On the Status of the Anterior Processes of the Male Genitalia in Homoptera.

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A number of workers have written upon the genitalia of Homoptera, and, while the majority agree that the posterior two pairs of gonapophyses in the two sexes are homologous, Kershaw and the writer appear to be the only two to regard the anterior pair in the two sexes as also homologous. It may, therefore, be well to restate, perhaps a little more fully, the evidence and reasons for so doing, and to point out that the question is not so simple as such writers as Crampton,[1] Hackman,[2] and Doering[3] appear to regard it.

In the female Homopteron the anterior genital processes, or ventral valvulae, arise as processes from the posterior margin of the eighth sternite or from the membrane immediately posterior to the eighth sternite; the posterior two pairs, the inner valvulae and the dorsal valvulae, arise from the membrane posterior to the ventral valvulae. There is no defined ninth sternite, and if all the ventral surface of the ninth segment be sternite, then these processes arise from the basal portion of the sternite. This is hardly likely to be the case, especially as in the orthopteroid insects they arise from the posterior margin. It is more likely that the ninth sternite is greatly reduced and the area posterior to the genital processes represents the connecting membrane between the ninth and tenth sternites. During ontogeny the ventral valvulae move away from the eighth sternite, and in the adult are often far from their point of origin, to which they are connected only by a membrane (i. e., *Diapheromera femorata*); they also become closely connected to the ninth tergite, either direct or through the valvifer. The valvifer appears to be all that remains of the ninth sternite in the adult, and it is larger in the Homoptera than in the Orthoptera (sens. lat.); as it is situ-

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[1] Crampton, Bull. Brooklyn Ent. Soc., XVII, pp. 46-55, 1922.

[2] Science Bull., University of Kansas, XIV (7), pp. 189-209, 1922.

[3] Science Bull., University of Kansas, XIV (21), pp. 515-587, 1922.

ated at the base of the dorsal valvula, it seems reasonable to suppose that the latter arises from the posterior margin of the ninth sternite. The fact that the ventral valvulae leave the eighth sternite and become intimately related to the posterior angles of the ninth tergite is important, as *this is the condition of the genital plates in the male.*

In the male Homopteron the anterior processes or genital plates arise from the membrane immediately posterior to the eighth sternite, and the posterior two pairs of processes (the aedeagus and the genital styles) arise from the membrane immediately posterior to the genital plates. The ninth tergite is no more defined in the male than in the female in the nymphal stages, and as most writers on this subject consider that the aedeagus and genital styles are the homologies of the inner and dorsal valvulae, and, therefore, arise from the posterior margin of the ninth sternite, it appears to follow that the area posterior to those processes must be the connecting membrane between the ninth and tenth sternites, as in the female.

In this respect the condition found in Odonata is of interest, for here the ninth sternite, with its appendages, is but a small anterior portion of the large area that forms the ventral surface of the ninth segment.

Doering states that "the three pairs of valves in the male arise from a genital area on the ninth segment, while in the female one pair comes from the eighth and two from the ninth." Hackman also states that "The male genitalia, consisting of three pairs of valves arise from a genital area on the ninth abdominal segment" and "The ventral pair (of appendages of the ovipositor) arises from the eighth sternum, and the dorsal and lateral pairs arise from the ninth sternum, the dorsal pair from its cephalic margin, and the lateral pair from its caudal margin." But no explanation is given why it should be "a genital area" in the male and a "ninth sternite" in the female, and Hackman's figures do not bear out his statement that, in the female, the "dorsal pair arise from the cephalic margin, and the lateral pair from its caudal margin." In fact, this statement runs counter to our knowledge of the origin of the organs in Orthoptera, and to the generally accepted belief in their homology to certain parts of the appendages of crustaceans.

Even if the ventral valvulae of the ovipositor always arose from the eighth sternite and the genital plate from the membrane immediately behind the eighth sternite, this would be no evidence that they were not homologous. The ventral valvulae always leave that position and take up one similar to the genital plates, viz., connected with the posterior angles of the ninth tergite. It would only indicate that development in the male was a stage in front of the female, which should not be wholly unexpected if we consider the greater specialization of the male. This is one of the foundations of the biogenetic law, that specialization in the adult causes preceding stages to appear earlier.

In discussing the hypandrium, Crampton says: "The hypandrium or sternite beneath the genital apparatus of the male insect may occur as a distinct plate such as the one labeled *ha* in Figs. 1 and 9, or it may be indistinguishably united with the pleural region of the ninth uromere. In the insect shown in Fig. 3, a pair of posterior lobes *hv* are beginning to form in the hinder region of the hypandrium *ha,* and in the insect shown in Fig. 13 (compare also Figs. 17 and 18) these lobes have assumed the form of the hypovalvae *hv* or hypandrial valves. In the insect shown in Fig. 12, these valves became proportionately larger, and in the insect shown in Fig. 25 the hypovalvae *hv* are demarked from the remainder of the hypandrium *ha* by a faint suture. In the insects shown in Figs. 22 and 26, these valves *hv* have developed an articulation with the remainder of the hypandrium *ha,* and during copulation they fit on either side of the hypogynium or subgenital valve *hg* of the female insect, as is shown in Fig. 26."

The above statements take it for granted that the line of evolution of the hypandrium (or genital plates) is from small, fixed processes to large articulated processes. If this were so, then we should expect to find them absent or only slightly developed in the more generalized groups of Homoptera, and largest and most highly developed in the more specialized. As a fact, we find just the reverse. In the Jassidae, Cercopidae, and Membracidae, we find these processes most frequently represented and most highly developed. In the Sternorhynchi they appear to be absent, at least as independent organs. In the fulgorids they are absent in most cases, or so highly modified and incorpo-

rated into the pygofer that they are difficult to recognize. Among the fulgorids they are most plainly to be seen in the Tettigometridae, the most generalized of the superfamily. The genus *Eurymela* and its allies form some of the most generalized of the Jassidae, and among them we find the genital plates large, free, and with a movable process. The fact that these first appear as paired processes and afterwards join together or amalgamate with the pygofer does not bear out Crampton's contention.

The solution of this matter lies in the disposition of the ninth sternite; in the nymph there is no sternite which we can recognize as such, and during ontogeny no such sternite can be recognized. In the adult *Eurymelus* there is a very slender strip of chitin which runs across the ventral surface from the basal angles of the pygofer or ninth tergite; it may be a development of this which forms the triangular plate called the ventral valve in some of the higher forms. But there is no evidence that this has anything to do with the ninth sternite.

In the Cicadidae the medio-ventral portion of the pygofer is membraneous, and it is possible that it is not homologous with the ventral portion of the pygofer in other Homoptera. Crampton has also recognized a difference, for in the Cicadidae he calls the eighth sternite the hypandrium, while in other Homoptera it is the ventral portion of the pygofer, a view which agrees with the writer's.

Turning to the opposition interpretation, we have some strong evidence in such insects as *Nicoletia.* Here we find in the male a well-developed ninth sternite bearing styles between which arise a pair of "appendices genitales,"[1] and posterior to these a distinct median penis. It appears probable that the articulated "appendix urosterni" of the fourth sternite of *Nicoletia ruckeri* are homologous with the unarticulated appendages on the same sternite of *N. wheeleri,* and both with the "appendices genitales" of the ninth segment. If we use the condition found in *Nicoletia* to explain the conditions in Homoptera, we can then understand the ventral part of the pygofer, the genital plates and the genital styles, but we then have to find another origin for the penis, as

[1] Silvestri, Redia, II (1905), pp. 111-120, PL. XI.

the endopodite and exopodite are already accounted for. If we accept it as a median organ arising from the intersegmental membrane between the ninth and tenth sternite, then all is well, but there is no evidence of a third pair of organs on the ninth segment which we can call upon for an explanation.

And here we can call in question the advisability of transferring our interpretation in one order where the evidence is plain to other orders where the evidence is conflicting. The gonopore has shifted its position in a number of cases among insects, and it is quite possible that the armature around it are not always arranged in the same manner.

Thus the status of the anterior genital processes (genital plates, hypovalvae or hypandrium) in male Homoptera is still uncertain, and the evidence that they are the homologues of the ventral valvulae of the female is strong enough to merit consideration.