

# **A revision of the Upper Jurassic-Lower Cretaceous dragonfly family Tarsophlebiidae, with a discussion on the phylogenetic positions of the Tarsophlebiidae and Sieblosiidae (Insecta, Odonoptera, Panodonata)**

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**ABSTRACT**

The Upper Jurassic-Lower Cretaceous dragonfly family Tarsophlebiidae is revised. The type species of the type genus *Tarsophlebia* Hagen, 1866, *T. eximia* (Hagen, 1862) from the Upper Jurassic Solnhofen Limestones, is redescribed, including important new information on its head, legs, wings, anal appendages and male secondary genital apparatus. The type specimen of *Tarsophlebiopsis mayi* Tillyard, 1923 is regarded as an aberrant or unusually preserved *Tarsophlebia eximia*. One new species of *Tarsophlebia* and three new species of *Turanophlebia* are described, i.e. *Tarsophlebia minor* n. sp., *Turanophlebia anglicana* n. sp., *T. mongolica* n. sp., and *T. vitimensis* n. sp. A new combination is proposed for *Turanophlebia neckini* (Martynov, 1927) n. comb. The phylogenetic relationships of the Mesozoic Tarsophlebiidae are discussed on the basis of new body and wing venation characters. The present analysis supports a rather derived position for the Tarsophlebiidae, as sister group of the the Epiproctophora rather than of (Zygoptera + Epiproctophora). Also, through the present discussion, the Oligo-Miocene family Sieblosiidae seems to be more closely related to the Epiproctophora than to the Zygoptera. But the present study and previous analyses suffer of the lack of informations concerning the more inclusive groups of Odonatoptera, viz. Protozygoptera, Triadophlebiomorpha, Protanisoptera, etc. The significance of the tarsophlebiid secondary male genital apparatus for the reconstruction of the evolution of odonate copulation is discussed.

**KEY WORDS**

Insecta,  
Odonatoptera,  
Zygoptera,  
Epiproctophora,  
Tarsophlebiidae,  
Sieblosiidae,  
Upper Jurassic-Lower  
Cretaceous,  
Cenozoic,  
fossil,  
copulation,  
phylogeny,  
revision,  
new species.

**RÉSUMÉ**

*Révision des Tarsophlebiidae du Jurassique supérieur et Crétacé inférieur, discussion sur les positions phylogénétiques des Tarsophlebiidae et des Sieblosiidae (Insecta, Odonatoptera, Panodonata).*

La famille de libellules mésozoïques des Tarsophlebiidae est révisée. L'espèce type du genre type *Tarsophlebia* Hagen, 1866, *T. eximia* (Hagen, 1862) du calcaire lithographique du Jurassique supérieur de la Bavière, est redécrite, incluant de nouvelles données sur les structures de la tête, des pattes, des ailes, des appendices anaux et des pièces génitales secondaires du mâle. Le type de *Tarsophlebiopsis mayi* Tillyard, 1923 est considéré comme un spécimen aberrant ou curieusement préservé de *Tarsophlebia eximia*. Une nouvelle espèce de *Tarsophlebia* et trois nouvelles espèces de *Turanophlebia* sont décrites : *Tarsophlebia minor* n. sp., *Turanophlebia anglicana* n. sp., *T. mongolica* n. sp. et *T. vitimensis* n. sp. Une nouvelle combinaison est proposée pour *Turanophlebia neckini* (Martynov, 1927) n. comb. Les relations phylogénétiques des Tarsophlebiidae sont discutées sur la base des nouveaux caractères du corps et des ailes. Notre analyse conclut à une probable position des Tarsophlebiidae comme groupe frère des Epiproctophora, plutôt que des (Zygoptera + Epiproctophora). Au travers de la présente discussion, il ressort que la famille cénozoïque des Sieblosiidae semble plus proche des Epiproctophora que des Zygoptera. Il apparaît aussi clairement que toutes ces analyses phylogénétiques souffrent du manque de données concernant les groupes plus basaux, comme les Protozygoptera, Triadophlebiomorpha ou Protanisoptera. L'intérêt des pièces génitales secondaires des mâles des Tarsophlebiidae pour l'analyse de l'évolution de la copulation chez les Odonatoptera est discuté.

**MOTS CLÉS**

Insecta,  
Odonatoptera,  
Zygoptera,  
Epiproctophora,  
Tarsophlebiidae,  
Sieblosiidae,  
Jurassique supérieur-  
Crétacé inférieur,  
Cénozoïque,  
fossile,  
copulation,  
phylogénie,  
révision,  
nouvelles espèces.

## INTRODUCTION

The Tarsophlebiidae Handlirsch, 1906 is one of the most enigmatic Mesozoic family of Odonoptera. Its phylogenetic relationships with the Zygoptera and the Epiproctophora remain very uncertain. Nel *et al.* (1993) considered them as the most inclusive lineage within the “Anisozygoptera” + Anisoptera (= Epiproctophora). Bechly (1996) and Rehn (2003) proposed to place them as sister group of the (Zygoptera + Epiproctophora). After our recent studies at PIN and MCZ, we could revise and describe several species. This study also revealed that the alleged calopterygoid-like anal appendages of *Tarsophlebia*, with apparently two pairs of claspers, are clearly based on misinterpretations due to artifacts of preservation. Indeed *Tarsophlebia* definitely does not possess zygopteroid but rather unique appendages. There are no visible paraprocts, the epiproct must have been reduced or inconspicuous since it is not visible in any specimen, and the cerci are very long, with a double-barrelled basal petiole and a curious distal plate-like expansion. The broken double-barrelled petioles of the two cerci have been commonly misinterpreted as two pairs of claspers, while the distal plates have been overlooked or regarded as preservational artifacts. This new result is of particular phylogenetic relevance, since the previous interpretation of the appendages would have represented a putative synapomorphy with Zygoptera. We comment on the characters that are used for the phylogenetic position of the Tarsophlebiidae.

## ABBREVIATIONS

*Institutions*

BSPGM	Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich;
JME	Jura-Museum, Eichstätt;
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge;
PIN	Arthropod Laboratory, Palaeontological Institute, Academy of Science of Russia, Moscow;

*Names of body and wing structures*

AA	Analís Anterior;
Ax1 and Ax2	primary antenodal cross-veins;

Bq	series of cross-veins between RP1+2, IR2 and oblique vein;
C	costal vein or costa;
Cr	nodal cross-vein;
CuA	Cubitus Anterior;
CuAb	first posterior branch of Cubitus Anterior;
CuP	Cubitus Posterior;
IR	intercalary vein of radial area;
MA	Median Anterior;
MAB	first posterior branch of Median Anterior;
MP	Median Posterior;
RA	Radius Anterior;
RP	Radius Posterior;
ScA	Subcosta Anterior
ScP	Subcosta Posterior;

## MATERIAL AND METHODS

All drawings were made with a camera lucida and a binocular microscope. The nomenclature of the dragonfly wing venation is based on the interpretations of Riek & Kukalová-Peck (1984), amended by Nel *et al.* (1993) and Bechly (1996). The systematic analysis is based on the principles of consequent phylogenetic systematics (*sensu* Hennig 1966, 1969, 1981), especially character polarisation based on outgroup comparison.

## SYSTEMATICS

Order ODONATOPTERA Martynov, 1932  
Suborder PANODONATA Bechly, 1996

Family TARSOPHLEBIIDAE Handlirsch, 1906

Tarsophlebiidae Handlirsch, 1906: 467, 468, 580, 581.

TYPE GENUS. — *Tarsophlebia* Hagen, 1866, original designation of Handlirsch (1906) by monotypy.

INCLUDED GENERA. — *Tarsophlebia* Hagen, 1866 (= *Tarsophlebiopsis* Tillyard, 1923) and *Turanophlebia* Pritykina, 1968. Since Bechly (1996, 1997) demonstrated that the genera *Euthemis* Pritykina, 1968 (Upper Jurassic) and *Sphenophlebia* Bode, 1953 (Upper Liassic) are isophlebioid “anisozygoptères” and thus not related to Tarsophlebiidae, there is no more

evidence for a Lower Jurassic occurrence of Tarsophlebiidae and also no need for a further redundant taxon Tarsophlebioidea or Tarsophlebioptera.

STRATIGRAPHIC AND GEOGRAPHIC RANGE. — Only known from the Upper Jurassic and Lower Cretaceous of Eurasia.

EMENDED DIAGNOSIS. — Nel *et al.* (1993) proposed a diagnosis of the Tarsophlebiidae. We here emend this diagnosis with the following characters: 1) primary antenodal braces Ax1 and Ax2 stronger than the secondary antenodal cross-veins; 2) in all fore and hind wings, there are pairs of secondary longitudinal concave veins “above” and “below” the convex veins CuA, MA, and IR2, and closely parallel to them. We propose to name them respectively antero-CuA, postero-CuA, antero-MA, postero-MA, antero-IR2 and postero-IR2 intercalary veins. These veins are more or less long and defined in the different taxa. The postero-intercalaries are always longer than the associated antero-intercalaries; and 3) in male, one pair of well separated anal appendages visible, of very particular shape, basally strongly sclerotized, with high humps and a non-sclerotized paddle-like distal part. No median anal appendage visible. These body characters are only known for *Tarsophlebia eximia* and *Turanophlebia vitimensis* n. sp.

The monophyly of Tarsophlebiidae is supported by several strong autapomorphies (Nel *et al.* 1993), such as: hypertrophied hind wing subdiscoidal cell, developed as “pseudo discoidal cell”; in hind wing, fusion of veins [MAB + MP + CuA] for a considerable distance before separation of MP and CuA; vein AA strongly bent at insertion of CuP-crossing; extremely acute distal angles of fore wing discoidal and subdiscoidal cell. The characters “distinctly prolonged legs, with very long tarsi” and “male cerci with strange distal expansions” are present in both *T. eximia* and *T. vitimensis* n. sp., and probably also in other Tarsophlebiidae. The “extremely prolonged female ovipositor” could be an autapomorphy of the family, too, but it is only known from *T. eximia*. A further alleged autapomorphy mentioned by Nel *et al.* (1993) rather seems to be a symplesiomorphy (Bechly 1996), viz. “veins [RP + MA] - MAB - CuA aligned”. It is also present in the Epiophlebiidae Muttkowski, 1910, Isophlebioptera and Heterophlebioptera.

### Genus *Tarsophlebia* Hagen, 1866

*Tarsophlebia* Hagen, 1866: 65.

TYPE SPECIES. — *Heterophlebia eximia* Hagen, 1862, original designation of Hagen (1866) by monotypy.

OTHER SPECIES. — We transfer *Tarsophlebia neckini* Martynov, 1927 into the genus *Turanophlebia*. *Tarsophlebia westwoodii* Hagen, 1850 from the Lower

Liassic of Gloucestershire in England was correctly transferred to the heterophlebioid genus *Liassophlebia* by Tillyard (1925).

EMENDED DIAGNOSIS. — Nel *et al.* (1993) proposed a diagnosis, erroneous in some points. We emend it as follows: primary antenodal braces stronger than secondaries, as in other Tarsophlebiidae (*contra* Nel *et al.* 1993); cubito-anal areas of fore and hind wings with four rows of cells or less; 16 or less postnodal cross-veins; less than ten secondary antenodal cross-veins in hind wing; and IR1 relatively short.

### REMARKS

Nel *et al.* (1993) noted that the genus *Turanophlebia* is very close to *Tarsophlebia*.

### *Tarsophlebia eximia* (Hagen, 1862)

(Figs 1; 2)

*Heterophlebia eximia* Hagen, 1862: 102, 106.

*Euphaea longiventris* Hagen, 1862: 106, 121, pl. 13, figs 7, 8.

*Tarsophlebia eximia* – Hagen 1866: 65, pl. 2, figs 1-6, 11.

*Agrion latreillei* [sensu Meunier] Meunier, 1896: pl. 1.

*Agrion exhaustum* [sensu Meunier] Meunier, 1896: pl. 2.

*Tarsophlebia major* Handlirsch, 1906: 580.

?*Tarsophlebia longissima* Handlirsch, 1906: 581.

*Tarsophlebiopsis mayi* Tillyard, 1923: 149 (n. syn.).

HOLOTYPE OF *HETEROPHLEBIA EXIMIA*. — Specimen No. AS-VI-44a-b (BSPGM). The holotype of *T. major* is in the collection of the National Museum in Prague (Malz & Schröder 1979: 26). *Tarsophlebiopsis mayi* is known by the holotype specimen, only represented by three wing fragments, located in the collection of Sedgwick Museum, Cambridge, UK.

GEOLOGICAL SETTING. — Upper Jurassic (“Oberer Weißjura”, Malm  $\xi$  2b), lower Tithonian, Hybonotum-Zone, Solnhofen Formation (Solnhofen Lithographic Limestone), Eichstätt area, near Solnhofen, southern Franconian Alb, Bavaria, SW Germany. The type specimen of *T. mayi* was found at the Boulder Clay (probably derived from the Amphill Clay, Corallian), Hertfordshire, UK (Tillyard 1923: 146).

DIAGNOSIS. — That of the genus. The fore wing length varies from 35–41 mm, and the hind wing length from 30–39 mm. The wing lengths of *Tarsophlebia major* Handlirsch, 1906 (39 mm) and *Tarsophlebia longissima* Handlirsch, 1906 (42 mm) still fit in this continuous

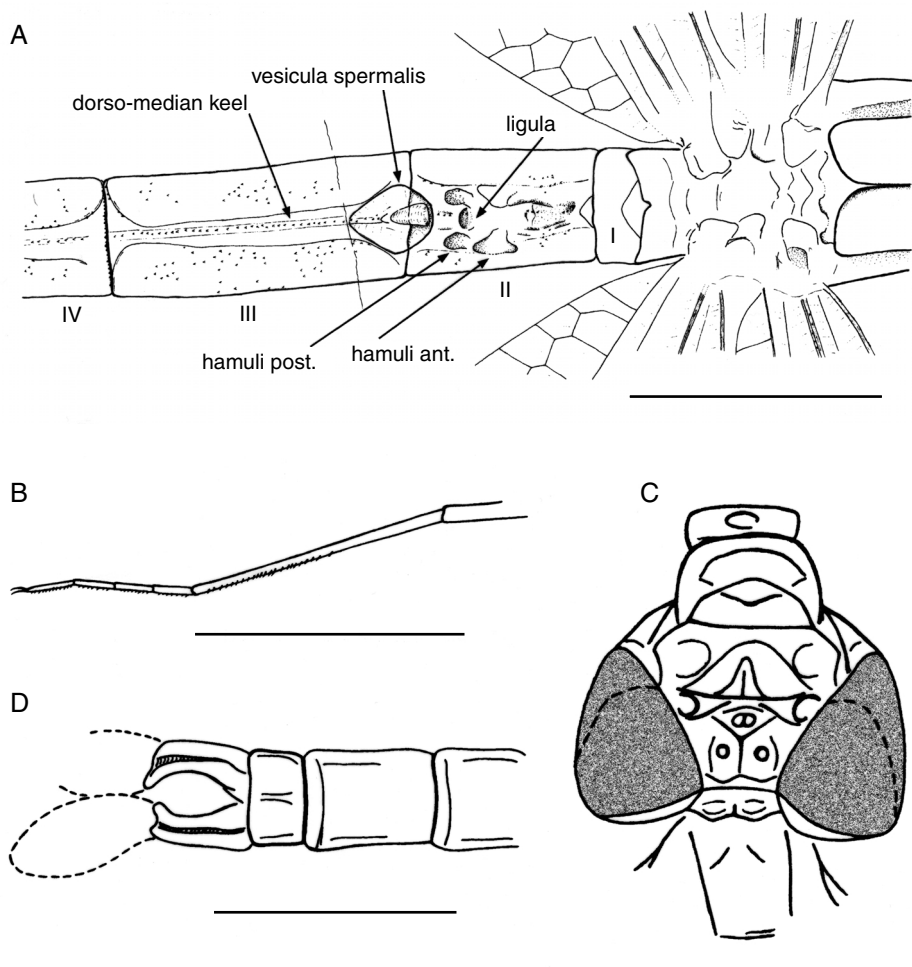


FIG. 1. — *Tarsophlebia eximia* (Hagen, 1862); **A**, male specimen (SOS 1720, JME), secondary genital apparatus; **B**, male holotype (BSPGM AS-VI-44b), counterpart, right hind leg; **C**, male (No. 6129, coll. Carpenter, MCZ), head; **D**, male (No. 6222, coll. Carpenter, MCZ), male genital appendage. Scale bars: A, B, D, 5 mm; C, 10 mm.

range of variability. Since there are no other diagnostic characters known, we tentatively concur with the synonymization of Nel *et al.* (1993), even though the unusually large range of size would well allow the recognition of a distinct larger species of *Tarsophlebia*.

#### REDESCRIPTION

##### Head

A well preserved head is only known from specimen No. 6129 in coll. Carpenter of MCZ, which is labelled “*Tarsophlebia eximia* Hag. - mas. -

Counterpart - Solenhofen - Dr. Krantz” and indicated as “Type”. Hagen (1866) figured this specimen (reproduced by Nel *et al.* 1993: fig. 53a-b). Our re-examination of the specimen showed that the original figures were rather imprecise. We give a new figure, after the direct examination of the holotype (Fig. 1C).

##### Thorax

Nel *et al.* (1993: 85) remarked that all specimens with the 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. However, they estimate that the skewness was probably more important than in recent Zygoptera, Lestidae Calvert, 1901. The very elongated humeral region (mesepisternum) of the synthorax with a very long dorsal carina (visible in specimens No. SOS 1705/1720 in JME) strongly supports a hypertrophied skewness.

### Legs

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 & Nel, 1996 from the same locality (Martínez-Delclòs & 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. As example, only three tarsomeres could be identified on all tarsi of the specimen No. 1951/73K (JME) (Nel *et al.* 1993: 86), with the following putative lengths: the foreleg length of first tarsomere 3.0 mm, length of second tarsomere 1.5 mm, length of third tarsomere 2.0 mm; median leg length of first tarsomere 2.5 mm, length of second tarsomere 1.2 mm, length of third tarsomere 1.0 mm; hind leg length of first tarsomere 3.0 mm, length of second tarsomere 2.0 mm, length of third tarsomere 1.0 mm. Nevertheless, we found two well preserved specimens which clearly confirm the original description of four-segmented tarsi because they show four segment borders and the segments are angled and not aligned with each other. The right hind leg of the holotype specimen AS-VI-44b in BSPGM indeed shows four tarsomeres, with the following dimensions: length of first tarsomere 1.46 mm, length of second tarsomere 1.40 mm (both could correspond to the putative first tarsomere of specimen No. 1951/73K), length of third tarsomere 1.45 mm, length of fourth tarsomere

1.68 mm. The left foreleg of specimen No. 1960/66K in JME also shows four tarsomeres of more or less equal length.

The tarsi of all specimens show a pair of elongate tarsal claws that do not seem to have a subapical tooth (putative plesiomorphy, even though a reduction or artifact of preservation cannot be excluded).

### Wings

They are extensively described in Nel *et al.* (1993), except for the following emendations: primary antenodal braces stronger than the secondaries; presence of 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”); presence of a relatively long not zigzagged secondary vein (“postero-MA vein”) closely parallel to distal part of MA, in postdiscoidal area and another one in area between RP3/4 and MA (“antero-MA vein”).

### Abdomen

Several specimens (e.g., specimen No. SOS 1720 in JME) show the presence of a longitudinal medio-dorsal carina on the abdominal terga, which is covered with a row of small spines. Specimen No. SOS 1720 also shows numerous tiny spines on the lateral parts of the abdominal terga, very similar to extant odonates (e.g., *Calopteryx* Leach, 1815).

### Male secondary genital apparatus

There is a single male specimen (No. SOS 1720 in JME) that shows the male secondary genital apparatus, even though the specimen is preserved in dorsal aspect, since the ventral side is pressed through. Nel *et al.* (1993: fig. 54) figured this specimen, but the genitals were apparently difficult to interpret. The alleged male “auricles” of *Tarsophlebia eximia*, described by Nel *et al.* (1993: fig. 68) from the second abdominal segment of specimen No. 1650/57a-b in JME, are obviously based on a misinterpretation of the hamuli posteriors (Bechly 1996; Rehn 2003: 201). We propose a new interpretation of the male secondary genital apparatus (see Fig. 1A).

*Female ovipositor*

The female ovipositors are very long, extending well beyond the abdomen. They were already figured and described in Nel *et al.* (1993), on the basis of specimen No. SOS 3609, in JME. Fleck & Nel (2003) noted that, despite the fact they both have long ovipositor, its structure is different in the extant family Cordulegastridae Hagen, 1875 and the Mesozoic Aeschnidiidae Needham, 1903. In the latter group, the valvula 1 is distinctly longer, narrower and weaker than in Cordulegastridae. The exact structure of the ovipositor cannot be established in *Tarsophlebia* because of the poor state of preservation of the available material.

*Male anal appendages*

The presence of a long ovipositor in female specimen supports the hypothesis that the specimens without such a structure are male. The anal appendages were always interpreted as calopterygoid-like, thus consisting of two pairs of long and curved claspers (cerci and paraprocts). Also, Nel *et al.* (1993: fig. 52) described such appendages from the holotype specimen. The discovery of very curious anal appendages of *Turanophlebia vitimensis* n. sp. (see below) stipulated the thorough re-examination of these structures in *T. eximia*. Indeed we could identify appendages of the same type in specimen No. 6222 in coll. Carpenter of MCZ, which is also labelled “*Tarsophlebia eximia* Hag. - mas. - Counterpart - Solenhofen - Dr. Krantz” and indicated as “Type”. The previous misinterpretations are based on artifacts of preservation.

## THE STATUS OF THE ENIGMATIC

*TARSOPHLEBIOPSIS MAYI* TILLYARD, 1923

Tillyard (1923) described *Tarsophlebiopsis mayi* based on two wing fragments that were found in the body chamber of an ammonite from the Upper Jurassic of England. Fraser (1955) revised this specimen and provided a reconstruction of the complete wing. Nel *et al.* (1993: 92) considered that the holotype of this taxon could be just an aberrant specimen in the plesiomorphic character state “basal separation of the stems of M and Cu

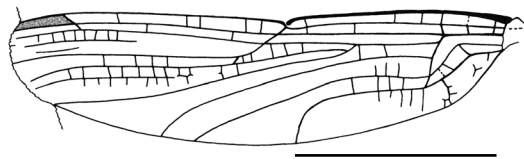


Fig. 2. — *Tarsophlebia minor* n. sp., holotype (No. 55, coll. Carpenter, MCZ), left hind wing. Scale bar: 10 mm.

with several cross-veins between their stems”. We completely agree with this statement and now formally synonymize *Tarsophlebiopsis mayi* with *Tarsophlebia eximia*. The reasons are as follows: Nel *et al.* (1993: 92) falsified two of the four diagnostic characters mentioned in the original description of Tillyard (1923). Nel *et al.* (1993: 92) accepted the better-defined primary antenodal cross-veins Ax1 and Ax2 as valid diagnostic character. This state also occurs in *Tarsophlebia eximia*. Thus, except for two character states (“M and Cu basally separated”; “submedian space with two rows of cells”), all preserved characters (including size and fore wing venation) of *Tarsophlebiopsis mayi* are absolutely identical with *Tarsophlebia eximia*. Both taxa are from the Upper Jurassic of Middle Europe. The first mentioned difference is very strange, since this character state (“M and Cu basally separated”) would represent a unique plesiomorphy within Panodonata (= Tarsophlebiidae + Odonata), which is only known from older and more basal stemgroup representatives of Odonata (e.g., Meganisoptera, Protanisoptera, Triadophlebiomorpha, and Protozygoptera). All other tarsophlebiids agree with the derived character state of extant odonates. The second character state (“submedian space with two rows of cells”) is in the same area of the wing and could be related to the aberrant structure of veins M and Cu. Therefore, both character states of the holotype of *Tarsophlebiopsis mayi* could be related to an individual atavistic aberration (also known from other wing venational structures in extant Odonata), or even as an artifact of preservation. The latter case could occur when the two membranes of the wing are separated and partly detached, which is for example a common phenomenon in amber damselflies.

*Tarsophlebia minor* n. sp.

(Fig. 2)

HOLOTYPE. — Specimen No. 55 in coll. Carpenter of MCZ, which is labelled “Agrion spec. - Solnhofen - Dr. Krantz”.

ETYMOLOGY. — Named after the relatively small size (hind wing length only about 26 mm), compared to the other species of the same genus.

GEOLOGICAL SETTING. — Hybonotum-Zone, Solnhofen Formation (Solnhofen Lithographic Limestone), lower Tithonian, Upper Jurassic (“Oberer Weißjura”, Malm  $\xi$  2b), Eichstätt area, near Solnhofen, southern Frankonian Alb, Bavaria, SW Germany.

DIAGNOSIS. — This new species is distinguished by its distinctly smaller size than *T. eximia* (fore wing about 26 mm long instead of 35–41 mm long in *T. eximia*). Also, the angle between MAb and MP + CuA is distinctly more opened than in the fore wing of *T. eximia*.

## DESCRIPTION

The holotype is an isolated left fore wing with missing apex. Length of preserved part, 25.0 mm, probable length of wing, about 26.0 mm; although the venation is rather poorly preserved, some characters can be determined with accuracy. Wing probably hyaline, pterostigma dark brown; distance from base to arculus, 3.2 mm; from arculus to nodus, 7.8 mm; from nodus to pterostigma, 10.3 mm, pterostigma elongated and narrow, about 3.5 mm long, 0.5 mm wide, not basally recessed; pterostigmal brace oblique and strong, opposite pterostigma base; median and submedian areas free of cross-veins; CuP strongly curved, basal of Ax2, basally closing subdiscoidal space; at least primary antenodal brace and Ax2 stronger than secondary antenodal cross-veins; arculus slightly opposite Ax2; only few secondary antenodal cross-veins preserved distal of Ax2, probably less than 10 in the living animal; all secondary antenodal cross-veins not aligned with the cross-veins of second rank between ScP and RA; MP + CuA strongly curved just before its fusion with MAb; a sharp angle between MP + CuA and MAb, but more opened than in *T. eximia*; no fusion between MAb and MP + CuA before CuA separates from MP. Thus it is a fore wing, as the tarsophlebiid hind wings have such a long fusion; 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 two cells by a cross-vein; AA without any strong posterior branches; anal area with two or three rows of cells; posterior wing margin rounded; petiole short, about 0.8 mm long; AA reaching free part of CuA at sharp angle; no CuAb (*sensu* Fleck *et al.* 2003); CuA without strong posterior branches; less than five rows of small cells between CuA and posterior wing margin; “postero-CuA vein” and “antero-CuA vein” not preserved; CuA reaching posterior wing margin just basal to nodus level; area between MP and CuA with one row of cells in its basal part but greatly widened in its distal half; postdiscoidal area slightly widened distally; bases of RP3/4 and IR2 between arculus and nodus, distinctly nearer to nodus, base of RP3/4 3.5 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; numerous Bq cross-veins; less than 11 postnodal cross-veins between C and RA, not aligned with the postsubnodal cross-veins; IR1 well defined, not zigzagged and only slightly curved; one row of cells between RP1 and IR1; area between RP2 and IR2 distinctly widened distally, “antero-IR2” and “postero-IR2” veins not preserved; area between IR2 and RP3/4 distally widened; area between RP3/4 and MA distally widened; “antero-MA” and “postero-MA” veins not preserved.

Genus *Turanophlebia* Pritykina, 1968

*Turanophlebia* Pritykina, 1968: 42.

TYPE SPECIES. — *Turanophlebia martynovi* Pritykina, 1968 by monotypy.

OTHER SPECIES INCLUDED. — *Turanophlebia sibirica* Pritykina, 1977, *Turanophlebia anglicana* n. sp., *Turanophlebia mongolica* n. sp., *Turanophlebia vitimensis* n. sp., *Turanophlebia neckini* (Martynov, 1927) n. comb.

EMENDED DIAGNOSIS. — Differs from the Upper Jurassic *Tarsophlebia eximia* and *Tarsophlebia minor*



n. sp. in its denser wing reticulation, mainly visible through: 1) the presence of more than 25 postnodal cross-veins (against 16 in *T. eximia* and around 11 in *T. minor* n. sp.); 2) six (or more) rows of cells between CuA and posterior hind wing margin (against less than five rows in *T. eximia* and *T. minor* n. sp.); 3) more than 10 secondary antenodal cross-veins in hind wing (against less than 10 in *T. eximia*); 4) IR1 longer than in *T. eximia*; and 5) presence of long secondary longitudinal not zigzagged veins in area between IR2 and RP2.

#### REMARKS

Jarzembowski (1990) considered that *Tarso-phlebia* and *Turanophlebia* differ in: 1) general density of venation; 2) width of cubito-anal area; and 3) form of “discal cell” in hind wing (“pseudo-discal cell” *sensu* Nel *et al.* 1993). The shape of the “pseudo-discal” cell is variable in both *Tarsophlebia eximia* and the different species of *Turanophlebia*, thus the character 3) is not constant.

#### *Turanophlebia martynovi* Pritykina, 1968 (Fig. 3)

*Turanophlebia martynovi* Pritykina, 1968: 43, 44, text-fig. 14, pl. 3, fig. 4. — Carpenter 1992: 73, fig. 46.4. — Nel *et al.* 1993: 89, 90, fig. 70.

HOLOTYPE. — Specimen No. 2554/21 (PIN).

GEOLOGICAL SETTING. — Upper Jurassic, Callovian-Kimmeridgian or Oxfordian-Kimmeridgian (Zherikhin & Gratshev 1993; Mostovski & Martínez-Delclòs 2000), Karatau, Chimkent region, Southern Kazakhstan, C.I.S.

DIAGNOSIS. — *T. martynovi* differs from *T. sibirica* and *T. anglicana* n. sp. in the following character states: pterostigma covering six cells; arculus opposite Ax2; two rows of cells between C and RA distal of pterostigma. *T. martynovi* has two rows of cells in hind wing anal area, unlike *T. neckini* n. comb. *T. martynovi* has a strong angle in its hind wing arculus; its subdiscoidal space is divided into three small cells, unlike other *Turanophlebia* species. It differs from *T. vitimensis* n. sp. in the presence of only six rows of cells in cubito-anal area between CuA and posterior wing margin. It differs from *T. mongolica* n. sp. in the presence of its vein “O” oblique.

#### ?*Turanophlebia sibirica* Pritykina, 1977

*Turanophlebia sibirica* Pritykina, 1977: 84, 85, text-fig. 2, pl. 1, fig. 2. — Nel *et al.* 1993: 91.

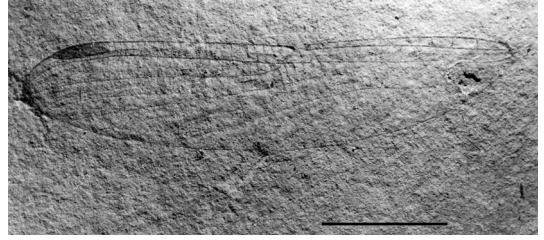


FIG. 3. — *Turanophlebia martynovi* Pritykina, 1968, holotype (PIN 2554/21). Scale bar: 10 mm.

HOLOTYPE. — Specimen No. 1289/1258 (PIN).

GEOLOGICAL SETTING. — Lower Cretaceous, Zaza Formation, Neocomian or Barremian-Aptian (Zherikhin *et al.* 1999; Mostovski & Martínez-Delclòs 2000). Baissa, Vitim river, Transbaikalia, C.I.S.

DIAGNOSIS. — ?*T. sibirica* differs from *T. martynovi* in the presence of only one row of cells in the area between C and RA distal of pterostigma. It differs from *T. anglicana* n. sp. in its longer wings. It differs from *T. neckini* n. comb. in the presence of two or three rows of cells in the hind wing anal area.

#### REMARKS

The type specimen of ?*T. sibirica* is very poorly preserved and incomplete. It is nearly impossible to be accurate of its attribution to the genus *Turanophlebia*: its cubito-anal area is too fragmentary to determine the exact number of cells rows between CuA and posterior wing margin (Pritykina’s wing reconstruction is optimistic); its vein IR1 is badly preserved. The only argument is the large number of cells in the apical part of its wing.

#### *Turanophlebia neckini* (Martynov, 1927) n. comb. (Fig. 4)

*Tarsophlebia neckini* Martynov, 1927: 757, 758, figs 1, 2. — Nel *et al.* 1993: 87.

HOLOTYPE. — Specimen No. 2452/3 (PIN).

GEOLOGICAL SETTING. — Upper Jurassic, Callovian-Kimmeridgian or Oxfordian-Kimmeridgian (Zherikhin & Gratshev 1993; Mostovski & Martínez-Delclòs 2000), Karatau, Chimkent region, Southern Kazakhstan, C.I.S.

DIAGNOSIS. — *T. neckini* n. comb. differs from the other *Turanophlebia* species in the presence of only one or two rows of cells in the hind wing anal area.

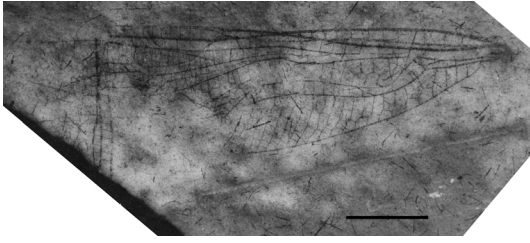


FIG. 4. — *Turanophlebia neckini* (Martynov, 1927) n. comb., holotype (PIN 2452/3). Scale bar: 10 mm.

#### REDESCRIPTION

There is some imprecision in the original description of Martynov (1927), thus a redescription is necessary. Imprint of a hind wing, with the distal half partly destroyed. Wing probably hyaline, pterostigma missing; wing about 39.0 mm long; 7.3 mm wide; distance from base to arculus, 6.0 mm; from arculus to nodus, 10.2 mm; median and submedian areas free of cross-veins; CuP strongly curved, nearly opposite Ax2, basally closing subdiscoidal space; primary antenodal braces Ax1 and Ax2 stronger than secondary antenodal cross-veins, without cross-veins between them, 2.0 mm apart; Ax1 is 3.8 mm from wing base; arculus opposite Ax2; 14 secondary antenodal cross-veins distal of Ax2, not aligned with the cross-veins of second rank between ScP and RA; numerous cross-veins in the area between RA and RP, between arculus and nodus; a long “gap” without cross-veins between arculus and RP3/4 in the area between RP and MA; MP + CuA strongly curved just before its fusion with MAb; a sharp angle between MP + CuA and MAb; presence of a long fusion between MAb and MP + CuA before CuA separates from MP, 1.1 mm long, characteristic of the Tarsophlebiidae (Nel *et al.* 1993); RP + MA, MA and MAb, MP + CuA + MAb, and basal free part of CuA well aligned in arculus, as in other Tarsophlebiidae (Nel *et al.* 1993); discoidal space basally opened; presence of a two-celled “tarsophlebiid pseudo-discoidal space” just distal of MAb in postdiscoidal area; subdiscoidal area divided into two cells by a cross-vein; AA without any strong posterior branches; anal area with one

or two rows of cells; posterior wing margin rounded; a short petiole, 1.4 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 in cubito-anal area; CuA reaching posterior wing margin just distal of nodus level; area between MP and CuA with one row of cells in its basal part but greatly widened in its distal half; postdiscoidal area with two rows of cells in its basal part, narrowed in its mid part and slightly widened distally; bases of RP3/4 and IR2 between arculus and nodus, midway between arculus and nodus, 5.2 mm from nodus; apparent base of IR2 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; numerous Bq cross-veins, but apparently no cross-vein in basal part of area between RA, RP, RP3/4 and IR2; numerous postnodal cross-veins between C and RA, not aligned with the postsubnodal cross-veins; base of IR1 about 10 cells distal of that of RP2; IR1 well defined, long, not zigzagged and only slightly curved; one row of cells between RP1 and IR1; area between RP3/4 and MA distally widened.

#### DISCUSSION

This fossil has the diagnostic characters of the genus *Turanophlebia*, i.e. cubito-anal area broad, with six rows of cells between CuA and posterior wing margin, more than 25 postnodal cross-veins, more than 10 secondary antenodal cross-veins in hind wing, IR1 longer than in *Tarsophlebia eximia*. Thus, we propose to transfer it into the genus *Turanophlebia*.

#### *Turanophlebia anglicana* n. sp.

(Fig. 5)

HOLOTYPE. — Specimen No. 018531, part and counterpart, Booth Museum of Natural History, Brighton, UK.

ETYMOLOGY. — After the latinised name of England.

GEOLOGICAL SETTING. — Lower Cretaceous, Lower Weald Clay, Upper Hauterivian, Clockhouse (Butterley) Brickworks, UK, National Grid Reference TQ 175385.

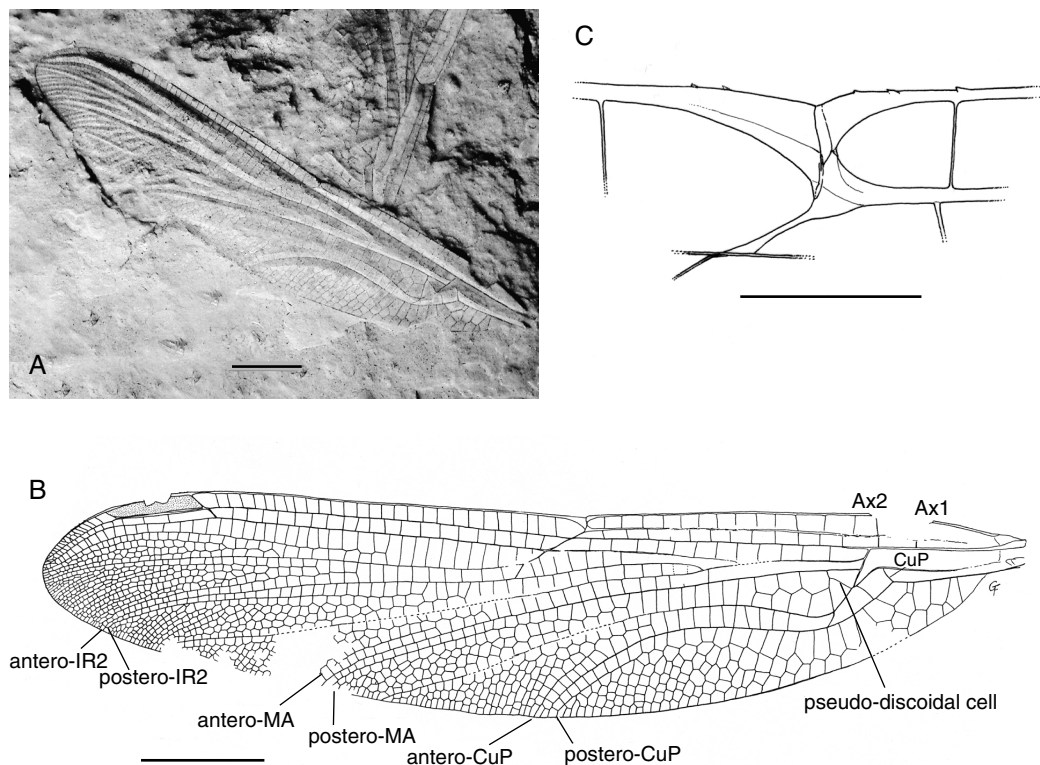


FIG. 5. — *Turanophlebia anglicana* n. sp., holotype (No. 018531, Booth Museum of Natural History, Brighton, UK); **A**, complete wing, other wing is that of a Libelluloidea; **B**, reconstruction of the hind wing; **C**, detail of hind wing nodus. Abbreviations: **Ax1**, **Ax2**, primary antenodal cross-veins; **CuP**, Cubitus Posterior; **IR2**, intercalary vein of radial area; **MA**, Median Anterior. Scale bars: **A**, 10 mm; **B**, 5 mm; **C**, 1 mm.

DIAGNOSIS. — Nel & Jarzembowski (1996: 91, fig. 4) attributed erroneously this specimen to a Campterophlebiidae genus and species *incertae sedis*. *T. anglicana* n. sp. differs from *T. martynovi* in the following character states: pterostigma covering only three cells instead of six; arculus slightly distal of Ax2; Ax1 shifted more distally; only one row of cells between C and RA distal of pterostigma. It differs from ?*T. sibirica* in its smaller size (wing about 40 mm long against 45 mm for ?*T. sibirica*). It differs from *T. neckini* n. comb. in the presence of two to three rows of cells in the anal area instead of one to two rows in *T. neckini* n. comb. *T. anglicana* n. sp. differs from *T. mongolica* n. sp. in its vein “O” oblique and of better defined secondary longitudinal veins parallel to CuA. It differs from *T. vitimensis* n. sp. in the presence of only six rows of cells between CuA and posterior wing margin, instead of nine or 10, and of one row of cells in the most narrow part of postdiscoidal area instead of two.

#### DESCRIPTION

Imprint and counterimprint of a nearly complete hind wing. The counterpart was previously described alone by Nel & Jarzembowski (1996) and erroneously attributed to the Campterophlebiidae Handlirsch, 1920. The error was due to its poor state of preservation. Fortunately, the imprint is very well preserved. The present redescription is based on its study. Wing probably hyaline, pterostigma dark brown; wing 39.7 mm long; 8.3 mm wide; distance from base to arculus, 6.4 mm; from arculus to nodus, 11.4 mm; from nodus to pterostigma, 15.5 mm, to apex, 22.1 mm; pterostigma elongated and narrow, 3.7 mm long, 0.5 mm wide, covering three cells, not basally recessed; pterostigmal brace oblique and strong, opposite

pterostigma base; median and submedian areas free of cross-veins; CuP strongly curved, nearly opposite to Ax2, basally closing subdiscoidal space; primary antenodal braces Ax1 and Ax2 stronger than secondary antenodal cross-veins, with no visible cross-veins between them, 1.5 mm apart; Ax1 is 4.4 mm from wing base; arculus slightly distal of Ax2 (0.4 mm); 13 secondary antenodal cross-veins distal of Ax2, not aligned with the cross-veins of second rank between ScP and RA; 12 cross-veins in the area between RA and RP, between arculus and nodus; a long “gap” without cross-veins between arculus and RP3/4 in the area between RP and MA; MP + CuA strongly curved just before its fusion with MAB; a sharp angle between MP + CuA and MAB; presence of a long fusion between MAB and MP + CuA before CuA separates from MP, 1.4 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; presence of a two-celled “tarsophlebiid pseudo-discoidal space” just distal of MAB in the postdiscoidal area; subdiscoidal area divided into two cells by a cross-vein; AA without any strong posterior branches; anal area with two or three rows of cells; posterior wing margin rounded; petiole short, 1.5 mm long; AA reaching free part of CuA at sharp angle; no CuAb (*sensu* Fleck *et al.* 2003); CuA without strong posterior branches; six or seven 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 thirteen rows of cells along posterior wing margin; postdiscoidal area with two rows of cells in its basal part, narrowed in its mid part and slightly widened distally, with five or six 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 5.0 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; numerous Bq cross-veins, but apparently no cross-vein in the basal part of areas between RA and RP, and between RP3/4 and IR2; 27 postnodal cross-veins between C and RA, not aligned with the 20 postsubnodal cross-veins; base of IR1 11 cells distal of that of RP2; IR1 well defined, not zigzagged and only slightly curved; one row of small cells in the area between C and RA distal of pterostigma; one row of cells between RP1 and IR1; five rows of cells in the 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.

#### DISCUSSION

Because of the structures of the anal area, the basally opened discoidal space, the strongly curved MP + Cu, the long MAB + MP + CuA, the sharp angle between MP + Cu and MAB and the presence of a “tarsophlebiid pseudo-discoidal space”, this fossil is clearly a tarsophlebiid hind wing (Nel *et al.* 1993). It can be attributed to the genus *Turanophlebia* rather than to *Tarsophlebia*, because of its broad cubito-anal area, long IR1, numerous postnodal and antenodal cross-veins.

#### NOTES

1) As this fossil is not a Campteropteroptera but a Tarsophlebiidae, the Isophlebioidea Handlirsch, 1906 remains unknown in the British Weald Clay.

2) Nel & Jarzembowski (1996) described *Proeuthemis pritykinae* from the Lower Weald Clay (Upper? Hauterivian), UK. Bechly (1997) attributed it to the Sphenophlebiidae Bechly, 1997 (in Isophlebioptera, Parazygoptera). Bechly (1997) also transferred the Euthemistidae Pritykina, 1968 from the Tarsophlebioidea to the Isophlebioptera Bechly, 1996.

3) Jarzembowski (1990) described two fossil fore wings from the British Lower Weald Clay (Durlston Bay), he attributed to “*Tarsophlebia?*” rather than to *Turanophlebia*, on the basis of the presence of only one row of cells in the area between C and RA, unlike *Turanophlebia martynovi*. As we can see above, this character alone is not sufficient to separate the two genera. Thus, the generic placement of these two fore wings within the Tarsophlebiidae is uncertain.

*Turanophlebia mongolica* n. sp.

(Fig. 6)

HOLOTYPE. — Specimen No. 3559/69 (PIN).

ETYMOLOGY. — Named after the country of Mongolia.

GEOLOGICAL SETTING. — Lower Cretaceous, Barremian-Aptian (Mostovski & Martínez-Delclòs 2000), Bon-Tsagaan series, Bon-Tsagaan, Bayanhongor Aimak, Central Mongolia.

DIAGNOSIS. — *T. mongolica* n. sp. differs from all other *Turanophlebia* species as follows: 1) presence of a complete secondary antenodal cross-vein between Ax1 and Ax2; 2) vein “O” not oblique, visible because of an angle of RP2; and 3) postdiscoidal area not distinctly narrowed in its mid part. It differs from *T. martynovi* and *T. anglicana* n. sp. in its base of vein IR1 only three cells distal of base of RP2, instead of more than 10 cells and the presence of only 15 rows of cells between MP and CuA along posterior wing margin, instead of more than 25 in *T. martynovi* and *T. anglicana* n. sp. It differs from ?*T. sibirica* in its cells of the cubito-anal area distinctly transverse. It differs from *T. neckini* n. comb. in the presence of two to three rows of cells in the anal area instead of one to two rows in *T. neckini* n. comb. The veins “antero-CuA” and “postero-CuA” are less well defined than in other *Turanophlebia* species.

DESCRIPTION

Imprint of a hind wing with the apical third missing and the region of discoidal cell partly destroyed. Wing probably hyaline; preserved part of wing 29.5 mm long; wing probably about 41.0 mm long; 9.7 mm wide; distance from base to arculus, 5.7 mm; from arculus to nodus, 12.0 mm; median and submedian areas free of cross-veins; CuP strongly curved, just distal of Ax2, basally closing subdiscoidal space; primary antenodal braces Ax1 and Ax2 2.9 mm apart,

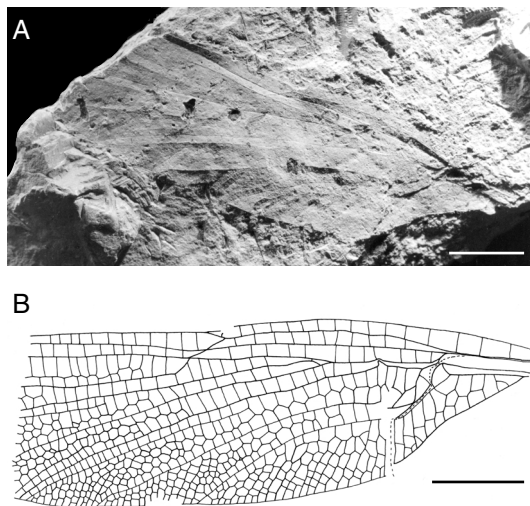


Fig. 6. — *Turanophlebia mongolica* n. sp.; A, holotype (PIN 3559/69); B, holotype, reconstruction of hind wing. Scale bar: A, 10 mm; B, 5 mm.

stronger than secondary antenodal cross-veins, with a complete secondary antenodal cross-vein between them; Ax1 is 2.0 mm from wing base; arculus distinctly distal of Ax2 (0.5 mm); 11 secondary antenodal cross-veins distal from Ax2, not aligned with the cross-veins of second rank between ScP and RA; 12 cross-veins in the area between RA and RP, between arculus and nodus; a long “gap” without cross-veins between arculus and RP3/4 in the area between RP and MA; MP + CuA strongly curved just before its fusion with MAb; a sharp angle between MP + CuA and MAb; presence of a long fusion between MAb and MP + CuA before CuA separates from MP, about 1.5 mm long, characteristic of the Tarsophlebiidae; MP + CuA + MAb and basal free part of CuA well aligned in arculus, as in other Tarsophlebiidae; discoidal space basally opened; presence of the two-celled “tarsophlebiid pseudo-discoidal space” just distal of MAb in the postdiscoidal area; subdiscoidal area divided into two cells by a cross-vein; AA without any strong posterior branches; anal area with three rows of elongate transverse cells; posterior wing margin rounded; a short petiole, about 1.5 mm long; AA reaching free part of CuA at sharp angle; no

CuAb (*sensu* Fleck *et al.* 2003); CuA with no strong posterior branches; seven rows of small cells between CuA and posterior wing margin; “antero-CuA” and “postero-CuA” veins present, relatively long but weakly zigzagged; CuA reaching posterior wing margin just distal of nodus level; area between MP and CuA with one row of cells in its basal part but rapidly greatly widened in its distal part, with about 15 rows of cells along posterior wing margin; postdiscoidal area with two rows of cells in its basal half, not distinctly narrowed in its mid part, and slightly widened distally, with a distal secondary longitudinal straight vein closely parallel to MA and six rows of cells between MA and MP near posterior wing margin; bases of RP3/4 and IR2 midway between arculus and nodus, 6.0 mm from nodus; base of IR2 apparently on RP3/4; nodal Cr and subnodus strongly oblique; base of RP2 aligned with subnodus; vein “O” not oblique, visible because of an angle of RP2, two cells distal of base of RP2; numerous Bq cross-veins, but no cross-vein in basal part of area between RA, RP, RP3/4 and IR2; numerous postnodal cross-veins between C and RA (12 of them being preserved), not aligned with the numerous postsubnodal cross-veins; base of IR1 only three cells distal of that of RP2; IR1 well defined, basally zigzagged but straighter distally; area between RP2 and IR2 widened distally; area between IR2 and RP3/4 distally widened; “antero-IR2 vein” not preserved; “postero-IR2 vein” elongate; area between RP3/4 and MA distally widened; “antero-MA” and “postero-MA” veins elongate.

#### DISCUSSION

This fossil is clearly a tarsophlebiid hind wing, because of the structures of the anal area, the basally opened discoidal space, the strongly curved MP + Cu, the long common stem MAb + MP + CuA, the sharp angle between MP + Cu and MAb and the presence of a “tarsophlebiid pseudo-discoidal space”. It can be attributed to the genus *Turanophlebia* rather than to *Tarsophlebia*, because of its broad cubito-anal area, long IR1, and numerous postnodal and antenodal cross-veins.

#### *Turanophlebia vitimensis* n. sp.

(Fig. 7)

HOLOTYPE. — Specimen No. 2361/1, part and counterpart (PIN).

ETYMOLOGY. — Named after Vitim River.

GEOLOGICAL SETTING. — Lower Cretaceous, Zaza Formation, Neocomian or Barremian-Aptian, Romanovka, right side of Vitim River downstream Romanovka village, Eravna district, Buryat Republic, Russia (Zherikhin pers. comm.).

DIAGNOSIS. — *T. vitimensis* n. sp. differs from all other *Turanophlebia* species in: 1) presence of nine to 10 rows of cells in the cubito-anal area between CuA and posterior wing margin; 2) CuA reaching posterior wing margin distinctly distal of nodus level, as in *T. neckini* n. comb.; 3) oblique vein “O” four cells distal of base of RP2. It shares with *T. mongolica* n. sp. the presence of two or more rows of cells in postdiscoidal area, instead of one in other *Turanophlebia* species; and 4) base of RP3/4 closer to nodus than to arculus.

#### DESCRIPTION

Part and counterpart of a body with the bases of the two fore wings and a nearly complete hind wing. Wings hyaline.

Preserved part of hind wing 20.0 mm long; hind wing probably about 47.0 mm long; 10.1 mm wide; distance from base to arculus, about 7.0 mm; from arculus to nodus, 15.0 mm; median and submedian areas free of cross-veins; CuP not preserved; only primary antenodal brace Ax2 preserved, stronger than secondary antenodal cross-veins; Ax2 about 6.0 mm from wing base; arculus distinctly distal of Ax2 (0.6 mm); 14 secondary antenodal cross-veins distal of Ax2, not aligned with the cross-veins of second rank between ScP and RA; more than 10 cross-veins in the area between RA and RP, between arculus and nodus; a long “gap” without cross-veins between arculus and RP3/4 in the area between RP and MA; MP + CuA not preserved basal of its fusion with MAb; long fusion between MAb and MP + CuA before the separation between CuA and MP, 2.5 mm long, characteristic of the Tarsophlebiidae; MA, MAb, MP + CuA + MAb and basal free part of CuA well aligned in arculus, as in other Tarsophlebiidae; discoidal space pro-

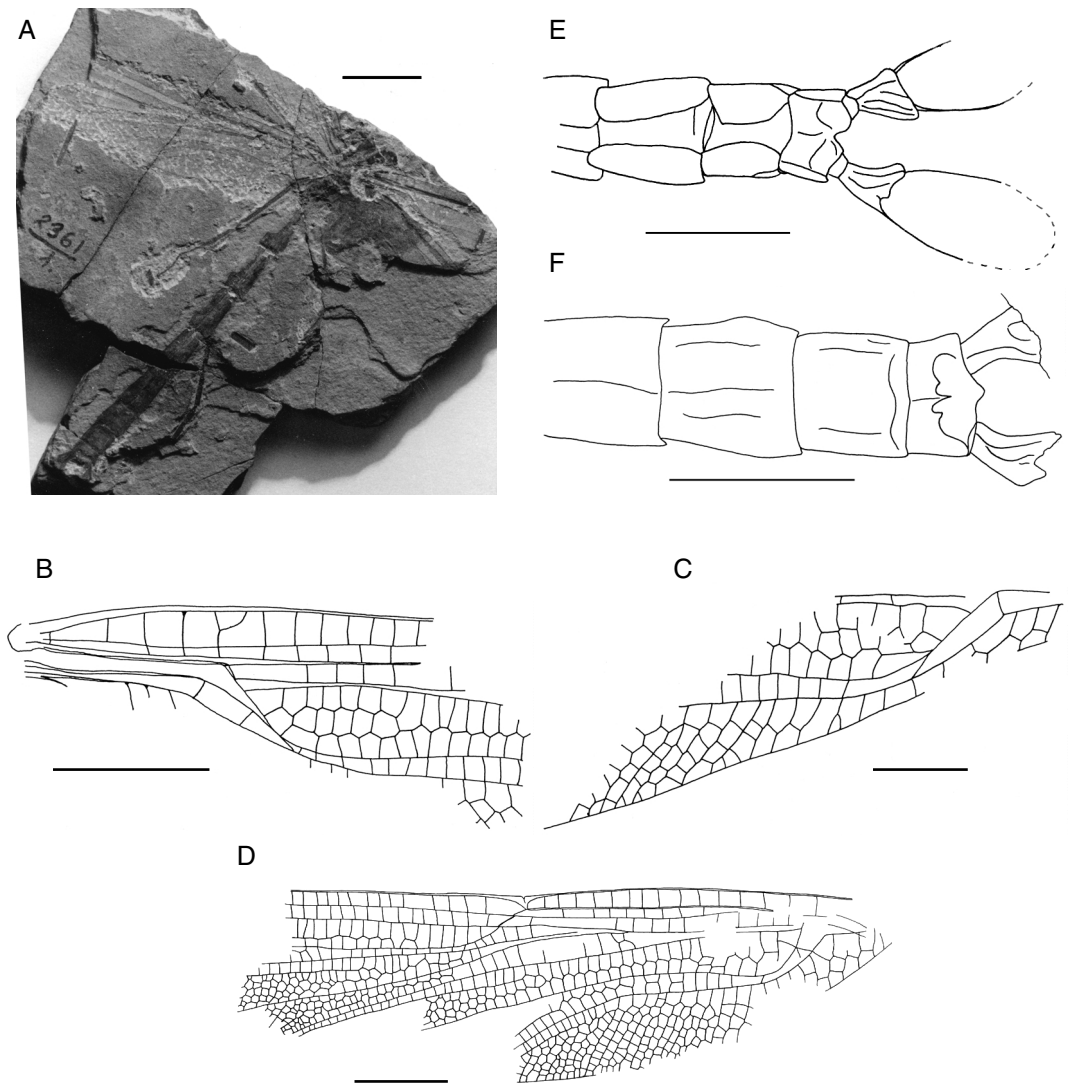


FIG. 7. — *Turanophlebia vitimensis* n. sp., holotype (PIN 2361/1); **A**, imprint; **B**, right fore wing; **C**, left fore wing; **D**, left hind wing; **E**, **F**, apex of the abdomen; **E**, counterimprint; **F**, imprint. Scale bars: **A**, 10 mm; **B**, **D**-**F**, 5 mm; **C**, 3 mm.

bably basally opened; presence of the two-celled “tarsophlebiid pseudo-discoidal space” just distal of MAb in the postdiscoidal area; subdiscoidal area divided into two cells by a cross-vein; AA without any strong posterior branches; anal area with three rows of cells; posterior wing margin rounded; AA reaching free part of CuA at sharp angle; no CuAb; CuA with no strong posterior branches; nine or 10 rows of small cells between

CuA and posterior wing margin; “antero-CuA” and “postero-CuA” veins elongate; CuA reaching posterior wing margin distinctly distal of nodus level; area between MP and CuA with one row of cells in its basal part but rapidly greatly widened in its distal part; postdiscoidal area with three rows of cells in its basal part, narrowed with two rows in its mid part, and slightly widened distally, with a distal secondary longitudinal straight

vein closely parallel to MA and five or six rows of cells between MA and MP near posterior wing margin; bases of RP3/4 and IR2 between arculus and nodus, nearer to nodus, 5.5 mm from nodus; nodal Cr and subnodus oblique; base of RP2 aligned with subnodus; vein "O" oblique, four cells distal of base of RP2; numerous Bq cross-veins; numerous postnodal cross-veins between C and RA (15 of them being preserved), not aligned with the numerous postsubnodal cross-veins; base of IR1 only six to eight cells distal of that of RP2; IR1 well defined, basally zigzagged but straighter distally; area between RP2 and IR2 widened distally; area between IR2 and RP3/4 distally widened; "postero-IR2" vein elongate; area between RP3/4 and MA distally widened; "antero-MA" and "postero-MA" veins elongate. Preserved part of fore wing 17.0 mm long; 6.7 mm wide (in its preserved part); distance from base to arculus, 7.0 mm; median and submedian areas free of cross-veins; CuP distinctly curved; Ax1 and Ax2 preserved, only slightly stronger than the secondary antenodal cross-veins; two secondary antenodals basal of Ax1 and one between Ax1 and Ax2; arculus between Ax1 and Ax2; numerous secondary antenodal cross-veins distal from Ax2, not aligned with the cross-veins of second rank between ScP and RA; numerous cross-veins in the area between RA and RP, between arculus and nodus; a long "gap" without cross-veins between arculus and RP3/4 in the area between RP and MA; MP + CuA strongly curved just before its fusion with MAb; presence of a very short fusion between MAb and MP + CuA before CuA separates from MP, better preserved on the right fore wing; MA, 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 two cells by a cross-vein; AA without any strong posterior branches; anal area with two rows of cells; AA reaching free part of CuA at very sharp angle; no CuAb; CuA with no strong posterior branches; more than seven rows of small cells in cubito-anal area; area between MP and CuA with one row of cells in its basal part but rapidly widened in its distal part; postdiscoid-

al area with three rows of cells in its basal half, narrowed with two rows in its mid part.

Thorax thin and elongate. Metathoracic leg well preserved, very long, as long as that of *Tarsophlebia eximia*, femora distinctly shorter than tibia, tibia 12.5 mm long, tarsus 8.5 mm long; tarsus very long and slender, with three brakes, probably corresponding to three visible tarsomeres.

Abdomen long and slender, about 45.0 mm long and 3.7 mm wide, the widest part being at the level of segment eight; presence of two lateral carinae on the posterior part of the abdominal segments. One pair of well separated anal appendages visible, of very particular shape, basally strongly sclerotized, with high humps and a non-sclerotized paddle-like distal part. No median anal appendage visible. The presence of only a pair of anal appendages shows that this specimen is a male, as the female Tarsophlebiidae have a very long ovipositor (Nel *et al.* 1993).

#### DISCUSSION

Because of the structures of the anal area, the basally opened discoidal space, the strongly curved MP + Cu, the long common stem MAb + MP + CuA, the sharp angle between MP + Cu and MAb and the presence of a "tarsophlebiid pseudo-discoidal space", this fossil is clearly a tarsophlebiid hind wing. It can be attributed to the genus *Turanophlebia* rather than to *Tarsophlebia*, because of its broad cubito-anal area, long IR1, and numerous postnodal and antenodal cross-veins.

#### PHYLOGENETIC POSITION OF THE TARSOPHLEBIIDAE

Nel *et al.* (1993) proposed that the Tarsophlebiidae are the most inclusive clade of the "Anisozoptera" + Anisoptera. The alleged putative synapomorphies mentioned by Nel *et al.* (1993), e.g., the less separated and relatively large eyes, the presence of two cephalic sutures, and the small leg spines, are at least characters of uncertain primary polarity because they are unknown in the Protozoptera, sister group of the Panodonata.



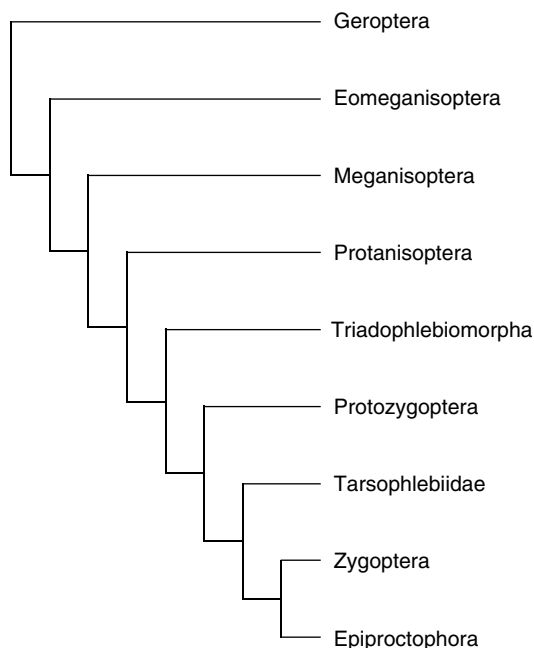


FIG. 8. — Phylogeny of the major groups of Odonatoptera, hypothesis of Bechly (1996).

Bechly (1996) excluded the Tarsophlebiidae from the Epiproctophora (= “Anisoptera” + Anisoptera) and considered them as the sister group of the Odonata (= Zygotera + Epiproctophora) within the Panodonata (= Tarsophlebiidae + Odonata), the sister group of the Panodonata being the Protozygotera, and the sister group of the (Panodonata + Protozygotera) being the Triadophlebiomorpha (see Fig. 8). More recently, Rehn (2003) proposed a new analysis that supports Bechly’s hypothesis on the position of the Tarsophlebiidae.

#### DISCUSSION ON THE CHARACTERS

We propose to re-examine some of the characters that would be available to clarify the problem of the phylogenetic position of the Tarsophlebiidae.

##### (A) Number of adult tarsomeres

Bechly (1999) indicated that the Protozygotera (sister group of the Panodonata) have four tarsomeres. In all the described Protozygotera, the

body is not preserved or too poorly preserved to observe the number of tarsomeres. Thus, we consider that it is still unknown in this group. After our observations, *Tarsophlebia eximia* seems to have four tarsomeres but *Turanophlebia vitimensis* n. sp. seems to have only three tarsomeres (see Figs 1B and 7A). Thus, some uncertainty remains concerning the exact number of tarsomeres in Tarsophlebiidae. The body structures of fossil insects from Solnhofen Lithographic Limestone are frequently poorly preserved, and difficult to interpret.

Under the hypothesis that the Tarsophlebiidae had four tarsomeres, this would correspond to a symplesiomorphy of the family with the more inclusive groups of Odonatoptera even though this character is unknown in the sister group of Panodonata and all more inclusive groups between Protozygotera Tillyard, 1925 and Meganeuridae Handlirsch, 1906. It is under a different state in the Meganisoptera, Meganeuridae, which have five tarsomeres (clearly visible in specimen MNHN-LP-R.52938 of *Meganeura monyi* Brongniart, 1884; Nel pers. obs.). Thus, three evolutionary scenarios are possible: 1) a progressive reduction of the number of tarsomeres from five in Meganeuridae to four in Protozygotera and Tarsophlebiidae and then to three in Odonata. In this case, this character state would be a striking symplesiomorphy of the Tarsophlebiidae; 2) a reduction from five tarsomeres in Protozygotera and more inclusive lineages to four in the stemgroup of Panodonata, maintained in the Tarsophlebiidae lineage, and a parallel reduction from four to three in Zygotera and Epiproctophora. This hypothesis is supported by the present phylogenetic analysis (see below); and 3) this theoretical possibility would be a reversal from three tarsomeres to four in Tarsophlebiidae, but it is not only less parsimonious, but also seems to be an evolutionary impossibility because no such example is known from any other insect. The problem will be definitely solved when the tarsal structures of the Protozygotera will be known.

Under the hypothesis that the Tarsophlebiidae had three tarsomeres, 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. Thus, it could correspond to an intermediate situation towards the three-segmented legs with a short basal tarsomere of the Odonata. There is no evidence of such a fusion in available fossils. In *Meganeura monyi* and in all Panodonata, except Tarsophlebiidae, the first tarsomere is the shortest. There is still no way to determine if some of the meganeurid's five tarsomeres have fused or were atrophied during the evolution.

Note. Under both the hypotheses of four- or three-segmented tarsi, all tarsomeres are very long in Tarsophlebiidae. This is a unique character in known Odonoptera. It could represent a synapomorphy of this family.

#### (B) Tarsal claws

Bechly (1996) indicated that the Odonata have "tarsal claws with a ventro-apical claw-hook" (autapomorphy) and that this structure is "apparently absent" in Tarsophlebiidae. The observations we have made support this hypothesis. Nevertheless, such structures could be hard to observe in some fossils. As example, the species of the modern libellulid genus *Oligoclada* have very reduced ventro-apical claw-hook that could be hardly visible in fossils. The basal odonopterid family Meganeuridae have simple tarsal claws, thus this structure could 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 suggests a position inclusive of the Odonata for the Tarsophlebiidae.

#### (C) Male secondary genital apparatus of second and third abdominal segment

Recent and fossil Panodonata have a complex secondary genital apparatus of second abdominal segment that has no homology in other insects. Such a structure can be observed in some Protozygoptera with the body preserved (pers. obs.), but it is not possible to interpret and compare correctly the secondary genital apparatus of the Protozygoptera to those of the recent

Zygoptera, Epiophlebiidae and Anisoptera. The secondary genital apparatus of these three lineages strongly differ but these differences concern structures that are nearly impossible to interpret in fossil specimens, even if very well preserved and closely related to well known recent taxa.

Bechly (1996) indicated that the Odonata have their "male vesicula spermalis more advanced and anteriorly elongated" (synapomorphy). After the present observations, this structure is indeed distinctly shorter and not anteriorly elongated in Tarsophlebiidae (Fig. 1A). Nevertheless, this structure remains unknown in Protozygoptera and all the more inclusive lineages within Odonoptera. Thus, it is not possible to primarily polarize this character by outgroup comparison. However, from the viewpoint of evolutionary biology the vesicula originated as sternal outgrowth and therefore a shorter vesicula would have to be considered as plesiomorphic.

The secondary male genital apparatus of Tarsophlebiidae turns out to be of high significance for the understanding of the evolution of odonate copulation. In the groundplan of Odonoptera (e.g., *Namurotypus sippeli* Brauckmann & Zessin, 1989) there was no secondary genital apparatus but primitive primary genitalia that were most similar to those of wingless insects who still deposit external spermatophores (Bechly *et al.* 2001). Such a deposition of spermatophores, first on the substrate and later on the basal male abdominal venter, is also the only possibility for the evolution of the complex secondary apparatus and mating wheel in Odonata (Bechly *et al.* 2001). In extant Odonata the secondary genital apparatus is without doubt homologous and is always composed by the following substructures: a pair of hamuli anteriores, a pair of hamuli posteriores, an unpaired median sternal process of segment II (ligula), and a pouchlike and unpaired median sternal outgrowth of segment III (vesicula spermalis). All these structures are present in all three major subgroups of Recent Odonata, viz. Zygoptera, Epiophlebiidae and Anisoptera. It is a most curious phenomenon that in each of these three groups a different structure of this apparatus is

developed as copulatory organ for sperm transfer and removal of foreign sperm (ligula in Zygoptera, hamuli posteriores in Epiophlebiidae, and vesicula spermalis in Anisoptera). Based on the well established phylogenetic hypothesis that Zygoptera form the sister group of Epiproctoptera, which comprises the Epiophlebiidae and Anisoptera, a hypothetical groundplan of the secondary genital apparatus can be reconstructed:

1) Hamuli anteriores: they are platelike in Zygoptera and Anisoptera, but hooklike in Epiophlebiidae. The most parsimonious interpretation is that the state in Epiophlebiidae is derived, so that platelike hamuli anteriores belong to the common groundplan.

2) Hamuli posteriores: they are platelike and small in Zygoptera and Anisoptera, and greatly enlarged and modified as copulation organs in Epiophlebiidae. The most parsimonious interpretation again is that the state in Epiophlebiidae is derived, so that small platelike hamuli posteriores belong to the common groundplan.

3) Ligula: the ligula is simple and small in Epiophlebiidae and Anisoptera, but greatly enlarged, subsegmented, and modified as copulation organ in Zygoptera. It can be regarded as very probable that the ligula is derived from the processus caudalis of this segment, a posteromedian sternal process that is still present on other abdominal segments of Epiophlebiidae and Anisoptera (probably reduced in Zygoptera). This process is simple, small and unmodified, so that the state in Zygoptera would have to be considered as derived, by using these serial homologous structures as kind of "outgroup". Consequently, a small and simple ligula seems to belong to the common groundplan. Nevertheless, this structure remains unknown in more inclusive groups of Odonatoptera, viz. Protozygoptera, Triadophlebiomorpha, Protanisoptera, etc. Thus, it is not possible to propose a primary polarisation of this character on the basis of the outgroup comparison.

4) Vesicula spermalis: it is relatively short and unsegmented in Zygoptera, somewhat elongated but unsegmented in Epiophlebiidae, and greatly elongated, subsegmented and modified as copu-

lation organ in Anisoptera. The most parsimonious interpretation is that the state in Zygoptera is plesiomorphic. Therefore, a relatively short, unsegmented and unmodified vesicula would belong to the common groundplan.

To sum up, the secondary genital apparatus in the hypothetical reconstruction of the odonate groundplan includes small and platelike hamuli anteriores and posteriores, a small and simple ligula, and a short and unmodified vesicula spermalis. However, this groundplan reconstruction implies a surprising problem: there is no structure left that would be suited to function as a copulation organ for sperm transfer and sperm removal. If this reconstruction would be correct, one would be forced to make two assumptions: 1) the stemspecies of Odonata did not transfer liquid sperm and did not remove foreign sperm, but did only partly conceal a spermatophore in the vesicula that was fetched by the female from this place; and 2) the transfer of liquid sperm and the mechanism of sperm removal developed three times as parallelism in Zygoptera, Epiophlebiidae, and Anisoptera. The latter hypothesis would explain why very different and non-homologous structures were developed as functional penis in each of these groups. The assumption that any of these highly specialised organs represents the primitive condition would hardly be explainable from the viewpoint of evolutionary biology, because it would imply the reduction of a perfect organ for sperm transfer and removal, only to be subsequently replaced by another organ that fullfills the same function. This clearly would not make sense and can be considered as unlikely.

What does secondary genital apparatus of Tarsophlebiidae contribute to this discussion: the secondary genital apparatus of Tarsophlebiidae exactly agrees with the hypothetical groundplan reconstruction, and therefore strongly confirms the latter! Vice versa, the primitive secondary genital apparatus of Tarsophlebiidae could be congruent with the assumed inclusive position of this fossil group relative to all extant Odonata, but would also be compatible with a position at the very base of Epiproctoptera. However, the

fact that the vesicula spermalis is even shorter than in Zygoptera rather supports the former alternative. It is obvious that Tarsophlebiidae were unable to transfer liquid sperm or to remove foreign sperm during an internal copulation. Therefore, we here propose that Tarsophlebiidae did still transfer spermatophores that were attached within the vesicula spermalis and fetched by the female in wheel position. The other structures of the secondary genital apparatus most probably served as holding and guiding devices for the female ovipositor.

*(D) Male auricles*

Nel *et al.* (1993) misinterpreted the hamuli posteriors as possible epiproctophorid male auricles, as noted by Bechly (1996).

*(E) Male genital appendages*

In males of both *Tarsophlebia eximia* and *Turanophlebia vitimensis* n. sp., no median anal structure is visible thus the epiproctal process is certainly absent in Tarsophlebiidae, which could exclude them from Epiproctophora *sensu* Bechly (1996) if this structure would be primitively absent and not reduced. Rehn (2003: 193) considered that the “complete or nearly complete absence of the epiproct” is a “unique zygopteran apomorphy, that seemingly provides strong support for the monophyly of the suborder” but as this character is unknown in more inclusive groups (Protozygoptera, Triadophlebiomorpha, Protanisoptera, etc.), it is not possible to propose a correct primary polarization of this character. After the present phylogenetic analysis (see below), the absence of the epiproct would appear plesiomorphic, *contra* Rehn (2003).

In both Zygoptera and Epiproctophora, the cerci are always well developed. In *Tarsophlebia eximia*, the structures that were interpreted as two pairs of appendages by Nel *et al.* (1993) or Bechly (1996) correspond to the strongly sclerotized parts of the two appendages of *Turanophlebia vitimensis* n. sp. These two appendages strongly resemble the cerci of a Campterophlebiidae (Epiproctophora, Isophlebioidea) from the Mesozoic of China (Fleck & Nel 2002). Some

Anisoptera (Petaluridae) also have basally sclerotized and spatulate cerci but no Odonata have spatulate paraprocsts. Thus, these tarsophlebiid appendages are probably the cerci. Three interpretations of tarsophlebiid male genital appendages remain possible: 1) the Tarsophlebiidae have no developed paraprocsts and no epiproct. Thus they would have “lost” the paraprocsts (which are a groundplan feature of insects) but not yet developed the epiproctal process of Epiproctophora. The very strongly sclerotized cerci would fulfill the function of both paraprocsts and epiproct, for grasping the female during mating; 2) the paraprocsts are not visible on these fossils, hidden below the cerci. Nevertheless, nothing in these fossils supports this hypothesis; and 3) the tarsophlebiid appendages are uniquely shaped paraprocsts and the cerci are reduced. The loss of the cerci would then be a unique autapomorphy of the Tarsophlebiidae.

All three hypotheses concerning the paraprocsts would be compatible with any of the discussed phylogenetic positions for Tarsophlebiidae.

*(F) Hind wing discoidal cell*

Bechly (1996) proposed to consider the basal closure of the hind wing discoidal cell as a strict synapomorphy of the Odonata, not shared by the Tarsophlebiidae. Rehn (2003) also considered that the absence of the posterior part of arcus in Tarsophlebiidae is plesiomorphic. This character would support a very inclusive position for this family, as sister group of Odonata. After the present phylogenetic analysis (see below), the sister group relationship with the Epiproctophora implies the convergent closure of the discoidal cell in Zygoptera and Epiproctophora, or the loss of the closure of the discoidal cell in the Tarsophlebiidae, which are of course less parsimonious solutions than the former hypothesis. Nevertheless, the Tarsophlebiidae have developed a closed “pseudo-discoidal cell” that has the function of the close discoidal cell of the Odonata. The basal opening of the discoidal cell could be “correlated” with the development of this highly specialized structure.

*(G) Vein CuAb*

Fleck *et al.* (2003) reinterpreted the structure of the fusion of vein AA with vein CuA. In Protozygoptera, Zygoptera and Tarsophlebiidae, there is no postero-proximal branch CuAb of CuA (plesiomorphy). Such a branch is present in all Epiproctophora (the Steleopteridae being excluded, Fleck *et al.* 2001). This vein CuAb is fused with the distal part of AA in Epiohlebiidae, Heterophlebiomorpha and Anisoptera. These veins are more or less separated in Isophlebioptera. Thus, this character is congruent with a very inclusive position for the Tarsophlebiidae, either as sister group of Odonata or as sister group of Epiproctophora.

*(H) Nodal structures*

Bechly (1996) also characterized the Zygoptera by the following three potential synapomorphies in the wing venation, i.e. characters (1) “reduction of the terminal kink of the CP”, (2) “reduction of the nodal furrow”, and (3) “obliteration of the tubular sclerotized canal of ScP along the venter of the postnodal costal margin”. The Tarsophlebiidae and Epiproctophora have the contrary character states (see Fig. 5C and Nel *et al.* 1993). Bechly (1996) polarized these characters after the assumption that Tarsophlebiidae are the sister group of Odonata. The more inclusive clades Protanisoptera, Triadophlebiomorpha and Protozygoptera have the same states for characters (1) and (2) as Zygoptera (Nel *et al.* 2001; Huguet *et al.* 2002). The principle of parsimony suggests that the polarities of these characters are contrary to that proposed by Bechly (1996) and that the character states are plesiomorphic in Zygoptera. As he apparently neglected the works of Nel *et al.* (1993) or Huguet *et al.* (2002), Rehn (2003) ignored the state of these important characters (coded “?”) for the most inclusive clades of Odonatoptera (Geroptera, Meganisoptera, Protanisoptera, Protozygoptera, even Tarsophlebiidae) in his analysis. After the present analysis, these characters support the clade (Tarsophlebiidae + Sieblosiidae + Epiproctophora) (see below).

Concerning the third character, the situation is different because the distal wing margin is a

fusion of the three longitudinal veins CA, ScA and ScP (Bechly 1996). Consequently, the presence of the tubular sclerotized canal of ScP is probably a plesiomorphy. The Tarsophlebiidae and the Epiproctophora would share only one putative synapomorphy, i.e. “presence of a strong kink of CP aligned with nodal Cr”, “correlated” with “a strong nodal furrow”. While the state “ScP ventrally visible along costal margin” must represent a symplesiomorphy. The Sieblosiidae Handlirsch, 1906 also have the same structures proper to Epiproctophora (*contra* Nel & Paicheler 1994).

Note: in Tarsophlebiidae, the nodus is distally shifted (between 44 and 47% of wing length), as in Epiproctophora. In Sieblosiidae, it is in basal position as in Protozygoptera and Zygoptera (probable plesiomorphic state).

*(I) Vein CuP*

In the most inclusive lineages of the Epiproctophora, i.e. Epiophlebiidae, Isophlebioptera, Heterophlebioptera, the Anisoptera, Liassogomphidae Tillyard, 1935, some Gomphidae Rambur, 1842 and Aeshnidae Leach, 1815 (but less pronounced), the vein CuP is strongly curved and seems to begin on AA rather than on MP + Cu. The same character is present in Tarsophlebiidae. In Zygoptera (except the Cenozoic family Sieblosiidae Handlirsch, 1906), Protozygoptera and more inclusive groups of Odonatoptera, the vein CuP is straight, which is thus probably the plesiomorphic character state. Their curved CuP suggests close relationships between the Tarsophlebiidae, the Sieblosiidae, and the Epiproctophora. Within the Sieblosiidae, the CuP of the *Stenolestes* species, *Parastenolestes* Nel & Paicheler, 1994 and *Paraoligolestes* Nel & Escuillié, 1993 are of epiproctophorid type. The exact structure of CuP is still unknown in *Oligolestes* Schmidt, 1958 because of some preservation problems (Schmidt 1958; Nel & Escuillié 1993; Nel & Paicheler 1994). Bechly (1996) included the Sieblosiidae within the Zygoptera in a very inclusive position, close to the Eucaloptera Bechly, 1996. As we have seen above, the nodal structures of the Sieblosiidae are of epiproctophorid-type and not

of zygopterid-type. Bechly (1996) proposed the following venational synapomorphies of the Zygoptera, which could be potentially visible on the fossil Sieblosiidae:

1) “both wing pair distinctly stalked with a petiole that is at least somewhat longer than broad”. In the Sieblosiidae, the petioles are short, shorter than those of some Epiproctophora, Stenophlebiidae (Fleck *et al.* 2003). Furthermore, in the Calopterygidae, the petiole can be extremely short, but it is long in the “basal” calopterygid *Caliphaea* Hagen, 1859 and the calopterygid sister group Dicteriadidae. Also, the protozygopterid petioles are very long. This wing petiolation has been convergently acquired at least six times by very different groups of Odonoptera. Thus, it is highly homoplastic;

2) “both wing pair of identical shape and venation”. The Triadophlebiomorpha and Protozygoptera (sister group of Panodonata) have this character state as convergence. Thus, this character is homoplastic as well;

3) “on the ventral wing surface the posterior part of the basal brace (Ax0) is obliterated or covered by a rather extensive sclerotization of the wing base”. This character is unknown in Triadophlebiomorpha and Protozygoptera, thus its primary polarization is uncertain. Furthermore, this character occurs also in Anisoptera, Aeshnidae (*Aeshna cyanea* (Müller, 1764), *Cordulegaster boltoni* (Donovan, 1807), etc.), in which this structure is identical to what occurs in the Zygoptera *Mecistogaster linearis* Olivier, 1792 and *Pseudostigma* Selys, 1860. Lastly, in Sieblosiidae, this sclerotization is absent and Ax0 is in a rather distal position. Thus it is probably homoplastic;

4) “reduction of the long spines of the dorsal surface of the RP and MP”. This character cannot be observed on the available material of Sieblosiidae. Furthermore, in the Epiproctophora, Heterophlebiidae Needham, 1903, these spines are reduced: on very well preserved specimens from the Liassic of Bascharage (Grand-Duché-du-Luxembourg), the spines of RA and of the net of transverse veins are clearly visible but none is visible on RP and MP. In the Anisoptera, Liassogomphidae from the same outcrop, the spines of RP

and MP are clearly visible. Thus, these spines are absent on the RP and MP of the Heterophlebiidae. It is possibly “correlated” with the smaller diameters of these veins in these taxa. Also, in the recent Epiproctophora *Epiophlebia superstes* (Selys, 1889), there are very few and very small spines on RP. Thus, this character cannot be used to attribute the Sieblosiidae to the Zygoptera, it is homoplastic and of uncertain primary polarity, as it is unknown in Protozygoptera and more inclusive Odonoptera;

5) “significant increase of spine-density at the apical costal margin”. This character is unknown in the Triadophlebiomorpha and Protozygoptera, thus, its exact polarity remains unknown. Furthermore, the Sieblosiidae have no such increase (clearly visible on the very well preserved specimen MNHN-LP-R.10375 of *Stenolestes couletti* Nel & Papazian, 1986) (Nel & Escuillié 1992). The Tarsophlebiidae have no such increase either (visible on type specimen of *Turanophlebia anglicana* n. sp.), which could confirm the polarity assumed by Bechly (1996) if Tarsophlebiidae indeed represent the sister group of all crown-group Odonata. Other autapomorphies of the Zygoptera proposed by Bechly (1996) are not visible in the known specimens of Sieblosiidae.

In conclusion, the Sieblosiidae do not share any known unambiguous apomorphy with the Zygoptera. Furthermore, the sieblosiid nodal and CuP structures suggest closer affinities with the Epiproctophora than with the Zygoptera.

In addition to these potential synapomorphies, the Sieblosiidae have the arculus shifted basally in a position between Ax1 and Ax2. Nevertheless, it is very close to Ax2. In Zygoptera, the arculus is aligned with Ax2 or very slightly basally recessed. In Protozygoptera, the arculus is in a rather variable position but generally aligned with Ax2 or in a distal position. Furthermore, this potential synapomorphy of the Sieblosiidae with the Epiproctophora is in fact homoplastic, *contra* Rehn (2003: 201): 1) Fleck *et al.* (2003) described a Epiproctophora, Stenophlebiidae having the arculus aligned with Ax2, as in Zygoptera; 2) also, the Calopterygoidea, Dicteriadidae (*Heliocharis amazona* Selys, 1853) has its arculus

TABLE 1. — Matrix of taxa/characters used in the phylogenetic analyses (see Appendix 1).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Tarsophlebia</i>	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Epiophlebia</i>	1	1	1	0	1	1	1	1	1	1	0	0	0	1	0	1	1
<i>Calopteryx</i>	1	1	1	1	0	0	0	0	0	0	1	1	1	0	1	0	0
<i>Permolestes</i>	?	?	?	?	?	?	?	?	0	0	1	1	?	0	0	?	0
<i>Bellabrunetia</i>	1	1	1	0	0	0	1	1	1	1	0	0	0	1	0	1	1
<i>Lestes</i>	1	1	1	1	0	0	0	0	0	0	1	1	1	0	1	0	0
<i>Stenolestes</i>	0	0	?	?	?	?	0	?	0	0	?	?	?	?	0	?	?

closer to Ax1 than to Ax2; and 3) inversely, the arculus of the Anisoptera *Synthemis montaguei* Campion, 1921 is shifted well distally from Ax2. Rehn (2003) proposed the following two main synapomorphies for the Zygoptera (but he ignored the group Sieblosiidae): “head transversely elongate”; “eyes separated by more than their own width” Although deformed, the head of the Sieblosiidae are not very transversely elongate and their eyes are not so separated. Other characters he proposed are subject to numerous homoplasies or are unknown in the Panodonata sister group. The Sieblosiidae do not have the male anal angle of the Epiroctophora. They do not have any visible epiroctophorid vein CuAb either but there is no visible furrow at the point of fusion between AA and CuA, thus it is not possible to determine if they have a CuAb completely fused with AA as in modern Anisoptera or fossil Stenophlebiidae, or a CuAb absent, as in Tarsophlebiidae (Fleck *et al.* 2003). Thus, the Sieblosiidae are probably in a very inclusive position within the Epiroctophora.

#### (J) Other characters

1) In some Tarsophlebiidae, the arculus is between Ax1 and Ax2, in others, it is opposite to Ax2 or distal of Ax2. Thus, this character is nearly useless. 2) The eyes of *Tarsophlebia eximia* are more similar to those of the modern Anisoptera and Epiophlebiidae and Permo-Triassic Protozygoptera than to those of the Zygoptera, not strongly separated of more than their diameter. However, this could well be a symplesiomorphy,

because the widely separated eyes of Zygoptera could be “correlated” with the apomorphic hammer-shaped head of Zygoptera and therefore probably are derived rather than primitive.

3) The ocelli of *Tarsophlebia eximia* are more of “zygopterid” type rather than of “anisopterid” type, in equilateral triangle, with the lateral ocelli posteriorly rejected. Unfortunately, the polarities of these characters remain uncertain because the head structures are still unknown in Protanisoptera, Triadophlebiomorpha, and Protozygoptera. 4) Thoracic skewness. The skewness was probably more important in Tarsophlebiidae than in recent Zygoptera, Lestidae. The presence of a strong thoracic skewness in some Permian Protozygoptera (among others, in the holotype of *Permolestes gracilis* Martynov, 1932; Nel pers. obs.) suggests that this similarity with Zygoptera is not a synapomorphy but a symplesiomorphy, or at least be due to convergence. Note that Rehn (2003) erroneously indicated that the important thoracic skewness is a unique synapomorphy of the Zygoptera, but he ignored the structure of the thorax of the Protozygoptera and the work of Nel *et al.* (1993) who first established the important skewness of the Tarsophlebiidae.

5) “Subdiscoidal cross-vein” *sensu* Rehn (2003). Rehn (2003) amended the wing venation nomenclature of Riek & Kukalová-Peck (1984) as follows: he supposed that the transverse vein named “CuP” by Riek & Kukalová-Peck (1984) is the vein “CuA + CuP” and he named “subdiscoidal cross-vein” the transverse vein called “CuA” by Riek & Kukalová-Peck (1984). Rehn

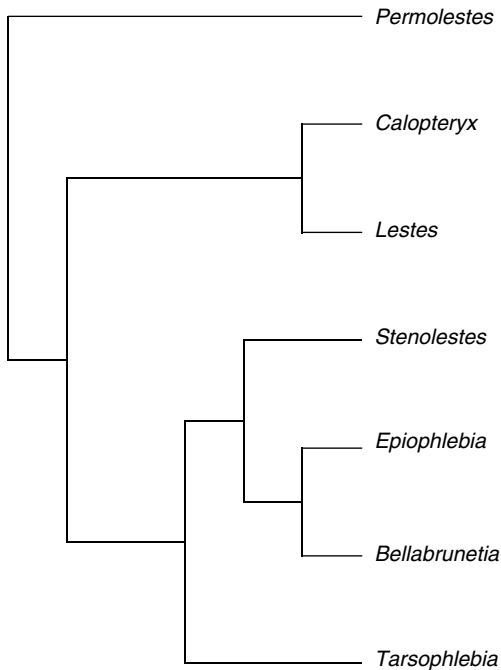


FIG. 9. — Most parsimonious tree T1 (obtained with PAUP4.0b10, Branch and Bound option), Consistency Index CI: 0.9375, CI excluding uninformative characters: 0.9231, Retention Index RI: 0.9375, and RC (RC = CI × RI): 0.8789.

(2003) apparently ignored the work of Nel *et al.* (1993) who confirmed the hypothesis of Riek & Kukalová-Peck (1984), after the study of the situation in *Isophlebia aspasia* Hagen, 1866 (Epiproctophora), in which there is no distal fusion between the vein AA + CuP and CuA (both *sensu* Riek & Kukalová-Peck 1984). Furthermore, the presence of the alleged “subdiscoidal cross-vein” is supposed to be one the two synapomorphies supporting the clade “Zygoptera + Epiprocta” *sensu* Rehn (2003) (= Zygoptera + Epiproctophora), but as this vein is in fact CuA, it is present in the more inclusive groups Protozygoptera and Triadophlebiomorpha. The character “CuA separating from MP at the point of fusion of MAb (“discoidal vein” *sensu* Rehn 2003) and aligned with it” is shared by the Tarsophlebiidae and Zygoptera + Epiproctophora, as already indicated in Nel *et al.* (1999). Thus, it cannot constitute a synapomorphy of the (Zygoptera + Epiproctophora).

6) Oblique vein “O” present. Rehn (2003: 201) considered that the presence of the oblique vein is a synapomorphy of the Epiproctophora (= former “Anisozygoptera” + Anisoptera, without the Tarsophlebiidae), with a convergency with the Zygoptera, Lestinoidea. Nel *et al.* (1993) and Fleck *et al.* (2003) demonstrated that this vein is absent in some Epiproctophora, Stenophlebiidae. Thus it is subject to more homoplasies than currently suspected. It is also present in the Tarsophlebiidae, as indicated in Nel *et al.* (1993) and the present paper, *contra* Rehn (2003).

## PHYLOGENETIC ANALYSIS

We made a computer phylogenetic analysis of the relationships of the Tarsophlebiidae, based on the set of characters discussed above. It is based on 17 characters, equally weighted and unordered (see Table 1 and Appendix 1). The taxa we considered are as follows: *Tarsophlebia* (Tarsophlebiidae), *Permolestes* Martynov, 1932 (Protozygoptera), *Epiophlebia* Calvert, 1903 (Epiproctophora, Epiophlebiidae), *Bellabrunetia* Fleck & Nel, 2002 (Epiproctophora, Isophlebiomorpha, i.e. anisopterid lineage), *Stenolestes* Scudder, 1895 (Sieblosiidae), *Lestes* Leach, 1815 (Zygoptera, Lestidae), and *Calopteryx* Leach, 1815 (Zygoptera, Calopterygidae). The analysis was made using the computer software PAUP4.0b10 (Swofford 1998), Branch and Bound option. *Permolestes* was chosen as outgroup. The analysis gave one more parsimonious tree T1: (*Permolestes* & (*Lestes* + *Calopteryx*) & [*Tarsophlebia* + (*Stenolestes* + (*Epiophlebia* + *Bellabrunetia*))]), with a length of the minimal trees of 16 steps, Consistency Index CI: 0.9375, CI excluding uninformative characters: 0.9231, Retention Index RI: 0.9375, and RC (RC = CI × RI): 0.8789 (see Fig. 9). Both clades Zygoptera and [*Tarsophlebia* + (*Stenolestes* + (*Epiophlebia* + *Bellabrunetia*))] are present. The clade [*Tarsophlebia* + (*Stenolestes* + (*Epiophlebia* + *Bellabrunetia*))], corresponding to the (Tarsophlebiidae + Epiproctophora), is supported by the apomorphic character states “11 (0) terminal kind of CP in nodus not reduced”, “12 (0) nodal fur-



TABLE 2. — Implications of the studied structures on the phylogenetic position of the Tarsophlebiidae. Abbreviations: **CuAb**, first posterior branch of Cubitus Anterior; **CuP**, Cubitus Posterior.

Character	Phylogenetic implication	Remark
A, number of adult tarsomeres	Basal to Odonata	Uncertain observations
B, tarsal claws	Basal to Odonata	Uncertain observations
C, male vesicular spermalis	Basal to Odonata	
D, male auricle	Erroneous	
E, male genital appendages	Basal to Odonata or to Epiproctophora	
F, hind wing discoidal cell	Basal to Odonata	
G, vein CuAb	Basal to Odonata or to Epiproctophora	
H, nodal structure	Basal to Epiproctophora	
I, vein CuP	Basal to Epiproctophora	

row not reduced”, and by the two unpolarized characters “4 (0) male ligula simple and small”, “13 (0) tubular sclerotized canal of ScP not obliterated”. The clade (*Stenolestes* + (*Epiophlebia* + *Bellabrunetia*)) is supported by the character state “17 (1) thoracic skewness not very important”. The clade (*Epiophlebia* + *Bellabrunetia*), representing the true Epiproctophora, is supported by the five apomorphies “7 (1)”, “8 (1)”, “9 (1)”, “10 (1)”, and “16 (1)”. The clade (*Lestes* + *Calopteryx*) is supported by the character state “15 (1) eyes of adults strongly separated”, unknown in *Triadophlebia*. The analysis does not support the clade [Tarsophlebiidae + (Zygoptera + Epiproctophora)] proposed by Bechly (1996) and Rehn (2003).

After the present observations, the Tarsophlebiidae seem to have four-segmented tarsi, which is probably a plesiomorphic condition because the Meganeuridae have five-segmented tarsi. Thus, their position in the same clade with the Epiproctophora would imply that the presence of three-segmented tarsi in both Zygoptera and Epiproctophora is either due to a convergence or that the “four-segmented tarsi” of the Tarsophlebiidae corresponds to an autapomorphy. The fact that they have extremely particular, very long tarsi would support this last hypothesis. Nevertheless, we tested the hypothesis that the Protozygoptera also had four-segmented tarsi

(state “0” for character “1”). We obtained the same parsimonious tree T1 as above. We also tested the hypothesis that the reduction of the nodal furrow is “correlated” with the reduction of the terminal kink of the CP in nodus, by excluding the character “12” from the analysis. We obtained the same results as above.

The phylogenetic implications of the characters examined above are summarized in the Table 2. They are rather favouring a derived position of Tarsophlebiidae close to the Epiproctophora than a position basal to the (Zygoptera + Epiproctophora) (Appendix 2). Nevertheless, the phylogenetic position still remains a matter of discussion, partly because of the uncertain primary polarization of some characters currently used to define the Zygoptera as a monophyletic group. The problem of the position of Tarsophlebiidae is related to a better relative characterization of Zygoptera and Epiproctophora. Also, this analysis clearly demonstrates the weakness of our knowledge on several characters that cannot be correctly polarized because of the lack of information in the Permo-Triassic Protozygoptera and Triadophlebiomorpha. The same remark can be made for the phylogeny proposed by Rehn (2003) in which no less than 34 characters per 112 (about 30%) are unknown in all the most inclusive (out)groups. Part of solution may come through the discovery of better preserved material

of Tarsophlebiidae and above all, a better knowledge of the body structures of the Protozgyopera, Triadophlebiomorpha, and Protanisoptera.

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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* Böblingen, Special Volume 1, 341 p.
- 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* Böblingen, Special Volume 2, 402 p.
- BECHLY G. 1997. — New fossil Odonata from the Upper Triassic of Italy, with a redescription of *Italophlebia gervasutti*, and a reclassification of Triassic dragonflies. *Rivista del Museo Civico di Scienze Naturale E. Caffi* Bergamo 19: 31-70.
- BECHLY G. 1999. — *Phylogeny and Systematics of Fossil Dragonflies (Insecta: Odonatoptera) with Special Reference to some Mesozoic Outcrops*. Ph.D. thesis, Eberhard-Karls-Universität Tübingen, Germany, x + 755 p.
- BECHLY G., BRAUCKMANN C., ZESSIN W. & GRÖNING E. 2001. — New results concerning the morphology of the most ancient dragonflies (Insecta: Odonatoptera) from the Namurian of Hagen-Vorhalle (Germany). *Journal of Zoological Systematics and Evolutionary Research* Berlin 39: 209-226.
- CARLE F. L. 1982. — The wing vein homologies and phylogeny of the Odonata: a continuing debate. *Societas Internationalis Odonatologica, Rapid Communications* Utrecht 4: 1-66.
- CARPENTER F. M. 1992. — Superclass Hexapoda, in MOORE R. C. & KAESLER R. L. (eds), *Treatise on Invertebrate Paleontology*. The Geological Society of America and the University of Kansas, Boulder, Colorado, (R), Arthropoda 4, 3/4, xxii + 655 p.
- FLECK G. & NEL A. 2002. — The first isophlebioid dragonfly (Odonata: Isophlebioptera: Camptero-phlebiidae) from the Mesozoic of China. *Palaeontology* 45: 1123-1136.
- FLECK G. & NEL A. 2003. — Revision of the Mesozoic family Aeschnidiidae (Odonata: Anisoptera). *Zoologica* 153: 1-180.
- FLECK G., NEL A., BECHLY G. & MARTÍNEZ-DELCLÒS X. 2001. — Revision and phylogenetic affinities of the Jurassic Steleopteridae Handlirsch, 1906 (Insecta: Odonata: Zygoptera). *Insect Systematic Evolution* 32: 285-305.
- FLECK G., BECHLY G., MARTÍNEZ-DELCLÒS X., JARZEMBOWSKI E. A., CORAM R. & NEL A. 2003. — Phylogeny and classification of the Stenophlebioptera (Odonata, Epiproctophora). *Annales de la Société entomologique de France* (N.S.) 39 (1): 55-93.
- FRASER F. C. 1955. — Note on *Tarsophlebiopsis mayi* Tillyard (Odonata: Tarsophlebiidae). *Psyche* 62: 134, 135.
- 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.
- HAGEN H. A. 1862. — Über die Neuropteren aus dem lithographischen Schiefer in Bayern. *Palaeontographica* 10: 96-145.
- HAGEN H. A. 1866. — Die Neuroptera des lithographischen Schiefers in Bayern. *Palaeontographica* 15: 57-96.
- HANDLIRSCH A. 1906-1908. — *Die fossilen Insekten und die Phylogenie der rezenten Formen. Ein Handbuch für Paläontologen und Zoologen*. Engelman V.W., Leipzig, 1430 p.
- HENNIG W. 1966. — *Phylogenetic Systematics*. University of Illinois Press, Urbana, 263 p.
- HENNIG W. 1969. — *Die Stammesgeschichte der Insekten*. Kramer, Frankfurt am Main, 436 p.
- HENNIG W. 1981. — *Insect Phylogeny*. Wiley & Sons, New York, xxii + 514 p.
- HUGUET A., NEL A., MARTÍNEZ-DELCLÒS X., BECHLY G. & MARTINS-NETO R. 2002. — Preliminary phylogenetic analysis of the Protanisoptera (Insecta: Odonatoptera). *Geobios* 35: 537-560.
- JARZEMBOWSKI E. A. 1990. — Early Cretaceous zygopteroids of Southern-England with the description of *Cretacoenagrion alleni*, gen. nov., spec. nov. (Zygoptera, Coenagrionidae, "Anisozygoptera": Tarsophlebiidae, Euthemistidae). *Odonatologica* 19: 27-37.
- MALZ H. & SCHRÖDER H. 1979. — Fossile Libellenbiologisch betrachtet. *Kleine Senckenberg-Reihe* Frankfurt am Main 9: 1-46.
- MARTÍNEZ-DELCLÒS X. & NEL A. 1996. — Discovery of a new Protomyrmeleontidae in the Upper Jurassic from Germany (Odonatoptera, Odonata, Archizygoptera). *Archaeopteryx* 14: 67-73.

- MARTYNOV A. V. 1927. — Jurassic fossil insects from Turkestan. 7. Some Odonata, Neuroptera, Thysanoptera. *Bulletin de l'Académie des Sciences de l'URSS, Classe des Sciences mathématiques et naturelles* 20 (13-14): 757-768.
- MEUNIER F. 1896. — Les Agrionides fossiles des musées de Munich et de Harlem. *Annales de la Société entomologique de France* 65: 30-35.
- MOSTOVSKI M. B. & MARTÍNEZ-DELCLÒS X. 2000. — New Nemestrinoidea (Diptera: Brachycera) from the Upper Jurassic-Lower Cretaceous of Eurasia, taxonomy and palaeobiology. *Entomological Problems* 31: 137-148.
- NEL A. & ESCUILLIÉ F. 1992. — Présence du genre *Stenolestes* Scudder, 1895 dans les laminites oligocènes du Revest-des-Brousses (Lubéron, France) (Insecta, Odonata, Zygoptera, Lestoidea, Sieblosiidae). *L'Entomologiste* 48: 1-13.
- NEL A. & ESCUILLIÉ F. 1993. — Découverte d'un nouveau genre de Sieblosiidae dans le Miocène supérieur de l'Ardèche (France) (Odonata, Zygoptera, Lestoidea, Sieblosiidae). *Nouvelle Revue d'Entomologie* (N.S.) 10: 233-242.
- NEL A. & PAICHELER J.-C. 1994. — Les Lestoidea (Odonata, Zygoptera) fossiles : un inventaire critique. *Annales de Paléontologie* 80: 1-59.
- NEL A. & JARZEMBOWSKI A. É. 1996. — Description and revision of some dragonflies ("Anisozygoptera") from the Lower Cretaceous of England (Odonata: Stenophlebiidae, Campterophlebiidae?, Epiophlebiidae, Euthemistidae). *Cretaceous Research* 17: 87-96.
- NEL A., GAND G., FLECK G., BETHOUX O. & LAPEYRIE J. 1999. — *Saxonagrion minutus* nov. gen. et sp., the oldest damselfly from the Upper Permian of France (Odonatoptera, Panodonata, Saxonagrionidae nov. fam.). *Geobios* 32 (6): 883-888.
- NEL A., MARTÍNEZ-DELCLÒS X., PAICHELER J.-C. & HENROTAY M. 1993. — Les "Anisozygoptera" fossiles. Phylogénie et classification (Odonata). *Martinia* Bois d'Arcy, numéro hors série 3: 1-311.
- NEL A., BETHOUX O., BECHLY G., MARTÍNEZ-DELCLÒS X. & PAPIER F. 2001. — The Permian-Triassic Odonatoptera of the "protodonate" grade (Insecta: Odonatoptera). *Annales de la Société entomologique de France* 37: 501-525.
- PRITYKINA L. N. 1968. — Strekozy Karatau (Odonata) [= Dragonflies from Karatau (Odonata)], in PANFILOV D. V. (ed.), *Yurskie nasekomye Karatau*. [= *Fossil Insects from Karatau*]. Academy of Sciences of the SSSR, Nauka, Moscow: 26-55 (in Russian).
- PRITYKINA L. N. 1977. — [New dragonflies from Lower Cretaceous deposits of Transbaikalia and Mongolia], in Fauna, flora i biostratigrafiya mezozoya i kaynozoya Mongolii [= Fauna, flora and biostratigraphy of the Mesozoic and Cenozoic of Mongolia]. *Trudy Sovmestnaya Sovetsko-Mongol'skaya Paleontologicheskaya Ekspeditsiya* Moscow 4: 81-96 (in Russian).
- REHN A. C. 2003. — Phylogenetic analysis of higher-level relationships of Odonata. *Systematic Entomology* 28 (2): 181-239.
- RIEK F. & KUKALOVA-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.
- SCHMIDT E. 1958. — Bemerkungen über Lestiden III. (Odonata). *Decheniana* 111: 1-7.
- SWOFFORD D. 1998. — *PAUP\**. *Phylogenetic Analysis Using Parsimony (\* and Other Methods)*, Version 4. Sinauer, Sunderland, Massachusetts, software.
- TILLYARD R. J. 1923. — *Tarsophlebiopsis mayi* n. gen. et n. sp., a dragon-fly, found in the body-chamber of a Corallian ammonite. *Geological Magazine* 60: 146-152.
- TILLYARD R. J. 1925. — The British Liassic dragonflies. *British Museum (Natural History), Fossil Insects* London 1: 1-39.
- TILLYARD R. J. & FRASER F. C. 1940. — A reclassification of the order Odonata based on some new interpretations of the venation of the dragonfly wing. *The Australian Zoologist* 9: 124-396.
- ZHERIKHIN V. V. & GRATSHEV V. G. 1993. — Obrieniidae, fam. nov., the oldest Mesozoic weevils (Coleoptera, Curculionoidea). *Paleontological Journal* 27 (1A): 50-69.
- ZHERIKHIN V. V., MOSTOVSKI M. B., VRANSKY P., BLAGODEROV V. A. & LUKASHEVICH E. D. 1999. — The unique Lower Cretaceous locality Baissa and other contemporaneous fossil insects sites in North and West Transbaikalia. *AMBA Projects Publications No. AMBA/AM/PFCIM98/1.99: Proceedings of the 1<sup>st</sup> Palaeontological Conference*, Moscow, 1998: 185-191.

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## APPENDIX 1

List of characters used in the phylogenetic analysis (see Table 1). Abbreviations: **AA**, Analis Anterior; **CP**, Costa Posterior; **CuA**, Cubitus Anterior; **CuAb**, first posterior branch of Cubitus Anterior; **CuP**, Cubitus Posterior; **MP + Cu**, Median Posterior + Cubitus; **ScP**, Subcosta Posterior.

1. Number of adult tarsomeres: 4 or more, **0**; 3, **1**.
2. Tarsal claws: without ventral-apical claw-hook, **0**; with a ventro-apical claw-hook, **1**.
3. Male vesicula spermalis: short and not anteriorly elongated, **0**; long and anteriorly elongated, **1**.
4. Male ligula: simple and small, **0**; greatly enlarged, subsegmented, and modified as copulation organ, **1**.
5. Male hamuli posteriors: platelike and small, **0**; greatly enlarged and modified as copulation organs, **1**.
6. Male hamuli anteriores: platelike, **0**; hooklike, **1**.
7. Male auricles: absent, **0**; present, **1**.
8. Male epiproctal process: absent, **0**; present, **1**.
9. Hind wing discoidal cell: basally opened, **0**; basally closed, **1**.
10. Postero-proximal branch CuAb of CuA: absent, **0**; present, even if more or less fused with AA, **1**.
11. Terminal kink of the CP in nodus: not reduced, **0**; reduced, **1**.
12. Nodal furrow: not reduced, **0**; reduced, **1**.
13. Tubular sclerotized canal of ScP along the venter of the postnodal costal margin: not obliterated, **0**; obliterated, **1**.
14. Vein CuP: straight, **0**; strongly curved and seems to begin on AA rather than on MP + Cu, **1**.
15. Eyes of adults: not strongly separated of more than their diameter, **0**; strongly separated, **1**.  
Remark: we prefer to consider on the character that concerns the distance between the eyes because the character "head transversely elongate" is "geometrically" correlated to it.
16. Ocelli: "zygoterid" type, in equilateral triangle, with the lateral ocelli posteriorly rejected, **0**; "anisopterid" type, not in equilateral triangle, **1**.
17. Thoracic skewness: very important, **0**; not very important, **1**.

## APPENDIX 2

List of synapomorphies of Tarsophlebiidae and Odonata (= synapomorphies of Panodonata Bechly, 1996). Abbreviations: **Ax0**, **1**, **2**, primary antenodal cross-veins; **CP**, Costa Posterior; **CuA**, Cubitus Anterior; **IR2**, intercalary vein of radial area; **MAB**, first posterior branch of Median Anterior; **MP**, Median Posterior; **RP**, Radius Posterior; **ScP**, Subcosta Posterior.

Presence of a costal triangle as broad and strong sclerotisation of the basal costal margin (even the most basal part of the CP is completely fused to the costal margin); the distal discoidal vein MAB (= distal side of discoidal cell) and the subdiscoidal vein (origin of the CuA on MP) are aligned and dorsally enforced by a strong sclerotisation, so that this structure appears to cross the vein MP and the concave fold along this vein (formation of a "discal brace" *sensu* Carle [1982], which is not an autapomorphy of Zygoptera, *contra* Bechly [1995]; this discal brace is aligned with the arculus in the groundplan, but this character state was only retained in some taxa with an open discoidal cell and in the fore wings of *Eptophlebia*); the midfork (first fork of RP and base of IR2) is shifted basally, with the RP3/4 generally arising basal of the subnodus (reversed in some Platycnemidoidea) and RP2 arising close to the subnodus (in the groundplan); more derived type of nodus, with a kink in ScP; the oblique basal brace (still present in Protanisoptera and Protozygoptera) is transformed into a transverse "basal bracket" Ax0 which looks like a primary antenodal cross-vein. Note that the presence of two strong primary antenodal cross-veins Ax1 and Ax2 is a synapomorphy also present in some Protozygoptera since they are aligned and enforced by a chitinous bracket in some well preserved specimens (Upper Permian of Russia, specimen No. 1/276, PIN), although difficult to observe in some fossils (Nel pers. obs.); pterostigma distinctly braced by an oblique post-subnodal cross-vein beneath the basal margin of the pterostigma; presence of a tracheated "lestine oblique vein" between RP2 and IR2 (secondarily absent in Caloptera, Coenagrionomorpha and Oreopterida); in the median space (= basal space) the convex vestige of the Media-stem ("vestigial CuA" *sensu* Fraser 1957) is suppressed since it is fused with the cubital stem to a common medio-cubital-stem (the alleged presence of this vestige in *Tarsophlebiopsis* is either an individual aberration, teratology, or preservational artifact), convergent to some Protanisoptera, Triadophlebiomorpha and Protozygoptera.