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The first Chinese Tarsophlebiidae from the Lower Cretaceous Yixian Formation, with morphological and phylogenetic implications (Odonatoptera: Panodonata)

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ABSTRACT

The Early Cretaceous *Turanophlebia sinica* sp. nov. is the first Chinese representative of the enigmatic family Tarsophlebiidae. The exquisite preservation of the type specimen allows to precise several important morphological structures of phylogenetic importance, i.e. three-segmented tarsi, with basal tarsomere very long; and absence of subapical tooth on tarsal claw. If the first character not longer supports a basal position for Tarsophlebiidae, the second confirms it. The presence of a fore leg tibial comb supports the hypothesis that the reduced tibial comb of the Hemiphlebiidae is apomorphic for this last group.

1. Introduction

The Tarsophlebiidae is a small family of Mesozoic dragonflies, distributed in the Upper Jurassic to Lower Cretaceous of Europe, Siberia, and Mongolia. It is still one of the most enigmatic Mesozoic families of Odonatoptera. Nevertheless its knowledge has greatly increased during these last years with new data on its body and wing venation (Nel et al., 1993; Bechly, 1996; Fleck et al., 2004). As sister group of the (Zygoptera + Epiproctophora) (see Bechly (1996), confirmed by the analysis of Fleck et al. (2004)), they are of crucial importance for the phylogeny of the Odonata. Therefore every additions of accurate information on their morphology are welcome. In particular, there was a controversy on their exact number of tarsal segments between one of us (AN) and G. Bechly, due to the poor preservation of the available material. The present discovery is the first record of a Chinese Tarsophlebiidae. Furthermore, its wings and body structures are exquisitely preserved, allowing to finally precise the leg structures in Tarsophlebiidae.

2. Systematic palaeontology

We follow the wing venation nomenclature of Fleck et al. (2004). We use the following standard abbreviations: AA anal vein, AP anal posterior, Ax0 Ax1 Ax2 primary antenodal cross-veins, CuAa distal branch of cubitus anterior, CuAb proximal branch of cubitus anterior, IRi intercalary radial veins, MAa distal branch of median anterior, MAb posterior branch of median anterior, MP median posterior, N nodus, O oblique vein, Pt pterostigma, RA radius anterior, RP radius posterior.

Order: Odonatoptera Martynov, 1932
Suborder: Panodonata Bechly, 1996
Family: Tarsophlebiidae Handlirsch, 1906
Genus *Turanophlebia* Pritykina, 1968

Turanophlebia sinica sp. nov.
Figs. 1–10

Derivation of name. Named after the Latin name for China.

Material. Holotype specimen 148201, collection housed in Nanjing Institute of Geology and Palaeontology.

Type locality and horizon. Yixian Formation, Lower Cretaceous; Western Liaoning, China.

Diagnosis. Wings large, 48–50 mm long; nearly 25 postnodal cross-veins; six rows of cells between CuA and posterior hind wing margin; more than 10 secondary antenodal cross-veins in hind wing; IR1 long; long secondary longitudinal not zigzagged veins in area between IR2 and RP2; hind wing pterostigma covering 5–6

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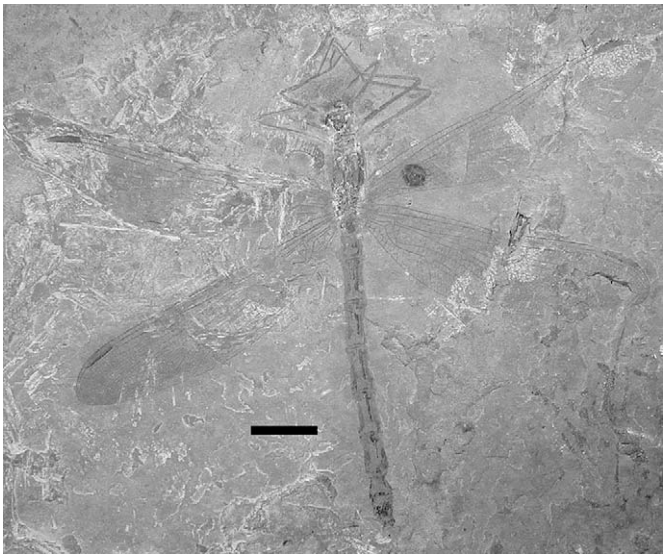

Fig. 1. *Turanophlebia sinica* sp. nov., holotype 148201, photograph of general habitus (scale bar represents 10 mm).

cells; subdiscoidal area divided into three cells instead of two; postdiscoidal area distinctly narrowed in mid part.

Description. Imprint of a nearly complete specimen with wings and legs in connection to body. Head 5.0 mm long, 5.3 mm wide, not transversely elongate; eyes large, 3.0 mm long, 2.0 mm wide, 2.0 mm apart (posterior part of head) and 4.0 apart (anterior part of head); mouthparts poorly preserved; mandibles strong; clypeo-frontal suture very deep; a triangular structure visible on dorsal surface, which corresponds to sutures between the three ocelli.

Thorax 13.5 mm long, 5.0 mm wide, with synthorax preserved are in dorsal aspect, so that it is not possible to quantify exactly the degree of skewness ('prognathisme' sensu Nel et al., 1993) of the thorax, but it was probably very high as in other Tarsophlebiidae.

Abdomen 48.0 mm long, 3.2 mm wide; presence of a longitudinal mediodorsal carina on abdominal terga, which is covered with a row of small spines; numerous tiny spines on lateral parts of abdominal terga, very similar to extant odonates. Both these structures were already indicated for other Tarsophlebiidae (Fleck et al., 2004). Secondary genital apparatus on segment 2 present but very poorly preserved (male specimen), confirmed by the absence of ovipositor; strongly sclerotized basal parts of one pair of well separated anal appendages visible; no median anal appendage visible.

Forewing hyaline, pterostigma dark brown; wing 49.5 mm long, 10.4 mm wide; distance from base to arculus 5.8 mm; from arculus to nodus 17.8 mm; from nodus to pterostigma 17.7 mm, to wing apex 26.1 mm; pterostigma elongated and narrow, 5.1 mm long, 0.8 mm wide, covering four cells, not basally recessed; pterostigmal

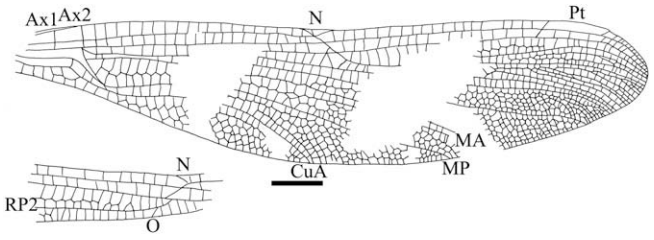

Fig. 2. *Turanophlebia sinica* sp. nov., holotype 148201, right forewing and nodal region of left forewing (scale bar represents 4 mm).

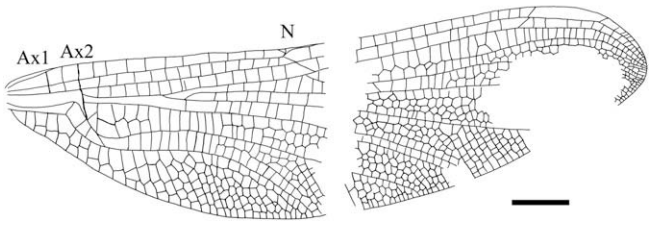

Fig. 3. *Turanophlebia sinica* sp. nov., holotype 148201, right hind wing (scale bar represents 4 mm).

brace oblique and strong, opposite pterostigma base; median and submedian areas free of cross-veins; CuP strongly curved, midway between Ax1 and Ax2, basally closing subdiscoidal space; primary antenodal braces Ax1 and Ax2 stronger than secondary antenodal cross-veins, 2.3 mm apart, with no secondary cross-vein between them; Ax1 is 3.5 mm from wing base; arculus aligned with Ax2; 19 secondary antenodal cross-veins distal of Ax2, not aligned with the cross-veins of second rank between ScP and RA; about 18 cross-veins in area between RA and RP, between arculus and nodus; a long 'gap' without cross-veins between arculus and RP3/4 in area between RP and MA; MP + CuA curved just basal of its fusion with MAb; a sharp angle between MP + CuA and MAb; a long fusion between MAb and MP + CuA before CuA separates from MP, 0.5 mm long, characteristic of the Tarsophlebiidae; RP + MA, MA and MAb, MP + CuA + MAb, and basal free part of CuA well aligned in arculus, as in other Tarsophlebiidae; discoidal space basally opened; subdiscoidal area divided into three cells by two cross-veins; AA without any strong posterior branches; anal area with two rows of cells; posterior wing margin straight; AA reaching free part of CuA at sharp angle; no CuAb (sensu Fleck et al., 2003); CuA without strong posterior branches; 6–7 rows of small cells between CuA and posterior wing margin; a relatively long not zigzagged secondary vein ('postero-CuA vein') closely parallel to distal part of CuA in cubito-anal area, and another one in area between MP and CuA ('antero-CuA vein'); CuA reaching posterior wing margin opposite nodus level; area between MP and CuA with one row of cells in its basal part but greatly widened in its distal half, with about 25 rows of cells along posterior wing margin; postdiscoidal area with two rows of cells in its basal to mid part, narrowed in its mid part and widened distally, with about eight rows of cells between MA and MP near posterior wing margin; bases of RP3/4 and IR2 between arculus and nodus, distinctly nearer to arculus, base of RP3/4 9.2 mm from nodus; base of IR2 apparently on RP3/4; nodal Cr and subnodus strongly oblique; base of RP2 aligned with subnodus; oblique vein "O" three small cells distal of base of RP2 in

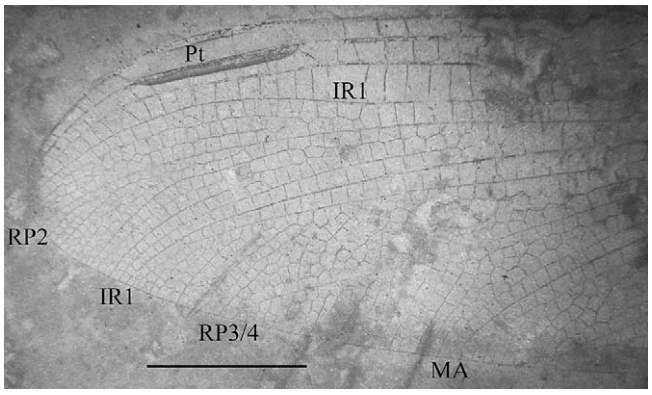

Fig. 4. *Turanophlebia sinica* sp. nov., holotype 148201, photograph of left hind wing apex (scale bar represents 5 mm).

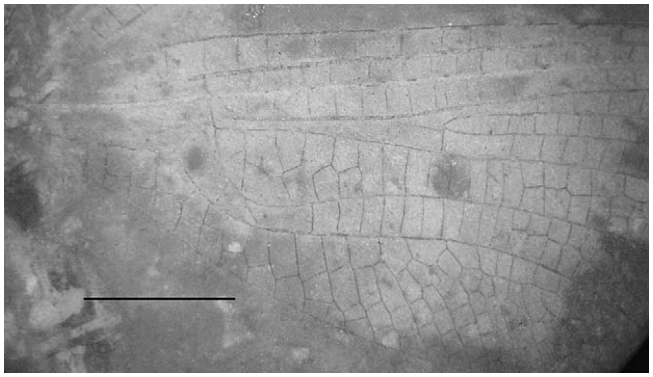

Fig. 5. *Turanophlebia sinica* sp. nov., holotype 148201, photograph of right hind wing base (scale bar represents 5 mm).

right wing but aberrantly just basal of base of RP2 in left wing; numerous Bq cross-veins; about 19 postnodal cross-veins between C and RA, not aligned with the 16 postsubnodal cross-veins; base of IR1 about 8–9 cells distal of that of RP2; IR1 well-defined, slightly curved distally; one row of small cells in area between C and RA distal of pterostigma; one row of cells between RP1 and IR1; three rows of cells in area between IR1 and RP2, in its widest part; area between RP2 and IR2 distinctly widened distally, antero-IR2 and postero-IR2 veins long; a secondary longitudinal vein closely parallel to RP2; area between IR2 and RP3/4 distally widened; area between RP3/4 and MA distally widened; 'antero-MA' and 'postero-MA' veins long.

Hind wing hyaline, pterostigma dark brown; wing 45.5 mm long, 12.1 mm wide; distance from base to arculus 5.4 mm; from arculus to nodus 14.7 mm; from nodus to pterostigma 17.4 mm, to wing apex 25.5 mm; pterostigma elongated and narrow, 5.5 mm long, 0.8 mm wide, covering 5–6 cells, not basally recessed; pterostigmal brace oblique and strong, opposite pterostigma base; median and submedian areas free of cross-veins; CuP strongly curved, midway between Ax1 and Ax2, basally closing subdiscoidal space; primary antenodal braces Ax1 and Ax2 stronger than secondary antenodal cross-veins, 2.1 mm apart, with a secondary cross-vein between them; Ax1 is 3.1 mm from wing base; arculus aligned with Ax2; 10 secondary antenodal cross-veins distal of Ax2, not aligned with the cross-veins of second rank between ScP and RA; 16 cross-veins in area between RA and RP, between arculus and nodus; a long 'gap' without cross-veins between arculus and RP3/4 in area between RP and MA; MP + CuA strongly curved just basal of its fusion with MAb; a sharp angle between MP + CuA and MAb; a long fusion between MAb and MP + CuA before CuA separates from MP, 0.3 mm long, characteristic of the Tarsophlebiidae; RP + MA, MA and MAb, MP + CuA + MAb, and basal free part of CuA

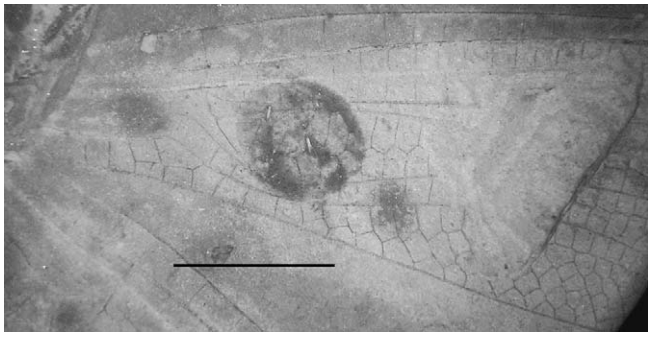

Fig. 6. *Turanophlebia sinica* sp. nov., holotype 148201, photograph of right forewing base (scale bar represents 5 mm).

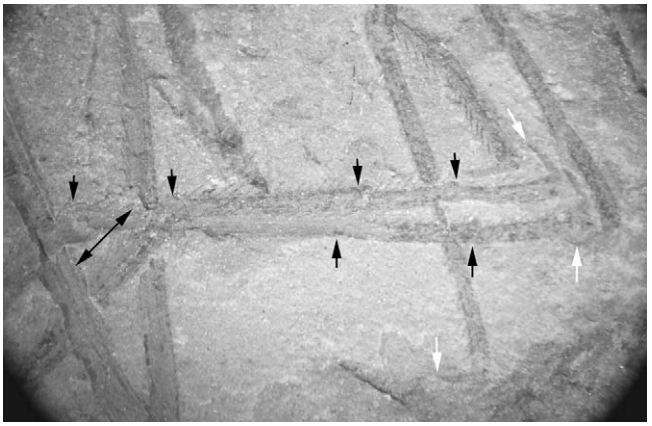

Fig. 7. *Turanophlebia sinica* sp. nov., holotype 148201, photograph of hind (below) and mid (above) tarsi, double arrow: apical long setae; simple back arrows: points of separations between tarsal segments; white arrows: claws.

well aligned in arculus, as in other Tarsophlebiidae; discoidal space basally opened; presence of a two-celled 'tarsophlebiid pseudo-discoidal space' just distal of MAb in postdiscoidal area; subdiscoidal area divided into three cells by two cross-veins; AA without any strong posterior branches; anal area with two rows of cells; posterior wing margin rounded; petiole short, 0.5 mm long; AA reaching free part of CuA at sharp angle; no CuAb (sensu Fleck et al., 2003); CuA without strong posterior branches; six rows of small cells between CuA and posterior wing margin; a relatively long not zigzagged secondary vein ('postero-CuA vein') closely parallel to distal part of CuA in cubito-anal area, and another one in area between MP and CuA ('antero-CuA vein'); CuA reaching posterior wing margin just distal to nodus level; area between MP and CuA with one row of cells in its basal part but greatly widened in its distal half, with about 17 rows of cells along posterior wing margin; postdiscoidal area with two rows of cells in its basal part, narrowed in its mid part and widened distally, with eight rows of cells between MA and MP near posterior wing margin; bases of RP3/4 and IR2 between arculus and nodus, distinctly nearer to arculus, base of RP3/4 9.1 mm from nodus; base of IR2 apparently on RP3/4; nodal Cr and subnodus strongly oblique; base of RP2 just basal of subnodus; oblique vein "O" four small cells distal of base of RP2; numerous Bq cross-veins, but apparently no cross-vein in basal part of areas between RA and RP, and between RP3/4 and IR2; about 17–18 postnodal cross-veins between C and RA, not aligned with the 15 postsubnodal cross-veins; base of IR1 about five cells distal of that of RP2; IR1 well-defined, basally zigzagged and slightly curved distally; one row of small cells in area between C and RA distal of pterostigma; one row of cells between RP1 and IR1; five rows of cells in area between IR1 and RP2, in its widest part; area between RP2 and IR2 distinctly widened distally, antero-IR2

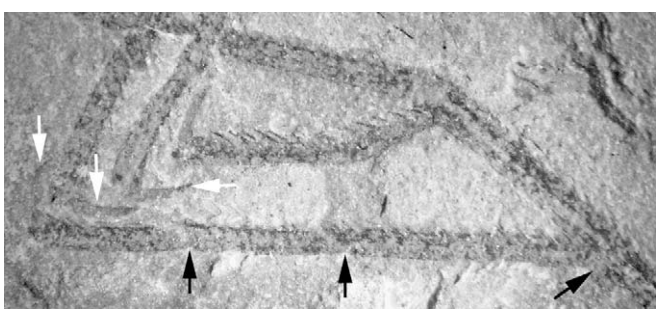

Fig. 8. *Turanophlebia sinica* sp. nov., holotype 148201, photograph of left fore tarsus (below) and of claws of right hind and mid (above) legs; simple back arrows: bases of tarsal segments; white arrows: claws.

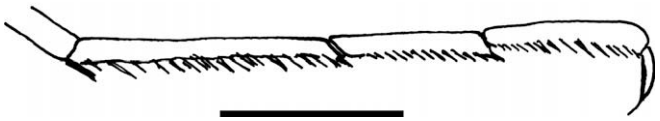

Fig. 9. *Turanophlebia sinica* sp. nov., holotype 148201, drawing of left fore tarsus (scale bar represents 2 mm).

and postero-IR2 veins long; a secondary longitudinal vein closely parallel to RP2; area between IR2 and RP3/4 distally widened; area between RP3/4 and MA distally widened; 'antero-MA' and 'postero-MA' veins long.

Legs and tarsi very slender; femora with two rows of inner stout spines (0.2 mm long) and two rows of outer small spines; tibiae with two inner rows of long spines, 0.5 mm long, these spines being longer and denser in apical part of fore tibia (presence of a tibial comb), and two outer rows of small spines. Tarsi with two inner rows of long spines (0.4 mm long), and two outer rows of small spines, three-segmented, with the separations between segments clearly visible and oblique; fore femur 9.0 mm long (preserved), tibia 9.0 mm long, first tarsomere 2.5 mm long, second 1.3 mm long, third 1.6 mm long; middle femur 13.5 mm long, tibia 9.5 mm long, first tarsomere 3.0 mm long, second 1.5 mm long, third 1.6 mm long; hind femur 14.0 mm long, tibia 10.5 mm long, first tarsomere 4.5 mm long, second 2.2 mm long, third 1.9 mm long; claws very long, 0.8 mm long, sharp and narrow, without subapical tooth.

Discussion. This fossil is easily attributable to the Tarsophlebiidae on the basis of numerous wing venation structures (in particular discoidal cells, etc.), but also the very long legs, compact head, the presence of a pair of particular anal appendages similar to those of *Turanophlebia vitimensis* Fleck et al., 2004. Two genera are currently recognized in this family, viz. *Turanophlebia* Pritykina, 1968 and *Tarsophlebia* Hagen, 1866. *Turanophlebia sinica* sp. nov. rather falls in the former genus on the basis of the following characters: wing reticulation denser than in *Tarsophlebia*, mainly visible through presence of around 25 postnodal cross-veins (against 16 in *Tarsophlebia eximia* Hagen, 1866 and around 11 in *T. minor* Fleck et al., 2004); six (or more) rows of cells between CuA and posterior hind wing margin (against less than five rows in *T. eximia* and *T. minor*); more than 10 secondary antenodal cross-veins in hind wing (against less than 10 in *T. eximia*); IR1 longer than in *T. eximia*; and presence of long secondary longitudinal not zigzagged veins in area between IR2 and RP2.

Turanophlebia comprises six species, viz. *Turanophlebia martynovi* Pritykina, 1968, *T. sibirica* Pritykina, 1977, *T. anglicana* Fleck et al., 2004, *T. mongolica* Fleck et al., 2004, *T. vitimensis* Fleck et al., 2004, and *T. neckini* (Martynov, 1927). *T. sinica* differs from *T. martynovi*, *T. neckini*, *T. anglicana* and *T. mongolica* in its distinctly larger wings (48–50 mm long instead of 39–41 mm long). It also differs from *T. anglicana* in the hind wing pterostigma covering 5–6 cells instead of three, subdiscoidal area divided into three cells instead of two. *T. mongolica* has its postdiscoidal area not distinctly narrowed in the mid part, less rows of cells between MP and CuA along posterior wing margin, broad anal area, unlike *T. sinica*. The wings of *T. vitimensis* and *T. sinica* are of similar sizes, but the former has 9–10 rows of cells in hind wing cubito-anal area between CuA and posterior wing margin, unlike *T. sinica*. *T. sibirica* has also a cubito-anal area broader than that of *T. sinica* (7–8 rows of cells instead of six).

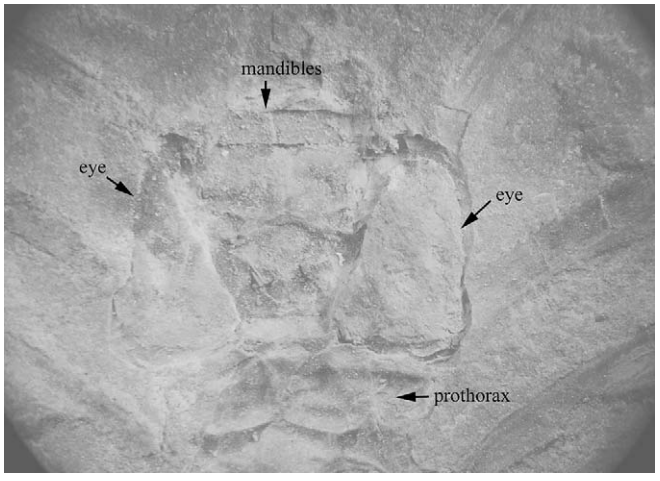

Fig. 10. *Turanophlebia sinica* sp. nov., holotype 148201, photograph of head.

3. Morphological and phylogenetic implications

The very long legs and tarsi stipulated the generic name *Tarsophlebia*. Legs of similar relative length are only known from the fossil protomyrmeleontid *Malmomyrmeleon viohli* Martínez-Delclòs and Nel, 1996 from the Late Jurassic of Germany (Martínez-Delclòs and Nel, 1996).

Hagen (1866) described a four-segmented tarsus, which was accepted by all subsequent authors, except Nel et al. (1993) who rejected this interpretation, since the type specimen is not sufficiently preserved. In fact, the tarsi of most specimens are far too poorly preserved to recognize the true number of tarsomeres. It is extremely hard to identify the different tarsomeres of the legs of these fossils, especially those from the lithographic limestones of Germany. As example, only three tarsomeres could be identified on all tarsi of the German specimen No. 1951/73 K (JME) (Nel et al., 1993: 86). Fleck et al. (2004) found two specimens from Germany with (apparently) four-segmented tarsi, but it was not possible to find four segments in the type specimen of *T. vitimensis* (Nel, pers. obs.). The exquisitely preserved legs of *T. sinica* only show three-segmented tarsi, with the basal segments very long. Thus the problem of the number of tarsal segments in Tarsophlebiidae is solved in favour of three tarsomeres, as in other Panodonata. This character is unknown in the sister group of Panodonata and all more basal groups between Protozygoptera Tillyard, 1925 and Meganeuridae Handlirsch, 1906. It is under a different state in the Meganisoptera: Meganeuridae, which have five tarsomeres (Fleck et al., 2004).

In *Meganeura monyi* Brongniart, 1884 and in all Panodonata, except Tarsophlebiidae, the first tarsomere is the shortest. Bechly (1996) suggested that the presence of a very long basal tarsomere in all Tarsophlebiidae could correspond to the fusion of two basal protozygopterid tarsomeres, but there is no evidence of such a fusion in all available fossils. Their very long basal tarsomeres could as well correspond to an apomorphy proper to this family.

The tarsi of all previously described Tarsophlebiidae show a pair of very elongate tarsal claws that do not seem to have a subapical tooth. The new fossil confirms that the subapical tooth is absent in these Odonata, unlike all other Panodonata. The basal odonatopterid family Meganeuridae have simple tarsal claws, thus this structure probably correspond to a plesiomorphy. But it is still unknown in Protozygoptera. Thus, it is not possible to conclude with certainty in which clade it appeared. Nevertheless, it supports a position basal of the Odonata for the Tarsophlebiidae, unlike their three-segmented tarsi.

Bechly (1996) proposed as a synapomorphy of *Hemiphlebia* (Zygoptera: Hemiphlebiidae) the tibial comb of fore legs degenerated, but this hypothesis was weakly supported because the structure of the tibial comb was unknown in Odonatoptera in a more basal position than the (Zygoptera + Epiproctophora), i.e. Tarsophlebiidae, Protozygoptera, etc. The presence of a tibial comb

in Tarsophlebiidae now confirms that its reduction in the damselfly family dHemiphlebiidae is an apomorphy. It can be of interest as we have recently found an Early Cretaceous damselfly in amber that can be attributed to the Hemiphlebiidae on the basis of this character (Lak et al., in prep.).

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