COMPARATIVE STUDIES OF THE MALE GENITALIA OF THE HEMIPTERA (Homoptera-Heteroptera)[1]

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This paper presents the results of a comparative morphological study of the male genitalia of the Hemiptera (Homoptera-Heteroptera). Many different names have been given to the structures that make up the copulatory apparatus of the males of the Hemiptera. This situation has led to much confusion among both the taxonomists and the morphologists as to a nomenclature which is both morphologically accurate and suitable for the use of the taxonomist.

The present study was taken up at the suggestion of Dr. C. D. Michener whose interest in the homologies of the genitalia throughout the various orders of insects resulted in a paper suggesting a uniform nomenclature based on interordinal homologies of the structures which make up the genitalia (Michener, 1944). The nomenclature suggested in that paper will be followed insofar as is possible.

Considerable work has been done on this problem and many speculations have been made concerning the homologies of the structures found in the genitalia of the Hemiptera. Most of this work has been summarized and evaluated by Singh Pruthi (1925) who has published a comprehensive study of the genitalia of the Hemiptera. His numerous figures, representing most of the major groups, are excellent and should be consulted by anyone wishing to study such genitalia in detail. The comprehensibility of his paper, however, is somewhat limited by the system of nomenclature used and by the vagueness of the author regarding the homologies of some of the structures involved.

Snodgrass (1935) in his excellent work on insect morphology gives the genitalia of the Hemiptera only a superficial treatment and suggests that further study is needed to determine the homologies of the parts.

The present study was undertaken to coordinate the works of these three authors and to point out the homologies existing between the genitalic structures of the Homoptera and Heteroptera. A nomenclature is proposed for these parts which, it is hoped, will be acceptable to the taxonomist and the morphologist alike. The origin of the somewhat complicated internal capsule of the Heteroptera from the simple condition existing in the Homoptera is also explained on a comparative morphological basis. It should be emphasized that the genital capsule of the Hemiptera is the ninth segment and that the internal capsule is entirely different in structure. Table I compares the nomenclatures used by the three previously mentioned authors and contains certain addition which now seem necessary.

In the present study, members of the following families were examined: Cicadidae, Fulgoridae, Psyllidae, Cicadellidae, Cercopidae, Membracidae,

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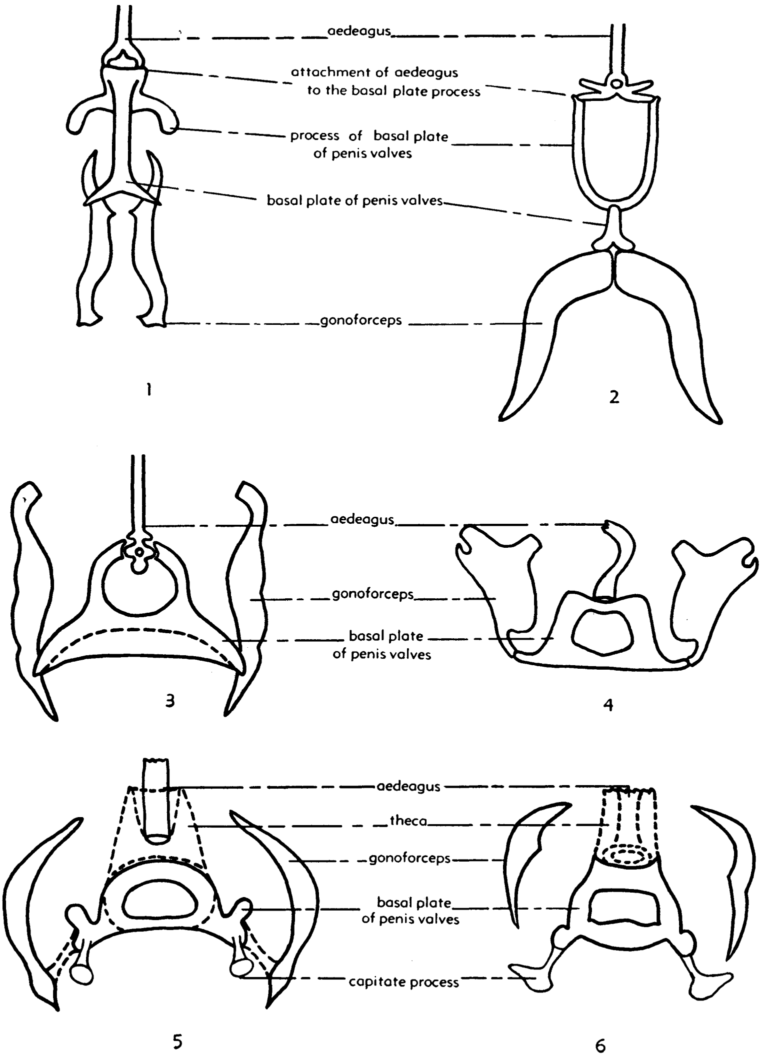


PLATE I

EXPLANATION OF PLATES

Plate I. Ventral view of hard parts of male genitalia dissected out and laid out flat.
Fig. 1. *Oecleus snowi* Ball (Fulgoridae)
Fig. 2. *Pachypsylla venusta* Osten Sacken (Psyllidae)
Fig. 3. *Leparonia quadrangularis* (Say) (Cercopidae)
Fig. 4. *Locris* sp. (Cercopidae)
Fig. 5. *Pentacora signoretti* (Guérin-Méneville) (Saldidae)
Fig. 6. Miris dolobratus (Linnaeus) (Miridae)

TABLE I

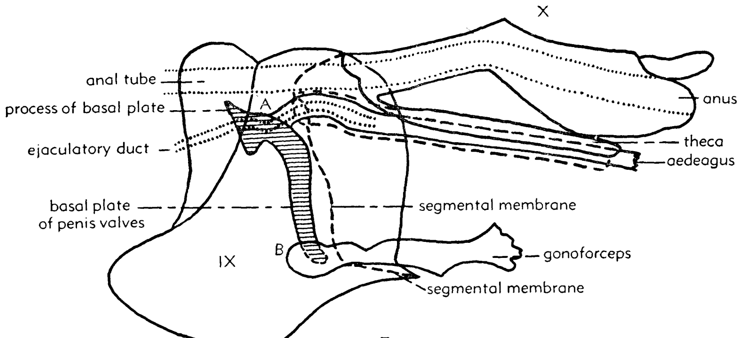
SINGH PRUTHI	SNODGRASS	MICHENER	MARKS
parameres	harpagones	gonoforceps	gonoforceps
basal plate	phallobase (basal plate no. 1)	fused basal portions of the gonopophyses	basal plate of the penis valves
basal plate prolongation	basal plate no. 2	————	lateral process of the basal plate
phallosoma	phallobase	————	theca
aedeagus	aedeagus	aedeagus	aedeagus
————	————	————	capitate process
segmental membrane	segmental membrane	segmental membrane	segmental membrane
genital chamber	genital chamber	————	genital chamber (internal capsule)
ninth sternum	ninth sternum	ninth sternum	ninth sternum

Saldidae, Miridae, Pentatomidae, Lygaeidae, Gerridae, and Corixidae. In all over a hundred dissections were made. From this series six insects were selected as representing a graded series depicting the homologies of the structures described in this paper. The specimens were cleared in warm ten percent caustic soda, washed in weak acetic acid, and stained in acid fuchsin. The dissections were made in a drop of glycerine under a binocular microscope.

In a hypothetical primative homopteron the genitalia may be described as follows; The gonoforceps, representing the fused gonocoxite and gonostylus or perhaps the gonocoxite alone, are articulated to the ventral, caudal edge of the ninth sternum. The basal plate of the penis valves, representing the fused proximal portions of the gonopophyses, is articulated to the gonoforceps at the point of attachment of the latter to the ninth sternum. From this point, lying in the segmental membrane, it projects dorsad articulating at the dorsal extremity with the base of the aedeagus. The latter extends caudad and is composed of the primative penis and the fused distal portion of the penis valves (i.e. the distal portions of the gonopophyses). The closing or segmental membrane between the margin of the ninth sternum and the base of the tenth is attached at the edges of the ninth segment and is produced caudad to form more or less of a theca around the aedeagus.

The condition described above is closely approximated in the fulgorid, *Oeclus snowi* Ball. As seen in fig. 1 Plate I, in which the hard parts of the genitalia have been dissected out and laid flat, the gonoforceps are articulated to the lower edge of the basal plate of the penis valves. This plate is articulated at its distal end to the base of the aedeagus. Just below this point of articulation two lateral processes belonging to the basal plate are present. As will be noted in fig. 7 plate II, the gonoforceps are attached to the segmental membrane just behind the ninth sternum while the basal plate and the basal portion of the aedeagus have moved inward and have lost their connection to the segmental membrane. In addition to this, the venter of the tenth segment is produced to form a dorsal support for the aedeagus. These latter adaptations, however, appear to be secondary in nature.

Fig. 2 plate I shows the hard parts of the genitalia of *Pachypsylla venusta* Osten Sacken dissected out and arranged in a comparable position. Here it



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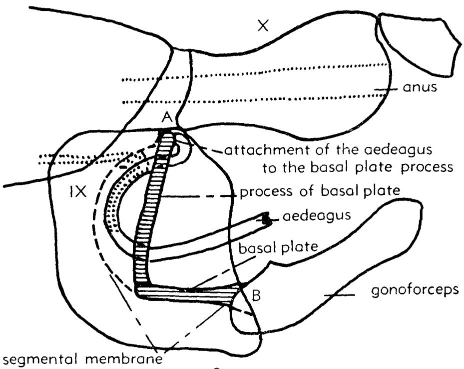

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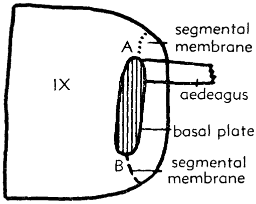

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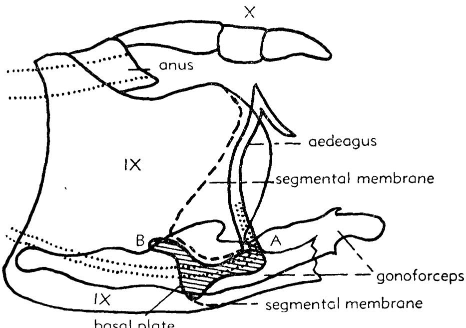

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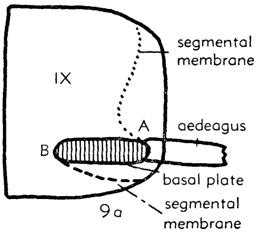

PLATE II

Plate II. Lateral view of the ninth segment and genital appendages.

Fig. 7. *Oecleus snowi* Ball (Fulgoridae)

Fig. 8. *Pachypsylla venusta* Osten Sacken (Psyllidae)

Fig. 8a. Diagram illustrating positions of the aedeagus and basal plate as seen in fig. 8.

Fig. 9. *Leparonia quadrangularis* (Say) (Cercopidae)

Fig. 9a. Diagram illustrating positions of the aedeagus and basal plate as seen in fig. 9.

will be seen that, as before, the gonoforceps are articulated to the basal plate of the penis valves which have been greatly reduced. The lateral processes of the basal plate are greatly elongated and have become articulated to the latter by a secondary articulation. At the distal ends of the elongated basal plate processes, the aedeagus is articulated, having shifted upward from the end of the basal plate.

In the cercopid, *Leparonia quadrangularis* (Say), as is seen in fig. 3 plate I, the basal plate is still farther modified until it appears as a bar connecting the gonoforceps. The processes, again fused with the basal plate and articulating with the base of the aedeagus, form an almost complete ring. In another cercopid *Locris* sp. fig. 4 plate 1, this trend of fusion and reduction is continued resulting in a complete ring with the aedeagus attached to the outer margin. It is not too clear, however, whether the basal portion of the aedeagus is actually incorporated in the ring or not.

It is of interest to note that the three above types of genital structure represent the three major types of homopteron genitalia and that all of those observed by the author or figured by Singh Pruthi can easily be related to one of these three types. The type found in the cicada is perhaps the most difficult to interpret. In this case the gonoforceps are absent. The basal plate of the penis valves is present however and resembles that of the fulgorid. The aedeagus in the specimens examined is membranous. The presence of a basal plate in the position typical of the fulgorid type indicates a relationship to the latter, the major differentiation being the reduction of the gonoforceps and the desclerotization of the aedeagus.

In relating the heteropteron type of genitalia to the homopteron type described above, several difficulties are encountered. These may be resolved most easily if we limit our observations for the present to the sclerotized ring found at the base of the internal capsule. This ring, figs. 5 and 6 Plate I, as can be seen by comparison with fig. 4, is homologous with the basal plate of the penis valves of the Homoptera. Fig. 5 plate 1 shows the basal plate of *Pentacora signoretti* (Guérin-Méneville), a saldid. The connection of the basal plate to the gonoforceps has become ligamentous. The fused penis valves of the aedeagus are no longer in evidence, the connection of the aedeagus to the basal plate being membranous and connecting around the edges of the ring. A secondary structure, which will be called the capitate process, has developed near the point of attachment of each gonoforcep to the basal plate. The homology of the basal plate of the Heteroptera to that found in the Homoptera is, however, quite evident.

In the type of genitalia found in the mirid, *Miris dolobratus* (Linnaeus) fig. 6 plate I, and, indeed in several of the other groups of Heteroptera examined, the attachment of the gonoforceps to the basal plate is very delicate and in some species appears to be completely missing. The position of the capitate processes, however, will serve to mark the original point of attachment. The attachment of the aedeagus to the basal plate is essentially similar to that found in the saldid. There is considerable variation in the different groups of the Heteroptera as can be seen from examining Singh Pruthi's plates. An understanding of the mirid type of structure will enable the reader to determine the necessary homologies for most of the group.

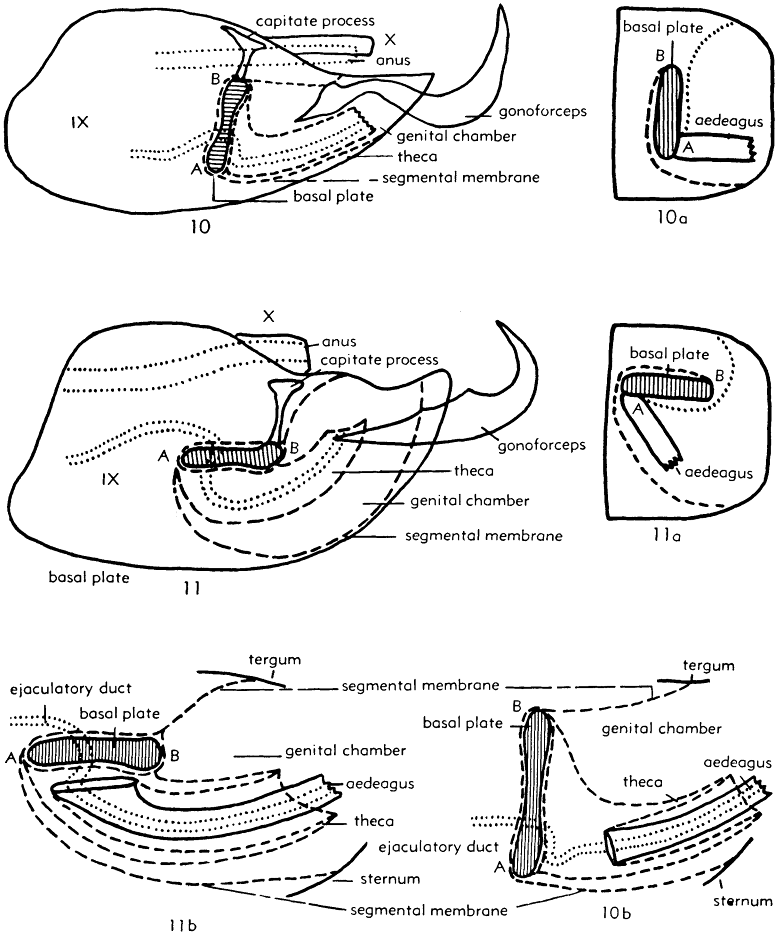

PLATE III

Plate III. Lateral view of ninth segment and genital appendages

Fig. 10. *Pentacora signoretti* (Guérin-Menéville) (Saldidae)

Fig. 10a. Diagram illustrating the positions of the aedeagus and basal plate as seen in fig. 10.

Fig. 10b. Detail of genital chamber as seen in fig. 10.

Fig. 11. *Miris dolobratus* (Linnaeus) (Miridae)

Fig. 11a. Diagram illustrating positions of the aedeagus and basal plate as seen in fig. 11.

Fig. 11b. Detail of the genital chamber as seen in fig. 11.

At this point the author wishes to make it clear that the series of insects described in this paper is not to be regarded as a phylogenetic series. These insects were selected because they show a graded series of steps in the development of the hemipteron type of genitalia. The author does imply that the sequence leading to the hemipteron type followed a similar developmental series. The ancestoral types are of course extinct and therefore unavailable for study but the phylogenetic sidelines have preserved enough of the intermediate stages in genitalic structure so that the homologies between the more primative Homoptera and the specialized Heteroptera can be established.

The contention that the forms discussed above show a developmental progression is strengthened by a study of the segmental membrane and the corresponding changes in the ninth segment and the basal plate. Plates II and III show diagrammatically the orientation of these parts in the normal resting position. Accompanying each of these figures is a diagram showing the relative positions of the genital parts. Figs. 7 and 8 Plate II show lateral views of a fulgorid and a psyllid respectively. The situation in these two insects is essentially the same and is diagrammed in fig. 8a. The basal plate is shaded and shown as a straight bar to facilitate visualization. The point of articulation of the aedeagus to the basal plate is marked as point A. The point of articulation of the basal plate to the gonoforceps is marked as point B. The position of the membrane which extends upward from point A to the base of the tenth segment is shown as a dotted line. The membrane which extends downward from point B to the posterior margin of the ninth sternum is shown as a broken line. In these insects the basal plate lies in the dorsoventral plane.

Fig. 9 Plate II shows the genitalia of a cercopid. In this case the basal plate of the penis valves has rotated ninety degrees and now lies in the anteroposterior plane. The dorsal portion of the segmental membrane extends downward and inward while the ventral portion extends upward and inward. The basal plate and the gonoforceps have moved inward, the latter being attached to the segmental membrane. Fig. 9a is a diagram showing the rotation that has taken place and the relative positions of the segmental membranes.

In the saldid, fig. 10 plates III, the basal plate has rotated another ninety degrees, again lying again in the dorsoventral plane but in a reversed position. The dorsal portion of the segmental membrane extends downward and inward, becoming attached to the edges of the basal plate. It now forms the dorsal wall of the genital chamber and is bulged outward around the base of the aedeagus. The ventral portion of the segmental membrane extends inward and upward, forming the ventral wall of the genital chamber and covering the anterior side of the basal plate. Coinciding with this development of a genital chamber, the ventral edge of the ninth sternum protrudes upward and outward, carrying with it the gonoforceps which are articulated to it. As a result the opening of the genital chamber lies on the upper surface of the ninth segment. With this change, the gonoforceps have been pulled away somewhat from the basal plate. The capitate processes extend upward toward the dorsal wall of the ninth segment. Fig. 10a illustrates this rotation and the relative positions of the segmental membrane. With the pulling away of the gonoforceps from the basal plate and the membranous condition of the base of the aedeagus, the articulation point of the gonoforceps to the basal plate is marked by the position of the capitate process. Similarly the articulation point of the aedeagus to the basal plate is marked by the position of the ejaculatory duct which is plainly visible in all cases, and which in all of the hemiptera examined passes between the processes of the basal plate before entering the base of the aedeagus. These two structures thus can be used as landmarks in following the rotation of the basal plate in the formation of the genital chamber.

In the mirid type of genitalia, fig. II Plate III, the basal plate undergoes further rotation and now lies again in an anteroposterior plane, having rotated a full two hundred and seventy degrees from the primative position found in the fulgorid. The rotation which results in the formation of the genital chamber can be visualized by following the series of figures: 8a, 9a, 10a, and 11a. The rotation illustrated in each case is ninety degrees, the total thus being two hundred and seventy degrees occurring between figures 8a and 11a. The attachment of the gonoforceps to the basal plate has become very delicate and in some cases appears to be absent entirely. The walls of the genital chamber which are membranous in the saldid have become sclerotized forming a definite internal capsule, often being firmly attached to the ventral wall of the ninth sternum. The aedeagus is a long membranous tube which is telescoped in the resting position so that its true structure can be determined only by teasing it out to its full length. There is some question as to just what structures are involved in the makeup of the hemipterous aedeagus. The aedeagus of the homopteron is well sclerotized, in all probability representing the fused penis valves and the primative penis which originates as an evagination of the segmental membrane. In the Hemiptera the penis valves have become desclerotized or are absent. Also the dorsal portion of the segmental membrane, due to the rotation of the basal plate, has become adnate to the latter and bulges outward forming a theca around the base of the aedeagus. These developments make it difficult to determine whether the aedeagal structure of the hemipteron is entirely homologous to that of the homopteron, or whether the dorsal portion of the segmental membrane enters into its consruction. Further study will be necessary to clarify this point. The work of F. S. Truxal (in press) on the genitalia of the Notonectidae shows a progressive reduction of the basal plate accompanied by an increase in the complexity of the aedeagus, showing a continuation of the line of development suggested here.

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