

# AUSTRALIAN MUSEUM SCIENTIFIC PUBLICATIONS

Evans, J. W., 1975. The external features of the heads of leafhoppers (Homoptera, Cicadelloidea). *Records of the Australian Museum* 29(14): 407–439. [5 May 1975].

doi:10.3853/j.0067-1975.29.1975.188

ISSN 0067-1975

Published by the Australian Museum, Sydney

nature culture **discover**

Australian Museum science is freely accessible online at  
[www.australianmuseum.net.au/publications/](http://www.australianmuseum.net.au/publications/)  
6 College Street, Sydney NSW 2010, Australia



# The External Features of the Heads of Leafhoppers (Homoptera, Cicadelloidea)<sup>1</sup>

*By*

J. W. EVANS

Research Associate, Australian Museum, Sydney

(47 Bundarra Road, Bellevue Hill, Sydney 2023)

Manuscript received 12th March, 1974

Figures 1-65

---

<sup>1</sup> For the purpose of this study, the Membracidae, and related families (Aetalionidae, Nicomiidae, Biturritidae) which have been grouped together by Strümpel (1972) into the superfamily Membracoidea, are here included in the Cicadelloidea.

Rec. Aust. Mus., 29, page 407.

G 72922—1

## CONTENTS

	Page
Summary .. .. .	3
1. Introduction .. .. .	3
2. Head characteristics of the Fulgoroidea, Cercopoidea, and Cicadoidea ..	3
3. Head characteristics of the Cicadelloidea .. .. .	5
4. Discussion of insect heads illustrated .. .. .	7
5. General discussion .. .. .	22
I. Generalized and specialized heads .. .. .	22
II. Evolutionary trends .. .. .	23
III. Head stability .. .. .	23
IV. Some factors possibly associated with head shape .. .. .	23
V. Head shape and structure as a guide to classification .. .. .	23
VI. A comparison of the evolutionary levels of the heads of the Cicadelloidea, Cercopoidea, and Cicadoidea .. .. .	24
6. The external features of the heads of Cicadelloidea .. .. .	25
I. Sutures and clefts .. .. .	25
II. Clypeus and lora .. .. .	25
III. Maxillary plates and genae .. .. .	26
IV. Frons .. .. .	27
V. Ocelli .. .. .	27
VI. Antennae and anterior tentorial pits .. .. .	28
7. Source of material .. .. .	28
8. Acknowledgments .. .. .	28
9. References.. .. .	29

*Appendix.* The systematic position; distribution; primitive and specialized ratings, and periods of possible origin of species illustrated in figures 1-63.

## SUMMARY

The external features of the heads of insects comprised in the superfamily Cicadelloidea are described and they are shown to be extremely unstable in comparison with those of insects in the other superfamilies of the Auchenorrhyncha.

By using a series of weighted characters an attempt is made to assess the evolutionary levels, and periods of geological origin, of the species selected for illustration. Possible homologies of the sclerites, sutures, and clefts, of the heads of leafhoppers are discussed.

### 1.

## INTRODUCTION

The heads of adult insects comprised in a single family or superfamily are usually stabilized at approximately the same level of evolutionary development and, moreover, resemble each other in general appearance. For this reason, insect groups, to which neither of these generalizations apply, are of unusual interest.

Outstanding, and possibly pre-eminent amongst such groups, is the superfamily Cicadelloidea. It is the purpose of this paper to draw attention to this phenomenon in leafhopper heads and to discuss its varied significance.

A claim that cicadelloid heads may differ more from each other in general appearance than do insects comprised in other superfamilies would, by itself, be impossible to substantiate. Thus, for example, the heads of insects in a related superfamily, the Fulgoroidea, are even more diverse in appearance. The differences, however, which separate fulgoroid heads from each other are essentially of a superficial nature unlike those between the heads of many of the Cicadelloidea. Some of the latter differ from others so considerably that heads of insects of presumed Mesozoic origin can be readily distinguished from others of more recent development, and differences may exist between the heads of species belonging to a single genus of a greater magnitude than the ones separating from each other the heads either of all the Cercopoidea or of all the Cicadoidea.

For purposes of comparison with the Cicadelloidea the basic structural characteristics of the heads of insects comprised in each of the three other superfamilies of the Auchenorrhyncha need to be noted.

## 2. HEAD CHARACTERISTICS OF THE FULGOROIDEA, CERCOPOIDEA AND CICADOIDEA

### *Fulgoroidea*

The transclypeal suture is incomplete. The lora are *always* laterally associated with the postclypeus for its entire length. The maxillary plates are *always* narrow and largely concealed. The epistomal suture is *always* retained and facially situated, and subgenal sutures are sometimes present. The tentorium is complete but the anterior arms are weakly developed and their pits are difficult to locate. Except in the Tettigometridae, the paired ocelli are *always* close to the antennal bases and a median ocellus is occasionally retained. The frons is *always* separately defined and ventrally situated. The antennae, which arise from ring-like structures, are situated either in front of the eyes, or adjacent to their anterior margins.

*Cercopoidea*

The transclypeal suture is *always* complete. The lora lie alongside the postclypeus for approximately the same length of the latter in *all* species. The narrow maxillary plates are *always* largely concealed. The epistomal suture is *always* present and is situated on the crown of the head. There is seldom any trace of subgenal sutures. The tentorium is complete and the pits of the anterior arms are adjacent to the antennal bases. The paired ocelli are *always* on the crown. The frons is likewise *always* on the crown and *always* rectangular in shape. The antennae are situated under overhanging marginal ledges which are *always* in approximate alignment with the transverse epistomal suture.

*Cicadoidea*

The transclypeal suture is *always* complete and well defined. The lora, which lie alongside the greater part of the sides of the postclypeus, *always* terminate posteriorly adjacent to the antennae. The maxillary plates are *always* narrow and largely concealed. The epistomal suture is *always* present and there is little, if any, trace of subgenal sutures. The tentorium is complete and the pits of the anterior arms are adjacent to the antennal bases. The paired ocelli are *always* on the crown. The frons, which is *always* triangular in shape and bears a median ocellus, is likewise *always* on the crown. The many-segmented antennae are situated under overhanging ledges which are *always* in approximate alignment with the epistomal suture.

If, from among the characteristics listed above, primitive ones are separated from those of a secondary nature, the situation is as follows:

**Primitive Head Characteristics***Fulgoroidea*

An incomplete transclypeal suture; the lateral association of the lora with the entire length of the postclypeus; narrow, and largely concealed, maxillary plates; a ventral epistomal suture; the occasional retention of subgenal sutures; a complete tentorium; ventrally situated ocelli; the occasional retention of a median ocellus; a completely defined, ventrally situated, frons; anteriorly situated antennae, approximately in alignment with the epistomal suture.

*Cercopoidea*

Narrow maxillary plates, which may be completely concealed; a well-defined epistomal suture; a complete tentorium; a distinct frons; antennae in approximate alignment with the epistomal suture.

*Cicadoidea*

Lora which are laterally associated with the postclypeus for the greater part of its length; largely concealed maxillary plates; an epistomal suture; a separate, though reduced, frons; a complete tentorium; a median ocellus; segmented antennae in approximate alignment with the epistomal suture.

### Secondarily-acquired Head Characteristics

#### *Fulgoroidea*

Highly specialized antennae with unsegmented flagellae.

#### *Cercopoidea*

A complete transclypeal suture; a dorsal epistomal suture; infrequently retained subgenal sutures; dorsal ocelli; a dorsal frons; posteriorly situated antennae.

#### *Cicadoidea*

A complete transclypeal suture; a dorsal, or marginal, epistomal suture; subgenal sutures lacking; dorsal ocelli; a dorsal frons; posteriorly situated antennae.

The aspect of the head characteristics of these three superfamilies, which it is particularly desired to emphasize, is their almost complete stability. The situation which obtains in the Cicadelloidea, and which is described below, is a very different one.

### 3. HEAD CHARACTERISTICS OF THE CICADELLOIDEA

The transclypeal suture *may* be complete or incomplete. The lora *may* terminate posteriorly close to the antennal bases or be widely separated from them. The maxillary plates *may* be entirely concealed, and if exposed, then either wide or narrow; the epistomal suture *may* be retained and either facially, or marginally, situated. Subgenal sutures *may* be present. The short anterior arms of the tentorium lack association with the posterior arms and they *may* be branched or simple. The pits of the anterior arms are adjacent to the antennal bases. The paired ocelli *may* be on the face of the head, or on the crown, marginally situated, or lacking. The frons, which *may* be separately differentiated, or continuous with the postclypeus, *may* be on the face, or on the crown of the head. The antennae, which *may* be short, or long, *may* be anteriorly, or posteriorly situated and supra-antennal ledges *may* be present or absent.

The numbers in the right hand column of the tables which follow, represent the extent to which leafhopper head characteristics are here regarded as primitive (P), or secondary (S). The reason weighting has been given to some primitive, but to no secondary characters, is that it is assumed that some of the former, though possibly none of the latter, may be of greater significance than others.

While it has been a simple matter to select characteristics for inclusion in the first table, and, in fact, it has been unnecessary to use all those available (such as the position of the base of the antennal ledges in relation to the eyes), it has not been so easy to choose characters for the second one. Moreover, in order to avoid obscuring a picture which is otherwise reasonably clear, certain frequently occurring types of head development have needed to be omitted.

Table 1

*Primitive head characteristics of Cicadelloidea*

		P
1	Posterior apices of lora, hence the point of attachment of the mandibular levers to the cranium, close to the ATP's and the antennal bases	4
2	Subgenal sutures well, or moderately, developed	3
3	An entirely ventral frons enclosed by well, or obscurely, defined postfrontal and epistomal sutures	2
4	A transverse, or slightly arched, epistomal suture, which may be obscure, situated on the face of the head, more or less between the antennal ledges	
5	The frons, or frontoclypeus, situated entirely on the face of the head, but the former not separately defined	
6	Ventral ocelli, not closely adjacent to the hind margin of the face	1
7	Transverse, or approximately transverse, antennal ledges	1
	<b>Possible Total</b> .. .. .	14

Table 2

*Secondarily-acquired head characteristics of Cicadelloidea*

		S
1	Posterior apices of lora widely separated from the ATP's and antennal bases	2
2	Subgenal sutures lacking	2
3	An entirely dorsal, well defined, frons	2
4	An entirely dorsal frons, not separated anteriorly from the postclypeus	
5	An entirely dorsal frons, not completely separated from the vertex	2
6	Marginal or dorsal ocelli, or ocelli lacking	2
7	Postfrontal suture entirely lacking	2
8	Strongly arched, steeply oblique, or no, antennal ledges	2
9	Anteclypeus completely separated from the postclypeus by a transverse suture	2
	<b>Possible Total</b> .. .. .	14

#### 4. DISCUSSION OF INSECT HEADS ILLUSTRATED

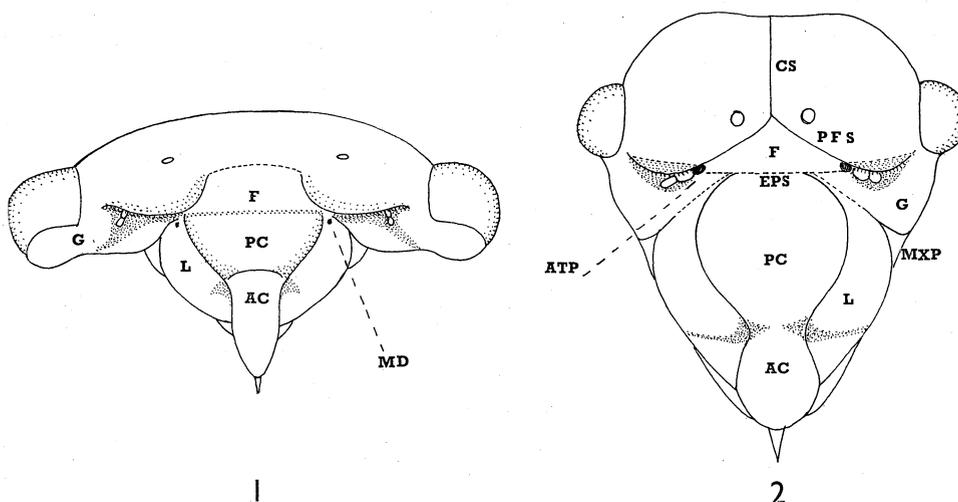
Figs 1 and 2 represent leafhopper heads with more primitive characteristics than those of any others illustrated.

Figure 1. *Coloborrhis reticulata* Evans (P 13: S 2)

The genus *Coloborrhis* Germar contains 17 described species. The type species, *C. corticina* Germar, is of widespread distribution in Africa. It occurs also in Madagascar, to which island the remaining 16 species are confined. These differ very considerably from each other in external features and it has been suggested their speciation may have been of an "explosive" nature, (Evans, 1959). Some indication of the extent of the differences separating *Coloborrhis* spp. may be obtained by comparing fig. 1 with figs 36 and 37. The two latter represent the head of *C. ledroides* Evans in facial and dorsal aspects.

While differing from the heads of other species comprised in the same genus, the head of *C. reticulata* resembles those of some membracids. This may be appreciated by comparing fig. 1 with fig. 4 (*Holdgatiella chepuensis* Evans). It resembles even more closely the head of the nicomiid, *Nicomia cicadoides* Walker, illustrated in Evans, 1948 (fig. 4).

At one time the genus *Coloborrhis* was included in the Membracidae (Funkhouser, 1950). Its present inclusion in the cicadellid subfamily, the Ulopinae, is, however, probably correct and the genus can be regarded as one of a complex of relict Mesozoic genera possessing both cicadelloid and membracoid affinities.



Its membracoid affinities are further emphasized by the fact that several species in the genus (*C. cristata* Ev., *C. cornuta* Ev. and *C. monstrosa* Ev.) have enlarged pronota. In respect to its presumed antiquity, it is of interest to note that in common with *Nicomia cicadoides*, some species (*C. enigma* Ev., *C. rugosa* Ev. and *C. planata* Ev.) have retained a venational characteristic of infrequent occurrence in the tegmina of present day leafhoppers but usual in Palaeozoic and Mesozoic forms. This is the presence of an acute proximal bend in vein CuA.

Although the head of *C. reticulata* retains an unusually large number of primitive features and some other species in the genus have, as well, both primitive tegminal and abdominal characteristics, this cannot necessarily be taken as an indication that these insects are actual Mesozoic relicts as their specific differentiation may well have taken place subsequent to the isolation of Madagascar, which may date from Tertiary times. It is for this reason that no entry has been made in the last column of the appendix in respect to this species.

Figure 2. *Darthula hardwickii* Gray (P 14: S 0)

The monotypic genus *Darthula* Gray is the sole genus in the Darthulinae, one of the two subfamilies of the Aetalionidae. *D. hardwickii* is the largest of all extant leafhoppers, having a length of 30 mm. Part of this length consists of an apical sword-like extension of the 9th abdominal tergum, common to both sexes. Previously I have suggested this process might be homologous with the similar one of the Lower Permian archescytinid, *Permoscytina kansasensis* Carpenter (Evans, 1957). Bekker-Migdisova, however, has shown that the Archescytinidae are ancestral to the Aphidoidea, hence do not lie on the same line of descent as the Auchenorrhyncha (Bekker-Migdisova, 1960).

Although the Aetalionidae are one of the families of the Membracoidea, as defined by Strümpel (1972), their heads differ in proportions from those of most of the Membracidae, being longer than wide, rather than, as is usual in membracids, wider than long. In this they resemble the biturritid, *Tropidaspis carinata* (Fabricius) (fig. 5) which, likewise, is of membracoid stock.

In having a score of fourteen for primitive features and zero for specialized ones, the head of *D. hardwickii* can be regarded, not only as more primitive in external features than those of any other known cicadelloid, but also, possibly, as more primitive than the heads of any other living Auchenorrhyncha.

Figs 3, 4 and 5 illustrate the heads of three membracoids, two of them belonging to the Biturritidae (figs 3 and 5) and one (fig. 4) to the Membracidae.

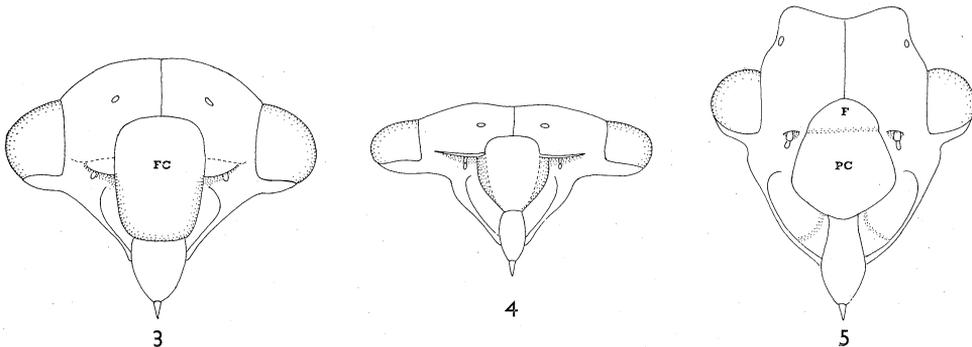


Figure 3. *Melizoderes darwini* Funkhouser (P 9: S 4)

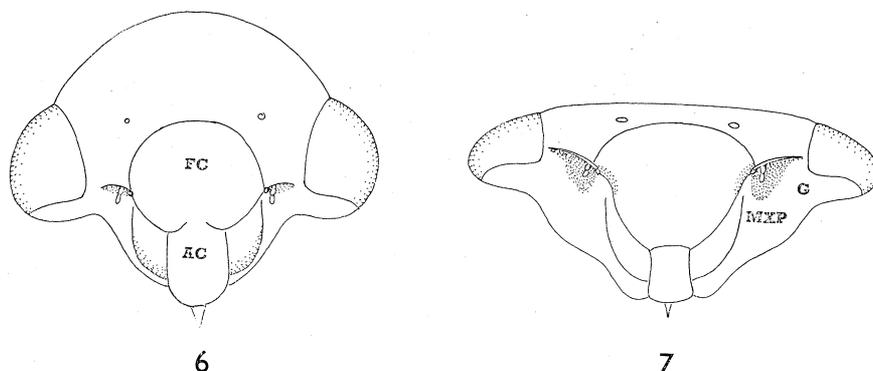
This head has been selected for illustration to re-emphasize the close resemblance that may exist between the heads of representatives of the Cicadelloidea and of the Membracoidea.

Figure 4. *Holdgatiella chepuensis* Evans (P 9: S 4)

While *H. chepuensis* cannot be regarded as a typical membracid, since its pronotum is of normal proportions, undoubtedly it belongs to this family. This head can be regarded as representing the generalized head-type of the family as a whole.

Figure 5. *Tropidaspis carinata* (Fabricius) (P 3: S 9)

Although the head of this biturritid retains a fairly distinct frons and in proportions resembles the heads of aetalionids, rather than those of membracids, it, nevertheless, is highly specialized. In its particular specializations it resembles the head of *Endoiastus productus* Osborn (illustrated in Evans, 1948, fig. 5B), which likewise, has been attributed to the Biturritidae. A consideration of the proportions and characteristics of the heads illustrated in figs 1–5 inclusive suggests the possibility that the family Biturritidae may be a composite one made up of ulopine (figs 1, 3, 4) and aetalionid (figs 2, 5) derivatives.



Heads of insects comprised in the Macropsinae and Jassinae are illustrated in figs 6 and 7. Because of certain shared characteristics, in particular the position of the ocelli, *Macropsis* Lewis and *Jassus* Fabricius were at one time assigned to the same subfamily grouping. Both heads retain numerous generalized characteristics, but in having an incomplete transclypeal suture and narrow maxillary plates, that of *Stenopsoides turneri* may be regarded as the more primitive.

Figure 6. *Stenopsoides turneri* Evans (P 10: S 2)

While no trace of a separate frons is evident in the head illustrated, one can be discerned in that of another species in the same subfamily, *Stenoscopus drummondi* Evans, which, likewise, is confined to southwest Australia. The latter has been figured previously and its general resemblance to the head of a biturritid, *Melizoderes* sp., noted (Evans, 1971). *S. turneri* has an enormously enlarged pronotum which serves to support the supposed affinity of the Macropsinae to the Membracidae.

Figure 7. *Jassulus brunneus* Evans (P 9: S 4)

Unlike the heads of the Macropsinae those of representatives of the Jassinae are very varied in shape, proportions and ocelli position. The head of *J. brunneus* has been chosen for illustration as representing the most generalized head-type known in this subfamily.

Figs 8–13, inclusive, illustrate the heads of leafhoppers belonging to the tribe Ulopini. These display an unusual assemblage of primitive and specialized features. Among the former are the retention of a ventral frons and the possession of more complete subgenal sutures than occur in the heads of cicadellids belonging to any other groups. Specialized characters include the dorsal position of the ocelli and the wide separation of the posterior corners of the lora from the inner apices of the antennal ledges.

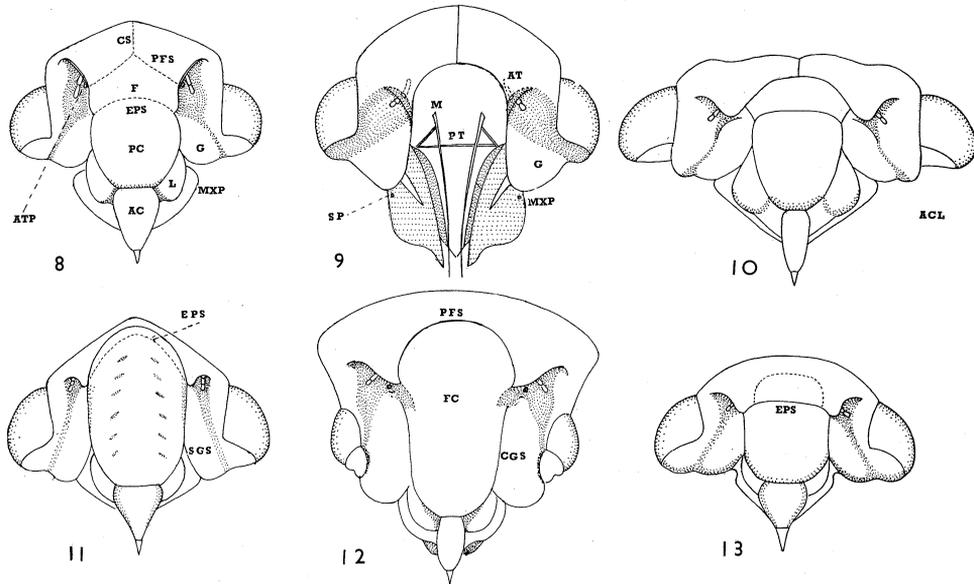


Figure 8. *Woodella wanungarae* Evans (P 7: S 8)

Even although more specialized, than primitive, characters are recorded for this head, it is nevertheless the most generalized one known within the Ulopinae. The nature and extent of its specializations can best be appreciated by comparing fig 8 with figs 1 and 2.

Figure 9. *Austrolopa brunensis* Evans (P 7: S 8)

The head illustrated, from which the frons and clypeus have been removed, resembles that of *W. wanungarae* (Fig. 8) in general features. It differs in the broader association of the maxillary plates with the cranium and in having the postclypeus, anteriorly, forming a lip-like structure which overhangs the anteclypeus. A somewhat similar, though less pronounced, development occurs also in the heads of some eurymelids. In the Ulopini the sensory process on the maxillary plate, which I have suggested may represent a reduced and modified maxillary palp (Evans, 1973) is always at the base of the maxillary plate.

Figure 10. *Moonia variabilis* Distant (P 8: S 5)

The head of *M. variabilis* bears a close resemblance, both in structure and proportions, to that of *Coloborrhis reticulata* (fig. 1). The principal differences are of ocelli position and the separation of the lorai bases from the antennae and the tentorial pits. As has been mentioned previously *Coloborrhis* and *Moonia* Distant are the sole genera of the Ulopini to be known only in the fully-winged form (Evans, 1971b).

Figure 11. *Taslopa montana* Evans (P 6: S 6)

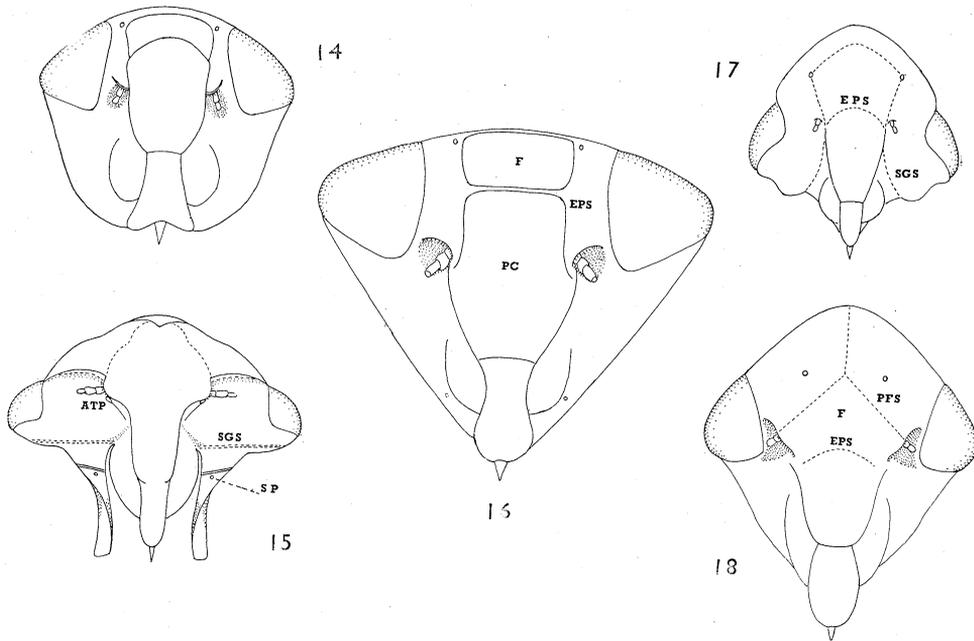
In this head the postclypeus has encroached so far on to the frontal area as to result in the epistomal and postfrontal sutures almost coinciding. There is also an extensive development of the clypeogenal sulcus.

Figure 12. *Megulopa sahlbergorum* Lindberg (P 6: S 6)

This is the most specialized of all known ulopine heads, not solely on account of its shape and proportions, but also because of the very wide separation of the points of attachment of the mandibular levers from the anterior tentorial pits; the lack of a transverse epistomal suture, and the long clypeogenal sulcus.

Figure 13. *Novolopa townsendi* Evans (P 6: S 6)

While in the head of *Taslopa montana* (fig. 11) the postfrontal suture is the most prominent posterior cephalic suture, in this head the epistomal suture is the one most strongly developed.



Figs 14–15 illustrate heads in which a distinct and separate frons is retained.

Figure 14. *Caelidoides tristis* Signoret (P 4: S 6)

This insect is one of several which have been referred to the Coelidiinae but are of uncertain relationships. As well as being unusual in retaining a distinct frons, this head is remarkable for the size of the maxillary plates, which are continuous with the extensive genae.

Figure 15. *Khyphocotis tessellata* Kirkaldy (P 8: S 2)

Although an epistomal suture is lacking, the extent of the frons is clearly evident. An unusual feature is the occurrence of a transverse line of strengthening on the maxillary plates anterior to the subgenal sutures and adjacent to the sensory processes. Such a line, which is present also on the head of *Nicomia cicadoides*, might possibly represent the margin of the stipes.

Figure 16. *Tartessus* sp. (nymph) (P 4: S 7)

In the heads of the nymphs of some species of *Tartessus* Stål the frons is better defined as a distinct sclerite than in the heads of any other known cicadelloids.

Figure 17. *Koebelia californica* Baker (P 8: S 6)

This is one of the few species of relict leafhoppers which has retained a food plant association with a gymnosperm. The extensive genal area is a further development of the condition found in the heads of ulopines (e.g. fig. 9).

Figure 18. *Agalliana pauliana* Evans (P 5: S 8)

This head retains more primitive characteristics than is suggested by its rating, in particular in respect to the shape of the postfrontal suture and the size of the lora in relation to the postclypeus.

Figs 19–21 lack particular association with each other but display individual points of interest.

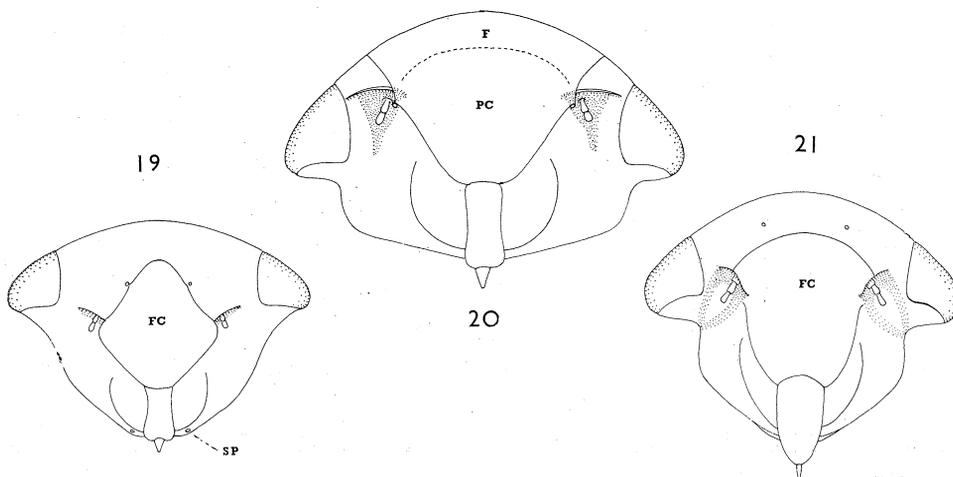


Figure 19. *Opio multistrigia* (Walker) (P 5: S 5)

Apart from a few species, which have an anterior lip-like enlargement of the frontoclypeus, and one, which has horn-like extensions on the head (*Cornutipo tricornis*, fig. 57), the heads of eurymelids are extremely stable. The frontoclypeus is always diamond-shaped; the ocelli are always close to the postfrontal suture; the maxillary plates are always wide and the sensory pits are always anteriorly placed.

Figure 20. *Eryapus gibbus* Evans (P 3: S 10)

The head of *E. gibbus* which is unusually wide and has extensive maxillary plates, differs from those on either side of it in retaining an obscure epistomal suture; in the frons extending onto the crown of the head and in the ocelli being marginally situated. It differs from the head of *O. multistrigia* (fig. 19) also in the presence of an acute ante-ocular emargination. This, presumably, marks the separation of the genae from the maxillary plates, although a similar curve in the heads of some leafhoppers appears to be associated with the retreat of the antennae from a former, more anteriorly situated, position (see figs 29, 50).

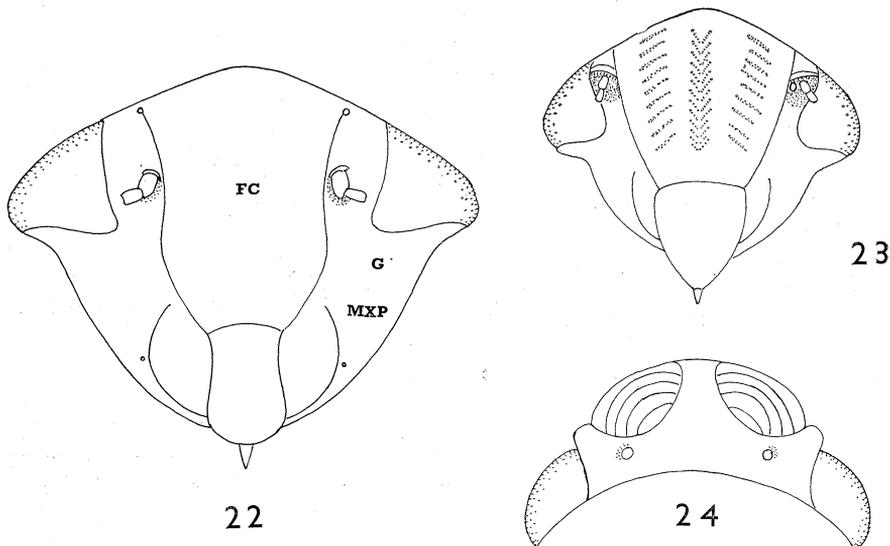
Figure 21. *Tiaja* sp. (P 4: S 8)

Uncertainty exists as to the relationships of the Megophthalmini. Thus, Oman (1949), and Wagner (1951), have associated them with the Agalliinae, while I, for reasons given previously, prefer to regard them as a tribe of the Ulopinae, though acknowledging their affinity with the former subfamily (Evans, 1947, 1968). Their heads are of special interest since the ocelli are either facially situated, as shown in fig. 21, or else lie in marginal depressions, hence are more primitively situated than those of any other ulopids, all of which have dorsal, or no, ocelli.

The heads illustrated in figs 22–24 are representatives of the Deltocephalinae and Cicadellinae. These are the dominant leafhopper subfamilies at the present time.

Figure 22. *Idiodonus cockerelli* (Ball) (P 2: S 12)

The Deltocephalinae, which are of worldwide distribution, are by far the most abundant of all cicadellid subfamilies. With the exception of the Platymetopiini, and some aberrant genera, their heads lack specialized features but have lost many of a primitive nature. The extent of this loss will be appreciated if fig. 22 is compared with fig. 1. Thus, in the head of *I. cockerelli* the lora,



posteriorly, lie at a considerable distance from the antennae; the maxillary plates, which are wide and exposed, are continuous with the genae; supra-antennal ledges are lacking, likewise the epistomal suture and the hind margin of the postfrontal suture, and the ocelli are marginally situated.

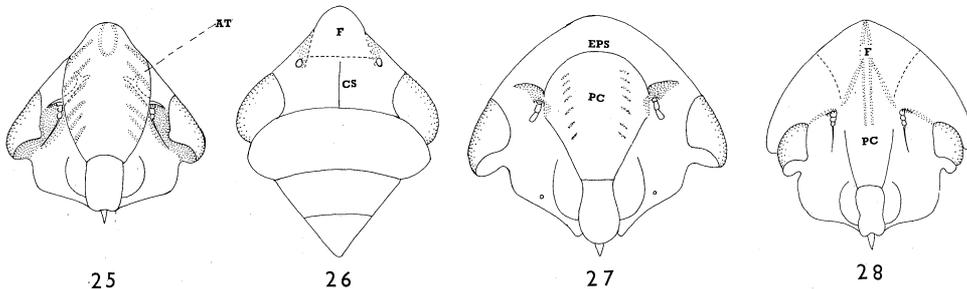
*Figures 23, 24. Cicadella spectra* (Distant) (P 1: S 12)

The Cicadellinae are essentially insects of the tropics and subtropics but also occur sparingly in cool temperate regions. The most notable features of their heads are the encroachment of the cibarial muscles onto the frontal region and their extension onto the crown of the head. Also to be noted is the position of the antennal ledges adjacent to the hind margin of the face, and the dorsal position of the ocelli.

In the group of heads illustrated in figs 25–28 the frons, or frontoclypeus, extends onto the crown of the head and the ocelli are either marginally, or dorsally, situated.

*Figures 25, 26. Chiasmus varicolor* (Kirkaldy) (P 1: S 10)

Formerly this species, which is of widespread distribution in the warmer parts of the world, was known as *Kosmiopelix varicolor* and was regarded as belonging to the tribe Aphrodini of the subfamily Aphrodinae (Evans, 1966). Recently it has been transferred to the genus *Chiasmus* Mulsant and Rey (Evans, 1974) and Ribaut's assignment of this genus to the Deltocephalinae accepted (Ribaut, 1952). The heads illustrated in figs 25 and 23 provide two different examples of the effect of the backward migration of the cibarial muscles on the shape, position and extent, of the postclypeus.



*Figure 27. Hecalus afzelii* (Stål) (P3: S 10)

In this head, in which the epistomal, but not the postfrontal suture, is retained, the frontal region is not separately defined and the ocelli are marginal in position.

*Figure 28. Eupelix cuspidata* (Fabricius) (P 0: S 12)

This highly specialized head, which also has marginal ocelli, differs from that of *H. afzelii* in the loss of the epistomal suture and in having the frons faintly defined. Unusual features are the extension of the vertex around part of the sides of the eyes and very extensive maxillary plates.

Although the heads illustrated in figs 29–31 are of insects belonging to different subfamilies they share in common an unusual feature, the occurrence of the ocelli on marginal rims separating the face from the crown of the head.

Figure 29. *Selenomorphus nigrovenatus* Evans (P 4: S 10)

While lacking a venational characteristic common to all other tribes of the Jassinae (the apical fusion, in the hind wings, of veins Rs and M1+2) the Selenomorphini are almost certainly correctly regarded as belonging to this subfamily (Evans, 1974). The head of *S. nigrovenatus* is more generalized than the two adjacent ones, since the antennal ledges are close to the anterior margins of the eyes and the postfrontal suture lies at a considerable distance from the hind margin of the face.

Figure 30. *Drabescus heroni* Evans (P 3: S 8)

This head closely resembles the adjacent one to the right (fig. 31) and for this reason at one time I regarded the genus *Drabescus* Stål as a component of the Selenocephalini (Evans, 1947) and not, as is now accepted, meriting separate subfamily status. Differences to be noted between the two heads are the position of the ocelli in relation to the eyes, and of the postfrontal sutures, laterally, in relation to the antennal ledges.

Figure 31. *Selenocephalus* sp. (P 3: S 8)

This figure requires no separate discussion.

Sexual dimorphism, apart from differences in the size of the sexes is of infrequent occurrence in the Cicadelloidea. In the heads of the two species illustrated in figs 32–35 the frons is narrowly produced in female, but not in male, insects.

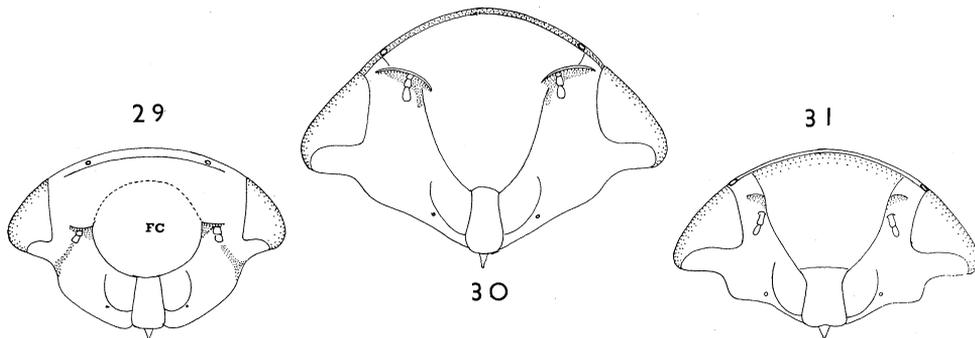


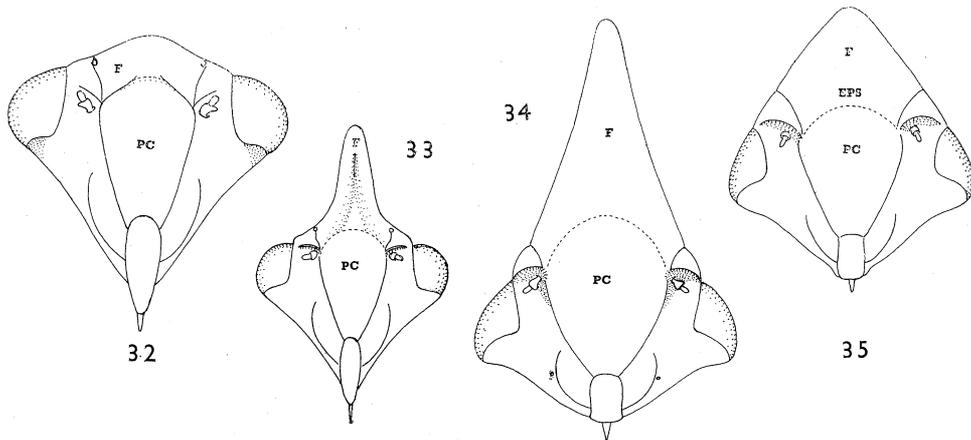
Figure 32, ♂, Figure 33, ♀, *Tartessoides griseus* Evans (P 3: S 8)

It needs to be noted, although the frons is retained as a separate sclerite in these heads, that the P rating is a low one.

Figure 34, ♀, Figure 35, ♂, *Stenotartessus mullensis* (Evans) (P 3: S 8)

Although having the same rating as *T. griseus* this pair of heads is even more specialized, since the antennal ledges lie posterior to the eyes and the frontal region is enormously enlarged.

The heads illustrated in figs 36–45, like those in figs 29–31, provide an example of parallel evolution, for they are of insects belonging to five separate subfamilies.



Figures 36, 37. *Coloborrhis ledroides* Evans (P 4: S 6)

Fig. 36 should be compared with fig. 1, which illustrates the head of an insect ascribed to the same genus. Apart from shape, the principal differences which separate these two heads, are associated with an increase, in the head of *C. ledroides*, of the postclypeus and genae. It will be noted in both heads, that the lora retain the same position in relation to the eyes, while the genae, in fig. 36, are considerably enlarged.

Figures 38, 43. *Platyscopus badius* Evans (P 3: S 10)

The frons is not separately defined and the backward extension of the postclypeus is, in part, associated with head lengthening.

Figure 39. *Mapochiella collaris* Distant (P 0: S 12)

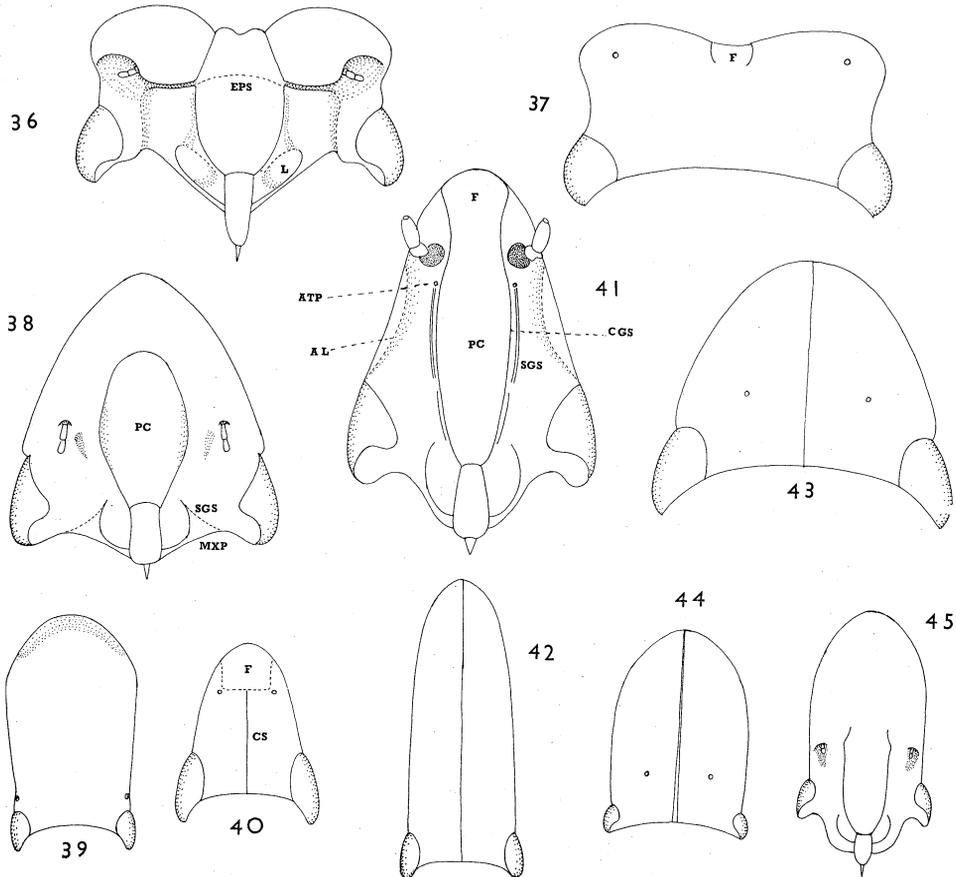
Most Paradorydiini have heads which taper apically (see fig. 49) but a few occurring in India, Africa and Australia, have spatulate heads. The ocelli are more marginally situated than truly on the crown but, as in the adjacent head (fig. 40), they have retained their primitive position close to the sides of the postfrontal suture.

Figures 40, 41. *Occinirvana eborea* Evans (P 0: S 8)

As in the head of *C. ledroides* (fig. 37), the frons in this species is, in part, on the crown but, while in *O. eborea* the ocelli have retained their primitive situation, they have not in the head of *C. ledroides*. Because of the backward extension of the head, as viewed facially, the antennae have become posteriorly situated and, moreover, the antennal ledges have come to margin the sides of the face. It is tentatively suggested that the pair of narrow channels on either side of the postclypeus, which terminate posteriorly at the anterior tentorial pits, may represent the subgenal sutures and, in support of this suggestion, fig. 41 should be compared with fig. 11.

Figure 42. *Dorycephalus hunnorum* Emeljanov (P 2: S 10)

I have not been able to distinguish the ocelli on this head but, if retained, they will be situated in a position similar to those of *M. collaris* (fig. 39) and not, as in the Ledrini, which they so closely resemble, where they are on the disc of the crown.



Figures 44, 45. *Ledropsis crocina* Distant (P 3: S 8)

The crown of this head, as well as being similar in general appearance to those illustrated in figs 38, 40, 42 and 43 bears a particularly close appearance to that of *P. badius* (fig. 43), since in both heads the ocelli are similarly situated. The Ledrini and the Penthimiinae, nevertheless, are not closely related groups and in the former, which have been derived from the Ulopini, dorsal ocelli are an ancient feature, while in the Penthimiinae, most of which do not have spatulate heads, they represent a more recent evolutionary development.

Although many salient primitive characters are lacking in the heads of some ledrids, in others, traces of the epistomal suture, subgenal sutures, and a separate frons, are retained.

The heads illustrated in figs 46–49 provide a further example of parallel evolution occurring in two widely separated groups of leafhoppers. In both series can be traced from forms with short, to others with very long, heads. Climax forms in both the Cephalelini and the Paradorydiini are similar in size, shape and general appearance. It is of interest to note that while short headed Cephalelini occur in Australia they have never been recorded from either South Africa or New Zealand. This suggests the possibility that the original derivation of the Cephalelini from a ulopine stock may have taken place within the Australian component of Gondwanaland.

Figure 46. *Cephalelus bulbosa* Evans (P. 3: S 8)

Although this is one of the climax forms of the Cephalelini, the head still retains an ancient feature in the form of subgenal sutures.

Figure 47. *Cephalelus minutus* (Evans) (P 3: S 8)

This represents the head of a “basic” representative of the Cephalelini.

Figure 48. *Cephalus ianthe* (Kirkaldy) (P 3: S 8)

In this intermediate form, in which the subgenal sutures are obscure, the association of the subocular emargination with the point of junction of the genae and the maxillary plates can be recognized. This enables an interpretation to be made of the similar emargination in the adjacent head of *P. menalaus* (fig. 49), in which, unlike the head of *C. ianthe*, the maxillary plates are extremely wide.

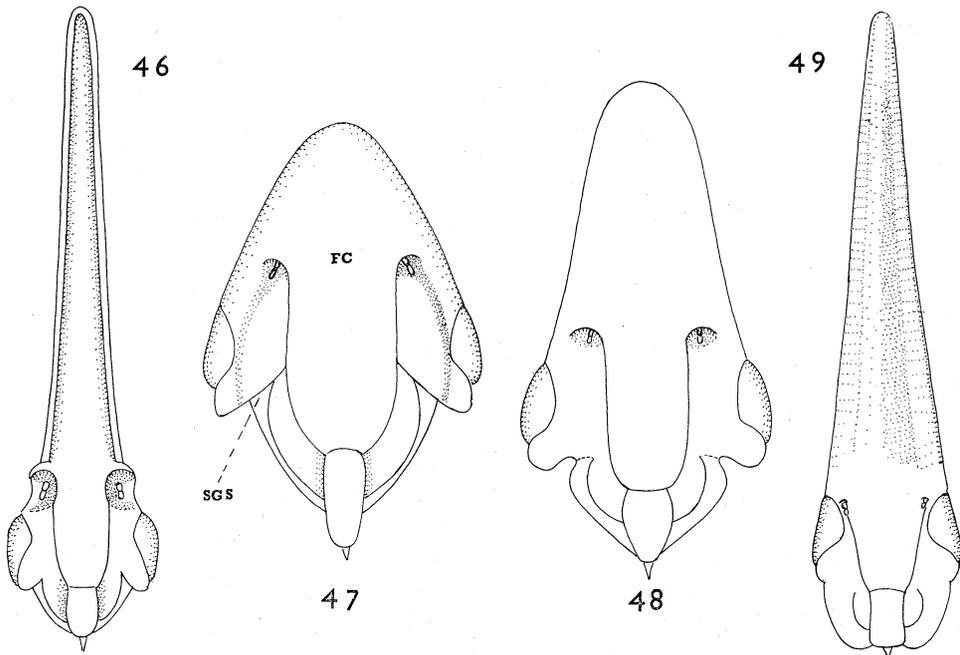


Figure 49. *Paradorydium menalaus* (Kirkaldy) (P 0: S 12)

This is a climax species of the genus *Paradorydium* Kirkaldy. While in the heads of representatives of the Cephalellini the ocelli are situated on the disc of the crown, in the Paradorydiini, they lie on its margin.

The heads illustrated in figs 50–55 all have narrowly produced heads. They belong to widely separated subfamilies and all but one have dorsal ocelli.

Figure 50. *Uloprora risdonensis* Evans (P 6: S 8)

The head of this ulopid, like that of another aberrant species in the same tribe (*M. sahlbergorum*, fig. 12) has unusually extensive genae. In consequence, the lora are widely separated from the anterior margins of the eyes.

Figure 51. *Ahenobarbus assamensis* Distant (P 0: S 12)

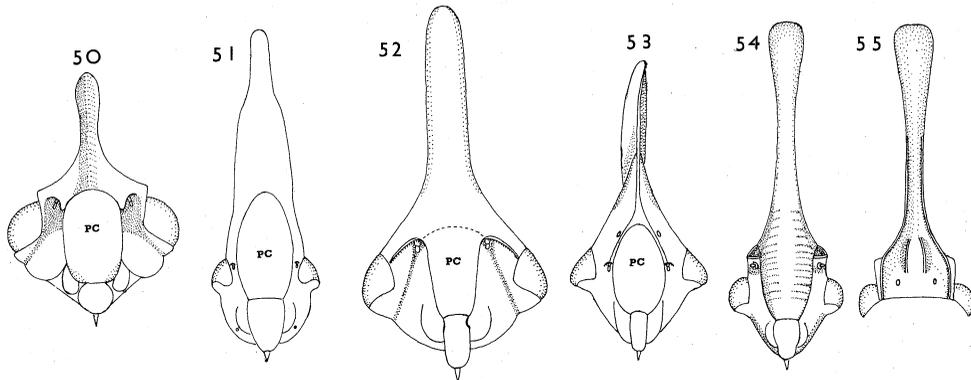
The Hylicidae, although highly specialized, are undoubtedly an ancient group of leafhoppers and most of the comprised genera are only distantly related to each other. In addition to *A. assamensis*, several species have narrowly produced heads (see figs 62, 63) and all have dorsal ocelli, the eyes close to the sides of the postclypeus, and weakly developed antennal ledges.

Figure 52. *Ledraprora compressa* Evans (P 3: S 10)

The Thymbrini, a tribe of the Ledorinae are confined to Australia and New Zealand. Their ocelli may be ventrally, marginally, or dorsally situated. One of their characteristics is the possession of strong transverse antennal ledges which separate the postclypeus widely from the eyes.

Figure 53. *Adelungia calligoni* Oshanin (P 2: S 8)

Like the Thymbrini, the Melicharellinae are of restricted distribution, being confined to the Eremian zone of the Palaearctic region. They, likewise, have species with ventral and dorsal ocelli. *A. calligoni* is the only cicadellid known to me which has ventral ocelli and an extensively produced head.



Figures 54, 55. *Namsangia garialis* Distant (P 1: S 12)

This is the most aberrant species of the several belonging to the Cicadellinae which have extensively produced heads.

Figures 56–60 illustrate some examples of grotesque developments in leafhopper heads.

Figure 56. *Euleimonios flavidiventrus* Stål (P 2: S 12)

The extensive lora in this head, which overlap the anteclypeus laterally, are not continuous with the ventral surface of the sucking pump.

Figure 57. *Cornutipo tricornis* (Evans) (P 10: S 4)

Although, with its horn-like projections, this head appears highly specialized, it retains primitive features. Thus, the posterior apices of the lora are close to the inner margins of the antennal ledges and the maxillary sense organs are less anteriorly placed than is usual in the Eurymelidae.

Figure 58. *Listrophora evansi* Boulard (P 1: S 10)

It is seemingly impossible, in this grotesque head, to recognize the line of separation of the genae from the maxillary plates.

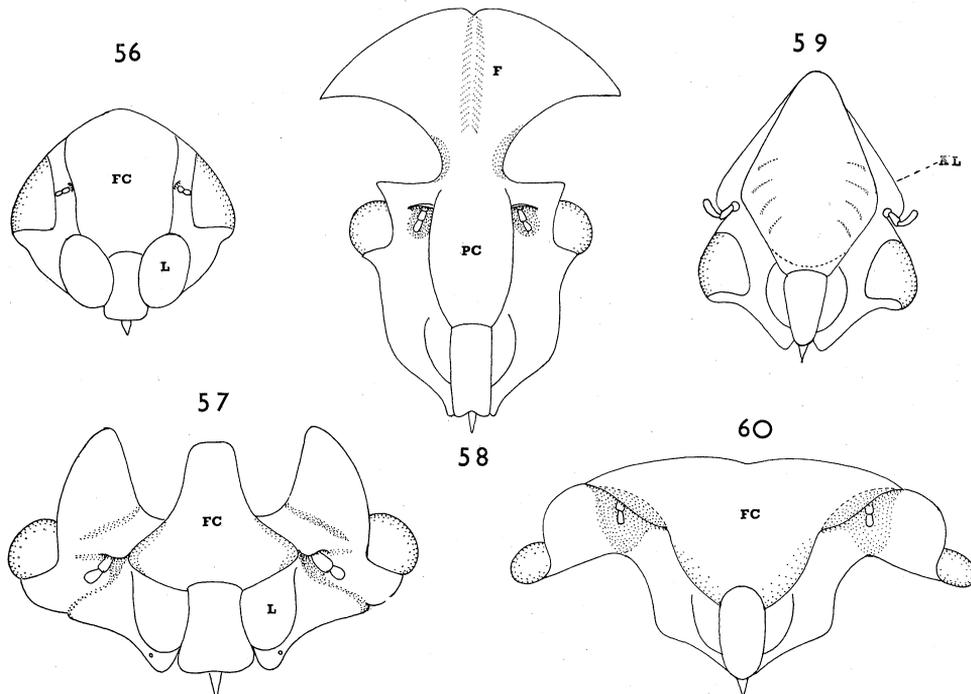


Figure 59. *Stenotortor madangensis* Evans (P 0: S 14)

This head has a higher *S* rating than any of the others illustrated. Unusual features include the extreme flattening of the face; the extension of the posterior apices of the lora to between the anterior margins of the eyes, and the bordering of the head, postero-laterally, by the antennal ledges.

Figure 60. *Evansiola kuscheli* China (P 1: S 10)

The head of *E. kuscheli* extends, laterally, well beyond the sides of the rest of the body and, like those of all the Myerslopiini, lacks ocelli. In the head of a less bizarre form belonging to the same genus, *E. selkirki* Evans, the genae are laterally emarginate anteriorly, as well as below the antennae, so that their line of junction with the maxillary plates can be recognized (Evans, 1968, fig. 3, E).

Figs 61–63 illustrate heads of insects belonging to two different families of the Cicadelloidea, which have heads with long, narrow, frontal extensions.

Figure 61. *Vangama steneosaura* Distant (P 4: S 6)

This is the sole recorded representative of the Evacanthini to have such an extensively produced crown. It is of interest to note how this highly specialized head retains traces of subgenal sutures.

Figure 62. *Wolfella krameri* Boulard (P 0: S 10)

Both this head, and the one illustrated in fig. 63, could equally well have been included in the group of bizarre heads.

Figure 63. *Wolfella caternauti* Spinola (P 1: S 8)

The distinctiveness of the frons is more apparent in this figure than in either of the two adjacent ones.

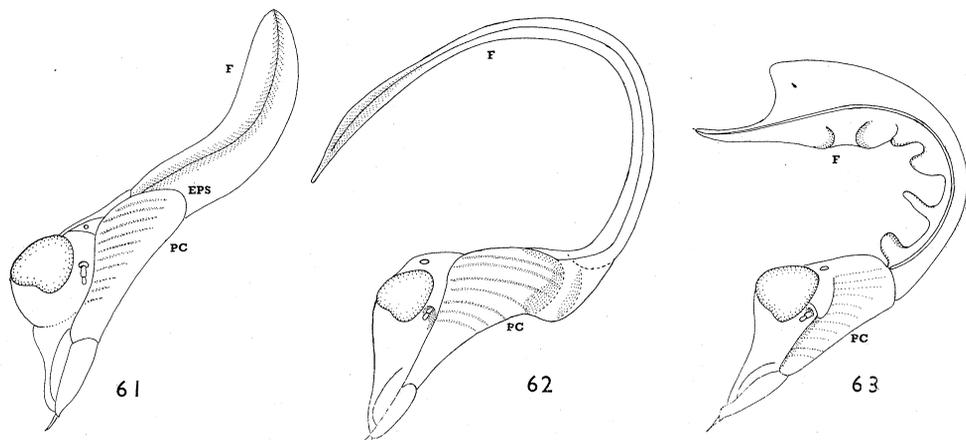
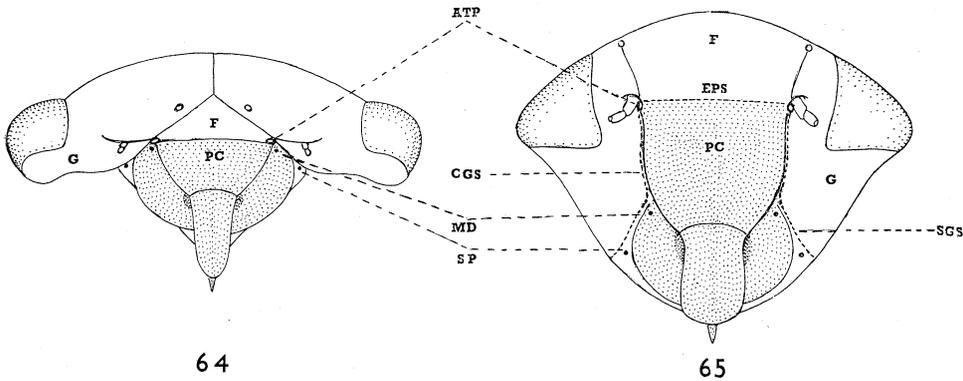


Figure 64. Reconstruction of primitive leafhopper head (based on figs 1 and 2).

Figure 65. Head based on fig. 22 with obsolete sutures added.



## 5.

### GENERAL DISCUSSION

#### I. Generalized and Specialized Heads

In the most generalized of the leafhopper heads illustrated (figs 1, 2), the maxillary plates, including the maxillary sense organs, are largely concealed by the extensive lora and they are separated from the genae by subgenal sutures. The mandibular levers are attached to the cranium close to the junctions of the subgenal and epistomal sutures, and they are also adjacent to the anterior tentorial pits and the antennal bases. The epistomal suture, which is transverse, is situated between the eyes, the transverse antennal ledges, and the anterior margins of the eyes, and it forms the anterior margin of a separately defined frons. The ocelli are on the face of the head adjacent to a three-sided, or a V-shaped, postfrontal suture.

In heads of representatives of the two dominant present-day leafhopper groups (figs 22–24), the lora may be small, or of medium size. The extensive maxillary plates, and the maxillary sense organs, are exposed and the former are continuous with the genae. Subgenal and epistomal sutures are lacking and likewise a separately defined frons. Antennal ledges may also be lacking and, if retained, form the lateral boundaries of the hind margin of the face. The ocelli may be marginally, or dorsally, situated and if a postfrontal suture is retained, then it lies close to the hind margin of the face, or on the crown of the head.

Apart from the loss of landmarks provided by the basic cephalic sutures the principal differences between the generalized cicadellid heads and those referred to in the last paragraph, is the wide separation, in the latter, of the lora, posteriorly, and hence of the points of attachment of the mandibular levers from the antennal bases and the anterior tentorial pits.

## II. *Evolutionary Trends*

The principal trends evident in the heads of leafhoppers are a tendency for the progressive extension of the postclypeus posteriorly accompanied by the backward movement of the antennae and the anterior tentorial pits. Independently of this trend, since it is not related to the pull of the cibarial muscles, is a tendency for the ocelli to migrate posteriorly and to become dorsally, instead of ventrally, situated.

In respect to shape the principal trends are for heads to become progressively, either narrowly, or broadly, produced and when broadly, then subsequently flattened.

## III. *Head Stability*

While the Cicadelloidea differ from other superfamilies comprised in the Auchenorrhyncha in their variable head developments, insects comprised in several of its subdivisions nevertheless have completely stable heads. It is possible also, that some groups with variable heads may be artificial rather than natural, ones.

Examples of groups with stable heads are the Membracidae, Eurymelidae, Macropsinae, Idiocerinae and Cicadellinae. Groups with variable heads include the Ulopini, Ledrini, Stenocotini, Jassinae and Pentthimiinae.

## IV. *Some Factors possibly associated with Head Shape*

Many of the unusual shapes of leafhopper heads are clearly of an adaptive nature. Thus, flattened heads enable an insect to press closely against, and to blend with, a leaf or branch (figs 36-45, 59), and long, narrow, heads may also aid concealment (figs 46, 49).

There are, however, many leafhoppers which have unusual heads seemingly lacking adaptive features.

Some of these occur on islands and their peculiarities may be associated with population isolation and a consequent period of genetic instability (figs 36, 60). Others, however, live in continental areas (figs 56, 58, 61, 63).

## V. *Head shape and Structure as a guide to Classification*

Several years ago I suggested the Cicadellidae could be separated into two series, the Ulopides and the Macropsides, the genera comprised in the former having, supposedly, been derived from a ulopine, and in the latter, from a macropsine stem (Evans, 1947).

No useful purpose would be served by repeating arguments used to support this suggestion, but a comparison of fig. 6 with fig. 8 will demonstrate the nature of the differences which separate the heads of insects comprised in these two primitive groups.

Since the Membracidae, Aetalionidae, Biturritidae and Nicomiidae comprise genera more closely related to each other than they are to genera of any of the other cicadelloid families, much is to be said in favour of Strümpel's segregation of these families into a single unit of classification (Strümpel, 1972). It

is, nevertheless, unfortunate that category limitations have made necessary the assignment of these groups to a superfamily, since this, misleadingly, suggests the Membracoidea have a degree of distinctiveness corresponding with those of the other superfamilies of the Auchenorrhyncha.

While the Membracoidea can be regarded as a sister group of possibly all the other cicadelloid families collectively, it is the common ancestor of the Membracoidea and the Cicadelloidea which corresponds in distinctiveness with the Cercopoidea and the Cicadoidea.

#### VI. *A Comparison of the Evolutionary Levels of the Heads of the Cicadelloidea, Cercopoidea and Cicadoidea*

The heads of cicadas and cercopoids are always primitive anteriorly and specialized posteriorly. Thus, insects in both groups have heads in which the anterior tentorial pits, the position of the attachment of the mandibular levers, and the antennal bases, are all adjacent to each other, while the frons and ocelli have lost their original ventral situation and are on the crown. It is of interest to note, accordingly, that among the Cicadelloidea there are not only species with primitive anterior head features and specialized posterior ones (figs 8, 38), but also others in which this situation is reversed (fig. 14).

Previously I have suggested the heads of cicadelloids might owe their potential for variability to their lack of a complete tentorium (Evans, 1938). Nevertheless, in spite of their many and varied heads developments, which may, or may not, be associated with tentorial reduction, among them are still to be found insects whose heads retain, collectively, a greater assemblage of primitive head features than are to be found in the heads of any cicadas or cercopoids. Thus, apart from lacking a median ocellus, such as is present in cicada heads, and in having a reduced tentorium, the heads illustrated in figs 1 and 2, as well as retaining all the primitive features of cicada and cercopoid heads, have the following additional ones: anteriorly situated antennae; a transverse epistomal suture, in front of, or between, the eyes; subgenal sutures; a ventral frons, and ventral ocelli.

### 6. THE EXTERNAL FEATURES OF THE HEADS OF THE CICADELLOIDEA

#### I. *Sutures and clefts*

*Epistomal suture.* In leafhoppers with primitive heads this suture is transverse and lies entirely in front of the eyes and the lora, posteriorly, terminate close to its lateral apices (figs 1, 2).

From such heads have developed ones in which, while the suture remains transverse, and in front of the eyes, the lora no longer terminate close to its apices, but are more anteriorly situated (figs 5, 18).

In further developments the distance separating the lora from the apices of the epistomal suture increases although the suture itself remains between the eyes (figs 8, 11, 17, 52). This suture may also become posteriorly arched (figs 14, 16), or obliterated, and in such instances the postclypeus becomes continuous with the frons (figs 6, 7, 19).

*Subgenal suture.* The position and extent of this suture is often difficult to determine. Thus, while it can be readily recognized in the heads of many ulopines (figs 8–13), it is absent or obscure in the heads of most leafhoppers. In the head illustrated in fig. 41 there are a pair of lateral channels on each side of the postclypeus which terminate at the tentorial pits. These have been labelled “subgenal sutures”, but this possibly is an error.

*Clypeogenal suture.* The clypeogenal suture is the cleft which extends from near the posterior apices of the lora to the tentorial pits and the antennal bases and it separates the postclypeus laterally from the genae. It varies in length and may be short (figs 15, 18), or long (figs 12, 16), and it is lacking in primitive heads (figs 1, 2). Its homologies are uncertain but as it extends from the genal margin to the lateral apices of the epistomal suture, it may be derived, in part, from the subgenal suture (*see* figs 8, 11, 12, 13, 15).

In order to explain this suggestion further a hypothetical primitive head, based on figs 1 and 2, is illustrated in fig. 64 and beside it (fig. 65), one derived from the head shown in fig. 22. These figures are self explanatory.

A clypeogenal suture is indicated in the head of a Thysanopteran illustrated in Matsuda, 1965 (fig. 17,B). As this terminates posteriorly at the point where the subgenal sutures meet the epistomal suture, it cannot be homologous with the clypeogenal suture of leafhopper heads since the areas bordering it laterally are of pre-, and not postgenal, origin. Nor can the clypeogenal sutures of the heads of Psocoptera be homologous with those of cicadelloids, since in the former the anterior tentorial pits lie at its anterior apices. Consequently the whole of the suture surrounding the postclypeus in psocid heads must represent the epistomal suture.

## II. *Clypeus and lora*

The clypeus is “the area of the cranium upon which arise the dilator muscles of the cibarium and the dorsal muscles of the buccal cavity, or the part of the stomadeum just within the mouth” (Snodgrass, 1935).

In Homoptera it is bounded laterally by the “lora”, or “mandibular plates”, and the identity of these presents the most intriguing problem associated with the Homopteran head.

In a recent paper Parsons has discussed three separate theories of the origin of the loral lobes (Parsons, 1974). These, respectively, are the hypopharyngeal, genal-sub-genal and the clypeal theories.

Two other hypotheses have been advanced. According to one the lora may have developed from paraclypeal lobes identical with those that occur in the heads of larval Megaloptera (Ferris, 1943). The other, which may be called the “stipal hypothesis”, is based on the assumption that the lora and maxillary plates are homologous structures and that their respective stylets are likewise homologous. Accordingly, as the maxillary stylet is presumed to have been derived from the lacinia of a biramous appendage, so must the mandibular stylet have a similar origin. This leads on to the assumption that the earliest insects had three pairs of biramous mouthparts and that in the Mandibulata the first pair have become reduced and modified (Heslop-Harrison, 1956).

In her *Conclusions* Parsons selected the hypopharyngeal theory as furnishing the most generally acceptable explanation of the origin of the lora, and she suggested that the clypeal theory was the most improbable one.

The generalized mandibulate head figured in her paper, for purposes of comparison with the heads of Hemiptera, is that of an Orthopteran and in her two diagrams illustrating Orthopteran heads, the clypeus, posteriorly, is shown as laterally continuous with a narrow subgenal area. In the heads of the supposedly primitive cicadelloids illustrated in figs 1 and 2, not only is there no evident association between the clypeus and the genae, but subgenae are lacking. They are also lacking in the heads of larval Mecoptera, which, surely, retain more primitive features than the heads of any Orthoptera? (See Matsuda, 1965, fig. 21B.)

Apart from the lack of genae, the heads of larval Mecoptera resemble those of the primitive leafhoppers referred to above in having the clypeus situated entirely in front of the eyes, and the antennae in alignment, or approximately so, with the transverse epistomal suture, which meets the subgenal sutures laterally, adjacent to the position of the anterior tentorial pits.

For the above reasons, and also because in cicadelloids the lora lie entirely in front of the genae, it seems improbable that they could be either of genal, or subgenal, origin.

One of Parsons' major criticisms of the clypeal theory of loral origin is concerned with innervation and another with the fact that this theory not only is the most complex of the three hypotheses, but that it requires two separate independent processes.

Her third major criticism is that it makes necessary the assumption that the originally united clypeus and lora became increasingly separated during the evolutionary development of the heads of Homoptera, while exactly the opposite phylogenetic trend is evident in the heads of Heteroptera. Moreover, this trend in the Heteroptera is consistent with both the genal-subgenal and with the hypopharyngeal theories of loral development.

The genal-subgenal theory has already been referred to. In respect to the hypopharyngeal hypothesis, surely, since the lora, as stated by Parsons, seemingly lack close association with the greater part of the postclypeus in the heads of the more specialized Cicadelloidea (see figs 12, 41, 65), although they embrace it laterally for the whole of its length in generalized ones (figs 1, 2), this fact, contrary to Parsons' interpretation, would seem to support the clypeal, rather than hypopharyngeal interpretation of loral development. For, otherwise, the reverse situation would presumably obtain, that is to say in primitive forms the lora would lack close association with the greater part of the postclypeus even although they might acquire it in subsequently evolved ones.

### III. Maxillary plates and genae

In a recent paper in which the possible morphological significance of the maxillary plates of the Auchenorrhyncha was discussed, the claim of Parsons (1964) that this plate is not part of the maxilla, but rather a non-appendicular parietal lobe, was rejected, and it was suggested that a sense organ present on the maxillary plates might have been derived from the maxillary palp (Evans, 1973).<sup>1</sup>

<sup>1</sup> Since this paper was written I have become aware that the same suggestion had previously been made by Heslop-Harrison (1956).

If the structure referred to is of palpal origin, then its reduction may have been associated with the growth of the lora, which in the heads of the more primitive leafhoppers overlap the greater part of the maxillary plates.

In some such heads the sense organ is situated at the base plates, close to where they meet the genae (figs 9, 15). Accordingly, in heads in which the genae and maxillary plates are continuous, the position of the organ might make possible the determination of the extent of the two components of the maxillary plates. Such a possibility, however, is not supported by an examination of a series of heads, for, while an increased genal and a reduced maxillary component might be an expected development (figs 16, 29-31) the extreme anterior position of the sense organ in the heads of most eurymelids (figs 19, 31) seemingly disproves the suggestion.

#### IV. *Frons*

Ferris has stated that the frons is nothing more than the facial portion of the antennal segment and not a separate morphological element (Ferris, 1943); also, that the postfrontal suture, because of its origin, must, at its greatest extent, pass between the compound eyes and the antennal foramina.

If Ferris is correct in his definition of the frons and in his description of the postfrontal suture, and there is no reason to suppose otherwise, then the frons and the postfrontal suture in their most primitive known condition in cicadelloid heads must be as illustrated in figs 2 and 8, and doubtless the supra-antennal ledges must be derived from the apical parts of the suture. It must, accordingly, be assumed that the condition in which the frons occurs as a separate and distinct sclerite is a secondary, even although an ancient, development, both in the Cicadelloidea (figs 10, 14, 17, 61, 63) and in the Fulgoroidea.

#### V. *Ocelli*

In leafhoppers with primitive heads there is little, or no, development of a crown, hence the ocelli are necessarily ventral, or situated on a vertical plane, and they are widely separated from the hind margin of the face (figs 1-6, 17-19). In some species with more specialized heads, although ocelli remain ventral in position they may be close to the hind margin of the face (figs 14, 16, 22, 32, 33); in marginal depressions (certain Megophthalmi and Stenocotini), or lie on a marginal rim separating the face from the crown (figs 29-31).

The transfer of the ocelli from the face to the crown of the head has been achieved in several ways. In the Penthimiinae, for example, a series can be traced from insects with convex heads and ventral ocelli to others with flattened spatulate head and dorsal ocelli (Evans, 1937, Text—fig. 1). However, in the heads of the Ledrini, which superficially resemble some penthimiids, no corresponding series can be followed, nor can it either in the Ulopini, from which it is supposed the Ledrinae were derived.

Bearing in mind the presumed selective advantage of dorsal ocelli it is surprising to find that, while ocellar rudiments in the nymphs of certain Thymbrini (*Rhotidoidea* spp.) are on the crown, in adult insects of the same species the ocelli are ventrally situated (Evans, 1969). In a few cicadellids, particularly in the Ulopiinae and Typhlocybinae, ocelli are lacking.

## VI. *Antennae and anterior tentorial pits*

While the antennae of most cicadellids have short flagellae, in a few groups, such as in the Coelidiinae and Platymetopiini, they are very long.

Their position on the head is variable. Thus, while on the heads of the more primitive forms they may be approximately in alignment with the anterior margins of the eyes (figs 1-7), they may also lie between their hind margins (figs 8-10), or even be more posteriorly situated (fig. 12). In highly specialized species the antennae are usually situated posterior to the eyes (figs 36, 38, 41, 45, 46) but they may also be placed near their centres (figs 53, 61-63).

The antennal muscles are attached to the dorsal arms of the tentorium (Matsuda, 1965, p. 22). This suggests the possibility, in cicadelloids that they have either migrated from the dorsal to the anterior arms, or else, in instances where the tentorium is unbranched, that true anterior arms are lacking.

## 7.

### SOURCE OF MATERIAL

All the insects illustrated in this paper are contained in the author's leafhopper collection. This has been assembled, with the co-operation of entomological colleagues, over a long period of years and, apart from the one in the British Museum may contain more species of a particularly interesting nature than are to be found in any other collection. When no longer needed for purposes of personal research it will be transferred to the Australian Museum.

It is regrettable, with the growth of nationalism in many parts of the world, that regional collections of insects are tending to be strengthened at the expense of those concerned with the fauna of the world as a whole, since, for studies of a varied nature, of which the present one is an example, collections representative of the world fauna are an absolute necessity.

## 8.

### ACKNOWLEDGMENTS

My interest in the structure of the heads of Homoptera is of long standing and my first paper on this subject was published nearly 40 years ago. Interests can grow stale, and the research incorporated in the present paper would never have been undertaken had it not been for the stimulus derived from long continued correspondence with Dr Margaret Parsons, to whom appreciative thanks are expressed. I am grateful also to my wife for help in the preparation of the illustrations.

## REFERENCES

- Bekker-Migdisova, E. E., 1960. Die Archescytinidae als vermutliche Vorfahren der Blattläuse. *Proc. XI Internat. Congr. Entomol.* 1: 298-301.
- Evans, J. W., 1937. Australian Leafhoppers, Part 6, Pentimiidae. *Mem. Qd. Mus.* 11: 149-156
- 1938. The morphology of the heads of Homoptera. *Pap. and Proc. Roy. Soc. Tasm.* 1937: 1-20.
- 1947. A natural classification of Leafhoppers, pt 3. *Trans. R. ent. Soc. Lond.* 98: 105-221.
- 1948. Some observations on the classification of the Membracidae and on the ancestry, phylogeny and distribution of the Jassoidea. *Trans. R. ent. Soc. Lond.* 99: 447-515.
- 1959. Quelques nouveaux Cicadellidae de Madagascar. Observations sur la signification évolutive de la spécialisation dans le genre *Coloborrhis* Germar. *Mem. Inst. Sci. Madagascar* E, II: 481-507.
- 1964. The periods of origin and diversification of the superfamilies of the Homoptera Auchenorrhyncha. *Proc. Linn. Soc. Lond.* 175: 171-181.
- 1966. The Leafhoppers and Froghoppers of Australia and New Zealand. *Aust. Mus. Mem.* XII: 1-347.
- 1968. Some relict New Guinea leafhoppers and their significance in relation to the comparative morphology of the head and prothorax of the Homoptera Auchenorrhyncha. *Pacif. Ins.* 10: 215-229.
- 1971, a. Leafhoppers from New Guinea and Australia belonging to the subfamilies Macropsinae and Agalliinae with notes on the position of *Nionia* Ball and *Magnentius* Pruthi. *Pacif. Ins.* 14: 169-200.
- 1971, b. Some New African Ulopini. *J. nat. Hist.* 5: 441-445.
- 1973. The maxillary plate of the Homoptera-Auchenorrhyncha. *J. ent.* (A) 48: 43-47.
- 1974. New Caledonian leafhoppers and the systematic position of *Kosmiopelix* Kirkaldy and *Euacanthella* Evans. *Pacif. Ins.*, 16: 165-175.
- Ferris, G. F., 1943. The basic materials of the insect cranium. *Microentomology* 8 (1): 8-24.
- Funkhouser, W. D., 1950-52. *Genera Insectorum*, Fasc. 208.
- Heslop-Harrison, G., 1956. The age and origin of the Hemiptera with special reference to the sub-order Homoptera. *Proc. Univ. Durham Phil. Soc.* 12: 150-169.
- Matsuda, R., 1965. Morphology and evolution of the insect head. *Mem. Amer. Ent. Inst.* 4: 1-334.
- Oman, P. W., 1949. The Nearctic Leafhoppers. *Mem. ent. Soc. Wash.* 3: 1-253.
- Parsons, M. C., 1964. The origin and development of the insect cranium. *Canad. J. Zool.* 42: 409-432.
- 1974. The morphology and possible origin of the Hemipteran loreal lobes. *Canad. J. Zool.* 52: 189-202.
- Ribaut, H., 1952. Homoptères Auchenorrhynques II (Jassidae), *Faune de France.* 57: 1-474.
- Snodgrass, R. E., 1935. *Principles of Insect Morphology.* McGraw-Hill Book Company, New York.
- Stümpel, H., 1972. Beitrag zur phylogenie der Membracidae Rafinesque. *Zool. Jb. Syst.* 99: 313-407.
- Wagner, W., 1951. Beitrag zur phylogenie und systematik der Cicadellidae nord- und mitteleuropas, *Comment. Biol.* 12 (2): 1-44.

## APPENDIX

*The Systematic Position; Distribution; Primitive and Specialized Ratings and Periods of Possible Origin of Species Illustrated in Figures 1-63*

Although remains, consisting principally of wings, of many Permian and Triassic cicadelloids have been described, few have been recorded from Jurassic and Cretaceous strata (Evans, 1964). For this reason the possible periods of geological origin, listed in the right-hand column, are not based on fossil evidence but on a balance of structural and distributional factors.

Fig.	Name	Systematic position	Distribution	Rating		Periods of possible origin
				P	S	
1	<i>Coloborrhis reticulata</i> Evans	Cicadellidae Ulopinae Ulopinae	Madagascar	13	2	(See p. 080).
2	<i>Darthula hardwickii</i> Gray	Aetalionidae Darthulinae	S.E. Himalayas	14	0	Jurassic.
3	<i>Melizoderes darwini</i> Funkhouser.	Biturritidae	Neotropical region.	9	4	Cretaceous.
4	<i>Holdgatiella chepuensis</i> Evans.	Membracidae	Chile	9	4	Cretaceous.
5	<i>Tropidaspis carinata</i> Fabricius.	Biturritidae	Neotropical region.	3	9	Cretaceous.
6	<i>Stenopsoides turneri</i> Evans.	Cicadellidae Macropsinae	S.W. Australia	10	2	Cretaceous.
7	<i>Jassulus brunneus</i> Evans.	Cicadellidae Jassinae Jassini	Tropical Africa	9	4	Cretaceous.
8	<i>Woodella wanungarae</i> Evans.	Cicadellidae Ulopinae Ulopini	E. Australia (montane fauna).	7	8	Jurassic.
9	<i>Austrolopa brunensis</i> Evans.	Cicadellidae Ulopinae Ulopini	S.E. Australia (montane fauna).	7	8	Jurassic.
10	<i>Moonia variabilis</i> Distant.	Cicadellidae Ulopinae Ulopini	India	8	5	Jurassic.
11	<i>Taslopa montana</i> Evans.	Cicadellidae Ulopinae	S.E. Australia (montane fauna).	6	6	Jurassic.
12	<i>Megulopa sahlbergorum</i> Lindberg.	Cicadellidae Ulopinae Ulopini	Israel	6	6	Cretaceous.
13	<i>Novolopa townsendi</i> Evans.	Cicadellidae Ulopinae	New Zealand	6	6	Jurassic.

## APPENDIX—continued

Fig.	Name	Systematic position	Distribution	Rating		Periods of possible origin
				P	S	
14	<i>Caclidoides tristis</i> Signoret.	Cicadellidae Coelidiinae (?)	Madagascar	4	6	Cretaceous.
15	<i>Khyphocotis tessellata</i> Kirkaldy.	Cicadellidae Ledrinae Stenocotini	Australia	8	2	Cretaceous.
16	<i>Tartessus</i> sp. (nymph)	Cicadellidae Tartessinae	Australia	4	7	Cretaceous.
17	<i>Koebelia californica</i> Baker.	Cicadellidae Ledrinae Koebeliini	California	8	6	Jurassic.
18	<i>Agalliana pauliana</i> Evans.	Cicadellidae Agalliinae	Madagascar	5	8	Cretaceous.
19	<i>Opio multistrigia</i> (Walker).	Eurymelidae Ipoini	Australia	5	5	Cretaceous.
20	<i>Eryapus gibbus</i> Evans	Cicadellidae Acostemminae (?)	Madagascar	3	10	Tertiary.
21	<i>Tiaja</i> sp.	Cicadellidae Ulopinae (?) Megophthalmiini	W.N. America	4	8	Jurassic.
22	<i>Idiodonus cockerelli</i> Ball.	Cicadellidae Dectocephalinae	N. America	2	12	Tertiary.
23 24	<i>Cicadella spectra</i> (Distant).	Cicadellidae Cicadellinae	Tropics and sub- tropics generally.	1	12	Tertiary.
25 26	<i>Chiasmus varicolor</i> (Kirkaldy).	Cicadellidae Dectocephalinae	Widely distributed in warmer parts of world.	1	10	Tertiary.
27	<i>Glossocratus afzelii</i> (Stål).	Cicadellidae Hecalinae Hecalini	South Africa	3	10	Tertiary.
28	<i>Eupelix cuspidata</i> (Fabricius).	Cicadellidae Hecalinae Eupelicini	Warmer regions of Palaeartic.	0	12	Tertiary.
29	<i>Selenomorphus nigrovenatus</i> Evans.	Cicadellidae Jassinae Selenomorphini	New Caledonia	4	10	Tertiary.
30	<i>Drabescus heroni</i> Evans.	Cicadellidae Drabescinae	N.E. Australia and New Guinea.	3	8	Tertiary.

## APPENDIX—continued

Fig.	Name	Systematic position	Distribution	Rating		Periods of possible origin
				P	S	
31	<i>Selenocephalus</i> sp.	Cicadellidae	Central Africa	3	8	Tertiary.
32	<i>Tartessoides griseus</i> Evans.	Cicadellidae Tartessinae	Australia (semi arid regions).	3	8	Tertiary.
33	(♂) (♀)	.....	.....	..	..	.....
34	<i>Stenotartessus mullensis</i> (Evans).	Cicadellidae Tartessinae	Australia	3	8	Tertiary.
35	(♀) (♂)	.....	.....	..	..	.....
36 37	<i>Coloborrhis ledroides</i> Evans.	Cicadellidae Ulopiniae Ulopini	Madagascar	4	6	Tertiary.
38	<i>Platyscopus badius</i> Evans.	Cicadellidae Penthimiinae	S.W. Australia	3	10	Tertiary.
39	<i>Mapochia collaris</i> Distant.	Cicadellidae Hecalinae Paradorydiini	South Africa	0	12	Tertiary.
40 41	<i>Occinirvana eborea</i> Evans.	Cicadellidae Nirvaninae Occinirvanini	W. Australia	0	8	Jurassic.
42	<i>Dorycephalus hunnorum</i> Emeljanov.	Cicadellidae Hecalinae Dorycephalini	U.S.S.R.	2	10	Cretaceous.
43	(See 38).					
44 45	<i>Ledropsis crocina</i> Distant.	Cicadellidae Ledrinae Ledrini	Australia	3	8	Jurassic.
46	<i>Cephalelus bulbosa</i> Evans.	Cicadellidae Ulopiniae Cephalelini	W. Australia	3	8	Jurassic.
47	<i>Cephalelus minutus</i> Evans.	Cicadellidae Ulopiniae Cephalelini	Southern Australia.	3	9	Jurassic.
48	<i>Cephalelus ianthe</i> (Kirkaldy).	Cicadellidae Ulopiniae Cephalelini	S.E. Australia	3	8	Jurassic.
49	<i>Paradorydium menalaus</i> Kirkaldy.	Cicadellidae Hecalinae Paradorydiini	S.E. Australia	0	12	?

## APPENDIX—continued

Fig.	Name	Systematic position	Distribution	Rating		Periods of possible origin
				P	S	
50	<i>Uloprora risdonensis</i> Evans.	Cicadellidae Ulopiniae Ulopini	E. Australia	6	8	Jurassic.
51	<i>Ahenobarbus assamensis</i> Distant.	Hylicidae	Assam	0	12	Cretaceous.
52	<i>Ledraprora compressa</i> Evans.	Cicadellidae Ledrinae Thymbrini	W. Australia	3	10	Cretaceous.
53	<i>Adelungia calligoni</i> Oshanin.	Cicadellidae Melicharellinae Adelungiini	Turkey (Eremian sub-region).	2	8	Cretaceous.
54 55	<i>Namsangia garialis</i> Distant.	Cicadellidae Cicadellinae	S.E. Asia	1	12	Tertiary.
56	<i>Euleimonios flavidiventris</i> Stål.	Cicadellidae Dectocephalinae	S.E. Australia	2	12	Tertiary.
57	<i>Cornutipo tricornis</i> (Evans).	Eurymelidae Ipoini	Tropical Australia.	10	4	Cretaceous.
58	<i>Listrophora evansi</i> Boulard.	Cicadellidae Hecalinae Listrophorini	Central Africa	1	10	Tertiary.
59	<i>Stenotortor madangensis</i> Evans.	Cicadellidae Nirvaninae Nirvanini	New Guinea	0	14	Tertiary.
60	<i>Evansiola kuscheli</i> China.	Cicadellidae Ulopiniae	Juan Fernandez Island.	0	12	Tertiary.
61	<i>Vangama steneosaura</i> Distant.	Cicadellidae Aphrodinae Evacanthini	N.W. India	4	6	Tertiary.
62	<i>Wolfella krameri</i> Boulard.	Hylicidae	Central Africa	0	10	Tertiary.
63	<i>Wolfella caternaulti</i> Spinola.	Hylicidae	Central Africa	1	8	Tertiary.

## Abbreviations used in Figures

AC, anteclypeus; AL, supraantennal ledge; AT, anterior arm of tentorium; ATP, anterior tentorial pit; CGS, clypeogenal cleft; CS, coronal suture; EPS, epistomal suture; F, frons; FC, frontoclypeus; G, gena; L, lorum; M, maxillary stylet; MD, attachment of mandibular lever; MXP, maxillary plate; PC, postclypeus; PFS, postfrontal suture; PT, posterior tentorial bar; SGS, subgenal suture; SP, sensory process.