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Response to Trueman and Rowe (2019) 'The wing venation of Odonata. *International Journal of Odonatology*"

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Trueman and Rowe (2019) claimed that they have finally solved the wing venation homologies for the Odonatoptera, refuting the previous models, and especially that of Riek and Kukalová-Peck (1984). Nevertheless, their proposal has several failures, viz. nature of the distal part of their "anal vein", nature of the "MA", and incongruence with recent results obtained by Jacquelin et al. (2018) on the morphology of the extreme wing base. Currently the only pattern of venation in total accordance with the known data is that of Riek and Kukalová-Peck (1984), as modified in Nel et al. (1993) and Jacquelin et al. (2018).

Keywords: Odonatoptera; wing venation; homologies; dragonfly

Trueman and Rowe (2019) recently proposed a new hypothesis of nomenclature of the wing venation of the Odonatoptera, claiming that they solved all the problems concerning the strange venation in this superorder. They also indicated that Riek and Kukalová-Peck's (1984) system "invokes vein mergers, 'lost crossings' and the relocation of veins from one wing surface to the other, all of which in evolutionary terms are highly implausible". Their work is of great interest for the origin of the insects' wings and articulation to body. Nevertheless, Trueman and Rowe were not aware of corrections made to the system of Riek and Kukalová-Peck (1984) by Nel, Martínez-Delclòs, Paicheler, and Henrotay (1993), who proposed to consider that the vein MA is basally fused to RA and RP in a common stem in which the three veins are still visible, solving the problem of the "jump" that M would make between its basal part and its fusion with RP in the arculus after Riek and Kukalová-Peck's (1984) hypothesis. Also Trueman and Rowe (2019) were not aware of the important works of Bechly (1995, 1996) and of Jacquelin et al. (2018) that explored the extreme base of a wing of an extant Aeshnidae, clearly showing several hidden structures, and resolving the pattern of the veins and of the basivenale bullae from which they emerge. As a result, Trueman and Rowe's (2019) hypothesis leads to several major issues.

In this Response, the names of veins between quotation marks correspond to the nomenclature of Trueman and Rowe (2019); those not in quotation marks correspond to the venation nomenclature of Nel et al. (1993).

First, the situation in the Mesozoic Isophlebiidae (typically *Isophlebia* or *Anisophlebia*) for the vein Trueman and Rowe (2019) named "AA" is sufficient to reject their hypothesis: the part

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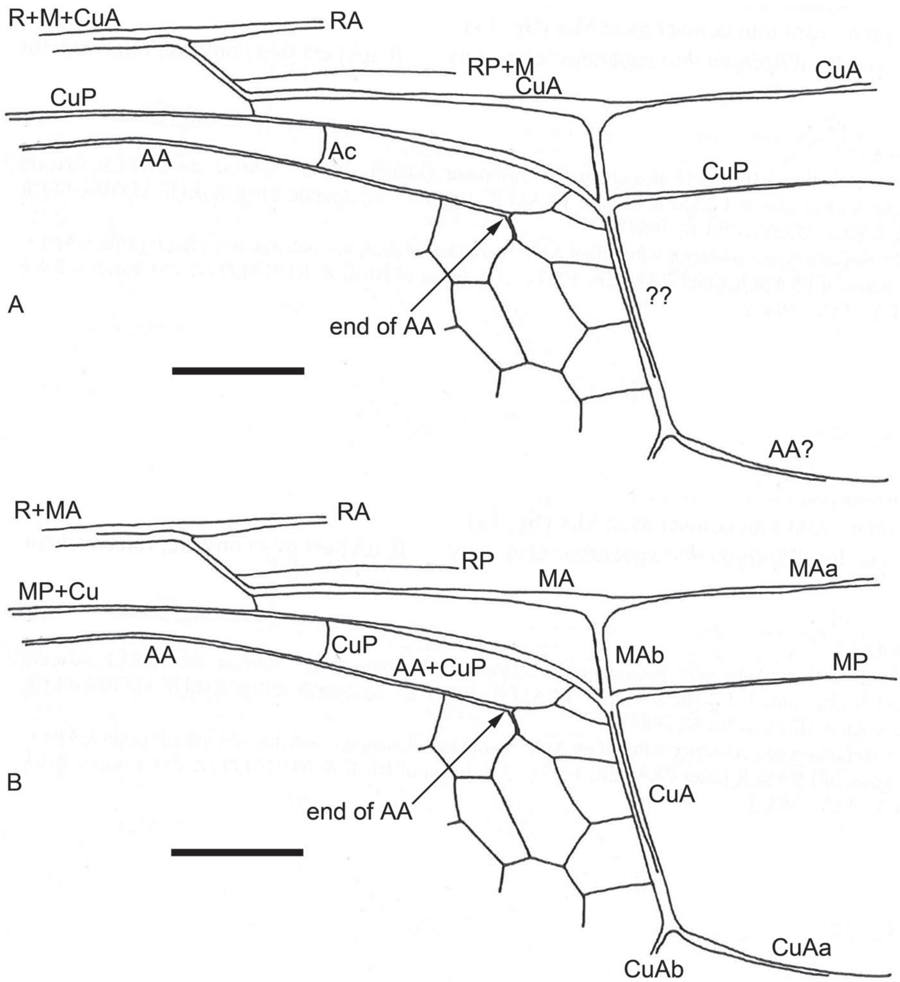

Figure 1. *Anisophlebia helle* (Hagen, 1862). Basal part of hind wing, reconstruction. (A) Trueman and Rowe's (2019) hypothesis; notice the vein "AA" making a "jump". (B) Nel et al.'s (1993) hypothesis. Scale bars = 2 mm.

of this vein distal to the discoidal cell is completely disjoint from its basal part (see Figure 1). Nel et al. (1993) already refuted the hypotheses of Tillyard and Fraser (1938), Fraser (1957) and Carle (1982) on the basis of the same argument. This convex distal part of vein "AA" emerges from the posterodistal angle of the discoidal cell, makes a short stem, and is fused with "AA" in all modern Odonata; but in the Isophlebiidae, this vein is very long, and not connected to "AA". It is a convex vein without name, posterior to the concave "CuP" of Trueman and Rowe (2019) and anterior to their "AA".

The second problem with Trueman and Rowe's (2019) hypothesis is the vein "MA". It is convex but it "emerges" from the main vein "R + MA" as a typical longitudinal intercalary vein (Figure 2), a feature present also in the palaeopteran Ephemeroptera. For instance, in the Odonatoptera: Triadophlebiomorpha, this vein has its base on a crossvein. It does not correspond to the theoretical division of a main vein into two branches as figured in Trueman and Rowe (2019, figure 4), but it has the typical aspect of a secondary vein or a crossvein as showed in Nel et al. (1993, figures 11, 12). Thus it is not a main vein and it cannot be MA. Trueman and Rowe (2019) accepted the existence of longitudinal intercalary veins in the radial area of the

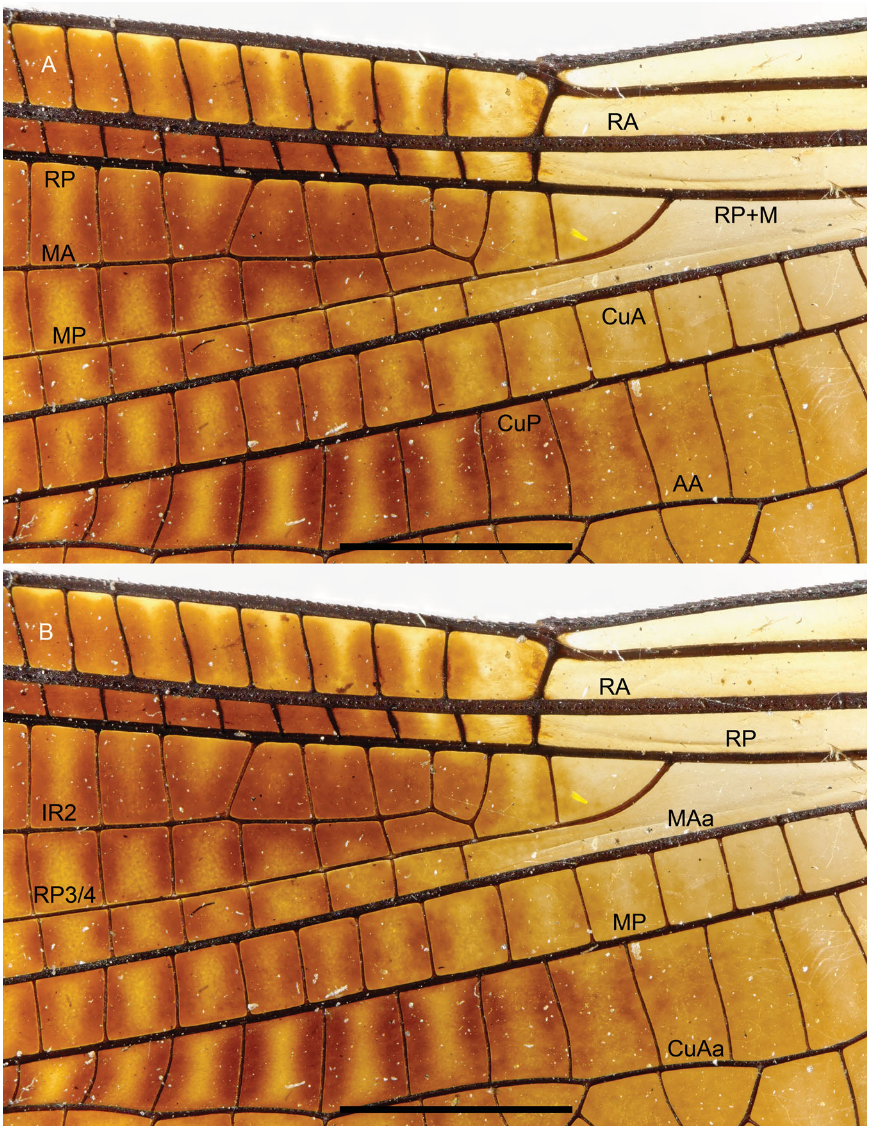

Figure 2. *Thaumatoneura inopinata* McLachlan, 1897. Photograph of mid part of forewing. (A) Trueman and Rowe's (2019) hypothesis; notice the vein "MA" emerging as a secondary longitudinal vein. (B) Nel et al.'s (1993) hypothesis. Scale bars = 2 mm.

Odonatoptera as they accepted the presence of a vein "IR1". The base of "IR1" is identical to that of the vein "MA" (in fact this "MA" is IR2).

Third, as showed in Jacquelin et al. (2018), the vein named "R + M + CuA" in Trueman and Rowe (2019) is constituted of three veins, as Nel et al. (1993, figure 4) and Bechly (1995, 1996) already showed. Two of them emerge from the same bulla, while the third one emerges from another bulla, posterior to the first bulla. Therefore these veins cannot be the "radius", the "media" and the "CuA", because these three main veins emerge from three different radial, median, and cubital bullae. These veins are in fact RA and RP emerging from the radial bulla, and MA emerging from the median bulla. Another vein emerges with MA from the same median bulla. This vein MP is distally fused at the extreme wing base with two veins that emerge from another, more posterior, bulla: CuA and CuP emerging from the cubital bulla.

Fourth, the vein named "CuP" should be a simple vein but it is quite clear in many Palaeozoic Odonatoptera that this vein is in fact the result of the fusion of two veins, one anterior and concave or neutral MP, plus one posterior and rather convex Cu (see the extensive discussion on this point in Jacquelin et al., 2018). This is in exact correspondence with the 3D CT-scan results.

Fifth, Trueman and Rowe (2019, figure 5A, B) supposed that "ScA" would be fused to an "edge-vein tube Ev", "CA", and "CP". In their figures, the basal part of wing, "ScA" is in the inner margin of this composite vein, while at the nodus level, it would be the outer margin (in fact the "Ev"). Jacquelin et al. (2018) showed that, if ScA is really present, it is a short vein that is independent at the extreme base of the wing, distally fused to CA and CP, and constitutes distally the most basal brace Ax0. It is not obvious that there is any anterior part of ScA going to the nodus level.

Lastly Nel, Roques, Prokop, and Garrouste (2018) have showed in the Carboniferous Odonatoptera *Enigmaptera magnifica* Nel et al., 2018 the presence of a MA closely parallel to R and a MP separated from MA at wing base and going into Cu. Under the hypothesis of Trueman and Rowe (2019), the single vein R would be "R", the MA would be "M", and there would be no "CuA" going parallel or fused to "M", then the MP would be "CuA" but this vein would not emerge from the same point as "CuP", which is highly improbable because the two branches of Cu should emerge from the same bulla (Figure 3).

The existence of a precostal and of a jugal vein in the venation of Odonatoptera and more generally of all insects, as proposed by Kukalová-Peck (1991), leave two important unsolved issues. Jacquelin et al. (2018) found no trace of these veins in the extant Odonata and fossil Zygophlebiidae. Further studies will be necessary to solve them for other insects, using the toll of 3D reconstruction with micro-CT scan.

In conclusion, Trueman and Rowe's (2019) hypothesis is much more complicated than that proposed by Nel et al. (1993) and Jacquelin et al. (2018). Also, Trueman and Rowe's (2019) hypothesis is not in accordance with the nature of their vein "AA" in the Isophlebiidae, the fact that their "MA" is a secondary longitudinal vein, and in the recent 3D microtomography exploration of the extreme wing base of an extant Aeshnidae, confirmed by the study of a fossil Triadophlebiomorpha (see Jacquelin et al., 2018). The hypothesis of Jacquelin et al. (2018) is much simpler, in accordance with the relative convexity of the veins, and does not imply any

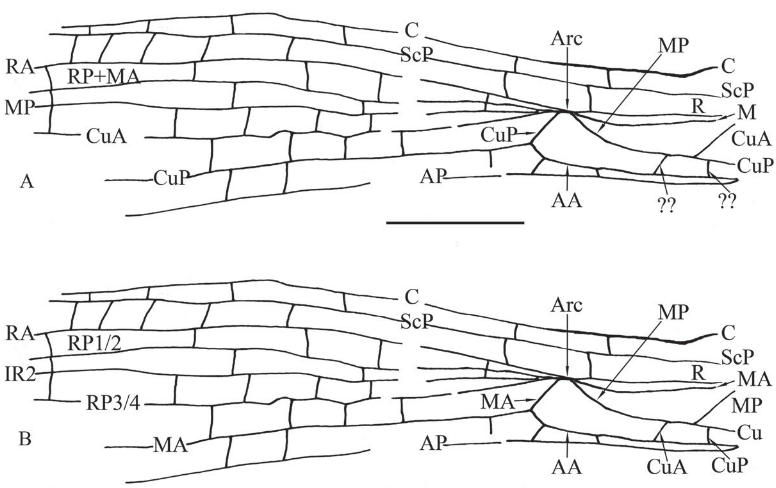

Figure 3. *Enigmaptera magnifica* Nel et al., 2018. Reconstruction of wing. (A) Trueman and Rowe's (2019) hypothesis; notice the vein "CuA" base very far from that of "CuP". (B) Nel et al.'s (1993) hypothesis. Scale bars = 2 mm.

"lost crossings" or relocation of veins from one wing surface to the other. Therefore, it is the only pattern of venation that has not been refuted by the known data. We can reasonably keep it as a basis for the venation of the Odonatoptera.

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References

Bechly, G. (1995). Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata), unter besonderer Berücksichtigung der Phylogenetischen Systematik und des Grundplanes der Odonata. *Petalura*, *Special Volume 1*, 1–341.

Bechly, G. (1996). Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata), unter besonderer Berücksichtigung der Phylogenetischen Systematik und des Grundplanes der Odonata. *Petalura*, *Special Volume 2*, 1–402.

Carle, F. L. (1982). The wing vein homologies and phylogeny of the Odonata: a continuing debate. *Societas Internationalis Odonatologica, Rapid Communications*, *4*, 1–66.

Fraser, F. C. (1957). A reclassification of the order Odonata, based on some new interpretations of the venation of the dragonfly wing. *Handbook of the Royal Zoological Society of New South Wales*, *12*, 1–133.

Jacquelin, L., Desutter-Grandcolas, L., Chintauan-Marquier, I., Boistel, R., Zheng, D.-R., Prokop, J., & Nel, A. (2018). New insights on basivenal sclerites using 3D tools and homology of wing veins in Odonatoptera (Insecta). *Scientific Reports*, *8*(238), 1–7.

Kukalová-Peck, J. (1991) Chapter 6: Fossil history and the evolution of hexapod structures. In Naumann, I. D. (Ed.), *The insects of Australia: A textbook for students and research workers* (2nd ed.) (pp. 141–179). Melbourne: Melbourne University Press, CSIRO.

Nel, A., Martínez-Delclòs, X., Paicheler, J.-C., & Henrotay, M. (1993). Les 'Anisozygoptera' fossiles. Phylogénie et classification (Odonata). *Martinia, Numéro Hors Série 3*, 1–311.

Nel, A., Roques, P., Prokop, J., & Garrouste, R. (2018). A new, extraordinary 'damselfly-like' Odonatoptera from the Pennsylvanian of the Avion locality in Pas-de-Calais, France (Insecta: 'Exopterygota'). *Alcheringa*, https://doi.org/10.1080/03115518.2018.1489561

Riek, E. F., & Kukalová-Peck, J. (1984). A new interpretation of dragonfly wing venation based upon early Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wings. *Canadian Journal of Zoology*, *62*, 1150–1166.

Tillyard, R. J., & Fraser, F. C. 1938. A reclassification of the order Odonata based on some new interpretations of the venation of the dragonfly wing. Part 1. *The Australian Zoologist*, *9*, 124–169.

Trueman, J. W. H., & Rowe, R. J. 2019. The wing venation of Odonata. *International Journal of Odonatology*, *22*(1), 73–88. https://doi.org/10.1080/13887890.2019.1570876