1923. Dyar (1940) neglects *Comadia* and includes these species just under *Hypopta* again. Brown (1975) revises the genus, synonymizes *H. edwardi* and *C. stabilis* with *H. bertholdi*, and includes also under *Comadia*: *Zeuzera redtenbacheri* Hammerschmidt, 1848, *Heterocoma albistriga*, *C. subterminata* Barnes & Benjamin, 1923, *C. suaedivora* Brown & Allen, 1973, *C. intrusa* Barnes & Benjamin, 1923, *C. dolli* Barnes & Benjamin, 1923, *C. arenae* Brown, 1975, *C. speratus* Brown, 1975, and *C. alleni* Brown, 1975. *Hypopta palmata* Barnes & McDunnough, 1910 belongs possibly to *Comadia* too.

In this study material of *bertholdi*, *edwardi*, *stabilis* and *albistriga* has been examined. Characteristics of the genus, which are noted by Brown (1975: 191), are one stout sensillum on the outer margin of the rami of the ♂ antenna and a very shortly bilobed ♀ antenna. The position and length of the sensillum varies amongst the species. In all species except *albistriga* the rami of the ♂ antenna are moderately flattened and moderately broad, with many short hairs on the proximal side (see fig. 43a). In *albistriga* the antennal rami have approx. two rows of moderately long hairs on the inner margin, which is presumably a reversal. The lobes of the ♀ antenna are bi- or trifid, with short stout sensilla at the apexes and with a moderate number of very short hairs on the proximal side (see fig. 43b). A further characteristic of the genus appears to be the presence of a moderate number of fine, pale brown spines on the fifth tarsomere next to the short, stouter and darker spines. The species further share the following apomorphies: Bs II with very short and very shallow grooves laterally (see fig. 21), mesomeron approx. 1.3 to 1.5 times width of eucoxa II, I-epiphysis reaching little short of or nearly as far as tibia-apex (not examined in *albistriga*), arolium wanting, ♂ frenulum spine moderately long or moderately short, ♂ retinaculum wanting, and humeral plate approx. 1.5 times size of radial bridge (not examined in *albistriga*). See also. fig. 51.

Vertex of *bertholdi* has an arcuate Pos up to (nearly) dorso-posterior margin. Vestiture of labial palpi is moderately short mixed moderately long, or ventrally moderately short and dorsally moderately long. Sections of the thorax of *bertholdi* are shown in fig. 21. An is moderately high in *stabilis*, and low in *bertholdi* and *edwardi*. K lacks (usually ?) a cross-suture. Mesepimeron is rather high or high. Intersclerite III is wanting. Tibial spurs are moderately short and slightly unequal in length. Fringes are long. Number of ♀ frenulum bristles is four to more than five and these are moderately short or short. Venation: areole moderately large to small, sometimes open; R3, R4+5 connate to shortly stalked; R4+5 shortly stalked up to for 0.4 times their length; Sc-Rs rarily present; Rs-M1 short to very shortly stalked. Scale plate is in *edwardi* distinctly shorter than radial bridge, but in *bertholdi* as long as. Radial plate is subapically rather wide. 4Ax is distally more or less membranous. Median arm is rather long and moderately narrow.

Brown (1975) provides distribution maps of all species. Most species occur in southwest U.S.A. *C. dolli* is also known from west U.S.A. *C. subterminata, manfredi* and *albistriga* occur in south U.S.A. *C. bertholdi* has the widest range; distributed over a large part of the U.S.A. *C. redtenbacheri* is known from Texas and Mexico.

A host of *redtenbacheri* in Mexico is *Agave salmiana* Otto. A 15% infestation of this host has been found in the regions of Mexico where it is of economic importance for the production of a distilled drink (Ancona, 1930, according to Brown, 1975: 210).

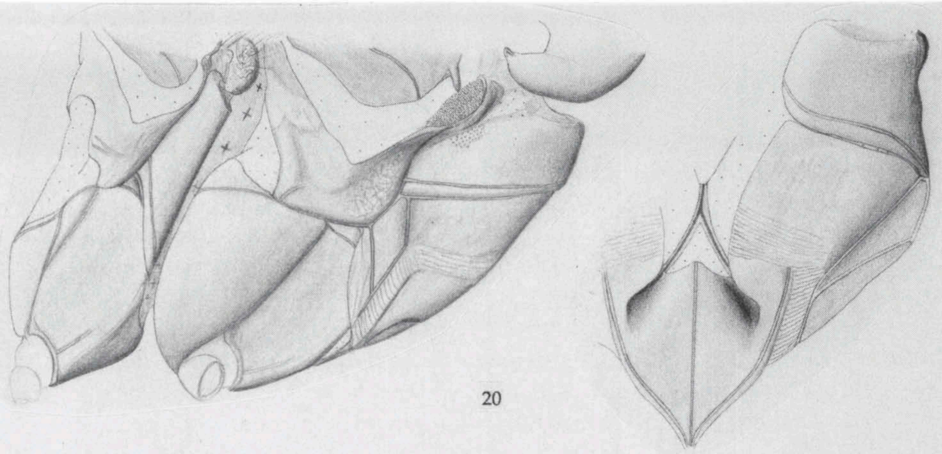
Material: (all U.S.A.)
bertholdi —series of both sexes (BMNH).
edwardi —1♂, California, Santa Maria (ITZ).
stabilis —long series of males (BMNH).
albistriga —1♂ (possible paratype), Arizona, Cochise Co., Paradise, vi (coll. Barnes) (USNM); 1♂, s. Arizona (BMNH).

Genus **Mormogystia** gen. nov.

Type species: *Cossus reibellii* Oberthür, 1876: 40, pl. 4: fig. 1 (female).

Etymology: "mormo" (Greek) means hobgoblin + "gystia" is an anagram of the genus-name *Stygia*. Gender: feminine.

A new genus is here established for *reibellii* from northern Africa and Arabia. *Eremocossus proleuca* Hampson is a junior synonym of *Cossus reibellii*. The species does not fit in *Cossus, Eremocossus, Isoceras* Turati, or any other genus. *Cossus* has been restricted by Daniel (1956a) to species of which both the ♂ and ♀ antenna are unilobed. In *reibellii* the ♂ antenna is moderately strongly bipectinate and the ♀ antenna is very shortly bilobed. *Eremocossus* species have no fine, pale brown spines on the fifth tarsomere, which are present in *reibellii*, and have hairs only on the lateral margins of the rami of the ♂ antenna. In *reibellii* the rami of the ♂ antenna are very much rounded, and have very short hairs on the proximal side, one stout sensillum at the apex, and one stout one on the outer margin (see fig. 44a). In *Isoceras bipunctatum* these rami have also two stout sensilla, but the rami are distinctly less rounded. Daniel (1960: 111) figures the ♀ antenna of *bipunctatum* approx. as strongly bipectinate as the ♂ one, without short hairs on the proximal side but with sensilla on the lateral margins. In *reibellii* the lobes of ♀ antenna have very short hairs on the proximal side and two or three stout sensilla near and at the apex (see fig. 44b). In *Isoceras* the fifth tarsomere is longer than fourth, whereas in *reibellii* as long.



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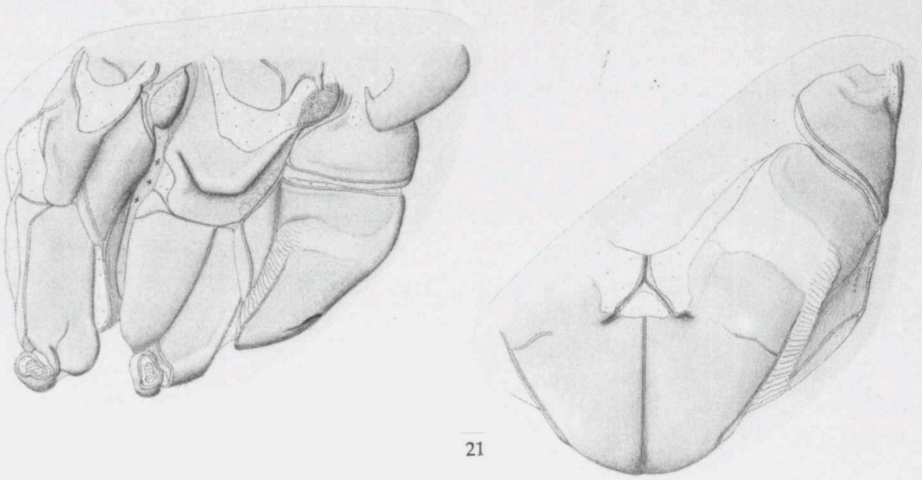
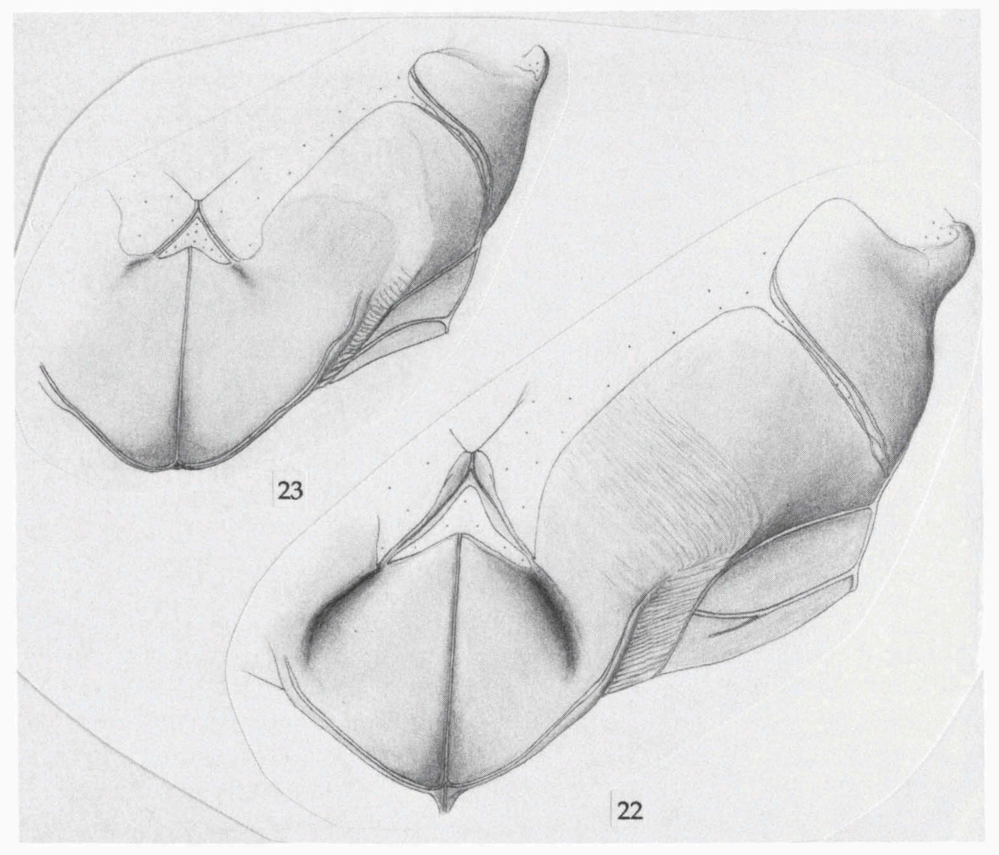


21

Figs. 20-21, sections of thoraces of cossid species. 20, unidentified *Rhizocossus* species (b), Chile; 21, *Comadia bertholdi*, U.S.A., Texas, Davis Mts.



Figs. 22-23, sternopleural regions of cossine species. 22, *Stygia australis*; 23, *Mormogystia reibellii*.

In *reibellii* the labial palpi are two- or three-segmented. It has furthermore the following apomorphies: tegula ventro-posteriorly (nearly) rounded, An varying from low to very low, Bs II with very short and shallow grooves laterally (see fig. 23), I-epiphysis reaching little short of tibia-apex, arolium small to minute, ♂ retinaculum wanting, and humeral plate approx. 1.5 times size of radial bridge. See also fig. 51. The species is moderately small and has silvery white and buff areas on the forewing.

Vertex is more or less swollen and has an arcuate or nearly triangular Pos up to approx. 0.8 times its length. K is variable in shape and size and has sometimes/often a cross-suture. Mesepimeron varies from high to moderately high. Intersclerite III is wanting. Tarsal claws are moderately slender. Fringes are long. Male frenulum spine is rather long. Number of ♀ frenulum bristles is four or five, and these are moderately or rather long. Venation: areole small or very small, sometimes wanting; R3, R4+5 usually/often shortly stalked, occasionally for more than half their length; R4+5 shortly stalked; inner cell small or wanting; sometimes a short cross-vein Sc-Rs present or Sc and Rs shortly stalked; Rs, M1 usually stalked for 0.3 to 0.6 times their length, but sometimes completely coalescent; inner cell (hindwing) small or wanting. 4Ax is distally partly thin or more or less membranous. Median arm is rather long and varies from narrow to very narrow. Tip of ♀ abdomen is moderately elongate, and ovipositor is little or distinctly protruberant.

Material:

reibellii —1♀ (holotype of *reibellii*), ALGERIA: Biskra, 14.v.1875 (MNHN); 1♂ (holotype of *proleuca*), SOUTH YEMEN: Aden, Yerbury, 27.ii.1895 (BMNH); 1♂ (type of *reibellii* ssp. *equatorialis* Le Cerf), KENYA: Lake Turkana, Mts. Lubur, Lokitang, 560 m., 22-24.i.1933, Gen. slide no. Viette ♂ 2386 (MNHN); long series of both sexes from Saudi Arabia, South Yemen, Algeria and Mauritania (BMNH).

Genus **Isoceras** Turati, 1924

Isoceras Turati, 1924: 51-52.

Type species: *Isoceras kruegeri* Turati, 1924: 51-52, pl. 2: figs. 8-9 (males), 10-11 (females).

Turati (1924: 51-52) suggests a new genus *Isoceras* for *kruegeri*, since this species has the ♂ and ♀ antenna as strongly bipectinate. Daniel (1960: 113-118) includes under this genus also *Endagria bipunctata* and *Hypopta sibirica*. The latter is here excluded and placed in a new genus *Eogystia*. Daniel (1965b: 100, pl.: fig. 4) describes the new *Isoceras kaszabi*.

According to Daniel (1960: 113-118), the ♀ antenna of *bipunctatum* is also as strongly bipectinate as the ♂ one. The rami of the ♀ antenna have only a series of sensilla on the outer margin and at the apex (Daniel, 1960: 111). Only males of *bipunctatum* and *kruegeri* have been examined. The rami of the ♂ antenna are rather broad and apically rounded, are in pairs at an acute angle, and have very short hairs on the proximal side. In *bipunctatum* the labial palpi are two-segmented, whereas in *kruegeri* three-segmented. The patagium is lower than the pronotum in at least *bipunctatum*. In both species the fifth tarsomere is approx. 1.3 to 1.5 times length of fourth. The male frenulum spine and retinaculum are wanting. The two species share furthermore the following apomorphies: Bs II with short and shallow grooves laterally, mesomeron approx. 1.5 times width of eucoxa II, fifth tarsomere with many fine and pale brown spines, and arolium wanting. In at least *bipunctatum* the I-epiphysis reaches as far as or slightly farther than the tibia-apex. See also fig. 51. When a lowered patagium will be also found in *kruegeri* and *kaszabi*, the genus should be placed at a lower branch in the cladogram (fig. 51). In section 3 such a patagium is further known in *Dyspessa* and its presumed sister-group.

I. kruegeri has been partially examined. Vertex of *bipunctatum* has a slightly sinuate Pos up to approx. 0.9 times its length. Vestiture of labial palpi is long mixed rather long. Latero-cervical sclerites are reduced for half length in at least *bipunctatum*. An is moderately low in at least *bipunctatum*. K is wide or rather wide but moderately small, and (usually ?) without cross-suture. Mesepimeron varies from high to moderately high in *bipunctatum* and is high in the examined specimen of *kruegeri*. Intersclerite III is wanting. Fringes are long. Venation: areole moderately small or small; R3, R4+5 connate to shortly stalked; R4+5 connate to stalked for 0.4 times their length; Rs-M1 stalked for 0.2 to 0.6 times their length. 4Ax is distally partly thin or more or less membranous. Median arm is moderately wide in *kruegeri* and moderately narrow to narrow in *bipunctatum*.

I. kruegeri is known from Libya. *I. bipunctatum* is distributed from Israel to Turkey, south U.S.S.R. (Caucasus) and Iran. *I. kaszabi* is recorded from Mongolia (Daniel, 1965b).

Material:
kruegeri —1♂, LIBYA: Cyrenaica, R.U. Agrario, Buhasal (Krüger) (BMNH).
bipunctatum —4♂♂, SYRIA (BMNH); 6♂♂, Hadjin (BMNH); 1♂, Mesop (BMNH); 2♂♂, Amasia (BMNH); 1♂, Taurus (RMNH); series of males, IRAQ: Kurdistan (BMNH); series of males, s.w. IRAN (BMNH).

Genus **Stygioides** Bruand, 1853

Stygioides Bruand, 1853: 18.
  Type species: *Stygia colchica* Herrich-Schäffer, 1851: pl. 2: fig. 10.
Bruandia Desmarest, 1857: 37. [Junior objective synonym].
  Type species: *Stygia colchica* Herrich-Schäffer, 1851: pl. 2: fig. 10.
Psychidostygia Daniel, 1955: 164. [Junior objective synonym].
  Type species: *Stygia colchica* Herrich-Schäffer, 1851: pl. 2: fig. 10.
Danielostygia Reisser, 1962: 198-199. **Syn. nov.**
  Type species: *Danielostygia persephone* Reisser, 1962: 199-200, pl. 21: fig. 14 (female, holotype).

Stygioides was established in the Psychides, now Psychidae. Kirby (1892: 869) places the type species in *Stygia*. Seitz (1912: 428) treats *colchica* and many other species under *Stygia*. Daniel (1955) excludes most of these species and places most of them in the new genus *Psychidostygia*, which is a junior synonym of *Stygioides*. Daniel includes the following species: *colchica*, *Stygia tricolor* Lederer, 1858, *Stygia dercetis* Grum-Grshimailo, 1900 and *Stygia aethiops* Staudinger, 1887. He synonymizes *Stygia angheri* Grum-Grshimailo, 1902 with *Stygia ledereri* Staudinger, 1871, a senior synonym of *Dieida persa* Strand, 1911. Daniel erroneously includes *Stygia psyche* Grum-Grshimailo also in *Dieida* Strand, 1911. The latter species is here added to *Stygioides*.

Danielostygia persephone Reisser is also included in *Stygioides*. It appears that there are several species known under the name *tricolor* (see also Daniel, 1955), and that there are several undescribed species most closely resembling *psyche* and *colchica*. Daniel (1965c: 82) provides an illustration of the ♂ antenna of *tricolor*, but this antenna is of a different type than that of the specimen examined from the Lederer collection. The speciman which Daniel examined most probably belongs to another species.

Koshantschikov (1923: 25-27) describes the new species *Stygia* (?) *gerassimovii* from the neighbourhood of Minussinsk (U.S.S.R.). No material of this species was available. Daniel (1955: 174), who had studied only the original description, suggests that this species probably belongs to the Zeuzerinae, since approx. the last six segments of the antenna is "simple". Daniel points out that in certain *Phragmataecia* species the antenna is mostly bipectinate but prismatic at apex. The described colour pattern is very different from that of a *Phragmataecia* species. The indicated size (17-21 mm.) and the bright colours on body and wings would suggest that it concerns a species of *Stygioides*, if it is actually a cossid. *S. gerassimovii* would have yellowish fringes, in contrast to the dark ones in (other) *Stygioides* species. The author of this paper doubts that the species actually belongs to the Cossidae. The status of *gerassimovii* thus remains obscure.

So far only *persephone* has been placed in *Danielostygia*. Reisser (1962: 198-200) compares *persephone* to *Stygioides colchica*. *D. persephone* would especially differ from *colchica* in the venation and vestiture on the forewing. Reisser's figures of the venation are incorrect. The venation of *persephone* closely resembles that of e.g. *psyche* (fig. 29), but the holotype of *persephone* has a long cross-vein Sc-Rs and its M of the hindwing is proximally indistinct. A cross-vein Sc-Rs is sometimes/often present in several *Stygioides* species. A more or less indistinct M of the hindwing is also known in *colchica*. The inner cell of the hindwing is present in *persephone* in contrast to what Reisser's figure shows. The characteristics of the venation which Reisser notes to distinguish *Danielostygia* from *Stygioides* are also found in e.g. *colchica* and *psyche*. The undescribed species (e) and (f) have similar vestiture on the wings as *persephone*. The ♀ antenna of *persephone* closely resembles that of *colchica*, but is symmetrically bilobed and lobes have approx. one stout sensillum apically. *D. persephone* shows furthermore the characteristics of *Stygioides*. Because there are no good differences, *Danielostygia* is here synonymized with *Stygioides*.

In this study material of *colchica, psyche, tricolor, persephone,* and several unidentified species has been examined. The types of *aethiops* have been briefly examined. The species are small and are reminiscent of certain psychids. The shape and vestiture of the antenna varies considerably amongst the species (see below). The eyes are slightly to distinctly reduced in size. In most species there are dorsally broad margins along the eyes. The frons is more or less widened. The pronotum is distinctly lower than the patagium in *colchica* and unidentified species (e), and this is presumed to be a characteristic of the whole genus. The labial palpi are in most species two-segmented and have long and fine vestiture. The vestiture on the thorax and abdomen is mainly long and nearly hair-like. The thoracic sclerites have been examined in *colchica, psyche, tricolor, persephone* and a few unidentified species. The sclerites are dark brown. Bs II is at least in these species distinctly flattened and rounded, and has very short shallow lateral grooves and very short anterior arms (see fig. 36). The mesepimeron does often/normally not show a paler band medio-posteriorly. The mesomeron is at least twice width of the eucoxa II. The fifth tarsomere is in all species, except *persephone* and unidentified species (b), 1.3 to 1.5 times length of the fourth. The fifth tarsomere has many fine, pale brown spines instead of stout, dark brown spines. The male retinaculum is wanting. The humeral plate is at most 1.5 times size of the radial bridge. The wings are in most species mainly sparsely covered with minute scales, but in the female of *persephone* and unidentified species (f) the scales are larger and cover nearly the whole surface of the wing. It appears that the wings of the female are generally more covered than those of the male. The females are generally darker than the males. See also fig. 51.

Vertex of *colchica* has a slightly sinuate Pos up to approx. 0.8 times its length. Vertex of unidentified species (e) has an arcuate Pos up to approx. 0.8 times its length, and in the specimens examined anterior protuberances are wanting. Female antenna of unidentified species (e) is moderately shortly bilobed; rami are moderately flattened and bluntly pointed, with rather short hairs on inner margin, and with scales and one to a few stout sensilla on outer margin (fig. 46). Male antenna of *psyche* is rather strongly bipectinate; rami are slightly flattened, and have moderately long hairs in approx. 2 rows on inner margin, and rather short hairs and small scales on outer margin. This state with 2 rows of hairs on inner margin is here presumed to be a reversal. In a ♀ specimen from Transcaspia and labelled as *psyche* the antenna is moderately bipectinate; rami are moderately flattened and moderately narrow, with moderately long hairs on inner margin and one stout sensillum subapically on outer margin. Male antenna of *colchica* is moderately bipectinate; rami are much flattened, with many very short hairs on proximal side; rami in pairs of unequal length and shape (see fig. 45a). Female antenna of *colchica* is shortly bilobed; lobes are in pairs of unequal length, distinctly flattened, with many short hairs on proximal side and two stout sensilla near apex (see fig. 45b). Male antenna of *tricolor* is very similar to that in *colchica*, but is a little more strongly bipectinate. Female antenna of *persephone* closely resembles that of *colchica*, but antenna is symmetrically bilobed and lobes have approx. one stout sensillum apically. In unidentified species (d) antenna is moderately bipectinate; rami are moderately flattened and distinctly thickened subapically. Labial palpi are three-segmented in unidentified species (d). In most or all other species the third segment of the labial palpi is wanting and the second segment is medially thickened.

Latero-cervical sclerites are reduced for half length in at least*colchica*. Tegula is in *colchica* moderately upturned and bluntly pointed. In at least *persephone* and unidentified species (e) the tegula shows the plesiomorphic state. K is small and plus or without cross-suture. Subalare-process II is short in at least *colchica, psyche* and unidentified species (e). Mesepimeron is high in *colchica, psyche,* and *persephone.* Mesepimeron is very high in unidentified species (e). Accessory plate II varies from rather wide to moderately narrow in *colchica,* and is moderately wide in *psyche* and unidentified species (e). Intersclerite III is sometimes or normally present in several unidentified species.

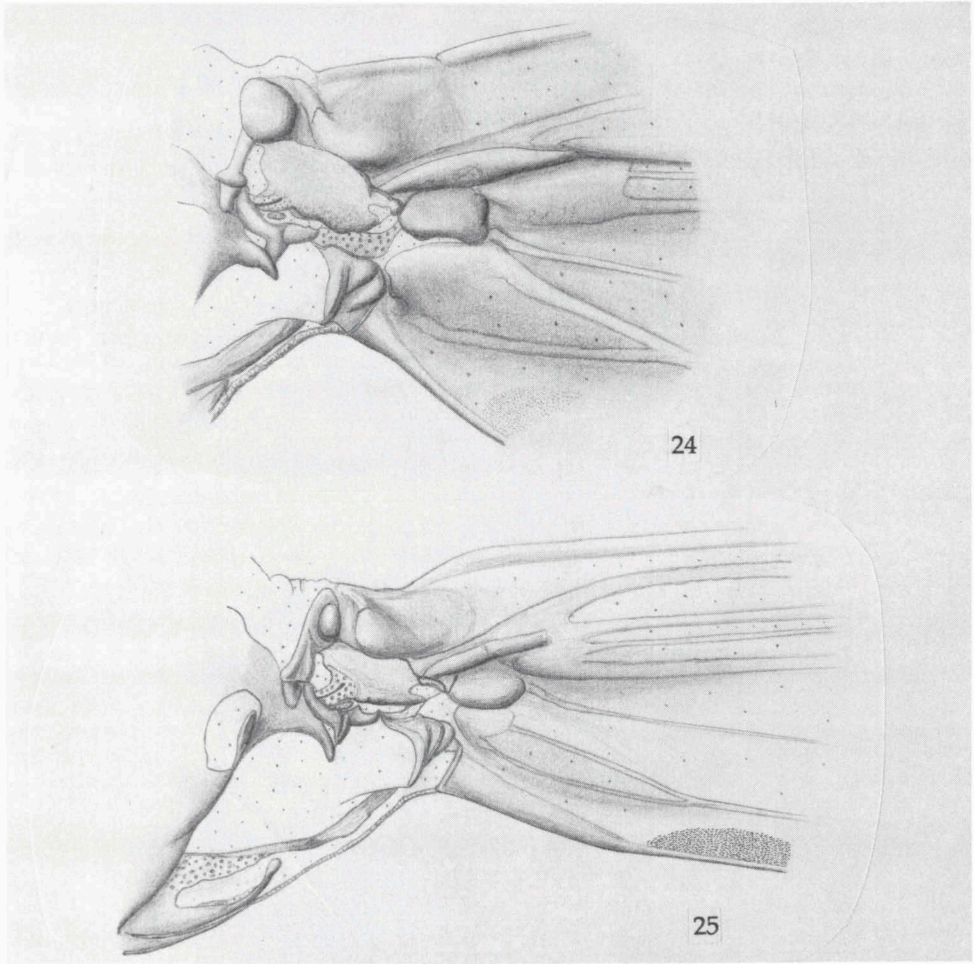
I-epiphysis reaches distinctly short of tibia-apex in the unidentified species (d). In *colchica, psyche, persephone* and unidentified species (e) I-epiphysis reaches approx. as far as tibia-apex. Tibial spurs are moderately long or moderately long and moderately short. Fifth tarsomere is as long as fourth in *persephone* and unidentified species (d). In the other species of which material has been examined fifth tarsomere is 1.3 to 1.5 times length of fourth. Tarsal claws are slender in certain species.

Fringes are long. Male frenulum spine varies interspecifically from moderately to rather long. Number of ♀ frenulum bristles is approx. four or five and these are moderately long in unidentified species (e). Venation (see also fig. 29): areole small to minute, but often/usually wanting in *colchica,* unidentified species (b) and (e), and perhaps more species; M sometimes/often proximally indistinct in at least *colchica* and *persephone;* M2, M3 sometimes/often connate in *colchica* and occasionally shortly stalked; a cross-vein Sc-Rs often present in *colchica* and unidentified species (b) and (e); in *colchica* Sc-Rs short to very short; in unidentified species (e) Sc-Rs moderately short; in unidentified species (b) Sc-Rs long; in holotype of *persephone* a long Sc-Rs present; in specimen from Lebanon of unidentified species (c) traces of Sc-Rs present; Sc-Rs normally proximal to Rs-M1; Rs-M1 shortly stalked up to 0.6 times their length, sometimes/occasionally completely coalescent; inner cell usually wanting or indistinct. Forewing base of *colchica* is shown in fig. 25. Humeral plate is approx. 1.5 times size of radial bridge in at least *colchica, tricolor* and unidentified species (e). In *colchica* humeral plate is variable in shape and is sometimes/often partly lowered (see fig. 25). 4Ax is distally partly thin or more or less membranous. Posterior notal wing process is in *colchica* and unidentified species (e) sometimes/often more or less proximally reduced in width (see fig. 25). Median arm is rather long and narrow to/or very narrow.

Tip of ♀ abdomen is distinctly elongate and ovipositor is often distinctly protruberant.

Representatives of the genus are known from south U.S.S.R. (Armenia, Caucasus, Kazakhstan, Transcaspia and Kyzylkum), Turkey, Syria, Lebanon, and Greece (Crete).

The holotype of *persephone* was caught during the day in the sunshine according to one of its labels.



Figs. 24-25, forewing bases of cossine species (localities unknown). 24, *Stygia australis*; 25, *Stygioides colchica*.

Material:

colchica —1♂, 1♀ (holotype), U.S.S.R.: Namangan (MHUB); 3♂♂, 1♀, U.S.S.R.: Sarepta (BMNH); 1♂, SYRIA (BMNH); 3♂♂, ? (BMNH).

psyche —2♂♂ (syntypes), U.S.S.R.: Kyzylkum, 4.iv.1892 (BMNH); (conspecific ?) 1♀, U.S.S.R.: Transcaspia, Jol tan (MNHN).

persephone —1♀ (holotype), GREECE: east Crete, Wurwulitis, Ep. Kaenurgion, north of Messará, 22.v.1925 (Schulz) (MHUB).

aethiops —1♀ (holotype), U.S.S.R.: Namangan (MHUB); 1♂ (paratype), Margilan (MHUB).

Unidentified species (a) (labelled as *dercetis*) —2♂♂, 1♀, U.S.S.R.: Kulp (BMNH).

Unidentified species (b) (labelled as *tricolor*) —1♂, SYRIA (BMNH); 1♂, U.S.S.R.: Ural'sk (BMNH).

Unidentified species (c) (labelled as resp. *angheri* and *ledereri*) —1♂, LEBANON: Beyruth (BMNH); 1♂, SYRIA: Marash (BMNH).

Unidentified species (d) (closely resembling *tricolor*) —1♀, SYRIA: Aleppo (MNHN).

tricolor —1♂, TURKEY: Manisa [Magnesia] (coll. Lederer) (MHUB).

Unidentified species (e) (placed under *nigritula*) —2♀♀, U.S.S.R.: Transcaspia, Imambaba (BMNH); 1♀, U.S.S.R.: Kyzylkum, Capsu-Kydurz (BMNH).

Unidentified species (f) (placed under *taurica*) —1♀, Taurus Oil. (BMNH).

Genus **Dieida** Strand, 1911

Dieida Strand, 1911: 162-163.

Type species: *Dieida persa* Strand, 1911: 163. [Synonymized with *Stygia ledereri* Staudinger, 1871 by Seitz, 1912: 428].

Dieida was established in the Zygaenidae. Seitz (1912: 428) synonymizes *persa* with *Stygia ledereri*, and notes *Typhonia stygiella* Bruand, 1852 as a possible synonym of *ledereri*. Daniel (1955: 174-181) revises the genus and erroneously includes *Stygia psyche*. He had not examined material of the latter species, which is here included in *Stygioides*. Daniel (1955: 179-180) synonymizes *Stygia angheri* with *ledereri*, and treats *persa* as a subspecies of the latter.

The most important characteristic of the genus which Daniel (1955: 174-175) notes is the absence of the midtibial spurs of the hindlegs, which is further known only in *Psychidocossus infantilis* within the Cossinae. The ♂ antenna of *ledereri* is dark fuscous and rather strongly bipectinate. The rami are slightly flattened, with many moderately long hairs on the inner margin. This type of antenna is presumably a reversal. The ♀ antenna is also bipectinate, but the rami are broad and somewhat thickened apically. The labial palpi are three-segmented, rather thick, and approx. 3.5 times length of the eye-diameter. The vestiture on these palpi is long, hair-like and blackish. *D. ledereri* shares with *Stygioides* the following apomorphies: eyes moderately reduced and frons widened, Bs II wide, rounded, flattened and with short, shallow grooves laterally, and mesomeron at least twice width of eucoxa II. The eucoxa II is narrow, and the mesomeron is nearly 3 times as wide as the former structure. The mesepimeron is high and nearly quadrangular in shape. The mesepimeron does (normally ?) not show a paler band medio-posteriorly. An accessory plate II is not visible. The I-epiphysis reaches approx. as far as tibia-apex. The fifth tarsomere is 1.5 times length of the fourth, and has probably many fine, pale brown spines. The tarsal claws are moderately slender. The fringes are moderately long. The male retinaculum is wanting and perhaps the frenulum spine too. In the male specimen examined Rs and M1 are completely coalescent. The median arm is moderately long and moderately wide. The species is moderately small and has long, hair-like vestiture on the thorax and abdomen. The wings are mainly sparsely scaled and not completely covered.

Vertex has not been examined. K is moderately small and has sometimes/usually a cross-suture. Subalare-process II is short. Intersclerite III is wanting. Tibial spurs are moderately long and moderately short. Dorsum of hindwing is very weakly invaginated between CuA2 and CuP. Venation (1 ex.): areole wanting; R4+5 shortly stalked; inner cell wanting; Rs-M1 completely coalescent; inner cell (hindwing) wanting.

The species occurs in Syria and Iran (Daniel, 1955: 180), and is further known from Iraq and U.S.S.R.

Material:
ledereri —1♂, U.S.S.R.: Ordubad (BMNH); 1♀, IRAQ: Mesopotamia, Hatschin (MNHN).

Genus **Semagystia** gen. nov.

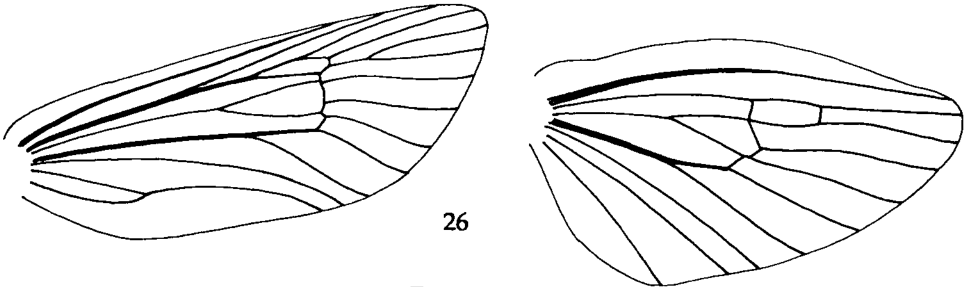
Type species: *Endagria agilis* Christoph, 1884: 113, pl. 7: fig. 3a-b (resp. female and male).

Etymology: "sema" (Greek) means blaze + "gystia" is an anagram of the genusname *Stygia*. Gender: feminine.

Semagystia is established for a series of species which were previously placed in *Dyspessa*, a senior synonym of *Endagria* Boisduval, [1837]. Daniel (1961) includes these species under *Catopta*, making this genus very heterogeneous. In this study *Catopta* is restricted to a few species with paronychia and a moderately long anal plate. *Dyspessa* is here restricted to a series of species with a very high mesepimeron. In *Semagystia* the mesepimeron is just high or rather high. Species of *Dyspessa* are generally smaller and have shorter, broader and more rounded antennal rami or lobes. In *Semagystia* the antennal rami are only moderately flattened. An important characteristic of *Semagystia* is a whitish or pale median band on the frons (see fig. 35a), which has not been noticed in *Dyspessa*. *Semagystia* shares with *Dyspessa* the following apomorphies: labial palpi two-segmented, patagium lower than pronotum, An at most moderately low, Bs II with short and shallow grooves laterally, mesomeron at least 1.5 times width of eucoxa II, fifth tarsomere with few short stout spines and many fine ones, arolium wanting and humeral plate at most 1.5 times size of radial bridge. See also fig. 51. These species are moderately small. In most species the cell of the forewing is mainly whitish.

The following species are included in *Semagystia*: *Endagria agilis* (plate 1: fig. F), *E. clathrata* Christoph, 1884, *E. cossoides* Graeser, 1892, *E. lacertula* Staudinger, 1887 and *Dyspessa tristis* Bang-Haas, 1912. Daniel (1961: 196-198) synonymizes *Dyspessa bucharana* Bang-Haas, 1910 and *D. magna* Seitz, 1912 with *agilis*. Daniel (1964a: 218) synonymizes *Dyspessa affinis* Rothschild, 1912 with *tristis*. Perhaps *Endagria alpheraky* Christoph, 1885, *E. monticola* Grum-Grshimailo, 1890 and certain species which Daniel (1964a) included in *Dyspessa* should also be placed in *Semagystia*.

Vertex of *agilis* has an arcuate Pos up to approx. 0.8 times its length and small membranous areas laterally to Pos (see fig. 35b). Male antenna of *agilis* is moderately bipectinate; rami have small scales and one or a few stout sensilla on outer margin (see fig. 47a). Male antenna of *cossoides* is rather strongly bipectinate; rami have small



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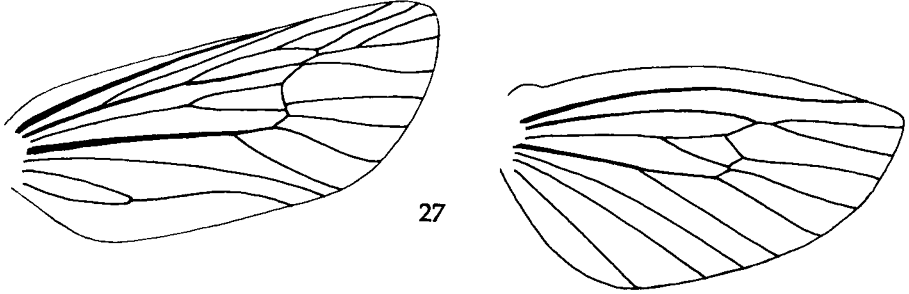

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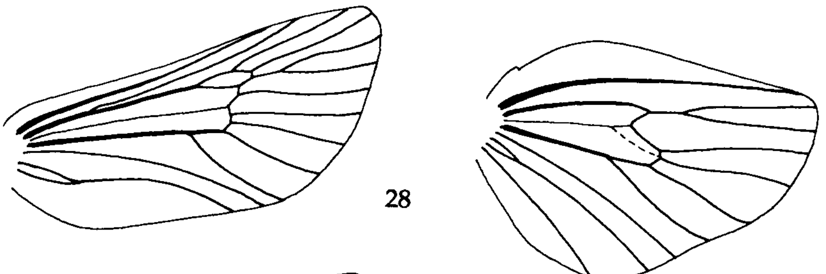

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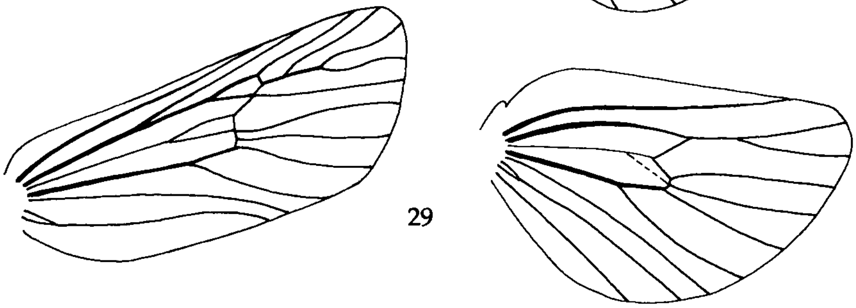

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Figs. 26-29, venation of cossid species. 26, unidentified *Rhizocossus* species (b); 27, *Catopta albonubilus*; 28, *Stygia australis*; 29, *Stygioides psyche*.

scales on outer margin. Male antenna of *clathrata* is moderately bipectinate; rami with a row of short hairs on outer margin (see fig. 48). In these species rami of ♂ antenna are slightly flattened and have approx. two rows of moderately long hairs on inner margin. This state of rami is presumably a reversal. Male antenna of *lacertula* and *affinis* is moderately bipectinate; rami are moderately but distinctly flattened. In *lacertula* rami have short hairs on proximal side. In *affinis* rami have moderately long hairs on margins and proximal side. Female antenna of *agilis* is a little variable, up to moderately bipectinate; rami are moderately flattened, with rather short hairs on inner margin, small scales on outer margin and one stout sensillum at apex (see fig. 47b). Female antenna of *cossoides* is shortly bilobed with short hairs on proximal side of rami. Female antenna of *clathrata* is moderately bipectinate. Labial palpi: second segment is often subapically narrowed and vestiture is mostly long and partly nearly hair-like.

Latero-cervical sclerites are reduced for approx. half length in at least *agilis*. An is moderately low or varies from moderately low to low. Apc terminates sometimes dorsally to K in *agilis*. K is variable in shape and size, plus or without a cross-suture. Bs II has in most species short and shallow grooves laterally, but in *agilis* these grooves are sometimes/often rather deep (see fig. 37). Mesepimeron is in most species high, and it varies from high to rather high in *agilis*. Mesepimeron does (normally ?) not show a paler band medio-posteriorly. Mesomeron is at least 1.5 times width of eucoxa II, and in *clathrata* even twice. Intersclerite III is (usually ?) wanting. I-epiphysis of *lacertula* reaches little short of tibia-apex, and is bluntly pointed.

Fringes are long. Male frenulum spine varies interspecifically from rather long to moderately short. Number of ♀ frenulum bristles is four or five and in *cossoides* approx. seven, and these are moderately short. Venation: areole moderately large to small; R3, R4+5 separate to very shortly stalked; R4+5 (very) shortly stalked; inner cell moderately large to small; Rs-M1 connate to shortly stalked. Humeral plate of *agilis* is approx. 1.5 times size of radial bridge (see fig. 30). Humeral plate has not been examined in the other species. 4Ax is distally partly very thin or more or less membranous. Median arm is narrow or very narrow, but in *clathrata* moderately wide.

Ovipositor is little or distinctly protruberant.

Representatives of the genus occur in south U.S.S.R. and some also in Afghanistan.

Material:

agilis —long series of both sexes, U.S.S.R.: from Ashkhabad, Repetek, Arwas, Dortkuju, Sumbar, Kopet-Dag, Buchara, Tekke, Altaï, Oase Tedshan, Almatinka, Garm and Aidasa (BMNH); series, AFGHANISTAN: Kuliab (BMNH); 1♂, U.S.S.R.: Ashkhabad (RMNH).

cossoides —1♂, 1♀, U.S.S.R.: Juldus (BMNH); 1♀, U.S.S.R.: Fergana, Namangan, Fl. Palscha-ata and Toste (BMNH); 1♀, U.S.S.R.: Gultscha, Osch (BMNH); 1♀, U.S.S.R.: Issyk-Kul (BMNH); 1♂ (syntype of ssp. *tsimgana* Zukowsky, 1936), U.S.S.R.: Tyan-Shan', Bolshoj Tshimgan, 2000 m., 15.vii.1934 (Sheljuzhko) (ex coll. Bang-Haas) (ITZ).

clathrata —long series of both sexes, U.S.S.R.: from Mary, Issyk-Kul, Samarkand, Imambaba and Kopet-Dag (BMNH); 1♂, U.S.S.R.: Mary (RMNH).

lacertula —1♂, CHINA: Aksu (BMNH); 2♂♂, 1♀, U.S.S.R.: Issyk-Kul (BMNH); 1♂, central Asia (RMNH).

tristis —2♂♂, U.S.S.R.: Karagai Tau (BMNH); 1♂, U.S.S.R.: Gultscha, Osch (BMNH).

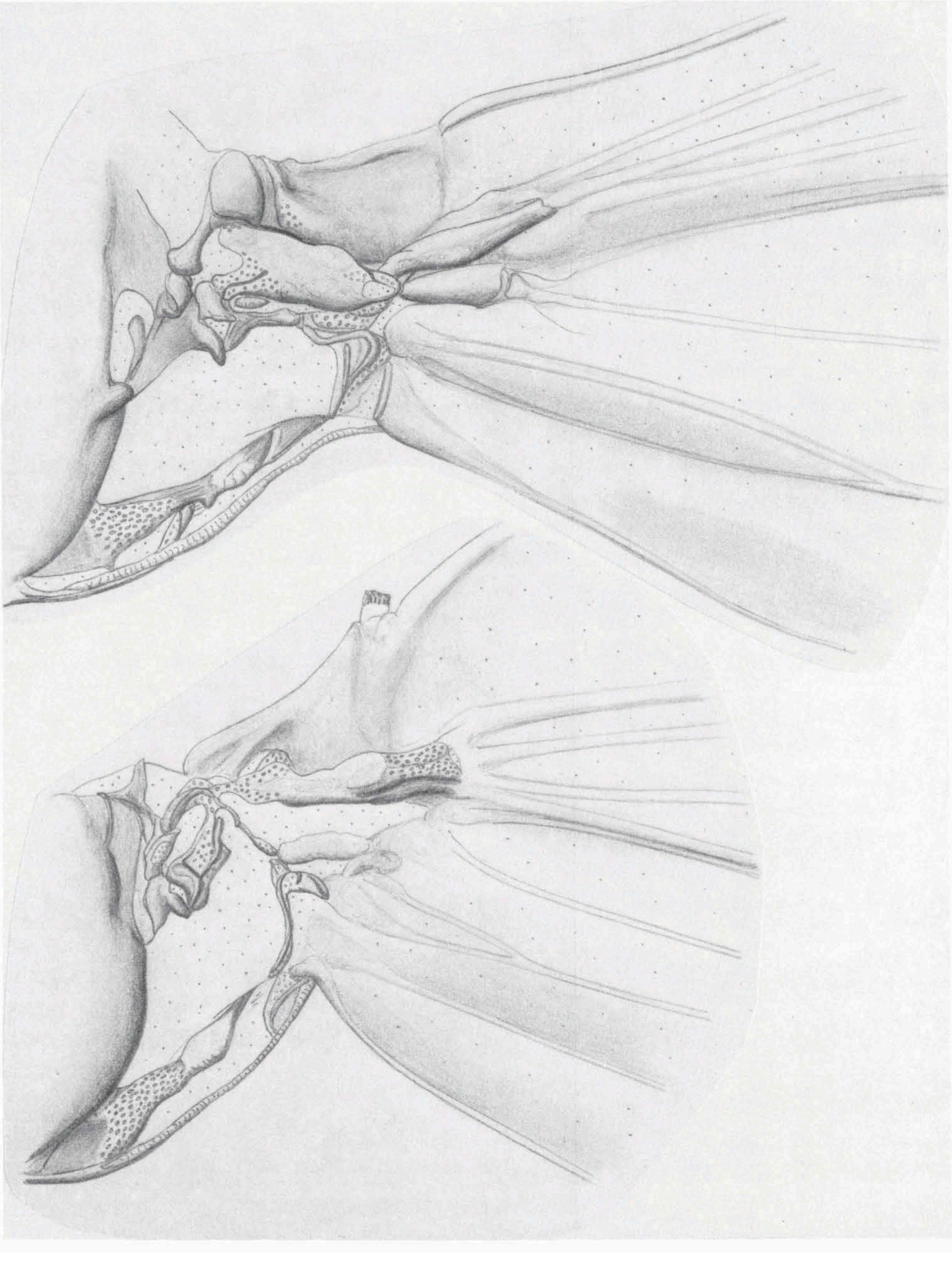


Fig. 30, wing bases of *Semagystia agilis*, Afghanistan, Kuliab.

Genus **Dyspessa** Hübner [1820] 1816

Dyspessa Hübner, [1820] 1816: 194.

Type species: *Phalaena pantherina* Hübner, 1790: 29-30 [as *hepialina*], pl. 4: fig. 10. [Synonymized with *Phalaena ulula* Borkhausen, 1790 by Kirby, 1892: 869].

Endagria Boisduval, 1834: 176. [Junior objective synonym].

Type species: *Phalaena pantherina* Hübner, 1790: 29-30.

Reference should be made to Fletcher & Nye (1982: 55) for synonyms of the type species and information on the type-designation.

Many species from several other genera had previously been included in *Dyspessa* and *Endagria*. Daniel (1962b; 1964a) revises the genus. Reference should be made to Daniel's revision for a list of *Dyspessa* species and their forms and subspecies. Daniel (1962b) includes *vaulogeri*, which is placed in *Eremocossus* in this study. Perhaps certain species included by Daniel (1964a) should be placed in *Semagystia*. Daniel (1962b) notes that *Endagria saxicola* Christoph, 1885 should probably be excluded, since it has a different type of antenna.

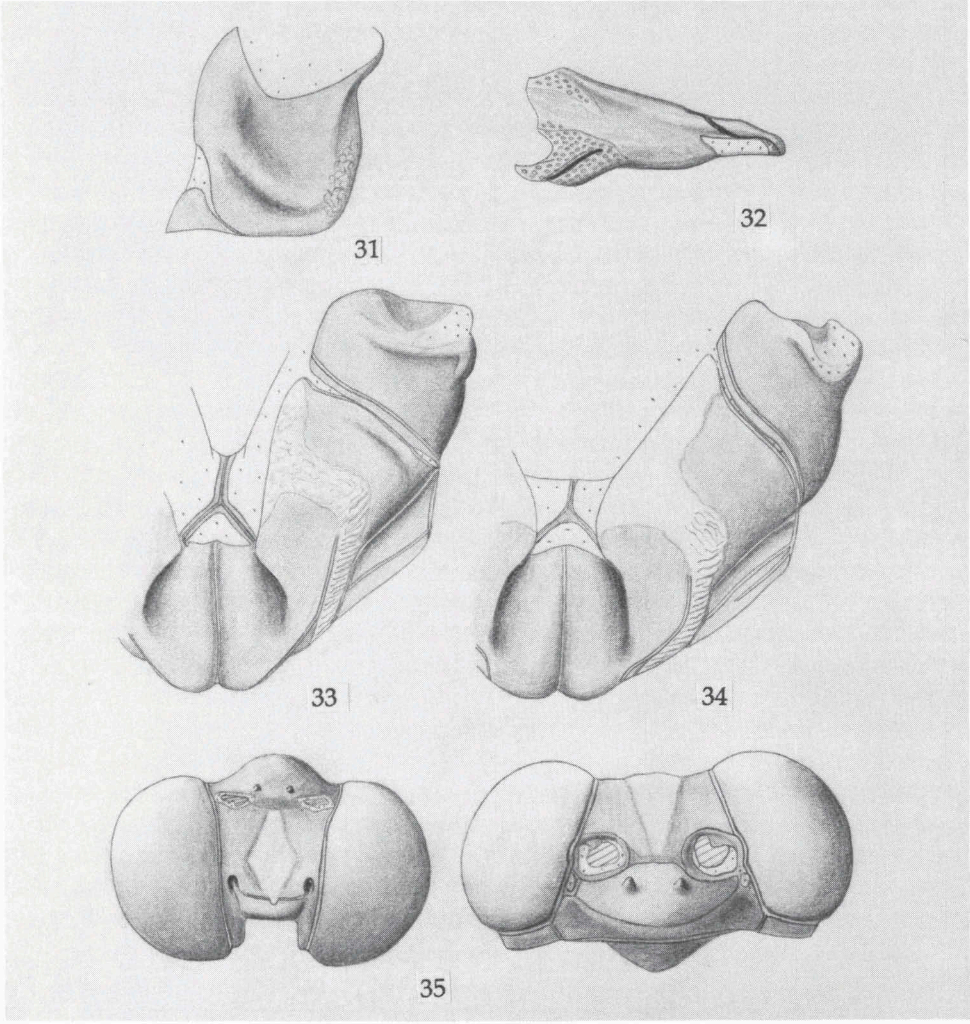
The following species have been examined and are certainly included: *ulula*, *Cossus salicicola* Eversmann, 1848, *Dyspessa aculeata* Turati, 1909 and *Endagria emilia* Staudinger, 1878.

The rami of the ♂ antenna are much flattened, broad and much rounded, and have (rather) short hairs on the proximal side and laterally (see fig. 50a). The ♀ antenna of at least *ulula* and *salicicola* is shortly and indistinctly bilobed, with short hairs on the proximal side of lobes and approx. two stout sensilla near the apex of the lobe (see fig. 50b); in *ulula* the antenna may look like as if it is unipectinate. An important characteristic of the genus appears to be a very high mesepimeron (see fig. 31). Furthermore Bs II is widened (see figs. 38-39). The mesepimeron does (normally ?) not show a paler band medio-posteriorly. *Dyspessa* shares with *Semagystia* that the patagium is distinctly lower than the pronotum and the labial palpi are two-segmented. Species of *Dyspessa* are generally smaller than those of *Semagystia*, which have a pale band over the frons and narrower rami of the ♂ antenna. *Dyspessa* has furthermore the following apomorphies (see also fig. 51): vestiture on labial palpi long and partly nearly hair-like, An approx. low or vey low, Bs II with short or very short, shallow grooves laterally (see figs. 38-39), fifth tarsomere with many fine and pale brown spines, arolium wanting, ♂ retinaculum wanting and humeral plate approx. 1.5 times size of radial bridge.

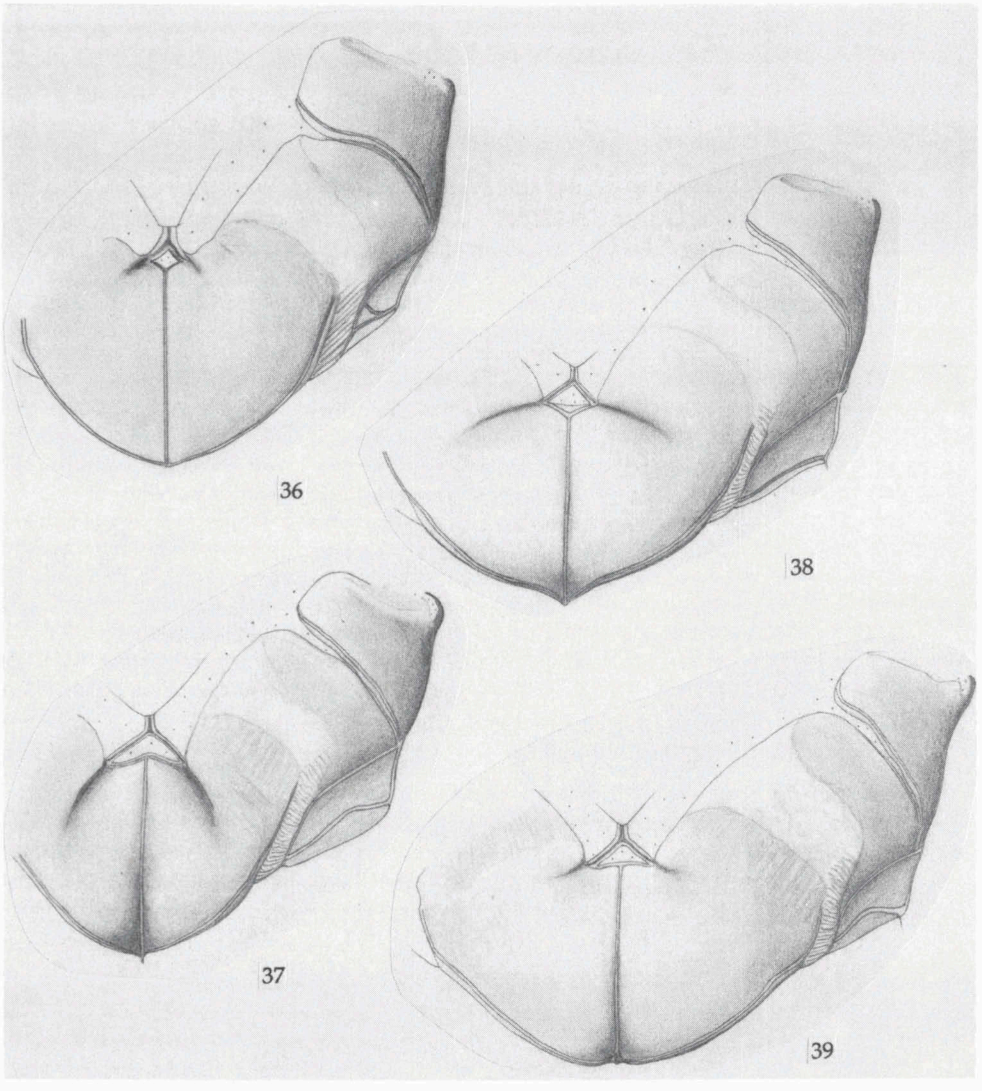
Vertex of *ulula* and *salicicola* has an arcuate Pos reaching far posteriorly. Rami of ♂ antenna have small scales on outer margin and near and at apex in at least *emilia*. Latero-cervical sclerites are reduced for approx. half length in at least *ulula* and *salicicola*. Bs II is (normally ?) gradually curved in at least *salicicola* (see fig. 38) and very rounded in at least *ulula* (see fig. 39). In *ulula* and *salicicola* Bs II has short anterior arms. K is variable in shape and size, plus or without a cross-suture. Intersclerite III appears to be normally wanting. I-epiphysis reaches as far as tibia-apex and is pointed in at least *ulula* and *salicicola*. Fifth tarsomere is 1.3 times length of fourth in *aculeata*. Fringes are long. Male frenulum spine varies from moderately long to moderately short. Number of ♀ frenulum bristles is in *ulula* and *salicicola* three or four, and these are moderately long or moderately short. Venation: areole variable, sometimes wanting; R3, R4+5 connate to shortly stalked; R4+5 shortly stalked; inner cell moderately small; a cross-vein Sc-Rs occasionally present in at least *ulula*; Rs-M1 shortly separate to shortly stalked; inner cell (hindwing) sometimes wanting. Wing bases closely resembling those of *Semagystia agilis* (see fig. 30). 4Ax is distally partly very thin or more or less membranous. Median arm is narrow or varies from moderately narrow to narrow.

The genus is represented in southern U.S.S.R., Afghanistan, Iran, Iraq, Syria, Turkey, northern Africa (Mauritania and Morocco to Egypt) and throughout a large part of Europe, including Sicily, Cyprus and Crete.

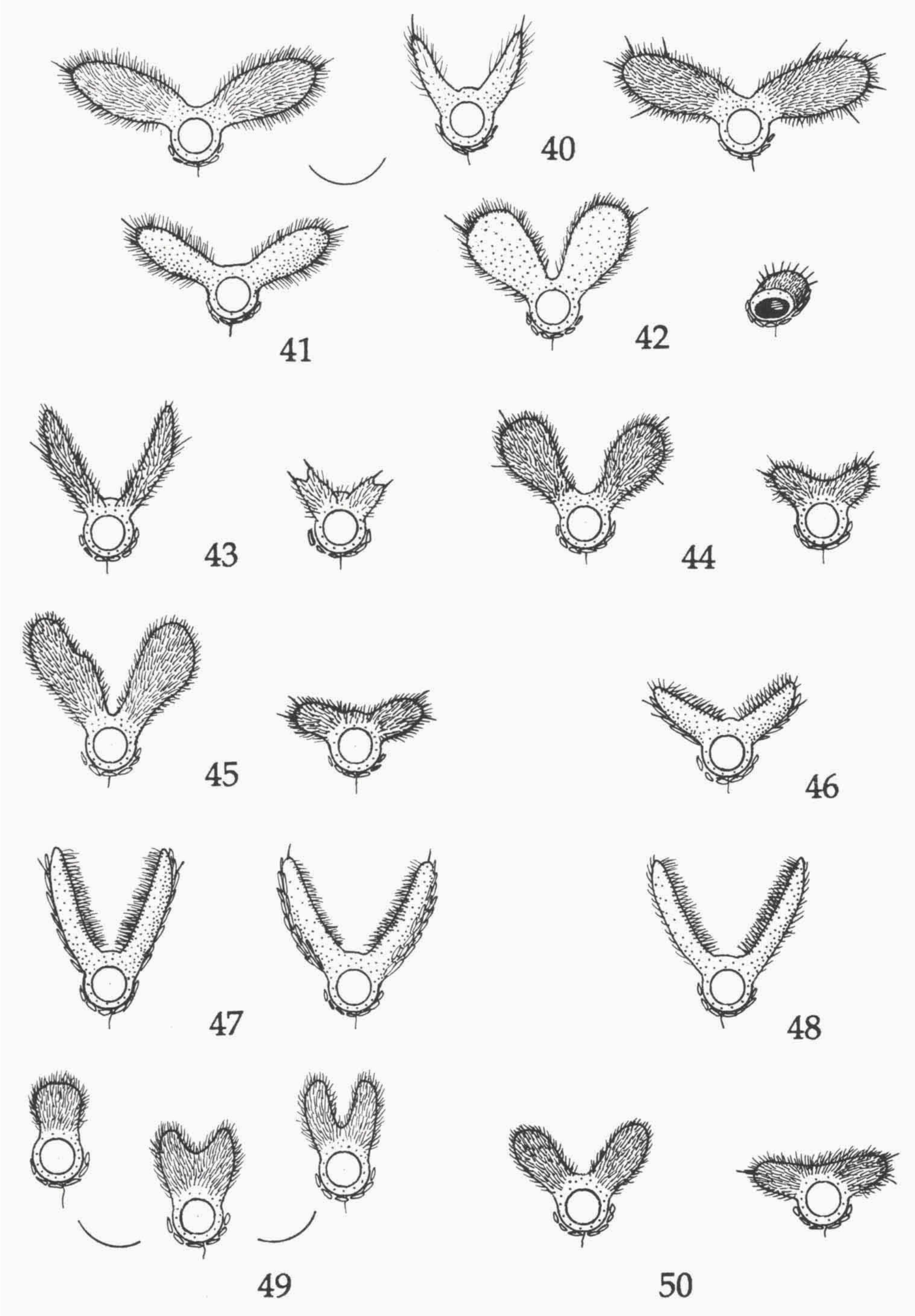
D. ulula has been recorded as a pest species in Garlic bulbs in the Ukraine (see Daniel, 1964a: 183).



Figs. 31-35, sections of cossine species. 31, mesepimeron and accessory plate II of *Dyspessa ulula* (aculeate area not depicted); 32, radial plate of *Prionoxystus robiniae*; 33, sternopleural region of *Cossus cossus*; 34, sternopleural region of *Prionoxystus robiniae*; 35a-b head of *Semagystia agilis*: a, frontal view; b, dorsal view.



Figs. 36-39, sternopleural regions of cossine species. 36, *Stygioides colchica*; 37, *Semagystia agilis*; 38, *Dyspessa salicicola*; 39, *Dyspessa ulula*.



Figs. 40-50, antennal segments of cossine species (a, male; b, female). 40, *Eogystia sibirica*; 41, male *Eremocossus faeda*; 42, *Eremocossus vaulogeri*; 43, *Comadia bertholdi*; 44, *Mormogystia reibellii*; 45, *Stygioides colchica*; 46, unidentified *Stygioides* species (e); 47, *Semagystia agilis*; 48, male *Semagystia clathrata*; 49, male *Cossulus herzi*; 50, *Dyspessa ulula*.

Material:

ulula —very long series of both sexes from at least Spain, France (central and south), Italy, Austria, Hungary, Yugoslavia, U.S.S.R. (Armenia and Turkmeniya), Syria and Algeria (BMNH); long series of both sexes from France, Austria, Hungary and U.S.S.R. (Caucasus and Turkmeniya) (RMNH).

salicicola —very long series of both sexes from Afghanistan, U.S.S.R. (Armenia, Caucasus, Ukraine, Kazakhstan), Syria, Turkey, and Yugoslavia (BMNH); 1♂, U.S.S.R.: Ashkhabad (RMNH).

aculeata —8♂♂, ITALY: Sicily (BMNH).

emilia —4♂♂, U.S.S.R.: Amasiya (BMNH); 1♂, ? TURKEY: Taurus Mts. (BMNH); 1♂, ? (BMNH).

Table 7. Apomorphies in fig. 51 (section 3B).

1a. Mesomeron approx. 1.3 or 1.5 times width of eucoxa II.
b. Mesomeron at least 2 times width of eucoxa II.
2. I-epiphysis reaching slightly short of or approx. as far as tibia-apex.
3. Bs II with moderately long to/or very short and more or less shallow grooves laterally, and Bs II more or less flattened (and widened), and more or less rounded (figs. 38-39). N.B. Within *Semagystia*, Bs II is usually/often normally vaulted and ovate in certain species.
4. Male retinaculum wanting, and frenulum spine reduced in length.
5a. Fifth tarsomere with moderate number of fine, pale brown spines.
b. Fifth tarsomere with many fine, pale brown spines.
6a. Arolium distinctly reduced to wanting.
b. Arolium wanting.
7. Labial palpi with much (rather) long vestiture ventrally.
8. Patagium distinctly lower than pronotum.
9. Labial palpi two-segmented.
10. Female antenna unilobed. N.B. The female of only one species from *Dyspessacossus* is known.
11. Male retinaculum distinctly reduced.
12. Labial palpi: third segment ovate, instead of conical.
13. An at most moderately low.
14a. Median arm varying from moderately narrow to moderately wide.
b. Median arm moderately wide.
15a. Male antenna: rami with one stout sensillum.
b. Male antenna: rami with two stout sensilla.
16. Fifth tarsomere approx. 1.5 times length of fourth.
17. Female antenna filiform. Of only one species of *Eremocossus* the female is known.
18. Female antenna bilobed.
19. Labial palpi three- or two-segmented.
20. Tarsal claws moderately slender.
21. Fifth tarsomere approx. 1.3 to 1.5 times length of fourth.
22. Male frenulum spine wanting.
23. Eyes more or less reduced in size, and frons more or less widened.
24. Pronotum distinctly lower than patagium.
25. Male antenna: rami with approx. two rows of hairs on inner margin.
26a. Mesepimeron high.
b. Mesepimeron very high (fig. 31).
27. Midtibial spurs (of hindleg) wanting.
28. Fringes moderately long.
29. Frons with whitish or very pale brown median band (fig. 35a).

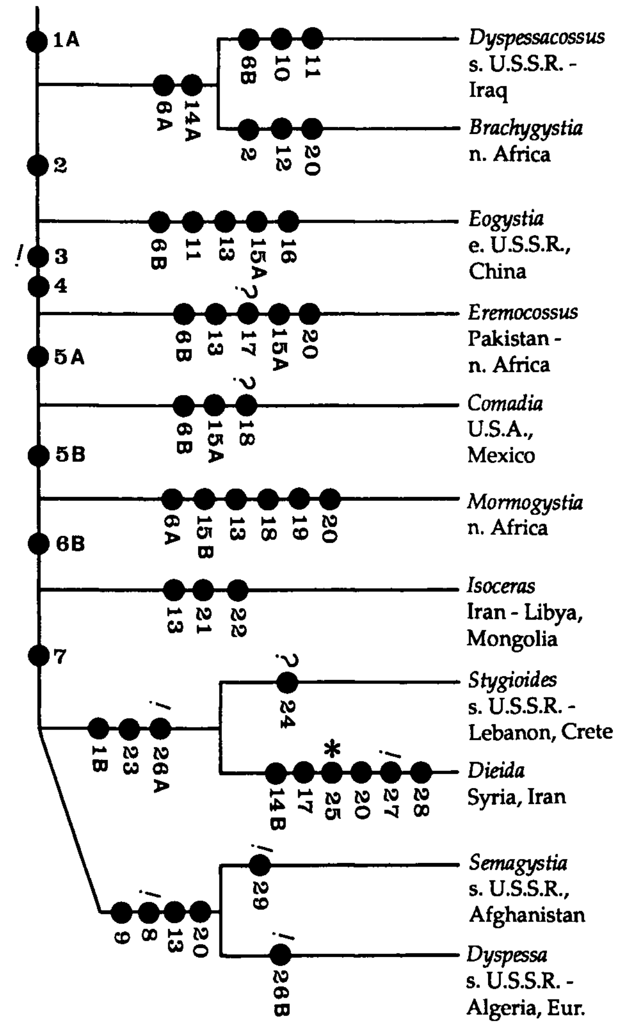


Fig. 51, cladogram of section 3B.

Uncertain position

Genus **Pecticossus** Gaede, 1930

Pecticossus Gaede, 1930: 542.
Type species: *Pecticossus castaneus* Gaede, 1930: 543.

Originally only *castaneus* was placed in *Pecticossus*. Daniel (1956b) includes his new species *gaerdesi* in this genus. Both Gaede and Daniel give hardly any diagnostic character. Clench (1959) treats *Pecticossus* tentatively as a synonym of *Arctiocossus*, although he supposes that it is a good genus. No material of *Pecticossus* was available, so that the genus cannot be defined and its position in the cladogram remains obscure.

P. castaneus is known from South Africa (Transvaal). *P. gaerdesi* has been caught in Namibia (environment of Swakopmund, Wlotzabakken) (Daniel, 1956b). The larva of *gaerdesi* lives in the roots of *Zygophyllum stapffii* in a desert-like environment near the coast (Daniel, 1956b).

Genus **Bifiduncus** Chou & Hua, 1988

Bifiduncus Chou & Hua, 1988: 225-227.

Type species: *Bifiduncus longispinalis* Chou & Hua, 1988: 225-228.

Bifiduncus has been described from a single male specimen from Pingxiang in Jiangxi Province (China) (deposited in the Entomological Museum of Northwestern Agricultural University, Shaanxi, China).

The author selected from the original description the following important characteristics: ocelli wanting, ♂ antenna completely bipectinate, midtibial spurs very short, first tarsomere of hindleg not swollen, areole small, Sc+Rs very shortly coalescent, uncus distinctly bifid, valva distinctly tapering in distal half, spina basalis longer than half length of valva, and aedeagus without cornuti.

Judging from the original description, I wonder whether a new genus for *longispinalis* is justified and which species are its closest relatives. Among the Cossinae, a bifid uncus is also known in some *Holcocerus* species, and thus may vary within the new genus. A not swollen first tarsomere of hindleg has also been found in *Prionoxystus robiniae*. The other characteristics of the external morphology in *longispinalis* are found within many other cossine taxa.

Discussion - Cossinae

Most genera of Cossinae have so few special characteristics and/or so much interspecific variation, that it is difficult to give a simple, generic diagnosis. Daniel (1955-1965) used particularly the characteristics of the antenna to distinguish the genera. In this study it appears that the type of antenna is very important but not sufficient for classification. The characteristics of the thoracic sclerites are apparently helpful in classification. The wing bases are mostly very similar amongst a great number of genera. In this study several main groups of genera are distinguished, but these groups cannot be placed in a dichotomous cladogram. There are apparently so few diverging characteristics of the external morphology within the larger genera, that it is impossible to elucidate the phylogeny of these on the species level. The proposed cladograms can be tested and improved by a study of other characters, such as those of the genitalia.

If the cladograms are followed, a distinction can be drawn between developments which seemingly occurred on many occasions and those which seemingly occurred a few times. A survey of these two categories can be helpful for studies of other primitive Ditrysian families.

Developments which seemingly occurred at least three times are: disappearance of anterior protuberances of vertex, reduction of antennal rami (particularly in the females), evolution of one or more stout sensilla on antennal segments, lowering of An, lowering of mesepimeron, probably reduction of accessory plate II, widening of mesomeron, disappearance of intersclerite III, lengthening of I-epiphysis, shortening of tibial spurs, lengthening of fifth tarsomere, narrowing of tarsal claws, reduction of arolium, reduction of ♂ frenulum spine, reduction of male retinaculum, reduction in length of ♀ frenulum bristles, reduction of areole, evolution of Sc-Rs, stalking of Rs-M1, reduction of distal plate of 4Ax in forewing, and widening of median arm.

Developments which seemingly occurred one or several times: disappearance of ocelli, reduction of eye-size, widening of frons, evolution of several types of antenna, reduction of third segment of labial palpi, reduction in length of vestiture ventrally on labial palpi, lowering of patagium, lowering of pronotum, flattening of Bs II, increase in height of mesepimeron, further widening of mesomeron up to at least 2 times width of eucoxa II, disappearance of I-epiphysis, shortening of ♀ I-epiphysis, disappearance of midtibial spurs, evolution of fine and pale brown spines on fifth tarsomere, disappearance of paronychia, disappearance of ♀ frenulum bristles, considerable reduction of fringes, considerable reduction of radial bridge, elongation of radial plate, lengthening of scale plate, shortening of median arm, and shortening of anal plate. The disappearance of ocelli and paronychia and the shortening of anal plate seemingly occurred at the base of the cladogram (fig. 10) after divergence of *Catopta*.

The following character-states noticed in the following cases are presumed to be reversals: the ocelli-like protuberances in the unidentified/undescribed *Holcocerus* species; the plesiomorphic state of the antenna in *Comadia albistriga, Styioides psyche, Dieida ledereri* and certain *Semagystia* species; an ovate third segment of the labial palpi in e.g. *Brachygystia;* partly moderately long vestiture ventrally on the labial palpi in *Holcocerus inspersus;* a moderately high An in *Stygioides* and *Dieida;* a rather high mesepimeron in *Prionoxystus macmurtrei;* and a moderately narrow median arm in *Parahypopta sheljuzhkoi.*

The significance of most developments is obscure. A few developments may be related to better flight capability. The lowering of An provides perhaps a more aerodynamic shape. The presence of a cross-vein Sc-Rs probably strengthens the wing. The widening of the median arm may strengthen the hindwing base. However, a reduction of the vestiture on the wings as in *Stygioides* seems to be disadvantageous to flight. Scales have a positive impact on the aerodynamic qualities of the wing; the presence of scales increases significantly the lift generated by a moth's wing (Ward-Smith, 1984: 124).

Other developments may be due to loss of significance of a structure. Most developments are reductions of structures. The reduction of e.g. arolium, paronychia, ♂ frenulum spine and retinaculum and ♀ frenulum bristles may have to do with loss of function. In many species the ♂ retinaculum is well-developed, while the frenulum spine is distinctly reduced in length. The combination of a long frenulum spine and small retinaculum is known only of *Eogystia sibirica.* In many other species the ♂ retinaculum is rudimentary or wanting, while the frenulum spine is moderately long. Only in a few genera is the ♂ frenulum spine wanting. It appears that the reduction of the ♂ frenulum spine generally precedes that of the retinaculum, but that the latter has gone further than the former in many cases.

In many species the ♀ antenna is unilobed or prismatic, while the ♂ antenna still is more or less bipectinate. This general reduction of the antennal rami in the female may be related to a less mobile role played by the female in sexual contact. However, in many other species the ♂ antenna is also unilobed or prismatic, although in many cases thicker than the ♀ one.

There is a record of attraction of many males of *Prionoxystus robiniae* by a female kept in a house (Bruce, 1883: 190). The males flew in a rapid direct flight. This would indicate that the female makes use of pheromones for sexual attraction. It has been recorded (Korb, 1910: 26), that the female of *Stygia australis* displays a type of flight during the day which is presumably for sexual attraction. In *australis* the ♂ antenna is distinctly bipectinate and the ♀ one is bilobed. The author does not know any other record of sexual behaviour in the Cossinae.

Yellowish or orange vestiture evolved apparently several times. In the female of *Neostygia postaurantia* and the male of *Stygia australis* the hindwing has a large yellowish area. It has been recorded (Korb, 1910: 26), that *S. australis* flies during the day. *Stygia hades* is also known to fly in the day-time (reference in Daniel, 1955: 163), but the male of *hades* is unknown and the female does not have bright colours. Bruce (1883: 190) records afternoon flights by males of *Prionoxystus robiniae*; the male and occasionally the female of *robiniae* also have a large yellowish area on the hindwing. The holotype of *Stygioides persephone* is labelled as having been collected flying during the day. The male of *persephone* is unknown and the female is dark fuscous. Two specimens of *Dieida ledereri* have been caught in copula (Staudinger, 1878: 342), which probably means in the day-time. Two females of *ledereri* have been caught when ovipositing (see Daniel, 1955: 179), which probably also means during the day. Several *Stygioides* species and *D. ledereri*, suggested here to be the sister-group, also have a more or less yellowish vestiture on the bodies and wings, particularly in the male. Possibly that most or all *Stygioides* species are diurnal. Females of *Dyspessa ulula* were seen in a kind of sexual flight from 8.00 until 9.45 a.m. in Greece (Daniel, 1964a: 192). None of the *Dyspessa* species has any yellow or orange vestiture. Yellow or orange markings are further known only in *P. fulvosparsa*; its forewing has many orange markings, but it is unknown whether it is day-flying. It may be that the presence of yellowish vestiture is correlated to diurnal activity and that the bright colour has a role in sexual attraction.

Only a few species show a marked increase in size: *Macrocossus toluminus* and certain *Cossus* species. Only the species of *Stygioides* and *Dieida*, presumed to be sister-groups, show considerable reduction in size.

Key to the genera of Cossinae (males only)

This key is only for male specimens, because the females of many species are unknown. Of *Neostygia* only the female is known. It is supposed that the ♂ antenna in *Neostygia* is bipectinate and that the rami have only short hairs on their proximal side. *Pecticossus* and *Bifiduncus*, of which no material has been personally examined, are not included in this key.

1. Ocelli present, sometimes small but distinct. Paronychia small but present. Anal plate approx. moderately long .... *Catopta*

- Ocelli wanting, but there may be small protuberances at terminations of Pos. Paronychia absent. Anal plate approx. moderately short 2
2. Vestiture on labial palpi ventrally only short and dorsally moderately long 3
- Vestiture on labial palpi ventrally (moderately) short mixed with moderately long, or mainly (rather) long 16
3. Male antenna more or less unilobed 4
- Male antenna completely bipectinate, or partly bipectinate and further prismatic, or completely prismatic 6
4. Palaearctic species. Male antenna completely rounded unilobed .... ***Cossus***
- Oriental species. Male antenna may be completely unilobed, but lobes often two-pointed. Male antenna of certain species proximally unilobed and distally prismatic, or proximally bipectinate and distally more or less unilobed.......... 5
5. Male antenna proximally bipectinate and distally unilobed, and rami with hairs only irregularly distributed (scattered) on their proximal side .... ***Isocossus***
- When ♂ antenna proximally bipectinate and distally unilobed, rami with approx. two rows of hairs on the inner margin and one row of hairs on the outer one. Male antenna may be also completely unilobed, or proximally unilobed and distally prismatic .... ***Paracossus***
6. Male antenna partly bipectinate and further prismatic 7
- Male antenna completely bipectinate or completely prismatic 8
7. Flagellum dorsally with approx. one sensillum on each segment .... ***Paracossus***
- Flagellum dorsally with many short hairs on each segment .... Undescribed genus (section 2)
8. Antenna completely prismatic 9
- Antenna completely bipectinate 10
9. American species .... ***Miacora***
- Asian or African species .... ***Holcocerus***
10. Rami of antenna with many short hairs only on the proximal side 11
- Rami of antenna with approx. two rows of hairs on the inner margin and may have hairs on the outer one 12
11. Species from India or Egypt and perhaps neighbouring countries . ***Alcterogystia***
- Species from Madagascar and perhaps southern Africa .... ***Planctogystia***
12. American species 13
- Asian or African species 14
13. Midtibial spurs absent .... ***Psychidocossus***
- Midtibial spurs present .... ***Fania/Toronia***
14. Antennal rami with approx. two rows of moderately long hairs on the inner margin, and may have approx. one row of hairs on the outer margin 15
- Antennal rami with approx. two rows of moderately short hairs on the inner margin and many short or very short hairs irregularly distributed (scattered) on the outer margin .... ***Hirtocossus***
15. Asian species .... ? ***Paracossus***
- African species .... Undescribed genus/genera
16. Antennal rami with approx. two rows of hairs on the inner margin 17
- Antennal rami with hairs only on the proximal side or antenna completely unilobed 27
17. Antennal rami with approx. two rows of moderately short hairs on the inner

margin, and many short or very short hairs irregularly distributed (scattered) on the outer one or approx. one row of hairs on the outer margin. Fifth tarsomere approx. 1.3 to 1.5 times length of the fourth 18
- Antennal rami with approx. two rows of moderately long hairs on the inner margin and may have one row of hairs on the outer one. Fifth tarsomere approx. as long as the fourth 21

18. Species from America 19
- Species from Africa, Europe or Asia 20

19. Frons moderately narrow. Radial plate moderately long and subapically moderately wide (see fig. 30) .... ***Acossus***
- Frons rather wide. Radial plate little elongate and subapically rather slender (fig. 32) .... ***Prionoxystus***

20. Species from Africa .... ***Macrocossus***
- Species from Europe and/or Asia .... ***Lamellocossus***

21. Mesomeron (halfway along its length) approx. as wide as the eucoxa II 22
- Mesomeron at least 1.3 times width of the eucoxa II 23

22. Species from South Africa and perhaps southern Africa .... ***Rethona***
- Species from northern Africa, Arabia and Asia .... ***Paropta***

23. Fifth tarsomere with only dark brown, stout spines, often reduced in length and number compared to other tarsomeres 24
- Fifth tarsomere with many fine, pale brown spines, and few or no dark brown, stout spines 25

24. I-epiphysis absent .... ***Arctiocossus***
- I-epiphysis present .... ***Mirocossus***

25. Midtibial spurs (of hindleg) present 26
- Midtibial spurs (of hindleg) absent .... ***Dieida***

26. Eyes small. Fifth tarsomere longer than the fourth. Forewing not completely covered by scales .... ***Stygioides***
- Eyes moderately large. Fifth tarsomere approx. as long as the fourth. Forewing completely covered by scales .... ***Semagystia***

27. Antenna at least partly bipectinate 28
- Antenna completely unilobed .... ***Parahypopta***

28. Antenna proximally unilobed and distally bipectinate or bilobed 29
- Antenna completely bipectinate 30

29. All present rami proximally fused at their inner side .... ***Dyspessacossus***
- Antenna partly bipectinate and at least a number of rami not proximally fused at their inner side .... ***Cossulus***

30. I-epiphysis absent. Humeral plate at least 2.5 times size of the radial bridge 31
- I-epiphysis present. Humeral plate at most approx. 2.5 times size of the radial bridge 32

31. Mesepimeron rather high .... ***Neostygia***
- Mesepimeron moderately high .... ***Stygia***

32. Fifth tarsomere with moderate number or many fine, pale brown spines and few or no stout, dark brown spines 33
- Fifth tarsomere with only stout, dark brown spines, which may be reduced in length and number compared to other tarsomeres 38

33. Labial palpi ventrally with much (rather) long vestiture 34

- Labial palpi ventrally with moderately short scales mixed with fewer moderately long ones 36

34. Pronotum distinctly higher than the patagium. Mesomeron (halfway along its length) approx. 1.5 times width of the eucoxa II and in few species twice as wide 35
- Pronotum distinctly lower than the patagium. Mesomeron (halfway along its length) at least twice as wide as the eucoxa II .... *Stygioides*

35. Mesepimeron very high (fig. 31). Frons completely brownish .... *Dyspessa*
- Mesepimeron at most high. Frons with whitish median band (fig. 35a) .... *Semagystia*

36. Species from Africa or Asia 37
- Species from America .... *Comadia*

37. Fifth tarsomere approx. as long as the fourth .... *Mormogystia*
- Fifth tarsomere approx. 1.3 to 1.5 times length of the fourth .... *Isoceras*

38. Mesomeron (halfway along its length) approx. 1.3 to 1.5 times width of the eucoxa II 39
- Mesomeron (halfway along its length) approx. as wide as the eucoxa II 41

39. An (II) at most moderately low 40
- An (II) moderately high .... *Brachygystia*

40. Antennal rami of male with only very short hairs on their lateral margins and further one stout sensillum at their apex (see figs. 41-42a). Female antenna filiform in at least one species (fig 42b). Forewing more or less whitish with fuscous striae. Species from Africa or southern Asia eastward to Pakistan .... *Eremocossus*
- Antennal rami in both male and female with many hairs on their proximal side and one or more stout sensilla on their lateral margins (see fig. 40). Forewing with silvery white and sandy brown areas. Species from northeast U.S.S.R., Mongolia or China .... *Eogystia*

41. Species from southern Africa .... *Brachylia*/*Coryphodema*
- Species from south or eastern Europe or U.S.S.R. .... *Paracossulus*

Subfamily **Pseudocossinae** Heppner, 1984

Pseudocossinae Heppner, 1984: 99.
Type genus: *Pseudocossus* Kenrick, 1913: 590.

The subfamily Pseudocossinae was proposed by Heppner (1984: 99) for the following three genera: *Pseudocossus*, *Chilecomadia* and *Rhizocossus*. The only significant characteristic shared by these three genera is a bifid uncus (see also Clench, 1957). Clench (1959b) notes a prototympanum for *Pseudocossus* and *Chilecomadia*. As explained in the introduction of the subfamily Chilecomadiinae, the state of the abdominal base which is found in the three mentioned genera is considered a plesiomorphy of the Cossidae and several other taxa. The species of *Pseudocossus* differ considerably from those of the other two genera. For reasons given under Chilecomadiinae, *Rhizocossus* and *Chilecomadia* are excluded from the Pseudocossinae. There thus is now only the type genus in the Pseudocossinae.

The Pseudocossinae share with the Zeuzerinae and Hypoptinae the following apomorphies: An at most moderately high, mesomeron wider than eucoxa II, and tibia and first tarsomere of hindleg not partly swollen.

Pseudocossus shares with the subfamily Zeuzerinae the following apomorphies: third segment of labial palpi conical, mesoscutellum elongate and more or less pointed apically, Pre II antero-dorsally elongate, mesepimeron at most moderately high, male retinaculum with long base, and median arm moderately long and moderately wide.

Pseudocossus has the following autapomorphies: pronotum low (reversal), An low, tergite I mainly sclerotized, I-epiphysis finely toothed, inner cell of forewing indistinct to/or wanting, CuA1 and CuA2 very close or connate, 1Ax apically rather large, lateral process of posterior notal wing process in forewing separate from main structure for approx. one-third its length (reversal). See also fig. 7. *Pseudocossus* is characterized by the presence of distinct ocelli. Within the Cossidae ocelli are further known only in *Catopta* (Cossinae). The antenna of members of *Pseudocossus* is prismatic. In most or all species of *Pseudocossus* CuP and A1+2 of the forewing are often or usually distally very close, linked by a cross-vein or more or less coalescent. The inner cell of the hindwing is probably normally wanting. See further under *Pseudocossus*.

All species of *Pseudocossus* are restricted to Madagascar.

Genus **Pseudocossus** Kenrick, 1913

Pseudocossus Kenrick, 1913: 590.
Type species: *Pseudocossus uliginosus* Kenrick, 1913: 590.

Pseudocossus was erroneously included in the Dudgeoneidae by Munroe (1982: 630). Munroe (1988: 79) corrected this view by noting that this family includes only one genus (thus *Dudgeonea*).

Pseudocossus includes two named species and three undescribed ones. No females were available in the collections of BMNH and MNHN. The species are medium-sized. The wings are chestnut brown with dark brown and dark fuscous areas, and are more or less speckled with white.

Vertex of *uliginosus* is anteriorly swollen and has an arcuate Pos up to approx. 0.7 or 0.8 times its length (fig. 18). In all species ocelli are present and these seem to be hypertrophic. Male antenna is prismatic, proximally rounded and more distally flattened. Third segment of labial palpi is small and conical. Vestiture on labial palpi is dense and moderately long. An is low. Lower suture of Apc reaches up to approx. 0.8 times length of An. Pre II is antero-dorsally elongate (fig. 53). Upper Pas is situated at approx. 0.4 times length of Pre II plus Pa. K is long and (normally ?) with cross-suture. Bs II has narrow anterior arms. Mesepimeron is moderately high. Accessory plate II is often/normally narrow in at least *uliginosus*. Mesomeron is approx. 1.3 times width of eucoxa II. Intersclerite III is small.

I-epiphysis is broad, apically tapering and finely toothed. Tibial spurs are distinctly unequal in length, moderately long and long. Tarsi: scales are ovate and dorsally approx. similar as ventrally; many stout spines ventrally, but these are mostly more or less reduced in length and longer near apexes of tarsomeres. Paronychia are short. Arolium is more or less membranous in distal half.

Fringes are rather long. Male retinaculum has a long base. Dorsum of hindwing is without incision. Venation (see fig. 52): areole moderately long and narrow; chorda thin, or in *boisduvalli* Viette sometimes partly to completely wanting; R1 proximal to areole, at approx. one-third wing-length; R5 more or less stalked with R4 in *boisduvalli*; in the other species R5 separate from R4, posterior to areole and slightly sinuate; M in forewing cell proximally or for most of its length wanting; furcation of M in forewing cell usually/often wanting, or very short and indistinct; CuA1 and CuA2 often/normally connate at bases; CuP and A1+2 of forewing normally apically coalescent in *uliginosus* and *boisduvalli*; in undescribed species (b) CuP and A1+2 usually apart, sometimes linked by a cross-vein or apically coalescent; in undescribed species (c) (3 ex.) both the separate and coalescent state occurs; in undescribed species (a) (1 ex.) CuP wanting; CuP often/usually distally more or less wanting in *boisduvalli*; sometimes a very short, incomplete cross-vein from Rs towards Sc; Rs-M1 short to moderately short; M in hindwing cell more or less wanting and not furcate; M3 and CuA1 very close or connate.

Wing bases of *uliginosus* are shown in fig. 54. Humeral plate is approx. 1.7 to 2 times size of radial bridge. Radial plate is elongate and distally slender. Scale plate is distinctly shorter than radial bridge and moderately wide. 1Ax is apically rather large. Lateral process of posterior notal wing process in forewing is separate for approx. one-third of its length. Median arm is moderately long and moderately wide. Anal plate is rather long.

Pseudocossus Gaede, 1933 (originally Cossidae) and *Pseudocossus* Martynov, 1931 (Palaeohemiptera) are junior homonyms of *Pseudocossus* Kenrick. Viette (1951a: 134) proposes *Zyganisus* as objective replacement name for *Pseudocossus* Gaede. *Zyganisus* seems to be most closely related to *Culama* Walker and is excluded from the Cossidae in this paper (see chapter on excluded and obscure taxa).

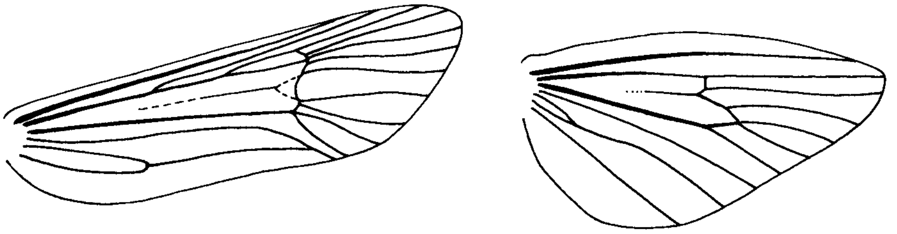


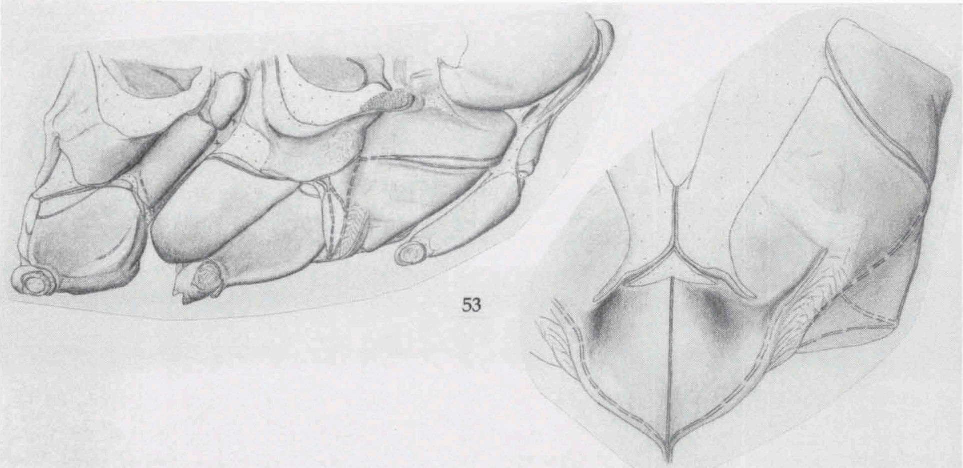
Fig. 52, venation of *Pseudocossus uliginosus*.

Pseudocossus uliginosus Kenrick, 1913: 590.

Material (all MADAGASCAR (BMNH)). —3♂♂ (syntypes), central Madagascar, 2500 ft., i-iii.1911 (Pratt); 2♂♂ (syntypes), Fort Dauphin, Mandena, 100 m., 14-18.v.1968; long series of males from various localities.

Pseudocossus boisduvalli Viette, 1955: 89-90, 1 fig. (male genitalia).

Material (all MADAGASCAR). —1♂ (holotype), east Madagascar, near Perinet, forêt d'Anala-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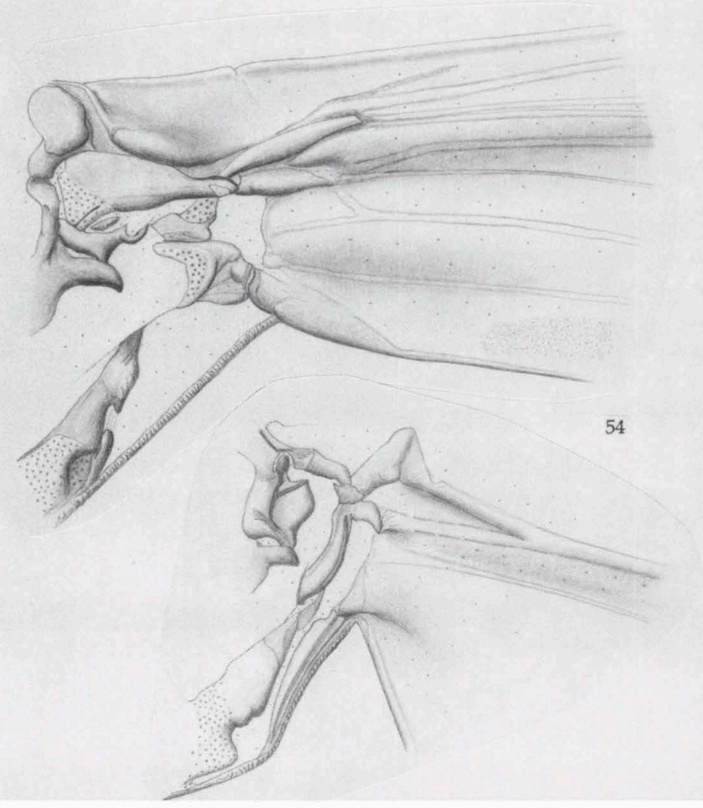

54

Figs. 53-54, sections of *Pseudocossus uliginosus*. 53, sections of thorax, Madagascar, Fort Dauphin; 54, forewing base and part of hindwing base, Madagascar.

mazoatra, 910 m., 19.iv.1955 (Viette) (MNHN); 14♂♂, various localities (BMNH).

Undescribed species (a)

Material. —1♂, MADAGASCAR: Station Perinet, 149 km east of Tananarive, i.1933 (d'Olsoufieff) (BMNH).

Note. Closely resembling *boisduvalli*, but smaller and paler.

Undescribed species (b)

Material. —24♂♂, MADAGASCAR (BMNH).

Note. Closely resembling *uliginosus*, but slightly smaller and with CuP and A1+2 usually separate.

Undescribed species (c)

Material. —3♂♂, MADAGASCAR: Station Perinet, 149 km east of Tananarive, i.1933 (d'Olsoufieff) (BMNH).

Note. Closely resembling *uliginosus*, but with a different colour pattern on forewing.

Subfamily **Zeuzerinae** Boisduval, [1828] 1829

Zeuzerinae Boisduval, [1828] 1829: 51 (as Tribus Zeuzeridi).
Type genus: *Zeuzera* Latreille, 1804: 186.
Zeuzerinae sensu Neumoegen & Dyar, 1894: 160.
Eulophonotinae sensu Zerny & Beier, 1936: 1696.

All representatives of the Zeuzerinae are characterized by the following apomorphies: midtibial spurs of hindleg wanting, Pre II with antero-dorsal process (see e.g. figs. 57-58, 82-83), upper Pas situated in extremely ventral position (see figs. 57-58, 82-83), and (at least) ♂ antenna proximally bipectinate and distally prismatic.

The subfamily Zeuzerinae shares with the Pseudocossinae the following apomorphies: third segment of labial palpi conical, mesoscutellum elongate and more or less pointed apically, Pre II antero-dorsally elongate, mesepimeron at most moderately high, ♂ retinaculum with long base, and median arm moderately long and moderately wide.

The subfamily Zeuzerinae has further the following autapomorphies: ocelli wanting, frontal tuft moderately or rather long, tegula ventro-posteriorly bluntly pointed, Apc rather wide and its lower suture reaching up to approx. 0.3 times length of An, mesepimeron moderately low with sinuate upper margin, accessory plate III wide, apical spurs short or very short, areole very long, and R1 from areole and at approx. half wing-length. Of several of these apomorphies one or more reversals are known.

In most Zeuzerinae the scale plate is as long as the radial bridge and the posterior M of the forewing terminates on or posterior to M3. In most representatives 2Ax (hindwing) has sometimes/often an elevated scaled area (see fig. 68). In all Zeuzerinae the median plate is apically narrowed and in many of them it is often reduced in length.

The subfamily is cosmopolitan but has most genera in Africa and tropical Asia. It is the only subfamily of the Cossidae which is represented in Australia.

Table 8. Apomorphies in fig. 55 (Zeuzerinae).

1. Ocelli wanting.
2. Antenna bipectinate for approx. 0.7 times its length and further prismatic. (*)
3. Lower suture of Apc reaching up to approx. 0.3 times length of An. (*)
4. Pre II with an antero-dorsal process.
5. Upper pas situated in extremely ventral position.
6. Mesepimeron moderately low and with sinuate upper margin. (*)
7. Accessory plate III rather wide to wide. (*)
8. Tegula ventro-posteriorly bluntly pointed and moderately upturned.
9. Midtibial spurs wanting.
10. Areole very long. (*)
11. R1 from areole and at approx. half wing-length. (*)
12. R4, R5 (normally) more or less stalked.
13. 2Ax of hindwing with or without an elevated scaled area. (*)
14. Metascutum medially narrow or very narrow, distinctly invaginated.
15. Female abdomen longer than hindwing. (*)
16. Vertex with one to few very small protuberances in invaginated area laterally to terminations of Pos.
17. Mesepimeron with rounded upper margin.
18. Mesomeron 2 to/or 2.5 times width of eucoxa II.
19. I-epiphysis reaching little short of or nearly as far as tibia-apex.
20. Tarsal spines wanting.
21. Anterior M in cell of forewing very close to or partly coalescent with chorda.
22. Scale plate approx. as long as radial bridge. (*)
23. Median arm rather wide, approx. as wide as Cu2.
24. 4Ax more or less antero-distally reduced or invaginated.
25. Tarsomeres only slightly or hardly widened apically.

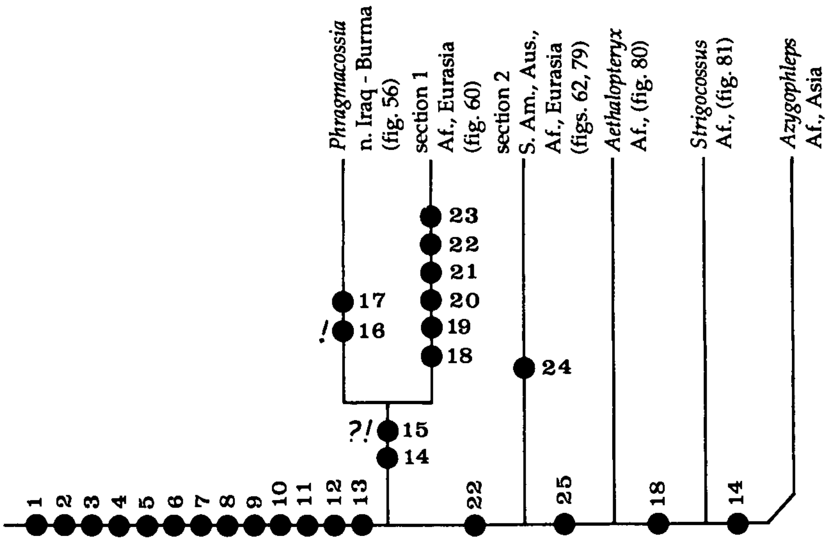


Fig. 55a, cladogram of the Zeuzerinae.

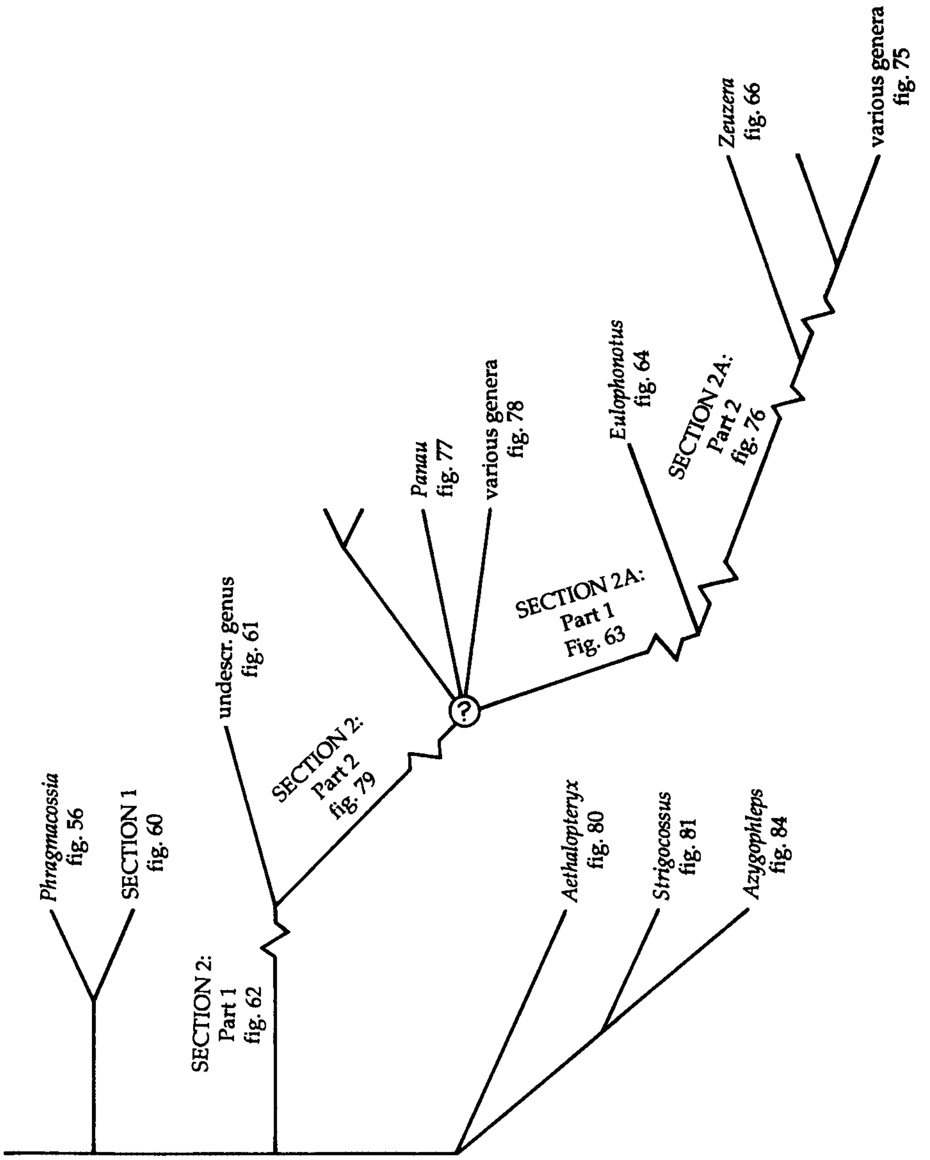


Fig. 55b, survey of cladograms and corresponding taxa of Zeuzerinae.

Genus **Phragmacossia** Schawerda, 1924

Phragmacossia Schawerda, 1924: 161-162.
Type species: *Pragmatoecia reticulata* Püngeler, 1900: 115, pl. 4: fig. 2.

Phragmacossia has been established for *reticulata* only. Here the name is applied to a group of species with a special vertex. The vertex has one or few small protuberances in an invaginated area laterally to the terminations of Pos (see fig. 86). However in *reticulata* this area may be very small (see fig. 85). The species of this genus are of moderate size, though *territa* (Staudinger, 1878) is sometimes/often small. The mesepimeron has a rounded upper margin whether it is low or moderately high. In many *Phragmacossia* species the median arm is rather short. *Phragmacossia* shares with the species of section 1 the following apomorphies: metascutum medially distinctly invaginated and narrow or very narrow, and ♀ abdomen longer than hindwing. In certain species the ♀ abdomen is approx. as long as hindwing, which is presumably a reversal. The species of section 1 have the chorda terminating very close to or partly coalescent with anterior M and median arm rather wide. See also fig. 56.

Vertex is in most species gradually curved, but in *reticulata* antero-laterally moderately ridged (see figs. 85-86). Vestiture of labial palpi is in most species long. Thoracic sclerites of *reticulata* are shown in fig. 57. Bs II of *reticulata* has distinctly bulbed lateral margins. Bs II of *territa* is elongate and ovate (see fig. 73). K is long, moderately narrow or moderately wide and has often a cross-suture. Subalare-process II varies amongst the species from moderately short to short. Mesomeron varies from 1.5 times in *reticulata* to twice width eucoxa II in most other species. Intersclerite III is sometimes present but often only traces of it are visible. Tarsi have long vestiture in *pallidalae* (Hampson, 1892) and the undescribed species. Dorsum of hindwing is weakly or not invaginated. Venation (see also fig. 91): R1 from areole; R3, R4+5 connate to very shortly stalked; R4+5 stalked for approx. 0.3 to 0.4 times their length; M1 below areole or sometimes from tip; Rs-M1 short in *territa* and moderately long or long in other species; Sc-Rs occasionally present in *reticulata*. Median plate is in most species usually reduced in length and is at least sometimes wanting in *pallidalae*.

Specimens of *Xyleutes clara* Bryk, 1950 and *X. obliquifascia* Bryk, 1950 were not available for personal comparison, but judging from the descriptions by Arora (1976: 91-94, 97-100) these come most close to *stigmatica* (Moore, 1879). Perhaps *Phragmataecia terebrifer* Fletcher, 1926-27 and *Phragmataecia dudgeoni* Arora, 1974 should also be included in *Phragmacossia*. According to Arora (1974: 157-159; 1976: 82-85, 88-91), the chorda does not terminate closely to anterior M in these species. Therefore the two do not fit in *Phragmataecia* Newman, 1850. Judging the figures provided by Arora, the two species closely resemble *parvipuncta*.

No material of *Phragmacossia paghmana* Daniel, 1963, *P. libani* Daniel, 1933 and *P. vartianae* Daniel, 1963 has been examined either and it is here not certain, if these species actually belong to this genus.

Since only the holotype of *tigrisia* Schawerda, 1924 was here available, its sclerites of the wing bases and of thorax have not been examined and the species couldnot be placed in the cladogram. The presented cladogram (fig. 56) is thus incomplete and

Cossus parvipunctus Hampson, 1892: 306.

Material. —1♂ (holotype), INDIA: Naga Hills, 1500 ft.,ix-x.1889 (Doherty) (BMNH).

Note. Dammerman (1929: 72) records that the species lives in Sugar-cane in Malaya, but the present author presumes that this record concerns another species.

Undescribed species

Material. —long series of both sexes, SRI LANKA: a.o. Maskeliya and Travancore (BMNH).

Note. Most closely resembling *parvipuncta*. Judging from the given locality data, *parvipuncta* sensu Arora (1976: 85-88) concerns this species. Arora notes *Saccharum officinarum* L. as a host-plant.

Phragmatoecia reticulata Püngeler, 1900: 115, pl. 4: fig. 2.

Material. —7♂♂, 1♀, AFGHANISTAN: province Kuliab, e.g. Ak-sou-Thal (BMNH).

Phragmacossia tigrisia Schawerda, 1924: 161-162, fig. 22.

Material. —1♂ (holotype), IRAQ: Mosul (NMW).

Phragmacossia paghmana Daniel, 1963: 154, pl. 27: fig. 18.

Not examined. From Afghanistan.

Phragmacossia vartianae Daniel, 1963: 153-154, pl. 27: figs. 13-14 (female), figs. 15-17 (male).

Not examined. From Afghanistan.

Phragmacossia libani Daniel, 1933: 107-108, pl. 1: fig. 33 (male).

Not examined. From Lebanon.

Phragmatoecia territa Staudinger, 1878: 341-342.

Material (all BMNH). —long series of both sexes from U.S.S.R. (Armenia, Amasiya, Turkmeniya, Repetek and Samarkand), Iran (Damavand) and Afghanistan.

Zenzera stigmatica Moore, 1879: 86.

Material (all BMNH). —1♂ (holotype), INDIA: Khasia Hills, Assam, Nissary; 2♂♂, INDIA: Khasia Hills; 4♂♂, INDIA: Sikkim, Geopaldhara and Mirik; 1♂, INDIA; 1♂, BHUTAN.

Xyleutes clara Bryk, 1950: 47-48, pl. 3: fig. 1 (male, holotype).

Not examined. From India, Bhutan and Burma.

Xyleutes obliquifascia Bryk, 1950: 46-47, pl. 3: fig. 3 (male, holotype).

Not examined. From north Burma and India.

Cossus pallidalae Hampson, 1892: 306.

Material (all BMNH). —1♂ (holotype), INDIA: Sikkim, 1888 (Möller); 1♂, BHUTAN; 1♂, ? (coll. Archbald).

Table 9. Apomorphies in fig. 56 (*Phragmacossia*).

1. Vertex with one to few small protuberances in small (invaginated) areas laterally to terminations of Pos.
2. Mesepimeron with rounded upper margin.
3. Median arm rather short.
4a. Metameron nearly moderately wide. (*)
b. Metameron moderately narrow.
5. Mesomeron at least twice as wide as eucoxa II.
6. Vertex gradually curved and (normally ?) without anterior protuberances.
7a. Humeral plate approx. as large as radial bridge.
b. Humeral plate approx. 1.8 times size of radial bridge.
8a. An moderately low (not examined in *parvipuncta*).
b. An low.
9. Forewing-apex very obtuse and much rounded (see fig. 91).
10a. Mesepimeron (rather) low.
b. Mesepimeron distinctly low.
c. Mesepimeron moderately high.
11. Tarsal spines wanting.

b. Female antenna moderately strongly bipectinate.
13. Subalare-process II very short and very blunt.
14a. Anal plate moderately to rather long.
b. Anal plate moderately long.
15a. Arolium rudimentary.
b. Arolium moderately long to distinctly reduced.
16a. Bs II with prominently bulbed posterior margins (see fig. 57).
b. Bs II very long (elongate) and ovate.
17. Scale plate as long as radial bridge and wide.
18. Paronychia wanting.
19. Labial palpi two-segmented.
20. Male antenna moderately strongly bipectinate.
21. Tegula ventro-posteriorly very bluntly pointed to (nearly) rounded.
22. Accessory plate III narrow.
23. Antenna bipectinate for 0.8 times its length.
25. Apc (usually ?) terminating dorsally to K.

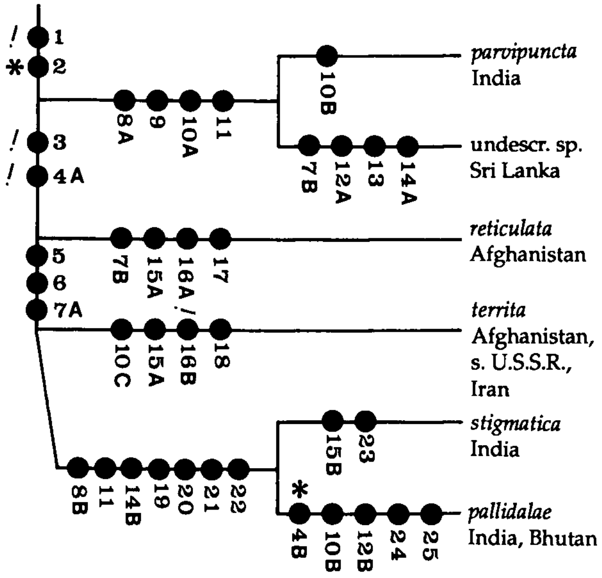


Fig. 56, cladogram of *Phragmacossia*.

Section 1

The species of section 1 are characterized by the following apomorphies: metascutum medially very narrow, mesomeron at least twice as wide as eucoxa II, I-epiphysis reaching little short of or nearly as far as tibia-apex, tarsal spines wanting, chorda terminating very closely to anterior M or being more or less coalescent with it, and median arm approx. as wide as Cu2. Distal plate of 4Ax is not anteriorly reduced. In certain genera of section 2 the chorda and anterior M show a similar state, but in these the distal plate of 4Ax is anteriorly reduced, R5 is stalked with R4 for more than half its length, the radial plate is elongate and the aculeate area at the mesepimeron is wanting.

Section 1 is considered the sister-group of *Phragmacossia*, since they share the following apomorphies: metascutum medially distinctly invaginated and narrow or very narrow, and ♀ abdomen longer than hindwing. In certain species of these taxa the ♀ abdomen is approx. as long as hindwing, which is presumably a reversal. The species of section 1 differ especially from those of *Phragmacossia* in that the chorda terminates very closely to or is partly coalescent with anterior M.

This group has many undescribed species from Madagascar. The naming of these species and of new genera is left to Dr. J. Minet (MNHN), who will investigate the Madagascaran material including their genitalia.

Genus **Eburgemellus** gen. nov.

Type species: *Xyleutes geminatus* Gaede, 1930: 546.

Etymology: "ebur" (Latin) means ivory + "gemellus" (Latin) means double. Gender: masculine.

The new genus *Eburgemellus* is established for *geminatus*. It is a large and easy recognizable species. It has formerly been placed in *Xyleutes* Hübner, [1820] 1816. In this study *Xyleutes* is restricted to three species with the ♀ I-epiphysis short, the fringes very short, the 4Ax antero-distally invaginated, and the humeral plate approx. 2.5 to 3 times size of the radial bridge. See further under *Xyleutes*. In the examined specimen of *geminatus* the chorda is partly coalescent with anterior M. The species shows the following other characteristics: second segment of labial palpi proximally narrowed, metascutum medially very narrow, mesepimeron moderately high, mesomeron approx. twice width of eucoxa II, I-epiphysis reaching little short of tibia-apex, stout spines on tarsi wanting, paronychia wanting, arolium minute, fringes moderately short, and median arm moderately long. The accessory plate II is nearly moderately narrow in the specimen examined. R5 is stalked with R4 for approx. half its length. Rs-M1 is moderately long. 1Ax is apically rather large. The species differs from other species of section 1 in that e.g. the anal plate is rather long. See also fig. 60.

Because this species apparently does not fit in any available genus, a new genus is established for it.

Xyleutes geminatus Gaede, 1930: 546.

Material. —1♂, IVORY COAST: Azaguié (MNHN).

Note. The type is from Cameroon.

Genus **Oreocossus** Aurivillius, 1910

Oreocossus Aurivillius, 1910: 50, 52 (key).
Type species: *Duomitus kilimanjarensis* Holland, 1892: 94.

For long only two species were included in *Oreocossus*. Rougeot (1977: 17-18) describes a third species, *ungemachi*. Rougeot considers *O. kilimanjarensis* synonymous with *O. occidentalis* Strand, 1913. The present author doubts if *kilimanjarensis* and *occidentalis* actually are one and the same species, and these are therefore kept tentatively separate.

The three species share the following apomorphies: tarsal spines wanting, chorda terminating very closely to anterior M or more or less coalescent with the latter, and anal plate moderately long. *O. kilimanjarensis* and *occidentalis* have further the following apomorphies: Apc terminating on K to distinctly dorsally to K, mesepimeron moderately high, mesomeron approx. twice width of eucoxa II, I-epiphysis reaching nearly as far as tibia-apex, and scale plate little to distinctly shorter than radial bridge. It seems that *Oreocossus* is the first taxon of section 1 in which the anal plate is only moderately long (see fig. 60).

Vertex of *kilimanjarensis* has a nearly straight Pos at approx. 0.8 times its length and lacks perhaps sometimes anterior protuberances. Female antenna is bipectinate for approx. 0.7 times its length, up to moderately. In at least *ungemachi* ♀ antenna is unequally bipectinate; anterior row of rami up to moderately shortly and posterior row up to moderately. Antenna is distally moderately strongly prismatic and in female prismatic segments have ventrally one stout sensillum. Lower suture of Apc reaches up to one-third length of An. Intersclerite III is complete or wanting, and in latter case metameron with a more or less distinct membranous split. Tarsus I has a few rather long scales in at least *kilimanjarensis* and *occidentalis*. Number of ♀ frenulum bristles amounts 4 to 6 and these are moderately to rather long. Dorsum of hindwing is not invaginated. Venation: R1 from areole; R3 connate or usually very shortly stalked with R4+5; R4 and R5 shortly stalked; M1 from areole; chorda usually terminating very closely to anterior M and sometimes shortly coalescent with it; in *kilimanjarensis* sometimes a cross-vein Sc-Rs; Rs-M1 long; M2, M3 very close to connate. Humeral plate of at least *kilimanjarensis* and *occidentalis* is approx. as large as radial bridge. 2Ax has sometimes/often a hardly elevated, scaled area (fig. 68). Median plate is at least sometimes reduced in length.

Duomitus kilimanjarensis Holland, 1892: 94.
Material. —1♂, ETHIOPIA: province Sidamo, Borana (ITZ); long series of both sexes from central Ethiopia, Kenya and Tanzania (-6000 ft.) (BMNH).
Note. Rougeot (1977: 17) treats this species as a form or subspecies of the following one.

Oreocossus occidentalis Strand, 1912: 35.
Material. —long series of both sexes from Zaire, Uganda, Kenya (-8000 ft.), Tanzania, Malawi and Mozambique (BMNH).

Oreocossus ungemachi Rougeot, 1977: 17-18, pl. 2: fig. 5.
Material. —1♀, ETHIOPIA: Ioubdo (Birbir), xi.1926, Gen. slide no. Rougeot 661 (MNHN).

An undescribed species from Madagascar and *Phragmataecia grandis* Viette, 1951 have the apomorphies no.'s 1-8a in fig. 60. The second segment of the labial palpi of *grandis* is shorter than the first one. In *grandis* the lower suture of Apc reaches up to from 0.7 to 0. 8 times length of An, and in the undescribed species up to 0.8 times. This is less far than in *Phragmataecia* and *Zeuzeropecten* Gaede, 1930. *P. grandis* does not show the characteristics of *Phragmataecia*. It is also much larger than the species of the latter. Both *grandis* and the undescribed species seem to take separate places in the cladogram of section 1 (see fig. 60). Thus they should most probably be placed in new genera.

The undescribed species has only moderately long fringes. It is much smaller than *grandis*, which has a very different colour pattern. This species should probably also be placed in a new genus.

Only the female of *grandis* is known. Female antenna of *grandis* is completely and unequally bipectinate; anterior row of rami up to moderately shortly and posterior one slightly shorter. The rami have one stout sensillum at apex. Male antenna of the undescribed species is bipectinate for approx. 0.6 times its length and further strongly prismatic. The prismatic segments have one stout sensillum ventrally. Tegula of *grandis* is ventro-posteriorly bluntly pointed and moderately upturned. Subalare-process II of *grandis* is short. Accessory plate II of *grandis* varies from wide to narrow. Vestiture on tibiae II and III is short. Number of ♀ frenulum bristles of *grandis* varies from five to seven and these are rather long. Venation of *grandis*: R4+5 shortly stalked; Rs-M1 long. Venation of undescribed species: R3, R4+5 very shortly stalked; R4+5 shortly stalked; Rs-M1 rather long.

Undescribed species

Material. —1♂, MADAGASCAR: near Perinet, forest of Analamazoatra, 910 m. (MNHN).

Phragmataecia grandis Viette, 1951a: 137-138, pl. 3: fig. 9 (female), fig. (female genitalia).

Material (all MNHN). —1♀ (holotype), MADAGASCAR: east coast, Gen. slide ♀ no. 2307; 5♀♀, east MADAGASCAR.

Genus **Phragmataecia** Newman, 1850

Phragmataecia Newman, 1850: 2931.

Type species: *Phalaena (Bombyx) arundinis* Hübner, [1802-1808]: pl. 48: figs. 200-201. [Synonymized with *Phalaena (Bombyx) castaneae* Hübner, 1790 by Hampson, 1892: 313].

Macrogaster Duponchel, [1845] 1844: 81. [Junior homonym of *Macrogaster* Thunberg, 1805].

Type species: *Phalaena (Bombyx) arundinis* Hübner, [1802-1808]: pl. 48: figs. 200-201.

? *Phragmatoecioides* Strand, 1914: 103.

Type species: *Phragmatoecioides pectinicornis* Strand, 1914: 103.

? *Synaptophleps* Hering, 1923: 15.

Type species: *Synaptophleps pelostema* Hering, 1923: 15.

The genus is well-known, particularly by the occurrence of *castaneae* in Europe. Other species occur in Africa and Asia. Most species are medium-sized and very brownish, and have a striate or reticulate fuscous pattern on the forewing. The lower suture of Apc reaches up to approx. 0.8 times length of An. The metascutum is more or less abruptly narrowed laterally. The tegula is ventro-posteriorly very blunt to (nearly) rounded. The mesepimeron is moderately high with a rounded upper margin. The subalare-process II is very short and blunt. See also the apomorphies no.'s 1-9 in fig. 60.

Zeuzera boisduvalii Herrich-Schäffer, [1854], of which the forewings are spotted, is here included in *Phragmataecia*. In this species and certain others the labial palpi are still three-segmented. In most species the labial palpi are two-segmented, and in a few these have only one segment.

Vertex of at least *castaneae* and *boisduvalii* is gradually elevated and has Pos at 0.5 or 0.7 times its length. Antenna is bipectinate for 0.5 to 0.8 times its length, in female varying from very shortly to moderately. In most or all species rest of antenna is in male strongly prismatic, while in female shortly. Sections of thorax of *castaneae* are shown in fig. 58. K is moderately to rather long, and has often/usually a cross-suture. Intersclerite III appears to be normally wanting. In *boisduvalii* I-epiphysis reaches still nearly as far as tibia-apex, but in many species it is shortened. Vestiture of tarsi is in many species short. Arolium is sometimes/often reduced in certain species. In *boisduvalii* fringes are shortened to moderately long. Venation (see also fig. 92): R1 from areole; R3, R4+5 connate to very shortly stalked; R4+5 shortly stalked; M1 from areole; Rs-M1 moderately long to long; M2, M3 usually very close and occasionally shortly stalked. Wing bases of *castaneae* are shown in fig. 59. Humeral plate is approx. as large as radial bridge. 2Ax is with or without an elevated scaled area.

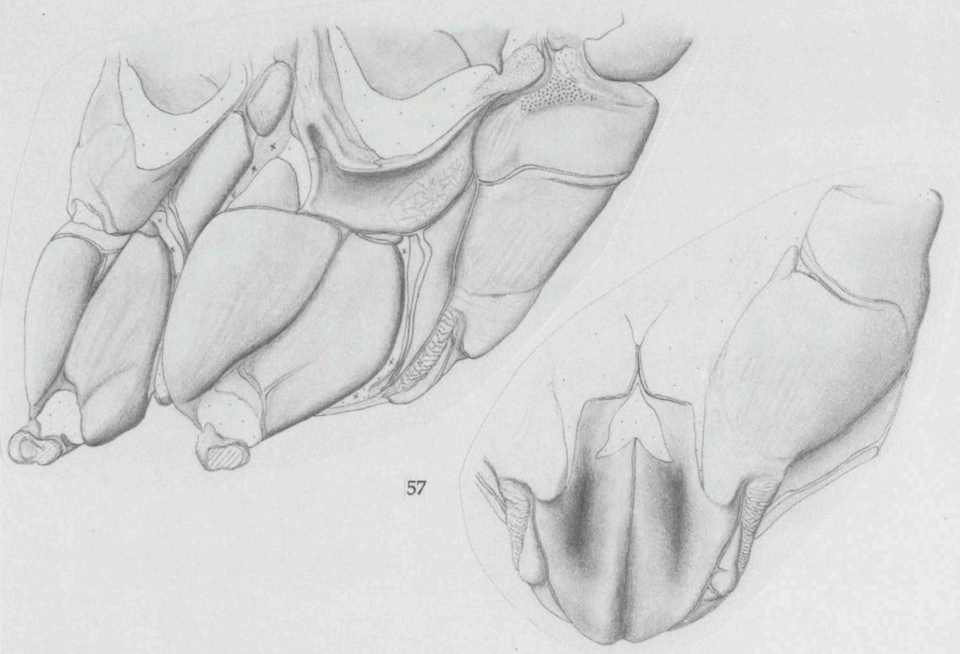
It seems impossible to produce a cladogram of the species on the basis of the external morphology, since there is too little interspecific variation amongst them. Besides certain characters, such as reduction of vestiture or labial palpi, often vary intraspecifically.

Phragmatoecites has so far known only been used by Oppenheim (1885: 333, pl. 10: fig. 3) for a fossil without the statement that it is a new genus. Oppenheim figures the fossil and notes that the hindwing venation of *Phragmatoecites damesi* Oppenheim closely resembles that of *Phragmatoecia*, an incorrect subsequent spelling of *Phragmataecia*. The venation of *damesi* is quite different from that of cossid species. *P. damesi* has been transferred to the Homoptera.

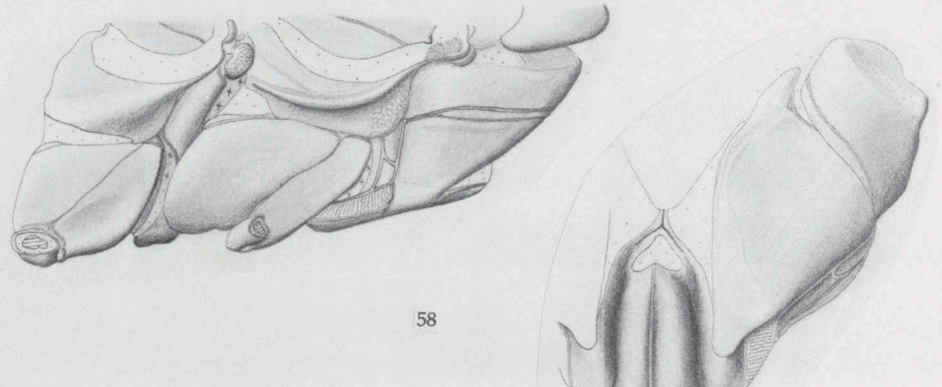
Phragmatoecioides is perhaps synonymous with *Phragmataecia*. Strand (1914: 103) notes that *pectinicornis* looks like a *Phragmataecia* species. Strand gives as a single characteristic distinguishing *pectinicornis* from species of *Phragmataecia* that the areole is absent. Perhaps the chorda is not wanting but more or less coalescent with the anterior M, which is normally the case in *Phragmataecia*. Gaede (1930: 548) notes that *pectinicornis* may be synonymous with *Phragmataecia pelostema* (Hering, 1923). Therefore *Phragmatoecioides* is tentatively placed as a synonym of *Phragmataecia* with a question mark.

Rhizona is noted by Herrich-Schäffer as a genus-name given by Boisduval and synonymous with *Phragmataecia*.

No material of *Synaptophleps pelostema* Hering was available. Judging from the figure given by Seitz (1930: pl. 80: fig. row d), it concerns a *Phragmataecia* species and Gaede (1930: 548) treats it like this. In the original description of *Synaptophleps* by Hering (1923: 15), the single characteristic given which differs from those in *Phragmataecia* is a cross-vein Sc-Rs. Hering (1923: 15) included *boisduvalii* in *Synaptophleps*. In the latter such a cross-vein is wanting. The presence of a cross-vein is here considered insufficient to warrant a separate genus, and therefore *Synaptophleps* is tentatively placed as a synonym of *Phragmataecia*.



57



58

Figs. 57-58, sections of thoraces of zeuzerine species. 57, *Phragmacossia reticulata*, locality unknown; 58, *Phragmataecia castaneae*, Netherlands, Weerribben.

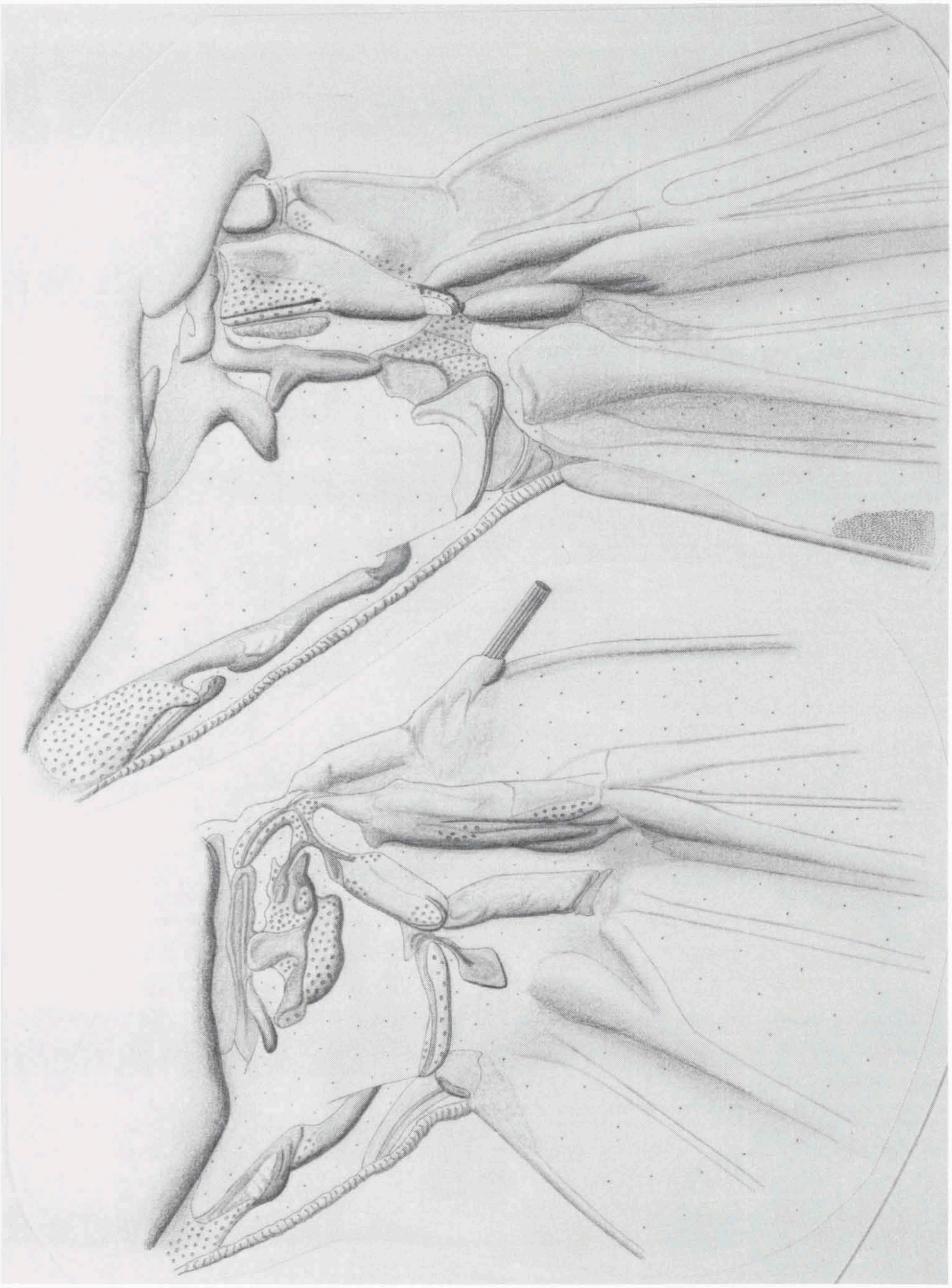


Fig. 59, wing bases of *Phragmataecia castaneae*, locality unknown.

No material of *P. capucina* Wallengrén, 1860 (Australia), *P. albicans* Walker, 1856 (Brazil), *P. testacea* Walker, 1856 (Brazil) and *P. rubescens* Walker, 1856 (Brazil) was here available, but these species presumably belong to other genera, because of their distribution. *P. impedita* Wallengrén, 1860 from South America has been synonymized with *Morpheis strigillatus* (Felder, 1874) by Gaede (1933b: 822).

No material of *P. terebrifer* Fletcher and *P. dudgeoni* Arora was available. According to Arora (1976: 82-85, 88-91) the chorda of these species does not terminate very closely to anterior M and the species closely resemble superficially *Phragmacossia parvipuncta*. It is here not certain, but these two species probably belong to *Phragmacossia*.

Zeuzera boisduvalii Herrich-Schäffer, [1854] 1850-1858: 58, fig. 167.

Material. —1♂ (holotype), SIERRA LEONE: Gatam (MNHN); long series of both sexes from Senegal, Ivory Coast, Sierra Leone, Nigeria, Uganda, Zimbabwe, Malawi and Sudan (BMNH).

Phragmataecia itremo Viette, 1974: 212-213.

Material. —1♂, MADAGASCAR: central massif of Itrema, 1615 m. (MNHN).

Azygophleps psyche Le Cerf, 1919a: 28-29.

Material. —1♂ (holotype), 1♀ (paratype), DAHOMEY: Plain of Zaguanado and Ketou, Forest of Hollis, d'Adia-Ouéré Illéman, 1910 (Ducorps) (MNHN).

Xyleutes gyldenstolpei Aurivillius, 1925: 20, fig. (male).

Not examined. From Zaire.

Note. The colour pattern of this species is quite different from that of the other species and it is not certain whether it actually belongs to this genus.

Phragmataecia brunni Pagenstecher, 1892: 245.

Not examined. From Tanzania.

Phragmatoecia irrorata Hampson, 1910a: 128.

Material (all BMNH). —1♂ (holotype), ZIMBABWE: Mashonaland (Dobbie); 1♂, ZIMBABWE: Mashonaland; few specimens from Zimbabwe and South Africa.

Phragmataecia pallens Herrich-Schäffer, [1854] 1850-1858: 58, fig. 169.

Material. —1♀ (holotype), Guinea (ex musaeo Boisduval) (MNHN); long series from Sierra Leone, Nigeria and Uganda (BMNH).

Note. The larva mines in roots of *Pennisetum purpureum* in Uganda (Le Pelley, 1959: 73).

Phragmatoecia fuscifusa Hampson, 1910a: 128.

Material. —1♂ (syntype), W. Africa (Dudgeon) (BMNH); 1♀ (syntype), SIERRA LEONE: i.1909 (Dudgeon) (BMNH).

Phragmatoecia sericeata Hampson, 1910a: 129.

Material (all BMNH). —1♂ (holotype), NIGERIA: Vivet, v.1906 (Dudgeon); long series from Ghana and Nigeria.

Synaptophleps pelostema Hering, 1923: 15.

Not examined. From Togo, Cameroon and Nigeria.

Phragmatoecioides pectinicornis Strand, 1914: 103.

Not examined. From Egypt/Sudan.

Phragmataecia andarana Clench, 1959a: 9-10.

Not examined. From Namibia.

Phragmataecia okovangae Clench, 1959a: 10-11.

Not examined. From Namibia.

Phragmataecia innominata Dalla Torre, 1923: 47.

Phragmatoecia reticulata Hampson, 1910a: 128-129. [Synonymized by Gaede, 1930: 548].

Material (all BMNH). —1♂ (holotype of *reticulata*), SOUTH AFRICA: Natal, Mooi River; 1♀, MOZAMBIQUE: Port E. Africa, east of Mt. Chiperone, 2200 ft.; 1♂, 1♀, MALAWI: Mt. Mlanje.

Phalaena (Bombyx) castaneae Hübner, 1790: 9. [The Reed Leopard].

Phalaena (Bombyx) arundinis Hübner, [1802-1808]: pl. 48: figs. 200-201. [Synonymized by

Hampson, 1892: 213].

Zeuzera innotata Walker, 1865: 587. [Synonymized by Hampson, 1892: 313].

Phragmataecia minor Moore, 1879: 87. [Synonymized by Hampson, 1892: 313].

Phragmataecia saccharum Moore, 1879: 87. [Synonymized by Hampson, 1892: 313].

Phragmataecia pygmaea Graeser, 1888: 119 [Synonymized by von Dalla Torre, 1923: 47].

Phragmataecia furia Grum-Grshimailo, 1890: 542, pl. 20: fig. 4. [Synonymized by Daniel, 1964: 7].

Phragmataecia minima Hampson, 1891: 66, pl. 144: fig. 14. [Synonymized by Hampson, 1892: 313].

Material. —very long series of both sexes from many localities in Europe, and further from Israel and U.S.S.R. (Turkmeniya and Vladivostok) (BMNH).

Note. Hosts are *Phragmites australis* (Cav.) and *Saccharum spontaneum* L. Skinner (1985: 70) provides a map of distribution in Great Britain. Inoue (1982: 61) records the species also from Japan.

Phragmataecia purpureus Fletcher, 1926-1927: 58, pl. 1: fig 1.

Not examined. From India.

Note. Hosts are *Andrapogon sorghum* Brot. (= Jowar), *Erianthus arundinaceus* Jeswiet (= *Saccharum arundinaceum* Retz) (roots), *Saccharum spontaneum*, Maize and Jowar (Arora, 1976: 77).

Phragmataecia cinnamomea Wileman, 1911: 151.

Material. —10 (including holotype), TAIWAN: Formosa (BMNH).

Phragmataecia fusca Wileman, 1911: 151.

Not examined. From Taiwan (Kanshirei, 1000 ft.).

Phragmataecia obscura Wileman, 1911: 151.

Not examined. From Taiwan (Kanshirei, 1000 ft.).

Phragmataecia hansi Strand, 1915: 41.

Not examined, From Taiwan.

Note. It is obscure whether this is a good species, as with the other species from Taiwan. Gaede (1933b: 821) notes *hansi* under *castaneae*, but the present author doubts that the two species are synonymous.

Phragmataecta longivittata Candèze, 1926-1927: 122.

Not examined. From Laos.

Phragmataecia impura Hampson, 1891: 66. pl. 144: fig. 7.

Material. —1♀ (holotype), INDIA: Nilgiris (BMNH); series from Sri Lanka, Thailand and Malaysia (BMNH); series from Indonesia (Sumatra and Java) (RMNH).

Note. It is not certain if the southeast Asian material actually concerns *impura*.

Phragmataecia sumatrensis Snellen, 1892: 29-30.

Material (all RMNH). —1♂ (holotype), INDONESIA: Sumatra; long series from Indonesia (mostly Sumatra and further Java).

Note. Gaede (1933b: 822) includes this species under *castaneae*.

Phragmataecia gummata Swinhoe, 1892: 285, pl. 8: fig. 14 (male).

Phragmataecia lata Snellen, 1895: 134-135. [Synonymized by Roepke, 1957: 40].

Phragmataecia sordida Snellen, 1900: 44. [Synonymized by Roepke, 1957: 40].

Material. —long series from Indonesia (Sumatra and Java) (RMNH).

Note. Both in *sumatrensis* and *gummata* the labial palpi may be two- or three-segmented.

Phragmataecia roborowskii Alphéraky, 1897: 235.

Material. —2♂♂, Kai Hi area (BMNH).

Note. The antenna is bipectinate for 0.8 times its length.

Phragmatoecia albida Erschoff, 1874: 34. [Established as a variation of *castaneae*].

Material. —long series from U.S.S.R. (Transcaspia) and Afghanistan (BMNH).

Note. The antenna is bipectinate for 0.7 times its length. Two examined males from Tekke (NMW) are not conspecific with the material of the BMNH and do not belong to *Phragmataecia*. These two specimens may concern *Phragmacossia territa*. It is here uncertain if the subspecies *minos* Reisser (1962: 200-208, fig. 7 (male genitalia), pl. 22: figs. 19-22) really concerns *albida*.

Phragmataecia erschoffi Reisser, 1962: 204, fig. 9 (male genitalia), pl. 22: fig. 26.

Not examined. From Crete.

Phragmataecia furiosa Sheljuzhko, 1943: 84-85, pl. 7: figs. 16-17.

Not examined.

Phragmataecia hummeli Bryk, 1942: 153.
Not examined. From China.

Genus **Zeuzeropecten** Gaede, 1930

Zeuzeropecten Gaede, 1930: 547.
Type species: *Zeuzeropecten lactescens* Gaede, 1930: 548.

So far only *lactescens* has been included in *Zeuzeropecten*. A number of species which had previously been placed in *Duomitus* Butler, 1880 are here added to *Zeuzeropecten*. In this paper *Duomitus* is restricted to one species of which the rami of the ♂ antenna are approx. in one plane, the ♀ antenna is simple, and 4Ax is antero-distally invaginated.

Zeuzeropecten is a group of species with the lower suture of Apc up to approx. 0.8 times length of An and occasionally over complete length of An. This is also the case in *Phragmataecia*. Only in one undescribed species of *Zeuzeropecten* the lower suture of Apc reaches up to from 0.7 to 0.8 times length of An. The subalare-process II in *Zeuzeropecten* is only short, whereas in *Phragmataecia* very short. In *Zeuzeropecten* the metascutum is laterally not abruptly narrowed. The distal two-fifths to one-fourth of the male antenna is rather strongly prismatic, although Gaede (1930: 547-548) erroneously notes shortly. The genus is furthermore characterized by the following apomorphies: labial palpi when three-segmented second segment shorter than first one, mesomeron at least twice width of eucoxa II, chorda normally partly coalescent with anterior M, tarsal spines wanting, median arm rather wide, and anal plate moderately long. The humeral plate of at least *lactescens* and *castaneum* (Kenrick, 1913) is as large as the radial bridge. The species are moderately large to large. It seems impossible to define the genus more accurately on the basis of the external morphology. There are in the MNHN at least 9 undescribed species from Madagascar which should be placed in this genus.

Vertex of *occultoides* (Kenrick, 1913) and *combustum* (Kenrick, 1913) is moderately transversely ridged, lacks anterior protuberances but has very small pits instead, and has Pos at approx. 0.8 times its length. Antenna is bipectinate for 0.5 times (e.g. in *castaneum*) to 0.7 times (in *lactescens* and *argillosum* (Le Cerf, 1979)) or 0.8 times (in undescribed species) its length. In *castaneum* the second segment of labial palpi is very short and seems to be thickened, while the first one is lengthened. In *combustum* and two undescribed species labial palpi are only two-segmented. Metameron of *lactescens* is nearly moderately wide. In *lactescens* and two undescribed species I-epiphysis reaches distinctly short of tibia-apex, which is presumably a reversal. In *castaneum* and an undescribed species fringes are only moderately long. Number of ♀ frenulum bristles varies in one undescribed species from five to seven and is in another approx. eight. There are sometimes/often shorter frenulum bristles in between. Dorsum of hindwing is hardly or not invaginated. Venation: R1 from areole; R3, R4+5 connate to very shortly stalked; R4+5 stalked for 0.3 to 0.5 times their length; M1 from areole; Rs-M1 rather long to long; M2, M3 (moderately) shortly separate. Median arm of *castaneum* is rather long. 2Ax has sometimes/often an elevated scaled area (fig. 68). Median plate is often/usually reduced in length, and is sometimes/often wanting in *lactescens*.

The named species of this genus are listed here below.

Zeuzeropecten lactescens Gaede, 1930: 548.
Material (all MADAGASCAR and BMNH). —1♂ (holotype), west of Mahonoro, Ambinanindrano, 12.v (Kestell-Cownish); 1♂, Ambinanindrano; 4♂♂, Tananarivo; 1♂, station Perinet; 1♀, Diego Suarez.

Phragmataecia argillosa Le Cerf, 1919d: 161.
Material. —1♂ (holotype), MADAGASCAR: Tananarive, 1916 (Waterlot), Gen. slide no. Viette ♂ 915 (MNHN).

Duomitus combustus Kenrick, 1913: 589. (plate 1: fig. G)
Material (all MADAGASCAR). —1♂ (holotype), 4♂♂, central Madagascar, 2500 ft., i-iii.1911 (Pratt) (BMNH); 10♂♂, various localities (BMNH); 4♂♂, near Moramanga, forest of Sandrangato (RMNH).

Duomitus castaneus Kenrick, 1913: 589.
Azygophleps hova Le Cerf, 1919a: 28. [Synonymized by Viette, 1951a: 134].
Material (all MADAGASCAR). —1♂ (holotype of *castaneus*), 4♂♂, central Madagascar, 2500 ft., i-iii.1911 (Pratt) (BMNH); 1♂ (holotype of *hova*), forest of Perinet, 1915, Gen. slide Viette ♂ no. 911 (MNHN); 1♀, Tananarive (BMNH).

Duomitus occultoides Kenrick, 1913: 589.
Material (all MADAGASCAR and BMNH). —1♂ (holotype), central Madagascar, 2500 ft., i-iii.1911 (Pratt); 2♂♂, east of Tananarive, station Perinet.

Duomitus lecerfi Viette, 1957: 102-104, fig. 3 (male genitalia).
Material (all MADAGASCAR). —1♂ (holotype), 3♂♂ (paratypes), Ampalomita, east Belanitra (Griveaud) (MNHN); long series from various localities (MNHN); 1♂, Ampalomita, east Belanitra (BMNH).

Duomitus altitudinis Viette, 1957: 104-105.
Material. —1♂ (holotype), 1♂ (paratype), MADAGASCAR: Massif de l'Ankaratra, Manjakamtompo, forest of Ambahano, 1850 m., 20/ 21.ii.1952 (Viette) (MNHN).

Table 10. Apomorphies in fig. 60 (section 1).

---

1. Mesomeron 2 to/or 2.5 times width of eucoxa II.
2. I-epiphysis reaching little short of or nearly as far as tibia-apex. (*)
3. Tarsal spines wanting.
4a. Chorda terminating very closely to anterior M or more or less coalescent with the latter.
b. Chorda often or normally partly coalescent with anterior M.
5. Scale plate approx. as long as radial bridge.
6. Median arm rather wide, approx. as wide as Cu2.
7. Anal plate moderately long.
8a. Lower suture of Apc up to from 0.7 to 0.8 times length of An.
b. Lower suture of Apc up to from 0.8 to 0.9 times length of An and narrow to moderately narrow.
9. Labial palpi, when three-segmented: second segment at most as long as first.
10. Mesepimeron moderately high.
11. Paronychia wanting.
12. Arolium minute.
13a. Fringes moderately short.
b. Fringes moderately long.
14. Female abdomen approx. as long as hindwing. N.B. In certain species of section 1 this couldnot be examined, since no females were available.
15. Metascutellum transversely only rather long to short, abruptly narrowed laterally and continu-

ing as a narrow rim.
16. Tegula ventro-posteriorly very blunt or (nearly) rounded.
17. Subalare-process II very short and blunt.

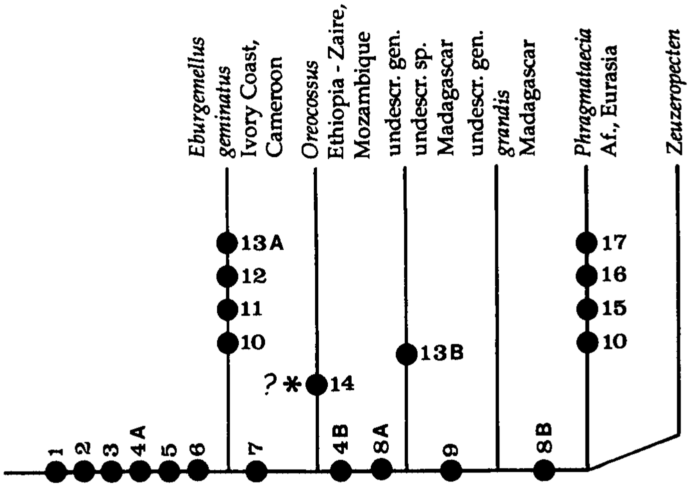


Fig. 60, cladogram of section 1 (Zeuzerinae).

Section 2

The species of section 2 have a more or less antero-distally reduced 4Ax; the distal plate of 4Ax is anteriorly reduced or invaginated (see figs. 65 and 74). In *Azygophleps nurella* Swinhoe, 1894, which is placed in a new genus, this reduction may be indistinct. In most species placed further in the cladogram this reduction is distinct. In most species of Cossinae the distal plate of 4Ax is more or less membranous but not anteriorly reduced or invaginated. Many species of section 2 are known to have a distinctly invaginated metascutum, but this has not been examined in many others.

For convenience, section 2 is split into several parts (see fig. 55b).

Genus **Relluna** gen. nov.

Type species: *Azygophleps nurella* Swinhoe, 1894: 440.

Etymology: an anagram of the species-name *nurella*. Gender: feminine.

Relluna nurella had formerly been placed in *Azygophleps* Hampson, 1892. The species differs from actual *Azygophleps* species in e.g. that the 4Ax is more or less reduced antero-distally. It differs from species of *Endoxyla* Herrich-Schäffer, [1853] and *Sympycnodes* Turner, 1932 in that the anal plate is still rather long, the ♂ antenna is only moderately bipectinate, and the median arm has the anterior invagination up to from $^1/_3$ to $^1/_4$ its length. The ♂ antenna is bipectinate for approx. half its length.

The labial palpi are two-segmented. In *Endoxyla* paronychia are wanting, and in *Sympycnodes* these are minute to wanting. In *Sympycnodes* the tarsomeres are slightly to hardly widened apically, whereas in *nurella* these are distinctly widened distally. See also figs. 55 and 62.

Lower suture of Apc reaches up to approx. 0.3 times length of An. Mesepimeron is rather low. Tarsi have long vestiture. I-epiphysis reaches distinctly short of tibia-apex. Arolium and paronychia are well-developed.

Venation: R1 from areole; R2, R3 may be shortly stalked; R3, R4+5 very shortly stalked; R4+5 shortly stalked; M1 from chorda or posteriorly to it; M2, M3 very close to connate; costa of hindwing gradually curved; Rs-M1 moderately long; M2, M3 well separate. Humeral plate is approx. 1.3 times size of radial bridge and more or less ovate in shape. Head of 1Ax is rather large. Median plate is often narrowed but not reduced in length. 2Ax is (normally ?) without elevated scaled area.

Azygophleps nurella Swinhoe, 1894: 440.

Material (all BMNH). —1♂ (holotype), INDIA: Khasi Hills, Cherra, Punji, Gen. slide no. ♂ 97; 1♂, PHILIPPINES: Palawan Plains, Taytay; 2♂♂, Borneo.

Genus **Endoxyla** Herrich-Schäffer, [1854] 1850-1858

Endoxyla Herrich-Schäffer, [1854] 1850-1858: 7.

Type species: *Endoxyla durvilli* Herrich-Schäffer, [1854] 1850-1858: 7, figs. 163-164.

Xyrena Herrich-Schäffer, [1854] 1850-1858: pl. 34: fig. 162. **Syn. nov.**

Type species: *Xyrena casuarinae* Herrich-Schäffer, [1854] 1850-1858: pl. 34: fig. 162. [Junior subjective synonym of *Cossus lituratus* Donovan, 1805: pl. [37]: fig. ** (female)].

Cossimorphus Houlbert, 1916: 76, 105, 107. **Syn. nov.**

Type species: *Cossus edwardsi* Tepper, 1891: 63, pl. 1.

Dictyocossus Houlbert, 1916: 77, 105, 108. **Syn. nov.**

Type species: *Xyleutes phaeocosma* Turner, 1911: 130-131.

Melanocossus Houlbert, 1916: 77, 105, 111. **Syn. nov.**

Type species: *Cossus tenebrifer* Walker, 1865: 585.

The genus-names listed above were treated as synonyms of *Xyleutes* by Gaede (1933b) and Turner (1945), and actually synonymized by Roepke (1957: 18). The genus *Endoxyla* is here resurrected. Probably all species (over fifty) listed by Turner under *Xyleutes* belong to *Endoxyla*. Oberthür (1916) treats the species also under *Xyleutes* and provides many figures. In this study *Xyleutes* is restricted to a few species from southern and southeast Asia with a short ♀ I-epiphysis, very short fringes, a humeral plate approx. 2.5 to 3 times size of the radial bridge, and a radial plate elongate with a rather slender apex. See further under *Xyleutes* and figs. 55 and 62. Reference should be made to Turner (1945) for a list of species and their synonyms.

It is difficult to define the genus. The species range in wingspan from approx. 30 to 230 mm (Common, 1970: 797). In many species the female is normally distinctly larger than the male. The distal plate of 4Ax is anteriorly reduced or invaginated. The anal plate is moderately long. Paronychia are wanting. Most other characters seemingly show a plesiomorphic state. The humeral plate seems to be in most species 1.3 to 1.5 times size of the radial bridge. All but two species occur in Australia.

There seems to be little interspecific variation in *Endoxyla*. One remarkable development is the shortening and narrowing of the ♀ I-epiphysis. In e.g. *durvilli* the ♀ I-epiphysis is bluntly pointed and in e.g. *edwardsi, pulchra* (Rothschild, 1896) and *boisduvali* (Rothschild, 1896) it has become sharply pointed. Species such as *tigrina* (Herrich-Schäffer, [1854]) and *vittata* (Walker, 1856) still have long fringes and an intersclerite III. In most species the fringes are moderately long or shorter. In an unidentified species close to *tigrina* the ♀ antenna is still proximally (shortly) bipectinate. In *tigrina* and e.g. *opposita* (Walker, 1865) this structure has become proximally bilobed, and as a further development it becomes proximally simple. In the plesiomorphic state the antenna is bipectinate or bilobed for 0.7 times its length and further shortly prismatic. In many species it has become for only 0.5 or 0.6 times length of antenna bipectinate, bilobed or simple. It may be that in e.g. *durvilli* it has become secondarily again a ratio of 0.7 to 0.3.

In most species the tip of the ♀ abdomen is enlarged and conspicuous, often with a different colour of vestiture than the rest of the abdomen.

Only in a few species, e.g. *phaeocosma*, the fifth tarsomere is longer than fourth. General trends amongst the species appear to be: shortening of fringes, reduction to disappearance of arolium, shortening of vestiture on tibiae II and III, lengthening of cross-vein Rs-M1, lengthening of Apc with two sutures, and heightening of mesepimeron.

McCoy (1879: 47-50, pl. 30) provides a description of a species, which he identified as belonging to *Zeuzera* (*Endoxyla*) *eucalypti* (Herrich-Schäffer, [1854]). The author of this paper doubts that the species figured by McCoy actually concerns *eucalypti*, a synonym of *durvilli*, since the colour pattern seems to differ from that figured by Herrich-Schäffer ([1854] 1850-1858: figs. 163-164). McCoy names the species the Wattle Goat-Moth, as its larvae would feed exclusively in Wattle (a species of *Acacia* Mill.), a plant of economic importance. McCoy describes and figures the various life-stages. The female of the Wattle Goat-Moth would produce millions of eggs, which is probably exaggerated. Fereday (1876: 460) notes that he found thousands of eggs in the abdomen of a specimen which probably belongs to an *Endoxyla* species. Common (1970: 797) states that the number of eggs deposited by a single female of *durvilli* exceeded 18.000, and that the mass of eggs is covered with a glutinous secretion. According to Common, the larvae of *durvilli* tunnel in the larger roots of *Acacia*, and those of many other species, such as *boisduvali* and *affinis* (Rothschild, 1896), bore singly in the trunk of *Eucalyptus* L'Hérit. The larvae of *leucomochla* (Turner) would tunnel in the soil feeding externally on the roots of *Acacia ligulata* A. Cunn. (Common, 1970: 798), a junior synonym of *Acacia salicina* Lindl.

The figure given by Seitz (1934: pl. 99: fig. row d) with the name *tigrina* appears to concern a specimen in the MHUB which has been erroneously identified by Gaede as belonging to *Xyleutes plesseni* Schultze, 1925. The figure given by Seitz (1934: pl. 99: fig. row d) with the name *plesseni* apparently concerns *tigrina*.

The genus is represented in Western Australia, South Australia, Northern Territory, Queensland, New South Wales, Tasmania (Turner, 1945) and Sulawesi. The occurrence of few species outside Australia is secondary (by dispersal), judging from their character-states. *E. celebesa* (Walker, 1865) is known from Sulawesi and was once caught on a ship in the Flores Sea, and Gaede (1933: 816) notes also Tonkin. The occasional occurrence in New Zealand of *E. durvilli* (= *eucalypti* Herrich-Schäffer), *E. boisduvali* and perhaps other *Endoxyla* species is due to import of infested timber (Fereday, 1876; Philpott, 1927: 708).

The species mentioned and a few more have been extensively examined, and many others briefly. The author did not succeed in producing a cladogram of the species, since there is too little interspecific variation within this large group. Species such as *tigrina* and *vittata* would probably take the lowest branches in a cladogram. See further the descriptions by Turner (1945).

Genus **Sympycnodes** Turner, 1932

Sympycnodes Turner, 1932: 194-195.
Type species: *Sympycnodes trigonocosma* Turner, 1932: 195.

Turner (1945:48) notes as most important characteristics for this exclusively Australian genus: labial palpi very short and slender, thorax with rounded anterior crest, forewings without inner cell and hindwing with small or no inner cell. However, in an unidentified specimen of a species very close to *rhaptodes* Turner, 1941 there is (still) a well-developed inner cell of the forewing. The labial palpi are two-segmented in all species and are moderately slender in *trigonocosma* and *rhaptodes*. The paronychia are minute or wanting. The lower suture of Apc reaches up to from 0.8 to 1.0 time length of An. Most other characters have a plesiomorphic state. See also fig. 62.

The genus is represented in Queensland and New South Wales (Australia).

Sympycnodes trigonocosma Turner, 1932: 195.
Not examined. From Queensland.
Sympycnodes rhaptodes Turner, 1941: 80.
Material. —8♂♂, AUSTRALIA: Victoria, Red Hill (ITZ).
Undescribed species (a)
Material. —1♀, AUSTRALIA: Morwell (ITZ).
Note. The specimen has in the forewing an inner cell. The species closely resembles superficially *rhaptodes*. It has a rounded dark spot at the cell-margin on the forewing.
Undescribed species (b)
Material. —2♂♂, AUSTRALIA: Red Hill (ITZ).
Note. The species has a rounded dark spot at the cell-margin and one at approx. one-third winglength between CuA and A1+2 on the forewing. The inner cell of the hindwing is sometimes/often wanting.

Notes on some Australian genera

Turner (1945) introduces several new genera for new species. They are monotypic and restricted to Australia. According to Turner the tibial spurs are absent in *Catoxophylla cyanauges* Turner, 1945 and *Brevicyttara cyclospila* (Turner, 1945), and are very short or wanting in *Brephomorpha cineraria* (Turner, 1945). Turner probably means that the midtibial spurs are absent or very short. This would mean that *Catoxophylla* and *Brevicyttara* most probably belong to the Zeuzerinae, but that this is not certain for *Brephomorpha*. No material of these species was available. The genera are tentatively placed in the Zeuzerinae. For biogeographical reasons the present author supposes that these genera are most closely related to *Sympycnodes* and *Endoxyla*. The genera in question are indicated below.

Catoxophylla Turner, 1945: 48.
  Type species: *Catoxophylla cyanauges* Turner, 1945: 49.
Brephomorpha Fletcher, in Fletcher & Nye, 1982: 26. [Objective replacement name for *Nepiomorpha* Turner, 1945].
  Type species: *Nepiomorpha cineraria* Turner, 1945: 63.
  Nepiomorpha Turner, 1945: 63. [Junior homonym of *Nepiomorpha* Pearman, 1936].
Brevicyttara Fletcher, in Fletcher & Nye, 1982: 26. [Objective replacement name for *Brachycyttara* Turner, 1945].
  Type species: *Brachycyttara cyclospila* Turner, 1945: 64.
  Brachycyttara Turner, 1945: 64. [Junior homonym of *Brachycyttara* Turner, 1933 (Noctuidae Latreille, 1809)].

Genus **Hamilcara** Barnes & McDunnough, 1910

Hamilcara Barnes & McDunnough, 1910: 465-466.
  Type species: *Hamilcara atra* Barnes & McDunnough, 1910: 466.

Barnes & McDunnough (1910: 466) include *atra* and the also new *Hamilcara gilensis*. Barnes & McDunnough (1911: 22) add *Zeuzera ramuscula* Dyar, 1906, a junior synonym of *Z. ramosa* Schaus, 1892, to *Hamilcara*. Dyar (1940: 1268) excludes *gilensis* from *Hamilcara* and places it in *Psychonoctua* Grote, 1865. No material of *gilensis* has been examined, but judging from the figure given by Barnes & McDunnough (1911: pl. 4: fig. 3) this species should indeed be placed in *Psychonoctua*.

Barnes & McDunnough (1910) note the following characteristics of *Hamilcara*: palpi minute, ♂ antenna bipectinate in basal half only, and R1 from cell. In both *atra* and *ramosa* the labial palpi are two- or three-segmented and approx. as long as the eye-diameter and thus not minute. In *atra* the ♂ antenna is bipectinate for approx. 0.6 times its length and that of *ramosa* for approx. 0.4 to 0.5 times its length. R1 is indeed proximal to the areole in *atra*, but branches off from the areole in *ramosa*. *Z. ramosa* differs further considerably from *atra*; e.g., ♀ antenna proximally simple, lower suture of Apc reaching up to from 0.5 to 0.8 times length of An, Apc terminating on to distinctly dorsally to K, mesepimeron moderately high, ♀ I-epiphysis shorter and narrower than ♂ one, paronychia wanting, number of ♀ frenulum bristles varying from six to eleven, and humeral plate approx. twice size of radial bridge. *Z. ramosa* seems to take a higher branch in the cladogram (fig. 62) after *Carohamilia* Dyar, 1940. Therefore, *ramosa* is excluded from *Hamilcara*. There thus appears to be only *atra* in *Hamilcara*.

H. atra has furthermore the following apomorphies: male antenna proximally only moderately bipectinate, ♀ antenna very shortly bipectinate for approx. 0.6 times its length, lower suture of Apc reaching up to from one-third to complete length of An, accessory plate II moderately narrow to narrow, I-epiphysis reaching approx. as far as tibia-apex, vestiture of tibiae II and III short, and paronychia minute, distal plate of 4Ax more or less reduced anteriorly, and anal plate moderately long.

Vertex of *atra* is swollen and has an arcuate Pos up to approx. 0.8 times its length. Intersclerite III is present or wanting. Dorsum of hindwing is weakly invaginated. Venation: areole long; R5 very shortly stalked with R4; Rs-M1 short to rather long. 2Ax lacks elevated scaled area.

Hamilcara atra Barnes & McDunnough, 1910: 466.
Material (all BMNH). —8♂♂, 1♀, U.S.A.: Arizona, Pima Co., Babaquivera Mts.; 1♀, U.S.A.: Kny-Scheerer Co.

Genus **Carohamilia** Dyar, 1940

Carohamilia Dyar, 1940: 1269.
Type species: *Lentagena ophelia* Schaus, 1921: 393.

Dyar (1940: 1269) includes *ophelia*, *Zeuzera itys* Druce, 1911 and *Givira lineaeplena* Dognin, 1911 in *Carohamilia*. Dyar notes as a characteristic of *Carohamilia* that the inner cell of the forewing is usually wanting. Furthermore, *ophelia* has a cross-vein distally in between CuP and A1+2 of forewing.

No material of *lineaeplena* was available. Judging from the figures provided by Seitz (1940: pl. 167: fig. row g), *lineaeplena* differs considerably from *ophelia* in colour pattern and most closely resembles

Schreiteriana pectinicornis (Dyar, 1940), which belongs to the Cossulinae. Dyar (1940: 1269) notes that in half of the specimens he examined a cross-vein Sc-Rs is present. Seitz figures the species, indicated as *lineaplena*, with short, completely bipectinate ♂ antennae, which would imply that this species should be excluded from the Zeuzerinae. Perhaps *lineaeplena* should be placed in *Schreiteriana* Fletcher, 1982 or *Givira* Walker, 1856. *Z. itys* differs considerably from *ophelia*; e.g., it has longer labial palpi, has not a cross-vein CuP-A1+2 in the forewing, and its median arm is rather long. The author supposes that *itys* is the sister-group of *Psychonoctua* (see also fig. 62). Therefore *itys* is excluded from *Carohamilia*.

C. ophelia has the following apomorphies: labial palpi short, An moderately low, lower suture of Apc reaching up to from approx. 0.7 to 1.0 time length of An, mesepimeron moderately high, I-epiphysis reaching nearly or approx. as far as tibia-apex, fringes varying from long to moderately long, inner cell of forewing sometimes present but small and often/usually wanting, CuP and A1+2 of forewing distally linked by a cross-vein or shortly coalescent, 1Ax apically large, distal plate of 4Ax anteriorly reduced, median arm rather wide and with anterior invagination up to approx. 1/3 its length, and anal plate moderately long. See also fig. 62.

In *ophelia* vestiture of tarsi is dorsally rather long but shortening apically. Venation: areole long and rather wide in *ophelia*; R3, R4+5 connate to shortly stalked; R4+5 stalked for approx. 0.4 to 0.6 times their length; in *ophelia* cross-vein CuP-A1+2 moderately short to very short, or CuP and A1+2 shortly coalescent; a cross-vein Sc-Rs sometimes/occasionally present in *ophelia*; Sc-Rs often present in *lineaeplena* (Dyar, 1940: 1269); Rs-M1 approx. moderately long in *ophelia*. Humeral plate of *ophelia* is approx. as large as radial bridge. 2Ax is (normally ?) without elevated scaled area.

Lentagena ophelia Schaus, 1921: 393.

Material. —1♂ (possible paratype), GUATEMALA: Cayuga, iii (coll. Schaus and Barnes) (USNM); 2♂♂, MEXICO: Yucatan, Chichen Itza (CMNH); 2♂♂, MEXICO: near Concordia, Sinoloa (CMNH); 1♂, MEXICO: Concordia, Sinaloa (NHMA).

Givira lineaeplena Dognin, 1911: 55.

Not examined. From French Guiana.

Note. This species has a very different colour pattern than *ophelia* and possibly belongs to another genus.

Genus **Aramos** gen. nov.

Type species: *Zeuzera ramosa* Schaus, 1892: 329.

Etymology: "aramos" is an anagram of the species-name *ramosa*. Gender: masculine.

Z. ramosa had been placed in *Hamilcara* by Barnes & McDunnough (1911: 22). This species is excluded from the latter, since it differs too much from the type species of *Hamilcara* and it seems to branch off farther in the cladogram after *Carohamilia*. *A. ramosus* has the following apomorphies: female antenna proximally simple, labial palpi two- or three-segmented, An moderately low, Apc terminating on to distinctly dorsally to K, lower suture of Apc reaching up to from approx. 0.5 to 0.8 times length of An, mesepimeron moderately high, accessory plate II moderately narrow to narrow, ♂ I-epiphysis reaching nearly or approx. as far as tibia-apex, ♀ I-epiphysis distinctly shorter and narrower than ♂ one, paronychia wanting, number of ♀ frenulum bristles varying from six to eleven, humeral plate 1.5 to 2 times size of radial bridge, 1Ax apically large, and anal plate moderately long. See also fig. 62.

A. ramosus shares with *Zeuzera masoni* Schaus, 1894 and *Zeuzera itys* Druce, 1911 that An is moderately low. *Z. masoni* differs from the other two species in e.g. that R1 is proximal to the areole, the I-epiphysis reaches distinctly short of the tibia-apex, and the median arm varies from moderately to rather long. *A. ramosus* and *masoni* differ from *Carohamilia ophelia* in that the humeral plate is larger; approx. 1.5 to 2 times size of the radial bridge. The author supposes that *itys* has a similarly large humeral plate. *A. ramosus* and *masoni* closely resemble each other in colour pattern. *Z. itys* has a different colour pattern than the other two. *Z. itys* has a rather long median arm, and is presumably the sister-group of the latter. *Z. itys* lacks the inner cell of the forewing. However, only one specimen of *itys* has been partially examined, and it may be that there is more intraspecific variation of e.g. median arm and that the mesepimeron is moderately high. Perhaps *itys* should be regarded as the sister-species of *masoni*.

The three species seemingly do not fit in *Psychonoctua*; in the latter the antenna is bipectinate/bilobed for 0.6 to 0.7 times its length, An is low, and the forewing has a special colour pattern. Besides *ramosus* differs further considerably from *Psychonoctua* species. It is not quite certain if the three species form a monophyletic group with *Psychonoctua*, as depicted in the cladogram (fig. 62). The lowering of An seemingly happened on many occasions within the Zeuzerinae and is also known in *Hamilcara atra* and *Carohamilia ophelia*. The presence of this apomorphic state in *ramosus, masoni, itys* and *Psychonoctua* could thus well be due to parallel developments. Perhaps study of the genitalia will provide more evidence of their relationships. The author has chosen to propose a new genus for *ramosa*, and to include tentatively *masoni* and *itys*.

Vertex of *ramosus* is slightly swollen and has nearly straight Pos at approx. 0.7 times its length. Male antenna of *ramosus* is bipectinate up to approx. 0.4 or 0.5 times its length. Male antenna of *masoni* is bipectinate for approx. half its length. Male antenna of *itys* (1 ex.) is bipectinate for approx. 0.6 times its length. Mesomeron of at least *ramosus* varies from 1.5 to 2 times width of eucoxa II. Intersclerite III is (normally ?) wanting. Male I-epiphysis of *ramosus* is bluntly to sharply pointed. Fringes of at least *ramosus* and *masoni* vary from long to moderately long. Venation: areole of at least *ramosus* and *masoni* long and rather wide; R3, R4+5 separate to very shortly stalked; R4+5 stalked for 0.3 to 0.6 times their length in *ramosus*, for approx. 0.4 to 0.5 times in *masoni*, and for approx. 0.5 times in *itys* (1 ex.); M1 from areole in *masoni*; inner cell of *ramosus* sometimes/occasionally wanting; inner cell of *itys* (normally ?) wanting; chorda of *ramosus* terminating sometimes very close to anterior M and occasionally very shortly coalescent with the latter; Rs-M1 short to rather long, but usually moderately long in *ramosus*. Median plate is sometimes/often reduced in length in at least *ramosus*. Anal plate is moderately long.

Zeuzera ramosa Schaus, 1892: 329.
  Zeuzera aeetes Druce, 1901: 436. [Synonymized by Dyar, 1940: 1266].
  Zeuzera ramuscula Dyar, 1906: 200. [Synonymized by Dyar, 1940: 1266].
  Material. —14♂♂, 3♀♀, U.S.A.: Texas (BMNH); 1♂, BRAZIL: Sao Paolo (BMNH); 2♂♂, SURINAM: distr. Marowijne (RMNH).
Zeuzera masoni Schaus, 1894: 235.
  Material (all GUATEMALA and BMNH). —2♂♂, Quirigua (coll. Schaus and Barnes); 1♂, Cayuga; 1♂, Queriflia.
Zeuzera itys Druce, 1911: 291.
  Material. —1♂ (type), COLOMBIA: Jimenea, Rio Dagua, 1600 ft., viii.1907 (coll. Druce) (BMNH).

Genus **Psychonoctua** Grote, 1865

Psychonoctua Grote, 1865: 249-251.
  Type species: *Psychonoctua personalis* Grote, 1865: 251.

Psychonoctua is here resurrected as a genus, after Dyar (1940) had treated it as a subgenus of *Xyleutes*. It is a complex of very similar species from Central America and the Caribbean. Characteristic of the genus is a low An, the antenna bipectinate for 0.6 or/to 0.7 times its length and the fifth tarsomere as long as the fourth. All species have a small dark spot at the distal cell-margin on the forewing. In most species there is proximally for approx. one-third wing-length a dark band anteriorly to CuA, but this is lacking in *benestriata* (Hampson, 1904). The species share with *Aramos itys* that the median arm is rather long, but in the latter the anterior invagination of the median arm reaches up to approx. 1/3 length of the arm. See further the position of the genus in the cladogram (fig. 62). It seems impossible to define the genus more accurately on the basis of the external morphology.

The author did not succeed in producing a cladogram of the species, since there is seemingly too little interspecific variation amongst them. *P. jamaicensis* (Schaus, 1901) and *personalis* seem to be sister-species, since both have only very narrow and stiff scales on the first tarsomere of the proleg. In *poam* Dyar, 1918, *terrafirma* Schaus, 1911 and two undescribed species from resp. St. Martin and Panama the fringes are seemingly only moderately long.

In *terrafirma* the lower suture of Apc reaches up to from 0.5 to 0.7 times length of An, while in most other species it is up to 0.7 times and it may be even 0.8 times in *jamaicensis*. Mesomeron is 1.5 times width of eucoxa II. Venation: R1 from areole; R3, R4+5 connate to very shortly stalked; R4+5 stalked for 0.1 to 0.4 times their length; M1 below areole; Rs-M1 moderately long to long. Humeral plate appears to be in most species twice size of radial bridge. Median plate is at least sometimes reduced in length. 2Ax has sometimes/often elevated, scaled area.

Psychonoctua personalis Grote, 1865: 251.
Material. —2♂♂, CUBA: Santiago (BMNH).
Note. A host is Coffee (species of *Coffea* L.) (Le Pelley, 1968: 210).
Dumitus jamaicensis Schaus, 1901: 46.
Material. —long series (most ♂♂, 1♀), JAMAICA (BMNH).
Note. A host is Coffee (Le Pelley, 1968: 210).
Psychonoctua lillianae Lindsey, 1926: 35.
Not examined. Dyar (1940: 1267) notes the species from Antigua, Montserrat and Barbados, and bred in Coffee and *Cassia glauca* Lam.
Xyleutes muricolora Dyar, 1940: 1267.
Not examined. From Puerto Rico and bred in Coffee (Dyar, 1940; Wolcot, 1933: 315-316).
Duomitus benestriata Hampson, 1904a: 180.
Material. —1♂ (holotype), BAHAMAS (BMNH).
Psychonoctua poam Dyar, 1918: 366-367.
Material. —8♂♂, GUATEMALA (various localities) (BMNH).
Psychonoctua terrafirma Schaus, 1911: 629.
Psychonoctua nullifer Dyar, 1914: 349. [Synonymized by Dyar, 1940: 1268].
Material. —2♂♂, COSTA RICA: Sixola River (BMNH).
Undescribed species (a)
Material. —4♂♂, PANAMA; Taboga (ZMUC).
Undescribed species (b)
Material. —2♂♂, FRANCE, Antilles: St. Martin (RMNH); 3♂♂, NETHERLANDS, Antilles: St. Maarten, i.1966 (Kruseman) (ITZ).
Undescribed species (c)
Material. —6♂♂, 1♀, ST. THOMAS: Ch. Amalie (ZMUC).
Unidentified species (d)
Material. —4♂♂, NETHERLANDS, Antilles: Saba, 12/16.iii.1953 (Croockewit) (ITZ).
Hamilcara gilensis Barnes & McDunnough, 1910: 466.
? *Psychonoctua unilinea* Dyar, 1925: 19.
Not examined. Dyar (1940: 1268) notes that he is convinced that *unilinea* and *gilensis* are the same. The first species is known from Mexico and the latter from U.S.A. (Arizona).
Xyleutes xuna Dyar, 1940: 1268, pl. 181: fig. row e.
Not examined. From Mexico.

A Kenyan species-group

It seems that an ancestral species most close to *Psychonoctua* and *Carohamilia* spread from South America to Africa. There are at least four undescribed species from Kenya in this group. The species still have the fifth tarsomere as long as fourth.

The paronychia are minute to/or wanting. The group is further only characterized by the apomorphies no.'s 1-12a in fig. 62. There seems to be no distinctive autapomorphy of the genus.

Three species (see also fig. 61) have shortened and narrowed labial palpi with a shortly ovate third segment. Lower suture of Apc may vary up to 0.7 times length of An. In the examined specimens of the four species the mesepimeron is moderately low with a sinuate upper margin. Most of these species were further hardly examined concerning the thoracic sclerites, since only few specimens of each were available. Venation: R1 from areole; R3, R4+5 connate to very shortly stalked; R4+5 stalked for 0.2 to 0.3 times their length; M1 usually below areole; Rs-M1 varies amongst the species from moderately short to rather long.

Because the species are unnamed and not described, no genus-name is yet given.

Undescribed species (a)

Material. —2♂♂, KENYA: Karisia Hills, 16 km e. of Maralal, 2400-2700 m., 2-5.xi.1978 (de Jong & Krikken) (RMNH).

Undescribed species (b)

Material. —2♂♂, KENYA: Samburu Game Reserve, near Uasa Ngira, 7.xi.1978 (de Jong & Krikken) (RMNH).

Undescribed species (c)

Material. —6♂♂, 2♀♀, KENYA: Nyiru, 02.09°N and 36.50°E, 2100 m., 29.iv.-1.v.1983 (de Jong & Krikken) (RMNH).

Undescribed species (d)

Material. —1♂, KENYA: Nguruman Escarpment, 01.55°S and 36.00°E, 900 m., 12/13.v.1983 (de Jong & Lepelaar) (RMNH).

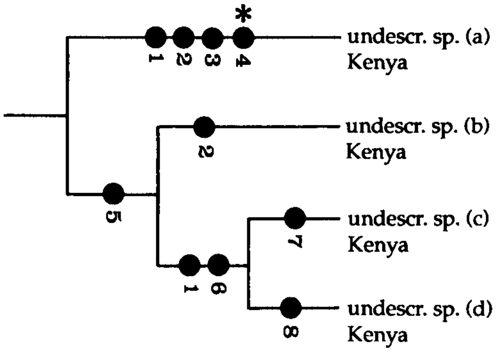


Fig. 61, cladogram of undescribed genus (section 2).

Table 11. Apomorphies in fig. 61 (undescribed genus).

1. Arolium wanting.
2. Fringes only moderately long.
3. Median arm rather long and with anterior invagination up to $^1/_3$ its length.
4. Anal plate rather long.
5. Labial palpi moderately slender and approx. as long as eye-diameter; third segment (shortly) ovate.
6. Tarsal claws moderately slender.
7. I-epiphysis reaching distinctly short of tibia-apex.
8. Inner cell of forewing wanting.

Genus **Voousia** gen. nov.

Type species: *Duomitus punctifer* Hampson, 1898: 259-260.

Etymology: the name is in honour of Prof. Dr. K.H. Voous, emeritus professor of Systematics and Zoogeography, The Netherlands. Gender: feminine.

Duomitus punctifer was placed in *Xyleutes* by Dyar (1940: 1268). This species does not fit in *Xyleutes* or *Duomitus* (see under these genera). It seems to take a place in the cladogram (fig. 62) after the Kenyan species-group. The species shares with an undescribed species from Venezuela that the mesepimeron is moderately high, the fifth tarsomere is 1.5 times length of the fourth, the arolium is much reduced in size, the paronychia are wanting, and M2 and M3 of the forewing connate or very shortly stalked. The two species have furthermore the following apomorphies: male antenna bipectinate for approx. half its length, An at most moderately low, lower suture of Apc reaching up to at least half length of An, accessory plate II moderately wide, fringes moderately long, 1Ax apically rather large or large, and anal plate is moderately long.

In *punctifer* An varies from moderately low to low and the humeral plate is approx. twice size of the radial bridge. In *Psychonoctua* species An is low. In the undescribed species the humeral plate is approx. 1.3 times size of the radial bridge, which is presumably a reversal. Furthermore, M is unforked in the forewing of the undescribed species. In *punctifer* the number of ♀ frenulum bristles amounts approx. six, and these are moderately long. The female of the undescribed species is unknown.

Since the two species seemingly do not fit in any available genus, they are placed in a new one.

Frontal tuft of *punctifer* is dorsally moderately long in the male and long in the female. In *punctifer* the lower suture of Apc reaches up to from 0.5 to 0.7 times length of An. In the undescribed species (1 ex.) the lower suture of Apc reaches up to approx. half length of An. Intersclerite III is wanting in *punctifer* and is small in the undescribed species. Accessory plate III is narrow. First tarsomere of proleg in *punctifer* has dorsally rather long scales. Venation: R1 from areole; R3, R4+5 shortly stalked; R4+5 stalked for 0.4 to 0.6 times their length; inner cell of forewing wanting in the undescribed species; in *punctifer* the anterior M of forewing very close or close to chorda and the posterior M anterior to M2; M1 from areole; M2 and M3 connate to very shortly stalked; Rs-M1 in *punctifer* moderately short and in the undescribed species moderately long. 2Ax has sometimes/often elevated scaled area.

Duomitus punctifer Hampson, 1898: 259-260.

Material (all BMNH). —1♂ (holotype), GRENADA; long series of both sexes from Grenada, Dominica, St. Lucia and St. Vincent.

Undescribed species

Material. —1♂, VENEZUELA: Estebos Valley, Las Quigas (BMNH).

Note. The species is mainly greyish brown but has whitish vestiture on the tegulae.

Table 12. Apomorphies in fig. 62 (section 2 - part 1).

1.	4Ax more or less antero-distally reduced.
2.	Anal plate only moderately long. (*)
3a.	Antenna bipectinate/bilobed for approx. 0.4, 0.5 or 0.6 times its length. (*)
b.	Antenna bipectinate/bilobed for approx. 0.6 to 0.7 times its length.
4a.	I-epiphysis reaching little short of or approx. as far as tibia-apex.
b.	I-epiphysis reaching distinctly short of tibia-apex.
5.	Tarsomeres only slightly or hardly widened distally.

6a. Median arm with anterior invagination up to approx. $^{1}/_{4}$ its length. (*)
b. Median arm with anterior invagination up to from $^{1}/_{3}$ to $^{1}/_{4}$ its length.
c. Median arm rather wide and with anterior invagination up to approx. $^{1}/_{3}$ its length.
d. Median arm with anterior invagination up to approx. $^{1}/_{3}$ its length.
7a. Lower suture of Apc (usually) up to at least half length of An.
b. Lower suture of Apc up to at least 0.8 times length of An.
c. Lower suture of Apc up to from 0.3 to 1.0 time length of An.
8a. Fringes long to moderately long or only moderately long.
b. Fringes at most moderately long.
9. 1Ax apically rather large or large.
10a. Female antenna proximally bilobed. (*) Not examined in e.g. *Carohamilia ophelia* and *Aramos masoni*.
b. Female antenna proximally simple.
11. Humeral plate 1.5 to/or 2 times size of radial bridge.
12a. Paronychia minute to/or wanting.
b. Paronychia only minute.
c. Paronychia only wanting.
13. Fifth tarsomere at least 1.3 times length of fourth.
14a. Number of ♀ frenulum bristles more than five, up to approx. twenty.
b. Number of ♀ frenulum bristles at least eight.
15. Tegula ventro-posteriorly gradually tapering and slightly upturned to bluntly pointed and moderately upturned.
16. Male antenna only moderately bipectinate.
17a. Labial palpi two-segmented.
b. Labial palpi two- or three-segmented.
18a. An moderately low.
b. An moderately low or low.
19. Accessory plate II moderately narrow to narrow.
20. Vestiture of tibia II short.
21. Vestiture of tibia III short.
22. R1 proximal to areole.
23. Labial palpi short; approx. 0.5 times as long as eye-diameter.
24. Mesepimeron moderately high, with rounded upper margin.
25a. Inner cell of forewing sometimes small but usually/often wanting.
b. Inner cell of forewing (normally ?) wanting.
26. Apc terminating on to distinctly dorsally to K.
27. I-epiphysis in female shorter and narrower than in male.
28a. Median arm moderately to rather long.
b. Median arm only rather long.
29. Arolium much reduced in size.

Section 2A

There is a group of species with a distally elongate radial plate with a rather slender apex (see figs. 65 and 74). In most of these species the ♂ I-epiphysis is more or less blunt and the tegula is ventro-posteriorly very blunt. See also figs. 63 and 76. There are two main divisions in section 2A; the species showing a well-developed aculeate area at the mesepimeron, and those in which such an area is wanting as well at the mesepimeron as on the forewing-base. The last genus of this section in the cladogram is the new genus *Tarsozeuzera*.

The species of section 2A further share the following apomorphies (see also figs.

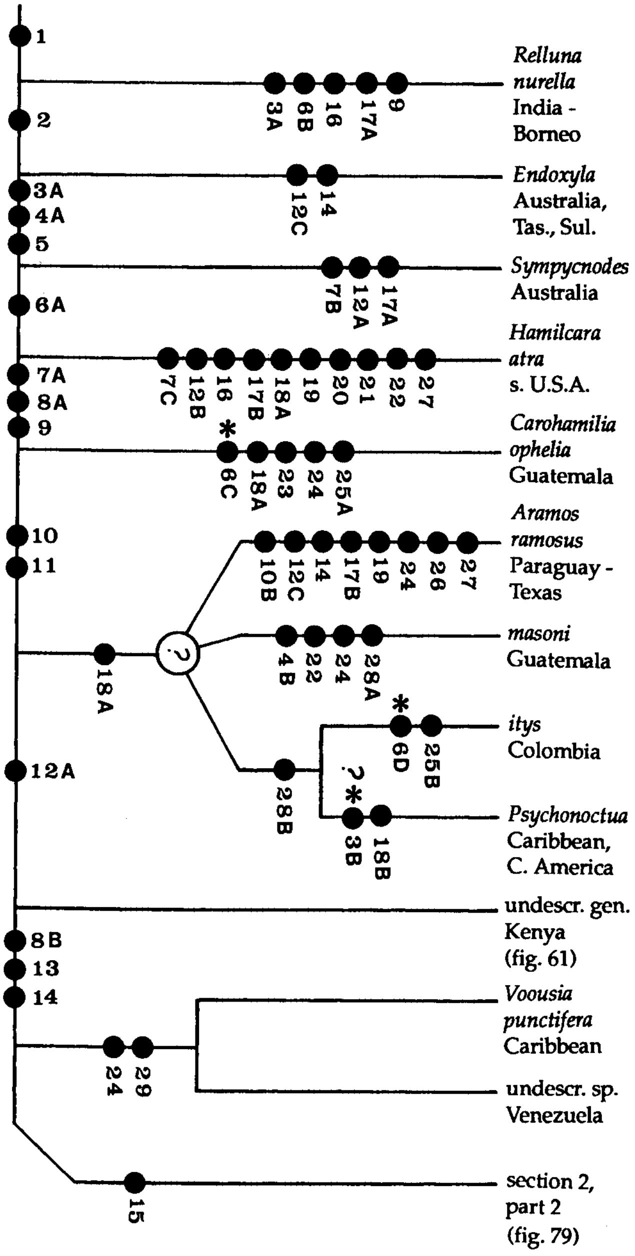


Fig. 62, cladogram of section 2 - part 1 (Zeuzerinae).

55, 62 and 79): male antenna bipectinate for less than 0.6 times its length, female antenna proximally bilobed or simple, lower suture of Apc reaching up to at least half length of An, ♂ I-epiphysis reaching little short of or approx. as far as tibia-apex (with reversals), paronychia wanting, fifth tarsomere at least 1.5 times length of fourth, tarsomeres only slightly or hardly widened apically, fringes at most moderately long, number of ♀ frenulum bristles more than five, distal plate of 4Ax anteriorly reduced, and 1Ax of forewing apically large.

A great number of species from this section and from other sections had previously been placed under *Xyleutes*. In this study *Xyleutes* is restricted to only three species. Many genus-names formerly synonymized with *Xyleutes* are excluded. See under *Xyleutes* for actual synonyms.

Genus **Morpheis** Hübner, [1820] 1816

Morpheis Hübner, [1820] 1816: 196.
  Type species: *Phalaena pyracmon* Cramer, 1782: 169, pl. 287: fig. 13.
Neocossus Houlbert, 1916: 89. [Synonymized by Donahue, 1980: 179].
  Type species: *Endoxyla strigillata* Felder, 1874: pl. 81: fig. 5.
Xylotrypa Turner, 1918: 162. [Synonymized by Donahue, 1980: 179].
  Type species: *Endoxyla strigillata* Felder, 1874: pl. 81: fig. 5.

Morpheis was resurrected by Donahue (1980: 173-174), after it had been synonymized with *Xyleutes* by Roepke (1957: 18). It is a complex of very similar species. Many species greatly resemble each other, also in colour pattern. Even the ratios in tarsomere-length is in all species similar; the fifth tarsomere is 1.5 to 2 times length of the fourth. The radial plate has the typical shape of section 2A. In all species, except *melanoleucus* (Burmeister, 1878), the tegula is ventro-posteriorly very blunt. The species, except *melanoleucus*, still have an arolium, though it is rudimentary. The median arm is rather long, and has the anterior invagination up to $^1/_4$ its length. The anal plate is rather long, but in *cognatus* (Walker, 1856) it varies from moderately to rather long. The forewing shows a longitudinal band of darker areas and has further many fuscous striae.

Xyleutes s.s. is restricted to southern and southeast Asia. In *Morpheis* the gnathos is well-developed, whereas it is absent in *Xyleutes*, and in *Xyleutes* the aedeagus has a digitate process, whereas such a process is absent in *Morpheis* (Donahue, 1980: 175). See further under *Xyleutes* for other differences.

An is moderately low to low. Lower suture of Apc reaches up to from 0.6 to 0.8 times length of An. Mesepimeron is moderately high. Accessory plate II is moderately wide, but may be moderately narrow in *cognatus* and *putridus* (Percheron, 1838). Intersclerite III is sometimes/often completely present in *pyracmon*. Metameron has usually a membranous split. Accessory plate III is narrow. In *pyracmon* the ♀ I-epiphysis is sometimes or often shortened, but only a little. In *xylotribus* (Herrich-Schäffer, [1853]) the tarsi are allover dark fuscous. In *pyracmon*, *putridus* and *fractus* (Walker, 1856) the fringes are shortened to moderately short or short. In the other species the fringes are moderately long. Number of ♀ frenulum bristles varies from approx. six to twelve. Venation: R1 from areole; R3, R4+5 (very) shortly stalked; R4+5 stalked for 0.3 to nearly 0.5 times their length; M1 from or posterior to areole; a cross-vein CuP-A1+2 appears to be usually present in *cognatus* and sometimes in *pyracmon*; cross-vein Sc-Rs sometimes/often present in *strigillatus* and *oberthuri* (Houlbert, 1916); Rs-M1 moderately short to rather long; M2, M3 distinctly separate. Humeral plate is approx. twice size of radial bridge or varies from 1.5 or 1.8 to 2 times as large. Median plate is often reduced in length. Anal plate is rather long or varies from rather to moderately long.

M. melanoleucus seems to take the first branch of the section 2A (see fig. 63), separately from the rest of *Morpheis*. For the sake of convenience and since *melanoleucus* does not differ much from other members of *Morpheis*, it is provisionally placed in this genus. It seems impossible to produce an acceptable cladogram of the species on the basis of the external morphology; there is too little interspecific and too much intraspecific variation. Furthermore, it is obscure if certain names stand for subspecies or good species.

Endoxyla melanoleuca Burmeister, 1878: 407.
  Material. —3♂♂, Argentina: La Rioja (BMNH).
Zeuzera cognata Walker, 1856: 1532.
  ? *Zeuzera comisteon* Schaus, 1911: 628.
  ? *Xyleutes discreta* Dyar, 1940: 1267.
  ? *Xyleutes mexicana* Houlbert, 1916: 88-89, fig. 23 (male).
  Material. —1♂ (holotype of *cognata*), HONDURAS (BMNH); 8♂♂, 1♀, MEXICO (BMNH); 3♂♂, GUATEMALA (RMNH); 1♂, MEXICO (MNHN); 1♂ (holotype of *mexicana*), MEXICO: Misantia, iv-v.1912 (Gugelmann) (MNHN).
  Note. Appearing as a smaller and duller version of *oberthuri*.
Duomitus mathani Schaus, 1901: 45-46.
  Xyleutes oberthuri Houlbert, 1916: 86-88, fig, 21 (males), fig. 22 (females). [Synonymized by Donahue, 1980: 179].
  Xyleutes cognatus ssp. *distinctus* Bryk, 1953: 267. [Synonymized by Donahue, 1980: 179].
  Material. —1♂ (holotype of *oberthuri*), 1♀ (paratype), PERU: Huambo, 1889 (de Mathan) (MNHN); 5♂♂, 2♀♀, PERU: a.o. Charape and San Gaban, -2500 ft. (BMNH); 1♀, ECUADOR: Paramba (BMNH); 1♀, Cachi (BMNH).
Endoxyla strigillata Felder, 1874: pl. 81: fig. 5.
  Phragmataecia impedita Wallengrén, 1860: 44. [Synonymized by Gaede, 1933b: 822].
  Material examined: 1♂, 1♀, Buenos Aires (BMNH).
  Note. Appearing as a smaller and duller version of *pyracmon*.
Phalaena pyracmon Cramer, 1782: 169, pl. 287: fig. 13.
  Endoxyla palmarum Herrich-Schäffer, [1853] 1850-1858: 58, fig. 36 [Established as a synonym of *Zeuzera putrida* Percheron]. [Synonymized by Dyar, 1940: 1266].
  Duomitus pyracmonides Schaus, 1901: 45. [Synonymized by Dyar, 1940: 1266].
  Material. —long series of both sexes from Mexico, Venezuela, Peru, Colombia and Brazil (BMNH).
Zeuzera fracta Walker, 1856: 1542.
  Material. —1♂ (holotype), ? (BMNH); 10♂♂, 2♀♀, VENEZUELA: Andes-Bricenno, 1500-4000 m., and Merida, 1900 m. (RMNH).
  Note. Appearing as a smaller and duller version of *pyracmon*, but white areas on forewing mixed with fuscous and thus appearing "dirtier".
Zeuzera putrida Percheron, 1838: text to pl. 4 (3 pages), pl. 4: fig. 1 (male and various parts).
  Material (all RMNH). —1♂, PERU: Iquitos; 1♂, Trinidad; 2♂♂, SURINAM: Raleigh Vallen.
  Note. Closely resembling *pyracmon*, but wing-pattern a little heavier.
Endoxyla xylotribus Herrich-Schäffer, [1853] 1850-1858: 58, figs. 37-38.
  Material. —long series of both sexes from Venezuela, Panama, Peru (-4500 ft.), Guatemala, Brazil, Bolivia and Paraguay (BMNH); 2♂♂, BRAZIL (RMNH).

Xyleutes vatani Schaus, 1934: 95.
Not examined. From Argentina.
Zeuzera lelex Dognin, 1891: 121.
Not examined. From Venezuela.
Morpheis clenchi Donahue, 1980: 176-177, figs. 3-4 (male, holotype), figs. 7-9 (male genitalia).
Not examined. From U.S.A. (Arizona).

Genus **Xyleutes** Hübner, [1820] 1816

Xyleutes Hübner, [1820] 1816: 195.
Type species: *Phalaena* (*Noctua*) *strix* Linnaeus, 1758: 508.
Strigoides Guérin-Méneville, [1829-1844] 1829-1838: 505. [Synonymized by Roepke, 1957: 18].
Type species: *Strigoides leucolophus* Guérin-Méneville, [1829-1844] 1829-1838: 505.
Hinnaeya Moore, 1882-1883: 153. [Synonymized by Roepke, 1957: 18].
Type species: *Phalaena* (*Noctua*) *strix* Linnaeus, 1758: 508.
Melanostrigus Houlbert, 1916: 78, 112. [Synonymized by Roepke, 1957: 18].
Type species: *Cossus personus* Le Guillou, 1841: 257.

In the species of section 2A which seemingly follow *Morpheis* in the cladogram (fig. 63) the ♀ I-epiphysis is distinctly shorter than the ♂ one (see figs. 69-71). There are three species with very short fringes and a large humeral plate. These species are considered to form *Xyleutes*. The frons is medio-dorsally more or less elevated. The genus is further characterized by the apomorphies no.'s 1-13a and 20-21a in fig. 63. In these species there may be considerable size differences between the sexes; the female is generally considerably larger than the male. X. *keyensis* Strand, 1919 belongs to the largest known cossid species.

Vertex of at least *strix* and *personus* is more or less distinctly antero-laterally ridged, and has small anterior protuberances. In *strix* the ♀ antenna is proximally simple. In the other two species the ♀ antenna is indistinctly bilobed with a pair of lateral stout sensilla on each segment. Third segment of labial palpi is shortly ovate. An is very low in *strix* and only low in *keyensis* and *personus*. Lower suture of Apc reaches up to from 0.8 to 0.9 times length of An. In *strix* the Apc terminates sometimes or often dorsally to K. Mesepimeron is moderately high. Accessory plate II is at least sometimes moderately narrow in *personus* and varies from wide to narrow in *keyensis*. Mesomeron is twice as wide as eucoxa II. Intersclerite III is present. Accessory plate III is moderately narrow to narrow. I-epiphysis in female is rather short and in *personus* it is sometimes even very short, further narrow and pointed. The tarsi are sometimes/often allover dark fuscous in *personus*. Number of ♀ frenulum bristles varies from approx. nine to thirty-two, and these bristles are short. Dorsum of hindwing is weakly to not invaginated. Venation: R1 from areole; R3, R4+5 (very) shortly stalked; R4+5 stalked for 0.4 to nearly 0.5 their length in *keyensis* and *personus*, and for 0.5 to 0.7 times in *strix*; Sc-Rs occasionally present in *strix* and *personus*; Rs-M1 rather long to long in *strix*, moderately long to long in *keyensis*, and moderately short to long in *personus*. Humeral plate is 2.5 to 3 times size of radial bridge. Median arm is rather long in *personus* and has the anterior invagination up to $^1/_3$ its length. In *strix* this invagination goes up to half length of the arm. 2Ax lacks (normally ?) elevated scaled area. Anal plate is only moderately long.

Many genus-names have previously been synonymized with *Xyleutes* (see

Roepke, 1957: 18). *Xyleutes* had become a mixture of genera from various sections, including *Psychonoctua*. In this study *Xyleutes* is applied to only the three species listed below.

Phalaena (*Noctua*) *strix* Linnaeus, 1758: 508.
Zeuzera signata Walker, 1856: 1537. [Synonymized by von Dalla Torre, 1923: 54].
Zeuzera bubo Butler, 1882b: 228. [Synonymized by von Dalla Torre, 1923: 54].
Xyrena tigrata Houlbert, 1916: 114. [Synonymized by Gaede, 1933b: 817].
Range: India, eastward to Philippines and Solomon Islands.
Material. —1♂ (holotype of *signata*), ? (BMNH); 1♀ (holotype of *bubo*), PAPUA NEW GUINEA: New Britain (BMNH); 1♂ (holotype of *tigrata*), INDONESIA: Sulawesi or Ambon (MNHN); very long series from most countries of its range (BMNH); long series from Indonesia (RMNH and ITZ).
Note. Roepke (1957: 19-22) distinguishes the following subspecies: *strix*, *bubo*, *tigrata* and *formosicola* Strand. A host is *Sesbania grandiflora* Pers. (Snellen, 1877: 22).
Xyleutes keyensis Strand, 1919: 93.
Range: Indonesia: Kepulauan Kai and Kepulauan Tanimbar (Roepke, 1957: 23), and perhaps Irian Jaya (see material examined).
Material (all INDONESIA). —1♀ (holotype), [INDONESIA: Kepulauan Kai] (BMNH); 1♀, Kepulauan Tanimbar (MNHN); 1♂, Kepulauan Tanimbar (ITZ); 2♂♂, 1♀, Kepulauan Tanimbar, Ulilit Saumlakki (RMNH); (conspecific ?) 1♀, Irian Jaya, Jayapura (RMNH).
Cossus personus Le Guillou, 1841: 257.
Strigoides leucolophus Guérin-Méneville, [1829-1844] 1829-1838: 505. [Synonymized by Roepke, 1955: 283].
Zeuzera leuconota Walker, 1856: 1537. [Symonymized by von Dalla Torre, 1923: 53].
Range: India, eastward to Philippines and New Guinea.
Material. —1♂ (holotype of *personus*), INDONESIA: Samarang (MNHN); 1♂ (holotype of *leuconota*), SRI LANKA (BMNH); long series of both sexes from most countries of its range (BMNH); long series of both sexes from Indonesia (RMNH and ITZ).
Note. Roepke (1957: 23) describes a subspecies *biakensis* from Biak and Schouten Islands (Irian Jaya). Host-plants are *Durio zibethinus* Murr., *Cassia fistulata* L., *C. multijuga* Rich., *C. nodosa* Ham., *C. renigera* Wall., *C. siamea* Lam., and a species of *Premna* L. (Beeson, 1961: 445; Arora, 1976: 118; Roepke, 1957: 22-23).

Genus **Alophonotus** gen. nov.

Type species: *Chalcidica* (*Duomitus*) *rauana* Strand, 1909: 130.

Etymology: "a" (Greek) means non- + genus-name *Eulophonotus* minus "eu". Gender: masculine.

Gaede (1930: 544) includes *rauanus* in *Callocossus* Aurivillius, 1910, which is a junior subjective synonym of *Eulophonotus* Felder, 1874. Although *rauanus* (Strand) most closely resembles superficially the females of *Eulophonotus*, it is separated from this genus in the cladogram (fig. 63) by many species which have lost the aculeate area at the mesepimeron. In *Xyleutes* the humeral plate is larger and the fringes shorter. In *rauanus* the fringes are only short and R1 is proximal to the areole. An is moderately low to low. The body and wings have many yellow-orange markings. In contrast to species of *Eulophonotus*, the male and female of *rauanus* have approx. the same size and colour pattern. This African species does not fit in any available genus and is therefore placed in a new genus. See further fig. 63.

Vertex is more or less antero-laterally ridged, and has at least sometimes small pits instead of anterior protuberances. Male antenna is bipectinate for little less than half its length. Female antenna is proximally simple. Tegula is ventro-posteriorly very blunt. Lower suture of Apc reaches up to 0.9 to 1.0 time length of An, and terminates often or usually dorsally to K. K is long, moderately narrow, and has a cross-suture. Subalare-process II is moderately short and thick. Aculeate area at mesepimeron is well-developed. Mesepimeron is moderately high. Mesomeron is twice as wide as eucoxa II. I-epiphysis of male is blunt and reaches nearly or approx. as far as tibia-apex. I-epiphysis is in female very short, narrow and pointed. Fifth tarsomere is 2.5 times length of fourth. Arolium and paronychia are wanting. Fringes are short. Number of ♀ frenulum bristles varies from approx. eight to twenty, and these bristles are rather short. Dorsum of hindwing is weakly to distinctly invaginated at CuA. Venation: R1 well proximal to areole; R3, R4+5 shortly stalked; R4+5 stalked for approx. 0.5 to 0.8 times their length; no Sc-Rs; Rs-M1 moderately long to (often) long. Humeral plate is 1.3 to 2.3 times size of radial bridge. Radial plate is distally elongate with slender apex. 1Ax is apically large. Median arm is moderately long, and has the anterior invagination up to approx. $^1/_3$ to half its length. Median plate is sometimes slightly reduced in length. Anal plate is moderately long.

Chalcidica (Duomitus) rauana Strand, 1909: 130.
Callocossus langi Holland, 1920: 318-319, pl. 14: fig. 8 (female). [Synonymized by Gaede, 1930: 544].
Material. —series of both sexes from Angola, Senegal, Uganda, Zimbabwe, Kenya and Malawi (BMNH).

Genus **Chalcidica** Hübner, [1820] 1816

Chalcidica Hübner, [1820] 1816: 197.
Type species: *Phalaena (Bombyx) minea* Cramer, 1779: 52, pl. 131: fig. D.

Chalcidica has been established for *minea* (Cramer) (plate 1: fig.I). The genus is here resurrected after *minea* had previously been treated as a *Xyleutes* species by most authors. This species is one of the most brightly coloured cossid species. The forewing is often yellowish with dark fuscous markings, but in certain material from New Guinea it is mainly darkened. The dark areas of the wings and body have a distinct metallic lustre. It is a rather large species and the female is generally larger than the male. It seems to be the first species in the cladogram (fig. 63) that lacks an aculeate area at the mesepimeron. It has a rather to moderately long median arm, a distally elongate and moderately slender radial plate, a rather long anal plate and the fifth tarsomere twice length of the fourth.

Vertex is more or less antero-laterally ridged. Male antenna is bipectinate for approx. 0.4 times its length. Female antenna is proximally simple. An is low. Lower suture of Apc reaches up to 0.9 to 1.0 time length of An. K is long and has at least sometimes a cross-suture. Subalare-process II is moderately short and thick. Mesepimeron is moderately high. Accessory plate II varies from wide to narrow. Intersclerite III is completely present but small. Accessory plate III is narrow. Female I-epiphysis is short, slender and much tapering apically. Vestiture of tibia II is short. Tarsi are allover dark fuscous. Fifth tarsomere is twice length of fourth. Fringes are short. Number of ♀ frenulum bristles is approx. fifteen and these are moderately short. Dorsum of hindwing is weakly to hardly invaginated. Venation: areole very long and rather narrow; R1 from areole; R3, R4+5 connate to shortly stalked; R4+5 stalked for approx. 0.4 to 0.6 times their length; M1 posterior to areole; no Sc-Rs; Rs-M1 moderately long; M2, M3 distinctly separate. Humeral plate is approx. twice size of radial bridge. Median arm is moderately long, and has the anterior invagination up to approx. $^1/_4$ its length. Median plate is sometimes slightly reduced in length. 2Ax lacks elevated scaled area. Anal plate is rather long.

Phalaena (Bombyx) minea Cramer, 1779: 52, pl. 131: fig. D.
Phalaena (Bombyx) hyphinoe Cramer, 1779: 91, pl. 154: fig B. [Synonymized by Gaede, 1933b: 818].
Zeuzera viridicans Eschscholtz, 1821: 219, pl. 11: fig. 29. [Synonymized by Walker, 1856: 1535].
Zeuzera alboatra Walker, 1865: 589. [Synonymized with *hyphinoe* by von Dalla Torre, 1923: 51].
Range: India, eastward to Philippines and Solomon Islands.
Material. —long series of both sexes from most countries of its range, including Bismarck Archipelago (BMNH); long series (♂, ♀) from Indonesia (RMNH and ITZ).
Note. Roepke (1957: 25-26) distinguishes the following subspecies: *minea*, *hyphinoe* (fig. 114) and *pallescens* Roepke, 1955 with a forma *archboldi* Roepke, 1955.

Genus **Bergaris** gen. nov.

Type species: *Xyleutes malayica* Roepke, 1957: 32.

Etymology: "bergaris" (Indonesian) means striped. Gender: masculine.

Bergaris is established for five species which had formerly been placed in *Xyleutes*. In this study *Xyleutes* is restricted to a few species of section 2A with a large humeral plate and very short fringes. An important characteristic of *Bergaris* is that the aculeate area at the mesepimeron is wanting. The fringes are only short and the humeral plate is approx. twice size of the radial bridge. The vertex is probably in all species medio-posteriorly elevated. The species of the following genera of section 2A have shorter fringes and a moderately short Pre II. *Bergaris* species are all medium-sized and have brown or buff wings with fuscous striae. They further have the following apomorphies: tegula ventro-posteriorly very blunt, An low, lower suture of Apc reaching up to from 0.8 to 1.0 time length of An, mesepimeron moderately high, ♂ I-epiphysis long and more or less blunt, vestiture on tibia II short, arolium and paronychia wanting, median arm rather long (reversal), and anal plate moderately long. See also figs. 62-63. Most species occur in Malaysia and/or Indonesia and one species is known from Vietnam.

B. ruficeps (Joannis, 1929) has been partially examined. Only males were available. Vertex of at least *jacobsoni* (Roepke, 1957) and *lutescens* (Roepke, 1957) is medio-posteriorly moderately elevated. Male antenna is bipectinate for slightly less than or approx. half its length. Tegula is ventro-posteriorly very blunt. An is low. Lower suture of Apc reaches up to approx. 0.8 to 1.0 time length of An. K is long and plus or without a cross-suture. Subalare-process II is short and thick. Mesepimeron is moderately high. Accessory plate II is wide to moderately wide. Intersclerite III is (usually ?) present. Accessory plate III is narrow. Fifth tarsomere is twice length of fourth. Fringes are short. Venation: R1 in most species from areole, but is sometimes just proximal to areole in *lutescens* and *malayicus*; R3, R4+5 (very) shortly stalked; R4+5 stalked for 0.3 to 0.4 or 0.5 times their length; M1 posterior to areole; Rs-M1 moderately short to moderately long; M2, M3 distinctly separate. Humeral plate is approx. twice size of radial bridge. 1Ax of forewing is apically large. Radial plate is distally elongate with slender apex. Distal plate of 4Ax is anteriorly reduced. Median arm is rather long, and has the anterior invagination up to from 1/4 to 1/3 its length. Median plate is normally reduced in length. 2Ax is plus or without an elevated scaled area. Anal plate is moderately long.

Azygophleps ruficeps Joannis, 1929: 551-552, pl. 3: fig. 18.

Material. —1♂ (holotype), VIETNAM: Hanoi, Gen. slide Viette no. 2559 (MNHN).

Note. See Roepke (1957: 32-33) approx. confusion with and differences from the following two species. The holotype is damaged and its wings are rather worn off. The vestiture on the vertex is orange, and that on the prothorax orange with blackish dots.

Xyleutes malayica Roepke, 1957: 32.

Xyleutes ruficeps sensu Gaede, 1933b: 891.

Range: Malaysia; Indonesia: Sumatra and Kalimantan; Brunei.

Material. —2♂♂, INDONESIA: Sumatra, Lebong Tandai (BMNH); 1♂, INDONESIA: Kalimantan, Kariorang (RMNH); 1♂, INDONESIA: Kalimantan, 85 miles north of Pontianak (MNHN); 5♂♂, BRUNEI: Badas Forest Res., Labi and Serias (BMNH).

Xyleutes jacobsoni Roepke, 1957: 32-33, pl. 3: fig. 6 (male, holotype).

Range: Indonesia: Sumatra, Simalur and Flores.

Material (all INDONESIA). —1♂ (holotype), 2♂♂, Simalur, Sinabang (Jacobson), (holotype) Gen. slide Xyl. no. 13 (RMNH); 5♂♂, Flores: Bea, Nio, Kai, Kisoa and Ruteug, -1200 m. (ITZ).

Undescribed species

Material. —1♂, New Guinea (BMNH).

Note. Most closely resembling *jacobsoni*, but lacking the paler spot in the cell of the forewing. It was placed under *malayica* when it was identified by Roepke.

Xyleutes lutescens Roepke, 1957: 33.

Xyleutes lutescens ssp. *lutescens* Roepke, 1957: 33-34, pl. 3: fig. 7 (male, paratype). (plate 1: fig. H)

Material. —1♂ (holotype), 1♂ (paratype), INDONESIA: Lingga Arch., Singkep, Tji Gapur, 12.i.1955 (Cardinaal) (RMNH); 4♂♂, BRUNEI: Telisai and Labi (BMNH).

Xyleutes lutescens ssp. *griseola* Roepke, 1957: 34.

Material. —1♂ (holotype), 1♂ (paratype), MALAYSIA: Malaya, Gunong Angsi, Negri Sembilan, 2000-2700 ft., iv.1918 (BMNH); 6♂♂ (paratypes), MALAYSIA: Bukit Kutu (BMNH).

Genus **Rapdalus** gen. nov.

Type-species: *Zeuzera pardicolor* Moore, 1879: 86.

Etymology: "rapdalus" is partly an anagram of the species-name *pardalis*. Gender: masculine.

Rapdalus is here established for *Z. pardicolor*. This species differs from *Bergaris* species in that Pre II is moderately short, the fringe of the forewing is very short, and R5 is stalked with R4 for approx. 0.8 times its length. In the following genera of section 2A the wings of at least the males are not completely covered by scales. *R. pardicolor* has the following additional apomorphies: vertex gradually swollen, labial palpi slender, tegula ventro-posteriorly very blunt, lower suture of Apc reaching up to nearly or approx. complete length of An, aculeate area at mesepimeron wanting, mesomeron approx. twice width of eucoxa II, ♂ I-epiphysis more or less blunt and long, fifth tarsomere twice as long as fourth, arolium and paronychia wanting, R1 proximal to areole, radial plate distally elongate with slender apex, 1Ax apically large, and median arm moderately long. See also figs. 62-63.

Male antenna is bipectinate for nearly half its length. An is moderately low to low. Subalare-process II is short and thick. Mesepimeron is moderately high. Accessory plate II varies from wide to moderately wide. Accessory plate III is narrow. Intersclerite III is wanting. Tibia II has only short vestiture. Fringe of hindwing is short. Anal region is distinctly to nearly prominently elongate. Venation: R1 proximal to areole; R3, R4+5 shortly stalked; R4+5 stalked for approx. 0.8 times their length; M1 from tip of or posterior to areole; Rs-M1 long to moderately short. Humeral plate is approx. twice as large as radial bridge. Scale plate is approx. as long as radial bridge. Anterior invagination of median arm reaches up to approx. ¼ length of arm. 2Ax is with or without an elevated scaled area. Anal plate is moderately long.

Xyleutes kapuri Arora, 1976 closely resembles superficially *pardicolor*, but has partly semihyaline wings (Arora, 1976: 107-109) and should therefore be placed further in the cladogram, possibly in a new genus.

Zenzera pardicolor Moore, 1879: 86.

Duomitus pardalis Dudgeon, 1899: 645-646, pl. 1: fig. 17 (male). [Synonymized by Gaede, 1933b: 819].

Range: n.e. Himalaya, Burma, Vietnam, Malaysia (incl. Sarawak), Indonesia (Sumatra and Kalimantan).

Material. —1♂ (holotype of *pardalis*), INDIA: Sikkim, 1800 ft., ix.1877 (Dudgeon) (BMNH); 1♂, BURMA: Maulmain (BMNH); 1♂, VIETNAM: Cochin, Laokai (BMNH); 1♂, VIETNAM: Ha Giang (MNHN); 2♂♂, MALAYSIA: Selangor, Bukit Kutu (BMNH); 3♂♂, MALAYSIA: Sarawak, Mulu (BMNH); 1♂, INDONESIA: Sumatra, Lebong Tandai (BMNH); 1♂, INDONESIA: Kalimantan (RMNH).

Note. The two specimens from Selangor are of a separate form or subspecies.

Genus **Rugigegat** gen. nov.

Type species: *Zeuzera nigra* Moore, 1877: 348.

Etymology: "rugi" (Indonesian) means damage + "gegat" (Indonesian) means moth. Gender: feminine.

Rugigegat is here established for *Z. nigra*. It is uncertain if *Xyleutes kapuri* Arora, 1976 from India should also be included. No material of this species was available for personal examination. *X. kapuri* differs from *nigra* at least in that R1 is proximal to the areole (cf. Arora, 1976: 107-109).

R. nigra differs from *Rapdalus pardicolor* and other foregoing species of section 2A in that the wings of at least the male are not completely covered by scales and that the fringe of the hindwing is very short. In the following genera of section 2A the median arm is approx. moderately long. *R. nigra* has the following additional apomorphies: vertex gradually swollen, eyes more or less reduced in size, frons more or less widened, labial palpi slender, tegula ventro-posteriorly blunt, An very low, lower suture of Apc reaching up to nearly or approx. complete length of An, aculeate area at mesepimeron wanting, mesomeron approx. twice width of eucoxa II, ♂ I-epiphysis more or less blunt and long, fifth tarsomere twice length of fourth, arolium and paronychia wanting, fringes very short, humeral plate 1.3 to 1.8 times size of radial bridge, radial plate distally elongate with slender apex, 1Ax apically large, and anal plate varying from moderately to rather long. See also figs. 62-63. The ♀ antenna is proximally simple, and the ♀ I-epiphysis is moderately short and slender.

Male antenna is bipectinate for approx. half its length. Apc terminates with upper suture slightly to distinctly dorsally to K. Subalare-process II is short and thick. Mesepimeron is moderately high. Accessory plate II is approx. moderately wide. Accessory plate III is narrow. Intersclerite III is small or wanting. Anal region is distinctly or nearly prominently elongate. Number of ♀ frenulum bristles varies from approx. eight to twelve, and these are approx. moderately long. Venation: R1 from areole; R3, R4+5 (very) shortly stalked; R4+5 stalked for from 0.7 to 0.8 times their length; M1 from tip of or posterior to areole; Rs-M1 long to moderately long. Scale plate is approx. as long as radial bridge. Median arm is rather long. Anterior invagination of median arm reaches up to approx. 1/3 length of arm. 2Ax is without an elevated scaled area.

Zenzera nigra Moore, 1877: 348.

Range: Sri Lanka and Singapore.

Material. —1♀ (holotype), SRI LANKA (BMNH); 1♂, SRI LANKA: Haldamulla (BMNH); 4♀♀, SRI LANKA: Kandy (BMNH); 1♀, SRI LANKA: Kandy (MNHN); 1♀, SINGAPORE (BMNH); 1♀, ? (BMNH).

Note. Moore (1882-1883: 155) notes Coffee as a host-plant.

Table 13. Apomorphies in fig. 63 (section 2A - part 1).

1. Female antenna proximally bilobed or simple.
2. Male I-epiphysis more or less blunt.
3. Radial plate distally elongate and moderately slender (see figs. 65 and 74).
4a. Anal plate moderately to rather long. (*)
b. Anal plate moderately long only. (*)
c. Anal plate rather long only.
5a. An moderately low to low.
b. An low.
c. An very low.
6. Tegula ventro-posteriorly blunt.
7a. Median arm rather long. (*)
b. Median arm moderately long.
8. I-epiphysis in female distinctly shorter and narrower than in male or wanting.
9. Paronychia wanting.
10. Arolium wanting.
11a. Fifth tarsomere 2 to 2.5 times length of fourth. (*)
b. Fifth tarsomere approx. 3 times length of fourth.
12a. Fringes short.
b. Fringes (at least of forewing) very short.
13a. Median arm with anterior invagination up to from 1/4 to 1/3 or half its length.
b. Median arm with anterior invagination up to 1/3 its length.
14. Lower suture of Apc reaching up to 0.8 to 1.0 time length of An.

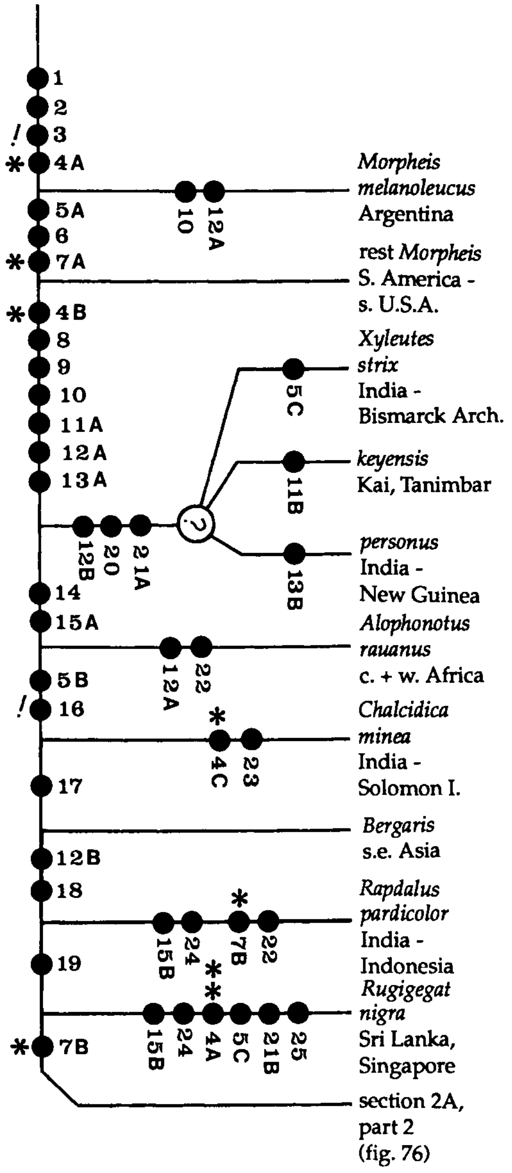


Fig. 63, cladogram of section 2A - part 1 (Zeuzerinae).

15a. R5 stalked with R4 for at least half its length.
b. R5 stalked with R4 for at least 0.7 times its length, up to 0.8 times.
16. Aculeate area at mesepimeron and corresponding one at wing base wanting.
17. Vertex distinctly swollen or posteriorly more or less elevated, but not ridged.
18. Pre II slightly shortened to moderately short.
19. Male wings with areas not completely covered by scales.
20. Frons medio-dorsally slightly to distinctly elevated.
21a. Humeral plate 2.5 to 3 times size of radial bridge.
b. Humeral plate 1.3 to 1.8 times size of radial bridge.
22. R1 proximal to areole.
23. Accessory plate II rather wide to narrow.
24. Labial palpi slender.
25. Eyes more or less reduced in size.

Genus **Pseudozeuzera** gen. nov.

Type species: *Duomitus biatra* Hampson, 1910a: 131-132.

Etymology: "pseudos" (Greek) means false + genus-name *Zeuzera*. Gender: feminine.

Pseudozeuzera is established for *biatra* and an undescribed species from Ivory Coast. In both species the thorax is dorsally whitish speckled with dark fuscous, which is special within the Zeuzerinae. In *biatra* R1 is proximal to the areole, as in most other species of section 2A following below. Since the colour pattern of the thorax is more special than the move of R1, the two species are placed together on a side-branch in the cladogram (fig. 76). The male forewing is not completely covered by scales. The colour pattern of the wings of *biatra* very closely resembles that of *Zeuzera* species. The forewing of *biatra* has however a rather large, blackish marking along costa at approx. 0.8 times wing-length. In the undescribed species the colour pattern of the forewing closely resembles that of *Morpheis xylotribus*; the forewing has a dark fuscous band posteriorly to the cell, and dark streaks distally in between the veins. In the undescribed species the labial palpi are three-segmented, but approx. as long as the eye-diameter. In *biatra* the labial palpi are two-segmented and shorter than the eye-diameter, as in *Zeuzera*. In the latter genus the subalare-process II is very short, whereas moderately short in at least *biatra*. The vestiture on the tibiae II and III is short. The tarsi are completely dark fuscous or blackish. The areole is moderately small in *biatra*. There is no cross-vein Sc-Rs, in contrast to *Zeuzera* species. The median arm is moderately long and nearly or approx. rather wide. The anal plate is moderately long in the undescribed species and moderately short in *biatra*.

Only males are known. Male antenna is bipectinate for nearly one-third its length. Thoracic sclerites have not been examined in the undescribed species. Tegula is ventro-posteriorly very blunt. An is low. Lower suture of Apc reaches up to complete length of An. Pre II is moderately short. Aculeate area at mesepimeron is wanting. Mesepimeron is moderately high. Accessory plate II is wide. Mesomeron is twice width of eucoxa II. Intersclerite III is moderately small. Accessory plate III is moderately narrow. I-epiphysis of male is blunt and reaches little short of or approx. as far as tibia-apex. Fifth tarsomere is approx. twice length of fourth. Arolium and paronychia are wanting. Fringes are very short. Dorsum of hindwing is distinctly invaginated. Venation: areole short and narrow in *biatra*, but long and moderately wide in the undescribed species; R1 proximal to areole in *biatra*, but from tip of or distinctly from areole in the other species; R3, R4+5 shortly stalked; R4+5 stalked for approx. 0.6 to 0.7 times their length; M1 posterior to areole; no cross-vein Sc-Rs; Rs-M1 rather long in *biatra*, but moderately long in the undescribed species; M2, M3 distinctly separate. Humeral plate is approx. twice size of radial bridge. Radial plate is distally elongate with slender apex. 1Ax of forewing is apically large. Distal plate of 4Ax is anteriorly distinctly reduced. Median arm of *biatra* is moderately long, slightly wider than Cu2, and has the anterior invagination up to approx. half its length. Median arm of the undescribed species is nearly as wide as Cu2 and is anteriorly invaginated up to approx. $^2/_5$ its length. Median plate is (normally ?) well-developed. 2Ax lacks elevated scaled area. Anal plate is moderately short.

Duomitus biatra Hampson, 1910a: 131-132.

Material. —1♂ (holotype), NIGERIA: Old Calabar (Crampton) (BMNH); long series of males from Sierra Leone, Ghana and Uganda (BMNH); 2♂♂, IVORY COAST: Adiopodoumé (MNHN).

Undescribed species

Material. —1♂, IVORY COAST: Adiopodoumé, x.1963 (Griveaud) (MNHN).

Genus **Paralophonotus** gen. nov.

Type species: *Zeuzera auroguttata* Herrich-Schäffer, [1854] 1850-1858: 58, fig. 173.

Etymology: "para" (Greek) means near + genus-name *Eulophonotus* minus "eu". Gender: masculine.

Z. auroguttata was transferred to *Callocossus* by Aurivillius (1910) (see *Eulophonotus*). Von Dalla Torre (1923: 49) places this species in *Xyleutes*. Gaede (1930: 544) includes *auroguttata* again in *Callocossus*.

P. auroguttatus resembles certain species of *Eulophonotus* in colour pattern; the species has also yellow-orange spots on the body and wings. This type of colour pattern is also found in *Alophonotus rauanus*. In contrast to *rauanus*, *auroguttatus* and *Eulophonotus* species show considerable sexual dimorphism. The male of *auroguttatus* is generally much smaller than the female and has a different colour pattern and shape of the hindwing. Another difference is that in *auroguttatus* and *Eulophonotus* species the aculeate area at the mesepimeron is wanting, whereas it is still present in *rauanus*. In most of the preceding species of section 2A R1 branches off from the areole, whereas in *auroguttatus* and the following species it is proximal to the areole. In *auroguttatus* the subalare-process II is short, whereas it is very short in the following species of section 2A. It thus seems that *auroguttatus* takes a separate place in the cladogram of this section (see fig. 76). Therefore a new genus is proposed for *auroguttatus*. *P. auroguttatus* has the following autapomorphies: eyes in both sexes more or less reduced in size, frons more or less widened, female frons considerably elevated medio-dorsally, second segment of labial palpi proximally narrowed, patagium considerably widely curved, An very low, fifth tarsomere 2 to 3 times length of fourth, humeral plate 2 to 2.3 times size of radial bridge, and anal plate approx. rather long. The species further has the characteristics of section 2A and the apomorphies no.'s 1-18 in fig. 63 and no.'s 1-3 in fig. 76.

Vertex is slightly swollen, has Pos at approx. 0.7 times its length, and lacks sometimes/often anterior protuberances. Male antenna is bipectinate for approx. 0.4 or 0.5 times its length. Female antenna is proximally simple. Metascutum is medially very narrow. Lower suture of Apc reaches up to nearly or actually complete length of An. Accessory plate II varies from moderately narrow to narrow. Accessory plate III is narrow. Intersclerite III varies from moderately large to small. I-epiphysis in male reaches approx. as far as tibia-apex and is more or less blunt. I-epiphysis in female is very short and pointed, and is perhaps sometimes wanting. Fringes are very short. Number of ♀ frenulum bristles varies from approx. five to thirteen, and these are moderately short. Dorsum of ♂ hindwing is considerably invaginated. Venation: areole rather long; R3 and R4+5 connate to very shortly stalked; R5 stalked with R4 for approx. 0.5 to 0.7 times its length; a cross-vein Sc-Rs sometimes/often present in one or both wings; Rs-M1 approx. moderately long. Radial plate has the shape typical for section 2A, but is slightly less elongate in the female than the male. Median arm is moderately long and moderately wide, and has its anterior invagination up to approx. half its length. 2Ax has elevated scaled area.

Zeuzera auroguttata Herrich-Schäffer, [1854] 1850-1858: 58, fig. 173.

Material. —long series (most ♀♀) from Ghana, Sierra Leone, Cameroon, Zaire and Angola (BMNH).

Genus **Eulophonotus** Felder, 1874

Eulophonotus Felder, 1874: pl. 82: fig. 9.

Type species: *Eulophonotus myrmeleon* Felder, 1874: pl. 82: fig. 9.

Engyophlebus Karsch, 1900: 2. [Synonymized by Gaede, 1930: 549].

Type species: *Engyophlebus obesus* Karsch, 1900: 3. [Synonymized with *Eulophonotus myrmeleon* Felder by Gaede, 1930: 549].

Callocossus Aurivillius, 1910: 51.

Type species: *Callocossus elegans* Aurivillius, 1910: 51.

Zeuzerops Strand, 1910: 143. Syn. nov.

Type species: *Zeuzerops hyalinipennis* Strand, 1910: 143-144.

So far only *myrmeleon* had been placed in *Eulophonotus*. *E. myrmeleon* appears to share many distinctive characteristics with *Duomitus armstrongi* Hampson, 1914-15 and two undescribed species. It seems that *Callocossus* is a paraphyletic genus, when it is not included in *Eulophonotus*. Therefore *Callocossus* is here synonymized with *Eulophonotus*. See also figs. 62-63 and 76.

Aurivillius (1910: 51) includes *elegans* and *Zeuzera auroguttata* in *Callocossus*. He further states that *Zeuzera stephania* Druce, 1887 probably belongs to *Callocossus* too. Gaede (1930: 544) includes *auroguttata*, *Alophonotus rauanus*, *elegans* and *stephania* in *Callocossus*. Gaede places *Zeuzerops* as a separate genus, but states that, if there were not little difference in venation, one would suppose that the examined male of *Zeuzerops hyalinipennis* Strand, 1910 concerns the male of *rauana* or *stephania*. *Zeuzerops hyalinipennis* is probably synonymous with *Eulophonotus stephanius*. *Z. auroguttata* has been placed here above in the new genus *Paralophonotus*.

All the species included share the following apomorphies: considerable sexual dimorphism in size and colour pattern, ♂ eyes varying from moderately large to distinctly reduced or only reduced, ♀ eyes moderately reduced, subalare-process II very short, ♂ forewings narrowed, R5 stalked with R4 for more than 0.8 times its length, and humeral plate at most 1.3 times size of radial bridge. Several of these apomorphies couldnot be checked in *armstrongi*, since its male is unknown. Pronotum is distinctly reduced in size in at least *stephanius*, undescribed species (a) and *myrmeleon*. The author supposes that also in the other species of this genus the pronotum is moderately low or low. The ♀ radial plate is sometimes/often not distally elongate and not narrowed, and thus of the normal zeuzerine type. The species further show the characteristics of section 2A and have the apomorphies no.'s 1-18 in fig. 63 and no.'s 1-4 in fig. 76. Since there is a wide morphological gap between the species formerly included in *Callocossus* and the others here included, a further description of the genus is split for the two sections.

Section A:

The species of the first section have yellow-orange spots on the wings and body. The species are generally smaller than *Alophonotus rauanus* and *Paralophonotus auroguttatus*. See also under *Alophonotus* and *Paralophonotus*.

Vertex of *stephanius* has Pos at approx. 0.8 times its length. Female frons of at least *stephanius* is medio-dorsally bulbed. Male antenna is bipectinate for approx. half its length. Female antenna is proximally simple. Labial palpi are two-segmented and have rather long vestiture in *stephanius*. An is very low. Lower suture of Apc reaches up to complete length of An. Pre II is moderately short. Mesepimeron is moderately high or nearly rather high. Mesomeron is at least twice (up to 2.5 times) as wide as eucoxa II. Accessory plate III is narrow. Intersclerite III is present or wanting. Male I-epiphysis reaches approx. as far as tibia-apex and is bluntly pointed. Female I-epiphysis is very short. Fifth tarsomere is 1.5 or 2 times length of fourth. Fringes are very short. Number of ♀ frenulum bristles varies from approx. seven to eleven, and these vary from moderately short to long. Dorsum of ♂ hindwing is more or less invaginated. Venation: R1 proximal to areole; areole rather long; R3, R4+5 shortly stalked; R4+5 stalked for most of their length or completely coalescent; M1 posterior to areole; Sc-Rs often distally present in *stephanius*; Rs-M1 moderately long to long in *stephanius*, and moderately short to rather long in *elegans*; M2, M3 sometimes connate in *stephanius*. Forewing base of *stephanius* is shown in fig. 74. Humeral plate is approx. 1.3 times size of radial bridge in *elegans*, and at most as large as radial bridge in *stephanius*. Median plate is moderately long and approx. as wide as Cu2, and has its anterior invagination up to approx. half its length. Median plate is usually well-developed. Anal plate is moderately long.

Section B:

The species of this section lack yellow-orange spots. They have mainly or completely black and white vestiture. The species of this section further differ from the other species in this genus in the following apomorphies: mesepimeron ventrally extended (see fig. 72), eucoxa II narrow and eucoxa III narrow and both approx. as wide as metameron, venation more or less reduced, radial plate plus narrow antero-lateral extension (see fig. 67), abdomen dorsally and laterally with very long tufts, and female abdomen with fur-like tuft at tip. Several of these apomorphies are unique within the Cossidae. The fur-like tuft couldnot be checked in undescribed species (b) and (c), since only the males of them are known.

The state of the radial plate couldnot be checked in undescribed species (b). Unique is that in *myrmeleon* and undescribed species (c) the labial palpi are wanting; the head showing only a tuft of scales on the place. In the other two species the labial palpi are two-segmented and have long vestiture. In the female of *myrmeleon* the Apc vanishes at approx. half length of An. In undescribed species (c) the lower suture of Apc is wanting. The males are moderately small or small and the females are medium-sized. The male forewing has areas which are not covered by scales.

Vertex of *myrmeleon* has slightly arcuate Pos at approx. 0.7 times its length and lacks at least sometimes anterior protuberances. Male antenna is bipectinate for slightly less than or approx. half its length. Female antenna of at least *myrmeleon* and *armstrongi* is simple for approx. half its length. Frons is rather wide. Male eyes of *myrmeleon* vary from moderately large to distinctly reduced. In the other material examined the eyes are reduced in size. Patagium of at least *myrmeleon* is considerably widely curved and more or less sclerotized. Tegula is ventro-posteriorly very blunt. An is seemingly moderately high in undescribed species (c), which is presumably a reversal. An is moderately low in undescribed species (b) and low in *armstrongi* (1♀). An is low in the female of *myrmeleon* and very low in the male of this species. Pre II is moderately short. Subalare-process II is very short and blunt in at least *myrmeleon* and *armstrongi*. Accessory plate III is narrow in at least *myrmeleon* and *armstrongi*. Male I-epiphysis is blunt and reaches nearly or approx. as far as tibia-apex. Female I-epiphysis is moderately long in *myrmeleon* and moderately short in *armstrongi*, and is in both species thin and pointed. Fringes are short or very short. Number of ♀ frenulum bristles amounts approx. ten in *armstrongi* (1 ex.), and varies from approx. nine to twenty in *myrmeleon*, and these are moderately long to short. Anal region is reduced in size and dorsum is invaginated in *myrmeleon* and undescribed species (c). Anal region is distinctly elongate in undescribed species (b). Anal region of hindwing is narrowed but distally elongate in *myrmeleon* and undescribed species (c). Venation (see figs. 93-95): chorda is short or wanting in *armstrongi*; chorda is mostly obsolescent and distally present in undescribed species (b); chorda is wanting in the other species; R3, R4+5 may be connate or even very shortly stalked; R4+5 is mainly stalked in undescribed species (b), and completely coalescent in the other species; M1 at least sometimes from tip of areole in *armstrongi*; M2 sometimes/often wanting in *myrmeleon*; cell of *armstrongi*, *myrmeleon* and undescribed species (c) is distally backward invaginated, but in undescribed species (b) distal margin of cell is normal; CuP and A1+2 are often very close distally, linked by a cross-vein or more or less coalescent in *myrmeleon*; in most species costal region of hindwing is widest at approx. half wing-length, but in undescribed species (c) at approx. two-thirds wing-length; Sc-Rs is wanting in one wing of the holotype and further very short in *armstrongi*; M1 of *armstrongi* is wanting; venation of hindwing especially in *myrmeleon* is further reduced; CuP, A1+2 and A3 with approx. equal distances in between their terminations in *myrmeleon* and undescribed species (b); anal veins are perhaps wanting in undescribed species (c). Wing bases have not been examined in undescribed species (b). Humeral plate of at least *armstrongi* and *myrmeleon* is approx. as large as radial bridge. Median arm is moderately long and as wide as or sligthly wider than Cu2 in at least *myrmeleon* and *armstrongi*. Anal plate is moderately long to/or moderately short. Abdomen has particularly in the female long tufts dorsally and laterally. Female abdomen of at least *myrmeleon* and *armstrongi* has at tip a fur-like tuft of special, grey mixed fuscous scales.

Section A

Callocossus elegans Aurivillius, 1910: 51.

Material. —5♀♀ from Ivory Coast, Sierra Leone and Zaire (BMNH); 1♂, 1♀ (in copula), IVORY COAST: Adiopo [Adiopodoumé ?] (MNHN).

Undescribed species (a)

Material. —1♀, UGANDA (BMNH).

Note. The specimen shows great similarity to *elegans*, but has a rather long and dark frontal tuft.

Zeuzera stephania Druce, 1887: 685, pl. 55: fig. 3.

? *Zeuzerops hyalinipennis* Strand, 1910: 143.

Material. —1♀ (holotype of *stephanius*), MALAWI (BMNH); long series (4♂♂, most ♀♀) from Ivory Coast, Tanzania and Malawi (BMNH).

Section B

Duomitus armstrongi Hampson, 1914-1915: 245.

Material. —1♀ (holotype), GHANA: Aburi, 27.xii.1910, in Coffee (Armstrong) (BMNH); 1♀, SIERRA LEONE: Njala, Guana (BMNH).

Note. The species is a stem-borer in Coffee (see above and Le Pelley, 1968: 209).

Undescribed species (b)

Material. —1♂, IVORY COAST: Adiopodoumé, ix.1965 (Griveaud) (MNHN). Note. Male forewing has a blackish spot in the cell and between CuP and dorsum of the forewing.

Eulophonotus myrmeleon Felder, 1874: pl. 82: fig. 9.

Engyophlebus obesus Karsch, 1900: 3. [Synonymized by Gaede, 1930: 549].

Material. —long series (most ♀♀) from Ghana, Guinea, s. Nigeria, Cameroon, Zaire, Uganda and South Africa (BMNH); 1♀, SOUTH AFRICA: Natal, Durban (RMNH); 1♂, 1♀, ZAIRE: Eala (MRAC); 1♂, IVORY COAST (MNHN).

Note. The larva may cause serious damage to Cocoa (Gaede, 1930: 549). The species also bores in the stem of a species of *Acalypha* L. in Ghana (Forsyth, 1966: 79). A parasite of this species (at least in Ghana) is *Amicrocentrum* (*Amicrocentrum*) *exilis* van Achterberg (Hymenoptera: Braconidae Nees,1812) (van Achterberg, 1979: 16).

Undescribed species (c)

Material. —1♂, tropical Africa (MNHN).

Note. Male has mainly whitish vestiture on head and thorax.

Table 14. Apomorphies in fig. 64 (*Eulophonotus*).

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1. Considerable sexual dimorphism; considerable differences in size and colour pattern.
2. Male eyes varying from moderately large to distinctly reduced in size or only reduced, and ♀ eyes (normally) moderately reduced. When eyes are reduced, frons is widened.
3. Pronotum distinctly reduced in size.
4. Male forewing narrowed.
5. Cell of forewing distally backward invaginated and cell shortened (see figs. 93-95). N.B. Distal margin of cell normal in an undescribed species of *Eulophonotus*.
6. R5 stalked with R4 for more than 0.8 times its length or even completely coalescent.

7a. Humeral plate at most 1.3 times size of radial bridge.
 b. Humeral plate as large as or smaller than radial bridge.
8. Median arm rather wide, approx. as wide as Cu2.

9a. Labial palpi two-segmented.
 b. Labial palpi wanting.
10. Fifth tarsomere 1.5 times length of fourth.
11. Mesepimeron ventrally extended, nearly triangular in shape (see fig. 72).
12. Eucoxa II narrowed, approx. as wide as eucoxa III.
13. Accessory plate II moderately wide to moderately narrow, or only moderately wide.

14. Eucoxa III narrowed, appr, as wide as metameron.
15. Reduction of venation; e.g., chorda present to wanting or only wanting, and M1 or M2 of hindwing wanting.
16. CuP and A1+2 of hindwing terminating at approx. equal distance compared to A1+2 and A3 (see figs. 94-95); these veins distally nearly parallel to each other. N.B. Anal veins of hindwing are perhaps wanting in undescribed species (b).
17. Radial plate plus narrow antero-lateral extension (fig. 67).
18. Abdomen dorsally and laterally with very long tufts.
19. Female abdomen with fur-like tuft at tip.
20. Fringes may consist of bi- and/or multipointed scales. N.B. Shortened fringes generally consist (normally) of ovate scales.
21. CuP, A1+2 and A3 of hindwing approx. parallel distally and with approx. equal distances in between their terminations (see fig. 95)
22. Costal region of hindwing widest at approx. two-thirds wing-length.
23. Hindwing with special shape (figs. 94-95); costal region distally reduced, wing shortened, and male anal region reduced.
24a. Male An very low.
b. An seemingly approx. moderately high.
25a. Female Apc up to half length of An and further (normally ?) vanished.
b. Lower suture of Apc (normally ?) wanting.
26. CuP and A1+2 in forewing normal to distally very close, or linked by a cross-vein or more or less coalescent.

Genus **Zeuzera** Latreille, 1804

Zeuzera Latreille, 1804: 186.
Type species: *Phalaena aesculi* Linnaeus, 1767: 833. [Synonymized with *Phalaena pyrina* Linnaeus, 1761 by Walker, 1856: 1529].
Aegolia Billberg, 1820: 83.
Type species: *Phalaena aesculi* Linnaeus, 1767: 833.
Latagia Hübner, [1820] 1816: 196. [Synonymized by Walker, 1856: 1528].
Type species: *Phalaena aesculi* Linnaeus, 1767: 833.

As with *Xyleutes* the genus name *Zeuzera* had often been used for many species from various other sections; the genus had become a mixture of various genera. In *Zeuzera* the aculeate area at the mesepimeron and the corresponding one at the basis of the forewing are wanting. The labial palpi are two-segmented. Pre II is moderately short. The subalare-process II is very short. A cross-vein Sc-Rs is present. The humeral plate is nearly triangular in shape. The radial plate has the typical shape of section 2A. The anal plate varies first from moderately long to moderately short and becomes shorter higher in the cladogram (fig. 66). The species are whitish with blackish or dark fuscous markings, and these markings have a greenish or bluish metallic lustre. See also the cladogram (fig. 66).

Frons in female is often prominently medio-dorsally bulbed. Vertex is more or less swollen, has Pos at nearly 0.5 to 0.6 times its length, and has (usually ?) small anterior protuberances (fig. 87). Antenna in male is bipectinate for approx. 0.5 to 0.6 times its length. Antenna in female of *caudata* Joicey & Talbot, 1916, *postexcisa* Hampson, 1893 and *aeglospila* Turner, 1915 is proximally indistinctly bilobed. In these three species vestiture on ♀ antenna is in longitudinal rows. In the other species the ♀ antenna is proximally simple. Labial palpi are short to very short. Sections of tho-

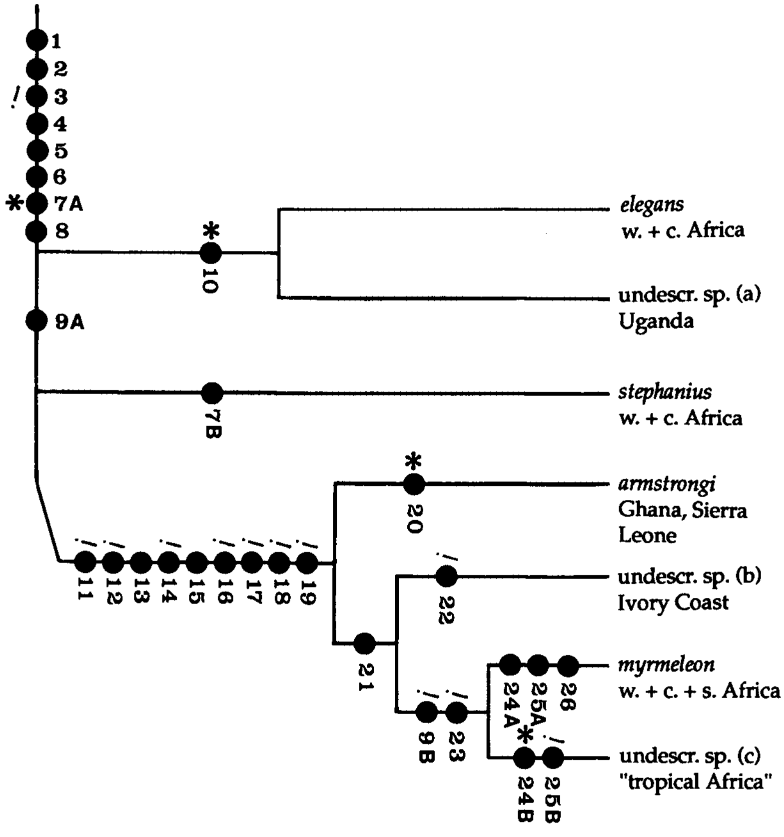


Fig. 64, cladogram of *Eulophonotus*.

rax of *pyrina* are shown in fig. 82. An varies from moderately high to moderately low amongst the species. Lower suture of Apc reaches up to from 0.8 to 1.0 time length of An. Mesepimeron is moderately high. Accessory plate II is (moderately) narrow in certain species. Mesomeron is at least twice width of eucoxa II. Intersclerite III is (normally) wanting, but in *indica* Herrich-Schäffer, [1854] still present. Accessory plate III is (usually) narrow. I-epiphysis in female is small to very small and pointed (figs. 70-71), but in *conferta* Walker, 1856 minute to wanting. Fifth tarsomere is in most species 2 to 2.5 times length of fourth. In *coffeae* Nietner, 1861, *lineata* Gaede, 1933 and the unnamed species (closely resembling the latter) fifth tarsomere is shortened and only 1.5 to 2 times length of fourth. In certain species tarsi are allover dark fuscous or blackish. Invagination of dorsum of hindwing varies amongst the species from very weak to distinct. Venation (see also fig. 96): areole moderately to rather long and moderately wide; R1 proximal to or from areole; R3, R4+5 connate to shortly stalked; R4+5 stalked for 0.4 to 0.7 times their length, and in *conferta* for 0.7 to 0.8 times; M1 usually posterior to areole; Sc-Rs in most species short to very short, but in *caudata* rather long; in *pyrina* sometimes an extra cross-vein Sc-Rs more proximally;

Rs-M1 in most species moderately to rather long but long or short in certain species. Wing bases of *pyrina* are shown in fig. 65. Humeral plate is still twice size of radial bridge in *indica*, and in the other species at most 1.5 times as large. Median arm is variable in length and width amongst the species. Median plate is at least sometimes reduced in length and/or narrowed in certain species. 2Ax has sometimes/often an elevated scaled area. Anal plate varies inter- and intraspecifically and is very short in quite a few species.

Most of the species included most closely resemble one another in their external features. See a.o. Roepke (1955; 1957) and Holloway (1986) for descriptions of a great number of them. The relative ratios in length of the tarsomeres can be very helpful for identifications. Seitz (1912: 428) explains that the colour pattern of these species must be regarded as warning colours.

Z. indica seems to take the first branch in the cladogram (fig. 66). This is the largest species and it has a wide range in the Oriental region and even occurs in Australia. This species still has an intersclerite III. A special subgroup is formed by *aeglospila*, *caudata* and *postexcisa*. These species have normally dark blocks and stripes on the thorax, but in the subspecies *caudata caudata* the thorax is dotted. The ♀ antenna is proximally indistinctly bilobed in these species, whereas in the others it is simple. Besides the vestiture on the ♀ antenna is in longitudinal rows, a special feature of this subgroup. Amongst the rest of the species the median arm and accessory plate II vary in length and/or width, but not in a way that a cladogram could be produced. In certain of these species R1 branches at least sometimes off from areole, which is considered a reversal.

Zeuzera (*Azygophleps*) *ariana* Grum-Grshimailo (1899: 468) seems not to belong to *Zeuzera* and *Azygophleps*, since it is mainly ochreous according to the original description. Its status remains obscure.

Zeuzera indica Herrich-Schäffer, [1854] 1850-1858: 58, fig. 166.

Zeuzera paucipunctata Walker, 1856: 1537. [Synonymized by Moore, 1881: 327].

Range: India, throughout southeast Asia eastward to Philippines, New Guinea and Australia.

Material. —1♂ (holotype of *indica*), BANGLADESH: Sylhet (ex musaeo Boisduval) (ex coll. Oberthür) (MNHN); 1♀ (holotype of *paucipunctata*), ? (BMNH); long series of both sexes from Bengal, Malaysia, Indonesia and Philippines (BMNH); long series of both sexes from Indonesia (RMNH and ITZ).

Zeuzera aeglospila Turner, 1915: 53-54.

Range: Australia (Queensland).

Material. —2♂♂, 2♀♀, AUSTRALIA: Cairns district (BMNH); 4♂♂, 6♀♀, ? (MNHN).

Zeuzera caudata Joicey & Talbot, 1916: 88-89.

Zeuzera rhabdota Jordan, 1932: 24-25. [Synonymized by Roepke, 1955: 283].

Zeuzera celebensis Roepke, 1957: 17-18. **Syn. nov.**

Range: Japan, Malaysia, Indonesia and Solomon Islands (Holloway, 1986: 32).

Material. —1♂ (holotype of *caudata*), INDONESIA: Irian Jaya, Wandammer Mts., 3000-4000 ft., xi.1914 (Pratt) (coll. Joicey) (BMNH); 1♂ (holotype of *celebensis*), INDONESIA: northern Sulawesi, Gorontala (coll. Van den Bergh) (ITZ); 7♂♂, PAPUA NEW GUINEA: various localities, -3600 ft. (BMNH); 3♂♂, INDONESIA: Irian Jaya, -2000 ft. (BMNH); 1♂, PAPUA NEW GUINEA: Goodenough Island, 2500-4000 ft. (BMNH); 2♂♂, INDONESIA: central BURU, Kako Tagalago, 2700 ft. (BMNH); 5♂♂, INDONESIA: Irian Jaya (ITZ); 1♂, INDONESIA: Sumatra, near Padang, 300 m. (RMNH); 1♀, INDONESIA: Sumatra, Padang (MNHN).

Note. Roepke (1957: 17-18) already states that perhaps in the future *celebensis* may prove to be a subspecies of *caudata*. Since there are no good differences in the external features and genitalia

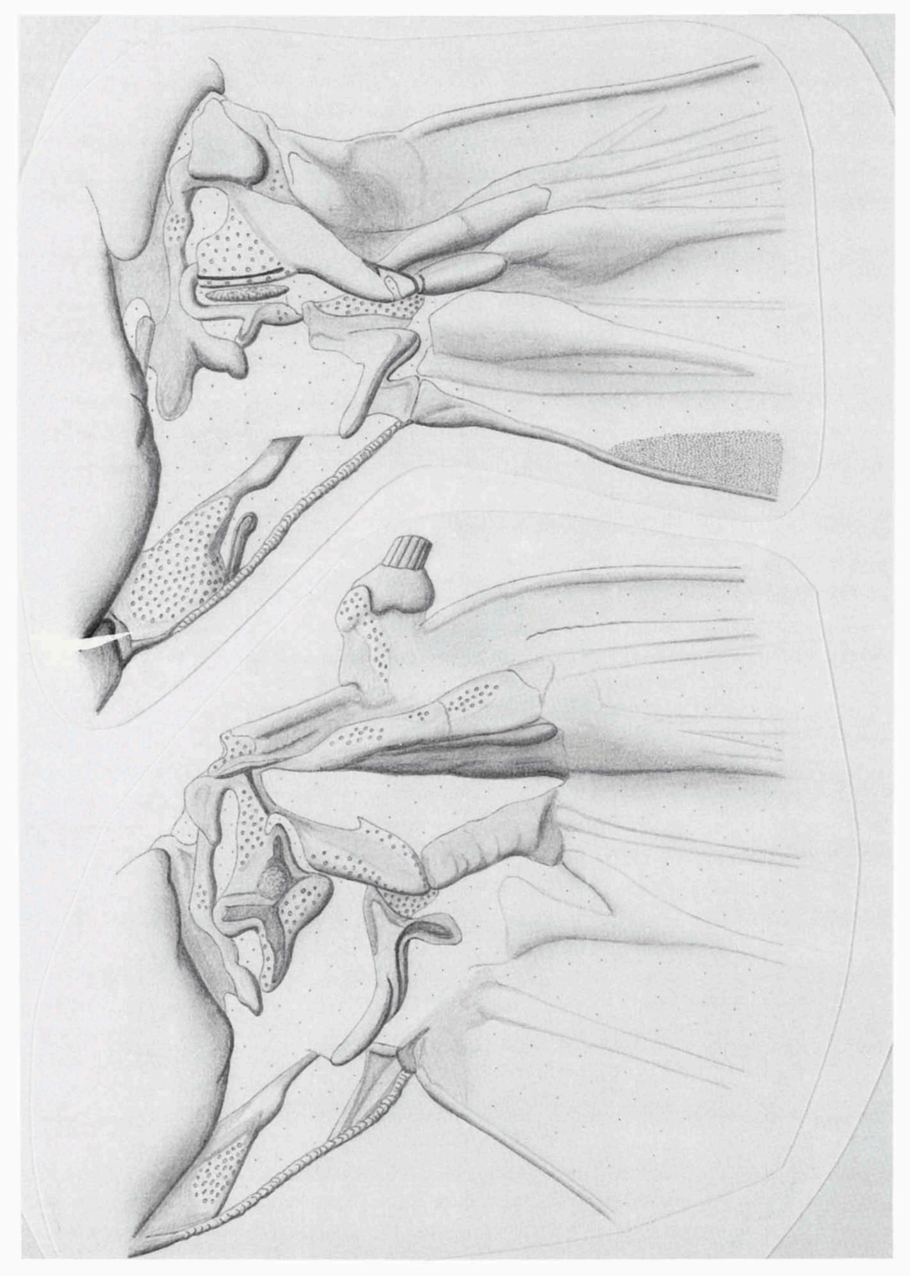


Fig. 65, wing bases of *Zeuzera pyrina*, Germany, Herkulesbad.

characters, *Z. celebensis* is here synonymized with *Z. caudata*. The author does not know if *celebensis* is a good subspecies. The thorax of *celebensis* shows a block-pattern more or less similar to that in the subspecies *rhabdota*, which is known only from Sumatra. The subspecies *caudata* is recorded from New Guinea, Buru and Solomon Islands (Roepke, 1957: 14).

Zeuzera postexcisa Hampson, 1893: 68, pl. 159: fig. 18 (male).

Range: India, Sri Lanka and Indonesia (Java) (Arora, 1976: 142).

Material. —1♂ (holotype), SRI LANKA (coll. Green) (BMNH); 5♂♂, 1♀, SRI LANKA: Maskeliya, Shevaray Hills, Kandy and Kitulgala (BMNH).

Note. A host is *Phoebe excelsa* Nees (Arora, 1976: 139).

Phalaena pyrina Linnaeus, 1761: 306. [The Leopard Moth].

Phalaena aesculi Linnaeus, 1767: 833. [Synonymized by Walker, 1856: 1529].

Zeuzera octopunctata Boisduval, 1832: 181, pl. 68: fig. 6 (male). [Synonymized by Gaede, 1933a: 244].

Zeuzera decipiens Kirby, 1892: 871. [Synonymized by Dyar, 1940: 1268].

Range: Throughout Europe, west to Ireland (Skinner, 1985: 71), northwest to Norway up to approx. 61°N (Opheim & Fjeldså, 1983: 18-19), and also occurring on Corsica, Sicily and Cyprus; known from Morocco and Algeria; east to U.S.S.R. (Vladivostok); and imported into U.S.A. (New York) (see Barnes & McDunnough, 1911: 20).

Material. —very long series of both sexes from United Kingdom, West Germany, East Germany, France, Italy (including Sicily), Greece (Cyprus), Morocco, Algeria, Egypt, Lebanon, [Kurdistan], U.S.S.R. (Vladivostok) and China (BMNH); long series of both sexes from Portugal (Lisboa), Spain (Santander and Abarracin-1200 m.), France (e.g. Corsica), Italy (Sila Grande-1100 m., Mt. Sambughetti-1200 m., Mt. Castelli-1050 m., Desenzano, Bologna, Sicily), Switzerland (Lugano), Austria (Stiermark), Yugoslavia (Dalmatia), and Cyprus (Limassol) (ITZ); long series of both sexes, NETHERLANDS (RMNH); 1♂, U.S.A.: New York (RMNH).

Note. Schultz (1905: 121-122) describes an aberration in colour pattern and names it *conflua*. Stichel (1918-1919: 199-200, fig. 2) distinguishes a form *paulomaculata*. Haggett (1950) provides information approx. the life-history, including a list of host-plants. Hackray et al. (1985: 33) gives a long list of food-plants. The species has a wide host-plant range. The larvae occasionally cause damage of economic importance to e.g. fruit trees (Skinner, 1895: 71).

Zeuzera biebingeri Speidel & Speidel, 1986: 82-84, figs. (adult and genitalia).

Material. —1♂ (paratype), GREECE: Crete, Vrysses, 60 m., 6.vi.1967 (coll. Reisser) (LNK); 1♂, 1♀ (paratypes), GREECE: Crete, Assites, 550 m., 14.vi.1958 (coll. Reisser) (LNK).

Zeuzera multistrigata Moore, 1881: 327.

Zeuzera leuconotum Butler, 1881: 22. [Synonymized by Daniel, 1962a: 7].

Range of subspecies *multistrigata*: Iran, northern India, China (Province Yuennan, Shansi and southern Shensi) (Daniel, 1962: 7; 1963: 153). Range of subspecies *leuconotum*: China (Province Chekiang), Korea, China/U.S.S.R. (Ussuri region), Japan and Taiwan (Daniel, 1962: 7). Further known from Philippines and Taiwan (Ulenberg et al., 1986: 34), and from Bangladesh and Burma (Arora, 1976: 138).

Material. —1♂ (holotype of *multistrigata*), INDIA: Darjiling (coll. Moore) (BMNH); 1♀ (holotype of *leuconotum*), JAPAN: Tokei (BMNH); long series of both sexes from Japan (ssp. *leuconotum*), and further India, Bhutan and upper Burma (BMNH); 4♂♂, 2♀♀, INDIA: Khasi Hills, Assam (ITZ); 10♂♂, INDIA: Assam and Chera (RMNH); 5♂♂, 1♀, INDIA: Jainta Hills, Tsekou, Sikkim and Darjeeling (MNHN); 9♂♂, ? (MNHN).

Note. The species is known to mine in: *Quercus*, *Buxus* L. and *Streblus* Lour. (Inoue et al., 1983); *Cryptomeria japonica* (L.f.), *Ilex* L., *Mahonia nepalensis* DC., *Mussaenda frondosa* L., *Pyrus malus* L., *Santalum album* L. and *Quercus lineata* Bl. (Arora, 1976: 236); In The Netherlands the species was found in bonsais of resp. a *Buxus* species from Taiwan and of *Streblus asper* Lour. from Philippines (Ulenberg et al., 1986: 34).

Zeuzera nepalense Daniel, 1962a: 7.

Not examined. From Nepal (Tukucha) and India (Sikkim and Gangtok).

Zeuzera yuennani Daniel, 1940: 1016-1017, pl. 30: figs. 15-16.

Not examined. From China (North Yuennan) and Tibet (Yangtse Valley).

Zeuzera nuristanensis Daniel, 1964b: 6.

Not examined. From Afghanistan.

Zeuzera borneana Roepke, 1957: 14-15, pl. 2: fig. 1 (male).

Range: Indonesia (east Kalimantan).

Material. —1♂ (holotype), INDONESIA: e. Kalimantan (Quarles de Quarles) (RMNH); 1♂ (paratype), INDONESIA: e. Kalimantan, Kariorang (Quarles de Quarles) (RMNH).

Note. Markings on the moth with greenish lustre. Forewing with a larger spot over bases of CuA up to A1+2; rest of wing moderately spotted, but less than in e.g. *coffeae*.

Zeuzera lineata Gaede, 1933b: 812, pl. 96: fig. row b (male).

Range: Malaysia and Indonesia.

Material. —1♂ (holotype), MALAYSIA: Sabah, Kinabalu (Waterstr.) (MHUB); 4♂♂, INDONESIA: Sumatra, N. Korintji Valley, 5000 ft., and Mt. Tanggamus, 2100 m. (RMNH); 2♂♂, INDONESIA: s.w. Sumatra, slopes of Mt. Korintji, 5000-7300 ft. (BMNH); 1♂, MALAYSIA: Sarawak, Baram (BMNH).

Undescribed species

Material (all INDONESIA: Sulawesi). —3♂♂, Dumoga Bone, 1000-1400 m. (RMNH); 2♂♂, Minahassa, Mt. Muajat, 1780 m. (ITZ); 1♂, Minahassa (ITZ); 3♂♂, s.w. Sulawesi, district Goa, Malino, 1100 m. (ITZ); 1♂, s.w. Sulawesi, Ereng-Ereng, 500 m. (ITZ); 2♂♂, w. Sulawesi, Palu, Mt. Rangkunan, 1800 ft. (BMNH); 1♂, w. Sulawesi, Palu, Mt. Tompu, 2700 ft. (BMNH).

Note. Most closely resembling *lineata*, but has a dark fuscous, V-shaped marking in the cell of the forewing, and the veins in the central region of the hindwing darkened.

Zeuzera conferta Walker, 1856: 1536.

Zeuzera roricyanea Walker, 1862: 177. [Synonymized by Holloway, 1986: 32].

Zeuzera neuropunctata Gaede, 1933b: 812, pl. 96: fig. row b (male). [Synonymized with *roricyanea* by Toxopeus, 1948: 171].

Range: n.e. Himalaya, Indochina and Indonesia (east to New Guinea) (Holloway, 1986: 32); further known from Bangladesh and Philippines.

Material. —1♀ (holotype of *conferta*), BANGLADESH: Sylhet (BMNH); series, INDONESIA: Sumatra, Kalimantan, Sulawesi and Irian Jaya (RMNH); 1♂, PHILIPPINES: Culion Isl., San Pedro (RMNH); long series of both sexes from Vietnam, Selangor, Sarawak, Kalimantan, Sumatra, Java, Sulawesi, and Obi Major (BMNH).

Note. This species can easily be recognized by the yellow ringed tarsi. Hosts are Cocoa, Balsa, *Barringtonia* J. R. & G. Forst., and probably Coca (Toxopeus, 1948: 174).

Zeuzera coffeae Nietner, 1861: 21-22. [The White Borer or Red Coffee Borer].

Zeuzera oblita Swinhoe, 1890: 198, pl. 6: fig. 9. [Synonymized by Hampson, 1982: 313].

Zeuzera reticulata Joicey & Talbot, 1916: 89. [Synonymized by Roepke, 1955: 282].

Zeuzera buergersi Gaede, 1933b: 812. [Synonymized by Roepke, 1955: 282].

Range: Pakistan, India, Sri Lanka, Thailand, Malaysia, Taiwan, Indonesia (including Krakatau) and Papua New Guinea.

Material. —1♂ (holotype of *buergersi*), INDONESIA: Irian Jaya, Mäanderberg, 670 m., 7.viii.1913 (Bürgers) (MHUB); long series of both sexes from most countries of its range (BMNH); long series of both sexes from Indonesia (RMNH and ITZ).

Note. Nietner (1861: 21) provides a description of the larva and notes that it destroys many young and old plants of Coffee in Sri Lanka. A long list of hosts is given by Dammerman (1929: 71-72), Toxopeus (1948: 170), Beeson (1961: 446), and Arora (1976: 130). Remarkable is that the hosts belong to many genera of different families. Certain hosts are of economic importance; e.g., Coffee, Tea, Cotton, Cocoa, Kapok, Coca, and Teak. Toxopeus (1948: 167-170) distinguishes the subspecies *oblita*, *coffeae*, and the new *virens* from Java. Arora (1976: 134-135) describes a fourth subspecies, *angulata*, from India.

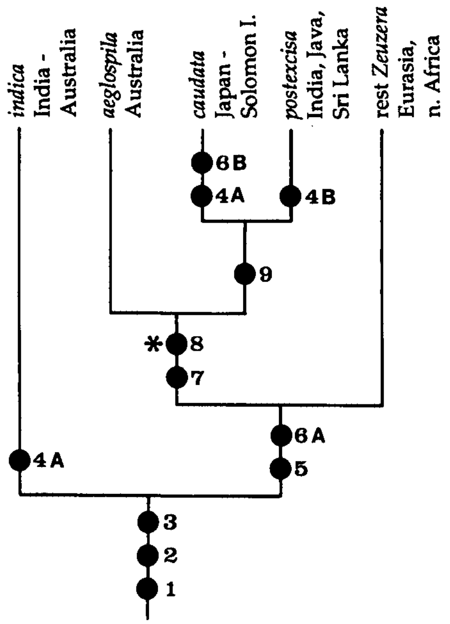


Fig. 66, cladogram of *Zeuzera*.

Table 15. Apomorphies in fig. 66 (*Zeuzera*).

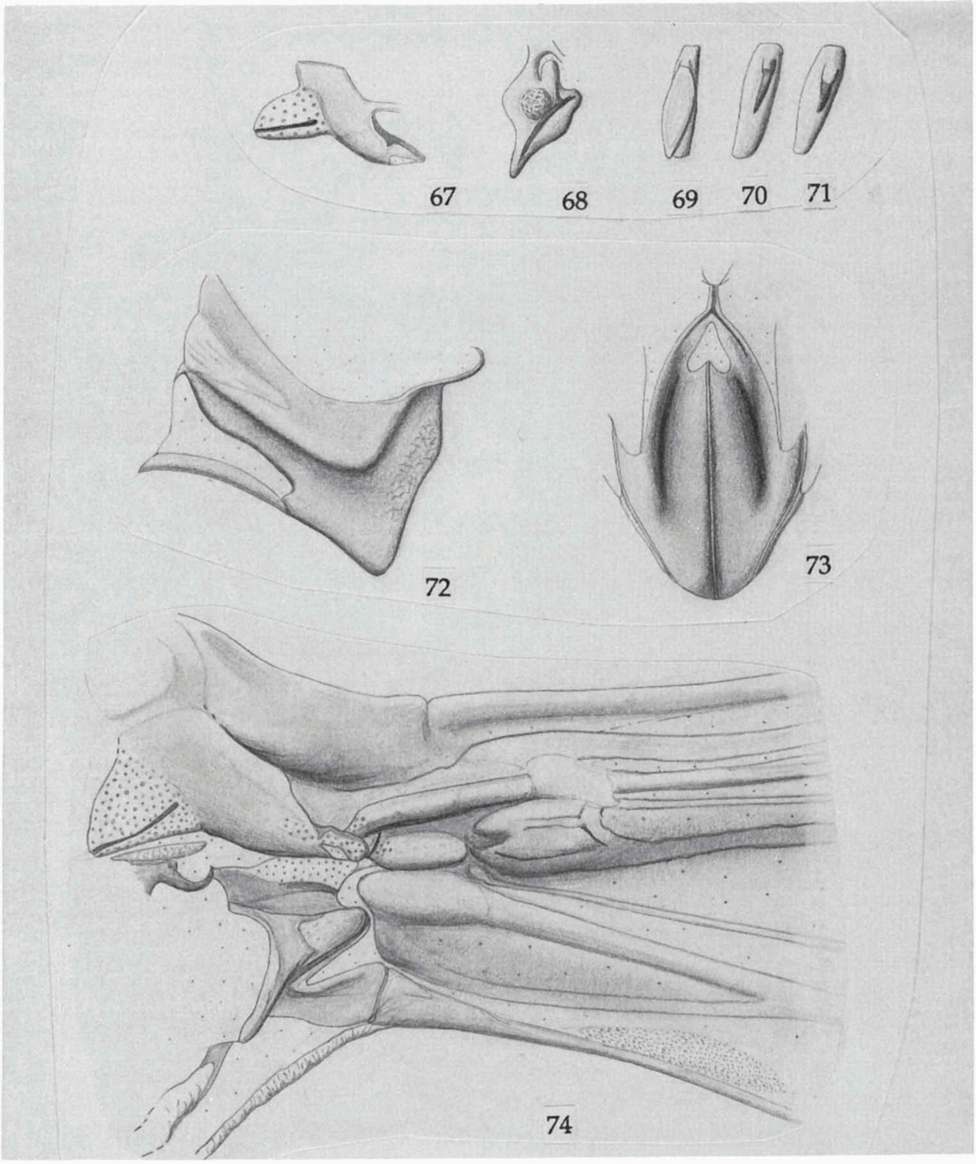
1. Cross-vein Sc-Rs present.
2. Humeral plate approx. triangular in shape.
3. Anal plate moderately long to moderately short.
4a. Median arm moderately long to rather short.
 b. Median arm rather long, with the anterior invagination up to $^1/_4$ its length.
5. Accessory plate II moderately wide to narrow or only narrow.
6a. Humeral plate at most 1.3 times size of radial bridge.
 b. Humeral plate 0.8 to 1 time size of radial bridge.
7. Vestiture on ♀ antenna in longitudinal rows.
8. R1 proximal to distinctly from areole.
9. Anal region of hindwing prominently extended in the male, and in the female of *postexcisa* and *caudata*.

Genus **Hermophyllon** gen. nov.

Type species: *Endoxyla anceps* Snellen, 1900: 40.

Etymology: "Hermes" is a Greek god + "phyllon" (Greek) means leaf. Gender: neuter.

H. anceps differs from actual *Endoxyla* species in that e.g. its radial plate is distally elongate with a rather slender apex, the aculeate area at the mesepimeron is wanting, and Pre II is moderately short. It differs from species of *Zeuzera* in the following characteristics: female eyes slightly reduced in size, humeral plate rounded and nearly quadrangular, anal plate varying from moderately to rather long, and cross-vein Sc-Rs wanting. *H. anceps* has yellow-buff wings with blackish markings and thus does not look like a species of *Zeuzera*. It has further the following apomorphies: labial palpi two-segmented, tegula ventro-posteriorly very blunt, An moderately low, lower suture of Apc reaching up to approx. 0.8 or 1.0 time length of An, subalare-process II very short, ♀ I-epiphysis rather short and distinctly shorter than ♂ one, fifth tarsomere 2.5 times length of fourth, arolium and paronychia wanting, fringes very short, R1 proximal to areole, and median arm moderately long. The ♀ I-epiphysis is moderately wide and blunt and not as short as in most species of section 2A, which is considered a reversal. *H. anceps* does not fit in *Zeuzera* or any other available genus and seems to stand on a lonely place in the cladogram (fig. 76). Therefore a new genus is established for it.



Figs. 67-74, sections of zeuzerine species. 67, radial plate of *Eulophonotus armstrongi*; 68, 2Ax of a zeuzerine species with an elevated area; 69, tibia of proleg of male *Zeuzera pyrina*; 70-71, tibiae of prolegs of females *Z. pyrina*; 72, mesepimeron and accessory plate II of *Eulophonotus armstrongi*; 73, basisternum II of *Phragmacossia territa*; 74, forewing base of *Eulophonotus stephanius*.

Male antenna is bipectinate for nearly half its length. Female antenna is proximally simple. Tegula is ventro-posteriorly very blunt. An is moderately low. K is rather long, moderately narrow, and has at least sometimes a cross-suture. Subalare-process II is very short and blunt. Mesepimeron is moderately high. Accessory plate II is wide. Mesomeron is approx. twice width of eucoxa II. Intersclerite III is (normally ?) present, but small. Accessory plate III is narrow. Male I-epiphysis is blunt and reaches nearly as far as tibia-apex. I-epiphysis of female reaches distinctly short of tibia-apex. Number of ♀ frenulum bristles varies from approx. six to ten and these are moderately short. Dorsum of hindwing is in both sexes distinctly invaginated. Venation: areole moderately long and moderately wide; R1 proximal to areole; R3, R4+5 shortly stalked; R4+5 stalked for 0.5 to 0.8 times their length; M1 from tip of or posterior to areole; Rs-M1 moderately short. Humeral plate is twice size of radial bridge. 1Ax is apically large. Distal plate of 4Ax is anteriorly distinctly reduced. Median arm is moderately long and moderately wide, and has the anterior invagination up to approx. $^{1}/_{3}$ its length. 2Ax lacks elevated scaled area.

The figure of *Xyleutes plesseni* Schultze (1925: pl. 1: fig. 5) shows the easily recognizable *anceps* and the description corresponds with the latter. Therefore, *Xyleutes plesseni* is synonymized with *Endoxyla anceps*.

The only specimen in the MHUB which has been identified by Gaede as *plesseni* corresponds with the specimen figured by Seitz (1934: pl. 99: fig. row d) with the name *tigrina*. This specimen is from Perak as noted by Gaede (1933b: 818-819). The figure with the name *plesseni* (Seitz, 1934: pl. 99: fig. row d) appears to concern *Endoxyla tigrina*. Apparently the captions of the figures have been interchanged. The specimen of *plesseni* sensu Gaede is here identified as belonging to a probably undescribed species of the new genus *Panau*.

Endoxyla anceps Snellen, 1900: 40.

Xyleutes plesseni Schultze, 1925: 571-572, pl. 1: fig. 5 (male). Syn. nov.

Range: Malaysia (Sabah), Indonesia (Sumatra, Nias, Kalimantan and Java) and Philippines.

Material. —3♂♂, MALAYSIA: Sabah, Tawau distr. and distr. Sandakan (BMNH); 1♂, PHILIPPINES (BMNH); 3♂♂, BRUNEI: Ulu Temburong (BMNH); 4♂♂, 1♀, INDONESIA: w. Sumatra, Nias and Java (BMNH); 2♂♂, 4♀♀, INDONESIA: w. Sumatra, w. Java and e. Kalimantan (RMNH).

Note. The label of one ♀ specimen from Padang is with "*Derris* branch" (*Derris* Lour.), and that of one female from Tjipetir (w. Java) with "ex stem of *Derris elliptica*" (*Derris elliptica* Benth).

Genus **Cecryphalus** gen. nov.

Type species: *Zeuzera nubila* Staudinger, 1895: 341.

Etymology: "kekryphalos" (Greek) means hairnet. Gender: masculine.

Cecryphalus is established for *nubilus* and *Zeuzera helenae* Le Cerf, 1924. Their body and wings are darker and more striated than in species of *Zeuzera*. They further differ from *Zeuzera* species in the following characteristics: An very low, ♂ I-epiphysis pointed and in *helenae* even slender, vestiture on tarsi long, and chorda terminating very closely to or partly coalescent with anterior M. The genus is further characterized by: labial palpi two-segmented, tegula ventro-posteriorly very blunt, sutures of Apc posteriorly diverging, lower suture of Apc reaching up to from 0.7 to 0.8

times length of An in *nubilus* and up to approx. 0.7 times length in *helenae*, Pre II moderately short, subalare-process II very short, aculeate area at mesepimeron wanting, accessory plate II moderately wide, ♀ I-epiphysis short and moderately slender, fifth tarsomere 2.5 times length of fourth, arolium and paronychia wanting, fringes very short, R1 proximal to areole, humeral plate as large as radial bridge, 1Ax apically large, radial plate distally elongate with slender apex, and distal plate of 4Ax anteriorly distinctly reduced. The species are medium-sized. See also figs. 62, 76 and 75.

Vertex of *nubilus* is gradually swollen with a suture at approx. 0.7 times length of vertex, and has at least sometimes anteriorly small pits instead of protuberances (see fig. 88). Eyes are perhaps slightly reduced in the female of *helenae*. Male antenna is bipectinate for approx. 0.4 times its length. Female antenna is proximally bilobed. Pre II is moderately short and slightly shorter than in *Zeuzera*. K is moderately long and moderately wide, and has a cross-suture. Mesepimeron is moderately high. Mesomeron is approx. twice width of eucoxa II. Accessory plate II is moderately wide. Accessory plate III is narrow. Intersclerite III is at least sometimes wanting. Fifth tarsomere is 2.5 times length of fourth. Number of ♀ frenulum bristles is more than ten and these are moderately short in *nubilus*, and approx. eight and moderately long in *helenae* (1 ♀). Dorsum of hindwing is distinctly invaginated in male of *nubilus* and in both sexes of *helenae*. Venation: R3, R4+5 shortly stalked; R4+5 stalked for more than half their length; M1 from areole; M2, M3 in forewing sometimes very close or connate; in 1 ex. of *nubilus* a cross-vein present in between chorda and anterior M; Sc-Rs sometimes present in *nubilus* and usually present in *helenae*; Rs-M1 long. Humeral plate is more or less ovoid in shape with a slight indent anteriorly. Median arm is moderately long, moderately wide, and has the anterior invagination up to $^{1}/_{4}$ to $^{1}/_{3}$ its length. Median plate is not reduced. 2Ax has at least sometimes elevated scaled area. Anal plate is moderately long.

Zeuzera nubila Staudinger, 1895: 341.

Zeuzera strix Grum-Grshimailo, 1895: 292. [Synonymized by Staudinger, 1896: 401].

Zeuzera speyeri Austaut, 1897: 45. [Synonymized by Seitz, 1912: 429].

Material (all BMNH). —1♂ (holotype of *speyeri*), IRAN: Abisata; series (most ♂♂, 1♀), U.S.S.R.: Repetek, Imambaba, Baigacum, Mary, Kushka and Maralbasa.

Zeuzera helenae Le Cerf, 1924: 27.

Material. —1♂ (holotype), 1♀ (paratype), MOROCCO: Meknès, vii. 1909 (MNHN); 2♀♀, ? (MNHN); 1♂, ? (BMNH); 1♀, ALGERIA: Hassi Bahbah, El Mesroue (BMNH).

Genus **Tarsozeuzera** gen. nov.

Type species: *Zeuzera kochi* Semper, 1896-1902: 439-440.

Etymology: "tarsos" (Greek) means foot + genus-name *Zeuzera*. Gender: feminine.

The last group of section 2A shows a thickened first tarsomere of the proleg and/or midleg. This is a unique feature amongst the Cossidae and separates four species from the rest. Two of the four species are undescribed ones from Africa and the named ones are *kochi* and *Duomitus fuscipars* Hampson, 1892. The four share with *Cecryphalus* species that the chorda terminates very closely to anterior M or is more or less coalescent with the latter. Since the four species (seemingly) form a separate monophyletic group, a new genus is proposed for them.

The male forewing is partly sparsely and minutely dark scaled and thus partly semi-transparent. The male wings show a pale area with dark striae in the anal region. *Tarsozeuzera* is further characterized by the following apomorphies: labial palpi two-segmented, tegula ventro-posteriorly very blunt, lower suture of Apc reaching up to at least 0.7 times length of An, Pre II moderately short, subalare-process II very short, aculeate area at mesepimeron wanting, tarsi with long vestiture (reversal), fifth tarsomere at least 1.5 times length of fourth, arolium and paronychia wanting, fringes very short, number of ♀ frenulum bristles more than five, R1 proximal to areole, radial plate distally elongate with slender apex, 1Ax apically large, distal plate of 4Ax distinctly reduced anteriorly, and anal plate moderately long.

Only of *kochi* the female is known. Vertex of *fuscipars* is very similar to that in C. *nubilus* (see fig. 88). Male antenna is bipectinate for approx. half its length. Female antenna of at least *kochi* is proximally simple. An is low in *fuscipars* and undescribed species (a), and very low in *kochi*. Lower suture of Apc reaches up to 0.7 times length of An in *fuscipars* and up to approx. complete length of An in the other species, and these sutures are parallel. K is plus or without a cross-suture. Accessory plate II is moderately narrow in *fuscipars* and undescribed species (a). Intersclerite III is sometimes/often completely present but small. Male I-epiphysis reaches little short of or approx. as far as tibia-apex in *nubilus* and *fuscipars*. Male I-epiphysis of the undescribed species reaches distinctly short of tibia-apex, which is presumably a reversal. Male I-epiphysis of *fuscipars* is blunt, whereas in the other species moderately slender and bluntly pointed. I-epiphysis is in female of *kochi* rather short, slender and pointed. Fifth tarsomere of *kochi* is 2.5 to 4 times length of fourth. In undescribed species (b) fifth tarsomere is 1.5 to 2 times length of fourth, and in the other two species only 2 times. Hindwing is weakly to moderately invaginated at approx. CuP. Number of ♀ frenulum bristles varies from approx. ten to fifteen in *kochi* and these are moderately short. Venation (see also fig. 97): areole moderately long and moderately to rather wide; chorda of *kochi* varying from shortly separate from to connate with anterior M, and in the other species chorda more or less coalescent with anterior M; R1 proximal to areole; R3, R4+5 (very) shortly stalked; R4+5 stalked for 0.7 to 0.8 times their length; M1 from areole; in *kochi* and *fuscipars* a cross-vein Sc-Rs present; in *kochi* this cross-vein very short or Sc and Rs varying from connate to shortly coalescent; Rs-M1 long in *kochi*, and in the other species moderately or rather long. Humeral plate of *kochi* is 1.5 times size of radial bridge and is sometimes nearly triangular in shape. In the other species humeral plate is as large as radial bridge, more or less ovate and slightly indented anteriorly. Median arm is rather long in *fuscipars* and moderately long in the other species. Anterior invagination of median arm varies in length amongst the species. Median plate is often reduced to half its length. 2Ax lacks elevated scaled area.

Zeuzera kochi Semper, 1896-1902: 439-440.

Range: Indonesia and Philippines.

Material (all BMNH). —1♂, INDONESIA: Sulawesi, Dumoga-Bone; 1♀, INDONESIA: Sulawesi, Palu, Mt. Rangkunau, 1800 ft.; 9♂♂, 4♀♀, PHILIPPINES: Manila.

Duomitus fuscipars Hampson, 1892: 309.

Range: northern India, and Malaysia and Borneo (Barlow, 1982: 42).

Material. —1♂ (holotype), INDIA: Sikkim, 1887 (Möller) (coll. Elwes), Gen. slide Cossidae no. 96 (BMNH); 1♂, INDIA: Gopaldhara (BMNH).

Note. According to Barlow (1982), the species feeds in *Gliricidia* Kunth. in India.

Undescribed species (a)

Material: 1♂, SOUTH AFRICA: Durban (Clark) (BMNH).

Note: Most closely resembling *kochi* and *fuscipars*, but has the first tarsomere of as well the proleg as the midleg much thickened.

Undescribed species (b)

Material. —1♂, ZAIRE: Dimonika, 11/12.ii.1978 (Menier) (MNHN).

Note. Very similar to the previous species, but only the proleg has the first tarsomere thickened and this tarsomere is 1.5 times length of the second instead of twice as long, as in the previous species.

Table 16. Apomorphies in fig. 75 (*Cecryphalus* and *Tarsozeuzera*).

1a. An very low. (*)
b. An low. N.B. Not examined in undescribed *Tarsozeuzera* species (b).
2a. Accessory plate II moderately wide.
b. Accessory plate II moderately narrow.
3. At least first tarsomere with rather long or long vestiture on dorsal side.
4a. Anterior M of forewing terminating very closely to to partly coalescent with chorda (see fig. 97).
b. Anterior M and chorda partly coalescent.
5a. Humeral plate approx. as large as radial bridge.
b. Humeral plate 1.5 times size of radial bridge.
6a. Lower suture of Apc up to 0.7 or 0.8 times length of An and sutures posteriorly diverging.
b. Lower suture of Apc up to 0.7 times length of An.
7a. Male I-epiphysis bluntly to distinctly pointed.
b. Male I-epiphysis reaching little to distinctly short of tibia-apex.
c. Male I-epiphysis slender and reaching distinctly short of tibia-apex.
8. Frontal tuft very long.
9a. First tarsomere of proleg more or less thickened.
b. First tarsomere of proleg and midleg much thickened.
10. R5 stalked with R4 for 0.7 to 0.8 times its length.
11a. Fifth tarsomere 2.5 to 4 times length of fourth.
b. Fifth tarsomere 1.5 to 2 times length of fourth.
12. Male retinaculum only moderately long.
13. Median arm rather long, with the anterior invagination up to $^{1}/_{4}$ or $^{1}/_{5}$ its length.
14. Cross-vein Sc-Rs (normally) wanting.

Table 17. Apomorphies in fig. 76 (section 2A - part 2).

1. Male wings partly not completely covered by scales.
2. Median arm moderately long.
3. R1 proximal to areole. (*)
4. Subalare-process II very short; subalare II nearly anteriorly rounded.
5. Labial palpi two-segmented.
6. An very low.
7. Accessory plate II only moderately wide.
8. Tarsi: at least first tarsomere with rather long or long vestiture on posterior side.

9. Chorda terminating very closely to anterior M or more or less coalescent with the latter.
10a. Humeral plate approx. 1 to/or 1.3 times size of radial bridge.
b. Humeral plate 2 to 2.3 times size of radial bridge.
c. Humeral plate at most 1.3 times size of radial bridge.
11. First tarsomere of proleg and/or midleg distinctly thickened.
12a. R5 stalked with R4 for 0.7 to 0.8 times its length.
b. R5 stalked with R4 for more than 0.8 times its length, or completely coalescent.
13. Thorax dorsally white speckled with dark fuscous.
14. Median arm rather wide.
15a. Anal plate moderately short.
b. Anal plate rather long only.
c. Anal plate moderately long to moderately short.
d. Anal plate varying from moderately to rather long.
16a. Eyes more or less reduced.
b. Female eyes slightly reduced in size.
c. Male eyes varying from moderately large to distinctly reduced in size or only reduced, and ♀ eyes (normally) moderately reduced. When eyes are reduced, frons is widened.
17. Labial palpi: second segment proximally narrowed up to subapically.
18. Female frons prominently elevated.
19. Patagium considerably widely curved.
20. Fifth tarsomere 2 to 3 times length of fourth.
21. Pronotum distinctly reduced in size.
22. Cross-vein Sc-Rs present.
23. Humeral plate more or less triangular in shape.
24. Lower suture of Apc up to 0.7 or 0.8 times length of An and sutures posteriorly diverging.
25. Male I-epiphysis bluntly to distinctly pointed.
26. Considerable sexual dimorphism; considerable differences in size and colour pattern.
27. Male forewing narrowed.
28. Cell of forewing distally backward invaginated and cell shortened (see figs. 93-95). N.B. Distal margin of cell normal in an undescribed species of *Eulophonotus*.

Notes on the species of section 2A

The ♀ antenna varies amongst the species from bilobed to simple but not in a distinct pattern. It seems that the bilobed state evolved at least once from the simple one, which is presumably a reversal.

As well in *Xyleutes* as in *Zeuzera* the frons may be elevated or bulbed. Of many species no females were available, so that this couldnot be checked in these.

The invagination of the median arm tends to lengthen up to $^1/_3$ or $^1/_2$ length of the arm in many species and the arm itself is often widened. The 2Ax has sometimes/often an elevated scaled area and this seems to be normally present in *Morpheis* species. In the rest of the section it varies from present to wanting or (normally) lost. It may well be that such an area can easily (re)develop from a dormant stage. At least there is no clear pattern of its loss. Remarkable is that the anal plate can be as well lengthened (e.g. in *Chalcidica minea*) as shortened. A general trend in the Zeuzerinae is only shortening of this stucture.

A general trend amongst the species as in the rest of the Zeuzerinae is the shortening of the vestiture on the tibiae II and III. In many species the tarsi are (nearly) unicoloured, often dark fuscous. The relative length of the fifth tarsomere is increased

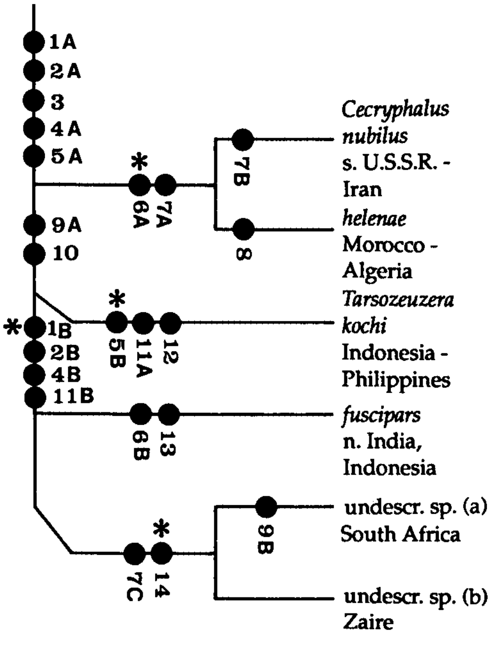


Fig. 75, cladogram of *Cecryphalus* and *Tarsozeuzera*.

in many species, but without a clear pattern.

While in *Eulophonotus* and *Zeuzera* the ♀ I-epiphysis is very short or even minute to wanting, in the genera following in the cladogram (fig. 76) this structure is only rather short. It seems that its relative length is not quite fixed and can lengthen again.

In all the species the ♀ frenulum bristles are reduced in length and their number is normally more than eight and in certain species considerably more. The degree of reduction and the number of these bristles vary amongst the species, but without a clear pattern.

In most species the thoracic sclerites are often darkened to dark brown. The patagia are often more or less sclerotized.

Remarkable is that *Alophonotus rauanus* so closely resembles the females of certain *Eulophonotus* species, while it is so widely separated from these in the cladogram (fig. 63). Furthermore, *Pseudozeuzera biatra* closely resembles *Zeuzera* species, while it seems to be separated from these by *Eulophonotus*. It may be that both colour patterns have been relatively easily (re)developed (within section 2A) from a basic (dormant) stage, which may have to do with a warning function against

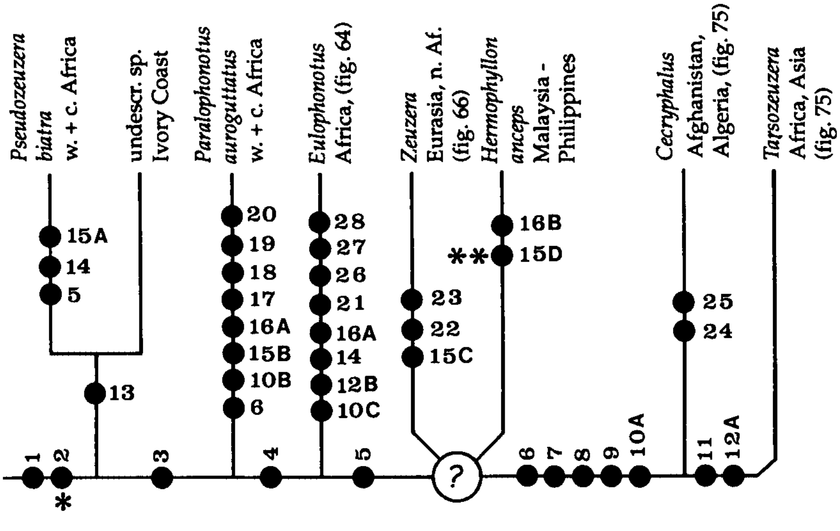


Fig. 76, cladogram of section 2A - part 2 (Zeuzerinae).

predation (see also Seitz, 1912: 428).

Note on the following genera of section 2

The following genera do not belong to section 2A. It seems impossible to produce a dichotomous cladogram for these genera on the basis of the external morphology. However, a distinction is drawn between South American and Asian taxa in the cladogram (fig. 79).

Genus **Brypoctia** gen. nov.

Type species: *Xyleutes strigifer* Dyar, 1910: 169.

Etymology: "brypoctia" is an anagram of the genus-name *Cryptobia*. Gender: feminine.

Dyar (1940: 1267) uses the name *strigifera* and still places this species in *Xyleutes*. In this study *Xyleutes* is restricted to a few species with the following characteristics: male I-epiphysis distinctly shorter than ♂ one, fringes very short, humeral plate approx. 2.5 or 3 times size of radial bridge, and radial plate distally elongate with slender apex. *X. strigifera* does not fit in *Xyleutes*. *X. strigifera* shares with species of *Allocryptobia* Viette, 1951 the following characteristics: accessory plate II at most moderately narrow, arolium distinctly reduced, fringes at most moderately short, and median arm with anterior invagination up to from $^1/_3$ to $^1/_4$ its length. The species differs otherwise considerably from *Allocryptobia* species. See also its position in the cladogram (fig. 79). The species does not fit in any available genus and is therefore placed in a new one.

B. strigifera has further the following apomorphies: male antenna bipectinate for approx. 0.4 times its length, labial palpi slender and approx. 0.5 times length of eye-diameter, second segment of labial palpi apically slightly thickened, tegula ventroposteriorly bluntly pointed, An moderately low, lower suture of Apc reaching up to from approx. 0.5 to 0.8 times length of An, mesepimeron moderately high, I-epiphysis reaching nearly or approx. as far as tibia-apex, fifth tarsomere 1.5 to 2 times length of fourth, paronychia wanting, fringes moderately short, inner cell of forewing often very small and sometimes wanting, humeral plate 1.5 to 2 times size of radial bridge, 1Ax apically large, distal plate of 4Ax distinctly reduced anteriorly, and anal plate moderately long. The species is medium-sized. The forewing is whitish and regularly striated fuscous.

Female is unknown. Vertex is moderately elevated and has a nearly straight Pos at approx. 0.8 times its length. Lower suture of Apc reaches usually up to 0.7 times length of An. Apc is moderately sinuate. Accessory plate III is narrow. Intersclerite III is wanting. Metameron has a membranous split. Venation: areole rather large; chorda sometimes partly coalescent with anterior M; R3, R4+5 shortly stalked; R4+R5 stalked for 0.5 to 0.6 times their length; inner cell often very small, sometimes wanting; M1 from areole; M2, M3 very close or connate; Sc-Rs occasionally present; Rs-M1 varying from short to moderately long but usually moderately short. Median arm is rather wide. Median plate varies from complete to distinctly reduced in length.

In the BMNH there is a specimen from Colombia labelled as type of *Zeuzera lasea* Druce. This specimen is placed under *strigifera* and appears to belong indeed to this species. The name *Zeuzera lasea* seems to be unpublished.

Xyleutes strigifer Dyar, 1910: 169.
Material (all BMNH). —long series of males from Mexico, Costa Rica, Honduras and Guatemala, and 1♂ from Colombia.

Genus **Allocryptobia** Viette, 1951

Allocryptobia Viette, 1951b: 38. [Objective replacement name for *Cryptobia* Herrich-Schäffer, [1854] 1850-1858].
Type species: *Cryptobia musae* Herrich-Schäffer, [1854] 1850-1858: 58, fig. 165.
Cryptobia Herrich-Schäffer, [1854] 1850-1858: 58, fig. 165. [Junior homonym of *Cryptobia* Leidy, 1846].

Herrich-Schäffer (1850-1858) does not give a description of *Cryptobia*, but notes *musae* and *mucoreus* Herrich-Schäffer, [1853] under the name *Cryptobia*. Fletcher & Nye (1982: 8) point out that *mucoreus* was not placed in *Cryptobia* until 1858. Dyar (1940: 1266) describes a third species, *phobifera*, which appears to concern the male of *mucorea*.

C. phobifera was described from a single male specimen from Paraguay. The holotype of *phobifera* is similar to a male specimen from Venezuela in the BMNH, which has been identified together with a female from the same locality as belonging to *mucorea*. Dyar notes that the hindwings are partly without scales due to damage. It appears to be a characteristic that a moderately broad band along the hindwing dorsum is unscaled, since the male in the BMNH has this too. There are apparently no good differences between the two species. Therefore *phobifera* is synonymized with *mucorea*.

The species show distinct sexual dimorphism; the female is distinctly larger and has a different colour pattern. In *mucorea* the ♀ hindwing is mainly yellow, while the ♂ one only very anteriorly. In the male of *mucorea* the forewing is narrowed and the hindwing shows a prominent elongation of the anal region. In the female of *musae* and in both sexes of *mucorea* the frons is moderately but distinctly widened. In the male of *musae* the frons varies from moderately wide to wide.

The two species have further the following apomorphies: female antenna proximally simple, An low, accessory plate II at most moderately narrow, arolium distinctly reduced, and scale plate shorter than radial bridge. The labial palpi of *mucorea* are two-segmented. The tegula of *mucorea* is ventro-posteriorly very blunt or rounded. The accessory plate II of *mucorea* is narrow. The fringes of *mucorea* are short or very short, and those of *musae* are moderately short. The anterior invagination of the median arm in *musae* reaches up to from $^1/_3$ to $^1/_4$ length of arm, and in *mucorea* up to half length. See also figs. 62 and 79. The species occur in South America.

Vertex of *musae* has Pos at approx. half length of vertex, has small invaginated areas at lateral terminations of Pos, and lacks anterior protuberances in the examined specimens. In *musae* antenna is for nearly 0.3 to 0.4 times its length bipectinate in the male and simple in the female. Antenna of *mucorea* is for approx. half its length bipectinate in the male and simple in the female. Lower suture of Apc in *musae* reaches up to from 0.3 to 0.5 times length of An; the state of 0.3 times is presumably a reversal. Lower suture of Apc in *mucorea* reaches up to from 0.5 to 0.8 times length of An. Mesepimeron is moderately high. Mesomeron is twice width of eucoxa II in both species. In *mucorea* the accessory plate II is narrow. Accessory plate III is moderately narrow or narrow. Intersclerite III is sometimes/often present and when absent metameron has a membranous split. I-epiphysis reaches nearly or approx. as far as tibia-apex. Fifth tarsomere of *musae* is approx. twice length of fourth and tarsal spines are wanting. Venation: R1 from areole in *mucorea*, but at least sometimes proximal to areole in *musae*; R3, R4+5 connate to very shortly stalked; R4+5 stalked for 0.3 to 0.4 times their length in *musae*, and for 0.6 to 0.7 times in *mucorea*; M1 posterior to areole; Rs-M1 short to moderately long. Humeral plate of *musae* is twice and that of *mucorea* 1.3 to 1.5 times size of radial bridge. Scale plate is approx. 0.8 times length of radial bridge and moderately wide. 1Ax is apically large. Distal plate of 4Ax is distinctly reduced anteriorly. Median arm of *musae* is sometimes/often approx. as wide as Cu2. Median arm of *mucorea* is approx. as wide as Cu2. Anal plate is moderately long.

Cossus mucoreus Herrich-Schäffer, [1853] 1850-1858: 58, fig. 39.

Cryptobia phobifera Dyar, 1940: 1266. **Syn. nov.**

Material. —1♂, 1♀, VENEZUELA: Valencia (BMNH); 3♀♀, PERU: Chanchamayo, 1000-1500 m. (BMNH); 1♀, BRAZIL (BMNH); 1♀, Porto Cabello (MNHN); 1♂ (holotype of *phobifera*), PARAGUAY: Villa Rica, iii.1922 (Jörgensen) (USNM).

Cryptobia musae Herrich-Schäffer, [1854] 1850-1858: 58, fig. 165.

Material. —1♀ (holotype), Rio Grande (ex musaeo Boisduval) (MNHN); 2♂♂, 10♀♀, VENEZUELA: Merida (BMNH); 1♀, GUATEMALA: Guatemala City (BMNH).

Genus **Panau** gen. nov.

Type species: *Xyleutes variegata* Roepke, 1957: 28-29, pl. 2: fig 3 (male, holotype), pl. 8: figs. 4-4a (male genitalia).

Etymology: "panau" (Indonesian) means a white spot on the skin. Gender: neuter.

Panau is established for a number of species from southeast Asia, which had previously been included in *Xyleutes*. Most of these species have been described by Roepke (1957). *Xyleutes* species differ from these species in that e.g. the humeral plate is approx. 2.5 to 3 times size of the radial bridge, the ♀ I-epiphysis is short, the fringes are very short, and the radial plate is distally elongate with a slender apex. The material of most species of this new genus is medium-sized, but that of *princeps* (Roepke, 1957) and *stenopterum* (Roepke, 1957) is somewhat larger. All but one species have a whitish marking on the forewing, and most of them dark streaks, particularly distally in between the veins. It is difficult to define the genus. Most species share that the median arm has its anterior invagination up to $^{1}/_{3}$ its length, which is presumably a reversal within section 2. In several others this invagination reaches up to $^1/_4$ length of the arm, which is presumably a reversal within this genus. See also figs. 77 and 79.

An undescribed species (a) from Sulawesi and New Guinea is rather different from the other species of *Panau*. This is a dark species without whitish spot; wings are fuscous with a blackish striate or reticulate pattern. It further differs from the other *Panau* species in that the labial palpi are two- or three-segmented and R1 is proximal to the areole. The undescribed species shares with the other species the type of median arm. It seems to branch off from the base of the cladogram of *Panau* (fig. 77). The undescribed species is tentatively included, pending a more thorough study including the genitalia.

Vertex has been examined in a few species. Pos is at 0.6, 0.7 or 0.8 times length of vertex and anterior protuberances are very small or indistinct. In *euphanes* (West, 1932) the ♂ antenna is bipectinate for approx. half its length. In the other species the ♂ antenna is bipectinate for 0.4 to 0.6 times its length. Female antenna of at least *adustum* (Roepke, 1957) is proximally simple. Lower suture of Apc reaches up to half length of An in *euphanes*, and up to 0.8 times length of An in the other species. K is rather long and with or without a cross-suture. Mesepimeron is moderately low in *brunnescens* (Roepke, 1957). Mesomeron is in most species 1.5 times width of eucoxa II, but in *brunnescens* apparently 2 times width. Accessory plate II is at least sometimes moderately narrow in *quarlesi* (Roepke, 1957), *princeps* and *stenopterum*. Accessory plate III seems to be normally (very) narrow. Intersclerite III may be completely present in certain species. I-epiphysis reaches nearly or approx. as far as tibia-apex in most species, but distinctly less far in *princeps*. Fifth tarsomere is 1.5 or 2 times length of fourth, but in *adustum* up to 2.5 times and in *princeps* 2.5 times. Arolium is well-developed in *brunnescens*, varies from moderately long to moderately short in *variegatum* (Roepke, 1957), is distinctly reduced in undescribed species (a), and is wanting in the other species. Paronychia are wanting. Fringes vary inter- and intraspecifically from moderately long to short. Number of ♀ frenulum bristles of *adustum* (1 ♀) amounts approx. nine, and these are moderately short. Venation: R1 from areole, but occasionally proximal to the latter; R3, R4+5 stalked for 0.2 to 0.3 times their length in *euphanes*, and for 0.3 to 0.7 times in other species; Rs-M1 moderately short to rather long. Humeral plate varies interspecifically from 1.5 to 2 times size of radial bridge. 1Ax is apically large. 4Ax is antero-distally distinctly reduced. Median plate varies amongst the species; the anterior invagination reaches up to $^1/_3$ or $^1/_4$ length of arm. 2Ax lacks (normally ?) elevated scaled area. Anal plate is moderately long.

A tentative cladogram of the genus is proposed (fig. 77). There seem to be several reversals. It seems that a shorter invagination of the median arm evolved twice as a reversal, while in *princeps* this seems to have reversed again.

Undescribed species (a)

Material (all INDONESIA and BMNH). —1♂, Irian Jaya, Arfak Mts., Ansi Lakes, 6000 ft., i/ii.1914 (Pratt & Pratt); 1♂, w. Sulawesi, Lindu Palu, 3700 ft., iv.1937 (Kalis).

Xyleutes euphanes West, 1932: 220.

Material (all PHILIPPINES). —1♂ (holotype), Luzon, subprov. Benguet, Klondyke, 800 ft., 7.iv.1912 (Wileman) (BMNH); 1♂, Luzon, Ifugao, Mayoyao, 1000-1500 m. (BMH); 2♂♂, Camarines Sur, Mt. Isarog, 750-800 m. (BMH); 3♂♂, Misamis Or., Hindangon, 20 km. south of Gingoog, 500-700 m. (BMH).

Undescribed species (b)

Material (all BMNH). —series of males from Irian Jaya (Snow Mts., -3500 ft., Mt. Goliath and Fak-Fak), Papua New Guinea (Ekeikai, -1500 ft.) and Little Kai.

Note. Most closely resembling *adusta*.

Xyleutes variegata Roepke, 1957: 28-29, pl. 2: fig. 3 (male, holotype), pl. 8: figs. 4-4a (male genitalia).

Material (all INDONESIA). —11♂♂ (types), n. Sulawesi: Minahassa, Tonsealama and Menado (RMNH); 3♂♂, n. Sulawesi (ITZ); 1♂, n. Sulawesi (BMNH).

Undescribed species (c)

Material. —1♂, MALAYSIA: Perak (MHUB).

Note. Most closely resembling *variegata*, but the latter seems to differ in colour pattern and to occur only on Sulawesi. This specimen has been erroneously identified as *plesseni* by Gaede, and figured with the name *tigrina* by Seitz (1934: pl. 99: fig. row d).

Xyleutes brunnescens Roepke, 1957: 29, pl. 2: fig. 6 (male, holotype), pl. 8: fig. 2 (male genitalia).

Material. —1♂ (holotype), INDONESIA: Kepulauan Banggai, Nulion Peling (ITZ); 1♂, INDONESIA: Kepulauan Kai (BMNH).

Undescribed species (d)

Material. —1♂, ? (ITZ).

Note. Most closely resembling *quarlesi*.

Xyleutes adusta Roepke, 1957: 30, pl. 3: fig. 3 (female), pl. 8: figs. 6-6a (male genitalia).

Material (all INDONESIA). —1♂ (holotype), Sumatra, Dolok Ilir, 18.ii.1936 (Uil), Gen. slide Xyl. no. 9 (RMNH); 3♂♂, 1♀ (paratypes), w. Java, Bogor (RMNH); 1♂ (paratype), Belitung (RMNH); 1♂, w. Belitung, Tg. Pandan (RMNH); 4♂♂, Singkep, Tji Gapur (RMNH); 3♂♂, Sumatra: Lebong Tandai (BMNH); 1♂, MALAYSIA: Pinang, 1800 ft. (BMNH).

Xyleutes quarlesi Roepke, 1957: 28, pl. 2: fig. 4 (male, paratype), pl. 7: figs. 6-6a (male genitalia).

Material. —1♂ (holotype), INDONESIA: n.e. Kalimantan, Sesajap (ITZ); 5♂♂, MALAYSIA: Selangor, Bukit Kutu, -3300 ft. (BMNH); 3♂♂, SINGAPORE (BMNH); 1♂, INDONESIA: Sumatra, Lebong Tandai; 2♂♂, INDONESIA: e. Kalimantan (RMNH); 7♂♂, INDONESIA: Bali, Baturiti (ITZ); 14♂♂, INDONESIA: Bali, Mondok Lumpang and Baturiti, -3500 ft. (BMNH).

Note. Material from Bali appears to differ in having a slightly wider and more rounded whitish spot.

Xyleutes stenoptera Roepke, 1957: 27, pl. 3: fig. 4 (male, holotype), pl. 7: figs. 5-5a (male genitalia), pl. 8: figs. 3-3a (male genitalia).

Material (all INDONESIA). —1♂ (holotype of ssp. *stenoptera* Roepke, 1957), w. Java, Perbawattee (Walsh) (RMNH); 2♂♂, Perbawattee (RMNH); 1♂, Singkep, Raja (RMNH); 3♂ ♂, Singkep, Tji Gapur (RMNH); 1♂, w. Belitung, Tg. Pandan (RMNH); 1♂ (holotype of ssp. *sumatrana* Roepke, 1957), 9♂♂, Sumatra, Lebong Tandai (BMNH).

Note. Roepke (1957: 27) distinguishes a new subspecies *sumatrana*, known from Sumatra.

Xyleutes princeps Roepke, 1957: 26-27, pl. 2: fig. 2 (male, holotype).

Material. —1♂ (holotype), INDONESIA: Sulawesi, Minahassa (ITZ).

Table 18. Apomorphies in fig. 77 (*Panau*).

1a. Median arm with anterior invagination up to $^1/_3$ its length. (*)
b. Median arm with anterior invagination up to $^1/_4$ its length.
2a. An moderately high to moderately low.
b An moderately low only.
c. An low.
3. Frontal tuft moderately short to short.
4a. Fringes moderately short.
b. Fringes short.
c. Fringes moderately long to short.
5a. Fifth tarsomere twice length of fourth.
b. Fifth tarsomere twice to 2.5 times length of fourth.

c. Fifth tarsomere 2.5 to 3 times length of fourth.
6a. Arolium wanting.
b. Arolium moderately long to wanting.
7. Humeral plate 2.5 times size of radial bridge.
8. Labial palpi: second segment proximally narrowed up to subapically.
9. I-epiphysis reaching distinctly short of tibia-apex.
10. Female antenna proximally simple.
11. Median arm rather long.
12. Labial palpi two- or three-segmented.
13. R1 proximal to areole.

Genus **Duomitus** Butler, 1880

Duomitus Butler, 1880: 68.

Type species: *Duomitus ligneus* Butler, 1880: 68-69. [Synonymized with *Zeuzera ceramica* Walker, 1865 by Hampson, 1892: 307].

Duomitus has often been used for many species from various sections. The ♂ antenna of the type species of *Duomitus*, *ceramicus*, is unique amongst the Cossidae; the rami are nearly straight, and opposite ones are placed nearly in one plane. The antennal rami have dorsally a row of moderately long sensilla. The male antenna is rather strongly bipectinate for approx. 0.4 times its length and further very shortly prismatic. The ♀ antenna is proximally simple and distally very shortly prismatic. *D. ceramicus* is a rather large to large, brownish and easily recognizable species. Most species that had erroneously been placed in *Duomitus* have not an antero-distally reduced or invaginated 4Ax. *D. ceramicus* has further the following characteristics: second segment of labial palpi usually slightly thickened apically, tegula ventro-posteriorly bluntly pointed, Bs II only moderately vaulted, An moderately low, lower suture of Apc reaching up to from 0.7 to 0.8 times length of An, upper suture of Apc often or usually posteriorly bifid, I-epiphysis reaching little short of tibia-apex, tarsomeres slightly to hardly widened apically, fifth tarsomere twice length of fourth, arolium and paronychia wanting, forewing moderately elongate, fringes short to very short, number of ♀ frenulum bristles usually more than fifteen, areole very long, 1Ax apically large, median arm with its anterior invagination up to approx. $^1/_3$ length of arm, and anal plate moderately long. The species occurs in southern and southeast Asia. See also figs. 62, 78 and 79.

Vertex is moderately bulbed or swollen, has Pos at approx. 0.8 times its length, and has very small anterior protuberances or these are wanting. Mesepimeron is moderately high. Mesomeron is 1.5 times width of eucoxa II. Accessory plate III is very narrow. Intersclerite III is wanting and metameron has a membranous split. Dorsum of hindwing is (very) weakly invaginated. Female frenulum bristles are moderately short. Venation: areole very long; R1 from areole; R3, R4+5 shortly stalked; R4+5 stalked for 0.4 to 0.6 times their length; M1 posterior to areole; inner cell of forewing long; Rs-M1 rather to moderately long. Humeral plate is twice size of radial bridge. Median plate seems to be usually not reduced in length. 2Ax lacks (normally ?) elevated scaled area.

Zeuzera ceramica Walker, 1865: 587. [The Large Teak Borer or Beehole Borer].

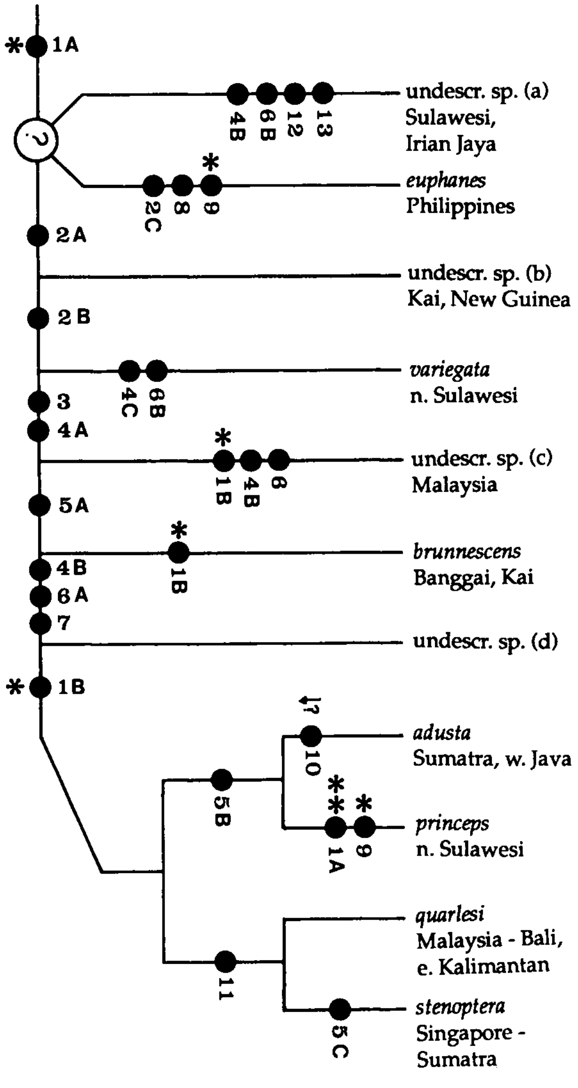


Fig. 77, cladogram of *Panau*.

Duomitus ligneus Butler, 1880: 68-69. [Synonymized by Hampson, 1892: 307].

Eudoxyla bosschae Heylaerts, 1892: 45-47. [Synonymized by Houlbert, 1916: 113].

Range: From India to Philippines and Solomon Islands.

Material. —1♀ (holotype of *ligneus*), INDIA: Darjiling (BMNH); long series of both sexes from most countries of its range (BMNH); long series of both sexes from Indonesia (RMNH, ITZ).

Note. Roepke (1957: 25) distinguishes a new subspecies *eichhorni* from the Solomon Islands. A host is Teak in Indonesia (Dammerman, 1929: 70). Hosts in other parts of its range are *Callicarpa arborea* Roxb., *Clerodendron infortunatum* L., *Duabanga sonneratioides* Buch.-Ham., *Sesbania grandiflora, Spathodea campanulata* P. Beauv., *Tectonia grandis, Vitex parviflora* Juss., *Gmelina arborea* Roxb. (Beeson, 1961: 440; Arora, 1976: 118).

Genus **Skeletophyllon** gen. nov.

Type species: *Xyleutes euphyes* West, 1932: 219.

Etymology: "skeletos" (Greek) means skeleton or dried + "phyllon" (Greek) means leaf. Gender: neuter.

The new genus-name *Skeletophyllon* is applied to three species from southeast Asia. These species are medium-sized and have regularly striated or marbled forewings. The labial palpi are moderately slender. The first tarsomere of the proleg has rather long vestiture in the two named species. The fringes are moderately short. R1 branches off proximally to the areole. The humeral plate is 1.3 times size of the radial bridge. The fifth tarsomere is approx. 1.3 to 1.5 times length of the fourth. The number of ♀ frenulum bristles in *perdrix* (Roepke, 1955) amounts approx. ten, and these are rather long. *Skeletophyllon* species differ especially from those of the following (new) genus in that their labial palpi are moderately slender. The species of the next genus have generally more irregularly spotted wings with few more or larger dots. See also figs. 62, 78 and 79.

Only of *perdrix* the female is known. Male antenna is bipectinate for approx. 0.4 or 0.5 times its length. Female antenna of at least *perdrix* is proximally indistinctly bilobed. Labial palpi: third segment is ovate in *perdrix* and the undescribed species. An is moderately low. Lower suture of Apc reaches up to 0.8 or 0.9 times length of An and is at least sometimes even complete length in the undescribed species. K is rather long or long, and has sometimes/often a cross-suture. Mesepimeron seems to be normally moderately high in *perdrix* and is sometimes/often moderately high in the undescribed species. Accessory plate II is sometimes/often narrow in *perdrix* and moderately narrow in *euphyes*. Mesomeron is 1.5 to 2 times width of eucoxa II. Intersclerite III is (normally ?) wanting. I-epiphysis reaches nearly or approx. as far as tibia-apex. Arolium is wanting in *euphyes* and the undescribed species, and is sometimes/often reduced in *perdrix*. Paronychia are wanting. Number of ♀ frenulum bristles amounts approx. ten in *perdrix* (1 ex.), and these are rather long. Venation: R1 proximal to areole; R3, R4+5 shortly stalked; R4+5 stalked for 0.3 to 0.7 times their length; M1 posterior to or from areole; Rs-M1 very short to moderately long; M2, M3 very to moderately shortly separate. 1Ax is apically rather large or large. 4Ax is anteriorly slightly to distinctly reduced. Median plate is sometimes/often reduced in length. Median arm is moderately long and moderately wide, and has its anterior invagination up to approx. $^{1}/_{4}$ its length. Anal plate is moderately long.

A more extensive investigation, including the genitalia, is needed to solve the trichotomy of the last three genera of section 2, amongst which *Skeletophyllon*, in the cladogram (fig. 78).

Xyleutes euphyes West, 1932: 219.

Xyleutes sibolgae Roepke, 1957: 31, pl. 3: fig. 10 (male, holotype). [Synonymized by Holloway, 1982: 180].

Material (all ♂♂). —1 (holotype of *euphyes*), PHILIPPINES: Luzon, subprov. Benguet, Klondyke, 800 ft., iii.1912 (Wileman) (BMNH); 1 (holotype of *sibolgae*), INDONESIA: Sumatra, Bonan Dolok, Sibolga, 500 m., 19/20.vi.1930 (Van der Meer Mohr) (RMNH); 1, MALAYSIA: Bukit Kutu, 3300 ft. (BMNH); 2, INDONESIA: Sumatra, Benkoelen, Lebong Tandai (BMNH); 1, MALAYSIA: Pinang, 2260 ft. (BMNH); long series, INDONESIA: w. Sulawesi (BMNH); 4, INDONESIA: Pulau Saleier (ITZ); 1, INDONESIA: Pulau Djampea, Lember (ITZ); 1, INDONESIA: s.w. Sulawesi, Pangean (ITZ).

Note. Holloway (1986: 40) records the species also from Borneo.

Xyleutes perdrix Roepke, 1955: 286, pl. 1: fig. 6.

Material. —1♂ (holotype), INDONESIA: Irian Jaya, Bewani R. terr., Ampas, 10.xi.1938 (Stüber) (RMNH); 3♂♂, INDONESIA: Irian Jaya, Ampas (ITZ); 4♂♂, INDONESIA: Irian Jaya (ITZ); 9♂♂, INDONESIA: Irian Jaya, Arfak Mts., Ninay Valley, 3500 ft. (BMNH); 1♂, INDONESIA: Irian Jaya, Kratke Mts., 4000-5000 ft. (BMNH); 1♂, 1♀, PAPUA NEW GUINEA: Upp. Aroa R. (BMNH); 1♂, PAPUA NEW GUINEA: Hydrographer Mts., 2500 ft. (BMNH); 1♂, PAPUA NEW GUINEA: Kumusi R. (BMNH).

Undescribed species

Material. —1♂, INDONESIA: Irian Jaya, Ampas (ITZ); 1♂, INDONESIA: Irian Jaya, Jayapura (ITZ).

Note. Closely resembling *euphyes*. The forewing is striated but less densely between CuA and A1+2, and has a more densely striated patch in between CuP and dorsum.

Genus **Trismelasmos** gen. nov.

Type species: *Cossus maculatus* Snellen, 1879: 125-126, pl. 10: fig. 4 (female).

Etymology: "tris" (Greek) means thrice + "melasmos" (Greek) means a blackening. Gender: masculine.

The species of *Trismelasmos* were originally placed in various genera. Roepke (1955; 1957) treats several of them under *Xyleutes*.

The genus consists mostly of very similar species. The forewing is whitish and more or less striated, and has in most species proximally a dark anterior marking, a dark anterior spot at approx. two-thirds wing-length, and often a small dark marking in between CuP and A1+2. The vertex of at least *papuanus* (Roepke, 1955), *minimus* (Houlbert, 1916), and the undescribed species (d) and (j) is distinctly antero-laterally ridged, and has small membranous areas laterally to Pos (see fig. 89). The author supposes that this type of vertex is characteristic for most of the species. However, the vertex of *maculatus* (Snellen, 1879) lacks the special membranous areas. The species have further the following characteristics: third segment of labial palpi shortly ovate, lower suture of Apc reaching up to at least half length of An, An at most moderately low or only low, I-epiphysis reaching little short of or as far as tibia-apex, tarsomeres only slightly or hardly widened apically, fifth tarsomere at least 1.5 times length of fourth, paronychia wanting, number of ♀ frenulum bristles more than five, fringes at most moderately long but in most species moderately short, R1 in most species proximal to areole, 1Ax apically rather large or large, and anal plate moderately long. See also figs. 62 and 78-79. Most species occur in Indonesia, particularly Irian Jaya, and a few on the Solomon Islands or in the Bismarck Archipelago.

Male antenna is in most species bipectinate for 0.3 to 0.4 times its length, but in a few species for approx. half its length. Female antenna seems to be in most species proximally slightly bilobed, but in *papuanus* it is moderately bipectinate (reversal). Lower suture of Apc varies amongst the species; up to from 0.5 to 0.7 times or from 0.7 to 0.8 times length of An, and in *papuanus* from 0.9 to 1.0 time length of An. Mesepimeron is moderately low or moderately high. Mesomeron varies from 1.5 to 2 times width of eucoxa II. Accessory plate II is at least sometimes narrow in certain species. Accessory plate III is narrow. Intersclerite III is wanting and metameron has usually a membranous split. Fifth tarsomere is 1.5 or/to 2 times length of fourth. Arolium is sometimes/often well-developed in *maculatus*, but is in most species minute or wanting. Number of ♀ frenulum bristles varies from approx. six to fifteen and these are moderately to rather long. Venation: R1 in all species, except *maculatus*, proximal to areole; R3, R4+5 (very) shortly stalked; R4+5 stalked for approx. 0.3 to 0.4 times their length, but in *minimus* for 0.4 to 0.8 times; M1 usually posterior to areole; Rs-M1 very short to rather long; M2, M3 more or less separate. Humeral plate is in *maculatus* and certain other species twice size of radial bridge but becomes smaller higher in the cladogram and in certain species it is as large as. Scale plate is in certain species, e.g. *minimus*, shorter than radial bridge. 2Ax (normally) without an elevated scaled area. Anterior invagination of median arm reaches up to $^1/_4$ length of arm in many species; in many others up to $^1/_3$ length; in some varying from $^1/_4$ to $^1/_3$ length; in *maculatus* from $^1/_3$ to $^1/_5$ length of arm. Median plate is sometimes/often reduced in length.

In the cladogram (fig. 78) there is an unsolved trichotomy of *Trismelasmos* with

Skeletophyllon and *Duomitus*. Perhaps research of the genitalia will help to produce two dichotomies.

The author did not succeed in producing a well-founded cladogram for the entire genus, since many species most closely resemble each other in their external features and the state of the specimens of some species did not allow examination of all characters (e.g. humeral plate). However, the base of the cladogram is provided (see fig. 78). Reduction in size of humeral and scale plate and shortening of fringes are developments of significance for distinguishing relatively derived groups within *Trismelasmos*. The humeral plate of *dictyograptus, mixtus* and *cinerosus* is approx. 2 times size of the radial bridge. This plate is approx. 1.3 times size of the radial bridge in at least *minimus, papuanus* and the undescribed species (k). In at least *minimus* and the undescribed species (c) and (j) the scale plate is shortened, and in these undescribed species the humeral plate is approx. as large as the radial bridge.

Cossus maculatus Snellen, 1879: 125-126, pl. 10: fig. 4 (female).

Xyleutes pygmaea Roepke, 1957: 38-39, pl. 2: fig. 7 (male, holotype), pl. 9: figs. 5, 5a (male genitalia). Syn. nov.

Range: Java, Flores, Jampea, Brunei, Sulawesi, Banggai (see below), and furthermore Singapore, Sarawak and Adonara (Roepke, 1957: 37-38); a ♀ specimen from Kepulauan Tanimbar (ITZ) may also belong to this species.

Material. —2♂♂ (paratypes of *maculatus*), INDONESIA: Sulawesi, Uju Pandang (RMNH); 1♂ (holotype of *pygmaea*), 1♂, 1♀ (paratypes), INDONESIA: Java, Siluwok Sawangan, in Randu, iii (RMNH); long series (most ♂♂), INDONESIA: Java (RMNH); 1♂, INDONESIA: Kepulauan Banggai, Lambiut (RMNH); long series of males, INDONESIA: Sulawesi (BMNH); series, BRUNEI (BMNH); series of males, INDONESIA: Sulawesi, Palu (ITZ); 1♂, INDONESIA: Sulawesi, Bonthain (ITZ); 4♂, INDONESIA: Djampea (ITZ); series of males, INDONESIA: Sulawesi, Dumoga Bone National Park (ITZ); long series of males, INDONESIA: Flores (ITZ).

Notes. There are *maculatus* specimens from the same host and the same localities as types of *pygmaea* in RMNH. There are no differences between *maculatus* and *pygmaea*, except that the types of *pygmaea* are small. Therefore the two species are here synonymized.

A host is *Ceiba pentandra* Gaertn., and according to Snellen (1879) probably also *Canarium commune* L.

Duomitus tectorius Swinhoe, 1901: 125.

Material (all SOLOMON ISLANDS and BMNH). —1♂ (holotype); 1♂, Bougainville, Arawa; 3♂♂, Tugela; 4♂♂, Tulagi Is.

Undescribed species (a)

Material (all INDONESIA: Irian Jaya). —2♂♂, Humboldt Bay dist. (Uskwar and Pukusam dist.) (BMNH); 1♂, Sawia (BMNH); 17♂♂ from Arso, Wembi, Wambis, Parfi and Ampas (ITZ); 8♂♂ from Ampas, Bernhard Camp, Jayapura and Biak (RMNH).

Note. This is *Xyleutes tectoria* sensu Roepke (1955: 285-286). In the collections of BMNH and RMNH, Roepke had placed the material apart and in the RMNH under "*toxopei*" (manuscript-name).

Undescribed species (b)

Material (all BMNH). —10♂♂, 1♀, PAPUA NEW GUINEA: Manam Isl. [= Vulcan Isl.]; 1♂, INDONESIA: Irian Jaya.

Note. Closely resembling *papuanus*, but generally smaller.

Xyleutes dictyograpta Roepke, 1957: 30, pl. 4: fig. 5 (male, holotype).

Material. —1♂ (holotype), INDONESIA: Kalimantan, Kariorang, 16.i.1957 (Quarles de Quarles), Gen. slide no. 10 (RMNH); 1♂, INDONESIA: Karimon, Djawa (RMNH); 3♂♂, MALAYSIA: Sabah, Kretam (BMNH); 1♂, MALAYSIA: Sarawak, Mt. Dulit (BMNH); 8♂♂, BRUNEI (BMNH).

Zeuzera mixta Pagenstecher, 1888: 126-127.

Material (all INDONESIA). —2♂♂, Ambon (BMNH); 1♂, Obi Major (BMNH); 3♂♂, Buru, Kako Tagalago (BMNH); 5♂♂, Ambon (RMNH); 1♂, Buru, Leksula (RMNH).

Xyleutes ? minimus Houlbert, 1916: 80, fig. 15 (males).

Material. —1♂, Doom Isl. (RMNH); 2♂♂, INDONESIA: Irian Jaya, Jayapura (ITZ); long series of males from Irian Jaya, New Ireland, New Hannover, New Britain, Dampier Isl., St. Matthias, Sudest Isl. and Rook Isl. (BMNH); 2♂♂, Rook Isl. (MNHN); 4♂♂, Dampier Isl. [= Karkar Isl.] (MNHN).

Note. This species is quite distinct from *mixtus*. It has e.g. a smaller scale plate and humeral plate, and R5 is stalked for approx. 0.7 times its length. The author couldnot find the types of *minimus* in the MNHN. Houlbert did not note a type-locality. Since there are many species of *Trismelasmos* corresponding with the figure of the types, the identity of *minimus* is obscure.

Xyleutes papuana Roepke, 1955: 285, pl. 1: fig. 8 (male), pl. 2: fig. 3 (male genitalia).

Material. —long series (most ♂♂, 1♀) from New Guinea and Dampier Isl. (BMNH).

Note. The dwarfed specimen from Biak recorded by Roepke (1955) has been here identified as belonging to *albicans* (Roepke).

Undescribed species (c)

Material. —1♂, PAPUA NEW GUINEA: Hydrographer Mts., 2500 ft. (BMNH); 1♂, PAPUA NEW GUINEA: Goodenough Isl., 2500-4000 ft. (BMNH).

Note. Closely resembling *papuanus*, but appears to be generally larger. The humeral plate is relatively slightly smaller than in *papuanus* and the fringes are short.

Xyleutes cinerosa Roepke, 1955: 284-285, pl. 1: fig. 2 (male), pl. 2: fig. 1 (male genitalia).

Material. —1♂ (holotype), INDONESIA: Irian Jaya, Humboldt Bay territorium, Mt. Haga, 3600 m., 18.ii.1939 (RMNH); 2♂♂, INDONESIA: Irian Jaya, Humboldt Bay territorium and Ampas (RMNH); 1♂, INDONESIA: Irian Jaya, Keerom, Mt. Haga, 1000 m. (ITZ); 1♂, INDONESIA: Irian Jaya, Arfak Mts., Ninay Valley, 3500 ft. (BMNH); 1♂, New Guinea, Garaine, 600 m. (MNHN).

Note. This is a large species.

Xyleutes elegans Roepke, 1955: 286, pl. 1: fig. 4 (male), pl. 2: fig. 5 (male genitalia).

Not examined. From New Guinea.

Undescribed species (d)

Material. —3♂♂, INDONESIA: Irian Jaya (RMNH); long series (most ♂♂, 1♀), INDONESIA: Irian Jaya: Ampas, Uskwar, Bagea, Sorong, Wemti, Wambis and Arso (ITZ).

Note. Apparently closely resembling *elegans* and perhaps concerning the latter.

Undescribed species (e)

Material. —1♂, INDONESIA: Irian Jaya, Jayapura (ITZ).

Note. Closely resembling the previous species.

Xyleutes major Roepke, 1957: 38, pl. 4: fig. 2 (male, holotype).

Material. —1♂ (holotype), INDONESIA: Bacan (RMNH).

Undescribed species (f)

Material. —2♂♂, PHILIPPINES: Misamis Or., Hindangon, 20 km. south of Gingang, 600-700 m., 20-24.iv.1960 (Torrevillas) (BMH).

Undescribed species (g)

Material. —2♂♂, INDONESIA: Irian Jaya, Penunungan Sterren, Sibil, 1260 m. (RMNH); (conspecific ?) 1♂, PAPUA NEW GUINEA: Dinawa, 4000 ft. (RMNH).

Note. Closely resembling *major*, but lacking the marking distally on the forewing between CuP and A1+2.

Xyleutes jordani Roepke, 1955: 285, pl. 1: fig. 9 (male), pl. 2: fig. 2 (male genitalia).

Material. —1♂ (holotype), INDONESIA: Irian Jaya, Cyclops Mts., 900 m. (RMNH).

Undescribed species (h)

Material. —1♂, INDONESIA: Irian Jaya (ITZ); 1♂, INDONESIA: Irian Jaya, Jayapura (ITZ).

Note. Closely resembling *minimus*.

Undescribed species (i)

Material. —2♂♂, INDONESIA: Irian Jaya: Jayapura and Teminabuan (ITZ).

Note. The dark patches on the forewing are more or less dissolved and there is a vague band on the forewing at approx. two-thirds wing-length.

Undescribed species (j)

Material. —8♂♂, INDONESIA: Irian Jaya, Snow Mts., 3500 ft. (BMNH); 9♂♂, PAPUA NEW GUINEA: Angabunga River, 6000 ft. (BMNH); 1♂, INDONESIA: Irian Jaya, Mistkamp, 1800 m.

(RMNH).

Note. This species has a dark transverse stripe on the forewing at approx. one-fourth wing-length.

Xyleutes albicans Roepke, 1955: 286, pl. 1: fig. 5 (male), pl. 2: fig. 6 (male genitalia).

Material. —1♂ (holotype), INDONESIA: Irian Jaya, Biak, 16.viii.1946 (Straatman) (RMNH); 1♂, INDONESIA: Irian Jaya, Biak (Straatman) (RMNH).

Undescribed species (k)

Material. —1♂, Indonesia, Irian Jaya, Savia (ITZ); 1♂, INDONESIA: Irian Jaya, Keerom, 1000 m(ITZ).

Note. This species has a white spot in the proximal anterior marking on the forewing.

Xyleutes kalisi Roepke, 1957: 35-36, pl. 3: fig. 2 (male, holotype).

Not examined. From southern Sulawesi.

Undescribed species (l)

Material. —2♂♂, PAPUA NEW GUINEA: Hydrographer Mts., 2800 m. (MNHN).

Note. Looking a bit like a distinctly smaller version of *cinerosus*.

Undescribed species (m)

Material. —1♂, PAPUA NEW GUINEA: West Sepik Province, Telefomin, viii.1975 (Gerrits) (ITZ).

Table 19. Apomorphies in fig. 78 (*Duomitus*, *Skeletophyllon*, and *Trismelasmos*).

1. An at most moderately low.
2. Male antenna: rami nearly straight and nearly in one plane.
3. Female antenna proximally simple.

4a. Arolium wanting.
b. Arolium moderately long to short.
c. Arolium minute to wanting.

5a. Fringes short to very short.
b. Fringes moderately short.

6. Median arm with anterior invagination up to approx. $^{1}/_{3}$ its length.
7. Labial palpi moderately slender.
8. R1 proximal to areole.
9. Humeral plate 1.3 times size of radial bridge.
10. Labial palpi: third segment (shortly) ovate.
11. Vestiture of tibia II short.
12. Forewing: proximal one-third only for anterior half or less than that darkened or with transverse stripe at approx. one-third wing-length.
13. Fifth tarsomere 1.5 to 2 times or twice length of fourth.

Table 20.Apomorphies in fig. 79 (section 2 - part 2).

1. Tegula ventro-posteriorly gradually tapering and slightly upturned to bluntly pointed and moderately upturned.

2a. Female antenna proximally bilobed or simple.
b. Female antenna proximally simple.

3. Male I-epiphysis bluntly pointed to apically rounded.
4. Radial plate distally elongate with rather slender apex.
5. Anal plate moderately to rather long. (*)

6a. An moderately low.
b. An at most moderately low.
c. An only low.

7. Arolium distinctly reduced in size.
8. Fringes at most moderately short.
9a. Median arm with anterior invagination up to from $^1/_4$ to $^1/_3$ its length.
b. Median arm with anterior invagination up to approx. $^1/_3$ its length.
10. Accessory plate II moderately narrow.
11. Frons in female or both sexes moderately widened.
12. Considerable sexual dimorphism; in colour pattern, size and shape.
13. Scale plate shorter than radial bridge.

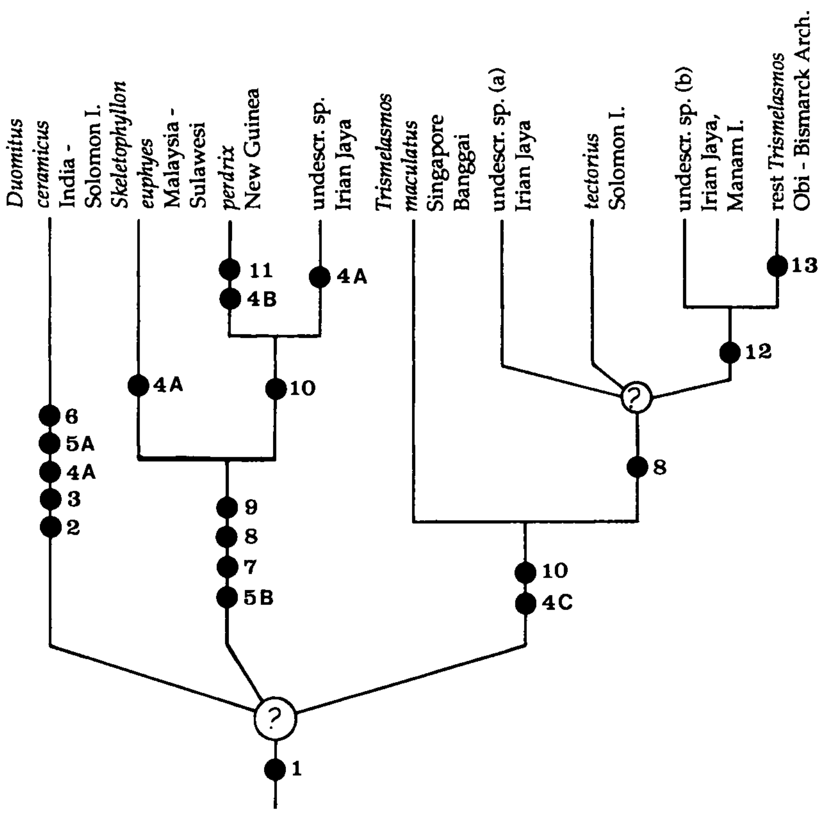


Fig. 78, cladogram of *Duomitus*, *Skeletophyllon* and *Trismelasmos*.

Genus **Aethalopteryx** gen. nov.

Type species: *Phragmatoecia atrireta* Hampson, 1910a: 129.

Etymology: "aithalos" (Greek) means soot + "pteryx" (Greek) means wing. Gender: feminine.

Aethalopteryx does not belong to section 2. It is here established for a group of African species which had formerly been placed under *Duomitus*, *Xyleutes* or

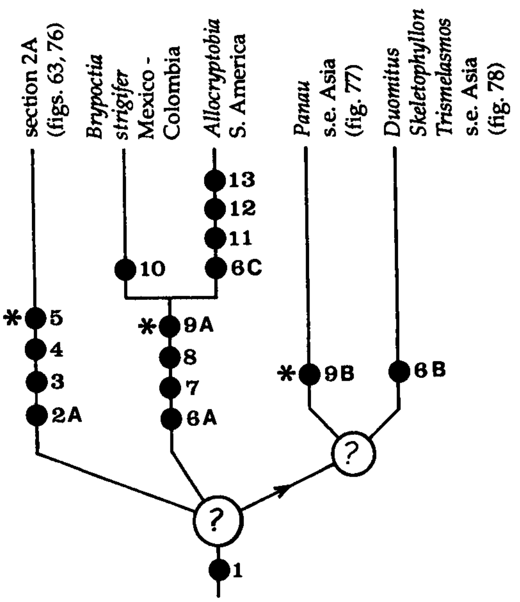


Fig. 79, cladogram of section 2 - part 2 (Zeuzerinae).

Azygophleps. The species of this new genus differ from those of *Xyleutes* and *Duomitus* in e.g. that they lack an antero-distal reduction of the 4Ax. In *Xyleutes* the humeral plate is approx. 3 times as large as the radial bridge, the ♀ I-epiphysis is short, and the radial plate is distally elongate and moderately slender. In *Duomitus* the rami of the ♂ antenna are straight and nearly in one plane. In *Aethalopteryx* the mesomeron is only 1.5 times as wide as the eucoxa II, whereas in *Azygophleps* it is twice as wide. The tarsomeres are only very slightly widened apically in both these genera. In *Aethalopteryx* the anal plate is moderately long, whereas in many *Strigocossus* and *Azygophleps* species this structure is rather long. The species are medium-sized and most of them have dark fuscous areas on the forewing. All the species occur in Africa. It seems impossible to define the genus as a whole more accurately. See also fig. 55. There seem to be two main sections within this genus – see fig. 80. The species of one of the main branches all lack an arolium. Those of the other section have the following characteristics: I-epiphysis reaching little short of or nearly as far as tibia-apex, humeral plate approx. 2 times size of radial bridge, and anterior invagination of median arm reaching up to 0.3 times length of arm.

In *squamea* (Distant, 1902) the ♀ antenna is moderately strongly bipectinate, while in the undescribed species (a) and in *steniptera* (Hampson, 1916) it is indistinctly bilobed. Of the other species no ♀ specimens with antennae were available. In most species the lower suture of Apc reaches up to at least 0.5 or 0.6 times length of An, but in *grandiplaga* (Gaede, 1930) it is still at 0.3 times. Although the humeral plate of the undescribed species (d) has not been examined, the species is tentatively placed next to *grandiplaga*. A general trend is the reduction of the arolium. Median plate is sometimes/often reduced in length. In both main branches of the cladogram (fig. 80) the anterior invagination of the median arm seems to shorten to 0.3 times length of this structure. See also fig. 80 for variation.

No material of *Xyleutes obscurascens* Gaede, 1930, *Xyleutes dictyotephra* Clench, 1959 and *X. forsteri* Clench, 1959 was available. These three species probably belong to *Aethalopteryx*.

Phragmatoecia atrireta Hampson, 1910a: 129.
Material. —1♂ (holotype), BOTSWANA: Ngami (Lugard) (BMNH).
Undescribed species (a)
Material. —2♀♀, ETHIOPIA: Daoua (Ulenhuth) (BMNH).
Note. Most closely resembling *atrireta*.

Duomitus steniptera Hampson, 1916: 166, pl. 2: fig. 31 (male).

Material. —1♂ (holotype), SOMALIA: Mandera, 47 miles southwest of Berbera, 3000 ft., 27.iv.1908 (Feather) (BMNH); 9♂♂, 1♀, SOMALIA (BMNH).

Undescribed species (b)

Material. —8♂♂, KENYA: Suna, s. Kavirondo (Feather) (BMNH).

Note. Most closely resembling *pindara*, but darker.

Duomitus pindarus Fawcett, 1916: 733.

Material. —2♂♂ (syntypes), KENYA: Kedai, 23-25.xi.1911 (Feather) (BMNH); (conspecific ?) 1♂, UGANDA: Bukuni (BMNH).

Note. This species is also known from Saudi Arabia (Wiltshire, 1986: 265).

Duomitus simillima Hampson, 1916: 166, pl. 2: fig. 32 (male).

Material (all BMNH). —1♂ (holotype), SOMALIA: Mandera, 47 miles southwest of Berbera, 3000 ft., 20.ix.1908 (Feather); 1♂, SOMALIA: Hargeisa, 4300 ft.; 4♂♂, ETHIOPIA: west of Harar, Diredoua.

Xyleutes grandiplaga Gaede, 1930: 547.

Material. —1♂ (paratype), CHAD: Oubangui, Chari, Bangui (coll. Moult) (BMNH); 2♂♂, NIGER: Warri (BMNH); 1♂, IVORY COAST: Adiopodoumé (MNHN).

Undescribed species (c)

Material. —1♂, GHANA: Bibianaha, 3.ii.1912, 700 ft. (Spurrell) (BMNH); 1♂, IVORY COAST: Bingervill, 1915 (Melou) (BMNH).

Undescribed species (d)

Material. —1♂, GHANA: Akoon, 23.ii.1914 (Harrison) (BMNH).

Note. The groundcolour of the forewing is white, and the forewing has a vague reticulate fuscous pattern.

Hyleutes tristis Gaede, 1915: 147-148.

Duomitus mesosticta Hampson, 1916: 165, pl. 2: fig. 30 (male). [Synonymized by Gaede, 1930: 547].

Material. —1♂ (holotype of *mesosticta*), SOMALIA: Mandera, 3000 ft., 7.x.1909 (Feather) (BMNH); 1♂, SOMALIA: Mandera (BMNH).

Undescribed species (e)

Material. —6♂♂, KENYA: Kibwezi (Feather) (BMNH); 1♀, TANZANIA: 100 miles west of Dar-es-Salam, Morogoro, at foot of Mt. Uluguru, 2000 ft. (Loveridge) (BMNH).

Note. The forewing shows a large dark anterior marking at its base, and has a dark spot at the costa at approx. half wing-length.

Duomitus squameus Distant, 1902: 213.

? *Azygophleps atriplaga* Le Cerf, 1919b: 30-31.

Material. —1♂ (holotype), SOUTH AFRICA: Pretoria (coll. Distant) (BMNH); 5♂♂, GHANA: Wassaw district (BMNH); 1, MALAWI: Lingadji (BMNH); 1♀ (*atriplaga*), ANGOLA (MNHN).

Undescribed species (f)

Material. —1♂, NAMIBIA: Tsumeb (BMNH).

Note. Closely resembling *squamea*. The forewing has a small spot at the costa at approx. half wing-length.

Undescribed species (g)

Material. —1♂, SIERRA LEONE (Bainbridge) (BMNH).

Table 21. Apomorphies in fig. 80 (*Aethalopteryx*).

1a.	Arolium wanting.
b.	Arolium reduced up to small.
2.	Labial palpi two-segmented.
3a.	Lower suture of Apc up to approx. 0.7 times length of An.
b.	Lower suture of Apc up to approx. 0.8 times length of An.
c.	Lower suture of Apc up to approx. 0.6 or 0.7 times length of An.
d.	Lower suture of Apc at approx. complete length of An.
4a.	Mesepimeron moderately low to moderately high, or moderately high.
b.	Mesepimeron moderately high.

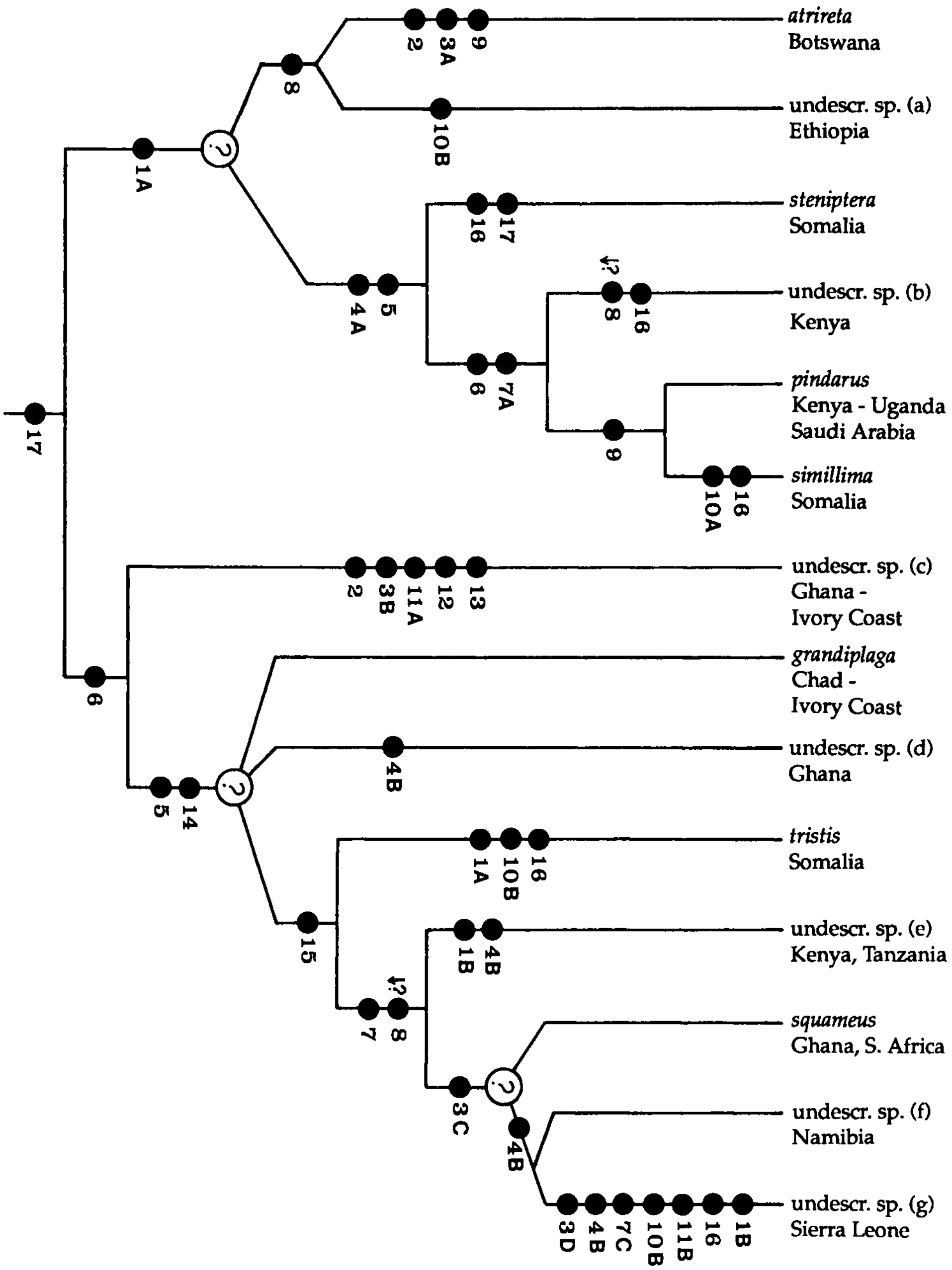


Fig. 80, cladogram of *Aethalopteryx*.

5. Median arm with anterior invagination up to approx. 0.3 times its length.
6. I-epiphysis reaching nearly or approx. as far as tibia-apex.
7a. Fringes only rather long.
b. Fringes at most moderately long.
c. Fringes short.
8. Intersclerite III wanting.
9. Male antenna moderately strongly bipectinate.
10a. Paronychia wanting.
b. Paronychia reduced to very small.
11a. Fifth tarsomere approx. 1.3 times length of fourth.
b. Fifth tarsomere approx. 1.5 times length of fourth.
12. Inner cell of forewing wanting.
13. Inner cell of hindwing wanting.
14. Humeral plate twice as large as radial bridge.
15. Tarsi dorsally mainly dark fuscous and not or indistinctly ringed white.
16. Labial palpi slender.
17. Anal plate approx. moderately long.

Genus **Strigocossus** Houlbert, 1916

Strigocossus Houlbert, 1916: 78.
Type species: *Strigocossus leucopteris* Houlbert, 1916: 84.
Xylocossus Houlbert, 1916: 85. Syn. nov.
Type species: *Zeuzera capensis* Walker, 1856: 1533.

Gaede (1930: 546) does not mention *Xylocossus*, its type species and *Strigocossus*, and he places *capensis* and several other species here included in *Xyleutes*. Roepke (1957: 18) synonymizes *Strigocossus* and *Xylocossus* with *Xyleutes*. In this paper, *Xyleutes* is restricted to a few species of section 2 in which the ♀ antenna is proximally bilobed or simple, the ♀ I-epiphysis is short and pointed, the arolium and paronychia are wanting, the fringes are very short, the humeral plate is approx. 2.5 to 3 times as large as the radial bridge, the radial plate is elongate with a rather slender apex, and the distal plate of 4Ax is anteriorly reduced. The *Xyleutes* species occur in Asia. See further under *Xyleutes*.

Strigocossus is here resurrected and *Xylocossus* is synonymized with the former.

Strigocossus shares with *Azygophleps* Hampson that the mesomeron is at least twice as wide as the eucoxa II, and the tarsomeres are only slightly or hardly widened distally. In *Azygohleps* the metascutum is medially distinctly invaginated and narrow or very narrow, whereas in *Strigocossus* it is only moderately narrow. In *Strigocossus* the second segment of the labial palpi is proximally narrowed, and the ♂ antenna is bipectinate for 0.4 to 0.5 or 0.6 times its length. See also fig. 55.

There is further much interspecific variation within *Strigocossus* (see fig. 81).The type species of *Strigocossus* seems to take the first branch in the cladogram (fig. 81). It is a large species with a dark lunulate marking at the wing-apex, as the others of the left section in the cladogram. In the right section of the cladogram only *capensis* may show such a marking. The species of the right section are only moderately large. The positions of *leucopteris*, *malgacicus* (Houlbert, 1916), *kilimandjarae* (Le Cerf, 1914) and the undescribed species in the cladogram (fig. 81) are tentative, since there was only one specimen of each available and these have partially been examined.

Vertex of *crassus* is gradually bulbed, whereas in *capensis*, *ochricostus* and probably the other species of the right section it is moderately antero-laterally ridged. K varies amongst the species from rather long to long, moderately wide to moderately narrow, and plus or without a cross-suture. There is no intersclerite III, and metameron often shows a membranous split. Vestiture of tarsi is short. In *leucopteris*, *cretaceus* and *malgacicus* the tarsi are dark fuscous, whereas in *crassus* these are ringed brown and in *moderatus* there may be a few white scales at bases of tarsomeres. Venation: R1 normally from areole, but is sometimes/often proximal to it in certain species; in *capensis* the chorda and anterior M may be more or less coalescent; R3, R4+5 connate to shortly stalked; R4+5 stalked for 0.2 or 0.3 times their length; M1 posterior to or from areole; Rs-M1 connate or short to rather long. Median plate is at least sometimes reduced up to approx. half length. 2Ax is plus or without elevated scaled area.

Strigocossus leucopteris Houlbert, 1916: 84.
  Material. —1♀ (holotype), CAMEROON: Johan Albrechts Hohe, Station Kamerun, 1896 (Konradt) (MNHN).
Xyleutes malgacica Houlbert, 1916: 81.
  Material. —1♂ (holotype), MADAGASCAR: Tananarive, 1889 (Camboué) (MNHN).
Zenzera cretacea Butler, 1878: 463.
  Material (all MADAGASCAR). —1♂ (holotype), 1♂, Ellongo (BMNH); 6♂♂, 2♀♀, various localities (BMNH); 1♂ (holotype of ssp. *ambahona* Viette), 3♂♂ (paratypes), Massif de l'Anaratra, Manjakatompe, 1850 m. (MNHN); 11♂♂ (ssp. *ambahona*), Behara, Lake Iotry, Plateau Mahafaly, Valley Maroakaho, near Belaha, and Sakahara (MNHN).
Zeuzera moderata Walker, 1856: 1533.
  Material. —1♂ (holotype of *moderatus*) (BMNH); series of both sexes from Ghana, Sierra Leone, Nigeria, Cameroon and Kenya.
Phalaena (Noctua) crassa Drury, 1782: 2, pl. 2: fig. 1 (female).
  Duomitus lunifera Hampson, 1910a: 130-131. [Synonymized by Gaede, 1930: 546].
  Duomitus polioplaga Hampson, 1910a: 131. [Synonymized by Gaede, 1930: 546].
  ? *Xyleutes speciosus* Houlbert, 1916: 83.
  Material. —1♂ (holotype of *polioplaga*), NIGERIA: Lagos, Olo-Kemeji, iv.1906 (Dudgeon) (BMNH); 1♂ (holotype of *lunifera*), SIERRA LEONE, 11.ii.1896 (Clements) (BMNH); series (most ♂) from Ghana, Sierra Leone, Nigeria and Uganda (BMNH); 1♂ (holotype of *speciosus*), Quanga Strom, Majorw. Mechow (coll. Biedermann) (*Xyl. crassa*) (MNHN); 1♂, GABON: Gamba Terminao (ITZ).
Zeuzera capensis Walker, 1856: 1533.
  ? *Xyleutes sjoestedti* Aurivillius, 1910: 50-51, pl.1: figs. 14-15.
  Azygophleps flavitincta Hampson, 1910a: 130. Syn. nov.
  Material (all BMNH). —1♀ (holotype of *capensis*), ?; 1♂ (holotype of *flavitincta*), KENYA: Njoro (Cholmley); long series of both sexes from South Africa, Kenya and Uganda.
  Note. Host-plants are: *Cassia bicapsularis* L. (Uganda), *C. siamea* Lam. (Uganda), *C. laevigata* Willd. (Uganda), *C. didymobotrya* Fresen. (East Africa), and *Ricinus communis* L. (eastern Africa) (Le Pelley, 1959: 73).
Xyleutes guillemei Houlbert, 1916: 82-83, fig. 18 (male).
  Not examined. From Zaire.
Azygophleps tandoensis Bethune-Baker, 1927: 330.
  Material (all BMNH). —1♂ (holotype), 1♀, ANGOLA: N'Dalla Tando, 2700 ft., 26.x.1908 (Ansorge); 4♂♂, MALAWI: Zomba (a.o. 3000 ft.); 2♂♂, 1♀, UGANDA/KENYA: Mt. Elgon; 1♂, UGANDA: Ruwenzori, Bugoye; 1♀, ?.
Undescribed species
  Material. —1♂, ETHIOPIA: Province Sidamo-Borana, Malghe-Wando farm, 24-31.iii.1960 (De Koster) (ITZ).

Note. Closely resembling *mediopallens* Fletcher and *ochricostus* Fletcher, but with brown mixed fuscous along the costa of the forewing.

Azygophleps mediopallens Fletcher, 1968: 327.

Material. —1♂ (holotype), 4♂♂ (paratypes), UGANDA: Ruwenzori Range, Namwamba Valley, xii.1934-i.1935 (Edwards) (BMNH).

Azygophleps ochricosta Fletcher, 1968: 327.

Material (all BMNH). —1♂ (holotype), 1♂ (paratype), ZIMBABWE: Vumba, 7.xi.1936 (Drysdale); 1♂ (paratype), ZIMBABWE: Mountain Inn, Melsetter; 1♂ (paratype), GUINEA: Boukouni, near Masenta, 1750 ft.; 1♂ (paratype), 2♂♂, ZAIRE: Lake Kivu, 7000 ft.; 1♂ (paratype), TANZANIA: Stang terr., Mbeya, 28.xi.1950; 1♂, TANZANIA: Njombe, 6000-6500 ft.; 1♂, TANZANIA: Temlong, 3800 ft.

Azygophleps kilimandjarae Le Cerf, 1914: 399.

Material. —1♂ (holotype), KENYA: Kilimanjaro, Neu-Maschi, iv.1912 (MNHN).

Table 22. Apomorphies in fig. 81 (*Strigocossus*).

---

1. Labial palpi: second segment proximally narrowed up to subapically.
2a. Male antenna bipectinate for 0.4 to 0.5 or 0.6 times its length. (*)
b. Male antenna bipectinate for approx. 0.7 times its length.
3. Female frenulum bristles (usually) at least eight in number. N.B. In *crassus* the number varies from three to five.
4a. Median arm with anterior invagination up to approx. $^{1}/_{3}$ its length. (*)
b. Median arm rather long and rather wide.
c. Median arm with anterior invagination up to from $^{1}/_{3}$ to $^{1}/_{2}$ times its length.
d. Median arm with anterior invagination up to approx. $^{1}/_{4}$ times its length.
e. Median arm rather short. (*)
f. Median arm moderately long.
5. Female antenna shortly to indistinctly bilobed.
6. Vestiture of tibia II short.
7. Vestiture of tibia III short.
8a. Paronychia minute.
b. Paronychia very small to wanting.
c. Paronychia wanting.
9a. Arolium distinctly reduced to membranous and rod-like.
b. Arolium short and rod-like.
c. Arolium moderately long to minute.
d. Arolium reduced to rather short or very short.
e. Arolium wanting.
10a. Fifth tarsomere approx. 1.5 times length of fourth.
b. Fifth tarsomere approx. 1.3 times length of fourth.
c. Fifth tarsomere 1.3 to 1.5 times length of fourth.
11. Female labial palpi: third segment ovate.
12. Female eyes slightly reduced; little smaller than those of male.
13a. I-epiphysis reaching little short of to as far as tibia-apex. (*)
b. I-epiphysis reaching distinctly short of tibia-apex.
14a. Lower suture of Apc up to from 0.3 to 0.4 times length of An.
b. Lower suture of Apc up to from 0.6 to 0.7 times length of An.
c. Lower suture of Apc up to approx. 0.7 times length of An.
d. Lower suture of Apc up to approx. 0.8 times length of An.
e. Lower suture of Apc up to from 0.5 to 0.6 times length of An and terminating dorsally to K.
15a. Mesepimeron moderately low to moderately high.
b. Mesepimeron moderately high and its upper margin sometimes/often slightly sinuate.
c. Mesepimeron moderately high and with rounded upper margin.
16a. Fringes only moderately long.
b. Fringes moderately long to moderately short.

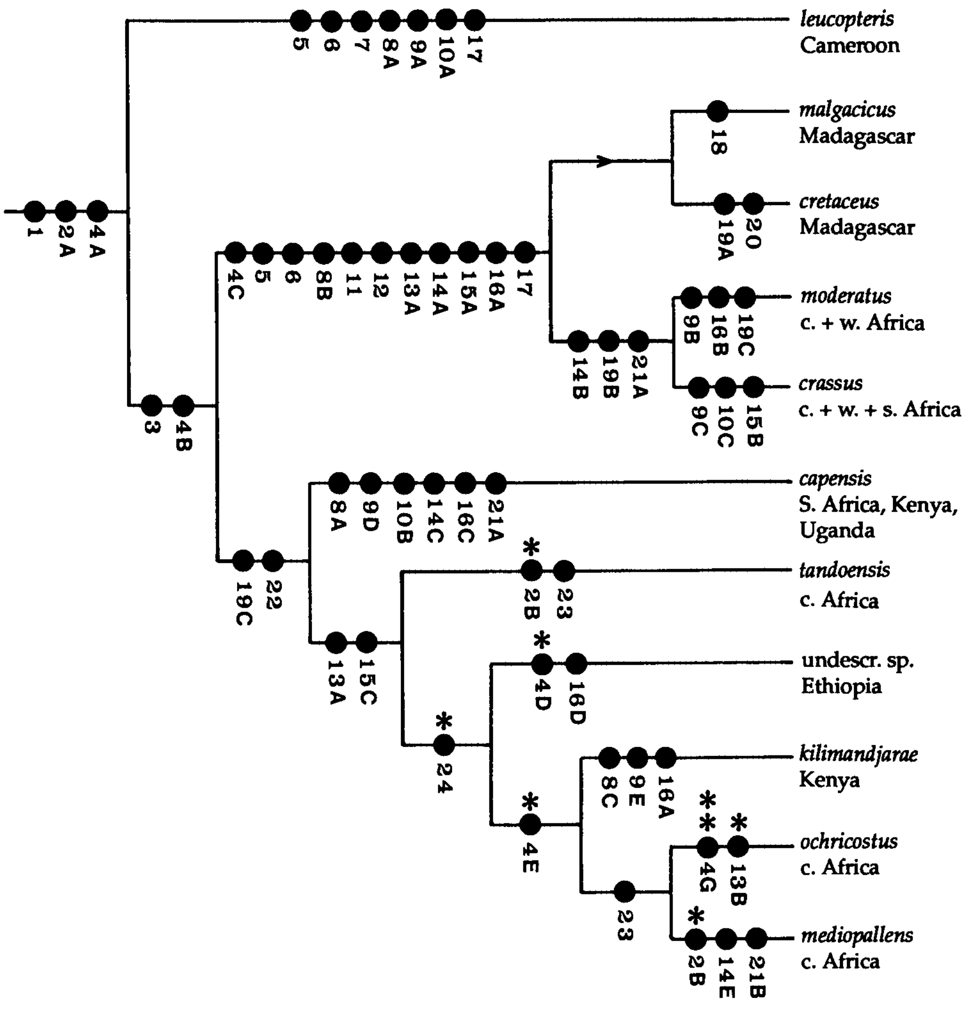


Fig. 81, cladogram of *Strigocossus*.

c. Fringes moderately short.
d. Fringes only rather long.
17. 1Ax apically rather large or large.
18. Abdominal segments ringed yellow-ochreous.
19a. An moderately high to moderately low.
b. An moderately low (only).
c. An low.
d. An approx. moderately high.
20. Accessory plate III narrow.
21a. Humeral plate twice as large as radial bridge.
b. Humeral plate approx. as large as radial bridge.
22. Tegula gradually tapering and hardly upturned to bluntly pointed and moderately upturned.
23. Scale plate shorter than radial bridge.
24. Anal plate moderately long.

Genus **Azygophleps** Hampson, 1892

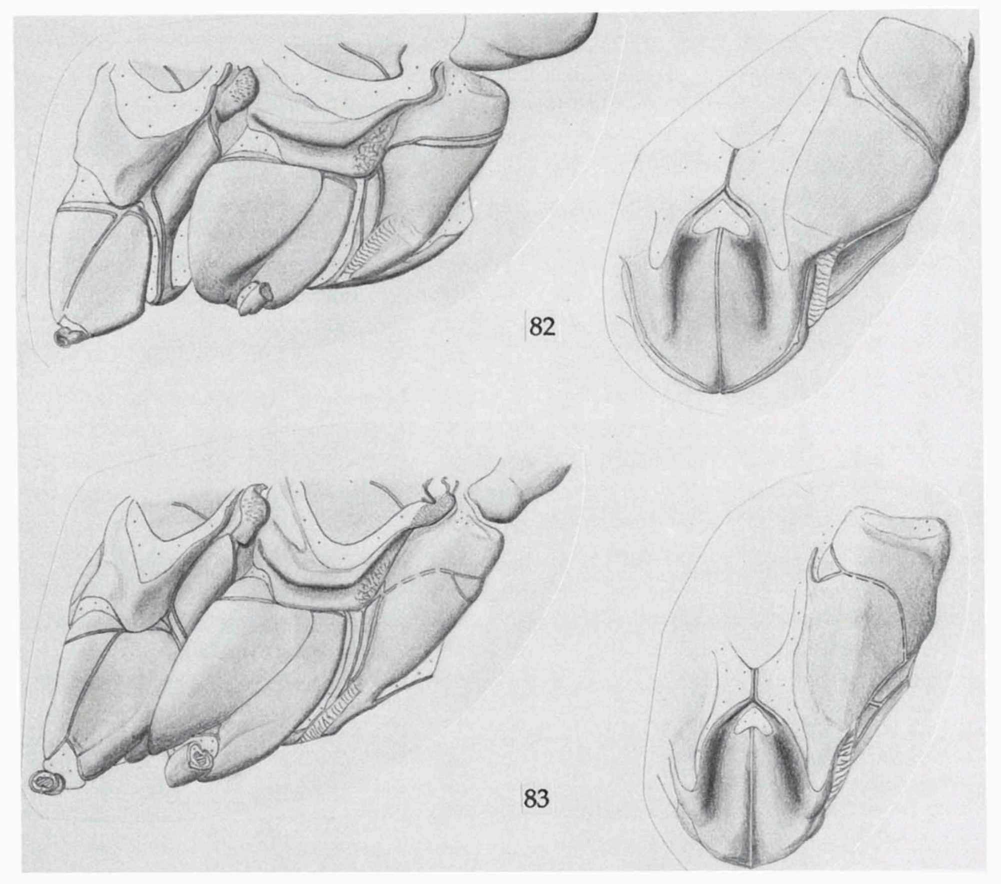
Azygophleps Hampson, 1892: 309.
Type species: *Hepialis scalaris* Fabricius, 1775: 590.

Azygophleps is a well-known genus, in which many species have been included. It is difficult to define accurately the whole of the genus. A significant characteristic is that the metascutum is medially distinctly invaginated and narrow or very narrow. This is also found in *Phragmacossia*, section 1 and certain species of section 2. In *Phragmacossia* and section 1 the ♀ abdomen is in most species longer than the hindwing and the tarsomeres are distinctly widened apically. In *Phragmacossia* the vertex has one to few protuberances laterally to Pos. In section 1 the chorda terminates very closely to or is partly coalescent with the anterior M. In section 2 the distal plate of 4Ax is anteriorly reduced.

Azygophleps shares with *Aethalopteryx* and *Strigocossus* that the tarsomeres are only very slightly or hardly widened apically. *Azygophleps* differs from *Aethalopteryx* that the mesomeron is at least twice as wide as the eucoxa II. In *Strigocossus* the metascutum is only moderately narrow and the second segment of the labial palpi is proximally narrowed. See also fig. 55. A large section of *Azygophleps* is characterized by a posteriorly shortened and more or less rounded Bs II (see figs. 84 and 83). The species of this section of *Azygophleps* resemble one another more or less closely in their colour pattern of the forewing. Remarkable is that the fringes are slightly lengthened in certain species of *Azygophleps*, while the general trend is shortening of the fringes within the Zeuzerinae. There is a fair amount of interspecific variation within *Azygophleps* (see fig. 84).

Vertex is antero-laterally ridged (see fig. 90) in at least *inclusa* (Walker, 1856), *albovittata* Bethune-Baker, 1908 and *scalaris*. Female antenna varies amongst the species in degree to how strongly bipectinate it is. In *pusilla* Walker, 1856 and *inclusa* it varies intraspecifically; in *inclusa* from shortly to moderately bipectinate. Sections of thorax of *albovittata* are shown in fig. 83. K is long and moderately narrow, and has in most species usually a cross-suture. Subalare-process II varies amongst the species from moderately short to short. Accessory plate III is in many species narrow. Intersclerite III is sometimes present, but in most species there are usually traces of sutures of it. In *scalaris* the wings are moderately elongate (fig. 98). Number of ♀ frenulum bristles varies sometimes/often from three to seven in several species. Venation (see also fig. 98): R1 from areole; R3, R4+5 connate to very shortly stalked; R4+5 stalked for 0.1 to 0.3 times their length; Rs-M1 in most species short to moderately long, but in *scalaris* up to long; M2, M3 may be connate in certain species. Median plate is normally reduced in length and is at least sometimes wanting in *scalaris*. 2Ax has in most species usually elevated scaled area.

Zeuzera liturata Aurivillius, 1879: 48-49.
Zeuzera aurivillii Kirby, 1892: 872. [Synonymized by von Dalla Torre, 1923: 37].
Material (all NAMIBIA). —4♂♂, Tsumeb (BMNH): 1♂, Tsumeb (RMNH); 1♂, Tsumeb (MNHN).
Azygophleps leopardina Distant, 1902: 213-214.
Azygophleps borchmanni Grünberg, 1910: 140. [Synonymized by Gaede, 1930: 545].
Material (all BMNH). —1♂ (holotype of *leopardina*), SOUTH AFRICA: Transvaal, Pretoria (coll. Distant); 4♂♂, SOUTH AFRICA: Natal, Durban and Pretoria; 1♂, NAMIBIA: Tsumeb; 1♂, KENYA: Mombasa; 1♂, KENYA: Kibwezi.



Figs. 82-83, sections of thoraces of zeuzerine species. 82, *Zeuzera pyrina*, Germany, Herkulesbad; 83, *Azygophleps albovittata*, Ghana, Kete-Krachi.

Azygophleps nubilosa Hampson, 1910a: 129.

Material. —1♀ (holotype), UGANDA (Doggett) (BMNH); 1♂, KENYA: Teita Hills (BMNH).

Undescribed species

Material. —1♀, TANZANIA: Livingstone Mts., 15.x.1931 (Zimmer) (ITZ).

Note. This is a rather large specimen with uniformly fuscous forewings and bronzy brown hindwings.

Zeuzera (?) *regia* Staudinger, 1891: 253-254, pl. 3: fig. 6 (male).

Material. —1♂, IRAQ (BMNH); 1♂, TURKEY: Pontus (BMNH).

Note. Daniel (1964: 6) distinguishes a subspecies *afghanistensis*.

Zenzera albofasciata Moore, 1879: 87.

Material. —1♂, INDIA: Darjiling (BMNH); 1♂, 2♀♀, INDIA: Sikkim, Mand (BMNH); 2♂♂, 1♀, INDIA: Scind Valley, 8000 ft. (BMNH); 1♂, 1♀, INDIA: Kulu (BMNH); 1♂, YAMMU AND KASHMIR: Srinagar, 1600 m. (MNHN); 1♀, Chio-Kou-Ho, 1700 ft. (BMNH); 3♂♂, Siao Lou (MNHN).

Azygophleps atrifasciata Hampson, 1910b: 481.

Material (all BMNH). —1♂ (holotype), ZIMBABWE: district Kalungwisi, High Plateau, 4-4500 ft., 26.ix.1908 (Neave); 1♀, ZIMBABWE: Mumbwa; 1♀, UGANDA: Entebbe; 1♀, ZAIRE: Lufira R., near Likasi Cap. M., 4000 ft.; 1♂, ANGOLA; 1♂, MALAWI: Zomba.

Zeuzera inclusa Walker, 1856: 1534.

Zeuzera petax Wallengrén, 1860: 43. [Synonymized by Gaede, 1930: 545].

Material (BMNH and RMNH). —long series from Ethiopia, Uganda, Kenya, Malawi, and Tanzania; 1♂, 1♀, NORTH YEMEN: near Dhamar, Risabab (ITZ).

Note. The species has also been recorded from Saudi Arabia and Oman (Wiltshire, 1986: 266). The larva is known as a root-borer in a species of *Indigofera* L. in Uganda (Le Pelley, 1959: 73).

Azygophleps melanophele Hampson, 1910a: 130.

Material. —1♂ (holotype), NIGERIA: Sapelo (Sampsom) (BMNH); 1♂, GHANA; district Wassaw, 45 miles inland from Sekondi (BMNH); 1♂, ? (BMNH); 1♂, IVORY COAST, Barr. d'Ayarné (MNHN); 1♂, GABON: Belinga (MNHN); 3♂♂, CAMEROON: Lolodorf (MNHN).

Zeuzera pusilla Walker, 1856: 1538.

Material (all BMNH). —1♂ (holotype), 5, north INDIA; 18, INDIA: Deccan, Jubbulpore, Madros, Mynporee, Jhansi and Bangalore; 1, Bengal, Chapro; 1, upper BURMA: Meiktil.

Zeuzera aburae Plötz, 1880: 77.

Material (all BMNH). —1♂, ZIMBABWE: Mumbwa; 1♂, KENYA: Suna, s. Kavirondo.

Phalaena (Noctua) asylas Cramer, 1779: 62, pl. 137: fig. c.

Zeuzera strigulosa Walker, 1856: 1534. [Synonymized by Kirby, 1892: 871-872].

Zeuzera canadensis Herrich-Schäffer, [1854] 1850-1858: 58, fig. 168. [Synonymized by Holland, 1898: 59-60].

Range: central Africa to South Africa (Gaede, 1929: 545).

Material. —long series from South Africa (BMNH); series of males, SOUTH AFRICA: Natal (MNHN).

Note. The locality recorded by Herrich-Schäffer for *canadensis*, Quebec, is probably erroneous, or it should be that the species had been imported into North America.

Azygophleps albovittata Bethune-Baker, 1908: 263.

Material (all BMNH). —1♂ (lectotype), 1 (paralectotype), north NIGERIA (Cator); 3 (paralectotypes), UGANDA: s.e. Ruwenzori, 3500 ft., iv. 1906 (Legge & Wollaston); long series from Ghana, Nigeria, Guinea, Zaire and Uganda.

Note. Carter & Deeming (1980: 399) record the species as a pest on Groundnuts in northern Nigeria.

Azygophleps simplex Aurivillius, 1905: 42.

Not examined. From Nigeria.

Phalaena (Hepialis) scalaris Fabricius, 1775: 590.

Zeuzera bivittata Walker, 1865: 586-587. [Synonymized by Hampson, 1892: 310].

Material. —long series of both sexes from Pakistan and India, and from Senegal, Ivory Coast, Ghana, Nigeria, Zaire, Angola, Tanzania and Sudan (BMNH); 2♂♂, CHAD (ITZ).

Note. Arora (1976: 55-58) notes that the species is also known from Indochina, China and Sri Lanka. The species is known as a stem-borer in species of *Sesbania* Scop. in Ghana. In India, the larva also mines in *Sesbania* spp. (at least stem) (Arora, 1976: 58; Agrawal & Agrawal, 1960, according to Carter & Deeming, 1980: 401), and in Sunnhemp (Arora, 1976: 55).

Table 23. Apomorphies in fig. 84 (*Azygophleps*).

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1. Metascutum medially narrow or very narrow, distinctly invaginated.
2a. Antenna bipectinate/bilobed for approx. 0.4 times its length.
b. Antenna bipectinate/bilobed for at least 0.7 (up to 0.8) times its length.
c. Antenna bipectinate/bilobed for approx. half its length.
3. Tegula gradually tapering and only slightly upturned.
4a. Mesepimeron moderately high and with rounded upper margin.
b. Mesepimeron moderately low to moderately high and with rounded upper margin.
5. Fifth tarsomere 1 to 1.5 times length of fourth.
6. Forewing regularly spotted.
7. An moderately low.
8a. Fringes moderately long.
b. Fringes little lengthened, very long. (*)
9a. Anal plate moderately long. (*)

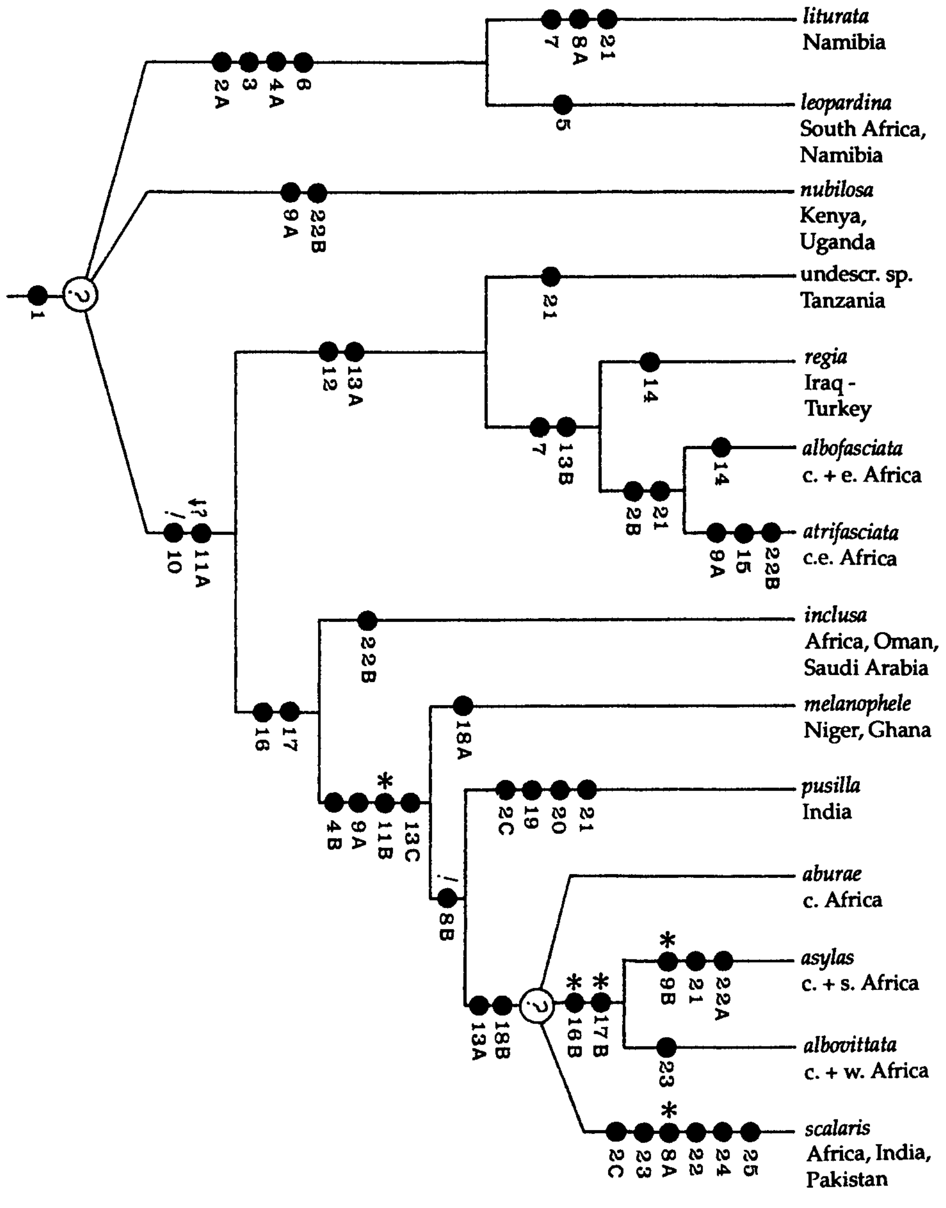
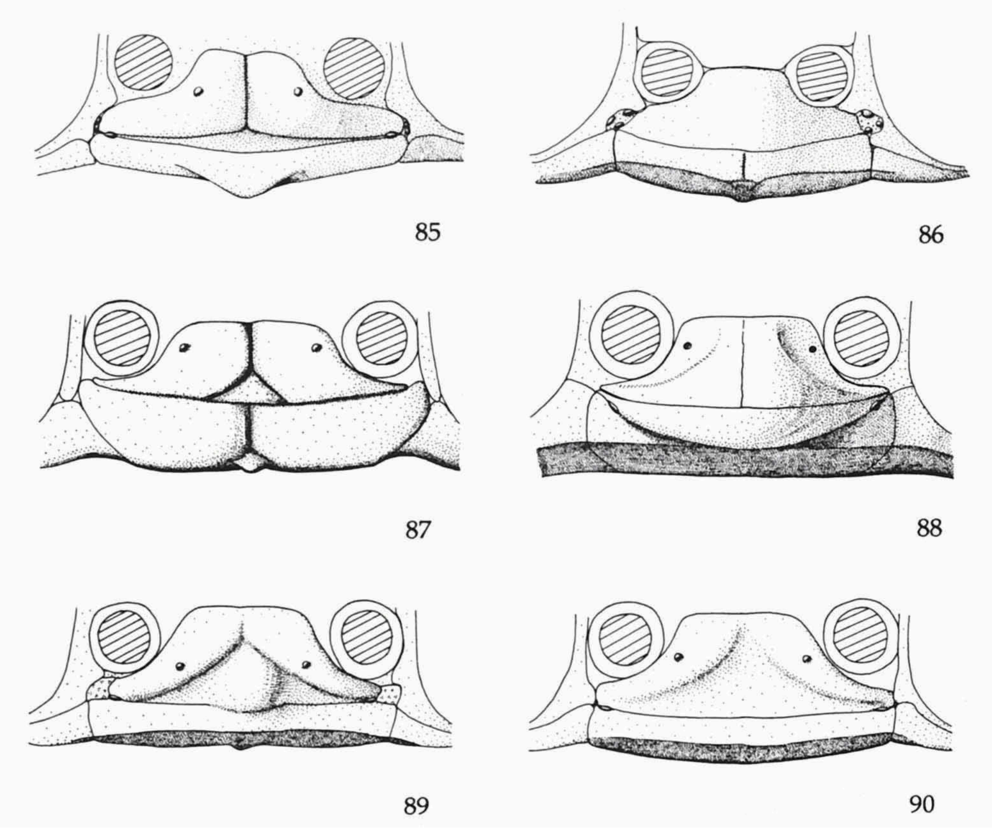


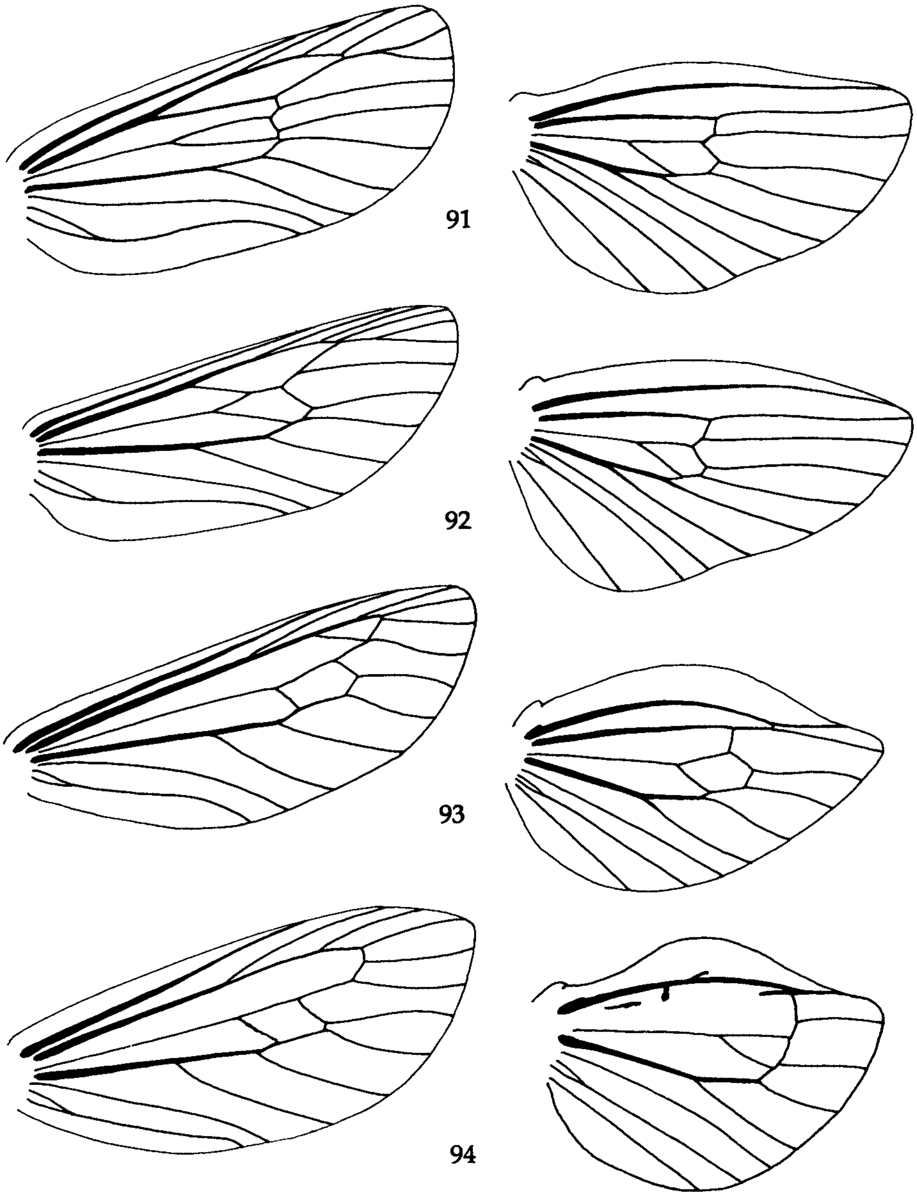
Fig. 84, cladogram of *Azygophleps*.

b. Anal plate rather long.
10. Bs II posteriorly shortened and rounded.
11a. Humeral plate 2 times size of radial bridge. (*) It may be that this is also found in species placed lower in the cladogram.
b. Humeral plate 1.5 to/or 1.8 times size of radial bridge.
12. Female antenna slightly bilobed.
13a. Median arm rather wide. N.B. In *albovittata* the median arm varies from rather to moderately

wide.
b. Median arm rather long.
c. Median arm varying from moderately to rather long, or rather long.
14. Lower suture of Apc up to from 0.5 to/or 0.7 or more times length of An.
15. Tegula ventro-posteriorly rounded.
16a. Subalare-process II short. (*)
b. Subalare-process II moderately short.
17a. Forewing with yellow streak, dots or striae. (*)
b. Forewing without yellow markings.
18a. I-epiphysis reaching approx. as far as tibia-apex.
b. I-epiphysis reaching little short of or approx. as far as tibia-apex, or varying from little to distinctly short of tibia-apex.
19. Male antenna moderately to rather strongly bipectinate for approx. half its length.
20. Female antenna for approx. half its length shortly bipectinate to bilobed.
21. Vestiture of tibia II short.
22a. Scale plate shorter than radial bridge.
b. Scale plate varying from shorter to as long as radial bridge.
23. Arolium narrowed.
24. Paronychia wanting.
25. Forewing more or less elongate.



Figs. 85-90, vertices of zeuzerine species. 85, *Phragmacossia reticulata*; 86, *Phragmacossia territa*; 87, *Zeuzera pyrina*; 88, *Cecryphalus nubilus*; 89, *Trismelasmos papuanus*; 90, *Azygophleps inclusa*.



Figs. 91-94, venation of zeuzerine species. 91, *Phragmacossia parvipuncta*; 92, *Phragmataecia castaneae*; 93, female *Eulophonotus armstrongi*; 94, female *Eulophonotus myrmeleon*.

Discussion - Zeuzerinae

There is sufficient variation in the structure of the sclerites of the thorax and wing bases within the subfamily Zeuzerinae to propose a cladogram of the genera based on external morphology. A few genera are so large and so homogeneous that no cladogram of their species can be provided. Cladograms of the species from the other genera have been constructed.

Certain developments have seemingly occurred on many occasions and in various lineages. These are here called trends. Trends within the Zeuzerinae with a more or less regular pattern are: lowering of An, lengthening of lower suture of Apc (reversal), tegula becoming ventro-posteriorly blunter, widening of mesomeron, lengthening of fifth tarsomere, shortening of fringes, reduction of arolium, reduction of paronychia, R1 moving to a position proximally to areole, R5 becoming stalked with R4 for more of its length, and shortening of anal plate. The developments of tegula, mesomeron, arolium, paronychia and fringes appear to be particularly helpful for the elucidation of phylogeny. These show a regular pattern, probably without reversals.

Trends without a simple pattern in the cladograms and thus less useful for the elucidation of the phylogeny of the Zeuzerinae are: reduction of rami of ♀ antenna, reduction of labial palpi, shortening of subalare-process II, heightening of mesepimeron, narrowing of accessory plates II and III (reversals), disappearance of intersclerite III, shortening of vestiture on legs, reduction of length and increase of number of ♀ frenulum bristles, enlargement of apex of 1Ax, shortening of vestiture of abdomen, and (further) "hardening" and darkening of most sclerites.

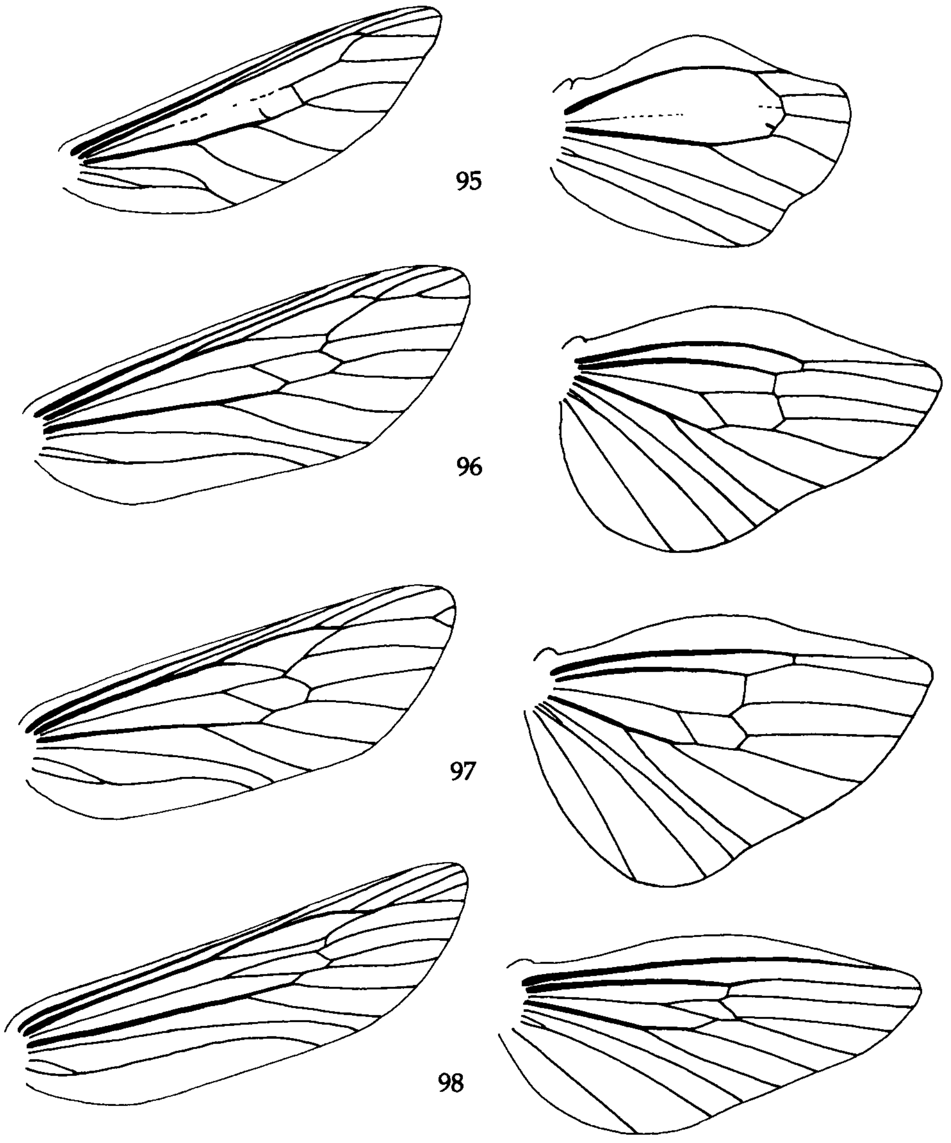
It is probable that certain trends involve aerodynamic improvement, such as lowering of An and shortening of the vestiture. It seems that 1Ax functions as a blocking structure against backward turning of the forewing during flight. It would thus be understandable that it increases in size in species with a greater mobility and/or a relatively larger forewing. Other trends possibly relate to loss of function, such as shortening of the ♀ frenulum bristles and the anal plate. It is remarkable that the ♀ frenulum bristles are often reduced in length, though the costal region of the hindwing is hardly or not extended. It is unknown why the number of frenulum bristles is increased in so many species, though they seem to have lost their function. With an increase in number these bristles are generally finer and often shorter.

When the fifth tarsomere is lengthened, it is similarly in all legs, although the relative ratios in length of the other tarsomeres often differ between the pairs.

It seems that reduction in size of certain sclerites is sometimes followed by an enlargement of that sclerite; e.g., An becomes sometimes higher again, and the anal plate and I-epiphysis are sometimes lengthened again. Enlargement of certain sclerites is apparently sometimes followed by reduction in size; e.g., the fifth tarsomere and I-epiphysis are sometimes shortened again, and the humeral plate often becomes smaller again. It seems that the factors determining the size of these structures can more or less easily reverse.

The presence or absence of a cross-suture on K and of an elevated scaled area on 2Ax varies often intraspecifically and show further a very irregular pattern.

There seems to be a positive correlation between a distinct invagination of the dorsum of the hindwing or extension of its anal region and the lengthening and/or narrowing of the forewing. This appears to be particularly the case in the males. The



Figs. 95-98, venation of zeuzerine species. 95, male *E. myrmeleon*; 96, *Zeuzera pyrina*; 97, *Tarsozeuzera kochi*; 98, *Azygophleps scalaris*.

females usually have a weaker invagination and broader wings than the males. Such a correlation may point to a function of the form of the anal region for greater steadiness in flight. It further seems that such a correlation is often in combination with the move of R1 proximal to the areole, probably for the consolidation of the (lengthened) wing. R5 is apparently less important, since it becomes more stalked with R4 on many occasions. R5 is sometimes even completely coalescent with R4 in distinctly narrowed wings (males of *Eulophonotus* species).

Coloration of the moths is usually whitish, brown and/or fuscous. In many species the dark fuscous areas show a distinct metallic lustre, normally bluish and sometimes greenish. Yellow or yellow orange wing coloration evolved on four occasions; present in *Chalcidica, Alophonotus, Paralophonotus, Eulophonotus, Allocryptobia* and certain species of *Azygophleps*. In *Hermophyllon anceps* the body and wings are partly yellowish. In *Bergaris* there are some species with buff or yellowish buff forewings, and one with orange vestiture on the head and thorax. In *Relluna nurella* the forewing is partly yellowish buff. In *Zeuzera conferta* the tarsi have yellowish rings. In certain *Endoxyla* species the abdomen has yellowish rings in combination with black and white ones.

There are, however, no records of day-time activities by these species. The bright colours may not have a role in diurnal sexual behaviour, but may have a warning function against predators.

It is remarkable that *Paralophonotus rauanus* so closely resembles the females of *Eulophonotus* species in colour pattern, while it is so widely separated from these in the cladogram (figs. 63 and 76). Furthermore, *Pseudozeuera biatra* closely resembles *Zeuzera* species superficially, while it seems to be separated from these by *Paralophonotus* and *Eulophonotus*. It may be that both colour patterns have been relatively easily (re)developed (within section 2A) from a basic (dormant) stage, which may have to do with a warning function against predation (see also Seitz, 1912: 428). A colour pattern which resembles that in *Zeuzera* is found in species from various genera of Zeuzerinae, e.g. *Endoxyla* and *Azygophleps*.

One or more hosts of a small number of species are known. Several species from different continents mine in stems and trunks of Coffee. Certain *Zeuzera* species are known to mine in plants of a diversity of families. Most species mine in trees, but certain or all *Phragmataecia* species feed in certain Grasses.

Key to the genera of Zeuzerinae

1. Distal plate of 4Ax well-developed (see fig. 59) 2
- 4Ax antero-distally reduced (see figs. 65 and 74 10
2. Metascutum medially much invaginated narrow or very narrow 3
- Metascutum medially slightly or not invaginated, moderately narrow 9
3. Tarsomeres distinctly widened apically and often with (rather) long vestiture ... 4
- Tarsomeres only slightly or hardly widened apically and with only short vestiture . ... *Azygophleps*
4. Terminations of Pos forming small pits or not marked. Median arm moderately long and approx. as wide as Cu2. Tarsal spines absent. Chorda terminating very closely to anterior M or more or less coalescent with the latter 5
- Vertex with one or few small protuberances at terminations of Pos (figs. 85-86). Median arm rather short and narrower than Cu2. Tarsal spines present in most

species. Chorda terminating at distinct distance from anterior M ... ***Phragmacossia***

5\. Anal plate moderately long ... 6

\- Anal plate rather long ... ***Eburgemellus***

6\. Lower suture of Apc reaching up to at least 0.6 times length of An ... 7

\- Lower suture of Apc reaching up to approx. 0.3 times length of An .. ***Oreocossus***

7\. Lower suture of Apc normally reaching up to from 0.8 to 0.9 times or complete length of An ... 8

\- Lower suture of Apc reaching up to from 0.6 to 0.7 times length of An ... undescribed genera (section 1, e.g. *grandis*)

8\. Tegula ventro-posteriorly bluntly pointed and slightly or moderately upturned. Subalare-process II short but distinct ... ***Zeuzeropecten***

\- Tegula ventro-posteriorly very blunt, nearly rounded. Subalare-process II very short and indistinct ... ***Phragmataecia***

9\. Mesomeron approx. 1.5 times as wide as the eucoxa II ... ***Aethalopteryx***

\- Mesomeron at least 2 times width of the eucoxa II ... ***Strigocossus***

10\. Male antenna proximally only moderately bipectinate ... 11

\- Male antenna proximally rather strongly bipectinate (as in *Zeuzera*) ... 12

11\. Forewing partly buff or yellowish brown. Asian species ... ***Relluna***

\- Forewing with white and dark fuscous areas. American species ... ***Hamilcara***

12\. Australian species ... 13

\- Asian, African, European or American species ... 15

13\. Labial palpi two-segmented ... 14

\- Labial palpi three-segmented ... ***Endoxyla***

14\. Radial plate distally elongate with moderately slender apex (figs. 65 and 74). Thorax white with blackish markings ... ***Zeuzera***

\- Radial plate distally moderately wide with moderately narrow apex. Thorax greyish or brownish ... ***Sympycnodes***

15\. Radial plate distally elongate with slender apex (figs. 65 and 74). Male I-epiphysis more or less blunt ... 16

\- Radial plate distally moderately wide with moderately narrow apex. Male I-epiphysis bluntly pointed ... 29

16\. Aculeate area at mesepimeron wanting ... 17

\- Aculeate area at mesepimeron well-developed ... 27

17\. Fringes only short ... 18

\- Fringes (at least of the forewing) very short ... 19

18\. Wings with yellowish areas ... ***Chalcidica***

\- Wings brownish or buff with fuscous striae ... ***Bergaris***

19\. R5 stalked with R4 for less than 0.8 times its length. When R5 is stalked with R4 for approx. 0.8 times its length, the first tarsomere of the pro- and/or midleg distinctly thickened ... 20

\- R5 stalked with R4 for at least 0.8 times its length or even completely coalescent. First tarsomere of the pro- and/or midleg not thickened ... ***Eulophonotus***

20\. Labial palpi three-segmented ... 21

\- Labial palpi two-segmented ... 23

21\. Male forewing completely covered by scales. Median arm rather long ... ***Rugigegat***

\- Male forewing partly semi-transparent; areas not completely covered by scales. Median arm moderately long ... 22

22. Labial palpi: second segment proximally narrowed. Thorax mainly blackish .... ***Paralophonotus***
- Labial palpi: second segment moderately thick along its whole length. Thorax white speckled with dark fuscous .... ***Pseudozeuzera***

23. First tarsomere of pro- and midleg approx. as thick as the second of that leg. R5 stalked with R4 for less than 0.7 times its length 24
- First tarsomere of pro- and/or midleg thickened. R5 stalked with R4 for 0.7 to 0.8 times its length .... ***Tarsozeuzera***

24. Chorda terminating at distinct distance from anterior M 25
- Chorda terminating very closely to or partly coalescent with anterior M .... ***Cecryphalus***

25. Forewing white with blackish markings 26
- Forewing with yellowish and blackish markings .... ***Hermophyllon***

26. Subalare II with a very short process, nearly rounded. Thorax white with blackish dots or blocks .... ***Zeuzera***
- Subalare II with an only short and distinct process. Thorax white speckled with dark fuscous .... ***Pseudozeuzera***

27. R5 stalked with R4 for less than half its length. Body and wings with brown, fuscous and/or whitish but no yellowish markings 28
- R5 stalked with R4 for at least half its length. Body and wings with yellow-orange markings .... ***Alophonotus***

28. Fringes very short. Humeral plate 2.5 to 3 times size of the radial bridge .... ***Xyleutes***
- Fringes moderately long or only short. Humeral plate approx. 1.5 to 2 times size of the radial bridge .... ***Morpheis***

29. Asian species 30
- American species 34
- African species .... Undescribed genus (section 2, undescribed species)

30. Forewing mainly whitish, with dark fuscous markings 31
- Forewing mainly brown 33

31. Forewing regularly striated dark fuscous or with larger dark markings along the costa and often in between CuP and A1+2 32
- Forewing with dark fuscous longitudinal streak over the central area .... ***Panau***

32. Labial palpi moderately slender .... ***Skeletophyllon***
- Labial palpi moderately thick .... ***Trismelasmos***

33. Forewing distally with some greyish markings, sometimes indistinct, and further mainly brown. Rami of the ♂ antenna nearly in one plane .... ***Duomitus***
- Forewing with a whitish spot posterior to the cell, sometimes indistinct, or with whitish area along the costa, or mainly brownish, or forewing brown with fuscous striae. Rami of the ♂ antenna in pairs at an obtuse but distinct angle from each other .... ***Panau***

34. Fringes long to/or moderately long. Scale plate approx. as long as the radial bridge. Little sexual dimorphism 35
- Fringes moderately short. Scale plate shorter than the radial bridge. Considerable sexual dimorphism. Groundcoulour of the forewing brownish .... ***Allocryptobia***
- Fringes moderately short. Scale plate approx. as long as the radial bridge. Little sexual dimorphism. Forewing whitish and regularly striated fuscous .... ***Brypoctia***

35. Fifth tarsomere approx. as long as the fourth 36

- Fifth tarsomere 1.3 to 1.5 times length of the fourth .... ***Voousia***

36. Labial palpi at least as long as the eye-diameter. Humeral plate approx. 1.5 to/or 2 times size of the radial bridge. Median arm moderately wide, slightly narrower than Cu2 37

- Labial palpi approx. half as long as the eye-diameter. Humeral plate approx. as large as the radial bridge. Median arm approx. as wide as Cu2 .... ***Carohamilia***

37. Male antenna bipectinate for approx. 0.4, 0.5 or 0.6 times its length. An moderately low. Median arm moderately long with an anterior invagination up to 0.3 times its length, or median arm rather long and the anterior invagination up to one-third its length .... ***Aramos***

- Male antenna bipectinate for 0.6 to/or 0.7 times its length. An low. Median arm rather long with an anterior invagination up to one-fourth its length ....***Psychonoctua***

Subfamily **Hypoptinae** Neumoegen & Dyar, 1894

Hypoptinae Neumoegen & Dyar, 1894: 160, 163.
Type genus: *Hypopta* Hübner, 1818: 25.

Neumoegen & Dyar originally included *Hypopta* and *Cossula* Bailey, 1882. Barnes & McDunnough (1911: 22) transfer *Cossula* to the Cossinae. Hodges (1983: 31) introduces the subfamily Cossulinae for *Cossula*. In this paper *Cossula* and most closely related taxa are excluded from the Cossidae (see chapter on excluded and obscure taxa).

The Hypoptinae are especially characterized by the state of 3Ax and 4Ax in the hindwing, which is unique within the Cossidae; these structures are only anteriorly fused and 4Ax is along most of its length approx. as dorsal as 3Ax. The upper Pas is situated in an extremely ventral position (see figs. 99-100), as in the Zeuzerinae. M of both the fore- and hindwing is close to CuA in most Hypoptinae. The subfamily Hypoptinae has further the following autapomorphies: ocelli wanting, frontal tuft moderately or rather long, vestiture on second segment of labial palpi moderately long, tegula bluntly pointed and moderately upturned or gradually tapering, CuP and A1+2 of forewing distally linked by a cross-vein or more or less coalescent (exceptions), a cross-vein Sc-Rs present (exceptions), and anal plate at most moderately long. In probably all Hypoptinae intersclerite III is wanting. These apomorphies occur also within other cossid subfamilies.

All species are distributed in America, and most of them in the Neotropics.

Genus **Hypopta** Hübner, 1818

Hypopta Hübner, 1818: 25.
Type species: *Hypopta ambigua* Hübner, 1818: 25, figs. 145-146.
Dolecta Herrich-Schäffer, [1854] 1850-1858: 58. Syn. nov.
Type species: *Dolecta scariosa* Herrich-Schäffer, [1854] 1850-1858: 58, fig. 148.
Philanglaus Butler, 1882a: 28. Syn. nov.
Type species: *Philanglaus ornatus* Butler, 1882a: 28-29.
Breyeriana Orfila, 1957: 124-125. Syn. nov.

Type species: *Breyeriana cistransandina* Orfila, 1957: 125-128, figs. 1-2 (resp. venation and male genitalia, and male and female).

Hypopta, Dolecta, Philanglaus and *Breyeriana* are genera which are much alike. In some of them, particularly *Hypopta,* many species had been placed but later transferred to other hypoptine genera.

Hübner (1818: 25) originally includes only *ambigua* in *Hypopta.* Hübner ([1820] 1816: 195) adds four other species to *Hypopta.* These four do not fit in *Hypopta;* most of them belong to the Cossinae. Kirby (1892: 863-864) erroneously designates *Hypopta caestrum* Hübner as the type species, and includes even more species from various genera, particularly cossine ones. Von Dalla Torre (1923: 20-24) follows Kirby and adds erroneously even more species to *Hypopta;* all these species other than *ambigua,* of which some occur in Eurasia, actually belong to many different genera of Hypoptinae and Cossinae. A problem is that these authors do not draw distinction between the two subfamilies.

Schaus (1905: 343) adds three new species, *inguromorpha, crassiplaga* and *triarctata,* to *Hypopta.* Dyar (1940: 1285) synonymizes *inguromorpha* and *crassiplaga* with *Langsdorfia polybia* Schaus, 1892, and places the latter and *triarctata* in *Inguromorpha* Edwards, 1888, which is probably correct.

Barnes & McDunnough (1911: 9) point out that *ambigua* is the type species of *Hypopta,* the type genus of Hypoptinae. They further include *Ravigia arcifera* Dyar, 1906 and *Hypopta palmata* Barnes & McDunnough, 1910. They had not examined *arcifera,* but were probably led by the original description, which states that *arcifera* is superficially much alike *Hypopta triarctata* Schaus. Dyar (1940: 1284-1285) places *arcifera* and *triarctata* in *Inguromorpha,* which is probably correct. The figure of *palmata* provided by Barnes & McDunnough (1911: pl. 4: fig. 1) shows a species more like one of *Comadia* (Cossinae). That *palmata* occurs in Arizona (U.S.A.) is more likely for a *Comadia* species than for a *Hypopta* one. It may well be that *palmata* should be excluded from *Hypopta.*

Barnes & McDunnough (1911: 10) make *Hypopta itzalana* Strecker, 1900 the type species of the new genus *Pomeria.* Barnes & McDunnough (1911: 16-17) place several species which were described under *Hypopta* by Dyar or Neumoegen & Dyar in *Givira* Walker, 1856.

Dyar (1910: 271-273; 1918: 367) includes two new species in *Hypopta,* and Schaus (1921: 394-395) places four new species in this genus. Most of these species described by Schaus or Dyar are placed in *Givira* or neglected by Dyar (1940). Judging the figures provided by Seitz (1940), most of these species transferred belong indeed to *Givira* or one of the genera most closely related to the latter. *Hypopta actileuca* Dyar, 1918 has, however, the outward appearance of a *Hypopta* species (see Seitz, 1940: pl. 184: fig. row a).

Hering (1923: 13-14) describes two new species under *Hypopta.* These were neglected by Dyar (1940). It is obscure to which genus Hering's species belong.

Dyar (1940: 1275) erroneously notes *caestrum* as type species of *Hypopta,* as Kirby (1892) did. Dyar (1940: 1275-1276) includes probably all cossine species, of which most belong to *Comadia,* under *Hypopta.*

Dyar (1940: 1283) erroneously places *ambigua* and *Lasiocampa aquila* Dognin, 1916 in *Langsdorfia* Hübner, [1821]. Dyar synonymizes *Endagria tigrina* Boisduval, 1859 with *ambigua.* The author of this paper examined the holotype of *tigrina* and a series of *ambigua* specimens, and doubts this synonymy, since the holotype has a rather high mesepimeron whereas this structure is moderately low in *ambigua*. The holotype of *tigrina* lacks antennae and legs, so that possible differences in these structures could not be revealed.

Dyar (1940: 1283) notes that the figure of *Langsdorfia demissa* (Maassen, 1890) shows a species much like a dark *aquila*. Perhaps *demissa* should be included in *Hypopta*.

Ureta (1957: 140-142, pl.: fig. 5a) describes and figures the new species *Hypopta monsalvei*, including the ♂ genitalia. It is here uncertain if this species from Chile actually belongs to *Hypopta*.

Daniel (1961: 160-161) discusses briefly the confusion approx. the actual type species of *Hypopta*, and introduces *Parahypopta* (Cossinae) for *caestrum* and some most closely related species. *Parahypopta* is restricted to the Palaearctic.

Gentili (1985: 102) erroneously includes *ambigua* in *Philanglaus*.

Philanglaus was originally monotypic and placed in the Hepialidae Stephens, 1829, but transferred to the Cossidae by Schaus (1905: 339). Schaus (1905: 342) adds the new species *sobrana* to *Philanglaus*. Schaus (1921: 393-394) describes the new species *Philanglaus beatrix*. Von Dalla Torre (1923: 26) notes also *Philanglaus metana* Dognin, 1910. Dyar (1940: 1282-1284) places *metana* and *beatrix* in *Langsdorfia*. Judging from the figure of *metana* given by Seitz (1940: pl. 184: fig. row e), this species looks indeed like a species of *Langsdorfia* Hübner. *P. beatrix* as figured by Seitz (1940: pl. 184: fig. row g) looks like a *Givira* species. Dyar (1940) neglects *Philanglaus ornatus*. Ureta (1957: 149) erroneously places *ornatus* in *Langsdorfia*. Clench (1957: 137-139, pl. 6: figs. 1, 4) describes the new species *Philanglaus penai*. Gentili (1985: 100) synonymizes *penai* with *ornatus*, and includes this species again in *Philanglaus*.

Originally only *scariosa* was included in *Dolecta*. Schaus (1892: 328) describes *Dolecta juturna*, *D. macrochir* and *D. invenusta*. Dyar (1940: 1277-1278, 1283) places *juturna* and *invenusta* in *Givira*, and *macrochir* in *Langsdorfia*. Judging from the figures of these species given by Seitz (1940: pl. 182: fig. row d, pl. 183: fig. row e, and pl. 184: fig. row g), these species should indeed be excluded from *Hypopta*, and *macrochir* looks indeed like a *Langsdorfia* species.The author is unaware of other species originally placed in *Dolecta*.

Breyeriana seems to be still monotypic. Orfila (1957) describes the male and female of *cistransandina*, including the genitalia, and records the species from Argentina and Chile.

In this study types of *Breyeriana cistransandina*, *Philanglaus ornatus* and *Dolecta scariosa*, and many specimens of *Hypopta ambigua* have been examined. These species share that the labial palpi have an ovate third segment, the arolium is wanting, the ♂ frenulum spine and retinaculum are distinctly reduced. At least in *cistransandina* the anal plate is moderately long and in certain others it is moderately short. The fringes of these species are still long. The mesomeron of *ambigua* is only 1.5 times width of the eucoxa II. In probably most or all other species the mesomeron is twice width of the eucoxa II. *Givira chiclin* Dognin, 1905 and *Lasiocampa aquila* Dognin are added to this group. *Langsdorfia pallida* Druce, 1911 is probably synonymous with *chiclin*. Furthermore, an unidentified specimen in the RMNH and erroneously identified as *pallidicosta* seemingly belongs to an unidentified *Hypopta* species.

It seems that these species included form a monophyletic group, although there are more species, such as *actileuca* and *demissa*, which should probably be included.

These species differ little from each other in their external morphology other than the colour pattern. Only of *Hypopta ambigua, Philanglaus penai, Breyeriana cistransandina* the genitalia are known (see Gentili, 1985: 96-97, 129, figs. 97b, 99a, 100a, 151-154, 165-166, and 174-177). In both *ambigua* and *ornatus* the ♂ genitalia have a pair of long processes near the valve, whereas in *cistransandina* these processes are only short and bulbed.

It seems impossible to produce a dichotomous cladogram based on the external morphology for these species. The author believes that when the concerning genera are maintained, certain ones will appear to be paraphyletic. Therefore *Dolecta, Philanglaus* and *Breyeriana* are synonymized with *Hypopta.*

Hypopta is thus characterized by the absence of an arolium and the distinct reduction of the ♂ frenulum spine and retinaculum. The frontal tuft is approx. rather long. The vestiture on the second segment of the labial palpi is rather long and probably in most species fine. As far known a ♂ frenulum spine and retinaculum is only present in *cistransandina,* and is wanting in probably all other species. In other hypoptine genera the mesomeron is at least twice width of the eucoxa II, whereas within *Hypopta* it is only 1.5 times as wide in at least *ambigua.* Within the Hypoptinae only in *Langsdorfia, Givarbela* Clench, 1957 and *Philiodoron* Clench, 1957 midtibial spurs are also present. These three genera differ from *Hypopta* in that their costal region of the hindwing is narrowing at approx. 0.4 or 0.5 times wing-length.

Vertex of *ambigua* has a nearly straight Pos at approx. half its length. Anterior protuberances of vertex are in one specimen examined of *ambigua* hypertrophied and horn-like. Male antenna of *ambigua* is moderately strongly bipectinate; rami have one stout sensillum at apex and one dorsally in between scales. Female antenna of *ambigua* is similar to that of male but with shorter hairs. Male antenna of *ornatus* is moderately shortly bipectinate; rami are much flattened and ovate, and have short hairs on inner margin. Male antenna of *scariosa* is moderately shortly bilobed; lobes are distinctly flattened, and have many rather short hairs and one or two sensilla on proximal side. Male antenna of *aquila, cistransandina* and *chiclin* is rather strongly bipectinate.

An is moderately high in at least *ambigua* and *aquila.* Mesepimeron of *ambigua* and *ornatus* is moderately low. Mesepimeron is still rather high in *tigrina* and the unidentified species. Mesepimeron of *aquila, cistransandina* and *chiclin* is approx. moderately high. Accessory plate II is narrow in *ambigua* and *tigrina,* whereas moderately wide in *aquila, cistransandina, chiclin* and *ornatus.* Accessory plate III is narrow in at least *ornatus.* Intersclerite is probably wanting in most or all species.

Tibial spurs are rather long in most species, but moderately long in *chiclin.* I-epiphysis reaches nearly or approx. as far as tibia-apex in *ambigua* and *scariosa.* Of the holotype of *tigrina* the legs are missing. Of the holotype of *scariosa* most legs and all tarsi are missing. Fifth tarsomere of *aquila* is slightly longer than fourth. Paronychia are very short in *ambigua, cistransandina,* and the unidentified species.

Fringes are long. Male frenulum spine of *cistransandina* is moderately short. Male retinaculum of *cistransandina* is small. In the other species examined ♂ frenulum spine and retinaculum are wanting. Venation (see also fig. 101): areole moderately small; R4 and R5 at least sometimes stalked in *ambigua, tigrina, aquila,* and the unidentified species; inner cell very small in *scariosa;* cross-vein CuP-A1+2 at least sometimes wanting in *ambigua, ornatus,* and the unidentified species; Sc-Rs long in most species, but approx. moderately long in *ambigua* and wanting in the unidenti-

fied species; Rs-M1 moderately short to short, but shortly stalked in *scariosa* and the unidentified species.
Humeral plate has not been examined in any of the species. Anal plate of at least *ambigua, chiclin* and *ornatus* is moderately short, but is moderately long in *tigrina* and *cistransandina.*

Several species occur in Argentina and/or Chile. *H. aquila* is known only from Colombia. *H. chiclin* occurs in Peru and Chile. The holotype of *scariosa* is from Rio Grande, but there are many localities in America with this name. Two species which probably belong to *Hypopta, demissa* and *actileuca,* are known from resp. Ecuador and Mexico. The unidentified species is from Mexico.

H. ornatus occurs in mixed forest of *Nothofagus* and *Araucaria* A.L. Jussieu, at altitudes between 1100 and 1400 m. (Gentili, 1985: 102). *H. cistransandina* has been found particularly in steppes, and further in zones transitional between forest and steppe, at altitudes between sea level and 1400 m. (Gentili, 1985: 130).

Material:
ambigua —(all BMNH) —12 (♂, ♀), ARGENTINA: Córdoba, Villa Ana, El Jabali, Jucuman, Soledad, and Chaco de Santiago; 1, Madras; 1♂, URUGUAY: Montevideo; 2, ? (coll. Zeller).
tigrina —1♂, ARGENTINA: B?ayses (ex musaeo Boisduval) (MNHN).
aquila —1♂ (type), 1♂, COLOMBIA: Bogotá (BMNH).
Unidentified species —1♂, MEXICO (RMNH).
scariosa —1♂ (holotype), Rio Grande (ex musaeo Boisduval) (MNHN).
chiclin —(all BMNH) —1♂, PERU: Trujillo; 2♂♂, PERU: Callao; 1♂, CHILE: Arica; 1♂ (type of *Langsdorfia pallida* Druce), CHILE: Wa?ka (coll. Druce).
cistransandina —1♂ (paratype), ARGENTINA: Neuquén, Catán-Lil, 25.i.1963 (Schajovskoi) (BMNH).
ornatus —1♂ (holotype), CHILE, Gen. slide no. 124 (BMNH); 1♂, CHILE: Mulchén, Gen. slide no. 126 (BMNH).

Genus **Langsdorfia** Hübner, [1821] 1806

Langsdorfia Hübner, [1821] 1806: [4].
Type species: *Langsdorfia franckii* Hübner, [1821] 1806: [4], pl. 194.

Originally only *franckii* (plate 1: fig. J) was included in *Langsdorfia.* Various authors added new species to this genus. Dyar (1940: 1282-1284) provides a list of species which he places in *Langsdorfia.* Dyar erroneously includes the following *Hypopta* species: *ambigua, aquila, chiclin,* and probably *demissa.* Judging the figures given by Seitz (1940: pls. 182, 184), the following species should probably also be excluded: *Ravigia basiplaga* Schaus, 1905, *Philanglaus beatrix* Schaus, 1921, and *Hypopta palmata.* Material of *Philanglaus sobrana,* which Dyar also includes in *Langsdorfia,* has been examined and this species appears to belong to *Givira.* Dyar (1940: 1277) places *Langsdorfia aroa* Schaus, 1874 in *Givira,* but this species appears to actually belong to *Langsdorfia.* Dyar (1940: 1285) places *L. polybia* Schaus, 1892 in *Inguromorpha,* which is correct. Schaus (1892: 329) notes that *polybia* is allied to *L. forreri* Druce, 1887. Perhaps the latter should also be placed in *Inguromorpha.* Ureta (1957: 148-151, pl.: figs. 4c, 5d) describes the new species *Langsdorfia albescens,* but also places two *Hypopta* species in *Langsdorfia.* The present writer doubts that *albescens* is correctly placed. In this paper *Langsdorfia andensis* Felder, 1874 is added to Dyar's list. *Trypanus garleppi* Staudinger is probably an unpublished name. There are probably several undescribed species amongst the unidentified material in the BMNH and ZMUC, and various species under the name *L. adornata* Dognin, 1889 in the BMNH.

Langsdorfia seems to be characterized by the following apomorphies: antennal rami with one, few, or up to five stout sensilla at and/or near apex, mesepimeron at most moderately high, mesomeron at least twice width of eucoxa II, arolium distinctly reduced or wanting, paronychia minute, costal region of hindwing abruptly narrowing at approx. 0.4 or 0.5 times wing-length, ♂ frenulum spine distinctly reduced in length or wanting, ♂ retinaculum wanting, ♀ frenulum bristles distinctly reduced or wanting, and anal plate approx. moderately short. In most or all species the frontal tuft is approx. moderately long and the areole is moderately small to/or small. In certain species, such as *adornata*, the clypeus is much pronounced. In certain species the third segment of the labial palpi is conical. In certain species the mesepimeron is moderately low and its upper margin is irregular or rounded and not squared. In probably all species the tarsal claws are moderately slender.

Within the Hypoptinae only in *Hypopta*, *Philiodoron* and *Givarbela* midtibial spurs are also present. *Givarbela* species differ from those of *Langsdorfia* in that their aculeate area at the mesepimeron is wanting. In *Philiodoron* the ♂ frenulum spine and retinaculum are well-developed and the cross-vein Sc-Rs is wanting. In *Hypopta* the costal region of the hindwing is narrowing at approx. 0.7 or 0.8 times wing-length. Several *Langsdorfia* species have one or few small, silvery white spots on the forewing, which is special within the Hypoptinae.

Few species have been extensively examined and several others briefly. Only of *franckii*, *adornata*, *garleppi*, and unidentified species (c) and (e) females were available. Vertex of *franckii* has a more or less indistinct Pos at approx. half its length, and lacks at least sometimes anterior protuberances. Male antenna is rather strongly bipectinate. Female antenna of *franckii* and *adornata* is similar to that of male but with shorter hairs. Female antenna of unidentified species (e) is unequally bipectinate, up to moderately strongly. Female antenna of unidentified species (c) is moderately shortly bipectinate. Number of stout sensilla on rami varies interspecifically; e.g., one or two in *franckii* and *L. malina* Dognin, 1891, and three to five in unidentified species (b). Third segment of labial palpi is conical in at least *franckii*, but ovate in most species examined. Vestiture on second segment of labial palpi is rather short in unidentified species (f), but moderately long in at least *franckii*.

Thoracic sclerites of *franckii* are shown in fig. 99. An is moderately high in at least *franckii* and *malina*. Mesepimeron is moderately high in *franckii*, *malina* and unidentified species (a). Mesepimeron is moderately low in *garleppi*, and unidentified species (d), (e) and (f). Mesomeron is at least twice width of eucoxa II, up to 3 times. Accessory plate III is narrow in at least *franckii* and *malina*. Intersclerite III is wanting in *franckii* and probably most or all other species.

Tibial spurs are moderately long in unidentified species (c), (d) and (e), but rather long in most or all other species examined. Fifth tarsomere is 1.5 times length of fourth in unidentified species (f). Arolium is wanting in at least *garleppi*, *malina*, and unidentified species (d) and (e). Stout spines are seemingly wanting in at least *franckii*.

Fringes of unidentified species (d) and (e) are long. Fringes of *franckii*, *malina*, and unidentified species (f) are moderately long. Male frenulum spine is rather long in unidentified species (d) and short or very short in at least *andensis*, *garleppi* and unidentified species (a). Male frenulum spine is wanting in *franckii* and *malina*. Female frenulum bristles are moderately long in *garleppi*, moderately short in unidentified species (e), and wanting in *franckii*. Venation (see also fig. 102): areole moderately to very small; radial veins all separate in probably most or all species; inner cell variable in size; CuP and A1+2 is at least sometimes wanting in *franckii*; Sc-Rs long to moderately long; Rs-M1 moderately short to very short. Humeral plate of at least *franckii* is approx. 1.3 times size of radial bridge. Anal plate is moderately short in most or all species.

Most species are restricted to South America. Many species occur in Peru, Ecuador and/or Colombia. At least some of these occur in high altitudinal ranges (see material examined). Many others are known from Brazil and/or Argentina. Several species, such as *centrosoma* (Dyar, 1925), are known from Mexico (Dyar, 1940: 1283). *L. rufitincta* Dyar, 1940 is distributed from Venezuela to Mexico, and *L. lunifera* and *aroa* occur from French Guiana to Mexico (Dyar, 1940: 1282). *L. franckii* is known from Mexico to Surinam.

Dyar (1940: 1282) notes that the larva of *lunifera* mines the lower end of the stalk and main roots of "Pigeon Pea".

Material:
franckii —long series of both sexes from various countries (BMNH); long series of both sexes from Brazil, Surinam (Paramaribo, Boramaca and Victoria), and Venezuela (Andes, Bricenno and Merida) (RMNH); few ♂ from Brazil and Mexico (Misantla) (ITZ); few ♂ from Brazil, Bolivia (Buena Vista), Peru (Chauchamaya) and Costa Rica (ZMUC).
aroa —(all BMNH) —1, VENEZUELA: north Venezuela; 1, MEXICO; 1, ? COSTA RICA: Tuis.
malina —(all BMNH) —4♂♂, COLOMBIA: San Antonio, 5800 ft.; 1♂, COLOMBIA: Rio Cauca, Guabinas; 1♂, PERU: River Tabaconnas, 6000 ft.
adornata —series of both sexes (BMNH).
andensis —series of males (BMNH).
garleppi —series of both sexes (BMNH).
plataea Schaus —3, Castro Paraná (BMNH).
Unidentified species (a) —1♂, PERU: s.e. Peru, Agualani, 9000 ft., xii.1905 (Ockenden) (BMNH).
Unidentified species (b) —3♂♂, PERU: s.e. Peru, Oconeque, Carabaya, 7000 ft. (Ockenden) (coll. Druce) (BMNH).
Unidentified species (c) —1♀, PERU: c. Peru, La Merced, 3000-4500 ft., i/ii.1920 (Watkins) (coll. Joicey) (BMNH).
Unidentified species (d) —1♂, ECUADOR: Guachayacu, ix/x.1926 (ZMUC).
Unidentified species (e) —1♀, ECUADOR: Guachayacu, ix/x.1926 (ZMUC).
Unidentified species (f) —1♂, ? (RMNH).
Unidentified species (g) —2♂♂, PANAMA: Taboga (ZMUC).

Genus **Philiodoron** Clench, 1957

Philiodoron Clench, 1957: 139-140.
Type species: *Philiodoron cinereum* Clench, 1957: 140-141, pl. 6: figs. 2 (venation, antennal segments, head), 4 (male genitalia).

Clench (1957: 139-142) originally includes in addition to *cinereum* a new species *frater* in *Philiodoron*. As far as the author knows only these two species have been included in this genus.

Philiodoron is characterized by the combination of the absence of a cross-vein Sc-

Rs in the hindwing and the presence of midtibial spurs. *Philiodoron* has the autapomorphies: mesepimeron moderately low and tarsal spines wanting. *Philiodoron* shares with *Langsdorfia* and *Givarbela* the following apomorphies: antennal rami with one stout sensillum apically, arolium more or less reduced (wanting in *cinereum* and *frater*), paronychia at most short, and costal region of hindwing narrowing at approx. 0.4 or 0.5 times wing-length. *Philiodoron* shares with only *Givarbela* the following apomorphies: mesepimeron (normally ?) without pale band, tarsal claws moderately slender, arolium wanting, forewing inner cell more or less narrowed and M approx. median in cell, and humeral plate reduced in size. *Givarbela* differs from *Philiodoron* in that the aculeate area at the mesepimeron is wanting in the former. In *Langsdorfia* and *Givarbela* the ♂ frenulum spine is reduced in length and the ♂ retinaculum is small or wanting, whereas these structures are well-developed in *Philiodoron*.

The present author couldnot discover the prominence which Clench (1957: 139) notes as a characteristic. Clench (1957) describes and figures the genitalia of the two species. The uncus is long and digitate. The valve has a short lobe at its dorsal margin. The vinculum is slender and curved.

Male antenna is rather strongly bipectinate. Antennal rami have a sensillum dorsally. Mesepimeron is distinctly angled and its upper margin has an acute angle. Mesomeron is more than twice width of eucoxa II in at least *frater*. Tibial spurs are approx. rather long. Venation (see also Clench, 1957: pl. 6: fig. 2A): areole narrow in specimen examined of *frater*; all radials separate or R3, R4 and R5 connate in *cinereum*; R3, R4 and R5 very shortly stalked in *frater* (1 ex.); CuP and A1+2 not linked in specimen examined of *frater*; Sc-Rs wanting; Rs-M1 short to shortly stalked; M2 and M3 connate in *frater* (1 ex.). Humeral plate is approx. size of radial bridge. Anal plate is approx. moderately long.

The two species are known only from Chile.

Material:

cinereum —1♂ (holotype), CHILE: La Leonera, 1700 m., 28.xii.1954 (Peña), Gen. slide no. C-510, slide legs no. C-515 (CMNH).

frater —1♂ (paratype), CHILE: La Leonera, Rancagua, 1.ii.1953 (Peña) (CMNH).

Genus **Givarbela** Clench, 1956

Givarbela Clench, 1956: 897-898.

Type species: *Givarbela steinbachi* Clench, 1956: 898-900, figs. 1-3 (resp. male genitalia, venation and head).

Schausisca Gentili, 1985: 105-107. **Syn. nov.**

Type species: *Schausisca desantisi* Gentili, 1985: 107-109, figs. 20, 21, 108, 126-127, 157-158, and 188.

So far only *steinbachi* has been included in *Givarbela*. This species is in many respects unusual for a cossid. It has the following autapomorphies: labial palpi approx. 3 times as long as eye-diameter, subalare II without process, mesepimeron moderately low, metameron slightly wider than eucoxa III, I-epiphysis wanting, midtibial spurs wanting, paronychia wanting, ♂ frenulum spine wanting, areole wanting, R2 stalked with R3 and R4 while R5 separate, M in forewing sometimes/often wanting, M1-M2 obsolescent or wanting, costal region of hindwing distally (further) reduced in width, hindwing inner cell wanting, anal region of hindwing reduced in width and anal veins of hindwing wanting, radial plate rather squared and moderately short, and anal plate moderately short. The type of venation and the shape of the radial plate are unique for the Cossidae. Also the types of uncus and valve (male genitalia) seem to be unique for a cossid (see Clench, 1956).

G. steinbachi shares with *Schausisca desantisi* the following apomorphies: I-epiphysis distinctly reduced in length, ♂ retinaculum wanting and scale plate wanting. In *desantisi* the I-epiphysis reaches up to approx. half length of the tibia, and is slender and acute. *G. steinbachi, desantisi* and *Schausisca marmorata* Gentili, 1985 share the apomorphies: aculeate area at mesepimeron wanting, accessory plate II partly or completely fused with mesomeron, and ♂ frenulum spine and retinaculum reduced. In *desantisi* and *marmorata* the ♂ frenulum spine is moderately or rather long. In the specimen examined of *marmorata* the ♂ retinaculum is small. Both in *marmorata* and *steinbachi* tarsal spines are wanting, whereas these are well-developed in *desantisi.* Only of *desantisi* the female is known and the ♀ antenna is bilobed in this species. *S. marmorata* greatly resembles superficially *Philiodoron* species, whereas *desantisi* more closely resembles superficially certain *Hypopta* species.

Gentili (1985: 105-111) includes only *desantisi* and *marmorata* in *Schausisca.* In the diagnosis of *marmorata* Gentili compares this species to ones of *Philiodoron,* but does not state in which subfamily *Schausisca* should be included. Gentili (1985) bases her diagnosis of the genus particularly on *desantisi,* and overlooks the presence of a well-developed I-epiphysis, the reduction of the ♂ frenulum spine, and the presence of a (small) ♂ retinaculum in *marmorata.* The present author does not know any other species which would fit in *Schausisca.* Since *desantisi* is the type species of *Schausisca* and since *marmorata* is seemingly the sister-group of *desantisi* and *steinbachi* together, it would be necessary to propose a new genus for *marmorata* to maintain *Schausisca* as a genus. The present author prefers one monophyletic genus to three monobasic genera, and hence *Schausisca* is here synonymized with *Givarbela.*

Givarbela includes here three species and is especially characterized by the absence of an aculeate area at the mesepimeron and the partial or complete fusion of the accessory plate II with the mesomeron, unique features within the Hypoptinae. *Givarbela* shares with *Philiodoron* the following apomorphies: mesepimeron (normally ?) without pale band, tarsal claws moderately slender, arolium wanting, forewing inner cell narrowed and M (sometimes/often wanting in *steinbachi*) approx. median in cell, and humeral plate reduced in size (at most as large as radial bridge). In *steinbachi* the humeral plate is approx. 0.5 times size of the radial bridge, whereas it is approx. as large as in the other species of *Givarbela* and those of *Philiodoron. Givarbela* and *Philiodoron* share with *Langsdorfia* the apomorphies: arolium more or less reduced, paronychia reduced, costal region of hindwing narrowing at approx. 0.4 or 0.5 times wing-length, and antennal rami with at least one stout sensillum apically (not certain of *desantisi* and *marmorata*). In *Philiodoron* both the ♂ frenulum spine and retinaculum are well-developed and Sc-Rs is wanting. See also fig. 105.

Vertex has a slightly arcuate Pos at approx. half its length. Male antenna is rather strongly bipectinate. Antennal rami have a sensillum dorsally in at least *steinbachi.* Mesomeron is approx. 2.3 to 2.5 times width of eucoxa II. Tibial spurs are approx. moderately long in *desantisi* and *marmorata.* Apical spurs are approx. moderately short in *steinbachi.* Venation of *marmorata* and *desantisi*: all radial veins separate; CuP and A1+2 sometimes/often separate (reversal). Venation of *steinbachi* (see also above and Clench, 1956: 899, fig. 2): R2+(3+4) stalked for respectively approx. 0.3 and 0.4

times their length; Sc-Rs short (not depicted by Clench); Rs-M1 moderately short; CuP (hindwing) indistinct.

G. steinbachi is known only from Bolivia. *G. desantisi* occurs in Argentina (Neuquén, Río Negro and Chubut) (Gentili, 1985: 108). *G. marmorata* is also known only from Argentina (Neuquén, Río Negro and Santa Cruz) (Gentili, 1985: 111).

G. desantisi is particularly found in zones transitional between forest and steppe close to *Nothofagus* galleries along brooks, and at altitudes between 640 and 850 m. (Gentili, 1985: 108). *G. marmorata* is found in forest of *Nothofagus pumilio* and also in zones transitional between forest and steppe, and at altitudes between 200 and 1750 m. (Gentili, 1985: 110-111).

Material:

marmorata —1♂ (paratype), ARGENTINA: Neuquén, Quilguihue, 750 m., 12.i.1982 (Gentili) (IPCN).

desantisi —2♂♂, ARGENTINA: Neuquén, Aeropto Chapelco, 780 m., 14.ii.1988 (Gentili) (IPCN).

steinbachi —all BOLIVIA and (Steinbach) (CMNH) —2♂♂ (paratypes), Prov. del Sara, -450 m., Gen. slide no. C-476; 1♂ (paratype), Rio Japacani; 1♂ (paratype), Buena Vista, 400 m., ix.1914, slide venation no. C-338.

Genus **Pomeria** Barnes & McDunnough, 1911

Pomeria Barnes & McDunnough, 1911: 10-11.
Type species: *Hypopta itzalana* Strecker, 1900: 30.

Barnes & McDunnough (1911) include only *itzalana* in *Pomeria*. Dyar (1940: 1284-1285) neglects *Pomeria* and places *itzalana* in *Inguromorpha*. Hodges (1983: 30) treats *Pomeria* as a synonym of *Inguromorpha*. In both genera the inner cells of both the fore- and hindwing are wanting. In *Pomeria* the mesepimeron is moderately low and has a more or less rounded upper margin, whereas in *Inguromorpha* this upper margin is more or less squared. In the latter paronychia are wanting, whereas these are at least sometimes present in *itzalana*. Thus *Pomeria* presumably occupies a separate position in the cladogram (fig. 105), and is here resurrected.

P. itzalana is an easily recognizable, very greyish species. Barnes & McDunnough note a number of characteristics of this species. The most important of these are: third segment of labial palpi conical, midtibial spurs wanting, ♂ frenulum spine well-developed, R4 and R5 stalked, inner cells wanting, and Rs and M1 connate or stalked. These characteristics, except the well-developed ♂ frenulum spine, are apomorphies. They also note that the vestiture of frons is composed of hair-like scales. The frontal tuft of *itzalana* is moderately long and its scales are only narrow and mostly two-pointed.

Vertex of *itzalana* has an arcuate Pos up to approx. its dorso-posterior margin. Terminations of Pos may have small, more or less swollen protuberances or ridges. Male antenna is moderately bipectinate. Female antenna is moderately shortly bilobed, and has many moderately short hairs on proximal and lateral sides of rami. Vestiture on second segment of labial palpi is moderately long. Accessory plate III is narrow. Intersclerite III is probably normally wanting. Arolium is more or less membranous and is sometimes/often small. Paronychia are small, minute or wanting. Male retinaculum varies in length of its base; from moderately to rather long. Female frenulum bristles are moderately short. Venation (see fig. 103): areole moderately small; R4 and R5 stalked up to for approx. 0.4 times their length; Sc-Rs sometimes with short side-branch; Rs and M1 connate to shortly stalked; M2 and M3 of hindwing connate or very shortly stalked. Anal plate is moderately short.

P. itzalana is known from southern U.S.A.; Arizona, New Mexico and Texas (see material examined).

Material:

itzalana —(all U.S.A. and BMNH) —1♂, 1♀, Arizona, Paradise; 2♂♂, Arizona, Prescott; 1♂, Texas, Brewster Co., 5000-7000 ft; 3♂♂, 1♀, New Mexico, Otaro Co.; 1♂, New Mexico, High Roile.

Genus **Givira** Walker, 1856

Givira Walker, 1856: 1510 (key), 1526-1527.
Type species: *Givira tristis* Walker, 1856: 1527.
Eugivira Schaus, 1901: 73. [Synonymized by Barnes & McDunnough, 1911: 11].
Type species: *Eugivira sabulosa* Schaus, 1901: 74.
Lentagena Dyar, 1905: 178. [Synonymized by Dyar, 1940: 1277-1281].
Type species: *Eugivira nudaria* Schaus, 1901: 75.
Stenocyttara Turner, 1918: 164-165. [Junior objective synonym].
Type species: *Eugivira sabulosa* Schaus, 1901: 74.
Acyttara Turner, 1918: 165-166. [Noted as synonym by Gentili, 1985: 112].
Type species: *Givira tigrata* Schaus, 1911: 631.
Anastomophleps Hering, 1923: 12-13. **Syn. nov.**
Type species: *Anastomophleps claosticha* Hering, 1923: 13.

Walker (1856: 1526-1527) introduces *Givira* for *tristis* only. He notes as most significant characteristics of *tristis*: labial palpi very short and its third segment very small, ♂ antenna moderately bipectinate, and hind tibiae with four rather small spurs. The labial palpi of *tristis* are approx. 1.2 times length of the eye-diameter, and thus not very short. Third segment of the labial palpi is conical and just small. The author supposes that the hind tibiae have only an apical pair of spurs.

Schaus (1901: 48) redefines the genus, but includes species which were later included in *Langsdorfia* or *Inguromorpha* by Dyar (1940). Schaus gives the following characteristics: antenna bipectinate, labial palpi extending beyond frons, CuP and A1+2 of forewing linked by a cross-vein, R4 and R5 stalked, and Rs and M1 from cell. The present author doubts that the latter is correct for all the species included by Schaus. In two specimens examined of *tristis* Rs and M1 are shortly stalked. Schaus distinguishes two subgroups of the genus; one with Sc-Rs and another one without this cross-vein. Schaus's definition of *Givira* does not help very much and is even confusing.

Schaus (1901: 73) introduces *Eugivira* for fifteen species, without denoting a type species. Viette (1951b: 42) designates *sabulosa* as the type. Schaus distinguishes two sub-groups, as he does for *Givira;* one with a cross-vein Sc-Rs and the other one without such a bar. Schaus gives as characteristics: antenna bipectinate, forewing venation as in *Givira,* and Rs and M1 stalked. This is a very poor definition and one which does not warrant a separate genus. Also in *tristis,* the type of *Givira,* Rs and M1 are at least sometimes stalked. The venation varies considerably amongst the species included. Schaus even transfers *Langsdorfia aroa* to *Eugivira,* although this species actually belongs to *Langsdorfia.* Barnes & McDunnough (1911: 11) point out that Dyar evidently united *Eugivira* with *Givira* in 1905, and they note *Eugivira* (partim) as a synonym of *Givira*. Dyar (1940: 1277-1281) neglects *Eugivira* again and lists the species, including *sabulosa*, under *Givira*. See also the discussion on *Stenocyttara* here below.

Barnes & McDunnough (1911: 11-12) treats *Givira* even in a wider sense; they synonymize *Inguromorpha* to *Givira*, although they had not examined material of *Inguromorpha slossoni* Edwards, 1888, the type species.

Dyar (1940: 1284) resurrects *Inguromorpha* and notes as an important characteristic that the inner cells of both the fore- and hindwing are wanting.

Dyar (1940: 1279-1281) treats *Lentagena* as subgroup of *Givira*, characterized by the absence of a cross-vein Sc-Rs. In *nudaria*, the type of *Lentagena*, the areole and the inner cell of the hindwing are wanting, which characteristics Dyar (1905: 178) uses to define the genus. There are more species, such as *Lentagena tristani* Schaus, 1911 and *Zeuzera roxana* Druce, 1911, with the same characteristics as *nudaria*. Turner (1918: 165) points out that he found an areole present in the single specimens he examined of *tristani*, *nudaria* and *Cossula albicosta* Schaus, 1911. There are also species seemingly belonging to *Givira* with the areole minute to/or wanting and no cross-vein Sc-Rs, but with a well-developed inner cell of the hindwing; e.g. *Eugivira quadra* Schaus, 1901. There are other species seemingly belonging to *Givira* with a minute areole but also a cross-vein Sc-Rs and an inner cell of the hindwing; e.g. *Philanglaus sobrana* Schaus, 1905. It thus seems that the venation varies amongst these species and that this variation could be regarded as intrageneric amongst the species of *Givira*. Therefore the author of this paper follows Dyar and treats *Lentagena* as a synonym of *Givira*, but not as a subgroup characterized by the absence of Sc-Rs.

Turner (1918: 164-165, fig. 18) introduces *Stenocyttara* for *Eugivira sabulosa* Schaus. The latter was designated as the type of *Eugivira* by Viette (1951b: 42). *Stenocyttara* has thus become a junior objective synonym of *Eugivira*, which has been synonymized with *Givira*. Turner notes that *Stenocyttara* is near *Givira*, but lacks Sc-Rs. Furthermore, *sabulosa* would have a narrow inner cell in the forewing and a small one in the hindwing. The cross-vein CuP-A1+2 would be absent and CuP would be distally wanting. Turner (1918: 165) treats *Lentagena* as a separate genus, of which the species also lack Sc-Rs. Dyar (1940: 1278) neglects *Stenocyttara* and places *sabulosa* and *Lentagena* in *Givira*. No material of *sabulosa* was available. It is known in several hypoptine species that CuP-A1+2 is sometimes wanting. The present author presumes that also in *sabulosa* CuP and A1+2 are usually linked, but that the coalescence has become obscure since CuP is distally wanting in the specimen(s) examined by Clench. The size of the inner cells varies inter- and intraspecifically within *Givira*. A more or less similar venation as in *sabulosa*, apart from CuP-A1+2, is also known in *Eugivira plagiata* Schaus, 1901. Dyar (1940: 1279-1281) includes a large group of species which lack Sc-Rs in *Givira*. In my opinion the noted differences in venation do not warrant a distinct genus separate from *Givira*. Therefore *Eugivira* and *Stenocyttara* are also treated as synonyms of *Givira* in this paper, pending a thorough study of *Givira* and closely related taxa.

Turner (1918: 165-166) proposes *Acyttara* for *tigrata*, which had been placed in *Givira*. *G. tigrata* lacks an areole, has Rs and M1 stalked, has a Sc-Rs, and lacks the inner cell of the hindwing. It thus seems to be a transitional type of venation in between that for which *Lentagena* was introduced and that which was thought typical of *Givira*. In this paper the type of venation in *tigrata* is regarded as to fit in the intrageneric variation of *Givira*. Gentili (1985: 112) notes *Acyttara* as a synonym of *Givira*, but does not note who made the synonymy.

Anastomophleps was introduced by Hering for *claosticha*. Hering notes that *Anastomophleps* comes near to *Hypopta*, but differs from the latter by the coalescence of R1 and R2. In *claosticha* R1 and R2 are shortly coalescent near the areole. This coalescence is here considered an aberration and not sufficient to warrant a separate genus. For the rest the species fits well in *Givira*. Therefore *Anastomophleps* is synonymized with *Givira*.

P. sobrana is erroneously placed in *Langsdorfia* by Dyar (1940: 1284). Other species listed by Dyar under *Langsdorfia* but which should probably be placed in *Givira* are *Ravigia basiplaga* and *Philanglaus beatrix*. *Hypopta actileuca* had probably erroneously been placed in *Givira*; this species has the outward appearance of a *Hypopta* species. *Zeuzera undulosa* Druce, 1911 and *Z. roxana* are added to Dyar's list of *Givira* species. *Zeuzera dolens* Druce (probably a manuscript-name) is seemingly synonymous with *nudaria*. Perhaps the species of *Puseyia* Dyar, 1940 should also be added to Dyar's list (see under *Puseyia*). Dyar neglects *Eugivira quadroides*, which was described by Hering (1923: 14-15). It is here uncertain if *quadroides* fits in *Givira*. Dyar (1940: 1269) places *Givira lineaeplena* Dognin, 1911 in *Carohamilia* (Zeuzerinae). No material of *lineaeplena* has been examined. Dyar notes that this species has a cross-vein Sc-Rs and that the inner cell is usually wanting. Judging from the figure of *lineaeplena* provided by Seitz (1940: pl. 167: fig. row g), this species has the ♂ antenna completely bipectinate and most closely resembles *Schreiteriana pectinicornis* (Cossulinae). For a cossuline species it is exceptional or unusual that Sc-Rs is present. It is here uncertain if *lineaeplena* should indeed be excluded from *Givira*. After the publication of Dyar's list at least two new species of *Givira* have been described: *Givira leonera* Clench, 1957 and *G. brunneoguttata* Gentili, 1985.

Givira appears to be a rather large genus with a fair amount of interspecific variation. It is difficult to define the genus. Only in certain species, such as *tristis*, the third segment of the ♂ labial palpi is conical. *Givira* seems to have the following apomorphies: mesepimeron moderately low with a more or less squared upper margin (see fig. 100), mesomeron at least twice width of eucoxa II (up to three times), midtibial spurs of hindleg wanting, paronychia wanting, R4 and R5 more or less stalked, and Rs and M1 usually connate to/or shortly stalked. These apomorphies are shared by several other genera (see fig. 105). There is seemingly no distinctive autapomorphy of *Givira*.

In a number of species the inner cell of the hindwing is wanting. The fringes are long, rather long or moderately long. In *Psychogena* the fringes are short and the anal region is distinctly elongate. In *Inguromorpha* the inner cell of both the fore- and hindwing are wanting. In *Puseyia puseyiae* Dyar, 1940 the inner cell of the forewing is wanting, the ♂ retinaculum is wanting, the ♂ antenna is shortly bipectinate, the third segment of ♂ labial palpi is conical, and the vestiture on the second segment of the labial palpi is short.

Material of a number of species has been partially or briefly examined and that of several species has been extensively examined. Only of *mucidus* (Edwards, 1882), *cleopatra* (Barnes & McDunnough, 1912), *marga* Barnes & McDunnough, 1910, *roxana*, and unidentified species (c) females were available.

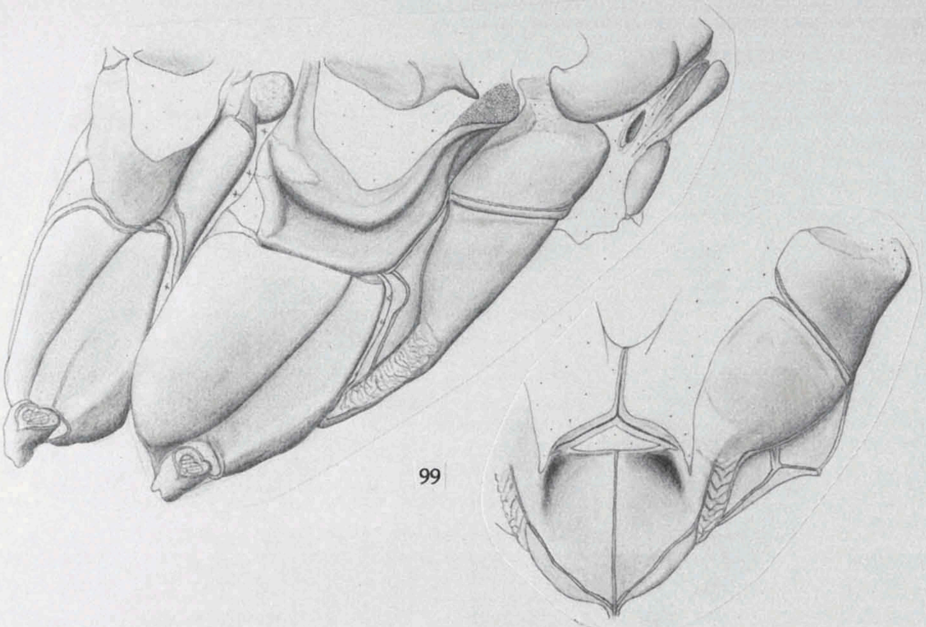
Vertex of *mucidus* and *sobrana* has a nearly straight Pos at approx. half its length. Pronotum of *sobrana* seems to be lower than patagium. Male antenna varies interspecifically from moderately strongly bipectinate to bilobed. Male antenna of *tristis, marga, cleopatra,* and *undulosa* is moderately bipectinate. Male antenna of at least *mucidus* and unidentified species (b) is moderately strongly bipectinate. Male antenna of *plagiata, quadra* and unidentified species (b) is moderately shortly bipectinate. Male antenna of *nudaria* is shortly bipectinate. Male antenna of *claosticha* and unidentified species (c) is bilobed. Antennal rami of at least *plagiata* has a row of hairs dorsally. In certain species there is a more or less conspicuous, haired protuberance in between rami; in e.g. *tristis* this protuberance is indistinct, but in at least *cleopatra* tooth-like. Female antenna of *cleopatra* is moderately bipectinate. Female antenna of *mucidus* is shortly bipectinate with many moderately long hairs on proximal side of rami and one stout sensillum at apex of rami. Female antenna of unidentified species (c) is bilobed. Female antenna of *roxana* is shortly bilobed. Frontal tuft of at least *tristis, marga, cleopatra, plagiata, nudaria* and *claosticha* is moderately short. Frontal tuft of *undulosa, roxana,* and unidentified species (a) and (b) is moderately long. Third segment of labial palpi is conical in at least the males of *tristis, mucidus, cleopatra,* and *plagiata.* Vestiture on second segment of labial palpi is moderately short in at least *tristis, mucidus,* and *roxana.*

Thoracic sclerites of *mucidus* are shown in fig. 100. An is moderately high in probably all species. Bs II is in many or most species less rounded than in figure of *mucidus.* Accessory plate II is narrow in *undulosa,* and moderately narrow in *roxana* and *claosticha.* Accessory plate III is narrow. Intersclerite III is wanting in probably all species. Apical spurs of tibiae are rather long and moderately long or moderately long in many species. Arolium is more or less reduced in *marga, cleopatra* and *claosticha,* but well-developed in many other species.

Fringes are rather long in at least *marga, cleopatra, plagiata,* and *nudaria.* Fringes of at least *tristis* are moderately long. Male frenulum spine is rather long in *claosticha,* moderately long in *tristis,* and moderately short in *quadra* and unidentified species (b) and (c). Male retinaculum is wanting in at least *tristis.* In *marga, sobrana* and unidentified species (a) both ♂ frenulum spine and retinaculum are wanting. Number of ♀ frenulum bristles amounts more than five in *mucidus* and *cleopatra.* Female frenulum bristles are seemingly wanting in *marga.* Length of frenulum bristles varies interspecifically from moderately long to short. Venation (see also fig. 104): areole is moderately small in many species, but is moderately large in certain others; areole is small to minute in *marga* and *cleopatra,* minute in *sobrana,* minute to wanting in *quadra* and *tristani,* and (usually ?) wanting in *nudaria* and *roxana;* R3 and R4+5 are stalked in *quadra,* and is sometimes/often connate in certain other species; inner cell is at least sometimes small in *quadra;* Sc-Rs is normally wanting in at least *plagiata, undulosa, roxana, nudaria, tristani,* and unidentified species (c) (see also Dyar, 1940: 1279-1281); inner cell is wanting in *nudaria, roxana* and *tristani.* Anal plate is moderately short in most species, but moderately long in certain ones.

Many species occur in South America, up to approx. 41° South (see Gentili, 1985: 115). Several species are known from Central America. Approx. fourteen species occur in southern U.S.A. (see Hodges, 1983: 31).

G. leonera occurs particularly in zones transitional between forest and steppe with galleries of *Nothofagus antarctica,* or in pampas surrounded by forest zones (Gentili, 1985: 117). *G. brunneoguttata* has been found in forest with one or more *Nothofagus* species, at altitudes between 100 and 1700 m. (Gentili, 1985: 120-121).



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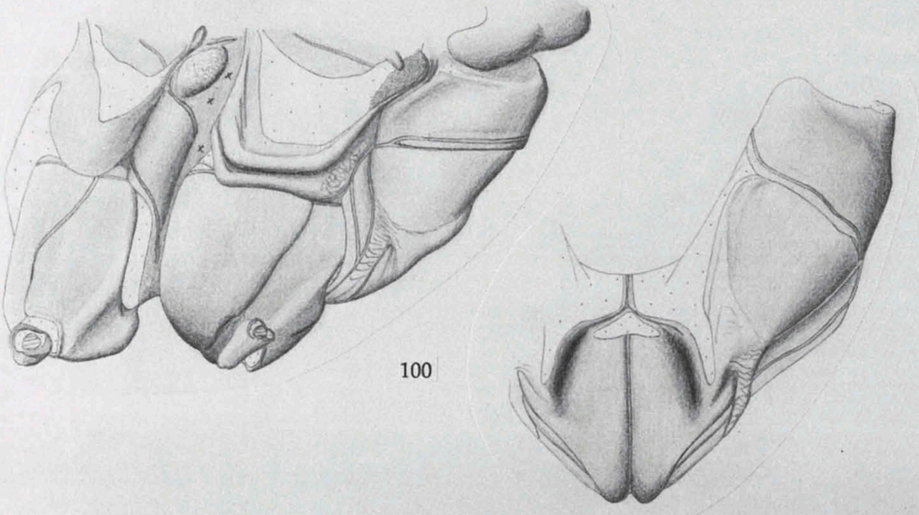

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Figs. 99-100, sections of thoraces of hypoptine species. 99, *Langsdorfia franckii*, Guatemala, Guatemala City; 100, *Givira mucida*, U.S.A., Arizona, Paradise.

Material:

tristis —1♂, ?, Gen. slide no. 125 (BMNH); 1♂, COLOMBIA: Muzo, 400-800 m. (BMNH).

mucidus —series of both sexes, U.S.A.: e.g. Paradise (BMNH).

ethela —series of males, U.S.A.: Eureka (BMNH).

Hypopta francesca Dyar —series of males, U.S.A. (BMNH).

marga —long series of both sexes, U.S.A. (BMNH).

cleopatra —long series of both sexes, U.S.A.: e.g. Eureka (BMNH).

plagiata —(all BMNH) —1♂ (holotype of *Duomitus daphne* Druce), COLOMBIA: Minca, 2000 ft. (Smith); 1♂, COSTA RICA: Avangares; 1♂, HONDURAS: La Cambre; 1♂, HONDURAS: Punta Gorda; 1♂, GUATEMALA: Cayuga.

quadra —(all BMNH) —6, COSTA RICA: Tuis, 2500 ft.; series from Brazil, Paraguay and Castro Paraná.

sobrana —(all BMNH) —2♂♂, Alto da Serra, Santos, 800 m.; 3♂♂, BRAZIL: Agulhas Negras [= Itatiaia], Est. do Rio, Maromba, 1100 m.; 1♂, BRAZIL: Agulhas Negras [= Itatiaia], Est. do Rio, Sede, 800 m.; 1♂, BRAZIL: Boraceá, Sao Paulo, Travassos.

nudaria —(all BMNH) —1♂ (holotype of *Zeuzera dolens* Druce, 1901), BRAZIL: south Brazil, Rio Grande do Sul; 1♂, BRAZIL: Est. do Rio, Teresópolis, Barreira, 400 m.; 1♂, GUYANA: Omai; 1♂, VENEZUELA: Estebon Valley, Las Quigas; 1♂, PERU: Yahuarmaye, 1200 ft.; 1♂, COLOMBIA: El Tigre, Rio Tamaua, 320 ft.

undulosa —1♂ (holotype), COLOMBIA: Tado Rio San Juan, 250 ft. (BMNH); 1♂, COLOMBIA: Ob. Rio Negro, 800 m. (BMNH).

roxana —1♀, COLOMBIA: Tado Rio San Juan, 250 ft. (BMNH).

tristani —(all BMNH) —1♂, COLOMBIA: Ob. Rio Negro, 800 m.; 1♂, GUATEMALA: Guirigua (coll. Schaus and Barnes); 1♂, HONDURAS: La Cambre; 1♂, MEXICO: Jalapa, M. Trujillo.

claosticha —1♂ (holotype), ARGENTINA: Mendoza, i. 1905 (Jensen-Haarup) (MHUB).

Unidentified species (a) —1♂, MEXICO: Plaevado Mazatlán, 2.v.1959 (Lemche) (ZMUC).

Unidentified species (b) —1♂, ECUADOR: Guachayaca, ix/x.1926 (Vorbeck) (ZMUC).

Unidentified species (c) —(all BMNH) —3♂♂, PANAMA: Bambito, V. de Chiriquí, 20.i.1948 (Ellison); 1♂ (labelled as *Eugivira pallidicosta* Schaus), Castro Paraná; 1♂, 1♀, Castro Paraná.

Unidentified species (d) —1♂, BRAZIL: Neu Bremen (RMNH).

Unidentified species (e) —1♂, BRAZIL, 29.ix.1929 (RMNH).

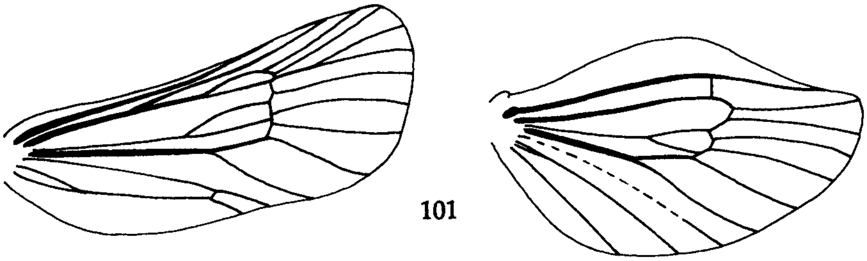
Unidentified species (f) —4♂♂, SURINAM: along river Pata Makka, and airport Käyser Gebergte. (RMNH).

Unidentfied species (g) —3♂♂, SURINAM: e.g. along river Pata Makka (RMNH).

Genus **Psychogena** Schaus, 1911

Psychogena Schaus, 1911: 633.
Type species: *Psychogena miranda* Schaus, 1911: 633-634.

Schaus (1911: 633) introduces *Psychogena* for *miranda* only. Dyar (1940: 1281) adds *Prionoxystus duplex* Schaus, 1905 to the genus. Only a single ♂ specimen of each species is known. Dyar notes that the venation is similar to that in *Givira*, but that Rs and M1 are stalked and there is a cross-vein Sc-Rs. He further points out that the ♂ hindwing is sharply triangular. The ♂ hindwing of the two species is indeed distally more or less triangular. The anal region of the hindwing is elongate, particularly in *miranda*. Rs and M1 are stalked for approx. 0.4 or 0.5 times their length, which is sometimes/often also the case in certain species of *Givira*. The two species share the following other apomorphies: mesepimeron moderately low with a more or less squared upper margin, midtibial spurs of hindleg wanting, paronychia wanting, fringes short, ♂ frenulum spine approx. moderately long, ♂ retinaculum wanting,



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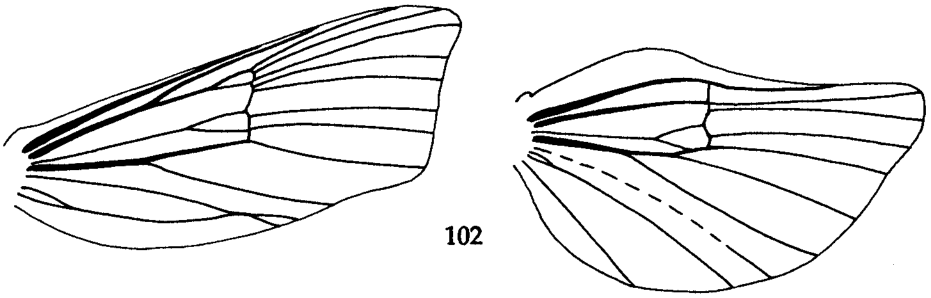

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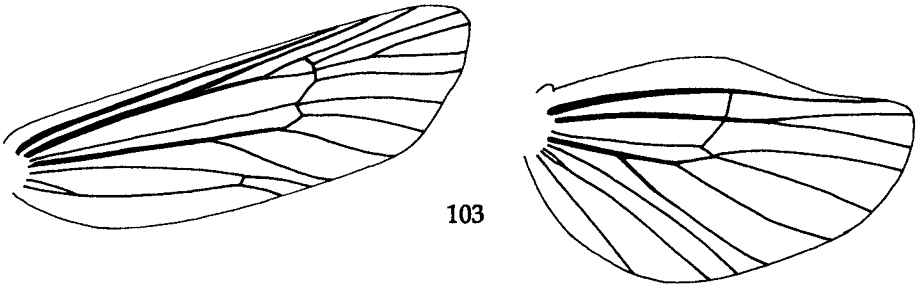

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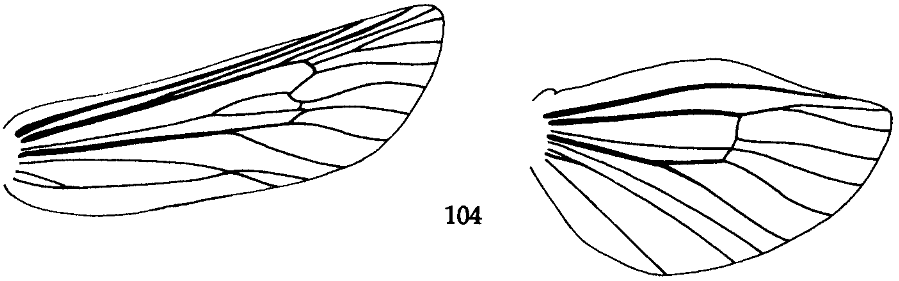

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Figs. 101-104, venation of hypoptine species. 101, *Hypopta ambigua*; 102, *Langsdorfia franckii*; 103, *Pomeria itzalana*; 104, *Givira nudaria*.

areole small or very small, R4 and R5 shortly stalked, and anal plate moderately short. Perhaps tarsal spines are wanting. In both species the arolium is more or less membranous, and in *duplex* it is moderately small. *P. miranda* has the following autapomorphies: male antenna shortly bipectinate with distinctly flattened rami, third segment of labial palpi conical, fifth tarsomere approx. twice length of fourth, and CuA2 of forewing at approx. 0.6 times length of cell. The state of labial palpi is not known in *duplex*. In both species the valves and uncus are bilobed; in *miranda* the lobes of the uncus are bifid.

Psychogena differs especially from the other hypoptine genera without midtibial spurs in that the fringes are short, the anal region of hindwing is elongate, and both valve and uncus are bilobed. In *Givarbela steinbachi* the uncus and valve are also bilobed and the midtibial spurs are also wanting. In *steinbachi* the fringes are long, the uncus is only very slightly bilobed and widened subapically, R2 is stalked with R3 and R4, and areole is wanting. See also under *Givarbela* above.

Male antenna of *miranda* is partly shortly bipectinate and partly bilobed. The antennal lobes are triangular and have many hairs on proximal side. Male antenna of *duplex* is rather strongly bipectinate. Frontal tuft of *miranda* is moderately long. Vestiture on second segment of labial palpi is moderately long in *miranda*. The states of frontal tuft and labial palpi in *duplex* are unknown. Tibial spurs are approx. moderately long. Venation: areole small in *miranda* and very small in *duplex*; Rs and M1 stalked for approx. 0.4 times their length in *miranda*, and for 0.5 times in *duplex*.

The genus is represented in South and Central America.

Material:
miranda —1♂ (holotype), COSTA RICA: Tuis, viii (USNM).
duplex —1♂ (holotype), FRENCH GUIANA: St. Laurent, Maroni (coll. Schaus) (USNM).

Genus Puseyia Dyar, 1940

Puseyia Dyar, 1940: 1284.
Type species: *Puseyia puseyiae* Dyar, 1940: 1284.

In the original description of *Puseyia*, three new species are included in this genus. These are *puseyiae*, *P. hiscelis* Dyar, 1940 and *P. ban* Dyar, 1940. The type species has a special colour-pattern. The other two are much smaller than *puseyiae* and look different (see Seitz, 1940: pl. 184: figs. row h). Dyar (1940: 1284) gives the following characteristics of the genus: antenna shortly bipectinate, ♂ frenulum well-developed, inner cells of both fore- and hindwing wanting, Sc-Rs present, and Rs and M1 considerably stalked. The male and ♀ antenna of *hiscelis* are actually bilobed. The female antenna of *ban* is moderately strongly bipectinate. Of *ban* only the female is known. In *puseyiae* the ♂ frenulum spine is reduced in length, and retinaculum is wanting. The forewing inner cell is present in *hiscelis*, and the hindwing inner cell is well-developed in *puseyiae*. Sc-Rs is wanting in *hiscelis*. Dyar's definition is thus incorrect. The genus thus appears to be a heterogeneous group.

The three species share the following apomorphies: mesepimeron moderately low with more or less squared upper margin, mesomeron at least twice width of eucoxa II, arolium more or less reduced, paronychia wanting, R4 and R5 stalked for approx. 0.3 to 0.4 times their length, and Rs and M1 stalked for approx. 0.3 to 0.7 times their length. The frontal tuft is moderately short in at least *puseyiae* and *hiscelis*. The third segment of the labial palpi is conical in the males of *puseyiae* and *hiscelis* and in the female of *ban*. An seems to be moderately low in *hiscelis*. The hindlegs of the holotype of *puseyiae* are missing, but it is presumed that the midtibial spurs are wanting as in the other two species. The areole is small in *puseyiae*. CuP and A1+2 are distally separate in the holotype of *ban*. The anal plate seems to be moderately long in *ban*, but is moderately short in the other two species.

It thus seems to be difficult to define *Puseyia* including the three species. The absence of the forewing inner cell may distinguish *Puseyia* from *Givira*, but then *hiscelis* should be excluded. The ♂ genitalia do not help very much. The uncus of at least *puseyiae* and *hiscelis* is long and slender. The valve of *puseyiae* is elongate and distally moderately slender, whereas that of *hiscelis* is broadly rounded. The outward appearance of the three species would not suggest that they are congeneric. For none of the species it can be ruled out that they should not be placed in *Givira*. It may well be that *Puseyia* should be synonymized with *Givira*, but it seems impossible to define *Givira* properly. The special shape of the valve in *puseyiae* may be an indication that this species does not fit in *Givira*. Therefore *Puseyia* is tentatively left as a separate genus, pending a more thorough study including the genitalia. *P. hiscelis* and *ban* do not seem to be congeneric with *puseyiae* and should probably be placed in *Givira*. The position of the genus in fig. 105 is tentative.

Material:
puseyiae —1♂ (holotype), PERU: Collao (coll. Pusey) (USNM).
hiscelis —1♂, 1♀ (syntypes), BRAZIL: Fonte Boa, Amapones (Fassl) (coll. Dognin) (USNM).
ban —1♀ (holotype), ARGENTINA: La Rioja, xii.1919 (coll. Dognin) (USNM).

Genus **Inguromorpha** Edwards, 1888

Inguromorpha Edwards, 1888: 182-183.
Type species: *Inguromorpha slossoni* Edwards, 1888: 183. [Synonymized with *Cossus basalis* Walker, 1856 by Dyar, 1898: 213-214].
Ravigia Dyar, 1905: 178. [Synonymized by ? Hodges, 1983: 30].
Type species: *Givira polybioides* Schaus, 1901: 48.

Inguromorpha was introduced for only *slossoni* and established in the Bombycidae Latreille, [1802]. Dyar (1898: 213-214) synonymizes *slossoni* with *Cossus basalis* Walker and makes clear that *Cossula magnifica* (Strecker, 1876) is different from the latter. Barnes & McDunnough (1911: 11) synonymize *Inguromorpha* to *Givira*. Barnes & McDunnough (1911: 15) point out that the type-locality of *basalis* is probably east Florida, which agrees with that of *slossoni*. Dyar (1940: 1284-1285) resurrects *Inguromorpha*, and includes ten species. Dyar neglects *Pomeria* and includes *itzalana*. In this paper *Pomeria* is resurrected (see above). Dyar notes the following characteristics of *Inguromorpha*: antenna bipectinate, ♂ frenulum well-developed, inner cells of both fore- and hindwing wanting, and some obscure ones for the venation. It is uncertain which species included by Dyar actually fit in *Inguromorpha*.

Ravigia was described by Dyar for *polybioides*. Dyar notes the following characteristics of *Ravigia*: male antenna shortly bipectinate, labial palpi slender, R3 and R4+5 stalked, and Sc-Rs present. Dyar (1940: 1284-1285) neglects *Ravigia* and places its type species in *Inguromorpha*. Hodges (1983: 30) notes probably for the first time *Ravigia* as a synonym of *Inguromorpha*. Several species described as belonging to *Ravigia* have been transferred to *Givira*.

In this study the holotype of *basalis* has been partially examined. Furthermore, material of *Langsdorfia polybia* and an unidentified species, which is perhaps *I. entone* Dyar, has been investigated. It is not certain if *basalis* and *polybia* are separate species. The most important characteristic of the genus appears to be the absence of the inner cell in both the fore- and hindwing. The male antenna of the unidentified species is moderately bipectinate. The male antenna of *polybia* is moderately shortly bipectinate. The female antenna of *polybia* is proximally unilobed and more distally bilobed, and has many hairs on the ventral side of the lobes. The third segment of the ♂ labial palpi is conical in *polybia* and the unidentified species. The mesepimeron is moderately low with a more or less squared upper margin. The fringes are rather long in the unidentified species. Midtibial spurs and paronychia are wanting. The male frenulum spine is rather long in the unidentified species. The male retinaculum is well-developed in *polybia* and the unidentified species. The areole is minute in *polybia*, and is wanting in the available specimen of the unidentified species. R4 and R5 are shortly stalked. M2 and M3 of the forewing are connate in the unidentified species. Sc-Rs is wanting in at least the species examined. Rs and M1 are shortly stalked. The anal region of the hindwing is moderately elongate in the unidentified species. Many species have one or two special markings at the wing-apex (see Dyar, 1940, and Seitz, 1940), which may be cryptic.

Pomeria, in which the inner cells are also wanting, differs in that the upper margin of the mesepimeron is more or less rounded and paronychia may be present. Therefore, *Pomeria* is placed at a lower branch than *Givira* in the cladogram (fig. 105). In *Givarbela steinbachi* the inner cells are also wanting, but this is a very distinct species (see under *Givarbela*). *Inguromorpha* is tentatively placed as the sister-group of *Puseyia*, of which the type species also lack the inner cell of the forewing. It cannot be ruled out that the absence of both inner cells fits in the intrageneric variation of *Givira*, but it is very difficult to define the latter.

Material:
basalis —1♂ (holotype), [? U.S.A.: east Florida] (BMNH).
polybia —(all BMNH) —1, ?; 1, PERU: s.e. Peru, Santo Domingo, 6000 ft.; 6, Corcovado, Rio, 800 ft.; 3, Corcovado; 2, BRAZIL: Estado do Rio; 2, FRENCH GUIANA; 3, GUYANA; 1, Trinidad; 1, La Rioja.
Unidentified species (? *entone*) —1♂, PANAMA: Taboga (ZMUC).

Table 24. Apomorphies in fig. 105 (Hypoptinae).

1. Ocelli wanting.
2. Frontal tuft moderately or rather long. (*)
3. Vestiture on second segment of labial palpi approx. moderately long. (*)
4. Tegula bluntly pointed and moderately upturned or gradually tapering.
5. Upper Pas situated in extremely ventral position (see figs. 99-100).
6. M of forewing close to CuA. (*)

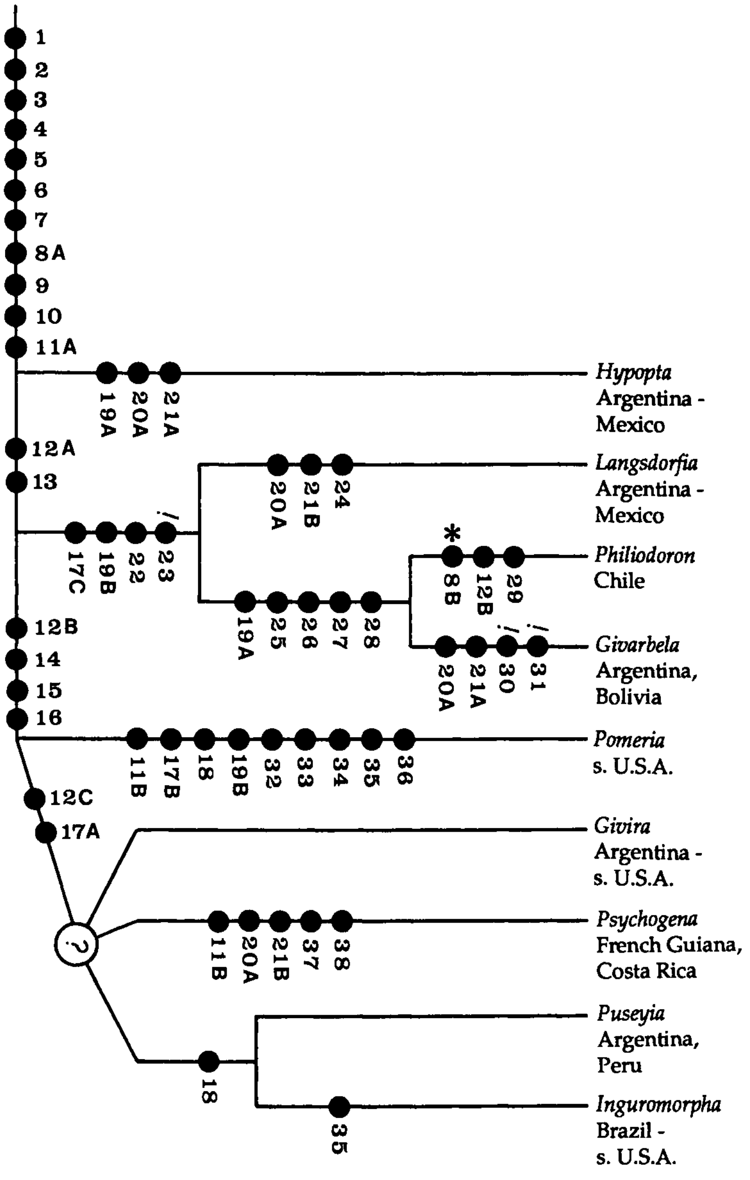


Fig. 105, cladogram of Hypoptinae.

7. CuP and A1+2 of forewing normally distally linked by a cross-vein or more or less coalescent. (*)
8a. Sc and Rs of hindwing linked by a cross-vein, which is usually rather long to long. (*)
  b. Cross-vein Sc-Rs wanting.
9. M of hindwing close to CuA.
10. 3Ax and 4Ax only anteriorly fused and 4Ax approx. as dorsal as 3Ax along most of its length.
11a. Anal plate at most moderately long.
  b. Anal plate approx. moderately short.
12a. Mesepimeron at most moderately high.
  b. Mesepimeron approx. moderately low.
  c. Mesepimeron with more or less squared upper margin.
13. Mesomeron at least twice width of eucoxa II, up to three times.
14. Midtibial spurs of hindleg wanting. N.B. This is not certain of all species of Givira Walker.
15. R4 and R5 stalked, usually for approx. 0.3 to 0.4 times their length.
16. Rs and M1 connate or shortly stalked, up to for approx. half their length. (*)
17a. Paronychia wanting.
  b. Paronychia minute.
  c. Paronychia short to wanting.
18. Inner cell of forewing wanting.
19a. Arolium wanting.
  b. Arolium more or less reduced in size.
20a. Male frenulum spine more or less reduced in length to/or wanting.
  b. Male frenulum spine only wanting.
21a. Male retinaculum small and rudimentary, or wanting.
  b. Male retinaculum only wanting.
22. Antennal rami with at least one stout sensillum at apex.
23. Costal region of hindwing narrowing at approx. 0.4 or 0.5 times wing-length.
24. Female frenulum bristles reduced in length or wanting.
25. Mesepimeron (normally ?) without pale band (medio-posteriorly).
26. Tarsal claws moderately slender.
27. Forewing cell narrowed and M approx. median in cell.
28. Humeral plate at most approx. as large as radial bridge.
29. Tarsal spines wanting.
30. Aculeate area at mesepimeron wanting.
31. Accessory plate II partly or completely fused with mesomeron.
32. Pos arcuate and reaching up to approx. dorso-posterior margin of vertex.
33. Male antenna moderately bipectinate.
34. Base of ♂ retinaculum varying from moderately short to rather long.
35. Inner cell of hindwing wanting.
36. M2 and M3 of hindwing connate to very shortly stalked.
37. Fringes short; consisting of approx. one layer of scales.
38. Anal region of hindwing elongate.

Notes on Hypoptinae

The following developments seem to have happened on at least three occasions within the Hypoptinae: shortening of rami (particularly in female), shortening of tibial spurs, reduction of arolium, reduction of paronychia, shortening of fringes, reduction of ♂ frenulum spine, disappearance of areole, disappearance of Sc-Rs, disappearance of inner cell of hindwing, shortening of anal plate. Developments which seem to have happened on two occasions are: lengthening of fifth tarsomere, disappearance of ♂ retinaculum, elongation of hindwing anal region.

There is no species especially large or small. None of the species have special bright colours.

There appears to be considerable variation in character-states of the ♂ genitalia amongst the hypoptine genera. It seems worthwile to investigate the genitalia to improve the cladogram (fig. 105).

Tentative key to the genera of Hypoptinae

1. Midtibial spurs of the hindleg present 2
- Midtibial spurs of the hindleg wanting (not certain of all *Givira* species.) 5
2. Costal region of the hindwing narrowing at approx. 0.4 or 0.5 times wing-length (see fig. 102) 3
- Costal region of the hindwing narrowing at approx. 0.6 or 0.7 times wing-length (see fig. 101) .... ***Hypopta***
3. Male frenulum spine and/or retinaculum distinctly reduced in size. Cross-vein Sc-Rs normally present 4
- Both male frenulum spine and retinaculum well-developed. Cross-vein Sc-Rs absent .... ***Philiodoron***
4. M of forewing closer to CuA than to R. Aculeate area at the mesepimeron present .... ***Langsdorfia***
- M of forewing approx. median in cell. Aculeate area at the mesepimeron absent .... ***Givarbela***
5. Mesepimeron with a more or less rounded or irregular upper margin (see fig. 99) 6
- Mesepimeron with a more or less squared upper margin (see fig. 100) 7
6. Areole wanting. R2 stalked with R3 and R4, while R5 separate. Anal veins of the hindwing absent .... ***Givarbela***
- Areole present. R2 and R3 separate from R4, and R4 stalked with R5. Anal veins of the hindwing present .... ***Pomeria***
7. Fringes at least moderately long; consisting of at least two layers of scales (ventral view). Anal region of the hindwing in most species not elongate 8
- Fringes short; consisting of one layer of scales (ventral view). Anal region of the hindwing elongate .... ***Psychogena***
8. Inner cell of the forewing and/or hindwing present 9
- Inner cell of both the fore- and hindwing absent .... ***Inguromorpha***
9. Inner cell of the forewing present .... ***Givira***
- Inner cell of the forewing absent .... ***Puseyia* (*puseyiae*)**

Checklist of subfamilies and their genera

Chilecomadiinae subfam. nov.

Chilecomadia Dyar, 1940
    Diarthrosia Bryk, 1945
    Allocossus Bryk, 1945

- *Rhizocossus* Clench, 1957

Cossinae Neumoegen & Dyar, 1894

- *Catopta* Staudinger, 1899
  - *Newelskoia* Grum-Grshimailo, 1900
  - *Sinicossus* Clench, 1958 **syn. nov.**
- *Paropta* Staudinger, 1899
- *Rethona* Walker, 1855
- *Arctiocossus* Felder, 1874
- *Mirocossus* **gen. nov.**
- *Macrocossus* Aurivillius, 1900
- *Lamellocossus* Daniel, 1956
- *Prionoxystus* Grote, 1882
  - *Xystus* Grote, 1874
- *Acossus* Dyar, 1905
- *Fania* Barnes & McDunnough, 1911
- *Toronia* Barnes & McDunnough, 1911
- *Psychidocossus* Fletcher, 1982
  - *Psychopsis* Dyar, 1940
- *Miacora* Dyar, 1905
- *Paracossus* Hampson, 1904
- undescribed genus (Africa)
- *Hirtocossus* **gen. nov.**
- undescribed genus (Zaire)
- *Cossus* Fabricius, 1793
  - *Teredo* Hübner, 1805/1806
  - *Lyonetus* Rafinesque, 1815
  - *Trypanus* Rambur, 1866
- *Holcocerus* Staudinger, 1884
  - ? *Holcoceroides* Strand, 1913
- *Neostygia* Wiltshire, 1980
- *Stygia* Latreille, [1802]
  - *Cryphia* Meigen, 1830
  - *Hyalida* Sodoffsky, 1837
- *Isocossus* Roepke, 1957
- *Alcterogystia* **gen. nov.**
- *Planctogystia* **gen. nov.**
- *Brachylia* Felder, 1874
- *Coryphodema* Felder, 1874
- *Paracossulus* **gen. nov.**
- *Cossulus* Staudinger, 1887
  - *Cossulinus* Kirby, 1892
- *Parahypopta* Daniel, 1961
- *Dyspessacossus* Daniel, 1953
- *Brachygystia* **gen. nov.**
- *Eogystia* **gen. nov.**
- *Eremocossus* Hampson, 1892

Comadia Barnes & McDunnough, 1911
Mormogystia **gen. nov.**
Isoceras Turati, 1924
Stygioides Bruand, 1853
    Bruandia Desmarest, 1857
    Psychidostygia Daniel, 1955
    Danielostygia Reisser, 1962
Dieida Strand, 1911
Semagystia **gen. nov.**
Dyspessa Hübner, 1816
    Endagria Boisduval, 1834
Pecticossus Gaede, 1930
Bifiduncus Chou & Hua, 1988

Pseudocossinae Heppner, 1984
Pseudocossus Kenrick, 1913

Zeuzerinae Neumoegen & Dyar, 1894
Phragmacossia Schawerda, 1924
Eburgemellus **gen. nov.**
Oreocossus Aurivillius, 1910
undescribed genus (Madagascar)
undescribed genus (Madagascar)
Phragmataecia Newman, 1850
    Macrogaster Duponchel, [1845] 1844
    ? *Phragmatoecioides* Strand, 1914
    ? *Synaptophleps* Hering, 1923
Zeuzeropecten Gaede, 1930
Relluna **gen. nov.**
Endoxyla Herrich-Schäffer, [1853] 1850-1858
    Xyrena Herrich-Schäffer, [1854] 1850-1858
    Cossimorphus Houlbert, 1916 **syn. nov.**
    Dictyocossus Houlbert, 1916 **syn. nov.**
    Melanocossus Houlbert, 1916 **syn. nov.**
Sympycnodes Turner, 1932
? *Catoxophylla* Turner, 1945
? *Brephomorpha* Fletcher, 1982
    Nephiomorpha Turner, 1945
? *Brevicyttara* Fletcher, 1982
    Brachycyttara Turner,1945
Hamilcara Barnes & McDunnough, 1910
Carohamilia Dyar, 1940
Aramos **gen. nov.**
Psychonoctua Grote, 1865
undescribed genus (Kenya)
Voousia **gen. nov.**
Morpheis Hübner, [1820] 1816

        - *Neocossus* Houlbert, 1916
        - *Xylotrypa* Turner, 1918
- *Xyleutes* Hübner, 1822
    - *Strigoides* Guérin-Méneville, [1829-1844] 1829-1838
        - *Hinnaeya* Moore, 1882-1883
        - *Melanostrigus* Houlbert, 1916
    - *Alophonotus* **gen. nov.**
    - *Chalcidica* Hübner, [1820] 1816
    - *Bergaris* **gen. nov.**
    - *Rapdalus* **gen. nov.**
    - *Rugigegat* **gen. nov.**
    - *Pseudozeuzera* **gen. nov.**
    - *Paralophonotus* **gen. nov.**
    - *Eulophonotus* Felder, 1874
        - *Engyophlebus* Karsch, 1900
        - *Callocossus* Aurivillius, 1910 **syn. nov.**
        - *Zeuzerops* Strand, 1910 **syn. nov.**
    - *Zeuzera* Latreille, 1804
        - *Aegolia* Billberg, 1820
        - *Latagia* Hübner, [1820] 1816
- *Hermophyllon* **gen. nov.**
    - *Cecryphalus* **gen. nov.**
    - *Tarsozeuzera* **gen. nov.**
    - *Brypoctia* **gen. nov.**
    - *Allocryptobia* Viette, 1951
        - *Cryptobia* Herrich-Schäffer, [1853] 1850-1858
    - *Panau* **gen. nov.**
    - *Duomitus* Butler, 1880
    - *Skeletophyllon* **gen. nov.**
    - *Trismelasmos* **gen. nov.**
    - *Aethalopteryx* **gen. nov.**
    - *Strigocossus* Houlbert, 1916
        - *Xylocossus* Houlbert, 1916 **syn. nov.**
    - *Azygophleps* Hampson, 1892

- **Hypoptinae** Neumoegen & Dyar, 1894
    - *Hypopta* Hübner, 1818: 25
        - *Dolecta* Herrich-Schäffer, [1854] 1850-1858 **syn. nov.**
        - *Philanglaus* Butler, 1882a **syn. nov.**
        - *Breyeriana* Orfila, 1957 **syn. nov.**
    - *Langsdorfia* Hübner, [1821] 1806
    - *Philiodoron* Clench, 1957
    - *Givarbela* Clench, 1957
        - *Shausisca* Gentili, 1985 **syn. nov.**
    - *Pomeria* Barnes & McDunnough, 1911
    - *Givira* Walker, 1856
        - *Eugivira* Schaus, 1901

Lentagena Dyar, 1905
Stenocyttara Turner, 1918
? *Acyttara* Turner, 1918
Anastomophleps Hering, 1923 **syn. nov.**
Psychogena Schaus, 1911
Puseyia Dyar, 1940
Inguromorpha Edwards, 1888
Ravigia Dyar, 1905

Survey of taxonomic changes at specific level

Cossus niloticus Joannis is resurrected and placed in *Alcterogystia*.
Cossus punctulatus Walker is resurrected and excluded from *Coryphodema*.
Holcocerus bolshoji Zukowsky is resurrected and placed in *Cossulus*.
Cossus osthelderi Daniel is resurrected and placed in *Dyspessacossus*.
Planctogystia gaedei is proposed as an objective replacement name for *Cossus fuscibasis* Gaede.
Catopta minor Rungs is synonymized with *Cossus mauretanicus* Lucas, which is placed in *Brachygystia*.
Zeuzera celebensis Roepke is synonymized with *Zeuzera caudata* Joicey & Talbot.
Xyleutes plesseni Schultze is synonymized with *Endoxyla anceps* Snellen, which is placed in *Hermophyllon*.
Cryptobia phobifera Dyar is synonymized with *Cryptobia mucoreus* Herrich-Schäffer, which is in *Allocryptobia*.
Xyleutes pygmaea Roepke is synonymized with *Cossus maculatus* Snellen, which is placed in *Trismelasmos*.
Azygophleps flavitincta Hampson is synonymized with *Zeuzera capensis* Walker, which is placed in *Strigocossus*.
Endagria tigrina Boisduval should probably be resurrected and placed in *Hypopta*.

Survey of host-plants

A survey of the hosts known for cossids is provided below. The species are listed in the same sequence as in the systematic treatment. The sequence of the plants is arbitrary. For references to publications on host data see the systematic treatment. Unless otherwise indicated the species are stem-borers.

Chilecomadia moorei — Quince (= *Cydonia* Mill.), Palto.
Chilecomadia valdiviana — *Nothofagus antarctica, N. pumilio, Weinmannia trichosperma*, Quince, Apple (= *Malus*), Pear (= *Pirus*), Olive (= *Olea* L.), Palto, Willow (= *Salix*).
Rhizocossus munroei — *Nothofagus pumilio.*
Paropta paradoxus — *Ficus carica, F. pseudosycomorus, Albizia lebbeck, Vitis vinifera.*
Pecticossus gaerdesi — *Zygophyllum stapffii* (roots).
Prionoxystus robiniae — Locust-tree (= *Robinia pseudacacia* L.), and other trees.
Paracossus acronyctoides — *Tamarix articulata.*
Cossus cossus — *Cydonia, Betula, Fraxinus, Pirus, Alnus, Populus, Salix, Sorbus, Quercus, Ulmus, Sambucus, Malus*, and other fruit trees.
Holcocerus verbeeki — *Acacia tomentosa.*
Stygia australis — unidentified *Echium* species (roots).
Aciterogystia cadambae — *Ficus, Nauclea cadamba, Tectona grandis.*

Parahypopta caestra — *Asparagus officinalis* and perhaps other *Asparagus* species (roots).
Comadia redtenbacheri — *Agave salmiana.*
Dyspessa ulula — Garlic (= *Allium sativum* L.) (bulb).
undescribed *Phragmacossia* species (from Sri Lanka) — *Saccharum officinarum.*
(*Phragmataecia* ?) *terebrifer* — *Saccharum spontaneum, Erianthus arundinaceus, Andropogon sorghum.*
Phragmataecia castaneus — *Phragmites australis, Saccharum spontaneum.*
Phragmataecia purpureus — *Andropogon sorghum* (roots), *Erianthus arundinaceus, Saccharum spontaneum,* Maize (= *Zea* L.).
Endoxyla durvilli — *Acacia* (roots).
Endoxyla boisduvali — *Eucalyptus.*
Endoxyla affinis — *Eucalyptus.*
Endoxyla leucomachla — *Acacia salicina* (externally on roots).
Psychonoctua personalis — Coffee (= *Coffea*).
Psychonoctua jamaicensis — Coffee.
Psychonoctua lillianae — Coffee, *Cassia glauca.*
Psychonoctua muricolora — Coffee.
Xyleutes strix — *Sesbania grandiflora.*
Xyleutes personus — *Cassia nodosa, C. fistulata, C. multijuga, C. renigera, C. siamea, Durio zibethinus, Premna* sp.
Rugigegat nigra — Coffee.
Eulophonotus armstrongi — Coffee.
Eulophonotus myrmeleon — Cocoa (= *Theobroma cacao* L.), *Acalypha.*
Zeuzera postexcisa — *Phoebe excelsa.*
Zeuzera pyrina — *Fraxinus, Aesculus* L., *Betula, Alnus, Castanea* Mill., *Crataegus* L., *Corylus* L., *Euonymus* L., *Ilex, Juglans* L., *Malus, Pyrus, Populus, Quercus, Sorbus, Syringa* L., *Tilia* L., *Ulmus, Acer* L., *Cornus* L., *Ligustrum* L., *Viburnum* L., *Carpinus* L., *Fagus* L., *Lonicera* L., *Ribes* L., *Prunus* L.
Zeuzera multistrigata — *Quercus* (at least *lineata*), *Buxus, Streblus* (at least *asper*), *Cryptomeria japonica, Ilex, Mahonia nepalensis, Mussaenda frondosa, Pyrus malus, Santalum album.*
Zeuzera conferta — Cocoa, Balsa, *Barringtonia,* and probably Coca (= *Erythroxylum* P. Br.).
Zeuzera coffeae — Coffee, Tea (= *Camellia sinensis* (L.)), Cotton (= *Gossypium* L.), Cocoa, Kapok (= *Ceiba pentandra* Gaertn.), Cinchona (= *Cinchona* L.), Coca, Teak (= *Tectona grandis*), Sandalwood (*Santalum album*), Indigo (= *Indigofera* L.), Soursop (= *Annona muricata* L.), Rose, Avocado Pear (= *Persea gratissima* Gaertn.), Guayava (= *Psidium* L.), Mahogany (= *Swietenia* Jacq.), Damur, *Citrus* L., *Caryocar nuciferum* L. (= Butternuts), *Casuarina* Adans., and many other plant species (see Arora, 1976: 130).
Hermophyllon anceps — *Derris* (at least *elliptica*).
Tarsozeuzera fuscipars — *Gliricidia.*
Duomitus ceramicus — Teak, *Callicarpa arborea, Clerodendron infortunatum, Duabanga sonneratioides, Sesbania grandiflora, Spathodea campanulata, Tectonia grandis, Vitex parviflora, Gmelina arborea.*
Trismelasmos maculatus — *Ceiba pentandra* and probably *Canarium commune.*
Strigocossus capensis — *Cassia bicapsularis, C. siamea, C. laevigata, C. didymobotrya, Ricinus communis.*
Azygophleps inclusa — *Indigofera* (roots).
Azygophleps albovittata — Groundnuts.
Azygophleps scalaris — *Sesbania,* Sunnhemp (= *Crotalaria* L.).
Langsdorfia lunifera — Pigeon Pea (lower end of stem and main roots).

Character matrices

The abbreviations used in the matrices are explained below.

0 = the first alternative, which is considered a plesiomorphy (apart from reversals), occurs.
1 = the second alternative, which is considered an apomorphy (apart from reversals), occurs.
9 = unknown or uncertain, which alternative occurs.
d = both alternatives that are indicated occur.
p = more states than the alternatives indicated occur, or the situation is more complicated than a "d" could indicate.
- = not applicable.

Table 25. Character-matrix 1, subfamilies of Cossidae.

Chilecomadiinae	10000d00d0	00d0d00100	10000d0000	000000d0
Cossinae	dpppdp0dp0	00p0d0dpdd	100011p000	p0pd00d0
Pseudocossinae	0000111010	1010101001	11000d1010	00110101
Zeuzerinae	111pdp1ppp	111111d111	d1dd0dp00d	d0p100d0
Hypoptinae	101pd001p0	01pd1000d1	1p000dpd01	d10d1010

Table 25. List of characters (cossid subfamilies).

1. Ocelli present / ocelli absent.
2. Antenna completely bipectinate, unilobed or prismatic / antenna proximally bipectinate and distally prismatic.
3. Frontal tuft short to moderately short / frontal tuft moderately or rather long.
4. Vestiture on second segment of labial palpi mainly short / this vestiture mainly approx. moderately long.
5. Third segment of labial palpi ovate / this segment conical.
6. Pronotum (very) high / pronotum low.
7. Mesoscutellum posteriorly rounded and not elongate / mesoscutellum posteriorly elongate and more or less pointed.
8. Tegula ventro-posteriorly distinctly upturned and distinctly pointed / tegula bluntly pointed and moderately upturned or gradually tapering.
9. An high / An at most moderately high.
10. Apc narrow and its lower suture reaching up to nearly or approx. full length of An / Apc rather wide and its lower suture reaching up to approx. 0.3 times length of An.
11. Antero-dorsal corner of Pre II not elongate / antero-dorsal corner of Pre II elongate.
12. Upper Pas at approx. 0.4 or 0.5 times length of Pre plus Pa / Upper Pas situated in extremely ventral position.
13. Mesepimeron rather high / mesepimeron at most moderately high.
14. Mesepimeron with rounded upper margin / mesepimeron with sinuate upper margin.
15. Mesomeron (halfway along its length) approx. as wide as eucoxa II / mesomeron at least approx. 1.5 times width of eucoxa II.
16. Accessory plate III narrow or very narrow / accessory plate III wide.
17. I-epiphysis bluntly pointed / I-epiphysis finely toothed.
18. Tibial spurs long and rather long / tibial spurs at most moderately long and moderately short.
19. Midtibial spurs present / these spurs absent.
20. First tarsomere of hindleg partly swollen / first tarsomere of hindleg not swollen.
21. Paronychia moderately short and moderately narrow / paronychia distinctly reduced or absent, at most short.

22. Male retinaculum with moderately long base / male retinaculum with long base.
23. R1 proximal to areole / R1 branching off from areole.
24. Areole at most moderately long / areole very long.
25. R3 and R4 nearly straight or slightly arcuate / R3 and R4 (normally) sinuate.
26. R4 and R5 separate / R4 (normally) stalked with R5.
27 Forewing inner cell well-developed / this cell indistinct or absent.
28. M of forewing approx. median in cell / M distinctly closer to CuA than to R.
29. CuA1 and CuA2 of forewing distinctly separate / CuA1 and CuA2 very close or connate.
30. CuP and A1+2 of forewing separate / CuP and A1+2 normally distally linked by a cross-vein or more or less coalescent.
31. Sc and Rs of hindwing normally separate / Sc and Rs normally linked by a cross-vein.
32. M of hindwing approx. median in cell / M close to CuA.
33. 1Ax of forewing apically moderately small / 1Ax apically rather large.
34. Median arm rather long / median arm at most moderately long.
35. 3Ax and 4Ax of hindwing much fused, and 4Ax mostly more ventral than 3Ax / 3Ax and 4Ax mainly separate, and 4Ax normally approx. as dorsal as 3Ax along most of its length.
36. Posterior notal wing process of forewing: lateral process mainly separate from main structure / this lateral process separate from main structure for approx. 0.3 times its length.
37. Anal plate rather long / this plate at most moderately long.
38. Tergite I mainly membranous / tergite I mainly sclerotized.

Table 26. Character-matrix 2, Cossinae.

Catopta	00101000--	0--0--0091	0d-0000000	0-d0-00000	-000d0--00	910000-000	0
Sinicossus	10901000--	0--9990099	0p-9999999	0-99999900	-00000--09	9100099901	0
Paropta	10001000--	0-----0099	0d-9900000	d-0d-0d900	-01d110-d1	11dd099991	1
Rethona	10909099--	0--9990091	0119990000	0-00-99900	-01110--11	9110099990	1
? Arctiocossus	10009099--	0-----0091	00-9991999	d-11d1--00	-0111d--11	910109999d	1
Mirocossus	10909099--	0--9990091	00-9991999	0-01001900	-01000--11	9100099991	1
Macrocossus	1000111---	0-----0091	0100010000	1001101900	-110111011	1100010011	1
Lamellocossus	1010111---	0--0--0091	0100000000	1001000100	-11011d-11	1110010011	1
Acossus	1000111---	0-----0091	00-0011000	100100d900	-11011d-11	91910d011	1
Prionoxystus	1100111---	0-----0191	0100001010	d-01100000	-110111111	1191011101	1
Fania	10901001--	0--9990091	0100100000	10d9901900	-010110-11	9190099991	1
Toronia	10d01009--	0-----0091	dd-9990999	10d0-d0000	-01d110-11	11dd099991	1
Psychidocossus	10909099--	0--9990091	0999999999	1011000900	-010d10-11	9110099991	1
Miacora	109-------	0-----1091	0109901000	1001099900	-910111011	919d099991	1
Paracossus	101ppppp--	ppp1d-0091	010000d000	d-d0-01000	-d10d1d-dd	1190d1d01d	1
undescr. gen.	10909999--	0--9990099	9999999999	9999999999	9919999999	9199999999	1
Hirtocossus	1090111---	0--9990091	010990d999	d-d1001900	-010010-11	910000-01d	1
undescr. gen.	10109099--	11-9991091	0109999999	0-99999900	-010099911	9110011011	1
Cossus	101-------	0-011-0091	0100000010	d-dd-01000	-01d1d--1d	11000110dd	1
Holcocerus	d01-------	0-11101091	0d-0001010	d-dd-01900	-01ddd--dd	11d00d-01d	1
Holcoceroides	101-------	0-19999091	0109901099	1000-01900	-010099911	9110099991	1
Neostygia	1191999999	999---0191	00-9900999	0-0991--00	-01110--99	1110011010	1
Stygia	1d01----10	0-----0d91	00-0010000	10d101--00	-01d10--00	d1d00110dd	1
Isocossus	9011----0-	11-999-091	010000d000	0-10-00900	-010110-01	919010-010	1
Alcterogystia	1011----0-	0--1d-0091	010999d999	d-9d-0d900	-0101d--11	1190099991	1
Planctogystia	10d1----0-	0--p--0091	0d-990d000	d-dd-d1000	-01d0d--91	11d009900d	1
Brachylia	1011----0-	0--1100091	00-9991999	0-00-01900	-010110-11	1d10099991	1
Coryphodema	1011----0-	0--10-0091	00-9901099	0-d0-01900	-01010--11	1110099991	1
Paracossulus	1011----0-	0--1110091	0110091099	1090-01900	-01110--11	1190011911	1
Cossulus	1091----0-	10-9990091	0d-9991000	d-0d-0d90d	-0111d--d1	91d00d-911	1
Parahypopta	1d1-------	0--10-0991	0110001000	d-d0-01900	-01110--11	11100d-01d	1

Dyspessacossus	1091----0-	10-9990091	010999d999	d-01000900	-01d110-11	9100099991	1
Brachygystia	1001----10	0-----0191	00-9900000	0-11001900	-01110--00	d190099999	9
Eogystia	1001----10	0-----0991	00-9901000	d-09901000	-11010--10	119000-010	1
Eremocossus	101-------	---0--0091	0110001191	11d1001900	01110---11	119000-010	1
Comadia	191d------	0--0--0991	0d-000d191	d-01001001	001d10--11	119900-900	1
Mormogystia	1011----11	0--0--0001	d0-0011191	d-01001901	101110--11	1110d0-090	1
Isoceras	1091----d-	0--9990991	d110001191	d-01001901	111d10--11	910000-01d	1
Stygioides	111d------	0-----0101	d1109d0191	11d110d901	1d1d1d--11	11d9d0-00d	1
Danielostygia	1019999999	9990--0191	1119990191	1101101001	101010--99	9109099990	9
Dieida	10909099--	0--9990191	0119990191	11-1101011	1111110-19	911010-091	1
Semagystia	101d------	0-----009-	111100119d	d-d1d01901	101110--11	11d000-00d	1
Dyspessa	1011----0-	0--0--0001	0111001191	1101001901	1d1110--11	1190d10010	1

Table 26. List of characters (Cossinae).

1. Ocelli present / ocelli absent.
2. Eyes not reduced in size / eyes reduced in size.
3. Both male and female antenna completely bipectinate / male and/or female antenna at least partly bilobed, unilobed, prismatic or filiform.
4. Rami of male and/or female antenna not distinctly or slightly flattened and with roughly 2 rows of hairs on inner margin / rami of male and/or female antenna distinctly flattened and with many hairs on proximal side, and without neat rows of hairs on inner margin.
5. Rami of male antenna with hairs on inner margin and not more than 1 hair or stout sensillum on outer margin / these rami similar but with many hairs on outer margin.
6. Rami of male antenna with moderately long hairs in approx. 2 rows on inner margin / these rami with moderately short hairs in approx. 2 rows on inner margin.
7. Rami of male antenna with approx. 1 row of hairs on outer margin / these rami with many (very short) hairs scattered on outer margin.
8. Rami of male antenna with approx. 1 row of moderately long hairs on outer margin / these rami with approx. 1 row of moderately short hairs on outer margin.
9. Rami of male antenna distinctly flattened and with many hairs on proximal side and no stout sensillum / these rami similar but with 1 or 2 stout sensilla.
10. Rami of male antenna distinctly flattened, with many hairs on proximal side, and with 1 stout sensillum/ these rami similar but with 2 stout sensilla.
11. Male antenna (nearly) completely bipectinate, unilobed, or prismatic / male antenna partly bipectinate and further unilobed or prismatic (for approx. or more than 10 segments when at base).
12. Male antenna partly bipectinate and further unilobed / male antenna partly bipectinate and further prismatic.
13. Male antenna (completely) unilobed / male antenna (completely) prismatic.
14. Female antenna (completely) bilobed / female antenna (completely) unilobed, prismatic, or filiform.
15. Female antenna (completely) unilobed / female antenna (completely) prismatic or filiform.
16. Female antenna (completely) prismatic / female antenna (completely) filiform.
17. Each flagellomere with approx. 1 hair dorsally / each flagellomere with many (very) short hairs dorsally.
18. Frons not widened / frons moderately widened.
19. Frons roughly uniformly coloured / frons brownish with whitish or very pale brown median band.
20. Third segment of labial palpi (when present) ovate / this segment conical.
21. Labial palpi three-segmented / labial palpi two-segmented.
22. Vestiture on second and third segment of labial palpi ventrally with (moderately) short vestiture mixed with fewer moderately long scales / this vestiture ventrally only short, or mostly moderately or rather long, or long.

23. Vestiture ventrally on second and third segment of labial palpi only short / this vestiture ventrally mostly moderately or rather long, or long.
24. Patagium well-developed (high) / patagium reduced in height (much lower than pronotum).
25. Pronotum well-developed (high) / pronotum reduced in height (much lower than patagium).
26. Tegula ventro-posteriorly distinctly pointed / tegula ventro-posteriorly only slightly pointed or nearly rounded.
27. An approx. moderately high / An at most moderately low.
28. Bs II with long, deep grooves laterally / Bs II with moderately long to very short and more or less shallow grooves laterally.
29. Bs II moderately long, ovate and gradually tapering posteriorly / Bs II posteriorly shortened and more or less rounded.
30. Bs II distinctly ovate, moderately wide and vaulted / Bs II more or less flattened (and widened) and more or less rounded posteriorly.
31. Mesepimeron rather high / mesepimeron moderately high, high, or very high.
32. Mesepimeron moderately high / mesepimeron high or very high.
33. Accessory plate II wide / this plate at most moderately wide.
34. Mesomeron approx. as wide as eucoxa II / mesomeron distinctly wider than eucoxa II.
35. Mesomeron approx. 1.3 to 1.5 times width of eucoxa II / mesomeron at least 2 times width of eucoxa II.
36. I-epiphysis present / I-epiphysis absent.
37. I-epiphysis (when present) reaching distinctly short of tibia-apex / I-epiphysis reaching nearly or at least as far as tibia-apex.
38. Female I-epiphysis at least moderately long and ovate / female I-epiphysis short and tooth-like.
39. Midtibial spurs of hindleg present / these spurs absent.
40. Fifth tarsomere with only stout, dark brown spines / fifth tarsomere with moderate or great number of fine, pale brown spines.
41. Fifth tarsomere with moderate number of fine, pale brown spines / fifth tarsomere with great number of fine, pale brown spines.
42. Fifth tarsomere approx. as long as fourth / fifth tarsomere approx. 1.3 to 1.5 times length of fourth.
43. Paronychia present / paronychia absent.
44. Tarsal claws moderately thick / tarsal claws moderately slender.
45. Arolium well-developed / arolium distinctly reduced or wanting.
46. Fringes long / fringes at most rather long.
47. At least male fringes approx. moderately or rather long / male and/or female fringes at most moderately short.
48. Male (and female) fringes approx. moderately short / male fringes at most short.
49. Male retinaculum well-developed / male retinaculum reduced or wanting.
50. Male frenulum spine well-developed (i.e. long) / this spine reduced in length or wanting.
51. Female frenulum bristles well-developed / these bristles reduced in length or wanting.
52. R4 and R5 separate / R4 stalked or connate with R5.
53. Forewing inner cell well-developed / forewing inner cell distinctly reduced in size.
54. Sc and Rs separate / cross-vein Sc-Rs present.
55. Hindwing inner cell present / hindwing inner cell absent.
56. Humeral plate approx. 1.5 to 1.7 times size of radial bridge / humeral plate at least 2 times size of radial bridge.
57. Humeral plate approx. 2 times size of radial bridge / humeral plate at least 2.5 times size of radial bridge.
58. Radial plate moderately long and with moderately slender apex / radial plate slightly elongate (rather long) and apically slender.
60. Median arm moderately narrow / median arm at least moderately wide.
61. Anal plate approx. moderately long / anal plate at most moderately short.

* - restricted to its type-species.

Table 27. List of characters (Zeuzerinae).

1. Male and female with approx. the same colour pattern / considerable differences in colour pattern between male and female.
2. Vertex not ridged / vertex more or less antero-laterally ridged.
3. Vertex nearly flat / vertex distinctly swollen.
4. Terminations of Pos not marked / terminations of Pos marked by one or few very small protuberances in special area, or by small membranous areas.
5. Terminations of Pos marked by one or few very small protuberances in special area / terminations of Pos marked by small membranous areas only.
6. Eyes moderately large / male and/or female eyes reduced in size.
7. Antenna bipectinate/bilobed/simple for approx. at least 0.7 times its length / antenna bipectinate/bilobed/simple for less than 0.7 times its length, or variably from 0.6 to 0.7 times its length.
8. Male antenna rather strongly bipectinate / male antenna moderately bipectinate.
9. Male antenna with distinctly arcuate rami / rami of male antenna nearly straight and nearly in one plane.
10. Female antenna proximally bipectinate / female antenna proximally bilobed or simple.
11. Female antenna proximally bilobed / female antenna proximally simple.
12. Frons of both male and female not elevated / frons of at least female (often/usually) medio-dorsally more or less elevated.
13. Frons moderately narrow / frons moderately widened in female and/or male.
14. Frontal tuft mostly moderately or rather long / frontal tuft mostly long or very long.
15. Labial palpi present / labial palpi absent.
16. Labial palpi three-segmented / labial palpi two-segmented.
17. Third segment of labial palpi (when present) ovate / this segment (when present) conical.
18. Labial palpi moderately thick / labial palpi (moderately) slender, or second segment proximally narrowed, or second segment thickened apically.
19. Labial palpi at least approx. as long as eye-diameter / labial palpi distinctly shorter than eye-diameter.
20. Second segment of labial palpi, when these palpi three-segmented, distinctly longer than first / second segment of labial palpi, when these palpi three-segmented, at most as long as first.
21. Thorax not speckled with dark fuscous when (mostly) white / thorax white speckled with dark fuscous.
22. Patagium flat to moderately curved / patagium considerably widely curved.
23. Pronotum well-developed (very high) / pronotum distinctly reduced in size (much lower than patagium).
24. Metascutum medially moderately narrow (not distinctly or slightly invaginated) / metascutum medially distinctly invaginated, and medially narrow or very narrow.
25. Metascutellum gradually tapering laterally / metascutellum abruptly narrowed laterally.
26. Tegula ventro-posteriorly distinctly pointed and distinctly upturned / tegula ventro-posteriorly bluntly pointed or (nearly) rounded, and moderately or slightly upturned.
27. Tegula ventro-posteriorly bluntly pointed / tegula ventro-posteriorly blunt.
28. An moderately high / An at most moderately low.
29. An moderately low / An at most low.
30. An low / An very low.
31. Lower suture of Apc reaching up to approx. 0.3 times length of An / this suture reaching up to more than 0.3 times length of An, or variably from 0.3 times to more than 0.3 times length of An.
32. Lower suture of Apc reaching up to 0.4, 0.5 or 0.6 times length of An, or variably from 0.3 to more than 0.3 times length of An / this suture reaching up to more than 0.6 times length of An, or variably from 0.6 times to more than this.
33. Sutures of Apc, when over complete length of An, nearly parallel / sutures of Apc posteriorly considerably diverging.
34. Pre II moderately long / Pre II approx. moderately short.
35. Subalare-process II moderately short or short / this process very short (subalare II nearly rounded anteriorly).

Table 27. Character-matrix 3, Zeuzerinae.

Phragmacossia	0d1100pdod	-90d0d10d0	000101dp--	d--000pddd	0000d0dd0-	-dd000----	0010-0000p	--0ddd-dd-	-0d--d
Eburgemellus	9999901009	990-001100	0999999999	9999001109	1009901199	911001110-	9011-00109	9991110110	-00--9
Oreocossus	0990-00000	-900001000	0101010999	0--0000001	d90900110-	-00000----	0010-00101	0-00p10111	1011-0
undescr. gen. (a)	9999991009	9900001000	0999999999	11-0900011	100910910-	-000019---	9010-00109	9999910111	1011-9
undescr. gen. (b)	9999990990	-900000001	09910100--	11-00011d1	199900010-	-00000----	1010-00101	0-01919111	1011-9
Phragmataecia	0dd0-9p000	-90d0p11d1	0001111d--	11-0101911	d000d0010-	-0d00d----	010-00101	0-0d9d-d1d	-011-1
Zeuzeropecten	0dd0-dp000	-90d0ddddd	0001019d--	11-000ddd1	d000d0010-	-dd00d----	dd10-00101	0-01pd-d11	1011-d
Relluna	9999901109	990001-91-	099100-999	0--0000099	000900000-	-00000----	9010-00001	0-01110011	010--9
Endoxyla	01-0-ddd0d	-99p00dd00	999d010d--	d--000dddd	d00d90d0d-	-1d00p----	1010-0000d	--0dd10d1p	-111-d
Cossimorphus *	0999901001	190-001000	0999999999	9999901109	000-90900-	-110011111	1010-00009	9999010011	01110
Dictyocossus *	0999991001	1999000100	0999999999	9999901109	000-90901-	-110011111	1010-00009	9999110111	0111-0
Melanocossus *	01-0-01001	090-001100	0990099999	9999901009	000990900-	-11001110-	1010-00001	0-01110011	0111-0
Sympycnodes	9000-d1109	999-01-d1-	00000100--	110000ddd1	090900100-	-10000----	0010-d0000	--010d-01d	-111-0
Hamilcara	0010-01100	-9000d1dd0	000001010-	1000000d10	100910100-	-1d000----	0110-0000d	--01d10d10	-111-0
Carohamilia	9999991009	9900001010	099001010-	1100901109	190900100-	-000010---	9010-10091	0-01110111	1111-9
Aramos	0010-91d01	199d0ddd00	0090010d--	1d-00011dd	d009d0900-	-9d00d----	1010-0000d	--01d1dd1-	-111-0
Psychonoctua	0010-0d001	090-001d00	00010101d-	1d-0001190	190910100-	-0d00d----	0010-00009	9901d1d010	-111-0
undescr. gen. (c)	09999d1001	099p00ddd0	09999100--	1d-00000d0	d00910100-	-1100d----	0010-90009	999911dd1d	-1d--0
Voousia	0010-01009	999-001100	00000101d-	1d-0001110	9999009010	-1100110--	101d-9000d	--91119010	-111-0
Morpheis	01-9901001	100-00dd00	000001d1d-	11000011d1	d10d101010	-110011p--	1010-0009d	--1111d010	-1d--0
Xyleutes	01-0-01001	d10p001d00	000001111d	11-00011d1	1101101011	0110011111	1010-00001	111111d01p	-111-0
Alophonotus	01-0-01001	1000009000	00099111d-	11000011d1	d101101011	0110011110	111100000d	--11110d1p	-111-0
Chalcidica	01-0-01001	1d00001100	0009911110	11000111d1	1101101011	-110011110	1010-00001	1011111010	-10--0
Bergaris	9999991009	9990001000	0000099110	110001d9d1	110910101d	-110011110	9d10-00001	1011111010	-111-9
Rapdalus	9010-01009	990-001110	00009111d-	11010111d1	1109101011	011001111d	9111000001	1011110010	-111-9

Table 27 (continued).

Rugigegat	0010-11001	1110001190	0000011111	1101011111	1101101011	0111011111	101100000d	--11111011	1110-0
Pseudozeuzera	9999991009	999-0d10d0	1999911110	1109011191	1109101011	0111011111	9ddd-00001	1011110d1-	-111-9
Paralophonotus	0010-11001	1119001100	0101011111	1101011111	1101101011	0111011111	1111000001	191111001-	-10--0
Eulophonotus	11-0-11001	111pd--190	0119911d--	d-011111d1	110110101d	-111111111	11d110d0p1	0--1110d11	1111-0
Callocossus *	1090-11001	111-01-19-	0019911111	110111-101	1101101011	0111111111	1111101001	0--111911-	-111-0
Zeuzerops *	1090-11001	111-01-19-	0019911111	110111-101	1101101011	0111111111	1111101001	0--111911-	-111-0
Zeuzera	09999d1001	dd0-01-11-	0000011d--	1101d111d1	110110101d	-111011111	1d1d-0001d	--1111dd1p	-111p0
Hermophyllon	0010-11001	101001-0d-	000991110-	1101111101	1101101011	0111011111	1111000001	1011110011	1110-0
Cecryphalus	0010-d1001	090d01-11-	0000011111	1111111111	d0d1001011	0119011111	1111000001	0-11110011	0111-0
Tarsozeuzera	0010-01001	110d01-11-	099991111d	1101111111	ddd101101d	-111011111	111110019d	--1111dd1p	-111-0
Brypoctia	901--91009	999-001110	000009910-	1d-0001111	100910101d	-11001110-	9011000p0d	--01110111	0111-9
Allocryptobia	100--11001	101d0d0000	0000011110	d--00011d1	100010101d	-1100111d-	1d1d-0000d	--00110d1p	-111-0
Panau	0010-11001	191p0d1dd0	0009010d--	1d-00011dd	d00910101d	-1d0011d--	1d1d-0000d	--0111d01d	-111-0
Duomitus	0000-01011	110-001100	000001010-	1100001d00	1000101011	011001111d	101d-00001	1001110011	1111-0
Skeletophyllon	0010-11011	099d00d1d0	000001010-	110000dddd	1009d01010	-1d001110-	111d-00001	0-0d110d10	-111-0
Trismelasmos	019d-0101d	-90000dd00	00099101d-	d-0000dddd	100010101d	-1d0011d--	1d1d-00001	d-0d11001d	-111-0
Aethalopteryx	0999901d0d	-90p0dddd0	099d0100--	d-0000ddd0	d000d010d-	-dd00p----	0010-0000p	--01dd-d1d	-011-0
Strigocossus	0dd0-1100d	-99p00dd00	0000010p--	1d-000ddd1	d0001010d-	-dd00p----	pd10-00d0d	--01dd-d1p	-0d--0
Azygophleps	0110-0dd0d	-90p001d00	000101dd--	d--000dd01	d000d0100-	-0d00p----	p010-0000d	--0dd1dd1d	-0d--0

36. Aculeate area at mesepimeron present / aculeate area at mesepimeron absent.
37. Mesepimeron moderately low / mesepimeron moderately high.
38. Mesepimeron with sinuate upper margin / mesepimeron with rounded upper margin.
39. Accessory plate II approx. wide or rather wide / this plate at most moderately wide.
40. Mesomeron approx. 1.5 times width of eucoxa II / mesomeron at least 2 times as wide as eucoxa II.
41. I-epiphysis of at least male reaching distinctly short of tibia-apex / I-epiphysis of at least male reaching only slightly short of or approx. as far as tibia-apex.
42. Male I-epiphysis distinctly pointed or distinctly tapering apically / male I-epiphysis with more or less blunt apex.
43. Male I-epiphysis moderately wide / male I-epiphysis slender.
44. Female I-epiphysis similar to male one / female I-epiphysis shorter and/or narrower than male one, or absent.
45. Vestiture of at least first tarsomere partly rather or moderately long / vestiture of at least first tarsomere short.
46. First tarsomere of proleg and/or midleg as thick as second / first tarsomere of proleg and/or midleg thickened, distinctly thicker than second.
47. Tarsomeres distinctly widened apically / tarsomeres only slightly or hardly widened apically.
48. Tarsal spines present / tarsal spines absent.
49. Fifth tarsomere approx. as long as fourth / fifth tarsomere at least 1.3 times length of fourth.
50. Fifth tarsomere approx. 1.5 times length of fourth / fifth tarsomere at least 2 times length of fourth.
51. Fifth tarsomere approx. 2 to 3 times length of fourth / fifth tarsomere more than 3 times length of fourth.
52. Paronychia moderately short or short / paronychia minute or absent.
53. Arolium moderately long and moderately wide / arolium distinctly reduced in size, or absent.
54. Male forewing completely covered by scales / male forewing not completely covered by scales.
55. Male forewing moderately wide / male forewing narrowed.
56. Fringes long or rather long / fringes at most moderately long, or varying from long to moderately long.
57. Fringes varying from long to moderately long / fringes at most moderately long.
58. Fringes moderately long / fringes at most moderately short.
59. Fringes moderately short / fringes at most short.
60. Fringes short / fringes very short.
61. Number of female frenulum bristles normally 3 to 5 (occasionally 6) / this number normally more than 5.
62. R1 branching off from areole / R1 proximal to areole.
63. Areole moderately long / areole approx. long or very long.
64. R4 and R5 connate or shortly stalked (up to approx. half their length) / R5 stalked with R4 for at least half its length.
65. R5 stalked with R4 for approx. 0.5 to 0.8 times its length / R5 stalked with R4 for more than 0.8 times its length.
66. Forewing inner cell (usually) present / forewing inner cell (usually) absent.
67. Forewing cell moderately long / forewing cell shortened (distinctly invaginated distally).
68. Anterior M of forewing distinctly separate from chorda / anterior M of forewing normally very close to to partly coalescent with chorda.
69. Cross-vein Sc-Rs normally absent / Sc-Rs normally present.
70. Humeral plate approx. 1.5 times size of radial bridge / humeral plate distinctly smaller or larger than 1.5 times size of radial bridge.
71. Humeral plate at most 1.3 times size of radial bridge / humeral plate distinctly more than 1.5 times size of radial bridge.
72. Humeral plate approx. 2 to 2.3 times size of radial bridge / humeral plate at least 2.5 times size of radial bridge.
73. Radial plate moderately long and moderately wide / radial plate rather long and moderately

slender.

74. Scale plate distinctly shorter than radial bridge / scale plate approx. as long as radial bridge.
75. 1Ax apically moderately small to moderately large / 1Ax apically rather large or large.
76. Median arm rather short / median arm moderately or rather long.
77. Median arm moderately long / median arm rather long.
78. Median arm moderately wide / median arm rather wide.
79. Median arm without antero-proximal invaginaton / median arm with antero-proximal invagination.
80. Median arm with anterior invagination up to approx. $^1/_4$ its length / median arm with anterior invagination up to approx. $^1/_3$ its length, or variably from $^1/_4$ to $^1/_3$ its length.
81. Median arm with anterior invagination variably up to from $^1/_4$ to $^1/_3$ its length / median arm with anterior invagination up to (only) $^1/_3$ its length.
82. 4Ax well-developed and not invaginated antero-distally (it may be vaulted) / 4Ax more or less reduced or invaginated antero-distally.
83. Anal plate only rather long / anal plate varying from moderately to rather long, or only moderately long, or shorter.
84. Anal plate varying from rather long to moderately long / anal plate only moderately long, or moderately short, or varying from moderately long to moderately short.
85. Anal plate varying from moderately long to moderately short / anal plate only moderately short.
86. Female abdomen shorter than or approx. as long as hindwing / female abdomen longer than hindwing.

Table 28. Character-matrix 4, Hypoptinae.

Hypopta	0pd000p00d	0000010p11	900d000d00	9d
Langsdorfia	0p1000d001	00d0ddpp11	1100000000	01
Philiodoron	9010001011	0010110000	910d109d0d	10
Schausisca	9990010011	d0d0110p11	9100100000	10
Givarbela	0010911011	1101110-11	9100110011	11
Pomeria	1100001001	0000009100	1001010111	91
Givira	0p0dd01101	000100ppdd	90010pdddd	0d
Psychogena	9p00d01101	0091001-11	9011000100	91
Puseyia	9p01101101	00910d0pdd	10010dd1d0	9d
Inguromorpha	9900901101	009100900d	90d1019119	99

Table 28. List of characters (Hypoptinae).

1. Pos nearly straight and situated at approx. half length of vertex / Pos arcuate and reaching up to approx. dorso-posterior margin of vertex.
2. Male rather strongly bipectinate / male antenna moderately bipectinate.
3. Antennal rami of male without stout sensillum at apex / rami of male with at least one stout sensillum at apex.
4. Frontal tuft moderately or rather long / frontal tuft moderately short.
5. Vestiture on second segment of labial palpi at least moderately long / this vestiture at most moderately short.
6. Aculeate area at mesepimeron well-developed / this area absent.
7. Mesepimeron moderately high / mesepimeron moderately low.
8. Mesepimeron with rounded or sinuate upper margin / mesepimeron with more or less squared upper margin.
9. Mesepimeron (normally) with pale band medio-posteriorly / mesepimeron (normally) without pale band medio-posteriorly.
10. Mesomeron approx. 1.5 times width of eucoxa II / mesomeron at least twice width of eucoxa II.

11. Accessory plate II separated from mesomeron by a suture / this plate partly or completely fused with mesomeron.
12. Midtibial spurs of hindleg present / these spurs absent.
13. Tarsal spines present / these spines absent.
14. Paronychia present / paronychia absent.
15. Tarsal claws moderately thick / tarsal claws moderately slender.
16. Arolium present / arolium absent.
17. Fringes long / fringes short.
18. Male retinaculum with moderately long base / male retinaculum with its base varying from moderately short to rather long.
19. Male retinaculum well-developed / male retinaculum distinctly reduced or wanting.
20. Male frenulum spine well-developed / this spine more or less reduced in length or wanting.
21. Female frenulum bristles well-developed / these bristles reduced in length or wanting.
22. Costal region of hindwing narrowing at approx. 0.6 or 0.7 times length of hindwing / this region narrowing at approx. 0.4 or 0.5 times length of hindwing.
23. Anal region of hindwing not elongate / this region elongate.
24. R4 and R5 separate / R4 stalked with R5.
25. Forewing cell moderately wide / forewing cell narrowed.
26. Forewing inner cell present / forewing inner cell absent.
27. Cross-vein Sc-Rs normally present / Sc-Rs normally absent.
28. Rs and M1 (of hindwing) (normally/often) separate / Rs and M1 (normally/often) connate or shortly stalked.
29. Hindwing inner cell present / this inner cell absent.
30. M2 and M3 of hindwing separate / M2 and M3 connate or (very) shortly stalked.
31. Humeral plate distinctly larger than radial bridge / this plate at most as large as radial bridge.
32. Anal plate approx. moderately long / anal plate approx. moderately short.

Table 29. Character-matrix 5, *Zeuzera*.

indica	1010011110	d-
aeglospila	019991d111	0-
caudata	0119010111	d-
postexcisa	019991d111	10
multistrigata	1091919111	0-
pyrina	1001111111	99
biebingeri	1099991199	0-
borneana	9999001199	0-
lineata	9999111199	0-
undescr. sp.	9911111111	0-
conferta	1001d0d111	0-
coffeae	101910d111	0-

Table 29. List of characters (*Zeuzera*).

1. Female antenna proximally bilobed / female antenna proximally simple.
2. Vestiture dorsally on female antenna irregularly distributed / this vestiture mostly arranged in longitudinal rows.
3. An moderately high / An moderately low.
4. Subalare-process II moderately short / this process very short.
5. Accessory plate II wide or rather wide / accessory plate II moderately wide to/or narrow.

6. Anal region of male hindwing not or only slightly extended / anal region of hindwing distinctly or considerably elongate.
7. R1 branching off from areole / R1 proximal to areole.
8. Cross-vein Sc-Rs absent / Sc-Rs present.
9. Humeral plate nearly quadrangular in shape / humeral plate nearly triangular in shape.
10. Humeral plate approx. 2 times size of radial bridge / humeral plate at most 1.5 times size of radial bridge.
11. Median arm moderately long / median arm rather long or moderately short.
12. Median arm rather long / median arm moderately short.

Table 30. Character-matrix 6, *Panau*.

undescr. sp. (a)	90100--010	-011110-91
euphanes	900111110-	-00--0d-01
undescr. sp. (b)	900010-00-	-10--d0-01
variegata	900011000-	-00--01001
brunnescens	9100110010	-011001010
undescr. sp. (d)	9109999010	-111101101
adusta	110911001d	-111101100
princeps	9001999111	0111109901
quarlesi	9101110010	-111101110
stenoptera	9100110011	d111101110

Table 30. List of characters (*Panau*).

1. Female antenna proximally bilobed / female antenna proximally simple.
2. Frontal tuft moderately or rather long / frontal tuft moderately short or short.
3. Labial palpi three-segmented / labial palpi three- to two-segmented.
4. Second segment of labial palpi moderately thick along their whole length / second segment of labial palpi proximally narrowed up to subapically.
5. An only moderately high / An varying from moderately high to moderately low, or at most moderately low.
6. An varying from moderately high to moderately low / An at most moderately low.
7. An moderately low / An low.
8. I-epiphysis reaching slightly short of or approx. as far as tibia-apex / I-epiphysis reaching distinctly short of tibia-apex.
9. Fifth tarsomere approx. 1.5 times length of fourth / fifth tarsomere at least 2 times length of fourth.
10. Fifth tarsomere approx. 2 times length of fourth / fifth tarsomere at least 2.5 times length of fourth.
11. Fifth tarsomere approx. (only) 2.5 times length of fourth / fifth tarsomere 2.5 to 3 times length of fourth.
12. Arolium well-developed or varying from well-developed to distinctly reduced / arolium only distinctly reduced.
13. Fringes moderately long / fringes varying from moderately long to short, or only moderately short or short.
14. Fringes varying from moderately long to short / fringes at most moderately short.
15. Fringes moderately short / fringes at most short.
16. R1 branching off from areole / R1 proximal to areole.
17. Humeral plate approx. 1.5 times size of radial bridge / humeral plate at least 2 times size of radi-

al bridge.

19. Median arm moderately long / median arm rather long.
20. Median arm with anterior invagination up to $^{1}/_{4}$ its length / median arm with anterior invagination up to $^{1}/_{3}$ its length.

Table 31. Character-matrix 7, *Aethalopteryx*.

atrireta	1191019999	90–00001
undescr. sp. (a)	909001d901	10–00001
steniptera	0011100000	10–00091
undescr. sp. (b)	0010111-00	110-00011
pindarus	1000d01000	110-00011
simillima	1011109001	110-00011
undescr. sp. (c)	0191011910	00–11001
grandiplaga	0000d01000	010-00111
undescr. sp. (d)	0999191000	099900991
tristis	0019991101	110-00911
undescr. sp. (e)	001d111100	111000111
squameus	0001011100	011000111
undescr. sp. (f)	0001111109	011000111
undescr. sp. (g)	0011111111	111100111

Table 31. List of characters (*Aethalopteryx*).

1. Male antenna rather strongly bipectinate / male antenna moderately strongly bipectinate.
2. Labial palpi three-segmented / labial palpi two-segmented.
3. Labial palpi moderately thick / labial palpi slender.
4. Lower suture of Apc reaching up to approx. 0.3, 0.4 or 0.5 times length of An / this suture reaching up to at least 0.6 times length of An.
5. Mesepimeron moderately low / mesepimeron moderately high, or varying from moderately low to moderately high.
6. Intersclerite III present / intersclerite III absent.
7. I-epiphysis reaching distinctly short of tibia-apex / I-epiphysis reaching nearly or approx. as far as tibia-apex.
8. Tarsi with distinct whitish rings at its base and apex / tarsi dorsally mainly dark fuscous and not or indistinctly ringed whitish.
9. Fifth tarsomere approx. as long as fourth / fifth tarsomere approx. 1.3 to 1.5 times length of fourth.
10. Paronychia moderately short or short / paronychia reduced to very small or wanting.
11. Arolium well-developed / arolium reduced to small, or wanting.
12. Fringes long / fringes at most rather long.
13. Fringes rather long / fringes at most moderately long.
14. Fringes moderately long / fringes short.
15. Forewing inner cell present / forewing inner cell absent.
16. Hindwing inner cell present / hindwing inner cell absent.
17. Humeral plate approx. 1.5 times size of radial bridge / humeral plate approx. 2 times size of radial bridge.
18. Median arm with anterior invagination up to approx. $^{1}/_{3}$ times its length / median arm with ante-

rior invagination up to $^1/_4$ times its length.

19. Anal plate approx. rather long / anal plate approx. moderately long.

Table 32. Character-matrix 8, *Strigocossus*.

leucopteris	0911099999	9990111110	110-999011	10000
malgacicus	9199999999	999110010-	110-910911	10001
cretaceus	1119111-1d	1d1110010-	110-10-010	-d000
moderatus	1111111111	0-01100110	1111110011	10000
crassus	1111111011	1d011011d-	110-d10011	11000
capensis	9111911111	0-90991110	1111110091	11000
tandoensis	900991110-	1101990099	0---10-911	11000
undescr. sp.	9190999999	999010000-	10--90-010	-1110
kilimandjarae	9190999991	9999900110	110-999091	00010
ochricostus	919091110-	1100000d-	0---90-110	-1010
mediopallens	90909911d-	1100901999	0---9--119	99010

Table 32. List of characters (*Strigocossus*).

1. Female eyes moderately large / female eyes slightly reduced.
2. Male antenna bipectinate for approx. 0.7 times its length / male antenna bipectinate for approx. 0.4 to 0.5 or 0.6 times its length.
3. Female antenna proximally strongly bipectinate / female antenna proximally shortly to indistinctly bilobed.
4. Second segment of labial palpi moderately thick / second segment of labial palpi proximally narrowed up to subapically.
5. Third segment of female labial palpi conical / third segment of female labial palpi ovate.
6. Tegula distinctly pointed and distinctly upturned / tegula gradually tapering and hardly upturned to bluntly pointed and moderately upturned.
7. An moderately high / An varying from moderately high to moderately low, or at most moderately low.
8. An moderately low / An low.
9. Lower suture of Apc reaching up to approx. 0.3 times length of An / this suture reaching variably up to from 0.3 to 0.4 times length of An, or at least 0.4 times length of An.
10. Lower suture of Apc reaching up to approx. 0.5 to 0.6 times length of An / lower suture of Apc reaching up to from 0.6 to 0.8 times length of An.
11. Mesepimeron moderately low / mesepimeron varying from moderately low to moderately high, or moderately high.
12. Mesepimeron moderately high with sinuate upper margin / mesepimeron moderately high with rounded upper margin.
13. Accessory plate III wide to/or moderately wide / this plate at most moderately narrow.
14. I-epiphysis reaching distinctly short of tibia-apex / I-epiphysis reaching little short of to as far as tibia-apex.
15. Vestiture of tibia II at least moderately long / this vestiture short.
16. Vestiture of tibia III at least moderately long / this vestiture short.
17. Fifth tarsomere approx. as long as fourth / fifth tarsomere approx. 1.3 to 1.5 times length of fourth.
18. Paronychia moderately short / paronychia distinctly reduced or wanting.
19. Arolium moderately long and moderately wide / arolium distinctly reduced or wanting.
20. Arolium distinctly reduced but present / arolium absent.
21. Fringes long / fringes at most rather long.

22. Fringes rather long / fringes at most moderately long.
23. Fringes only moderately long / fringes varying from moderately long to moderately short, or only moderately short.
24. Fringes varying from moderately long to moderately short / fringes only moderately short.
25. Female frenulum bristles 3 or 4 in number, occasionally 5 / these bristles (usually) at least 8 in number.
26. Humeral plate approx. 1.3 to/or 1.5 times size of radial bridge / humeral plate approx. as large as radial bridge or approx. 2 times size of radial bridge.
27. Humeral plate approx. 2 times size of radial bridge / humeral plate approx. as large as radial bridge.
28. Scale plate approx. as long as radial bridge / scale plate shorter than radial bridge.
29. 1Ax apically moderately small / 1Ax apically rather large, or large.
30. Median arm moderately long / median arm rather short or rather long.
31. Median arm rather short / median arm rather long.
32. Median arm moderately wide / median arm rather wide.
33. Median arm with anterior invagination up to approx. $^{1}/_{3}$ or $^{1}/_{2}$ times its length / median arm with anterior invagination up to $^{1}/_{4}$ times its length.
34. Anal plate rather long / anal plate moderately long.
35. Abdominal segments without yellowish vestiture / abdominal segments ringed yellow-ochreous.

Table 33. Character-matrix 9, *Azygophleps*.

liturata	1-09911000	1101000100	1-0000000
leopardina	1-09110000	1109100100	000000000
nubilosa	0109119000	000d000-00	0099d0001
undescr. sp.	0191191110	0001000-00	001-00110
regia	0009111110	000-000000	001-01100
albofasciata	0101111110	0101900000	001-01100
atrifasciata	0101911010	0001900000	001-d9991
inclusa	0101110111	0000000010	001-d0000
melanophele	0009911011	9910000010	009901109
pusilla	1-11111111	1101000010	010000001
aburae	9999911999	9919000010	019991109
asylas	0009119990	0011000000	019911100
albovittata	0001111010	d119001000	01000ddd1
scalaris	1-00111011	11d0011011	1-0111111

Table 33. List of characters (*Azygophleps*).

1. Antenna bipectinate/bilobed for at least 0.6 times its length / antenna bipectinate/bilobed for less than 0.6 times its length.
2. Antenna bipectinate/bilobed for approx. 0.6 times its length / antenna bipectinate/bilobed for at least 0.7 times its length.
3. Male antenna only rather strongly bipectinate / male antenna varying from moderately to rather strongly bipectinate.
4. Female antenna rather or moderately strongly bipectinate / female antenna shortly bipectinate or bilobed.
5. Metascutum medially moderately narrow, not or slightly invaginated / metascutum narrow or very narrow, distinctly invaginated.
6. Tegula distinctly pointed and distinctly upturned / tegula bluntly pointed and slightly upturned,

or ventro-posteriorly rounded.
7. An moderately high / An moderately low.
8. Lower suture of Apc reaching up to 0.3 times length of An / this suture reaching variably up to from 0.3 to 0.5 times or more than half length of An.
9. Bs II moderately long and ovate / Bs II posteriorly shortened and rounded.
10. Subalare-process II moderately short / this process short.
11. Mesepimeron moderately low / mesepimeron moderately high.
12. Mesepimeron with sinuate upper margin / mesepimeron with rounded upper margin.
13. I-epiphysis reaching distinctly short of tibia-apex / I-epiphysis reaching little short of or approx. as far as tibia-apex.
14. Vestiture of tibia II partly at least moderately long / this vestiture only short.
15. Fifth tarsomere approx. as long as fourth / fifth tarsomere varying from 1 to 1.5 times length of fourth.
16. Paronychia present / paronychia absent.
17. Arolium moderately wide / arolium narrowed.
18. Forewing striate (without dots) / forewing regularly spotted.
19. Forewing without yellowish vestiture / forewing with yellow streak, dots or striae.
20. Forewing moderately long / forewing more or less elongate.
21. Fringes at least long / fringes moderately long.
22. Fringes long / fringes very long (little lengthened).
23. Humeral plate less than 2 times size of radial bridge / humeral plate at least 2 times size of radial bridge.
24. Humeral plate approx. 1.5 times size of radial bridge / humeral plate approx. 1.5 to 1.8 times size of radial bridge.
25. Scale plate approx. as long as radial bridge / scale plate shorter than radial bridge.
26. Median arm moderately long / median arm rather long.
27. Median arm moderately wide / median arm rather wide.
28. Median arm with anterior invagination up to approx. $^1/_3$ times its length / median arm with anterior invagination up to approx. $^1/_4$ times its length.
29. Anal plate rather long / anal plate moderately long.

Excluded and obscure taxa

The taxa which still had been placed in the Cossidae by Fletcher & Nye (1982) but which should probably be excluded are indicated below. They are treated in alphabetical sequence. For references to publications see Fletcher & Nye (1982) and the list in this paper.

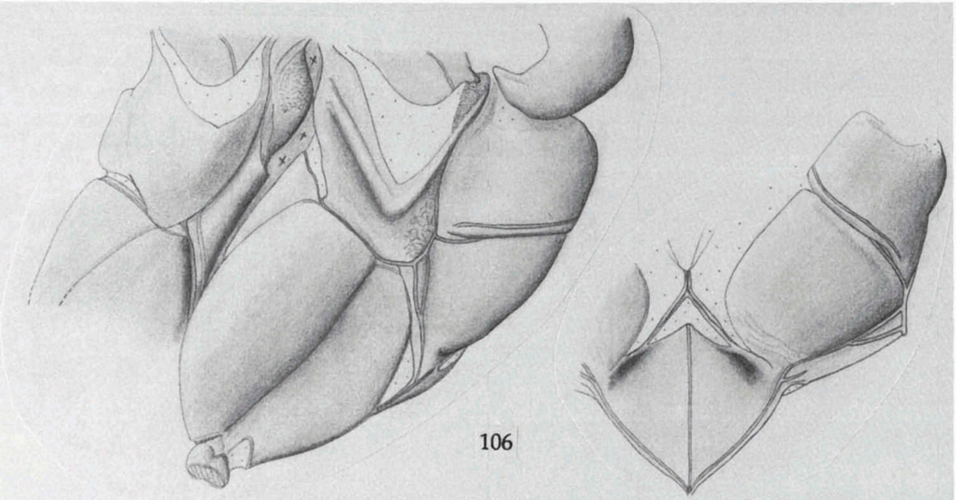
All the taxa excluded below, except the metarbelids and perhaps the ones incompletely known by fossils, do not have a cossoid type of mesepimeron and thus should probably be excluded from the Cossoidea. The other differences noted below suggest in most cases that the absence of a pale band over the mesepimeron is not secondary. Most of these taxa seem to be of a more primitive grade than the Cossidae, considering their states of patagium, pronotum, maxillary palpi, labrum, mesomeron, fifth tarsomere, CuA2 of forewing, lateral process of posterior notal wing process in forewing, and/or anal plate. The author supposes that a number of these should be placed in one or more new families.

Acousmaticus Butler, 1882 is monotypic and was established in the Psychidae. The genus was transferred to the Argyrotypidae, but Bryk (1937) include it in the Cossidae. Clench (1957: 136-137) places this genus in the *Givira-Langsdorfia* group. This is understandable, since CuP and A1+2 of the forewing are distally more or less coalescent in *A. magnicornis* Butler, 1882. Two ♂ specimens from Chile (BMNH), amomg which the holotype, have been examined. The state of 3+4Ax in the hindwing of *magnicornis* is similar to that in the Hypoptinae. A difference from the Hypoptinae is that M of both fore- and hindwing is not close to CuA in *magnicornis*. The mesepimeron of *magnicornis* (see fig. 106) closely resembles that of certain hypoptine species, but lacks a pale band. *A. magnicornis* does not have the psychid type of mesepimeron (see below). The species has the following other characteristics: vertex very short, antenna nearly or approx. as long as forewing, ♂ antenna strongly bipectinate, antennal rami with rather long, spine-like scales dorsally, tentorial pits rather large, ♂ labial palpi approx. 3 times as long as eye-diameter, labrum small, patagium probably very low and pronotum probably very high, K unusually narrow (see fig. 106), lower Pas rudimentary or absent, metepimeron seemingly wide, I-epiphysis probably wanting, tarsal spines wanting, Rs and M1 of hindwing very close to shortly stalked, and anal region of hindwing rather narrow. Clench (1957: 136-137, pl. 5: fig. 3, pl. 6: fig. 5) figures the venation and genitalia. The uncus has a dorsal lobe. See also the description by Gentili (1985: 119-121). *Acousmaticus* does not fit in the Cossidae and is therefore excluded from this family.

Acritocera Butler, 1886 is monotypic. A series of specimens, including the holotype, of *A. negligens* Butler, 1886 in the BMNH has been examined. A significant difference from the Cossidae is the presence of a pair of well-developed abdominal tympanic organs, which closely resemble those in *Dudgeonea* Hampson, 1900. The latter genus was orginally included in the Cossidae, but later placed in a family of its own by Berger (1957). The mesepimeron of *negligens* closely resembles that of *Dudgeonea* species (see fig. 112) and lacks a pale band. Other important differences between *A. negligens* and the Cossidae are: vertex seemingly with an extra suture, ♂ antenna very strongly unipectinate, ♀ antenna rather strongly unipectinate, clypeus pronounced and pointed, pronotum very low, subalare II ventrally elongate, Pas seemingly wanting, aculeate area at mesepimeron wanting, mesomeron distinctly narrower than eucoxa II, intersclerite III long, areole narrow and with only R2 and R3 branching off, CuP of forewing in distal half wanting, costal region of hindwing narrowing very distally, M of hindwing very close to CuA, inner cell of hindwing large, link M3-CuA1 in hindwing wanting, and posterior notal wing process of hindwing slender. The states of pronotum and intersclerite III are also found in *Dudgeonea*, but the other ones listed are also differences from the latter. Perhaps *Acritocera* should be included in the Dudgeonidae, though there are many differences between the former and *Dudgeonea*. *Acritocera* certainly does not fit in the Cossidae, and is therefore excluded from this family.

Adelopsyche Cockerell, 1926 was proposed for a new species *frustrans*, described from a fossil fragment. Cockerell (1926: 16-17) figures the forewing venation. R1 branches off close and proximally to the areole, while R4 and R5 are connate and M is close to CuA. Such a type of venation seemingly does not fit in the Cossidae, and therefore *Adelopsyche* is excluded from the Cossidae.

Allostylus Hering, 1923 was proposed for *Cossula caerulescens* Schaus, 1911. Dyar (1940: 1269) neglects *Allostylus* and places *caerulescens* in *Cossula*. Perhaps *Allostylus* should be synonymized with *Cossula*. *C. caerulescens* probably belongs to the



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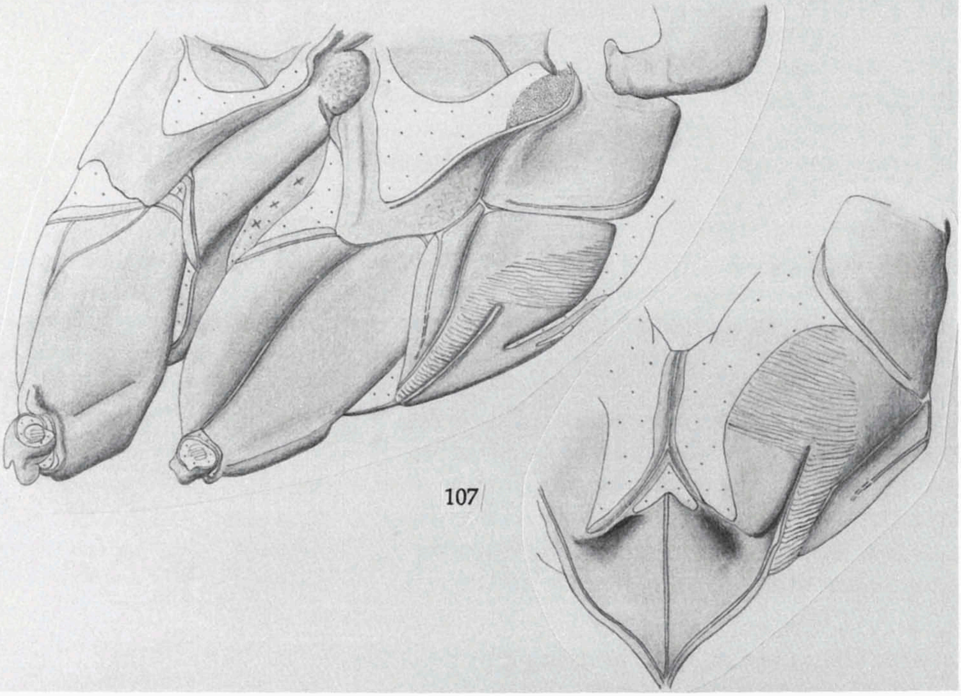

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Figs. 106-107, sections of thoraces. 106, *Acousmaticus magnicornis*, Chile; 107, *Archaeoses polygrapha* Australia, Blackwood.

Cossulinae. The Cossulinae are excluded from the Cossidae (see Cossulinae and *Cossula*).

Andesiana was introduced for three new species by Gentili (1985: 73-77), which are: *lamellata*, *similis* and *brunnea*. Two ♂ paratypes of *similis* (IPCN) and two males of *lamellata* (IPCN) have been examined. These two species greatly resemble one another superficially. The maxillary palpi are four-segmented in at least *lamellata*. In both species CuA2 branches off far distally, which is exceptional for the Cossidae. *A. similis* has the following characteristics: ocelli wanting, ♂ antenna bipectinate, metascutum wide, metascutellum moderately wide, An high, Apc reaching up to approx. half length of An, mesepimeron moderately high and without pale band, accessory plate II seemingly absent, mesomeron slightly narrower than eucoxa II, metameron very narrow, eucoxa III wide, intersclerite III moderately large, tibiae with conspicuous spines, midtibial spurs at approx. half length of tibia, fringes long, ♂ retinaculum with long base, all radial veins of forewing separate, M of forewing proximally close to R, costal region of hindwing narrowing very gradually, scale plate absent, lateral process of posterior notal wing process in forewing shortly separate, median arm rather wide, median plate rather long, 2Ax of hindwing mostly moderately narrow, 4Ax with large lobe, and anal plate approx. rather long. The present author supposes that *lamellata* has similar characteristics. The outward appearance of *Andesiana* species is very unusual for the Cossidae. The ♂ genitalia differ considerably from the generalized type of the Cossidae; e.g., the vinculum is very large and excavated, and the juxta has conspicuous processes. *Andesiana* does not fit in the Cossidae and is therefore here excluded from this family.

Archaeoses Turner, 1932 was proposed for a new species *neurotenes*. Turner (1945: 67) notes that the latter is a junior synonym of *Cossus polygrapha* Lower, 1893. A long series of *polygrapha* specimens in the BMNH has been examined. The mesepimeron is rather triangular and lacks a pale band (see fig. 107). Other differences from the Cossidae are: labrum with well-developed pilifers, pronotum low, metascutum medially rather wide, metascutellum medially wide and medio-anteriorly extended, mesomeron distinctly narrower than eucoxa II, midtibial spurs slightly to distinctly beyond half length of tibia, fifth tarsomere approx. 0.8 times length of fourth, forewing widened at approx. one-third wing-length, anterior M of forewing very shortly furcate, CuA2 of forewing branching off very distally and sinuate, costal region of hindwing sometimes very shortly furcate, lateral process of posterior notal wing process in forewing very shortly separate (see fig. 108), and anal plate long. *Archaeoses* is so different from the Cossidae, that it is excluded from this family.

Austrocossus was proposed for the new species *minutus* by Gentili (1985: 85-87). Judging from the descriptions and figures provided by Gentili (1985), *minutus* has the following characteristics: male and ♀ antenna prismatic, maxillary palpi four-segmented, I-epiphysis short and with base beyond half length of tibia, forewing widened at approx. one-third wing-length, and ♀ frenulum bristles short. One paratype (IPCN) has been examined by the present writer. *A. minutus* has the following other characteristics: ocelli wanting, clypeus pronounced and bluntly pointed, tentorial pits rather long and ovate, metascutum rather wide, metascutellum moderately wide, An high, mesepimeron rather triangular and without pale band, accessory plate II seemingly absent, mesomeron slightly narrower than eucoxa II, metameron very narrow, eucoxa III wide, intersclerite III rather long, costal region of

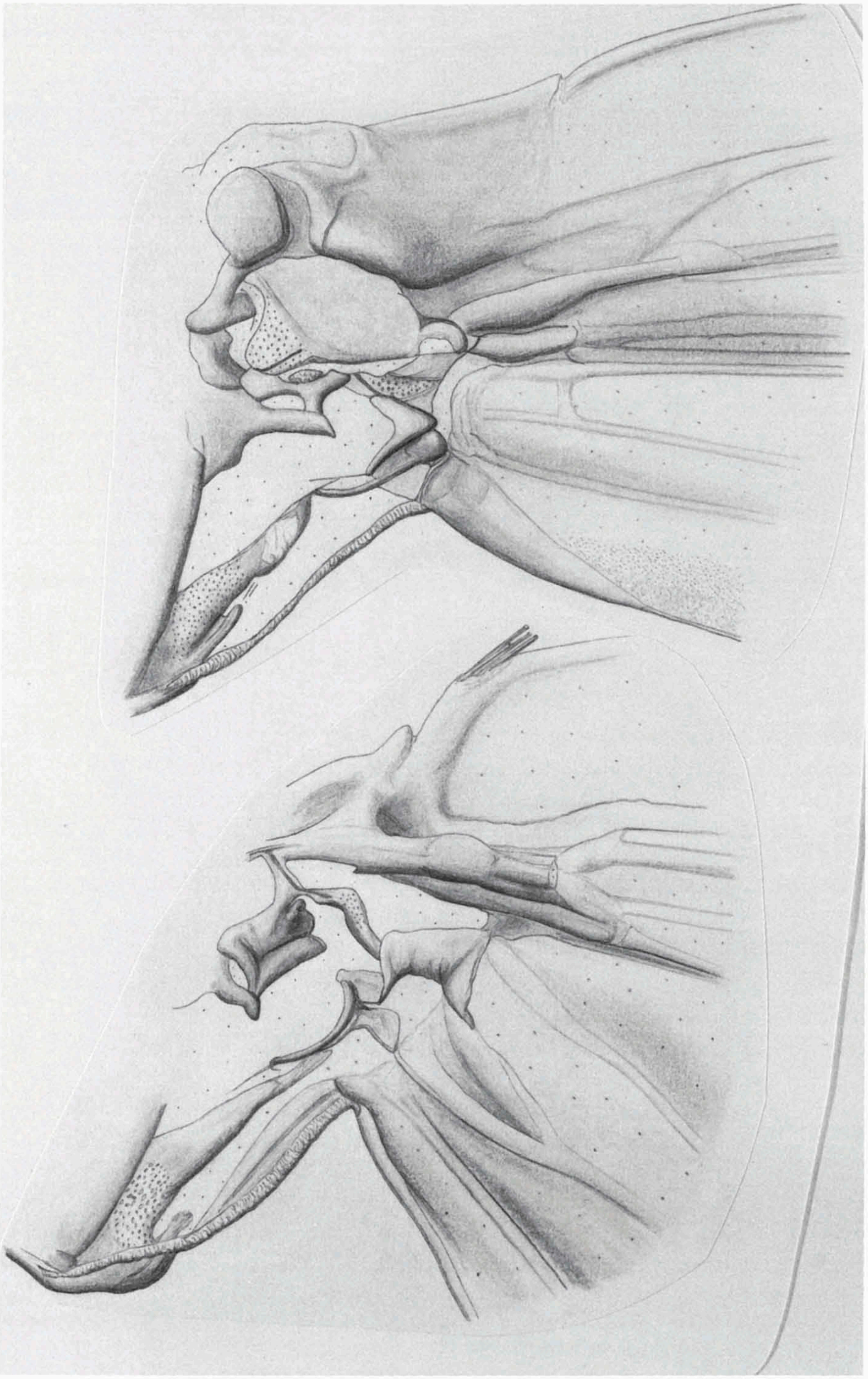


Fig. 108, wing bases of *Archaeoses polygrapha*, Australia.

forewing rather wide, all radial veins of forewing separate, CuA2 branching off rather far distally, costal region of hindwing moderately narrow and narrowing very gradually distally, scale plate approx. as long as radial bridge, lateral process of posterior notal wing process in forewing shortly separate, median arm rather long and moderately wide, and anal plate long. The outward appearance of *minutus* is very unusual for the Cossidae. This species does not fit in the Cossidae, and therefore *Austrocossus* is here excluded from this family.

Charmoses was introduced for a new species *dumigani* by Turner (1932: 194). According to the original description, *dumigani* has the following characteristics: male antenna completely bipectinate, R3 and R4 stalked, and inner cell of hindwing wanting. The state of the ♂ antenna and the distribution outside America would mean that *dumigani* probably belongs to the Cossinae, if it actually is a cossid. It would be the only cossine species known to occur in Australia. It is unusual for the Cossinae to have R3 and R4 stalked while R5 is separate. Therefore the author doubts that *Charmoses dumigani* belongs to the Cossidae.

Citharalia was proposed by Clench (1956: 904-905) for the new species *idiosetoides* from South America. Two ♂ paratypes (CMNH) have been examined. The ♂ antenna is unipectinate. The rami are moderately long and much flattened and have many short hairs on their proximal side. There is no (distinct) patagium/pronotum. An is high. The mesepimeron is moderately high, has a rounded upper margin, and lacks a pale band. Areole and forewing inner cell are wanting. The male retinaculum has a moderately short base. *Citharalia* does not fit in the Cossidae and is excluded from this family. The genus should perhaps be included in the Cossulinae.

Cossodes White, 1841 is monotypic with *Cossodes lyonetii* White, 1841 as type species. *Tirema* Herrich-Schäffer, [1854] 1850-1858 is a junior objective synonym, although *lyonetii* was (erroneously) ascribed to Boisduval. Two specimens of *lyonetii* in the BMNH have been examined. Both ♂ and ♀ antenna are prismatic. The labial palpi are approx. 2.5 times length of the eye-diameter. The mesepimeron has an unusual shape (see fig. 126), which is reminiscent of that of *Saalmulleria stumpfii* (Saalmüller, 1884) (Metarbelidae) (see fig. 120). The mesepimeron of *lyonetii* has a short pale band, whereas that in *stumpfii* reaches far anteriorly. The fuscous areas on the wings of *lyonetii* have a bright blue metallic lustre as in certain metarbelids, such as *Melisomimas metallica* Hampson, 1914. Especially because of the shape of the mesepimeron, *Cossodes* is excluded from the Cossidae and tentatively placed in the Metarbelidae.

Cossula Bailey, 1882 has as type species *Cossula magnifica*, which is a junior synonym of *Cymatophora magnifica* Strecker, 1876. Dyar (1940: 1269-1273) includes many species in *Cossula*. In this study material of *magnifica* and several other *Cossula* species has been examined. The mesepimeron lacks a pale band (see fig. 109). The patagium varies from very low to moderately high within *Cossula*. The lateral grooves of Bs II are rather short, moderately shallow, and approx. transverse (see fig. 109). The accessory plate II is long. The crochets of the larvae are arranged in two transverse bands in *Cossula*, whereas these are in a complete circle in the Cossidae (Fracker, 1915: 77-78). Because of these differences, *Cossula* is excluded from the Cossidae.

Cossulinae Bailey was proposed for *Cossula*. *Cossula* and thus also the subfamily Cossulinae have been excluded from the Cossidae in this paper (see above). The following genera should probably be included in the Cossulinae: *Cossula*, *Costria* Schaus, 1892, *Trigena* Dyar, 1905, *Allostylus*, *Schreiteriana* Fletcher, 1982, *Dimorphoctena*, Clench, 1957 and (perhaps) *Citharalia*.

Cossus lepta West, 1932 closely resembles superficially certain cossine species. A long series of this species, including the types, in the BMNH has been examined. The mesepimeron of *lepta* is moderately low, lacks a pale band, and has a regularly rounded upper margin (see fig. 114). This type of mesepimeron is also known in the Psychidae, and a more or less similar type is also found in the Acrolophidae Busck (see fig. 113). Other differences in *lepta* from the Cossidae are: patagium very low, M of forewing proximally very close to Rs, R3 and R4 or only R2 and R3 stalked, CuA2 of forewing distally coalescent with CuP for approx. 0.8 times its length, costal region of hindwing narrow, lateral process of posterior notal wing process in forewing shortly separate, and 3+4Ax of hindwing rather broad and seemingly swollen (see fig. 115). Since *lepta* does not fit in the Cossidae, it is excluded from this family. The author does not know if *lepta* has already been transferred to another family. *C. lepta* shows great similarity to species of *Westia* Fletcher, 1982. Differences from *Westia* species seem to be: R1 branching off before areole at approx. 0.3 or 0.4 times wing-length, costal region of hindwing narrow, mesomeron wider than eucoxa II, and anal plate moderately long. Clench (1959c: 223) places *Westia* as a member of the Melasinidae Tutt, 1900, and notes that the Melasinidae are probably most closely related to the Psychidae. Robinson (1988: 120) places *Melasina* Boisduval, 1840 (s.s.) as a genus of the Psychidae. *C. lepta* probably belongs also to the Psychidae.

Costria Schaus, 1892 was proposed for the new species *abnoba*. Dyar (1940: 1270) neglects *Costria* and includes its type species in *Cossula*. *Costria* should probably be included in the Cossulinae. The Cossulinae are excluded from the Cossidae (see under *Cossula* and Cossulinae). The author supposes that the mesepimeron of *Costria* species most closely resembles that in *Cossula magnifica* (see fig. 109) and also lacks a pale band.

Culama was proposed for a new species *australis* by Walker (1856: 1524-1525). Walker (1856: 1522) places the new species *caliginosus* in *Cossus*, while this species most closely resembles *australis*. *C. caliginosus* and several other species have been included in *Culama*.

Turner (1918: 160) establishes *Macrocyttara* for *Culama expressa* Lucas, 1902. Turner notes that *expressa* differs especially from *Culama* species in that all radial veins of the forewing are separate. A long series of *expressa* specimens in the BMNH has been examined. The ♀ antenna of *expressa* is prismatic, whereas that of *Culama* species is bipectinate. The anal plate of *expressa* is slightly shorter than in *Culama* species. In *caliginosa* all radial veins of the forewing are sometimes/often also separate, or R3 and R4 are shortly stalked. *C. expressa* is further very similar to *Culama* species. Gaede (1933b: 810) neglects *Macrocyttara* and includes *expressa* in *Culama*. The differences noted here do not warrant a separate genus in my opinion. Therefore *Macrocyttara* is synonymized with *Culama*.

The mesepimeron of *Culama* species lacks a pale band (see fig. 110). Other differences from the Cossidae are: female labial palpi at least three times as long as eye-diameter, maxillary palpi three-segmented in certain species, pronotum moderately high, accessory plate II long, mesomeron slightly narrower than eucoxa II, ♂ retinaculum with short base, forewing widened at approx. one-third wing-length, M of forewing proximally close to Rs, and lateral process of posterior notal wing process in forewing shortly separate. The larvae excavate galleries beneath the bark of trees (Common, 1970: 797). Because of these differences, *Culama* is excluded from the Cossidae.

Culama treicleiota Bethune-Baker, 1911 is neither a species of *Culama* nor a cossid. Two male specimens of *treicleiota* in the BMNH, including the holotype, have been examined. The species is primitive in many respects; ocelli present, maxillary palpi three-segmented, labrum with well-developed pilifers, galeae rather long, mesomeron approx. 0.5 times width of eucoxa II, CuA2 of forewing branching off very distally, A1 and A2 coalescent for approx. half their length, costal region of hindwing narrowing very distally, lateral process of posterior notal wing process in forewing very shortly separate, and anal plate long. The mesepimeron is rather triangular but ventrally moderately wide, and lacks a pale band (see fig. 116). The shape of the mesepimeron is different from that in *Culama* (see fig. 110). *C. treicleiota* is excluded from the Cossidae, but it is uncertain as to which family *treicleiota* belongs.

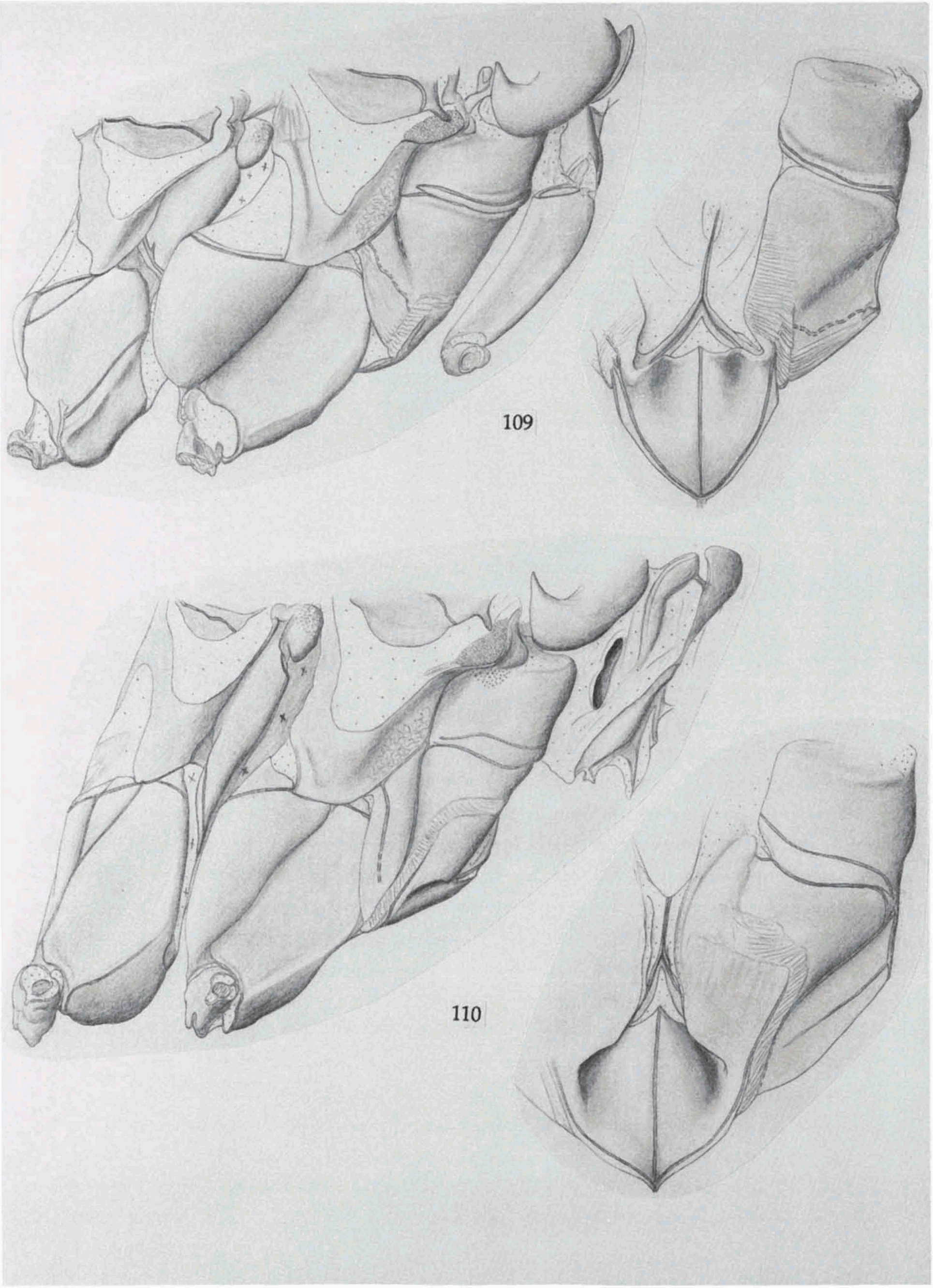
Dimorphoctena was introduced by Clench (1956: 900-901) for the new species *egregia* from Brazil. Two ♂ paratypes (CMNH) have been examined. The ♂ antenna is unipectinate in a way which is exceptional for the Cossidae. The mesepimeron lacks a pale band and closely resembles that in *Cossula* (see fig. 109). The accessory plate II is long. R1 branches off from the areole. R2 is stalked with R3 and R4. CuA2 branches off far distally. The colour pattern greatly resembles that in certain *Cossula* species. *Dimorphoctena* does not fit in the Cossidae and is excluded from this family. It should most probably be included in the Cossulinae.

Duomitella was established for the new species *relicta* by Koshantschikov (1923: 24-25). According to the original description, *relicta* would look like a smaller version of *Xyleutes personus* (Zeuzerinae). Koshantschikov notes the following characteristics: male antenna shortly unipectinate, ♀ antenna laminate, and legs without spurs. In certain cossine species the ♂ antenna is also unipectinate, but the hindlegs have two pairs of distinct spurs. In the Zeuzerinae the midtibial spurs are wanting, but the ♂ antenna is proximally bipectinate. Therefore the author supposes that this monotypic genus should be placed in another family.

Gurnetia Cockerell, 1921 was proposed for a new species *durranti*, based on a fossil fragment of a forewing. The type of forewing venation is so unusual for the Cossidae (see chapter on fossils), that *Gurnetia* is excluded from the Cossidae.

Idioses Turner, 1927 is monotypic, and has *I. littleri* Turner, 1927 as its type species. A long series of *littleri* specimens in the ITZ and four borrowed from the C.S.I.R.O. Division of Entomology (Canberra City, Australia) have been examined. The mesepimeron of *littleri* is ventrally rather squared, and lacks a pale band (comparable to fig. 117). The ocelli are small to wanting. The special venation of *littleri* is figured by Common (1970: 798). The males have a kind of pterostigma. Other differences from the Cossidae are: pronotum probably very low, M of forewing proximally very close to Rs, M3 and CuA1 of forewing shortly stalked, lateral process of posterior notal wing process in forewing very shortly separate, and anal plate long. Because of these differences, *Idioses* is excluded from the Cossidae.

Macrocyttara Turner, 1918 has been synonymized with *Culama* Walker, 1856 (see *Culama*).



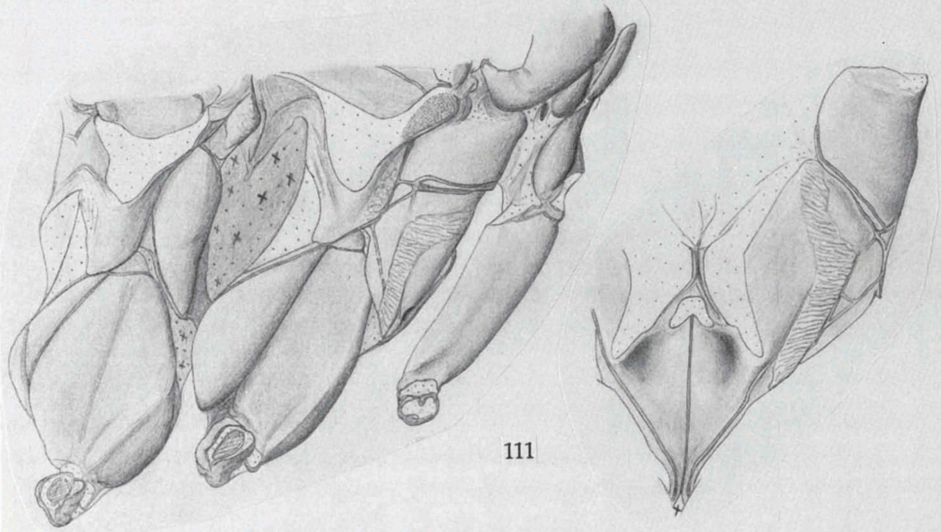
Figs. 109-110, sections of thoraces. 109, *Cossula magnifica*, U.S.A., Florida, St. Petersburg; 110, *Culama caliginosa*, Australia, Toowong.

Meharia Chrétien, 1915 was established in the Tineidae Latreille, 1810, but transferred to the Cossidae by Bradley (1951). The type species is *M. incurvariella* Chrétien, 1915. *Blalia vittata* Rungs, 1943, the type species of *Blalia* Rungs, 1943, is a junior synonym of *incurvariella*. There are five other species in *Meharia*. Material of most of these species in the BMNH and the types of *incurvariella* and *vittata* in the MNHN have been examined. The species are mostly very similar, apart from colour pattern. The mesepimeron is rather triangular and lacks a pale band (see fig. 111). Other differences from the Cossidae are: labrum with more or less developed pilifers, pronotum low, metascutum medially wide, metascutellum medially wide and more or less antero-medially extended, tergite I membranous in anterior half, Pa anteriorly well separate from Bs II, upper Pas diagonally over Pre II, mesomeron slightly narrower than eucoxa II, eucoxa III wide, midtibial spurs at or slightly beyond half length of tibia, fifth tarsomere approx. 0.8 times length of fourth, forewing widened at approx. one-third wing-length, CuA2 of forewing very distal, costal region of hindwing narrowing very distally, and anal plate long. Because of these differences, *Meharia* is excluded from the Cossidae.

Mekla Swinhoe, 1892 was proposed for *Degia deficiens* Walker, 1862. *Mekla deficiens* looks like a psychid. The mesepimeron of this species lacks a pale band, is moderately low, and has a regularly rounded upper margin, as in fig. 114. This type of mesepimeron is also found in the Psychidae, e.g. *Trichocossus* Hampson, 1910 and *Gymnelema* Heylaerts, 1891. *Trichocossus* and *Gymnelema* were originally included in the Cossidae, but later transferred to the Psychidae. *Mekla* is excluded from the Cossidae and tentatively included in the Psychidae.

Metarbelidae Strand, 1909 has as type genus *Metarbela* Holland, 1893. Teragridae Hampson, 1920 and Lepidarbelidae Dalla Torre & Strand, 1923 are junior synonyms. Arbelidae Hampson, 1892 and Hollandiidae Karsch, 1896) are invalid names for the same family.

The Metarbelidae were included as a subfamily in the Cossidae by Handlirsch (1925) and Zerny & Beier (1936). Most authors regarded the Metarbelidae as a separate family. Minet (1986: 298-299) includes the Metarbelidae again in the Cossidae, apparently because of the similar types of pronotum in the two families. A problem is that the (primary) types of pronotum of other cossoid families are unknown and that the possibility that a similar type is also found in certain other Cossoidea cannot be ruled out. If it actually is a synapomorphy of the Metarbelidae and Cossidae sensu Neumoegen & Dyar, this does not necessarily imply that the taxon Metarbelidae should be regarded as a subfamily of the Cossidae. An overriding problem is that there is no modern definition of the (sub)family Metarbelidae should be defined, the phylogeny of its constituent groups is unresolved and its monophyly is unproven. Most Metarbelidae have a reduced venation, dissimilar to that of the Cossidae sensu Neumoegen & Dyar. Within the Metarbelidae, a generalized primitive ditrysian type of venation is known only in *Cossodes lyonetii*, which has been transferred from the Cossidae to the Metarbelidae in this paper (see above). In *C. lyonetii* the shape of the mesepimeron (see fig. 136) is most unusual for the Cossidae, but is reminiscent of that in *Saalmulleria stumpfii* (Metarbelidae) (see fig. 120). The mesepimeron of *lyonetii* is moderately low and nearly crescent-like. In many other Metarbelidae, such as *Lebedodes* species, the mesepimeron has a rather squared outline, but less than in the (other) Cossidae. It is more parsimonious to place the Metarbelidae as the sister-group of the Cossidae than in the Cossidae. Extensive research on Metarbelidae and



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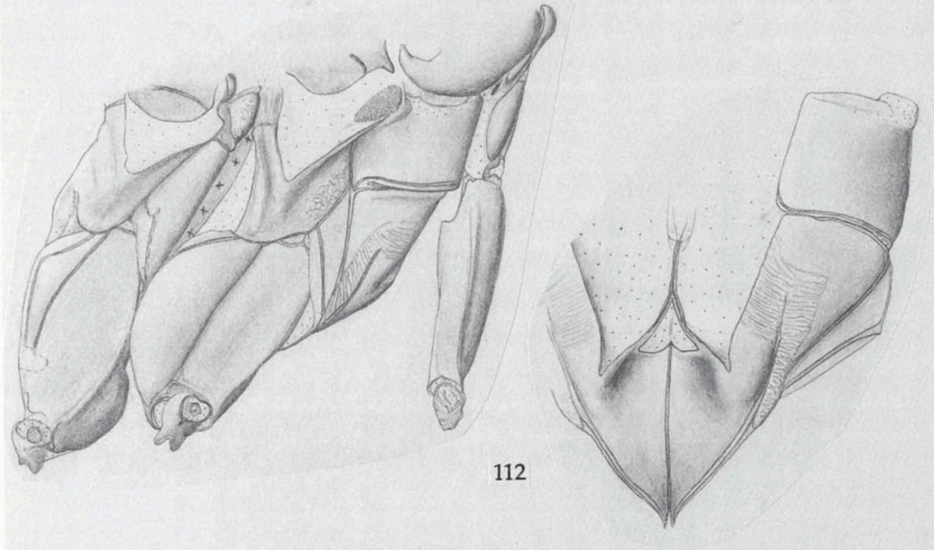

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Figs. 111-112, sections of thoraces. 111, *Meharia semilactea* (Warren, 1905), Arabia, Wadi Qarma; 112, *Dudgeonea nummata* Roepke, 1957 (Dudgeoneidae), Papua New Guinea, Rossel Island.

other Cossoidea is needed to verify this idea. The Metarbelidae are here tentatively regarded as a separate family, pending further investigation.

Nomima Durrant, 1916 is a senior synonym of *Theatrista* Meyrick, 1917, *Zesticodes* Meyrick, 1918 and *Pectitinea* Amsel, 1953. Attention to these synonymies was drawn by Dr. G.S. Robinson (pers. comm.). *Theatrista* was established in the Tineidae, but had been transferred to the Limacodidae by Gozmány & Vári (1973). Fletcher & Nye (1982: x, 161) transfer the genus to the Cossidae on the advice of a colleague. *Nomima* includes five species; the type species is *N. prophanes* Durrant, 1916. Two ♂ specimens of the latter in the BMNH have been examined. This species is greatly reminiscent of *Meharia* species. The thorax most closely resembles that of *Meharia* species (see fig. 111). The mesepimeron is rather triangular and lacks a pale band. Other differences from the Cossidae are: male antenna nearly or approx. as long as forewing, pronotum very low, metascutum wide, metascutellum wide and at least sometimes slightly extended medio-anteriorly, upper Pas approx. diagonally over Pre II, mesomeron slightly narrower than eucoxa II, metameron very narrow, eucoxa III wide, I-epiphysis probably wanting, midtibial spurs before half length of tibia, approx. 2 stout apical spines on each tarsomere, fifth tarsomere approx. 0.8 times length of fourth, forewing approx. as wide as hindwing and widened at approx. one-third wing-length, M of forewing indistinct or obsolescent and unforked, CuA2 of forewing branching off rather far distally, costal region of hindwing moderately narrow and gradually tapering very distally, lateral process of posterior notal wing process in forewing shortly separate, and anal plate long. Because *Nomima* does not fit in the Cossidae, it is excluded from this family.

Porthetes West, 1932 is a junior homonym of *Porthetes* Schoenherr, 1838 (Coleoptera). See under *Westia* Fletcher.

Pseudocossus Gaede, 1933 is a junior homonym of *Pseudocossus* Kenrick, 1914. See under *Zyganisus* Viette, 1951.

Pseudurgis Meyrick, 1908 was established in the Tineidae, but later transferred to the Limacodidae by Gozmány & Vári (1973). Fletcher & Nye (1982: 137) include *Pseudurgis* in the Cossidae on the advice of a colleague. The type species is *P. tectonica* Meyrick, 1908. Material of eleven named species, including *tectonica*, and few undescribed ones in the BMNH has been examined. The thorax of these species closely resembles that in *Meharia* (see fig. 111). The mesepimeron lacks a pale band. Ocelli are well-developed, small or wanting. The ♂ antenna is rather strongly or strongly unipectinate, but the last five to ten segments are prismatic. The labial palpi vary interspecifically from 2 to 4 times length of the eye-diameter. The clypeus is pronounced and more or less pointed or rounded. Pa is not partly overhanging Bs II. The mesomeron varies interspecifically from distinctly narrower than to nearly as wide as eucoxa II. The intersclerite III may be long. Other differences from the Cossidae are: patagium moderately high, pronotum very low, metascutellum wide and medio-anteriorly extended or rather wide and oval, tergite I membranous in anterior one-third, half or three-fifths, I-epiphysis slender, fifth tarsomere approx. 0.8 times length of fourth, costal region of hindwing narrow, lateral process of posterior notal wing process in forewing hardly separate, and anal plate long. Because of these differences, *Pseudurgis* is excluded from the Cossidae.

Ptilomacra Walker, 1855 was established in the Notodontidae Stephens, 1829, but placed in the Cossidae by Kirby (1892). *Ptilomacra senex* Walker, 1855 is a senior synonym of *Cossus longicornis* Walker, 1856, *Ptilomacra antiqua* Walker, 1869, and *Pachyphlebius thoracicus* Felder, 1874. *Pachyphlebius* Felder, 1874 is a synonym of *Ptilomacra*. The genus is monotypic. A long series of *senex* in the BMNH has been examined. The mesepimeron (see fig. 127) is high, narrower than in the Cossidae, and lacks a pale band. Other differences from the Cossidae are: male antenna strongly bipectinate, pronotum low, median arm seemingly fused with median plate, costal region of hindwing narrowing very gradually, and anal region of hindwing moderately narrow. Because of these differences *Ptilomacra* is excluded from the Cossidae.

Schreiteria Dyar, 1940 is a junior homonym of *Schreiteria* Melzer, 1933 (Coleoptera). See *Schreiteriana* Fletcher, 1982.

Scheiteriana Fletcher, 1982 is an objective replacement name for *Schreiteria* Dyar, 1940, which has *Schreiteria pectinicornis* Dyar as type species and is monotypic. The syntypes of *pectinicornis* (USNM) have been examined. The thorax of *pectinicornis* is very similar to that in *Cossula magnifica* (see fig. 109). The mesepimeron lacks a pale band. The ♂ retinaculum has a very long base. The uncus is broad and gradually rounded. Because of these differences, especially the type of mesepimeron,

Schreiteriana is excluded from the Cossidae. *Schreiteriana* is seemingly closely related to *Cossula*.

Squamura Heylaerts, 1890 is still reckoned as belonging to the Cossidae by Fletcher & Nye (1982: 154). Holloway (1986: 42) places *Squamura* in the Metarbelidae, which is correct in my opinion.

Surcossus was proposed for the new species *perlaris* by Heimlich (1960: 102-103). The original description is very short and provides hardly any information to warrant a new genus. Gentili (1985: 90-91, figs. 16, 35, 39, 50, 58, 67, 107 and 123), who examined the type-material of *perlaris*, provides a better description and correcter figures. According to Gentili, the midtibial spurs are rudimentary. Two ♀ specimens (IPCN) have been personally examined. *S. perlaris* has the following characteristics: ocelli wanting, ♀ antenna is shortly and partly unequally bilobed, ♀ eyes small and frons wide, mesepimeron moderately high and without pale band, accessory plate II moderately short and moderately narrow, mesomeron nearly or approx. twice as wide as eucoxa II, I-epiphysis reaching distinctly short of tibia-apex and (normally ?) finely toothed, apical spurs approx. moderately long, paronychia rather wide, fifth tarsomere approx. as long as fourth, fringes moderately long, ♀ frenulum bristles many and moderately short, CuA2 of forewing branching off rather far distally, scale plate small, lateral process of posterior notal wing process in forewing mainly separate, median arm approx. moderately long and moderately wide, and anal plate moderately short. With this combination of characteristics *perlaris* does not fit in the Cossidae. The outward appearance is also quite unusual for a cossid. Therefore *Surcossus* is here excluded from the Cossidae.

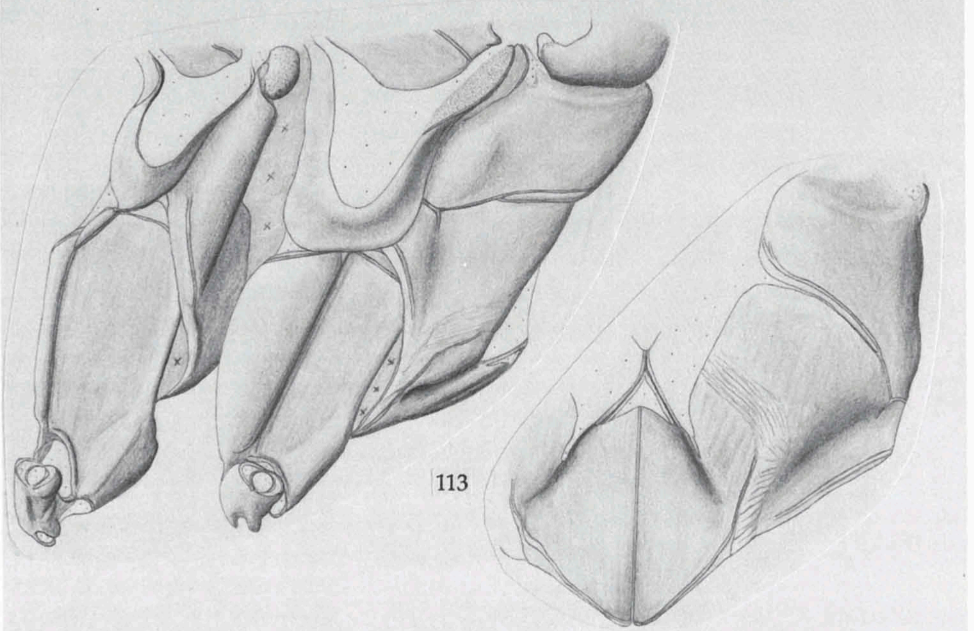
Theatrista Meyrick, 1917 is a junior subjective synonym of *Nomima* Durrant, 1916, which was pointed out by Dr. G.S. Robinson (BMNH) (pers. comm.). See under *Nomima*.

Trigena was proposed for *Cossus parilis* Schaus, 1892 by Dyar (1905: 178). Dyar (1940: 1269) includes further three other species. *Schausiania* Strand, 1910 is an objective replacement name for *Hemipecten* Dyar, 1905. The type species of the latter is *H. ecparilis* Dyar, 1905, which is junior subjective synonym of *Cossus parilis*. *Hemipectrona* Schaus, 1921 is an unnecessarily replacement name for *Hemipecten*. Material of *parilis* and some other species in the BMNH has been examined. The mesepimeron of *Trigena* species lacks a pale band and closely resembles that in *Cossula magnifica* (see fig. 109). The labrum has more or less developed pilifers. The patagium is very low. Bs II is similar to that in *Cossula magnifica* (see fig. 109). The accessory plate II is long. Because of these differences, especially the type of mesepimeron, *Trigena* is excluded from the Cossidae. *Trigena* seems to be closely related to *Cossula* and should most probably be included in the Cossulinae.

Trigonocyttara was proposed for a new species *clandestina* by Turner (1945: 65). Common (1970: 799) places *clandestina* in the Psychidae. Fletcher & Nye (1982: 165) still reckon *Trigonocyttara* as belonging to the Cossidae. A specimen of *clandestina* borrowed from the Queensland University (Australia) has been examined. This species shows indeed characteristics of a psychid species, such as the psychid type of mesepimeron; the mesepimeron is moderately low, lacks a pale band, and has a regularly rounded upper margin. *Trigonocyttara* should probably indeed be included in the Psychidae.

Westia Fletcher, 1982 is an objective replacement name for *Porthetes* West, 1932. *Porthetes* was proposed for a new species *cyrtozona* by West (1932: 220). Material of *Westia* species in the BMNH has been examined. The mesepimeron of these species is moderately low, lacks a pale band, and has a regularly rounded upper margin. The mesepimeron is similar to that of *Cossus lepta* (see fig. 114). This type of mesepimeron is also known in the Psychidae. An unidentified *Westia* species from Sulawesi (ITZ) has been extensively examined. The thorax of this species is nearly similar to that of *Cossus lepta* (see fig. 114), but the mesomeron is approx. as wide as eucoxa II. The wing bases of the unidentified species closely resembles those of *lepta*, including the special type of 3Ax in hindwing (see fig. 115). The scale plate is short and the anal plate is long in the *Westia* species. As in *lepta*, CuA2 of the forewing is distally coalescent with CuP for approx. 0.8 times its length. Clench (1959: 223) places *Porthetes* as a member of the Melasinidae Clench and suggests that the Melasinidae are most closely related to the Psychidae. Robinson (1988: 120) places *Melasina* (s.s.) as a genus of the Psychidae. Fletcher & Nye (1982) erroneously reckon *Westia* as still belonging to the Cossidae.

Zyganisus Viette, 1951 is an objective replacement name for *Pseudocossus* Gaede, 1933, preoccupied by *Pseudocossus* Kenrick, 1914. Gaede (1933b: 811) proposes *Pseudocossus* for a new species *fulvicollis*. Gaede notes that the ♀ body has a special shape. Two specimens of *fulvicollis*, borrowed from the C.S.I.R.O. Division of Entomology (Canberra City, Australia), have been examined. The ♀ abdomen has indeed a special shape; it seems to be short and the tip is narrow. *Z. fulvicollis* most closely resembles superficially *Culama* species. Pre II is not antero-dorsally extended in *fulvicollis*, whereas it has an antero-dorsal process in most or all *Culama* species. *Z. fulvicollis* differs from most or all *Culama* species in the following details: upper pas diagonally over Pre II up to antero-dorsal corner of the latter, mesepimeron slightly lower, accessory plate II very narrow, and ♀ abdomen with narrow tip. *Z. fulvicollis* is otherwise very similar to *Culama*. See also under *Culama*. If the two are indeed separate genera, they are most probably sister-groups. The mesepimeron lacks a pale band. *Zyganisus* is here excluded from the Cossidae.



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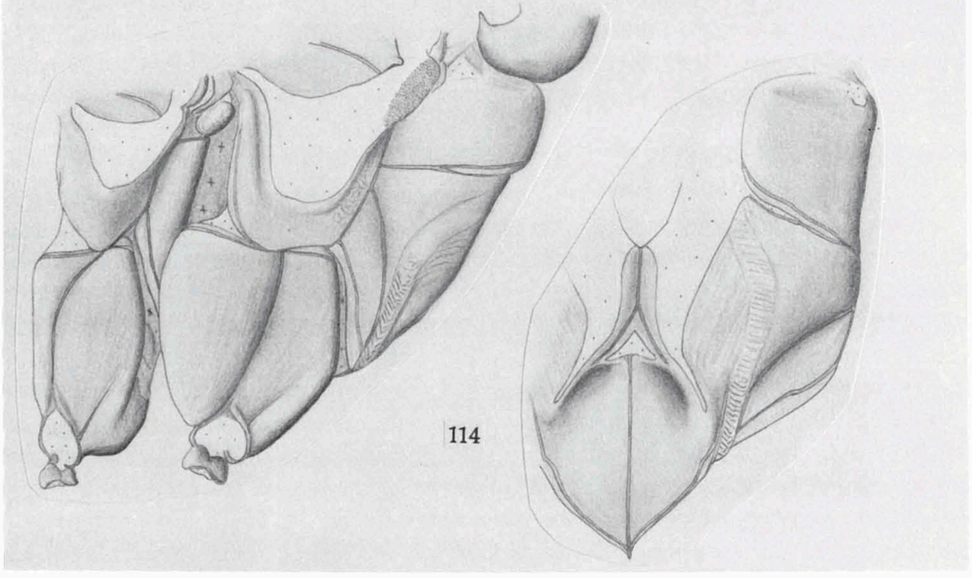


114

Figs. 113-114, sections of thoraces. 113, unidentified species of *Acrolophus* Poey, 1832, Brazil, La Soledad; 114, *"Cossus" lepta*, Indonesia, Sumatra.

Supposed close relationships of the Cossidae

Position of Cossoidea. – The group Ditrysia, to which the Cossoidea belong, had been for long more or less a jumble of superfamilies until the publication by Brock (1971), in which he distinguishes two main types of second abdominal sternite: a "tineoid" and "tortricoid" type (found in the Cossoidea). Kyrki (1983) redefines these types. Minet (1983) establishes the Apoditrysia for the taxa with the tortricoid type and points out that the remaining Ditrysia are the Tineoidea, Gelechioidea and Yponomeutoidea (including Glyphipterigidae Rebel, 1901). Minet (1986: 294) establishes the Obtectomera for the Apoditrysia without mobility of the first four abdominal segments of the pupa. Nielsen (1989: 288) provides a cladogram with an unsolved polytomy for the non-obtectomerous Apoditrysia: Cossoidea, Tortricoidea, Castinioidea Boisduval, [1828], Sesioidea Boisduval, 1828, Zygaenoidea Latreille, 1809, Immoidea Heppner, 1978, Urodoidea Kyrki, 1988, Schreckensteinioidea Fletcher, 1929, and Copromorphoidea Meyrick, 1905 (without Glyphipterigidae). Robinson (1988) shows that the superfamily Tineoidea (non-apoditrysian) consists of two lineages and suggests that the tineoid lineage (including Tineidae, Eriocottidae Nielsen, 1978, Acrolophidae Busck, 1912 and Psychidae) is the sister-group of the remaining Ditrysia. The gracillarioid lineage (including Bucculatricidae Borner, 1939, Gracillaridae Wocke, 1861 and Roeslerstammiidae Bruand, 1850) would form with the Yponomeutoidea Stephens, 1829 and Gelechioidea the remaining non-apoditrysian superfamilies. It is obscure, which of these three (non-apoditrysian) superfamilies is the sister-group of the Apoditrysia (including Cossoidea) (Nielsen, 1989). Minet (1988) believes that the non-obtectomerous Apoditrysia are most likely paraphyletic.

Nielsen (1989: 290) considers it pertinent to reassess the validity of the Obtectomera against other characters, since unambiguous assignment is difficult for several families. Brock (1971: 93-94) believes that "Obtectae" superfamilies have only "recently" reached obtect rank. Brock (1971) places the Bombycoidea (obtectomerous according to Nielsen, 1989) as the sister-group of the Cossoidea, because of a similarity in mesothoracic postphragma.

Brock (1971: 84) notes that three of the endophagous, ditrysian superfamilies (Sesioidea (as Aegeroidea, including Dudgeoneidae), Cossoidea, and Castnioidea) show an extremely high correlation of characteristics with the Tortricoidea (Tortricidae Latreille, [1802]). According to Brock, all three exhibit similarities in the structure of the metathoracic furca, the second abdominal sternite, and larval chaetotaxy, many of which characters have undoubtedly evolved within the spectrum of the Tineoid (sensu lato) complex. It is not clear what the similarity is in the metathoracic furca between the Cossoidea and Tortricoidea. Brock states that little can be said as to the lines of origin of the Sesioidea, Cossoidea, Castnioidea and Pyraloidea Latreille, 1809. According to Brock, these groups are best conceived as having originated on a common stem from an ancestral form related to the extant Tortricoidea, from which all have diverged to some extent.

Fracker (1915: 71) states that the larval strucure in the Tortricidae indicates rather close relationship with both Cossidae and Gelechioidea but is not relied upon, for all these groups are typical Microlepidoptera in most respects and may belong to wholly different but only slightly specialized stocks.

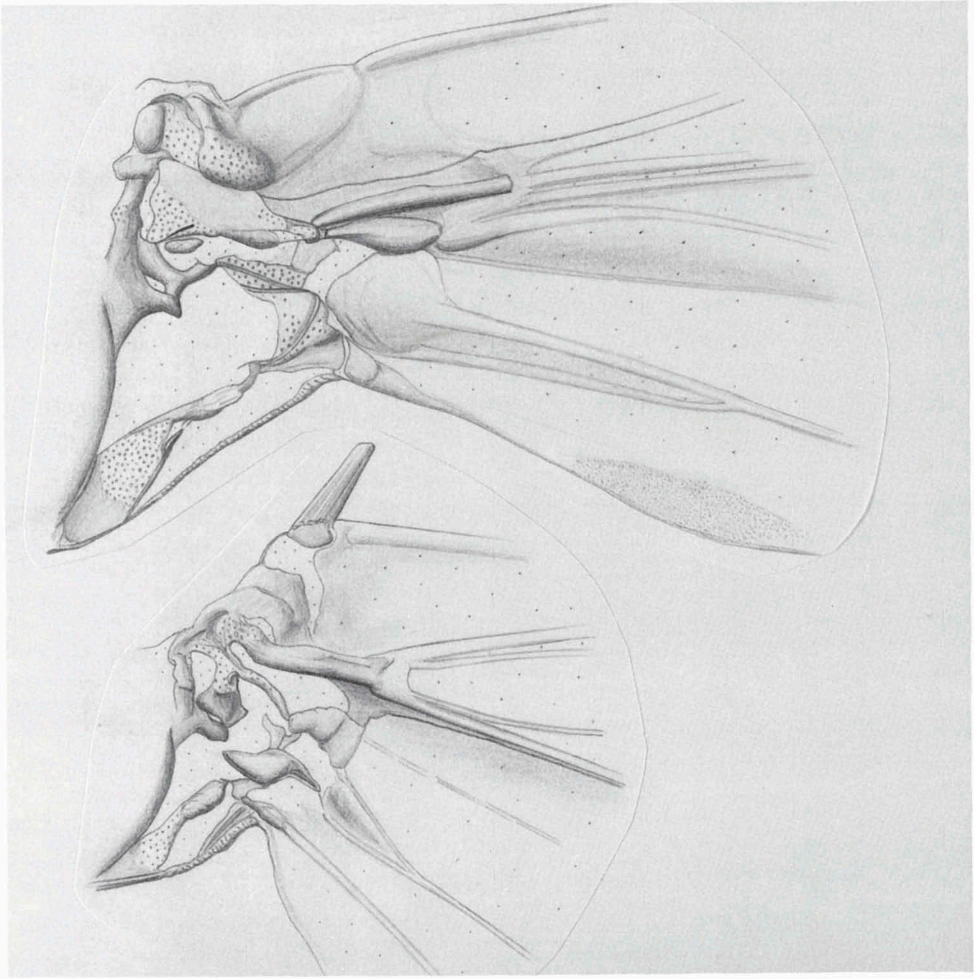


Fig. 125, wing bases of *"Cossus" lepta*, Indonesia, Sumatra.

Hessel (1969: 361) provides a cladogram with the Cossoidea, Hesperoidea Latreille, 1809, and Papilionoidea Latreille, [1802] on one branch separately from the other ditrysian superfamilies. Hessel based his cladogram on morphological data of the dorsal vessel. He found aortal polymorphism in the Cossidae. Hessel places the Megalopygidae Herrich-Schäffer, 1855 in the Zygaenoidea. In the Megalopygidae the aortal pattern is different from the types found in the Cossidae. Brock (1971) places the Megalopygidae in the Cossoidea. Minet (1988) considers the Hedyloidea, Hesperoidea and Papilionoidea a monophyletic group (thus without the Cossoidea) on the basis of the type of imaginal aorta. It thus seems that the aortal polymorphism within the Cossoidea is not so useful for elucidating their position.

Several authors suggested a close relationship between the Cossidae and Tortricidae (e.g. Forbes, 1923). Common (1970: 797) suggests that the Tortricidae may have been derived from cossoid stock, because of the resemblance in chaetotaxy and male genitalia. The genitalia and the larva of the Cossidae are seemingly just generalized primitive apoditrysian. There are several important differences between the Tortricidae and Cossidae. In the Tortricidae chaemosemata are present. In certain Tortricidae the maxillary palpi are four-segmented. According to Schultz (1914: 30, figs. 18-20), the Tortricina do not have a (distinct) pronotum. Unlike the more primitive Tortricoidea, the metathoracic furcal stem is always short in the Cossoidea (Brock, 1971: 56). The Tortricidae seem to be generally more primitive than the Cossidae in many respects: metascutum wide, Bs II rather triangular in shape and with short and shallow lateral grooves, mesepimeron rather triangular, mesomeron narrower than eucoxa II, metameron very narrow, midtibial spurs of hindleg at approx. half length of tibia, fifth tarsomere shorter than fourth, lateral process of posterior notal wing process in forewing shortly separate, and anal plate long (in many Tortricidae). It thus seems unlikely that the Tortricidae have been derived from cossoid stock, considering that the Cossidae are probably of the most primitive grade within the Cossoidea. I do not know good reasons to place the Tortricoidea as the sister-group of the Cossoidea.

It is thus still obscure which (non-obtectomerous apoditrysian) superfamily is the sister-group of the Cossoidea, if it is not the Bombycoidea.

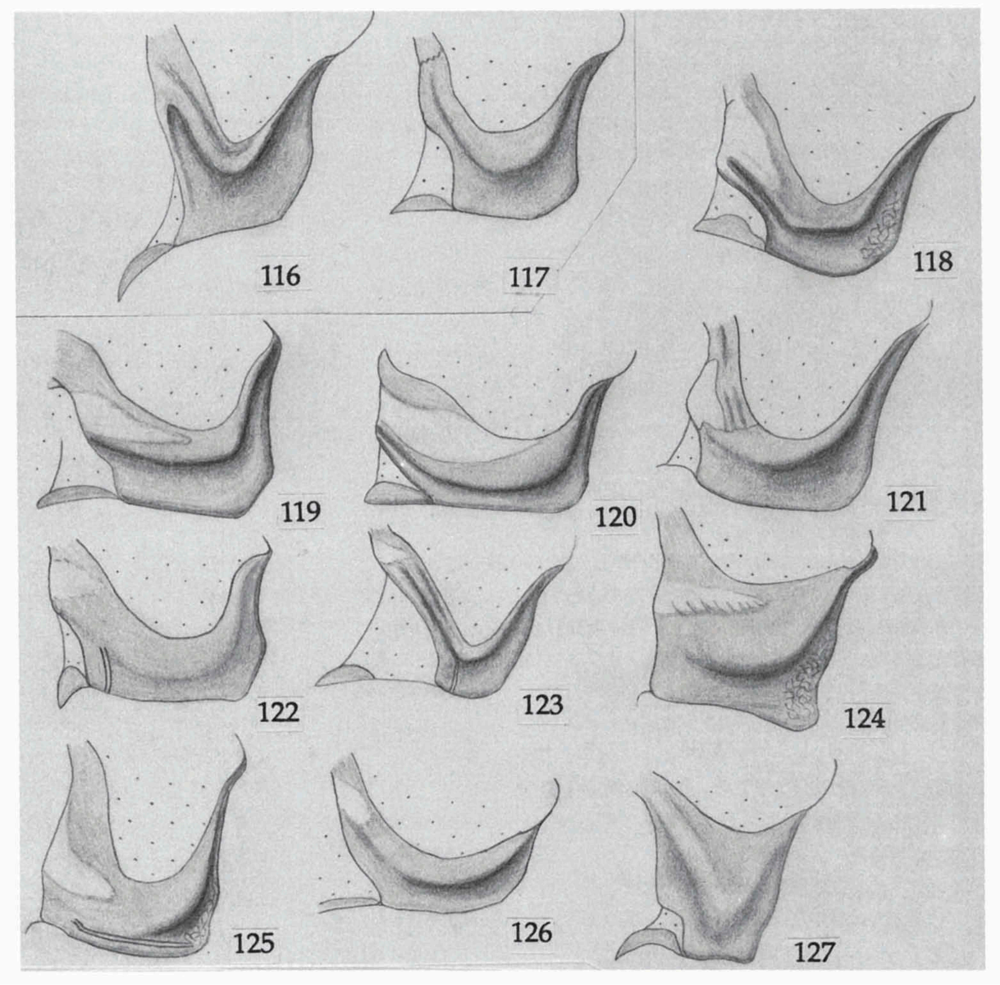
Cossoid families

The Cossidae had been placed in various (other) superfamilies, until Turner (1946: 338) includes them with the Metarbelidae in the Cossoidea. Most sound of the classifications of Cossoidea is that by Brock (1971), since he supports it by (syn)apomorphies.

Brock (1971) includes the Cossidae, Ratardidae, Metarbelidae, Megalopygidae, Dalceridae, Limacodidae and Chrysopolomidae in the Cossoidea. Brock (1971: 52) points out that the primary type of mesepimeron in the Cossoidea has a broad membranous area just ventrad to the fusion of the mesepimeron with the secondary arms of the mesothoracic furca (see figs. 118-126). This special area of the mesepimeron is normally paler than the rest of the mesepimeron and appears to be a different type of sclerotization. Brock thinks that it is highly likely that the absence of such a pale band, which occurs in few cossoid taxa, is secondary. Within the Cossidae this seems to be indeed the case. Brock did not find such a pale band in all other Ditrysia which he examined. Brock (1971: 54) notes that there is usually a deep fold along the line of fusion of the basisternum with the parepisternum in all cossoid families.

In the Cossoidea the tergal phragma of the dorsal thoraco-abdominal articulation has become sclerotized, lightly fusing across the frontal wall of the tergite (Brock, 1971: 55-56). According to Brock, this feature is a secondarily derived and found only in the Cossoidea. The mesothoracic postphragma shows a slightly special development in the cossoid families; it takes the form of a very deep emargination resulting in a distinctly bilobed contour (Brock, 1971: 53). According to Brock, this characteristic is unusual but also found in the Bombycoidea.

Common (1974: 104) points out that the Cyclotornidae Meyrick, 1912, of which Brock (1971) had not examined material, should also be included in the Cossoidea on the basis of Brock's diagnosis. Fletcher & Nye (1982: iii) include the Cyclotornidae in the Zygaenoidea, perhaps having overlooked Common's remark.



Figs. 116-127, mesepimerons of various species (no Cossidae) (aculeate areas not depicted). 116, *"Culama" treicleiota* (ex Cossidae); 117, *Idioses littleri* (ex Cossidae); 118, unidentified species of *Lebedodes* Holland (Metarbelidae); 119, *Melisomimas metallica* Hampson, 1914 (Metarbelidae); 120, *Saalmulleria stumpffii* (Metarbelidae); 121, *Ratarda furvivestita* Hampson (Ratardidae); 122, unidentified species of *Chilena* Walker, 1855 (Lasiocampidae); 123, *Sibine flora* (Schaus, 1911) (Limacodidae); 124, *Langucys bicolor* Möschler, 1883 (Megalopygidae); 125, *Dalcerina tijucana* Schaus, 1892 (Dalceridae); 126, *Cossodes lyonetii* (ex Cossidae); 127, *Ptilomacra senex* (ex Cossidae).

Minet (1986: 298) criticizes Brock's diagnosis and opines that only the Cossidae, including the Metarbelinae, should be included in the Cossoidea (see remarks in the notes on the taxonomic history). Minet (1986: 307) removes the Ratardidae from the Cossoidea to the Bombycoidea on the basis of the following characteristics: ocelli and galeae wanting, female antenna sometimes bipectinate (perhaps a ground-plan characteristic), frenulum absent, and midtibial spurs of hindleg wanting. Minet (1986: 307) regards these characteristics as synapomorphies. These apomorphies are also found within the Cossidae and could "easily" have occurred further within the Cossoidea. The present author believes that it would be better to include the Ratardidae in the Cossoidea, since Brock (1971) supports this idea with more sound evidence in my opinion.

Nielsen (1989: 289) notes that the Cossoidea, including Dudgeoneidae, are tentatively regarded as monophyletic, referring to Nielsen & Common (in press). Brock (1971: 35) includes the Dudgeoneidae in the Aegerioidea. Fletcher & Nye (1982: iii) places this family in the Sesioidea. Munroe (1988: 79) includes the Dudgeoneidae in the Pyraloidea and notes that the family includes one genus. The tympanic organs found in *Dudgeonea* are of the type found in some Pyralidae, according to Brock (1971: 82). This is probably why Munroe (1988) includes the family in the Pyraloidea. Perhaps that *Acritocera* should also be included in the Dudgeoneidae. In both *Acritocera* and *Dudgeonea,* at least two of the cossoid characteristics are absent: a pale band of the mesepimeron and a deep fold between basisternum II and parepisternum (see fig. 122). In combination with the presence of tympanic organs, this does not lend support to a classification of the family within the Cossoidea.

Relationships within Cossoidea

Of the families that Brock included in the Cossoidea, the Cossidae seem to be of the most primitive grade, particularly in their venation. It may well be that the family Metarbelidae is the sister-group of the Cossidae (see chapter with notes on taxonomic history, and the one on excluded and obscure taxa). If *Cossodes* (*lyonetii*) should indeed be included in the Metarbelidae, this genus is probably of the most primitive grade within Metarbelidae; in *lyonetii* the venation is also generalized primitive apoditrysian. Other important characteristics of *lyonetii* are: ocelli wanting, antenna in both sexes prismatic, I-epiphysis reaching much less far than tibia-tip, tibia and first tarsomere of hindleg partly swollen, fifth tarsomere approx. as long as fourth one, ♂ retinaculum with moderately short base, number of ♀ frenulum bristles approx. six and these moderately long, all radial veins of forewing separate or R4 shortly stalked with R5, Rs and M1 sometimes/often very shortly stalked, lateral process of posterior notal wing process in forewing mainly separate, median arm moderately long and moderately narrow, and anal plate moderately long. As in the Cossidae, the primary type of pronotum in the Metarbelidae is probably high. However, the states of the pronotum in other cossoid families are unknown. It is obscure how the rest of the cladogram of the Cossoidea should be depicted.

Additional notes

Several taxa originally established in the Cossidae more or less closely resemble the hypothetical archetype of the Cossidae but lack the cossoid type of mesepimeron. Of these taxa *Culama* seems to show the greatest similarity to the cossid archetype; in certain *Culama* species the pronotum is moderately high, the metascutum is moderately narrow, Bs II has deep lateral grooves, Pa partly overhangs Bs II, and accessory plate II is wide. *Culama* is more primitive than the cossid archetype in certain respects: mesomeron narrower than eucoxa II, and lateral process of posterior notal wing process in forewing shortly separate. Sections of the thorax of *Culama caliginosa* (Walker) are shown in fig. 110. An investigation of internal structures, such as the thoracic furcae and genitalia, is needed to obtain a better idea of the relationship of *Culama* with the Cossoidea. At present it is speculative to suggest that *Culama* is most closely related to the ancestral form of the Cossoidea.

It is not clear in which family or families many of the genera excluded from the

Cossidae, such as *Culama* and *Cossula*, should be placed. No distinctive (syn)-apomorphies of the external morphology could be found in most of them. It seems necessary to establish several new families for them and perhaps one or more superfamilies for these. A study of internal structures is needed to find characteristics for a justification to propose the new families. It might be that *Meharia*, *Aeonoxena* and *Meharia*, perhaps together with *Pseudurgis* and *Titanomis*, should be placed in one (new) family. At least in *Pseudurgis* the second abdominal sternite is of the "tortricoid" type. It also may be that *Archaeoses* and *Idioses*, perhaps together with *Ptilomacra*, *Culama* and *Cossula*, should be placed in another new family.

General discussion

Detailed comments are provided for individual subfamilies in the treatment above, and the significance of certain developments has been discussed. This chapter provides more general discussion.

A rather high mesepimeron (of the cossoid type) is considered an autapomorphy of the Cossidae. Within the family the mesepimeron is often lowered and occasionally heightened.

Characteristics of significance — in combination — of the hypothetical archetype of the Cossidae are probably: Pos at approx. half length of vertex, labial palpi three-segmented, maxillary palpi two-segmented, labrum without pilifers, galeae short, metascutum moderately narrow, upper Pas at approx. 0.4 or 0.5 times length of Pre II plus Pa, accessory plate II wide and moderately long, mesomeron approx. as wide as eucoxa II, tibia and first tarsomere of hindleg swollen, fifth tarsomere approx. as long as fourth, ♂ retinaculum with moderately long base, costal region of hindwing moderately wide and distinctly narrowing at approx. 0.6 or 0.7 times wing-length, R1 branching off at approx. 0.3 or 0.4 times wing-length, areole and inner cell present, all radial veins of forewing separate, CuA2 of forewing branching off at approx. 0.8 times length of CuA, 1Ax of forewing apically moderately small, lateral process of posterior notal wing process in forewing mainly separate, median arm rather long and (moderately) narrow, and anal plate rather long. See also chapter on the supposed plesiomorphies. Many of these characters vary within the Cossidae. Most of them could probably also be postulated in the archetype of the Metarbelidae.

Each of the subfamilies Pseudocossinae, Zeuzerinae and Hypoptinae appear to have many autapomorphies, of which several are more or less distinctive within the Cossidae. Many other apomorphies found in these taxa, such as loss of ocelli, are also found in other families. Many developments were found in more than one subfamily.

Developments of the external morphology which seemingly occurred independently in two or more subfamilies are: reduction of eye-size, widening of frons, disappearance of anterior protuberances of vertex, disappearance of ocelli, reduction of antennal rami, evolution of one or more stout sensilla on each ramus, reduction of labial palpi, lengthening of vestiture on labial palpi, lowering of An, posteriorly shortening of Bs II, disappearance of aculeate area at mesepimeron, change in height of upper margin of mesepimeron, narrowing of accessory plate II, widening of mesomeron, disappearance of intersclerite III, change in length of I-epiphysis, shortening of tibial spurs, reduction of tarsal spines, change in relative length of fifth tarsomere, reduction of arolium, reduction of paronychia, shortening of fringes, reduction of ♂ frenulum spine, reduction of ♂ retinaculum, shortening of ♀ frenulum bristles, increase in number of ♀ frenulum bristles, reduction of vestiture on wings, reduction of areole, reduction of forewing inner cell, stalking of radials, partial coalescence of CuP and A1+2 in forewing, evolution of Sc-Rs, elongation of anal region in hindwing, change in relative size of humeral plate, elongation of radial plate, lengthening of scale plate, enlargement of 1Ax apically, reduction of distal plate of forewing 4Ax, change in width and length of median arm, shortening of anal plate, reduction of anal tufts, lengthening of vestiture on body, and evolution of yellowish vestiture.

Most of the developments listed above are thus reductions in size of the structures. Several of the reductions are often complete, such as loss of arolium or paronychia. Many of these developments seem to have happened independently within other families. Lowering of An, widening of mesomeron, disappearance of intersclerite III, widening of metameron and shortening of anal plate seem to be more or less general trends amongst the Ditrysia. Although these developments seemingly occurred in various taxa, they appear to be very useful for the elucidation of the phylogeny within these taxa.

The significance of most developments listed above is obscure. It may well be that many reductions are due to loss of function.

Shortening of the I-epiphysis in the female only seemingly happened on several occasions within the Zeuzerinae and once within the Cossinae (*Lamellocossus terebra*). It is not clear why such a reduction is found particularly in the female.

In this study it appears that investigation of thoracic sclerites provides many useful data for the elucidation of phylogeny. The other characters of the external morphology alone are insufficient to assess relationships within the Cossidae. Within the Zeuzerinae there is much diversity amongst the characters of the thorax, and for several zeuzerine genera it appears possible to elucidate the phylogeny at the level of species using these. Within the Cossinae and Hypoptinae there appears to be less diversity amongst these characters, and for these two subfamilies a study of the genitalia is needed to improve the cladograms.

Considerable diversity amongst the characters of the thorax may perhaps be found in other ditrysian families. Amongst the sclerites of the lateral and ventral side of the thorax particularly the type of Bs II and the mesepimeron seem to be most useful in assessing relationships amongst higher Ditrysia. Amongst the characters of the wing bases the following characteristics seem to be most useful: the shape of the radial plate, the type of 4Ax in the forewing, the length along which the lateral process of the posterior notal wing process in the forewing is separate from the main process, the type of median arm, the shape of 3+4Ax in the hindwing, and the length of the anal plate.

There are two publications in which the phylogeny of the Cossidae is discussed. That by Turner (1918) is based mainly on wing venation. Turner erroneously includes *Cossodes* and *Dudgeonea* and regards these as two of the most primitive genera. According to Turner, *Ptilomacra* is not far removed from *Cossus* considering their types of venation. In the present paper *Ptilomacra* is excluded from the Cossidae.

Holcocerus and *Rethona* are closely related, according to Turner. These two genera both belong to the Cossinae, but no close relationship between them has been found in this study. Turner neglects too many genera to be able to give a right interpretation of relationships. Venation as a character alone appears to be far from sufficient to elucidate phylogeny amongst cossid genera.

Arora (1976: 146-149) discusses the phylogeny of the Indian Cossidae and provides a cladogram. Since Arora deals with only nine genera, it is not surprising that her cladogram shows many differences from the ones presented in this paper. For example *Azygophleps* and *Phragmataecia* are supposed to be sister-groups by Arora, whereas these genera are here placed in very different sections of the Zeuzerinae.

It seems that cossid larvae feed primarily in the trunks and/or branches of trees. Mining in the stem and roots of herbs is a secondary development. Only *Endoxyla leucomochla* is known to live as a larva outside the plant; this is also considered a secondary development. For many species, only one or two host species of economic importance are known, and other hosts are to be expected. The mining in several plant species from different families is known in a number of species: e.g., *Chilecomadia valdiviana, Paropta paradoxus, Cossus cossus,* several *Zeuzera* species, *Duomitus ceramicus, Trismelasmos maculatus*. It may well be that a wide host-tolerance is a plesiomorphy of the Cossidae.

Biogeography

Introduction – The following account concerns historical biogeography sensu de Lattin (1967: 18-20) and Wiley (1981: 278). The author's aim is to point out some interesting biogeographic details inferred from the cladograms in the light of what is known of biotic patterns and earth history. Corroborations by distribution patterns within other groups are not really analyzed, since this is not the aim here and there is a vivid discussion of the techniques proposed (cf. e.g., Ball, 1976; Nelson & Rosen, 1981; Platnick & Nelson, 1988; Myers & Giller, 1988: e.g. chapters 12-14; Rosen, 1988; Wiley, 1988a and 1988b; Cracraft, 1988; Sober, 1988; discussion of Brooks Parsimony Analysis forthcoming in Systematic Zoology). The author does not adhere to the progression rule (Hennig, 1966; see also explanations by Pielou, 1979 and Wiley, 1981). For critiques of this aprioristic principle see, for example, Howden (1972), Croizat et al. (1974), Ball (1976: 419-420, 426-427), and Nelson & Rosen (1981: e.g. chapter 3).

Underlying assumptions in this biogeographic account are: (1) the cladograms provided give the right picture of the phylogenetic hierarchy; (2) the speciations were allopatric; (3) both (eco)geographic vicariant events and dispersal played an important role in the history of the distribution patterns; (4) the dispersive power of Cossidae is at least moderate, as suggested by the distribution patterns of certain species in Malesia, often reaching as far east as the Solomon Islands; (5) an ancestral species had the same preference for climatic and vegetational conditions as its descendants and its closest, extant relatives, unless there is evidence to the contrary; (6) many cossids have a wide host plant tolerance and can adapt to other host-plants after dispersal (a number of cossids are known to mine in plants imported into their ranges, such as Coffee, Apple, Pear, and Groundnuts).

Gondwanaland

In the cladograms for the Zeuzerinae most continents of austral origin are involved. Fig. 128 shows a reduced area cladogram for *Aethalopteryx* (with *Strigocossus* and *Azygophleps*) and zeuzerine section 2. The sequence Africa-Indo-Malesia-Australia-Middle America is of particular interest. It would be simplest to explain this distribution type, shown in fig. 128, by postulating that the ancestral stock of *Aethalopteryx* and section 2 was distributed over Gondwanaland before the final breakup of East Gondwanaland. The fragmentation of East Gondwanaland is held responsible for some of the austral vicariances indicated.

The three areas from which *Relluna nurella* is known, viz. India, Burma and Borneo, are fragments of Gondwanaland (Audley-Charles, 1983, 1987). The absence of Australia in the sequence of *Phragmacossia*, section 1, *Aethalopteryx* and allied genera, and *Relluna* is taken as evidence that the ancestor of *Relluna* was present on the Indian part of Gondwanaland and not in the parts which broke away from the northern margin of the Australian region in the Jurassic (Audley-Charles, 1987). *R. nurella* would have (secondarily) spread into southeast Asia.

The occurrence of two *Endoxyla* species, viz. *celebesa* and *liturata*, outside Australia (respectively in Sulawesi and Tasmania) is secondary (by dispersal), judging from their character-states.

Furthermore, there is the link between Australia and America. The explanation above implies a former population or migration across Antarctica and thus a much milder climate and more luxurious vegetation in this region than at present. Fossil floras from Antarctica's borders suggest that much of this continent was covered with temperate (at least cool-temperate), evergreen forests from Early Tertiary until Early Miocene (Cracraft, 1973: 488-489; Raven & Axelrod, 1974: 620). A *Lystrosaurus* zone (Mesozoic reptile association) is known from Antarctica (Keast, 1971: 370). Many different groups are supposed to have inhabited or migrated across Antarctica (see below, and especially Brundin, 1966 and Gauld, 1983). Certainly not all of these groups are now confined to temperate regions.

The explanation above implies that the ancestral stock of *Hamilcara* and remaining genera of section 2 became extinct in most of South America. *Hamilcara, Carohamilia,* certain *Aramos* species and *Psychonoctua* would later have retracted in Middle America. It is assumed that the ancestor of the undescribed genus (represented in Kenya) reached Africa from (northeast) South America prior to the Palaeocene (in the Cretaceous), when a biotic interchange between these two continents was still possible.

The explanation of the vicariances is partially in concordance with what is known of the breakup sequence of Gondwanaland inferred from both geological and biological evidence (cf. Humphries, 1981b: fig. 12). For data on the fragmentation, reference can be made to Audley-Charles (1981, 1983 and 1987), Cracraft (1973; 1975), Crook (1981), Foster (1974), Howarth (1981), Keast (1971), Kennett et al. (1974), Owen (1976), Powell et al. (1981) and Tarling (1972). The breakup of Australia-Antarctica-South America cannot be held responsible for the speciation of the ancestral stock of *Sympycnodes* and *Hamilcara,* since both *Endoxyla* and *Sympycnodes* are represented in Australia. This breakup probably cannot be held responsible either for the speciation of the ancestral strock of *Hamilcara* and the other American taxa, regarding the occurrence of the undescribed genus in Africa (viz. Kenya); the final rupture between

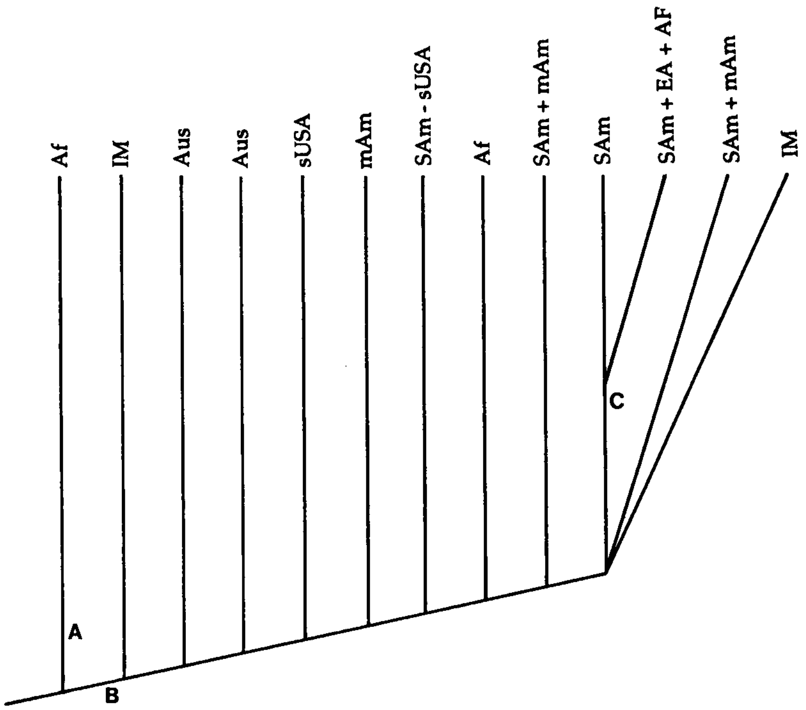


Fig. 138, reduced area cladogram derived from the phylogenetic hypothesis for the Zeuzerinae (in part); A = *Aethalopteryx, Strigocossus* and *Azygophleps*; B = section 2; C = section 2A; Af = Africa; Aus = Australia; EA = Eurasia; IM = Indo-Malesia; mAm = Middle America; SAm = South America; sUSA = southern U.S.A.

South America and Africa dates farther back than that between South America and Antarctica. There is thus concordance with at least the breakup sequence of Africa-(Antarctica)-India-Australia.

Two alternative hypotheses will be compared to the one suggested above. One may postulate that the ancestral stock of zeuzerine section 2 was distributed along the southern margin of Laurasia. This would require the following extra steps to explain the present-day vicariances: (1) dispersal into India, (2) twice waif dispersal into Australia, (3) a population distributed over a vast area or dispersal over long distances (enabling the vicariance between the Australian and Middle American groups), and (4) extinction in at least Europe and western Asia, or some of these steps combined with elements from the following scenario. If one postulates that the ancestral stock was present on the Indian fragment of Gondwanaland, this would require: (1) spreading over the mainland of Asia, (2) twice waif dispersal into Australia, (3) migration across Beringia, and (4) extinction in most of Asia. The advantageous implication of these two hypotheses is that a population or migration across Antarctica is not required. However, it would be more difficult to explain the occurrence of the undescribed genus in Africa. This would imply as extra steps: (1) (waif) dispersal across the wide ocean gap (with islands) between the American continents or from South America into Africa, or dispersal via a land bridge across the North Atlantic through Europe and across a land bridge into Africa with (2) subsequent extinction in North America and Europe. An advantage of the initial explanation is the partial concordance with the breakup sequence of Gondwanaland.

A search for corroboration by a biotic pattern leads to numerous publications. Surveys of taxa with austral disjunctions presumed to have derived from Gondwanan stocks are provided by several authors: e.g., Jeannel (1942: 195-217, 261-264) for Coleoptera in particular, Evans (1959: 158-159) for insects, Riek (1959: 255-257) for insects, Keast (1971: 355-357) for various groups, Cracraft (1973: e.g. 502) for birds, Raven & Axelrod (1974: 550-558) for vertebrates, Main (1981: 1068-1069) for invertebrates, Humphries (1981b: 199-204) for various groups, and Noonan (1985: 337) for Carabidae (Coleoptera). Most of these austral distributions do not involve India.

Among insects, putative examples of a Gondwanan distribution type which includes Africa and/or Madagascar, Australia and South America are known of: Notonemourinae (Plecoptera) (Illies 1965: e.g fig. 6), Podonominae and Diamesinae (Chironomidae) (with multiple transantarctic relations) (Brundin, 1966), certain taxa of Diptera (Paramonov, 1959: 187), and certain taxa of Coleoptera (Howden, 1981: 1027-1029).

Among insects, a Gondwanan distribution type including South America and Australia but not Africa is supposed for: several families of Ephemeroptera (Edmunds, 1972: 28, 30, 33), Nannochoristidae (Byers, 1973), several taxa of Trichoptera (Ross, 1967), Peloriidae (Homoptera) and Migadopini (Coleoptera: Carabidae) (Darlington, 1965), Idiostolidae (Hemiptera) (associated with *Nothofagus*) (Schaefer & Wilcox, 1969), *Neuquenaphis* and its sister-group *Sensoriaphis* (Aphidae) (both associated with *Nothofagus*) (Schlinger, 1974), Aphroteniinae (Chironomidae) (Brundin, 1966), Labeninae (Hymenoptera: Ichneumonidae) (with multiple transantarctic relations) (Gauld, 1983), Archiperlaria, Austroperlidae, Gripopterygidae and Penturoperlidae (Plecoptera) (Illies, 1960; 1965), and *Australosymmerus* s.l. (Diptera) (Munroe, 1974). All of these distributions presumably imply former population(s) in or migration across Antarctica.

Faunal and floral affinities are less marked between Africa and Australia than between South America and Australia (Evans, 1959: 162; Keast, 1968: 227). One reason for this is probably that the biotic interchange overland (via Antarctica) between South America and Australia was severed later than that between Africa and Australia.

Most faunal affinities between Australia and Africa and/or Madagascar seemingly exclude India (c.f. Raven & Axelrod, 1972: 1381; 1974: 553, 619), and there are no certain cases suggesting that Africa and Australia at one time exchanged vertebrates directly via Antarctica (Cracraft, 1975: 44). On the other hand, there are several examples of animal groups with austral distributions involving India but not Australia: e.g., certain dinosaurs, and the *Lystrosaurus* and *Cynognathus* zones (Mesozoic reptile associations) (see Keast, 1971: 353, 370), and Pelecidae (Coleoptera) (Jeannel, 1942: 299).

There seem to be only few animal groups with a (presumed) Gondwanan distribution including Africa, India and/or Sri Lanka and Australia: Sphaerotheriidae (Diplopoda) (Jeannel, 1942: 261, fig. 106), Acavidae (Mollusca) (Jeannel, 1942: 251-252), Leptophlebiidae (Ephemeroptera) (Peters & Edmunds, 1970; 1964), Ledrinae

(Cicadelloidea) (Evans, 1959: 155), and Phraetoicoidea (freshwater Crustacea) (Riek, 1959: 253). Of these taxa, only the Acavidae, Leptophlebiidae and Ledrinae are also known from South America. It is, however, not known if India comes directly in between Africa (or Madagascar) and Australia in the cladograms for these groups. In his reconstruction of the development of the Australasian insect fauna, Evans (1959, according to Keast, 1971) postulates an initial stratum of Indian origin and indicates that this stratum antedates an "Antarctican" one. Thus, the evidence of faunal links between India and Australia is meagre in extant groups.

Floral affinities tell a different story. Of the tropical Australasian plant species, nearly 500 (classified in 273 genera) are either identical with continental or with peninsular Indian species, and over half of these are also found in tropical Africa and sometimes in tropical America (Specht, 1981: 272). However, it remains uncertain which of these links have been directly derived from Gondwanan stocks. Fossils provide a better picture. The Triassic *Glossopteris-Gangamopteris* floras are known from all southern continents (see Darlington, 1965: 111; Keast, 1971). *Thinnfeldia (Discoidum) odontopteroides* is known in the Early Jurassic from Graham Land, southern Africa, Madagascar, Kerguelen, New Zealand and Norfolk Islands (Jeannel, 1942: 196). Mesozoic fossils of *Podocarpus* are known from India, Australia, New Zealand, Antarctica, and South America (Jardine & McKenzie, 1972: 24). Reference should be made to Dettmann (1981: 370-371) for Early Cretaceous floral links between Australia and India and in some cases also Patagonia.

In most of the presumed Gondwanan distributions, southern Africa and southern South America are involved. At least several of the groups concerned are not confined to the temperate regions of these continents. For example, *Australosymmerus* s.l. (Diptera) shows a morphological-chorological progression from Tierra del Fuego to Mexico (Munroe, 1974). The subfamily Ledrinae (Cicadelloidea) has its richest representation in India, and is also represented elsewhere in the Indo-Malesian Region (= Oriental Region), in Australia, southern and tropical Africa, and in central America, with derivatives in North and South America, and in Europe (one representative) (Evans, 1959: 155). The pulmonate family Charopidae (Mollusca) with an austral distribution is also represented in North America (van Bruggen, 1980: 219, fig..2). The monotypic genera *Merope*, represented in eastern U.S.A., and *Australomerope*, represented in Australia (Perth), of the Meropeidae (Mecoptera) are also supposed by Byers (1973) to be derivatives of a Gondwanan stock. The three monotypic genera of the Bittacidae (Mecoptera) are known from respectively Australia, Chile and California. The pleistocene glaciations in southern South America may have been responsible for the extinction of certain groups derived from a Gondwanan stock in this region.

The occurrence of *Hamilcara* (Cossidae) and most closely related genera in respectively southern U.S.A., Middle America and northern South America can be explained by assuming that these genera have derived from a South American stock and that a number of their species retracted later in more northern areas. Raven & Axelrod (1974: 626) state that for most groups (e.g., plants, fishes, amphibians, reptiles, birds, insects) tropical North America (including Central America and West Indies) has been populated mainly by a biota that evolved in isolation in South America. This picture seems to be corroborated by distribution patterns among the Hypoptinae. Most hypoptine species occur in South America and certain derivatives are endemic to Middle America or southern U.S.A. (see also fig. 105). The mayfly (Mecoptera) fauna of the West Indies is Neotropical in origin (Peters, 1988: 20). It thus is not unreasonable to presume that *Hamilcara* and allies are Neotropical in origin. *Hamilcara* is thought to have a relict distribution (in Arizona).

Faunal links between South America and Africa independent of East Gondwanaland include taxa of many groups: e.g., certain freshwater fish taxa (Ostariophysi) and in particular characids and their parasites (Lowe & McConnell, 1975: 17; Robert, 1972: 117; Novacek & Marshall, 1976), trigoniid molluscs and nonmarine ostracods (see Cracraft, 1973: 467), certain caecilians (Amphibia) (Estes & Wake, 1972; Estes & Reig, 1973: 46; Estes, 1976), Gekkonidae (see Raven & Axelrod, 1974: 553), a few mammals (Thenius, 1980: 55), Trichoptera (Ross, 1967: 195), various coleopteran families (Jeannel, 1942: 304, 346-347; Noonan, 1985), Baetidae (Ephemeroptera) (Edmunds, 1972: 28). Raven & Axelrod (1974: 603-604) and Wolfe (1981) discuss floral links between the two continents.

By the Palaeocene, Africa and South America were separated by a gap of approx. 800 km with volcanic islands that aided east-west and west-east dispersal of tropical taxa (Raven & Axelrod, 1974: 635). Migration across the Atlantic between these continents in the Eocene, Oligocene or Early Miocene is presumed for a few taxa from various plant families, but a general exchange of floral elements is definitely not visible in the Tertiary palynological record (Germeraad et al., 1968: 276-284). Therefore, the author supposes that the ancestor of the undescribed zeuzerine genus reached Africa prior to the Palaeocene.

Some examples of exclusive affinities between South or Middle America and Madagascar are found among Coleoptera (see Jeannel, 1942: 346-347; Noonan, 1985: 335-337). For example, numerous species of *Syrbatus* (Coleoptera: Pselaphidae) occur in South America, some in North America, some in Mashonaland (Zimbabwe) and three on Mt. Kilimanjaro. The link between northern South America and Kenya within zeuzerine section 2 is thus not surprising.

While searching for corroborating biotic patterns, the lack of cladograms in most of the literature is a serious problem. Humphries (1981b: 199-204) provides a survey of the known (reduced) cladograms with austral disjunctions. The pattern Africa+(Australia+South America) is found in the cladograms of *Drimys* (Winteraceae), Gevuineae (tribe of Proteaceae), Macadamiae (tribe of Proteaceae) (Humphries, 1981b: fig. 17B), and Podominae and Diamesinae (Chironomidae) (see Brundin, 1966, and Humphries & Parenti, 1986: fig. 4.7). The pattern Madagascar+(Australia+South America) is found in the one for *Leptocarpus* with *Calopsis* (see Humphries, 1981b: fig. 17C).

Summarizing, there are partial corroborations among other groups for the initial explanation (for zeuzerine section 2). These corroborations and the partial concordance with the breakup sequence of Gondwanaland make an explanation postulating random dispersal less plausible. The main deviation from a palaeantarctic distribution pattern is that South America is absent in the sequence. This is also known in another group presumed to have derived from a Gondwanan stock, viz. Meropidae (Mecoptera). The two alternative hypotheses discussed, which seem to be the most reasonable among the alternative ones, require more steps of explanation and are therefore regarded as less acceptable.

The view preferred is that the ancestral stock of zeuzerine section 2 and *Aetha-*

lopteryx was distributed over Gondwanaland in the Early Cretaceous. The fragmentation of this supercontinent is held responsible for the vicariances between Africa, India, and Australia.

The hypothesis could be falsified by refutation of the (part of the) phylogeny upon which it is based, or by discovery of fossils of certain taxa of inappropriate date in Laurasia. A similar distribution pattern attendant on good evidence of a Laurasian stock would also make the explanation less plausible.

A deduced consequence of the explanation concerning the distribution of the Zeuzerinae is that the clade Apoditrysia dates back as far as at least the Early Cretaceous. There seems to be no fossil evidence in support of this. The superfamily Papilionoidea (Apoditrysia: Obtectomera) dates back as far as at least the Middle Eocene (see Tindale, 1981). The oldest lepidopteran fossils so far known seem to be those of one or two undescribed species and *Eoses triassica* of the Late Trias (see Tindale, 1981), although several authors (see e.g. Hennig, 1981: 410-411) ascribe *Eoses* to the Mecoptera. Definitely lepidopteran fossils (presumably belonging to the Zeugloptera, and an unidentified larva) are known from the Early Cretaceous (see Hennig, 1981: 412-413; Tindale, 1981: 968-969).

Another consequence of the explanation given is that Gondwanan distributions should be found for more pre-apoditrysian and possibly other apoditrysian taxa. Tindale (1981: 970) suggests that certain hepialid (Neolepidoptera: Exoporia) and castnioid taxa (Apoditrysia) show the Australia-South America link in their present distributions. Jeannel (1942: 254-255) suggests that the Castniidae had a Gondwanan distribution. This family is represented in South and Middle America, South Africa, Madagascar, Burma, Singapore, the Philippines and Australia (see Strand, 1930, 1933, 1940). However, no cladograms of these groups are available. Holloway (1984: 139-141) points out that certain vicariances within the Oenochrominae (Lepidoptera: Apoditrysia: Obtectomera: Geometridae) may date from the Early Cretaceous. However, there does not seem to be an actual Australian group within this geometrid taxon. The author is unaware of other supposedly Gondwanan distributions among Lepidoptera.

The occurrence of certain *Phragmacossia* species (Zeuzerinae) in India and Sri Lanka, while section 1 is restricted to Africa, may be an indication of an earlier distribution of this genus on the Indian part of Gondwanaland, as the eastern vicariant of section 1. There is no evidence of an earlier or original occurrence of the Hypoptinae and Pseudocossinae in the Northern Hemisphere. The subfamily Hypoptinae may be regarded as the western vicariant of the ancestral stock of the Pseudocossinae and Zeuzerinae. The present cladograms for the Cossinae give too little insight for an inference of the original distribution in the Early Cretaceous. The Chilecomadiinae, only known from southern South America, have an association with *Nothofagus* (forests as habitat, and in some cases also the plants as hosts). *Nothofagus* probably had a Gondwanan distribution (cf. e.g. Humphries, 1981a and 1981b). This association between the moths and the plants may thus date back as far as the Cretaceous.

Beringia

Considering the cladograms, the ancestral species/stocks of the following taxa may be supposed to have migrated across Beringia: (1) *Acossus* and *Prionoxystus*; (2) *Comadia*; (3) *Xyleutes* and remaining genera of zeuzerine section 2 (except *Morpheis*);

(4) *Panau, Duomitus, Skeletophyllon* and *Trismelasmos.* The possibility that the vicariance between *Paracossus* in Indo-Malesia and the group of *Fania, Toronia, Psychidocossus* and *Miacora* in America has been derived from a Laurasian stock cannot be excluded at present. The expansion of the ancestral species of *Panau* resulting in a distribution of this genus in southeast Asia was perhaps separate from the one by the ancestral stock of *Duomitus, Skeletophyllon* and *Trismelasmos.*

Since the branching off of the initial Asian taxa in the phylogeny of zeuzerine section 2 is at approx. the same height, it may be supposed that the expansion of their ancestors took place via the same route. Expansion by way of Beringia is regarded as the most parsimonious explanation. Postulating expansion via a North Atlantic land bridge would imply extinction in Europe and western Asia as an extra step. Assuming a route via (western) Africa would imply extinction in Africa without good reason, such as loss of tropical climate. Therefore, it is suggested that the concerning stocks invaded North America (see paragraph on Panama Isthmus), expanded their ranges to the north, subsequently spread across Beringia and eventually invaded Asia. Progressive climatic deterioration would have pushed the populations to the south and caused extinction in North America.

Migration across Beringia is supposed for many taxa of: e.g., birds (Mayr, 1946: e.g. table 1; Cracraft, 1973: 531-533), (nonvolant) mammals (Simpson, 1947; Kurtén, 1971), Dugesiidae (freshwater Planaria) (Ball, 1976), Carabidae (Coleoptera) (Ball, 1963; Ball & Negre, 1972; Goulet, 1983; Kavanaugh, 1988), Cerambycidae (Coleoptera) (Linsley, 1963), Trichoptera (Ross, 1967), Ephemeroptera (Peters & Edmunds, 1970; Peters, 1988), Mecoptera (Byers, 1988), Plecoptera (Hynes, 1988), Psylloidea (Hodkinson, 1980), Odontiinae (Lepidoptera: Pyralidae) (Munroe, 1975), Noctuidae (Lepidoptera) (Lafontaine & Wood, 1988), Fanniinae (Diptera: Muscidae) (Chilcott, 1960), Chrysolampinae (Hymenoptera: Chalcidoidea) (Darling, 1986). In most cases, these migrations are supposed to have happened in several waves, in view of the different climatic preferences and diversifications within the groups. For data on the past geology, climates and vegetations of Beringia and its neighbourhoods, reference should be made to Hopkins (1967), Wolfe (1978; 1980) and Matthews (1980).

The first wave of cossid migration would concern the ancestral stock of *Xyleutes* and following taxa of section 2 and that/those of *Panau, Duomitus, Skeletophyllon* and *Trismelasmos.* These taxa and their close allies are tropical with most probably a preference for (rain) forest. Subtropical to tropical forests occurred near the land bridge during the Palaeocene (Wolfe, 1980: 315-316; Matthews, 1980), and a boreotropical flora was certainly present in Beringia during the middle Eocene (Wolfe, 1980: 318). The mid-Eocene entomofauna of lowland areas in Canada was undoubtedly tropical to subtropical in character (Matthews, 1980: 1098). The climatic deterioration at the end of the Eocene resulted in a major vegetation shift (Wolfe, 1980: 318). Large regions of the Northern Hemisphere were, for the first time, occupied by microthermal broad-leaved deciduous forest (Wolfe, 1980: 318). This initial wave of migration thus probably happened in the Palaeocene or more probably in the Eocene prior to climatic deterioration.

There is some dispute approx. the pan-pacific distributions of plants. Van Steenis (1963) provides a list of entirely or mainly pantropical plant families, and discusses seven categories of explanations of these distributions. Smith (1963) believes that the Beringian and Antarctican pathways suffice in this. According to Wolfe (1980), tropical plants with Old World affinities moved via Beringia into North America. MacGinitie (1969: 64) provides a list of Asiatic plant elements supposed to have dispersed across Beringia in the Early Tertiary. Melville (1981) disputes the role of Beringia in plant migration around the Pacific, and he and Humphries & Parenti (1986) are tempted to explain these distributions by involving a "Pacifica" continent. Haugh (1981) explains (convincingly in my opinion) that the assumption of such a Pacifica" is naive in terms of the known geology of the American regions. In the case of the cossids, the theory of Pacifica cannot account for the pan-pacific distributions.

Among animals, there seem to be few (good) examples of tropical taxa presumed to have migrated across Beringia. The vicariance between *Penichrolucanus* (Coleoptera: Lucanidae) (present in tropical Asia) and *Brasilucanus* (in tropical South America) is probably the result of a spreading across Beringia in the Early Tertiary (cf. Ratcliffe, 1984). The turtle genus *Geoemyda* (Chelonia: Testudinidae) is known from tropical America and Indo-Malesia (Dunn, 1931: 109-111; Simpson, 1943: 419). The Bering route was probably a major dispersal corridor for the primitive oscines (Aves) that eventually gave rise to the New World oscine radiations (Cracraft, 1973: 501). The Eocene to Pliocene Eogruidae (Aves) of Asia were probably derived from a North American ancestor (Cracraft, 1973: 501). Other pantropical elements among (extant) land birds in America are the trogons (Trogonidae), parrots (Psittacidae), and the barbets (Capitonidae) (Mayr, 1946: 16). Some New World and Asian trogons are found in temperate montane zones, and they are thus not typically tropical elements. Furthermore, Eocene trogons are known from France (Mayr, 1946). Trogons thus may have spread across a North Atlantic land bridge. The parrots may be derivatives of a Gondwanan stock (see Cracraft, 1973: 508-509). The degree of difference between their DNA's indicate that the African barbets last shared an ancestor with the New World barbets approx. 55 Ma (Sibley & Ahlquist, 1986). This was thus in the Palaeocene and in this era there was no direct floral interchange anymore between Africa and South America (Germeraad et al., 1968). Another interesting case among birds is the range of *Picumnus*. This genus has 25-30 species in tropical America and one species in southern and southeast Asia (see Short, 1973: 265-268; Platnick & Nelson, 1988: 415). It thus seems that a *Picumnus* species spread across Beringia. Among the primarily freshwater birds, the pantropical elements are seemingly not good indicators of migration across Beringia (cf. Mayr, 1946: 15-16). According to Simpson (1947: e.g. 651), there is no evidence from the mammals that any truly tropical or subtropical animal ever migrated across Beringia after the Early Eocene. However, Cracraft (1973: 501) points out that our knowledge of the Early Tertiary mammals (mostly extinct groups) is probably not sufficient to make this claim. Tapirs (Perissodactyla) are the only extant mammals found exclusively in the Asian and American tropics. Pliocene and later tapirs (*Tapirus*) are known from Eurasia and North America (see e.g. Kurtén, 1971: 138), but it is not certain how far back this genus dates.

Evidence of exchange of tropical biota(s) across Beringia is thus meagre at present. This seems at least partly due to the lack of cladograms for taxa of interest. Mammal fossils suggest that Beringia was a corridor rather than a filter (sensu Simpson, 1940) in the Early Eocene (Simpson, 1947). It is still questionable whether Beringia was also a corridor for tropical taxa for a sufficiently long time.

The ancestor of *Comadia* would have had a preference for warm temperate to subtropical conditions, judging by the present-day ranges of this genus and its close allies. The conditions in Beringia were probably favourable for this ancestor prior to the Miocene but not during the Middle Eocene (cf. Wolfe, 1980; Matthews, 1980). It seems likely, from the present ranges of its allies, that it was an open country element. The first major wave of open country elements across Beringia was probably in the Late Eocene, and open formations became widespread in North America thereafter (Webb, 1977: 359, 362). Ranges that are more or less similar to those of *Comadia* and close allies are found among the Odontiinae (Lepidoptera: Pyralidae) (cf. Munroe, 1975).

Acossus, Prionoxystus and *Lamellocossus* have their ranges mainly in the cool- to warm-temperate regions, and their species probably have a preference for forest. The ancestor of *Acossus* and *Prionoxystus* would have crossed Beringia between the middle Eocene and Pleistocene.

Examples of warm-adapted but not tropical taxa presumed to have crossed Beringia are found among: Aves (Mayr, 1946), Trichoptera (Ross, 1967), Mecoptera (Byers, 1988), Psylloidea (Hodkinson, 1980), and Pyralidae (Lepidoptera) (Munroe, 1975). Evidence of cool-temperate biotic interchange via Beringia is great, and is found among most of the various non-cossid groups listed above in this paragraph.

Panama Isthmus

Among the Cossidae, the following taxa or their ancestors presumably spread from South to Central or North America or vice versa: one or more *Miacora* species, *Hamilcara, Carohamilia,* certain *Aramos* species, *Psychonoctua, Voousia punctifera, Morpheis cognata, M. clenchi, Brypoctia strigifer,* several hypoptine taxa, the ancestor of *Xyleutes* and the remaining genera of section 2A (except *Morpheis*), and the ancestor(s) of *Panau, Duomitus, Skeletophyllon* and *Trismelasmos*. Only the *Miacora* species probably migrated from North to South America.

The two Americas were widely separated by an ocean gap scattered with islands during the Cretaceous and most of the Tertiary (see Raven & Axelrod, 1974: 544-549; Pielou, 1979: 34-35; Matthews, 1980; Adams, 1981). There is now general agreement that a land bridge between the two continents came into existence in the Pliocene, but there is still controversy about the exact date (cf. e.g., Webb, 1978a; Pielou, 1979: 34-35; Matthews, 1980; Adams, 1981). The oldest date inferred from marine fossils is around 5.7 Ma (cf. Emiliani et al., 1972). A number of taxa must have at this stage already crossed the ocean gap by island hopping. An increase in mammalian interchange is noticeable between 3 and 1 Ma (Whitmore & Stewart, 1965; Webb, 1976; Marshall et al., 1979; Marshall et al., 1982; cf. Marshall & Knecht, 1978, and Webb, 1978b). Webb (1978a) discusses the probable environmental types of the land bridge and its neighbourhood.

There is overwhelming evidence of biotic interchange between the Americas. It has been reported by Raven & Axelrod (1974; 1975) for plants, by Mayr (1946: 25-27) and Cracraft (1975: 519-521) for birds, by Marshall et al. (1979) for various terrestrial vertebrates, and by Webb (1976; cf. Simpson, 1940) for mammals. Most of the data probably concerns interchange in the Pliocene or later. Fossils suggest that raccoons and their allies (Procyonids), megalonychids and mylodontids (ground sloths), and sigmodontinids (cricetid rodents) had crossed the ocean gap in the Miocene (Marshall et al., 1979: 277). Certain hylid frogs presumably crossed in the Oligocene (Raven & Axelrod, 1975: 425). Certain taxa of Carabidae (Coleoptera) are supposed to have crossed in the Oligocene or Miocene (Noonan, 1985).

For most cossid migrations from one American continent to the other, an overland expansion in the Pliocene is probably sufficient explanation. However, for the ancestor of *Xyleutes* and the one(s) of *Panau, Duomitus, Skeletophyllon* and *Trismelasmos*, which are considered Neotropical in origin (see paragraph on Gondwanaland), a much earlier crossing (oversea) would have happened, since these taxa probably migrated across Beringia prior to the end of the Eocene (see paragraph on Beringia). Therefore, these zeuzerine ancestors would have invaded North America in the Late Cretaceous, Palaeocene or Eocene by island hopping.

A Late Mesozoic or Early Cenozoic migration (waif dispersal) from one to the other American continent is presumed for a considerable number of taxa. Raven & Axelrod (1974) provide a list of Angiosperm taxa which are supposed to be primarily Neotropical elements and of which Late Palaeocene and Eocene fossils are known from North America. Other fossils suggest an early crossing of: teiid lizards in the Late Cretaceous and iguanid lizards in the Eocene, toads of the genus *Bufo* in the Eocene (Raven & Axelrod, 1974: 553-554; 1975: 425), a *Testudo* species (Chelonia: Testudinidae) in the Early Tertiary (Simpson, 1943: 420), aniliid and boid snakes (see Webb, 1978a), and certain mammals (see Raven & Axelrod, 1975: 425; Webb, 1978a: 394). From observed diversification, such an early dispersal is presumed to have happened for: many taxa of the Trichoptera (Ross, 1967), *Bittacus* (Mecoptera: Bittacidae) (Byers, 1988: 28), and among birds at least the Icteridae (Mayr, 1946: 23-27). Considering these data, it is not surprising that certain cossids, which presumably have a much greater vagility than many of the taxa mentioned, would also have made this journey.

Peninsular Arabia

Considering the cladograms and the ranges, a number of cossid taxa have probably invaded the Afrotropics from Asia or vice versa. Among the Cossinae, the ancestors of the following taxa may have done so: (1) *Rethona*; (2) *Lamellocossus, Acossus* and *Prionoxystus* or the ancestor of section 1 (but it is possible that the migration took place through Europe); (3) the two undescribed genera and *Hirtocossus* (section 2); (4) *Planctogystia, Brachylia* and *Coryphodema*. A problem with most of the vicariances within the Cossinae is that the possibility of the fragmentation of Gondwanaland (Africa-India) as their cause cannot be excluded at present. Among the Zeuzerinae, the ancestors of the following clades presumably crossed Arabia: (1) *Alophonotus* (into Afrotropics); (2) *Pseudozeuzera, Paralophonotus* and *Eulophonotus* (into Afrotropics); (3) *Zeuzera, Hermophyllon, Cecryphalus* and *Tarsozeuzera* (into Asia); (4) the two undescribed *Tarsozeuzera* species (into Afrotropics); (5) *Azygophleps pusilla* and (possibly separately) *A. scalaris*. From the present ranges, the ancestor of both *Azygophleps regia* and *albofasciata* may have followed a more northern route across Arabia than the others. The other invasions presumably took place through the southern half of the Arabian peninsula.

What is now known as Peninsular Arabia was part of the African continent and had various shapes during the Mesozoic and Palaeogene (see Howarth, 1981; Adams, 1981). A temporary disconnection of the strait separating Arabia from Asia may have happened (as early as) in the Oligocene (Adams, 1981). The final disconnection of the Mediterranean from the Indian Ocean took place in the Burdigalian (19-14.5 Ma) (Adams, 1981). During the middle Eocene the Persian Gulf was shorter than at present and the Red Sea was closed at its southern end, but open to the north (Adams, 1981). The Red Sea was open to the south and closed at its northern end since Early Pliocene (Adams, 1981). In the Late Pliocene the Red Sea, and probably also the Persian Gulf, had attained their present shape (Adams, 1981). The lowering of the ocean level during the Glacial Periods has certainly affected (temporarily) the shape of the Persian Gulf, possibly almost eliminating it. The Red Sea and Suez Isthmus have always been narrow (Moreau, 1952).

There was thus opportunity for direct biotic interchange overland between Asia and Africa during the Miocene (from the Burdigalian onward) and possibly temporarily in the Oligocene. In the Pliocene the faunal route overland was across the Suez Isthmus and ran against the Saharan desert to the south. The narrow gap formed by the Red Sea would not have been an unassailable barrier for mammals (cf. Cooke, 1968), and most probably also not for flying animals, such as birds and moths.

The Miocene vegetation of East Africa would certainly have affected further dispersal of invaders into Africa. No fossil flora is known from the Horn of Africa. Data on vegetation in eastern Africa during the Miocene and Pleistocene are provided by Hamilton (1974). Miocene floras of East Africa suggest that both forest and savanna existed then in this region. A surprising feature of the Miocene plant species is that many are referable to present day East Africa. The Miocene mammalian fauna of Kenya includes both savanna and evergreen-forest types (Moreau, 1952: 881). Fossils and other data suggest that the climate of lowland East Africa was tropical during the Miocene (Hamilton, 1974: 206).

In the Red Sea area the climate seems to have been hot and dry with minor, temporary ameliorations (lowering in temperatures and increase in humidity) throughout post-Miocene times (see Moreau, 1952: 882). The climate of the southern part of the Arabian Peninsula is likely to have resembled that of the Horn of Africa, which was probably never better than semi-arid at any time during the Pleistocene (see Moreau, 1966: 114). The mountain masses of Yemen and Gebel Akhdar and the elevated, southern rim may have had a savanna-like vegetation during humid periods in the Pleistocene and Neolithic (around 6000 Ma) (Moreau, 1966: 114, 117). There are evidences of two major pluvial periods in Yemen, which were equated with the Kamasian and Gamblian in East Africa (see Ripley, 1954: 243).

There are strong floral and faunal affinities between the Afrotropical Region and the Palaearctic and/or Indo-Malesian Region. Some of these may date back as far as the Cretaceous (cf. e.g. Mani, 1974). Part of the interchange between Africa and Asia took place via Europe. For taxa from various groups migration is supposed to have taken place across Arabia (see e.g., Edmunds, 1972: 39; Lowe-McConnell, 1975; Novacek & Marshall, 1976; Sibley & Ahlquist, 1986).

Mammal fossils suggest that a limited number of taxa migrated across Arabia, particularly in the Late Miocene and Late Pliocene (Cooke, 1968: 245-257). According to Cooke (1968: 257), the connection(s) must have been filter bridges or sweepstake routes (sensu Simpson, 1940), since apparently the mammal faunas as a whole did not become deeply involved in the interchange. Fossils suggest that hominids and gomphoteriids (Cooke, 1968: 245-257), and also proboscids and cricetid mice (Kingdon, 1971: 57) had migrated out of Africa in the Late Oligocene.

Post-Miocene invasions into the Afrotropical (= Ethiopian) Region from Eurasia or vice versa must have happened during several periods and along various routes (see Moreau, 1966; de Jong, 1976, 1978).

In view of the diversifications, any cossine migration would have happened prior to the Pleistocene, if they took place. Migration by the ancestor(s) of *A. pusilla* and *scalaris* would have been recent, in the Pleistocene or possibly in the Pliocene, as there is no morphological difference between *scalaris* specimens from Asia and those from Africa. The same applies to the invasions into Peninsular Arabia by *Aethalopteryx pindarus* and *Azygophleps inclusa*. In view of the diversifications, the other zeuzerine migrations were probably earlier.

Judging from the ranges of the close allies of the first four listed zeuzerine invaders (see above in this paragraph), these invaders had a preference for tropical forest.

According to Moreau (1952-1966), a forest connection probably never existed across Arabia and the Horn of Africa in the Pleistocene. Moreau (1952: 905) finds it difficult to imagine how any extensive interchange of forest elements could have taken place across Arabia.

Some Miocene plants from Mount Elgon (Kenya) have features referable to the Dipterocarpoidea (Hamilton, 1974: 191). Today, members of this group are characteristic trees of the southeast Asian forests and are entirely absent from Africa (Hamilton, 1974). This may support the idea of a forest connection across Arabia in or prior to the Miocene, but these dipterocarpoids may also be derivatives from a Gondwanan stock in Africa.

De Beaufort (1951: 92) notes the following vicariances among mammals as evidence of a forest connection: *Hyemoschus* in western Africa and *Tragulus* (chevrotains) in the woods of Indo-Malesia; the pottos (*Perodictius*) and *Arctocebus* in western Africa and the slender and slow lorises (*Loris* and *Nycticebus*, Lorisinae) in Indo-Malesia; the guereza (*Colobus*, monkeys) in Africa and the South Asiatic langur (*Presbytes*); and the forest-dwelling porcupines of the genus *Atherurus* in western Africa as well as in Indo-Malesia.

Among birds, none of the species common to tropical Africa and India (not including its Palaearctic zone in the north and the higher montane areas) is a forest element (Moreau, 1966: 117). There are only four forest species in southwest Arabia, three of which are actually montane birds from Africa (Moreau, 1966: 113-114) and one a woodpecker with relatives in Indo-Malesia (including Himalaya) (Lees-Smith, 1986). Expansions of their ranges are presumed to have been possible as late as (a humid period in) the Pleistocene or Neolithic (Moreau, 1966: 117; Lees-Smith, 1986: 73). Both *Phodilus prigoginei* (an owl) and *Artisornis* (/*Orthotomus*) *metopias* (a warbler) are sedentary and known only from montane evergreen forest in Africa, while their closest relatives occur in India and are not typical of this habitat (Moreau, 1966: 117). De Beaufort (1951: 92) points out that Indo-Malesia and the Afrotropics share the following forest elements: barbets (Capitonidae), hornbills, broadbills (Eurylaemidae), and ground thrushes (Pittidae).

Among butterflies (Papilionidae, Pieridae, Hesperidae, Danaidae, Lycaenidae, Nymphalidae, Satyridae, Acraeidae, Libytheidae and Riodinidae), most species common to the Afrotropics and Indo-Malesia are known from arid habitats, whereas common genera are frequently sylvan (Carcasson, 1964: 151). These common genera do not involve affinities at the specific level (Carcasson, 1964: 151-151).

Summarizing, the mammal data suggest that there were several acmes of migration of land animals, but that the routes concerned were filter bridges or sweepstake routes. The other data indicate that a forest connection occurred only prior to the Pleistocene or the Pliocene. If the Red Sea area was really hot and dry (with only minor, temporary "ameliorations") throughout post-Miocene times (see Moreau, 1952: 882), a forest connection should have been in the Miocene and/or the Oligocene.

Turkestan

The term "Turkestan" is applied here to a region including Turkmeniya, Uzbekistan, Tadzhikistan, Kirgiziya, Pamir and Altaï. In Turkestan (including Kuliab, near the border in Afghanistan), there is a clustering of species of *Cossulus, Parahypopta, Stygioides, Semagystia* and *Holcocerus* (all cossine genera). For distribution data, reference should be made to Daniel (1955-1965). The following species are endemic to Turkestan: *Cossulus strigillatus, C. stertzi, Parahypopta issyca, P. putrida, P. sheljuzhkoi, Stygioides aethiops, S. psyche,* unidentified *Stygioides* species (e), *Semagystia agilis, S. clathrata, S. cossoides, S. tristis,* (?) *S. albina,* (?) *S. albosignata, Holcocerus pulverulentus, H. praeclarus, H. puengeleri, H. brunneogrisea, H. tekkensis, H. gracilis, H. muscosus, H. musculus, H. murinus,* and *H. sacarum.* The following species occur in Turkestan as well as in neighbouring areas (southwest China, northern Iran and/or Afghanistan): *Cossulus turcomanica, C. herzi, Semagystia lacertula, Holcocerus campicola, H. consobrinus, H. nobilis,* and *H. inspersus.* Among these species, only *P. sheljuzhkoi* is endemic to Tyan-Shan', and *C. herzi* (*bolshoji*) and possibly *Semagystia cossoides* (? *tsimgana*) have subspecies endemic to this subregion. The percentages of species belonging to the two categories that are indicated above are moderately to very high within the genera mentioned. Furthermore, there are many cossine species with a wider distribution including Turkestan: e.g., *Holcocerus arenicola, H. gloriosus, H. holosericeus, Stygioides colchica* and *S. tricolor.*

Turkestan at present consists mainly of steppe and desert, but some of its areas have been irrigated more or less recently (e.g. Cerny, 1986). It is to be expected that most or all of the cossine species occurring there prefer steppe- and/or desert-like habitats. However, only for *Stygioides colchica, Dieida ledereri, Holcocerus campicola* and *H. praeclarus,* are there records of their habitat that support this idea (see Daniel, 1955-1965c). Several other species from section 3 have also been recorded from such habitats. Judging from their ranges, it seems that all species of section 3 and *Holcocerus* prefer high day temperatures during the summer. All species are restricted to areas south of the July isotherm of 20°C, and most of them south of the 25°C isotherm (cf. Voous, 1960: 8-map 3). Ground temperatures may be more relevant than air temperatures as limiting factors for these species, since their larvae are perhaps root-borers (only positively known of *Stygia australis, Parahypopta caestra* and *Dyspessa ulula*). Reference should be made to Mani (1968) for data on the considerable differences between ground and air temperatures in the mountains. This may aid in understanding the altitudinal range of certain species, and the occurrence of others only in the mountains while closely related species are known from the lowlands. Most of the species from section 3 and *Holcocerus* occur in areas indicated as desert or steppe by Udvardy (1975). Therefore, it may be presumed that most species from section 3 and *Holcocerus* prefer steppe- and/or desert-like habitats with high day temperatures during the summer and with certain herbs (as hosts). The author assumes that these species had this preference already before the vicissitudes of the Pleistocene.

In the Pliocene, great areas in inner Asia were steppe or desert, gradually intergrading into savanna and finally into rain forest in the monsoon areas (Kurtén, 1971: 135). A vegetation related to the present *Haloxylon*-association (desert vegetation) was present in Turkmeniya during the entire Pliocene, as indicated by palynological records (see Kryzhanovskij, 1961: 427). The ranges of the species mentioned were presumably scattered over a vast area. The species would have been forced to the south by the climatic deteriorations of the Glacial Periods and would have little or hardly spread after the Pleistocene. Turkestan is thus considered a main refuge area for the species of *Cossulus, Parahypopta, Stygioides, Semagystia* and *Holcocerus*.

Reinig (1937: 46-57) considers Turkestan also a main refugium for steppe elements and provides many examples of such Turkestan elements among *Bombus* species (Hymenoptera: Apidae). These elements could later have invaded the mountains of Middle Asia (e.g. Pamir) (Reinig, 1937).

De Lattin (1967: 322-fig. 96, 398) names part of Turkestan (with an extension to Ozero Balkhash) the Turano-eremic Centre, a centre of post-glacial dispersal of eremic species. De Lattin (1967: 398-fig. 136) notes *Podoces pander* (Aves: Corvidae) as an example of Turano-eremic elements. According to de Lattin (1967: 322-fig. 96), the eastern part of Turkestan (including Tyan-Shan') was a centre (of post-glacial dispersal) of arboreal elements (named the Turkestan Centre). According to de Lattin (1967: fig. 96), the south of Turkestan and parts of Iran and Afghanistan were also a centre of arboreal elements. Other parts of Iran and Afghanistan are indicated as the Irano-eremic Centre by de Lattin (1967: 322).

Among the Cossinae, there are at least two *Holcocerus* species, viz. *nobilis* and *holosericeus*, with one subspecies in Turkestan and another one in Afghanistan (see Daniel, 1959). This may be an indication of separate refugia in these two regions.

Turkestan is thus considered a main Pleistocene refugium for organisms which prefer steppe- and/or desert-like habitats.

New Guinea and surroundings

Most cossid species occurring in New Guinea belong to the Zeuzerinae and only one to the Cossinae (viz. the undescribed *Paracossus* species). *Chalcidica minea, Zeuzera caudata, Duomitus ceramicus* are distributed from India to the Solomon Islands, *Xyleutes strix* from India to the Bismarck Archipelago, *Zeuzera indica* from India to Australia, and *X. personus* from India to New Guinea. Two undescribed *Panau* species and certain *Trismelasmos* species occur in New Guinea as well as on other islands of Malesia or Melanesia. Endemics to New Guinea are *Skeletophyllon perdrix*, an undescribed *Skeletophyllon* species and several *Trismelasmos* species.

The insect faunas of New Guinea and the Solomon Islands are considered basically of Asian origin (Gressitt, 1958: 768; Peters & Edmunds, 1970: 233; Edmunds, 1972: 39; Raven & Axelrod, 1972), a view concordant with the cossid data.

New Guinea is a composite area with remnants of several island arcs. For surveys of the geological history of New Guinea and surroundings, reference should be made to Holloway (1979; 1984), Coleman (1980), Duffels (1983), Audley-Charles (1983; 1987), Duffels & De Boer (in press). The biogeographic relations between the components in this region have been investigated in detail by only few authors (see below), and there are still uncertainties in this field. The following discussion of distribution patterns within certain cossid taxa may contribute to a better understanding.

Chalcidica

Chalcidica minea has at least three subspecies. The nominate one is distributed from India eastward to Flores, Sulawesi (= Celebes), the Philippines and the northern Moluccas (Halmahera and Bacan). *C. minea hyphinoe* is known from the southern Moluccas (Ambon and Seram), Sulawesi (Pangean and a locality in eastern Sulawesi), Salayar, Kepulauan Kai (= Kai Islands), and Irian Jaya (Biak, Sorong, Fakfak, Tanah Merah). *C. minea pallescens* is positively known from midnorthern New Guinea (Hollandia = Jayapura, the Humboldt Bay area, Kota Nica, Pim, Uskwar, Wembi, Ampas, Bernhard Camp). The other localities of *pallescens* were not specified ("New Guinea" and "W. Irian") or couldnot be located on maps (Kroinni, Wambis, Wembis/Wambis). The two subspecies *hyphinoe* and *pallescens* both have an enlarged dark pattern in the forewing, but in *pallescens* the ground colour is paler (yellowish white) than in *hyphinoe*. Only *minea* material in RMNH and ITZ has been considered. The material in BMNH (from e.g. Aru, islands northeast of New Guinea, Solomon I.) has not been checked for subspecific status.

The area from which *pallescens* is positively known (New Guinea, roughly north of Taritatu = Idenburg River) is considered to be a remnant of the Outer Melanesian Arc (cf. Holloway, 1979: 15). The southern Moluccas, Kepulauan Kai and midnorthern New Guinea (areas where *hyphinoe* occurs), and part of Sulawesi were probably parts of the Inner Melanesian Arc (Holloway, 1984: 132). The island Biak and possibly (at least the northern part of) the Vogelkop (northwestern peninsula of New Guinea) were probably parts of the Outer Melanesian Arc (Holloway, 1984: 132; Duffels & De Boer, in press).

From this distribution pattern it may be inferred, that the ancestor of *hyphinoe* and *pallescens* originally occurred on one or both Melanesian Arcs (as the eastern vicariant of ssp. *minea*), and that *pallescens* has developed from a *hyphinoe*-like population on the midnorthern New Guinean component of the outer arc, when this was still a separate island. It would be interesting to see to which subspecies the material (BMNH) from Aru, the islands northeast of New Guinea, and the Solomon Islands belong.

Panau

Two *Panau* species occur in New Guinea, but they are not endemic to this island. Undescribed species (a) is only known from Palu (3700 ft.) in Sulawesi and the Arfak Mountains (6000 ft.) in Irian Jaya. The Arfak Mountains (northern Vogelkop) were probably part of the Outer Melanesian Arc. The closely related *euphanes* (see fig. 77) is restricted to the Philippines. Gressitt (1958: 768) points out that there are affinities, at least in part independent from Sulawesi, between New Guinea and the Philippines through the Moluccas.

Undescribed species (b) is known from several localities on new Guinea (Fakfak, central ranges of Irian Jaya, and Papua New Guinea) and from Kepulauan Kai. These areas are considered former parts of the Inner Melanesian Arc.

It is uncertain if there was a vicariance event between ancestral populations of, on the one hand, the undescribed species (a) and, on the other hand, those of the undescribed species (b) and the following species of *Panau* in western Melanesia and on the Inner Melanesian Arc. There seems to have been two vicariance events between ancestral populations on the Inner Melanesian Arc, remnants of which are inhabited by the undescribed species (b) and *brunnescens*, and species in western Malesia, including northern Sulawesi.

Trismelasmos

Trismelasmos is represented from Singapore eastward to the Solomon Islands. *T. maculatus* seems to take the first branch in the cladogram for the genus (see fig. 78). This species occurs from Singapore eastward to Banggai and possibly Kepulauan Tanimbar. There is an unsolved trichotomy in the cladogram (fig. 78) for undescribed species (a), *tectorius*, undescribed species b, and the rest of the genus. Undescribed species (a) is known from Irian Jaya. One record of this species is from Biak, and at least six from the other eight known localities are situated northeast of or along the Taritatu, particularly in the area of the river Arso; two more localities, viz. Parfi and Wambis, couldnot be located. *T. tectorius* is known from the Solomon Islands (Bougainville, Tugela and Tulagi Isl.). Undescribed species (b), which follows *tectorius* and undescribed species (a) in the cladogram, is known from Manam Island and a not specified locality in Irian Jaya.

Trismelasmos dictyograptus, mixtus, cinerosus and perhaps some undescribed species are supposed to follow undescribed species (b).(as a middle section of *Trismelasmos*) in the cladogram (see systematic section). *T. dictyograptus* is known from eastern Kalimantan (Indonesian Borneo) and Karimunjawa (islands north of Java) (see material examined and Roepke, 1957). *T. mixtus* is known with certainty from Ambon, Buru and Obi Major; Roepke (1957: 37) notes also (Kepulauan) Kai, New Guinea, Lang Island and possibly Java as localities of *mixtus*. One locality of *cinerosus* concerns the Arfak Mountains (northern Vogelkop) and at least four from the six other known localities are situated northeast of or along the Taritatu; the other two localities, viz. Slager and Garaine, couldnot be located.

Most other species of *Trismelasmos* are known from New Guinea and/or neighbouring islands. Several of these species seem to be restricted to the area north of the Taritatu. A few species are known from mountains in central New Guinea. Two species are only known from the eastern part of the island. *T. minimus* is known from northwest and northern Irian Jaya and islands close to New Guinea, such as Dampier Island, St. Matthias and New Ireland. Several other species occur outside New Guinea. *T. kalisi* is only known from southern Sulawesi. *T. major* occurs on Bacan (Moluccas). Undescribed species (f) is known from the Philippines.

Undescribed *Trismelasmos* species (a) and (b), *tectorius, cinerosus* and some other species are perhaps restricted to areas which are considered to be remnants of the Outer Melanesian Arc. *T. maculatus*, which is the sister-species of all other *Trismelasmos* species, is known from parts of the Inner Melanesian Arc as well as from other islands of (western) Indonesia. There was probably an east-west vicariance event between *maculatus* (western Malesia and possibly Inner Melanesian Arc) and the ancestor of the rest of *Trismelasmos* (Outer Melanesian Arc), which probably involved Sulawesi and Banggai. It is unclear whether the ancestral species of the genus spread from Malaysia over the Indonesian Archipelago or originated on one of the Melanesian arcs. The possibility that both *Skeletophyllon* and *Trismelasmos* originated on the Outer Melanesian Arc cannot be excluded. There was probably a vicariance event between (1) some New Guinean parts of the Outer Melanesian Arc (Biak, midnorthern New Guinea and Manam Island), where the undescribed species (a) and (b) occur, and (2) the parts now forming the Solomon Islands, where *tectorius* is found. The Outer Melanesian Arc was probably already open as a dispersal route for Asian immigrants into the Pacific in Early Miocene times (Duffels, 1983: 39). There was apparently a great radiation on New Guinea; 17 species are known from this island. The Pleistocene climatic vicissitudes and the Pliocene and Pleistocene orogenesis may have caused this radiation. A spreading from New Guinea to the west happened apparently on several occasions.

There are affinities between the Vogelkop and adjacent islands and midnorthern New Guinea; *cinerosus* occurs both in midnorthern New Guinea and in the Arfak Mountains, *minimus* is known from midnorthern New Guinea, neighbouring islands, the Arfak Mountains and Doom Island, and undescribed species (d) is represented in both midnorth New Guinea and in Sorong. These affinities seem to support the idea that the Vogelkop was at least in part also a component of the Outer Melanesian Arc (cf. Holloway, 1979: 15; Duffels, 1985: 279; Duffels & De Boer, in press).

Other groups

Duffels (1986) and Duffels & De Boer (in press) provide a survey of distribution patterns which show biogeographic relations between the areas in eastern Malesia and Melanesia. On the basis of distribution patterns within the Cicadoidea (Homoptera), Duffels (1986: 330) distinguishes at least three biogeographic areas in New Guinea: (1) central mountains, (2) northern mountain range, and (3) Vogelkop area with Waigeo, Salawati and Misoöl.

From cicadoid distribution patterns, Duffels (1986: 330-331) supposes an isolated position of the Vogelkop in the past, and a relation of it with the fragments of the Outer Melanesian Arc and the Moluccas. This is possibly corroborated by distribution patterns within *Platymantis* (Ranidae: Platymantinae), but no cladogram for this group is available (see Zweifel & Tyler, 1982: 787-788; cf. Duffels, 1986: 332). Among the Cicadoidea, only *Cosmopsaltria delfae* is known from both northern Vogelkop and midnorthern New Guinea. Within *Trismelasmos*, the ranges of at least four species suggest a close relation between the (northern) Vogelkop and midnorthern New Guinea. Van Welzen (1990: 113) suggests that the Vogelkop "features" together with the central mountain range. Only the distribution of *Guioa subericea* (Sapindaceae) suggests this, to my opinion, whereas that of *Guioa membranifolia* indicates a close relationship between the Vogelkop and northern New Guinea.

Within the fruitbat genus *Dobsonia* there are affinities between, on the one hand, respectively Japen and Biak (with Owii Islands) and, on the other hand, northern New Guinea and/or the islands off its northern coast (Bergmans & Sarbini, 1985). *Baeturia bloetei* (Cicadoidea) occurs on Japen and Biak as well as in (mainly) northern Irian Jaya (see De Boer, 1989). Within *Trismelasmos*, the ranges of undescribed species

(a) also suggest a close relation between Biak and midnorthern New Guinea.

Duffels (1986: 329-332) lists examples among the Cicadoidea of a vicariance event between the Sulawesi Arcs and both Melanesian arcs (within Prasiini), vicariances between the two Melanesian arcs (within Cosmopsaltriaria), and close biogeographic relations of northern New Guinea with the Solomon Islands, the Bismarck Archipelago and the Moluccas (within *Diceropyga*). The ancestors of the cicadoid groups endemic to central New Guinea are supposed to have migrated from the Outer to the Inner Melanesian Arc (in the Late Miocene or the Pliocene) (Duffels, 1986: e.g. 330), which was probably also the case within *Trismelasmos*. De Boer (1989) notes that the distribution pattern of the *Baeturia bloetei* group (Cicadoidea) largely coincides with remnants of the Outer Melanesian Arc.

Holloway (1984: 150-158) suggests that a two-arc pattern among Lepidoptera is found within *Nadagarodes* (Geometridae), *Cyana* (Arctiidae) and *Ophyx* (Noctuidae), but these examples are not convincing in my opinion.

For example, Thornton (1980: 252-255) and Möller Andersen (1989) provide other interesting data of distribution patterns in eastern Malesia.

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Index to genera

Valid names are in bold, and the names of obscure taxa or ones excluded from the Cossidae are asterisked.