THE PHYLOGENY OF THE HOMOPTERA[1]

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The Hemiptera, which is the most isolated phylogenetically of all orders of insects, is the largest group of the Hemimetabola. The characters which distinguish the major taxonomic units are well-defined and, as far as the Homoptera are concerned, the fossil record, which extends from Lower Permian or even Carboniferous times, is remarkable. There are, furthermore, numerous relict Homoptera in existence which almost certainly have changed very little since Mesozoic times.

On account of these factors, it might be anticipated that there is a reasonably clear understanding of the nature of the inter-relationships existing between the various principal groups. This, however, is not yet the case partly from the very great antiquity of each group and partly because, though each has distinctive characteristics, a number of morphological features occur in different combinations among their various representatives.

Metcalf (42), in a consideration of the phylogeny of the Homoptera Auchenorrhyncha, was of the opinion that it was not sufficient to divide the Hemiptera into two suborders as is usually done, and proposed that each be regarded as an order of the superorder Hemipteriforma. On a descending scale, he then divided each order into suborders, phalanxes, cohors, subcohors, and superfamilies. While not denying that such a system has much to recommend it, it is proposed for the purposes of this review to regard each of the nine distinctive groups of the Homoptera as superfamilies, as follows: Peloridoidea, Aphidoidea, Aleurodoidea, Psylloidea, Coccoidea, Fulgoroidea, Cicadoidea, Cercopoidea, and Cicadelloidea. The Membracidae, which, in most works are given equal status with other divisions of the Auchenorrhyncha, are included in the Cicadelloidea and reasons for this will be explained later.

Recent works in which views based on comparative morphology have been expressed on the phylogeny of the Homoptera and summaries given of earlier opinions, include those of Kramer (41), Heslop-Harrison (38, 39), Bekker-Migdisova (5, 6), and Vondráček (54).

Some preliminary cytogenetic investigations have been made with a few Homoptera and phylogenetic deductions drawn, but these are of too restricted a nature to yield information which bears on phylogeny in its broader aspects (29, 30).

It would be confusing if conflicting views on homopterous phylogeny were to be discussed without first stating, in the space permitted, the salient characteristics of each group and defining some of the terms used. Therefore, an hypothesis will first be presented (see Fig. 1), and after it has been examined in the light of the available knowledge, the conclusions reached will be compared with those presented in other recent publications.

In order to interpret the features of any particular superfamily as defined in Figure 1, it is necessary to begin with those given for the Protohomoptera and then to make the amendments indicated in intervening circles. Thus, for example, if the Cercopoidea is selected it will be found that they have the following characteristics: Head C; two ocelli; a three-segmented tarsus; wings with "complete" venation, the hind wings being larger than the forewings and having an anal fan and a marginal vein; timbals in both sexes; male genitalia with both harpogones and subgenital plates and a filter chamber belonging to Type B.

It should be noted that some of the characteristics ascribed to the various superfamilies may not be of universal occurrence within the group; and furthermore, some may be known only from fossil representatives or from nymphal stages, or, be of an obsolete nature.

Thus, for instance, most fulgoroids have only two ocelli; but as some retain three, all are shown in the diagram as having the primitive number. Further, no Recent cercopoid has "complete" venation, although such a pattern of venation has been recorded from Palaeozoic and Mesozoic insects ascribed to this group (21, 24, 25). Finally, while timbals may not be of universal occurrence in both sexes within the Cercopoidea, Fulgoroidea, and Cicadelloidea, they have been recorded from some representatives of each group (46).

The base of the line connecting the three left-hand circles is shown leaving the one representing the Psylloidea at a tangent. This is intended to suggest that coccids, aphids, and aleurodids were derived from forms that had, at some time in their evolutionary history, acquired certain modifications which differed from those of their protohomopterous ancestors and resembled some of those now characteristic of the Psylloidea. It is not to be inferred, however, that psyllids as such were directly ancestral to the three other superfamilies, particularly as one of the characters listed in the psyllid circle, relating to the labium being associated with the prosternum, is not found in aleurodids or aphids, and only to a certain extent, in coccids.

DEFINITION OF TERMS

Head A.—The clypeus is not transversely differentiated into an ante- and post-clypeus, and the lora, or "mandibular plates," which are linked with the hypopharynx by a narrow bridge, are not separated posteriorly from the rest of the clypeus; prominent anterior tentorial pits are sometimes present and there is a complete tentorium, the anterior arms being
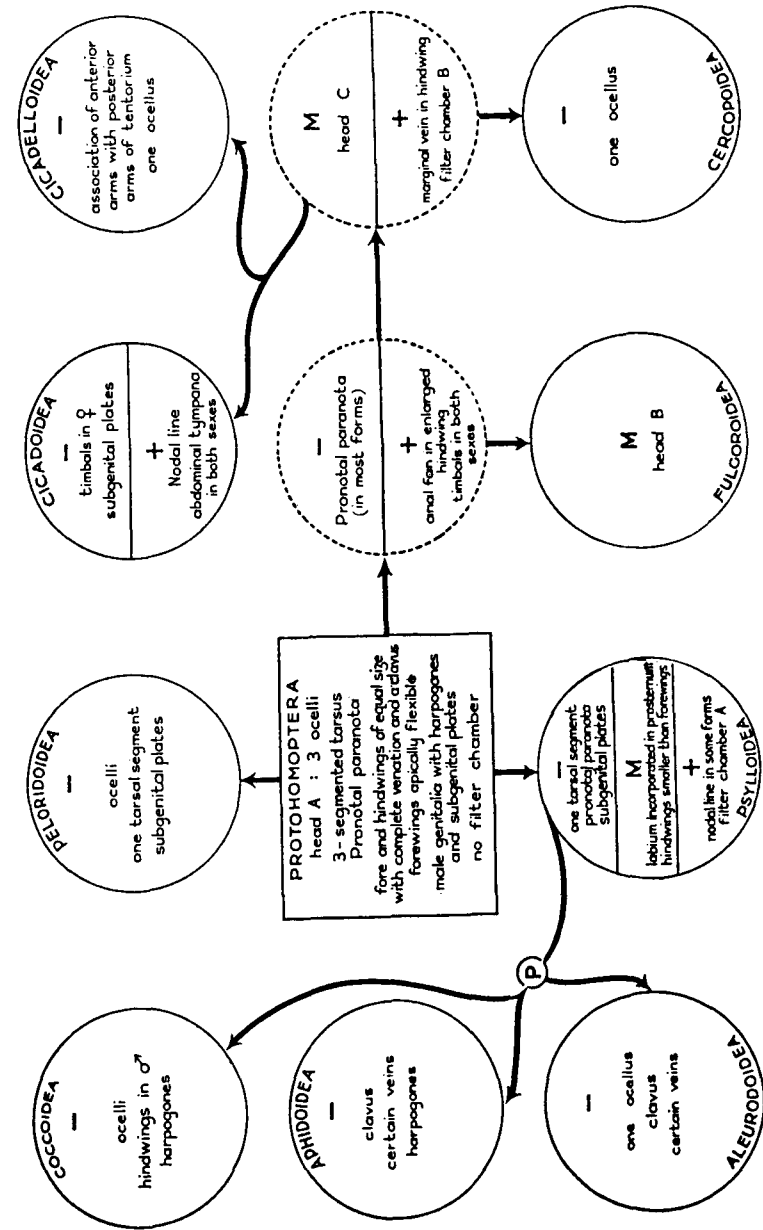

FIG. 1. Hypothetical phylogeny of the Homoptera. A minus symbol represents the loss, a plus symbol the acquirement of a characteristic, while M indicates a character modification and P, the occurrence of parthenogenesis. For simplicity, the number of characters listed has been kept to a minimum.

joined to the posterior tentorial bar. There is a clypeo-frontal sulcus in nymphal, even if not in adult stages, and the maxillary plates are not associated externally with the genae. The antennae may have a few or as many as ten segments, and are never setiform.

Head B.—The ante-clypeus is not separated from the post-clypeus by a complete transverse suture, and the lora, which are connected to the hypopharynx by a narrow bridge, are separated by longitudinal sutures from the rest of the clypeus. The post-clypeus is always distinct from the frontal region, a ridge marks the former clypeo-frontal sulcus and, in adult insects, the post-clypeus never extends posteriorly to the mid-antennal region.

The tentorium is usually complete and, while the maxillary plates are continuous with the genae, their junction is usually discernible. The stylets have single protractor and retractor muscles. The antennae, which are variable in shape and situated below the eyes, have an enlarged pedicel, with conspicuous sensory organs.

Head C.—The clypeus is usually separated into two parts by a transverse suture and a clypeo-frontal sulcus is usually lacking. If present (as in certain cicadelloids), it is, except in some nymphal stages, ill-defined. The lora are connected to the hypopharynx by a wide bridge; the tentorium, except in the Cicadelloidea, is complete and the antennae, which may have a few or as many as nine segments which are usually apically setiform, are situated between the eyes and are overhung by ledges. The maxillary plates are continuous with the genae although, particularly in a few cicadelloids, their junction may be discernible as a subgenal suture. The stylets have multiple protractor and retractor muscles (10, 41, 51).

Filter chamber.—It is assumed, as shown in Figure 1, that a filter chamber has been developed independently on at least two occasions. This is a reasonable assumption since Pesson has shown that the filter chamber of coccids (Type A) differs from that of cicadoids, cercopoids, and cicadelloids (Type B). These differences arise from the fact that in the Sternorrhyncha the Malpighian tubules are not associated (Type A) with the filter chamber as they are (Type B) in the Auchenorrhyncha (48).

The nodal line.—For the discussion of the Cicadoidea and Cicadelloidea, it is necessary to mention the nodal line, or furrow, and to define the use of the term in Figure 1.

In general, a nodal line is understood to be a transverse line of weakness, associated with the mechanics of flight, which occurs in the forewings of many Hemiptera. Because of its presence in most Heteroptera, and in representatives of both the Auchenorrhyncha and the Sternorrhyncha among the Homoptera, it must, presumably, have been a characteristic of some Protohemiptera.

In a family of Permian Homoptera, the Prosbolidae; in the living Mesozoic relicts, *Tettigarcta* spp., and in nearly all cicadids, such a transverse

line of weakness is accompanied by the splitting of the veins and their proximal thickening at those points where they are crossed by the nodal line. This specialised condition of the forewings, which enables them to be apically flexed in a downward direction, is the one referred to in the two places where a "nodal line" is mentioned in Figure 1.

Formerly, a nodal line has been reported as occurring also in the forewings of some of the representatives of a family of cicadelloids, the Hylicidae (17). It is believed that while the condition in these particular insects is homologous with that found in various Hemiptera, it should not be regarded as being strictly comparable with the nodal line of cicadoids. Heslop-Harrison, who has suggested that a nodal line may formerly have been associated with wing-shedding, has recorded its presence in certain psyllids (37).

Protohomoptera

No certain information is available concerning the characteristics of the earliest representatives of the Homoptera, hence, to attempt to describe them would be pure speculation. All of those features which are ascribed to the Protohomoptera in this study are ones which are known to have been possessed by representatives of the order at some stage in their evolutionary development, and they are all features from which the characteristics of every present-day group could have been derived.

The earliest Homoptera, very possibly, had reticulate venation, and Bekker-Migdisova ascribes to the Homoptera the wings of two Carboniferous insects which had such a pattern of venation (*Protoprosbole straeleni* Laurentiaux and *Blattoprosbole tomiensis* Bekker-Migdisova) (6). Heslop-Harrison, likewise, regards a Carboniferous forewing as belonging to this order (*Dictyocicada antiqua* Brongniart) (38). There is, however, no certainty in regard to the ordinal position of the wings of any of these three insects.

In every superfamily of the Auchenorrhyncha there are some insects which have reticulate venation, but there is reason to suppose that this always represents a secondary condition, even in those families of the Fulgoroidea in which it is of usual, though not of universal occurrence. Accordingly, the term "complete venation" as ascribed to the Protohomoptera in Figure 1 does not refer to a hypothetical pattern of full venation in which R_s had four branches, and M and Cu each had four anterior and four posterior ones, but rather to the actual pattern of generalised venation which is known to have occurred in some Lower and Upper Permian archescytinids and in Upper Permian scytinopterids and prosbolids. This pattern is to be found also in certain present-day cicadoids (e.g., *Tettigarcta* spp.) (21), and from it can be derived nearly all other types of homopterous venation. It consists of the following veins; *Sc.*, which may be distinct, or incorporated in the costal margin; R_{1a}, R_{1b}, Rs, M_1, M_2, M_3, M_4, Cu_{1a}, Cu_{1b}, Cu_2, and, in the clavus *1A* and *2A*. Whether

or not M consists of MP (posterior branch of M) as suggested by Fennah (26), or the anterior branches represent MA_{1+2} and MA_{3+4} and the posterior ones MP_{1+2} and MP_{3+4} as suggested by Heslop-Harrison (36), is immaterial for the purposes of the present discussion, as is the question of whether the cubital veins represent CuA and CuP.

It is assumed that the Protohomoptera had three tarsal segments since some Lower-Permian Archescytinidae, as recorded by Carpenter, are known to have had this number (7). Archescytinids also had fore and hind wings of similar size and shape.

The brief notes on each superfamily which follow will serve to supplement the information provided in Figure 1. At the same time, and in order to provide an indication of the known or assumed age of each, mention will be made of some of the earliest fossils. Unfortunately, space does not permit consideration of the interrelationships with Recent groups of the greater number of extinct families of Homoptera.

COLEORRHYNCHA

Peloridoidea.—Peloridiids are small, slow-moving, cryptically coloured and dorsoventrally flattened insects which range in length between 2 and 5 mm. To the present time, nineteen species comprising nine genera, all of which live in the Southern Hemisphere, have been described (9, 23). They feed on moss growing in humid places (34). The morphology of the head (10), thorax (11), and internal anatomy (47) have been investigated.

Because of their restriction to a terrestrial environment of a specialised nature, it is improbable that peloridiids, as they are known today, could ever have become preserved as fossils.

Bekker-Migdisova, nevertheless, has described some insects from Triassic strata in Central Asia which she has placed in a family, the Cicadocoridae, which she ascribes to the Coleorrhyncha (a homopterous series which otherwise comprises only the family, Peloridiidae). She has also assigned to the same family some other fossils which had been placed by Handlirsch in the family, Procercopidae (3). An examination of the illustrations of the forewings of *Cicadocoris kuliki* Bekker-Migdisova and *Olgamartynovia truncata* Bekker-Migdisova, the two new species placed in the Cicadocoridae, lends no support to the suggestion that they had any close affinity with the Peloridoidea. Very possibly, they were Heteroptera and related to, even if not identical with, a group, the Actinoscytinidae, which has been recorded from the Upper Triassic of Australia (21).

In spite of the lack of fossil evidence, it is, however, believed that the Peloridoidea are Palaeozoic relicts which, though highly specialised in certain respects, nevertheless, retain several primitive characteristics.

AUCHENORRHYNCHA

Hypothetical stages.—In Figure 1, there are two circles which represent hypothetical stages in homopterous evolution. It is well known that in

many groups of organisms differential evolution occurs so that in the several representatives of a particular group there may be some in which certain structural feaures are at a more, and others at a less, advanced stage of evolutionary development than is the norm for the group as a whole.

For example, as already mentioned, while most fulgoroids have only two ocelli, certain cixiids have three; most cercopoids have veins M and Cu_1 in the tegmen fused together proximally, although in some these veins retain their separate identity for the whole of their length (e.g., *Cosmocarta* spp.); most cicadelloids lack pronotal paranota homologous with wings, though in a few they are retained (Myerslopiini); in most cicadas, vein Sc is incorporated in the costal margin of the forewing, but in some (e.g., *Yanga* spp.) it retains its separate identity. It is to be expected that a similar state of affairs will have occurred in former geological periods, hence it cannot be anticipated that fossils will ever be found having a combination of all the features noted in either of the two middle right-hand circles.

Bekker-Migdisova has illustrated the head of a Permian homopteron, *Scytoneura elliptica* Martynova, which she regards as combining certain of the characteristics of the Sternorrhyncha, Coleorrhyncha, and Auchenorrhyncha (5). She has ascribed this insect to the Cicadopsyllidae, Cicadopsyllidea, Psyllaria. (However, as *S. elliptica*, as indicated in a figure of a reconstruction, had a three-segmented tarsus and the venation of the forewing was similar to that of the Scytinopteridae), it was doubtfully a psyllid and it could well have been an insect in the stage of evolution indicated in the circle immediately to the right of the Protohomoptera. The acquirement of enlarged hind wings with and without a marginal vein, and of heads at evolutionary stage C are developments which are known to have taken place during the Permian period.

Fulgoroidea.—Muir has given a key to the 18 families of Fulgoroidea, which were recognised in 1930 (45). Since then, two additional ones have been described, the Gengidae, known only from South Africa (28), and the Hypochthonellidae (8). Metcalf separated his phalanx Fulgorina into two cohors, the Fulgorida and Flatida, each comprising various subcohors and superfamilies (42).

A tegula is present on the mesothorax, the pronotum is usually narrow, a pleural wing groove is lacking and the middle coxae are widely separated. The anal veins always form a Y-vein, although this is not a characteristic confined to the Fulgoroidea. Fennah has given an interpretation of fulgoroid venation which differs from that of many other authors (26). Heslop-Harrison, however, has suggested that the venation of this group is basically identical with that of other representatives of the older (37).

A nodal line, which is comparable to, though not identical with that of cicadas, is sometimes developed in the Fulgoroidea; the distal part of the

tegmen is thinner and more flexible than the basal area in representatives of several families, and in some genera the membrane is hinged to the corium, along a line from the junction of C and Sc to the apex of the clavus where Cu meets the commissural margin (26).

Many fossil impressions have been ascribed to this superfamily on the basis of wing venation as well as head structure, but several of these probably have other relationships. Among undoubted Mesozoic fossil fulgoroids are *Boreocixius sibiricus* Bekker-Migdisova from the Permo-Triassic of Siberia (2), and numerous ones have been described from Jurassic strata by Handlirsch (32).

Cercopoidea.—Some authors regard the Cercopoidea as comprising four families [e.g., Metcalf (42)], but only three are recognised here. These are the Cercopidae, Aphrophoridae, and Machaerotidae. The two former are of world-wide distribution, although most richly represented in the tropics. The Machaerotidae are confined to the Oriental Region, tropical Africa, and Australia.

The nymphs of the Cercopidae and Aphrophoridae live surrounded by "spittle" of their own making. Those of the Machaerotidae live in calcareous tubes on their food plants. These tubes are formed from excretory products and the insects live immersed in their liquid excretions (12). Both froth production and tube-living habits are adaptations preventing desiccation and suggest that cercopoids at one time lived under atmospheric conditions of high humidity.

The hind coxae are short, conical, and not laterally dilated as in the Cicadelloidea, the meron articulates with the epimeron, and the hind tibiae are cylindrical with one or two strong spurs. The scutellum may be enlarged and extended posteriorly to form a spine-like process.

There have been differences of opinion in regard to the recognition of fossil wings as belonging to insects ascribed to this superfamily. Hence, it is necessary to discuss certain venational features. The forewing of *Trifidella perfecta* Evans from the Upper Triassic of Queensland seems to be that of a cercopoid and it resembles the forewing of a Recent species. *Aufidus tripars* Walker in several features (21, 25). Thus, in both wings Sc is short, R is multi-branched, and M and Cu proximally form a single vein. The two arms of Cu_1 have a very characteristic shape, Cu_{1a} being curved and Cu_{1b} straight and almost in alignment with the undivided portion of Cu_1. If the forewing of *T. perfecta* is compared with that of the forewing of *Belmontocarta perfecta* Evans, an insect from the Upper Permian of New South Wales (24), it will be appreciated that the latter insect is almost certainly also a cercopoid, even though the family Eoscarterellidae, to which it has been ascribed, is regarded by Bekker-Migdisova to be of uncertain position (5). The only significant features in which it differs from *T. perfecta* are that the four branches of M are not reduced as they are in the Triassic wing, and in having Cu_1 proximally separate

from M. Both wings are rugose, both have a multi-branched R_1 and both have a similarly shaped Cu_{1a} and Cu_{1b}.

Cicadelloidea.—Leafhoppers may be grouped into seven families as follows: Aetalionidae, Biturritidae, Nicomiidae, Membracidae, Hylicidae, Cicadellidae, and Eurymelidae (16, 18). All of these families except the Membracidae, Cicadellidae, and Eurymelidae are relict groups. The reasons for the belief that the Membracidae do not merit special segregation but are best included within the Cicadelloidea, are as follows: in the heads of both cicadellids and membracids, as in all representatives of the Cicadelloidea, the anterior arms of the tentorium lack association with the posterior arms. The prothorax of all membracids is enlarged as it is in certain cicadellids which resemble membracids also in general head shape. In the basic pattern of the venation of the forewings of cicadellids, M and R form a single vein proximally, while in most membracids M and Cu_1 are basally incorporated in a single vein. However, in some membracids, R, M, and Cu_1 are all separate proximally, while in some leafhoppers in the family Biturritidae, which, by many authors, are included within the Membracidae, R and M are basally joined. Fennah (27) has shown how the pretarsal structure of membracids and cicadellids is identical yet differs from those of cercopids and cicadas. Cicadellids have been supposed to differ from membracids in lacking a filter chamber; but this feature is common to both groups. The nymphs of membracids are ant-attended, as are those of a few species of cicadellids and all of the representatives of another family of the Cicadelloidea, the Eurymelidae.

Very numerous Palaeozoic and Mesozoic fossils have been ascribed, probably correctly, to the Cicadelloidea. While the greater number belong to extinct families, some have been ascribed to families and even sub-families and tribes of Recent Cicadelloidea. Thus, Bekker-Migdisova (3) has described some wings from the Upper Triassic of Central Asia which she has ascribed, not only to the Membracidae, but also to particular sub-families which almost certainly were not differentiated until the isolation of the Neotropical Region during the Tertiary. It is probable that these wings are not those of membracids but that they belonged rather to the Heteroptera.

While no undoubted membracids have been recorded as Pre-Tertiary fossils, several wings have been described which may, with confidence, be ascribed to the Cicadellidae. These include *Mesojassoides gigantea* Oman from the Cretaceous of Colorado, and *Eurymelidium australe* Tillyard from the Upper Triassic of Queensland (21). A wing of a possible eurymelid has also been described from the same strata.

The Cicadelloidea differ in an important respect from the rest of the Homoptera since they are less stereotyped, both structurally and biologically, and include a greater range of evolutionary stages occurring in various combinations.

Whereas, the head structure of any aphid, fulgorid, cicada, and cercopid is basically identical with that of every other aphid, fulgorid, cicada, and cercopid this is not the case for the Cicadelloidea. Such features in which they may differ from their relatives in the same superfamily, are almost entirely associated with secondary loss, as of an ocellus, or of secondary change in superficial shape, as happens, for instance, in the vertex of some fulgoroids and cercopids. A similar comparison, if made for wing venation or even tibial armature, would give the same result. One explanation of this state of affairs could be that the Cicadelloidea, unlike the other groups, are polyphyletic. Another, and more probable one, is that they include a number of forms which have become stabilised at different evolutionary levels.

It has previously been shown how, in wing venational characteristics, all of the existing families of the Cicadelloidea could have been derived from a Permian form, such as *Homaloscytina plana* Tillyard (16) and that certain Cicadelloidea retain pronotal paranota (22). It has also been suggested that the apical process of the aetalionid, *Darthula hardwickii* Gray might be homologous with one recorded from a Lower Permian archescytinid, *Permoscytina kansasensis* Tillyard (17).

The retention of these and of several other archaic features, particularly in relation to head structure, in representatives of a single superfamily, might seem to suggest that perhaps the Cicadelloidea could have been ancestral to the rest of the Auchenorrhyncha. This, however, cannot have been the case because of their lack of certain features, such as a median ocellus, which have been retained in representatives of other superfamilies.

Cicadoidea.—Metcalf has separated this superfamily into the families Cicadidae with 136 genera and the Tibicinidae with 139 (42). It is suggested that a preferable arrangement is to recognise the family Tettigarctidae (1, 22) with one living and several extinct genera and the family Cicadidae. The morphology of *Tettigarcta* has been investigated (13, 50).

Cicadas are remarkable for their anomalous life cycle, the greater part of which is passed underground, and for the adaptive features associated with a subterranean existence. Although, today, they are essentially associated with warm temperate and tropical climates, it is possible that their larval habits originated in response to cold climatic conditions.

Formerly, it was suggested that *Tettigarcta* followed a different line of descent from other cicadas (21), but Heslop-Harrison has correctly queried this opinion (39). In Figure 1, the Cicadoidea are shown as having harpogones in the male genitalia and as lacking timbals in the female sex. Harpogones, however, are retained only in the Tettigarctidae, which also have timbals, though no tympana, in both sexes (13).

Fossil Cicadoidea, other than the Prosbolidae, and those described from the Tertiary strata, are comprised of three families, the Tettigarctidae,

Palaeontinidae,[3] and Mesogereonidae (1, 21, 22). Australian representatives of the Palaeontinidae have been recorded from the Middle Triassic strata and of the Mesogereonidae from the Upper Triassic. In the Northern Hemisphere, wings of insects belonging to these families have been recorded from Mesozoic rocks of later date.

The most distinctive feature of the forewings of tettigarctids and palaeontinids is the presence of a well-defined nodal line. This is absent in the the forewings of the Mesogereonidae, doubtless due to secondary loss associated with their greater elongation.

STERNORRHYNCHA

Psylloidea.—The following families are recognised: Aphalaridae, Lividae, Psyllidae, Triozidae, Carsidaridae, Pauropsyllidae, and Ceriacremidae (35, 54).

In its most complete expression, the venation of the forewings of psyllids consists of R_{1a}, R_{1b}, Rs, M_{1+2}, M_{3+4}, Cu_{1a}, Cu_{1b}, $1A$, and $2A$. Veins R and M are always proximally incorporated together in a single vein and M and Cu_1 also proximally consist of a single vein. A pterostigma may be developed between R_{1a} and R_{1b}.

In spite of their small size, psyllids are known as abundant fossils from the Upper Permian strata onward. The principal feature in which the fossil wings differ from those of present-day species is that in the former, M has sometimes more than two apical branches.

Heslop-Harrison has suggested that *Austroprosbole maculata* Evans, from the Upper Permian of New South Wales, which had a forewing 13 mm in length, may have been a psyllid (37). If this is a correct interpretation, it means that some Palaeozoic psyllids were considerably larger than Recent ones which have, in general, like their Permian and Triassic forerunners, a wing length of no more than 5 mm.

Aleurodoidea.—Aleurodids, which are very small insects ranging in size between one and three millimetres, are highly specialised both biologically and structurally. The venation of their forewings is very considerably reduced, and in its most complete state only R_1, Rs, M, Cu_1, and $1A$ are represented. There is no fully developed clavus, and the wings are not coupled in flight.

[3] The family Palaeontinidae derives its name from *Palaeontina* Butler. An examination of illustrations of *P. oolitica* Butler, as figured by Handlirsch (31), suggested that the wings were not those of Homoptera. The substitution of the family name Cicadomorphidae was therefore proposed to comprise those Mesozoic Homoptera which were formerly known as the Palaeontinidae (21). However, as it seems probable that the drawings were made from badly preserved specimens which might actually have been Homoptera, it seems preferable to retain the family name Palaeontinidae.

Because of their size and fragility, it would not be anticipated that adult aleurodids would have been preserved as fossils, still less, their larvae. Nevertheless, Bekker-Migdisova has described a larval form from the Upper Permian of the Kuznetsk Basin which she has attributed to this group and named *Permaleurodes rotundatum* Bekker-Migdisova (4). It is a flattened oval insect, 2.5 mm long, with developing wing pads on the meso- and meta-thorax. Possibly, the placing of this insect in the Aleurodoidea is correct, but this must remain uncertain. It differs from a small homopterous nymph recorded from the Upper Permian of New South Wales, in having the head and prothorax incorporated in a single sclerite (15).

Aphidoidea.—All of the very numerous species of aphids exhibit various degrees of polymorphism. There are four families, the Aphididae, Eriosomatidae, Phylloxeridae, and Adelgidae. The female genitalia are usually reduced but in the Phylloxeridae and Adelgidae a true basic ovipositor seems to have been retained (49).

In Figure 1, the Aphidoidea are shown as having a filter chamber, although its occurrence is restricted almost exclusively to one subfamily, the Lachninae (49). Mordwilko has suggested that aphids "originated in a moderate climate" (43). This view is based on the fact that the greatest diversity of forms is found in temperate climates, and adaptations to life in the tropics seem to be of a secondary nature.

Bekker-Migdisova has described some insects from the Permian of Archangelsk and the Kuznetsk Basin which she has placed in the Aphidaria, Family Permaphidopseidae (4, 5). Among these, the species which would seem to resemble Recent aphids most closely in wing shape and in venation is *Permaphidopsis sojanensis* Bekker-Migdisova. The only details in which this wing, which is 5.9 mm long, differ from those possessed by Recent aphids are in the more proximal separation of Rs from R, the less thickened $Sc + R$, the presence of an additional vein in the anal area, and the greater proximal width. A wing, from *Triassoaphis cubitus* Evans found in the Upper Triassic strata of Queensland, resembles Recent aphids even more (21).

Coccoidea.—Female coccids which are neotenic, are much better known than the males, but because of their varying degrees of specialisation as characterised by their loss of structural features, can provide very little information on phylogeny. While most coccids have only a single tarsal segment, all species in the subfamily Xylococcinae (Margarodidae) have two (44).

Theron, who has studied the morphology of male coccids, states that the male genitalia consist of a simple tubular, heavily sclerotized organ, not unlike those of aleurodids (52).

It would seem that the only pre-Cretaceous fossil to have been ascribed to this superfamily is *Mesococcus asiatica* Bekker-Migdisova from the Per-

mian period of Central Asia. This is an oval insect with the appearance of a mealybug (4).

Mention should be made of the Permian family Coleoscytidae which, until the present time, has been recorded only from the Northern Hemisphere. Formerly, I have regarded it as being related to the Scytinopteridae (21), but Bekker-Migdisova, with good reason, ascribes it to the Sternorrhyncha (5).

DISCUSSION

Spooner, on the basis of comparative studies of the head capsule, recognized the distinctiveness of the Fulgoroidea but derived all other Homoptera, apart from the Peloridiidae, from the Cercopidae (51). In commenting on these views I suggested that while it might be possible, on the basis of cephalic structure, to derive the Aphididae and Psyllidae from the protohomopterous stem close to the origin of the Peloridiidae and Fulgoroidea, there were no reasons to suggest that the Sternorrhyncha could have had a cercopoid origin (14).

Subsequently, three primary divisions for the Auchenorrhyncha were proposed, one to comprise fulgoroids, another cicadoids, and a third division for cercopoids and cicadelloids (16). Later, cicadids, cercopids, and cicadellids were grouped together in a single series distinct from fulgoroids (20).

Heslop-Harrison, whose paper is illustrated by a hypothetical phylogenetic tree, has stated that although all of the major groups of higher Homoptera, or approximations of them, appear to have had representation in the latter part of the Permian, it might be difficult to place their evolution in its proper sequence. Furthermore, that while the stages between the Fulgoridomorpha and the Cicadomorpha and Jassidomorpha are obscure, clear lines of affinity lie between the Cicadidomorpha and the Jassidomorpha by way of the Cercopidae, and that the latter include many forms which are venationally transitional between the two extremes. He has suggested also, that perhaps an even more primitive cercopoid type might have existed at one time which linked the two major natural groups, the Cicadidomorpha and the Jassidomorpha, through a common ancestral plexus and that from this the Fulgoridomorpha could also have been derived. He added that while venationally there were no difficulties in visualising the form of such an ancestral type, it would also need, among other things, a simple gut (38).

The position of the Cercopoidea in relation to other groups of Homoptera presents a special and difficult problem. Cicadas cannot possibly be related to leafhoppers by way of cercopoids as both the two former groups retain different combinations of primitive characteristics which are absent from the Cercopoidea. However, both could have been evolved from a common ancestral plexus, as suggested by Heslop-Harrison and as represented in Figure 1 by the central right-hand circle. Nevertheless, the Fulgoroidea must presumably have become differentiated as such before the

Procercopoidea and hence could not have been derived from a "primitive cercopoid type."

Heslop-Harrison has stated that the Prosbolidae should be regarded as belonging to the Cicadidoidea (39), and Bekker-Migdisova has suggested that the Permian Scytinopteridae, in particular the subfamily Ingruinae may have been ancestral to the Cicadelloidea (5). It seems improbable that the Ingruinae could have lain on a direct line of descent of any Recent cicadelloids, since they were already highly specialised in certain respects, for example, in having a Y-vein in the clavus; it is preferable in any case to regard the Scytinopteridae as belonging to the Cicadelloidea rather than as having been ancestral to them.

Bekker-Migdisova has also suggested that the Biturritidae, a Recent family of the Cicadelloidea, may be relict scytinopterids and, while this is a possibility, they would not seem to belong in this category to any greater extent than, for example, either the Aetalionidae or the Ulopinae (Cicadellidae).

In the same work, Bekker-Migdisova gives a table in which the several extinct and existing families of the Homoptera are listed in relation to geological periods. In referring to this, it must be remembered that interpretations of relationships between fossil and living forms differ appreciably. For instance, as has already been mentioned, opinions differ as to whether the Membracidae were, as shown in the table, in existence during the Triassic, and as to whether or not any Cercopoidea have been recorded from the Palaeozoic strata. The Prosbolidae, in this table, are shown as being represented in the Carboniferous but in the accompanying text it is mentioned that the only known Carboniferous prosbolid belongs to the genus *Archeglyphis* Martynov. It has previously been suggested that the wing of *Archeglyphis crassinervis* Martynov may be that of an archescytinid, and that very possibly it is not that of a homopteron at all (21).

If the Prosbolidae are regarded as belonging to the Cicadoidea, and the Scytinopteridae to the Cicadelloidea, then the differentiation of these two superfamilies will have taken place no later than Permian times and both the Cercopoidea and Fulgoroidea will have had an even earlier origin.

In Heslop-Harrison's opinion, as both psyllids and coccids possess complicated filter chambers, their affinities lie with the main cicadoid-jassoid stem, while the absence of a filter chamber in aleurodids and aphids brings them nearer to the main fulgoroid stem. He has further stated that venationally aphids can be traced directly to archescytinids (38).

Some aphids and aleurodids have been recorded as having simple filter chambers (49), hence there is no good argument for associating psyllids and coccids closely together for the reasons given above. Several authors have sought to derive the Aphidoidea directly from the Archescytinidae and, as presumably the latter family had many features in common with

the "Protohomoptera," the hypothetical line of descent presented in Figure 1 does not necessarily conflict with this assumption.

In later works, Heslop-Harrison has mentioned that psyllids produce sound by means of a complicated apparatus, the structure of which precludes the possibility of their ever having had cicada-type timbals (39, 40). At the same time, he has suggested that psylloids must, at some time in the past, have converged on the cicadoid-prosboloid ancestral stem, and at a time which is more recent than the ultimate convergence of the latter with a joint aphidoid-fulgoroid stem, "which may or may not have involved the ancestors of the archescytinids."

While the above suggestions are in general agreement with Figure 1, it is doubtful whether there are any special characteristics which link closely together aphids and fulgoroids.

Bekker-Migdisova (5) supports Haupt (33) in uniting the Psyllina and Aleuridina into the Psylloidea, and considers that the wings of Permian insects, which she ascribes to the family Permapheidopseidae, furnish a link between Recent aphids on the one hand and small Permian archescytinids on the other. The arrangement in Figure 1, in which the Psylloidea and Aleurodoidea are shown in adjacent circles, is in agreement with the first part of the above suggestion, while the position of the psyllid circle in respect to the rest of the Sternorrhyncha is in agreement with the views of Vondráček (54).

Thus, it is apparent that the differentiation of the Sternorrhyncha into existing superfamilies took place also during the Permian period at the latest.

Origin of the Heteroptera

Although this topic does not properly lie within the scope of this review, it is of such considerable interest as to merit brief mention. Several presumed Palaeozoic Heteroptera have been described. A suggestion that one of these, *Paraknighta magnifica* Evans (15, 19), is a representative of the Heteroptera has been supported by Heslop-Harrison (38). On the other hand, a suggestion that the wing of an insect which was thought by Tillyard, in a letter to "Nature" (53), to be that of a "specialised scytinopterid in process of becoming a true Heteropterous type" is, in fact, that of a cercopoid, has been queried by Bekker-Migdisova, who named the insect to which the wing belonged, *Prosbolopsites tillyardi* (5). This name is a synonym of *Eoscarterella media* Evans (25). Bekker-Migdisova, who supports Tillyard in his opinion that the wing of *E. media* represents a transitional form between the two suborders, states that she is uncertain whether it should be placed in the Coleorrhyncha or should be regarded as a representative of the Heteroptera. As has been previously stated, while it may be assumed that early Heteroptera had a venational pattern similar to early

Homoptera although they will have differed in other respects, such wings as show increased apical overlap cannot necessarily be interpreted as indicating that their bearers were "becoming Heteroptera" (21).

A suggestion made by the present author that the Homoptera and Heteroptera were derived from a common ancestral stock prior to the commencement of the Permian (19), has been supported by Heslop-Harrison (36).

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