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Venation pattern of Orthoptera

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Abstract

The revision of several taxa previously attributed to the plesion 'Protorthoptera' yielded information about the venation pattern of Orthoptera and the sister-group relationships of Orthoptera. A new wing venation pattern is proposed, *i.e.*, (1) a basal composite stem $M + CuA$, distally separated into M and CuA ; (2) distal free CuA fused with the anterior branch of $CuPa$ ($CuPa$ 'alpha'). We consider the clade Orthoptera as an apomorphy-based group (*sensu* Brochu & Sumrall), on the basis of this complex structure and, also by the presence of two branches of MA , $MA1$ and $MA2$ (but reversed in some recent taxa, having a MA simple). In the stem group of Orthoptera, the free part of CuA is fused with $CuPa$, *i.e.*, $CuPa$ is not ramified into $CuPa$ 'alpha' and $CuPa$ 'beta'. Also, MA is simple.

Key words

Insecta, 'Protorthoptera', Orthoptera, Ensifera, Caelifera, apomorphy, fossil, forewing venation pattern

Introduction

The wing venation of Orthoptera is highly derived compared to those of its currently accepted recent potential sister groups (Wheeler *et al.* 2001). Thus the vein homology is difficult to establish for this group. This situation is confused by a multiplicity of interpretations (Sharov 1968, Kukalová-Peck 1991, Carpenter 1992), all based on different interpretations of the median and cubital veins of the available fossil taxa.

In order to establish a cladistic phylogeny of the Orthoptera through a set of clearly homologous characters, we revised several fossil taxa of the plesion 'Protorthoptera' because this group potentially contains the stem group of Orthoptera. A new interpretation of the forewing venation pattern is proposed.

Re-interpretation of the forewing venation of Orthoptera and relatives.—The present study utilizes the widely accepted method of homologization of insect wing veins, based on relief and branching of veins. In the pterygote ground plan, each vein is divided in two sectors, an anterior convex sector and a posterior concave sector (if the wing is observed on its dorsal side) (Redtenbacher 1886; Brongniart 1893;

Laurentiaux 1953; Kukalová-Peck 1983, 1991; Carpenter 1992). Wings of insects are supposed to have eight veins in the ground plan (Kukalová-Peck 1983). They are, from the anterior to posterior wing margin: Precosta (presence debatable), Costa, Subcosta, Radius, Media, Cubitus, Anal and Jugal, respectively abbreviated PC , C , SC , R , M , Cu , A , J .

The venational patterns for the different lineages can be interpreted on the basis of this general pterygote pattern. Among concurrent patterns, we prefer to choose the one that implies the minimal number of changes of convexity of the main veins, because it implies fewer *ad hoc* hypotheses. Various venational patterns have been proposed for Orthoptera. That of Ragge (1955), followed by Sharov (1968: Fig. 1) and Gorochov (1995 a, b) is incongruent with the pterygote ground plan pattern, because the vein these authors named MP (referred to below as vein '1') is distinctly convex, and consequently should not correspond to a posterior sector. Also, the branches of 'CuA' *sensu* Sharov, are concave instead of being convex, as branches of an anterior sector. Moreover, the first posterior branch of the vein MA *sensu* Sharov is concave. Thus, the pattern proposed by Sharov implies three inversions of 'convexity' that concern main veins.

Kukalová-Peck (1991) and Carpenter (1992) proposed to consider the vein MA *sensu* Sharov as the concave MP . After Carpenter (1992), the vein '1' is a pseudovein, but this author did not demonstrate its alleged secondary origin. Kukalová-Peck (1991) proposed two other different patterns. The first one is similar to Carpenter's hypothesis. Her second pattern is based on a composite basal vein $CuA + M$, from which emerges a free part of CuA (convex vein '1') connected to a branch of CuP by a pseudovein (concave vein '2'). But these expected pseudoveins are always present as strong, convex and concave veins in all Paleozoic Orthoptera or relatives, which is incongruent with her hypothesis.

In order to clarify the situation, we revised *Gerarus bruesi*. Sharov (1968) proposed this taxon as sister-group of the whole of Orthoptera. We do not agree with the 'hemipteroid' interpretation of its forewing venation proposed by Kukalová-Peck & Brauckmann (1992, Fig. 27), because there is no visible fusion of MA with the radial stem at the extreme wing base. Its MA is branched, with a $MA1$ close to RP . We

Fig. 1. Venational pattern of Orthoptera.

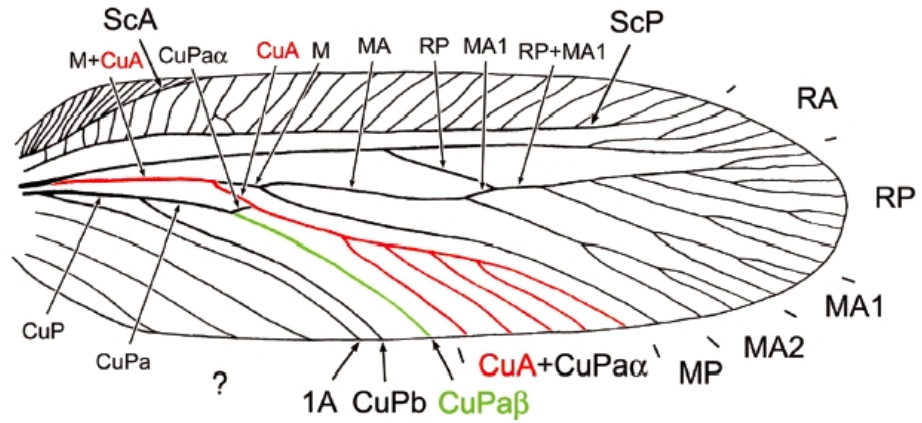


Fig. 2. Venational pattern of Ensifera.

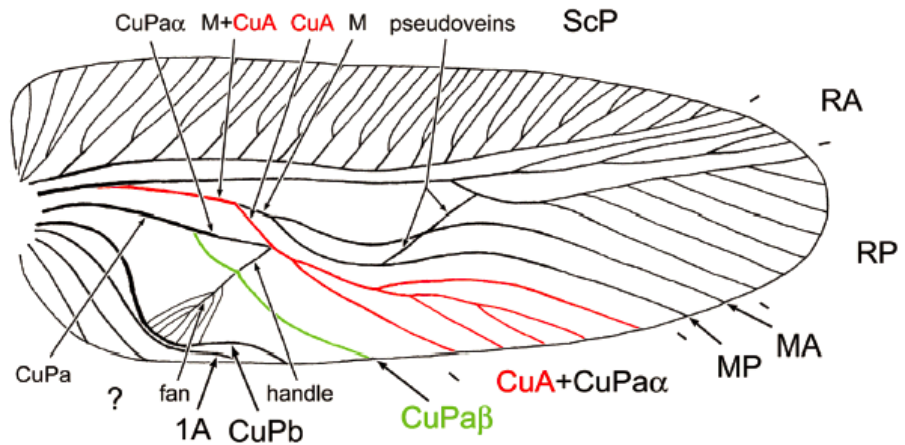
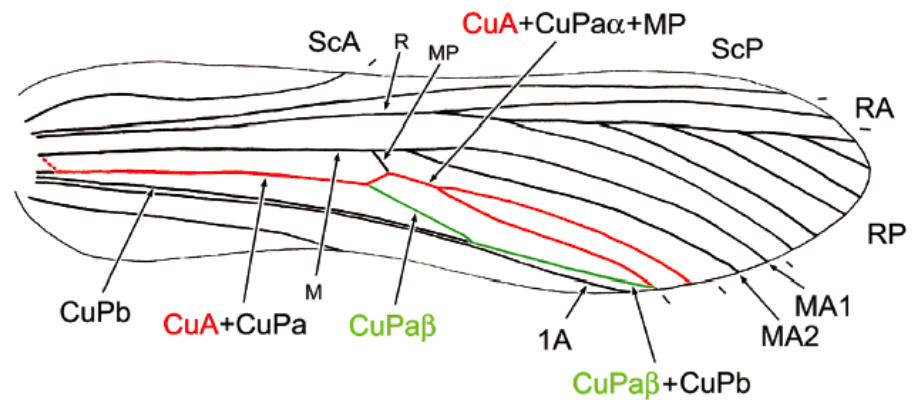


Fig. 3. Venational pattern of Caelifera.



emend the interpretation of the medio-cubital area proposed by Kukalová-Peck & Brauckmann (1992), as follows: a convex composite vein, M + CuA, distally divided into a basally neutral vein M and a strongly convex vein CuA (vein '1'), which is fused with a clearly concave vein (vein '2'). Contrary to Kukalová-Peck & Brauckmann (1992), we consider this last vein as the anterior branch of CuPa, *i.e.*, CuPa 'alpha'. The resulting composite vein, CuA + CuPa 'alpha' is distally convex.

The true Orthoptera have the same organization of veins M, MA, MP, CuA and CuP as *Gerarus*, but these are more easily visible in the Paleozoic and Early Mesozoic than in more recent taxa.

We also examined specimens assigned to the Narkeminidae (Pinto & Pinto de Ornellas 1991). The course of CuA (the strongest vein in the medio-cubital area) is very clear in these fossils. They have the same medio-cubital pattern, except for the number of ramifications of CuP. Their CuPa is simple. Consequently, the composite vein is CuA + CuPa. Several other fossil taxa assigned to the plesion 'Protorthoptera' (*sensu* Carpenter 1992) share this pattern, such as *Heterologopsis* (Brauckmann & Koch 1982), *Carpenteroptera* (Pinto 1990), and the Tococladidae (Carpenter 1966).

This 'orthopteroid' venation pattern is based on the hypothesis of the occurrence of a very basal fusion of CuA

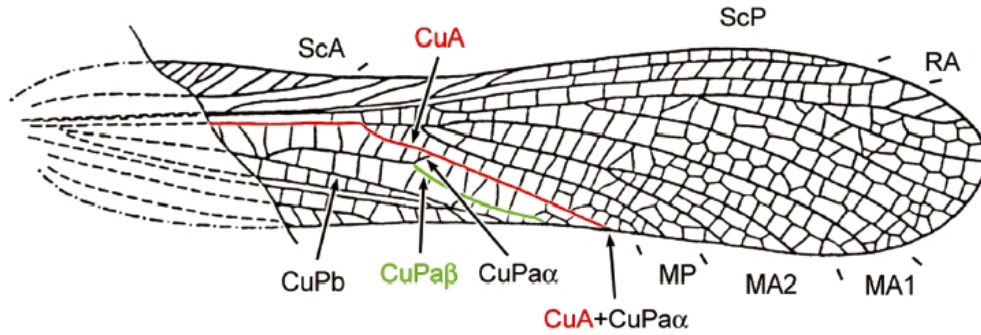


Fig. 4. New interpretation of forewing venation of *Plesioschwinzia thalassophila* (Caelifera; drawing after Zessin, 1988).

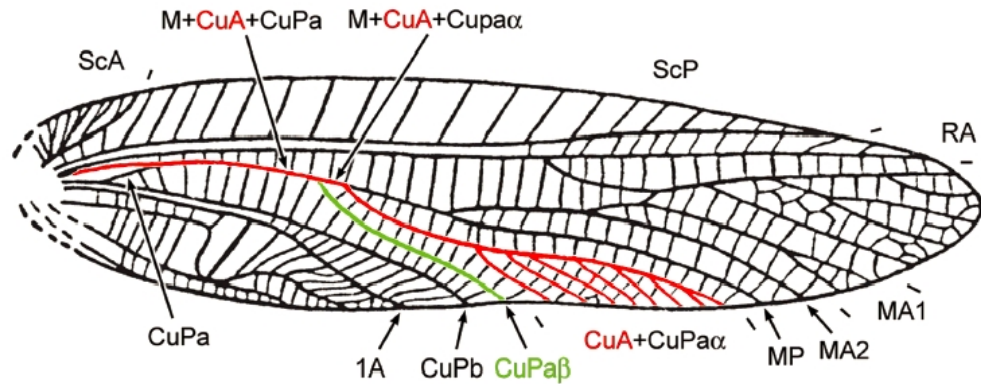


Fig. 5. New interpretation of forewing venation of *Elcana media* (Orthoptera; drawing after Zessin, 1988).

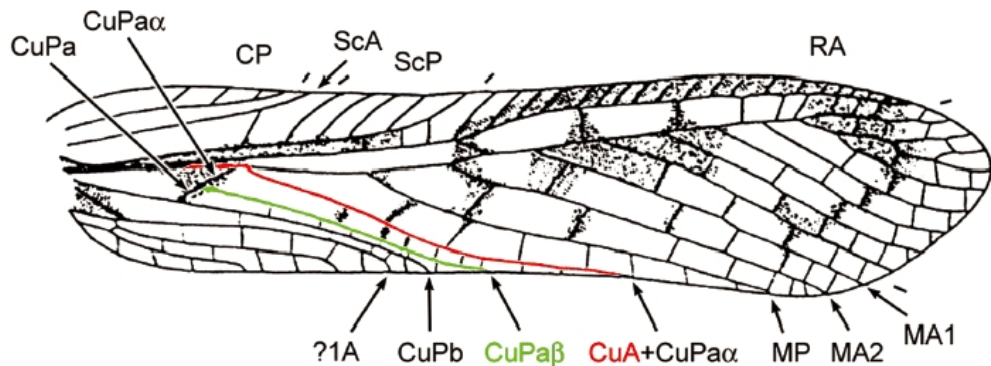


Fig. 6. New interpretation of forewing venation of *Mesoedischia madygenia* (Orthoptera; drawing after Sharov, 1968).

and M. Similar fusions are frequent in several pterygote insects (among others Odonoptera). It does not imply any supplementary hypothesis of change of convexity of one or several main veins and it is congruent with the strong convexity of vein '1' and strong concavity of vein '2'.

New 'Orthopteroid' venation pattern with implications on forewing structures of extant taxa.—Our aim here is neither to propose a new diagnosis of Orthoptera, nor to exhaustively review the relationships within this clade, but only to propose a new interpretation of the venation, underlining its major phylogenetic implications. The pattern has no implications for the classification of extant Orthoptera.

We propose to characterize the 'orthopteroid lineage' (as an apomorphy-based clade *sensu* Brochu & Sumrall 2001)

on the basis of the following autapomorphic structure of cubito-median veins: fusion of distal free part of CuA (emerging from common stem M + CuA) with concave anterior branch (CuPa or CuPa 'alpha') of CuP. We include in this group the true Orthoptera, the Titanoptera, the Caloneurodea and several Paleozoic families formerly included in the 'Protorthoptera' (Béthoux *et al.*, forthcoming; Béthoux & Nel, submitted).

Within this group, we propose to characterize the Orthoptera on the basis of the following autapomorphies: 1) jumping metathoracic legs; 2) (Fig. 1) differentiation of MA into MA1 and MA2 (MA1 is primitively close to RP, connected with it by a short cross-vein or fused with it; reversed in several derived Ensifera); 3) (Fig. 1) MP strongly concave. This last character is more variable than the others.

In the 'Ensifera' ('gryllids' and 'tettigoniids') (Fig. 2), numerous complex pseudo-veins occur, related to sound producing organs (enclosure of a distinct vibrating area; production of pure tones). The ramification of CuA + CuPa 'alpha' characterizes the Ensifera *sensu nov.*, with the first branch directed posteriorly and the second branch directed anteriorly (Béthoux *et al.* 2002). Note that CuA + CuPa 'alpha' are uniformly posteriorly pectinate or simple in other Orthoptera. The name 'Ensifera' does not have the same significance depending on the authors and even corresponds to a paraphyletic group of Gorochov (1996). Nevertheless, we choose to maintain it for this clearly defined clade, including all extant taxa currently assigned to this group. The composition of the Ensifera *sensu nov.* matches that of the (Gryllidea + Tettigoniidea) *sensu* Gorochov (1996).

In the ground plan of the currently accepted group Caelifera, the distal free part of CuA is present, as in *Plesioschwinzia thalassophila* (Zessin 1988) (Fig. 4) and some other Locustopsidae (*Praelocustopsis*) and Locustavidae (*Locustavus*) (see Sharov 1968, Figs 34A, D). In the more derived Caelifera, it is basally rejected or 'cross-vein-like', and MP is fused with CuA + CuPa 'alpha', enclosing the discoidal cell (Fig. 3). The Caelifera are mainly characterized by the absence of fusion between RP and MA1 (a convergence with the recent taxa of the 'ensiferan' lineage).

We applied this pattern to several fossil Orthoptera, which are neither Ensifera nor Caelifera. In the male Mesoedischiiidae, CuPa is basally fused with M + CuA (Fig. 5). Note the occurrence in this group of a stridulatory apparatus not homologous with that of the Ensifera. In the Elcanidae ground plan, the distal free part of CuA is not independent, but fused at its origin with CuPa 'alpha', and CuA + CuPa 'alpha' is simple, as in the Caelifera (Fig. 6).

Conclusion

The extensive use of crucial Paleozoic fossils permits us to propose a new venation pattern of Orthoptera. It already allows us to give new wing venational autapomorphies of the 'orthopteroid lineage' and Orthoptera. Such information is of crucial importance for the resolution of the phylogeny of this taxon, based on the cladistic outgroup comparison method (Béthoux & Nel, submitted).

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