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The Structure of the Male Genitalia in Tachinidae (Diptera) and their Taxonomic Value*

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The present contribution is to be considered as an abstract of a recently published, more extensive paper dealing with the same matter (J. Verbeke, 1962).

Two main phenomena appeared when studying the male genital structures in view of their affinities: first the transformation of types of structures (typogenesis); second the formation of species (speciation). In the process of evolution the former obviously precedes the latter, the formation of species being but an achievement and a further differenciation of the type formation process.

On the basis of these principles, we attempted to define the different types of organization found in the most important parts of the male genitalia, to identify their affinities and establish their relationships. The parts found to be of special interest with regard to the discovery of the mutual affinities among Tachinidae are (1) the nature of the connection between basiphallus and distiphallus, (2) the distiphallus and (3) the posterior paramere. Their characters will be described briefly below. The present investigation was based upon the examination of more than 400 species from all biogeographical regions of the world.

(1) Regarding the connection between basiphallus and distiphallus, our comparative work led us to the discovery of two main structural types, affecting in a certain way the whole aedeagus, either type being combined with other characters. The one is a direct and non-mobile connection; it is the common structure among Tachinidae and has been indicated as "type I" (Pl. I, fig. 7—9, Pl. II); the other is an indirect and mobile connection, typical for most Dexiinae, Voriinae and for some Dufouriini and it has been defined as "type II" (Pl. I, fig. 1—6).

Between these two extreme types we met a series of intermediate types, whose connection is generally indirect but non-mobile (Pl. II, fig. 18); they belong in fact to the "type I" as indicated by the association of a certain number of other characters. These transitional structures are less common among Tachinidae and do not justify a special type definition in the present state of our investigation.

(2) The most important structural particularities, however, revealed by our work concern the proper macro- and microstructure of the distiphallus, the "distiphallus type" as we call it, and its various subtypes.

Here also we distinguish two main types, each containing three subtypes. The first is defined as the "POS type", because it is composed of the subtypes representative of *Phasia, Ocyptera* and *Strongygaster (= Tamiclea)*. This "POS type" includes all genera characterized by a complete lack of longitudinal ventral microstructures on the distiphallus; moreover this part of the aedeagus shows a structure that is fundamentally different from that in the remaining Tachinidae (Pl. III). The three subtypes

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are those indicated by the typical genera. *Leucostoma*, although slightly different, is included in the subtype designation of *Ocyptera*, but occupies in fact an intermediate situation between *Ocyptera* and *Strongygaster* (Pl. III, fig. 25—27).

This "POS type" is typical for the true Phasiinae, i. e. those Tachinids parasitizing most often Hemiptera-Heteroptera; *Strongygaster* and allied genera are an exception hereto.

The second main distiphallus type is indicated as the "DEG type", being derived from the genera *Dexia*, *Echinomyia* and *Gonia* that are representative for the various subtypes; this type includes in fact all Tachinidae except for the Phasiinae (nob.). It is characterized by the presence of longitudinal rows of ventral microstructures or secondary structures derived from the latter; its fundamental structure is entirely different from that of the Phasiinae and is characterized by more or less distinct dorsal and ventral strata or parts; it varies strongly in shape and size and sometimes shows additional structures or a pronounced development in width or length; the apical part or praeputium, if present, is less differenciated but sometimes more developed than with the Phasiinae. On the other hand the three subtypes are rather less distinct from each other than in the "POS type" and they are connected by several intermediate forms (Pl. I & II).

The *Dexia* subtype groups all Dexiini, except for the genera *Microphthalma* and *Dexiosoma*, all Rutiliini, Campylochaetini, Voriini (= Athryciini), Rhamphinini and Thelairini, the Macquartiini *Phyllomyiina*, some *Dufouriina* and some Macquartiini *Macquartiina* (e. g. *Blepharomyia*) sensu MESNIL (1939).

The *Echinomyia* subtype is typical for all Larvaevorini, Leskiini, Minthoini, for some Macquartiini (e. g. *Brachymerina*, *Zophomyiina*, *Macquartiina* p. p.) and some Phasiini (e. g. *Melisoneurina*, *Dufouriina* p. p.) sensu MESNIL (1939) and also for both the above mentioned genera (Pl. I, fig. 7). There is less variation within this subtype than there is in both remaining subtypes; the Ormiini and Aulacocephalini belong to this category; examples of this subtype are shown in Pl. I, fig. 7—8; Pl. II, fig. 16—17.

The *Gonia* subtype represents by far the greatest number of genera; it is typical for all Salmaciinae (= Goniinae) and Phorocerinae sensu MESNIL (1939). These two subfamilies, later considered as tribes by MESNIL (1944), cannot be distinguished by the male genital structures. In fact the genitalia indicate an entirely different structuration of this complex group. Within the latter, the Ethillini and Winthemiini occupy an intermediate position between some higher or more specialized forms and some less specialized genera, which were wrongly classified by MESNIL (1939) among his Phasiinae: *Acemyia*, *Ceracia*, *Thrixion*, etc. The two subfamilies referred to above, must be grouped together with the mentioned tribes and genera, in one and the same subfamily, that could be named Eutachininae or Exoristinae, as did HERTING (1957, 1960). The Blondeliini constitute herein a well defined group with a very typical distiphallus. Some illustrations of this highly varying subtype are given in Pl. I, fig. 9, and Pl. II, fig. 18.

Among this DEG distiphallus type two tribes, the Dufouriini and the Macquartiini, are somewhat isolated by a more exceptional combination of characters and we proposed the fusion of both tribes into a separate subfamily. The reasons for creating this new subfamily will appear better from our explaining hereinafter the various types of parameres we met among the male genital structures.

(3) We distinguish three types of posterior parameres, the A, B and C types, the second, the B or basic type being intermediate between the A (sensorial) and the C (connective) types. The B type is typical for both tribes above mentioned, but is not limited to them.

The posterior paramere of the C type is in the shape of a strip or plate and has a connective function; it lies between the arms or the posterior part of the hypandrium,

and constitutes a bridge between the latter and the basical part of the aedeagus. This type of paramere generally occurs in combination with the aedeagus of type II, i. e. with mobile connection basiphallus-distiphallus.

The distiphallus occuring in the previous combination is of the *Dexia* subtype; it is uniform in structure, more or less flattened and slender in form, sometimes extremely elongated, bearing frequently a differenciated apical part or praeputium. This first combination of characters is typical for most of the Dexiinae and Voriinae.[1] We proposed to classify in the former subfamily all genera showing a total lack of differenciation in the posterior paramere and the distiphallus, and to maintain in the latter subfamily all forms showing a slight differenciation in these parts. Examples are given in Pl. I, fig. 1—6.

The posterior paramere of the A type has a marked sensorial function. It is lobe-shaped or palp-like and often of a structure similar to that of the anterior paramere; it is more or less mobile resulting from a weaker attachment to the hypandrium arms and more or less differenciated by the presence of pores, points, spines, microchaetae, etc., the latter being often more developed at the anterior edge. Sometimes this type of paramere cannot be distinguished so well (or not at all) because of the fusion with the hypandrium arm or with the anterior paramere.

This type of paramere generally occurs in combination with the aedeagus of type I, i. e. the type with direct and non-mobile connection basiphallus-distiphallus. Certain intermediate structures characterized by an indirect but non-mobile connection are also combined with the posterior paramere of the A type. The accompanying distiphallus is of the *Echinomyia* or *Gonia* types; here the distiphallus is less uniform in structure, more differenciated and often cylindrical in shape, without distinct apical part or praeputium, sometimes reduced in length but never very elongated. This second combination of characters is typical for most of the Echinomyiinae or Larvaevorinae and of the Eutachininae or Exoristinae. Examples are shown in Pl. I, fig. 7—8, and Pl. II, fig. 15 and 18.

The posterior paramere of the B type is exactly intermediate between the two above mentioned types; it is more or less plate-shaped and firmly attached to the hypandrium, but shows in its apical or distal part some more or less pronounced differenciation, either due to the presence of lobes, points, spines, etc. or to a special shape of its distal edge. This type of paramere occurs in combination with an aedeagus of type II in the Dufouriini and with an aedeagus of type I in the Macquartiini, thus constituting a bridge between the two above mentioned complex groups.

The distiphallus occuring in combination with this paramere is either of the *Dexia* or of the *Echinomyia* type, but frequently also of an intermediate structure and sometimes strongly reduced in size. In a general way, however, the Dufouriini combine an aedeagus of type II and a distiphallus of the *Dexia* subtype, whereas the Macquartiini combine an aedeagus of type I and a distiphallus of the *Echinomyia* subtype. Many other characters prove the intermediate situation of both tribes and for this reason we fused them into a new subfamily: the D u f o u r i i n a e. Examples are given in Pl. II, fig. 10—14.

The Dufouriinae, which are often parasites of adults of insects, mainly Coleoptera, could be related to the Phasiinae through the intermediary of such genera like *Hyalo-*

[1] We must draw attention here to the fact that certain authors described only a single paramere as typical for the Dexiinae, etc. The interpretation of a single paramere is based on a misunderstanding of the simplified structure of the second or posterior paramere in this subfamily and some other categories. In fact, two parameres are present in all Tachinidae. In the Dexiinae, the Voriinae and some Dufouriini, however, the posterior paramere is developed perpendicularly to the anterior paramere or produced from the latter and is for these reasons less distinct, whereas in the other subfamilies and tribes both parameres are developed in the same plane.

myiodes, parasite of beetles, and *Strongygaster*, attacking flying ants. Further research will, however, be needed in order to establish the exact position of these and allied genera and the actual way of connection between the Phasiinae (nob.) and the remaining Tachinidae.

Our investigations suggest certain remarks and general conclusions of great importance with a view to the establishment of a satisfactory classification of the Tachinidae.

The first remark to be made is that among the above selected characters the type of distiphallus shows by far the greatest stability and that a given type occurs in large natural groups. In the main categories, this stability or uniformity occurs in combination with a great number of other, biological as well as morphological characters and these combinations are more or less constant.

Another important item to be pointed out is that some of the above described structures repeat themselves in all or at least in most of the larger groups, as outlined by the distiphallus type and subtypes. This is true particularly for the posterior paramere; indeed, the A, B and C types occur as well among the Phasiinae as among the Exoristinae, for instance. The intermediate type of connection between basiphallus and distiphallus also appears in most of the main groups.

This repeated appearance of similar structures in different groups implicates a parallelism between the male genitalia of these groups; this parallelism also appears in a great number of other characters and is commonly qualified as "convergence".

Various hypotheses have been formulated in order to explain these phenomena of parallel evolution. One of them supposes that living matter disposes of only a limited number of solutions to the same problems; this condition increases or favours the coincidences and reduces the evolutionary possibilities of the living creature (P.-P. Grassé, 1950). Another hypothesis by the same author proposes that the evolutionary lines, having a "common genetic basis", have been transformed in a similar way for a certain number of characters (correlated characters).

A last general observation concerns the correlation between the host specificity and the structure of the male genitalia as a whole and more especially of the distiphallus. This correlation clearly appears among the Phasiinae (nob.) but to a certain extent also among the Dexiinae, the Voriinae, the Echinomyiinae and the Salmaciini or Goniini; it is less constant among the Blondeliini and the Dufouriinae (nob.). The Dufouriinae with their wide range of morphological structures could be considered as the predecessors of most of the numerous recent tribes. Further research will, however, be needed in order to verify this and other facts.

Certain data resulting from our investigation could usefully contribute to a satisfactory classification of the Tachinidae. Various solutions seem possible as suggested by our tables pp. 144 and 147 (J. Verbeke, 1962). On a purely tentative basis we proposed a system composed of six major groups or subfamilies: the Phasiinae, the Dexiinae, the Voriinae, the Dufouriinae, the Echinomyiinae or Larvaevorinae and the Eutachininae or Exoristinae. Another acceptable solution could be to fuse the *Dexia-Voria-Dufouria* complex on the one hand and the *Echinomyia-Exorista-Gonia* complex on the other hand, thus constituting together with the Phasiinae three subfamilies. Above all, the structure of the male genitalia will prove to be of most valuable aid in delimiting the numerous tribes and sub-tribes that are the only true taxonomic units in Tachinidae.

Finally, as to the Palpostomatini, the Acemyiini and related genera we must state that, in our opinion, these groups cannot be integrated within the Phasiinae (nob.) notwithstanding the fact that certain characters are clearly convergent.

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Plate I

Figs. 1—6: Examples of the aedeagus of type II; the distiphallus is of the *Dexia* subtype; the posterior paramere of the C type.

Figs. 7—9: Examples of the aedeagus of type I; the distiphallus is of the *Echinomyia* (7—8) or the *Gonia* (9) subtype; the posterior paramere of the A type.

Figs. 1, 3 and 4 shows connection between posterior paramere and hypandrium.

1. — *Psecacera chilensis* Bigot; 2. — *Prosena siberita* Fabricius; 3. — *Freraea gagathea* Robineau-Desvoidy; 4. — *Dufouria (Pseudoptilops) nitida* Rondani; 5. — *Kirbya moerens* Meigen; 6. — *Blepharigena trepida* Meigen; 7. — *Microphthalma europaea* Egger; 8. — *Hyalurgus diaphanus* Fallen; 9. — *Gonia capitata* de Geer.

Figs. 1, 3 and 4: aedeagus, parameres and hypandrium (shown partly in fig. 1); figs. 2 and 5—8: aedeagus and parameres; fig. 9: aedeagus. Abbr.: *ap*, anterior paramere; *bph*, basiphallus; *dph*, distiphallus; *hy*, hypandrium; *ppA*, posterior paramere of the A type; *ppC*, posterior paramere of the C type; *pr*, praeputium; *sp*, spinus.

Plate II

Figs. 10—18: Examples of the distiphallus of the DEG type, the *Dexia* subtype being shown in figures 10—14, the *Echinomyia* subtype in figures 16 and 17, the *Gonia* subtype in figure 18; the distiphallus is intermediate between the *Dexia* and *Echinomyia* subtypes in figure 15.

The posterior paramere is of the C type in figure 10, of the B type in figures 11, 12 and 14, of the A type in figures 13, 15 and 18; it is intermediate between the B and the A types in figure 16 and intermediate between the C and the B types in figure 17.

The connection between basiphallus and distiphallus is of type I.

Figs. 10 and 13 shows connection between posterior paramere and hypandrium.

10. — *Redtenbacheria insignis* Egger; 11. — *Macroprosopa atrata* Fallen; 12. — *Myiophasia nigrifrons* Townsend; 13. — *Imitomyia kivuensis* Verbeke; 14. — *Ptilopsina nitens* Villeneuve; 15. — *Graphogaster brunnescens* Villeneuve; 16. — *Proscissio cana* Hutton; 17. — *Aulacocephala maculithorax* Macquart; 18. — *Prodegeeria javana* Brauer-Bergenstamm.

Abbr.: *ap*, anterior paramere; *bph*, basiphallus; *dph*, distiphallus; *hy*, hypandrium; *ppA*, posterior paramere of the A type; *ppB*, posterior paramere of the B type; *ppC*, posterior paramere of the C type; *sp*, spinus.

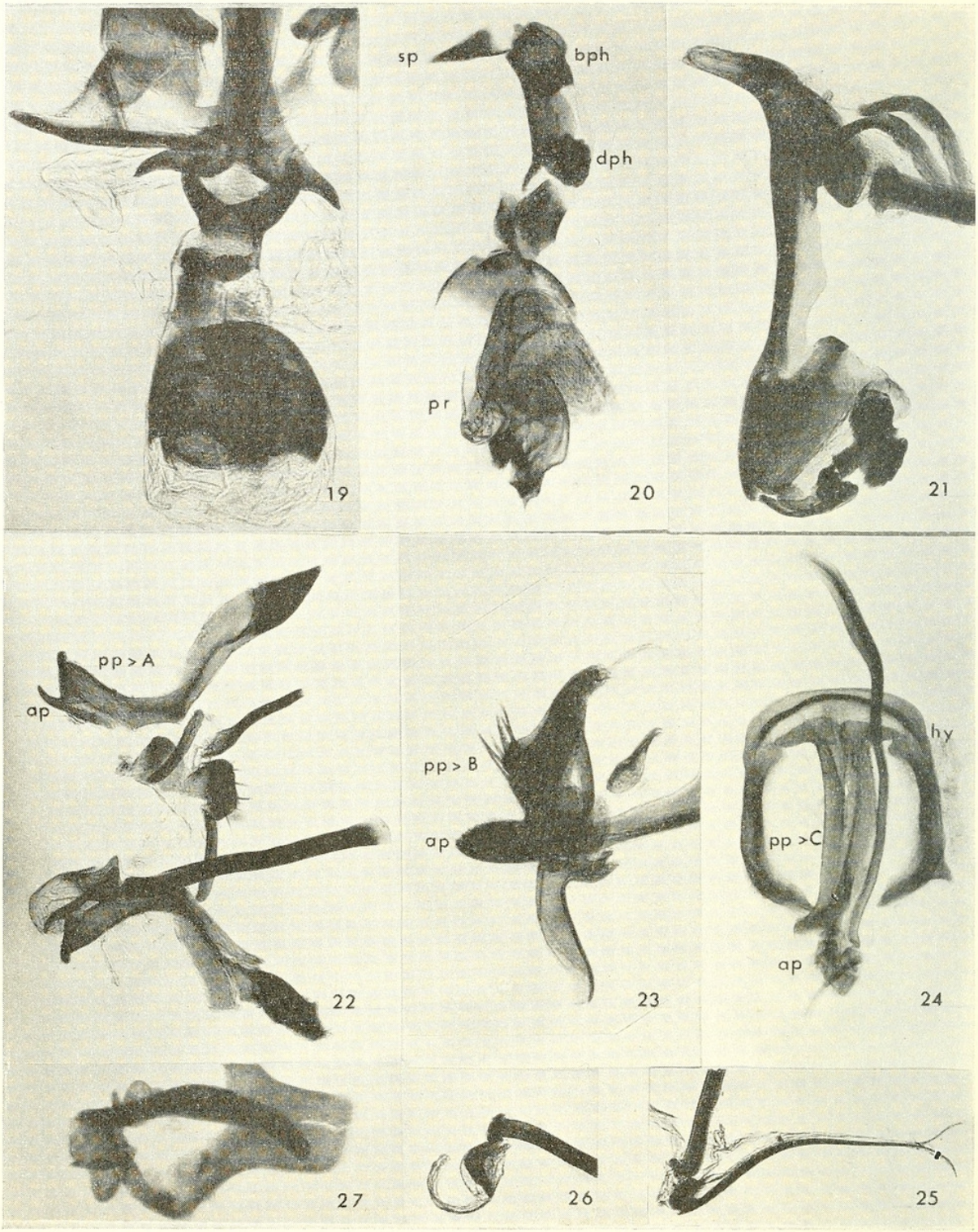

Plate III

Figs. 19—27: Examples of the distiphallus of the POS type, the *Phasia* subtype being shown in figures 19—21, the *Ocyptera* subtype in figures 22—26 and the *Strongygaster* subtype in figure 27. Among the *Ocyptera* subtype, figures 22—24 show three types of posterior parameres similar to those found in the DEG type (plate II) but of heterogeneous structure (indicated by the sign >). A strongly developed praeputium is shown in figures 19—21; it is reduced or absent in the other forms.

Figs. 22—24 shows connection between posterior paramere and hypandrium.

19. — *Trichiopoda* sp.; 20. — *Gymnosoma* sp.; 21. — *Hermyia diabolus* WIEDEMANN; 22. — *Leucostoma* sp.; 23. — *Weberia curvicauda* FALLEN; 24. — *Ocyptera auriceps* MEIGEN; 25. — *Ocyptera brassicaria* FABRICIUS; 26. — *Leucostoma* sp.; 27. — *Rondaniooestrus apivorus* VILLENEUVE.

Figs. 22, 23, 24 and 27: aedeagus, parameres and hypandrium; fig. 19: aedeagus and parameres; figs. 20, 21, 25 and 26: aedeagus. Abbr. *ap*, anterior paramere; *bph*, basiphallus; *dph*, distiphallus; *hy*, hypandrium; *pp > A*, posterior paramere approaching the A type; *pp > B*, posterior paramere approaching the B type; *pp > C*, posterior paramere approaching the C type; *pr*, praeputium; *sp*, spinus.