SYSTEMATICS AND PHYLOGENY OF HOLARCTIC GENERA OF NEPTICULIDAE (LEPIDOPTERA, HETERONEURA: MONOTRYSIA)

by

ERIK J. VAN NIEUKERKEN

Nieukerken, E.J. van: Systematics and phylogeny of Holarctic genera of Nepticulidae (Lepidoptera, Heteroneura: Monotrysia).

Zool. Verh. Leiden 236, 31-xii-1986: 1-93, figs. 1-135, tables 1-3. — ISSN 0024-1652.

Key words: Lepidoptera; Monotrysia; Nepticulidae, phylogeny; hostplant relationships; leafminers.

A revised classification of the Holarctic genera of Nepticulidae is provided. Eight genera belonging to the nominal subfamily are recognised and redefined. They are *Enteucha* Meyrick (= *Johanssonia* Borkowski, *Artaversala* Davis, *Oligoneura* Davis), *Stigmella* Schrank (including *Astigmella* Puplesis), *Simplimorpha* Scoble in the Nepticulini and *Acalyptris* Meyrick (= *Microcalyptris* Braun, *Niepeltia* Strand), *Trifurcula* Zeller, *Parafomoria* Van Nieukerken, *Bohemannia* Stainton and *Ectoedemia* Busck in the Trifurculini. *Trifurcula* is divided into the subgenera *Glaucolepis* Braun (= *Fedalmia* Beirne), *Levarchama* Beirne and *Trifurcula* s.str. *Ectoedemia* is divided into the subgenera *Etainia* Beirne, *Fomoria* Beirne, *Laqueus* Scoble, *Zimmermannia* Hering and *Ectoedemia* s.str. The genera and subgenera are (re)described and data on biology and distribution are given. The species *Simplimorpha promissa* (Staudinger) and *Acalyptris psammophricta* Meyrick are redescribed. A phylogeny of the family in cladistic sense is presented and discussed. The monophyly of *Ectoedemia* is uncertain, and monophyly of the subgenus *Fomoria* could not be demonstrated. Current opinions about the phylogenetic position of the Nepticulidae and the division of the Heteroneura are reviewed and discussed. The biogeography and hostplant relationships of the family are reviewed.

E.J. van Nieukerken, Rijksmuseum van Natuurlijke Historie, Postbus 9517, 2300 RA Leiden, The Netherlands.

CONTENTS

INTRODUCTION

The Nepticulidae form by far the largest family of non-Ditrysian Lepidoptera with about 600 described species and probably at least as many undescribed species, occurring in all zoogeographic regions, except Antarctica. Despite their comparatively high uniformity in morphology they reached a great diversity in most regions and form a large proportion of all leaf-mining insects.

During the second half of the 19th century most species were assigned to the genus *Nepticula* Heyden, a junior synonym of *Stigmella* Schrank, with only a small number of species placed in *Trifurcula* Zeller and *Bohemannia* Stainton. In the first half of this century some other genera have been described, but Beirne (1945) was the first to divide the family into several genera on the basis of the male genitalia of the British species. However, his scheme was rarely adopted elsewhere and the correct place of most other Holarctic species remained unknown. In the early seventies the interest in the family increased and resulted into several accounts on the classification of Nepticulidae, such as Johansson (1971), Borkowski (1972) and Wilkinson & Scoble (1979) who all adopted and refined Beirne's scheme. Recently, Scoble (1983) provided a revised classification, the first which strictly followed cladistic principles. Although his classification was intended to treat the family world-wide, Scoble mainly studied the South-African species and several Holarctic genera were treated by him as "incertae sedis". Scoble was also the first to introduce suprageneric categories within the family. Also Puplesis (1984b, 1985a,b) provided a review of the generic classification, the only major change being the upgrading of Scoble's tribes into subfamilies, and creating some new tribes. However, Puplesis did not follow cladistic principles.

The work by Scoble (1983) provides an important starting point for the classification of the Holarctic Nepticulidae; in this study I was able to corroborate most of the branching points proposed by him and to refine others. I also could resolve some of the existing uncertainties in a few Holarctic genera, not studied by Scoble. Further a detailed study of adult and larval morphology, partly with the aid of a scanning electron microscope lead to the discovery of several important characters previously not used in the classification of Nepticulidae. Finally the study of some overlooked generic names lead to a number of nomenclatorial changes.

The classification proposed here has been used in my check-list of western Palaearctic species (Van Nieukerken, 1986), and the new synonymies of genera discussed here were formally established in that paper.

All genera and subgenera recognised are redescribed, except those which I recently revised (Van Nieukerken, 1983b and 1985b), and a diagnosis and list of apomorphies are provided for each. Further, the known information on biology and distribution is summarised. The distribution of the (sub)genera is also provisionally mapped, except that of *Stigmella,* which is almost cosmopolitic. Illustrations are mainly additional to previous publications. No complete lists of species, neither of specimens examined are given, but reference is made to published lists per genus.

The references under the genus headings are confined to the first descriptions of all nominal genera; important treatments are cited in relevant places in the text, especially under "Species included".

Descriptions of immature stages are not given; not enough material of pupae was available (but see Scoble, 1983 for some notes) and the larvae will be subject of a future publication. However, important apomorphies in immature stages are included in this work, but will be elaborated on later (Van Nieukerken & Jansen, in prep.).

MATERIAL AND METHODS

This study is based on an extensive study of the western Palaearctic Nepticulidae. Almost all described species have been examined, except a few belonging to *Stigmella* and *Trifurcula*. For these the generic placement was clear from literature data. For the eastern Palaearctic fauna much information became recently available through the works of Puplesis (1984a-e, 1985b,c), Puplesis & Ivinskis (1985) and Kemperman & Wilkinson (1985), a large part of the species described by them has also been examined by me. Other Japanese species are currently studied, and a large collection of Chinese Nepticulidae made by J.W. van Driel and me in cooperation with Liu Youqiao of the Academia Sinica in Beijing provided some additional information. The Nearctic species are known through the works of Davis (1978b), Wilkinson (1979, 1981), Wilkinson & Newton (1981), Wilkinson & Scoble (1979) and Newton & Wilkinson (1982); several Nearctic species have been examined by me.

The type-species of all described nepticulid genera have been examined, except those of *Varius* Scoble, *Areticulata* Scoble and *Pectinivalva* Scoble. Representatives of about 10 undescribed species of *Pectinivalva* were examined (ANIC). Larvae of many European and some other species were examined, belonging to all genera and subgenera recognised; a detailed treatment will be given by Van Nieukerken & Jansen (in prep.).

Material from the following institutions has been studied for this revision: ANIC, Australian National Insect Collection, Division of Entomology, CSIRO, Canberra, Australia; BMNH, British Museum (Natural History), London, U.K.; EIHU, Entomological Institute, Faculty of Agriculture, Hokkaido University, Sapporo, Japan; ELUO, Entomological Laboratory, College of Agriculture, University of Osaka Prefecture, Osaka, Japan; LNK, Landessammlungen für Naturkunde, Karlsruhe, West Germany; MHUB, Museum für Naturkunde der Humboldt-Universität, Berlin, East Germany; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NMW, Naturhistorisches Museum Wien, Vienna, Austria; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands; RMS, Naturhistoriska Riksmuseum, Stockholm, Sweden; USNM, U.S. National Museum of Natural History, Smithsonian Institution, Washington DC, USA; ZIAB, Zoological Institute, Academia Sinica, Beijing, Peoples Republic of China; ZIAS, Zoological Institute, Academy of Sciences of the USSR, Leningrad, USSR; ZMA, Instituut voor Taxonomische Zoologie (Zoölogisch Museum), Amsterdam, Netherlands; ZMUC, Zoological Museum, University of Copenhagen, Copenhagen, Denmark; and from the private collections of R. Johansson (Växjo, Sweden) and the author (EvN).

Genitalia and wing slides were prepared as described in Van Nieukerken (1985b). From several species complete adults were macerated in KOH and examined in glycerin or permanent mounts.

Specimens for scanning electron microscopy were air-dried, mounted on stubs and gold coated. They were examined with an ISI-40 scanning electron microscope, using a beam current of 5 or 10 kV.

Plant family names follow Dahlgren (1983), thus with preference for type-genus based names such as Asteraceae instead of Compositae. Betulaceae, however, comprises also Corylaceae here, and Rosaceae includes Malaceae and Amygdalaceae.

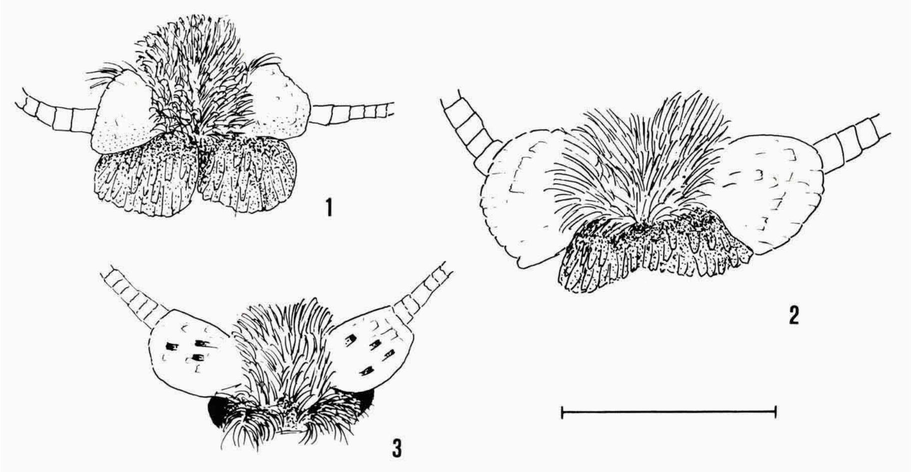
Localities are spelled according to The Times Atlas of the World (Comprehensive Edn, 1975), deviating names on labels are cited in brackets.

Nomenclature follows the most recent International Code of Zoological Nomenclature (3rd edn., 1985), which is referred to as the "Code".

This study follows the basical concepts and tenets of phylogenetic systematics as outlined by Hennig (1966). The methods of this school were recently described and reviewed in several textbooks, such as Eldredge & Cracraft (1980), Nelson & Platnick (1981) and Wiley (1981). No attempt has been made here to use a computerized algorithm for pattern analysis. Monophyletic groups were firstly hypothesized on the basis of uniquely derived characters and overall similarity. Later additional apomorphies were searched by means of outgroup analysis (for reviews on this method see Watrous & Wheeler, 1981 and Maddison, Donoghue & Maddison, 1984) and the original hypotheses of monophyly either corroborated or falsified. Characters represented by evolutionary novelties were given more weight than reductions or characters showing frequent parallelisms. On the basis of the apomorphies found, cladograms were constructed.

ADULT MORPHOLOGY

Several authors provided a detailed account of the adult morphology of Nepticulidae, the most extensive being that of Scoble (1983), in which also results of earlier workers are summarised. Van Nieukerken (1985b) presented a discussion of the morphology of *Ectoedemia* (partim). Further Davis (1986b) made many morphological observations on Monotrysia in his treatment of the Palaephatidae. To present a detailed account of adult structure here, therefore, would be highly repetitive, and the following treatment is thus confined to those structures which have received less attention previously, or are considered especially important to understand the phylogeny of the family.



Figs. 1-3. Head, dorsal aspect, showing scape, frontal tuft and collar. 1, *Stigmella aurella* (Fabricius), England; 2, *Bohemannia quadrimaculella* (Boheman), Sweden; 3, *Ectoedemia (Fomoria) septembrella* (Stainton), The Netherlands. Scale: 0.5 mm.

Head

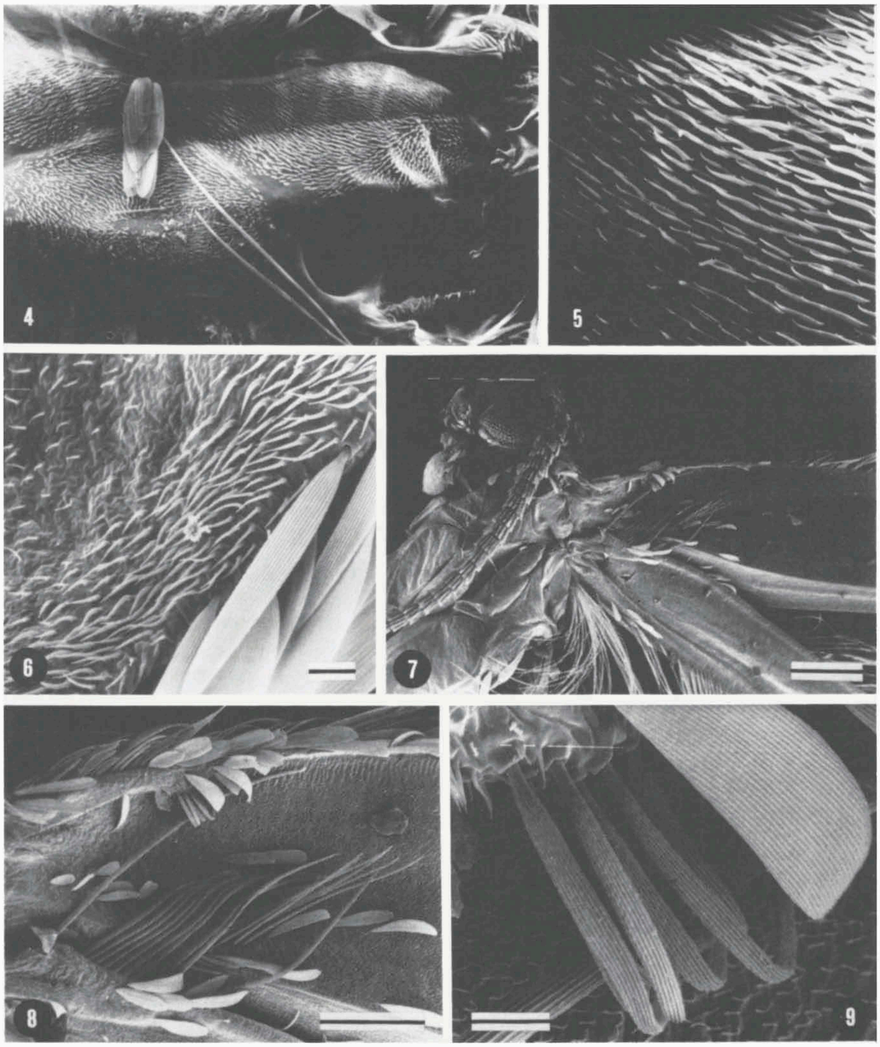
A feature, overlooked by most authors is the conditions of the so called "collar", viz. the two groups of scales inserted on the back of the head. These scales are piliform in most Nepticulidae, forming relatively inconspicuous tufts (fig. 3), but lamelliform in *Stigmella* (fig. 1), *Enteucha* and part of *Bohemannia* (fig. 2), forming a large structure, often overlapping the thorax.

Morphology of antennae has been treated by Van Nieukerken & Dop (1984, 1986).

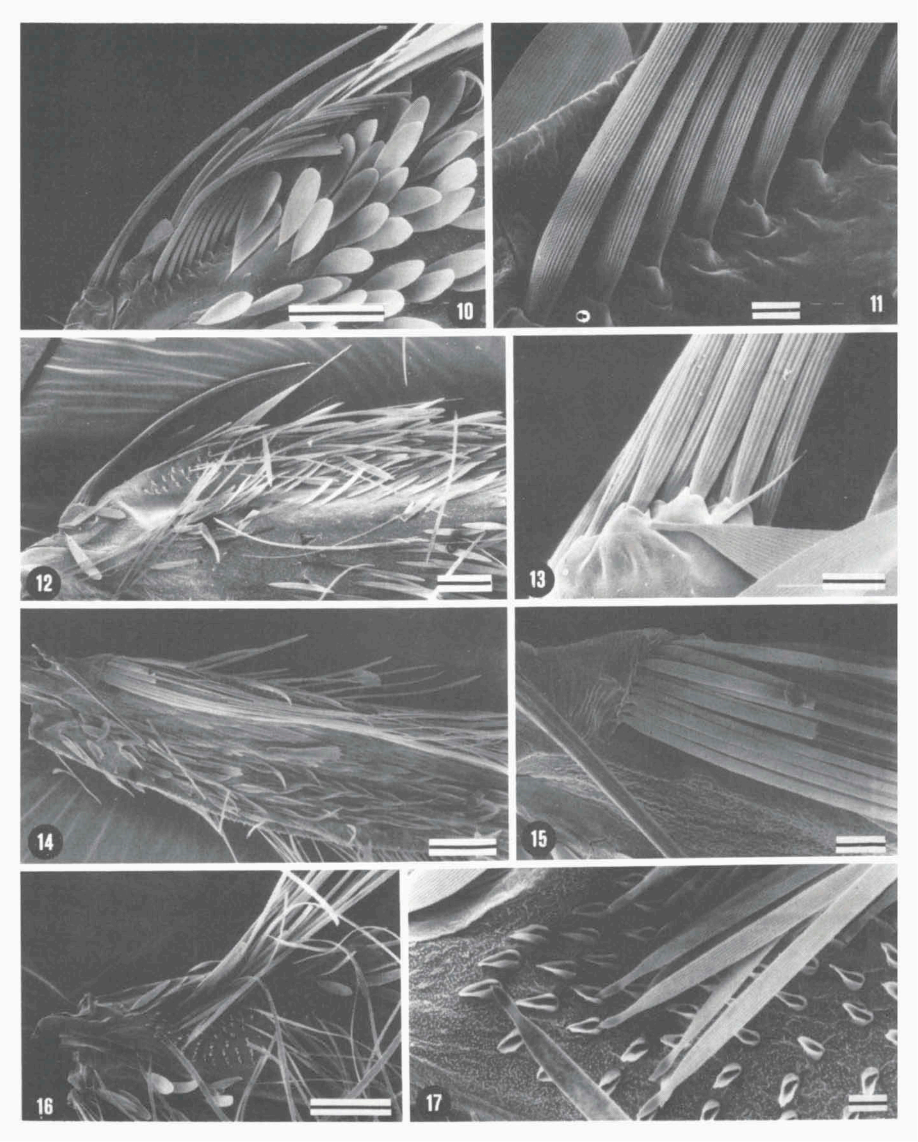
Thorax

The structure of the thorax has not received much interest from nepticulid workers, but seems to be very uniform throughout the family. Minet (1984) described the prothoracal structure, which will be discussed further in the section on phylogeny.

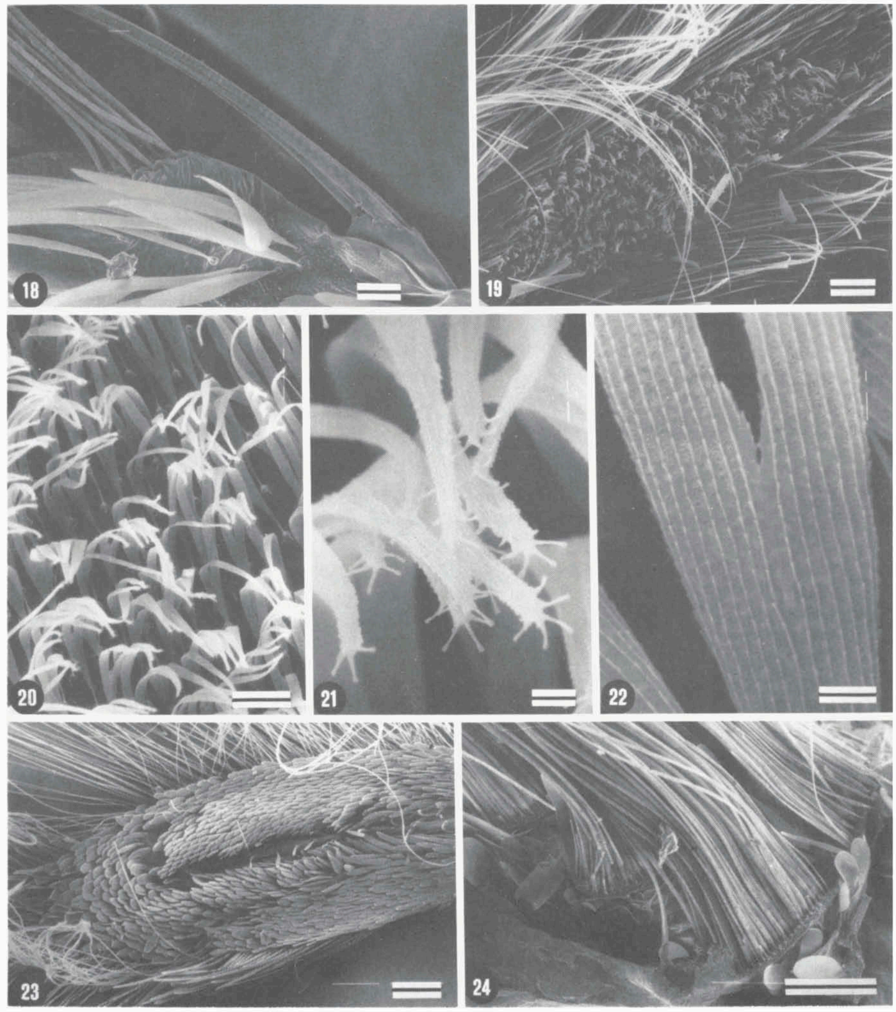
The wing-locking device, composed by a field of microtrichia on the metascutum and an area of microtrichia along the anal margin on the forewing underside, has been reported previously for Nepticulidae by Kuijten (1974) and Scoble (1983) and for the Nepticuloidea by Common (1969). It is here illustrated by scanning micrographs (figs. 4-6).



Figs. 4-9. Adult structure. 4, *Ectoedemia albifasciella* (Heinemann), metathorax with "wing-locking" microtrichia; 5, idem, detail; 6, *Trifurcula immundella* (Zeller), underside of forewing with "wing-locking" microtrichia; 7, *Stigmella malella* (Stainton), male, wing coupling; 8, idem, detail; 9, detail of costal retinaculum. Scales: 0.2 mm (7); 0.1 mm (8); 10 μm (9).



Figs. 10-17. Male hindwing structures, upperside. 10, 11, *Stigmella suberivora* (Stainton), frenulum and costal bristles; 12, 13, *Bohemannia quadrimaculella* (Boheman), frenulum and diffuse "hair-pencil"; 14, 15, *Parafomoria helianthemella* (Herrich-Schäffer), hair-pencil; 16, 17, *Acalyptris* near *minimella* (Rebel), diffuse "hair-pencil", frenulum broken. Scales: 0.1 mm (10, 12, 14, 16); 10 µm (11, 13, 17); 20 µm (15).



Figs. 18-23. Male hindwing structures. 18, *Trifurcula (Levarchama) cryptella* (Stainton), hair-pencil and frenulum on hindwing underside; 19-22, *Trifurcula* (s.str.) *immundella* (Zeller), raised androconial scales on hindwing underside, details of tips and incision; 23, *Acalyptris platani* (Müller-Rutz), androconial scales on hindwing upperside; Fig. 24, *Acalyptris falkovitshi* (Puplesis), paired tufts of hair-scales on T5-6. Scales: 0.1 mm (19, 23, 24); 20 μm (18, 20); 2 μm (21, 22).

Wings

The vestiture of the wings is highly diagnostic, but usually hardly or not correlated with phylogenetic relationships. The presence of a fascia and a cilia-line on the forewing are believed to be part of the groundplan of Nepticulidae.

The wing-coupling in the males basically comprises a double mechanism (figs. 7-10): firstly a composite frenulum arising on the hindwing base hooking into the costal retinaculum formed by some hooked scales; secondly a row of costal bristles (pseudofrenular bristles) arising on the humeral lobe, coupling with a subdorsal retinaculum composed of some hairscales. In the females only the second mechanism is present. The double coupling is found throughout the family, but the costal bristles are secondarily lost or modified in the males of several genera: in *Pectinivalva* they are lamellar scales rather than spines (Scoble, 1983), in *Parafomoria* (figs. 14, 15) and many species of *Ectoedemia* they are modified into a hair-pencil (Van Nieukerken, 1983b; 1985b). Hair-pencils in other genera appear to be analogous to this hair-pencil, since they occur together with costal bristles, such as in *Acalyptris minimella* (Rebel) (figs. 16, 17), or are doubtfully homologous as in *Bohemannia* (figs. 12, 13) of *Trifurcula* (fig. 18).

Several other types of sex-linked scales occur in males of many species scattered throughout the genera. They comprise patches of differently coloured lamellar scales on the underside of the forewing and both sides of the hindwing (fig. 23), or elongate scales extending into the fringe, the latter especially in *Stigmella*. The occurrence of these types of scales is usually not much correlated with phylogenetic relationships, they often occur in one species of a pair of sister-species, or in a part of an otherwise distinct monophyletic species group. These androconial scales must therefore be regarded as parallelisms or more likely underlying synapomorphies (sensu Saether, 1979). Despite their scattered occurrence, in one genus the type is often unique. So are the long black scales which occur in *Stigmella atricapitella* (see Johansson, 1971) typical for the *ruficapitella* and *hemargyrella* (or *suberivora*) species groups and found in several distantly related species throughout the Palaearctic region. A patch of yellow scales on the underside of the forewing occurs in some species of the subgenera *Glaucolepis* and *Trifurcula* s.str., and can therefore be regarded as an underlying synapomorphy for the genus *Trifurcula*.

A sharp contrast forms the occurrence of an unusual kind of raised scales on the underside of the male hindwing in *Trifurcula*: they occur in all species in the genus, except a few members of the subgenus *Glaucolepis*, and are therefore regarded as an autapomorphy for *Trifurcula*. These scales (figs. 19-22) are long and deeply bifurcate. Both divisions are narrow and curved and bear papillate appendages near the apex. They form a "velvet-like" patch on the apical half of the hindwing. The exact function is unknown, but it is striking that they occur together with three pairs of abdominal tufts (see further), which most likely contact this velvet patch in rest. Which of these structures is scent-producing or just serving in spreading the scent, is an interesting object for further study.

Venation. Despite the reduced condition of the venation in Nepticulidae, it shows important diagnostic characters at the generic level. The venation has been studied in detail by Braun (1917a) and Scoble (1983). The labelling of the veins used here, conforms with the latter treatment. Interspecific variation is mainly exhibited in the number of terminal branches of the main trunk in the forewing and the visibility and length of Cu. Other important characters, such as the presence of a closed cell and the situation of R1 and R2 + 3 remain very constant throughout a given (sub)genus. Scoble's (1983) observation that R1 separates from the base in *Niepeltia* is refuted here by the finding of a persistent trachea, representing the main trunk of Rs in all species examined (figs. 27, 28, 103, 104).

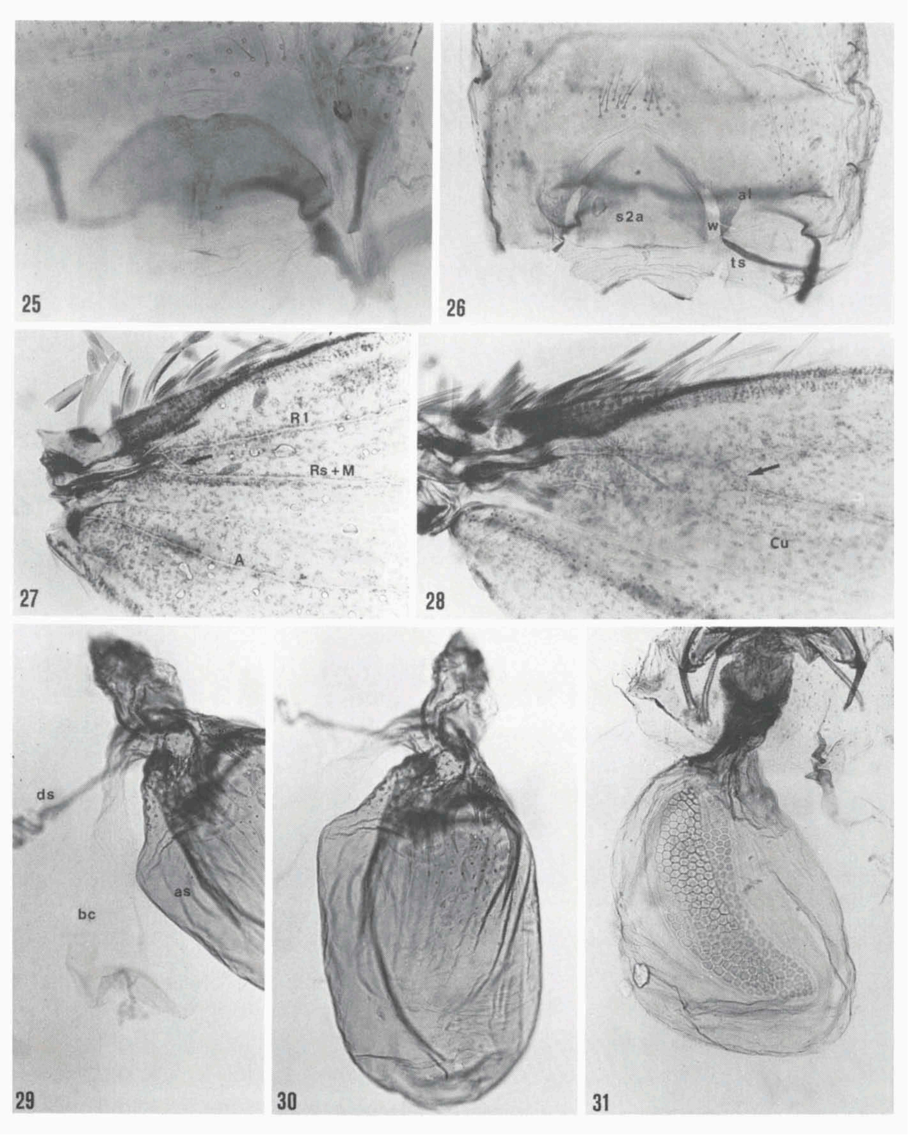
Abdomen

In general the abdominal segments in Nepticulidae are weakly sclerotised only; distinct tergal or sternal sclerites are rarely present, so that it is hardly possible to distinguish between tergal, pleural or sternal parts of each segment.

Segment 1 comprises only a tergum, sternum 1 is lacking as in all other Heteroneura (Kristensen & Nielsen, 1980). From tergum 1 (T1) the lateral margins are strongly sclerotised bars articulating with the anterior margin of T2. According to Börner (1939) and Kyrki (1983) the tergosternal connection between T1 and S2 ("hintere Seitenspänge"), which is present in Incurvarioidea, is possibly lost in Nepticulidae. However, this probably applies only to part of the Nepticulidae, since a distinctly sclerotised tergosternal connection is often visible (fig. 26). It articulates with the anterolateral ridges of S2 (see further). According to Kristensen & Nielsen (1979) the tergosternal connection is part of the lepidopteran groundplan.

The morphology of sternum 2 (S2) has been the subject of phylogenetic studies on family level both in the primitive Lepidoptera (Kristensen & Nielsen, 1980) and the Tineoid Lepidoptera (Kyrki, 1983), but little attention has been paid to the variation of this character on generic or species level. Davis (1986b) observed a varied condition of S2 in the Palaephatidae and in this study a similar variation is reported within the Nepticulidae (figs. 25, 26, 33-55).

Basically sternum 2 is composed of two intimately connected parts: a small anterior sclerite (S2a), fitting into an anterior excavation of the main body of S2. S2a is slightly more sclerotised than S2. The shape of S2a varies considerably within the family and is sometimes more or less characteristic for a genus or group of species. The plesiomorphic condition is more or less quadrate or trapezoid, in advanced forms the lateral margins are becoming



Figs. 25-31. Adult structure. 25, *Pectinivalva* spec., ♂, 2nd abdominal sternite, slide VU 988; 26, *Acalyptris* spec., Algeria, ♂, abdominal sternum 2, slide BM 22597, al = anterolateral ridges, ts = tergosternal connection, w = "window"; 27-28, *Acalyptris* spp., forewing base, showing reduced closed cell with persistent trachea (arrow); 27, *A.* sp., Greece, slide VU 959; 28, *A. bicornutus* (Davis) comb. n., slide VU 961; 29-30, *Stigmella atricapitella* (Haworth), ♀ genitalia, with reduced bursa copulatrix (bc), accessory sac (as) and ductus spermathecae (ds), slide VU 1462; 31, *Acalyptris psammophricta* Meyrick, Holotype, ♀ genitalia.

shorter and the shape of S2a is more or less triangular. Laterally S2a is bordered by less sclerotised tissue which represents the so called "windows", which are less obvious in some genera. The border of S2 next to those windows is often more sclerotised, and represents the anterolateral ridges of Davis (1986b). They are secondarily lost in *Ectoedemia* (figs. 54, 55). It should be noted here, that the interpretation of Kristensen & Nielsen (1980) that in *Ectoedemia* s.str. (named *Trifurcula*) S2 is devoid of anterolateral processes, is not completely correct: not well sclerotised portions of S2p, which project anteriorly at either side of S2a, could be regarded as such. Posterior of S2a, S2 possesses a group of small setae which most likely serve as proprioreceptors, registrating the position of the abdomen.

Some specialisations of S2 include the posterior processes of S2a in *Bohemannia* (figs. 47-49) and the spinose conditions of S2a in *Pectinivalva* (figs. 25, 33). In *Opostega auritella* (Hübner) (Opostegidae) (fig. 32) the situation is principally not different, but S2a is relatively large, and there are no windows or anterolateral ridges visible.

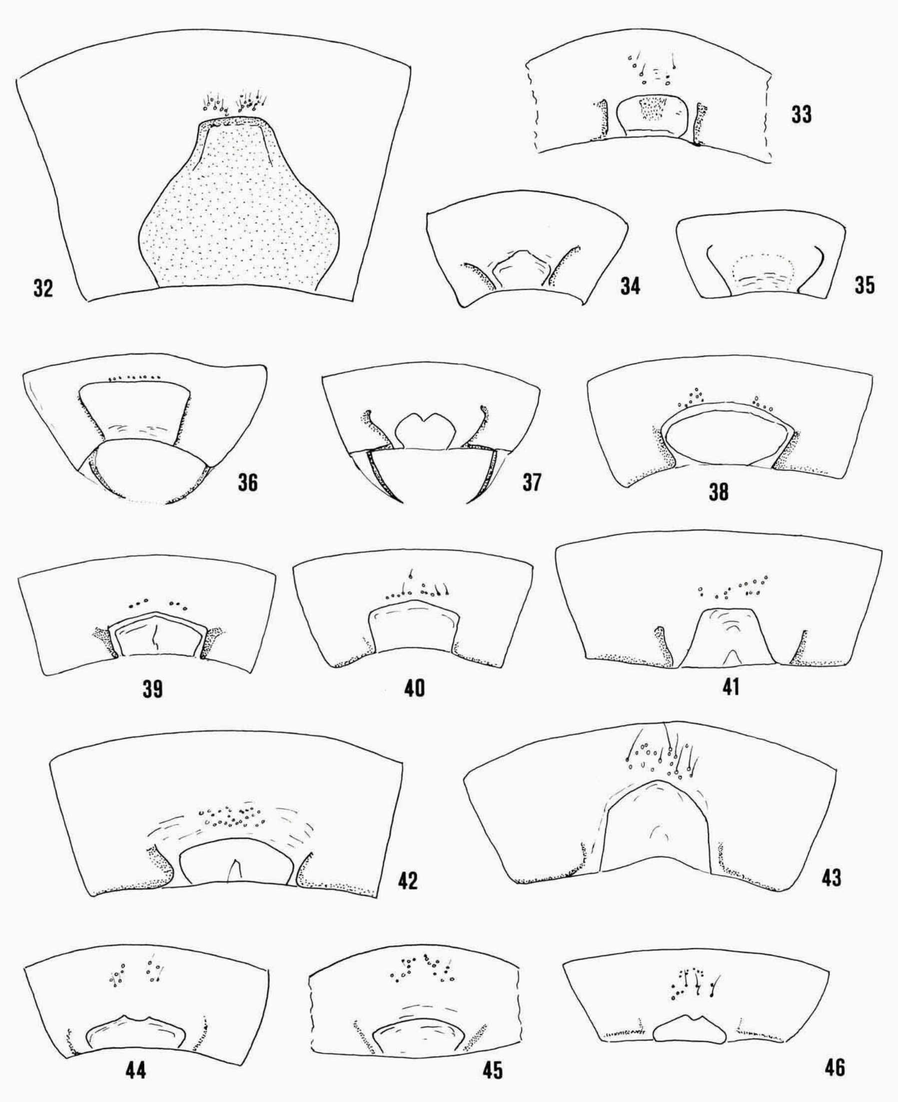
T2 has the anterior margin strongly sclerotised. In some genera this sclerotisation shows some small membranous unmelanized patches, in most species of *Enteucha* there are two of these patches at either side, which might be an apomorphy for this genus (fig. 56).

Segments 3 to 6 (and 7 in the males as well) usually do not show any particular characters except S4 which bears in the female of all species examined a pair of fenestrae (see also Davis, 1975; Scoble, 1983). These fenestrae are possibly associated with some sort of pheromone producing glands, although they do not represent a glandular opening themselves, in contrast to the sternum 5 openings of *Eriocrania* (Davis, 1978a). The internal structure associated with the nepticulid fenestrae requires further study.

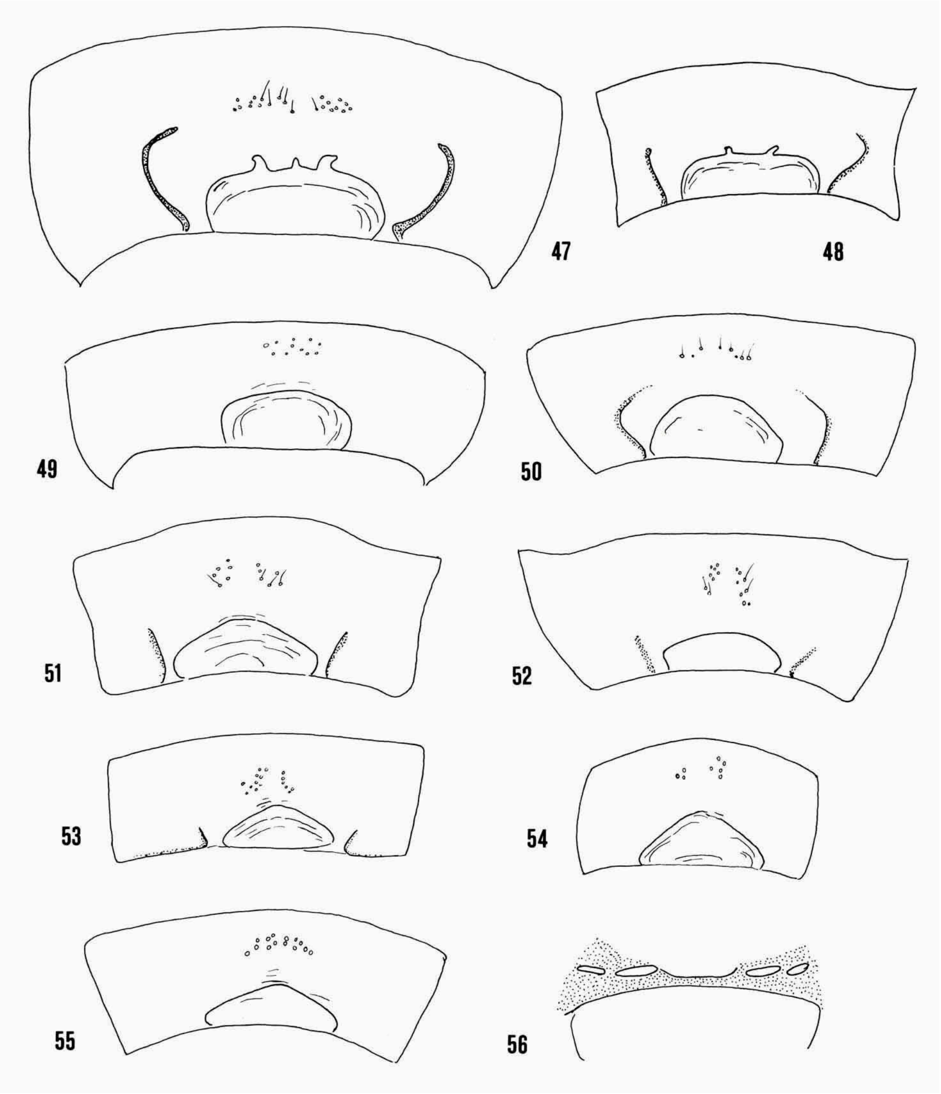
The males of most species possess a pair of anal tufts on T8, which are only lost secondarily in a number of species within *Stigmella*. These tufts comprise long, erect piliform scales, arising from two small patches close to the attachment of the tegumen to T8. In the *Stigmella ruficapitella* species group these tufts arise from strongly sclerotised plates.

In addition to the anal tufts, similar, but smaller tufts are found on T6 and T7 in all species of *Trifurcula*, and hence form another autapomorphy for this well defined genus.

A peculiar specialisation of the male abdomen occurs in most species belonging to the *repeteki* species group of *Acalyptris* (Puplesis, 1984c). Here terga 4 to 8 bear paired tufts, which comprise extremely long piliform scales, which are folded backwards, completely covering the abdomen (fig. 31). These tufts are usually associated with T-shaped sclerotisations on the tergites.



Figs. 32-46. Abdominal sternum 2, in 36-37 tergum 1 also partly shown. 32, *Opostega auritella* (Hübner), ♂, slide VU 1484; 33, *Pectinivalva* spec., ♂, slide VU 1483; 34, *Enteucha* spec., Nepal, ♂, slide VU 1337; 35, *E. gilvafascia* (Davis), ♂, slide VU 1366; 36, *E. cyanochlora* Meyrick, ♂, Holotype; 37, *E. acetosae* (Stainton), ♂, slide RJ 1407; 38, *Simplimorpha promissa* (Staudinger), ♀, slide VU 1181; 39, *Stigmella suberivora* (Stainton), ♀, slide VU 1919; 40, *Acalyptris minimella* (Rebel), ♀, slide VU 1434; 41, *A.* spec., near *psammophricta*, Iran, ♀, slide VU 1272; 42, *A. bipinnatellus* (Wilkinson) **comb. n.**, ♀, slide USNM 17428; 43, *A.* spec., Algeria, ♀, slide BM 22615; 44, *Trifurcula (Glaucolepis) rosmarinella* (Chrétien), ♀, slide VU 1411; 45, *T. (Levarchama) anthyllidella* Klimesch, ♀, slide VU 1932; 46, *Parafomoria pseudocistivora* Van Nieukerken, ♀ Paratype, slide VU 1320. All on same scale.



Figs. 47-55. Abdominal sternum 2 of *Bohemannia* and *Ectoedemia*. 47, *B. quadrimaculella* (Boheman), ♀, slide VU 1277; 48, *B. auriciliella* (Joannis), ♀, Holotype; 49, *B. pulverosella* (Stainton), ♀, slide VU 1280; 50, *E. (Etainia) decentella* (Herrich-Schäffer), ♀, slide VU 1285; 51, *E. (Laqueus) vincamajorella* (Hartig), ♀, slide VU 1425; 52, *E. (Fomoria) weaveri* (Stainton), ♀, slide VU 1079; 53, *E. (Fomoria) groschkei* (Skala), ♀, slide VU 1781; 54, *E. (Zimmermannia) liebwerdella* Zimmermann, ♂, slide VU 1832; 55, *E.* (s.str.) *heringiella* (Mariani), ♂, slide VU 1837. All on same scale. Fig. 56. *Enteucha* spec., Nepal, ♂, slide VU 1337, base of tergum 2, with unmelanized patches in sclerotisation.

Male genitalia

Exhaustive treatments of the male genitalia have been given by Scoble (1983) and Van Nieukerken (1985b). An important contribution towards the understanding of the evolution of male genitalia in Lepidoptera is Kristensen's (1984a) study of the lepidopteran ground plan.

Segment 8 is slightly modified to accommodate the genital capsule, such that T8 extends further posteriorly than S8.

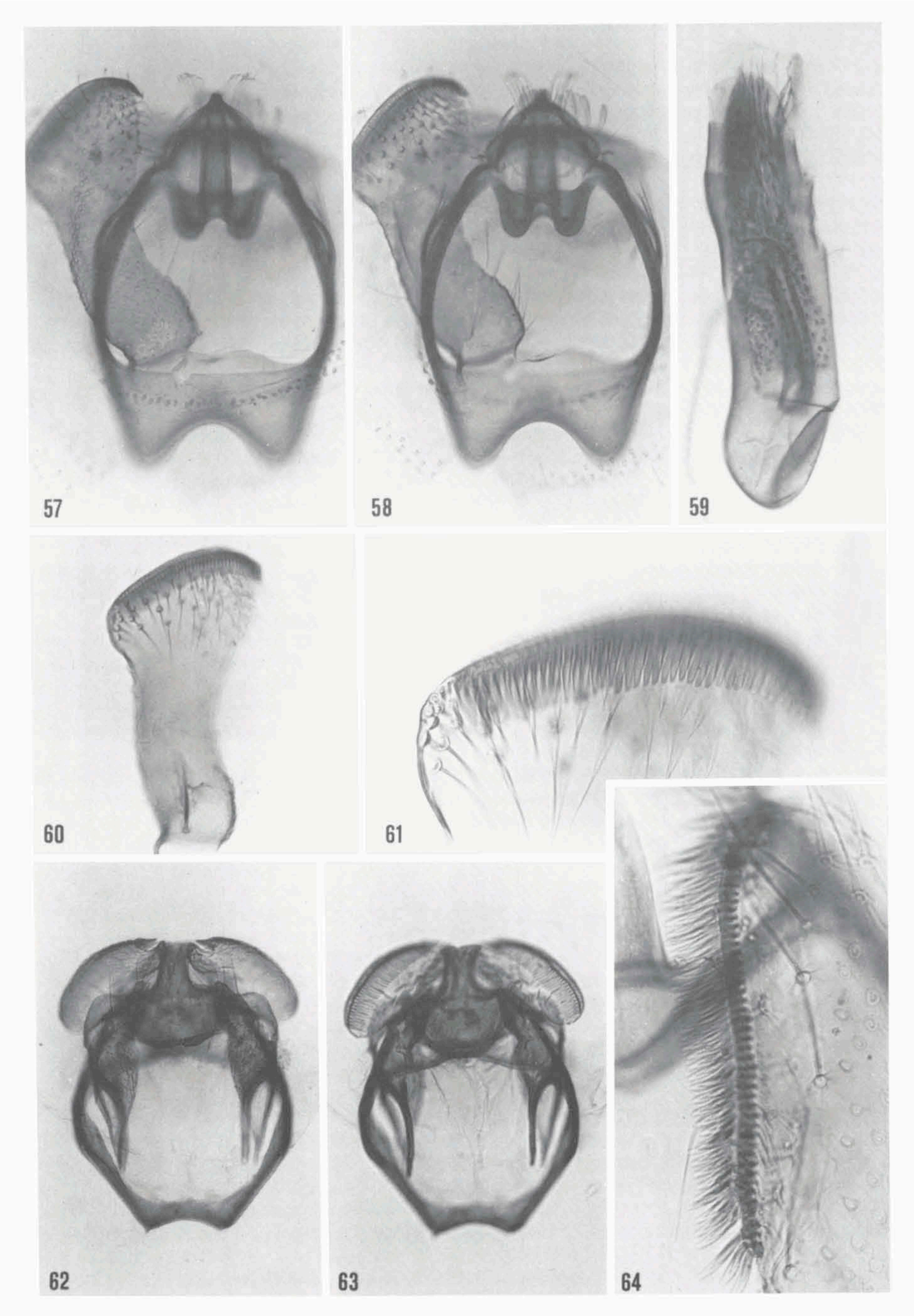
The Nepticulidae can be divided in two groups according to the condition of segment 9: either a separate tegumen and vinculum, or forming a complete ring without a recognisable separate tegumen. Scoble (1983) assumed that the fused condition is derived, a reasonable assumption considering the fact that the Opostegidae and Incurvarioidea have the separate condition as well. However, Kristensen (1984a) considers the complete ring to be most likely part of the lepidopteran groundplan, and the division of tegumen and vinculum to be secondary. If this is correct one should question if the fused ring in Trifurculini could be plesiomorphic, or a tertiary development or reversal. I am in favour of the latter possibility, since the first is in contradiction with a whole array of characters and upsets the most parsimonous cladogram. .

The valvae show considerable diversification within the Nepticulidae, and are often diagnostic for individual species. In *Pectinivalva* Scoble there is a well developed pectinifer (figs. 57-61) either along the inner margin or along the distal margin of the valva (Scoble, 1982; 1983); it resembles more or less the pectinifer of *Opostega* (figs. 62, 63). A similar row of spines occurs in the species of the *Acalyptris repeteki* group (Puplesis, 1984c) as illustrated in fig. 64. It is not clear if this pectinifer has independently evolved or is retained as a plesiomorphy although the latter possibility seems less likely since it involves the independent loss in many clades.

Apart from a distinct pectinifer, rows of strong spines occur in many Nepticulidae, and in *Ectoedemia (Etainia)* there are several strong, hooked spines on the inner surface near the tip of the valva.

It is strongly dissuaded to use terms like "style" or "cuiller" for parts of the valva since homology with such structures in Ditrysia is at least questionable (Scoble, 1978b, Schoorl et al., 1985). Simple descriptive terms like valval tip, digitate process, distal process, inner lobe, etc. are recommended instead. The often strongly developed valval tip, with many tactile setae on the inner surface, possibly replaces functionally the pectinifer during copulation.

A well developed transtilla, joining the two valvae dorsally, is absent from *Pectinivalva, Enteucha, Trifurcula (Glaucolepis)* and many species of *Acalyptris*. Scoble (1983) assumed that the presence of a well developed



Figs. 57-64. Male genitalia with pectinifers. 57-61, *Pectinivalva* spec., slide VU 988; 57, 58, Genitalia without aedeagus and right valva, ventral aspect; 59, Aedeagus, lateral aspect; 60, 61, Right valva, dorsal aspect; 62, 63, *Opostega auritella* (Hübner), slide VU 1484, ventral aspect; 64, *Acalyptris falkovitshi* (Puplesis), right valva, slide VU 940.

transverse bar belongs to the ground plan of the family, since it is found in many Incurvarioidea. However, the transverse bar in Nepticulidae is not completely similar to that in Incurvarioidea, and since it seems to be absent in the Opostegidae (own observations) and the most basal taxa of the Nepticulidae (*Pectinivalva, Enteucha*), the alternative solution that the transverse bar is evolved independently in the Nepticulidae cannot be ruled about completely. The anteriorly directed processes of the transtilla which are usually named the ventral arms (Beirne, 1945; Scoble, 1983; Van Nieukerken, 1985b) are invariably present, also if the transverse bar is lacking. Although these processes are slightly more ventral in position than the transverse bar, the term "ventral arms" is not very appropriate and could better be replaced by the more suitable term sublateral processes as used in the Incurvarioidea (e.g. Nielsen, 1985b).

The aedeagus is a well-sclerotised tubular structure, closed anteriorly, and with the opening through which the ductus ejaculatorius enters on the ventral side, usually slightly anterior of middle. The position of this opening, infrequently illustrated in taxonomic papers, could be diagnostic, it is shifted anteriorly in several species. Posterior of the opening there is a group of microsetae or pores, probably representing some kind of sensilla with unknown function. The primitive aedeagus in Nepticulidae appears to be a rather long smooth tube, with a vesica covered by many spiculate cornuti. This type is found in *Pectinivalva, Enteucha* and most species of *Stigmella*.

In several Holarctic species of *Stigmella* the distal portion of the aedeagus is surrounded by a more or less sclerotised membrane, covered by denticles, which is believed to be the innermost layer of the anellus: the manica (cf. Klots, 1970). The manica is more closely associated with the aedeagus than with the remaining diaphragm; when the aedeagus is removed from the genitalia it usually remains in position on the aedeagus.

In the Trifurculini the aedeagus is frequently adorned with processes near the phallotrema, which are called carina or carinate processes (Scoble, 1983; Van Nieukerken, 1985b). These carinae are hollow spinelike processes, of which the inner side is invisibly fused with the aedeagal tube, and the outer side with membranes belonging to the diaphragm (anellus). These membranes unite the aedeagus to the valvae, transtilla and vinculum. Ventrally there is often a ventral process – a juxta-like structure – which hinges the carinae to the vinculum.

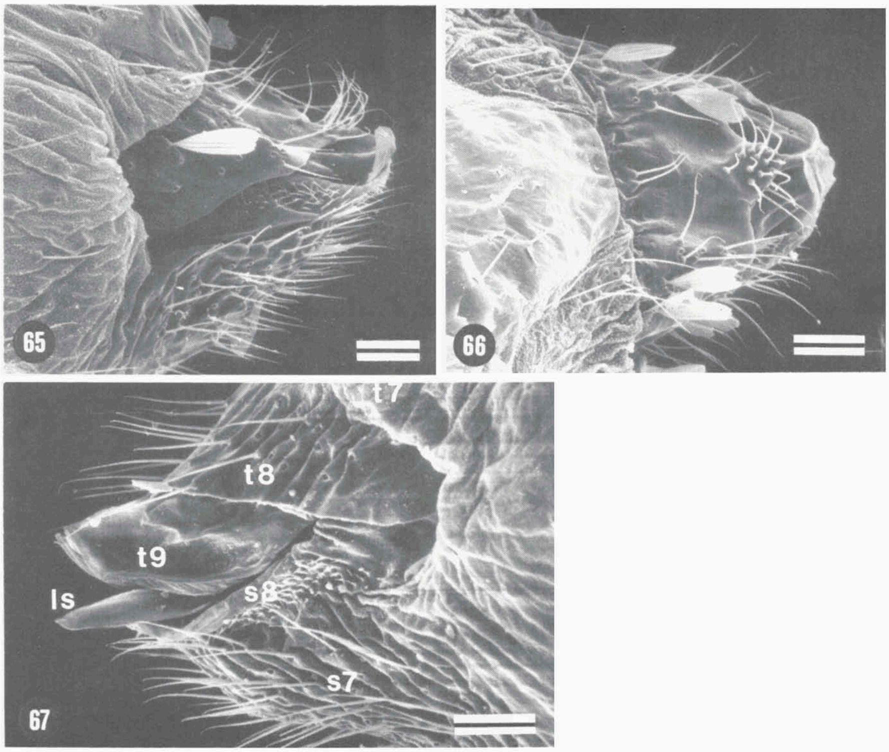
The base of the ductus ejaculatorius is surrounded in most Nepticulinae by a striate thickening (Scoble, 1983), for which the name cathrema has been proposed (Schoorl et al., 1985). According to Scoble (1983) it is absent in the Pectinivalvinae, but at least in some species there is a more or less tubular structure, which seems to surround the ductus as well and hence could be a homologue of the cathrema (fig. 59). The smooth cathrema in *Enteucha,* here assumed to be autapomorphous, slightly resembles the condition in *Pectinivalva,* and might therefore after all appear to be the plesiomorphous condition. Further work on the genital morphology of *Pectinivalva* and *Enteucha* is therefore much needed.

A well developed juxta is present in several species of *Stigmella,* especially in more generalised members of the genus, such as the *betulicola* species group (Schoorl & Wilkinson, 1986). Scoble (1983) questioned the homology of this juxta and the incurvarioid juxta, although there is some resemblance. In any case, the apomorphy "loss of juxta" for the Nepticuloidea (Kuznetsov & Stekolnikov, 1978; Davis, 1986b) should be viewed with some suspicion.

Female genitalia

The morphology of the female postabdomen (segments 7-9) has been described by Van Nieukerken (1983b, 1985b) respectively for *Parafomoria* and *Ectoedemia* (partim). In general the structure is not much different in the other genera, the situation in *Stigmella* is here illustrated in some detail (figs. 65-67). T8 is always a distinct sclerotised plate, usually with two groups of scales and setae, but occasionally with special patterns of setae, such as the posterior medial group of setae in *S. anomalella* (fig. 66). In the *Stigmella ruficapitella* group T8 has two longitudinal grooves alternating with rows of setae. In many species throughout the family the scales on T8 are lost and often long setae or large patches of setae develop instead, apparently as an adaptation to oviposition on special surfaces. S8 is represented by an almost semicircular sclerotised bar, which often forms the posterior end of the abdomen, and which anteriorly is joined to the anterior apophyses and to T8. It is normally covered with a spinose membrane as in figs. 65 and 67 (see also fig. 30 in Van Nieukerken, 1985b). T9 is a weakly sclerotised plate often represented by a pair of anal papillae (setose pads), which are often absent in *Stigmella* (as in figs. 65-67). A pair of lateral sclerites, probably representing a caudal part of the posterior apophyses can often be observed in *Stigmella* (fig. 67) and are projecting out of the abdomen.

The ovipositor – the complex of T8, T9, S7 and S8 together – is usually blunt and not extendable, but in several not closely related species it is elongate and pointed. These long ovipositors are apparently adaptations to hidden oviposition sites, such as hairy leaves or in narrow hairy axils between veins. Some examples include *Stigmella zelleriella* (Snellen) ovipositing on *Salix repens* (cf. Van Nieukerken, 1983a), *S. tityrella* (Stainton) on *Fagus* (in the hairy axils on the leaf-underside), *Ectoedemia turbidella* (Zeller) on



Figs. 65-67. *Stigmella,* female abdominal tip. 65, 66, *S. anomalella* (Göze), lateral (65) and dorsal (66) aspects (note medially pointed and setose t8); 67, *S. aurella* (Fabricius), lateral aspect. ls = lateral sclerite; s = sternum; t = tergum. Scales: 30 μm.

Populus alba and *Trifurcula (Glaucolepis) rosmarinella* (Chrétien) on *Rosmarinus* (in the furrow between the enrolled leaf-margins).

The internal genitalia comprise a short vagina, often enlarged into a heavily folded vestibulum and a globose bursa copulatrix. A ductus bursae is difficult to recognise as separate structure, possibly part of the structure here named vestibulum and elsewhere colliculum (e.g. Wilkinson & Scoble, 1979; Davis, 1986b) belongs to it. The vestibulum shows many specialisations, in many Trifurculini elaborate sclerotisations surround it or occur internally, and several evaginations occur, such as the spiculate pouch in *Ectoedemia* s.str. (Van Nieukerken, 1985b) or a small accessory sac in some *Bohemannia* species. In many *Stigmella* species there is a large elaborate accessory sac or bursa accessorius (see Schoorl et al., 1985; Kemperman & Wilkinson, 1985), which is often better sclerotised and more folded than the corpus bursae. In some species it is arcuate or coiled, such as in *S. hybnerella* (Hübner). It is very likely that the accessory sac replaces in such cases the bursa during copulation by receiving the male vesica. A strong indication for this assumption was the finding of a female *S. hybnerella* (Dutch material) with a complete set of male cornuti inside the accessory sac. The most specialised situation occurs in the *ruficapitella* species group (cf. Johansson, 1971). Here the structure hitherto believed to be the bursa itself is in fact a greatly enlarged accessory sac. The following points lead to this interpretation. 1. The inner wall of the sac is covered with strong spines: such spines have never been found inside a *Stigmella* bursa, but in some other species they occur in the accessory sac; 2. The point of entrance of the ductus spermathecae is often on this sac, far away from the posterior end, whereas in other groups this point is always on the vestibulum or accessory sac, never on the bursa itself. 3. The bursa proper is shown to be present at least in preparations of *S. atricapitella* (Haworth), but very weakly sclerotised and therefore probably often lost during preparation (figs. 29, 30); 4. In the closely related species of the *suberivora* group (sensu Kemperman & Wilkinson, 1985) the accessory sac is always strongly developed and better sclerotised than the bursa itself. Hence, the accessory sac of the *ruficapitella* group is considered as a further specialisation of the type present in the *suberivora* group.

The inner wall of a typical nepticulid bursa is covered with rows of small spines: pectinations, which often locally have special patterns, forming more or less distinct signa. Paired signa occur in some *Stigmella* species and most Trifurculini, in which they have a reticulate pattern.

The ductus spermathecae resembles the typical lepidopteran pattern described by Dugdale (1974), with a sclerotised internal canal and a more membranous external canal, both coiled and leading to a sclerotised vesicle. The angulated condition of the ductus noted by Dugdale (1974) is a derived condition occurring within some groups of *Stigmella*. The coiled ductus is in fact another apomorphy of the Neolepidoptera, not listed by Kristensen (1984b), as appears from Dugdale's table 2. The number of convolutions appears to be a strong diagnostic character for nepticulid species, as is often the shape of the vesicle. The part of the spermatheca distal of the vesicle is hardly sclerotised and usually not preserved in KOH treated specimens. The few observations made show that the description given by Dugdale (1974) applies to most Nepticulidae.

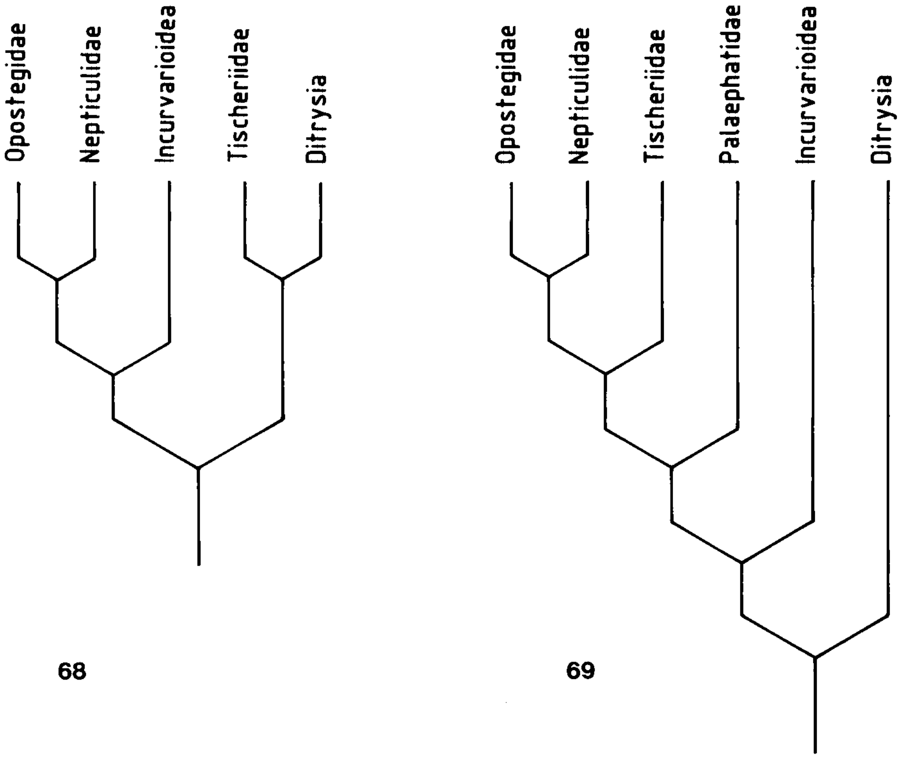
The paired collaterial glands are very large and always present, but have to be removed from slides made for taxonomical purposes, since they often distort the remaining genitalia by their sticky substance.

PHYLOGENY

Position of the Nepticuloidea

By most modern authors the Nepticulidae are considered to form together with their sister-group the Opostegidae the superfamily Nepticuloidea and to belong to the monotrysian grade of the Heteroneura (= Frenatae). The phylogeny and monophyly of the Heteroneura have recently been discussed by Kristensen (1984b), Nielsen (1985a) and Davis (1986b) (see also figs. 68, 69). However, since the views of Nielsen and Davis are partly at variance with each other, and the monophyly of the Heteroneura has been questioned by Minet (1984), I will discuss these views shortly and present my own opinion about the position of the Nepticuloidea.

The monophyly of the Heteroneura is based on at least 7 apomorphies (Kristensen, 1984b), including the heteroneurous venation, frenate wing-



Figs. 68, 69. Phylogeny of the Heteroneura, alternatives showing the views of Nielsen (1985) (fig. 68) and Davis (1986b) (fig. 69). See text for discussion.

coupling, loss of abdominal sternum 1, and three characters of the wing base structures. The seventh character, presence of a prosternal bridge ("pont précoxal") has been refuted as an apomorphy by Minet (1984) on the basis of its absence in Opostegidae and its weak sclerotisation in Nepticulidae. However, I am with Davis (1986b) of the opinion that this structure in Nepticulidae, although weakly sclerotised, resembles more the apomorphous condition as found in Incurvarioidea than the plesiomorphous condition, and hence can better be regarded as a secondary reduction. The complete absence of this structure in Opostegidae is of course remarkable, but must tentatively be regarded as a further reduction. Also more species of Opostegidae, and primitive Nepticulidae should be studied with regard to this character. Minet also questioned the validity of three other characters (he did not discuss the wing base structures) on the basis of the occurrence of parallelisms in non-related groups (heteroneury, reduction sternum 1) or because it does not apply to a single, well defined structure (wing coupling). The questioning of an apomorphy because it occurs elsewhere as a parallelism is methodologically not justified, since only ingroup parallelisms can weaken or refute a supposed apomorphy. If such an argument is universally accepted, it would lead to dismissing many well founded apomorphies. An apomorphy such as heteroneury is based on out-group comparison: in the three taxon comparison Neopseustina, Exoporia, Heteroneura, the homoneurous condition is found in the Exoporia and the out-group Neopseustina and also in all other more primitive groups (except the parallel situation in Zeugloptera as indicated by Minet) and hence heteroneury is assumed to be the apomorphy for the Heteroneura. Also on grounds of parsimony, the monophyly of the Heteroneura based on at least seven characters must be preferred to Minet's solution, which is based on two characters for the monophyly of Exoporia and Eulepidoptera and two for the monophyly of the Eulepidoptera (= Heteroneura without Nepticuloidea), including the prosternal bridge. Thus, in conclusion I agree with Kristensen (1984b) and Davis (1986b) that monophyly of the Heteroneura is at present the best hypothesis available.

The phylogeny of the monotrysian families in the Heteroneura is still far from resolved, and the problem has become more difficult to solve due to the discovery of an entirely new family, the Palaephatidae, in austral South America (Davis, 1986b) and later in Australia (Nielsen, in press). Nielsen (1985a) and Minet (1984) excluded in Tischeriidae from the monophyletic pair Nepticuloidea + Incurvarioidea (which could be named Monotrysia) and regarded the Tischeriidae as the sister-group of the Ditrysia on the basis of the female frenulum. Davis (1986b), however, reestablished the Monotrysia, including the Tischeriidae and Palaephatidae, as the sister-group of the

Ditrysia, mainly on the base of the metafurcasternum. Both phylogenies are reproduced in figs. 68 and 69. The only synapomorphy for the Tischeriidae + Ditrysia, female frenular bristles arising from a single socket, has been questioned by Davis (1986b), since there is also a concentration of pseudofrenular (= costal) bristles in some Palaephatidae and Prodoxidae. I want to stress here the point that in my opinion the pseudofrenular setae – at least in the Nepticuloidea – are not homologous with the male frenulum. In fact, similar setae (costal bristles) occur on the same position in the male hindwing (see section on morphology) and no setae occur on the same place as the frenulum. A frenulum as in female Ditrysia and Tischeriidae is similar to the male frenulum and in my opinion a true homologue. Acquisition of this character in the female could therefore be a novelty, but I must admit that I have not examined the situation of the so-called pseudofrenular bristles in Prodoxidae and Palaephatidae.

Some weak points in Davis' cladogram include the absence of a pectinifer in Tischeriidae and Palaephatidae and the overall weakness of the characters supporting the monophyly of the Nepticulina and the monophyly of the Tischeriidae + Nepticuloidea, all being regressive traits. Davis also indicates an alternative sister-group relationship of Palaephatidae + Ditrysia on the basis of three characters.

The lack of characters makes it impossible to make a firm and final choice between Nielsen's and Davis' cladograms, but intuitively I have a slight preference for Nielsen's cladogram with the Palaephatidae included somewhere near the Tischeriidae. Detailed morphological studies on the lower Heteroneura, including immature stages, seems now of paramount importance to solve this "monotrysian heteroneuran phylogeny puzzle".

Phylogeny of the Nepticuloidea

The sister-group relationship between the Opostegidae and Nepticulidae – together forming the Nepticuloidea – is well documented (Nielsen, 1985a; Davis, 1986a; 1986b; Minet, 1984) and supported by a whole array of characters listed by these authors. Amongst these are the expanded scape and several larval characters. To these can be added the presence of special branched sensilla and the overall very similar configuration of the flagellar segments (Van Nieukerken & Dop, 1984; 1986).

The monophyly of the Nepticulidae is based on the following characters: 1. M and R in forewing coalescent. This is the situation in the Pectinivalvinae and Nepticulini. The condition in Trifurculini with M + Cu coalescent and M meeting Rs later is thought to be secondary; 2. Flagellar segments with paired sensillum vesiculocladum (Van Nieukerken & Dop, 1984; 1986); 3. Genital capsule of male, in particular vinculum, well sclerotised (Scoble, 1983); 4. Tegumen band-shaped (Scoble, 1983); 5. Uncus hood-shaped (Scoble, 1983); 6. Aedeagus broad and well sclerotised (Scoble, 1983); 7. Cornuti of aedeagus numerous (Scoble, 1983); 8. Pupa with large and numerous spines on dorsum (Scoble, 1983). The doubts on the validity of this character expressed by Scoble can be partly removed, since similar spines are absent from Opostegidae (Davis, 1986a); 9. Larval abdominal segments 1-8 with 6 pairs of setae only (Van Nieukerken & Jansen, in prep.).

Scoble (1983) lists another three characters which are here regarded as ancestral: 1. fusion of M1 and M2 belongs to the groundplan of the Nepticuloidea and the Tischerioidea (Davis, 1986b); 2. vinculum U-shaped belongs to the ground plan of Monotrysia (Nepticuloidea + Incurvarioidea) and 3. gnathos with undivided central element belongs probably to the ground plan of Nepticuloidea.

For a better understanding of the ground plan of Nepticulidae and Nepticuloidea detailed and comparative morphological studies on Opostegidae and Pectinivalvinae including immature stages are much needed.

Phylogeny of the Nepticulidae

Scoble (1983) presented for the first time a phylogeny of Nepticulidae based on cladistic principles. His primary divisions of the family into Pectinivalvinae + Nepticulinae (= Nepticulini + Trifurculini) are here maintained and supported by some new characters. Further an attempt has been made to refine the cladogram on the generic and subgeneric level, resulting in the phylogeny presented in fig. 70. Apomorphies for each clade are numbered both in text and figure, but autapomorphies for genera and subgenera are listed only in their respective treatments.

As noted above, the primary dichotomy in the Nepticulidae falls between the Pectinivalvinae and Nepticulinae. The Pectinivalvinae (genus *Pectinivalva*), which are only known from Australia and thus fall outside the scope of this paper, are characterised by the following apomorphies (all from Scoble, 1983): 10. Deflection of R + M towards costa of hindwing; 11. Form of uncus (possibly); 12. Modification of ends of lateral arms of vinculum (possibly). Another autapomorphy might be the hostplant family, the Myrtaceae, in which all species of which the life-history is known appear to feed.

The Nepticulinae are defined by the following set of apomorphies: 13. Subdorsal retinaculum present on forewing (Scoble, 1983); 14. Trunk 1 + 2A thickened in forewing (Scoble, 1983); 15. Pectinifer lost (Scoble, 1983). It is tentatively assumed that the pectinifer-like structure in an infrageneric group of *Acalyptris* is a novelty, rather than a retained plesiomorphy, which involves the independent loss in many clades; 16. Cathrema present as striate thickening (Scoble, 1983). The aberrant condition in *Enteucha* and *Varius*, where there is only a smooth tubular structure is at present considered to be secondary, but its resemblance to the more open sclerotisation in *Pectinivalva* might sug-

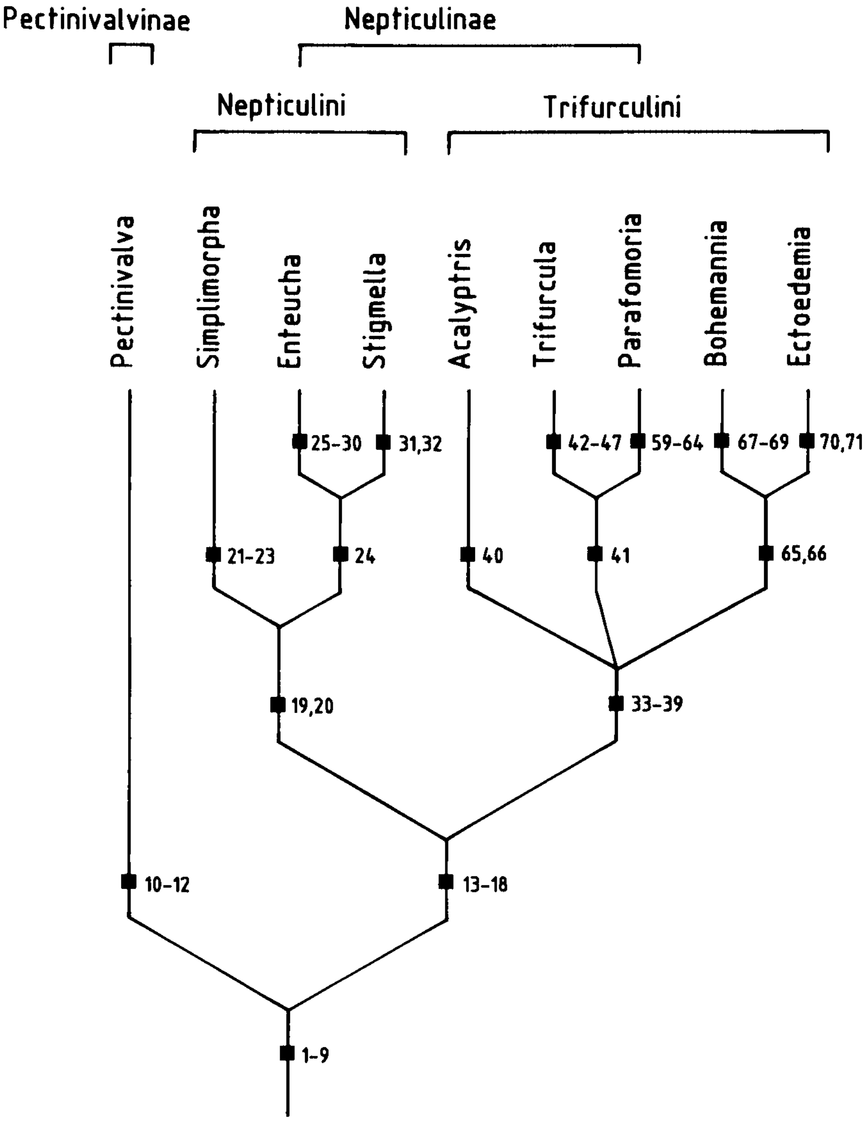


Fig. 70. Cladogram of the Nepticulidae, demonstrating the phylogenetic relationships between the genera. Numbers refer to apomorphies, explained in text.

gest rather a plesiomorphous condition. This possibility is at present refuted on grounds of parsimony; 17. Larval antenna reduced to one cushion-like segment (Van Nieukerken & Jansen, in prep). The important finding that the larval antenna of *Pectinivalva* has the plesiomorphic condition with three segments as in most Lepidoptera (including the Opostegidae), further corroborates the primary division of the Nepticulidae and the monophyly of the Nepticulinae; 18. Signa on corpus bursae paired (Scoble, 1983).

A further character listed by Scoble, reduction of Cu in forewing, is a doubtful apomorphy, since so much variability of this character occurs at and below the species level.

The next dichotomy, between Nepticulini (Stigmellini) and Trifurculini, introduced by Scoble, is maintained, but the Nepticulini, still monotypic in Scoble's concept, are widened here. This tribus is characterised by the following larval characters (see further Van Nieukerken & Jansen, in prep.): 19. Labrum with one pair of setae dorsally. All other Nepticulidae and Opostegidae have two setae or one seta and one setal pore; 20. Labial palpus with two segments only. The three-segmented palpus is the condition in *Pectinivalva* and many Trifurculini, but some Trifurculini also have two segments.

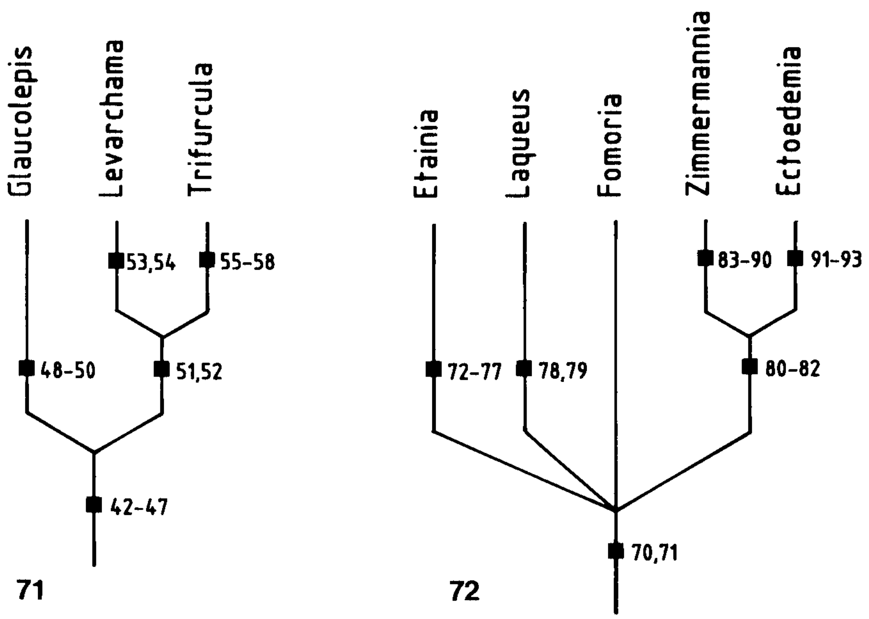
There are at present no adult characters, which can be regarded as synapomorphies for the Nepticulini, the similarity of the three genera is largely based on symplesiomorphies. The basic dichotomy is tentatively assumed to lay between *Simplimorpha* (apomorphies 21-23) and the remaining genera, *Enteucha* (25-30) and *Stigmella* (31-32). The last two are regarded as sister-genera on the basis of the single apomorphy: 24. Collar in adult conspicuous, comprising lamellar scales. This character is only as a parallelism evolved in parts of *Bohemannia* and *Acalyptris*. *Varius* Scoble could be the sister-group of *Enteucha* on the basis of characters 28 and 29 or be a synonym of the latter, see discussion under *Enteucha*.

The Trifurculini form a tight monophyletic assemblage on the basis of the next apomorphies (33-38 also listed by Scoble, 1983): 33. Vinculum ring-shaped (see also morphological discussion); 34. Tegumen extended posteriorly, forming a pseuduncus; 35. M coalesced with Cu at base of forewing, and subsequently deflected to meet Rs at branching point between R2 + 3 and R4 + 5; 36. Uncus forms thickened band in shape of inverted V or Y; 37. Vestibulum (or ductus bursae) with prominent sclerotisation; 38. Signa on corpus bursae reticulate; 39. Paired carinae and ventral process present in male aedeagus. The almost universal occurrence of carinae in Trifurculini and the absence in other nepticulids makes this a very likely apomorphy for the Trifurculini. However, a few carina-like structures in *Stigmella* should be examined carefully to see if they are real homologues or different structures as in *S. naturnella* (Klimesch), where it is probably a complex juxta.

The phylogeny of the genera within the Trifurculini is the most difficult to solve. Scoble (1983) presented it as an unresolved polytomy with at least six branches. By synonymising some genera I have reduced the number of them to five, but I am only able to indicate one more or less strong sister-group relationship, that between *Bohemannia* and *Ectoedemia*. Tentatively I regard *Parafomoria* as sister-genus of *Trifurcula,* although there is an alternative placement, so that the resulting cladogram shows an unresolved trichotomy at the basis of the Trifurculini (fig. 70).

No synapomorphies have been found to link *Acalyptris* (apomorphy 40) to any other genus, although overall the genus resembles most the pair *Trifurcula-Parafomoria*. The latter pair is here regarded tentatively as a monophyletic entity on the basis of a single character: 41. Female T8 longitudinally divided. Sometimes the division is only indicated by a medial incision of T8.

The evidence for monophyly of *Trifurcula* (42-47) plus *Parafomoria* (59-64) is not very strong, since the latter also shows some similarity to *Ectoedemia,* as for instance in the typical male hair-pencil, so that alternatively *Parafomoria* could be the sister-group of *Bohemannia* + *Ectoedemia*.



Figs. 71, 72. Cladograms of the genera *Trifurcula* (fig. 71) and *Ectoedemia* (fig. 72), demonstrating the relationships between the subgenera. Numbers refer to apomorphies, listed in the text.

The phylogeny of the subgenera of *Trifurcula* is shown in fig. 71.

The monophyly of *Bohemannia* (67-69) plus *Ectoedemia* (70-71) is based on the following larval characters (Van Nieukerken & Jansen, in prep.): 65. Frontoclypeus approximately stirrup-shaped or triangular. 66. Anterior tentorial arms much longer than posterior arms. Both characters are closely correlated, since the shape of the frontoclypeal ridges influences the position of the tentorial arms. In all other Nepticulini the tentorial arms are similar in length and the frontoclypeus is rectangular.

The phylogeny of the subgenera of *Ectoedemia* is problematic, and presented as an unresolved polytomy of four branches (fig. 72). *Etainia* shows some similarities with *Zimmermannia* in the larva and also the loss of the uncus, but there are other arguments against a sister-group relation between *Etainia* and *Zimmermannia*.

BIOGEOGRAPHY

Biogeographical considerations on Nepticulidae are really hampered by the lack of knowledge on the nepticulid fauna from such major areas as the Neotropic and Oriental regions. Also from the major part of Africa hardly any species is known and from Australia only unpublished information is available (Scoble, pers. comm.). However, information on distribution is increasing and the present knowledge is mapped below for all (sub)genera, except for *Stigmella,* which is almost cosmopolitic.

It is striking that most (sub)genera have a very wide distribution, and endemism seems almost absent. Only *Pectinivalva* is confined to one continent: Australia. Two taxa seem to be predominantly Ethiopian, viz. *Simplimorpha* and *Ectoedemia (Laqueus),* but both occur in southern Europe as well. *Parafomoria* is only known from the West Palaearctic, and *Trifurcula* (s.s.) is at present only known from the old world.

When comparing the distribution patterns with the phylogenies presented above, no distinct vicariant patterns become visible, so that knowledge on biogeography at present neither corroborates nor falsifies the phylogenetic hypothesis as presented above.

HOSTPLANT RELATIONSHIPS

Nepticulidae are for a major part known through collecting and rearing of leaf-mines, so that there is a large amount of knowledge available on hostplants and degree of polyphagy. This knowledge led in the past to the general idea that nepticulid species are strictly monophagous and that closely related species feed on related hosts. Although the *a priori* use of this idea has given rise to many mistakes at the species level (Wilkinson & Scoble, 1979;

Table. 1. Hostplant families and subclasses for world Nepticulidae. A: number of nepticulid species recorded per hostplant family; C: idem per subclass; B and D: given as percentage of total moth-hostplant records. An asterisk denotes records of oligophagous species, feeding in several families or subclasses. Not given are records of unknown nepticulid species for subclasses NYMPHAEIFLORAE (Piperaceae, mines in Brazil, unpublished observation) and PROTEIFLORAE (Proteaceae, species in Australia, Powell, 1980).

Plant Subclass	Plant family	A	B	C	D
POLYGONIFLORAE	Polygonaceae	10	1.8	10	1.8
PLUMBAGINIFLORAE	Limoniaceae	2	0.4	2	0.4
MALVIFLORAE	Cistaceae	8	1.4	86	15.1
	Tiliaceae	9	1.6		
	Malvaceae	5	0.9		
	Ulmacceae	16	2.8		
	Moraceae	5	0.9		
	Euphorbiaceae	10	1.8		
	Rhamnaceae	33	5.8		
	various	6	1.1		
VIOLIFLORAE	Salicaceae	30*	5.3	34*	6.0
	various	4	0.7		
THEIFLORAE	Clusiaceae	9	1.6	11	1.9
	various	2	0.4		
PRIMULIFILORAE	(mainly Ebenaceae)	15	2.6	15	2.6
ROSIFLORAE	Fagaceae	88	15.5	235*	41.4
	Betulaceae	33*	5.8		
	Rosaceae	104*	18.3		
	various	14*	2.5		
MYRTIFLORAE	Myrtaceae	10	1.8	17	3.0
	various	7	1.2		
FABIFLORAE	Fabaceae	28	4.9	28	4.9
RUTIFLORAE	Anacardiaceae	12	2.1	42*	7.4
	Aceraceae	15	2.6		
	various	15*	2.6		
SANTALIFLORAE	(mainly Celastraceae)	10	1.8	10	1.8
ARALIFLORAE	Apiaceae	3	0.5	3	0.5
ASTERIFLORAE	Asteraceae	19	3.3	19	3.3
SOLANIFLORAE	Convolvulaceae	2	0.4	2	0.4
CORNIFLORAE	Ericaceae	16*	2.8	22*	3.9
	various	6	1.1		
GENTIANIFLORAE	various	8	1.4	8	1.4
LAMIFLORAE	Lamiaceae	11	1.9	19	3.3
	various	8	1.4		
COMMELINIFLORAE	(Cyperac., Poac.)	3	0.5	3	0.5
total		568	100%	568	100%

Van Nieukerken, 1986), the general idea is true. Monophagy, at least at generic plant level, and often at species level, is the common condition in Nepticulidae, and oligophagy even on family level is rare. Real polyphagy has not been reported, but a few cases of disjunct oligophagy are known: *Stigmella corylifoliella* (Clemens) feeds on four families in two subclasses (Wilkinson & Scoble, 1979) and *S. aurella* (Fabricus) and *Ectoedemia atricollis* (Stainton) are both oligophagous on Rosaceae and feed on one host in a different family and subclass (Van Nieukerken, 1986).

That closely related species often feed on closely related, or the same hosts, can for instance be seen in the check-list for the West Palaearctic region (Van Nieukerken, 1986), where many species-groups of *Stigmella* and *Ectoedemia* are monophagous on a single host family. However, Scoble (1983) stated that "*major* nepticulid lineages are not, in general, associated with particular hostplant lineages". This holds true for the large genera *Stigmella, Acalyptris* and *Ectoedemia* (s.l.), but certainly not for several of the smaller (sub)genera, which are (almost) completely associated with one hostplant family: *Pectinivalva* (on Myrtaceae), *Simplimorpha* (Anacardiaceae), *Enteucha* (Polygonaceae), *Trifurcula* s.l. (Fabaceae), *Parafomoria* (Cistaceae) and *Ectoedemia (Zimmermannia)* (Fagaceae).

Powell (1980) presented a survey of major hostplant families for Nepticulidae, but because many more data became available recently, an updated survey is presented in table 1. The plant taxonomy is taken from Dahlgren (1983), which although not strictly cladistic comes most close to a cladistic system. In contrast with Dahlgren I included Corylaceae in Betulaceae and took the Rosaceae in the wide sense, including the trees.

The host-records are taken from published accounts on the Nearctic (see under material), western Palaearctic (Van Nieukerken, 1986) and South African species (Scoble, 1978-83). The data on eastern Palaearctic species are compiled from the works of Puplesis (1984-1985) and Kemperman & Wilkinson (1985) and unpublished data on Nepticulidae from China, Japan and Nepal. From other regions the published data are scanty and include amongst others Gustafsson (1985) on Gambia and Donner & Wilkinson (in press) on New Zealand. For Australia only the record of about ten species of *Pectinivalva,* feeding on Myrtaceae, is included. Other data are from unpublished sources.

As in many similar accounts (Powell, 1980) there is a strong bias towards the Holarctic region, where for 430 species the host is known on a total of 568 species world-wide. To stress the enormous difference between northern and southern hemisphere fauna's, the host record for southern Africa and the Holarctic are given separately per genus in tables 2 and 3.

The very strong dominance of the Rosiflorae in the host record of the Holarctic (almost 53%) strongly influences the world percentage of 41, since only four species in the southern Hemisphere are recorded from this subclass. This is not surprising, because the Rosiflorae are inconspicuous in the southern hemisphere flora in contrast to their dominant position in the forests of the Holarctic, which are often entirely formed by trees belonging to Fagaceae, Betulaceae and Rosaceae.

Despite the discrepancies between the different regions, a few general trends can be observed. Two subclasses are well represented hosts in both hemispheres: the Malviflorae and Rutiflorae. Also striking is the almost complete

Table 2. Hostplant families and subclasses for the Nepticulidae of South Africa based on studies of Scoble. Refer for subclass names to table 1. Abbreviations of (sub)genera: Si = *Simplimorpha,* V = *Varius,* S = *Stigmella,* Ac = *Acalyptris,* L = *Laqueus,* F = *Fomoria,* E = *Ectoedemia* s.str.

		Si	V	S	Ac	L	F	E	Ar	totaal	%	subclass
M	Sterculiaceae			2						2	3.1	25.4
	Tiliaceae			3						3	4.8	
	Malvaceae			1						1	1.6	
	Ulmaceae			1						1	1.6	
	Moraceae			2						2	3.1	
	Euphorbiaceae			3	1					4	6.3	
	Rhamnaceae			1			2			3	4.8	
V	Flacourtiaceae						1			1	1.6	4.8
	Capparaceae				1		1			2	3.1	
T	Ochnaceae		1							1	1.6	1.6
P	Ebenaceae					12				12	19.0	19.0
R	Rosaceae								1	1	1.6	1.6
M	Rhizophoraceae				1					1	1.6	9.5
	Myrtaceae				1					1	1.6	
	Combretaceae				3					3	4.8	
	Chrysobalanaceae			1						1	1.6	
F	Fabaceae			1	1					2	3.1	3.1
R	Anacardiaceae	1		1			2			4	6.3	15.9
	Sapindaceae			1			1			2	3.1	
	Rutaceae				1					1	1.6	
	Burseraceae							2		2	3.1	
	Geraniaceae			1						1	1.6	
S	Celastraceae					6				6	9.5	9.5
G	Oleaceae						1			1	1.6	4.8
	Rubiaceae				2					2	3.1	
L	Bignoniaceae						1			1	1.6	4.8
	Scrophulariaceae						1			1	1.6	
	Verbenaceae						1			1	1.6	
total		1	1	18	11	18	11	2	1	63	100%	

Table 3. Hostplant families and subclasses for the Holarctic Nepticulidae. Refer to table 1 for subclass names. Abbreviations of (sub)genera: S = *Stigmella*, A = *Acalyptris*, G = *Glaucolepis*, F = *Fomoria*, E = *Ectoedemia* s.str., remaining (sub)genera pooled under "other". Asterisks denote oligophagous species, recorded more than once.

		S	A	G	F	E	other	total	%	% subclass	
P	Polygonaceae						10	10	2.3	2.3	P
M	Cistaceae	1					7	8	1.9	13.3	M
	Tiliaceae	5						5	1.2		
	Ulmaceae	11				3	1	15	3.5		
	Rhamnaceae	21	1					22	5.1		
V	Salicaceae	21*				9*		30	7.0	7.0	V
T	Clusiaceae				9			9	2.1	2.3	T
R	Fagaceae	46				32	7	85	19.8	52.8	R
	Betulaceae	26*				5*	2	33	7.7		
	Rosaceae	78*				23*	2	103	24.0		
F	Fabaceae	4		1			14	19	4.4	4.4	F
R	Anacardiaceae	2	4			1	1	8	1.9	6.5	R
	Aceraceae	7		1		2	5	15	3.5		
C	Ericaceae	11*			1	3	1	16	3.7	4.9	C
L	Lamiaceae			11				11	2.6	3.7	L
various families/subcl.		15	7	7	4	8*	5	46	10.7		
total		245	12	20	14	84	55	430			

absence in the host record of the subclasses Magnoliiflorae, Nymphaeiflorae, Ranunculiflorae, Caryophylliflorae and all Monocotyledoneae – with only three nepticulid species recorded. This absence seems to be a general phenomenon within the microlepidoptera, with the exception of the grass-like monocots (Powell, 1980). The common feature of these subclasses, seems to be the presence of highly poisonous chemicals such as benzylisoquinoline alkaloids in the first three (Dahlgren, 1980).

Generalised, Nepticulidae tend to feed on woody apparent dicotyledons, which have quantitative chemical defense systems using tannin accumulation, and are as such not different from many other primitive Lepidoptera (Boomsma, 1984; pers. comm.; Powell, 1980). "Apparent" plants, such as trees or grasses, are in the terminology of Feeny (1976) "bound to be found" by insects, and thus more often attacked by parasites, which forces the plant to develop a chemical defense. This concept of quantitative defense by apparent plants (Feeny, 1976), using tannins, has recently been challenged both from research on the tannins themselves (Zucker, 1983) and from research on oak insects (Faeth, 1985).

Discussion on the evolutional significance of hostplant relationships is often obscured by the fact that hostplant data are treated statistically only and pooled for a certain taxon and by neglect of the known phylogenetic relationships of the insect group in question. In fact hostplant records should be treated in a similar way as morphological characters, divided into ancestral and derived states, and superimposed on a cladogram which has been inferred from morphological data. Only then can sound conclusions about the evolutionary history be made. When this is done roughly, the Nepticulidae appear to be conservative in hostplant choice, since species groups which originated on a certain host, rarely jump to another host-family (compare Van Nieukerken, 1985b and 1986). Hostplant choice is a complex, inherited character, which does not change at each speciation event. Speciation is probably primarily allopatric or parapatric (see also Menken & Brouwer, 1984), and often leads to the proliferation of species on a single host family or genus (such as *Quercus*). When a host shift occurs, this will most likely be on hostplants with similar chemical defences, which involves less difficulties in adaptation of the larval physiology. This probably explains the rarity of Nepticulidae feeding on "poisonous" plants and the relatedness of the species which have adapted to such plants. The palatability of such hosts as Rosaceae on the other hand explains probably the numerous shifts towards this family and also weakens considerably the argument of such hosts in phylogenetic reasoning.

There has been a strong belief in a co-evolution between insects and plants ever since Ehrlich & Raven's (1964) famous paper, but an accumulation of evidence has, amongst others, prompted Jermy (1984) to propose a sequential evolutionary model, where phytophagous insects do not affect plant evolution, but follow that of the plants. The situation in the Nepticulidae also fits better in Jermy's theory, and does not provide any evidence for real co-evolution.

It seems not possible to indicate the plant group on which the Nepticulidae most likely originated, because the most primitive genera have probably a derived hostplant choice. On the other hand it is tempting to speculate that they originated on Fagales, since the primitive Lepidoptera groups Heterobathmiina, Eriocranioidea, Tischerioidea and Incurvarioidea are either only known from Fagales or have at least a group of species on Fagales. Further, a fossil mine reported to be nepticulid, from the upper Cretaceous is found on a Fagales-leaf (Skalski, 1984 and pers. comm.).

All we can say about the origin of Nepticulidae is that they probably originated in the Cretaceous as leafminers on woody dicots. The recent discovery of the larva of *Heterobathmia* (Kristensen & Nielsen, 1983), suggests that leaf-mining is a ground plan character for the Heterobathmiina + Glossata. This is further corroborated by the predominancy of the leaf-mining habit in the Dacnonypha, Monotrysia and primitive Ditrysia. Other feeding strategies, as root boring, bark mining or external feeding were probably derived from leaf-mining.

CLASSIFICATION

The classification presented here is a phylogenetic (cladistic) one, in the sense that it represents phylogenetic relationships between the taxa recognised. In other words, the classification is a linear transcription of the cladograms which are thought to represent the phylogeny of the group in question. The way in which a classification should be formed as suggested by Hennig (1966) – naming each clade at each branching point in a formal taxonomic rank – has met much opposition because of the numerous taxonomic changes necessary and the complex nature of such classifications. Several authors have attempted since to suggest conventions in order to make a classification less complex, but still phylogenetic, and they were eventually combined in a useful system by Wiley (1981): the annotated Linnean classification. A major thought behind this system is that the number of taxonomic changes should be kept minimal to construct the classification. This includes "phyletic sequencing", use of informal ranks and annotation with "sedis mutabilis" (of interchangeable position) or "incertae sedis" (of uncertain placement).

I have adopted Wiley's (1981) conventions, and therefore followed Scoble (1983), who previously constructed a classification of Nepticulidae. The classification presented here therefore only deviates slightly from Scoble's. There are some nomenclatorial changes in the generic names, and one genus *(Obrussa = Etainia)* is sunk as subgenus; further some "incertae sedis" species have now a more permanent position. The most difficult decision was the delimitation of genera and subgenera. The genus name is not only a label for a monophyletic entity, but also serves as part of the binomen, and is therefore used by many people who are not so much interested in the phylogeny. Therefore the number of genera is kept small, no new genera are erected and some distinct monophyletic entities are rather recognised as subgenus than genus. In the case of *Ectoedemia* the decision is a provisional one, since its monophyly is not very certain (see further). I considered to lump *Ectoedemia* and *Bohemannia,* since the monophyly of this assemblage seems better supported, but this suggestion was considered impractical on the grounds of an enormous number of necessary name changes and the fact that the characters supporting this monophyly are only found in the larva, and actually the larva of only one species of *Bohemannia* has been studied. The genus delimitation used here has the advantage that all genera can be recognised on adult external or venational characters, which makes sorting of unidentified material easier than with genitalia characters.

The uncertainties in the basic divison of the Trifuculini prompted me to use informal names for the three lineages instead of introducing new suprageneric names.

Classification of the Nepticulidae on a world basis:

- Family NEPTICULIDAE
  - Subfamily PECTINIVALVINAE
    - Genus *Pectinivalva*
  - Subfamily NEPTICULINAE
    - Nepticulinae *incertae sedis: Areticulata leucosideae* (cf Scoble, 1983)
    - Tribe NEPTICULINI
      - Nepticulini *incertae sedis: Varius ochnicolus* (cf Scoble, 1983)
      - Genus *Simplimorpha*
      - Genus *Enteucha*
      - Genus *Stigmella*
    - Tribe TRIFURCULINI
      - *Acalyptris* assemblage, sedis mutabilis
        - Genus *Acalyptris*
      - *Trifurcula* assemblage, sedis mutabilis
        - Genus *Trifurcula*
          - Subgenus *Glaucolepis*
          - Subgenus *Levarchama*
          - Subgenus *Trifurcula*
        - Genus *Parafomoria*
      - *Bohemannia* assemblage, sedis mutabilis
        - Genus *Bohemannia*
        - Genus *Ectoedemia*
          - Subgenus *Etainia,* sedis mutabilis
          - Subgenus *Laqueus,* sedis mutabilis
          - Subgenus *"Fomoria",* sedis mutabilis
          - *Ectoedemia* subgenus pair, sedis mutabilis
            - Subgenus *Zimmermannia*
            - Subgenus *Ectoedemia*

TAXONOMIC PART

Family Nepticulidae

Nepticulidae Stainton, 1854: 295. Type-genus: *Nepticula* Heyden.
Stigmellidae Hampson, 1918: 387. Type-genus: *Stigmella* Schrank.

Diagnosis. — Small heteroneuran moths, recognised by enlarged scape (eyecap), vestiture of head comprising erect hair-scales, except collar in some species, usually very short galea, maxillar palpi not reduced. Forewings relatively broad, often with pale spots or fascia, hindwing in male with frenulum, in female and often in male as well with well developed costal bristles; both wings with long fringe. Venation characteristic (figs. 24, 80, 81, 83-86, 103, 104, 106-108, 119-126), with branched veins. Closely related Opostegidae only have unbranched veins. See further apomorphies listed in section on phylogeny.

Description. — Adult. Very small to moderately small, forewing length 1-5 mm, wingspan 2.5-11 mm. Head. Vestiture of erect piliform scales covering frons and vertex, collar comprising two groups of lamellar or piliform scales. Mandibles reduced. Maxilla with haustellate galea, usually short, but functional; maxillar palpi folded, 5-segmented. Labial palpi two- or three-segmented, short. Antenna with enlarged scape (eyecap), covering eye in rest; pedicel slightly larger than flagellar segments, total number of segments 14-70; flagellomeres moniliform, with regular whorls of scales and sensillum vesiculocladum present at least in terminal part of flagellum. Thorax with small tegulae, mesoscutum large, metascutum devoid of scales, spinose (fig. 4). Forewing relatively broad, often with pale spots or fascia, a cilia-line frequently present. Subcostal retinaculum on costal fold, comprising hooked scales, present in male, subdorsal retinaculum present or absent in both sexes. Special scales occur in males of several species on underside. Venation reduced, Sc short, M coalescent with R or Cu or both, R2 and R3 always fused; 1 + 2A entirely fused or forming anal loop. Hindwing narrow, with long cilia, rarely with colour pattern, frenulum present in male, costal bristles in female and often in male well developed. Special androconial scales often present in male. Venation reduced: Sc, Cu and A present as short single branches, R + M bifurcate or trifurcate. Legs: tibial spurs 0-2-4, epiphysis absent; vestiture comprising long spine-like scales. Abdomen with S1 absent, T1 only sclerotised along margins, forming tergosternal connection, articulating with S2. S2 divided into S2a and S2p. Female S4 with pair of fenestrae. Male with anal tufts on T8, occasionally also on other tergites.

Male genitalia. Capsula well-sclerotised. Vinculum often bilobed anteriorly, sometimes extended, not forming true saccus; lateral arms articulate or fuse with tegumen. Uncus and gnathos present as well sclerotised structures, sometimes reduced, gnathos usually with single medial element. Valvae saclike, approximately triangular, with or without pectinifer. Transtilla comprising sublateral processes and often a well-developed transverse bar. A separate juxta sometimes present. Aedeagus tubular, well sclerotised, with ventral opening for ductus ejaculatorius. Vesica armed with well sclerotised cornuti.

Female genitalia. Monotrysian, with single genital, terminal opening, separate from anal opening, cloaca absent. Ovipositor usually not extended, but broadly rounded, T8 band-shaped, joining anterior apophyses, which terminally form narrow S8. T9 reduced to flimsy tergite with anal papillae, posterior apophyses, and lateral sclerites. Segment 7 encircling segments 8 and 9. Vestibulum well developed, often with sclerotisations. Corpus bursae large, often covered with pectinations and paired signa. Ductus spermathecae coiled, internal canal well sclerotised.

Biology. — Larva leaf-miner on mostly woody dicotyledons, few species on herbs and only three species known to feed on monocotyledons. Secondary shift of larval feeding habits in several Trifurculini to stem-, bark-, bud- or fruit-mining. Eggs deposited on the surface of the leaf or the plant part in which the larva actually feeds. The egg itself has not been studied; it is covered by a smooth helmet shaped case, formed by secretion from the female collaterial glands.

The larva, after hatching, eats the egg-shell and enters the plant tissue immediately. The hole remains usually covered by the egg case. In principle the larva never quits its mine before it ceases feeding, but in *Ectoedemia (Etainia)* larvae seem to be able to enter a new bud from the outside. Larvae in some *Trifurcula (Glaucolepis)* species use more than one leaf, but reach the second leaf through the stem and petioles. Larvae generally with four of five instars (Boomsma et al., 1986, van Nieukerken & Jansen, in prep.), but in *Ectoedemia (Zimmermannia)* up to eight instars. The final instar larva usually leaves the mine via a semicircular slit and spins an oval, tough cocoon. Few species spin their cocoon inside the mine.

Pupation takes place inside the cocoon, often after a diapause of the larva, but in other species the diapause is in the pupal stage.

Adults probably short-living, but no detailed data on duration of life known. Active feeding has been observed on leaf-nectaries (Downes, 1968) and in captivity on sugar water or honey (personal observations). Courtship has often been observed in captivity within few hours after emergence. Detailed observations on courtship only published by Schönherr (1958). Males are often active flyers and come in numbers at light, although sometimes also females are collected at light. Many species fly actively just before sunset.

KEY TO THE (SUB)GENERA OF HOLARCTIC NEPTICULIDAE

1\. Collar smooth, comprising lamellar scales, in rest overlapping thorax (figs. 1, 2) 2

– Collar rough, comprising piliform (hair)scales, small, in rest not overlapping thorax (fig. 3) 5

2\. Venation: main trunk in forewing (R + M) distinctly curved beyond point of divergence of R1; R1 confluent with Rs in basal third; main trunk with 2 to 4 branches 3

– Venation: main trunk in forewing (R + M) straight or very slightly curved beyond divergence of R2 + 3; R1 separate from Rs from wing base or apparently so; main trunk with 4 to 7 branches including R1 ... 4

3\. Forewing: R2 + 3 absent, main trunk with 2 or 3 branches (figs. 83-86). Male genitalia: transtilla without transverse bar; aedeagus with long tubular cathrema or without; gnathos with single medial element. Female genitalia: anterior apophyses without anterior apodemes (fig. 77, 78), bursa very small .... *Enteucha*

– Forewing: R2 + 3 present, main trunk with 4 branches (fig. 80). Male genitalia: transtilla with transverse bar; aedeagus with normal, short striate cathrema; gnathos usually with two posterior processes, occasionally with one medial process. Female genitalia: anterior apophyses with distinct apophyses, bursa distinct, often large and with accessory sac often present .... *Stigmella*

4\. Forewing with main trunk Rs + M + Cu (excluding R1) with 5 or 6 branches (figs. 119-121). Larger species, usually with metallic colours .... *Bohemannia* (part)

– Forewing with main trunk Rs + M + Cu (excluding R1) with 3 branches (figs. 103, 104). Smaller species, uniformly sand coloured or irrorate .... *Acalyptris* (part, Japan only)

5\. Male with three pairs of tufts of hair-scales on T6-T8; male hindwing underside in almost all species with "velvet patch" of raised androconial scales (figs. 19-22). Hindwing with trifurcate Rs + M (figs. 106-108) (genus *Trifurcula*) 6

– Male with paired anal tufts on T8 only, or (in one group of *Acalyptris* species) with five pairs of very long tufts of hair-scales; no velvet patch. Hindwing with Rs + M bifurcate 8

6\. Forewing with closed cell, connection between R2 + 3 and R4 + 5 present, Cu often separate (figs. 106, 107). Male genitalia: transtilla without transverse bar; inner wall of aedeagus often with spines near phallotreme, vesica with only one, often very long and curved cornutus (figs. 109-112) .... subgenus *Glaucolepis*

– Forewing without closed cell, connection between R2 + 3 and R4 + 5 absent, Cu completely coalescent with M (fig. 108). Male genitalia: transtilla complete; aedeagus without spines near phallotreme, vesica with 2 or 3 large and several smaller cornuti 7

7\. Male genitalia: uncus split longitudinally (in ventral view) (fig. 114); aedeagus with two large cornuti and a group of strongly sclerotised curved cornuti at left side (fig. 115); vinculum anteriorly excavate. Leaf miners of Fabaceae .... subgenus *Levarchama*

– Male genitalia: uncus split in lateral view, not in ventral view; aedeagus with two or three large cornuti, without a similar group of curved cornuti, but a large group of needle-like cornuti at right side; vinculum anteriorly rounded. Larvae stem or barkminers of Fabaceae .... subgenus *Trifurcula*

8\. Male genitalia: vinculum U-shaped, gnathos and uncus absent, valva deeply cleft. Forewing without closed cell, R1 confluent with Rs for at least some distance (fig. 81). Only one Holarctic species, redescribed below .... *Simplimorpha*

– Male genitalia: vinculum ring-shaped, completely fused with tegumen; gnathos mostly normally developed, uncus present or absent; valva never deeply cleft. Forewing with closed cell, or if without than R1 separating almost from wing-base 9

9\. Forewing with distinct closed cell, R2 + 3 (if present) branching off approximately at junction of Rs and M, R1 branching off away from wing-base (figs. 122-126) 11

– Forewing without closed cell, or closed cell shifted basewards and difficult to recognise; R2 + 3 branching off far beyond junction of Rs and M, R1 separate from wing-base (figs. 103, 104, 119-121) 10

10\. Forewing with main trunk Rs + M + Cu (excluding R1) slightly curved, with 6 branches, no closed cell visible (fig. 119) .. *Bohemannia* (part)

– Forewing with main trunk Rs + M + Cu (excluding R1) straight and with 3 branches only (occasionally an indistinct Cu as well), closed cell recognisable because of persistent trachea (figs. 103, 104) .... *Acalyptris* (largest part)

11\. Forewing with R2 + 3 absent. Vinculum with large rounded ventral plate and expanded lateral arms. Female genitalia with reduced bursa without signa. Larva on Cistaceae .... *Parafomoria*

– Forewing with R2 + 3 present. Vinculum usually excavated anteriorly and lateral arms not so expanded. Female genitalia with normal or large bursa, usually with paired reticulate signa. Larva on other hosts (genus *Ectoedemia*) 12

12. Forewing with anal loop (figs. 123, 124). Uncus present .... subgenus *Laqueus*
– Forewing without anal loop. Uncus either present or absent 13
13. Male genitalia: valva with long dorsal apodeme; vinculum posteriorly with approximately U-shaped excavation; vesica with H-shaped sclerotisation. Female genitalia: ductus bursae with group of spines, bursa with very large signa .... subgenus *Etainia*
– Male genitalia: valva without such apodeme; vinculum not excavate; vesica without H-shaped sclerotisation. Female genitalia: ductus bursae only in few species with spines but frequently with pectinations, bursa usually with elongate not very large signa 14
14. Uncus present .... subgenus *"Fomoria"*
– Uncus absent 15
15. Male genitalia: aedeagus with 2-3 pairs carinae, ventral carinae usually very large and prominent; valval tip hardly or not curved inwards, inner margin often with a process. Female genitalia: vestibulum without vaginal sclerite, only with inconspicuous sclerotisation or spines. Hindwing in male often with pronounced costal emargination. Larva barkminer in Fagaceae or Ulmaceae .... subgenus *Zimmermannia*
– Male genitalia: aedeagus with 1-2 pairs carinae, occasionally absent; valval tip usually curved inwards, inner margin never with process. Female genitalia: vestibulum usually with vaginal sclerite and often with dense concentration of pectinations. Hindwing never emarginate. Larva leaf-miners or petiole-feeders (miner or gall-maker) .... subgenus *Ectoedemia*

Subfamily Nepticulinae Stainton

This is the only subfamily represented in the Holarctic region, whereas the other subfamily, Pectinivalvinae Scoble, 1983, is confined to Australia. Scoble (1983) named the nominotypical ("nominate") subfamily Stigmellinae and the nominotypical tribe Stigmellini, after their common type-genus *Stigmella* (a senior synonym of *Nepticula*). According to the Code (Art. 37a) however, the name of the subordinate taxon that contains the type-genus of the superior taxon, bears the same name, except for suffix. Hence, the names should be Nepticulinae and Nepticulini, with the same author and date as the family.

Diagnosis. — Forewing usually with subdorsal retinaculum. Venation: 1 + 2A thickened in forewing; in hindwing R + M not deflected towards costa.

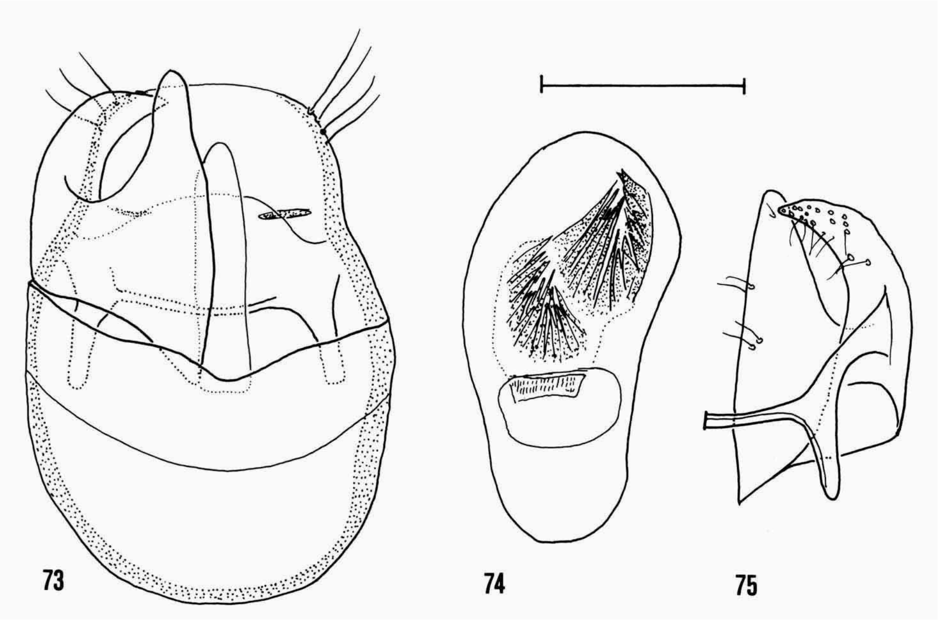
Male genitalia: pectinifer absent (but see *Acalyptris*), valvae often joined by transverse bar of transtilla; cathrema normally present (apomorphies 13-18).

Tribus Nepticulini Stainton

This tribe, in Scoble (1983) monobasic and redundant, is here enlarged to contain the genera *Simplimorpha, Varius, Enteucha* and *Stigmella.*

Diagnosis. — Collar conspicuous, comprising lamellar scales (except *Simplimorpha*). Forewing: M coalescent with R from base, with 2-4 terminal branches; Cu separate, or absent. Hindwing: costal bristles present in male and female. Male genitalia: vinculum U-shaped, articulating with band-shaped tegumen. Aedeagus without carinal processes. Juxta often present. Gnathos either with single medial process or with two posterior processes. Uncus hood-like, often bilobed. Female genitalia: reticulate signa absent. Vestibulum often enlarged into accessory sac, sclerotisations absent.

Distribution. — This is the most widespread tribe, with the distribution actually coinciding with that of its largest genus, *Stigmella,* and occurring in all continents except Antarctica.



Figs. 73-75. *Simplimorpha promissa* (Staudinger), male genitalia, slide VU 1810. 73, capsule, ventral aspect; 74, aedeagus, ventral aspect; 75, valva, dorsal aspect. Scale: 0.1 mm.

Biology. — Invariably leaf-miners, with a wide range of hostplant families (see under generic descriptions). Mines principally linear (gallery)mines. Pupation in soil.

Genus **Simplimorpha** Scoble, 1983
(fig. 82)

Simplimorpha Scoble, 1983: 15. Type-species: *Stigmella lanceifoliella* Vári, 1955: 331, by original designation and monotypy.

Scoble (1983) proposed this genus for *Stigmella lanceifoliella* Vári, since this species does not share any synapomorphies with *Stigmella*. The European *Nepticula promissa* Staudinger shows some striking similarities with *lanceifoliella* in external features, hostplant choice and to some extent in the genitalia as well. Therefore I consider these two species as congeneric, forming a monophyletic group, tentatively placed at the basis of the Nepticulini (fig. 70).

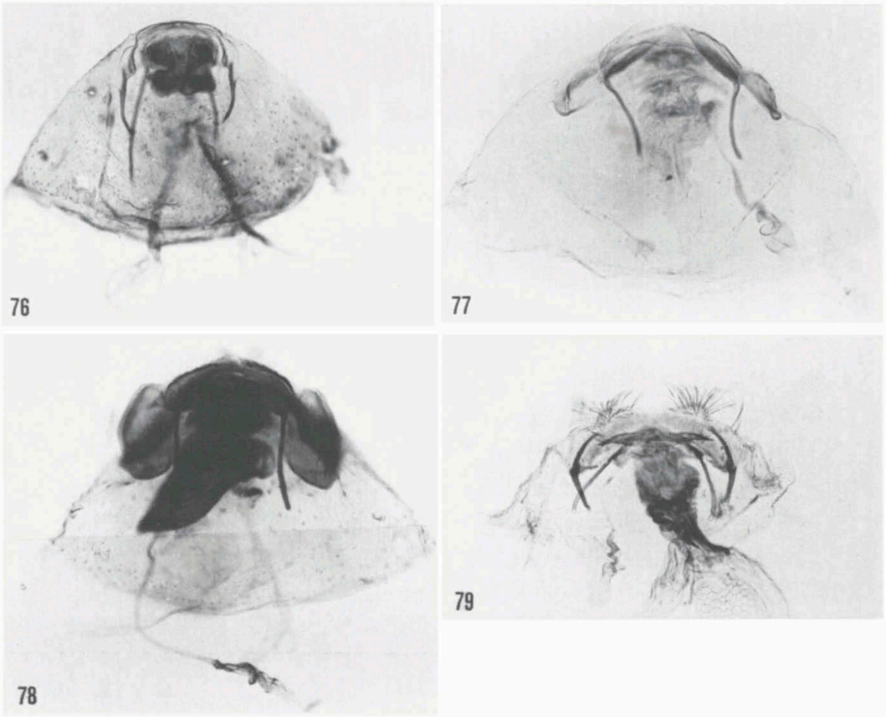
Diagnosis. — *Simplimorpha* resembles *Stigmella* in venation but can be separated by the absence of lamelliform scales in the collar and the simple male genitalia without uncus and gnathos.

Apomorhies. — 21. Hostplant: Anacardiaceae; 22. Uncus absent. 23. Gnathos reduced or absent.

Description. — Adult. Small moths, forewing length 1.7-2.2 mm. Head. Collar small, comprising pilliform scales. Antennae with 20-30 segments. Sensillum vesiculocladum not examined. Labial palpi with three segments. Forewing irrorate, without distinct pattern. Cilia-line distinct. Venation (fig. 81) as in *Stigmella*, Cu either inconspicuous (in *promissa*) or curving upwards to meet Rs + M (in *lanceifoliella*). Hindwing with costal bristles in male and female, no special scales in the two species. Venation as in *Stigmella*. Abdomen. Anterior part of sternum 2 pentagonal (fig. 38) as in *Stigmella*. Male with anal tufts on tergum 8.

Male genitalia (figs. 73-75). Vinculum lateral arms articulate with sides of tegumen; ventral plate anteriorly rounded. Tegumen broad, weakly sclerotized. Uncus absent. Gnathos absent or occasionally inconspicuous (Scoble, 1983). Valva deeply divided, ventral lobe less developed in *lanceifoliella*; transtilla with distinct transverse bar. Juxta present (according to Scoble a ventral process). Aedeagus simple, without carinae. Vesica with spiculate cornuti; cathrema present.

Female genitalia (fig. 76). T8 large, quadrate; T9 with setose anal papillae. Apophyses long and pointed. Vestibulum and bursa weakly sclerotised, small, without signa or other sclerotisations.



Figs. 76-79. Female genitalia. 76, *Simplimorpha promissa* (Staudinger), slide VU 1440; 77, *Enteucha acetosae* (Stainton), slide VU 1364; 78, *E.* spec., Nepal, slide VU 1369; 79, *Acalyptris psammophricta* Meyrick, Holotype (see also fig. 31).

Biology. — Hostplants. Anacardiaceae, both species being oligophagous. Mine. A linear gallery. Pupation in a cocoon in the soil. Life history. With several generations a year.

Distribution (fig. 82). — The genus is at present only known from southern Africa and the mediterranean region.

Species included. 1. *S. lanceifoliella* (Vári, 1955), southern Africa. See Vári (1955) and Scoble (1983). 2. *S. promissa* (Staudinger, 1870), redescribed below.

Simplimorpha promissa (Staudinger, 1870)
(figs. 38, 73-76, 81)

Nepticula promissa Staudinger, 1870: 325. Syntypes, France: Celles-les-Bains (Ardèche), mines 14.ix.1866, *Pistacia lentiscus, Cotinus coggyria,* (Staudinger) (MHUB) [examined].

Nepticula robiniella Gustafsson, 1973: 197. Holotype ♀, Greece: City of Rodhos, mine on 1.v.1973 on *Pistacia atlantica* [misidentified as *Robinia*], e.l. 14.v.1973 (Janzon) (RMS) [examined] (Synonymised by Van Nieukerken, 1986: 6).

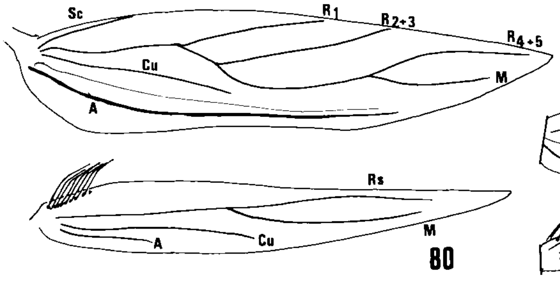
Material examined. — 8♂, 6♀. Corsica: 3♂, 3♀, Porticcio, SE of Ajaccio, beach, 10.v.1982, *Pistacia lentiscus*, e.l. 28.v-4.vi.1982 (Van Nieukerken) (EvN, ZMA); Greece: 1♀, Lakonia, 7 km SW Monemvasia, 6.x.1980, (Christensen) (ZMUC); Hungary: 1♂, 1♀, Csákvár, 5-6.v.1964, *Cotinus*, (Szőcs) (ZMUC); Italy: 1♀, Ospedaletti Riv., 25.iv.1932, mine on *Cistus salvifolius* (sic!, probably mistaken hostplant) (Hering) (MHUB); 1♂, Monti Aurunci, 800 m, 6 km N. Itri, 15.viii.1972 (Johansson); 1♂, Monti Aurunci, 400 m, 4 km NW Castelforte, 22-23.vi.1969 (Johansson) (coll. Johansson); Yugoslavia: 1♂, Hrvatska, Dvorine, 8 km NW Crikvenica, 15.x.1985, *Cotinus coggyria* e.l. 10-12.iii.1984 (Boomsma, Van Nieukerken); 1♂, Slovenia, 7 km SE Piran: Cedle, 300 m, 12.x.1983, *Cotinus coggyria*, e.l. 8.iii.1984 (Boomsma, Van Nieukerken) (ZMA).

Male. Forewing length 1.7-2.4 mm. Head: frontal tuft white with small contrasting brown tuft on vertex; collar white; scape very small, white with brown scales, antenna with about 30 segments. Thorax fuscous black with white tips of mesoscutum and tegulae. Forewing fuscous black irrorate with white scales; white scales concentrated in basal half, along dorsal margin and at 2/3, tending to form two fasciae or fascia and costal and dorsal spot; cilia-line distinct, terminal cilia silvery white. Hindwing grey, with costal bristles.

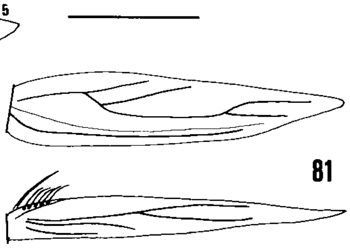
Female. Forewing length 1.9-2.4 mm. Antenna with 19-22 segments.

Venation. As in *Stigmella*, with R1, R2 + 3, R4 + 5, and M as separate branches. Cu inconspicuous or absent.

Male genitalia (figs. 73-75). Capsule 250 μm long. Vinculum with large ventral plate. Tegumen weakly sclerotised, rounded, with setose pads laterally; a pair of indistinct sclerotised bars dorsally belongs probably to tegumen. Uncus and gnathos absent. Juxta long and narrow, not tightly fused to aedeagus. Valva ± 150 μm long, deeply divided, dorsal part curved, pointed; ventral part rounded distally; transtilla with long transverse bar and short sublateral



80



81

Fig. 80. Venation of *Stigmella zelleriella* (Snellen), ♀, slide VU 257; Fig. 81. Venation of *Simplimorpha promissa* (Staudinger), ♂, slide VU 477. Scale : 0.5 mm.

processes. Aedeagus 200 μm long, distally widest, no carinae present; vesica with many long spiculate cornuti of variable size and form.

Female genitalia (fig. 76). T8 large, quadrate, covered with scales and setae. Anal papillae with 6-7 setae. Both pairs of apophyses long, straight and pointed. Bursa very small, hardly sclerotised. Ductus spermathecae with 8 narrow convolutions.

Biology. — Larva leaf-miner in Anacardiaceae: recorded from *Rhus coriaria* L., *Cotinus coggyria* Scop., *Pistacia lentiscus* L., *P. terebinthus* L. and *P. atlantica* Desf. Mine a long gallery, filled with contorted frass, resembling the mine of *Acalyptris minimella* (Rebel). Almost continuously breeding in mediterranean area, but bi- or trivoltine in places where only deciduous *Cotinus* occurs.

Distribution. — Widely distributed in southern Europe with northern limit approximately along southern slopes of Alps and along Danube.

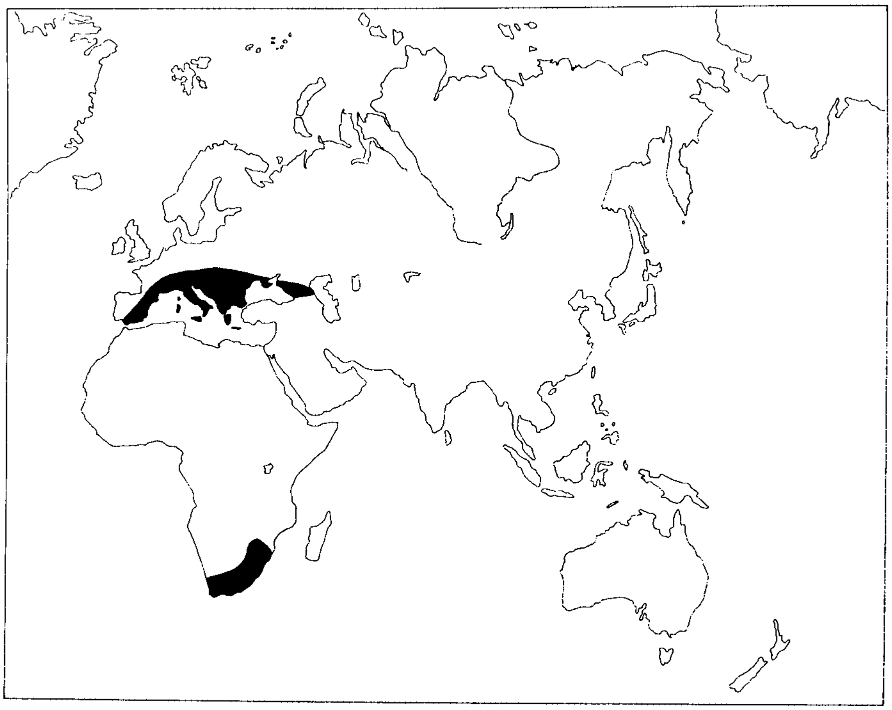


Fig. 82. Distribution of *Simplimorpha*.

Genus **Enteucha** Meyrick, 1915
(figs. 34-37, 56, 77, 83-102)

Enteucha Meyrick, 1915: 241. Type-species: *Enteucha cyanochlora* Meyrick, 1915: 241, by monotypy.

Johanssonia Borkowski, 1972: 702. Type-species: *Nepticula acetosae* Stainton, 1854: 303, by original designation and monotypy (Synonymised by Van Nieukerken, 1986: 7).

Oligoneura Davis, 1978b: 217. Type-species: *Oligoneura basidactyla* Davis, 1978b: 218, by original designation and monotypy (Synonymised by Van Nieukerken, 1986: 7).

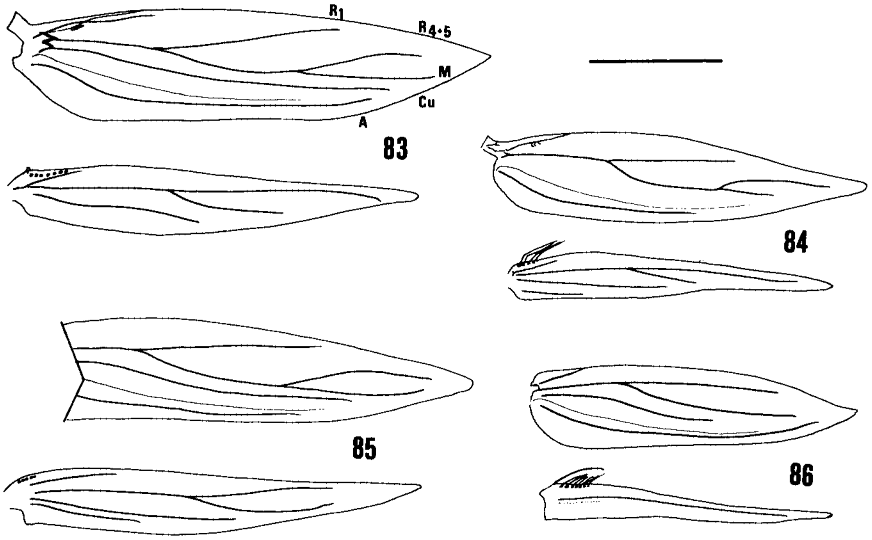
Artaversala Davis, 1978b: 219. Type-species: *Artaversala gilvafascia* Davis, 1978b: 221, by original designation and monotypy (Synonymised by Van Nieukerken, 1986: 7).

Manoneura Davis, 1979: scientific note, replacement name for *Oligoneura* Davis nec Bigot, 1878.

Johanssoniella Koçak, 1981: 99, replacement name for *Johanssonia* Borkowski nec Selensky, 1914.

Stigmella (Johanssonia); Leraut, 1980: 49.

The genus *Enteucha* was originally proposed for a single species from British Guiana in the Lyonetiidae and thought to be related to *Opostega*. Davis (1984, 1985) placed it in the Nepticulidae, and here it is for the first time treated as a polytypic genus. The genera *Johanssonia, Artaversala* and *Oligoneura* were all proposed for single nepticulid species, and no other species have been added hitherto. When comparing the descriptions of these three genera and the redescription of *Enteucha cyanochlora* by Davis (1985),



Figs. 83-86. Venation of *Enteucha* spp. 83, *E.* spec., Japan, ♂, slide VU 723; 84, *E. acetosae* (Stainton), ♀, slide VU 385; 85, *E.* spec., Nepal, ♀, slide VU 957; 86, *E. gilvafascia* (Davis), ♂, slide USNM 18401. Scale: 0.5 mm.

the proposed genus seems to be a rather heterogenous assemblage of a few aberrant Nepticulini. However, in closer examination, there are several striking similarities in the venation, male genitalia and biology, as already noted by Davis (1978b). The discovery of a group of undescribed species in east Asia, mining *Polygonum,* which share characters either with the European *acetosae* or the Nearctic species, made it likely that all these Polygonaceae-feeding species belong to one monophyletic taxon. Apart from the venation, the hostplant seems to form one of the best apomorphies for this genus, notwithstanding the fact that the hostplant of *cyanochlora* is still unknown. Although the species *cyanochora* and *gilvafascia* are quite aberrant in their male genitalia, they are tentatively regarded as a very autapomorphic group within the genus, since they share all apomorphies listed below.

The complex gnathos described for *Oligoneura* (Davis, 1978b), is in my opinion based on a misinterpretation of a downfolded uncus which is entangled with the gnathos. I saw this also happen in other species during preparation. When folded apart, the gnathos and uncus in *basidactyla* resemble those structures in other species of the genus.

The genus *Varius* Scoble was proposed for the single species *Stigmella ochnicola* Vári, 1955, which did not fit into any other known genus. It appears to resemble *Enteucha* in various ways, such as the shape of the valva and uncus, the absence of a transverse bar of the transtilla and possibly the thickening in the aedeagus (Scoble, 1983). I did not examine the species, but since it does not share the venation and hostplant characters, I do not synonymise *Varius* with *Enteucha.* The best solution might be tentatively to regard *Varius* as the sistergroup of *Enteucha.*

Diagnosis. — Externally *Enteucha* species resemble *Stigmella* because of the collar and general appearance, but they are separated by the listed apomorphies.

Apomorphies. — 25. Hostplant: Polygonaceae; 26. R2 + 3 absent in forewing; 27. Transtilla lacking transverse bar; 28. Aedeagus with long tubular, smooth cathrema; 29. Anterior apophyses without anterior apodemes; 30. Anterior margin of T2 with two unsclerotised patches on each side (see section on morphology).

Description. — Adult. Very small moths, forewing length 1.5-3.0 mm. Head. Collar conspicuous, comprising lamelliform scales, overlaying thorax. Antennae not very long, a maximum of 36 segments has been counted. Sensillum vesiculocladum five-branched. Labial palpi with two *(acetosae)* or three segments *(basidactyla, gilvafascia).* Forewing with pale fascia, spots or two fasciae, often metallic, on dark background. Cilia-line absent. Venation (figs. 83-86) more reduced than in other nepticulid genera. Sc weak, R1 distinct. Rs fused with M, forming a single branch in *cyanochlora* and *gilvafascia,* or bifurcate (probably in R4 + 5 and M) in other species; R2 + 3 always absent. Cu either present and long (most species) or absent *(basidactyla, acetosae)*, but Scoble (1983) observed a faint Cu in *acetosae.* Hindwing with costal bristles in ♂ and ♀, no special scales observed in known species. Venation as in *Stigmella* or more reduced in *gilvafascia* and *basidactyla* (Davis, 1978b). Abdomen. Anterior part of sternum 2 pentagonal (figs. 34-37), but hardly recognisable in *cyanochlora* and *gilvafascia*; windows in sternum 2 bordered by arcuate rodlike sclerotised structures. Male tergum 8 with pair of anal tufts.

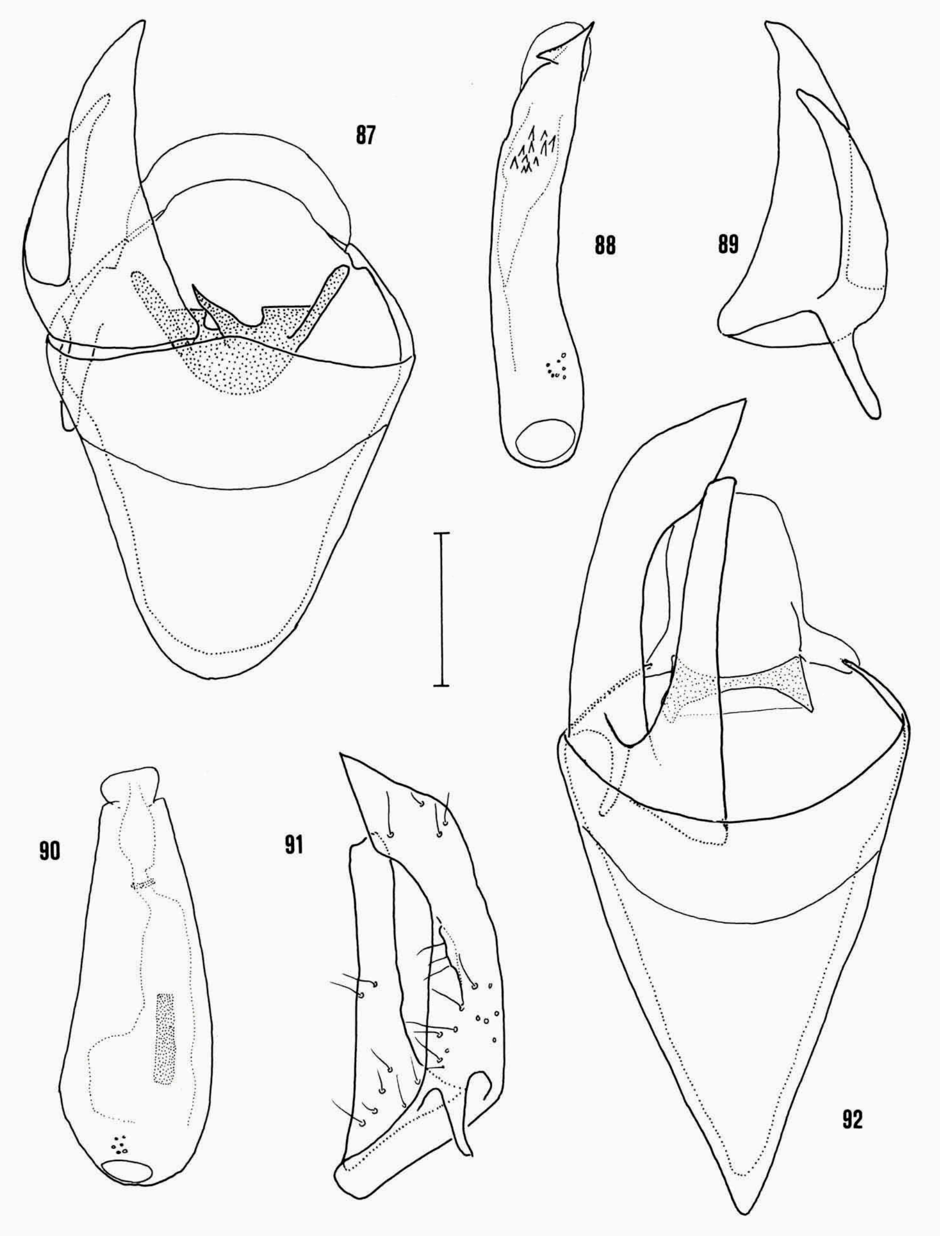
Male genitalia. (figs. 87-101). Vinculum lateral arms articulate with sides of tegumen; ventral plate considerably expanded in some species. Tegumen narrow, or slightly enlarged. Uncus strongly sclerotised, hood-like, with medial posterior process, but absent in *cyanochlora* and *gilvafascia.* Gnathos with single medial element, sometimes reduced. Valva approximately triangular, with distinct distal digitate process, sometimes valva completely divided in two lobes (figs. 89, 92). Transtilla lacking transverse bar. Aedeagus with vestigial carinate processes, hinging to valva and vinculum; vesica usually with small cornuti; cathrema different from other Nepticulinae: a long smooth tubular sclerotisation, encircling base of ductus ejaculatorius (figs. 91, 97), but not observed in *acetosae, basidactyla* or *cyanochlora;* ventral opening in aedeagus approximately in middle or shifted anteriorly.

Female genitalia (figs. 77, 78). T8 comparatively large, covered with scales and setae, overlapping T9, with or without setose anal papillae. Anterior apophyses not extending into abdomen, ending blunt near anterior margin of T8. Posterior apophyses long and pointed. Vestibulum and bursa vestigial, hardly sclerotised, without sclerotisations or signa. Ductus spermathecae with conspicuous vesicle, usually with few convolutions.

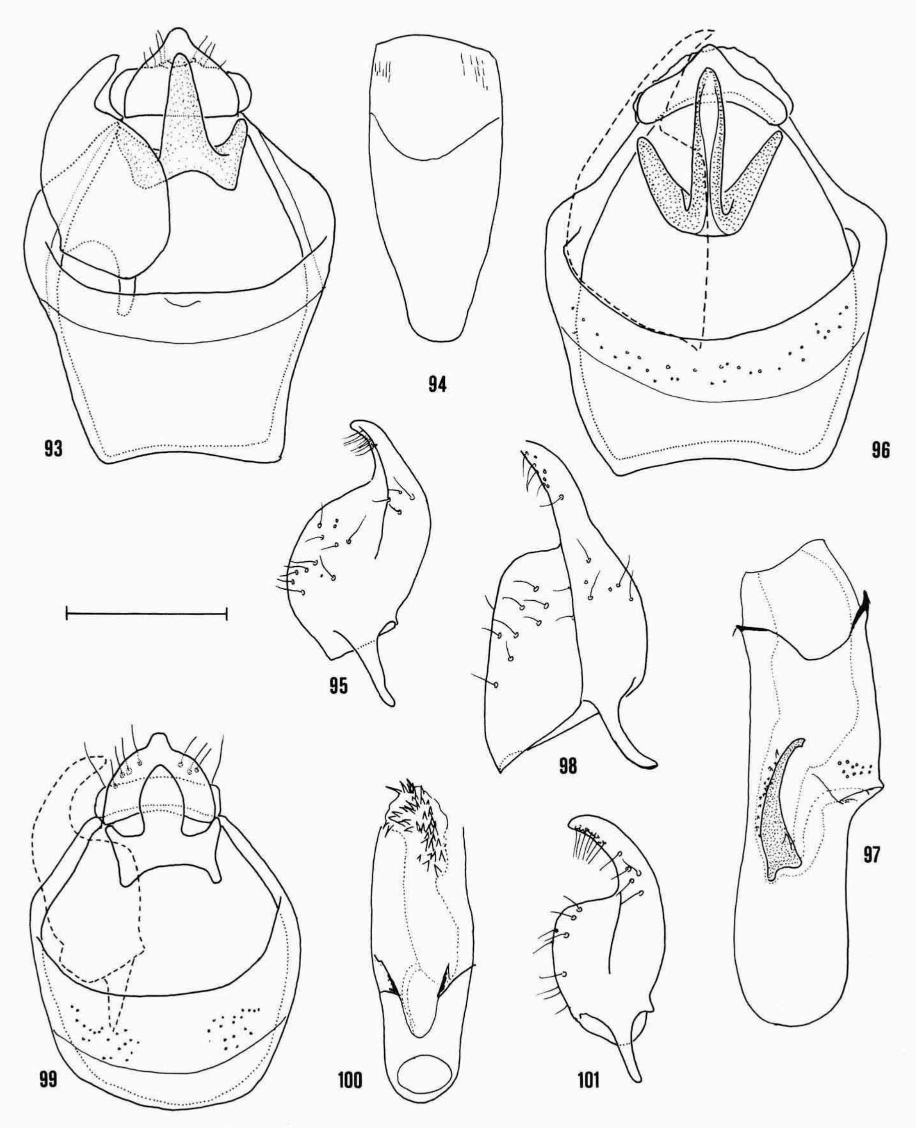
Biology. — Hostplants. Polygonaceae, genera *Rumex (E. acetosae), Polygonum* (Asiatic species), *Coccoloba (E. basidactyla, gilvafascia)* and *Eriogonum* (undescribed species from California, D. Wagner in litt. to Wilkinson); unknown for *cyanochlora.* Mine. A gallery, often much contorted, in leaf (cf Emmet, 1976). Pupation in a cocoon in the soil. Life history. The known species are bivoltine or multivoltine.

Distribution (fig. 102). — The genus comprises at present at least ten species from Holarctic, Oriental and Neotropical regions: Europe, Nepal, China: Yunnan, North Burma, Japan, Thailand (mines on *Polygonum* reported by Karsholt, in litt. and Kuroko, in litt.), North America and Guyana.

Species included. — 1. *E. cyanochlora* Meyrick, 1915, Guyana (figs. 87-89). Redescribed by Davis (1985). Davis did not describe the venation, but as far



Figs. 87-92. *Enteucha*, male genitalia; 87-89. *E. cyanochlora* Meyrick, holotype; 90-92. *E. gilvafascia* (Davis), slide VU 1366, paratype. 87, 92, capsule, ventral aspect, right valva and aedeagus omitted; 88, 90, aedeagus, ventral aspect; 89, 92, valva, dorsal aspect. Scale: 0.1 mm.



Figs. 93-101. *Enteucha,* male genitalia, 93-95. *E. acetosae* (Stainton), slide RJ 1407; 96-98, *E.* spec., Japan, slide VU 723; 99-101, *E.* spec., Japan, slide VU 678. 93, 96, 99, capsule, ventral aspect, right valva and aedeagus omitted; 94, 97, 100, aedeagus, ventral aspect; 95, 98, 101, valva, dorsal aspect. Scale: 0.1 mm.

as I can see without making a preparation of the wings, the venation matches that of *Artaversala gilvafascia* very well. In my opinion the gnathos is not membranous (Davis, 1985), but of the usual nepticulid type with a pointed central element as visible in Davis fig. 2 between the valvae (fig. 87). This structure was interpreted by Davis as the juxta. 2. *E. gilvafascia* (Davis, 1978b) **comb. n.**, Florida. See original description, and figs. 86, 90-92. 3. *E. basidactyla* (Davis, 1978b) **comb. n.**, Florida. See original description, and note about gnathos above. 4. *E. acetosae* (Stainton, 1854), Europe. See Borkowski (1972), Emmet (1976), Scoble (1983) and figs. 84, 93-95. 5. Two species from Japan, currently studied (coll. EIHU, ELUO) (figs. 96-101). 6. Two undescribed species from Nepal (coll. Van Nieukerken) (fig. 78). 7. Two undescribed species from Yunnan, China (coll. ZIAB, ZMA). 8. One undescribed species from Burma (coll. RMS). 9. At least one undescribed species from Thailand (mines, coll. ZMUC). 10. One undescribed species from California (Wagner, in litt. to Wilkinson), probably belonging to *Enteucha*.

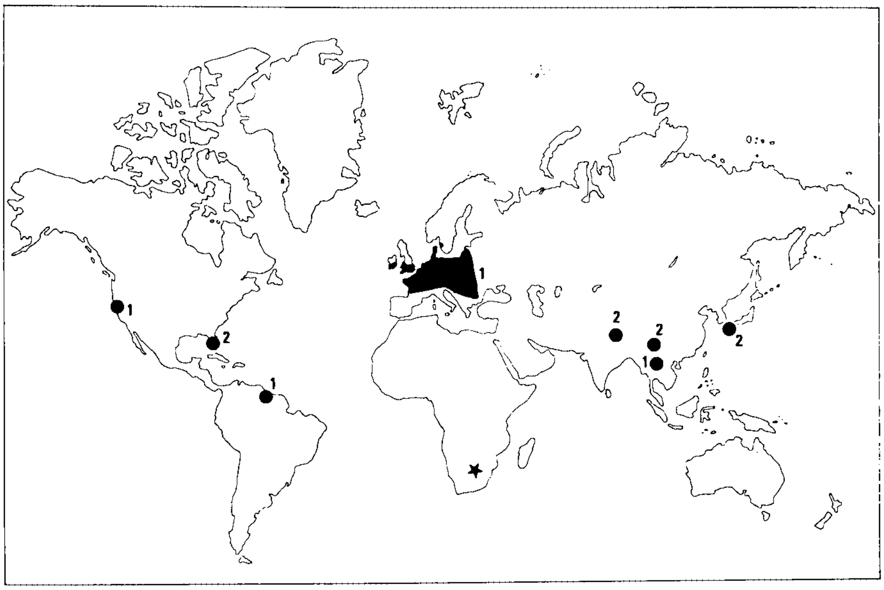


Fig. 102. Distribution of *Enteucha*, with number of species indicated, and *Varius ochnicolus* (Vári) (star).

Genus **Stigmella** Schrank, 1802
(figs. 1, 7-11, 29, 30, 39, 65-67, 80)

Stigmella Schrank, 1802: 169. Type-species: *Phalaena (Tinea) anomalella* Göze, 1783: 168, by subsequent designation (Walsingham, 1907: 1008).

Nepticula van Heyden, 1843: 208. Type-species: *Tinea aurella* Fabricius, 1775: 666, by subsequent designation (Tutt, 1899: 184) (Synonymised by Walsingham, 1907: 1008).

Dysnepticula Börner *in* Bröhmer, 1925: 370. Type-species: *Phalaena (Tinea) anomalella* Göze, 1783: 168, by original designation (an objective junior synonym).

Astigmella Puplesis, 1984a: 111. Type-species: *Astigmella dissona* Puplesis, 1984a: 112, by original designation (Synonymised by Van Nieukerken, 1986: 7).

Until recently most Nepticulidae were described in *Stigmella* or more often under its junior synonym *Nepticula*. The present concept of *Stigmella* is a combination of Beirne's *Stigmella* and *Nepticula* and was first strictly used by Johansson (1971) and Borkowski (1972). Although many species were subsequently removed from *Stigmella,* it remains the largest genus of Nepticulidae in probably all parts of the world. The nomenclature was discussed by Wilkinson (1978).

Astigmella was recently described by Puplesis for two east Asiatic species probably living on *Betula*. The type-species, *A. dissona* is probably a synonym of *Stigmella naturnella* (Klimesch). These species have the plesiomorphic type of gnathos and an atypical uncus resembling the plesiomorphic condition, which therefore makes placement in *Stigmella* difficult. On the other hand *S. naturnella* and *A. dissona* resemble the species of the *lapponica* species-group and the Nearctic *procrastinella* species-group both in morphology and biology and these groups are considered to belong to *Stigmella* on the grounds of at least one synapomorphy (32). Without a thorough knowledge of the phylogeny within *Stigmella* I am therefore in favour of keeping *Astigmella* at present within *Stigmella.*

Several authors treated *Stigmella* recently: Wilkinson & Scoble (1979) and Newton & Wilkinson (1982) treated the Nearctic species, Scoble (1978b) the South African species and Kemperman & Wilkinson (1985) the Japanese species. Also several East Palaearctic species were described by Puplesis (1984a, b, d, e, 1985b, c). Three groups of western Palaearctic species were revised by Johansson (1971), Schoorl, Van Nieukerken & Wilkinson (1985) and Schoorl & Wilkinson (1986).

Diagnosis. — *Stigmella* species are recognised by the combination of a collar comprising lamelliform scales, R + M coalescent in forewing and R2 + 3 present in forewing. The collar character can be used as a preliminary sorting character, since only few other species – belonging to *Enteucha* and *Bohemannia* – have a similar collar. Male genitalia are usually recognised by the U-shaped vinculum, bilobed uncus, gnathos with two posterior processes and transtilla present, but exceptions on the last three characters occur. Female genitalia lack reticulate signa and vaginal sclerites, an accessory sac is often present.

Apomorphies. — 31. Uncus bilobed; 32. Larval antennae with sensilla placed cross-wise (Van Nieukerken & Jansen, in prep.).

The following apomorphies probably do not belong to the ground-plan of *Stigmella*, but are present in a large part of the genus. Since they are unknown outside *Stigmella* they are sufficient but not necessary diagnostic characters: a. Gnathos with two posterior processes; b. Aedeagus with surrounding manica (often spinose); c. Female with large accessory sac (enlargement of vestibulum); d. Uncus with four lobes.

Description. — Adult. Very small to small moths, forewing length 1-4 mm. *Stigmella* comprises the smallest known Lepidoptera. Head. Collar conspicuous, comprising lamelliform scales, overlapping thorax in rest (fig. 1). Antennae not very long, usually with approximately 20-30 segments, but species with fewer (14) or many more (up to 50) segments occur. Sensillum vesiculocladum five-branched. Labial palpae with three segments. Forewing with variable pattern, either fasciate, with number of spots or unicolorous, often with metallic reflections. Cilia-line often absent, but present in several groups. Venation (fig. 80) with R + M coalescent from base, R1, R2 + 3, R4 + 5 and M present. Cu present as separate branch. Hindwing with costal bristles in ♂ and ♀. Androconial scales occur in many species, often extending into fringe. Venation with Sc, Rs + M bifurcate, Cu and A present. Abdomen. Anterior part of sternum 2 pentagonal or trapezoïd (fig. 39), "windows" bordered by rodlike arcuate structures. Male with anal tufts on tergum 8, but these are often absent. In some species female with anal tufts on tergum 7.

Male genitalia. Vinculum lateral arms articulate with sides of tegumen; ventral plate usually bilobed. Tegumen narrow, band-like. Uncus hood-like, usually bilobed or almost quadrangular, often each lobe bilobed again, sometimes uncus rounded off. Gnathos with single medial element in *lapponica, procrastinella, ingens,* and *caesurifasciella* species groups (Kemperman & Wilkinson, 1985), but with two laterally placed posterior processes in all other species; often with two anterior processes as well. Valva approximately triangular, often with distinct distal digitate process and an inner lobe. Transtilla with transverse bar, sometimes divided in middle; sublateral processes often absent. Aedeagus without carinae, but some loose processes present in *S. naturnella, S. dissona* **comb. n.**, *S. mirabella* (Puplesis) **comb. n.** (cf. Puplesis, 1984a, e) and species of *ingens* species-group (Scoble, 1978b).

Vesica usually with numerous denticulate cornuti, sometimes reduced; cathrema broad. In several Holarctic species groups (such as *aurella, marginicolella, pomella* and *ruficapitella* species groups) aedeagus surrounded by spinose manica. Juxta frequently present.

Female genitalia. T8 distinct, covered with scales and setae, often in groups or rows; posterior margin sometimes medially pointed. T9 often indistinct, without setose anal papillae, sometimes with distinct anal papillae. Anterior and posterior apophyses rather straight. Vestibulum often heavily folded, without sclerotisations; in many groups enlarged into bursa-like accessory sac (bursa accessorius), sometimes armed with large spines (*ruficapitella* species group) (figs. 29, 30); corpus bursae usually covered with pectinations, which tend to form signa-like concentrations in some species; paired signa (not reticulate) sometimes present. Ductus spermathecae often very long and coiled, but straight in other species.

Biology. — Hostplants. A large number of families have been recorded as hosts, mostly woody dicotyledons. Important host-families in Holarctic: Betulaceae, Fagaceae, Rosaceae, Salicaceae and Rhamnaceae. Other families from which *Stigmella* species are recorded comprise Aceraceae, Anacardiaceae, Apocynaceae, Asteraceae (New Zealand!), Caprifoliaceae, Celastraceae, Chrysobalanaceae, Cistaceae, Convolvulaceae, Cucurbitaceae, Cyperaceae, Epacridaceae, Ericaceae, Euphorbiaceae, Fabaceae, Geraniaceae, Hamamelidaceae, Juglandaceae, Linaceae, Malvaceae, Moraceae, Myricaceae, Poaceae (1 species, Japan), Sapindaceae, Sterculiaceae, Styracaceae, Tiliaceae, Ulmaceae, Urticaceae, Vitaceae. Mine. All species make leaf-mines, usually galleries, occasionally blotches. Pupation in a cocoon in soil or leaf-litter, occasionally on hostplant, not in mine. Life history. Dependent on climate, strategies from univoltine to polyvoltine occur.

Distribution. — Worldwide, except Antarctica, in Holarctic found northwards to Arctic sea. Also occurring on large islands such as New Zealand, Fiji, but not recorded from Hawai and many smaller islands.

Species included and subdivision. At least 300 described species. From West Palaearctic 99 species (Van Nieukerken, 1986), in East Palaearctic 68 (Puplesis, 1984a, b, d, e, 1985b, c; Kemperman & Wilkinson, 1985), in Nearctic 51 species (Newton & Wilkinson, 1982); from South Africa 34 (Scoble, 1978b), from Gambia 7 species (Gustafsson, 1985) and from New Zealand 29 species (Donner & Wilkinson, in press). Number of species from Neotropical, Oriental and Australian regions unknown since the few described species are unrevised, but *Stigmella* occurs commonly in all these regions.

Several attempts have been made to divide this large and uniform genus into smaller entities, the species groups. Johansson (1971) provided a first subdivision of the northern European species and his scheme has been adopted and refined by Emmet (1976), Kemperman & Wilkinson (1985) and Van Nieukerken (1986). Wilkinson & Scoble (1979) and Newton & Wilkinson (1982) made a similar division for the Nearctic species, using different names. Some of their groups clearly fall within Johansson's scheme, others however, do not. Scoble (1978b) divided the South African species merely into two groups according to the type of gnathos. The scarcity of good apomorphies on group-level, makes a worldwide subdivision of *Stigmella* very difficult, especially for species of which only one sex is known. Many of the groups in the Holarctic appear to be monophyletic entities, but their relative relationships are hard to assess.

Several Holarctic species-groups show the apomorphies b-d, as listed above, whereas these characters are comparatively seldom seen in southern hemisphere species of *Stigmella,* which show a predominance of generalised features (Scoble, 1978b; Donner & Wilkinson, in press). On comparison, the South-African species of *Stigmella* show similarities to the Holarctic *lapponica, freyella, paliurella, tiliae* and *betulicola* species groups.

On the basis of these apomorphies and several other characters (unpublished work of van Driel & Van Nieukerken), the linear sequence of Palaearctic species groups, as presented in my check-list (Van Nieukerken, 1986), is tentatively assumed to approach the phylogenetic relationships most.

Tribus Trifurculini Scoble

Trifurculini Scoble, 1983: 16. Type-genus: *Trifurcula* Zeller, 1848: 330.

Scoble (1983) erected this tribe for those Nepticulidae which have a ring-shaped vinculum in the male and reticulate signa in the female. This group has previously been treated as the single genus *Trifurcula,* by Johansson (1971) and some other authors, but is here, following Scoble, divided into a number of very diverse and (partly) large genera: *Acalyptris, Trifurcula, Parafomoria, Bohemannia* and *Ectoedemia.*

Diagnosis. — Distinguished from the Nepticulini by the following characters: Collar usually inconspicuous, comprising piliform scales (hair-scales), but lamellar in some species of *Bohemannia* and *Acalyptris.* Forewing: M coalescent with Cu from base, but diverging later to coalesce with Rs, thus forming a closed cell (secondarily reduced or lost in *Acalyptris* and *Bohemannia*). Hindwing: costal bristles in male often present, often secondarily lost or transformed into hair-pencil. Male genitalia: vinculum ring-shaped, invisibly fused with tegumen, which usually extends into a pseuduncus. Aedeagus with carinal processes and often a juxta-like ventral process. Gnathos with single medial process. Uncus usually with medial process V- of Y-shaped, or absent. Female genitalia: usually with reticulate signa present. Vestibulum sometimes with small evaginated pouch and usually with various sclerotisations.

Distribution. — World-wide, but not yet recorded from South America and absent from at least New Zealand (Donner & Wilkinson, in press).

Biology. — Principally leaf-miners, but also species feeding in bark, shoots, buds and fruits occur. Pupation normally in soil, but sometimes in the mine.

Genus **Acalyptris** Meyrick, 1921
(figs. 16, 17, 23, 24, 26-28, 40-43, 64, 103-105)

Acalyptris Meyrick, 1921: 410. Type-species: *Acalyptris psammophricta* Meyrick, 1921: 410, by original designation and monotypy.

Microcalyptris Braun, 1925: 224. Type-species: *Microcalyptris scirpi* Braun, 1925: 225, by original designation and monotypy (Synonymised by Van Nieukerken, 1986: 14).

Weberia Müller-Rutz, 1934a: 122. Type-species: *Weberia platani* Müller-Rutz, 1934a: 122, by original designation and monotypy (Synonymised by Van Nieukerken, 1986: 14).

Niepeltia Strand, 1934: 241, replacement name for *Weberia* Müller-Rutz nec Robineau-Desvoidy, 1830.

Weberina Müller-Rutz, 1934b: "slip", replacement name for *Weberia* Müller-Rutz.

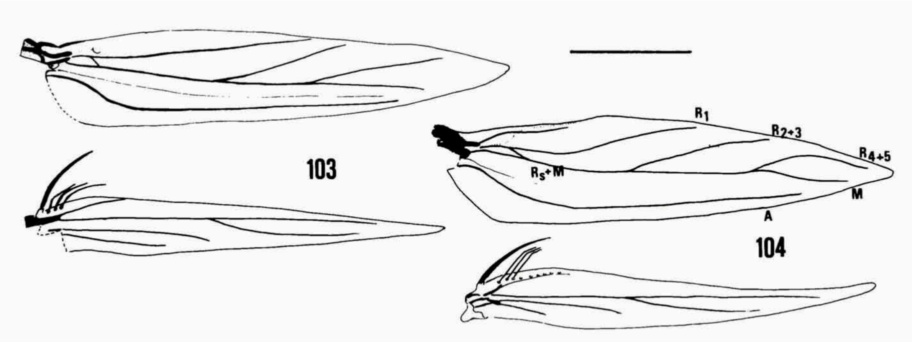
Acalyptris was described on the base of a single specimen, which Meyrick thought lacked the expanded scape, typical of the family. However, on reexamination the scape appeared to form a normal, although relatively small eyecap, partly hidden in the vestiture of the head. Further examination of the female revealed that it is very close to some undescribed species from West Asia which I at the time regarded as belonging to the old world genus *Niepeltia* in the sense of Scoble (1980b). In between such species have been described by Puplesis (1984c) in *Microcalyptris* – previously only recorded from North America – forming the species-group *repeteki* Puplesis. Careful reexamination of the type-species of these genera and several additional species showed that a separation of *Microcalyptris* and *Niepeltia* is no longer tenable. All species share the typical venation, with the towards the base shifted closed cell (figs. 27, 28, 103, 104). The closed cell is still visible because a persistent trachea runs from R1 to Rs + M, a feature previously overlooked, but present in all species examined. Other characters, thought to be typical for *Microcalyptris*, such as the lateral support rods, occur also in many species believed to be *Niepeltia*. Also the supposed *Niepeltia* apomorphy (Scoble, 1980b), the absence of the transverse bar of the transtilla, although widespread, is not universal: two species in northern Africa, several Asian and some Nearctic species have a distinct transverse bar. It is still possible that the Nearctic species form a subordinate monophyletic entity, but keeping it as separate taxon almost certainly makes the old-world genus paraphyletic. Thus I have synonymised *Niepeltia* and *Microcalyptris* with the senior *Acalyptris*.

Diagnosis. — Species of *Acalyptris* can most easily be recognised by the venation (figs. 27, 28, 103, 104): the almost straight Rs + M and the very small, hardly visible closed cell. Many species are unicolorously pale, but some have colour patterns.

Apomorphy: 40. Closed cell in forewing shifted towards base, vestigial.

The following apomorphic trends can be observed in many members of this taxon, but since also the plesiomorphic condition occurs in *Acalyptris,* they cannot be regarded as part of the ground-plan: a. Transverse bar of transtilla lost; b. Ventral plate of vinculum reduced to flimsy membrane; c. Lateral support rods present.

Description. — Adult. Very small to moderately small moths, forewing length 1-4.2 mm. Head. Collar small, comprising piliform scales. Antenna with 22-73 segments. Sensillum vesiculocladum variably branched. Labial palpi three segmented. Forewing usually uniformly pale, occasionally with longitudinal stripe or various patterns, not often fasciate; cilia-line normally present, but often indistinct. Underside occasionally with special scales or a hair-pencil. Venation (figs. 27, 28, 103, 104): closed cell shifted towards base, hardly visible, R1 seeming separate from wing-base, but a persistent trachea (or two tracheae) runs from R1 to Rs + M. Main trunk Rs + M approximately straight, with three branches: R2 + 3, R4 + 5 and M. Cu usually not present as separate vein, but present in some species (fig. 28). Hindwing with costal bristles in ♂ and ♀, occasionally lost in ♂. In some species special scales



Figs. 103, 104. Venation of *Acalyptris*. 103, *A*. spec., Greece, ♂, slide VU 378; 104, *A. loranthella* (Klimesch), ♂, slide VU 376. Scale: 0.5 mm.

present, sometimes as hair-pencil, but different from hair-pencil in *Ectoedemia*. Venation as in *Stigmella*. Abdomen. Anterior part of sternum 2 (figs. 40-43) comparatively large, pentagonal or trapezoid, "windows" bordered by rod-like structures. Male with paired anal tufts on tergum 8, but most species in *repeteki*-group with pairs of very long piliform scales on tergites 4-8 (Puplesis, 1984c); in addition these species have special sclerotisations on the tergites.

Male genitalia. Vinculum invisibly fused with tegumen, forming complete ring; ventral plate usually bilobed, often reduced to flimsy membrane. Tegumen forming variably shaped pseuduncus. Uncus with single medial process, usually divided dorsoventrally. Gnathos with single medial element. Valva variously shaped, often with prominent inner processes; in *repeteki* species group inner margin with comb of closely set spines, resembling pecten of *Pectinivalva* and Incurvarioidea. Transtilla usually without transverse bar, occasionally with. Aedeagus with one or two pairs of carinae, the ventral pair fused to a ventral process; vesica with small denticulate cornuti and often additional larger sclerotisations.

Female genitalia. Terminalia usually blunt and broad. T8 a single plate, often narrow, with single setae or groups of setae. T9 comprising distinct pair of anal papillae. Posterior apophyses sometimes (in Nearctic species) much

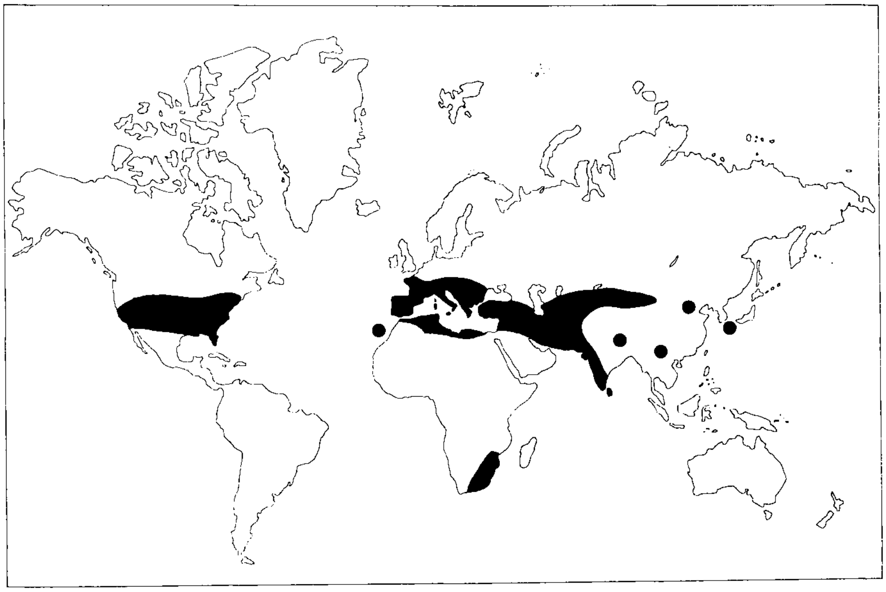


Fig. 105. Distribution of *Acalyptris*.

longer than anterior ones. Vestibulum with elaborate sclerotisations and often additional pectinations. Ductus spermathecae coiled, vesicle prominent. Corpus bursae long, usually with pectinations and long reticulate signa.

Biology. — Hostplants. Known for less than 50% of species, there are no plant families which comprise the hosts for a considerable part of the genus. Recorded from: Anacardiaceae, Capparaceae, Combretaceae, Cyperaceae, Euphorbiaceae, Fabaceae (Leguminosae), Limoniaceae, Loranthaceae, Lythraceae, Myrtaceae, Platanaceae, Rhamnaceae, Rhizophoraceae, Rubiaceae, Rutaceae and Theaceae. Mine. Leaf-miners, usually a long gallery. Pupation in soil.

Distribution (fig. 105). — In Nearctic region mainly in southern half of USA, in Palaearctic region mainly in desert and steppe regions of North Africa, Middle East and Central Asia, few species in southern Europe, Japan and China. In Oriental region at least in India and Sri Lanka, and common in southern part of Africa.

Species included. — 1. *A. psammophricta* Meyrick, redescribed below. 2. 16 species in West Palaearctic and Central Asia (Puplesis, 1984c; Van Nieukerken, 1986). 3. 20 species in southern Africa and one from India described by Scoble (1980b). 4. 7 species in USA (Davis, 1978b; Wilkinson, 1979). 5. 2 species from Japan at present under study (ELUO).

Acalyptris psammophricta Meyrick, 1921
(figs. 31, 79)

Acalyptris psammophricta Meyrick, 1921: 410. Holotype ♀, India: Ahmedabad, Bombay, 5.x.1918 *(Maxwell),* Meyrick coll., Genitalia slide 22601 (BMNH) [examined].

Male unknown.

Female. Forewing length 2.3 mm. Head: frontal tuft very pale yellow; collar almost white; scape white, antenna with 35 segments. Thorax white. Forewing white with few scattered yellowish scales. Hindwing white. Venation (examined in intact specimen) as described for genus.

Female genitalia (figs. 31, 79). T8 narrow, laterally produced into setose lobes, no scales present. T9 ending in two widely separate hairy anal papillae, in dorsal view overlapped by T8. S7 with row of long setae. Vestibulum folded, with indistinct sclerotisation at right side. Corpus bursae bulbous, 550 μm long, without pectinations; signa long, 405 μm. Ductus spermathecae with 3 convolutions.

Remarks. — Nothing is known of the biology of the species. *A. psammophricta* comes very close to females found in Iran, which are associated with males clearly belonging to the *repeteki* group of Puplesis (1985c).

Genus **Trifurcula** Zeller, 1848
(fig. 71)

Trifurcula Zeller, 1848: 330. Type-species: *Trifurcula pallidella* Zeller, 1848: 332, by subsequent designation (Tutt, 1899: 355).

Glaucolepis Braun, 1917b: 201. Type-species: *Nepticula saccharella* Braun, 1912: 97, by original designation and monotypy (Synonymised by Van Nieukerken, 1986: 14).

Levarchama Beirne, 1945: 206. Type-species: *Nepticula cryptella* Stainton, 1856: 41, by original designation (Synonymised by Johansson, 1971: 246).

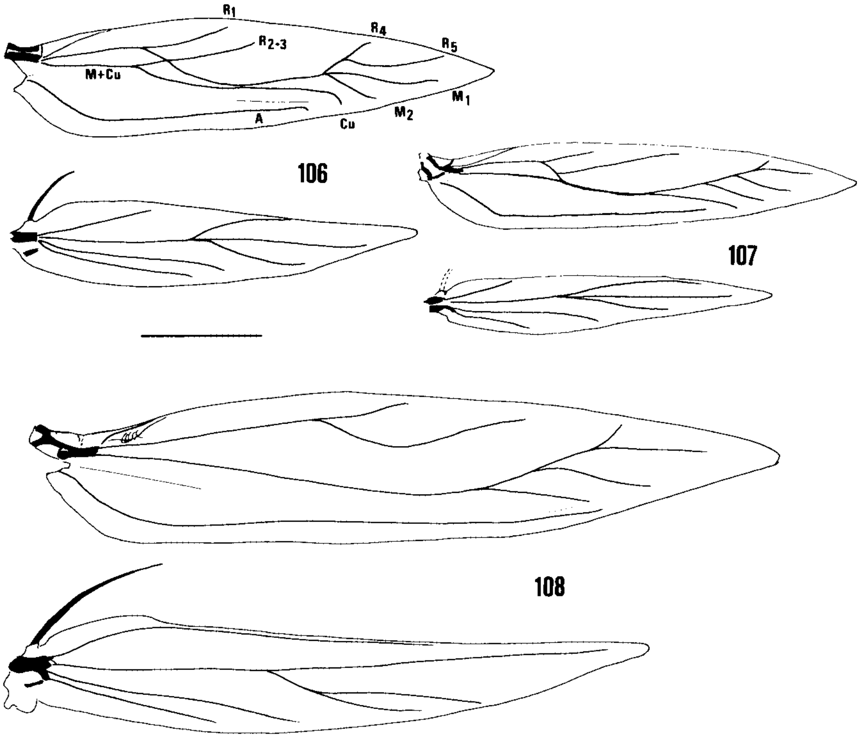
Fedalmia Beirne, 1945: 207. Type-species: *Nepticula headleyella* Stainton, 1854: 300, by original designation and monotypy (Synonymised by Johansson, 1971: 245).

The genus *Trifurcula* was proposed by Zeller (1848) for two species with a three-branched (trifurcate) R + M vein in the hindwing, opposed to the bifurcate condition in other nepticulids. In fact this character still holds as an autapomorphy for *Trifurcula* in the present sense, which follows Scoble's (1983) concept. *Trifurcula* is one of the best defined nepticulid genera, with at least three autapomorphies. Apart from the name-giving character, there are two secondary sexual characters in the male, present in almost all species: the three pairs of abdominal tufts and the "velvet" patch on the hindwing underside. Also the genitalia exhibit a high uniformity, which lead Scoble (1980a) to postulate two other possible apomorphies: shape of valva and short tegumen. A possible other apomorphy is the hostplant family: Fabaceae (Leguminosae). All species of the subgenera *Trifurcula* s.str. and *Levarchama* of which the life-history is known feed on this family, but from the subgenus *Glaucolepis* only one species in Japan is known to feed on Fabaceae. I assume tentatively that the Japanese species retained the plesiomorphic hostplant and that most *Glaucolepis* species shifted to another hostplant. If this later appears to be untrue, the hostplant family is in any case an apomorphy for the subgenera *Levarchama* and *Trifurcula*.

Diagnosis. — *Trifurcula* males are easily recognised by the three first apomorphies, only two species of *Glaucolepis* are known to miss the "velvet" patch. Females can be recognised by the hindwing venation, but are externally easily confused with *Acalyptris* or *Ectoedemia* species.

Apomorphies. — 42. Hindwing with three-branched R + M (figs. 106-108) (Zeller, 1848; Scoble, 1980a); 43. Male abdomen with paired tufts on tergites 6, 7 and 8; 44. Male hindwing on underside with "velvet" patch of special scales (figs. 19-22); 45. Hostplant: Fabaceae (Leguminosae); 46. ?short tegumen (Scoble, 1980a); 47. ?triangular valva with pointed distal process (Scoble, 1980a).

Description. — Adult. From very small to (for Nepticulidae) relatively large moths, forewing length 1.7-5.0 mm. Head. Collar small, comprising piliform scales. Antennae with 23-55 segments. Sensillum vesiculocladum five-branched. Labial palpi three segmented. Forewing usually uniformly white, ochreous, grey, etc., usually composed by two or three types of scales. A tornal spot is often present, a costal spot rarely. Other wing markings occur scarcely, a cilia-line is more or less distinct. Underside frequently with lamellar androconial scales. Venation (figs. 106-108) complete in *T. (Glaucolepis),* with closed cell, branches R1, R2 + 3, R4, R5, M1, M2, a long Cu and A present. In *Trifurcula* s.str. and *T. (Levarchama)* closed cell secondarily lost, junction between R2 + 3 and M + R4 + 5 lost. Hindwing with costal bristles usually present in ♂, always in ♀. Underside in ♂ with "velvet" patch of androconial scales in 95% of species; occasionally additional androconial scales on upperside. Venation: Rs + M with three branches. Abdomen. Anterior part of sternum 2 pentagonal or with convex posterior margin, "windows" bordered by rod-like structures (figs. 44, 45). Male with



Figs. 106-108. Venation of *Trifurcula*. 106, *T. (Glaucolepis) headleyella* (Stainton), ♂, slide VU 963; 107, *T. (G.) sanctaecrucis* (Walsingham), ♂, slide VU 276; 108. *T. (T.) immundella* (Zeller), ♂, slide VU 247. Scale: 0.5 mm.

paired tufts of piliform scales on tergum 6, 7 and 8, those on 8 being the largest.

Male genitalia. Vinculum invisibly fused with tegumen, forming complete ring, ventral plate often expanded, occasionally bilobed. Tegumen produced into triangular pseuduncus. Uncus V or Y shaped. Gnathos basically with single medial element, but this often reduced. Valva basically triangular, terminating in pointed distal process. Transtilla with or without transverse bar. Aedeagus with single ventral carina, often bifurcate, tightly fused to ventral process; vesica with one or more large cornuti and often several smaller cornuti.

Female genitalia. T8 comprising two approximately triangular plates, each covered with a group of setae, and usually scales. T9 comprising a distinct pair of setose anal papillae. Few species with long pointed ovipositor. Vestibulum folded, without sclerotisations, but usually a few pectinations present. Ductus spermathecae strongly sclerotised and coiled, with up to ten convolutions, vesicle conspicuous. Bursa long, elongate, covered with pectinations, and pair of long, narrow reticulate signa, with irregular margins.

Biology. — See under subgenera.

Distribution. — Recorded from most continents, except South America and Australia, but reaching its highest diversity in the mediterranean region, see further under subgenera.

Species included. — The genus is here (as in Scoble, 1983) divided into three subgenera: *Glaucolepis, Levarchama* and *Trifurcula.*

Subgenus **Glaucolepis** Braun, 1917
(figs. 44, 106, 107, 109-113)

Glaucolepis Braun, 1917b: 201. Type-species: *Nepticula saccharella* Braun, 1912.
Fedalmia Beirne, 1945: 207. Type-species: *Nepticula headleyella* Stainton, 1854 (Synonymised by Puplesis, 1985b).

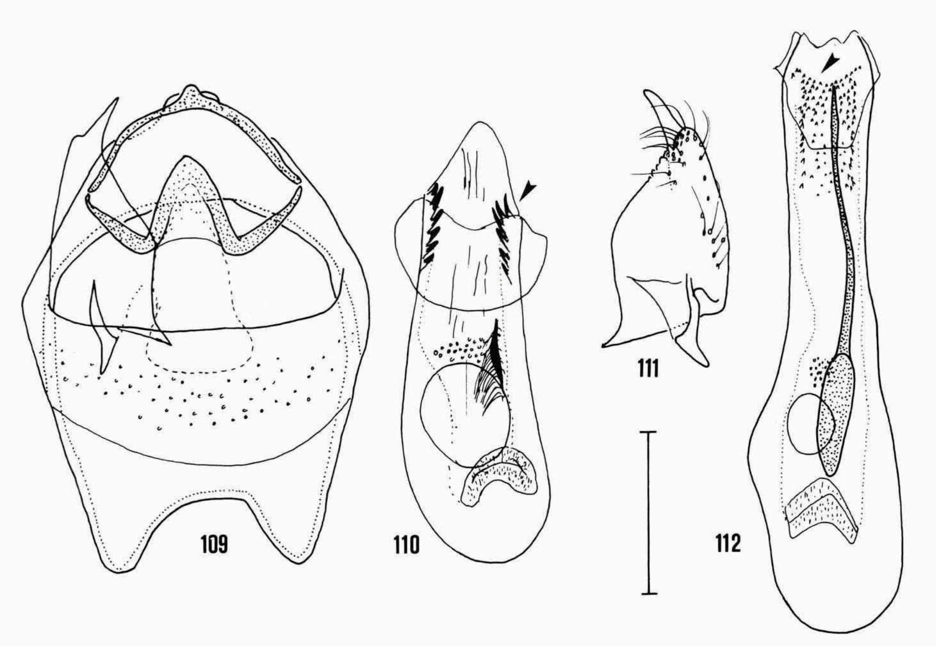
Braun (1917b) described *Glaucolepis* for a single, *Acer*-feeding species in North America. Examination of this species corroborated the earlier suggestion by Johansson (see Scoble, 1983) that it is congeneric with the single species, included by Beirne (1945) in *Fedalmia,* sharing most apomorphies for the genus and subgenus. After Beirne's work it became apparent that many species in the mediterranean region, especially those mining Labiatae, belong to the same taxon. The subgenus is very uniform in the male genitalia, but exhibits a large variation in externals and biology.

Diagnosis. — Externally most species in *T. (Glaucolepis)* cannot be distinguished from the next subgenera. The venation of the forewing is the best character plus the male genitalia (see apomorphies).

Apomorphies. — 48. Transverse bar of transtilla lost (fig. 111); 49. Aedeagus with spines on innerside near phallotreme (fig. 110, 112); 50. Vesica with single, very long and often curved cornutus (fig. 112).

Description. — Adult. Forewing usually without colour pattern or with tornal spot only, but some species, especially outside Europe, have shining metallic spots and/or fasciae. Underside in male in many species with small or large patch of androconial scales. Venation (figs. 106, 107) complete, with closed cell; Cu often very long, running partly parallel or confluent with Rs + M. Hindwing occasionally without "velvet" patch, as in *T. saccharella,* but usually this patch present. Occasionally there are other androconial scales on the upperside.

Male genitalia (figs. 109-112). Vinculum usually slightly concave anteriorly, sometimes long and truncate. Uncus with pointed or bilobed ventral process. Gnathos with single medial element. Valva triangular, with prominent, often separate, distal process. Transtilla without sclerotised transverse bar, a mem-



Figs. 109-112. *Trifurcula (Glaucolepis),* male genitalia; 109-111. *T. headleyella* (Stainton), slide VU 2292; 112. *T. rosmarinella* (Chrétien), slide VU 1821; 109, capsule, ventral aspect; 110, 112, aedeagus, ventral aspect; 111, valva, dorsal aspect. Spines near phallotrema arrowed (apomorphy 49). Scale: 0.1 mm.

branous connection seems sometimes present. Aedeagus with ventral process; inner side of aedeagal wall often with spines laterally and occasionally ventrally, near phallotreme, the spines resemble cornuti but belong to the aedeagus proper. Vesica with only one cornutus, usually very long and curved, sometimes longer than aedeagus, other cornuti absent, but vesica often grooved or fluted.

Female genitalia. Ovipositor sometimes extremely long and pointed (in *T. rosmarinella* (Chrétien) and *stoechadella* Klimesch), associated with very long apophyses, otherwise as described for genus. Signa with the cells often incomplete.

Biology. — Hostplants. In Nearctic on deciduous trees: Aceraceae, in Japan on Fabaceae (Leguminosae). In West Palaearctic on dwarf shrubs and herbs, usually occurring in mediterranean habitats (so-called Garrigue, Maquis, Mattoral vegetations), or even deserts: Lamiaceae (Labiatae) (for at least 12 species), Globulariaceae (3 spp.), Apiaceae (Umbelliferae) (2 spp.), Linaceae (1 sp.) and Asteraceae (Compositae) (1 sp.). Mine. In principle leaf-miners, making long galleries. Species on Lamiaceae often use two or three leaves to complete feeding, which they reach by mining through the petioles and stem. Occasionally the larva only mines the stem (summer generation of *T. saturejae* (Parenti); *T. bleonella* (Chrétien)). Life-history. Mostly

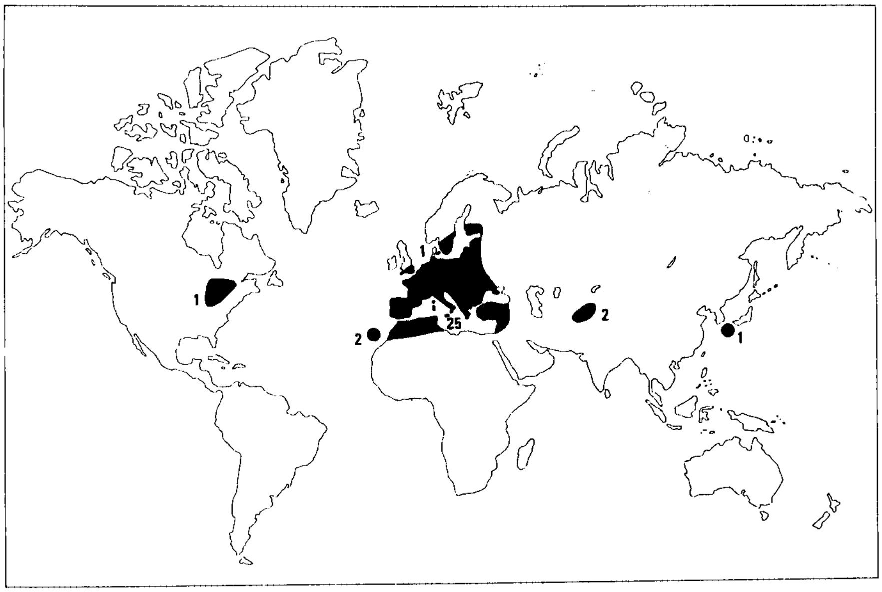


Fig. 113. Distribution of *Trifurcula (Glaucolepis)* with approximate number of species per region.

univoltine, occasionally bivoltine. Mediterranean species often feed during winter.

Distribution (fig. 113). — At present known from North America, Japan and western Palaearctic region, northwards to Sweden, westwards to Canary Islands, southwards to Sahara and eastwards to Afghanistan and Tadzhikistan. Especially common around Mediterranean.

Species included. — 1. *T. saccharella* (Braun, 1912) **comb. n.**, North America, see Wilkinson & Scoble (1979). 2. 18 described West Palaearctic species, see Van Nieukerken (1986), Klimesch (1975a, b; 1976; 1977; 1978b; 1979), Borkowski (1970) and Emmet (1976). There are at least 10 more undescribed species present in collections. 3. *T. raikhonae* (Puplesis, 1985c) **comb. n.**, from Central Asia. 4. One species from Japan, at present under study (EIHU, ELUO).

Subgenera **Levarchama** and **Trifurcula**

Apomorphies for subgenera *Levarchama* and *Trifurcula*. — 51. Forewing: connection between R2 + 3 and R4 + 5 lost (fig. 108); 52. Aedeagus with two or three large cornuti.

Subgenus **Levarchama** Beirne, 1945
(figs. 18, 45, 114-117)

Levarchama Beirne, 1945: 206. Type-species: *Nepticula cryptella* Stainton, 1856.

This is a very small and uniform subgenus of species making leafmines in certain leguminosous herbs and shrubs. Although it is similar to *Trifurcula* s.str., the morphology of the genitalia and the biology warrant a separate subgeneric status, rather than species-group, thus following Scoble (1983).

Diagnosis. — Externally not separable from other subgenera. In venation similar to *Trifurcula* s.str. Male genitalia characterised by split uncus and characteristic set of cornuti. Female by high number of convolutions in ductus spermathecae.

Apomorphies. — 53. Uncus split (in ventral view) (fig. 114); 54. Aedeagus with a group of strongly sclerotised curved cornuti at left side (fig. 115).

Description. — Adult. Forewing pale or darker with dorsal and sometimes costal spot, no metallic colours. Velvet patch on hindwing always present, other special scales absent.

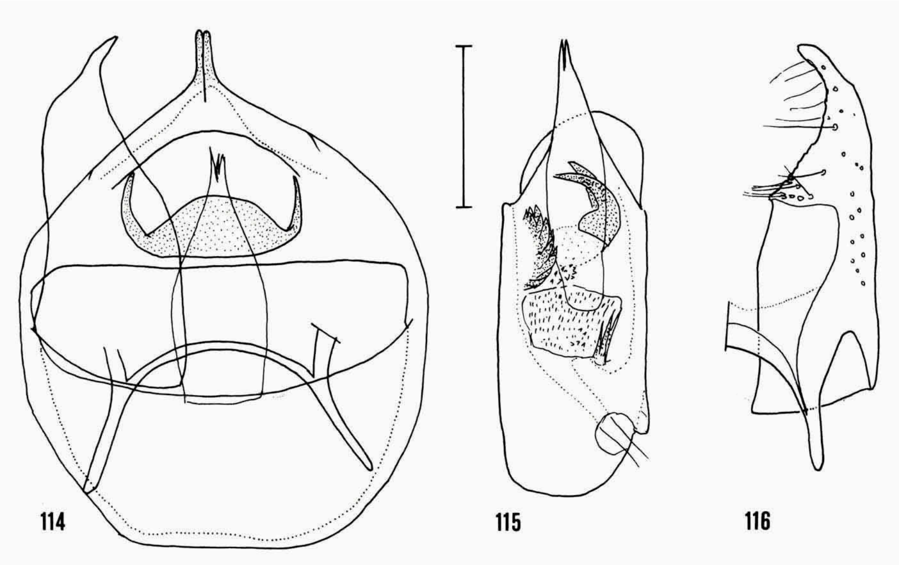
Male genitalia (figs. 114-116). Vinculum slightly excavate anteriorly. Uncus with long pointed central process, completely split longitudinally (in ventral view). Gnathos simple, central element hardly developed. Valva more or less triangular, gradually narrowing into pointed tip. Transtilla with transverse bar. Aedeagus with long, bifid ventral carina, tightly fused to ventral process; aedeagal tube with asymmetric lobe at right side. Vesica with two large, usually curved cornuti, a group of closely set, strongly sclerotised and curved cornuti at left side and many small cornuti, comprising few needle-like.

Female genitalia. Ductus spermathecae long coiled, with many convolutions (7-9), otherwise as described for genus.

Biology. — Hostplants. Fabaceae (Leguminosae), tribes Loteae *(Lotus, Dorycnium, Anthyllis)* and Coronilleae *(Coronilla)*. Mine. Leaf-mine in a single leaflet, first a gallery, later blotch. One species pupates inside mine. Life-history. Voltinism variable.

Distribution (fig. 117). — Europe, northwards to Sweden and Scotland, eastwards unknown, widespread in southern Europe, also in Canary Islands.

Species included. — Five species (Van Nieukerken, 1986). For descriptions see Emmet (1976) and Klimesch (1951a, b, 1975b, 1977).



Figs. 114-116. *Trifurcula (Levarchama) eurema* (Tutt), male genitalia, slides Kl. 837 (114) and VU 2296. 114. capsule, ventral aspect; 115, aedeagus, ventral aspect; 116, valva, dorsal aspect. Scale: 0.1 mm.

Subgenus **Trifurcula** Zeller, 1848 s.str.
(figs. 6, 19-22, 108, 117)

Trifurcula Zeller, 1848: 330. Type-species *Trifurcula pallidella* Zeller, 1848.

The concept of this subgenus is similar to the original concept of the genus and – amongst others – to that of Klimesch (1953), and Scoble (1980a).

Diagnosis. — Forewings without colour pattern, or with a longitudinal stripe only. Venation as in *Levarchama*. Male genitalia with uncus split in lateral view and characteristic pattern of cornuti. Female genitalia very similar to other subgenera.

Apomorphies. — 55. Uncus divided dorsoventrally (Scoble, 1980a); 56. Aedeagus with large group of needle-like cornuti at right side; 57. Anterior extension of vinculum rounded (Scoble, 1980a); 58. Larva feeding in stem or bark-mining (or otherwise?), but not leaf-mining.

Description. — Adult. Forewing usually uniformly pale or irrorate with two or three types of scales, occasionally with a dark longitudinal stripe, but without fascia or white spots. Underside in *griseella* species-group with patch of yellow and/or brown androconial scales. Venation with link between R2 + 3 and R4 + 5 lost (fig. 108), occasionally other veins reduced (Scoble, 1980a). Hindwing with velvet patch present, occasionally with additional sexual characters.

Male genitalia. Vinculum anteriorly rounded or extended. Uncus divided dorsoventrally, dorsal part more strongly sclerotised, and pointed, or slightly bilobed. Gnathos variable, often with large central element (*T. beirnei* Puplesis, *maxima* Klimesch), in general with different appearance from typical nepticulid gnathos, long anterior apodemes present in several species. Valva often with almost parallel margins, or triangular, ending in pointed tip. Transtilla with transverse bar. Aedeagus with pointed, often cleft, ventral carina, strongly fused to ventral process; vesica with 2 or 3 large cornuti, often curved and with large bases; in addition a group of long needle-like cornuti at right side and many indistinct small cornuti.

Female genitalia. As described for genus.

Biology. — Hostplants. Only known for some Palaearctic species: Fabaceae (Leguminosae), tribes Genisteae (*Cytisus, Genista, Lygos* and other genera) and Loteae *(Lotus)* or Coronilleae *(Coronilla)* for *griseella* species-group. For several species the hostplants are only known from association with the adult. Complete life-history only known for *T. immundella* (Zeller) and two undescribed species. They make gallery mines in the green, living bark of the hosts, and feed in winter or early spring; pupation in the soil. It is possible that ignorance of biology in other species is due to unusual, hidden habits of the larva, such as feeding in roots, buds or inside stems. Most species seem to be univoltine, flying late in the season.

Distribution (fig. 117). — Especially common in mediterranean region, extending northwards to Sweden, Estonia and Scotland, eastwards to Libanon and westwards to Canary Islands. Also in southern Africa, not yet known in between, probably in Sumatra (see further).

Species included. — 1. Eight described species from West Palaearctic (Van Nieukerken, 1986) and at least a further 10 undescribed species (see Klimesch, 1953; Wolff, 1957, Van Nieukerken & Johansson, 1986). 2. Two species in southern Africa (Scoble, 1980a). 3. One species in Sumatra. This refers to a single male present in LNK, very similar to some European species. To exclude any possibility of mislabelling, although unlikely, this record should be corroborated by finding more specimens.

Fig. 117. Distribution of *Trifurcula* s.str. The distribution of *Trifurcula (Levarchama)* almost coincides with the Palaearctic distribution of the typical subgenus.

Genus **Parafomoria** Van Nieukerken, 1983
(figs. 14, 15, 46, 118)

Parafomoria Borkowski, 1975: 498. Unavailable name.
Parafomoria Van Nieukerken, 1983b: 454. Type-species: *Nepticula helianthemella* Herrich-Schäffer, 1860: 60, by original designation.

The small genus *Parafomoria* was completely described and revised by Van Nieukerken (1983b), therefore the following treatment is kept short, and the description is not repeated.

Diagnosis. — Small moths with relatively long antennae, with or without pale spots or fascia, further recognised by listed apomorphies. See fig. 46 for sternum 2.

Apomorphies. — 59. Loss of R + 3; 60. Expansion of ventral plate of vinculum (parallelled in *Trifurcula* s.str.); 61. Expansion of lateral arms of vinculum; 62. Reduction of corpus bursae and loss of signa; 63. Costal bristles in ♂ transformed into hair-pencil or lost (figs. 14, 15); 64. Hostplant: Cistaceae.

Biology. — Hostplants. Cistaceae, genera *Cistus, Halimium, Helianthemum* and *Tuberaria.* Mine. Leaf-miners making gallery mines. Pupation in cocoon in the soil. Most species feed in winter.

Distribution. (fig. 118) and species included. — Seven species known in western Palaearctic region, with most species in west mediterranean region (Van Nieukerken, 1983b, 1985a).

Genus **Bohemannia** Stainton, 1859
(figs. 2, 12, 13, 47-49, 118-121)

Bohemannia Stainton, 1859: 439. Type-species: *Nepticula quadrimaculella* Boheman, 1853: 67, by monotypy.
Scoliaula Meyrick, 1895: 727. Unnecessary replacement name for *Bohemannia* Stainton.

Stainton erected this genus for the single species *Nepticula quadrimaculella,* which differed in its venation from all other species of *Nepticula,* known at the time. The genus remained monotypic until Borkowski (1975) placed the externally very different *B. pulverosella* (Stainton) in this genus on the basis of a similar venation and male genitalia. I also included *B. auriciliella* Joannis (= *bradfordi* Emmet) (Van Nieukerken, 1986) in this genus and Puplesis (1984b, 1985b, 1985c) recently added several eastern Palaearctic species.

Bohemannia is a characteristic genus with several apomorphies, although it has close affinities with *Ectoedemia* s.l. (see phylogenetic discussion),

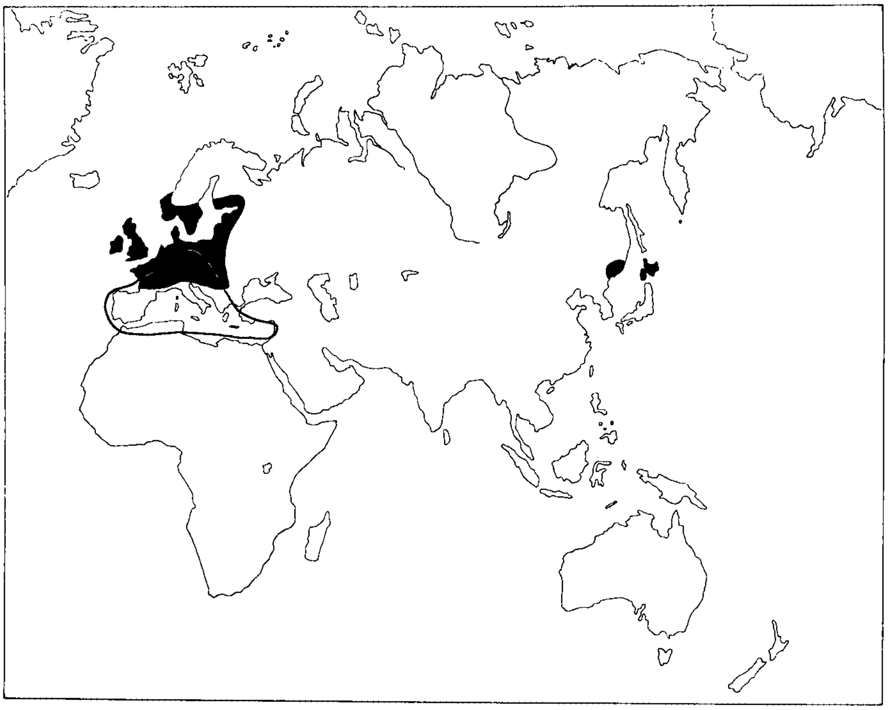


Fig. 118. Distribution of *Bohemannia* (black areas) and *Parafomoria* (solid line).

especially in the larva (Van Nieukerken & Jansen, in preparation). I have considered including *Bohemannia* into the enlarged concept of *Ectoedemia,* but since this would lead to an unfortunate large number of name changes – *Bohemannia* being the elder name – and since the evidence is not very strong, I prefer to keep these genera at present apart.

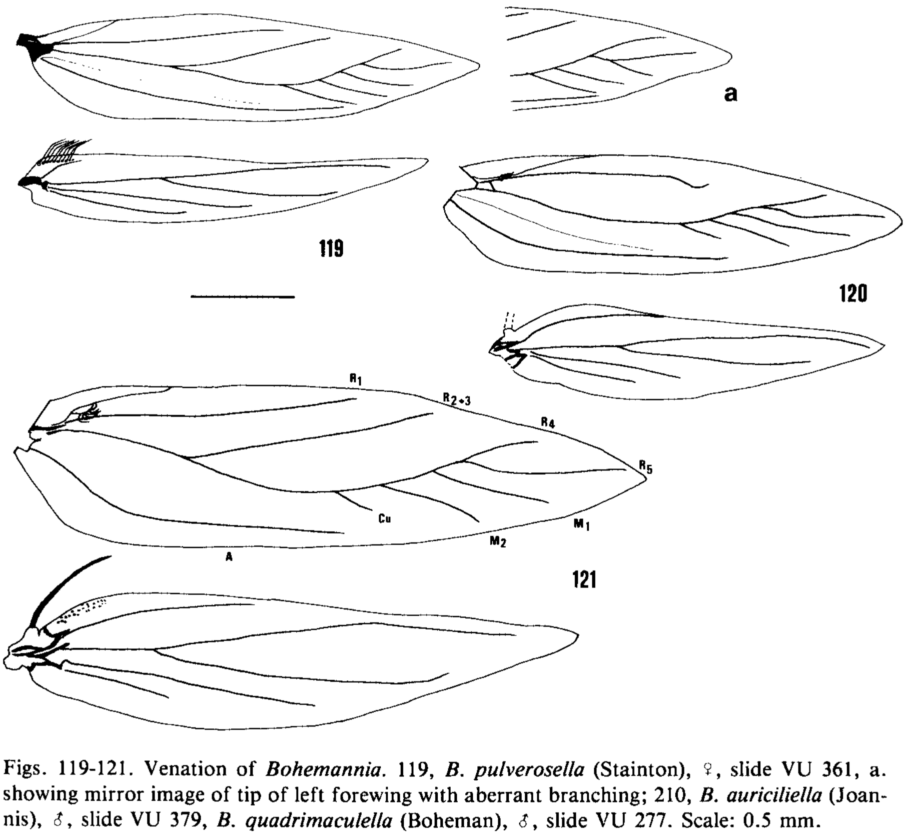
Within *Bohemannia,* the leaf-mining *B. pulverosella* and *B. piotra* Puplesis, 1984b, considered to be sister-species or possibly even synonyms, have more generalised characters than the other species, and lack some of the apomorphies of the remaining species; they are therefore considered to form the sister-group of the remaining part of the genus.

Diagnosis. — The most distinctive character is the venation (figs. 119-121). Except *pulverosella* and *piotra,* all species have a collar, comprising lamelliform scales similar to *Stigmella* and lack a cilia-line in forewing.

Apomorphies. — 67. Closed cell in forewing lost; 68. Uncus reduced to two setose pads; 69. Valva with inner (mesal), short process (secondarily lost in a few species).

The following characters are apomorphies for all species except *pulverosella* and *piotra*: a. Collar comprising lamellar scales; b. Cilia-line lost; c. Larva not leaf-mining.

Description. — Adult. Comparatively large, forewing length 2.8-4.0 mm. Head. Collar either comprising piliform scales *(pulverosella, piotra)* or lamellar scales, not very large (fig. 2). Antennae with 28-57 segments. Sensillum vesiculocladum five-branched. Forewing uniformly irrorate or with shining fascia or spots. Cilia-line present or absent. Venation: closed cell absent or reduced (recognisable by persistent trachea in *auriciliella,* fig. 120), R1 separate from main trunk of Rs + M + Cu, which normally comprises six branches: R2 + 3, R4, R5, M1, M2 and Cu, R2 + 3 absent in *auriciliella* and *ussuriella* Puplesis. Hindwing with or without costal bristles in ♂, or with small hair-pencil (figs. 12, 13), no other special scales observed; often broad and with enlarged humeral lobe. Venation not principally different from *Stigmella.* Abdomen. Anterior part of sternum 2 with rounded lateral



Figs. 119-121. Venation of *Bohemannia.* 119, *B. pulverosella* (Stainton), ♀, slide VU 361, a. showing mirror image of tip of left forewing with aberrant branching; 210, *B. auriciliella* (Joannis), ♂, slide VU 379, *B. quadrimaculella* (Boheman), ♂, slide VU 277. Scale: 0.5 mm.

margins, posterior margin straight or with some lobes (figs. 47-49). Arcuate rods present or absent. Male tergum 8 with pair of anal tufts.

Male genitalia. Vinculum ring-shaped, fused with tegumen. Tegumen rounded, not forming a pseuduncus. Uncus a curved or angulate bar with two lateral setose pads, central element not prominent. Gnathos of generalised type with large central element. Valva approximately triangular, with inwards curved tip; on inner (dorsal) surface with small inwards directed process in most species. Transtilla with transverse bar. Aedeagus with complex carinal structures; vesica with numerous small and one or two large cornuti.

Female genitalia. Ovipositor broad or produced. T8 with setae and with or without scales. Anal papillae distinct and setose. Vestibulum with lateral, folded, pouch (a small accessory sac), sometimes with internal sclerotisations. Corpus bursae with reticulate signa (or secondary lost) and small spicules placed in groups of 3 on small cushions. Ductus spermathecae coiled.

Biology. — According to biology the species can be divided into the same groups as on morphological grounds:

1. The species *B. pulverosella* and *piotra* are leaf-miners on *Malus* (Rosaceae), univoltine, with larvae feeding in early summer.
2. From the remaining species the biology is largely unknown. *B. quadrimaculella* is associated with *Alnus glutinosa* (Betulaceae) and *B. ussuriella* Puplesis with *Quercus* spp. (Fagaceae). *B. quadrimaculella* most likely mines buds, since a nepticulid larva was discovered, when opening some buds of *Alnus* (Emmet, in litt.). It is supposed that most other species have a similar endophagous life-style, but no larva has been discovered yet.

Distribution (fig. 118). — Entirely Palaearctic, known from most of Central, West and northern Europe, the easternmost Soviet-Union (Primorye) and Japan, Hokkaido.

Species included. — Eight described species in total: three from West Palaearctic (Van Nieukerken, 1986) and five from East Palaearctic (Puplesis, 1984b, 1985b, 1985c).

Genus **Ectoedemia** Busck, 1907
(fig. 72)

Ectoedemia Busck, 1907: 97. Type-species: *Ectoedemia populella* Busck, 1907: 98, by original designation and monotypy.

Obrussa Braun, 1915: 196 nec Saalmüller, 1891. Type-species: *Nepticula ochrefasciella* Chambers, 1873: 128, by original designation and monotypy (Synonymised by Van Nieukerken, 1986: 16).

Zimmermannia Hering, 1940: 266. Type-species; *Ectoedemia liebwerdella* Zimmermann, 1940: 265, by original designation and monotypy (Synonymised by Klimesch, 1953: 163).

Dechtiria Beirne, 1945: 204. Type-species: *Tinea subbimaculella* Haworth, 1828: 583, by original designation (Synonymised by Svensson, 1966: 200).

Etainia Beirne, 1945: 208. Type-species: *Lyonetia sericopeza* Zeller, 1839: 215, by original designation (Synonymised by Van Nieukerken, 1986: 16).

Fomoria Beirne, 1945: 208. Type-species: *Nepticula weaveri* Stainton, 1855: 49, by original designation (Synonymised by Scoble, 1983: 19).

Laqueus Scoble, 1983: 20 (as subgenus of *Ectoedemia*). Type-species: *Nepticula grandinosa* Meyrick, 1911: 236.

Trifurcula partim; Johansson, 1971: 245.

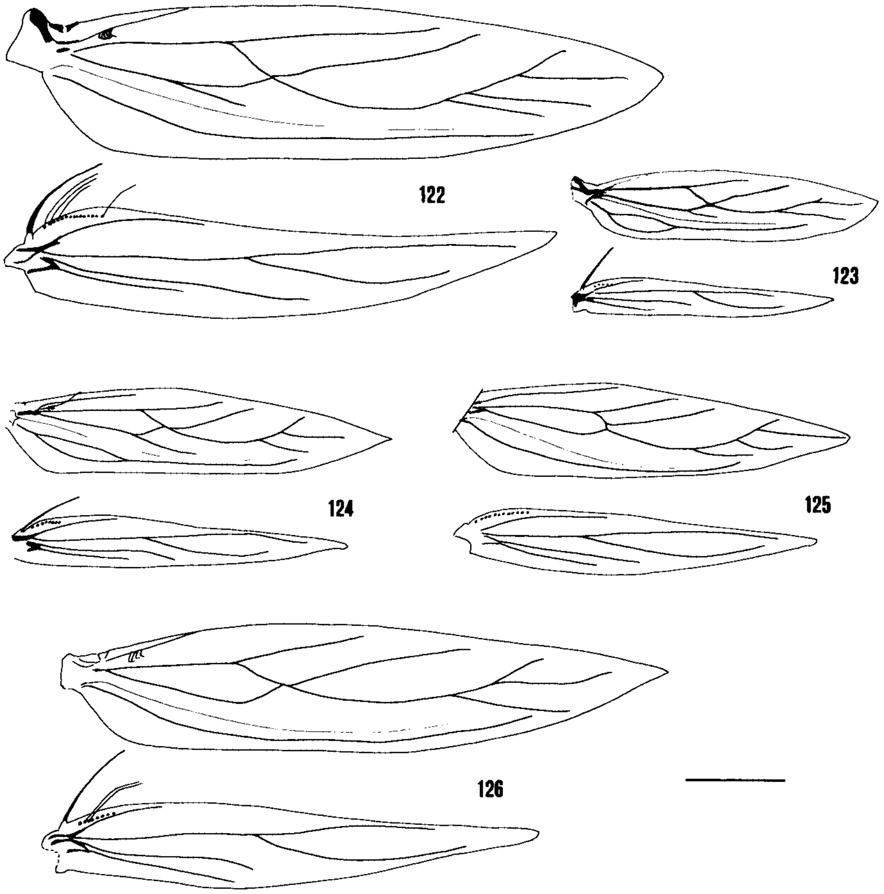
Ectoedemia was originally described for the gall-making *populella,* hence the name, but has been used in recent years for the group of species now included in the subgenera *Ectoedemia* and *Zimmermannia* (van Nieukerken, 1985b). Scoble (1983) expanded the genus considerably (although he added that its monophyly was uncertain) by adding the subgenera *Fomoria* and *Laqueus* and for similar reasons here the subgenus *Etainia* is added. See further the section on phylogeny.

Diagnosis. — Species of *Ectoedemia* can most easily be recognised by their venation: the closed cell is present and branches R1 and R2 + 3 are always present. A similar forewing venation is found in *Trifurcula (Glaucolepis),* but here Rs + M in the hindwing is trifurcate, whereas it is bifurcate in *Ectoedemia.* Also male *Ectoedemia* lack the two sexual characters of *Trifurcula. Parafomoria* lacks always R2 + 3, and in *Bohemannia* and *Acalyptris* the closed cell is reduced.

Apomorphies. — There are only two possible apomorphies found for this genus as a whole: 70. Abdominal sternum 2 with anterior plate almost triangular, lateral margins shortened; 72. Sensillum vesiculocladum reduced in various ways from basic 5-branched pattern (Van Nieukerken & Dop, 1986).

Description. — Adult. Highly variable in size and colour pattern, both some of the largest and smallest Nepticulidae occur in this genus. Head. Collar small, comprising piliform scales. Antennae variable, from 20 to 70 segments. Sensillum vesiculocladum very variable, usually with reduced or absent branching. Haustellum (galea) in some species very long (Scoble, 1983: some species in subgenus *Laqueus*). Forewing often with pale fascia or spots, but also uniformly coloured pale or dark species occur; cilia-line normally present. Underside in several species throughout the genus with androconial scales. Venation (figs. 122-126) with closed cell and branches R1, R2 + 3, A, always present, terminal portion of main branch (R4, R5, M1, M2) comprising two to four branches, Cu occasionally absent. Hindwing. Costal bristles present in ♂ of some species, but often replaced by hair-pencil. Venation as in *Stigmella.* Abdomen. Anterior part of sternum 2 (figs. 50-55) with shortened lateral margins, approximately triangular. Male with pair of anal tufts on tergum 8.

Male genitalia. Vinculum invisibly fused with tegumen, forming complete ring, ventral plate usually concave, occasionally expanded. Tegumen produced into pseuduncus. Uncus V- or Y-shaped, or absent. Gnathos with single central element. Valva approximately triangular, with inwards curved tip, but many variations known on this pattern. Transtilla principally with transverse bar. Aedeagus with paired carinae, the ventral pair almost always present; in addition lateral and dorsal pairs occur; ventral carinae fused to ventral pro-



Figs. 122-126. Venation of *Ectoedemia*. 122, *E. (Etainia) sericopeza* (Zeller), ♂, slide VU 384; 123, *E. (Laqueus) nigrifasciata* (Walsingham), ♂, slide VU 245; 124, *E. (Laqueus) vincamajorella* (Hartig), ♂, slide VU 1406; 125, *E. (Fomoria) nowakowskii* (Toll), ♀, slide VU 1486; 126, *E. (Fomoria) weaveri* (Stainton), ♂, slide VU 383. Scale: 0.5 mm.

cess, which is hinged to valvae and vinculum. Vesica basically with numerous denticulate cornuti but often with some large cornuti or other structures.

Female genitalia. T8 basically simple, undivided, with scales and setae, but many variations occur. T9 comprising pair of setose anal papillae. Vestibulum usually folded, with internal or external sclerotisations. Corpus bursae long, basically covered with pectinations and pair of reticulate signa. Ductus spermathecae coiled, on several occasions with many convolutions; vesicle conspicuous.

Biology. — See under subgenera.

Distribution. — Almost world-wide, but not found in New Zealand (Donner & Wilkinson, in press), and not yet positively recorded from South America.

Species included. — The genus is divided into the subgenera *Etainia, Laqueus, Fomoria, Zimmermannia* and *Ectoedemia.*

Subgenus **Etainia** Beirne, 1945
(figs. 50, 122, 127)

Obrussa Braun, 1915: 196 (preoccupied). Type-species: *Nepticula ochrefasciella* Chambers, 1873.
Etainia Beirne, 1945: 204. Type-species: *Lyonetia sericopeza* Zeller, 1839 (Synonymised by Wilkinson & Scoble, 1979: 98).

The species belonging to this taxon form a well defined monophyletic unit, usually given the rank of genus (e.g. Scoble, 1983). However, the species of *Etainia* share several attributes with the other subgenera of *Ectoedemia* which cannot be merely regarded as plesiomorphies, such as the two possible apomorphies listed under the genus. Further the larva has many similarities to some other *Ectoedemia* species, which means that *Etainia* is probably the sister group of one of the other subgenera. Although the exact relationships of these subgenera are not yet resolved, excluding *Etainia* would almost certainly make *Ectoedemia* paraphyletic.

Diagnosis. — The Holarctic species usually have two fasciae and males possess androconial scales on underside forewing and both sides of hindwing. Further recognised by the listed apomorphies.

Apomorphies. — 72. Valva with long dorsal apodeme (Beirne, 1945; Scoble, 1983); 73. U-shaped excavation in vinculum (Scoble, 1983); 74. Vesica with H-shaped sclerotisation; 75. Vestibulum with lobed sclerotisation; 76. Ductus bursae with group of spines; 77. Larvae not leaf-mining, but feeding in buds, shoots, fruits.

Description. — Adult. Forewing usually with two fasciae (often interrupted) and often additional spots, sometimes pale colour dominant. Underside in many species with dark androconial scales, leaving one or two areas bold except for a central row of scales. Venation (fig. 122) in Holarctic species complete, with four terminal branches, but more or less reduced in some South African species. Hindwing with costal bristles in ♂ and ♀, in ♂ often with androconial lamellar scales. Abdomen sternum 2 fig. 50.

Male genitalia. Vinculum with U-shaped excavation between valvae. Tegumen produced into a variably shaped pseuduncus. Uncus absent in Holarctic species, but according to Scoble (1983) present in South African species (in my opinion this could be a different interpretation of the same structure, here interpreted as tegumen). Valva approximately triangular, terminally rounded, with many prominent setae; dorsally with long, inwardly directed apodeme. Transtilla with transverse bar, with only narrow attachment to valva. Aedeagus with pair of ventral carinae. Vesica with basal H-shaped sclerotisation (not the cathrema), and a few large terminal cornuti, small cornuti absent.

Female genitalia. Terminal segments often complex. T8 with rows of setae, often with medial incision. Vestibulum with more or less ring-shaped large sclerotisation, ending ventrally in paired lobes. Ductus bursae with group of spines, corpus bursae without pectinations, signa relatively large. Ductus spermathecae indistinctly coiled.

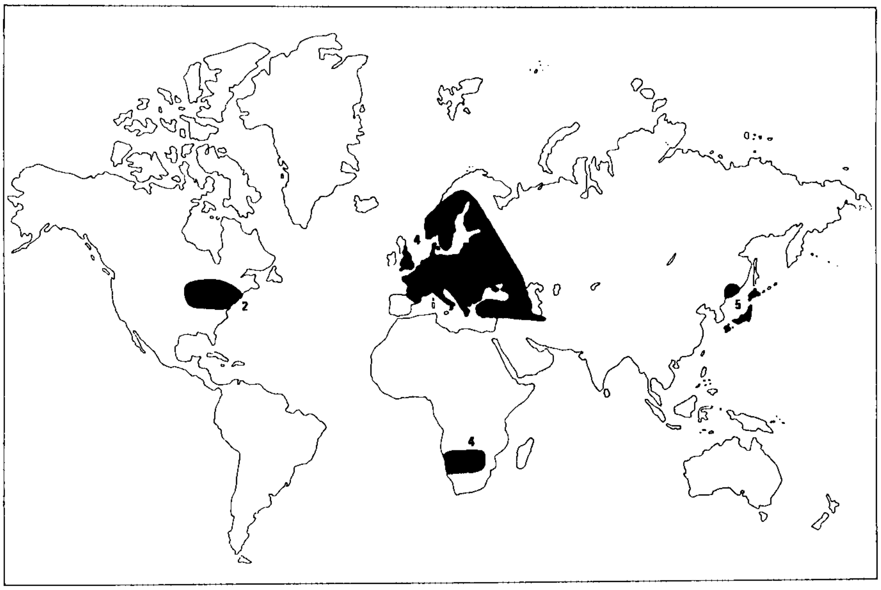


Fig. 127. Distribution of *Ectoedemia (Etainia)*, with number of species indicated.

Biology. — Hostplants. Only known for five Holarctic species: four on *Acer* (Aceraceae) and one on *Arctostaphylos* (Ericaceae). Biology partly known (Jäckh, 1951; Emmet & Johnson, 1977; Emmet, 1984). Larvae of *Acer*-feeding species mine the fruits (keys or samaras) in summer and attack various parts in winter: buds, petioles or probably shoots. *E. albibimaculella* (Larsen) mines shoots of *Arctostaphylos* (Adamczewski, 1947).

Distribution (fig. 127). — Widely distributed in Europe, known from West Asia (Anatolia, Iran, Caucasus). In East Palaearctic probably common, as yet known from Primorye and Japan. Further in North America and southern Africa.

Species included. — 1. Four species in West Palaearctic (Van Nieukerken, 1986), see Emmet (1976) and Jäckh (1951). 2. Four or five species in East Palaearctic (Puplesis & Ivinskis, 1985; current studies on Japanese species). 3. Two species in North America (Wilkinson & Scoble, 1979). 4. Four species in Southern Africa (Scoble, 1983).

Subgenus **Laqueus** Scoble, 1983
(figs. 51, 123, 124, 128-130)

Laqueus Scoble, 1983: 20. Type-species: *Nepticula grandinosa* Meyrick, 1911.

Scoble erected this subgenus for a number of species in southern Africa which have a so called "anal-loop" in the forewing (figs. 123, 124), which in fact is a reversal of a ground plan character of the Amphiesmenoptera (Kristensen, 1984b). Subsequently this character was discovered in a number of southern European species, especially those feeding on *Euphorbia,* which form a tight monophyletic group. Since these species resemble *E. grandinosa* and some other species included in *Laqueus*, this group was placed in *Laqueus* (Van Nieukerken, 1986). It is also of interest to note that all species feed on plants (belonging to five unrelated families) which have high contents of poisonous defence chemicals, such as glycosides or alkaloides.

Diagnosis. — Members of this subgenus are recognised by the anal loop in the forewing.

Apomorphies. — 78. Forewing with anal loop (Scoble, 1983); 79. Larval stipes with two setae (Van Nieukerken & Jansen, in prep.) (only known for Palaearctic species).

Description. — Adult. Forewing often uniform, occasionally with fasciae or spots. Special scales on fore- or hindwing present in few African species, not in Palaearctic species. Male with or without costal bristles. Abdomen segment 2 fig. 51. Venation (fig. 123, 124) as for genus, but with anal loop in forewing.

Male genitalia. (figs. 129, 130). See Scoble (1983) for African species. Palaearctic species: vinculum anteriorly excavate. Uncus with indistinct central process, laterally with two prominent setae on either side. Valva triangular, without specialisations. Aedeagus with minute carinae, vesica with denticulate cornuti.

Female genitalia. Palaearctic species: abdominal tip wide, both pairs of apophyses long and straight. Vestibulum with indistinct sclerotisation. Ductus spermathecae coiled; vesicle prominent, with one convolution itself.

Biology. — Hostplants. African species on Ebenaceae (genus *Diospyros, Euclea*) and Celastraceae *(Maytenus)*; Palaearctic species on Euphorbiaceae *(Euphorbia)*, Apocynaceae *(Vinca)* and Asclepiadaceae *(Periploca)*. Mine. All species leaf-miners, making galleries and/or blotches, except *E. nigrifasciata* (Walsingham), which makes galls and mines (Klimesch, 1972).

Distribution (fig. 128). — Mediterranean region eastwards to Greece; Canary Islands, further in southern Africa. Presumably a primary African subgenus extending just into southern Europe.

Species included. — Five described Palaearctic species (Van Nieukerken, 1986) and 28 species in southern Africa (Scoble, 1983).

Subgenus **Fomoria** Beirne, 1945
(figs. 3, 52, 53, 125, 126, 131-133)

Fomoria Beirne, 1945: 208. Type-species: *Nepticula weaveri* Stainton, 1855.

The subgenus *Fomoria* in the present sense follows the concept of Scoble (1983), who added that its monophyly had not been established: it is only characterised by the absence of apomorphies for the other subgenera in *Ectoedemia*. Thus, the subgenus might possibly be paraphyletic. This solution must be regarded as provisional until the relationships are better known. Although some species of *Fomoria* cluster into monophyletic units, splitting would lead to a large number of small genera, still with unknown affinities. Most Holarctic species of *Fomoria* belong to the monophyletic group which coincides with *Fomoria* in its original sense, here called the *weaveri*-group; this comprises a number of species feeding on *Hypericum* occurring throughout the Holarctic, and two closely related species on different hosts. The few other Holarctic species are added to the subgenus for similar reasons as the African species: lack of apomorphies.

Diagnosis. — Members of *Fomoria* can be recognised by the absence of all apomorphies listed under the other subgenera; an uncus is present.

Description. — Adult. Forewing variable, venation (figs. 125, 126) as for genus, Cu not separate in *weaveri*-group. Special scales absent on both wings in *weaveri*-group, present in some other species. Costal bristles in ♂ usually present, absent in some African species. Abdomen sternum 2 figs. 52, 53.

Male genitalia (figs. 131, 132). Vinculum often with posterior process, fused to carinae of aedeagus. Uncus Y-shaped. Valva often narrow or more or less triangular. Aedeagus with two pairs of carinal processes; vesica usually with some large terminal spines.

Female genitalia. Vestibulum usually with elaborate sclerotisations. Corpus bursae long.

Biology. — Hostplants. For *weaveri*-group: Clusiaceae *(Hypericum)*, but two species on respectively Ericaceae *(Vaccinium)* and Rutaceae *(Ptelea)*. Other Palaearctic species: Verbenaceae *(Vitex, Callicarpa)* and Apiaceae *(Peucedanum)*. African species recorded from Anacardiaceae, Bignoniaceae, Capparaceae, Flacourtiaceae, Oleaceae, Rhamnaceae, Sapindaceae, Scro-

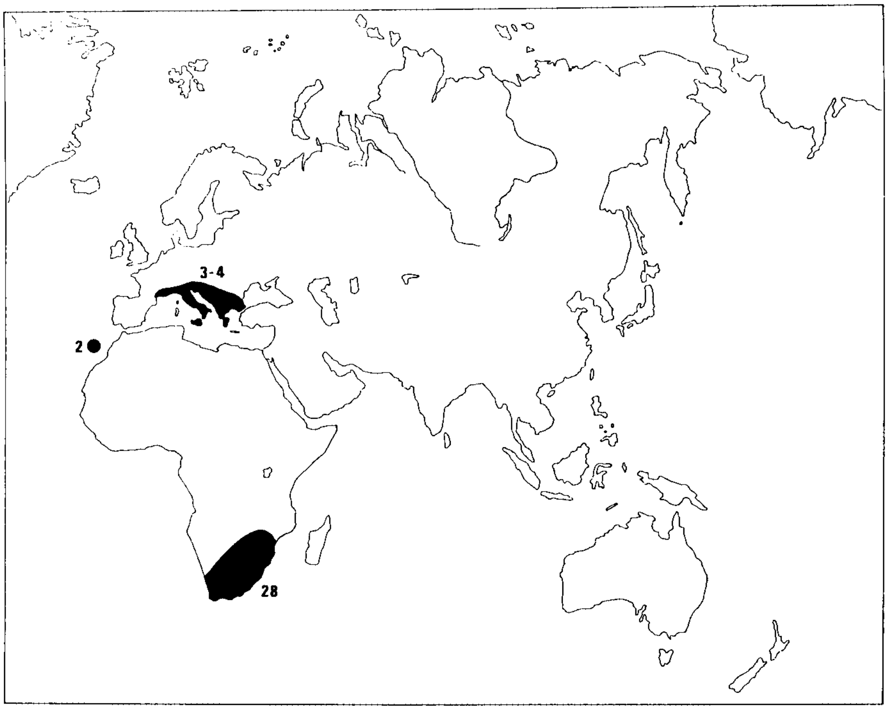


Fig. 128. Distribution of *Ectoedemia (Laqueus)*, with number of species indicated.

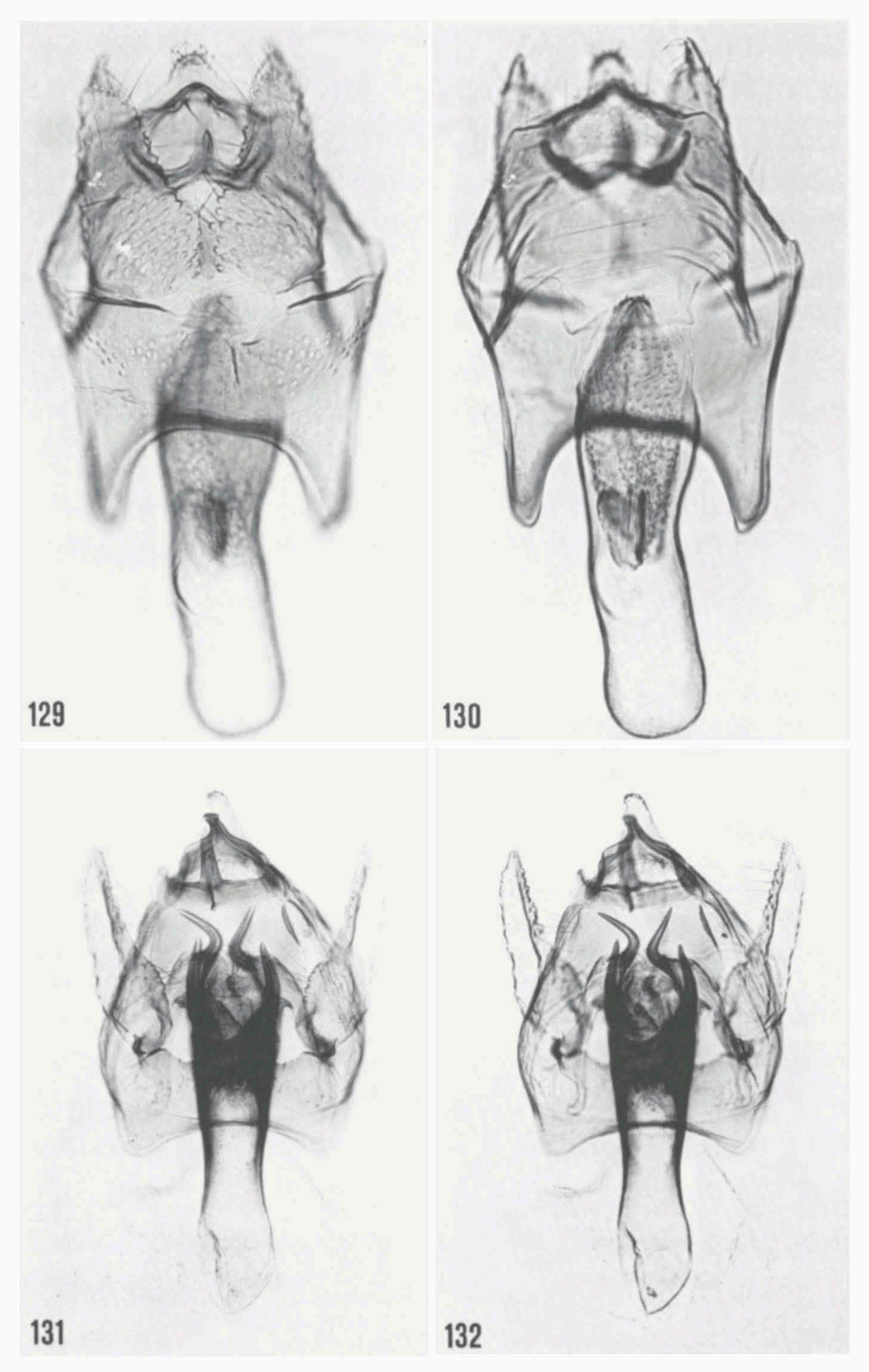


Fig. 129-132. Male genitalia of ***Ectoedemia*, ventral aspect**. 129, 130, *E. (Laqueus) euphorbiella* (Stainton), slide VU 1812; 131, 132, *E. (Fomoria) weaveri* (Stainton), slide VU 1707.

phulariaceae and Verbenaceae. Mine. Leaf-miners, making galleries, or galleries combined with blotches. Many species in *weaveri*-group pupate inside mine.

Distribution (fig. 133). — Widespread in Palaearctic region: Europe, northern Africa, Himalaya (Nepal), China, eastern USSR and Japan. Further in North America and southern Africa.

Species included. — A. *weaveri*-group: 1. Five species in West Palaearctic (Van Nieukerken, 1986), see descriptions in Emmet (1976), and Klimesch (1977, 1978a, 1978b). 2. Two or three species in North China, East USSR and Japan: *E. hypericifoliella* (Kuroko, 1982) **comb.n.** and *E. permira* (Puplesis, 1984b) **comb. n.** 3. One or two undescribed species in Nepal and Yunnan (China). 4. Two species in North America (Wilkinson, 1979).

B. other species: 5. Two species in Europe: *E. groschkei* (Skala) (see Klimesch, 1978b) and *E. nowakowskii* (Toll). 6. One species in Japan on *Callicarpa*, related to *groschkei* (ELUO). 7. Sixteen species in southern Africa (Scoble, 1983).

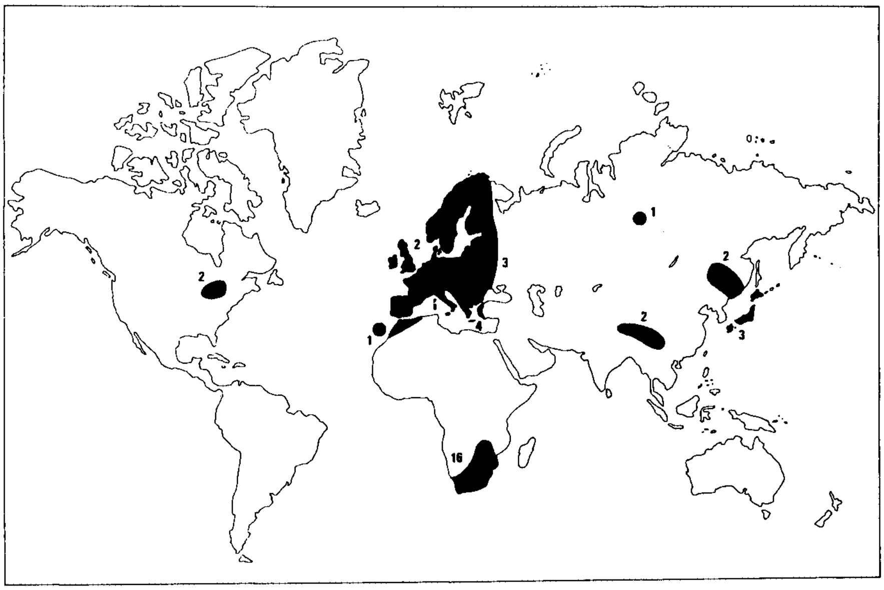


Fig. 133. Distribution of *Ectoedemia (Fomoria)*, with number of species indicated.

Subgenera **Zimmermannia** and **Ectoedemia**

The following two subgenera were treated in detail by Van Nieukerken (1985b), their treatment is therefore kept short and no description is given. These subgenera form a pair of sister-groups on the base of the following apomorphies: 80. Loss of uncus. 81. Sensillum vesiculocladum blisterlike. 82. Female with single sensillum vesiculocladum per segment.

Subgenus **Zimmermannia** Hering, 1940
(figs. 54, 134)

Zimmermannia Hering, 1940: 266. Type-species: *Ectoedemia liebwerdella* Zimmermann, 1940.

Diagnosis. — Comparatively large moths, usually dark and without colour pattern, further recognised by the listed apomorphies. They slightly resemble *Trifurcula* species, but differ in the absence of the *Trifurcula* apomorphies. Abdomen sternum 2 illustrated in fig. 54.

Apomorphies (all according to Van Nieukerken, 1985b). — 83. Larvae bark-mining; 84. Larval life lengthened, with 6-8 instars; 85. Colour pattern of forewings largely lost; 86. Male hindwing with pronounced costal emargination; 87. Large size of ventral carinae and corresponding dorsal fold of valva; 88. Female with long setae on tergites 7 and 8; 89. Bursa extremely long and narrow; 90. Margin of signa wider than individual cells.

Biology. — Hostplants. Probably for most species Fagaceae *(Quercus, Castanea, Fagus)* (known for 6 species), one species on Ulmaceae *(Ulmus)*. Mine. Bark-mining or occasionally gall-formers on bark. Pupation in soil. The larvae feed for one or two years, and overwinter in their mines.

Distribution (fig. 134) and species included. — Entirely Holarctic: twelve species in Nearctic (Wilkinson & Newton, 1981; Wilkinson 1981), eight in West Palaearctic (Van Nieukerken, 1985b) and four described from East Palaearctic (Puplesis, 1984b, 1985a, b).

Subgenus **Ectoedemia** Busck, 1907 s.str.
(figs. 4, 5, 55, 135)

Ectoedemia Busck, 1907: 97. Type-species: *Ectoedemia populella* Busck, 1907.
Dechtiria Beirne, 1945: 204. Type-species: *Tinea subbimaculella* Haworth, 1828.

Diagnosis. — Often fasciate or spotted species, usually smaller than *Zimmermannia*. Differ from other subgenera except *Etainia* by absence of uncus,

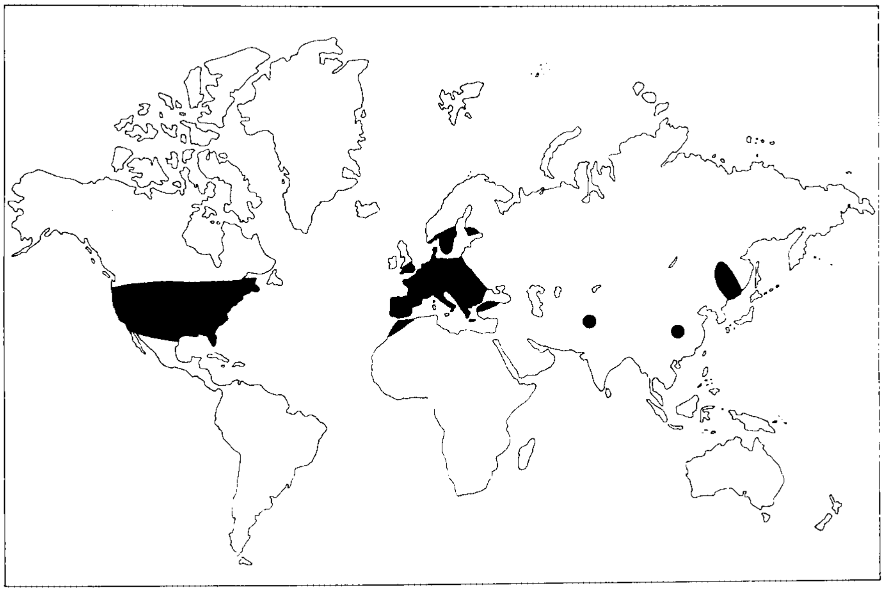


Fig. 134. Distribution of *Ectoedemia (Zimmermannia).*

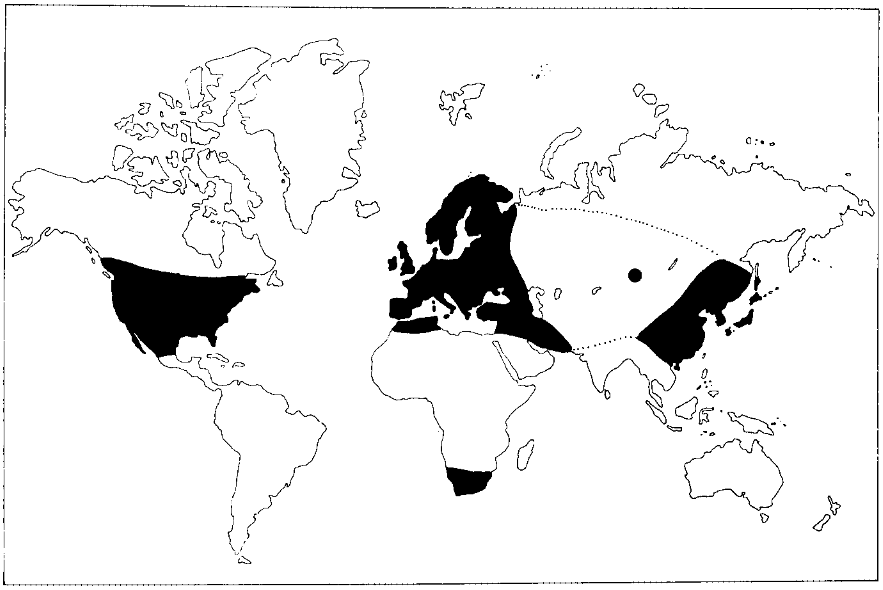


Fig. 135. Distribution of *Ectoedemia* s.str.

from *Etainia* by totally different genitalia and often different colour pattern. Further recognised by apomorphies. Abdomen sternum 2 illustrated in fig. 55.

Apomorphies (according to Van Nieukerken, 1985b). — 91. Vestibulum with circular vaginal sclerite; 92. Vestibulum with spiculate pouch; 93. Vestibulum with patch of densely packed pectinations.

Biology. — Hostplants. Most frequent on Fagaceae, Rosaceae and Salicaceae. Also recorded from Aceraceae, Anacardiaceae, Betulaceae, Burseraceae, Caprifoliaceae, Ericaceae, Hippocastanaceae, Juglandaceae, Nyssaceae, Platanaceae and Ulmaceae. Mine. Leaf-miners or petiole-miners (*E. populella* gall-maker in petiole). Mine usually starting as gallery, later forming a blotch, but many different types occur. Most species pupate in soil, but a few inside their mines.

Distribution (fig. 135) and species included. — Predominantly Holarctic: 18 in Nearctic (Wilkinson & Newton, 1981; Wilkinson, 1981); 42 in West Palaearctic, 15 described from East Palaearctic (Puplesis, 1984a, b, e, 1985b, c), a further 20 species from Japan are under study and several undescribed species are known from China. Further three species from southern Africa (Scoble, 1978a, 1979).

ACKNOWLEDGMENTS

This study is the result of eight years of taxonomic research in the "nepticulid-working group" in Amsterdam, and I am grateful to its leader, Prof. Dr. Christopher Wilkinson, for the opportunity to carry out this research, and for his criticism and helpful suggestions. I am particularly indebted to my former colleagues of this working group: Dr. Georgina Bryan, Dr. Koos Boomsma and Dr. Steph Menken for their excellent and stimulating cooperation. It is very sad that this group was sacrificed as a consequence of the economy policy at the Dutch Universities. It is a pleasure for me to extend my special thanks to my co-specialists in Nepticulidae Mr. Roland Johansson (Växjö, Sweden), Dr. Josef Klimesch (Linz, Austria), Dr. Rimantas Puplesis (Vilnius, USSR) and Dr. Malcolm Scoble (London, U.K.) for the stream of information received and the stimulating discussions. For material and information I would further like to thank the following persons: Dr. Roger Buvat (Marseille, France), Dr. Don R. Davis (USNM, Washington, USA), Mr. Hans Donner (Amsterdam, Netherlands), Mr. Hans van Driel (Amsterdam, Netherlands), Mr. Bert Gustafsson (RMS, Stockholm, Sweden), Prof. Dr. H.L. Hannemann (MHUB, Berlin, East Germany), Mr. Wim Hogenes (ZMA, Amsterdam, Netherlands), Mr. Ruud Jansen (Amsterdam, Netherlands), Dr. Rienk de Jong (RMNH, Leiden, Netherlands), Mr. Ole Karsholt (ZMUC, Copenhagen, Denmark), Dr. Friedrich Kasy (NMW, Vienna, Austria), Mr. Theo Kemperman (Amsterdam, Netherlands), Dr. Tosio Kumata (EIHU, Sapporo, Japan), Dr. Hiroshi Kuroko (ELUO, Osaka, Japan), Prof. Liu You-qiao (ZIAB, Beijing, China), Dr. Ebbe S. Nielsen (ANIC, Canberra, Australia), Dr. Gaden Robinson (BMNH, London, U.K.), Mr. Pim Schoorl (Amsterdam, Netherlands), Dr. Ernst Traugott-Olsen (Marbella, Spain) and Mr. Kevin Tuck (BMNH, London, U.K.).

I acknowledge with gratitude the technical support by Mr. Kees Alders (collecting, rearing, preparations), Mr. Remko Andeweg (idem), Mr. Bart Jan van Cronenburg (preparations), Mr. Ton Feijen (photographic work), Mrs. Daisy Kloos (preparations), Mrs. Silvia Richter (wordprocessing), Mr. Adri Rol (rearing, preparations), Mr. Nico Schaefers (printing) and Mrs. Mariet van Wissen (graphical work).

For critical comments on this manuscript I am indebted to Dr. Koos Boomsma, Dr. Rienk de Jong, Dr. Steph Menken, Dr. Niels Peder Kristensen (ZMUC, Copenhagen, Denmark) and Prof. Dr. J.T. Wiebes (RMNH, Leiden, Netherlands).

REFERENCES

Adamczewski, S., 1947. Notes on the Lepidoptera of Poland. — Entomologist 80: 102-106, 133-136.

Beirne, B.P., 1945. The male genitalia of the British Stigmellidae (Nepticulidae) (Lep.) — Proc. R. Ir. Acad. (B) 50: 191-218.

Boheman, C.H., 1853. Entomologiska Anteckningar under en resa i Södra Sverige 1851. — K. svenska VentenskAkad. Handl. 1852: 55-210.

Boomsma, J.J., 1984. Evolutionary aspects of larval food-plant exploitation in Microlepidoptera: an ecological approach to phylogenetic data. — Abstr. 17th int. Congr. Ent.: 33.

Boomsma, J.J., H. Timmermans, C.P.M. Cörvers & J. Kabout, 1986. Monophagous leaf-mining larvae of *Stigmella* (Lepidoptera: Nepticulidae) on birch: patterns and differentiation in exploitation of the host — Holarctic Ecol. (in press).

Borkowski, A., 1970. Studien an Stigmelliden (Lepidoptera) Teil II. *Fedalmia thymi* sp. n. — eine neue Art aus Mitteleuropa. — Polskie Pismo ent. 40: 69-78.

Borkowski, A., 1972. Studien an Nepticuliden (Lepidoptera). Teil IV. Bemerkungen zur Nomenklatur und Systematik der Familie Nepticulidae. — Polskie Pismo ent. 42: 689-709, 2 pls.

Borkowski, A., 1975. Studien an Nepticuliden (Lepidoptera) Teil VI. Die Verbreitung der Nepticuliden in Polen. — Polskie Pismo ent. 45: 487-535, 10 pls.

Börner, C., 1925. 22 Ordn. Lepidóptera, Schmetterlinge. — In: P. Brohmer (ed.), Fauna von Deutschland, 3., verbesserte Auflage, pp. 358-387.

Börner, C., 1939. Die Grundlagen meines Lepidopteren systems. — Int. Congr. Ent. 7, 1938, Verh. 2: 1372-1424.

Braun, A.F., 1912. Notes on North American species of *Nepticula,* with descriptions of new species (Lepidoptera). — J. Cincinn. Soc. nat. Hist. 21: 84-101.

Braun, A.F., 1915. New genera and species of Tineina. — Can. Ent. 47: 188-197.

Braun, A.F., 1917a. Observations on the pupal wings of *Nepticula,* with comparative notes on other genera. — Annls ent. Soc. Am. 10: 233-239, 1 pl.

Braun, A.F., 1917b. Nepticulidae of North America. — Trans. Am. ent. Soc. 17: 234-256, 1 pl.

Braun, A.F., 1925. Microlepidoptera of Northern Utah. — Trans. Am. ent. Soc. 51: 183-226.

Busck, A., 1907. New american Tineina. — Proc. ent. Soc. Wash. 8: 86-99.

Chambers, V.T., 1873. Micro-lepidoptera. — Can. Ent. 5: 124-128.

Common, I.F.B., 1969. A wing-locking or stridulatory device in Lepidoptera. — J. Aust. ent. Soc. 8: 121-125.

Dahlgren, R.M.T., 1980. A revised system of classification of the angiosperms. — Bot. J. Linn. Soc. 80: 91-124.

Dahlgren, R.M.T., 1983. General aspects of angiosperm evolution and macrosystematics. — Nord. J. Bot. 3: 119-149.

Davis, D.R., 1975. Systematics and zoogeography of the family Neopseustidae with the proposal of a new superfamily (Lepidoptera: Neopneustoidea). — Smithson. Contr. Zool. 210: 1-45.

Davis, D.R., 1978a. A revision of the North American moths of the superfamily Eriocranioidea with the proposal of a new family, Acanthopteroctetidae (Lepidoptera). — Smithson. Contr. Zool. 251: 1-131.

Davis, D.R., 1978b. New Leaf-mining moths of the family Nepticulidae from Florida. — Fla Ent. 61: 209-224.

Davis, D.R., 1979. *Manoneura,* a new name to replace the generic homonym *Oligoneura* Davis (Lepidoptera: Nepticulidae). — Fla Ent. 62(3): scientific notes.

Davis, D.R., 1984. Nepticulidae. — In: J.B. Heppner (ed.), Atlas of Neotropical Lepidoptera, Checklist: part I. Micropterigoidea — Immoidea, pp. 17-18.

Davis, D.R., 1985. A re-examination of *Enteucha cyanochlora* Meyrick and its subsequent transfer to the Nepticulidae (Lepidoptera: Nepticuloidea). — Proc. ent. Soc. Wash. 87: 142-145.

Davis, D.R., 1986a. Opostegidae. — In: F. Stehr (Ed.), An introduction to the immature insects of North America, vol. 1. Kendall/Hunt Publ. Co., Dubuque, Iowa.

Davis, D.R., 1986b. Monograph of a new family of Monotrysian moths from Austral South America (Lepidoptera: Palaephatidae) with a phylogenetic review of the Monotrysia. — Smithson. Contr. Zool. 434: 1-202.

Donner, J.H. & C. Wilkinson, in press. Nepticulidae (Insecta: Lepidoptera). — Fauna New Zealand, in press.

Downes, J.A., 1968. A nepticulid moth feeding at the leaf-nectaries of poplar. — Can. Ent. 100: 1078-1079.

Dugdale, J.S., 1974. Female genital configuration in the classification of Lepidoptera. — N.Z. Jl. Zool. 1: 127-146.

Ehrlich, P.R. & P.H. Raven, 1964. Butterflies and plants: a study in coevolution. — Evolution 18: 586-608.

Eldredge, N. & J. Cracraft, 1980. Phylogenetic patterns and the evolutionary process. — Columbia University Press, New York.

Emmet, A.M., 1976. Nepticulidae. — In: J. Heath (ed.), The moths and butterflies of Great Britain and Ireland 1: 171-267. Curwen, London.

Emmet, A.M., 1984. The feeding habits of overwintering larvae of *Etainia sphendamni* (Hering, 1937) (Lep.: Nepticulidae). — Entomologist's Rec. J. Var. 96: 22-26.

Emmet, A.M. & P.J. Johnson, 1977. *Etainia sericopeza* (Zeller, 1839) [Lep.: Nepticulidae] confirmed as a British species. — Entomologist's Rec. J. Var. 89: 257-264, pl. 20.

Fabricius, J.C., 1775. Systema entomologiae. — Flensburgi et Lipsiae, Kortii.

Faeth, S.H., 1985. Quantitative defense theory and patterns of feeding by oak insects. — Oecologia 68: 34-40.

Feeny, P., 1976. Plant apparency and chemical defense. — Recent Adv. Phytochem. 10: 1-40.

Göze, J.A.E., 1783. Entomologische Beiträge zu des Ritter Linné Zwölften Ausgabe des Natursystems. — Leipzig.

Gustafsson, B., 1973. A new species of *Nepticula* v. Heyden from Rhodes (Lep. Nepticulidae). — Ent. Tidskr. 94: 197-198.

Gustafsson, B., 1985. New species of *Stigmella* from The Gambia (Lepidoptera, Nepticulidae). — Tijdschr. Ent. 127: 165-177.

Hampson, G., 1918. Some small families of the Lepidoptera which are not included in the key to the families in the catalogue of Lepidoptera Phalaenae. — Novit. zool. 25: 366-394.

Haworth, A.H., 1828. Lepidoptera Brittanica, 4: 513-609. — London, J. Murray.

Hennig, W., 1966. Phylogenetic systematics. — University of Illinois Press, Urbana, Chicago, London.

Hering, E.M., 1940. *Zimmermannia liebwerdella* (Zimmermann). Ein Nachwort. — Mitt. zool. Mus. Berlin 24: 266.

Herrich-Schäffer, G.A.W., 1860. Revision der Europäischen Schmetterlingfauna. — KorrespBl. Sammler Ins. 1: 59-61.

Heyden, C. von, 1843. (no title) — Amtlicher Bericht der Versammlung der Naturforscher zu Mainz: 208.

Jäckh, E., 1951. Die fruchtminierenden Arten der Gattung *Nepticula* Heyd. (*Etainia* Beirne) an den vier deutschen Ahornarten (Lep. Nepticulidae). — Z. wien. ent. Ges. 36: 170-178, pls. 14-16.

Jermy, T., 1984. Evolution of insect/hostplant relationships. - Am. Nat. 124: 609-630.

Johansson, R., 1971. Notes on the Nepticulidae (Lepidoptera). I. A revision of the *Nepticula ruficapitella* group. — Ent. scand. 2: 241-262.

Kemperman, T.C.M. & C. Wilkinson, 1985 (with biological data provided by H. Kuroko & T. Kumata). Japanese species of the genus *Stigmella* (Nepticulidae: Lepidoptera). — Ins. matsum. n.s. 32: 1-107.

Klimesch, J., 1951a. Zur Kenntnis der Genitalmorphologie einiger *Nepticula*-Arten (Lep., Nepticulidae). — Z. wien. ent. Ges. 36: 4-9.

Klimesch, J., 1951b. *Nepticula (Levarchama) ortneri* spec. nov. (Lept., Nepticulidae). — Z. wien. ent. Ges. 36: 66-70.

Klimesch, J., 1953. Die europäischen *Trifurcula*- und *Ectoedemia*-Arten (Lep., Nepticulidae). — Z. wien. ent. Ges. 38: 160-170, 191-196.

Klimesch, J., 1972. *Dechtiria nigrifasciata* (Wlsm.) (Lep., Nepticulidae). Ein Beitrag zur Genitalmorphologie und Ökologie. — Mitt. münch. ent. Ges. 62: 1-12.

Klimesch, J., 1975a. Ergebnisse von Untersuchungen einiger Nepticuliden-Typen der Sammlung des Muséum national d'Histoire naturelle, Paris (Lep., Nepticulidae). — Bull. Mus. natn. Hist. nat. Paris 3e sér., zool. 221: 861-866.

Klimesch, J., 1975b. Über neue mediterrane und kanarische Nepticuliden. — Mitt. münch. ent. Ges. 65: 1-28.

Klimesch, J., 1976. Zur Genitalmorphologie und Lebensweise der *Fedalmia (Stigmella) saturejae* (Parenti, 1963) (Lep., Nepticulidae). — Z. ArbGem. öst. Ent. 28: 45-48.

Klimesch, J., 1977. Beiträge zur Kenntnis der Microlepidopteren-Fauna des Kanarischen Archipels. 1. Beitrag: Nepticulidae, Tischeriidae. — Vieraea 6: 191-218.

Klimesch, J., 1978a. *Fomoria luisae* n.sp. (Lep., Nepticulidae). — Z. ArbGem. öst. Ent. 29: 89-91.

Klimesch, J., 1978b. Beitrag zur Kenntnis der Nepticulidenfauna von Anatolien und der Insel Rhodos (Lepidoptera, Nepticulidae). — Tijdschr. Ent. 121: 239-278.

Klimesch, J., 1979. Beiträge zur Kenntnis der Nepticuliden. Beschreibung zweier neuer Arten (*Stigmella abaiella* n.sp. und *Trifurcula (Fedalmia) sanctibenedicti* n.sp.) (Lepidoptera, Monotrysia). — Z. ArbGem. öst. Ent. 31: 21-27.

Klots, A.B., 1970. Lepidoptera. — In: S.L. Tuxen (ed.), Taxonomist's glossary of genitalia in Insects, 2nd enlarged edition, pp. 115-120. Munksgaard, Copenhagen.

Koçak, A.Ö., 1981. On the nomenclature of some genera of Lepidoptera. — Priamus 1: 97-109.

Kristensen, N.P., 1984a. The male genitalia of *Agathiphaga* (Lepidoptera, Agatiphagidae) and the lepidopteran ground plan. — Ent. scand. 15: 151-178.

Kristensen, N.P., 1984b. Studies on the morphology and systematics of primitive Lepidoptera (Insecta). — Steenstrupia 10: 141-191.

Kristensen, N.P. & E.S. Nielsen, 1979. A new subfamily of micropterigid moths from South America. A contribution to the morphology and phylogeny of the Micropterigidae, with a generic catalogue of the family (Lepidoptera: Zeugloptera). — Steenstrupia 5: 69-147.

Kristensen, N.P. & E.S. Nielsen, 1980. The ventral diaphragm of primitive (non-ditrysian) Lepidoptera. A morphological and phylogenetic study. — Z. zool. Syst. EvolForsch. 18: 123-146.

Kristensen, N.P. & E.S. Nielsen, 1983. The *Heterobathmia* life history elucidated: immature stages contradict assignment to suborder Zeugloptera (Insecta, Lepidoptera). — Z. zool. Syst. Evolut-forsch. 21: 101-124.

Kuijten, P.J., 1974. On the occurrence of the hitherto unknown wing-thorax coupling mechanism in Lepidoptera. — Neth. J. Zool. 24: 317-322, 2 pls.

Kuroko, H., 1982. Nepticulidae. — In: H. Inoue, S. Sugi, H. Kuroko, S. Moriuti & A. Kawabe, Moths of Japan, 1: 49-50; 2: 448, pls. 1, 261, 262 [in Japanese].

Kuznetsov, V.I. & A.A. Stekolnikov, 1978. The system and evolution of the infraorders in the Lepidoptera (Micropterigomorpha-Papilionomorpha) in the light of the functional morphology of the genitalia. — Ent. Rev., Wash. 57: 601-622. (English translation of Ent. Obozr. 57: 870-890).

Kyrki, J., 1983. Adult abdominal sternum II in ditrysian tineoid superfamilies — morphology and phylogenetic significance (Lepidoptera). — Annls ent. fenn. 49: 89-94.

Leraut, P., 1980. Liste systématique et synonymique des Lépidoptères de France, Belgique et Corse. — Alexanor, Bull. Soc. ent. Fr., Suppl.: 1-334.

Maddison, W.P., M.J. Donoghue & D.R. Maddison, 1984. Outgroup analysis and parsimony. — Syst. Zool. 33: 83-103.

Menken, S.B.J. & J. Brouwer, 1984. Biochemical systematics and speciation in the leaf-mining genus *Ectoedemia* Busck (Nepticulidae, Lepidoptera). — Abstr. 17th int. Congr. Ent.: 10.

Meyrick, E., 1895. A handbook of British Lepidoptera. — London, Macmillan & Co.

Meyrick, E., 1911. Descriptions of Transvaal Micro-Lepidoptera. — Ann. Transv. Mus. 2: 218-240.

Meyrick, E., 1915. Descriptions of South American Micro-Lepidoptera. — Trans. ent. Soc. Lond. 1915: 201-256.

Meyrick, E., 1921. Exotic Microlepidoptera, 2 (13): 385-416.

Minet, J., 1984. Contribution a l'analyse phylogénétique des Néolépidoptères (Lepidoptera, Glossata). — Nouv. Rev. Ent., N.S. 1: 139-149.

Müller-Rutz, J., 1934a. Über Microlepidopteren. — Mitt. schweiz. ent. Ges. 16: 118-128, 1 pl.

Müller-Rutz, J., 1934b. Berichtigung. — Slip, published with Mitt. Schweiz. ent. Ges. 16(3).

Nelson, G. & N. Platnick, 1981. Systematics and biogeography, cladistics and vicariance. — Columbia University Press, New York.

Newton, P.J. & C. Wilkinson, 1982. A taxonomic revision of the North American species of *Stigmella* (Lepidoptera: Nepticulidae). — Syst. ent. 7: 367-463.

Nielsen, E.S., 1985a. The monotrysian heteroneuran phylogeny puzzle: a possible solution (Lepidoptera). — Proc. 3rd Congr. eur. Lepid. Cambridge 1982: 138-143.

Nielsen, E.S., 1985b. A taxonomic review of the adelid genus *Nematopogon* Zeller (Lepidoptera: Incurvarioidea). — Ent. scand., Suppl. 25: 1-66.

Nielsen, E.S., in press. The recently discovered primitive (non-ditrysian) family Palaephatidae in Australia (Lepidoptera). — Aust. J. Zool.

Nieukerken, E.J. van, 1983a. The identity of *Stigmella zelleriella* (Snellen, 1875), a senior synonym of *S. repentiella* (Wolff, 1955) (Lepidoptera, Nepticulidae). — Zool. Meded., Leiden 57: 59-65.

Nieukerken, E.J. van, 1983b. The Cistaceae-feeding Nepticulidae (Lepidoptera) of the western Palaearctic region. — Syst. Ent. 8: 453-478.

Nieukerken, E.J. van, 1985a. A new species of *Parafomoria* Van Nieukerken, and some additional notes on the genus (Lepidoptera; Nepticulidae). — Ent. Ber., Amst. 45: 24-28.

Nieukerken, E.J. van, 1985b. A taxonomic revision of the Western Palaearctic species of the subgenera *Zimmermannia* Hering and *Ectoedemia* Busck s.str. (Lepidoptera, Nepticulidae), with notes on their phylogeny. — Tijdschr. Ent. 128: 1-164.

Nieukerken, E.J. van, 1986. A provisional phylogenetic check-list of the western palaearctic Nepticulidae, with data on hostplants (Lepidoptera). — Ent. scand. 17: 1-27.

Nieukerken, E.J. van & H. Dop, 1984. Antennal sensilla of Nepticulidae (Lepidoptera: Nepticuloidea), morphology and phylogenetic implications. — Abstr. 17th int. Congr Ent.: 11.

Nieukerken, E.J. van & H. Dop, 1986. Antennal sensory structures in Nepticulidae (Lepidoptera) and their phylogenetic implications. — Z. zool. Syst. EvolForsch. (in press).

Nieukerken, E.J. van & R. Jansen, in preparation. Morphology and systematics of larvae of palaearctic Nepticulidae (Lepidoptera).

Nieukerken, E.J. van & R. Johansson, 1986. *Trifurcula pallidella* (Duponchel) and *T. beirnei* Puplesis (Lepidoptera: Nepticulidae): nomenclature, taxonomy and distribution. — Ent. scand. 17, in press.

Powell, J.A., 1980. Evolution of larval food preferences in Microlepidoptera. — Ann. Rev. Ent. 25: 133-159.

Puplesis, R.K., 1984a. Novye vidy molej-maljutok (Lepidoptera, Nepticulidae) iz juznogo Primor'ja. — Ent. Obozr. 63: 111-125.

Puplesis, R.K., 1984b. K sisteme molej-maljutok (Lepidoptera, Nepticulidae) palearkticeskoj fauny. — Ent. Obozr. 63: 582-597.

Puplesis, R.K., 1984c. Obzor vidov roda *Microcalyptris* (Lepidoptera, Nepticulidae) iz pystyn" Mongolii i SSSR (A review of nepticulid moths of the genus *Microcalyptris* (Lepidoptera, Nepticulidae) from the deserts of Mongolia and the USSR). — Nasekomye Mongolii 9: 484-507.

Puplesis, R.K., 1984d. Pervye nachodki rodov *Stigmella* i *Ectoedemia* (Lepidoptera, Nepticulidae) v Mongolii (First records of the genera *Stigmella* and *Ectoedemia* in Mongolia). — Nasekomye Mongolii 9: 508-510.

Puplesis, R.K., 1984e. New species of (Lepidoptera) Nepticulidae. — Ent. Rev., Wash. 63: 96-111 (a translation into English of Puplesis, 1984a).

Puplesis, R.K., 1985a. Moli-maljutki (Lepidoptera, Nepticulidae) Pribaltiki i Dal'nego vostoka (Nepticulidae of the Baltic states and the far east). — Avtoreferat, Ordena Trudovogo Krasnogo Znameni Zoologiceskij Institut AN SSSR, Leningrad: 1-23.

Puplesis, R.K., 1985b. Contribution to the classification of the palaearctic Nepticulidae (Lepidoptera). — Ent. Rev., Wash 63: 149-164 (a translation into English of Puplesis, 1984b).

Puplesis, R.K., 1985c. Novye vidy molej-maljutok (Lepidoptera, Nepticulidae) s juga dal'nego vostoka i Tadzhikistana (New species of the nepticulid moths from Southern far east and Tadzhikistan). — Trudy zool. Inst. Leningr. 134: 59-72.

Puplesis, R.K. & P.P. Ivinskis, 1985. Obzor fauny molej-maljutok roda *Obrussa* Braun SSSR i opisanie 4 novych vidov — *Obrussa capesella* sp. n., *O. tigrinella* sp. n., *O. peterseni* sp. n., *O. sabina* sp. n. (review of the nepticulid moths fauna of the *Obrussa* Braun genus in the USSR and a description of 4 new species). — Liet. TSR Mokslu Akad. Darb. Ser. B 4(92): 36-46.

Saether, O.A., 1979. Underlying synapomorphies and anagenetic analysis. — Zool. Scr. 8: 305-312.

Schönherr, J., 1958. Biologie und Morphologie von *Ectoedemia liebwerdella* Zimmerm., unter Berücksichtigung der übrigen rindenminierenden Nepticuliden (Lep.). — Dt. ent. Z. (N.F.) 5: 1-71.

Schoorl, J.W., E.J. van Nieukerken & C. Wilkinson, 1985. The *Stigmella oxyacanthella* species-group in Europe (Nepticulidae: Lepidoptera). — Syst. ent. 10: 65-103.

Schoorl, J.W. & C. Wilkinson 1986. The *Stigmella betulicola* species-group in Europe (Lepidoptera: Nepticulidae). — J. nat. Hist. 20: 225-244.

Schrank, Franz von Paula, 1802. Fauna Boica, 2(2) — J.W. Krüll, Ingolstadt.

Scoble, M.J., 1978a. Nepticulidae (Lepidoptera) of southern Africa: the genus *Ectoedemia* Busck. — J. ent. Soc. sth. Afr. 41: 81-86.

Scoble, M.J., 1978b. Nepticulidae of southern Africa: a taxonomic revision of the genus *Stigmella* Schrank (Lepidoptera: Monotrysia). — Ann. Transv. Mus. 31: 87-129, 1 pl.

Scoble, M.J., 1979. A new species of *Ectoedemia* Busck from Botswana with observations on its imaginal skeletal anatomy (Lepidoptera: Nepticulidae). — Ann. Transv. Mus. 32: 35-54.

Scoble, M.J., 1980a. *Trifurcula* Zeller: a critical analysis of the genus, cladistic relationships and descriptions of two new species from South Africa (Lepidoptera: Nepticulidae). — J. ent. Soc. sth. Afr. 43: 139-150.

Scoble, M.J., 1980b. The genus *Niepeltia* Strand: taxonomy, and comments on structure and relationships (Lepidoptera: Nepticulidae). — Ann. Transv. Mus. 32: 197-229.

Scoble, M.J., 1982. A pectinifer in the Nepticulidae (Lepidoptera) and its phylogenetic implications. — Ann. Transv. Mus. 33: 123-129.

Scoble, M.J., 1983. A revised cladistic classification of the Nepticulidae (Lepidoptera) with descriptions of new taxa mainly from South Africa. — Transv. Mus. Monograph 2: i-xi, 1-105.

Skalski, A.W., 1984. Mesozoic Lepidoptera with emphasis to early evolution of the order. — Abstr. 17th int. Congr. Ent.: 8.

Stainton, H.T., 1854. Insecta Brittanica. Lepidoptera: Tineina. — London, Lovell Reeve.

Stainton, H.T., 1855. Lepidoptera. The new British species in 1854. — Entomologist's Annu. 1855: 62-72, frontispiece.

Stainton, H.T., 1856. Lepidoptera. New British species in 1855. — Entomologist's Annu. 1856: 26-45.

Stainton, H.T., 1859. Manual of British Butterflies and Moths, 2. — Cooke & Son, London.

Staudinger, O., 1870. Beschreibung neuer Lepidopteren des europäischen Faunengebiets. — Berl. ent. Z. 14: 97-132, 193-208, 273-330.

Strand, E., 1934. *Niepeltia* novum genus Lepidopterorum. — Int. ent. Z. 28: 241.

Svensson, I., 1966. New and confused species of Microlepidoptera. — Opusc. ent. 31: 183-202, 4 pls.

Tutt, J.W., 1899. Natural history of the British Lepidoptera. A textbook for Students and Collectors. Vol. 1. — London, Berlin.

Vári, L., 1955. South african Lepidoptera I. Descriptions of new leafmining Tineina. — Ann. Transv. Mus. 22: 331-351, 2 pls.

Walsingham, Lord, 1907. Microlepidoptera of Tenerife. — Proc. zool. Soc. Lond. 1907: 911-1034, pls 51-53.

Watrous, L.E. & Q.D. Wheeler, 1981. The out-group comparison method of character analysis. — Syst. Zool. 30: 1-11.

Wiley, E.O., 1981. Phylogenetics. — John Wiley & Sons, New York, Chichester, Brisbane, Toronto, Singapore.

Wilkinson, C., 1978. On the *Stigmella-Nepticula* controversy (Lepidoptera). — Tijdschr. Ent. 121: 13-22, 2 pls.

Wilkinson, C., 1979. A taxonomic study of the micro-lepidopteran genera *Microcalyptris* Braun and *Fomoria* Beirne occurring in the United States of America (Lepidoptera, Nepticulidae). — Tijdschr. Ent. 122: 59-90.

Wilkinson, C., 1981. A supplement to the genus *Ectoedemia* Busck (Nepticulidae: Lepidoptera) in North America, dealing with some difficult species and also some new ones. — Tijdschr. Ent. 24: 93-110.

Wilkinson, C. & P.J. Newton, 1981. The microlepidopteran genus *Ectoedemia* Busck (Nepticulidae) in North America. — Tijdschr. Ent. 124: 27-92.

Wilkinson, C. & M.J. Scoble, 1979. The Nepticulidae (Lepidoptera) of Canada. — Mem. ent. Soc. Can. 107: 1-118.

Wolff, N.L., 1957. *Trifurcula griseella* nov. spec. (Lepidoptera, Nepticulidae). — Ent. Meddr 28: 19-22.

Zeller, P.C., 1839. Versuch einer naturgemässen Eintheilung der Schaben. — Isis, Jena 1839: 167-220.

Zeller, P.C., 1848. Die Gattungen der mit Augendeckeln versehenen blattminirenden Schaben. — Linn. ent. 3: 248-344, 1 pl.

Zimmermann, F., 1940. Eine neue Nepticulide aus Deutschland (Lep.) — *Ectoedemia liebwerdella* spec. nov. (Lep.). — Mitt. Zool. Mus. Berlin 24: 264-265.

Zucker, W.V., 1983. Tannins: does structure determine function? An ecological perspective. — Am. Nat. 121: 335-365.