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SOME RELICT NEW GUINEA LEAFHOPPERS AND THEIR SIGNIFICANCE IN RELATION TO THE COMPARATIVE MORPHOLOGY OF THE HEAD AND PROTHORAX OF THE HOMOPTERA-AUCHENORRHYNCHA (Homoptera : Cicadellidae : Ulopinae)

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Abstract: Three species of leafhoppers with relict characteristics, *Monteithia* spp. nov., from the high mountains of New Guinea, are described. Their possibe affinities are discussed and they are referred to a new tribe of the Ulopinae, the Monteithiini. The components of the Ulopinae are reviewed and the genus *Evansiola* China is transferred from the Megophthalmini to the Myerslopiini. A reason for the occurrence of relict insects in New Guinea is suggested and the significance of a subgenal suture in the heads of *Monteithia* spp. is considered in relation to the comparative morphology of the heads of Homoptera-Auchenorrhyncha. The occurrence of pronotal paranota in the Homoptera is reviewed and the phenomenon of alary polymorphism in the Ulopinae is discussed.

Although numerous cicadelloids have been described from New Guinea, the leafhopper fauna of the island is not well known. Sufficient material, however, has been described, or, if undescribed, is contained in collections, to enable an assessment to be made of its principal components and its origins. The principal faunal element is an Oriental one which is dominated by representatives of the Cicadellinae, of which there are several endemic genera. There is also an Australian element of restricted occurrence. This element, apart possibly from some Tartessinae, is of comparatively recent establishment and most of its components differ little, if at all, from related species occurring in northeast Australia. The leafhoppers described below cannot be ascribed either to the present Oriental or Australian faunas, but are relict forms of presumed great antiquity and of remarkable interest.

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1. Part of the specimens studied here were collected during fieldwork supported by the National Science Foundation (GB 3245 to the Bishop Museum).

Genus **Monteithia** Evans, n. gen.

Sexually dimorphic insects (in forms lacking hindwings) with face of head considerably wider than long and punctate and labium terminating between bases of hind coxa. The flattened, pear-shaped ante-clypeus sparsely pilose and lora convex and parallel-sided. Maxillary plates, which are separated from genae by a prominent subgenal ridge, are nearly as wide posteriorly as lora and their external margins posteriorly are at right-angles to genae. Post-clypeus parallel-sided, flattened medially and slightly convex laterally. Antennal ledges prominent and oblique and antennal depressions deep. Coronal suture sometimes discernible, and, although post-clypeus does not extend onto the frontal region, margins of frons are well defined. The combined frons and vertex flat, except laterally, where it slopes steeply towards antennal ledges. Eyes prominent. Crown of head coarsely pitted and foliaceous anterior to eyes, and appears to consist of secondarily developed lateral lobes which have become amalgamated with former anterior margin of crown. Pronotum, which is more or less flat, may have small lateral paranotal lobes and the scutellum is small. Hind tibiae, long and narrow and quadrilateral in section with marginal hairs and with 1, or a few, very small spines. Tegmina may be reduced to a varying extent and may have obscure, or distinct, venation, or lack veins altogether, and in ♀ insects be elytra-like. Forms with reduced tegmina with hind wings lacking.

Type-species: *Monteithia anomala*, n. sp.

Monteithia anomala Evans, new species Fig. 1 A-H.

Length: ♂, 7 mm, ♀ 8 mm; greatest width: ♂ 3.6 mm, ♀ 3.5 mm. General coloration, white, ivory, or pale brown with a variable pattern of bold, black markings.

♀. Face of head pale testaceous, ante-clypeus medially, post-clypeus laterally, antennal channels and vertex posterior to eyes, black. Crown of head yellowish, or whitish-testaceous with a pair of parallel-sided broad, oblique, black bands; area behind eyes black. Pronotum extending laterally as small paranotal lobes, with a pair of large, oval black markings. Tegmen convex, punctate, elytra-like, broadest at 3/4 of its length; lacking veins and a claval suture, with a flattened anterior proximal margin, a fringe of fine marginal hairs and extending nearly as far as apex of ovipositor; color white or yellowish brown with a variable pattern of bold, black markings. Legs with tibiae in part black, in part white.

♂. Face and crown of head resembling those of ♀. Pronotum similar in color to crown of head with, or without, a pair of black markings and with small posterolateral lobes. Tegmen brachypterous, convex, punctate, considerably broader apically than proximally, lacking veins and a claval suture and extending as far as 6th or 7th abdominal segments, white, grayish white or pale brown. Legs similar in color to those of ♀. Genitalia with long, parallel-sided parameres and subgenital plates which are broadest distally and apparently bi-segmented.

Holotype ♀ (BISHOP 7575) and allotype ♂, NE New Guinea, Keglsugl, Mt Wilhelm, 2500-2700 m, in Nothofagus forest 21. XI. 66, G. Monteith.

Paratypes: 1 ♀ same data as holotype, 1♂, Chimbu-Kerowagi div., 2800 m, British Mus. (Nat. Hist.); 1 ♂, 1 ♀, same data as holotype, Australian Mus.; 1 ♂, 1 ♀, same data as holotype, Dept. of Entomology, Univ. of Queensland.

SPECIMENS EXAMINED: 12 ♀♀, 2 ♂♂, Mt Wilhelm, 2600-3000 m, Sedlacek; 12 ♀♀, 3 ♂♂, Upper Chimbu-Kerowagi, 2800 m, Gressitt; 2 ♀♀, 2 ♂♂, Asaro-Chimbu div., 3000 m, Gressitt; 3 ♀♀, 1 ♂, Toromomburo, Mt Wilhelm, 2200 m, Gressitt; 1 ♂, Miramar-Gobayabe, Asaro Valley 2000 m, Gressitt; 2 ♀♀, Lake Sirunki (Iviva), 2800-2900 m, Sedlacek.

Monteithia nigra Evans, new species Fig. 2 A, B.

Length: ♂, 6 mm, ♀, 6.5 mm; greatest width: ♂, ♀, 3 mm.

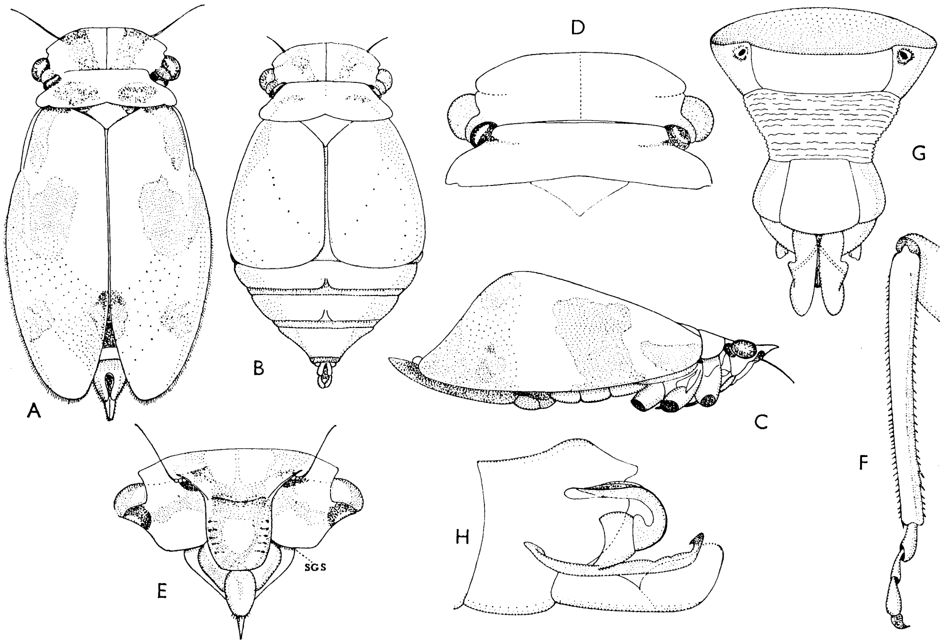


Fig. 1. *Monteithia anomola*: A, ♀; B, ♂; C, ♀ in lateral aspect; D, crown of head and thorax; E, face of head; F, hind tibia and tarsus; G, apical segments of ♂ in ventral aspect; H, ♂ genitalia. SGS, subgenal suture.

♀. General coloration, black. Face of head black, frontal region, yellowish brown. Crown of head black with a small, central yellowish brown stripe. Pronotum broadest posteriorly, black. Tegmen convex, punctate, elytra-like; hind margin beyond apex of clavus curving to a narrow apex and extending as far, or slightly further than, apex of abdomen; proximally black, distally dark hyaline brown with 2 obscure brown veins; curved margin broadly whitish. Legs, black.

♂. Face and crown of head resembling those of female. Pronotum black with irregular brown markings. Tegmen, brachypterous, convex punctate, broadest at 2/3 of its length and extending as far as 6th or 7th abdominal segment; reddish brown. Legs black. Genitalia closely resembling those of type species.

Holotype ♀ (Bishop 7576), NE New Guinea, E end Saruwaged Range, 20 km SSW of Kabwum, 2550 m, 5-12. VIII. 66, G. Samuelson. Allotype ♂ (Bishop), NE New Guinea, Morobe Distr., Lake Trist, 1600 m, 22-26. XI. 66, G. Samuelson.

Paratypes. 1♂ (Evans coll.), Morobe Distr., Lake Trist, 1820 m, Samuelson; 1♀ (Bishop), Mt Piora 6.45° S, 146° E, 2100 m, 13. VI. 1966, Gressitt & Wilkes.

Monteithia nigra differs from the type species in its smaller size, in coloration and in the very different shaped female tegmina.

Monteithia venata Evans, new species Fig. 2 C, D.

Length: ♂, 4.5 mm, ♀, 5.5-5.8 mm; greatest width: ♂, 2.1 mm, ♀, 2.2-2.6 mm.

♀. General coloration brown or pale yellowish brown with bold, black markings on head and thorax. Face of head brown or pale yellowish brown with a pattern of dark brown or black markings. Crown of head brown, or pale yellowish brown, with a pair of wedge-shaped dark brown or black markings which do not extend as far as hind margin of crown. Pronotum considerably wider posteriorly than anteriorly with 3 broad, black, longitudinal stripes. Scutellum with an approximately circular black marking. Tegmen convex, punctate; hind margin beyond clavus curving to a narrow apex, extending short of, as far as, or beyond, apex of abdomen; veins distinct but venation variable; in color having a variable pattern of mottled or pale yellowish brown. Legs black with pale markings.

♂. General coloration pale brown or brown. Face of head similar in color to ♀. Crown of head brown. Pronotum widest posteriorly, brown. Scutellum concolorous with crown of head and pronotum. Tegmen with obscure venation, brachypterous, convex, punctate, broadest at 3/4 of its length and extending as far as 6th abdominal segment; coloration brown. Legs black with pale markings. Genitalia closely resembling those of the type species.

Holotype ♀ (Bishop 7577) and allotype ♂, SE New Guinea (Papua), Owen Stanley Range, Goilala: Loloipa, 1-15.II.1956, W. W. Brandt.

Paratypes: 2♂♂, 1♂, Owen Stanley Range, Goloila: Tapini, 975 m, Brandt; 1 Wissel Lakes, 1530 m, Urapura, Kamo Valley, Gressitt; 1 same data as holotype; 3 Wau, Morobe Distr., 1200-1500, Sedlacek.

Monteithia venata differs from the type species and from *M. nigra* in its smaller size and different color and in having clearly discernible tegminal venation.

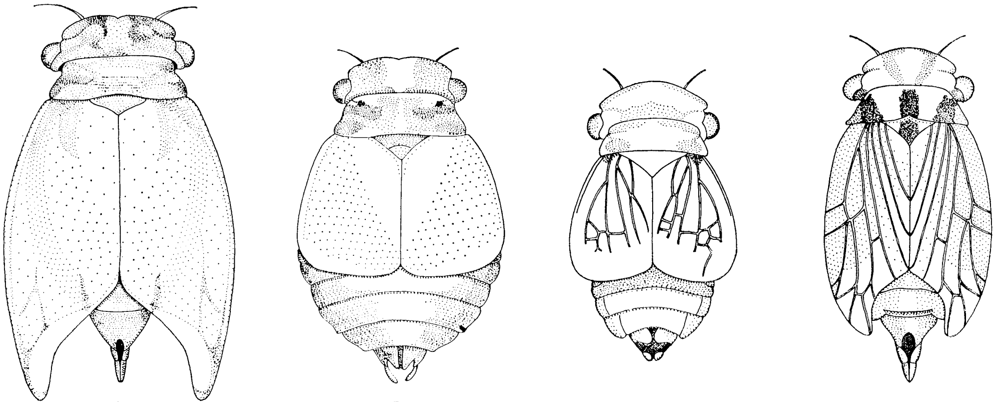


Fig. 2. A, *Monteithia nigra*, ♀; B, *M. nigra*, ♂; C, *Monteithia venata*, ♂; D, *M. venata*, ♀.

The Systematic Position *Monteithia*

Two characteristics of the specimens of *Monteithia* spp. available for study have been omitted both from the generic and specific descriptions. These are the absence of ocelli and of hind wings. This has been done since it is possible that fully winged forms of these species may occur which, almost certainly, would have ocelli situated on the crown of their heads.

At first sight, the 3 species of *Monteithia* seem so aberrant as to require the erection of a new subfamily of the Cicadellidae for their reception. An analysis of their salient morphological features discloses, however, that in spite of the comparatively large size of the type species they share sufficient characteristics with representatives of the Ulopinae to justify their inclusion within this subfamily. Thus, if the anterior part of the face of the head of *M. anomola* (Fig. 1, E) is compared to that of the Australian ulopid, *Woodella wanungarae* Evans (Fig. 3 A), and the hind part of the face with the corresponding area of the head of *Evansiola selkirki* Evans, from Juan Fernandez I., (Fig. 3 E) the following striking resemblances will be noted. Both *M. anomola* and *W. wanungarae* have well-defined subgenal ridges and maxillary plates which are not continuous with the genae laterally. Both *M. anomola* and *E. selkirki* bear similarities in the shape of the head and in having the frontal region extending to the crown instead of being confined to the face of the head as in the Ulopini.

While in the most generalized ulopids, such as in the Indian genus *Moonia* Distant, the crown of the head is narrow and the ocelli almost marginal in position (the majority of known species have a well developed crown and ocelli, when present, are dorsally situated). Some ulopids which have extensive crowns and lack ocelli are illustrated in Fig. 3 C (*Myerslopia magna* Evans, from New Zealand) and Fig. 3 F (*Evansiola kuscheli* China, from Juan Fernandez I.).

An unusual feature of the thorax of *M. anomola* is the presence of small lateral pronotal paranota. Among the Ulopinae, similar paranota occur in *Paulianiana dracula* Evans from Madagascar (Evans 1953: Fig. 1) and in *Myerslopia* spp. (Fig. 3 B, C, D). Another thoracic feature common to *M. anomola* and many Ulopinae is the lack of hind wings and the occurrence of brachypterous forms.

While in some ulopids the hind tibiae have an armature of strong spines those comprised in the Ulopini have hind tibia with small, evenly-spaced spines, similar to those of *M. anomola* (Fig. 1 F).

The male genitalia of *M. anomola* have large seemingly bisegmented sub-genital plates. Such a condition occurs also in an Australian ulopid, *Austrolopa brunensis* Evans, and in an African species, *Coloborrhis corticina* Germar. I have been informed by Dr J. P. Kramer that he has noted a similar condition in certain Agalliinae belonging to the genus *Agalliopsis* Kirkaldy.

Before discussing the position of *Monteithia* within the Ulopinae, a transfer of a genus from one tribe to another needs to be made and the position of the Megophthalmini discussed.

The Tribes of the Ulopinae

In Part 3 of my "Natural Classification of Leafhoppers" (Evans 1947) 3 tribes (Ulopini, Cephalelini and Megophthalmini) were ascribed to the subfamily Ulopinae. Subsequently a fourth tribe (Myerslopiini) was defined and added to this subfamily and a key given to the four component tribes (Evans 1957a). In the same paper 2 new species of *Evansiola* China were described and China's assignment of this genus to the Megophthalmini accepted, although it was noted that the 3 comprised species had certain characteristics in common also with genera in the Myerslopiini, a tribe which formerly contained only 2 named genera, *Myerslopia* Evans from New Zealand and *Paulianiana* Evans from Madagascar.

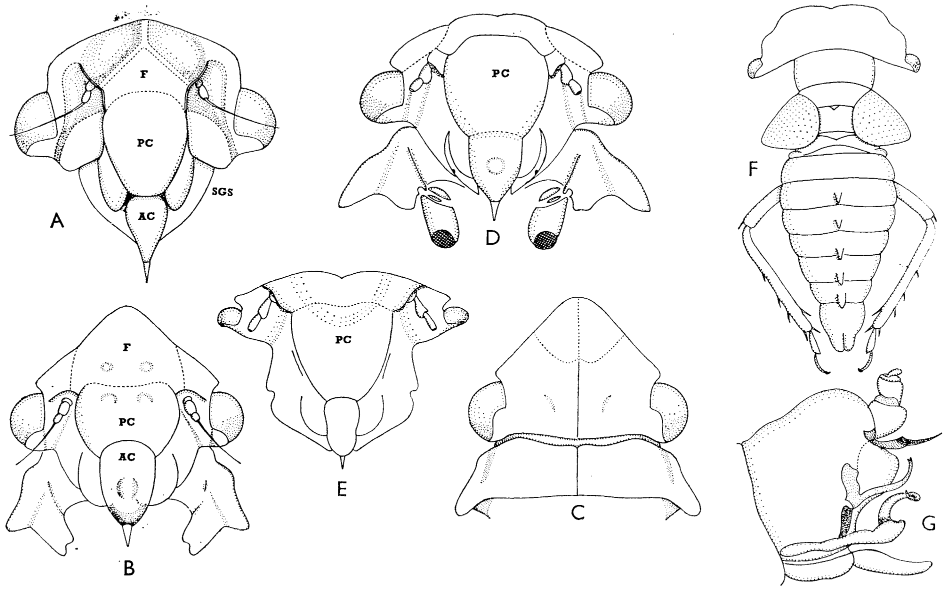


Fig. 3. A, *Woodella wanungarae*, face of head of adult insect; B, *Myerslopia magna*, face of head and prothorax of last instar nymph; C, *M. magna*, crown of head and pronotum of last instar nymph; D, *Myerslopia parva*, face of head and prothorax of last instar nymph; E, *Evansiola selkirki*, face of head of last instar nymph; F, *Evansiola kuscheli*, adult ♂ ; *E. selkirki*, ♂ genitalia

Evansiola spp. which are confined to Juan Fernandez I., resemble *Myerslopia* spp. (Fig. 3 B, C, D) in having the frontal region of the head extending onto the crown, in the development of an extensive crown and in lacking ocelli. Although lateral pronotal paranota are absent from two species of *Evansiola* they are present, though small, in the third species, *E. selkirki* Evans. In addition, both *E. selkirki* (Evans 1957: a, Fig. 1 D) and *E. kuscheli* (China) resemble *Paulianiana dracula* in having the tegmina reduced to short pads and in having median dorsal crests on the abdominal segments. Finally, both *E. kuscheli* and *E. insularis* Evans resemble *P. dracula* and *Myerslopia* spp. in, when found, being encrusted with hardened soil. None of the characteristics mentioned above occurs among the Megophthalmini which have the frons confined to the face of the head, ventral ocelli and little or no development of a crown. Moreover, although some species in this tribe have forms in which hind wings are lacking, their tegmina invariably extend as far as the apices of their abdomens. It is of interest to note that *Evansiola kuscheli* provides an example of metathetely, as defined by Southwood (1961) since it retains a juvenile characteristic in having only 2 tarsal segments in the adult (Fig. 3 F). As the male genitalia of no representatives of the Myerslopiini have previously been figured, those of *Evansiola selkirki* are illustrated in Fig. 3 G.

Opinions have differed on the position of the Megophthalmini. Thus, while I had earlier regarded them as one of the tribes of the Ulopinae (Evans 1947, 1951), Oman (1949) considered them as a distinct subfamily more closely related to the Agalliinae, and Wagner (1951) has illustrated *Megophthalmus* Curtis as lying on a different branch of a hypothetical phylogenetic tree from *Ulopa* Fallen and *Ledra* Fabricius. While studies have been made of the chromosome structure of *Ulopa reticulata* F. (Halkka 1959) none has been made of any *Megophthalmus* sp. Hence cytogenetic evidence which might have been helpful in assessing affinities is unavailable.

It is presumed that the opinions of Oman and Wagner on the systematic position of the Megophthalmini are due to these insects having ventral, rather than dorsally situated, ocelli. However, in the light of the many characteristics which the Megophthalmini and the Ulopini share in common, it is suggested that the position of the ocelli need not be given over-riding significance. Furthermore, although Wagner placed *Megophthalmus* on a different line of descent from *Ulopa* and *Ledra*, these 3 genera nevertheless are shown on his tree as lying nearest to the point of its initial branching and hence as very close to each other. Then, in an Australian species, *Kahavalu gemma* Kirkaldy (Evans 1966, Fig. 15 G, H) although lacking a subgenal suture would, nevertheless, seem to belong to the Ulopini. The ocelli are so anteriorly placed on the crown of the head as to be almost marginal in position and they lie in lateral depressions similar to those of *Megophthalmus* spp.

As a result of a re-examination of European specimens of *Megophthalmus scanicus* Fallen, the eastern North American *Tiaja interrupta* Ball and *Brenda arborea* Oman, and of illustrations of the East African *Odomas myops* Jacobi, and of a reconsideration of their salient structural characteristics, my former opinion that the Megophthalmini are best regarded as a tribe of the Ulopinae remains unchanged. This is not to indicate that I do not recognize that Megophthalmini and the several tribes of the Ulopinae are as a whole closely related to the Agalliinae as this is evident from their many shared characteristics. Thus, for example, if the illustration of the male genitalia of *Evansiola selkirki* (Fig. 3 G) is compared with those of representatives of the Agalliinaes described from the same locality (Evans 1957 a), several striking resemblances will be noted. Then, many Agalliinae like most Ulopini have a deep transverse sulcus on the scutellum and some also have a pitted appearance. However, unlike the tribes comprised in the Ulopinae, the Agalliinae cannot be regarded as a relict Mesozoic group of possible Jurassic origin as they are essentially a more recently evolved one of probable Tertiary radiation.

The only tribes of Ulopinae to which *Monteithia* might possibly be assigned to are the Ulopini or the Myerslopiini. This is because in the retention of a well-developed subgenal ridge *Monteithia* resembles many genera in the Ulopini, while the features it shares with Myerslopiini include an extensive crown, the lack of ocelli and the presence of pronotal paranota. Since, however, *Monteithia* does not resemble 1 tribe more than the other and because the comprised species have several distinctive features of their own, such as the large size of the type species and unusually long hind tibia, it seems preferable to assign it to neither tribe but instead to create a new one, the Monteithiini, for its sole present reception.

The 5 tribes now comprised in the Ulopinae can be distinguished by the following key.

1. Face of head with well-developed subgenal ridge 2
   Face of head lacking a subgenal ridge 4
2. Not sexually dimorphic; pronotum lacking pronotal paranota.. 3
   Sexually dimorphic insects; pronotum sometimes with small pronotal paranota............

.... **Monteithiini**

3. Narrow, elongate, insects, the crown of the head extensive and apically acute......**Cephalelini**
   Crown usually small, and if produced, not acute..**Ulopini**
4. Lacking ocelli, crown of head extensive; pronotal paranota sometimes present... **Myerslopiini**
   Ocelli present on the face of head, crown small; lacking pronotal paranota ... **Megophthalmini**

Monteithia spp. have several features of unusual interest. These include their geographical occurrence, the retention of 2 presumed protohomopterous characteristics, a subgenal suture and, in the type species, pronotal paranota, and their flightless and sexually dimorphic condition. These features are discussed below.

The Geographical Occurrence of *Monteithia* spp.

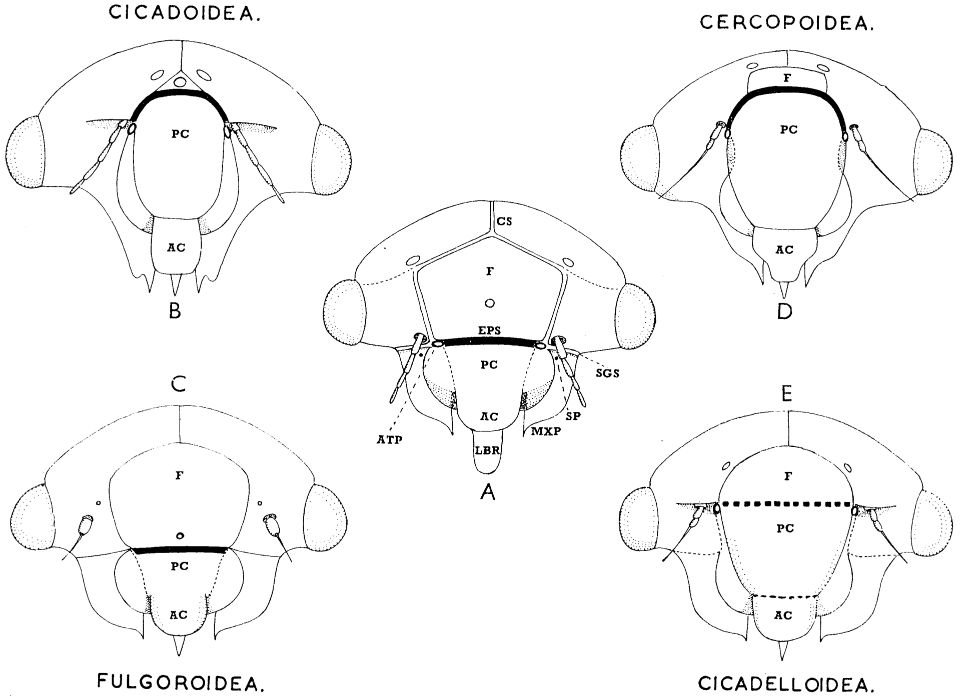
A previous paper suggested that the Ulopinae became differentiated in the Southern Hemisphere not later than Jurassic times (Evans 1965). This hypothesis is based on their primitive structural features and discontinuous distribution. The Ulopini, which are the most widely distributed tribe, although sparsely represented in the Palaearctic fauna, are most abundantly represented in India and in southern land areas. The Cephalelini have been recorded only from South Africa, Australia and New Zealand and the Myerslopiini from Madagascar, New Zealand, Juan Fernandez I. and Chile. The Megophthalmini, on the other hand, have not been recorded from anywhere in the Southern Hemisphere, and I (1965) suggested that their present geographical distribution might be associated with post-Eocene dispersal factors.

The insect fauna of New Guinea, as already mentioned, is predominantly an Indo-Malayan one with an Australian element and the latter is essentially part of the autocthonous and not of the relict Australian fauna. Since *Monteithia* would seem to be a component of neither the Indo-Malayan nor of the Australian elements of the New Guinea fauna but of the "Antarctic" fauna, its occurrence on the island requires explanation. The island of New Guinea owes its origin, in its present form, to Miocene-Pliocene tectonic movements; but, as well as Tertiary mountain ranges, there are also remnants of a much older mountain system. It has been suggested that these mountains provide evidence that some part of the area of the island has been continuously above the sea since Palaeozoic times and hence can have provided a refuge for a relict fauna and flora (Cheesman 1951).

The Facial Sclerites of the Heads of Homoptera

In the illustration of the face of the head of *M. anomola* (Fig. 1 E) the transverse ridge separating the genae from the maxillary plates has been named the "subgenal suture." Although Kramer (1950) has called the corresponding ridge in the head of the fulgoroid *Scolops pungens* Germar by this name in previous papers, I have always, because of uncertainty of its homology, referred to it as the "maxillary suture." Should this well-differentiated ridge be, in fact, homologous with the subgenal suture of mandibulate insects, then some of the recent conclusions of Parsons (1964) on the homologies of the cranial sclerites of the Hemiptera may need revision.

Parsons, who considers the views of Muir & Kershaw (1911 a, b) on the origin of the maxillary plates of Hemiptera to be incorrect, has suggested that these plates have been


CICADOIDEA.

CERCOPOIDEA.

FULGOROIDEA.

CICADELLOIDEA.

Fig. 4. Generalized heads of A, a hypothetical Protohomopteron; B, Cicadoid; C, Fulgoroid; D, Cercopoid; E, Cicadelloid. AC, ante-clypeus; ATP, anterior pit; CS, coronal suture; EPS, epistomal suture; F, frons; LBR, Labrum; MXP, maxillary plate; PC, post-clypeus; SGS, subgenal suture; SP, sensory pit.

derived from "flap-like outpocketings of the genal and postgenal regions." This implies they cannot be directly homologous with the cardo and stipes of mandibulate insects and that a true subgenal suture cannot be present in the heads of any Hemiptera.

In a series of figures illustrating the transition from a psocid to a cicada head Duporte, who accepts Muir & Kershaw's views of the origin of the maxillary plates, has indicated, though he has not so labelled it, a subgenal suture (Duporte 1962: Fig. 5 B). However, in his illustration of a presumed ancestral psocid-like head (Fig. 5 A) he has shown the subgenal suture as a lateral extension of the one separating the ante-clypeus from the post-clypeus and not, as in mandibulate insects, as an extension of the clypeo-frontal or epistomal suture.

Among insects, the Hemiptera, and in particular the Homoptera, are remarkable for the survival of an abundance of forms in which various structural features occur in different stages of evolutionary development. They are remarkable also on account of their fossil record. In consequence, it is suggested in seeking to elucidate problems associated with the Hemipterous head that studies of the comparative morphology of selected forms retaining different characteristics are likely to be more rewarding than those confined to representatives of a single superfamily and also that fossils may provide more fruitful information than embryological studies. This is especially so when it is remembered that embryology provides information relating largely to the development of existing structural features and that these may be very different from those of an organism's remote ancestors.

Bekker-Migdisova (1946, 1948) has described and figured the heads of several Permian Homoptera. Some of these, in their salient features, resemble those of most present-day Auchenorrhyncha (*Permocicada integra* B. M., *Scytinoptera cubitalis* B. M., *Sojanoneura kazanensis* Zalessky.) On the other hand, others have heads which differ very considerably from those of most Recent Homoptera, though as pointed out by Bekker-Migdisova (1946) they resemble the heads of the nymphs of the Peloridiidae (*Scytoneura elliptica* Martynov, *Prosbolopsis* spp.).

The principal features in which these 2 types of insect heads differ from each other are in the presence, or absence, of a transverse suture separating the ante- from the post-clypeus and the extent to which the lora are differentiated from the clypeus. In heads belonging to both groups, the maxillary plates are apparently separated from the genae by a subgenal ridge.

The most instructive of the fossil heads listed above is that of *Scytoneura elliptica* (Bekker-Migdisova 1948: Fig. 12 a, b). This head has the following features; a large labrum (labelled "ante-clypeus" in the figure) ; a clypeus which is not separated into an ante- and post-clypeus; lora which seemingly consist of lateral clypeal lobes; subgenal sutures; extensive frons bounded anteriorly by epistomal suture and enclosed by both lateral and posterior sutures. As in a former paper (Evans 1957b) I have made comparisons between the heads of some fossil and Recent Homoptera and have sought to establish homologies between various sclerites in the 2 groups; arguments previously used need not be repeated. The reason for once more referring to this topic is because my views on the identity of the several facial sclerites, which are presented in Fig. 3, differ very considerably from ones recently advanced by Duporte and Parsons.

Fig. 4 A represents a reconstruction of the head of a hypothetical Protohomopteron. This head is based on a consideration of the external features of the heads of Permian fossil Homoptera, in particular of *Scytoneura elliptica*, on the heads of peloridiid nymphs and on the heads of selected fulgoroids and cicadelloids such as of the cixiid, *Achaemenes resurgens* (Walker), the fulgoroid *Scolops pungens*, the aetalionid *Darthula hardwickii* (Gray), the ulopid *Woodella wanungarae* and the cicadellids *Tartessus ferrugineus* (Walker) and *Stenopsoides turneri* Evans. It has the following characteristics: a large labrum; an undivided clypeus with lateral lobes; maxillary plates bearing sensory pits and separated from the genae by subgenal sutures; 4-segmented antennae situated adjacent to the anterior tentorial pits; a completely differentiated frons; 3 ocelli. The antennae have been shown as 4-segmented as this would seem to be their basic number in the Heteroptera and hence possibly is a Protohemipterous characteristic. Their position close to the anterior tentorial pits accords with the situation found in the Cicadoidea, Cercopoidea and Cicadelloidea.

The head of the cicada illustrated (Fig. 4 B) differs from the Protohomopterous head in having a smaller labrum, a transversely divided clypeus, an enormously enlarged and more posteriorly situated post-clypeus, no subgenal sutures and a greatly reduced frons. It resembles the Protohomopterous head in having 3 ocelli. Sensory pits situated on the maxillary plates are not shown in this, or in the other, side illustrations because of their wide variation in position within the Homoptera.

In the illustration of the fulgoroid head (Fig. 4 C) the position of the anterior tentorial pits is not indicated, since although posterior tentorial pits are easier to locate in representatives of this superfamily than in those of the others, anterior tentorial pits apparently are lacking. While most fulgoroids lack a subgenal suture and a median ocellus, as both features are retained in some, they have been included in the figure. It will be noted that apart from having a reduced labrum and specialised antennae the fulgoroid head very closely resembles the hypothetical reconstruction illustrated (Fig. 4 A).

The cercopoid head (Fig. 4 D) resembles that of the cicada in the extent and position of the post-clypeus, in having an arched epistomal suture and in lacking subgenal sutures. It differs from the cicada head in lacking a median ocellus and strong supra-antennal ledges and in having a more extensive and different shaped frons. It differs also in having the posterior extensions of the lora concealed under the post-clypeus and not entirely exposed.

In the head of the cicadelloid (Fig. 4 E) both the epistomal suture and the transclypeal suture are shown as broken lines. This is because although a complete epistomal suture is absent in most leafhoppers, it is retained in a few (such as in some *Tartessus* spp.) ; and while most leafhoppers have a transversely divided clypeus, some such as *Aetalion* spp. do not. In spite of the fact that a median ocellus is lacking in leafhoppers and an epistomal suture seldom retained, the head illustrated in Fig. 3 E, more closely resembles the reconstruction of a Protohomopterous head than do those of either the cicadoid or the cercopoid.

Parsons, in her study of the head of Hemiptera has illustrated progressive hypothetical stages in the development of the cranium and of these the last is "stage-4" (Parsons 1964 ; Fig. 2 E ; 9 A, B). It is appropriate to compare the figures referred to above with Fig. 4 A, since it represents a different concept of an Hemipteran head at approximately the same stage of development. Such a comparison reveals very few points of correspondence. Thus, in Parsons' illustrations a trans-clypeal sulcus, which is absent in Fig. 4 A, is shown ; the transfrontal sulcus (which corresponds to the "epistomal suture" in Fig. 4 A) is arched and not transverse ; a subgenal suture is lacking and the "post-frons", which presumably corresponds with the "frons" of Fig. 3A, is not defined as a separate sclerite.

If next a comparison of Parsons' illustrations is made with Fig. 4 B, representing the head of a cicada, many similarities will be observed. This is not surprising since her interpretation, in part, follows that of Duporte, whose studies were largely based on the heads of cicadas.

No indication is given in Parsons' figures of her "stage-4" Hemipteran head of the presence of a separately differentiated frontal region ; yet whatever its homologies, such as a separate sclerite, presumably they must have been present in pre-Hemipterous ancestors and, moreover, have occupied a considerable part of the central area of the cranium. The reason for this ommission is doubtless associated with the assumed derivation of the Hemiptera from machilid or psocopteroid-like ancestors neither of which have a separately differentiated frons. Matsuda (1965) in a figure of the head of the psocid *Stenopsocus stigmaticus* (Imhoff & Labram) has labelled the large, central, enclosed sclerite of this head as the "frons" on the grounds that it cannot represent the post-clypeus since it is preoral in position. This sclerite, however, is not homologous with the frontal areas illustrated in Fig. 4.

While an enclosed frontal region is lacking in adult insects other than in many Homoptera, it is present in certain larval Holometabola, in particular in the larvae of Mecoptera, which also have anteriorly situated antennae. This suggests the possibility that the Hemiptera may have been derived from insects possessing cephalic characteristics similar to those now otherwise retained in certain larval insects.

It is not proposed to discuss the long disputed topic of the origin of the lora, or "mandibular plates", except to point out that while in the Auchenorrhyncha the mandibular levers are always attached to the hind apices of the lora, in the Peloridiidae they are more anteriorly placed, their points of attachment lying towards the lateral apices of the shaded areas of the clypeus, as illustrated in Fig. 4 A. This would seem to support what has been suggested previously by several authors, that the lora are in part of clypeal, and in part of hypopharyngeal origin.

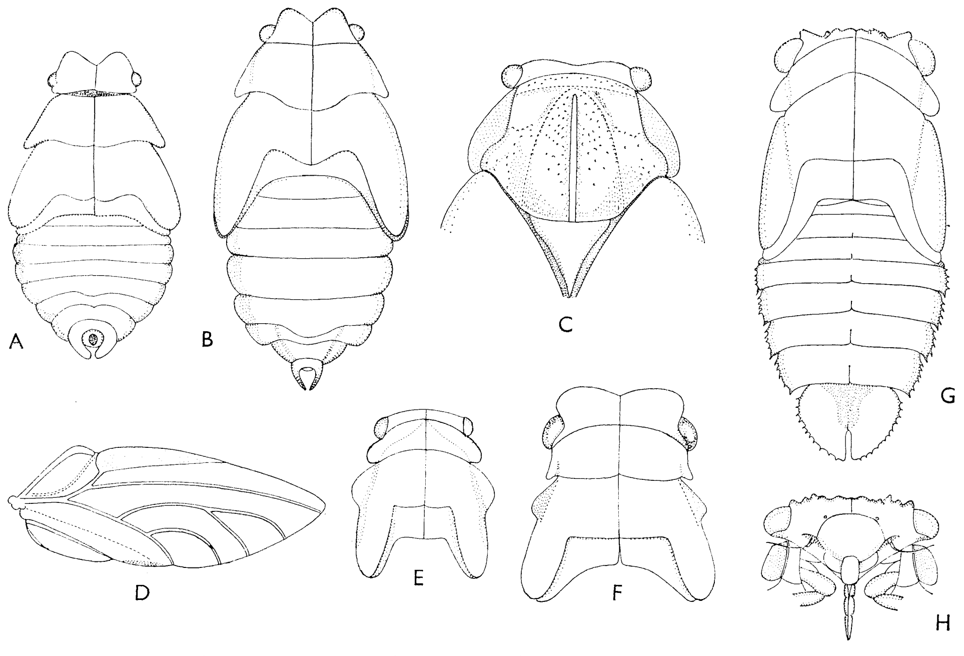


Fig. 5. A, *Aetalion parviceps*, last instar nymph; B, *A. parviceps*, penultimate instar; C, *Schiza* sp. (Aetalionidae), head and thorax in dorsal aspect; D, tegmen of *Cometopsylla* sp.; E, *Macropsis* sp., head and thorax of last instar nymph; F, *Coloborrhis corticina*, head and thorax of last instar nymph; G, *Macropsis* sp., last instar nymph; H, *Macropsis* sp. face of head and prothorax of last instar nymph.

The Significance of Pronotal Paranota

Although the pronotal paranota of *Monteithia anomola* are not so extensively developed as in some of the Myerslopiini, they are nevertheless a distinctive feature of this species.

In an earlier discussion of these structures, as developed in the Homoptera, I referred to their presence in several Palaeozoic and Mesozoic Homoptera as well as in the Peloridiidae and in the Myerslopiini (Evans 1957b). At the time I was unaware that they were to be found also in certain other relict Homoptera belonging both to the Cicadoidea and Cicadelloidea.

Although within the Cicadoidea paranota are lacking in the Tettigarctidae, they are apparently present in some Cicadidae, such as in *Yanga* spp., from Madagascar, while within the Cicadelloidea they are retained in some Neotropical Aetalionidae, and in the nymphs of some Ulopini and Macropsinae. Some examples of lateral expansions of the pronotum in the Aetalionidae are illustrated in Fig. 5 A–C. The paranota of the *Macropsis* nymph illustrated in Fig. 5 G and H, which was collected on Mt Kosciuscko in New South Wales, are of particular interest. This is because they are separated ventrally from the rest of the prothorax, as happens also in the nymphs of the Peloridiidae, by a longitudinal line of weakness (Fig. 5 H).

An ulopid, *Coloborrhis corticina* Germar, of widespread distribution in Africa, which has rudimentary nymphal pronotal expansions, is illustrated in Fig. 5 F. This nymph has an additional relict thoracic feature of interest which consists of a wedge-shaped expansion of the anterior costal border of the tegmen. Such tegminal expansions are to be found also in certain *Macropsis* nymphs, and a nymph with this characteristic from Western Australia is illustrated in Fig. 5 E. Similar costal expansions occur in the tegminal pads of some membracids, such as in those of an Australian species, *Sextius virescens* Fairmaire.

A consideration of the significance of this nymphal structure suggests it may be homologous with the proximal costal expansions of the tegmina of certain adult cicadas and psyllids, such as are found in the Madagascan cicada, *Yanga brancsiki* Distant (illustrated in Distant 1912: Fig. 7a), in an Australian psyllid belonging to the genus *Cometopsylla* Froggatt (Fig. 5 D). In both of these insects the costal expansion is supported medially by the subcostal vein, although in the psyllid the vein is only weakly developed. Since in cicadas, vein Sc is usually incorporated in the costal margin of the tegmen and is usually lacking in psyllids, it seems possible that this development, like pronotal paranota, may represent the retention of a very ancient structural characteristic.

Within extant Heteroptera, pronotal paranota are to be found in the Gelastocoridae and Tingidae; and although in the latter family they may well be secondary developments, in the former they are more likely to be ancient structures. Since the Gelastocoridae lie close to the base of the Heteropterous evolutionary stem and since paranota occurred in the Permian Heteropteran *Paraknightia magnifica* Evans and in the Triassic *Triassodoecus chinai* Evans (Evans 1963), these structures may be assumed to have been characteristics of the Protohemiptera at the time of their separation into 2 suborders.

Wing Polymorphism in the Ulopinae

Although alary, or pterygo-polymorphism, is widespread in the Heteroptera and occurs in all major groups except the Pentatomoidea and Hydrocorisae (Southwood 1961), its occurrence in the Homoptera-Auchenorrhyncha is exceptional. Within the Cicadellidae, apart from the Ulopinae, it occurs, other than very occasionally, only in the Hecalini, Aphrodini, Erhomenellini, Evacanthini and Deltocephalinae.

In 3 of the tribes of the Ulopinae, the Ulopini, Cephalelini and Megophthalmini, forms may occur which have either fully developed fore and hind wings, lack hind wings but have fully developed tegmina, or lack hind wings and have the tegmina reduced to short pads. In the Myerslopiini and Monteithini, up to the present, forms are known in only 1 or the other of the 2 last-named categories.

Kalmus (1945) has pointed out how flightlessness in insects is frequently accompanied by lack of ocelli and such an association is of frequent occurrence within the Ulopini and Cephalelini. In explanation of this phenomenon, Southwood (1961) has suggested that ocelli are an adult character and their correlation with fully developed wings is simply the association of 2 adult characters controlled by the same hormonal condition. The same author has also drawn attention to the fact that brachypterism is frequently associated with high altitudes where low prevailing temperatures act on the hormonal balance and lead to the production of metathetelous adults, i. e., adults which retain juvenile characters. This hypothesis has support in the fact that while most representatives of the Ulopini and Cephalelini are particularly, though not necessarily exclusively associated with montane conditions in both Australia and New Zealand, such few ulopids as are known solely as fully-winged forms live in areas where warm temperate to tropical conditions prevail (*Moonia* spp. in India and *Coloborrhis corticina* in Africa).

Monteithia spp. though dimorphic, and thus conforming with the Ulopinae generally, differ from all other known species in this subfamily in the nature of their dimorphism. This is because in these species an association exists between sex and wing morphology. Although hind wings are lacking in both sexes of known forms, females have the elytra-like tegmina extending almost as far as, or beyond the apex of the ovipositor, while the males have the greater part of the abdomen exposed.

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