

Systematic position of *Triplosoba*, hitherto the oldest mayfly, from Upper Carboniferous of Commeny in Central France (Insecta: Palaeodictyoptera)

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Abstract. A revision of the holotype of *Triplosoba pulchella* (Brongniart, 1883), the 'oldest mayfly', provides evidence for new attribution to Palaeodictyoptera sensu Bechly. New character states derived from the venation pattern, namely the basal connection of the median anterior with the radius and radius posterior in the forewing, the median anterior remote from the radius posterior and basally fused with the median posterior in the hindwing, and a strong costal margin formed by two connected or fused veins with a series of small spines (costa and subcosta anterior), support an ordinal placement of *Triplosoba* into Palaeodictyoptera (inclusive of Diaphanopteroidea sensu Bechly) versus Ephemeroptera as supposed by previous authors. It shares with Diaphanopteroidea a potential synapomorphy in the presence of long curved connections between the three stems of the radius, media, and cubitus in the basal part of the forewing, a character not present in other groups of Palaeodictyoptera.

Introduction

Ephemeroptera are considered one of the oldest lineages of winged insects (Pterygota). Therefore, the re-examination of the putative oldest representative of this group is rather important for the phylogeny of mayflies and also for the significance of its venation pattern in the context of pterygote insect evolution.

The holotype of *Triplosoba pulchella* (Brongniart, 1883) from the Upper Carboniferous Commeny Basin, Allier, France, was studied and revised by several authors, resulting in different interpretations of wing venation, but a precise description and drawing of the fossil specimen has yet to be provided. Brongniart (1893) described *Blanchardia pulchella* and attributed the species to basal Ephemeroptera (Protephemerida). Handlirsch (1906–1908) created a new family, Triplosobidae, and established a new genus, *Triplosoba*, because *Blanchardia* was preoccupied. He placed this taxon in the suborder Protephemeroidea due to what he considered an 'intermediate' state of characters between Ephemeroptera and Palaeodictyoptera. Lameere (1917) later reinterpreted and

discussed several venation characters indicated by Brongniart according to the current state of preservation. Demoulin (1956) revised the species on the basis of a photograph only, because the type specimen was not at his disposal at that time. In revising the specimen, Carpenter (1963) discussed possible relationships of *Triplosoba* to Ephemeroptera. Other authors, such as Forbes (1943: 398), or more recently Willmann (1999: 300), doubted its attribution to Ephemeroptera, because of the presence of venational characters such as the basal fusion of the radius anterior (RA) and the radius posterior (RP) with the median anterior (MA) in the forewing and differences in the cubital area. Tillyard (1932: 100–104) reviewed and discussed controversial characters supporting attribution to Ephemeroptera versus Palaeodictyoptera (Dictyoneuridae). Rasnitsyn (2002: 88) considered Triplosobida as a separate lineage in his phylogeny and system of Ephemeroptera, indicating questionable synapomorphies of a simple MA and cubitus anterior (CuA). Kluge (2004: 56) attributed *Triplosoba* to Ephemeroptera sensu latissimo (Protephemeroidea) and listed characters with unclear phylogenetic status in contrast to Ephemeroptera as follows: (i) RP basally fused with RA and independent from MA; (ii) RP2 non-branched on hindwings; (iii) MA non-branched.

The main goal of this work was the revision of the holotype specimen, providing more evidence to elucidate its

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higher systematic placement. After re-examination of the type specimen, we found significant characters in the basal part of the wings that enabled its attribution to Palaeodictyoptera rather than to Ephemeroptera.

Materials and methods

The Commentry Basin, Allier department, France, is one of the classical insect localities from the Upper Carboniferous (Stephanian B–C). Its insect fauna was primarily studied by Brongniart (1893), Meunier (1909, etc.) and later revised by Lameere (1917) and other authors. The holotype of *T. pulchella* is housed in the collection of the Muséum National d'Histoire Naturelle, Sciences de la Terre, Paris, France.

The holotype specimen was studied with a stereomicroscope (Olympus SZX 9) and observed under a thin layer of ethyl alcohol, providing higher clarity of the venation pattern. The line drawing of venation was drawn directly using a stereomicroscope with a camera lucida and finally readjusting to the photograph scales using image-editing software (Adobe Photoshop). Photographs were made using a digital camera (Olympus 5050) by single-sided cross-light exposure.

Abbreviations of wing veins throughout the text are given as: AA, anal anterior; AP, anal posterior; CuA, cubitus anterior; CuP, cubitus posterior; IMP, intercalary median posterior; IR, intercalary radial; MA, median anterior; MP, median posterior; RA, radius anterior; RP, radius posterior; ScA, subcosta anterior; ScP, subcosta posterior.

Systematics

Palaeodictyoptera sensu Bechly (1996, 2007)

Forbes, 1943: 398; Willmann, 1999: 298–302.

Family *Triplosobidae* Handlirsch, 1906

Type genus. *Triplosoba* Handlirsch, 1906

Revised diagnosis. *Forewing.* Costal margin strong and slightly serrate, with two veins costa and ScA partly connected (Fig. 1A), with a series of small spines on both; ScP long, ending near wing apex; RA simple, ending close to wing apex; stems of radius, media, and cubitus strongly basally approximate and shortly connected; cubitus divided into CuA and CuP, media basally separates into MA and MP; MA separated from radial vein, but there is no space between them, RP separates from RA at the same point MA diverges from radial vein; RP with three main terminal branches and two intercalary longitudinal veins between them emerging secondarily on cross-veins; MA simple and nearly straight; MP with two branches and one intercalary between them; CuA and CuP simple; two anal veins visible, both simple.

Hindwing similar to forewing, except in the following points that concern the bases of the radius, median and cubital veins:

stems of cubitus and media strongly approximate that of radius, basal stem of media connected but not fused to that of radius; separation of media into MA and MP close to wing base; MA remote from RP; anal area well preserved with four major branches of AA and AP and longitudinal intercalary veins between them.

Genus *Triplosoba* Handlirsch, 1906

Type species. *Triplosoba pulchella* (Brongniart, 1893)

Revised diagnosis. As for the family.

Triplosoba pulchella (Brongniart, 1893)

(Figs 1–3)

Blanchardia pulchella Brongniart, 1893: 325–328, pl. 18, figs 8–9, fig-text 14.

Triplosoba pulchella Handlirsch, 1906: 312, pl. 32, figs 6, 7; Handlirsch, 1911: 183, pl. 8, fig. 12; Lameere, 1917: 103; Martynov, 1924: 158, fig. 3; Tillyard, 1932: 101, fig. 1; Demoulin, 1956: 1–8, fig. 1; pl. 1; Carpenter, 1992: 19; Carpenter & Burnham, 1985: 303; Wootton, 1981; Willmann, 1999: 289–302; Rasnitsyn, 2002: 87–89, fig. 84; Kluge, 2004: 56–57, fig. 14A.

Material. Holotype no. R51092 (imprint and counterimprint), Muséum National d'Histoire Naturelle, Paris, France, Sciences de la Terre, with the label '*Blanchardia pulchella* Brongn. (Brongniart, 1893: pl. 18. fig. 8)'.

Age and layer. Stephanian (B–C), Upper Carboniferous; Commentry, Allier (Central France).

Redescription. Body structures visible from dorsal view are not very well preserved, head fragmentary, prothorax short, enlarged meso- and metathorax, four elongated legs preserved without distinct segmentation of the tarsi; slender abdomen with about 11 visible segments bearing three distal segmented appendages as two shorter cerci and a distinctly elongated paracercus (terminal filament). There is no clear evidence of presence of gonostyli on the fossil.

Wings. Forewings slightly slender than hindwings, forewing 21.5 mm long and approximately 6 mm wide, hindwing 20 mm long and 7 mm wide, wingspan 42 mm, both pairs probably originally cloudy, wing membrane not thickened. Numerous simple cross-veins between the main longitudinal veins and their branches exhibit a rather coarse network of cells.

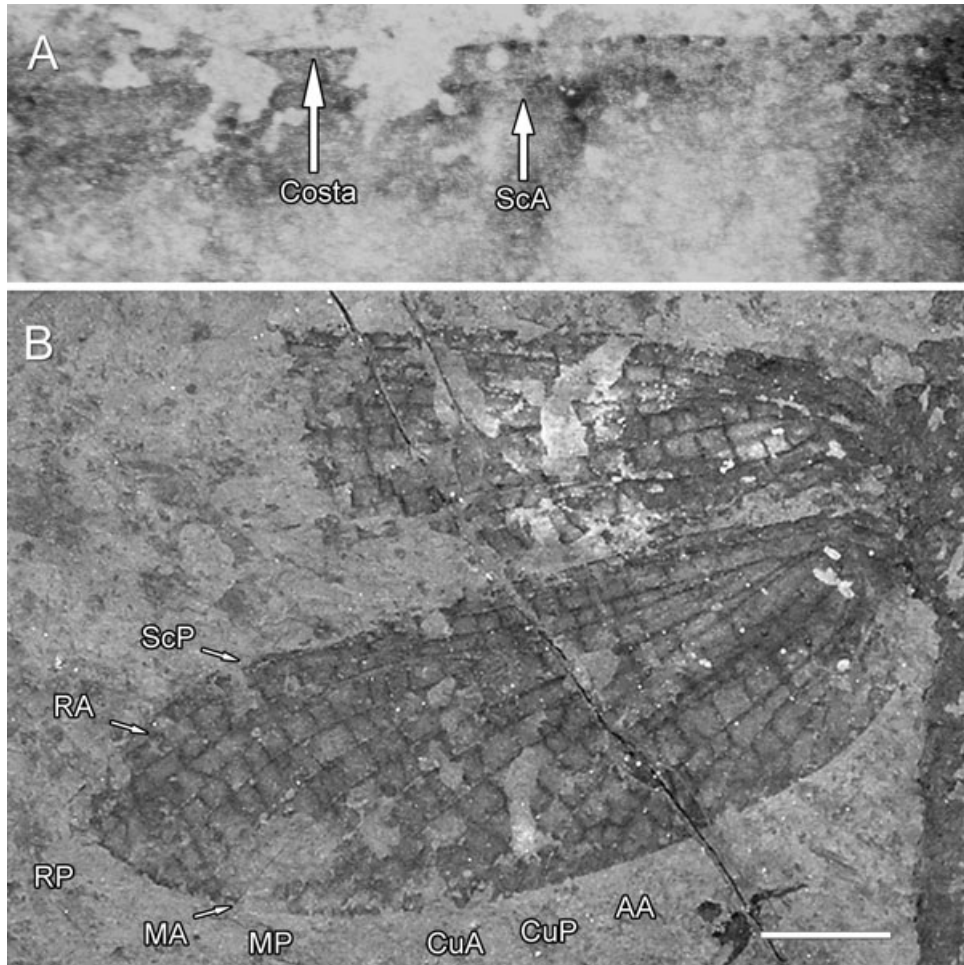


Fig. 1. *Triplosoba pulchella* (Brongniart, 1893), holotype specimen no. R51092 (imprint). (A) Photograph of the anterior margin of the forewing (connection of veins costa and subcosta anterior), (B) photograph of the forewing and hindwing venation (scale bar represents 3 mm).

Forewing. Costal margin rather slightly serrate, and very strong, with two veins fused (or connected?), with a series of small spines on both; ScA not visible as a separate brace near wing base; ScP very long, parallel to costa and probably ending near wing apex, with a regular series of simple cross-veins between them; RA simple, ending very close to wing apex, also with a series of cross-veins between it and ScP; stems of radius, media, and cubitus very strongly approximate (or even fused?), and shortly connected at wing base, even the stem of media cannot be distinguished in a rather broad sclerotized area between the two stems of cubitus and radius; cubitus divided into CuA and CuP approximately 1 mm from wing base, just distally, the median vein becomes visible and separates into MA and MP; MA separated from radial vein without space between them, MA narrower than radial vein; RP separates from RA 4.5 mm from wing base, at the same point MA diverges from radial vein; RP with three branches and two intercalary longitudinal veins IR1 and IR2 between them; MA simple and nearly straight; MP with two branches and one

intercalary IMP between them; CuA and CuP simple; two anal veins visible, both simple, but anal area poorly preserved.

Hindwing. Broader than forewing in basal part; venation pattern very similar except in the following points that concern the bases of the radius, median and cubital veins: stems of cubitus and media strongly approximate that of radius, basal stem of media connected but not fused to that of radius; separation of media into MA and MP 2.3 mm from wing base; MA remote from RP; anal area well preserved with four major branches of AA and AP and longitudinal intercalary veins between them, but basal part of anal veins not clearly visible.

Discussion. This controversial fossil bears the main diagnostic characters of the Palaeodictyoptera sensu Bechly (2007): basal connection of MA with radius and RP (forewing) and MA remote from RP and basally fused with MP (hindwing) previously indicated by Willmann (1999). In addition, CuA and CuP are basally arched, the stem of the cubital vein

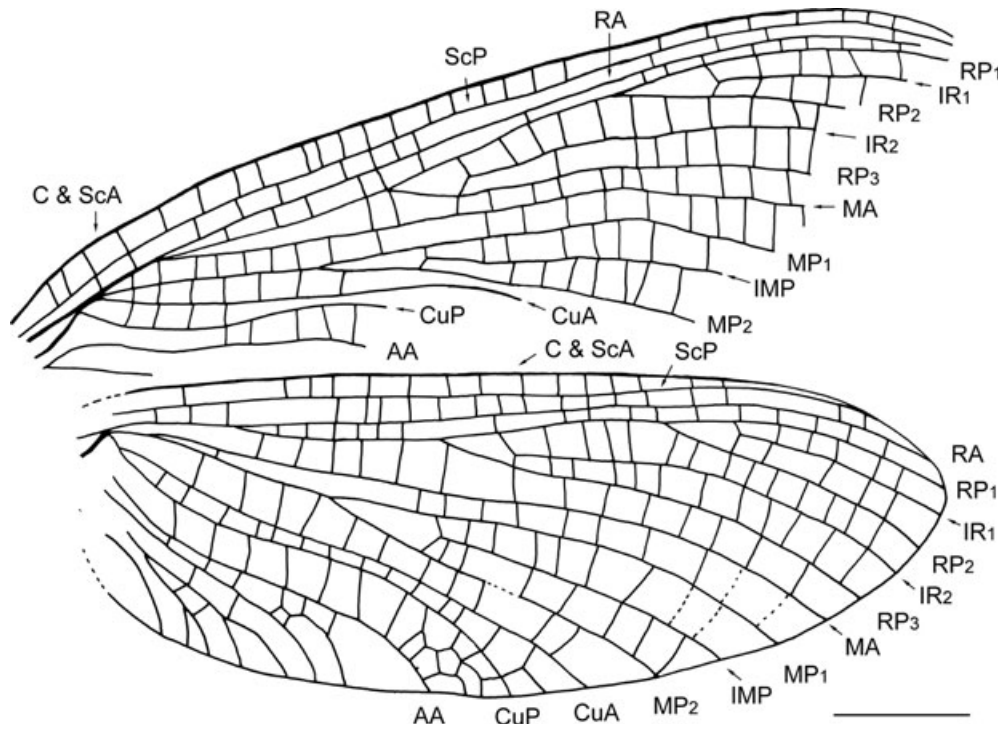


Fig. 2. *Triplosoba pulchella* (Brongniart, 1893), holotype specimen no. R51092, composite line drawing of forewing and hindwing (scale bar represents 3 mm).

is well connected to the radius and media in the forewing, and the stem of the cubital vein is basally arched and probably connected to the radius and media in the hindwing. The difference in venation pattern in the forewing and hindwing is probably due to the different widths in wing basal parts. Characters such as the presence of intercalary veins, simple cross-veins between main veins, and the absence of archedictyon, would rather support affinities with Ephemeroptera and Odonatoptera, but they are also present in some Palaeodictyoptera, as several taxa within Palaeodictyoptera (Calvertiellidae, Namuronigxiidae) bear these characters as well (see Béthoux *et al.*, 2007; Prokop & Ren, 2007). The lack of a well-developed ScA brace typical for Permian taxa of Ephemeroptera (Proteismatidae) and Odonatoptera also supports that *Triplosoba* is remote from this last clade (see Carpenter, 1992). Nevertheless, the lack of a costal brace does not per se preclude a sister-group relationship to the remaining mayflies or to Eupalaeoptera. The wing venation of *Triplosoba* is superficially similar to that of Permian ephemerid *Protereisma* Sellards, 1907, in the general wing shape, the presence of numerous cross-veins and of intercalary longitudinal veins (IR1, IR2 and IMP). However, *Protereisma* strongly differs from *Triplosoba* in the cubital and median stems completely separated from that of the radius in fore- and hindwings, and more developed MA and CuA both with intercalary veins (Carpenter, 1979). *Triplosoba* shares with the Syntonopteridae, another Carboniferous group closely related to the Ephemeroptera, the absence of brace ScA (Prokop, Nel & Tenny, unpublished results), but it differs from them in the

same distinct separation of the stems of the radius, media and cubitus as in *Protereisma*.

In Palaeodictyoptera Goldenberg, 1877, the stems of the radius, media, and cubitus are also not connected, unlike in *Triplosoba*. The majority of Palaeodictyoptera have their MA and CuA branched. In nearly all the families with these veins simple, there is no connection between CuA and the radius and media. One point of contact between these veins is only present in Calvertiellidae Martynov, 1931 and Tchirkovaeidae Sinichenkova, 1979. In Permothemistida Martynov, 1938, MA and the cubitus are very far from the radial stem. The stems of the radius and media (but not that of the cubital vein) are connected in Megasecoptera, but in relation to the strong petiolation of their wings. They do not have the particular strong curve of the cubital vein present in *Triplosoba*.

Triplosoba shares with the Diaphanopteroidea Handlirsch, 1919 the presence of long connections between the three stems of the radius, media, and cubitus in the basal part of the wing. These three stems are also basally curved as in *Triplosoba*. The presence in *Triplosoba* of a very strong costal margin constituted by two veins fused (or connected?), with a series of small spines on both of them, is a very special character, already noted by Béthoux & Nel (2003) for *Diaphanoptera* Brongniart, 1893, and interpreted as a costa and ScA fused or strongly connected. It is a potential synapomorphy of the order and would be interesting to check on other taxa. A similar structure also occurs in Odonatoptera. Many of Diaphanopteroidea also have a vein MA long connected to

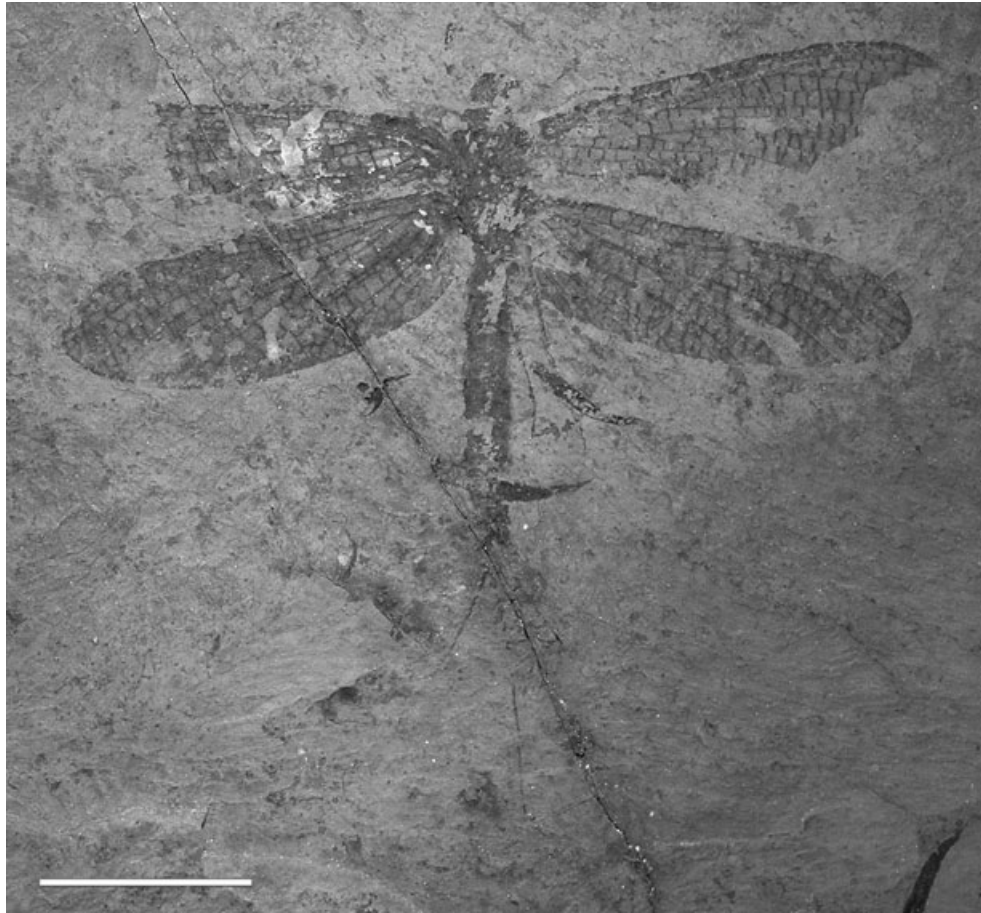


Fig. 3. *Triplosoba pulchella* (Brongniart, 1893), holotype specimen no. R51092 (imprint), photograph of holotype (scale bar represents 10 mm).

the radius and separating from it at or near the base of RP. *Triplosoba* also shares with the Diaphanopteroidea simple MA and CuA.

The main difficulty with an attribution of *Triplosoba* to the Diaphanopteroidea is the presence of three anal appendages instead of only two, as in the Permian representatives of this order in which they are preserved (e.g. Rasnitsyn & Novokshonov, 1997). However, these fine morphological structures are fragile with considerably low potential for preservation and the majority of the Carboniferous taxa lack any abdominal appendages. The presence versus absence of the terminal filament is rather variable in recent Ephemeroptera. Nevertheless, the presence of a terminal filament is probably a plesiomorphy as it is also present in Apterygota, so useless for an attribution to the Ephemeroptera. The completeness of the fossil insect specimens from Commentry is unique and could possibly reveal unexpected discoveries in the future (see e.g. Béthoux, 2003).

If the Permian forms and the Carboniferous Parabrodiidae Carpenter, 1933 generally have more 'simplified' venations with few to very few branches of main veins and few cross-veins, then the two Carboniferous families Diaphanopteridae Handlirsch, 1906 and Prochoropteridae Handlirsch, 1911 share

with *Triplosoba* the presence of RP and MP and of numerous cross-veins. However, these taxa differ from *Triplosoba* in the vein MA distinctly separated from the radial stem (Béthoux & Nel, 2003). A vein MA connected to the radius can be found in the Permian diaphanopteroidean genus *Asthenohymen* Tillyard, 1924 (Asthenohymenidae Tillyard, 1924).

The exact affinities of *Triplosoba* within the Diaphanopteroidea remain uncertain because of the lack of phylogenetic analysis of this order, which is not within the scope of the present paper.

Conclusions

Carboniferous insects from Commentry (France) preserved with solid well-sclerotized parts as well as delicate body structures represent a unique source of fossils to palaeontologists and morphologists (see Béthoux, 2003; Béthoux & Nel, 2005). In spite of *Triplosoba* being a rather controversial fossil, as noted by several authors, we provide a set of new and revised characters that support its attribution into the Palaedictyodoptera and close relationships to the order Diaphanopteroidea. It is supported by major characters as follows: (i) presence of long curved connections between the three

stems of the radius, media, and cubitus in the basal part of the wing (possible synapomorphy of Diaphanopteroidea); (ii) basal connection of MA with the radius and RP (forewing) and MA remote from RP and basally fused with MP (hindwing); (iii) strong costal margin formed by two connected or fused veins with a series of small spines (costa and ScA). Therefore, its systematic placement to the order Ephemeroptera based on few venation characters and the presence of terminal abdominal filament (plesiomorphy) can be rejected.

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