CHIEF TYPES OF MALE GENITALIA IN DIPTERA

In order to have an understanding of the natural affinities of various groups of Diptera, a comparative study of the male genitalia is of basic importance. In view of the great degree of confusion that exists in this field, it is necessary to establish certain basic patterns of genital structures, before making an effort to interpret the various homologies in the entire series. Instead of exploring morphology as a primary tool for bringing forth the natural affinities of the various taxa, earlier workers on Diptera seem to have been mostly contented with describing the structural features of the genitalia, taking rather for granted the genuineness of the major groupings of the classificatory scheme in vogue. A major objective of the present study was to rehabilitate morphology to its position of importance in a natural scheme of classification.

Morphologically, the male genitalia of Diptera can be grouped in two broad categories, viz., the Orthopygous type and the Campylopygous type. The former are in line with the longitudinal axis of the abdomen and possess the outer parameres, whereas the latter are tucked underneath so as to be invisible from above and lack the outer parameres.

(1) The Orthopygous Genitalia:

This type is the characteristic feature of the erstwhile Nematocera and the Brachycera, possessing the following distinguishing characters.

(a) The terga and sterna of the abdominal segments are symmetrically orientated, and are not displaced from the position normally occupied by them.

(b) In some cases, the last three or four segment of the abdomen
undergo a process of rotation through 180 which reverses the normal position of the terga and sternae of the segments affected by rotation.

(c) The ninth segment is an independent feature, and its tergum does not fuse with the succeeding tergum.
(d) The surstyli are usually absent.
(e) The ninth sternum is always in the form of a transverse plate.
(f) The outer parameres are present; and are well developed.
(g) The inner parameres spicily fuse with each other to form a composite structure.
(h) The intramittent organ always points backwards, and is not provided with a movable articulated internal apodeme.
(i) The tenth and the eleventh segments together form the proctiger.

The Orthopygous genitalia can further be subdivided into the Tipulomorphic type, and the Bibiomorphic type.

(a) The Tipulomorphic Type: (Figs. Pd.1-4)

An important outcome of the present study has been the discovery of the Tipulomorphic genitalia. The family Tipulidae is one of the most primitive families of Diptera, and the study of the skeleto-muscular system of the male genitalia of *Pachyrrhina dorsomaculata* has brought to light some very interesting features. For instance, it has exploded the myth that the Tipulidae are of little phylogenetic importance since their line of development was said to have ended blindly, without leading to any other 'neuroptocerous' family,— a contention put forward by Crampton (1942).

The present study has shown that so far as the genital pattern is concerned, the Tipulidae are not alone in the field. The Anisopodidae, the Tanyderidae, the Ptychopteridae, the Asilidae, the Empididae, and the Dolichopodidae, to cite some examples, possess Tipulomorphic type of genitalia.
The chief distinguishing characters of the Tipulomorphic genitalia can be summarised as under:

(a) The intromittent organ is very peculiar in the sense that it is derived from the ejaculatory duct, instead of the phallic buds.

(b) The intromittent organ is not straight. Shortly after its point of origin, it bends upon itself in the vertical plane before finally taking a posteriorly directed course.

(c) The intromittent organ is partially or fully enclosed in a membranous sac, the genital chamber, which originates as an invagination between the ninth and the tenth sterna.

(d) The genitalia may or may not undergo a process of rotation.

(e) The ninth segment is a prominent feature and is well developed.

(f) The outer parameres are not pronouncedly claw-, or pincer-like in appearance. Each paramere consists of a basimere and a telomere. The basimere may be independent, or fuse with its counterpart from the other side, or with the ninth sternum. The telomere is usually single, but in some instances may be represented by two or more pieces.

(g) The inner parameres usually present a complicated structure and are apically fused with each other to form a composite structure. They, however, retain their individual identity in the basal portion. In some instances, such as the Asilidae, the inner parameres may be lost.

(h) The genitalia are usually, though not invariably, somewhat laterally flattened.

(b) *The Bibiomorphic Type:* (Figs. Aa.1-2,5)

The present study which was based on the skeleton-muscular system of the male genitalia of *Aedes aegypti* has brought to light the second basic type of genitalia in Diptera. Since structurally the genitalia of this type are similar
to those of the primitive family Bibionidae, it has been named as the Bibiomorphic type. The Cecidomyiidae, the Dixidae, the Chironomidae, the Simuliidae, and the Tabanidae, besides the Culicidae and the Bibionidae, are some of the families which possess the Bibiomorphic type of genitalia.

The chief distinguishing characters of the Bibiomorphic Genitalia can be summarised as under:

(a) The well developed claw-like or pincer-like outer parameres are the most conspicuous feature of this type. The basimere is very well developed. It may be independent or get fused with its counterpart from the other side, or with the ninth sternum. The telomere which is basally articulated with the distal end of the basimere, works in a pincer-like manner.

(b) The inner parameres are intimately associated with the aedeagus and have, therefore, been regarded as 'penis valves' by many workers. Even if they fuse with each other, the inner parameres do not lose their identity in the basal portion.

(c) The aedeagus is relatively a short and stout structure and never pronouncedly bends upon itself.

(d) There is no membranous genital chamber.

(e) The ninth segment is relatively much reduced as compared to its counterpart in the Tipulomorphic type.

(f) The genitalia may or may not undergo rotation.

(g) The genitalia are usually, though not invariably, somewhat dorso-ventrally flattened.

(2) The Campylopygous Type of Genitalia:

The Campylopygous genitalia are a characteristic feature of the erstwhile Cyclorrhapha, possessing the following distinguishing characters.

(a) The genitalia undergo a process of retro-inversion so as
to be concealed from view from above. The strain of this process results in the displacement and modification of the terga and sterna of the preceding three or four segments.

The fifth tergum is not affected by retro-inversion. The fifth sternum, however, is usually somewhat displaced from its normal position.

The sixth tergum may or may not be reduced or lost. The sixth sternum is drawn into a more or less lateral position in the left side of the abdomen. Its upper end is closely associated, even fused, with the antero-ventral aspect of the seventh sternum.

The seventh tergum, with the exception of certain Syrphidae and Dorilaidae, is usually atrophied. The seventh sternum is drawn into the left side of the abdomen still higher up than the sixth sternum, and gets partially or totally merged with the eighth tergum (and not eighth sternum, as generally believed).

The eighth tergum is usually closely associated with the genital syn-tergum. The eighth sternum, with certain exceptions, is incorporated in the antero-ventral aspect of the genital syn-tergum, as revealed by the studies of the present writer.

(b) The ninth tergum is always fused with the tenth tergum to form the genital syn-tergum.

(c) The outer parameres are absent.

(d) The inner parameres may be vestigeal or well developed.

(e) The surstyli are present.

(f) The ninth sternum is U-shaped or horse-shoe shaped.

(g) The aedeagus points forwards or downwards.

(h) The tenth sternum may be partially or totally lost as a definite sclerite.

(i) The eleventh segment forms the protiger.
The Campylopygous genitalia can further be divided into the Syrphomorphous type, the Drosophilomorphous type, the Muscomorphous type, the Tachinomorphous type, the Hippoboscomorphous type, and the Nycteribomorphous type.

(A) **The Syrphomorphous Type:** (Figs. S1.1-2)

The Syrphomorphous genitalia are possessed by a number of families such as the Syrphidae, the Dorilidae, the Pyrgotidae, the Trypetidae, the Ortalidae, the Coelopidae, and the Richardiidae etc.

The chief distinguishing features of this type of genitalia can be summarised as under:

(a) The genitalia do not fully complete the process of retro-inversion and, therefore, lie orientated towards the right side of the abdomen, a little away from the median axis. Since they do not return to their original position, the genitalia do not assume a secondarily acquired symmetry with the rest of the abdomen.

(b) The fifth sternum is not deeply cleft on the posterior margin to produce any copulatory lobes.

(c) The surstyli are conical to more or less plate-like structures in shape which are either continuous with the genital tergum, or articulated with the latter. They never, however, have the elongated, conical, tusk-like shape commonly met with in the Tachinomorphous type.

(d) Posterior surstyli are usually absent.

(e) The phallobase does not form any movably articulated pre-, or post-gonites.

(f) The aedeagus may be short, or elongated and coiled.

(g) The tenth sternum is either incorporated with the inner parameres to form the composite shield, or the inner
parameres may be present as separate structures movable by means of muscles.

(B) **The Drosophilomorphic Type:**

The Drosophilomorphic genitalia differ from those of the Syrphomorphio type primarily in their secondarily acquired symmetry with the rest of the abdomen, as a result of the completion of retro-inversion which enables the genitalia to return to their original position. Besides the Drosophilidae, many other families such as the Platyzoeidae, the Micropozaedae, and the Calobatidae etc. possess this type of genitalia.

Other features in which the Drosophilomorphic genitalia differ from the Syrphomorphio type are summarized as under:

(a) The sixth segment is usually normal in position and is not modified or displaced.

(b) The aedeagus may be short or elongated, but is never coiled.

(c) The ninth sternum is usually sub-divided or provided with secondary features.

(C) **The Muscomorphic Type:** (Figs. Mn.1-2,5)

The Muscomorphic genitalia are possessed by a number of families such as the Muscidae, the Oestridae, the Stomoxzyidae, and the Glossinidae etc. Pollock (1973) has put forward the hypothesis that the Glossinidae are taxonomically closely related to the Gasterophilidae so much so that the two may be taken to have descended from the same gasterophiloid stock. However, quite contrary to his contention, so far as the genitalial morphology is concerned, the Glossinidae certainly belong to the Muscomorphic type. The Gasterophilidae, on the other hand, possessing two pairs of pre-, and post-gonites (besides other structural features) belong to the Tachino-
The chief distinguishing characters of the Heteromorpho genitalia can be summarised as under:

(a) The fifth sternum is not deeply cleft on the posterior margin to produce any prominently developed copulatory lobes. Such lobes, if present, are only vestigeal.

(b) There are two pairs of surstyli. The anterior pair is always more or less plate-like, never forming an elongated, conical, tusk-like structure as in the case in the Tachinomorpho type.

The posterior surstyli, however, may be plate-like or elongated and conical as in the Tachinomorpho type.

(c) The inner parameres may be vestigeal or fused with the posterior arms of the horse-shoe shaped ninth sternum, but never in the form of lateral rods.

(d) The phallobase forms only a single pair of movably articulated hook-like structures, viz., the pre-gonites. The post-gonites are absent.

(e) The aedeagus is relatively simple in structure, usually composed of a basal sclerotized portion, the rest being more or hyaline. The basal spine of the aedeagus is present, and is usually slightly spatulate at its tip.

(D) The Tachinomorpho Type: (Figs. Ss.1-2,5; Sr.1-2,4)

The Tachinomorpho genitalia are possessed by a large number of dipterous families such as the Tachinidae, the Calliphoridae, the Sarcophagidae, the Scatophagidae, the Cuterebridae, the Gasterophilidae, the Phasiidae, and the Anthomyiidae etc., to cite some well known examples.

The chief distinguishing characters of the Tachinomorpho genitalia can be summarized as under:

(a) The genitalia assume secondarily acquired symmetry with the rest of the abdomen due to completion of retro-
inversion.

(b) There are two pairs of surstyli, which are usually in the form of elongated, conical, tusk-like structures. In some cases, the anterior surstyli may be more or less plate-like as in the Sarcophagidae, whereas in certain other cases such as the Scatophagidae and Cordyluridae, the posterior surstyli may be so. It must, however, be borne in mind that in both the above instances, at least one pair will be elongated and conical. In no instance, both pairs will be plate-like.

(c) The inner parameres may be rod-like, or in the form of sclerotized sclerites. In the first case, the rods are basally articulated with the postero-lateral arms of the ninth sternum, and distally with the base of the anterior surstyli.

In the second case, the sclerotized sclerites are always located in the vicinity of the postero-lateral arms of the ninth sternum.

(d) The phallobase forms two pairs of movably articulated pre-, and post-gonites. The pre-gonites articulate with the phallobase at one end and with the post-gonites at the other. The post-gonites, in turn, articulate either directly with the base of the aedeagus as in the Calliphoridae, or indirectly through the basal plate of the aedeagus as in the Sarcophagidae.

(e) The aedeagus is usually complex in structure, consisting of a basal sclerotized portion, and an apical portion which usually contains a number of sclerotic pieces embedded in its walls.

(f) The basal spine of the aedeagus is usually present and is pointed at its tip. In some cases such as the Sarcophagidae, the basal spine may be absent.

(g) The fifth sternum is invariably deeply cleft to produce the
well developed copulatory lobes.

(B) The Hippoboscomorphic Type: (Figs. Hm.1-3)

The Hippoboscomorphic genitalia are possessed by the families Hippoboscidae and Streblidae.

The families Hippoboscidae, Streblidae and the Nycteribiidae have usually been regarded as members of the series Pupipara by most workers on Diptera. Crampton (1944) placed these in the super-family Hippoboscoidea (Acalptratae), along with the Braulidae. In his earlier work (1942) he regarded the Pupipara as a synonym of the Hippoboscomorpha, and found it difficult to properly place this group in the phylogenetic scheme. He, however, pointed out the difference between the genitalia of the Hippoboscidae and the Nycteribiidae. Schlein and Theodor (1971) also concluded that the genitalia of Hippoboscidae and Nycteriboscinae (Streblidae) are different from those of Nycteribiidae. They, however, regarded the differences to be a new development in their phylogenetic history.

The present studies on the genitalia of Hippobosca maculata coupled with those of Jeve (1963) on Trichobius spp. (Streblidae), and Schlein and Theodor (1971) on Ascodipteron, Nycterophila, and Brachytarsina (Streblidae), have finally confirmed that the genitalia of the two families are strikingly similar to each other, and belong to the same basic type.

The chief characteristic features of the Hippoboscomorphic genitalia can be summarized as under:

(a) The entire genitalia are characteristically retracted inside the abdomen for the greater part of their length.
(b) The genitalia are quite symmetrical with the rest of the
abdomen, there being no external evidence of the retro-inversion. The occurrence of this process, however, is amply supported by the internal anatomical evidence.

(c) The posterior ends of the U-shaped ninth sternum project outwards in the form of a pair of forcep-like claspers, which, however, have nothing to do with the parameres or the post-gonites as maintained by Jeve (1963), and Schlein and Theodor (1971), respectively.

(d) The ninth sternum for the greater part projects into the abdominal cavity in the form of a very well developed internal inflection.

(e) The well developed aedeagus points downwards, and is provided with a well developed internal apodeme.

(f) The surstyli are in the form of a pair of flap-like structures laterally flanking the claspers.

(g) Just before its end, each arm of the ninth sternum mesally sends out a narrow sclerotic strip which fuses with the composite plate formed by the fusion of the inner parameres with the tenth sternum. This arrangement serves to work as a check mechanism, preventing the excessive intrusion of the aedeagus.

(h) The sixth and the seventh terga occupy a lateral position on either side of the abdomen. They are divided into two plates each. The eighth tergum gets completely membranized.

(F) The Nycteribomorphic Type: (Figs. Hb.1-3)

Crampton (1942) pointed out the great resemblance between the male genitalia of the Nycteribiidae and the Braulidae, and accordingly suggested that the two should be grouped together in the super-family Brauloidea. He also recorded the fact that the genitalia of these two families do not resemble that of the Hippoboscidae. In a later work (1944b),...
however, he seems to have reversed his earlier stand and included the Nycteribiidae and the Braulidae in the super-family Hippoboscoidea, along with the Streblidae and the Hippoboscidae.

In the light of the studies made by the present writer, the Nycteribiidae and the Braulidae seem to be very closely related in so far as the genitalic morphology is concerned.

The chief distinguishing characters of the Nycteribomorphia genitalia can be summarized as under:

(a) The genitalia are apparently quite symmetrical with the rest of the abdomen. There is no external evidence of the retro-inversion which, however, is fully corroborated by evidence of the internal anatomy.

(b) The genitalia, unlike those of the Hippoboscomorphic type, are fully exerted.

(c) The sharply tapering, points downwards.

(d) The phallobase gives rise to a pair of lateral flaps which closely flank the aedeagus.

(e) The sixth tergum is the last unmodified tergum of the abdomen. The terga of segments 7-10 seem to coalesce together to form a syn-tergum.

(f) The anterior surstyli may be absent or vestigeal. The posterior surstyli, however, are present and elongated, conical in shape.

(g) The aedeagal apodeme is well developed.