BEAUFORTIA

INSTITUTE OF TAXONOMIC ZOOLOGY (ZOOLOGICAL MUSEUM)
UNIVERSITY OF AMSTERDAM

Vol. 37, no. 7 February 2, 1988

CHARACTER ANALYSES FOR DISCRIMINATION AND AFFINITY RECOGNITION OF THE NORTH AMERICAN MICROLEPIDOPTERA IN THE GENUS *ECTOEDEMIA* BUSCK (NEPTICULIDAE: LEPIDOPTERA)

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ABSTRACT

Character analyses have been carried out on the North American species in the genus *Ectoedemia* Busck in order to obtain a measure of their phenetic affinities. The characters used (140) were not only morphological but ranged widely through aspects of biology, and led to the production of up-dated descriptions. Diagnoses based on, and interpreted through, the numerical results are also given. The most important results from seven cluster analyses and principal co-ordinates analyses with minimum spanning trees, contouring, nearest neighbours and similarity coefficients are discussed.

CONTENTS

INTRODUCTION

Ectoedemia is a large genus of microlepidoptera in the family Nepticulidae. It is almost world wide, occurring on all the larger land masses. The moths and their larvae are very small, the latter being flattened and adapted for mining or forming galls in leaves, petioles, twigs or bark. Larval feeding in the cortex has also been cited in the literature, but this has not been corroborated. Other genera may also attack fruits.

In North America the family has attracted attention only since the middle of the last century, but in Europe a good deal earlier. The moths were known to Linnaeus and excellent pre-Linnean accounts of one or two life histories exist (e.g. De Geer, 1752). However, their habits are secretive and for the majority of bark miners, life cycles are not known and the taxonomy of a number of species complexes is obscure.

An account of the North American species, including their taxonomic history and biology, can be found in Wilkinson & Scoble (1979), Wilkinson & Newton (1981), Wilkinson (1981), together with plates and figures of externals and male and female genitalia for each species.

The descriptions provided here have been revised and up-dated as part of the process for making them amenable to numerical analysis. They include major characters used in the analyses, provide diagnoses for phenetically similar species and account for the main cophenetic differences between taxa. Thus the need to provide similarity matrices, character tables and codings is alleviated. For taxonomic work, the descriptions can also be used in conjunction with illustrations in the publications referred to above. The terminology, therefore, follows these earlier papers, notwithstanding that in recent works dealing with other regions, a few terms (e.g. saccus and anellar spines) have been changed. However, the internal classification of the genus is modified to correspond with the results of the computer tests.

Formerly it was the intention to present here the results of a comparison between the cladistic and numerical methods of classification. However, the cladistic method when applied to these species added very little to conclusions already drawn elsewhere. There was often not enough evidence to make sound choices between alternative character states and decisions concerning synapomorphies. Thus reference to Scoble (1983) and van Nieukerken (1985) will indicate the present state of the art and its attendant problems.

The results of character analyses exhibited here demonstrate degrees of phenetic relationship between taxa on a diversity of characters from external features, genitalia, biology and life histories, and gives a classification which is acceptable and unlikely to be contested on present evidence.

NUMERICAL ANALYSIS

The genus *Ectoedemia* in North America lends itself to numerical analysis. Many species have more than one form and some are geographically polymorphic. Others are difficult or impossible to distinguish without including non-morphometric data, so it is a good test of numerical methods to produce satisfactory classifications of this genus. The analyses, therefore, demonstrate the necessity of including larval information and details of biology, for it is on this basis that some taxa are separated, rather than the morphometric data of adults.

Seven principal co-ordinates and cluster analyses have been computed for thirty-six taxa from the genus *Ectoedemia* in North America. One species from the genus *Trifurcula* was also included as a control and to obtain a measure of its' dissimilarity.

The analyses were as follows:

1. Principal co-ordinates analysis based on all observed morphological and biological characters, including reproductive structures, life histories, host plants, mines and voltinism (figs. 1-7).
2. Cluster analysis based on the same characters (fig. 8).
3. Cluster analysis for all male characters.
4. Cluster analysis for all female characters.
5. Cluster analysis based on a random selection of thirty characters from both sexes.

The principal co-ordinates analysis was interpreted by graphing combinations of two dimensional plots of the variaus co-ordinates. Three dimensions were also represented by means of contouring and sectioning. The cluster analyses were illustrated by dendrograms and similarity coefficients. The nearest neighbours were also calculated and a minimum spanning tree derived from this data. This tree was then superimposed on the plots of the co-ordinates.

The above analyses were followed by a further two, which included the European species. These results are reserved for another publication, apart from some relevant remarks here.

Modifications of Gower's principal co-ordinates and cluster analysis (CLASP) were applied, although in the early stages BIOPAT was also used. The mean square distance coefficient and unweighted pair group method using arithmetic averages (UPGMA) were applied. Minimum spanning trees were also calculated to indicate possible distortions in two dimensional space representations, because reducing three (or more) dimensions to a two dimensional piece of paper can produce misleading effects in perspective. A method for sectioning three dimensional space was used which was first developed by Wilkinson (1973).

An algorithm has been devised to represent on a line printer any selection of three dimensions from a multi-dimensional array. As shown in the figures (e.g. fig. 5), the coordinate corresponding to the first selected dimension is plotted across the page, a second upward and the third is used to generate a level variable *h* after the first two are reduced to interger grid locations. Four plotting strategies are possible, depending on how level *h* is interpreted. In these analyses it is used for cumulative plotting in which each level includes cases belonging to, or below it.

A multi-dimensional model of *Ectoedemia*, with its' constituent species, was produced and reduced to the three most significant dimensions. The computer can be programmed to section the model at as many levels as required, in this case, four. Thus each dot in the scattergrams represents a cut through a rod at a given level, and each rod represents a species. The longer the rod, the more sections will pass through it and the greater is dimension 3. The scattergram of the lowest level, the base, shows all the points under consideration. As well as sectioning, the minimum spanning tree is superimposed, thus providing information from both types of analysis.

The characters were assessed as binaries and multi-states. However, for the purpose of these analyses the multi-states were transformed to binaries. A total of 140 characters in 430 states were tested for each species, but where information was not known the results had to recorded as N.T. (no test). Therefore, the number of tests applied per species varied. The species descriptions are based on the characters used, but a complete list of the characters and their states can be obtained by contacting the author.

The phenetic affinities of each species are discussed in the descriptions and a diagnosis is given for all species with high similarity.

CONCLUSIONS

The results (e.g. fig. 7) show that the taxa fall into two distribution patterns, a tight cluster on the right (points 16-32 excl. 24 and 28), and a dispersed scatter on the left (1-15). In addition, there is one solitary point (35) clearly isolated. The right cluster corresponds to the subgenus *Zimmermannia* Hering, whilst the point (35) represents the only species (*saccharella*) included from the separate genus *Trifurcula* Zeller *comb. n.* which was tried as a test case. In each analysis the separate nature of *Trifurcula* has been clearly identified. At a lower level of differentiation the two other subgenera computed, *Etainia* Beirne (33 and 34) and *Fomoria* Beirne (36 and 37, not illustrated) are separate from *Ectoedemia s. str.* and *Zimmermannia* and so retain their identities.

Zimmermannia was erected by Hering in 1940 for European species. In North America it corresponds to what has previously been called the *castaneae* species group (Wilkinson *et al.*, 1981; Wilkinson, 1981). Their synonymy has been demonstrated in the numerical analysis of both European and American species by forming a homogenous cluster (*in litt.*). Alone, each species has more than a 40% similarity with all the others, except *reneella* (30). Not only does this group have morphological characters in common, but also features of their biology. As far as is known, these species damage bark either by tunelling or forming galls, which contrasts with the species of other subgenera, which mine leaves or petioles. So perhaps it is not surprising that this group shows a high measure of independence.

Cluster analysis (fig. 8) shows that the most closely related species within this group are *heinrichi* (19) and *castaneae* (20), having a 70% similarity coefficient. From the descriptions it can be seen that morphologically the two species have not yet been separated, not even by differences in genitalia. The diagnosable characters are to be found in the food plants of the larvae, location of the egg-laying site, damage caused and response of the host plant to it. *E. heinrichi* is a bark miner feeding on *Quercus palustris*, whilst *castaneae* forms galls on *Castanea*. This example illustrates the limitations which would be imposed if only morphological characters were to be used in a numerical analysis. The specimen 90 (27) shows an 80% similarity to *castaneae*, but when the species this single specimen represents is better known perhaps its' affinity will not be quite so high.

E. phleophaga (21) links with *mesoloba* (23) before joining the *castaneae* group and *helenella* in the cluster analysis where features of the male genitalia dominate, due to lack of information on the female and life cycle of *mesoloba*. In the principal co-ordinates analysis *phleophaga* is thus associated with *heinrichi* at level 2 (fig. 6). *E. obrutella* (16) and *acanthella* (17) are also closely related (60%), and together with *piperella* (18) form a group within the subgenus (figs. 3 and 8), although *Zimmermannia* cannot be so readily divided as *Ectoedemia s. str.* As shown in the base set (figs. 4 and 7), this is because all the *Zimmermannia* species radiate from *castaneae* except *chlorantis* (22). All species, therefore, belong with *castaneae* in the same group. *E. chlorantis* is known only by a single female specimen. Its' affinities, therefore, are uncertain.

The species of lowest phenetic similarity in the dendrogram *reneella* is not shown to be exceptionally dissimilar when its' position is seen in three dimensions or using the minimum spanning tree method (fig. 4). The density of this group in comparison with the much wider scatter of the leaf miners implies much less diversity of characters in *Zimmermannia*. For some reason there is much more uniformity, either because this subgenus has not had so long to diverge or, more likely, the conditions within the bark mining habit are more constant so limiting differentiation and such differences as do exist are not so easily measured (e.g. mine characters).

Thus the character analyses show a complete separation of the bark miners from the leaf miners which, under the circumstances, would have been more surprising if they had not done so.

From the figures it can be seen that the species *grandisella* (25) (e.g. fig. 4) provides the link between the two subgenera. This is reasonable, but it is probably a typical member of *Zimmermannia*. Owing to lack of material and damaged male genitalia the features have, to some extent, been reconstructed.

The subgenus *Ectoedemia s. str.* Busck (1-16) is much more diverse and this is demonstrated in all forms of analysis and representation.

The species which attack petioles, *populella* (1) and *canutus* (3), form a separate group, together with *argyropeza* (2) which first bores into the petiole and later continues in the lamina (e.g. fig. 4). *E. populella* forms galls on the petioles of *Populus* species whilst *argyropeza* and *canutus* mine the leaves. *E. argyropeza* and *canutus* are very similar except that the former is parthenogenetic, only having females, whilst *canutus* is bisexual, like all the other species here, as far as is known.

In the descriptive work (Wilkinson *et al.*, 1981) these species formed the *populella* species group, together with two leaf miners *trinotata* (4) and *marmaropa* (5). At the time doubts were expressed about the true relationships of the leaf miners. The phenetic results suggest that they do not belong here and for *trinotata* at least, the *rubifoliella* group is more appropriate. For the first three however, the general analyses and those for females only (not illustrated) showed them to be a distinct unit with close affinities. The male analyses are not relevant since *argyropeza* is parthenogenetic.

The *platanella* species group (6-10) comes out as a discrete cluster, with the exception of *clemensella* (7) which is peripherally connected to the *rubifoliella* group (11-15). *E. clemensella* is the most dissimilar of the *platanella* group and lacks a number of the essential features joining the rest of the group together. (See also *clemensella* species description). According to these analyses, species *trinotata* (4) should be assigned to this group.

The *rubifoliella* group (11-15), as determined by classical taxonomic methods, should now also include *canadensis* (24) and *andrella* (28 and 29). The numerical position of *canadensis* in this species group is probably also correct phylogenetically. In fact, it may be synonymous with *lindquisti* (11), there then being two forms having different food plants. The difficulty is that there are no known extant specimens of *canadensis*, as Braun's holotype is now missing. *E. andrella* is similar to *ulmella* (13).

The dendrogram (fig. 8) and minimum spanning tree link *canadensis* to *rubifoliella* (12), which is convenient for this concept of the species group. Unfortunately, however, *rubifoliella* is exceedingly peripheral to its' own species group, although in the male only analysis *ulmella* (13) was given as its' nearest neighbour. Actually, when character analyses of both the North American and European species were carried out together, *rubifoliella* was transferred to the European *angulifasciella* group, whilst the other species co-incided with the *occultella* group.

Taken overall, the results of the numerical analyses suggest that *nyssaefoliella* (14) should be placed in a new group with *marmaropa.* In the description of *nyssaefoliella* (Wilkinson *et al.*, 1981) it was predicted that on the basis of the female characteristics association with the *rubifoliella* group was justifiable. This was borne out by the numerical analysis of females only. In the general classification (fig. 8) and minimum spanning tree (fig. 4) *nyssaefoliella* takes a very peripheral position on the edge of the *populella* group. This favours the male characters and apart from the lack of spines on the aedoeagus the males are typical of this group. It is now demonstrated that if only one sex or part of a life cycle is represented, a group can easily be assigned which has all the characteristics of being 'natural', but will not correspond when aspects of the other sex are added.

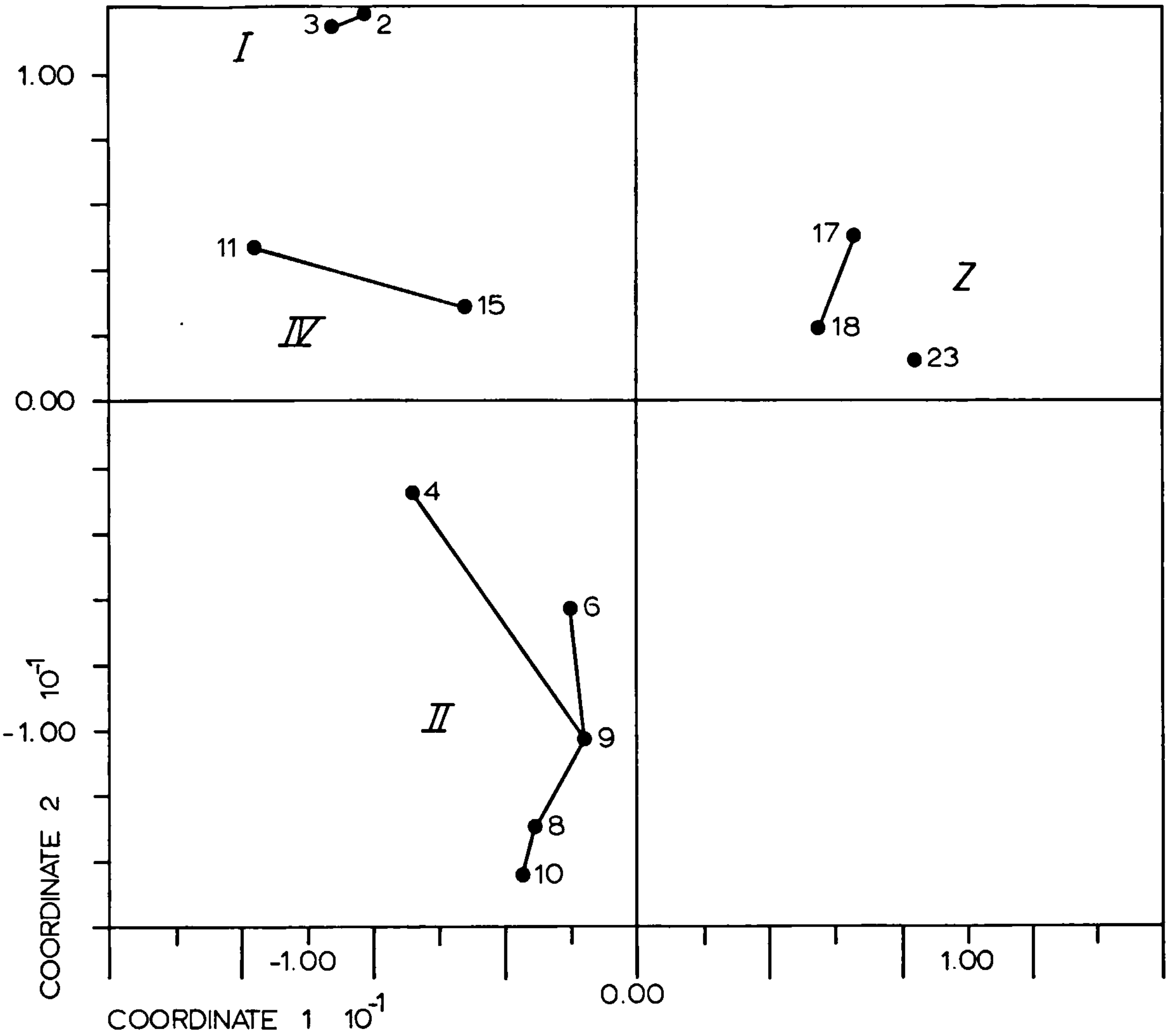
It may be concluded that taxa can be easily placed into species groups on the basis of a limited character set (e.g. food plants or male genitalia characters) if others are ignored. Using a wide range of characters, often makes assignment to a pre-establishment non-phenetic species group more difficult, and at least a number of taxa will fall outside the range applicable to that group. On the other hand, these outliers are often found to belong to new groups when the sample is increased to include, for example, both European and North American species in the same analysis e.g. *rubifoliella* (12). The possibility that computer analyses can select the characters and their order of priority for cladistic analyses has not yet been fully investigated.

The character analyses expressed in the cluster and principal co-ordinates analyses have demonstrated the value of the numerical method in producing meaningful and useful classifications. The innovations of contouring and minimum spanning trees have done much to overcome the distortions brought about by two dimensional representations of multi-dimensional concepts. In the main, they seem to lead to recognition of true affinities between taxa, especially at species level. In some cases, they have proposed reasonable associations between taxa which had not been previously suspected by other forms of approach. Occasionally species were placed peripheral to the group in which they were thought to belong, but with the phenetic approach the 'rationale' can usually be traced and considered. Taxa found later can be added to the matrix and the phenetic associations assessed by Add-a-Point program (Wilkinson, 1970).

Classification apart, the numerical methods provide for each taxon, a useful indication of which species should be compared for diagnosis. It is apparent that 'nearest neighbours' should always be checked. The description of phenetic affinities given for each species provides a measure of its' typicality and a ready awareness of the taxa with which it is associated.

ACKNOWLEDGEMENTS

My thanks are due to Huib Welker who carried out a numerical analysis using BIOPAT (D. Povel, Leiden) as part of his undergraduate project in 1983. He derived his character



Figs. 1-5. Principal co-ordinates analysis of the genus *Ectoedemia*, showing vectors 1 and 2 with contour levels and minimum spanning tree. I-V = species groups of *Ectoedemia* s. str. Z = subgenus *Zimmermannia*. E = subgenus *Etainia* and T = single species *saccharella* from the genus *Trifurcula*.

Fig. 1. Contour level 4.

matrix from the published works and his findings suggested that a more in depth study would be useful. I have retained the same dimensions for the figures in order to see if my larger data matrix produced from the specimens, gave significantly different results. Mr Welker's analysis showed broadly similar groupings, but differed in some very important interspecific detail, resulting from uncertain character tests.

I also wish to acknowledge the art work of D. A. Langerak who produced the figures from my line-print diagrams and rough sketches.

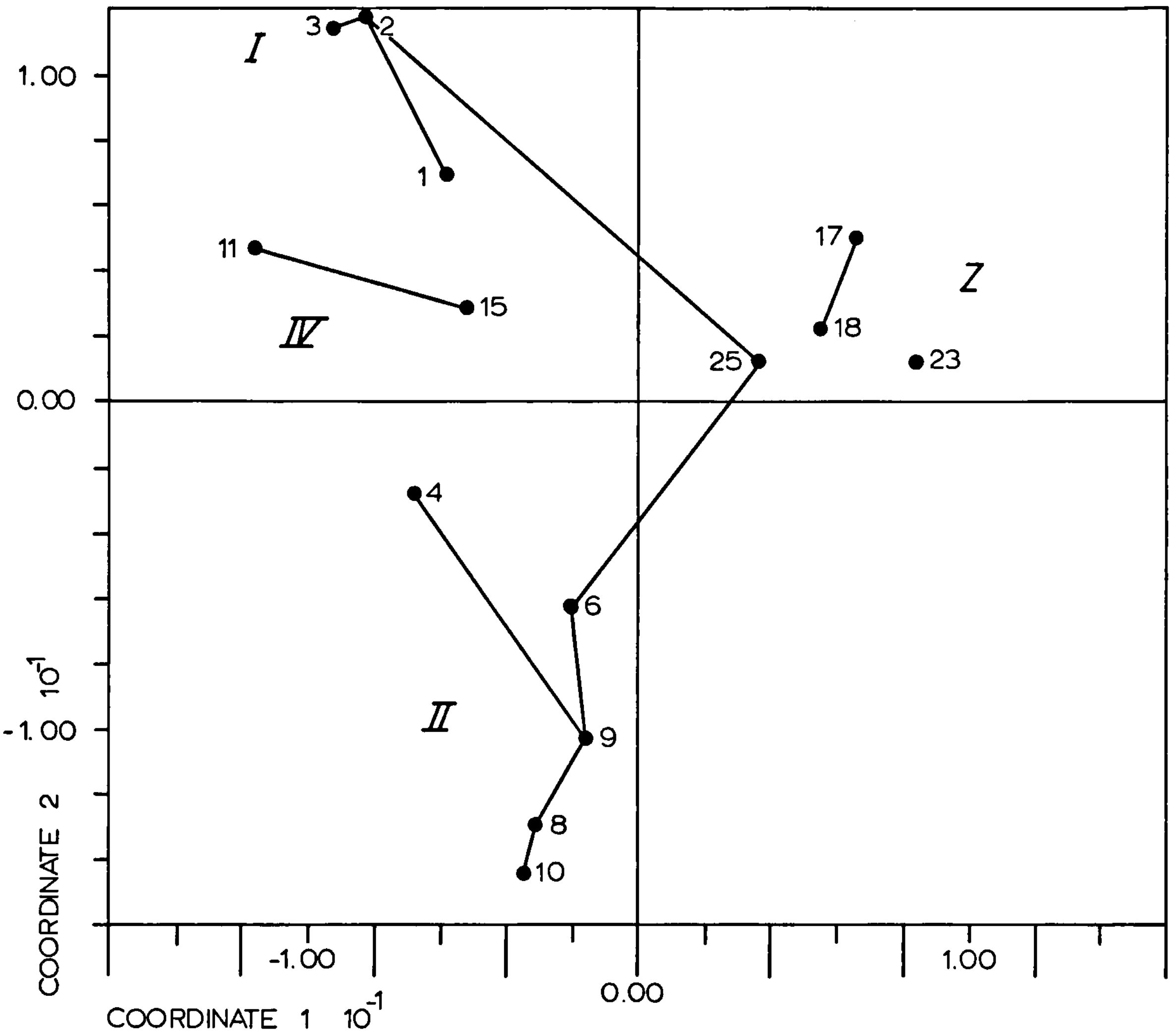


Fig. 2. Contour level 3.

CHECK LIST TO THE SPECIES OF THE GENUS *ECTOEDEMIA* IN NORTH AMERICA AS DETERMINED BY NUMERICAL ANALYSIS

Ectoedemia Busck, 1907
  Ectoedemia (*Ectoedemia*) *s. str.*
    populella group I
      (1) *populella* Busck, 1907
      (2) *argyropeza* (Zeller, 1839)
      (3) *canutus* Wilkinson & Scoble, 1979

    platanella group II
      (6) *platanella* (Clemens, 1861)
      (8 & 9) *similella* (Braun, 1917)
      (10) *virgulae* (Braun, 1927)
      (7) *clemensella* (Chambers, 1873)
      (4) *trinotata* (Braun, 1914)

    rubifoliella group III
      (12) *rubifoliella* (Clemens, 1860)

    numerical group IV
      (11) *lindquisti* (Freeman, 1962)
      (24) *canadensis* (Braun, 1917)
      (13) *ulmella* (Braun, 1912)
      (15) *quadrinotata* (Braun, 1917)
      (28 & 29) *andrella* Wilkinson, 1981)

numerical group V
- (5) *marmaropa* (Braun, 1925)
- (14) *nyssaefoliella* (Chambers, 1880)

Ectoedemia (*Zimmermannia*) Hering, 1940
- (16) *obrutella* (Zeller, 1873)
- (17) *acanthella* Wilkinson & Newton, 1981
- (18) *piperella* Wilkinson, 1981
- (19) *heinrichi* Busck, 1914a
- (20) *castaneae* Busck, 1913
- (21) *phleophaga* Busck, 1914b
- (22) *chlorantis* Meyrick, 1928
- (23) *mesoloba* Davis, 1978
- (25) *grandisella* (Chambers, 1880)
- (26) *coruscella* Wilkinson, 1981
- (27) specimen 90 Wilkinson, 1981
- (30) *reneella* Wilkinson, 1981
- (31) *helenella* Wilkinson, 1981
- (32) specimen 180 Wilkinson, 1981

Ectoedemia (*Etainia*) Beirne, 1945
- (33) *ochrefasciella* (Chambers, 1873)
- (34) *sericopeza* (Zeller, 1839)

Ectoedemia (*Fomoria*) Beirne, 1945
- (36) *pteliaeella* (Chambers, 1881)
- (37) *hypericella* (Braun, 1925)

Also included in the numerical analyses:
- (35) *Trifurcula saccharella* (Braun, 1912)

SPECIES GROUP *POPULELLA*

This genus is the *populella* group of Wilkinson & Scoble, 1979 and Wilkinson & Newton, 1981. Although *argyropeza* is the older name and also occurs in Europe, *populella* is used for the group because it is the type species for the genus.

In North America the species contained therein are *populella*, *argyropeza* and *canutus*. Formerly *trinotata* and *marmaropa* were included, but according to this numerical study these two leaf blotch miners are misplaced here, the analyses preferring to place them within other leaf-mining groups, notwithstanding that the associated species are serpentine miners. The minimum spanning tree specifically associated *trinotata* with *similella* and *marmaropa* with *nyssaefoliella*.

The group characters are a broadly triangular pseuduncus, a well developed transverse bar, a straight or weakly concave anterior border to the male genital capsule. The aedoeagus has very large spines - usually four. The female has sclerotised colliculum in the ductus bursae. The accessory sac appears to be wanting. The apophyses are approximately equal.

Associated species in Europe include *argyropeza argyropeza* (Zeller, 1839), *turbidella* (Zeller, 1848) = *populialbae* (Hering, 1934), *hannoverella* (Glitz, 1872), *klimeschi* (Skala, 1933), *intimella* (Zeller, 1848) and *wilkinsoni* (Puplesis, 1984a). This group includes the petiole and midrib miners.

Ectoedemia (Ectoedemia) populella Busck (1)

Ectoedemia populella Busck, 1907,
Proc. Ent. Soc. Wash., 8:98

The ground colour of the dorsal surface of the forewing is cupreous brown, dusted with grey and with characteristic copper reflections.

E. populella is generally larger than most other species in the genus excepting those in the bark-mining group. The fringe on the forewing is variously irrorate with scales of the forewing ground colour, but the scales are not arranged in a band over the cilia as in many leaf-mining *Ectoedemia* species including *platanella* and *clemensella*.

The species *argyropeza* and *canutus* appear to be closely related to *populella*, but *argyropeza* is thought to be parthenogenetic and without males, while the male genitalia of *populella* differ from those of *canutus* in the more pointed pseuduncus, the shorter and broader valves and the gnathos, which is not bifid laterally, in *populella*. Also, the outer pair of anellar projections on the aedoeagus are shorter than the inner pair and much shorter than those in *canutus*. The female genitalia are distinguished from those of *argyropeza*, *canutus* and most of the leaf-mining *Ectoedemia* species by the comparatively small signa and cells that comprise them.

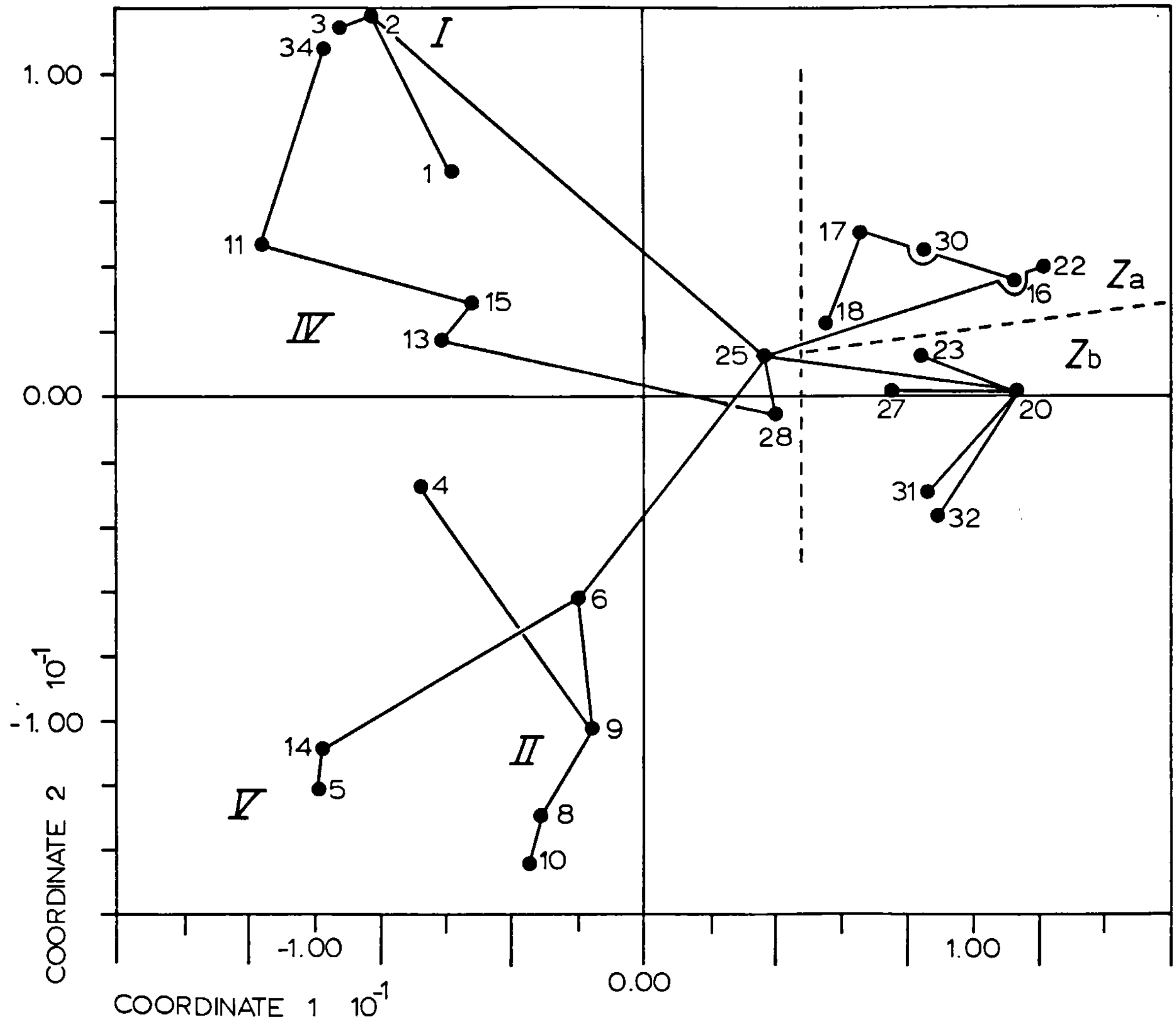


Fig. 3. Contour level 2. Za and Zb possible divisions of subgenus *Zimmermannia.*

The larvae of *populella* form galls on the leaf petiole of trembling aspen, *Populus tremuloides* A. Michaux and large tooth aspen, *P. grandidentata* A. Michaux. The galls take the form of swellings in the petiole close to the leaf and thus distinguish *populella* from *argyropeza*, which makes a mine in the petiole and leaf-blade of *Populus*. Possibly *canutus* forms similar petiole galls to those of *populella*, but on balsam poplar. The larvae mature in October and early November and the imagines emerge in May and June of the following year; *populella* is univoltine. The species is recorded from Ontario and Manitoba in Canada; New York, Ohio, New Hampshire and Massachusetts in the U.S.A. All numerical analyses show this species to be closely related to *argyropeza* (2) and *canutus* (3), but not so closely as the latter pair are to each other. Features of the biology of *populella* account for this, particularly the formation of galls in the petiole. However, the minimum spanning tree (fig. 2) clearly shows its' affinity to *argyropeza*, as does an analysis only using females (not illustrated).

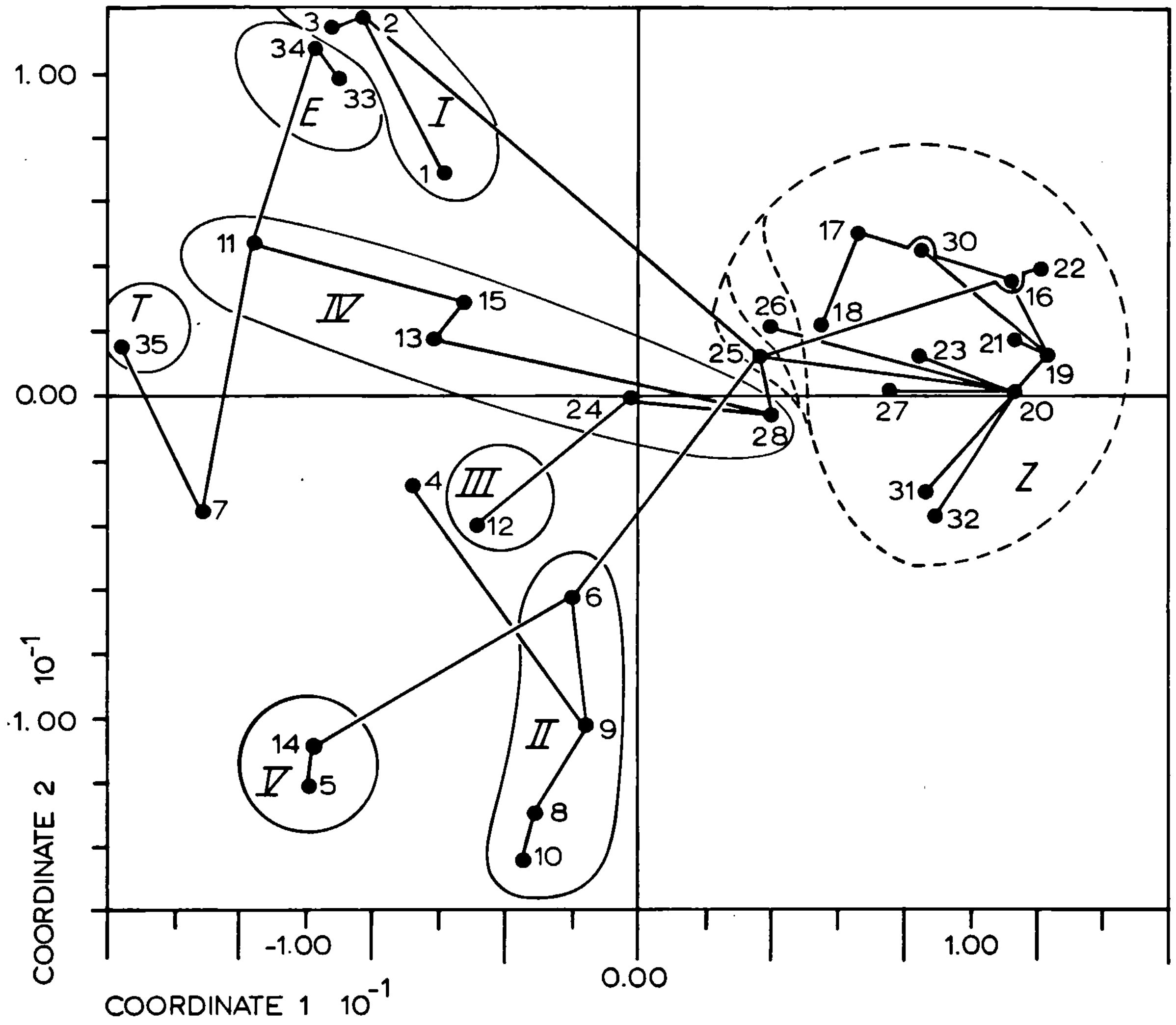


Fig. 4. Contour level 1 (base set) showing subgenera and species groups as suggested by numerical analysis of characters.

Ectoedemia (Ectoedemia) argyropeza (Zeller) (2)

Lyonetia argyropeza Zeller, 1839,
Isis von Oken, 23:215

E. argyropeza has been regarded as having two subspecies, although this has not been borne out by recent biochemical work (Menken, in preparation). Differences in externals may represent limited gene flow in a recently introduced population. The nominate sub-species *argyropeza argyropeza* (Zeller) is European only.

Ectoedemia argyropeza downesi Wilkinson & Scoble, 1979, *Can. Ent.*, 107:80

The ground colour of the forewings of this subspecies is grey, heavily irrorate with purplish brown scales distally, more lightly irrorate proximally. Some specimens have a patch of white scales on the costal edge forming an incomplete postmedial fascia. The following species, *canutus*, is externally very similar to *argyropeza downesi*, but the more scattered irrorations of scales on the forewing tend to give *canutus* a slightly darker overall appearance.

Both subspecies of *argyropeza* are parthenogenetic; only females are known. The female genitalia have a very wide and characteristic ovipositor with broad apophyses; the ovipositor of *canutus* is considerably less wide and the signa of *populella* considerably smaller in comparison with those of *a. downesi.*

The larvae form first a petiole-mine and then continue to form a stigmatonome at the base of the leaf blade. Like *populella*, the host trees of *a. downesi* are *Populus tremuloides* and *P. grandidentata.* However, while a certain amount of callus tissue is formed in the petiole of *P. tremuloides*, in *P. grandidentata* this may block the mine, preventing the larvae from developing and *a. downesi* seldom reaches maturity on the latter host. The egg is laid on the petiole. The larva remains in the mine until after leaf-fall and a green zone remains around the mined portion of the leaf-blade after the rest has turned yellow. The larva then overwinters in ground litter or soil, in the cocoon, and pupates in the early spring.

This species is univoltine, adults emerging in May or June, and it is known only from Ontario and Quebec in Canada.

It is unique in being parthenogenetic and this feature has influenced the numerical analyses. In the cluster analysis for all characters (fig. 8), the nearest neighbour is clearly *canutus* (3) with a 75% similarity. In an analysis of female characters only, *populella* (1) is closest. The principal co-ordinates analyses also link the species very closely with *canutus*, both species appearing at level 4 in the sectioning and linked by the minimum spanning tree (fig. 1). The second nearest neighbour is *populella.*

Ectoedemia (Ectoedemia) canutus
Wilkinson & Scoble (3)

Ectoedemia canutus Wilkinson & Scoble, 1979, *Mem. Ent. Soc. Can.*, 107:81

The forewing of *canutus* is pale greyish; irrorate with a variable number of cupreous brown scales with weak copper and silvery grey reflections. The wings are more uniformly irrorate and appear generally darker than those of *argyropeza downesi* and they lack the stronger cupreous reflections of the wings of *populella.* Males have a pale yellow tuft of cilia arising from the base of the costal margin of the hindwing.

The male genitalia have longer, narrower valves than *populella*; the pseuduncus is more rounded in *canutus* and the laterally bifid arms of the W-shaped gnathos are characteristic and possibly unique in *Ectoedemia.* Also, the outer anellar projections of the aedoeagus are much longer in *canutus* than in *populella.* In the female genitalia the ovipositor of *canutus* is narrower and more pointed than that of *a. downesi*, while the signa are larger and made up of larger cells compared with the signa of *populella.*

The host plant of *canutus* is balsam poplar, *Populus balsamifera* L. and there is some evidence to suggest that the larvae form galls on the petioles of the leaves, similar to those made by *populella* on other *Populus* species.

There is very little material of this species, but it is probably, like *populella* and *argyropeza*, univoltine, emerging in the late spring. The only known locality is that of the type series, in Ontario. *E. canutus* is phenetically closely associated with *argyropeza* (2) and to a lesser extent *populella* (1), which together form one discrete group. The analyses shown (figs. 3, 7 and 8) suggest no great affinity with the former members of the species group - *trinotata* (4) and *marmaropa* (5) which, considering their biology, is not surprising. However, by confining analyses to genitalia characters (not shown) both males and females demonstrate high cophenetic levels with *trinotata.*

SPECIES GROUP *PLATANELLA*

The five species - *platanella, virgulae, similella, clemensella* and *trinotata* form the species group in North America. They all have fasciae or patches and a fringe of broad scales overlapping the hair scales. In males the first three species

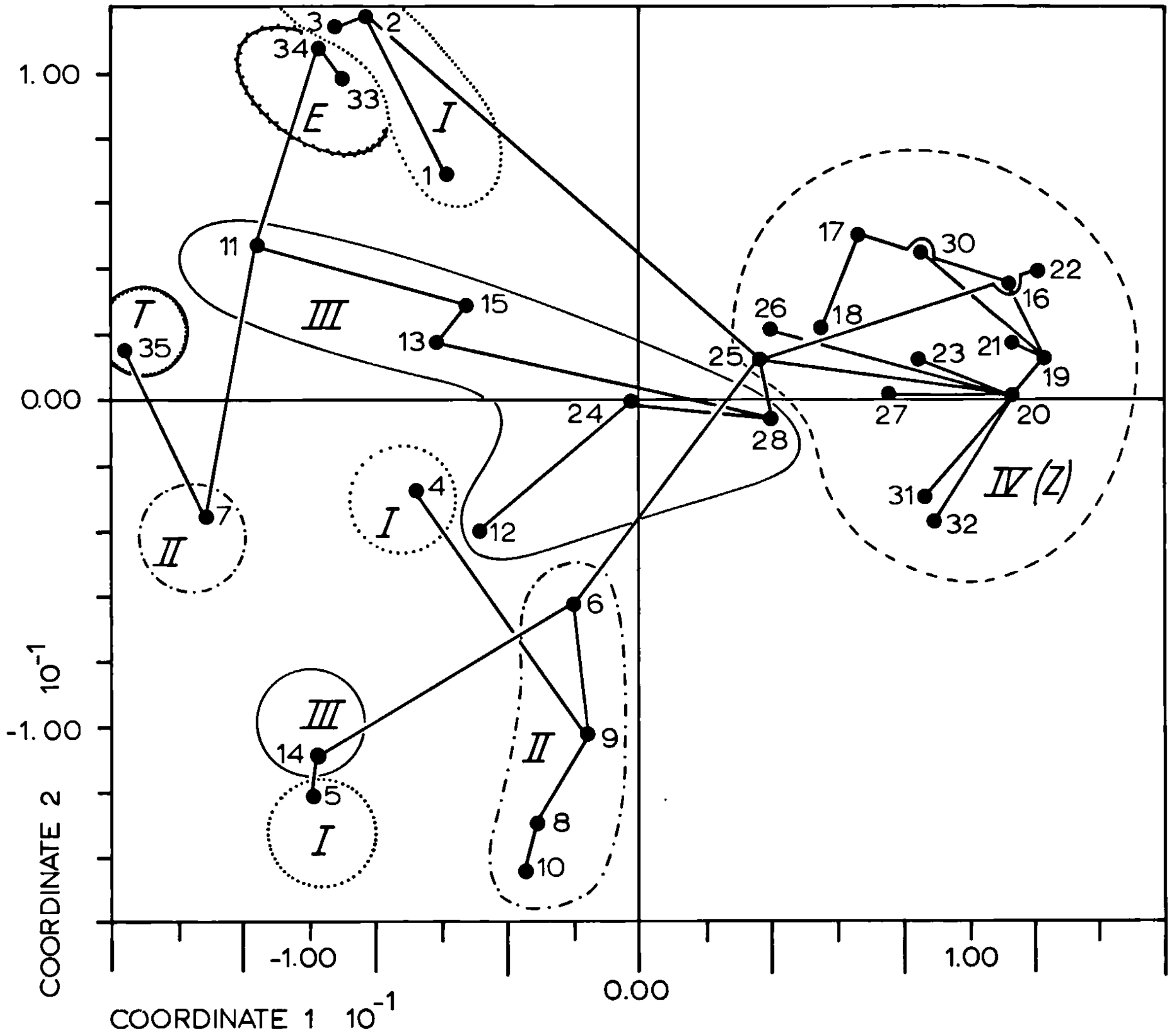


Fig. 5. Contour level 1 (base set) showing subgenera and species groups as earlier proposed by classical (non-numerical) techniques.

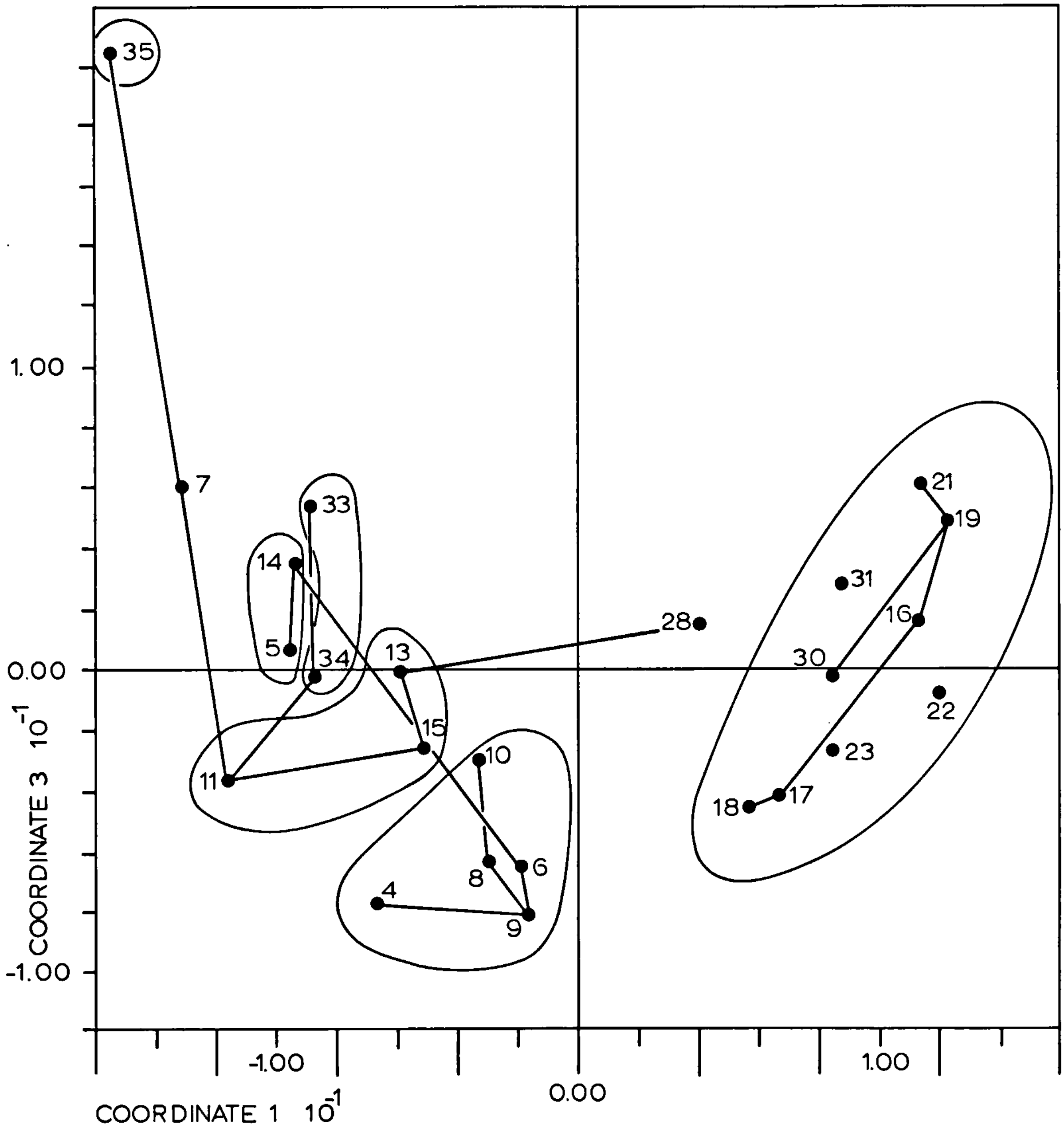
also have a lance-shaped chitinous plate along the fore edge of the hindwing.

The males have the same tapering pseuduncus, usually terminating in a point and W-shaped gnathos as in the previous species group. Particularly notable in these five species are the multi-branched setae, or scales, on the inner surface of the valves, (only weakly developed in *clemensella* and absent in *trinotata*) which are not found in other groups. The aedoeagus terminates in well developed spines, but this feature is also seen in other species groups.

There is a double sclerotised collicula ring in females, which are all very similar.

In Europe there is no exact counterpart to this group, although some species of the *subbimaculella* (Haworth, 1828) group may be associated.

All are leaf miners confining themselves to the lamina.



Figs. 6-7. Principal co-ordinates analysis of the genus *Ectoedemia*, showing vectors 1 and 3 with contour levels and minimum spanning tree.

Fig. 6. Contour level 2 showing affinity groups.

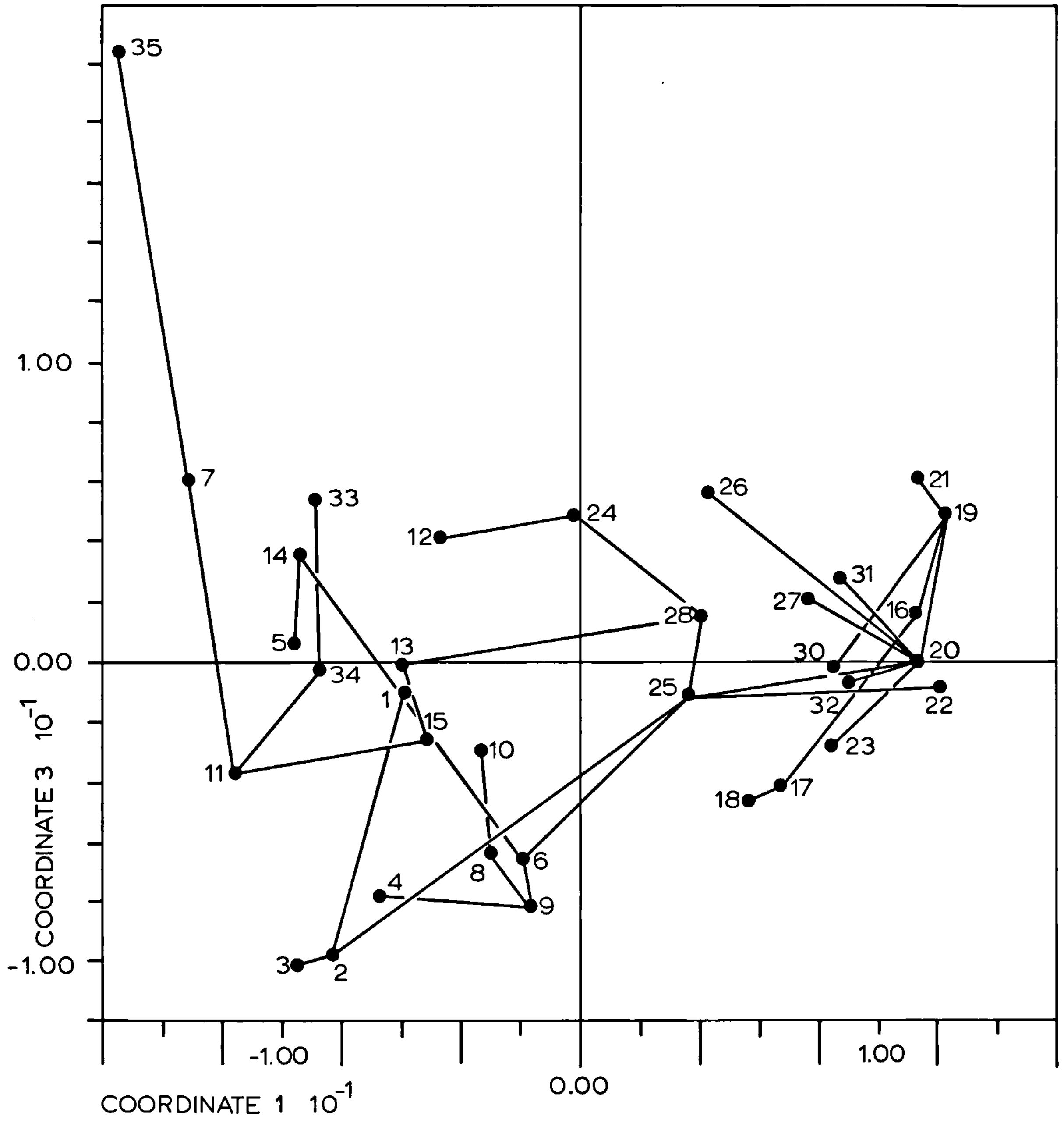


Fig. 7. Contour level 2 (base set).

Ectoedemia (Ectoedemia) platanella (Clemens) (6)

Nepticula platanella Clemens, 1861,
Proc. Ent. Soc. Philad., 1:83

The forewing of *platanella* is dark brown with bronze reflections; there are two white, medial streaks—one on the fore and the other on the hind margin—which are occasionally linked in the middle by a few white scales so forming a complete fascia; the fringe is whitish, with an apical band of dark brown wing scales. In males a lance-shaped chitinous plate extends along the fore-edge of the hindwing to the middle of the costa. Although similar to *clemensella*, *platanella* is usually larger and browner and the males of *clemensella* lack the specialized chitinous plate on the hindwing.

The male genitalia of *platanella* and *clemensella* differ in the form of the weakly bilobed saccus, the shorter, more furcate valves and the two pairs of spine-like anellar projections on the aedoeagus in *platanella*. The female genitalia are similar to those of *similella* and *virgulae*, but are distinguished by the spines on the lobe associated with the colliculum, which are large and single in *platanella*. Also, the signa and cells that comprise them are comparatively large in *platanella*.

The host plant of *platanella* and of the following species, *clemensella*, is sycamore, *Platanus occidentalis* L., although there is a record of a single male specimen of *platanella* from red oak, *Quercus rubra* L. The upper surface ophistigmatonome of the two species are easily distinguished: the mine of *platanella* is a very short, linear tract, filled with frass and a large round blotch, whereas in *clemensella* the linear portion is long, straight, with a central line of frass, broadening suddenly into a small terminal blotch.

In *platanella* the egg is laid on the lower surface of the leaf, sometimes near a vein. The mine is a circular blotch which often eclipses the earlier linear portion of the mine and the frass is scattered evenly throughout the blotch. The larva emerges on the upper surface of the leaf and the cocoon is ochreous brown.

There are three generations per year; adults have emerged or been taken from early May through to late July, with a peak in late June and early July. The species is reported from Ohio, New Jersey, Washington D.C., Kentucky and from Ontario in Canada.

The affinities of *platanella* are not in question, since in all analyses the highest phenetic bonding goes to *similella* (8, 9) and *virgulae* (10). When selected or random characters are used, sometimes *similella* is assessed as nearest to *platanella*, in others *virgulae*, but together they clearly form a close species group.

Ectoedemia (Ectoedemia) similella (Braun) (8, 9)

Nepticula similella Braun, 1917,
Trans. Amer. Ent. Soc., 43:188

The pattern of wing markings, although resembling that of other members of the species group, is most variable in *similella* and there are two forms. The Ohio form has a brown forewing with scattered blue and purple reflections, distally irrorate, with a single, medial, oblique fascia, shining silver, and occasionally reduced to marginal streaks as in *platanella* and *clemensella*; it is found in Ohio, New Jersey and Virginia. The Florida form has a very dark brown to black forewing, uniformly dusted with grey reflections, the markings barely visible as marginal patches of not more than five whitish scales and with an apical patch of off-white ciliae in the fringe. The Ohio form is generally more iridescent than *platanella* and *clemensella* and differs in the irrorate nature of the forewing ground colour; it is very similar to *virgulae*. The markings of the Florida form are characteristic. There is a single female from Arkansas with externals intermediate between the two forms: the forewings are dark chocolate brown with an apical patch of cream, as in the Florida form, but there is a single medial fascia, as in the Ohio form.

The male genitalia do not vary as the externals do. The saccus is more markedly bilobed than in *platanella* and *virgulae*, but less than in *clemensella*. The broad fan-like scales of the valves are characteristic. The female genitalia resemble those of the other members of the group and differ only in the unequal size of the relatively small signa and the very small spicules on the lobe associated with the colliculum.

The host plants of *similella* are pin oak, *Quercus palustris* Muench., and red oak, *Q. rubra* L. The egg is laid on the upper surface of a leaf and the larva initially mines a very narrow tract, contorted in close S-shaped curves and with frass scattered throughout its breadth. Later the larva mines a lower surface blotch with frass accumulated as a congealed mass toward the beginning of the blotch. The larva

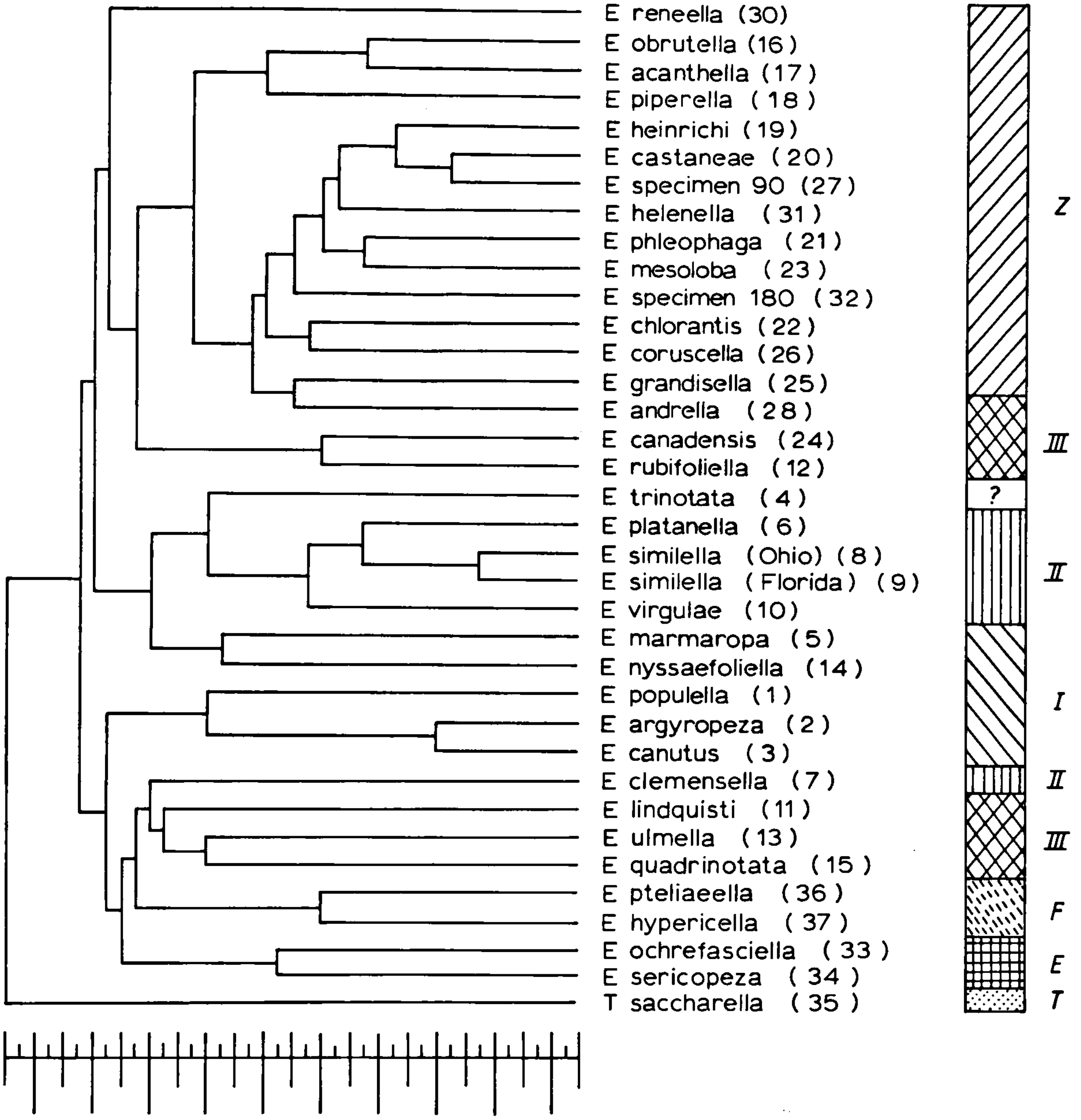


Fig. 8. Dendrogram of genus *Ectoedemia* derived from cluster analysis. Pattern code indicates species groups as determined by non-phenetic methods. I-III = subgenus *Ectoedemia* species groups, Z = subgenus *Zimmermannia*, E = subgenus *Etainia*, F = subgenus *Fomoria*, T = genus *Trifurcula*.

usually emerges from the lower surface of the leaf and spins an ochreous cocoon. The mine of *similella* is easily separated from the very long lower surface ophionome produced by *Stigmella altella* (Braun), which is also found on *Quercus palustris*.

Adults have been taken in May, throughout June and early July, while late instar larvae are found from July to October. It is possible that there are up to three generations per year. The species is known only from the U.S.A.: Ohio, New Jersey, Virginia, Arkansas and Florida.

The two forms of this species were tested separately, but the cluster analysis dendrogram (fig. 8) shows that their similarity was 'recognised' and given the highest percentage (83%) similarity of any taxon pair. That *platanella* (6) and *virgulae* (10) are its' cohorts is demonstrated by the contouring (fig. 1) of the principal co-ordinates analysis.

Whilst the dendrogram (fig. 8) might suggest otherwise, in the vast majority of co-ordinate tests *virgulae* is given as *similella's* nearest neighbour. However, the three together comprise a well knit group.

Ectoedemia (Ectoedemia) virgulae (Braun) (10)

Nepticula virgulae Braun, 1927,
Trans. Amer. Ent. Soc., 53:198

The ground colour of the forewing of *virgulae* varies from brown to very dark chocolate brown with bronze and purple reflections distally, with each scale darker at the tip; there is a single, oblique, medial fascia, variable in breadth, shining silver and markedly concave inwardly. As in *similella*, there is geographic variation in wing colour and markings. The forewing ground colour varies in intensity from a pale brown in Ohio to dark chocolate brown in Florida and Texas; the breadth of the fascia varies and is broader in those specimens from Florida.

E. virgulae is generally smaller than *platanella* and differs from *platanella* and *clemensella* in the irrorations and reflections of the forewings.

Unlike *similella*, the variation in externals is correlated with variation in the male genitalia of *virgulae*. The pseuduncus ranges in length and shape from a short, blunted form in Florida, to a longer, more tapering form in Ohio and Texas. The setae of the valves are more heavily sclerotised and larger in Florida males than in those from Ohio and Texas. There are just two males known from Texas and these have much stouter transtillae than the type which is possibly a geographical or seasonal difference. The saccus is more weakly bilobed and the valves more concave along the inner margin than in *similella* or *clemensella*. The setae of the valves differ from those of *platanella*, *clemensella* and *similella*, in the longer shaft. The female genitalia resemble those of the above mentioned species, but are distinguished by the large triple spines on the lobe associated with the colliculum and the relatively small equal-sized signa in *virgulae*.

The larvae mine an upper surface ophionome on American hazel, *Corylus americana* Walter. The mine is long, gradually broadening to a width of about 1.5 to 2.0 mm at its' end and the frass is more or less scattered, usually forming a broad tract. The mine is broader than that of *Stigmella corylifoliella* (Clemens), but narrower than that of *S. ostryaefoliella* (Clemens), both of which are also found on hazel.

The species is possibly bivoltine in Ohio, with adults emerging in April, May and July. Adults have also been taken in May from Florida and in September from Texas.

The principal co-ordinates of *virgulae* (e.g. fig. 3) are most similar to those of *similella* (8, 9) and *platanella* (6) is also close. The cluster analysis shows *platanella* to have the greatest similarity with *virgulae* (63%) using all characters (fig. 8) and male characters only (not illustrated), whilst on the basis of female characters *similella* is nearer. The contouring (fig. 1) shows that these species form a valid species group.

Ectoedemia (Ectoedemia) clemensella (Chambers) (7)

Nepticula clemensella Chambers, 1873,
Can. Ent., 5:125

The ground colour of the forewing of *clemensella* is purplish black with bronze and purple reflections; there are two medial white patches, weakly shining silver, one on the costa and one on the anal edge, usually meeting to form a fascia.

The species is similar to *platanella*, but generally smaller and paler, and males lack the chitinous plate of the hindwing that is found in *platanella*, *similella* and *virgulae*.

The setae of the valves in the male genitalia of *clemensella* are smaller and less furcate than those of other closely related species. The saccus is markedly bilobed, with each lobe pointed, distinguishing *clemensella* from *platanella* and *virgulae* in which the saccus is only very weakly bilobed and from *similella* in which it is less markedly bilobed. The female genitalia are similar to those of *platanella*, *similella* and *virgulae*, but the signa are smaller than in *platanella* and relatively larger than those of *similella* and *virgulae* and the anterior apophyses are broad and complex.

The host plant of *clemensella* is *Platanus occidentalis* and the mine is easily distinguished from that of *platanella*, which also mines sycamore, by the characters given above. The long linear portion of the mine, with a central line of frass, gradually increases in breadth and the small terminal blotch has a diameter about three or four times the width of the end of the linear portion; the frass-line is absent in a large part of the blotch.

E. clemensella, like *platanella*, has three generations per year and adults have emerged or been taken from May to early August.

E. clemensella is much less common than *platanella*, but it is known from Ohio, Pennsylvania, Kentucky, Maryland, New York and Ontario in Canada.

Numerically *clemensella* appears to have no special affinities, in fact in some tests it was more dissimilar than species from other subgenera. During the taxonomic studies this species was placed in the *platanella* group (6-10) which, although some of its' diagnostic characters are weak, still seems to belong there. *E. clemensella* lacks the chitinous plate of the hind wing, the branched hairs of the male valves and some of the mine characteristics found in other members of the group.

Ectoedemia (Ectoedemia) trinotata (Braun) (4)

Nepticula trinotata Braun, 1914,
Can. Ent., 46:18

The ground colour of the forewing of *trinotata* is very dark brown, the basal third with purple reflections and the apical two thirds irrorate, with the base of each scale greyish. The fringe is whitish, shining silver, with an apical band of dark brown wing scales. There is a small, diffuse, antemedial spot on the costal margin, which is occasionally eclipsed by greyish reflections when viewed from certain angles, followed by two distinct postmedial spots, shining silver, one at each margin. There is a band of wing scales in the fringe of many of the leaf-mining *Ectoedemia* species, but the forewing markings of *trinotata* are characteristic; they are similar to those of *quadrinotata*, but *trinotata* has only one antemedial spot on the forewing whereas *quadrinotata* has two.

The male genitalia are easily differentiated from those of other members of the genus by the unusual narrow, rounded lobe of the pseuduncus and the form of the transtillae. In *trinotata* the transtillae are in the form of an inverted U, with the lateral arms short and broad, the ventral arms short and narrow and the long, narrow transverse bars fused to form a strongly arcuate strap. There are two pairs of anellar projections on the aedoeagus, as in *populella* and *canutus*, but the inner pair are short and spine-like and the outer pair are long and strongly curved. The overall form of the female genitalia, especially the sclerotised double ring of the colliculum, is typical of many *Ectoedemia* species. The large spiculate lobe associated with the colliculum, the pair of long narrow signa and the loosely spiralling accessory duct may be characteristic for *trinotata.*

The larva forms an upper surface ophistigmatonome on leaves of bitternut hickory, *Carya cordiformis* (Wangenheim) K. Koch. The egg is laid on the upper or lower surface of the leaf, usually near a vein. At first the mine is a very narrow, much contorted linear tract which rapidly enlarges into an extensive blotch; the frass is scattered throughout. The larva emerges from the mine on the upper surface of the leaf and spins a pale reddish brown cocoon. The mine of *trinotata* is transparent throughout and is thus distinguished from the whitish mines of *Stigmella judlandifoliella* (Clemens), also found sometimes in hickory.

E. trinotata has two generations: the mines of the first appearing during the early part of July and the second in the beginning of September. The adults are on the wing in June and then in late July and August. The species is known from Ohio, Arkansas and Illinois.

The relationships of *trinotata* were uncertain from taxonomic study and the species was nominally placed in the *populella* species group. The principal co-ordinates analyses (fig. 1) suggests that it is more correctly an outlier to the *platanella* species group (II). This view is supported by the cluster analysis (fig. 8) where it is seen to have a 35% affinity with the *platanella* group, whilst with the *populella* group the similarity value varies from 13%-25%. It is the male genitalia that show similarity to *canutus* (3) in the cluster analysis and the much stronger similarity of the female characters that relates *trinotata* to *virgulae* (10).

Ectoedemia (Ectoedemia) rubifoliella (Clemens) (12)

Nepticula rubifoliella Clemens, 1860,
Proc. Acad. Nat. Sci. Philad., 12:214

The forewing of *rubifoliella* is brownish black with a single, shining silver, medial fascia. It resembles *virgulae* in externals, although *rubifoliella* is generally darker and males lack the chitinous plate of the hindwing found in *virgulae.* There are only a few known specimens of this species, all are small.

The pseuduncus of the male genitalia is short and rounded, as in the bark-mining species of *Ectoedemia*, but in *rubifoliella* the valves are short, broad basally and emarginated distally; the vesica lacks denticulate cornuti, but bears strong, curved striate thickening. The female genitalia lack a colliculum on the ductus, as do those of *ulmella* and *nyssaefoliella*, but are distinguished by equal-sized signa comprising very large cells.

The larvae of *rubifoliella* mine leaves of blackberry *Rubus* sp., forming at first a very narrow linear tract, which closely follows a vein or the margin of the leaf, before enlarging into an elongate, rather irregular, blotch. The frass in the linear portion of the mine is in a broken, central line and in the blotch, irregularly dispersed. The cocoon is dark brown.

E. rubifoliella appears to have two generations per year; mines containing larvae being found in July and September. Adults have been taken in late May, early June and mid-August in Ohio and Kentucky. Clemens originally described this species from mines collected in Pennsylvania but *rubifoliella* is now also known from Ontario and Quebec in Canada.

From the principal co-ordinates analyses and minimum spanning trees it can be seen that *canadensis* (24), *andrella* (28), *ulmella* (13), *quadrinotata* (15) and *lindquisti* (11) are phenetically associated and probably form a valid species group. *E. rubifoliella* is somewhat peripheral to this group. It is interesting that the computer should have separated this species so far away from them. In the taxonomic study of the American species alone, *rubifoliella* does not seem to be so separate. However, when comparing European and American species together, then *rubifoliella* falls into another species group, i.e. the European *angulifasciella* group, whilst the others would be in the *occultella* group. In a dendrogram for the analysis of female characters only, *nyssaefoliella* (14) was drawn as nearest neighbour, but the affinity is weak. In that for males, *ulmella* was nearest. In the cluster analysis dendrogram (fig. 8) *canadensis* is again the closest and a loose relationship (23%) with *Zimmermannia* subspecies (16-23, 30-32)—those attacking bark—is seen.

NUMERICAL GROUP IV

At present this group has five members in North America, *ulmella*, *andrella*, *quadrinotata*, *lindquisti* and *canadensis.*

The pseuduncus in males is bluntly rounded, more tapering in *lindquisti*, and the aedoeagus has two large terminal spines. Anteriorly the capsule is straight or only weakly concave. Females are without the sclerotised colliculum, except *lindquisti*, otherwise the characters are typical for *Ectoedemia.* All mine the lamina.

This group probably corresponds with the *angulifasciella* (Stainton, 1849) group in the old world, which also contains *Rubus* and *Ulmus* feeding species. However, comparison of the genitalia shows that at least some of the *subbimaculella* (Haworth, 1828) group could also be associated here. This latter group of some 17 species is almost exclusively found on oaks (*Quercus*) which is not, as yet, known as a food plant for this new world group. The traditional European species groups have been based largely on similarities in life cycles.

E. canadensis and *lindquisti* could be regarded as forming a subgroup in North America which would also include *argentipedella* (Zeller, 1839) and *mediofasciella* (Haworth, 1828) from Europe. These are leaf miners on *Betula* and *Alnus* and the North American pair appear to be homologous with the European species and possibly even synonymous. For further discussion see species descriptions.

The male genitalia (unknown in *canadensis*) are characterised by a tapering, pointed pseuduncus, uniformly arcuate valves, a well developed transverse bar and long ventral arms to the transtillae. The female has a sclerotised figure-of-eight shaped colliculum. *E. lindquisti* has no well developed accessory sac and the apophyses are sub-equal.

Ectoedemia (Ectoedemia) lindquisti (Freeman) (11)

Nepticula lindquisti Freeman, 1962,
Can. Ent., 94:522

The forewing of *lindquisti* is dark brownish grey with grey, bronze and purple reflections, and a single, emarginated, postmedial fascia with silver reflections; the fringe is grey, irrorate with scales of forewing ground colour, which do not form a band across the terminal cilia as in many leaf-mining *Ectoedemia* species. The position of the fascia also distinguishes *lindquisti* from those species with a single medial fascia and it differs from *marmaropa*, which also possesses a postmedial fascia, in the absence of a lustrous basal patch.

The male genitalia resemble those of *platanella*, *clemensella*, *similella* and *virgulae*, but differ in the absence of setae on the valves. Also, the aedoeagus of *lindquisti* has a characteristic pair of simple bifid anellar projections. The female genitalia have a colliculum as a sclerotized double ring, which distinguishes them from those of *rubifoliella*, *ulmella* and *nyssaefoliella*, but the associated spiculate lobe, present in all the preceding species, is absent in *lindquisti*. The anterior apophyses are broad and longer than the narrower posteriores.

Most specimens of *lindquisti* have been reared from white birch, *Betula papyrifera* Marshall and one specimen from yellow birch *Betula lutea* (F. Michaux) (= *B. alleghaniensis* Britton). The egg is laid on the under surface of the leaf. The mine is an upper surface stigmatonome; the blotch is more or less rectangular and is made between two lateral leaf veins and the frass is deposited in circular patches. The cocoon is yellow-brown, darkening with age.

Lindquist (1962) describes the biology of this species and, according to him, *lindquisti* is univoltine in Ontario with adults present from late June to late July. However, some of the paratypes from Ontario were taken in early June and one on the 1st August. Besides localities in Ontario, *lindquisti* has also been taken in Maine, U.S.A.

This species has been difficult to assign to a group. During the general taxonomic study *lindquisti* was provisionally placed in the *rubifoliella* group (11-15) on the grounds of similarities in the males genitalia, especially *quadrinotata* (15) which has smaller anellar spines and more pointed pseuduncus. Generally, there are resemblances to the *platanella* group (6-10) but differ again in the absence of specialised setae on the valves of males and the lobes on the colliculum in females. The female is, however, more like those in the *populella* group (1-5).

The cluster analysis (fig. 8) places the species in the *rubifoliella* group, although at a low phenetic level of 28%. The contouring and minimum spanning tree of the principal coordinates analysis (fig. 1) links *lindquisti* with *quadrinotata* (15) in the same group, but not closely, and together they have tenuous links with other species via *andrella* (28). A cluster analysis of female characters only, joins this species with the *populella* group and the *platanella* group equally, whilst the males only analysis, also favours the *platanella* group.

Thus the affinities of this species are weak and, on balance, *lindquisti* can best remain in the *rubifoliella* group to which it has already been assigned.

Ectoedemia (Ectoedemia) canadensis (Braun) (24)

Nepticula canadensis Braun 1917, *Trans. Amer. Ent. Soc.*, 43:185

The tufts and vertex are black or very dark brown and match the background of the wings. There is a single, white, medial fascia and in these points somewhat resembles *lindquisti* which differs in that its' fascia is postmedial and the tuft and vertex are ochreous. The genitalia are unknown.

The mine starts as a short, contorted, serpentine mine which abruptly enlarges to form an irregular blotch and thus forms an upper surface ophistigmatonome. There are frequently numerous mines on a single leaf of the food plant, which is Mountain Alder *Alnus tenuifolia* (Nutt.). It is thought to be univoltine.

Although Braun collected a number of mines, the only adult ever known was the holotype which cannot be located since it is no longer in the author's collection. For a full discussion on the status of this species and its' diagnosis as *Ectoedemia* see Wilkinson 1981: 94. The two European species referred to as homologues in this reference are probably no longer to be regarded as separate species. It seems possible, therefore, that *canadensis* and *lindquisti* (11) are also conspecific.

E. canadensis has been correctly associated with the leaf miners as opposed to the bark miners in the principal co-ordinates analysis, and both types of analysis link it with *rubifoliella* (12). The same characteristics which have caused workers to regard it as separate from *lindquisti* have also contributed to lack of association in the numerical tests.

Ectoedemia (Ectoedemia) ulmella (Braun) (13)

Nepticula ulmella Braun, 1912, *Jour. Cincinn. Soc. Nat. Hist.*, 21:87

The wings of *ulmella* are covered in grey scales with purplish brown tips giving a variously mottled ground colour of purplish brown and grey, with bronze reflections. There is a single medial fascia, with weak reflections, formed by the union of costal and anal patches. This species is large and less iridescent than *rubifoliella*; the fringe is not irrorate with wing scales and males lack a chitinous plate on the hindwing, but have a large basal patch of buff to pale ochreous androconia.

The male genitalia resemble those of *rubifoliella*, but the valves are narrower, the gnathos broad with the lateral arms shorter than the medial projection and the anellus has two pairs of projections, the medial pair in the form of spines arising from large basal processes, in *ulmella*. The female genitalia also resemble those of *rubifoliella* in the absence of a colliculum, but may be separated by the smaller signa and the cells that comprise them and the outwardly curving posterior apophyses in *ulmella*.

The host plants of *ulmella* are various species of elm. At first the upper surface mine is very narrow and winding; at about half its' length it abruptly widens and from then on gradually increases; this portion of the mine is so contorted that it is impossible to trace the course of the mine, the whole having the appearance of an irregular blotch. The cocoon is reddish brown and contrary to the usual habit of *Ectoedemia* species which pupate in the surface soil or leaf litter, most *ulmella* larvae, especially those of the overwintering generation, spin cocoons within the mines, generally in the centre of the blotch.

There are two generations per year in *ulmella*, mature larvae being found in July and September. Adults have been taken in June, July, August and September. The species is reported from Ohio, Pennsylvania and Kentucky in the U.S.A., Ontario and Quebec in Canada.

Numerically *ulmella* has most overall affinity with *quadrinotata* (15) in the analyses given, but when using only male genital characters, *rubifoliella* (12) is closest and female characters show *nyssaefoliella* (14) to be the nearest. From the principal co-ordinates analysis (fig. 7) it can be seen that *andrella* (28) and *canadensis* (24) are also related.

Ectoedemia (Ectoedemia) quadrinotata (Braun) (15)

Nepticula quadrinotata Braun, 1917, *Trans. Amer. Ent. Soc.*, 43:168

The externals resemble those of *trinotata*. The forewing is dark greyish brown with greenish bronze reflections and there are four patches, reflecting silver, two on the costa in antemedial and subterminal positions and two on the hind margin, one postmedial and one basal. Thus there are four spots in *quadrinotata*, while there are only three in *trinotata*, which has only a single antemedial spot on the costal margin.

The male genitalia of *quadrinotata* are quite distinctive. The pseuduncus is short and tuberculate. The gnathos comprises a pair of stout lateral horns fusing at the bases to form a very thick short medial projection and the anellar projections are complex, in the form of a crown of thorn-like spines surrounded by longer spines and processes. The female genitalia lack a double sclerotised ring-like colliculum, but it is not absent as in *rubifoliella*, *ulmella* and *nyssaefoliella:* there is a weakly sclerotised structure, but no associated denticulate lobe.

E. quadrinotata mines leaves of hornbeam, *Carpinus caroliniana* Walter and American hazel, *Corylus americana* Walter. A few specimens have been reared from hop hornbeam or ironwood, *Ostrya virginia* (Miller) K. Koch and yellow birch, *Betula lutea* (F. Michaux). The mine begins as a narrow linear tract extending along the midrib or between two leaf veins, broadening to fill the area between the veins, in what Braun considered to be a blotch. The frass is dark and initially in a broken line, becoming less compact and later diffuse. The cocoon is brown, usually with an olive green tinge. There appear to be two generations per year, adults of *quadrinotata* being taken in May and June and later in July. Mines are found in July and from late August to the middle of October. The species is known from Ohio, Kentucky and Arkansas in the U.S.A. and Ontario in Canada.

This species is numerically closest to *ulmella* (13). Although the cluster analysis gives a relatively low percentage similarity (35%) between *quadrinotata* and *ulmella*, the principal co-ordinates analyses demonstrate a strong affinity. *E. lindquisti* (11) and *canadensis* (28) are also shown to be close relatives and more information about these species will almost certainly demonstrate this to be the case.

Ectoedemia (Ectoedemia) andrella Wilkinson (28, 29)

Ectoedemia andrella Wilkinson, 1981, *Tijdschr. Ent.*, 124:102

This species is similar in external appearance to *ulmella* but differs in its' more dowdy appearance and weaker lustre. In the male genitalia the pseuduncus is broader and larger, the gnathos is more strongly W-shaped and the valves more evenly tapering than in *ulmella.*

The palps and antennae are buff and the tuft is white deepening to brown or dark brown on the vertex. A shining white medial fascia is present on a dark brown forewing background. Hindwings, fringe and hair scales greyish brown to buff.

The male genitalia have a rounded pseuduncus prolonged posteriorly. The saccus is small and bilobed with the long, narrow, triangular valves arising low on the capsule. The aedoeagus is flask-shaped and with two arcuate spines. The specimen believed to represent the female of this species has a long bursa copulatrix with a pair of equal reticulate signa. The anterior apophyses are unusually long in comparison with the posteriores.

The biology, and consequently the early stages and host plant are unknown.

In the first analyses carried out the males and female of *andrella* were computed separately (28, 29). Since the association between them was 'recognised' by adjacent plots they were later amalgamated (28 only). At first sight the analyses show *grandisella* (25) to have the greatest numerical affinity with *andrella*, but reference to the contouring plots in which the third dimension is incorporated (e.g. fig. 6) shows that species *ulmella* (13), *quadrinotata* (15) and *lindquisti* (11) are joined to *andrella* by the minimum spanning tree and probably represent the true relationships, together with *canadensis* (24) and *rubifoliella* (12) which appear at the next level of similarity (fig. 7). In the cluster analysis for females, *ulmella* and *nyssaefoliella* (14) are nearest neighbours.

NUMERICAL GROUP V

Two species have been placed in this group: *marmaropa* and *nyssaefoliella*. Their genitalia are similar, having a tapering pseuduncus, weakly W-shaped gnathos, small valves with simple styles and weakly concave anterior margin to the tegumen. The aedoeagus in *marmaropa* has strong cornuti which are absent in *nyssaefoliella*. The female of the former also has a colliculum which is missing from the latter. Larvae of both species make blotch mines.

Ectoedemia (Ectoedemia) marmaropa (Braun) (5)

Nepticula marmaropa Braun, 1925, *Trans. Amer. Ent. Soc.*, 51:225

The forewing of *marmaropa* is dark brown with bronze and gold reflections, becoming irrorate distally; there is a basal patch dusted with grey and a convex, shining silver, postmedial fascia.

The lustrous basal patch separates this species from any other in the genus with a single fascia, known at present from North America. In external features and forewing markings *marmaropa* bears a close superfical resemblance to *Trifurcula saccharella* (Braun), but generic characters, including wing venation differences, separate the two.

The male genitalia resemble those of *lindquisti* in overall form, but differ in the nature of the more rounded lobe of the pseuduncus, the short, broad, quadrate valves and the more complex anellar processes on the aedoeagus in *marmaropa*. The female genitalia can be distinguished from those of other *Ectoedemia* species with a similar colliculum by the small associated spiculate lobe and the long posterior apophyses, which reach well beyond the anteriores, although they are not as long as those of the bark-mining species.

The larva of *marmaropa* mines an upper surface ophistigmatonome on leaves of Woods' Rose, *Rosa woodsii* Lindley. The egg is laid on the lower surface of the leaf next to the midrib. The mine begins as a very narrow linear tract, but abruptly enlarges into a blotch which may consume half the area of the leaf; frass is scattered throughout the blotch. The larva emerges from the upper surface of the leaf and the cocoon formed is at first bluish green, later turning a dark reddish brown.

The specimens that Braun described in 1925 were collected at altitudes of 5,500 and 6,000 feet in Utah. She later reared a single specimen from Phelps Lake in Wyoming. The mines containing fully-grown larvae were collected in Ohio in July and the adults emerged in April the following year. The specimen from Wyoming emerged in May.

All analyses demonstrate *nyssaefoliella* (14) to be the nearest neighbour to *marmaropa*, with *rubifoliella* (12) and *ulmella* (13) as second and third in the nearest neighbour listing. The principal co-ordinates representation (fig. 3) suggests a closer affinity with *nyssaefoliella* than does the cluster analysis (fig. 8), but there is no doubt that on the basis of the characters analysed a relationship exists which was not recognised during the orthodox taxonomic study. The cluster analysis of male characters demonstrates a close similarity with *similella* (8, 9), and perhaps accounts for why *marmaropa* plus *nyssaefoliella* have been attached to the *platanella* group (6-10), (figs. 3, 7). So it is not yet clear to which species group *marmaropa* naturally belongs, but probably a new one, together with *nyssaefoliella.*

Ectoedemia (Ectoedemia) nyssaefoliella (Chambers) (14)

Nepticula nyssaefoliella Chambers, 1880, *Psyche*, 3:66

This species resembles several other *Ectoedemia* species in possessing a single, shining silver, medial fascia and an apical band of dark wingscales in the fringe. However, *nyssaefoliella* is generally darker than those species; the wings are dark brown with bronze reflections and the distal scales are darker at the tips; also, the biconcave fascia is generally narrower in *nyssaefoliella.*

The male genitalia of *nyssaefoliella* are easily differentiated from those of any other member of the genus figured here, by the absence of any form of anellar processes or projections on the aedoeagus. The female genitalia, like those of *rubifoliella* and *ulmella*, lack a colliculum, but are characterised by the unequal signa, one of which is constricted proximally in *nyssaefoliella* and the anterior apophyses, which are extremely broad basally and taper markedly distally.

The host plant of *nyssaefoliella* is sour gum, *Nyssa sylvatica* Marshall. There are two female specimens reared from serviceberry, *Amelanchier* sp., with genitalia indistinguishable from those of *nyssaefoliella*, but with small differences in the externals. These differences may result from the different host plants or the females may represent a separate species, but there is at present insufficient evidence to support the latter supposition, although Clemens (1861: 84) described a species *Nepticula amelanchierella* from mines on *Amelanchier.* From Clemens' description the mine of *amelanchierella* would appear to be an upper surface ophionome, sometimes much contorted, with a dark brown frass line.

In the single case observed the egg of *nyssaefoliella* was laid on the lower surface of the leaf, next to the midrib. The mine begins as a narrow linear tract which abruptly broadens into an elongate blotch on the upper surface. The frass is deposited as a continuous black line in the centre of the linear portion and in much contorted track throughout the blotch. The larva emerges on the upper surface of the leaf and spins a pale green cocoon.

There are two or possibly three generations per year; adults have been taken from May through to August. The specimens reared from *Amelanchier* were collected in Virginia; *nyssaefoliella* is known from Ohio, Kentucky, New Jersey and also Virginia.

In the analyses provided, *nyssaefoliella* has the greatest numerical affinity with *marmaropa* (5), but the percentage is not high (42%). This is also borne out in the dendrogram. In females *ulmella* (13) is closest, but the association is distant. The numerical analyses propose a new group for this species, together with *marmaropa.*

SUBGENUS *ZIMMERMANNIA*

This subgenus includes the species which may be bark miners or gall makers. They are *obrutella* and *heinrichi* associated with oaks, *castaneae* and *phleophaga* which are found on *Castanea* and the following whose host plants are as yet unknown or uncertain: *acanthella*, *piperella*, *chlorantis*, *mesoloba*, *grandisella*, *coruscella*, *reneella*, *helenella*, plus two other specimens representing new species.

The subgenus is characterised by the genitalia, especially in males by the broad rounded pseuduncus, weak transverse bar of the transtillae and usually long ventral arms. The aedoeagus is typically adorned with long spines, palmate plates, denticles and cathrema. The female is typified by a thickening of the ductus bursae, but lacks the sclerotised figure-of-eight colliculum of other groups. The number of spiral twists in the spermathecal duct is often consistent and diagnostic within a range. Usually the apophyses are unequal, the posteriores being very long.

In western Europe the subgenus includes *atrifrontella* (Stainton, 1851) and *longicaudella* (Klimesch, 1953), both have oaks as the host, as do two of the above American species. Other species in the group are *liebwerdella* (Zimmermann, 1940) on *Fagus*; *amani* (Svensson, 1966) on *Ulmus* and *ligburicella* (Klimesch, 1953) host plant uncertain, but possibly evergreen oaks.

Ectoedemia (Zimmermannia) obrutella (Zeller) (16)

Trifurcula obrutella Zeller, 1873, *Verh.k.-k. zool.-bot. Ges. Wien*, 23:316

In *obrutella* the forewing is variously irrorate with creamy white and brown scales, sometimes with the impression of a medial, pale fascia. The forewing markings resemble those of *heinrichi*, *castaneae* and *phleophaga*. However, the tufts on the head and vertex and the collar are dark chocolate brown in *obrutella*, while the tufts are white or buff in *phleophaga* and the collar white in *heinrichi* and *castaneae*.

The male genitalia are similar to those of the bark-mining *Ectoedemia* species figured here, in the rounded pseuduncus and the form of the anellar projections. They are distinguished by the form of the gnathos, which more strongly resembles an inverted V rather than a W, and the shape of the plate of minute papillae and distribution of denticles on the vesica of the aedoeagus are characteristic. The female genitalia of *obrutella* are very similar to those of *heinrichi*, *castaneae*, *phleophaga* and *chlorantis*, but the ductus bursae is relatively longer and the bursa copulatrix relatively short in *obrutella*.

The large size and certain external and genital characters of *obrutella* suggest that it is a bark-mining species. Several adults have been taken on the trunks of *Quercus*.

Specimens have been taken in May, June and early July, suggesting that *obrutella* is univoltine. Apart from Texas, the species is also known from Pennsylvania and Massachusetts.

E. obrutella is, perhaps, the first of the subgenus *Zimmermannia* species. The mining habits are unknown, but even so the numerical analysis demonstrates its' strong affinity with the bark miners. The complete character set and female character set analyses show close affinities with *heinrichi* (9), *castaneae* (20) and *phleophaga* (21). In males, *heinrichi*, *castaneae* and *acanthella* are closest.

Ectoedemia (Zimmermannia) acanthella Wilkinson & Newton (17)

Ectoedemia acanthella Wilkinson & Newton 1981, *Tijdschr. Ent.* 124:75 and 108

External features resemble *obrutella* except that the abdomen of this species is creamy white. The background colour of the forewing is grey-white with scattered brown scales, weakly lustrous and reflecting purple. The hindwing and fringe are also buff, shining pale bluish purple.

The male genitalia are also similar to *obrutella* except that the saccus is narrow and markedly bilobed. The pseuduncus is a single flattened lobe. The valves extend just beyond the pseuduncus, arise high up on the capsule and are narrow, tapering markedly. The lack of knobs on the inner margins separate *acanthella* from *mesoloba* and *phleophaga*. The aedeagus is long with a vesica evenly distributed with small denticles and a plate of minute papillae.

The female, biology and host plant are unknown.

The principal co-ordinates analysis shows this species and the following, *piperella*, to have a high similarity co-efficient. The contour linkages on the minimum spanning tree show *acanthella* and *piperella* to be connected at the earliest level, before other species have appeared (fig. 1). Dendrograms for the complete cluster analysis (fig. 8) and that for the male characters (not illustrated), show *acanthella* to have strong affinity with *obrutella* (16). The larva of this species is presumed, like *grandisella* (25), to attack bark. Although the life histories are not known, structures of the male genital capsule are typical of other known bark mining species. However, the aedoeagus is not so characteristic. The principal co-ordinates analysis enables this classification to be made with greater confidence, especially as *acanthella* is spatially not far from *grandisella* (e.g. fig. 7).

Ectoedemia (Zimmermannia) piperella Wilkinson (18)

Ectoedemia piperella Wilkinson, 1981, *Tijds. Ent.*, 124:104

The tufts on the front of the head and vertex are orange-ochreous and the collar pale brown. The ground colour of the forewing is yellowish, irrorate with purplish brown scales, particularly at the base and along the costal margin, reflecting purple. The externals of *piperella* are similar to those of *chlorantis*, but the tufts are yellowish-brown in *chlorantis* and that species lacks the purplish reflections of the forewing.

The male genitalia are most similar to those of *obrutella* in the form of the inverted V-shaped gnathos and the anellar projections. However, the saccus is more strongly bilobed and the valves stouter in *piperella* than in *obrutella*. The female of *piperella* is not yet known.

The immature stages and host plant are unknown.

The few specimens that have been collected were taken in late May and June and all from the typelocality in Arkansas.

The cluster analysis shows *acanthella* (17) and *obrutella* (16) as the nearest relatives of *piperella*, but this is based on too limited a knowledge of the species to express certainty. *E. chlorantis* (22) could also be close, but only females are known for this species, whilst *piperella* is only known by males. The minimum spanning tree demonstrates that *piperella* is closest to *acanthella* and, together, they unite with *obrutella* which then links with *heinrichi* (19) where more certain affinities begin.

Ectoedemia (Zimmermannia) heinrichi Busck (19)

Ectoedemia heinrichi Busck, 1914*a*, *Proc. Ent. Soc. Wash.*, 16:149

The forewing of *heinrichi* is irrorate with white and brown scales, variable on each wing as well as between specimens; the hindwing is greyish buff. The tufts on the front of the head and on the vertex are dark brown and the collar white. This species is very similar to *castaneae* and the two are almost impossible to diagnose on externals, although *heinrichi* appears to be a slightly larger species. However, *obrutella* can be distinguished from *heinrichi* by a darker, brown collar and paler hindwings and *phleophaga* has pale white or buff tufts.

The male genitalia have a rounded pseuduncus, a W-shaped gnathos with the lateral arms shorter than the inner arms, a weakly bilobed saccus and anellar projections as a part of tooth-like spines and rows of saw-like sclerotisations; they are indistinguishable from those of *castaneae* as are the female genitalia. The bursa copulatrix is long, as in *phleophaga* and *chlorantis*, but in *phleophaga* the signa are more elongate and in *chlorantis* the small lobe on the ductus bursae bears large spicules.

The host plant of *heinrichi* is pin oak, *Quercus palustris* Muench. The larvae mine the bark and the eggs are laid on young branches. The mine is a narrow linear track coiled into an oval spiral, showing very plainly in the bark, with the empty egg at the centre. The mine appears to be commoner on the twigs of young saplings, although Busck (1914*a*: 149) reports finding a few mines on the outer branches of larger trees. In the autumn, October-November, the mature larvae leave the mine and fall to the ground, where they pupate in a flattened, oval, reddish brown cocoon.

The species is univoltine, with moths emerging from May to June. Besides the typelocality in Virginia, *heinrichi* is known also from Ohio and Kentucky.

Not surprisingly, *castaneae* (20) has the greatest affinity with this species (70%), and the differences are largely based on life histories. *E. obrutella* (16) is also very close, as is borne out by the principal co-ordinates analysis and minimum spanning tree (figs. 4 and 7).

Ectoedemia (Zimmermannia) castaneae Busck (20)

Ectoedemia castaneae Busck, 1913, *Proc. Ent. Soc. Wash.*, 15:103

The tuft on the front of the head is chocolate brown and on the vertex brown, whilst the collar is white. The forewing is white, but many scales are tipped with dark brown, making the surface variously irrorate. It is impossible to distinguish *castaneae* from *heinrichi* on external features, although it is perhaps smaller.

The male and female genitalia of *castaneae* are also indistinguishable from those of *heinrichi.*

Although it is impossible to diagnose *castaneae* and *heinrichi* on externals and the morphology of the genitalia, with regard to biology, *heinrichi* mines the bark of *Quercus*, whereas the host plant of *castaneae* is chestnut, *Castanea* sp., and the larvae do not mine, but form small spherical galls around young twigs. In form and size the galls resemble "the egg masses of the forest tent-caterpillar" (loc. cit.).

Busck's original material from Virginia emerged in April and there are a few specimens from Pennsylvania collected in June; *castaneae* appears to be bivoltine or more probably trivoltine. The species is also reported from Kentucky.

All analyses give *heinrichi* (19) as the nearest relative to *castaneae* with over 70% similarity. Too much attention should not be attached to the supposed high similarity of the single specimen 90 (27) in the dendrogram. The principal co-ordinates analyses (fig. 7) well illustrate how a species, (20), can be at the centre of a number of associations where others (19, 21, 23, 31 and 32) can be closely related to it and not so closely to each other. This can only be indicated in a limited way on a dendrogram.

Ectoedemia (Zimmermannia) phleophaga Busck (21)

Ectoedemia phleophaga Busck, 1914, *Ins. Insc. Mens.*, 2:3

The tufts on the front of the head and on the vertex are white or buff and the collar brown. The forewing is brown with some white scales, sometimes forming an antemedial and postmedial spot and occasionally a postmedial fascia. The basal half of the wing sometimes appears dark bluish fuscous. The species is similar to *castaneae*, but *phleophaga* is easily distinguished by its' larger size, darker wings and lighter tufts and abdomen. The white or buff tufts also distinguish it from *obrutella* and *heinrichi*, in which they are dark brown.

Considering the male genitalia, *phleophaga* is the only bark-miner with the inner arms of the W-shaped gnathos equal in length to the lateral arms, although this feature may vary according to preparation. It also has a central boss on the middle of the valves, as does *mesoloba*, but in *phleophaga* the form of the boss is more complex. The female genitalia are typical of the *Ectoedemia* species attacking bark figured here: they lack the strongly sclerotised colliculum and have very long posterior apophyses. It is possible that *phleophaga* can be diagnosed by the anterior apophyses, which are narrower and straighter than in other similar species, especially *obrutella*, *heinrichi* and *castaneae.*

Like the previous species, the host plant of *phleophaga* is chestnut, *Castanea dentata* (Marsh.) Borkh. However, unlike the larvae of *castaneae* which live in galls, the larvae of *phleophaga* mine the bark. The biology of *phleophaga* is well known because of its' association with the spread of the chestnut bark disease, *Endothia parasitica* and it is commonly referred to as the Chestnut Bast Miner. The egg is laid on the bark and the larva tunnels into the lower layers of the bark and the cambium. It hibernates in the mine and starts feeding again in the spring until fully-grown, in April to early June, when the larva tunnels out and drops to the ground. The exit-hole is the only external indication of the mine. The closely woven, reddish brown cocoon is rather seed-like.

The species is univoltine with adults appearing in August and September. Only the type series of specimens from Virginia is known although *phleophaga* is also reported from Pennsylvania.

The minimum spanning trees (figs. 4 and 7) for co-ordinates 1 + 2 and 3 + 4 demonstrate clearly the close relationship between this species and both *heinrichi* (19) and *castaneae* (20). The contouring indicates similarity in the third dimension. The linkage of *phleophaga* with *mesoloba* (23) in the dendrogram draws attention to the common characters of the male genitalia, but also shows the possible distortions which arise by illustrating a multi-dimensional concept on a flat piece of paper.

Ectoedemia (Zimmermannia) chlorantis Meyrick (22)

Ectoedemia chlorantis Meyrick, 1928, *Exotic Microlepidoptera*, 3:462

The forewing of *chlorantis* is yellowish buff, speckled lightly with light grey or fuscous and more heavily speckled in the distal half. The tufts on the front of the head and vertex are yellowish brown and the collar brownish buff. The forewing coloration of *chlorantis* is similar to that of *piperella*, but lacks the purple reflections. It is also similar to that of *mesoloba*, however there is not enough material to know whether there are reliable diagnostic differences, although *chlorantis* is possibly a much larger species.

The male of *chlorantis* is not known. The female genitalia lack the characteristic collicular ring of most leaf- and petiole-mining *Ectoedemia* species, although there is a weak sclerotisation; they strongly resemble those of *Ectoedemia* species attacking bark in the long bursa copulatrix and very long posterior apophyses, reaching well beyond the anteriores.

The immature stages and host plant are unknown, although the external morphology and form of the genitalia suggest that *chlorantis* may be a bark-mining species.

The holotype was taken in September and no other specimens are known.

From the foregoing it will be realised that the associations to be claimed for *chlorantis* are limited. The cluster analysis dendrogram (fig. 8) suggests it has greatest affinity with *coruscella* (26) whilst the principal co-ordinates analysis (fig. 7) proposes *grandisella* (25). On present knowledge, either association is distant.

Ectoedemia (Zimmermannia) mesoloba Davis (23)

Ectoedemia mesoloba Davis, 1978, *Florida Ent.*, 61:209

The tufts on the front of the head and vertex are buff to white. The thorax is white with some pale brown above and the abdomen buff with much pale brown marking above. The forewings are irrorate with buff and pale brown and the hindwings pale buff. Externally *mesoloba* is mainly light-coloured, like *chlorantis*, but *mesoloba* is very much smaller.

The male genitalia have a rounded pseuduncus, as in the bark-mining *Ectoedemia* species figured here, but the W-shaped gnathos with the medial projection markedly shorter than the lateral arms, is more similar in form to those of some leaf-mining species. Only *mesoloba* and *phleophaga* possess a central boss on the valves and it is more complex in *phleophaga*. The anellar projections in the form of tooth-like spines and lateral spinose plates appear to be characteristic. The female of *mesoloba* is not known.

The host plant and immature stages are unknown.

The holotype was taken on November 12th, 1961, and no other specimens are known.

The nearest relative for *mesoloba* is *phleophaga* (21), according to the general cluster analysis (fig. 8) and the one for males only. The principal co-ordinates analyses emphasise the central nature of *castaneae* (20) in its' relationship with the bark miners.

Ectoedemia (Zimmermannia?) grandisella (Chambers) (25)

Nepticula grandisella Chambers, 1880, *J. Cincinn. Soc. Nat. Hist.*, 2:193

The tufts on the front of the head and vertex are ochreous to brown and the general colour is brown and on the wings it is speckled with darker brown. The male genitalia have a simple, smoothly flattened pseuduncus; a weakly invaginated saccus and valves with two concavities along the inner margin; the aedoeagus is adorned with a pair of large dentate spines; the vesica is covered with small denticles and a plate separates the sperm duct and vesica. These genital characters are together diagnostic and, as with the externals, are typical of the bark miners in *Ectoedemia.* For this reason the species has been transferred to this genus.

The female, host plant and immature stages are unknown.

In all the phenetic analyses *grandisella* has served as a species from which all the bark, petiole and leaf miners have 'radiated'. The probable reason for *grandisella* taking this position as the 'basic stock' is because of uncertainty about the male reproductive structures, which are damaged in the single known specimen. Knowledge of them is through reconstruction. The analyses are biased towards *grandisella*'s association with the bark miners, which is probably correct because the extant parts of the genital capsule appear to be similar to *Zimmermannia*, although the aedoeagus is not so characteristic. Thus, when all its' features are known, *grandisella* is less likely to have such an important intermediate position in the subgenera classification.

Ectoedemia (Zimmermannia) coruscella Wilkinson (26)

Ectoedemia coruscella Wilkinson, 1981, *Tijdschr. Ent.*, 124:99

This species exhibits the general external brown colour with heavily speckled wings that is typical of the bark miners of this genus. Subterminally a pair of light buff triangular spots, lacking the darker speckling are to be found. They are to date diagnostic.

The male genitalia are characterised primarily by the shape of the valves and the flask-shaped aedoeagus which are best understood by reference to the figures. It will be seen that the aedoeagus lacks the palmate plates of *obrutella* but is more spinose than *acanthella. E. mesoloba* differs in the gnathos and has relatively smaller valves.

The female, host plant and mine are unknown but it may be a bark miner thus perhaps indicating why the immature stages have eluded collectors.

E. coruscella is not closely related to any other species. In the cluster analysis of males only, specimen 90 (27) was given as closest 'relative'. Also, owing to similarities in males, the species were described consecutively in the classical treatment. The principal co-ordinates analyses with minimum spanning tree, associate the species, probably correctly, with those attacking bark, particularly *castaneae* (20). On the basis of general characters, excluding genitalia, one analysis put this species next to *andrella* (28).

Ectoedemia (Zimmermannia) specimen 90 (27)

Ectoedemia specimen 90 Wilkinson, 1981, *Tijdschr. Ent.*, 124:100

The tufts and vertex are dark brown and the background colour of the forewing is brown. Fasciae are absent, but the wing is speckled with white scales. The ground colour of the hind wing is brownish grey and the legs are buff.

Whilst there is nothing characteristic about the externals, the male genitalia are distinct, especially the aedoeagus which is adorned with very long spines and cornuti. The gnathos and valves are not unlike those of *coruscella*, the gnathos being W-shaped with a central boss about half the length of the outer arms, and the valves are about two-thirds the length of the capsule.

The female, host plant and mine are unknown, but this specimen has the characteristics of a species which attacks bark.

The numerical analyses classify this specimen as *Zimmermannia*, but having no particular overall affinities with any other species except *castaneae* (20), which is the 'root' species for the subgenus, as shown by the minimum spanning tree (figs. 4 and 7). A cluster analysis for males places this specimen very close to *coruscella* (26), which was anticipated from general taxonomic studies.

Ectoedemia (Zimmermannia) reneella Wilkinson (30)

Ectoedemia reneella Wilkinson, 1981, *Tijdschr. Ent.*, 124:104

A wholly light coloured species totally white or buff and rarely with brown scales. Fasciae are absent.

The male genitalia show a pseuduncus smoothly rounded, a deeply bilobed saccus with unornamented valves arising comparatively high up the capsule but not extending beyond the capsule. The aedoeagus is flask-shaped and strongly spinose as is the vesica which also has two pairs of digitate plates. The excessively spiny aedoeagus, together with the lack of processes developed on the inner margins of the valves, is characteristic.

The female, biology and food plant are unknown.

In the dendrogram of general characters (fig. 8), *reneella* appears to be something of an outlier to the bark miners (*Zimmermannia*). However, in a cluster analysis of males only (not shown), *piperella* (18) had the closest affinity to *reneella* and should, therefore, also be checked for diagnosis with this species.

The principal co-ordinates analysis shows *reneella* to have affinities with *heinrichi* (19) and *castaneae* (20), however, by reference to the contour sections of co-ordinates 1 + 2 (figs. 1-4), *reneella* appears on level 2 and remains unattached until the base set, level 1, when *heinrichi* is also present. Certain characteristics account for *reneella*'s position as a 'super' bark miner (fig. 8), e.g. the even more strongly spinose aedoeagus than is typical for *Zimmermannia.*

Ectodemia (Zimmermannia) helenella Wilkinson (31)

Ectoedemia helenella Wilkinson, 1981, *Tijdschr. Ent.*, 124:105

This species is small and in that is similar to *mesoloba* but *helenella* is darker having a brown head, dark brown vertex and dark brown forewing scales scattered on a buff background. The hindwings are also buff but with proximal dark brown scales in the costal region of males. The wings are lustrous and shine silver subbasally and on forewing tips.

The male genitalia are similar to those of the larger species *heinrichi.* The pseuduncus is small and the saccus more or less flat and not bilobed. The aedoeagus has spine cornuti and a pair of spinose palmate plates.

The female, biology and host plant are unknown.

In all the analyses *helenella* is closely related to *heinrichi* (19) and *castaneae* (20). There is close, but rather less affinity with *mesoloba* (23) and *phleophaga* (21). These species should all be checked for positive identification.

Ectoedemia (Zimmermannia?) specimen 180 (32)

Ectoedemia specimen 180 Wilkinson, 1981, *Tijdschr. Ent.*, 124:107

This is a single unique female specimen. It can be easily diagnosed by the golden eye-caps, the intensely dark brown antennae and tufts. The former have lighter annulations. The forewings are brown but the edge and fringe are buff. The hindwings are probably more diagnostic being grey and therefore contrast with the buff fringe and wing edge.

The genitalia resemble those of *obrutella* having a broad complex ductus bursae, long spiculate bursa copulatrix with double reticulate signum. The anterior apophyses are long, arcuate and narrow but less so than the posteriores which are narrower, longer and straighter.

The male is unknown, although it is possible that one specimen (no. 170) also from Alabama might belong here. It has white eye-caps and is 1 mm smaller. Unfortunately the abdomen is missing.

The biology and host plant are unknown. Possibly the species is a bark miner.

For interest, this unnamed species was included in the numerical analyses, but from a single female specimen not so much can be said regarding affinities. The cluster analysis for female characteristics (not illustrated) is perhaps the most meaningful and shows close association with *pleophaga* (21) and *chlorantis* (22).

SUBGENUS *ETAINIA*

In this work two North American species are included for analysis: *ochrefasciella* and *sericopeza.*

The ventral surface of the forewing and dorsal surface of the hindwing in males have a patch of brightly coloured and specialised scales. The male genitalia has the tegumen extended into a tapering or lobed pseuduncus; the uncus is reduced and membranous and the gnathos without large anteriorlydirected lateral processes. The anterior edge of the vinculum is concave; the valves are blunt distally and each has a large dorsal arm projecting transversely to reach the opposite side of the capsule. The aedoeagus has complex paired spines or plates. The female genitalia have a plate-like sclerotisation proximal to the genital aperture and a signum comprising two ovate patches of reticulate cells.

The larvae mine the fruits of *Acer* spp.

Ectoedemia (Etainia) ochrefasciella (Chambers) comb. n. (33)

Nepticula ochrefasciella Chambers, 1873, *Can. Ent.*, 5:128

The moth is darker than that of *sericopeza*, with the ground colour of the forewing purplish black. Males of *ochrefasciella* have ochreous specialised scales on the ventral surface of the forewing and at the base of the hindwing, as compared with blue-black scaling in *sericopeza* males.

The male genitalia are diagnosed by the truncated pseuduncus, the W-shaped gnathos, the shape of the valves and serrate nature of the associated spine-like processes and the form of the transtillae. The female genitalia differ from those of *sericopeza* in the form of the antrum, which is more complex, and in the invaginated anal sclerotisation, which is absent in *ochrefasciella.*

There are no rearing records, mines, nor references about the life of the larva. However, it is strongly suspected that *ochrefasciella* makes a carponome in *Acer* keys, like *sericopeza*; several adult specimens have been taken on sugar maple, *Acer saccharum* Marshall.

All but one specimen, a male taken in November, have been collected in June or July; *ochrefasciella* is, therefore, possibly bivoltine. The species is quite widely distributed in northeastern North America: Quebec and Ontario in Canada; Ohio, Pennsylvania, New York, Illinois, New Hampshire and Maryland in the U.S.A.

This is the first of two species assigned to the subgenus *Etainia* Beirne (1945) included in the numerical analyses. As was to be expected, the two *Etainia* species showed close affinity with each other in all analyses, but lacked close associations with the other subgenera. The dendrograms placed them on the periphery of the cluster analyses.

In the principal co-ordinates analyses they are also seen to be peripheral but with some coordinates no more so than for other species which do fall within *Ectoedemia s. str.* (figs. 4 and 8).

However, the contouring shows the species to appear at different levels, i.e. *Ectoedemia s. str.* (species 1-3) at level 3 (fig. 2), *Etainia sericopeza* (34) at level 2 (fig. 3) and *ochrefasciella* at level 1 (fig. 4). This not only indicates a greater dissimilarity between *Ectoedemia s. str.* and *Etainia*, but also gives greater separation between the *Etainia* species. This species is less similar to *Ectoedemia s. str.* than *sericopeza.*

The contouring and minimum spanning tree have proved valuable methods here. Without them, a close relationship between these two subgenera might have been concluded. Due to distortion in representation, through ignoring other dimensions, it might have seemed appropriate to have only one species group for these five species.

Ectoedemia (Etainia) sericopeza (Zeller) (34)

Lyonetia sericopeza Zeller, 1839, *Isis von Oken*, 32:215

The ground colour of the forewing of *sericopeza* is very dark grey, irrorate with pale grey and with bronze reflections. It is paler than the purplish-black forewing of *Ochrefasciella.* In *sericopeza* there is a single fascia, rather irregular, broad and creamy white; there are also three creamy white patches with silver reflections: one postmedial on the costa, one subterminal on the anal edge and one basal. In the male the ventral surface of the forewing and base of the hindwing each bear a blue-black androconial patch.

The male genitalia also differ from those of *ochrefasciella* in the longer tapering pseuduncus and U-shaped, rather than W-shaped, gnathos. In the female the bifid, V-shaped anal plate with an upturned base, is characteristic.

The host-plant of *sericopeza* is Norway maple, *Acer platanoides* L. The larva mines in the fruit, forming a carponome in the parenchyma.

Moths have been taken in May and June in New York and Connecticut; in July and August in Ontario. This species is widely distributed, occurring in many parts of the Holarctic.

General comments regarding this species affinities have already been made in the description of *ochrefasciella* (33), its' nearest neighbour, and with which it has been associated in every numerical analysis.

SUBGENUS *FOMORIA*

The two U.S.A. species, *hypericella* (Braun) and *pteliaeella* (Chambers) have been included in this subgenus on the basis of venation and genital morphology. They are tested here in the numerical analyses.

The male genitalia of the two species known in the U.S.A. are similar to European representatives, in the form of the uncus, pseuduncus, gnathos and cornuti; the dorsal projections of the valves, however, are peculiar to the North American species. Similarities in venation and male genitalia between Nearctic and Palaearctic species are also sustained in the female genitalia especially the complex sclerotisation of the ductus, and the long, paired signum are characteristic.

The vinculum is always ring-shaped and the tegumen, which is fused to the vinculum dorsally, extends into a long, bluntly pointed pseuduncus; the uncus is bridge-like with a spatulate medial projection, whilst the gnathos has medial arms fused to form a posterior central boss or tapering process, rarely with anterior medial projection. The lateral arms are usually broad and straight. The valves taper markedly and in Nearctic species have large dorsal spines. The transtillae are broadly W-shaped and the transverse bar continuous. The aedoeagus is regular or weakly flask-shaped, usually equal to the length of the capsule whilst the vesica is usually adorned with small denticles and the cathrema with minute papillae. It also has several pairs of heavily sclerotised cornuti.

In the female genitalia there are complex plates, proximal to the genital aperture and a spiral accessory duct and sac. The bursa copulatrix is large and variously pectinate with a signum comprising two weakly sclerotised, linear, reticulate patches.

The larvae are often, but not always, recorded as pupating within the mines in North American representatives.

Ectoedemia (Fomoria) pteliaeella (Chambers) comb. n. (36)

Nepticula pteliaeella Chambers, (1881), Psyche, 3:137

This species differs externally from *hypericella.* The thorax of *pteliaeella* is very dark brown to black and strongly iridescent silver. In the forewing the ground colour of the dorsal surface is dark brown with bronze reflections and the fringe is greyish brown, shining silver at the apex, with an apical band of dark brown wing scales. There is a silver basal patch on the dorsal margin followed by a shining silver antemedial fascia, widening on the margin, and two postmedial marginal streaks, almost touching in the middle, also shining silver.

Both male and female genitalia resemble those of *hypericella* in overall form, particularly the male in the possession of the large dorsal spine of the valves, but they may be separated by the pointed median process of the gnathos, the relatively shorter aedoeagus and the larger and more numerous cornuti at the phallotreme in *pteliaeella* males. The females differ in that the funicular antrum of *pteliaeella* lacks the heavy sclerotisation and the lance-shaped plate found in *hypericella.*

The host plant of *pteliaeella* is the hop-tree, *Ptelea trifoliata* L.

The mine starts as a small blotch, but continues in the upper surface as a much contorted linear mine. The frass is at first green and scattered evenly across the breadth of the mine; later the frass is black and in the distal portion of the mine forms a continuous central line. The larva emerges on the upper surface of the leaf prior to pupation.

The cocoon is yellowish to dark brown.

From mines collected in August, moths emerge at the end of May and June the following year. Their larvae may be collected in July, August and September, thus the species is bivoltine. All the adult specimens available (nineteen from Braun's collection) appear to represent a single generation, being taken in late May and June. Chambers reared moths from mines collected at the type locality in Kentucky and Braun collected and reared material in Ohio.

According to the cluster analysis, the two *Ectoedemia* (*Fomoria*) species (36 and 37) have 55% co-phenetic similarity, but their association with *Ectoedemia s. str.* is at a low 23% level. The subgenus *Fomoria* is not shown in the principal co-ordinates analysis, but the two species (apart from each other) could be expected to have *sericopeza* (34) as their nearest neighbour, although not close. The co-ordinates of the *Fomoria* species would be plotted beyond those illustrated in the current analyses and joined by the minimum spanning tree to *sericopeza.*

Ectoedemia (Fomoria) hypericella (Braun) comb. n.
(37)

Nepticula hypericella Braun, 1925, *Trans. Amer. Ent. Soc.,* 51 : 17

The thorax of *hypericella* is dark brown with a greyish lustre, but not iridescent as in *pteliaeella.* In the forewing the ground colour of the dorsal surface is greyish brown; each scale is darker at the tip and there are predominently grey and bronze reflections; the fringe is greyish, shining metallic grey, with an apical band of dark brown wing scales. The uniform colour of the forewing and the absence of any markings separate *hypericella* from *pteliaeella.*

The quadrate median process of the gnathos, the larger aedoeagus and more complex anellar projections in *hypericella* distinguish the male genitalia from those of *pteliaeella*; the more heavily sclerotised antrum of *hypericella* distinguishes the female genitalia.

The larva makes a very long, slender mine in the upper surface of leaves of St. John's wort, *Hypericum prolificum.* The frass is deposited centrally as a continuous line in the early portion, but is later more generally scattered. The larva emerges on the lower surface of the leaf but often pupation occurs within the mine. The cocoon is bright pale brown in colour.

Mines occur in July and adults emerge in August. The type series was collected at Eastwood, Ohio and no additional specimens are known to have been taken since.

The nearest neighbour to *hypericella* is *pteliaeella* (36). In the cluster analysis, *Fomoria* species show little more dissimilarity than those of *Etainia* and some clusters in *Ectoedemia s. str.*, e.g. the petiole miners of the *populella* species group or leaf miners of the *rubifoliella* group. This underlines how readily identifiable characters have been of primary importance in determining classification by other taxonomic methods.

Trifurcula saccharella (Braun) (35)

Nepticula saccharella Braun, 1912, *Jour. Cincinn. Soc. Nat. Hist.*, 21:97

The ground colour of the forewing is purplish black with reddish bronze reflections and with a poorly defined basal to sub-basal shining silver patch. There is a single shining silver postmedial fascia; the fringe is grey and irrorate with scales of forewing ground colour, which form a band across the terminal cilia. The hindwing of the male *saccharella* bear an oval patch of ochreous androconia, proximally on the dorsal surface.

In the male genitalia the gnathos comprises a pair of lateral arms, which articulate with lateral arms of the vinculum, and meet and fuse to form an inverted V-shaped medial process. The transtilla lacks a horizontal bar, but lateral arms are present. The aedoeagus bears long hooked spine-like processes and striate thickening. In the female the anal papillae are simple, the ductus bursae very short and the bursa copulatrix long, with a pair of long signa comprising rows of characteristic pectinations.

The larva mines leaves of sugar maple, *Acer saccharum* Marshall and occasionally red maple, *Acer rubrum* L. and one specimen has been reared from red oak, *Quercus rubra* L. The mine is an upper surface ophionome, about 13 to 14 cm in length. The larva often crosses the midrib of the leaf, sometimes about half-way through its mining life, but also at quite an early stage. The frass is deposited as a dense, but broken line at first and it is more dispersed later. The cocoon is ochreous, regularly oval, much flattened and smooth, with a projecting rim extending entirely around it.

Mined leaves may be collected in early July and late August and sometimes the larvae of a third generation are found in October. Adults have emerged or been collected in June, July and August. The species is known only from Ohio, Ontario and Quebec.

Trifurcula saccharella was included in the *Ectoedemia* analysis to test if the numerical methods 'recognised' the uniqueness of this species as proposed by classical techniques. In all analyses the completely separate identity of this taxon is demonstrated, in spite of its' superficial resemblance to some *Ectoedemia* species, e.g. *marmaropa* (5). Conversely, it reinforces the view that *Ectoedemia* in its' totality as a genus, including all subgenera, is a discrete entity.

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REFERENCES

DEGEER, C., 1752. Memoires pour servir à l'histoire des insectes, **1**: 440-458 (Grefing, Stockholm).

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

SCOBLE, M. J., 1983. A revised cladistic classification of the Nepticulidae (Lepidoptera), mainly from South Africa. Transvaal Mus. Monogr., **2**: 1-105.

WILKINSON, C., 1970. Adding a point to a principal coordinates analysis. Syst. Zool., **19** (3): 258-263.

——, 1973. Graphical methods for representing computer classifications. J. Ent. (B), **42** (1): 103-112.

——, 1981. A supplement to the genus Ectoedmia Busck (Nepticulidae) in North America, dealing with some difficult species and also some new ones. Tijdschr. Ent., **124** (3): 93-110.

WILKINSON, C. & P. J. NEWTON, 1981. The Microlepidopteran genus Ectoedemia Busck (Nepticulidae) in North America. Tijdschr. Ent., **124** (2): 27-92.

WILKINSON, C. & M. J. SCOBLE, 1979. The Nepticulidae (Lepidoptera) of Canada. Mem. ent. Soc. Can., **107**: 1-129.

Received: September 30, 1987.

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