

Fig. 1

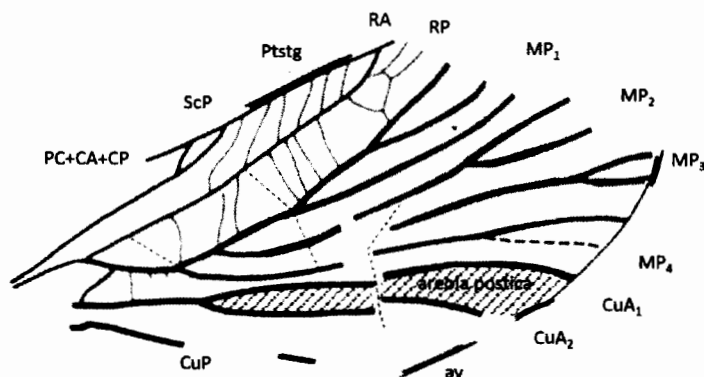
A new interpretation of the venation of oldest Euhemiptera: *Aviorrhyncha magnifica* Nel, Bourgoïn, Engel et Szwedo, 2013 (Hemiptera, Aviorrhynchoidea)

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In the shadow of Palaeozoic-era 'giant' insects, paraneopteran Hemiptera were already present as small size insects (Laurentiaux 1952; Nel *et al.* 2013). Scarcely visible against the dark matrix while most researchers hunt for the more familiar 'giants' of these periods, their small size of less than one centimetre probably explains why they were hitherto generally overlooked. In 2013, the authors described the Pennsylvanian Moscovian *Aviorrhyncha magnifica* Nel *et al.*, 2013 (310 Mya), the second Carboniferous and oldest hemipteran known after *Protoprosbole straeleni* Laurentiaux, 1952, known from Serpukhovian Mississippian Carboniferous (325 Mya). *Aviorrhyncha* was reported to the Euhemiptera lineage, suggesting a separation from the Sternorrhyncha dating back at least to the Moscovian and older than suggested by molecular dating (Song & Liang 2013). In the supplementary information available (online version), we mentioned that alternative interpretations of the venation were possible.

After a careful re-analysis of the data on new photos we provide here the most probable of them (Fig. 1) considering that basal and anal parts of the wing are missing. Particularly, basal cell is not observable (cua-cup not visible) and, separated from MP (with 9 terminals), CuA encloses a long areola postica; ambient vein (av) is observed in the wing margin starting from



pterostigma (Ptstg) to clavus (apex of CuP). The separated four veins at the base of the wing is an artefact due to a crack of the substrate. This new interpretation does not change the conclusions already published, but it obscures the evolution of some interesting and key morphological characters present in the Hemiptera ground plan.

Discussion

Protoprosbole shares with *Aviorrhyncha* a richer venation network than observed in other (and later) Permian Hemiptera Archescytinoidea (286-248 Mya), which are characterized by: the complete fusion of costal veins complex (PC+CA+CP), a complete apomorphic fusion of ScP+R except at apex where they separate forming a pterostigma in between, and by a rather simplified venation. Basal cell is long and pointed and the basicubital triangle ends where the CuP branch starts. Two free veins are present in the clavus and ambient vein is absent (Shcherbakov 1996, fig. 3).

In *Protoprosbole*, according to Laurentiaux (1952), costal vein is absent and the 3 veins ScP, R and MP are basally close but independent, not forming a common stem in a suggested plesiomorphic condition; CuA remains isolated. We interpreted however these 3 veins as PC+CP, ScP+R and MP+CuA as the first vein reaching the costal margin after the end of CP is clearly concave (ScP). Moreover on the published photo, structure between this ScP (–) and the more or less rectilinear RA (+) and the costal margin looks different, darker, with microsculptures identifying it as a pterostigma. RP and MP are multibranching but their exact respective pattern needs to be re-analysed. Basal cell is elongated ending with separation of MP and CuA. Basicubital triangle is long and wide ending at a curved and apically forked CuP: anterior margin of clavus is not straight. According to the published photo and although not reported by Laurentiaux, an ambient vein is present.

Conclusions

At the very base of the Hemiptera tree, Protoprosboloidea with *Protoprosbole* is characterized by ScP+R and MP+CuA basally joined but still not connected, a pterostigma (being part of the ground plan of Hemiptera), a curved CuP apically forked, and an ambient vein running from pterostigma up to apex of clavus. The lineage (forgotten in Bourgoin *et al.* 2004) is sister to all other Hemiptera taxa with a straighter anterior margin of clavus (CuP) and in which first division between Sternorrhyncha and Euhemiptera appeared already at least 310 Mya respectively with:

- Archescytinoidea (represented by *Archescytina s. str.* as the group is probably polyphyletic) characterized by an autapomorphic reduction of PC+CP (complete fusion of veins of costal complex) and ambient vein, a reduced venation with main veins rarely forking more than once, very few transverse veins. They retain a plesiomorphic elongated and apically pointed basal cell (Shcherbakov 1996).
- Euhemiptera with plesiomorphic characters as ambient vein and pterostigma present, a more complete venation with main veins forking more than once and transverse veins present. The shorter basal cell is only characteristic of Fulgoromorpha (Shcherbakov 1996). Currently, no clear apomorphic wing character allows characterizing Euhemiptera.

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