PAP. & PROC. ROY. SOC. TASMANIA, 1937 (20TH MAY, 1938)

1

The Morphology of the Head of Homoptera

By

J. W. EVANS, M.A., F.R.E.S.

(Read 8th November, 1937)

Although a great deal of attention, on the part of several workers, has been devoted to a study of the head structure of Hemiptera, the interpretation of which presents one of the most controversial questions in external insect anatomy, uncertainty still exists as to the correct homologies of the various sclerites. Hence in taxonomic papers the same part of the head may be named differently according to the views held by the respective authors.

The present work has been made possible by the recent discovery of abundant material of *Hemiodoecus fidelis* Evans, a representative of the Peloridiidae, which is undoubtedly the most archaic hemipterous family still in existence.

PELORIDIIDAE

The Peloridiidae, which comprise the whole of the series Coleorrhyncha, have been fully discussed by Myers and China (1929), China (1932), and Helmsing and China (1937), and, as pointed out by Helmsing and China, 'may well be descended in an almost direct line from proto-hemipterous ancestors'.

The first interpretation of the head-structure of an insect belonging to this family was given by Myers and China, and was based on an adult specimen of *Hemiodoecus leai* China. The sutures that limit the sclerites of the head, though distinct with the nymphal instars, are unrecognisable in the adult head, hence these authors made certain errors in their interpretation. The present author, in an earlier paper (Evans, 1937, *b*), also incorrectly interpreted part of the head of a peloridiid, since he based his interpretation on a specimen mounted on a slide, without previous dissection.

Figure 1 represents the head of a pre-imaginal nymph of *Hemiodoecus fidelis* Evans. Between the eyes lies the large vertex, which, owing to the opisthognathous nature of the head, is entirely ventral in position, and which is divided medially by the coronal suture. This branches anteriorly as the epicranial suture, which lies along the posterior margin of the frons. On either side of the frons is the frontal suture, and separating the frons from the clypeus, the epistomal suture. From the point of junction of the epistomal suture with the frontal suture, on each side of the head, arise the sub-genal sutures. The genae bear the antennae, and are separated from the vertex on each side by an ill-defined suture that does not continue as far as the eyes.

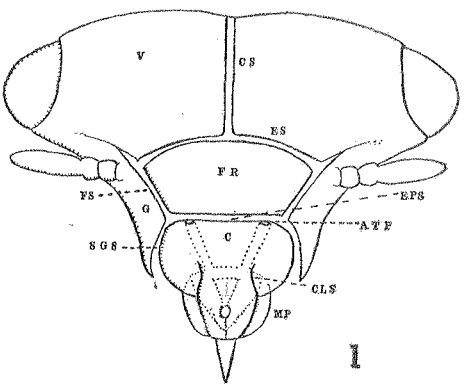
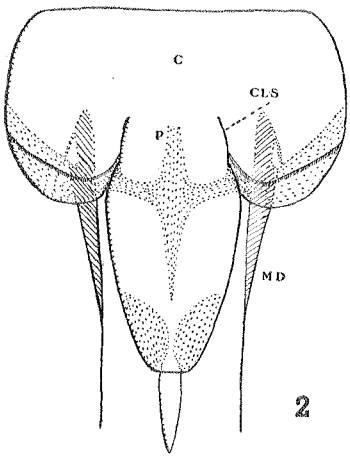


FIG. 1.—Head of *Hemiodoecus fidelis* in facial aspect.
v., vertex; *cs.*, coronal suture; *es.*, epicranial suture; *fr.*, frons; *fs.*, frontal suture; *g.*, gena; *eps.*, epistomal suture; *atp.*, anterior tentorial pit; *sgs.*, sub-genal suture; *c.*, clypeus; *cls.*, clypeal suture; *mp.*, maxillary plate.

It will be noticed that, apart from the epistomal and sub-genal sutures, three sutures have been named separately, instead of two as is usual. Myers (1928), under the term 'epicranial suture', includes doth the coronal and epicranial sutures, whilst Snodgrass (1935) retains the present coronal suture, but includes both the epicranial and frontal sutures under the term 'frontal suture'.

The clypeus is divided into two parts (Fig. 2), an anterior part from the ventral wall of which arises the labrum, known usually as the labrum-epipharynx, and a posterior part which bears antero-medially the impressions of the dilator muscles of the sucking-pump, and extends laterally on either side as swollen lobes (the 'frontal lobes' of Myers and China). These lobes are recurved antero-laterally, and each has an external ridge close to its anterior margin. The sides of the anterior portion of the clypeus extend posteriorly

into the body of the post-clypeus, and the sutures that divide the clypeal lobes from the median part of the clypeus, are the clypeal sutures. The clypeal lobes continue under the ante-clypeus medially, and are joined to the ventral wall of the sucking-pump, whilst the mandibles are attached to a ridge on the anterior internal margin of each lobe.



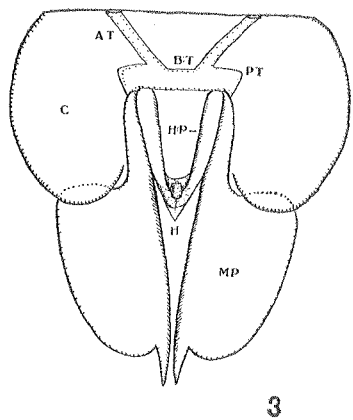


FIG. 2.—Clypeus of *H. fidelis*.

p., posterior extension of floor of sucking-pump; *md.*, mandible.

FIG. 3.—Maxillary plates and post-clypeus of *H. fidelis*.

at., anterior arm of tentorium; *bt.*, body of tentorium; *pt.*, posterior arm of tentorium; *hp.*, apodeme of hypopharynx; *h.*, hypopharynx;. Other lettering as Figure 1.

Figure 3 is a diagram of the same part of the head shown in Figure 2, after the removal of the ante-clypeus and floor of the sucking-pump. Arising from pits on the epistomal suture are the anterior arms of the tentorium; these join the posterior arms which form a transverse bar through the back of the head; the median part of the bar is the body of the tentorium. Whilst in orthopteroid insects the tentorial structure is X-shaped, according to Snodgrass the π form, rather than the X form, is the more primitive type. Attached to the tentorial bar anteriorly are the apophyses of the hypopharynx and processes of the maxillary plates; the maxillary stylets are attached to the latter processes. The maxillary plates, which are largely hidden by the clypeus, and which may be removed as distinct sclerites, are not in any way connected with the genae.

FULGOROIDEA

The head-structure of members of this group have been studied by Muir (1926) and Snodgrass. The interpretation that follows is based on that already given for the head of *Hemiodoecus*.

Figure 4 represents the head of *Achilus flammeus* Kby., which differs from that of *Hemiodoecus* in that the clypeal suture entirely separates the median clypeus from the lateral lobes, the mandibular stylets are attached to the posterior internal corners of the clypeal lobes, and the maxillary plates are fused with the genae. Although in *Achilus flammeus* the clypeus is divided by a superficial transverse suture into an ante- and post-clypeus, with many fulgoroids (e.g., *Platybrachys* spp.), it still consists of a single sclerite.

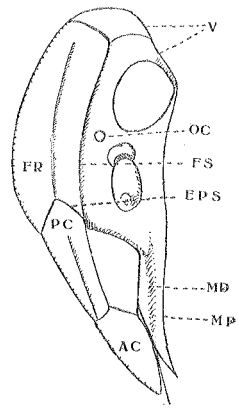


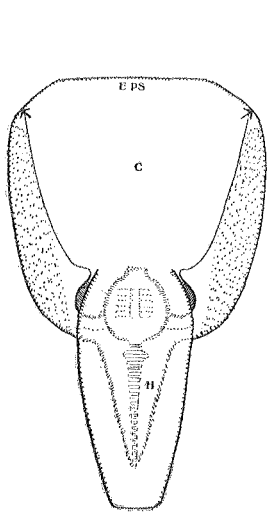
FIG. 4.—Head of *Achilus flammeus*.
p.c., post-clypeus; *a.c.*, ante-clypeus; *oc.*, ocellus. Other lettering as in previous figures.

Figure 5 represents the clypeus of *Eurinopsyche doddi* Dist. (Fulgoridae). The ante-clypeus projects from the post-clypeus, and bears the dorsal wall of the sucking-pump on its ventral surface. The ventral wall of the sucking-pump, anterior to the point at which it narrows posteriorly, is apparently joined to the rounded anterior internal margins of the sides of the post-clypeus. The median part of the post-clypeus supports the dilator muscles of the sucking-pump, and is separated from the lateral parts by superficial sutures; and the sides of the clypeus are recurved marginally, and to them are attached the mandibles at the points indicated by arrows.

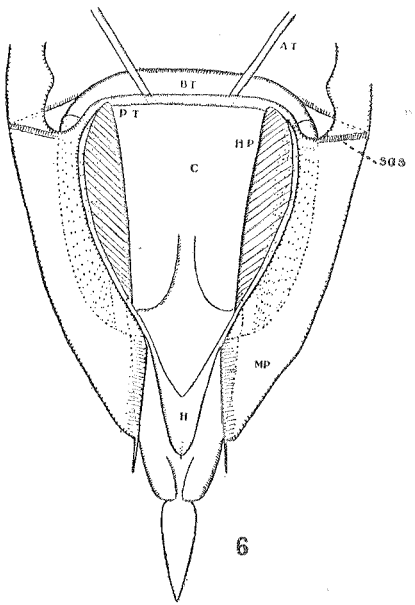
The epistomal suture separates the clypeus from the frons, and the vertex forms the crown and sides of the head. Just as the presence of a median ocellus on a sclerite is sufficient evidence that the sclerite is of frontal original, so may the position of the lateral ocelli be used in determining the vertex.

Figure 6 represents the anterior part of the head of *E. doddi* viewed from behind, and is reproduced to indicate how the maxillary plates are separated from the genae by sub-genal sutures, and how

the maxillary apodemes are fused with the posterior arms the tentorium. The apophyses of the hypopharynx lies below the tentorial bar (above in the figure). In all members of the Fulgoroidea that have been examined, the proximal ends of the anterior arms of the tentorium have been found unattached, but from their position it is probably that they originate on the epistomal suture. Dorsal tentorial arms occur in some genera, and arise from the anterior arms close to their approximation with the body of the tentorium.



5



6

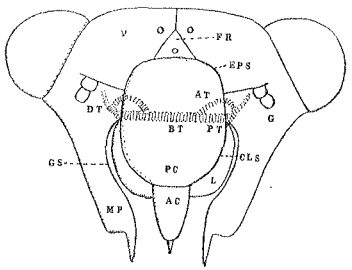
FIG. 5.—Clypeus of *Eurinopsyche doddi* in facial aspect.
FIG. 6.—Anterior part of head of *E. doddi* from behind. Lettering as in previous figures.

CICADIDAE

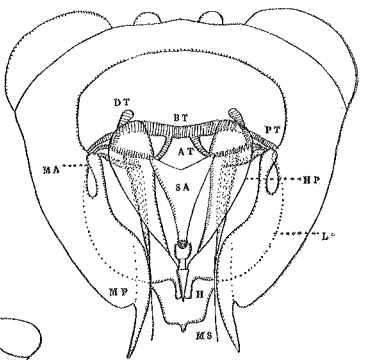
Although the morphology of the cicadan head has been investigated more thoroughly than that of any other hemipterous type, uncertainty still exists as to the homologies of the various parts.

Figure 7 is a diagram of a head of a cicada in facial aspect. Posteriorly between the eyes is the vertex, on which occur the paired ocelli. The larger part of the vertex lies on the crown of the head (Fig. 9), and is divided medially into two halves by the coronal suture which branches anteriorly into the epicranial suture; the arms of this suture enclose the frons which bears the median ocellus. Anterior to the frons, and separated from it by the epistomal suture, is the post-clypeus. The epistomal suture extends laterally on either

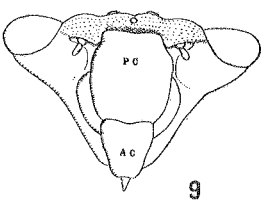
side of the post-clypeus, to a position slightly in front of the antennae, where it joins the clypeal suture. The clypeal suture then extends to a position just in front of the suture separating the ante- and post-clypeus, where it meets the genal suture, whilst its apodeme, which narrows posteriorly, close to each antenna, widens anteriorly, and the apodemes from each side of the head meet under the ventral surface of the sucking-pump and may be fused with it. The lorae, or mandibular plates, are joined to the genae posteriorly, to the apodemes of the clypeal suture laterally, and to the circular membranous plate already described, medially; they thus have no apparent connection



7



8



9

FIG. 7.—Diagram of the head of a cincada in facial aspect. *gs.*, genal suture; *l.*, lorum.

FIG. 8.—Head of *Tettigarcta tomentosa* from behind. *sa.*, apodeme of salivary syringe; *ms.*, maxillary stylet; *ma.*, maxillary apodeme. Other lettering as in previous figures.

FIG. 9.—Head of *Macrotristria angularis*.

with the clypeus. On either side of the lorae are the maxillary plates, which are suspended from the genae, but not separated from them by a sub-genal suture. The head of the cicades differs from those of fulgoroids, in that the maxillary plates are widely visible in facial aspect; in the reduction in size of the frons; in the absence of a sub-genal suture; in the posterior extension of the clypeal suture; in the arching of the epistomal suture; and in the separation of the lorae from the clypeus.

Figure 8 is a diagrammatic representation of the head of *Tettigarcta tomentosa* White; the maxillary plates have been pulled apart to disclose the hypopharynx, and to separate the apodemes of the

latter from those of the maxillary plates, to which the maxillary stylets are attached. Medially behind the hypopharynx is the salivary syringe and its apodeme. The apodemes of the hypopharynx, though closely apposed to the posterior arms of the tentorium, are not fused with them. The anterior arms of the tentorium arise from the epistomal suture, where it meets the clypeal suture, at the posterior apices of the lorae, and the dorsal arms branch from the anterior arms close to their points of origin.

CERCOPIDAE

The head structure of the Cercopidae, which has been studied previously by Doering (1922), is very similar to that of the Cicadidae, differing principally in the absence of a median ocellus. The greater part of the face of the head is occupied by the post-clypeus, which is separated from the vertex posteriorly by a small rectangular frons. The frons, which may be distinct, or amalgamated with the post-clypeus, always lies on the crown of the head, whilst the post-clypeus may be entirely ventral or extend on to the dorsal surface.

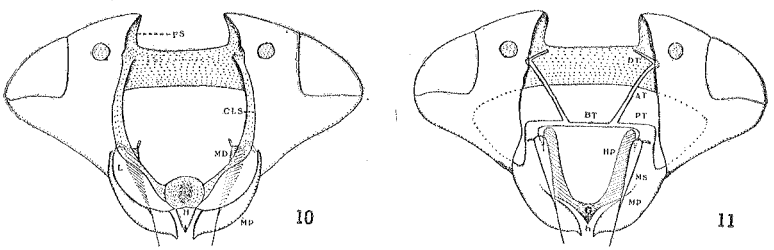


FIG. 10.—Head of *Hindola compacta* in facial aspect, the frons and clypeus having been removed.

FIG. 11.—Same as Figure 10, the lorae also having been removed. Lettering as in previous figures.

Figure 10 represents the head of *Hindola compacta* Walk. (Machaerotinae), from which the ante-clypeus, post-clypeus, frons, and antennae have been removed. Attention is directed to the clypeal sutures and their apodemes, which terminate close to the antennae, and to the attachment of the lorae to these apodemes and to the genae posteriorly. Figure 12 represents the lorae, clypeal apodemes, and mandibular stylets of the above species after removal from the head capsule, and shows the point of attachment of the stylets to the lorae. To the backward prolongation of each stylet are attached the retractor muscles, which arise on the dorsal wall of the head, whilst the protractor muscles are inserted on the bi-segmented connecting strut, and extend to the inner anterior margin of each lorum. Figure 11 represents the head after the removal of the lorae and their attachments. It will be noticed that the posterior

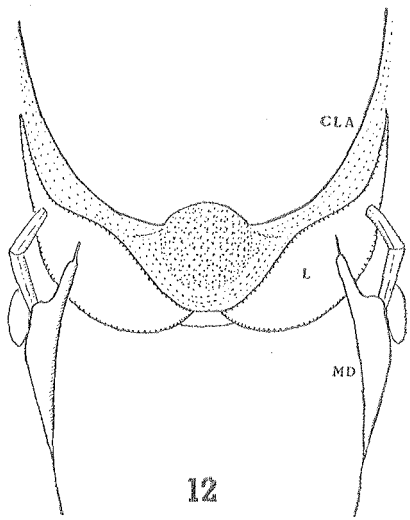


FIG. 12.—Lorae, mandibles, and clypeal apodeme of *H. compacta*. *cla.*, clypeal apodeme.

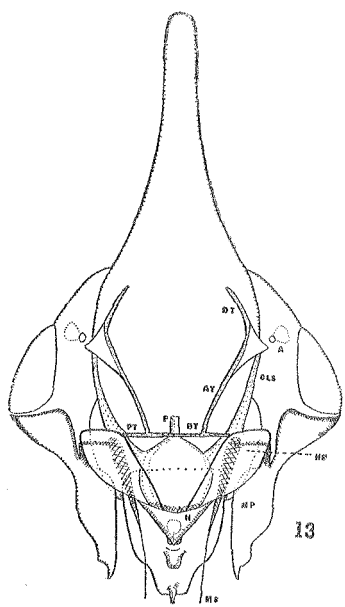


FIG. 13.—Head of *Philagra parva* from behind, the dorsal surface of the post-clypeus frons and vertex having been removed.
a., antenna. Other lettering as in previous figures.

arms of the tentorium are fused with the maxillary apodemes, and that the latter are not fused with the hypopharyngeal apophyses distally, although joined to them anteriorly. Each maxillary stylet is articulated with a maxillary apodeme by means of a short transverse lever. The anterior arms of the tentorium, as in the Cicadidae, arise from the apices of the epistomal suture, where they join the clypeal suture.

In *Philagra parva* Don. (Fig. 13) the apodemes of the maxillary plates are reduced in size, whilst the posterior arms of the tentorium are fused with the hypopharynegeal apophyses. The narrow posterior prolongation of the ventral surface of the sucking-pump, shown in the figures, lies above the anterior junction of the clypeal apodemes, and connects with the pharynx.

JASSOIDEA

The heads of jassoid insects differ from those of the groups already considered, in that with the majority there is no trace of the frons as a distinct sclerite, and the anterior arms of the tentorium, which serve to support the antennal muscles, are not attached to the body of the tentorium. Also, in the majority of jassoid families, although the clypeal suture is distinct, there is little development of a clypeal apodeme.

Figure 14 represents the head of *Eurymeloides pulchra* Sign., which has been chosen for description, since but for a narrow crown all the head lies in one plane. Between the eyes is the vertex, and medio-anteriorly lies the fronto-clypeus. As pointed out elsewhere (Evans, 1936, *a*), in the nymphs of some species of *Tartessus* (Euscelidae) a distinct rectangular plate occurs immediately behind the sclerite bearing the impressions of the dilator muscles of the sucking-pump, which in adult insects is fused with the post-clypeus. The rectangular sclerite referred to is the frons, hence the large median sclerite of most jassoid insects may be assumed to consist of all the frons and part of the clypeus. The rest of the head in facial aspect needs no further description.

When viewed from behind (Figs. 15, 16), just above the antennal scrobes are short struts, which are attached at their proximal ends to the antennal scrobes close to the point of junction of the clypeal and frontal sutures, and presumably at the apices of the lost epistomal suture. These are the anterior arms of the tentorium, the pits of which have been seen in the heads of nymphs of certain genera *(Aethalion* and *Rubria).* Joining the distal ends of the hypopharyngeal apodemes is a narrow bar; this bar consists of the apposed posterior arms of the tentorium. The apodemes of the maxillary plates are fused with those of the hypopharynx, and the maxillary stylets are attached to the former. With the Eurymelidae the ventral wall of the sucking-pump and its support are intimately joined to the hypopharynx, and form its dorsal wall.

As has been pointed out by previous workers, the homologies of the various parts of the labium are uncertain. It is possible that the segments labelled in Figure 15, mentum, prementum, and paraglossa, are derived from the corresponding parts of the mandibulate labium, but this not certain. A pair of small structures lying between the paraglossae may represent the glossae.

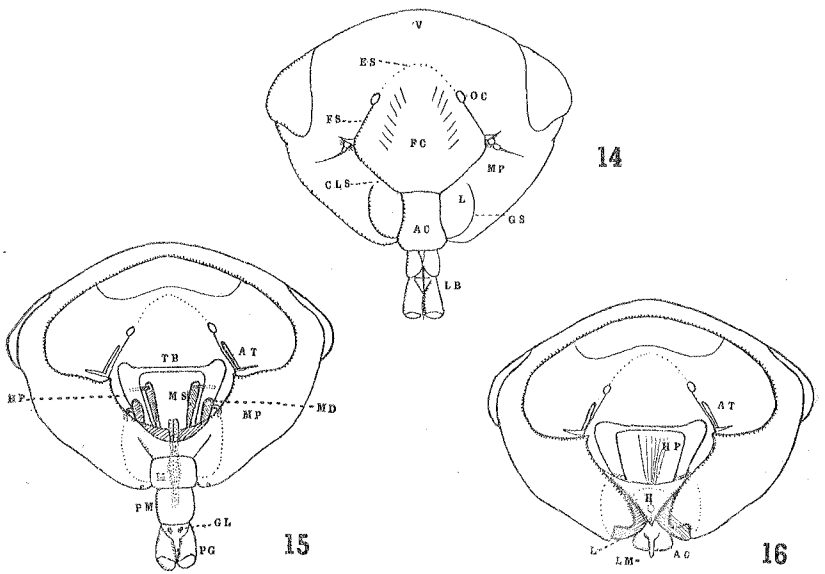


FIG. 14.—Head of *Eurymeloides pulchra* in facial aspect.
lb., labium; *fc.*, fronto-clypeus.

FIG. 15.—Head of *E. pulchra* from behind.
tb., tentorial bar; *m.*, mentum; *pm.*, prementum; *gl.*, glossa; *pg.*, paraglossa.

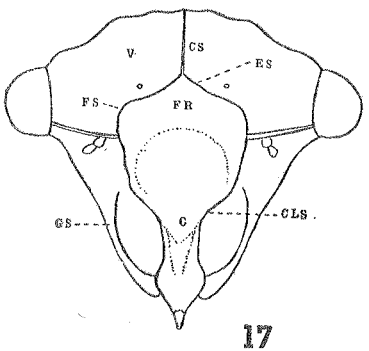
FIG. 16.—Same as Figure 15 after the removal of the labium and the stylets.
lm., labrum. Other lettering as in previous figures.

Figure 17 represents the head of *Aethalion reticulatum* L., after treatment in caustic potash, and is reproduced to show the presence of the coronal suture, which is absent in the majority of adult jassoids. There is no suture present between the ante-clypeus and post-clypeus, but an indistinct trace of a suture occurs, as shown, on the fronto-clypeus. This may indicate the boundary between the frons and post-clypeus; hence the suture branching anteriorly from the coronal suture is the epicranial suture, the suture that extends from the termination of the epicranial suture to the antennae, the frontal suture, which in turn connects with the clypeal suture. If this interpretation is correct, the rounded suture faintly discernible

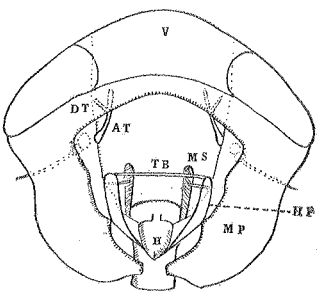
on the fronto-clypeus must be the epistomal suture, traces of which remain in a number of jassoids, as, for instance, *Smicrocotis obscura* Kirk.

Figure 18 represents the head of *Deltocephalus* sp., and is reproduced to show the presence of dorsal tentorial arms, which have not been noticed in any jassoid genera, other than with those that belong to the family Euscelidae.

It is possible that the diversity in the shape of the head that occurs among jassoid insects, may be due, in part, to the reduction in size of the anterior arms of the tentorium, since those muscles which were formerly attached to these arms will have taken upon new positions and set up new stresses. Whilst in the majority of jassoid



17



18

FIG. 17.—Head of *Aethalion reticulatum* in facial aspect.
FIG. 18.—Head of *Deltocephalus* sp. from behind. Lettering as in previous figures.

families the frons is incorporated in the same sclerite as the post-clypeus, and the suture (when present) that divides the fronto-clypeus from the vertex is the epicranial suture, it is believed that in the Signoretidae, Pythamidae, and Eucanthidae, the frons is a distinct sclerite. In these families a small-circular area occurs on the crown of the head, bounded by the edge of the head anteriorly and by a raised carina posteriorly. The area referred to is the frons, the carina marks the epicranial suture, and the edge of the head separating the post-clypeus from the frons, the epistomal suture. The vertex consists of a narrow margin to the back of the head, which extends anteriorly on each side of the frons, and the ocelli lie on these extensions.

MEMBRACIDAE

The membracid head is similar to that of the Jassoidea in the possession of a tentorial bar which has no connection with the anterior arms of the tentorium. It differs from them (apart from

the Aethalionidae) in the retention of the coronal suture in the adult head. Muir was of the opinion that the one characteristic possessed by the head of Membracidae, which was different from those of the rest of the Cicadoidea, was that the post-clypeus (his frons) overlaps and often entirely hides the ante-clypeus. However, this character also occurs in the jassoid genus *Austrolopa* Evans (Ulopidae). In some of the membracid heads examined, the clypeal suture was not well-defined, so that the lorae appeared to be separated from the sides of the head rather by folds than by sutures.

STERNORRHYNCHA

The present study is principally concerned with the Colerrhyncha and Auchenorrhyncha, and only a few Sternorrhynchous types have been examined, belonging to the Aphididae and Psyllidae.

The principal feature in the head structure of these families is the separation of the head into two parts by a deep cleft, formed by the epistomal and sub-genal sutures. Posterior to this cleft the only distinct suture, which may be present or absent, is the coronal suture. With the Aphididae the frons is not defined as a distinct sclerite, and with the Psyllidae, only the median ocellus remains to mark its position.

The anterior portion of the head of certain aphides (e.g., *Pineus pini* Koch.) bears a striking resemblance to that of *Hemiodoecus*, in the development of the clypeal lobes, to the sides of which the mandibular stylets are attached, and in the small maxillary plates which are not fused with the genae. With the Psyllidae, clypeal lobes are not evident, and the maxillary plates are greatly reduced. Whilst with certain aphides the anterior tentorial pits occur close together towards the centre of the epistomal suture, with others, and with all the psyllids examined, they lie at the apices of the suture, which is somewhat arched medially. In the latter family the anterior arms of the tentorium are strong struts, that serve to brace the sides of the anterior part of the head.

Discussion.

Apart from the work of Snodgrass, the most recent and detailed study of the structure of the homopterous head is that of Myers, who, although particularly concerned with the cicadan head, referred to other groups and reviewed the earlier literature. In a paper published two years before that of Myers, Muir revised the views he had presented in earlier papers written in collaboration with Kershaw, and in a short note published in 1929 he altered his previous interpretation in so far as the tentorium was concerned.

VERTEX.—Little discussion has centred round the identity of the vertex, excepting with the Fulgoroidea, but confusion has been caused by the misuse of the term. The vertex is that part of the head that lies directly above the frons, whether the latter is distinct or incorporated in the fronto-clypeus. As pointed out by Baker (1923), the term is not synonymous with 'crown', since the vertex may lie in part on the face and in part on the crown, and the fronto-clypeus, post-clypeus, or frons, may extend on to the crown.

FRONS.—The frons is present as a distinct sclerite in the Peloridiidae, Fulgoroidea, and Cicadidae. With the Cercopidae it may consist of a small rectangular plate on the crown of the head, or appear to be absent, in which event it must comprise the hindmost portion of the post-clypeus. Muir considered the frons of fulgoroids to be the vertex, as does Snodgrass, although the latter believes a small triangular area bearing the median ocellus, such as occurs with some species, is of frontal origin.

With most jassoids and all membracids, the frons is incorporated in the same sclerite as the post-clypeus.

CLYPEUS AND LORAE.—According to Comstock (1920), although the clypeus almost always appears as a single sclerite, it really consists of a row of three sclerites, one in the median line and one on each side. The lateral sclerites are the ante-coxal pieces of the mandibles.

The clypeal lobes of *Hemiodoecus* may well be homologous with the ante-coxal pieces of certain mandibulate insects (e.g., the larvae of *Corydalus*), because of their position, and because of the attachment of the mandibular stylets to the surface of the anterior recurved margins. It is not difficult to trace the relationship between the clypeal lobes of *Hemiodoecus*, and of members of the Fulgoroidea, with the lorae of other groups. The transition will have been associated with the stresses set up by the dilator muscles of the sucking-pump, and their gradual backward migration on the clypeal plate, resulting in the enlargement of the median clypeus and the arching of the epistomal suture. This will have been accompanied by the simultaneous backward extension of the clypeal sutures and their apodemes.

The floor of the sucking-pump consists of a more or less circular membranous plate that is joined to the clypeal apodemes and the lorae. As pointed out by Muir, this plate is of double thickness, the two layers usually being fused together, but with insects shortly after ecdysis their separation is possible, when it is found that the lorae are attached to the ventral layer, and thus the median continuation does not actually constitute the lower surface of the mouth cavity, but its support.

Whilst with all types studied, with the exception of *Hemiodoecus*, the mandibles are articulated with the posterior corners of the lorae, their protractor muscles still retain their position on the inner anterior

margins. That the lorae are not part of the mandibles, although frequently referred to as 'mandibular plates', has been shown by the embryological studies of Muir, who demonstrated that all the embryonic rudiment of the mandible becomes the stylet and its attachment. Both Muir and Myers considered the lorae as part of the genae, though Imms (1925) states that they are lateral developments of the clypeus, and reference to his figure shows that the sclerite in question is the post-clypeus. It is quite certain that Imms is correct and that their attachment to the genae is a secondary development.

Myers, following Muir, regarded the ante-clypeus as the whole of the clypeus, and the post-clypeus of the cicada as the frons. This is because he was not in agreement with Snodgrass in believing that the sucking-pump is part of the mouth-cavity, but considered it to be of pharyngeal origin. The suture that divides the ante-clypeus from the post-clypeus is a secondary development and not of universal occurrence.

MAXILLARY PLATES.—The maxillary plates have been shown by previous workers to consist of part of the maxillae, the embryonic rudiment of which becomes bi-segmented at an early stage, the basal joint becoming the maxillary plate and the distal joint the maxillary stylet.

Each maxillary plate consists of a wide, flat plate that tapers anteriorly to a point, and which is produced into the head-capsule posteriorly as an apodeme (possibly the cardo), or process, to which the maxillary stylet is attached. Although in *Hemiodoecus* the maxillary plates are distinct sclerites, in all Auchenorrhynchous families they are fused postero-laterially with the genae, and joined posteriorly by a thin membrame that lies between the floor of the hypopharynx and the base of the labium.

LABRUM.—The labrum is a narrow lobe suspended from the ventral wall of the ante-clypeus, and is usually known as the labrum-epipharynx. Imms, Doering, and Branch (1913) all identify the ante-clypeus with the labrum, but the attachment of the dorsal wall of the sucking-pump to the hind portion of the former sclerite, and the fact that no suture may occur between it and the post-clypeus, render their interpretation improbable.

HYPOPHARYNX.—The hypopharynx consists of a conical lobe that lies below the sucking-pump. Myers states that 'the lateral wings of the hypopharynx seem to be directly continuous with the lorae', which would suggest that the lorae are homologous with the superlinguae. However, though the dorsal wall of the hypopharynx is formed by the ventral wall of the sucking-pump and its support, the latter are not part of it. The salivary syringe is enclosed in the hypopharynx, and the aperture of the salivary canal is at its apex.

The hypopharyngeal apophyses are the most conspicuous structures within the homopterous head, and are probably homologous with supports of the hypopharynx such as occur in other orders.

SUCKING-PUMP.—Snodgrass has given a full and clear account of the origin and mechanism of the sucking-pump of Hemiptera, and as there appears to be no reason to doubt his interpretation, it need not be discussed here.

TENTORIUM.—The tentorium is an endoskeletal structure that serves to brace the cranial walls and give attachment to certain muscles. Snodgrass has suggested that all these muscles should take their origins on the sterna of the gnathal segments or on apodemal processes of the sterna, yet the tentorium appears to be a tergal structure. Helmsing and China have suggested that paired pits visible on the dorsal surface of each segment of the thorax of nymphs of *Hemiodoecus veitchi*, may be the ends of the thoracic apodemes similar to the frontal pits which mark the apodemes of the head. This suggestion lends support to the hypothisis that the tentorium is a tergal structure.

Considerable confusion has existed in the past over the tentorium. Myers accepted Muir's interpretation of 1926, and identified the anterior arms as the dorsal arms, although he drew attention to the fact that these arms joined the body of the tentorium, and that the latter was connected to the outer wall of the head capsule by invaginations which probably corresponded with the posterior arms of the tentorium. Although the dorsal arms of the pterygote tentorium may be united with the epicranial walls in the neighbourhood of the antennae, they are merely secondary outgrowths of the anterior arms, and can have no connexion with the posterior arms or body of the tentorium. Doering identified the tentorial arms correctly in the cercopid *Lepyronia quadrangularis* (Say), as did Snodgrass with the cicada *Magicicada septemdecim* L.

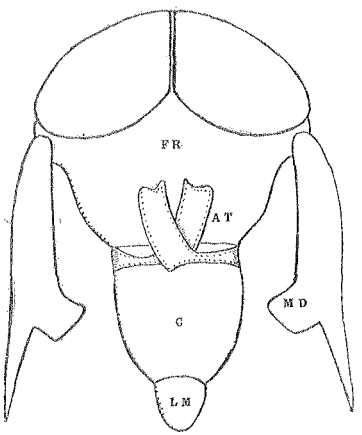
In 1929 Muir modified his views concerned with the tentorium, following the publication of a paper by Snodgrass (1928) on the morphology and evolution of the insect head, and advanced the view that the anterior arms of the tentorium arise from the hypopharynx and not from the anterior portion of the head-capsule. This assumption was based on Snodgrass's suggestion that endoskeletal arms, that spring from the base of the hypopharynx in Chilopods and Apterygota, may be homologous with the anterior arms of the pterygate tentorium. Hence Muir was of the opinion that the Hemiptera have not arisen from an orthopteroid stem, but from a more primitive one related to the Myriapoda and Apterygota.

It is, however, more probable that, whilst the hypopharyngeal apodemes of *Heterojapyx*, as figured by Snodgrass, are homologous with similar apodemes present in Hemiptera, and that apodemes

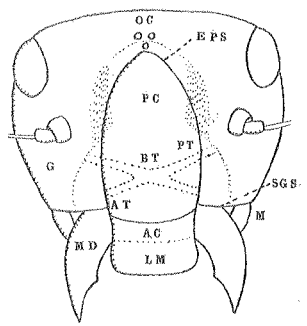
such as occur with the Machilidae (Fig. 19), which arise from the margin of the head-capsule just anterior to the epistomal suture, are homologous with the anterior arms of the tentorium of pterygote insects, the two sets of apodemes referred to are not homologous with each other.

A study of the head of *Hemiodoecus* suggests that the Hemiptera have arisen from an early orthopteroid stem, and possess, in common with the Orthoptera, sternal apophyses that arise from the hypopharynx, in addition to two pairs of tergal invaginations that give rise to the anterior and posterior arms of the tentorium.

Tentorial arms that arise from pits on the epistomal suture, such as occur in *Hemiodoecus*, must be the anterior arms and not dorsal



19



20

FIG. 19.—Diagram of the head-capsule of *Allomachilis froggatti*.
FIG. 20.—Head of *Myopsocus australis*.
m., maxilla. Other lettering as in previous figures.

arms, and with their determination it is a simple matter to decide upon the homologies of similar structures in other groups, even though with the arching of the epistomal suture, the anterior tentorial pits lie at the apices of the suture and not towards its centre. In all the homopterous types examined, the posterior arms of the tentorium occur as a transverse bar, usually attached to either or both of the paired apodemes of the hypopharynx and maxillary plates. The pits of the posterior arms have not been located, but doubtless occur on the post-occipital suture, which is ill-defined, since it occurs on the membrame that separates the head from the thorax.

SUTURES.—It is believed that the various sutures that appear in the head capsule, with the exception of the post-occipital suture, have no relation to original metamerism, being only secondary inflexions of the cuticle.

Muir distinguished four sutures on each side of the head, the frontal, genal, maxillary, and labial sutures. His frontal sutures in the cicada delimited the lateral extent of the frons, continued beyond the antennae, and met in a middle line, and are thus identical with the epistomal suture of Snodgrass and the epistomal suture + clypeal suture of the present author. The apodeme of the clypeal suture, which is narrow near each antenna, and widens anteriorly, finally joining the one from the opposite side, was believed by Muir (1926) and Myers to represent the anterior arms of the tentorium; the circular membrane joining the apodemes, which forms the ventral wall of the sucking-pump or its support, was considered by them to be homologous with the frontal plate of the tentorium in some Orthoptera, and they identified the depressions that occur laterally at the junction of the ante- and post-clypeus with the pits of the anterior arms of the tentorium. Later, Muir (1929) considered the apodemes of the clypeal suture to be 'invaginations at the anterior end of the frontal suture', and not the anterior arms of the tentorium.

If it is accepted that the lorae are lateral developments of the post-clypeus, then that part of the suture that lies on either side of the post-clypeus anterior to the antennae can be neither the frontal nor the epistomal suture, but is the clypeal suture, its limit being marked by its apodeme. True frontal sutures, such as occur in *Hemiodoecus*, are elsewhere found only with fulgoroids and cercopids, where they lie on either side of the frons, and in some jassoids, where they lie between the epicranial and clypeal sutures. In the cicadas there is no trace of a frontal suture, the frons being defined laterally by the epicranial sutures, and anteriorly by the epistomal suture.

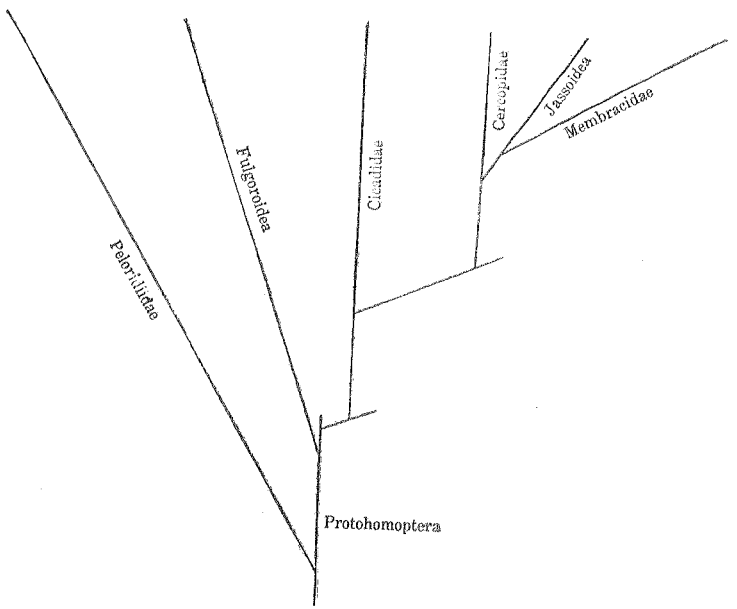
The genal sutures, which separate the lorae from the maxillary plates, must not be confused with the sub-genal sutures, since the latter, though distinct in *Hemiodoecus* and the aphides and psyllids that have been examined, are lost in other groups consequent upon the fusing of the genae with the maxillary plates.

The maxillary suture of Muir is 'very indistinct, and only recognizable as a crease'; it lies on the other side of the maxillary plate from his genal suture. Muir regarded the processes of the maxillary plates which lie alongside the apophyses of the hypopharynx, and which may be fused with the tentorial bar, as being the apodemes of the maxillary suture, and since he stated that the maxillary apodeme 'is the most complex and conspicuous structure in the head of the

cicada', it would seem that he had failed to separate the processes of the maxillary plates, to which the maxillary stylets are joined, from the apophyses of the hypophraynx.

The labial suture of Muir must be homologous with the post-occipital suture, since on it occur the pits of the posterior arms of the tentorium.

Only one more suture need be considered: that is the epistomal suture, which separates the frons from the clypeus. Snodgrass identified the suture that lies at the back and sides of the large median swollen sclerite in psocids and cicadas as the epistomal suture. Whilst not disputing this interpretation in so far as psocids are concerned, where no clypeal suture occurs, it is maintained that in



cicadas the epistomal suture extends anteriorly only as far as the neighbourhood of the antennae, where it meets the clypeal suture, which, as has been mentioned in an earlier paragraph, may be recognized by its apodeme. The anterior tentorial pits occur at the junctions of the two sutures. With cercopids the epistomal suture is seldom distinct, whilst with most jassoids no trace of it remains in adult insects, the posterior margin of the fronto-clypeus being limited by the epicranial suture.

PHYLOGENY.—Various views have been advanced in the past concerned with the phylogeny of the Auchenorrhyncha. Osborn (1895) considered the Cicadidae to be the most generalized, followed by the

Membracidae, Fulgoroidae, Cercopidae, and Jassoidea, in that sequence. Kirkaldy (1906), whilst in agreement with Osborn in so far as the position of the Cicadidae was concerned, believed the fulgoroids to be the most specialized, and linked the membracids closer to the cercopids than to the jassoids. Singh-Pruthi (1925), as a result of a study based on the characters of the male genitalia, derived the Fulgoroidea from a lower level of the homopterous stem than the other groups, and the Membracidae from the same line as the Jassidae and Cercopidae, but at a lower level. The possible relationships of the various groups, as suggested by a comparison based principally on head-structure, are set out in the phylogenetic tree given above.

After the Peloridiidae, the Fulgoroidea are derived from the lowest level of the protohomopterous branch, not only because in the structure of the head, especially the clypeus, they resemble *Hemiodoecus*, but because of the primitive type of their genitalia, no subgenital plates being developed, and also on account of their tegminal venation. Certain fulgoroid genera have more complete venation, and less specialization by reduction, than is found in any other group of homoptera.

After the Fulgoroidea, there is little doubt that the Cicadidae represent the most primitive family, and next to them come the Cercopidae, which are possibly related to the mesozoic Scytinopteridae, since the tegminal venation of the latter is very similar to that of the present-day Machaerotinae.

The Cercopidae resemble the Cicadidae in the complete development of the tentorium, and in the presence, with many genera, of a distinct frons. The Jassoidea and Membracidae are placed at a higher level than the Cercopidae, because of their reduced tentorium, and since it is believed that the fusion of the post-clypeus with the frons, and in some genera the fusion of the front-clypeus with the vertex, is a recent development, brought about by the progressive backward migration of the dilator muscles of the sucking-pump on the cranial walls.

REFERENCES.

BAKER, C. F., 1923.—The Jassoidea related to the Stenocotidae. *Phillipine Journ. Sci.* 23 (4) ; 348.

BRANCH, H. E., 1913.—Morphology and Biology of the Membracidae of Kansas. *Kansas Univ. Sci. Bull.* 8 (3).

CHINA, W. E. 1932.—On the Occurrence of the Peloridiid Genus *Hemiodoecus* in Queensland. *Ann. & Mag. Nat. Hist.* (10), 10; 392.

COMSTOCK, J. H., 1920.—*An Introduction to Entomology.* Comstock Publishing Co., Ithaca, N.Y.

DOERING, K., 1922.—Biology and Morphology of *Lepyronia quadrangularis. Kansas Univ. Sci. Bull.* 14 (21).

EVANS, J. W., 1937,—(*a*) Australian Leaf-Hoppers, Pt. 5. *Papers Roy. Soc. Tas.* 1936, 69.

EVANS, J. W., 1937.—(*b*) A New Species of Peloridiidae from Tasmania. *Proc. Roy. Ent. Soc. London.* B. 6 (6); 107.

HELMSING, I. W., and CHINA, W. E., 1937.—On the Biology and Ecology of *Hemiodoecus veitchi. Ann. & Mag. Nat. Hist.* (10), 19; 473.

IMMS, A. D., 1925.—*A General Text Book of Entomology.* Metheun and Co., London.

KIRKALDY, G. W., 1906.—Leaf-Hoppers and their Natural Enemies. *Bull. Hawaii Sug. Ass. Ent.* 1 (9).

MUIR, F., 1926.—Reconsideration of Some Points in the Morphology of the Head of Homoptera. *Ann. Ent. Soc. America.* 19; 67.

————, 1929.—The Tentorium of Hemiptera Considered from the Point of View of the Recent Work of Snodgrass. *Ent. Month. Mag.* 65; 86.

MYERS, J. G., 1928.—The Morphology of the Cicadidae. *Proc. Zool. Soc. London.* (2), 365.

————————, and CHINA, W. E., 1929.—The Systematic Position of the Peloridiidae. *Ann. Mag. Nat. Hist.* (10), 3; 282.

OSBORN, H., 1895.—The Phylogeny of the Hemiptera. *Proc. Ent. Soc. Washington.* 3; 185.

SING-PRUTHI, H., 1925.—The Morphology of the Male Genitalia in Rhynchota. *Trans. Ent. Soc. London;* 127.

SNODGRASS, R. E., 1928.—Morphology and Evolution of the Insect Head and Its Appendages. *Smithsonian Misc. Coll.* 81 (3), no. 20.

————————, 1935.—*Principles of Insect Morphology.* McGrath Hill Book Co.