

Preliminary phylogenetic analysis of the Protanisoptera (Insecta: Odonoptera)

Essai d'analyse phylogénétique des Protanisoptera (Insecta : Odonoptera)

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Abstract

The Permian suborder Protanisoptera (Insecta: Odonoptera) is revised and a new phylogenetic hypothesis proposed after analyses based on wing venation and different outgroups. After our study the families Camptotaxineuridae and Kaltanoneuridae are excluded from the Protanisoptera. After a new phylogenetic analysis, the family Permaeschnidae is redefined and the families Pholidoptilidae, Polytaxineuridae, Callimokaltaniidae and Hemizygopteridae are restored, as already proposed for the latter three families by Bechly (1996). The new genus *Proditaxineura* is described. The genus *Gondvanoptilon* RÖSLER et al., 1981 is excluded from the Meganisoptera: Erasipteridae and re-included in the Permaeschnidae, as already proposed by Bechly (1998). *Permaeschna proxima* MARTYNOV, 1931 is considered as a junior synonym of *Permaeschna dolloi* MARTYNOV, 1931. *Pholidoptilon camense* ZALESSKY, 1931 is excluded from *Permaeschna* MARTYNOV, 1931 and the genus *Pholidoptilon* ZALESSKY, 1931 is restored. *Ditaxineurella stigmalis* MARTYNOV, 1940 is excluded from the Hemizygopteridae and considered as a Protanisoptera Incertae sedis. © 2002 Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

Résumé

Le sous-ordre permien des Protanisoptera (Insecta : Odonoptera) est révisé et une nouvelle hypothèse phylogénétique est proposée d'après des analyses basées sur la nervation alaire et différents groupes externes. D'après la présente étude, les familles Camptotaxineuridae et Kaltanoneuridae doivent être exclues des Protanisoptera. La famille Permaeschnidae est redéfinie et les familles Pholidoptilidae, Polytaxineuridae, Callimokaltaniidae et Hemizygopteridae sont restaurées, comme déjà proposé pour les trois dernières familles par Bechly (1996). Le nouveau genre *Proditaxineura* est décrit. Le genre *Gondvanoptilon* RÖSLER et al., 1981 est exclu des Meganisoptera: Erasipteridae et reconsidéré comme un Permaeschnidae, comme déjà proposé par Bechly (1998). *Permaeschna proxima* MARTYNOV, 1931 est considéré comme un junior synonyme de *Permaeschna dolloi* MARTYNOV, 1931. *Pholidoptilon camense* ZALESSKY, 1931 est exclu de *Permaeschna* MARTYNOV, 1931 et le genre *Pholidoptilon* ZALESSKY, 1931 est restauré. *Ditaxineurella stigmalis* MARTYNOV, 1940 est exclu des Hemizygopteridae et considéré comme un Protanisoptera Incertae sedis. © 2002 Éditions scientifiques et médicales Elsevier SAS. Tous droits réservés.

Keywords: Insecta; Odonoptera; Protanisoptera; Revision; Phylogenetic analysis; Gen. nov.; Sp. nov.

Mots clés: Insecta; Odonoptera; Protanisoptera; Révision; Analyse phylogénétique; Gen. nov.; Sp. nov.

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1. Introduction

Protanisoptera is a group of Odonoptera that was apparently flourishing all over the World during the Permian (recorded from Russia, USA, Australia and Brazil) and became extinct before or at the end of this period.

There is a recent relative consensus concerning its phylogenetic position within the Odonoptera. **Trueman (1996)** considered that the Protanisoptera are the sister group of the ‘modern’ Odonoptera [‘Protozygoptera’ and ‘Archizygoptera’ and Zygoptera and ‘Anisozygoptera’ and Anisoptera], the clade [Protanisoptera + modern Odonoptera] being the sister group of the Meganeuromorpha. **Bechly (1995, 1996)** proposed a similar hypothesis, i.e. Nodialata [= Protanisoptera + Discoidalina] as sister group of Meganeuromorpha and the Discoidalina being the Triadophlebioptera + Stigmoptera [= Protozygoptera + Panodonata]. **Nel et al. (1999)** added the Lapeyriidae as sister group of the Nodialata, after the Meganeuromorpha, but did agree with the hypothesis of **Bechly (1996)**.

The phylogenetic relationships within the Protanisoptera are more problematic. **Tillyard and Fraser (1940)** and **Fraser (1957)** divided the Protanisoptera into the Ditaxineuridae TILLYARD, 1926 and Polytaxineuridae TILLYARD, 1935 (including the Pholidoptilidae ZALESSKY, 1931 and the Permaeschnidae MARTYNOV, 1931 without any care of the priority rules). Among the recent contributions to the problems, **Carpenter (1992)** followed this hypothesis and divided the Protanisoptera into Ditaxineuridae TILLYARD, 1926 and Permaeschnidae MARTYNOV, 1931. He also synonymized the Pholidoptilidae ZALESSKY, 1931, the Polytaxineuridae TILLYARD, 1935, the Callimokaltaniidae ZALESSKY, 1955 and the Hemizygopteridae ZALESSKY, 1955 with the Permaeschnidae, without explanation. **Carpenter** proposed no phylogenetic analysis.

Bechly (1996) proposed the following phylogenetic classification of the Protanisoptera: [Polytaxineuridae + (Permaeschnidae + (Hemizygopteridae + Ditaxineuridae))]. In his thesis, **Bechly (1998, in press)** slightly modified this classification by regarding Callimokaltaniidae as sister-group of Ditaxineuroidea (= Hemizygopteridae + Ditaxineuridae). Both groups together were named Ditaxineurida and the name Ditaxineuromorpha was used for the putative monophylum of Permaeschnidae and Ditaxineurida. **Bechly (1998, in press)** also re-transferred *Gondvanoptilon* from Erasipteridae to Permaeschnidae and restored the original spelling of the specific name of the type species to *G. brasiliense*, because the spelling change to *Gondvanoptilon brasiliensis* by **Martins Neto (1996)** was not justified, since the Greek stem ‘ptlion’ is neutral. **Bechly (1998, in press)** even questioned the justification of *Gondvanoptilon* as a genus distinct from *Permaeschna* due to the strong similarity of *G. brasiliense* and *Permaeschna dolloi*.

The monophyly of (Permaeschnidae + (Callimokaltaniidae + (Hemizygopteridae + Ditaxineuridae))) = Ditaxineuromorpha sensu **Bechly (1998)** is perhaps supported by the

following synapomorphies: (1) only a single antesubnodal cross-vein retained; (2) only one cross-vein present in the space between RP and MA from arculus to midfork; (3) all true cubito-anal cross-veins reduced – the apparent cubito-anal cross-veins are the two stems of CuA and CuP and an intercubital cross-vein.

These characters are dubious because: (1) some of them are unknown for many taxa supposed to belong to this clade (wing base structures unknown in the *Permaeschna* spp., etc.); (2) after the present analysis, some taxa clearly related to the Permaeschnidae (i.e. the *Gondvanoptilon* spp.) do not verify character. Therefore, it is clearly necessary to make a new phylogenetic analysis in order to test the hypotheses of **Bechly (1996, 1998)**.

We had the opportunity to describe one new species and revise a part of the type material of species previously described from the Palaeoentomological Institute, Academy of Science, Moscow, Russia (= PIN) and from the British Museum of Natural History, London. After this revision, we propose a new phylogenetic analysis of the Protanisoptera.

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 Odonoptera proposed by **Bechly (1996, 1997, 1998)** (**Table 1**).

Table 1
Matrix of taxa/characters states
Tableau 1
Caractères et taxons de la matrice

Taxa/characters	1	2	3	4	5	6	7	8	9	10
I1. <i>P. zherhikini</i>	0	0	0	0	1	0	0	1	1	2
I2. <i>P. dolloi</i> (3353/75)	?	1	1	0	0	0	?	1	0	1
I3. <i>P. camense</i>	0	0	0	1	1	0	0	1	0	2
I4. <i>P. stanleyi</i>	0	0	0	1	0	0	1	1	1	0
I5. <i>C. martynovi</i>	0	0	1	1	1	0	?	1	1	1
I6. <i>H. uralense</i>	0	0	1	1	1	1	0	1	1	2
I7. <i>G. brasiliense</i>	?	1	1	0	0	0	?	1	0	0
I8. <i>P. proxima</i>	?	?	?	?	?	?	?	?	?	?
I9. <i>D. anomalostigma</i>	0	0	0	1	1	1	0	0	0	2
I10. <i>D. cellulosa</i>	?	?	0	?	1	1	1	2	1	1
I11. <i>D. cellulosa</i> type	?	?	0	?	?	?	?	?	?	?
O1. ‘Geropterid’	0	0	0	1	0	0	0	0	?	0
O2. ‘Tupus’	0	0	0	0	0	0	1	0	0	0
O3. <i>L. magnifica</i>	?	?	?	?	?	0	?	0	0	0
O4. <i>P. uralica</i>	?	?	?	?	?	?	?	0	0	1&2
O5. <i>T. guillaumei</i>	1	?	?	?	?	?	?	?	0	0
O6. <i>M. schucherti</i>	0	0	1	0	0	0	1	0	0	0
Taxa/characters	11	12	13	14	15	16	17	18	19	20
I1. <i>P. zherhikini</i>	1	2	1	1	1	1	1	1	0	1
I2. <i>P. dolloi</i> (3353/75)	0	0	2	2	0	1	0	1	1	1
I3. <i>P. camense</i>	1	0	?	?	0	1	1	1	1	1
I4. <i>P. stanleyi</i>	0	1	1	?	2	1	1	1	1	1
I5. <i>C. martynovi</i>	0	1	1	1	1	1	1	2	0	1
I6. <i>H. uralense</i>	2	2	1	1	1	?	1	1	0	1
I7. <i>G. brasiliense</i>	0	0	2	2	2	1	1	1	1	2
I8. <i>P. proxima</i>	?	?	?	?	?	?	?	?	?	?
I9. <i>D. anomalostigma</i>	1	2	0	0	1	0	0	2	0	2
I10. <i>D. cellulosa</i>	0	1	0	0	1	0	1	2	0	2
I11. <i>D. cellulosa</i> type	?	?	0	0	?	?	?	?	?	2
O1. ‘Geropterid’	0	0&1	0	0	2	1	1	0	0	0
O2. ‘Tupus’	0	0	0	0	2	1	1	0	0	0

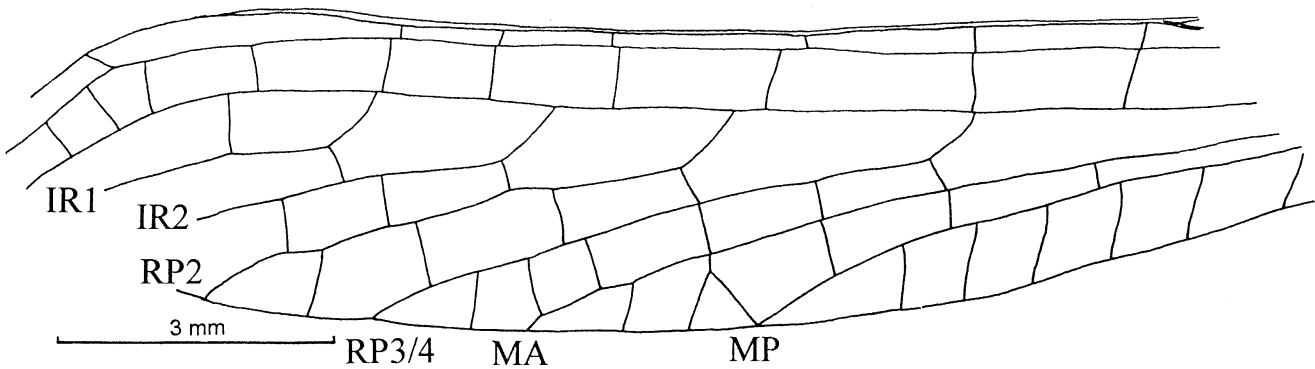


Fig. 1. *Kaltanoneura bartenevi* ROHDENDORF, 1961, holotype specimen PIN 600/485, print (scale bar represents 3 mm).

Fig. 1. *Kaltanoneura bartenevi* ROHDENDORF, 1961, holotype PIN 600/485, empreinte (l'échelle représente 3 mm).

2. Systematic palaeontology

2.1. Remarks about some families previously placed within Protanisoptera

Family: CAMPTOTAXINEURIDAE Tillyard, 1937 (formerly in Odonatoptera: Protanisoptera)

Type genus: *Camptotaxineura* TILLYARD, 1937.

Remark: This taxon was originally attributed to the Protanisoptera (Tillyard, 1937) but it probably does not belong to the Odonatoptera.

Genus: *Camptotaxineura* TILLYARD, 1937

Type species: *Camptotaxineura ephialtes* TILLYARD, 1937.

Camptotaxineura ephialtes TILLYARD, 1937

1937 *Camptotaxineura ephialtes* – Tillyard, 88–91, Fig. 3 (original description).

1992 *Camptotaxineura ephialtes* – Carpenter, 88 (in Odonata family undetermined, without explanation).

Material: Specimen holotype No. 15590, Yale University Collection (Tillyard, 1937). The apical portion of a wing.

Horizon and type locality: Lower Permian, Elmo, Kansas, USA.

Discussion: The original attribution of this taxon to the Odonatoptera: Protanisoptera proposed by Tillyard (1937) is weakly supported by one character, i.e. the presence of a weakly sclerotized pterostigma crossed by vein RA. *Camptotaxineura* has none of the other synapomorphies of the Protanisoptera, i.e. no forked RA; no oblique postsubnodal cross-vein; base of the alleged first basal branch of RP not aligned with subnodus; no undulation of distal part of RP1 below pterostigma.

Tillyard (1937) does not indicate anything about the concavity of the wing veins. Thus, it is very difficult to determine the exact nature of the various veins. Nevertheless, the vein RP has five posterior distal parallel branches, which is unlikely in Odonatoptera, which have only the four branches RP3/4, IR2, RP2 and IR1. Furthermore, this wing has two successive main veins, named MA and CuP by

Table 1
Tableau 1

Taxa/characters	1	2	3	4	5	6	7	8	9	10
O2. 'Tupus'	0	0	0	0	2	1	1	0	0	0
O3. <i>L. magnifica</i>	0	0	1	1	2	1	1	0	0	1
O4. <i>P. uralica</i>	0	0	1	0	0	1	1	0	0	2
O5. <i>T. guillaumei</i>	0	0	0	0	?	1	?	0	0	2
O6. <i>M. schucherti</i>	0	0	0	0	2	1	1	0	0	0
Taxa/characters	21	22	23	24	25	26	27	28	29	30
I1. <i>P. zherhikini</i>	2	2	1	0	0	1	0	2	1	1
I2. <i>P. dolloi</i> (3353/75)	1	2	2	1	0	1	0	2	2	2
I3. <i>P. camense</i>	2	2	?	?	?	?	?	?	?	?
I4. <i>P. stanleyi</i>	2	2	1	0	1	0	?	?	?	?
I5. <i>C. martynovi</i>	1	2	1	0	0	1	0	2	1	2
I6. <i>H. uralense</i>	1	1	1	0	0	1	0	2	1	1
I7. <i>G. brasiliense</i>	1	2	2	1	0	1	0	2	2	2
I8. <i>P. proxima</i>	?	?	2	1	?	?	?	2	2	2
I9. <i>D. anomalostigma</i>	1	2	1	0	1	1	0	2	1	1
I10. <i>D. cellulosa</i>	1	2	1	0	1	1	1	2	1	1
I11. <i>D. cellulosa</i> type	1	1	?	?	1	1	1	2	1	1
O1. 'Geropterid'	0	0	0	1	0	0	0	0	0	0
O2. 'Tupus'	0	0	0	0	0	0	0	0	0	0
O3. <i>L. magnifica</i>	2	2	0	0	0	0	0	0	0	0
O4. <i>P. uralica</i>	1	1	0	1	0	0	0	0	0	0
O5. <i>T. guillaumei</i>	2	2	0	1	0	0	0	0	?	0
O6. <i>M. schucherti</i>	0	0	0	0	1	0	0	0	0	0
Taxa/characters	31	32	33	34	35	36	37	38	39	40
I1. <i>P. zherhikini</i>	0	0	0	0	0	1	1	1	0	1
I2. <i>P. dolloi</i> (3353/75)	0	1	1	1	1	0	0	1	0	1
I3. <i>P. camense</i>	?	?	?	?	?	1	?	?	0	?
I4. <i>P. stanleyi</i>	?	?	?	0	?	1	0	?	0	?
I5. <i>C. martynovi</i>	1	0	1	0	0	1	0	1	?	2
I6. <i>H. uralense</i>	1	1	0	0	0	1	0	1	0	1
I7. <i>G. brasiliense</i>	0	1	?	1	1	0	0	1	0	1
I8. <i>P. proxima</i>	0	1	1	1	1	0	?	1	?	1
I9. <i>D. anomalostigma</i>	1	0	0	0	0	1	1	1	0	1
I10. <i>D. cellulosa</i>	1	0	0	0	0	1	1	1	0	1
I11. <i>D. cellulosa</i> type	1	1	0	?	?	1	?	1	?	1
O1. 'Geropterid'	0	0	0	0	0	1	0	0	1	0
O2. 'Tupus'	0	0	0	0	1	1	0	1	?	0
O3. <i>L. magnifica</i>	0	0	0	0	1	1	0	1	?	0
O4. <i>P. uralica</i>	0	0	0	0	0	1	0	?	?	0
O5. <i>T. guillaumei</i>	0	0	0	0	0	1	0	?	?	0
O6. <i>M. schucherti</i>	0	0	0	0	1	1	0	1	1	0

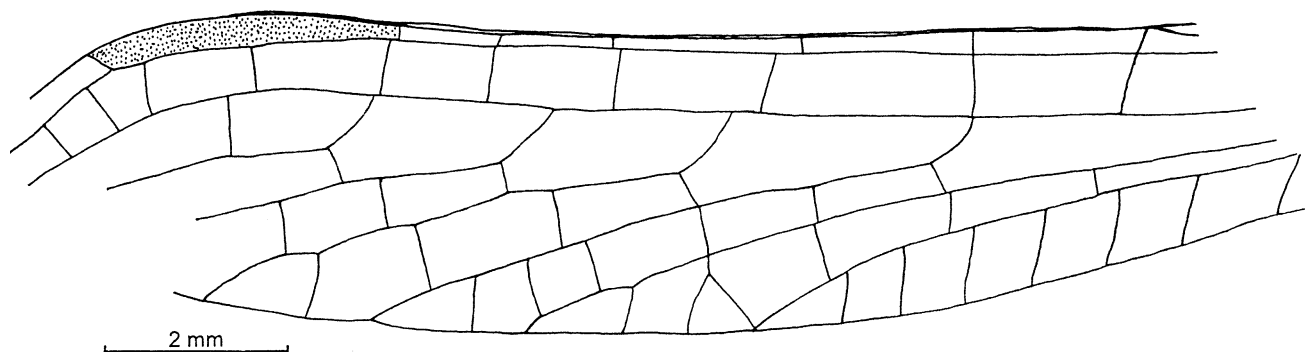


Fig. 2. *Kaltanoneura bartenevi* ROHDENDORF, 1961, holotype specimen PIN 600/485, counterprint (scale bar represents 2 mm).

Fig. 2. *Kaltanoneura bartenevi* ROHDENDORF, 1961, holotype PIN 600/485, contre-empainte (l'échelle représente 2 mm).

Tillyard (1937) clearly forked, which is also unlikely in Odonoptera. Thus, this fossil wing possibly does not correspond to Odonoptera. The Palaeodictyoptera: Permothemistidae have an apical pterostigma crossed by a longitudinal vein similar to that of *Camptotaxineura*. Furthermore, in Palaeodictyoptera, the genus *Dunbaria* TILLYARD, 1924 has a series of posterior simple parallel branches of RP and two more basal veins distinctly forked. The main differences between *Camptotaxineura* and *Dunbaria* are the absence of a sclerotized pterostigma and the vein ScP reaching wing apex or so. Nevertheless, the ScP of *Dunbaria* is very close to RA, thus such a vein could be present in *Camptotaxineura*, but not visible and thus not figured by Tillyard.

In conclusion, *Camptotaxineura* has to be excluded from the Protanisoptera and could belong to the Palaeodictyoptera. Examination of the holotype is necessary before any definite attribution of this enigmatic taxon can be made.

ODONATOPTERA (sensu Bechly, 1996).

PROTOZYGOPTERA (sensu Bechly, 1996).

KALTANONEURIDAE (Rohdendorf, 1961) (formerly in Protanisoptera).

Type genus: *Kaltanoneura* ROHDENDORF, 1961.

Diagnosis: Pterostigma very long with a proximal side perpendicular to RA and Costa and a distal side oblique, together with the little number of postnodal cross-veins; a broad area between RA and RP, relative to area between Costa and RA; few postnodals nearly aligned with corresponding postsubnodals; three cross-veins below the pterostigma.

Genus *Kaltanoneura* ROHDENDORF, 1961.

Type species: *Kaltanoneura bartenevi* ROHDENDORF, 1961.

Diagnosis: That of the family.

Kaltanoneura bartenevi ROHDENDORF, 1961, Figs. 1 and 2.

1958 *Kaltanoneura martynovi* – Rohdendorf, 856, Fig. 24 (nomen nudum, in Kennedyidae).

1961 *Kaltanoneura bartenevi* – Rohdendorf, 86, text-Fig. 35, pl. 2, Fig. 10 (original description).

1962 *Kaltanoneura bartenevi* – Rohdendorf, 75, text-Fig. 131 (in Protanisoptera).

1992 *Kaltanoneura bartenevi* – Carpenter, 88 (in Odonoptera family uncertain, without explanation).

Material: Specimen holotype PIN 600/485, print and counterprint of the distal two-thirds of a fore- (?) wing.

Horizon and type locality: Upper Permian, Kusnetsk Basin, Kaltan, Kemerovo region, Russia.

Redescription (Figs. 1 and 2): Rohdendorf (1958) only figured the wing of this taxon but described it in Rohdendorf (1961). There are some errors in the original description, thus it is necessary to redescribe it.

Apex and basal third of wing not preserved; length of the preserved part, 23 mm; width, 5 mm; nodus preserved, nodal cross-vein aligned with subnodus but weakly oblique; area between RA and RP is about three times wider than that between Costa and RA; no apical branch of RA; four postnodal cross-veins, not exactly aligned with the corresponding postsubnodal cross-veins; none of the postsubnodal veins oblique; pterostigma sclerotized, between Costa and RA, very long and narrow, 3.5 mm long and 0.5 mm wide, with its proximal side not oblique but its distal side distinctly oblique; no pterostigmal brace, but three cross-veins below pterostigma; MA and MP not zigzagged; area between MP and posterior wing margin 0.9 mm wide, with one row of cells between these veins; area between MA and MP distally widened near posterior wing margin; no supplementary vein IMA between MA and MP; MA, RP3/4, IR2, RP2 and IR1 more or less parallel; base of RP3/4: 1.7 mm distal of subnodus; base of IR2: 2.6 mm distal of base of RP3/4; base of RP2: 2 mm distal of base of IR2; base of IR1: 2 mm distal of base of RP2; no supplementary longitudinal veins between main branches of radial vein.

Discussion: This fossil has none of the main synapomorphies of the Protanisoptera, i.e. no oblique postsubnodal cross-vein; pterostigma not crossed by RA; no apical branch of RA; no IMA. Thus, we exclude it from this group. The presence of a very long pterostigma with a proximal side perpendicular to RA and Costa and a distal side oblique, together with the little number of postnodal cross-veins and suggest strong affinities with the Protozygoptera (as already

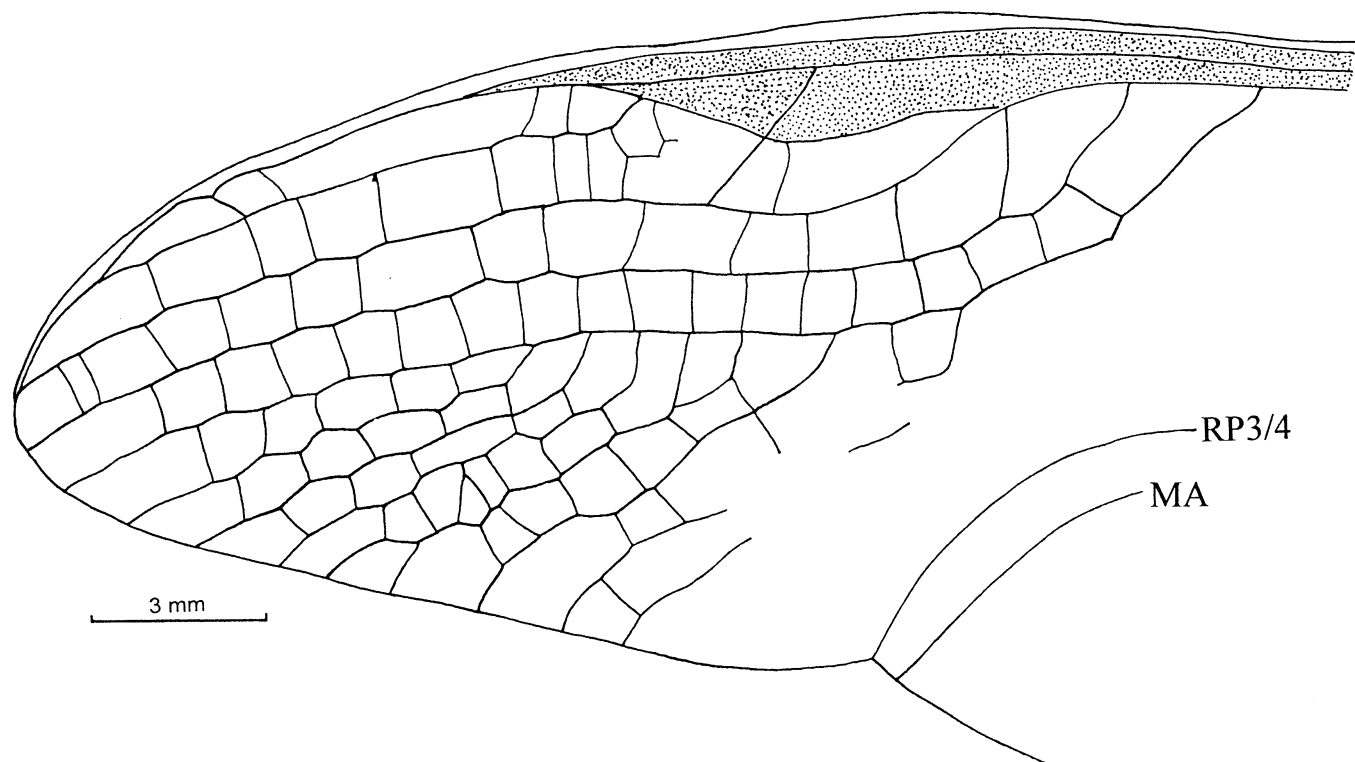


Fig. 3. *Permaeschna dolloi* MARTYNOV, 1931, holotype specimen PIN 2334/2-3, print (scale bar represents 3 mm).

Fig. 3. *Permaeschna dolloi* MARTYNOV, 1931, holotype PIN 2334/2-3, empreinte (l'échelle représente 3 mm).

proposed by Bechly (1998, in press)), and more precisely with the kennedyid genus *Progoneura* CARPENTER, 1931. *Kaltanoneura* shares with the latter the presence of a broad area between RA and RP, relative to the area between Costa and RA, and few postnodals nearly aligned with the corresponding postsubnodals. The main difference between the two genera is the presence of only one cross-vein below the pterostigma in *Progoneura*, instead of three in *Kaltanoneura*.

Nevertheless, the phylogenetic relationships of *Kaltanoneura* will be, perhaps, solved after a general reanalysis of the phylogeny of 'Protozygotera'.

2.2. Suborder Protanisoptera CARPENTER, 1931 (junior synonyms *Permanisoptera* MARTYNOV, 1931, in Carpenter (1992))

Included families: Permaeschnidae MARTYNOV, 1931, Callimokaltaniidae ZALESSKY, 1955 stat. rest., Pholidoptilidae ZALESSKY, 1931 stat. rest., Polytaxineuridae TILLYARD, 1935 stat. rest., Hemizygoteridae ZALESSKY, 1950 stat. rest., Ditaxineuridae TILLYARD, 1926.

Diagnosis: Bechly (1996) proposed a diagnosis of the Protanisoptera. We agree with it, except for the character 'distal free part of the CuP seems to be absent...' proposed by Bechly (1996) as an autapomorphy of the Protanisoptera, which has to be excluded, as already noted by Bechly (1998, in press), because in *P. dolloi* MARTYNOV, 1931 and *G.*

brasiliense RÖSLER et al., 1981, there is a long distal free part of CuP in the cubito-anal area.

PERMAESCHNIDAE Martynov, 1931 sensu nov.

Type genus: *Permaeschna* MARTYNOV, 1931.

Other genus: *Gondvanoptilon* RÖSLER et al., 1981.

Diagnosis: This family is characterized by the following synapomorphies, after the present phylogenetic analysis (see below): (1) IMA divided into two main branches, the posterior branch being parallel to MP, the anterior branch being parallel to MA, and with secondary branches beginning on the posterior branch; (2) RA with a long distal posterior branch; (3) two or more distinctly transverse cells between RP1 and IR2, near the base of IR2; (4) numerous secondary longitudinal veins between RP3/4 and IR2.

The 'wings large with many cells' of the Permaeschnidae is probably a more homoplastic character. The pterostigma basally and distally prolonged is also present in *Callimokaltania martynovi* ZALESSKY, 1955, that does not fall in the same clade, after the present phylogenetic analysis (see below). Also, the presence of two or more cross-veins between RP1 and the posterior margin of the pterostigma is a character shared by *Hemizygoteron uralense* ZALESSKY, 1955 and *Ditaxineura cellulosa* CARPENTER, 1933.

Junior synonyms: Carpenter (1992, 66–67) synonymized the Callimokaltaniidae ZALESSKY, 1955 (type genus: *Callimokaltania* ZALESSKY, 1955); the Pholidoptil-

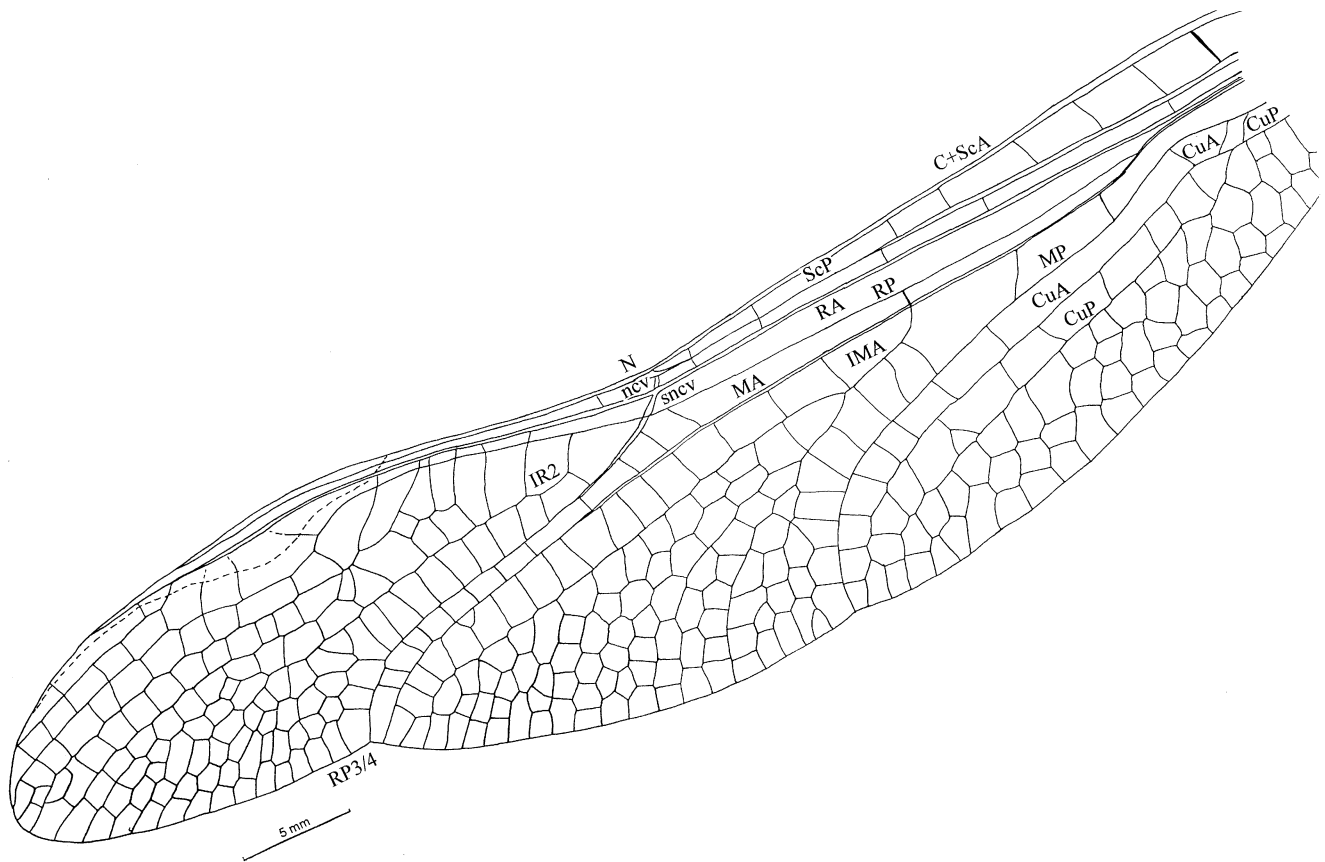


Fig. 4. *Permaeschna dolloi* MARTYNOV, 1931, specimen PIN 3353/75, print (scale bar represents 5 mm).

Fig. 4. *Permaeschna dolloi* MARTYNOV, 1931, spécimen PIN 3353/75, empreinte (l'échelle représente 5 mm).

idae ZALESSKY, 1931 (type genus: *Pholidoptilon* ZALESSKY, 1931); the Polytaxineuridae TILLYARD, 1935 (type genus: *Polytaxineura* TILLYARD, 1935), and the Hemizygopteridae ZALESSKY, 1950 (type genus: *Hemizygopteron* ZALESSKY, 1950), with the Permaeschnidae, all without explanation. Bechly (1996) already restored the Hemizygopteridae, as sister group of the Ditaxineuridae. After our phylogenetic analysis, all these taxa never fall with the clade (*Permaeschna* + *Gondvanoptilon*). Thus, the Callimokaltaniidae, Pholidoptilidae, Polytaxineuridae, and Hemizygopteridae cannot be considered as junior synonyms of the Permaeschnidae. We exclude the corresponding genera and species from this last family.

Genus: *Permaeschna* MARTYNOV, 1931

Type species: *Permaeschna dolloi* MARTYNOV, 1931.

Diagnosis: Characterized by: (1) absence of any cross-vein in the antesubnodal area; (2) absence of a well-defined distal portion of AA; (3) less antenodal cross-veins than for *Gondvanoptilon*. Characters (1) and (3) are related to absence of cross-veins, and may be due to the poor preservation of these areas in the fossil wings. Character (2) may be related to the fact that the known wings of *Permaeschna* are forewings and the unique specimen of *Gondvanoptilon* is probably a hindwing that has a broader cubito-anal area and a better developed distal free part of

AA. Only the future discovery of new material may help to solve the delicate problem of the possible identity between these two genera.

Permaeschna dolloi MARTYNOV, 1931 (= *Permaeschna proxima* MARTYNOV, 1931 new junior synonym), Figs. 3–5.

1931a *Permaeschna dolloi* – Martynov, 141, 143–144, Fig. 1–2 (original description).

1931a *Permaeschna proxima* – Martynov, 145–146, Fig. 3 (original description).

1931b *Permaeschna dolloi* – Martynov, 246 (phylogenetic position).

1931c *Permaeschna dolloi* – Martynov, 24–25, text-Fig. 10 (revision).

1931c *Permaeschna proxima* – Martynov, 24 (discussion).

1938 *Permaeschna dolloi* – Martynov, 44, Fig. 21 (phylogenetic position discussed).

1992 *Permaeschna dolloi* – Carpenter, 66–67, text-Fig. 42.2 (listed in Permaeschnidae).

Material: Holotype (*P. dolloi*) specimen PIN 2334/3 (print) and 2334/2 (counterprint), the apical two-thirds of a forewing. Other specimens: PIN 2334/4: holotype of *P. proxima*, the apical half of a wing; and specimen 3353/75: a nearly complete wing, well preserved.

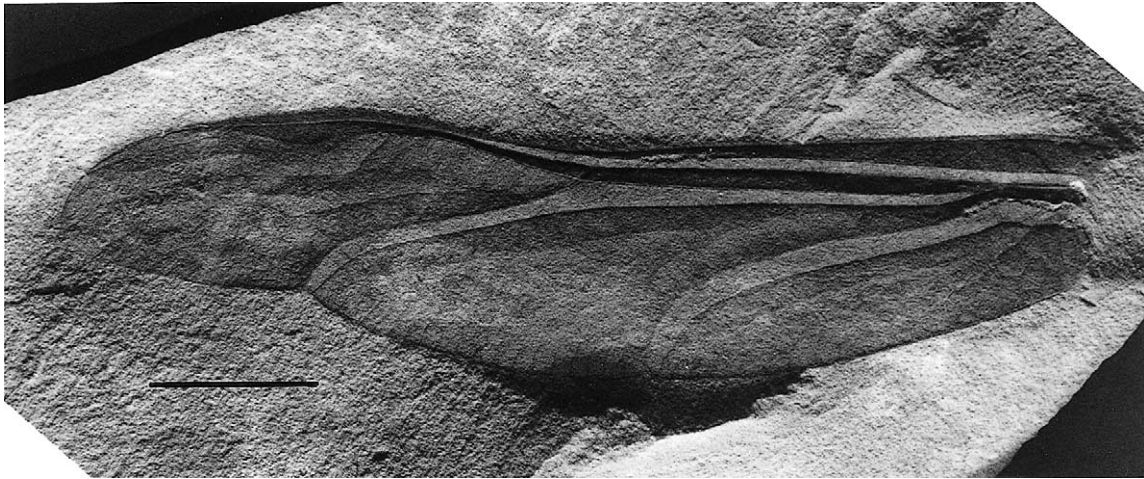


Fig. 5. Photograph of *Permaeschna dolloi* MARTYNOV, 1931, specimen PIN 3353/75, print (scale bar represents 10 mm).

Fig. 5. Photographie de *Permaeschna dolloi* MARTYNOV, 1931, spécimen PIN 3353/75, empreinte (l'échelle représente 10 mm).

Horizon and localities: Holotype PIN 2334/2-3 and specimen PIN 2334/4: Upper Kazanian, Permian, Iva-Gora, Arkhangelsk; specimen PIN 3353/75: Upper Kazanian, Upper Permian, Soyana, Russia.

Description of the material:

- Holotype of *P. dolloi* PIN 2334/2-3 (Fig. 3): poorly preserved. In its original description (Martynov, 1931),

some errors occurred in the interpretation of the wing venation:

- in median area, IMA very long, running parallel to MA and with numerous secondary branches nearly perpendicular to the main one and reaching posterior wing margin: the vein named MP by Martynov, parallel to MA is in fact the distal portion of IMA.

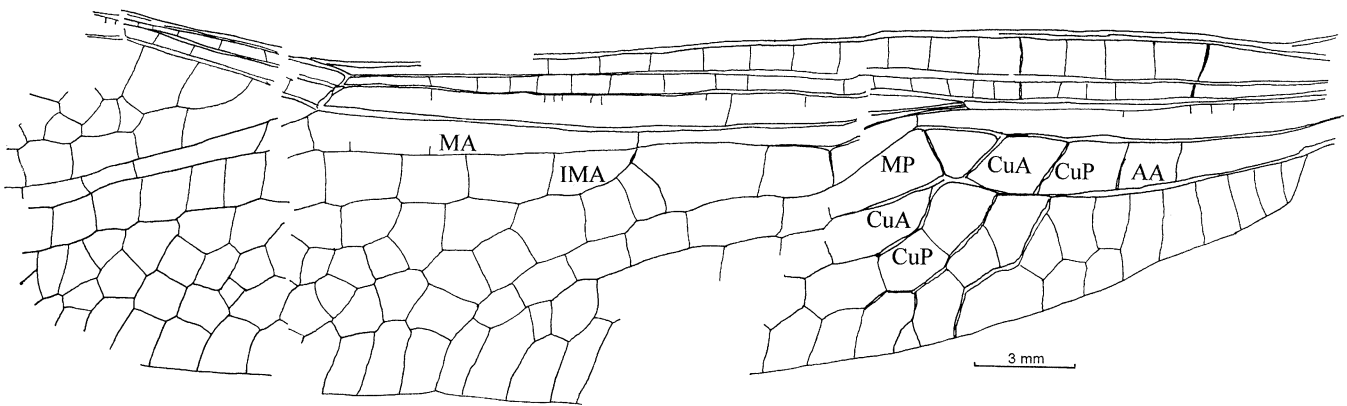


Fig. 6. *Polytaxineura stanleyi* TILLYARD, 1935, holotype specimen in 46395, print (scale bar represents 3 mm).

Fig. 6. *Polytaxineura stanleyi* TILLYARD, 1935, holotype in 46395, empreinte (l'échelle représente 3 mm).

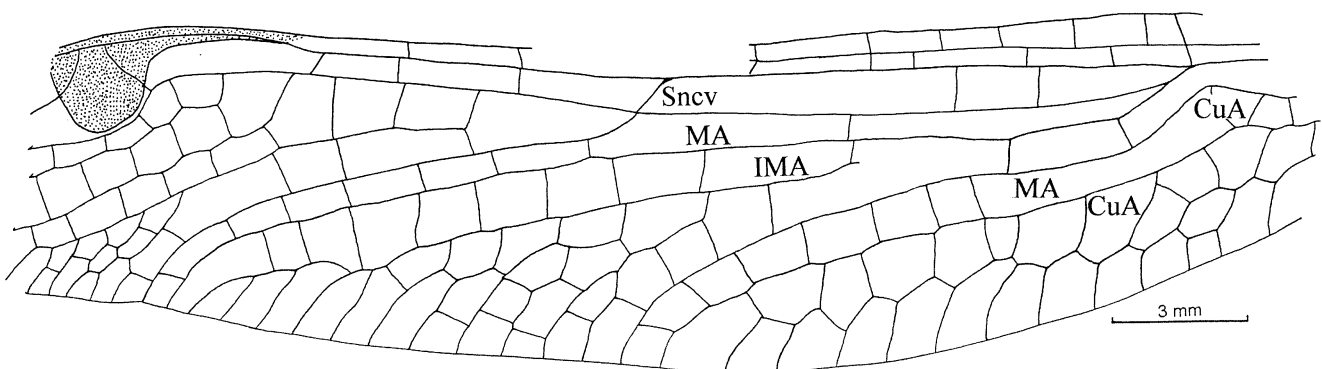


Fig. 7. *Callimokaltania martynovi* ZALESSKY, 1955, holotype specimen PIN 504/246 (scale bar represents 3 mm).

Fig. 7. *Callimokaltania martynovi* ZALESSKY, 1955, holotype PIN 504/246 (l'échelle représente 3 mm).

After Martynov (1931), there would be two rows of cells between IMA and MA but this is very dubious because this area is very poorly preserved. The exact organization of the area below IMA cannot be determined. The vein called CuA by Martynov is one of the zigzagged secondary branches of IMA. Also, CuP, A1 and A2 sensu Martynov are respectively, MP, CuA and CuP;

- on the apical part of the wing, RA forked in the distal part of pterostigma with a long posterior branch; at the end of this branch, two cross-veins between RA and C; posterior branch of RA, RP1, IR1 and RP2 parallel, with one row of cells between them; RP1 strongly bent below pterostigma; RP2 with more than five secondary branches until posterior wing margin; RP3/4 strong and parallel to distal part of MA, separated by one row of cells; posterior wing margin strongly notched at the end of RP3/4.
- Holotype of *P. proxima*, PIN 2334/4: only a wing apex, rather poorly preserved. The preserved characters are nearly identical to the two other specimens.
- Specimen 3353/75 (Figs. 4 and 5): a nearly complete wing, well preserved; probably a hindwing because of the rather broad cubito-anal area; extreme base missing, anyway it was obviously not petiolate; wing length, about 64 mm; greatest width, 14 mm at the level of end of CuP and 10 mm at the level of end of RP3/4; surface of the rock uniformly grey, so the wing was probably hyaline with no coloured pattern, excepted the darker pterostigma; Costa strongly serrated along its anterior margin; eight antenodal cross-veins of first rank perpendicular to Costa, first one being very strong but not homologous to Ax0 because it is not prolonged between ScP and RA; five antenodal cross-veins of second rank; second, seventh and height antenodals of the first rank corresponding to the first, fourth and fifth of second rank; only one postnodal and 15 postsubnodal cross-veins; just basal of point of fusion of ScP with C, ncv and sncv strong and directed towards apex; sncv well aligned with ncv and joining RP at bifurcation between RP1 and RP3/4; nodus at 29 mm from wing base; RA forked in distal part of pterostigma; pterostigma thin and very elongated, nearly reaching wing apex, crossed by the seventh, eighth, ninth and further postsubnodal cross-veins, distal of fork of RA, by two cross-veins between posterior fork of RA and anterior wing margin; RP1 strongly bent towards pterostigma; IR1 and RP2 parallel to RP1 and to distal part of RA; only one row of cells between RA and RP1, RP1 and IR1 and between IR1 and RP2; basal parts of IR1 and RP2 fused; distal part of IR2 not clearly defined; base of IR2 parallel to RP3/4 with only one row of cells between them; no cross-vein in antesubnodal area between RA and RP; one row of cells between MA and RP and distally RP3/4; opposite third antenodal cross-vein of second rank, presence of a

strong cross-vein between RP and MA aligned with IMA; IMA making a fork in a large and broad area with numerous cells between MA and MP, 82 cells in area between the two main forks of IMA; MP strongly curved towards arculus; MP, CuA and CuP long, straight and parallel, curved just before joining posterior wing margin; one row of cells between MP and CuA and between CuA and CuP; cubito-anal area long and containing 52 cells in preserved part of wing; three rows of cells between CuP and posterior wing margin.

Discussion:

- Comparison of *P. proxima* with *P. dolloi*. After Martynov (1931), *Permaeschna proxima* differs from *P. dolloi* as follows:
 - base of IR1 and RP2 (RS1 and RS2 sensu Martynov) separated in *P. dolloi* but fused into a common stem (RS2 + 3 sensu Martynov) in *P. proxima*. The examination of the holotype PIN 2334/4 of *P. proxima*, which is very poorly preserved, shows that the bases of these veins are nearly completely destroyed, so this ‘common pedicel’ seems to be an artefact;
 - RP2 (RS3 sensu Martynov) with several secondary branches until posterior wing margin in *P. dolloi*; RP2 and IR2 (RS3 and RS4 sensu Martynov) ‘straight and separated by two rows of cells’ in *P. proxima*. After the examination of the specimens PIN 2334/3 and PIN 2334/2 (print and counterprint of the same specimen), which are both poorly preserved, it appears that RP2 has several secondary branches until posterior wing margin as it occurs on *P. dolloi*;
 - on the drawing of *P. dolloi* proposed by Martynov, it seems that this taxon has two rows of cells between IMA and MA, unlike only one in *P. proxima*. This character is not clearly visible on the holotype specimen of *P. dolloi*. Furthermore, it is not sufficient for a specific separation, because nothing is known concerning the intraspecific variability within the Protanisoptera.

Because of the poor state of preservation of the type material of both species and of the lack of clear differences between the two species, we propose to consider *Permaeschna proxima* MARTYNOV, 1931 as a junior synonym of *Permaeschna dolloi* MARTYNOV, 1931. *P. proxima* is described in second by Martynov (1931).

- Comparison between *Permaeschna* and *Gondvanoptilon*. The main differences between *P. dolloi* and *G. brasiliense* are as follows: (1) there is no cross-veins in the antesubnodal area between RA and RP for *P. dolloi*, instead of one for *G. brasiliense*; (2) the distal portion of AA in cubito-anal area is well defined, appearing as a long longitudinal vein in *G. brasiliense* instead of being reduced in *P. dolloi*; (3) presence of 14 antenodal cross-veins of the first rank in *G. brasiliense*, after the figures of Martins Neto (1996), instead of seven for *P. dolloi*. The structures of the radial and ‘postdiscoidal’ areas of the type specimens of *P. dolloi* and *P. proxima*

are very poorly preserved but they are nearly identical in the type of *G. brasiliense* and specimen PIN 3353/75.

Genus: *Gondvanoptilon* RÖSLER et al., 1981 (in Permaeschnidae stat. rest.).

Type species: *Gondvanoptilon brasiliense* – Rösler et al. (1981).

Diagnosis: Characterized by the presence of a cross-vein in the antesubnodal area, the presence of a well-defined distal portion of AA and more antenodal cross-veins than for *Permaeschna*.

Phylogenetic position: Rösler et al. (1981) included this genus in the Protanisoptera: Permaeschnidae. More recently, Martins-Neto (1996) revised the type species and transferred it into the Meganisoptera: Erasipteridae CARPENTER, 1939. This fossil clearly has several of the wing venational autapomorphies of the Protanisoptera, as defined by Bechly (1996): ‘presence of an ‘abnormal’ pterostigma that is crossed by the RA’; ‘RA with an apical secondary branch’; ‘undulating course of the distal part of the RP1 beneath the pterostigma’; ‘midfork (origin of RP [= RP3/4]) shifted to a very distal position at ca. 60% of wing length’; ‘presence of a concave intermedian intercalary vein IMA that is arising on MA between MA and MP’. The characters listed by Martins-Neto to support his attribution to the Meganisoptera are either erroneous (pterostigma and nodus present) or symplesiomorphies (basal structures of the veins RA, RP, MA and MP). Therefore, we consider that *Gondvanoptilon* as a true Protanisoptera. After our phylogenetic analysis, it falls as the sister group of *Permaeschna*, within the Permaeschnidae. It shares no less than four unique synapomorphies with *Permaeschna*.

Gondvanoptilon brasiliense RÖSLER et al., 1981

1981 *Gondvanoptilon brasiliense* RÖSLER et al., 221–232, Fig. 2 (original description).

1996 *Gondvanoptilon brasiliensis* – Martins-Neto, 42–45, Figs. 1 and 2 (revision, in Erasipteridae).

Gondvanoptilon brasiliensis – Pinto and Adami-Rodrigues 1999, 120, 122 (list, in Erasipteridae).

Material: Holotype specimen GP/1T505, Departamento de Paleontologia e Estratigrafia do Instituto de Geociência da Universidade de São Paulo, a nearly complete wing, but with the colour of the pterostigma partly destroyed.

Horizon and type locality: Pedreira da Mineração, Amaral Machado, Formação Irati, Grupo Passa Dois, Bacia do Paraná, Upper Permian, Brazil.

PHOLIDOPTILIDAE Zalesky, 1931

Type genus: *Pholidoptilon* ZALESSKY, 1931.

Diagnosis: Wing large, with many cells; antenodal cross-veins of the first rank between C and ScP numerous, more numerous than for *Permaeschna dolloi*, comparable to *Gondvanoptilon brasiliense*. No other clear characters would be sufficient to characterize this taxon. In fact, the type specimen should have never been named.

Phylogenetic position: Because of its poor preservation, all the synapomorphies of the Permaeschnidae (see list above) cannot be observed on the type specimen of *P. camense*. This taxon only shares the ‘wings large with many cells’ with the Permaeschnidae, but this character is highly homoplastic and not sufficient to attribute *Pholidoptilon* to the Permaeschnidae. Therefore, we exclude *P. camense* from *Permaeschna* and restore the family Pholidoptilidae and genus *Pholidoptilon*. The exact relationship of this taxon within the Protanisoptera remains undetermined.

Genus: *Pholidoptilon* ZALESSKY, 1931

Type species: *Pholidoptilon camense* ZALESSKY, 1931.

Pholidoptilon camense ZALESSKY, 1931, stat. rest.

1931a *Pholidoptilon camense* – Zalesky, 36–41, text-Fig. 1, pl. 5 (original description).

1931b *Pholidoptilon camense* – Zalesky, 855–861, Figs. 1 and 2 (original description).

1933 *Pholidoptilon camense* – Zalesky, 501, Fig. 1 (morphology, phylogenetic position within Odonoptera).

1935 *Pholidoptilon camense* – Tillyard, 375 (in Polytaxineuridae).

1992 *Permaeschna camense* – Carpenter, 66, Fig. 42.2b (listed in *Permaeschna* sit. nov., without explanation).

Material: Location of the holotype unknown, a forewing.

Horizon and type locality: Permian, Fikhiiia Gory, Kama River Basin, Russia.

Remark: The ‘postdiscoidal’ area of this wing between MA and MP is partly destroyed. Also, all the apical third with the structures around the pterostigma are missing.

POLYTAXINEURIDAE Tillyard, 1935

Type genus: *Polytaxineura* TILLYARD, 1935.

Diagnosis: Bechly (1996) proposed to characterize the Polytaxineuridae after the ‘RP’ (= RP3 and 4) and MA parallel and straight, not distally curved towards the hind margin’. Unfortunately, this alleged character and the other characters listed below were based on the reconstruction of the wing of *Polytaxineura stanleyi* proposed by Tillyard (1935). The distal parts of these veins are not preserved in the holotype specimen, thus this character is highly putative, if not false, and cannot be used. Numerous antenodal cross-veins of the first (14) and second ranks (19); a supernumerary strong cubito-anal vein, basal of CuP; possible presence of cross-veins in the median area; in submedian area, two cross-veins between MP&Cu and AA, basal to the base of free part of CuP.

Phylogenetic position: Because of its poor preservation, all the synapomorphies of the Permaeschnidae (see list above) are absent or cannot be observed on the type specimen of *P. stanleyi*. Furthermore, the synapomorphy ‘IMA divided into two main branches, the posterior branch being parallel to MP, the anterior branch being parallel to MA, and with secondary branches beginning on the posterior branch’ is absent in *Polytaxineura*. This taxon only shares the ‘wings large with many cells’ with the Permae-

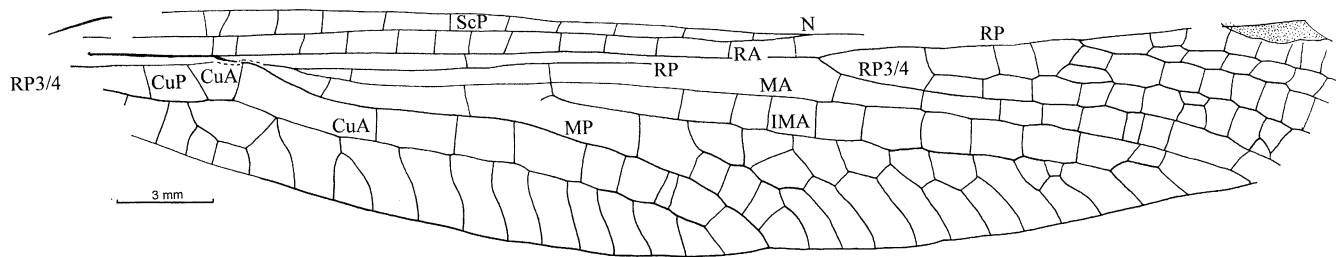


Fig. 8. *Proditaxineura pritykinae* (NOVOKSHONOV, 1992) comb. nov., specimen PIN 1700/3247, right hindwing, print (scale bar represents 3 mm).
 Fig. 8. *Proditaxineura pritykinae* (NOVOKSHONOV, 1992) comb. nov., spécimen PIN 1700/3247, aile postérieure droite, empreinte (l'échelle représente 3 mm).

schnidae, but this character is highly homoplastic and not sufficient to attribute *Polytaxineura* to the Permaeschnidae. Therefore, we exclude *P. stanleyi* from the Permaeschnidae and concur with the restoration of the family Polytaxineuridae by Bechly (1996). The exact relationship of this taxon within the Protanisoptera remains undetermined.

Genus: *Polytaxineura* TILLYARD, 1935.

Type species: *Polytaxineura stanleyi* TILLYARD, 1935.

Diagnosis: That of the family.

Polytaxineura stanleyi TILLYARD, 1935, Fig. 6.

1935 *Polytaxineura stanleyi* – Tillyard, 374–382, text-Figs. 1–3, pl. 12, Figs. 1–3 (original description).

1938 *Polytaxineura stanleyi* – Martynov, 48, Fig. 22 (phylogenetic position discussed).

1957 *Polytaxineura stanleyi* – Fraser, 27, Fig. 11.

1992 *Polytaxineura stanleyi* – Carpenter, 67, text-Fig. 42.5 (listed in Permaeschnidae without explanation).

Material: Holotype specimen No. In 46395, British Museum (Natural History), London, a nearly complete forewing and fragments of supposed hindwings.

Horizon and type locality: Upper Permian, Warner's Bay, New South Wales, Australia.

Redescription: The original description, although complete, contains some imprecision that must be discussed after a new examination of the specimen holotype No. In 46395 which was labelled S343 in Tillyard's text.

In the preserved portion of the forewing: 14 antenodal cross-veins of first rank; 19 antenodals of second rank; presence of a thin basal brace directed towards apex (perhaps homologous to Ax0); seven postnodal cross-veins between C and RA and three postsubnodal cross-veins

between RA and RP1; in median area, the presence of five cross-veins between arculus and MP&Cu basal to a stronger sixth cross-vein, which is perhaps a rudimentary MAb, so the basal cell which would be a 'discoidal cell' is not open basally; in submedian area, two cross-veins between MP&Cu and AA, basal to the base of free part of CuP; IMA long, weakly zigzagged, parallel to MP with only one rank of cells between IMA and MP; 13 cells between IMA and MP along posterior wing margin; posterior margin with a slight notch at the end of MP; one cross-vein between RP and MA exactly aligned with IMA; MP strongly bent towards arculus just distal to 'prequadrangular' cell sensu Tillyard (1935); rather large cubito-anal area with three strong veins basal to CuA, the concavity of these veins is not visible on the specimen, so CuA and AA cannot be clearly identified; however, there is a supernumerary strong cubito-anal vein.

All the apical structures, reconstructed by Tillyard (1935) are unknown, especially, the pterostigma, distal part of postnodal area, distal end of RA, RP1, IR1, and RP2.

DITAXINEURIDA Bechly (taxon nov.)

Included families: Callimokaltaniidae ZALESSKY, 1955, Hemizygopteridae ZALESSKY, 1955 and Ditaxineuridae TILLYARD, 1926.

Wing venational autapomorphies: The present hypothesis of closest relationships between the Callimokaltaniidae, Hemizygopteridae and Ditaxineuridae is supported by the analysis of Bechly (1998) who created the clade Ditaxineurida for [Callimokaltaniidae + Ditaxineuroidea (= Hemizygopteridae + Ditaxineuridae, sensu Bechly (1996))]. The clade Ditaxineurida is supported by the following synapo-

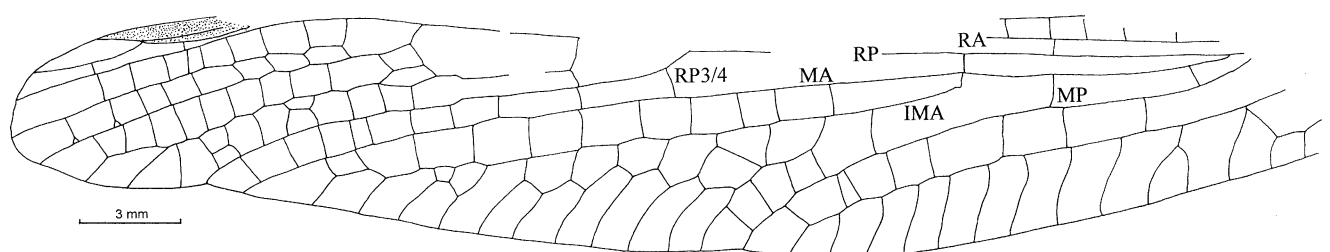


Fig. 9. *Proditaxineura pritykinae* (NOVOKSHONOV, 1992) comb. nov., specimen PIN 1700/3247, right hindwing, counterprint (scale bar represents 3 mm).
 Fig. 9. *Proditaxineura pritykinae* (NOVOKSHONOV, 1992) comb. nov., spécimen PIN 1700/3247, aile postérieure droite, contre-empreinte (l'échelle représente 3 mm).

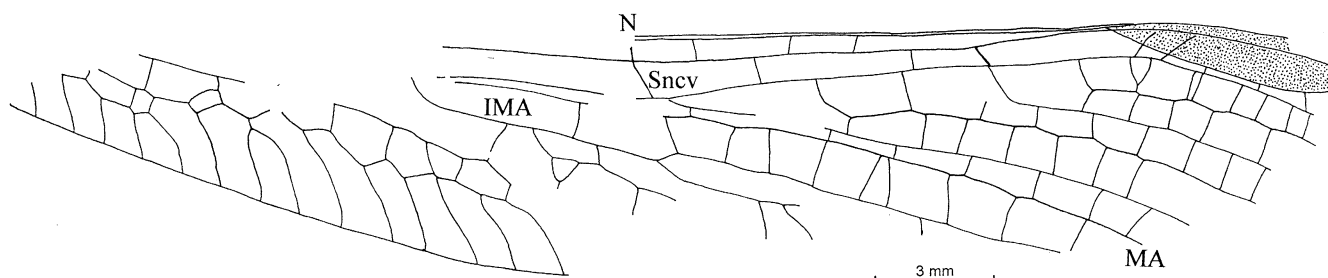


Fig. 10. *Proditaxineura pritykinae*, specimen PIN 1700/3247, right forewing, print (scale bar represents 3 mm).

Fig. 10. *Proditaxineura pritykinae*, spécimen PIN 1700/3247, aile antérieure droite, empreinte (l'échelle représente 3 mm).

morphy: 'free part of CuP between MP&Cu and AA nearly perpendicular to MP&Cu and AA'.

The 'presence of only few cross-veins in the antesubnodal area between RA and RP' is also a synapomorphy shared by these taxa. The 'presence of only a short distal posterior branch of RA' could also be a synapomorphy of this clade but the polarization of this character remains difficult because it is unknown in the possible outgroups, as the 'presence of a distal posterior branch of RA' is a synapomorphy of the Protanisoptera.

CALLIMOKALTANIIDAE Zalesky, 1955 (stat. rest.)

Type genus: *Callimokaltania* ZALESSKY, 1955.

Diagnosis: Pterostigma with its central part rounded and very broad and basally prolonged; pterostigma crossed by two veins between RA and RP1, one directed towards the wing base and the other towards the apex; wing of medium size; antenodal cross-veins numerous (seven being visible); two cross-veins between RA and RP basal of the nodus; MP with a strong curve opposite the arculus; a very large triangular cell between RP1 and RP3/4 just distal of the base of RP3/4.

Phylogenetic position: After our phylogenetic analysis, *Callimokaltania* falls in the clade {*Callimokaltania martynovi*, *Hemizygopteron uralense*, *Proditaxineura pritykinae*, *Ditaxineura anomalostigma*, *Ditaxineura cellulosa*}, as sister group of [*Hemizygopteron uralense*, (*Proditaxineura pritykinae* gen. nov., (*Ditaxineura anomalostigma*, *Ditaxineura cellulosa*)))] in nearly all the minimal cladograms. Nevertheless, for some (few) choices of outgroups, there is an unresolved polytomy between *Callimokaltania*, *Hemizygopteron*, *Proditaxineura* gen. nov. and the clade of the *Ditaxineura* spp. Thus, an uncertainty remains concerning the position of *Callimokaltania* within this group. We restore the family Callimokaltaniidae and include it in the Ditaxineurida sensu novo.

Genus: *Callimokaltania* ZALESSKY, 1955

Type species: *Callimokaltania martynovi* ZALESSKY, 1955.

Diagnosis: That of the family.

Callimokaltania martynovi ZALESSKY, 1955, Fig. 7.

1955 *Callimokaltania martynovi* – Zalesky, 630–631, Fig. 1 (original description).

1956 *Callimokaltania martynovi* – Rohdendorf, Fig. 22.

1961 *Callimokaltania martynovi* – Rohdendorf, 87–88, text-Fig. 36, pl. 2, Fig. 11 (redescription).

1992 *Callimokaltania martynovi* – Carpenter, 66–67, text-Fig. 42.3 (list, in Permaeschnidae without explanation).

Material: Holotype specimen PIN 504/246 (print) and PIN 1197/17 (counterprint), nearly complete wing, only the base is missing. Rohdendorf (1961) labelled the specimen PIN 504/246 under the number 504/250 and erroneously considered PIN 1197/17 as a different specimen. He also listed two other specimens PIN 1197/18 and PIN 1197/21.

Horizon and type locality: Lower Permian, Kuznetsk Formation, Mitino Member, Kaltan, Kemerovo region, Russia.

Remark: There are very few and small errors in the original description of Zalesky (1955) (see Fig. 7).

DITAXINEUROIDAE Tillyard, 1926

Included families: Hemizygopteridae ZALESSKY, 1955, and Ditaxineuridae TILLYARD, 1926.

Remark: The superfamily Ditaxineuroidea (= Hemizygopteridae + Ditaxineuridae, sensu Bechly (1996)) is present in nearly all our phylogenetic analyses, but with few choices of outgroup combinations, *Hemizygopteron* is no longer the sister group of the Ditaxineuridae and falls in an unresolved polytomy within the Ditaxineurida (see Table 2). Thus, an uncertainty remains concerning the position of *Hemizygopteron* within the Ditaxineurida and the monophyly of the Ditaxineuroidea.

DITAXINEURIDAE Tillyard, 1926.

Type genus: *Ditaxineura* TILLYARD, 1926.

Other genera: *Proditaxineura* gen. nov.

Diagnosis: Tillyard (1926) characterized this family by the presence of 'only two cross-veins between consecutive branches of the main veins in the distal portion of the wing'. This character is far from being sufficient to define correctly a family of Odonatoptera, because it is simply due to the relatively few number of cells in the wing. We propose to characterize this family by the following synapomorphy: 'presence of a large cell in cubito-anal area between CuP and CuA, at the base of distal free part of CuP'. These taxa also have a relatively reduced cubito-anal area and narrow wings, with few cells. They also have a relatively narrow area between MP and IMA.

Table 2

Organisation of the 'ingroup' in the various strict consensus trees depending of the choice of the outgroup(s), I3 being excluded. N: number of equally minimal cladograms; L: length of the minimal cladograms; CI: consistency index; CI–: consistency index, excluding uninformative characters; RI: retention index

Tableau 2

Organisation des groupes internes dans les différents arbres consensus stricts dépendant du choix du/des groupe(s) externe(s), I3 étant exclu. N: nombres de cladogrammes minimaux; L: longueur des cladogrammes minimaux; CI: index de consistance; CI–: index de consistance excluant les caractères non informatifs; RI: index de rétention

Outgroup(s)	clades of the 'ingroup'	N	L	CI	CI–	RI
All outgroups	T1 [I4((I7,I2)(I5(I6(I1(I9(I10,I11)))))))]	1	96	0.594	0.577	0.719
O1	T1 [I4((I7,I2)(I5(I6(I1(I9(I10,I11)))))))]	1	79	0.680	0.653	0.696
O3	T1 [I4((I7,I2)(I5(I6(I1(I9(I10,I11)))))))]	1	81	0.691	0.653	0.675
O4	T2 [(I7,I2)(I4(I5(I6(I1(I9(I10,I11)))))))]	1	78	0.654	0.623	0.654
O5	T2 [(I7,I2)(I4(I5(I6(I1(I9(I10,I11)))))))]	1	76	0.658	0.620	0.667
O6	T2 [(I7,I2)(I4(I5(I6(I1(I9(I10,I11)))))))]	1	81	0.679	0.649	0.687
O2	T3 [(I7,I2)(I4(I5(I1&I6(I9(I10,I11)))))))]	2	80	0.675	0.649	0.679
(O1,O2)	T5 [I4&(I7,I2)&(I5(I1&I6&(I9(I10,I11))))]	3	84	0.655	0.643	0.434
(O1,O3)	T1 [I4((I7,I2)(I5(I6(I1(I9(I10,I11)))))))]	1	82	0.671	0.659	0.675
(O1,O4)	T3 [(I7,I2)(I4(I5(I1&I6(I9(I10,I11)))))))]	2	85	0.659	0.635	0.642
(O1,O5)	T4 [I4&(I7,I2)&(I1&I5&I6&(I9(I10,I11))))]	6	83	0.675	0.654	0.654
(O1,O6)	T2 [(I7,I2)(I4(I5(I6(I1(I9(I10,I11)))))))]	1	85	0.647	0.635	0.659
(O2,O3)	T4 [I4&(I7,I2)&(I1&I5&I6&(I9(I10,I11))))]	12	79	0.671	0.671	0.468
(O2,O4)	T3 [(I7,I2)(I4(I5(I1&I6(I9(I10,I11)))))))]	2	85	0.635	0.624	0.631
(O2,O5)	T4 [I4&(I7,I2)&(I1&I5&I6&(I9(I10,I11))))]	12	85	0.647	0.631	0.674
(O2,O6)	T2 [(I7,I2)(I4(I5(I6(I1(I9(I10,I11)))))))]	1	80	0.675	0.667	0.705
(O3,O4)	T2 [(I7,I2)(I4(I5(I6(I1(I9(I10,I11)))))))]	1	81	0.630	0.617	0.639
(O3,O5)	T1 [I4((I7,I2)(I5(I6(I1(I9(I10,I11)))))))]	1	79	0.646	0.636	0.654
(O3,O6)	T2 [(I7,I2)(I4(I5(I6(I1(I9(I10,I11)))))))]	1	80	0.675	0.667	0.701
(O4,O5)	T4 [I4&(I7,I2)&(I1&I5&I6&(I9(I10,I11))))]	3	80	0.637	0.625	0.633
(O4,O6)	T2 [(I7,I2)(I4(I5(I6(I1(I9(I10,I11)))))))]	1	85	0.635	0.624	0.640
(O5,O6)	T2 [(I7,I2)(I4(I5(I6(I1(I9(I10,I11)))))))]	1	83	0.651	0.642	0.651
(O1,O2,O3)	T1 [I4((I7,I2)(I5(I6(I1(I9(I10,I11)))))))]	1	85	0.655	0.643	0.713
(O1,O2,O4)	T3 [(I7,I2)(I4(I5(I1&I6(I9(I10,I11)))))))]	2	89	0.629	0.611	0.673
(O1,O2,O5)	T4 [I4&(I7,I2)&(I1&I5&I6&(I9(I10,I11))))]	6	87	0.644	0.628	0.677
(O1,O2,O6)	T2 [(I7,I2)(I4(I5(I6(I1(I9(I10,I11)))))))]	1	85	0.647	0.647	0.714
(O1,O3,O4)	T5 [I4&(I7,I2)&(I5(I1&I6&(I9(I10,I11))))]	3	88	0.636	0.618	0.670
(O1,O3,O5)	T1 [I4((I7,I2)(I5(I6(I1(I9(I10,I11)))))))]	1	84	0.667	0.651	0.702
(O1,O3,O6)	T6 [I4&(I7,I2)&(I5(I6(I1(I9(I10,I11)))))]	2	87	0.632	0.632	0.689
(O1,O4,O5)	T3 [(I7,I2)(I4(I5(I1&I6(I9(I10,I11)))))))]	2	87	0.655	0.628	0.674
(O1,O4,O6)	T2 [(I7,I2)(I4(I5(I6(I1(I9(I10,I11)))))))]	1	90	0.622	0.604	0.670
(O1,O5,O6)	T2 [(I7,I2)(I4(I5(I6(I1(I9(I10,I11)))))))]	1	88	0.636	0.621	0.673
(O2,O3,O4)	T3 [(I7,I2)(I4(I5(I1&I6(I9(I10,I11)))))))]	2	86	0.628	0.628	0.677
(O2,O3,O5)	T4 [I4&(I7,I2)&(I1&I5&I6&(I9(I10,I11))))]	12	83	0.651	0.646	0.698
(O2,O3,O6)	T2 [(I7,I2)(I4(I5(I6(I1(I9(I10,I11)))))))]	1	83	0.663	0.651	0.750
(O2,O4,O5)	T3 [(I7,I2)(I4(I5(I1&I6(I9(I10,I11)))))))]	2	87	0.632	0.616	0.660
(O2,O4,O6)	T2 [(I7,I2)(I4(I5(I6(I1(I9(I10,I11)))))))]	1	87	0.632	0.616	0.686
(O2,O5,O6)	T2 [(I7,I2)(I4(I5(I6(I1(I9(I10,I11)))))))]	1	85	0.647	0.634	0.691
(O3,O4,O5)	T6 [I4&(I7,I2)&(I5(I6(I1(I9(I10,I11)))))]	2	86	0.616	0.593	0.683
(O3,O4,O6)	T2 [(I7,I2)(I4(I5(I6(I1(I9(I10,I11)))))))]	1	87	0.632	0.616	0.680
(O3,O5,O6)	T2 [(I7,I2)(I4(I5(I6(I1(I9(I10,I11)))))))]	1	84	0.655	0.642	0.701
(O4,O5,O6)	T2 [(I7,I2)(I4(I5(I6(I1(I9(I10,I11)))))))]	1	87	0.632	0.616	0.667

Phylogenetic position: In nearly all the present phylogenetic analyses, Ditaxineuridae falls the sister group of the Hemizygopteridae ZALESSKY, 1955. But, in some analyses (see below), there is a polytomy of the clade {*Calimokaltania martynovi*, *Hemizygopterum uralense*, *Proditaxineura pritykinae*, (*Ditaxineura anomalostigma*, *Ditaxineura cellulosa*)}. Nevertheless, as *Ditaxineura* and *Proditaxineura* share a strong potential synapomorphy (see above), we choose to include them in the same family Ditaxineuridae.

Genus: *Ditaxineura* TILLYARD, 1926

Type species: *Ditaxineura anomalostigma* TILLYARD, 1926.

Emended diagnosis: Tillyard (1926) characterized this genus by the presence of an 'abnormal' pterostigma, crossed by RA. Thus, we propose to characterize this genus as follows: 'no strong notch of the posterior wing margin at the distal end of MP and at the distal end of MA and RP3/4' (reversions); 'less than five antenodal cross-veins of the first row, between C and ScP' (strict synapomorphy).

Phylogenetic position: Sister group of the genus *Proditaxineura* gen. nov.

Ditaxineura anomalostigma TILLYARD, 1926

1926 *Ditaxineura anomalostigma* – Tillyard, 69–73, Fig. 8 (original description).

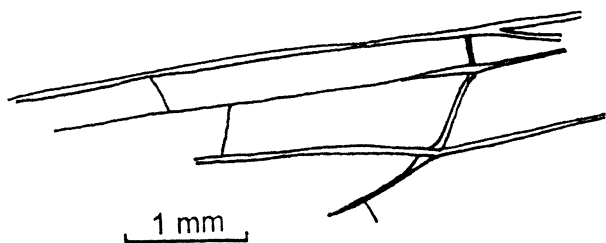


Fig. 11. *Proditaxineura pritykinae*, specimen PIN 1700/3247, nodal area of right forewing, counterprint (scale bar represents 1 mm).

Fig. 11. *Proditaxineura pritykinae*, spécimen PIN 1700/3247, aire nodale de l'aile antérieure droite, contre-empreinte (l'échelle représente 1 mm).

1931 *Ditaxineura anomalostigma* – Carpenter, 123–129, Figs. 1.1 and 4.1 (revision).

1938 *Ditaxineura anomalostigma* – Martynov, 43, Fig. 19 (phylogenetic position discussed).

1939 *Ditaxineura anomalostigma* – Carpenter, 44–45, Fig. 10 (revision).

1957 *Ditaxineura anomalostigma* – Fraser, 27, Fig. 11.

1992 *Ditaxineura anomalostigma* – Carpenter, 66, text-Fig. 42.1.

Material: Holotype specimen No. 5054a, b (the apex of a wing), Yale University (Peabody Museum) and Cawthron Institute (after Tillyard, 1926; Carpenter, 1931). Carpenter (1931) attributed two other fossils to this species, i.e. No. 3046 (a complete forewing), No. 3045 (a wing base), No. 3044 (a costo-apical part of a wing), Museum of Comparative Zoology, USA.

Horizon and type locality: Lower Permian, Wellington Shales, Elmo, Kansas, USA.

Diagnosis: See below the diagnosis of *D. cellulosa*.

Remark: The holotype specimen is very fragmentary. It has no character that could be used for a diagnosis of the species. It is nearly impossible to be accurate of its exact relationships with the other specimens that were attributed to this species by Carpenter (1931).

Furthermore, Carpenter (1939) also described and figured a hindwing (specimen No. 3972ab, Museum of Comparative Zoology, USA) he attributed to *D. anomalostigma*.

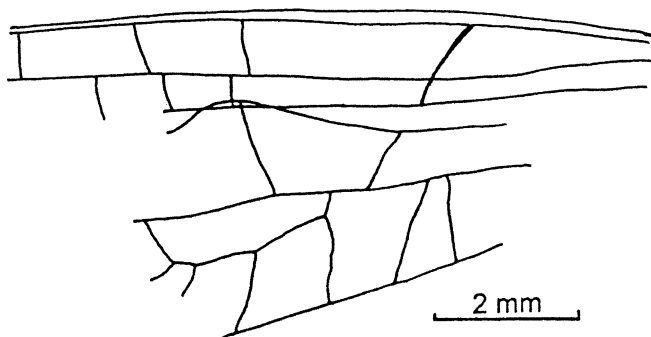


Fig. 12. *Proditaxineura pritykinae*, specimen PIN 1700/3247, base of left forewing, print (scale bar represents 2 mm).

Fig. 12. *Proditaxineura pritykinae*, spécimen PIN 1700/3247, base de l'aile antérieure gauche, empreinte (l'échelle représente 2 mm).

This last specimen differs from the most complete specimen described by Carpenter (1931) in the following points: 'postdiscoidal' area between MP and MA very narrow opposite the nodus in the specimen No. 3972ab, instead of being very broad in specimen No. 3046. The structure of the 'postdiscoidal' area of specimen No. 3972ab is very strange, as figured by Carpenter (1939), because there is no trace (and place!) for a vein IMA. It is possible that there is a brake in this wing in the 'postdiscoidal' area or an error in Carpenter's interpretation. The broad cubito-anal area of specimen No. 3972ab is probably a hindwing character.

A revision of all the specimens described by Carpenter (1931, 1939) is necessary in order to be accurate that they belong to the same species.

Ditaxineura cellulosa CARPENTER, 1933

1933 *Ditaxineura cellulosa* – Carpenter, 419–423, Fig. 4 (original description).

1962 *Ditaxineura cellulosa* (?) – Tasch and Zimmerman, 1332–1333, Fig. 22 (description of a new specimen).

Material: Specimen No. 3222ab, Museum of Comparative Zoology, Harvard, USA, the apical half of a wing. Other specimen: No. 1025, Tasch Collection, University of Wichita, USA, a complete wing.

Horizon and locality: Lower Permian, Elmo, Kansas, USA.

Diagnosis: This species differs from *D. anomalostigma* in the presence of five rows of cells between RP1 and the posterior wing margin in the radial area, instead of three, and by the presence of five cells in the area between MA and IMA, instead of three.

Genus: *Proditaxineura* gen. nov.

Type species: *Proditaxineura pritykinae* NOVOKSHONOV, 1992 comb. nov.

Etymology: After its affinities with the genus *Ditaxineura*.

Diagnosis: Characterized as follows: RP1 with only a slight bent below the pterostigma; cubito-anal area narrow, with one or two rows of cells between CuA and the posterior wing margin; IMA and MA long parallel, with one row of cells between them; all branches of RP parallel, with one row of cells between them; antenodal cross-veins numerous.

Note: Novokshonov (1992, 1998) included this species in the genus *Ditaxineurella* MARTYNOV, 1940. Its type species *D. stigmatis* MARTYNOV, 1940 is based on a very incomplete specimen (see below). We exclude *P. pritykinae* from *Ditaxineurella* because it strongly differs from *D. stigmatis* in its narrow wings, the presence of more than five cells in the area between MA and RP3/4; a basally prolonged pterostigma; nodus and pterostigma not approximate.

Proditaxineura pritykinae (NOVOKSHONOV, 1992) comb. nov. Figs. 8–14.

Material: We could not find the original description of Novokshonov (1992) but the same author gave a good figure of this species in 1998. We could examine two specimens we attribute to this species, i.e. specimen PIN

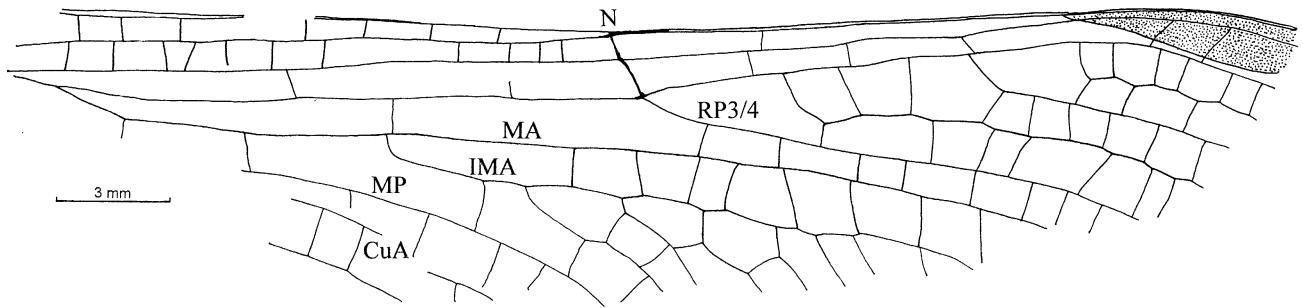


Fig. 13. *Proditaxineura pritykinae* (NOVOKSHONOV, 1992) comb. nov., specimen PIN 1700/461, left hindwing, counterprint (scale bar represents 10 mm).
 Fig. 13. *Proditaxineura pritykinae* (NOVOKSHONOV, 1992) comb. nov., spécimen PIN 1700/461, aile postérieure gauche, contre-empainte (l'échelle représente 10 mm).

1700/3247, print and counterprint and specimen PIN 1700/461, print and counterprint.

Horizon and type locality: Lower Permian, Chekarda, Russia.

Descriptions:

– Specimen PIN 1700/3247 (Figs. 8–12): print and counterprint of the thorax with four legs, the two forewings and the right hindwing in connection, together with three basal abdominal segments. The wings are dark brown but they are of the same colour of the rock, thus they were probably

hyaline on the living animal. The forewings are partly destroyed but the hindwing is nearly complete.

Forewing about 40 mm long and 6 mm wide; a strong and oblique basal brace (maybe homologous to Ax0 sensu Chao (1951)), 2.5 mm from wing base; antenodal cross-veins of the first rank between C and ScP not aligned with those of the second rank, between ScP and RA, but rather numerous, probably about 10; no primary antenodal cross-vein Ax1 nor Ax2 stronger than the secondaries; distance between wing base and nodus, about 18 mm; base of CuP

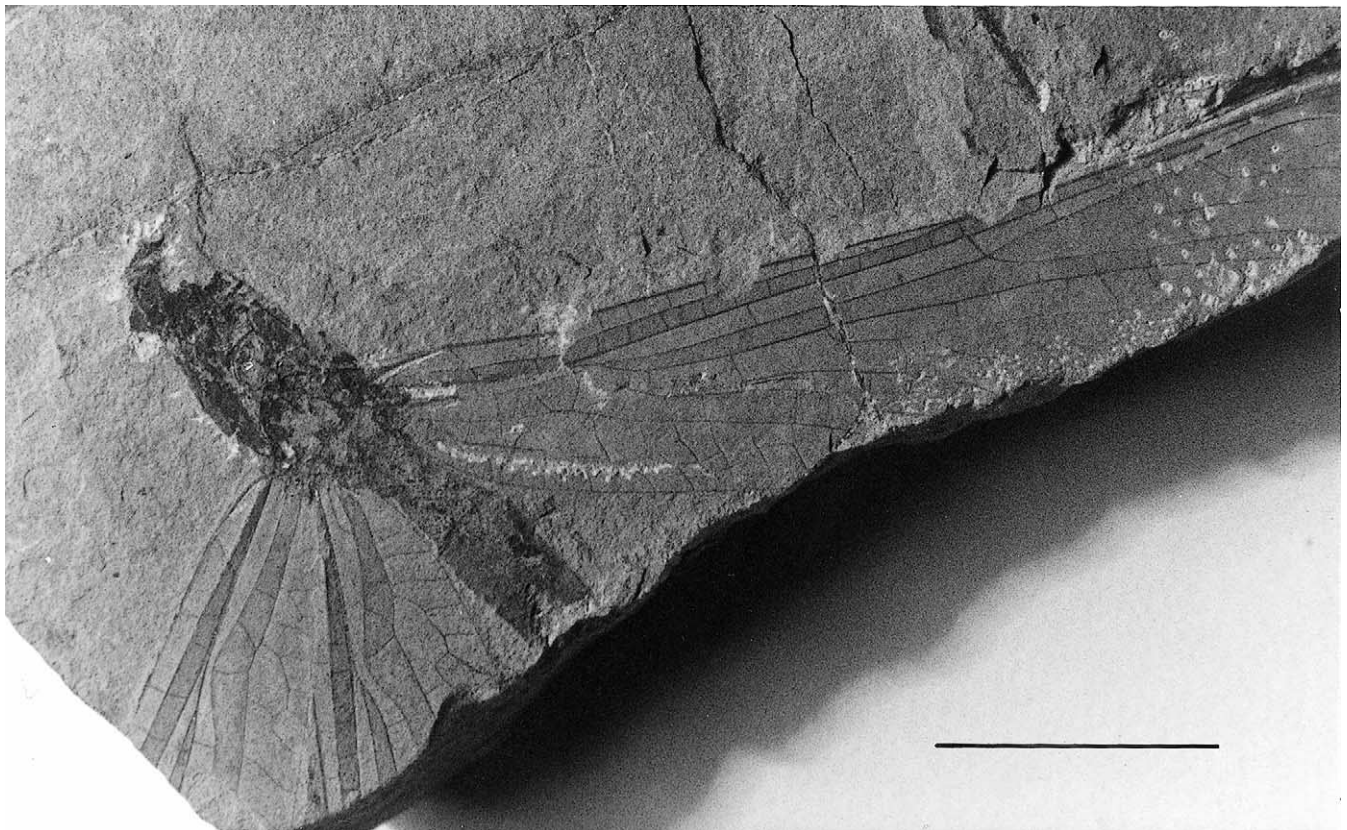


Fig. 14. Photograph of *Proditaxineura pritykinae*, specimen PIN 1700/461, print (scale bar represents 10 mm).
 Fig. 14. Photographie de *Proditaxineura pritykinae*, spécimen PIN 1700/461, empreinte (l'échelle représente 10 mm).

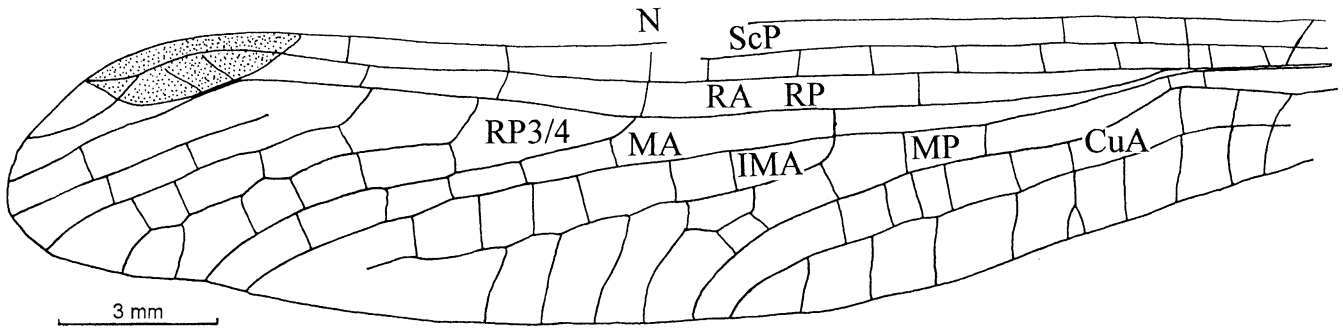


Fig. 15. *Hemizygopteron* sp. cf. *uralense* ZALESSKY, 1955, specimen PIN 1700/470, print (scale bar represents 3 mm).

Fig. 15. *Hemizygopteron* sp. cf. *uralense* ZALESSKY, 1955, spécimen PIN 1700/470, empreinte (l'échelle représente 3 mm).

not preserved; CuA separating from MP 3.5 mm from wing base, as a strong cross-vein between MP and AA&CuP; a strong cross-vein between MP and AA&CuP&CuA directed towards wing base, 1.5 mm distally; area between AA&CuP&CuA and posterior wing margin narrow, 1.5 mm wide, with one row of cells; presence of three supplementary cells below AA&CuP&CuA opposite the cross-vein between MP and AA&CuP&CuA, distal free part of CuP zigzagged and being the posterior margin of these cells; distal free part of AA being probably reduced to a simple short cross-vein basal of these cells; distal part of CuA long, zigzagged, parallel to MP, with one row of cells between them; the presence of a well-defined vein IMA in the area between MP and MA, beginning as a secondary branch of MA; two secondary longitudinal branches of IMA between MP and IMA; one row of cells between MA and IMA; nodal

cross-vein ncv slightly in a distal position to the point of fusion between ScP and C, well aligned with subnodal cross-vein sncv; ncv nearly perpendicular to C and RA; sncv obliquely directed towards wing apex; base of RP3/4 just distal of subnodal cross-vein; RP3/4 nearly straight; base of IR2: 4 mm distal of subnodus; IR2 weakly zigzagged; base of RP2: 9 mm distal of subnodus; distal part of RP2 nearly straight; base of IR1: 11 mm distal of subnodus; IR1 weakly zigzagged; only one row of cells between MA and RP3/4, RP3/4 and IR2, IR2 and RP2, RP2 and IR1, IR1 and RP1; RP1 not strongly curved below pterostigma; three postnodal cross-veins between C and RA, not aligned with the three postsubnodal cross-veins between RA and RP1; the most distal postsubnodal cross-vein is strongly oblique, directed towards wing apex, about midway between nodus and apex, aligned with RP2; pterostigma sclerotized, darker

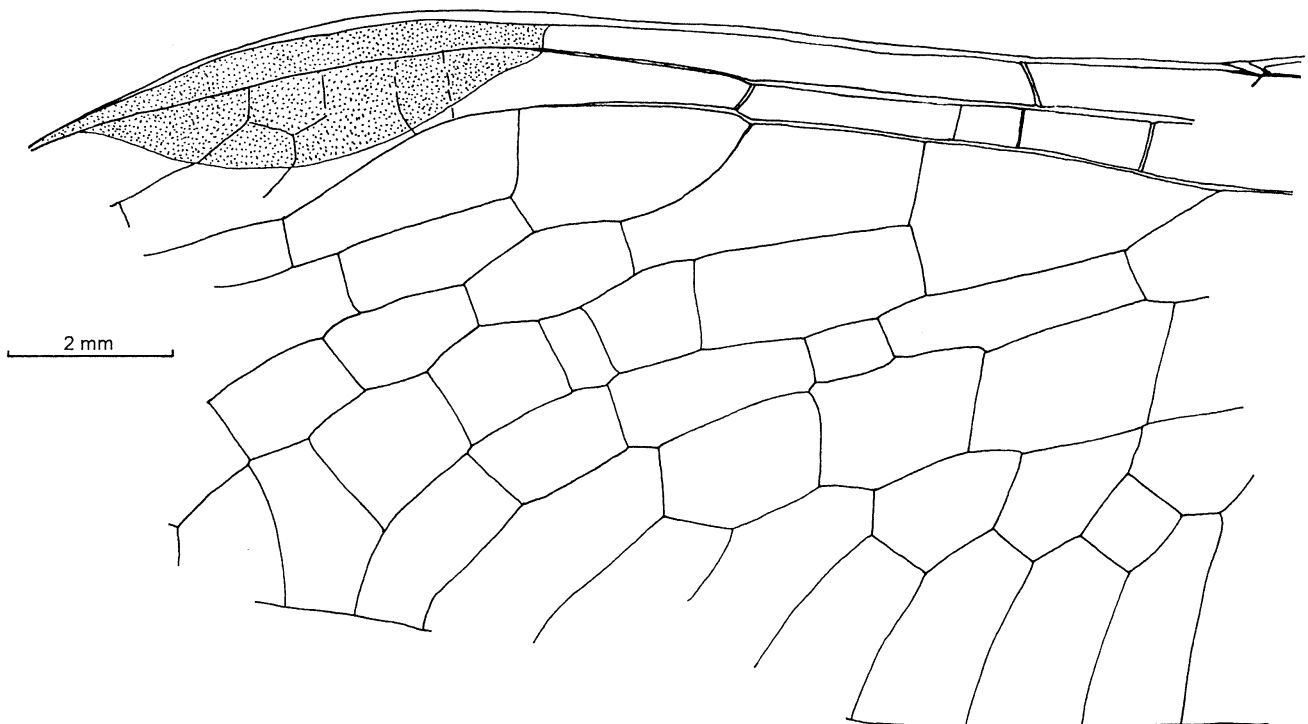


Fig. 16. *Ditaxineurella stigmalis* MARTYNOV, 1940, holotype specimen PIN 102/118 (scale bar represents 2 mm).

Fig. 16. *Ditaxineurella stigmalis* MARTYNOV, 1940, holotype PIN 102/118 (l'échelle représente 2 mm).

than the wing, crossed by vein RA and by two cross-veins between RA and RP1; pterostigma not touching RP1; pterostigma about 7–8 mm long and 1–1.5 mm wide, six times longer than wide, not basally prolonged in the postnodal area; distal fork of RA not preserved, if present.

Hindwing length, about 40 mm, width, 6.5 mm; basal brace between C and ScP not preserved; 11 antenodal cross-veins of the first rank between C and ScP not aligned with those of the second rank, between ScP and RA, but rather numerous; no primary antenodal cross-vein Ax1 nor Ax2 stronger than the secondaries; distance between wing base and nodus, about 24 mm, between wing base and arculus, 5 mm; distance between base of arculus and fork between MA and RP, 4 mm; CuP separating from MP 2.5 mm from wing base, as a strong cross-vein between MP and AA&CuP; CuA separating from MP 5 mm from wing base, appearing as a strong cross-vein between MP and AA&CuP; a strong cross-vein between MP and AA&CuP&CuA directed towards wing base 1 mm distally; area between AA&CuP&CuA and posterior wing margin narrow, 2 mm wide, with one row of cells; presence of one supplementary cell below AA&CuP&CuA opposite the cross-vein between MP and AA&CuP&CuA, distal free part of CuP zigzagged and being the posterior margin of this cell; distal free part of AA reduced to a simple short cross-vein basal of these cells; distal part of CuA long, weakly zigzagged, parallel to MP, with one row of cells between them; presence of a well-defined vein IMA in the area between MP and MA, beginning as a secondary branch of MA; a series of about 10 parallel zigzagged secondary veins between IMA and posterior wing margin; one row of cells between MA and IMA; one or two rows of cells between IMA and posterior wing margin; only two cross-veins between MA and MP basal of IMA, none of them being stronger than the other (no well-defined discoidal vein MAb), distance between these cross-veins, 4 mm, distance between the most distal cross-vein and base of IMA, 3 mm; presence of a incomplete cross-vein at the base of IMA, between IMA and MP; a strong cross-vein between RP and MA exactly opposite the base of IMA; nodal cross-vein ncv slightly in a basal position to the point of fusion between ScP and C; subnodal cross-vein snvc not preserved; ncv nearly perpendicular to C and RA; base of RP3/4 just distal of nodal cross-vein; RP3/4 nearly straight; base of IR2: 4 mm distal of subnodus; IR2 weakly zigzagged; base of RP2: 9 mm distal of subnodus; distal part of RP2 weakly zigzagged; base of IR1: 11 mm distal of subnodus; IR1 weakly zigzagged; nearly always one row of cells between MA and RP3/4, RP3/4 and IR2, IR2 and RP2, RP2 and IR1, IR1 and RP1; RP1 not strongly curved below pterostigma; postnodal and postsubnodal cross-veins between C and RA not preserved; pterostigma sclerotized, darker than the wing, crossed by vein RA; pterostigma not touching RP1; pterostigma very poorly preserved but about 1.5 mm wide, distinctly longer than wide; part of RA between nodus and pterostigma not preserved but distal fork of RA visible, not

beginning in the pterostigma; one cell between the two branches of RA; anterior branch of RA is the distal margin of pterostigma.

– Specimen PIN 1700/461 (Figs. 13 and 14): print and counterprint of the thorax with meso- and meta-thoracic legs well preserved, and femora of right prothoracic leg; the right forewing and the two hindwings in connection, together with three basal abdominal segments; first abdominal segment short, as in modern Odonata; abdomen broad, 3 mm wide; thorax about 10 mm long and 4.5 mm wide, partly deformed but larger than in modern Zygoptera; wings of the same colour as rock, thus they were probably hyaline on the living animal. Apical part of right wings destroyed but left hindwing nearly complete.

Differences with the holotype. Preserved part of forewing, about 12 mm long and 6 mm wide; a strong and oblique basal brace, 3 mm from wing base; CuP separating from MP 4 mm from wing base, CuA separating from MP 5 mm from wing base; two strong cross-veins between MP and AA&CuP&CuA directed towards wing base, 2 and 4 mm distal of CuA-crossing; MP strongly curved towards M opposite arculus; area between AA&CuP&CuA and posterior wing margin narrow, 2.5 mm wide, with one row of cells; presence of two supplementary cells below AA&CuP&CuA opposite cross-vein between MP and AA&CuP&CuA.

Hindwing length, about 45 mm, width, 7 mm; basal brace between C and ScP strong and oblique; about 10 antenodal cross-veins of first rank between C and ScP, not aligned with those (11) of second rank, between ScP and RA; distance between wing base and nodus, about 22 mm, between wing base and arculus, 7 mm; distance between base of arculus and fork between MA and RP, 3 mm; CuP separating from MP 4 mm from wing base; two strong cross-veins between MP and AA&CuP&CuA directed towards wing base, 2 and 4 mm distally; MP strongly curved towards MA opposite arculus; area between AA&CuP&CuA and posterior wing margin narrow, 3 mm wide, with one row of cells; presence of two supplementary cells below AA&CuP&CuA opposite cross-vein between MP and AA&CuP&CuA, distal part of CuA not well preserved but it was probably long; one row of cells between MA and IMA; only two cross-veins between MA and MP basal of IMA, distance between these cross-veins, 3.5 mm, distance between the most distal cross-vein and base of IMA, 4 mm; ncv and subnodal cross-vein snvc aligned, directed toward wing apex; base of RP2: 9 mm distal of subnodus; distal part of RP2 weakly zigzagged; only one postnodal cross-vein between C and RA and five postnodal cross-veins between RA and RP, the third being distinctly oblique, directed towards wing apex; pterostigma crossed by vein RA and the two most distal cross-veins between RA and RP1, both directed towards wing base; distal fork of RA not visible on preserved part of pterostigma.

HEMIZYGOPTERIDAE *Zalessky, 1955*

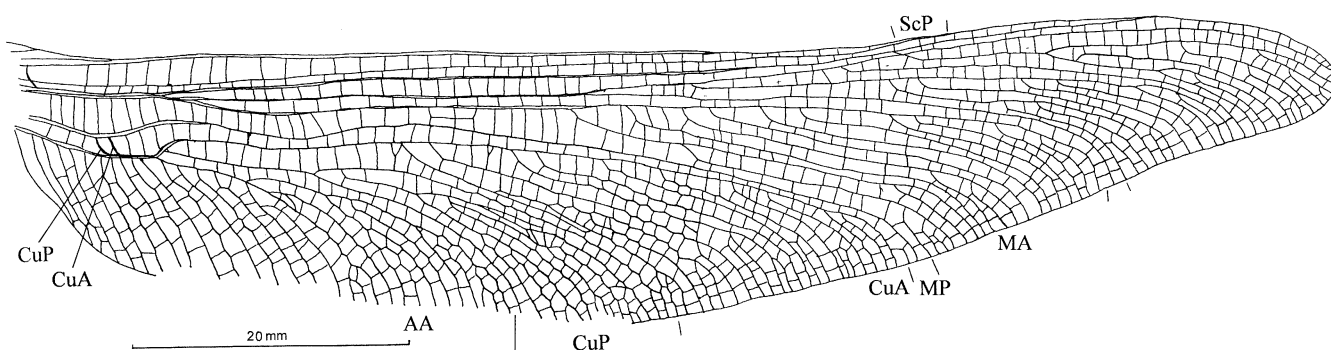


Fig. 17. Meganeuridae: Tupinae genus and species undetermined from the Upper Permian of Lodève (France), labelled 'Tupus', specimen Ld LAP 156 (Lapeyrie Collection) (scale bar represents 20 mm).

Fig. 17. Meganeuridae: genre et espèce indéterminés de Tupinae du Permien supérieur de Lodève (France), noté 'Tupus', spécimen Ld LAP 156 (collection Lapeyrie) (l'échelle représente 20 mm).

Type genus: *Hemizygopterion* ZALESSKY, 1955. [Bechly \(1996\)](#) also included *Ditaxineurella* in this family, but we prefer to consider this last taxon as an Incertae sedis because of the very incomplete state of preservation of its type specimen.

Diagnosis: [Bechly \(1996, 1998, in press\)](#) indicated that there is no known autapomorphy of this family. We failed to find one in our phylogenetic analysis, because of the incomplete state of preservation of the available material.

Genus: *Hemizygopterion* ZALESSKY, 1955 stat. rest.

Type species: *Hemizygopterion uralense* ZALESSKY, 1955.

Diagnosis: Only one row of cells in the cubito-anal area between CuA and the posterior wing margin (unique state of character within the Protanisoptera). Apparently, the bent of RP1 below the pterostigma is weak.

Phylogenetic position: This taxon falls in the clade {*Callimokaltania martynovi*, *Hemizygopterion uralense*, *Proditaxineura pritykinae* gen. nov., *Ditaxineura anomalostigma*, *Ditaxineura cellulosa*}. Thus, we exclude it from the Permaeschnidae.

Hemizygopterion uralense ZALESSKY, 1955 stat. rest.

1955 *Hemizygopterion uralense* – Zalesky, 632–633, [Fig. 2](#) (original description, in Hemizygopteridae).

1958 *Hemizygopterion uralense* – [Laurentiaux](#), 47 (listed in Hemizygopteridae).

1992 *Ditaxineurella uralense* – [Carpenter](#), 67 (listed, synonymized without revision with *Ditaxineurella*, transferred in Permaeschnidae).

Material: Holotype location unknown, a wing with the central part missing.

Horizon and type locality: Upper Permian, Ural, Russia.

Hemizygopterion cf. *uralense* ZALESSKY, 1955, [Fig. 15](#).

Material: Specimen PIN 1700/470, print and counterprint of a nearly complete wing.

Horizon and locality: Lower Permian, Chekarda, Russia.

Description: This fossil is probably a forewing because of the narrow cubito-anal area; extreme base missing; wing length, about 25 mm; greatest width, 5.5 mm at the level of end of CuA and 4.5 mm at the level of end of RP3/4; surface of the rock uniformly grey, so the wing was probably hyaline with no coloured pattern, excepted for the darker pterostigma; almost three antenodal cross-veins of first rank perpendicular to Costa, nine antenodal cross-veins of second rank; first antenodal of the first rank corresponding to the third cross-vein of second rank; only two postnodal cross-veins and four postsubnodal cross-veins, the two most distal crossing pterostigma; presence of a strong basal brace between C and RA directed towards apex, perhaps homologous to Ax0; point of fusion of ScP with C not preserved, ncv and sncv weak and nearly perpendicular to C; sncv well aligned with ncv and joining RP at bifurcation between RP1 and RP3/4; nodus at 13 mm from the most basal part of the preserved part of the wing; RA forked into two short branches in distal part of pterostigma; pterostigma not elongated, about 4 mm long; greatest width, 1 mm, only one cell basal of wing apex, crossed by the third and the fourth postsubnodal cross-veins; RP1 touching posterior margin of pterostigma; RP1, IR1, RP2, IR2, RP3/4, distal part of MA and IMA parallel, with only one row of cells between them; only one row of cells between IMA and posterior wing margin distal of end of MP; one cross-vein in antesubnodal area between RA and RP; presence of four cross-veins in median area between MA and MP basal to IMA; presence of a strong cross-vein between RP and MA, well aligned with IMA; MP strongly curved towards arculus; CuP long, straight and parallel to MP with one row of cells between them; extreme base of AA not preserved; free part of CuA and CuP between AA and MP&Cu weakly oblique; cubito-anal area long and narrow, with few cells in preserved part of wing; only one row of cells between CuA and posterior wing margin; distal free parts of CuP and AA not defined, either absent or reduced to cross-veins between CuA and posterior wing margin as it occurs in *Hemizygopterion uralense* ZALESSKY, 1950.

Comparison with the type specimen of *Hemizygopteron uralense* ZALESSKY, 1955.

The main differences between this specimen PIN 1700/470 and the holotype of *H. uralense* are as follows:

- nine antenodal cross-veins of second rank in PIN 1700/470, only two in the type specimen of *H. uralense* (after ZALESSKY, 1955) in preserved part of the wing;
- presence of a strong basal brace between C and RA, directed towards apex in PIN 1700/470, absent in *H. uralense* (after ZALESSKY, 1955);
- third and fourth postsubnodal cross-veins crossing pterostigma in PIN 1700/470, absent in *H. uralense* (after ZALESSKY, 1955);
- end of RP1 simple in PIN 1700/470, forked in *H. uralense* (after ZALESSKY, 1955);
- end of RA forked at the end of the pterostigma in PIN 1700/470, not forked in *H. uralense* (after ZALESSKY, 1955).

These differences remain dubious because it would be necessary to verify the reconstruction of the wing of *H. uralense* proposed by Zalesky (1955). Nevertheless, the two fossils are closely related because they share the same organization of the cubito-anal area, shape of pterostigma, radial area, base of IMA and wing dimensions. As the reconstruction of *H. uralense* proposed by Zalesky is dubious, we prefer to keep the new specimen in open nomenclature, under the name of *Hemizygopteron cf. uralense*.

Genus: *Ditaxineurella* MARTYNOV, 1940

Type species: *Ditaxineurella stigmalis* MARTYNOV, 1940.

Diagnosis: Although the very incomplete state of preservation of its holotype, this taxon can be characterized as follows: wings relatively broad, wider than those of *Proditaxineura* and *Ditaxineura*, with five long cells in the area between MA and RP3/4; a distally but not basally prolonged pterostigma; numerous cross-veins and cells between RP1 and RA in the pterostigma; nodus and pterostigma approximate, so either the wing is short or the nodus is in a very distal position.

Phylogenetic position: Because of its incomplete state of preservation, it was not possible to include this taxon in the phylogenetic analysis. Nevertheless, it does not have the synapomorphies of the Permaeschnidae, i.e. its RA has no long distal posterior branch, there is no distinctly transverse cell between RP1 and IR2, near the base of IR2, and there is no secondary longitudinal vein between RP3/4 and IR2. It is more probably related to the superfamily Ditaxineuroidea, but we prefer to maintain it in an open position, as a Protanisoptera Incertae sedis.

Ditaxineurella stigmalis MARTYNOV, 1940, Fig. 16.

1940 *Ditaxineurella stigmalis* – Martinov, 11–12, 48–49, text Fig. 5, pl. 2, Fig. 3 (original description).

1992 *Ditaxineurella stigmalis* – Carpenter, 67, text-Fig. 42.4 (list, in Permaeschnidae without explanation).

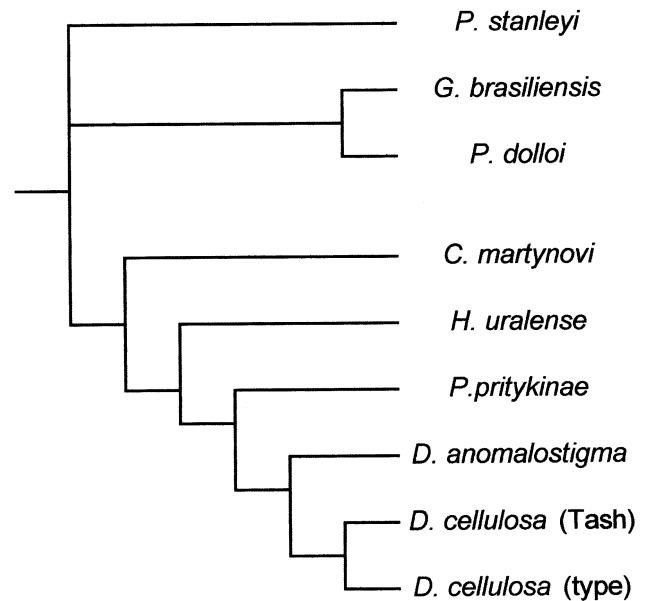


Fig. 18. Strict consensus tree obtained using particular outgroup(s): tree T1.
Fig. 18. Arbre consensus strict obtenu en utilisant des groupes externes particuliers: arbre T1.

Material: Holotype specimen PIN 102/118, the distal two-third of a wing.

Horizon and locality: Permian, Kungurian, Cherkada, Urals, Russia.

Redescription: Only one postnodal cross-vein between C and RA, directed towards base of the wing; four postsubnodal cross-veins basal to pterostigma on the preserved part of the wing, the last one strong and directed towards the apex ('Schrägader' sensu Bechly, 1996); RA forked in distal part of the pterostigma; pterostigma distally prolonged between RA and C; pterostigma crossed by several cross-veins between RP1 and RA; RP1 strongly bent below pterostigma; RP1, IR1, RP2, IR2 and RP3/4 parallel and separated by one row of cells; posterior wing margin not notched at the end of PR3/4 or MA.

Discussion: Carpenter (1992) listed and synonymized without revision, *Hemizygopteron* with *Ditaxineurella*. As the holotype of *D. stigmalis* is a very fragmentary specimen, no clear evidence supports this synonymy. Furthermore, the pterostigma of *D. stigmalis* is distally prolonged between RA and C, which is not so in *Hemizygopteron*. Thus, we propose to restore the genus *Hemizygopteron*.

3. Phylogenetic analysis

We propose a phylogenetic analysis of the Protanisoptera. We have excluded from the analysis the taxa that have too many unknown characters because of their incomplete state of preservation of the type material, i.e. *Permaeschna proxima*, *Ditaxineurella stigmalis* and *P. camense*. We have examined the impact of the different choices of the outgroup(s). Six potential outgroups have been selected i.e.:

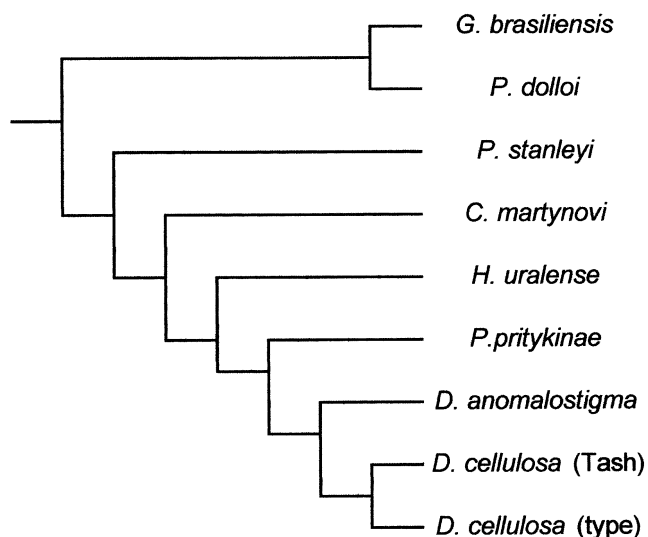


Fig. 19. Strict consensus tree obtained using particular outgroup(s): tree T2.
Fig. 19. Arbre consensus strict obtenu en utilisant des groupes externes particuliers: arbre T2.

- an ‘undescribed geropterid from Westphalian of Rioja, Argentina’, figured in [Wootton and Kukalová Peck \(2000\)](#), called herein ‘Geropterid’ (Outgroup O1), chosen because it has a very basal position within the Odonatoptera;
- an undescribed Meganeuridae: Tupinae genus and species undetermined from the Upper Permian of Lodève (France), called herein ‘Tupus’ (Outgroup O2) ([Fig. 17](#));
- *Lapeyria magnifica* [NEL et al., 1999](#) (Outgroup O3), chosen because [Nel et al. \(1999\)](#) considered it as the sister group of the Nodialata (= Protanisoptera + more modern Odonatoptera);
- *Pemphlebia uralica* [NEL et al., submitted](#) (Upper Permian of Russia) (Outgroup O4);
- *Triadotypus guillaumei* [GRAUVOGEL and LAURENTIAUX, 1952](#) (revised by [Nel et al., submitted](#)), (Outgroup O5), both these taxa have been chosen as potential outgroups because they belong to the more modern Odonatoptera, but are in a basal position ([Nel et al., submitted](#));
- *Megatypus schucherti* [TILLYARD, 1925](#) (from the Permian of Elmo, USA), after an unpublished new drawing of [Bechly \(1998\)](#) and personal communication) (Outgroup O6). ‘Tupus’ and *Megatypus schucherti* belong to the Meganisoptera, sister group of the Lapeyriidae + Nodialata.

The ‘ingroup’ is as follows: *Proditaxineura pritykinae* (I1); *Permaeschna dolloi*, specimen PIN 3353/75 (I2); *Pholidoptilon camense* (I3); *Polytaxineura stanleyi* (I4); *Callimokaltania martynovi* (I5); *Hemizygopteron uralense* (I6); *Gondvanoptilon brasiliense* (I7); *Permaeschna dolloi*, specimen PIN 2334/4 (holotype of *P. proxima*) (I8); *Ditaxineura anomalostigma*, specimen No. 3046 (Museum of Comparative Zoology, USA) (I9); *Ditaxineura cellulosa* (?),

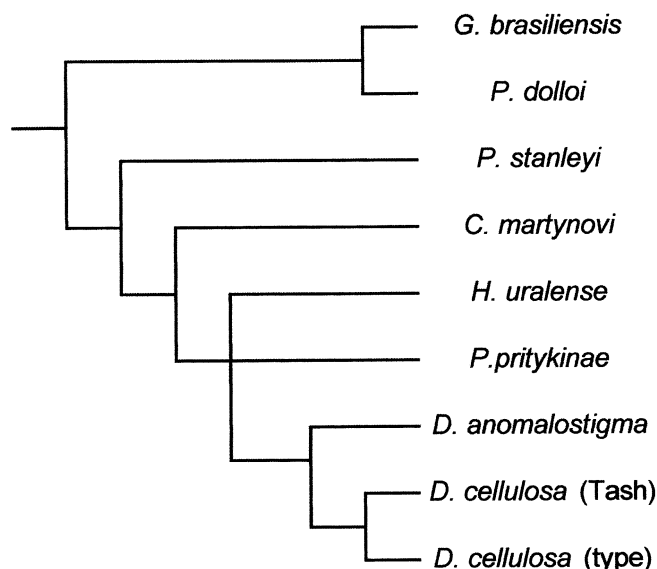


Fig. 20. Strict consensus tree obtained using particular outgroup(s): tree T3.
Fig. 20. Arbre consensus strict obtenu en utilisant des groupes externes particuliers: arbre T3.

specimen figured in [Tasch and Zimmerman \(1962\)](#) (I10); *Ditaxineura cellulosa*, type specimen (I11).

We defined 40 characters, all concerning the wing venation (see Appendix 1). The body structures of these fossils are poorly known or even unknown. All characters are considered unordered and equally weighted. No constraint was imposed about the monophyly of the ingroup, i.e. the option ‘outgroup rooting: root tree at internal node with basal polytomy’ was used. Nevertheless, the option ‘outgroup rooting; make ingroup monophyletic’ has led to the same results. The analyses were performed using the computer software Paup 3.1.1. The ‘heuristic search’ and ‘branch and bound search’ options gave the same results. The repartition of the character states among the branches of the most parsimonious cladograms was analysed and compared using the computer software MacClade 3.07.

We first performed the analyses excluding I3 because of its very incomplete state of preservation.

Several analyses were attempted, based on different choices of outgroup(s). We first explored analyses based on the six outgroups all together. [Barriel and Tassy \(1998\)](#) noted that, in some cases, with the computer software Paup 3.1.1., the choice of the prime outgroup can influence the result and leads to different resulting minimal cladograms. Thus, we change the order of introduction of the prime outgroup in the data matrix, i.e. test the following combinations of outgroups: (O1,O2,O3,O4,O5,O6); (O2,O3,O4,O5,O6,O1); (O3,O4,O5,O6,O1,O2); (O4,O5,O6,O1,O2,O3); (O5,O6,O1,O2,O3,O4); (O6,O1,O2,O3,O4,O5). All analyses gave the same result, i.e. the minimal tree T1, with the same length, C.I. and R.I. The present example shows that the assumption of [Barriel and Tassy \(1998\)](#) is not a general rule.

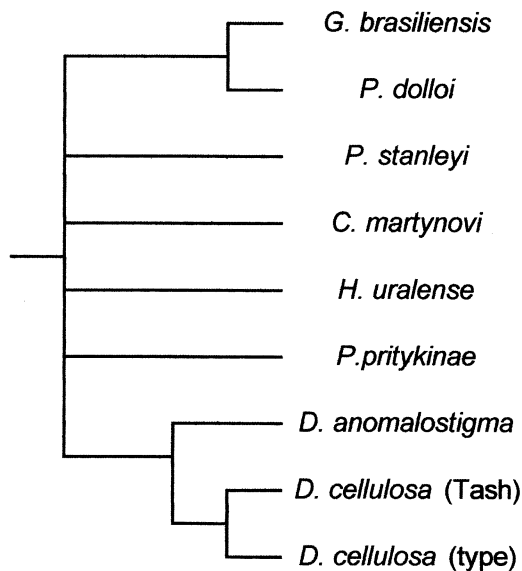


Fig. 21. Strict consensus tree obtained using particular outgroup(s): tree T4. Fig. 21. Arbre consensus strict obtenu en utilisant des groupes externes particuliers: arbre T4.

We also performed analyses based on different combinations of outgroups in singles, pairs and triplets. The order of introduction of the prime outgroups in pairs and triplets was also tested and had no impact on the results. Nevertheless, the different analyses gave six different strict consensus trees, T1, T2, T3, T4, T5 and T6, depending on the combinations in pairs and triplets, showing that it is not always sufficient to examine the order of introduction of the prime outgroup to explore the impact of the choice of outgroup(s) on the ingroup topology (see Table 2 and Figs. 18–21).

Some clades are present in all the minimal trees of the various analyses, i.e. clades (I9(I10,I11)) and (I7,I2). T1 and T2 differ in the position of I4 (sister group of all the rest of the ingroup) in T1 but sister group of {I5,I6,I1,I9,I10,I11} in T2. The strict consensus tree T3 is generated by T2 and T'2 that is very similar to T2 but 'exchanges' the positions of I1 and I6. The strict consensus tree T4 of 12 minimal trees fails to define the order of the clade {I5&I6&I1&(I9(I10,I11))}, except for the subclade (I9(I10,I11)), but T1 and T2 are present among these 12 trees. The strict consensus tree T5 of three minimal trees fail to define the order of the clade {I6&I1&(I9(I10,I11))}, but T2 is present among these three trees. The tree T6 is the strict consensus of T1 and T2.

In T1 and T2, the clade (I7,I2) [Permaeschnidae sensu novo] is supported by the strict synapomorphies '23 (2)' (IMA is present, divided into two main branches, the posterior branch being parallel to MP, the anterior branch being parallel to MA, and with secondary branches beginning on the posterior branch), '29 (2)' (RA with a long distal posterior branch), '34 (1)' (two or more distinctly transverse cells between RP1 and IR2, near the base of IR2 present), '35 (1)' (numerous secondary longitudinal veins between

RP3/4 and IR2 present), and '36 (0)' (wings large with many cells). The clade {I1,I9,I10,I11} = {*Proditaxineura pritykinae* and *Ditaxineura anomalostigma* and *Ditaxineura cellulosa* (?) and *Ditaxineura cellulosa* type} is supported by the strict synapomorphies '3 (0)' (basal brace 'Ax0' between C and ScP distinctly oblique) and '37 (1)' (a large cell in cubito-anal area between CuP and CuA, at the base of distal free part of CuP present). The clade {I6,I1,I9,I10,I11} = {*Hemizygopteron uralense* and *Proditaxineura pritykinae* and *Ditaxineura anomalostigma* and *Ditaxineura cellulosa* (?) and *Ditaxineura cellulosa* type} is supported by the strict synapomorphy '30 (1)' (pterostigma present but not basally and distally prolonged).

A Bremer's test gives a high stability of the clade (I7,I2), which remains present in trees six steps longer than the corresponding minimal cladograms. It gives a lower stability for the clade (I9(I10,I11)), which is still present in trees two steps longer than the minimal cladograms. In all analyses, other clades are not preserved in trees one step longer than the minimal cladograms (Bremer, 1994). Therefore, it is not possible to make a comparison through a Bremer's test of the relative value of the different solutions obtained using different outgroups.

The clade {I6,I1,I9,I10,I11} is present in T3 but absent in T4. The clade {I1,I9,I10,I11} is absent in T3 and T4 but present in some of the minimal trees from which T3 and T4 are generated. Among the twelve minimal trees that generate T4, the order among I5, I6 and I1 varies greatly: either I5 is in basal position within the clade {I5,I6,I1,I9,I10,I11}, or it is I6 or I1, I5 and I6 can also be sister groups in some of these trees. All these perturbations concerning the clade {I5,I6,I1,I9,I10,I11} are due to the use of O2 as outgroup. The incompleteness of the information concerning O2 cannot be at the origin of these differences with other analyses because O2 has very few unknown character states. There are few differences in the character state distribution between O1 and O2 (only 6 or 7 characters). This result suggests that the organization of the clade {I5,I6,I1,I9,I10,I11} remains very ambiguous and would need the discovery of more characters. The combination of the very incomplete O5 with O2 or O1 increases the perturbation (tree T4).

The two clades present in all the analyses are [*Ditaxineura anomalostigma* (I9) + [*Ditaxineura cellulosa* (?) (sensu Tasch and Zimmerman, 1962) (I10) + *Ditaxineura cellulosa* (type specimen) (I11)]], corresponding to the genus *Ditaxineura*; and [*Permaeschna dolloi* (I2) + *Gondvanoptilon brasiliense* (I7)].

The present study only partly supports the hypotheses of Bechly (1996, 1998, in press), who proposed the following phylogenetic classification of the Protanisoptera: [Polytaxineuridae + (Permaeschnidae + (Callimokaltaniidae + (Hemizygopteridae + Ditaxineuridae)))]]. The Hemizygopteridae sensu Bechly (1996) comprise *Hemizygopteron* and *Ditaxineurella*. We excluded *Ditaxineurella* from our analyses because of its very incomplete state of preservation.

Hemizygopteron (I6) falls as sister group of the Ditaxineuridae + *Proditaxineura* (trees T1 or T2), which is congruent with the hypothesis of Bechly. The Permaeschnidae sensu Bechly (1996) [= *Permaeschna* (I2) + *Callimokaltania* (I5) + *Pholidoptilon* (I3)] are no longer monophyletic, but polyphyletic, in our analyses. Bechly (1998) named Ditaxineuomorpha the clade (Permaeschnidae + (Callimokaltaniidae + (Hemizygopteridae + Ditaxineuridae))) and proposed the following synapomorphies to characterize it:

- ‘only a single antesubnodal cross-vein retained’. This character is false for *Callimokaltania* (two cross-veins) and possibly *Pholidoptilon* (no cross-vein). Note that ‘no cross-vein’ could be reformulated as ‘less the two antesubnodal cross-veins retained’ to solve the problem of *Pholidoptilon*;
- ‘only one cross-vein present in the space between RP and MA from arculus to midfork’. Characters (1) and (2) are considered as synapomorphies of the Ditaxineuomorpha because *Polytaxineura* (supposed to be the sister group of the Ditaxineuomorpha) is supposed to have numerous cross-veins in these areas. But, this character remains dubious for this last taxon;
- ‘all true cubito-anal cross-veins reduced’. This character is false for *Gondvanoptilon* that has such numerous cross-veins.

We also performed the analyses including I3 (*Pholidoptilon camense*). Using 15 different combinations of outgroups (all outgroups, or (O1,O2,O6), (O3,O4,O5) etc.), we obtain a consensus tree very similar to T1, with I3 as sister group of {I1,I5,I6,I9,I10,I11}. Using O1, O4, or O6 alone, or (O1,O4,O6), we obtain a tree similar to T2 and I3 falls as sister group of I1. Using O2 or O5, we obtain a tree similar to T4, with I3 in an unresolved polytomy with [I1&I5&I6&(I9(I10,I11))]. It appears clearly that the introduction of this very incompletely known taxon adds noise to the original trees of the preceding analysis. I3 (*P. camense*) is in a very uncertain position. There is no clear argument to support the hypothesis of Carpenter (1992) concerning the attribution of *P. camense* to the genus *Permaeschna*.

On the contrary, if we add the type specimen of *Permaeschna proxima* (I8) to the analyses, it always falls as sister group of *Permaeschna dolloi*. This result supports the close affinities, if not identity, of the two taxa.

Note: Pfau (2000) considered the Protanisoptera as a ‘transition stage’ between the Odonatoptera ‘stemgroup’ and the Protozygoptera and the Odonata because of their alleged ‘primitive ‘distal’ nodus and a very oblique (‘soft’) anterior and mid arculus’. If the protanisopterid arculus structure is clearly plesiomorphic, it is not so obvious for their nodal structures. Pfau (2000, Fig. 6) obviously followed the erroneous wing venation interpretation of Fraser (1957). After the present study, the nodal structures of the Protanisoptera are not in a more distal position than in many modern Anisoptera and have all the specializations of the

true Odonata, i.e. nodal furrow at the point of fusion of ScP with C and well-aligned nodal Cr and subnodus below this structure. The nodal structures of the Permian Lapeyriidae (Nel et al., 1999) are clearly more ‘primitive’ than those of the Protanisoptera, but Pfau (2000) ignored this last paper.

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Appendix 1

List of characters

1. A basal triangular sclerotized area between C and ScA ...
present: 0
absent: 1
2. A strong basal brace between C and ScP (homologous to Ax0?) ...
at the apical angle of the basal sclerotized area between C and ScA. 0
distal of the apical angle: 1
3. The basal brace ‘Ax0’ between C and ScP ...
distinctly oblique: 0
not so oblique: 1
4. The basal brace ‘Ax0’ ...
is prolonged by a cross-vein between ScP and RA: 0
is not prolonged by a cross-vein between ScP and RA: 1
5. The free part of CuP between MP&Cu and AA ...
is distinctly oblique: 0
is nearly perpendicular to MP&Cu and AA: 1
6. The free part of CuA between MP&Cu and AA ...
is distinctly oblique: 0
is nearly perpendicular to MP&Cu and AA: 1
7. Cross-veins between MP&Cu and AA basal of CuP ...
absent: 0
present: 1
8. Prequadrangular cell (sensu Tillyard, 1935) ...
absent: 0
present, trapezoidal with its base distinctly shorter than its anterior part: 1
present, but nearly rectangular: 2
9. At the level of the base of the arculus, MP and CuA (&CuP&AA) ...
remain parallel: 0
move aside, the distance between the two veins greatly increases, and approximate again distally, so that MP is strongly arched at this point: 1

10. The distal portion of AA in cubito-anal area is ...
 well-defined, appearing as a long longitudinal vein: 0
 not well-defined, appearing as a strongly zigzagged vein: 1
 as a cross-vein: 2
11. The distal portion of CuP in the cubito-anal area is ...
 a well-defined, long longitudinal vein parallel to distal part of CuA, with one row of cells between them: 0
 not well-defined, appearing as a strongly zigzagged vein, diverging from distal part of CuA: 1
 as a cross-vein: 2
12. The cubito-anal area is ...
 very wide, with more than four rows of cells between CuA and posterior wing margin: 0
 wide, with three rows of cells between CuA and posterior wing margin: 1
 narrow, with less than two rows of cells between CuA and posterior wing margin: 2
13. At the distal end of MP, the posterior wing margin has ...
 no notch: 0
 a weak notch: 1
 a strong notch: 2
14. At the distal end of MA and RP3/4, the posterior wing margin has ...
 no notch: 0
 a weak notch: 1
 a strong notch: 2
15. In the antesubnodal area between RA and RP ...
 no cross-veins: 0
 few cross-veins: 1
 many cross-veins: 2
16. The antenodal cross-veins of the first row, between C and ScP are ...
 few, less than five: 0
 numerous, more than six: 1
17. The antenodal cross-veins of the second row, between ScP and RA are ...
 few, less than five: 0
 numerous, more than seven: 1
18. The cross-vein in the area between RP and MA, opposite the base of IMA, is ...
 absent: 0
 exactly aligned with IMA: 1
 slightly in a distal position relative to the base of IMA: 2
19. The cross-veins in the area between RP and MA, between the cross-vein opposite the base of IMA and the base of RP3/4, are ...
 absent: 0
 present: 1
20. The nodal cross-vein ncv and the subnodal cross-vein sncv are ...
 absent: 0
 present but not well-aligned: 1
 well-aligned: 2
21. The nodal cross-vein ncv is ...
 absent: 0
 present, not distinctly directed towards the apex: 1
 present, distinctly directed towards the apex: 2
22. The subnodal cross-vein sncv is ...
 absent: 0
 not distinctly directed towards the apex: 1
 distinctly directed towards the apex: 2
23. IMA is ...
 absent: 0
 present, simple, with several veins beginning on IMA and directed towards posterior wing margin: 1
 present, divided into two main branches, the posterior branch being parallel to MP, the anterior branch being parallel to MA, and with secondary branches beginning on the posterior branch: 2
24. The median area between MA and MP is ...
 wide, with more than six rows of cells between MA and the posterior wing margin: 0
 narrow, with less than seven rows of cells between MA and the posterior wing margin: 1
25. Postnodal cross-veins between C and RA ...
 present: 0
 absent: 1
26. A distinctly oblique postsubnodal cross-vein between RA and RP ...
 absent: 0
 present: 1
27. Other postsubnodal cross-veins ...
 present: 0
 absent: 1
28. Pterostigma ...
 absent: 0
 present, not crossed by RA: 1
 present, crossed by RA: 2
29. RA ...
 with no distal posterior branch: 0
 with a short distal posterior branch: 1
 with a long distal posterior branch: 2
30. Pterostigma ...
 absent: 0
 present, not basally and distally prolonged: 1
 present, basally and distally prolonged: 2
31. RP1 ...
 not curved below the pterostigma: 0
 strongly curved below the pterostigma: 1
32. Cross-veins between RP1 and the posterior margin of the pterostigma ...
 one or less: 0
 two or more: 1
33. A cross-vein between RP1 and the posterior margin of the pterostigma, directed towards the apex, and more or less developed as a secondary branch of RP1 is ...

- absent: 0
present: 1
34. Two or more distinctly transverse cells between RP1 and IR2, near the base of IR2 ...
absent: 0
present: 1
35. Numerous secondary longitudinal veins between RP3/4 and IR2 ...
absent: 0
present: 1
36. Wings ...
large with many cells: 0
smaller with fewer cells: 1
37. A large cell in cubito-anal area between CuP and CuA, at the base of distal free part of CuP ...
absent: 0
present: 1
38. ScP, RA and RP1 ...
ScP arrives near the wing apex or ScP ends far from the apex, but the apices of RA and RP1 are very Distant: 0
ScP ends far from the apex, but the apices of RA and RP1 are approximated: 1
39. Antenodal cross-veins basal of basal brace 'Ax0' ...
absent: 0
present: 1
40. Pterostigma ...
absent: 0
present, but not widely widened: 1
present, widely widened: 2

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