

New griffenfly, *Bohemiatus elegans* from the Late Carboniferous of western Bohemia in the Czech Republic (Odonoptera: Meganisoptera: Meganeuridae)

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Abstract. A new griffenfly, *Bohemiatus elegans* n. gen., n. sp. (Meganeuridae) is described from the Upper Carboniferous (Bolsovian) deposits of the Ovčín near Radnice in western Bohemia (Czech Republic). The new taxon based on fore- and hindwing venation is compared with the other meganeurid genera. It is the first record of a large griffenfly from the continental basins of the Bohemian Massif supplementing the other giant insects such as *Bojophlebia prokopi* Kukalová-Peck 1985 or *Carbotriplura kukalovae* Kluge 1996 from the same strata.

Résumé. Une nouvelle « libellule géante », *Bohemiatus elegans* du Carbonifère supérieur de la Bohême de l'ouest (République Tchèque) (Odonoptera: Meganisoptera : Meganeuridae). Un nouveau genre et une nouvelle espèce de Meganeuridae (Meganisoptera), *Bohemiatus elegans* n. gen., n. sp. est décrit du Carbonifère supérieur d'Ovčín près de Radnice (ouest de la Bohême, République Tchèque). Ce nouveau taxon est basé sur la nervation des ailes antérieures et postérieures. Il est comparé aux autres Meganisoptera décrits. Il s'agit de la première « libellule géante » des bassins continentaux du massif de Bohême, mais pas du premier insecte géant des mêmes aire et étage (*Bojophlebia prokopi* Kukalová-Peck 1985, *Carbotriplura kukalovae* Kluge 1996).

Keywords: Taxonomy, Tupindae, Insecta, Bolsovian, Radnice Basin, Paleozoic.

Paleozoic odonatopteran order Meganisoptera Martynov 1932 (so-called 'Protodonata') represents the 'stem group' to true Odonata. However, the members of Meganisoptera differ from Odonata by absence of nodus and pterostigma in wing venation, as well as males lacking secondary genitalia (Bechly *et al.* 2001). Above all, this group is well known for the insects with largest wingspan that have ever lived such as *Meganeuropsis permiana* Carpenter 1939 from Early Permian of Kansas that reached wingspan more than 700 mm (Carpenter 1939, 1947).

The clade Odonatoptera is first recorded about 320 million years ago in the Namurian, and its main subgroups Odonatoclada Bechly, 2003 (= the clade that comprises the Lapeyriidae Nel *et al.* 1999, the Campylopteridae Tillyard 1928 and the Nodialata Bechly 1996 viz. the Odonatoptera with a true nodus), Meganisoptera, and Geroptera Brodsky 1994 suddenly appeared in Westphalian (Brauckmann & Zessin 1989; Riek & Kukalová-Peck 1984; Jarzembowski and Nel 2002). Meganisoptera are not very frequent in the fossil record of Namurian and Westphalian deposits, viz.

the Westphalian *Carpentertypus durhami* (Carpenter 1960), *Piesbergtypus hielscheri* Zessin 2006, *Arctotypus diluculum* (Whalley 1980), *Palaeotherates pennsylvanicus* Handlirsch 1906, and *Gallotupus oudardi* Nel *et al.* 2008; and the Namurian *Sinomeganeura huangheensis* Prokop *et al.* 2008, *Shenzhousia qilianshanensis* Zhang *et al.* 2006, and *Namurotypus sippeli* Brauckmann & Zessin 1989 (Zessin 2006; Zhang *et al.* 2006; Ren *et al.* 2008; Nel *et al.* 2008, 2009).

The continental basins of the Bohemian Massif are represented by a number of insect localities ranging in age from the Duckmantian (Westphalian B) to the Middle Stephanian. In the central and western Bohemia the most famous localities are in the Radnice Member of Bolsovian age (Westphalian B-C), which involves localities like Lubná, Příčina, Štílec, Vrapice and Otovice or in the Nýřany Member of the Asturian age where Nýřany and Třemošná belong among the most famous ones. Predominance of the Blattodea is significant in Nýřany and Lubná (Kušta 1883; Fritsch 1901; Handlirsch 1920; Kukalová 1955), while others are represented by single records of palaeopterous insects (Ephemeroptera, Paleodictyoptera), (Fritsch 1880; Kukalová 1958; Kukalová-Peck 1985; Novák 1880).

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Accepté le 15 janvier 2010

New insect material was recently discovered at Ovčín near Radnice during extensive excavations by palaeobotanists in tuff layers so called „whetstone horizon“ from the roof of the Lower Radnice Seam (Lower Bolsovian) with well known buried plants preserved *in situ* (see Opluštil *et al.* 2007, 2009; Libertín *et al.* 2009). Insect fauna is very rare with two other undescribed specimens of palaeodictyopterid larvae and orthopteroid insect (Prokop unpubl.).

Material and methods

The fossil specimen was observed under stereomicroscopes Zeiss Cytoplast in dry state and under ethyl alcohol. Due to large dimensions of the specimen the venation pattern line drawing was redrawn from color photograph and revised by parallel observation under stereomicroscope. Drawing was finally readjusted to the photograph scale using of graphic software (Adobe Photoshop). Photographs were made in dry state and

under ethyl alcohol by digital camera Nikon D80 with macro lens Nikon AF-S VR Micro-Nikkor 105 mm in the highest contrast as possible by single sided cross-light pre-exposure.

Type material was collected in 2006 during extensive excavations by group of palaeobotanists so called “Czech mafia” in Ovčín near Radnice and housed in the collection of West Bohemian Museum in Plzeň, Czech Republic.

We use the wing venation nomenclature of Nel *et al.* (1993), and Bechly (1996). Systematic and divisions follows the concept of higher phylogenetic classification of Odonatoptera proposed by Bechly (1996, 2007).

The venational symbols used here specified as follows: symbols in capitals denote the longitudinal veins (CA / CP – costal anterior / posterior, ScA / ScP – subcostal anterior / posterior, RA / RP – radial anterior / posterior, IR – intercalary radial posterior, MA / MP – medial anterior / posterior, CuA / CuP – cubital anterior / posterior, AA – anal anterior).

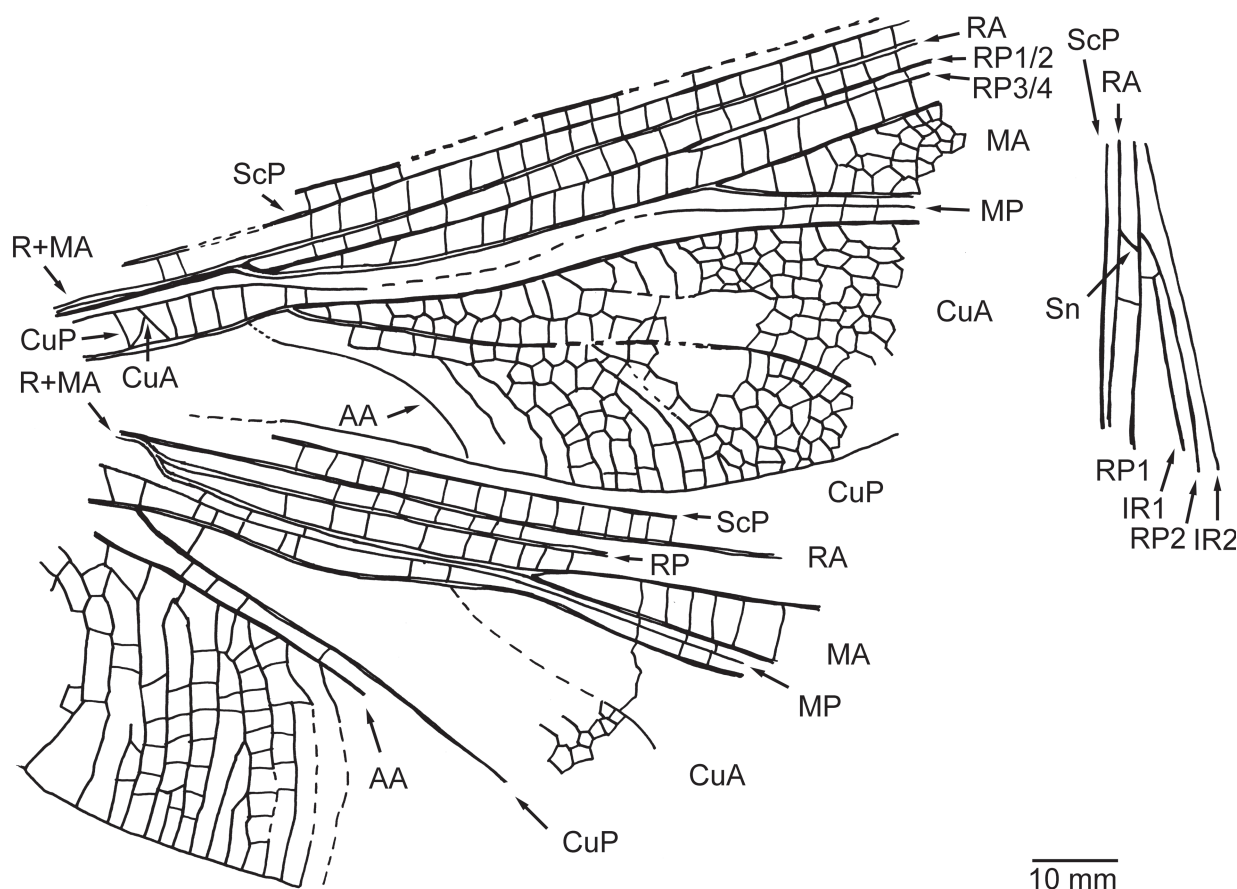


Figure 1

Bobemiatupus elegans n. gen., n. sp. (Meganeuridae), holotype M00485 (negative imprint) – line drawing of fore- and hindwing venation, isolated apical part drawn as preserved.

Results

Superorder Odonatoptera Martynov 1932

Order Meganisoptera Martynov 1932

Family Meganeuridae Handlirsch 1906

Subfamily Tupinae Handlirsch 1919

Genus *Bohemiatus* n. gen.

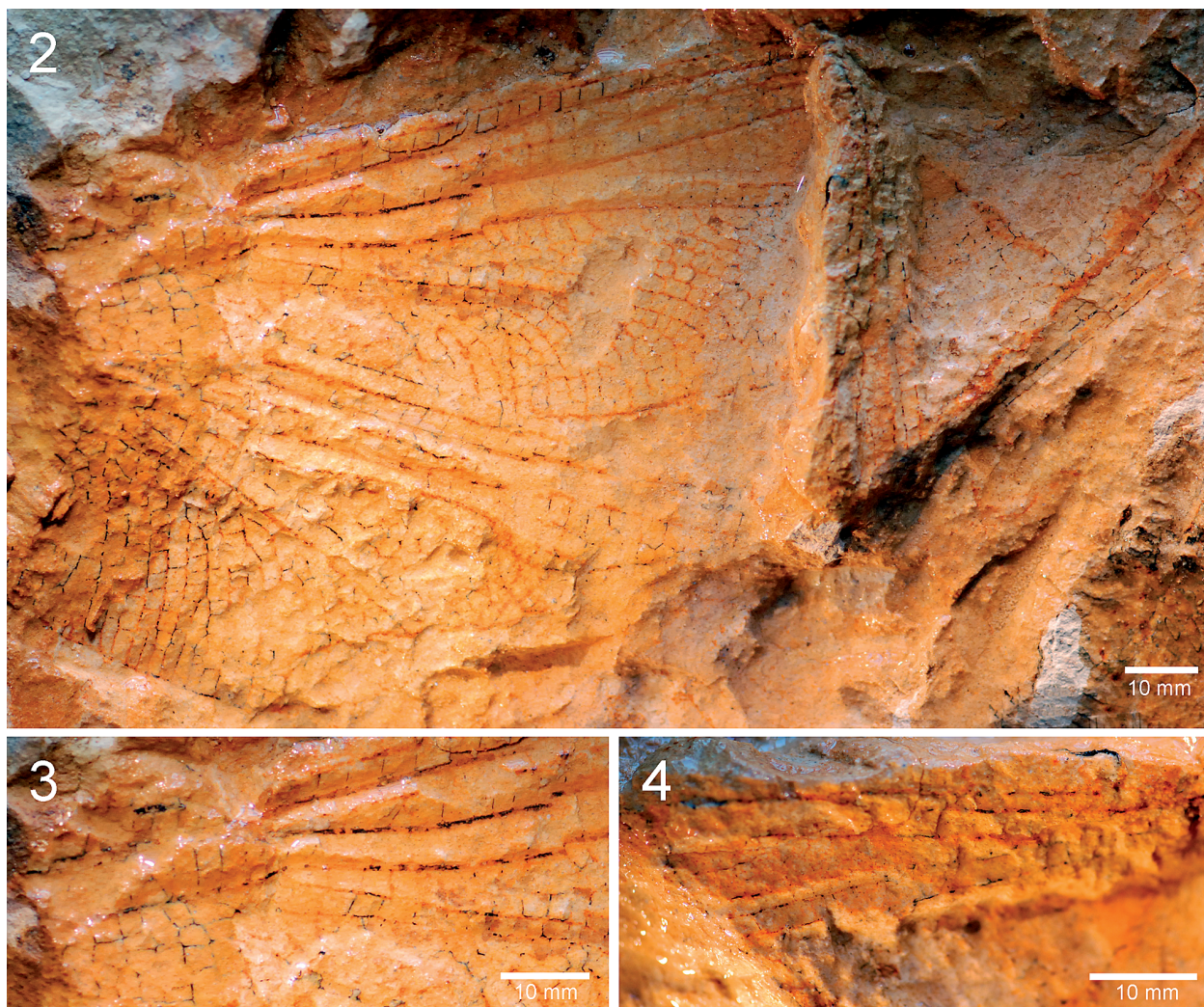
Type species. *Bohemiatus elegans* n. sp.

Etymology. Composite name after Bohemia (historical region in central Europe, occupying the western two-thirds of the traditional Czech Lands, currently the Czech Republic) and *Tupus* (genus name), masculine in gender.

Diagnosis. ScA short; ‘subnodus’ present between RA and RP near base of RP2; parts of CuA and CuP between MP and AA separated and oblique, with only one cells between them; AA1 with posterior branches; CuP very long and straight, with more than three concave branches, but area covered by posterior branches of CuP distinctly narrower than those of CuA and AA1; hind wing distinctly broader and with anal and cubito-anal areas distinctly broader than in forewing.

Bohemiatus elegans n. sp. (Figs. 1–4)

Holotype. Specimen M00485, well preserved basal and medial part of fore- and hindwing, apical part of fore wing distorted and medioapical part of hindwing not preserved, negative imprint, collection of West Bohemian Museum in Plzeň, Czech Republic.



Figures 2–4

Bohemiatus elegans n. gen., n. sp. (Meganeuridae), holotype M00485 (negative imprint). 2, photograph of wing venation, ventral view; 3, detail photograph of basal part of forewing; 4, detail photograph of forewing isolated apical part.

Derivation of name. Named after magnificent state of preservation, *elegans* in Latin.

Type locality. Ovčín opencast mine near Radnice, Radnice Basin, Czech Republic

Type strata. Upper Carboniferous, Westphalian B-C, Bolsovian, Kladno Formation, Radnice Member, Lower Radnice Coal, Whetstone Horizon.

Description. Negative imprint of a fore and a hindwing in life position, probably hyaline. Forewing broadest part at about midwing; length of fragment to first distortion break about 115 mm, probable total length about 260 mm; wing width 49 mm; estimate ratio (wing length/width) about 5.3; precostal area of CA and CP not preserved, but ScA is certainly short as it is absent above arculus level; simple concave ScP nearly parallel to anterior wing margin, and reaching it in apical part of wing, at least distal of 190 mm from wing base, but extreme apex of ScP not preserved; nine visible ‘antenodal’ cross-veins in area between ScP and C, more or less aligned with cross-veins in area between ScP and RA; the most basal cross-vein perpendicular to C, ScP, and RA, stronger than others ‘antenodals’, and making a distinct brace corresponding to the primary antenodal cross-vein Ax0 not preserved; ‘subnodus’ between RA and RP near base of RP2; stem of radial veins dividing 34 mm from wing base forming ‘arculus’, RA strong, simple, parallel to ScP, and ending probably in wing apex; R and MA fused in their basal parts; RP bifurcating into RP1/2 and RP3/4 88 mm from wing base; only basal part of RP3/4 preserved, simple; IR2 and other distal branches of RP partly preserved on isolated apical part; MA nearly straight with its most basal posterior branches partly preserved, first opposite bifurcation between RP1/2 and RP3/4; only fragments of MP vein preserved and visible at level of arculus, its medial part being hidden under rock, but MP probably simple; at least CuA forming strongly oblique cross-vein but remains of an oblique cross-vein CuP also visible in area between MP and AA, CuP 15 mm from wing base, CuA one cell distally; CuP separating from CuA 36 mm from wing base and six cells distal of CuP-crossing; distal part of CuA with numerous main posterior branches; CuP very long and rather straight, with four main simple posterior branches covering a relatively small area, basal part before its first furcation long and straight, about 4 mm long, width of area of CuP along posterior wing margin 51 mm; distal part of AA forming a relatively large are, width of this are along posterior wing margin 49 mm; basal part of AA (+ Cu) forming a very weak curve; anal and cubito-anal areas rather broad, 17 mm wide, with numerous posterior branches.

The preserved parts of the hindwing are very similar to the forewing in pattern of venation except for the cubito-anal area, hindwing slightly broader than forewing; length of wing fragment about 85 mm, probable total length as about fore wing; wing width 50 mm; estimated ratio (wing length/width) 5.2; anal and cubito-anal areas distinctly broader than in the fore wing, 30 mm wide; preserved basal part of CuP long and nearly straight but distal part not preserved; distal part of AA forming a relatively large area with 8–9 main posterior branches.

Discussion

This Odonatoptera is clearly related to the Meganisoptera that comprises the ‘families’ Namurotypidae Bechly 1996, Meganeuridae Handlirsch 1906, Kohlwaldiidae Guthörl 1962, and Paralogidae Handlirsch 1906. Relationships with the Namurotypidae are excluded because *Bohemiatus n. gen.* has a distally branched CuP, instead of being simple. The Paralogidae have a long and straight CuP as in *Bohemiatus n. gen.*, but with numerous branches covering a broader area than CuA and distal branch of AA. The Kohlwaldiidae are characterized by having the distal parts of CuP and AA strongly reduced, which is not the case of *Bohemiatus n. gen.* (Nel *et al.* 2009). The Meganeuridae are characterized by the presence of a typical ‘subnodal’ oblique vein between RA and RP near the base of RP2, which is preserved in our fossil. The very large size of *Bohemiatus n. gen.* supports affinities with this family even if several Meganeuridae have distinctly smaller dimensions (Nel *et al.* 2009). *Bohemiatus n. gen.* cannot be attributed to the Meganeurinae because its vein ScA is short. The Carpentertypinae Zessin 1983 [type genus *Carpentertypus* Zessin 1983, based on one species *C. durhami* (Carpenter 1961)] is based on a very fragmentary fossil, with no information on any of the basal halves of the wings. Nevertheless it differs from *Bohemiatus n. gen.* in its distinctly less numerous cells and narrower area covered by MA. The Piesbergitupinae Zessin 2006 (type genus *Piesbergitupus* Zessin 2006) is characterized by the narrow anal area of fore wing and presence of one oblique cross-vein distal of the oblique braces CuP and CuA and basal of the distal branch of CuP re-emerging from CuA+CuP, plus the long CuP and AA1 (Zessin 2006, 2008; Nel *et al.* 2009). The pattern of wing venation of *Bohemiatus n. gen.* fits very well with the Tupinae. The monophyly of this last group is not very clearly established (Bechly 1996; Nel *et al.* 2009), but we can now restrict the comparison of *Bohemiatus n. gen.* to the genera that are currently attributed to it. After the key to the tupine genera of Nel *et al.* (2009), *Bohemiatus n. gen.* would fall

near the Permian genus *Tupus* Sellards 1906 because of the following characters: the two braces CuP and CuA oblique, not fused into a long, oblique vein; AA1 with several posterior branches; and CuP with more than three concave branches. *Bohemiatus n. gen.* greatly differs from *Tupus* in its hindwing cubito-anal area distinctly broader than that of fore wing. Some 'enigmatic' genera are based on incomplete wings, i.e. the Carboniferous genera *Shenzhousia* Zhang *et al.* 2006 and *Boltonites* Handlirsch 1919, and the Permian *Petrotypus* Zalessky 1950. *Petrotypus* needs a complete redescription, and it is based on a very poor fossil. Nevertheless, its CuP seems to be simple and very straight after Zalessky (1950), unlike *Bohemiatus n. gen.* *Shenzhousia* shares with *Bohemiatus n. gen.* a very long and straight CuP but with numerous posterior branches covering a broad area, unlike *Bohemiatus n. gen.* (Zhang *et al.* 2006). After the figure of Bolton (1922: fig. 44), *Boltonites* has a distinctly curved CuP, shorter than that of *Bohemiatus*.

Conclusions

Bohemiatus n. gen. is established for *Bohemiatus elegans n. sp.* (type species) that exhibits unique combination of characters within Meganeuridae. The present discovery represent the first record of large griffenfly from the continental basins of the Bohemian Massif supplementing the other giant insects such as *Bojophlebia prokopi* Kukalová-Peck 1985 or *Carbotriplura kukalovae* Kluge 1996 from the same strata.

Moreover, the material from Ovčín near Radnice represents an extraordinary source of fossil plants *in situ* and other animals like arachnid, fish and amphibian trace fossils those enable study of developed peat mire ecosystem into a shallow lake gradually filled by redeposited volcanic ash from Bolsavian of western Bohemia (Czech Republic).

Acknowledgements. The authors are grateful to Radek Labuřa (National Museum in Praha) who discovered the present specimen and to group of the Czech paleobotanists so called "Czech mafia" for large excavations at Ovčín locality. We especially thank to Josef Pšenička (West Bohemian Museum in Plzeň) for the loan of the material. The first author (JP) acknowledges the research support from the Grant Agency of Academy of the Czech Republic No. KJB301110701 and Ministry of Schools MSM 0021620828. We sincerely thank Dr Gunther Fleck for his useful comments on the first version of the paper.

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* Böblingen Special Volume 2: 1-402.
- Bechly G. 2007. *Phylogenetic systematics of Odonata*. Homepage on Internet. <http://www.bernstein.naturkundemuseum-bw.de/odonata/index.htm>
- Bechly G., Brauckmann C., Zessin W., Gröning E. 2001. New results concerning the morphology of the most ancient dragonflies (Insecta: Odonoptera) from the Namurian of Hagen-Vorhalle (Germany). *Zeitschrift für Zoologische Systematik und Evolutionsforschung* 39: 209-226.
- Bolton H. 1922. A monograph of the fossil insects of the British coal measures. *Palaeontographical Society Monograph* London 74: 81-156.
- Brauckmann C., Zessin W. 1989. Neue Meganeuridae aus dem Namurium von Hagen-Vorhalle (BDR) und die Phylogenie des Meganisoptera. *Deutsche Entomologische Zeitschrift* (N.F.) 36: 177-215.
- Carpenter F.M. 1939. The Lower Permian insects of Kansas. Part 8. Additional Megasecoptera, Protodonata, Odonata, Homoptera Psocoptera, Plecoptera, and Protoperlaria. *Proceedings of the American Academy of Arts and Sciences* 73: 29-70.
- Carpenter F.M. 1947. Lower Permian insects from Oklahoma. Part 1. Introduction and the orders Megasecoptera, Protodonata, and Odonata. *Proceedings of the American Academy of Arts and Sciences* 76: 25-54.
- Fritsch A. 1880. Dva noví členovci z útvaru kamanouhelného v Čechách [Two new arthropods from the coal system in Bohemia.]. *Vesmír* 9: 241-242.
- Fritsch A. 1901. Fauna der Gaskohle und der Kalksteine der Permformation Böhmens. Bd. IV, Prag, 92 pp.
- Handlirsch A. 1920. Beiträge zur Kenntnis der Palaeozoischen Blattarien. *Sitzungsberichte der Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse*, Wien, (1), 129: 8.
- Jarzemkowski E. A., Nel A. 2002. The earliest damselfly-like insect and the origin of modern dragonflies (Insecta: Odonoptera: Protozygoptera). *Proceedings of the Geologist's Association* 113: 165-169.
- Kukalová J. 1955. *Permoedischia n. gen.* (Protorthoptera) a *Moraviptera n. gen.* (Palaeodictyoptera) z moravského permu. *Sborník Ústředního Ústavu Geologického, oddíl Paleontologický* 21: 541-575.
- Kukalová J. 1958. Paoliidae Handlirsch (Insecta, Protorthoptera) aus dem Oberschlesischen Steinkohlenbecken. *Geologie* 7: 935-959.
- Kukalová-Peck J. 1985. Ephemeroid wing venation based upon new gigantic Carboniferous mayflies and basis morphological phylogeny and metamorphosis of pterygote insects (Insecta, Ephemerida). *Canadian Journal of Zoology* 63: 933-955.
- Kušta J. 1883. Über einige neue böhmische Blattinen. *Sitzungsberichte Königlich Böhmisches Gesellschaft Wissenschaften*, Pragae 1883: 211-215.
- Libertín M., Opluštil S., Pšenička J., Bek J., Sýkorová I., Dašková J. 2009. Middle Pennsylvanian pioneer plant assemblage buried in situ by volcanic ash-fall, central Bohemia, Czech Republic. *Review of Palaeobotany and Palynology* 155(3-4): 204-233.
- Nel A., Garrouste R., Roques P. 2008. A new griffenfly genus from the Late Carboniferous of northern France (Odonoptera: Meganeuridae). *Insect Systematics & Evolution* 39: 231-239.
- Nel A., Fleck G., Garrouste R., Gand G., Lapeyrie J., Bybee S.M., Prokop J. 2009. Revision of Permo-Carboniferous griffenflies (Insecta: Odonoptera: Meganisoptera) based upon new species and redescription of selected poorly known taxa from Eurasia. *Palaeontographica* (A) 289: 89-121.
- Nel A., Martínez-Declos X., Paicheler J.-C., Henrotay M. 1993. Les 'Anisozygoptera' fossiles. Phylogénie et classification (Odonata). *Martinia* Numéro Hors Série 3: 1-311.
- Novák O. 1880. Ueber Gryllacris Bohemica, einen neuen Locustidenrest aus der Steinkohlenformation von Stradonitz in Böhmen. *Jahrbuch der k.k. Geologischen Reichsanstalt* 30: 69-75.
- Opluštil S., Pšenička J., Libertín M., Šimůnek Z. 2007. Vegetation patterns of Westphalian and Lower Stephanian mire assemblages preserved in tuff beds of the continental basins of Czech Republic. *Review of Palaeobotany and Palynology* 143: 107-154.
- Opluštil S., Pšenička J., Libertín M., Bashforth A.R., Šimůnek Z., Drábková J., Dašková J. 2009. A Middle Pennsylvanian (Bolsavian) peat-forming forest preserved in situ in volcanic ash of the Whetstone Horizon in the Radnice Basin, Czech Republic. *Review of Palaeobotany and Palynology*, 155 (3-4): 234-274.

- Ren D., Nel A., Prokop J. 2008.** New early griffenfly, *Sinomeganeura huangheensis* from the Late Carboniferous of northern China (Meganisoptera: Meganeuridae). *Insect Systematics & Evolution* **38**: 223-229.
- Riek E.F., Kukalová-Peck J. 1984.** A new interpretation of dragonfly wing venation based upon Early Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic characters states in pterygote wings. *Canadian Journal of Zoology* **62**: 1150-1166.
- Zalessky G. 1950.** [New representatives of fossil insects of order Protodonata.] *Byulleten Moskovskogo obshchestva ispytatelej Prirody, otdel Geologicheskii* **25**: 98-108. [in Russian].
- Zessin W. 2006.** Zwei neue Insektenreste (Megasecoptera, Odonatoptera) aus dem Westfalium D (Oberkarbon) des Piesberges bei Osnabrück, Deutschland. *Virgo, Mitteilungsblatt des Entomologischen Vereins Mecklenburg* **9**: 37-45.
- Zessin W. 2008.** Überblick über die paläozoischen Libellen (Insecta, Odonatoptera). *Virgo, Mitteilungsblatt des Entomologischen Vereins Mecklenburg* **11**: 5-32.
- Zhang Z.-J., Hong Y.-C., Lu L.-W., Fang X.-S., Jin Y.-G. 2006.** *Shenzhousia qilianshanensis* gen. et sp. nov. (Protodonata, Meganeuridae), a giant dragonfly from the Upper Carboniferous of China. *Progress in Natural Science* **16**: 328-330.