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THE GENITALIA OF THE AUCHENORHYNCHOUS HOMOPTERA.

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Most students of insect morphology consider that the male and female genitalia of insects are homologous, but it is also considered that in some groups of insects the female genital opening, or gonopore, is situated between the eighth and ninth abdominal sternites and the male gonopore between the ninth and tenth. So far as the Hemiptera are concerned these two views have never been reconciled, and the fact that the gonapophyses of the two sexes appear to pertain to different segments has been ignored, or used as an argument against the organs being homologous.

Observations made by one of the authors in England upon Cercopidæ and by the other in Honolulu upon Cicadellidæ and Fulgoroidea, agree in showing that the difference is only apparent and is due to development during the last nymphal instar. The gonopore in both sexes is between the eighth and ninth abdominal sternite (or at the base of the ninth sternite) and the three pairs of gonapophyses form the genital appendages.

CERCOPID FEMALE.

Observations were made upon more than one species of this family and our remarks in general apply to all, but the details refer to *Philaenus leucophthalmus* (Linn) which was the chief species used.

In the nymphs the sexes can be recognized in the second instar and it is possible that in carefully prepared specimens they could be recognized in the first instar. In the later nymphal stages they are quite distinct.

Between the eighth and tenth sternites there is an area the anterior portion of which we will call the genital area; anterior to this is the eighth sternite, which is well defined; posterior to it, and between it and the tenth, is an area which may represent the ninth, or it may represent the conjunctiva between the ninth and tenth, and the ninth may be represented in the genital area. From the genital area arises the gonapophyses.

In the female nymphs during the last instar the gonapophyses consist of three pair of subangular, fairly flat processes reaching more than half way back to the tenth sternite. The anterior pair (Fig. 1, g1) arise from the posterior edge of eighth sternite, although at an earlier period their connection with that sternite is not so apparent. The median pair (Fig. 1, g2) are smaller and lie immediately posterior to g1, and as they both point backward and g1 are larger than g2, therefore they lie beneath, or are covered up by g1. The posterior pair (Fig. 1, g3) are larger and hold a more lateral position and are concavo-convex. The genital opening or gonopore is at the base of g2.

In the adult female the eighth abdominal segment is short but well defined. That the segment in question is the eighth can be demonstrated by counting them, especially on the dorsal aspect; the presence of the last, or eighth, spiracle also indicates which segment it is. From the hind margin of the eighth sternite arises two processes (Figs. 2, 3, g1), which form the anterior or ventral process of the ovipositor. These are long, thin and narrow and *their outer basal angles are joined to the outer basal angles of the ninth tergite.* The eighth sternite overlaps their bases, but the membranous connection shows the relationship to the posterior margin of that segment. The ninth segment forms the pygofer (Fig. 2, pg), the tergite being large, but the extent of the sternite obscure and depends upon the composition of the genital area of the nymph. Two sclerites (Fig. 2, bp) which appear to be the valvifers of

Orthoptera, may represent the only chitinized portion of the ninth sternite; they form the supports of the posterior processes.

The median processes (Figs. 2 and 4, g2) lie immediately posterior to the anterior processes and are represented by a single, median process bifurcate on apical third and grooved along the ventral surface. This process is joined to the anterior processes by a tongue and groove joint and together they operate as the ovipositor, the gonopore opening at the base of g2 and the eggs passing along the ventral groove between g1 into the puncture made by the ovipositor. The posterior processes (Figs. 2 and 4, g3) are large and hold a lateral position slightly posterior to g2, and form a sheath for g1 and g2 when at rest. Beyond the pygofer is the anal segment (Fig. 2, 10 and 11) which is composed of the tenth and eleventh segment. Beneath the anus is the anal style (Fig. 2, a. s.), a median organ grooved along its dorsal surface. In no Homopteron, in either the young or adult, are the cerci present so far as we have observed.* Whether an anal style is present in Psocidæ where cerci are absent we are unable to say.

If we dissect an immature imago from the nymphal skin just before it moults we find that the apices of the adult, g1, g2 and g3 rest within the nymphal g1, g2 and g3 so there can be no question as to their homology.

Walker† in his admirable study of the ovipositor of Orthoptera, has shown good reasons for considering g3 as the coxites of the ninth sternite. In the nymphal stages of some Orthoptera g3 carry the styles which are lost before the adult stage is reached. In many Odonata these styles are retained in the adult. In the Cercopidæ there is evidence to indicate that g1 are the coxites of the eighth sternite but none to indicate that g3 are the coxites of the ninth. If they be, then the area between them and the tenth sternite is not the ninth sternite. This leaves g2 as the only true gonapophyses and their origin is open to speculation.

If we consider the genital organs as representing the "legs" of the eighth and ninth segments, then g1 would represent

*Huxley, in The Anatomy of Invertebrated Animals, p. 364, fig. 104, figures an Aphis in which cerci are present. Whether this is supposed to be drawn from an actual specimen or is only a composite figure, we are unable to state.

†Walker, 1919, Ann. Ent. Soc. Am. XIII, p. 267-316.

the coxites* of the eighth sternite, g2 the endopodites and g3 the coxites of the ninth sternite. The style of the abdominal sternites cannot represent the "legs" (endopodites) but the exopodites, unless we consider that the styles on the thoracic coxæ are not their homologies. In *Machilis heteropus* Silv. the "ovipositor" consists of two pair of appendages, one of which represents the endopodite of the ninth sternite and the other the endopodite of the eighth. A careful comparison of the male and female genitalia in a representative series of species of *Machilis* and allied genera would be of great morphological value.

CERCOPID MALE.

In the male nymph of *Philaenus leucophthalmus* (Linn) the gonapophyses arise in exactly the same place as in the female. In the earliest instar of the nymph g2 is a small, single median process, in the following instar it is bilobed at the apex (Figs. 5 and 6). In the last instar the genital processes are smaller than in the female and g1 are not in such close connection with the eighth sternite. A comparison of Figures 1 and 7 indicates the differences between the sexes.

In the adult male the segment behind the eighth forms a ring-like pygofer with the ventral margin produced into a pair of narrow, flat processes (gp) with a longitudinal line of weakness along the middle of the ventral surface (Figs. 8 and 9, g1 or gp). The tenth and eleventh segment form the anal segment, the posterior margin of the former being produced into two large, thick spines curved downward (Fig. 8) and the anterior margin into two small curved processes (Fig. 8). From the middle of the area between the anal segment and the gp of the pygofer arises three processes, a median penis or aedeagus (Fig. 8, p) and a pair of genital styles (Fig. 8, gs). The latter project well into the pygofer as apodemes (Fig. 8, gss) for the attachment of muscles.

If we dissect out an immature imago from the nymphal skin shortly before the final moult we find that the apices of gp lie

*Walker considers g1 and g2 to be similar organs of the eighth and ninth segments. This would make them both endopodites. Certain of the evidence appear to favor his view and we are quite prepared to accept it, but we have used the term coxites as their development in the Homoptera appear to indicate that they are those organs, rather than the endopodites.

within g1, the apex of p within g2 and the apices of gs within g3, but the last is obscure and the more difficult to trace. This shows their true homologies and also shows the homologies of the male and female, which can be represented as follows:

	Nymph	Adult ♂	Adult ♀
Anterior gonapophyses	g1	Genital plates	Outer { Processes of
Median gonapophyses	g2	Aedeagus	Inner { ovipositor
Posterior gonapophyses	g3	Genital styles	Ovipositor Sheaths

In many species of Cercopidæ g1 in the adult male are joined together into a single plate.

COMPOSITION OF THE ÆDEAGUS.

The ædeagus is a complex structure and the homologies of its parts not clear. In the adult *Philaenus leucophthalmus* (Linn) there is a large, chitinous bulb (Fig. 8, pa) which may represent the periandrium, and a straight penis (Fig. 8, p). On the ventral aspect of the apex of the penis is the orifice or gonopore (Fig. 8, gpr). It is possible that during copulation the ejaculatory sac may be protruded or evaginated and the gonopore or functional orifice be situated upon it. Figure 8 shows this sac slightly protruded. At the apex of the penis there are two large, curved hooks, the penis hooks (Fig. 8, ph), and below them four smaller processes in a circle. In the later nymphal stages the area around the base of g2 is invaginated, carrying with it both g2 and the bases of g3, (Fig. 10). The penis hooks (ph) of the adult lie within the bifurcations of g2, (Fig. 11). The bulb or periandrium (pa) evidently arises from the body wall, round the base of g2. The fact that g2 first arises as a single lobe and the bifurcation arises later may indicate that it is only the penis hooks that are homologous to the paired processes of the female and the rest of the ædeagus (the penis and bulb) are formed by outgrowths of the body wall.

Membracidæ

One of the authors* has published notes on the development of the genitalia of a membracid (*Tricentus*). In all its main features it is similar to the Cercopidæ.

Cicadellidæ.

Observations on *Eurymela* and *Deltocephalus mollipes* also show the same development as in the Cercopidæ.

Cicadidæ

No remarks are needed on the female genitalia, as they are the same as in Cercopidæ.

In the male Cicadidæ we have a very distinct type of genitalia. Although we have not followed the details of development so thoroughly as in Cercopidæ, yet enough is known to clearly indicate the line of development and the homologies.

In forms such as *Pompomia maculaticollis* the seventh sternite is large and produced considerably posteriorly where it is slightly emarginate in middle or broadly and slightly bilobed. Whether this extension represents a development of the seventh coxites we cannot say. The eighth sternite forms a large plate which almost conceals the pygofer from below. Posteriorly it narrows to a blunt point at apex, which has a cleft in middle, thus making it bilobed. This represents the eighth sternite and coxites and the eighth spiracles are situated near its basal angles. The pygofer is large, its medioventral surface membranous. From the lateral margins arise a pair of non-articulated processes which represent the much reduced g3. From the middle of the opening of the pygofer arises the ædeagus, which in most Cicadidæ is long, thin and tubular, but in some complex and trilobed. The anal segment is similar in composition to that of the Cercopidæ; in some species it is complex.

If our interpretation of the large plate below, or anterior to, the pygofer, be correct, then it will represent a more generalized type than the Cercopidæ so far as this structure is concerned; but the reduced and non-articulate genital style is a specialization. The plate in question represents the hypandrium.

*Kershaw, 1913, Ann. Soc. en Belgique, 57 (191-201).

The Cicadidæ differ from all other Cicadoidea and Fulgoroidea in that the coxites of the eighth sternites, or g1, are not incorporated into the pygofer, whereas in all the other families they are.

Fulgoroidea.

In the Fulgoroidea we have a third type, which is a development of the Cercopid type. There is a complete pygofer often forming a more or less complete chitinous ring, one pair of articulate genital styles and an ædeagus, which is often very complex. The genus *Tettigometra* is an exception, for along with other Cicadoidean characters it has a pygofer similar to Cercopids, with two pairs of styles. In the genus *Hilda* g1 are more completely amalgamated to the pygofer. On account of the availability of material *Perkinsiella saccharicida* Kirk (Delphacidæ) has been selected as a type, although its small size makes it unsuitable for observing the development.

In the female nymph the ninth tergite forms nearly a complete circle, having a small opening on the ventral aspect (Figs. 12, 9), the anal segment and genital area being sunk into this ring. At the posterior edge of the eighth sternite, between the lateral margins of the ninth tergite, arises the gonapophyses. Only the paired g1 and the single, median g2 are visible, but upon dissecting the g3 are found beneath the larger anterior processes (Fig. 13); g2 is not bilobed at the apex. The homologies of the adult processes can be demonstrated by the apices of the processes of the immature imago lying within the nymphal processes. They are similar to those of the Cercopidæ, but much longer, and as the imago develops within the nymph the base of the ovipositor has to move forward towards the thorax, taking along with it the median portion of the preceding sternites. This causes the abdominal sternites of the adult to be V-shaped and the ovipositor to appear as if arising far anterior to the apex of the abdomen. The pygofer is also carried forward so that it is long and narrow. In many Fulgorids the ovipositor is short and projects beyond the end of the abdomen, or is nearly or quite abortive; in these cases the abdominal sternites are not V-shape.

In the male nymph of *P. saccharicida* the ninth tergite is similar to that of the female, but the gonapophyses are much

smaller and more obscure. In the adult the pygofer forms a ring; from its medio-ventral edge arises two small, laterally flattened spines; a pair of moderately small, flattened genital styles arise near the ventral margin, with a more or less chitinous wall, the diaphragm, dividing them from the ædeagus which is subcylindrical, flattened laterally, with the orifice at the apex on dorsal aspect, with two spines near the orifice. A chitinization of the body wall connects the base of the ædeagus with the base of the anal segment, and there is a chitinous connection between the base of ædeagus and the base of the genital styles.

If we dissect out the immature male from the nymphal skin we find that the body wall at the base of the ædeagus is invaginated, but the genital styles are not carried with it, there being a fold of the body wall between them, (Fig. 19, dia). It is this fold which forms the diaphragm of the adult. At an early stage of development the ædeagus is a simple tubular body with the opening slightly before the apex; the genital styles are proportionally short and flat and the two processes on the ventral margin of pygofer (g1) are relatively large. (Figs. 15, 16 and 17). At the stage shown in Figure 19 they are more than half the length of the genital styles.

In most of the Delphacidæ there is no trace of g1 in the fully developed pygofer; in a few there is a single median process, but the genus *Perkinsiella* has a pair of processes which varies in shape and size in each species. The genus *Pissonotus* shows g1 very well developed (Fig. 20). Among other fulgorids g1 are often well developed (i. e., *Olonia picea*, Eurybrachidæ and *Eurynomeus granulatis*, Achilidæ).

Among the thousand and more genera of the Fulgoroidea the differences of ædeagus are very great, but they can be reduced to three sub-types, which we will refer to as Tettigometroid (A), Delphacoid (B) and Flatoid (C). The Tettigometroid, for other reasons besides the type of male genitalia, we consider as the most primitive type of fulgorid. In the genus Tettigometra the pygofer is of the Cercopid type. In *Hilda breviceps* g1 are incorporated into the pygofer; the periandrium is large and bulb-like and the ædeagus very short, the conjunctiva being distinct; the penis-styles apodemes are well developed. The medio-ventral margin of pygofer is produced.

The more common form of this subtype is found among the Cixiidæ (i. e., *Oliarus*), where the periandrium forms a fairly long tube more or less chitinous and often bearing large spines and other processes, the penis is often complex and produced into processes and more or less membranous so that the conjunctiva is not sharply defined; the penis apodeme passes through the periandrium and joins the base of the penis. The following families have this subtype: Tettigometridæ; Cixiidæ in part; Delphacidæ in part; Tropiduchidæ in part; Derbidæ modified.

In the Flatoid subtype the periandrium is shorter and wider, and generally funnel shape and the penis is invaginated into the periandrium and is also often funnel shape. Both the periandrium and the penis often form a short tube or ring bearing lateral processes. The complexity is very great in some forms (i. e., *Capelopterum maculifrons*, Issidæ). The Meenoplinæ of the Cixiidæ come under this type and thereby add one more character by which they approach the Flatidæ. The following families have this type of ædeagus: Flatidæ, Acanaloniidæ, Ricaniidæ, Issidæ, Dictyophoridæ, Fulgoridæ, Achilidæ, Eurybrachidæ, Lophopidæ and Cixiidæ in part.

The Delphacoide subtype contains Delphacidæ in part and Tropiduchidæ in part. In it the periandrium is greatly reduced or absent and the penis alone forms the ædeagus and is generally tubular. The periandrium generally forms a small ring at the base of the ædeagus and is joined by a chitinous structure to the base of the anal segment.

FURTHER SPECULATIONS.

We consider that the facts briefly stated in this paper are sufficient to demonstrate the homology between the genitalia of the two sexes, and between the Fulgoroidea and the Cicadoidea. There is much work still to be done in all the groups, especially in the Fulgoroidea where the variation in detail, especially in the ædeagus, is very great. Exactly what becomes of the ninth sternite has yet to be shown, also the nature of the area between the ædeagus and the anal segment.

Turning to other orders we find that the Lepidoptera and Trichoptera appear to be built upon the same morphological plan as the Fulgorids. There is a ring-like segment which

appears to be the ninth, a small anal segment, one pair of articulate genital styles and a median ædeagus. They are so similar that it appears only logical to conclude that they have a similar origin and development. At least it urges us to study the pupal stage and the immature imago to see if any evidence of such a development can be found. The Lepidoptera possess no cerci in the males while the Trichoptera possess cerci.

Elsewhere one of the authors has insisted that no evidence has been brought forward to show the homology between the male and female gĕnitalia of Coleoptera, and that in many forms the male gonopore appears to open between the ninth and tenth sternites. If in the Homoptera the coxites can be disassociated from the eighth sternite and become amalgamated with the ninth tergite so as to appear as the ninth sternite, it is highly probable that the same has happened in Coleoptera. But until direct evidence is brought forward showing that such is the case, we must not dogmatically assert that it has. Wherever the hypandrium appears as the ninth sternite we must bear in mind the possibility of it being the coxites of the eighth sternite.

If this homology of the sexes in Coleoptera can be demonstrated, it helps us to understand the wonderful coadaptation between the internal sac and the uterus, for they are then true homologies and the cause which modifies one can modify the other in the same manner. The question is worthy of further study.

EXPLANATION OF PLATE XIII.

Philænus leucophthalmus.

Fig. 1. ♀. Ventral view of VIII-X sternites of nymph, last instar.
Fig. 2. ♀. Lateral view of apical abdominal segments of adult.
Fig. 3. ♀. Anterior processes of ovipositor.
Fig. 4. ♀. Median and posterior processes of ovipositor.
Fig. 5. ♂. Gonapophyses at an early stage.
Fig. 6. ♂. Gonapophyses penultimate nymphal stage.
Fig. 7. ♂. Ventral view of VIII-X sternites of nymph, last instar.
Fig. 8. ♂. Lateral view of apical segments of adult.
Fig. 9. ♂. Ventral view of pygofer.
Fig. 10. ♀. Aedeagus and one genital style of immature adult.
Fig. 11. ♂. Median gonapophyses, last nymphal stage, showing the immature adult stage within it.

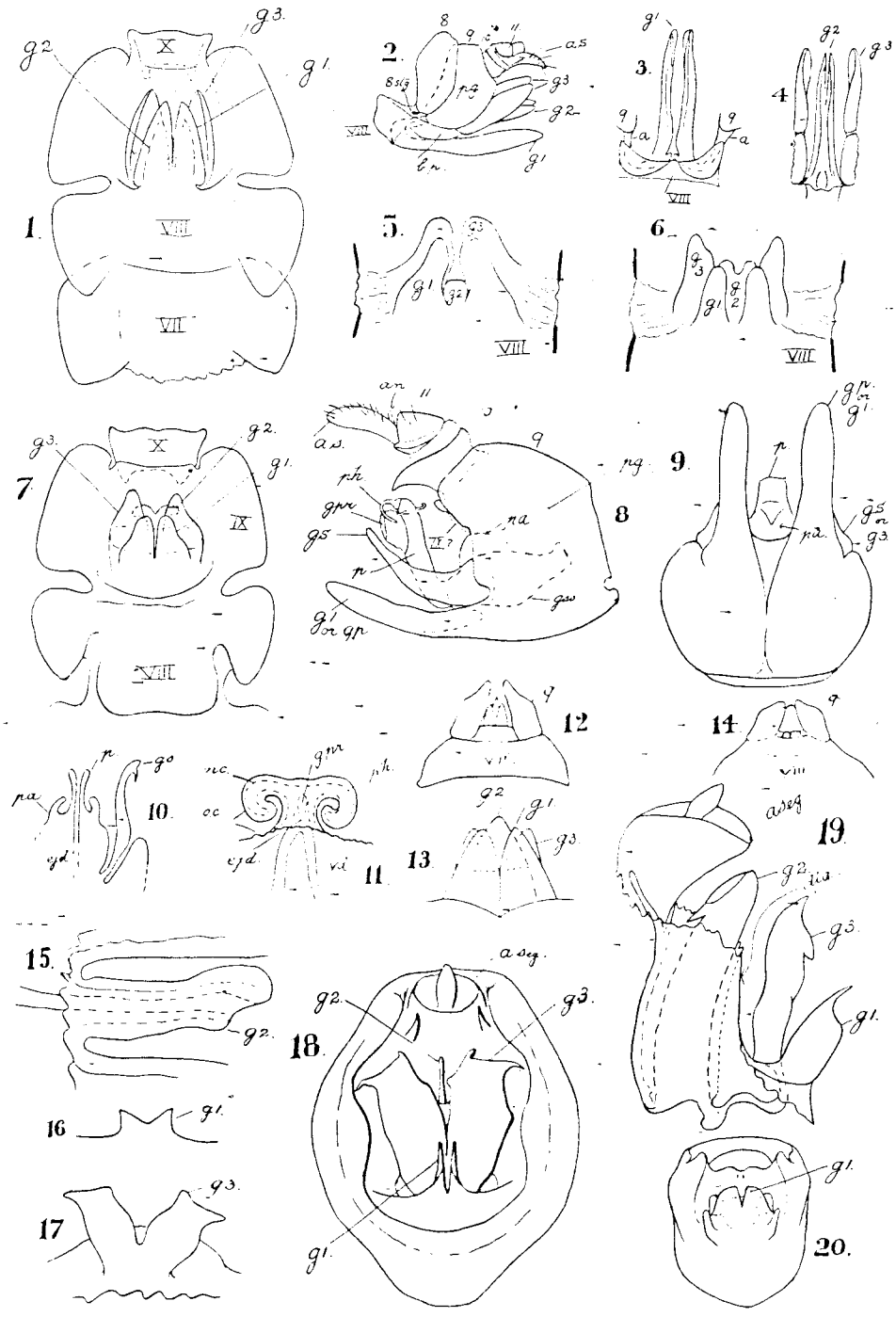
Perkinsiella saccharicida.

Fig. 12. ♀. Ventral view of last abdominal segment of nymph, last instar.
Fig. 13. ♀. Gonapophyses of same, enlarged.
Fig. 14. ♂. Ventral view of last abdominal segments of nymph, last instar.
Fig. 15. ♂. Aedeagus of immature adult.
Fig. 16. ♂. Anterior gonapophyses of immature adult.
Fig. 17. ♂. Posterior gonapophyses of immature adult.
Fig. 18. ♂. Full view of pygofer of immature adult.
Fig. 19. ♂. Lateral view of anal segment æedeagus, anterior and posterior gonapophyses of immature adult just before final larval moult.

Fig. 20. *Pissonotus frontalis.* Full view of ♂ pygofer.

LETTERING OF FIGURES.

a. seg. = Anal segment.
an = Anus.
as = Anal style.
bp = basal plate.
dia = diaphragm.
ejd = ejaculatory duct.
gpr = gonopore.
gss = apodeme of genital style.
g1 = anterior gonapophyses = *gp* or genital plates.
g2 = median gonapophyses.
g3 = posterior gonapophyses = gs or genital styles.
nc = new cuticle.
oc = old cuticle.
p = penis.
pa—periandrium.
pg = pygofer.
ph = penis hooks.
8 *stg* = 8th stigma.
8, 9, 10. 11 = tergites.
VIII, IX, X = sternites.



Kershaw and Muir.