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THE PERMO-TRIASSIC ODONATOPTERA OF THE "PROTODONATE" GRADE (INSECTA : ODONATOPTERA)

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Résumé. – Les Odonatoptera permo-triassiques du grade 'protodonate' (Insecta : Odonatoptera). – Nous décrivons un nouvel Odonatoptera fossile *Permophlebia uralica,* gen. n., sp. n. que nous attribuons à une nouvelle famille Permophlebiidae. Plusieurs Odonatoptera permo-triassiques sont redécrits, dans la famille Triadotypidae, et dans les genres *Kargalotypus* Rohdendorf, 1962 et *Liadotypus* Martynov, 1937. Les positions phylogénétiques sont discutées, et plusieurs décisions taxinomiques modifiées. Les Piroutetiidae Nel, 1989 sont transférés dans les Triadophlebiomorpha, superfamille indéterminée **sit. nov.** Les Kargalotypidae Zessin, 1983 sont transférés dans les Triadophlebiomorpha: Zygophlebiida **sit. nov.** Les Liadotypidae Grauvogel & Laurentiaux, 1952 (non Martynov, 1937) sont transférés dans les Isophlebiida **sit. nov.** famille *incertae sedis,* **stat. nov.** L'analyse cladistique des Zygophlebiida (**nouveau clade**) est proposée.

Abstract. – We describe a new fossil dragonfly *Permophlebia uralica,* gen. n., sp. n. that we attribute to a new family Permophlebiidae. Several Permo-Triassic odonate taxa are redescribed, viz. the taxa of the family Triadotypidae, and the genera *Kargalotypus* Rohdendorf, 1962, and *Liadotypus* Martynov, 1937. Their phylogenetic positions are discussed, and some earlier taxonomic decisions re-evaluated. The Piroutetiidae Nel, 1989 is transferred in the Triadophlebiomorpha, superfamily undetermined **sit. nov.** The Kargalotypidae Zessin, 1983 is tranferred in the Triadophlebiomorpha: Zygophlebiida **sit. nov.** The Liadotypidae Grauvogel & Laurentiaux, 1952 (non Martynov, 1937) is transferred in the Isophlebiida **sit. nov.** family *incertae sedis* **stat. nov.** The cladistic analysis of the Zygophlebiida (**new clade**) is proposed.

Our knowledge of the Permo-Triassic Odonatoptera has greatly increased during last years with the reinterpretation of the wing venational characters, the phylogeny proposed by Bechly (1996, 1997) and the recent discovery of the new Upper Permian family Lapeyriidae Nel, Gand & Garric, 1999, which is situated at the very base of the clade Nodialata Bechly, 1996 (Nel *et al.*, 1999b). After the opportunity to study the material housed in the Laboratory of Palaeoentomology (PIN) of the Academy of Science in Moscow (Russia) and the

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Laboratory of Palaeontology of the University of Strasbourg (France), we here describe a new fossil dragonfly *Permophlebia uralica* gen. n., sp. n. that we attribute to a new family Permophlebiidae. Several Permo-Triassic odonate taxa are redescribed, their phylogenetic positions discussed, and some earlier taxonomic decisions are re-evaluated.

In the following study we use the wing venation nomenclature of NEL *et al.* (1993) and BECHLY (1996). We mainly follow and base our study on the phylogenetic classification of Odonatoptera proposed by BECHLY (1996, 1997, 1998).

SYSTEMATIC PALAEONTOLOGY

Order **Odonatoptera** (*sensu* Brauckmann & Zessin, 1989)

Clade **PANDISCOIDALIA, new clade**

Included groups. – Triadotypomorpha Bechly, 1996 and Discoidalia Bechly, 1996.

Wing venational autapomorphies. – (1) highly developed nodus with a kink in ScP; (2) nodal furrow present; (3) nodal and subnodal crossveins aligned; (4) primary antenodal crossvein Ax1 present. Note that the second distal primary antenodal crossvein *Ax2* is plesiomorphic absent in the groundplan.

We exclude the Triadotypomorpha species from the Discoidalia *sensu* BECHLY (1996), because they do not share several important autapomorphies of Discoidalia, i.e. (1) presence of a specialized oblique crossvein *MAb*, distally closing a well-defined discoidal cell; (2) separate origin of *CuA* on *M* + *Cu*, developed as an oblique vein parallel to the *CuP*-crossing, lost.

BECHLY (1996) listed the following presumed autapomorphies of his clade Triadophlebioptera [= Triadotypomorpha + Triadophlebiomorpha]: (1) 'very elongate and slender wings with a very dense reticulation' — this character state is present in numerous other groups as well, such as Meganeuromorpha Bechly, 1996, and thus is either highly homoplasic or even plesiomorphic; (2) 'wings distinctly petiolated' — this character state is highly homoplasic, too, and not even shared by *Triadotypus*, type genus of Triadotypomorpha; (3) 'nodus in a very basal position' — this character state is uncertain in *Triadotypus*; (4) 'large number of postnodal crossveins' — a character of uncertain polarity, which is present in many unrelated subgroups of Odonatoptera; (5) 'secondary branching of *RP2*' (also see BECHLY, 1997) — this character state is erroneous for *Triadotypus guillaumei* Grauvogel & Laurentiaux, 1952 and *Reisia sodgianus* (Pritykina, 1981) (see the redescription of *Triadotypus* below); (6) 'secondary branching of *RP3/4*' — a somewhat homoplasic character, which is also present in several groups (e.g. the Protomyrmeleontidae) that are certainly not closely related to Triadotypomorpha and Triadophlebiomorpha; (7) 'secondary branching of *MP*' — character state erroneous for *Triadotypus*. Consequently, there is only weak evidence in favour of a sister group relationship between Triadotypomorpha and Triadophlebiomorpha.

We here consider Triadotypomorpha as the sister group of Discoidalia, together constituting the new monophylum Pandiscoidalia, which is the sister group of the Protanisoptera within Nodialata Bechly, 1996. Since Triadotypomorpha is here excluded from the Triadophlebioptera Bechly, 1996, this latter taxon becomes redundant with Triadophlebiomorpha Pritykina, 1981 and therefore could be regarded as obsolete.

Clade **TRIADOTYPOMORPHA** Bechly, 1996 (**sens. nov.**)

Included groups. – Triadotypidae Grauvogel & Laurentiaux, 1952. BECHLY (1996) proposed to include Piroutetiidae Nel, 1989 in this group. We prefer to transfer the latter family to Triadophlebiomorpha.

Wing venational autapomorphies. – BECHLY (1996) proposed the two following putative synapomorphies for Triadotypidae and Piroutetiidae: (1) 'MA and MP apically converging'; (2) 'wing pleating hypertrophied (wing extremely corrugated)'. However, some Triadophlebiomorpha (*Triadophlebia* Pritykina, 1981, *Xamenophlebia* Pritykina, 1981, etc.) share the first character state, while the second character state is rather difficult to evaluate since it may not be preserved due to fossilisation processes in many fossils, especially in the type specimen of *Triadotypus guillaumei* Grauvogel & Laurentiaux, 1952. Since we exclude Piroutetiidae from Triadotypomorpha, we propose the following wing venational character states as possible autapomorphies of Triadotypomorpha s.str. (= Triadotypidae): (1) vein AA with several posterior branches, at least two of them being directed towards the wing base; (2) RP&MA with a very long common basal stem in the arculus. However, it must be emphasized that these two characters are currently only known in the type species *Triadotypus guillaumei*.

Family **TRIADOTYPIDAE** Grauvogel & Laurentiaux, 1952 (= **REISIIDAE** Laurentiaux, 1958, **syn. nov.**)

Type genus. – *Triadotypus* Grauvogel & Laurentiaux, 1952.

Other genus. – *Reisia* Handlirsch, 1912, which is only tentatively attributed to this family (see below).

Wing venational autapomorphies. – Those of the Triadotypomorpha, which is a redundant taxon.

Remark. – LAURENTIAUX (1958) synonymized the Triadotypidae with the 'Reisiidae Handlirsch, 1911'. But HANDLIRSCH (1912) created the genus name *Reisia* in 1912 and never created the family name Reisiidae. Thus the family name Reisiidae has to be attributed to LAURENTIAUX (1958), and considered as a junior synonym of Triadotypidae.

Genus **TRIADOTYPUS** Grauvogel & Laurentiaux, 1952, **bonus genus**

Triadotypus Grauvogel & Laurentiaux, 1952 : 124 (original description).
Reisia : LAURENTIAUX, 1958 : 7 (discussion, synonymy); BECHLY, 1997 : 53 (synonymy).

Type species. – *Triadotypus guillaumei* Grauvogel & Laurentiaux, 1952.

Other species. – *Triadotypus nana* (Bechly, 1997).

Diagnosis. – This genus is distinguished by the following combination of characters: (a) base of *RP3/4* aligned with nodus; base of *IR2* distinctly distal of nodus; (b) *IR1* secondarily branching on *RP2*; (c) *MP* simple, with very few (or without any) secondary veins between it and posterior wing margin; (d) distal part of *AA* not strongly curved and reaching posterior wing margin opposite nodus.

Remark. – Originally described by GRAUVOGEL & LAURENTIAUX (1952), this genus was synonymized with the genus *Reisia* Handlirsch, 1912 (type species *Handlirschia gelasii* Reis, 1909) by LAURENTIAUX-VIEIRA *et al*. (1952) (nec Grauvogel & Laurentiaux, as erroneously stated by BECHLY, 1997), but without considering the correct taxonomic consequences, as already noted by BECHLY (1997). Nevertheless, *R. gelasii* greatly differs from *T. guillaumei* and *T. nana* in its *MP* clearly being pectinate, with a wide area between *MP* and *CuA* (see below). Thus we prefer to restore the genus *Triadotypus* and consider *Reisia* as a distinct genus.

Triadotypus guillaumei Grauvogel & Laurentiaux, 1952, **comb. rest**. (figs 1-3)

Triadotypus guillaumei Grauvogel & Laurentiaux, 1952 : 124 (original description); LAURENTIAUX-VIEIRA, RICOUR & LAURENTIAUX, 1952 : 320.
Reisia gelasii (Reis, 1909) : LAURENTIAUX, 1958 : 37 (synonymy, redescription).
Triadotypus guillaumei : PRITYKINA, 1981 : 9 (comparison with *T. sodgianus* Pritykina, 1981); CARPENTER, 1992 : 70, text-fig. 44.2a.; NEL *et al*., 1996 : 32, fig. 5 (redescription of the nodal structures).
Reisia guillaumei : BECHLY, 1997 : 53 (discussion on systematic position).

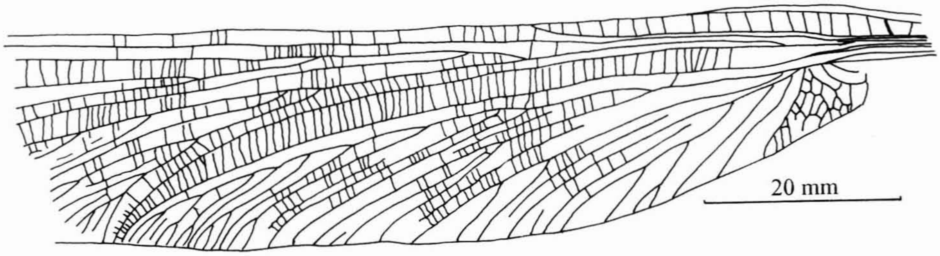

Fig. 1, *Triadotypus guillaumei* Grauvogel & Laurentiaux, 1952, comb. rest. Wing of the holotype specimen 57.32, collection Grauvogel and Gall.

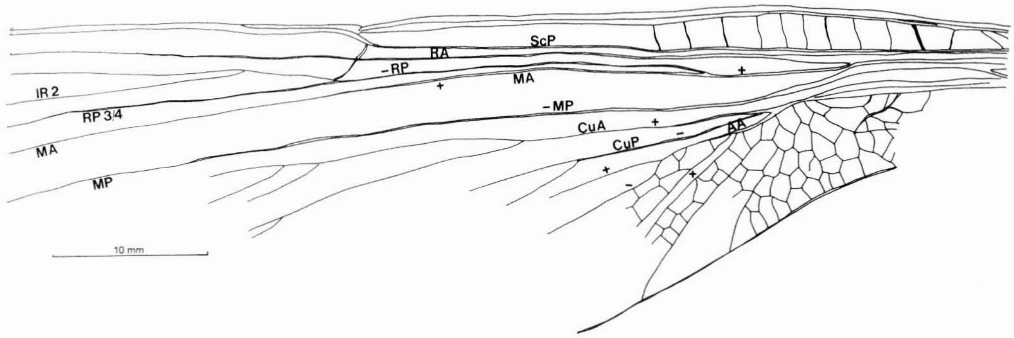

Fig. 2, *Triadotypus guillaumei* Grauvogel & Laurentiaux, 1952, comb. rest. Wing base of the holotype specimen 57.32, collection Grauvogel and Gall.

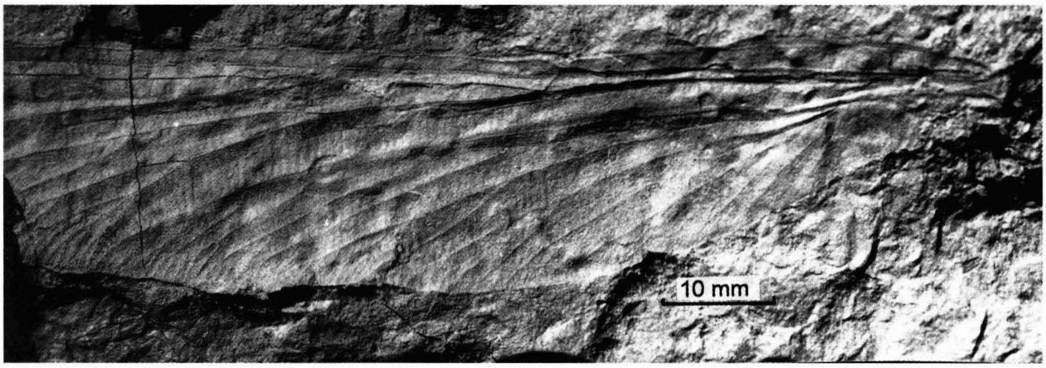

Fig. 3, *Triadotypus guillaumei* Grauvogel & Laurentiaux, 1952, comb. rest. Photograph of the holotype specimen 57.32, collection Grauvogel and Gall.

Material. – Holotype specimen 57.32, collection Grauvogel & Gall, Institut de Géologie de l'Université Louis Pasteur, Strasbourg, France.

Type horizon. – Upper Buntsandstein, Lower Anisian, Middle Triassic.

Type locality. – Outcrop of Bust, department of Bas-Rhin, France.

Redescription. – There are several errors in the original description and figure of the holotype (GRAUVOGEL & LAURENTIAUX, 1952), especially concerning the structures of the wing base. Therefore, a redescription is necessary.

Imprint of a wing with the extreme base and apex missing. No trace of coloration is preserved. Wing probably 136 mm long, 21.5 mm wide at nodus; distance between base and nodus, 42.5 mm; between wing base and base of arculus, 11 mm; nodal structures well preserved, showing a nodal furrow, a posteriorly bent *CP*, a strong oblique nodal crossvein (= *Cr*), and an oblique subnodus, aligned with *Cr* (NEL *et al.*, 1996, fig. 5); 21 preserved antenodal crossveins between *C* and *ScP*; antenodal crossveins of the second row between *ScP* and *RA* poorly preserved, only the more distal ones being visible; *ScP* strongly approximating *RA*, distance between *C* and *ScP*, 2.1 mm, and between *ScP* and *RA*, 0.4 mm; one antenodal crossvein distinctly stronger than others, 6.6 mm from wing base, probably corresponding to *Ax1* and not to *Ax0*, because of the presence of a secondary crossvein in a more basal position; no *Ax2* stronger than the distal secondary antenodal crossveins; *R* and *MA* with a common stem and separating into *RA* and *RP* + *MA* in the arculus; basal stem *RP* + *MA* is a long convex vein; *RP* and *MA* separating 9.2 mm distal of base of arculus; no specialized posterior vein *MAb*, distally closing a discoidal cell; basal stem of *MP* + *Cu* rather poorly preserved and basal parts of *CuA* and *CuP* not preserved between *MP* + *Cu* and *AA*; nevertheless, *AA*, *CuP* and *CuA* distally separating nearly at the same point, 16.2 mm from wing base, similarly to the homologous structures in Meganeuridae; distal part of *CuP* long, concave, with four branches reaching posterior wing margin; *AA* with numerous posterior branches, at least two of them being directed towards wing base; more distal branch of *AA* divided into five main branches, one of them being subdivided into four branches; all these branches directed towards posterior wing margin; *CuA* closely parallel to *MP* and with about eight posterior branches reaching posterior wing margin; *MP* slightly curved, without any branches, and closely parallel to *MA*, with only one row of cells inbetween; 'postdiscoidal' area between *MP* and *MA* distinctly narrowed near posterior wing margin; concave vein *RP3/4* separating from *RP1/2* below subnodus, and distally divided into two main branches with a convex longitudinal secondary vein between them; main branches of *RP3/4* subdivided into several branches; *IR2* straight, simple, separating from *RP1/2* 5.8 mm distal of base of *RP3/4*; *RP2* separating from *RP1* 15.7 mm distally; convex *IR1* secondarily branching on concave *RP2*; *RP2* not basally forked as in Triadophlebiomorpha; distal parts of these veins not preserved; a pterostigma is not visible; postnodal crossveins between *C* and *RA* very numerous but not aligned with second row of crossveins between *RA* and *RP1*.

Discussion. – Contrary to the original interpretation of the wing venation by GRAUVOGEL & LAURENTIAUX (1952), *Triadotypus guillaumei* has a genuine arculus and an organization of the distal parts of veins *CuA*, *CuP* and *AA* identical to that of the Meganeuridae. Thus, a new discussion of its phylogenetic position is necessary.

GRAUVOGEL & LAURENTIAUX (1952), PRITYKINA (1981) and ZESSIN (1983) regarded Triadotypidae as Meganeuromorpha (protodonate grade). In their phylogenetic analysis of the plesion Meganisoptera *sensu* MARTYNOV (1932a) (= Protodonata Brongniart, 1885), BRAUCKMANN & ZESSIN (1989) included the Triadotypidae in a clade [Paralogidae + Meganeuridae (considered as polyphyletic) + Triadotypidae], as a sister-group of the more 'rezente Odonata'. CARPENTER (1992) transferred Triadotypidae to Triadophlebiomorpha Pritykina, 1981 without explanation. BECHLY (1996) discussed the position of Triadotypidae and considered this taxon as the sister group of Triadophlebiomorpha within the clade [Discoidalia – Triadophlebioptera].

The Triadotypidae share several important synapomorphies with Nodialata, i.e. (1) presence of a true odonatoid nodus, with oblique nodal and subnodal veinlets; (2) *RA* and *RP* basally fused into a long double-barrel radial stem; (3) *MA* unbranched. These characters are not shared by Meganeuromorpha *sensu* BECHLY (1996) [= Paralogidae + Kargalotypidae + Kohlwaldiidae + Meganeuridae]. Likewise, *Triadotypus* does not show any potential synapomorphies with Protanisoptera, i.e. (1) specialized basal brace *Ax0*; (2) specialized protanisopteran pterostigma structure crossed by *RA*; (3) *RA* with a second apical branch; (4) one of the postsubnodal crossveins midway between nodus and pterostigma distinctly oblique. Furthermore, *T. guillaumei* has a nodus with a kink in *ScP* and a nodal furrow (NEL *et al.*, 1996), which have to be considered as strong synapomorphies with the Discoidalia *sensu* BECHLY (1996).

Nevertheless, *T. guillaumei* has no specialized oblique crossvein *MAb*, distally closing a well-defined discoidal cell, unlike the Discoidalia *sensu* BECHLY (1996). The area between *MP* + *Cu* and *AA* is too poorly preserved to show the origin of *CuA* on *MP* + *Cu*, but the organization of the distal parts of *CuA*, *CuP* and *AA*, which are nearly identical with those of the more basal odonatoid groups (Protanisoptera and Meganeuromorpha), suggests that the *CuA* of *T. guillaumei* had a separate origin on *MP* + *Cu* that was developed as an oblique vein parallel to the *CuP*-crossing, unlike the derived state in Discoidalia.

The development of the anal area suggests that *T. guillaumei* probably had a non-petiolated wing, and its nodus was not in a very basal position, unlike the derived states in Triadophlebiomorpha. With the latter clade it only shares the secondary branching of *RP3/4* as a potential synapomorphy. Unlike the Triadophlebioptera, its *MP* is simple. *RP2* is not bifurcate near its base as in Triadophlebioptera. Since such branchings are convergently present in the unrelated Protozygoptera – Protomyrmeleontidae as well, they represent homoplasic characters, which are not sufficient as evidence for an attribution of *T. guillaumei* to the Triadophlebioptera *sensu* BECHLY (1996). The inclusion of the Triadotypomorpha within [Discoidalia – Triadophlebioptera] *sensu* BECHLY (1996) is only weakly supported and would imply an important reversal of the main wing venational autapomorphy of the Discoidalia, i.e. presence of a vein *MAb*.

Triadotypus nana Bechly, 1997

Triadotypus guillaumei var. *nana*, Laurentiaux-Vieira, Ricour & Laurentiaux, 1952 : 320 (original description).
Reisia nana Bechly, 1997 : 54.

Material. – Holotype specimen without number, originally in the collection of the 'Ecole des Mines de Paris'. This collection has been transferred to the University Claude Bernard, of Lyon-Villeurbanne, where this specimen is now missing, so that the type has to be regarded as lost.

Geological age. – Keuper, Middle Triassic.

Type locality. – Dent de Villard, Vanoise, department of Savoie, France.

Remarks. – Due to a lapse, BECHLY (1997) erroneously attributed the original description of this fossil to Grauvogel & Laurentiaux. The distinctly smaller size of this specimen than the holotype of *T. guillaumei* with a difference of one-third in the total length is clearly sufficient to justify a specific separation between *T. nana* and *T. guillaumei*, as already mentioned by BECHLY (1997). We propose the following two further distinctions: presence of secondary veins between *MP* and posterior wing margin near apex of *MP*, unlike the unbranched *MP* of *T. guillaumei*; vein *CuP* simple and very weak between *CuA* and *AA*, unlike the distally forked *CuP* of *T. guillaumei*.

T. nana differs from *Reisia sodgianus* (Pritykina, 1981) in its distal part of *AA* not strongly curved. Nevertheless, because of its very fragmentary condition, its attribution to the genus *Triadotypus* has to be regarded as very tentative. Among other missing characters, there is no available information on the relative positions of nodus and bases of veins *RP3/4* and *IR2*.

Note. – LAURENTIAUX-VIEIRA *et al.* (1952) misinterpreted the organization of the cubito-anal area of *T. nana* in the following point: since they considered the three veins *CuA*, *CuP* and *AA* as mere branches of the anal vein *A1*, they named the alternatively concave and convex branches of *CuA* 'f', 'e', 'd', 'c', 'b' and considered *CuP* and *AA* as subdivisions of the branch 'a' in the type specimen of *T. nana*. Similarly they named the *CuP* of the type specimen of *T. guillaumei* 'branch c', and the branches of *AA* 'b' and 'a', without any consideration about the different convexities of these alleged homologous branches.

Genus **REISIA** Handlirsch, 1912
(*in* Triadotypidae ?)

Type species. – *Reisia gelasii* (Reis, 1909).

Other species. – *Reisia sodgianus* (Pritykina, 1981), **comb. nov.**

Diagnosis. – *Reisia* differs from *Triadotypus* as follows: area between *MP* and *CuA* greatly widened distally, with numerous weak posterior secondary veins between *MP* and posterior wing margin (known in *R. gelasii* and *R. sodgianus*). The following other characters are not preserved in the holotype of *R. gelasii* and thus only known in *R. sodgianus*: *AA* reaching posterior wing margin well basal of level of nodus; bases of *RP3/4* and *IR2* distinctly basal of nodus, between nodus and arculus, instead of being distal of nodus. These differences are sufficient to justify a generic separation between *Reisia* and *Triadotypus*.

Remark. – Both types of *R. gelasii* and *R. sodgianus* lack the basal parts of wings. Nearly all the venational characters of the distal two thirds of *Triadotypus*, *Reisia* and Triadophlebiomorpha are identical. The two groups Triadotypomorpha and Triadophlebiomorpha differ in the branching of the veins *MP*, *CuA*, *CuP*, and *AA* and in the presence of *MAb*. These characters are unknown in the two *Reisia* species. There is only one character suggesting that *R. sodgianus* could be related to Triadotypidae rather than to Triadophlebiomorpha — Triadophlebiidae Pritykina, 1981, i.e. its vein *CuA* is strong, with many well-defined posterior branches, unlike *Triadophlebia* Pritykina, 1981. However, we only suggest a very tentative attribution of *Reisia* to Triadotypidae, since the mentioned single character is hardly sufficient for a definite attribution.

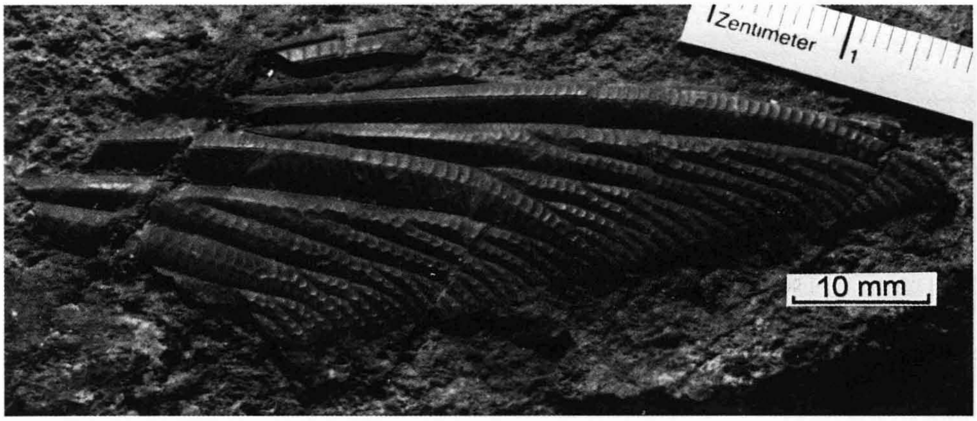

Fig. 4, *Reisia gelasii* (Reis, 1909). Photograph of the holotype specimen no. 1908 I 49 at BSPGM in Munich.

Reisia gelasii (Reis, 1909) (fig. 4)

Handlirschia gelasii Reis, 1909 : 661-694, figs 1-7 (original description).
Reisia gelasii : HANDLIRSCH, 1912 : 3 (new generic name); LAURENTIAUX, 1958 : 37 (citation); BECHLY, 1997 : 53 (position discussed).

Material. – Holotype specimen no. 1908 I 49 at BSPGM in Munich; a fragment of the mid part of a wing.

Type horizon. – 'Schaumkalk', Lower 'Muschelkalk', Middle Triassic.

Type locality. – Münnerstadt, Lower Franconia, Germany.

Remarks. – All the preserved parts of the wing of *Reisia gelasii* are nearly identical with those of *R. sodgianus*. Although there is no clear difference between the two fossils, the geographical and stratigraphical separation suggests that it is not very likely that both indeed belong to the same species. Anyway, due to the fragmentary state of preservation of the holotype of *R. gelasii*, this last fossil perhaps should have never been named at all.

Reisia sodgianus (Pritykina, 1981), **comb. nov.** (fig. 5)

Triadotypus sodgianus Pritykina, 1981 : 9-11 (original description).
Triadotypus sodiques : CARPENTER, 1992 : 71; BECHLY, 1997 : 57 (listed).

Material. – Holotype specimen PIN 2785/21, Moscow.

Type horizon. – Madygen Formation, Norian, Upper Triassic.

Type locality. – Dzhayloucho, South Fergana, near Shurab, Batkensk region, Kyrgyastan.

Remarks. – There are some ambiguous points in the original figure of PRITYKINA (1981, text-fig. 1), i.e. the concave *RP2* is not really bifurcate because its alleged costal branch is a convex vein; the exact position of the base of *IR1* is not clear because this part of the wing is destroyed, thus it is impossible to determine whether *IR1* is secondarily branching on *RP2*, as in *T. guillaumei*, or not. Furthermore, the complete basal part of the wing is not preserved.

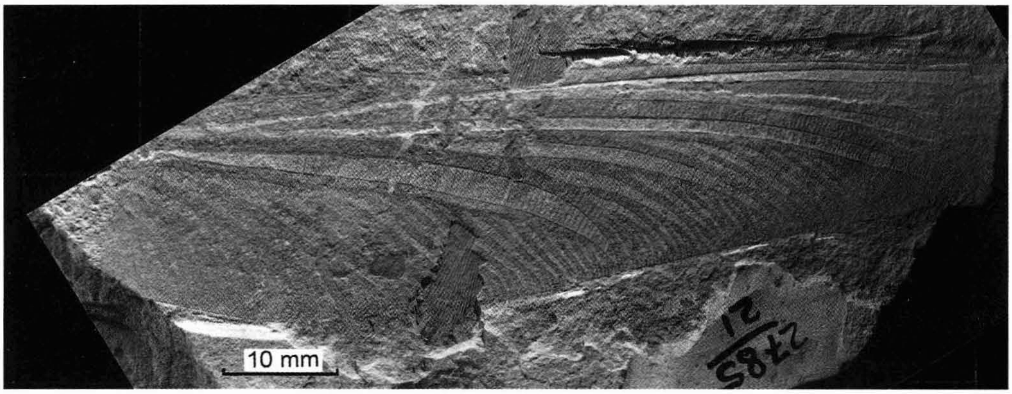

Fig. 5, *Reisia sodgianus* (Pritykina, 1981). Photograph of the holotype PIN 2785/21.

The exact nature of the concave and convex veins present in the basal part of the area between CuA and the posterior wing margin of *P. sodgianus* needs to be discussed. PRITYKINA (1981) interpreted them as a concave '*A2*' (that would be *CuP* in the present venational nomenclature, if we consider *P. sodgianus* as a Triadotypidae) and a convex '*A3*' (that would be *AA*). An alternative solution would be to consider that *CuA* is basally bifurcate in *P. sodgianus* and has a strong secondary concave vein between its two main branches. Such a hypothetical structure of *CuA* is unknown in other Odonatoptera, so that this hypothesis is clearly less probable than the preceding one. Consequently, we consider that *P. sodgianus* has a distal organisation of the veins *CuA*, *CuP* and *AA* nearly identical to that of *Triadotypus*. With this hypothesis, the wing venation of *P. sodgianus* agrees with an attribution to Triadotypidae.

Clade **DISCOIDALIA** Bechly, 1996

Included groups. – Triadophlebiomorpha Pritykina, 1981, and Stigmoptera Bechly, 1996. This latter clade includes the Protozygoptera (incl. Archizygoptera) and the more 'modern' Panodonata.

Diagnosis. – BECHLY (1996) proposed a list of wing venational autapomorphies for this taxon. Since we exclude the Triadotypomorpha from Discoidalia, we here propose to amend the list of wing venational autapomorphies of Discoidalia as follows: (1) presence of a typical odonatoid discoidal cell that is distally delimited by a characteristically oblique crossvein *MAb*, developed as a secondary branch of *MA*; and (2) the separate origin of *CuA* on *M* + *Cu*, that was developed as an oblique vein parallel to the *CuP*-crossing and the partial fusion of *CuA* with *AA* + *CuP* is lost.

Remark. – The second primary antenodal crossvein *Ax2*, which is absent in Triadotypomorpha, seems to be present in at least some representatives of Triadophlebiomorpha (see below) and is clearly present in Stigmoptera. Therefore, this character represents a further putative autapomorphy of Discoidalia.

Clade **TRIADOPHLEBIOMORPHA** Pritykina, 1981

Included families. – BECHLY (1996) proposed the division of this clade into two subclades, the Zygophlebioidea Pritykina, 1981 and the Triadophlebiida Bechly, 1996. Since we add the new family Permophlebiidae as sister group of Xamenophlebiidae, we propose the following new division of this clade into two taxa:

– Zygophlebiida **taxon n.** that includes Zygophlebioidea Pritykina, 1981 (Zygophlebiidae Pritykina, 1981), and Xamenophlebioidea Pritykina, 1981 (Xamenophlebiidae Pritykina, 1981, and Permophlebiidae, **fam. n.**).

– Triadophlebiida Bechly, 1996 that includes Mitophlebiidae Pritykina, 1981 *sensu* Bechly, 1996, and Triadophlebioidea Pritykina, 1981 (Triadophlebiidae Pritykina, 1981, Paurophlebiidae Bechly, 1996).

Diagnosis. – BECHLY (1996) proposed a list of wing venational autapomorphies of this group: (1) 'wing with a very long petiolus'; (2) 'a unique type of petiolus' (in the petiolus of Triadophlebiomorpha, veins *MP*, *Cu* are basally separated, and distally fused together with *AA*, more distally, *CuA* + *CuP* + *AA* separate from *MP*); (3) '*MP* distinctly curved distal of its origin at the distal angle of the discoidal cell'; and (4) 'very long and oblique discoidal vein *MAb*'. It should be noted that these characters are difficult to recognize in many fossil specimens because of their incomplete state of preservation. Other useful characters such as vein *CuA* without distal posterior branches can help to distinguish Triadophlebiomorpha from Triadotypomorpha (see below for Piroutetiidae).

Family **PIROUTETIIDAE** Nel, 1989
(*in* Triadophlebiomorpha, superfamily undetermined, **sit. nov.**)

Type genus. – *Piroutetia* Meunier, 1907.

Diagnosis. – NEL (1989) provided a diagnosis for this family. The presence of several parallel concave veins between *RP1* and *RP2* with pectinate origin on *RP1* appears to be a unique autapomorphy of this family within Triadophlebiomorpha (BECHLY, 1996).

Discussion. – The synapomorphies proposed by BECHLY (1996) in favour of an attribution of Piroutetiidae to Triadotypomorpha were already critically discussed above. The structures of the cubito-anal veins of *Piroutetia* are clearly different from those of *Triadotypus*. The *CuA* of *Piroutetia* is a relatively weak zigzagged vein, without posterior secondary branches, beginning on a strong concave vein *CuP*, instead of being a strong vein with numerous posterior branches.

The wing of *Piroutetia* strongly resembles that of some Triadophlebiidae (e.g. *Cladophlebia* Pritykina, 1981 and *Paurophlebia* Pritykina, 1981) in numerous characters, such as the cubito-anal, radial, and median veins. Nevertheless, *Piroutetia* differs from all other known Triadophlebiomorpha in its subnodal veinlet being not very long and oblique (contrary to Triadophlebiida Bechly, 1996), and in its radial veins being normally branched on *RP1* (contrary to Zygophlebioidea Pritykina, 1981 *sensu* BECHLY, 1996). We therefore prefer to consider *Piroutetia* as a basal representative of Triadophlebiomorpha with uncertain affinities.

Genus **PIROUTETIA** Meunier, 1907

Type species. – *Piroutetia liasina* Meunier, 1907.

Diagnosis. – That of the family.

Piroutetia liasina Meunier, 1907

Piroutetia liasina Meunier, 1907a : 521-522 (original description); MEUNIER, 1907b :1-2; NEL, 1989 : 15-19 (redescription); BECHLY, 1996 : 354 (*in* Triadotypomorpha).

Material. – Holotype specimen MNHN-LP-B.9711, Laboratoire de Paléontologie, Muséum national d'Histoire naturelle, Paris.

Geological age. – Rhaetian, Upper Triassic.

Type locality. – Fort-Mouchard, Arçures, Jura, France.

Clade **ZYGOPHLEBIIDA, new clade**

Included groups. – [Zygophlebiidae + (Xamenophlebiidae + Permophlebiidae)].

Diagnosis. – (1) very broad and long wings, with numerous small cells; (2) *RP2* apparently branched on *IR2* rather than on *RP1*; (3) *IR1* apparently branched on *RP2* rather than on *RP1*; (4) *RP4*, *MA* and *MP* strongly approximate near posterior wing margin; (5) veins *CuA* and *CuP* closely parallel, with only one row of cells between them; (6) *CuA* without any posterior branch.

Remarks. – The character '*AA* reduced to a oblique crossvein between the posterior margin and the branching of *Cu* + *AA* into *CuA* and *CuP*', proposed by BECHLY (1996) in his diagnosis of Zygophlebioidea, is only known in the Zygophlebiidae, because the structures of the wing bases of Xamenophlebiidae and Permophlebiidae are unknown. Nevertheless, *AA* of *Permophlebia uralica,* gen. n., sp. n. (see below) was probably very short and similar to those of the Zygophlebiidae. Nevertheless, we prefer to avoid this character in the diagnosis of the Zygophlebioidea.

– The character 'basal part of *RP2* looking like a bridge between *IR2* and *IR1*", proposed by BECHLY (1996) is present in Zygophlebiidae and Xamenophlebiidae, but less developed in Permophlebiidae. This character is developed by convergence in Protomyrmeleontidae.

– The very special structure of vein *CuP* + *AA*, making a strong zigzag between the point of separation of *CuA* from *CuA* + *CuP* + *AA* and the point of separation between *CuP* and *AA* (see fig. 8) is a derived character present in *Zygophlebia*, *Zygophlebiella*, and *Mixophlebia*. This character is unknown in *Cyrtophlebia*, *Xamenophlebia* and *Permophlebia*.

Family **ZYGOPHLEBIIDAE** Pritykina, 1981

Type genus. – *Zygophlebia* Pritykina, 1981.

Other genera. – *Zygophlebiella* Pritykina, 1981, *Mixophlebia* Pritykina, 1981, *Cyrtophlebia* Pritykina, 1981. BECHLY (1996) noted that the latter genus could be more closely related to the Xamenophlebiidae.

Wing venational autapomorphies. – Not yet known (BECHLY, 1996).

Genus **ZYGOPHLEBIA** Pritykina, 1981

Type species. – *Zygophlebia ramosa* Pritykina, 1981.

Diagnosis. – Six rows of cells in area between *CuP* and posterior wing margin; *CuA* straight; wing broad with many cells, but less than in *Mixophlebia*.

Zygophlebia ramosa Pritykina, 1981 (figs. 6-7)

Material. – Holotype specimen PIN 2785/20. Other specimens PIN 2555/619, 2555/656, 2555/4101.

Type horizon. – Madygen Formation, Norian, Upper Triassic.

Type locality. – Dzhayloucho, South Fergana, near Shurab, Batkensk region, Kyrgyastan.

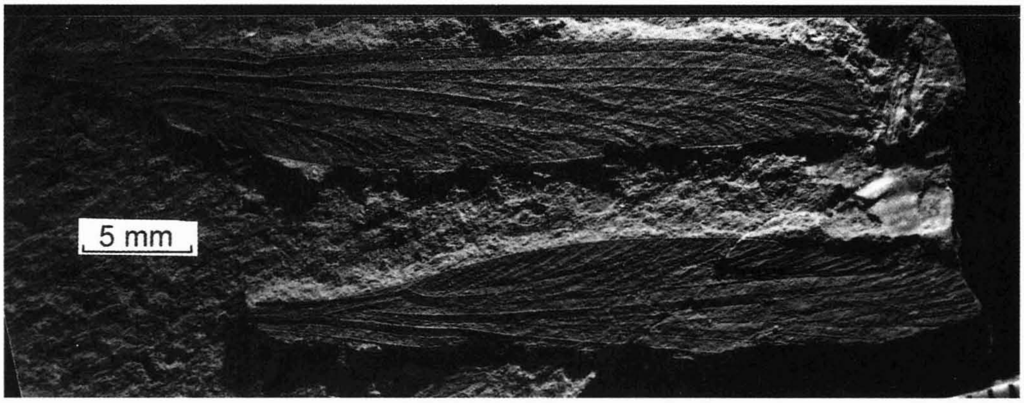

Fig. 6, *Zygophlebia ramosa* Pritykina, 1981. Photograph of the holotype PIN 2785/20.

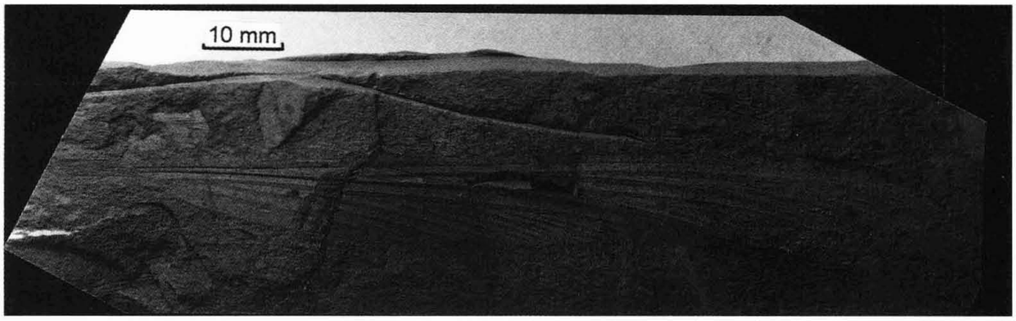

Fig. 7, *Zygophlebia ramosa* Pritykina, 1981. Photograph of the paratype PIN 2555/619.

Genus ZYGOPHLEBIELLA Pritykina, 1981

Type species. – *Zygophlebiella curta* Pritykina, 1981

Diagnosis. – Two or three rows of cells in the area between *CuP* and posterior wing margin; *CuA* more zigzagged than in *Zygophlebia* and *Mixophlebia*; wing narrower than those of *Zygophlebia* and *Mixophlebia*.

Remark. – We have examined the specimen PIN 2555/631 at PIN in Moscow. It has several structures different from those of the holotype PIN 2785/20: (a) presence of numerous crossveins in the postdiscoidal area just distal of *MAb*; (b) *IR2* zigzagged at its base; (c) *CuA* more zigzagged than that of the holotype. Nevertheless, it shares with the holotype the structure of the stem of *CuA + CuP + AA* and the shape and size of the cubito-anal areas. Thus, specimens 2555/631 and 2785/20 probably belong to the same species, or at least very closely related species of the same genus.

Zygophlebiella curta Pritykina, 1981 (fig. 8)

Material. – Holotype specimen PIN 2555/633. Other specimen PIN 2555/631.

Type horizon. – Madygen Formation, Norian, Upper Triassic.

Type locality. – Dzhayloucho, South Fergana, near Shurab, Batkensk region, Kyrgyastan.

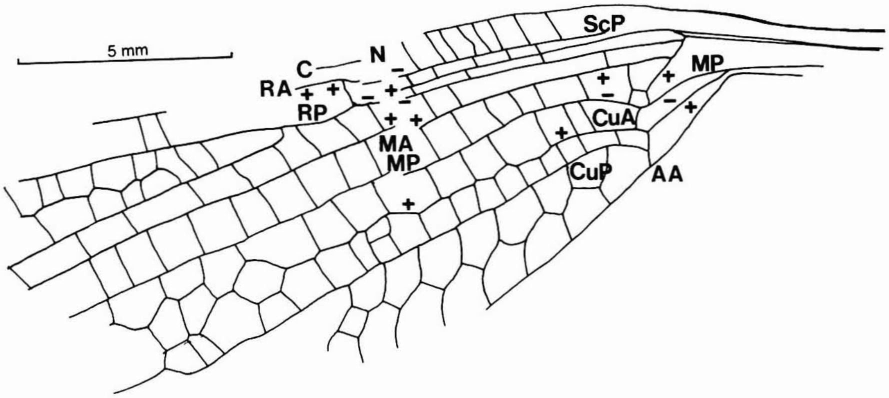

Fig. 8, *Zygophlebiella curta* Pritykina, 1981. Holotype PIN 2555/633.

Genus **MIXOPHLEBIA** Pritykina, 1981

Type species. – *Mixophlebia mixta* Pritykina, 1981.

Diagnosis. – This genus is characterized by its veins *MPb*, *CuP + AA* and *AA* aligned, forming a transverse vein at the base of cubito-anal areas; wings very wide and longer than those of *Zygophlebia* and *Zygophlebiella*.

Mixophlebia mixta Pritykina, 1981 (figs. 9-10)

Material. – Holotype specimen PIN 2555/625. Other specimen PIN 2785/8.

Type horizon. – Madygen Formation, Norian, Upper Triassic.

Type locality. – Dzhayloucho, South Fergana, near Shurab, Batkensk region, Kyrgyastan.

Genus **CYRTOPHLEBIA** Pritykina, 1981

Type species. – *Cyrtophlebia sinuosa* Pritykina, 1981.

Remark. – Since the basal halves of the wings of the type specimen of *Cyrtophlebia* are not preserved, the main characters of Zygophlebiidae are unknown for this taxon. The single visible synapomorphy with Zygophlebioidea is the basal part of *RP2* looking like a bridge between *IR2* and *IR1*, which can be regarded as a rather strong evidence.

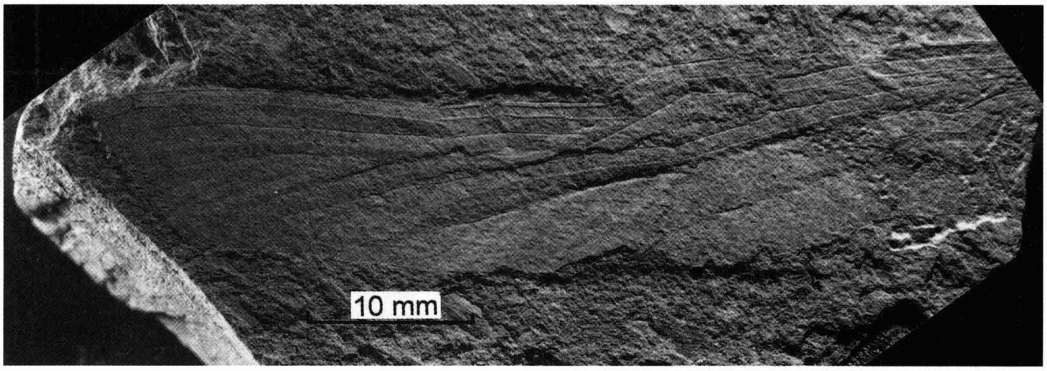

Fig. 9, *Mixophlebia mixta* Pritykina, 1981. Photograph of the holotype PIN 2555/625.

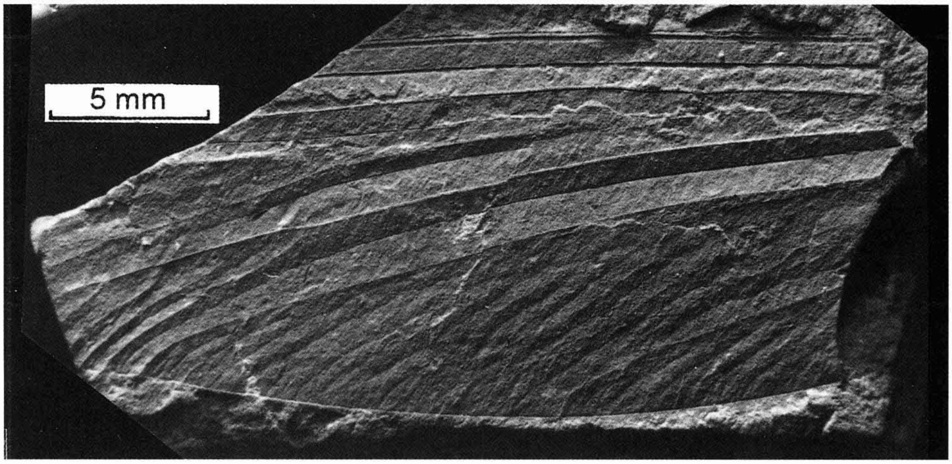

Fig. 10, *Mixophlebia mixta* Pritykina, 1981. Photograh of the paratype PIN 2785/8.

Cyrtophlebia sinuosa Pritykina, 1981

Material. – Holotype specimen PIN 2785/25.

Type horizon. – Madygen Formation, Norian, Upper Triassic.

Type locality. – Dzhayloucho, South Fergana, near Shurab, Batkensk region, Kyrgyastan.

Superfamily **XAMENOPHLEBIOIDEA** Pritykina, 1981

Included groups. – Xamenophlebiidae Pritykina, 1981 and Permophlebiidae, **fam. nov.**

Wing venational autapomorphies. – (1) Area between *RP3* and *RP4* very broad, with more than 15 rows of cells along posterior wing margin; (2) a long and straight concave vein '*Mspl*' closely parallel to *CuA*; (3) the three veins '*Mspl*', *CuA* and *CuP* arranged in a converging triplet and apparently not reaching the posterior wing margin; (4) *RP3/4* is bifurcated in all Triadophlebiomorpha and Triadotypomorpha but, in Xamenophlebiidae, the fork is asymmetric, *RP3* being clearly secondarily branched on *RP4* (based on our study of the type material of *Xamenophlebia*).

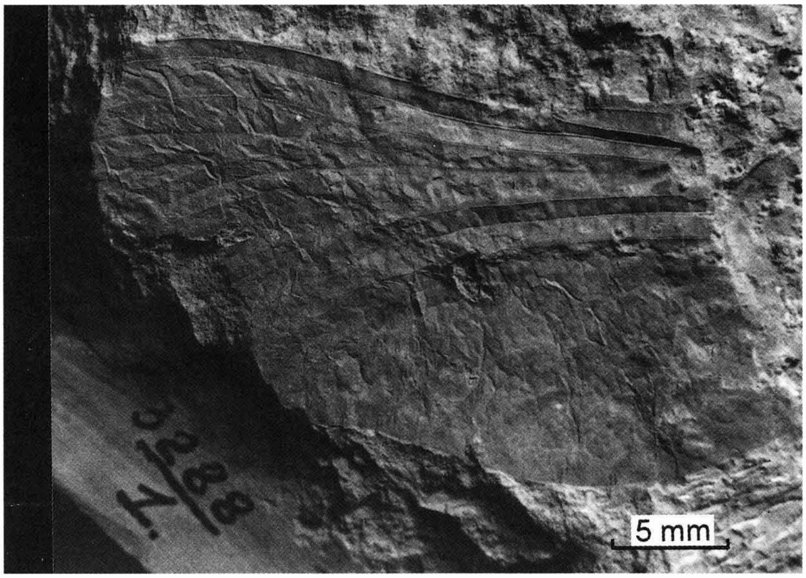

Fig. 11, *Xamenophlebia ornata* Pritykina, 1981. Photograph of the holotype PIN 3288/1.

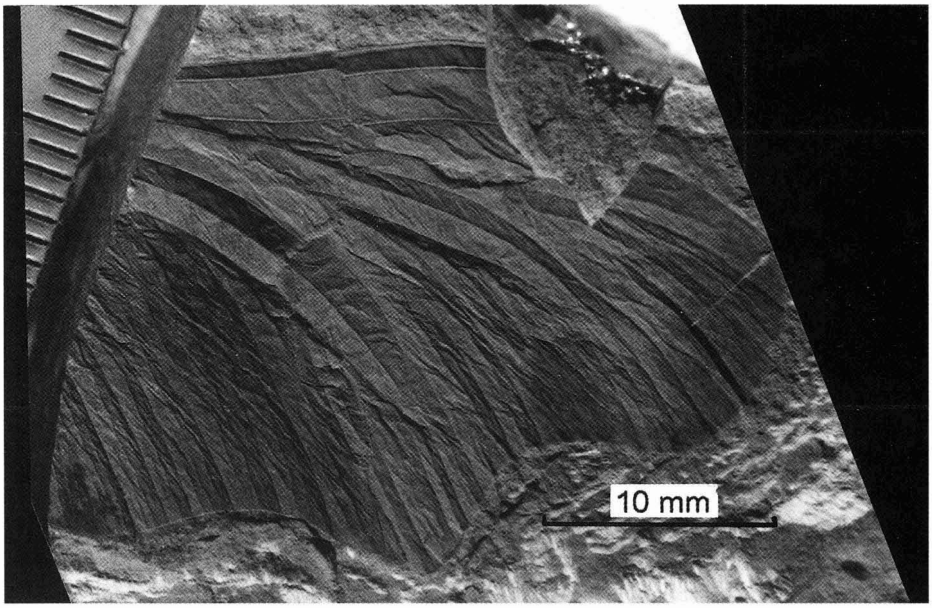

Fig. 12, *Xamenophlebia ornata* Pritykina, 1981. Photograph of the paratype PIN 2555/2074.

Family **XAMENOPHLEBIIDAE** Pritykina, 1981

Type genus. – *Xamenophlebia* Pritykina, 1981.

Wing venational autapomorphies. – *RP4*, *MA* and *MP* arranged in a converging triplet; *RP3*, *IR2* and *IR2* arranged in a converging triplet; an extremely undulating posterior wing margin along the triplet *RP4-MA-MP*.

Genus **XAMENOPHLEBIA** Pritykina, 1981

Type species. – *Xamenophlebia ornata* Pritykina, 1981.

Diagnosis. – That of the family.

Xamenophlebia ornata Pritykina, 1981 (figs. 11-12)

Material. – Holotype specimen PIN 3288/1. Other specimens PIN 2555/2074 and PIN 2240/1789.

Type horizon. – Madygen formation, Norian, Upper Triassic.

Type locality. – Dzhayloucho, South Fergana, near Shurab, Batkensk region, Kyrgyastan.

Family **PERMOPHLEBIIDAE, fam. nov.**

Type genus. – *Permophlebia,* gen. nov.

Wing venational autapomorphies. – (1) Presence of an oblique 'pseudo-subnodus' basal of the subnodus that is directed towards the wing base; (2) presence of a '*pseudo-Cr*' basal of the nodal '*Cr*'; (3) primary antenodal crossveins very approximate and on a level with arculus; (4) presence of a secondary longitudinal concave vein closely parallel to *CuA*, in postdiscoidal area; (5) wing reaches maximum width just distal of nodus. The strong convergence of *MP* and *MA* near posterior wing margin is more likely a convergence to the state in Triadotypomorpha.

Remarks. – PRITYKINA (1981) did not figure any primary antenodal crossveins in all the Triadophlebiomorpha she described. Our re-examination of the fossil material confirmed that these structures are not preserved in the fossil wings, thus they remain unknown for nearly all the Triassic Triadophlebioidea. Nevertheless, we could observe the presence of two primary antenodal crossveins on the type specimen of *Cladophlebia parvula* Pritykina, 1981 (specimen PIN 2555/617) and on specimen 2555/628 that was correctly attributed to *Paurophlebia lepida* by PRITYKINA (1981). On both specimens, these veins are well basal of the arculus, more approximate in *P. lepida* than in *C. parvula*, but clearly less approximate than in *Permophlebia uralica,* gen. n., sp. n.

Genus **PERMOPHLEBIA, gen. nov.**

Type species. – *Permophlebia uralica,* sp. n.

Etymology. – Named after the Greek word for 'vein', and the Permian age.

Diagnosis. – That of the family.

Permophlebia uralica, sp. n. (figs. 13-14)

Holotype. – Specimen PIN 4706/1 (part and counterpart), Moscow.

Geological age. – Early Upper Permian.

Type locality. – Vostochno-Novikbozhskay borehole, depth int. 1254.3-1261.9 m, Vorkuta Basin, North Ural, Russia.

Etymology. – Named after the Ural region in Russia.

Diagnosis. – That of the family (monotypy).

Description. – Part and counterpart of a wing with the apex and base missing. No trace of coloration preserved. Length of preserved part of wing, 61.3 mm; maximum width, 19.7 mm; wing elongate and broad, its broadest part being just distal of the nodus; vein *ScP* reaching costal margin 22.2 mm from base of arculus, in basal half of wing; no nodal furrow visible in costal margin; nodal crossvein '*Cr*' present but obliquely directed towards wing base; a short crossvein '*pseudo-Cr*' closely parallel to '*Cr*', 1.3 mm basally, between *ScP* and *RA*; subnodal crossvein perpendicular to *RA* and *RP* and aligned with '*Cr*'; a strong and long crossvein 'pseudo-subnodus' between *RA* and *RP* aligned with '*pseudo-Cr*', and obliquely directed towards wing base; numerous antenodal crossveins in antenodal area between *ScP* and *C*, viz. 19 secondary crossveins and 2 strongly approximate primary antenodal crossveins *Ax1* and *Ax2*, 1.6 mm apart and both on a level with arculus; the two rows of secondary antenodal crossveins are not well-aligned; no antesubnodal crossveins in area between *RA* and *RP*, between arculus and 'pseudo-subnodus'; costal margin concave at nodus; postnodal crossveins very numerous between *C* and *RA*, not aligned with postsubnodal crossveins between *RA* and *RP1*; *RA*, *RP* and *MA* basally fused into a common stem; *RP* + *MA* separating from *RA* in arculus; RP separating from *MA* 1.1 mm distal of base of arculus; *MA* with a strong angle 1 mm distally; a strong posterior branch *MAb* of *MA* between *MA* and *MP*; basal stem of *RP* + *MA*, *MA* and *MAb* well-aligned in a very strong oblique 'composite' vein ending in *MP*; base of *RP3/4* aligned with nodus, 20.6 mm distal of base of *RP*; base of *IR2* 4 mm distally, that of *RP2* 12.6 mm distally, and that of *IR1* 8.4 mm distally; *RP3/4*, *IR2*, *RP2*, and *IR1* all simple, without any branches; *IR2* apparently branched on *RP3/4* rather than on *RP1*; *RP2* apparently branched on *IR2* rather than on *RP*; *IR1* apparently branched on *RP2* rather than on *RP1*; *RP3/4*; *RP3/4* bifurcate, with a straight concave anterior *RP3*, branching on *RP3/4*, with two rows of cells between it and *IR2* and a very broad area between it and *RP4*; *RP3/4* undulating but more or less parallel to *MA*; areas between *RP3/4* and *IR2*, and *IR2* and *RP2* distally widened; *MA* simple, without any posterior branches; two rows of cells between *MA* and *RP3/4*, in their distal parts; 'postdiscoidal' area between *MA* and *MP* distally narrowed, with one or two rows of cells between these veins near wing margin; area between *MP* and posterior wing margin very large and broad, 20 mm wide along posterior wing margin and with 22 to 25 rows of cells between *MP* and posterior wing margin; *MP* without distal posterior branches; about 20 secondary long secondary veins between *MP* and posterior wing margin; *MP* with a basal posterior branch *MPb* aligned with *MAb*; a long, concave and straight secondary vein '*Mspl*' closely parallel to *CuA* in area between *MP* and *CuA*; a longitudinal concave vein (probably *CuP*) closely parallel to *CuA*, with one row of cells in area between *CuA* and it; area between *CuP* and posterior wing margin broad, 5.6 mm wide, with about 20 rows of cells and 25 long secondary oblique veins; veins '*Mspl*', *CuA* and *CuP* arranged in converging triplet and apparently not reaching the posterior wing margin; basal branchings of *CuA* and *CuP* not preserved but the preserved part of these veins looks like those of the Zygophlebiidae; *AA* not preserved; as *AA* was not extending distal of the level of arculus, it was probably very short; wing probably petiolate, indicated by relative directions of basal part of posterior wing margin and *CuA*, *CuP*, and *MP*; precise length of petiole unknown.

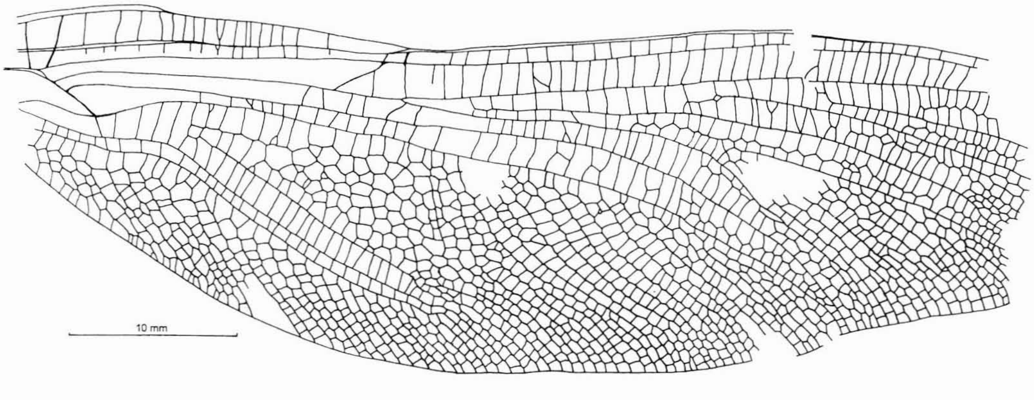

Fig. 13, *Permophlebia uralica,* sp. n. Print of the holotype wing PIN 4706/1.

Discussion. – *Permophlebia uralica,* gen. n., sp. n. shares several important synapomorphies with Panodialata *sensu* NEL *et al.* (1999b) (= Lapeyriidae Nel *et al.*, 1999 + Nodialata Bechly, 1996): (1) presence of a true odonatoid nodus, with nodal and subnodal veinlets; (2) RA and RP basally fused into a long double-barrel radial stem; (3) archaedictyon reduced. Furthermore, its *MA* is unbranched, which is an important synapomorphy with Nodialata (*sensu* BECHLY, 1996, amended by NEL *et al.*, 1999b) (= Protanisoptera + Discoidalia). Thus, it obviously cannot be closely related to Lapeyriidae. It also does not show any of the autapomorphies of Protanisoptera, as listed in BECHLY (1996), i.e. it has no postnodal crossveins developed as an oblique vein, no specialized pterostigma, proper to this group, no apical secondary branch of *RA*, etc. Furthermore, it shares the venational autapomorphies of the Discoidalia sens. n., i.e. 'presence of a typical odonatoid discoidal cell', distally delimited by a characteristically oblique and very strong vein *MAb*; vein *CuA* not fused with *AA* + *CuP* but directly beginning on *MP* + *Cu* (BECHLY, 1996).

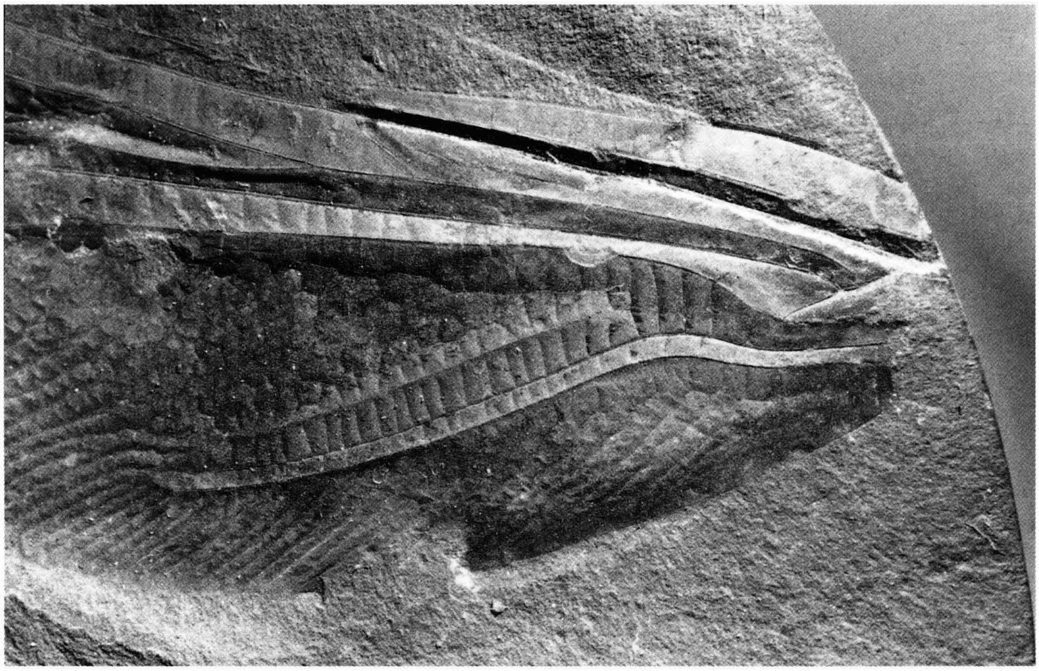

Fig. 14, *Permophlebia uralica,* sp. n. Photograph of the counterpart of the holotype PIN 4706/1.

The distal free part of *CuP* seems to have been convergently reduced in some Protanisoptera like *Hemizygopteron* Zallesskiy, 1955 (correlated with the reduction of the anal area) and the majority of taxa in Discoidalia, since the protanisopteran genera *Polytaxineura* Tillyard, 1935 and *Permaeschna* Martynov, 1931 (BECHLY, 1998; NEL, unpublished data) have retained a long distal free part of *CuP*. Thus, the presence of a long distal free part of *CuP* in *Permophlebia,* gen. n. is not conflicting with a closer relationship with the Discoidalia rather than with Protanisoptera. Furthermore, *Triadotypus guillaumei* Grauvogel & Laurentiaux, 1952 has a well-developed distal free part of *CuP* as well. The presence of a plesiomorphic well developed distal free part of *CuP*, basally independent of *CuA* in *Permophlebia*, implies that it has a rather basal position within the Discoidalia.

According to BECHLY (1996), in Triadophlebiomorpha, *AA* has been captured by *MP* + *Cu* (autapomorphy) and the distal free part of *CuA* is not beginning directly on *MP* but is still on a common basal stem *CuA* + *CuP* + *AA*. In *Permophlebia*, at the extreme base of the preserved part of the wing, *CuA*, *CuP* and *MP* are still well separated, thus the exact organization of the respective branchings between these veins remains unknown. Nevertheless, *Permophlebia* shares with Zygophlebiida, and more precisely with the Xamenophlebiidae, the presence of long and straight '*Mspl*', *CuA* and *CuP*, arranged in a converging triplet and apparently not reaching the posterior wing margin, which appears to be a good putative synapomorphy.

Family **KARGALOTYPIDAE** Zessin, 1983 (family rank proposed by BECHLY, 1996)
(= **MEGANEURIDAE** subfamily **KARGALOTYPINAE** Zessin, 1983)
(*in* Triadophlebiomorpha: Zygophlebiida, **sit. nov.**)

Type genus. – *Kargalotypus* Rohdendorf, 1962.

Diagnosis. – ZESSIN (1983) characterized this taxon as follows: (1) 'unique type of *MA*-field with the shape of an isosceles triangle' (BECHLY, 1996); (2) the point of separation between *RP2* and *RP1* ('*R2+3*' *sensu* ZESSIN, 1983) in a distal position; (3) no specialized subnodal vein (ZESSIN, 1983). After the present reinterpretation of the wing veins, the vein named *MA* by ZESSIN corresponds to *RP3/4*, thus character (1) (unique autapomorphy of the family after Bechly) is invalid. With the new interpretation of the wing venation, the characters (2) and (3) are no longer valid as well. We propose to transfer this taxon within Triadophlebiomorpha close to Zygophlebiida (see discussion below). The characters 'nodal and subnodal veins not oblique' is also present in this latter taxon. Compared to Zygophlebiida, *Kargalotypus* differs from *Zygophlebia* and *Permophlebia* in the presence of a more pronounced undulation of posterior wing margin; and it differs from *Zygophlebia* and *Xamenophlebia* in the absence of a bridge between *IR2* and *IR1*. Since all the structures of the basal half of the wing are unknown, it is impossible to determine the precise affinities of *Kargalotypus* within Triadophlebiomorpha.

Genus **KARGALOTYPUS** Rohdendorf, 1962

Type species. – *Kargalotypus kargalensis* (Martynov, 1932)

Kargalotypus kargalensis (Martynov, 1932) (fig. 15)

Megatypus (?) *kargalensis* Martynov, 1932b : 19-21, text-fig. 9 (original description).

Kargalotypus kargalensis : ROHDENDORF, 1962 : 74, fig. 127 (*in* gen. nov.); ZESSIN, 1983 : 60, 68 (*in* Kargalotypinae subfam. nov.); BRAUCKMANN, 1991 : 137 (list); CARPENTER, 1992 : 89 (*in* uncertain family); BECHLY, 1996 : 352 (*in* Kargalotypidae fam. nov.).

Material. – Holotype specimen PIN 968/1, Moscow.

Type horizon. – Kazanian, Upper Permian.

Type locality. – Kargala, Ural, Russia.

Redescription. – There are several errors in the original description and figure of MARTYNOV (1932b), reproduced by ROHDENDORF (1962). Therefore, a redescription is necessary.

Print and counterprint of the apical part of a wing, 46.6 mm long and about 22 mm wide; no trace of coloration visible; vein *ScP* reaching costal margin about 43 mm basal from apex; *RA* reaching costal margin near wing apex; about 40 cells between *C* and *RA* from nodus and point of fusion between *RA* and *C*; no oblique or specialized nodal or subnodal veins. As bases of veins *IR2*, *RP3/4*, *MA* and *MP* are not preserved, it is difficult to determine the exact nature of the longitudinal veins. Nevertheless, the respective concavity and convexity of these veins allow to identify them. Convex vein *IR1* originating 22 mm from wing apex; *IR1* basally weakly zigzagged but distally straight; concave vein *RP2* originating 27,2 mm from wing apex; *RP2* not zigzagged but with a distinct curvature; base of convex *IR2* not preserved but probably basal of or very close to the nodus (point of fusion between *ScP* and *C*); *IR2* nearly straight; base of *RP3/4* probably basad of nodus, *RP3/4* not zigzagged but distinctly forked into *RP3* and *RP4*, 13.9 mm from posterior wing margin; a broad area, 10.5 mm wide along posterior wing margin, with eight long secondary longitudinal veins between *RP3* and *RP4*; area between *IR2* and *RP3* distally narrowed near posterior wing margin; *MA* unbranched and nearly straight; area between *RP4* and *MA* distally narrowed near posterior wing margin; *MP* nearly straight; two or three rows of cells in the area between *MA* and *MP*; area between *MP* and posterior wing margin very broad, with numerous long secondary veins originating on *MP* and reaching posterior wing margin; posterior wing margin very undulating between the ends of veins *RP4* and *MP*.

Discussion. – *Kargalotypus* has to be excluded from the Meganisoptera for the following evidences: (1) its vein *RA* nearly reaching the wing apex is a character present in odonatopteran groups distinctly more advanced than the Meganisoptera. In the less advanced Meganisoptera but also in the Lapeyriidae, even in the Protanisoptera, *RA* is reaching the Costa well basad of the wing apex (plesiomorphy); (2) its *MA* is unbranched (synapomorphy of the Nodialata *sensu* BECHLY, 1996); *ScP* ist short, so that the nodus is in a very basal position (synapomorphy of the Nodialata).

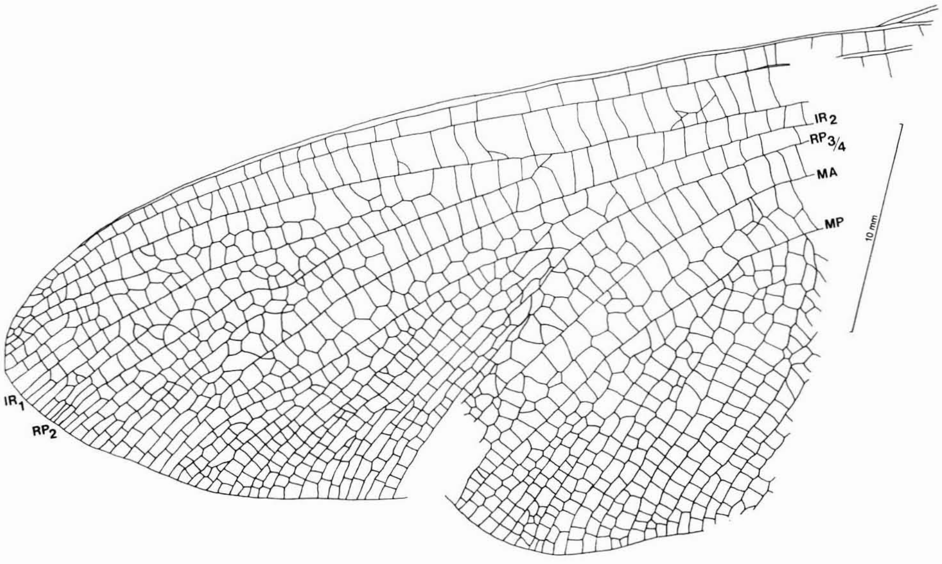

Fig. 15, *Kargalotypus kargalensis* (Martynov, 1932). Print of the holotype wing PIN 968/1.

Furthermore, *Kargalotypus* shares several putative synapomorphies with the clade Triadophlebiomorpha: Zygophlebiida within Nodialata: (1) very undulating posterior wing margin; (2) *RP4* and *MA* strongly approximate near posterior wing margin; (3) *RP3* and *IR2* strongly approximate near posterior wing margin; (4) *RP3* and *RP4* distinctly separated into two branches, with a broad area between them; (5) wing very broad with many cells.

Nevertheless, the fact that *IR1* and *IR2* are not fused with *RP2* and the absence of the 'oblique vein' (= vestigial *RP2* stem) between *RP1* and *IR1* + *RP2* are two plesiomorphic characters that exclude a position of *Kargalotypus* within Zygophlebiida [= Zygophlebiidae + (Permophlebiidae + Xamenophlebiidae)], since a convergence or reversal of such a unique fusion is very unlikely. An undulating hind margin is also present in Mitophlebiidae, so that it could either be a convergent tendency or parallel trend within Triadophlebiomorpha or (less likely) a symplesiomorphy. Since the peculiar bridge structure is developed in Zygophlebiidae and Xamenophlebiidae and (less distinct) Permophlebiidae, Kargalotypidae can at best be the sistergroup of Zygophlebiida as a whole but not be the sistergroup of Xamenophlebioidea [= Permophlebiidae + Xamenophlebiidae].

CLADISTIC ANALYSIS OF THE ZYGOPHLEBIIDA

We have performed a cladistic analysis of the genera of Zygophlebiida, based on 17 characters (see character list and matrix fig. 18), using *Triadotypus* and two members of

List of characters used in the cladistic analysis of ZYGOPHLEBIIDA

1. AA.
   - not reduced to a oblique crossvein between posterior margin and branching of *Cu + AA* into *CuA* and *CuP* (0)
   - reduced to a oblique crossvein between posterior margin and branching of *Cu + AA* into *CuA* and *CuP* (1)
2. **RP2.**
   - branched on *RP* (0)
   - apparently branched on *IR2* rather than on *RP1* (1)
3. **IR1.**
   - branched on *RP* (0)
   - apparently branched on *RP2* rather than on *RP1* (1)
4. **RP4, MA** and **MP.**
   - not strongly approximate near posterior wing margin (0)
   - strongly approximate near posterior wing margin (1)
5. **CuA.**
   - with posterior branches (0)
   - without posterior branch (1)
6. **CuA** and **CuP.**
   - not closely parallel and with more than one row of cells between them (0)
   - closely parallel and with one row of cells between them (1)
7. **Basal part** of **RP2.**
   - not looking like a bridge between *IR2* and *IR1* (0)
   - looking like a bridge between *IR2* and *IR1* (1)
8. **CuP** + **AA.**
   - is not making a strong zigzag between the point of separation of *CuA* from *CuA + CuP + AA* and the point of separation between *CuP* and *AA* (0)
   - is making a strong zigzag between the point of separation of *CuA* from *CuA + CuP + AA* and the point of separation between *CuP* and *AA* (1)
9. **Area between RP3** and **RP4.**
   - not very broad (0)
   - very broad, with more than 15 rows of cells along posterior wing margin (1)
10. **A long** and **straight concave vein 'Mspl' closely parallel** to **CuA.**
    - absent (0)
    - present, the three veins '*Mspl*' being arranged in a converging triplet (1)
11. **CuA** and **CuP.**
    - reaching the posterior wing margin (0)
    - apparently not reaching the posterior wing margin (1)
12. **The fork** of **RP3/4 is.**
    - symmetric (0)
    - asymmetric, *RP3* being secondarily branched on *RP4* (1)
13. **CuA.**
    - is zigzagged (0)
    - straight (1)
14. **RP3.**
    - with strong secondary branches (0)
    - no strong secondary branches (1)
15. **RP4.**
    - with strong secondary branches (0)
    - no strong secondary branches (1)
16. **Subnodal veinlet.**
    - not very obliquely directed towards the apex of the wing (0)
    - very obliquely directed towards the apex of the wing (1)
17. **CuA** + **CuP** + **AA.**
    - not fused to *MP* (0)
    - fused to *MP*, but separating basal of the base of arculus (1)
    - fused to *MP*, separating distal of the arculus (2)

Triadophlebiida (*Triadophlebia* and *Mitophlebia*) as outgroups. The characters were considered as unordered, but the results are the same if the two characters having three states ('16' and '17') are considered as ordered. The results concerning the ingroup are identical if the analyses are performed with one, two or three outgroups. The analysis was performed using the computer software packages Paup 3.1.1. and MacClade 3.07. The 'branch and bound' analysis yielded 9 most parsimonious trees of equal length (17 steps), with a consistency index CI 0.88, a consistency index excluding uninformative characters CI 0.85, and a retention index RI 0.91. The strict consensus tree is given in figure 19. The ingroup Zygophlebiida is monophyletic, with a subclade [*Xamenophlebia* + *Permophlebia*]. A calculation of the BREMER's 'decay' indices (1994) shows:

(1) the search for trees with 18 steps or less only yields the nine equally parsimonious trees;

(2) the search for trees with 19 steps or less preserves the clade Zygophlebiida but not the subclade Xamenophlebioidea;

(3) the search for trees with 20 steps or less results in a totally unresolved consensus tree.

Table 1. – Table of character states for the present cladistic analysis of Zygophlebiida.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Xamenophlebia	?	1	1	1	1	1	1	?	1	1	1	1	1	1	1	?	?
Permophlebia	?	1	1	1	1	1	0	?	1	1	1	1	1	1	1	1	1
Zygophlebia	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	1
Zygophlebiella	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	1
Mixophlebia	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	1
Cyrtophlebia	?	1	1	1	?	?	1	?	0	?	?	0	?	1	1	?	?
Mitophlebia	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	2	2
Triadophlebia	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	2	2
Triadotypus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0

The clade Xamenophlebioidea is supported by the state changes 0 > 1 for characters '9', '10', '11', and '12'. The clade Zygophlebiida is supported by the state changes 0 > 1 for characters '2', '3', and '4'. There is no known character supporting the family Zygophlebiidae, which does not appear as a monophyletic clade.

Clade **ISOPHLEBIIDA** Bechly, 1996

Family **LIADOTYPIDAE** Grauvogel & Laurentiaux, 1952 (non MARTYNOV, 1937)
(*in* **ISOPHLEBIIDA**, **sit. nov.**, family *incertae sedis*)

Type genus. – *Liadotypus* Martynov, 1937

Remarks. – MARTYNOV (1937) included *Liadotypus relictus* in the Meganeuridae. GRAUVOGEL & LAURENTIAUX (1952) discussed briefly on this taxon and considered that it belongs to a different family Liadotypidae that they erroneously attributed to MARTYNOV (1937), even though they were the first authors to cite this family.

Wing venational autapomorphies. – Unknown. This family name should not have been erected at all, because of the very fragmentary state of preservation of the type.

Genus **LIADOTYPUS** Martynov, 1937

Type species. – *Liadotypus relictus* Martynov, 1937.

Liadotypus relictus Martynov, 1937 (figs. 16-17)

Liadotypus relictus Martynov, 1937, : 110-111, fig. 64 (original description); GRAUVOGEL & LAURENTIAUX, 1952 : (refigured, position discussed); LAURENTIAUX, 1958 : 44 (position discussed); ZESSIN, 1983 : 59 (list).

Material. – Holotype specimen PIN 3621/23a, b, Moscow.

Geological age. – Liassic/Middle Jurassic.

Type locality. – Shurab, Ferghana, Russia.

Redescription. – There are numerous errors in the original description of MARTYNOV (1937), due to the poor and fragmentary state of preservation of the holotype.

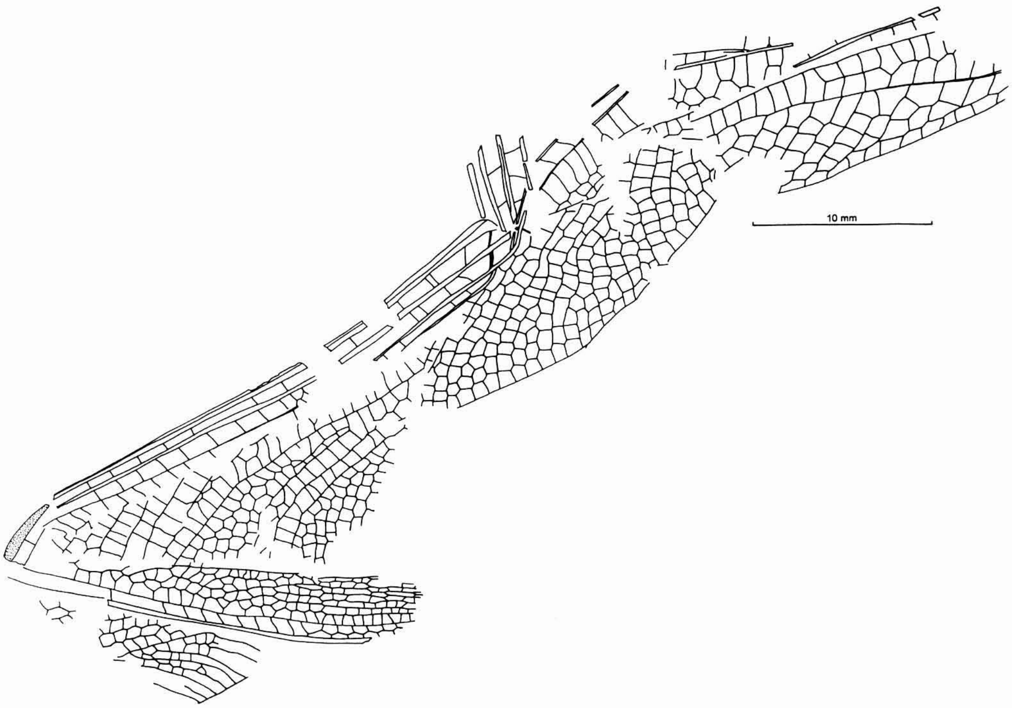

Fig. 16, *Liadotypus relictus* Martynov, 1937. Wing of the holotype PIN 3621/23a,b.

It is the print and counter print of a forewing. Since there is no trace of coloration, the wing probably was hyaline; wing base missing and apex partly destroyed; length of preserved part about 85 mm; width of wing unknown; fragments of a sclerotized narrow and probably rather long pterostigma visible; true nodus clearly preserved, with fusion between *ScP* and Costa, and aligned nodal and subnodal oblique veinlets; only distal part of antenodal area preserved, with several antenodal crossveins of second row between *ScP* and *RA*; postnodal area relatively well preserved, with about 11 postnodal crossveins not aligned with postsubnodals; area between *MP* and posterior wing margin very well developed, with numerous secondary veins below *MP*; mid part of postdiscoidal area between *MP* and *MA* preserved with two rows of cells between these vein basally, and a distinct distal narrowing of this area; numerous small cells and secondary veins in radial area; *CuA* weak and short, with only one row of cells in cubito-anal area.

Discussion. – *Liadotypus* was previously included in the meganisopteran grade (ZESSIN, 1983). It has to be excluded from it because of the presence of a sclerotized pterostigma and of a true nodus. Furthermore, its very long wing, the hypertrophied area between *MP* and the posterior wing margin, the reduced cubito-anal area and the distal narrowing of the postdiscoidal area represent autapomorphies of the Isophlebiida [= Archithemistidae + Campterophlebiidae + Isophlebiidae] within the clade Epiproctophora Bechly, 1996 [= 'anisozygoptères' + Anisoptera]. Thus, *Liadotypus* has to be excluded from the Meganeuridae and the Meganeuromorpha and is here transferred to Isophlebiida. The presence of antesubnodal crossveins between *ScP* and *RA* and the absence of antenodal crossveins between *ScP* and *C* suggest that closer affinities with the Isophlebiidae are unlikely. Likewise, the long pterostigma and long wing with numerous cells suggest that closer affinities with the Archithemistidae are unlikely either. The poor and fragmentary state of preservation of the type does not allow a more precise estimation of its phylogenetic position and affinities.

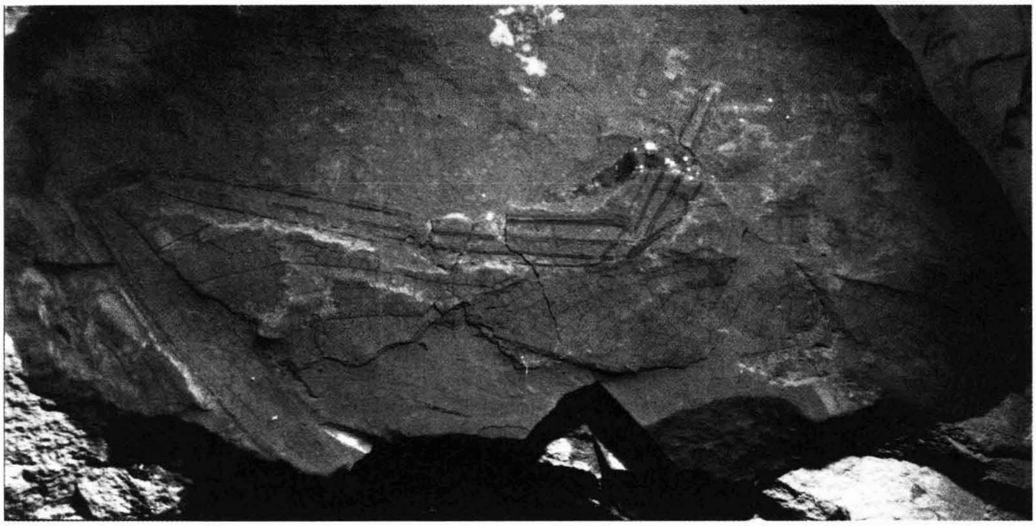

Fig. 17, *Liadotypus relictus* Martynov, 1937. Photograph of the holotype PIN 3621/23a,b.

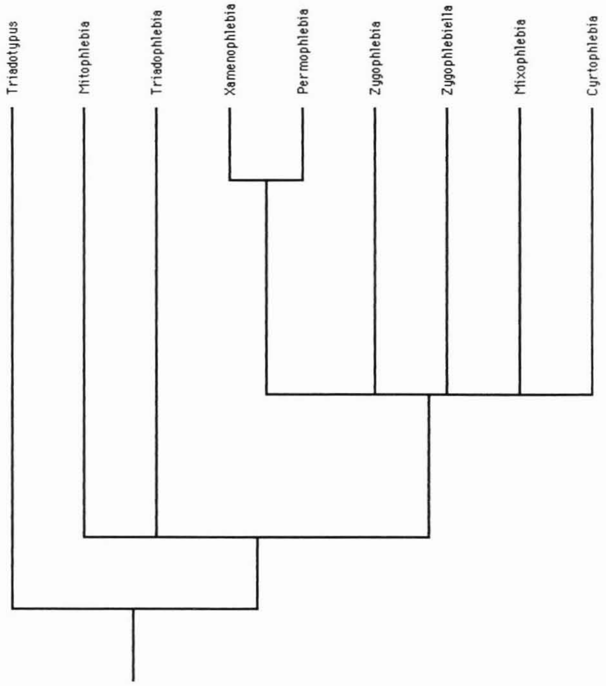

Fig. 18, Strict consensus cladogram of the 9 equally minimal parsimonious trees.

CONCLUSIONS

GRAUVOGEL & LAURENTIAUX (1952) considered *Liadotypus* as the most recent Meganeuromorpha. Because of our attribution of *Liadotypus* to the [Epiproctophora – Isophlebiida] and the attribution of *Triadotypus* to the Nodialata, the Meganeuromorpha now appear to be exclusively restricted to the Carboniferous and Permian, as suggested by BECHLY (1997, 1998). The presence of *Permophlebia* as a genuine representative of Discoidalia in the Early Upper Permian of Russia shows that this group, which was previously only known after the Middle Triassic, is much more ancient, and was present before the Permo-Triassic boundary. This finding is supported by the discovery of a representative of the sister group of Nodialata (viz *Lapeyria magnifica* Nel, Gand & Garric, 1999) and of a true Stigmoptera (viz *Saxonagrion minutus* Nel *et al.*, 1999) in the Upper Permian of Lodève (France) (NEL *et al.*, 1999a, b). Furthermore, a member of Discoidalia has recently been discovered in the Westphalian of England (JARZEMBOWSKI & NEL, in prep.), and BECHLY (1998: 424, text-fig. 132) even figures an undescribed new genus and species of Protozygoptera from the Virgillian of Carrizo Arroyo in New Mexico (specimen No. 1/19981 in coll. Jarmila Kukalová-Peck, Ottawa). All these new discoveries strongly suggest that the Odonatoptera were not affected by a major crisis at the Permo-Triassic boundary, as already noted by NEL *et al.* (1999b).

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