

The Phylogeny of the Homoptera

By

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The question of the phylogeny of the Homoptera does not remain unsettled for want of discussion, as several authors have expressed most definite, though often contradictory, views on the subject. A few years ago a Bulletin entitled 'The Phylogeny of the Hemiptera based on the Study of the Head Capsule' was published in the United States (Spooner, 1938). This work is no mere short paper, but a considerable contribution of over one hundred pages, containing close on four hundred figures. For this reason, quite apart from its obvious worth as a contribution to the comparative morphology of insects, it merits close attention. It consists of two parts; the first part deals with the Homoptera and the second with the Heteroptera, and at the end of each part the conclusions reached by the author with respect to phylogeny are expressed as trees. As far as the Heteroptera are concerned, no comment is offered, but the present paper has been written to dispute certain conclusions reached by Spooner regarding the inter-relationships of the Homoptera, and to present alternative proposals.

In the phylogenetic tree for the Homoptera three main lines of descent are shown radiating from the Protohomopterous stem. Two of these give rise to the Fulgoridae and Peloridiidae respectively and the third to the Cercopidae, all the several other groups of Homoptera, apart from those mentioned above, then being derived direct from the Cercopidae. The separate derivation of the Fulgoridae and Peloridiidae from the Protohomopterous stem is not questioned, in fact an identical suggestion has been made previously (Evans, 1938). The points disputed are the derivation of the Sternorrhyncha from the Cercopidae and the dual origin claimed for the Jassoidea.

Crawford (1914) in his monumental work on the Psyllidae suggested that many characters borne by the group point to a close relationship with the higher Homoptera, especially the Cicadidae, Membracidae, and related families. At the same time he acknowledged that he was not prepared to make a definite pronouncement on relationships. Muir (1930) was of the opinion that the Psyllidae represent a specialization, considerably by reduction, of the Cicadoidea, and Myers (1929) believed that the relative simplicity of the Sternorrhyncha was a secondary specialization. Tillyard (1926), as a result of a study of the wing venation of Lower Permian Homoptera, suggested that the Sternorrhyncha were less primitive than the Auchenorrhyncha. Nevertheless, although there would seem to be fairly general agreement that the Sternorrhyncha, and the Psyllidae in particular, are derived from the Auchenorrhyncha, contrary views have been expressed. Thus Kirkaldy (1906) mentions that Ashmead, in a discussion of Osborn's paper on the phylogeny of the Homoptera (Osborn, 1895), put forward the suggestion that the Auchenorrhyncha were derived from the Sternorrhyncha.

Ideas on relationships based on the study of a single character are notoriously unreliable, but it is believed that, so far as the Homoptera are concerned, the structure of the head-capsule, correctly interpreted, offers a reasonable basis for phylogenetic conclusions.

If a comparison is made between the heads of an aphid, a psyllid, and a nymph of a peloridiid, it will at once be seen that they possess a striking characteristic in common. This is the separation of the head into two parts by the epistomal and subgenal sutures. There are other resemblances as well which can best be appreciated by reference to published figures. If first the head of a nymph of the peloridiid *Hemiodoecus fidelis* (illustrated in Evans, 1938, 1942; Snodgrass, 1938) is compared with the head of the psyllid *Paurocephala magnifrons* (Crawford, Pl. 3, fig. 16), the following points will be noted. Both have a distinct five-sided frons, from the posterior corners of which postgenal sutures arise, and both have a small distinct clypeus which is not separated into two parts by a transverse suture. Spooner gives a figure of the head of the psyllid *Pachypsylla celtidis-mamma* (Pl. 2, fig. 34) in which the clypeus is indicated as possessing two parts. This is because the genal cones have been labelled 'post-clypeus' and the actual complete clypeus 'ante-clypeus'.

The retention of a postgenal suture in the Psyllidae is of considerable interest. It extends from the lateral apices of the frons on each side in the direction of the eyes, and then from close to the eyes continues posteriorly, more or less at right angles to its former direction, as far as the hind margin of the head. On the crown it may either lie against the internal margins of the eyes or be slightly separated from them. The paired ocelli lie close to the apices of these sutures. Apart from in the Psyllidae and in the nymphs of the Peloridiidae, postgenal sutures do not occur in any other Homopterous types, although they are present in a few other groups of insects, such as the Dermaptera and Perlaria. In these, where lateral frontal sutures are absent, the true identity of postgenal sutures as such, has not been recognized and they have been referred to as 'postfrontal sutures' (Snodgrass, 1935). Such postfrontal sutures actually comprise combined epicranial and postgenal sutures (Evans, 1942).

If next the head of an aphid, such as *Lachnus* sp. (Spooner, Pl. 2, fig. 33), is compared with the head of *Hemiodoecus*, two noteworthy resemblances will be apparent. Both have complete small maxillary plates which are not attached in any way to the genae, and both have a clypeus without a transverse division, but with lateral lobes. These lobes are homologous with the lora of the Auchenorrhyncha.

The following characters of the Homopterous head are believed to be primitive: the complete separation of the clypeus from the frons; the complete separation of the maxillary plates from the genae; the possession of a clypeus lacking a median transverse division; the possession of a clypeus with lateral lobes which are separated from the median part of the clypeus by sutures that do not extend as far as the epistomal suture. The following are believed to be secondary developments: the partial or complete fusion of the frons with the clypeus and the enlargement of the clypeus at the expense of the frons; the fusion of the maxillary plates with the genae; the separation of the clypeus into two parts by a transverse division; the backward extension of the longitudinal clypeal sutures, their junction with the lateral frontal sutures, and the partial or complete obliteration of the epistomal suture.

Snodgrass (1938) has suggested that one of the characters claimed above as primitive is actually a secondary development. According to him, the lateral lobes of the clypeus are of hypopharyngeal origin and their connexion with the

post-clypeus a secondary union. In his opinion the obliteration of the clypeolateral sutures which occurs in the Peloridiidae, Aphididae, and certain Fulgoroidea is a progressive development from the condition which occurs in the majority of the Auchenorrhyncha, where separate loral plates are present. Whilst unable to offer an alternative explanation to account for the union of the lora with the hypopharynx, the hypothesis proposed by Snodgrass is not accepted. This is because of the supporting array of characters in the Peloridiidae, which are undoubtedly of a primitive nature.

In the cercopid head, not only are the maxillary plates fused with the genae, but no trace remains of the subgenal suture; the clypeus is divided into two parts and enormously enlarged posteriorly, and the epistomal suture, in those species where it may still be recognized, is so arched that the anterior tentorial pits lie close to the antennae. No trace of postgenal sutures remains, and, in the adult head, even the coronal suture is not distinct.

Thus it is clear that, on the basis of cephalic structure, whilst it might be justifiable to derive the Aphididae and the Psyllidae from the Protohomopteran stem close to the origin of the Peloridiidae and Fulgoroidea, no adequate reasons can be presented to explain a cercopid origin for the Sternorrhyncha. Carpenter (1932) has proposed the name Palaeorrhyncha for a division of the Homoptera that occurred in Permian times and which, with respect to wing venation, combined the main features of recent groups. It may well be that the Auchenorrhyncha and the Sternorrhyncha have both arisen from the Palaeorrhyncha. This suggestion obviates the necessity of attempting to derive either of the two principal present-day Homopteran divisions from the other.

In regard to the origin of the Jassoidea, Spooner has suggested that the group represented by *Oncometopia* Stål (Cicadellidae) may have been derived from the Cercopinae and all the several other jassoid families from the Aphrophorinae. Whilst not disputing that the suggestion is reasonable if head structure alone is considered, other characters lend it no support. For instance, in the hind-wings of insects in all jassoid families, with the exception of the Aethalionidae, the media has two branches ($M_1 + 2$ and $M_3 + 4$) although occasionally $M_3 + 4$ may be fused apically with $M_1 + 2$, also the first cubital vein is undivided. In both the Cercopinae and the Aphrophorinae the media terminates as a single vein, whilst Cu_1 has two branches, Cu_{1a} and Cu_{1b} . This common characteristic which the Cicadellidae share with other jassoid families is only one of several that could be chosen to stress the fact that, although the Jassoidea may well have arisen from the Cercopidae, they are a monophyletic group. Our present knowledge is insufficient to make definite pronouncements possible concerning other derivations presented in Spooner's phylogenetic tree. Nevertheless, though the Membracidae may have arisen direct from the Cercopidae as suggested in the tree, there is much to be said in favour of deriving them instead from the Jassoidea.

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