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# Phylogeny and classification of the Stenophlebioptera (Odonata: Epiproctophora)

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**Résumé – Phylogénie et classification des Stenophlebioptera (Insecta, Odonata, Epiproctophora) –** Les Juraheterophlebiidae, nouvelle famille de la lignée "hétérophlebioïde", les Henrotayiidae, nouvelle famille de la lignée "anisoptéroïde", les Prostenophlebiidae et les Liassostenophlebiidae, nouvelles familles de Stenophlebioptera, et trois nouveaux genres et espèces de Stenophlebiidae sont décrits du Mésozoïque d'Allemagne, Espagne, Angleterre, Kazakhstan et Mongolie. Les positions phylogénétiques des familles Erichschmidiidae et Gondvanogomphidae sont discutées. Un essai d'analyse phylogénétique des Anisopteromorpha est proposé. Ces nouvelles données étendent significativement nos connaissances sur la distribution paléogéographique des Stenophlebioptera et des Epiproctophora.

**Abstract** – The Juraheterophlebiidae, new family of the "heterophlebioid" lineage, the Henrotayiidae, new family of the "anisopteroid" lineage, the Prostenophlebiidae and the Liassostenophlebiidae, new families of the Stenophlebioptera, and three new genera and species of the Stenophlebiidae are described from the Mesozoic of Germany, Spain, England, Kazakhstan, and Mongolia. The phylogenetic positions of the families Erichschmidiidae and Gondvanogomphidae are discussed. A tentative phylogenetic analysis of the Anisopteromorpha is proposed. This significantly extends our knowledge on the palaeogeographical distribution of the Stenophlebioptera and the Epiproctophora ("dragondamselflies").

The family Stenophlebiidae was established by Needham (1903) and Handlirsch (1908) for the species *Stenophlebia amphitrite* (Hagen, 1866), *S. casta* (Hagen, 1862) and *S. latreillei* (Germar, 1839) (= *S. latreillei* + *S. aequalis* (Hagen, 1862) + *S. phryne* (Hagen, 1862), *sensu* Handlirsch, 1908) from the Upper Jurassic of Eichstätt - Solnhofen, Germany. Pritykina (1980) erected the superfamily Stenophlebioidea for the sole family Stenophlebiidae and included it in the suborder "Lestomorpha" (= Zygoptera). Nel *et al*. (1993) considered Stenophlebiidae to be the sister group of the Epiophlebiidae Muttkowski, 1910, and both families as the sister group of the (Anisoptera + "Heterophlebioidea") + "Isophlebioidea". Bechly (1995) agreed with this hypothesis and included both families in the superfamily Epiophlebioidea as part of the Epiproctophora (= "Anisozygoptera" + Anisoptera) *sensu* Bechly (1995). Bechly (1996) erected the Stenophlebioptera Bechly, 1996 (= Gondvanogomphidae Bechly, 1996 + Stenophlebiidae) and transferred this group into the Trigonoptera (= Stenophlebioptera + Anisoptera), itself considered to be the sister group of the Heterophlebioptera (= Heterophlebioidea *sensu* Nel *et al*. 1993) within the Anisopteromorpha (= Heterophlebioptera + (Stenophlebioptera + Anisoptera)) (Bechly 1996).

The following taxa have been added to the Stenophlebiidae since Handlirsch (1908): *Stenophlebia eichstaettensis* (Nel *et al*., 1993), *Stenophlebia karatavica* Pritykina, 1968, *Stenophlebia corami* Nel & Jarzembowski, 1996, *Sinostenophlebia zhanjiakouensis* Hong, 1984, *Prostenophlebia jurassica* Nel & Martínez-Delclòs, 1993 (in Nel *et al*. 1993).

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The present study of new taxa from the Lower and Upper Jurassic and Lower Cretaceous of Germany, Spain, England Kazakhstan and Mongolia demonstrates that the diversity of this family was higher than supposed during the Mesozoic. Also the revision of the holotype of *Prostenophlebia jurassica* Nel *et al.*, 1993 shows that some errors of interpretation were made in the original description and that a new description was necessary.

**Systematic Palaeontology** – We follow the wing venation nomenclature of Riek & Kukalová-Peck (1984), amended by Kukalová-Peck (1991), Nel *et al.* (1993) and Bechly (1996). The higher classification of fossil and extant Odonatoptera is mainly based on the new phylogenetic system of Bechly (1996).

## Order **ODONATA** Fabricius, 1792

## Suborder TRIGONOPTERA Bechly, 1996

## Clade **Heterophlebioptera** Bechly, 1996

**Included taxa** – Myopophlebiidae Bode, 1953, Liassophlebiidae Tillyard, 1925, Heterophlebiidae Needham, 1903, Juraheterophlebiidae n. fam. (Nel *et al.* 1993; Bechly 1996).

**Problem of the monophyly of the Heterophlebioptera** – The analysis of stenophlebiid phylogenetic affinities would be facilitated by an accurate analysis of the relationships between major clades within the Anisopteromorpha. Following new discoveries herein, the clade Heterophlebioptera Bechly, 1996 (= Heterophlebioidea *sensu* Nel *et al.* (1993)) no longer appears well supported. It was characterized by the following synapomorphies that we discuss below:

**(1)** Unique unicellular "anal loop" (Nel *et al.* 1993) lying beneath the subdiscoidal cell and ventrally closed by CuAb that is parallel to AA and thus directed towards the wing base instead of the posterior wing margin". Nel *et al.* (1993) and Bechly (1996) suggested that this structure is probably not homologous with the anisopteroid anal loop.

In "heterophlebioid" taxa, and more generally in the Isophlebioptera, Epiophlebiidae, and Anisopteromorpha, the vein CuA is clearly forked into two branches, CuAb directed towards wing base and CuAa directed towards wing apex, and AA secondarily reaches CuAb at right angle. This structure is clearly visible in the myopophlebiid specimens MNHN-DHT R10384 (female paratype of *Paraheterophlebia marci* Nel & Henrotay, 1993, in Nel *et al.* 1993) (fig. 1), MNHN-DHT R10385 (holotype of *Paraplagiophlebia loneuxi* Nel & Henrotay, 1993, in Nel *et al.* 1993) (fig. 2). It is also clearly visible on some Liassophlebiidae (*Liassophebia jacksoni* Zeuner, 1962) that CuA is divided into the same veins CuAa and CuAb, independently of AA that reaches CuA before this bifurcation at right angle and the vein AA + CuA is distally aligned with basal part of CuA, not with AA, as in Anisoptera (fig. 3). In the holotypes of *Liassophlebia magnifica* Tillyard, 1925 and *Liassophlebia pseudomagnifica* Whalley, 1985, the main branch of AA vanishes in the partial fusion of the "anal loop" with the subdiscoidal space.

Furthermore, the long basal free part of CuAb before its fusion with the branches of AA, present in "heterophlebioid" taxa, is also present in Isophlebioptera (Selenothemistidae, Architemistidae, Campterophlebiidae, Isophlebiidae, etc.). In Isophlebioptera, CuA is also forked, independently of AA. This last vein never reaches CuAb in many of these taxa (many Campterophlebiidae and Isophlebiidae).

The "heterophlebioid" anal loop is anteriorly and distally closed by the main branch of AA (tentatively interpreted as the distal part of CuP by Pfau 2000), basally closed by a strong secondary branch of AA (tenta-

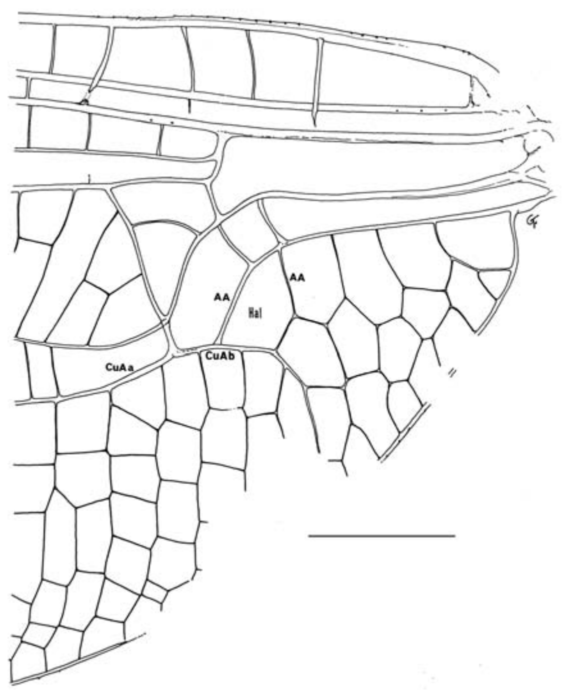



**Figure 1**
Hindwing base of *Paraheterophlebia marci* Nel & Henrotay, 1993, specimen MNHN-DHT R10384 (IB 959a,b) (Myopophlebiidae). AA, analis anterior; CuAa and CuAb, basal branches of cubitus anterior; Hal, "heterophlebioid" anal loop (scale bar represents 2 mm).

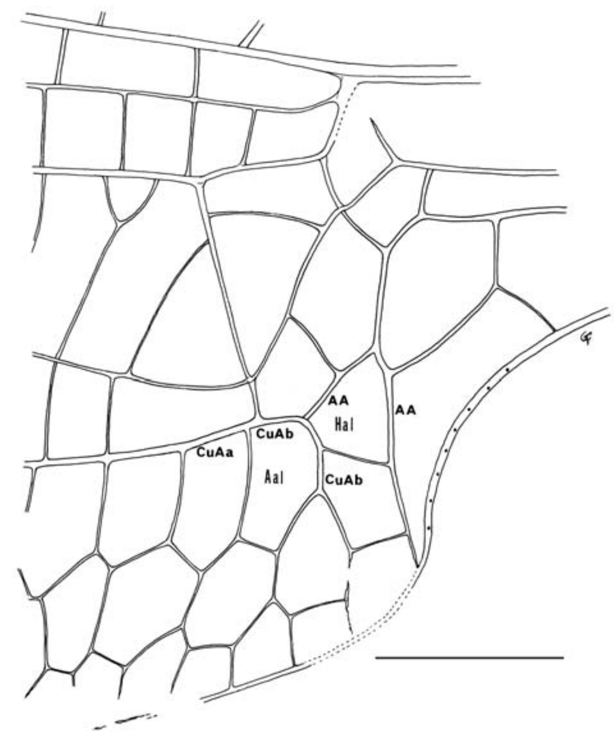



**Figure 2**
Hindwing base of holotype specimen MNHN- DHT R10385 of *Paraplagiophlebia loneuxi* Nel & Henrotay, 1993 (Myopophlebiidae). AA, analis anterior; CuAa and CuAb, basal branches of cubitus anterior; Hal, "heterophlebioid" anal loop; Aal, "anisopteroid" anal loop. Note the curved long free CuAb (scale bar represents 2 mm).

tively interpreted as the distal part of AA by Pfau 2000), and posteriorly by CuAb and/or the continuation of this secondary branch of AA. CuAb is long before its contact with the two branches of AA that surround the "anal loop". Such a structure is also present in *Juraheterophlebia kazakhstanensis* n. gen., n. sp. (Juraheterophlebiidae n. fam.). The only difference is the more basal position of the "anal loop" than in "heterophlebioid" taxa, related to a longer CuAb.

Note that in the Myopophlebiidae *Paraplagiophlebia loneuxi* Nel & Henrotay, 1993 (in Nel *et al.* 1993), the "heterophlebioid" anal loop is posteriorly open (only posteriorly closed by a weak cross-vein) and CuAa has a very basal posterior branch defining a different cell, which is in a more distal position and corresponds to a primitive posteriorly open "anisopteroid" anal loop (fig. 2), also reduced in the Henrotayiidae n. fam.

In the anisopteroid lineage (*sensu stricto*) and the stenophlebioid lineage, the fork of CuA into CuAa and a long CuAb is not longer visible, but the very base of CuAb is still visible at the point of fusion of AA with CuA. Such structure is clearly visible in Liassic Liassogomphidae, and still present but less visible in some modern Gomphidae or Petaluridae and fossil Aeschnidiidae (Fleck *et al.* 2002) (figs. 3-4). In nearly all Anisoptera, the posterior part of discoidal triangle and the crossing between CuA and AA are membranous. The main branch of CuA reaches the main branch of AA at right angle, and the heterophlebioid CuAb is rudimentary, nearly completely reduced. The end of the main branch of AA no longer makes an angle with CuAb (as in Heterophlebioptera and in some Stenophlebiidae (*S. katatavica* and forewing of *S. latreillei*) but is aligned with basal free part of CuAb, with no clear limit between the two veins. Thus this structure is not homologous to the fusion of AA with CuA in the Zygoptera, due to the absence of vein CuAb in Zygoptera, as it can be seen from: (1) ontogeny, i.e. in Zygoptera, the anal trachea directly reaches the CuA trachea but, in Anisoptera, it reaches the trachea corresponding to CuAb (see


**Figure 3**
Hindwing base of a Liassogomphidae, *Phtitogomphus angulatus* (Handlirsch, 1939), specimen IB'8a,b (Henrotay coll., Laboratory of Palaeontology, MNHN, Paris). AA, analis anterior; 1: CuAb; 2: (AA + CuA)a and 3: (AA + CuA)b, branches of distal part of AA + CuA; Hal, "heterophlebioid" anal loop; Aal, "anisopteroid" anal loop. Note the still visible long CuAb, fused with AA (scale bar represents 5 mm).

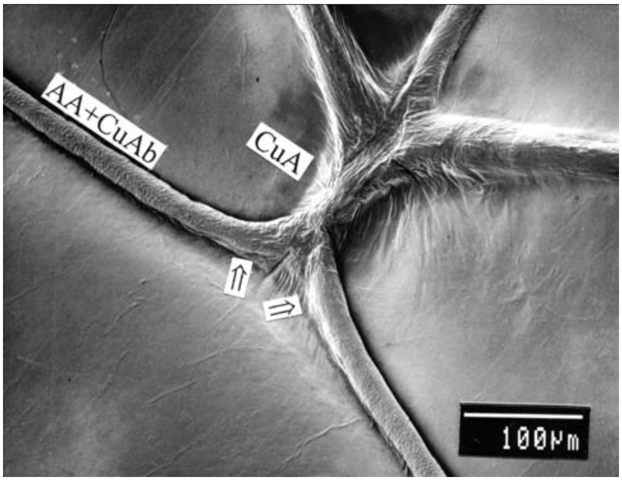



**Figure 4**
Electron scanning photograph of the hindwing of an extant *Gomphus vulgatissimus* (Anisoptera: Gomphidae), area of fusion between AA and CuA, the arrows indicate the two residual branches CuAa and CuAb.

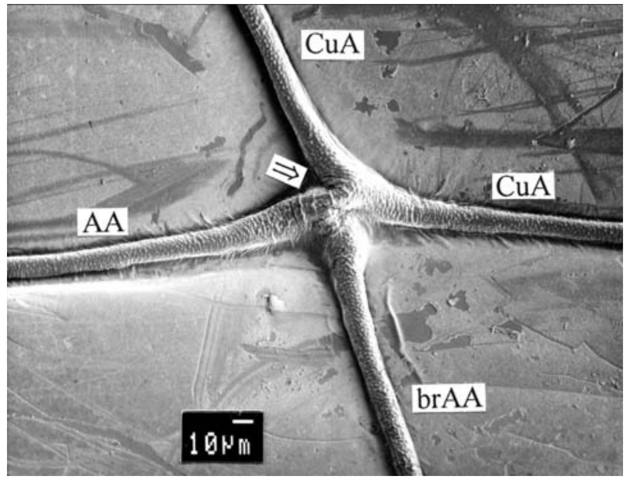



**Figure 5**
Electron scanning photograph of the hindwing of an extant *Coeliccia cyanomelas* (Zygoptera: Coenagrionoidea: Platycnemididae), area of fusion between AA and CuA, brAA: posterior branch of AA, the arrow indicates the furrow between AA and CuA.

Needham 1903: pl. 31, fig. 1-2; Tillyard 1915); (2) AA is secondarily fused on CuA in the Zygoptera, at least in *Pseudolesmus mandarinus* McLachlan, 1870 and *Calopteryx* spp. (but less visible) (both Calopterygidae), *Lestes sponsa* (Hansemann, 1823) (Lestidae), *Coenagrion puella* (Linnaeus, 1758), *Pyrrhosoma nymphula* (Sulzer, 1776) and *Coeliccia cyanomelas* Ris, 1912 (both Coenagrionoidea) (figs. 4-8), and probably in Tarsophlebiidae.

In the Epiophlebiidae, CuAb is still present as a true vein directed towards wing base as in Heterophlebioptera but it is very short and AA is secondarily branching on it as in a Myopophlebiidae (fig. 9). Because of its wing petiolation, the hindwing venation of a male *Epiophlebia* superficially resembles that of a Zygoptera: Lestidae but the structure of AA and CuAb is completely different.

As there is a fusion of AA with CuA, the two anisopteroid veins currently named “CuAa” and “CuAb” are not homologous to those of the “heterophlebioid” and stenophlebioid taxa and should be named (AA + CuA)a and (AA + CuA)b (fig. 3). The vein (AA + CuA)b corresponds to the first posterior branch of CuAa of the Myopophlebiidae *Paraplagiophlebia loneuxi* (fig. 2). The “anisopteroid” anal loop is not homologous to the “heterophlebioid” anal loop but to the more distal small cell of *Paraplagiophlebia*. In Anisoptera: Liassogomphidae, the “heterophlebioid” anal loop is still present but reduced and posteriorly open as the true “anisopteroid” anal loop (see fig. 3).

In the Stenophlebiidae, the “heterophlebioid” anal loop is smaller than in “heterophlebioid” families, even reduced and/or posteriorly open (probably in relation to the wing petiolation in *Hispanostenophlebia* n. gen. and *Cretastenophlebia* n. gen.). The vein AA is not secondarily reaching CuAb, but is fused and more or less aligned with it (clearly visible on the hindwing of *Stenophlebia latreillei*, fig. 10), even if there is still a weak distal free part of CuAb below the “heterophlebioid” anal loop in *S. karatavica* and the forewings of *S. latreillei*. Thus, we consider that the Stenophlebiidae have a reduced CuAb, aligned with distal end of AA, of “anisopteroid” type.

We conclude that: (a) the “heterophlebioid” anal loop is present in Stenophlebiidae and in Anisoptera (ground plan); (b) this “heterophlebioid” anal loop is not homologous to the “anisopteroid” anal loop; (c) the basal position of the “heterophlebioid” anal loop is related to the long free part of CuAb, which is a plesiomorphic condition, lost in Anisoptera; (d) the main difference between Heterophlebioptera and Anisoptera is due to a different mode of fusion of AA with CuA, basal of the division of CuA into CuAa and CuAb in “heterophlebioid” groups.

Character **(1)**, as defined above, is not an autapomorphy of the Heterophlebioptera but a synapomorphy of the whole clade Anisopteromorpha Bechly, 1996, i.e. the “heterophlebioid”, stenophlebioid and anisopteroid ground plan.

**(2)** Forewings briefly petiolated (Nel *et al.* 1993).

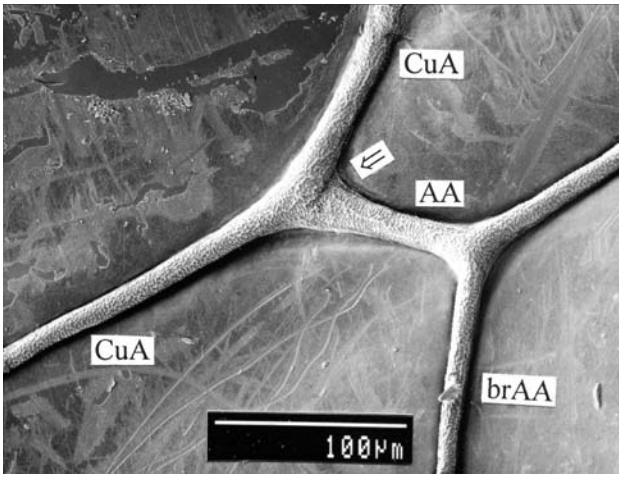



**Figure 6**
Electron scanning photograph of the hindwing of an extant *Lestes sponsa* (Zygoptera: Lestidae), area of fusion between AA and CuA, brAA: posterior branch of AA, the arrow indicates the direct furrow between AA and CuA.

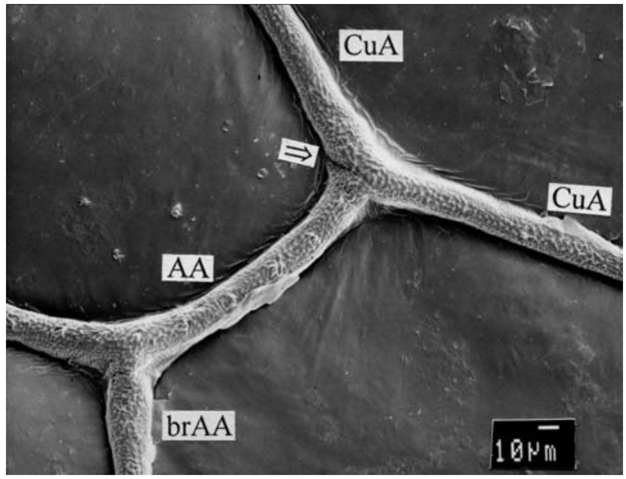



**Figure 7**
Electron scanning photograph of the hindwing of an extant *Pyrrhosoma nymphula* (Zygoptera: Coenagrionidae), area of fusion between AA and CuA, brAA: posterior branch of AA, the arrow indicates the furrow between AA and CuA.

The wing petiolation is a highly homoplastic character within the Epiproctophora. Thus, this character is of uncertain polarity and of little use. Furthermore, some Stenophlebiidae also have a short petiolation of the forewing. The petiolation is only slightly more pronounced in the Heterophlebioptera than in the Anisoptera: Liassogomphidae, and therefore might even represent a symplesiomorphy.

**(3)** Subdiscoidal cell of the hindwing with a convex curved or angulated posterior margin (Nel *et al.* 1993).

The subdiscoidal space has such a structure in some Isophlebioptera (Selenothemistidae, Architemistidae). Furthermore, this space is poorly defined in many Heterophlebioptera (see above).

**(4)** Unique shape of the forewing discoidal cell that is very transverse and narrow (Bechly 1996).

More precisely, the "heterophlebioid" forewing discoidal cell has the following features: (a) a distinct angle between MA and MAb; (b) a strongly bent MP + CuA; (c) an acute angle between MP + CuA and MAb; (d) long basal part of MA and MAb; (e) the discoidal cell may be open or closed, depending on the species (even on the specimens!) within the "heterophlebioid" families.

Character (a) is not confined to "heterophlebioid" taxa but it is also present in stenophlebioid and anisopteroid taxa. It is absent in *Paraheterophlebia marci* Nel & Henrotay, 1993 (Myopophlebiidae). This character corresponds to the division of the discoidal cell into a triangle and a hypertriangle. It is probably a synapomorphy of the Anisopteromorpha, with, maybe, the Myopophlebiidae excluded (see the phylogenetic analysis below). The corresponding plesiomorphic state is the alignment of the basal part of RP + MA, basal part of MA, and MAb, present in Triadophlebiomorpha, Tarsophlebiidae, Isophlebioptera (except the highly specialized Isophlebiidae), some Zygoptera (see Nel *et al.* 2001).

Character (b) is also present in stenophlebioid and anisopteroid taxa as well as Tarsophlebiidae, some Isophlebioptera (hindwing of the Campterophlebiidae *Adelophlebia* Pritykina, 1980), and Epiophlebiidae (but less pronounced in these two last groups), although absent in Zygoptera. Thus, either it is plesiomorphic or a specialization that would support the Epiproctophora clade.

Character (c) is also present in Tarsophlebiidae, Epiophlebiidae and Stenophlebiidae, thus it is probably a plesiomorphy for the Odonata (Bechly 1996, 1998) or of the Epiproctophora.

Character (d) is also present in Stenophlebiidae and thus is not a strict "heterophlebioid" synapomorphy. Furthermore, the basal part of MA is short in the Myopophlebiidae *Paraheterophlebia marci*. The main difference between the "heterophlebioid" families and the stenophlebioid forewing discoidal cell is the fact that in the former it is not divided into a triangle and a hypertriangle. Also, there is a more distinct angle between the

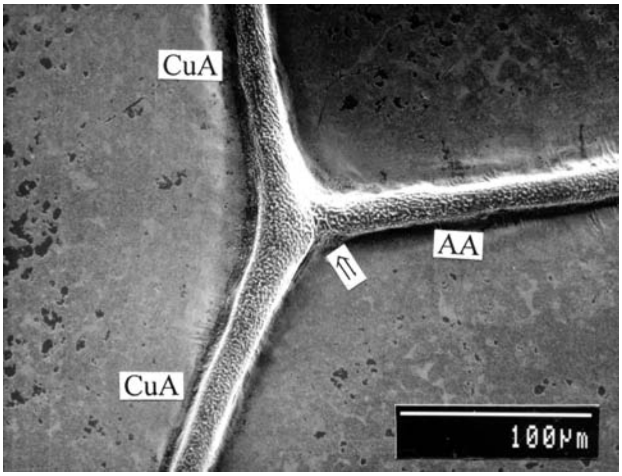



**Figure 8**
Electron scanning photograph of the hindwing of an extant male *Psolodesmus mandarinus* (Zygoptera: Calopterygidae), area of fusion between AA and CuA, the arrow indicates the furrow between AA and CuA.

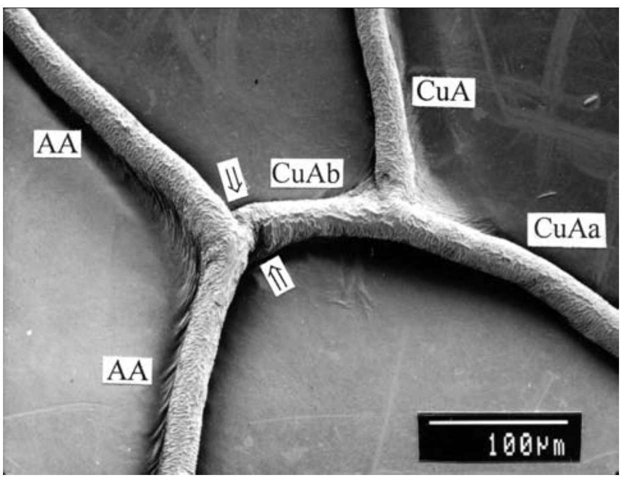



**Figure 9**
Electron scanning photograph of the hindwing of an extant male *Epiophlebia superstes* (Epiophlebiidae), area of fusion between AA and CuA, the arrows indicate the furrow between AA and CuA.

veins MA and MAb in Stenophlebioidea than in the "heterophlebioid" families.

**(5)** Strong "tendency" towards the development of a second incomplete arcular veinlet in the hindwings, and a single incomplete arcular veinlet in the forewings (but the basal closure of the forewing discoidal cell is still very variable, in many specimens being completely open or completely closed) (Bechly 1996). This character is variable in the "heterophlebioid" taxa and thus too weak as a single character for a large clade.

In conclusion, the potential synapomorphies of the putative Heterophlebioptera proposed by Nel *et al.* (1993) and Bechly (1996) are either plesiomorphies or synapomorphies of the Anisopteromorpha. After this preceding re-evaluation of the phylogenetic evidence, the monophyly of the group Heterophlebioptera is not supported by strict synapomorphies.

After the new phylogenetic analysis (see below), the clade Heterophlebioptera *sensu* Nel *et al.* (1993) or Bechly (1996) (= Myopophlebiidae + (Liassophlebiidae + (Juraheterophlebiidae + Heterophlebiidae))) is only supported by the character "hindwing subdiscoidal space foot-shaped, 33 (state 1)", also present in the *Stenophlebia* spp., *Cretastenophlebia*, and the (Liassogomphidae + (Aeschnidiidae + modern Anisoptera)). Thus, this study confirms that we can neither exclude the monophyly, nor the paraphyly of the Heterophlebioptera. The present result needs confirmation after a detailed analysis of the phylogenetic relationships of the species attributable to the Heterophlebioptera. Note that the Henrotayiidae n. fam. superficially resembles the "heterophlebioid" families, although it falls near the Anisoptera, after our phylogenetic analysis (see below).

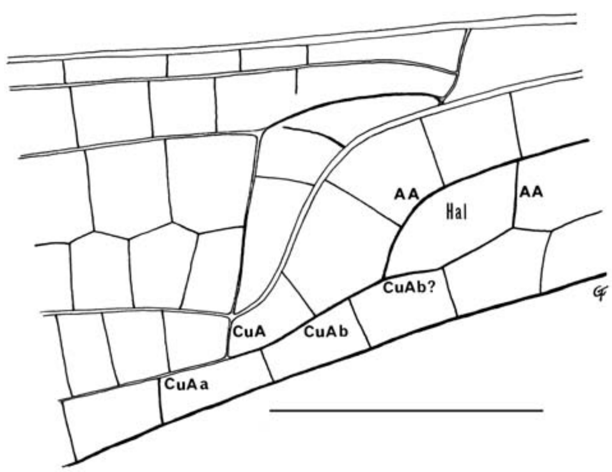



**Figure 10**
Discoidal area of left forewing of *Stenophlebia latreillei* (Germar, 1839), specimen 1870/VII/35, Museum of Munich (scale bar represents 3 mm).

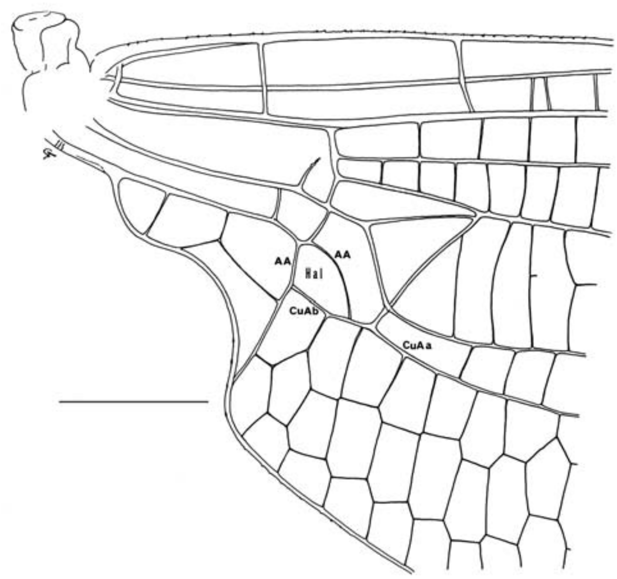



**Figure 11**
Hindwing base of *Heterophlebia buckmani* (Brodie, 1849), specimen IB 1004a,b (Heterophlebiidae) (scale bar represents 2 mm).

## Family **JURAHETEROPHLEBIIDAE** n. fam.

**Type genus** – *Juraheterophlebia* n. gen.

**Diagnosis** – (1) wing long but not falked; (2) discoidal cell divided into a free equilateral transverse triangle and a free quadrangular hypertriangle; (3) angle between MAa and MAb distinctly more than 90°; (4) subdiscoidal space broad, foot-shaped, of "heterophlebiid" type (see figs. 11-12); (5) AA strongly curved before subdiscoidal space; (6) a typical "heterophlebioid" anal loop, anal area narrow; (7) wing long petiolated; (8) Ax1 and Ax2 close, with no secondaries between them; (9) no secondary antenodal cross-veins between C and ScP, distal of Ax2; (10) nodal Cr not very oblique, short, without any cross-veins reaching it; (11) subnodus well aligned with nodal Cr, not very oblique, with no cross-veins reaching it; (12) pterostigma relatively long, not basally shifted; (11) pt-brace absent; (13) oblique vein "O" present in a basal position; (14) a long Mspl in postdiscoidal space; (15) no supplementary veinlet below subnodus, just basal RP2, between RP and IR2; (16) CuA long, reaching posterior wing margin well distal of nodus; (17) two rows of cells between C and RA distal of pterostigma; (18) pterostigma covering few cells; (19) CuAa and CuAb perfectly aligned.

After the phylogenetic analysis (see below), this taxon falls as sister group of the Heterophlebiidae, from which it mainly differs in its well petiolated hindwing and longer free part of CuAb. This Upper Jurassic taxon represents the youngest known representative of the Liassic "heterophlebioid" lineage. *Juraheterophlebia* superficially resembles *Prostenophlebia* Nel & Martínez-Delclòs, 1993 (RP2 not aligned with subnodus, presence of a long Mspl, pterostigma shape, wing petiolation). These characters are either homoplastic or plesiomorphies. Their structures of discoidal and subdiscoidal areas are different.

## Genus ***Juraheterophlebia*** n. gen.

**Type species** – *Juraheterophlebia kazakhstanensis* n. sp.

**Etymology** – After the Jurassic age of the material and genus *Heterophlebia*.

### ***Juraheterophlebia kazakhstanensis*** n. sp.
(figs. 12-13)

**Holotype** – Specimen PIN 2297/11, Arthropod Laboratory, Palaeontological Institute, Moscow, Russia.

**Etymology** – After Kazakhstan.

**Stratum typicum** – Upper Jurassic, Callovian-Kimmeridgian or Oxfordian-Kimmeridgian (Zherikhin & Gratshev 1993; Mostovski & Martínez-Delclòs 2000).

**Locus typicus** – Karatau, Chimkent region, Southern Kazakhstan, C.E.S.

**Description** – Impression of a nearly complete hindwing. Length, about 43 mm; width, 10.0 mm (distal of nodus); distance between nodus and base, 16.7 mm; between arculus and base, 5.7 mm; between arculus and nodus, 11.0 mm; RP separating from RP + MA closer to bend of MA than to base of RP + MA; posterior part of arculus (bdcv), between MA and MP + Cu not aligned with anterior part; CuP separating from MP + Cu and fused with AA at end of petiole, opposite Ax1, well basal of arcu-

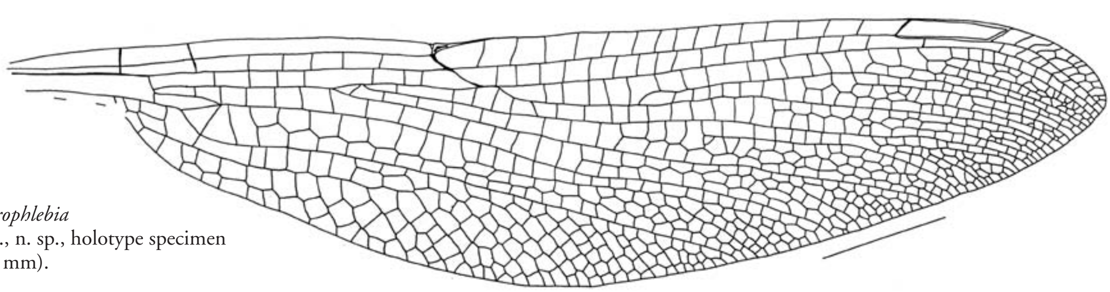


**Figure 12**
Hindwing of *Juraheterophlebia kazakhstanensis* n. gen., n. sp., holotype specimen (scale bar represents 5 mm).

**Figure 13**
Photograph of the hindwing of *Juraheterophlebia kazakhstanensis* n. gen., n. sp., holotype specimen.

lus; MA divided into MAa and MAb, at an angle of 120°; MAa basally nearly straight but distally slightly undulate; MAb straight; median and probably submedian spaces free of cross-veins; discoidal space divided into a nearly equilateral, transverse free discoidal triangle and a longitudinal free hypertriangle, separated by a cross-vein stronger than the others, beginning at bend of MP + CuA, and fused with MAb in costo-distal angle of discoidal space; discoidal triangle broad, 1.5 mm long, 1.0 mm wide, length of its costal side, 1.5 mm, of distal side, 1.4 mm, of posterior side, 1.2 mm; hypertriangle subtriangular, 2.6 mm long, 0.4 mm wide at base; subdiscoidal space broad, nearly identical to that of Heterophlebiidae (see above and Nel *et al.*, 1993), 3.3 mm long, 1.2 mm wide; AA strongly curved and angular, with a strong posterior branch, enclosing a unicellular "anal loop" of "heterophlebioid" type, well basal of discoidal triangle; anal margin not angular (female specimen?); CuA separating from MP in posterior angle of discoidal triangle and reaching AA at a right angle; CuA (+ AA) long but distally zigzagged and disappearing, with about six or seven strong posterior branches and intercalary longitudinal veins between them; basal free part of CuA relatively long (0.5 mm); CuA (+ AA) reaching posterior margin opposite nodus; area between MP and posterior wing margin large, with numerous secondary veins; base of wing not well preserved but distinctly petiolated, petiole more than 4 mm long and 2.1 mm wide; anal area narrow, with one or two rows of cells; seven or eight rows of cells between CuA and posterior wing margin; postdiscoidal area basally narrow with two rows of cells and distally widened; a concave Mspl and a long secondary zigzagged longitudinal convex vein parallel to MP, beginning two cells after discoidal triangle; MP and RP3/4 straight; nodus well preserved, vein Cr between nodus and RA quite oblique but not well aligned with general trend of ScP; subnodus (Sn) long and oblique; base of RP2 one cell distal of end of Sn; no supplementary veinlet just basal of base of RP2, between RP and IR2; antenodal area well preserved; primary antenodal cross-veins distinctly stronger than secondaries, 2.8 mm apart; arculus between primary antenodals, slightly closer to Ax1 than to Ax2; no secondary antenodal cross-veins between ScP and C, five antenodal cross-veins of second rank between ScP and RA, distal of Ax2; no secondary antenodals between the two primaries; 15 postnodal cross-veins, not aligned with the subpostnodals; pterostigma elongate, 3.6 mm long, 0.6 mm wide, covering one and a half cells and one cross-vein, not shifted basally; pterostigmal brace absent; area between C and RA distal of pterostigma broadened with two rows of cells; bases of RP3/4 and IR2 between nodus and arculus, closer to nodus (about 2.5 mm for IR2 and 3.8 mm for RP3/4) than to arculus; one cell between these bases; oblique vein "O" present, in a proximal position, only two cells distal of base of RP2; area between MA and RP3/4 slightly widened. IR1 apparently branching on RP2, not zigzagged; numerous long supplementary longitudinal veins between main veins; more veins and cells in apical half than in basal half of wing, with venation closer in distal half than in basal half.

## Clade **Anisoptera** *sensu lato*
## (= Henrotayiidae + Liassogomphidae + Aeschnidiidae + modern Anisoptera)

## Family **HENROTAYIIDAE** n. fam.

**Type genus** – *Henrotayia* n. gen.

**Diagnosis** – (1) discoidal triangle and hypertriangle of "primitive" shapes, similar to those of the Heterophlebiidae, i.e. hypertriangle pentagonal and triangle broad transverse; (2) subdiscoidal space not foot-shaped; (3) AA reaching CuAb as in Anisoptera, not at right angle as in "heterophlebioid" taxa; (4) "heterophlebioid" anal loop rudimentary; (5) "anisopoteroid anal loop" absent; (6) no secondary antenodal cross-veins between C and ScP, as in Heterophlebiidae; (7) postdiscoidal area narrower along posterior wing margin than the areas between CuA and MP and between MA and RP3/4; (8) a long gap free of cross-veins between RP and MA basal of RP3/4.

**Discussion**. Some characters of the Henrotayiidae n. fam. appear plesiomorphic (relative widths of the areas between CuA and MP, between MA and RP3/4 and between MA and MP; shape of discoidal triangle and hypertriangle) but some very derived (fusion of CuAb with AA of "anisopteroid" type). Although the Henrotayiidae are probably closely related to the Anisoptera, their phylogenetic position remains somewhat uncertain (see the phylogenetic analysis below).

### ***Henrotayia*** n. gen.

**Type species** – *Henrotayia marci* n. sp.

**Diagnosis** – That of the family.

**Etymology** – After Dr Michel Henrotay, in recognition to his contributions to Palaeoentomology.

## *Henrotayia marci* n. sp.
(fig. 14)

**Material** – Holotype specimen MNHN-DHT R55234a,b (IBMH 16a,b), Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris, France.

**Etymology** – After the latinised first name of Marc Henrotay, son of Michel Henrotay.

**Stratum typicum** – Lower Toarcian, Upper Liassic.

**Locus typicus** – Bascharage, Grand-Duché-du-Luxembourg.

**Description** – A complete hindwing, 32.0 mm long, 8.7 mm wide, just distal of nodus; distance from base to arculus, 4.3 mm, from arculus to nodus, 9.7 mm, from nodus to pterostigma, 10.6 mm, from nodus to apex, 17 mm; median and submedian spaces free of cross-veins; strongly curved CuP just distal of level of Ax1, closing subdiscoidal space; discoidal space divided by a rather weak curved vein into a broad transverse free triangle and a broad pentagonal free hypertriangle; costal side of discoidal triangle 0.9 mm long, distal side 1.2 mm long, basal side 1.1 mm long; costal side of hypertriangle 1.1 mm long, distal side 0.5 mm long, posterior side 1.2 mm long, basal side 0.5 mm long; subdiscoidal space divided into two cells by a cross-vein, but not foot-shaped; AA strongly curved at the base of subdiscoidal space; anal area broad with two rows of cells between AA and posterior wing margin; no anal angle; AA with only weak posterior branches; basal free part of CuA long, 0.5 mm long; no angle between AA and CuAb, these veins being aligned, as in Anisoptera, but a small structure, 0.1 mm long, that could correspond to a relictual CuAb, is visible 0.1 mm before the fusion of AA with CuA; no strong posterior branch (AA + CuA)b (see fig. 14), thus there is no "anisopteroid-anal loop"; the "heterophlebioid-anal loop" is not well defined below the angle of AA; distal CuA (+ AA) with numerous weak posterior branches and reaching posterior margin distal of nodus; five or six rows of cells between CuA and posterior wing margin; area between CuA and MP and area between MA and RP3/4 greatly widened distally, both distinctly wider than postdiscoidal area along posterior wing margin; a short basal gap without cross-veins in the area between CuA and MP; postdiscoidal area with two rows of cells just distal of discoidal triangle, narrower in its mid part and widened distally, the two primary antenodal cross-veins Ax1 and Ax2 stronger than secondaries, 3.2 mm apart, with one secondary cross-vein between them in the area between C and ScP; no secondary antenodal cross-vein between C and ScP distal of Ax2; eight secondary antenodals of second row between ScP and RA, distal of Ax2; arculus between Ax1 and Ax2, closer to Ax1; RP and MA well separated in the arculus; 14 cross-veins in the area between RA and RP, basal of subnodus; a long gap without cross-veins in the area between RP and MA, basal of RP3/4, 5.6 mm long; bases of RP3/4 and IR2 nearly midway between arculus and nodus, base of RP3/4 is 4.7 mm distal of arculus; base of IR2 1.6 mm distally; Bq space with seven cross-veins; nodal Cr distinctly oblique, less than that of a Heterophlebiidae but more than that of an Anisoptera; subnodus distinctly oblique; base of RP2 aligned with subnodus; oblique vein "O" two cells, 0.8 mm, distal of base of RP2; 17 postnodal cross-veins, not aligned with the 14 postsubnodal cross-veins; pterostigma elongate, 3.3 mm long and broad, not basally recessed, covering at least about three cells; pterostigmal brace strong and aligned with basal margin of pterostigma; base of IR1 6.1 mm, 10 cells distal of base of RP2; IR1 not zigzagged, well defined and with a strong curve below the pterostigma; area between IR2 and RP2 distinctly wider than that between IR2 and RP3/4 along posterior wing margin.

## Clade STENOPHLEBIOPTERA Bechly, 1996

**Included taxa** – Liassostenophlebiidae n. fam., Prostenophlebiidae n. fam., Stenophlebiidae Needham, 1903. We exclude the Gondwanogomphidae Bechly, 1996 from the Stenophlebioptera.

Position of the Gondvanogomphidae and Sonidae. Bechly (1996) included the fossil family Gondvanogomphidae in the Stenophlebioptera and also added the Sonidae Pritykina, 1986 to the Stenophlebioidea, but Bechly *et al.* (1998) considered that this hypothesis is weakly supported. Lohmann (1996) suggested that the "Sonidae" belong to the stem-group of Exophytica. Bechly (1999 in litt.) tentatively considered them as

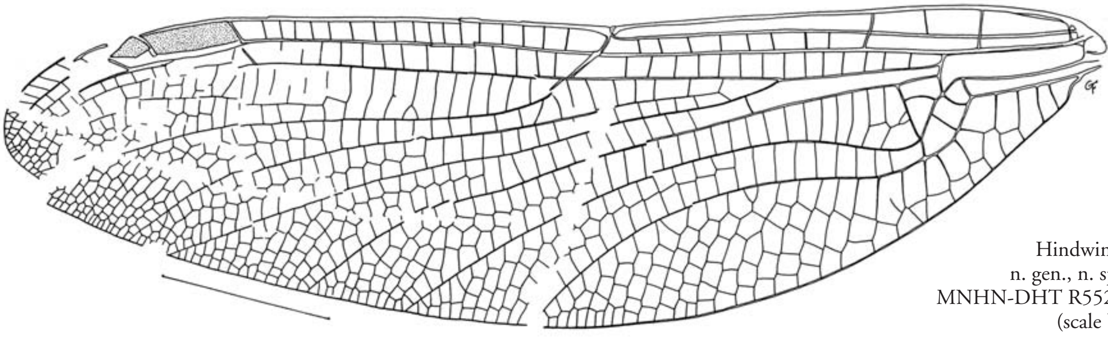


**Figure 14**
Hindwing of *Henrotayia marci* n. gen., n. sp., holotype specimen MNHN-DHT R55234a,b (IBMH 16a,b) (scale bar represents 5 mm).

**Figure 15**
Photograph of the hindwing of *Henrotayia marci* n. gen., n. sp., holotype specimen MNHN- DHT R55234a,b (IBMH 16a,b) (scale bar represents 5 mm).

junior synonyms of the Aeschniididae. After Fleck *et al.* (2002), the Sonidae are not aeschnidiids but Anisoptera of uncertain position.

Bechly (1996) proposed the following autapomorphies of the Stenophlebioptera: (1) IR2 and RP3/4 arising close together, correlated with a very long and narrow bridge space; (2) base of RP2 not strongly aligned with subnodus (more probably a plesiomorphy); (3) cubito-anal area of hindwings reduced, thus both wings of similar shape.

Character (1) is also present in at least Tarsophlebiidae, some Isophlebioptera (Asiopteridae), some Heterophlebioptera (*Heterophlebia buckmani* (Brodie, 1849), *Juraheterophlebia* n. gen.), and even some Gomphidae. Furthermore, if RP3/4 and IR2 are basally parallel to their bases very close together in *Gondvanogomphus* Schlüter & Hartung, 1982, it is not the case in many Stenophlebiidae (specimen 1870.VIII.35 of *Stenophlebia latreillei* (Germar, 1839) among others). Character (2) is also very frequently present in taxa of other groups (some Anisoptera: Gomphomacromiidae (*Gomphomacromia* Brauer, 1864) and Libellulidae (*Nannothemis* Brauer, 1868) and in many Isophlebioidea, among other). In *Stenophlebia latreillei*, RP2 is aligned with the subnodus in the forewing and not aligned in the hindwing. Character (3) is also present in *Gondvanogomphus* but not in various *Stenophlebia* spp. (specimen 1960/I/311 of *Stenophlebia phryne* (Hagen, 1862), see Nel *et al.*, 1993). Since all these alleged autapomorphies have to be rejected, there remains no argument favouring a sister group relationship between the Gondvanogomphidae and the Stenophlebiidae. In particular, the Gondvanogomphidae lack several synapomorphies of the Stenophlebiidae (stenophlebiid diagnostic characters (1), (3) and (4) listed below). Nevertheless, *Gondvanogomphus* has a division of the forewing discoidal cell into a triangle and a hypertriangle, corresponding to the main synapomorphy of the Trigonoptera Bechly, 1996 (= Stenophlebioptera + Anisoptera sensu *lato*, see below). It cannot be excluded that the Gondvanogomphidae are indeed related to Stenophlebiidae, but at present we still have to consider the Gondvanogomphidae as Trigonoptera of uncertain position.

**New diagnosis** – The Stenophlebioptera are characterized, within the Trigonoptera, by the following synapomorphies, after the present phylogenetic analysis (see below): (1) nodal Cr very oblique, i.e. angle (Cr, RA) > 140°; (2) subnodus Sn very oblique, with or without cross-veins reaching it; (3) CuAa with a broad area between the two most distal posterior branches (it may happen that CuAa has only two strong posterior distal branches, with secondary veins between them, and a short basal branch); (4) presence of straight supplementary longitudinal veins in the areas between IR2 and MP, near posterior wing margin (recessed in *Liassostenophlebia*, maybe due to its small size). Character (1) is also present in *Erichstmidtia* Pritykina, 1968, taxon of uncertain position (see below). Character (3) is reversed in *Prostenophlebia*. Note that all Stenophlebioptera, except *Liassostenophlebia*, have a long straight "Mspl" and a long straight convex longitudinal secondary vein in the postdiscoidal area, convergently present (but less clearly defined) in *Juraheterophlebia*. These structures may be recessed in *Liassostenophlebia*, correlated to its very small size.

## Family **LIASSOSTENOPHLEBIIDAE** n. fam.

**Included taxa** – *Liassostenophlebia* n. gen.

**Diagnosis** – (1) forewing small and rounded, not falcate; (2) discoidal cell divided into a free equilateral triangle and a free triangular hypertriangle; (3) angle between MAa and MAb slightly more than 90°; (4) subdiscoidal space not foot-shaped; (5) AA not strongly curved below subdiscoidal space; (6) presence of an "heterophlebioid" anal loop; (7) Ax1 and Ax2 well spaced, with numerous secondaries between them; (8) nodal Cr slightly oblique, and rather short; (9) subnodus well aligned with nodal Cr, oblique, with two cross-veins reaching it; (10) pterostigma relatively short, not shifted basally; (11) pt-brace absent or weak and displaced distally (?); (12) oblique vein "O" present but in a distal position; (13) no Mspl, but a long zigzagged secondary longitudinal vein in postdiscoidal space beginning just distal of triangle; (14) a short veinlet below subnodus, just basal of RP2, between RP and IR2; (15) CuA long, reaching posterior wing margin opposite nodus.

## Genus ***Liassostenophlebia*** n. gen.

**Type species** – *Liassostenophlebia germanica* n. sp.

**Etymology** – After the Liassic age of the material and genus *Stenophlebia*.

**Diagnosis** – That of the family.

### ***Liassostenophlebia germanica*** n. sp.
(fig. 16)

**Holotype** – Specimen n° 1, coll. Hartwig O.W., Naturhistorische Gesellschaft Nürnberg, Germany.

**Etymology** – After the latinised name for Germany.

**Type horizon** – Lower Toarcian, "Epsilon" Liassic, Lower Jurassic.

**Type locality** – Rhine-Danube canal, Km 112/ca 400, Geodenlage 2, Bavaria, Germany.

**Diagnosis** – That of the family.

**Description** – Impression of an incomplete small fore-(?) wing (petiole very short or absent). Length of preserved part, 21.0 mm; width of wing, 5.6 mm; distance between nodus and base, about 10.5 mm; between arculus and base, about 2.3 mm; between arculus and nodus, 8.1 mm; RP separating from RP + MA closer to bend of MA than to base of RP + MA; posterior part of arculus between MA and MP + Cu not aligned with anterior part; CuP separating from MP + Cu and fused with AA well basal of arculus; MA divided into MAa and MAb, at an angle of 105°; MAa basally nearly straight but posteriorly slightly curved distally; MAb straight; visible parts of median and submedian spaces free of cross-veins; discoidal space divided into an equilateral transverse free discoidal triangle and a longitudinal free hypertriangle, separated by a cross-vein stronger than the others, beginning at

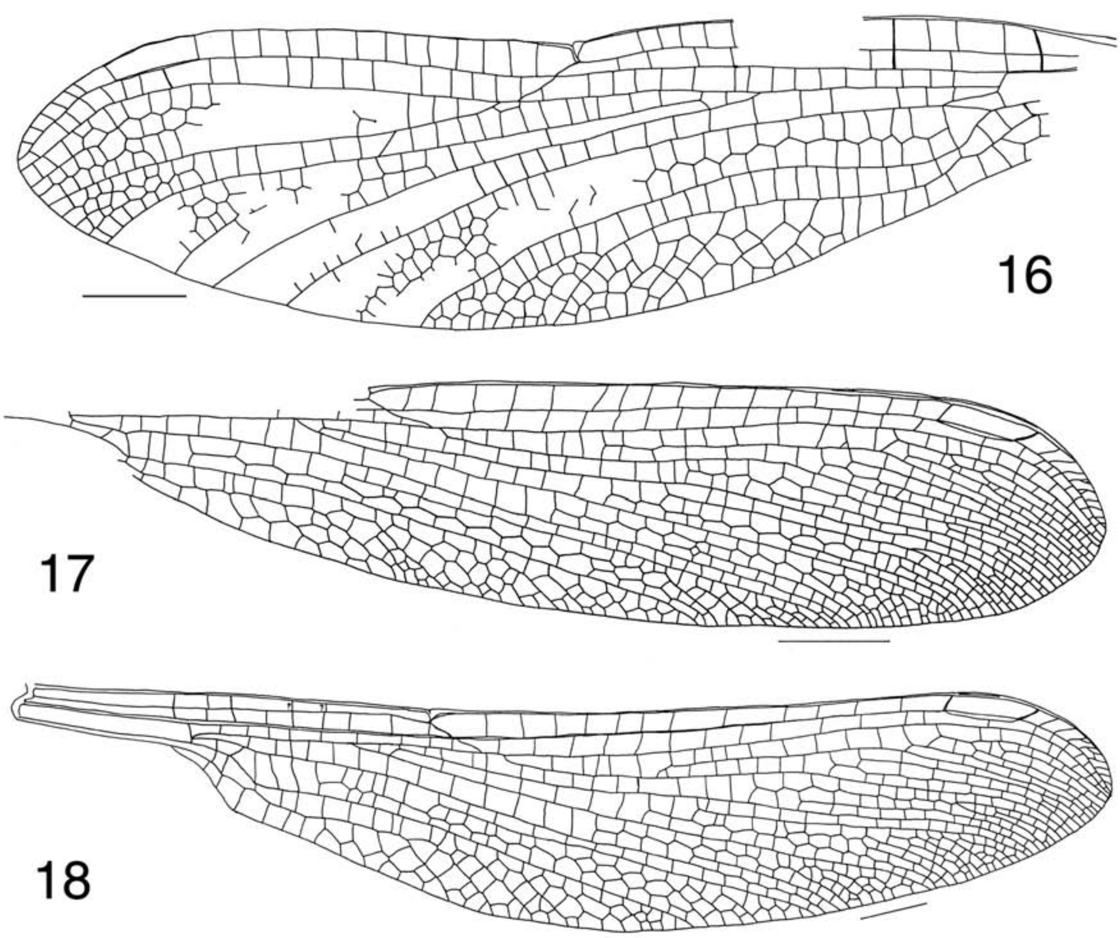



**Figure 16-18**
16, forewing of *Liassostenophlebia germanica* n. gen., n. sp., holotype specimen (scale bar represents 2 mm). – 17, forewing of *Prostenophlebia jurassica* Nel & Martínez-Delclòs, 1993, holotype specimen (scale bar represents 3 mm). – 18, hindwing of *Prostenophlebia jurassica* Nel & Martínez-Delclòs, 1993, holotype specimen (scale bar represents 2 mm).

bend of MP + CuA, and fused with MAb in costo-distal angle of discoidal space; discoidal triangle broad, 0.9 mm long and 0.9 mm wide; length of its costal side, 0.9 mm; distal side, 0.9 mm; posterior side, 1.0 mm; hypertriangle triangular, 1.2 mm long, 0.3 mm wide at base; subdiscoidal space 1.3 mm long, 0.5 mm wide, with one row of three cells; AA only slighly curved, with weak posterior branches; presence of an unicellular "anal loop", well basal of discoidal triangle, in the same position as in *Stenophlebia* spp.; CuA separating from MP in posterior angle of discoidal triangle and reaching AA at a right angle; CuA (+ AA) with about three-four strong posterior branches and three intercalary longitudinal veins between them; basal free part of CuA 0.2 mm long; CuA (+ AA) reaching posterior margin slightly distal of nodus; area between MP and posterior wing margin narrow, with few secondary short veins; base of wing not preserved thus it is impossible to determine whether it was shortly petiolated or not, but the basal widening of the costal vein suggests that the missing basal part of the wing is very small, thus only very briefly petiolated; anal area narrow, with only one row of cells; five rows of cells between CuA and posterior wing margin; postdiscoidal area basally narrow with two rows of cells and distally widened; no concave Mspl but a long secondary zigzagged longitudinal convex vein parallel to MP, beginning just after discoidal triangle; nodus well preserved, vein Cr between nodus and RA oblique and aligned with general trend of ScP; subnodus (Sn) long and oblique, with two cross-veins reaching it; base of RP2 one cell distal of end of Sn; presence of a supplementary cell just basal of base of RP2, between RP and IR2; antenodal area poorly preserved; primary antenodal cross-veins distinctly stronger than secondaries, well separated (2.8 mm apart); arculus between primary antenodals, closer to Ax1 than to Ax2; secondary antenodal cross-veins numerous, five preserved distal of Ax2 and three between Ax1 and Ax2, not aligned with the antenodal cross-veins of second rank between ScP and RA; 12 postnodal cross-veins, not aligned with the subpostnodals; pterostigma rather elongate, 1.8 mm long, 0.5 mm wide, covering three cells; pterostigmal brace apparently in a distal position, below the middle of pterostigma; bases of RP3/4 and IR2 between nodus and arculus, closer to nodus (about 2.3 mm for IR2 and 3.4 mm for RP3/4) than to arculus; two cells between these bases; oblique vein "O" present, in a distal position, six cells distal of base of RP2; area between MA and RP3/4 slightly widened. IR1 zigzagged; no long supplementary longitudinal veins between main veins; venation more open than in other Stenophlebiidae.

## Superfamily **STENOPHLEBIOIDEA** Prikykina, 1968

**Included taxa** – Prostenophlebiidae n. fam., Stenophlebiidae.

**New diagnosis** – The Stenophlebioidea are characterized, within the Stenophlebioptera, by the following synapomorphies, after the present phylogenetic analysis (see below): (1) a long and not zigzagged (or slightly zigzagged) secondary longitudinal convex vein in postdiscoidal area, parallel to MP, the base of this vein being about two or three cells or just distal of discoidal triangle; (2) a long and not zigzagged concave Mspl; (3) oblique vein "O" absent; (4) wing elongate. Characters (1) and (2) are also present in the enigmatic taxon *Erichschmidtia*, but character (3) is not shared by this last taxon. *Prostenophlebia* also differs from *Erichschmidtia* by the presence of small cross-veins reaching subnodus, which is also a character present in Stenophlebiidae.

## Family **PROSTENOPHLEBIIDAE** n. fam.

**Type genus** – *Prostenophlebia* Nel & Martínez-Delclòs, 1993 (in Nel *et al.* 1993).

**Emended diagnosis** – Nel *et al.* (1993) gave a diagnosis of the genus *Prostenophlebia*. We need to amend it as follows: (1) long fore- and hindwing petioles; (2) no secondary antenodal cross-veins between C and ScP distal of Ax2; (3) no oblique vein "O"; (4) hindwing discoidal triangle not transverse; (5) fore- and hindwing hypertriangles short; (6) "heterophlebioid" anal loop reduced, due to wing petiolation; (7) nodal Cr and subnodus quite oblique but relatively short, compared to those of the Stenophlebiidae; (8) presence of cross-veins reaching subnodus. Note that the wing petiolation has also been acquired by the genuine Stenophlebiidae *Hispanostenophlebia* n. gen., even with a more advance step (basal fusion of AA and MP&Cu).

### Genus **Prostenophlebia** Nel & Martínez-Delclòs, 1993 (in Nel *et al.* 1993)

*Prostenophlebia* Nel & Martínez-Delclòs, 1993 : 127-132, text-fig. 100a, b (in Stenophlebiidae).
*Prostenophlebia* : Bechly 1996 : 370-371 (in Erichschmidtiidae).
*Prostenophlebia* : Bechly 1999 (in Erichschmidtiidae).

**Type species** – *Prostenophlebia jurassica* Nel & Martínez-Delclòs, 1993 (in Nel *et al.* 1993).

**Phylogenetic position** – Bechly (1996) included *Prostenophlebia* in the Erichschmidtiidae Bechly, 1996 (type genus: *Erichschmidtia* Pritykina, 1968). The phylogenetic position of *Erichschmidtia* Pritykina, 1968 remains uncertain. Based on a single hindwing, this taxon was originally considered as in Heterophlebiidae (Pritykina 1968). Nel *et al.* (1993) showed that it is not a "heterophlebioid" taxon and considered it as Zygoptera or "Anisozygoptera" *incertae sedis*. Bechly (1996) erected the family Erichschmidtiidae for this taxon and included it in the Epiophlebioidea on the basis of the wing petiolation and RP2 not being strictly aligned with the subnodus. Both these characters are clearly homoplastic. Bechly (in litt.) considered it as the sister group of the Anisopteromorpha Bechly, 1996 (= Heterophlebioptera + Trigonoptera). This last group is characterized by the following synapomorphies: (1) hindwing discoidal cell divided by a longitudinal trigonal vein into a posterior triangulum and an anterior hypertriangulum. This character is obviously absent in *Erichschmidtia*; (2) [M + Cu] distinctly bent at the arculus of both pairs of wings (also absent in Erichschmidtiidae); (3) male hindwings with a perpendicular secondary posterior branch AA2b which runs to the anal angle and distally delimits the anal triangle (absent in Erichschmidtiidae) that is divided into three cells in the groundplan (absent in Erichschmidtiidae). As none of the synapomorphies of the Anisopteromorpha are present in *Erichschmidtia*, we consider that the sister group relationship between these two taxa remains unproven. *Erichschmidtia* shares with the Stenophlebiidae three characters: (1) numerous intercalary veins, especially in the distal half of the wing; (2) presence of the two characteristic longitudinal intercalaries in the postdiscoidal space; (3) very oblique subnodal and nodal veinlets. The characters (1) and (2) are homoplastic in Epiproctophora (= "Anisozygoptera" + Anisoptera). Character (1) is also present in some Tarsophlebiidae and Heterophlebioptera. We indicate in the diagnosis of Stenophlebiidae that character (2) is also present in some Isophlebiidae and Anisoptera. Only character (3) could represent a real synapomorphy of *Erichschmidtia* and the Stenophlebiidae, but the subnodus and nodal veinlet are only slightly less oblique in some Tarsophlebiidae than in *Erichschmidtia*. Furthermore, if *Erichschmidtia* is considered as a basal Stenophlebioptera, its entire discoidal cell would imply that the division of the discoidal cell into a triangle and a hypertriangle would have been convergently acquired by the Stenophlebioptera and a lineage comprising Heterophlebioptera and Anisoptera. *Erichschmidtia* could be a critical taxon for analysis of the relationships of Stenophlebiidae, Heterophlebioptera and Anisoptera but it is still too poorly known (forewing unknown) for a certain determination of its affinities. We consider it as an Epiproctophora *incertae sedis*.

Bechly (1996) based the inclusion of *Prostenophlebia* in Erichschmidtiidae on the following putative synapomorphies:

(1) Numerous intercalary veins in the apical part of the wing with a "unique" pattern, i.e. numerous closely parallel intercalaries and a characteristic pattern of small longitudinally elongated cells in the distal part of the wing. These characters are also present in Stenophlebiidae, Euthemistidae, and in Tarsophlebiidae;

(2) Two characteristic intercalaries in the narrow postdiscoidal space between MA and MP. This character is one of those proposed by Bechly (1996) for the diagnosis of the Stenophlebiidae;

(3) MA and MP closely parallel, correlated with a very narrow postdiscoidal space. This character is incorrect for *Prostenophlebia*;

(4) Very oblique nodal and subnodal veinlet. This is also one of the main diagnostic characters of the Stenophlebioptera;

(5) IR2 apparently arising on RP3/4. This character is homoplastic, also present in some Heterophlebioptera, but not all of them;

(6) Antenodal cross-veins between costal margin and ScP suppressed distal of Ax2. In the original description of *Prostenophlebia*, it was erroneously stated that there were secondary antenodals distal of Ax2 (Nel *et al*. 1993). This character state should be verified in *Erichschmidtia*. Furthermore, such a character is clearly highly homoplastic within the whole clade Epiproctophora (presence of secondary cross-veins in Isophlebiidae Handlirsch, 1908 versus absence in its sister group Campterophlebiidae Handlirsch, 1920).

All these characters are either wrong or also present in Stenophlebiidae. Furthermore, *Prostenophlebia* has the diagnostic characters of the Stenophlebioidea, especially the division of the discoidal cell into a triangle and hypertriangle by a cross-vein secondarily branched on MP + CuA, on all four wings, and the absence of oblique vein "O", present in *Erichschmidtia*.

**Nota**. The discoidal "hypertriangle + triangle" of *Prostenophlebia* is nearly identical to that of the Libellulidae *Palaeothemis tillyardi* Fraser, 1923 or the Cordulephyidae *Cordulephyia pygmaea* Selys, 1871. These specialized structure of the discoidal cells, appearing as reversions in the case of these Libelluloidea, may be correlated to the very short, small and narrow wings of these taxa. The same situation may occur in *Prostenophlebia*.

### ***Prostenophlebia jurassica*** Nel & Martínez-Delclòs, 1993 (figs. 17-19)

**Material** – Holotype specimen SOS 2047, Jura-Museum, Eichstätt, Germany. Other material. Specimen MC7, coll. Carpenter, Harvard University, Cambridge, Massachusetts, U.S.A. This last specimen was figured by Needham (1903, text-fig. 9) under the caption "fossil undescribed agrionid genus".

**Stratum typicum** – Upper Jurassic, Malm zeta 2b ("oberer Weißjura"), Lower Tithonian, *Hybonotum*-Zone, Solnhofen Lithographic Limestone.

**Locus typicus** – Eichstätt, southern Frankonian Alb, Bavaria, Germany.

**Redescription** – The description proposed by Nel *et al.* (1993) was partly erroneous.

Holotype. Impression of a complete body with one fore- and one hindwing in connection with the body. No trace of colouration is preserved.

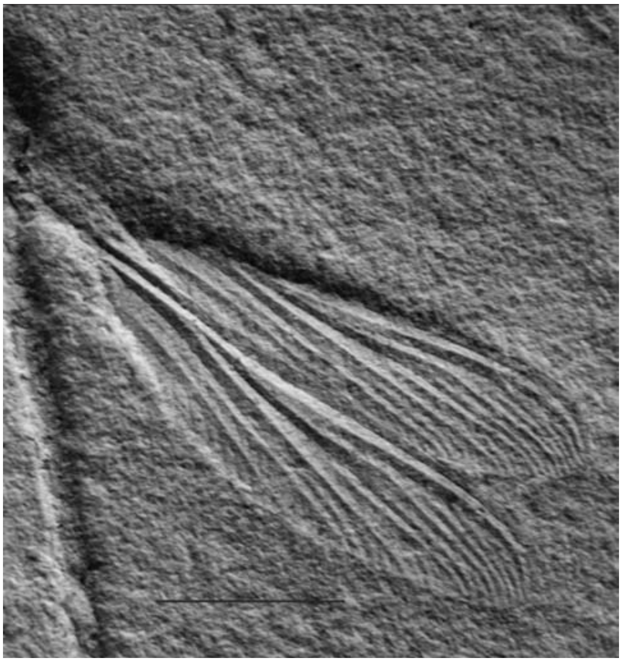


**Figure 19**
Photograph of the wings of *Prostenophlebia jurassica* Nel & Martínez-Delclòs, 1993, holotype specimen, (scale bar represents 10 mm).

Preserved part of forewing 34.0 mm long, 7.3 mm wide (distal of nodus), distance from nodus to base, about 11.3 mm; from nodus to pterostigma, 17.4 mm; nodus in a basal position; distance from arculus to nodus, 9.4 mm; pterostigma 2.8 mm long and 0.7 mm wide; posterior side of arculus between MA and MP + Cu strong; CuP not preserved. MA divided into MAa and MAb; these two veins make an angle of 85°; MAb nearly straight; median and submedian spaces poorly preserved but probably free of cross-veins; discoidal space divided into an elongate discoidal quadrangle and a longitudinal hypertriangle, separated by a strong cross-vein reaching MA basal of costo-distal angle of discoidal space (fig. 17); branching of this cross-vein on MP + CuA of secondary type (presence of a furrow); free discoidal quadrangle broad (1 mm long and 0.7 mm wide); length of its costal side, 0.4 mm; of distal side, 0.7 mm, thus MAb is short relative to those of *Stenophlebia* spp.; length of proximal side of quadrangle, 0.4 mm; hypertriangle 1.2 mm long, 0.3 mm wide; subdiscoidal space and basal portion of AA poorly preserved; CuA separating from MP in posterior angle of discoidal quadrangle and fused with AA at right angle (95°), length of its free part, 0.2 mm; CuA reaching posterior margin opposite nodus, with only two strong posterior branches with two intercalary veins between them; area between MP and posterior wing margin broad, with numerous secondary veins; petiole not preserved; three rows of cells between CuA and posterior wing margin; postdiscoidal area narrow with two rows of cells but distally broadened; a long vein Mspl beginning below nodus and a long secondary zigzagged longitudinal convex vein parallel to MP in postdiscoidal area, beginning three cells distal of discoidal cell; nodus poorly preserved; vein Cr between nodus and RA very oblique and directly aligned with basal part of ScP; subnodus Sn also very oblique and directly aligned with Cr between RA and RP; no postnodal cross-vein reaching Cr but one reaching subnodus; base of RP2 distal but nearly opposite point of fusion between Sn and RP1; no secondary longitudinal "stenophlebiid veinlet" between RP and IR2 below the nodus, (which would be distally fused with RP2, see Nel *et al.* (1993: figs. 84, 91a), unlike in the *Stenophlebia* spp.); antenodal area not preserved; 16 postnodal cross-veins, not well aligned with corresponding subpostnodal cross-veins between RA and RP1; pterostigma slightly elongate and narrow, with a very weak basal brace between RA and RP1 basally displaced; pterostigma covering about two long cells and one cross-vein and not proximally recessed; bases of RP3/4 and IR2 between nodus and arculus, closer to nodus (1.4 mm for IR2 and 2.2 mm for RP3/4) than to arculus, with one cell between their respective bases; cross-vein "O" absent; IR1 well defined, nearly straight and parallel to RA in its proximal part, bent distally; at least four long secondary longitudinal veins between MA and RP3/4, three others between IR2 and RP3/4, two between RP2 and IR2, two between RP2 and IR1 and three between MA and MP; there are shorter longitudinal veins between these secondary veins.

Hindwing 39.4 mm long and 8.0 mm wide (well distal of nodus); distance from nodus to base, 14.5 mm; from nodus to pterostigma, 18.4 mm; nodus in a basal position; distance from arculus to base, 6.3 mm; from arculus to nodus, 8.4 mm; pterostigma 3.1 mm long and 0.6 mm wide; in arculus, RP separating from RP + MA at bent of MA (fig. 18); posterior part of arculus between MA and MP + Cu strong; CuP separating from MP + Cu and fused with AA 0.9 mm distal of base of arculus; MA divided into MAa and MAb, at an angle of 82° between these two veins; MAb (distal margin of discoidal triangle) nearly straight; median and submedian spaces free of cross-veins; discoidal space divided into a nearly transverse discoidal quadrangle and a longitudinal hypertriangle, separated by a cross-vein stronger than the others, fused with MA basal of costo-distal angle of discoidal space; branching of this cross-vein of secondary type (presence of a furrow); discoidal quadrangle broad (1.1 mm long and 0.9 mm wide) and free of cross-veins, length of costal side of discoidal quadrangle, 0.4 mm, of distal side (MAb), 1.1 mm, of posterior side (MP + CuA), 1.3 mm; hypertriangle 2.0 mm long, 0.5 mm wide, with one cross-vein; subdiscoidal space 1.9 mm long and 0.7 mm wide, divided into two cells; AA with a basal bend, more or less parallel to posterior side of discoidal quadrangle; anal area narrow, divided into three cells; CuA separated from MP in posterior angle of discoidal triangle and fused with AA at nearly right angles; length of free part of CuA, 0.2 mm; CuA with only two or three posterior branches and reaching posterior margin opposite nodus; area between MP and posterior wing margin broad, with numerous secondary veins; wing long petiolated; petiole 5.6 mm long; a distinct angle below discoidal quadrangle on the posterior wing margin (male specimen); cubito-anal area with three or four rows of cells between CuA and posterior wing margin; postdiscoidal area narrow with three or four rows of cells, and distally broadened; a long straight vein Mspl and a long secondary zigzagged longitudinal convex vein parallel to MP, beginning three cells distal of discoidal cell; nodal furrow very weak, with nearly no interruption of costal margin; vein Cr between nodus and RA very oblique and aligned with general direction of ScP; no postnodal cross-vein reaching Cr; subnodus Sn also very oblique and aligned with Cr between RA and RP; small cross-vein present between ScP and RA opposite base of Cr; base of RP2 one cell distal of point of fusion between Sn and RP1; no secondary longitudinal "stenophlebiid veinlet" between RP and IR2 (below nodus and distally fused with RP2); antenodal area well preserved; primary antenodal cross-veins Ax1 and Ax2 distinctly stronger than secondaries; distance between Ax1 and Ax2, 2.1 mm; arculus between the two primary antenodals, but closer to Ax1 than to Ax2; one complete secondary cross-vein between Ax1 and Ax2 but probably no other antenodal cross-vein in distal portion of area between C and ScP; five cross-veins in area between ScP and RA; 12 postnodal cross-veins not aligned with corresponding subpostnodal cross-veins in area between RA and RP1; pterostigma slightly elongate and narrow, not basally braced, covering about two long cells and not proximally recessed; bases of RP3/4 and IR2 between nodus and arculus, closer to nodus (1.1 mm for IR2 and 2.7 mm for RP3/4) than to arculus, with two cells between their respective bases; cross-vein "O" absent; IR1 well defined, basally more or less parallel to RA but distally slightly curved; at least two long secondary longitudinal veins between MA and RP3/4, two others between IR2 and RP3/4, two between RP2 and IR2, two between RP2 and IR1 and three between MA and MP; shorter longitudinal veins present between these secondary veins.

Specimen MC7, coll. Carpenter. There are few differences from the previous specimen listed in the shortened description below: forewing about 35 mm long and 6.5 mm wide (well distal of nodus); distance from nodus to base, about 12 mm; from nodus to pterostigma, about 15 mm; nodus in a basal position; distance from arculus to base, about 3 mm; from arculus to nodus, 9.4 mm; pterostigma, 2.5 mm long and 0.6 mm wide; forewing petiolation nearly as long as hindwing's; subdiscoidal space long and narrow, similar to that of the hindwing; Ax1 and Ax2 strong, 1.9 mm apart; arculus between primary antenodals, but very close to Ax1, few secondary antenodal cross-veins of second rank between ScP and RA; antenodals of first rank not preserved; no oblique cross-vein "O"; CuAa apparently with more numerous posterior branches than in holotype.

Hindwing 7.4 mm wide (well distal of nodus); distance from nodus to base, 13.1 mm; nodus in a basal position; distance from arculus to base, 4.2 mm; from arculus to nodus, 8.9 mm; RP2 slightly closer to subnodus than on holotype; no angle on posterior wing margin (female specimen); no pterostigmal brace; discoidal space divided by a cross-vein into a hypertriangle and quadrangle.

## Family **STENOPHLEBIIDAE** Needham, 1903

Stenophlebinae Needham, 1903 : 750 (n. subfam.) (nom. imperf.).
Stenophlebiidae *sensu* Handlirsch 1906 : 581 (stat. n. et nom. correct.) [partim: "Anisozygoptera" Handlirsch 1908 (taxon n.)].
Stenophlebiinae *sensu* Tillyard 1917 : 311 and 319 (*in* Calopterygidae).
Stenophlebiidae *sensu* Pritykina 1968 : 45-46 (*in* Tarsophlebiidea).
Stenophlebioidea *sensu* Pritykina 1980 (stat. n.) [partim: "Heterophlebiina" Pritykina (taxon n., suborder, not subtribe)].
Stenophlebiidae *sensu* Ross & Jarzembowski 1993 in Benton, 372.
Stenophlebioidea *sensu* Nel *et al.* 1993 : 107 (revision of the family).
Stenophlebiidae *sensu* Bechly 1996 : 373 (*in* Trigonoptera).
Stenophlebiidae *sensu* Bechly 1999 (*in* Trigonoptera).

**Type genus** – *Stenophlebia* Hagen, 1866.

**Included taxa** – *Stenophlebia* Hagen, 1866, *Sinostenophlebia* Hong, 1984, *Cretastenophlebia* n. gen., *Hispanostenophlebia* n. gen., *Mesostenophlebia* n. gen., but not *Prostenophlebia* Nel & Martínez-Delclòs, 1993 (in Nel *et al.* 1993).

**Diagnosis** – Bechly (1996) proposed the following venational autapomorphies:
**(1)** Discoidal triangle of unique and similar shape in both pairs of wings (transversely elongated, narrow, and strictly triangular).

**Comments**. – The discoidal cells of Stenophlebiidae are identical in the four wings and divided into two parts by a transverse vein which is secondarily branched on MP + CuA. These two parts are a quadrilateral hypertriangle and a transverse discoidal triangle with a sharp apico-posterior angle. The discoidal triangle is free or divided into small cells by parallel cross-veins. This subdivision into triangle and hypertriangle is visible in *Stenophlebia* spp., *Mesostenophlebia* n. gen. and *Hispanophlebia* n. gen.; it is more rudimentary in the Prostenophlebiidae and unknown in *Sinostenophlebia* (due to lack of preservation). This shape of discoidal "triangle" and hypertriangle is reminiscent of the forewing discoidal cell [= triangle + hypertriangle] of extant Libellulidae such as *Diplacodes* Kirby, 1889 and *Neodythemis* Karsch, 1889. Nel *et al.* (1993) considered that Stenophlebiidae and Anisoptera convergently acquired the division of the discoidal cell into a triangle and a hypertriangle, but Bechly (1996) had the reverse opinion. In Heterophlebioptera: Liassophlebiidae, the discoidal cell is unicellular but transverse with a rudimentary incomplete cross-vein. In Myopophlebiidae, the division of the discoidal cell is more or less acquired in hindwings (cross-vein not well defined) but not in forewings. In Heterophlebiidae and Paraheterophlebiidae, the transverse vein separating the hypertriangle and the triangle is still secondarily branched on MP + CuA. In the *Stenophlebia* spp., this vein is present in the fore- and hindwing and is strongly concave as in Anisoptera, more than those of Heterophlebioptera. In the Liassic "anisopteroid" family Liassogomphidae, this vein is primarily branched on MP + CuA. A gradation schema could be proposed for this structure, as follows: "liassophlebiid-myopophlebiid undivided or poorly divided unicellular transverse discoidal cell" "heterophlebiid type of hindwing discoidal cell divided into hypertriangle and transverse triangle by a secondarily branched vein" "trigonopterid, i.e. stenophlebioid and anisopteroid type of fore- and hindwing discoidal cells, both divided into a hypertriangle and a transverse triangle by a primarily branched vein". Nevertheless, the sister group relationship between the Heterophlebioptera and the Trigonoptera suggests that the "heterophlebiid" type could have been independently acquired of the "trigonopterid" type (see phylogenetic analysis below).

**(2)** Wings very long and slender.

**Comments**. – This character is present in *Stenophlebia* spp. and *Hispanostenophlebia* but not in the Liassostenophlebiidae and Prostenophlebiidae. The wings are shorter in *Cretastenophlebia*. This character is unknown in *Mesostenophlebia*.

**(3)** Nodal and subnodal veinlet extremely oblique (Nel *et al*. 1993).

**Comments**. – Nel *et al.* (1993) noted that, in the *Stenophlebia* spp., the nodal veinlet Cr is well aligned with the main part of ScP, and seems to distally continue this vein, between the nodus and RA, so that ScP apparently reaches RA, which is of course not so (ScP reaches the costal margin, as in other Odonata). Nodal veinlet Cr is similar to those of extant Zygoptera: Chlorocyphidae such as *Libellago* Selys, 1840, *Rhinocypha* Rambur, 1842, *Euthore fasciata* (Hagen, 1853) (Polythoridae) and *Mnais andersoni* McLachlan, 1873 (Calopterygidae) representing evolutionary convergence between these families, as they do not share any other synapomorphy.

**(4)** Presence of a "stenophlebiid" oblique vein between RP1 and RP2.

**Comments**. – This "stenophlebiid" oblique vein (*sensu* Bechly 1996) is in fact the real base of RP2. In *Stenophlebia* spp., there are two rows of cells between RP and IR2, basal of the base of RP2, with a short longitudinal and zigzagged secondary vein that reaches RP2. In *Liassostenophlebia* n. gen., this structure is reduced to a short veinlet below the base of RP2. In *Stenophlebia karatavica*, the secondary vein is straight and long and the true base of RP2 appears as an oblique vein between RP1 and RP2. Therefore, we prefer to replace the character "presence of a stenophlebiid oblique vein between RP1 and RP2" by "presence of a secondary longitudinal vein just basal of base of RP2, between RP and IR2". Note that this character is absent in some genuine Stenophlebiidae (*Cretastenophlebia* n. gen.).

**(5)** Nodal furrow reduced (Nel *et al*. 1993).

**Comments**. – Bechly (1996) considered that this character is convergent with Epiophlebiidae and Aeschnidiidae.

**(6)** Hindwings with a short but distinct petiole (Nel *et al*. 1993).

**Comments**. – The most characteristic pattern is the petiolated hindwings but not forewings. The petiole of *Hispanostenophlebia* is clearly very long, reaching the level of arculus.

**(7)** Numerous intercalary veins with a characteristic pattern between MA and MP.

**Comments**. – In Stenophlebioptera, there is at least one nearly straight convex secondary longitudinal vein between MA and MP that begins less than three cells distal of the discoidal triangle and another one (concave "Mspl") in a more distal position. Bechly (1996) noted that the same structure is present in the enigmatic Erichschmidtiidae. It is also present in some Isophlebiidae (*Isophlebia aspasia* Hagen, 1866) and some Anisoptera (*Petaliaeschna fletcheri* Fraser, 1927).

**(8)** Basal secondary antenodal cross-veins present between Ax0 and Ax1.

**Comments**. – If this structure is present in some *Stenophlebia* spp., such a structure is generally too poorly preserved to be certain that it is found generally in Stenophlebiidae. It is absent in *Cretastenophlebia*.

**(9)** Pterostigma shifted basally.

**Comments**. – Bechly (in litt.) indicated that this character is convergent with Isophlebiidae, Aeschnidiidae, and Petaluridae. It is not stable in all Stenophlebiidae (clearly absent in *Cretastenophlebia*). Thus we prefer to exclude this character from the family diagnosis.

**(10)** Terminal part of male abdomen dilated (Nel *et al*. 1993).

**Comments**. – This character is only known in some Upper Jurassic German *Stenophlebia*. Bechly (1996) noted that it is convergent with certain Liassophlebiidae, many Gomphidae and some Libellulidae. In *Prostenophlebia* (sister group of the Stenophlebiidae), it is not broadened (Nel *et al*. 1993).

**(11)** Female ovipositor strongly reduced, so that it is not clearly visible in the fossils.

**(12)** Pterostigmal braces basally recessed or absent (new character).

**(13)** Oblique vein "O" absent.

**Comments**. – The oblique vein is absent in Stenophlebioidea, but not in *Liassostenophlebia*.

**(14)** Presence of numerous secondary antenodal cross-veins distal of Ax2.

**Comments**. – This character is highly homoplastic but after the present phylogenetic analysis, it would be a plesiomorphy within the Anisopteromorpha.

**(15)** Pterostigma elongate, ratio length/width ≥ 6 (convergent with Petaluridae).

We propose the following new diagnosis for the Stenophlebiidae (synapomorphies): (1) a long not zigzagged secondary longitudinal convex vein in postdiscoidal area, parallel to MP, the base of this vein being just distal of discoidal triangle; (2) Cr long or very long, covering more than one or two cells between RA and RP; (3) pterostigma basally shifted (not very in *Cretastenophlebia* n. gen.); (4) pterostigma very long; (5) hindwing subdiscoidal space transverse and crossed by two veins or more; (6) the four wings elongate and more or less falcate; (7) forewing discoidal triangle long transverse. This last character was convergently acquired by some Aeschnidiidae; (8) numerous and well defined straight intercalary secondary longitudinal veins reaching posterior wing margin.

## Genus ***Hispanostenophlebia*** n. gen.

**Type species** – *Hispanostenophlebia barremiana* n. sp.

**Etymology** – After Hispania, the latin name for Spain.

**Diagnosis** – Small species (the hindwing is only 36 mm long); (1) wing elongate but weakly falcate; (2) nodal structure similar to that of *S. latreillei* and *S. amphitrite* but Cr shorter than in *S. eichstaettensis* (plesiomorphy); (3) the secondary longitudinal "stenophlebiid veinlet" between RP and IR2 that is in basal continuity with RP2, opposite the nodus, is short (three cells long), as in *S. latreillei* and *S. amphitrite* (plesiomorphy); (4) Sn short (one or two cells long; plesiomorphy); (5) in the arculus, RP separates from RP + MA midway between the bend of MA and the base of RP + MA (autapomorphy); (6) only one row of cells in subdiscoidal space; (7) discoidal triangle (and maybe hypertriangle) crossed by two cross-veins (apomorphy); (8) AA nearly straight (apomorphy); CuA and AA with a sharp angle (polarity uncertain); a well-defined Mspl; (9) the second primary antenodal cross-vein Ax2 opposite arculus; (10) pterostigma covering at least 12 cells between RA and RP1 (autapomorphy); (11) oblique cross-vein "O" absent or rudimentary (apomorphy); (12) CuAa short with only two main branches (apomorphy); (13) AA + AP and MP + Cu fused basally in a long petiole, correlated with a submedian area extremely reduced (autapomorphy); (14) area between MP and posterior wing margin slightly shorter than cubito-anal area.

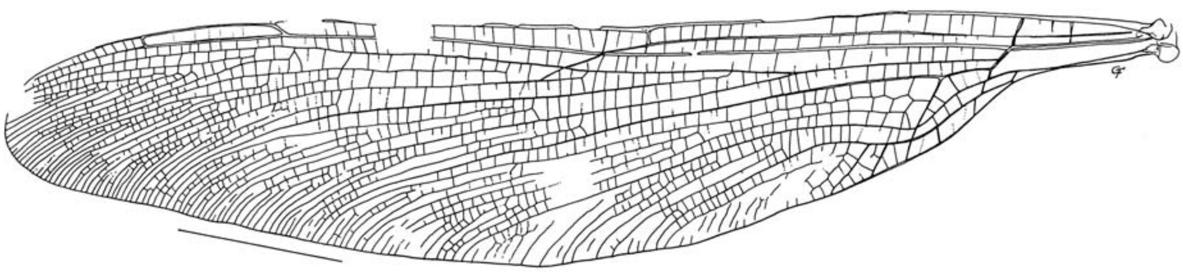


**Figure 20**
Hindwing of *Hispanostenophlebia barremiana* n. gen., n. sp., holotype specimen ADR–0315–I, (scale bar represents 5 mm).

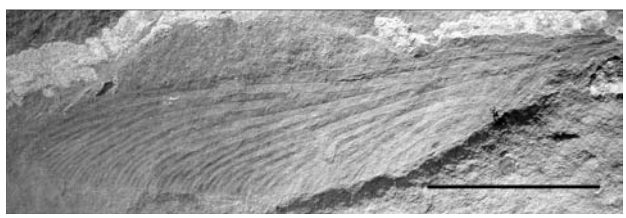


**Figure 21**
Photograph of *Hispanostenophlebia barremiana* n. gen., n. sp., holotype specimen ADR–0315–I (scale bar represents 10 mm).

### ***Hispanostenophlebia barremiana*** n. sp.
(figs. 20-21)

**Holotype** – Specimen ADR–0315–I, coll. Armando Díaz–Romeral of Cuenca, it is to be deposited in the Museo de Cuenca.

**Etymology** – After the Barremian stage.

**Type horizon** – Second member of the Formation Calizas de la Huérguina, Upper Barremian - Aptian (Diéguez *et al.* 1995), Lower Cretaceous.

**Type locality** – Outcrop at Las Hoyas, 4 km NW of Pueblo de La Cierva, Spain.

**Diagnosis** – As for genus.

**Description** – The holotype is an impression of a hindwing; no trace of coloration preserved; only the main longitudinal veins are clearly visible, the cross-veins being badly fossilised; it is 36.1 mm long, 7.5 mm wide; distance between nodus and base, 16.2 mm, between arculus and base, 4.6 mm, between arculus and nodus, 11.6 mm, between nodus and pterostigma, 11.2 mm, pterostigma 4.3 mm long, 0.4 mm wide; RP separating from RP + MA midway between bend of MA (in the discoidal triangle) and base of RP + MA in arculus; posterior side of arculus between MA and MP + Cu strong; CuP separating from MP + Cu and fused with AA opposite base of arculus; MA divided into MAa and MAb, these two veins being at an angle of 65°; MAa nearly straight, its distal part being curved near posterior wing margin; MAb straight; median and submedian spaces free of cross-veins; discoidal space divided into a transverse discoidal triangle and a longitudinal hypertriangle separated by a cross-vein slightly stronger than the others, between bend of MP + CuA and MA; discoidal triangle extended transversely, broad, 1.8 mm long and 0.6 mm wide, and crossed by two cross-veins; costal side of discoidal triangle 1.5 mm long, distal side (MAb), 1.8 mm, posterior side, 1.7 mm; hypertriangle 1.4 mm long, 0.5 mm wide, probably with two cross-veins; subdiscoidal space 2.6 mm long and 0.5 mm wide, with one row of cells; AA nearly straight and parallel to posterior side of discoidal triangle, with two short posterior branches; CuA separating from MP in posterior angle of discoidal triangle and fused with AA, with a sharp angle (45°);

length of free part of CuA, 0.3 mm; CuA reaching posterior wing margin a little basal of nodus, with only two strong posterior branches and two intercalary veins between them; area between MP and posterior wing margin broad, with numerous secondary veins; wing well petiolated, petiole 4.5 mm long; AP nearly parallel to AA; anal area narrow with only one row of cells; anal vein AA + AP fused basally with M + Cu, separated opposite Ax2, 3.3 mm distal of wing base; three or four rows of cells between CuA and posterior wing margin; postdiscoidal area with three rows of cells basally; unlike in *Stenophlebia*, a vein Mspl and a long secondary longitudinal convex vein beginning just distal of MAb; vein ScP clearly fused with costal margin; nodal furrow very weak; nearly no interruption of costal margin; vein Cr very oblique and directly aligned with general trend of ScP; two postnodal cross-veins reaching Cr; subnodus (Sn) very oblique and aligned with Cr, with one cross-vein reaching it; true base of RP2 aligned with Sn; a secondary longitudinal "stenophlebiid veinlet" between RP1 +2 and IR2 below subnodus, distally fused with RP2; antenodal area poorly preserved; primary antenodal cross-vein Ax1 and Ax2 distinctly stronger than the numerous secondaries between C and ScP (about 20 preserved) not aligned with antenodal cross-veins of second row between ScP and RA; postnodal area also incompletely preserved; exact number of postnodal cross-veins undetermined but 12 are visible; pterostigma elongate, narrow, covering about 12 small cells and slightly basally shifted; basal side of pterostigma very oblique; pterostigmal brace six cells basally recessed and very weak; bases of RP3/4 and IR2 between nodus and arculus, closer to nodus (4.6 mm for RP3/4 and 1.7 mm for IR2) than to arculus, about four cells between their respective bases; oblique vein "O" absent or very weak; IR1 well defined, straight and proximally parallel to RA; numerous secondary longitudinal veins between the main veins.

## Genus ***Mesostenophlebia*** n. gen.

**Type species** – *Mesostenophlebia anglicana* n. sp.

**Etymology** – After the Mesozoic age of the material and genus *Stenophlebia*.

**Diagnosis** – Although *Mesostenophlebia* n. gen. has no clear autapomorphy, it can be distinguished by the following features: (1) discoidal cell somewhat "intermediate" between that of *Prostenophlebia* and those of *Stenophlebia* and *Hispanostenophlebia*, i.e. free hypertriangle pentagonal and free discoidal triangle less transverse than those of *Stenophlebia* spp. and *Hispanostenophlebia*; (2) numerous antenodal cross-veins, like *Stenophlebia* spp. and *Hispanostenophlebia*; (3) shares with *Stenophlebia* and *Hispanostenophlebia* long secondary longitudinal convex vein in postdiscoidal area, less developed in *Prostenophlebia;* (4) a clear bifurcation of CuA into two branches, three cells distal of its fusion with AA; (5) CuA reaches posterior margin well basal of nodus; (6) hypertriangle somewhat broad and pentagonal.

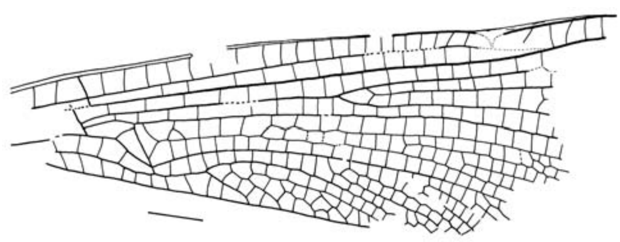


**Figure 22**
Forewing of *Mesostenophlebia anglicana* n. gen., n. sp., holotype specimen (scale bar represents 2 mm).

### ***Mesostenophlebia anglicana*** n. sp.
(fig. 22)

**Holotype** – Specimen MNEMG 1996.93a,b, Maidstone Museum, coll. R. Coram.

**Etymology** – After the latinised name for England.

**Type horizon** – Clements' (1993) Bed DB36c, Lower Purbeck beds, Earliest Berriasian, Lower Cretaceous.

**Type locality** – Durlston Bay, Dorset, U.K. National Grid Reference SZ 035781.

**Description** – The species is known from the impression of an incomplete wing. Length of preserved part, 23 mm; width of wing, 7.6 mm; distance between nodus and base, about 19 mm; between arculus and base, about 3 mm; between arculus and nodus, 16 mm; RP separating from RP + MA closer to bend of MA than to base of RP + MA; posterior part of arculus (bdcv), between MA and MP + Cu, strong and aligned with anterior part; CuP separating from MP + Cu and fused with AA well basal of arculus; MA divided into MAa and MAb at an angle of 68°; MAa basally nearly straight but posteriorly curved distally; MAb straight; visible parts of median and submedian spaces free of cross-veins; discoidal space divided into a transverse free discoidal triangle and a longitudinal free hypertriangle, separated by a cross-vein stronger than the others, beginning at bend of MP + CuA, and fused with MAb below costo-distal angle of discoidal space; discoidal triangle broad, 1.7 mm long and 0.8 mm wide; length of its costal side, 0.8 mm; of distal side, 1.6 mm; of posterior side, 1.7 mm; hypertriangle somewhat pentagonal, 1.9 mm long, 0.7 mm wide; subdiscoidal space 3.9 mm long, 0.8 mm wide, with one row of four cells; AA only slighly curved, with weak posterior branches; CuA separating from MP in posterior angle of discoidal triangle and reaching AA in a sharp angle; CuA (+ AA) with only two strong posterior branches and three intercalary longitudinal veins between them; free part of CuA 0.3 mm long; CuA (+ AA) reaching posterior margin distinctly basal of nodus; area between MP and posterior wing margin broad, with numerous secondary veins; base of wing not preserved thus it is impossible to determine whether it was petiolated or not; AP nearly parallel to AA; anal area narrow, with only one row of cells; over three rows of cells between CuA and posterior wing margin; postdiscoidal area basally narrow with two rows of cells and distally widened; a long straight Mspl and a long secondary longitudinal convex vein parallel to MP, beginning just after discoidal triangle; nodus not preserved, but vein Cr between nodus and RA probably very oblique and aligned with general trend of ScP, because there are three cross-veins between RA and RP, below the nodus; subnodus (Sn) and RP2 not preserved; antenodal area poorly preserved; primary antenodal cross-vein Ax2 apparently not distinctly stronger than secondaries; arculus between primary antenodals, closer to Ax2 than to Ax1; secondary antenodal cross-veins numerous, about 24 preserved, and not aligned with the less numerous antenodal cross-veins of second rank between ScP and RA; postnodal area only partly preserved, thus exact number of postnodal cross-veins unknown; pterostigma not preserved; bases of RP3/4 and IR2 between nodus and arculus, closer to nodus (about 5 mm for IR2 and 6 mm for RP3/4) than to arculus; only one cell between these bases; oblique vein "O" and IR1 not preserved; area between MA and RP3/4 not widened in preserved part of wing.

**Remark** – There is no preserved part in common between the types of *Mesostenophlebia anglicana* n. gen., n. sp. and the only other Lower Cretaceous English stenophlebiid, *Stenophlebia corami*, due to the poor preservation of the nodal region of the former and the incompleteness of the latter. Thus, it is nearly impossible to compare these two fossils.

## Genus *Cretastenophlebia* n. gen.

**Type species** – *Cretastenophlebia mongolica* n. sp.

**Etymology** – After the Cretaceous age of the material and genus *Stenophlebia*.

**Diagnosis** – (1) wing long and falked; (2) discoidal cell divided into a crossed elongate transverse triangle and a free hypertriangle; (3) angle between MAa and MAb about 90°; (4) subdiscoidal space foot-shaped; (5) AA curved below subdiscoidal space; (6) no "heterophlebioid" anal loop, anal area very narrow; (7) Ax1 and Ax2 close, with no secondaries between them; (8) nodal Cr quite oblique, long, with numerous cross-veins reaching it; (9) subnodus well aligned with nodal Cr, quite oblique, with two cross-veins reaching it; (10) pterostigma elongate, not shifted basally; (11) pt-brace absent or very weak and basally shifted (?); (12) oblique vein "O" absent; (13) a long Mspl, and a long zigzagged secondary longitudinal vein in postdiscoidal space beginning just distal of triangle; (14) no supplementary veinlet below subnodus, just basal RP2, between RP and IR2; (15) CuA short, reaching posterior wing margin well basal of nodus; (16) male hindwing anal angle well pronounced and distally shifted below the distal side of discoidal cell (probable unique character, autapomorphy); (17) Ax0 in a relative distal position.

## *Cretastenophlebia mongolica* n. sp.

(figs. 23-24)

**Holotype** – Specimen PIN 3559/10180, part and counterpart, Arthropod Laboratory, Palaeontological Institute, Moscow, Russia.

**Etymology** – After Mongolia.

**Stratum typicum** – Lower Cretaceous, Barremian-Aptian (Mostovski & Martínez-Delclòs 2000), Bon-Tsagaan series.

**Locus typicus** – Bon-Tsagaan, Bayanhongor Aimak, Central Mongolia.

**Description** – Impression of a nearly complete hindwing, 40.0 mm long, 8.4 mm wide (distal of nodus); distance between nodus and base, about 16 mm; between arculus and base, 4.7 mm; between arculus and nodus, about 12 mm; RP separating from RP + MA distinctly closer to bend of MA than to base of RP + MA; posterior part of arculus (bdcv), between MA and MP + Cu, well aligned with anterior part; CuP separating from MP + Cu and fused with AA at end of petiole, opposite Ax1, well basal of arculus; MA divided into MAa and Mab at

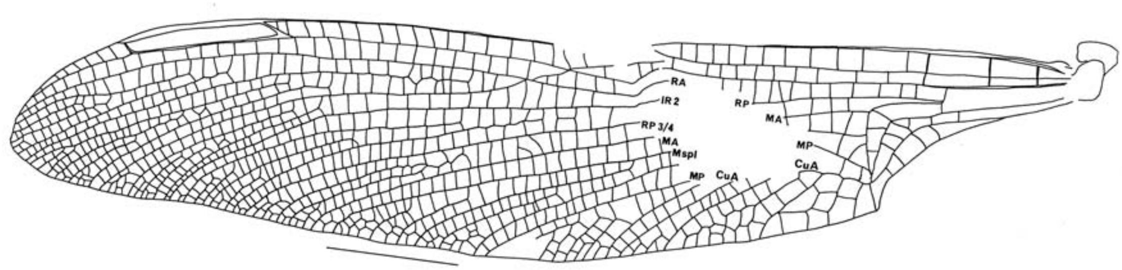



**Figure 23**
Hindwing of *Cretastenophlebia mongolica* n. gen., n. sp., holotype specimen (scale bar represents 5 mm).

**Figure 24**
Photograph of the hindwing of *Cretastenophlebia mongolica* n. gen., n. sp., holotype specimen.

an angle of 84°; MAa nearly straight; MAb slightly curved; median and submedian spaces free of cross-veins; discoidal space divided into a very transverse crossed discoidal triangle and a longitudinal free hypertriangle, separated by a cross-vein stronger than the others, beginning at bend of MP + CuA, and fused with MAb in costo-distal angle of discoidal space; discoidal triangle narrow and long, 2.5 mm long and 0.9 mm wide, length of its costal side, 0.9 mm, of distal side, 2.5 mm, of posterior side, 2.2 mm; hypertriangle quadrangular, 2.2 mm long, 0.4 mm wide at base; subdiscoidal space long and foot-shaped, 4.5 mm long, 0.8 mm wide, divided into five cells by cross-veins; AA curved, with no strong posterior branch basal of its fusion with CuA, no "heterophlebioid" anal loop; anal margin angular (male specimen); wing very narrow between base and discoidal triangle; CuA separating from MP in posterior angle of discoidal triangle and reaching AA at an acute angle; a strong cross-vein between point of fusion of AA and CuA directed towards anal angle of wing; CuA (+ AA) long, with three strong posterior branches and intercalary longitudinal veins between them; basal free part of CuA 0.3 mm long; CuA reaches posterior margin opposite nodus; area between MP and posterior wing margin with several secondary veins; base of wing distinctly petiolated, petiole 2.5 mm long and 2.0 mm wide; anal area very narrow, with one row of cells; 10-12 rows of cells between CuA and posterior wing margin; postdiscoidal area basally narrow with two rows of cells and distally greatly widened; a concave Mspl and a long secondary straight longitudinal convex vein parallel to MP, beginning just distal of discoidal triangle; MP and RP3/4 straight; nodus not well preserved but vein Cr between nodus and RA quite oblique and aligned with general trend of ScP, with several cross-veins reaching it from above and below; subnodus (Sn) long and oblique, with two cross-veins reaching it; base of RP2 just distal of end of Sn; no supplementary cell just basal of base of RP2 between RP and IR2; antenodal area well preserved; primary antenodal cross-veins distinctly stronger than secondaries, well spaced, 2.4 mm apart; arculus between primary antenodals, slightly closer to Ax2 than to Ax1; Ax0 in a rather distal position; no secondary antenodal cross-veins between Ax0 and Ax2 but 11 distal of Ax2, not aligned with the 10 antenodal cross-veins of second rank between ScP and RA; 18 postnodal cross-veins, not aligned with the subpostnodals; the two most distal postnodals reach the very oblique basal margin of the pterostigma; pterostigma elongate, 5.5 mm long, 0.5 mm wide, covering eight cells, not shifted basally; pterostigmal brace absent or very weak and basally shifted (?); area between C and RA distal of pterostigma with one row of cells; bases of RP3/4 and IR2 between nodus and arculus, apparently closer to nodus than to arculus; oblique vein "O" absent; area between MA and RP3/4 slightly widened. IR1 long not zigzagged, beginning three cells distal of base of RP2; numerous long supplementary longitudinal veins between main veins; more veins and cells in apical half than in basal half of wing.

## Genus ***Sinostenophlebia*** Hong, 1984

*Sinostenophlebia* Hong, 1984 : 136 (original description).
*Sinostenophlebia* : Nel *et al.* 1993 : 127 (discussion).

**Type species** – *Sinostenophlebia zhangjiakowensis* Hong, 1984.

**Stratum typicum** – Mesozoic.

**Locus typicus** – North of China.

**Remark** – This fossil would need a redescription because of the poor original description and figures. Its position remains uncertain.

## Genus ***Stenophlebia*** Hagen, 1866

**Type species** – *Stenophlebia amphitrite* (Hagen, 1862), designated by Nel *et al.* (1993).

**Other species** – *Stenophlebia eichstaettensis* (Nel *et al.*, 1993), *Stenophlebia latreillei* (Germar, 1839), *Stenophlebia lithographica* (Giebel, 1857) (Odonata of uncertain position), *Stenophlebia phryne* (Hagen, 1862) stat. rest., *Stenophlebia karatavica* Pritykina, 1968, ?*Stenophlebia casta* (Hagen, 1862), ?*Stenophlebia corami* Nel & Jarzembowski, 1996. A new species of *Stenophlebia* from the Upper Jurassic limestone of Nusplingen (Germany) will be described by Bechly & Schweigert (in prep.). It seems to be "intermediate" between *S. amphitrite* and *S. eichstaettense*.

**Diagnosis** – (1) wing very elongated and falked; (2) discoidal cell divided into a crossed elongate transverse triangle and a narrow hypertriangle; (3) angle between MAa and MAb around 90°; (4) subdiscoidal space more or less foot-shaped; (5) an "heterophlebioid" anal loop; (6) nodal Cr quite oblique, long, with cross-veins reaching it; (7) subnodus well aligned with nodal Cr, quite oblique, with cross-veins reaching it; (8) pterostigma elongate, basally shifted; (9) pt-brace basally shifted or absent; (10) oblique vein "O" absent; (11) a long Mspl, and a long zigzagged secondary longitudinal vein in postdiscoidal space beginning just distal of triangle; (12) one or more cells below subnodus, just basal of RP2, between RP and IR2; (13) CuA short, reaching posterior wing margin well basal of nodus; (14) male abdomen distally broadened; (15) no strong ovipositor. These two last characters are unknown in several *Stenophlebia* spp. and other Stenophlebioidea.

### *Stenophlebia amphitrite* (Hagen, 1862)

(fig. 25)

*Heterophlebia amphitrite* Hagen, 1862 : 105.
*Stenophlebia amphitrite* : Hagen 1866 : 83-86.
*Stenophlebia amphitrite* : Handlirsch 1908 : 581.
*Stenophlebia amphitrite* : Carpenter 1992 : 88 (listed).
*Stenophlebia amphitrite* : Nel *et al.* 1993 : 109-113.

**Material** – Lectotype specimen AS I 1025a,b, Munich Museum (designated by Nel *et al.* 1993).

**Other specimens** – Specimen 1951/20/aK, Jura Museum, Eichstätt (described in Nel *et al.* 1993). Specimen 4D, private Kümpel coll., Wuppertal, Germany (part and counterpart). Mr. Kümpel has willed the latter specimen to the Jura Museum, Eichstätt.

**Stratum typicum** – Upper Jurassic, Malm zeta 2b ('oberer Weißjura"), Lower Tithonian, *Hybonotum*-Zone, Solnhofen Lithographic Limestone.

**Locus typicus** – Eichstätt, southern Frankonian Alb, Bavaria, Germany.

**Diagnosis** – Nel *et al.* (1993) gave a diagnosis. We amend it as follows: (1) wings large and narrow, more than 80 mm long; (2) nodal vein Cr long, with two or three cross-veins reaching it, and well aligned with general trend of ScP; (3) subnodus short, one cell long; (4) supplementary veinlet below subnodus short, two cells long, (5) pterostigma elongate and basally recessed; (6) pterostigmal brace very basally recessed; (7) two rows of cells in anal area, with a secondary zigzagged vein more or less parallel to AP; (8) Ax1 and Ax2 well spaced, with numerous cells between them; (8) forewing Ax2 opposite MAb; (9) MP reaching posterior margin opposite nodus; (10) AA strongly curved, and subdiscoidal space large and broad, foot-shaped; (11) "Heterophlebioid" anal loop present, two-celled; antenodal and postnodal cross-veins very numerous; MAa and MAb perpendicular, i.e. discoidal triangle very transverse

**Description** – The lectotype and specimen 1951/20/aK have already been described by Nel *et al.* (1993). We describe herein the new specimen n° 4D, coll. Kümpel.

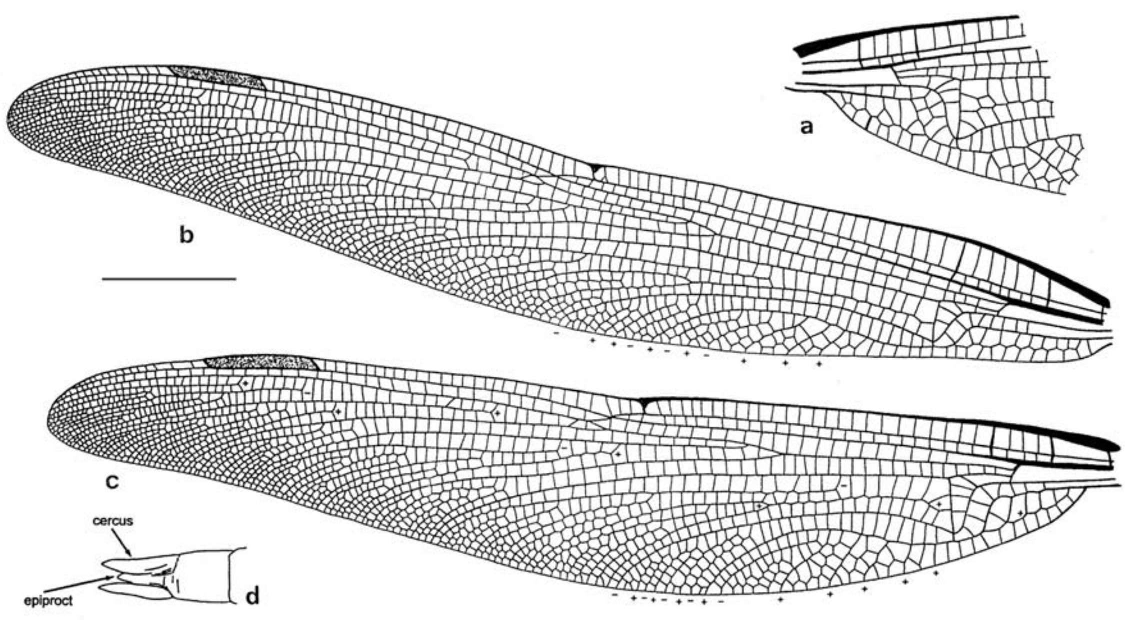



**Figure 25**
*Stenophlebia amphitrite* (Hagen, 1866), specimen n° 4D, coll. Kümpel, a. Forewing; b. Left hindwing; c. Base of Right hindwing; d. apex of the abdomen (scale bar represents 10 mm).

Forewing (fig. 25b), 84.0 mm long, 13.0 mm wide (distal of nodus); distance between nodus and base, 39.8 mm; between arculus and base, 8.2 mm; between arculus and nodus, 32.4 mm; RP separating from RP + MA distinctly closer to bend of MA than to base of RP + MA; posterior part of arculus (bdcv), between MA and MP + Cu, not aligned with anterior part; CuP separating from MP + Cu and fused with AA immediately opposite arculus; MA divided into MAa and MAb, at an angle of 90°; MAa basally nearly straight and distally curved; MAb straight; median space free of cross-veins; submedian space with two cross-veins basal of CuP; discoidal space divided into a transverse (crossed?) discoidal triangle and a longitudinal crossed hypertriangle, separated by a cross-vein not stronger than the others; discoidal triangle broad and long, 3.2 mm long and 1.6 mm wide, length of its costal side, 1.6 mm, of distal side, 3.2 mm, of posterior side, 2.9 mm; hypertriangle pentagonal, 4.7 mm long, 0.3 mm wide at base; subdiscoidal space long and foot-shaped, 4.8 mm long, 1.0 mm wide, divided into four cells by parallel cross-veins; AA curved, with a strong posterior branch basal of its fusion with CuA, an two-cells “heterophlebioid” anal loop; CuA separating from MP in posterior angle of discoidal triangle and reaching AA at right angles; CuA (+ AA) not very long, with four strong posterior branches and intercalary longitudinal veins between them; basal free part of CuA 0.3 mm long; CuA reaching posterior margin well basal of nodus; MP reaching posterior wing margin opposite nodus; area between MP and posterior wing margin smaller than the cubito-anal area, with several secondary veins; base of wing not petiolated; anal area broad, with two row of cells; six-seven rows of cells between CuA and posterior wing margin; postdiscoidal area basally narrow with two rows of cells and distally greatly widened; a concave Mspl beginning well distal of discoidal triangle; a long secondary straight longitudinal convex vein parallel to MP, beginning just distal of discoidal triangle; MP and RP3/4 curved; nodus well preserved, vein Cr between nodus and RA long, oblique and perfectly aligned with general trend of ScP, with three cross-veins reaching it from above and below; subnodus (Sn) one cell long and quite oblique, with no cross-veins reaching it; base of RP2 just distal of end of Sn; supplementary veinlet below subnodus very short, covering one cell; antenodal area well preserved; primary antenodal cross-veins distinctly stronger than secondaries, very well spaced, 7.4 mm apart; arculus between primary antenodals, slightly closer to Ax1; Ax2 opposite MAb; Ax1 and Ax2 greatly separated (7.5 mm) with five secondary antenodal cross-veins between them, but 26 distal of Ax2, not aligned with the antenodal cross-veins of second rank between ScP and RA; 27 postnodal cross-veins, not aligned with the subpostnodals; pterostigma elongate, 5.8 mm long, 0.9 mm wide, covering six cells, considerably shifted basally, 11 mm basal of wing apex; pterostigmal brace absent or maybe very weak and shifted four cells basal of the pterostigma (?); area between C and RA distal of pterostigma very long, with one row of cells; bases of RP3/4 and IR2 between nodus and arculus, closer to nodus than to arculus (RP3/4 10.0 mm and IR2 7.5 mm basal of nodus); oblique vein “O” absent; area between MA and RP3/4 widened; IR1 long not zigzagged, beginning four cells distal of base of RP2; numerous long supplementary longitudinal veins between main veins; more veins and cells in apical half than in basal half of wing.

Hindwing (fig 25 a,c). 81.0 mm long, 15.7 mm wide (basal of nodus); distance between nodus and base, 36.0 mm; between arculus and base, 7.7 mm; between arculus and nodus, 28.1 mm; RP separating from RP + MA closer to bend of MA than to base of RP + MA; posterior part of arculus (bdcv), between MA and MP + Cu, well aligned with anterior part; CuP separating from MP + Cu and fused with AA just distal of arculus; MA divided into MAa and MAb, at an angle of 96°; MAa basally straight and distally curved; MAb straight; median space free of cross-veins; submedian space crossed; discoidal space divided into a transverse crossed discoidal triangle and a longitudinal hypertriangle, separated by a cross-vein stronger than the others, beginning at bend of MP + CuA, and fused with MA above costo-distal angle of discoidal space; hypertriangle free on left wing but with one cross-vein in right wing; discoidal triangle more transverse than that of forewing, narrow and long, 4.6 mm long and 1.9 mm wide, length of its costal side, 1.7 mm, of distal side, 4.5 mm, of posterior side, 4.1 mm; hypertriangle quadrangular, 3.8 mm long, 0.5 mm wide at base; subdiscoidal space long and distinctly foot-shaped, 6.0 mm long, 1.8 to 2.1 mm wide, very broad and divided into five cells by cross-veins in left wing and into seven cells, in two rows in right wing; AA strongly curved, with a strong posterior branch basal of its fusion with CuA, a two- or three-celled “heterophlebioid” anal loop; anal margin not angular (female specimen); CuA separating from MP in posterior angle of discoidal triangle and reaching AA at a right angle; CuA (+ AA) with four strong posterior branches, and intercalary longitudinal veins between them; basal free part of CuA 0.6 mm long; CuA reaching posterior margin well basal of nodus; MP reaching posterior margin opposite nodus; area between MP and posterior wing margin smaller than the cubito-anal area, with several secondary veins; base of wing briefly petiolated, petiole 2.8 mm long and 4.0 mm wide; anal area with two rows of cells; six to eight rows of cells between CuA and posterior wing margin; postdiscoidal area basally narrow with two rows of cells and distally greatly widened; a concave Mspl beginning well distal of discoidal triangle; a long secondary straight longitudinal convex vein parallel to MP, beginning just distal of discoidal triangle; MP and RP3/4 curved; nodus well preserved, vein Cr between nodus and RA quite oblique and well aligned with general trend of ScP and with several cross-veins reaching it from above and below; subnodus (Sn) one-cell short and oblique, with one cross-vein reaching it; base of RP2 one cell distal of end of Sn; two supplementary cells and a short secondary longitudinal “stenophlebiid vein” aligned with RP2, just basal of base of RP2, between RP and IR2; antenodal area well preserved; primary antenodal cross-veins distinctly stronger than secondaries, well separated, 4.7 mm apart; arculus between primary antenodals, midway between Ax1 and Ax2; Ax2 above middle of hypertriangle; three secondary antenodal cross-veins between Ax1 and Ax2 and 25 distal of Ax2, not aligned with the antenodal cross-veins of second rank between ScP and RA; 28 postnodal cross-veins, not aligned with the subpostnodals; pterostigmal brace absent or maybe very weak and basally shifted (?); pterostigma elongate, 7.9 mm long, 1.0 mm wide, covering six cells, shifted basally, 11.0 mm basal of wing apex; area between C and RA distal of pterostigma elongate, with one row of cells; bases of RP3/4 and IR2 between nodus and arculus, closer to nodus than to arculus (RP3/4 10.2 mm and IR2

7.9 mm basal of nodus); oblique vein "O" absent; area between MA and RP3/4 widened. IR1 long not zigzagged, beginning six cells distal of base of RP2; numerous long supplementary longitudinal veins between main veins; more veins and cells in apical half than in basal half of wing.

Female abdomen with long cerci and a long epiproct (or maybe ovipositor?) (fig. 25d).

### ***Stenophlebia eichstaettensis*** (Nel *et al.*, 1993) nom. corr.

*Stenophlebia eichstattense* Nel *et al.*, 1993 : 125-127 (original description).

**Material** – Holotype specimen SOS 2329, Jura Museum, Eichstätt, Germany. We amend the name *eichstattense* (incorrect original spelling) to *eichstaettensis*.

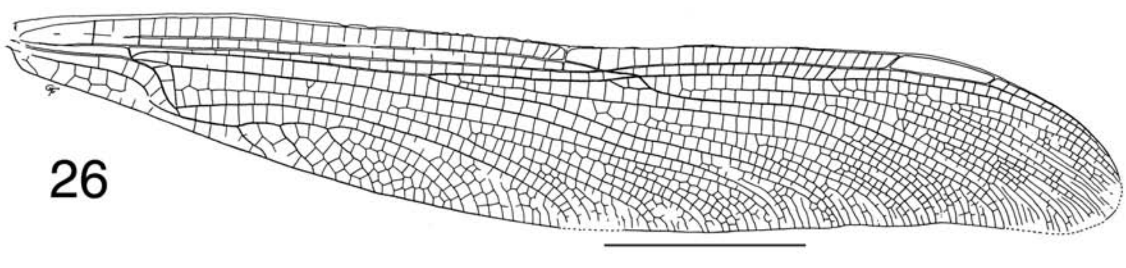
**Stratum typicum** – Upper Jurassic, Malm zeta 2b ('oberer Weißjura"), Lower Tithonian, *Hybonotum*-Zone, Solnhofen Lithographic Limestone.

**Locus typicus** – Eichstätt, southern Frankonian Alb, Bavaria, Germany.

**Diagnosis** – *S. eichstaettensis* (Nel *et al.*, 1993) differs from other species in the following features: (1) slightly smaller than *S. amphitrite* (wing length 69 mm instead of more than 80 mm in *S. amphitrite*); (2) Cr longer than in other *Stenophlebia* spp., except for *S. lithographica*, with eight cross-veins; (3) subnodus longer than in all other *Stenophlebia* spp., with three cross-veins; (4) Ax2 opposite the middle part of the hypertriangle, instead of MAb; (5) anal area narrower than that of *S. amphitrite*; (6) space between primary antenodal cross-veins narrower than in *S. amphitrite*, with only two secondary antenodals between them; (7) secondary longitudinal vein basally aligned with RP2 and longer than in other *Stenophlebia* spp., except *S. karatavica*, covering four cells in *S. eichstaettensis*; (8) angle between MAa and MAb 90° or so.

### ***Stenophlebia latreillei*** (Germar, 1839) (figs. 10, 26-29)

*Agrion latreillei* Germar, 1839 : 218 (original description).
*Calopteryx latreillei* : Charpentier 1840 : 172.
*Cordulegaster muensteri* Hagen 1850 : 360.
*Diastatomma muensteri* : Giebel 1856 : 276.
*Heterophlebia latreillei* : Hagen 1862 : 139.
*Heterophlebia aequalis* : Hagen 1862 : 124-127 (original description).
*Stenophlebia aequalis* : Hagen 1866 : 86.
*Stenophlebia phryne* : Hagen 1866 : 91.
*Stenophlebia latreillei* : Deichmüller 1886 : 44.
*Stenophlebia aequalis* : Deichmüller 1886 : 43.
*Stenophlebia latreillei* : Kirby 1890 : 170.
*Stenophlebia aequalis* : Meunier 1897 : pl. 1, fig. 1, pl. 2, fig. 2.
*Stenophlebia aequalis* : Meunier 1898 : pl. 8, fig. 16.
*Stenophlebia latreillei* : Handlirsch 1908 : 581 (synonymized with *S. Phryne*, *S. aequalis*).
*Stenophlebia latreillei* : Carpenter 1932 : 106-107.
*Stenophlebia aequalis* : Carpenter 1932 : 106 (synonymized with *S. latreillei*, without explanation).
*Stenophlebia latreillei* : Carpenter 1992 : 88 (listed).
*Stenophlebia latreillei* : Nel *et al.* 1993 : 115-125 (redescription).



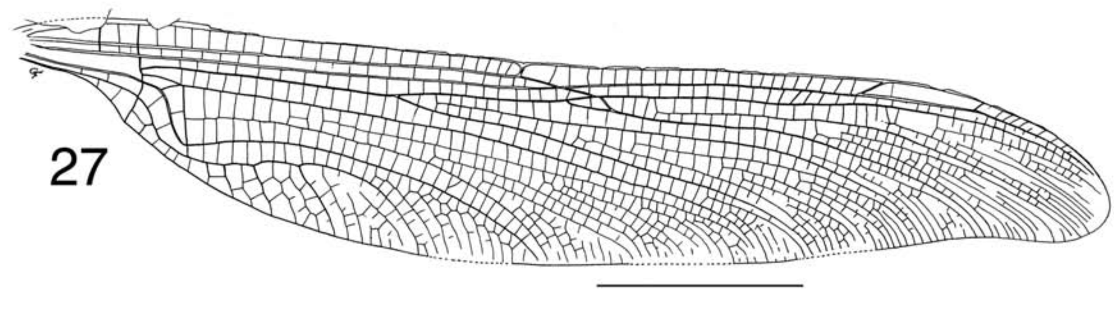




**Figure 26-27**
26, right forewing of *Stenophlebia latreillei* (Germar, 1839), specimen 1870/VII/35, Museum of Munich (scale bar represents 10 mm). – 27, right hindwing of *Stenophlebia latreillei* (Germar, 1839), specimen 1870/VII/35, Museum of Munich (scale bar represents 10 mm).

**Material** – No holotype was designated. Nel *et al.* (1993) listed the material attributed to both *S. latreillei* and *S. aequalis* and redescribed several specimens. We propose to designate as lectotype the syntype specimen 1870/VII/35, Museum of Munich, Germany.

**Stratum typicum** – Upper Jurassic, Malm zeta 2b ('oberer Weißjura"), Lower Tithonian, *Hybonotum*-Zone, Solnhofen Lithographic Limestone.

**Locus typicus** – Eichstätt, southern Frankonian Alb, Bavaria, Germany.

**Diagnosis** – Nel *et al.* (1993) proposed a revised diagnosis. We complete it as follows: (1) wing shorter than in *S. amphitrite* and *S. eichstaettensis* (wing length between 48 and 65 mm); (2) vein Cr shorter than in *S. eichstaettensis* and *S. amphitrite*; (3) subnodus nearly as long as Cr, but only one cell long, distinctly shorter than in *S. eichstaettensis*; (4) forewing Ax2 just distal of arculus; (5) hindwing Ax2 opposite arculus; (6) forewing posterior part of arculus very short; (7) angle between MAa and MAb less than 90° (discoidal triangles less transverse than in *S. eichstaettensis* and *S. amphitrite*); (8) two rows of cells in anal area of forewing; (9) anal area of hindwing narrow, with the "heterophlebioid" anal loop posteriorly opened; (10) subdiscoidal area narrow; (11) vein AA smoothly curved (unevenly curved in *S. eichstaettensis* and *S. amphitrite*); (12) pt-brace shifted three cells basally; (13) discoidal triangles very narrow.

**Note** – Carpenter (1932) synonymized *S. aequalis* with *S. latreillei*. He also figured the discoidal area of a specimen (n° 3796, Carnegie Museum, U.S.A.), which he attributed to *S. latreillei*. Unfortunately, his drawing has a probable error: the point of separation of RP from MA in the arculus is closer to the base of RP + MA than to the posterior part of arculus, unlike all the specimens of *Stenophlebia* spp. we have examined. Furthermore, this specimen would have a discoidal triangle more oblique than the lectotype of *S. latreilli* (see below), a free discoidal triangle, unlike the lectotype of *S. latreilli* and a posterior part of the arculus distinctly longer than in the lectotype of *S. latreilli*. Thus, if we consider Carpenter's drawing to be true concerning these structures, these specimens do not belong to the same species.

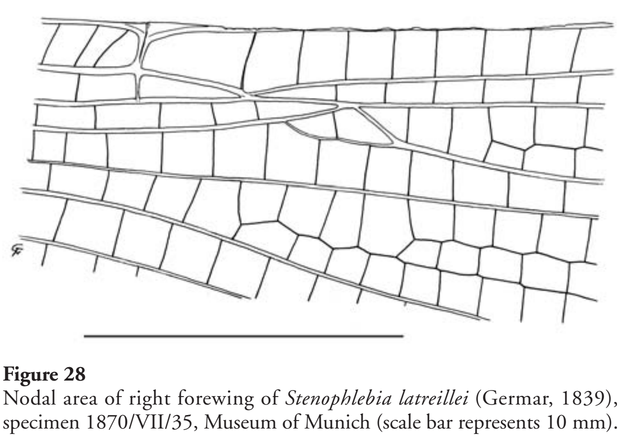


**Figure 28**
Nodal area of right forewing of *Stenophlebia latreillei* (Germar, 1839), specimen 1870/VII/35, Museum of Munich (scale bar represents 10 mm).

**Redescription** – Lectotype specimen 1870/VII/35 (after a cast of the specimen). Impression of a nearly complete specimen, with the four wings in connection with the body. This specimen was not completely prepared when Nel *et al.* (1993) studied it. But one of us (A.N.) had the opportunity to prepare it, so that the antenodal and postnodal areas are now clearly visible.

Forewing, 54.0 mm long, 9.2 mm wide (distal of nodus); distance between nodus and base, 27.1 mm; between arculus and base, 5.7 mm; between arculus and nodus, 21.6 mm; RP separating from RP + MA distinctly closer to bend of MA than to base of RP + MA; RP + MA nearly touching MP + Cu so that posterior part of arculus (bdcv) is extremely short; CuP not stronger than other cross-veins between MP + Cu and AA; MA divided into MAa and MAb, at an angle of 78°; MAa basally nearly straight; MAb straight; median space free of cross-veins; submedian space with cross-veins; discoidal space divided into a transverse free discoidal triangle and a longitudinal crossed hypertriangle, separated by a cross-vein stronger than the others, beginning at bend of MP + CuA, and fused with MA above costodistal angle of discoidal space; discoidal triangle wide and long, 2.0 mm long and 0.9 mm wide, length of its costal side, 0.8 mm, of distal side, 2.0 mm, of posterior side, 2.1 mm; hypertriangle triangular, very narrow, 1.6 mm long, less than 0.1 mm wide at base; subdiscoidal space long and distinctly foot-shaped, about 3 mm long, 1.0 mm wide, divided into three cells by cross-veins; AA strongly curved, with a strong posterior branch basal of its fusion with CuA, an unicellular "heterophlebioid" anal loop; CuA separating from MP in posterior angle of discoidal triangle and reaching AA at acute angle; CuA (+ AA) long, with four strong posterior branches and intercalary longitudinal veins between them; basal free part of CuA 0.4 mm long; CuA reaching posterior margin well basal of nodus; MP reaching posterior margin just distal of nodus; area between MP and posterior wing margin smaller than the cubito-anal area, with several secondary veins; base of wing not petiolated; anal area not narrow, with two rows of cells; six rows of cells between CuA and posterior wing margin; postdiscoidal area basally narrow with two rows of cells and greatly widened distally; a concave Mspl beginning well distal of discoidal triangle; a long secondary straight longitudinal convex vein parallel to MP, beginning just distal of discoidal triangle; MP and RP3/4 curved; nodus well preserved, vein Cr between nodus and RA long, oblique and perfectly aligned with general trend of ScP, with one or two cross-veins reaching it from above and below; subnodus (Sn) nearly as long as Cr, quite oblique, with one cross-vein reaching it; base of RP2 opposite end of Sn; two supplementary cells and a secondary longitudinal short "stenophlebiid" vein, well aligned with RP2, just basal of base of RP2, between RP and IR2; antenodal area well preserved; primary antenodal cross-veins distinctly stronger than secondaries, approx-

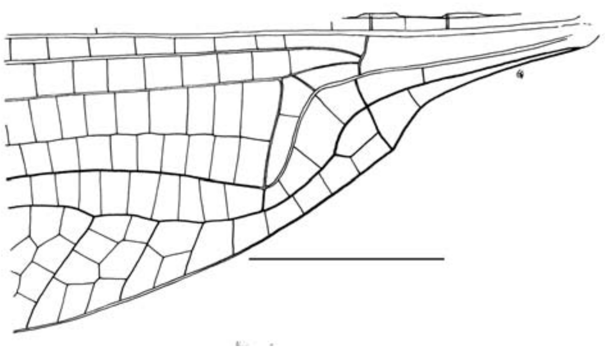


**Figure 29**
Discoidal area of left hindwing of *Stenophlebia latreillei* (Germar, 1839), specimen 1870/VII/35, Museum of Munich (scale bar represents 5 mm).

imate, 2.2 mm apart; arculus between primary antenodals, very near to Ax2; one secondary antenodal cross-vein between Ax1 and Ax2 but 29 distal of Ax2, not aligned with the antenodal cross-veins of second rank between ScP and RA; 23 postnodal cross-veins, not aligned with the subpostnodals; pterostigma elongate, 4.8 mm long, 0.8 mm wide, covering six or seven cells, relatively shifted basally; pterostigmal brace shifted three to five cells basal of pterostigma; area between C and RA distal of pterostigma elongate, with one row of cells; bases of RP3/4 and IR2 between nodus and arculus, closer to nodus than to arculus (RP3/4 6.2 mm and IR2 5.0 mm basal of nodus); oblique vein "O" absent; area between MA and RP3/4 widened; IR1 long not zigzagged, beginning three cells distal of base of RP2; numerous long supplementary longitudinal veins between main veins; more veins and cells in apical half than in basal half of wing.

Hindwing, 53.5 mm long, 9.7 mm wide (distal of nodus); distance between nodus and base, 24.3 mm; between arculus and base, 6.0 mm; between arculus and nodus, 18.4 mm; RP separating from RP + MA closer to bend of MA than to base of RP + MA; posterior part of arculus (bdcv), between MA and MP + Cu, not aligned with anterior part but of normal length, not as in forewing; CuP separating from MP + Cu and fused with AA opposite arculus, slightly curved; MA divided into MAa and MAb, at an angle of 78°; MAa nearly straight; MAb straight; median space free of cross-veins; submedian space with one or two cross-veins; discoidal space divided into a transverse crossed discoidal triangle and a longitudinal free hypertriangle, separated by a cross-vein stronger than the others, beginning at bend of MP + CuA, and fused with MA just above costo-distal angle of discoidal space; discoidal triangle more narrow and transverse than that of forewing, relatively narrow and long, 2.9 mm long and 1.0 mm wide, length of its costal side, 1.0 mm, of distal side, 2.9 mm, of posterior side, 3.1 mm; hypertriangle quadrangular, 1.8 mm long, 0.2 mm wide at base; subdiscoidal space long and weakly foot-shaped, 3.9 mm long, 0.9 mm wide, rather narrow and divided into three or four cells by cross-veins; AA not strongly curved, with a strong posterior branch aligned with CuP and reaching anal angle; a "heterophlebioid" anal loop, but more or less posteriorly opened; anal margin angular (male specimen); CuA separating from MP in posterior angle of discoidal triangle and reaching AA at an acute angle; CuA (+ AA) with four strong posterior branches, and intercalary longitudinal veins between them; basal free part of CuA, 0.5 mm long; CuA reaching posterior margin well basal of nodus; MP reaching posterior margin slightly distal of nodus; area between MP and posterior wing margin broad, but smaller than the cubito-anal area, with several secondary veins; base of wing petiolated, petiole about 2 mm long and 2.4 mm wide; anal area with one row of cells; six rows of cells between CuA and posterior wing margin; postdiscoidal area basally narrow with two rows of cells and distally greatly widened; a concave Mspl; a long secondary straight longitudinal convex vein parallel to MP, beginning just distal of discoidal triangle; MP and RP3/4 curved; nodus well preserved, vein Cr between nodus and RA very oblique and well aligned with general trend of ScP, with two cross-veins reaching it from above and below; subnodus (Sn) long and oblique, with two cross-vein reaching it; base of RP2 just distal of end of Sn; two supplementary cells and a short secondary longitudinal "stenophlebiid" vein aligned with RP2, just basal of base of RP2, between RP and IR2; antenodal area well preserved; primary antenodal cross-veins distinctly stronger than secondaries, strongly approximate, 1.8 mm apart; arculus opposite Ax2; one secondary antenodal cross-vein between Ax1 and Ax2 and 23 distal of Ax2, not aligned with the antenodal cross-veins of second rank between ScP and RA; 24 postnodal cross-veins, not aligned with the subpostnodals; pterostigmal brace basally recessed by four cells; pterostigma elongate, 5.3 mm long, 0.8 mm wide, covering eight cells, shifted basally; area between C and RA distal of pterostigma elongate, with one row of cells; bases of RP3/4 and IR2 between nodus and arculus, closer to nodus than to arculus (RP3/4 5.6 mm and IR2 3.8 mm basal of nodus); oblique vein "O" absent; area between MA and RP3/4 widened. IR1 long not zigzagged, beginning four cells distal of base of RP2; numerous long supplementary longitudinal veins between main veins; more veins and cells in apical half than in basal half of wing.

**Discussion** – The wing lengths of the various specimens attributed to *S. latreillei* vary greatly. Also, the lectotype specimen has its vein RP basally very close to RA and the posterior part of the arculus very short in both forewings, unlike other specimens attributed to this species. It is difficult to determine if these differences are intra- or interspecific. Only a revision based on as many specimens as possible will permit the determination of the variability within the *S. latreillei* – *S. aequalis* complex.

### *Stenophlebia lithographica* (Giebel, 1857)
(*in* Stenophlebiidae gen. and sp. *incertae sedis* n. sit.)

*Calopteryx lithographica* Giebel, 1857 : 380-382 (original description).
*Heterophlebia lithographica* : Hagen 1862 : 105 (very short redescription, synonymy).
*Stenophlebia lithographica* : Deichmüller 1886 : 45.
*Stenophlebia lithographica* : Kirby 1890 : 170.
*Stenophlebia latreillei* : Handlirsch 1908 : 581-582 (tentatively synonymized).
*Stenophlebia latreillei* : Nel *et al.* 1993 : 115.

**Material** – The type specimen of Giebel (1857) is probably lost. Deichmüller (1886) indicated that it should be in the University of Heidelberg.

**Stratum typicum** – Upper Jurassic, Malm zeta 2b ("oberer Weißjura"), Lower Tithonian, *Hybonotum*-Zone, Solnhofen Lithographic Limestone.
**Locus typicus** – Eichstätt, southern Frankonian Alb, Bavaria, Germany.

**Note** – The successive descriptions of this species are nearly useless for separating it from other *Stenophlebia* spp., in particular *S. phryne*. Hagen (1862) indicated that "*Calopteryx lithographica*" would fall near the genus "*Heterophlebia*" (in fact in *Stenophlebia*). He added that it has a wing 55 mm long, as *S. phryne*, but is of uncertain position. The exact location of the type material remains unknown. Therefore, we prefer to consider this taxon as *incertae sedis*.

### ***Stenophlebia phryne*** (Hagen, 1862)
(figs. 30-32)

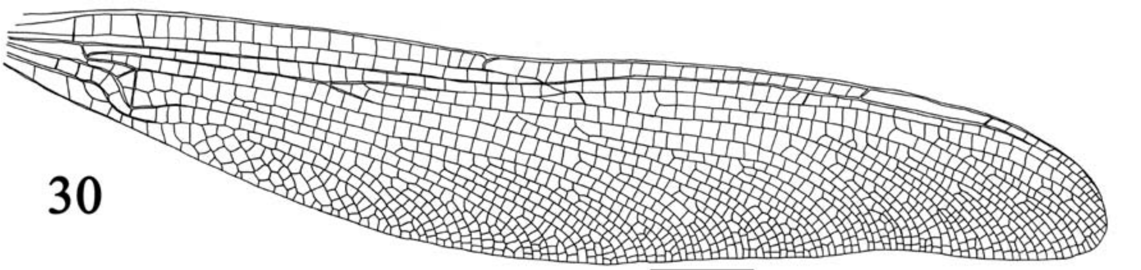
*Heterophlebia phryne* Hagen, 1862 : 105 (very brief original description).
*Stenophlebia phryne* : Hagen 1866 : 91-92.
*Stenophlebia phryne* : Deichmüller 1886 : 43.
*Stenophlebia latreillei* : Handlirsch 1908 : 582 (synonymy with *S. latreillei*).
*Stenophlebia phryne* : Nel *et al.* 1993 : 115 (listed as synonym of *S. latreillei*).

**Material** – Lectotype specimen MCZ Coll. Carpenter 6212, with the original labels "*Stenophlebia phryne* Hag., Palaeont. XV. p. 35 no 21. Type, Solnhofen. Dr. Krantz" and "*Stenophlebia latreillei* Germar, Solenhofen Jurassic", at the "Museum of Comparative Zoology, Harvard University, U.S.A. Hagen (1862) indicated that his type series comprises six specimens of unknown location. Hagen (1866) indicated five specimens in the Museum of Munich and four from the Krantz collection. Thus, it is possible or even likely that the specimen n° 21 of coll. Krantz belongs to the type series of 1862. Anyway, we here designate it as lectotype to clarify this taxonomic problem. Further new specimen n° 70/29, coll. Tischlinger H., Germany.

**Stratum typicum** – Upper Jurassic, Malm zeta 2b ("oberer Weißjura"), Lower Tithonian, *Hybonotum*-Zone, Solnhofen Lithographic Limestone.

**Locus typicus** – Eichstätt, southern Frankonian Alb, Bavaria, Germany.

**Diagnosis** – The original [and early] descriptions of "*S. phryne*" are very poor (Hagen 1862, 1866). Deichmüller (1886) noted that it is very hard to separate "*S. aequalis*" and "*S. phryne*". After the present study, it appears clear that these are two different species. *S. phryne* differs



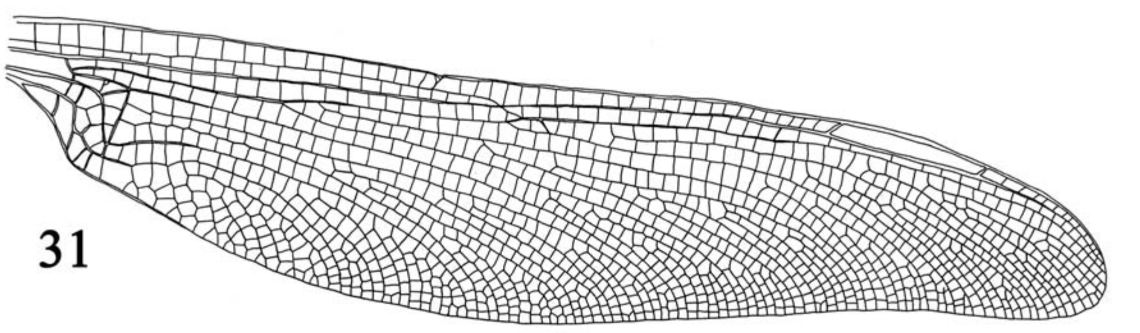


**Figure 30-31**
30, right forewing of *Stenophlebia phryne* (Hagen, 1862), specimen 70/29, coll. Tischlinger (scale bar represents 5 mm). – 31, right hindwing of *Stenophlebia phryne* (Hagen, 1862), specimen 70/29, coll. Tischlinger (scale bar represents 5 mm).

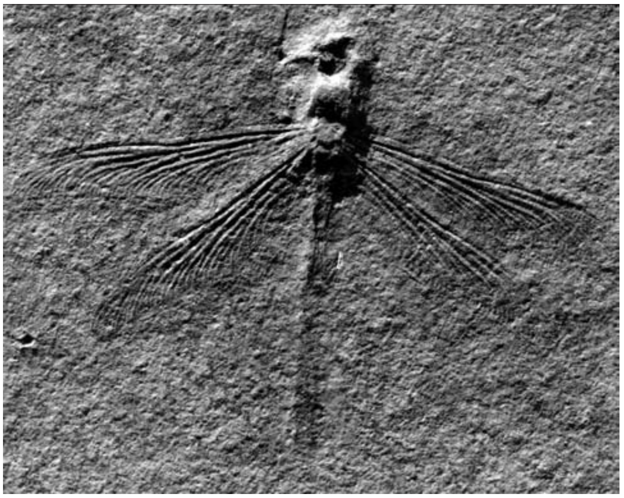


**Figure 32**
Photograph of *Stenophlebia phryne* (Hagen, 1862), specimen 70/29, coll. Tischlinger.

from *S. latreillei* in the presence of a very long nodal vein Cr (character shared with *S. eichstaettensis*), but it has a very short, one-cell long subnodus, unlike *S. eichstaettensis*. Furthermore, it has a short supplementary longitudinal vein basal of RP2 and aligned with this vein. Its discoidal triangle is narrower and longer than that of *S. eichstaettensis* (see Nel *et al.*, 1993); hindwing length 57 mm, instead of 69 mm in *S. eichstaettensis*; subdiscoidal space broad and distinctly foot-shaped; vein AA with a strong curve. Forewing Ax2 opposite MAb; hindwing arculus midway between Ax1 and Ax2. Pterostigmal brace distinctly recessed basally. Area between MP and posterior wing margin large and broad.

**Description** – The original descriptions of "*S. phryne*" are very poor (Hagen 1862, 1866), i.e. the differences between "*S. phryne*" and "*S. aequalis*" proposed by Hagen are: wing shorter and the female abdomen slightly narrower in *S. phryne* than in *S. aequalis*. As the lectotype specimen is poorly preserved, we redescribe *S. phryne* based on the new, well-preserved specimen 70/29. It is an impression of a nearly complete individual, with the four wings in connection with the body.

Forewing, 55.0 mm long, 10.1 mm wide (distal of nodus); distance between nodus and base, 23.0 mm; between arculus and base, 3.5 mm; between arculus and nodus, 19.6 mm; RP separating from RP + MA distinctly closer to bend of MA than to base of RP + MA; posterior part of arculus, between MA and MP + Cu, not aligned with anterior part; CuP separating from MP + Cu and fused with AA immediately opposite arculus; MA divided into MAa and MAb, at an angle of 90°; MAa basally nearly straight and curved distally; MAb straight; median space free of cross-veins; submedian space with one cross-vein basal of CuP; discoidal space divided into a transverse crossed discoidal triangle and a longitudinal crossed hypertriangle, separated by a cross-vein stronger than the others, beginning at bend of MP + CuA, and fused with MAb in costo-distal angle of discoidal space; discoidal triangle wide and long, 1.9 mm long and 0.8 mm wide, length of its costal side, 1.0 mm, of distal side, 1.9 mm, of posterior side, 1.5 mm; hypertriangle quadrangular, 2.2 mm long, 0.2 mm wide at base; subdiscoidal space long and slightly foot-shaped, 4.6 mm long, 0.7 mm wide, divided into four cells by cross-veins; AA curved, with a strong posterior branch basal of its fusion with CuA, an unicellular "heterophlebioid" anal loop; CuA separating from MP at posterior angle of discoidal triangle and reaching AA at right angle; CuA (+ AA) with three strong posterior branches and intercalary longitudinal veins between them; basal free part of CuA, 0.3 mm long; CuA reaching posterior margin well basal of nodus; area between MP and posterior wing margin smaller than the cubito-anal area, with several secondary veins; base of wing not petiolated; anal area narrow, with one row of cells; six rows of cells between CuA and posterior wing margin; postdiscoidal area basally narrow with two rows of cells and greatly widened distally; a concave Mspl and a long secondary straight longitudinal convex vein parallel to MP, beginning just distal of discoidal triangle; MP and RP3/4 curved; nodus well preserved, vein Cr between nodus and RA very long, oblique and perfectly aligned with general trend of ScP, with several cross-veins reaching it from above and below; subnodus (Sn) one cell long but quite oblique, with no cross-veins reaching it; base of RP2 one cell distal of end of Sn; two supplementary cells and a secondary longitudinal short "stenophlebiid" vein, well aligned with RP2, just basal of base of RP2, between RP and IR2; antenodal area well preserved; primary antenodal cross-veins distinctly stronger than secondaries, well separated, 3.3 mm apart; arculus between primary antenodals, very near to Ax1; Ax2 opposite MAb; two secondary antenodal cross-veins between Ax1 and Ax2 but 20 distal of Ax2, not aligned with the 17 antenodal cross-veins of second rank between ScP and RA; 22 postnodal cross-veins, not aligned with the subpostnodals; pterostigma elongate, 6.1 mm long, 0.6 mm wide, covering five cells, relatively shifted basally; pterostigmal brace shifted three cells basal of pterostigma; area between C and RA distal of pterostigma elongate, with one row of cells; bases of RP3/4 and IR2 between nodus and arculus, closer to nodus than to arculus (RP3/4 7.2 mm and IR2 5.6 mm basal of nodus); oblique vein "O" absent; area between MA and RP3/4 widened; IR1 long not zigzagged, beginning four cells distal of base of RP2; numerous long supplementary longitudinal veins between main veins; more veins and cells in apical half than in basal half of wing.

Hindwing, 52.0 mm long, 11.2 mm wide (distal of nodus); distance between nodus and base, 20.0 mm; between arculus and base, 2.9 mm; between arculus and nodus, 17.0 mm; RP separating from RP + MA closer to bend of MA than to base of RP + MA; posterior part of arculus (bdcv), between MA and MP + Cu, not aligned with anterior part; CuP separating from MP + Cu and fused with AA opposite arculus; MA divided into MAa and MAb, at an angle of 97°; MAa basally straight and distally curved; MAb straight; median and submedian spaces free of cross-veins; discoidal space divided into a transverse crossed discoidal triangle and a longitudinal crossed hypertriangle, separated by a cross-vein stronger than the others, beginning at bend of MP + CuA, and fused with MAb in costo-distal angle of discoidal space; discoidal triangle more transverse than that of forewing, narrow and long, 2.6 mm long and 1.1 mm wide, length of its costal side, 1.3 mm, of distal side, 2.6 mm, of posterior side, 2.2 mm; hypertriangle quadrangular, 2.5 mm long, 0.2 mm wide at base; subdiscoidal space long and distinctly foot-shaped, very broad and divided into five cells by cross-veins; AA strongly curved, with a strong posterior branch basal of its fusion with CuA, "heterophlebioid" anal loop present, but posteriorly opened; anal margin angular (male specimen); CuA separating from MP in posterior angle of discoidal triangle and reaching AA at a right angle; CuA (+ AA) short, with three strong posterior branches, and intercalary longitudinal veins between them; basal free part of CuA, 0.5 mm long; CuA reaching posterior margin well basal of nodus; area between MP and posterior wing margin smaller than the cubito-anal area, with several secondary veins; base of wing shortly petiolated, petiole less than 1.2 mm long and 2.6 mm wide; anal area with one row of cells; six to eight rows of cells between CuA and posterior wing margin; postdiscoidal area basally narrow with two rows of cells and distally greatly widened; a concave Mspl and a long secondary straight longitudinal convex vein parallel to MP, both beginning just distal of discoidal triangle; MP and RP3/4 curved; nodus well preserved, vein Cr between nodus and RA very oblique and well aligned with general trend of ScP, with several cross-veins reaching it from above and below; subnodus (Sn) one-cell long and oblique, with one cross-vein reaching it; base of RP2 one cell distal of end of Sn; two supplementary cells and a short secondary longitudinal "stenophlebiid" vein aligned with RP2, just basal of base of RP2, between RP and IR2; antenodal area well preserved; primary antenodal cross-veins distinctly stronger than secondaries, well separated, 2.6 mm apart; arculus between primary antenodals, slightly closer to Ax1 than to Ax2; Ax2 opposite bend of MP + CuA in discoidal triangle; two secondary antenodal cross-veins between Ax1 and Ax2 and 16 distal of Ax2, not aligned with the 16 antenodal cross-veins of second rank between ScP and RA; 24 postnodal cross-veins, not aligned with the subpostnodals; pterostigmal brace recessed basally by two cells; pterostigma elongate, 7.0 mm long, 0.7 mm wide, covering six cells, shifted basally; area between C and RA distal of pterostigma elongate, with one row of cells; bases of RP3/4 and IR2 between nodus and arculus, closer to nodus than to

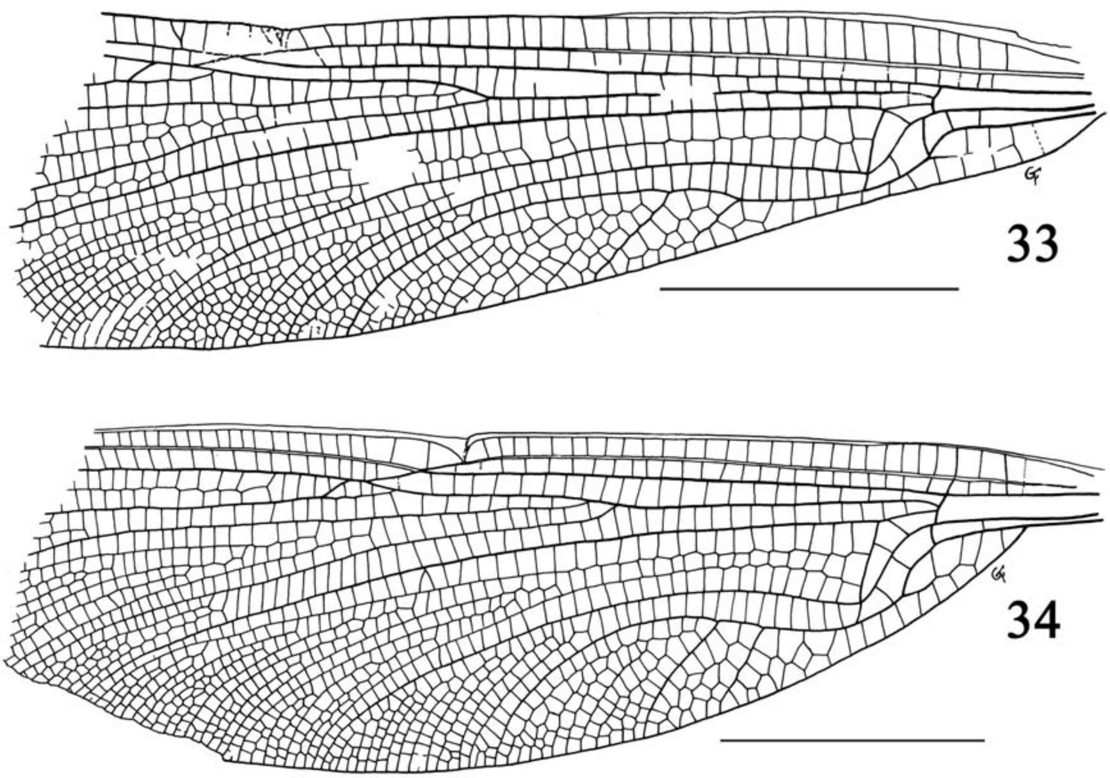



**Figure 33-34**
33, left forewing of *Stenophlebia karatavica* Pritykina, 1968, holotype specimen (scale bar represents 10 mm). – 34, left hindwing of *Stenophlebia karatavica* Pritykina, 1968, holotype specimen (scale bar represents 10 mm).

arculus (RP3/4 6.7 mm and IR2 5.1 mm basal of nodus); oblique vein "O" absent; area between MA and RP3/4 widened. IR1 long, not zigzagged, beginning four cells distal of base of RP2; numerous long supplementary longitudinal veins between main veins; more veins and cells in apical half than in basal half of wing.

**Remark** – The lectotype specimen shares with specimen 70/29 the following characters: a very long Cr and a short subnodus, wing length similar (57 mm long in lectotype specimen). It differs from specimen 70/29 in the following points: discoidal triangle narrower, base of RP2 opposite end of subnodus instead of being one cell distal; subnodus shorter and less oblique; anal area apparently very wide, with the posterior margin rounded (female specimen).

We also tentatively attribute the specimen 1960/I/311 (Museum of Munich), that Nel *et al.* (1993) included in *S. latreillei*, to the same species because it shares several characters with specimen 70/29 of *S. phryne*, i.e. a very large subdiscoidal space of the same shape; a secondary branch of AA reaching the posterior margin in the posterior angle of the wing; the same shape of the cubito-anal area; same dimensions; similar discoidal triangle and hypertriangle.

### ***Stenophlebia karatavica*** Pritykina, 1968
(figs. 33-37)

*Stenophlebia karatavica* Pritykina, 1968 : 45-46, text-fig. 16, pl. 4, fig. 2 (original description).
*Stenophlebia karatavica* : Nel *et al.* 1993 : 127 (discussion).

**Holotype** – Specimen PIN 2066/26, Arthropod Laboratory, Palaeontological Institute, Moscow, Russia.

**Stratum typicum** – Upper Jurassic, Callovian-Kimmeridgian or Oxfordian-Kimmeridgian (Zherikhin & Gratshev 1993; Mostoski & Martínez-Delclòs 2000).

**Locus typicus** – Karatau, Chimkent region, Southern Kazakhstan, C.E.S.

**Diagnosis** – (1) hindwing broader than those of other *Stenophlebia* spp. (in hindwing, ratio [distance (nodus, wing base) / max. width of wing], 1.86 instead of 1.95 in *S. phryne*, > 2 in other species); (2) vein Cr relatively short; (3) subnodus slightly longer than Cr, two-cells long, distinctly shorter than in *S. eichstaettensis*; (4) forewing Ax2 probably opposite arculus; (5) hindwing Ax2 opposite arculus; (6) angle between MAa and MAb less than 90°; (7) hindwing discoidal triangle longer and more transverse than in forewing; (8) two rows of cells in anal area in forewing; (9) anal area of hindwing wide, with the "heterophlebioid" anal loop posteriorly closed; (10) vein AA abruptly curved and making a angle with CuAb; (12) cubito-anal area wide, with three long posterior branches of CuA; (13) postdiscoidal area broad, with Mspl and convex secondary longitudinal vein beginning on discoidal triangle; (14) forewing area between MP and CuA very narrow along posterior margin; (15) base of IR2 one cell distal of that of RP3/4, instead of more than two cells in other Stenophlebiidae; (16) supplementary longitudinal vein basally aligned with RP2 is four-cells long.

**Description** – Impression of a thorax with the four wings in connection. The wing apices are missing. The two meso- or metathoracic (?) legs are short and strong. Femora 9.1 mm long and 2.0 mm wide. Tibia 7.0 mm long. Tarsus about 3.0 mm long. Two rows of short and strong spines along inner margin of femora and two rows of slightly stronger spines along inner margin of tibia. Thorax compressed, with strips of coloration, 1.1 mm high.

Forewing preserved part, 37 mm long, 11.2 mm wide (distal of nodus); distance between nodus and base, 27.3 mm; between arculus and base, 5.7 mm; between arculus and nodus, 21.9 mm; RP separating from RP + MA closer to bend of MA than to base of RP + MA; posterior part of arculus (bdcv), between MA and MP + Cu, not aligned with anterior part; CuP separating from MP + Cu and fused with AA just opposite arculus; MA divided into MAa and MAb, at an angle of 75°; MAa basally nearly straight and distally curved; MAb straight; median space free of cross-veins; submedian space with one or two cross-veins basal of CuP; discoidal space divided into a transverse free discoidal triangle and a longitudinal free rather short hypertriangle, separated by a cross-vein stronger than the others, beginning at bend of MP + CuA, and fused with MAb at costo-distal angle of discoidal space; discoidal triangle narrow and long, 2.3 mm long and 1.0 mm wide, length of its costal side, 1.0 mm, of distal side, 2.3 mm, of posterior side, 2.2 mm; hypertriangle quadrangular, 1.7 mm long, 0.3 mm wide at base; subdiscoidal space long and slightly foot-shaped, 4.4 mm long, 1.2 mm wide, divided into three cells by cross-veins; AA curved and with a angle with CuAb, with a strong posterior branch basal of its

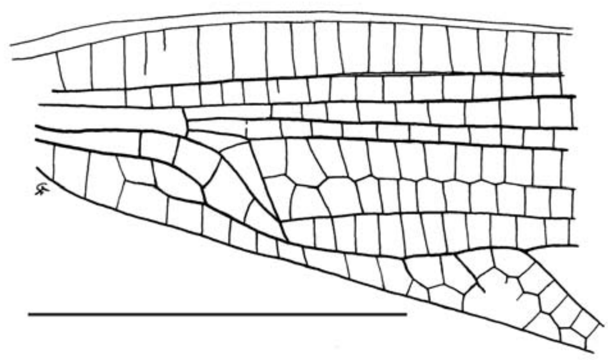


**Figure 35**
Base of right forewings of *Stenophlebia karatavica* Pritykina, 1968, holotype specimen (scale bar represents 10 mm).

fusion with CuA, an unicellular "heterophlebioid" anal loop; CuA separating from MP in posterior angle of discoidal triangle, long, slightly curved, and reaching AA at nearly a right angle; CuA (+ AA) very long, with three strong posterior branches and several intercalary longitudinal veins between them; basal free part of CuA, 0.7 mm long; CuA (+ AA) reaching posterior margin well basal of nodus; area between MP and posterior wing margin distinctly smaller than the cubito-anal area; base of wing not petiolated; anal area with two rows of cells; six or seven rows of cells between CuA and posterior wing margin; postdiscoidal area basally narrow with two rows of cells and greatly widened distally; a concave Mspl and a long secondary straight longitudinal convex vein parallel to MP, beginning just distal of discoidal triangle; MP and RP3/4 curved; nodus not well preserved, vein Cr between nodus and RA one cell long, oblique and perfectly aligned with general trend of ScP, with maybe one cross-vein reaching it from above; subnodus (Sn) long and quite oblique; base of RP2 two cells distal of end of Sn; two supplementary cells and a secondary longitudinal short "stenophlebiid" vein, well aligned with RP2, just basal of base of RP2, between RP and IR2; antenodal area well preserved; primary antenodal cross-veins not stronger than secondaries; arculus between primary antenodals; presence of secondary antenodal cross-veins between Ax1 and Ax2 but about 30 distal of Ax2, not aligned with the numerous antenodal cross-veins of second rank between ScP and RA; more than 25 postnodal cross-veins, not aligned with the subpostnodals; pterostigma not preserved; bases of RP3/4 and IR2 between nodus and arculus, closer to nodus than to arculus; oblique vein "O" absent; area between MA and RP3/4 widened; numerous long supplementary longitudinal veins between main veins.

Hindwing preserved part, 43.0 mm long, 13.0 mm wide (distal of nodus); distance between nodus and base, 24.4 mm; between arculus and base, 6.2 mm; between arculus and nodus, 18.1 mm; RP separating from RP + MA closer to bend of MA than to base of RP + MA; posterior part of arculus (bdcv), between MA and MP + Cu, nearly aligned with anterior part; CuP separating from MP + Cu and fused with AA opposite arculus; MA divided into MAa and MAb, at an angle of 72°; MAa basally straight and distally curved; MAb straight; median space free of cross-veins; submedian space with one cross-vein; discoidal space divided into a transverse crossed discoidal triangle and a longitudinal free hypertriangle, separated by a cross-vein slightly

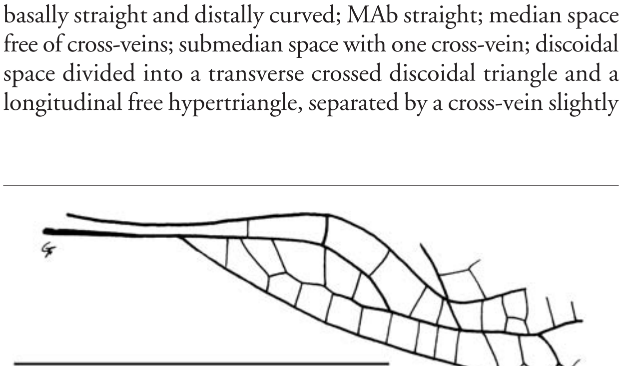


**Figure 36**
Base of right hindwing of *Stenophlebia karatavica* Pritykina, 1968, holotype specimen (scale bar represents 10 mm).

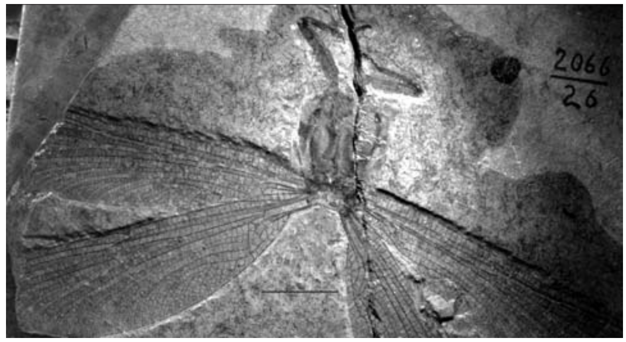



**Figure 37**
Photograph of *Stenophlebia karatavica* Pritykina, 1968, holotype specimen (scale bar represents 10 mm).

stronger than the others, beginning at bend of MP + CuA, and fused with MAb just above costo-distal angle of discoidal space; discoidal triangle more transverse than that of forewing, narrow and long, 3.2 mm long and 1.1 mm wide, length of its costal side, 1.0 mm, of distal side, 3.1 mm, of posterior side, 3.0 mm; hypertriangle quadrangular, 1.8 mm long, 0.4 mm wide at base; subdiscoidal space long and distinctly foot-shaped, 4.5 mm long, very broad and divided into three cells by cross-veins; AA strongly curved and with a angle with CuAb, with a strong posterior branch basal of its fusion with CuA, a one or two celled "heterophlebioid" anal loop; anal margin rounded (female specimen); CuA separating from MP in posterior angle of discoidal triangle and reaching AA at nearly a right angle; CuA (+ AA) with four strong posterior branches, and intercalary longitudinal veins between them; basal free part of CuA, 0.8 mm long; CuA reaching posterior margin opposite nodus; area between MP and posterior wing margin smaller than the cubito-anal area, with several secondary veins; base of wing shortly petiolated, petiole 3.2 mm long and 2.6 mm wide; anal area with one or two rows of cells; nine to ten rows of cells between CuA and posterior wing margin; postdiscoidal area basally rather broad with three rows of cells and distally greatly widened; a concave Mspl and a long secondary straight longitudinal convex vein parallel to MP, both beginning just distal of discoidal triangle; MP and RP3/4 curved; nodus well preserved, vein Cr between nodus and RA quite oblique and well aligned with general trend of ScP, but short and with two cross-veins reaching it, one directly below nodus; subnodus (Sn) two-cells long and oblique, with one cross-vein reaching it; base of RP2 one cell distal of end of Sn; five supplementary cells and a relatively long secondary longitudinal "stenophlebiid" vein aligned with RP2, just basal of base of RP2, between RP and IR2; antenodal area well preserved; primary antenodal cross-veins stronger than secondaries, approximated, 1.9 mm apart; arculus between primary antenodals just opposite Ax2; 25 secondary antenodal cross-veins distal of Ax2, not aligned with the antenodal cross-veins of second rank between ScP and RA; more than 20 postnodal cross-veins, not aligned with the subpostnodals; pterostigma not preserved; bases of RP3/4 and IR2 between nodus and arculus, closer to nodus than to arculus; oblique vein "O" absent; area between MA and RP3/4 widened. IR1 long not zigzagged, beginning four cells distal of base of RP2; numerous long supplementary longitudinal veins between main veins.

### *?Stenophlebia casta* (Hagen, 1862) (figs. 38-39)

*Heterophlebia casta* Hagen, 1862 : 106 (original description).
*Heterophlebia casta* : Weijenbergh 1869 : 235 (list, synonymized with *Libellula brevialata* Münster).
*Heterophlebia casta* : Kirby 1890 : 169 (list, synonymized with doubt with *Libellula brevialata* Münster).
*Stenophlebia casta* : Handlirsch 1908 : 582 (in *Stenophlebia*).
*Stenophlebia casta* : Nel *et al.* 1993 : 125 (in *Stenophlebia incertae sedis*).

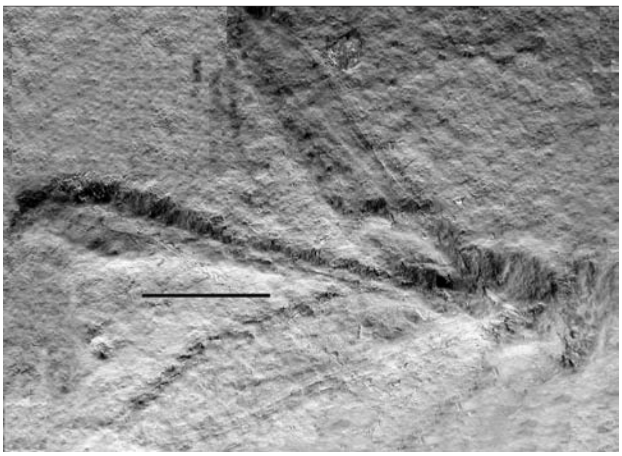


**Figure 38**
Photograph of *Stenophlebia casta* (Hagen, 1862), Neotype specimen SOS 4656, Jura Museum (scale bar represents 10 mm).

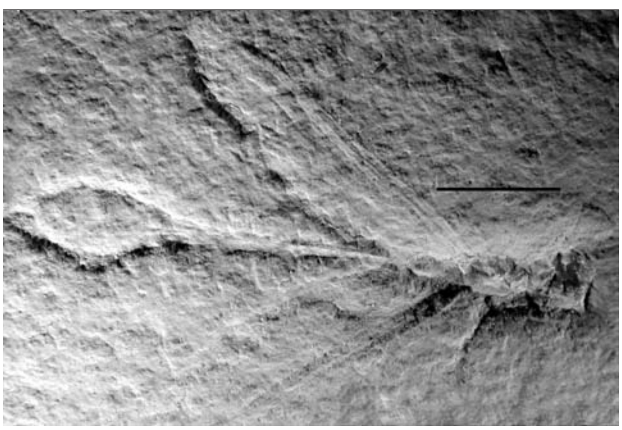


**Figure 39**
Photograph of *Stenophlebia casta* (Hagen, 1862), specimen BMMS 266a,b, Bürgermeister Müller Museum (scale bar represents 10 mm).

**Material** – Location of the holotype unknown, it seems to have been lost during the Second World War. Neotype specimen SOS 4656, Jura Museum, Eichstätt, Germany (ex coll. Schäfer). Specimen BMMS 266a,b, Bürgermeister Müller Museum, Solnhofen, Germany. Three further specimens are present in private collection of Mr. Knodel (Ilze, Germany), the best of which was figured *in* Frickhinger (1999: 57, fig. 96). Finally, there is a specimen no. "MA 237 A" in the private collection of Mr. G. Stöbener (Staufenberg, Germany).

**Stratum typicum** – Upper Jurassic, Malm zeta 2b ('oberer Weißjura"), Lower Tithonian, *Hybonotum*-Zone, Solnhofen Lithographic Limestone.

**Locus typicus** – Solnhofen, southern Frankonian Alb, Bavaria, Germany.

**Remark** – Weijenbergh (1869) proposed to synonymize *Heterophlebia casta* with *Libellula brevialata* Münster. This last species is probably a *nomen nudum*, since Münster (1839) did not name any of the fossil Solnhofen Odonata he briefly described. In the forthcoming redescription of *Stenophlebia casta* by Bechly (in prep.) it will be demonstrated that this enigmatic taxon does neither belong to the genus *Stenophlebia* nor to Stenophlebiidae at all. It represents a new family and genus of Heterophlebioptera, close to Liassophlebiidae.

### *?Stenophlebia corami* Nel & Jarzembowski, 1996

*Stenophlebia corami* Nel & Jarzembowski, 1996 : 87-91, figs. 1-3.

**Material** – Holotype specimen n° 018957/-8, Robert Coram Coll.

**Stratum typicum** – Lower Cretaceous, Middle Purbeck Beds, Clement's Bed 175.

**Locus typicus** – Durlston Bay, Dorset, U.K., National Grid Reference SZ 038784.

**Remark** – This species was described on the basis of the costo-median part of a wing, showing the nodal Cr, subnodus and RP2 base characteristic of the Stenophlebiidae. Nevertheless, in the same levels, there is a Stenophlebiidae that belongs to a different genus, *Mesostenophlebia anglicana* n. gen., n. sp., and that could correspond to the same taxon because there is no part in common to the two fossils. Thus, if *Stenophlebia corami* is a Stenophlebiidae, it is less certain that it belongs to the genus *Stenophlebia*.

## PHYLOGENETIC ANALYSIS

We have performed a cladistic analysis of the species attributable to the Stenophlebioptera, based on 42 characters mainly defined on wing venation, having max. three states (see character list and matrix in plate 1), using the Zygoptera (represented by a *Lestes* sp., a *Calopteryx* sp., and a *Coenagrion* sp.), Tarsophlebiidae (represented by the type species *Tarsophlebia eximia* (Hagen, 1862)), Isophlebioidea (represented by *Isophlebia aspasia* Hagen, 1866 and *Bellabrunetia catherinae* Fleck & Nel, 2002), and Epiophlebiidae (represented by *Epiophlebia superstes* (Selys, 1889)) as potential outgroup(s), because of the uncertainty in the basal phylogeny of the Epiproctophora. The analysis was performed using the computer software packages Paup 4.0b.10 and MacClade 3.08 (to examine the character distribution), with the Branch and Bound option. We have tested all combinations of outgroups. The results were independent of the combinations and the order of introduction of outgroups in the matrix.

The "ingroup *sensu stricto*" comprises the species attributable to the Stenophlebiidae, Prostenophlebiidae n. fam., Liassostenophlebiidae n. fam., the Liassogomphidae (represented by *Liassogomphus brodiei* (Buckmann, 1843)), modern Anisoptera (represented by taxa of the main extant families, i.e. Petaluridae, Aeshnidae, Gomphidae, Libellulidae), Aeschnidiidae (checked after all the described taxa of this highly diverse family, after Fleck & Nel submitted), Henrotayidae n. fam., Liassophlebiidae (represented by *Liassophlebia magnifica* Tillyard, 1925), Heterophlebiidae (represented by *Heterophlebia buckmani* (Brodie, 1849)), Myopophlebiidae (represented by *Paraheterophlebia marcusi* Nel & Henrotay, 1993), and Juraheterophlebiidae n. fam. Depending on the analyses, we have added the Epiophlebiidae and Isophlebioptera to an "ingroup *sensu lato*". The characters were first considered as unordered. In a second time, the twenty multistate characters (with at least states 0, 1, and 2) were considered as ordered (option ORD of Paup).

The analyses made with unordered characters gave nine most parsimonious trees (length = 113 steps, consistency index = 0.5664, consistency index excluding uninformative characters = 0.5625, retention index = 0.7742, RC = 0.4383) (see fig. 40). The analysis made with ordered multistate characters gave two most parsimonious trees (length = 123 steps, consistency index = 0.5203, consistency index excluding uninformative characters = 0.5164, retention index = 0.7958, RC = 0.4141).

Several important results concerning the topology of the "ingroup *sensu lato*" are independent of the choice of the character status (ordered versus unordered), i.e. the following clades are present in all most parsimonious trees:

(**1**) The clade [Isophlebioidea + (Epiophlebioidea + Anisopteromorpha)] is supported by the characters "7 (state 1)', "27 (state 1)', "39 (state 1)', and "40 (state 1)".

(**2**) The clade Epiophlebioidea + Anisopteromorpha is supported by the character "42" (state 1), and the characters "30 (state 1)", "31 (state 1)", and "32 (state 1)", which are unknown in many of these fossil taxa, but the avalaible information is congruent with this hypothesis (no known case of homoplasy). The larvae of the Heterophlebiidae and Stenophlebiidae were probably of anisopteroid type.

(**3**) The clade Anisopteromorpha is supported by five characters: "5 (states 2)" (but state 2 is also present in Henrotayiidae and Liassophlebiidae), characters "9" and "10" (all corresponding to the division of hindwing discoidal cell in triangle and hypertriangle, but unknown in Liassostenophlebiidae), and "27 (state 2)", corresponding to the presence of a "heterophlebioid" anal loop and to the structure of the branching of AA on CuA. These structures are important for the flight.

(**4**) The clade Heterophlebioptera *sensu* Nel *et al.* (1993) or Bechly (1996) (= Myopophlebiidae + (Liassophlebiidae + (Juraheterophlebiidae + Heterophlebiidae))) is less strongly supported than the preceding, by the character "33 (state 1)". This character state is also present in the *Stenophlebia* spp., *Cretastenophlebia*, and the (Liassogomphidae + (Aeschnidiidae + modern Anisoptera)). The Juraheterophlebiidae fall as sister group of the Heterophlebiidae but the clade (Juraheterophlebiidae + Heterophlebiidae) is supported by only character "17 (state 0)" that concern the pterostigma. The clade [Liassophlebiidae + (Heterophlebiidae + Juraheterophlebiidae)] is supported by the character "11 (state 1, no secondary antenodal cross-veins between C and ScP)". This character is highly homoplastic within the Odonata (present in some Isophlebiomorpha and absent in others, same thing in Zygoptera). Thus, the monophyly of this group is weakly supported. The Myopophlebiidae is supported by the reversal of character "28" to state 0 (forewing MA and MAb strictly aligned). The structures of their subdiscoidal space and of the "heterophlebioid" anal loop are very variable within this family. Thus, it could be paraphyletic, but only a more precise phylogenetic analysis of the relationships between the "heterophlebioid" taxa is necessary before any conclusion on this point.

(**5**) The clade Trigonoptera (= [Stenophlebioptera & (Liassogomphidae + (Aeschnidiidae + modern Anisoptera)) & Henrotayiidae], sister group of

Heterophlebioptera, is supported by the characters states "4 (state 1)", "36 (state 1)", "37 (state 1)", which all concern the division of the forewing discoidal cell in a triangle and a hypertriangle, and "40 (angle between CuAb and AA very weak or absent)". These are "twist" structures, important during the flight.

The situation diverges between the two options of treatment of the multistate characters in the inner topology of this last clade. Using the unordered option, the Henrotayiidae falls at the base of the "anisopterid" clade [Henrotayiidae + (Liassogomphidae + (Aeschnidiidae + modern Anisoptera))], this clade being supported by the character state "23 (state 0)" (reversal). Using the ordered option, the Henrotayiidae falls in a trichotomy with the Stenophlebioptera and (Liassogomphidae + (Aeschnidiidae + modern Anisoptera)). Nevertheless, if we exclude the character "4" (division of discoidal cell in triangle and hypertriangle, unknown in *Henrotayia*) and the character "5" that concerns the same structure in the hindwing, from the "ordered" analysis, the Henrotayiidae falls again at the base of the "anisopterid" group. If we only consider the character "23" as ordered, it is not sufficient to change anything to the analysis under the option "all characters unordered".

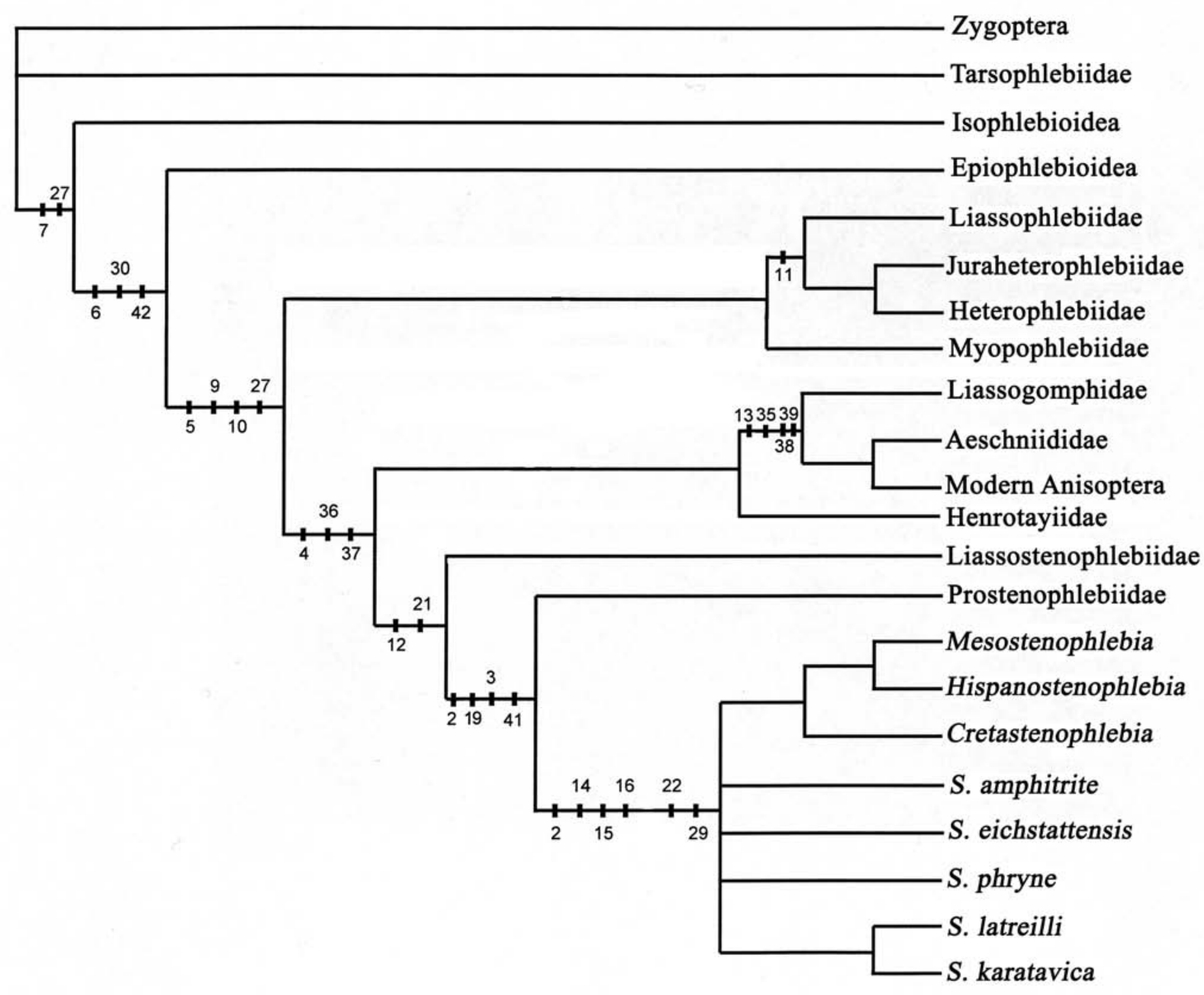



**Figure 40**
Strict consensus cladogram ("tree T1") of the phylogenetic analysis of the Stenophlebioptera. The numbers correspond to the characters supporting the branches.

**Table 1** – Matrix of character states for the phylogenetic analysis of the Anisopteromorpha and Stenophlebioptera.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Prostenophlebia* | 0 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 |
| *Hispanostenophlebia* | 2 | 2 | 2 | 1 | 2 | 2 | 1 | ? | 2 | 2 | 0 | 1 | 0 | 1 |
| *Mesostenophlebia* | 2 | 2 | 1 | 1 | ? | ? | 1 | 0 | ? | ? | 0 | 1 | 0 | 2 |
| *Liassostenophlebia* | 1 | 0 | 0 | 1 | ? | ? | 1 | 1 | ? | ? | 0 | 1 | 0 | 0 |
| *Cretastenophlebia* | 2 | 2 | 1 | ? | 2 | 2 | 1 | ? | 3 | 2 | 0 | 1 | 0 | 2 |
| *S. amphitrite* | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 0 | 3 | 2 | 0 | 1 | 0 | 2 |
| *S. latreilli* | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 0 | 2 | 2 | 0 | 1 | 0 | 1 |
| *S. eichstaettensis* | 1 | 2 | 1 | 1 | 2 | 1&2 | 1 | 1 | 3 | 2 | 0 | 1 | 0 | 2 |
| *S. phryne* | 2 | 2 | 2 | 1 | 2 | 1 | 1 | 1 | 2 | 2 | 0 | 1 | 0 | 2 |
| *S. karatavica* | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 0 | 2 | 2 | 0 | 1 | 0 | 1 |
| *Juraheterophlebia* | 0 | 0 | 1 | ? | 2 | 1 | 1 | ? | 2 | 1 | 1 | 0 | 0 | 0 |
| Heterophlebiidae | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 0 |
| Myopophlebiidae | 0 | 0 | 0 | 0 | 1&2 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| Liassophlebiidae | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 0 |
| Liassogomphidae | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 1 | 0 |
| Aeschnidiidae | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 0 | 3 | 2 | 0 | 0 | 1 | 0 |
| modern Anisoptera | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 0 | 2&3 | 1 | 0 | 0 | 1 | 0 |
| Epiophlebiidae | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Isophlebioidea | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0&1 | 0 | 0 | 0 |
| Tarsophlebiidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0&1 | 0 | 0 | 0 | 0&1 | 0 | 0 |
| Zygoptera | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0&1 | 0 | 0 | 0&1 | 0 | 0 | 0 |
| *Henrotayia* | 0 | 0 | 0 | ?/0 | 1 | ? | 1 | ? | 1 | 1 | 1 | 0 | 0 | 0 |

| | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Prostenophlebia* | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 2 | 1 | 0 | 1 | 2 | 1 |
| *Hispanostenophlebia* | 1 | 1 | 1 | ? | 1 | 2 | 2 | 1 | 2 | ? | 2 | 1 | 2 | 1 |
| *Mesostenophlebia* | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 2 | 1 | 2 | 1 |
| *Liassostenophlebia* | 0 | 0 | 1 | 2 | 0 | 1 | 2 | ? | ? | 0 | 0 | 1 | 2 | 1 |
| *Cretastenophlebia* | 1 | 1 | 1 | 2 | 1 | 0 | 2 | 1 | 1 | ? | 2 | 1 | 2 | ? |
| *S. amphitrite* | 1 | 1 | 1 | 2 | 1 | 1&2 | 1 | 1 | 1 | 0 | 1 | 1 | 2 | 1 |
| *S. latreilli* | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 0 | 2 | 1 | 2 | 1 |
| *S. eichstaettensis* | 1 | 1 | 1 | 2 | 1 | 2 | 2 | 1 | 1 | 0 | 0 | 1 | 2 | 1 |
| *S. phryne* | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 0 | 0 | 1 | 2 | 1 |
| *S. karatavica* | ? | ? | ? | ? | 1 | 2 | 2 | 1 | 1 | 0 | 2 | 1 | 2 | 1 |
| *Juraheterophlebia* | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 | ? | 0 | 0 | 2 | 1 |
| Heterophlebiidae | 0 | 0 | 0 | 0&1&2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 1 |
| Myopophlebiidae | 0 | 0 | 0&1 | 0&1 | 0 | 0&1 | 0 | 0&1 | 1 | 0 | 0 | 0 | 2 | 0 |
| Liassophlebiidae | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 1 |
| Liassogomphidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 |
| Aeschnidiidae | 0&1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 |
| modern Anisoptera | 0&1 | 0&1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 |
| Epiophlebiidae | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0&1 | 1 | 1 |
| Isophlebioidea | 0&1 | 0&1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0&1 |
| Tarsophlebiidae | 0 | 0 | 1 | 0 | 0 | 0 | 0&1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| Zygoptera | 0 | 0 | 0&1 | 0 | 0&1 | 0 | 0 | 0 | 0&1&2 | 0&1 | 2 | 1 | 0 | 0&1 |
| *Henrotayia* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 2 | ? |

| | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Prostenophlebia* | 0 | ? | ? | ? | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 2 | 1 | 1 |
| *Hispanostenophlebia* | 1 | ? | ? | ? | 0 | 0 | 0 | ? | ? | 0 | ? | 3 | 1 | 1 |
| *Mesostenophlebia* | ? | ? | ? | ? | 0 | ? | ? | 2 | 2 | 0 | ? | 3 | 1 | 1 |
| *Liassostenophlebia* | 0 | ? | ? | ? | 0 | ? | ? | 1 | 1 | 0 | ? | 3 | 0 | 1 |
| *Cretastenophlebia* | 1 | ? | ? | ? | 1 | 1 | 0 | ? | ? | 0 | 1 | 3 | 1 | 1 |
| *S. amphitrite* | 2 | ? | ? | ? | 1 | 2 | 0 | 2 | 2 | 0 | 1 | 2 | 1 | 1 |
| *S. latreilli* | 2 | ? | ? | ? | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 2 | 1 | 1 |
| *S. eichstaettensis* | 2 | ? | ? | ? | 1 | 1&2 | 0 | 2 | 2 | 0 | ? | 2 | 1 | 1 |
| *S. phryne* | 2 | ? | ? | ? | 1 | 1&2 | 0 | 2 | 2 | 0 | 1 | 2 | 1 | 1 |
| *S. karatavica* | ? | ? | ? | ? | 1 | 0 | 0 | 1 | 2 | 0 | ? | 2 | 1 | 1 |
| *Juraheterophlebia* | 0 | ? | ? | ? | 1 | 2 | 0 | ? | ? | 0 | ? | 1 | 0 | 1 |
| Heterophlebiidae | 0 | ? | ? | ? | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| Myopophlebiidae | 0 | 1 | 1 | ? | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| Liassophlebiidae | 0 | 1 | 1 | ? | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| Liassogomphidae | 0 | ? | ? | ? | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 3 | 0 | 1 |
| Aeschnidiidae | 0 | ? | 1 | 1 | 1 | 2 | 1 | 2 | 2 | 1 | ? | 3 | 0 | 1 |
| modern Anisoptera | 0 | 1 | 1 | 1 | 0&1 | 2 | 1 | 2 | 1 | 1 | 2 | 3 | 0 | 1 |
| Epiophlebiidae | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| Isophlebioidea | 0&1&2 | 0 | ? | 0 | 1 | 1&2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| Tarsophlebiidae | 0 | ? | ? | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Zygoptera | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0&1 | 0 |
| *Henrotayia* | 0 | ? | ? | ? | 0 | 2 | 0 | ?/0 | ?/0 | 0 | ?/1 | 3 | 0 | 0 |

We also tested the hypothesis that the Henrotayiidae had several structures of "heterophlebioid" type that are unknown in fact, i.e. "forewing discoidal cell not divided into a triangle and an hypertriangle", and "male hindwing anal triangle elongate". Thus, we coded the state 0 for characters "4", "36", "37" and state 1 for character "39". This hypothesis can be considered because of the great venational similarities between the "heterophlebioid" and henrotayiid hindwings in other characters. Under this hypothesis, the analysis based on unordered characters gives 57 most parsimonious trees, with no longer clade Heterophlebioptera and a polytomy affecting the "anisopterid" lineage, the Stenophlebioptera, and the families Henrotayiidae, Myopophlebiidae, Liassophlebiidae, and (Juraheterophlebiidae + Heterophlebiidae) in the corresponding strict consensus tree. This analysis shows that the hypothesis that the Henrotayiidae had several structures of "heterophlebioid" type is conflictual with the known characters of this family.

Whatever is the option of treatment of the multistate characters, the clade (Liassogomphidae + (Aeschnidiidae + modern Anisoptera)) is present, supported by the characters "13 (state 1)", "35 (state 1)", "38 (state 1)", and "39 (state 2)" (position of the nodal Cr, presence of "anisopteroid" anal loop, pseudo-IR1 present, male anal triangle transverse), which are important for flight or mating.

The Aeschnidiidae appear more closely related to modern "anisopteroid" families than to Liassogomphidae, contra Bechly (1996) who considered them as sister group of the Liassogomphidae within the Aeschnidioptera, itself sister group of the modern Anisoptera. No exclusive synapomorphy supports the grouping of the Aeschnidiidae with the modern Anisoptera, except for a character also present in Stenophlebiidae, i.e. character "36 (state 1, forewing hypertriangle long)". We can add the cross-vein between the hypertriangle and the discoidal triangle ending at the angle between MA and MAb, which is reversed in some Anisoptera with small wings and homoplastic in Stenophlebiomorpha. The aeschnidiid larva is of "cavilabiata", libelluloid type, but the larvae of the Liassogomphidae and of the Stenophlebiomorpha remain unknown. Note that the Aeschnidiidae have a strong, oblique and well-defined vein (AA + CuA)b, as other Anisoptera but it is very short because intercepted by a "neo-vein", the Aspl (Nel & Martínez-Delclòs 1993).

The Stenophlebioptera = [(Stenophlebiidae + Prostenophlebiidae) + Liassostenophlebiidae] is monophyletic in all analyses, supported by strict synapomorphies, characters "12 (state 1, structure of nodal Cr)" and "21 (very oblique subnodus)" and by a weaker character "1 (distal part of area between CuA and posterior wing margin very broad)", which is reversed in *Prostenophlebia*. *Liassostenophlebia* is mainly characterized by its small size, and by many plesiomorphic characters, i.e. presence of a vein "O", very few secondary longitudinal secondary veins between the main veins, etc. The Stenophlebioidea (= Prostenophlebiidae + Stenophlebiidae) is supported by character states "2 (state 1)", "3 (state 1, presence of a long straight concave 'Mspl' and convex longitudinal vein in postdiscoidal area)", "19 (state 1, vein 'O' absent)", and "41 (state 1)". *Prostenophlebia* is characterized by its long wing petioles, i.e. character states "23 (state 2)" and "24 (state 1)". The same character defines the Juraheterophlebiidae. Note that the wing petiolation is a highly homoplastic character within the Odonatoptera, which convergently occurred in Protozygoptera, Triadophlebioptera, many Zygoptera, Isophlebioptera, Epiophlebiidae, etc., and probably correlated with the flight.

The Stenophlebiidae is supported by numerous synapomorphies, viz. characters "2 (state 2)", "14 (Cr long to very long)" (although its distribution of the two states "Cr long" versus "Cr very long" is homoplastic in the family), "15 (state 1)", "16 (state 1)", and "22 (state 1)". The clade (*S. latreillei* + *S. karatavica*) is weakly supported by character "34 (state 0)", also present in *Hispanostenophlebia*. Only the character "29 (state 1)" supports the clade (*Cretastenophlebia* + (*Hispanostenophlebia* + *Mesostenophlebia*)), but it is unknown in *Mesostenophlebia*.

The inner topology of the Stenophlebiidae changes with the option characters "ordered" versus "unordered". Using unordered characters, there is a polytomy affecting the *Stenophlebia* spp., except for the group (*S. latreillei* & *S. karatavica*) and the clade (*Cretastenophlebia* + (*Hispanostenophlebia* + *Mesostenophlebia*)) (see tree T1 proposed in table 2). When using ordered characters this polytomy is solved as follows: ((*S. latreilli* + *S. karatavica*) + (*S.phryne* + (*S. eichstaettensis* + (*S. amphitrite* + (*Cretastenophlebia* + (*Hispanostenophlebia* + *Mesostenophlebia*)))))). The genus *Stenophlebia* appears paraphyletic. There are numerous differences between the *Stenophlebia* spp., i.e. (see descriptions above, also Nel *et al.* 1993) in the shape of the discoidal triangle, the relative position of the arculus and Ax2, the length of nodal Cr and subnodus, etc. The genera *Hispanostenophlebia*, *Mesostenophlebia* and *Cretastenophlebia* are characterized by autapomorphies.

**Notes**

(**1**) a calculation of the Bremer's indices (1994) shows, for the analysis based on [Zygoptera & Tarsophlebiidae] as outgroups, and all characters unordered (minimal tree length 113 steps):

(a) The search for trees with 114 steps or less yields to 213 trees. The clades Stenophlebiidae, (Stenophlebiidae + Prostenophlebiidae), (Liassostenophlebiidae + (Stenophlebiidae + Prostenophlebiidae)), Anisopteromorpha, and (Liassogomphidae + (modern Anisoptera + Aeschnidiidae)) are preserved, as for the relative positions of the Isophlebioptera, and Epiophlebiidae. Only the clade Heterophlebiomorpha, the basal position of the Henrotayiidae in the "anisopterid" lineage, and the inner organization of the Stenophlebiidae are no longer maintained;

(b) The search for trees with 115 steps or less yields to 2725 trees and preserves the clades Stenophlebiidae, Stenophlebioptera, (Liassogomphidae & modern Anisoptera & Aeschnidiidae), (Epiophlebiidae & Anisopteromorpha & Isophlebioidea), but with a polytomy.

(c) The search for trees with 116 steps or less only preserves the clades (Liassogomphidae & modern Anisoptera & Aeschnidiidae), Stenophlebiidae and the "ingroup *sensu lato*".

(d) The search for trees with 117 steps exceeds the capacity of our computer.

Thus, the Bremer" indices show that the character set best supports the clades within the Stenophlebioptera and the "anisopterid" lineage.

(**2**) The stratigraphic record of the concerned taxa is clearly incomplete, but more or less depending of the groups: if the oldest known representatives of the two sister groups Stenophlebioptera and "Anisoptera *sensu lato*" are both Liassic, the oldest representative of the clade Anisopteromorpha is Lower Liassic but its sister group Epiophlebiidae is only known by two extant species. Interestingly, the larvae of the two *Epiophlebia* spp. live in very particular biotas, in cold freshwater streams of Japan and Himalayas (Tillyard 1921; Asahina 1954; Tani & Miyatake 1979). Similarly, the very basal family Tarsophlebiidae is only known from the Upper Jurassic and Lower Cretaceous. As the oldest known Isophlebioptera are Triassic, the same minimal age should be attributed to the tarsophlebiid lineage. The known Tarsophlebiidae are highly specialized Odonatoptera, mainly characterized by their very long and slender legs and hypertrophied ovipositor, probably adapted to a very particular palaeoenvironment. A Protozygoptera: Protomyrmeleontidae that has been discovered in the same Upper Jurassic lithographic limestone with *Tarsophlebia eximia* (Hagen, 1862) also had very long and slender legs (Martínez-Delclòs & Nel 1996). The Triassic and Liassic taxa of the tarsophlebiid lineage, still unknown, may not have been fossilised because of their possible particular palaeoecology, as for the Epiophlebiidae.

The Liassogomphidae are still strictly Lower Jurassic. Ren (1994) described the genus and species *Chrysogomphus beipiaoensis* (based on an adult specimen from the Upper Jurassic of Liaoning, China) and attributed it to the Liassogomphidae. After the figure and photograph of Ren (1994), this taxon is clearly not related to this family because its hindwing discoidal triangle is not transverse but elongate, with a secondary longitudinal vein in the postdiscoidal area that begins in a strong angle in MAb. These characters suggest strong affinities with the Aeshnoptera. *Chrysogomphus* can be excluded from the Liassogomphidae but a redescription will be necessary to clarify its exact phylogenetic position within the Anisoptera. The family Liassogomphidae remains strictly Liassic and do not extend in the Upper Jurassic.

## CONCLUSION

The "Anisozygoptera" is a polyphyletic group (Nel *et al.* 1993; Bechly 1996), its maximal "diversity" occurring during the Jurassic and Cretaceous, with no definite Cenozoic record. The first representatives are known from the Upper Triassic of Australia, Southern Africa, and England (Triassolestidae, "isophlebioid" family of rather uncertain phylogenetic position, see Nel *et al.* 2003 in press). The "Anisozygoptera" is now reduced to the extant genus *Epiophlebia*. The Stenophlebioptera (Lower Jurassic - Lower Cretaceous) are known from numerous specimens in the Tithonian of Solnhofen-Eichstätt (Germany), the Upper Jurassic of Karatau (Kazakhstan, C.I.S.), and the Mid Mesozoic of North China. It is now also recorded from the Lower Jurassic of Luxembourg and the Lower Cretaceous of England. The new discoveries increase the knowledge of the palaeogeography of this clade. The present discovery of *Hispanostenophlebia* n. gen. also removes the problem of the apparent absence of the "Anisozygoptera" in the Lower Cretaceous of Spain, although this group is well documented in numerous Mesozoic outcrops in Europe, Asia, Australia and Antarctica. It is still perplexing that no "Anisozygoptera" have been discovered among the hundreds of fossil odonates from the Lower Cretaceous Crato Formation of NE Brazil. It was also the case for the Mesozoic strata of the Liaoning Province (China) since the recent discovery of a new genus of Campterophlebiidae (Fleck & Nel 2002).

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## REFERENCES


Asahina S. 1954 – *A morphological study of a relict Dragonfly* Epiophlebia superstes *Selys (Odonata, Anisozygoptera).* – The Japan Society for the Promotion of Science, Tokyo: 153 p.

Bechly G. 1995 – Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta: Odonatoptera), unter besonderer Berücksichtigung der Phylogenetischen Systematik und des Grundplanes der *Odonata. – *Petalura*, Böblingen, special–volume **1**: 1-341.

Bechly G. 1996 – Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata), unter besonderer Berücksichtigung der Phylogenetischen Systematik und des Grundplanes der *Odonata. – *Petalura*, Böblingen, Special Volume **2**, 402 p. (Revised edition of the 1995 publication, with an English appendix including a new phylogenetic system of fossil and Recent Odonata).

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. 1998 – *Phylogeny and systematics of fossil dragonflies (Insecta: Odonatoptera) with special reference to some Mesozoic outcrops*. – 765 p. PhD thesis, University Tübingen.

Bechly G. 1999 – Phylogenetic Systematics of Odonata. Website on the Internet, *http://www.bechly.de/phylosys.htm* (will be electronically published in 2003 on CD-Rom by Schorr M., Lindeboom M. (eds), in press. Fundamentals of Odonatological Research. *ODOLITonCD 1.0*, Tübingen).

Bechly G. in prep – A re-description of *Stenophlebia casta* and description of a new species of *Nannogomphus* (Odonata: Parastenophlebiidae n. fam. and Nannogomphidae) from the Upper Jurassic Solnhofen Limestone in Germany. – *Stuttgarter Beiträge zur Naturkunde*, (B).

Bechly G., Nel A., Martínez-Delclòs X., Fleck G. 1998 – Four new dragonfly species from the Upper Jurassic of Germany and the Lower Cretaceous of Mongolia (Anisoptera: Hemeroscopidae, Sonidae, and Proterogomphidae). – *Odonatologica*, **27**: 149-187.

Bremer K. 1994 – Branch support and tree stability. – *Cladistics*, **10**: 295-304.

Bode A. 1953 – Die Insektenfauna des ostniedersachsichen Oberen Lias. – *Palaeontographica* (A), **103**: 1-375.

Carpenter F.M. 1932 – Jurassic insects from Solenhofen in the Carnegie Museum and the Museum of Comparative Zoology. – *Annals of the Carnegie Museum*, **21**: 97-129.

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.

Charpentier T. de 1840 *De libellulinis petreficatis. Libellulinae Europaeae descriptae ac depictae, cum tabulis XLVIII coloratis*. Lipsiae, Leopold Voss: 170-173.

Clements R.G. 1993 (for 1992) – Type-section of the Purbeck Limestone Group, Durlston Bay, Swanage, Dorset. – *Proceedings of the Dorset Natural History and Archaeological Society*, **114**, 181-206.

Deichmüller J.V. 1886 – Die Insekten aus dem lithographischen Schiefer mit Dresdener Museum. – *Mitteilungen aus dem Königlichen Mineralogisch Geologischen und Prähistorischen Museum in Dresden*, Cassel, **37**: 1-84.

Diéguez C., Martín–Closas C., Meléndez N., Rodríguez–Lázaro J., Trinçao P. 1995 – Biostratigraphy. *In*: Meléndez, N. (coord.), *Las Hoyas. A lacustrine Konservat–Lagerstätte, Cuenca, Spain.* II International Symposium of Lithographic Limestones, Universidad Complutense de Madrid: 77-79.

Fleck G., Bechly G., Nel A., Escuillié F. 2002 – The larvae of the Mesozoic family Aeschnidiidae and their phylogenetic implications (Insecta: Odonata: Anisoptera) – *Palaeontology*, **45**: 165-184.

Fleck G., Nel A. 2002 – The first isophlebioid dragonfly (Odonata: Isophlebioptera: Campterophlebiidae) from the Mesozioc of China. – *Palaeontology*, **45**: 1123-1136.

Fleck G., Nel A. Submitted – Revision of the Mesozoic family Aeschnidiidae (Odonata: Anisoptera). – *Mémoires du Muséum National d'Histoire Naturelle*, Paris.

Fleck G., Nel A., Martínez-Delclòs X., Jarzembowski E.A., Bechly G., in press – A revision of the Mesozoic dragonfly family Tarsophlebiidae, with a discussion on the phylogenetic positions of the Tarsophlebiidae and Sieblosiidae (Odonatoptera: Panodonata). – *Geodiversitas*.

Frickhinger K.A. 1999 – *Die Fossilien von Solnhofen 2 - The fossils of Solnhofen 2*. Goldschneck Verlag: 190 p.

Giebel C.G. 1856 – *Fauna der Vorwelt mit steter Breucksichtigung der Lebenden Thiere*, **2** (1). *Die Insekten und Spinnen*, Brodhaus, Leipzig: xviii + 511 p.

Giebel C.G. 1857 – Zur Fauna des lithographischen Schiefers von Solenhofen. – *Zeitschrift für die Gesamten Naturwissenschaften*, Berlin, **9**: 373-383.

Germar E.F. 1839 – Die versteinerten Insekten Solenhofens. – *Nova Acta Leopoldiana Carola Akademia,* **19**: 187-222.

Hagen H.A. 1850 – Odonates fossiles. *In*: Selys-Longchamps E. de & Hagen H. A., Revue des Odonates ou libellules d'Europe. – *Mémoires de la Société Scientifique de Liège*, **6**: xxii + 406 p.

Hagen H.A. 1862 – Über die Neuropteren aus dem Lithographischen Schiefer im Bayern. – *Paleontographica*, **10**: 96–145.

Hagen H.A. 1866 – Die Neuropteren aus dem Lithographischen Schiefer im Bayern. – *Paleontographica*, **15**: 57–96.

Handlirsch A. 1906-1908 – *Die fossilen Insekten und die Phylogenie der rezenten Formen. Handbuch für Paläontologen und Zoologen*. Engelman W. (publ.), Leipzig: ix + 1430 p.

Handlirsch A. 1920 – Palaeontologie. Systematische Übersicht. *In*: Schöder, C. (ed.). *Handbuch der Entomologie*: 117-299, 377-1140.

Hong Y.-C. 1984 – Tracheata, Insecta. pp. 135-136. *In*: *Paleontological atlas of North China. 2. Mesozoic*. (ed. Tianjing Institute of Geology and Mineral Resources). Geological Publishing House, Beijing. [In Chinese].

Kirby F. 1890 – Appendix of fossil species. pp. 165-176. *In*: Kirby F. (ed.). *A synonymic catalogue of Neuroptera Odonata*. Gurney & Jackson (publs), London: 202 p.

Kukalová-Peck J. 1991 – Chapter 6: Fossil history and the evolution of hexapod structures. p. 141-179. *In*: Naumann, I.D. (ed.). *The insects of Australia, a textbook for students and research workers* (2nd ed.), **1**, (Melbourne University Press, Melbourne): 542 p.

Lohmann H. 1996 – Das Phylogenetische System der Anisoptera (Odonata). – *Entomologische Zeitschrift*, Essen, **106** (6): 209-252 (first part); **106** (7): 253-296 (second part); **106**: 360-367 (third part).

Martínez-Delclòs X., Nel A. 1996 – Discovery of a new Protomyrmeleontidae in the Upper Jurassic from Germany (Odonatoptera, Odonata, Archizygoptera). – *Archaeopteryx*, **14**: 67-73.

Meunier F. 1897 – Revue critique de quelques insectes fossiles du Musée Teyler. – *Archives du Musée Teyler*, Haarlem, (2), **5**: 7-23.

Meunier F. 1898 – Les insectes des temps secondaires. Revue critique des fossiles du Musée paléontologique de Munich. – *Archives du Musée Teyler*, Haarlem, (2), **6**: 87-149.

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.

Münster G. 1839 – Über einige neue Versteinerungen in den lithographischen Schiefern von Baiern. – *Neues Jahrbuch für Mineralogie, Geonosie, Geologie und Petregaktenkunde*, **1839**: 676-682.

Needham J.G. 1903 – A genealogic study of dragonfly wing venation. – *Proceedings of the United States National Museum*, Washington, **26**: 703-764.

Nel A., Bethoux, O., Bechly, G., Martinez-Delclos X., Papier F. 2001 – The Permo-Triassic Odonatoptera of the "protodonate" grade (Insecta: Odonatoptera). – *Annales de la Société Entomologique de France*, **37**: 501-525.

Nel A., Jarzembowski A.E. 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., Marie V., Schmeibner S. 2003 – Revision of the Lower Mesozoic damsel-dragonfly family Triassolestidae Tillyard, 1918 (Odonata: Epiproctophora). – *Annales de Paléontologie* (in press).

Nel A., Martinez–Delclos X., Paicheler J.–C, Henrotay M. 1993 – Les "Anisozygoptera" fossiles. Phylogénie et classification. (Odonata). – *Martinia*, Bois d'Arcy, numéro hors série **3**: 1-311.

Pfau H.K. 2000 – *Erasipteron larischi* Pruvost, 1933, *Eugeropteron lunatum* Riek, 1984 und die Evolution der Verstellpropeller-Flügel der Libellen. – *Mitteilungen der Schweizerischen Entomologische Gesellschaft*, **73**: 223-263.

Pritykina L.N. 1968 – Strekozy Karatau (Odonata). [Dragonflies from Karatau (Odonata)]. p. 26-55. *In*: Panfilov D.V. (coord.), *Yurskie Nasekomye Karatau*. [*Fossil insects from Karatau*]. Academy of Sciences of the S.S.S.R., Academyia Nauka, Moscow: 252 p. [in Russian.]

Pritykina L.N. 1980 – Odonata. p. 128–134. *In*: Rohdendorf B.B. (coord.). *Historic description of the class Insecta*. – *Trudy Paleontologiceskovo Instituta Akademie S.S.S.R.*, Moscow, **175**: 1-269. [in Russian.]

Ren D. 1994 – A new genus and species of Liassogomphidae (Insecta, Odonata) from Late Jurassic of Liaoning province, China. – *Geoscience*, **8**: 254-258.

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

Ross A. J., Jarzembowski E.A. 1993 – Arthropoda (Hexapoda; Insecta), p. 363-426. *In*: Benton M.J. (ed.), *The fossil record*, Chapman and Hall (publ.), London, **2**.

Schlüter T., Hartung M. 1982 – *Aegyptidium aburasiensis* gen. nov., spec. nov. (Aeschnidiidae) und *Gondvanogomphus bartheli* gen. nov., spec. nov. (Gomphidae) aus mutmasslicher Unterkreide Südwest-Ägyptens (Anisoptera). – *Odonatologica*, **11**: 297-307.

Tani K., Miyatake Y. 1979 – The discovery of *Epiophlebia laidlawi* Tillyard, 1921 in the Kathmandu Valley, Nepal (Anisozygoptera: Epiophlebiidae). – *Odonatologica*, **8**: 329–332.

Tillyard R.J. 1915 – On the development of the wing-venation in zygopterous dragonflies, with special reference to the Calopterygidae. – *Proceedings of the Linnean Society of New South Wales*, **47**: 212-230.

Tillyard R.J. 1917 – *The Biology of Dragonflies (Odonata or Paraneuroptera).* Cambridge University Press: London. xii + 396 p.

Tillyard R.J. 1921 – On an anisozygopterous larva from the Himalayas (Order Odonata). – *Records of the Indian Museum*, Calcutta, **22**: 93-107.

Tillyard R.J. 1925 – The British Liassic dragonflies. *British Museum Fossil insects*, **1**: 1-39.

Weijenbergh, H.Jr. 1869 – Prodromus en algemeene beschouwing der fossiele insekten van Beijeren. – *Tijdschrift voor Entomologie*, 12: 230-248.

Whalley P.E.S. 1985 – The systematics and palaeogeography of the Lower Jurassic insects of Dorset, England. – *Bulletin of the British Museum*, (*Natural History*), *Geology*, **39**: 107-187.

Zeuner F.E. 1962 – Fossil insects from the Lower Lias of Charmouth, Dorset. – *Bulletin of the British Museum*, (*Natural History*), *Geology*, **7**: 155-171.

Zherikhin V.V., Gratshev V.G. 1993 – Obrieniidae, n. fam., the oldest Mesozoic weevils (Coleoptera, Curculionoidea). – *Paleontological Journal*, **27** (1A): 50-69.

## APPENDIX

### List of characters

**1**. CuAa: with a narrow area between its two most distal posterior branches, when present or simple, without branches (0); with a broad area between the two most distal posterior branches (1); with two strong posterior distal branches, with secondary veins between them, and a short basal branch (2).
**2**. No long not zigzagged secondary longitudinal convex vein in postdiscoidal area (0); a long not zigzagged secondary longitudinal convex vein in postdiscoidal area, parallel to MP, the base of this vein being about two or three cells distal of discoidal triangle (1); a long not zigzagged secondary longitudinal convex vein in postdiscoidal area, parallel to MP, the base of this vein being just distal of discoidal triangle (2).
**3**. No long and not zigzagged concave "Mspl" (0); a long and not zigzagged concave "Mspl", its base being more than three cells distal of discoidal cell (1); base of "Mspl" just distal of discoidal triangle (2).
(Note. The "anisopteroid" Mspl, absent in the most basal Anisoptera (Liassogomphidae, Petaluridae, etc.), is not exactly homologous to that of the Stenophlebiidae because it is distinctly shorter and curved.)
**4**. Forewing discoidal cell: not divided into a triangle and a hypertriangle (0); divided into a triangle and a hypertriangle by a cross-vein (1).
**5**. Hindwing discoidal cell: not divided into a triangle and a hypertriangle (0); with at least a rudimentary vein between a triangle and a hypertriangle (1); well divided into a triangle and a hypertriangle (2).
**6**. In hindwing: no "heterophlebioid" anal loop limited by a secondary branch of AA, main branch of AA and CuAb, even if anal and cubital areas are broad (0); a "heterophlebioid" anal loop limited by a secondary branch of AA, main branch of AA and CuAb (1); anal loop reduced, due to the wing petiolation (2).
**7**. Hindwing CuAb: absent (0); present (1).
**8**. In forewing: two rows of cells (or more) in the anal area (0); one row of cells in the anal area (1).
**9**. Hindwing hypertriangle: absent (0); short, not distinctly longer than the discoidal triangle (1); longer than the discoidal triangle width (2); more than 1.5 times longer than the discoidal triangle width (3).
**10**. Hindwing discoidal triangle: absent (0); short, not distinctly transverse (1); long, clearly transverse (2).
**11**. Numerous secondary antenodal cross-veins between ScP and C (0); no secondary antenodal cross-veins between ScP and C (1).
**12**. Nodal Cr: oblique, but not very, i.e. 120° < angle (Cr, RA) < 140° (0); very oblique, i.e. angle (Cr, RA) > 140° (1).
**13**. Nodal Cr: oblique (0); nearly perpendicular to RA and ScP (1).
**14**. Nodal Cr short, with no short cross-veins reaching it (0); longer, covering one or two cells between RA and RP (1); very long, with more than two postnodal veins reaching it and/or covering more than two cells below it, between RA and RP (2).
**15**. Pterostigma: in a normal position (0); basally shifted (1).
**16**. Pterostigma: not very long (0); very long (1).
**17**. Pterostigma covering one or two cells (0); than two cells (1).
**18**. Pterostigma braced (0); Pterostigmal brace basally shifted (1); Pterostigmal brace absent (2).
**19**. A distinct oblique cross-vein "O" (0); vein "O" absent (1).
**20**. No longitudinal secondary vein basally aligned with RP2, below subnodus (0); a short longitudinal secondary vein basally aligned with RP2, below subnodus (1); this vein is long (2).
**21**. Subnodus Sn: not very oblique (0); very oblique, but with no cross-vein reaching it (1); very oblique, with one or more cross-veins reaching it (2).
**22**. Hindwing subdiscoidal space not so (0); transverse and crossed by two parallel veins or more (1).
**23**. Hindwing: very shortly or not petiolated (0); distinctly petiolated (1); long petiolated (AA and AP separated nearly opposite arculus) (2).
**24**. Forewing: not petiolated (0); petiolated (1).
**25**. Arculus between Ax1 and Ax2, close to Ax1 (0); midway between Ax1 and Ax2 (1); near Ax2 or opposite Ax2 (2).
**26**. A space between CuAa and MP without any cross-vein (gap), two or more cells longs, just distal of base of CuA (0); in hindwing, no gap between CuAa and MP, just distal of base of CuA (1).
**27**. CuAb: absent (0); not at right angle with CuAb (&AA) and CuAa (1); at right angle with CuAb (&AA) and CuAa. 2.
**28**. Forewing MA and MAb strictly aligned (0); a distinct angle between MA and MAb, in forewing (1).
**29**. Four wings: not falcate (0); falcate (1); very falcate (2).
**30**. Thoracic interpleural suture: dorsally present (0); dorsally absent (1).
**31**. Male genital appendages: of "zygopteroid" type (0); of "anisopteroid" type (1).
**32**. Larva: of "zygopteroid'-type (0); of "anisopteroid'-type, with an anal pyramid (1).
**33**. Hindwing subdiscoidal space: not foot-shaped (0); foot-shaped (1).
**34**. Hindwing Mab: directed towards wing apex (0); vertical (1); directed towards wing base (2).
**35**. No "anisopteroid" vein (AA + CuA)b in hindwing (0); a "anisopteroid" vein (AA + CuA)b in hindwing (1).
**36**. Forewing hypertriangle: absent (0); short (1); long (2).
**37**. Forewing discoidal triangle: absent (0); not transverse (1); long transverse (2).
**38**. Pseudo-IR1 (*sensu* Bechly, 1996): absent (0); present (1).
**39**. Male anal triangle: absent (0); present, but elongate (1); transverse (2).
**40**. CuAb absent (0); a strong angle between CuAb and AA (1); angle between CuAb and AA very weak (2); angle between CuAb and AA absent (3).
**41**. Not zigzagged secondary longitudinal veins in areas between IR2 and MP: absent (0); present (1).
**42**. Postdiscoidal area: less broad than area between MA and RP3/4 along posterior wing margin (0); broader than area between MA and RP3/4 along posterior wing margin (1).