
REVIEWS

On the Discussion of the Wing Venation of (Archae)Orthoptera (Insecta)

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Abstract—Alternative current approaches to homology and nomenclature of the insect wing venation are discussed. The differences between the opposing viewpoints are found to be not as deep as they have sometimes been supposed to be, and more so, there are some observations that could help to smooth current contradictions. However, this requires an understanding of the evidence presented by the disputants and, particularly, an understanding of their terminology.

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Current polemics on the wing venation of Orthoptera and related insects (Béthoux and Nel, 2002; Gorokhov, 2005; Béthoux, 2007) throw light on some important problems of meronomy and morphological nomenclature, and gives a convenient opportunity to discuss them.

In modern entomology, there are three main approaches to the homology and nomenclature of the wing veins in insects. One, developed by Kukalová-Peck (1978, 1991, etc.), proceeds from the metameric organization of the wing, with six homonomous vein systems, namely costal (C), subcostal (SC), radial (R), medial (M), cubital (Cu), and anal (A). Each system originally dichotomizes into a convex (raised above the membrane, labeled with +) anterior vein and a concave (slightly depressed and labeled with –) posterior one. The anterior of these veins is traditionally marked by the addition of the letter A (anterior), the posterior one by P (posterior): CA, CP, RA, RP, MA, MP, CuA, CuP, AA, AP. Each vein may be further subdivided, normally retaining its sign (+ or –). Béthoux (2007) described this pattern as classical, but I can see no sign of classicism here and do not use this term.

The second approach is historically a derivative of the first, but it accentuates obligatory preservation of the vein position rather than metamery (six homonomous principal veins); thus, if the visible CuA base is concave, then it is not CuA but CuP. This approach is now being developed by Béthoux (Béthoux and Nel, 2001, 2002; Béthoux, 2007).

The third approach would be worthy of the name classical, if the term had not already been used by Béthoux in a different sense. This is an old but constantly developing, changing and in general not too strict pattern including the veins C, SC, R with its pos-

terior branch RS (homologues of RA and RP in Kukalová-Peck's pattern), M, which is accepted as consisting of MA and MP when necessary, Cu with constant branches CuA and CuP, and one or several anal veins (A). Furthermore, the C, R, CuA and A are normally convex (+), while SC and CuP are concave (–), but this correspondence is not taken as too strict, and its violation itself is not considered sufficient to reconsider the vein homology. For example, in Hymenoptera of the family Diapriidae and superfamily Cynipoidea, the vein CuA in the hind wings is concave, but no one has yet doubted its homology. A very common situation in insects is when the CuA (in traditional sense) is convex in forewings and concave in hind wings (see, e.g., Rasnitsyn and Quicke, 2002, text-figs. 78, 110, 212, 360); this is not considered as an argument against their homology.

A variant of this old pattern is “the M_5 pattern,” as named by Béthoux, “of which Rasnitsyn... is the sole modern defender” (Béthoux, 2007, p. 338). This version (far from unique to myself, see, e.g., Sharov and Sinitchenkova, 1977; Shcherbakov et al., 1995; Novokshonov, 1997; Storozhenko, 1998; Aristov, 2004) supplements the old pattern with the convex posteriormost branch of M, conventionally termed M_5 , the fusion of which with the primarily concave vein results in the familiar convex CuA. The reasons for such a hypothesis have been given earlier (Rasnitsyn, 1980; Rasnitsyn and Quicke, 2002) and are not repeated herein (but see below).

Finally, Sharov–Gorokhov's pattern alternative to Béthoux's pattern in current polemics formally presents nothing new, being merely an adaptation of the old pattern to orthopterans. In these insects, the M shows no trend to dichotomize into two principal branches, but often gives off a short but strong, convex vein that devi-

ates backwards close to the M base and soon is fused with CuA. Therefore, taking into account the dichotomy of M into MA and MP in some insect groups, this posteriormost M branch was termed MP (while the M itself was termed MA). Since no special efforts to substantiate this homology have been undertaken so far, and because the MP of Sharov–Gorokhov entirely corresponds to my M_5 , I would like to state that Sharov’s and my patterns are substantially identical and differ only nomenclatorially. However, Béthoux is incorrect not only for this reason, when he accuses Gorokhov of inconsistency, pointing to his publication where my vein nomenclature is accepted. The point is that he refers to our joint publication (Gorokhov and Rasnitsyn, 2002), where the vein nomenclature reflects my opinion, not Gorokhov’s.

Nevertheless, discarding the details and intentionally simplifying the situation, in the above picture one may see the same two trends as I discussed recently using the example of taxonomy and taxonomic nomenclature (Rasnitsyn, 2002). I mean the alternative *class-individuum* or, more exactly, the triad *class-continuum-individuum*. *Class* in the philosophical meaning of the word is a unit of classification, whose attribution is unambiguously defined by the possession of a certain character or combination of characters. *Individuum* is an object characterized by its integrity and continuity rather than character: the baby and the old man may have nothing in common but name, and are nonetheless indisputably the same person (individuum). *Continuum* is an intermediate notion: it is integral enough to be named, but not enough for its proper name to be sufficient for its identification. For this purpose, it is necessary additionally to define the boundaries of the continuum by tracing hiatuses, i.e., gaps in the continuity of the character distribution. Naturally, the typical (paradigmatic) continuum is the taxonomical species and every other taxon; we trace the boundaries between species rather than set them using fixed characters. The same is applicable to morphology; the meron (a part of organism, analogue of taxon in meronomy, i.e., in classification of parts) is likewise separated by tracing the boundaries rather than assigning to it some defining character. Indeed, the leg is an organ of cursorial locomotion, whereas the wing is an organ of flight, but the hind leg of a flying frog is still a leg, because it is little modified compared to the legs of other frogs, while the foreleg of a bat is already a wing.

The old nomenclature for the insect wing venation emerged and developed just by means of tracing hiatuses in diversity of the wing structure variants. The Sharov–Gorokhov pattern appeared in the same way; Sharov noticed a constant presence of the posterior branch connecting M with CuA and, taking into account the widespread division of the median into two stable branches, MA and MP, decided that it is MP that fused into the anterior cubitus and that only anterior branch of the median is free; he found no serious counterarguments to this idea. In fact, Sharov used the main

(in my opinion) tool of cognition, the presumption method (thoroughly analyzed in a series of my papers: Rasnitsyn, 1988, 1992, 2002, 2006; Rasnitsyn and Dlussky, 1988). He applied the most universal **conservative presumption**: “accept the viewpoint of predecessors, unless and until sound contrary evidence is presented, and if it is not possible, modify it no more than is sufficient to overcome the controversy revealed.” Actually, this is nothing more than a modified formulation of the famous Ockham’s razor (parsimony principle), claiming that entities should not be multiplied beyond necessity, and that, in particular, one should use minimal means to reach the goal.

I followed the same presumption, restoring and additionally arguing the “ M_5 pattern” (Rasnitsyn, 1980; Rasnitsyn and Quicke, 2002). I noted the widespread occurrence of a short, often oblique convex vein running from M to CuA, often present when typical MA and MP are developed. A hypothesis of homology between this vein and MP seems to me doubtful; more so, this posterior M branch was found to be constantly convex, whereas, in the paradigmatic case (in the wings of Palaeoptera, i.e., in mayflies, dragonflies, and palaeodictyopteroids), the MP is concave and MA is convex, as it should be from the aerodynamic point of view (convex MA between concave RS and MP forms an additional reinforcing rib). However, the strongest argument for independence of the posterior convex branch of CuA was the venation of *Evenka archaica* (Rasnitsyn, 1977), showing in forewings the M_5 of typical structure and, in hind wings, a free vein running very close to CuA. Moreover, with some degree of confidence, the free M_5 was also revealed in the wings of many other insects from the Carboniferous to the Recent (for more detail, see Rasnitsyn, 1980, 1998; Rasnitsyn and Quicke, 2002). As a result, I concluded that the previous venation nomenclature is not adequate to these observations and needs correction.

In my opinion, other modifications of the initial pattern emerged in a more or less similar way, but were apparently self-actualized insufficiently to judge with confidence. Nonetheless, it is easy to note that different emphasis may be placed on the hiatus and on the character. In my opinion, Kukalová-Peck’s hypothesis suffers from a groundless conviction that the venation in the ancestor of winged insects was completely regular (metameric), and accordingly appoints to the veins properties (characters), the reliability of which is far from supported by observation. I have repeatedly commented on this (Rasnitsyn, 1981, 1998; Rasnitsyn and Quicke, 2002) and, since this hypothesis is not itself reality, will not discuss it further.

Béthoux’s hypothesis has inherited from Kukalová-Peck’s hypothesis an unnecessary (in my opinion) faith in the reliability of specific characters identifying a vein (confirming its homology). I mean first of all the vein position (convex/concave): overemphasis of this character and especially the obligatory convexity of CuA

forced Béthoux to accept fusion of CuA with the median from its very base in all the cases where I identify the presence of M_5 . Therefore, Béthoux's CuA is strictly my M_5 ; it leaves the M stem in the same manner not far from the wing base, and more or less soon merges with the next posterior vein, normally concave, termed CuP by Béthoux (and CuA by myself). Béthoux homologizes my M_5 with CuA, despite direct evidence of basal M plus CuA fusion (retention of the free CuA base near the wing base, proximal to the fusion with the M base) being absent or insufficiently convincing. Béthoux also does not attach significance to the fact that the CuA in common usage is usually a richly branching vein, while CuP is in most cases simple or has few branches, whereas, in the pattern proposed by him, conversely, only CuP is multibranching.

The main point, the vein termed CuA by Béthoux and M_5 by myself, is already present in the earliest pterygotes, and subsequently in all main groups of winged insects. The statement of Béthoux (2007) that the M_5 is unknown in Palaeoptera and Polyneoptera (except for Grylloblattida) is surprising; Béthoux introduces his taxa of high (but not specified) rank, Archaeorthoptera and Panorthoptera, based to a considerable extent just on the CuA (= M_5), which, deviating from M + CuA, merges very early with CuPa in Archaeorthoptera and with CuA α in Panorthoptera (Béthoux and Nel, 2002). It is also difficult to agree with the absence of M_5 in the remaining Polyneoptera and Palaeoptera. This vein is found in some of the earliest mayflies and palaeodictyopteroids, in the most primitive Carboniferous Grylloblattida, in the earliest cockroaches and (in the hind wings) in earwigs (Bolton, 1921, pl. 1, fig. 1; Vignon, 1929, pl. II, figs. 1, 2 (j); Sharov and Sinitchenkova, 1977, text-fig. 2; Carpenter, 1979, text-figs. 10B, 10C; Sinitchenkova, 1979, 1980; Laurentiaux-Vieira and Laurentiaux, 1980, text-figs. 2–3 (*m*); Kukulová-Peck, 1985, text-figs. 12–14 (*st*); Kukulová-Peck and Brauckmann, 1990, text-figs. 1–3 (*st*); Storozhenko, 1998, text-figs. 106, 109; Rasnitsyn and Quicke, 2002, text-figs. 87, 150, 353, 355, 356, 359–361, 420). The statement of Béthoux that, in Plecoptera, the absence of M_5 is proven by the CuA being convex from the base (l.c.) is not convincing. First, the change in the vein position is in my opinion not a very rare phenomenon (see above) and, when a vein changes position along its length (as in the case of CuA becoming convex after its fusion with M_5), the boundary between its convex and concave parts may shift easily. Second, the vein termed the arculus by Béthoux (2005) looks like the typical M_5 in the hind wings of most stoneflies figured by him; thus, the same homology of arculus can apply to the fore wings as well.

The wide occurrence of M_5 (in my sense, i.e., CuA + CuPa/CuPa α in the sense of Béthoux) in winged insects forces us to accept this character as having been acquired by a common ancestor of all known Pterygota, i.e., as a synapomorphy of the subclass. It means that

Béthoux's hypothesis, if realized consistently, requires a total renaming (in all insects) of M into M + CuA, and Cu into CuP. However, no direct evidence of basal fusion between M and CuA is presented, as mentioned above, and the immense rearrangement of the vein nomenclature turns out to be based solely on a hypothesis of a perfectly regular original venation in insect wings and strict retention of the vein position. Certainly, this does not mean that Béthoux's nomenclature is incorrect, but one must recognize that the basis of his hypothesis is problematical, and its introduction in terms of total renaming of the veins mentioned is premature.

Nevertheless, whatever is said here, it is unwise to expect that it will result in the acceptance of any point of view by all sides. Debate in general is not the most worthwhile occupation for thinking men; said it has been said many times that, in dispute, a quarrel is born, and only rarely understanding. It should simply be accepted that the vein termed the median by Sharov is named the same by me and M + CuA by Béthoux. Respectively, Sharov's MP is myself M_5 and Béthoux's CuA, while Cu of Sharov and myself is CuP of Béthoux. Of course, this jumble of synonyms and homonyms is inconvenient; it fairly hinders common understanding, especially if some people are involved in the dialog who are not going into the heart of the matter and are not familiar with the terminology of the disputants. However, this is true professionalism to know the details and understand your colleagues' language. With time, the disagreements and schism will be surmounted and forgotten, and other problems, which we do not even suspect, will arise.

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