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A new family of Anisoptera from the Upper Jurassic of Karatau in Kazakhstan (Insecta: Odonata: Juragomphidae n. fam.)

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With 2 Figures

Summary

A new dragonfly genus and species, *Juragomphus karatauensis*, from the Upper Jurassic of Karatau in Kazakhstan is described and attributed to a new family Juragomphidae. The phylogenetic position and relationships of this new taxon are discussed.

Zusammenfassung

Eine neue Großlibellen-Gattung und -Art, *Juragomphus karatauensis*, wird aus dem oberen Jura von Karatau in Kasachstan beschrieben und einer neuen Familie Juragomphidae zugeordnet. Die phylogenetische Stellung und Verwandtschaft dieses neuen Taxons werden diskutiert.

1. Introduction

The Liassogomphidae Tillyard & Fraser, 1940*) (= Gomphitidae Tillyard, 1925) is the oldest known and presumably most basal family of the anisopterid lineage (excluding the "anisozygopteroid" stem group). It is relatively abundant in the European Liassic outcrops (Switzerland, Germany, England, Luxembourg) (Tillyard, 1925; Cowley, 1935, 1942; Tillyard & Fraser, 1940; Bode, 1953; Fraser, 1957; Carpenter, 1992; Nel et al., 1993). Etter & Kuhn (2000) synonymized nearly all the previously described species with *Liassogomphus brodieri* (Buckman, 1843), except for *Elattogomphus latus* Bode, 1953 and *Proinogomphus bodei*

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*) Please note: Tillyard (1935: 381) cited the family name Liassogomphidae without any designation of the type genus or species and no diagnosis. Therefore, it was a nomen nudum. Tillyard & Fraser (1940) defined the "Liassogomphidae fam. nov.".

(Handlirsch, 1939), and with some doubt *Phthitogomphus angulatus* (Handlirsch, 1939).

Ren (1994) described a new genus and species *Chrysogomphus beipiaoensis* (based on an adult specimen from the Upper Jurassic of Liaoning, China) which he attributed to the Liassogomphidae. Based on the figure and photograph of Ren (1994), Fleck et al. (submitted) concluded that this taxon is clearly not related to this family and could have strong affinities with the Aeshnoptera. Thus, the family Liassogomphidae remains a strictly Liassic taxon.

We here describe a well-preserved liassogomphid-like dragonfly from the Upper Jurassic Karatau range as a new genus and species, *Juragomphus karatauensis,* within a new family Juragomphidae.

Methods

We follow the wing venation nomenclature of Nel et al. (1993) and Bechly (1996). The higher classification of fossil and extant Odonatoptera is based on the new phylogenetic system of Bechly (1996).

2. Systematic Palaeontology

Order Odonata Fabricius, 1792
Suborder Anisoptera Selys, 1854
Family Juragomphidae n. fam.

Type genus: *Juragomphus* n. gen.

Diagnosis. – This new family is characterized by the following combination of characters: Wings very long (about 70 mm); forewing discoidal triangle transverse, equilateral, divided into numerous cells, and very broad; numerous antenodal and postnodal crossveins; Ax1 distinctly stronger than Ax2; CuA curved; PsA weak; subdiscoidal space triangular, poorly defined but divided into five cells; no Mspl; no Rspl; postdiscoidal area very broad; 2 lestine oblique veins; no primary IR1; pseudo-IR1 present; pterostigma long, covering 6 cells; pterostigmal brace vein present, but not very oblique and not basally recessed; RP1 and RP2 not basally parallel up to the level of the pterostigma; anterior margin of supratriangle straight. All these characters are plesiomorphic within Anisoptera, except for the equilateral discoidal triangle which is probably an autapomorphy (but convergently present in some taxa within the Petalurida, Aeshnoptera and Cavilabiata).

Genus *Juragomphus* n. gen.

Type species: *Juragomphus karatauensis* n. sp.
Derivation of name: After the Jurassic age and the extant genus *Gomphus.*

Diagnosis. – That of the family.

Juragomphus karatauensis n. sp.

Figs 1–2

Holotype: Specimen PIN 2997/4431, Moscow, a nearly complete forewing.
Type locality: Karatau, Chimkent region, Southern Kazakhstan, C.E.S.

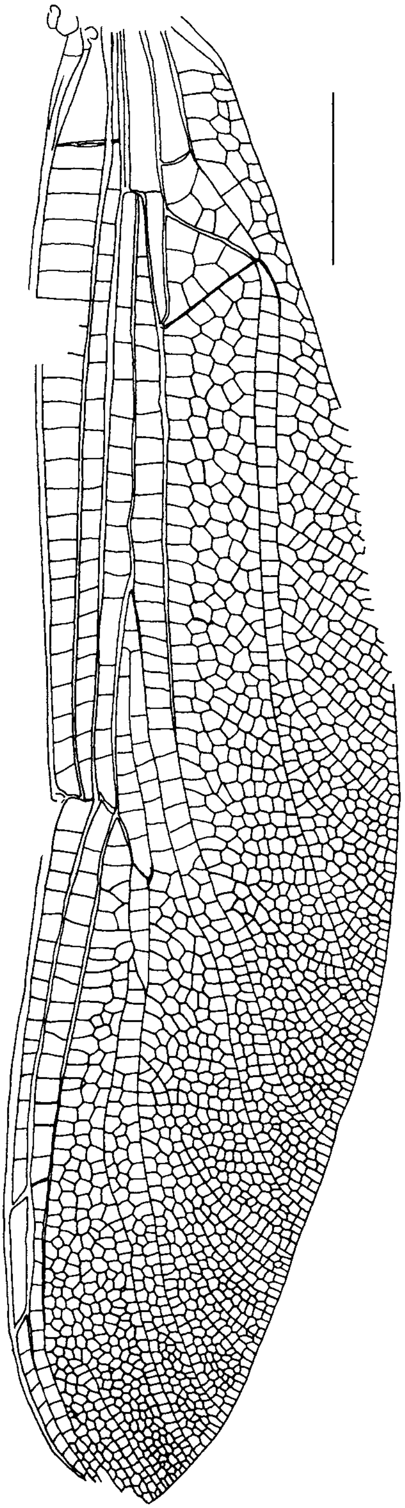

Fig. 1. *Juragomphus karatauensis* n. gen. n. sp., holotype specimen PIN 2997/4431, forewing reconstruction drawing. Scale 8 mm.

Type horizon: Upper Jurassic, Callovian-Kimmeridgian or Oxfordian-Kimmeridgian (Zherikhin and Gratshev, 1993; Mostovski and Martínez-Delclòs, 2000).
Derivation of name: Named after the type locality Karatau.

Diagnosis (female). – That of the family.

Description. – Forewing 70 mm long, 16.4 mm wide; ratio width / length, 0.23; distance from base to nodus, 36.4 mm; from nodus to apex, 33.2 mm; from nodus to pterostigma, 18.6 mm; from pterostigma to apex, 10 mm; from nodus to arculus, 28.4 mm; nodal furrow very distinct; pterostigma 6 mm long, 1.2 mm wide, with about 6 cells below pterostigma; pterostigmal brace vein slightly oblique, stronger than postnodal cross-veins, and aligned with basal side of pterostigma; about 16 postnodal cross-veins, not strictly aligned with corresponding postsubnodal cross-veins between RA and RP1; 24 secondary antenodal crossveins; antenodal cross-veins of second row between ScP and RA less numerous and not aligned with those of first row; 5 secondary antenodal cross-veins between the 2 strong primary antenodal cross-veins, but none basal of Ax1; Ax1 stronger than Ax2; Ax1 2.2 mm basal of arculus; distance between Ax1 and Ax2, 7.2 mm; Ax2 slightly basal of distal angle of discoidal triangle; RP and MA well-separated in arculus; posterior part of arculus aligned with anterior part; numerous cross-veins between RP and RA basal of RP3/4, between base of RP3/4 and nodus, and between RP and MA basal of RP3/4; 7 bridge-cross-veins (Bqs); discoidal triangle divided into 7 cells, transverse and nearly equilateral; length of its anterior side, 5.2 mm; of distal side, 5.4 mm; of basal side, 4.6 mm; supratriangle short and free of cross-veins; median space free of cross-veins; submedian space crossed by CuP which is distinctly curved and oblique; a well-defined PsA separating submedian space from a nearly triangular five-celled subdiscoidal triangle, the latter 5 mm long and 2.4 mm wide; 3 rows of cells in anal area; a row of two infrasubdiscoidal cells beneath anal vein, limited by a forward slanting secondary branch of AA; CuA divided into 8 posterior branches; CuA very long and reaching posterior wing margin on the level of nodus; 8–10 rows of cells between CuA and posterior wing margin; area between CuA and MP greatly widened near posterior wing margin with one row of cells behind discoidal triangle and about 17 rows near posterior wing margin; 4–5 rows of cells in postdiscoidal area distal of discoidal triangle; 2 longitudinal zigzagged secondary veins in postdiscoidal area, but no Mspl; postdiscoidal area slightly widened distally near posterior wing margin; area between MA and RP3/4 widened near posterior wing margin and developing eight rows of cells; MA and RP3/4 closely parallel, and somewhat distal of nodus, undulate; RP2 originating at subnodus; 2 lestine oblique cross-veins 'O'; no Rspl; area between IR2 and RP2 widened distally near posterior wing margin; IR2 gently curved; RP2 undulate a little basal of pterostigma; primary IR1 absent; a more or less zigzagged convex distal pseudo-IR1 (sensu Bechly, 1996) starting somewhat distal of pterostigma; 6–7 rows of cells in area between IR1 and RP2; 4 rows of cells in area between IR1 and RP1.

Discussion. – The Liassogomphidae were considered as "anisozygopteres" by Tillyard (1925, 1935), Tillyard & Fraser (1940), Fraser (1957), Carle (1982) and Carle & Wighton (1990). Cowley (1942) and Nel et al. (1993) included them in the Anisoptera. Bechly (1996) considered them as the sister group of the Aeschnidiidae, within the superfamily Aeschnidioidea sensu Bechly (1996), itself sister group of the Anisoptera. More recently, Bechly (1998) changed his mind and considered the Aeschnidiidae as the sister group of the modern Anisoptera, in the

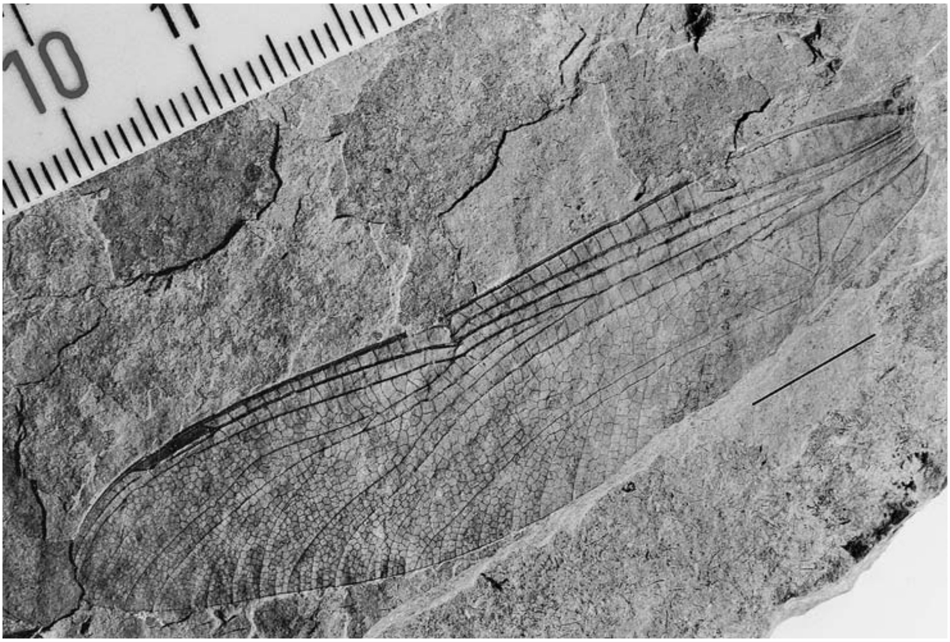

Fig. 2. *Juragomphus karatauensis* n. gen. n. sp., holotype specimen PIN 2997/4431, photo. Scale 10 mm.

Neoanisoptera Bechly, 1998. Fleck & Nel (submitted) argued against the potential synapomorphies of the Liassogomphidae with the Aeschnidiidae. After the same authors, the family Aeschnidiidae would fall within the more advanced Anisoptera – Cavilabiata, mainly on the basis of the larval characters (Please note that this view is not shared by the second author, Bechly, of the present paper who rather regards the spoon-shaped mask as a convergence within Aeschnidiidae). The exact affinities of the Liassogomphidae within the Anisoptera remain uncertain (Fleck & Nel, submitted).

Comparison with Anisoptera excluding Liassogomphidae:

Juragomphus n. gen. does not share the wing venational synapomorphies of the Aeschnidiidae, as listed in Bechly (1996): Discoidal triangle transversely elongate; subdiscoidal triangle hypertrophied; at least one secondary antenodal crossvein basal of Ax1; nodal furrow reduced; distinct Rspl and Mpsl present; pterostigma shifted basally.

It has none of the synapomorphies of the Aeshnoptera sensu Bechly (1996) or Bechly et al. (2001): (1) RP1 and RP2 basally parallel up to the pterostigma, with a single row of cells in-between; (2) at least, a weakly defined Rspl is present; (3) RP3/4 and MA more or less undulating. Note that these veins are no more undulating in *Juragomphus* than in *Liassogomphus*. *Juragomphus* shares with *Paramesuropetala gigantea* Bechly et al., 2001 (Aeshnoptera – Liupanshaniidae) a large equilateral discoidal triangle but they strongly differ in the presence of a Rspl, of a strong PsA, and of a straight CuP in *Paramesuropetala* (Bechly et al., 2001).

The Petalurida sensu Bechly, 1996 have the following forewing synapomorphies (Nel et al., 1998): (1) Postnodal space very narrow, with many cells distal of pterostigma; (2) primary IR1 very well defined; (3) wing space between RP1 and RP2 strongly expanded; (4) forewing pseudo-anal vein PsA hypertrophied; (5) subdiscoidal triangle widened, with many cross-veins. The characters (1), (2) and (4) are absent in *Juragomphus*. The characters (3) and (5) are convergently present in Aeschnidiidae (but more pronounced) and Liassic Liassogomphidae (but less pronounced). Thus, *Juragomphus* shares no strong synapomorphy with the Petalurida. Within this group, the Aktassiidae – Aktassiinae (*Aktassia* Pritykina, 1968 and *Aeschnogomphus* Handlirsch, 1906) also share with *Juragomphus* wings with many cells, a subequilateral forewing discoidal triangle, and the presence of two oblique veins 'O'. But the former two characters are likely convergences while the last character is a symplesiomorphy. Furthermore, they strongly differ in the three characters (2), (4), and (5).

The Exophytica sensu Bechly (1996) (= Gomphides + Cavilabiata) have only a weak wing venational synapomorphy, viz. "the second distal oblique vein 'O' obsolete" which is not so in *Juragomphus*. The Gomphides sensu Bechly (1996) have also a weak forewing synapomorphy, viz. the "supratriangle with a distinctly curved anterior margin", also absent in *Juragomphus*. The Cavilabiata have only one forewing synapomorphy, viz. the "cordulegastrid gap" which is absent in *Juragomphus*.

Comparison with the Liassogomphidae:

Bechly (1996) indicated that there is no known synapomorphy of the Liassogomphidae. Thus, it is rather difficult to attribute a species to this family. Etter & Kuhn (2000) proposed an emended diagnosis of the Liassogomphidae: (1) Pterostigma long; (2) antenodals and postnodals numerous; (3) upper side of discoidal triangle ending approximately below distal angle of supratriangle; (4) triangle crossed; (5) no true subtriangle present, but a more primitive crossed subquadrilateral cell; (6) pseudo-IR1 (IR1 sensu Etter & Kuhn, 2000) present (short, with its origin near the distal end of the pterostigma). This character seems to be a synapomorphy of the Anisoptera (including the Liassogomphidae) (after Fleck et al., submitted); (7) area between RP2 and IR2 very narrow near the lestine oblique vein 'O' (at least in the forewing); (8) hindwing with extensive area behind CuA reaching level of nodus; (9) male hindwing with anal angle. The characters (1), (2), (3), (5), (8) and (9) are symplesiomorphies of the Anisoptera, also present in the sister group Stenophlebioptera (Fleck & Nel, submitted). Thus, they are of little use. The character (7) seems to be an apomorphy of the Liassogomphidae (but also convergently present in the Cavilabiata – Araripelibellulinae Bechly, 1996). It is absent in *Juragomphus* n. gen.

Juragomphus n. gen. shares with the Liassogomphidae the following characters: (10) Presence of two infrasubdiscoidal cells beneath the anal vein, limited by a forward slanting secondary branch of AA. This character is convergently present in the Aeschnidiidae and some Libellulidae (*Diastatops*). It seems to be correlated to the large number of cells in the forewing basal half. Thus, we regard it as only a weak potential synapomorphy of *Juragomphus* with the Liassogomphidae; (11) absence of primary IR1. In the "heterophlebioid" lineage and the Stenophlebioptera, sister group of the Anisoptera, IR1 is present. Thus its complete reduction could be a synapomorphy of *Juragomphus* with the Liassogomphidae; (12) CuP distinctly curved. In the most basal lineages of the Epiproctophora, i.e. Epiophlebiidae, Isophlebioptera, the "heterophlebioid" lineage, the Liassic Anisoptera – Liassogomphidae and some Gomphidae and Aeshnidae (but less pronounced), the vein CuP is strongly curved and seems to begin on AA rather than on MP + Cu. The same character is present in Tarsophlebiidae and in the Cenozoic family Sieblosiidae HANDLIRSCH, 1906 of rather uncertain position (FLECK et al., in prep.). Thus the character "CuP strongly curved" is probably a symplesiomorphy within the Anisoptera; (13) no Rspl. This is probably a plesiomorphy, as this vein is absent in both the Stenophlebioptera and the "heterophlebioid" lineage; (14) no Mspl. This character is rather homoplastic in the Stenophlebioptera and the "heterophlebioid" lineage (FLECK et al., submitted). Thus its polarity within the Anisoptera remains uncertain; (15) triangular-shaped and broad subdiscoidal space, limited by a weak PsA vein. This is probably plesiomorphic as very similar to the situation in the Stenophlebioptera, sister group of the Anisoptera (FLECK et al., submitted); (16) forewing discoidal triangle rather transverse. The polarity of this character is uncertain and it is subject to numerous homoplasies within the different anisopterid lineages.

Furthermore, *Juragomphus* differs from the Liassogomphidae in the following characters: (17) Forewing discoidal triangle equilateral and very broad, very different of those of the Liassogomphidae. Note that similar equilateral triangles are convergently present in Aeshnoptera, Petalurida and in the Cavilabiata Eocene family Palaeomacromiidae (PETRULEVICIUS et al., 1999); (17) two lestine oblique veins 'O', instead of one. This plesiomorphic character is also highly homoplastic within the clade [Stenophlebioptera + Anisoptera] (FLECK & NEL, submitted). As example, the Stenophlebiidae have no oblique veins but the Liassostenophlebiidae FLECK & NEL (nomen nudum) have one; (18) second primary antenodal crossvein distinctly weaker than Ax1, unlike the Liassic Liassogomphidae; (19) pterostigma covering six cells, instead of two or three in the Liassic taxa; (20) wing distinctly longer than those of the Liassogomphidae (forewing 70 mm long compared to only 40 to 50 mm in Liassogomphidae).

In conclusion, *Juragomphus* shares several characters with the Liassogomphidae which are probably all symplesiomorphies of the Anisoptera. Several important differences with the Liassogomphidae justify its attribution to a new family Juragomphidae n. fam. Its affinities within the Anisoptera are not clear, but it has probably a very basal position since it shares no synapomorphies with any of the modern anisopterid lineages, except for the following character: In *Juragomphus* there is a broad and long membranule, as in modern Anisoptera, but not in Liassogomphidae and more basal taxa ("heterophlebioid" and stenophlebioid lineages). This could support a more advanced position than that of the Liassogomphidae within Anisoptera.

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4. References

BECHLY, G. (1996): Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata), unter besonderer Berücksichtigung der Phylogenetischen Systematik und des Grundplanes der *Odonata. – Petalura, Special Volume, **2**, 402 pp.; Böblingen.

– (1998): A revision of the fossil dragonfly genus *Urogomphus*, with description of a new species. – Stuttgarter Beitr. Naturk., B, **270**: 1–47; Stuttgart.

BECHLY, G., NEL, A., MARTÍNEZ-DELCLÒS, X., JARZEMBOWSKI, E. A., CORAM, R., MARTILL, D., FLECK, G., ESCUILLIÉ, F., WISSHAK, M.M. & MAISCH, M. (2001): A revision and phylogenetic study of Mesozoic Aeshnoptera, with description of several new families, genera and species (Insecta: Odonata: Anisoptera). – N. Paläont. Abh., **4**, 219 pp.; Dresden.

BODE, A. (1953): Die Insektenfauna des ostniedersächsischen oberen Lias. – Palaeontographica, (A), **103**: 1–375; Stuttgart.

CARLE, F. L. (1982): The wing vein homologies and phylogeny of the Odonata: a continuing debate. – S.I.O. Rapid Comm., **4**: 1–66; Utrecht.

CARLE, F. L. & WIGHTON, D. C. (1990): Chapter 3. Odonata. pp. 51–68. – *In*: GRIMALDI, D. A. (ed.): Insects from the Santana Formation, Lower Cretaceous, of Brazil. – Bull. Amer. Mus. nat. Hist., **195**, 191 pp.; New York.

CARPENTER, F. M. (1992): Superclass Hexapoda. – *In*: MOORE, R. C. & KAESLER, R. L. (eds): Treatise on Invertebrate Paleontology. (R), Arthropoda 4, **3–4**, xxii + 655 pp.; Boulder & Lawrence (Geological Society of America & University of Kansas).

COWLEY, J. (1935): Nomenclature of Odonata: three generic names of Hagen. – Entomologist, **68**: 283–284; London.

– (1942): Descriptions of some genera of fossil Odonata. – Proc. R. ent. Soc. London, (B), **11**: 63–78; London.

ETTER, W. & KUHN, O. (2000): An articulated dragonfly (Insecta, Odonata) from the Upper Liassic Posidonia shale of Northern Switzerland. – Palaeontology, **43**/5: 967–977; London.

FLECK, G. & NEL, A. (submitted): Revision of the Mesozoic family Aeschnidiidae (Odonata: Anisoptera). – Zool. J. linn. Soc.; London.

FLECK, G., NEL, A., BECHLY, G., MARTÍNEZ-DELCLÒS, X., JARZEMBOWSKI, E. A. & CORAM, R. (submitted): Phylogeny and classification of the Stenophlebioptera. (Insecta, Odonata, Epiproctophora). – Ann. Soc. ent. France; Paris.

FLECK, G., NEL, A., MARTÍNEZ-DELCLÒS, X., JARZEMBOWSKI, E. A. & BECHLY, G. (in prep.): New Mesozoic Tarsophlebiidae, with a discussion on the phylogenetic positions of the Tarsophlebiidae and Sieblosiidae (Odonatoptera: Panodonata).

FRASER, F. C. (1957): A reclassification of the order Odonata, based on some new interpretations of the venation of the dragonfly wing. – Handbook R. zool. Soc. N. S. Wales, **12**: 1–133; Sydney.

KUKALOVÁ-PECK, J. (1991): Chapter 6: Fossil history and the evolution of hexapod structures. – *In*: NAUMANN, I. D. (ed.): The insects of Australia, a textbook for students and research workers (2nd ed.), **1**, 542 pp.; Melbourne (Melbourne University Press).

MOSTOVSKI, M. B. & MARTÍNEZ-DELCLÒS, X. (2000): New Nemestrinoidea (Diptera: Brachycera) from the Upper Jurassic – Lower Cretaceous of Eurasia, taxonomy and palaeobiology. – Entomological Problems, **31**/2: 137–148; Bratislava.

NEL, A., BECHLY, G., MARTÍNEZ-DELCLÒS, X. & JARZEMBOWSKI, E.A. (1998): A new revision of the Recent and fossil Petaluridae (Insecta, Odonata, Anisoptera). – Paleontologia Lombarda, (N.S.), **10**: 1–68; Milano.

NEL, A., MARTÍNEZ-DELCLÒS, X., PAICHELER, J.-C. & HENROTAY, M. (1993): Les “Anisozygoptera” fossiles. Phylogénie et classification. (Odonata). – Martinia, numéro hors série, **3**: 1–311; Bois d’Arcy.

PETRULEVICIUS, J. F., NEL, A. & MUZON, J. (1999): A new libelluloid family in the Palaeocene of Argentina. – Palaeontology, **42**: 677–682; London.

REN, D. (1994): A new genus and species of Liassogomphidae (Insecta, Odonata) from Late Jurassic of Liaoning province, China. – Geoscience, **8**/3: 254–258; Beijing.

RIEK, F. & KUKALOVÁ-PECK, J. (1984): A new interpretation of dragonfly wing venation based upon early Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wings. – Can. J. Zool., **62**: 1150–1166; Ottawa.

Tillyard, R. J. (1925): The British Liassic dragonflies. – British Museum Fossil Insects, **1**: 1–39; London.

– (1935): Upper Permian insects of New South Wales. 4. The order Odonata. – Proc. linn. Soc. N. S. Wales, **60**: 374–384; Sydney.

Tillyard, R. J. & Fraser, F. C. (1940): A reclassification of the order Odonata based on some new interpretations of the venation of the dragonfly wing. – Aust. Zool., **9**: 124–396; Sydney.

Zherikhin, V. V. & Gratshev, V. G. (1993): Obrieniidae, fam. n., the oldest Mesozoic weevils (Coleoptera, Curculionoidea). – Paleont. J., **27**/1A: 50–69; Washington.

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