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# UPPER PERMIAN HOMOPTERA FROM NEW SOUTH WALES.

By J. W. EVANS, M.A., D.Sc.

(Figures 1-64.)

In the twenty-five years which have elapsed since the first descriptions were published of Upper Permian Homoptera preserved in volcanic tuff in New South Wales, much new and interesting material has been brought to light. Former collections have been described by Tillyard (1921, 1922, 1926*a*), Davis (1942) and Evans (1943).

The present collection, comprising some 124 specimens, has been made principally by Mr. Malcolm Stanley. A few specimens, comprising some of the very greatest interest, have been contributed by Mr. O. le M. Knight. Both Mr. Stanley and Mr. Knight have generously presented their material to the Australian Museum.

It is but seldom that a taxonomist interested in recent insects is given the opportunity to study new fossil material in his chosen group, and appreciation and thanks are expressed to the Director and Trustees of the Australian Museum for having afforded me this privilege.

Unless otherwise indicated, all specimens dealt with in this paper were found in Upper Permian strata between Belmont and Warner's Bay and are contained in the Malcolm Stanley collection of fossil insects at the Australian Museum, Sydney. The photograph reproduced in Fig. 24*a* was made available by Mr. Knight.

## Division PALAEORRHYNCHA.

### Family ARCHESCYTINIDAE.

In a recent paper (Evans, 1943) a remarkably preserved small Homopteron from the Upper Permian of Belmont (*Permocephalus knighti* Ev.) was placed in the Archescytinidae. This was an error, the result of confusion induced by the following circumstances. In 1926, Tillyard (1926*b*) erected a new family, the Permopsyllidae, in which he placed a single genus, *Permopsylla* Till. The genotype, *P. americana* Till., was found in Lower Permian strata in Kansas. Tillyard, following a definition of the family, stated that it was a specialized offshoot from the Archescytinidae which had undergone reduction in size and in the length of the tegmen compared with its breadth, together with great reduction in the clavus. The latter character Tillyard considered brought the type of wing definitely within the Sternorrhyncha. In the same year (Tillyard, 1926*a*) he described three more genera, *Permothea*, *Protopsyllidium* and *Permopsyllidium*, all from Upper Permian strata in New South Wales, and these he also included in his family Permopsyllidac.

In 1931 Carpenter transferred *Permopsylla* to the Archescytinidae and pointed out that the reduction of the clavus was more apparent than real, due to the incomplete preservation of the type specimen. For this family he proposed a new division, the Palaeorrhyncha. Insects in the Palaeorrhyncha, according to Carpenter, combine primitive features of both the Auchenorrhyncha and the Sternorrhyncha, as Archescytinids were furnished with long antennae, consisting of twenty-five segments; three-segmented tarsi and a fully developed clavus in each tegmen with two anal veins. At the same time he proposed the family name Protopsyllidiidae for the genera *Permothea*, *Protopsyllidium* and *Permopsyllidium*.

Davis, in 1942, referred to Carpenter's action in transferring *Permopsylla* to the Archescytinidae, but apparently overlooked the new family name Protopsyllidiidae, as he continued to include the three genera from New South Wales previously defined

by Tillyard, in the Permopsyllidae and at the same time added a further five genera to the same family.

*Permocephalus* was originally placed in the Archescytinidae, as it was erroneously supposed that this family was identical with the Permopsyllidae of Tillyard. *Permocephalus knighti* has short antennae and is related to species in genera comprised in the Protopsyllidiidae, not to *Permopsylla* spp. It is accordingly transferred from the Archescytinidae to the Protopsyllidiidae.

Thus, up to the present, no true Archescytinids have been described from the Upper Permian of New South Wales. Two specimens in the present collection would seem to belong to this family. One is described below; the other, a fragment, is figured in a later section (Fig. 59).

#### Austroscytina, gen. nov.

The hind-wing is of stout consistency and the costal space is narrow.  $R_{1a}$  meets the costal margin only slightly beyond its centre.  $R_{1b}$  does not extend as far as the apex of the wing and the space separating the apices of  $R_{1a}$  and  $R_{1b}$  along the costal margin is only slightly greater than the space between  $R_{1b}$  and  $Rs$ .  $M$  has three branches, and  $M$  and  $Cu_1$  have separate origins. The clavus is unknown.

#### *Austroscytina imperfecta*, sp. nov. (Genotype.) (Fig. 3.)

*Length of wing*, 8 mm.; greatest width, 3.3 mm. The dotted line shown in the figure occurs as a furrow in the wing in the position indicated. It may represent  $Sc$ .  
*Holotype wing*—F 40084, Malcolm Stanley Collection.

### Division AUCHENORRHYNCHA.

#### Family PROSBOLIDAE.

Three tegmina and one wing, from the Upper Permian of New South Wales, have been ascribed previously to this family. They are of *Mitchelloneura permiana* Till. (1921), and *Permoglyphus belmontensis* Till., *Permodiphthera robusta* Till., and *Permodiphthera dubia* Till. (1926a).

In describing the family characteristics, Tillyard states that there is a differentiation in the texture of the membrane of the basal and distal portions of the tegmen and that the costa may be notched either at, or before, the apex of  $R_{1a}$ , forming a kind of nodus.

In *Prosbote hirsuta* Handl. from the Upper Permian of Russia, the tegmen is divided into two parts as described by Tillyard. However, the nodal line in all those Russian Prosbolidae in which it is present, invariably extends from where  $R_{1a}$  meets the costa<sup>1</sup> to the point where  $M$  first branches, thence to the fork of  $Cu_1$ . Martynov (1935b) has grouped also in this family certain tegmina which lack all trace of a transverse division.

It is suggested that the "nodal lines" indicated in Tillyard's figures of *Permoglyphus belmontensis* and *Permodiphthera robusta* are merely creases, the result of slight crumpling. Accordingly, *Permoglyphus* Till. and *Permodiphthera* Till. are transferred from the Prosbolidae to a new family, the Permoglyphidae. *Mitchelloneura* Till., being known only from a hind-wing, is retained in the Prosbolidae.

Martynov (1928) has suggested that the genera *Orthoscytina* Till. and *Homaloscytina* Till., placed by Tillyard in the Scytinopteridae, belong rather to the Prosbolidae. This suggestion is not supported.

#### Austroprosbote, gen. nov.

The tegmen is long, broad and delicate. A break occurs in the costal margin where it is in contact with  $R_{1a}$ , and there is a distinct nodal line in the position indicated in the illustration of the tegmen of the genotype. The costal space is wide, and  $Rs$  is bent and in close contact with  $M_1$ .  $M$  has four branches, and  $M_1$  and  $M_2$  are shorter than  $M_3$  and  $M_4$ . The clavus is broad, the two anal veins meet at their distal apices, and the anal margin is not in alignment with the rest of the hind margin of the tegmen.

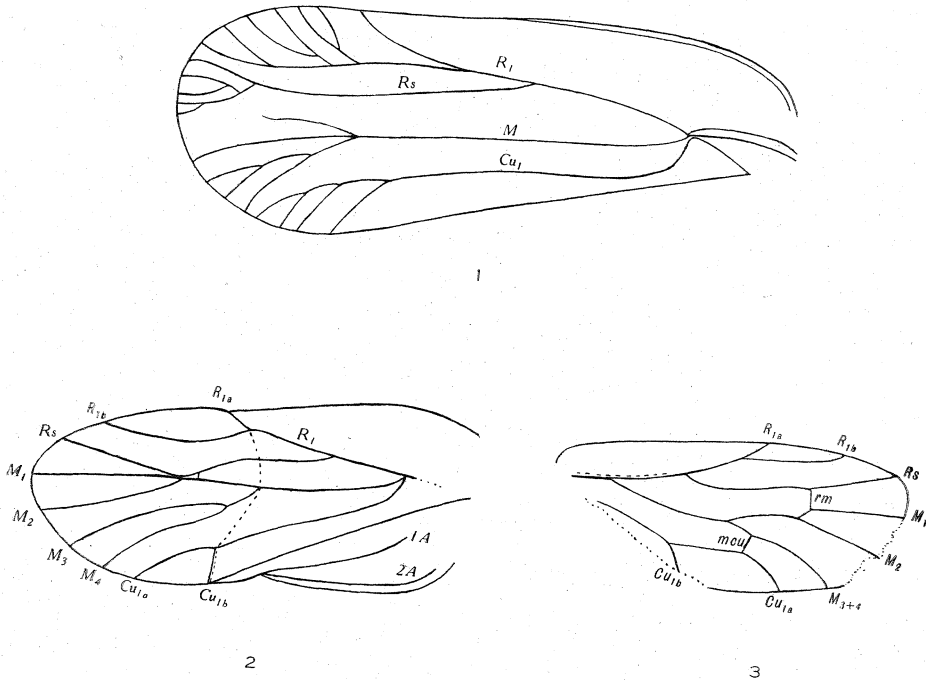
<sup>1</sup>The costa may be interrupted at  $R_{1a}$  without the development of a nodal line, as for instance in the recent Psyllid, *Cometopsylla rufa* Frogg. (Froggatt, 1900).

***Austroprosbole maculata*, sp. nov. (Genotype.) (Fig. 2.)**

*Length of tegmen*, 13 mm.; greatest width, 5 mm. The whole tegmen has a mottled colour pattern and no apparent differentiation in texture.

*Holotype tegmen*—F 40048, Malcolm Stanley Collection.

In all other known Prosbolidae, with the exception of *Dictyoprosbole membranosa* Mart. (Martynov, 1935a), the anal veins are distinct for their entire length, but reasons exist for believing that the presence or absence of a V- or Y-vein in the clavus is a character of limited significance.



Figs. 1-3.—1, *Permobrachus magnus*, holotype tegmen. 2, *Austroprosbole maculata*, holotype tegmen. 3, *Austroscytina imperfecta*, holotype tegmen.

Tillyard (1918) suggested that species in the Triassic family Dunstaniidae were related to the Permian family Prosbolidae and at the same time ancestral to the Heteroptera. In 1926 (1926c) he confirmed his former hypothesis and stated that "the family Dunstaniidae belongs to the Gymnocerata and is clearly an early type ancestral to the Pentatomoidea". In the same year (1926a) he had already written that the Prosbolidae appear to have been ancestral to recent Fulgoroidea, especially the Trophiduchidae. It is agreed that the Prosbolidae may have been on the same line of descent as the Fulgoroidea, as might equally well have been the Permogliphidae and Pereboridae,<sup>1</sup> but the mere tendency of a tegmen to divide into a coriaceous proximal portion and an overlapping membranous distal part does not necessarily imply any ancestral relationship with the Heteroptera. On another occasion, Tillyard (1936) figured a Triassic tegmen which he stated was "a specialized Scytinopterid type in process of becoming a true Heteropterous type". The only explanation offered in support of such a startling pronouncement was the shape of the tegmen, which was not unlike that of a recent Achilid.

<sup>1</sup>The closest approach to a Fulgoroid type, of any known Australian Permian Homoptera, is to be found in the tegmen of *Eochiliocycla angusta* Davis, which should be compared with recent Achilids.

## Family PERMOGLYPHIDAE.

This family has characteristics in common both with the Scytinopteridae and the Ipsviciidae. *Permoglyphus belmontensis* resembles the former in the shape of the tegmen, in the shape of the proximal half of  $Cu_1$ , in having a complete media with four branches, and in the complete separation of the anal veins. It resembles *Paraknightia magnifica*, gen. et sp. nov. (Ipsviciidae), in the short transverse Sc, in the transverse nodal break which extends from the costa, to the point of separation of R and M from R + M, in having R parallel with the costal margin, and in the possession of separate anal veins. *Permodiphthera robusta*, *Permodiphthera dubia* and *Permobrachus magnus*, gen. et sp. nov., lack certain of these characteristics, but all have Rs with more than a single branch, and for the moment it is convenient to group them together with *P. belmontensis*. Tillyard suggested that *P. dubia* might not be congeneric with its genotype. It is now transferred to the new genus *Permobrachus* which is described below. *Permobrachus magnus* resembles *Permopibrocha ramosa* Mart. (fam. Pereboridae) in the development of numerous subsidiary veins and it is possible that it would be better placed in this family.

*Permobrachus*, gen. nov.(Genotype, *Permobrachus dubia* (Till.).)

The tegmen is long and somewhat narrow. R, Rs, M and  $Cu_1$  all have subsidiary veins.  $Cu_1$  is curved following its separation from R and M, and the costal space is extensive. The clavus is unknown.

*Permobrachus magnus*, sp. nov. (Fig. 1.)

*Length of tegmen*, 16 mm.; greatest width, 5.8 mm. The proximal third is somewhat roughened and the apical two-thirds smooth. This effect is believed to be due to the manner of preservation and not to a difference in the consistency of the original tegmen.

*Holotype tegmen*—F 40029, Malcolm Stanley Collection.

## Family SCYTINOPTERIDAE.

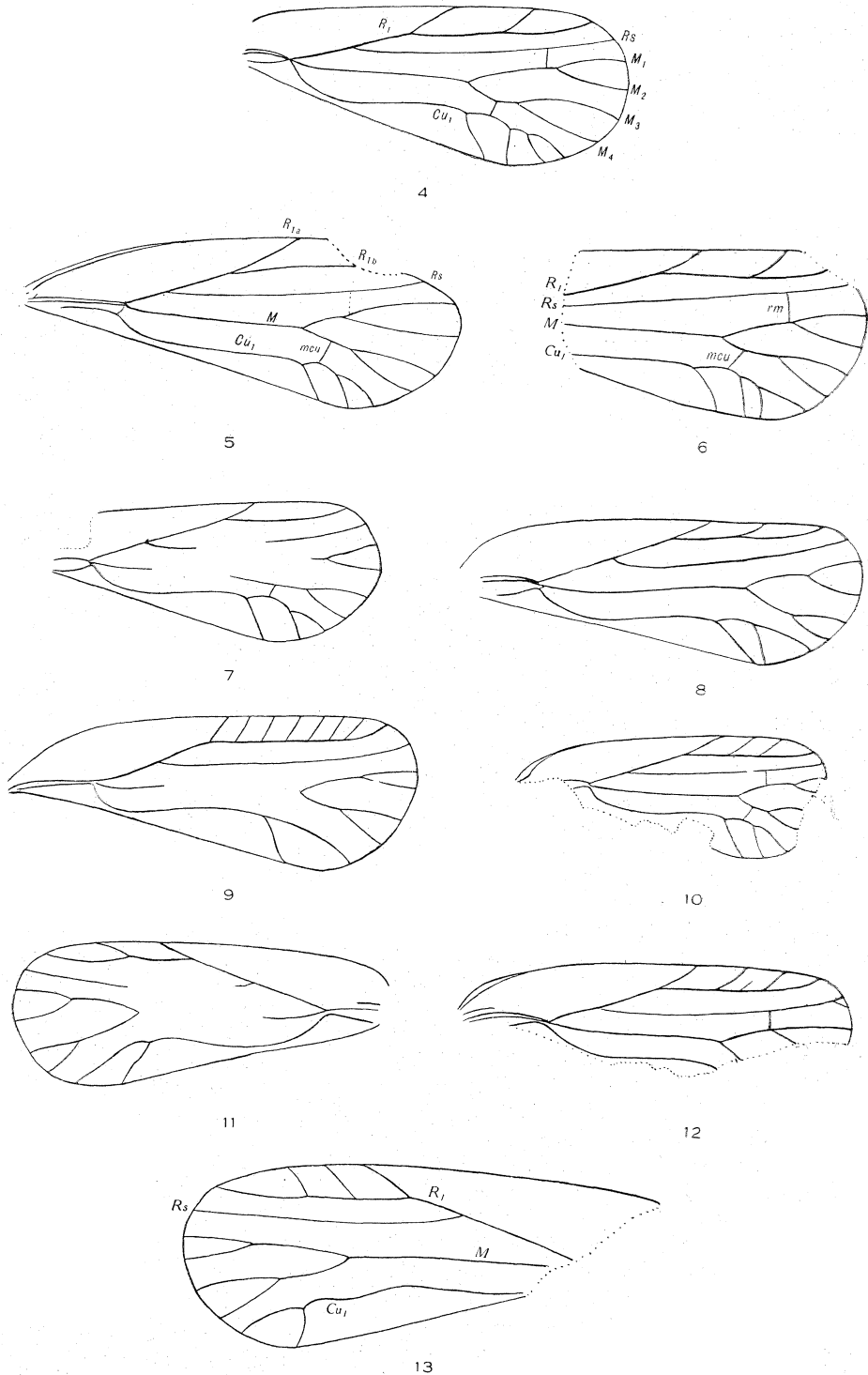
The following genera of Upper Permian Homoptera from New South Wales have been placed in this family by their respective authors: *Permoscarta* Till., *Permojassus* Till., *Stenoscytina* Till., *Orthoscytina* Till., *Actinoscytina* Till., *Elliptoscarta* Till., *Homaloscytina* Till., *Psocoscytina* Davis, *Anomaloscytina* Davis, *Eochiliocycla* Davis, and *Permagra* Ev. Davis has mentioned that *Eochiliocycla* is only tentatively placed in the Scytinopteridae, where it certainly does not belong. *Permoscarta* and *Permagra* are herewith transferred to the Ipsviciidae.

*Orthoscytina* Till., 1926.

If the number of tegmina found preserved as fossils provide any indication of abundance, then species included in the genus *Orthoscytina* would appear to have been the dominant Auchenorrhyncha of Upper Permian times in Australia. The following diagnostic characters of the genus may now be added to those furnished previously by Tillyard: clavus of the tegmen with two widely separated anal veins, pronotum rectangular, scutellum long, but shorter than the pronotum. These additions have been made possible by the discovery of F 39885, which is illustrated in Fig. 58.

While the generic characters of *Orthoscytina* are well defined and characteristic, the specific ones are otherwise, and it is doubtful whether all the nine species described by Tillyard are justified. This, however, is unimportant when a name is associated merely with a particular specimen and not with a group of individual organisms.

Figures 4-13 are illustrations of the tegmina of the better preserved specimens of *Orthoscytina* which occur in the present collection. Figs. 8 and 11 represent the obverse and reverse of a single tegmen and have been included to indicate the extreme caution which must be observed in drawing conclusions based on minor differences in the venation of fossil wings.

*Orthoscytina* spp.

Figs. 4-13.—4, F 40014 (10 mm.). 5, F 39941 (9 mm.). 6, F 40051 (5.8 mm., fragment).  
 7, F 40019 (6 mm.). 8, F 40023 (7.8 mm.). 9, F 40001 (9 mm.). 10, F 40025 (8.8 mm.).  
 11, F 39993 (7.8 mm.). 12, F 40090 (9 mm.). 13, F 39988 (7 mm.).

When the ten figures of *Orthoscytina* spp. presented here are compared with Tillyard's illustrations, it is found that exact correspondence cannot be found in a single instance. Figs. 5, 8 and 11 might well be ascribed to *O. belmontensis* Till. and Fig. 12 to *O. tetra-neura* Till. In the present instance, it is considered adequate merely to figure the tegmina contained in this collection. When further material is brought to light and a better appreciation becomes possible of the limits of specific differentiation and intra-specific variation, it may be advisable to sink some of Tillyard's species as synonyms or to propose new species. Details of the lengths of the tegmina illustrated are given in the description of the figures.

#### Homaloscytina Till., 1926.

The same problem of specific differentiation is met with in this genus. Figs. 14–23 are illustrations of the best preserved tegmina representing the several variations which occur in the present collection. Not a single figure is identical with that of the holotype of *H. plana* Till., yet no useful purpose would be served by describing any of the several forms as new species. The differences concern the shape of the apex of the tegmen, the presence, absence and exact position of cross-veins, especially of m-cu, and the length of the branches of M and Cu<sub>1</sub>. Variations in details of tegminal venation are not unusual in recent Homoptera. An example occurring in the Jassoidea is illustrated in the Appendix. Details of the specimens of *Homaloscytina* figured are given in the descriptive text. Numbers F 39909 and F 39904 were collected by Mr. Knight at the Pincombe outcrop between Belmont and Warner's Bay.

The tegmen of *H. plana* is clearly that of an insect closely related to various Homoptera of the Russian Permian, such as *Sojaneura aberrans* Mart. (Martynov, 1935b). It is not clear why this latter species, among others, was included by its author in the Prosbolidae and not in the Scytinopteridae.

#### Family IPSVICIIDAE.

Up to the present no representatives of this family have been recorded from Upper Permian strata; they have been known only from the Triassic of Ipswich, Queensland. Five new genera, each with a single species, are described below. In addition, *Permagra*<sup>1</sup> and *Permoscarta* are transferred from the Scytinopteridae to the Ipsviciidae.

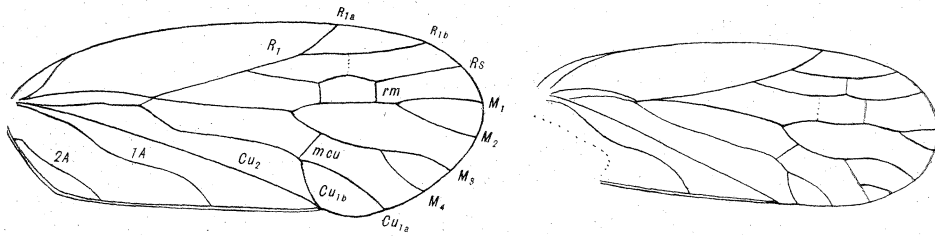
Tillyard (1920) regarded the Ipsviciidae as "early Fulgoroidea", doubtless because of the presence of a Y-vein in the single specimen with a complete clavus. It has already been suggested that the presence of a Y-vein is a character of but limited diagnostic value. It is more probable that the Ipsviciidae were related, if not directly ancestral, to the Cercopidae.

The Upper Permian representatives of the Ipsviciidae described below resemble those from Triassic strata in the shape of the tegmen, which narrows apically, in the indistinctness of the venation towards the apex of the tegmen, and in the basal fusion of M and Cu<sub>1</sub>. Of the two specimens occurring with the clavus intact, one has a Y-vein; in the other the anal veins are separate.

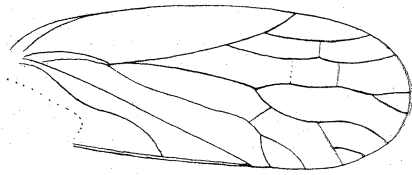
#### Paraknightia, gen. nov.

The pronotum has large and well developed paranotal expansions and is narrowly produced anteriorly. In the tegmen Cu<sub>1</sub>, proximally, is parallel to M and to R. The costa is thickened and Sc short and transverse. A nodal line extends from the costal margin to the point where R diverges from M. R is parallel to the costa for the greater part of its length and in the clavus the two anal veins are parallel with each other. The tegmen narrows apically; it is rugose, excepting close to the apex where it is smooth, suggesting that the apex was membranous.

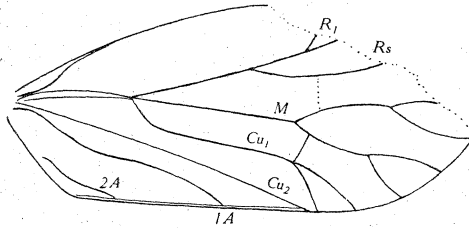
<sup>1</sup> Certain changes in the venational interpretation of *Permagra* are necessary. The vein labelled R<sub>1</sub> is R<sub>1a</sub>; R<sub>2+3</sub> is R<sub>1b</sub>; R<sub>4+5</sub> is Rs.



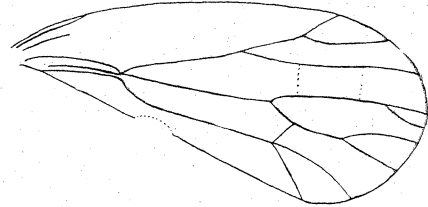
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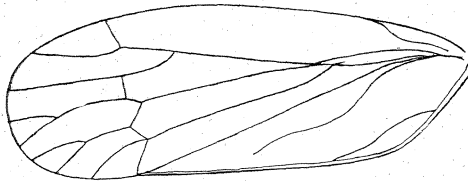
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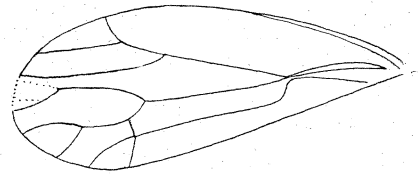
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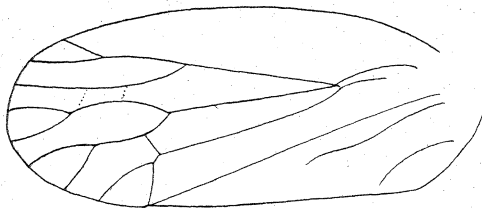
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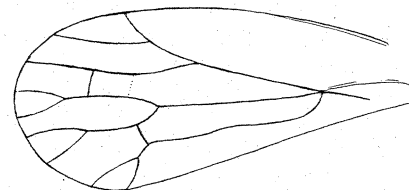
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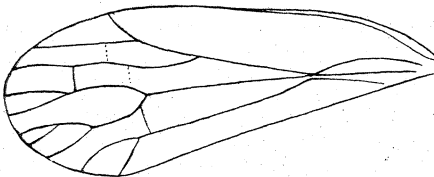
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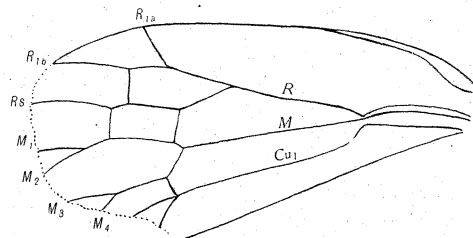
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23

*Homaloscytina plana.*

Figs. 14-23.—14, F 40015 (6 mm.). 15, F 40057 (5.8 mm.). 16, F 40011 (5.8 mm.). 17, F 40012 (5.8 mm.). 18, F 40010 (6 mm.). 19, F 40071 (5.8 mm.). 20, F 39909 (6 mm.). 21, F 39904 (6 mm.). 22, F 40085 (6 mm.). 23, F 40004 (5 mm., fragment).



*Paraknightia magnifica*, sp. nov. (Genotype.) (Fig. 24.)

*Length*, from the anterior margin of the pronotum to the tip of the ovipositor, 17 mm. *Length of tegmen*, 12 mm.; greatest width, 4 mm.

*Holotype*—F 40450, found by Mr. Knight in Upper Permian strata at Lake Macquarie, N.S.W.

This striking fossil is excellently preserved as a ventral impression. The insect is pale brown and the surrounding rock white. The dotted lines in the fork of  $Cu_1$ , shown in the figure, represent veins of the hind-wing. In the original description of *Permagra distincta* it was suggested that pronotal paranota might be present, but their recognition was uncertain. In *Paraknightia magnifica* there is no doubt as to their presence. Other interesting structural features are the nodal line and the long ovipositor. The nodal line is not homologous with that occurring in *Prosbote*. Such transverse lines of weakness are of wide occurrence in both fossil and recent Homoptera. With regard to the ovipositor, a few recent Homoptera have unusually long ovipositors; for instance, the Australian Ledrid, *Ledramorpha planirostris* Don. In none are they so long as in *Permoscytina kansasensis* Till. as figured by Carpenter (1939). Whether such a terminal structure as that possessed by *P. kansasensis* functioned as an ovipositor, or, as suggested by Carpenter, as a respiratory tube, must remain uncertain. In the author's opinion the latter explanation is improbable, likewise Carpenter's suggestion that the nymphs of Archescytinids were aquatic.

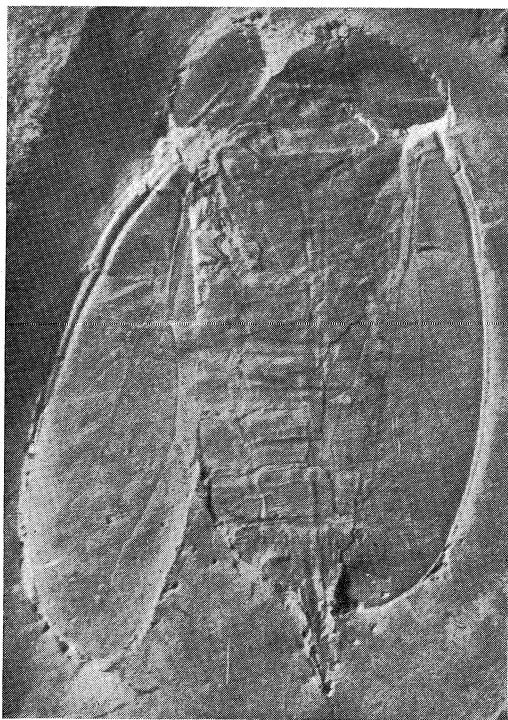


Fig. 24a.

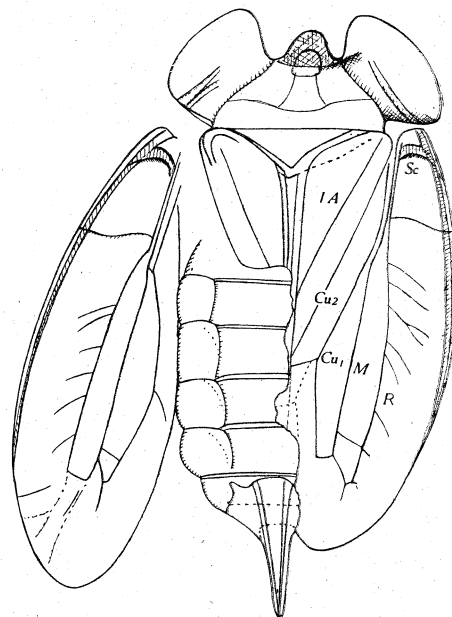


Fig. 24b.

Figs. 24a-b.—*Paraknightia magnifica*, holotype.

At first sight the inclusion of *P. magnifica* in the Ipsviciidae might appear unwarranted; but, if Fig. 24b is compared with Tillyard's illustration of the tegmen of *Ipsvicia jonesi* Till., the genotype of the genus *Ipsvicia* Till., the following resemblances between the two tegmina will be apparent. In both,  $R_s$  is parallel to the costa and has numerous transverse costal veinlets; the venation is indistinct ante-apically and the apex of the tegmen narrow. In the position of the nodus of *P. magnifica* Tillyard has

drawn a line in his figure, which does not break the costal border. This line, he indicates, represents Sc, but it is possible that it is a nodal break. The condition in *I. jonesi*, where M and  $Cu_1$  are fused for part of their course, is foreshadowed in *P. magnifica*, where these veins, though distinct, lie closely apposed to one another.

**Stanleyana**, gen. nov.

The tegmen narrows apically. R is parallel with the costal margin for the greater part of its length, and M and  $Cu_1$  are fused basally. M consists of  $M_1$ ,  $M_2$  and  $M_{3+4}$ .  $Cu_{1a}$  and  $Cu_{1b}$  are longer than  $M_1$  and  $M_2$ . An ambient vein is developed. The clavus is unknown.

**Stanleyana pulchra**, sp. nov. (Genotype.) (Fig. 25.)

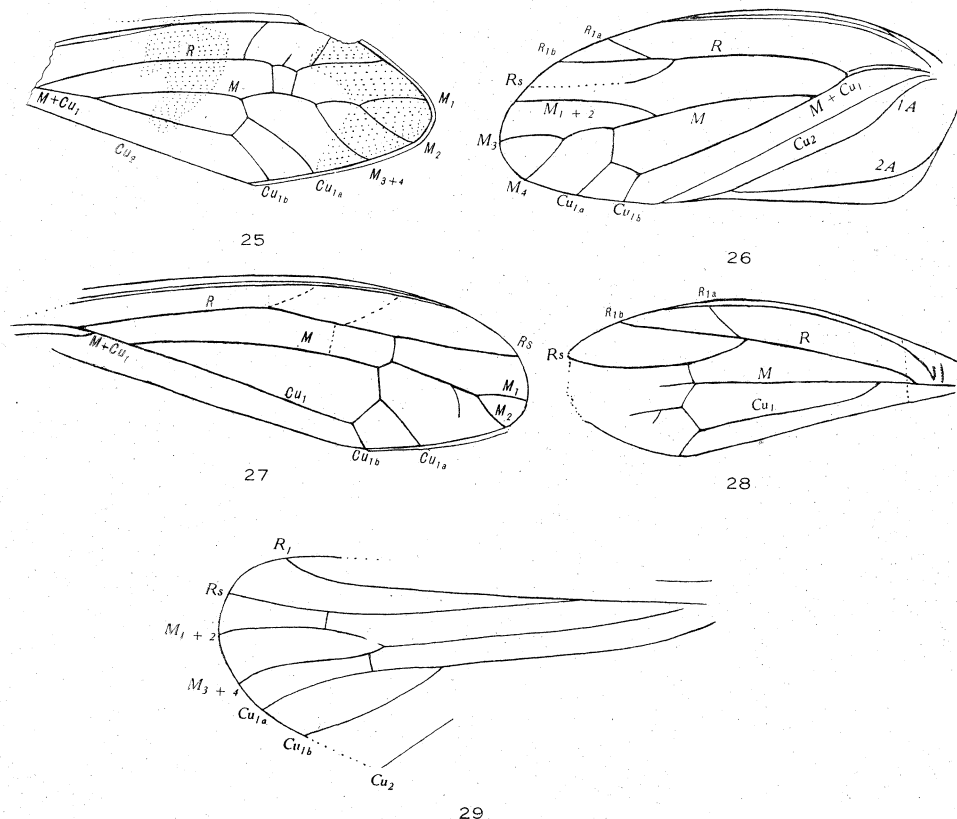
Length of tegmen, 7 mm.; greatest width, 2.8 mm. Colour pattern well developed, the shaded portion, as shown in the figure, being pale brown, the remainder black. The whole tegmen is smooth and was probably coriaceous with the apex membranous.

*Holotype tegmen*—F 40016, Malcolm Stanley Collection.

*S. pulchra* represents a later development than *P. magnifica* and shows a further approach to the condition of the tegmina found in Triassic representatives of the Ipsiviciidae.

**Stenovicia**, gen. nov.

The tegmen is narrow and the costa is thickened.  $R_1$  is parallel to the costa for the greater part of its length. M and  $Cu_1$  are fused close to their point of contact with R.  $M_1$  and  $M_2$  are short, and  $Cu_{1a}$  is almost twice the length of  $Cu_{1b}$ . The clavus is unknown.



Figs. 25-29.—25, *Stanleyana pulchra*, holotype tegmen. 26, *Palaeoviccia incerta*, holotype tegmen. 27, *Stenovicia angustata*, holotype tegmen. 28, *Permoviccia obscura*, holotype tegmen. 29.—*Anomaloscytina incompleta*, holotype wing.

**Stenovicia angustata**, sp. nov. (Genotype.) (Fig. 27.)

*Length of tegmen*, 6 mm.; greatest width, 2 mm. It is uncertain whether an ambient vein is developed or merely an appendix.

*Holotype tegmen*—F 40008, Malcolm Stanley Collection.

**Permoviccia**, gen. nov.

The tegmen is short and broad. Sc is short, wide and transverse, and R and R<sub>1b</sub> are more or less parallel to the costal margin. Rs is widely curved, and M and Cu<sub>1</sub> are fused for a short distance basally. The apical terminations of M and Cu<sub>1</sub> are unknown. A nodal break may be present in the position indicated in the figure of the genotype. The clavus is unknown.

**Permoviccia obscura**, sp. nov. (Genotype.) (Fig. 28.)

*Length of tegmen* (fragment), 4.8 mm.; greatest width, 1.6 mm. State of preservation of holotype, poor.

*Holotype tegmen*—F 40059, Malcolm Stanley Collection.

**Palaeoviccia**, gen. nov.

The tegmen is broad and narrows apically. R and R<sub>1b</sub> are parallel to the costal margin. Rs is short and straight, and M has three branches, M<sub>1+2</sub> and M<sub>3</sub> and M<sub>4</sub>. M and Cu<sub>1</sub> are fused basally. The clavus is broad and the anal veins form a Y-vein.

**Palaeoviccia incerta**, sp. nov. (Genotype.) (Fig. 26.)

*Length of tegmen*, 5.7 mm.; greatest width, 2 mm. The whole tegmen is somewhat rugose. A poor impression, especially in the neighbourhood of Rs and M<sub>1+2</sub>.

*Holotype tegmen*—F 39999, Malcolm Stanley Collection.

Family **SCYTINOPTERIDAE?****Anomaloscytina incompleta**, sp. nov. (Fig. 29.)

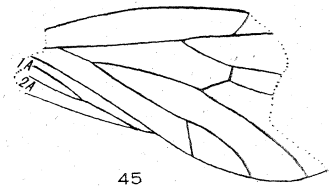
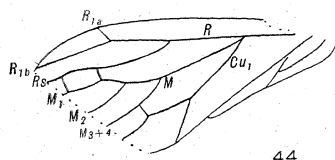
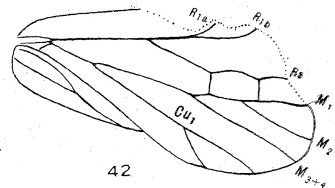
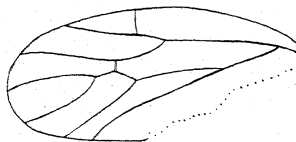
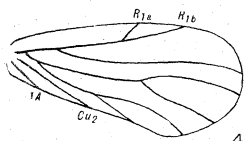
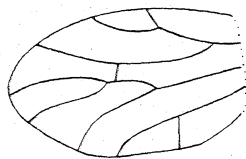
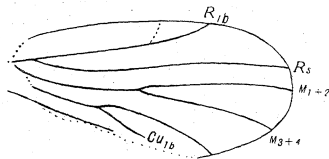
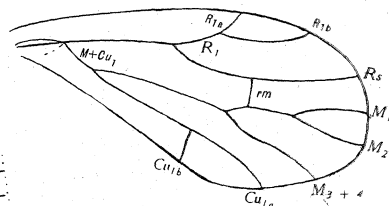
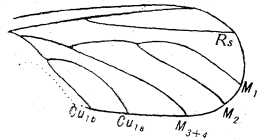
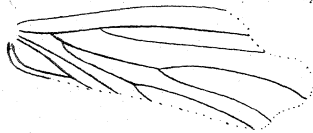
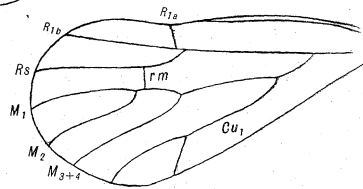
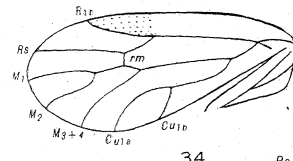
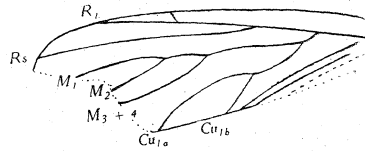
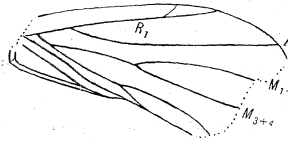
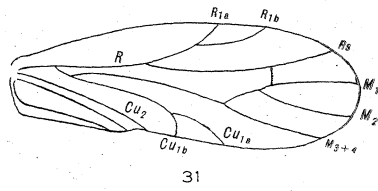
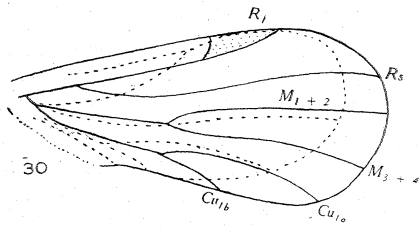
*Length of hind-wing* (fragment), 10 mm. This wing differs from that of *A. metapteryx* Davis in the greater length of Rs and in having the branches of M shorter than those of Cu<sub>1</sub>.

*Holotype wing*—F 40009, Malcolm Stanley Collection.

Hind-wings of Homoptera, as might be expected, are seldom found in a fossil condition. Even more seldom are they found with their corresponding tegmina. The wing described and figured above may or may not be that of a Scytinopterid. It is of interest to note that up to the present no hind-wings of Permian Homoptera have been found with an ambient vein developed. They thus resemble, in this respect, those of recent Fulgoroidea. Yet the principal characteristics of the tegmina of both the Scytinopteridae and the Ipsviciidae suggest relationships rather with recent Cercopidae and Jassoidea.

Division **STERNORRHYNCHA.**

It is clear that the small Homoptera described in the families Protopsyllidiidae and Pincombeidae belong neither to the Palaeorrhyncha nor to the Auchenorrhyncha. On the other hand, they possess several characteristics which separate them from recent Sternorrhyncha. Several authors (e.g. Singh Pruthi, 1925; Muir, 1930) have pointed out that the separation of the Homoptera, apart from the Peloridiidae (Coleorrhyncha), into the Auchenorrhyncha and Sternorrhyncha results in an unnatural grouping. However, because of inadequate morphological knowledge, no satisfactory alternative system has yet been proposed, although it is generally acknowledged that the Fulgoroidea need further separation from the rest of the Auchenorrhyncha. Because of the close correspondence evident between the venation of the Protopsyllidiidae and recent Psyllids, it is convenient to regard them both as members of the same division. Whether such action is justified on phylogenetic grounds is uncertain.



Family **PROTOPSYLLIDIIDAE.**

The Protopsyllidiidae comprise small Homoptera from the Upper Permian of New South Wales which resemble recent Psyllidae in size and in the venation of the tegmen, apart from the clavus. They differ from the Psyllidae in the structure of the head and ovipositor. In the head the frons is triangular, the clypeus is joined to the frons and the antennae, which are short, arise from close to the apices of the epistomal suture. In recent Psyllids the frons is so reduced that the median ocellus is all that remains, the clypeus is detached, distinct and of a different shape, and the antennae, which are long, arise from the sides of the head close to the eyes. The ovipositor of the Protopsyllidiidae is of the primitive basic type which is found in recent Auchenorrhyncha, apart from many Fulgoroidea. It consists of paired median valves (presumably three pairs). The ovipositor of recent Psyllids is of a specialized type and does not consist of three pairs of median valves.

With the exception of *Psocopsyllidium media* Davis (Fig. 47), *Eopsyllidium delicatulum* Davis and *Permopsyllioides insolita*, gen. et sp. nov. (Fig. 46), all the known tegmina of the Protopsyllidiidae, including those described and figured below, are very similar in general appearance and can be grouped into two clear-cut divisions, differing in the structure of the media. In one group the media has two branches, in the other it has three. The anal veins also show minor differences. Whether, for the purpose of separating the several varieties of tegmina, the erection of numerous genera, instead of two only, is justified, is a debatable question.

Figs. 30-47, with the exception of Fig. 44, represent the best preserved of the various types of tegmina of the Protopsyllidiidae contained in the present collection. A few well-preserved tegmina, identical with some of those figured, also occur. These are not figured.

**Protopsyllidium** Till., 1926.

This genus contains two species, the genotype *P. australe* Till., and *P. sinuatum* Davis. Davis has drawn attention to the possibility that too little allowance for individual variation and variation in the state of preservation has been made in the past in deciding on interspecific differences between representatives of this family. So far as this genus is concerned, it would appear that due caution has been observed and that two species are certainly justified. The specimen illustrated in Fig. 41 is identified as *P. australe*. It was found by Mr. Knight at Kimble's Hill near Belmont. The tegmina illustrated in Figs. 30, 32, 35 and 38 are all considered as *P. sinuatum*. Details of the index numbers of the specimens figured and of their size (length) are given in the description of the figures.

**Permopsyllidium** Till., **Permothea** Till., 1926, **Permotheëlla** Davis,—**Permopsyllidops** Davis, **Clavopsyllidium** Davis, 1943.

The association of tegmina contained in fresh collections with species in the above genera will always be a difficult matter. It is suggested that the tegmina reproduced in the following figures belong here: Figs. 31, 34, 39, 40, 43 and 45. Those illustrated in Figs. 33, 36, 37 and 42, while clearly belonging to the same group of genera, are considered to be sufficiently distinct to merit the definition of new genera.

It would seem that all the material of the Protopsyllidiidae originally handled by Tillyard consisted of tegmina lacking a clavus. On this account, except in one instance where 1A was preserved, Tillyard assumed that anal veins were lacking in these insects.

Figs. 30-45.—30, *Protopsyllidium sinuatum* (F 40067: 5 mm.). 31, *Permopsyllidium mitchelli* Till. (F 40069: 3.5 mm.). 32, *Protopsyllidium sinuatum* (F 39997: 3 mm.). 33, *Psyllidiana davisia*, holotype tegmen. 34, *Permopsyllidium affine* (F 40062: 2.8 mm.). 35, *Protopsyllidium sinuatum* (F 39983: 4.5 mm.). 36, *Psyllidella magna*, holotype tegmen. 37, *Protopsyllidops minuta*, holotype tegmen. 38, *Protopsyllidium sinuatum* (F 39981: 3 mm.). 39, *Permotheëlla scytinopteroides* (F 39985: 4.8 mm.). 40, *Permopsyllidium mitchelli* (F 40006: 2.4 mm.). 41, *Protopsyllidium australe* (F 40724: 2.8 mm.). 42, *Belpsylla reticulata*, holotype tegmen. 43, *Permopsyllidium mitchelli* (F 40040: 2.6 mm.). 44, *Protopincombea obscura*, holotype tegmen. 45, *Permopsyllidium mitchelli* (F 39901: 4.7 mm.).

Davis was the first to show that the Protopsyllidiidae had a small but well developed clavus with two anal veins. Of necessity a personal bias must operate in determining identifications such as these. For instance, the tegmen reproduced in Fig. 34 has been associated with *Permopsyllidium affine* Till., although it might equally well have been identified as that of *Permotheëlla scytinopteroides* Davis. The specimen (F 39901) illustrated in Fig. 45 was found by Mr. Knight at the Pincombe outcrop between Belmont and Warner's Bay.

**Psyllidiana**, gen. nov.

The tegmen is narrow, and  $R_1$  and  $R_s$  are both straight. M has three branches,  $M_1$ ,  $M_2$  and  $M_{3+4}$ .  $Cu_{1a}$  is longer than the basal portion of  $Cu_1$ . The clavus of the holotype of the genotype is incomplete; but it is probable that the anal veins are separate for their entire length.

**Psyllidiana davisia**, sp. nov. (Genotype.) (Fig. 33.)

*Length of tegmen*, 3 mm. A poor impression suggesting a delicate tegmen.

*Holotype tegmen*—F 40711, collected by Mr. Knight at the Pincombe outcrop between Belmont and Warner's Bay.

**Psyllidella**, gen. nov.

The tegmen is broad and the costal margin is thickened and sinuate.  $R_1$  is straight, and  $R_s$  leaves R at a point in line with the first bifurcation of M. The clavus is unknown.

**Psyllidella magna**, sp. nov. (Genotype.) (Fig. 36.)

*Length of tegmen*, 5 mm.; greatest width, 2 mm. A pale yellowish-brown negative impression on white coarsely grained rock.

*Holotype tegmen*—F 40043, Malcolm Stanley Collection.

*P. magna* resembles *Psocoscytina bifida* Davis in size and superficial appearance, although the latter has been placed by its author in the Scytinopteridae. It differs in having  $R_s$  single and in having  $M_3$  and  $M_4$  fused together and not  $M_1$  and  $M_2$ .

**Protopsyllops**, gen. nov.

The tegmen is short and broad.  $R_1$  lies close to the costal margin,  $R_s$  is long, and the first branching of M occurs close to the junction of M and  $Cu_1$ . All the three branches of M are long, and  $Cu_{1b}$  is parallel to  $Cu_{1a}$ .

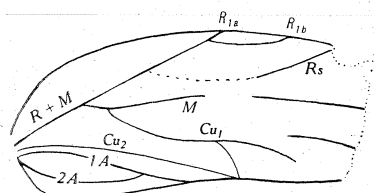
**Protopsyllops minuta**, sp. nov. (Genotype.) (Fig. 37.)

*Length of tegmen*, 3.1 mm.; greatest width, 1.1 mm.

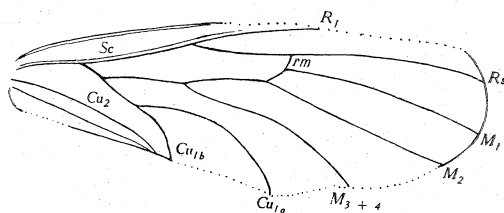
*Holotype tegmen*—F 40005, Malcolm Stanley Collection.

**Belipsylla**, gen. nov.

The tegmen is long and apically broad.  $R_{1a}$  and  $R_{1b}$  curve towards the costa. There are two cross-veins between R and M, all three branches of M are straight, and  $Cu_1$  is narrowly forked. The clavus has a well-developed Y-vein.



46



47

Figs. 46, 47.—46, *Permopsylloides insolita*, holotype tegmen. 47, *Psocopsyllidium media* (F 39953: 4.7 mm.).

**Belpsylla reticulata**, sp. nov. (Genotype.) (Fig. 42.)

*Length of tegmen*, 3.8 mm.

*Holotype tegmen*—F 39992, Malcolm Stanley Collection.

The tegmina illustrated in Figs. 46 and 47 are quite distinct from the remainder of the Protopsyllidiidae, the former on account of its wide costal space and short straight radius, the latter on account of its size, shape and general appearance. Fig. 47 is the tegmen of *Psocopsyllidium media*. In the specimen figured, R is convex, and there is a depression alongside this vein which has been indicated in the figure and labelled Sc. Whether it actually represents Sc is uncertain.

**Permopsylloides**, gen. nov.

The tegmen is of even width for its entire length. The costal space is wide, and  $R_{1a}$  meets the costal border slightly beyond its centre and Rs is curved towards the costa. The number of branches of M is unknown. The clavus is wide and long, and the anal veins form a Y-vein.

**Permopsylloides insolita**, sp. nov. (Genotype.) (Fig. 46.)

*Length of tegmen*, 4 mm.; greatest width, 1.5 mm. A poor impression.

*Holotype tegmen*—F 40727, found by Mr. Knight at Kimble's Hill, near Belmont.

Family **PINCOMBEIDAE**.

The genera *Pincombea* Till. and *Eupincombea* Davis have previously been placed in this family. The tegmen illustrated in Fig. 44 is herewith added because it resembles *Pincombea mirabilis* Till. in having M and  $Cu_1$  arising separately from the same point on R without a basal common stem. It is, however, doubtful whether adequate justification exists for the separation of this family from the Protopsyllidiidae.

**Protopincombea**, gen. nov.

The tegmen is broad and the clavus short and narrow. R is parallel with the costal margin and there are two cross-veins between Rs and M and one between M and  $Cu_1$ . M has three branches,  $M_1$ ,  $M_2$  and  $M_{3+4}$ . M and  $Cu_1$  arise from the same point on R, but lack a common stem. The anal veins form a Y-vein.

**Protopincombea obscura**, sp. nov. (Genotype.) (Fig. 44.)

*Length of tegmen* (fragment), 4.2 mm.; greatest width, 2 mm. As well as the tegmen, the thorax and abdomen of the holotype are preserved. Their total length is 3.5 mm., and that of the abdomen alone, 2 mm.

*Holotype tegmen*—F 40075, Malcolm Stanley Collection.

Attention is drawn to the resemblance which exists between the tegmen of *P. obscura* and the hind-wing of *Sojanoscytina* (?) *latipennis* Mart. (1933). It is suggested that the latter wing is actually a tegmen of an insect belonging to the Pincombeidae or Protopsyllidiidae, and not part of an Archescytinid as suggested by Martynov, even though Rs has two branches. Carpenter (1939) is also of the opinion that *Sojanoscytina* (?) *latipennis* is not an Archescytinid.

**Head-structure.**

In an earlier paper (Evans, 1943) the head-structure of two Upper Permian Homoptera was described and figured. One of these, *Permagra distincta* Ev., belonged to the Auchenorrhyncha. The other, *Permocephalus knighti*, which was originally placed in the Palaeorrhyncha, has, in an earlier section of this paper, been transferred to the Sternorrhyncha.

Five moderately well preserved heads occur in the present collection. These are illustrated in Figs. 48–52. A new genus and species are necessary for the head reproduced in Fig. 48; the remainder are considered as specimens of *P. knighti*.

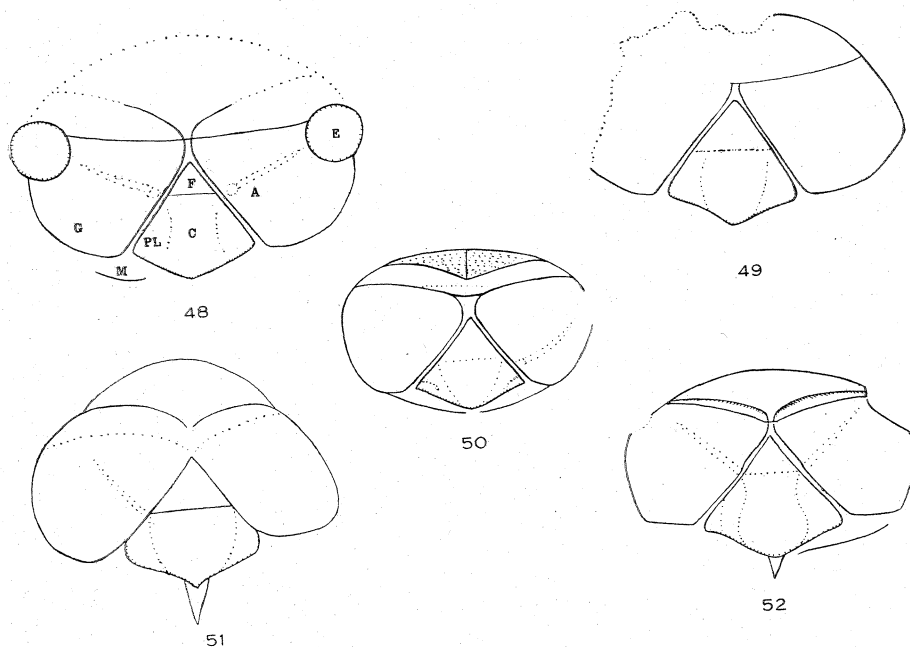
In Evans (1943) the statement was made that *P. knighti* lacked traces of clypeal sutures. By "clypeal sutures" is understood the sutures which separate the lora,

paraclypeal lobes or mandibular plates, from the clypeus proper. In all the heads now figured, faint indications of such sutures occur. They are indicated in the figures by dotted lines. A small triangular frons lies posterior to the clypeus in every specimen.

Ferris in a recent paper (1943) gives a figure (Fig. 1) of a generalized insect head which, in some respects, bears a striking resemblance to Fig. 48. The differences evident between the two heads would appear to be bridged by Ferris's diagram (Fig. 2D). If the interpretation given by Ferris is correct, the wide V-shaped suture towards the back of the head in Fig. 48 is the premandibular suture and the line joining the eyes a secondary ridge of no structural significance. The inverted V-suture is made up, according to Ferris, of the postfrontal + tentorial sutures, while the suture referred to in a former paragraph as the clypeal suture must together with the transverse epistomal suture make up Ferris's clypeo-frontal suture. It is, however, more probable that the paraclypeal lobes are part of the clypeus and that the clypeo-frontal suture is restricted to the transverse suture which lies between the antennal bases. Unfortunately, the fossils do not throw any light on the principal problem of the Homopterous head, and a satisfactory explanation is still needed to show how the paraclypeal lobes come to continue under the ante-clypeus and to form medially the ventral surface of the sucking-pump.

Ocelli are not preserved in the fossils, but a median ocellus, if present, would lie on the triangular frons, anterior to the post-frontal suture. Both Ferris and Cook (1943) are of the opinion that the inverted Y-suture of the heads of *Corydalid* larvae is the clypeo-frontal suture, although the corresponding suture in the heads of adult insects lies posterior to the median ocellus and anterior to the paired ocelli!

If the heads illustrated in Figs. 48-52 are compared with those of a recent Psyllid, correspondence will be found between the wide genae of the two types, which in neither instance are fused facially with the maxillary plates. The small triangular frons is lost in recent representatives, only the median ocellus remaining to indicate its position. The antennae in most, though not in all, recent Psyllids are long, and in all consist of ten segments. Upper Permian Psyllids had short antennae containing an unknown



Figs. 48-52.—48, *Permocapitus globulus*, holotype head, in facial aspect. F., frons; A., antenna; G., gena; C., clypeus; PL., paraclypeal lobe; M., maxillary plate (?). 49-52, *Permocephalus knighti*, head in facial aspect.



number of segments. Further, the position of the antennal bases has moved from close to the apices of the epistomal suture to the neighbourhood of the eyes.

**Permocapitus**, gen. nov.

The head is oval in shape, the eyes globular and the frons small. A transverse ridge lies between the eyes, and a suture (the premandibular suture?) separates a wide V-shaped area at the back of the head from the rest of the face.

**Permocapitus globulus**, sp. nov. (Genotype.) (Fig. 48.)

*Length* (of whole insect), 5 mm. *Width of head*, 1.2 mm. A complete median ovipositor is present in the abdomen. No trace of wings is retained in the holotype.

*Holotype*—F 40078, Malcolm Stanley Collection.

**Permocephalus knighti**. (Figs. 49–52.)

For convenience, the remaining heads are identified with this species. Particulars of the various specimens follow:

Fig. 49 (F 39967). *Width of head*, 1.4 mm. Part of the abdomen and legs are also preserved and a wing fragment. The latter suggests affinities with *Permotheëlla scytinopteroides*.

Fig. 50 (F 39944). *Width of head*, 1.2 mm. The posterior quarter of the head, divided medially by the coronal suture and shaded in the figure, is almost certainly part of the crown; the rest of the head consists of the face. No trace of wings is preserved.

Fig. 51 (F 40449). *Width of head*, 1.1 mm. Seven abdominal segments, having a total length of 2.2 mm., are also preserved, but no trace of wings. This specimen was found by Mr. Knight at Lake Macquarie.

Fig. 52 (F 33945). *Width of head*, 1.2 mm. *Length of whole insect*, 5.6 mm. The abdomen of this specimen is illustrated in Fig. 57.

**Fragments.**

A well preserved nymph and various fragments are illustrated in Figs. 53–59. With the exception of Fig. 58 (*Orthoscytina* sp.), none of the specimens is named, although the practice is often observed of naming even less complete specimens of fossil insects.

Fig. 53 (F 40448). *Length of whole insect* 9 mm.; *width*, at widest point, 4 mm. Part of the crown of the head and the pronotum and scutellum are well preserved. A coronal suture is discernible, and the lateral flanges on the pronotum suggest possible relationship with the Ipsviciidae. The proximal costal area of each tegmen is distinct, but no veins are visible. Found by Mr. Knight at Lake Macquarie.

Fig. 54 (F 40083). A splendidly preserved impression of a nymph, 1.5 mm. long and 0.8 mm. wide, which may well belong to the Protopsyllidiidae. It is remarkable to find such a minute insect so well preserved.

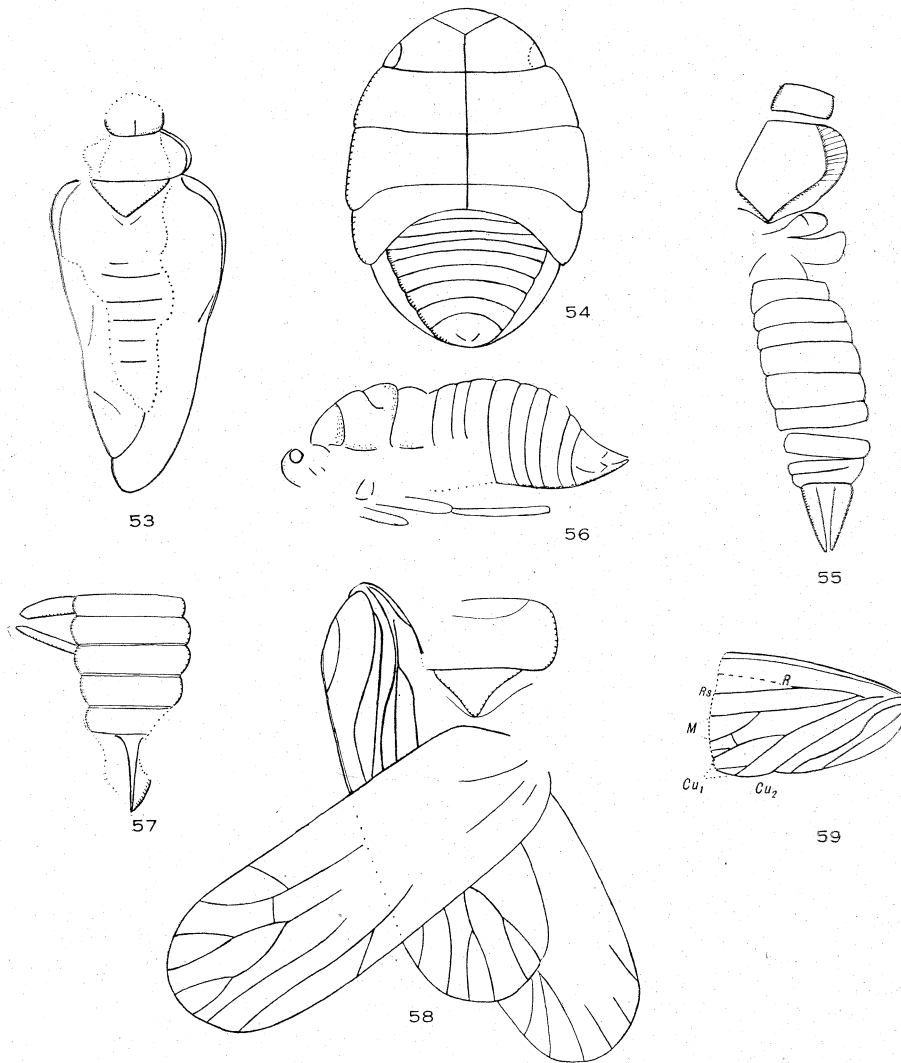
Fig. 55 (F 40077). *Length of specimen*, 6 mm. It is possible that the small rectangular pronotum is neither complete nor in position and the wide mesonotum may have been partially concealed by the pronotum. The affinities of this specimen are quite unknown.

Fig. 56 (F 39951). A good impression of a small Homopteron in lateral aspect. The process suggesting a labium is believed to be part of a leg, as reason exists for believing that the labia of Permian Sternorrhyncha were short. The genital segments, in outline, are reminiscent of those of recent female Psyllids.

Fig. 57 (F 39945). The head of this specimen is illustrated in Fig. 52. The figure of the abdomen is reproduced to illustrate the type of ovipositor possessed by Permian Sternorrhyncha.

Fig. 58 (F 39885). This is the first specimen of an *Orthoscytina* to be found with the clavus intact. The width of the hind margin of the pronotum is 3 mm. and the length of each tegmen 9 mm. The venation of only a small part of the hind-wing is distinguishable. Found by Mr. Knight at the Pincombe outcrop between Belmont and Warner's Bay.

Fig. 59 (F 39977). This interesting fragment may be part of the tegmen of an Archescytinid. The length of the fragment is 4.2 mm. and its greatest width 2 mm.



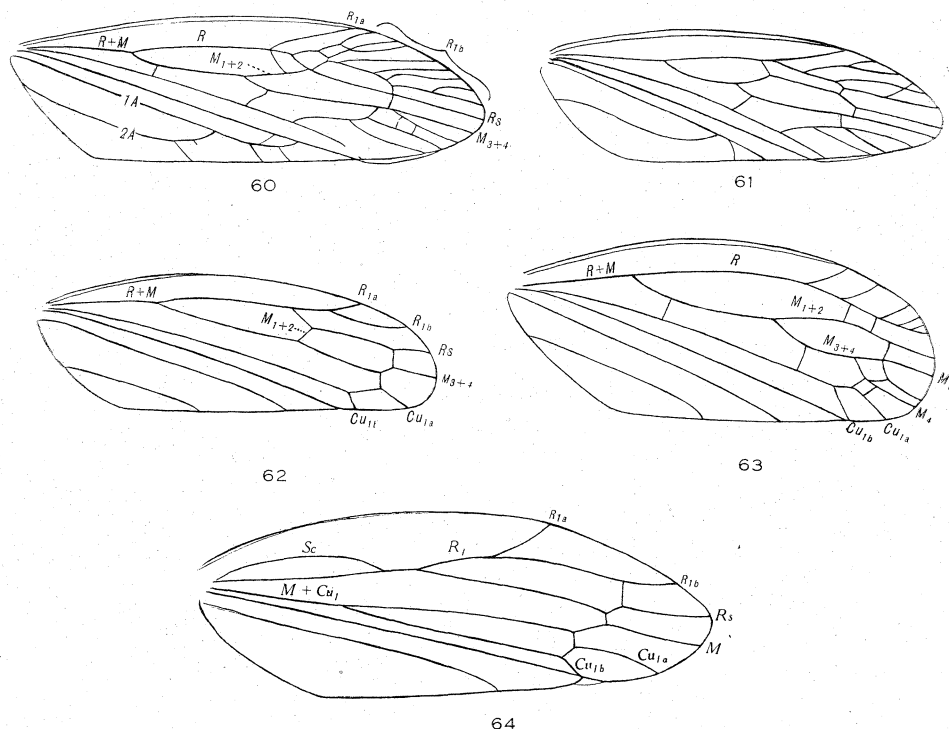
Figs. 53-59.—54, Nymph (Protopsyllidiidae). 58, *Orthoscytina* sp., part of thorax, tegmina and wing. 53, 55, 56, 57, 59, un-named fragments; for description see text.

#### Appendix.

The tegmina illustrated in Figs. 60-64 are those of four recent Jassoids and a recent Cercopid. They are presented here for three purposes. The first purpose is to give some idea of the wide variation in minor details of venation which may occur in recent insects belonging to a single species. The second is to show how, even within the same family or super-family, marked differences in major venational features may occur. The third is to give an example of how fossil wings may be used to assist in the interpretation of the venation of the wings of recent insects.

Figs. 60 and 61 represent the tegmina of a female and male respectively of *Stenocotis depressa* Walk. (Stenocotidae, Jassoidea). The two tegmina are drawn to the same scale, so that their difference in size as well as in venational details is evident.

Figs. 62 and 63 represent the tegmina of *Macroceps fasciatus* Sign. (Thymbridae, Jassoidea) and *Cornutipo scalpellum* Ev. (Eurymelidae, Jassoidea) respectively. Differences to note in comparing the four Jassooid tegmina are the presence of a Y-vein in the clavus of *Stenocotis* and the separate anal veins of *Macroceps* and *Cornutipo*. *Stenocotis* and *Macroceps* have Rs well developed; in *Cornutipo* R is unbranched. In *Stenocotis* and *Macroceps*,  $M_{1+2}$  is reduced to a cross-vein; in *Cornutipo* it is fully developed.



Figs. 60-64.—60, *Stenocotis depressa*, tegmen (female). 61, *S. depressa*, tegmen (male). 62, *Macroceps fasciatus*, tegmen. 63, *Cornutipo scalpellum*, tegmen. 64, *Philagra parva*, tegmen.

Metcalf (1913, 1917) has investigated the venation and preceding tracheation of the Jassoidea and Cercopidae. With regard to the former he has advanced the opinion that the two branches of the typical Jassooid radius represent  $R_{2+3}$  and  $R_{4+5}$ . The three branches of the Cercopid radius he considered as  $R_1$ ,  $R_{2+3}$  and  $R_{4+5}$ .

In an earlier paper (Evans, 1939) Metcalf's interpretation was followed, so far as the Jassoidea are concerned, although Tillyard (1926a) had previously drawn attention to the incorrectness of such an interpretation.

As a result of the study of the fossils contained in the present collection, Tillyard's interpretation is accepted, and in the figures of the four Jassooid tegmina and the Cercopid tegmen (Fig. 64, *Philagra parva* Don.) the veins have been labelled in accordance with this interpretation. Thus the hypothetical tegmen of the common ancestor of recent Jassoidea as presented in Evans (1939), Pl. v. fig. 2, becomes identical with Carpenter's (1933) reconstruction of the common ancestor of Lower Permian Homoptera.

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