Beitr. Ent. · Bd. 20 · 1970 · H. 1/2 · S. 5–10 · Berlin

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Two main factors in the formation of the wing venation of Diptera

With 3 text figures

The order Diptera can be divided into many categories, more than 50 in number, according to their wing venation (ROHDENDORF 1951). The ways and stages of wing specialization and, to some extent, the phylogenetic relationships are reflected in this preliminary system. However, the estimation of such groups from the standpoint of functional morphology is very difficult now. In this connection the theory of the flapping flight may be regarded as making no satisfactory advance in distinguishing the groups.

The present paper intends to give a model for studying the influence of the main factors on the wing venation and to analyse a number of concrete examples on the basis of this model.

At first we must find out the trends of the progressive alteration of the wing venation in Diptera. Five infraorders, most important for this purpose, may be chosen: Tipulomorpha, Bibionomorpha, Anisopodomorpha, Asilomorpha and Myiomorpha. The common trends of all the infraorders are the following: 1) the reduction of free branches of *RS*; 2) the strengthening of a membrane between the radial and medial fields; 3) the formation of the discoidal cell and the gradual approach of its distal margin to the wing border; 4) the reduction of free branches of *M*; 5) the shortening and the elimination of the cubital and anal veins. This results in the hardening of the front third of the wing, in lightening the hind third of the wing and forming, in the middle part of the wing, flexible structures connecting the front and hind parts.

Let us assume now that the reason for these changes is the combination of two factors which are the lifting force and the dragging force, and the mechanism of these changes is the interaction of the process of costalization and the process that we will here call the process of stabilization. We determine the process of costalization as a mechanism directly related to the increase of the lifting force and causing the following alterations: 1) the shift of the radial system of the veins to the costal border of the wing and their thickening; 2) the lightening of the hind part of the wing; 3) the reduction of free branches of certain veins or their bases only (this includes the reduction of *C* along the anal border of the

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DOI: 10.21248/contrib.entomol.20.1-2.5-10

wing); 4) the general enlargement of the wing area and the preservation of its wide base. We determine the process of stabilization as a mechanism directly related to the increase of the dragging force and causing the following alterations: 1) the even development and distribution of the longitudinal veins on the wing surface; 2) the strengthening of the longitudinal veins with the help of various additional veins; 3) the non-enlargement of the wing area and the distinct isolation of the marginal regions (apex, anal lobe, alula); 4) the narrowing of the wing base.

To give examples. It is known that the length of the branches of R_4—R_5 and their position with respect to the wing apex are very important for ascertaining the degree of phylogenetic relationship within the lower Asilomorpha (STEYSKAL,

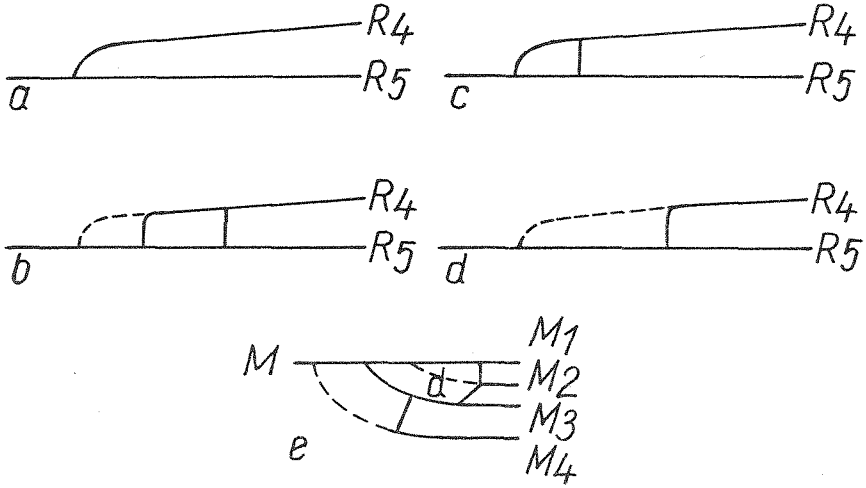

Fig. 1. The phases of the shift of longitudinal veins. Explanations in the text

1956). How does the shortening of the fork R_4—R_5 occur? According to the definition of the processes stated above, we assume that this alteration, i.e. the movement of the base of R_4 along R_5 to the wing apex, consists of new formations and reductions following one another. At first a cross-vein appears between R_4 and R_5. This phase obviously depends upon the process of stabilization (cf. the 2nd point of the definition of the process). Then the base of R_4 disappears for the extent from the point where R_4 branches off R_5 up to the new cross-vein (cf. the 3rd point of the definition of the process of costalization). This leads to the shift of the base of R_4 resulting from the cross-vein towards the wing apex (fig. 1 a—d).

We believe that the same explanation can be given for some other facts too, e.g. the shifts of veins to the wing base, termed a process of basalization by TUOMIKOSKI (1966). The movement of the base of *RS* along R_1 is another example. Looking at the wing of *Mesophantasma tipuliforme* (fig. 2) we see that *RS* arises from *R* with two veins which are shortly after wards fused together (ROHDENDORF 1962: 319). Is this character the aberrant one? It might be. But more

DOI: 10.21248/contrib.entomol.20.1-2.5-10

probably it testifies to the movement of the veins. In fact, a distal branch can correspond to an extra crossing vein whereas a poorly developed proximal branch corresponds to the gradually reduced base of *RS*. The analogous changes are peculiar to all longitudinal veins and consist of two phases: 1) the formation of the cross-vein between two longitudinal stems; 2) the reduction of the base part of the smaller longitudinal vein. First of all it concerns the formation of the discoidal cell, namely a loss of M_2 at its base (fig. 1 e). Besides there is a junction of R_{2+3} and R_1 realized in the same way among some Olbiogastridae, Eremochaetidae, Asilidae, Mydaidae, Apioceridae and several genera of Rhagionidae.

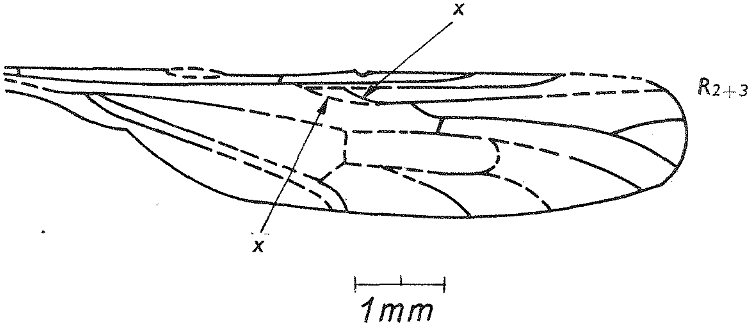

Fig. 2. The wing of *Mesophantasma tipuliforme* ROHDENDORF (After ROHDENDORF).

Another example of the way the main factors act is provided by the formation of the first vein of *RS* in Brachycera. The problem is: what veins are fused in this case? As suggested by HENNIG (1954: 330—333) these are the veins R_3 and R_4 that mix and form the anterior branch of *RS*. To prove it he mentioned two facts: 1) a bend of R_2 in *Lampromyia pallida* MEIGEN; 2) the presence of a recurrent appendage near the base of R_4 in many Tabanidae. But if we agree with HENNIG we shall not be able to explain why the so-called R_3 is always absent in Stratiomyidea and Tabanidea and is often detected in Asilidea, Bombyliidea and especially Empididea possessing fairly apomorphic patterns of wing venation. Isn't it better to assume that this "R_3" in Asilomorpha appears irrespective of other veins, simply as an extra crossing vein in the course of the stabilization of the wing venation? Then the recurrent appendage in a cell r_3 can be regarded as a remnant of the former base of R_4.

We want to stress here that it is wrong to derive the additional cross-veins from the general plan of wing venation in Diptera. NEEDHAM (1908) was the first to develop this method, using the material on Tipulidae. HARDY further developed NEEDHAM's ideas in "The reticulation theory of wing venation in Diptera" (1951), where the deviating types of wing venation are constructed from the reticulum by the consecutive reduction of crossing veins. The attempt to interpret all cross-veins in this way is justifiable only in TILLYARD's archedictyon, i.e. at the level of infraclasses, cohorts and superorders. As to the

DOI: 10.21248/contrib.entomol.20.1-2.5-10

lower taxa, e.g. the family Nemestrinidae, the presence of the organized system of extra crossing veins can be explained by their secondary origin in the course of the process of stabilization.

A few examples, mentioned above, clearly show that longitudinal veins are shifting along the main axis of the wing. On the other hand, such movements conform very well to the interaction between the processes of costalization and stabilization. On the basis of these principles it is possible to explain many structural alterations in the wing venation of Diptera. Now we shall try to show that they also give a key for solving a more general problem.

Since the beginning of the 20th century the problem of the veins separating adjacent fields of the wing has been a matter of controversy. In particular, the authors could be divided into three groups according to their assumptions about the nature of the vein which is intermediate between M_3 and Cu_1 in Diptera. For instance, Tillyard (1919) held it to be the last vein of M, namely M_4. Comstock (1918) believed that it was the anterior branch of cubitus, Cu_1. Finally, Hennig (1954) interpreted this vein in analogy to two other fields ($Sc-R$ and $R-M$) as a product of junction of M_4 and Cu_{1a}. In his argument with Tillyard he advanced two considerations (p. 252). First, that „die fragliche Ader wohl sehr oft keine Verbindung zur Media, häufig aber nur eine solche zum Cubitus (Cu_{1b}) hat". Secondly, „handelt es sich hierbei um eine deutlich konvexe Ader".

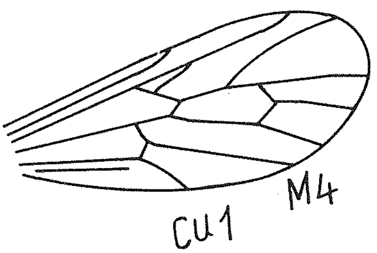

Fig. 3. The wing of *Parer̆emochaetus minor* Ussatchov

Hennig's former objection is untenable because of the secondary connection between M_4 and Cu_1 resulting in the formation of the so-called cubital fork, while the anterior branch of the true cubital fork doesn't mix with M_4 but is gradually reduced in Mecopteroidea and entirely lost in Diptera. On the other hand, there is no doubt the natural cohesion of M_4 and the main stem of M (fig. 3). These veins are joined not only in such Nematocera sa Tipulomorpha (Psychodidae) and Bibionomorpha (some Fungivoridea, Scatopsidea, Cecidomyiidea) but, as we know now, in the initial forms of Asilomorpha (Ussatchov 1968).

As to his latter objection, Hennig proceeds from Adolf's criterion (1879) of identifying veins by their convexity or concavity in the wing surface. Though he warns against placing too many hopes in the furrows of the undulating wing membrane, still he himself investigates the nature of the convex veins R_1, R_5, M_4 in connection with this principle. The final conclusion is that the vein lying on a convex ridge draws up a concave one situated just before, so that convex veins R_1^+, Ma^+, Cu_{1a}^+ and corresponding concave veins Sc_2^-, R_5^-, M_4^- are fused two by two.

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Using the definition of the two main factors stated above, we could take a different view of the phenomena that occur between adjacent fields of the wing. If the veins had been under the influence of the process of stabilization only, the scheme of HENNIG would have remained valid. However, it is necessary to to take into consideration the process of costalization which decreases in its effect toward the anal margin of the wing. Then it would be logical to assume that Sc_2 and R_1 are mixed together and that an additional longitudinal fold (vena spuria) appears, between R_5 and M_1 while M_4 and Cu_1 remain joined by the crossing vein *mcu*. That means that a vein M_4+Cu_1 does not exist.

Returning now to the beginning of the paper let us consider five infraorders, chosen for our purpose, in connection with the suggested model.

The process of stabilization is predominant in Tipulomorpha and is the cause of the isolation of the wing base and the primary formation of a discoidal cell, its distal margin approaching the terminal border of the wing while shifting with the whole cell. In Bibionomorpha, on the contrary, the process of costalization prevails and causes the strong reduction of veins, especially in Cecidomyiidae, some Mycetophilidae and Keroplatidae. On the whole both groups were, so-to-speak, "experimental" for the formation of the venation in higher Diptera.

A more successful combination of these processes gives rise to Anisopodomorpha. Until recently this infraorder had been included in Bibionomorpha as a sister-group of Bibionidea+Fungivoridea. However, TUOMIKOSKI (1961) demonstrated peculiar characters within this group and established a new infraorder. With respect to the wing venation it even keeps two very plesiomorphic features, the retention of A_2 and four branches of M, indicating old links with Tipulomorpha. In other venation characters which are the location of the discoidal cell and the structure of RS (R_{2+3}; R_4-R_5), Anisopodomorpha differs greatly from the rest of Nematocera and gives the foundation for constructing the wing venation of Asilomorpha.

The full reciprocal co-ordination of the two processes is completed in Myiomorpha, where we find branches of RS and M in twos, a long discoidal cell and a considerable shortening of Cu_1.

So the results of this study have organized the meaningful pattern of the interaction between the process of costalization and the process of stabilization. Such an interaction, as we have seen, is a main cause of various alterations in the wing membrane's venation.

In bringing this paper to a close it is perhaps necessary to stress that we have created a rather idealized scheme in which the shape of the wing, the distribution of microchaetae and sensillae, the structure of the wing base and the wing root have not been taken into account. Nevertheless such restrictions seem to be justified, for the shape of the wing is to a greater extent related to the characteristics of the whole body, the distribution of the chaetae — to the manoeuvrability during the flight, while the transmissive sclerites depend on other laws of mechanics than the veins of the wing membrane.

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Zusammenfassung

Bei Betrachtung verschiedener Geädertypen des Dipterenflügels kann man zwei Grundprozesse feststellen und unterscheiden, den Prozeß der Kostalisierung und den Prozeß der Stabilisierung, die für die Formierung und die Entwicklung des Systems der Adern und Zellen verantwortlich sind. In ihrer Eigenschaft als allgemeinere anschauliche Anlage der untersuchten Mechanismen wurde eine Reihe aus fünf Infraordnungen aufgestellt und der Versuch gemacht, die progressiven Veränderungen in dieser Reihe auf der Basis dessen zu erklären, daß die vorliegenden Prozesse Wechselwirkungszeiten eines Widerspruchs darstellen. In Abhängigkeit von den Existenzbedingungen wird eine dieser Seiten zur Hauptrichtung.

Summary

If we examine various types of the venation of the wings of Diptera, we find and distinguish two basic processes which determine the formation and the development of the system of veins and cells, the process of costalization and the process of stabilization. As a more general and instructive arrangement of the mechanisms under consideration, a series of five infra-orders was established, and an attempt was made to explain the progressive changes in this series by the assumption that the existing processes represent the interacting sides of a contradiction. As a result of the habitat conditions, one of these sides becomes the main trend.

Резюме

При рассмотрении различных типов жилкования крыла у двукрылых насекомых можно выделить и определить два основных процесса, процесс костализации и процесс стабилизации, ответственных за формирование и развитие системы жилок и ячей. В качестве наиболее общего наглядного приложения изученных механизмов представлен ряд из пяти ключевых инфраотрядов и сделана попытка объяснить прогрессивные изменения в этом ряду на основе того, что данные процессы составляют взаимодействующие стороны одного противоречия. В зависимости от условий существования главной оказывается одна из этих сторон.

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