A NATURAL CLASSIFICATION OF LEAF-HOPPERS (JASSOIDEA, HOMOPTERA)

PART 1.
EXTERNAL MORPHOLOGY AND SYSTEMATIC POSITION.

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SINCE the time when attention was first paid to insects as plant pests, the injurious nature of the feeding activities of leaf-hoppers has been well known. It is only of recent years, however, that full realisation has been possible of the true importance of these insects. This is because it is now known that in addition to causing direct injury to growing plants by the removal of their sap, many species are also vectors of virus diseases of plants.

As well as being an important group of insects from the economic aspect, leaf-hoppers can claim attention for other reasons. One such reason is their age, and it is probable that they have changed but little since late Palaeozoic times.

Their classification presents great difficulties, largely because they are, on the whole, a homogeneous group and lack well-defined characters in many of the middle categories.

Several systems of classification have been proposed at different times, notably those of Baker (1923) and Haupt (1929), but none has secured general acceptance. My views on the classification of leaf-hoppers (Evans, 1939b; 1941c) differ widely from those of other workers and as at present it seems probable that my task in the future will be to describe a large amount of new material, it may prove helpful to those who follow if I present a full account of them.

Leaf-hoppers, although an old group of insects, which retain certain primitive characteristics lost in other Orders, are also, in certain respects, extremely specialised.

For reasons which will become apparent, the system to be outlined cannot be explained by means of keys. Instead, illustrations will be used; and it is hoped that these will make possible the assignment of any leaf-hopper to its correct position in a natural classification.

As a preliminary, some appreciation of the structure of these insects is necessary, primarily because systematic studies are to a large extent applied comparative morphology, but also because confusion might otherwise arise between instances of convergence and true relationship.

The purpose of the present paper, which is the first in a series, is to offer an interpretation of certain controversial points concerned with the structure of the head, to illustrate and describe the external morphology of a representative species and to discuss the position of leaf-hoppers with respect to the rest of the Homoptera–Auchenorrhyncha. In succeeding papers of the series an attempt will be made to describe and illustrate the principal diagnostic features of every

distinct natural group and at the same time to place in its correct group as many genera as possible of those which have already been described, and which total approximately 1000.

The Structure of the Head.

Fig. 10 represents the head of a leaf-hopper (*Putoniessa nigra* Walk.). Attention is drawn to the three median sclerites, the most anterior of which is a small triangular lobe which projects beyond the margin of the head-capsule. A student commencing descriptive work and wishing to learn how to name these structures correctly will, on referring to the established literature, become extremely puzzled. Snodgrass (1935 : 330, fig. 177c) refers to them as the clypeus, ante-clypeus and labrum respectively and Imms (1934 : 348, fig. 346) as the clypeus, labrum and epipharynx. On turning for enlightenment to works dealing exclusively with the Hemiptera, his confusion will increase. Thus Haupt (1929 : 180, fig. 4) names the two anterior median sclerites of a fulgoroid the labrum. Posterior to these is a part he calls the clypeus, while to the large median plate lying between the eyes he gives the name vertex. Spooner (1938) names the hind part of the large median plate in leaf-hoppers the frons, and the part immediately anterior to the antennae the post-clypeus; while the rectangular sclerite is called by him the ante-clypeus and the small triangular one the labrum. I have done likewise except that I have employed the term fronto-clypeus for the whole of the large sclerite in leaf-hoppers and the term frons for Haupt's vertex in fulgoroids (Evans, 1938).

Ferris (1943) denies the occurrence of an unpaired median plate posterior to the clypeus in any insect. He suggests that the term " frons " signifies nothing more than the facial portion of the antennal segment, and that frontal sutures have no existence in fact. By " frontal sutures " are meant sutures which lie between the antennae and which extend anteriorly from the apices of the epicranial (or postfrontal) sutures as far as the epistomal (or clypeo-frontal) suture (Snodgrass, 1935 : fig. 35).

Attention is next directed to a pair of plates shown in fig. 10, which lie on each side of the median sclerites. These have been claimed to be of mandibular origin (Smith, 1892); to be part of the genae (Muir, 1926); to be part of the clypeus (Spooner, 1938; Evans, 1938); to be part of the hypopharynx (Snodgrass, 1938; Butt, 1943); and to belong to the antennal segment (Ferris, 1943). Other debated points concerned with the head are the extent of the maxillae and the position of the pits of the anterior arms of the tentorium. Finally, confusion often exists in descriptive work because the terms " crown " and " vertex " are used as if they were synonymous.

I suggest that among the Pterygota the most primitive type of insect development is to be found among the larvae of the Mecoptera and the Sialioidea (Megaloptera). This is because the Mecoptera and Sialioidea lie at the base of the Holometabola and have polypod larvae, which represent an earlier onto-

FIGS. 1–9.—Illustrations of steps leading to the development of the jassid head. AC., ante-clypeus; AT., anterior arms of the tentorium; ATP., anterior tentorial pit; C., clypeus; CLS., clypeal suture; CS., coronal suture; EPS., epistomal suture; F., frons; FS., frontal suture; H., hypopharynx; L., lorum; LAB., labium; LABAP., labial apodeme; LABR., labial retractors; LABRP., labial protractors; LBR., labrum; MA., maxillary stylet; MAPR., maxillary protractors; MAR., maxillary retractors; MD., mandibular stylet; MDAT., attachment of mandibular stylet to head capsule; MDPR., mandibular protractors; MDR., mandibular retractors; MP., maxillary plate; PC., post-clypeus; PT., posterior arms of tentorium; SALAP., apodeme for reception of muscles of salivary pump; SALPMP., salivary pump.
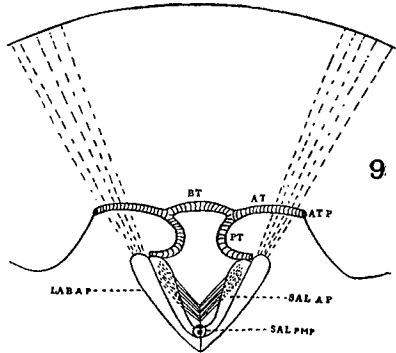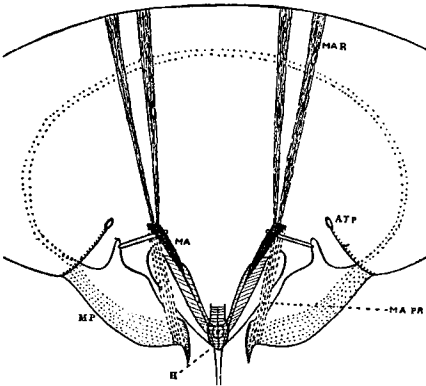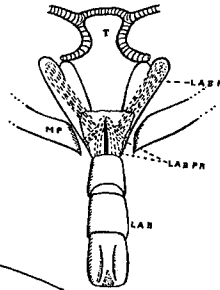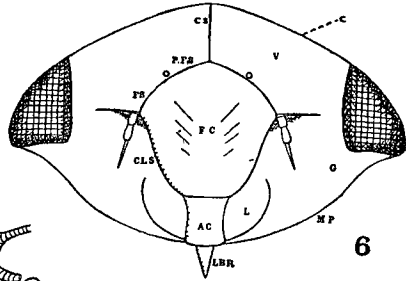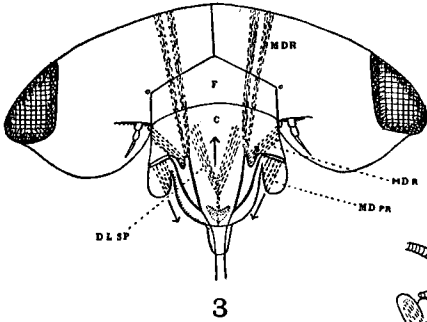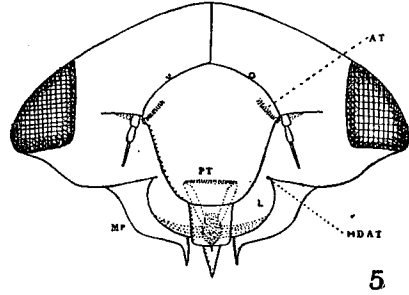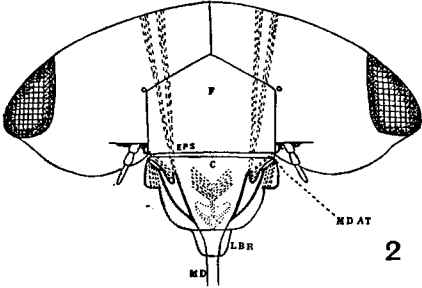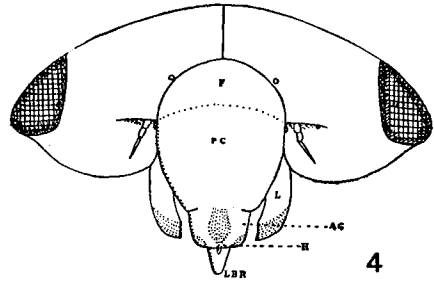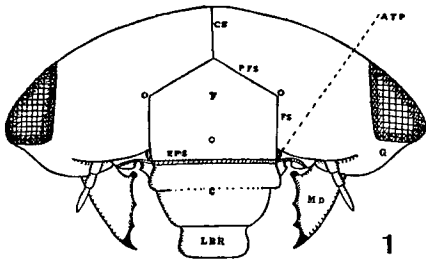
genetic stage than the post-oligopod nymphs of the Hemimetabola. Illustrations of the heads of such larvae have been given in several recent papers. Ferris (1942 : fig. 21) figures the head of a corydalid, and Cook (1943 : fig. 7) reproduces the same figure. Applegarth (1939) figures the head of a mecopteron and Evans (1942) the heads of a mecopteron and a corydalid. All these heads have a feature in common. This is the presence of a median unpaired sclerite similar to that shown in fig. 1. This sclerite is bounded posteriorly by an inverted V-shaped suture and laterally by a pair of sutures which extend anteriorly as far as the lateral margins of the clypeus. In the mecopteron larva figured by Evans there is a transverse suture which forms the anterior boundary of the sclerite. Close to the apices of this transverse suture are the pits of the anterior arms of the tentorium, and the antennae are at the sides of the head, more or less in line with the pits. The heads of corydalid larvae lack a transverse suture between the pits, and the anterior boundary of the median sclerite lies well in front of the antennae. Such a suture is, however, present in the heads of the sialid larvae (e.g. *Sialis lutaria*).

Fig. 1 is a reconstruction of a hypothetical insect head which is identical in essentials with the head of the larval mecopteron figured previously. The median unpaired sclerite is the frons which is bounded posteriorly by the postfrontal sutures, laterally by the frontal sutures, and anteriorly by the epistomal suture. The epistomal suture separates the frons from the clypeus, and the anterior tentorial pits lie close to its apices. Such an unpaired median sclerite occurs in the heads not only of larval Mecoptera, corydalids and sialids, but also in certain larval Coleoptera and in larvae belonging to other Orders. It also occurs in several Homoptera, notably in the Fulgoroidea, but also in the psyllid, *Paurocephala magnifrons* (Crawford, 1914), the nymphs of *Tartessus* spp. (JASSIDAE) and the nymphs of *Hemiodoecus* spp. (Evans, 1937, 1941c; Snodgrass, 1938; Ferris, 1943).

I have suggested in an earlier paper (1942) that in corydalids that part of the median plate posterior to the tentorial pits is the frons, the clypeus being the part anterior to the pits. Ferris (1942) and Cook (1943) believe that in corydalid and mecopterous larvae the whole of the median plate belongs to the clypeus, although, as already pointed out (Evans, 1943), in adult corydalids the median ocellus occurs on this sclerite. Similarly in *P. magnifrons* and certain fulgoroids, the median ocellus occurs on a well-defined central frons.

Consider now the head of a leaf-hopper (JASSIDAE). The following features are noted in fig. 6 : posteriorly a median longitudinal suture, the coronal suture; and centrally a large sclerite bearing muscle impressions, bounded posteriorly by a pair of divergent sutures which extend as far as the antenna on each side. Close to, and midway along these latter sutures, are the ocelli and at right-angles to their terminations, near the antennae, is a pair of transverse ledges which overhang the antennae. These ledges are a very constant feature of the Homoptera–Auchenorrhyncha, with the exception of the Fulgoroidea. Directly anterior to the large central sclerite is a smaller rectangular one, on either side of which is a pair of rounded flaps. If the rectangular plate is raised, so that it is attached to the head only at its posterior margin, it will be found that the lateral flaps continue in a medial direction underneath it and are attached to the sides of a ventral bowl-shaped depression (fig. 12). On either side of these flaps is a pair of plates which extend from the eyes and the antennae as far as the anterior margin of the head. Finally there is a small anteriorly-projecting lobe.

An attempt will now be made to trace certain steps which have led to the

development of the type of head shown in fig. 6 from sôme such type as that illustrated in fig. 1.

The hypothetical head.shown in fig. 1, while agreeing with the head of the mecopterous larva figured previously in the presence of the coronal suture and in the position of the frons, eyes, antennae, anterior tentorial pits, anterior mandibular articulations and post-antennal ledges, differs in having two additional features. These are the presence of paired ocelli close to the posterior corners of the frons and the partial sub-division of the clypeus. The position of the ocelli in the figure is their actual position in the majority of leaf-hoppers; any other position is a secondary development. A division of the clypeus, as indicated, is found commonly among the Orthoptera as well as in other Orders.

The sole articulations of the mandibles of certain Thysanura (*Machilis*) are at the back of the head, on the mandibular segment. Mandibulate pterygote insects have two articulations; a primary one on the mandibulate segment and a secondary one close to, or on, the posterior-lateral corners of the clypeus. In heads which retain primitive features the actual anterior condyle of the mandible fits into a depression on a small plate, termed by Ferris (1943) the " paraclypeal lobe." The suture limiting this plate posteriorly, Ferris terms the " tentorial suture." These plates, according to Ferris, are not parts of the clypeus but belong to the antennal segment. He further states that their origin is obscure and suggests that the lora of Homoptera (fig. 6, L) are derived from them.

In all Homoptera the sole points of contact of the mandibular stylets with the head capsule are at the posterior inner angle of each lorum (fig. 13). In fig. 2 the hypothetical first stage of the development of the lora is represented. The points of attachment of the mandibular stylets correspond to the anterior articulations of the mandibles as shown in fig. 1, only the epistomal suture now separates the anterior tentorial pits from the attachments of the mandibles and the latter are placed on the inner corner of the clypeus. In the nymphs of *Hemiodoecus* the pits are close to the posterior corners of the clypeus. Muir and Kershaw (1921) have shown that in the head of *Siphanta acuta* (Fulgoroidea) the frons, clypeus and labrum are not separated from each other by transverse sutures at an early embryological stage. Possibly they are all derived from the primitive prostomium and the epistomal suture is a secondary fold which developed in the first place as a direct result of the acquisition of the anterior articulations of the mandibles. While this suture, which encloses a thickened fold, serves to give added strength to the anterior part of the head capsule of biting insects, its loss in many Homoptera can be associated with the acquisition of piercing mandibles and the change in the position of their attachment.

If fig. 3 is compared with fig. 2, it will be noted that the epistomal suture and the antennal ledges, which are derived from the tentorial sutures, have been shifted in a posterior direction. I suggest that this backward development of the clypeus which is accompanied by a reduction in the size of the frons, a development found also in cicadas and cercopids, is the direct result of the backward pressure of the dilator muscles of the sucking-pump, together with those of the mandibular-tentorial retractor muscles. I wish to stress the fact that the direction of the extension of the sclerite is the same as the direction of the pressure of the muscles inserted on its surface. In direct apposition to these retractor muscles and to those mandibular muscles which are inserted on the base of the head capsule are the protractor muscles of the mandibles. The pressure exerted by these is in the direction of the front of the head.

It is now possible to suggest the probable course of development from a type of head such as that illustrated in fig. 1 to a type resembling fig. 6 as far as the

frons, clypeus, labrum and lora are concerned. In the change from biting to piercing mandibles the functions of the original abductor and adductor muscles changed to those of protractors and retractors. This change resulted in the abductors assuming a reversal of direction from the posterior to the anterior part of the head (Börner, 1929). If, as is here assumed, the protractors became attached to the sides of the clypeus, the effect of their pressure may well have resulted in the development of lateral clypeal lobes, as shown in fig. 3. At the same time the clypeus increased in size posteriorly and the frons and labrum decreased in size. In fig. 4 the epistomal suture has almost disappeared and the clypeal lobes have lengthened and have been cut off at their bases by the backward extension of the sides of the clypeus. In addition a new transverse suture has partially appeared, which separates the anterior part of the clypeus, overhanging the sucking-pump, from the posterior part bearing the dilators of the sucking-pump. It is not suggested that the clypeal lobes ever hung free as shown in fig. 4, but that they were directed inwards, in the direction of the pull of the protractors of the mandibles, and that the development of the new transverse suture was contemporaneous with their attachment to the sides of the base of the hypopharynx (ventral surface of the sucking-pump).

The final stages, as shown in figs. 5 and 6, were probably the completion of the transverse sutures separating the ante- from the post-clypeus, the fusion of the bases of the clypeal lobes with the anterior margins of the genae, the complete obliteration of the epistomal suture (consequent on the backward migration of the cibarial dilators on to the frons), and the loss of the separate identity of the postfrontal and frontal sutures.

This hypothesis is based on several facts. In several fulgoroids, as shown by Spooner, and in *Hemiodoecus*, there is a complete frons as illustrated in fig. 2. Further, not only is the ante-clypeus not separated from the post-clypeus by a transverse suture, but also the lora are not separated postero-laterally from the rest of the clypeus. Also, the tentorial pits in *Hemiodoecus* are on the sides of the clypeus, close to the ends of the epistomal suture. The Fulgoroidea are the most primitive group of the Auchenorrhyncha and the PELORIDIIDAE are undoubtedly the most primitive surviving Homoptera (Evans, 1937, 1939a, 1941a). In addition, a few leaf-hoppers have a complete frons in their nymphal stages and many retain traces of a frons when adult.

I do not accept the suggestion of Snodgrass that the lateral parts of the hypopharynx, on which in Orthoptera muscles of the mandibles are attached, have been expanded in Hemiptera to form the loral plates. My reason for disagreeing on this point is that it involves the growth of the lora in a direction contrary to the pull of the mandibular retractors.

That the lora are not part of the mandibles has been shown by the embryological studies of Muir and Kershaw. Ferris' suggestion that they are developments of the paraclypeal lobes of mandibulate insects is difficult to understand, because according to my interpretation, the ledges overhanging the antennae are derived from the continuation of the suture termed by Ferris the " tentorial suture." In this connection the position of the anterior pits in fig. 13 should be noted and this figure compared with figs. 2 and 3. The area immediately anterior to the antennae on each side would thus seem to correspond with the paraclypeal lobes of Ferris. There is, however, a further possibility to consider. In the mecopteron larva figured earlier (Evans, 1942) I have shown that the epistomal fold continues beyond the apices of the frontal sutures as far as the antennae on each side. The anterior tentorial pits are posterior to the lateral continuations of the fold and the articulations of the

mandibles are anterior to it. In the mecopteron, a suture (the continuation of the frontal suture) separates the mandibular articulations from the clypeus, but in the larva of *Sialis lutaria* no such suture exists. In other words, that part of Ferris' paraclypeal lobes, on which the mandibles articulate, has become incorporated in the clypeus. Hence the lora may in part be of paraclypeal origin.

Finally, that the lora cannot be derived from the gena is evident from the fact that the genae of Homoptera are secondary developments and cannot have formed part of the ancestral head capsule.

The maxillae have been omitted from figs. 1–4 but are shown in figs. 5, 6 and 8. In the Sternorrhyncha, Coleorrhyncha (PELORIDIIDAE) and certain Auchenorrhyncha, the maxillary plates either have no contact with the face of the head or are attached to the genae but are not completely fused with them (fig. 5). Fig. 8 shows the relation of the maxillary stylets and the maxillary plates to the rest of the head before the development of their association with the genae.

In fig. 9 the tentorium is shown as it occurs in the PELORIDIIDAE and as it is assumed to have been in the stages of development reproduced in figs. 2 and 3. The backward movement of the frons and antennae will have been accompanied by the backward shifting of the pits of the anterior arms. While in fulgoroids, cicadas and cercopids this movement was accompanied by a progressive lengthening of the anterior arms, the same effect did not occur in jassids. Instead the anterior arms lost contact with the posterior arms. The final result is illustrated in fig. 5, where the anterior arms are short and have no connection with the posterior arms. The latter consist of a transverse strut joining the apices of a pair of apodemes which arise from the base of the hypopharynx and on which are inserted the dilator muscles of the salivary syringe. In addition to these hypopharyngeal apodemes there is also another pair, and the two pairs are in close association with one another. The second pair supports the retractors of the labium distally and also one set of labial protractors, close to the point where they arise from the labium. The other set of protractors is inserted on the base of the labium itself (fig. 7). Although in some Homoptera the apophyses of the hypopharynx dwarf those of the labium, the two pairs are quite distinct in leaf-hoppers.

Before turning to the description of the structure of an actual leaf-hopper, it is desirable to explain the terms used to describe the various parts of the jassid head in fig. 6.

That part of the head which is visible from above and is on a plane with the pronotum is the crown. The term has no morphological significance, and may comprise part of the frons and part of the post-clypeus as well as part of the vertex. In facial aspect the coronal suture divides the vertex longitudinally as far as the point of divergence of the arms of the epicranial suture, here called the postfrontal suture. The lateral apices of the postfrontal sutures are usually close to the ocelli. The frontal sutures are a continuation of the postfrontal sutures as far as the antennae. Two terms are necessary to describe what might appear to be a single suture. This is because in some forms one pair is lost and in other forms the other pair is not developed. That part of the median sclerite posterior to the antennal ledges is of frontal origin, but because the muscles of the sucking-pump may extend on to its inner surface the whole plate is termed the " fronto-clypeus." The suture bordering the post-clypeus, from the antennae as far as the ante-clypeus, is termed the " clypeal suture." The other terms used, lorum, maxillary plate and labrum, need no comment.

The External Morphology of a Leaf-hopper (*Putoniessa nigra* Walker).

Many works exist in which some mention is made of the morphology of leaf-hoppers. In some the insect is dealt with as a whole; in others a comparative study is made of a single part. Nevertheless, the need still exists for further studies of the structure of representative Homoptera. The present study is not intended to be complete but is intended to serve three purposes : namely, to demonstrate the musculature of the stylets; to explain the venation
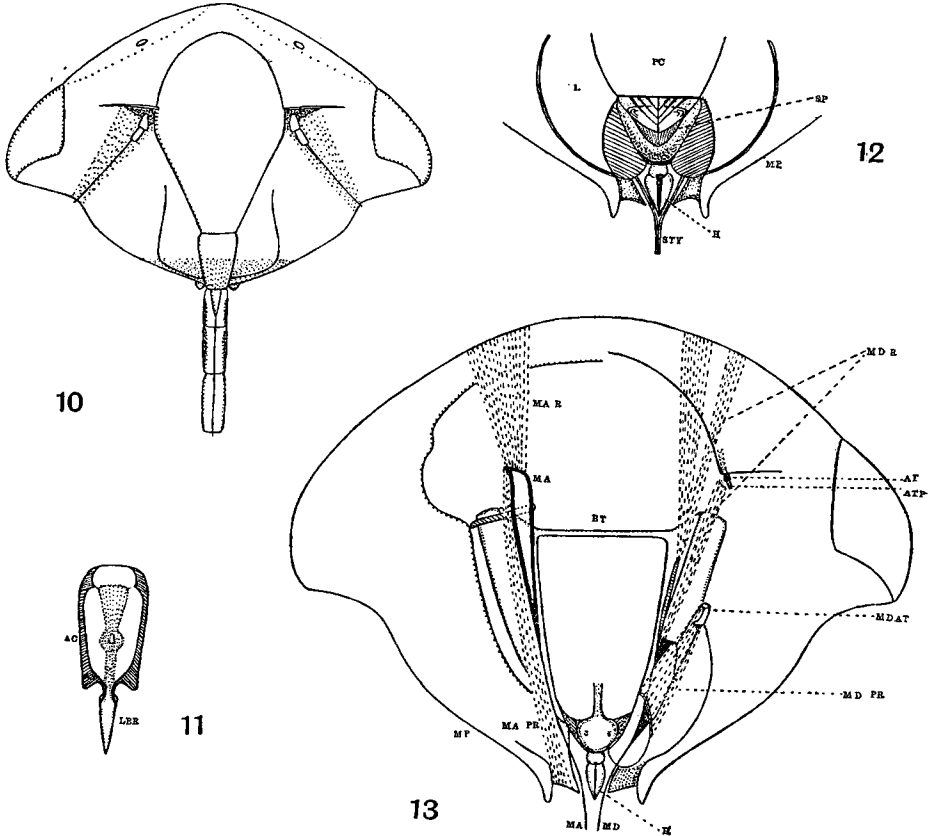

Fig. 10.—Head of *Putoniessa nigra*. Fig. 11.—Epipharyngeal surface of ante-clypeus and labrum. Fig. 12.—Anterior part of head after removal of ante-clypeus and labrum. Fig. 13.—Head, showing musculature of maxillary and mandibular stylets. AF., antennal foramen; BT., body of tentorium; SP., dorsal surface of sucking-pump; STY., stylets; other lettering as in figs. 1–9.

of the tegmen, and to compare it with the venational plan of certain other leaf-hoppers; and to describe the structure of the rest of the body in order to draw attention to certain primitive features.

The Head.

The complete head in facial aspect is illustrated in fig. 10. It will be noted that the ocelli·do not retain their primitive position. Fig. 11 represents the epipharyngeal surface of the ante-clypeus and labrum, and fig. 12 the anterior part of the head after the removal of the ante-clypeus and labrum. The cone-

'shaped structure shown in fig. 12 is the dorsal surface of the sucking-pump. The insertions of the dilator muscles of the sucking-pump (the cibarial muscles) are on its inner surface, and their distal attachments are on the fronto-clypeus. The ventral surface of the sucking-pump is the U-shaped trough from which the anterior lobe of the hypopharynx is suspended. The lora are attached to the sides of the trough on each side. The salivary syringe is enclosed by the hypopharynx and the salivary duct opens at its apex, where it makes contact
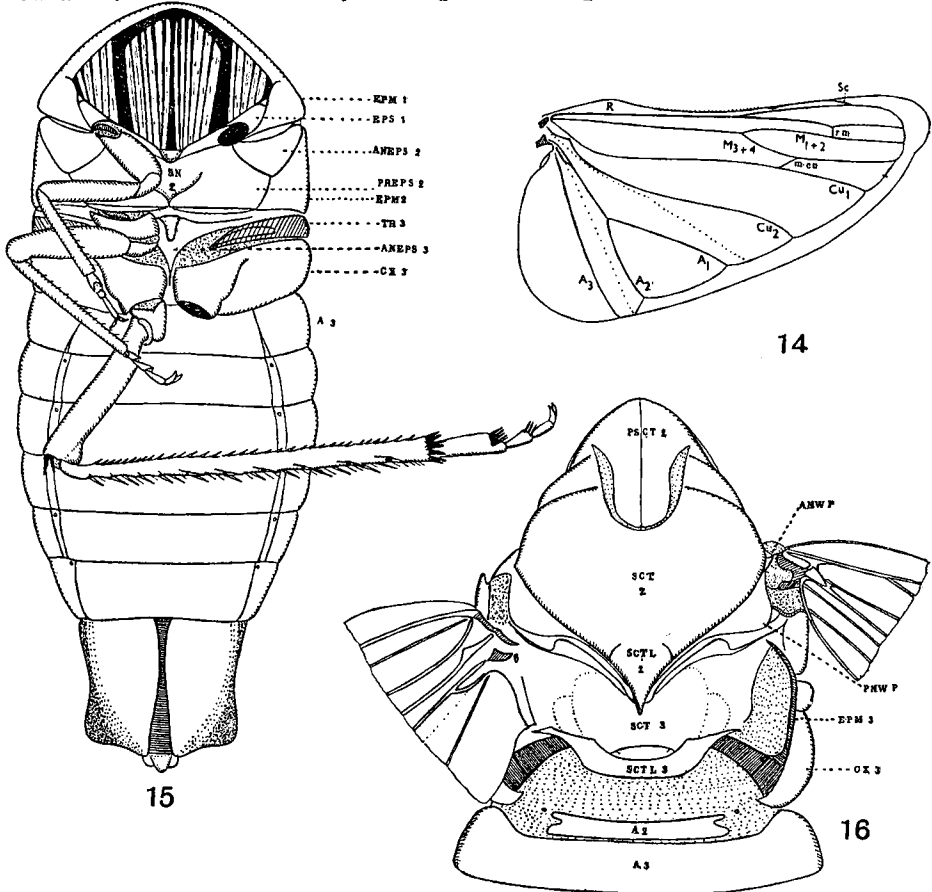
FIG. 14.—*P. nigra*, wing. FIG. 15.—*P. nigra*, thorax and abdomen, ventral aspect. FIG. 16.—*P. nigra*, meso- and meta-thorax and part of abdomen, dorsal aspect. A., abdominal segment; ANEPS., anepisternum; ANWP., anterior notal wing process; CX., coxa; EPM., epimeron; EPS., episternum; PNWP., posterior notal wing process; PREPS., pre-episternum; PSCT., pre-scutum; SCT., scutum; SCTL., scutellum; SN., sternum; TR., trochantin.

with the apposed stylets. The musculature of the mandibular and maxillary stylets is shown in fig. 13, the head being viewed in facial aspect. Comment on this figure is unnecessary.

The Thorax and Abdomen.

Fig. 15 illustrates *P. nigra* in ventral aspect, the head having been removed. The muscles shown are the median dorsal longitudinal muscles of the tegmina

and laterally the coxal muscles of the fore legs. The dorsal surface of the pro-
thorax consists of an undivided plate, the pronotum. Laterally and ventrally
the episterna are reduced and the visible sternum small, although the pits of the
sternal apophyses are widely separated. The apophyses are fused at their
extremities with processes arising from the pleural sutures.

In the mesothorax each episternum is divided into an anepisternum and
a pre-episternum, the epimera are undivided and the sternal apophyses arise
from paired invaginations situated at the sides of the triangular sternum.

In the metathorax the trochantins and hind coxae are enormously enlarged,
a development associated with the use of the hind legs for jumping. The
episterna and epimera are concealed by the coxae. The epimera extend around
the leg bases and, together with the post-coxale on each side, they form strong
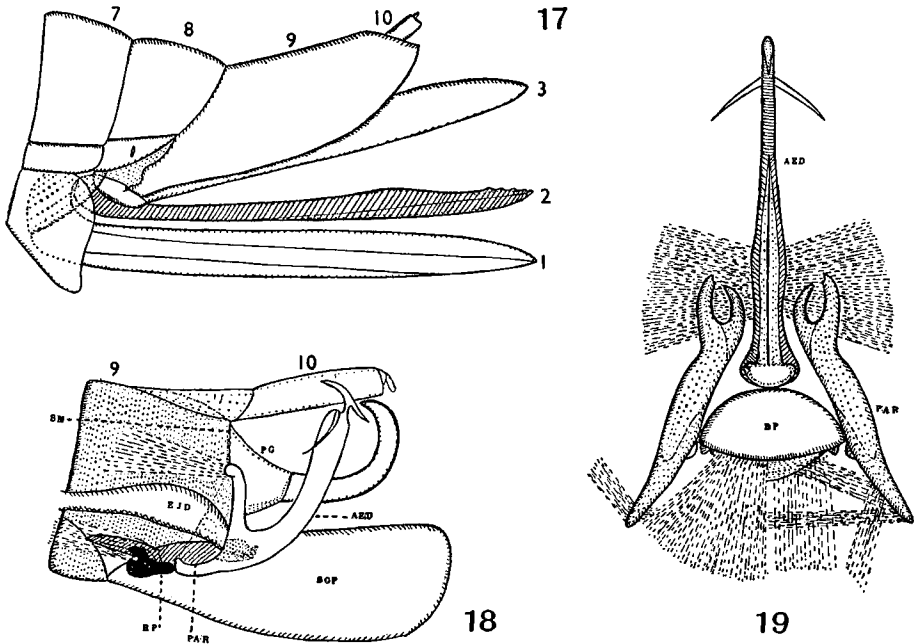

Fig. 17.—*P. nigra*, female genitalia. Fig. 18.—*P. nigra*, male genitalia. Fig. 19.—
    Aedeagus, parameres and basal plate, dorsal aspect. AED:, aedeagus; BP., basal
    plate; EJD., ejaculatory duct; PAR., paramere; PG., pygophore; SM., segmental
    membrane.

struts which meet just behind the sternal invaginations. The sternal apophyses
are short and arise from a single pit.

The mesonotum and part of the metanotum are shown in fig. 16, which also
shows the axillary sclerites and the bases of the fore- and hind-wings. The
area anterior to the U-shaped suture (which separates the attachments of the
median dorsal longitudinal muscles from the tergo-sternal muscles of the teg-
mina) is called the pre-scutum in the figure. As I have explained in a previous
paper (Evans, 1941b), in reference to the cicada *Tettigarcta tomentosa*, it is
uncertain whether all this area or just that part anterior to the first pair of
transverse folds belongs to the true pre-scutum. The post-notum of the
mesothorax is concealed beneath the scutum and scutellum and its phragma
support the lateral dorsal wing muscles. The post-notum of the metathorax

is reduced and hidden by the meta-scutellum, and the meta-pleural epimera are joined to it on each side by strong processes which lie immediately posterior to the wing bases.

The spines on the hind tibiae, as in many leaf-hoppers, are in four distinct rows; one row of spines is hair-like and another row is mounted on enlarged bases. The other two rows consist of widely-spaced long spines and closely set small spines respectively. (The venation of the tegmen (fig. 25) and of the wing (fig. 14) will be discussed in a later section.)

The first abdominal segment is reduced and its tergum is concealed by the scutellum of the metathorax. The spiracles shown in fig. 16 belong to the second abdominal segment, which is also reduced.

The female genitalia (fig. 17) are structurally identical with the type common to all the Auchenorrhyncha, with the exception of certain Fulgoroidea. According to Snodgrass (1935), the three pairs of valvifers of the ovipositor of Homoptera more nearly retain their original segmental connections than they do in other Orders. No purpose would be served by describing the various parts of the ovipositor, since these are clearly shown in the figure, and Snodgrass' account of the ovipositor of a cicada applies equally to that of a leaf-hopper.

The male genitalia are illustrated in figs. 18 and 19. Attention is drawn to the attachment of the aedeagus and that of the parameres (harpogones) to the basal plate. In *P. nigra* the separate identity of the sternum of the ninth segment is retained; it is lost in many leaf-hoppers. The large clasper shown in the figure lying between the tenth (anal) segment and the sub-genital plate is a process of the pygophore. Accessory clasping organs, associated either with the pygophores or the sub-genital plates, are of frequent occurrence in leaf-hoppers.

The Position of Leaf-hoppers within the Homoptera–Auchenorrhyncha.

This series of papers will be concerned only with leaf-hoppers, but as a preliminary some attention must be given to their relationships with other groups of Homoptera.

The usual practice is to start with two primary divisions of the Auchenorrhyncha, one comprising the Fulgoroidea and the other all the remainder. While acknowledging the very wide gap which separates the Fulgoroidea from the other groups, I consider that it is misleading to associate the cicadas so intimately with the cercopids, jassids and membracids. Hence a primary separation into three divisions, instead of two, is proposed.

1. Tegulae almost always present; middle coxae elongate, articulated far apart, free and capable of lateral movement; hind coxae immobile; wing without a marginal vein . . . . Fulgoromorpha.
   Tegulae absent; middle coxae short, articulations near together; hind coxae mobile; wing with a marginal vein . . . . 2.
2. Head with a swollen post-clypeus, the crown with a small triangular frons bearing a median ocellus . . . . Cicadomorpha.
   Head with a large, but not necessarily swollen post-clypeus, which may or may not be distinct from the frons; frons without a median ocellus
   Jassidomorpha.

The next step is the sub-division of the Jassidomorpha into two super-families :—

In the head, the anterior arms of the tentorium fused with the posterior arms; hind coxae short, conical, not transversely dilated; hind tibiae with one or a few strong spurs but lacking spines . . . . Cercopoidea.

In the head, the anterior arms of the tentorium not in contact with the posterior arms; hind coxae transverse, laterally dilated; hind tibiae armed with spines, some of which may be mounted on enlarged bases . . . . . Jassoidea.

In the past, following Baker (1923), I have recognised (Evans, 1939b) a large number of jassoid groups as families, and it is quite certain that many merit this status. There are, however, apart from the MEMBRACIDAE, four outstandingly distinctive groups, and it is now proposed to regard only these as families. The families recognised in the Jassoidea are the MEMBRACIDAE, AETHALIONIDAE, HYLICIDAE, EURYMELIDAE and JASSIDAE. All of these except the MEMBRACIDAE will be dealt with in the papers to follow.
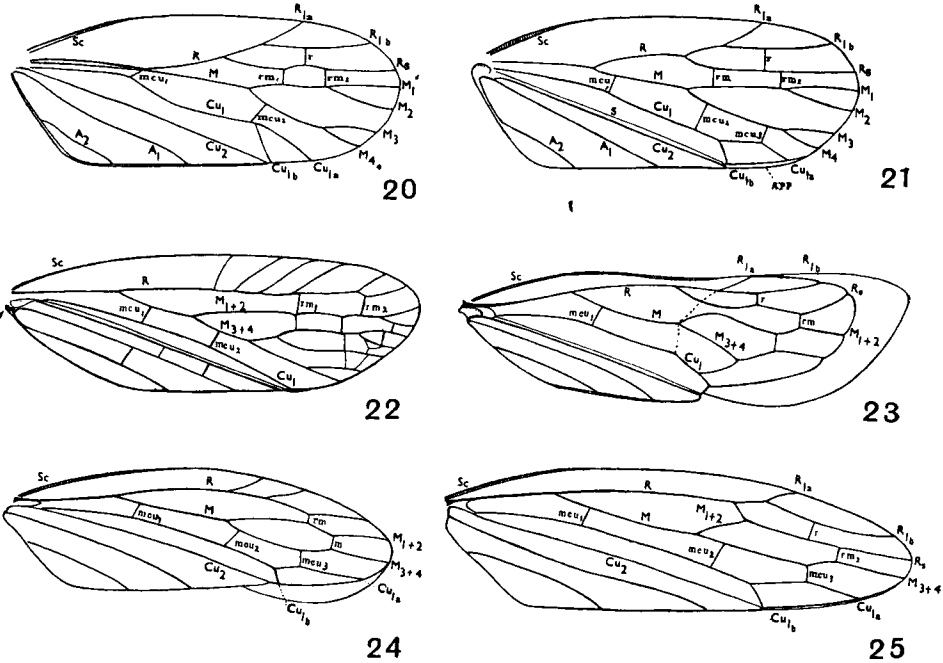
FIG. 20.—*Homaloscytina plana*, tegmen. FIG. 21.—Reconstruction of tegmen of hypothetical ancestor of recent jassoids. FIG. 22.—*Aethalion reticulatum*, tegmen. FIG. 23.—*Balala fulviventris*, tegmen. FIG. 24.—*Eurymeloides bicincta*, tegmen. FIG. 25.—*Putoniessa nigra*, tegmen.

Full definitions of the various families will be given when they come to be considered in turn. Here it will be sufficient to separate them on the characters supplied by the tegmen.

Fig. 25 represents the venation of the tegmen of *Putoniessa nigra* and will serve to illustrate the type of venation common to all the JASSIDAE. From this basic type many others have been derived, either by reduction of the principal veins, or by the addition of supernumerary cross-veins or by the meeting and anastomosing of adjacent veins.

The interpretation of the venation given in fig. 25 differs from that of Metcalf (1913) in the following respect: although Metcalf recognised the trachea of R_1 in certain jassids, he was of the opinion that the two main branches of the radius were derived from the radial sector (R_{2+3} and R_{4+5}). A study of Metcalf's figures of tracheation supported by the findings of Carpenter (1933), Tillyard

(1926) and myself (1943) with respect to fossil Homoptera, suggests that R_s is always unbranched in jassids.

Figs. 22–24 represent the tegmina of *Aethalion reticulatum* L. (AETHALIONIDAE), *Balala fulviventris* Dist. (HYLICIDAE) and *Eurymeloides bicincta* Erichs. (EURYMELIDAE) respectively. The tegmen of *A. reticulatum* differs from the jassid type in the absence of R_s, the extension of M_{1+2} to the apex of the tegmen, the presence of M_3 and M_4 as separate veins and the unbranched condition of Cu_1. All known representatives of this family share these characteristics, except that in *Darthula hardwicki* Gray, from Southern India, all four branches of the media are distinct.

The HYLICIDAE, represented here by *B. fulviventris*, have not in the past received the attention their interest merits. The venation illustrated in fig. 23 differs from the jassid type in having M_{1+2} extending to the apex of the tegmen and M_{3+4} fused apically with Cu_{1a}. This involves the suppression of cross-vein m-cu$_3$. The wide apical appendix is a further constant characteristic and attention is drawn to the presence of a nodal line.

The tegmen of the eurymelid (fig. 24) differs from fig. 25 in the absence of R_s and in the extension of M_{1+2} to the apex of the tegmen.

The same stability in basic tegminal venation does not occur in the MEMBRACIDAE. Thus M may be fused basally either with R or with Cu_1. Funkhouser (1913) was of the opinion that Cu_1 was unbranched in the MEMBRACIDAE. As a result of a study of his figures of tracheation and venation and of the examination of a wide range of material, including *Nicomia cicadoides* Walk. from British Guiana, I suggest that Cu_1 has two branches in membracids, as in other jassoid families, apart from the AETHALIONIDAE.

Fig. 21 represents the venation of a hypothetical form which could serve as a common ancestor to the four types illustrated in figs. 22–25, and fig. 20 represents the tegmen of *Homaloscytina plana* Tillyard, from the Upper Permian of New South Wales. The two figures differ from each other in the following features : the wide costal space of *H. plana* is lacking in fig. 21; R and M are not completely fused basally in *H. plana* as they are in fig. 21; cross-vein m-cu$_3$ is absent in *H. plana* and present in fig. 21.

Homaloscytina plana belongs to the family SCYTINOPTERIDAE, a family of Permian Homoptera from which it is probable that both the Jassoidea and Cercopoidea have been derived. The hind-wings of scyntinopterids lacked a marginal vein, which is therefore probably a secondary development. Fig. 14 represents the wing of *P. nigra*. It will be noticed that the two branches of R are not labelled in the figure. This is because it is uncertain whether they represent R_{2+3} and R_{4+5}, as suggested by Metcalf, or R_1 and R_s as would seem more probable.

contribution to our knowledge of leaf-hoppers could never have been made.
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