THE EXTERNAL MALE GENITALIA OF FULGOROIDEA
(Homoptera)

By R. G. FENNAH

The external genitalia of the male in Fulgoroidea develop in association with the posterior margin of the ninth abdominal segment and comprise a tubular intromittent organ, or *phallus* (Fig. 1, *ph*) and a pair of claspers, genital styles or *harpagones* (*hrp*), all emerging through the conjunctival membrane between the sterna of the ninth and tenth segments. The ninth abdominal segment is ring-like and on its inner walls are attached all but one pair of the muscles of the genitalia.

On the posterior ventral margin of this segment there is frequently developed a median process (Fig. 9, *mvp*), usually simple (Cixiidae, most Derbidae), but sometimes forked (*Malaxa:* Delphacidae), or paired (*Burnilia, Perkinsiella, Pissonotus:* Delphacidae), or showing evidence of having been formed by the fusion of paired immovable processes (many Achilidae): this structure has been considered homologous with the more prominent *subgenital plates* of the Cicadoid superfamilies. Functionally it wedges the first and second valvulae of the ovipositor between the bases of the harpagones during coitus. The harpagones are free from the ventral surface of the ninth segment and are invariably inter-connected near their internal (basal) extremities by a transverse bar (Fig. 4, *tvs. st*)—the "basal plates" of Singh-Pruthi—from the mid-point of which a vertical sclerotised rod passes upward to a sclerotised ring surrounding the apex of the *ejaculatory duct* (Fig. 13, *ejd*) where it joins the *endophallus* (*enp*) or innermost lining of the phallus. The latter consists of a *phallobase* (*phb*), which is suspended from the posterior margin of the tergum of segment IX on each side of the insertion of segment X and passes distally into a tubular aedeagus (*aed*) which is invaginated at its apex, the invaginated portion passing anteriorly as the endophallus to join the ejaculatory duct. The sclerotised arms which suspend the phallobase from the tergum are in some families fused for part of their length, and assume the shape of a Y, but their points of attachment remain constant.

The musculature of these organs comprises four elements: (1) paired protractor and retractor muscles of the phallus; (2) a

pair of muscles from the transverse strut between the harpagones to the anterior ventral margin of the pygofer; (3) a pair from the basal ends of the harpagones to the phallobase and (4) a pair from the harpagones to the ventrolateral walls of the pygofer. There is in addition a small pair of muscles attached to the posterolateral wall of the ninth segment close to the points of insertion of the suspensorial arms of the phallobase and attached dorsally to the tergum. In Jassoidea and Cercopoidea there is an unpaired transverse zygomatic abductor muscle joining the basal ends of the harpagones: no counterpart of this has been found in Fulgoroidea.

(1) The protractor muscles of the aedeagus are attached to the dorsal surface of the sclerotised roof over the apex of the ejaculatory duct and pass obliquely to the lateral margins of the pygofer where they are broadly inserted and invariably reach the posterior margin (Fig. 1, 1). The retractor muscles (Fig. 1, 2) are inserted on the anterior margin or on the ventrolateral surface of the sclerite which bears the protractors and pass to a lip on the anterior ventral or ventrolateral margin of the pygofer. (2) The muscles which connect the transverse strut of the harpagones to the anterior margin of the pygofer (Fig. 1, 3) are always paired and apparently serve to retract the harpagones; they are often attached along the major portion of the strut, but sometimes converge from the anterior margin to lie immediately at each side of the base of the vertical apodeme. (3) The muscles directly associated with the phallobase (Fig. 1, 4) are attached ventrolaterally to a slight flange at its junction with the conjunctival membrane; proximally they join the inner faces of the basal arms of the harpagones and serve as abductors and depressors of the latter. (4) The muscles attaching the harpagones to the pygofer are antagonistic to the last mentioned and are inserted on the outer surface of their basal arms whence they pass laterally to unite broadly with the ventrolateral wall (Fig. 1, 5).

The above arrangement of the genital musculature occurs in almost all families of Fulgoroidea: it is accordingly of interest to find it strikingly modified in the families Derbidae and Achilidae. In both it is the phallic musculature which is involved, and in both the base of the aedeagus is withdrawn into the body— excessively so in Achilidae—but whereas in the latter the median apodeme from the transverse strut of the harpagones is greatly elongated, in the Derbidae it is absent. The condition found in Achilidae is shown in fig. 7. Here the retractor muscles of the aedeagus are absent, otherwise the musculature is normal (though it may be noted that the dorsal muscles near the insertion of the phallobase on the tergal margin are unusually well developed). It is presumed that in such an arrangement retraction of the aedeagus is brought about by the median

apodeme to the harpagones becoming flexed when the protractor muscles are contracted and pulling antagonistically as their tension is reduced.   In the Derbidae also it is the paired retractors of the aedeagus which are aborted, but here their function appears to have been assumed by the muscles which pass from the phallobase to the harpagones.   These muscles in Derbidae are exceptionally large (Fig. 8, 4), and the basal arms of the harpagones on which they are inserted extend deeply into the abdomen with the result that the muscles pull antagonistically to the aedeagal protractors.

The ninth segment, or pygofer, is normally ring-like.   In Derbidae its tergal region is reduced to a narrow rim firmly attached to the basal margin of the tenth segment (*Cedusa*, *Phaciocephalus*) or almost indistinguishably incorporated into the tenth tergite (*Neocenchrea* (Fig. 8), *Zeugma*).   In this family the eighth and sometimes the seventh abdominal sternite may also be suppressed.

Kershaw and Muir (1922) and Muir (1925) considered the medioventral process of the pygofer in Fulgoroidea and the closely similar subgenital plates in other Auchenorhyncha to be homologous with the first valvulae of the Hemipterous ovipositor: they postulated a movement of the posterior (coxopodite) area of the eighth sternite in the male, on which they believed genital appendages (gonapophyses) subsequently to develop, to a position below the ninth tergum and fusion with it to form the pygofer, and justified this view by citing the example of the female in which the valvifer, or coxopodite of the eighth sternite, with its gonapophysis (the first valvula) during nymphal development becomes attached to the ninth tergum.   Muir's contention, as he pointed out, rests on a claim that the ninth abdominal sternite has not been demonstrated in the homopterous male either in the nymphal or adult form.   This claim, however, is no longer tenable: the writer has examined all stages of the delphacid *Peregrinus maidis* (Ashm.) and has found this sternite initially present in both sexes, and in the male continuously so during development (Figs. 14, 15). There is no trace of posterior drift of any portion of the eighth sternite in the male (compare figs. 14–17 and 21–26).   Moreover, the first valvulae of the ovipositor, notwithstanding their migration, still retain their original muscular relation with the coxopodite of the eighth segment (the valvifer), while the muscles of the second valvulae are restricted to the ninth segment, of which these valvulae are the gonapophyses.   An inevitable corollary of Muir's view of the nature of the ventral portion of the pygofer is that the paired muscles which pass from the transverse strut between the harpagones to the anterior ventral margin of the pygofer, the adductor muscles of the harpagones and the retractor muscles of the aedeagus all connect appendages of the

ninth segment with the coxopodite area of the eighth, a condition at variance with that in the female with which homology is claimed. Muir found it difficult to accept what he considered to be the alternative to his interpretation, namely that the sub-genital plates of Homoptera are "new processes not represented in the other sex or in other insects". Such apodemes of the sternite of the ninth segment, however, have arisen by parallel development in the males of certain Mecoptera (e. g. *Panorpa*). In contrast to Muir, Singh-Pruthi (1924:71) interpreted the sub-genital plates as "coxites" (of the ninth segment) "and therefore homologous to the lateral pair of ovipositor-lobes" (third valvulae). In *Peregrinus* the third valvulae of the ovipositor arise in the membrane behind the posterior margin of segment IX laterad of the second valvulae (Fig. 26a): buds arising in a corresponding position in the male nymph (i. e. laterad of the median phallogenic area of the membrane behind segment IX) (Fig. 18) develop into the harpagones, as may readily be seen by dissecting teneral fifth instars and adults from their respective fourth and fifth instar cuticulae. Sub-genital plates are not developed in *Peregrinus*, but if fourth and fifth instars of the Jassoid *Entogonia* be examined it may be seen that the subgenital plates arise posteriorly on each side of the middle line of the ninth sternum and represent an outpushing of the sternal margin itself. Above them, in the membrane, are developed the buds of the harpagones and phallus exactly as seen in *Peregrinus*. The ontogeny of the subgenital plates thus shows them to be adventitious apodemes of the ventral margin of the ninth segment: this conclusion is corroborated by their anatomy, since they are at no stage provided with muscles.

It is appropriate at this point to draw attention to a pair of processes prominently developed in all nymphal stages of *Peregrinus maidis* (Ashm.) on the dorsolateral hind margin of the pygofer at the level of a line through the middle of the tenth segment (Fig. 15, *dlp*). Similar processes are of widespread occurrence in nymphal Fulgoroidea and may prove to be universal in the superfamily: as far as has been ascertained these have not previously been mentioned in the literature on this group. In *Peregrinus* each process is unsegmented, devoid of musculature, subquadrate and rugose-verrunculate; in the Dictyopharidae *Hyalodictyon* and *Toropa* and the Flatidae *Antillormenis* and *Ilesia* it is lanceolate and smooth. Their position on the ninth segment indicates that, resemblances notwithstanding, they cannot be cerci: their condition remains unchanged throughout nymphal life but in the adult, if present at all, they appear in rudimentary form as a slight inwardly-directed lobe on the hind margin of the pygofer. In *Peregrinus* this eminence is feeble and minutely granular. In adult Fulgoroidea various immovable apodemes may be developed on

the posterolateral margins of the pygofer, sometimes asymmetrically (as in the Kinnarid *Quilessa*), while in certain Delphacidae (e. g. *Burnilia*) they may form a comparatively elaborate armature.

The harpagones, the development of which is considered along with that of the aedeagus below, are symmetrical, rod-like or triangularly or subquadrately spatulate, and are always interconnected by the transverse strut. In *Tettigometra* they are styliform, while in *Euphyonarthex* they are fused in a broad plate resting on the coxosternum of the pygofer. Union of the apposed ventral margins of the harpagones is not common but is of wide occurrence in Acanaloniidae.

The phallus varies considerably in shape but its morphological composition is far more uniform. The different arrangements of the phallobasic and aedeagal elements are shown diagrammatically in fig. 29; these diagrams are self-explanatory and comment may accordingly be restricted to a few of the more interesting points. The phallus of Tettigometridae is generally considered to represent one of the most primitive types; the phallobase is well developed, with paired suspensorial arms, and passes distally into a simple tubular aedeagus which is apically membranous and devoid of accessory processes. In the Asiracinae, the least specialised subfamily of the Delphacidae, the phallus closely resembles that of the pintaliine Cixiidae, and comprises a phallobase and an exserted aedeagus (Fig. 13): in the tribe Delphacini the aedeagus has become largely withdrawn into a crypt (Fig. 12), and the phallobase, still recognisable by the attachment of the harpagonal depressor muscles, is formed dorsally by the median sclerotised suspensorial arm passing upward to the tergum and ventrally by a sclerotised and usually pigmented plate lying transversely across the conjunctival membrane; this is the "diaphragm" (Fig. 11, *dpm*) of systematic terminology. Kershaw and Muir (1922:209) homologised "a small ring at the base of the aedeagus" with their "periandrium" (phallobase): their view was questioned by Singh Pruthi (1925:228), who considered the delphacine aedeagus to correspond to the phallobase of Cixiidae. If this contention were correct it would be necessary to look for the attachment of the harpagonal depressors ventrally at the base of the aedeagus: they do not, however, occur in this position, but as indicated above, on the sclerotised transverse plate across the conjunctival membrane. Singh-Pruthi's interpretation accordingly leaves unexplained both the presence of the "diaphragm" and its relation to the dorsal insertion of the harpagonal depressor muscles. In the kinnarid genus *Bytrois* (Fig. 10) only the phallobase is present, and assumes the form of a wide tube produced distally to form a *theca;* the gonopore opens medially at its base. Muir's figure of the Old World

genus *Kinnara* (1923:236) indicates that in this family the aedeagus may be fully developed within the theca; other genera (*Quilessa*, *Prosotropis*, and *Atopocixius*) appear to occupy an intermediate position between these two forms. As in Kinnaridae the phallus in Meenoplidae shows considerable variation: in *Nisia* and *Robigalia* the phallobase appears to combine with the aedeagus in a short tube which is traversed by the endophallus; in *Phaconeura* the aedeagus itself forms a tube and is surrounded basally and roofed over for most of its length by the extended phallobase. No adequate account has yet been given of the phallus in Achilixiidae: it is possible that it may be found to be similar to that of *Bytrois* as in *Achilixius* the phallus is simple and is attached to a transverse bar across the conjunctival membrane. In Acanaloniidae the phallus consists in some species merely of a thecal extension of the phallobase in the shape of a spinose bag decurved laterally to form an incomplete tube, while the aedeagus is represented by a small triangular lip medially at its base. In the ricanioid group of families with which the Acanaloniidae are generally associated the aedeagus proper is reduced to a short tube with the phallotreme, or external opening of the endophallus (Fig. 13, *pt*), occupying the dorsal, apical or ventral surfaces; the condition of the aedeagus in Acanaloniidae merely represents a reduction of this type.

Suggestions have been put forward (Kershaw and Muir 1922:208, Muir 1923:245, Singh-Pruthi 1925:232) for a phylogenetic arrangement of the families of Fulgoroidea in which the form of the phallus is treated as the paramount character, the principle division of the superfamily being considered as occurring between groups in which the phallotreme is situated proximally, when the aedeagus is usually surrounded by a theca, and others in which the phallotreme is situated distally, when the aedeagus is exserted well beyond the phallobase. If this distinction be employed rigorously as a criterion of natural relationship through common ancestry then it would appear that the small family Meenoplidae, which embraces both types, is not of monophyletic origin; moreover it is to be suspected that with the examination of the genitalia of many more species other families would come to be regarded as being in a similar condition. The writer is not prepared to endorse such an extreme view, and while he is provisionally disposed to recognise a community of origin between the Cixiidae and Delphacidae, the Dictyopharidae and Fulgoridae, and members of the ricanioid complex respectively, does so on the basis of characters which are not necessarily subordinate to that of phallic structure. Between families other than those indicated above considerable latitude must be allowed for local modifications and for parallel trends of development, and evidence of natural relationship must be accumulated from their ontogeny, anatomy and biology.

The phallus in *Peregrinus* and *Toropa* arises medially in the membrane behind segment IX and between the harpagonal buds (Fig. 18 *ph*). A T-shaped sclerotisation of the membrane, with the transverse arm composed of two layers and the vertical strut occupying the middle line of the body, advances into the body cavity. In *Peregrinus* (Figs. 19, 19a, 19b) two invaginations of the membrane are thus developed, the first forming a flattened pocket between the upper and lower surfaces of the cross-bar of the T-shaped sclerite which in the adult forms the crypt in which the aedeagus lies, the second lying below the preceding between the posterior margin of the sternum and the buds of the harpagones and persisting in the adult as the chamber in which the medio-basal portion of the harpagones is contained. The latter develop from small buds by rapid proliferation during the fifth nymphal stage. The transverse strut which connects the harpagones together develops in the membrane below them and from the first is in contact with the lower end of the T-shaped sclerite. In Achilidae, Flatidae and possibly in other families the vertical apodeme of this sclerite may lose its mesal connection with the conjunctival membrane in the adult though in such cases it retains its normal attachments at each end. In *Peregrinus* the dorsal plate of the cross-bar of the T-shaped sclerite, which forms the roof of the aedeagal crypt, becomes more strongly sclerotised at its posterior lateral angles to form the suspensorial arms of the phallobase; from the outset of its development it is in contact with the laterodorsal hind margin of the tergite. These sclerotised arms in some families may be developed throughout their length as separate elements passing to each side of the phallobase, or as in *Peregrinus* they may unite mesally to form a short vertical bar in the middle line of the membrane. The ventral plate of the cross-bar of the T-shaped sclerite forms the floor of the aedeagal crypt and distally provides the areas of insertion of the dorsal ends of the harpagonal depressor muscles. The roof-like sclerite over the distal extremity of the ejaculatory duct is formed during the basad extension of the point of union of the dorsal and vertical elements of the T-shaped sclerite.

Singh-Pruthi (1924) on the basis of a study of late instars of two species of the jassoid *Idiocerus* by means of transverse sections concluded that in these species the aedeagus arises as a paired organ formed during division of what he regarded as an initial (and phylogenetically primitive) pair of common phallic-harpagonal buds. His figures 2e and 2f of the third instar and 3a and 3b of the fourth indicate that incipient aedeagal development in *Idiocerus* occurs as reconstructed diagrammatically in fig. 28. He expanded his account of phallic and periphallic differentiation in this genus into a general statement embracing both auchenorhynchous and

sternorhynchous Homoptera (pp. 87, 88) and claimed that the
phallus and harpagones in members of this Suborder are con-
jointly homologous with the second valvulae of the ovipositor
(p. 71).

While it may be accepted that in Auchenorhyncha differentia-
tion of the phallus, its associated basal sclerites, and its muscula-
ture occurs symmetrically about the axial line of the body,
observational evidence that the phallus is formed by the union
of two appendages developed independently in each half of the
ninth segment is still lacking. It must not be overlooked that in
Idiocerus the ectoderm of the middle line from the earliest stage
of development differentiates to form the dorsal surface of the
phallus throughout its length and at all times is in broad conti-
nuity with the flanges which grow downward on each side,
forming with them a single steeply tectiform plate, of which
the ventral margins finally become united. The implication
that the bilaterally symmetrical development of the phallus in
this genus may be taken as evidence of the presence of a pair
of gonapophyses, one on each side of the gonopore, in ancestral
forms of Homoptera must be evaluated in the light of possible
alternatives. In *Peregrinus* there appear to be grounds for
considering the harpagones as homologous with the third
valvulae of the ovipositor: both arise as buds in close association
with the lateral portion of the hind margin of the ninth segment
and occupy a morphologically similar position in the adult;
both are provided with muscles which are inserted on elements
of the ninth segment. The relation of these appendages in
Idiocerus as illustrated in Singh-Pruthi's figures 3a and 6 is
quite consistent with this interpretation. On this presumption,
if the aedeagus in Auchenorhyncha be regarded as a morphologi-
cally paired organ with a counterpart in the female, it can only
be homologised with the second valvulae of the ovipositor. In
view of the variability in the male genitalia of Auchenorhyncha
and of the unprecedented appearance or suppression of muscles
in different groups the writer considers that the evidence in
favour of such homology in this Series is still too inconclusive to
secure its general acceptance.

Divergent views have been expressed on the question whether
the accessory sclerites of the base of the aedeagus are homolo-
gous in Heteroptera and auchenorhynchous Homoptera (Singh-
Pruthi 1925: 135, 136; Muir 1926:328). No one has yet
attempted to homologise them with structures in the female
genitalia and it would seem not inappropriate here to anticipate
speculation on this point. If it be supposed that the aedeagus
in Auchenorhyncha is of paired composition and is homologous
with the second valvulae, and if it be assumed that the median
(though distally paired) vertical sclerites above and below the
aedeagus were also primitively paired throughout their length,
it will be noted that each sclerite so formed includes a limb to a

gonapophysis (one half of the aedeagus), a limb to a style (one of the harpagones) and a third limb to the posterior margin of the ninth tergum.   A similar series of relationships is found in the valvifer of the ninth segment in the female.   If these structures were considered homologous it would be expected that the muscles of the style would be inserted on the coxopodite from which it primitively arose: one such muscle, it may be claimed, exists in that which joins each of the harpagones to the phallobase; of the four remaining muscles of the genitalia on each side of the body, however, only one, the protractor of the aedeagus, has the anatomical relations of a muscle of the valvifer.   Moreover on ontogenic grounds it is to be supposed that the coxosternal area from which the gonapophyses originate is embodied in the ventral half of the pygofer.   Such a hypothesis, therefore, does not consistently account for the relations with the pygofer of all elements of the genitalia.   In the opinion of the writer it is more satisfactory to regard the sclerites supporting the male genital appendages in Auchenorhyncha as having recently arisen (perhaps by local sclerotisation of a basal and primitively segmental element in the conjunctival membrane) in adaptation to the functional requirements of a changing copulatory mechanism than to seek in them the modified remains of structures supposedly omnipresent in the earliest evolutionary stages of the Rhynchota.

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EXPLANATION OF FIGURES

Fig.   1. *Petrusa marginata* (L.) (Flatidae), lateral view of male genitalia with muscles and clasper of left side removed.

Fig.   2. Do., posterior view of male genitalia, slightly diagrammatic, left side showing muscles hidden by those on right.

Fig.   3. Do., dorsal view of male genitalia, slightly diagrammatic, aedeagal protractor muscle of right side removed.

Fig.   4. Do., ventral view showing harpagonal muscles of left side.

Fig.   5. *Toropa ferrifera* (Wlk.) (Dictyopharidae), lateral view of male genitalia, harpagonal muscles omitted.

Fig.   6. Do., lateral view of harpagonal muscles.

Fig.   7. *Catonia* sp. (Achilidae), lateral view of male genitalia.

Fig.   8. *Neocenchrea gregaria* Fenn. (Derbidae), lateral view of male genitalia.

Fig.   9. Do., harpagonal muscles with posterior process of segt. IX shown dotted.

Fig. 10. *Bytrois nemoralis* Fenn., (Kinnaridae), lateral view of male genitalia.

Fig. 11. *Peregrinus maidis* (Ashm.) (Delphacidae: Delphacini), posterior view of male genitalia, right clasper removed, its phallobasic attachment seen by transparency.

Fig. 12. Do., lateral view of male genitalia.

Fig. 13. *Punana portoricensis* Muir (Delphacidae: Asiracinae), lateral view of phallus.

Figs. 14-20. Stages in development of male genitalia of *Peregrinus maidis* (Ashm.).

Fig. 14. *Peregrinus maidis* (Ashm.), ventral view of posterior segments of first instar.

Fig. 15. Do., lateral view of same.

Fig. 16. Do., ventral view of IXth sternite of third instar; (a) lateral view.

Fig. 17. Do., posterolateral view of IXth and Xth abdominal segments, fourth instar.

Fig. 18. Do., anterior view of harpagonal buds and phallogenic area, fourth instar.

Fig. 19. Do., as above, fifth instar; (a) lateral view, (b) dorsal view.

Fig. 20. Do., lateral view of phallus and clasper of teneral adult.

Figs. 21-26a.   Stages in the development of the female genitalia of *Peregrinus maidis* (Ashm.).

Fig. 21. Do., ventral view of posterior segments of second instar of female.

Fig. 22. Do., ventral view of IXth sternite of second instar of female; (a) lateral view.

Fig. 23. Do., as above, third instar of female.

Fig. 24. Do., as above, fourth instar of female.

Fig. 25. Do., ventral view of genital appendages of fifth instar of female.

Fig. 26. Do., posterior view of abdominal segments IX and X of fifth instar of female; (a) ventro-posterior view of genital buds.

Fig. 27. Do., genital appendages of left side of IXth segment of adult female.

Fig. 28. Diagrammatic reconstruction of incipient phallus-formation in *Idiocerus* (Jassoidea) from sectional figures given by Singh-Pruthi (1924).

Fig. 29. Diagrams showing composition of phallus in various groups of Fulgoroidea.

EXPLANATION OF LETTERING

aed, aedeagus; *dlp*, dorsolateral process of IXth segment; *dpm*, diaphragm (phallobase of Delphacini); *ejd*, ejaculatory duct; *enp*, endophallus; *hrp*, one of harpagones; *mvp*, medioventral process of pygofer; *ph*, phallus; *phb*, phallobase; *pht*, phallotreme; *tvs. st.*, transverse sclerotised strut interconnecting the harpagones; *valv*, valvula of ovipositor; *vert. ap.*, vertical apodeme from transverse strut of harpagones to base of aedeagus.

PLATE 22   PROC. ENT. SOC. WASH., VOL. 47
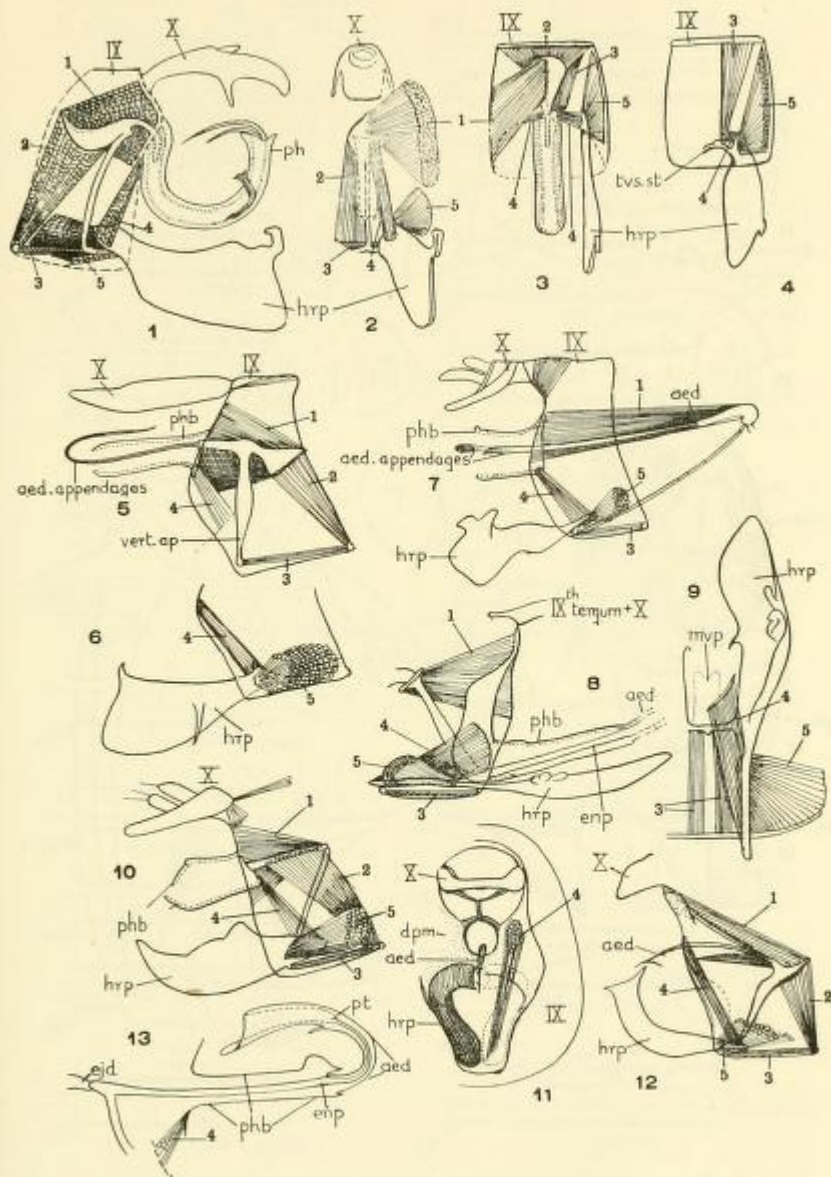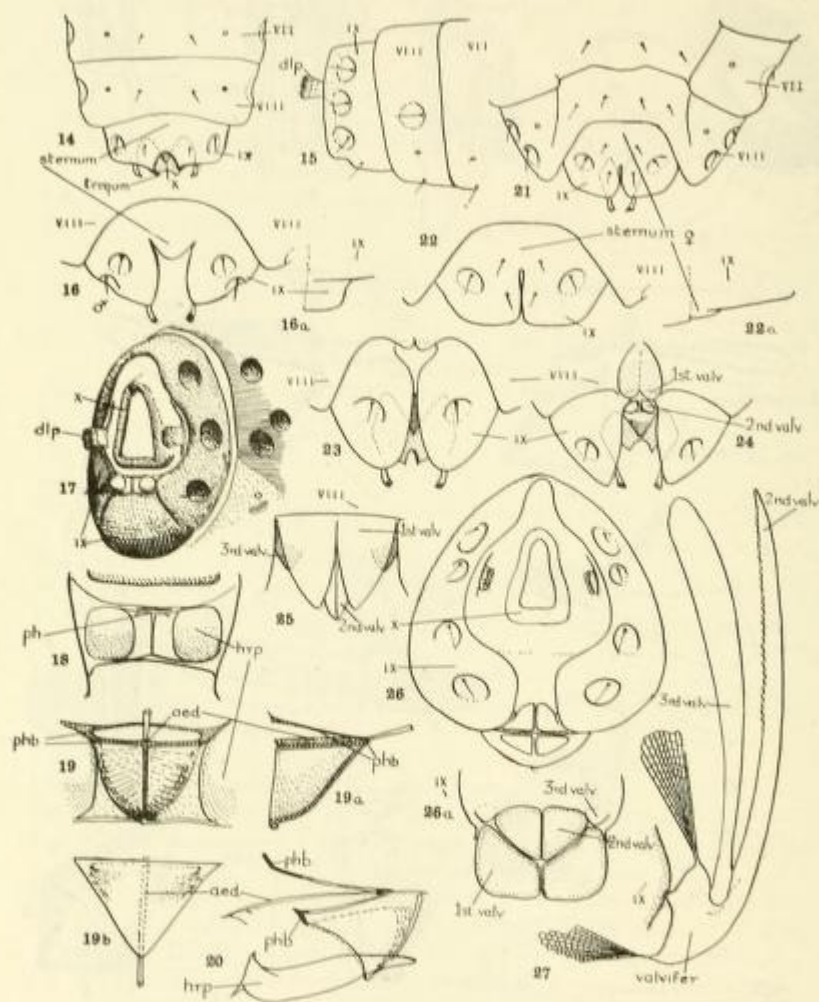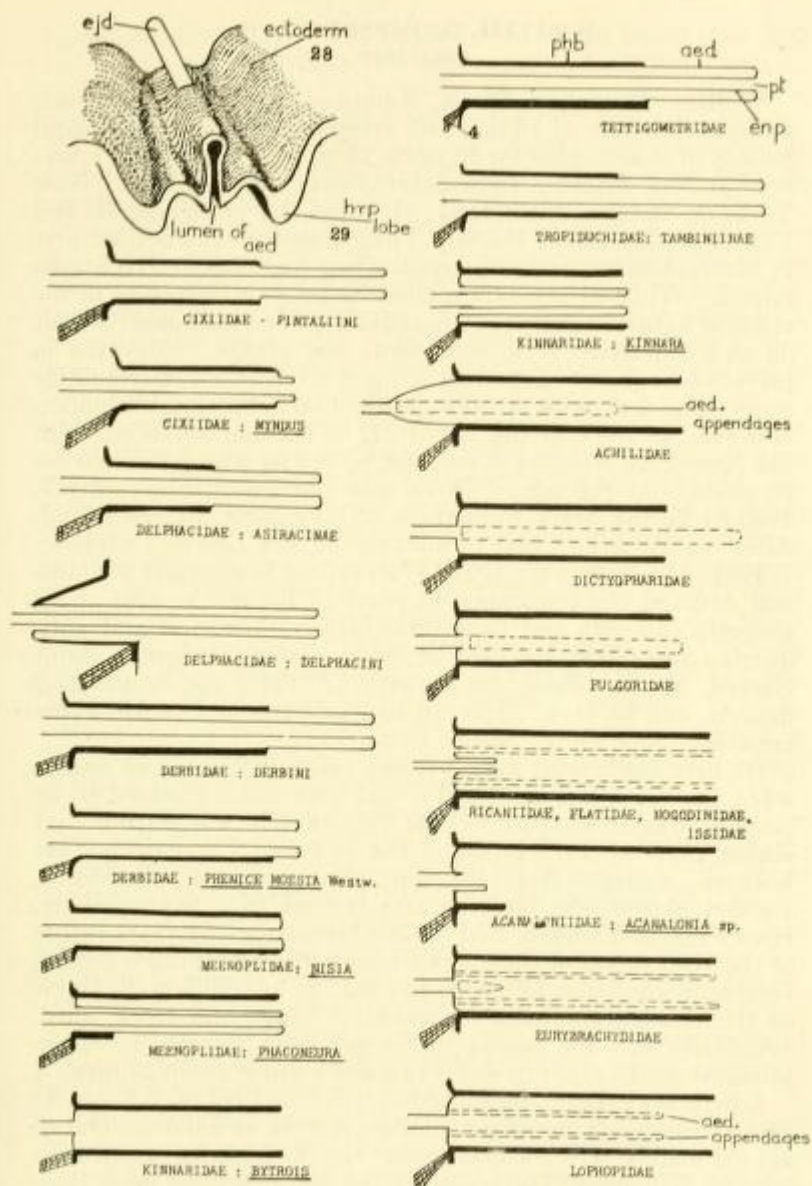
Footnote: For "Eurybrachydidae" above, read "Eurybrachyidae"