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THE NOMENCLATURE OF WING VENATION IN BEETLES (COLEOPTERA)

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Study of the structure of the hind wings of beetles is of great importance for establishment of their classification and the definition of their phylogeny. The venation and the system of folding the hind wings are purely imaginal structures and Dollo's law of the irreversibility of evolution is far more strictly fulfilled in their evolutionary modifications than in most other characters (Ponomarenko, 1969). There-fore, the series of forms with successive degrees of reduction of the venation which occur widely among beetles are highly convenient for the correction of assumed phylogenetic sequences in which forms with complete venation should not originate from forms with reduced venation. This accounts for the continuing interest in a study of the hind wings of beetles. Unfortunately there is one negative feature to the present stage of their investigation. Since the end of the twenties, after the work of Forbes, there have been no publications devoted to the structure of the wings of all beetles. The more recent papers deal only with the wing structure of beetles belonging to a single family or to a group of closely related families. Such an approach may be productive only if there is a good and widely accepted general outline by which to compare the views of different authors. The establishment of homologies in wing venation, without which a rational nomenclature is impossible, necessitates very broad comparisons. The veins of the beetle wing are not merely strengthening ribs, but include also a system of levers for the folding and unfolding of the wing blade along its folds. Therefore, crossveins are frequently converted into longitudinal veins and, conversely, longitudinal veins intersected by folds may lose the proximal part and the role of their base may be taken by a former crossvein. Moreover, an independent vein is frequently considered a branch of a completely different vein. This has had the result that completely different systems in general manuals and identification keys are used to designate veins and they cannot provide an adequate basis for the production of a unified nomenclature. The textbook of general entomology *by* B. N. Shvanvich (1949) serves to illustrate the situation with regard to the nomenclature of wing venation in beetles. The "nomenclature first proposed by Comstock and Needham (1898-1899) is used in the general section to designate the veins of the wings of beetles, although its incorrectness had been demonstrated long before the textbook was written, while in the special section of the book an illustration of a beetle is reprinted without any alterations from the Handbuch der Zoologie, which gives a nomenclature of venation borrowed from Handlirsch (1906-1908) that is completely different but also incorrect.

The nomenclature most widely used at present is that proposed by Forbes (1922, 1926). Having carefully worked through a large amount of material and having drawn on data on tracheation and the structure of the wing base, Forbes was able to make a correct homologization between the venation of beetles and that of other insects. He corrected the mistake of Comstock and Needham, who omitted the medial system of veins in homologization of the veins of beetles and other insects, since the medial trachea was lost in the longicorn beetles studied by them. Having demonstrated the presence of this system in beetle wings, Forbes proposed a general plan of beetle wing venation in which the veins really became homologous to those in the wings of other insects. However, the nomenclature which he proposed turned out to be not entirely correct. Forbes simply trans-posed mechanically forward by one system the names of veins proposed by Comstock, beginning with the medial sys-tem, and maintained the single trunk of the cubital system. This was comprehensible in the nomenclature of Comstock and Needham—after the loss of the medial system there was

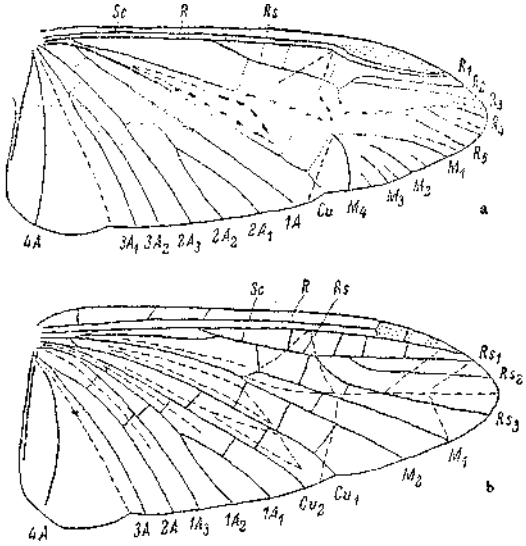

Fig. 1. Diagram of the primitive venation of the hind wings of beetles.

a) Taken from Forbes, 1922; b) original. The symbols employed for the veins are traditional, those employed for the folds are those given by Forbes, 1926. Here and in the next illustration folds are shown by dashed lines.

simply no place for a posterior trunk of the cubital system. Now it had appeared, but nevertheless Forbes retained the former nomenclature. As a result he was forced to assert that the vein in the Neuropteroidea regarded by all other investigators as the posterior trunk of the cubitus was in fact the anterior trunk of the anal system. The nomenclature proposed by Forbes coincided with the nomenclature of Cornstock (1918) for mecopteroids and differed from that for neuropteroids. Further research has revealed, however, that Comstock's nomenclature of mecopteroid venation was incorrect and was based, as in the case of the Coleoptera, on mistaken homology. This eliminated the final basis for Forbes interpretation of the vein running directly behind the anterior branch of the cubitus as the first anal vein and demonstrated that it should be regarded as the posterior branch of the cubitus.

It must be noted that such an interpretation of this vein had previously been accepted by many authors, but that it had been used in works not specially devoted 10 the wing venation of beetles. However, such was the prestige of Forbes' research that this interpretation is not used at the present time.

The nomenclature proposed by Forbes is shown in Fig. la. When modified to bring the nomenclature of the wing veins of beetles into conformity with that of the venation of other holometabolous insects, it assumes the form shown in Fig. 1, b. The first anal vein is then designated as the posterior branch of the cubital vein; the following three branches, designated as the second anal vein by Forbes should be called branches of the first anal vein; the following two veins, originating in a common trunk, should be called

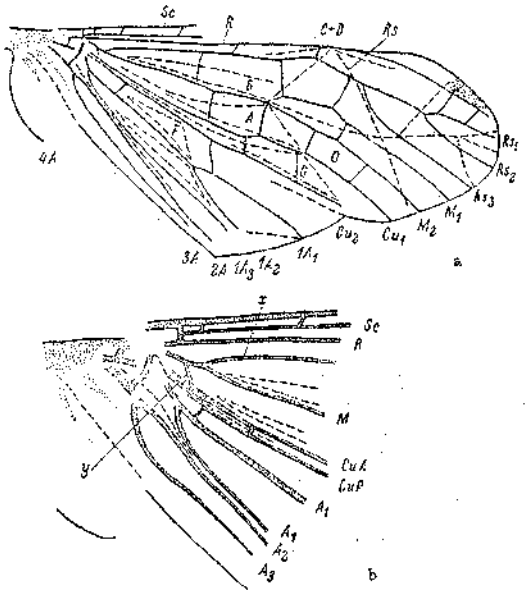

Fig. 2. Hind wing of a beetle from Upper Permian deposits near the village of Chepanikha (Urals), specimen PIN 3286/4.

a) general appearance (x 10); b) wing base (x 20); x, y—compound veins.

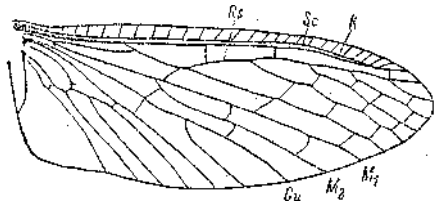

Fig. 3. Hind wing of Archichauliodes.

the third and fourth anal veins. In this case the veins of the hind wings of beetles acquire the same names as those of the hind wings in the Megaloptera, which are most similar to beetle wings in common structural plan.

Additional information on the homology of the venation of beetle wings is provided by study of an. outstanding new find of an excellently preserved beetle hind wing from Upper Permian deposits (Fig. 2,b). This is the best preserved impression of the hind wing of a beetle in all the more than 15,000 remains of extinct beetles in the collection of the Paleontological Institute, USSR Academy of Sciences. Unfortunately, this is an isolated wing, so that it is impossible to establish to which of the fairly varied Late. Permian beetles it belonged. On the other hand, had it been found connected to the body it probably would not have been so magnificently preserved and study of the particularly important basal part of the wing-would not have been possible.

The venation differs strongly from that of known beetle wings, including those of the Triassic beetles, so that it has even been doubted as to whether it is actually a beetle wing. However, fold are clearly to be seen on it (Fig. 6, b) which correspond almost entirely to the characteristic folds of the hind wing in beetles. It is difficult to believe that the folds, in precisely those places where they occur on beetle wings, simply resulted from crumpling of the wing in the course of fossilization. The shortening of the apical portion of the wing, so that the apex of the first anal vein lies in its distal half, is also characteristic for beetles.

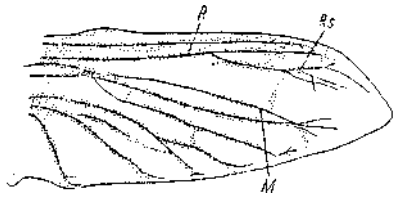

Fig. 4. Tracheation of the wing in a pupa of Tenebrio molitor L. Tracheae indicated by continuous lines, veins by dots (taken from Forbes, 1922).

The wing (Fig. 2) is of the shape characteristic for beetle wings with a dilated anal lobe and its anterior margin is completely straight. The main differences from the wings of present day beetles are the large number of crossveins, the practically total absence of differentiation of the veins with respect to thickness and their general weakness, and complete preservation of the base of the medial system, which is as complex as in the Megaloptera.

The subcostal and radial veins are noticeably removed from the anterior margin of the wing and one from the other, i. e. , their structure is the same as in other wings of Permian beetles, whereas in Mesozoic and Recent beetles they are converged and run practically along the extreme margin of the wing. There are crossveins in the subcostal area. The radial sector is pectinate and three-branched.

The vein terminating in pectinate branches typical of the radial sector does not, however, originate from the radius, but from the medial vein, extending forward from it. This vein is undoubtedly compound. Its apex is formed *by* the radial sector and its base by a vein extending obliquely on the wings of Megaloptera—Corydalidae to the base of RS from the base of M and sometimes even possessing its own base (Fig. 3). On the wing described it occupies a completely longitudinal position and is greatly elongate, while the base of RS is either completely lost or has been converted into one of the crossveins between the radius and the com-pound vein. This compound vein is therefore homologous to the recurrent vein of many beetles, which extends proximally from the base of the trachea RS (Fig. 4). On the wings of the Neuropteroidea the crossvein is usually referred to as 1r - m, but it is quite possible that, it is in fact the anterior branch of media, distally merged with the posterior branch of the radial sector. Such a nomenclature was proposed, for ex-ample, by O. M. Martynova (1960).

On the wing described the main free trunk of media is two-branched. On the wings of present-day beetles the anterior of these branches is basally lost, as often happens with veins intersected by folds. Slightly proximal of the base of the compound vein extending from RS another vein extends obliquely back from the base of M and this is also usually designated as a crossvein, 1m - cu, whereas in reality it may possibly be the base of M5 distally merged with the cubital system, as was considered by Tillyard (1926). The homology of the vein designated above as M1 (Fig. 2) also cannot be regarded as completely clear. It is possible that it is a compound vein consisting of the first branch of media and the last branch of the radial sector. In this case the vein designated as crossvein 2r - m is in origin a longitudinal vein forming its base. This facilitates the homologization of these veins in the wings of beetles and neuropteroids and renders explicable the tracheation of the veins designated by Forbes as the last branches of the radial sector (Fig. 1, a).

The cubital system is made up of two simple veins which, unlike the veins of present-day beetles, do not differ appreciably in thickness. Precise establishment of the nature of their connection is impossible, since an unopened fold runs between them. The cell usually designated as oblongum is not to be seen among the other cells of the area between the medial and cubital systems.

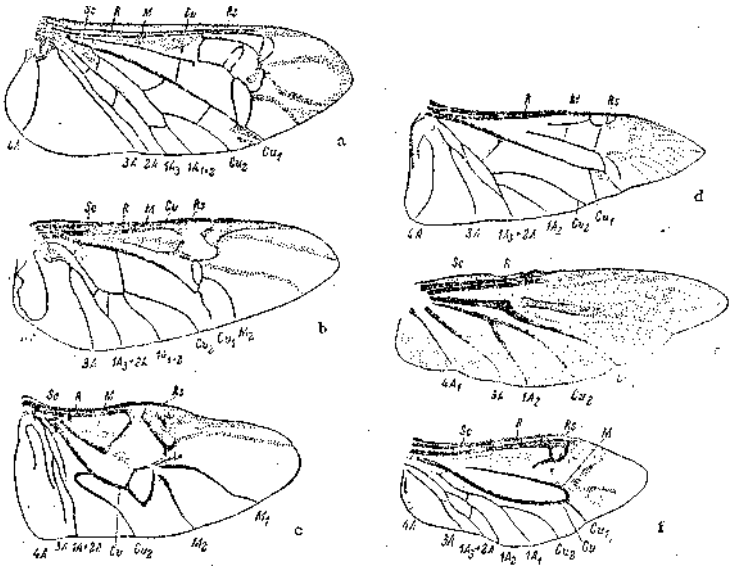

Fig. 5. Wing venation of beetles—Archostemata, Adephaga and Polyphaga.

a) Cupes clathratus Sols.; b) Calosoma sycophanta L.; c) Gyrinus sp. ; d) Hydrous piceus L. ; e) Necrophorus vespillo L. ; f) Permestes lardarius L. ;

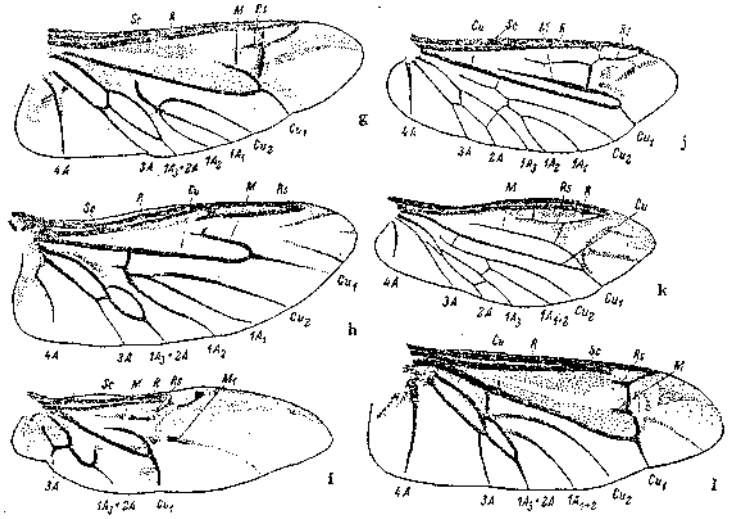

Fig. 5. (continuation), g) Dascillus cervinus L. ; h) Ancylocheira sp. ; i) Hippodamia tredecimpunctata L. ; j) Cebrio bicolor Leach (taken from Forbes, 1922); k) Athous niger L. ; l) Prionus corianus L.

The first anal vein divides near the base and its anterior branch again dichotomizes slightly distal of its middle. The crossvein between the first and second anal veins, lying proximal of their branching, can scarcely be said to be an anal arch, which is how it is designated by Forbes. It is simply a crossvein. The second and third anal veins are simple and begin with a fairly long common trunk, as is usual in beetles and neuropteroids. The anal region of the wing is distinctly divided into two lobes—anal and jugal.

The number of crossveins may be greater in all areas, except in the anal area, than on the wings of present day beetles. The arrangement of most of them makes it easily possible to homologize with them certain crossveins pre-served in present-day wings. These veins are apparently not homologous in different beetle families and their comparison with the venation of the wing described, which has a full complement of veins, provides new data for reconstruction of the phylogeny of beetles.

The folds clearly to be seen on the impression are of great interest. Their general pattern is extremely similar to the prototype worked out by Forbes (1926) on the basis of a comparative study of present day beetles. Only the large and strongly extended proximal fold B does not fit into this scheme. The folds C + D most probably formed a practically equilateral triangle with its vertex directed forward. The strong development of the fold G should be noted. In general the wing is more reminiscent of the wing of the primitive Polyphaga in the nature of the folds than of present-day members of the Archostemata, although it is probably from a member of the latter suborder.

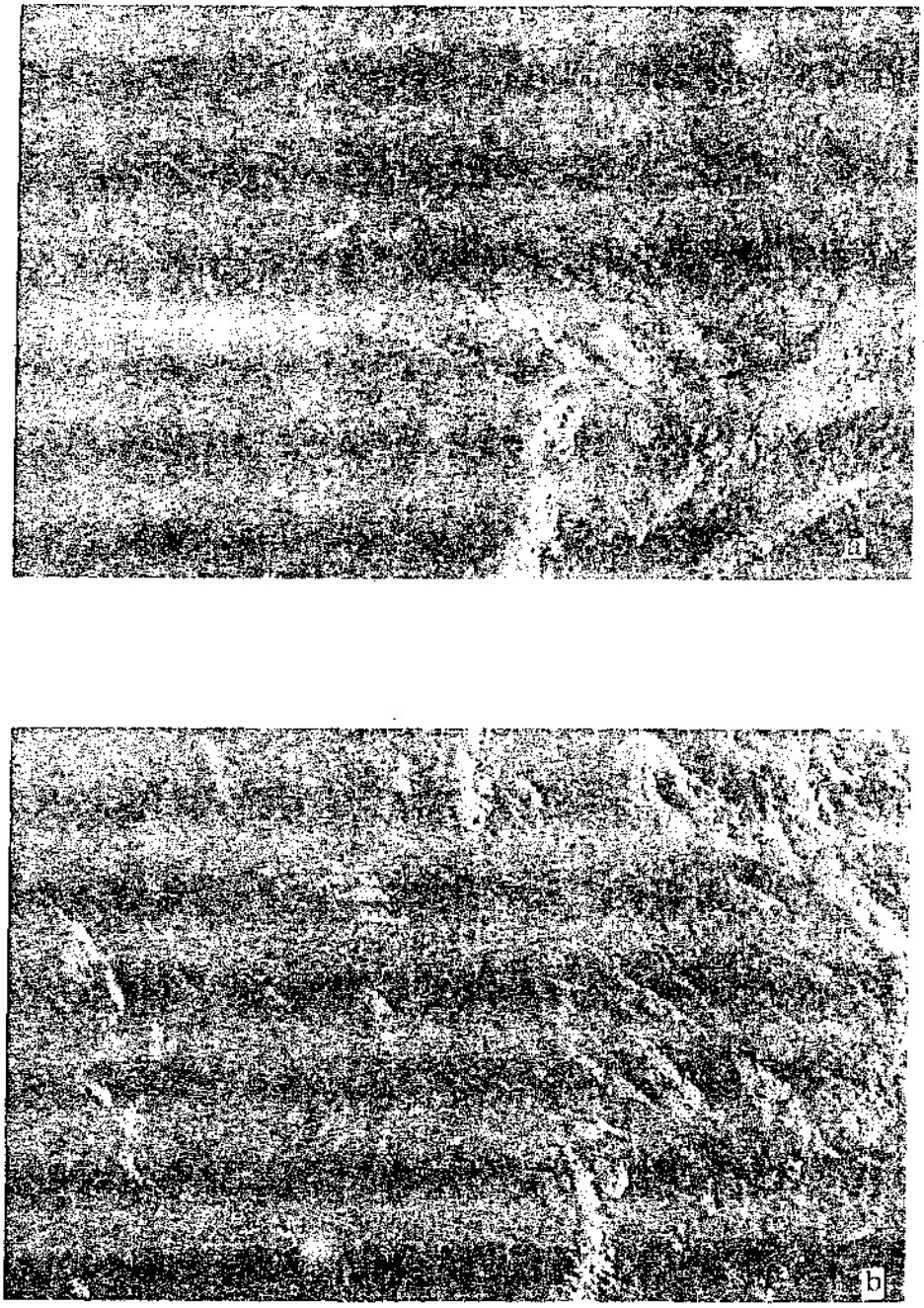

Fig. 6. Hind wing of a beetle from Upper Permian deposits near the village of Chepanikha (Urals), specimen PIN 3286/4 (x 7). a) direct lighting; b) side lighting.

In conclusion we should consider a rational nomenclature of the wings of the present-day families of beetles. The most widely employed system for the classification of wings is their separation into the caraboid, cantharoid and staphylinoid types. The most important characters for the discrimination of these types are usually said to be the presence of crossveins forming an oblongum in the first type and the total absence of crossveins in the last. Wings with cantharoid venation constitute an intermediate type. In such a form this division simply describes a degree of reduction of the venation and may be used only for identification purposes, but not for analysis of the classification of beetles owing to the very high frequency of parallelism in this process of the reduction of venation.

Nevertheless, caraboid venation (Fig. 5) is in fact characteristic of a natural group of beetles—the suborders Adephaga and Archostemata. The features most characteristic of it are not such primitive characters as the retention of the crossveins forming the oblongum but, on the contrary, features of reduction: the absence of the fold B, the presence of only two branches of the first anal vein and the absence of a recurrent vein on RS.

Beetles whose wings have venation of the other two types do not form natural groups. They incorporate groups which are different in origin but similar in the degree of reduction of the venation. Five types of wing structure were established in beetles of the suborder Polyphaga by Forbes (1926),

but the classification of the order proposed on their basis was found to differ sharply from that generally accepted. These conditions have scarcely been reflected at all in the present-day classifications of the order (Crowson, 1955) and they therefore merit attentive reexamination. At present we must confine ourselves to the presentation of a number of wings in the suborder Polyphaga and an indication of the nomenclature of their veins (Fig, 5). It should, however, be noted that there is in any case no doubt that the homology of the principle veins of beetles as proposed by Forbes is correct and that after appropriate modification of the nomenclature, as described above, it is fully capable of serving as a unified nomenclature for all beetles.

SUMMARY

Homology and the nomenclature of hind wing venation in beetles are discussed. A description is given of the venation of a beetle wing from the Permian of the Urals similar in many respects to the wings of the Megaloptera.. The wings of various beetles are illustrated showing a proposed nomenclature for the veins,

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