

NEPTICULIDAE (LEPIDOPTERA): A REVISED CLASSIFICATION,
AND DESCRIPTIONS OF SOME NEW TAXA PARTICULARLY
FROM SOUTHERN AFRICA

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TO DR L. VARI

*. . . a classification is not a neutral hat rack;
it expresses a theory of relationships that controls
our concepts.*

S.J. Gould 1977, *Ever Since Darwin*, p.114.

*. . . I believe this element of descent is the hidden
bond of connexion which naturalists have sought under
the term of the Natural System. On this idea of the
natural system being, in so far as it has been perfec-
ted, genealogical in its arrangement, . . . we can
understand the rules which we are compelled to follow
in our classification . . . We shall never, probably,
disentangle the inextricable web of affinities be-
tween the members of any one class; but when we have
a distinct object in view, . . . we may hope to make
sure but slow progress.*

C. Darwin 1859, *The Origin of Species*

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ABSTRACT

Previous classifications of the Nepticulidae were based on species from the northern hemisphere, primarily western Europe (including the United Kingdom) and North America. The revised classification presented in the present work was developed from a study of material primarily from southern Africa, but also from Australia, Europe, North America, and the Orient. Most of the descriptive section deals with the taxonomy of the Nepticulidae of southern Africa. Nevertheless, a guide to the supraspecific classification of the family was a major aim.

Cladistic methods were used to assess genealogy as far as possible. The degree to which it has been elucidated is incorporated into the classification. As a result of the study, the Nepticulidae are divided into two subfamilies. One of these subfamilies is divided into two tribes. Fifteen genera and six subgenera are recognised. Two keys are presented, one to subfamilies and tribes and the other to genera and subgenera.

The species from southern Africa are included in eight genera, three of which are new. One hundred and seventeen species from southern Africa are considered. Seventy-two new species are described in this work. Of these 40 have been published (reprints are bound into the thesis) and 32 appear as manuscript names. For some species described by previous workers lectotypes have been designated where appropriate. The primary types of all the known species from southern Africa have been examined.

Observations on adult structure are discussed from the viewpoint of phylogenetic relationships both within the Nepticulidae and between the family and other lepidopteran groups. This has led to a reinterpretation and expansion of some aspects of nepticulid morphology.

Numerical phenetic methods, which include cluster analyses and an ordination technique (principal component analysis), were used to check my personal assessment of phenetic relationships. The illustrations (phenograms and ordination diagrams) provide a visual summary of phenetic relationships of as wide a range of Nepticulidae as possible.

Aspects of the nature of taxonomic characters, ancestor-descendant relationships, and homoplasy are discussed. Brief comments are made on distribution, and host-plant choice and phylogeny.

PREFACE

Systematics has been in a state of ferment for the last decade or so, and the literature has been fraught with rhetoric and polemic. Views are strong as can be seen in the recent spirited debate in *Nature* where the philosophy of cladism, or phylogenetic systematics, has figured prominently and has reached a wide readership.

At present it is impossible to adopt one approach to systematics without dissent from persons who follow another, and so in parts of this thesis I explain *why* certain systematic principles were adopted as well as *how* they were applied. Some of the conflicting views are presented as commentaries at the end of the sections entitled 'Cladistic Analysis', 'Classification', and 'Numerical Phenetic Analysis'.

The classification adopted here, is based on cladistic methods. Historically, the methods of the cladistic school were articulated by Hennig (1966) in a book entitled *Phylogenetic Systematics*. Hennig never used the term cladistics; it was applied to him and his followers by others who considered his definition of phylogenetics too narrow. The word cladistics is based on 'clade' (*sensu* Huxley 1959), which itself is derived from the Greek *klados* - a branch. A clade is a group of organisms that share a common ancestor, and which includes all the descendents of that ancestor. This is clearly an evolutionary definition expressing genealogy.

Followers of cladism are not entirely agreed on the way they view it; some stress the independence of cladistics from phylogenetics, others do not. The distinction may seem no more than a quibble, but at least it emphasises the difference between a cladogram, in which all taxa - extant or extinct - are treated as terminal, and a phylogeny in which a time component is added. The key question is this: do cladistic classifications approximate phylogenies closer than other known methods? The answer is 'yes' if homoplasy (convergence and parallelism) is recognisable. The problem posed by homoplasy is serious for all systematic methods, not just cladistics. The recognition of homoplasy is an aim of character analysis rather than cladistics, but since cladists insist that classifications are derived directly from the most parsimonious cladogram without character weighting they have been criticised for implying that nature is parsimonious. The vexed question of parsimony is discussed in 'Classification'.

Cladistic methods were adopted in this work for two main reasons. First they are arguably the best means of discovering phylogeny, even if they are imperfect. Second, Farris (1979) contended that a classification derived by cladistic means is the most succinct (and therefore the most informative) way of indirectly storing a set of data, whether or not the phylogeny is historically accurate. The point is dealt with in 'Classification'.

Although the systematic principles discussed are of general application, they were adopted for a taxonomic study of a family of moths - the Nepticulidae - which this work is primarily about. The large descriptive section detailed in 'Systematic Treatment' precedes those entitled 'Cladistic Analysis' and 'Numerical Phenetic Analysis' in order of presentation. Of course the classification adopted in the Systematic Treatment depended on the analyses, but the order of presentation adopted means that the characters discussed in the analyses and the taxa involved are known to the reader from the descriptions.

Phenetics is generally anathema to cladists although most systematists who deal with large numbers of taxa make an intuitive assessment of general similarity at first. The so-called phenons that became apparent from my estimate of similarity were used as a basis for the cladistic work. Numerical phenetic methods were used to check these personally assessed phenons, and the results are presented in 'Numerical Phenetic Analysis'. The numerical work also stands in its own right as an illustration of phenetic relationships; phenotypic distances between taxa are of interest even if they are not the criteria used in the construction of a classification by cladistic principles.

The final part of the dissertation - 'Concluding Remarks' - acts as a vehicle for comment on the relationship of the phylogeny proposed to a broader body of evolutionary theory. Strictly, the conclusion of the work is the phylogeny and classification presented in the section entitled 'Classification'.

This preface would hardly be complete without comment on systematics and the philosophy of science, a topic that has been discussed a great deal of late. The debate has largely stemmed from claims by the cladists that their cladograms (and classifications) are testable in the sense of Karl Popper. The reason why this claim is made is explained under 'Cladistic

Analysis' p.184, but at this stage let us consider whether the application of Popper's philosophy to systematics is appropriate.

Popper argues that scientific hypotheses and theories are unverifiable but must be capable of falsification. Failure to refute an hypothesis after testing it leads to its corroboration, not proof. The philosophy is called the hypothetico-deductive approach to science.

In deduction, observations are collected to test the premise. Therefore 'deductive inference can only reveal the nature of our own constructed systems.', (Trusted 1979:2). By contrast, in induction the 'facts' precede the theory and we generalise from particular ('singular') instances. Critics of the inductive approach argue that facts are never collected entirely independent of theory; to Popper (1974) observations are interpretations of facts. Nevertheless, as Trusted has argued, the generation of hypotheses, which may lead to the formation of theories, often comes about by inductive inference - a process based on experience. Progress in systematics almost invariably results from the intuitive association of observations about organisms (Crowson 1970:5).

It seems that both inductive and deductive *inference* plays a part in systematics. Whether classifications and phylogenies are scientific *theories* in Popper's sense is another matter: Kitts (1977, 1978) criticised those systematists who have claimed that they are. He pointed out (Kitts 1978) that classifications are 'historical circumstances that call for an explanation' not 'theories that explain.' He argued that if we find that an historical pattern does not hold in the light of further information then 'how natural it would be to say that we had been mistaken about the course of history and how odd it would be to say that we had falsified a theory-like hierarchical pattern.' Kitts (1977:189) concluded that 'classifications are summaries of "facts", or "data", or "phenomena".' He pointed out that classifications are what Popper terms 'numerically universal statements' as opposed to 'strictly universal statements'.

Popper (1974) drew an important distinction between these two kinds of statements. Numerically universal statements 'relate only to certain finite regions of space and time.', (p.63), whilst strictly universal statements are claimed to be true for any place and any time. The former, therefore, are capable of verification, at least in principle, whilst the latter are non-verifiable and only falsifiable. Phylogenies and

classifications are statements about *history*, and are therefore confined to finite regions of space and time. In so being they fall outside Popper's concept of the theoretical sciences, which are concerned with the falsification of statements that are claimed as valid for any place and any time.

However, as Kitts (1978) pointed out, classifications may be validly considered as hypotheses and, indeed, is part of science. - He did not argue that a hypothetico-deductive *approach* to systematics was inappropriate, but simply found 'errors in the application of Popper's philosophy of science to systematics and set out to correct them.', (Kitts 1978:224).

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INTRODUCTION

This study began as an attempt to classify the Nepticulidae (Lepidoptera) of southern Africa and to provide descriptions of the taxa involved. Most of the specimens collected from the area are housed in the Transvaal Museum, Pretoria and were easily available for examination. The majority were painstakingly collected over the years by Dr L. Vári, and many were reared from the larval stage. Some of the species represented in this collection fell into higher taxa already described from Europe and North America. However, many did not.

This family includes the smallest lepidopterans, and the larvae of most species mine in the parenchyma of leaves although in some species they tunnel in bark, stems, petioles, winged-seeds and perhaps buds.

As the work progressed it soon became clear that the existing nepticulid classification, which was almost entirely based on Nearctic and Palearctic species, was inadequate. Clearly a new framework was required. However, a framework restructured from the existing one on the basis of the nepticulids from southern Africa would have been less sound than one based on a still wider sample. In order to make the study more inclusive, Australian material was borrowed from the Australian National Collection, Canberra through the courtesy of Dr I.F.B. Common who had collected most of the specimens himself. The Australian material proved to be of particular interest since it included representatives of several species that belong, collectively, to the sister-group of all other Nepticulidae.

The study of the southern hemisphere nepticulids was carried out against the background of earlier work on North American species (Scoble 1974; Wilkinson & Scoble 1979) and an examination of specimens of the type-species of most of the Palearctic genera. In addition, the extensive and scattered literature on the Nepticulidae was surveyed to support the study of specimens.

An area which has, until recently, been rather neglected by collectors of Nepticulidae is South America. As far as I know only two species have been described from the region. Collections are being made by European workers, and the proposed *Atlas of Neotropical Lepidoptera* should provide information of substance about the nepticulid fauna of the region.

The major aims of the present study therefore involved both the provision of a taxonomic treatise on the Nepticulidae of southern Africa, and a revised classification of the family as a whole down to generic level.

SYSTEMATIC PRINCIPLES

To achieve the classification finally presented I considered the following. First, how best could species be recognised?, second how could their relationships be assessed?, and third what method of classification should be used?

Much of the current disagreement about how to classify organisms can probably be attributed to predilection. Some systematists regard a classification primarily as a useful identification scheme and as an aid to memory, whilst others consider it an exact expression of the degree of resolution reached in the search for pattern in nature. The two are not completely exclusive of course.

The theme underlying the present work is the search for pattern and its expression in a classification. Since a gradual resolution of some existing problems in nepticulid systematics can be expected in the light of ongoing and future studies (particularly at the Vrije Universiteit, Amsterdam by Professor C. Wilkinson and his associates), a further aim of this work is to indicate the limits of resolution reached in the classification and the areas to which attention might be most fruitfully turned.

SPECIES: WHAT ARE THEY AND HOW WERE THEY RECOGNISED? Many biologists consider that species differ in kind from other taxa - that they have an objective reality. We talk about the process of speciation but not about a process by which say genera and families evolve. Supraspecific taxa are *groups* (classes) of species as opposed to discrete natural *units* (individuals), and processes such as natural selection and genetic drift do not act on them. Their categorical rank (e.g. genus, family, order) is arbitrary even though relative; it is a collective term to assist communication. This is not to say that a supraspecific taxon is an arbitrary collection of species; its species may all have evolved from a single ancestral species. A supraspecific *taxon* is not the same as a supraspecific *category*. In contrast, a species is not a collection; it is a unit, which may be subject to processes such as natural selection. If there is such a process as speciation then we can better treat a species as a unit, and an organism as a *part* of a species.

This concept was proposed by Ghiselin (1975) who suggested that we should consider a species as an *individual* as opposed to a *class*. I chose species as the fundamental units of this study because of their fundamental status in nature.

If species exist as individuals how may we recognise them? The species in the present work were recognised by morphological criteria supported, where information was available, by host-plant choice. Given that a species is a real entity then, however we may define it, those treated below are hypotheses of that entity.

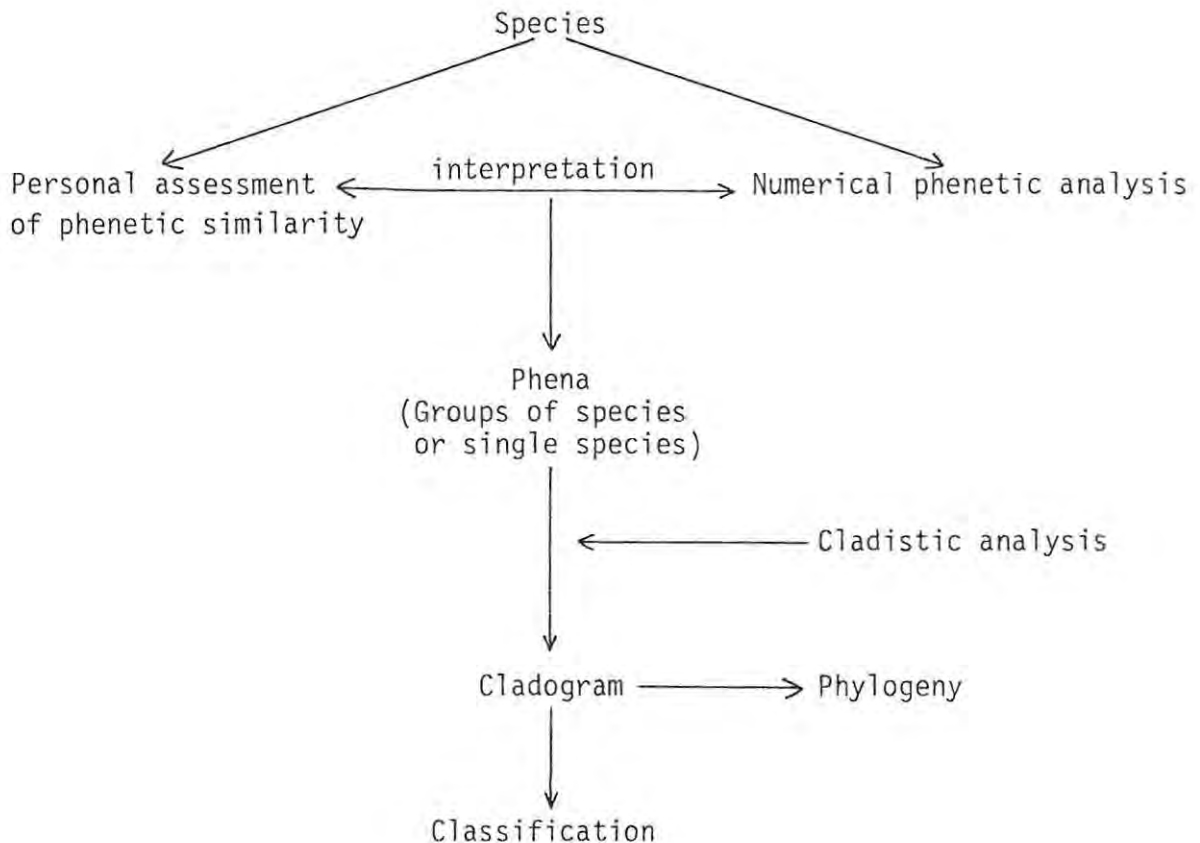
These species fall into line with what most persons working on the group recognise as such. This general agreement has come about by the empirical observation that there is little variation between certain specimens and, relatively, quite a lot between these and other such clusters. A detailed study of intraspecific variation in even a few purported nepticulid species would be a valued addition to our knowledge of this group. The major problem is the acquisition of a large number of specimens over a wide geographical range, but this should be practicable, particularly in Europe where various entomologists have collected and reared specimens at different periods over the last century or so. Large numbers of specimens are surprisingly hard to come by in the field.

Apart from sexual differences, the structures that exhibit little variation within purported species but significant variation between them were found to be the male genitalia, wing venation and, to a lesser degree, forewing colour. In the present study a species was recognised if specimens differed to the degree generally accepted as being specific for the Nepticulidae. This general principle was followed even if one specimen was involved.

Species have been designated from single specimens where characteristics are so distinct that valuable information would have been lost were it not done. The diagnostic characters of such species are of a sufficient degree that they do not, in my opinion, represent aberrations. The specimen had to be in a condition such that the diagnostic characters, in particular the genitalia, could be clearly seen. A species was not described from a single specimen if its differentiation was doubted. Species were not described from single females since females of different species are often difficult, or even impossible, to distinguish. As long as the custom is followed the possibility of conspecific males and females being

erroneously assigned to different species will not arise.

RELATIONSHIPS BETWEEN SPECIES. I have aimed to reflect phylogenetic relationship as closely as possible in the classification presented in this work. The steps in the procedure adopted are summarised in the scheme that follows.



Initially, species that resembled each other were grouped together. 'Resembled' means that they were similar on the basis of the attributes studied. This approach was carried out at first by observation and a personal assessment of similarity: later, numerical phenetic methods were used to check these intuitive groupings. Character-weighting was avoided in both phenetic studies and in the cladistic analysis that followed them.

The cladistic approach contrasts with the phenetic one however, since the latter involves an estimate of 'overall' similarity between species. Whether numerical methods are used or not 'So long as the intent . . . is to seek such groupings reflecting overall resemblance it is a phenetic approach.', (McNeill 1979:467). Cladistic or phylogenetic systematics is *not*

the same as this because taxa are recognised on the basis of shared derived characters.

The numerical phenetic analysis is detailed in the section so entitled, which begins on page 208. The methods are described there, and phenetic relationships are illustrated in phenograms and ordination diagrams.

The phenetic groups (phena) were then analysed cladistically. Cladistic methods are also described below in the section entitled 'Cladistic Analysis' (p.184). The method of analysis involves a search for taxa, based on uniquely derived characters (apomorphies, Hennig 1966), and their display on a dendrogram that reveals the hierarchical pattern so formed. Such a dendrogram is called a cladogram. In phylogenetic terms the groups of the hierarchical pattern are said to be monophyletic. 'Monophyly' is defined here in the sense of the cladists in that it includes *all* the known descendants of a hypothetical common ancestor. The meaning is the same as 'holophyletic' *sensu* Ashlock (1971).

Character-weighting was avoided. Although the experience that some attributes are more valuable than others is an influence that is hard to escape, an attempt was made to avoid *a priori* judgements in this work.

CLASSIFICATION. The results of the analysis of relationships between species were used to classify them. The classification presented is a cladistic one; it is a direct transposition of the hierarchy expressed in the cladogram into an indented list (p.207).

METHODS: COMMENTS ON TAXONOMIC PROCEDURE

The bulk of this study is descriptive. The descriptive work, phylogenetic implications, and the classification proposed required a critical reappraisal of nepticulid morphology. In addition to the usual approach of studying 'external characters' and genitalia, general observations were made on the whole skeleton of adult moths, which were macerated in potassium hydroxide (KOH), for species for which adequate material was available. The variation was assessed at general, light-microscopic level.

DISSECTION. The dissection and examination of such very small moths as nepticulids is much more difficult than it is in the case of larger lepidopterans.

Genitalia preparations were made in the standard way by heating the abdomen in KOH, dissecting, staining, dehydrating, clearing and mounting in Canada Balsam or Euparal. Whole skeletons were dissected and examined in glycerol after KOH treatment. Glycerol helps clear specimens and does not evaporate so it is particularly useful. Zeiss interference contrast microscopy was used for detailed studies of certain structures.

TYPES. Previous to the present work, South African species had been described by Meyrick (1895-1937), Janse (1948), and Vári (1955, 1963). Janse's type-series were frequently found to include representatives of more than one species, and the difficulties that this caused were considerable. I have fixed the identity of problem-species by the designation of lectotypes. Janse frequently labelled one male and one female as 'Type'. Each of the remaining specimens of the type-series was labelled 'Cotype'. Since no holotype was designated by Janse in print, all the specimens are syntypes in the eyes of the *International Code of Zoological Nomenclature* (1964). Following the recommendation of that work lectotypes have been designated from figured specimens.

The material from which Meyrick described South African species was sent to him by Janse, and that which was returned is housed in the Transvaal Museum. Meyrick rarely added type-labels to the specimens but they bear his accession numbers. Apparently Meyrick wrote to Janse concerning his intentions about the type-status of these specimens (see Janse 1968), but the original letters have not come to light. However, Janse (1968: Introduction) quoted the following sections from them. 'With regard to types, you can regard the example returned to you as being the type in every instance' (letter of 1909), and 'Wherever you have originally sent me two specimens of an insect which I have described as new, returning you one specimen and keeping the other myself, the specimen returned to you should always be regarded as the type', (letter of 1912). It was to these returned specimens that Janse added type-labels. The moths and their genitalia were illustrated by Janse (1948). In those species described by Meyrick from more than one specimen the individual figured by Janse has been designated as lectotype.

DESCRIPTIONS OF MONOTYPIC TAXA. Each equivalent division of a taxon is traditionally given the same rank, and each subdivision will belong to one of the primary divisions. For example, a family may be divided into

two or more subfamilies, and each genus in the family will belong to one of these subfamilies. The Nepticulidae have been divided into two subfamilies (below). One of them includes a single genus - that is, it is monotypic. Farris (1976) pointed out that in such a case the two taxa have the same membership, and that the different names they bear actually apply to one and the same group. To give a separate diagnosis or description for the two categories, which actually represent the same taxon, would therefore involve an arbitrary decision as to which characters diagnose the genus and which the subfamily. We would have to guess the characters that would be shared by the single genus included at present and by another genus (or other genera) *that might be described in future*. This would mean prejudging some attributes as generic and others as subfamily characters. *A priori* judgement has been widely criticised by systematists with different approaches to systematics (e.g., and compare, Sneath & Sokal 1973; Crowson 1970). A systematist may be quite experienced at guessing such common characters, but there is no objective way of providing such a diagnosis since it depends on taxa unknown to the systematist. For this reason formal diagnoses have not been given for monotypic taxa in the present work.

Farris (1976) suggested that monotypic taxa should be abandoned. He proposed that the hierarchy of a classification could still be retrieved from a list using a system of indentation. Since the rules of nomenclature require that each species is assigned to a genus, Farris pointed out that monotypic genera would have to be exempted from the suggestion. Wiley (1979) found the pure indented-list system impractical, and suggested that to abandon names of all monotypic taxa (even excluding genera) on grounds of logic might be counter productive. In the present work I have followed convention by retaining or introducing the names of monotypic taxa.

Monotypic genera pose an additional problem in cladistic classification. A species that does not share one or more apomorphies with others in a known genus does not strictly belong to that genus. The species may resemble others phenetically, because of retained generalised (primitive) features, but this does not mean that it belongs to the same monophyletic group. Under current regulations a species must be named as a binomen. Thereafter if it is excluded from all described genera it must be assigned to a new one. The ratio of monotypic genera to polytypic genera is growing, partly for this reason. The more monotypic genera described, the less informative the generic category becomes. The description of such a monotypic genus to

a cladist does not mean that the generic component of the binomen labels a taxon, but rather that it is simply a part of the species name. To a pheneticist with an 'outlier' species the monotypic genus would mean something different - a 'good' genus based on phenetic distinction.

A uninomial system for naming species would avoid the problem of numerous monotypic genera. It would also have the advantage that species for which phylogenetic relationships are unclear could be treated as unassigned until their affinities are better understood. A uninomial system was proposed by Michener (1964), but under the present regulations its use is not permissible.

PUBLISHED STUDIES. Five reprints on the taxonomy of Nepticulidae (Scoble 1978-1980) are bound in at intervals in this thesis under the genus to which each applies. They form a part of the dissertation.

SYSTEMATIC TREATMENT

PHYLOGENY OF THE NEPTICULIDAE

Previous to Börner (1939) the Nepticulidae were usually assigned to the Tineina, an heterogeneous assemblage comprising a large number of unrelated groups. Börner (1939) divided the Lepidoptera into the Monotrysia and the Ditrysia. In the former (into which the Nepticulidae fall) a single genital aperture in the female serves as a copulatory-pore and an egg-pore, whilst in the latter the egg-pore opens separately on a different segment. Since that time the monophyly of the Monotrysia (in Börner's sense) has been disputed.

Davis (1978a:36) recognised seven 'major phyletic lines' and retained (not actually stated but clearly implied) the Nepticuloidea and the Incurvarioidea in the Monotrysia, a category used in a much more restricted sense than that of Börner. Kristensen and Nielsen (1981) referred to the monotrysonian *grade* within the Heteroneura (monotrysians plus Ditrysia) since the monophyly of the group is unsettled. The grade includes the Nepticulidae and Opostegidae, the Incurvarioidea (comprising six families, E.S. Nielsen personal communication), and the Tischeriidae. All of these taxa are monophyletic. Further, objections to the sister-group relationship of the Nepticulidae and Opostegidae are now overcome (Scoble *in press*) by the discovery of a pectinifer (a series of comb-like teeth) on the valvae of many Australian Nepticulidae. Prior to this observation there was some doubt about the relationship since although the Nepticulidae and Opostegidae are jointly characterised by an expanded antennal scape ('eye-cap'), the presence of a pectinifer in the Opostegidae and the Incurvarioidea suggested an alternative sister-group relationship between these taxa (Kristensen & Nielsen 1980; Nielsen 1980).

The presence of a pectinifer is not necessarily apomorphic for the Nepticuloidea (Nepticulidae plus Opostegidae) since the structure is probably homologous with a similar structure in some Incurvarioidea and perhaps with that in a few Ditrysia. The best synapomorphy for the Nepticulidae and the Opostegidae is the presence of an expanded antennal scape; the weakly sclerotised terga and sterna of the abdomen is another possibility. Nielsen (*in press*) suggests that the prominent metatibial spurs may also be a nepticulid plus opostegid synapomorphy. (Detailed work on the sister-group

relationship between the Nepticulidae and the Opostegidae is being undertaken by D.R. Davis, Smithsonian Institution.)

CLASSIFICATION

Most persons working on the higher classification of the Lepidoptera are attempting to classify the group according to phylogenetic (cladistic) principles. Classifications have become refined as phylogeny has become better elucidated. At present the Nepticulidae can be said to belong to the Nepticuloidea within the monotrystian grade of the Heteroneura.

PREVIOUS TREATMENTS

Many naturalists, fascinated by the mining habits of the larvae and the small size of the adults, have been attracted to the study of the Nepticulidae. Most of the work published about the family is confined to descriptions of new species, and general observations on host-plant choice and mines made by the larvae. There have been relatively few broadly based studies on the systematics of the group, probably because of the technical difficulties involved in studying the anatomy of such small moths, and also because of the sporadic collecting from areas other than Europe and North America.

Borkowski (1972), and Wilkinson & Scoble (1979) discussed previous approaches to the classification of the Nepticulidae, and it would be superfluous to repeat the details here. The short outline that follows is added for the convenience of the reader so as to stress the main approaches to the classification of the group. Problems of nomenclature are considered under the relevant taxa.

Before the important paper of Beirne (1945) most species were assigned to *Stigmella* Schrank (or *Nepticula* Heyden, a junior synonym of *Stigmella*; see Wilkinson 1978). Only two other genera were recognised: *Trifurcula* Zeller and *Bohemannia* Stainton (= *Scoliaula* Meyrick). Beirne (1945) grouped the British species into nine genera based on a study of the male genitalia. Like some earlier authors (see Borkowski 1972 for details) Beirne noted that the genera fell into two groups. Johansson (1971) reflected this division in his list of the Scandinavian and British nepticulids by recognising only two genera, namely *Nepticula* and *Trifurcula*. He treated most of the genera accepted by Beirne as subgenera of *Trifurcula*.

Many papers describing new species have been published since these works; some authors have largely followed Beirne's scheme, others have adopted that of Johansson (see Scoble 1978b). Prior to the present work suprageneric categories within the family have not been introduced.

COMMENTS ON ADULT STRUCTURE

HEAD. Some general features are labelled in fig.1 p.145, and Scoble (1979: figs 18-23). The head is hypognathous and said to be 'rough-scaled', which means that the scales are not flattened down onto the head-capsule but extend outwards. Piliform (hair-like) scales arise from a large circular area on the front of the head, and also from two other patches on the vertex (Scoble 1979: fig.18). Two groups of lamellar scales, collectively called the 'collar' by many authors, are attached to the back of the head.

In contrast with many primitive moths, few sulci are present on the head-capsule of nepticulids. The curved, ridge-like thickening of *leucosideae* spec. nov. (fig.9) is atypical. Ocelli are absent, chaetosemata present, and compound eyes prominent. The chaetosemata (thought to be homologous with 'warts' of Trichoptera) are raised, elongated, cuticular patches on the top of the head (Scoble 1980b: fig.3a). The size of the compound eye relative to the head-capsule varies relatively little between the species for which this character was examined. In two species (*lanzeifoliella* Vári and *leucosideae* the eyes are much smaller than usual, figs 1,2).

The antenna rarely extends to the full length of the forewing. A feature shared by the Nepticulidae and the Opostegidae is the expanded scape, the significance of which is discussed above. Lamellar scales are flattened down and overlap this structure. Denuded, the scape varies somewhat in shape between species; it is comparatively narrow in *leucosideae* (fig. 9). The pedicel is slightly larger than each flagellar segment and in *vanifer* Meyrick a ball-shaped expansion, the function of which is unknown, is present in males (fig.8). The flagellar segments are submoniliform; the exact shape varies between species and is sometimes characteristic (e.g. *ochnicolus* Vári). (Detailed studies, using a scanning electron microscope, are being undertaken by E.J. van Nieukerken, Vrije Universiteit -personal communication.) In certain species the flagellum differs between the sexes, particularly in an undescribed Australian species where the proximal part of the antenna is swollen in the male.

The maxillary and labial palpi exhibit the primitive number of segments - five and three respectively. In the aberrant *leucosideae* the labial palpus has two segments, a situation I have seen in no other nepticulid. The fourth segment of the maxillary palpus in *royenicola* Vári is greatly enlarged and bears a dense patch of scales (fig.5). The galeae are haustellate and short although their length varies. In most of the species for which this character was examined, the galeae do not extend beyond the labial palpi. In representatives of a group of *Diospyros*-feeding species the length is about twice as long as the labial palpi, and in *insulata* Meyrick it is about two and a half times the length of the head-capsule, a fact that emphasises the functional aspect of the 'tongue' as observed for a Canadian nepticulid by Downes (1968). He also observed moths pressing their tongues against the surface of leaf-nectaries, and demonstrated that the crop was filled with fluid.

WINGS. The colour of the forewings falls into three main categories: 'metallic' in which there is usually a brightly shining, silver fascia or silver patches, and a variety of coloured reflections; ochreous, variously irrorated with fuscous; and grey-brown to very dark grey. Groups of related species often have predominantly one kind of colour pattern, but colour was generally found to be a weak indicator of relationship.

In both forewings and hindwings of some species, aculei (microtrichia) are densely scattered over the surface. In most species the aculei are sparsely distributed except for an elongated patch on the basal, anal edge of the ventral surface of the forewing where they are concentrated and larger. This area (the '*Haftfeld*' of earlier workers) is present in many adult Lepidoptera (Kuijten 1974). This author, and Common (1969) independently suggested that the function of the 'holding area' or 'alar zone' is to keep the wings in position at rest. The spines on the wing interlock with a corresponding patch on the metascutum of the thorax. Scoble (1979: 41) was in error in implying that the alar zone was absent in two *Ectoedemia* species. Although the area is not of the same shape as shown in the illustrations of Kuijten and of Common it does exist, and is present throughout the family.

The wings of the males of many nepticulid species bear secondary sexual characteristics. A hair-pencil, which is a bunch of long scales, is present in several groups of Lepidoptera. In the Nepticulidae it varies, when

present, in position and scale-shape between species and occurs on the forewings or the hindwings, so it probably developed independently on a number of occasions.

Specialised lamellar scales are present on representatives of many genera. These scales differ in shape, constitution and colour from the typical lamellar wing scales. When present they are found on the forewing or hindwing or both, and, rarely, on the abdominal terga. Their absence from the female suggests a function in courtship. The scales are visible under low magnification; they are often shiny purplish black but may be ochreous, and their position and arrangement varies according to species. Under light-microscope magnifications the scales appear granular. Specialised scales are found in many groups of Lepidoptera and are called androconia. Detailed studies of the scales using a scanning electron microscope would be of value to see if they are structurally similar in such distantly related groups as Nepticulidae and Papilionidae. They certainly resemble (in granulation, not shape) the specialised scales on the hindwings of *Argyroplote lutipennis* Meyrick (Tortricidae) at light-microscope magnifications.

Wing coupling. In males, a strong frenular spine on the hindwing hooks into a retinaculum on the forewing. In females there is no frenular spine; instead a series of scales modified into spines arises from the costa of the hindwing; they are not homologous with the frenulum. These costal spines are also found in males of many species. In some members of the Pectinivalvinae there are large lamellar scales rather than spines.

The retinaculum in the male comprises a series of 'looped, linear, and heavily chitinised scales' (Braun 1924:237) at the base of the forewing near the costal edge on the ventral surface. (Scoble 1979:54 provides a photograph of the frenulum hooked into the retinaculum.) In *Obrussa* Braun these spines are comparatively long. In the female the modified scales of the retinaculum are often spread-out along the costal fold for some way.

In addition to the subcostal retinaculum, a series of spines, situated on the ventral surface of the forewing near the base and close to the cubital vein, occurs in most species ('subdorsal retinaculum' of Braun 1924). Braun suggested that the presence of the subdorsal retinaculum is correlated with the presence of costal spines on the hindwing; the latter interlock with the former and so couple the wings. However, in several species with costal spines the subdorsal retinaculum is absent. In general, the stronger the costal spines the better developed is the subdorsal retinaculum, but this is not always the case. The subdorsal retinaculum is

probably absent in the Pectinivalvinae.

A jugum (a finger-like projection of the jugal lobe of the forewing) was said to be present in some nepticulids (Braun 1924). For doubts about this and a further discussion see Scoble (1979:41). The jugum is widespread in the homoneurous Lepidoptera: it overlaps the hindwing and is thought to assist in coupling the wings.

Venation. This is reduced to a degree equalled, within the Lepidoptera, only by a few species of Heliozelidae (Incurvarioidea) and surpassed only by the Opostegidae. In contrast to most lepidopterans no true crossveins exist and there are no accessory cells. Veins are labelled in figs 10 and 13, p.148, and in Scoble (1978a,b; 1980a,b).

Few authors include descriptions or figures of the venation of species that they describe. This is unfortunate since considerable interspecific variation exists, particularly in the forewing; even the venation of closely allied species may differ slightly. Much of our understanding of the venation of the Nepticulidae is the result of the valuable study by Braun (1917a) on pupal wings. Although Wootton (1979) points out the need for caution in assessing vein homology on tracheation alone, the weak veins, the persistent tracheae of the adults, and the extreme reduction of the venation in the Nepticulidae makes the study of tracheae one of the few methods available for doing so.

Of the major trunks in the forewing the subcosta (Sc) is very weak and often not visible although sometimes a trachea persists. The radius (R_1) diverges from the radial sector (R_s) usually about one-third of the way along the forewing, but in some genera (e.g. *Niepelitia*) it separates from the base of the wing. (Wootton (1979) recommends that the branches of R_s in insects should be labelled R_{s_1} , R_{s_2} etc., not R_2 , R_3 etc. This reasonable suggestion is not adopted in the present work for the sake of conformity with the parts already published.) R_2 is always completely fused with R_3 ; in some species the branch is absent.

The course run by the media (M) of the forewing varies considerably within the Nepticulidae. The association of M and the cubitus (Cu) at the base of the wing in many nepticulids, or for some distance along it, is also found in some Opostegidae. In the latter M is a thick vein that runs

undeflected towards the apex of the wing. In the Pectinivalvinae and the nominate tribe of the Stigmellinae M coalesces with R_5 almost from the base of the wing. In some slide preparations a persistent trachea (presumably that of M) runs from the base of Cu obliquely forward to near the base of R_5 . Braun (1917a: fig.3) also illustrates this condition in the pupal wings of *Stigmella rosaefoliella* (Clemens). Borkowski (1972:700) showed M as being fused with Cu in *Stigmella plagiocolella* (Stainton) for the entire length of the latter, an interpretation that the above observations suggest to be erroneous. In many members of the tribe Trifurculini M is fused with Cu for about a third of the way along the wing. M then diverges to meet R_5 at or near the point at which R_{2+3} (if present) arises. From this condition other modifications have developed.

The anal veins are usually coalesced throughout their length (1+2A), but in several South African species they are separated at the base of the wing for a short distance. This condition, found elsewhere in the Lepidoptera, has presumably developed independently on several occasions. It has been referred to as the 'anal loop' in a hepialoid species by Kristensen (1978:17, fig.30); the term is adopted in the present work.

In the Stigmellinae, p.35, (but not the Pectinivalvinae, p.31) 1+2A is thickened and forms a slight ridge on the ventral surface of the wing. This thickening was noted by Braun (1917b:157; 1+2A called the 'second anal vein' by her) as a family characteristic since the Pectinivalvinae were unknown at that time. Braun suggested that this ridge might function as a 'fastening for the row of spines along the costal margin on the upper side of the hindwing of the female', but since these spines are also found in the Pectinivalvinae, where 1+2A is not thickened, this interpretation is open to doubt.

The hindwing exhibits a relatively uniform condition. M and R share a common trunk from the base of the wing before they diverge. M is usually represented by one branch but in *Trifurcula* Zeller (in the sense of this study, see below) it is divided into M_1 and M_2 .

LEGS. There is no epiphysis on the foreleg. As far as I know such a structure is absent from Opostegidae and Tischeriidae. Tibial spurs are absent from the foreleg, a single pair is present distally on the midleg and there are two pairs on the hindleg - one pair is distal the other pair

varies somewhat in its position. Each pair of spurs on the midlegs and the hindlegs comprises a short member and a longer one.

The position of the proximal pair of spurs on the hindtibia was used by Braun (1917b, and elsewhere) as a character of taxonomic importance within the Nepticulidae. The character-states used by Braun were above, below, or in the middle of the hindtibia. Certainly species within a genus tend to exhibit one of these states, but there are exceptions.

ABDOMEN. *Pregenital segments.* Lamellar scales cover the sterna and terga. Usually the dorsum of the abdomen is grey-brown or grey, sometimes it is ochreous. The ventral surface is always pale. In the male two lateral patches of piliform scales are present on the posterior margin of tergum 8. These scales, which arise from prominent sockets, form an 'anal tuft', although it has a double origin.

In their study of the ventral diaphragm of non-ditrysian Lepidoptera Kristensen & Nielsen (1980) suggested that no sternum 1 sclerites exist in any of the non-ditrysian heteroneurous moths (to which the Nepticuloidea belong). These authors observed that the anterior-most portion of the ventral diaphragm always originates from sternum 2 in homoneurous Lepidoptera even when sternum 1 is present. In the nepticulids studied by these authors (*argyropeza* Zeller and *argentipedella* Zeller) the anterior-most diaphragm muscles were seen to originate on the first visible sclerite and so they interpreted it as sternum 2. Sternum 2 is divided into anterior and posterior parts in Nepticulidae and Tischeriidae. Scoble (1979), who did not study the diaphragm, regarded the anterior part of sternum 2 in two *Ectoedemia* species as sternum 1 and is therefore probably in error.

In the female a pair of fenestrae is present on sternum 4 (see Davis 1975b for a summary of the distribution and position in representatives of many lepidopteran families). The fenestrae are difficult to see in the Nepticulidae because the sterna are but weakly sclerotised. Davis (1978a) observed that they demarcated the position of small, internal reservoirs in the North American Eriocraniidae. These structures have not been observed in the Opostegidae nor the Tischeriidae.

Male genitalia. Strongly sclerotised they form a well-defined capsule. Figs 51-53 are labelled to illustrate the general features p.158.

The vinculum comprises a ventral plate, which continues into an anterior extension (Scoble 1978b), and a pair of lateral arms. Beirne (1945) pointed out that the Nepticulidae could be divided into two groups partly on the basis of the arrangement of the lateral arms. In one group the arms form a U-shaped boundary to the capsule and their posterior ends unite with the sides of the tegumen. In the other group the ends of the arms meet to form a complete ring around the aedeagus. In a number of species it is not clear whether the vinculum is 'U-shaped' or 'ring-shaped'. In most species of Pectinivalvinae the lateral arms fuse with the sides of the tegumen but a pair of apodemes extends across the tegumen between the ends of the arms. This condition is described below as 'extended U-shaped'. In some Opostegidae the ring-shaped condition is approximated but the resemblance is weak.

The general shape of the vinculum, in ventral view, is broad, but in one species (*Artaversala gilvafascia* Davis) the anterior extension tapers to a point anteriorly, which makes the vinculum V-shaped.

The tegumen is generally in the form of a simple band, or it may be extended posteriorly into what Beirne (1945) has termed a pseuduncus. A pseuduncus is present only in those species with a ring-shaped vinculum. Since the degree of extension of the tegumen varies so much between species it is difficult to know at which point it should be called a pseuduncus: therefore the term has been avoided in the present work (excluding the earlier publications bound into this thesis). Usually single-lobed, in some species the tegumen is bilobed.

In general the uncus is either approximately hood-like (and often bilobed) or in the shape of a narrow inverted V-shaped thickening.

The gnathos is generally prominent, although in a few species it is reduced or even absent. In most nepticulids the structure appears approximately W-shaped in ventral view. The central member is ventral to the lateral processes and it is frequently large (long and narrow, or broad). The situation is illustrated diagrammatically by Scoble (1980a:144, figs 16 & 17). This type of gnathos is found in all the suprageneric taxa of Nepticulidae and is considered primitive. In most species of *Stigmella* the central element is divided but a few members of this genus retain the primitive state.

A pair of what Davis (1978b) termed 'lateral support rods' is present in *Microcalyptris* Braun. They extend from the base of the uncus to about halfway down the genital-capsule on each side. Structures that are possibly homologous are found in some species of *Niepeltia* Strand (Scoble 1980b: 200) where they are termed an 'apodeme'.

The valvae are paired clasping organs and exhibit considerable variation within the family. A pectinifer is present in the Pectinivalvinae. The nepticulid pectinifer often closely resembles that found in the Opostegidae in that it is composed of many fine, fairly long units. In some species the units are shorter and broader and resemble those of the Incurvarioidea. The discovery of this structure in the Nepticulidae affects the interpretation of the cladistic relationships within the group comprising the Nepticuloidea and the Incurvarioidea (Scoble *in press*, and see above).

The valva is usually approximately triangular or derived from this shape, a condition widespread in many monotrysian Lepidoptera, although not in the Opostegidae. In several species of Pectinivalvinae the valva is roughly mushroom-shaped, a condition that bears no resemblance to any other nepticulid.

The sclerotisations associated with the diaphragmata and the aedeagus are difficult to interpret. Dorsally a well-developed transtilla is usually present. Whether this is a derivation of the diaphragmata remains in doubt. A transverse bar of the transtilla, when present, results in a tight binding of the valvae. Loss of the transverse bar has occurred on a number of occasions within the family, its presence in the morphotype is hypothesised because it is found in species of Incurvarioidea.

The anellus (the central part of the diaphragm) surrounds the aedeagus. In one South African species it is covered with denticles.

In some species a thickened plate is present, which may act as an aedeagus-support. Whether this structure is homologous with the 'juxta' of other Lepidoptera, e.g. the Incurvarioidea, is unknown. Beirne (1945) used the single term to refer to what are in fact three non-homologous structures: (1) the posterior extension of the ventral plate of the vinculum (in his genus *Fomoria*); (2) carinate processes, which are part of the aedeagus (*Dechtiria* Beirne, a junior synonym of *Ectoedemia* Busck; *Trisfurcula*, *sensu stricto*), and (3) a well-defined thickening that resembles the 'juxta' in its accepted sense.

The characteristic aedeagus is broad and well-sclerotised and varies in length and width. Many different kinds of spines or other processes are associated with the aedeagus: some form part of the external aedeagus and others belong to the endophallus (vesica). The terms carina or carinate processes are reserved for the former. Frequently, these processes have been misinterpreted as sclerotised parts of the diaphragm (e.g. juxta, Beirne 1945:204; anellar projections, Wilkinson & Scoble 1979:75) or, by many authors, as cornuti, which are armatures of the vesica.

With few exceptions, the base of the ejaculatory duct of the Stigmellinae is surrounded by a striate thickening. This character is unique to the subfamily. Previously, authors have tended to follow Beirne (1945) who described the structure as a curved plate and regarded it as a cornutus. This particular thickening is absent in the Pectinivalvinae. The ejaculatory duct is difficult to discern and may best be seen by staining the genitalia in Chlorazol Black E. A long thickening of the vesica is present but this does not seem to surround the base of the ejaculatory duct and it is not striated.

Female genitalia. The general pattern was described by Dugdale (1974) in a paper that reviewed the system in the Lepidoptera in general. Features of particular note are the absence of a cloaca, and the presence of a lateral lagena of the spermatheca. The common oviduct enters the copulatory chamber ventrally as it does in the Micropterigoidea, the Eriocranioidea and the Incurvarioidea but not the rest of the Lepidoptera (Exoporia and Ditrysia). The internal canal of the spermatheca is angulated, not spiral, in *laqueorum* Dugdale (see Dugdale 1974) whereas in most nepticulids examined in the present work it is spiral.

Characters of importance in the internal classification of the Nepticulidae are derived from the apophyses and the bursa copulatrix (ductus bursae and corpus bursae). The structures are labelled in fig.104, p.171.

The end of the abdomen is usually broad, but in some species the ovipositor is pointed. In *insulata* Meyrick the apophyses are attenuated posteriorly to a degree remarkable for a nepticulid. Vári (1955:339) suggested that a pointed ovipositor might be an adaptation to laying eggs on a leaf densely covered with hairs, a point recently noted for several European species (E.J. van Nieuwerkerken, personal communication).

The sclerotisations on the ductus bursae, when present, are complex and difficult to homologise. On the corpus bursae in most species of the Trifurculini there is a pair of reticulate signa (signa reticulata). In several species of *Stigmella* pectinate marks are concentrated into bands or patches, a situation observed in at least one species of Opostegidae.

IMMATURE STAGES: SOME COMMENTS

LIFE-HISTORY. As far as is known the egg is always laid on the surface of the plant to be mined by the larva, not injected into it. However the ovipositor of the adult of *insulata* Meyrick (for which the host-plant is unknown) is remarkably long for a nepticulid so there may be exceptions to the general rule. The larva eats through the egg-shell and burrows into the plant-tissue.

Most nepticulid larvae are leaf-miners. This mode of life has been the subject of many narrative accounts by early and present day naturalists. Occasionally more detailed studies on life-history have been undertaken (e.g. Jones 1933; Van Frankenhuijzen & De Vries 1979). Much general information on leaf-mining is to be found in Needham et. al. (1928), Herring (1951), and, particularly for the Nepticulidae, Emmet (1976).

Usually leaf-mining nepticulids spend their entire larval life in one leaf, but in the European *Fedalmia* Beirne the larvae mine two or three leaves and move from one to another via the petioles (Emmet 1976). In some species the larvae mine the tissue of other parts of the plant: bark, winged-seeds, leaf-petioles or buds.

The cocoon, in which pupation takes place, is spun by the larva usually in the soil, but sometimes in the mine or on the trunks of trees.

LARVA. Most of our knowledge about the structure of nepticulid larvae comes from the works of Trägårdh (1913), Watt (1921; 1924), Jayewickreme (1940), MacKay (1972) and Gustafsson (1981). Virtually no identified specimens of the South African species have been preserved so most of the comments that follow are summarised from the works mentioned above and supported by some observations on larvae collected in England.

The larva is a leaf-miner. The head is prognathous, the body flattened dorsoventrally, and appendages are reduced. Pseudolegs ('ambulatory warts')

are present on the meso and metathorax and on the first seven abdominal appendages (MacKay 1972 - see particularly scanning electron micrograph of frontispiece). Apparently their number, and degree of development often depends on which way up the larva feeds (C. Wilkinson, personal communication). The antenna (fig.139) is one-segmented and cushion-like. Two setae, one long and one short, arise from each side of the segment; two large and one small basiconic sensillae are also present. The mandibles are prominent (fig.138) and have four teeth. The maxillary and labial palpi also bear basiconic sensillae (fig.138). The spinneret is broad (fig.138) in late instars, but absent in early stages (Jayewickreme 1940). Like the Tischeriidae and the Opostegidae the hypostomal areas are extended anteriorly.

PUPA. Even fewer observations have been made on the pupae than the larvae. Most of our knowledge is due to Moscher (1969) and Watt (1921, 1924).

Some degree of movement is possible between all the abdominal segments except the last three. Mandibles are reduced and not functional, and maxillary palpi are well-developed.

The presence of posteriorly directed spines on the abdominal terga (segments two to eight) found in many primitive Lepidoptera help prevent the pupa from sliding back as it moves forward in, and partly out of, the cocoon just before ecdysis (Common 1975). These spines can be examined by observing pupal exuviae (e.g. Scoble 1979); they vary in size and number between species. Exuviae should be saved after adults have emerged since these details are of systematic value.

AGE OF ORIGIN

Brooks (1955) illustrated a nepticulid mine from Eocene deposits of western North America. This is the earliest record of the Nepticulidae that has been published (Opler 1973). The discovery of a mined leaf from the Cretaceous (Dr A.W. Skalski, personal communication) pushes the age of origin of the family back considerably. Details of this find will be published by Dr Skalski and Dr A. Borkowski; a photograph of the specimen, kindly supplied by Dr Skalski, shows that there is little question that the mines are of a nepticulid.

A discussion of the age of origin and distribution in relation to phylogeny of the Nepticulidae is presented in 'Concluding Remarks'.

FAMILY NEPTICULIDAE STAINTON

Nepticulidae Stainton, 1854:295. Type-genus: *Nepticula* Heyden (a junior subjective synonym of *Stigmella* Schrank, see Wilkinson 1978).

Stigmellidae Hampson, 1918:387.

ADULT. Very small moths usually with a wingspan of about 5-6 mm.

Head. Hypognathous, rough-scaled. Sulci reduced, chaetosemata present on dorsal aspect, ocelli absent, compound eyes prominent. Mandibles reduced. Maxillae: laciniae absent; galeae haustellate, short, rarely longer than head; palpi folded, 5-segmented. Labium: palpi 3-segmented, rarely 2-segmented. Antenna: rarely extends to full length of forewing; scape expanded into a large eye-cap; pedicel larger than flagellar segments but much smaller than scape; flagellar segments approximately moniliform.

Thorax. Forewing narrow, jugum absent (questionably present in some North American species). Subcostal retinaculum present; subdorsal retinaculum present or absent; specialised scales in male present or absent. Venation reduced, veins usually weak. M associated with R or Cu or both; Cu associated with M for part or all of its length, or free from M; 1+2A weak or thickened, entirely fused or separated at base to form anal loop. Hindwing narrow to very narrow; grey or grey-brown, specialised scales in male present or absent, never present in females. Frenulum a strong spine in males, a series of non-homologous costal bristles in female; costal bristles present or absent in male. Venation reduced, veins weak; R and M coalesced for part of length, R one-branched, M sometimes two-branched; Cu and A short, sometimes absent. Foreleg without epiphysis or spurs; midleg with one pair of unequal tibial spurs at distal end of tibia; hindleg with two pairs of unequal spurs, one pair at distal end, the other in, above, or below the middle of tibia.

Abdomen. Pale ventrally. Specialised scales rarely present on terga. Pregenital segments weakly sclerotised; segment 1 absent. Female with pair of fenestrae on fourth sternum (possibly not universally present); absent in male. Male with anal tuft arising from eighth tergum.

Male genitalia. Capsule well-sclerotised; usually slightly elongated, rarely V-shaped. Vinculum: lateral arms fuse with sides of tegumen or

meet, or nearly meet, to form a ring around aedeagus. Tegumen extended to a point or not. Uncus hood-like, or in the form of a thickened band, or absent; strongly or weakly divided dorsoventrally at apex, or undivided. Gnathos with a pair of lateral members that lie dorsal to a central, ventral member which may be divided or not; occasionally gnathos is reduced, or very complex. Valvae of variable shape; pectinifer present or absent. Transtilla present; transverse bar present or absent. 'Juxta' present or absent. Aedeagus broad and well-sclerotised; with or without carinae. Vesica with or without cornuti or various thickenings; a striate thickening surrounds base of ejaculatory duct in Stigmellinae (rarely absent).

Female genitalia. Monotrysian, ovipore terminal, cloaca absent. Ovipositor flat, rounded, or pointed. Apophyses relatively short, rarely attenuated. Oviduct ventral. Ductus bursae with or without complex sclerotisations. Spermatheca with lateral lagena; internal canal usually spiral, sometimes angular. Corpus bursae with or without signa.

LARVA. *Head* (figs 138,139). Prognathous, partially retracted into thorax. Vertex deeply divided so posterior, dorsal prolongations are long. Hypostomal areas much extended anteriorly. A single ocellus on each side of head. Antenna one-segmented. Mandibles prominent, bearing four 'teeth'. Maxillary palpi and labial palpi with basiconic sensillae. Spinneret broad, present in late instars, absent in early instars.

Thorax. Pseudolegs (ambulatory warts) present on meso and metathorax.

Abdomen. Pseudolegs present on first seven abdominal appendages.

PUPA. Aedealous, some movement possible between most segments. Mandibles reduced; maxillary palpi well-developed. Abdominal terga two to eight with spines that vary in size and number.

DIAGNOSIS. The Nepticulidae include small, monotrysian moths with the scape of the antenna much expanded into an eye-cap. An eye-cap is present in certain Lyonetiidae (Leucopteriginæ), but the ditrysian arrangement of the female genitalia and the fuller venation in that group suggests that the expanded state of the scape is not homologous with that found in the Nepticulidae.

The presence of an eye-cap distinguishes the family from all monotrysian and exoporian moths except for the Opostegidae. In the Opostegidae

the eye-cap is larger than that found in the Nepticulidae. The broad, well-sclerotised aedeagus found throughout the Nepticulidae differs from that structure in the Opostegidae where it is either reduced to a narrow, poorly defined structure or is apparently absent. The wing venation of opostegids is reduced even more than in nepticulids. In the former M is strong in the forewing and runs, undeflected, on a line from base to apex; in the latter M is not so strongly developed and is coalesced with R from the base of the wing, or with Cu at the base and R from about one-third of the way along the forewing.

KEY TO SUBFAMILIES AND TRIBES

1. Male: pectinifer present on valva, rarely reduced; vesica with base of ejaculatory duct not surrounded by a striate thickening. Forewing: Cu long; 1+2A not thickened. Hindwing: trunk of R+M deflected towards costa..... Pectinivalvinae
- Male: without pectinifer on valva; base of ejaculatory duct surrounded by a striate thickening, or if not then valva is deeply cleft. Forewing: Cu usually short; 1+2A thickened. Hindwing: trunk of R+M not deflected towards costa..... Stigmellinae, 2

2. Forewing: Cu separates from M at base and continues as a short independent trunk; M coalesced with R from base. Male: ends of lateral arms of vinculum fuse with sides of tegumen. Female: signa reticulata never present on corpus bursae..... Stigmellini
- Forewing: Cu coalesced with M for about one-third of length of wing then M diverges to meet R_5 ; if M does not meet R_5 then signa reticulata are present on corpus bursae of female. Male: lateral arms of vinculum meet or almost meet; ends do not fuse with sides of tegumen. Female: corpus bursae rarely without signa reticulata..... Trifurculini

KEY TO GENERA AND SUBGENERA

The genera *Glaucolepis* Braun, *Microcalyptris* Braun and *Parafomoria* Borkowski are excluded; for reasons see under their respective headings, below.

1. Male: pectinifer present (rarely reduced). Forewing: 1+2A not thickened. Hindwing: trunk of R+M deflected towards costa *Pectinivalva*
- Male: pectinifer absent. Forewing: 1+2A thickened. Hindwing: trunk of R+M not deflected towards costa..... 2

2. Forewing: M coalesced with R_S from base, Cu runs independent of M or is absent. Female: signa reticulata absent (where female is known)..... 3
- Forewing: M coalesced with Cu from base but diverges to R_S later, or R, M, and Cu coalesced from base; if M is not concurrent with Cu at base then valva, in male genitalia, bears a long apodeme. Female: signa reticulata rarely absent 8

3. Male: vinculum V-shaped. Female: anterior apophyses almost form a sclerotised ring largely encircling posterior margin of seventh segment..... *Artaversala*
- Male: vinculum broad anteriorly, not V-shaped. Female: anterior apophyses not modified as above..... 4

4. Male: valva deeply cleft. Forewing: R₄ and R₅ represented by separate branches..... *Varius*
- Male: valva not cleft; gnathos with central, ventral element generally divided or absent. Forewing: R₄ and R₄ united 5

5. Male: uncus absent; gnathos reduced to narrow band..... *Simplimorpha*
- Male: uncus present; gnathos not reduced 6

6. Forewing: Cu absent. Male: uncus reduced, gnathos divided into posterior and anterior halves; valva with finger-like lobe *Manoneura*
- Forewing: Cu present. Male: uncus not reduced; gnathos not similarly modified; valva without finger-like lobe 7
7. Forewing: R_{2+3} absent. Male: transverse bar of transtilla absent *Johanssonia*
- Forewing: R_{2+3} present. Male: transverse bar of transtilla present 8
8. Labial palpi two-segmented; eyes very small. Male: uncus in form of a pair of weakly sclerotised lateral arms each of which terminates apically as a setose lobe *Areticulata*
- Labial palpi three-segmented; eyes not very small. Male: not so arranged, weakly bilobed *Stigmella*
9. Male: ventral plate of vinculum deeply excised; long apodeme arises from outer aspect of valva and runs behind valva across capsule - if these characters are absent then valva shaped as in fig.56 *Obrussa*
- Male: ventral plate of vinculum not deeply excised; long apodeme absent from valva or if present (rare) then of a different origin 10
10. Hindwing: M two-branched or if not then R_1 and R_{2+3} of forewing absent 11
- Hindwing: M undivided 13
11. Forewing: R_{2+3} not separated from rest of R_s . Male: uncus not divided dorsoventrally nor split in ventral view *Trifurcula (Fedalmia)*
- Forewing: R_{2+3} separated from rest of R_s or absent. Male: uncus divided dorsoventrally or split in ventral view 12

12. Uncus divided dorsoventrally *Trifurcula* (*Trifurcula*)
 - Uncus split in ventral view *Trifurcula* (*Levarchana*)
13. Forewing: R, M and Cu united at base to form
 a common trunk that divides into five branches
 terminally..... *Bohemannia*
 - Forewing: R, M and Cu either not united at base,
 or if united then not divided into five branches
 terminally..... 14
14. Forewing: R₁ separate from R_S from base. Male:
 ventral plate of vinculum generally a flimsy
 membrane; uncus weakly divided dorsoventrally at
 apex..... *Niepeltia*
 - Forewing: R₁ coalesced with R_S at base for about
 one-third of way along wing. Male: ventral plate
 of vinculum not a flimsy membrane; uncus not di-
 vided dorsoventrally at apex..... 15
15. Male: uncus absent..... *Ectoedemia* (*Ectoedemia*)
 - Male: uncus present..... 16
16. Forewing: anal loop present..... *Ectoedemia* (*Laqueus*)
 - Forewing: anal loop absent..... *Ectoedemia* (*Fomoria*)

Subfamily PECTINIVALVINAЕ subfam. nov.

Type-genus: *Pectinivalva* gen. nov.

The Pectinivalvinae is one of the two subfamilies into which the family Nepticulidae is divided in this work: the division represents the primary phylogenetic dichotomy of the family (see cladogram, fig. 140a). The subfamily is erected to show the sister-group relationship of the taxon to all other Nepticulidae. The apomorphies on which the group comprising the other nepticulids are based are numbers 10-15 in the 'Cladistic Analysis' pp 193, 194.

The Pectinivalvinae is itself a monophyletic group, the apomorphies being the deflection of R+M towards the costa of the hindwing, and possibly the form of the uncus and the modification of the ends of the lateral arms of the vinculum. The pectinifer on the valvae of the male genitalia is rarely reduced. This structure is not unique to the Pectinivalvinae. However, as far as I know it is absent from all other Nepticulidae and so, at present, it is an attribute which distinguishes the Pectinivalvinae from other nepticulids.

The subfamily includes one genus, which is described and diagnosed below, from Australia.

The description of all the Australian species of the subfamily represented in the Australian National Collection falls outside the scope of the present work. Nevertheless the venation, and male and female genitalia of many species have been examined and the range recorded in the generic description, below.

Genus *PECTINIVALVA* gen. nov.

Type-species *Pectinivalva commoni* spec. nov.

Pectinivalva includes about 40 undescribed species represented in the Australian National Collection. In order to validate the genus, one species is described following the generic description.

The species fall into two groups: those with a relatively symmetrical valva with a rounded apex, and those with an asymmetrical, roughly triangular valva.

The name is derived from the Latin *pecten* (a comb) and *valva* (referring to that structure in the male genitalia), and is of the feminine gender.

ADULT. ♂,♀. Large to small nepticulids.

Head. Tuft off-white, ochre, red-brown or black.

Thorax. Forewing varies considerably between species: ochreous variously irrorate with fuscous, ochreous with patches of fuscous, fuscous with off-white patches, charcoal, grey, dark glossy with a shining silver fascia or an off-white, incomplete fascia. Subdorsal retinaculum absent. Venation: R_1 and R_5 with common trunk from base of wing to about one-third of length of wing. R_{2+3} usually present but sometimes absent. R_4 and R_5 usually fused to form R_{4+5} but in some species present as separate branches. M coalesced with R, not Cu, and represented by a single branch terminally. Cu long, runs obliquely from its origin towards anal edge; not fused with any other vein. 1A and 2A coincident throughout length except for one species where the trunk is divided *terminally* (not at base); 1+2A weakly defined, not thickened.

Hindwing: in male wing is sometimes expanded at base. Specialised scales present or absent. Frenulum present in male absent in female. Venation: M represented by one branch, not divided. Trunk of R+M deflected towards costal margin, sometimes runs close to it for much of its length.

Abdomen. Dorsum fuscous.

Male genitalia. Vinculum: lateral arms occasionally meet to form a ring around aedeagus, generally fused with sides of tegumen but with two extensions continuing to meet their equivalents on the other side (fig.51); anterior extension weakly to moderately excavated. Tegumen a simple band,

not tapering to a point; occasionally the posterolateral corners are produced. Uncus hood-like, prominent and rather elongate; weakly bilobed, clearly bilobed, or pointed; a cluster of setae arises near apex on each side, and the areas from which they arise may be produced into small lobes. Gnathos well-sclerotised, fused, W-shaped in ventral view, central (and ventral) element variable - long and narrow, greatly expanded caudally, or shortish and broad at base. Valva either rounded at apex and approximately symmetrical, or triangular, or approximately rectangular; pectinifer rarely reduced; units of this structure fine and typically comb-tooth-like or, occasionally, short and dentate; pectinifer fringes apex of rounded valva, confined to apex of triangular valva. Transtilla: transverse bar absent; ventral arms present. Aedeagus: long, usually without any carinate processes, sometimes with lateral carinae but never a ventral process. Vesica with numerous spine-like cornuti, some of which are large and heavily sclerotised and sometimes extend beyond phallosome; base of ejaculatory duct *not* surrounded by a striate thickening.

Female genitalia. End of abdomen blunt, notably flat. Posterior and anterior apophyses present. Bursa copulatrix: ductus bursae with or without a weak, sclerotised band; corpus bursae pectinate, pectinations sometimes arranged in scallop shapes, sometimes present as minute denticles.

LARVA. The few species that have been reared are all leaf-miners. Host-plants include: *Callistemon salignus*, *Eucalyptus bicostata*, *E. ? gigantea*, *E. macarthuri*, *Leptospermum ? laevigatum*, *Tristania suaveolens*. All belong to the Myrtaceae.

PUPA. Only one specimen of one, undescribed species was available. Terga 2-8 are covered with relatively large spines.

DISTRIBUTION. Australia.

DIAGNOSIS. A pectinifer (rarely reduced) is present on the valva of the male, and this distinguishes the genus from all others known in the Nepticulidae. The shape of the uncus is also characteristic. The absence of a striate thickening around the base of the ejaculatory duct where it enters the aedeagus distinguishes *Pectinivalva* from all other nepticulid genera so far described except *Varius* (see below). The long, obliquely

running cubital vein seen in *Pectinivalva* is characteristic. In contrast to the Stigmellinae 1+2A in the forewing is not thickened, and the trunk of R+M in the hindwing is strongly deflected towards the costa. The general pattern of wing venation and the female genitalia resemble those of the Stigmellini, but the features of the venation mentioned above, and the particularly broad end to the abdomen of *Pectinivalva* enable females to be distinguished.

Pectinivalva commoni spec.nov., figs 10,51,103

ADULT ♂, ♀. Wingspan 5,8-6,0mm. Head-tuft ochre. Forewing dark, glossy, purplish brown with purple reflections. Hindwing: male with a number of large, purplish leaf-like scales arising from costal edge near base; female with costal spines but no purplish scales. Hindtibia: proximal pair of spurs above midpoint. Abdomen as forewing.

Venation (fig.10). Forewing: R_{2+3} present, arises very close to point at which R_1 diverges from common trunk, R_4 and R_5 represented terminally as separate branches. Hindwing: R+M runs close to costal edge for most of its length.

Male genitalia (fig.51). Vinculum: lateral arms in the shape of a U, from the end of which arise some thin rod like extensions, arrowed in figure; anterior extension weakly excavated. Tegumen in form of a band, slightly expanded laterally. Uncus tapers to a well-sclerotised point posteriorly. Gnathos with central (and ventral) element broad at base and comparatively short. Valva approximately symmetrical, rounded at apex and with a pectinifer (*pr* in fig.51) of about 30 units. Aedeagus about one and one third times length of genital capsule; no carinae. Vesica with a mass of spine-like cornuti and three larger spines.

Female genitalia (fig.103). Abdomen broad and flat posteriorly. Apophyses short, posteriores extend beyond anteriores. Ductus bursae with a weak sclerite; corpus bursae with minute denticles.

LARVA. A leaf-miner on *Eucalyptus ? gigantea* (Myrtaceae), information from label.

MATERIAL EXAMINED. ♂-Holotype, AUSTRALIA: New South Wales, 17 miles S.E. of Braidwood, 27.ii.1958, I.F.B. Common, genitalia slide no.MJS.26. Paratypes: data as holotype, 2♀ 7.ii.1958, 1♀ 22.ii.1958. Holotype and paratypes in Australian National Insect Collection, CSIRO, Canberra.

The shape of the gnathos of the male, and that of the weak sclerite on the ductus bursae of the female are distinguishing features of *P. commoni*.

The species is named after Dr I.F.B. Common in recognition of his work in collecting Neptculidae, and in gratitude for his allowing me access to the material.

Subfamily STIGMELLINAE subfam. nov.

Type-genus: *Stigmella* Schrank, 1802:169.

The subfamily is composed of all nepticulid genera so far described except for the Australian *Pectinivalva*, which has been assigned to the subfamily Pectinivalvinae above.

DIAGNOSIS. Distinguished from the Pectinivalvinae by the following characters. Forewing: subdorsal retinaculum usually present in both sexes; M often associated with Cu from base to about one-third of length of wing before diverging to R; if M coalesces with R from base and Cu is independent, then Cu is generally short and does not run obliquely down to trailing edge of wing (compare fig.10 with figs 11, 12 of the present work and fig.1 of Scoble 1978b); 1+2A thickened, prominent. Hindwing: trunk of R+M not deflected towards costal edge. Male genitalia: lateral arms of vinculum not produced into narrow extensions across tegumen where they fuse with tegumen; often lateral arms meet or nearly meet each other to form a ring around aedeagus; uncus not so prominent as in Pectinivalvinae, sometimes reduced to a thickened band, sometimes lost; valva without pectinifer; ejaculatory duct surrounded by a striate thickening where it enters aedeagus in all species in this work except where noted in descriptions. Female genitalia often with paired signa, which are generally reticulate; if signa absent then distinguish females by wing characters given above.

DISTRIBUTION. Worldwide except Antarctica: further information is given under generic descriptions, below.

Genus *VARIUS* gen. nov.

Type-species: *Stigmella ochnicola* Vári, 1955:336.

The species is removed from *Stigmella*, for although it shares some attributes with that genus they are not synapomorphies. The uncus of *ochnicolus* is not bilobed at the apex and so it lacks the best apomorphy of *Stigmella*, thus giving a sound cladistic reason for excluding the species from *Stigmella*. Phenetically the species is also separate (see 'Numerical Phenetic Analysis', below). Since the species does not belong to any described nepticulid genus it is assigned to a new one in accordance with the binomial system of nomenclature. No generic description is presented here, for since only one species is concerned the description applies to both. If a species is found later that shares one or more of what are now interpreted as unique characters of *ochnicolus*, then a formal generic description could be given. Further details about this point are given on pages 6-8.

The genus is named after Dr L. Vári and is to be treated as masculine.

Varius ochnicolus (Vári) comb. nov., figs 2, 12, 53

Stigmella ochnicola Vári, 1955:336.

The short Cu and the thickened 1+2A veins, and the presence of a subdorsal retinaculum in the forewing are attributes characteristic of the Stigmellinae. The species may represent the sister-species of all other members of the Stigmellinae, but since this possibility needs corroboration it is not incorporated into the classification. At present *Varius ochnicolus* is of uncertain position (*incertae sedis*) within the Stigmellinae. Further information on relationships is given in 'Cladistic Analysis', below.

This is a metallic species with a shining silver, postmedial fascia. The comments that follow augment the description of Vári (1955). The genitalia are redescribed.

ADULT ♂,♀. Head-capsule as in fig.2, flattened dorsoventrally. Antenna short, not extending more than halfway along forewing. Male with short, approximately triangular flagellar segments, female with short filiform segments. Scape relatively narrow. Galeae comparatively stout, not

extending beyond labial palpi. Compound eye small. Hindwing: costal spines present in male, very bunched together. No specialised scales on wings. Hindtibia: proximal pair of spurs above midpoint.

Venation (fig.12). Forewing: R_1 and R_5 share a common trunk from base of wing to where R_1 diverges. M runs with R from base of wing; not linked to Cu. R_4 and R_5 , and M_{1+2} represented by terminal branches. Cu free from M, and runs to about halfway along wing. Hindwing: M represented by a single, unbranched vein.

Male genitalia (fig.53). Vinculum: lateral arms fused with sides of tegumen, not forming a complete ring around aedeagus; ventral plate with thickened caudal margin; anterior extension not emarginated and not rounded. Tegumen a relatively narrow band, not extended into a point. Uncus in form of a hood, rather weakly sclerotised, not bilobed at the apex. Gnathos with single, well-sclerotised central process; each lateral process dorsally expanded. Valva deeply divided into an approximately triangular, ventral lobe, and a longer, narrow, slightly curved, dorsal element, which is continued anteriorly to meet the continuation of the opposite valva. Transtilla: transverse bar absent. Aedeagus narrow, expanded slightly anteriorly; carinate processes absent. Vesica marked only by a long thickening, which is not striate, but probably surrounds the base of the ejaculatory duct.

Female genitalia (Vári 1955: fig.22). Anal papillae form a fairly broad end to abdomen. Ductus bursae without sclerotisations. Corpus bursae without signa.

LARVA. Mines the leaves of *Ochma pulchra* (Ochnaceae). The mine is a gallery in its early stages and then suddenly broadens into a rather elongate blotch. For further details and an illustration of the mine see Vári (1955:337, and fig.31).

MATERIAL EXAMINED. The type-series (collected in Pretoria) as cited by Vári (1955:337); in Transvaal Museum except for one paratype in British Museum (Natural History), London and another in Museum für Naturkunde der Humboldt Universität, Berlin.

The species may be distinguished from all others, with the exception of the North American *Artaversala gilvafascia* Davis, by the deeply divided valva. The flagellar segments of the antenna of the male (fig.2) are of a shape not seen elsewhere in the Nepticulidae.

The ending of the original species name has been changed from feminine to masculine so that it agrees in gender with the new generic component of the name. (*International Code* 1964:Articles 30, 34b.)

Genus *SIMPLIMORPHA* gen. nov.

Type-species: *Stigmella lanceifoliella* Vári, 1955:22.

The species is removed from *Stigmella*, for although it shares several attributes with that genus they are not synapomorphies. A separate description is not given for this monotypic genus since it is equivalent to that of the species. The reasons are similar to those given under the preceding species, and they are discussed in detail on pages 6-8.

The word *Simplimorpha* refers to the simple structure of the male genitalia and is to be treated as feminine.

Simplimorpha lanceifoliella (Vári) comb. nov., figs 1, 11, 52

Stigmella lanceifoliella Vári, 1955:22.

The wing venation of *lanceifoliella* is similar to *Stigmella* and *Pectinivalva*. The species belongs to the Stigmellinae but cannot be placed in either *Stigmella* (Stigmellini) or the Trifurculini. The characters it shares with *Stigmella* are interpreted as generalised rather than mutually defining. This point is discussed in 'Cladistic Analysis', below. Therefore *S. lanceifoliella* is treated as of an uncertain placement in the Stigmellinae.

The remarks presented below are additional to those of Vári (1955). The genitalia are redescribed.

ADULT ♂,♀. Head-capsule as in fig.1. Antenna: flagellar segments elongate in both sexes. Compound eye small. Galeae short, approximately equal to length of labial palpi. No specialised scales on wings. Forewing of male with a circular structure at base between Sc and R. Hindwing of male, as well as female, with costal spines. Hindtibia: proximal pair of spurs approximately in middle.

Venation (fig.11). Forewing: R_{4+5} and M_{1+2} represented as terminal branches. M runs concurrently with R_s from base of wing. Cu runs independently from base of wing and curves upwards to just meet the trunk of R_s+M about three-quarters of way along wing.

Male genitalia (fig.52). Vinculum: lateral arms form a U-shaped boundary to genital capsule, not a ring around aedeagus; anterior extension

rounded, not emarginated. Tegumen: broad, and not extended into a point. Uncus absent. Gnathos usually an inconspicuous narrow band, sometimes absent. Valva broad at base in ventral view, approximately rectangular when examined from inner aspect. Transtilla: transverse bar present. Aedeagus large with inconspicuous ventral process - sometimes long and narrow, sometimes shorter and broader; no other carinae. Vesica: cornuti generally spiculate, but variable in shape, size and number, and sometimes absent; a striate thickening surrounds base of ejaculatory duct.

Female genitalia (Vári 1955: fig.14). Anal papillae form a blunt end to abdomen. Ductus bursae without sclerotisations. Corpus bursae without signa.

LARVA. Forms a linear leaf-mine. For illustration and further details see Vári (1955:332 and his fig.23). The following host-plants have been recorded: *Rhus chirindensis*, *R. dentata*, *R. lancea*, *R. leptodictya*, *R. lucida*, *R. pyroides*, *Protorhus longifolia*, *Schinus molle*. All belong to the Anacardiaceae; *Schinus molle* is the introduced South American pepper tree.

PUPA. Spines on abdominal terga 2-8 small and tooth-like, and arranged in a single row of about 14 units.

MATERIAL EXAMINED. The type-series (collected in Pretoria) as cited by Vári (1955:332); in Transvaal Museum except for one paratype in British Museum (Natural History), London and another in Museum für Naturkunde der Humboldt Universität, Berlin.

Other specimens. SOUTH AFRICA: Transvaal, Pretoria, 41♂, 46♀ January, March, June to December; Pretoria District, Hartebeespoortdam, 1♂ August; Hennops River, 1♂ August; Orange Free State, Golden Gate National Park 1♂, 2♀ February; Sasolburg, 1♂, September; Natal, Margate, 1♂, 8♀ May; Umdoni Park, 1♂ December; St. Lucia Bay, 1♂ September; Durban, 1♂ December; Cape Province, Cape Town, 1♂ September; Port Alfred, 1♂ November. ZIMBABWE: Mt. Edgecombe, 3♀ April; Umtali, 1♀ May. Most specimens collected by L. Vári, some by D.W. Rorke, D.M. Kroon, J. & H. Potgieter, A.J.T. Janse, B. Janse; in Transvaal Museum.

S. lanceifoliella is unlikely to be confused with any other described species. The general shape of the genital capsule of the male and its components are characteristic.

Genus *JOHANSSONIA* Borkowski

Johanssonia Borkowski, 1972:702. Type-species: *Nepticula acetosae* Stainton, 1854:303, by original designation and monotypy. (Synonymized by Karsholt & Nielsen 1976:17.)

The generic name was proposed for the European species *acetosae* Stainton. Borkowski (1975:529) treated *arifoliella* Klimesch as a subspecies of *acetosae* so the genus remains monotypic.

Johanssonia acetosae (Stainton)

Nepticula acetosae Stainton, 1854:303.

The species belongs to the Stigmellinae, but its position within the subfamily is uncertain. Comments on its relationship are made in 'Cladistic Analysis', p.187.

I have examined a male and a female, kindly donated by Colonel A.M. Emmet. The following comments are of particular note.

Hindtibia. Proximal pair of spurs below midpoint.

Venation. Forewing: R_{2+3} absent; M probably coalesced with R_S from base of wing; Cu faint, gradually curves up to meet R_S+M about halfway along wing (Cu omitted by Borkowski 1972:fig.20).

Male genitalia. Vinculum: lateral arms articulate with sides of tegumen. Tegumen approximately rectangular, not shown by Borkowski (1972: fig.8). Uncus large, hood-like, terminating in a point. Gnathos with central, tongue-shaped element and lateral processes (omitted from Borkowski's illustration). Valva approximately triangular. Transtilla: transverse bar absent. Aedeagus with no carinate processes.

Female genitalia. Abdomen ends broadly. Ductus bursae unmarked. Corpus bursae without signa.

MATERIAL EXAMINED. ENGLAND: Suffolk, Icklingham, 1♂, 1♀, 17-18.v.1974, A.M. Emmet; in Transvaal Museum.

The course run by Cu in the forewing resembles that of *Simplimorpha lanceifoliella* in that it curves up to meet R_S+M . Since one of the characteristics of the Trifurculini (see below) is that M curves up to meet R_S , the situation in *acetosae* is rather confusing: could 'Cu' in fact be M? Probably not, because M diverges rather sharply up to meet R_S about one-third of the way along the wing in the Trifurculini whereas in *acetosae*

the vein in question curves up gradually and meets R_s about halfway along the wing. *J. acetosae* lacks characters that are unique to the Trifurculini (e.g. a narrow band-like uncus in the male and signa reticulata in the female). It may be distinguished from *Stigmella* by the absence of the branch R_{2+3} in the forewing and the absence of a transverse bar of the transtilla.

Tribe STIGMELLINI trib. nov.

(Type-genus: *Stigmella* Schrank, as for subfamily.)

The diagnosis that follows applies to both the tribe and its single included genus, *Stigmella*. The name Stigmellini is strictly redundant, but it is included here to follow the convention of assigning equivalent taxonomic divisions the same rank. (For details see pages 6-8.)

DIAGNOSIS. The species from southern Africa are dealt with immediately below in the reprint.

Distinguished from the Trifurculini by the following: Forewing: M coalesced with R from base of wing, Cu runs independently throughout its length. Male genitalia: lateral arms of vinculum fuse distinctly with sides of tegumen and do not form a complete ring around aedeagus; uncus hood-like, not in the form of a narrow band. Female genitalia: signa reticulata never present.

In one species of Trifurculini M is probably united with R from the base of the forewing, but this species is otherwise quite distinct from any species of *Stigmella* (see *Obrussa zimbabwiensis*, described below). The absence of signa reticulata on the corpus bursae of the female in Trifurculini is rare. In females in which the signa are absent M is coalesced with Cu from the base of the forewing and then diverges to R about one-third of the way along the wing; this distinguishes such species from any presently assigned to *Stigmella*.

DISTRIBUTION. *Stigmella* is a large genus of worldwide distribution. (No records from South America are known to me.)

Genus *STIGMELLA* Schrank

See reprint bound in immediately below, (Scoble 1978b).

Tribe TRIFURCULINI trib. nov.

Type-genus: *Trifurcula* Zeller, 1848:330.

The name of the tribe is based on the oldest name of the remaining nepticulid genera. The concept of the Trifurculini in some ways resembles that of *Trifurcula* in the sense of Johansson (1971), see 'Previous Treatments' (p.10).

The larvae are generally leaf-miners, but various other kinds of tissues are mined.

DIAGNOSIS. Distinguished from the Stigmellini by the following characters. Forewing: M coalesced with Cu from base to about one-third of way along wing before M diverges to coalesce and run with R; or R (or just R_s), M and Cu are coalesced from base. Male genitalia: lateral arms of vinculum not distinctly fused to sides of tegumen but meet, or just fail to meet, and so form a ring around aedeagus. Tegumen frequently extended to a point, a blunt lobe, or a bifurcate or bilobed process. Female genitalia: signa reticulata usually present. The uncus, when present, is generally a thickened band approximately in the shape of an inverted V. This character is absent from all other nepticulids. With few exceptions the gnathos is fused so that it forms a strong, undivided central element that is ventral to the lateral elements (Scoble 1980b:fig.7). The basic shape of the gnathos is widespread in the Nepticulidae, but it is different from that of most *Stigmella* species and also from that of *Simplimorpha lanceifoliella*.

The pupal exuviae of only a few species were available for study. The spines on the abdominal terga are generally large and numerous, although sometimes they are smaller. This contrasts with the Stigmellini where the spines are very small and usually reduced to a single row.

DISTRIBUTION. Some of the genera included are found in both northern and southern hemispheres. Representatives of the tribe are found in most parts of the world.

Genus *OBRUSSA* Braun

Obrussa Braun, 1915:196. Type-species: *Nepticula ochrefasciella* Chambers, 1873:128, by original designation and monotypy.

Etainia Beirne, 1945:208. Type-species: *Lyonetia sericopeza* Zeller, 1839:215, by original designation. (Synonymized by Wilkinson & Scoble 1979: 98 see there for additional references.) Emmet *in* Heath, 1976:206 (details of life-history included).

The species from the Holarctic form a tight-knit group. The genitalia are modified and the larvae mine in the winged-seeds of *Acer* and (at least in one species) in bark, petiole and bud in addition.

Four species from southern Africa are assigned to *Obrussa*, below.

ADULT. *Head*. Tuft on front of head and vertex black, ferruginous or orange to yellow.

Thorax. Forewing with white fasciae or spots on a blackish background, or ochreous or off-white variously irrorated with fuscous or with a fuscous fascia. Male with or without a hair-pencil, and with or without specialised scales. Subcostal retinaculum in male, where observed, comprising unusually long hook-like units. Venation varies, see species descriptions. R_1 and R_{2+3} always present. R_4 and R_5 represented by separate branches terminally, or fused. M_1 and M_2 represented by separate branches terminally or fused. M is coalesced with Cu at base of wing, later diverges to R_5 , or interpretation of the M and Cu veins uncertain (see species descriptions). 1+2A fused throughout length; no anal loop. Hindwing brownish grey, with or without specialised scales in male. Venation: M unbranched. Hindtibia: proximal pair of spurs above or below midpoint.

Abdomen. Male genitalia: Vinculum: lateral arms form a complete, or almost complete, ring around aedeagus; ventral plate usually with deep (rarely shallow) U-shaped emargination of caudal edge; anterior extension generally not excavated, rarely weakly so. Tegumen rounded, not extended into a long point. Uncus not divided dorsoventrally at apex; bipapillate or undivided at apex in ventral view; a band approximately in shape of an inverted V. Gnathos with or without a divided or undivided central, ventral element. Valva: with a characteristic, long apodeme (rarely absent) arising from outer aspect that runs behind (i.e. dorsal to) the valva into

the genital capsule. Shape of valva varies, occasionally it is small. Strong setae arise from apex of valva, often these are prominent. Transstilla: transverse bar present or absent. Aedeagus: rarely a large process arises ventrally, which is probably an extension of inner wall of aedeagus. Vesica without denticulate or spiculate cornuti.

Female genitalia. End of abdomen broad, not attenuated to form pointed ovipositor. Ductus bursae variously sclerotised, generally with funicular markings, often with spines. Corpus bursae with a pair of large signa reticulata.

LARVA. No information on the species from southern Africa. In the Holarctic the species mine in the winged-seeds of *Acer* (for details see Emmet 1976). In *sericopeza* the first generation mines in winged-seeds whilst the second mines in petiole, bark and bud.

DIAGNOSIS. The two most striking unique characters of this genus are found in the male genitalia. They are the U-shaped excavation of the caudal edge of the ventral plate of the vinculum, and the long, heavily sclerotised apodeme associated with the valva. In *nigricapitella* Meyrick this apodeme is absent, but see there for why the species is included in the genus. Many prominent setae arise from the apical part of the valva; they are found in all species of *Obrussa* and are particularly prominent in *ochrefasciella* and the new species described from Zimbabwe, below.

In *decentella* (Herrich-Schäffer), see Emmet (1976:206), and in all the species from southern Africa, the head-tuft is black. A black head-tuft is unusual, but not unique in the Nepticulidae, and is probably an independently evolved apomorphy of *Obrussa*.

DISTRIBUTION. North America, Europe, Africa (records only from southern Africa).

Obrussa crypsixantha (Meyrick) comb.nov., figs 13,54

Nepticula crypsixantha Meyrick, 1918:43.

Nepticula crypsixantha Meyrick; Janse, 1948:164.

ADULT ♂. Wingspan 5,8-6,0mm. Head-tuft black. Antenna: eye-cap broad. Forewing pale ochre heavily (up to 50%) irrorated with fuscous. Subcostal retinaculum comprising a series of very long hook-like units. Hindwing broad at base and with a patch of specialised, pale ochre scales on ventral surface; costal spines absent. Hindtibia: proximal pair of spurs below midpoint. Abdomen pale grey.

Venation (fig.13). Forewing: R_4 and R_5 represented by terminal branches. M_{4+5} present. M concurrent with Cu from base to about a third of way along wing when it diverges to meet R_5 . Cu continues for a very short distance after M diverges.

Male genitalia (fig.54). Vinculum: U-shaped excavation of ventral plate moderate; anterior extension not emarginated. Tegumen well-fused to uncus. Uncus bipapillate. Gnathos with central element not greatly elongated. Valva triangular; apex weakly cleft and with several strong setae arising from it, but not as prominent as in *zimbabwiensis*; apodeme of valva long and tapering. Transtilla: transverse bar present. Aedeagus with pair of lateral carinae and a large finger-like process that is probably an extension of the inner ventral wall. Vesica with poorly-defined thickenings.

MATERIAL EXAMINED. I designate as Lectotype the syntype of Meyrick of which a photograph appears in Janse (1948: plate 93, fig.7). It is a male and bears the following label data: 'Pretoria, 27.ix.'13, A.J.T. Janse; [Genitalia slide] 7245; *Nepticula crypsixantha* M., Type No.125.'; in Transvaal Museum. Paralectotypes: SOUTH AFRICA: Transvaal, Pretoria, 1♂ 29.ix.1915, 'Cotype No.126', 1♂ 20.x.1915, 'Cotype No.143', A.J.T. Janse; in Transvaal Museum.

Other specimens: Pretoria North, 1♂ ix.1949, G. van Son; 1♂ 29.x.1948, L. Vári; 1♂ 28.x.1976, L. Vári; in Transvaal Museum.

This species may be distinguished from all the other known species of

Obrussa from southern Africa by the presence of a transtilla. The male genitalia are, in general, characteristic.

Obrussa zimbabwiensis spec.nov., figs 14,55,104

ADULT ♂, ♀. Wingspan 5,4-6,4mm. Head-tuft black. Antenna: eye-cap very large. Forewing very pale ochre with a black, postmedial fascia. In two males, collected from same locality as the holotype, shiny black, specialised scales cover proximal half of ventral surface and cause proximal half of dorsal surface to appear dark. In male, not female, an ochreous hair-pencil comprising a bunch of long, rather wide scales, arises from base of forewing near costa on ventral surface. Subcostal retinaculum in male consists of a series of very long hook-like units. Hindwing of male with shiny black, specialised scales on both surfaces; costal spines absent. Both wings densely covered with aculei. Hindtibia: proximal pair of spurs above midpoint.

Venation (fig.14). R_{4+5} and M_{1+2} present, or the R_S+M trunk terminates before branching. M does not diverge from Cu to meet R_S , so it is probably associated with R_S from base of wing. Cu present, or so weak as to be visible only as a persistent trachea.

Male genitalia (fig.55). Vinculum: U-shaped excavation of ventral plate broad and deep; anterior extension weakly emarginated. Uncus in shape of inverted V. Gnathos with central element long and narrow, extending beyond uncus. Valva triangular with several characteristic setae arising from apical part; base produced inwardly into a short, pointed process; apodeme attached to basal outer edge of valva, and hardly tapers. Transtilla: transverse bar absent. Aedeagus: projected ventrally into a short spatulate process; a pair of lateral carinae are present. Vesica with few poorly-defined thickenings.

Female genitalia (fig.104). Ductus bursae with characteristic funicular sclerotisation. Corpus bursae: signa reticulata long and broad.

MATERIAL EXAMINED. ♂-Holotype, ZIMBABWE (RHODESIA): Lundi, 13-16.iii.1964, Vári & van Son, genitalia slide no.10079; in Transvaal Museum. Paratypes: data as holotype, 2♂, 4♀; 6♂, 3♀ 2-5.ii.1964, Vári & van Son; Salisbury, 1♂ 25.vi.1956, C.N. Smithers; housed in Transvaal Museum.

The species can easily be distinguished from all other species of

Obrussa presently described by the colour of the forewing, and the form of the male and female genitalia.

Obrussa nigricapitella (Janse) comb.nov., figs 15,56,105

Nepticula nigricapitella Janse, 1948:170.

Nepticula irrorata Janse, 1948:168 *partim* (two misidentified paralectotypes, see also Scoble 1978a:95).

ADULT ♂, ♀. Wingspan 4,2-5,0mm. Head-tuft black. Antenna: with rather rounded, approximately moniliform segments in male. Compound eye very large, eye-index = 1,5. Galeae short and swollen, extending just beyond labial palpi. Maxillary palpi with segments 1 and 2 almost completely fused, and segments 2 and 3 poorly demarcated. Forewing pale ochre, weakly irrorated with fuscous. Subcostal retinaculum in male comprising a series of very long hook-like units. No specialised scales on either wing. Hindwing: no costal spines in male. Hindtibia: proximal pair of spurs below midpoint. Abdomen off-white.

Venation (fig.15). Forewing: R_{4+5} and M_{1+2} represented by terminal branches. M separate from R_5 at base, later meets R_5 about third of the way along wing. Cu weak, presumably fused with M at base of wing, or else lost.

Male genitalia (fig.56). Vinculum: U-shaped excavation of ventral plate shallow; anterior extension very weakly emarginated. Tegumen well fused to uncus. Uncus in form of a sclerotised band produced terminally into pair of prominent points. Gnathos with central element partly divided. Valva small, well fused to its opposite member at base, with a C shaped excavation from top of valva; strong setae arise from apex, not as prominent as in *zimbabwiensis*; apodeme of valva vestigial. Transtilla: transverse bar absent; ventral arm lies at about right angles to valva and sinks well back into genital capsule. Aedeagus with a pair of long narrow carinate processes. Vesica: a long thin apodeme is probably derived from it.

Female genitalia (fig.105). Ductus bursae with a characteristic marking, and a pair of plates from which arise comb-like teeth at the point at which the spermatheca enters the ductus. Corpus bursae: signa reticulata long and broad.

MATERIAL EXAMINED. I designate as Lectotype one of Janse's three syntypes. It is a male of which a photograph of the genitalia is given in Janse (1948: plate 90 fig.7). It bears the following label data: 'Abachaus, S.W.A. [South West Africa] Feb. 43 G. Hobohm; [Wing side] 1899; [genitalia slide] 4953; *Nepticula nigricapitella* Janse, Type No.2380'; in Transvaal Museum. Paralectotypes, SOUTH WEST AFRICA: Abachaub, 1♂, 1♀ x.1943, G. Hobohm, a photograph of the female moth appears in Janse (1948: plate 92 fig.7); in Transvaal Museum.

Other specimens. Paralectotypes of *Stigmella irrorata*, 1♂ labelled 'Abachaus [*sic*, Abachaub], S.W.A., No.43, G. Hobohm, paralectotype *Stigmella irrorata* Janse.'; 1♀ labelled 'Abachaus, S.W.A., April 43, G. Hobohm, paralectotype *Stigmella irrorata* Janse.'; SOUTH WEST AFRICA: Abachaub, 1♂ x.1943, 1♀ x.1944, 1♂, 2♀ xi.1945, G. Hobohm; in Transvaal Museum.

O. nigricapitella is similar to the next species but is easily distinguished from it by the absence of the apodeme associated with the valva. The shallow U-shaped depression of the ventral plate of the vinculum, and the general similarity of male and female genitalia to those of the next species shows that *nigricapitella* belongs to *Obrussa*.

The species has been collected only from South West Africa. The next species occurs in the eastern Transvaal in South Africa on the opposite side of the subcontinent.

Obrussa krugerensis spec.nov., fig.57

The species is closely allied to *nigricapitella* and the comments below include only the differences from that species.

ADULT ♂, ♀. Wingspan 4,0-4,8mm. Forewing of male with an ochreous hair-pencil arising from base of ventral surface on costa.

Male genitalia (fig.57). Vinculum: excision of caudal margin of ventral plate much deeper than in *nigricapitella*. Uncus not extended into two points. Gnathos: shape unusual (see figure) but central element not divided. Valva: apex weakly divided but not with a C-shaped excavation; long spine-like apodeme extends from base of valva across genital capsule.

The species has been found only in the Kruger National Park (Eastern Transvaal) and so has a quite different distribution from *nigricapitella*, which has only been found in South West Africa.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Kruger National Park, Letaba Camp, 28.iii.1952, Janse & Vári, genitalia slide no.10140; in Transvaal Museum. Paratypes: locality as holotype, K.N.P. Survey, 1♂, 1♀ 3-6.xii.1973, Potgieter & Scholtz; Shingwedzi, 1♂ 29.iii.1952, Janse & Vári; Punda Milia, K.N.P. Survey, 2♂, 2♀ 4-5.v.1970, Vári & Potgieter; in Transvaal Museum.

Genus *ECTOEDEmia* Busck

Ectoedemia Busck, 1907:97. Type-species: *Ectoedemia populella* Busck, 1907:98, by original designation and monotypy. (Treated as a subgenus of *Trifurcula* Zeller (*sensu* Johansson 1971) by Johansson 1971:245.)

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

Fomoria Beirne, 1945:208. Type-species: *Nepticula weaveri* Stainton, 1855:49, by original designation. (Treated as a subgenus of *Trifurcula* Zeller (*sensu* Johansson 1971) by Johansson 1971:245.)

Ectoedemia has been much expanded here to include a large number of species. All these species share certain attributes but no one feature is unique to them all, so the monophyly of the group is questionable. A discussion of the problem is presented under 'Classification' (p.200), and reasons for the treatment are given.

Further studies on species that fit the description presented below from other parts of the world are needed. Work by the group studying Nepticulidae at the Vrije University, Amsterdam may resolve the question of the monophyly of *Ectoedemia* in the future.

ADULT ♂,♀. *Head.* Orange, ochreous, off-white or mixed with red-brown. Compound eye not very small. Galeae either fail to extend beyond labial palpi or are about twice length of those structures, or, rarely, over twice length of head-capsule.

Thorax. Forewing metallic or non-metallic; colour varies between species, frequently ochreous lightly or heavily irrorated with fuscous, often grey-brown. Male with or without a hair-pencil, and with or without specialised scales. Venation varies between species. R_1 and R_{2+3} always present. R_4 and R_5 represented by separate branches terminally, or fused. M_1 and M_2 represented by separate branches terminally, or fused. M united with Cu at base and R_5 later. Cu sometimes long, or sometimes short and never separate from M. Hindwing with or without specialised scales. Venation: M unbranched. Hindtibia: proximal pair of spurs below midpoint, at least for species discussed in this work, except where hindlegs are missing.

Abdomen. Male genitalia. Vinculum: lateral arms form a complete ring around aedeagus; ventral plate without a deep excavation from caudal margin; anterior extension emarginated or not. Tegumen extended into a long point, or bilobed or bifurcate, or rounded. Uncus: absent, or present and approximately in form of an inverted V; apex undivided or weakly emarginated; occasionally with an additional pair of lobes. Gnathos usually with an undivided, pointed or bluntly rounded central and ventral element, sometimes modified, but always based on this plan. Valva approximately triangular in general but with considerable variation in detail, and sometimes greatly modified; without long *Obrussa*-type apodeme. Transtilla: transverse bar present. Aedeagus: with or without a ventral process; ventral process often long, narrow and forked at apex. Vesica: cornuti present or absent.

Female genitalia. End of abdomen broad, extended into a short point or, rarely, very long for a nepticulid. Ductus bursae with prominent sclerotisations that usually form a ring, and in some species rows of pectinate marks; rarely, ductus lacks sclerotisations. Bursa copulatrix with a pair of signa reticulata; these structures are rarely absent.

LARVA. Mining habits vary. Generally leaf-miners, some species mine petioles, where they induce the formation of galls, others are bark-miners.

PUPA. For the few species for which pupal exuviae were examined terga 2-8 are covered with medium-sized to large spines.

DIAGNOSIS. *Ectoedemia* is easy to distinguish from *Obrussa*; it lacks the long apodeme of the valva, and the ventral plate of the vinculum is not emarginated. The forewing venation differs from *Niepeltia* since R_1 and R_s run together from the base of the wing in the former whereas in the latter they are separate. The male genitalia of *Ectoedemia* differ from those of the homogeneous genus *Niepeltia* in shapes of the components, compare figures. The venation of the forewing of *Ectoedemia* differs from that of *Microcalyptris* in that in the latter M is stated to coalesce with R from base (Wilkinson 1979:62), whereas M only meets R_s about one-third of the way along the forewing in *Ectoedemia*.

In the hindwing M is not branched in *Ectoedemia* whereas in *Trifurcula* M is branched into M_1 and M_2 .

Ectoedemia is unlikely to be confused with any other genus. In all the species M diverges from the joint M+Cu trunk in the forewing and fuses with R_s about one-third of the way along the forewing. In all but a few species the ductus bursae is marked by an approximately ring-shaped sclerite. Neither of these characters is unique to the genus but their combination is, except for the few species where the markings on the ductus are absent and considered to be secondarily lost.

DISTRIBUTION. World-wide, except Antarctica. No information from South America.

Subgenus *ECTOEDEMIA* Busck

Type-species: *Ectoedemia populella* Busck, 1907:98.

The two reprints (Scoble 1978a, 1979) bound in below deal with three species from southern Africa. They are included in the nominate subgenus.

The subgenus is widespread although it is not represented in the Australian nepticulid material housed in the Australian National Collection.

A character common to all the species is the absence of an uncus. The general pattern of the wing venation is the same for all species examined, but not unique to the taxon since it occurs in species belonging to the other subgenera.

Subgenus *LAQUEUS* subgen. nov.

Type-species: *Nepticula grandinosa* Meyrick, 1911a:236.

In the forewing of all the species 1A and 2A are separate at the base of the wing, and subsequently unite. This arrangement was called an 'anal loop' by Kristensen (1978: fig.20) in the Prototheoridae. This is the only known character that is present in all the species. A well-developed ventral process of the aedeagus occurs in most, but not all species.

The group has not been found outside southern Africa.

A group of eleven closely allied species.

The 11 species that follow constitute a tight-knit group. They are not named more formally as a species-group because most of the other species in the subgenus do not fall into clusters of similar cohesion; to name these others would result in the anomaly of naming many single species each as a 'group'.

The eight species for which host-plant information is available feed on various species of *Diospyros* (Ebenaceae).

In the male genitalia the anterior extension of the vinculum is usually rounded anteriorly rather than emarginated or excavated. The apex of the tegumen is often in the form of a pair of small rounded knobs, or finger-like extensions, a situation rare in the Nepticulidae. The apex of the uncus is usually strongly bent ventrally, at least in dried specimens, and often weakly emarginated. The gnathos is of the generalised nepticulid-type in some species but in others the central element is weakly sclerotised and broad, which indicates that the lateral processes are weakly fused. The valva is approximately triangular and, in all except one species, is curved and narrows towards the apex. Four or five long setae with prominent, tuberculate bases arise from the valva, usually towards its base. The aedeagus is expanded anteriorly into a flattened flange-like structure, or a pair of lateral flanges. The prominent ventral process of the aedeagus is also found in some other species of the subgenus.

In the females, known for five species, the apophyses form a point at the end of the abdomen. Below the rather characteristic thickening on the ductus bursae are some minute pectinations. In some species they are few in number and faint, even using interference contrast microscopy;

in others they are numerous and distinct.

The galeae, in species where sufficient material was available for their examination, extend well beyond the labial palpi. In most other nepticulids examined they are considerably shorter.

The setae with the prominent bases on the valvae, and the flange of the aedeagus are characters unique to this group.

Ectoedemia (Laqueus) stimulata (Meyrick) comb.nov., fig.58.

Nepticula stimulata Meyrick, 1913:326.

Nepticula stimulata Meyrick; Janse, 1948:176.

Nepticula macrochaeta Meyrick, 1921:140 [synonymised by Janse 1948:176].

ADULT ♂. Wingspan 4,4-4,8mm. Head-tuft off-white. Forewing off-white with a few fuscous scales scattered over dorsal surface. Hindwing: no costal spines. No specialised scales on wings.

Venation. As *guerkliae*, below. R_{4+5} , and M_1 and M_2 represented by terminal branches. Cu continues for a short distance after M diverges to meet R_5 .

Male genitalia (fig.58). Vinculum: anterior extension not emarginated. Tegumen tapers to a single, undivided lobe. Uncus in form of a well-sclerotised band, with a small, weakly emarginated extension apically. Gnathos unremarkable. Valva divided at apex, with four prominent setae arising near base. Transtilla: transverse bar present. Aedeagus with a pair of small lateral flanges anteriorly; ventral process large, bifurcate; no other carinae. Vesica with some minute cornuti.

MATERIAL EXAMINED. ♂-Lectotype, here designated: it is one of Meyrick's syntypes and bears the following label data: 'Barberton, 5. Dec. 1910., A.J.T. Janse; 4894; G. [genitalia slide] 7241; *Nepticula stimulata* M., Type No.117; *N. stimulata*.' A photograph appears in Janse (1948: plate 94, fig.2); in Transvaal Museum. Paralectotype, SOUTH AFRICA: Transvaal, Barberton, 1♂ 19.xii.1910, A.J.T. Janse; 'Cotype No.118.'; in Transvaal Museum.

The shape of the valvae and of the ventral process of the aedeagus is characteristic of *stimulata*.

Ectoedemia (Laqueus) grandinosa (Meyrick) comb.nov., figs 16,59,106,122

Nepticula grandinosa Meyrick, 1911a:236.

Nepticula grandinosa Meyrick; Janse, 1948:166.

ADULT ♂,♀. Wingspan 4,8-5,8mm. Head-tuft pale ochre with variable number of fuscous hairs mixed in. Galeae not long, but extend significantly beyond labial palpi. Forewing pale ochre, usually heavily irrorated with fuscous, but sometimes not. Hindwing: no costal spines in male. No specialised scales on wings. Abdomen grey.

Venation (fig.16). Forewing: R_{4+5} and M_{1+2} represented by terminal branches. Cu continues for a short distance after M diverges to R_5 .

Male genitalia (fig.59). Vinculum: anterior extension very weakly excavated. Tegumen terminates at apex as a pair of widely separated, small, rounded lobes. Uncus turned ventrally at apex, which is weakly emarginated. Gnathos with flattened ends to tips of lateral processes. Valva with patch of prominent setae arising from near base. Transtilla: transverse bar present; ventral arms relatively long. Aedeagus broadened anteriorly into a pair of lateral flanges; ventral process pointed at apex, not forked; no other carinae. Vesica with some minute cornuti.

Female genitalia (fig.106). Apophyses form a short, pointed ovipositor. Ductus bursae with a curved sclerite and rows of pectinate marks. Corpus bursae with a pair of elongate, clearly bordered signa, the reticulations of which are strong.

LARVA. Mines the leaves of *Diospyros lycioides* subspecies *lycioides* (Ebenaceae). The mine (fig.122) is a short, narrow gallery in its early stages and broadens suddenly into a wider and much contorted one. The convolutions merge so forming a blotch. The larva forms a cocoon inside the mine occasionally.

PUPA. Numerous rather small spines on abdominal terga 2-8.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Pretoria,

6.ix.1906, A.J.T. Janse, genitalia slide no.7206, 'Type No.113'; housed in Transvaal Museum.

Other specimens. SOUTH AFRICA: Transvaal, Pretoria, labelled as a ♂ of *fuscata* by Janse, 10.xii.1916, A.J.T. Janse, 'Cotype No.2363' see p.121; 2♂, 3♀ October-December, A.J.T. Janse; 27♂, 20♀ August-January, L. Vári; in Transvaal Museum.

The undivided lobe of the ventral process of the aedeagus is a character useful for recognising *grandinosa*.

Larvae of *grandinosa* often mine the leaves of the same individual plant as the next species. The mines however are easily distinguished by the presence of a short gallery in the early stage in *grandinosa*, and the presence of a black spot on the inner side of the epidermis in the next species.

Ectoedemia (Laqueus) wilkinsoni spec.nov., figs 60,120

ADULT ♂, ♀. Wingspan 5,4-6,4mm, one female is 4,6mm. Head-tuft pale ochre with variable number of brown or red-brown hair-scales mixed in, often the darker hairs predominate. Galeae extend clearly beyond labial palpi. Forewing a mixture of pale ochre and fuscous giving a mottled appearance, some specimens are darker than others; no specialised scales. Hind-wing of male: no costal bristles; pale yellow specialised scales on dorsal and ventral surfaces and a concolorous costal hair-pencil that arises from base of wing. Abdomen grey.

Venation. As *grandinosa*, above.

Male genitalia (fig.60). Vinculum: lateral arms long so capsule is elongate; ventral plate with caudal margin thickened; anterior extension rounded, not emarginated. Tegumen terminates at apex in a pair of small rounded lobes. Uncus in form of a narrow band bent ventrally at apex. Gnathos with small pointed central element. Valva with four prominent setae arising from near base. Transtilla: transverse bar present; ventral arms long. Aedeagus with a pair of small flanges anteriorly; ventral process in form of a short ventral component and a large, longer, more dorsally situated, forked process; no other carinae. Vesica with a small patch of minute cornuti.

Female genitalia. As *grandinosa* except that curved sclerite on ductus bursae is slightly larger.

LARVA. Forms a blotch mine (fig.120) in the leaves of *Diospyros lycioides* subspecies *lycioides* (Ebenaceae). The inner surfaces of the upper and lower epidermis are stained black. On the lower epidermis the stained area forms a prominent black spot, on the upper epidermis it is more extensive.

PUPA. Terga 2-8 covered with many medium-sized spines arranged into two patches one on each side of the segment.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Pretoria,

accession no.439, 27.ii.1952, L. Vári, genitalia slide no.10542; in Transvaal Museum. Paratypes: 1♀ data as holotype, 25.ii.1952, L. Vári; accession no.345, 3♂, 7♀, 23.viii., 7, 13, 16, 17, 22.ix., 1.x.1951, L. Vári; 1♂, 9.ix.1952, L. Vári; in Transvaal Museum.

The elongate vinculum and the presence of specialised scales on the hindwing of the male are useful characters for identifying that sex. The dorsoventrally divided ventral process resembles that of the next species as do the female genitalia and the mine.

The species is often found mining leaves on the same plant as *grandinosa* but the mine differs from that made by *grandinosa* (compare figures and see under *grandinosa*, above).

E. wilkinsoni has been collected only from Pretoria in the Transvaal, whereas the closely allied next species has been found only in the southern Cape.

The species is named after Professor C. Wilkinson of the Vrije Universiteit, Amsterdam.

Ectoedemia (Laqueus) simicola spec.nov., figs 17,61,121

ADULT ♂, ♀. Wingspan 4,8-5,4mm. Head-tuft pale ochre with some darker hair-scales mixed into tuft on vertex in two specimens. Forewing pale ochre sparsely irrorated with fuscous, the irrorations being more prominent towards edge of wing. Hindwing: no costal bristles. No specialised scales on wings. Abdomen grey.

Venation (fig.17). Forewing: R_4 (a short spur) and R_5 , and M_{1+2} represented by terminal branches. Cu continues for a short distance after M diverges to R_5 .

Male genitalia (fig.61). Vinculum: anterior extension rounded, not emarginated. Tegumen narrows to a single blunt lobe, not bilobed; Uncus complex, weakly emarginated at apex medially, laterally extended into an additional process on each side (arrowed in figure). Gnathos with a fairly small central element. Valva with four setae arising from slightly below midpoint. Transtilla: transverse bar present; ventral arms long. Aedeagus with a flange around anterior end; ventral process with a short ventral component and a long, dorsal, weakly bifid process; a pair of well-developed dorsolateral carinae present. Vesica unmarked except for striate thickening around base of ejaculatory duct.

Female genitalia. Apophyses form a pointed end to abdomen. Ductus bursae with pectinations very weak and not extensive. Markings on ductus bursae and corpus bursae as *grandinosa*.

LARVA. Forms a blotch mine (fig.121) on the leaves of *Diospyros simi*, and possibly *D. dichrophylla* (Ebenaceae). The inside of the epidermis is stained black, particularly in a small central patch on the lower epidermis. A whitish spot is usually present on the outside of the upper epidermis, a character that distinguishes the mine from that made by *wilkinsoni*.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Cape Province, [Tsitsikama] Coastal National Park, Stormsriviermond [Storms River Mouth], accession no. 2905, 4.xii.1967, L. Vári, genitalia slide no. 9909; in Transvaal Museum. Paratypes: data as holotype, 5♀, 28,30.xi., 1,2.xii.1967, L. Vári;

Lake Pleasant, accession no. 1098, 1♂, 10.iv.1954, L. Vári; Knysna, accession no. 1396, 3♂, 19,20.xii.1954; in Transvaal Museum.

This species is closely allied to *wilkinsoni*. The male of *simicola* may be distinguished from that of *wilkinsoni* by the single-lobed, as opposed to bilobed, condition of the tegumen, the additional lateral processes on the uncus and the form of the ventral component of the ventral process. The ductus bursae of the female of *simicola* has less extensive, and weaker pectinations.

Ectoedemia (Laqueus) guerokiae spec.nov., figs 18,62,107,122

ADULT ♂, ♀. Wingspan 5,0-5,6mm. Head-tuft pale ochre. Galeae extend clearly beyond labial palpi. Forewing pale ochre, evenly and fairly well irrorated with fuscous. Hindwing without costal bristles in male. No specialised scales on wings. Abdomen grey.

Venation (fig.18). Forewing: R_{4+5} , and M_1 and M_2 represented by terminal branches. Cu continues for a short distance after M diverges to meet R_s .

Male genitalia (fig.62). Vinculum: anterior extension rounded, not emarginated. Tegumen terminates at apex in a pair of widely separated, small, slightly elongated lobes. Uncus broad, weakly sclerotised, and terminates in a single, small lobe at apex; apex not strongly bent ventrally. Gnathos characteristic; lateral processes long and distinctive (see figure). Valva with four prominent setae arising from near base. Transtilla: transverse bar present; ventral processes long. Aedeagus with a pair of small lateral flanges anteriorly; ventral process very broad, bifurcate at apex; a pair of dorsolateral carinae present and bound to each other by a narrow, transversely orientated bar. Vesica with a patch of minute cornuti.

Female genitalia (fig.107). Apophyses form a pointed end to abdomen. Ductus bursae: curved sclerite is notably narrow; pectinations few in number. Corpus bursae with signa reticulata elongated.

LARVA. Mines the leaves of *Diospyros lycioides* subspecies *guerkei* (Ebenaceae). The mine (fig.122) is a long narrow gallery in its early stages. It broadens suddenly into a wider, and much contorted tract. The contortions often merge to form a blotch. Many mines stored under accession numbers relating to this species look different in that they are blotches, probably formed by side to side feeding of the larva rather than the merging of the contorted gallery. They probably belong to the next species. The mine figured is considered to be that which correctly represents *guerokiae* because moths have been reared from batches of mines only represented by contorted galleries. The mines are difficult to distinguish from those of *grandinosa* but the early, narrow stage is longer in *guerokiae* and so

each species is probably confined to one subspecies of *D. lycioides*.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Pretoria, accession no. 300, 10.i.1951, L. Vári, genitalia slide no. 6789; in Transvaal Museum. Paratypes: data as holotype, 1♂, 11.i.1951; accession no. 61, 2♀, 14.xii.1948, L. Vári; accession no. 108, 1♂ 4.ii.1949; accession no. 359, 1♂ 7.ix.1951, L. Vári; Johannesburg, accession no. 227, 1♂ 21.ix.1950, L. Vári; Wylies Poort, 5 miles North, 1♂ 21-22.iii.1954, A.J.T. Janse; Blyde River Nature Reserve, 1♂ 24.xi.-1.xii.1975, Potgieter & Scoble; in Transvaal Museum.

The ventral process of *guerokiae* is broader than any other species. The shape of the lobes of the tegumen are rather elongate and less rounded than in *grandinosa*, a species that feeds on the same species of host-plant (although probably a different subspecies). The sclerotisation on the ductus bursae of the female of *guerokiae* is particularly narrow. Both sexes may further be separated from *grandinosa* by the median vein, which is branched, terminally, in *guerokiae*, but unbranched in *grandinosa*.

Ectoedemia (Laqueus) macrochaeta (Meyrick) comb.nov., figs 63,108,123

Nepticula macrochaeta Meyrick, 1921:140.

Nepticula stimulata Meyrick; *sensu* Janse, 1948:176 (*macrochaeta* treated as a junior synonym).

Nepticula primaria Meyrick, 1913:326, (*partim*), misidentified syntype.

Nepticula primaria Meyrick; Janse, 1948:174 (*partim*), misidentified syntype.

The species was described from a single female specimen from Pretoria. Janse (1948) synonymised *macrochaeta* with *stimulata*. The characteristic genitalia are similar to those of females of a long series reared from *Diospyros* from Pretoria. The males of this series have genitalia easily distinguishable from the males of *stimulata*. The two syntypes of *stimulata* come from Barberton in the eastern Transvaal. Therefore *macrochaeta* is withdrawn from synonymy.

The male genitalia illustrated by Janse (1948:plate 85, fig.9) are those of *macrochaeta*, not *primaria* as labelled.

To add to the confusion one of the paralectotypes of *primaria* Meyrick is a misidentified specimen of *macrochaeta*.

ADULT ♂, ♀. Wingspan 5,4-6,4mm. Head-tuft orange-ochre. Galeae about twice length of labial palpi. Forewing pale ochre variously, but rather lightly, irrorated with fuscous; in some specimens irrorations are almost absent. Hindwing: a few long costal hair-like scales arise from base of wing of male rather than costal bristles. No specialised scales on wings. Abdomen grey.

Venation. As *simicola*, above.

Male genitalia (fig.63). Vinculum: anterior extension not excavated. Tegumen extended into a deeply-forked process. Uncus weakly emarginated at apex, which is bent ventrally. Gnathos fused but rather weakly so, and not forming a pointed, well-differentiated central element. Valva with five prominent setae arising from near base. Transtilla: transverse bar present; ventral arms long. Aedeagus terminates in a flange anteriorly; ventral process forked, not very broad, similar to extension of tegumen; a pair of dorsolateral carinae present. Vesica unmarked except for striate

thickening around base of ejaculatory duct.

Female genitalia (fig.108). Posterior apophyses form a strong, sharp point to end of abdomen. Anterior apophyses particularly broad. Ductus bursae: sclerotised bands form a broken ring; a few minute pectinations are also present. Corpus bursae with signa reticulata elongated.

LARVA. Mines the leaves of *Diospyros lycioides* subspecies *guerkei* (Ebenaceae). The mine (fig.123) is a gallery followed by a true blotch. The subspecies of plant on which *macrochaeta* feeds is the same as that of the previous species, *E. guerkeiae*, see above, but the larva of *macrochaeta* makes a true blotch.

MATERIAL EXAMINED. ♀-Holotype, SOUTH AFRICA: Transvaal, Pretoria, 20.xii.1910, C.J. Swierstra, genitalia slide no. 7269, 'Type No. 2397', a further label, probably added by Meyrick, bears the number 837, and another states '*Nepticula macrochaeta* Meyrick Type'; in Transvaal Museum.

Other specimens. SOUTH AFRICA: Transvaal, Pretoria, ♀ paralectotype of *primaria* Meyrick, 'Cotype No. 121', 11.xi.1909, A.J.T. Janse; 21♂, 17♀ January, February, September, November; Pretoria North, 1♂ March; Johannesburg 4♂, 9♀ September, October, December. Marieps Mnt. [Marieps-kop], 2♀ December. Natal, Umdoni Park, 1♂ January. Most specimens collected by L. Vári, other collectors C.J. Swierstra, A.J.T. Janse, D.M. Kroon, G. van Son; in Transvaal Museum.

The species may be distinguished from *stimulata*, *primaria* and all others, except the next, by the forked extension of the tegumen in the male, and the particularly sharp point formed by the posterior apophyses in the female. *E. macrochaeta* is closely allied to the next species and is distinguished from it by the characters given under that species, below.

Ectoedemia (Laqueus) furcella spec.nov., fig.64

The description for this species is like that of *macrochaeta*, above, except for the following.

ADULT ♂. Black specialised scales on dorsal surface of hindwing. An ochreous hair-pencil arises from base of hindwing at costa.

Male genitalia (fig.64). Tegumen less deeply forked than in *furcella*. Aedeagus: dorsolateral carinae not completely separated from each other (see figure).

♀ indistinguishable from *macrochaeta*.

LARVA. The two reared specimens were collected from *Diospyros lycioides* subspecies *lycioides*. The mine is similar to that made by *macrochaeta*.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Brits District, Hartebeespoort Dam, accession no. 3677, viii.1977, L. Vári, genitalia slide no. 10312; in Transvaal Museum. Paratypes: 1♂ data exactly as holotype; Kruger National Park, Pretoriuskop, 3♂ 6-7.iv.1952, L. Vári; Barberton, 5♂ 28.ii.-1.iii.1974, L. & G. Vári; Blyde River Nature Reserve, 2♂, 2♀ 24.xi.-1.xii.1975, Potgieter & Scoble; in Transvaal Museum.

Ectoedemia (Laqueus) maritima spec.nov., figs 65,124

ADULT ♂. Wingspan 4,2-6,0mm. Head-tuft ochre to dull red-brown. Galeae about twice length of labial palpi. Forewing pale ochre, evenly and fairly well irrorated with fuscous. Hindwing without costal bristles. No specialised scales on wings. Abdomen grey.

Venation. As *grandinosa*, above.

Male genitalia (fig.65). Vinculum: anterior extension rounded, not emarginated. Tegumen terminates at apex as a pair of widely separated points. Uncus: apex bent ventrally and emarginated to form a weakly forked process. Gnathos fused but weakly so, similar to *macrochaeta* and *furcella*. Valva with six prominent setae arising near base. Transtilla: transverse bar present. Aedeagus terminates anteriorly in a small flange; ventral process not broad, forked at tip; pair of dorsolateral carinae present. Vesica with some minute cornuti.

LARVA. Mines the leaves of *Diospyros ? villosa* (Ebenaceae). The mine (fig.124) is a narrow gallery in its early stage, and expands into a blotch later. It resembles the mines of *macrochaeta* and *furcella*.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Cape Province, Alexandria, Langebos, accession no. 1437, 23.xii.1954, L. Vári; genitalia slide no. 7279; in Transvaal Museum. Paratypes: data as holotype, 4♂ 19,20, 24.xii.1954, L. Vári; Kenton-on-Sea, 24♂ 22-23.ii.1978, M.J. Scoble; in Transvaal Museum.

The species is allied to *macrochaeta* and *furcella* as can be seen from the male genitalia and the shape of the mine. The tegumen is not extended into a forked process and the ventral arms of the transtilla are not as long. The ventral process of the aedeagus is also different, compare figures.

Ectoedemia (Laqueus) umdoniella spec.nov., figs 19,66,

ADULT ♂. Wingspan 4,6mm. Head-tuft predominantly red-brown with some pale ochre. Forewing pale ochre irrorated with fuscous, particularly along costa and on distal half. Hindwing: no costal bristles; broad at base; with a costal hair-pencil (fig. 19) of black scales at base. No other specialised scales on wings. Hindlegs missing.

Venation (fig.19). Forewing: R_4 and R_5 , and M_1 and M_2 represented by terminal branches. Cu continues for a short distance after M diverges to meet R_5 .

Male genitalia (fig.66). Vinculum: anterior extension rounded, not emarginated. Tegumen extended into a pair of small rounded lobes at apex; lobes close together. Uncus strongly bent ventrally, single-lobed. Gnathos rather weakly fused, lateral process joined to form a weakly sclerotised central element. Valva with rounded rather than pointed apex; four prominent setae arise from basal half. Transtilla: transverse bar present. Aedeagus narrow, with small lateral flanges at anterior end; ventral process long, narrow and forked at tip; pair of dorsolateral carinae present. Vesica with minute cornuti.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Natal, Umdoni Park, 23.i.1977, D.M. Kroon, genitalia slide no.10453, wing slide no. 3879; in Transvaal Museum.

The shapes of the valva and the ventral process of the aedeagus are different from those of all other species. *E. umdoniella* is most closely allied to *maritima*, *furcella* and *macrochaeta*. In having a hair-pencil it particularly resembles *furcella*.

Ectoedemia (Laqueus) scabridae spec.nov., figs 20,67,125

ADULT ♂. Wingspan 5,6mm. Head-tuft pale ochre. Forewing grey. Hindwing ?without costal bristles. No specialised scales on wings. Abdomen dark brownish grey.

Venation (fig.20). Forewing: R_{4+5} and M_{1+2} diverge and then the branches split to form R_4 and R_5 , and M_1 and M_2 terminally. Cu continues for a short distance after M diverges to meet R_5 .

Male genitalia (fig.67). Vinculum: anterior extension hardly emarginated, but not rounded. Tegumen rounded at apex, not bilobed. Uncus broad; extended into a pair of small points apically and medially, lateral corners slightly produced. Gnathos fused, resulting central element is of an unusual shape, see figure. Valva with four prominent setae arising from apical (posterior) half. Transtilla: transverse bar present. Aedeagus with a bulb-shaped flange anteriorly; ventral process forked; pair of dorsal carinae present. Vesica with a large tooth, somewhat smaller divided process, and some minute cornuti.

LARVA. Forms a blotch mine (fig.125) on the leaves of *Diospyros ? scabrida* (Ebenaceae).

PUPA. Abdominal terga 2-8 covered with small spines arranged in about five irregular rows on each segment.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Natal, Otterburn, accession no.1213, v.1954, L. Vári, genitalia slide no.9908, wing slide no.3896; in Transvaal Museum.

The species is the only one of this group with grey wings. The forewing venation and the shapes of the gnathos and aedeagus are also unique.

Ectoedemia (Laqueus) jupiteri spec.nov., fig.68

ADULT ♂. Wingspan 5,2mm. Head-tuft pale ochre. Forewing pale ochre, about 50% irrorated with fuscous. Hindwing without costal bristles. No specialised scales on wings. Abdomen brownish grey.

Venation. As *guerksiae*, above. Forewing: R_4 is a barely visible spur.

Male genitalia (fig.68). Vinculum: anterior extension rounded, not emarginated. Tegumen extended into two lateral processes. Uncus tapers to a narrow, truncated apex, which is weakly divided. Gnathos reduced to a narrow band, central element hardly represented. Valva narrow; a few prominent setae arise from near inner edge of valva about halfway down. Transtilla: horizontal bar present; ventral arms extend broadly down from dorsal aspect of base of valvae. Aedeagus terminates anteriorly as a large flange, which is expanded laterally; ventral process divided, but not strongly, at tip; no other carinae. Vesica with prominent curved process near phallosome.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Blydepoort, 25-29.x.1976, Scholtz & Scoble, genitalia slide no.10286, hindleg slide 3914; in Transvaal Museum. Paratype: Northern Transvaal, near Pietersburg, Hanglip Forestry, 1♂ 3.ii.1976, D.M. Kroon; in Transvaal Museum.

The shapes of the tegumen, uncus, gnathos, valva and transtilla are characters by which this species may be recognised.

The name of the species is indirectly derived from the locality from which the holotype was collected. *Blyde* is an Afrikaans word meaning 'joy'. Jupiter is the planet of jolity in Holst's Planet Suite.

Other species in the subgenus

Ectoedemia (Laqueus) royenicola (Vári) comb. nov., figs 5, 21, 69

Stigmella royenicola Vári, 1955:335.

Comments additional to those of Vári (1955).

ADULT. ♂,♀. Wingspan 5,2-6,0mm. Maxillary palpus: fourth segment much enlarged in male (fig.5), and bears a group of long scales, which arise from an oval patch. No specialised scales on wings.

Venation (fig.21). Forewing: R_4 and R_5 present as terminal branches; M unbranched. Cu with persistent trachea extending almost to edge of wing after M diverges to R_5 .

Male genitalia (fig.69). Vinculum: posterior margin of ventral plate convex; anterior extension weakly emarginated anteriorly. Tegumen tapers to a single lobe (not with lateral lobes, see Vári 1955:335). Uncus in shape of a well-sclerotised inverted V with a pair of lateral lobes. Valva broad, but differs in shape from next species (compare figures). Aedeagus: ventral process composing a pair of long spines joined to form a common base; pair of lateral carinae present. Vesica with some prominent spines.

Female genitalia (Vári 1955:fig.18). Below the ring-like markings on the ductus there is a poorly-defined pectinate area.

LARVA. Mines the leaves of *Diospyros whyteana* (Ebenaceae). The mine is characteristic, see Vári (1955) and the comments below.

MATERIAL EXAMINED. The type-series (from Hennops River, Pretoria District), cited by Vári (1955:336); in Transvaal Museum except for one paratype in British Museum (Natural History) and one in Museum für Naturkunde der Humboldt Universität, Berlin (not examined).

Other material. SOUTH AFRICA: Transvaal, Hennops River, 6♂, 9♀ September, October; Pretoria, 14♂, 11♀ September, October, November; all collected by L. Vári; in Transvaal Museum.

Subsequent to the description of *royenicola*, Dr Vári has reared a large number of specimens mining the leaves of *Euclea* (also Ebenaceae). Whilst I have been unable to distinguish the specimens reared from *Diospyros* (i.e. *royenicola*) from those reared from *Euclea* on adult structure, the mines made by the larvae are different. In the specimens reared from *Euclea* the mine is long in the early stage, but not as narrow as that on *Diospyros*, and the blotch of the former is a gradual expansion of the linear section of the mine whilst in the latter it appears suddenly and is definitive. The moths are therefore not identified as *royenicola*, and may represent a new species.

Ectoedemia (Iaqueus) nigrisquama spec.nov., fig.70

This species is closely allied to *royenicola*. The following characters are diagnostic.

ADULT ♂. Wingspan 5,6-6,0mm. Maxillary palpi with fourth segment only slightly enlarged, and without patch of long scales. Forewing: proximal half of ventral surface covered with black specialised scales. Hindwing: expanded; proximal half of dorsal surface, and anal edge of ventral surface, with black, specialised scales.

Male genitalia (fig.70). Uncus: projected into a weakly sclerotised point on each side, not flanged like *royenicola* (compare figures). Valva broader than *royenicola*, subquadrate.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Pretoria, 14.ix.1952, L. Vári, genitalia slide no.6827; in Transvaal Museum. Paratypes: Pretoria, 1♂ 4.ix.1956, 2♂ 9.ix.1956, L. Vári; in Transvaal Museum.

Ectoedemia (Laqueus) denticulata spec.nov., figs 22,71,109,126

The strong ventral process of the male genitalia, and the host-plant of the larva demonstrate the affinity of this species to the preceding members of the subgenus.

ADULT ♂, ♀. Wingspan 5,0-6,0mm. Head-tuft off-white to very pale ochre with a few reddish brown hairs mixed in on the top of the head in some males. Antenna expanded slightly towards tip in male. Galeae extend beyond labial palpi; but not long. Forewing a mixture of fuscous and pale ochre, predominantly fuscous in most specimens. Hindwing male: costal bristles absent; a thickening is situated on trunk of R_5+M (fig.22); long yellowish scales form a hair pencil from base of wing on dorsal surface; female without these characters. Abdomen grey.

Venation (fig.22). Forewing: R_4 , R_5 , M_1 and M_2 all represented terminally. Cu continues for a short distance after M diverges to meet R_5 , or is never separate from M.

Male genitalia (fig.71). Vinculum: anterior extension not emarginated, or only weakly so. Tegumen terminates in a single, narrow lobe. Uncus: a well-developed caudal band, not bilobed. Gnathos with prominent central element. Valva rather small with an inwardly-directed projection near apex. Transtilla: transverse bar present; ventral arms long. Aedeagus surrounded by a glove-like annellus which is covered with denticles; ventral process well-sclerotised narrow, weakly bifid; no lateral carinae. Vesica unmarked except for striate thickening around base of ejaculatory duct.

Female genitalia (fig.109). Anal papillae form a fairly broad end to abdomen. Ductus bursae with sclerites forming an incomplete ring below which is a poorly defined pectinate area. Corpus bursae without signa reticulata.

LARVA. Forms a blotch mine (fig.126) in the leaves of *Diospyros glabra* (Ebenaceae). The mine is easy to recognise since the epidermal layer of the leaf becomes stained, which leaves a black spot surrounded by a pale periphery. The frass is tightly packed in the central area and sparse around

this area. The egg is laid on the lower epidermis in the centre of the mine.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA, Cape Province, Jonkershoek, accession no.2536, 16.x.1962, L. Vári, genitalia slide no.9848; in Transvaal Museum. Paratypes: data as holotype, 12♂, 9♀ 16,17,19,22.x., 5.xi.1962, L. Vári; Worcester, Fairy Glen 1♂ 15 and 19.x.1966, Vári & Potgieter; Paarl District, Du Toits Kloof, 1♂ 16 and 22.x.1966, Vári & Potgieter; Clanwilliam District, Algeria Forestry, 3♂, 1♀ 4-10.iii.1969; Tulbagh District, Kluitjieskraal Forestry, accession no.3762, 7♂, 8♀ 2, 3,4,5,8,15,17,18,19,22.x.1979, H. Geertsema; in Transvaal Museum.

The denticulate marks on the anellus, and the shape of the valva in the male genitalia are characters useful for the recognition of this species. In the female the absence of signa reticulata is rare in the Trifurculini.

Ectoedemia (Laqueus) undatae spec.nov., figs 23,72,110

ADULT ♂, ♀. Wingspan 5,4-6,0mm. Head-tuft red-brown. Forewing pale ochre irrorate with fuscous. Male with large patch of black, specialised scales on ventral surface, absent in female. Hindwing: in male slightly broadened at base, with specialised black scales covering most of dorsal surface, some are present on ventral surface along costal and anal edges. No costal spines in male. Abdomen grey.

Venation (fig.23). Forewing: R_{4+5} , and M_1 and M_2 present as terminal branches. Cu fairly long.

Male genitalia (fig.72). Vinculum: rather elongate; anterior extension not excavated. Tegumen extended into a single lobe. Uncus with a pair of small lateral lobes. Gnathos with a well-defined central element. Valva bulging inwardly. Transtilla: transverse bar present; ventral arms fairly long. Aedeagus long and broad; ventral process long, narrow, forked at tip; no other carinae. Vesica with a few large spines at phallosome and some minute denticles.

Female genitalia (fig.110). Anal lobes form a blunt, fairly broad end to abdomen. Ductus bursae with a large sclerite. Corpus bursae with a pair of elongate, reticulate signa.

LARVA. Records give a tentative identification of the host-plant as *Maytenus undata* (Celastraceae), but no mines have come to light so the record remains in doubt.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Pretoria District, Saartjiesnek, accession no.2312, 3.x.1961, L. Vári, genitalia slides no.9923; in Transvaal Museum. Paratypes: data as holotype, 2♀ 2,3.x.1961, L. Vári; in Transvaal Museum.

The shapes of the male genital capsule, valva, aedeagus, and ventral process are characteristic. The ventral process resembles that structure in *denticulata*, and in the group of *Diospyros*-feeding species. The valva lacks the inwardly directed process of *denticulata* but otherwise resembles the structure in that species.

Ectoedemia (Laqueus) bicarina spec.nov., figs 24,73

ADULT ♂. Wingspan 5,6-5,8mm. Head-tuft ochre. Forewing: holotype pale ochre irrorate with pale fuscous; paratype grey-brown; large patch of yellowish specialised scales on ventral surface. Hindwing: patch of yellowish specialised scales on dorsal surface; no costal spines present. Abdomen grey.

Venation (fig.24). Forewing: R_{4+5} and M_1 and M_2 present as terminal branches. Cu weak but long, extends almost to edge of wing.

Male genitalia (fig.73). Vinculum: anterior extension not emarginated. Tegumen extended into a single lobe. Uncus with small lateral flanges. Gnathos: lateral elements rather weakly sclerotised and broad. Valva bulges inwardly; ventral, outer corner extended into a long anteriorly directed apodeme. Transtilla: transverse bar indistinct. Aedeagus: ventral process narrow, divided at tip; a pair of prominent lateral forked carinae arises dorsally. Vesica with two sharp spines extending beyond phallosome, and some minute cornuti.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Cape Province, Cape Peninsula, Hout Bay, 10-15.xi.1954, L. Vári, genitalia slide no.10125, wing slide 3877; in Transvaal Museum. Paratype: Stormsrivierbrug, 1♂ 6-7.iii. 1972, L. & G. Vári, in Transvaal Museum.

The shape of the valva and the presence of its associated apodeme, and the forked dorsolateral carinae are characteristic of this species. The male genitalia demonstrate that the species is allied to *denticulata* and *undatae*.

Ectoedemia (Laqueus) craspedota (Vári) comb.nov., figs 25,74
Stigmella craspedota Vári, 1963:73.

Information additional to the original description follows.

ADULT. Hindwing of male without costal spines.

Venation (fig.25). Forewing: R_{4+5} and M_{1+2} present as terminal branches. Cu does not extend far beyond point at which M diverges to R_s .

Male genitalia (fig.74). Uncus with a pair of narrow, lateral lobes. Aedeagus: ventral process (called juxta by Vári) fairly small, narrow, weakly divided at tip; a pair of small lateral digitate carinae are visible. Vesica with a prominent, thick, curved spine, a few irregular thickenings, and several denticulate cornuti.

Female genitalia (Vári 1963: fig.10). Ductus bursae with complex, heavy sclerotisations roughly in form of a ring.

LARVA. Forms an elongated blotch mine on the leaves of *Maytenus undata* (Celastraceae) see Vári (1963).

MATERIAL EXAMINED. The type-series (from Plettenberg Bay, Knysna District, Cape Province), cited by Vári (1963:74).

The valvae most closely resembles those of *undatae*, and the shape of the aedeagus and digitate processes are like those of *digitata* and *limburgensis*. Details of the male genitalia provide the best way of distinguishing *craspedota*.

The host-plant of *craspedota* (*Maytenus undata*) is the same as *undatae*.

Ectoedemia (Laqueus) digitata spec.nov., figs 26,75

ADULT ♂. Wingspan 5,0mm. Head-tuft mostly lost, what remains is off-white. Forewing grey. Hindwing: very narrow scales, rather than spines, on costa. No specialised scales on wings. Abdomen silvery grey.

Venation (fig.26). Forewing: R_1 and R_5 , and M_1 and M_2 present as terminal branches. Cu not long, but extends slightly beyond point at which M diverges to meet R_5 .

Male genitalia (fig.75). Vinculum: ventral plate with a shallow emargination along caudal margin; anterior extension hardly emarginated. Uncus extended into a single, rounded lobe. Uncus pointed apically, arms fairly broad. Gnathos with a well-developed central element. Valva approximately triangular with many short setae arising from various parts. Transtilla: transverse bar present; ventral arms relatively long. Aedeagus broad; ventral process narrow, divided at tip; pair of lateral, digitate carinae present. Vesica with few spines near phallosome.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Pretoria North, 9.ii.1954, L. Vári, genitalia slide no.10022, wing slide no.3872; in Transvaal Museum.

The paired, lateral digitate processes are characteristic of this species, as is the weakly excavated posterior edge of the ventral plate of the vinculum. The strong ventral process is similar to that structure in the preceding species of the subgenus.

Ectoedemia (Laqueus) limburgensis spec.nov., figs 27,76

ADULT ♂. Wingspan 5,2mm. Head-tuft pale ochre. Forewing pale ochre irrorate with fuscous. Hindwing with costal spines present. No specialised scales on wings. Hindlegs missing. Abdomen grey.

Venation (fig.27). Forewing: R_4 represented by a short spur terminally, R_5 present; M unbranched (M_{1+2}). Cu continues weakly after M diverges to R_5 . R_4 and R_5 , and M_{4+5} present as terminal branches.

Male genitalia (fig.76). Vinculum: ventral plate with a slight depression in middle of posterior margin; anterior extension not emarginated. Tegumen extended into a single lobe. Uncus without lateral lobes. Gnathos with prominent central element. Valva approximately flask-shaped. Transstilla: transverse bar present. Aedeagus broad posteriorly; ventral process narrow with characteristic shape at tip (see figure); pair of lateral digitate carinae present. Vesica with a few minute, inconspicuous, denticulate cornuti.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Potgietersrus District, Limburg, 19-21.xi.1968, L. Vári, genitalia slide no.10305, wing slide no.3874; in Transvaal Museum.

The digitate carinae resemble those of *digitata* but the shape of the valvae, and other features of the male genitalia differ. The form of the ventral process allies the species to the previous members of the subgenus treated above.

Ectoedemia (Laqueus) subnitescens (Meyrick) comb.nov., figs 28,77

Trifurcula subnitescens Meyrick, 1937:90.

Nepticula subnitescens Meyrick; Janse, 1948:176.

Described by Meyrick (1937) and Janse (1948). The following comments are additional to those descriptions; the genitalia are redescribed.

ADULT ♂. Wingspan 8,2mm. No specialised scales on wings. Hindwing with costal spines present.

Venation (fig.28). Forewing: R_4 and R_5 , and M_1 and M_2 present as terminal branches. Cu long.

Male genitalia (fig.77). The genitalia of the only male specimen are damaged (see photograph of Janse 1948:plate 91, fig.1) and so the figure here is a reconstruction. Vinculum: anterior extension not emarginated. Tegumen extended into a single lobe. Uncus unremarkable. Gnathos with well-developed central element. Valva broad, rounded apically. Transtilla: transverse bar probably absent, may have been lost when right valva was removed. Aedeagus: ventral process narrow, divided at apex, broadly fused at base to aedeagus. Vesica: two spines present at phallosome probably associated with vesica, no denticulate cornuti; striate thickening around base of ejaculatory duct is pulled up to near phallosome in this specimen.

MATERIAL EXAMINED. ♂-Lectotype (from East London, Cape Province) here designated. It is the male of Meyrick's two syntypes and bears the following label data: 'E. London, Cape Prov. Oct. 1925, H.K. Munro; M335; G. [genitalia slide] 4185; [wing slide] 3910; *Trifurcula subnitescens* M. Type No.956.' In Transvaal Museum. The large brown cocoon is attached to the block of pith on which the moth is mounted.

This is a large nepticulid. The shape of the valva is characteristic. The prominent ventral process allies the species to the members of the subgenus described above.

The female paralectotype (not examined) is in the British Museum (Natural History).

Ectocdemia (Laqueus) capensis spec.nov., figs 29,78,111

ADULT ♂, ♀. Wingspan 6,2-9,0mm. Head-tuft orange-ochre to ochre. Antenna rather long, extends just under length of forewing. Galeae slightly longer than labial palpi but not long. Forewing grey with a mottled appearance due to the dark tips of the scales. Hindwing: costal spines not present in male. No specialised scales on wings. Abdomen grey.

Venation (fig.29). Forewing: R_4 and R_5 , and M_1 and M_2 represented by terminal branches. Cu extends nearly to wing margin.

Male genitalia (fig.78). Vinculum: anterior extension weakly emarginated. Tegumen extends into a single lobe. Uncus with a pair of prominent lateral lobes. Gnathos with fairly broad dorsolateral elements. Valva subquadrate in inner view. Transtilla: transverse bar present; ventral arms long. Aedeagus with complex sclerotisations, a pointed ventral process is present although it is difficult to distinguish from the other carinae; other carinae include a strong spine fixed to one side of aedeagus, and a pair of dorsolateral forked structures. Vesica with two long, well-sclerotised spines at phallosome, and a patch of denticulate cornuti.

Female genitalia (fig.111). Anal papillae elongate so forming a narrow, truncated end to abdomen. Apophyses relatively long. Ductus bursae with strong sclerotisations approximately forming a ring, and a pectinate patch. Corpus bursae with pair of long, narrow signa reticulata, the reticulations of which are rather weak.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Cape Province, Cape Peninsula, Hout Bay, 10-15.xi.1954, L. Vári, genitalia slide no.7275; in Transvaal Museum. Paratypes: 1♂, 4♀ data exactly as holotype; locality (spelled 'Houtbaai' on labels) as holotype, 4♂, 1♀ 21.x.1965, L. Vári; Cape Town, Kirstenbosch 3♂, 1♀ 5-29.xii.1954, A.J.T. Janse; central Cape Coast, Knysna, Sourflats, 1♂ 22-24.xi.1954, L. Vári.

Most of the specimens are large compared with nepticulids in general. In the male the shape of the ventral process of the aedeagus is characteristic and so is that of the valva. The form of the anal papillae is a

useful diagnostic character for the female. Although *capensis* is of about the same size as *insulata*, p.94, the colour of the forewings is different.

Ectoedemia (Laqueus) gymnosporiae (Vári) comb.nov., figs 30,79

Stigmella gymnosporiae Vári, 1955:334

Information additional to the original description. The male genitalia are fully redescribed.

ADULT ♂, ♀. Antenna: first few flagellar segments filiform, rest approximately moniliform. Compound eye slightly reduced, but not very small. Galeae extend about as far as labial palpi. Hindwing of male with costal spines present. No specialised scales on either wing.

Venation (fig.30). Forewing: R_4 and R_5 , and M_1 and M_2 represented by separate branches terminally. Cu does not extend beyond point at which M meets R_5 .

Male genitalia (fig.79). Vinculum: anterior extension emarginated; lateral arms with pair of lateral sclerites (arrowed in figure) not same shape as the support rods in *Microcalyptris* and *Niepeltia*. Tegumen extended into a single, pointed structure. Uncus narrows towards apex, but is expanded at that point, and with a pair of very narrow lateral lobes. Gnathos with central element broad and rounded, not pointed. Valva approximately triangular, margin at base thickened. Transtilla: transverse bar absent. Aedeagus narrow at base, broadening to phallosome; ventral process in form of a pair of long processes united at base where they arise from aedeagus; a pair of lateral carinae are present. Vesica with a complex of long spines that extend beyond phallosome, and some minute denticulate cornuti.

Female genitalia (Vári 1955: fig.17). Ductus bursae with strong sclerotisations approximately in form of a ring. Corpus bursae with reticulations of elongate signa reticulata weak.

LARVA. Forms a linear mine in the leaves of *Maytenus heterophylla* (= *Gymnosporia buxifolia*) (Celastraceae), for further details and an illustration see Vári (1955).

PUPA. Terga 2-8 of abdomen covered with small spines.

MATERIAL EXAMINED. The type-series (from Hennops River, Pretoria District, and Hartebeespoort Dam, Brits District), cited by Vári (1955:334); in Transvaal Museum, except for one paratype in British Museum (Natural History), and one in Museum für Naturkunde der Humboldt Universität, Berlin, (not examined).

Other material. SOUTH AFRICA: Transvaal, Pretoria District, Hartebeespoort Dam, accession no.1540, 1♀ 24.ii.1955; in Transvaal Museum.

The form of the ventral process, and the shapes of the valvae and aedeagus are characteristic. The irregular margin of the signa reticulata in the female is also unusual.

Ectoedemia (Laqueus) psarodes (Vári) comb.nov., figs 31,80
Stigmella psarodes Vári, 1963:70.

Information additional to the original description follows.

ADULT ♂. Hindwing of male without costal spines.

Venation (fig.31). Forewing: R_4 (a short spur) and R_5 , and M_1 and M_2 represented by branches terminally. Cu continues very weakly for a short distance after M diverges to meet R_5 .

Male genitalia (fig.80). Vinculum: anterior extension hardly excavated. Tegumen extends into a knob-like structure, unilobed. Uncus: apex truncated, and with a pair of lateral flanges. Gnathos: central element not large. Valvae fairly narrow, with short inwardly-pointing process at apex. Transtilla: transverse bar absent. Aedeagus: ventral process in form of a pair of long central spines arising from common base, a smaller lateral spine is fused with each of the central spines; a pair of dorsolateral carinae present. Vesica with a long spine that extends beyond phallos-treme, and a few poorly-defined minute cornuti.

LARVA. A miner on *Maytenus undata* (Celastraceae) see Vári (1963) for details and an illustration.

MATERIAL EXAMINED. The ♂-Holotype (from Louis Trichardt, Transvaal), which is the only specimen of this species known, cited by Vári (1963); in Transvaal Museum.

The form of the ventral process of *psarodes* bears some resemblance to that of *gymnosporiae*, but the additional lateral processes of the aedeagus in *psarodes* distinguishes that species. In both species the transtilla lacks a transverse bar, and the uncus is truncated at the tip. The shape of the gnathos, valvae and aedeagus are features by which the two species may easily be distinguished.

Ectoedemia (Laqueus) insulata (Meyrick), comb. nov., figs 6, 32, 81, 112
Nepticula insulata Meyrick, 1911b:79.
Nepticula insulata Meyrick; Janse, 1948:169.

Meyrick (1911) originally assigned the species to the Tineidae, although he put it in the genus *Nepticula*. Since Meyrick's description, from a single female, several more females have been collected, and recently a single male.

ADULT ♂,♀. Wingspan 7,6-9,2mm. Head-capsule (fig.6). Head-tuft orange-ochre. Galeae very long, over four times length of labial palpi, approximately twice as long as head-capsule. Forewing pale ochre tinged with copper, with fuscous scales along costa, particularly at base of wing, and a light scattering of fuscous-tipped scales near apex; some specimens have hardly any fuscous. Hindwing of male without costal spines. No specialised scales on either wing. Abdomen grey.

Venation (fig.32). Forewing: R_4 and R_5 , and M_1 and M_2 represented by branches terminally. Cu does not continue separately after M meets R_5 .

Male genitalia (fig.81). Vinculum: rather elongate; anterior extension very weakly emarginated. Tegumen extends into a single, fairly pointed lobe. Uncus truncated and slightly emarginated at apex, with narrow lateral flanges. Gnathos unremarkable. Valva approximately rectangular in ventral view. Transtilla: transverse bar not present, but replaced by a broad membrane joining the valvae. Aedeagus narrow: ventral process narrow, not forked at apex; lateral carinae of a similar shape to ventral process, but less strongly sclerotised. Vesica: cornuti absent.

Female genitalia (fig.112). Last segment, together with both apophyses, attenuated to form a pointed ovipositor, very long for a nepticulid. Anterior apophyses longer than posteriores. Ductus bursae unsclerotised. Corpus bursae without signa.

MATERIAL EXAMINED. ♀-Holotype, SOUTH AFRICA: Transvaal, labelled 'Woodb. Vill. [Woodbush Village], 13.xii.1909, C.J. Swierstra; G. [genitalia slide] 7259; *Nepticula insulata* Meyr. ♀ Type No.2377'; a further

handwritten label adds '*Nepticula insulata* Meyr. Type, C.J.Sw.'; in Transvaal Museum.

Other material. SOUTH AFRICA: Transvaal, Marieps Mnt. [Mariepskop], 6♀ December, G. van Son; Soutpansberg, Tshakoma, 1♀ November, G. van Son; Blyde River Nature Reserve, 1♂, 8♀ October, Scoble & Scholtz; in Transvaal Museum.

The long galeae are visible on the dried specimen, as noted by Meyrick (1911b). No other nepticulid known to me has a proboscis that nears this length. The pointed ovipositor is also exceptionally long for a nepticulid. The female is further remarkable in the absence of markings on the ductus and corpus. In lacking *signa reticulata* it resembles *denticulata* in this subgenus, but other features are quite different. These characters, together with the relatively large size of the moth and the cupreous tinge of the forewings, are useful for distinguishing the female of this species.

The narrow aedeagus is probably correlated with the very narrow ovipositor, a feature helpful in identifying the light-captured specimen as a male of *insulata*, a species previously known only from the female. The lateral carinae, and the wing colour further help to distinguish the male from any other nepticulid.

The presence of an anal loop in the forewing, and of a ventral process resembling that of several other species dealt with above, determined the placement of *insulata* in the subgenus *Laqueus* even though the species has a number of aberrant features. The absence of markings from the ductus bursae, and *signa* from the corpus are interpreted as secondary losses.

Ectoedemia (Laqueus) kowynensis spec. nov., figs 7, 33, 82, 127

ADULT ♂. Wingspan 4,4-5,4mm. Head-tuft orange-ochre. Head-capsule (fig.7) rather flattened dorso-ventrally. Compound eye reduced, but not very small. Galeae very short hardly extending as far as do labial palpi. Forewing fuscous, bases of scales often pale, which gives wing a weakly mottled appearance. Hindwing: costal bristles present in male. No specialised scales on wings. Abdomen very dark grey.

Venation (fig.33). Forewing: R_4 and R_5 present as separate branches terminally; M unbranched. Cu extends beyond point at which M diverges to meet R_5 .

Male genitalia (fig.82). Vinculum: anterior extension very weakly excavated. Tegumen tapers to a single lobe. Uncus unremarkable. Gnathos with a very broad, triangular central element. Valva bulbous inwardly, at base. Transtilla: transverse bar absent; ventral arms fairly long. Aedeagus: ventral process rather broad, divided at tip, not very strongly sclerotised; dorsally a pair of large carinae are present, which are produced into short spinose processes at their tips.

LARVA. Forms a linear mine (fig.127) on *Maytenus peduncularis* (Celastraceae). In nearly all of the many specimens examined, the larva mines approximately in a circle of variable diameter; the end of the tract almost meets the beginning but passes inside.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Kowyn's Pass, accession no.3689, 12.vii.1977, J.H. Potgieter, genitalia slide no.10546; in Transvaal Museum. Paratypes: data as holotype, 17♂ 27.vi., 5,7,10,12, 14,18,20,22,25.vii.1977, J.H. Potgieter; in Transvaal Museum.

The shapes of the gnathos and of the bulbous valvae of the male genitalia are characteristic. The ventral process is not easy to see, and it is of a different shape from that found in other species which have one. It is best seen by examining the aedeagus in lateral view.

Ectoedemia (Laqueus) nylstroomensis spec.nov., figs 34,83

ADULT ♂. Wingspan 5,2mm. Head-tuft orange-ochre. Forewing pale ochre with a few fuscous irrorations on distal half. Hindwing: costal spines absent. No specialised scales on wings. Abdomen dark grey.

Venation (fig.34). Forewing: R_4 and R_5 and M_1 and M_2 represented by terminal branches. Cu meets R_5 together with M. (A persistent trachea—arrowed in figure—of Cu runs from the fold to meet M in the only known specimen of this species.)

Male genitalia (fig.83). Vinculum: anterior extension very weakly excavated. Tegumen extended into a single lobe. Uncus with a pair of small, lateral flanges. Gnathos: central element not large. Valva approximately triangular. Transtilla: transverse bar absent. Aedeagus wide; ventral process broad, irregularly divided at apex; pair of small dorsolateral processes present. Vesica with a prominent, digitate sclerite, and other poorly-defined thickenings.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Nylstroom, 1.ii.1972, D.M. Kroon, genitalia slide 10270, wing slide 3873; in Transvaal Museum.

The shapes of the ventral process of the aedeagus, and the digitate sclerite on the vesica are characteristic.

Ectoedemia (Laqueus) rhabdophora spec.nov., figs 35,84,128

ADULT ♂. Wingspan 4,4-5,0mm. Tuft on front of head dull ochre, tuft on vertex mostly dark, dull ochre. Forewing pale ochre irrorated with fuscous. Hindwing: costal spines present. No specialised scales on wings.

Venation (fig.35). Forewing: R_{4+5} , and M_1 and M_2 represented by branches terminally. Cu meets R_S together with M.

Male genitalia (fig.84). Vinculum: ventral plate with caudal edge thickened centrally; anterior extension hardly emarginated. Tegumen extended into a single, blunt lobe. Uncus without lateral flanges. Gnathos with central element not pointed. Transtilla: transverse bar absent. Valva: shape unique, divided longitudinally, ventral part approximately L-shaped, dorsal component attenuated into a very long apodeme. Aedeagus: ventral process absent; a pair of long, narrow dorsolateral carinae are present. Vesica with some minute denticulate cornuti.

LARVA. Mines the leaves of *Maytenus heterophylla*. The mine (fig. 128) is a long gallery, which expands suddenly into a broader tract.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Natal, Umhlanga Rocks, accession no.2934, 18.vii.1968, L. Vári, genitalia slide no.9871, wing slide no.3854; in Transvaal Museum. Paratype: Transvaal, Pretoria, 1♂ ix.1952, accession no.537, L. Vári, in Transvaal Museum.

The species is easily recognised by the divided valva together with the very long apodeme associated with it. Although the anal loop in the forewing is present, the ventral process is absent and the affinities of the species are not clear. The long apodeme associated with the valva resembles that found in *Obrussa*, but the way it is attached to the valva is quite different. *E. rhabdophora* shares none of the other characteristic features of *Obrussa*.

Ectoedemia (Laqueus) crispae spec.nov., figs 36,85,113,129

ADULT ♂, ♀. Wingspan 5,6-7,6mm. Head-tuft pale to medium dark orange-ochre sometimes tinged with red-brown. Galeae extend beyond labial palpi but not far beyond. Forewing pale ochre lightly to very heavily irrorated with fuscous. Hindwing: no costal spines in male. No specialised scales on wings. Abdomen grey.

Venation (fig.36). Forewing: R_{4+5} , and M_1 and M_2 represented by terminal branches. Cu continues weakly after point at which M diverges to R_5 .

Male genitalia (fig.85). Vinculum: anterior extension hardly emarginated. Tegumen tapers to a single point. Uncus with a pair of small lateral flanges. Gnathos: central element broad at base. Valva very narrow. Transtilla: transverse bar absent. Aedeagus: ventral process absent; pair of short, lateral carinae dorsally. Vesica with several large spines.

Female genitalia (fig.113). Anal papillae form a relatively broad end to abdomen. Apophyses fairly short. Ductus bursae with complex sclerotisations, including a patch of denticles. Corpus bursae with a pair of long, narrow signa reticulata, the reticulations of which are weak.

LARVA. Mines the leaves of *Euclea crispa* (Ebenaceae). The mine (fig. 129) begins as a narrow gallery and then broadens gradually to form a wide gallery.

PUPA. Spines on terga 2-8 long and numerous, almost covering each segment.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Pretoria, accession no.370, 9.ix.1951, L. Vári, genitalia slide no.10547; in Transvaal Museum. Paratypes: data as holotype 12♂, 12♀ 9,12,13,15,16,18,19, 20.ix., 11.x., 26.xi.1951, L. Vári; accession no.180, 1♂ 30.ix.1949, L. Vári; accession no.348, 7♂, 10♀ 29,viii., 4,9,16,20,22,29.ix., 7.x., 13, 18.xi.1951, 17.iii., 16,27.v.1952, L. Vári; accession no.361, 1♂ 9.ix.1951, L. Vári; accession no.3297 1♂, 1♀ 20.viii., 3.ix.1974, L. Vári; accession no.3450, 7♀ 13,22,25,29.viii., 12.ix.1975, L. Vári; accession no.3604,

2♂, 5♀ 18.vii., 20,27.viii.1976, L. Vári; Suikerbosrand, 1♂ 17.iii.1978, D.M. Kroon; in Transvaal Museum.

E. crispae bears little resemblance to the other species in the subgenus except that the anal loop is present in the forewing. The ventral process of the aedeagus is absent, and the cornuti are quite different from other species since they are large and quite numerous; the valvae are very narrow. The sclerotisations on the ductus bursae are unique, and are dissimilar to the usual ring-shaped sclerite.

Subgenus *FOMORIA* Beirne

Genus *Fomoria* Beirne, 1945:208; Wilkinson, 1979:82. Type-species: *Nepticula weaveri* Stainton, 1855:49, by original designation.

The two European species (*weaveri* and *septembrella*) originally included in *Fomoria* by Beirne (1945) are very closely allied; the wing venation is identical and the genitalia are similar in detail. In general the species resemble many others from elsewhere and so Beirne's original concept of *Fomoria* is expanded. This approach is an extension of that of Wilkinson (1979) who transferred two North American species to *Fomoria* from *Nepticula* (= *Stigmella*) and broadened the definition of the genus.

An uncus is always present and this distinguishes *E. (Fomoria)* from *E. (Ectoedemia)*. In contrast to *E. (Laqueus)* there is no anal loop in the forewing of *E. (Fomoria)*.

Comments on *weaveri* (Stainton) and *septembrella* (Stainton), (European).

The hindwing of the males have costal bristles. The proximal pair of spurs on the hindtibia are below the midpoint.

Forewing venation. Borkowski (1972:fig.14) illustrated that of *septembrella*. The pattern is the same for both that species and *weaveri*. R_4 and R_5 , and M_{1+2} are represented by terminal branches. Cu never runs independent of M.

Male genitalia. The ventral plate of the vinculum is extended posteriorly and is linked to the aedeagus. Beirne states that the ventral plate 'is continuous with a large juxta, which is produced into a pair of heavily-sclerotised anellus lobes'. These 'anellus lobes' are carinate processes of the aedeagus. I can find no sclerotised plate and the term juxta is probably not appropriate. The 'pair of heavily-sclerotised, outwardly curving spines' referred to by Beirne are dorsal, carinate processes of the aedeagus, not 'situated *between* the transverse bar and the aedeagus' (my emphasis). The transverse bar of the transtilla is strongly curved.

Female genitalia. The ductus bursae bears strong sclerotisations of a form resembling many other species of *Ectoedemia*. The corpus bursae has a pair of signa reticulata.

MATERIAL EXAMINED. *Ectoedemia (Fomoria) weaveri* (2♂, 1♀), *Ectoedemia (Fomoria) septembrella* (2♂, 2♀).

Ectoedemia (Fomoria) oleivora (Vári) comb.nov., figs 37,86
Stigmella oleivora Vári, 1955:336.

Information additional to the original description. The genitalia are redescribed.

ADULT ♂, ♀. Galeae extend to about length of labial palpi. Antenna: flagellar segments longer in female than in male. Hindwing: costal spines present in male. No specialised scales on wings. Wings densely covered with aculei.

Venation (fig.37). Forewing: R_4 and R_5 , and M_1 and M_2 represented by branches terminally. Cu never separate from M, a persistent trachea runs with that of M to R_5 .

Male genitalia (fig.86). Vinculum: anterior extension hardly excavated. Tegumen extended into a blunt lobe. Uncus unremarkable. Gnathos: central element prominent. Valva narrow apically, broader basally in ventral view. Transtilla: transverse bar present. Juxta present, in form of a pair of connected lateral thickenings of anellus, not bound firmly to vinculum. Aedeagus: ventral process is a spine-like extension of the aedeagus; pair of lateral carinae present. Vesica with several large spines.

Female genitalia (Vári 1955: fig.19). Anal papillae form a broad, flat end to abdomen. Ductus bursae with prominent, complex sclerotisations (not 'ostium', Vári 1955:336). Corpus bursae: signa reticulata long, reticulations well-defined, margins irregular.

LARVA. Forms a gallery mine followed by a blotch in leaves of *Olea chrysophylla* (Oleaceae), see Vári (1955) for details and an illustration.

PUPA. Three or four irregular rows of medium-sized spines cover each of terga 2-8.

MATERIAL EXAMINED. The type-series (from Hennops River, Pretoria District), cited by Vári (1955:336); in Transvaal Museum, except for one paratype (not examined) in the British Museum (Natural History).

Other material. SOUTH AFRICA: Transvaal, Pretoria District, Hennops River (type-locality), accession no.3610, 4♂, 2♀ 27.viii.1976, L. Vári; in Transvaal Museum.

The species may easily be recognised by the shapes of the components of the male genitalia see fig.86 - particularly the ventral process and the juxta.

Ectoedemia (Fomoria) pappeivora (Vári) comb. nov., figs 38, 87
Stigmella pappeivora Vári, 1963:68.

Information additional to those of the original description. The genitalia are redescribed.

ADULT ♂,♀. Galeae about length of labial palpi. Male hindwing: with long scale-like hairs near base on costa rather than costal spines; base of wing broader than in female.

Venation (fig.38). Forewing: R_4 a short spur terminally, or coalesced with R_5 . M_1 and M_2 present. Cu does not continue beyond point at which M meets R.

Male genitalia (fig.87). Vinculum: anterior extension not emarginated. Tegumen extended into a short, nipple-like structure posteriorly. Uncus a prominent arch, not pointed at apex. Gnathos unremarkable. Valva: inner edge projected into a point at apex. Transtilla: transverse bar present; ventral arms fairly long. Aedeagus: expanded slightly at base; ventral process extends as a fairly narrow structure, not deeply divided at tip; back (dorsum) of aedeagus extended into a pair of short, pointed carinae. Vesica with a single spine and an additional poorly defined thickening.

Female genitalia (Vári 1963:fig.8). Anal papillae not pointed but not very broad. Apophyses fairly long. Ductus bursae with a relatively small sclerite forming an incomplete ring. Corpus bursae with signa reticulata elongate, well-defined, and bordered.

LARVA. Forms a gallery mine followed by a blotch in the leaves of *Pap-
pea capensis* (Sapindaceae). For details and an illustration see Vári (1963).

MATERIAL EXAMINED. The type-series (from the Hartebeespoort Dam, Brits District, Transvaal), cited by Vári (1963).

Other material. SOUTH AFRICA: Transvaal, Pretoria District, Roodeplaat, accession no.3664, 1♂, 1♀ 14,15.iv.1977, M.J. Scoble; in Transvaal Museum.

The shape of the base (anterior end) of the aedeagus resembles that of *stimulata* and its allies in the subgenus *Laqueus* but the absence of an anal loop in the forewing distinguishes *pappeivora* from all those species. The shape of the valva is characteristic and so is the ventral process of the aedeagus.

Ectoedemia (Fomoria) indicaevora spec.nov., figs 39,88,130

ADULT ♂. Wingspan 5,8mm. Head-tuft off-white. Forewing pale ochre, heavily irrorated with fuscous, a patch of ochre is present on posterior edge postmedially. Hindwing: very narrow scales, rather than spines, arise from costa at base. No specialised scales on wings. Abdomen grey.

Venation (fig.39). Forewing: R_4 and R_5 , and M_{1+2} represented as terminal branches. Cu does not continue beyond point at which M meets R_5 ; either Cu meets R_5 with M or it is absent (interpretation uncertain).

Male genitalia (fig.88). Vinculum: anterior extension hardly emarginated. Tegumen extended into a pointed apex. Uncus: apex bent ventrally in both holotype and paratype. Gnathos not prominent. Valva narrow at tip, broad at base. Transtilla: transverse bar present; ventral arms very short. Aedeagus: ventral process in form of a pair of prominent spines; dorsally aedeagus is extended into a pair of blunt carinae. Vesica unmarked, except for striate thickening surrounding base of ejaculatory duct.

LARVA. Forms a blotch mine (fig.130) on *Flacourtia indica* (Flacourtiaceae). The frass is deposited in a large central mass.

MATERIAL EXAMINED. ♂-Holotype, ZIMBABWE (RHODESIA): Lundi, accession no.1917, 18.v.1956, L. Vári, genitalia slide no.9920, wing slide no. 3853; in Transvaal Museum. Paratype: data as holotype, 1♂ 21.v.1956, L. Vári; in Transvaal Museum.

The male genitalia are quite distinct, and are adequate for the recognition of this species.

Ectoedemia (Fomoria) knysnaensis spec.nov., figs 40,89

ADULT ♂. Wingspan 7,2mm. Head-tuft ochreous. Forewing pale ochre; no specialised scales. Hindwing broad at base; without costal spines; with a small patch of pale ochre, specialised scales near base on ventral surface. Hindlegs missing. Abdomen silvery grey, weakly ribbed.

Venation (fig.40). Forewing: R_4 and R_5 , and M_1 and M_2 represented by terminal branches. Cu continues after M diverges to meet R_5 and then itself curves to almost touch $M+R_5$.

Male genitalia (fig.89). Vinculum: anterior extension hardly excavated. Tegumen narrows to apex. Uncus: apex bent over ventrally; laterally extended into particularly long apodemes that fuse with lateral arms of vinculum. Gnathos: lateral elements curved; central element prominent. Valva strongly curved at apex; inner (dorsal) part extended into a short, curved spine. Transtilla: transverse bar weakly sclerotised; ventral arms broad at origin. Aedeagus rather narrow; ventral process present as a pair of broad, spine-like structures; wall of aedeagus extended laterally into a pair of carinate processes; dorsally (probably an extension of the inner wall and not derived from the vesica) a pair of broad-based spines extend, each into a long process. Vesica unmarked, except for striate thickening that surrounds base of ejaculatory duct.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Cape Province, Knysna, 10-14.i.1955, A.J.T. Janse, genitalia slide no.9963, wing slide no.3881; in Transvaal Museum.

The very long dorsal processes of the aedeagus and the short spine associated with the valva are unique.

The spine of the valva superficially resembles the structure in *Obrussa*, but it is much shorter in *knysnaensis*. No other features characteristic of *Obrussa* are exhibited.

Ectoedemia (Fomoria) lucidae spec.nov., figs 41,90,131

ADULT ♂. Wingspan 5,0mm. Head-tuft ochreous. Forewing dark purplish brown. Hindwing: costal spines absent. No specialised scales on wings. Abdomen brownish grey.

Venation (fig.41). Forewing: R_4 and R_5 , and M_1 and M_2 represented by terminal branches. Cu with a persistent trachea extending fractionally beyond point at which M diverges to R_5 .

Male genitalia (fig.90). Vinculum: anterior extension not excavated. Tegumen narrows rather suddenly to apex. Uncus unremarkable. Gnathos: central element approximately triangular. Valva with medial, inwardly pointed projection. Transtilla: transverse bar present. Aedeagus large; ventral process in form of a pair of spinose extensions; a pair of carinae are present as dorsal extensions of aedeagus. Vesica with some large spines.

LARVA. Mines the leaves of *Halleria lucida* (Scrophulariaceae). The mine (fig.131) is unusual: it begins as an upper surface, possibly epidermal narrow, frass-free gallery and then expands suddenly into a broad, parenchymal gallery with a loose, central frass deposition. This gallery is so contorted that the mine appears like a blotch in some cases. The early narrow gallery is often obscured against the background of the later contorted section of the mine.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Orange Free State, Golden Gate National Park, accession no.2583, 22.ii.1964, L. Vári, genitalia slide no.9921, wing slide no.3851; in Transvaal Museum.

Reference to fig.90 shows that the male genitalia, in particular the valvae, are diagnostic. The shape of the leaf-mine (fig.131) aids identification of this species.

Ectoedemia (Fomoria) tecomariae (Vári) comb.nov., figs 42,91
Stigmella tecomariae Vári, 1955:333.

Information additional to the original description. The genitalia are redescribed.

ADULT ♂. Wingspan 4,4-5,4mm. Hindwing of male without costal bristles.

Venation (fig.42). Forewing: R_{4+5} , and M_1 and M_2 represented as branches terminally. Cu continues almost to anal edge of wing.

Male genitalia (fig.91). Vinculum: anterior extension emarginated although not deeply. Tegumen narrows to a point at apex. Uncus unremarkable. Gnathos: central element pointed. Valva approximately triangular, a strong ridge is present (arrowed in figure). Transtilla: transverse bar present, rather weak; ventral arms fairly long. Aedeagus: ventral process present, deeply divided; dorsolateral carinae present. Vesica with prominent, well-sclerotised spines near phallosome.

LARVA. Mines the leaves of *Tecomaria capensis* (Bignoniaceae). The mine is illustrated and described by Vári (1955:fig.26). It begins as a narrow gallery, which expands into a broader one and becomes so contorted that it resembles a blotch.

MATERIAL EXAMINED. The type-series (from Cape Town and Grahamstown, Cape Province, and Umhlanga Rocks, Natal), cited by Vári (1955:333); in Transvaal Museum.

Other material. SOUTH AFRICA: Natal, Umhlanga Rocks, accession no. 2945, 1♂ 25.vii.1968, L. Vári; in Transvaal Museum.

The species is unlikely to be confused with any other in this work. The shape of the valva is characteristic.

Ectoedemia (Fomoria) myrtinaecola spec.nov., Figs 43,92,114,132

ADULT ♂, ♀. Wingspan 5,0-6,0mm. Tuft on front of head reddish brown, sometimes less dark in female, to ochre; tuft on vertex ochre. Galeae extend about as far as labial palpi. Forewing: a mixture of dull ochre and fuscous giving a mottled appearance, with two dull ochreous, poorly defined postmedial patches. Male with shiny, black specialised scales on basal half of ventral surface, absent in female. Hindwing: male without costal bristles; with black, shiny specialised scales on dorsal surface of proximal half of wing, and as a streak running along the cubital vein for a short distance on ventral surface. Abdomen dark grey; terga in males with shiny, black specialised scales.

Venation (fig.43). Forewing: R_4 and R_5 , and M_{1+2} represented by terminal branches. Cu: a slight indication exists in stained specimens after M diverges to R_5 , but not a persistent trachea.

Male genitalia (fig.92). Vinculum: anterior extension slightly emarginated. Tegumen narrows to a point. Uncus unremarkable. Gnathos: central element broad and rounded. Valva long, narrow, tip extended into a narrow process. Transtilla: transverse bar present. Aedeagus: ventrally left side is extended as a long, well-sclerotised spine; ventral process absent; a pair of dorsolateral carinae are present on each side, one member curved, the other not. Vesica with a patch of spiculate cornuti.

Female genitalia (fig.114). Anal papillae form a broad end to abdomen. Posterior apophyses significantly longer than anteriores. Ductus bursae with complex, characteristic sclerotisations. Corpus bursae with *two pairs* of signa reticulata - one pair long, the other small and rounded and situated at anterior end.

LARVA. Forms a serpentine, gallery mine (fig.132) on the leaves of *Scutia myrtina* (Rhamnaceae).

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Cape Province, Grootvadersbos, accession no.2860, 20.xi.1966, L. Vári, genitalia slide no.10552;

in Transvaal Museum. Paratypes: data as holotype, 6♂, 14♀ 20,21,22,23,24, 28.xi.1966, L. Vári; in Transvaal Museum.

The species may be confused with the new species immediately following because the host-plant, the genitalia, and the mine are similar. The males of *myrtinaecola* bear black, shiny specialised scales on the wings and abdomen whilst those of the next species do not. Differences in the genitalia of the two species are noted below.

The presence of two pairs of signa reticulata on the corpus bursae of this species, and the following, is not found in any other known to me.

Ectoedemia (Fomoria) alexandria spec.nov., figs 93,133

The species is similar to *myrtinaecola* and the comments below include only the differences from that species.

ADULT ♂, ♀. Forewing slightly paler than in *myrtinaecola*. Wings without specialised scales. Abdomen pale grey, without specialised scales.

Male genitalia (fig.93). Gnathos with central element more rounded than in *myrtinaecola*. Aedeagus: ventrally extended into a process with a heavily sclerotised pointed tip, which tends to be associated more with the left side of aedeagus than the right; a pair of prominent, long, curved, carinate spines arises dorsolaterally, which is *attached* to the valvae by part of the membranous anellus but is not *part* of the valvae; a further spine arises mid-dorsally near the phallosome. Other carinae, and markings on vesica approximately as *myrtinaecola*.

LARVA. The mine (fig.133) is shorter than that of *myrtinaecola*. It is contorted in its later stages but is not nearly so markedly serpentine.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Cape Province, Alexandria, Langebos, accession No.1441, 22.xii.1954, L. Vári, genitalia slide no.9886, wing slide no.3802; in Transvaal Museum. Paratypes: 1♀, data as holotype, 19.xii.1954; 1♂, locality as holotype, not reared from larva, 27-29.xi.1954, L. Vári; in Transvaal Museum.

Ectoedemia (Fomoria) leptodictyae spec.nov., figs 44,94,115,134

ADULT ♂, ♀. Wingspan 4,0-5,6mm. Head-tuft orange-ochre rarely reddish brown. Galeae short, but extend beyond tips of labial palpi. Forewing ochre, heavily irrorated with fuscous; male generally darker than female with some overlap in degree of irroration between the sexes. Hindwing: no costal spines in male. No specialised scales on wings. Abdomen dark grey.

Venation (fig.44). R_{4+5} , and M_1 and M_2 represented by terminal branches. Cu continues after M diverges to meet R_s .

Male genitalia (fig.94). Vinculum: anterior extension slightly emarginated. Tegumen extended into a short lobe at apex. Uncus: caudal edge flat and broad. Gnathos: central element narrow. Valva: caudal-half emarginated. Transtilla: transverse bar present. Aedeagus extended ventrally into a pair of prominent spines; dorsally extended into a divided process. Vesica unmarked, except for striate thickening surrounding base of ejaculatory duct.

Female genitalia (fig.115). Anal papillae form a rounded, fairly broad end to abdomen. Ductus bursae: sclerotised thickening small, approximately in the form of a ring. Corpus bursae: signa reticulata long and narrow.

LARVA. Mines the leaves of *Rhus leptodictyae* (Anacardiaceae). The mine (fig.134) begins as a narrow gallery and broadens into a wider, contorted one.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Pretoria, accession no.169, 23.viii.1949, L. Vári, genitalia slide no.6148; in Transvaal Museum. Paratypes: data as holotype, 5♂, 16♀ 18, 21,22,24,25,26, 30.viii., 1.ix.1949; accession no.160, 1♂ 15.vii.1949, L. Vári; accession no.2061, 3♂, 4♀ 1,3,4,6,7,8.viii.1958, L. Vári; accession no.2087, 2♂ 28.viii.1958, L. Vári; accession no.3068, 2♂, 1♀ 18.viii.1970, L. Vári; accession no.3142, 4♂, 2♀ 10.vii., 18,21,23.viii.1971, L. Vári; 3♂ 27, 29.viii.1949, L. Vári; Pretoria North, accession no.2010, 2♂ 20.viii.1957,

L. Vári; in Transvaal Museum.

The species is similar to the one that follows, but the lack of specialised scales on the wings of *leptodictyae* distinguishes it. Further characters in which the two species differ are given below, under the next species description.

Ectoedemia (Fomoria) incisaevara spec. nov., figs 95, 135

The species is similar to *leptodictyae* and the comments below include only the differences from that species.

ADULT ♂,♀. Wingspan 4,0-4,4mm. Forewing of male with a patch of black, specialised scales on ventral surface. Hindwing of male broader at base than in *leptodictyae* and with black specialised scales on ventral surface, and a pale ochreous hair-pencil originating from base of wing on costa; no costal bristles.

Male genitalia (fig.95). Vinculum: anterior extension hardly emarginated, less so than that of *leptodictyae*. Valva: inner edge of both apical and basal half excavated so that it appears, approximately, E-shaped in ventral view - compare with figure of *leptodictyae*.

LARVA. Forms mines (fig.135) similar in shape to those of *leptodictyae*, but on *Rhus incisa* (Anacardiaceae).

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Cape Province, Worcester, accession no.2874, 20.xi.1967 L. Vári, genitalia slide no.9884; in Transvaal Museum. Paratypes: data as holotype, 1♂, 2♀ 20,21.xi.1967; in Transvaal Museum.

Ectoedemia (Fomoria) malelanensis spec.nov., figs 45,96

ADULT ♂. Wingspan 3,6mm. Head-tuft dark red-brown. Forewing pale ochre irrorated with an equal amount of fuscous so giving a mottled appearance. Hindwing with costal spines. No specialised scales on wings.

Venation (fig.45). Forewing: R_4 perhaps represented by a very weak spur separated from R_5 terminally. M present as a single branch terminally. Cu does not continue after M diverges to meet R_5 .

Male genitalia (fig.96). Vinculum: anterior extension weakly excavated. Tegumen weakly bilobed at apex. Uncus: apex truncated. Gnathos not large. Valva narrow, curved. Transtilla: transverse bar rather thick. Anellus weakly sclerotised on each side of aedeagus. Aedeagus fairly small; without any carinate processes. Vesica with strong spine and some minute cornuti.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Kruger National Park, Malelane, 24.iii.1952, Janse & Vári, genitalia slide no.10027, wing slide no.3871; in Transvaal Museum.

The species is unlikely to be confused with any other described at present. The bilobed tegumen and the shape of the valva are characteristic features.

Ectoedemia (Fomoria) thermae spec.nov., figs 46,97,136

ADULT ♂. Wingspan 4,8mm. Head-tuft pale ochre. Forewing pale ochre sparsely irrorated with fuscous; no specialised scales. Hindwing broad at base, without costal spines; with a patch of elongate, shiny, black specialised scales on dorsal surface, and a greyish hair-pencil at base of wing at costa. Abdomen silvery grey.

Venation (fig.46). Forewing: R_4 and R_5 , and M_1 and M_2 represented as branches terminally. Cu continues weakly for a short distance after M diverges to R_5 .

Male genitalia (fig.97). Vinculum: anterior extension rounded anteriorly. Tegumen narrows suddenly to a point. Uncus: apex bent ventrally. Gnathos: central process not large. Valva narrow, inward margin projected medially. Transtilla: transverse bar long. Juxta present in form of a weakly-sclerotised plate deeply excavated medially. Aedeagus: extended ventrally into a weakly-sclerotised triangular structure and dorsally into a forked process; pair of lateral carinae present. Vesica with a long, straight spine that extends well beyond phallosome and twists at base to be rooted deep into aedeagus, various other thickenings, one of which is a comma-shaped process, and numerous minute cornuti.

LARVA. Mines the leaves of *Vitex wilmsii* (Verbenaceae). The mine (fig.136) is a short gallery followed by a blotch.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Warmbaths, accession no.2737, 4.i.1965, L. Vári, genitalia slide no.9927, wing slide no.3868; in Transvaal Museum.

This species is best recognised by the following: the shapes of the valva, the genital capsule in general, the carinate processes of the aedeagus, and the markings on the vesica.

Ectoedemia (Fomoria) portensis spec.nov., figs 47,98

ADULT ♂. Wingspan 4,8-6,4mm. Head-tuft orange-ochre. Forewing off-white to pale grey-brown. Hindwing without costal spines, with thickening along trunk of R+M. No specialised scales on wings. Abdomen pale grey.

Venation (fig.47). Forewing: R_4 and R_5 , and M_1 and M_2 represented by terminal branches. Cu continues nearly to anal edge of wing after M diverges to meet R_5 .

Male genitalia (fig.98). Vinculum: anterior extension rounded anteriorly. Tegumen narrows to apex. Uncus extended well-beyond tegumen into a pointed apex. Gnathos with broad central element. Valva meets opposite member at base; a pair of short spines project inwardly one from near apex, one about halfway down inner margin of valva. Transtilla: transverse bar absent; ventral arms fairly long. Aedeagus: ventral process absent; pair of dorsal carinae present. Vesica with several moderately large spine-like cornuti.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Cape Province (N.W. of George), Seweweekspoort, 4-6.xii.1968, Potgieter & Jones, genitalia slide no.9935, wing slide no.3801; in Transvaal Museum. Paratypes: data as holotype 1♂; Transvaal, Blydepoort, 1♂ 25-29.x.1976, Scholtz & Scoble; in Transvaal Museum.

The shapes of the components of the male genitalia, particularly the valvae, are characteristic.

Ectoedemia (Fomoria) fuscata (Janse) comb.nov., figs 48,99,116
Nepticula fuscata Janse, 1948:165, (*partim*).

Janse's type-series includes representatives of several species see below, so his description, in part, is invalid. The species is redescribed here.

ADULT ♂. Wingspan 5,2-5,6mm. Head-tuft pale ochre. Forewing pale ochre with a few fuscous irrorations. Hindwing: costal bristles present.

Venation (fig.48). Forewing: R_{4+5} , and M_{1+2} present as terminal branches. Cu continues for a short distance, weakly, after M diverges to R_s .

Male genitalia (fig.99). Capsule rather elongate. Vinculum: combined ventral plate and anterior extension large; anterior extension hardly emarginated. Tegumen extended into a rounded lobe, not pointed at apex. Uncus with apex bent ventrally. Gnathos: central element fairly broad. Valva with a short, inwardly directed point; a weak setose pad, which resembles a pin-cushion, present near apex. Transtilla: transverse bar long; ventral arms short. Aedeagus: ventral process absent; pair of large, carinate lateral processes arises near phallosome; dorsally there is a pair of small, pointed carinae. Vesica with several medium sized spines.

Female genitalia (fig.116). Anal apophyses form a fairly rounded end to abdomen. Ductus bursae marked with sclerotisations as in figure. Corpus bursae with large, well-bordered signa reticulata.

TYPES. Janse (1948:165) cited the type material as follows: 'Abachaus, near Otjiwarongo, S.W. Africa; collected by Mr G. Hobohm in viii., xi., xi. and ii. ♂ and ♀ types, two ♂ paratypes and four ♀ paratypes in the Transvaal Museum (ex Janse collection)'.

I designate as Lectotype the '♂ type' the genitalia of which are illustrated in a photograph by Janse (1948 plate 91 fig.2), and which bears the following label data: 'Abachaus, S.W.A. x '45, G. Hobohm; G. [genitalia slide no.] 4971; [wing slide no.] 3883; *Nepticula fuscata* Janse. ♂ Type No.2357'. The collection dates of the material examined by Janse are cited by him (1948:166) as '... viii., xi., xi. and ii.' The double citation of 'xi' (November) is probably a misprint and one of the entries should presumably read 'x.' i.e. October, the date on the label of the

specimen of which Janse illustrated the genitalia. Janse's photograph of the genitalia leaves no doubt that this is a valid syntype.

The wing venation of the female paralectotype labelled 'Type No.2358' is identical to that of the lectotype and the wing pattern is similar. The two specimens were collected in the same year, the male in October and the female in November. This specimen is therefore considered to be a correctly identified specimen of *fuscata*.

The male labelled 'Cotype No.2363' bears a Pretoria locality label and has probably been mislabelled 'cotype' so I do not regard it as a paralectotype of *fuscata*. This specimen is a male of *grandinosa*.

The male paralectotype labelled 'Cotype 2359' was made a paratype of *commiphorella* Scoble (see Scoble 1978:84).

The male paralectotype labelled 'Cotype No.2364' represents an undescribed species of *Niepeltia* Strand (genitalia and wing venation examined). Janse (1948: plate 82 fig.4) illustrated the forewing venation and erroneously labelled what is a slight thickening as the cubitus.

The three remaining paralectotypes are females. Two were collected in February 1943 ('Cotype' numbers 2361 and 2362) and one in April 1943 ('Cotype No.2360'). The wing venation of number 2360 is quite different from that of *fuscata* and so are the genitalia. The genitalia of the other two specimens are also different from those of *fuscata* and so none of the three specimens belong to the species.

MATERIAL EXAMINED. ♂-Lectotype, SOUTH WEST AFRICA: Grootfontein District, near Otjiwarongo, 'Abachaus' [*sic*, Abachaub], x.1945, G. Hobohm; in Transvaal Museum. Paralectotype: data as lectotype, 1♀ xi.1945; in Transvaal Museum.

The male genitalia, resemble those of *vannifera* and *hobohmi*; particularly the valvae, the rounded, not pointed, tegumen, the long transverse bar of the transtilla and the numerous, fairly large spines on the vesica. The presence of R_{4+5} and M_{1+2} in the forewing is a further similarity. The species are easily distinguished by comparing the illustrations of the male genitalia. The female genitalia of *vannifera* are remarkable and distinct, see *vannifera* immediately following.

Ectoedemia (Fomoria) vannifera (Meyrick) comb.nov., figs 8,49,100,117

Nepticula vannifera Meyrick, 1914:203.

Nepticula vannifera Meyrick: Janse, 1948:178.

Nepticula irrorata Janse, 1948:168, (*partim*).

ADULT ♂. Wingspan 4,2-6,0mm. Head-tuft off-white with dark brown hair-scales, which often predominate on vertex and are also found on front of head. Antenna with a ball-like expansion of pedicel (fig.8); flagellar segments squat at base of antenna; segments get longer distally. Galeae extend only slightly beyond labial palpi. Forewing: degree and pattern of irrorations varies; in specimens from South West Africa, Abachaub, irrorations are generally heavy and uniform, in specimens from South Africa (various localities) the irrorations are often concentrated along midline along length of the wing. Ventral side of forewing with specialised, shiny black scales that form a long patch at base, posterior to fold, and a hair-pencil, comprising a series of long ochreous scales, which arises from base near anal edge and overlaps the black scales. Hindwing: expanded at base to give wing a characteristic shape; costal spines present; dorsal surface with an elongated patch of specialised, black scales; ventral surface with a few similar scales near base. Abdomen grey.

♀ as male except that there is no ball-like expansion of the pedicel, and no specialised black scales or hair-pencil. Hindwing: not expanded at base.

Venation (fig.49). Forewing: R_{4+5} and M_{1+2} represented by branches terminally. Cu does not continue after M diverges to R_s , and, since only a single persistent trachea is visible, it may be absent altogether.

Male genitalia (fig.100). Vinculum: anterior extension hardly emarginated. Tegumen broad, not extended into a long, gradually tapering apex. Uncus and gnathos unremarkable. Valva of a characteristic shape; a round setose pad or lobe is present posteriorly, and looks like a pin-cushion; a short process arises from about halfway down valva and points into genital capsule. Transtilla: transverse bar long. Aedeagus: ventral process absent; a lateral carinate spine curves around the phallosome on each side, and a bifurcate process is present dorsally. Vesica with many large spine-like cornuti.

Female genitalia (fig.117). Anal papillae form a fairly narrow, but not pointed, end to abdomen. Apophyses fairly long. Ductus bursae unmarked. Corpus bursae with the following sclerotisations: 1) a pair of elongate oval signa, *not* reticulate, with a strong boundary at caudal end, which becomes very weak anteriorly; each signum is covered with minute pectinations; 2) a single, subtriangular sclerite near posterior end; 3) a series of short spines arising from a curved, sclerotised line.

LARVA. Data from labels of reared specimens from Fort Beaufort gives "*Capparid oleoides*", now *Boscia oleoides* (Capparaceae), as the host-plant.

MATERIAL EXAMINED. Syntypes - SOUTH AFRICA: Transvaal, Pretoria, 1♀ 17.ix.1912, A.J.T. Janse, genitalia slide no.7244, Meyrick's no.3707, 'Type No.123'; 1♀ 12.x.1912, A.J.T. Janse, genitalia slide no.4032, Meyrick's no.3709, 'Cotype No.124'; in Transvaal Museum.

Other material. SOUTH AFRICA: Transvaal, Pretoria, 1♂, 3♀ September; Pretoria North, 1♂, 2♀ February, September; Blyde River Nature Reserve, 1♂ November-December; Kruger National Park, Letaba Camp, 1♂ March; Soutpansberg District, Rochdale, 4♂, 2♀ September; Orange Free State, Sasolburg, 4♂, 3♀ September; Cape Province, Fort Beaufort, 4♂, 1♀ October; Heidelberg District, Grootvadersbos, 1♂ November; Worcester, Fairy Glen, 6♂ October; Natal, Pietermaritzburg, Merrivale, 2♂ October. SOUTH WEST AFRICA: Grootfontein District, Abachaub, 9♀ paralectotypes of *Stigmella irrorata*, September, October, November; 13♂, 5♀ September, October, November. Specimens collected by G. Clark, G. Hobohm, A.J.T. Janse, Janse & Vári, Potgieter, Potgieter and Scoble, B.R. Stuckenberg, G. van Son, L. Vári, Vári & Potgieter; in Transvaal Museum.

The species is clearly allied to *fuscata* (for reasons see under that species, above). In *E. vannifera* the male is easily recognised by the shape of the pedicel of the antenna and the position of the hair-pencil, besides the genitalia. The markings on the corpus bursae of the female are characteristic and, except for the fact that the signa are double and bordered, bear little resemblance to any other species. The species is similar to the next species, *hobohmi* (known only from the male), but may be distinguished by the presence, in the former, of the expanded pedicel, a hair-pencil and black specialised scales, and by the shape of the valva and the smaller size.

Janse (1948: footnote on p.178) stated that Meyrick made no mention of the presence, in the male, of a hair-pencil and black, specialised scales. This is incorrect - Meyrick (1914:203) wrote 'Forewings on under-surface with a light yellowish subdorsal hairpencil from base surrounded with deep black scales.' Meyrick examined one male and sent the two female syntypes to the Transvaal Museum. The male syntype is in the British Museum (Natural History) and has not been examined by me. Meyrick's description shows that this specimen is conspecific with the males studied by me.

The slide G. 4961 was mislabelled by Janse as the 'Type' of *nigricapitella*. It is actually a specimen of *vannifera*. Slide 4962 is the slide of the 'Type' of *nigricapitella*. The slides have been relabelled. Both specimens came from Abachaub.

Ectoedemia (Fomoria) hobohmi (Janse) comb.nov., fig.101

Nepticula hobohmi Janse, 1948:167 *partim*.

The species, known only from the male, is similar to *vannifera* but may be distinguished from it by the following characters.

ADULT ♂. Larger than *vannifera*, wingspan 6,0-7,6mm. Antenna: scape without ball-like expansion. Forewing more heavily irrorated with fuscous; hair-pencil and black specialised scales absent. Hindwing not strongly expanded at base; specialised scales absent.

Male genitalia (fig.101). Vinculum: anterior extension more deeply emarginated. Valva with a longer spine that points posteriorly. Aedeagus: carinae differ (see figure). Vesica with rather fewer cornuti.

MATERIAL EXAMINED. I designate as Lectotype the male syntype from South West Africa of which a photograph appears in Janse (1948:plate 93, fig.2). A photograph of the genitalia of this specimen is given in the same work (plate 90,fig.1). The specimen bears the following label data 'Abachaus [*sic*, Abachaub]. S.W.A. Oct. 44, G. Hobohm; G. [genitalia slide no.] 4967; *Nepticula hobohmi* Janse ♂. Type No.2365.'; in Transvaal Museum. Paralectotypes, SOUTH WEST AFRICA: 'Abachaus' [*sic* Abachaub], 2♂ ix.1944, 1♂ ix.1945, G. Hobohm, 'Cotype' nos.2366, 2368, 2369; in Transvaal Museum.

A further male paralectotype of *hobohmi*, 'Cotype' No.2367', has genitalia similar to *vannifera* and also a hair-pencil characteristic of that species. However, there are no black specialised scales on the wings, nor is there a ball-shaped expansion on the scape. The size of the specimen, and the heavily irrorate forewing is typical of *hobohmi*. The specimen is not considered to belong to *hobohmi*.

Genus *NIEPELTIA* Strand

A paper dealing with this genus follows, (Scoble 1980b).

Genus *MICROCALYPTIRIS* Braun

Microcalyptris Braun, 1925:224. Type-species: *Microcalyptris scirpi* Braun, 1925:224, by original designation and monotypy.

Braun (1925) described this North American genus and its single included species from one specimen with a small, inconspicuous 'eye-cap'. Davis (1978b) added two new species, and Wilkinson (1979) described three more and transferred two others from *Nepticula* (= *Stigmella*).

The wing venation of *Microcalyptris* appears identical to that of *Niepeltia* (compare Wilkinson 1979: fig.11 with Scoble 1980b: figs 4,5). The dotted line between R_1 and R_{2+3} in Wilkinson's figure of the forewing should not be interpreted as a vein (C. Wilkinson, personal communication). Davis (1978) reported the presence of 'lateral support rods' in the male genitalia of *Microcalyptris* (p. 214). These structures are generally well-developed; possible homologues are present, although weak, in some species of *Niepeltia* (Scoble 1980b:200). However, other attributes show that *Microcalyptris* and *Niepeltia* are different.

Microcalyptris is excluded from the 'Key to Genera', above, because I have not studied any specimens of the genus and have been unable to find a key character for all the species in the existing literature.

Genus *TRIFURCULA* Zeller

Trifurcula Zeller, 1848:330. Type-species: *Trifurcula pallidella* Zeller, 1848:332, by original designation.

Fedalmia Beirne, 1945:207. Type-species: *Nepticula headleyella* Stainton, 1854:300, by original designation and monotypy. (Treated as a subgenus of *Trifurcula* Zeller (*sensu* Johansson 1971) by Johansson 1971:245.)

Levarechama Beirne, 1945:206. Type-species: *Nepticula cryptella* Stainton, 1856:41, by original designation. (Treated as a subgenus of *Trifurcula* Zeller (*sensu* Johansson 1971) by Johansson 1971:246.)

The affinities of the genus were discussed by Scoble (1980a, bound in below). At the time of writing a cladistic study of other genera had not been undertaken and *Trifurcula*, *Fedalmia* and *Levarechama* were retained as genera. Each of these taxa is monophyletic and thus treating them as subgenera is simply a change in rank that indicates their cladistic relationships within the Trifurculini. At this time I prefer to keep all at the same rank although it is likely that *T. (Trifurcula)* shares a common ancestor with *T. (Levarechama)* more recently than either of them does with *T. (Fedalmia)*. If this is so the fact should be reflected in the classification. Studies in progress by workers at the Vrije Universiteit are expected to test this hypothesis of relationship.

Subgenus *FEDALMIA* Beirne

Genus *Fedalmia* Beirne, 1945:207. Type-species: *Nepticula headleyella* Stainton, 1854:300, by original designation and monotypy. (Treated as a subgenus of *Trifurcula* Zeller (*sensu* Johansson 1971) by Johansson 1971: 245.)

There are no species from southern Africa; all members of the taxon come from Europe (including Britain). Unlike *T. (Trifurcula)* and *T. (Levarchama)* there is no loss of link between R_{2+3} and the rest of R_s . The uncus, at least in *T. (Fedalmia) headleyella*, is not divided dorsoventrally as in *T. (Trifurcula)* nor is it split in ventral view as in *T. (Levarchama)*. The larvae of many species of *T. (Fedalmia)* mine two or three leaves instead of the usual one. They move from leaf to leaf via the petioles (see, for example, Borkowski 1970; Emmet 1976; Klimesch 1976).

Mr R. Johansson has suggested (personal communication) that *Fedalmia* may be synonymous with the North American *Glaucolepis* Braun. The wing venation of the two seems to be identical, and the male genitalia of *Glaucolepis* are similar to some species included in *Fedalmia*. A synonymy may well be needed; if so *Glaucolepis*, being the older name, will take precedence.

Subgenus *TRIFURCULA* Zeller

Genus *Trifurcula* Zeller, 1848:330. Type-species: *Trifurcula pallidella* Zeller, 1848:332, subsequent designation by Beirne, 1945:207 (treated as the nominate subgenus by Johansson 1971:245); Scoble, 1980a (bound in below and in that reprint treated as a genus).

Characters that distinguish the taxon from *T. (Fedalmia)* and *T. (Levarchama)* are given in the reprint, below.

Subgenus *LEVARCHAMA* Beirne

Genus *Levarchama* Beirne, 1945:206. Type-species: *Nepticula cryptella* Stainton, 1856:41, by original designation. (Treated as a subgenus of *Trifurcula* Zeller (*sensu* Johansson 1971) by Johansson 1971:246.)

The subgenus, known only from Europe (including Britain), may be distinguished from *T. (Fedalmia)* and *T. (Trifurcula)* by the shape of the uncus, which is split in ventral view.

Genus *BOHEMANNIA* Stainton (European)

Bohemannia Stainton, 1859:439. Type-species: *Nepticula quadrimaculella* Boheman, 1851:67, by monotypy.

Scoliaula Meyrick, 1895:727. Type-species: *Nepticula quadrimaculella* Boheman, by monotypy.

Two species are included in this European genus, the type-species, and one added by Borkowski (1975:489) *B. pulverosella* (Stainton), although it was assigned to *Scoliaula*, a junior synonym of *Bohemannia*. A further species will probably be added (Mr R. Johansson *personal communication*).

Bohemannia is a senior synonym of *Scoliaula*. *Bohemannia* is not pre-occupied (cf. Johansson 1971:246) according to the *Nomenclature Zoologica* (Neave 1939), although *Bohemania* (spelled with a single 'n') was used earlier for an hemipteran. The species *quadrimaculella* was the only one included by Stainton (1859) in the original description of the genus and therefore it is the type-species (*International Code*: Article 68c).

Specimens of *quadrimaculella* and illustrations of the genitalia of *pulverosella* (all kindly provided by Mr R. Johansson) have been examined.

The presence of signa reticulata on the corpus bursae of the female shows that the genus falls within the Trifurculini.

DIAGNOSIS. The united trunk of R, M and Cu divides into five branches terminally. This feature distinguishes the genus from all others. In the male, the uncus is reduced to a pair of setose lobes, a condition bearing little resemblance to that found in other nepticulids except perhaps *Areticulata leucosideae* (described below), a species from which *Bohemannia* is otherwise quite distinct. A characteristic, short process arises from each valva.

DISTRIBUTION. Europe.

Some remarks about the type-species follow.

Bohemannia quadrimaculella (Boheman)

Nepticula quadrimaculella Boheman, 1851:67.

The male genitalia are illustrated by Beirne (1945:fig.72) and Borkowski (1975: fig.9).

ADULT. *Venation*. Borkowski (1972:fig.10) illustrated the wing venation. The labels on the figure of the forewing suggest that R_1 and R_5 are united at the base of the wing and that the section of R_5 that subsequently diverges to meet M+Cu is lost (broken line in Borkowski's figure). I have examined the forewing of a specimen and can see a persistent trachea running from the base of R_1 to the M+Cu trunk. This trachea continues with that of M and of Cu in a common vein and thus suggests that R_1 and R_5 are actually separated from the base and not united.

Male genitalia. Described and figured by Beirne (1945) who stated that the 'pseuduncus' (the tegumen extension) 'projects as a spined lobe on either side of the uncus'. The posterior edge of the tegumen is flat and not extended, so the term 'pseuduncus' is inappropriate, and nor is it projected on either side of the uncus - Beirne was probably referring to the setose lobes of the uncus itself. The juxta is large and characteristic. The ventral wall of the aedeagus is produced into a long, narrow, carinate process. (This process is probably one of Beirne's 'three very large and heavily sclerotised cornuti'.) Actually the vesica bears one enormous and one smaller cornutus, and a number of very small cornuti.

Female genitalia. Klimesch (1975) provided a figure of the genitalia of what he referred to as *quadrimaculella*, but the specimen cannot have represented that species since no signa reticulata were illustrated (and were stated to be absent) whereas these structures are present in *quadrimaculella* (and *pulverosella*). The reticulations of the signa on the corpus bursae are very weak. The markings on the ductus bursae comprise a pair of sclerotised rods.

MATERIAL EXAMINED. SWEDEN, Kullaberg, 2♂, 1♀ 2,9.viii.1969, R. Johansson; in Transvaal Museum.

Genus *ARETICULATA* gen. nov.

Type-species: *Areticulata leucosideae* spec. nov.

This monotypic genus is described for a species that has some remarkable attributes (see below under species description). A formal description of the genus is not presented since it is equivalent to that of the species. For details of this point see pages 6-8.

Areticulata leucosideae spec. nov., figs 9,50,102,118,137.

ADULT ♂,♀. Wingspan 3,6-4,4 mm. Head-capsule (fig.9): a well-developed thickening on each side runs from ventral edge of antennal socket to inner margin of eye and then curves down to labrum. Head-tuft dull ochre tinged with red-brown, or completely red-brown. Antenna: scape narrow; flagellar segments more elongate in female than in male. Compound eye very small, projecting from side of head. Galeae very short. Labial palpi two-segmented. Forewing: in male dark grey with some ochreous irrorations; in female pale ochre with a fuscous patch at apex. Hindwing very narrow, slightly broader at base in male; no costal spines in male. No specialised scales on wings. Hindtibia: proximal pair of spurs well-below midpoint. Abdomen grey.

Venation (fig.50). Forewing: R_{4+5} and M_{1+2} represented by terminal branches. M probably coalesced with R from base. Cu curves up gently to meet R+M about halfway along wing. Hindwing: M undivided, represented by a single branch arising from trunk of R_5+M .

Male genitalia (fig.102). Vinculum: lateral arms meet posteriorly to form a complete ring around aedeagus; anterior extension very weakly emarginated or flat, not rounded. Tegumen broadly rounded. Uncus in form of a pair of rather weakly sclerotised lateral arms each of which terminates apically as a setose lobe. Gnathos: approximately U-shaped, central element absent; lateral horns with an additional pair of processes. Valva divided into a ventral component, which tapers suddenly to a finger-like projection, and a dorsal component terminating in an apodeme. Transtilla: transverse bar present, fairly long. Aedeagus small; ventral process absent; pair of dorsolateral carinae present. Vesica with a patch of spiculate cornuti; striate thickening probably absent from base of ejaculatory duct, or if present very weak.

Female genitalia (fig.118). Anal papillae form a fairly narrow, but not a pointed, end to abdomen. Ductus bursae without sclerotisations. Corpus bursae with a pair of circular, bordered signa covered with pectinations, incompletely reticulate.

LARVA. Forms a gallery mine (fig.137) in the leaves of *Leucosidea sericea* (Roseaceae).

PUPA. Abdominal terga 2-8 with several small spines arranged in about three rows on each segment.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Heidelberg, Suikerbosrand Nature Reserve, accession no.3864, 8.xii.1980, D.M. Kroon; in Transvaal Museum. Paratypes: data as holotype, 2♂, 1♀ 8,9,10.xii.1980; accession no.3480, 1♂ 17.xi.1975, M.J. Scoble; Heidelberg accession no. 2921, 1♂, 2♀ 24.i.1968, 1♀ without date, L. Vári; Natal, Balgowan, Yello-woods, 1♂ 27.i.1965, L. Vári; in Transvaal Museum.

The shape of the gnathos is similar to many species of *Stigmella*, however the condition of the lateral arms of the vinculum and of the tegumen is atypical of *Stigmella* and the Stigmellini as a whole. The arrangement of the vinculum and tegumen could be analogous to that found in the Trifurculini (i.e. independently evolved), but, in the same way, the gnathos could be analogous to that of *Stigmella*. Some other characters are similar to those found in *Stigmella*, but these are not unique to that genus and they are interpreted as primitive so *leucosideae* cannot justifiably be included in *Stigmella*. These characters are as follows. M is probably fused to R from the base of the forewing; the vein that curves up to meet R is interpreted as Cu because it meets R about halfway instead of one-third of the way along the wing, and is not sharply bent up as is typical of the condition of M in the Trifurculini. The coalescence of M with R from the base of the wing is found not only in the other species in the Stigmellini but also in *Pectinivalva*. A pair of large signa is found in many species within the Stigmellinae. In the Trifurculini the signa are reticulate and characteristic of that group. Non-reticulate signa that in some ways resemble those of *leucosideae* are found in the North American *corylifoliella* species-group (Wilkinson & Scoble 1979).

A leucosideae exhibits many unique characters, particularly the prominent sulcus on the front of the head, the two-segmented labial palpi, the elongated scape of the antenna, and the shape of the valva.

The species may represent the sister-species of all the other Stigmellinae but this would mean an independent development of a gnathos like many species of *Stigmella*. It could be an aberrant member of *Stigmella* but that would mean an independent development of the condition of the lateral arms of the vinculum and of the tegumen found in the Trifurculini. It could be the sister-species of the Trifurculini but this would mean the independent development of a gnathos similar to many species of *Stigmella*. Therefore the position of *leucosideae* within the Stigmellinae is uncertain.

Genus *ARTAVERSALA* Davis

Artaversala Davis, 1978b:219. Type-species: *Artaversala gilvafascia* Davis, 1978b:221, by original designation and monotypy.

The generic name was proposed for a single species *gilvafascia* Davis (1978b) from Florida, North America. The venation is reduced and the male and female genitalia are aberrant. Most remarkable is the V-shaped vinculum and the deeply divided valva in the male, and the anterior apophyses, which almost form a ring encircling the seventh segment, and the very slender ductus bursae of the female.

Since M in the forewing is coalesced with R from the base, and as the corpus bursae of the female does not bear signa reticulata, *gilvafascia* does not belong to the Trifurculini. The position of the species within the Stigmellinae is uncertain.

Genus *MANONEURA* Davis

Manoneura Davis, 1979: scientific note, replacement name for *Oligoneura* Davis, 1978b:217 (preoccupied). Type-species: *Oligoneura basidactyla* Davis, 1978b:218 by original designation and monotypy.

The generic name was proposed for a single species *basidactyla* Davis (1978b) from Florida, North America. The gnathos is of a complexity unknown elsewhere in the Nepticulidae. As pointed out by Davis, the forewing venation resembles that of *Johanssonia acetosae*. *M. basidactyla* lacks the 'defining' characters of the Trifurculini. For example M is coalesced with R from the base of the forewing rather than Cu, and the uncus is very small and not in the form of a thickened band. Unfortunately the abdomen of the only female is lost (Davis 1978b) so the presence or absence of signa reticulata cannot be checked.

Relationships are discussed further in 'Cladistic Analysis'. I have not examined any of the few specimens in existence; the species is of an uncertain position in the Stigmellinae.

Genus *PARAFOMORIA* Borkowski

Parafomoria Borkowski, 1975:498.. Type-species: *Nepticula helianthemella* Herrich-Schäffer, 1960:60, by original designation and monotypy.

The European species *helianthemella* Herrich-Schäffer was removed from *Nepticula* (= *Stigmella*) by Borkowski (1975), because of the reduced wing venation, and given a new generic name.

Unfortunately Borkowski gave no figures and no other details. I have not examined material of the species, and because of this lack of information *Parafomoria* is not included in the key, above.

CHECK-LIST TO GENERA, SUBGENERA AND SPECIES FROM SOUTHERN AFRICA
(Synonyms are not italicised)

VARIUS gen. nov.

ochmicolus (Vári) comb. nov.

SIMPLIMORPHA gen. nov.

lanceifoliella (Vári) comb. nov.

STIGMELLA SCHRANK, 1802

The *fluida* group

charistis Vári, 1963

abutilonica Scoble, 1978 b

parinarella Vári, 1955

fluida (Meyrick, 1911a)

irrorata (Janse, 1948)

varii Scoble, 1978b

geranica Scoble, 1978b

satarensis Scoble, 1978b

allophylica Scoble, 1978b

tragilis Scoble, 1978b

hortorum Scoble, 1978b

potgieteri Scoble, 1978b

crotonica Scoble, 1978b

rhynchosiella Vári, 1955

platyzona Vári, 1963

celtifoliella Vári, 1955

generalis Scoble, 1978b

perplexa (Janse, 1948)

urbica (Meyrick, 1913)

androflavus Scoble, 1978^b

abachausi (Janse, 1948)

pallida Scoble, 1978b

nigrata (Meyrick, 1913)

triumfettica Scoble, 1978b

dombeyivora Scoble, 1978b

ampullata Scoble, 1978b

pretoriata Scoble, 1978b

protosema (Meyrick, 1921)

porphyreuta (Meyrick, 1917)

The *ingens* group

confinalis Scoble, 1978b

grewiae Scoble, 1978b

ingens (Meyrick, 1913)

angustivalva Scoble, 1978b

letabensis Scoble, 1978b

Species not assigned to a species group

caliginosa (Meyrick, 1921), comb. nov.

liota Vári, 1963

OBRUSSA BRAUN, 1915

ETAINIA BEIRNE, 1945

cryptixantha (Meyrick, 1918), comb. nov.

zimbabwiensis spec. nov.

nigricapitella (Janse, 1948), comb. nov.

krugerensis spec. nov.

ECTOEDEMIUM BUSCK, 1907

DECHTIRIA BEIRNE, 1945

FOMORIA BEIRNE, 1945

ECTOEDEMIUM (ECTOEDEMIUM)

commiphorella Scoble, 1978a

mauni Scoble, 1979

nigrimacula (Janse, 1948)

ECTOEDEMIUM (LAQUEUS) subgen. nov.

stimulata (Meyrick, 1913), comb. nov.

grandinosa (Meyrick, 1911a), comb. nov.

wilkinsoni spec. nov.

simicola spec. nov.

guerksiae spec. nov.

macrochaeta (Meyrick, 1921), comb. nov.

furcella spec. nov.

maritima spec. nov.

wundoniella spec. nov.

scabridae spec. nov.

jupiteri spec. nov.
royenicola (Vári, 1955), comb. nov.
nigrisquama spec. nov.
denticulata spec. nov.
undatae spec. nov.
bicarina spec. nov.
craspedota (Vári, 1963), comb. nov.
digitata spec. nov.
limburgensis spec. nov.
subrutescens (Meyrick, 1937), comb. nov.
capensis spec. nov.
gymnosporiae (Vári, 1955), comb. nov.
psarodes (Vári, 1963), comb. nov.
insulata (Meyrick, 1911b), comb. nov.
kowynensis spec. nov.
nylstroomensis spec. nov.
rhabdophora spec. nov.
crispae spec. nov.

ECTOEDEMA (FOMORIA)

oleivora (Vári, 1955), comb. nov.
pappeivora (Vári, 1963), comb. nov.
indicaevora spec. nov.
knysnaensis spec. nov.
lucidae spec. nov.
tecomariae (Vári, 1955), comb. nov.
myrtinaecola spec. nov.
alexandria spec. nov.
leptodictyae spec. nov.
incisaevora spec. nov.
malelanensis spec. nov.
thermae spec. nov.
portensis spec. nov.
fuscata (Janse, 1948), comb. nov.
vannifera (Meyrick, 1914), comb. nov.
hobohmi (Janse, 1948), comb. nov.

NIEPELTIA STRAND, 1934

combretella (Vári, 1955)

vumbaensis Scoble, 1980b
molleivora Scoble, 1980b
zeyheriae Scoble, 1980b
rubiacivora Scoble, 1980b
obliquella Scoble, 1980b
fagarivora (Vári, 1955)
fuscofascia Scoble, 1980b
undoniensis Scoble, 1980b
pundaensis Scoble, 1980b
lorantivora (Janse, 1948)
krooni Scoble, 1980b
acumenta Scoble, 1980 b
bispinata Scoble, 1980b
sellata Scoble, 1980b
mariepsensis Scoble, 1980b
lundiensis Scoble, 1980b
fulva Scoble, 1980b
vacuolata Scoble, 1980b
lanneivora (Vári, 1955)
vepricola (Vári, 1963), comb. nov.

TRIFURCULA ZELLER, 1848

TRIFURCULA (TRIFURCULA)

pullus Scoble, 1980 a
barbertonensis Scoble, 1980 a

ARETICULATA gen. nov.

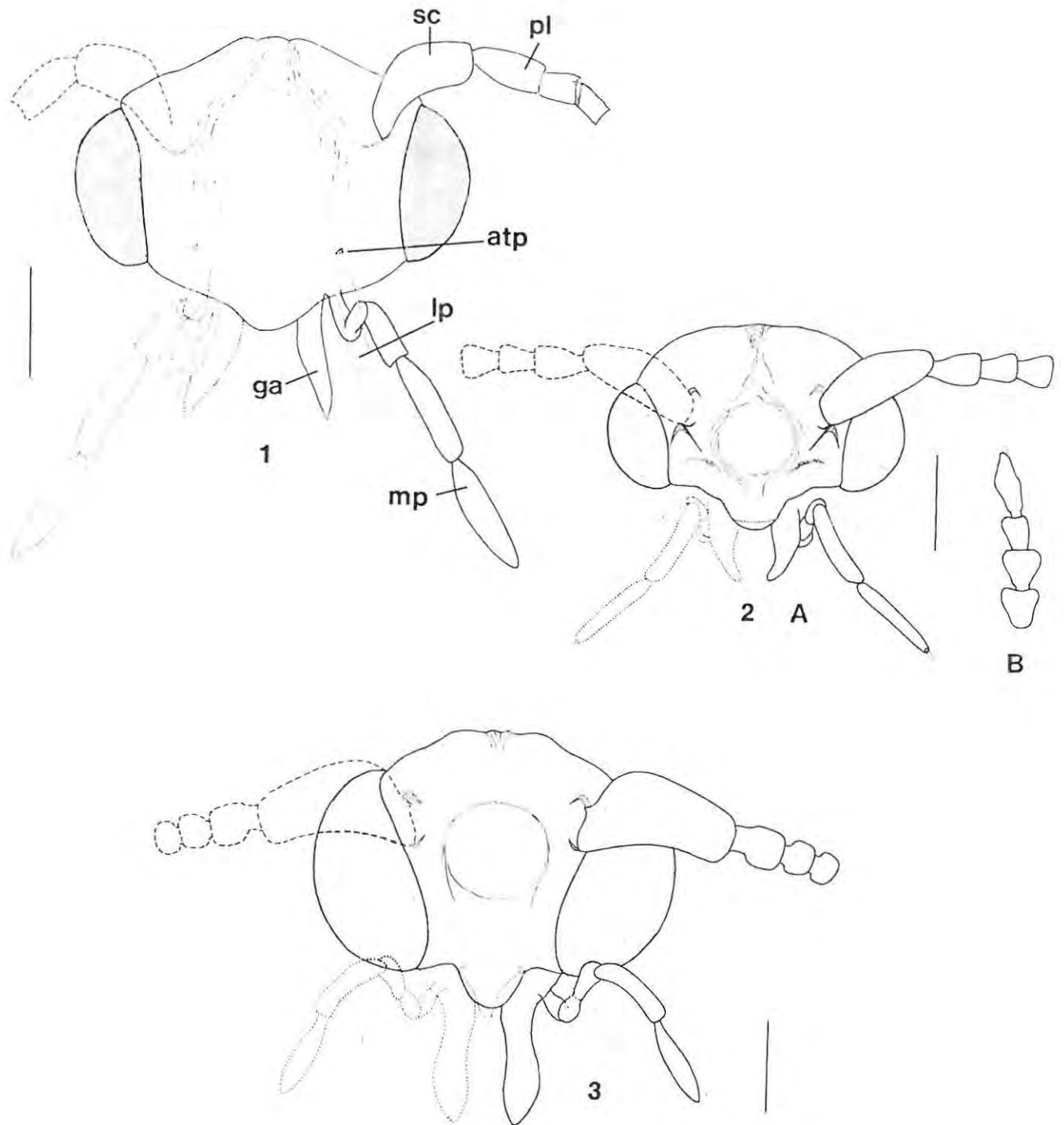
leucosideae spec. nov.

SPECIES OF UNDETERMINED GENERIC PLACEMENT

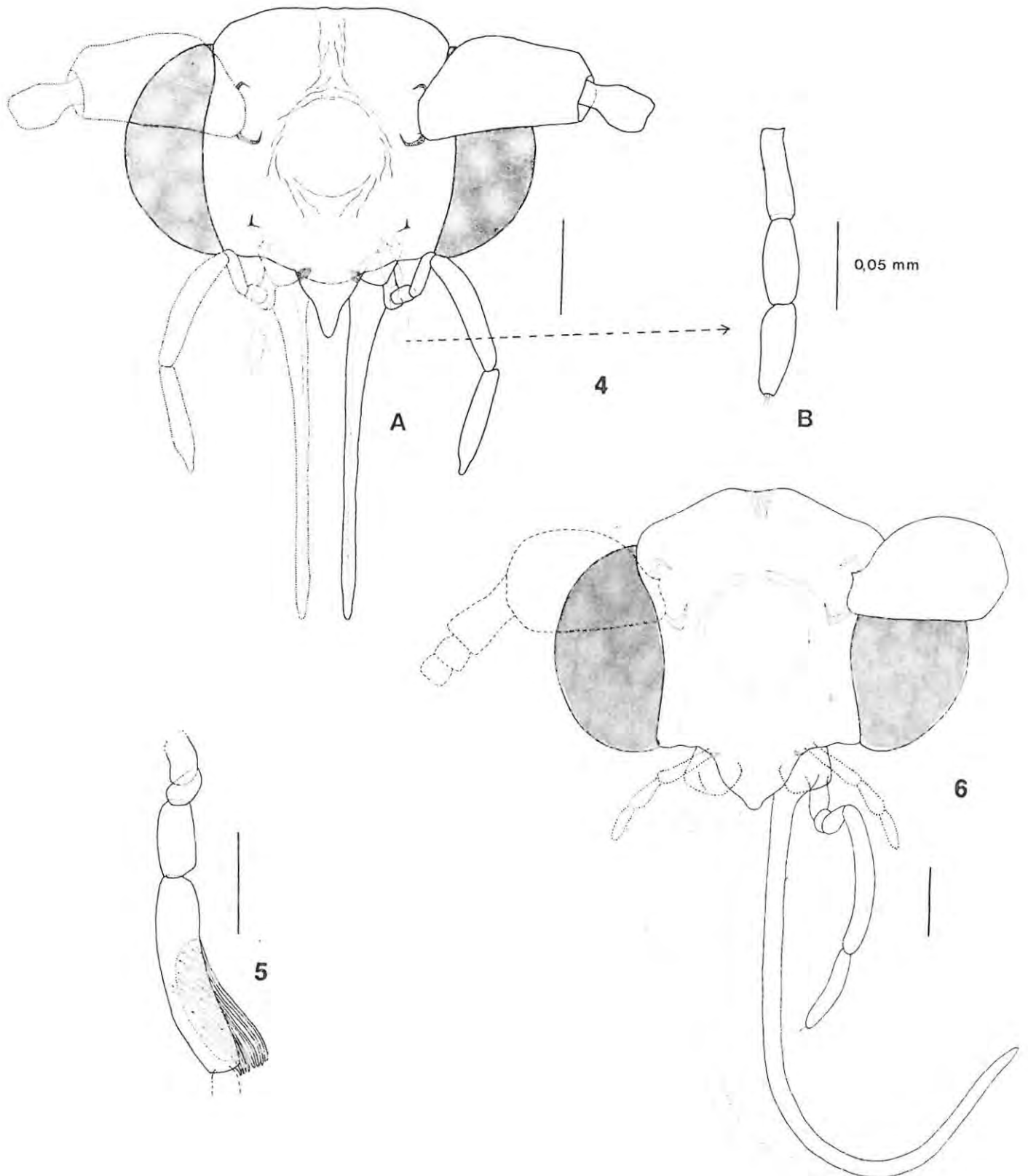
'Nepticula' *galactaema* Meyrick, 1924
 'Nepticula' *panconista* Meyrick, 1920
 'Nepticula' *xuthomitra* Meyrick, 1921
 'Stigmella' *krugeri* Vári, 1963

ABBREVIATIONS TO FIGURES

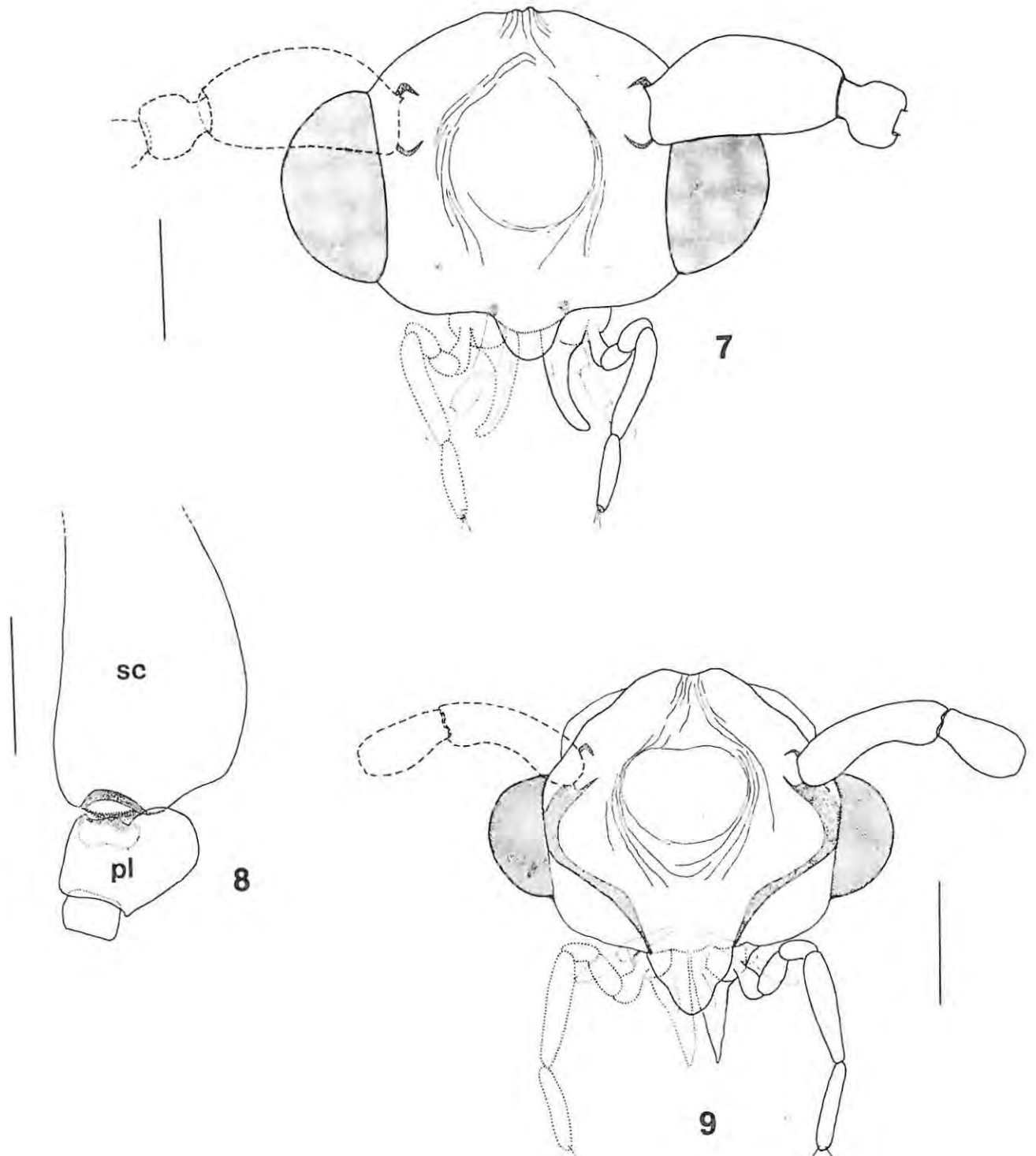
aa	anterior apophyses
ae	anterior extension of vinculum
al	anal loop
atp	anterior tentorial pit
cb	corpus bursae
db	ductus bursae
ga	galea
gs	gnathos
lav	lateral arm of vinculum
lp	labial palpus
lps	lateral carinate process of aedeagus
mp	maxillary palpus
pa	posterior apophysis
pl	pedicel
pr	pectinifer
sa	spermatheca
sc	scape
sd	sclerotisation of ductus bursae
sgm	signum
sm	sensillum
ta	transtilla
tn	tegumen
us	uncus
va	valva
vp	ventral process of aedeagus
vpl	ventral plate of vinculum



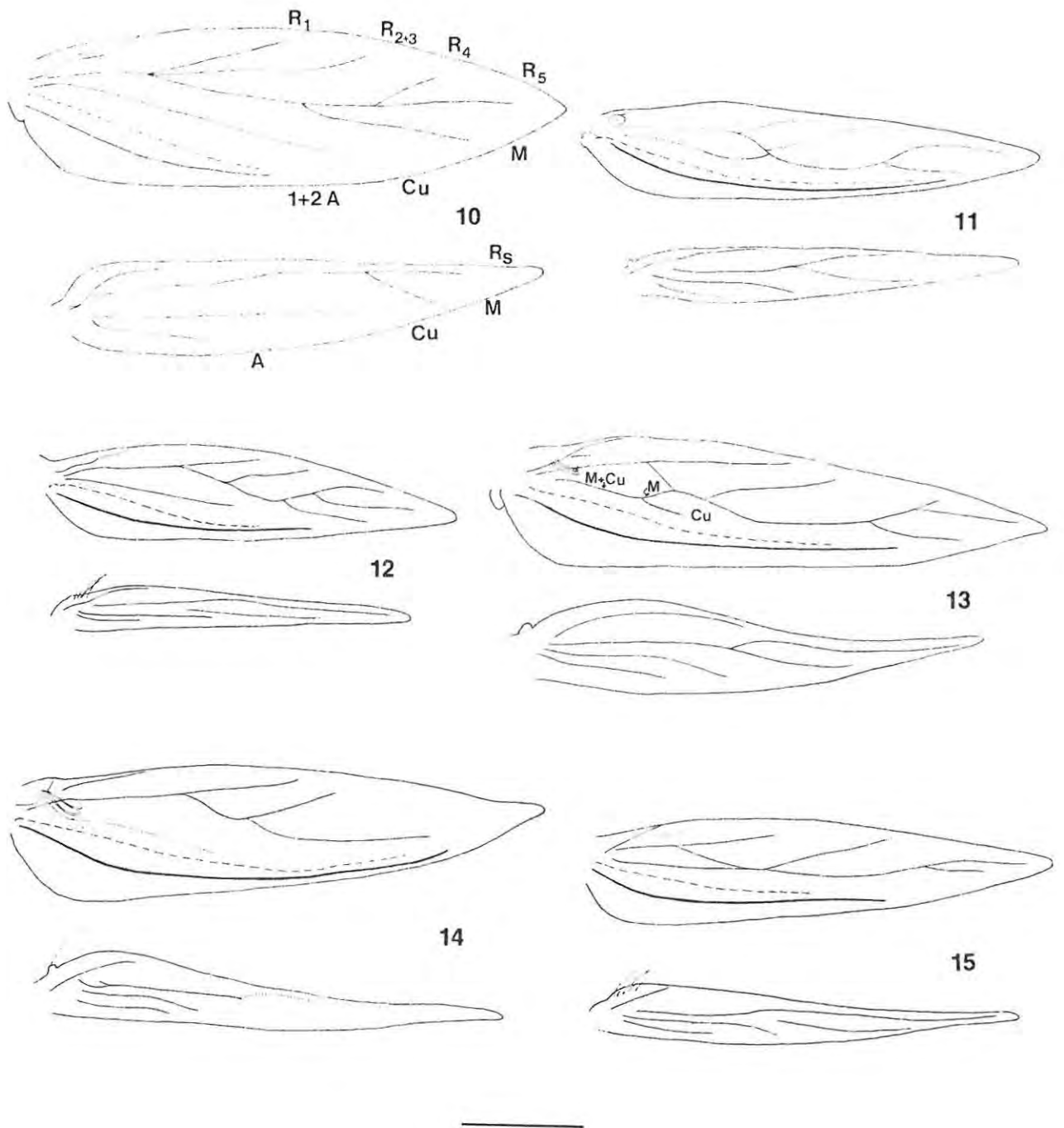
FIGS 1-3. Heads (anterior views). 1. *Simplimorpha lanceifoliella* (Vári).
 2. *Varius ochnicolus* (Vári), (B) terminal segments of antenna. 3.
Obrussa nigricapitella (Janse). Scale lines = 0,1 mm.



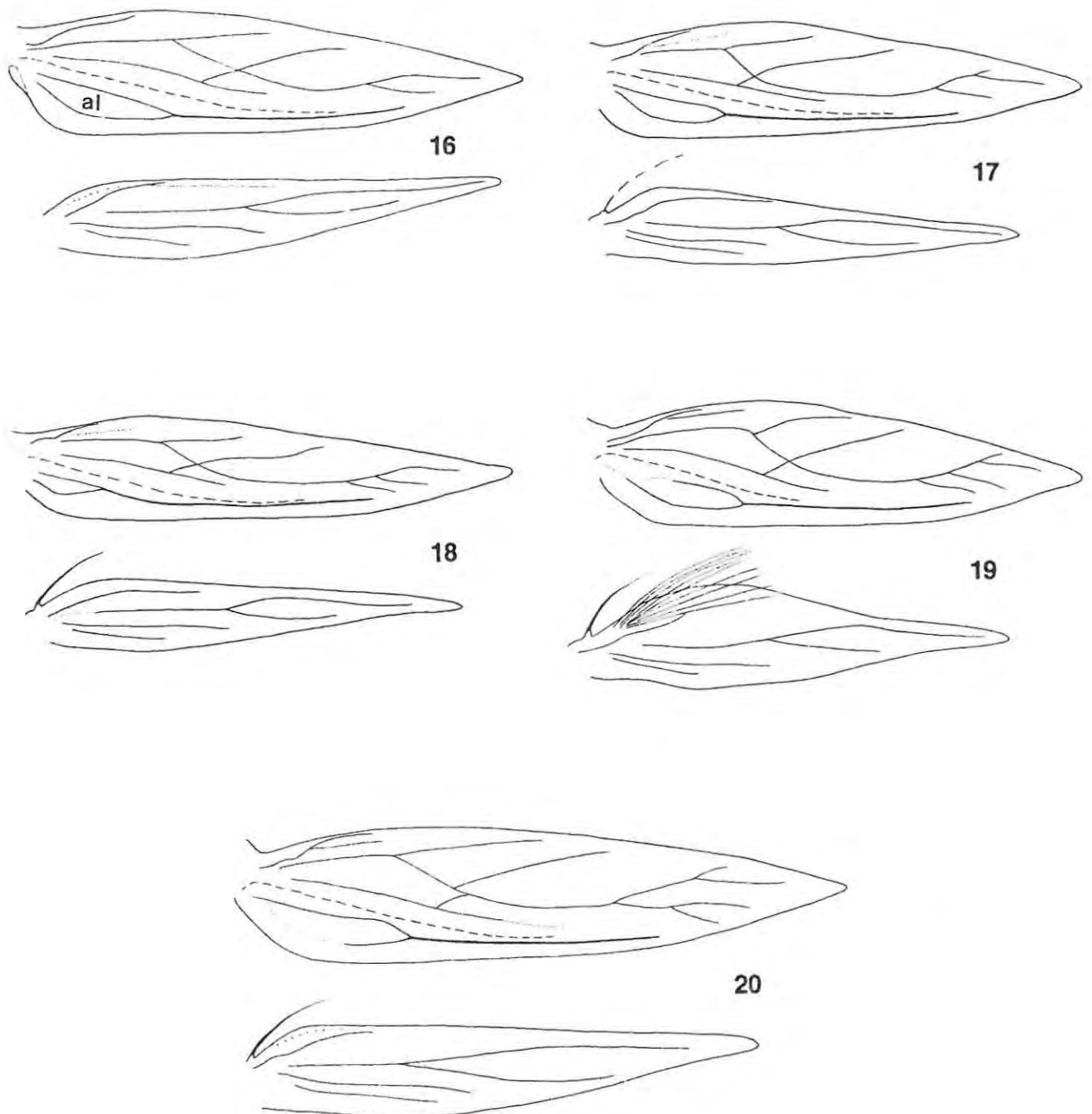
FIGS 4-6. Heads of *Ectoedemia* spp. 4. *E. (Laqueus) maritima* spec. nov., (B) labial palpus. 5. Part of maxillary palpus of *E. (L.) royenicola* (Vári). 6. *E. (L.) insulata* (Meyrick). Scale lines = 0,1 mm unless shown otherwise.



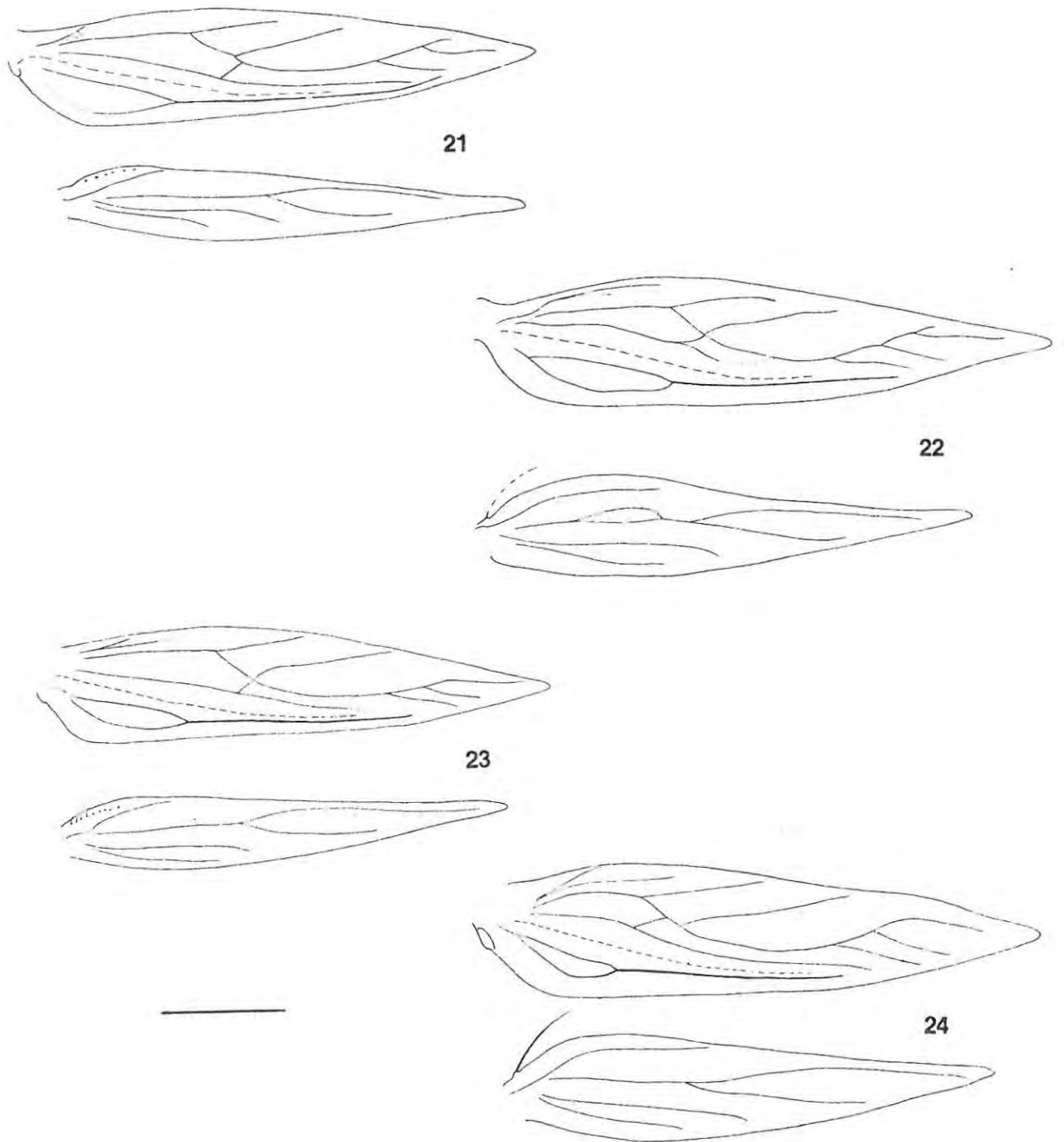
FIGS 7-9. Heads. 7. *Ectoedemia (Laqueus) kowynensis* spec. nov. 8. Scape, pedicel and first flagellar segment of antenna of *Ectoedemia (Fomoria) vannifera* (Meyrick). 9. *Areticulata leucosideae* spec. nov. Scale lines = 0,1 mm.



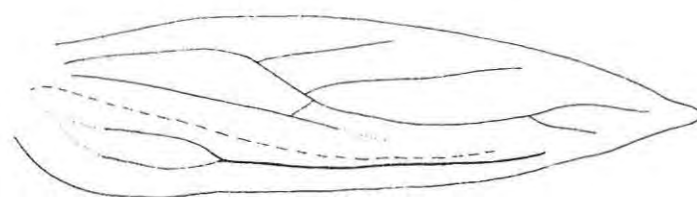
FIGS 10-15. Wing venation. 10. *Pectinivalva comuni* spec. nov. 11. *Simplimorpha lanceifoliella* (Vári). 12. *Varius ochricolus* (Vári). 13. *Obrussa crypsixantha* (Meyrick). 14. *Obrussa zimbabwiensis* spec. nov. 15. *Obrussa nigricapitella* (Janse). Scale 35 line = 0,5 mm.



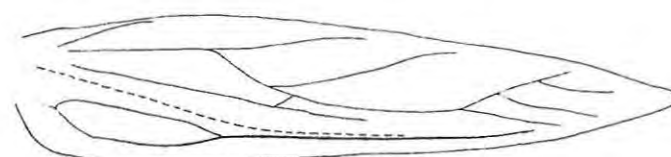
FIGS 16-20. Wing venation of *Ectoedemia* (*Laqueus*) spp. 16. *E.* (*L.*) *grandinosa* (Meyrick). 17. *E.* (*L.*) *simicola* spec. nov. 18. *E.* (*L.*) *guerkliae* spec. nov. 19. *E.* (*L.*) *undoniella* spec. nov. 20. *E.* (*L.*) *scabridae* spec. nov. Scale line = 0,5 mm.



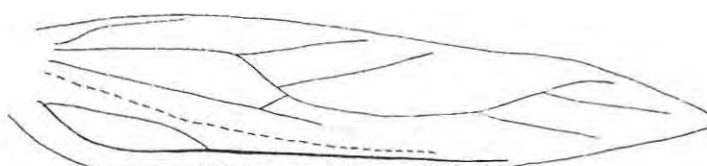
FIGS 21-24. Wing venation of *Ectoedemia (Laqueus)* spp. 21. *E. (L.) royenicola* (Vári). 22. *E. (L.) denticulata* spec. nov. 23. *E. (L.) undatae* spec. nov. 24. *E. (L.) bicarina* spec. nov. Scale line = 0,5 mm.



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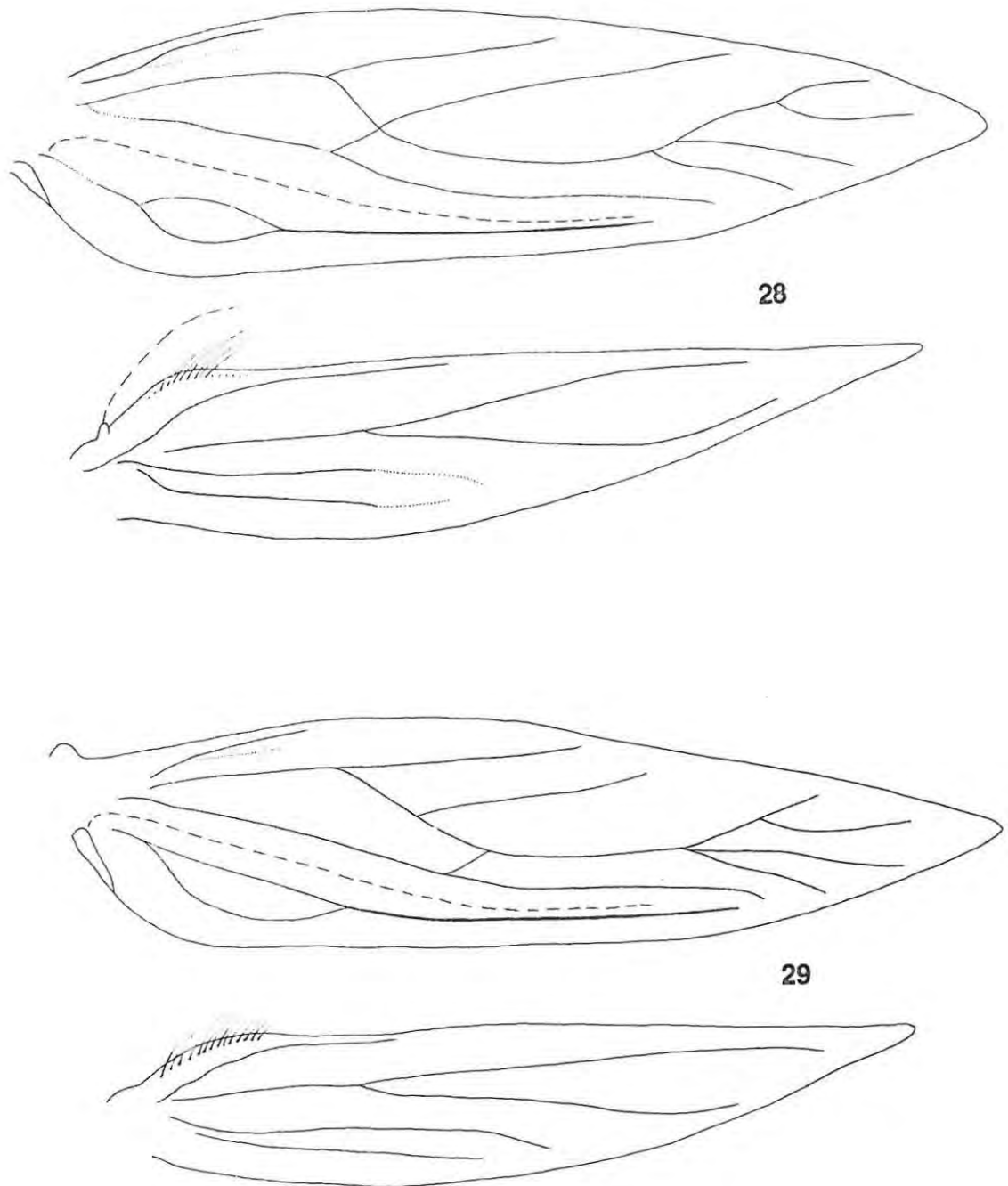
26



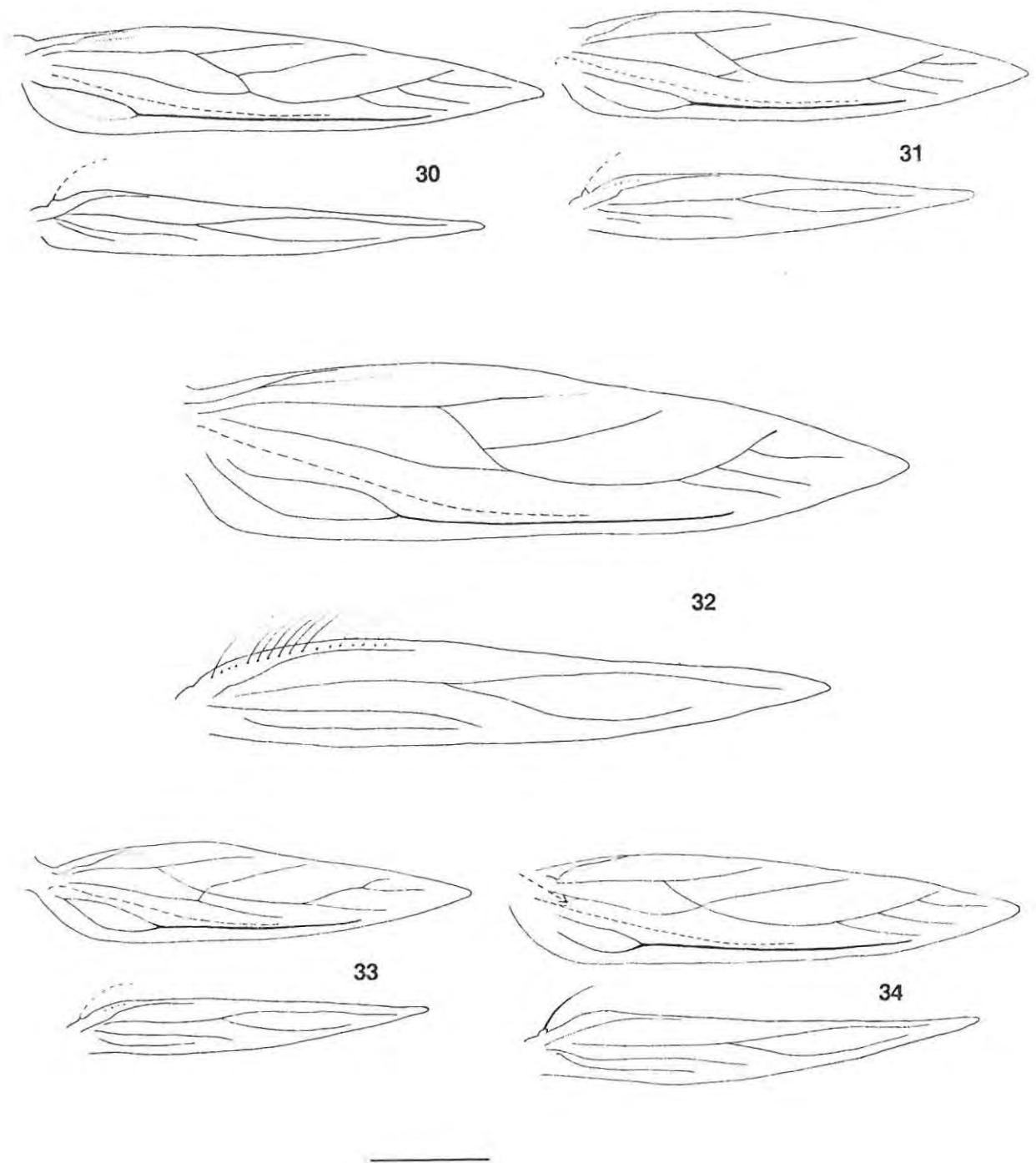
27



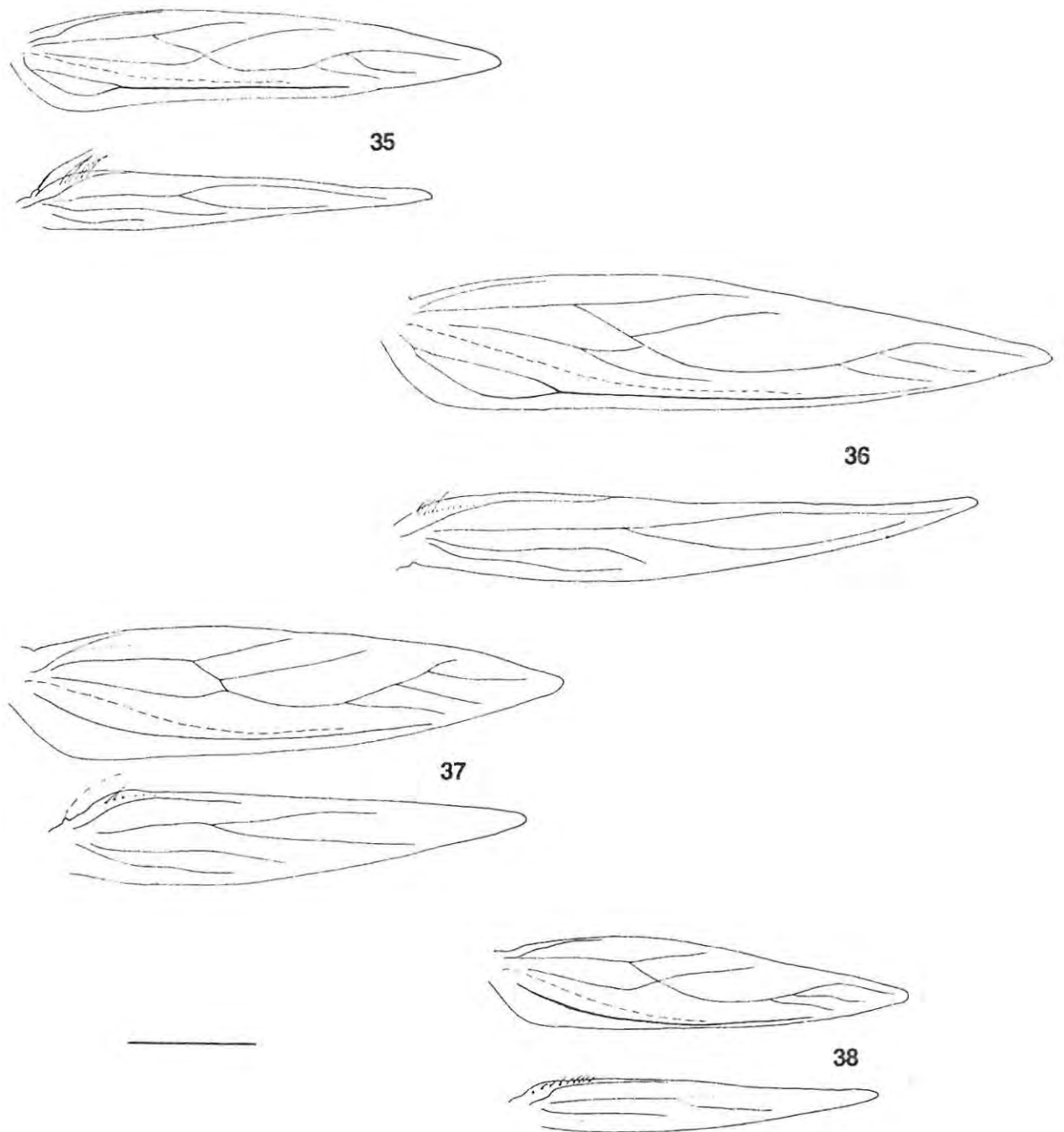
FIGS 25-27. Wing venation of *Ectoedemia* (*Laqueus*) spp. 25. *E.* (*L.*) *craspedota* (Vári). 26. *E.* (*L.*) *digitata* spec. nov. 27. *E.* (*L.*) *limburgensis* spec. nov. Scale line = 0,5 mm.



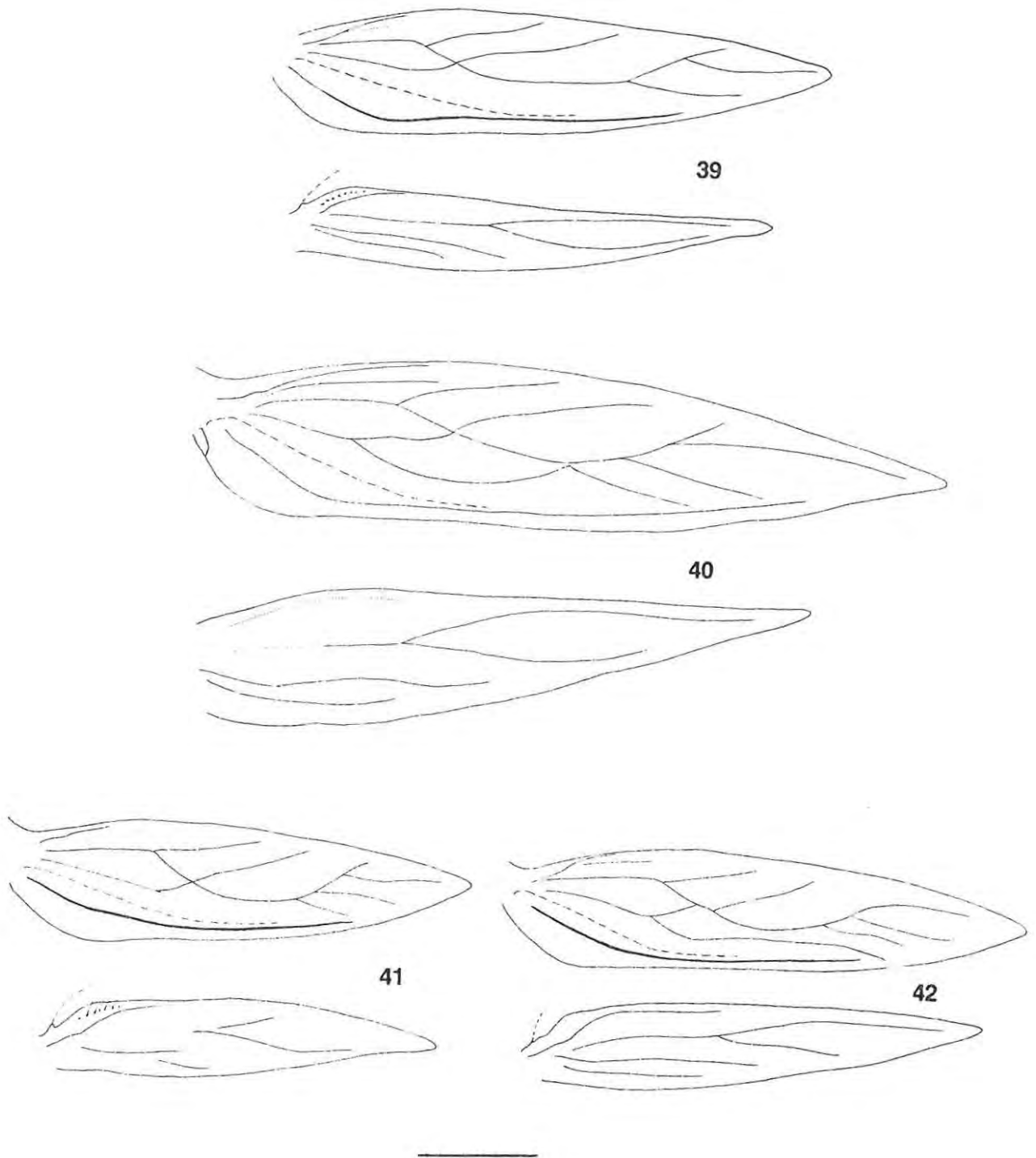
FIGS 28-29. Wing venation of *Ectoedemia* (*Laqueus*) spp. 28. *E. (L.) subnitescens* (Meyrick). 29. *E. (L.) capensis* spec. nov. Scale line = 0,5 mm.



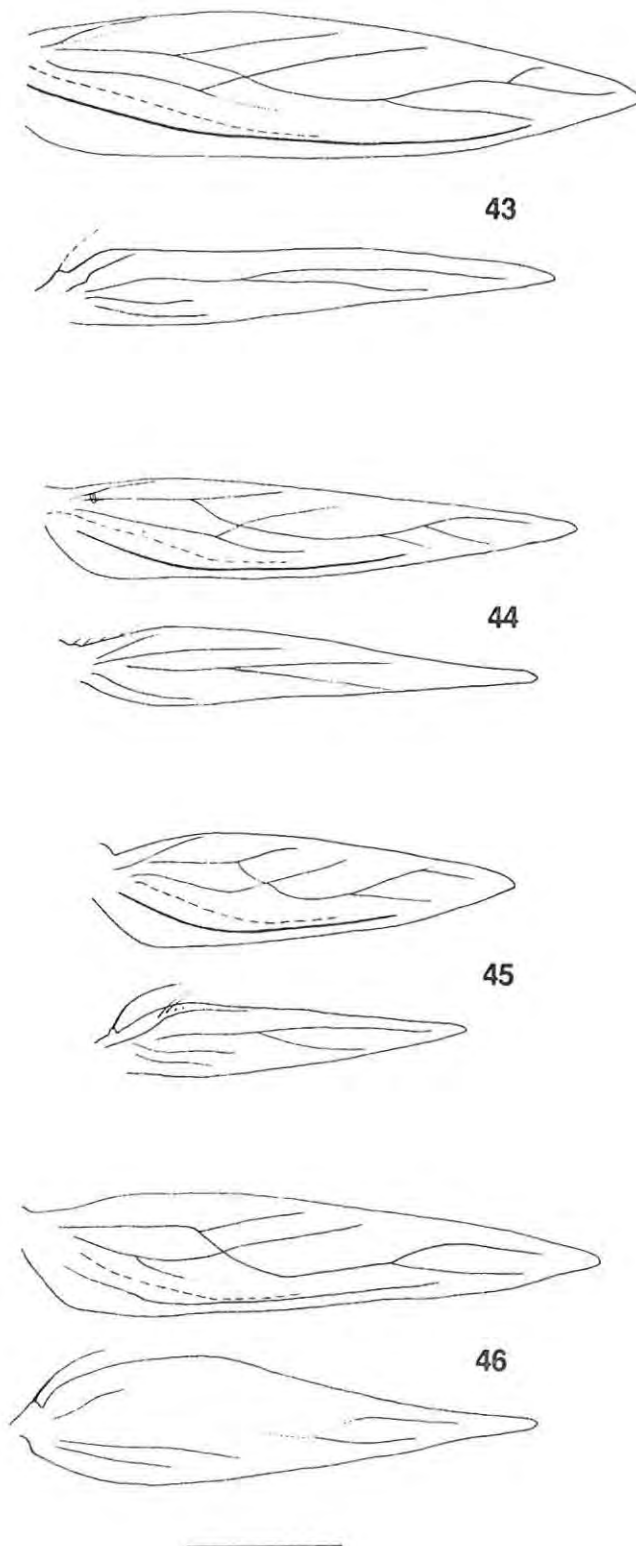
FIGS 30-34. Wing venation of *Ectoedemia* (*Laqueus*) spp. 30. *E.* (*L.*) *gymnosporiae* (Vári). 31. *E.* (*L.*) *psarodes* (Vári). 32. *E.* (*L.*) *insulata* (Meyrick). 33. *E.* (*L.*) *kowynensis* spec. nov. 34. *E.* (*L.*) *nylstroomensis* spec. nov. Scale line = 0,5mm.



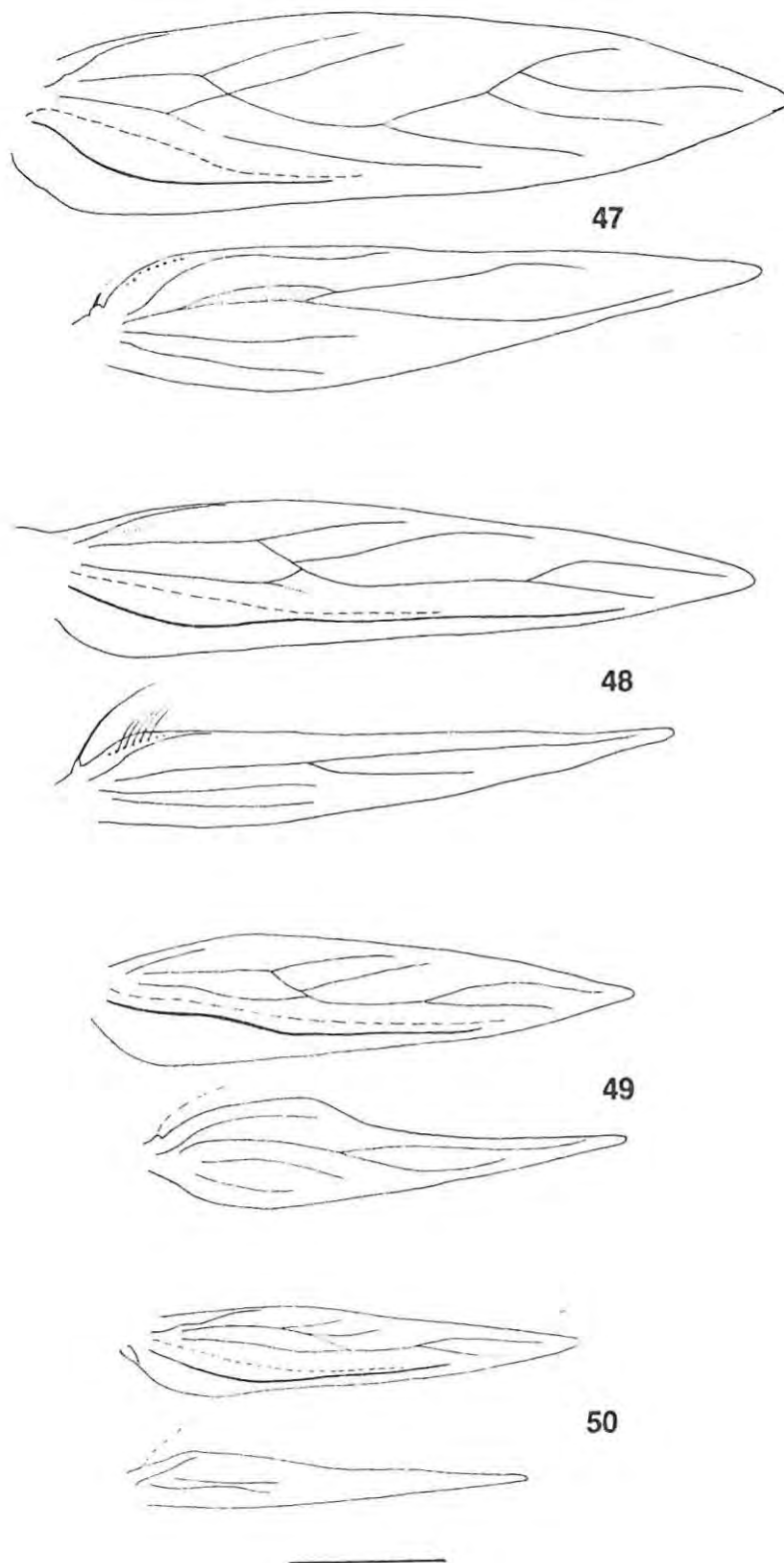
FIGS 35-38. Wing venation of *Ectoedemia (Laucus)* spp. and *Ectoedemia (Fomoria)* spp. 35. *E. (L.) rhabdophora* spec. nov. 36. *E. (L.) crispae* spec. nov. 37. *E. (F.) oleivora* (Vári). 38. *E. (F.) pappeivora* (Vári). Scale line = 0,5 mm.



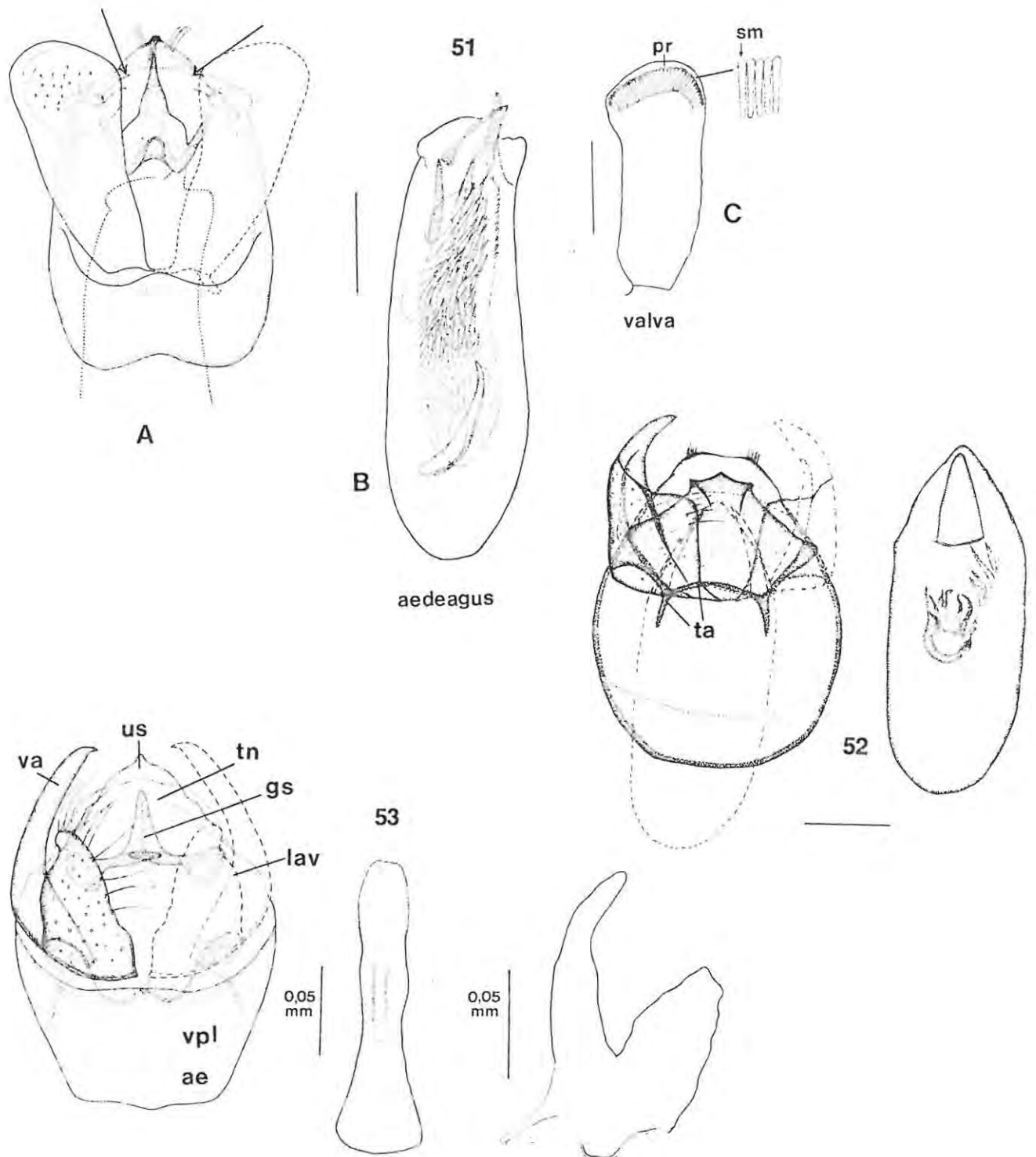
FIGS 39-42. Wing venation of *Ectoedemia (Fomoria)* spp. 39. *E. (F.) indicaevora* spec. nov. 40. *E. (F.) knysnaensis* spec. nov. 41. *E. (F.) lucidae* spec. nov. 42. *E. (F.) tecomariae* (Vári). Scale line = 0,5 mm.



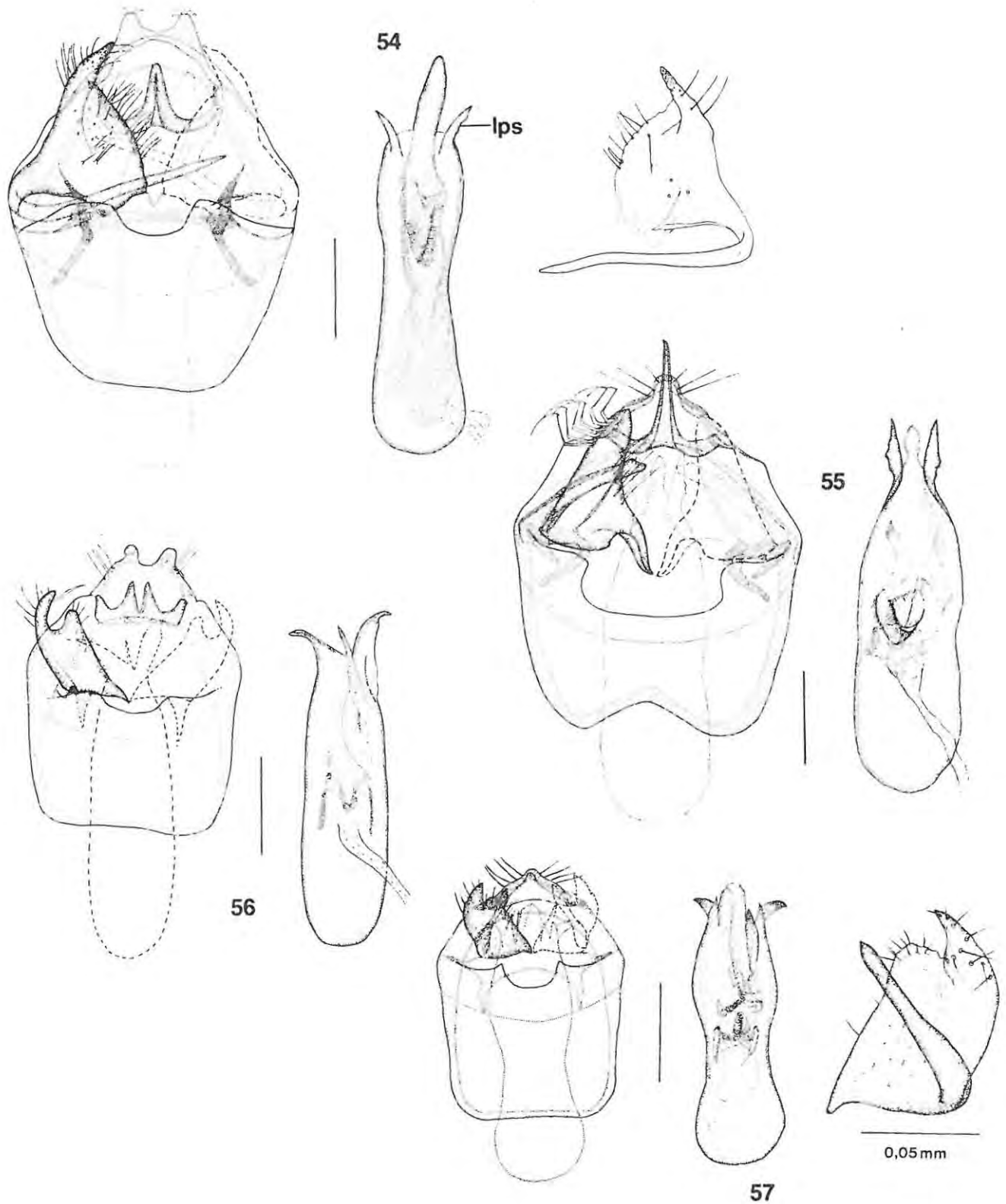
FIGS 43-46. Wing venation of *Ectoedemia (Fomoria)* spp. 43. *E. (F.) myrtinaecola* spec. nov. 44. *E. (F.) leptodictyae* spec. nov. 45. *E. (F.) malelanensis* spec. nov. 46. *E. (F.) thermae* spec. nov. Scale line = 0,5 mm.



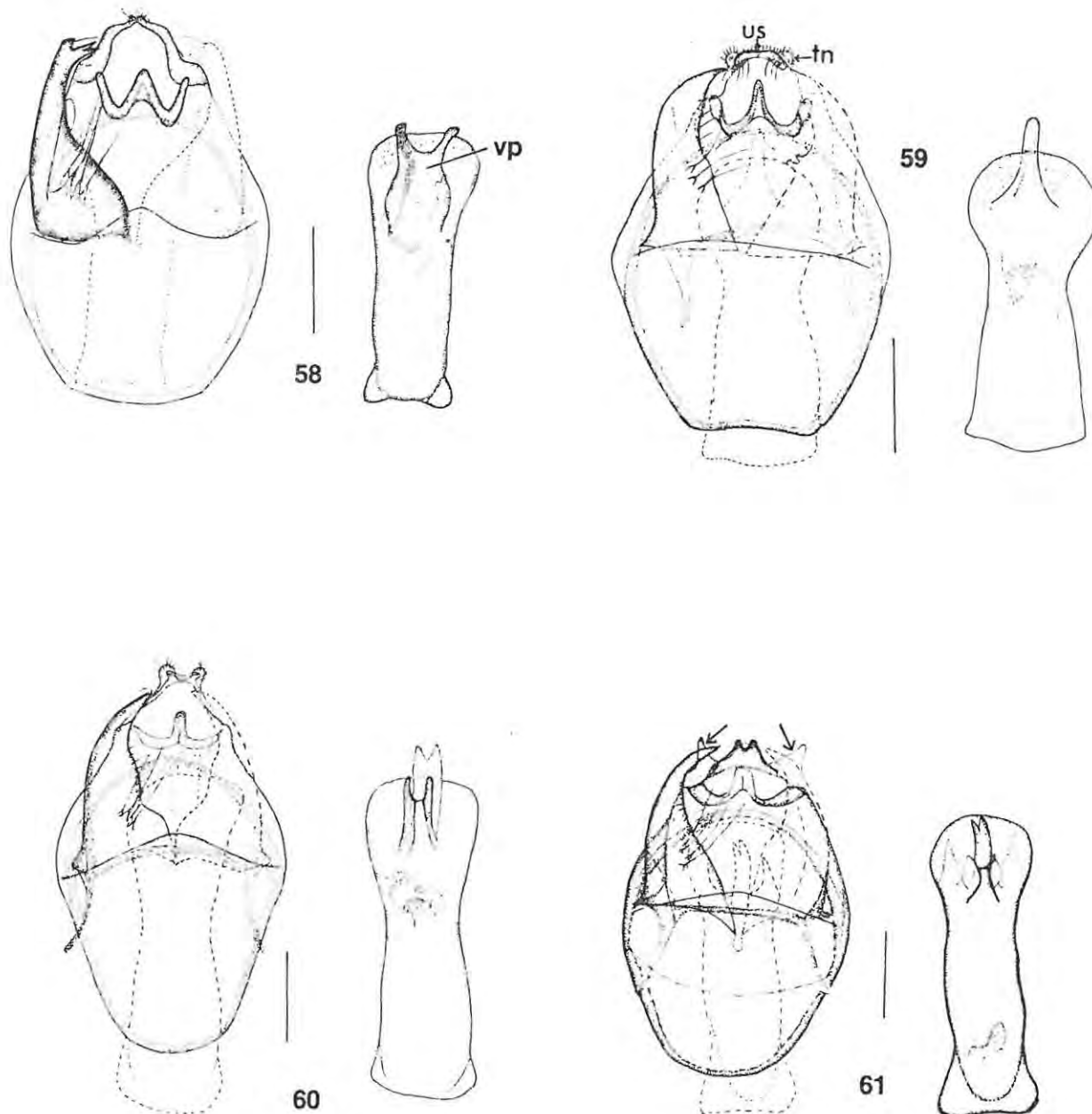
FIGS 47-50. Wing venation of *Ectoedemia* (*Fomoria*) spp. and *Areticulata* sp. 47. *E. (F.) portensis* spec. nov. 48. *E. (F.) fuscata* (Janse). 49. *E. (F.) vannifera* (Meyrick). 50. *A. leucosideae* spec. nov. Scale line = 0,5 mm.



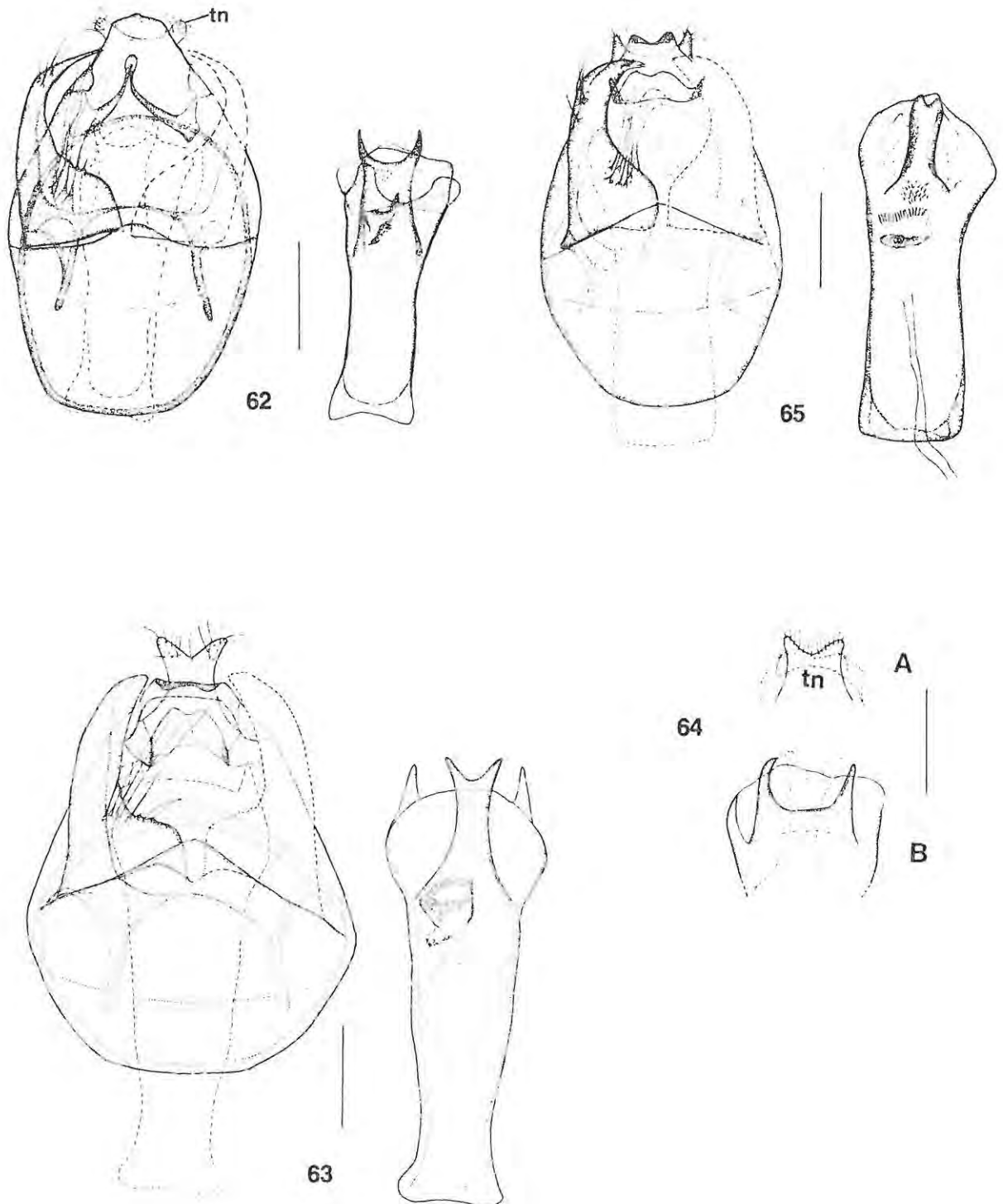
FIGS 51-53. Male genitalia (ventral view unless otherwise indicated).
 51. *Pectinivalva commoni* spec. nov., (A) with arrows to show rod-like extensions of lateral arms of vinculum, (C) right valva shown from inner (dorsal) view. 52. *Simplimorpha lanceifoliella* (Vári). 53. *Varius ochnicolus* (Vári), left valva also shown from inner (dorsal) view. Scale lines = 0,1 mm unless otherwise indicated.



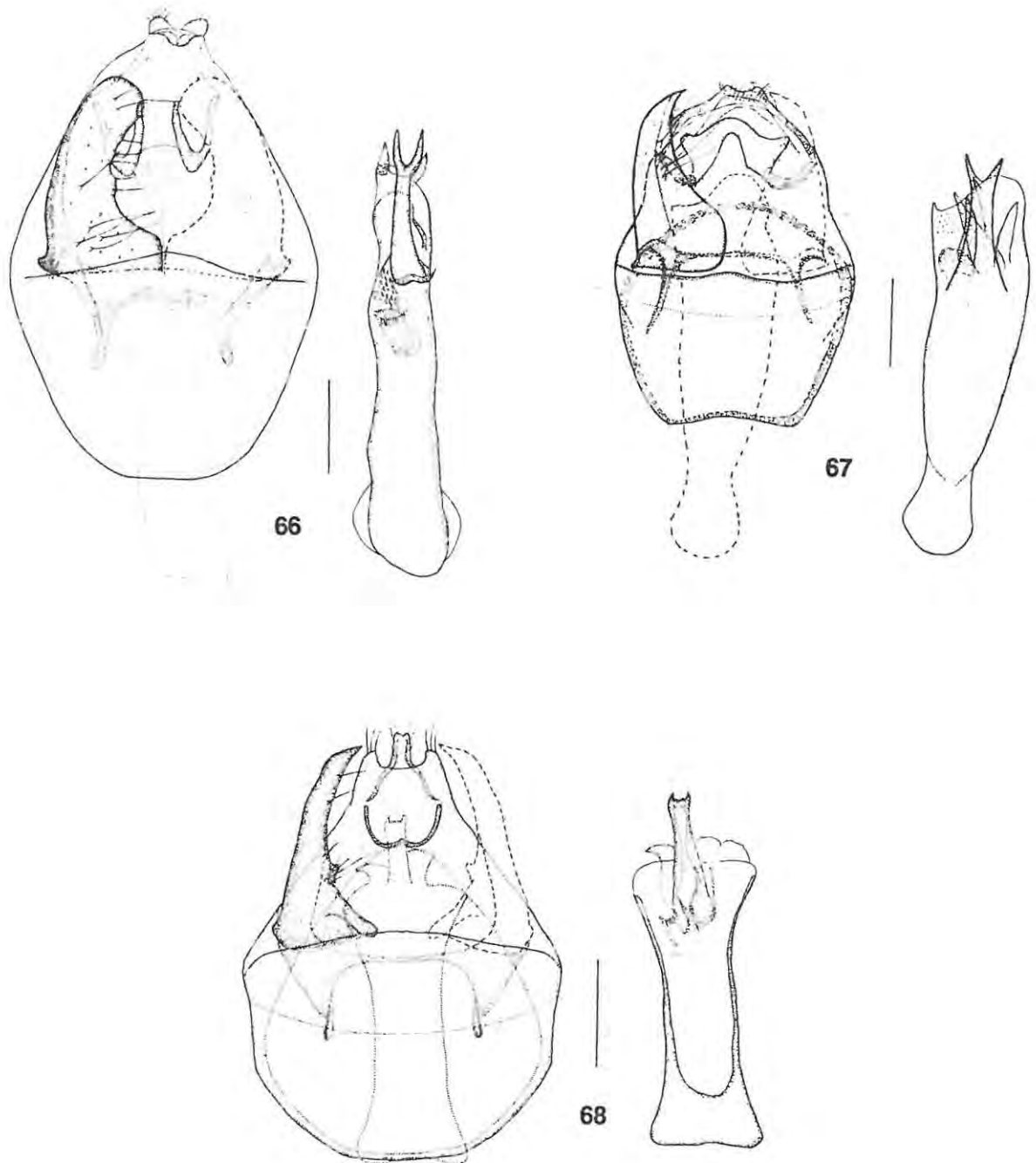
FIGS 54-57. Male genitalia of *Obrussa* spp. 54. *O. crypsixantha* (Meyrick), right valva also shown from inner (dorsal) aspect. 55. *O. zimbabwiensis* spec. nov. 56. *O. nigricapitella* (Janse). 57. *O. krugerensis* spec. nov., right valva also shown from inner (dorsal) aspect. Scale lines = 0,1 mm unless otherwise indicated.



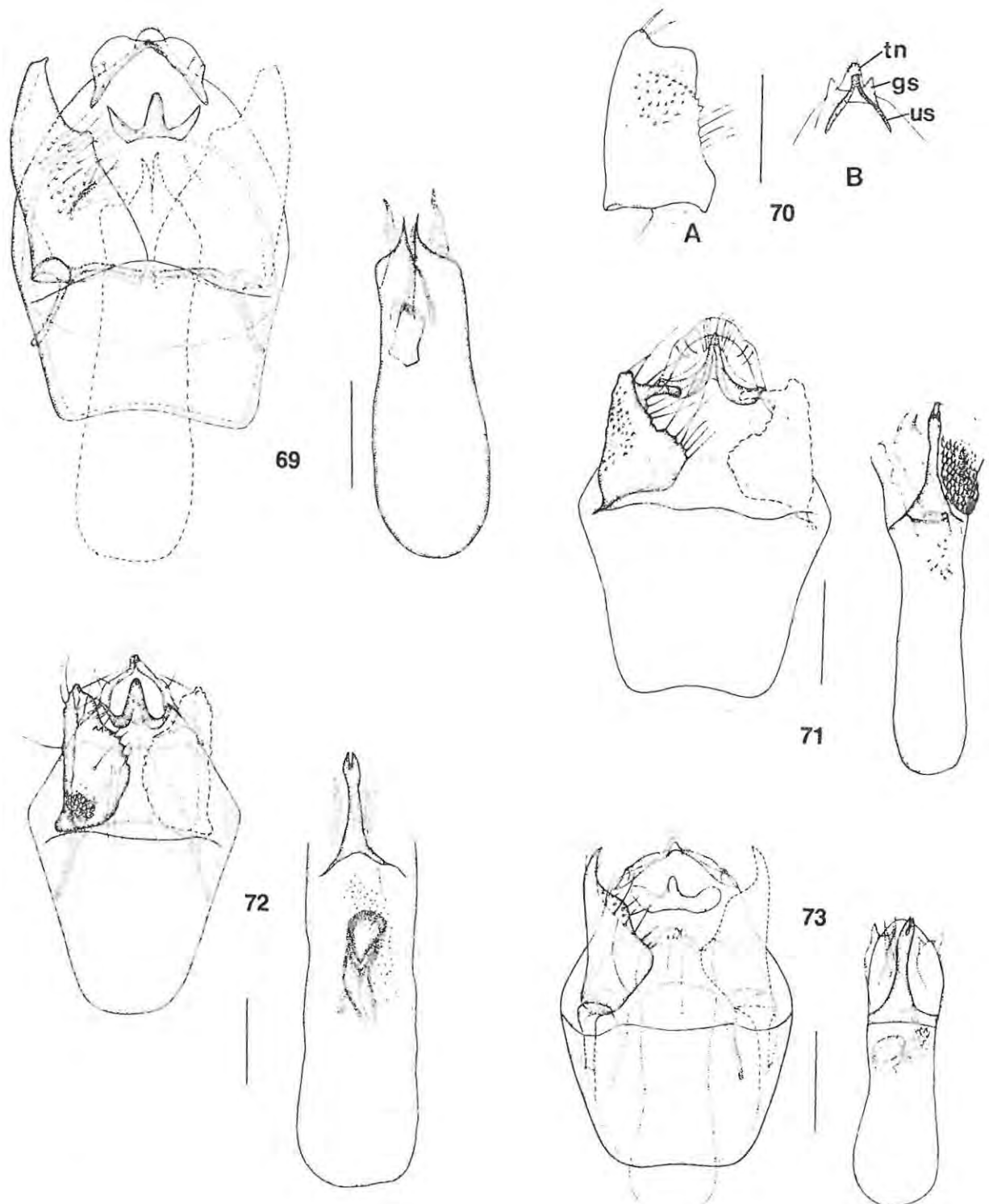
FIGS 58-61. Male genitalia of *Ectoedemia* (*Laqueus*) spp. 58. *E. (L.) stimulata* (Meyrick). 59. *E. (L.) grandinosa* (Meyrick). 60. *E. (L.) wilkinsoni* spec. nov. 61. *E. (L.) simicola* spec. nov. Scale lines = 0,1 mm.



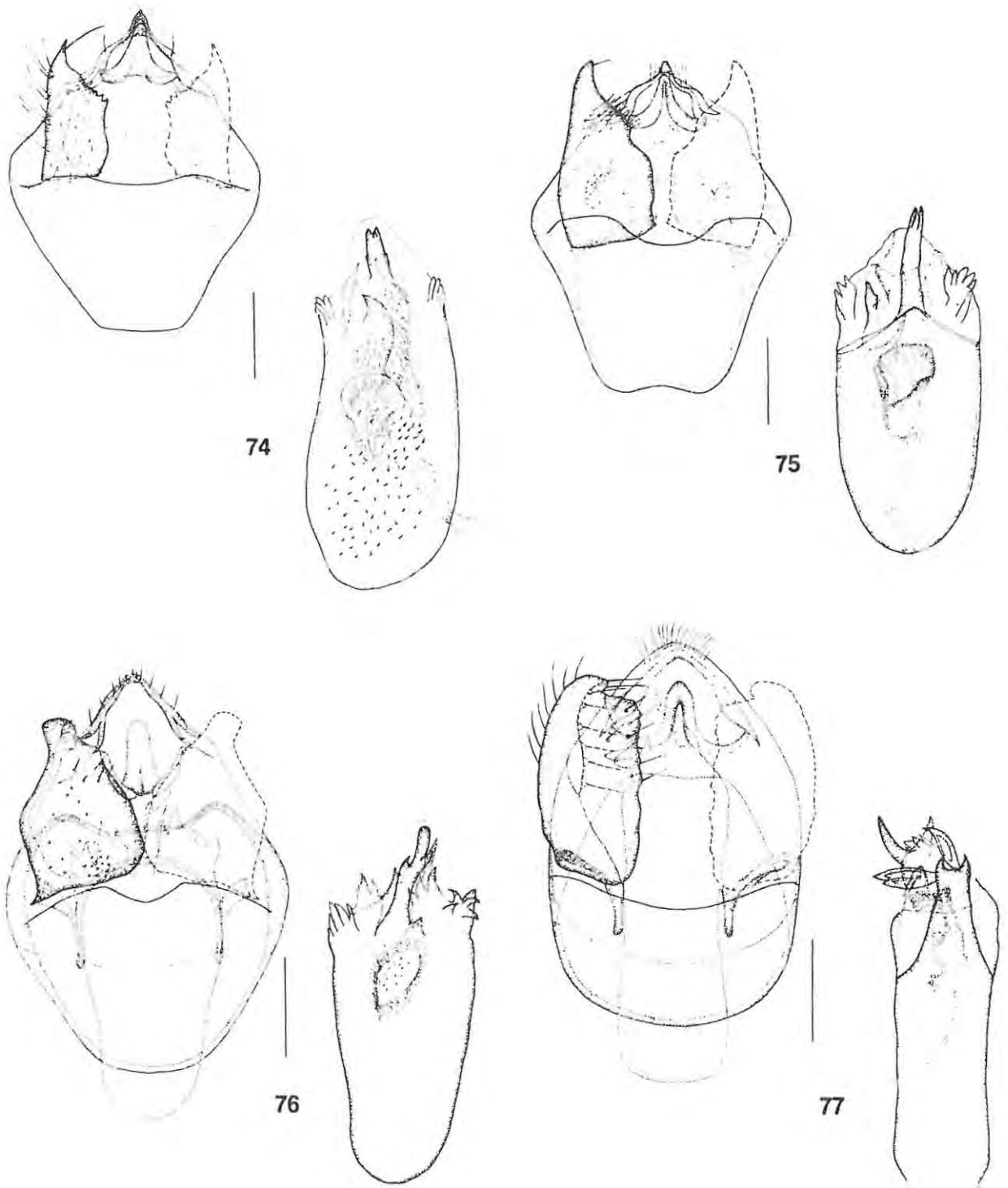
FIGS 62-65. Male genitalia of *Ectoedemia* (*Laqueus*) spp. 62. *E.* (*L.*) *guerckiae* spec. nov. 63. *E.* (*L.*) *macrochaeta* (Meyrick). 64. *E.* (*L.*) *furcella* spec. nov., (A) dorsal view of tegumen; (B) dorsal view of posterior part of aedeagus to show link between dorsolateral carinae (stippled). 65. *E.* (*L.*) *maritima* spec. nov. Scale lines = 0,1 mm.



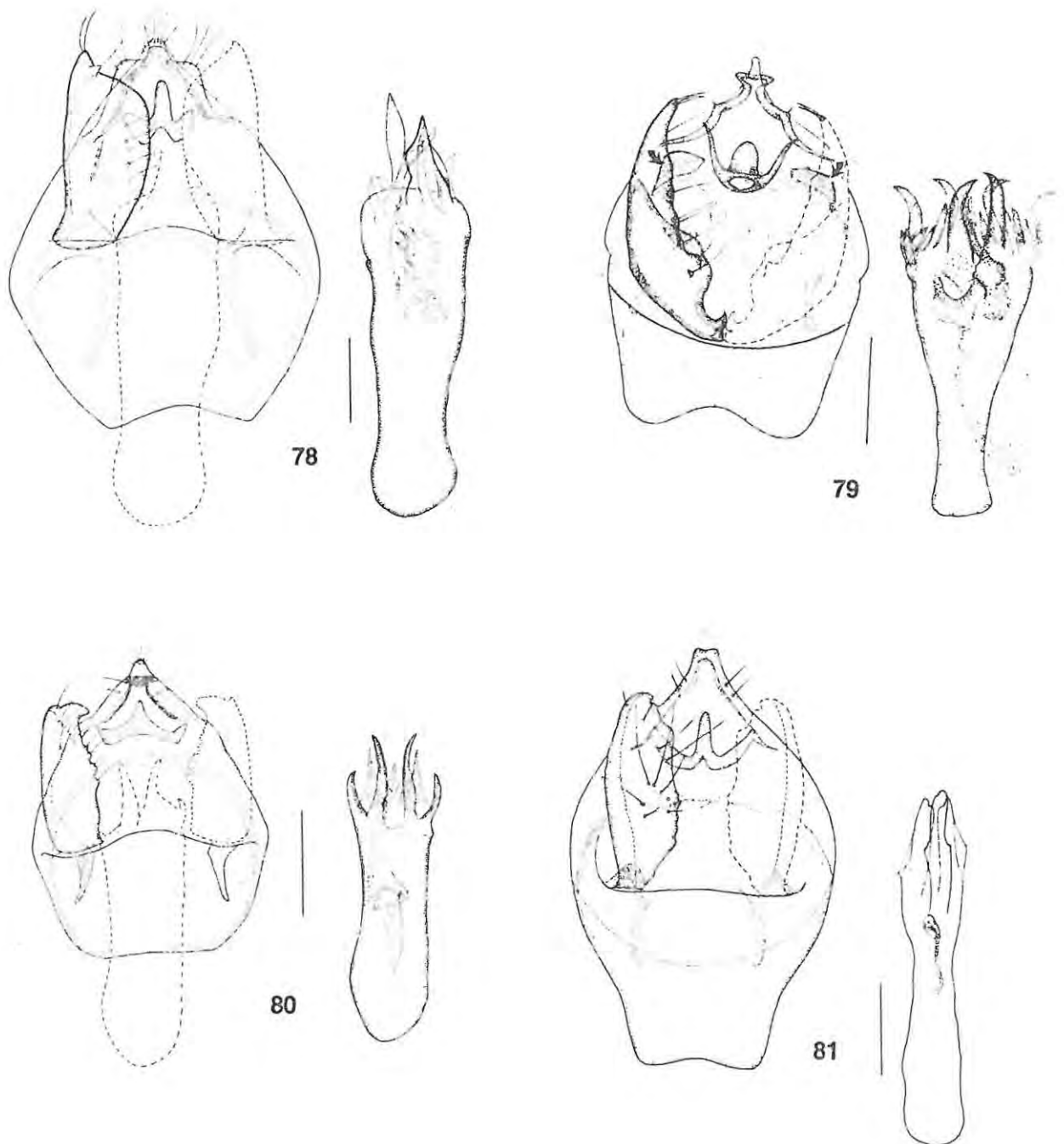
FIGS 66-68. Male genitalia of *Ectoedemia* (*Laqueus*) spp. 66. *E.* (*L.*) *undoniella* spec. nov. 67. *E.* (*L.*) *scabridae* spec. nov. 68. *E.* (*L.*) *jupiteri* spec. nov. Scale lines = 0,1 mm.



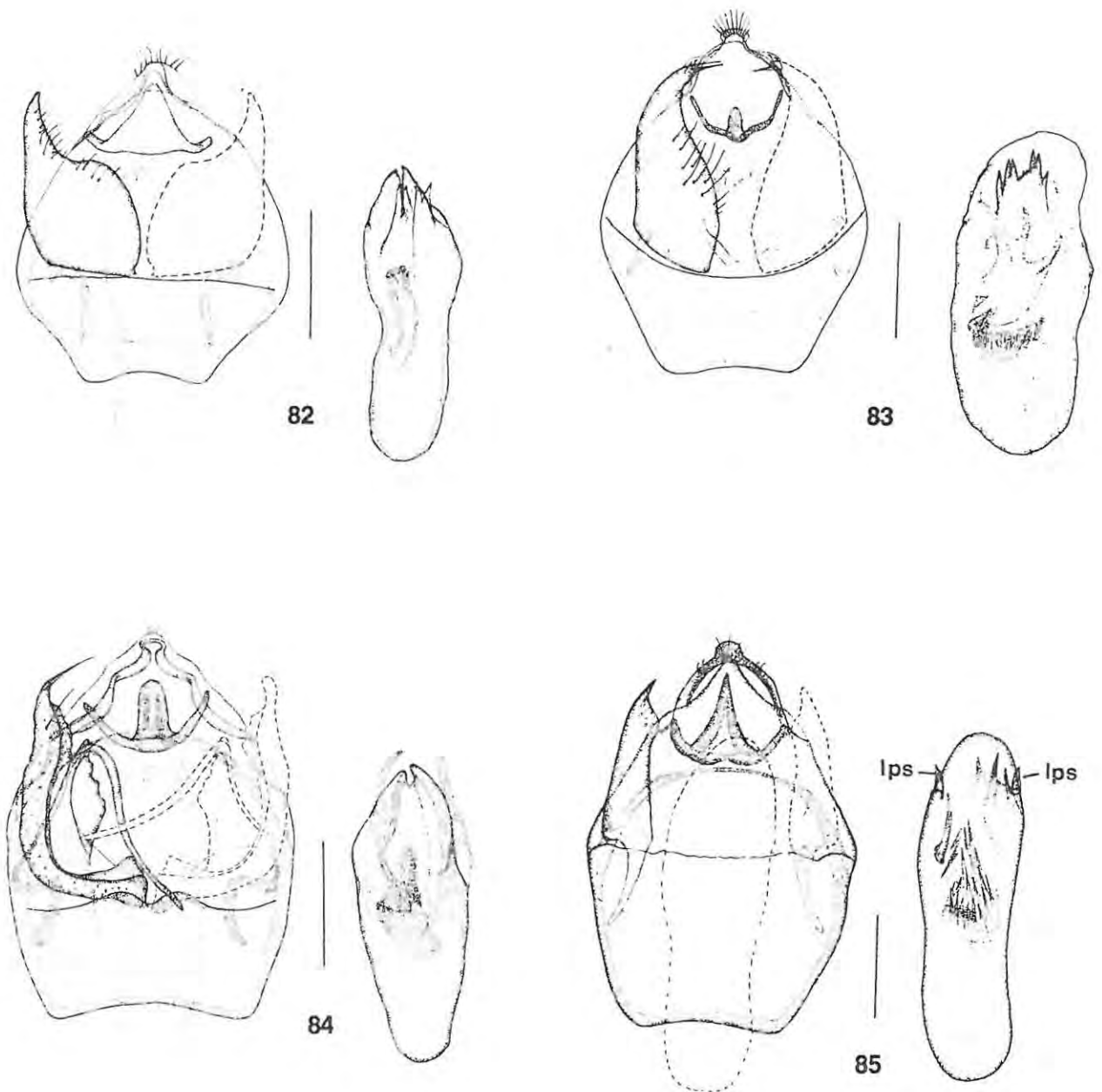
FIGS 69-73. Male genitalia of *Ectoedemia* (*Laqueus*) spp. 69. *E. (L.) royenicola* (Vári). 70. *E. (L.) nigrisquama* spec. nov., (A) valva; (B) tegumen, gnathos, and uncus. 71. *E. (L.) denticulata* spec. nov. 72. *E. (L.) undatae* spec. nov. 73. *E. (L.) bicarina* spec. nov. Scale lines = 0,1 mm.



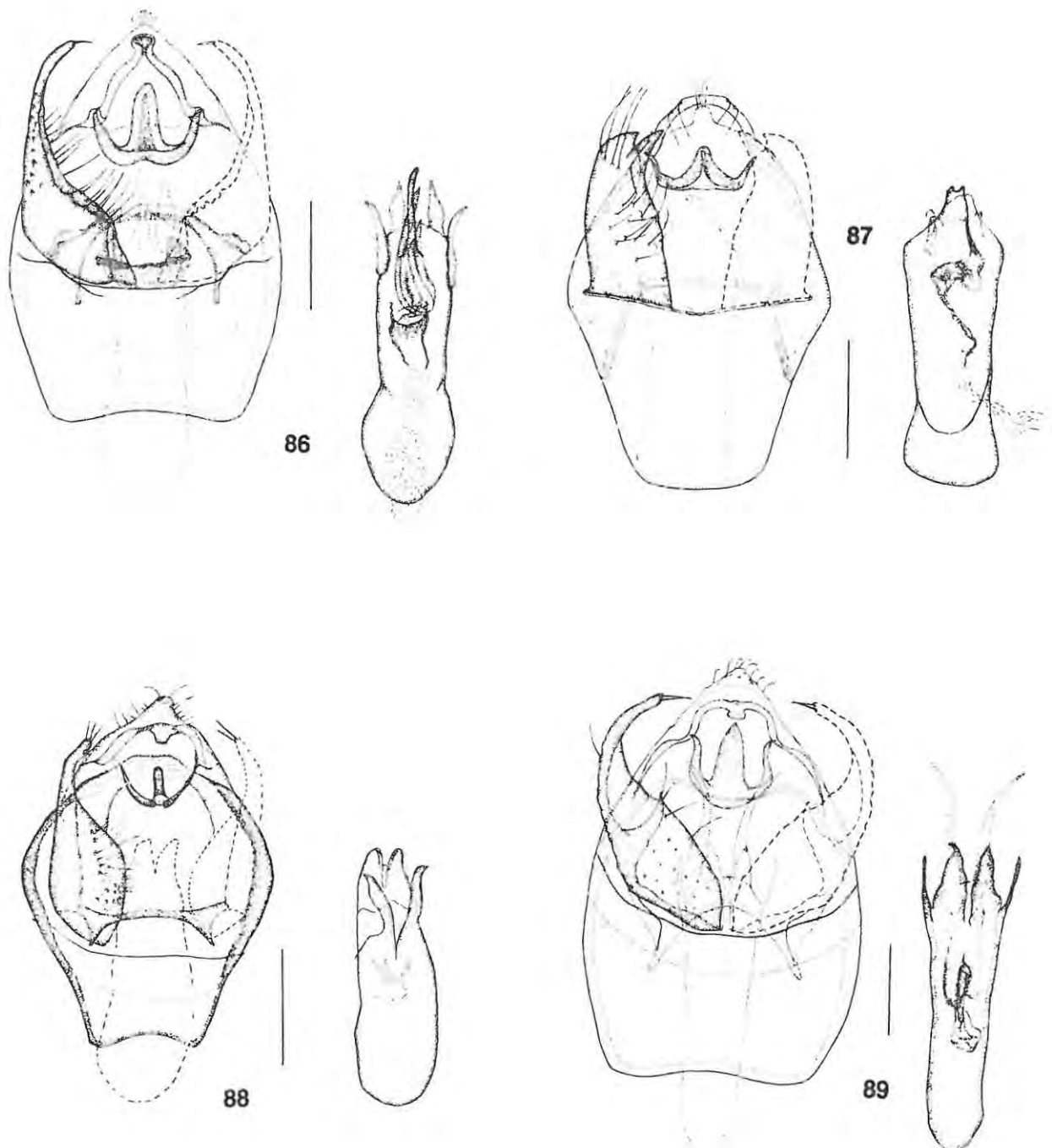
FIGS 74-77. Male genitalia of *Ectoedemia* (*Laqueus*) spp. 74. *E. (L.) craspedota* (Vári). 75. *E. (L.) digitata* spec. nov. 76. *E. (L.) limburgensis* spec. nov. 77. *E. (L.) subnitescens* (Meyrick). Scale lines = 0,1 mm.



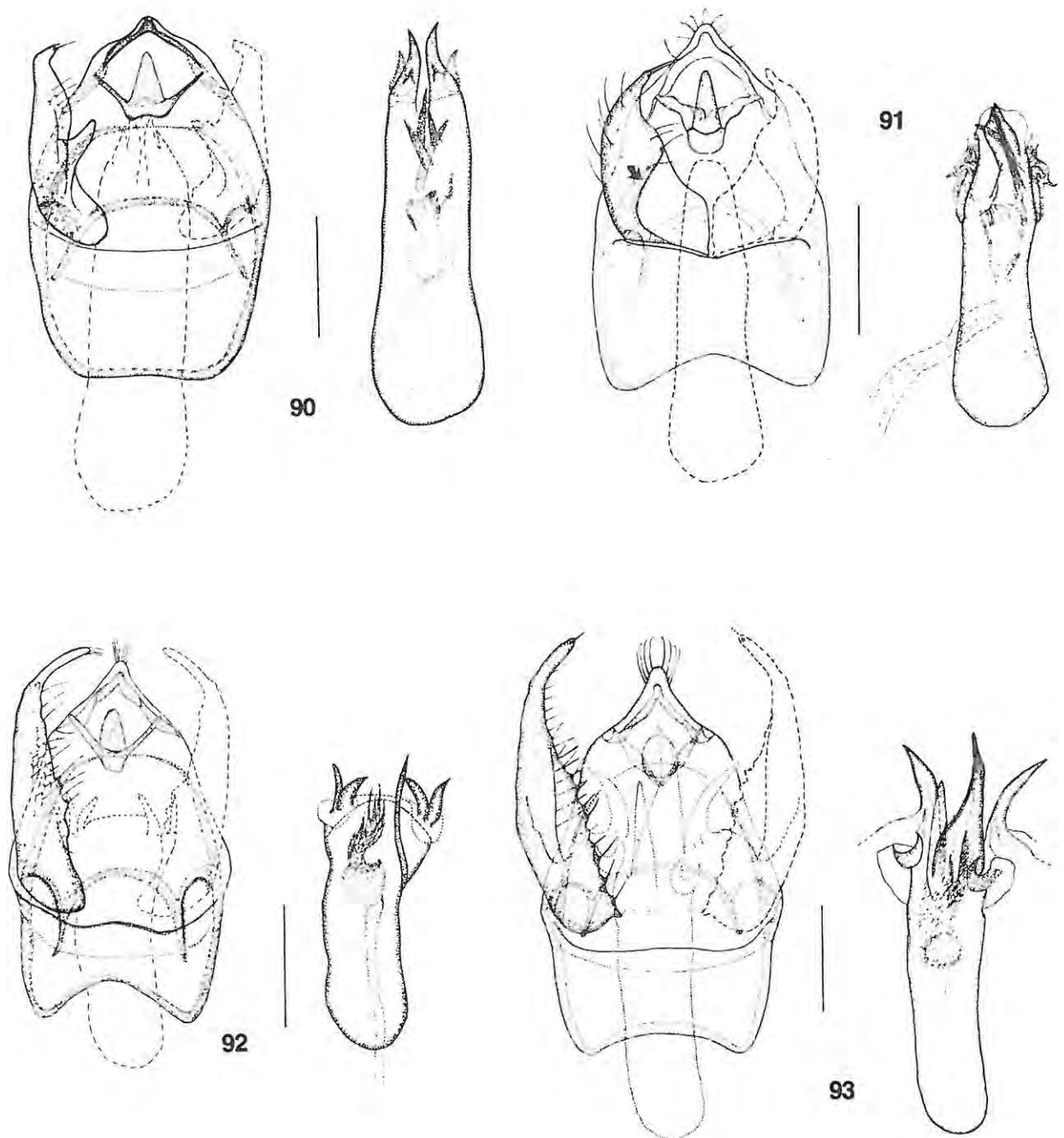
FIGS 78-81. Male genitalia of *Ectoedemia* (*Laqueus*) spp. 78. *E.* (*L.*) *capensis* spec. nov. 79. *E.* (*L.*) *gymnosporiae* (Vári), lateral sclerites of lateral arms of vinculum are arrowed. 80. *E.* (*L.*) *psarodes* (Vári). 81. *E.* (*L.*) *insulata* (Meyrick). Scale lines = 0,1 mm.



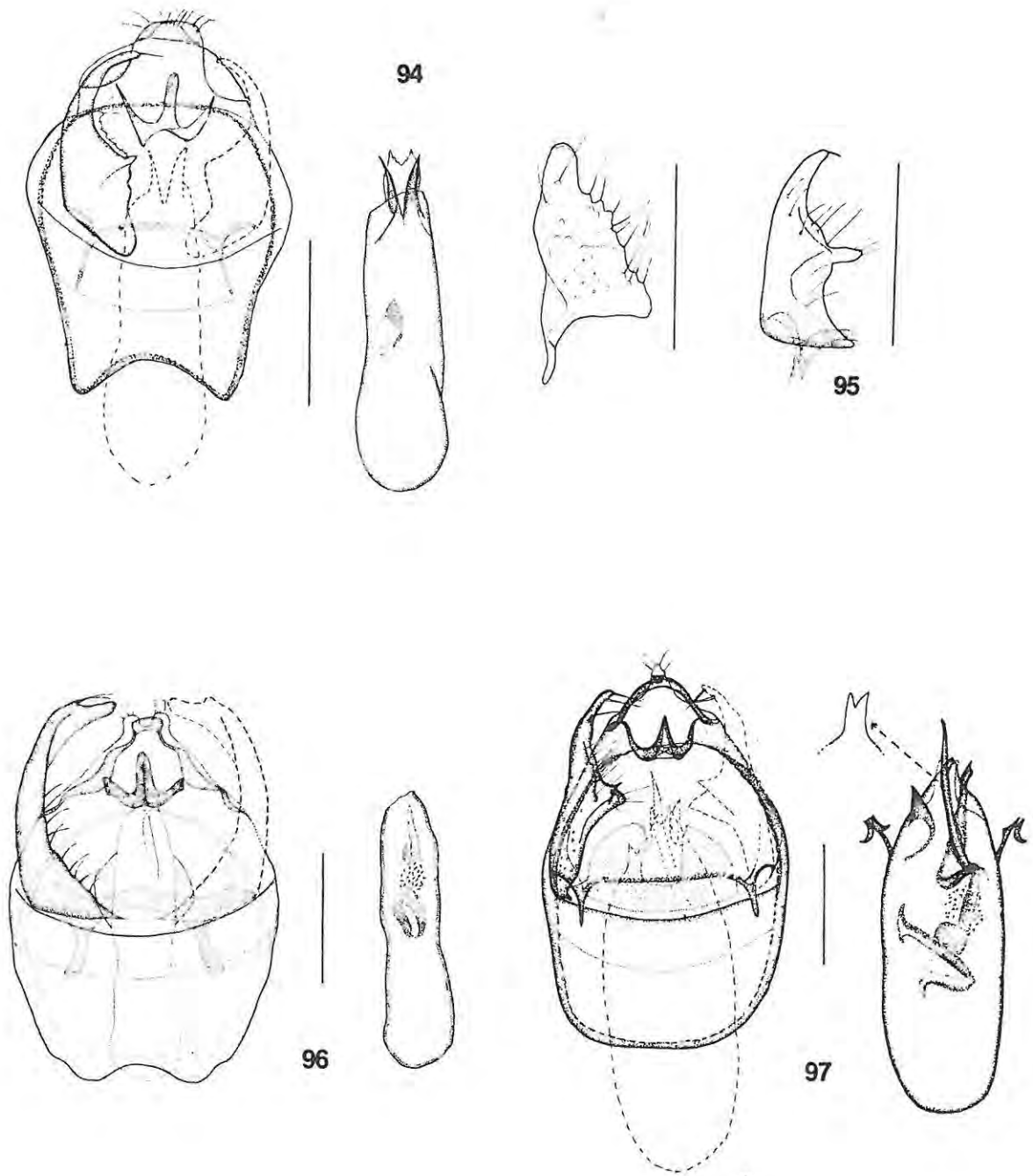
FIGS 82-85. Male genitalia of *Ectoedemia (Laqueus)* spp. 82. *E. (L.) kowynensis* spec. nov. 83. *E. (L.) nylstroomensis* spec. nov. 84. *E. (L.) rhabdophora* spec. nov. 85. *E. (L.) crispae* spec. nov. Scale lines = 0,1 mm.



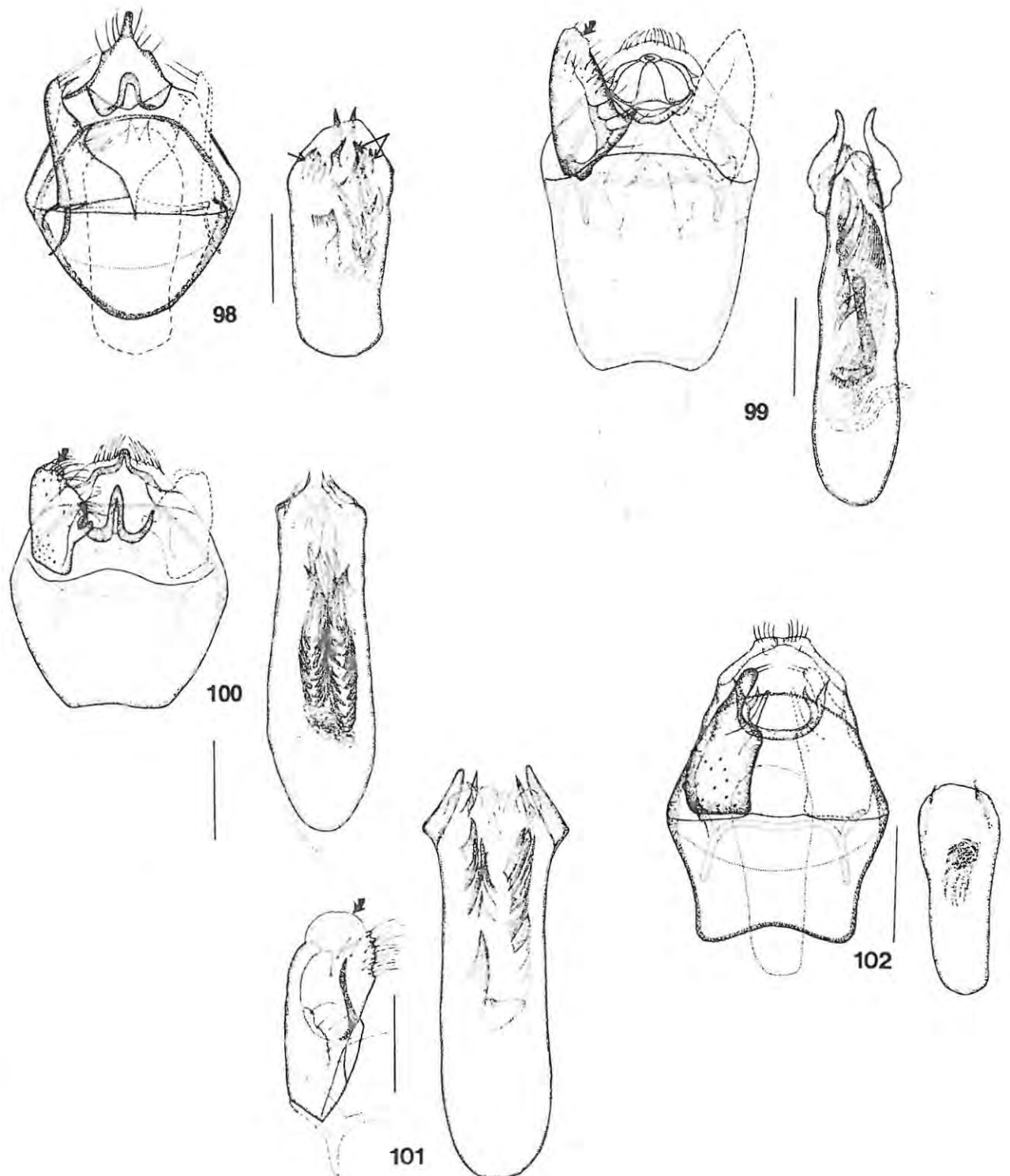
FIGS 86-89. Male genitalia of *Ectoedemia* (*Fomoria*) spp. 86. *E.* (*F.*) *oleivora* (Vári). 87. *E.* (*F.*) *pappeivora* (Vári). 88. *E.* (*F.*) *indicaevora* spec. nov. 89. *E.* (*F.*) *knysnaensis* spec. nov. Scale lines = 0,1 mm.



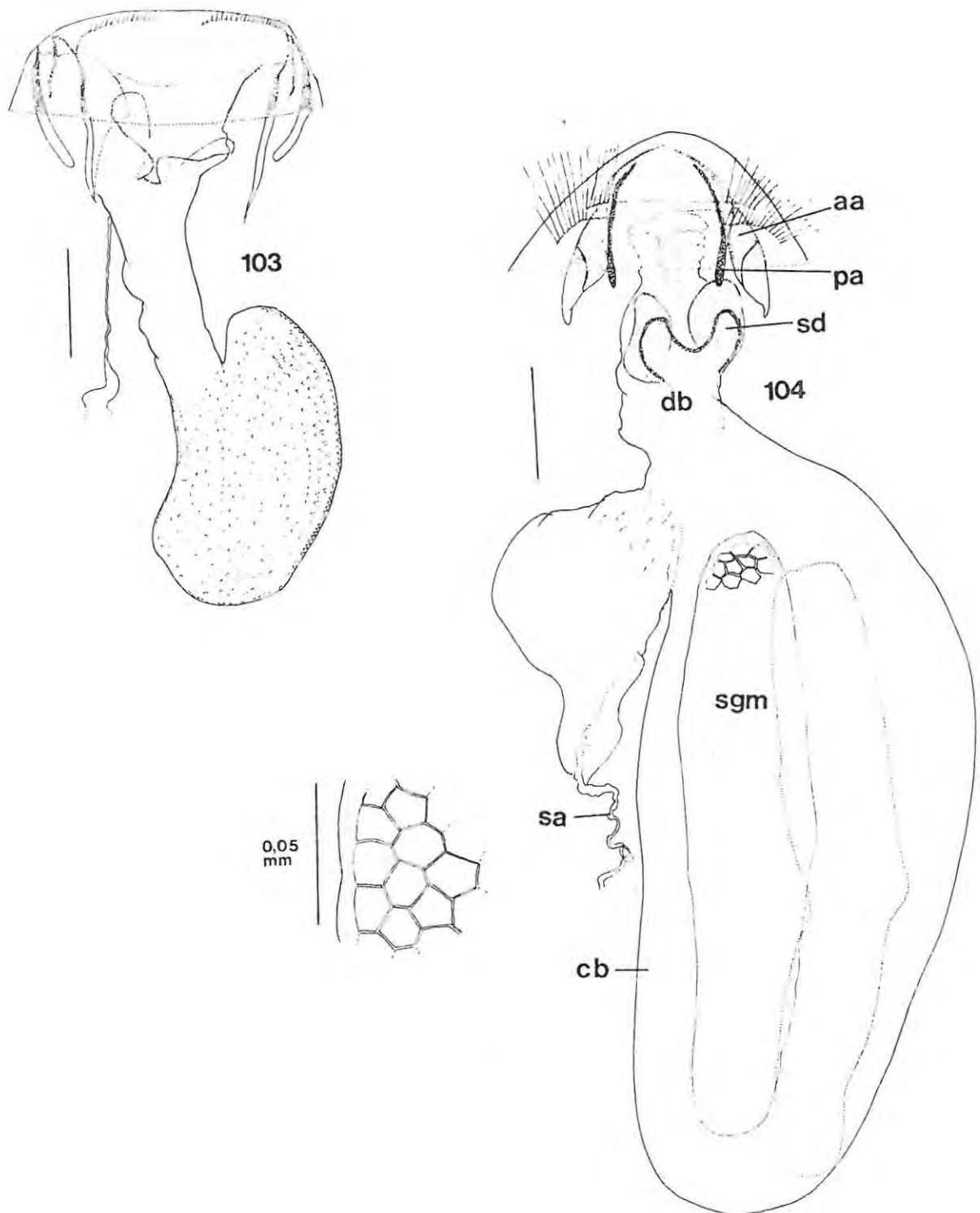
FIGS 90-93. Male genitalia of *Ectoedemia* (*Fomoria*) spp. 90. *E. (F.) lucidae* spec. nov. 91. *E. (F.) tecomariae* (Vári), ridge of right valva arrowed. 92. *E. (F.) myrtinaecola* spec. nov. 93. *E. (F.) alexandria* spec. nov. Scale lines = 0,1 mm.



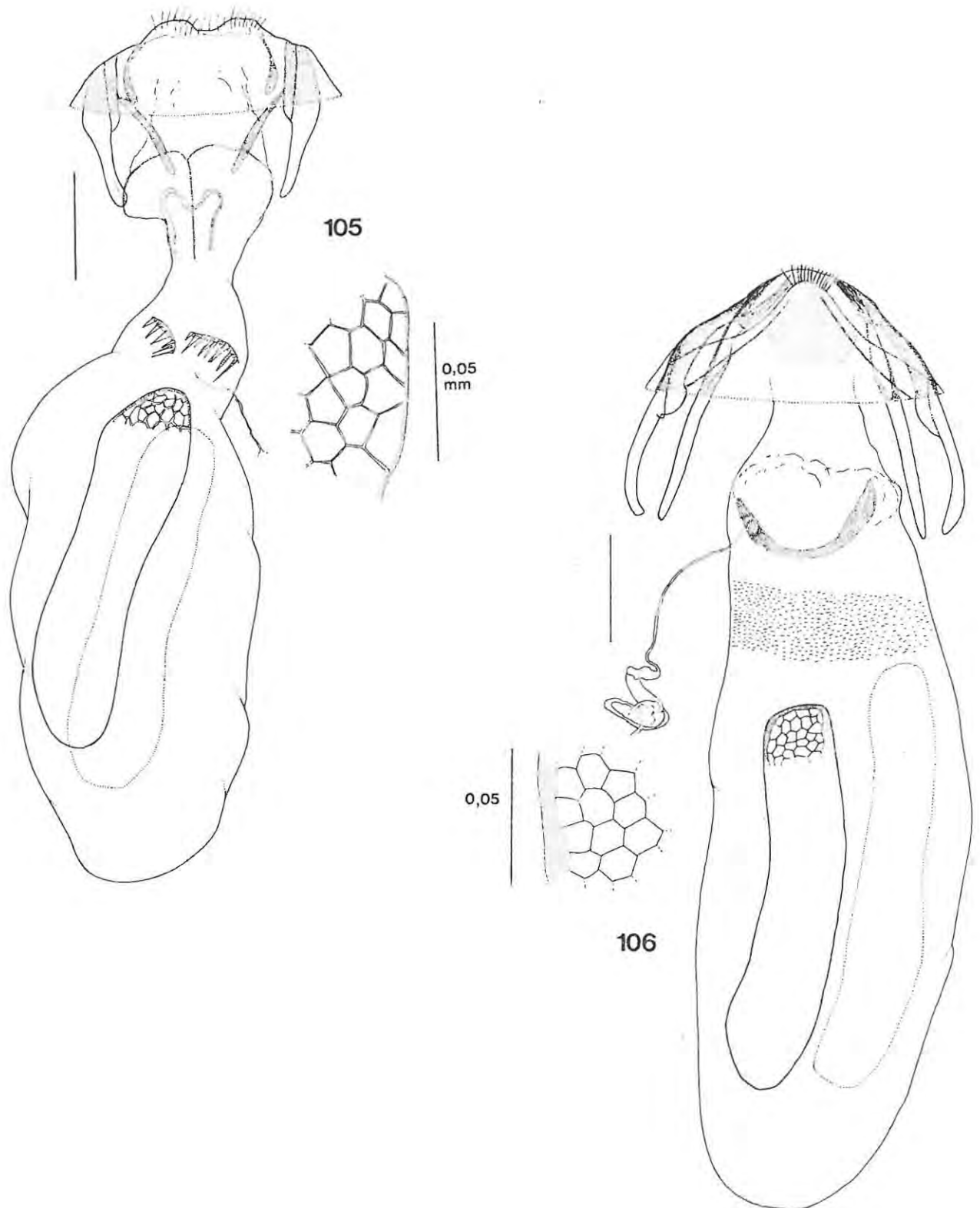
FIGS 94-97. Male genitalia of *Ectoedemia* (*Fomoria*) spp. 94. *E. (F.) leptodictyae* spec. nov., left valva also shown from inner (dorsal) aspect. 95. *E. (F.) incisaevora* spec. nov., right valva. 96. *E. (F.) malelanensis* spec. nov. 97. *E. (F.) thermiae* spec. nov., dorsal process of aedeagus also shown see text. Scale lines = 0,1 mm.



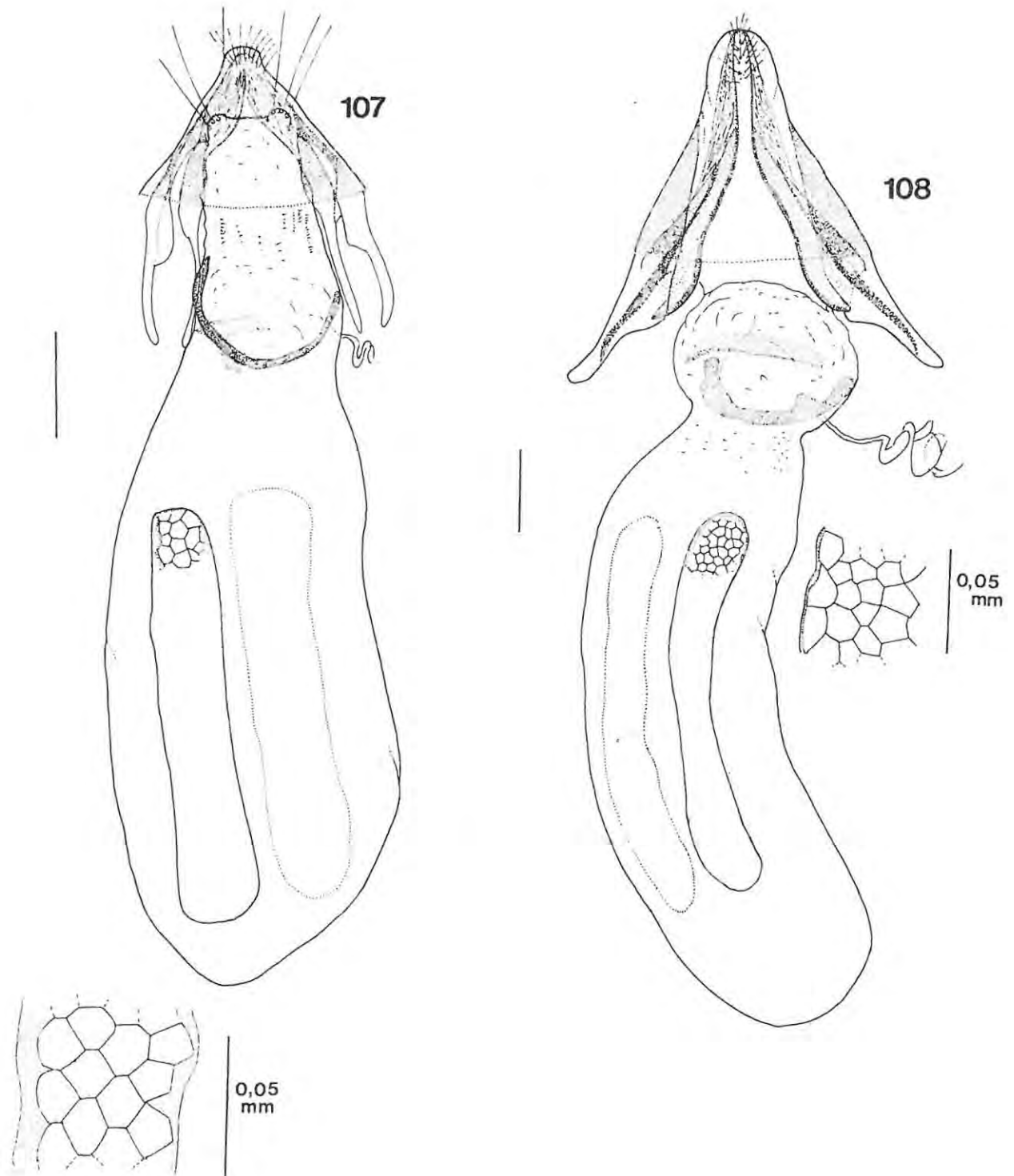
FIGS 98-102. Male genitalia of *Ectoedemia* (*Fomoria*) spp. and *Areticulata* gen. nov. sp. 98. *E. (F.) portensis* spec. nov., dorsal carinae arrowed. 99. *E. (F.) fuscata* (Janse), 'pin cushion' of right valva arrowed, see text. 100. *E. (F.) vannifera* (Meyrick), 'pin cushion' of right valva arrowed, see text. 101. *E. (F.) hobohmi* (Janse), right valva with 'pin cushion' arrowed, and aedeagus. 102. *A. leucosideae* spec. nov. Scale lines = 0,1 mm.



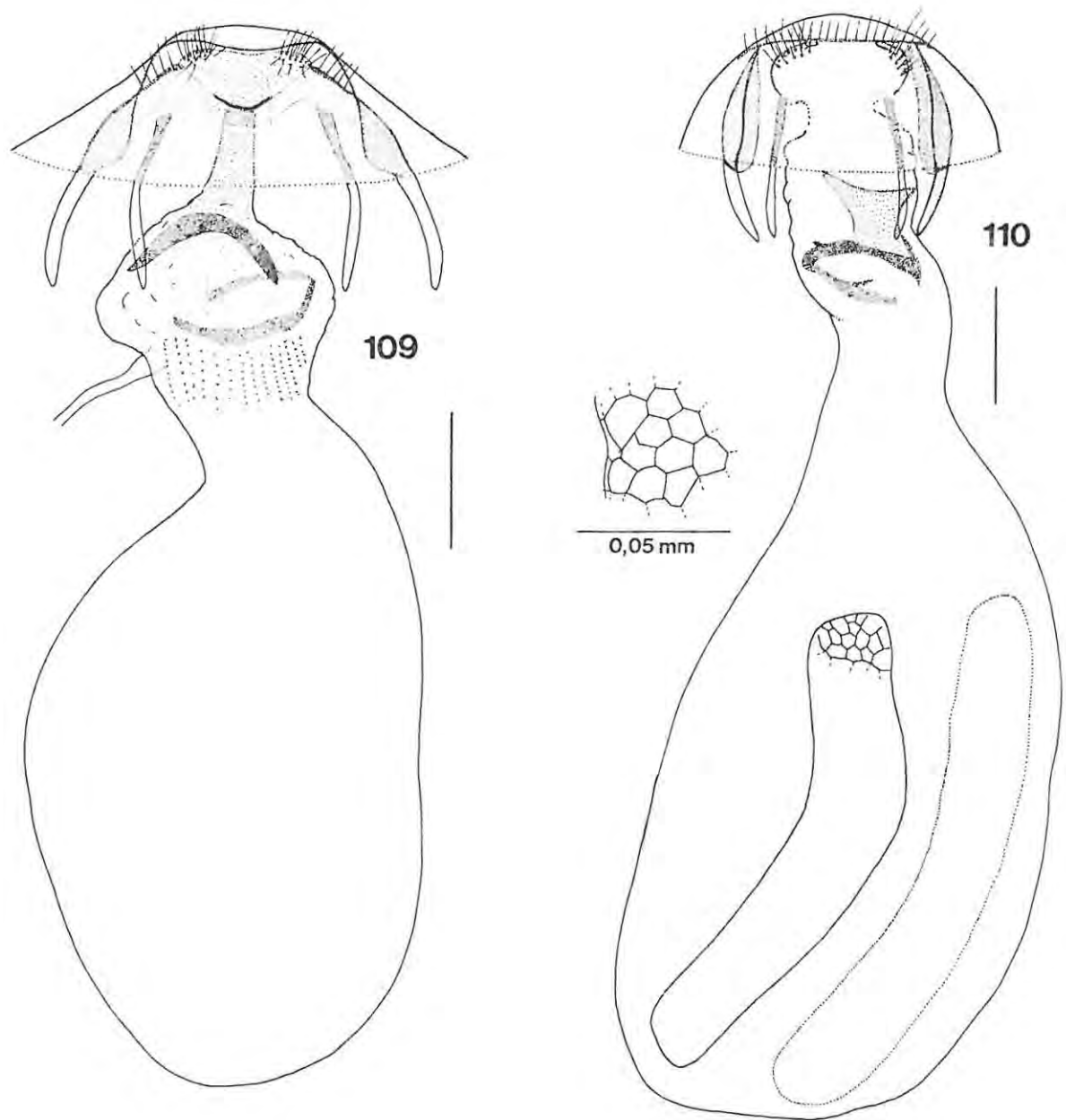
FIGS 103, 104. Female genitalia of *Pectinivalva* and *Obrussa*. 103. *P. comuni* spec. nov. 104. *O. zimbabwiensis* spec. nov., section of reticulations of signa also shown, enlarged. Scale lines = 0,1 mm unless shown otherwise.



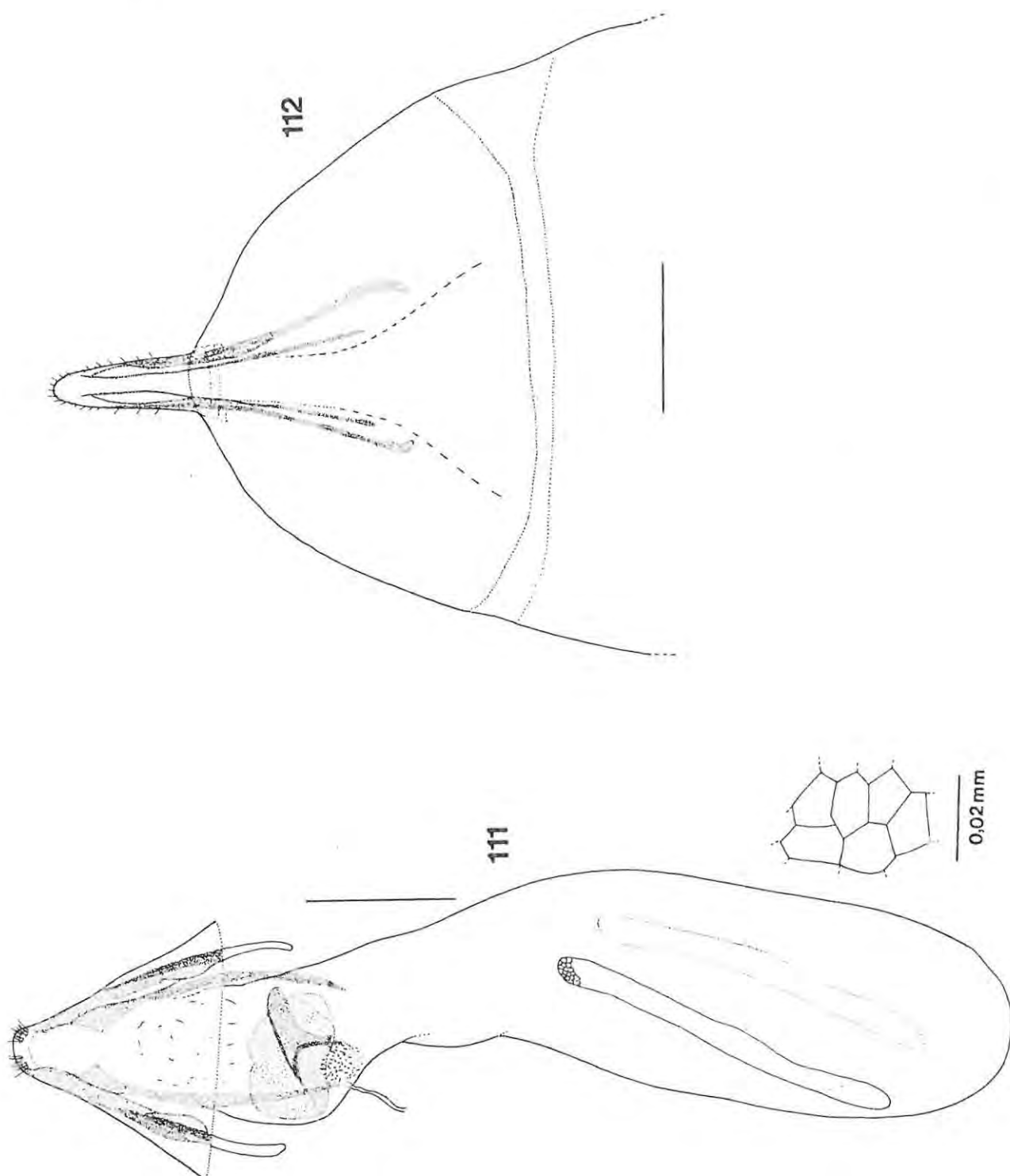
FIGS 105, 106. Female genitalia of *Obrussa* and *Ectoedemia* (*Laqueus*).
 105. *O. nigricapitella* (Janse). 106. *E. (L.) grandinosa* (Meyrick).
 Scale lines = 0,1 mm unless shown otherwise. Sections of reticulations of signa also shown, enlarged.



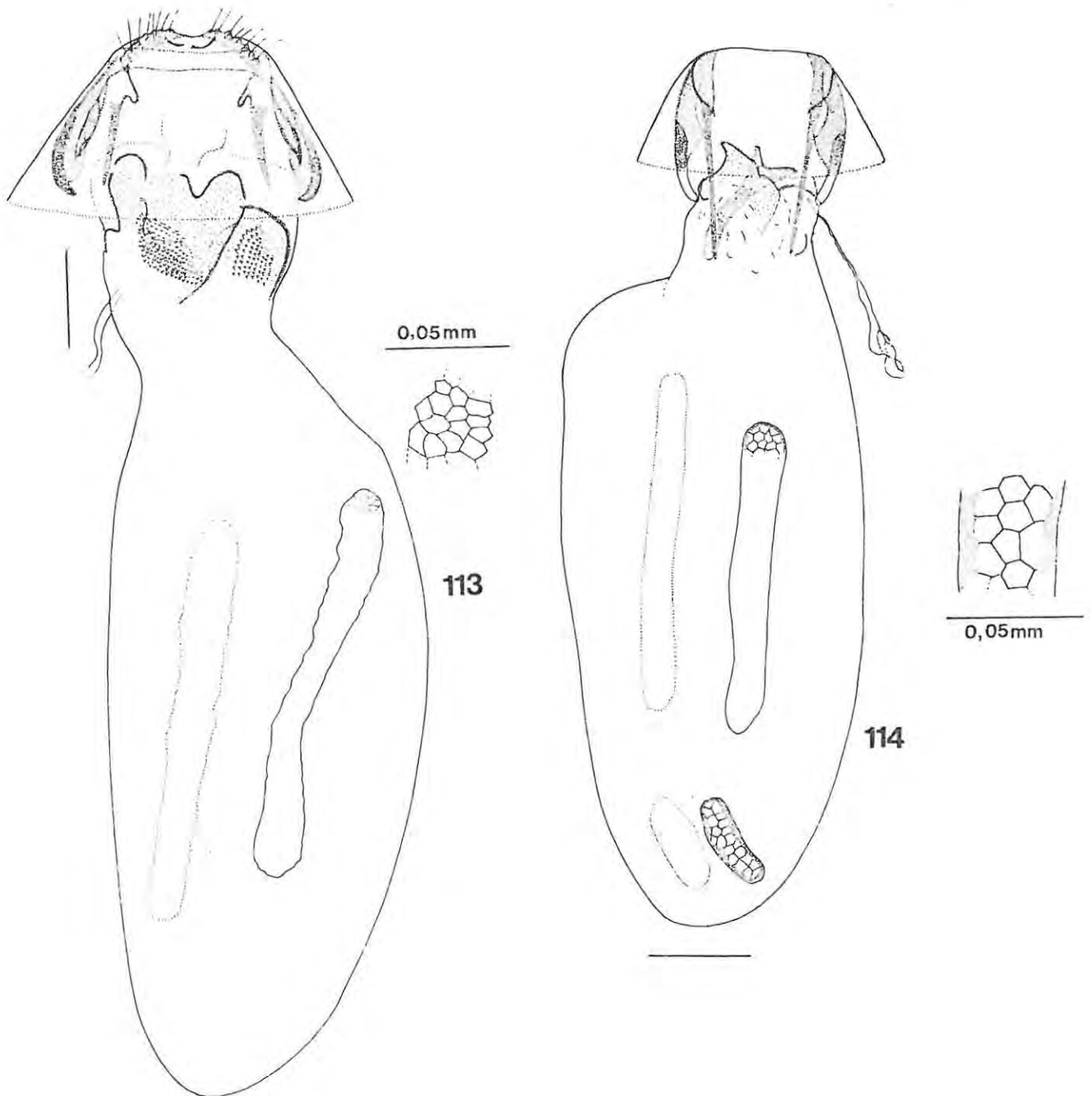
FIGS 107, 108. Female genitalia of *Ectoedemia (Laqueus)* spp. 107. *E. (F.) guerkliae* spec. nov. 108. *E. (F.) macrochaeta* (Meyrick). Scale lines = 0,1 mm unless shown otherwise. Sections of reticulations of signa also shown, enlarged.



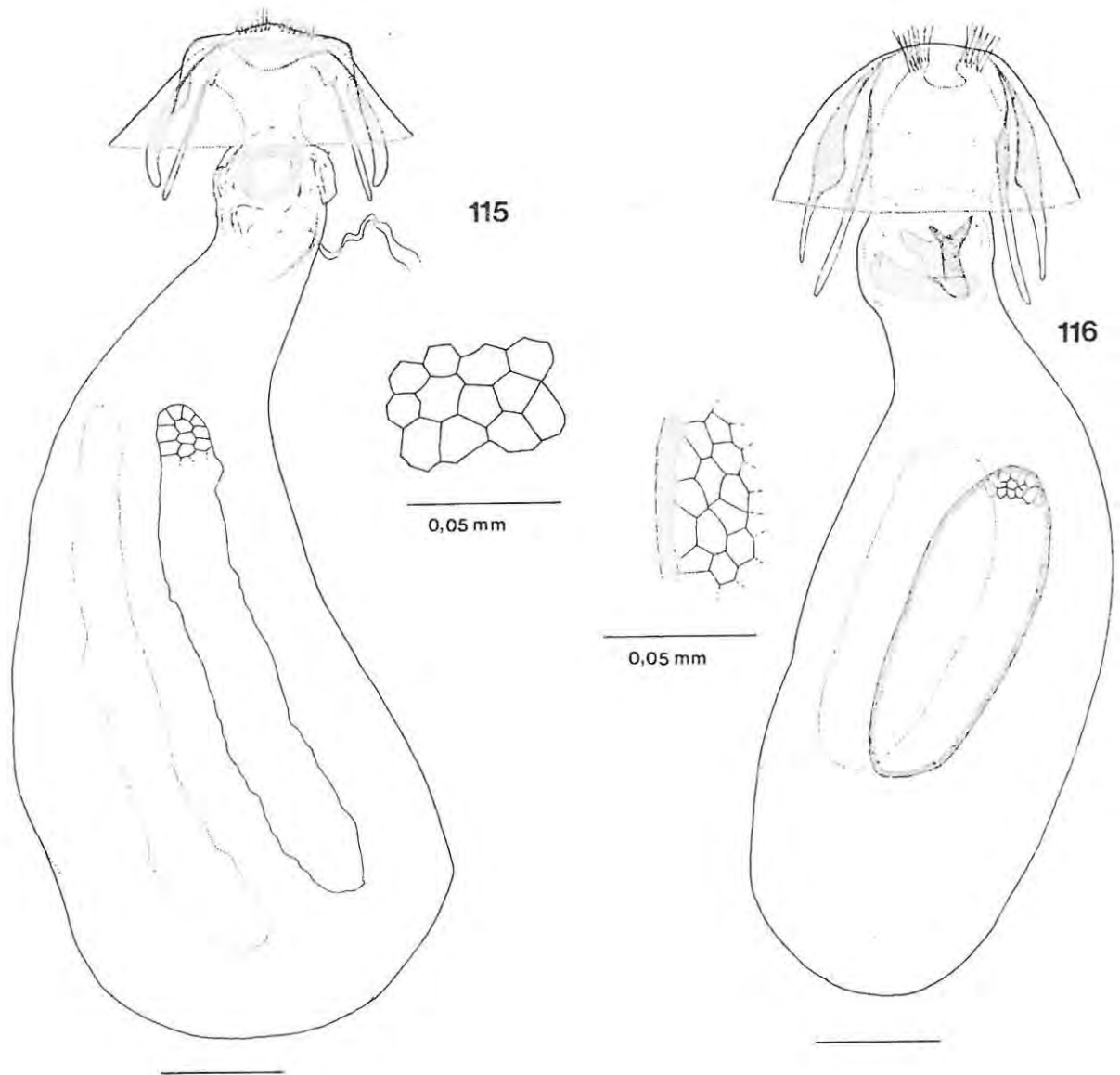
FIGS 109, 110. Female genitalia of *Ectoedemia (Laqueus)* spp. 109. *E. (L.) denticulata* spec. nov. 110. *E. (L.) undatae* spec. nov., section of reticulations of signum also shown, enlarged. Scale lines = 0,1 mm unless shown otherwise.



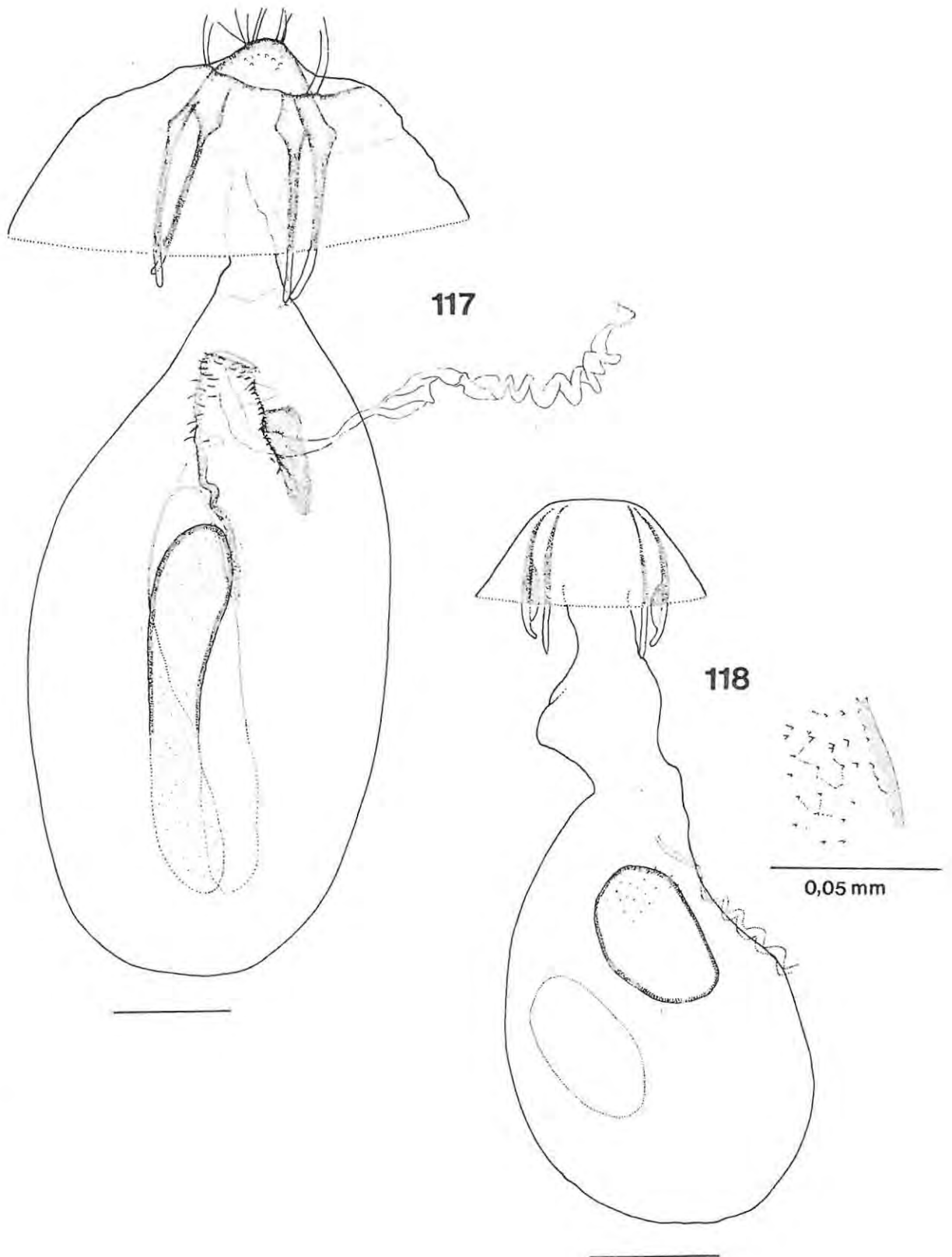
FIGS 111, 112. Female genitalia of *Ectoedemia (Laqueus)* spp. 111. *E. (L.) capensis* spec. nov., section of reticulations of signum also shown, enlarged. 112. *E. (L.) insulata* (Meyrick). Scale lines = 0,25 mm unless shown otherwise.



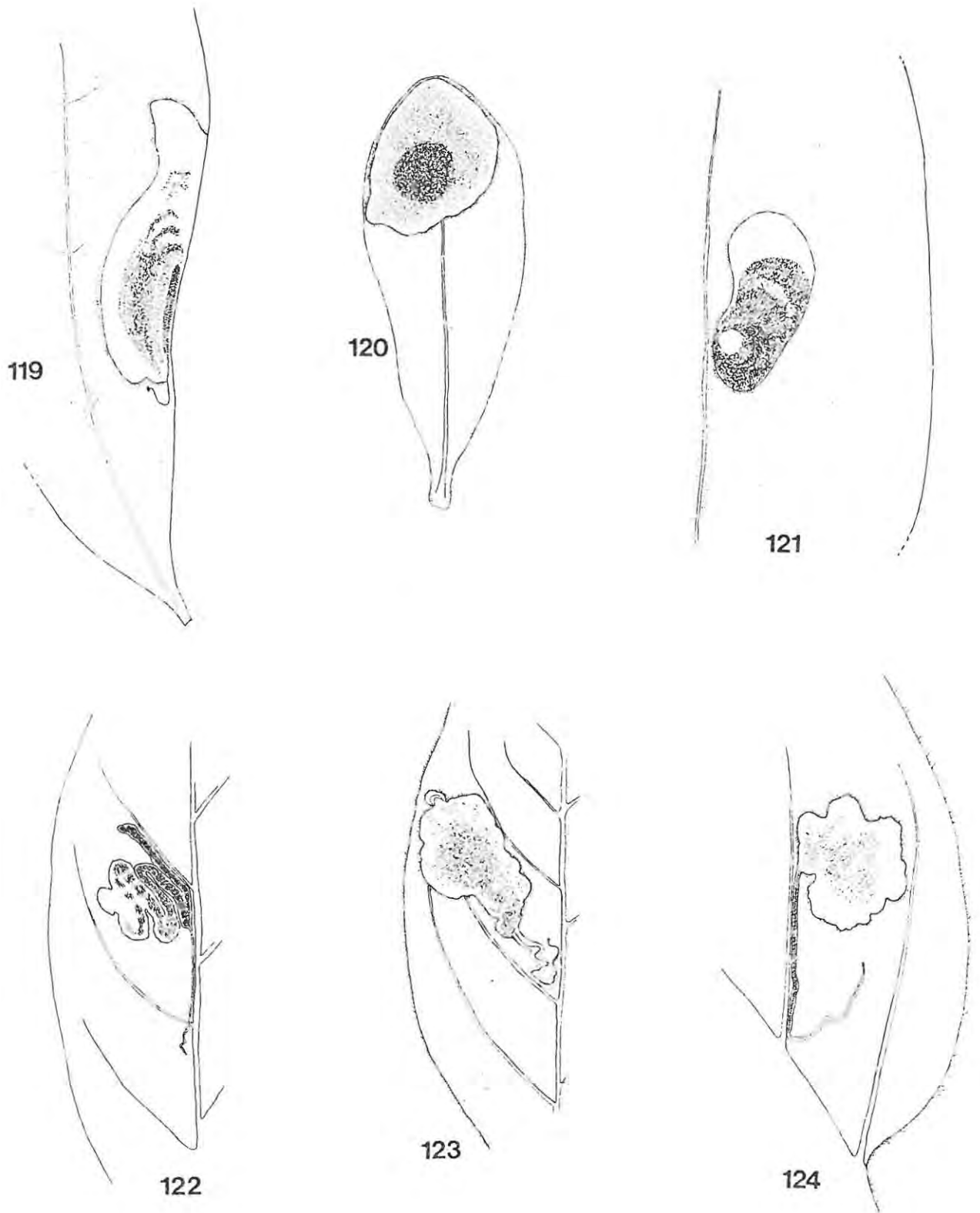
FIGS 113, 114. Female genitalia of *Ectoedemia (Laqueus)* sp. and *E. (Fomoria)* sp. 113. *E. (L.) crispae* spec. nov. 114. *E. (F.) myrtinaecola* spec. nov. Scale lines = 0,1 mm unless shown otherwise. Sections of reticulations of signa also shown, enlarged.



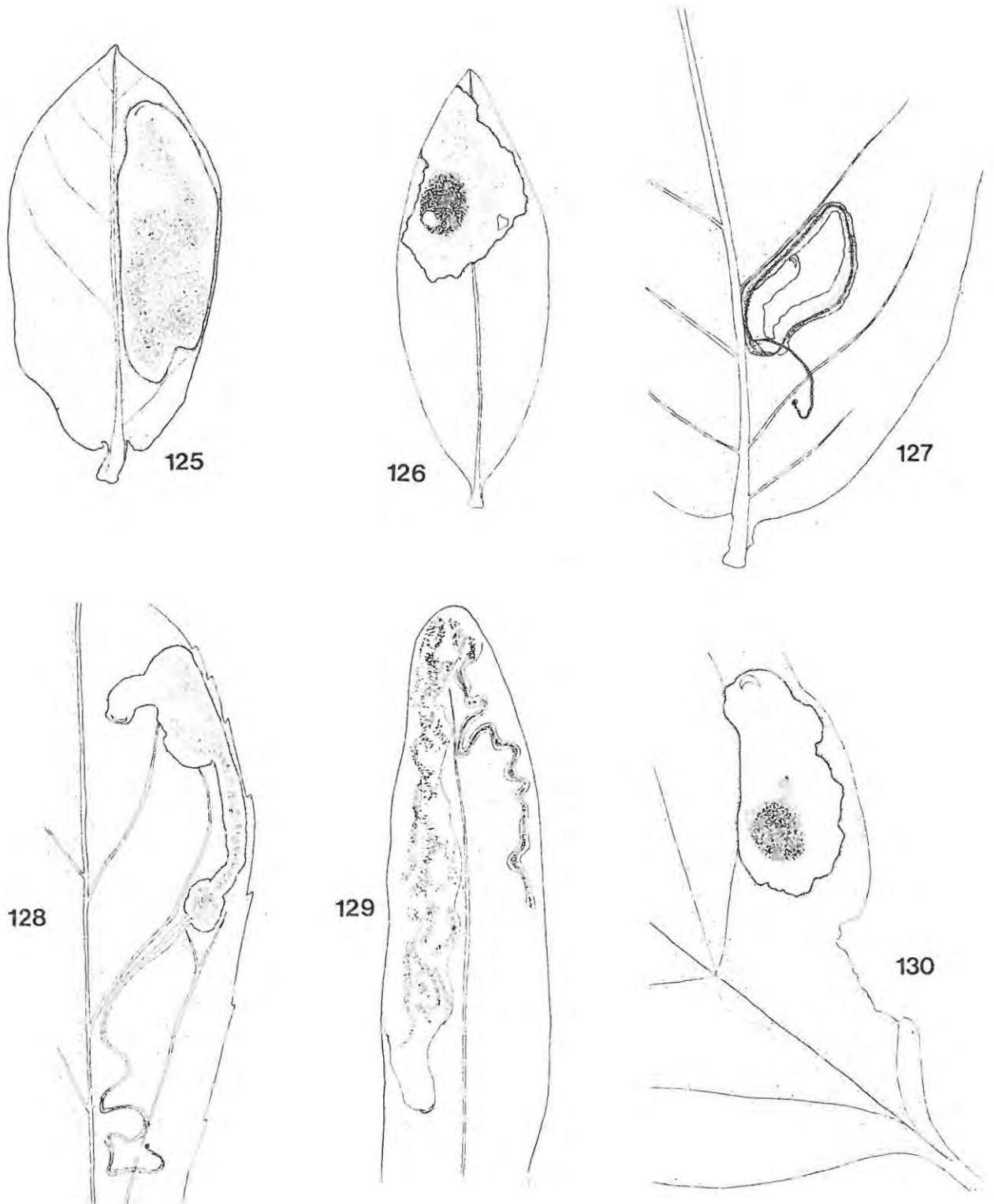
FIGS 115, 116. Female genitalia of *Ectoedemia (Fomoria)* spp. 115. *E. (F.) leptodictyae* spec. nov. 116. *E. (F.) fuscata* spec. nov. Scale lines = 0,1 mm unless shown otherwise. Sections of reticulations of signa also shown, enlarged.



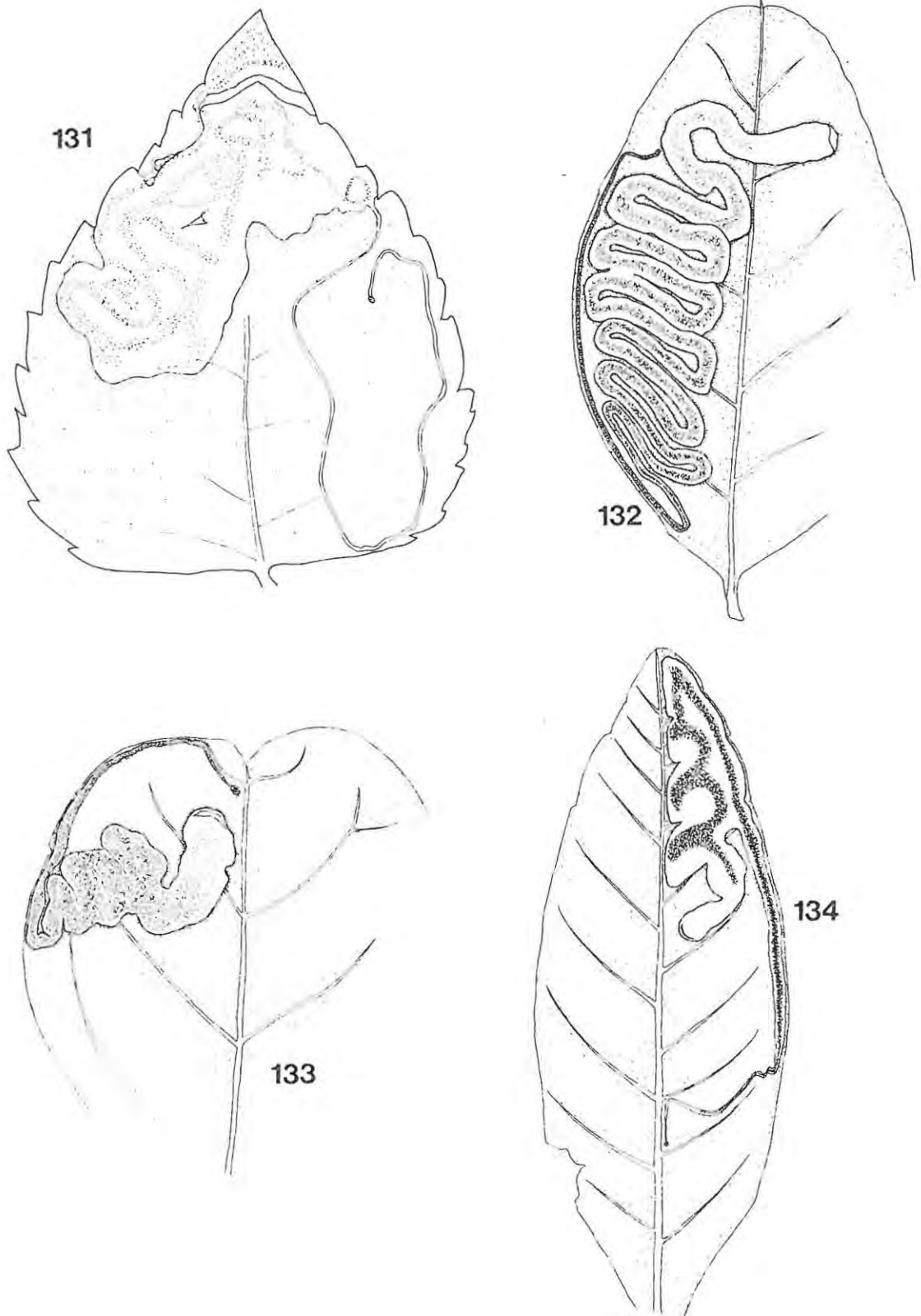
FIGS 117, 118. Female genitalia of *Ectoedemia (Fomoria)* sp. and *Areticulata* sp. 117. *E. (F.) vannifera* (Meyrick). 118. *A. leucosideae* spec. nov., section of markings on signum also shown, enlarged. Scale lines = 0,1 mm unless shown otherwise.



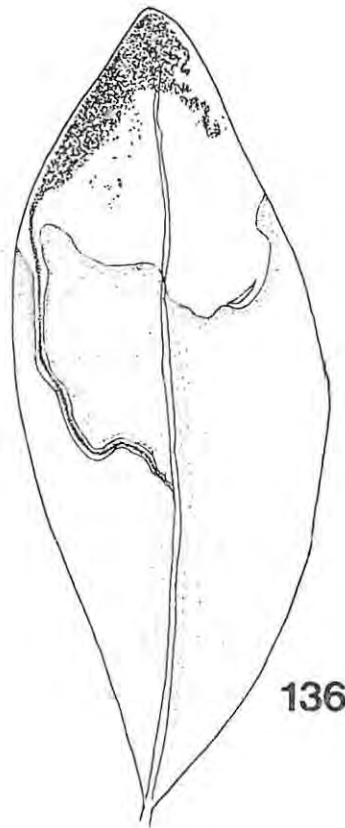
FIGS 119-124. Leaf-mines of *Ectoedemia* (*Laqueus*) spp. 119. *E. (L.) grandinosa* (Meyrick). 120. *E. (L.) wilkinsoni* spec. nov. 121. *E. (L.) simicola* spec. nov. 122. *E. (L.) guerkliae* spec. nov. 123. *E. (L.) macrochaeta* (Meyrick). 124. *E. (L.) maritima* spec. nov.



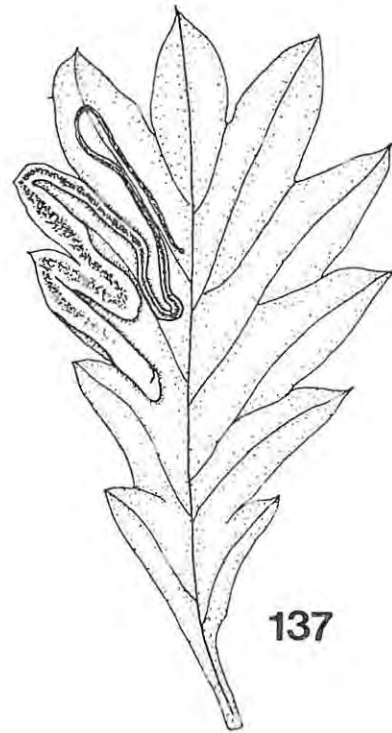
FIGS 125-130. Leaf-mines of *Ectoedemia* (*Laqueus*) spp. and *E.* (*Fomoria*) sp. 125. *E.* (*L.*) *scabridae* spec. nov. 126. *E.* (*L.*) *denticulata* spec. nov. 127. *E.* (*L.*) *kowynensis* spec. nov. 128. *E.* (*L.*) *rhabdophora* spec. nov. 129. *E.* (*L.*) *crispae* spec. nov. 130. *E.* (*F.*) *indicaevora* spec. nov.



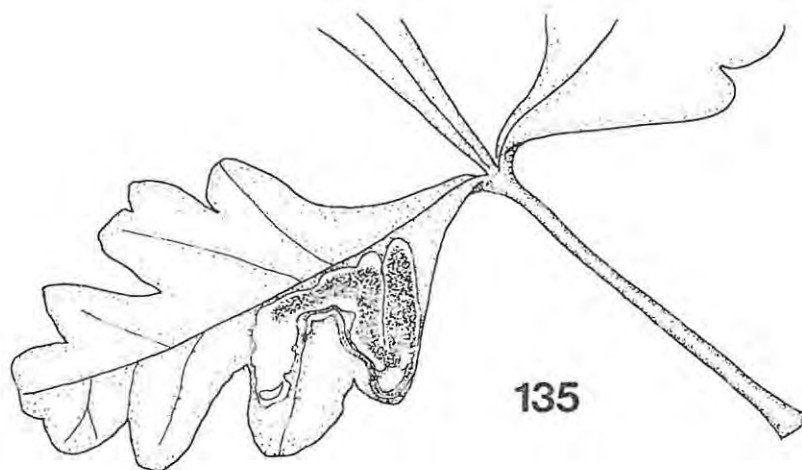
FIGS 131-134. Leaf-mines of *Ectoedemia* (*Fomoria*) spp. 131. *E. (F.) lucidae* spec. nov. 132. *E. (F.) myrtinaecola* spec. nov. 133. *E. (F.) alexandria* spec. nov. 134. *E. (F.) leptodictyae* spec. nov.



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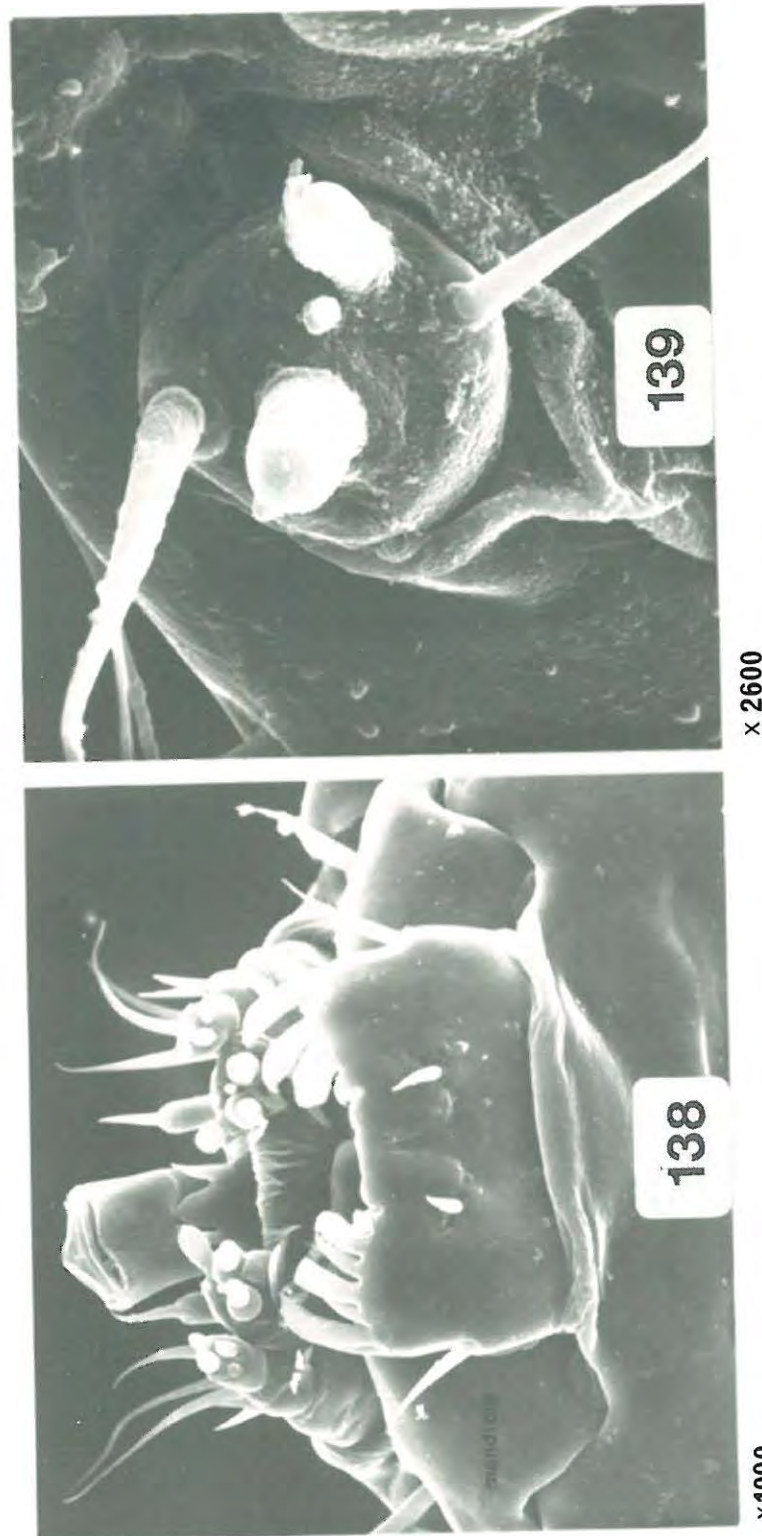


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FIGS 135-137. Leaf-mines of *Ectoedemia* (*Fomoria*) spp. and *Areticulata* sp. 135. *E. (F.) incisaevora* spec. nov. 136. *E. (F.) thermae* spec. nov. 137. *A. leucosideae* spec. nov.



FIGS 138, 139. Larvae of Nepticulidae spp. 138. Mouthparts (dorsal view) of *Ectoedemia (Ectoedemia) ? subbimaculella* (Haworth). 139. Antenna (anterior view) of *Stigmella anomalella* (Göze).

CLADISTIC ANALYSIS

PROCEDURE

The literature on cladistic methods is extensive. As stated in the Introduction cladistic analysis involves the search for taxa based on uniquely (or independently) derived characters termed *apomorphies* (Hennig 1966), or evolutionary novelties (Eldredge & Crickraft 1980). An apomorphy shared by two or more taxa is known as a synapomorphy. Apomorphies can be displayed on branched diagrams (cladograms) to reveal the hierarchical pattern of taxa so formed. For example, in this analysis characters 1-9 (see below) are synapomorphous for the family Nepticulidae; that is they have been found in all nepticulids examined except where interpreted as secondarily modified. They may be regarded as having been present in the 'morphotype' or 'ground-plan' of the Nepticulidae.

The most acceptable way to find apomorphies is by the method of out-group comparison. Thus characters present in nepticulids but not in non-nepticulids (out-groups) are regarded as synapomorphous for nepticulids. This method requires a knowledge of closely related relatives, and so particular attention was paid to Opostegidae, Incurvarioidea and other 'primitive' Lepidoptera.

Within the Nepticulidae cladistic analysis was carried out on 'Basic Taxa' (see below). These taxa are groups of species, or single species, the monophyly of which is discussed below by presenting the apomorphies on which they are recognised, provided that apomorphies have been found. The cladogram in figure 140a shows that three taxa are under consideration. There are two other theoretically possible cladograms: one in which *Pectinivalva* and *Stigmella* form a sister-group, and the other in which *Pectinivalva* and the Trifurculini form a sister-group. These possibilities were considered, but the cladogram presented is the best corroborated arrangement. The features that are shared by *Pectinivalva* and *Stigmella*, but that are absent from the Trifurculini were interpreted as present in the nepticulid ground-plan and subsequently *modified* in the Trifurculini. Therefore they are not apomorphies for *Pectinivalva* plus *Stigmella*. Nevertheless, certain attributes are common to *Pectinivalva* and *Stigmella*, for example the medial vein of the forewing is coalesced with the radial sector

so that the cubitus is free. In the Trifurculini M is united with Cu from the base and diverges to R_s further along the wing. Since neither of these conditions occurs in non-nepticulids why should the free Cu not be treated as a synapomorphy of *Pectinivalva* plus *Stigmella*? The answer is that there are attributes of *Stigmella* and the Trifurculini that do not occur in *Pectinivalva* or any other group. Such attributes can reasonably be regarded as unique to *Stigmella* and the Trifurculini and therefore as synapomorphous. This interpretation means that the divergence of M from Cu one third of the way along the forewing is the condition derived from the free Cu; it refutes the suggestion that a free Cu is synapomorphous for *Pectinivalva* and *Stigmella*.

A cladogram that is said to be the best corroborated arrangement of the taxa in question simply means that it is supported by more apomorphies than any other arrangement. It also means that 'Hypotheses of synapomorphy which refute a phylogeny [cladogram] also refute all hypotheses of synapomorphy which form a proper subset of the rejected phylogeny.', (Wiley 1975:243).

It is customary for characters to be divided into 'states' in cladistic and in numerical phenetic analysis. In the former, the states have been treated as generalised (plesiomorphous) or derived (apomorphous). However, all taxonomic attributes are apomorphous at some point on a cladogram and so their division into primitive and derived states is unnecessary (Platnick 1979). A primitive state is simply a more generalised attribute than its derived state. In this respect 'taxonomic character' means the same as 'apomorphy', but the word apomorphy is used in this work mainly to follow custom. In the numerical phenetic analysis, characters were divided into states because it is a requirement for the preparation of a data matrix.

Two other problems of practical importance were encountered; that of the loss of a structure and that of homoplasy (convergence and parallelism). If a structure is present in one group but not in another then its absence is due either to loss or to the fact that it has never developed. However, there is no *a priori* way by which we may know if the absence of a structure is due to the one or to the other - we have to rely on other characters to construct the cladogram. Once the cladogram is constructed *then* the absence of a feature may be interpreted as a loss or simply as never having been developed, by incongruence on the cladogram. This is how character 13 (below) was interpreted as a loss.

The problem of homoplasy in systematics arises when a systematist has failed to recognise that two apparently similar structures are really similar modifications of two independently derived features (Platnick 1979). An aim of morphological study and character analysis is to avoid such oversights, or to reduce their numbers. In the many trial cladograms constructed before the final product emerged, wing-colour and colour of head-tuft caused the most incongruence between sets of purported apomorphies. Neither of these attributes was ignored during the construction of the cladogram, but the scattered occurrence of similar colours in relatively unrelated taxa, according to the 'final' cladogram, means that homoplasy was extensive in these features. These attributes were not omitted from the character-list (below) by *a priori* rejection on the basis of *likely* homoplasy. They were excluded *a posteriori* because of their incongruence with what has turned out to be the cladogram with the least number of character reversals.

BASIC TAXA

Pectinivalva

A large genus, so far collected only in Australia. Synapomorphies include the deflection of the trunk of R+M towards the costa of the hindwing, and possibly the presence of apodemes that arise from the posterior end of each lateral arm of the vinculum and meet their equivalents from the other side. The apex of the valva is rounded in several species, which may be an apomorphy for them collectively or an apomorphy of the whole genus. The presence of a somewhat similarly shaped valva in many of the Tischeriidae may mean that the feature is considerably more generalised. The presence of a pectinifer on the valva is *not* an apomorphy of *Pectinivalva* since it is found in Opostegidae and Incurvarioidea.

Varius ochnicolus

The cladistic relationships of this species are uncertain. Unlike the general condition in the Stigmellinae, the base of the ejaculatory duct of the male is not surrounded by a striate thickening; therefore it is possible that *ochnicolus* represents the sister species of all the other Stigmellinae (fig.141). This suggestion requires corroboration so

it is not directly incorporated into the classification; hence *ochnicolus* is *incertae sedis* within the Stigmellinae.

Simplimorpha lanceifoliella

To have included the species in *Stigmella* would have meant widening the limits of what is already a very large genus. Although it is phenetically rather similar to *Stigmella*, the similarities (e.g. M of forewing coalesced with R from base) are considered not to be synapomorphous, but as more generalised. *S. lanceifoliella* lacks an uncus; whether this should be regarded as a modification of the characteristic bilobed uncus of *Stigmella* or an independent loss remains unknown. The structure of the tegumen, which forms a broad, undefined roof to the male genital capsule, is unique.

The absence of an uncus and the reduced gnathos makes it difficult to judge from which condition they were modified. Since the cladistic relationship of the species within the Stigmellinae is unclear it is treated as of uncertain position.

Johanssonia acetosae

Unlike *Stigmella*, the uncus of this species is not bilobed, and the transverse bar of the transtilla and R_{2+3} in the forewing are absent. *J. acetosae* is phenetically rather similar to *Stigmella* (see section on Numerical Analysis, below), and was included in the genus by Karsholt & Nielsen (1976). However, since it does not share an apomorphy with that genus its distinctness is indicated by retaining the generic name *Johanssonia*.

Like the two previous species, *acetosae* is treated as *incertae sedis* within the Stigmellinae.

Stigmella

With the exception of a few species, members of this large, world-wide genus exhibit a monotonously similar general structure. The usual shape of the uncus resembles that of *Pectinivalva*, but it is smaller and less prominent on the whole. Its bilobed condition in *Stigmella* (very weak in a few species) is an apomorphy for the genus.

Apart from a few species, the gnathos is modified. In contrast with

the widespread nepticulid condition of a ventral, undivided, central element, the structure is divided in *Stigmella*. A few species of the genus retain the generalised condition, for example the South African *ingens* group (Scoble 1978b) and the North American *procrastinella* group (Wilkinson & Scoble 1979). Each group may represent an independent lineage, but rather than erect new taxa for them they are retained in *Stigmella* since they share at least one derived character with the other species of the genus.

Obrussa

Represented by species in the Palearctic, the Nearctic and the Ethiopian (Afrotropical) regions. The monophyly of the group is demonstrated by the following synapomorphies: the U-shaped excavation of the ventral plate of the vinculum, the long apodeme associated with the valva, and the strong setae around the apex of the valva. The larval feeding habits are unique within the Nepticulidae, although no such information is available for the four species from southern Africa. A black head-tuft is found in species in both the northern and southern hemispheres. This character is not unique to *Obrussa* but is generally rare in the Nepticulidae, and probably independently evolved by the clade. In certain species of *Obrussa* the head is not black, but its presence in species so widely separated suggests that it is probably present in the ground-plan. The plate-like, often funicular, markings associated with the ductus bursae of the female may be an additional apomorphy for the genus, but in an illustration of the female genitalia of *albibimaculella* Larsen (received from Mr R. Johansson) the markings on the ductus resemble those found in *Ectoedemia* and *Niepeltia*. The ductus of many species is ornamented with spines - an additional possible apomorphy of the clade.

Ectoedemia

No apomorphies have been found for this assemblage of species, and so its monophyly has not been demonstrated. A detailed *world-wide* review of this genus is one of the most important tasks in nepticulid systematics. Studies on larvae may well shed light upon the problem.

Phenetically, the species now included in *Ectoedemia* form a loose aggregation (except for *grandinosa* and its relatives, which are closely allied and distinct - see Numerical Phenetic Analysis, below), and for this reason they are assigned to the same genus at present. The monophyly of

the assemblage may simply not yet have been demonstrated, but it is probable that at least some species will have to be removed if cladistic relationships are to be accurately expressed.

Although *grandinosa* and its relatives form a distinct cluster, they are included in the subgenus *E. (Laqueus)* because all the members of that group have an 'anal loop' in the forewing. This is a feature present in no other nepticulid, and is considered to be apomorphic for *E. (Laqueus)*.

In its original sense, *Ectoedemia* may be a monophyletic assemblage and it is retained as the nominate subgenus of the now expanded genus. However since the only hypothesized apomorphy is the loss of an uncus, corroboration of this suggestion is needed.

Fomorìa (originally a genus) has been included in *Ectoedemia* as a subgenus. The name was originally intended to include two species (Beirne 1945) that are very similar in detailed structure and in choice of host-plant. If generic status is given to such closely related species then it should likewise be given to many others representing a similar situation. This underlines the point made by Mitchener (1978) that the number of species united in a named monophyletic taxon (holophyletic in Mitchener's paper) depends on a phenetic decision (unless the genealogy has been completely worked out in which case every sister group can be named). The concept of *Fomorìa* was expanded by Wilkinson (1979) and is further broadened in the present work. Its monophyly is not established. It is possible that some of the South African species included in *E. (Fomorìa)* have secondarily lost the anal loop; certainly a few are phenetically close to species of *E. (Laqueus)*. However, in the absence of evidence that the loop has been secondarily lost in such species they cannot be included in *E. (Laqueus)* at present.

Niepeltia

This is a homogeneous genus represented in both northern and southern hemispheres. The venation is invariable, and the male genitalia exhibit a high degree of similarity between species. The coalescence of R_5 and M from the base of the forewing is probably unique to *Niepeltia*. The flimsy, very weakly sclerotised ventral plate of the vinculum, and the general

shape of the valva, with an inwardly projecting component, are apomorphic characters. The apex of the uncus is weakly divided dorsoventrally (Scoble 1980b: fig.7) and is probably a further apomorphy. In *Trifurcula* (*Trifurcula*) the uncus is deeply divided, and looks different (Scoble 1980a: figs 9-11). The presence of a ventral process of the aedeagus is shared by many species in *Ectoedemia*, but the shape in *Niepeltia* differs. Whether this structure is homologous is not known. The presence of lateral apodemes (lateral support rods of Davis 1978b) in some species may be synapomorphic with *Microcalyptris*.

Microcalyptris

The genus was described by Braun (1925) for a single species (*scirpi*), represented by a single male specimen. The genitalia were found to be damaged on dissection (Dr D.R. Davis, personal communication, and see Wilkinson 1979) and so it is difficult to assess whether the species now included in this genus actually constitute a monophyletic group. The long posterior apophyses of the female genitalia of most of the species currently assigned to *Microcalyptris* may be an apomorphy; unfortunately no female of the type-species has been collected. The lateral support rods (Davis 1978b) in the male genitalia of *Microcalyptris* may be homologous with the apodemes (Scoble 1980b) of *Niepeltia*, and therefore not an apomorphy for *Microcalyptris* itself.

Trifurcula

Scoble (1980a) discussed the cladistic relationships of *Trifurcula*, *Levarehama* and *Fedalmia*. In that work they were not combined as one genus, but after a general study of nepticulid genera I now follow the suggestion of Johansson (1971) in which all three are treated as subgenera of *Trifurcula*. To retain *Levarehama* and *Fedalmia* as full genera would obscure their cladistic relationship, see figure 140.

The forked condition of the medial vein in the hindwing is an apomorphy of the genus. Its absence in *T.* (*Trifurcula*) *barbertonensis* (Scoble 1980a:142) is considered to be a loss because that species has other apomorphies of the subgenus.

Bohemannia

Several apomorphies support the hypothesis of monophyly of this ditypic genus. The trunk R+M+Cu in the forewing is divided into five branches terminally (R_1 , R_2 , M_1 , M_2 , and Cu). This is the only genus where Cu is present as a terminal branch of this trunk. The short process on the valva is unique, and so is the shape of the juxta.

The cladistic relationships of *Bohemannia* within the Trifurculini are unclear. R_5 is coalesced with M+Cu (not R_1) from the base of the forewing, which is similar to the condition found in *Niepeltia*. However, no other characters suggest a relationship. The general form of the uncus bears a slight resemblance to the North American species *Glaucolepis sacharella* but this is probably only superficial.

Areticulata leucosideae

The relationships of this species are obscure as was noted above in Systematic Treatment. The suggestion that it represents the sister-species of the Trifurculini (fig.141) requires corroboration before it is incorporated into the classification, hence its treatment as *incertae sedis* within the Stigmellinae.

CHARACTERS (APOMORPHIES)

In cladistic analysis, all characters define monophyletic groups (taxa) at some point on a cladogram. Therefore the characters are not divided into 'states'.

1. *Forewing: M_1 coincident with M_2 terminally to form M_{1+2}*

This is the condition in the Pectinivalvinae, and is probably a synapomorphy for the Nepticulidae as a whole. The subsequent division of M terminally into M_1 and M_2 is an apomorphy of the Trifurculini, which has secondarily reverted to the fused condition in several species.

2. *Genital capsule of male very well sclerotised*

In the Nepticulidae the lateral arms of the vinculum are particularly well-sclerotised compared with non-nepticulids. The genital capsule of nepticulids is easy to recognise on account of this.

3. *Vinculum U-shaped or extended U-shaped*

In species not belonging to the Trifurculini the lateral arms of the vinculum articulate with the sides of the tegumen and do not, by themselves, form a ring around the aedeagus.

4. *Tegumen approximately in the shape of a band, usually flat along posterior edge, not extended posteriorly*

This is best understood by reference to the figures for the species not belonging to the Trifurculini. I have not observed the condition in other moths and so consider it to be character of the nepticulid morphotype.

5. *Uncus approximately hood-shaped*

The uncus is well-developed in *Pectinivalva* and the hood-shaped condition is basically retained in *Varius*, *Johanssonia* and *Stigmella*, but modified in the Trifurculini (see character 19). This form of uncus is probably not found outside the Nepticulidae.

6. *Gnathos with an undivided central element, which lies ventral to the lateral processes*

This is a character widespread in the Nepticulidae. A similar condition may be present in the North American species *Opostega nonstrigella* Chambers (figured by Eyer 1924) but this requires checking since it is not characteristic of the Opostegidae in general. If the shape is the same, the character will be a synapomorphy of the Opostegidae plus Nepticulidae rather than just the Nepticulidae as suggested here.

7. *Aedeagus broad and well-sclerotised*

The shape of the aedeagus is unique to the Nepticulidae. In *Incurvarioidea* and *Tischeriidae* the structure is very slender, and in *Opostegidae* it is poorly defined and weakly sclerotised.

8. *Cornuti of aedeagus numerous*

This condition is found in many species of *Pectinivalva* and *Stigmella*, but by no means in all, and in a few Trifurculini. Since cornuti are absent or few in number in many non-Trifurculini species they have probably

been lost or reduced many times. The condition may have evolved independently in many species, but since the pattern of the cornuti looks similar in a variety of species it is treated as a characteristic of the nepticulid ground-plan here.

9. *Spines on terga of pupa large and numerous*

Material of only a few species was available for examination and the feature has not been examined for any species of Opostegidae. The position of this character on the cladogram is therefore in considerable doubt. Large spines were observed in one species of *Pectinivalva*. In *Stigmella* the number and size of the structures are much reduced, as they are in *Simplimorpha lanceifoliella* and in *Nicpeltia*.

10. *Subdorsal retinaculum present on forewing*

The series of spines near the base of the underside of the forewing, on or near the cubitus, was termed the subdorsal retinaculum by Braun (1924).

11. *Length of cubitus reduced in forewing*

The cubitus is long in the Pectinivalvinae. Although it is short in most Stigmellinae, in some Trifurculini it is long. The hypothesis that a long cubitus has evolved independently in the Trifurculini on a number of occasions, rather than that it has been lost independently, is accepted on grounds of parsimony.

12. *Trunk 1+2A thickened in forewing*

13. *Pectinifer lost*

A pectinifer, previously known only in Opostegidae and Incurvarioidea, has now been found in Nepticulidae (subfamily Pectinivalvinae). Its absence in members of the subfamily Stigmellinae is therefore interpreted as a loss. The loss of a structure should not be prejudged as a character since a loss can occur more than once. The primary division of the Nepticulidae was made on other characters first; the absence of the pectinifer from one division was subsequently interpreted as a loss. The fact that this structure is reduced in some species of *Pectinivalva* underlines the need for caution. Since no species of Stigmellinae is known to possess a

pectinifer there is no reason to suggest that the loss occurred more than once.

14. *Striate thickening around base of ejaculatory duct*

15. *Signa of corpus bursae paired*

Paired signa are present in many nepticulid genera. In most species of *Stigmella* they are absent but they are found in a few members of the genus usually as accumulations of pectinate marks (e.g. in the North American *corylifoliella* group, Wilkinson & Scoble 1979). Their size is generally similar to the well-defined signa of the Trifurculini, and so this character is probably a character of the morphotype of the Stigmellinae.

16. *Vinculum 'ring-shaped'*

17. *Tegumen extended posteriorly*

The extension may only be slight, but it contrasts with the band-shaped condition of the non-Trifurculini.

18. *M is coalesced with Cu at base of forewing, and is subsequently deflected to meet R_s from about one-third of the way along wing*

This is considered to be a morphotype character for the Trifurculini. Within that group there have been modifications of this condition, such as in *Niepeltia* for example where Cu, M and R_s are coalesced from the base.

19. *Uncus in form of a thickened band, approximately in the shape of an inverted V*

In the subgenus *Ectoedemia* (*Ectoedemia*) the uncus is lost, and in *Bohemannia* it is strongly setose; these conditions are interpreted as secondary modifications.

20. *Ductus bursae with a prominent sclerotised thickening*

Although a small thickening has been observed in some species of *Pectinivalva*, the presence of a large, prominent one is confined to the Trifurculini. A variety of thickenings occur; in some species they are absent. Since these species fit into the Trifurculini in other respects,

the absence of the structures is considered to be a loss.

21. *Signa of corpus bursae reticulate*

Signa reticulata are rarely lost within the Trifurculini.

CLADOGRAMS

Figure 140 is the cladogram derived from the cladistic analysis. Excluded from it are the species treated as *incertae sedis*. This is the diagram on which the classification is based (see next section). In figure 141, an additional cladogram is presented in which the possible position of some of the species of uncertain placing are indicated.

The cladogram (fig.140) makes a specific statement about the relationships of the taxa involved. It cannot be proven; but it is capable of being corroborated or falsified by the finding of additional synapomorphies that support or refute the scheme respectively.

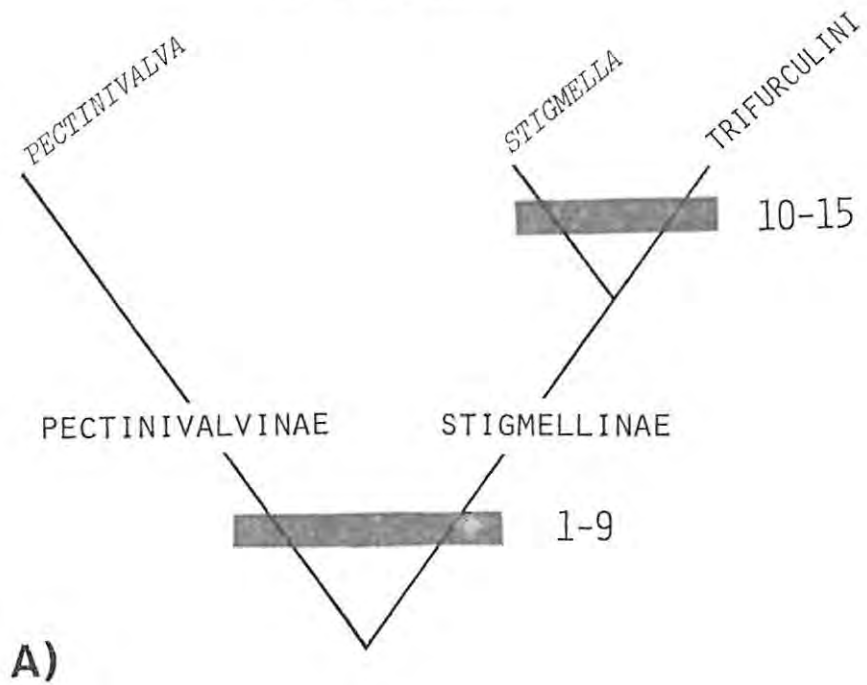
COMMENTS ON CLADISTIC ANALYSIS

As mentioned in the Preface some writers have stressed that further assumptions are required before a cladogram can be regarded as a phylogeny (e.g. Nelson 1979; Platnick 1979). A cladogram is atemporal since all taxa, even the extinct, are terminal on the diagram. In figures 140 and 141 there is no time axis; the schemes simply illustrate a hierarchy of groups based on apomorphies. Although the diagrams have no time axis the taxa represent species, or groups of species, that have arisen by descent with modification.

In figure 141 *Varius oehnicolus* could theoretically be the ancestor of all taxa to its right on the diagram. I do *not* propose that it is, but simply make the point that if it was then the cladogram would still be valid because the hierarchy of groups would be exactly the same. If we wanted to turn the cladogram into a phylogeny to show this assumption then *Varius oehnicolus* would have to be represented at its present branch-point (node) on figure 141, not as it is shown now.

In figure 140a the taxa are groups of species not single species. Since only species, but not higher taxa, evolve *Stigmella* could obviously

NEPTICULIDAE



TRIFURCULINI

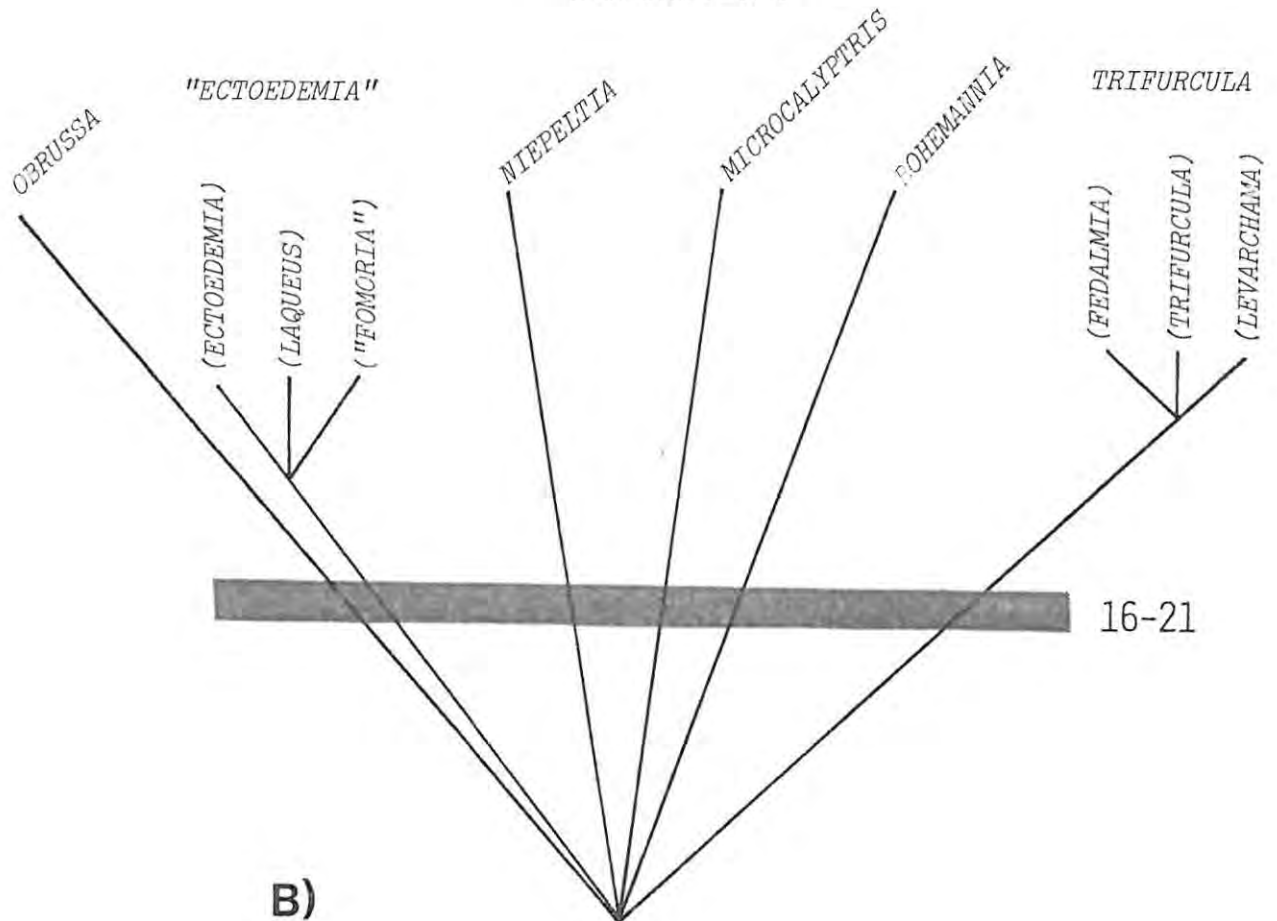


FIG. 140. Cladograms of A) major clades of Nepticulidae, and B) the Trifurculinae. Numbers refer to apomorphous characters (see text). Taxa in inverted commas are of doubtful monophyletic status.

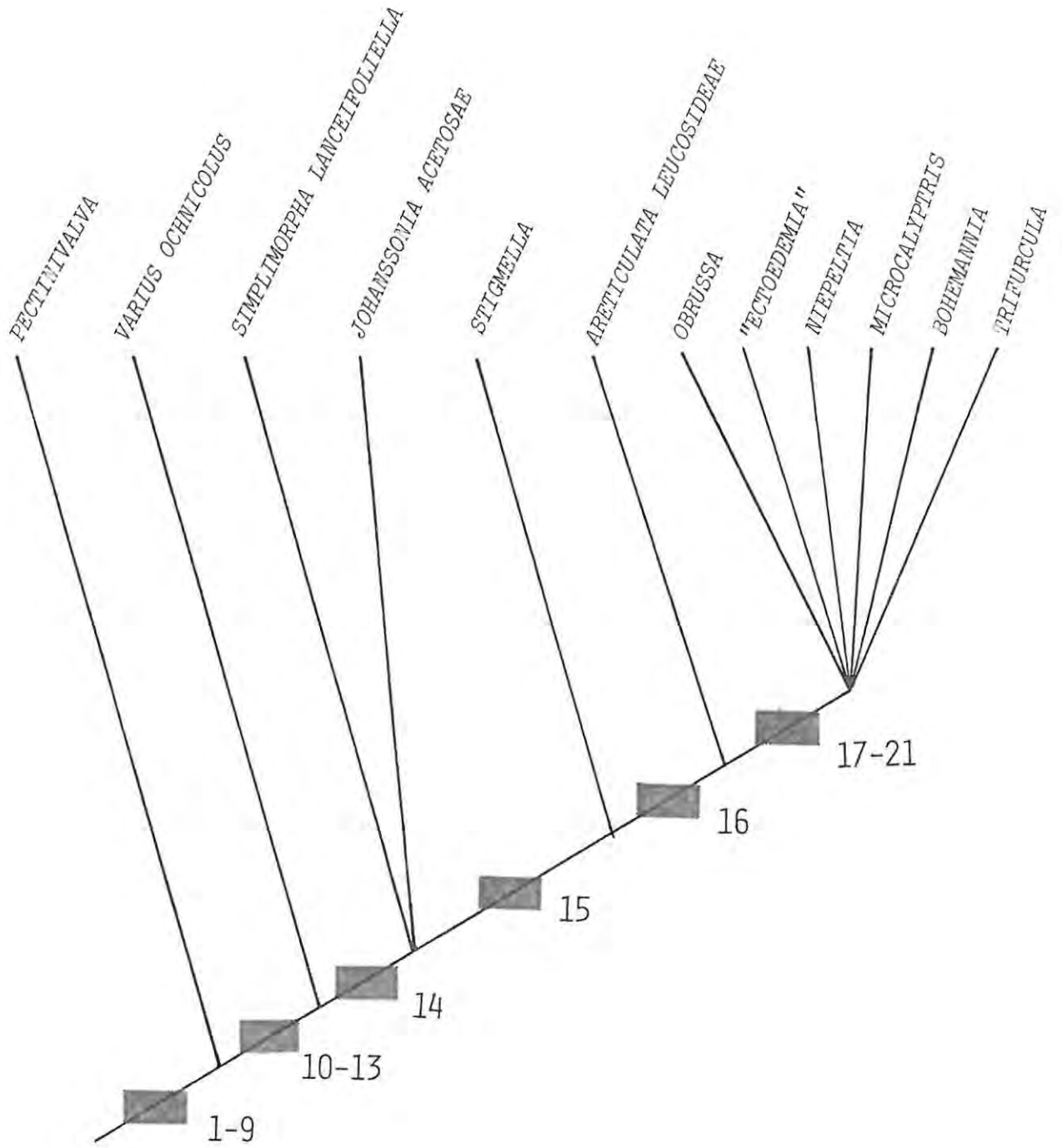


FIG. 141. Hypothetical cladogram, which indicates possible position of species of uncertain position (*incertae sedis*) in the classification adopted. Numbers refer to apomorphous characters (see text).

not be shown as the ancestor of the Trifurculini although it is theoretically possible that a species that belongs to *Stigmella* could be the ancestor.

Actually, the cladograms in this work (figs 140, 141) may indeed be regarded as phylogenies (postulates of kinship) *if one assumes, as I do, that the nodes represent unknown common-ancestral species of the taxa they subtend.*

The course of a particular history can only be completely illustrated by patterns of ancestry and descent. Therefore diagrams like figures 140 and 141, which include groups of species as well as - or instead of - single species, are only partial histories. Diagrams that do show patterns of ancestry and descent between species are called 'phylogenetic trees', or simply 'trees' (e.g. Eldredge & Cracraft 1980). Eldredge & Cracraft (1980:114) do not regard diagrams such as figures 140 and 141 as trees because they include *groups* of species as 'descendants' instead of single species, even though the branch-points may represent single ancestral species. The writers argue that because only species evolve, aggregates of species can never be regarded as ancestral *or* descendant units. Apparently there is no term for phylogenies of the kind described in the present work although there are many such diagrams in the literature.

Originally, Hennig (1966) presented his method of classification in terms of an evolutionary model and so the treatment of cladograms in the way described above represents a change of attitude. However, Platnick (1979:537) stressed that 'neither the value nor success of [Hennig's] methods is limited by the value or success of [his] evolutionary model.' As Hull (1979:419) has pointed out: 'Once the principles of cladism are recognised for what they are, *methodological principles*, the logic of the cladistic position on a variety of issues becomes much clearer.' Whilst few systematists would deny that evolution has occurred, its mechanism is disputed. Therefore if Hennig's methods depended on his evolutionary model, then refutation of the model would invalidate both the methods and classifications based on them. Certain questions about the process of evolution are hotly debated. Here are two. Is speciation generally the result of gradual transformation of lineages, or of a series of relatively sudden changes - or do both occur with about the same frequency? Does a species ever arise through the hybridization of two others? Eldredge & Cracraft (1980) argued that we should search for pattern in nature and express it in our classifications without making assumptions about the process by which

it has been brought about. The limits to which this can be achieved are the limits of cladism (Hull 1979).

The mechanism of speciation is not of great relevance to those systematists who are chiefly concerned with providing a classification of *groups* of species, although it may be of considerable interest. This is the case in the present work. The growing popularity of cladistics is probably mainly a result of its explicit methods and reasonable applicability.

However, the problems of cladistic analysis are considerable. Apomorphies are difficult to identify and homoplasy is a great source of confusion. Are these problems so great as to make the construction of cladograms and the search for genealogies a hopeless exercise? One argument is that genealogies are worth seeking however difficult to achieve. Another (Farris 1979, and see 'Classification', below) is that since cladograms are 'most parsimonious trees', their information content is higher than other dendrograms irrespective of whether or not they accurately represent genealogies.

This is the relevance of the issue of parsimony in cladistics - not whether nature is parsimonious or not. A systematist who states that he accepts the most parsimonious hierarchy utters a truism, for clearly if one arrangement (A) has fewer incongruent characters than another (B), then there is no reason for accepting (B). If a new study shows that some or all of the purported apomorphies of scheme (A) are invalid then the characters originally treated as incongruent for scheme (B) become congruent (and therefore apomorphic) for the latter and a new hypothesis is erected.

The important issue is this: given that phylogeny is worth estimating, are cladograms actually the best approximations? The actual course of phylogeny, like that of all historical narratives, will always elude us; therefore we have to recognise potential sources of error in our estimates. Recent commentators (e.g. Thomson 1981; Ghiselin 1981) have argued that homoplasy may be so extensive in nature that to simply accept the most highly corroborated (parsimonious) cladogram is to permit a major source of error in the estimation of phylogeny. Ghiselin (1981:141) stated that parallelism 'would be far more widely recognised if its non-existence were not used as a methodological posit.' However, if there is evidence from character analysis which suggests that similar structures in different clades are independent (not unique) modifications, then presumably no cladist would treat them as a single apomorphy.

CLASSIFICATION

The classification proposed (p.207) for the Nepticulidae is an exact, listed transposition of the cladogram in figure 140. In evolutionary terms, both the diagram and the list are hypotheses of genealogy (kinship). The list is a Linnean hierarchy indicated by indentation and a series of subordinate ranks. It is an expression of the degree to which nepticulid genealogy has been elucidated by the writer.

THE PROPOSED CLASSIFICATION

The taxa listed below under 'A Classification of the Nepticulidae' are, with the exception of *Microcalyptris* and *Ectoedemia* and one of its subgenera - *Fomoria*, supported by one or more apomorphies.

The genus *Ectoedemia* includes a large number of species, and the problems of their association are noted in 'Systematic Treatment' (above) and illustrated in 'Numerical Phenetic Analysis' (below). A conservative approach has been taken by the broadly inclusive use of the name *Ectoedemia*. Whilst the monophyly of the genus has not been demonstrated yet, by the finding of an apomorphy, it may be established in future. However it is equally, or more, likely that the group is not monophyletic. If *Ectoedemia* is not monophyletic it is objectionable. Since this possibility exists it is therefore a weak point in the classification and a prime area for future study.

I considered dealing with *Ectoedemia* in a different way from that finally proposed: (1) to retain *Ectoedemia* as a full genus as used in its original sense, (2) to treat the subgenus *E. (Iaqueus)* as a separate genus, and (3) to describe a series of monotypic or ditypic genera for the species of the subgenus *E. (Fomoria)* since no apomorphy has been found for this assemblage of species. This would have certainly been as 'correct' as the treatment actually presented, but it was not presented for the following reasons.

Point (1). The only apomorphy of *Ectoedemia* in its original sense (the nominate subgenus in the present work) is the loss of an uncus. Since the presence of an uncus is hypothesised as a ground-plan feature of the Nepticulidae, its absence in any nepticulid species must be interpreted as

a loss (a modification of the original condition). However, the loss could have occurred independently (as indeed it has in *Simplimorpha lanceifoliella* for example) on several occasions. Therefore its interpretation as an apomorphy in *E. (Ectoedemia)* requires corroboration from other characters. Certainly the species of this widespread group are phenetically similar in their wing venation and genitalia, but at present a confirmatory apomorphy, besides the loss of an uncus, has yet to be found. Since it is quite possible that the group is monophyletic it is still retained in the classification presented here. It is treated as a subgenus, not because that rank is arbitrarily considered to be more suitable than that of genus, but because, since the patterns of wing venation and genitalia resembles those of many other species, all the species should be associated in a genus to show their relative distinction from other genera. Until it is shown that some of the species of this assemblage are more closely related to those of other genera, it is preferable to retain them in a genus of their own.

Point (2). The phenetic similarity of some species of *E. (Laqueus)* to some of *E. (Fomoria)* is pronounced (see the positions of species 27-34 and 35-43 in figs 146, 147 in 'Numerical Phenetic Analysis', below). The only apomorphy for the former is the presence of an anal loop in the forewing. Although this is certainly a striking character, its absence in some of the closely phenetically related species of *E. (Fomoria)* suggests that it may have been secondarily lost in them. Since this possibility exists the species of *E. (Laqueus)* and *E. (Fomoria)* are included within the same genus because they, like the members of *E. (Ectoedemia)*, may be cladistically more closely related to each other than to species in any other genus. This inclusion is not intended as a compromise between phenetics and cladistics, but an attempt to demonstrate the degree to which nepticulid genealogy has been elucidated so far.

Point (3). *E. (Fomoria)* includes several species that are loosely associated phenetically. As noted above, some of them are phenetically, and possibly cladistically, allied to species of *E. (Laqueus)*. For this reason I prefer to retain them all in the same genus. At present, *E. (Fomoria)* is an assemblage for which no apomorphy has been found. I considered describing 12 new genera (nine monotypic, two ditypic, and one with three species) for the South African species included in *E. (Fomoria)*, above. This would have been shown on figure 140b as 12 extra lines that arise from the base of the cladogram. It would have represented the limits of

our knowledge of genealogy more accurately and would have been consistent with an aim of the study. However, species can only be described as binomina (*International Code* 1964), so a systematist is obliged, in a situation such as the present one, either to include many species of doubtful affinity in a genus or to describe them in small, often monotypic, genera.

To have split the subgenus *E. (Fomoria)* into several genera would have meant the introduction of many redundant names, to the probable irritation of other workers. It would also have implied that the same treatment should be applied to other species not dealt with in this work, particularly from Europe, which are difficult to place at present, but which show phenetic affinities to this somewhat heterogeneous assemblage. Since intensive studies on the Nepticulidae are being continued at the Vrije Universiteit, Amsterdam, I prefer to avoid the introduction of numerous additional generic names at present for practical reasons.

In order to show that monophyly has not been convincingly established for *Ectoedemia* as a whole, and *E. (Fomoria)*, the names are placed in quotation marks in the listed classification (p.207). The qualifications *sedis mutabilis* and *incertae sedis* are also used in the list. *Sedis mutabilis*, which means 'of interchangeable position' (Wiley 1979), is used to indicate taxa that form multiple furcations on the cladogram (fig.140b). Thus the arrangement of all the genera in the Trifurculini are interchangeable. The expression contrasts with *incertae sedis*, which means 'of uncertain placing'. Specimens of uncertain placing are also noted in the list. The uncertainty of position is not total of course and the species to which it applies are qualified as being *incertae sedis* within a particular subfamily.

COMMENTS ON CLADISTIC CLASSIFICATION

The debate over whether we should adopt phenetic or cladistic classifications, or those of the evolutionary (also called eclectic or synthetic) school have been discussed numerous times and are somewhat passé. However, since I have adopted a cladistic classification here, some justification of the approach seems necessary.

Cladistic classifications have been claimed to be more 'informative',

'stable', and 'natural' than other kinds. These claims are considered below.

Farris (1977, 1979, 1980) has argued that cladistic (he uses the term phylogenetic) classifications are more *informative* than phenetic or evolutionary ones. Since a classification is simply a list, then apart from the hierarchy it expresses, the information contained is indirect. Farris' claim rests upon the fact that cladograms, in contrast with other dendrograms, are 'most parsimonious trees'. Such trees 'allow data to be completely summarized by the most succinct diagnoses' (Farris 1979:483). Farris measured the information content of hypothetical data sets (1979) and data from organisms (1980) and found that the taxa of classifications based on cladograms were diagnosed more efficiently (in fewer terms) than those in other classifications. Farris stated that cladograms are preferable to phenograms because of this more efficient (informative) data description. One can derive a most parsimonious arrangement on the basis of *uniquely* shared characters from any data matrix. Most parsimonious trees are more informative irrespective of whether or not they accurately represent phylogeny.

Farris used the word diagnosis in a literal sense - that is, the fewest characters required to distinguish any group in a classification. This does not mean that 'diagnoses' in taxonomic revisions or field guides should necessarily be like this. In such cases they provide means of identification of a specimen and they may include more characters than the minimum strictly required for literal diagnosis.

Terms such as 'cladistic' and 'phylogenetics' stress kinship whilst saying nothing about the indirect information content or stability of classifications based on the methods. It is difficult to drop these controversial words since they are well-established in the literature. Terms used in information theory are precise, but they may prove unacceptable to biologists. Some may object to Farris' definition of 'informative' but it seems to be the only unequivocal one given, and the thought behind it cuts through the rhetoric that seems more to have confused than clarified the issue of the informativeness of classifications.

Concepts of what systematists mean by a *natural* classification are equally controversial. It is not just the definition of the word that has led to the problem, but the thought that lies behind it.

The word natural is the antonym of artificial or manufactured. Nelson (1979) pointed out that systematics is the discovery of nature's order, and that classifications may be natural (an embodiment of that order) or artificial. Whilst few would disagree that both kinds of classification have their uses, proponents of the three current major schools of systematic thought have as their primary aim the production of a natural classification. Since the methods of each school are claimed by their adherents to produce the most natural classifications, considerable controversy has arisen.

Gilmour (1937) defined a natural classification as 'one founded on attributes which have a number of other attributes correlated with them.' In this classic paper he distinguished between a natural and a phylogenetic classification. Gilmour pointed out that degree of similarity 'is frequently an indication of [phylogenetic] relationship ... but that it is an invariable indication certainly cannot be maintained.' Hardly any systematist would disagree about the last point. The contentious issue is whether a phylogenetic classification is, in contrast with Gilmour's view, natural. Certainly the pheneticists would argue, with Gilmour, that it is not.

Darwin (1859:Chapter 13) took the opposite view. He noted that descent was the 'hidden bond of connexion' that naturalists had been unconsciously seeking when constructing their classifications. Over one hundred years later this point has been 'rediscovered' by modern cladists. They have moved away from stressing the phylogenetic model of Hennig (1966) (although the methods are still accepted), and have noted that cladism is a return to the methods of classification prior to the development of Darwinian evolutionary theory, and is therefore, strictly, independent of it. Darwin's realisation that the *search* for the Natural System is essentially independent of the theory of evolution, even though the evolutionary process was the cause of it, demonstrates a remarkable understanding of what many present-day writers probably regard as a somewhat fashionable approach to phylogenetic systematics. This insight is acknowledged by the Darwinian epigraph to this work.

Farris (1977) has shown that whilst clustering by overall similarity can produce natural classifications (in Gilmour's sense) they do not always do so. Farris argued that the most natural classifications are achieved if attributes that are not unique to a taxon are eliminated. He found that the use of a similarity measure that excluded such non-unique attributes was superior (had a higher cophenetic correlation coefficient) to one that

included them.

Cladistic classifications are also claimed to be more *stable* than other kinds. Schuh & Polhemus (1980) used numerical methods to compare the congruence of numerically generated cladograms and phenograms (derived by Wagner and unweighted pair group methods respectively) on complete and partial data sets on Leptopodomorpha (Hemiptera). They found that the various cladograms generated were less subject to change (were more stable) than the phenograms when the original character set was reduced. Schuh & Polhemus used 35 and 38 character sets and a 19 character subset for most of their cladograms and phenograms. Whilst this supports the greater stability of cladistic techniques for relatively low numbers of characters, pheneticists would claim that their techniques are perhaps fairly judged only on large numbers. Nevertheless, the preference for relatively large numbers of characters seems to be a limitation of the methods. The problem of obtaining a large number of logically indivisible characters has been noted by Crowson (1970); it was a serious difficulty in the present study.

An objection levelled at cladistic classification is that, by incorporating only genealogy, it is impoverished by the loss of information about grades of organisation and 'adaptive zones' (e.g. Mayr 1974). Therefore to many, a classification should achieve a compromise between the expression of genealogy and degrees of divergence of genealogical lineages. In a study of the Aculeate Hymenoptera, Brothers (1975:578) stated, with regard to his cladogram, that 'The basic pattern (the result of cladogenesis) is only one aspect to be considered; degree of relative morphological or phenetic distinctness of taxa (the result of anagenesis) is another.' Brothers devised a method of calculating a measure of 'taxonomic distinctness', and used it as a guide to establish taxonomic rank.

The problem with such a compromise is that the genealogical component of a classification, and its stability - if the work of Schuh & Polhemus is of general validity, is then reduced. Clearly any given classification cannot, in theory, satisfy the goals of proponents of a cladistic, a phenetic or an eclectic approach at once.

Some suggest that the required adherence to the Linnean hierarchy is a constraint. Sneath & Sokal (1973:201) stated that hierarchical classifications are often poor representations of phenetic relationships in nature.

Without doubt, all kinds of objects could be arranged in many non-hierarchical ways by certain phenetic techniques. For example, diagrams derived from ordination methods (frequently used in numerical phenetic studies) are intrinsically inappropriate for hierarchical representation. However, the special property of living organisms is that they are assumed to have come about by a process of descent, so therefore one consistent pattern that is present in nature is that of genealogy; and that can only be represented hierarchically. The reason why cladists have found an hierarchy appropriate is not because of their constrained way of thinking, but because this pattern reflects one that is unequivocally expressed in nature. That Linneaus adopted an hierarchical system may have been because, as Darwin suggested in *The Origin*, systematists were unconsciously seeking it as a reflection of the natural pattern without recourse to evolutionary theory. Any other system can only compromise the one absolutely representable pattern for which there seems to be overwhelming evidence. Therefore is it not appropriate to accept the expression of this pattern as the goal for classification, and continue to examine grades, rates of evolution, and phenetic relationships as additional, and allied, projects?

A CLASSIFICATION OF THE NEPTICULIDAE

Family: NEPTICULIDAE

Subfamily: PECTINIVALVINAЕ

Genus: *PECTINIVALVA*

Subfamily: STIGMELLINAЕ

Tribe: STIGMELLINI

Genus: *STIGMELLA*

Tribe: TRIFURCULINI (All genera of interchangeable position,
sedis mutabilis.)

Genus: *OBRUSSA*

"*ECTOEDEμία*"

Subgenus: *ECTOEDEμία*

LAQUEUS

"*FOMORIA*"

NIEPELTIA

BOHEMANNIA

TRIFURCULA

Subgenus: *FEDALMIA*

TRIFURCULA

LEVARCHAMA

"*MICROCALYPTRIS*"

Species *incertae sedis* within the Stigmellinae

Varius ochnicolus

Simplimorpha lanceifoliella

Johanssonia acetosae

Areticulata leucosideae

Artaversala gilvafascia

Manoneura basidactyla

Parafomoria helianthemella

NUMERICAL PHENETIC ANALYSIS

The phenetic aspect of the study formed the basis on which the cladistic analysis was carried out, see Introduction and in particular the flow diagram on page 4 . The numerical analysis was used primarily to check my personal estimate of resemblance based on simple observation, but it also provided an illustration of phenetic relationships that may have value in its own right. The numerical work is presented at this point in the dissertation so as not to disrupt the flow of the cladistic style that runs through 'Systematic treatment', 'Cladistic Analysis', and 'Classification'.

The 'operational taxonomic unit', or OTU (e.g. Sneath & Sokal 1973) in this work is the species.

Two sets of analyses were undertaken. The preliminary one was carried out early in the study on a large body of data obtained from first-hand examination of specimens and from the literature. A matrix of 149 species and 45 characters was constructed and included as broad a sample of neptculid variation as possible. Many of these species are known only from the male, in which case female characters and life-history details were coded as 'missing data'. This meant a large number of gaps in the matrix.

Multivariate techniques, including cluster analyses and ordination methods were applied to the data to see how the resulting groups compared with those apparent to me without using these numerical methods. On the whole there was correspondence, so the preliminary numerical study acted as a summary of the data available at that time.

Further morphological examination was then undertaken on species whose phenetic relationships expressed in the numerical study were doubted. This involved obtaining representatives of a few European species (particularly type-species) for which aspects of morphology were thought to be either incorrectly interpreted in the literature or inadequately described. Further examination of South African and Australian species was also undertaken.

Since the subsequent work revealed misinterpretations of structure, which had been incorporated into the data matrix, a new matrix was constructed and subjected to further analysis.

Fewer species were included in the second group of analyses than in the first; the guiding principle adopted was to include as wide a range of nepticulids as possible. The reason for the smaller number of species are twofold. First it reflects the limits of my confidence in the morphological interpretation presented in much nepticulid literature, or the coverage of the descriptions. Second only species for which both males and females were known were included in order to reduce the amount of missing data.

The numerical analyses were carried out as follows. Characters were selected and coded for each species involved, and then a matrix was drawn up and the data were punched onto cards. The data were subjected to both cluster analyses and ordination methods. Both techniques give results that display different kinds of distortion; each acts as a check on the distortion inherent in the other.

CHARACTER SELECTION AND CODING

The principle of estimating what is known as 'overall' similarity is based on the assumption that similarity-measures derived from a sample of characters from the phenotype will approximate to overall similarity in its literal sense. Perhaps a better term for 'overall' is 'raw' similarity (Farris 1979) since it avoids the misleading implication of total similarity.

How many characters should be used before raw similarity will give a reasonable estimate of overall similarity in its literal sense? Sneath & Sokal (1973:106) 'still are unable to provide generally valid answers to this question.' They suggest that as large a number of characters as possible should be used because 'As more and more characters are added, it takes an increasingly large number of characters with quite different phenetic information to alter appreciably a given estimate of phenetic similarity.' The authors refer to this as a 'principle of inertia'.

In the present work an attempt was made to obtain as many characters as possible, not only for the numerical analysis but also for the personal assessment of phenetic similarity and for the cladistic study. Characters that would have given a large amount of 'missing data' in the sample were ignored. Since the species was the fundamental unit of the analysis, intraspecific variation was also excluded.

What is a taxonomic character to the numerical taxonomist? In the

numerical work the definition of a unit character given by Sneath & Sokal (1973:74) was adopted. A unit character is 'a taxonomic character of two or more states, which within the study at hand cannot be subdivided logically, except for subdivision brought about by the method of coding.' Although this might be described as a working definition it was very difficult to know when a potential character became logically indivisible in the present work. (The point has been made by Crowson 1970.) This in part accounted for what might be considered by some as a rather small number of characters.

In general, colour is very difficult to code in the Nepticulidae. Consider the colour of the head-tuft. At first glance black and orange would seem logical subdivisions of this feature. However the more species that were examined the more this division became obscured. There seems to be gradation from off-white, to orange, to orange infused with red-brown, to predominantly red-brown, to dark red-brown to almost black, to black. When I attempted to code the head-tuft colour of a species into what seemed at first reasonable subdivisions there were many examples that did not fit. The same problem occurred in the case of forewing colour. Whilst many nepticulid species are 'metallic', with silver or golden reflections, most are not. This seemed, at first, an obvious subdivision. But there are species that obscure this boundary, *Obrussa sericopeza* being one example. Again, ground-colour of the forewing ranges from off-white to very dark brown or black. It was impractical to divide the numerous grades of grey, brown and ochreous into logical subdivisions; indeed they may not even be divisible. Rather than force the data into arbitrary subdivisions these features were excluded from the list of characters.

The subjectivity involved in coding characters is considered as one of the shortcomings of numerical taxonomy by Sneath & Sokal (1973:427). Although a genuine attempt was made to remove subjectivity from this process in the present study, the way in which the shape of structures was coded depended, inevitably, on personal judgement. The more thoroughly I studied nepticulids, and the more species I examined, the fewer became the number of logically indivisible characters compared with the original list of potential ones.

A further problem is the virtual impossibility of coding subtle but detailed differences in shape, particularly of male genital components. The omission of this can lead to a false impression of closeness of

relationships within tight clusters. This is not a serious objection to the numerical work since the main object was to give a *broad* summary of nepticulid variation, not a detailed analysis of within-group phenetic relationships. Such an aim is a matter of approach expressed by Crowson (1970) who contrasts the 'synthetic' method in systematics, where species are grouped together and so on up the Linnean hierarchy, with the 'analytical' approach where the main groups are critically analysed from the highest levels downwards. Both approaches were used in this work, as in most systematic projects, but the broad summary of nepticulid variation was the chief object of the numerical and the cladistic analyses.

The 53 species involved in the analyses are listed in Table 1, the characters and their states in Table 2, and the matrix drawn up is given in Table 3. 'No comparisons', coded as '9', represent either lack of information, or the absence of a structure. For example character 22 (the condition of the apex of the uncus) cannot be compared in species where the uncus is absent. A separate character (21) records the general condition of the uncus, including its absence.

PROCEDURE

Computations were carried out on an IBM S/370 model 158 computer, at the Centre for Computing Services of the Council for Scientific and Industrial Research, Pretoria. The programs used come from the NT-SYS package devised by Rholf *et al.* (1974).

Characters were standardised by expressing each state as a deviation from the mean in standard deviation units (Sneath & Sokal 1973; Moss *et al.* 1977).

Average taxonomic distance and correlation matrices were computed and phenograms were printed for each. Since phenograms are subject to distortion at low clustering levels, the data were analysed by an ordination method. This took the form of Principal Component Analysis (PCA) based on a matrix of product-moment correlations between characters. A minimum spanning tree (MST), which indicates nearest neighbours, was imposed on the ordination diagrams.

Phenograms and ordination diagrams were interpreted reciprocally. Phenograms are reliable for expressing phenetic relationships within tightly clustered taxa, but become increasingly unreliable (prone to distortion) towards the base of the diagram (see, for example, Sneath & Sokal 1973;

Moss *et al.* 1977). Ordination methods give a better assessment of inter-group distances but tend to be less reliable for assessing phenetic relationships between closely related taxa. The MST was used to indicate the inevitable distortion present in reducing the results of the PCA to two dimensional diagrams.

In general the guidelines given by Sneath & Sokal (1973) for the presentation of a numerical taxonomic study were followed.

ANALYSES

The results refer to the second set of numerical analyses performed, not to the preliminary ones carried out early on in the study (see above).

53 SPECIES STUDY. Cluster analyses were performed on all 44 characters coded. The average taxonomic distance and correlation phenograms (figs 142, 143 respectively) show a number of differences. For example species 53 (*Artaversala gilvafascia*) is an extreme outlier in the distance phenogram but unites with species 13 (*Simplimorpha lanceifoliella*) at about the 0,4 level in the correlation phenogram. Species 12 (*Varius ochnicolus*) falls within the *Stigmella* to *Simplimorpha* cluster in the distance phenogram but is attached to *Pectinivalva* in the correlation phenogram. Other incongruences are also present and great care is required in interpreting the results presented in the phenograms.

However, perhaps the most notable feature of the phenograms is their congruence. The major clusters that appear represent *Pectinivalva* (1-4), *Obrussa* (15-18), *Niepeltia* (44-48), and *Ectoedemia grandinosa* and its relatives (21-26). The two *Trifurcula* species (49, 50) are also united on both diagrams. In the distance phenogram *Stigmella* (5-11), and the monotypic genera *Johanssonia* (14), *Varius* (12), *Areticulata* (52) and *Simplimorpha* (13) are united. Within this cluster *Stigmella* species (excluding species 9, *S. allophylica*) fall together. In the correlation phenogram *Varius ochnicolus* (12), and *Stigmella confinalis* (11) are divided from the group, *Simplimorpha lanceifoliella* (13) and *Areticulata leucosideae* (52) are united and attached to it, and *Johanssonia acetosae* (14) is attached low down on the diagram.

Ectoedemia is divided into two main groups; two species, 28 and 42, are isolated. The same general pattern is shown in the correlation phenogram; species 42 (*E. vannifera*) is again shown to fall outside either subgroup but its relationship to species 41 (*E. fuscata*) is indicated.

Except for the incongruent placing of species 51 and 53, the distance phenogram indicates a fundamental division within the sample between *Pectinivalva* and the rest. This corresponds to the subfamilial division of the Nepticulidae (p.207), but it is not apparent in the correlation phenogram. There is no justification for the tribal division of the Stigmellinae from either diagram.

Since the matrix correlations were high for both phenograms (0,917 for the distance and 0,814 for the correlation diagram, which indicates that the phenograms gave a good fit for the data), PCA was used to see if some of the incongruence could be explained. Before this was undertaken, species 53 (*Artaversala gilvafascia*) was removed because of its outlying position in the distance phenogram. In the preliminary set of analyses this species accounted for so much of the variation within the sample that the ordination diagrams showed *A. gilvafascia* on one side and all the other species displaced to the other, so that the relationships within the latter were obscured.

52 SPECIES STUDY. The deletion of species 53 (*A. gilvafascia*) resulted in one invariant character in the matrix. (Invariant characters are omitted automatically by the computer on the NT-SYS package.) A distance phenogram (not presented) was first produced and checked against the corresponding diagram of the 53 species study. There was hardly any difference between the two: species 13 (*Simplimorpha lanceifoliella*) was split away from the *Stigmella* to *Simplimorpha* group apparent in the 53 species phenogram, otherwise the species were in the same order. The alteration in species 13 emphasises its problematic affinities.

In order to perform the ordination all characters that included a state coded for 'no comparison' were removed. PCA is based on correlations between characters (see Procedure, above) so correlations can obviously not be made on missing data. The removal resulted in the standardisation of 34 characters, a reduction of the original number of about 23 percent. Even with this reduction the distance and correlation phenograms (figs 144, 145 respectively) show a high degree of resemblance to those of the 53 species/44 character study. The same main clusters are apparent; details within them vary somewhat. (The figures are only presented to indicate the degree of similarity and the differences; no further taxonomic structure is apparent.)

The first five components were computed, and components I against II, and I against III are compared to illustrate the ordination (figs 146, 147). Each principal component represents a linear combination of the original variables (characters) computed in such a way as to summarise major sources of variation. The five components accounted for 57,04 percent of the total variation. This figure is the sum of the following individual percentages: component I=22,39; component II=11,09; component III=9,18; component IV=7,95; and component V=6,43. Obviously the greater the fraction of the total variation accounted for in an ordination the more useful will be its results. Sneath & Sokal (1973:304) consider an ordination to be unsatisfactory if the variation explained is less than 40 percent, a figure clearly exceeded here. The plot of components I against II is given in figure 146. These components explain 33,48 percent of the total variation. The minimum spanning tree (MST), which connects nearest neighbours, is calculated from the average taxonomic distance matrix and is superimposed on the figure.

The major groups of the phenograms (figs 144 and 145) are also apparent as clusters in the ordination diagram (fig. 146). Within each cluster the species are interconnected by the MST. *Varius ochnicolus* (12) tends towards an intermediate position between *Pectinivalva* and *Stigmella*. This is better represented in fig. 146 than in the phenograms. The position of *ochnicolus* (12) is similar in the plot of component I against component III (fig. 147).

The isolated position of *Pectinivalva* (1-4) is apparent in both figures 146 and 147. Both *Stigmella* (5-11) (together with *Johanssonia* (14) and *Simplimorpha* (13)) and *Niepeltia* (44-48) are shown to be rather isolated from the large *Obrussa* (15-18), *Ectoedemia* (19-43) and *Trifurcula* (49, 50) conglomerate. The two *Trifurcula* species (49 and 50 each representing a different subgenus) are rather far apart but are, nevertheless, nearest neighbours as indicated by the MST. A similar indication is derived from the phenograms. That the proximity of species 51 (*Bohemannia quadrimaculella*) to species 45 and 48 in fig. 146 is due to distortion inherent in the two dimensional diagram can be seen from the MST and the position of the species in fig. 147. *Bohemannia* is phenetically distinct.

The position of *E. fuscata* (41) and *E. vanniifera* (42) appears more acceptable in the ordination diagrams than in the distance phenogram since their attachment to each other (by the MST) and to the loose *Ectoedemia* (19-43) aggregation is indicated. However, since the first three factors

explain only about 57% of the total variation the real phenetic positions of these species remains obscure.

The matrix for the first three components is given in Table 4, to indicate the character loadings.

Two of the three subgenera of *Ectoedemia* (*Laqueus*, 21-34, and *Fomoria*, 35-43) are certainly not apparent in the numerical analyses. In order to see if they could be distinguished by the techniques, a further analysis was carried out on the species of *Ectoedemia*. *Obrussa* and *Areticulata* were retained since they were closely associated with the loose *Ectoedemia* aggregation. No further resolution was obtained from an examination of the phenograms or ordination diagrams and so the results are not detailed. Again *grandinosa* and its relatives formed a discrete cluster.

DISCUSSION

The results of a numerical phenetic study are not generally converted directly into a classification without at least some modification. The results are usually interpreted in the light of what is termed the conventional or orthodox approach, although some workers consider that to do this threatens the operational or objective approach for which numerical pheneticists strive.

How would a phenetic classification based on the numerical phenetic techniques appear in the present study? The following groupings are fairly clear: (A) *Pectinivalva* (1-4), (B) *Stigmella* (5-11) plus *Simplimorpha lanceifoliella* (13) plus *Johanssonia acetosae* (14), (C) *Niepelitia* (44-48), (D) *Obrussa* (15-18), (E) *grandinosa* and its relatives (21-26) and possibly (F) *Trifurecula* (49, 50). *Artaversala gilvafascia* (53) and *Bohemannia quadrimaculella* (51) are outliers and independent taxonomic rank is indicated, (G) and (H). There is little structure apparent within the remaining species (*Ectoedemia*, less *grandinosa* and its relatives, plus *Areticulata leucosidae*), but their loose aggregation in the ordination diagrams suggests that they could be included in a group (I) for convenience.

The position of *Varius ochnicolus* (12) varies somewhat in the phenograms, and it is represented outside the *Stigmella*, *Simplimorpha*, *Johanssonia* group (5-14) in the ordination diagrams. In a phenetic classification it could be treated as a member of that group or named on its own (J).

If the phenetic distinctness of *Pectinivalva* from most other nepticulids

is recognised by a higher category (Pectinivalvinae) then, for consistency, *Artaversala* and *Bohemannia* should be treated in the same way. The tribal division of the Stigmellinae is not apparent from the numerical results.

A classification based on the numerical study would therefore probably include nine or ten genera. The differences between this and the classification presented on page 207 is that in the latter suprageneric categories are introduced, the indeterminate position of some species is noted by *incertae sedis* categorisations, *Ectoedemia* is divided into three subgenera, and, perhaps most controversial of all, *grandinosa* and its relatives are included in one of these subgenera. Although this represents a considerable refinement of the phenetic groups it is not, in itself, a criticism of phenetic techniques. Since the phenetic groups were used as a basis for subsequent cladistic analysis, alterations were to be expected.

I found that the numerical analysis produced similar groups to those of my own assessment achieved early on in this project. There is no direct evidence for this of course, but the tendency for the results of numerical phenetic analyses to broadly resemble those conceived by the systematist is well documented. The following quotes from various authors express this point.

In the main, the major phenetic divisions have corresponded with the classically derived genera ...

Wilkinson (1970:284) in

a study of some Indo-Australian Drepanidae (Lepidoptera).

In general, the numerical findings confirmed the existence of the nine new and nine described genera recognised earlier by conventional means.

Moss *et al.* (1977:400)

in a study of eustathid mites.

We may first consider what general taxonomic information may be obtained from numerical studies. The most obvious is that the numerical taxonomy confirms the broad outlines of existing orthodox taxonomy.

Sneath & Sokal (1973:430).

Since this point seems to be well-established perhaps the use of numerical methods might be reserved for special problems, particularly those dealing with the discrimination of taxa on the basis of measurements rather

than on coded characters. In some studies, particularly those involving measurements, the application of multivariate methods is essential. For example Dippenaar (1980) made extensive use of them in his work on African *Crocidura*, a genus of shrews. The data on which his phena (species) were delimited came from skull-measurements. Numerical taxonomy is not limited to phenetics of course. Methods for computing most parsimonious trees are used in phylogenetic systematics (e.g. Farris 1970; Sneath & Sokal 1973).

Sneath & Sokal (1973) consider, nevertheless, that the value of confirmation of conventional techniques should not be despised because: 'It increases the general credibility of the taxonomy of the group and of the numerical techniques appropriate for such study.', (p.430).

Table 1. Species used in the numerical analyses

(A - Australian, E - European, NA - North American; rest are from southern Africa.)

<i>Pectinivalva</i> (A)	<i>Ectoedemia</i> (<i>Ectoedemia</i>)	<i>Niepeltia</i>
1. <i>commoni</i>	19. <i>commiphorella</i>	44. <i>molleivora</i>
2. <i>species A</i>	20. <i>populella</i> (NA)	45. <i>rubiaevora</i>
3. <i>species B</i>		46. <i>lorantivora</i>
4. <i>species C</i>	<i>Ectoedemia</i> (<i>Iaqueus</i>)	47. <i>acumenta</i>
	(<i>grandinosa</i> and its relatives)	48. <i>larneivora</i>
<i>Stigmella</i>	21. <i>grandinosa</i>	
5. <i>abutilonica</i>	22. <i>wilkinsoni</i>	<i>Trifurcula</i> (<i>Fedalmia</i>)
6. <i>parinarella</i>	23. <i>simicola</i>	49. <i>headleyella</i> (E)
7. <i>varii</i>	24. <i>guerksiae</i>	
8. <i>geranica</i>	25. <i>macrochaeta</i>	<i>Trifurcula</i> (<i>Trifurcula</i>)
9. <i>allophylica</i>	26. <i>furcella</i>	50. <i>pallidella</i> (E)
10. <i>nigrata</i>	(Other species in the subgenus)	
11. <i>confinalis</i>	27. <i>royenicola</i>	<i>Bohemannia</i>
	28. <i>denticulata</i>	51. <i>quadrinaculella</i> (E)
<i>Varius</i>	29. <i>undatae</i>	
12. <i>ochnicolus</i>	30. <i>craspedota</i>	<i>Areticulata</i>
	31. <i>capensis</i>	52. <i>leucosideae</i>
<i>Simplimorpha</i>	32. <i>gymnosporiae</i>	
13. <i>lanceifoliella</i>	33. <i>insulata</i>	<i>Artaversala</i>
	34. <i>crispae</i>	53. <i>gilvafascia</i> (NA)
<i>Johanssonia</i>		
14. <i>acetosae</i> (E)	<i>Ectoedemia</i> (<i>Fomoria</i>)	
	35. <i>oleivora</i>	
<i>Obrussa</i>	36. <i>pappeivora</i>	
15. <i>zimbabwiensis</i>	37. <i>myrtinaecola</i>	
16. <i>nigricapitella</i>	38. <i>alexandria</i>	
17. <i>krugerensis</i>	39. <i>leptodictyae</i>	
18. <i>sericopeza</i> (E), (NA)	40. <i>incisaevora</i>	
	41. <i>fuscata</i>	
	42. <i>vannifera</i>	
	43. <i>septembrella</i> (E)	

TABLE 2. List of characters and character states.

Head

1. Pedicel of antenna: normal (0), with ball-shaped expansion in male (1).

Thorax: general

2. Hair-pencil of male: absent (0), underside of forewing on costal edge (1), underside of forewing near anal edge (2), upper surface of hindwing on costal edge (3).
3. Specialised scales on male: absent (0), laminate, granular (1), pilose (2).
4. Proximal pair of spurs on hindtibia: above midpoint (0), in middle (1), below midpoint (2).

Thorax: forewing venation

5. R_1 : coincident with stem of R_S , diverges later (0), coalesced with R_S throughout length (1), separate from R_S from base (2).
6. R_{2+3} : not represented by a separate branch (0), linked to rest of R_S (1), not continuous with rest of R_S (2).
7. R_4, R_5 : neither branch present (0), coalesced as R_{4+5} (1), both branches present terminally (2).
8. M: coalesced with R_S from base, not Cu (0), coalesced with Cu at base and R_S from about one-third of way along wing (1), coalesced with Cu from base and meets R_S terminally (2), coalesced with R_S and Cu from base (3).
9. M_1, M_2 : coalesced as M_{1+2} (0), both branches present terminally (1).
10. Cu: very long (0), short (1).

11. Cu: not represented as terminal branch of R+M+Cu trunk (0), represented as terminal branch of R+M+Cu trunk (1), no comparison (9).
12. 1+2A: not thickened (0), thickened (1).
13. Anal loop: absent (0), present (1).

Thorax: hindwing venation

14. Trunk of R+M, or R if veins are separate: deflected towards costa (0), not deflected towards costa (1).
15. M: a single branch (0), two-branched (1).

Male genitalia

16. Vinculum: broad (0), V-shaped (1).
17. Ventral plate of vinculum: unmodified (0), with a deep U-shaped excavation (1), extended posteriorly (2), flimsy except for thickened posterior margin (3).
18. Lateral arms of vinculum: extended U-shaped (0), U-shaped (1), ring-shaped (2).
19. Apodemes (support rods) of lateral arms of vinculum: absent (0), present (1).
20. Tegumen: a simple band (0), forms a broad back to capsule (1), extended (2), bifurcate or bilobed (3), very slender (4).
21. Uncus: absent (0), hood-like (1), a thickened band, approximately in the shape of an inverted V (2), a pair of small, setose lobes (3), a pair of prominent setose lobes (4).
22. Apex of uncus: not divided dorsoventrally (0), weakly divided dorsoventrally (1), deeply excavated dorsoventrally (2), no comparison (9).

23. Gnathos: reduced (0), not reduced (1).
24. Gnathos: central element undivided (0), central element divided or absent (1), no comparison (9).
25. General shape of valva: very broadly rounded at apex (1), deeply divided (1), approximately triangular (2).
26. Pectinifer of valva: absent (0), present (1).
27. Large, spine-like apodeme of valva: absent (0), present (1).
28. Short lobe-like process of valva: absent (0), present (1).
29. Pin-cushion-like lobe of valva: absent (0), present (1).
30. Cluster of prominent setae towards base of valva: absent (0), present (1).
31. Transverse bar of transtilla: absent (0), present, even if indistinct (1).
32. Diaphragmata: not denticulate (0), denticulate (1).
33. Juxta: absent (0), present (1).
34. Flanges of aedeagus: absent (0), present (1).
35. Ventral process of aedeagus: absent (0), present (1).
36. Shape of ventral process of aedeagus: prominent (0), not prominent (1), no comparison (9).
37. Striate thickening around base of ejaculatory duct: absent (0), present (1).

Female genitalia

38. Ovipositor: not distinctly pointed (0), distinctly pointed (1).
39. Ductus bursae: unmarked (0), with ring-shaped thickening (1), with funicular thickening (2), with narrow band-like thickening (3), with pair of short rods (4), as fig.113 (5).
40. Comb-like teeth near union of spermatheca and bursa copulatrix: absent (0), present (1).
41. Signa of corpus bursae: absent (0), present (1).
42. Makings of signa: absent or minute (0), reticulate (1), pectinate (2), knobs (3), no comparison (9).

Larval habits

43. Larva mines: leaf (0), petiole (1), seed/bud/stem (2), lamina/petiole of leaf (3).
44. Leaf-mine: gallery (0), gallery followed by blotch (1), true blotch (2), no comparison (9).

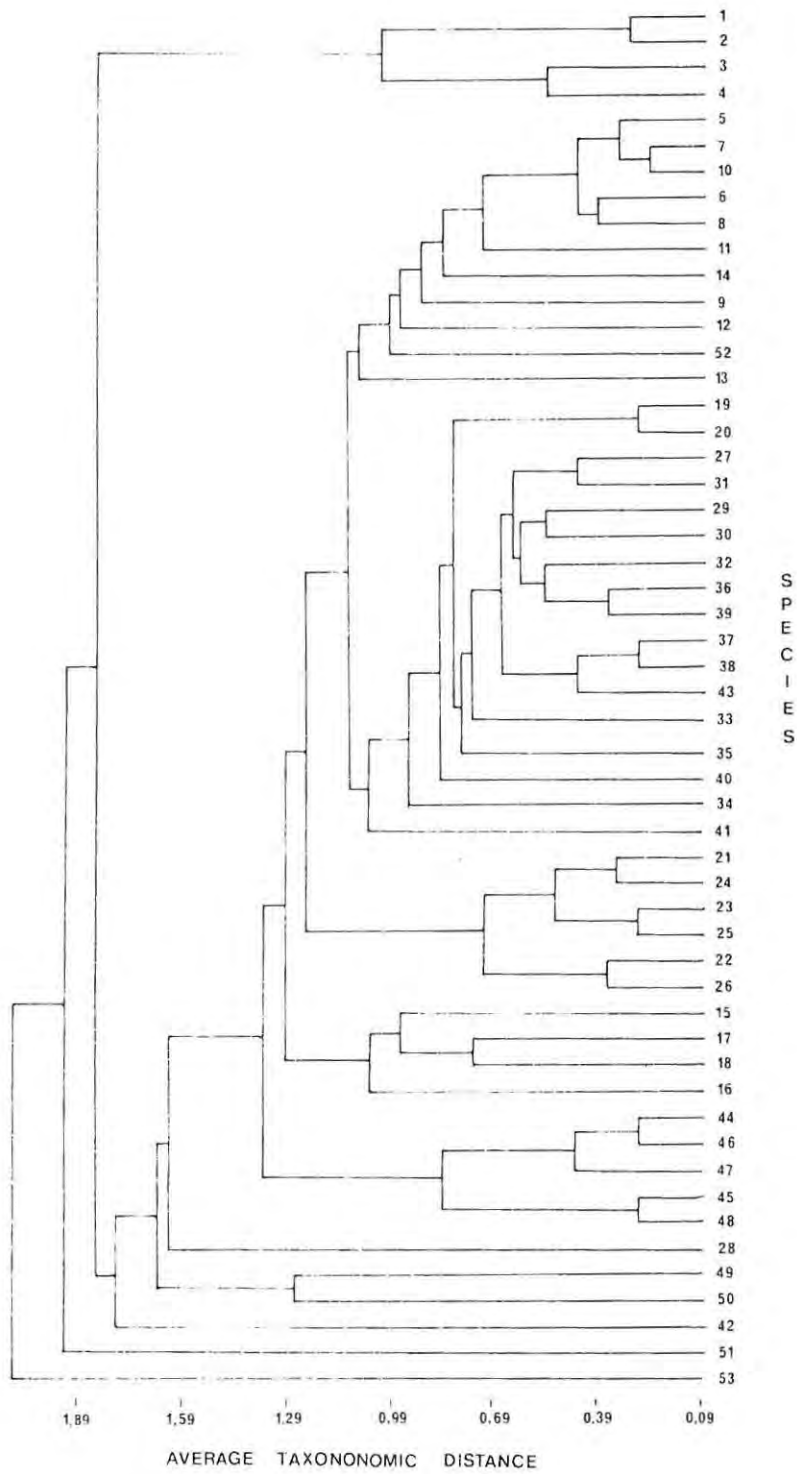


Fig. 142. Fifty-three species study. Phenogram based on taxonomic distances between species. Matrix correlation = 0,917.

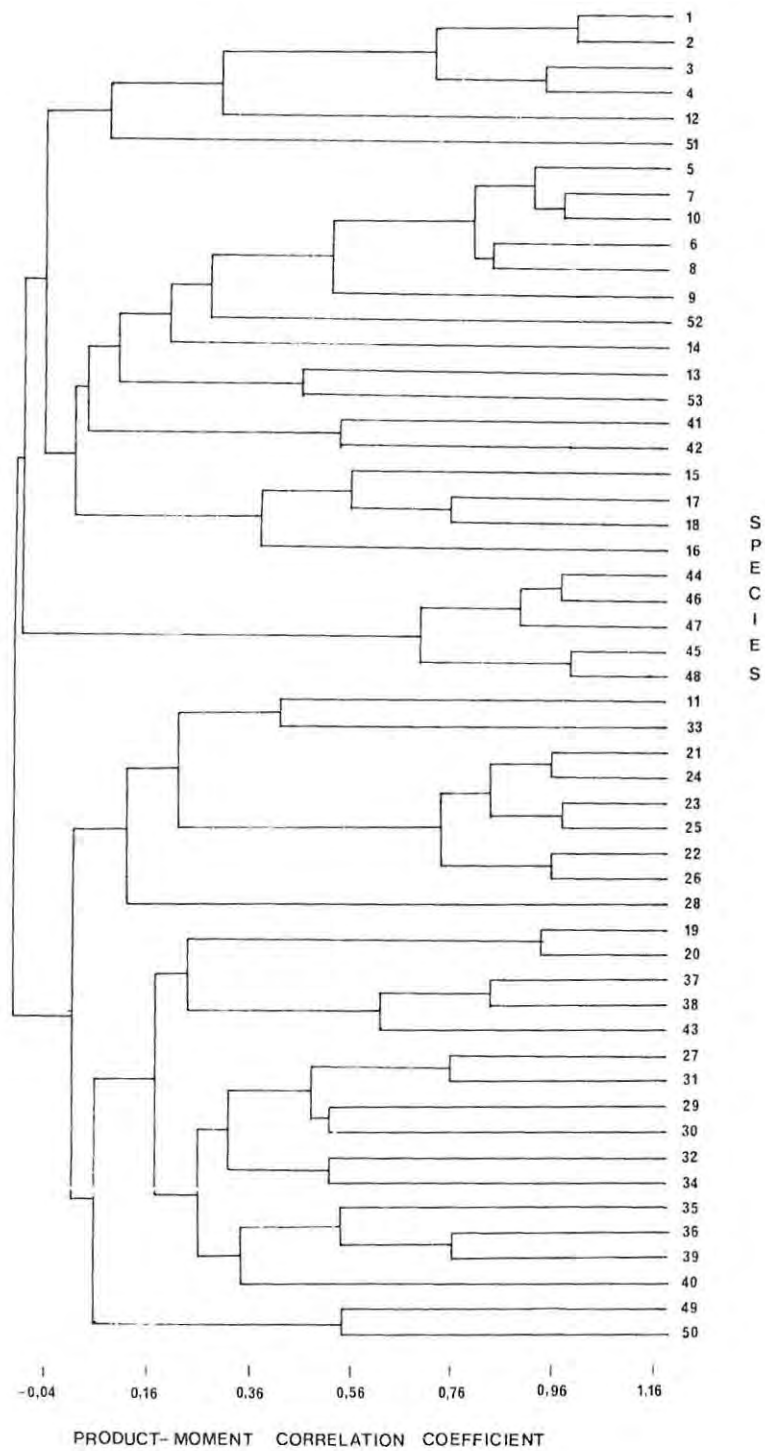


Fig. 143. Fifty-three species study. Phenogram based on correlations between species. Matrix correlation = 0,814.

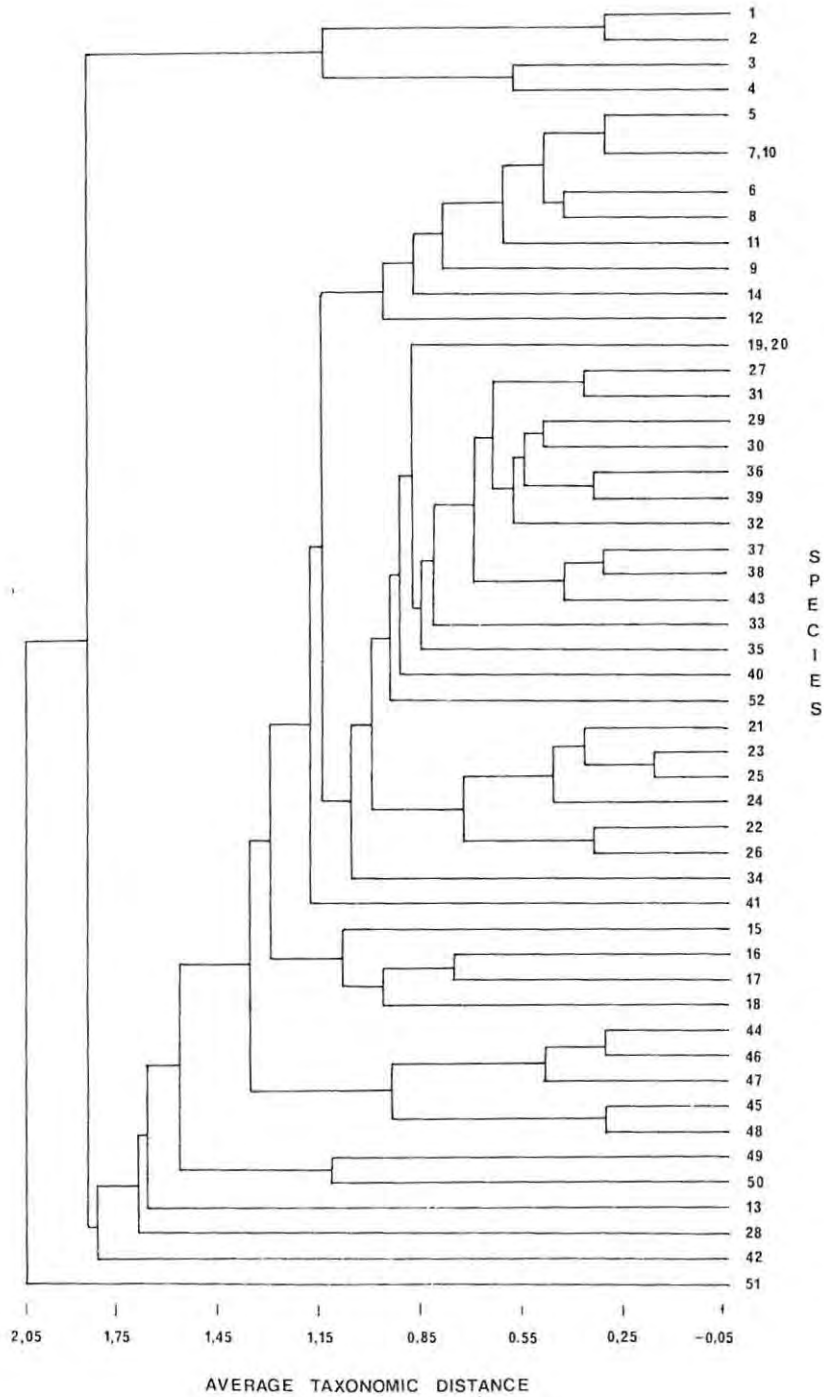


Fig. 144. Fifty-two species study. Phenogram based on taxonomic distances between species. Matrix correlation = 0,911.

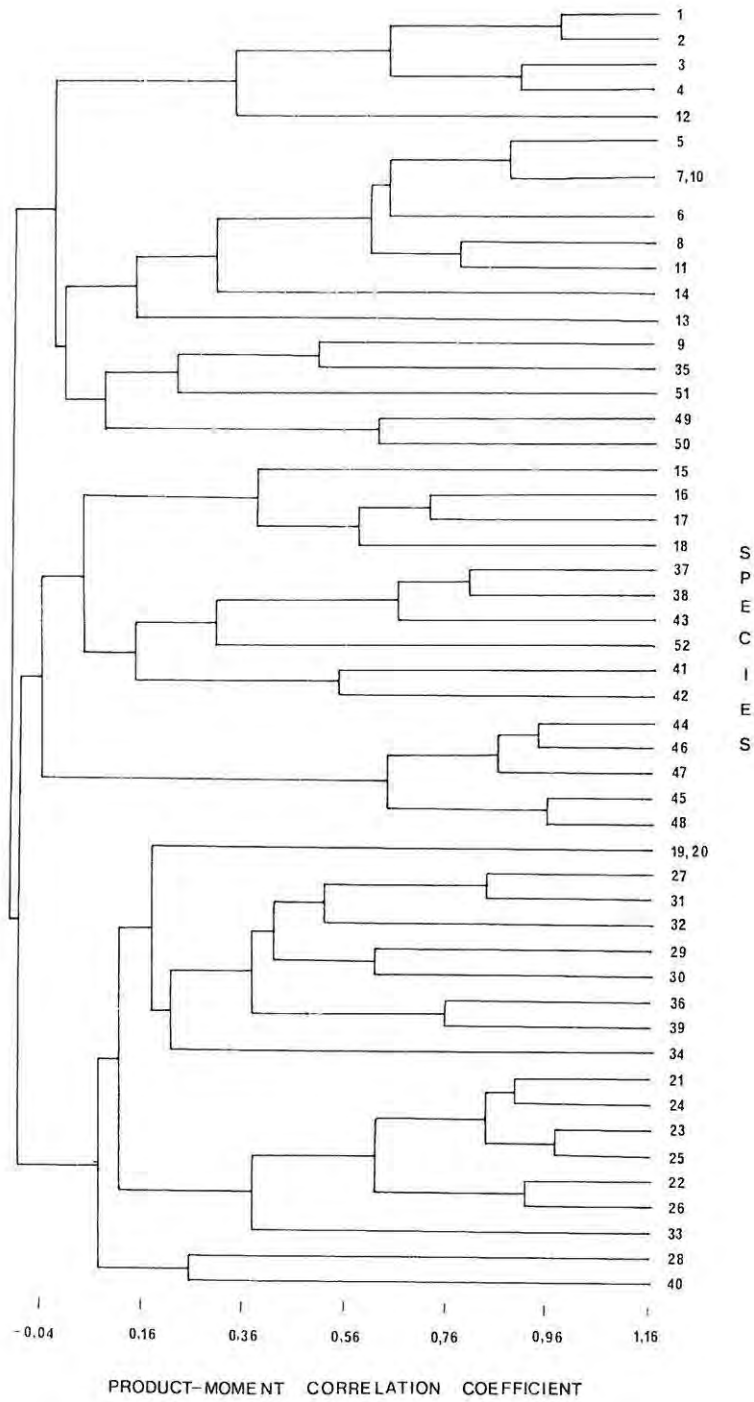


Fig. 145. Fifty-two species study. Phenogram based on correlation between species. Matrix correlation = 0,795.

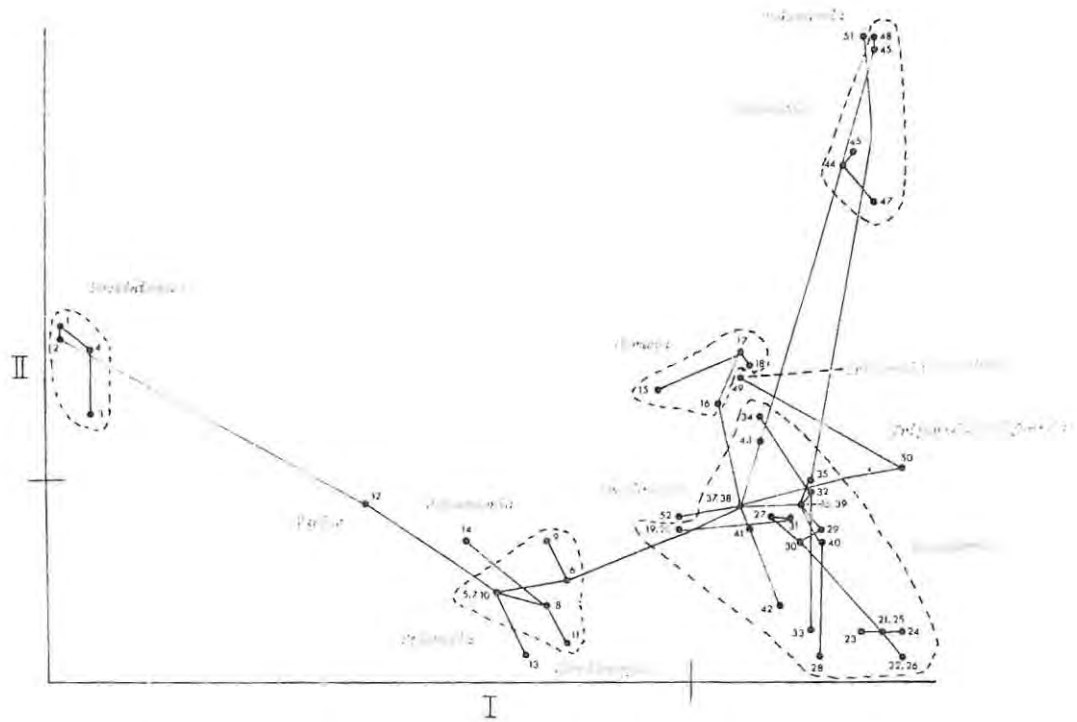


Fig. 146. Fifty-two species study. Ordination by principal component analysis; component I against II. Minimum spanning tree superimposed.

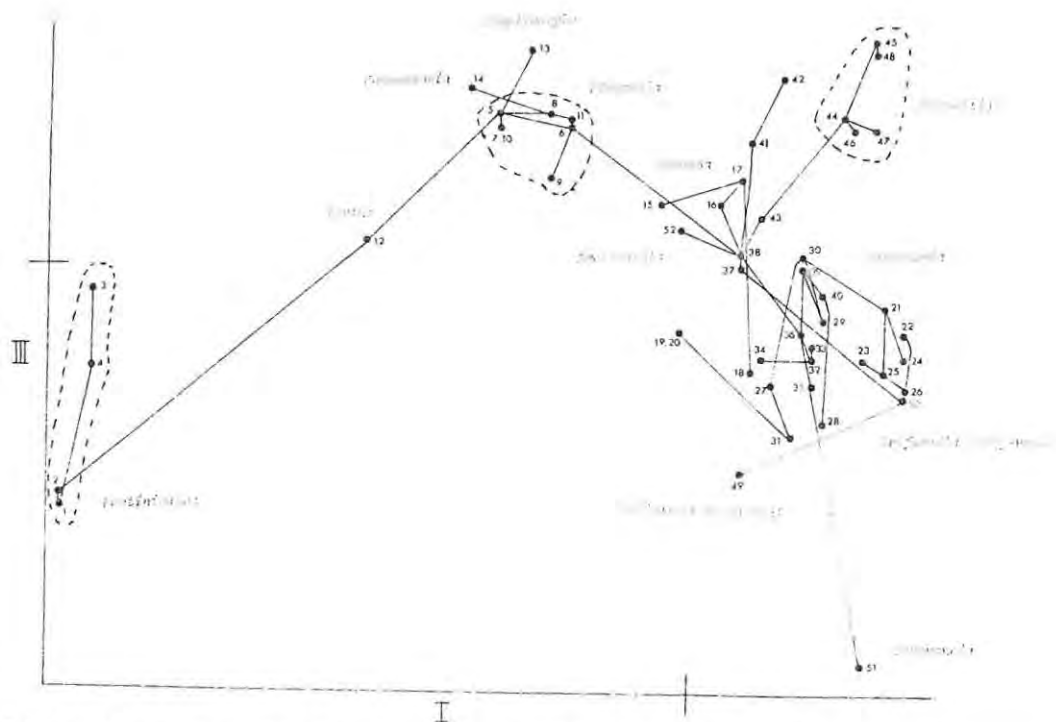


Fig. 147. Fifty-two species study. Ordination by principal component analysis; component I against III. Minimum spanning tree superimposed.

Table 4. Matrix for 52 species study to show character loadings for first three components.

	COMPONENT		
	1	2	3
1	0.057	-0.117	0.196
2	0.240	-0.281	-0.091
3	0.020	0.107	-0.119
4	0.747	-0.106	0.073
5	0.284	0.813	0.211
6	0.515	-0.048	-0.098
7	0.052	-0.051	-0.683
8	0.649	0.671	-0.011
9	0.350	-0.030	-0.555
10	0.440	-0.288	0.589
13	0.413	-0.415	-0.395
14	0.802	-0.202	0.317
15	0.118	0.060	-0.244
17	0.266	0.727	0.429
18	0.954	0.042	-0.044
19	0.165	0.532	0.327
20	0.852	0.034	-0.261
21	0.642	0.324	-0.359
23	0.100	0.169	-0.223
25	0.612	-0.152	0.322
26	-0.802	0.202	-0.317
27	0.032	0.160	0.033
28	0.112	0.372	-0.415
29	0.067	-0.120	0.235
31	0.345	-0.642	-0.102
32	0.084	-0.166	-0.156
33	0.067	0.203	-0.335
34	0.333	-0.381	-0.229
35	0.631	0.062	-0.220
37	0.762	-0.140	0.233
38	0.323	-0.340	-0.118
39	-0.069	0.454	-0.511
40	0.054	0.157	0.034
41	0.742	0.226	-0.106

CONCLUDING REMARKS

This work is first and foremost a systematic one, and the classification presented is its main result. Phenetics and cladistics are methods of assessing pattern; in themselves they prove nothing about the process of evolution.

The topics touched on below are related to systematics but they are ancillary, and more speculative. The issues all depend on phylogeny, and the degree to which they can be discussed is limited to existing hypotheses of neptculid phylogeny. Only a broad outline of neptculid phylogeny is known, and so general comments about the topics are all that can be made at present. Relatively few specimens of most species have been collected, and taxonomic work has been almost entirely confined to the adults. In terms of world coverage, collecting has been patchy.

PHENOTYPIC VARIATION AND TAXONOMIC CHARACTERS

There seem to be two different kinds of variation between living organisms. Some variation is relatively discrete, quantum, and easily observed, such as the presence or absence of a structure. The other sort is continuous, graded, and not divisible into discrete units. Both are used in systematic studies.

The first type is that which is generally understood as a taxonomic character. In the present study this was the only kind of variation used. In the numerical phenetic analysis the characters were divided into 'states': discrete divisions of the variation of a given structure. In the cladistic analyses the characters were the apomorphies that 'defined' the monophyletic taxa.

The second type, continuous variation, is used in systematic studies that rely on the statistical relationships of measurements. This may involve only two measurements (e.g. length and breadth of a structure) of a series of specimens thought to represent two or more phena. Such variation can be plotted on a scattergram. Usually, however, a series of measurements are taken, and multivariate statistics are used to examine the variation at the same time. Phenata that are not separable by inspection may be delimited by the use of these techniques.

Are non-continuous differences genuinely discrete or are they simply an artifact of the failure to collect species with intermediate conditions of a structure? If they are real do they represent phenetic changes that occur at the time of, or as a result of, speciation?

Some palaeontologists think that the 'gaps' in the fossil record are real and not always the result of its impoverishment (see particularly Eldredge & Gould 1972). They consider that speciation occurs relatively suddenly (in terms of geological time), and see the history of a species as relatively unchanged (static, constrained) until 'punctuated' by a speciation event. They term this model punctuated equilibrium and contrast it with phyletic gradualism, a view that speciation is a gradual process and that a lineage may change into several species through time.

With regard to phyletic change (i.e. undirected phenotypic change involving a whole species) the general expectation under gradualism is that it will be uniformly low with no increase at lineage splitting; in punctuated equilibrium it will be episodic - high during speciation and low to absent within a species (Vrba 1980). If, as Paterson (1978) suggests, 'a new species arises when all members of a subpopulation of an existing species acquire a new specific mate recognition system' then at least some phenotypic changes at speciation will be those involved in mate recognition. Discrete, species-specific characters may often be of this kind.

The punctuation model of speciation remains controversial. But here lies a possible explanation for the two kinds of variation used by systematists. The continuous variation used in multivariate analyses may be due to geographical variation within a species, or to a low rate of change between two species after speciation has taken place. It may be allometric. The discrete variation may come about rather suddenly: 'most morphological divergence of a descendant species occurs very early in its differentiation, when the population is small and still adjusting more precisely to local conditions.', (Eldredge & Gould 1972:95).

Since we cannot observe speciation events, the most direct assessment of phenotypic change at speciation is that apparent between ancestors and descendants. Eldredge & Cracraft (1980) proposed that a species can be postulated as an ancestor of another if the former has no apomorphies with respect to the latter (i.e. autapomorphies). Both would need to share at least one common apomorphy (synapomorphy) of course.

A pair of species that fit this criterion in the present work is *Obrussa krugerensis* and *O. nigricapitella*. The latter has three characters hypothesised as modifications of the conditions found in the former. These are: (1) the vestigial apodeme of the valva, (2) the almost non-existent depression of the ventral plate of the vinculum as opposed to the deep excavation of *krugerensis*, and (3) the C-shaped excavation of the apex of the valva. The presence of specialised scales in *krugerensis* is not considered to be apomorphic since they are present in other species of *Obrussa*. It is therefore possible that *krugerensis* is the direct, and persistent, ancestor of *nigricapitella*.

The differences between the species are certainly discrete, even though in general shape the male genitalia are extremely similar. Further possible examples of ancestor-descendant pairs of species are *Ectoedemia nigrisquama* and *E. royenicola*; *E. myrtinaecola* and *E. alexandria*; and *E. incisaevora* and *E. leptodictyae*. Collection of morphologically intermediate specimens between these species would, of course, falsify the possibility that they represent ancestor-descendant relationships, and even throw into doubt their valid designation as species.

Whilst the *krugerensis-nigricapitella* situation lends some support to the rather discrete changes in characters between these otherwise closely phenetically related species, the changes could also have developed gradually after speciation (Wiley 1978). They could also be the result of the failure to assess intraspecific variation. As in so much of the present work, a thorough analysis of intraspecific variation in nepticulids would be most relevant here. If the characters found to differ between these two species were generally invariable within each over a wide range, then we might reasonably suppose that they are stable, species specific, and linked with speciation. The suggestion that the genital characters involved (see above) reflect real variation between the species is based on six genital preparations of *nigricapitella* and four of *krugerensis*; a number that compares rather favourably with many insect taxonomy works. The fact that these two species did not cluster particularly closely in the numerical analyses is probably because of the discrete differences mentioned, and also because their similarity is seen in the shape of the male genitalia, which is very difficult to code in detail, as was pointed out in the numerical phenetic section.

HOMOPLASY

In evolutionary terms, similarity between two species may be of two kinds. It may be the result of common ancestry (patristic similarity *sensu* Cain & Harrison 1960; including primitive or derived similarities *sensu* Hennig 1966), or it may be the result of convergence (similarity derived from different phyletic lineages).

One of the aims of character analysis was to make a detailed study of similarity to avoid confusing artificial resemblance with *real* (genealogical) resemblance. Any similarity between species that remained unaccounted for by patristic similarity after the cladistic analysis had been completed was regarded as due to homoplasy. Homoplasy may result from convergence or from hidden patristic similarity (parallelism), see below.

MORPHOLOGICAL HOMOPLASY. The most apparent examples of homoplasy in this work are found in the colour of the forewing. Within several genera, both markedly 'metallic' (with gold, red, and green reflections and silver spots or fasciae) and drab species can be found. Metallic and drab species are found throughout the family. Although at first sight this seems a discrete difference, on close examination a rather continuous range of colour pattern is revealed. (No phylogenetic transformation series is implied by this statement.) To a degree, the colour patterns between the species can be compared, but it is extremely difficult to assess homology of forewing colour and pattern without making *a priori* assumptions about relationships. Is 'weakly metallic' homologous with 'strongly metallic'?; that is, is 'metallic' a homologous character in itself? A judgement of similarity is virtually impossible in such a case. However, it would be unreasonable to ignore the striking similarity of the bright silver fascia of say the North American *Ectoedemia rubifoliella* Clemens, an undescribed Australian species belonging to *Pectinivalva*, and *Stigmella celtifoliella* Vári. Each of these species belongs, not only to a different genus but to a different higher taxon. Many other examples exist.

The continuous discovery of new species that show this metallic colour pattern within and between monophyletic taxa leads us to ask whether this pattern is a ground-plan feature of the Nepticulidae; that is, whether it was present in the ancestral nepticulid species. If it was then metallic species from different lineages would not be convergent (independently

evolved) in this character. However, we would then be left to explain the widespread condition of the drab ochreous-fuscous condition. The problem of homoplasy would seem to arise for one or other pattern.

This kind of homoplasy is called parallelism and a possible genetic explanation was given by Throckmorton (1965). Throckmorton (p.229) stated that in *Drosophila* 'closely related species are complex mosaics of the characteristics of their nearest relatives.' A character present in one species may be absent from its closest relatives and then appear in a species of a less closely related lineage. Throckmorton argued that if two alternative character-states are homozygous (which they need not be), then their appearance would depend on the presence of the homozygous condition: neither would be present in the heterozygote. Hence persistent heterozygosity in a lineage, which would give rise to homozygotes by segregation of alleles at meiosis and pairing at zygote formation, may result in the appearance of homologous characters in species that are not sister pairs. Throckmorton suggests that heterozygosity may persist for a considerable period of time in a lineage. This could explain the frequent occurrence of strongly metallic species within quite different nepticulid lineages.

Another possible example of parallelism is in the head-tuft colour of the genus *Obrussa*. The black-headed condition, found in most members of this genus (all the species from southern Africa and several from the northern hemisphere), is generally rare within the Nepticulidae and is probably a ground-plan character for *Obrussa*. The orange or off-white head-tuft, characteristic of most Nepticulidae, is present in some species of *Obrussa*. This could be explained either by independent evolution (convergence) of the character, or as a consequence of persistent heterozygosity (parallelism).

LARVAL HABITS AND HOMOPLASY. Wilkinson & Scoble (1979:108) stated that 'The leaf-mining mode of life is polyphyletic being found in many families.' Actually, the fact that it is found in many families does not mean that it is polyphyletic as such: it may simply have been retained in these families as an ancestral condition. Indeed, this seems quite probable for many families at least. Leaf-mining is first exhibited in the Lepidoptera by the Eriocranioidea, although no information on the life-history of one of the two included families (the Acanthopteroctetidae) is known (Davis 1978a). Therefore the habit may represent an apomorphy for the whole of the Glossata (all the Lepidoptera except for the Micropterigidae (Zeugloptera)

and Agathiphagidae (Aglossata) - see Kristensen & Nielsen 1980). It is most unlikely that leaf-mining has been independently evolved in Tischerioidea, Nepticuloidea and Incurvarioidea.

COMMENTS ON HISTORICAL ZOOGEOGRAPHY

Only general impressions about the reasons for the present distribution of the Nepticulidae can be proposed at present since only a broad postulate of the phylogeny of the group has been presented. The patchy collection of the family also means that statements that suggest that a taxon is confined to an area are highly suspect. Therefore I give only a few comments concerning distribution instead of a detailed, and highly speculative, scenario.

A few South American nepticulids have been recently collected. These specimens will enable workers to make some general comparison of that fauna with nepticulids from elsewhere, and until this is done a major gap in nepticulid zoogeography will remain.

The Nepticulidae as a whole are widespread and so are many of the genera, which occur on several, or most, continents (e.g. *Stigmella*). Unless one assumes a great deal of relatively recent intercontinental dispersal, the only way to explain the present day distribution is to suggest an early origin of the family (and many of its lineages) and its presence on existing continents by the movement of tectonic plates (continental drift). Intercontinental dispersal would be inhibited not only by ocean barriers, but also by different host-plants since the Nepticulidae exhibit a fairly high degree of monophagy.

The probable explanation of present day distribution is that the Nepticulidae originated on Pangea before its division into Laurasia and Gondwanaland about 180 (Rosen 1978) to 150 (Irving 1977) million years ago.

Whilst the Stigmellinae are, as far as is known, of world-wide occurrence, the Pectinivalvinae have only been collected from Australia. The shape and arrangement of the pectinifer in Opostegidae (the sister-group of the Nepticulidae) is similar to many Pectinivalvinae and the absence of the pectinifer in the Stigmellinae is a secondary loss. There is no support for an independent development of the structure in Opostegidae and Pectinivalvinae. The Opostegidae are widespread, so why should the Pectinivalvinae have only been collected from Australia? It is possible that the latter may be found in South America, when we consider that Australia and South America

were connected via Antarctica until the upper Cretaceous. (For a cladistic representation of the break up of Pangea see Rosen 1978.) However this does not explain why the Pectinivalvinae should apparently be absent from Africa, North America, and Europe. We are left with the explanation that the Pectinivalvinae were once more widespread, and that they have been replaced. Future collecting may, of course, show otherwise.

In view of the extensive palaeobiological evidence of relationships between southern China and Gondwanaland (Cooper 1980) we may yet find Pectinivalvinae in areas other than Australia which have not been sampled.

HOST-PLANT CHOICE AND PHYLOGENY

It is a common observation, for many lepidopteran families, that closely related species tend to feed on closely related species of host-plant. Holloway & Hebert (1979) found this observation to be broadly true in their quantitative documentation of the association between macrolepidopteran species and host-plants using cluster analysis. The general observation is true for the Nepticulidae although no quantification of this has been carried out. However, *major* nepticulid lineages are not, in general, associated with particular host-plant lineages. Powell (1980) found this to be the usual case amongst microlepidopterans: 'no major microlepidopteran family is diversified (i.e. more than 12% of hostplant records) in association with a primitive angiosperm subclass.' The only major nepticulid lineage that may be exclusively associated with a family of host-plants is that of the Australian *Pectinivalva*, for which specimens have been reared only from species of Myrtaceae. However, records for only a few species are available.

Nepticulids probably co-evolve with their host-plants - that is speciation events of the moths may be associated with speciation of the host-plants. Co-evolution acts in a generally conservative way and accounts for the observation that related species of nepticulids tend to feed on related species of host-plant. Host-plant switching of nepticulids would therefore account for incongruence between nepticulid and plant phylogeny. The wide diversity of host-plants associated with major nepticulid lineages (including genera) can be explained in two ways. First, if we accept that nepticulids became isolated by continental drift then the stock on each continent would speciate with the host-plants. In time, the host-plants would

become distinct from their progenitors. Second, co-evolutionary pattern would be disrupted by host-plant switching by nepticulids. Over a time it is not surprising that there is a rather low level of association of nepticulids with major plant lineages.

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Nepticulidae (Lepidoptera) of southern Africa: the genus *Ectoedemia* Busck

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The first southern hemisphere record of *Ectoedemia*, based on two species collected from southern Africa, is given. A new species, *E. commiphorella*, is described and notes on the leaf-mining habit of the larva are presented. A species, *nigrimacula*, that was previously assigned to another genus (*Nepticula*, a junior synonym of *Stigmella*) is transferred to *Ectoedemia*.

INTRODUCTION

This paper deals with two southern African *Ectoedemia* species, one of which is new. As far as I know, these are the only *Ectoedemia* species collected in the area. The genus was described by Busck (1907) and originally included a single species from North America, namely *E. populella* Busck. Subsequently, other species were found in North America and Europe. The genus has not previously been recorded from southern Africa, nor from the southern hemisphere as a whole, for although *nigrimacula* Janse was described in 1948 from specimens collected in South West Africa it was assigned to *Nepticula* Heyden (now a junior synonym of *Stigmella* Schrank, see Wilkinson in press) and not to *Ectoedemia*. *Ectoedemia* is one of three nepticulid genera known to occur in both southern Africa and in the holarctic.

Svensson (1966) synonymized *Dechtiria* Beirne (1945) with *Ectoedemia*. Structural characters of the adults lend support to this synonymy despite variation in larval feeding habits within the expanded genus.

The larvae of *Ectoedemia* species mine either (i) in bark, (ii) in petioles of leaves from which they usually enter the leaf-blade later, or (iii) exclusively in the leaf-blade. Bark and petiole-feeding larvae induce the formation of variable amounts of callus tissue. According to Busck (1907) the larva of *populella* causes galls 'the size of a pea' on the petioles of *Populus* leaves. Borkowski (1972) suggested that *Ectoedemia* be subdivided into three subgenera each representing one of the three kinds of larval feeding habits. Although this recommendation was followed by Emmet in Heath (1976) for the British species, it is not adopted by the present author for the following reasons. Firstly, the feeding habits of the larvae of *nigrimacula* are unknown, so that it is not possible to assign it to one of the subgenera. Secondly, taxa are best defined by structural characters, perhaps eventually supported by features of the life-history, rather than by life-history alone.

ECTOEDEMIA Busck, 1907

Type-species *Ectoedemia populella* Busck, by original designation and monotypy. *Dechloria* Beirne, 1945:204. Type-species *Nepticula subbimaculella* Haworth, by original designation. Synonymized by Svensson, 1966:200.

A detailed description of the genus is given by Wilkinson & Scoble (*in press*) and is not repeated here. I have subsequently examined many southern African species representing several as yet undescribed genera, and the following remarks are made to emphasize the principal diagnostic features of *Ectoedemia* in the light of this additional material.

Ectoedemia is characterised by the absence of an uncus in the male genitalia. In most described genera (see figures of Beirne 1945) and in several undescribed ones, the uncus is approximately in the form of an inverted V. In the forewing (fig. 1) the medial vein (M) is unbranched in *Ectoedemia*, which distinguishes it from *Obrussa* Braun in which M is branched into M₁ and M₂. In the hindwing (fig. 2) M is also unbranched. Whilst this is the general condition in the Nepticulidae, it distinguishes *Ectoedemia* from four genera as yet recorded only from the holarctic, viz. *Fedalmia*, *Trifurcula* (*sensu stricto*), *Levarchama* and *Glaucoplepis*. As a whole, the venation is the same as some of the undescribed southern African genera, but differences in the genitalia are great enough to exclude their species from *Ectoedemia*. Janse (1948) figured the fore and hindwing venation of *nigrimacula* but incorrectly labelled the forewing fold as a vein.

***Ectoedemia commiphorella* spec. nov., figs. 3-5 and 12-13.**

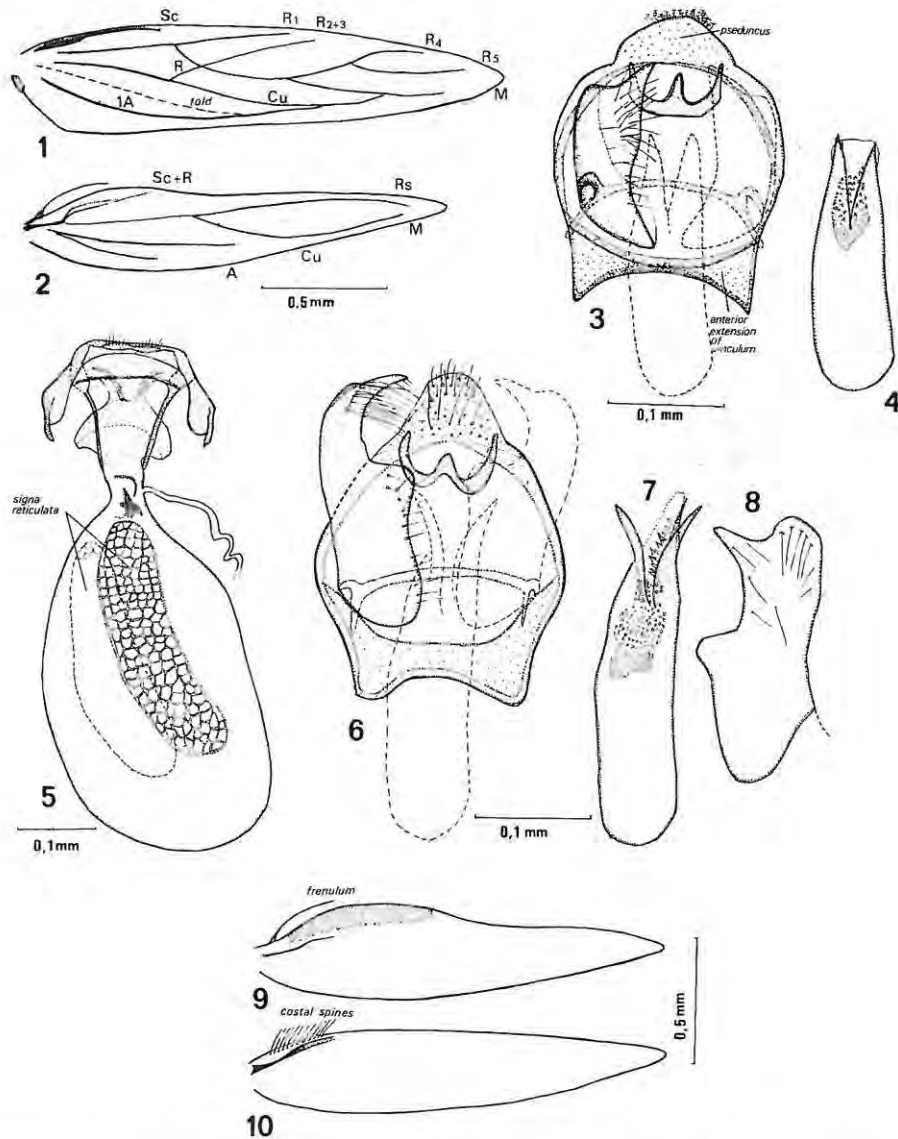
Nepticula fuscata Janse, 1948:165 *partim* (misidentified syntype).

Nepticula nigrimacula Janse, 1948:171 *partim* (misidentified syntype).

External characters. Fig. 12. ♂, ♀. (Wing-span of holotype: 5.0 mm). Mouthparts: palps off-white. Tuft on front of head off-white; tuft on vertex tinged with brown in holotype, unclear in paratypes. Eye-cap off-white; antenna pale grey-purple, extending to approximately half length of forewing. Thorax and abdomen greyish brown. Forewing: upperside pale ochreous, in holotype heavily irrorated with dark purplish brown by scales, the tips of which are so coloured; in paratypes irrorations less pronounced probably due to poor condition of specimens; underside grey; fringe pale ochreous, speckled at base and in middle but less densely than rest of wing. Hindwing: pale grey; fringe pale grey, base of component hair scales tinged with ochre at apex of wing. Legs grey and ochreous.

Male genitalia. Figs 3-4. Vinculum: ventral plate in form of a very narrow band; anterior extension with anterior and posterior edges emarginate so forming pair of pointed lobes. Tegumen produced into rounded pseuduncus crowned with cluster of flat-headed hairs. Gnathos well sclerotized, W-shaped. Valve not extending further than base of pseuduncus, inner aspect of apex terminating in a point. Transtilla: transverse bar long. Aedeagus approximately the length of genital capsule, with pair of large, strong, straight spines posteriorly; vesica with poorly defined patch of denticles and a weak, striate plate.

Female genitalia. Fig. 5. Anal papillae flattened. Anterior apophyses thin, longer than posteriores. Posterior apophyses with large basal plate. Ductus bursae with sclerotizations as in fig. 5. Bursa copulatrix with pair of large reticulate signa.



Figs 1-10. *Ectoedemia* spp. 1-2. Venation of genus. 1. Forewing. 2. Hindwing. 3-5. *E. commiphorella* spec. nov. 3. ♂ genital capsule. 4. Aedeagus. 5. ♀ genitalia. 6-10. *E. nigrimacula*. 6. ♂ genital capsule. 7. Aedeagus. 8. Inside (dorsal aspect) of left valve. 9. Hindwing ♂. 10. Hindwing ♀. All genitalia figured in ventral view except 8.

The species is distinguished from *nigrimacula* by the shorter and broader pseuduncus with the characteristic flat-topped hairs. The valve of *commiphorella* is much shorter relative to the length of the genital capsule than it is in *nigrimacula* and is differently shaped; compare fig. 3 with fig. 5. The forewing of the holotype of *commiphorella* is more heavily irrorated than in any of the *nigrimacula* specimens.

One of the male paratypes of *commiphorella* is a misidentified syntype of *nigrimacula* (see also under that species below) collected at Abachaus, South West Africa. Another is a misidentified syntype of *fuscata* Janse, a species belonging to a genus to be dealt with in a later publication. A female syntype of *nigrimacula* also collected at Abachaus probably, but not certainly, belongs to *commiphorella*. The genitalia resemble those of the only female paratype of *commiphorella* but, as is the general case in the Nepticulidae, these structures are of limited taxonomic value. The specimen was caught at light, so the food-plant of its larva, often a valuable clue to the identity of a species, is unknown. The forewings are badly rubbed, so that the colour cannot be compared with the holotype. For these reasons the specimen is not included in the type-series of *commiphorella*.

MATERIAL EXAMINED. Holotype ♂, SOUTH AFRICA: Transvaal, Langjan Nature Reserve, 21.xii.1964, L. Vári, accession number 2723. Paratypes: 1♀ data as holotype; 1♂ SOUTH WEST AFRICA: Abachaus, ii.1943, G. Hobohm, syntype of *fuscata* Janse labelled:— '*Nepticula fuscata* Janse ♂. Cotype No. 2359; 1♂ Abachaus ix.1943, G. Hobohm, syntype of *nigrimacula* labelled '*Nepticula nigrimacula* Janse, ♂, Cotype No. 2389'. All specimens housed in the Transvaal Museum.

BIOLOGY. Food-plant: *Commiphora pyracanthoides* Engl. Egg: laid on upper surface of leaf. Mine: fig. 13, an upper surface, gradually widening, linear tract entirely within the leaf-blade. Frass deposited as a central line within the mine. Larva exits from upper surface of leaf.

Ectoedemia nigrimacula (Janse) **comb. nov.**, figs 6–11.

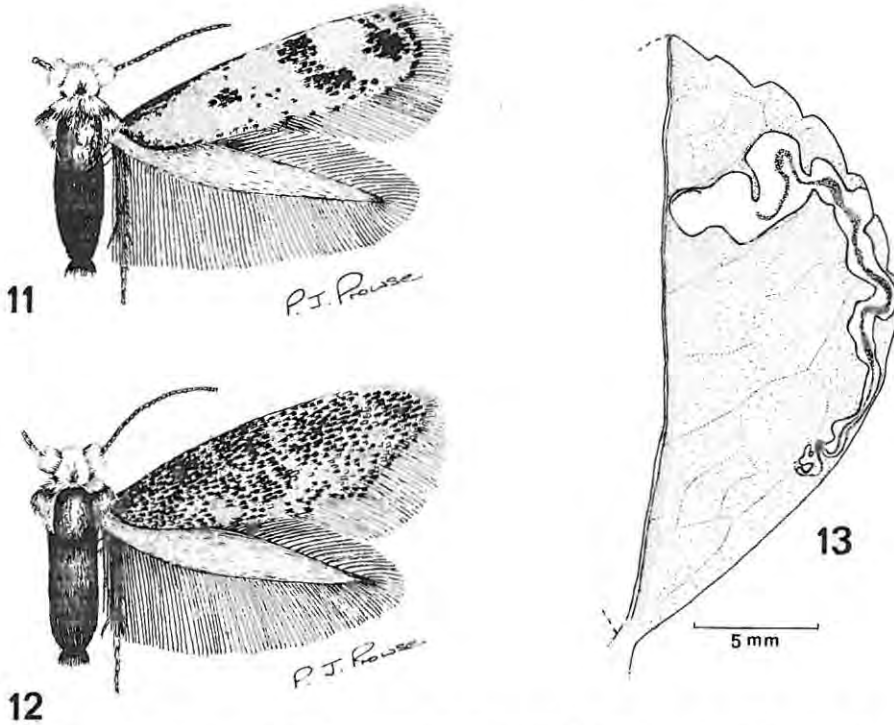
Nepticula nigrimacula Janse, 1948:171.

External characters. Fig. 11. Additional note to Janse (1948): hindwing of male with elongated thickened patch on base of costa, absent in female. For consequent differences in wing shape compare figs 9 and 10.

Male genitalia. Figs 6–8. Vinculum: ventral plate absent; anterior extension strongly excavated posteriorly, less so anteriorly. Tegumen produced into gradually tapering, blunt, membranous pseuduncus with stiff, posteriorly directed hairs. Gnathos well sclerotized, W-shaped. Valve extending to apex of pseuduncus, curved posteriorly by emargination of inner edge. Transtilla weakly sclerotized; transverse bar long. Aedeagus approximately length of genital capsule with long, strong, curved spines posteriorly; vesica with a poorly defined patch of denticles which become larger posteriorly, and a weak, striate patch.

Female genitalia. Uncertainty exists regarding the identity of the female, see below.

E. nigrimacula may be distinguished from *commiphorella* particularly by the emarginated inner aspect of the valve in the male, the longer pseuduncus and the different kind of hairs associated with the pseuduncus. The long spines of the aedeagus are more slender in *nigrimacula* and the forewing is not as heavily irrorated.



Figs 11-13. *Ectoedemia* spp. 11. *E. nigrimacula* ♂. 12-13. *E. commiphorella* spec. nov. 12. ♂ (holotype). 13. Leaf-mine.

Janse's type-series included a male 'type' and seven male paratypes, and a female 'type' and a further female paratype. According to article 73 of the International Code of Zoological Nomenclature, they are all syntypes. I have found only nine of these specimens in the Transvaal Museum collection. I designate as lectotype the male 'type' which bears the following label data:— 'Abachaus, S.W.A., Jan.44, G. Hobohm; *Nepticula nigrimacula* Janse, ♂, Type No. 2383'. The male syntype labelled 'Cotype No. 2389' has been misidentified. Although the specimen is in poor condition the genitalia clearly show that it belongs to *commiphorella*. The two female syntypes of *nigrimacula* are not conspecific as the genitalia are different. The specimen labelled 'Cotype No. 2391' probably, but not certainly, belongs to *commiphorella* (see also under that species above). I cannot tell whether or not the syntype labelled 'Cotype No. 2384' belongs to *nigrimacula*. The forewings of both these specimens are so badly rubbed that they do not assist identification. Neither of these female syntypes are regarded as *nigrimacula*.

MATERIAL EXAMINED: Lectotype ♂, SOUTH WEST AFRICA: Abachaus, i.1944, G. Hobohm. Transvaal Museum type number 2383. Paralectotypes, locality and collector as lectotype, 1♂ i.1944, type number 2386; 1♂ i.1943, type number 2390; 1♂ ii.1943, type number 2388; 2♂♂ iv.1945 type numbers 2385 and 2387. All specimens housed in the Transvaal Museum.

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I am very grateful to Dr L. Vári of the Transvaal Museum for his comments on a draft of this paper and to the Director and board of the Museum, where this work was undertaken, for facilities. I thank Mrs P. J. Prowse for her illustrations of the moths. Dr De Winter of the National Herbarium, Pretoria, kindly permitted the identification of the food-plant of *commiphorella* at that institute, and I am extremely grateful to Miss Retief who so willingly carried this out.

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NEPTICULIDAE OF SOUTHERN AFRICA:
A TAXONOMIC REVISION OF THE GENUS
STIGMELLA SCHRANK
(LEPIDOPTERA: MONOTRYSLA)

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(With one Plate and 51 Text-figures)

ABSTRACT

Thirty-four species of the leaf-mining genus *Stigmella*, of which 20 are new, are included in this revision; the species fall into two species groups. The primary type of each species was examined. Generic names of nine species are recombined with *Stigmella*; five lectotypes are designated. A key to the males is presented; taxonomic characters used in the descriptions are evaluated. Notes on the biology of those species for which such information is available are documented.

INTRODUCTION

The present paper is one of a series on the taxonomy of the Nepticulidae of southern Africa; it deals with the cosmopolitan genus *Stigmella* Schrank. The larvae of all the species, for which such data is available, are leaf-miners.

The name *Stigmella* was considered to be invalid by certain authors e.g. Braun (1917), Johansson (1971), Borkowski (1972). In the present paper, *Stigmella* is considered to be the valid name of the genus rather than *Nepticula* Heyden (for details see Wilkinson, 1978) mainly because there is no justification for rejecting the name *Stigmella*, which, as it is older, takes precedence over *Nepticula*.

There is a controversy over which nepticulid taxa should be assigned the rank of genus. The majority of recent authors (e.g. Borkowski, 1972, 1975; Emmet *in* Heath, 1976; Klimesch, 1953, 1975a, 1975b; Svensson,

1966; Wilkinson & Scoble, in press; Scoble, 1978; Newton, in preparation) have explicitly or implicitly agreed that most of the genera dealt with by Busck (1907), Braun (1915, 1917) and Beirne (1945) should indeed have that status. However, Johansson (1972) reduced all of Beirne's genera, except *Stigmella* (in the sense of the present paper), to subgenera of *Trifurcula* Zeller. He was followed by Klimesch (1975c).

Despite disagreement over rank of the non-*Stigmella* genera, authors have all agreed that *Stigmella* (*Nepticula* in the sense of several authors, see above) should indeed have generic status. The boundaries of the genus are more difficult to delimit. The five species comprising the *ingens* group in this paper all have a gnathos the shape of which is usually found in other genera and not in the type-species of *Stigmella*, nor in most other species of the genus. The species of the *ingens* group are included in *Stigmella* because, on balance, they have more characteristics in common with this genus than any other. The kind of gnathos present in these species resembles that of the North American *procrastinella* (Braun) (Wilkinson & Scoble, in press), a species that is also included in *Stigmella*. Apart from these relatively few exceptions, *Stigmella* is a large and structurally homogeneous genus.

All species of Nepticulidae from southern Africa were previously assigned to *Stigmella* or *Nepticula*. Many do not belong to this genus. Those *Stigmella* species described by Meyrick and by Janse are treated, in this paper, as follows: external characters are not redescribed although they are used in diagnoses where necessary. Where material is available, the female genitalia are described and figured. The male genitalia of Meyrick's species were described by Janse (1948). Because of the importance of these structures and as most workers follow the terminology of Beirne (1945), which differs somewhat from that used by Janse, the male genitalia of both Meyrick's and Janse's species are detailed. Neither the external characters, nor the genitalia of those species described by Vári (1955, 1963) are redescribed. A diagnosis is presented for each so that they may be distinguished from the new species described in this publication.

The characters used in this study are explained in appendix 1 and their taxonomic values are indicated. Of special note is that to avoid confusion the term 'saccus' has not been used in this work. The structure labelled 'saccus' by Beirne (1945) does not appear to be the true saccus i.e. an invagination of the vinculum. The part of the vinculum that extends anterior to the ventral plate is here termed 'the anterior extension of the vinculum' it has also been called the saccus in some papers on Nepticulidae.

Where possible each species is diagnosed from its nearest relatives. If there is no close relative diagnostic characters, or a combination of characters, are given that separate the taxon from all others described in this paper. The words 'relative', 'related' etc. imply structural similarity between taxa.

Eight of the new species recognized in this paper are described from single male specimens. Taxonomists usually prefer a series of representative specimens to allow for extremes of variation within a given species. However, characters used in the recognition of these species are constant

intraspecifically for species where large series are available, so significant variation may be excluded. These species are described to give a more accurate indication of the size of the genus, as the relative number of species in a given taxon indicates the rate of evolution of that group.

To obtain the adult wingspan specimens were measured from the centre of the thorax to the tip of the forewing; the distance was then doubled. The range, for each species, is given at the beginning of the description.

A key to males, based on the genitalia, is presented. External characters are also used, primarily as corroborative data. There is no key to females because identification is very difficult, and because there are several species of which no female specimens have been collected. As the colours and patterns of many of these moths are similar a key based on external features would be unreliable.

The five species for which half-tone illustrations of the moth have been made were selected to show the interspecific range of variation in the *Stigmella* species additional to those in Vári (1955, 1963).

A list of food-plants, where known, is included (see Table 1). As there is a high level of monophagy in the Nepticulidae a correctly identified food-plant is of great assistance for identifying the moth species feeding on it. The shape of the mine made by the larva is also of diagnostic value.

ABBREVIATIONS: BMNH: British Museum (Natural History), London, England.

NMHU: Museum für Naturkunde der Humboldt Universität, Berlin, East Germany.

TM: Transvaal Museum, Pretoria, R.S.A.

Code: International code of Zoological Nomenclature adopted by the XV International Congress of Zoology, 1958.

TAXONOMIC PART

Genus *STIGMELLA* Schrank

Stigmella Schrank, 1802. Fauna Boica 2:169.

Type-species: *Phalaena Tinea anomalella* Göze, 1783 = *Tinea rosella* Schrank, 1802:139 (by subsequent designation by Walsingham, 1907).

A full description of the genus *Stigmella* is given by Wilkinson & Scoble (in press) and is not repeated here. A combination of characters that typifies the genus *Stigmella* is as follows:

♂-GENITALIA: Vinculum U-shaped; lateral arms articulating with sides of tegumen. Tegumen not extended into pseuduncus. Uncus present. Gnathos generally with paired horns projecting posteriorly, sometimes with a single central element.

♀-GENITALIA: Corpus bursae unmarked, covered with spines, or pectinate; pectinations may be concentrated to form bands or approximately oval-shaped patches; signa never in the form of networks of 'cells' (signa reticulata).

WING-VENATION (fig. 1): Forewing: Rs represented by R_{2+3} and R_{4+5} . M fused with R1 and Rs; separates as a short branch near apex. Cu separate from other veins.

Hindwing: Rs and M each represented by a single branch.

KEY TO THE SPECIES AND SPECIES GROUPS: MALES

- 1 Gnathos with paired horns, single central element not large, e.g. fig. 2, if horizontal element has a protuberance it is very small – much shorter than length of horns *fluida*-group
2
- Gnathos with single, undivided, large central element e.g. fig. 43 *ingens*-group
29
- 2 Uncus emarginated or depressed so forming prominent papillae or lobes 8
- Uncus neither emarginated nor depressed or only very weakly so; if papillae present they are very small 3
- 3 Ventral arms of transtillae absent 4
- Ventral arms of transtillae present 5
- 4 Transtillae fused to form U-shaped band (fig. 31); gnathos approximately U-shaped; male with shiny black scales on underside of forewing and upper and lower surfaces of hindwing *nigrata*
- Transtillae as in fig. 30; gnathos approximately H-shaped; male without shiny black scales on wings *pallida*
- 5 Aedeagus with three large spines $\frac{3}{4}$ length of aedeagus; gnathos approximately H-shaped *triumfettica*
- Aedeagus without spines of $\frac{3}{4}$ length of aedeagus; gnathos not H-shaped 6
- 6 Valve $\frac{3}{4}$ length of capsule; vesica of aedeagus with two pairs of 'teeth' posteriorly, and a centrally placed thickening; collar dark purplish-brown, forewing uniformly charcoal *fragilis*
- Valve less than $\frac{3}{4}$ length of capsule; vesica of aedeagus with 'teeth' posteriorly or a thickening but not both 7
- 7 Tegumen? (see fig. 39) very large with pair of associated flask-shaped pouches; anterior extension of vinculum deeply excavated so forming pair of long, thin processes (fig. 39); juxta absent *ampullata*
- Tegumen small, without associated flask-shaped pouches; anterior extension of vinculum deeply excavated; juxta present *celtifoliella*
- 8 Posterior edge of ventral plate of vinculum lies in posterior half of genital capsule; valve less than half length of capsule; forewing with either white macula on costal and anal edges of forewing, or with wide ochreous-yellow fascia 9
- Posterior edge of ventral plate of vinculum lies in anterior half of genital capsule; valve more than half length of genital capsule; forewing not marked by maculae or a fascia 10
- 9 Anterior projection of vinculum deeply excavated; vesica of aedeagus with four 'teeth'; forewing with wide, ochreous-yellow fascia *platyzona*
- Anterior projection of vinculum with shallow excavation; vesica of aedeagus with three large, finger-like projections and a sclerotized plate; forewing with small white maculae, one on costal one on anal edge *protosema*
- 10 Uncus as in fig. 40; transtilla with broad lateral arm and short ventral bar; aedeagus notably short and narrow in relationship to capsule *pretoriata*
- Uncus and transtilla not as fig. 40; aedeagus not so small in relationship to capsule 11
- 11 Genital capsule as wide as long; uncus with pair of large ear-like lobes (fig. 27) *urbica*
- Genital capsule longer than wide; uncus without such lobes 12
- 12 Gnathos approximately U-shaped 13
- Gnathos not U-shaped 15
- 13 Gnathos with knob-like lateral process arising near tip of each horn; ventral arm long; hindwing yellow *androflavus*
- Gnathos with lateral processes at base of horns; ventral arm of transtilla not long; hindwing not yellow 14

- 14 Transtilla with associated 'tooth' positioned in middle of valve (fig. 29); ventral arm pointed; vesica of aedeagus with single, large 'tooth' and approximately rectangular thickening *abachausi*
 - Transtilla without associated 'tooth'; ventral arm rounded; vesica of aedeagus with three, thin, pointed spines and a triangular thickening *dombeyivora*
- 15 Aedeagus much longer, or slightly longer, than genital capsule 16
 - Aedeagus less than length of genital capsule 17
- 16 Aedeagus $1\frac{1}{2}$ times length of genital capsule; at base almost as wide as widest part of capsule; forewing dark brown with bright purple reflections *crotonica*
 - Aedeagus slightly longer than length of genital capsule but not $1\frac{1}{2}$ times its length, not nearly as wide as widest part of capsule at any point; forewing pale ochreous *potgieteri*
- 17 Gnathos approximately H-shaped 18
 - Gnathos not H-shaped 21
- 18 Uncus with rounded lobes (fig. 20); ventral arm of transtilla pointing nearly laterally *hortorum*
 - Uncus without such rounded lobes; ventral arm of transtilla reduced or not pointing nearly laterally 19
- 19 Vesica of aedeagus with prominent spines posteriorly; gnathos without lateral processes 20
 - Vesica of aedeagus with inconspicuous denticles arranged approximately in a ring; gnathos with clearly visible lateral processes *allophylica*
- 20 Lateral arm of transtilla clearly present, pointed; anterior extension of vinculum long, deeply excavated so forming pair of large lobes *perplexa*
 - Lateral arm of transtilla virtually absent, or reduced to short, rounded lobes; anterior extension of vinculum very short, weakly depressed *generalis*
- 21 Forewing uniformly pale, not irrorated 22
 - Forewing dark or, if pale, irrorated 23
- 22 Juxta absent; aedeagus with 'teeth' posteriorly on vesica *rhynchosiella*
 - Juxta present; aedeagus without 'teeth' on vesica *fluida*
- 23 Forewing pale ochreous, irrorated with dark scales 24
 - Forewing not as above 25
- 24 Uncus with pair of well developed papillae (fig. 2); forewing rather lightly irrorated *abutilonca*
 - Uncus with papillae less developed (fig. 6); forewing heavily irrorated *irrorata*
- 25 Underside of forewing with streak of yellow scales *varii*
 - Underside of forewing without streak of yellow scales 26
- 26 Forewing with incomplete silver fascia *parinarella*
 - Forewing without a fascia 27
- 27 Uncus bipapillate; forewing generally with bright yellow tip *charistis*
 - Uncus bilobed rather than papillate; forewing not yellow at tip 28
- 28 Uncus covered with denticles; anterior extension of vinculum rounded *satarensis*
 - Uncus not covered with denticles; anterior extension of vinculum depressed *geranica*
- 29 Valves broad, strongly produced inwardly (fig. 51); juxta heavily sclerotized and of a characteristic shape; genital capsule as wide as long, transtilla fused to form a U-shaped structure *letabensis*
 - Valves narrow; juxta absent; genital capsule longer than wide, transtilla not forming a U-shaped structure 30
- 30 Aedeagus less than length of genital capsule; anterior extension of vinculum large (fig. 49); forewing not irrorated; wingspan relatively large 9-10mm *ingens*
 - Aedeagus approximately equal to, or longer than length of genital capsule, anterior extension of vinculum shorter; forewing irrorated; wingspan not exceeding 6mm 31

- 31 Aedeagus with characteristic markings on vesica (fig. 50); anterior extension of vinculum weakly excavated; tegumen very large . . . *angustivalva*
 - Aedeagus with markings on vesica different from fig. 50; anterior extension of vinculum more deeply excavated; tegumen not very large . . . 32
- 32 Gnathos: central element broad (fig. 43); transtilla with lateral arm broad . . . *confinalis*
 - Gnathos: central element narrow (fig. 46); transtilla with lateral arm less broad . . . *greviae*

CHECK-LIST OF SOUTHERN AFRICAN SPECIES OF *STIGMELLA* SCHRANK

The <i>fluida</i> -group:	<i>S. urbica</i> (Meyrick) comb.nov.
<i>S. charistis</i> Vári	<i>S. androflavus</i> spec.nov.
<i>S. abutilonica</i> spec.nov.	<i>S. abachansi</i> (Janse) comb.nov.
<i>S. parinarella</i> Vári	<i>S. pallida</i> spec.nov.
<i>S. fluida</i> (Meyrick) comb.nov.	<i>S. nigrata</i> (Meyrick) comb.nov.
<i>S. irrorata</i> (Janse) comb.nov.	<i>S. triumfettica</i> spec.nov.
<i>S. varii</i> spec.nov.	<i>S. dombeyivora</i> spec.nov.
<i>S. geranica</i> spec.nov.	<i>S. ampullata</i> spec.nov.
<i>S. satarensis</i> spec.nov.	<i>S. pretoriata</i> spec.nov.
<i>S. allophylica</i> spec.nov.	<i>S. protosema</i> (Meyrick) comb.nov.
<i>S. fragilis</i> spec.nov.	<i>S. porphyreuta</i> (Meyrick) comb.nov.
<i>S. hortorum</i> spec.nov.	
<i>S. potgieteri</i> spec.nov.	The <i>ingens</i> -group:
<i>S. crotonica</i> spec.nov.	<i>S. confinalis</i> spec.nov.
<i>S. rhynchosiella</i> Vári	<i>S. greviae</i> spec.nov.
<i>S. platyzona</i> Vári	<i>S. ingens</i> (Meyrick) comb.nov.
<i>S. celtifoliella</i> Vári	<i>S. angustivalva</i> spec.nov.
<i>S. generalis</i> spec.nov.	<i>S. letabensis</i> spec.nov.
<i>S. perplexa</i> (Janse) comb.nov.	

The *FLUIDA*-group

In the males of the species of the *fluida*-group the gnathos has paired horns instead of a single, central element (compare e.g. fig. 2 with fig. 43); this character distinguishes the *fluida*-group from the *ingens*-group. The antenna does not generally extend to beyond the length of the forewing. However, this character is not very reliable (see appendix 1).

Stigmella charistis Vári

Stigmella charistis Vári, 1963. *Koedoe* 6:71, pl. 1:6; genitalia: text-figs. 5 & 12; mine: text-fig. 18.

In addition to the type-series three further specimens, two males and one female, have been examined. In the males of these the yellow at the apex of the forewing is characteristically present, but it is absent in the female. However the genitalia of the female are typically those of *charistis*, and the moth was reared from a larva feeding on the same plant as the larva from which one of the males was reared.

Generally the very bright, yellow forewing apex distinguishes *charistis* from its relatives. However, as one of the females examined lacks this feature, the character is not certainly diagnostic of the species. *S. charistis* is larger and darker than the closely related *abutilonica* with which it shares

a yellow, although not bright yellow, forewing apex and similar, although not identical, genitalia. In the male of *charistis* the valves are slightly broader, the transtilla more robust and the vesica of the aedeagus more strongly marked. The absence of silver patches on the forewing of *charistis* distinguishes it from *parinarella* although the genitalia of these two species show them to be related. *S. charistis* is much darker than *fluida* and the aedeagus is considerably shorter relative to the genital capsule than in *crotonella*. The absence of cornuti on the vesica of the aedeagus distinguishes *charistis* from *irrorata*.

MATERIAL EXAMINED: The type-series from Umhlanga Rocks, Natal (see Vári, 1963); in TM. Additional specimens: SOUTH AFRICA: Transvaal, Louis Trichardt, Accession no. 1585, 1 ♂ 20.iv.1955, 1 ♀ 19.iv.1955 (Vári); Kruger National Park, 1 ♂ 6-15.v.1975 (Potgieter & Scoble); in TM.

BIOLOGY: Food-plant: *Grewia occidentalis* L. (Tiliaceae).

Mine: In the sample of mined leaves from which the type-series was reared the eggs were laid on the lower surfaces and the larvae left the mine through the upper epidermis (Vári, 1963:72). In a large series of mined leaves bearing the same accession number as the two adults mentioned above the eggs are laid on the upper surface of the leaf. Amongst this series are two specimens from which the larvae have left from the lower surface.

Stigmella abutilonica spec.nov., text-figs. 2-4.

EXTERNAL CHARACTERS: ♂, ♀ (3,0-4,4mm). Head-tuft ranging from ochreous to the more usual red-brown. Collar and eye-cap off-white. Antenna grey-purple. Thorax and abdomen grey. Forewing pale ochre with bronze reflections, irrorated with brown-purple scales concentrated apically, the extent of irroration varying between individuals; fringe pale ochre at tip. Hindwing pale grey. Legs almost white at tips.

♂-GENITALIA (fig. 2): Vinculum: ventral plate short; anterior extension short, weakly excavated so forming a pair of points. Tegumen gently rounded. Uncus bipapillate. Gnathos: horns straight. Valve narrow, strongly curved apically. Transtilla with all elements thin; lateral arm long; ventral arm fairly long. Aedeagus $\frac{3}{4}$ length of genital capsule; vesica with a patch of denticulate cornuti and a small centrally placed thickening.

♀-GENITALIA (fig. 3): Apophyses relatively long. Corpus bursae covered with minute pectinations.

REMARKS: The pale ochreous forewing, irrorated with brown-purple, and the small size of the moth, distinguish this species from its relatives. In the male the valve is slightly narrower, the transtilla less robust and the vesica of the aedeagus less strongly marked than in *charistis*. The absence of silver patches on the forewing of *abutilonica* distinguishes it from *parinarella*. *S. abutilonica* is darker than the very pale *fluida*. The aedeagus, relative to the length of the genital capsule, is shorter than it is in *crotonella* and there are fewer cornuti on the vesica of the aedeagus than in *irrorata*.

MATERIAL EXAMINED: ♂-Holotype, SOUTH AFRICA: Natal, Umhlanga Rocks, Accession no. 2930, 5.vii.1968 (Vári); genitalia slide no.

10250; in TM; paratypes, data as holotype, 4♂♂ 7–10.xii.1953; Accession no. 2953, 52♂♂, 93♀♀ 1–11.vii.1968 (Vári); in TM.

BIOLOGY: Food-plant: *Abutilon grantii* A. Meeuse (Malvaceae).

Mine (fig. 4): An upper surface linear tract. Frass deposited as a narrow, central solid line. Larva exits through upper epidermis of leaf.

Egg: laid on upper surface of leaf.

Stigmella parinarella Vári

Stigmella parinarella Vári, 1955. *Ann. Transv. Mus.* 22:337, pl. 24:3; genitalia: text-figs. 10 & 21, mine: text-fig. 32.

This species is distinguished from its known relatives (*charistis*, *abutilonica*, *fluida* and *irrorata*) by the two silver patches on the forewing. The lobes of the uncus are rather more rounded than pointed, and the valve is markedly swollen at the base.

MATERIAL EXAMINED: The type-series (see Vári, 1955:338) except for two paratypes one of which is deposited in the BMNH and the other in the NMHU.

BIOLOGY: Food-plant: *Parinari capense* Harv. (Chrysobalanaceae).

Mine: (Additional notes to Vári, 1955). An upper surface linear tract. Larva exits through upper epidermis of leaf.

Stigmella fluida (Meyrick) **comb.nov.**, text-fig. 5.

Nepticula fluida Meyrick, 1911. *Ann. Transv. Mus.* 2:236; Janse, 1948. *The Moths of South Africa* 4:164, pl. 82:3, 87:8, 89:8, 93:6.

♂-GENITALIA (fig. 5): Vinculum: Ventral plate of medium length; anterior extension excavated so forming pair of approximately triangular structures. Tegumen only slightly curved. Uncus bipapillate. Gnathos: horns short and straight; lateral and anterior processes fused to form large, triangular plate; horizontal element short. Valve gently arcuate, curving more strongly apically, bulbous basally. Transtilla: lateral and ventral arms robust; ventral arm relatively long; transverse bar more narrow. Juxta in form of a small, curved, punctured plate situated between bases of valves. Aedeagus $\frac{3}{4}$ length of genital capsule; vesica with a weakly sclerotized thickening, cornuti absent.

♀-GENITALIA: Unknown. The only known specimen, which according to Meyrick's original description is a female, has lost its abdomen (Sattler, personal communication).

REMARKS: *S. fluida* is related to *charistis*, *abutilonica*, *parinarella* and *irrorata*. It may be distinguished by the off-white to very pale ochreous body and wings. The large triangular plate of the gnathos, formed by the union of the lateral and anterior processes, is a characteristic feature of the species.

In the original description Meyrick made no type designation. Of the two syntypes on which he based his description, one, a male, is housed in the Transvaal Museum and the other, believed to be a female, is in the British Museum (Natural History). The male is here designated as lectotype. It is labelled as follows: 'Pretoria, 17.9.06, A.J.T. Janse; 4295; *Nepticula fluida* M., Type no. 114'; G [genitalia slide no.] 7240.

MATERIAL EXAMINED: ♂-Lectotype, SOUTH AFRICA: Transvaal, Pretoria, TM type no. 114; Meyrick's number 4295, 17.ix.1906 (Janse);

in TM. Additional specimens: Pretoria, 3♂♂ 10.xi.1911, 22.xi.1913, 15.i.1915 (Janse); 2♂♂ 7.i.1949, 19.viii.1952 (Vári); Potchefstroom, 1♂ 27.ix.1951 (Vári); Ofcolaco, Cyprus Farm, 1♂ 20.ix.1960 (Vári); Suikerbosrand, Nature Reserve, 1♂ 17.iii.1978 (Kroon); in TM.

BIOLOGY: Unknown.

Stigmella irrorata (Janse) **comb.nov.**, text-fig. 6.

Nepticula irrorata Janse, 1948. The Moths of South Africa 4:168 (*partim*), pl. 82:7, 88:13 (♂-genitalia of lectotype), 90:2, 92:6.

♂-GENITALIA (fig. 6): Vinculum: ventral plate short, excavated anteriorly; anterior extension very short. Tegumen fairly wide. Uncus emarginated posteriorly so forming pair of short papillae. Gnathos: horns rather short, anterior and lateral processes forming an approximately triangular structure. Valve approximately triangular, slightly curved at tip. Transstilla: lateral arm and transverse bar relatively long. Aedeagus just over half the length of genital capsule; vesica with row of cornuti running longitudinally for most of length, and a rectangular thickening.

♀-GENITALIA: Unknown.

REMARKS: The well defined row of cornuti serves to distinguish *irrorata* from *charistis*, *abutilonica*, *parinarella* and *fluida*. The shape of the gnathos is characteristic.

Janse referred to twelve specimens in his original description and stated that the 'types' are in the Transvaal Museum. One male and one female are each labelled as 'Type' and a further five as 'Cotype'. Of the remaining five specimens four are females and one is a male. None of them bear a type label but I consider them to be part of the type series as they were in the collection under Janse's '*irrorata*' label, and because the number of specimens and their label data agree with that recorded in the original description. The male syntype labelled 'Type No. 2370' is here designated as lectotype of *irrorata* because (1) the genitalia were figured by Janse in the original description and (2) Janse's description fits this specimen more closely than it does the others. The lectotype is labelled: 'Abachaus, S.W.A., May 43, G. Hobohm. *Nepticula irrorata* Janse ♂, Type No. 2370, G.4950.'

None of the paralectotypes actually belong to *irrorata*. The only male is a specimen of *nigricapitella* Janse, one female probably belongs to this species, and the remaining nine females probably represent *vannifera* Meyrick. None of them belong to *Stigmella* species. They will be dealt with fully in a later paper. The label data of these paralectotypes is as follows: SOUTH WEST AFRICA: Abachaus, 6♀♀ Type Nos. 2371-2376, ix-x.1945, iv.1943 (Hobohm); 1♂ xi.1943 (Hobohm); 4♀♀ ix.1943, ix.1945 (Hobohm).

MATERIAL EXAMINED: ♂-Lectotype, TM type no. 2370; SOUTH WEST AFRICA: Abachaus, v.1943 (Hobohm); genitalia slide no. 4950; in TM.

BIOLOGY: Unknown.

Stigmella varii spec.nov., text-figs. 7-9.

EXTERNAL CHARACTERS: ♂, ♀ (4.0-5.0mm). ♂ Head-tuft ochreous. Collar and eye-cap off-white. Antenna, thorax and abdomen grey-brown

with purple and copper reflections. Forewing: upperside as antenna, thorax and abdomen; underside with streak of pale ochreous scales near base situated midway between costal and anal edges. Hindwing light grey. Legs light purplish grey.

♀ As male but without pale ochreous scales on underside of forewing.

♂-GENITALIA (fig. 7): Vinculum- ventral plate of medium length; anterior extension excavated so forming pair of roughly triangular processes. Tegumen gently curved posteriorly. Uncus weakly bilobed, sclerotized laterally. Gnathos: horns stout and straight; lateral and anterior processes jointly forming a pair of roughly triangular plates. Valve excavated, ventral aspect broad, rounded apically; dorsal aspect strongly curved at tip. Transtilla: lateral arms stout, extending into triangular basal process; transverse bar formed by union of triangular process of each transtilla. Aedeagus $\frac{3}{4}$ length of capsule; vesica with centrally placed arcuate thickening, cornuti absent.

♀-GENITALIA (fig. 8): Ductus bursae encircled by ring of sclerotizations where it merges with corpus. Corpus bursae unmarked.

REMARKS: The ♂-genitalia of this species are rather generalized: they have no strikingly differential characters. The following combination of characters may assist in identification: transtilla robust, valve excavated apically, capsule rather wide. In the ♀-genitalia a ring of denticulate marks, otherwise found only in *crotonella* amongst the species considered here, encircles the top of the bursa. The ♂-genitalia show the species to be most closely related to *irrorata*; *varii* differs from that species through lacking the forewing irrorations.

The species is named after Dr L. Vári of the Transvaal Museum.

MATERIAL EXAMINED: ♂-Holotype, SOUTH AFRICA: Transvaal, Brits District, Hartebeespoortdam, Accession no. 561, 4.ix.1952 (Vári); genitalia slide no. 9919; in TM; paratypes, data as holotype, 1♂ 4.ix.1952; Pretoria, Accession no. 57, 1♀ 8.xii.1948 (Vári); Accession no. 395, 1♂ 5.x.1951; Pretoria North 9♂♂, 13♀♀ ix.1949 (van Son); 2♂♂ 26.i.1954 (Vári); in TM.

BIOLOGY: Food-plant: *Croton gratissimus* Burch. var. *subgratissimus* (Prain) Burtt Davy (Euphorbiaceae).

Mine (fig. 9): An upper surface linear tract. Frass deposited as a dark, central line throughout. Larva exits through upper surface of leaf.

Egg: laid on upper surface of leaf.

Stigmella geranica spec.nov., text-figs. 10-12.

EXTERNAL CHARACTERS: ♂, ♀ (3,8-4,6mm). Head-tuft ranging from pale grey-brown to ochreous. Collar off-white. Eye-cap off-white to brownish-grey. Antenna, thorax, dorsal surface of abdomen, forewing and legs dark purplish-grey, with bronze and some purple reflections. Hindwing pale grey-brown. Legs becoming pale distally.

♂-GENITALIA (fig. 10): Vinculum: ventral plate bulging posteriorly between bases of valves; anterior extension of medium length, weakly excavated. Tegumen curved, swollen at ends. Uncus weakly bilobed. Gnathos: horns long, thin and slightly curved; horizontal element slightly swollen posteriorly. Valve relatively wide, gently arcuate, bul-

bous basally with small point at tip. Transtilla: ventral arm fairly long. Aedeagus just under $\frac{3}{4}$ length of genital capsule; vesica with pair of large 'teeth', a cluster of denticles posteriorly, and a centrally placed, arcuate thickening.

♀-GENITALIA (fig. 11): Corpus bursae unmarked.

REMARKS: The species is distinguished from *satarensis*, to which it is very closely related, by the horizontal element of the gnathos, which is in the form of a protuberance, and by the absence of denticles on the uncus. Compared with those of *tragilis*, the ♂-genitalia of *geranica* lack the denticles covering the uncus, and there is no sexual dimorphism in the external characters of *geranica*. The uncus of *geranica* has flattened lobes at the apex rather than rounded ones as in *hortorum*. The transtilla also differs. *S. germanica* has a darker head-tuft and a smaller wingspan than *allophylica*. In the male, the uncus and the valve of these two species are of a slightly different shape, although, overall, the genitalia are very similar.

MATERIAL EXAMINED: ♂-Holotype, SOUTH AFRICA: Natal, Everton, Accession no. 3404, 5.v.1975 (Vári); genitalia slide no. 9986; in TM; paratypes, data as holotype, 11♂♂, 14♀♀ 5-9.v.1975; in TM.

BIOLOGY: Food-plant: *Geranium* cf. *pulchrum* Brown (Geraniaceae).

Mine (fig. 12): A long, upper surface, linear tract remaining relatively narrow throughout length. Frass deposited centrally; compact for entire length of mine. Larva exits through upper epidermis of leaf.

Egg: laid on upper surface of leaf.

Stigmella satarensis spec.nov., text-fig. 13.

EXTERNAL CHARACTERS: ♂ 4.4mm. ♀ Unknown.

♂-GENITALIA (fig. 13).

REMARKS: *S. satarensis* is so similar to *geranica* that only diagnostic features are recorded here. It differs from *geranica* by the presence of denticles scattered over the uncus, and by the shape of the gnathos. *S. satarensis* is also related to *tragilis*. It is distinguished from that species by the anterior extension of the vinculum which is not excavated but rounded. The eye-cap of the male of *S. satarensis* is not as heavily shaded as it is in *tragilis*. However, there is some weak shading.

MATERIAL EXAMINED: ♂-Holotype, SOUTH AFRICA: Transvaal, Kruger National Park, Satara, 27.iii.1952 (Janse & Vári); genitalia slide no. 10025; in TM.

BIOLOGY: Unknown.

Stigmella allophylica spec.nov., plate 15:1, text-figs. 14-16.

EXTERNAL CHARACTERS: ♂, ♀ (5.0-5.6mm): Head-tuft off-white, orange-ochre, red-brown or pale brown. Collar and eye-cap off-white. Antenna purplish-grey dorsally, pale grey ventrally. Thorax, abdomen, forewing and legs purplish-grey, with bronze and a few purple reflections. Hindwing pale brownish-grey. Legs pale at tips.

♂-GENITALIA (fig. 14): Vinculum: ventral plate slightly curved posteriorly; anterior extension reduced to a short thickened margin. Tegumen comprising an arcuate band, slightly swollen at ends. Uncus weakly

bilobed. Gnathos: horns and anterior processes approximately of equal length; lateral processes short. Valve wide, swollen at base. Transtilla robust; ventral arm long. Juxta narrow, elongate. Aedeagus just over $\frac{1}{2}$ length of genital capsule; vesica with inconspicuous denticles arranged roughly in a ring posteriorly, and with a centrally placed, arcuate thickening.

♀-GENITALIA (fig. 15): Ductus with small toothed-plate where accessory sac branches. Corpus bursae with a pair of long pectinate bands.

REMARKS: This species is most closely related to *geranica*. However *allophylica* has a paler head-tuft and a larger wingspan than that species. The uncus and valve of the two species differ slightly in shape. The vesica of the aedeagus of *geranica* is marked with large 'teeth' in contrast to the inconspicuous ring of denticles in *allophylica*. The presence of a juxta in *allophylica* further distinguishes the species from *geranica*.

MATERIAL EXAMINED: ♂-Holotype, SOUTH AFRICA: Natal, Umhlanga Rocks, Accession no. 2937, 8.vii.1968 (Vári); genitalia slide no. 9847; in TM; paratypes, data as holotype, 3♂♂, 15♀♀ 5-14.vii.1968 (Vári); in TM.

BIOLOGY: Food-plant: *Allophylus natalensis* (Sond.) De Winter (Sapindaceae).

Mine (fig. 16): An upper surface linear tract. Frass deposited as a narrow compact line in early part, later laid down as zig-zag arcs. Larva emerges from upper epidermis of leaf.

Egg: laid on upper surface of leaf.

***Stigmella fragilis* spec.nov., text-figs. 17-19.**

EXTERNAL CHARACTERS: (3,6-4,6mm). ♂ Head-tuft off-white to pale ochreous. Collar dark purplish-brown. Eye-cap off-white, usually with a striking, dark purplish-brown patch posteriorly although this is absent in one specimen. Antenna dorsally dark purplish-brown, ventrally pale. Thorax, abdomen and forewing charcoal, with weak purple and bronze reflections. Hindwing grey. Legs a mixture of off-white and grey.

♀ As male except for: head-tuft reddish-ochre. Collar off-white. Eye-cap without dark patch.

♂-GENITALIA (fig. 17): Vinculum: ventral plate bulging posteriorly between bases of valves; anterior extension fairly short, weakly excavated. Tegumen in form of crescentic band. Uncus covered with denticles, posterior margin only very slightly depressed, not bilobed. Gnathos: horns long, thin and slightly curved; horizontal element in form of protuberance. Valve narrow, slightly bulbous at base. Transtilla with all elements thin; lateral arm long; transverse bar long and curved. Aedeagus $\frac{1}{2}$ length of genital capsule; vesica with four large teeth posteriorly and a centrally placed arcuate thickening.

♀-GENITALIA (fig. 18): Accessory sac with characteristic oval thickening where it branches from ductus bursae. Corpus bursae pectinate.

REMARKS: The species is most closely related to *satarensis*. It is distinguished by the dark patch on the eye-cap and the dark collar of the male. The valve is comparatively long and thin and the elements comprising the transtilla are very narrow. The female genitalia of *fragilis* are characterized by the oval thickening associated with the ductus.

MATERIAL EXAMINED: ♂-Holotype, SOUTH AFRICA: Natal, Margate, Accession no. 2995, 25.i.1969 (Vári); genitalia slide no. 10095; in TM; paratypes, data as holotype 13♂♂, 4♀♀ 24–28.i.1969; in TM.

BIOLOGY: Food-plant: *Tragia durbanensis* Kuntze (Euphorbiaceae).

Mine (fig. 19): An upper surface linear tract. Frass forms an unbroken line in the early stages but is deposited as separate granules later. Larva exits through upper epidermis of leaf.

Egg: laid on upper surface of leaf.

Stigmella hortorum spec.nov., text-fig. 20.

EXTERNAL CHARACTERS: ♂ (4,0–4,4mm). Head-tuft, eye-cap and collar off-white. Antenna grey. Thorax, abdomen and forewing dark grey-brown with bronze and purple reflections. Hindwing pale grey-brown. Legs pale grey.

♀ Unknown.

♂-GENITALIA (fig. 20): Vinculum: ventral plate bulging posteriorly between bases of valves; anterior extension short, weakly excavated, so forming two small, roughly triangular processes. Tegumen flat posteriorly, swollen laterally. Uncus with pair of rounded lobes. Gnathos robust; horns slightly curved; lateral processes short; anterior processes long; horizontal element in form of protuberance. Valve of medium width, gently arcuate becoming more strongly curved towards tip; inner margin denticulate. Transtilla: ventral arm fairly short and pointing nearly laterally so being almost in line with transverse bar. Aedeagus $\frac{1}{2}$ length of genital capsule; vesica with two short vertical rows of denticulate cornuti posteriorly, and a centrally placed ring-shaped thickening.

REMARKS: The rounded shape of the lobes of the uncus is diagnostic of this species, and so is the near laterally projected ventral arm of the transtilla which gives the structure a flattened appearance. The species seems to be most closely related to the four preceding ones.

MATERIAL EXAMINED: ♂-Holotype, SOUTH AFRICA: Transvaal, Kruger National Park, Pretoriuskop, 6–7.iv.1952 (Vári); genitalia slide no. 10138; in TM; paratype, data as holotype, 1♂ 6–7.iv.1952; in TM.

BIOLOGY: Unknown.

Stigmella potgieteri spec.nov., text-fig. 21.

EXTERNAL CHARACTERS ♂ (3,8mm): Head-tuft reddish-brown. Collar ?. Eye-cap off-white; antenna greyish-purple. Forewing pale ochreous. Hindwing light grey to off-white. Legs grey.

♀ Unknown.

♂-GENITALIA (fig. 21): Vinculum: ventral plate of medium width; anterior projection short, weakly excavated so forming a pair of small papillae. Tegumen slightly swollen laterally. Uncus weakly bilobed. Gnathos: horns curved; anterior processes fairly well developed; horizontal element with small tongue-shaped projection. Valve excavated at tip to form two small hooks. Transtilla: lateral arm long; ventral arm absent; transverse bar long and straight. Aedeagus approximately equal to length of genital capsule; pointed posteriorly; vesica with long sclerotized elements and an arcuate thickening.

REMARKS: The projection of the horizontal element of the gnathos of this species somewhat resembles *bortorum*, however the aedeagus is much larger, the ventral arms of the transtilla are absent, and the forewing is pale ochreous not dark grey-brown.

The species is named after Mr J.H. Potgieter of the Transvaal Museum.

MATERIAL EXAMINED: ♂-Holotype, SOUTH AFRICA: Transvaal, Kruger National Park, Satara, 6.v.1970 (Vári & Potgieter); genitalia slide no. 10170; in TM.

BIOLOGY: Unknown.

Stigmella crotonica spec.nov., plate 15:2, text-figs. 22-24.

EXTERNAL CHARACTERS: ♂, ♀ (3,6-5,6mm). Head-tuft orange-ochreous. Collar dark brown with bright purple reflections. Eye-cap off-white. Antenna purplish-grey, with purple reflections. Thorax and abdomen dark brown, with copper and a few purple reflections. Forewing ground-colour dark brown with bright purple reflections. Hindwing grey-brown. Legs dark brown with purple reflections, pale at tips.

♂-GENITALIA (fig. 22): Vinculum: ventral plate of medium length; anterior extension short, excavated so forming a pair of pointed papillae. Tegumen fairly large, rounded posteriorly. Uncus with corners of apex comprising a pair of pointed projections. Gnathos: horns long and thin; lateral processes short; anterior processes long. Valve excavated, front triangular in ventral view; back strongly curved at tip. Transtilla: ventral arm fairly long. Aedeagus large, approximately $1\frac{1}{2}$ times length of genital capsule, widening basally; vesica with long, longitudinally running band of cornuti, anterior to which is a thickening.

♀-GENITALIA (fig. 23): Corpus bursae encircled by a ring of longitudinally running, sclerotized markings near to point at which it meets ductus bursae, otherwise unmarked.

REMARKS: The combination of bright purple reflections from the forewing, the very long aedeagus, relative to the length of the genital capsule, and the papillate corners of the uncus are characteristic of *crotonica*. The ring of sclerotizations encircling the top of the corpus bursae in the female resembles those of *varii*; otherwise the two species are not similar. This ring of sclerotizations distinguishes the ♀-genitalia of *crotonica* from other *Stigmella* species considered in this paper.

MATERIAL EXAMINED: ♂-Holotype, RHODESIA: Mount Selinda, Accession no. 1793, 20.iv.1956 (Vári); genitalia slide no. 10179; in TM; paratypes, data as holotype; 7♂♂, 2♀♀ 20.iv.-3.v.1956; in TM.

BIOLOGY: Food-plant: *Croton sylvaticus* Hochst. (Euphorbiaceae).

Mine (fig. 24): An upper surface linear tract. Frass fills early part of mine, later breaks up into separate grains. Larva exits through upper epidermis of leaf.

Egg: laid on upper surface of leaf.

Stigmella rhynchosiella Vári

Stigmella rhynchosiella Vári, 1955. *Ann.Transv.Mus.* 22:338, pl. 24:4; genitalia: text-figs. 12 & 13; mine: text-fig. 34.

The uncus of *rhynchosiella* is rather similar to that of *platyzona*. However, in *rhynchosiella* the valve is relatively much larger and the anterior extension

of the vinculum much shorter. The pale colour of the forewing of *rhynchosiella* resembles that of *fluida*, however, the genitalia are quite different and the two species are not closely related. The ♀-genitalia of *rhynchosiella* have characteristically long apophyses, the anteriores are longer than the posteriores. The pseuduncus (see Vári, 1955) of this species is here regarded as the uncus.

MATERIAL EXAMINED: The type-series (Vári, 1955:339) except for two paratypes one of which is deposited in the BMNH and the other in the NMHÜ. Additional specimens: SOUTH AFRICA: Transvaal, Pretoria, Accession no. 161, 4♂♂ 28, 30.vi.1949; Accession no. 175, 4♂♂, 1♀ 18, 21, 23, 30.viii.1949; Accession no. 1661, 1♂, 2♀♀ 25, 26.v.1955 (Vári); Pretoria North, Accession no. 2013, 1♂, 1♀ (abdomen missing) 7, 9.viii.1957 (Vári); in TM.

BIOLOGY: Food-plant: *Rhynchosia nitens* Benth. (Leguminosae).

Mine: an upper surface linear tract.

Egg: laid on upper surface of leaf (compare Vári, 1955).

Stigmella platyzona Vári

Stigmella platyzona Vári, 1963. *Koedoe* 6:67, pl. 1:1; genitalia: text-figs. 1 & 7; mine: text-fig. 13.

Although it has a similar uncus to *rhynchosiella*, *platyzona* is easily distinguished by the relatively small valve and the very long anterior extension of the vinculum. The wide, transverse, ochreous-yellow fascia of the forewing is characteristic. The length of the valve is inversely proportional to the length of the ventral plate of the vinculum. This is why the ♂-genitalia of *platyzona* resemble those of *celtifoliella*. However, the uncus, gnathos and transtilla are different, and the anterior extension of the vinculum is deeply excavated in *platyzona*. The forewing markings of the two species are also different.

MATERIAL EXAMINED: The type-series (Vári, 1963:67). Additional specimen: SOUTH AFRICA, Transvaal, Sudwala Caves, 1♂ 12-13.iii.1974 (L. & G. Vári).

BIOLOGY: Food-plant: *Ficus burttidavii* Hutch., and *Ficus* species (Moraceae).

For further details of the biology see Vári (1963).

Stigmella celtifoliella Vári

Stigmella celtifoliella Vári, 1955. *Ann. Transv. Mus.* 22:338, pl. 24:1; genitalia: text-figs. 11 & 20; mine: text-fig. 33.

S. celtifoliella is one of the few South African species of Nepticulidae with a silver fascia on the forewing, a characteristic feature of so many holarctic species. The distinguishing features found in the ♂-genitalia are as follows: anterior extension of vinculum long, excavated, although not as deeply as that of *platyzona*. Valve small, bulbous at base. Aedeagus swollen posteriorly, narrowing at anterior end. In general appearance the male genitalia are similar to *platyzona* but the valve shape, transtilla, gnathos and uncus differ. The silver fascia on the forewing of *celtifoliella*

further distinguishes the species from *platyzona* which has a broad, ochreous-yellow fascia. In the female of *celtifoliella* there are characteristic markings on the ductus bursae, and on the corpus bursae very near to the point at which it meets the ductus.

The cubitus vein in the forewing is weak and not easy to see. However, it is definitely present and the venation is typically that of *Stigmella*.

MATERIAL EXAMINED: The type-series (Vári, 1955:338) except for two paratypes one of which is deposited in the BMNH and the other in the NMHU. Additional specimens: SOUTH AFRICA: Transvaal, Pretoria, Accession no. 99, 1♀ 18.i.1949; 1♀ 16.ix.1949; Accession no. 148, 1♂ 5.iv.1949; Accession no. 319, 1♂ ii.1951; Accession no. 1665, 1♀ 14.vii.1955; Accession no. 1670, 1♀ 22.vii.1955; 1♀ 11.iii.1971; Accession no. 3090, 1♀ 22.iii.1971; Accession no. 3603, 1♂, 1♀ 8.vii.1976 (Vári); Pretoria North, 1♂, 1♀ 9.ii.1954 (Vári); 3♂♂ 23.x.1960 (van Son); Natal, Umhlanga Rocks, Accession no. 2946, 1♀ 5.viii.1968 (Vári); in TM.

BIOLOGY: Food-plant: *Celtis africana* Burm. (Ulmaceae).

Mine: Additional notes to Vári (1955:338). It begins as a tract in the lower layer of the leaf. The larva then moves into the upper layers and the mine widens. It vacates the mine through the lower epidermis of the leaf. The initial part of the mine is frequently crossed by the later section of the tract. Frass almost fills the early part of the mine, but later becomes less tightly packed.

***Stigmella generalis* spec.nov., text-fig. 25.**

EXTERNAL CHARACTERS: ♂ (4,4mm). Head-tuft ochreous. Collar and eye-cap off-white. Antenna pale grey-purple. Thorax and forewing greyish-brown with weak copper and purple reflections. Hindwing light brown. Legs missing from specimen.

♀ Unknown.

♂-GENITALIA (fig. 25): Vinculum: ventral plate of medium length; anterior extension very short, very weakly excavated. Tegumen in form of narrow, curved band. Uncus fairly short, with pair of small, ear-like lobes apically, and swellings baso-laterally. Gnathos robust, approximately H-shaped; horns and anterior processes forming a continuous element tapering cephalad. Valve broad, approximately triangular. Transtilla: lateral arm broad. Aedeagus $\frac{3}{5}$ length of genital capsule, flask-shaped; vesica with characteristic spines posteriorly and an arcuate thickening centrally.

REMARKS: This species has no particularly close relatives. Although the gnathos resembles *platyzona*, *generalis* is easily distinguished from that species by the lack of a fascia on the forewing and in the general appearance of the ♂-genitalia capsule. The uncus, and to some extent the gnathos, of *generalis* resembles *perplexa*. However, the absence of a juxta in *generalis*, the general shape of the ♂-genitalia and the dark, as opposed to pale, forewing distinguish it.

MATERIAL EXAMINED: ♂-Holotype, SOUTH AFRICA: Cape Province, East London, viii.1946 (Clark); genitalia slide no. 5930; in TM.

BIOLOGY: Food-plant: *Rhus* species (from label data), (Anacardiaceae).

Stigmella perplexa (Janse) **comb.nov.**, text-fig. 26.

Nepticula perplexa Janse, 1948. *The Moths of South Africa* 4:172, pl. 83:1, 88:18, 90:9, 91:3.

♂-GENITALIA (fig. 26): Vinculum: ventral plate short slightly bulging posteriorly in mid-margin; anterior projection long, deeply excavated so forming pair of large lobes. Tegumen narrow, not curved. Uncus wide, weakly bilobed. Gnathos approximately H-shaped, all elements of about the same width; anterior processes long although shorter than horns. valve with large bulbous base. Transtilla: lateral arm stout, each terminating in roughly triangular swellings so that ventral arm is virtually absent; transverse bar formed by union of apices of triangular swellings. Juxta triangular at base from which a long element extends posteriorly. Aedeagus approximately $\frac{1}{2}$ length of genital capsule; vesica with pair of three-spine clusters posteriorly and a large, arcuate, centrally placed plate.

♀-GENITALIA: Of uncertain identity (see below).

REMARKS: The ♂-genitalia resemble those of *generalis* and *urbica*. They are distinguished from both by the long, deeply excavated, anterior projection of the vinculum. The presence of a juxta, and the virtual absence of ventral arms of the transtilla show that *perplexa* is closer to *urbica* than to *generalis*. The length/breadth ratio of the genital capsule is considerably greater in *urbica* than it is in *perplexa*.

As the specimens of the type-series are in a relatively poor condition I am unable to definitely associate the only female paratype of *perplexa* with the males. The specimen certainly belongs to *Stigmella* as the bursa copulatrix lacks signa and is covered with weak pectinations characteristic of the genus. It is labelled 'Abachaus. S.W.A., Feb. 43 G.Hobohm; *Nepticula perplexa* Janse, Cotype No. 2394.'

MATERIAL EXAMINED: ♂-Holotype, TM type no. 2392; SOUTH WEST AFRICA: Abachaus, i.1944 (Hobohm); genitalia slide no. 7266; in TM; paratypes, data as holotype, 1♂ i.1945 (TM type no. 2393); 1♂ xi.1945 (TM type no. 2395). Additional specimen: SOUTH AFRICA: Transvaal, Potgietersrus District, Limburg, 1♂ 19-21.xi.1968 (Vári); in TM.

BIOLOGY: Unknown.

Stigmella urbica (Meyrick) **comb.nov.**, text-fig. 27.

Nepticula urbica Meyrick, 1913. *Ann. Transv. Mus.* 4:326; Janse, 1948. *The Moths of South Africa* 4:177, pl. 86:1, 89:1, 91:5.

♂-GENITALIA (fig. 27): Vinculum with lateral arms short and widely separated making capsule wider than long; ventral plate bulging posteriorly; anterior extension short, excavated, so forming a pair of roughly triangular lobes. Tegumen comprising a narrow bar. Uncus with pair of ear-like lobes. Gnathos robust with horns curved; lateral processes triangular; anterior processes comprising short thin elements. Valve excavated, roughly triangular in ventral view. Transtilla: lateral arm broad terminating in a swelling; ventral arm absent; transverse bar formed by union of swellings of lateral arms. Juxta comprising a triangular plate the apex of which is continued for a short distance as a thin

process. Aedeagus $\frac{4}{5}$ length of genital capsule; vesica with two pairs of strong spines, one pair long the other short, and an arcuate thickening.

♀ Unknown.

REMARKS: The most characteristic feature of the ♂-genitalia of *urbica* is that the genital capsule is relatively wide compared with its length. The shapes of the transtilla and juxta resemble *perplexa*, but the anterior extension of the vinculum is much shorter and less deeply excavated in *urbica*. The spines on the vesica of the aedeagus of *urbica* are much larger than those of *perplexa*.

MATERIAL EXAMINED: ♂-Holotype, TM type no. 116; Meyrick's no. 4890; SOUTH AFRICA: Transvaal, Barberton, 26.i.1911 (Janse); genitalia slide no. 4028; in TM.

BIOLOGY: Unknown.

Stigmella androflavus spec.nov., text-fig. 28.

EXTERNAL CHARACTERS: ♂ (3,8–4,4mm). Head-tuft ochreous. Collar and eye-cap off-white. Antenna light purplish-grey. Thorax, abdomen and forewing greyish-brown with weak copper reflections. Hindwing with upper surface yellow. Legs off-white.

♀ Unknown.

♂-GENITALIA (fig. 28): Vinculum: ventral plate fairly short; anterior extension short, weakly excavated. Tegumen narrow, slightly swollen at ends. Uncus with sclerotized lateral elements that are produced into pair of papillae. Gnathos: lateral processes short, knob-like, arising near tips of horns; anterior processes very short and thin. Valve slightly arcuate, rather bulbous at base. Transtilla: lateral arm stout, expanding basally into triangular plate which is extended into long ventral arm; transverse bar formed by union of the triangular plates. Aedeagus $\frac{3}{5}$ length of genital capsule; vesica with arcuate, centrally placed thickening from which arises a pair of long, thin sclerites; cornuti absent.

REMARKS: *S. androflavus* is known only from the male. The species is characterized by the yellow hindwings. This is almost certainly a feature of the male only; it distinguishes that sex from males of the related *abachausi*. *S. androflavus* is also distinguished from the latter by the position of the lateral processes of the gnathos, the ventral arm of the transtilla, which is longer in *androflavus*, the absence of the tooth associated with the lateral arm of the transtilla, and by the shape of the valve.

MATERIAL EXAMINED: ♂-Holotype, SOUTH AFRICA: Transvaal, Pretoria, 17.xi.1948 (Vári); genitalia slide no. 5938; in TM; paratypes, data as holotype; 3♂♂ 16.ix.1949, 31.i.1951, 26.xi.1957 (Vári); in TM.

BIOLOGY: Unknown.

Stigmella abachausi (Janse) comb.nov., text-fig. 29.

Nepticula abachausi Janse, 1948. The Moths of South Africa 4:162 (*partim*), pl. 82:1, 88:14, 90:4, 92:1.

♂-GENITALIA (fig. 29): Vinculum: ventral plate narrow; anterior extension of medium length, weakly excavated. Tegumen swollen at both ends, narrow in middle. Uncus sclerotized apically and laterally, apical margin depressed. Gnathos: horns curved; lateral processes pointed; anterior processes absent; horizontal element thin. Valve arcuate, broad for $\frac{2}{3}$ of

its length then narrowing suddenly to tip. Transtilla with prominent, inwardly pointed 'tooth' arising from posterior part of lateral arm; lateral arm expanded basally into triangular plate; ventral arm short; transverse bar formed by union of triangular plates. Aedeagus $\frac{1}{2}$ to $\frac{3}{4}$ length of genital capsule. Vesica with large swollen spine and a pair of smaller ones posteriorly, and a centrally placed, arcuate thickening.

♀-GENITALIA: Of uncertain identity (see below).

REMARKS: The 'tooth' associated with the transtilla in the male is a characteristic feature of *abachausi*. Although related to *S. pallida*, *abachausi* is clearly distinguishable (see under *pallida* below).

In the original description Janse did not designate type material but stated '... 9♂♂ and 10♀♀, in collection Transvaal Museum...'. He labelled one male and one female 'Type' and eight others 'Cotype'. All these are syntypes according to the Code. I have found a further 11 specimens under Janse's *abachausi* label in the collection. These, together with the ten specimens bearing type labels, makes 21, two more than the number of specimens originally mentioned by Janse. The specimen labelled 'Cotype No. 2353' was not collected on a date given in the description. Another specimen, without hindwings or abdomen, is considerably darker than any of the other specimens. It was photographed by Janse (1948, pl. 92:1) and bears a handwritten label 'Ph'. Although this specimen does not bear a type label it clearly belongs to the type series. Apart from this specimen only those 10 specimens with type labels (seven males and three females) can be justifiably considered as syntypes. Of these, two of the males were incorrectly labelled as females by Janse. The genitalia show that the female syntypes appear to belong to two, or possibly three, species. Which, if any, actually represent *abachausi* (assuming *abachausi* to be the species of which the ♂-genitalia are figured by Janse) is not known.

The male labelled 'Type' is here designated lectotype. It is housed in the Transvaal Museum and bears the following label data: 'Abachaus S.W.A. [South West Africa] Jan. 1944, G. Hobohm'. '*Nepticula abachausi* Janse ♂ Type No. 2346.', 'G. [genitalia slide no.] 7247'. I consider the following paralectotypes either misidentified or of uncertain identity: SOUTH WEST AFRICA: Abachaus; 1♀ v.1943, ('Cotype' No. 2354); 1♀ ix.1945 ('Cotype' No. 2355); 1 ex. xi.1945; 1♀ x.1945 ('Type' no. 2347) (Hobohm); in TM.

MATERIAL EXAMINED: ♂-Lectotype (see above), in TM, paralectotypes, locality as lectotype; 1♂ xi.1943, 1♂ x.1945, 2♂♂ ix.1945, 1♂ xi.1945, 1♂ vi.1943 (Hobohm); type nos. 2346, 2348-2353; in TM. Additional specimens: SOUTH AFRICA: Transvaal, Kruger National Park, Satara, 1♂ 27.iii.1952 (Janse & Vári); Soutpansberg District, Kairo (Farm no. 212), 1♂ 22-27.iii.1978 (Kroon); in TM.

BIOLOGY: Unknown.

Stigmella pallida spec.nov., plate 15:3, text-fig. 30.

EXTERNAL CHARACTERS: ♂, ♀ (4.4-5.8mm). Head-tuft pale ochre. Collar and eye-cap off-white. Antenna grey. Thorax pale ochre. Abdomen grey. Forewing yellow to ochre. Hindwing greyish-brown. Legs grey and ochre.

♂-GENITALIA (fig. 30): Vinculum: ventral plate of medium length, deeply excavated so forming pair of lobes. Tegumen in form of a curved band. Uncus broad, rounded at apex, with pair of papillae. Gnathos approximately H-shaped; horns gently curved; anterior processes shorter than horns. Transtilla: ventral arm absent. Aedeagus approximately length of genital capsule, relatively wide; vesica with large patch of denticulate cornuti and a curved arcuate plate.

♀-GENITALIA: Description as *nigrata*.

REMARKS: The ♂- and ♀-genitalia of this species resemble those of *nigrata*. *S. pallida* is most easily distinguished from that species by the colour of the forewing which is yellow to ochre rather than very dark fuscous. In *pallida* the length/breadth ratio of the ♂-genitalia capsule is greater than that of *nigrata*, the anterior extension of the vinculum is more deeply excavated, the uncus is slightly wider and the gnathos has a different shape.

MATERIAL EXAMINED: ♂-Holotype, SOUTH AFRICA: Cape Province, Worcester, Fairy Glen, 15-19.x.1966 (Vári & Potgieter); genitalia slide no. 10208; in TM; paratypes, data as holotype, 2♂♂ (abdomen missing from one of these), 4♀♀ (abdomen missing from one of these); in TM.

BIOLOGY: Unknown.

Stigmella nigrata (Meyrick) **comb.nov.**, plate 15:4, text-figs. 31-33.

Nepticula nigrata Meyrick, 1913. *Ann. Transv. Mus.* 3:326; Janse, 1942. *The Moths of South Africa* 4:170 (*partim*), pl. 82:6, 86:6, 87:9, 89:6, 9, 92:2.

EXTERNAL CHARACTERS: ♂, ♀. (Additional remarks to Janse, 1942): Forewing of some specimens with weak, white postmedial maculae one on costa and one on posterior edge.

♂-GENITALIA (fig. 31): Vinculum: ventral plate narrow; lateral arms quite widely separated so making capsule rather wide; anterior extension short, weakly excavated. Tegumen comprising a broad, rounded band. Uncus rounded apically with pair of lateral, rod-like thickenings the apices of which are swollen and outwardly sinuate. Gnathos approximately U-shaped, horns gently curved; anterior processes absent. Valve deeply excised, approximately triangular in ventral view; back of valve arcuate. Transtilla fused with opposite member so forming a continuous, U-shaped band; ventral arm absent. Aedeagus approximately equal to length of genital capsule, wide; vesica with a large, irregular patch of denticulate cornuti and a curved, centrally placed thickening.

♀-GENITALIA (fig. 32): Apophyses: a small papilla arises from posterior edge of the segmental band that joins the anteriores. Accessory sac of ductus bursae covered with spicules. Corpus bursae heavily pectinate.

REMARKS: In the male the shiny black scales on the underside of the forewing and the upper and undersides of the hindwing distinguish *nigrata* from the closely related *pallida*.

Meyrick (1913:326) cites his material as follows: 'Waterval Onder (Janse); in November, one specimen'. This specimen is therefore the holotype. Janse (1948:170) stated that there is a 'type' from Abachaus South West Africa. He labelled it as female, type number 2379. However, it cannot be a type and it is, in any case, a male of *protosema* (see below) not a female of *nigrata*.

MATERIAL EXAMINED: ♂-Holotype, SOUTH AFRICA: Transvaal, Waterval Onder, 19.xi.1910 (Janse); in TM; genitalia slide no. 4027. Additional specimens. SOUTH AFRICA: Transvaal, Pretoria, Accession no. 3187, 12♂♂, 7♀♀ 23, 25.v., 8, 28.vi., 29, 31.viii., 4, 7, 8, 9.ix.1972 (Vári); Accession no. 96, 1♂, 1♀ 19, 11.i.1949 (Vári); Accession no. 815, 1♂ 22.vii.1953 (Vári); 1♂ 5.xi.1923 (Janse); 1♂ 13.xii.1966 (Vári); Pretoria North, 1♂ ix.1949 (van Son); 1♀ 9.ii.1954 (Vári); Barberton District, Nelshoogte Forestry, 1♂ 24–25.ii.1972 (Potgieter & Jones); Kruger National Park, Satara, 2♂♂, 1♀ 27.iii.1952 (Janse & Vári), 2♂♂ 6.v.1970 (Vári & Potgieter); Pretoriuskop, 1♂ 24–25.iv.1968 (Potgieter & Goode). Cape Province: Van der Kloof, P.K. le Roux Dam, 1♂ 19–25.x.1970 (Snyman & Jones). SOUTH WEST AFRICA: Abachaus, 2♂♂ iii.1943, 1♂ i.1944, 3♂♂ xi.1949 (Hobohm).

BIOLOGY: Food-plant: *Ziziphus mucronatus* Willd. (Rhamnaceae).

Mine (fig. 33): An upper surface linear blotch. Larva exits through upper epidermis of leaf.

Egg: laid on upper surface of leaf.

***Stigmella triumfettica* spec.nov., text-figs. 34–35.**

EXTERNAL CHARACTERS: ♂ (3,6mm). Head-tuft ochreous-brown. Eye-cap off-white. Collar grey-brown. Antenna grey-purple dorsally, pale below. Thorax, abdomen and forewing grey-brown with weak bronze and purple reflections. Hindwing grey. Legs pale ochre to off-white.

♀ Unknown.

♂-GENITALIA (fig. 34): Vinculum: ventral plate of medium width; anterior extension rather deeply excavated so forming pair of large lobes. Tegumen narrow in middle, swollen at ends. Uncus with apical margin slightly depressed. Gnathos robust; horns curved; lateral and anterior processes short; horizontal element stout. Valve swollen at base, gradually narrowing towards tip. Transtilla: ventral arm long. Aedeagus $\frac{1}{2}$ length of genital capsule; vesica with three long spines appearing to arise from centrally placed, ring-shaped thickening, and a pair of arcuate, toothed plates.

REMARKS: The uncus, gnathos and valve of this species are rather generalized. The strong spines and the ring-shaped thickening on the vesica of the aedeagus are characteristic.

MATERIAL EXAMINED: ♂-Holotype, SOUTH AFRICA: Transvaal, Pretoria District, Derdepoort, Accession no. 2049, 21.iv.1958 (Vári); genitalia slide no. 9926; in TM.

BIOLOGY: Food-plant: *Triumfetta* species (Tiliaceae).

Mine (fig. 35): An upper surface linear tract. Frass deposited as a compact, central line in early part of mine, later breaking up into zig-zag arcs.

Egg: laid on upper surface of leaf.

***Stigmella dombeyivora* spec.nov., text-figs. 36–38.**

EXTERNAL CHARACTERS: ♂, ♀ (4,2–4,8mm). Head-tuft ochreous. Collar and eye-cap off-white. Antenna dark purplish-grey. Thorax, abdomen and forewing dark purplish-grey with bronze and purple reflections. Hindwing pale greyish-brown. Hindleg purplish-grey, tarsi pale.

♂-GENITALIA (fig. 36): Vinculum: ventral plate short; lateral arms long, making capsule elongate; anterior extension very long, not excavated. Tegumen narrow in middle, swollen at ends. Uncus with corners extended as papillae. Gnathos U-shaped; horns long and straight; lateral processes short and stout; anterior processes very small. Valve approximately triangular, divided into pair of small projections apically. Transtilla fairly stout; lateral arm terminating in approximately triangular swelling; transverse bar formed by union of one corner of each of these swelling. Aedeagus approximately $\frac{2}{3}$ length of genital capsule, narrow for anterior $\frac{2}{3}$ then widening; vesica with pair of strong spines arising from a triangular thickening with a further pair of large spines, and single shorter ones, at apex.

♀-GENITALIA (fig. 37): Genital opening flanked by a pair of weakly sclerotized plates. Corpus bursae unmarked.

REMARKS: The shape of the anterior extension of the vinculum, the gnathos and the aedeagus are characteristic of this species. The presence of large spines on the vesica of the aedeagus resemble those of *triumfettica* only superficially.

MATERIAL EXAMINED: ♂-Holotype, RHODESIA: Umtali, Accession no. 1912, 7.v.1956 (Vári); genitalia slide no. 10094; in TM; paratypes, data as holotype, 3♂♂, 2♀♀ 7, 9.v.1956 (Vári); in TM.

BIOLOGY: Food-plant: *Dombeya* species (Sterculiaceae).

Mine (fig. 38): An upper surface tract. Frass deposited as a narrow line throughout. Larva exits through upper epidermis of leaf.

Egg: laid on upper surface of leaf.

Stigmella ampullata spec.nov., text-fig. 39.

EXTERNAL CHARACTERS: ♂ (3,8mm). Head-tuft ochreous. Collar and eye-cap off-white. Antenna dark grey-purple. Thorax and abdomen dark grey-brown. Forewing dark grey-brown with bronze reflections and a white, postmedial fascia which has shining silver reflections. Hindwing pale grey-brown. Legs grey and buff.

♀ Unknown.

♂-GENITALIA (fig. 39): Vinculum with ventral plate of medium length; anterior extension deeply excised so forming a pair of spine-like processes. Tegumen (?) comprising a large weakly sclerotized plate with pair of associated flask-shaped pouches. Uncus wide at base, narrowing gradually, truncated; lateral margins sclerotized. Gnathos: horns straight and short, lateral processes large. Valve wide at base, narrowing suddenly about half way to apex; apex divided into two small points. Transtilla with lateral arm expanded into approximately triangular plate; ventral arm fairly long; transverse bar formed by union of triangular plates. Aedeagus approximately $\frac{3}{4}$ length of genital capsule; vesica with large, ill-defined scattering of cornuti, and a centrally placed thickening.

REMARKS: The species is known from a single male specimen. The shape of the gnathos and the presence of flask-shaped pouches are diagnostic of *ampullata*.

MATERIAL EXAMINED: ♂-Holotype, SOUTH AFRICA: Transvaal, Kruger National Park, Punda Milia, 6-15.v.1975 (Potgieter & Scoble);

genitalia slide no. 9912; in TM.

BIOLOGY: Unknown.

Stigmella pretoriata spec.nov., text-fig. 40.

EXTERNAL CHARACTERS: ♂ (5,4mm). Head-tuft cream. Collar and eye-cap off-white. Antenna pale grey. Thorax, abdomen and forewing grey-brown with weak bronze and purple reflections. Hindwing pale grey with some brownish scales. Legs pale grey-brown.

♀ Unknown.

♂-GENITALIA (fig. 40): Vinculum with ventral plate of medium length; anterior extension deeply excavated so forming pair of large, pointed processes. Tegumen in form of a thin bar, not curved. Uncus bipapillate. Gnathos roughly H-shaped, horns slightly longer than anterior processes; lateral processes short. Valve curved gently for most of length, more strongly curved apically; apex with small characteristic knob. Transtilla: lateral arm broad; ventral arm short; transverse bar short. Juxta (?) roughly in shape of a parallelogram. Aedeagus $\frac{1}{2}$ length of genital capsule; vesica with pair of short spines posteriorly and a centrally placed thickening.

REMARKS: This species, known from a single male, may be recognized by the unusual shape of the uncus and the wide lateral arm of the transtilla. The aedeagus, relative to the size of the genital capsule, is small compared with other *Stigmella* species.

MATERIAL EXAMINED: ♂-Holotype, SOUTH AFRICA: Transvaal, Pretoria, 15.ix.1945 (Janse); genitalia slide no. 10129; in TM.

BIOLOGY: Unknown.

Stigmella protosema (Meyrick), **comb.nov.**, text-fig. 41.

Nepticula protosema Meyrick, 1921. *Ann. Transv. Mus.* 8:140; Janse, 1948. The Moths of South Africa 4:175, pl. 83:3, 87:10-11, 92:4.

♂-GENITALIA (fig. 41): Vinculum: ventral plate very large, posterior margin bulging slightly posteriorly; anterior extension excavated so forming a pair of lobes. Tegumen narrow. Uncus with pair of large, sclerotized lateral elements. Gnathos: horns fairly short. Valve excavated; back of each produced inwardly and fused to its opposite member to form a large, roughly triangular process, the apex of which is bifurcate. Transtilla: ventral arm long; transverse bar widely separating valves. Aedeagus just less than length of genital capsule; vesica with four large, finger-like processes and a centrally placed, arcuate thickening.

♀-GENITALIA: Of uncertain identity, see below.

REMARKS: The most notable feature of *protosema* is the large, roughly triangular process associated with the valves. The uncus, the large ventral plate of the vinculum, and the finger-like processes of the vesica of the aedeagus are also characteristic.

The holotype is in a poor condition. Nevertheless, the white macula on the costal edge of the forewing, referred to by both Meyrick and Janse, is clearly visible. Some of the other specimens that I have identified as belonging to *protosema* do not have such a patch and so this character cannot be considered to be diagnostic of the species. The genitalia of

female specimens I suspect of belonging to this species have a papilla associated with the apophyses. However, this is also a feature of *nigrata* (see above), and thus the identity of the female of *protosema* remains obscure.

MATERIAL EXAMINED: ♂-Holotype, SOUTH AFRICA: Pretoria North, 12.iv.1917 (Swierstra), type no. 2396; genitalia slide no. 4954; in TM. Additional specimens: SOUTH WEST AFRICA: Abachaus, 3♂♂ iii, v, viii.1943 (Hobohm); Abachaus, 1♂, paralectotype of *abachausi*, xi.1945 (Hobohm). SOUTH AFRICA: Transvaal, Kruger National Park, Lower Sabi, 1♂ 26.iii.1952 (Janse & Vári); Satara, 3♂♂ 6.v.1970 (Vári & Potgieter); Skukuza, 2♂♂ 7.v.1970 (Vári & Potgieter); Potgietersrus District, Limburg, 1♂ 12.xii.1963 (Vári). Cape Province, Heidelberg District, Grootvaderbos, 1♂ 4-6.xi.1966 (Vári & Potgieter). RHODESIA: Lundi, 1♂ 2-5.iii.1964 (Vári & van Son); in TM.

BIOLOGY: Unknown.

Stigmella porphyreuta (Meyrick) **comb.nov.**, text-fig. 42.

Nepticula porphyreuta Meyrick, 1917. *Ann.S.Afr.Mus.* 17:13; Janse, 1948. The Moths of South Africa 4:173, pl. 88:17 and 90:9 (♂-genitalia of lectotype).

Meyrick's two type specimens were deposited in the South African Museum, Cape Town. According to Janse (1948) they were mounted on the same block of pith. One of these specimens got severely damaged by pests. Janse prepared a slide of the genitalia of the other specimen (a male) which he figured and provided a photograph. Mr Prins of the South African Museum sent me this slide and informed me that the rest of the specimen had been destroyed by museum beetle. Thus the only existing material of *porphyreuta* is the genitalia slide prepared by Janse. As the specimen is clearly that figured by Janse (1948), who stated that it was one of Meyrick's original specimens, it is here designated as lectotype. The genitalia are mounted on a microscope slide labelled '*Nepticula porphyreuta* Meyr. Type, S.A. Museum'. Although this is the only material of the species known to me it is clear that *porphyreuta* is a valid species.

Unfortunately I received the specimen too late to incorporate the information in the key and in the body of the manuscript, so these details are given here.

♂-GENITALIA (fig. 42): Vinculum: ventral plate of medium length, slightly bulging posteriorly; anterior extension excavated so forming a pair of large lobes. Tegumen narrow. Uncus bipapillate. Gnathos relatively small; horns fairly short, horizontal element weak. Valve triangular, less than half length of genital capsule. Transtilla: lateral arms extending into triangular processes; transverse bar formed by union of triangular process of each transtilla. Aedeagus approximately $\frac{1}{2}$ length of genital capsule; vesica with eight stout cornuti and a pair of larger tooth-like sclerotizations posteriorly.

REMARKS: *S. porphyreuta* may be distinguished from the other species in the *fluida*-group by the characteristic sclerotizations at the anterior end of the aedeagus and the relatively small gnathos. The uncus resembles *charistis* and its relatives but *porphyreuta* differs from these species in having relatively small valves. Meyrick notes that there is a silvery-white

fascia on the forewing in the specimens. This further distinguishes *porphyreuta* from all the species in this paper except for *celtifoliella* and *ampullata*.

The *INGENS*-group

In the male of the species of the *ingens*-group, the gnathos has a single, central element instead of paired horns (compare e.g. fig. 43 with fig. 2). This character distinguishes the species from those of the *fluida*-group. The antenna extends to beyond half the length of the forewing.

Stigmella confinalis spec.nov., plate 15:5, text-figs. 43–45.

EXTERNAL CHARACTERS: ♂, ♀ (5.4–6.0mm). Tuft on front of head mainly red-brown with some off-white hairs; tuft on vertex off-white. Collar off-white. Eye-cap off-white, irrorated with purplish scales particularly posteriorly. Antenna grey. Thorax and abdomen grey. Forewing: upperside off-white, heavily irrorated with fuscous; underside with base of fringe yellow. Hindwing light grey. Legs off-white with dark patches.

♂-GENITALIA (fig. 43): Vinculum: ventral plate large bulging posteriorly; anterior extension bilobed. Tegumen curved, fairly wide. Uncus large, bipapillate. Gnathos comprising single, large, tongue-shaped medial projection with pair of shorter lateral processes. Valve narrow throughout length. Transtilla: lateral arm fairly stout; ventral arm short; transverse bar narrow. Aedeagus approximately $1\frac{1}{4}$ times length of genital capsule; vesica with longitudinally running band of spine-like cornuti in posterior half.

♀-GENITALIA (fig. 44): Anal papillae attenuated to form ovipositor. Apophyses: long and without basal plates; anteriores extending beyond posteriores posteriorly and total length greater than that of posteriores, anteriores slightly thicker. Accessory sac of ductus bursae very large, covered with spicules. Corpus bursae lightly pectinate.

REMARKS: *S. confinalis* is closely related to *greviae*, but is distinguished from it by the stouter gnathos in the male, and the weaker spines on the accessory sac in the female. The forewing is more heavily irrorated in *confinalis* than in *greviae*.

The apophyses of the ♀-genitalia of this species, and those of the next, are attenuated to form a short, pointed ovipositor reminiscent of that of *S. rhynchosiella*; Vári (1955:339) suggested that the shape of the ovipositor in the latter is an adaptation to laying eggs on the epidermis of the hirsute leaves of its food-plant.

MATERIAL EXAMINED: ♂-Holotype, RHODESIA: Beit Bridge, Accession no. 1940, 13.v.1956 (Vári); genitalia slide no. 10098; in TM; paratypes, data as holotype; 1♂ 10.v.1956, 1♂ 2♀♀ 12.v.1956, 1♀ 13.v.1956, 1♀ 16.v.1956 (Vári). SOUTH AFRICA: Transvaal, Kruger National Park, Lower Sabi, 1♂ 26.iii.1952 (Janse & Vári); in TM.

BIOLOGY: Food-plant: *Dombeya* species (Sterculiaceae).

Mine (fig. 45): As *greviae* except that frass is always spread around base of blotch. Sometimes the linear part of the mine is not visible.

Egg: laid on lower surface of leaf. Pale and conical; not dark and elliptical which is usual in the Nepticulidae.

Stigmella grewiae spec.nov., text-figs. 46–48.

EXTERNAL CHARACTERS: ♂, ♀ (4,4–4,6mm). Tuft on front of head orange-ochreous; tuft on vertex ochreous tinged with red-brown. Eye-cap off-white with a few fuscous scales in the case of two males. Collar off-white. Antenna, thorax and abdomen dark grey. Forewing ochreous, irrorated with greyish-purple scales that tend to be concentrated apically. Hindwing lead grey. Legs off-white with dark grey patches.

♂-GENITALIA (fig. 46) and ♀-GENITALIA (fig. 47): Descriptions as for *confinalis* except for certain diagnostic features (see Remarks, below).

REMARKS: This species is closely related to *confinalis*. In the male the tegumen is rounded posteriorly and not straight as in *confinalis*. In *grewiae* the papillae on the uncus are closer together and the central element of the gnathos is much thinner. In the female the spines of the long accessory sac associated with the ductus bursae are larger than they are in *confinalis*.

MATERIAL EXAMINED: ♂-Holotype, SOUTH AFRICA: Natal, Balgowan, Yellowwoods, Accession no. 2746, 22.i.1965 (Vári); genitalia slide no. 9894; in TM; paratypes, data as holotype, 1♂ 22.i.1965, 3♀♀ 20.i.1965 (Vári). Cape Province, Langebos, Alexandria, Accession no. 1429, 1♂ 15.xii.1954 (Vári); in TM.

BIOLOGY: Food-plant: *Grewia occidentalis* L. (Tiliaceae).

Mine (fig. 48): A linear-blotch. The frass is not always deposited around the base of the blotch as in *confinalis*, but extends into it.

Egg: laid on lower surface of the leaf.

Stigmella ingens (Meyrick) comb.nov., text-fig. 49.

Nepticula ingens Meyrick, 1913. *Ann.Transp.Mus.* 3:327; Janse, 1948. The Moths of South Africa 4:167, pl. 83:8, 85:1–6, 86:3, 89:3, 93:5.

♂-GENITALIA (fig. 49): Vinculum: ventral plate large; lateral arms long and close together making genital capsule long and narrow in appearance; anterior extension long, excavated, so forming a pair of lobes. Tegumen in form of curved band. Uncus rounded, sclerotized apically and laterally, with pair of ear-like lobes. Gnathos: deeply excised at base. Valve relatively broad. Transtilla robust, lateral arm long; ventral arm virtually absent. Aedeagus approximately $\frac{4}{5}$ length of genital capsule; vesica with pair of small spines, a patch of cornuti and a small curved thickening.

♀-GENITALIA: No females have been examined by me.

REMARKS: The long anterior extension of the vinculum, the base of the gnathos and the shape of the uncus distinguish *ingens* from the other species in the *ingens*-group. The moth is exceptionally large for a nepticulid.

Although Meyrick referred to only three specimens in his original description there are apparently five specimens of *ingens* in existence with label data corresponding to Meyrick's original citation. Three of these are in the TM and Dr Sattler informs me that there are two in the BMNH. One of the males housed in the TM, which also bears one of Meyrick's identification-number labels, is here designated as lectotype. It bears the following label data: 'Donkerhoek, 9.10.1910, A.J.T. Janse, *Nepticula ingens* M. Type No. 122'. Meyrick's identification no. '4843'. Meyrick's handwritten label adds '*N. ingens* 4843'; genitalia slide no. 7243. The two specimens in the BMNH are the paralectotypes.

MATERIAL EXAMINED: ♂-Lectotype, SOUTH AFRICA: Transvaal, Donkerhoek; in TM, for details see above. Additional specimens: Data as lectotype, 2♂♂ (Janse); in TM.

BIOLOGY: Unknown.

Stigmella angustivalva spec.nov., text-fig. 50.

EXTERNAL CHARACTERS: ♂ (5,8mm). Head-tuft ochreous tinged with red-brown. Collar and eye-cap off-white. Antenna purplish. Thorax, abdomen and forewing pale ochreous irrorated with a few purplish-brown scales. Hindwing light grey. Legs pale ochreous; tarsi mixed with grey.

♀ Unknown.

♂-GENITALIA (fig. 50): Vinculum: ventral plate fairly large; anterior extension short, weakly excavated so forming a pair of lobes. Tegumen large, comprising broad band, extending laterally beyond lateral arms of vinculum. Uncus rounded, with small notch apically. Gnathos: central projection long and thin. Valve long and very narrow. Transtilla: ventral arm long. Aedeagus large, approximately same length of genital capsule; vesica with pair of large curved horns apically, four others nearer middle and a large curved thickening.

REMARKS: The very narrow valve, the long, thin central process of the gnathos and the markings on the aedeagus distinguish this species from the others in the *ingens*-group.

MATERIAL EXAMINED: ♂-Holotype, SOUTH AFRICA: Cape Province, van der Kloof, P.K. le Roux Dam, 19-25.x.1970 (Snyman & Jones); genitalia slide no. 10147; in TM.

BIOLOGY: Unknown.

Stigmella letabensis spec.nov., text-fig. 51.

EXTERNAL CHARACTERS: ♂ (4,5mm). Head-tuft ochreous tinged with red-brown. Collar and eye-cap off-white. Antennae, thorax, abdomen and forewing pale ochreous. Underside of forewing pale brown. Hindwing pale brown-grey. Legs very pale ochreous.

♀ Unknown.

♂-GENITALIA (fig. 51): Vinculum: ventral plate of medium length; lateral arms widely separated so capsule, at widest part, is as wide as long; anterior extension short, weakly excavated so forming pair of small rather rounded lobes. Tegumen comprising a fairly broad band. Uncus weakly bilobed, lateral and apical margins sclerotized. Gnathos: central projection narrowing rapidly from triangular base to form finger-like projection. Valve large, base forming 45° angle with posterior margin of ventral plate of vinculum. Transtilla approximately U-shaped; ventral arm absent. Juxta W-shaped, heavily sclerotized. Aedeagus approximately $\frac{3}{4}$ length of genital capsule; vesica with arcuate thickening.

REMARKS: The shape of the valve and the juxta, together with the small length/width ratio of the capsule distinguish *letabensis* from the other species in the *ingens*-group. The U-shaped transtilla is also characteristic.

MATERIAL EXAMINED: ♂-Holotype, SOUTH AFRICA: Transvaal, Kruger National Park, Letaba Camp, 28.iii.1952 (Janse & Vári); genitalia slide no. 10146; in TM.

BIOLOGY: Unknown.

ACKNOWLEDGEMENTS

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APPENDIX 1: Taxonomic characters

EXTERNAL CHARACTERS: They are mostly based upon colour, which is virtually valueless for indicating relationships between species. Closely related species are frequently quite differently coloured and marked whilst unrelated species, even in different genera, may be similar.

HEAD-TUFT: The description refers to the tuft on the front of the head and the vertex.

COLLAR: Colour.

EYE-CAP: Colour.

ANTENNA: Besides colour, a further character used is whether the antenna extends beyond, below, or to half the length of the forewing. Antenna length varies between members of the same species, and frequently the tips of the antennae are broken off: consequently the exact length cannot be measured. For these reasons, the taxonomic value of this character is limited. It is referred to in the diagnoses of the species groups.

THORAX: Colour.

ABDOMEN: The description refers to the upperside unless otherwise stated. The underside is pale medially.

FOREWING: The description refers to the upperside unless otherwise stated.

HINDWING: The description refers to the upperside unless otherwise stated.

LEGS: Colour.

♂-GENITALIA: They are by far the most important structures for determination of relationships of the various species, and for their diagnoses; this also applies to genera. The complex of characters available from the genitalia is the major one by which the family has been classified in the holarctic; the present work is no exception.

Workers on the Nepticulidae have generally followed Beirne (1945) in their terminology. Although it is unlikely that all the terms used by Beirne are homologous with those similarly named in the Ditrisia (see e.g. Klots *in* Tuxen, 1970), for practical purposes many of Beirne's original terms are used in the present paper to describe the ♂-genitalia. These terms will be readily understood by other workers on the family. In addition some further terms have been proposed in this paper in order to shorten otherwise lengthy descriptions of certain characters.

VINCULUM: This is a large structure comprising *lateral arms*, a *ventral plate* and an *anterior extension* (see fig. 5). The posterior edge of the ventral plate is regarded as being slightly depressed anteriorly unless it is stated as bulging posteriorly. The anterior extension is usually excavated to a greater or lesser degree, so forming a pair of lobes.

SACCUS: The 'saccus' *sensu* Beirne (1945) does not appear to be the true saccus i.e. an invagination of the vinculum. The term is avoided in the present paper.

TEGUMEN: In *Stigmella* this structure articulates with the caudal end of the lateral arms of the vinculum. In most genera with a 'ring-shaped'

vinculum (see Beirne, 1945) the tegumen is extended caudad to form a pseuduncus.

UNCUS: In genera with a ring-shaped vinculum, and a pseuduncus, the true uncus may be absent (membranous according to Beirne) or in the form of a characteristic, inverted V-shaped structure e.g. *combretella*, see Vári (1955).

GNATHOS: It is represented by two main types in the Nepticulidae. In one case (see fig. 2) there are paired *horns* projecting posteriorly from which usually arise smaller *lateral processes* further up the horns. The base (*horizontal element*) varies in size and there is usually a pair of *anterior processes*, extending below the base, of variable length. In the other type there is a single, undivided process and a pair of shorter, arcuate lateral elements. This second type of gnathos is widespread in the family: it is characteristic of most genera. Although the first type is usual in *Stigmella* the second form is also represented in a few species. I consider the gnathos with the single central element to be primitive (plesiomorphic) to the derived (apomorphic) one with the paired horns.

VALVE: The descriptions are based on the ventral aspect. The valves have not been bent back to reveal their inner surfaces, which is the conventional method of display in most other Lepidoptera; such a process is prevented, in nepticulids, because the transtilla usually joins the valves tightly so that bending them back leads to distortion of the genital capsule. By differential focusing of the microscope the 'back' (dorsal aspect) of the valves can be distinguished from the ventral aspect. In lateral aspect the rounded, shell-like nature of the structures can be seen. Often the apex of the valves is excised, sometimes forming an irregular division into what Beirne called a rounded 'cuiller' and a pointed 'style'. In other species there is no such division. The terms cuiller and style are not used in the present work although many authors have followed Beirne. According to Klots 'style' was first applied to the valves of the Hesperidae by Rambur in 1837. It is unlikely that such a structure is homologous with the style (*sensu* Beirne) in the Nepticulidae. To use this term might imply a similarity to a term with a different meaning in the Ditrisia.

TRANSTILLA: The transtillae generally join the base of the valves tightly. Often, the three elements that comprise each transtilla, namely the *transverse bar* and the *lateral* and *ventral arms*, together form a roughly triangular structure that fuses with its opposite member e.g. fig. 7.

JUNTA: It is unlikely that this is homologous with the structure of that name in the Ditrisia.

AEDEAGUS: Relative size and markings on vesica.

♀-GENITALIA: They provide generic characters in the Nepticulidae, and to a certain extent, specific ones. The most useful characters are the sclerotizations of the ductus bursae and the corpus bursae.

APOPHYSES: The *posterior apophyses* (*posteriores*) are those that extend furthest posteriorly. They are the pair situated in the middle when the genitalia are viewed ventrally, and are nearly always longer and thinner than the *anteriores*. Unless otherwise stated the *posteriores* may be assumed to be longer than the *anteriores*. For a discussion of these, and other structures of the ♀-genitalia, see Mutuura (1972).

DUCTUS BURSAE: Usually has a membranous accessory sac which is often

difficult to see. The ductus merges imperceptibly with the corpus bursae. In some species of *Stigmella*, and particularly in other nepticulid genera, the ductus has various associated sclerotizations.

CORPUS BURSÆ: In *Stigmella* this may be pectinate, and the pectinations may be concentrated into a band, or pair of bands, or oval patches. In some species from the holarctic there is a concentration of heavily sclerotized spines.

MINES: Characters from the mines are of particular value in identification. The behaviour of the larva is manifest in the shape of mine it produces. The surface on which the egg is laid and the surface of the leaf from which the larva emerges are generally invariable for each species.

MINE PATTERN: Tract or blotch or a combination of the two.

FRASS: Nature of deposition of grains.

EGG: Whether laid on the upper or lower surface of the leaf.

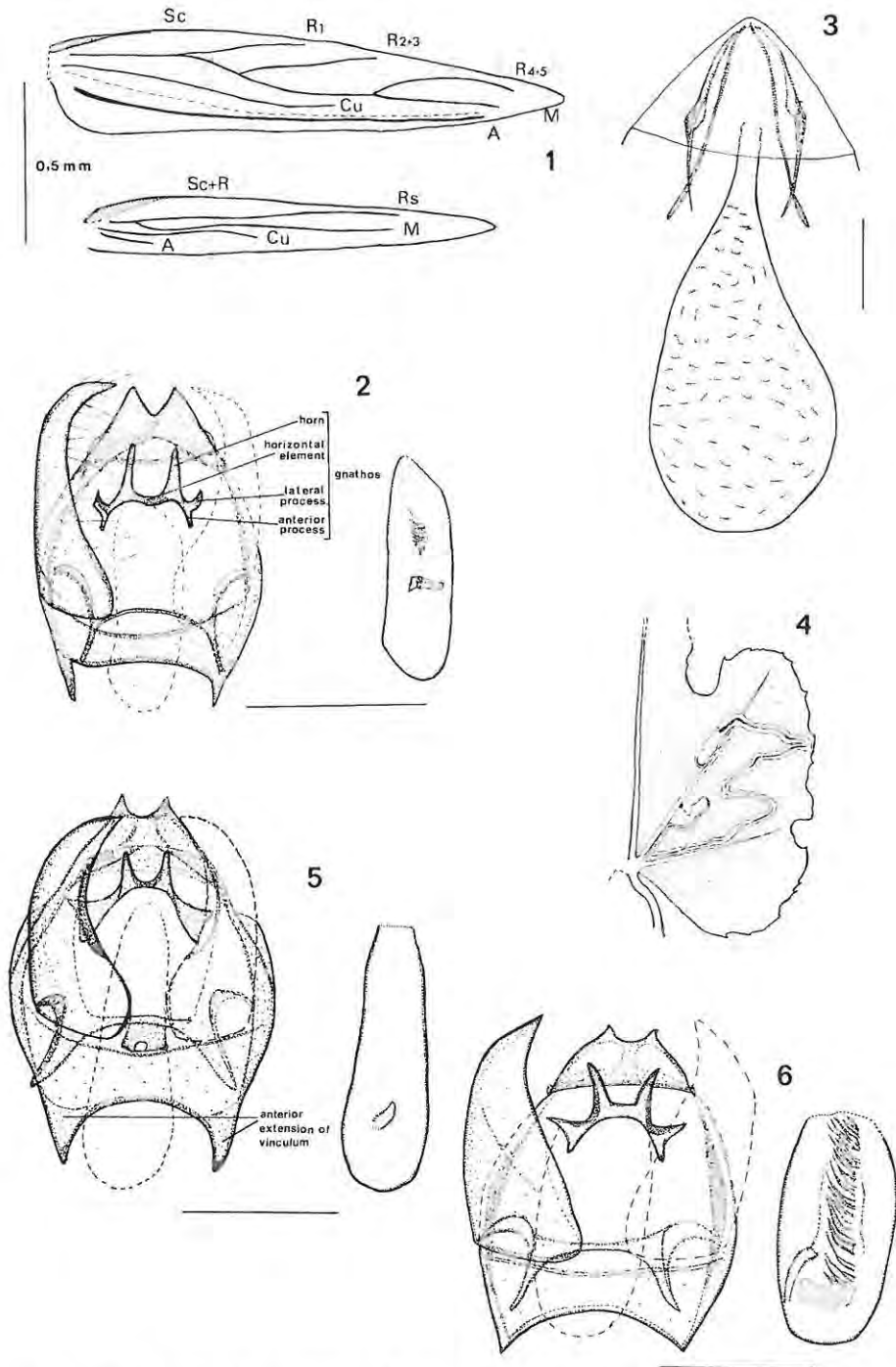
LARVA: The surface of the leaf from which it leaves the mine.

Amongst the Nepticulidae are found bark, fruit and leaf-petiole miners in addition to leaf-miners. As yet, no species have actually been reared from these other sources in Southern Africa.

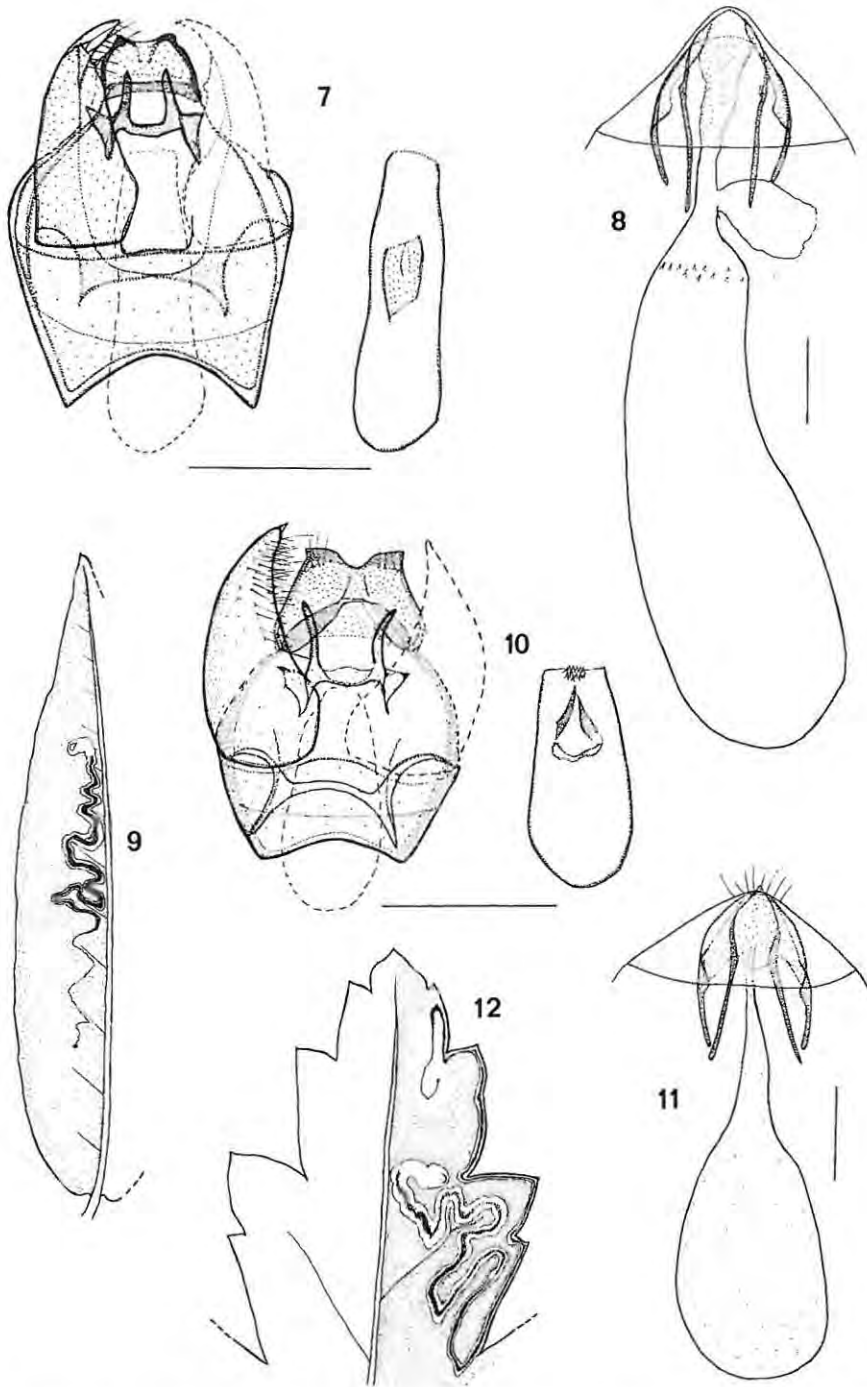
WING-VENATION: The venation of the forewing in particular is a major source of characters for defining genera.

TABLE 1: Food-plants of *Stigmella* species.

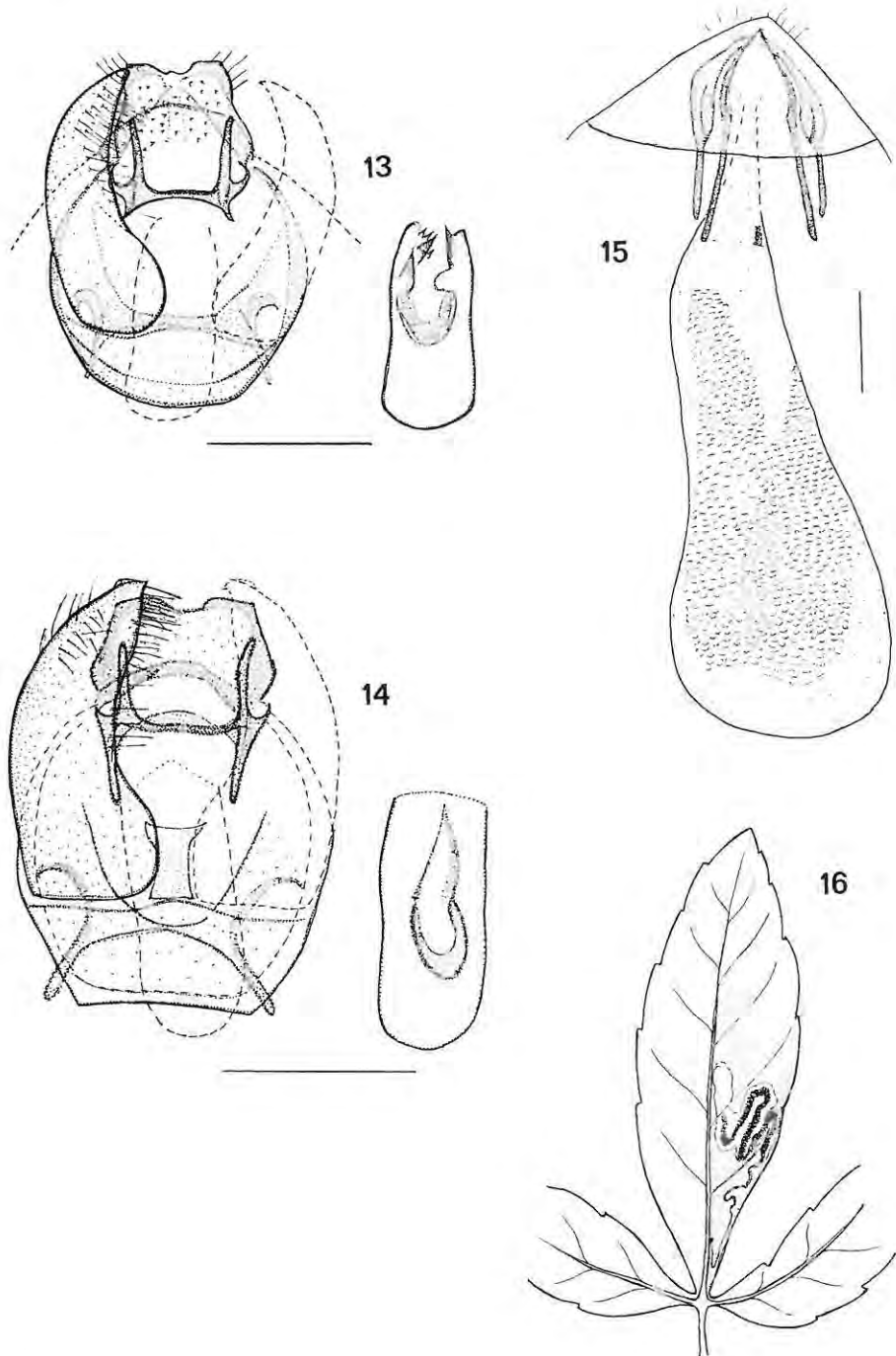
<i>Abutilon grantii</i>	<i>S. abutilonica</i>
<i>Allophylus natalensis</i>	<i>S. allophylica</i>
<i>Celtis africana</i>	<i>S. celtisfoliella</i>
<i>Croton gratissimus</i> var. <i>subgratissimus</i>	<i>S. varii</i>
" <i>sylvaticus</i>	<i>S. crotonica</i>
<i>Dombeya</i> species	<i>S. dombeyivora</i>
" species	<i>S. confinis</i>
<i>Ficus</i> spp.	<i>S. platyzona</i>
" <i>burttdavyi</i>	<i>S. platyzona</i>
<i>Geranium</i> cf. <i>pulchrum</i>	<i>S. geranica</i>
<i>Grewia occidentalis</i>	<i>S. charistis</i> , <i>S. grewiae</i>
<i>Parinari capense</i>	<i>S. parinarella</i>
<i>Rhus</i> species	<i>S. generalis</i>
<i>Rhynchosia nitens</i>	<i>S. rhynchosiella</i>
<i>Tragia durbanensis</i>	<i>S. tragilis</i>
<i>Triumfetta</i> species	<i>S. triumfettica</i>
<i>Ziziphus mucronatus</i>	<i>S. nigrata</i>



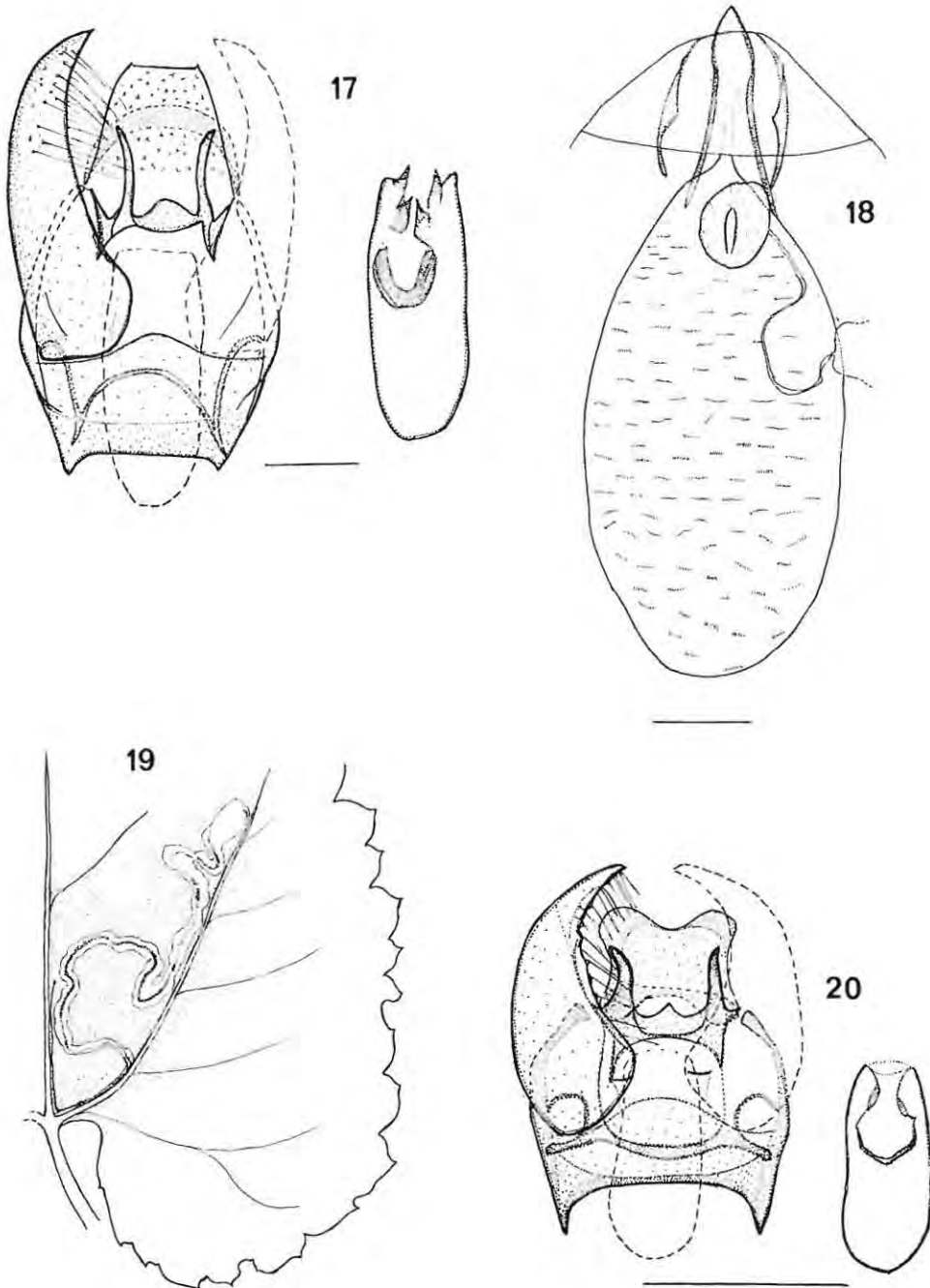
FIGS. 1. *Stigmella*, wing-venation of genus. 2-4. *S. abutilonica* spec. nov. 2. ♂-genitalia. 3. ♀-genitalia. 4. Leaf-mine. 5. *S. finida* (Meyrick), ♂-genitalia. 6. *S. irrorata* (Janse), ♂-genitalia. Scale-lines all 0,1mm unless otherwise indicated.



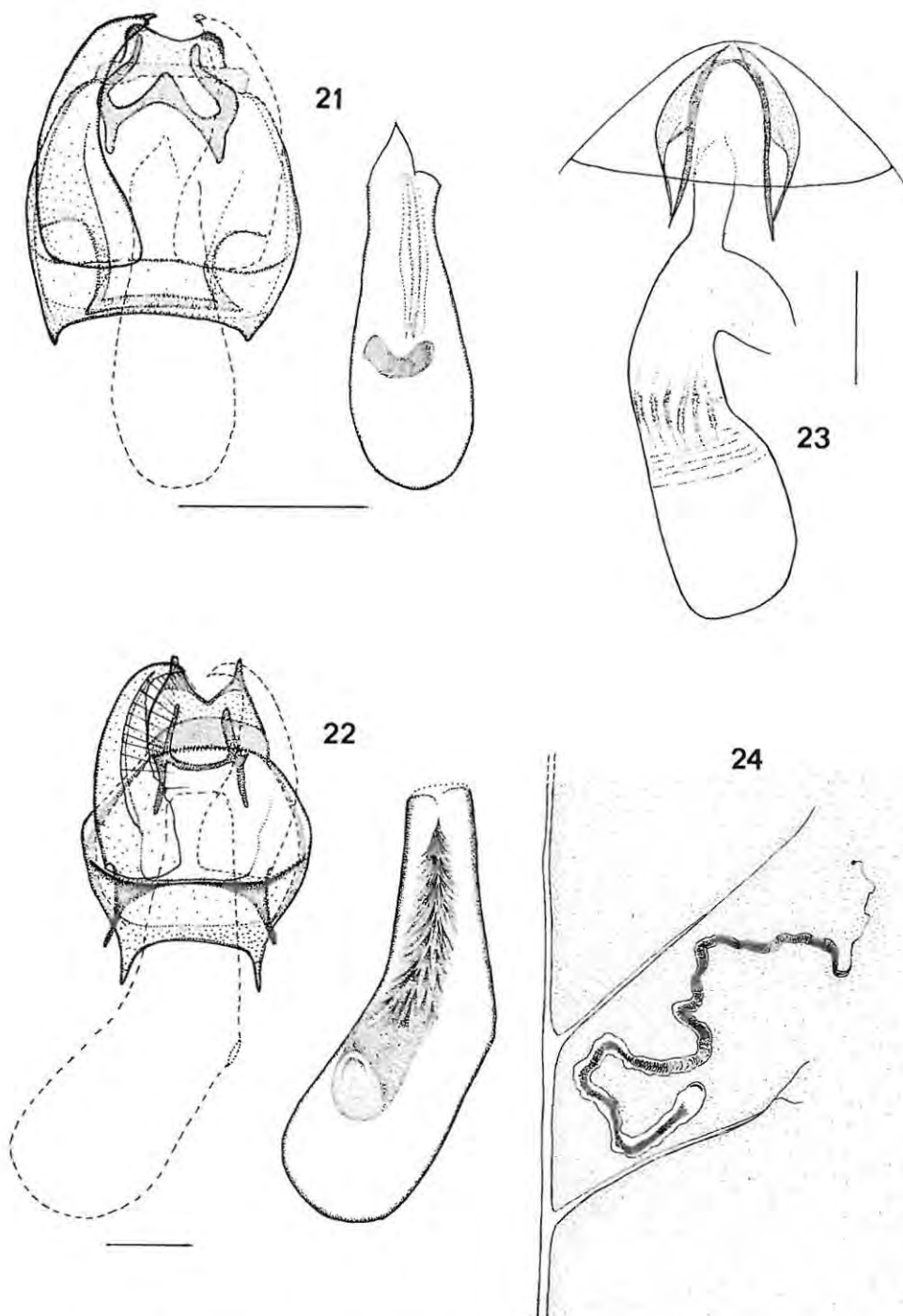
FIGS. 7-9. *S. variii* spec. nov. 7. ♂-genitalia. 8. ♀-genitalia. 9. Leaf-mine. 10-12. *S. geranica* spec. nov. 10. ♂-genitalia. 11. ♀-genitalia. 12. Leaf-mine. Scale-lines all 0,1mm.



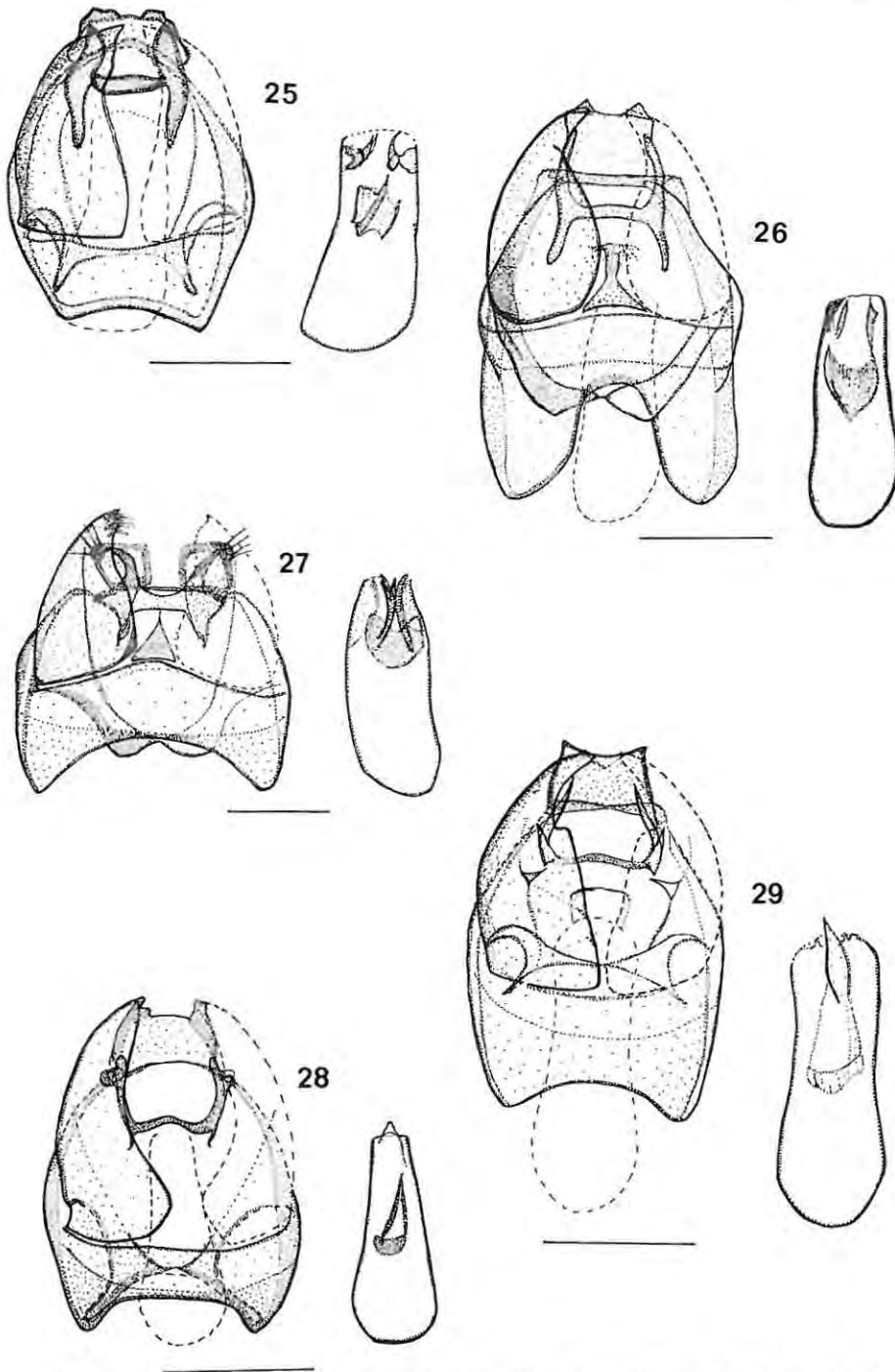
FIGS. 13. *S. satarensis* spec. nov., ♂-genitalia. 14–16. *S. allophylica* spec. nov. 14. ♂-genitalia. 15. ♀-genitalia. 16. Leaf-mine. Scale-lines all 0,1mm.



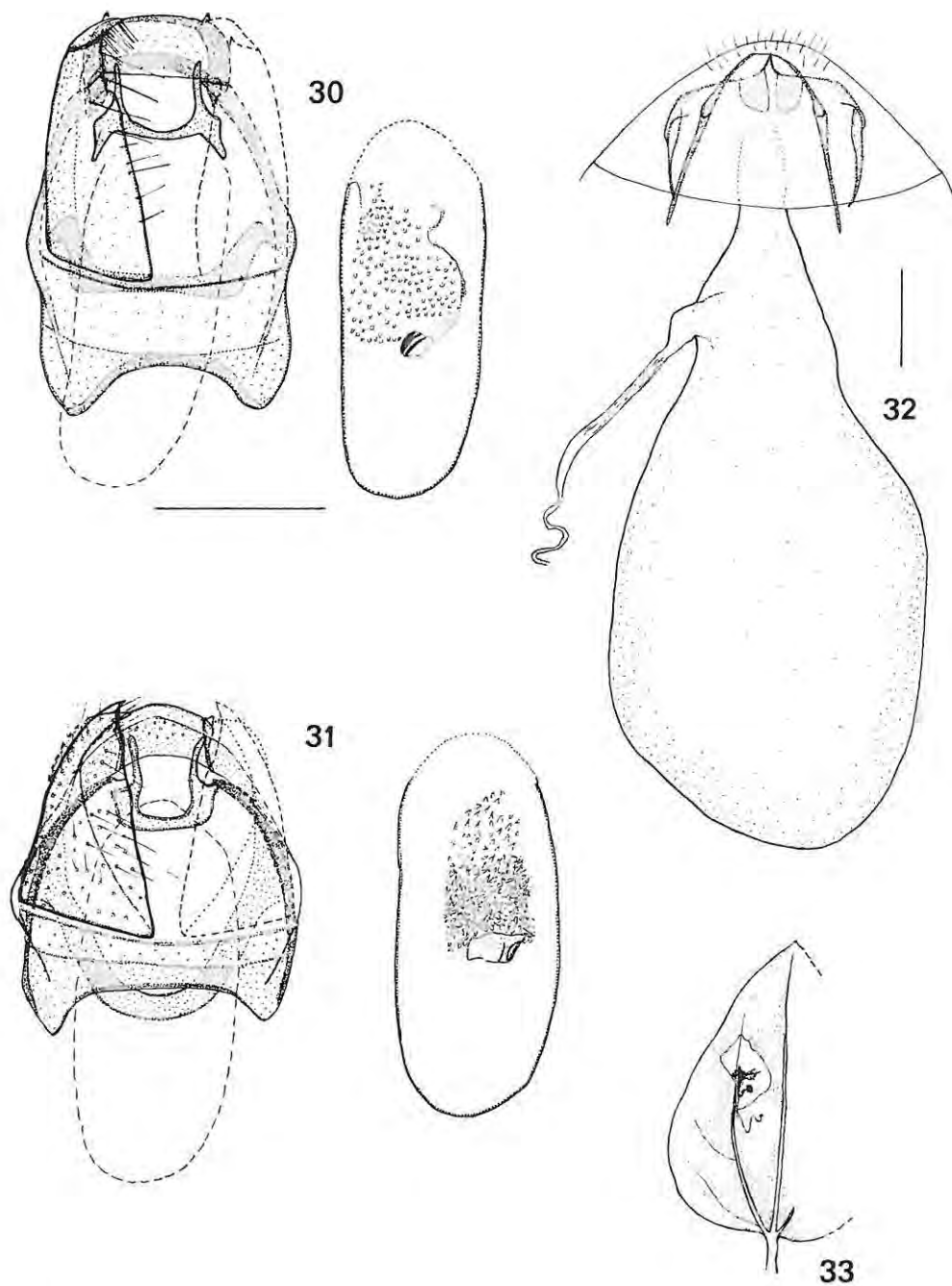
FIGS. 17-19. *S. fragilis* spec. nov. 17. ♂-genitalia. 18. ♀-genitalia. 19. Leaf-mine. 20. *S. hortorum* spec. nov., ♂-genitalia. Scale-lines all 0,1mm.



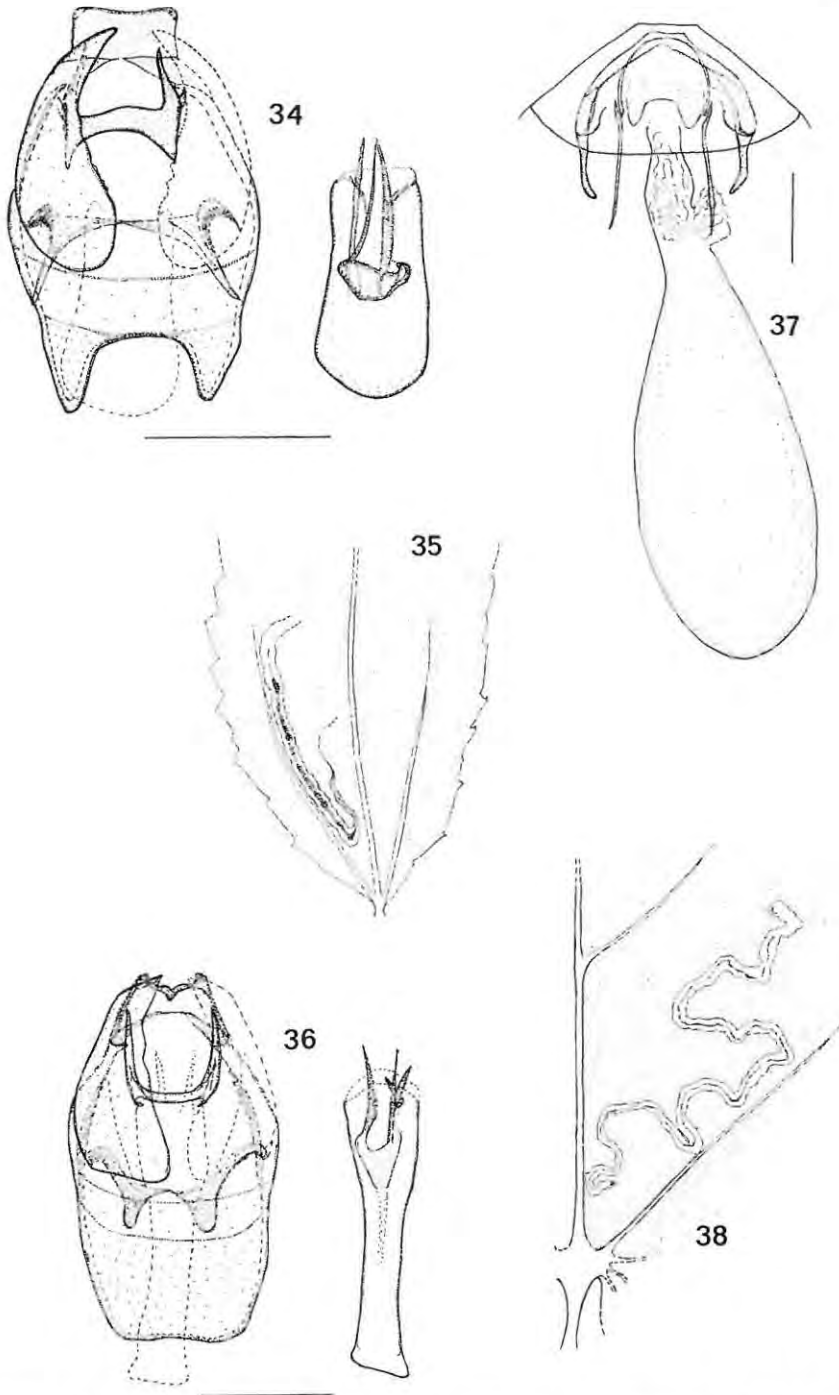
FIGS. 21. *S. potgieteri* spec. nov., ♂-genitalia. 22-24. *S. crotonica* spec. nov. 22. ♂-genitalia. 23. ♀-genitalia. 24. Leaf-mine. Scale-lines all 0,1mm.



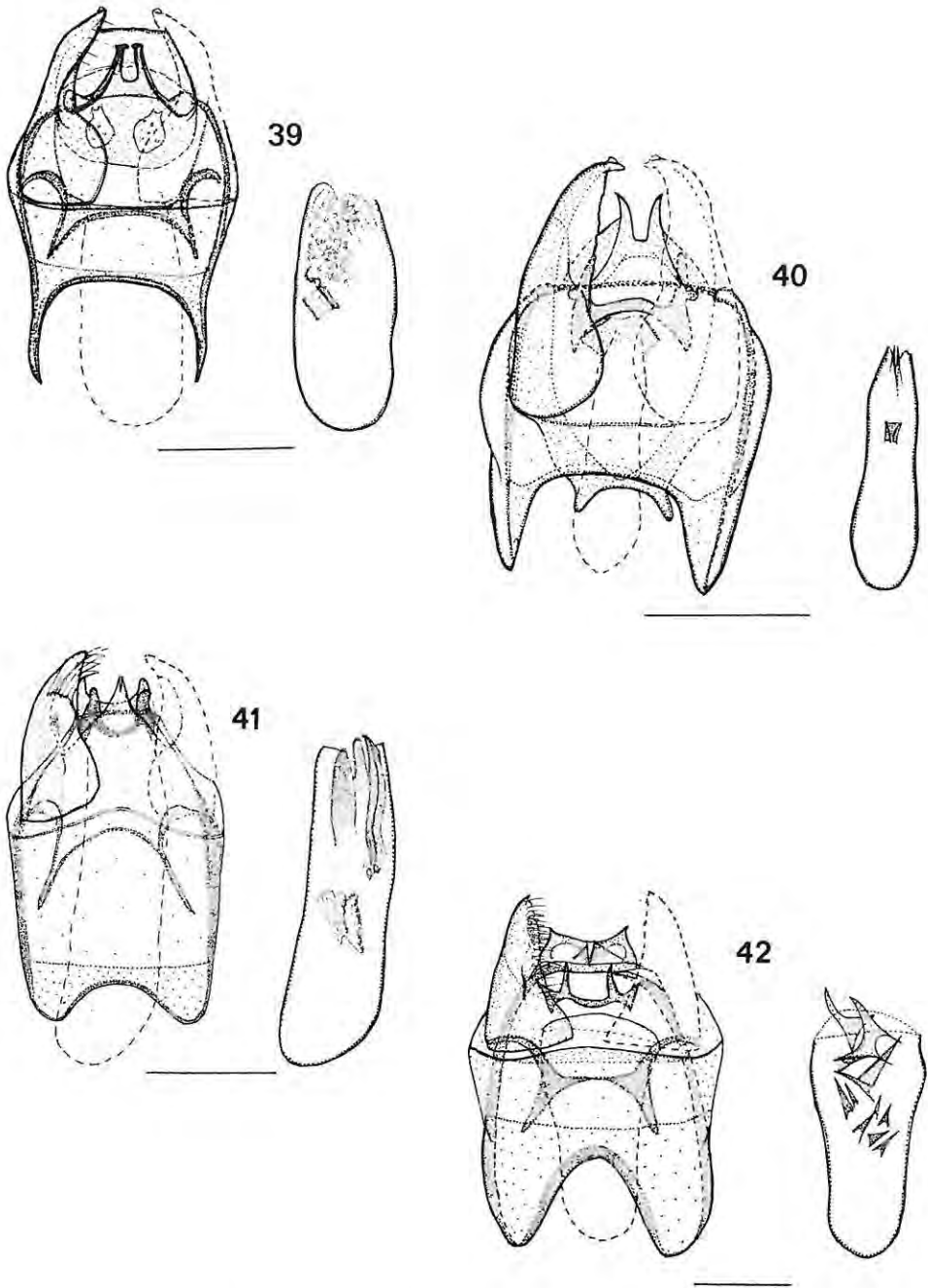
FIGS. 25. *S. generalis* spec. nov., ♂-genitalia. 26. *S. perplexa* (Janse), ♂-genitalia. 27. *S. urbica* (Meyrick), ♂-genitalia. 28. *S. androflavus* spec. nov., ♂-genitalia. 29. *S. abachausi* (Janse), ♂-genitalia. Scale-lines all 0,1mm.



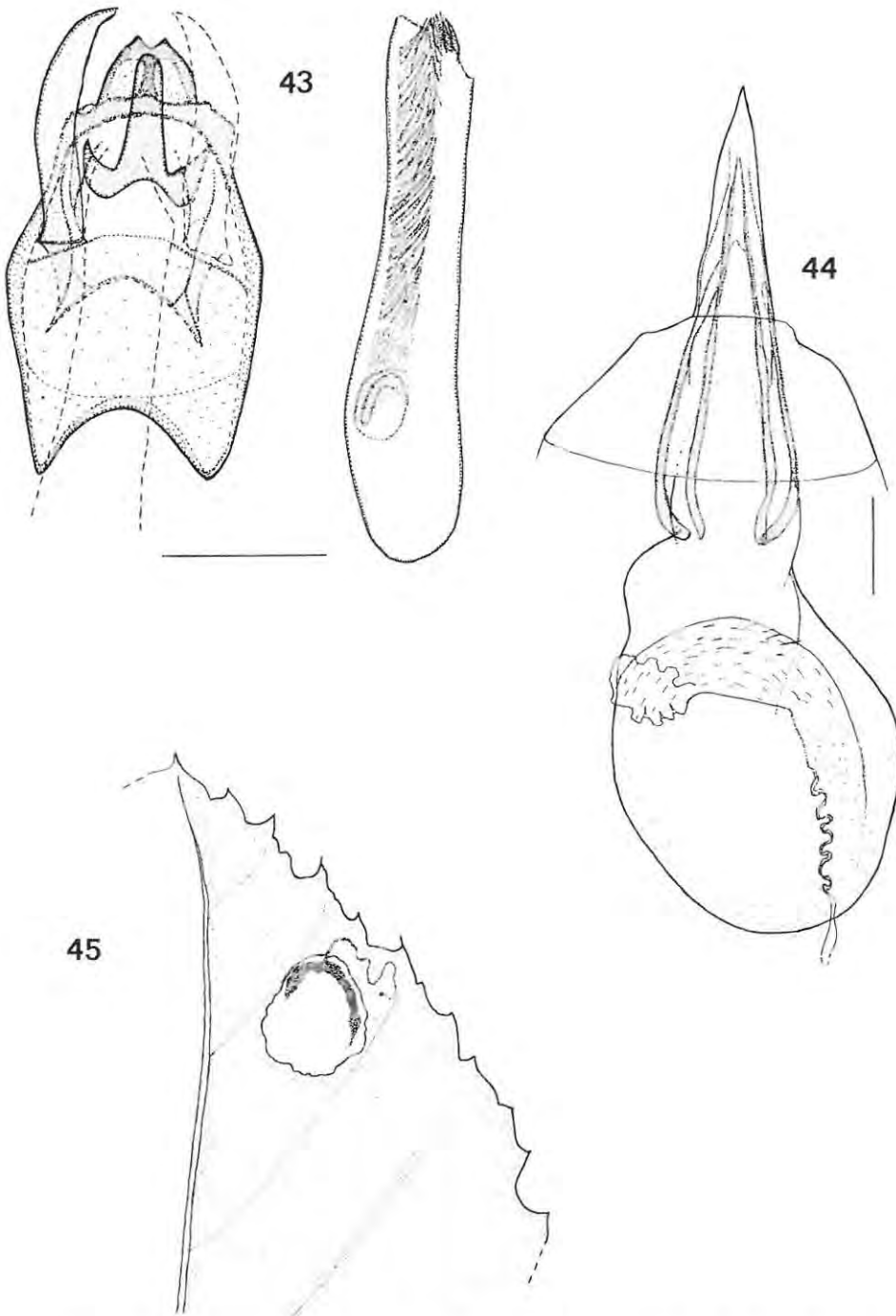
FIGS. 30. *S. pallida* spec. nov., ♂-genitalia. 31-33. *S. nigrata* (Meyrick), 31. ♂-genitalia
32. ♀-genitalia. 33. Leaf-mine. Scale-lines all 0,1mm.



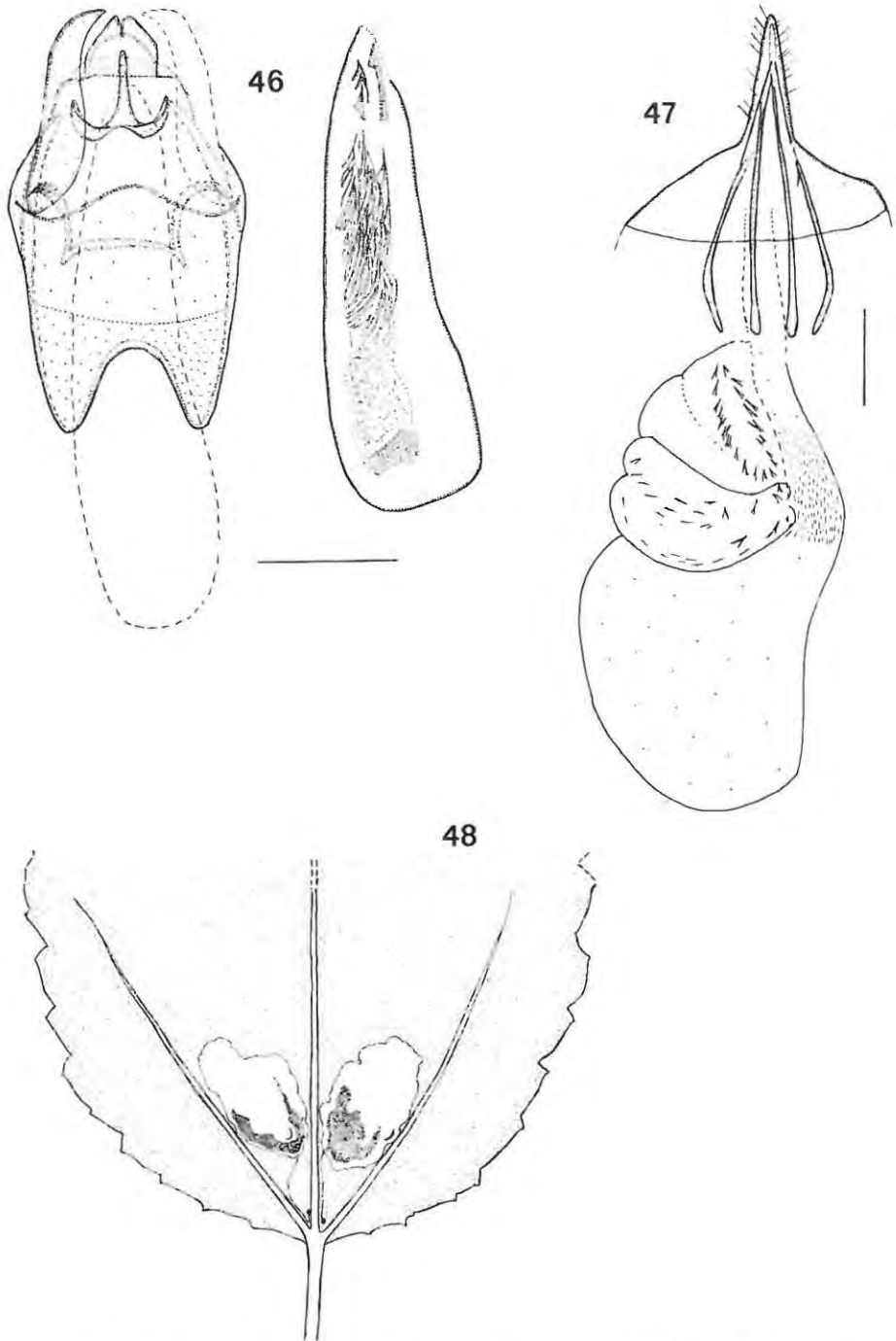
FIGS. 34-35. *S. triumfettica* spec. nov. 34. ♂-genitalia. 35. Leaf-mine. 36-38. *S. dombeyvora* spec. nov. 36. ♂-genitalia. 37. ♀-genitalia. 38. Leaf-mine. Scale-lines all 0,1mm.



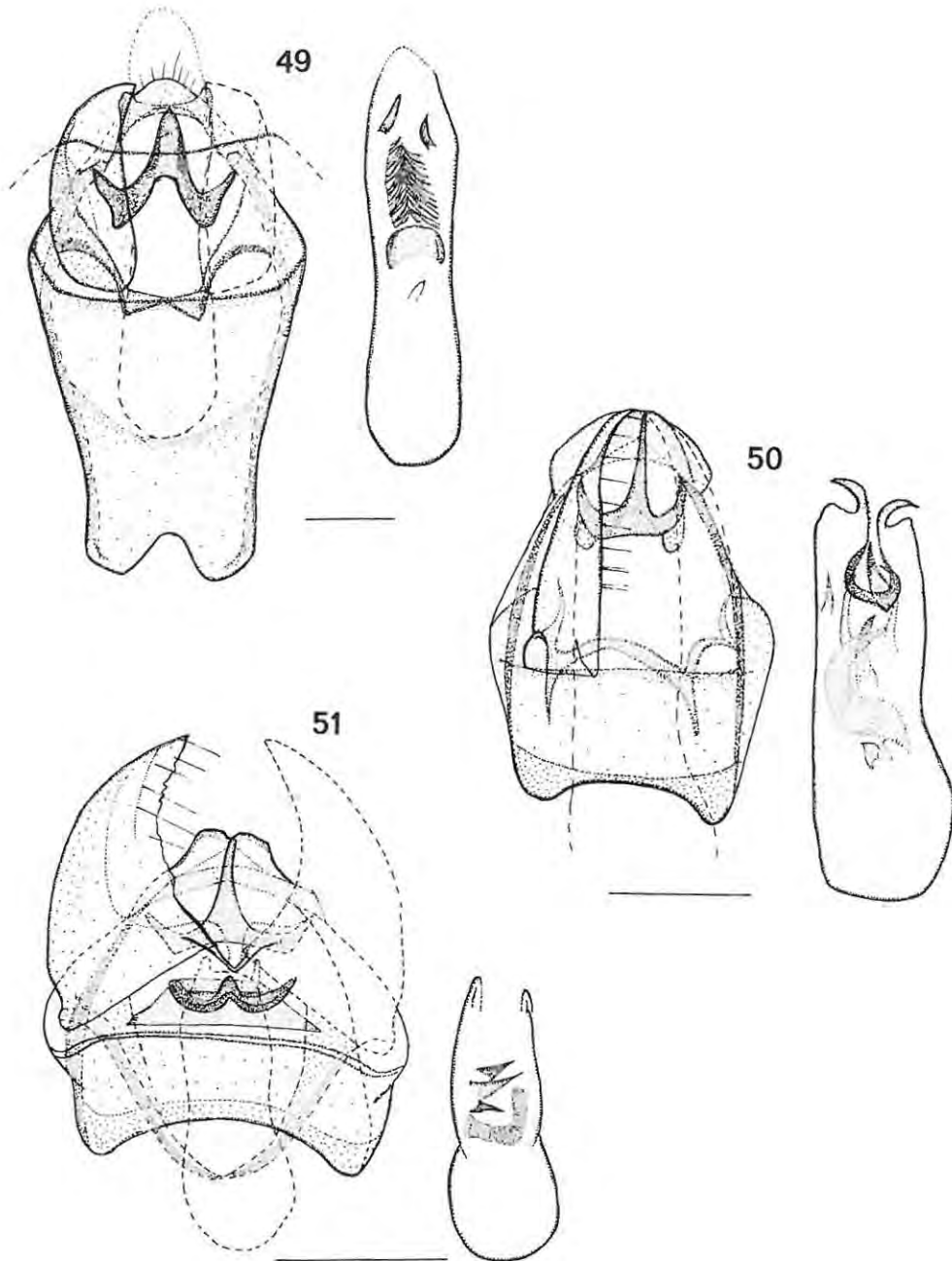
FIGS. 39. *S. ampullata* spec. nov., ♂-genitalia. 40. *S. pretoriata* spec. nov., ♂-genitalia.
 41. *S. protosema* (Meyrick), ♂-genitalia. 42. *S. porphyreuta* (Meyrick), ♂-genitalia.
 Scale-lines all 0,1mm.



FIGS. 43-45. *S. confinalis* spec. nov. 43. ♂-genitalia. 44. ♀-genitalia. 45. Leaf-mine.
Scale-lines all 0,1mm.



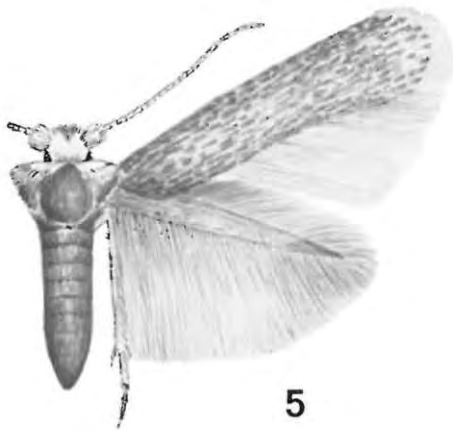
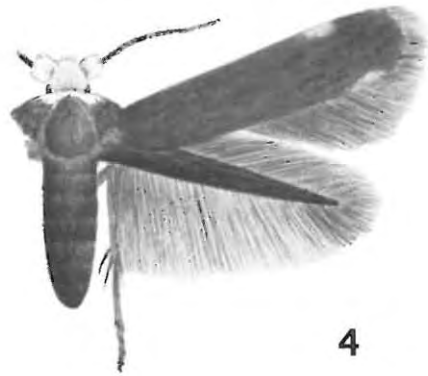
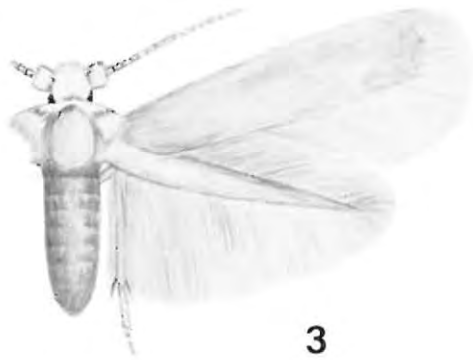
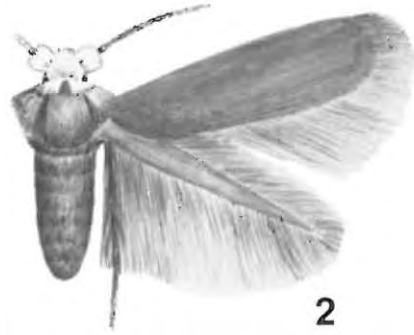
FIGS. 46-48. *S. greviae* spec. nov. 46. ♂-genitalia. 47. ♀-genitalia. 48. Leaf-mine. Scale-lines all 0,1mm.



FIGS. 49. *S. ingens* (Meyrick), ♂-genitalia. 50. *S. angustivalva* spec. nov., ♂-genitalia. 51. *S. letabensis* spec. nov., ♂-genitalia. Scale-lines all 0,1mm.

PLATE 15.

1. *Stigmella allophilica* spec. nov. 2. *S. crotonica* spec. nov. 3. *S. pallida* spec. nov. 4. *S. nigrata* (Meyrick), ♂. 5. *S. confinalis* spec. nov. Illustrations: Mrs P.M. Prowse.
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SCOBLE 1979

before p. 61

ANNALS OF THE TRANSVAAL MUSEUM
ANNALE VAN DIE TRANSVAAL-MUSEUM

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PART 2 DEEL

A NEW SPECIES OF *ECTOEDEmia* BUSCK FROM
BOTSWANA WITH OBSERVATIONS ON ITS
IMAGINAL SKELETAL ANATOMY
(LEPIDOPTERA: NEPTICULIDAE)

by M.J. SCOBLE

Transvaal Museum, Pretoria

ABSTRACT

A new species of Nepticulidae is described and a key to the species of *Ectoedemia* from southern Africa is provided. Some observations on the skeletal anatomy of the species and of *E. nigrimacula* (Janse) are recorded. This information is compared with that accrued from some morphological studies of other primitive Lepidoptera.

INTRODUCTION

Most published work on the Nepticulidae is confined to descriptions of species and genera based mainly on colouration, genitalia and wing venation of the adult. Some observations on the morphology of the imago of a new species of *Ectoedemia* and on *E. nigrimacula* (Janse) have been recorded in this work. They are presented firstly as a startingpoint for comparative work on the structure of nepticulid moths, in order to critically examine the internal classification of the family, and secondly to document information for comparison with that from studies on other primitive moths. The morphological work is by no means an exhaustive treatment.

TAXONOMY

Key to the species of *Ectoedemia* of southern Africa

1. Male genitalia: valve long, extending to apex (most caudal point) of pseuduncus, excavated inwardly (Fig. 11); hindwing of male with elongate, thickened patch along basal part of costa; forewing mainly ochreous with only a few fuscous scales *nigrimacula*
- Male genitalia: valve short, extending only to base of pseuduncus, not excavated inwardly; hindwing of male without elongated, thickened patch on costa; forewing grey or with many fuscous scales 2.
2. Male genitalia: pseuduncus appears to be thickened in ventral view; valve relatively broad, inwardly projecting process points at right-angles to anterior-posterior axis of valve (see Fig. 5); vinculum with anterior extension deeply excavated. Female genitalia: ductus bursae with ring-shaped sclerite. Larva feeds on *Commiphora africana* *mauni*
- Male genitalia: pseuduncus not so thickened; valve relatively narrow, inwardly projecting process points at 45° to anterior-posterior axis of valve (Fig. 12); vinculum with anterior extension not deeply excavated. Female genitalia: ductus bursae with associated sclerite not ring-shaped. Larva feeds on *Commiphora pyracanthoides* *commiphorella*

Ectoedemia mauni spec. nov.

ADULT (Fig. 15): Wingspan 4,2-5,0 mm. ♂ Head-tuft pale ochre. Antenna: eye-cap off-white; flagellum grey-purple. Thorax charcoal grey. Forewing grey with a very few, pale ochreous scales. Hindwing pale grey-brown. Abdomen: dorsal surface charcoal grey. ♀ As male except for greater number of pale ochreous scales on thorax and forewing.

Male genitalia (Figs. 5-8, 10): Vinculum: anterior extension rather deeply excavated; ventral plate narrow. Tegumen extended into blunt pseuduncus, the ventral surface of which is thickened, hood-like in lateral view, and with a strong central thickening. Uncus absent. Gnathos well sclerotized. W-shaped. Valve extending to base of pseuduncus, relatively broad, with an inward process caudally which points at right-angles to the anterior-posterior axis of valve. Transtilla well sclerotized. Aedeagus slightly longer than genital capsule.

Female genitalia (Fig. 13): Anal papillae broad. Bursa copulatrix: ductus with ring-shaped sclerotization; corpus large with pair of signa reticulata.

LARVA: Head-capsule shaped as in Figure 16. Larva forms a linear leaf-mine on *Commiphora africana* (A. Rich.) Engl. (Burseraceae) (Fig. 14) that resembles that made by *E. commiphorella* (see Scoble, 1978a). In the early stage frass almost fills the mine. The mine broadens considerably later.

PUPA (Fig. 17): Spines on dorsum of abdominal segments 2-8 large, and densely covering surface.

This is a drab, greyish moth. The male genitalia most closely resemble those of *E. commiphorella* Scoble (for figure see Scoble, 1978a). They can

be distinguished from those of the latter by the unusual thickening on the pseuduncus, the shape of the valve (compare Figs. 10 and 12), and the more deeply excavated anterior extension of the vinculum. The flat-topped hairs on the posterior edge of the pseuduncus of *commiphorella* are absent in *mauni*. In the female the sclerotization associated with the ductus bursae is ring-shaped in *mauni* and not like this in *commiphorella*.

The specimens were collected as larvae by the writer during a field-trip to the Okavango Swamps in January 1978. All were mining leaves of *Commiphora africana* bushes growing in sandy soil close to the edge of the Swamps.

MATERIAL EXAMINED. ♂-Holotype, BOTSWANA: 15 km N. of Maun, 27-29.i.1978, M.J. Scoble, accession number 3708. Paratypes: 9♂♂, 5♀♀ data as holotype. All specimens housed in the Transvaal Museum.

There is a male from South Africa with identical genitalia to those of the specimens from Maun, but with the antennae and forewings pale ochreous with a few fuscous scales, and hindwings a pale grey. This specimen bears the following label data: 'Limburg, Tvl. [Transvaal], Potgietersrus Distr. 19-21.xi.1968, L. Vári'. It is not included in the type-series of *mauni*.

MORPHOLOGY

METHODS

Examination of the skeletal anatomy of adults of *E. mauni* and *E. nigrimacula* was undertaken on specimens macerated in KOH. There was no need to so treat the limited amount of type-material of *nigrimacula* as I recently received additional specimens of this species. Some other nepticulids, and specimens of other monotrystian families referred to in the text, were treated in the same way.

The specimens from which the larval head-capsule and pupal spines are illustrated were prepared from exuviae salvaged from nepticulid cocoons. The head-capsule and the whole pupal 'skin' were soaked in a solution of KOH, stained, and mounted on slides. Pupal exuviae were inflated by jetting water from a syringe into them so that the spine-bearing abdominal segments were not squashed together. Abdominal spines are clearly visible and vary considerably in size and in number within the family.

OBSERVATIONS ON THE SKELETAL ANATOMY OF *E. MAUNI* AND *E. NIGRIMACULA*.

HEAD. The head is approximately oval (Figs. 18, 19) and the compound eyes are almost as high as the head-capsule. The "eye-index" (Powell, 1973) was 1,2 for a specimen of *E. mauni* and the "inter-ocular index" (Davis, 1975a) was 1,3 for a specimen of *mauni* and 1,5 for one of *nigrimacula*. The frons/clypeus and vertex are rough-scaled; the scales forming the tuft on the former arise from a large circular area (Fig. 18). The 'tuft' on the vertex is actually constituted by two adjacent patches of scales; these patches can only be distinguished by examining the denuded head-capsule.

A pair of raised cuticular patches, presumed to be chaetosemata are present on the dorsum of the head. Ocelli are absent. The post-occipital sulcus is prominent (Fig. 19). Subgenal processes are much reduced.

Both the scape and the pedicel (Fig. 18) of the antennae are larger than the segments of the flagellum; the scape forms a large eye-cap covered with flattened scales. There is a re-inforcement around the base of the antenna which is C-shaped rather than in the form of a complete ring. The pedicel is much smaller than the scape. The flagellum is filiform and the last segment conical (Fig. 1); the other segments of the flagellum are approximately rectangular. Each bears a ring of scales inserted at the base, and a ring of peg-like sensillae arises from near the apex. The antennae extend just beyond halfway along the forewing. The number of segments (scape and pedicel included) varies in *mauni* from 25 to 31, and in *nigrimacula* from 29 to 32.

The labrum is reduced to a pair of well-sclerotized pilifers. The epipharynx (Fig. 21) is membranous and triangular. There are no mandibles. The maxillary palps are five-segmented, the relative lengths of these segments in *nigrimacula* being approximately 1:1:1,7:3,7:2,5. There is a bend between the third and fourth segments, and the divisions between the first and second, and second and third segments are weak. Segments four and five bear prominent sensillae down the sides and at the tip. The galeae form a proboscis about threequarters the length of the head-capsule. The stipes/cardo is rather membranous; I am not able to distinguish these elements from one another. The labial palps are three-segmented and widely separated at their bases (Fig. 20). They bear three sensillae at the tip in a shallow pit (organ of von Rath). The boundary between the prementum and the postmentum is not visible.

The bottom of the sucking pump is a prominent, thickened plate (Fig. 22). The membranous hypopharynx is club-shaped (Fig. 23) and covered with small spines.

The tentorium lacks dorsal arms. The corporotentorium is prominent (Fig. 19).

The lateral cervical sclerites (Fig. 2) lack a postero-medial suture.

THORAX. The prothorax is small and mostly obscured by the mesothorax in dorsal view. The patagia are prominent. The mesonotum is bent down anteriorly. In dorsal view the ratio of the length of the mesothorax to that of the metathorax is approximately 1,4:1. The tegula is shaped as in Figure 3. The cephalic margin of the scutum of the metathorax is exposed mesally and is not concealed by the scutellum. The "metascutal zone" (Common, 1969) or "holding area" (Kuijten, 1974), a patch of minute curved spines on each side of the metascutum, is extensive.

The coxae of the forelegs are moveable, whereas those of the midlegs and hindlegs are fused to the sternites. The tibial spur formula is 0-1-2; the pair of spurs on the midtibiae are terminal (distal) and unequal in length. On the hind tibiae are two pairs of unequal spurs, one terminal and the other just below the midpoints of the tibiae (Fig. 24).

The wings are aculeate; aculei are most clearly observed at the borders of the wings. There is a strong frenulum in the male, arising from the base of the hindwing, that catches into a retinaculum comprising some hook-like spines on the costa of the underside of the forewing (Fig. 26). In the female

there is a row of costal bristles near the base of each forewing; the well-defined, costal retinaculum found in the male is absent.

A jugal lobe is present in both the male (Fig. 25) and the female of *E. mauni*; it is better defined in the male. This structure is also clearly visible in the male of *E. nigrimacula* (no females available).

The wing venation of *Ectoedemia* is figured by Scoble (1978a).

ABDOMEN. Abdominal sterna and terga are weakly sclerotized. Only the posterior part of sternum 1 is thickened. It comprises a narrow band (Fig. 4).

In the male, tergum 8 bears a pair of lateral patches from each of which arises a tuft of ochreous scales. The shapes of the genital components are useful for species diagnosis; they are described above. In ventral view the pseuduncus in *mauni* appears to be thickened. It appears like this because it is in the form of a hood-like extension of the tegumen as can be seen in lateral view (Fig. 7). The structure should not be confused with a true uncus. A schematized diagram (Fig. 9) of the uncus of a kind found extensively in the family, but not in *Ectoedemia*, shows how the pseuduncus and the uncus are usually situated. The ejaculatory duct enters the aedeagus lateromedially.

In the female, sternum 4 bears a pair of fenestrae (see Davis, 1975b for Neopseustidae and 1978 for Eriocraniidae). These lie very close together near the anterior edge of the sternum. They are not easy to see in the Nepticulidae mainly because the surrounding sternum is so weakly sclerotized. Each window is similar in appearance to those in Davis' photograph of *Apoplania chilensis* Davis (Neopseustidae).

The female genitalia are monotrysian. There is no cloaca — the ovipore opens independently from the alimentary canal. The anal papillae form a broad, flat posterior edge to the abdomen; there is no piercing ovipositor. Sternum 7 is large and curved upwards so that the genital opening and the anus, although terminal, are situated more dorsally than ventrally. The anterior apophyses are joined at their bases by a sclerotized band that runs around the end of the abdomen.

The internal canal of the spermatheca in *mauni* is spiral, a condition not universal in the Nepticulidae (see Dugdale, 1974).

DISCUSSION

The degree to which the structures described in the morphology section, above, varies with that of other nepticulid species awaits further comparative study. Most of the features probably vary between families rather than within them. The morphological work presented here was done with particular reference to the studies of Davis (1975b and 1978) and Kristensen (1968a and b) on certain families of Dacnonypha, and Brock (1971) who, in his work on the Ditrysia, also referred to the structure of primitive moths. In addition to these sources of comparison I personally examined representatives of a few other families of the Monotrysia.

Eye-size, relative to the size of the head-capsule is reasonably supposed to be related to time of flight (Powell, 1973). Powell's "eye-index" is the ratio of the maximum eye-diameter to the height of the head measured from the antennal base to the base of the frons/clypeus, Powell found that in night-flying Ethmiidae the range of the index was approximately 0,9-1,2 whilst in diurnal species it was about 0,7-0,8. The figure of 1,2 for *E. mauni* shows the relative eye-size to be high. Nepticulid species have been observed flying at dusk and have frequently been taken at light traps during the night. No information about flight-time is available for *E. mauni*.

The figures for relative eye-size of certain primitive moths were expressed as an "interocular index" by Davis (1975a). It is interesting to compare these figures with those for nepticulids that I have measured even though in future it may be better, for purposes of standardization, to use Powell's index (Davis, personal communication). The interocular index values for *E. mauni*, *E. nigrimacula* and *E. platanella* (Braun) (a North American leaf-mining species for which the value is 1,3) fall within the range given for the Neopseustidae (Davis, 1975b). A specimen of *E. populella* Busck (another N. American species, the larvae of which induce the formation of callus tissue in leaf-petioles of *Populus*) had an index of 0,9. This species is considerably larger than the other nepticulids examined. No information on flying time is available.

Loss of ocelli in the adult is a general feature of the Nepticulidae. This loss has occurred, presumably independently, in several families.

Antennal length relative to that of the forewing varies between *Ectoedemia* species. The scape is particularly large in the Nepticulidae compared with that of other families except for the Opostegidae in which it is larger. The reinforcements at the point at which the antennae articulate with the head-capsule do not form a complete rim as in the Neopseustidae (Kristensen, 1968a).

The mouthparts of nepticulid species are typically neolepidopteran (mandibles are reduced and a proboscis is developed); they have deviated considerably from the orthopteroid design exhibited most markedly in the Lepidoptera by the Micropterigidae. The galeae, although short, are haustellate and Downs (1968) has shown them to be functional in a species of *Ectoedemia* from North America. No other feeding records have been recorded for the Nepticulidae but the presence of a proboscis, and a well-developed sucking pump base suggests that Downes' observation is widely applicable. The number of segments in the maxillary palps is not exceeded elsewhere in the Lepidoptera. The relative lengths of the segments are approximately the same as those given for *Neopseustis meyricki* Hering by Kristensen (1968a). The prementum is a well-defined structure in *Eriocrania* (Eriocraniidae) and also clearly recognisable in the Mnesarchaeidae and the Nepticulidae, although in the last two families the structure is shaped like a palp segment on each side (see the papers of Kristensen and Davis cited above). In *E. mauni*, *E. nigrimacula* and some other monotrysiids (one specimen of Opostegidae and one of Tischeriidae were examined besides several additional Nepticulidae), the prementum is not defined from the postmentum and the labial palps are widely separated at their bases.

The general shape of the lateral cervical sclerites is similar to that found in other nepticulids, in *Opostega bellicosa* Meyrick (Opostegidae) and *Eriocrania* (Eriocraniidae) (see Kristensen, 1968b, Fig. 17). The suture demarcating the postero-medial part of each sclerite in *Eriocrania* is absent in nepticulids. In a tischeriid and a heliozelid species examined there is a triangular, rather membranous area in the middle of each lateral cervical sclerite. In an adeline incurvariid studied the broad ventral plate seen in the Nepticulidae is reduced to a narrow limb.

The unconcealed cephalic margin of the metascutum is a general feature of the thorax of primitive moths (see Brock, 1971).

Ventrally the basisternum of the mesothorax is apparently demarcated from the pre-episternum, which according to Brock, is unusual in the Lepidoptera. The basic layout of this region is essentially the same as that of the Incurvariidae illustrated by Brock.

The spines comprising the patches on the metascutum are modified aculei (microtrichia). Rather similar spines are found on the underside, and near the base, of the forewing in the elliptical patch in many Lepidoptera (Common, 1969; Kuijten, 1974 and personal communication). The two areas serve as a locking device when the wings are folded over the thorax. I have not found an alar zone in either *E. mauni* or in *E. nigrimacula*; aculei are densely and widely scattered over the wing surfaces.

There is a certain amount of confusion both in the use of the terms jugum and fibula, and about the presence or absence of these structures in the Lepidoptera. Comstock (1918) considered the jugum to be a finger-like projection of the jugal lobe that, when it functioned in amplexiform coupling, lay below the costa of the hindwing so that the hindwing was yoked between the jugum and the inner margin of the forewing. The fibula, similar in position to the jugum, was thought to act as a clasp and lie above the hindwing. Today the words jugum and fibula are used synonymously and it appears that the structure always lies on the upper surface of the hindwing.

Braun (1924) stated that the fibula is retained in females of the more primitive genera (presumably *Obrussa* and *Ectoedemia*, see Braun, 1923) of the Nepticulidae. In contrast to this in an earlier paper (Braun, 1919) she recorded the fibula as being present in the females of the specialized genera of the family. In the 1924 paper she figured the forewing bases of a male and a female of *Ectoedemia heinrichi* Busck and labelled the small finger-like structure on the illustration of the female as "fib." (fibula) but not the rather more rounded lobe on the figure of the male. Sharplin (1964) noted the presence of a jugum in two genera of "Stigmellidae" (i.e. Nepticulidae), but did not state which genera had been studied nor whether both sexes were examined or not. It is not known if the extension of the jugal area functions in wing-coupling at all in the Nepticulidae. I have not seen a finger-like projection in any nepticulid, although the figures of *Ectoedemia heinrichi* (see Braun, 1923; 1924) and *Obrussa ochrefasciella* (Chambers) (see Braun, 1923) suggest that such a structure sometimes exists. There is certainly a well-defined jugal lobe present in many species of Nepticulidae, including *E. mauni* and *E. nigrimacula*, and this is undoubtedly the generalized

condition in the family. The presence of a jugal lobe in the primitive Lepidoptera is widespread (Sharplin, 1963; 1964).

Epiphyses are absent throughout the Nepticulidae. Loss of these structures has occurred several times in primitive Lepidoptera so this character is of limited value in phylogenetic analysis. The exact position of the first (most basal) pair of tibial spurs on the hindleg varies within the Nepticulidae. In *E. mauni* and *E. nigrimacula* this pair is positioned just below the midpoint of the tibia; this is the usual condition in *Ectoedemia* species.

The fusion and loss of veins in *Ectoedemia* is a general feature of the Nepticulidae although this reduction is not as extreme as it is in the Opostegidae.

The main feature of note in the abdomen, apart from the genitalia, is the presence of a pair of circular fenestrae on the fourth sternum of the female of *mauni*. The presence or absence of these structures in several species of primitive moths from a wide variety of families was tabulated by Davis (1975b). To this information can be added the absence of such structures in a female of an undescribed species of *Tischeria* examined by me.

The variation in genital components is considerable within the Nepticulidae; for example the uncus may be present or absent, the transverse bar of the transtilla (*sensu* Beirne, 1945) is usually present but may be absent as in *Niepeltia* Strand (Scoble, in preparation). For this reason these structures are widely used for taxonomic purposes at the specific and generic levels. Much comparative study remains to be done before we can fully understand the phylogenetic value of the male genitalia of primitive moths at higher levels of classification.

The absence of a pointed ovipositor is the usual condition in female nepticulids although such structures are present in a few species (see Vári 1955; Scoble 1978b). Attenuated, piercing ovipositors are well developed in certain primitive families e.g. Eriocraniidae and Incurvariidae. Ovipositor form and function in the Lepidoptera was reviewed by Mutuura (1972).

The weakly upturned abdomen in the female of *Ectoedemia* is indicated in Mutuura's figure of '*Nepticula turbidella* (Zeller)' (this species is almost certainly *argyropeza* (Zeller), *turbidella* is not known from North America, and has been transferred to *Ectoedemia* by Wilkinson & Scoble, 1979) which shows the large, curved seventh sternum. This upturned condition is also seen in *E. mauni* but not in nepticulids belonging to other genera so far examined, nor in many other Lepidoptera (see the figures of Dugdale, 1974). The genital aperture and the anus are terminal in *mauni* despite their somewhat dorsal position. Mutuura's figure shows the genital opening as dorsal and distinctly aterminal, an interpretation open to doubt.

ACKNOWLEDGEMENTS

I am extremely grateful to Dr N.P. Kristensen, Zoologisk Museum, Copenhagen, for several incisive comments on an early draft of this work. I thank Dr Don R. Davis, Smithsonian Institute, Washington for further most helpful remarks. Dr L. Vári, Transvaal Museum and Professor C. Wilkinson, Vrije Universiteit, Amsterdam also kindly read and commented upon the manuscript. Dr P.J. Kuijten, University of Leiden drew my attention to the holding area on the metascutellum and let me see his many photographs of the holding mechanism in the Lepidoptera. Miss E. Retief, Botanical Research Institute, Pretoria, kindly confirmed my identification of the foodplant of *E. mauni*. I thank Dr D.M. Kroon, Sasolburg, for donating specimens of *E. nigrimacula* that were used in this study. The morphological observations were undertaken using a Zeiss Standard microscope fitted with interference contrast. This facility obtained by the Transvaal Museum with a grant from the Council for Scientific and Industrial Research, Pretoria, is greatly appreciated. I thank Dr E. Holm and other colleagues from the Entomology Department, University of Pretoria, for inviting me to go on a field-trip to Botswana with them during which time the specimens of *E. mauni* were collected.

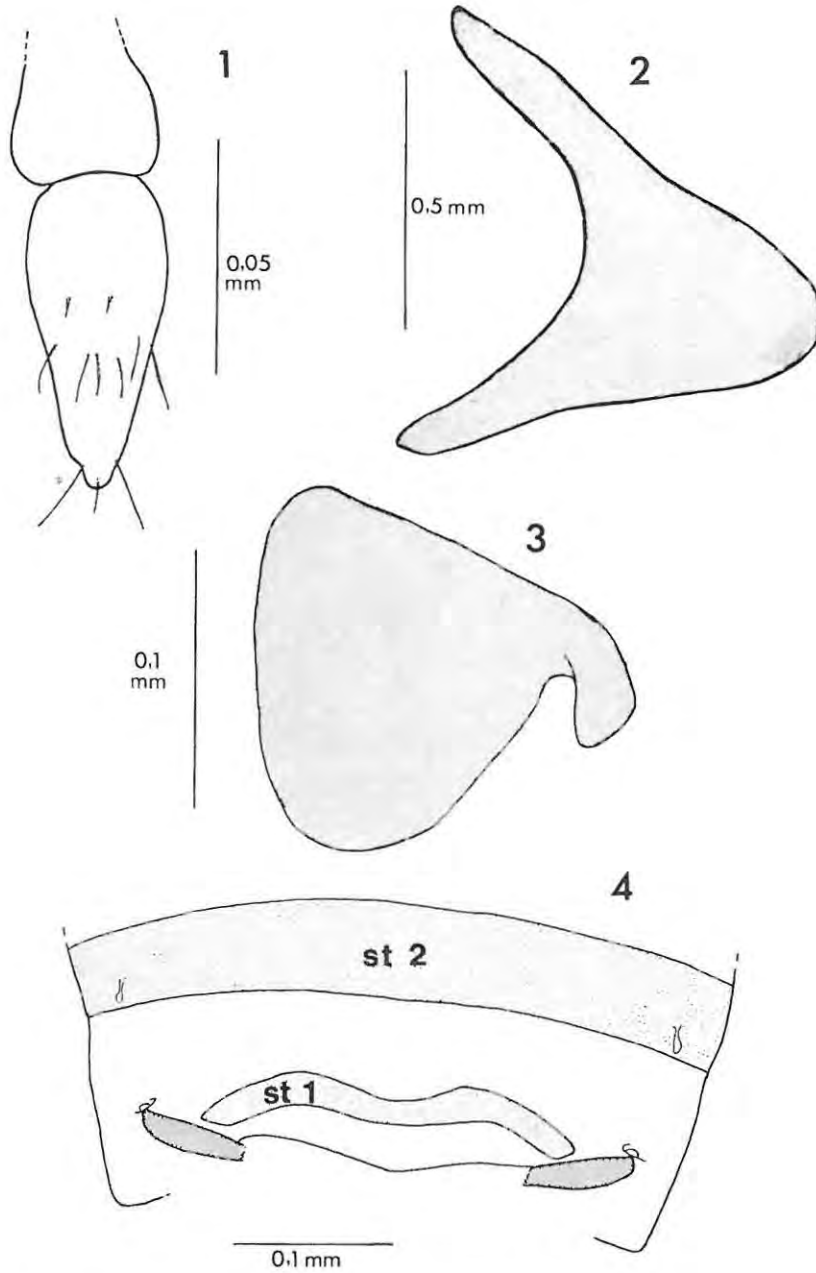
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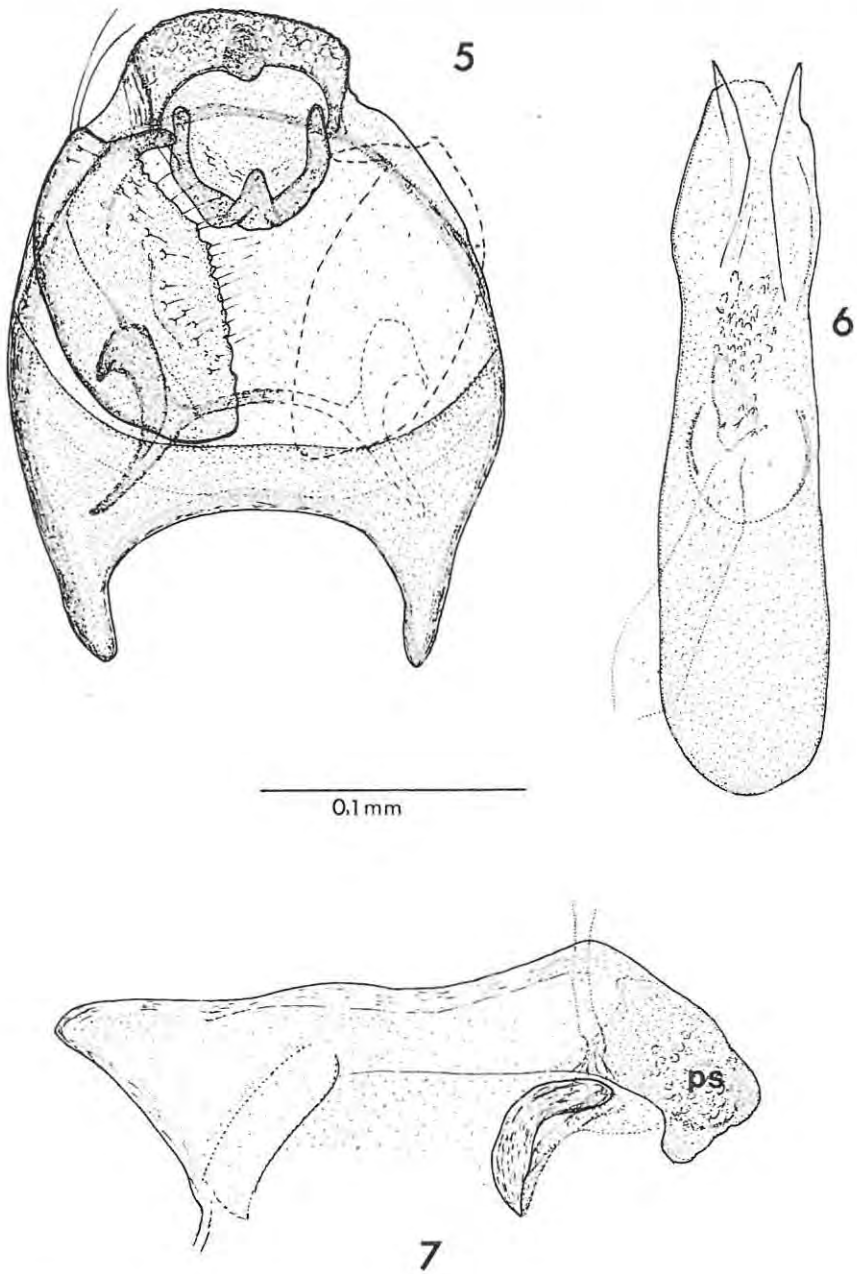
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ABBREVIATIONS

ct	corporotentorium
ej	ejaculatory duct
fr	frenulum
fw	forewing
hw	hindwing
jl	jugal lobe
pl	pedicel
pos	post-occipital sulcus
ps	pseuduncus
sc	scape
un	uncus
rm	retinaculum
st	sternum



E. mauni spec. nov. Figure 1. Apex of antenna.
 Figure 2. Left lateral cervical sclerite.
 Figure 3. Tegula (outer view).
 Figure 4. Abdominal sterna 1 and 2.



E. mauni spec. nov. Figure 5. ♂ genitalia, ventral view.

Figure 6. ♂ genitalia, aedeagus.

Figure 7. ♂ genitalia, lateral view.

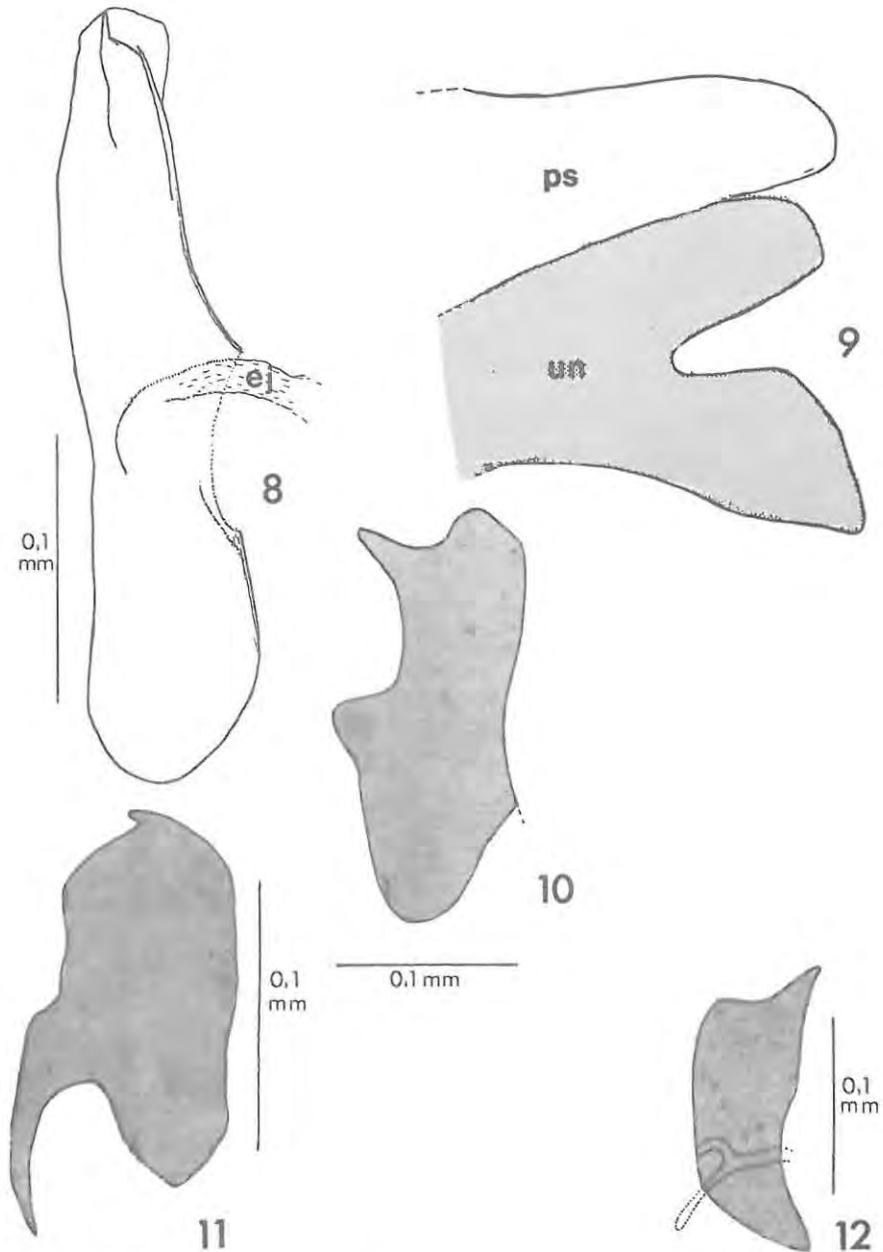


Figure 8. *E. mauni* spec. nov. Lateral view of aedeagus.

Figure 9. Nepticulidae, schematized figure, lateral aspect of generalized condition of uncus and pseuduncus *not* found in *Ectoedemia*.

Figure 10. *E. mauni* spec. nov. ♂ genitalia, inner view of left valve.

Figure 11. *E. nigrimacula* (Janse). ♂ genitalia, inner view of left valve.

Figure 12. *E. commiphorella* Scoble. ♂ genitalia, inner view of right valve.

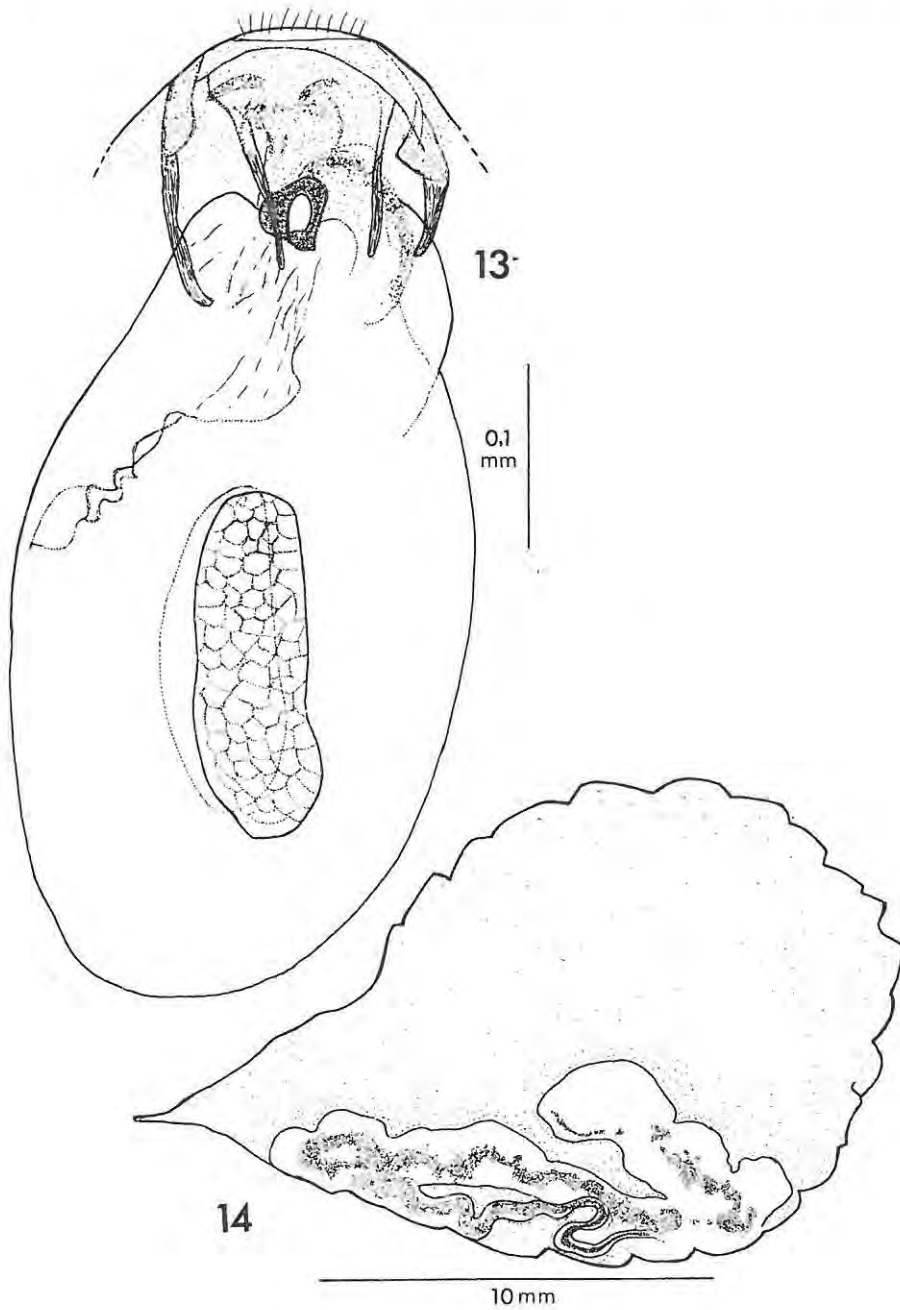


Figure 13 *E. mauni* spec. nov. ♀ genitalia.

Figure 14. *E. mauni* spec. nov. Leaf-mine.



Figure 15. *E. mauni* spec. nov. Adult, wingspan = 4,2 m.

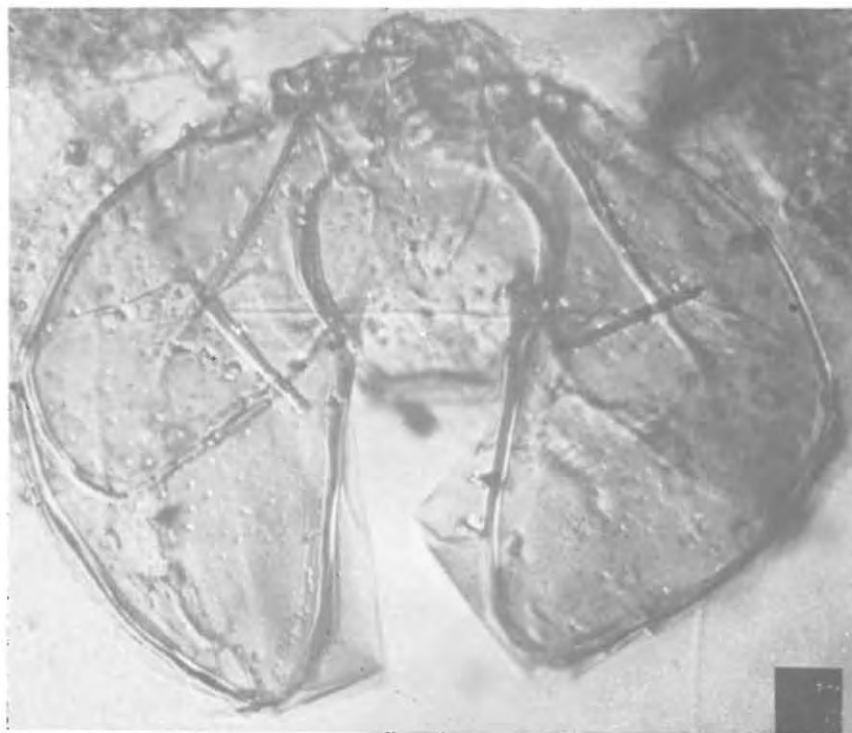


Figure 16. *E. mauni* spec. nov. Exuviae of larval head-capsule, approximately $\times 350$.

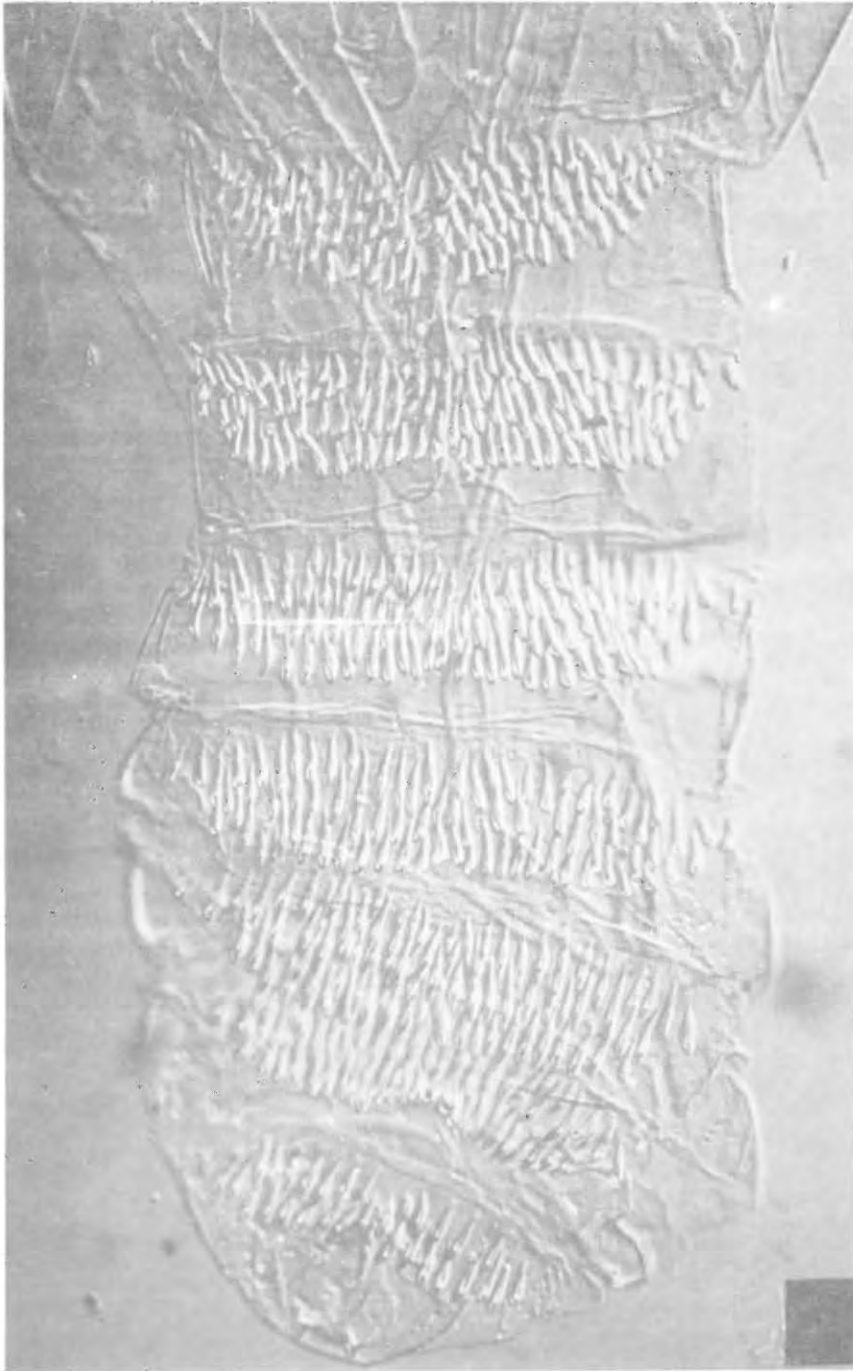


Figure 17. *E. mauni* spec. nov. Abdomen of pupal exuvia, approximately $\times 150$.

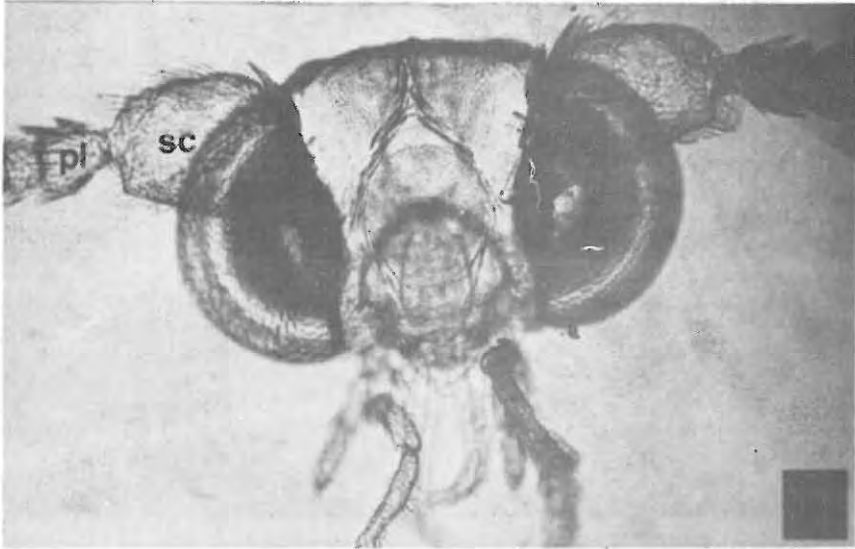


Figure 18. *E. mauni* spec. nov. Anterior view of head, approximately $\times 110$.

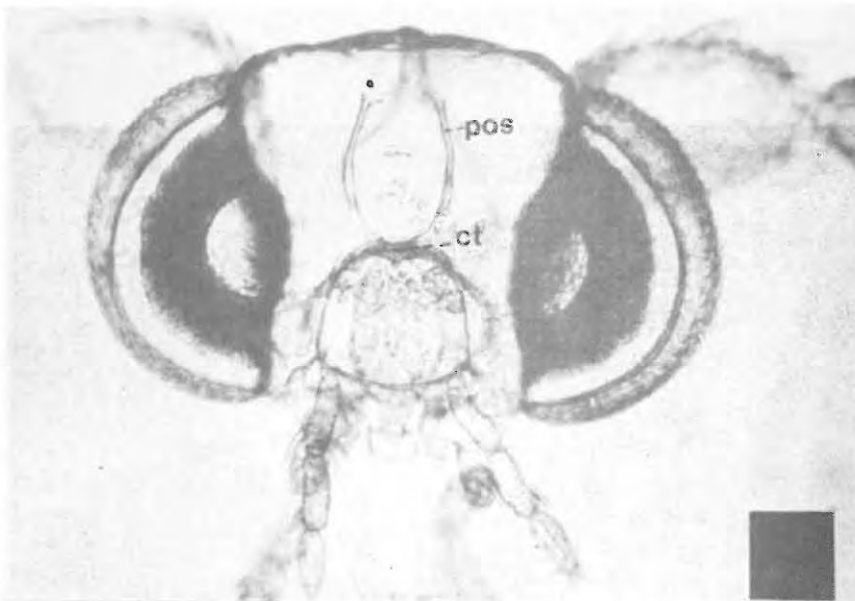


Figure 19. *E. mauni* spec. nov. Posterior view of head, approximately $\times 125$.



Figure 20. *E. mauni* spec. nov. Posterior view of bases of labial palps, approximately $\times 410$.

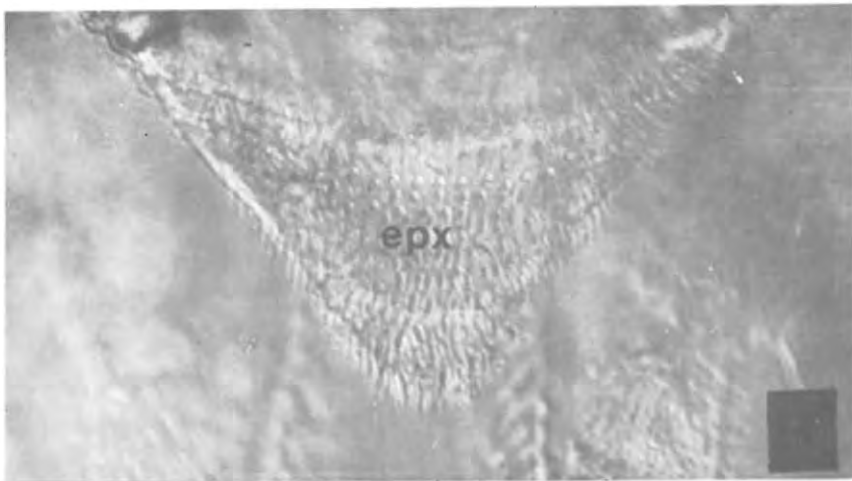


Figure 21. *E. mauni* spec. nov. Epipharynx, approximately $\times 880$.



Figure 22. *E. mauni* spec. nov. Floor of sucking pump, approximately $\times 400$.

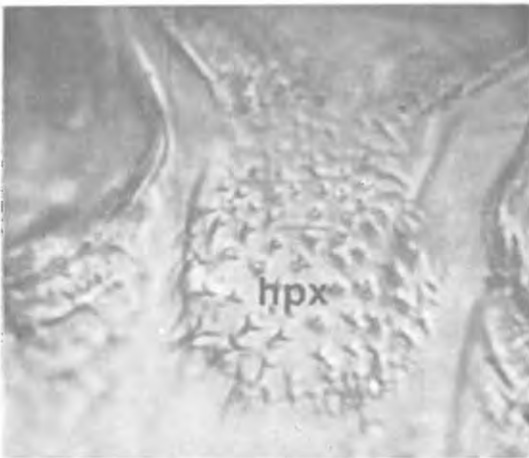


Figure 23. *E. mauni* spec. nov. Hypopharynx, approximately $\times 100$.



Figure 24. *E. mauni* spec. nov. Hind tibia, approximately $\times 140$.

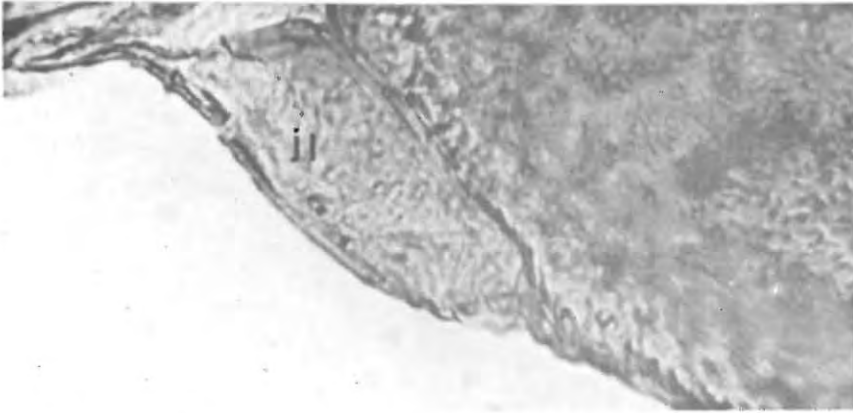


Figure 25. *E. nigrimacula* (Janse). Underside of base of forewing, approximately $\times 400$.

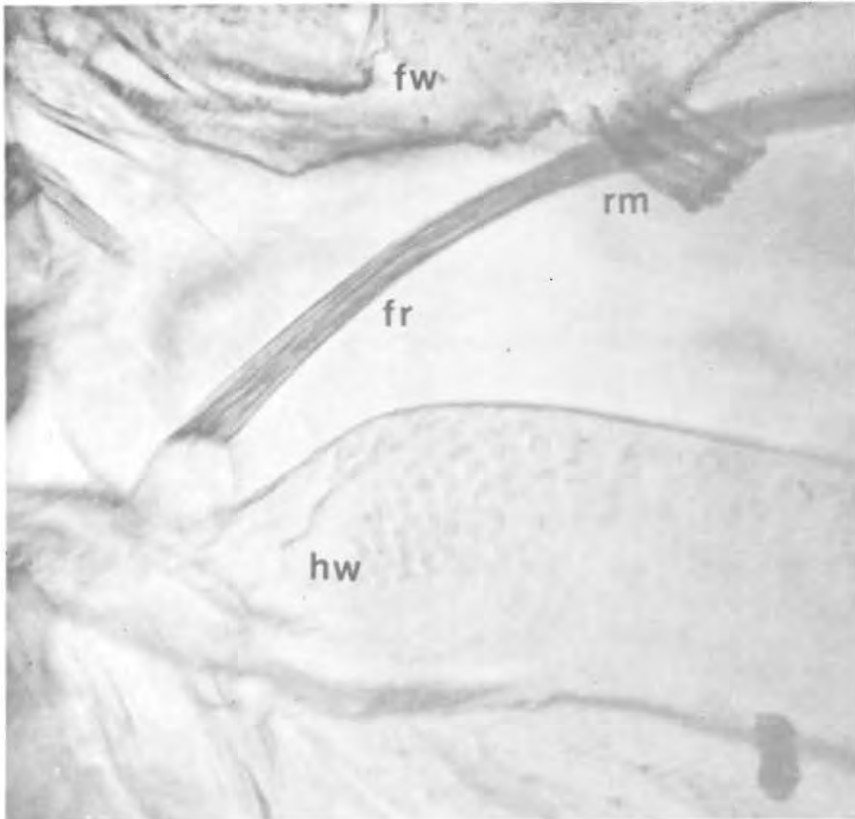


Figure 26. *E. nigrimacula* (Janse). Wing-coupling mechanisms, underside of wing, approximately $\times 140$.

Trifurcula Zeller: a critical analysis of the genus,
cladistic relationships and descriptions of two new
species from South Africa (Lepidoptera:
Nepticulidae)

by

M. J. SCOBLE

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The genus *Trifurcula* (*sensu* Beirne 1945 and Klimesch 1953) is recorded for the first time from South Africa based on two new species, *pullus* and *barbertonensis*. The genus is expanded to include the somewhat incongruous species *barbertonensis* because it shares derived (apomorphic) characters with the type-species. A more detailed description of the male genitalia of the type-species, *T. pallidella* Zeller, is provided and the cladistic relationships of the genus are discussed.

INTRODUCTION

This paper is concerned with two new South African nepticulid species. They are assigned to the genus *Trifurcula* Zeller (*sensu* Beirne 1945 and Klimesch 1953); this is the first record of the genus outside the palaeartic. The locality data given by Klimesch show that the genus has previously been recorded from Britain, central and southern Europe and Asia Minor.

The name *Trifurcula* was used by Beirne (1945) and Klimesch (1953) to refer to the taxon comprising *pallidella* Zeller and its close relatives. Johansson (1971) gave the taxon a subgeneric rank and used the name in a wider sense (for a discussion of this usage see Scoble 1978). A study of the new species, described below, has helped me to reassess the boundaries of the taxon. I have not adopted Johansson's subgeneric ranking, although the suggestion may be implemented in part later when more is known about the relationships amongst nepticulid taxa. Therefore, in the present paper, the name *Trifurcula* refers to those species discussed by Klimesch (1953), together with the new South African ones, and not to the members of the other taxa included in it by Johansson.

The two new species described below have helped to clarify the characters on which *Trifurcula* may be best conceived. Although they do not share all the features of the palaeartic species, their similarities to them are considerably more striking than their differences from them. Whilst a 'final' delimitation of the genus requires a wide-ranging study of nepticulid taxa, a critical assessment of its characters suggests to me that the boundaries can be drawn more usefully to indicate the relationships of its component species.

Of the two new South African species, the first can be assigned to the genus with little difficulty. It is the second of the two, particularly, that exhibits some unique features. I consider that to describe a new monotypic genus for this species is unwarranted, certainly at this stage, and would only obscure its relationships.

TAXONOMY AND CHARACTERS

During the course of this study I noted some features of the male genitalia not previously described for the type-species. Some of these, also present in the new species, are useful for indicating relationships. A new description of the male genitalia is presented below.

Trifurcula pallidella Zeller, figs 1-3, 9, 13

Trifurcula pallidella Zeller, 1848:332.

MALE GENITALIA. Vinculum: anterior extension rounded. Tegumen extended into short, relatively pointed pseuduncus. Uncus divided into dorsal and ventral components; dorsal component prominent in ventral view and extending well beyond tegumen (fig. 9). Gnathos fused, central element truncated, dorsolateral elements each comprising a narrow, relatively short, posteriorly directed apodeme and a more narrow, longer anteriorly directed one. Valva approximately triangular, undivided, extended into a point terminally. Transverse bar of transtilla present. Aedeagus narrows abruptly towards tip; ventral process (juxta of Beirne) fused to aedeagus and extended just beyond its tip; no other carinae; vesica with large spine-like cornuti, strong spines near phallosome, and a striate thickening.

The term 'juxta' has been used to describe several non-homologous structures in the Lepidoptera. The descriptive term 'ventral process' is used here, and in a study of another nepticulid genus, *Niepellia* Strand (Scoble, in preparation), to refer to the carinate process attached to the ventral aspect of the aedeagus.

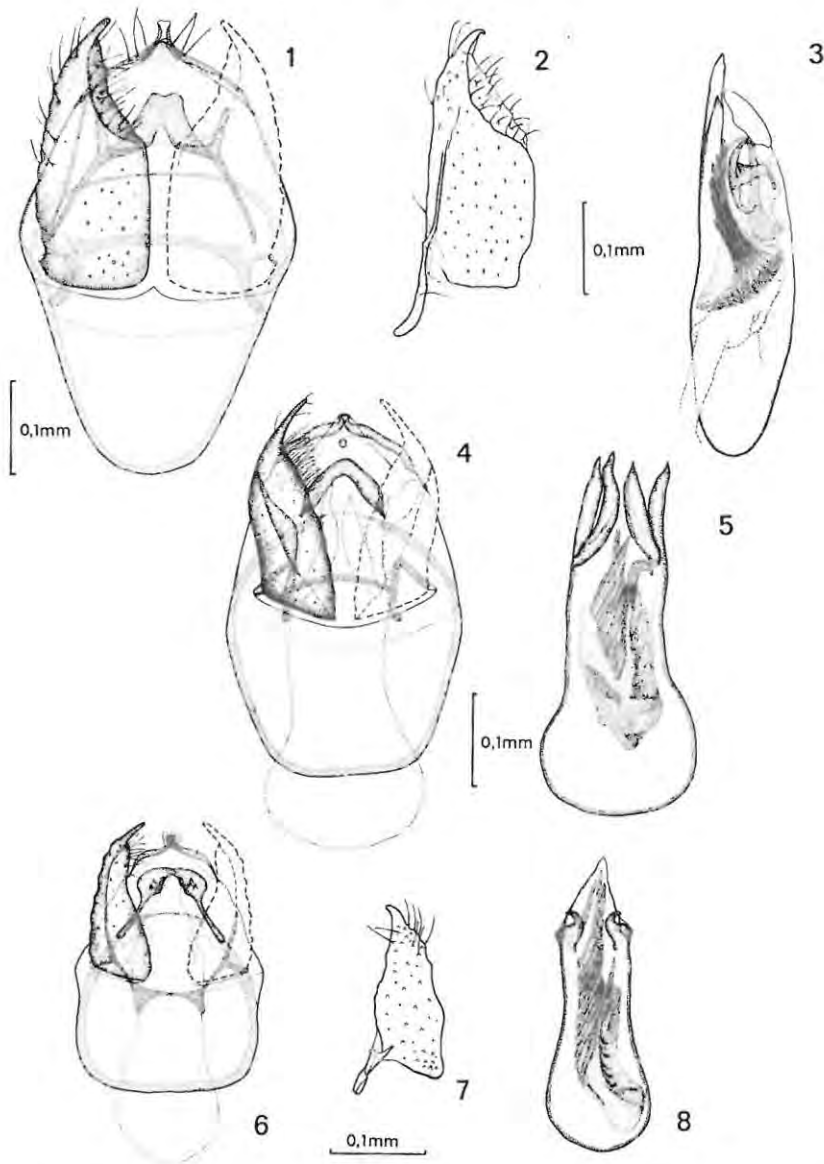
Trifurcula pullus spec. nov., figs 4-5, 10, 14, 20-21

ADULT. ♂. Wingspan of holotype 5.0 mm, of paratype 5.4 mm. Head-tuft orange-ochre. Antenna extends just beyond half length of forewing; 35 segments in holotype, 33 segments in paratype. Thorax and forewing dark grey, very dark in paratype, slightly more pale in holotype.

Forewing venation (fig. 20). R_1 and R_{2+3} fused to form R_{1+2+3} . R_4 and R_5 represented as terminal branches of $M+Cu$ trunk, no connection to R_{1+2+3} . Cu never free from M for any part of its length. $1+2A$ coincident throughout length, no 'anal loop' (Kristensen 1978:fig. 20).

Hindwing venation (fig. 21). R_s and M form a common trunk at base and subsequently diverge into the branches R_s , M_1 and M_2 .

Male genitalia (figs 4, 5, 10, 14). Vinculum with anterior extension rounded. Tegumen extended into short pseuduncus. Uncus in lateral view as in fig. 10. Gnathos fused, dorsolateral elements present, reduced (fig. 14) with anteriorly directed members longer than posteriorly directed ones. Valva approximately triangular, undivided, extended at apex and with an associated lobe on dorsal part (visible in fig. 4). Transverse bar of transtilla present. Aedeagus: swollen anteriorly, narrowing nearly to



Figs 1-8. *Trifurcula* spp., male genitalia. 1-3. *T. pallidella* Zeller. 1. Genital capsule, ventral view. 2. Inner aspect of valva. 3. Aedeagus, lateral view. 4-5. *T. pullus* spec. nov. 4. Genital capsule, ventral view. 5. Aedeagus, ventral view. 6-8. *T. barbertonensis* spec. nov. 6. Genital capsule, ventral view. 7. Inner aspect of valva. 8. Aedeagus, ventral view.

a point posteriorly; ventral process absent; two pairs of strong, ventral carinae extending beyond phallotreme; vesica with patch of spiculate cornuti, a row of stouter cornuti and a striate thickening.

MATERIAL EXAMINED. Holotype ♂, SOUTH AFRICA: Transvaal, Kruger National Park, Lower Sabi, 26.iii.1952, Janse and Vári; paratype, 1♂, data as holotype. Specimens housed in the Transvaal Museum.

T. pullus is darker than any known species of *Trifurcula*. Whilst the wing venation is similar to that of *pallidella*, in the forewing R_{2+3} is coincident with R_1 to form R_{1+2+3} . The shapes of the gnathos, the aedeagus and its ventral carinae are useful distinguishing features of the species.

***Trifurcula barbertonensis* spec. nov.**, figs 6–8, 11, 12, 15, 22, 23.

ADULT. ♂. Wingspan 3.8–4.6 mm. Head-tuft orange-ochre but more pale than in *pullus*. Antenna extends to just beyond half length of forewing; 27–28 segments; flagellum submoniliform. Thorax and forewing pale ochre with fuscous scales variously distributed but not extensive. Abdomen greyish.

Forewing venation (fig. 22). Reduced. R_1 and R_{2+3} absent. R_{4+5} present. Cu never free from M. M_{1+2} (?M+Cu) present as a single branch. $1+2A$ coincident throughout length, no anal loop.

Hindwing venation (fig. 23). Rs and M form a common trunk at base. M not branched into M_1 and M_2 apically.

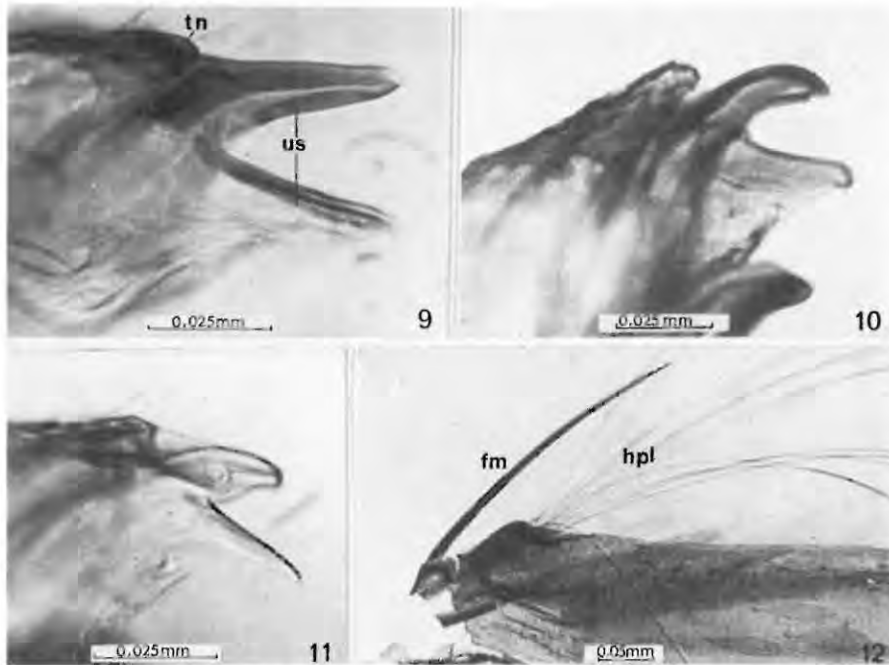
Male genitalia (figs 6–8, 11, 15). Vinculum with anterior extension rounded. Tegumen extended into short pseuduncus. Uncus in lateral view as in fig. 11. Gnathos fused, with pair of long, narrow lateral arms; central element with short, stout extensions (fig. 15) and sensillae. Valva undivided, approximately triangular, extended at apex. Transverse bar of transtilla present, short. Aedeagus narrows to a point posteriorly; ventral process absent; pair of ventrolateral, broad-based carinae present which terminate in short, outwardly curved spines; vesica with many long spiculate cornuti, a row of stouter cornuti and a striate thickening.

MATERIAL EXAMINED. Holotype ♂, SOUTH AFRICA: Transvaal, Barberton, 28.ii.-1.iii.1974, L. & G. Vári; paratypes, 5♂, data exactly as holotype; 2♂ Pretoria, 11.iii.1971, L. Vári; Heidelberg, Suikerbosrand Nature Reserve, 1♂ 17.iii.1978, D. M. Kroon. All specimens housed in the Transvaal Museum.

T. barbertonensis can be distinguished from all other members of the genus by the single branch of M in the hindwing. The venation of the forewing is unique in its extreme reduction. The shape of the gnathos and its remarkable small outgrowths (fig. 15) are very useful distinguishing features, and the shape of the paired carinae is characteristic.

The reasons for including *barbertonensis* in the genus *Trifurcula* are presented below.

The following information is recorded because although it has no bearing upon the diagnosis of *barbertonensis* it may be useful in assessing relationships amongst nepticulid species on a wider scale. Eyes not reduced, eye-index of Powell (1973) = 0.9. Galeae approximately three-quarters of dorsoventral length of head-capsule; maxillary



Figs 9-12. *Trifurcula* spp. 9-11. Male genitalia, lateral view of uncus (us) and tegumen (tn). 9. *T. pallidella* Zeller. 10. *T. pullus* spec. nov. 11. *T. barbertonensis* spec. nov. 12. *T. barbertonensis*, base of hindwing; frenulum (fm), hair pencil (hpl).

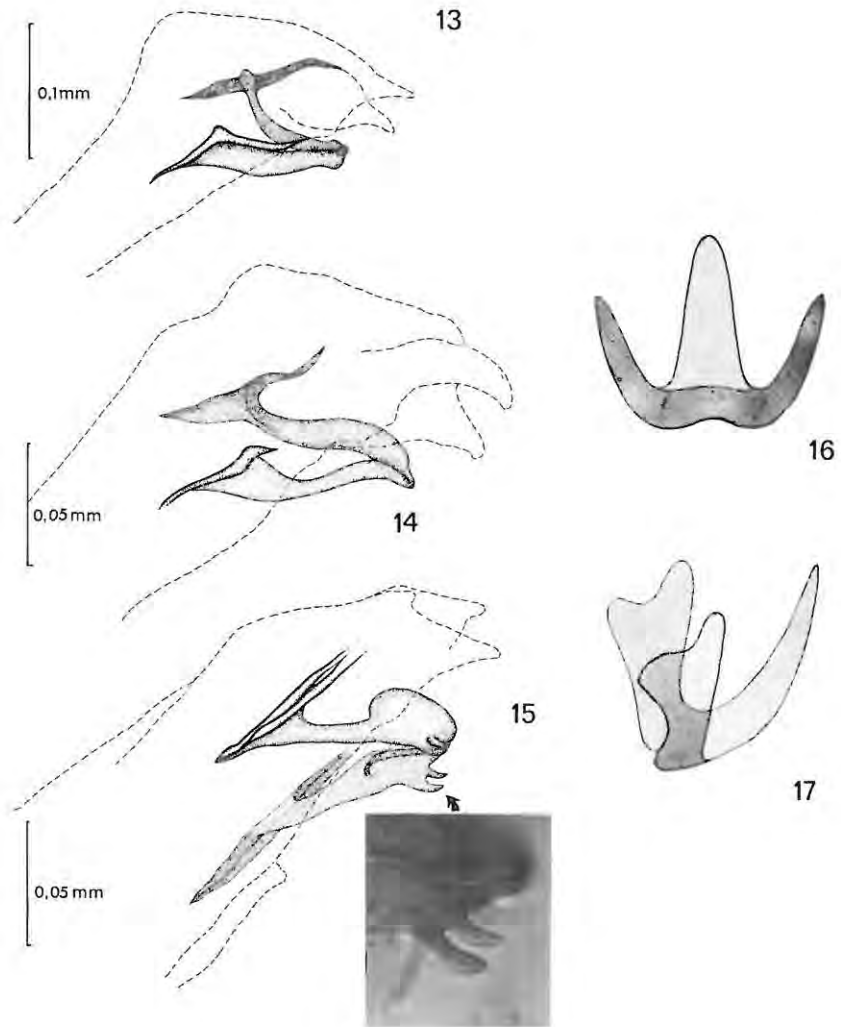
palpi five-segmented. Labial palpi three-segmented. Hindwing with frenulum and a small hair-pencil (fig. 12) arising on costa near base of wing.

There is a female with venation identical to that of *barbertonensis*. The forewings have very few fuscous scales and the abdomen is pale ochre. I am not convinced that the specimen belongs to *barbertonensis* and so it is not included in the type-series. The end of the abdomen is broadly rounded, the ductus bursae has an associated sclerotisation and the corpus bursae has a pair of very weakly sclerotised signa reticulata that are extremely difficult to see. Specimen data: SOUTH AFRICA: Transvaal, Pretorius Kop, 1.iv.1952, L. Vári. It is housed in the Transvaal Museum.

Characters

Some of the characters that are present in *Trifurcula*, including the South African species, also occur in the palaearctic genera *Fedalmia* Beirne and *Levarchama* Beirne. Borkowski (1972) and Emmet *in* Heath (1976) noted that *Trifurcula* and *Levarchama* species feed on Papilionoideae in their larval stages, and that all three genera share some characters in the wing venation.

The cladogram (fig. 24) was constructed on the basis of the following characters.



Figs 13-17. Nepticulidae. 13-15. *Trifurcula* spp., lateral view of gnathos (stippled). 13. *T. pallidella* Zeller. 14. *T. pullus* spec. nov. 15. *T. barbertonensis* spec. nov. 16-17. Generalised nepticulid gnathos. 16. Ventral view. 17. Lateral view.

1. *Uncus strongly divided dorsoventrally*

In lateral view, the uncus in *pallidella*, *pullus* and *barbertonensis* is divided into a well sclerotised dorsal part and a less well sclerotised ventral component (figs 9–11). This characteristic feature was omitted from the diagrammatic illustration of *Trifurcula* given by Beirne (1945). The uncus is also divided dorsoventrally in other nepticulids, e.g. *Niepelitia* Strand, but the division, which is very slight, is confined to the tip of the uncus. It would be of great value to know whether this character is also present in *Fedalmia* and *Levarchama*.

2. *Extension of tegumen (pseuduncus of Beirne) short*

The tip of the dorsal component of the uncus extends well beyond the extension of the tegumen (as in figs 9–11). The diagrammatic figures of Beirne show that this character is present in *Levarchama* and *Fedalmia*. The condition is also found in other nepticulids; it is a weak indicator of relationships.

3. *Gnathos differs from that of the generalised nepticulid type*

The basic design of the gnathos in *Trifurcula*, best seen in lateral view, is shown in figs 13–15. It is different from the generalised nepticulid gnathos, which has a characteristic tongue-shaped central element and short lateral processes (figs 16 & 17).

4. *Anterior extension of vinculum rounded*

The development of this character has probably occurred many times during the evolution of the Nepticulidae because it is present in a number of unrelated species. The vinculum is rounded in the South African and in nearly all the European *Trifurcula* species, and in *Levarchama*, which means that the feature is probably present in the morphotype of the *Trifurcula/Levarchama* sister group.

5. *Valva approximately triangular, terminating in a narrow tip*

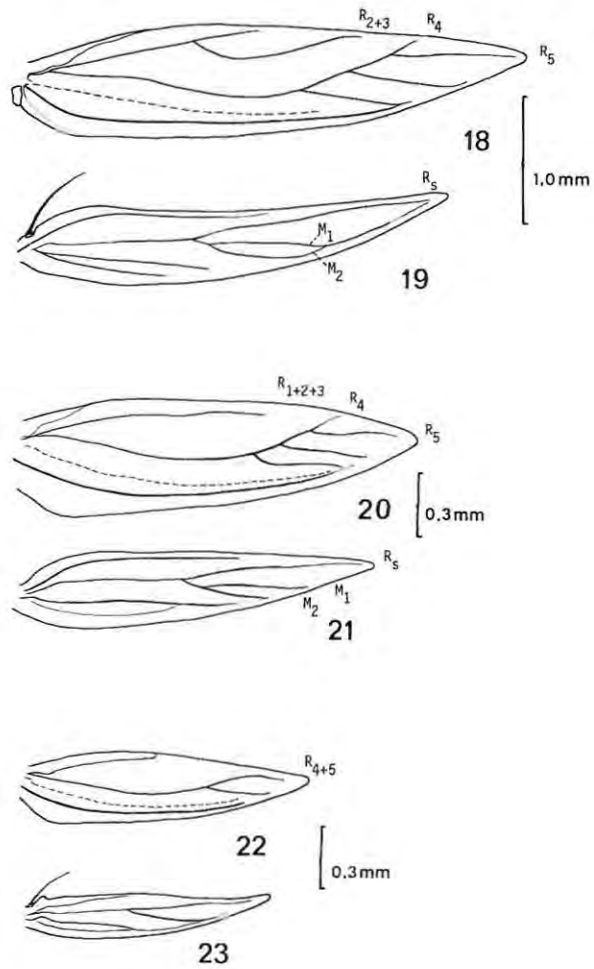
The shape of the valvae in the Nepticulidae is a character the taxonomic value of which is difficult to assess. The extended apex is of note, and although the valvae are not strong indicators of membership of the genus they certainly help in the exclusion of many species from it. The shape of these structures in *Fedalmia* and *Levarchama* basically conforms with that found in *Trifurcula*.

6. *Aedeagus narrows abruptly towards phallosome*

This is an unusual character in the Nepticulidae.

7. *Vesica (endophallus) with long, spiculate cornuti*

Several species of Nepticulidae have long spiculate cornuti. The presence of this type seems to be universal in *Trifurcula*. (The striate thickening present in all the species is a generalised feature widespread in the family.)



Figs 18-23. *Trifurcula* spp., wing venation. 18-19. *T. pallidella* Zeller. 18. Forewing. 19. Hindwing. 20-21. *T. pullus* spec. nov. 20. Forewing. 21. Hindwing. 22-23. *T. barbertonensis* spec. nov. 22. Forewing. 23. Hindwing.

8. Loss of link between R_{2+3} , and R_4 , R_5 (or R_{4+5}) in forewing

This is one of the most marked characteristics of *Trifurcula*. In *pullus* R_1 and R_{2+3} are coincident throughout their length. A further and more striking reduction occurs in *barbertonensis*, where $R_1 + R_{2+3}$ is lost. This is the last known phase of the transformation series from loss of the connection between R_{2+3} and R_4 , R_5 (e.g. *pallidella* fig. 18), through the fusion of R_1 and R_{2+3} (*pullus* fig. 20), to loss of this fused vein (*barbertonensis* fig. 22).

9. *M* represented by two branches after its divergence from *Rs* in the hindwing

This character is also present in *Fedalmia* and *Levarchama*. In *T. barbertonensis* the two branches of *M* are considered to have re-fused and thus they effectively exhibit the generalised condition in the Nepticulidae. It is unlikely that *Trifurcula* represents a particularly primitive element of the Nepticulidae. I consider that the condition of the media in *barbertonensis* is a secondary feature that parallels the general situation found in the family.

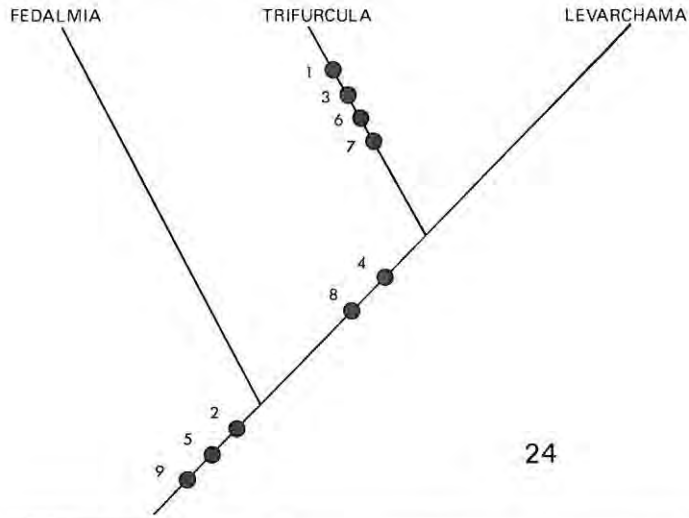
DISCUSSION

Three main questions arise from the preceding analysis. First, why should the apparently incongruous species *T. barbertonensis* be included in *Trifurcula* when the latter is a homogeneous taxon, with apparently little variation in wing venation and genitalia, in the palaeartic region? Second, what are the strengths and weaknesses of the cladogram that unites *Fedalmia*, *Trifurcula* and *Levarchama* (fig. 24)? Third, do the palaeartic *Trifurcula* species share a more recent common ancestor with the new South African species or with *Levarchama*, and how does this problem affect the taxonomic rank of the latter?

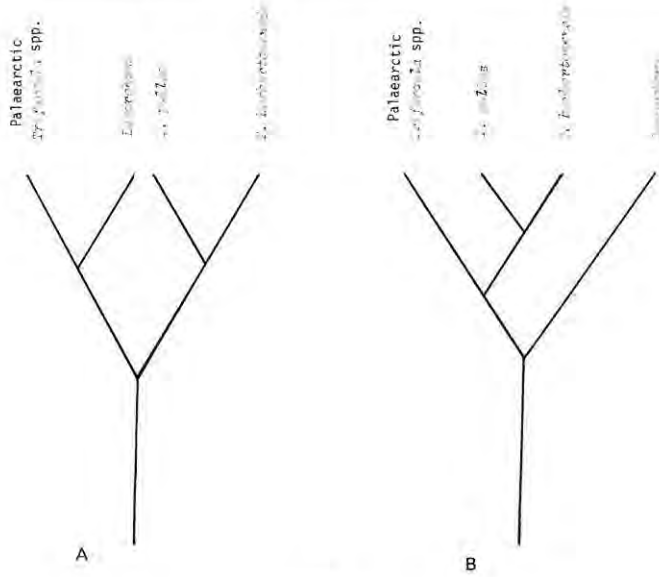
In addition to its unique features, *T. barbertonensis* possesses four characters (numbers 1, 3, 6, 7 above) that reveal its close relationship to *pallidella*. Although veins R_1 and R_{2+3} in the forewing of *barbertonensis* are lost, this reduction is merely the last stage of a transformation series derived from the *Trifurcula* morphotype (see character 8): the reduction is an autapomorphic (uniquely derived) character of *barbertonensis*. The synapomorphic (shared derived) condition of character 8 (the loss of the link between R_{2+3} and R_4 , R_5) for *Trifurcula* and *Levarchama* still applies to *barbertonensis*.

The examination of *barbertonensis* and *pullus* has helped me to delimit the boundaries of the genus *Trifurcula* more clearly. If the presence of related species geographically far apart from each other implies a long temporal isolation of them, then characters shared only by the isolates are probably present in the morphotype and therefore apomorphic for the clade to which the species belong. Chance dispersal of nepticulids is unlikely. Even if it did happen, the high degree of host-plant specificity in the Nepticulidae makes the chance of successful colonisation in areas with very different plants unlikely (for example, South Africa and Europe). The distribution of nepticulid taxa is best explained by continental drift, and a long and close association with their angiosperm hosts.

With regard to the second question, Beirne (1945) and particularly Borkowski (1972) noted similarities amongst *Fedalmia*, *Trifurcula* and *Levarchama*. However, neither of these writers clearly stated whether or not the relevant characters were derived or generalised. I consider that character 9, and also possibly characters 2 and 5, are synapomorphic for the whole cladogram (fig. 24). The two-branched condition



24



25

Figs 24-25. Cladograms. 24. Cladogram uniting *Fedalmia*, *Trifurcula* and *Levarchama*. 25A and B. Alternative hypotheses of cladistic relationships amongst palaeartic *Trifurcula* species, *Levarchama*, and South African *Trifurcula* species. Black circles represent apomorphies, numbered as in text. For details see text.

of the medial vein of the hindwing is considered to be a derived feature because the single-branched condition is present in the out-group of the Nepticulidae (the Opostegidae), and because it is the most widespread state within the Nepticulidae. The narrow, extended apex of the valvae (character 5) is a feature shared by *Fedalmia*, *Trifurcula* and *Levarchama* (see figures of Beirne 1945, and those in this paper) but, since such a condition exists in species belonging to other genera, it is an apomorphy of doubtful standing. The same argument applies to the short extension of the tegumen (character 2). Characters 2 and 5 probably evolved more than once within the Nepticulidae; they can still be apomorphic for their respective taxa however.

Borkowski (1972:704) noted similarities in the larval feeding habits of *Fedalmia* and *Trifurcula*. The larvae of *Trifurcula* and *Levarchama*, where known, feed on Papilionoidea. Unfortunately no information is available for the South African *Trifurcula* species. The phylogenetic interpretation of the larval feeding habits of the Nepticulidae remains unclear to me, and so no such information has been used in the construction of the cladogram (fig. 24). To relate larval structure to habits would be a rewarding study that would undoubtedly shed some further light upon cladistic relationship within the family.

Borkowski (1972) showed how the radial sector vein in the forewing of *Trifurcula* and *Levarchama* split, secondarily, into one component associated with the radius and one associated with the media (character 8). This is a very convincing apomorphy that reveals the sister group relationship between the two genera.

Of the four characters shared by the palaeartic and the South African *Trifurcula* species (see cladogram), numbers 1 and 3, which refer to the shapes of the uncus and the gnathos respectively, are of particular interest. Character 1 may be conservatively placed in fig. 24. In this paper it has been useful for revealing relationships between the type-species of *Trifurcula*, and *pullus* and *barbertonensis*. It may also be present in *Fedalmia* or *Levarchama* or both. Since Beirne omitted it from his diagrammatic lateral view of *Trifurcula* he may have overlooked it in these other genera as well. The usual shape of the gnathos in the Nepticulidae is illustrated in figs 16 & 17. The structure comprises a central tongue-shaped element and a pair of lateral processes. This is quite different from the condition found in *Trifurcula*, (compare fig. 16 with figs 1, 4, 6 and fig. 17 with figs 13-15). Although the shape of the gnathos differs amongst *pallidella*, *pullus* and *barbertonensis*, its basic design is the same: this is particularly clear from the lateral views. The type of gnathos shown in figs 16 & 17 is considered to be plesiomorphic because it is found in the nepticulid out-group, the Opostegidae, and because it is the most widespread condition within the Nepticulidae. Eyer (1924, plate 31 fig. 1) illustrated the male genitalia of *Opostega nonstrigella* Chambers (Opostegidae). This structure is of the same general shape as that of the usual nepticulid one (fig. 16)

The rounded shape of the anterior extension of the vinculum (character 4) is a feature that, if it is correctly assumed to be apomorphic, has been reversed in certain species.

The final question concerns the problem of the cladistic analysis of the holophyletic (the term is used in the sense of Ashlock 1971) group comprising *Trifurcula* and *Levarchama*. Do *Pullus* and *barbertonensis* form the sister group of the palaeartic *Trifurcula* species and *Levarchama*, or does *Levarchama* form the sister group of the palaeartic and South African *Trifurcula* species (cladograms A and B respectively in fig. 25)? A more detailed study of the male genitalia of *Levarchama* will help consider-

ably in deciding which of the two is correct. Since the present study is mainly about the relationship of the two new South African species to the type-species of *Trifurcula*, and as I have not examined representatives of *Levarchama*, the possible alternatives are presented but the problem is not resolved. *Levarchama* is only known from the palaeartic, and so the most parsimonious interpretation of the distribution data is that shown in the cladogram in fig. 25A; that is, *Levarchama* shares a more recent common ancestor with the palaeartic *Trifurcula* species than with the South African *pullus* and *barbertonensis*. If this is the case then, on cladistic grounds, *Trifurcula* and *Levarchama* should be regarded as congeneric.

ACKNOWLEDGEMENTS

I am indebted to Professor C. Wilkinson, Vrije Universiteit, Amsterdam, and to Dr E. S. Vrba, Transvaal Museum, Pretoria, for their incisive comments on an earlier draft of this manuscript. I thank Dr L. Vári for advice during the course of the work. The line drawings were prepared by Miss D. van Draanen; I am very grateful to her for producing work of such a high quality. I thank Mr H. Dullaart, Transvaal Museum, Pretoria, for photographic assistance, and also those persons, cited above, who collected the specimens on which this work was carried out.

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ANNALS OF THE TRANSVAAL MUSEUM
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**THE GENUS *NIEPELTIA* STRAND: TAXONOMY, AND
COMMENTS ON STRUCTURE AND RELATIONSHIPS
(LEPIDOPTERA: NEPTICULIDAE)**

By M.J. SCOBLE

Transvaal Museum, Pretoria

(With 80 Text-figures and one Table)

ABSTRACT

SCOBLE, M.J. 1980. The genus *Niepeltia* Strand: taxonomy, and comments on structure and relationships (Lepidoptera: Nepticulidae). *Ann. Transv. Mus.* 32(8):197-229.

The genus *Niepeltia* is redescribed and all the known species are reviewed. Structures of importance in the systematics of the genus are discussed, and the plesiomorphic/apomorphic states of the characters are evaluated. Twenty-three species are considered in this work; six names are recombined; of the 20 species found in southern Africa 16 are described as new. All the species, for which such information is available, are leaf-miners. The known distribution of the group is mapped, although it is stressed that this is unlikely to represent the true range of the genus.

INTRODUCTION

The genus *Niepeltia* Strand is well represented in southern Africa. Only three species belonging to this taxon, two from Europe and one from the Orient, are known to me from the rest of the world.

The localities from which species of *Niepeltia* have been collected are summarised on the maps (Figs 1a, b). This is certainly only a patchy indication of the true distribution of *Niepeltia*, and I hope it will encourage others to examine their nepticulid material so as to establish a more complete picture of the range of the genus.

A knowledge of the distribution of the Nepticulidae is of value because it indirectly gives us a clue to the approximate age of the component taxa, and tells us the geographical distribution of characters. The latter provides information by which the plesiomorphic or apomorphic nature of a character may be judged. Assuming that vicariance is responsible for the intercontinental distribution of *Niepeltia* then, in order to explain its widespread distribution, the genus must have originated before continental drift. *Niepeltia*, *Ectoedemia* Busck, *Stigmella* Schrank and *Trifurcula* Zeller (*sensu* Beirne, 1945) are the only four nepticulid genera that have been found both in the northern and southern hemispheres. *Ectoedemia* and

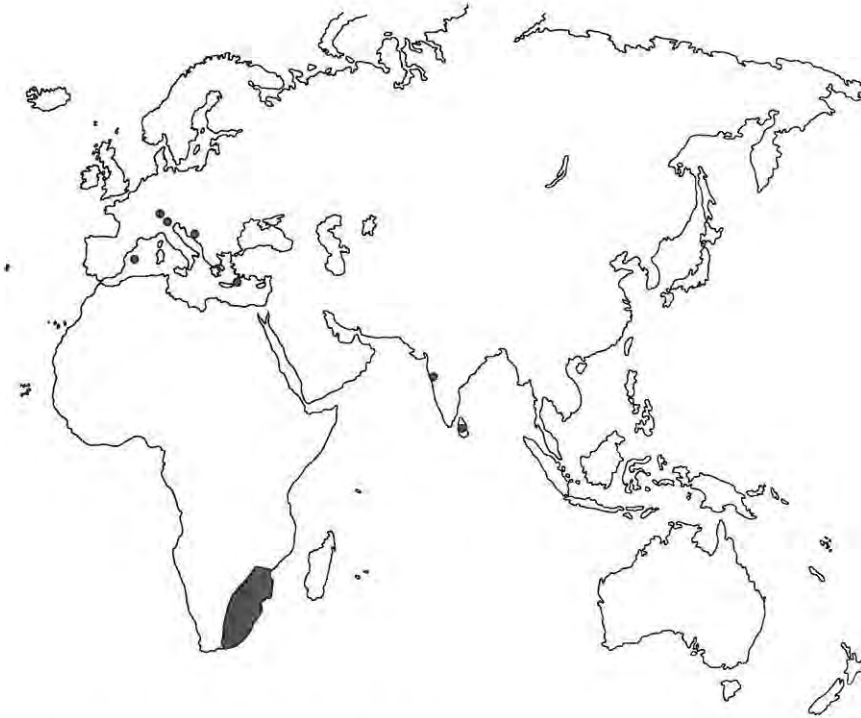


FIG. 1a. Known world distribution of *Niepeltia*.

particularly *Stigmella* are still more widely distributed than *Niepeltia*.

The nepticulid fauna of the world is but poorly collected, as pointed out by Davis (1978 *b*). Nevertheless, the fact that the above-mentioned genera have been found amongst nepticulid material collected from many parts of the globe suggests that our existing collections represent not simply chance samples, giving a purely biased impression of generic distribution, but rather that they provide a reasonable skeleton for the construction of a predictive classification. Sensible extrapolation is the essence of systematic biology; indeed all systematics is extrapolative as systematists can obviously work only on samples of any given taxon.

COMMENTS ON MORPHOLOGY AND RELATIONSHIPS

Whilst a full description of the genus is given below, certain features deserve further comment. The characters discussed include those that are (1) generalised (plesiomorphic) within the heteroneurous monotrysians, (2) generalised within the Nepticulidae, (3) unique (derived or apomorphic) to the genus *Niepeltia* and (4) present in a number of nepticulid species of different supra-specific taxa.

Characters that are considered to be generalised in the Nepticulidae include the reduction in head sulci, the five-segmented maxillary palpi and the three-segmented labial palpi, the loss of ocelli and the presence of chaetosemata.

The eye-index (Powell, 1973), which expresses the relative size of the compound eye to the head, is 1.0-1.2 in the four species of *Niepeltia* for which this feature was recorded. Certain species, or groups of nepticulid species, not belonging to this

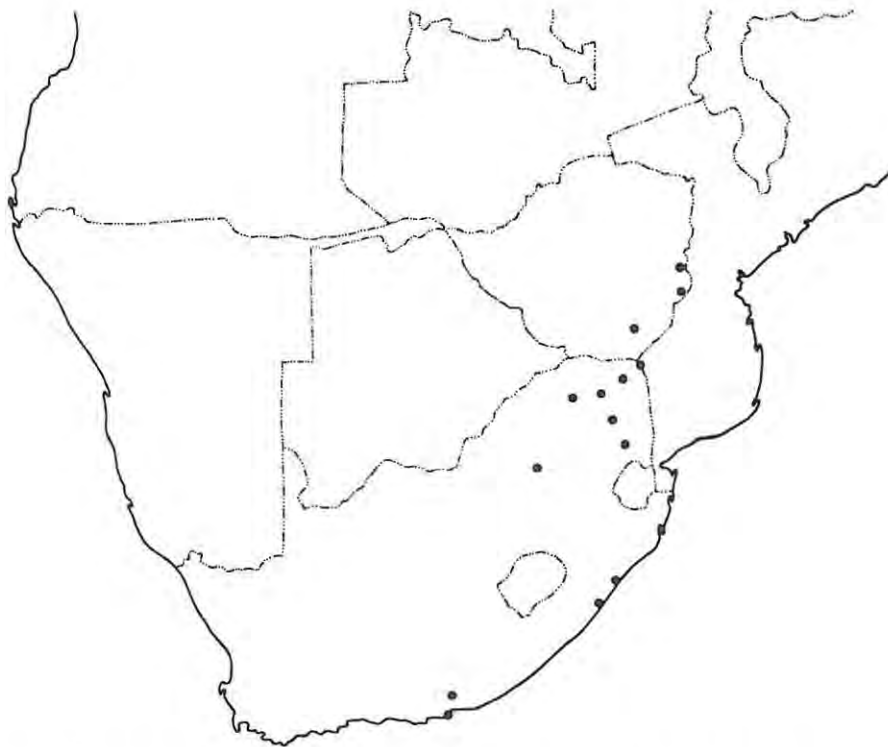


FIG. 1b. Localities in southern Africa from which *Niepeltia* species have been collected.

genus have a decidedly smaller eye. The larger eye is by far the most widespread condition within the Nepticulidae and that state is probably plesiomorphic for the family.

There is a pair of raised cuticular patches, presumed to be chaetosemata, on the dorsal surface of the head. These are similar to those in *Dyseriocrania griseocapitella* (Walsingham) (Eriocraniidae); see Davis (1978a, Fig. 16).

The galeae are short in *Niepeltia* (Fig. 2), a general, but not universal, condition of the Nepticulidae. In one undescribed nepticulid the galeae are two and a half times the length of the head-capsule.

In the thorax, features generalised for the Nepticulidae include, for example, the frenular-retinacular wing-coupling in the male, the representation of the radial and medial veins of the hindwing each by a single branch (Fig. 5) and the absence of epiphyses on the forelegs.

In general appearance the forewings of the moths are usually ochreous or pale off-white with variable amounts of fuscous scaling. So many nepticulid species from other taxa are similarly coloured that it is very difficult to recognise whether or not a specimen belongs to *Niepeltia* without examining other characters. However, the tone of the ochreous ground colour is a clue to the recognition of this genus and it should not be totally rejected as a means of identification. There is little value in colouration for assessing relationships.

Specialised scales, sometimes shiny black, sometimes ochreous, are present on the wings of the males of a number of *Niepeltia* species considered in this paper and

of several nepticulids. These scales always have approximately the same shape and striations when viewed under the light microscope. They are widely distributed in the family, but within a given supraspecific taxon they may occur only in a few representatives.

The most striking feature in the male genitalia of *Niepeltia* species is the absence of the transverse bar of the transtilla. The structure has also been lost in a few other nepticulids (e.g. *Microcalyptris tenuijuxta* Davis; see Davis, 1978b) independently. The presence of the transverse bar is so widespread in the Nepticulidae that I consider its presence to be generalised (plesiomorphic) and its absence derived (apomorphic).

The vinculum is in the form of a 'ring' (terminology of Beirne, 1945). The ring is formed by the lateral arms and ventral plate which surround the aedeagus. Strictly speaking the lateral arms frequently fail to meet or are difficult to distinguish from the tegumen with which they fuse. Nevertheless this ring-shaped vinculum contrasts with the U-shaped form found in *Stigmella* where the lateral arms fuse with the *sides* of the aedeagus. On the basis of the shape of the vinculum, together with a number of other features, the Nepticulidae may be divided into two basic lineages: one represented by *Stigmella*, and a few other undescribed taxa, and the other comprising many taxa, including *Niepeltia*, which are usually ranked as genera.

The ventral plate of the vinculum is generally reduced to a flimsy membrane in *Niepeltia*. This is a curious feature that I have not seen in other nepticulids. The caudal edge of this structure is often thickened, sometimes markedly (e.g. as in Fig. 30; *cvp*).

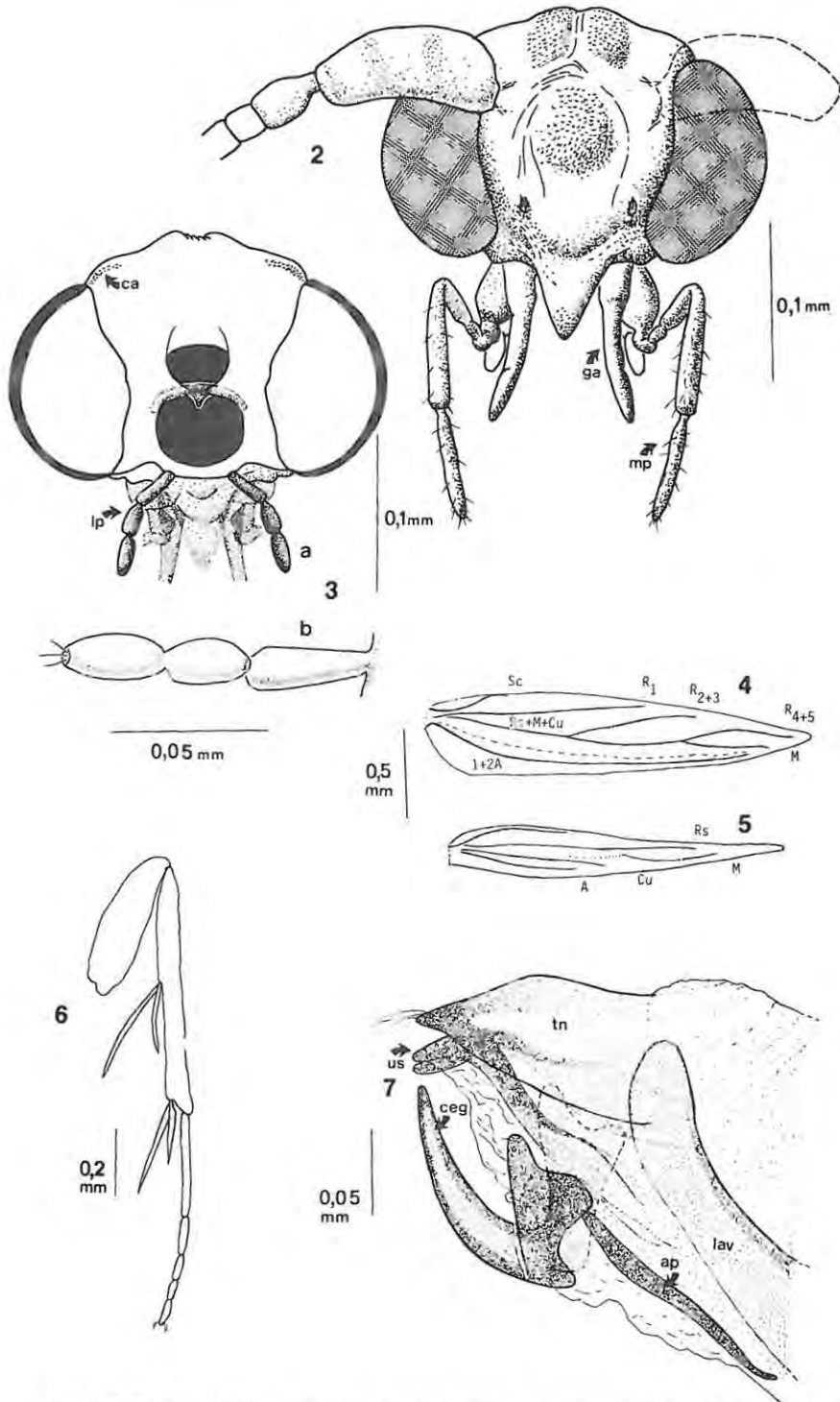
In *lanneivora* Vári an apodeme arises on each side of the genital capsule at the base of the gnathos and runs, for a short distance, alongside the lateral arm of the vinculum. The structure is best seen in lateral view (*ap* in Fig. 7). To a certain extent the bars resemble those in *Microcalyptris* Braun (see Davis, 1978b). An indication of these structures is present in some other *Niepeltia* species, but they are not well developed.

Fig. 7 also shows how the uncus is divided dorsoventrally at its tip. This division is confined to the tip of the uncus; it is much deeper in *Trifurcula* (*sensu stricto*) (Scoble, 1980). The general shape of the uncus is widespread in the Nepticulidae. In *Stigmella* the structure is of a different form, and in *Ectoedemia* it is absent (Scoble, 1978a).

The shape of the gnathos in *Niepeltia* is also similar to that of most other supraspecific taxa of the Nepticulidae.

Insufficient attention has previously been paid to the details of the complex of spines associated with the aedeagus in the Nepticulidae. Associated processes may form part of the external aedeagus or may be actually associated with the vesica (endophallus). The best way to differentiate these categories is to remove the aedeagus from the genital capsule, manipulate the spinose projections to see if they are fused or hinged to the aedeagus, and then to hook-out the vesica to examine the associated sclerotisations. In *Niepeltia* the large spinose 'lateral processes' (*lps* in Fig. 18) are associated with the outer layer of the aedeagus and not the vesica. In many non-*Niepeltia* species large spines found at the phallosome may be associated with the vesica. In *Niepeltia* the markings on the vesica are weak and comprise small denticulate cornuti and certain thickenings.

There is no ventral aedeagus-support (*juxta*) in *Niepeltia*. Such a structure is found in certain other nepticulids in which it is variously shaped and fused to the vinculum (e.g. *Stigmella allophylica* Scoble; see Scoble, 1978b). As the term 'juxta' has been used for this process it is not used for the 'ventral process' (*vp* in Fig. 18) hinged to the aedeagus of *Niepeltia* species. This ventral process (termed as such in



2-7, 2-3. *Niepeltia molleivora* spec.nov. 2. Head-capsule, anterior view. 3a. Head-capsule, posterior view. 3b. Labial palpus. 4-5. *N. lorantivora* (Janse). 4. Forewing. 5. Hindwing. 6. *N. fuscofascia* spec.nov., hindleg. 7. *N. lanneivora* (Vári), male genitalia, lateral view.

the descriptions) is a prominent structure hinged to the aedeagus by a pair of lateral arms. The process is present in the members of another supraspecific taxon at present under review.

In one of the species, described below, the female has a short *pointed* ovipositor (Fig. 72). Such a structure is present in a few other nepticulids although the abdomen generally ends bluntly. Although it is a useful species-distinguishing character the structure is not of systematic value in defining supraspecific taxa. The function of the pointed ovipositor in the Nepticulidae is obscure. Observation has not borne out the obvious suggestion that the structure is used to inject eggs into plant tissue.

The presence of spines on the dorsum of the abdomen of the pupa is widespread in primitive moths. Pupal exuviae were recovered from cocoons of a few species of *Niepeltia* and the spines were examined. They are considerably smaller than those of a species of *Ectoedemia* examined (Scoble, 1979). The value of these characters has not yet been fully assessed, but there appear to be notable differences between supraspecific taxa.

Niepeltia is easy to distinguish from all other described nepticulid genera (see the diagnosis below). Precise relationships, however, are less clear and will be more easy to assess when further information on the Nepticulidae is available. At present all that can be said is that *Niepeltia* is a member-lineage of the 'non-*Stigmella*' group of nepticulids that includes most of the supraspecific taxa of the family so far described. Within this group it is difficult to find apomorphic characters that unite *Niepeltia* to one rather than another genus. The present paper concentrates on the distinguishing features of the genus and of its component species, and includes general remarks on structure. An assessment of the cladistic and phenetic relationships of nepticulid taxa is in progress.

TAXONOMY

Genus *NIEPELTIA* Strand

Niepeltia Strand, 1934. Int. ent. Z. 28:241 [Replacement name for *Weberia* Müller-Rutz, 1934. *Mitt. schweiz. ent. Ges.* 16:122. Type-species: *Weberia platani* Müller-Rutz, 1934]

Weberina Müller-Rutz, 1934. *Mitt. schweiz. ent. Ges.* 16:122. [Replacement name for *Weberia* but published after the name *Niepeltia*]

The name *Weberia* was originally proposed for the genus by Müller-Rutz (1934) in *Mitteilungen der Schweizerischen entomologischen Gesellschaft*. It was discovered, however, that this name was preoccupied. Accordingly, Müller-Rutz changed the name to *Weberina* in an amendment published on a slip attached to the September issue of the journal. However, in August 1934 Strand proposed the name *Niepeltia* as a replacement for *Weberia*. Despite the unethical procedure of this action (duly expressed by the board of the Swiss Entomological Society in its journal, 1934:148 in a protest note pointing out that Strand had not examined the insects, nor given Müller-Rutz the opportunity to change the name himself) the replacement name *Niepeltia* was published before that of *Weberina* and is therefore the valid name of the genus according to the *International Code of Zoological Nomenclature*.

ADULT. *Head* (Figs 2, 3). Hypognathos. Rough scaled; tuft on front of head and vertex usually concolourous ochre or off-white; tuft on vertex occasionally darker. Antenna extends approximately half to three-quarters length of forewing; number of segments may vary within a given species, generally about 28; scape large, articulates with head fairly high up, forming a white to off-white eye-cap sometimes with a few fuscous scales; pedicel slightly larger than flagellar segments,

concolourous with, and considerably smaller than, scape (Fig. 2); flagellum darker above than below, submoniliform, terminal segment conical. Compound eye relatively large, eye-index 1.0-1.2. Galeae short, extend only slightly beyond labial palpi; approximately half length of maxillary palpi. Maxillary palpi five-segmented, segment two weakly demarcated from segment three. Labial palpi (Fig. 3b) three-segmented with shallow pit at end of third segment from which arise a few (usually three) sensilla.

Thorax. Dorsum, tegula and forewing concolourous. Wingspan (forewing) 3.2-6.0 mm. Forewing: dorsal surface ground colour generally ochre, sometimes pale off-white with variable amount of fuscous present either as irrorations, patches or fasciae; fringe grey; ventral surface dull fuscous or pale, a yellowish tinge to fringe at apex, with shiny black scales in male of one species. Venation (Fig. 4): Sc short, only present at base of wing; R_1 almost meets costal margin approximately halfway along the margin; R_1 runs separately from R_5 from base of wing; R_{2+3} nearly reaches costal margin; R_4 and R_5 represented by a single branch R_{4+5} ; M fuses with R_5 from base of wing to form $R+M$, represented by a single branch (M_{1+2}) terminally; Cu not present as a separate vein, either coincident with R_5 and M or possibly absent; 1A and 2A coincident throughout length, represented by single, thick vein, possibly a faint indication of 3A. Retinaculum in male comprising a series of hooked scales situated near base of wing on costal fold. Hindwing: grey, sometimes with special scales on dorsal and ventral surfaces in the male. Venation (Fig. 5): Sc short; R and M form a common trunk ($R+M$) basally, later diverge into separate branches; Cu and A each represented by a single branch. Frenulum present in male absent in female; costal spines present in female. Foreleg fuscous, without epiphysis or tibial spurs; midleg off-white, sometimes with fuscous on tibia and tarsus, with one pair of tibial spurs situated at distal end of tibia; hindleg more or less concolourous with mesothoracic leg, tibia with one pair of spurs near centre, the other distal, both pairs with one spur long and one short (Fig. 6).

Abdomen. Dorsum fuscous, unless otherwise stated in species descriptions; pair of tufts of ochreous, hair-like scales arising from caudal aspect of segment eight of male. Ventral surface pale, with pair of weakly defined fenestrae, situated close together, on sternum four of female; absent in male.

Male genitalia: vinculum with cephalic margin of anterior extension (Scoble, 1978b: 115) excavated to a variable degree; ventral plate frequently reduced to a flimsy membrane, sometimes with caudal margin heavily sclerotised; lateral arms nearly join caudally, articulate with base, not sides, of tegumen; occasionally with associated sclerotised apodeme (Fig. 7) associated with lateral arms, one on each side. Tegumen forms hood over genitalia, broad at base, tapering caudally. Uncus in shape of an inverted V, well sclerotised, tip divided dorso-ventrally. Gnathos fused, W-shaped in ventral view, central element (*ceg* in Fig. 7) extends ventral to lateral elements. Valva narrow, base often extended inwardly in form of a projection. Transverse bar of transtilla absent. Juxta (e.g. as in *Stigmella allophylica*; see Scoble, 1978b) absent. Aedeagus with (1) a ventral process, usually forked or emarginate caudally, with a pair of lateral arms which hinge to aedeagus, (2) a pair of lateral processes, the bases of which meet the bases of the lateral arms of the ventral process and the tips of which extend beyond the phallotreme (3) the vesica (endophallus) usually marked with small cornuti, and various thickenings. Ejaculatory duct enters aedeagus ventrally, approximately halfway along its length.

Female genitalia: anal papillae generally broad at base, apophyses rarely attenuated to form short, relatively pointed ovipositor. Bursa copulatrix; ductus with complex sclerotisations; corpus with pair of reticulate signa.

LARVA. Leaf-miner throughout life, forming linear mines, where known. Host-plants are summarised in Table I.

PUPA. Spines on dorsal aspects of segments two to eight of abdomen small, arranged in about four rows.

DIAGNOSIS. ADULT. Eye not small. Galeae short. Forewing: usually pale ochre, with fuscous irrorations or markings; venation: R_1 runs separately from R_2 from base of wing; R_{4+5} and M_{1+2} present as single branches; M fused with R_2 for most of its length; Cu coincident with R_2+M (or absent); $1+2A$ united throughout length. Hindwing venation: M represented as a single branch *not* as M_1 and M_2 as in *Trifurcula (sensu stricto)*. Male genitalia: vinculum with lateral arms *not* fused to sides of tegumen; uncus present in shape of an inverted V; gnathos fused, W-shaped in ventral view, central member not divided; transverse bar of transtilla absent; aedeagus with hinged ventral process and pair of lateral processes. Female genitalia: ductus bursae with complex sclerotisations; corpus bursae with pair of reticulate signa.

LARVA and PUPA. As description.

TABLE I. Host-plants of *Niepeltia* species

PLANT	NIEPELTIA SPECIES
ANACARDIACEAE	
<i>Lannea discolor</i>	<i>N. lanneivora</i>
<i>Pistacia lentiscus</i>	<i>N. minimella</i>
CAPPARACEAE	
<i>Boscia oleoides</i>	<i>N. lorantivora</i>
COMBRETACEAE	
<i>Combretum apiculatum</i>	<i>N. combretella</i>
<i>Combretum molle</i>	<i>N. molleivora</i>
<i>Combretum zeyheri</i>	<i>N. zeyheriae</i>
EUPHORBIACEAE	
<i>Bridelia micrantha</i>	<i>N. obliquella</i>
LEGUMINOSAE	
<i>Brachystegia</i> sp.	<i>N. fuscofascia</i>
PLATANACEAE	
<i>Platanus orientalis</i>	<i>N. platani</i>
RHIZOPHORACEAE	
<i>Cassipourea gerrardi</i>	<i>N. mariepsensis</i>
RUBIACEAE	
<i>Canthium gilfillanii</i>	<i>N. rubiaevara</i>
<i>Canthium inerme</i>	<i>N. rubiaevara</i>
<i>Tapiphyllum parvifolia</i>	<i>N. rubiaevara</i>
RUTACEAE	
<i>Zanthoxylum capense</i>	<i>N. fagarivora</i>

CHECK-LIST OF *NIEPELTIA* STRAND

(All species are from southern Africa unless otherwise indicated).

- N. platani* (Müller-Rutz) [type-species, Europe]
N. minimella (Rebel) comb.nov. [Europe]
N. combretella (Vári) comb.nov.
N. vumbaensis spec.nov.
N. molleivora spec.nov.
N. zeyheriae spec.nov.
N. rubiaevora spec.nov.
N. obliquella spec.nov.
N. fagarivora (Vári) comb.nov.
N. fuscofascia spec.nov.
N. umdoniensis spec.nov.
N. pundaensis spec.nov.
N. lorantivora (Janse) comb.nov.
N. krooni spec.nov.
N. acumenta spec.nov.
N. bispinata spec.nov.
N. sellata spec.nov.
N. mariepsensis spec.nov.
N. lundensis spec.nov.
N. fulva spec.nov.
N. vacuolata spec.nov.
N. lanneivora (Vári) comb.nov.
N. clinomochla (Meyrick) comb.nov. [India and Sri Lanka]

Niepellia platani (Müller-Rutz), Figs 8, 9, 15, 16.

Selected references.

Weberia platani Müller-Rutz, 1934. *Mitt. Schweiz. ent. Ges.* **16**:122.

Weberina platani Müller-Rutz; Klimesch, 1940. *Z. wien EntVer.* **25**:191.

Niepellia platani (Müller-Rutz); Strand, 1934. *Int. ent. Z.* **28**:241.

Niepellia platani (Müller-Rutz); Hering, 1957. *Bestimmungstabellen der Blattminen von Europa* **2**:789.

Trijuvcula (Weberina) platani (Müller-Rutz); Klimesch, 1978. *Tijdschr. Ent.* **121**:253.

ADULT. ♂ Wingspan 5,2-5,4 mm. Tuft on front of head ochre; tuft on vertex dark brown. Forewing pale ochre with three large areas of fuscous scales, one basal to sub-basal, one medial and one terminal. Hindwing: shape as in Fig. 9; upper and lower surfaces covered with ochre scales except at tip. ♀ Not examined.

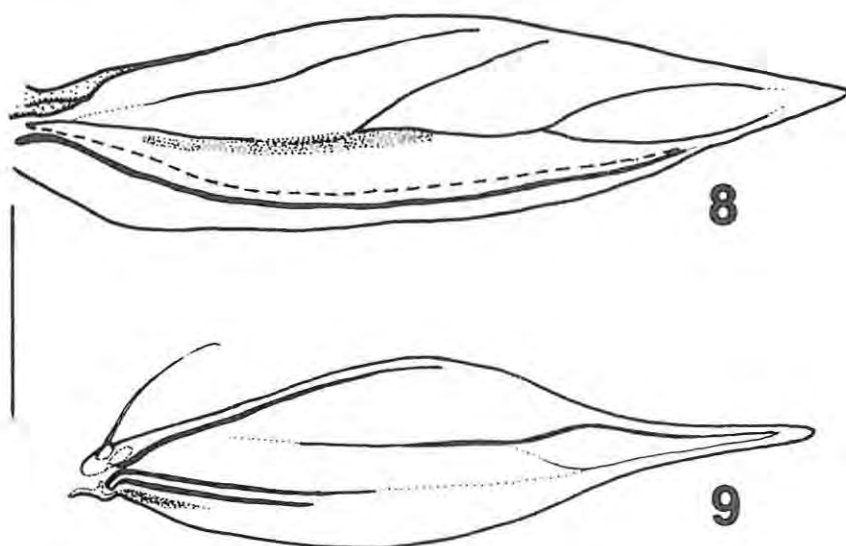
Male genitalia (Figs 15, 16). Anterior extension of vinculum deeply excavated, caudal edge in form of a thickened band. Valva approximately L-shaped. Aedeagus: ventral process subdivided at tip of each fork; cornuti on vesica present.

LARVA. Mines leaves of *Platanus orientalis* L. (Platanaceae), see figures of Hering (1957) and Klimesch (1978).

REMARKS. *N. platani* may be recognised by the pattern of the forewings, the thickened caudal edge of the anterior extension of the vinculum, the shape of the valves, and the form of the ventral process of the aedeagus.

The two male specimens examined came from Trento (Italy). Müller-Rutz collected the types in Mendrisio, Tessin (Switzerland), and Hering (1957) gives south and central Europe as the locality for the species. Klimesch (1978) has recorded leaf-mines of the species from the island of Rhodos.

The colour illustrations of *platani* in the original description (Müller-Rutz, 1934, pl.1) show the darker patches on the forewing to be considerably more purplish than the two male specimens I have examined, and also more so than any specimens of any other species of *Niepellia* that I have seen. Actually the ochre-



FIGS 8-9. *Niepeltia platani* (Müller-Rutz). 8. Forewing. 9. Hindwing. Scale = 0,5 mm.

fuscous pattern of this species is typical of *Niepeltia* species. The shape of the hindwing in the male of *platani* is very broad for two-thirds of its length; it then tapers to a point. In his colour illustrations and line drawings Müller-Rutz has labelled the moth with narrow hindwings as male and the one with broad wings as female: this error was pointed out by Klimesch (1940:191).

MATERIAL EXAMINED. EUROPE: Italy, Trento, Città, 2♂ emerged v.1946, mine on *Platanus occidentalis* x.-xi.1945 (Klimesch).

Niepeltia combretella (Vári) **comb.nov.**, Figs 17, 18.

Stigmella combretella Vári, 1955. *Ann. Transv. Mus.* 22:332, Pl.23:2; genitalia : Figs 2, 24; mine: Fig. 24.

ADULT. ♂ Wingspan 4,0-4,4 mm. Head-tuft ochreous. Forewing ground colour pale ochre above, fuscous near apex, and with a few dark scales scattered over proximal two-thirds of wing; underside with very small yellow patch at base.

Male genitalia (Figs 17, 18). Anterior extension of vinculum narrow; lateral arms with a notch near base of tegumen on both sides. Valva simple. Aedeagus: ventral process weakly forked; lateral processes comprising a pair of spines; vesica with a few minute cornuti, and thickenings.

LARVA. Forms a linear mine (Vári, 1955) in leaves of *Combretum apiculatum* Sonder (Combretaceae).

REMARKS. *N. combretella* is best distinguished from the next four species, with which it may be confused, by comparing the shapes of the valvae, and the ventral process of the aedeagus.

MATERIAL EXAMINED. ♂-Holotype, Transvaal Museum type no. 2974; SOUTH AFRICA: Transvaal, Pretoria, accession no. 241, 21.ix.1950 (Vári); paratype, Pretoria, accession no.101, 1♂ 25.i.1949 (Vári). Additional specimen, Pretoria, accession no.1692, 1♂ 29.xii.1955 (Vári); in Transvaal Museum.

Niepeltia minimella (Rebel) **comb.nov.**

Trifurcula minimella Rebel, 1926. *Verh. zool.-bot. Ges. Wien* **74/75**:110

Weberina lentiscella Groschke, 1944. *Mitt. Münch. ent. Ges.* **34**:117 [synonymy by Klimesch, 1978:256].

Niepeltia lentiscella (Groschke); Hering, 1957. *Bestimmungstabellen der Blattminen von Europa* **2**:781.

Trifurcula (Weberina) minimella (Rebel); Klimesch, 1978. *Tijdschr. Ent.* **121**:256.

Klimesch (1978) notes two subspecies, one from Rhodos and the other from Mallorca, and there are some striking differences in the genitalia figured by that author. The genitalia of the specimens from Mallorca resemble those of *platani*. I have not examined any Mallorca specimens, but the most noticeable difference between Klimesch's figure and the genitalia of *platani* is in the markings on the vesica of the aedeagus.

The larval host-plant of *minimella* is *Pistacia lentiscus* L. (Anacardiaceae).

Niepeltia vumbaensis spec.nov., Figs 19, 20.

ADULT. ♂ Wingspan 4,4 mm. Head-tuft deep ochre. Forewing pale ochre with a heavy, postmedial to subterminal band, much more clearly defined than apical scaling of *combretella*; fuscous scales present on fringe, a few on the costa, and on the tegulum.

Male genitalia (Figs 19, 20). Anterior extension very narrow; lateral arms without the notch characteristic of *combretella*. Valva simple. Aedeagus: ventral process broad at base, narrowing posteriorly; lateral processes divided at tip; vesica with cornuti more prominent than in *combretella*.

REMARKS. The presence of a fascia on the forewing distinguishes this species from *combretella*. The male genitalia are rather generalised and resemble those of several species. Useful distinguishing characters are the shapes of the valvae and the ventral process of the aedeagus, the divided tip of the lateral processes and the nature of the sclerotisations on the vesica.

MATERIAL EXAMINED. ♂-Holotype, RHODESIA: Vumba; accession no.2671, 1.iv.1964 (Vári); in Transvaal Museum.

Niepeltia molleivora spec.nov., Figs 21, 22, 66, 75.

ADULT. ♂, ♀ Wingspan 4,0-4,2 mm. Head-tuft pale ochre. Forewing pale ochre, lightly and fairly regularly irrorated with fuscous.

Male genitalia (Figs 21, 22). Ventral plate of vinculum with slightly thickened caudal edge. Fine apodeme stretching from near lateral process of gnathos to valva. Valva simple, fairly small. Aedeagus long; ventral process forked, each fork subdivided; vesica with cornuti larger than those of *combretella* and smaller than those of *vumbaensis*.

Female genitalia (Fig. 66). Ductus bursae with characteristic sclerotisations. Corpus bursae with long signa extending nearly its entirely length.

LARVA. Mines leaves of *Combretum molle* R. Br. ex G. Don (Combretaceae), Fig. 75.

REMARKS. The long aedeagus of *molleivora*, the relatively small valvae and the shape of the ventral process of the aedeagus serve to distinguish the species from *combretella* and *vumbaensis*. The fine apodemes stretching from the gnathos to around halfway down the valvae are difficult to discern. They are presumably homologous with the more prominent structures in some other species e.g. *lanneivora* (see below).

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Pretoria, accession no.191, 3.i.1950 (Vári); paratypes, all from Pretoria, accession no.191, 1♂ 3.i.1950; accession no.294, 1♂ 15.xi.1950, 1♂ 20.x.1961, 1♂ 15.xii.1968; accession no.191, 2♀ 2,5.i.1950; accession no.301, 2♀ 5,11.i.1951 (Vári); in

Transvaal Museum.

There are two specimens, a male and a female, reared from *Eugenia capensis* (Eckl. & Zeyh.) Harv. ex Sond. (Myrtaceae) (for leaf-mine see Fig. 76) that are excluded from the type-series of *molleivora* for the following reasons. The forewing of the female is heavily irrorated with fuscous at the apex, and the male, although not so strongly marked, has a heavier concentration of fuscous. The valvae of the male seem somewhat broader than those of *molleivora* at the apex but other structures are similar. The female genitalia are indistinguishable.

Although the host-plant of these specimens does not belong to the same family as that from which the types of *molleivora* were reared, the structural similarity of the moths precludes the recognition of a new species.

MATERIAL EXAMINED. SOUTH AFRICA: Natal, Umhlanga Rocks, accession no.2936, 1♂, 1♀ 22.vii.1968 (Vári); in Transvaal Museum.

Niepeltia zeyheriae spec.nov., Figs 23, 24, 77.

ADULT ♂ Wingspan 4,4 mm. Tuft on front of head ochre; tuft on vertex very dark brown. Forewing rather dark, fuscous predominates over ochreous scaling, no concentrations of either colour into patches.

Male genitalia (Figs 23, 24). Anterior extension of vinculum very narrow in middle; lateral arms with small notch near base of pseuduncus. Valva extends beyond tip of tegumen, ridge-like thickening present on inner (dorsal) side from base to halfway up valva. Aedeagus: ventral process forked; lateral processes rounded at tips, not pointed; vesica with minute cornuti present.

LARVA. Mines leaves of *Combretum zeyheri* Sond. (Combretaceae), Fig. 77.

REMARKS. The relatively dark colour of the moth, the long valvae and the shapes of the ventral and lateral processes of the aedeagus best distinguish *zeyheriae* from *combretella*, *vumbaensis* and *molleivora* with which it might be confused.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Louis Trichardt, accession no.1625, 30.iv.1955 (Vári); paratype, 1♂, data as holotype 1.v.1955; in Transvaal Museum.

Niepeltia rubiaeivora spec.nov., Figs 25-27, 67, 78.

ADULT ♂,♀ Wingspan 4,0-4,7 mm. Head tuft off-white to pale ochre. Forewing pale ochre, fuscous scales usually scattered fairly uniformly over surface sometimes with a greater concentration at apex.

Male genitalia (Figs 25-27). Anterior extension of vinculum very narrow. Valva simple, inner surface with small thickened ridge (arrowed in Fig. 27). Aedeagus long, ventral process weakly emarginate caudally; vesica lacks cornuti, sclerotised thickening present as usual.

Female genitalia (Fig. 67). Ductus bursae with complex sclerotisations. Corpus bursae with long signa extending its entire length.

LARVA. Mines the leaves of *Canthium inerme* (L.f.) Kuntze, *C. gilfillanii* (N.E. Br.) O.B. Miller, *Tapiphyllum parvifolia* (Sond.) Robyns (Rubiaceae), Fig. 78.

REMARKS. The absence of cornuti and the form of the valva in the male, and the shape of the sclerotisations on the ductus bursae of the female are the best distinguishing features of this species.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Pretoria, accession no.381, 19.i.1952 (Vári); paratypes, locality as holotype, accession no.381, 1♀ 21.xi.1951, 1♀ 21.xi.1951, 1♀ 24.i.1952, 1♀ 26.ii.1952; accession no.118 1♂, 1♀ 23.i.1949, 1♂ 24.ii.1949, 1♀ 25.ii.1949; accession no.3505, 1♀ 10.xii.1975 (Vári); Natal, Umhlanga Rocks, accession no.932, 1♂ 22.xii.1953 (Vári); in

Transvaal Museum.

There is a very dark male specimen with genitalia similar to *rubiaevora* but with a prominent patch of long spicules on the vesica and some small cornuti in addition to the sclerotised thickening. The host-plant is recorded as *Tricalysia lanceolata*, which is also a member of the Rubiaceae. Unfortunately the mine does not seem to have been preserved and so the identification cannot be checked. However, as *N. rubiaevora* has been reared from members of two genera of the Rubiaceae, another host-plant belonging to this family would not be surprising.

The specimen in question may represent a species distinct from *rubiaevora*. However, the differences in the genitalia are insufficient for me to be certain of this, and, although new species are recognised from only one specimen elsewhere in this paper, further material is required for a firm decision in this case. On balance the specimen is not considered to be a new species, and is not included in the type-series of *rubiaevora*.

MATERIAL EXAMINED. SOUTH AFRICA: Natal, Everton; accession no.3402, 1♂ 20.v.1975 (Vári); in Transvaal Museum.

Niepeltia obliquella spec.nov., Figs 28, 29, 68.

ADULT. ♂ Wingspan 4.4-5.0 mm. Head-tuft. Forewing pale ochre irrorate with fuscous, with an oblique, fuscous fascia postmedially, rather more pronounced than in *fagarivora*, which just fails to reach posterior edge.

Male genitalia (Figs 28, 29). Ventral plate of vinculum with caudal edge thickened but not nearly to such an extent as in *fagarivora*. Valva simple, long, extending beyond tegumen, narrow for apical two-thirds, swollen at base. Aedeagus: ventral process not forked, lateral processes each with prominent basal plate; vesica with some relatively large and some relatively small cornuti.

Female genitalia (Fig. 68). Ductus bursae with complex sclerotisations including a V-shaped spinose pocket. Corpus bursae with long signa extending its entire length.

LARVA. Possibly mines leaves of *Bridelia micrantha* (Hochst.) Baill. (Euphorbiaceae). There is doubt as to the validity of this record and the mines do not seem to have been preserved.

REMARKS. The shapes of the vinculum and the valvae, and the unforked ventral process of the aedeagus distinguish *obliquella* from other species treated in this paper.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Natal, Umdoni Park, accession no.3347, 8.v.1975 (Vári); paratypes, data as holotype, 1♀ 28.v.1975, 1♀ 8.v.1975 (Vári); in Transvaal Museum.

Niepeltia fagarivora (Vári) **comb.nov.**, Figs 30, 31, 69.

Stigmella fagarivora Vári, 1955. *Ann. Transv. Mus.* 22:334, Pl. 23:5; genitalia: Figs. 6, 16; mine: Fig. 28.

ADULT. ♂,♀ Wingspan 4.1-4.6 mm. Head-tuft ochre. Forewing pale ochre with oblique, fuscous, postmedial fascia (poorly defined in some specimens); fringe irrorated with fuscous at apex.

Male genitalia (Figs 30, 31). Caudal edge of ventral plate in form of a thick band. Valva with small, inwardly directed process, narrow at base as well as apex. Aedeagus: ventral process forked; cornuti on vesica few in number, not easily discernable.

Female genitalia (Fig. 69). Corpus bursae with signa long and narrow, extending almost its whole length.

LARVA. Mines leaves of *Zanthoxylum capense* (Thunb.) Harv. (= *Fagara*

magalimontana Engl.) (Rutaceae), see Vári (1955).

REMARKS. The external features and the male genitalia of *fagarivora* resemble those of the next species. The fascia of the former is less strong, and there are clear differences in the shape of the valvae and the ventral process of the aedeagus between the two species. The signa reticulata in the female are of quite a different shape.

MATERIAL EXAMINED. ♂-Holotype, TM type no.2994; SOUTH AFRICA: Pretoria, accession no.253, xii.1950 (Vári); paratypes, Pretoria, accession no.253, 1♀ 10.xii.1950; Pretoria, Hennops River, accession number 376, 1♀ 16.ix.1951, 1♀ 24.x.1951 (Vári). Additional specimen, Hennops River, accession no.376, 1♀ x.1951 (Vári); in Transvaal Museum.

There is a further paratype, not examined by me, in the British Museum (Natural History).

Niepeltia fuscofascia spec.nov., Figs 32-34, 70.

ADULT ♂,♀ Wingspan 4,0-4,8 mm. Head-tuft ochre. Forewing pale yellow with a prominent, dark fuscous, rather irregularly edged fascia situated postmedially; wing surface otherwise characteristically devoid of fuscous irrorations.

Male genitalia (Figs 32-34). Ventral plate of vinculum with caudal edge very thick medially, anterior extension narrow. Valva almost triangular with associated spine-like process. Aedeagus: ventral process characteristic; denticulate cornuti on vesica absent.

Female genitalia (Fig. 70). Ductus bursae with triangular spinose patch. Corpus bursae with signa relatively short and rounded.

LARVA. According to the rearing records the species mines leaves of *Brachystegia* (Leguminosae: Caesalpinioideae).

REMARKS. The forewing colour and pattern is characteristic of this species. The male genitalia resemble those of *fagarivora* (for distinguishing features see under that species, above) and those of the next species which, like *fuscofascia* have a thin process associated with the valvae. The pattern of the forewing, the shape of the ventral process of the aedeagus and the markings on the vesica are features which distinguish *fuscofascia* from the next species.

The female genitalia are remarkable for *Niepeltia* in having rounded signa reticulata rather than long narrow ones.

MATERIAL EXAMINED. ♂-Holotype, RHODESIA: Lundi, accession no.2625, 21.iii.1964 (Vári); paratypes, locality as holotype, accession no.2625, 2♂, 1♀ 20.iii.1964 (Vári); 5♂ 2-5.iii.1964 (Vári & Van Son); in Transvaal Museum.

Niepeltia umdoniensis spec.nov., Figs 35, 36.

ADULT. ♂ Wingspan 4,0 mm. Head-tuft ochreous. Forewing pale ochre with a poorly defined, fuscous, postmedial fascia, otherwise rather lightly irrorate with fuscous.

Male genitalia (Figs 35, 36). Caudal margin of ventral plate of vinculum well-thickened; anterior extension relatively broad. Valva small, with long associated spine-like process. Aedeagus: ventral process weakly emarginated at apex; cornuti on vesica present.

REMARKS. This species is characterised particularly by the shape of the genital capsule and the valvae. For additional characters by which *umdoniensis* may be distinguished from *fuscofascia* see under that species, above.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Natal, Umdoni Park, 15.xii.1974 (Kroon); in Transvaal Museum.

Niepeltia pundaensis spec.nov., Figs 37, 38.

ADULT. ♂ Wingspan 3,6-4,1 mm. Tuft on front of head pale ochre, tuft on vertex dark brown. Forewing pale ochre, sparsely irrorated with fuscous scales that are concentrated into a rather poorly defined oblique fascia.

Male genitalia (Figs 37, 38). Anterior extension of vinculum narrow. Valva with inner projection arising from near base and curving upwards. Aedeagus: ventral process divided at tip several times; lateral processes rather narrow and long; vesica with complex thickenings; cornuti absent.

REMARKS. The shape of the valva, the ventral process of the aedeagus and the thickening on the vesica are distinguishing features of this species.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Kruger National Park, Punda Milia, 4-8.v.1970 (Vári & Potgieter); paratype 1♂, data as holotype; in Transvaal Museum.

Niepeltia lorantivora (Janse) **comb.nov.**, Figs 4, 5, 39, 40, 71, 79.

Nepticula lorantivora Janse, 1948. *The Moths of South Africa* 4:169, Pls 82:9, 93:1.

ADULT. ♂ Wingspan 4,0-6,0 mm (see Remarks). Tuft on front of head pale ochre; tuft on vertex very dark brown. Forewing ochre, irrorate with rather pale fuscous scales, most specimens uniformly and densely speckled. Hindwing with pale yellow scales on upper surface nearly covering basal half of wing. ♀ As male except yellow scales on hindwing are absent.

ABDOMEN. Pale in both sexes.

Male genitalia (Figs 39, 40). Anterior extension of vinculum deeply excavated. Valva with large inner projection from which arises a spine. Aedeagus: broad; ventral process forked; lateral processes prominent, additional small spine-like process arises from one side of aedeagus; cornuti on vesica prominent.

Female genitalia (Fig. 71). Corpus bursae with long signa which run nearly the whole length of the structure.

LARVA. Mines leaves of *Boscia oleoides* (Burch. ex DC.) Tölken (Capparaceae), Fig. 79.

REMARKS. The holotype, a female, was collected by Gowan C. Clark who reared the specimen from the larval stage. Attached to the block of pith on which the moth is pinned are three cocoons, presumably from the series from which the type was reared. From one of these Dr Vári obtained a dead male pupa from which he mounted the genitalia. As a result males of the species can be readily identified.

According to Janse (1948), Clark reared the specimen from "caterpillars making a mine in the leaves of *Loranthus elegans*." The actual mine does not seem to have been preserved. Subsequently Clark reared a number of specimens from mined leaves, which were preserved, of *Boscia oleoides*. *Loranthus* is a parasite on *Boscia* (amongst other plants) and the two are not taxonomically related. It is likely that the record of *Loranthus* given for the holotype is wrong; the specimen was probably also reared from *Boscia*.

The particularly large wingspan range may be misleading because one specimen measures 4,0 mm and the next lowest figure is 5,4 mm.

Noteable distinguishing features of *lorantivora* are the shapes of the valvae and the ventral process of the aedeagus.

MATERIAL EXAMINED. ♀-Holotype, Transvaal Museum type no.2378, SOUTH AFRICA: Cape Province, Addobush, 2.vii.1942 (Gowan C. Clark), genitalia slide G7260, wing slide 1906, a further label '7260A' refers to the male genitalia of a pupa from one of the cocoons mounted with the type. Additional specimens: Cape Province, Port Elizabeth, accession no.178, 3♂ 12.ix.1949, 1♂ 14.ix.1949, 1♂

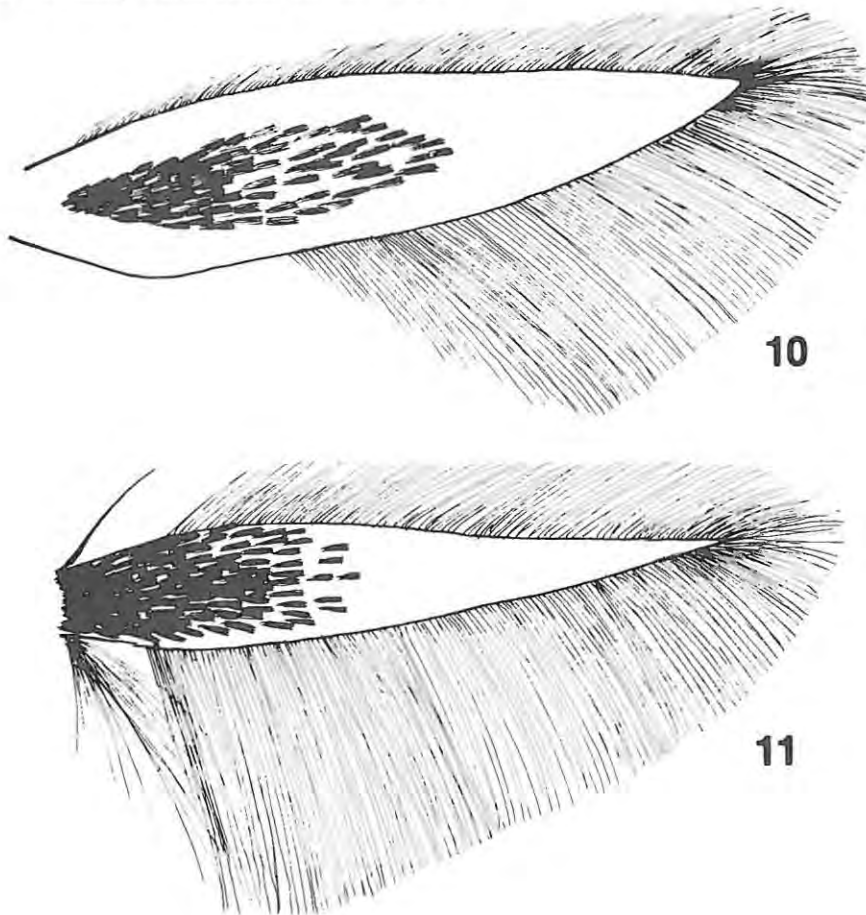
17.ix.1949, 2♀ 8.ix.1949, 2♀ 9.ix.1949, 2♀ 16.ix.1949, (G.C. Clark). All specimens in Transvaal Museum.

Niepeltia krooni spec.nov., Figs 10, 11, 41, 42.

ADULT. ♂ Wingspan 3,6 mm. Head-tuft ochreous. Forewing (Fig. 10) dorsal surface pale off-white, with a few pale fuscous irrorations and a few shiny black scales on costa near base; underside with shiny black scales extensive. Hindwing with shiny black scales covering dorsal surface (Fig. 11) from base to about half length of wing, similar on underside but interrupted by longitudinally running row of ochreous scales.

Male genitalia (Figs 41, 42). Anterior extension of vinculum noticeably excavated so that it is very narrow in middle but has a pair of prominent lateral lobes. Valva narrows gradually to base from just under halfway down its length. Aedeagus: ventral process well sclerotised laterally; cornuti on vesica very small, few in number and not easily visible.

REMARKS. The shapes of the vinculum, valvae and the ventral process of the aedeagus are useful distinguishing features of this species and so is the distribution of the shiny black scales on the wings.



FIGS 10-11. *Niepeltia krooni* spec.nov. 10. Ventral surface of forewing. 11. Dorsal surface of hindwing.

The species is named after Dr D.M. Kroon, Sasolburg.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Soutpansberg District, Kairo farm 212, NW. of Alldays, 22-27.iii.1978, (Kroon); paratypes, 1♂ data exactly as holotype; Transvaal, Kruger National Park, 1♂ data exactly as holotype; Transvaal, Kruger National Park, 1♂ 6.v.1970 (Vári & Potgieter); in Transvaal Museum.

Niepeltia acumentia spec.nov., Figs 43-46, 72.

ADULT. ♂,♀ Wingspan 3,9-5,0 mm. Head-tuft off-white. Forewing pale, off-white, lightly but variously irrorated with pale fuscous.

Male genitalia (Figs 43-46). Anterior extension of vinculum broad, hardly emarginated; ventral plate with caudal edge thickened in middle. Valva squared-off at base so that inwardly directed process is broad based. Aedeagus: lateral processes long, tapering to their bases; vesica with prominent, characteristic sclerotisation, cornuti absent.

Female genitalia (Fig. 72). Apophyses extended into short, pointed ovipositor. Corpus bursae, with signa elongate but not as long as corpus itself.

REMARKS. The weakly emarginated vinculum, the shape of the valvae, the long lateral processes of the aedeagus and the pointed ovipositor of *acumentia* distinguish this species from *lorantivora* to which it shows some resemblance. The ventral process and the lateral processes of the aedeagus differ in shape between *acumentia* and *bispinata*. In *acumentia* there are no spinose processes, typical of *bispinata*, on the inner projection of the valvae.

The specific name derives from the pointed ovipositor in the female (*acumen* — a point).

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Kruger National Park, Pretoriuskop, 6-7.iv.1952, (Vári); paratypes, locality and collector as holotype, 2♂, 1♀ 6-7.iv.1952, 2♂ 1.iv.1952; in Transvaal Museum.

Niepeltia bispinata spec.nov., Figs 47, 48.

ADULT. ♂ Wingspan 4,4 mm. Head-tuft off-white. Forewing very pale, off-white with fuscous scales concentrated near apex in a short, almost horizontal, streak.

Male genitalia (Figs 47, 48). Base of valva relatively broad with a pair of spines, one short one longer, projecting inwards. Aedeagus: ventral process prominent, heavily sclerotised, forked; lateral processes each with a plate at base; vesica with complex sclerotisations; cornuti minute, few in number, hardly visible.

REMARKS. The presence of a pair of spinose processes associated with the valvae of *bispinata* and the prominent ventral process of the aedeagus distinguish this species from *lorantivora* and *acumentia* to which it shows some resemblance.

There is a fine apodeme (*ap* in Fig. 47) arising from the area of the lateral arms of the gnathos on each side similar in position to *lanneivora*.

The two spinose processes on the valva suggested the species name.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Kruger National Park, Pretoriuskop, 6.vii.1952 (Vári); in Transvaal Museum.

Niepeltia sellata spec.nov., Figs 49, 50.

ADULT. ♂ Wingspan 4,2 mm. Tuft on front of head ochreous, tuft on vertex reddish brown, darker than tuft on front of head but not very dark. Forewing: dorsal surface pale, off-white with a few very pale fuscous scales; undersides with a patch of shiny black scales on basal half of dorsal surface.

Male genitalia (Figs 49, 50). Vinculum: anterior extension very deeply excavated so forming pair of long lobes, very narrow medially; ventral plate with caudal

edge thickened. Tegumen bluntly rounded. Valva: shape characteristic, squared-off at base with prominent inwardly directed process. Aedeagus: narrow, ventral process lacks anteriorly directed lateral arms; denticulate cornuti on vesica absent.

REMARKS. The shape of the valvae, a useful distinguishing feature of this species, suggested the specific name *sellata* — a chair. The long lobes of the anterior extension of the vinculum, the form of the ventral process of the aedeagus and the distribution of shiny black scales on the wings are further characters by which *sellata* may be recognised.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Pretoria North, 16.x.1960 (Van Son); paratype data as holotype, 1♂ 23.x.1960; in Transvaal Museum.

Niepeltia mariepsensis spec.nov., Figs 51, 52, 73, 80.

ADULT. ♂, ♀ Wingspan 4,0-4,9 mm. Head-tuft ochre or dark ochre. Forewing pale ochre, heavily irrorated with fuscous, particularly in one of the female specimens, with a rather weakly defined, oblique, fuscous fascia, difficult to discern in the females.

Male genitalia (Figs 51, 52). Anterior extension of vinculum broad, very weakly excavated; ventral plate with caudal edge slightly thickened medially. Valva with a pair of inwardly directed processes. Aedeagus: ventral processes well sclerotised, prominent; cornuti on vesica present.

Female genitalia (Fig. 73). Corpus bursae with elongate signa, one member of pair much shorter than the other in specimen dissected.

LARVA. Mines leaves of *Cassipourea gerrardi* (Schinz) Alston (Rhizophoraceae), Fig. 80.

REMARKS. The shape of the ventral process of the aedeagus and the projections of the valvae are characteristic of this species.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Mariepskop, accession no.1720, 11.ii.1956 (Vári); paratypes, RHODESIA: Mount Selinda, accession no.1821, 1♂, 1♀ 3.v.1956 1♀ 1.v.1956 (Vári); in Transvaal Museum.

Niepeltia lundensis spec.nov., Figs 53-57.

ADULT. ♂ Wingspan 3,4-3,6 mm. Head-tuft ochre. Forewing pale ochre with fuscous scales scattered fairly randomly over surface.

Male genitalia (Figs 53-57). Caudal margin of ventral plate of vinculum thickened. Valva long, narrow with inwardly directed spine-like process. Aedeagus: ventral process comprising a small forked projection and solid lateral thickenings; lateral processes very large, shell-like so that they curve around aedeagus; cornuti on vesica present.

REMARKS. The shape of the valvae of *lundensis* resemble those of the next species. The two species are easily distinguishable by the relative lengths of the valvae, the shape of the vinculum and its components, and the ventral process and lateral processes of the aedeagus.

MATERIAL EXAMINED. ♂-Holotype, RHODESIA: Lundi, 2-5.iii.1964 (Vári & Van Son); paratypes, data as holotype, 1♂ 2-5.iii.1964, 1♂ 13-16.iii.1964; in Transvaal Museum.

Niepeltia fulva spec.nov., Figs 58, 59.

ADULT. ♂ Wingspan 3,4 mm. Head-tuft rubbed, only a few hairs remain. Forewing pale, off-white with a few very pale fuscous scales. Hindwing with brown scales covering basal half of dorsal surface.

Male genitalia (Figs 58, 59). Anterior extension of vinculum broad; ventral plate

with lateral parts of caudal edge thickened. Tegumen rounded. Valva with inwardly pointing finger-like projection. Aedeagus relatively narrow; ventral process small; lateral processes long and narrow; vesica with complex sclerotisations, cornuti present.

REMARKS. The valvae of *fulva* resemble those of *lundensis*. For distinguishing features see under *lundensis*, above. The specific name *fulva* refers to the colour of the scales in the hindwing.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Kruger National Park, Pafuri, 8.v.1975 (Potgieter & Scoble); in Transvaal Museum.

Niepeltia vacuolata spec.nov., Figs 60, 61.

ADULT. ♂ Wingspan 5,0 mm. Head-tuft off-white. Forewing pale, off-white with fuscous scales concentrated into two patches, one near apex and a smaller one near centre of wing, and around base with a few scales scattered over wing surface. Hindwing with raised brown scales covering basal two-thirds.

Male genitalia (Figs 60, 61). Large. Vinculum: anterior extension broad. Valva with notable thickenings, and a pair of inwardly directed processes formed by a large vacuolate excavation; basal element straight, long and stout. Aedeagus: ventral process long; lateral processes of anellus small; vesica with cornuti prominent.

REMARKS. The shape of the valva is characteristic of this species and is the most useful diagnostic feature of it. The name of the species was suggested by the vacuolate emarginations of these structures. The brown scales on the hindwings are undoubtedly confined to the male sex although no females are available to confirm this.

MATERIAL EXAMINED. ♂-Holotype, SOUTH AFRICA: Transvaal, Kruger National Park, Punda Milia, 4-5.v.1970 (Vári & Potgieter); in Transvaal Museum.

Niepeltia lanneivora (Vári) **comb.nov.**, Figs 7, 12, 62, 63, 74.

Stigmella lanneivora Vári, 1955, *Ann. Transv. Mus.* 22:332, Pl. 23:3; genitalia: Figs 3, 15; mine: Fig 25.

ADULT. ♂,♀ Wingspan 4,6-5,6 mm. Tuft on front of head off-white, tuft on vertex dark brown. Forewing pale ochre, fairly regularly and heavily irrorate with fuscous. Hindwing: in type-series colour and shape as usual in genus, in two additional male specimens dorsal surface with shiny, yellowish scales from base to just under half length of wing; shape of wing as in Fig. 12.

Male genitalia (Figs 7, 62, 63). Anterior extension of vinculum broad, rounded not excavated; ventral plate with short process bearing a pair of setae arising from each side of aedeagus. Well sclerotised apodeme arises from near gnathos and extends along lateral arm of vinculum on each side. Valva squared-off at base, basal element of valva prominent; inwardly directed projection of valva short, rounded and broad based; short inwardly directed finger-like projection at tip; a membrane, extended into a pair of setae-bearing, finger-like projections joins valvae weakly to aedeagus ventrally. Aedeagus narrow, not large, markings on vesica characteristic, cornuti absent.

Female genitalia (Fig. 74). Corpus bursae with elongate signa.

LARVA. Mines leaves of *Lannea discolor* Engl. (Anacardiaceae), see Vári (1955).

REMARKS. The shape of the valvae, the rounded vinculum and the finger-like processes on the membrane associated with the valva and aedeagus are characteristic of this species.

The presence of brown scales on the hindwing of only two of the known males of *lanneivora* is surprising. As there do not appear to be any other differences these specimens are identified as *lanneivora*.

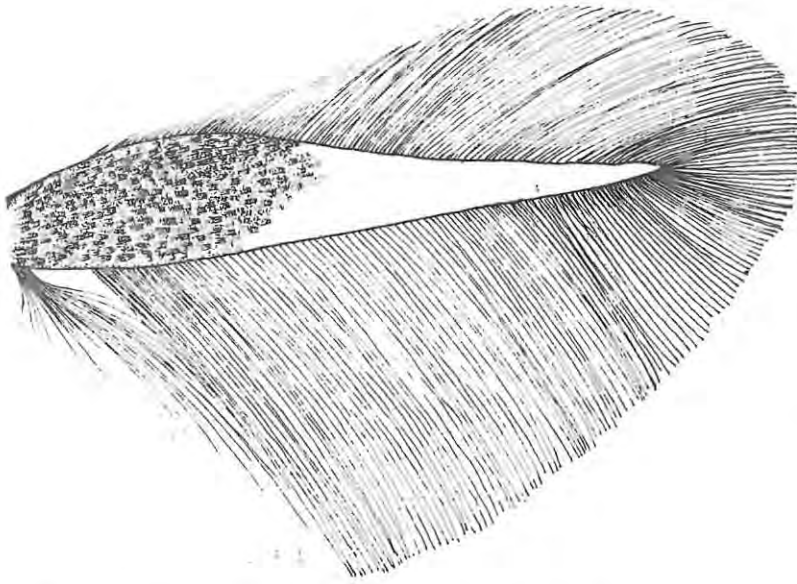


FIG. 12. *Niepeltia lanneivora* (Vári). 12. Hindwing, total length = 2 mm.

The well sclerotised bars running alongside the lateral arms of the vinculum are prominent (Fig. 7). For further remarks see under 'Comments on morphology and relationships' above.

MATERIAL EXAMINED. ♂-Holotype, Transvaal Museum type no.2976 SOUTH AFRICA: Transvaal, Pretoria, accession no.316, 3.ii.1951 (Vári); paratypes, locality as holotype; accession no.335, 1♂ 22.viii.1951; accession no.202, 3♀ 21, 26.iv.1950; accession no.316, 1♀ 2.ii.1951 (Vári). Additional specimens, Pretoria North, 1♂ 9.vi.1953, (Rorke); 1♂ 27.i.1951; Pretoria accession no.202, 1♀ 26.iv.1950 (Vári); in Transvaal Museum.

Niepeltia clinomochla (Meyrick) **comb.nov.** Figs 13, 14, 64, 65.

Nepticula clinomochla Meyrick, 1934. *Exotic Microlepidoptera* 4:468.

Trifurcula clinomochla (Meyrick); Gustafsson 1976. *Ent. Tidskr.* 97:47, Figs 3, 4, 6, 9, 10.

The species was redescribed by Gustafsson (1976) from a series of specimens from Sri Lanka. Meyrick's type was not available for comparison and so the identity of these specimens remains in question. However, Gustafsson gives his reasons for identifying his specimens as *clinomochla* (included amongst them is that this series was reared from the same species of host-plant as that from which Meyrick reared the type).

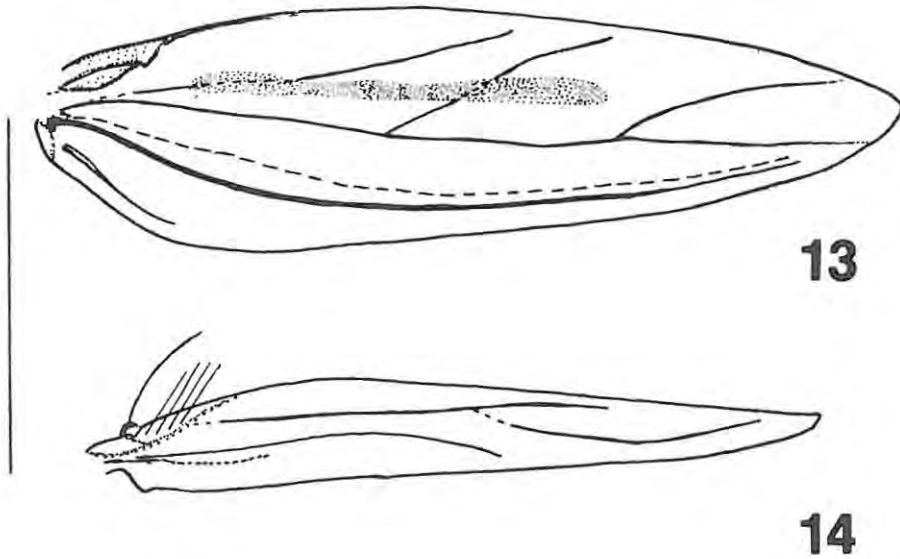
ADULT. See Gustafsson (1978). In addition, the forewing of the male has a long thickening (Fig. 13) visible after denudation of the scales.

Male genitalia (Figs 64, 65). Anterior extension of vinculum narrow, rounded, very characteristic; ventral plate with caudal edge thickened. Aedeagus: ventral process in form of a pair of hook-like apodemes.

Female genitalia. Corpus bursae with rather small signa.

LARVA. Forms a linear mine on *Bridelia retusa* (L.) Spréng. (Euphorbiaceae), see Gustafsson (1978).

MATERIAL EXAMINED, SRI LANKA: North Western Province, Ibbagamuwa, 1♂, 1♀ 7.iii.1974 (Gustafsson); in Swedish Museum of Natural History, Stockholm.



FIGS 13-14. *Niepeltia clinomochla* (Meyrick). 13. Forewing. 14. Hindwing. Scale = 0,5 mm.

ACKNOWLEDGEMENTS

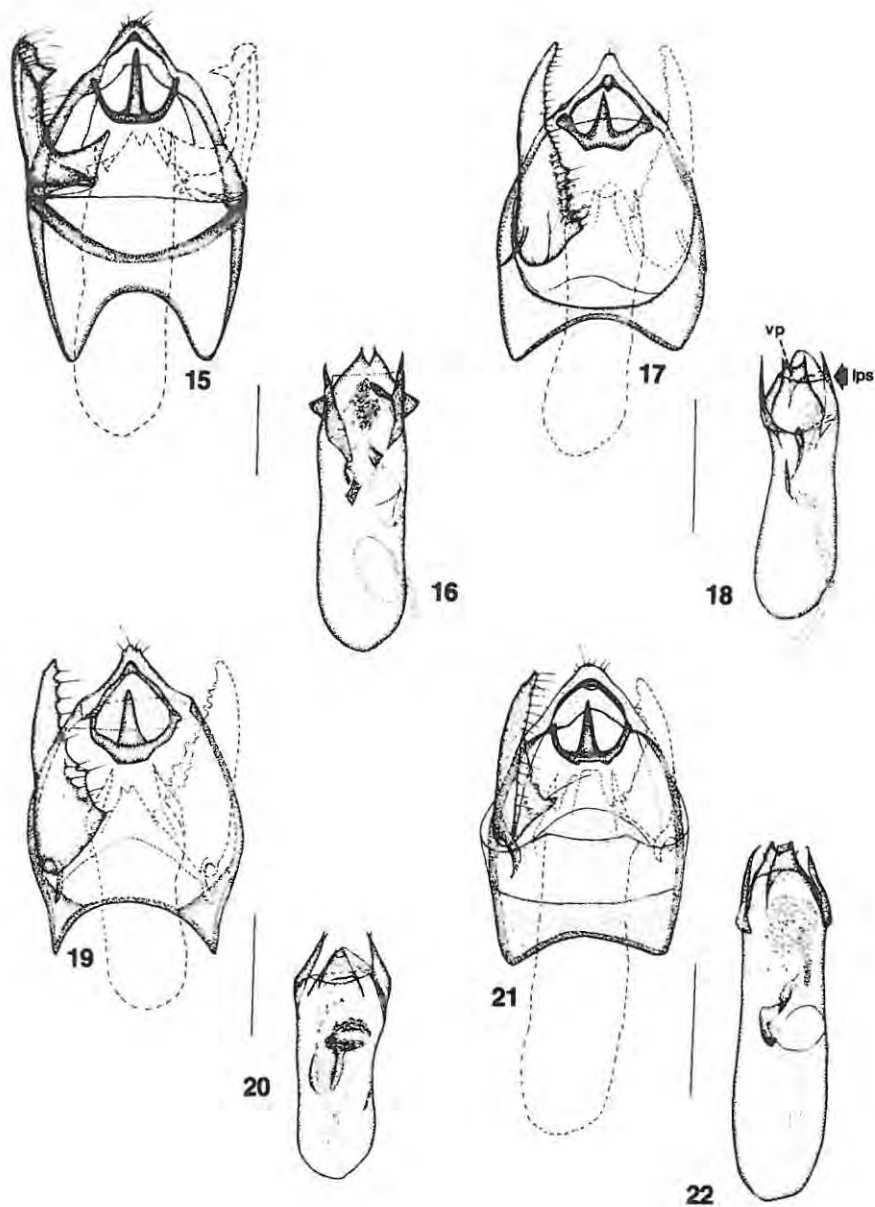
I thank Dr L. Vári, Transvaal Museum, Pretoria, and Professor C. Wilkinson, Vrije Universiteit, Amsterdam, for their comments on the manuscript. I am grateful to Dr J. Klimesch, Linz, Austria for his advice on a number of points, and for donating specimens of the type-species of *Niepeltia* to the Transvaal Museum, and to Drs E. van Nieukerken, Vrije Universiteit, Amsterdam, for drawing my attention to Grosche's reference to '*Weberina*' *lentiscella*. I thank Dr B. Gustafsson, Stockholm, for lending me specimens of *Niepeltia clinomochla*, and Dr D.M. Kroon, Sasolburg, for donating specimens of *Niepeltia* to the Transvaal Museum. Miss E. Retief, Botanical Research Institute, Pretoria, kindly checked the identification of the host-plant records. The illustrations were prepared by myself assisted by Mrs P.J. Prowse, Mr H. Dullaart, and Miss D. van Draanen. Most of the specimens on which this study is based were collected by Dr L. Vári.

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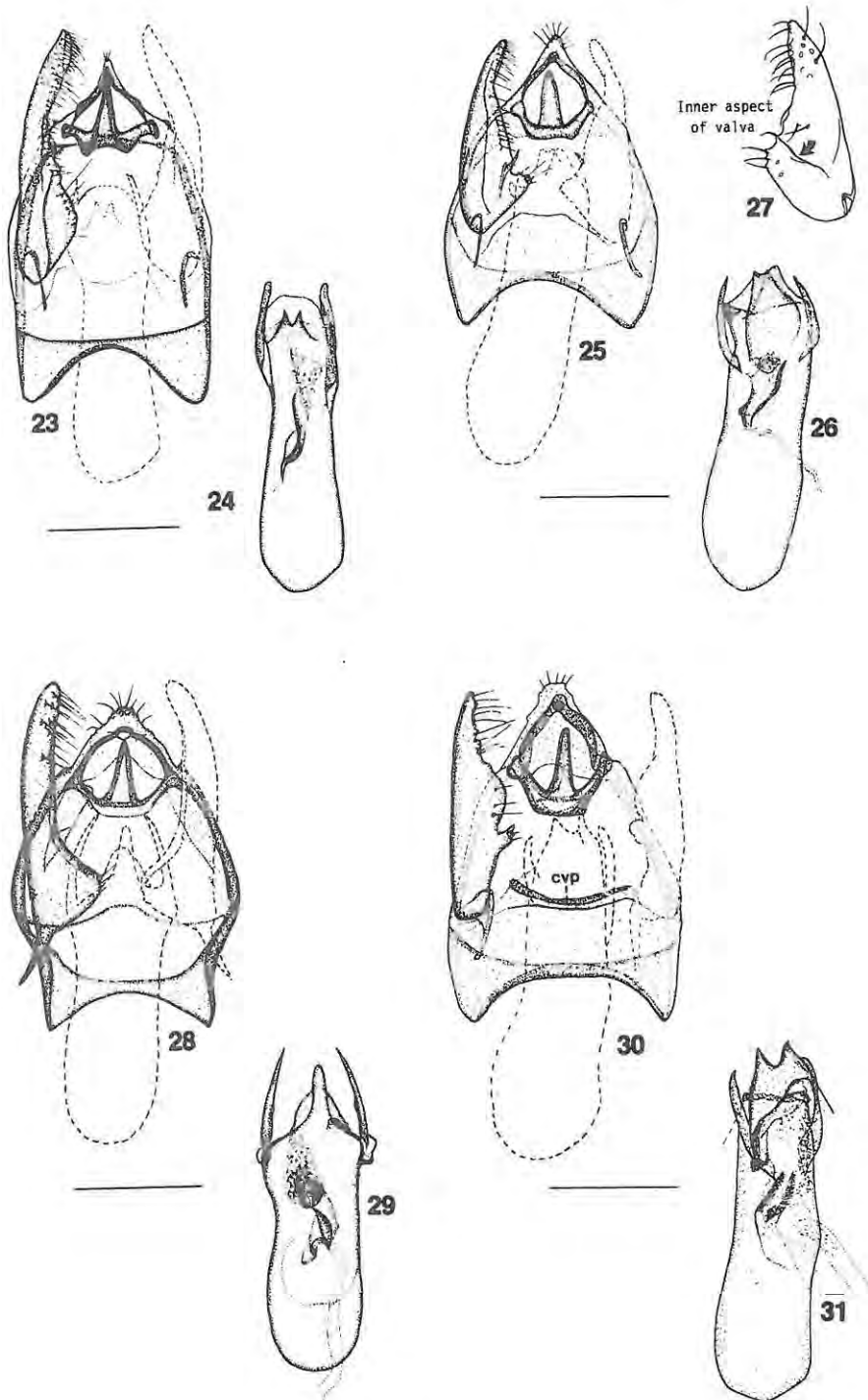
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ABBREVIATIONS

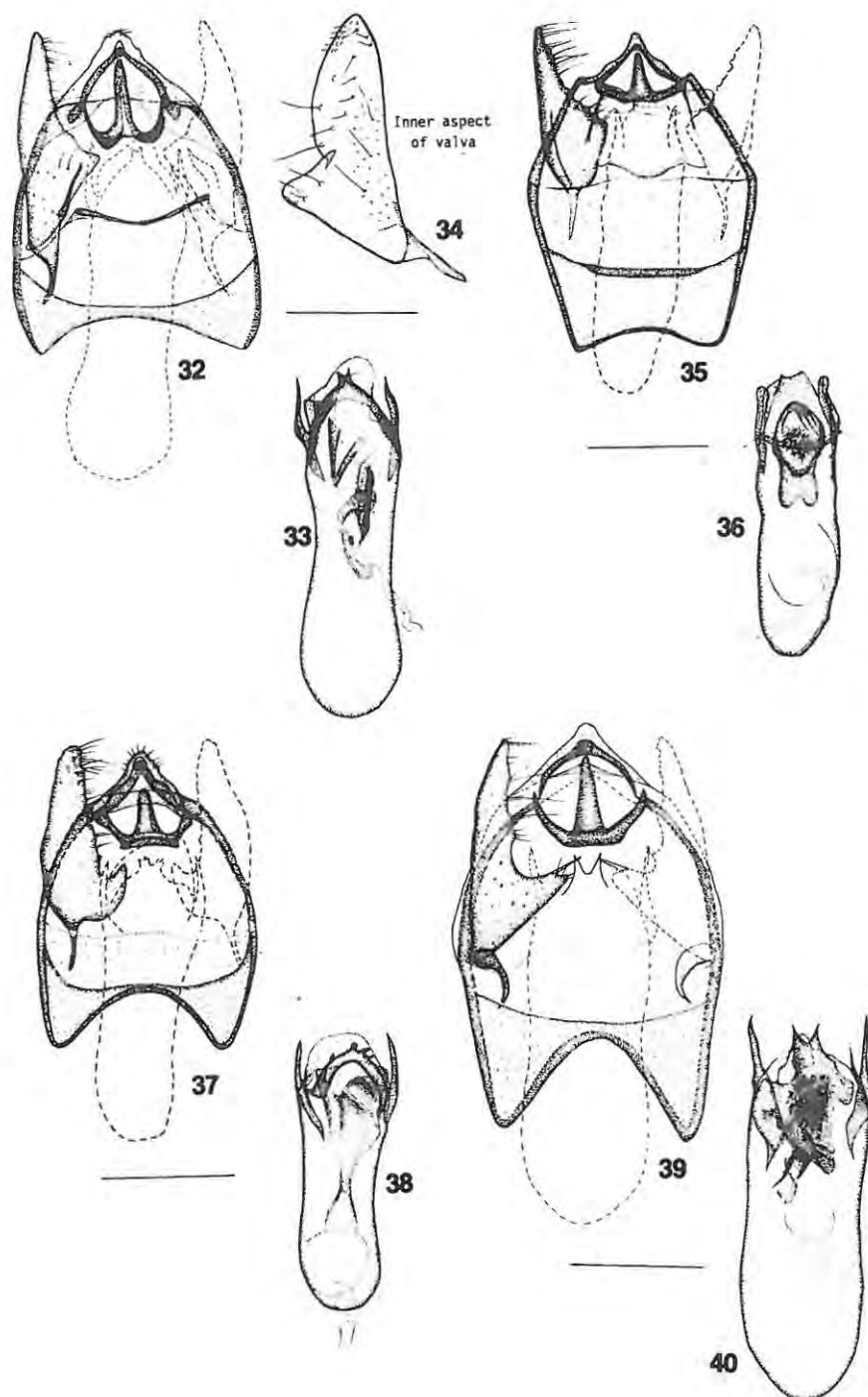
ap	apodeme
ca	chaetosema
ceg	central element of gnathos
cvp	caudal edge of ventral plate of vinculum
ga	galea
lav	lateral arm of vinculum
lp	labial palpus
lps	lateral process of aedeagus
mp	maxillary palpus
tn	tegumen (pseuduncus)
us	uncus
vp	ventral process of aedeagus



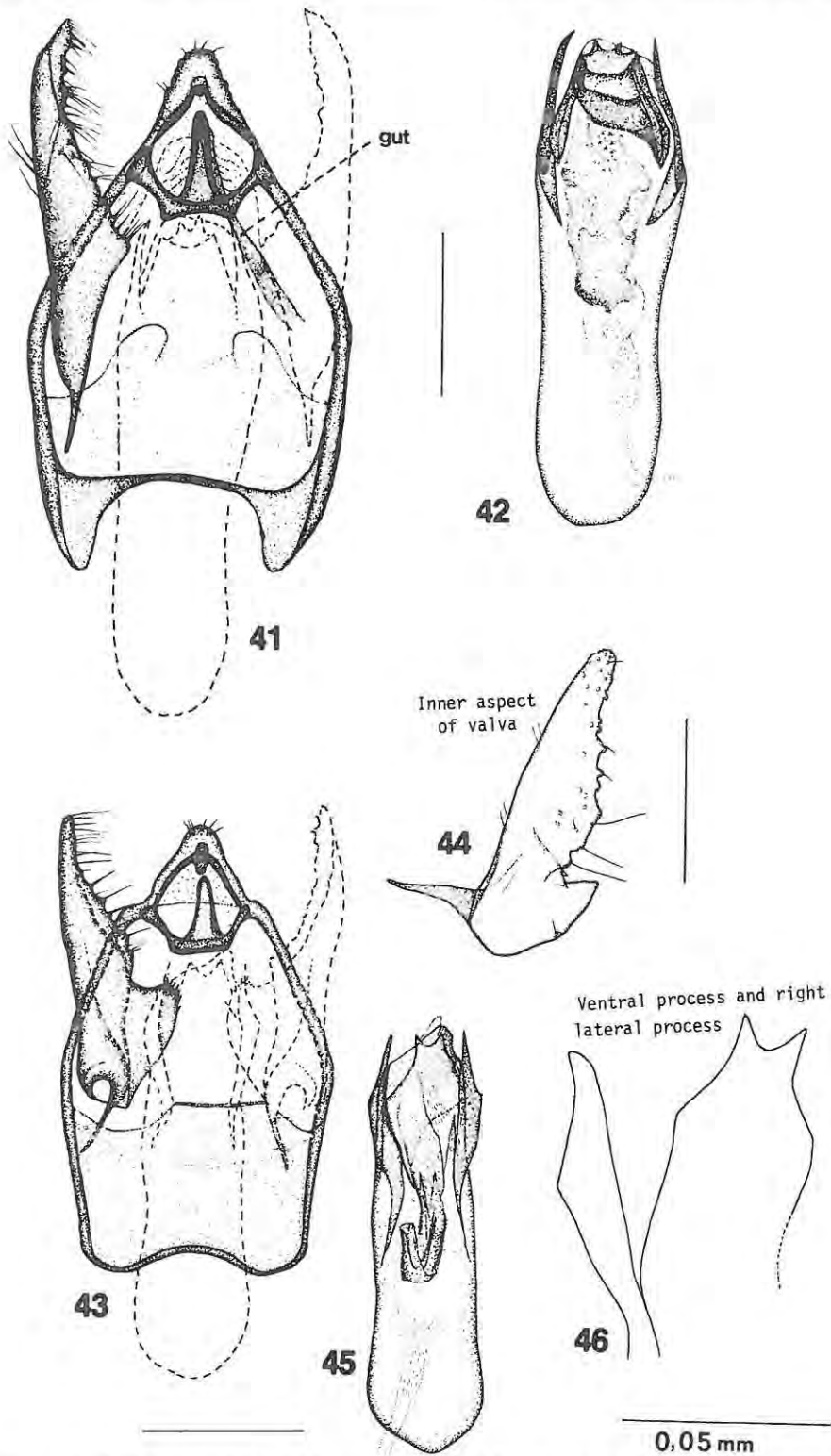
FIGS 15-22. Male genitalia of *Niepeltia* species, ventral view. 15-16. *N. platani* (Müller-Rutz). 17-18. *N. combretella* (Vári). 19-20. *N. vumbaensis* spec.nov. 21-22. *N. molleivora* spec.nov. Scales = 0,1 mm.



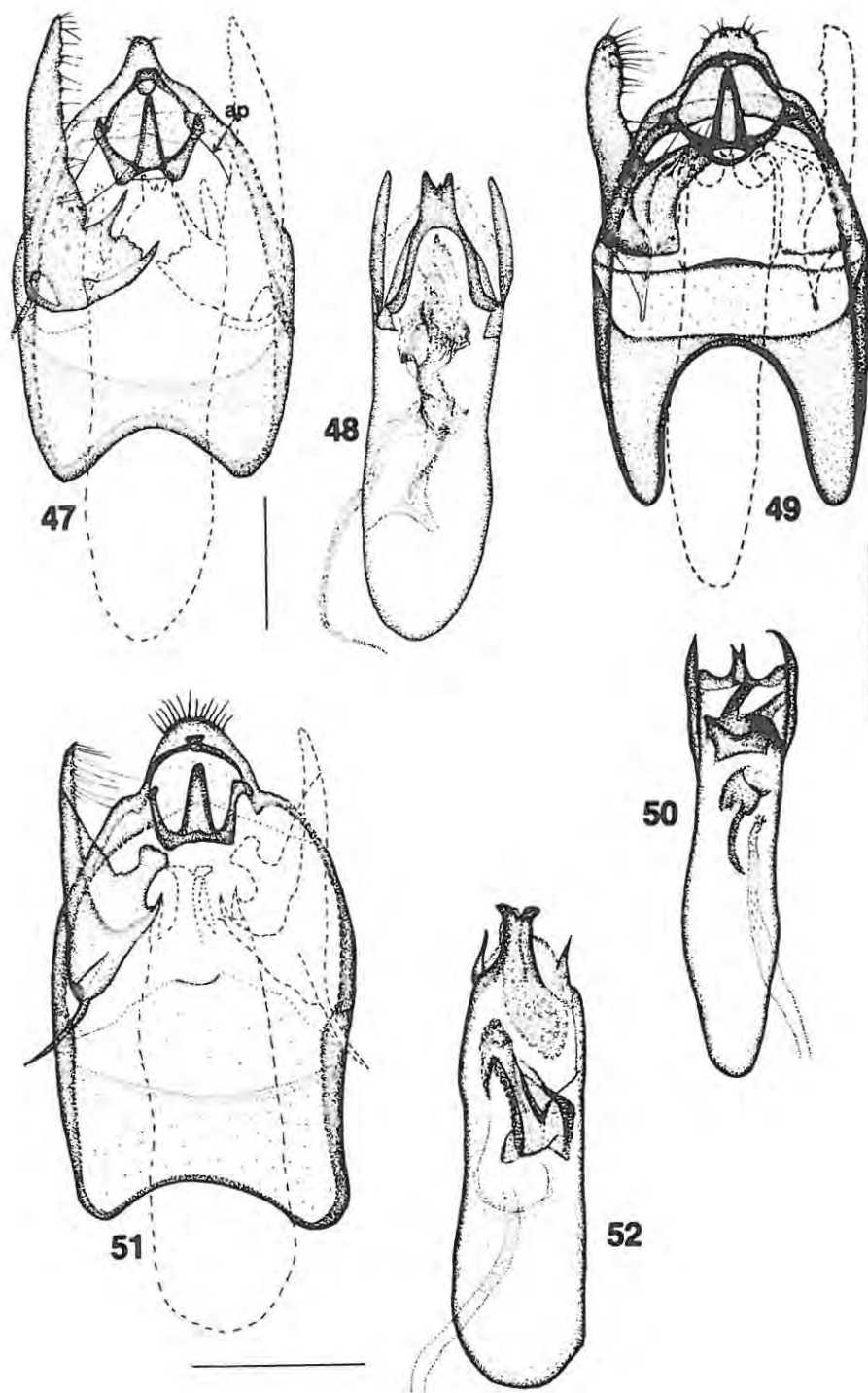
FIGS 23-31. Male genitalia of *Niepeltia* species. 23-24. *N. zeyheriae* spec. nov. 25-27. *N. rubiaevara* spec. nov. 28-29. *N. obliquella* spec. nov. 30-31. *N. fagarivora* (Vári). Scales = 0,1 mm.



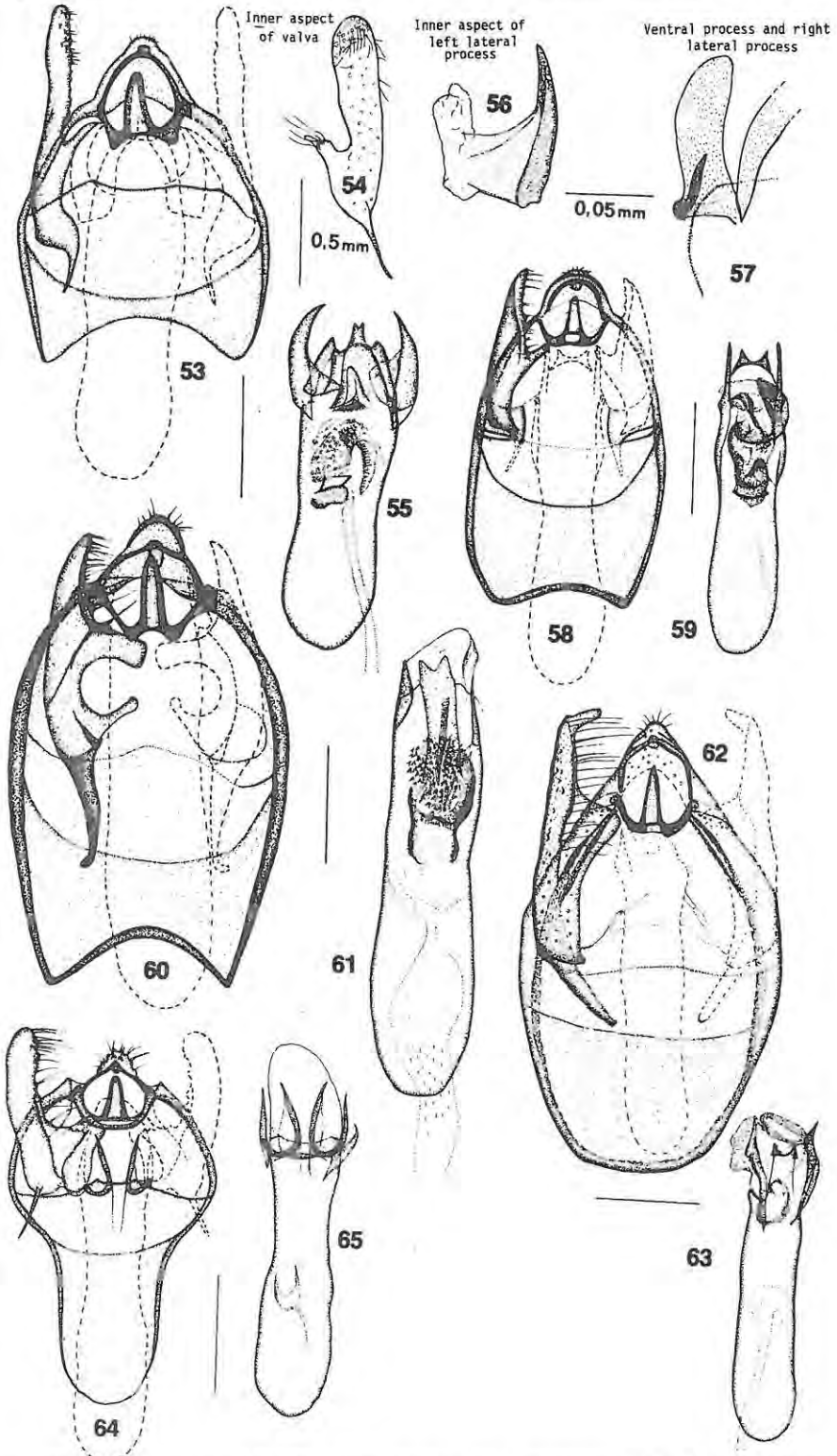
FIGS 32-40. Male genitalia of *Niepeltia* species. 32-34. *N. fuscifascia* spec.nov. 35-36. *N. undoniensis* spec.nov. 37-38. *N. pundaensis* spec.nov. 39-40. *N. lorantivora* spec.nov. Scales = 0,1 mm.



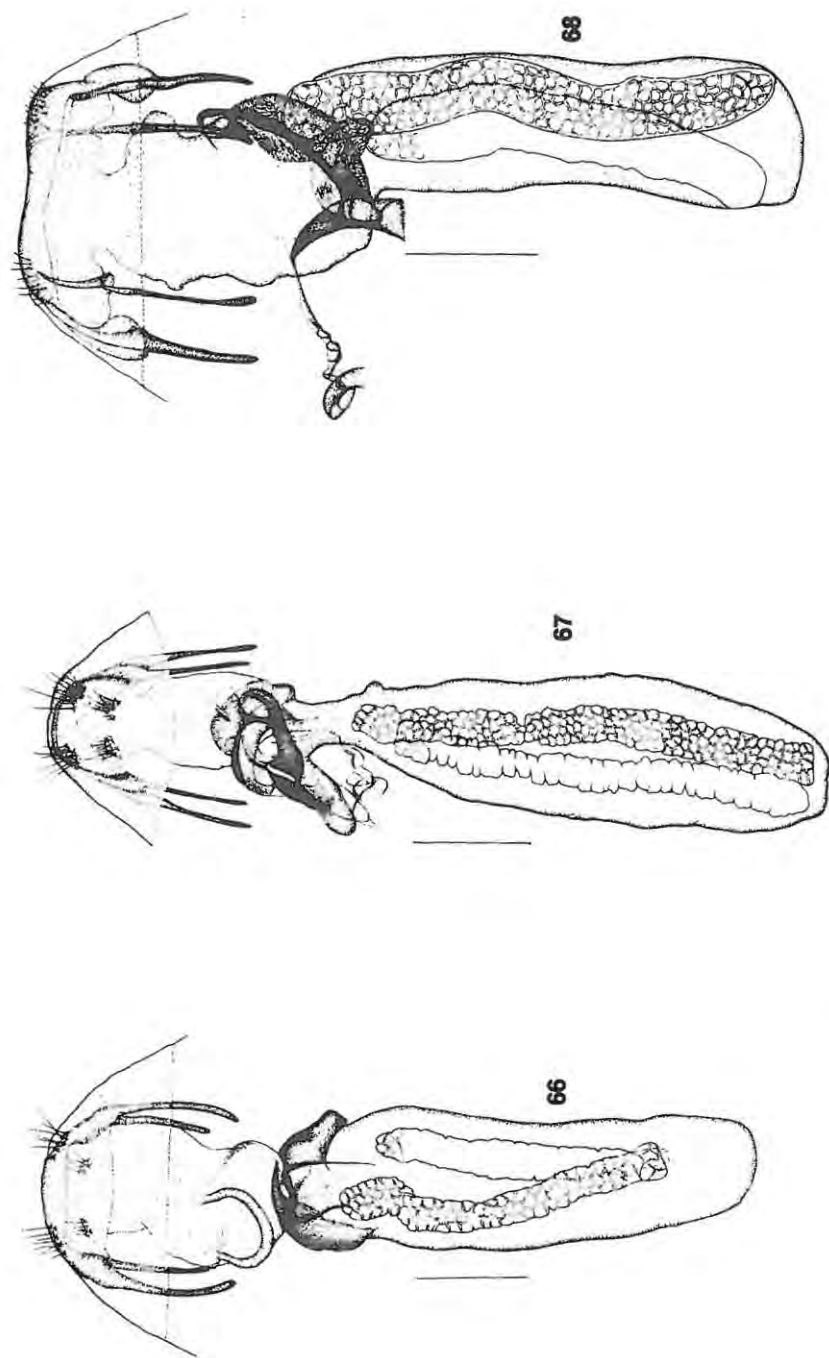
FIGS 41-46, Male genitalia of *Niepeltia* species. 41-42. *N. krooni* spec.nov. 43-46. *N. acumenta* spec.nov. Scales = 0,1 mm except where shown otherwise.



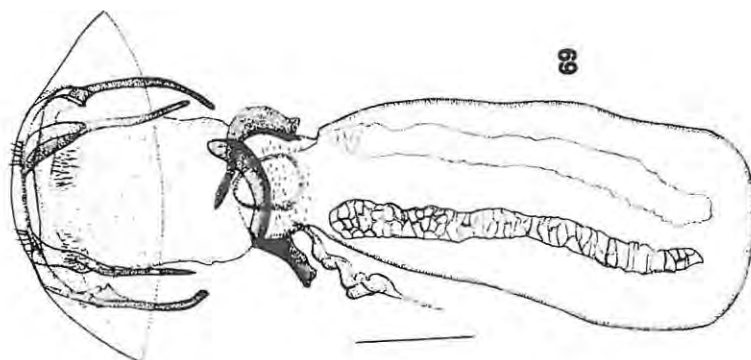
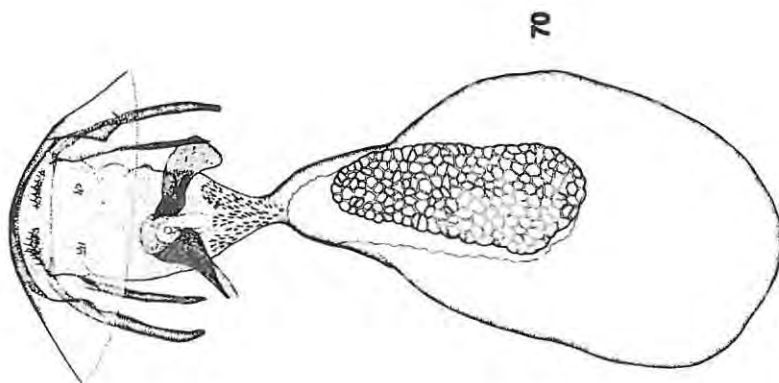
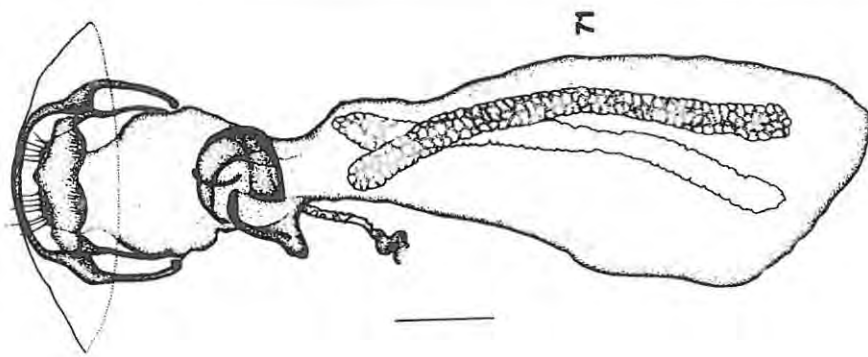
FIGS 47-52. Male genitalia of *Niepeltia* species. 47-50. *N. sellata* spec.nov. 51-52. *N. mariepsensis* spec.nov. Scales = 0,1 mm.



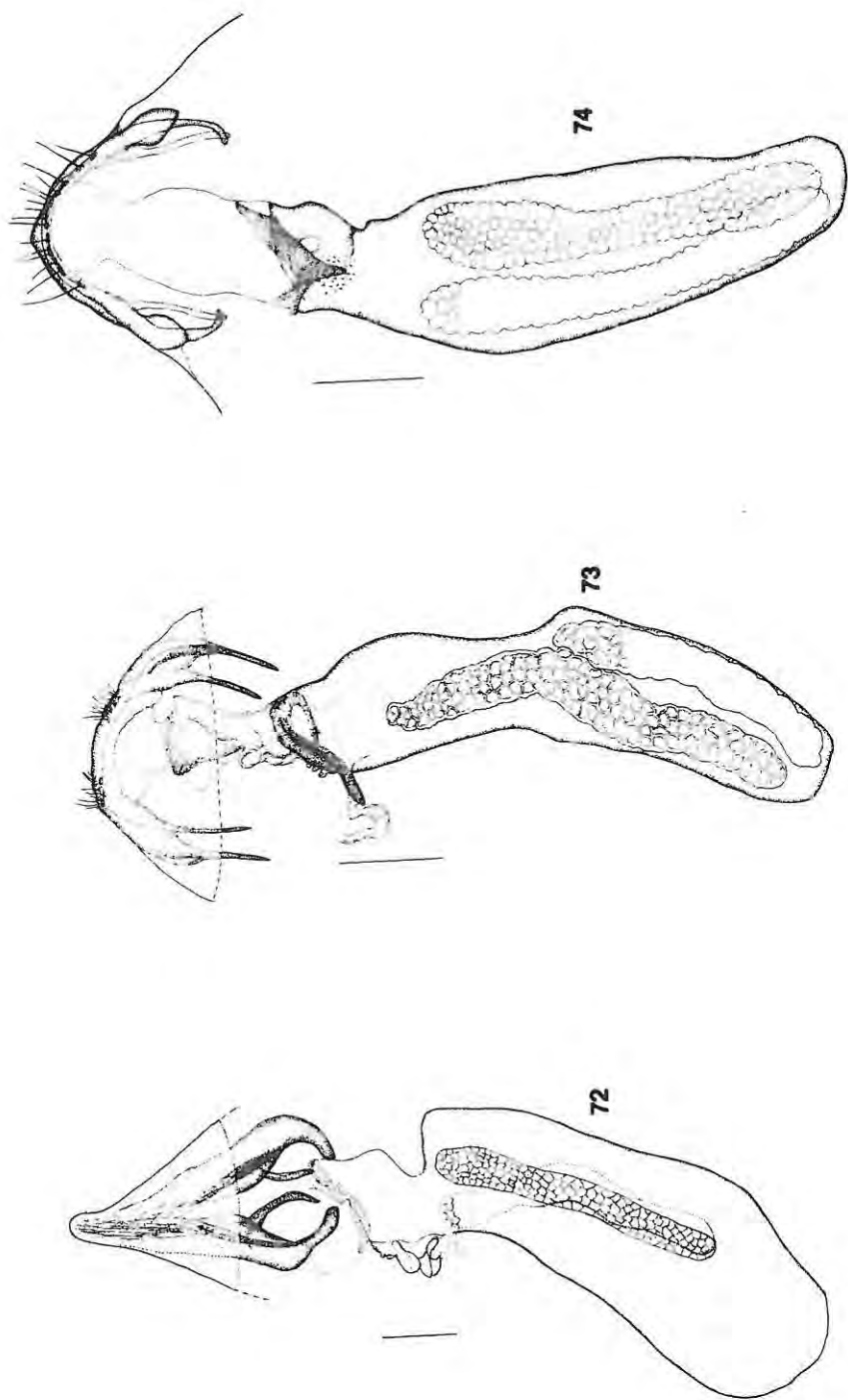
FIGS 53-65. Male genitalia of *Niepeltia* species. 53-57. *N. lundensis* spec.nov. 58-59. *N. fulva* spec.nov. 60-61. *N. vacuolata* spec.nov. 62-63. *N. lanneivora* (Vári). 64-65 *N. clinomochla* (Meyrick) Scales = 0,1 mm except where shown otherwise.



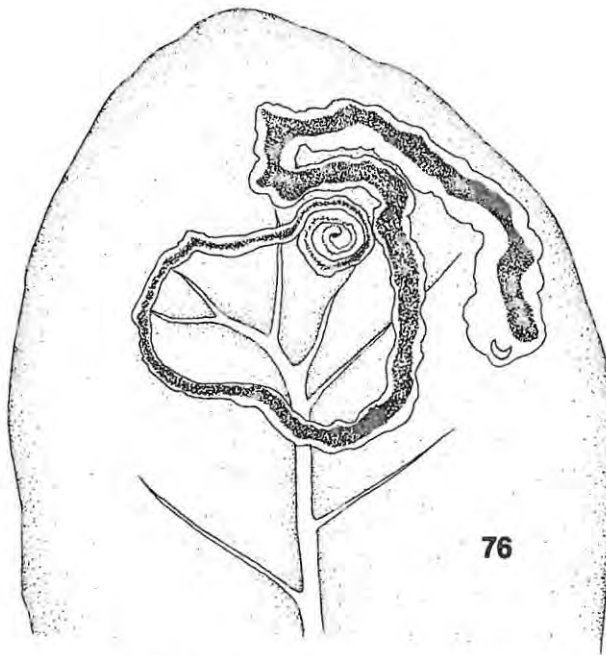
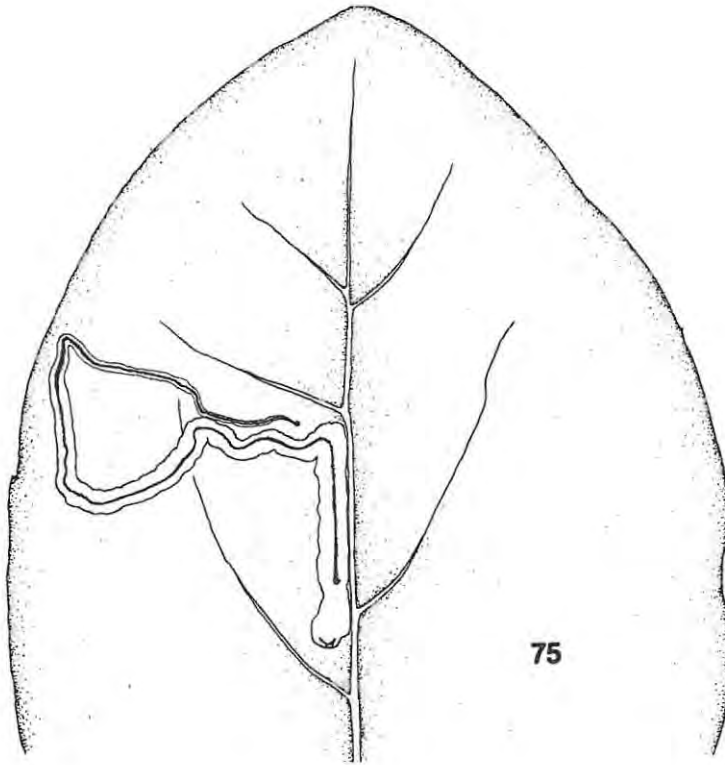
FIGS 66-68. Female genitalia of *Niepeltia* species. 66. *N. molleivora* spec.nov. 67. *N. rubiaevora* spec.nov. 68. *N. obliquella* spec.nov. Scales = 0,1 mm.



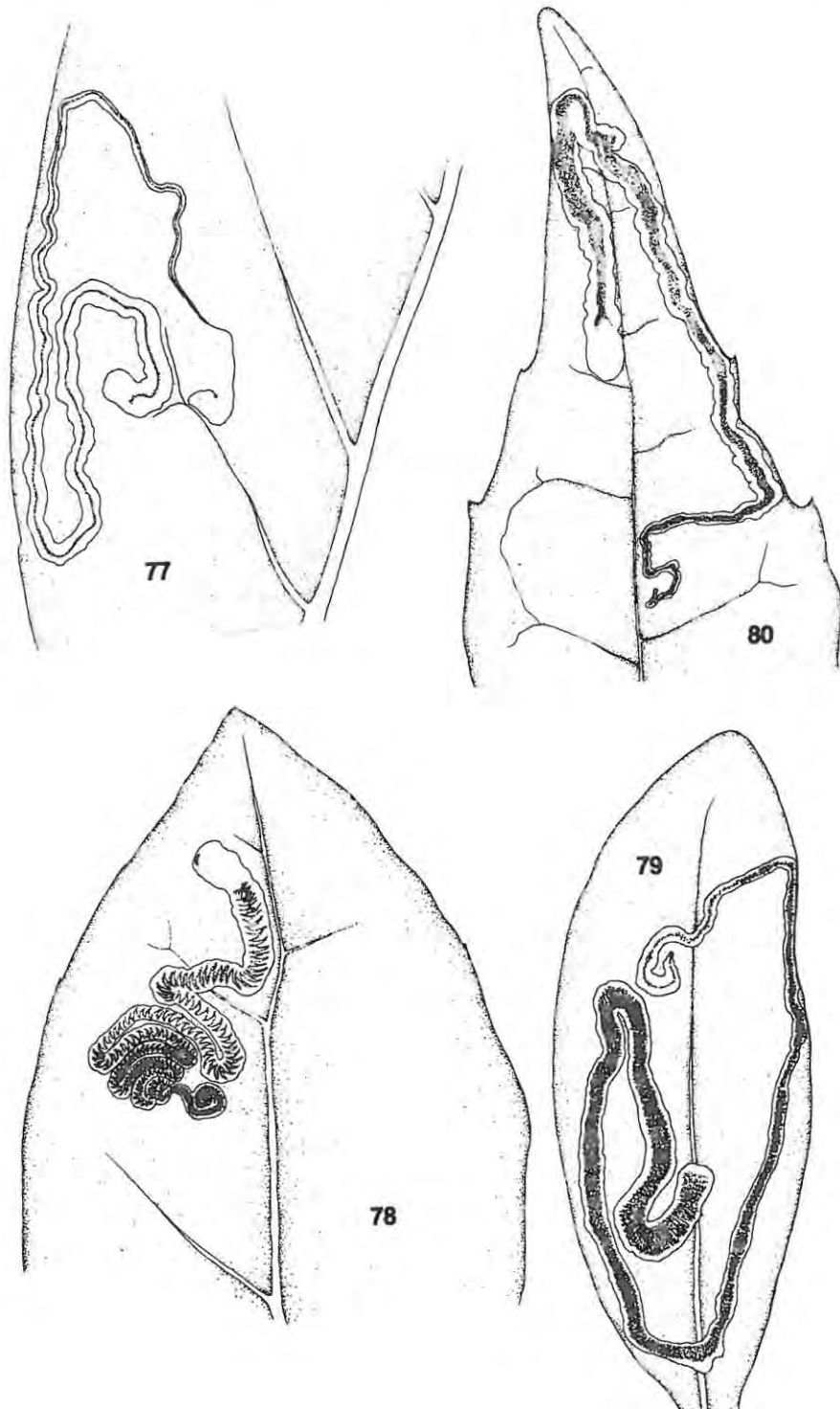
FIGS 69-71. Female genitalia of *Niepeltia* species. 69. *N. fagarivora* (Vári). 70. *N. fuscifascia* spec. nov. 71. *N. lorantivora* (Janse). Scales = 0,1 mm.



FIGS 72-74. Female genitalia of *Niepeltia* species. 72. *N. acumenta* spec. nov. 73. *N. mariepsensis* spec. nov. 74. *N. lanneivora* (Vári). Scales = 0.1 mm.



FIGS 75-76. Leaf-mines of *Niepeltia* species, 75. *N. molleivora* spec.nov., on *Combretum molle*. Un-identified *Niepeltia* species on *Eugenia capensis*.



FIGS 77-80. Leaf-mines of *Niepeltia* species. 77. *zeyheria* spec.nov., on *Combretum zeyherii*. 78. *N. rubiae-vora* spec.nov., on *Canthium inermis*. 79. *N. lorantivora* (Janse), on *Boscia oleoides*. 80. *N. mariep-sensis* spec.nov., on *Cassipourea gerrardi*.