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A new genus and species of Homoiopteridae from the Upper Carboniferous of the Intra-Sudetic Basin, Czech Republic (Insecta: Palaeodictyoptera)

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Abstract. New palaeodictyopterid *Paraostrava stanislavi* gen. n., sp. n. is described from the Upper Carboniferous (Duckmantian) deposits of the Jan Šverma Mine in northern Bohemia (Czech Republic). The new taxon based on hindwing venation is attributed to Homoiopteridae and compared with the other homoiopterid and heolid genera within Homoiopteroidea. Due to the poor state preservation of *Boltopruvostia robusta*, we consider this taxon as Palaeodictyoptera: Homoiopteridae of uncertain position and restore the well defined genus *Ostrava* Kukalová, 1960 (type species *Ostrava nigra* Kukalová, 1960). Some uncertainties in the current state of knowledge on the taxonomy and phylogeny of the Homoiopteridae are pointed out. The characters matrix used to separate the genera of Homoiopteroidea is included.

INTRODUCTION

The fossil insect order Palaeodictyoptera Goldberg, 1854 within superorder Dictyoneuridea Handlirsch, 1906 (Palaeodictyopteroida sensu Bechly, 1996) represents a widely diverse group of Palaeozoic insects ranging from the Lower Carboniferous (Namurian A) through Permian up to the Lower Triassic (Middle "Buntsandstein" by single record of *Thuringopteryx gimmi* Kuhn, 1937) with a peak of abundance in the Upper Carboniferous (Bechly, 1997; Sinitshenkova, 2002). Palaeodictyopteran insects with a distribution mainly restricted to the tropical belt of the northern hemisphere are commonly found in Euroamerican Upper Palaeozoic deposits, which indicate their probable thermophily (Sinitshenkova, 2002). The taxon Palaeodictyoptera is considered to be paraphyletic after Bechly (1996). Because of this state, it is necessary to revise the described species in the perspective of a future phylogenetic study of this group. But many species are based only on more or less complete wings. Thus, such analysis may be very difficult to achieve. Further orders of Palaeodictyopteroida like Megasecoptera, Diaphanopterodea and Permothemistida differ clearly in wing venation patterns and are therefore likely to be monophyletic groups (Grimaldi, 2001). We follow the wing venation terminology of Kukalová-Peck (1991). The systematics of Palaeodictyoptera is mainly based on the work of Sinitshenkova (2002), partly adapted from Riek (1976). Both systems are critically reviewed and discussed on the current position of Homoiopteridae.

The Intra-Sudetic Basin is a NW-SE extending structure situated in the northern part of former Bohemia (Czech Republic) (see Fig. 1). The major part of this basin lies in the territory of Poland while a narrow prominence is located in Žacléř surroundings and Broumov in the Czech Republic. The basin is filled with Lower Carboniferous to Triassic continental sediments (Spudil, 1999). Generally, the overlying deposits of Šverma mine group seams are of fluvial origin. Zoopalaeontological and phytopalaeontological records were reviewed by Tásler et al. (1979).

TAXONOMIC PART

Family Homoiopteridae Handlirsch, 1906

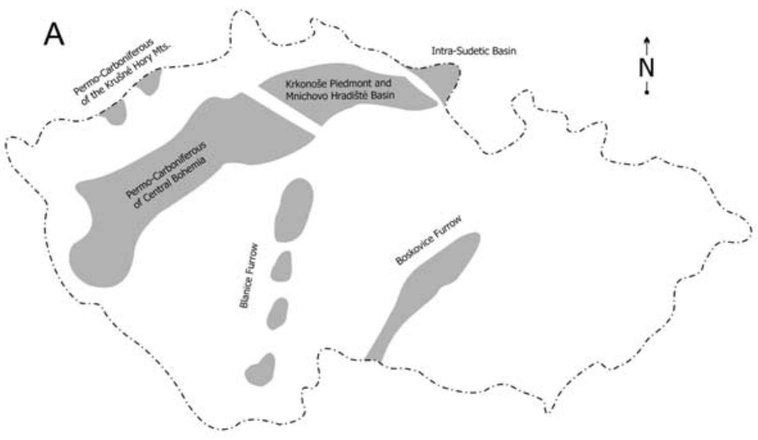
List of genera after Carpenter (1992) supplemented by Brauckmann & Becker (1992)*:

Adolarryia Kukalová-Peck & Richardson, 1983; *Ametretus* Handlirsch, 1911*; *Amousus* Handlirsch, 1911*; *Boltopruvostia* Strand, 1929; *Homoioptera* Brongniart, 1893; *Larryia* Kukalová-Peck & Richardson, 1983; *Mammia* Handlirsch, 1906*; *Mazonopterum* Kukalová-Peck & Richardson, 1983; *Mazothairos* Kukalová-Peck & Richardson, 1983; *Parathesoneura* Sinitshenkova, 1977; *Scepasma* Handlirsch, 1911*; *Thesoneura* Carpenter, 1944; *Turneropterum* Kukalová-Peck & Richardson, 1983.

Genus *Paraostrava* gen. n.

Type species. *Paraostrava stanislavi* sp. n. by present description.

Diagnosis. Homoiopterid genus; based on hind wing venation; *Paraostrava* gen. n. differs from all other homoiopterid genera by combination of the following characters: RA and RP diverging distally of division M into MA and MP; basal part of RP not very long; area between RP and RA with numerous long sigmoidal veinlets, twice as wide as that between RP and MA; MA simple; MP with seven branches; CuA with two weak branches; CuP with two branches; reticulate venation (so-called "archedictyon") reduced but still present through numerous irregular cells.



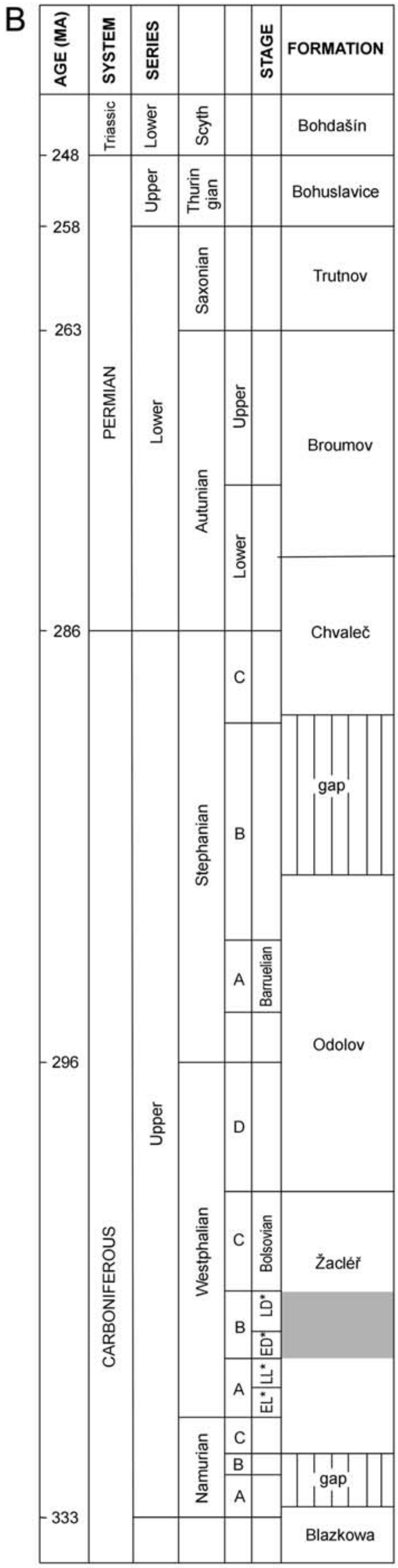
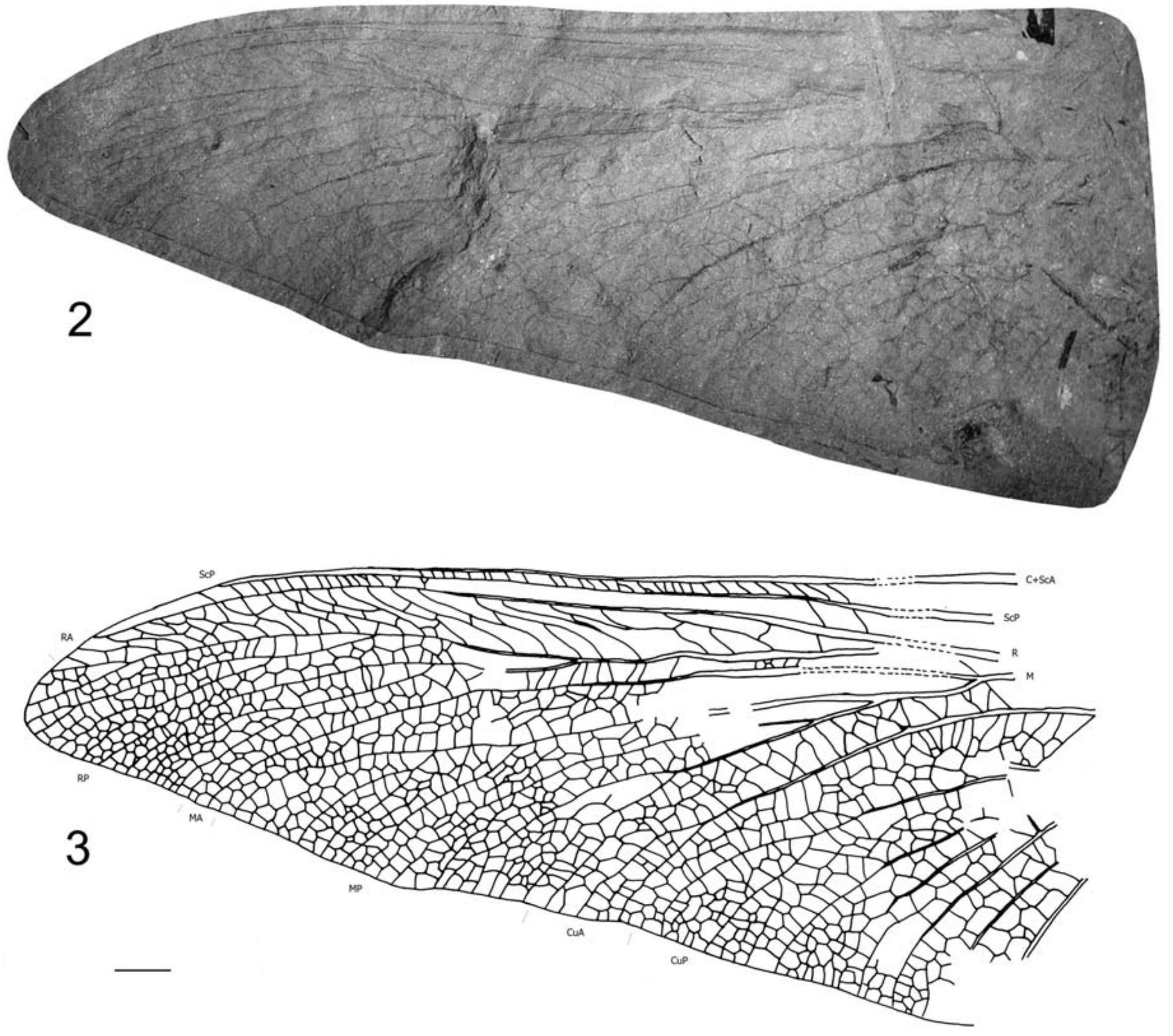


Fig. 1. A – Geographical map of Permo-Carboniferous limnic basins of the Bohemian Massif and position of the Intra-Sudetic Basin. B – Stratigraphic column of the Intra-Sudetic Basin division with proximate time level of the presented fossil (gray box). Abbreviations: EL – Early Langsettian, LL – Late Langsettian, ED – Early Duckmantian, LD – Late Duckmantian.

Etymology. Para – meaning similar to the genus *Ostrava*; feminine in gender.

***Paraostrava stanislavi* sp. n.**
(Figs 2–3)

Description. Wing membrane probably hyaline; wing covered with a dense irregular network, except in the more poorly preserved regions, i.e. the basal parts of areas between ScP and R, R and M, and MA and MP; extreme apex of convex ScA visible at its point of fusion with anterior wing margin, 87.9 mm from wing apex; concave ScP straight, reaching anterior wing margin very distally, 20.4 mm close to wing apex; numerous small simple cross-veins in area between C and ScP; basal part of area between ScP and R poorly preserved but with some visible cross-veins, distal part of same area with several short cross-veins; RA simple and straight, ending on anterior margin 8.6 mm from wing apex; RA and RP area with numerous long sigmoidal cross-veins; base of RP 48.4 mm from wing apex, 25.7 mm distal to division fork: M divides into MA and MP; first fork of RP 12.9 mm distal to its base, both two basal forks of RP divided into three branches; RP reaching wing apex; MA simple, slightly curved, ending on posterior wing margin 17.8 mm from wing apex; MP divided dichotomously into seven branches; MP area very broad reaching the posterior wing margin from 20.4 to 47.3 mm of wing apex; a rather strong oblique cross-vein between M and R, emerging from M at the point of division of M into MA and MP; at the same point, another strong oblique cross-vein between CuA and M; CuA slightly curved, with two short but strong branches ending on posterior wing margin; fork of Cu into CuA and CuP poorly preserved, probably 95 mm from wing apex; CuP slightly curved, more or less parallel to CuA and forked into two branches, first 51.4 mm and second 55.0 mm from posterior wing margin; five anal veins preserved, forming a large anal area (hind wing).



Figs 2–3: *Paraostrava stanislavi* gen. n. et sp. n. 2 – Holotype specimen No. NM-Me128; 3 – hind wing venation. Scale = 5 mm.

Dimensions. Length of fragment about 95 mm, probable total length about 125 mm (wingspan more than 250 mm); width of fragment about 40 mm.

Holotype. Specimen NM-Me128 the distal two-thirds of a well-preserved hind wing, secondary coloured in red by iron-oxide, National Museum, Prague, Czech Republic

Type locality. Jan Šverma (formerly Julia) Mine in Žacléř (Schatzlar in German literature), Intra-Sudetic Basin, Czech Republic.

Type strata. Upper Carboniferous, Duckmantian (formerly Westphalian B), Žacléř Formation.

Etymology. Patronymic; named after Stanislav Opluštil, donator of this fossil.

Discussion. The current state of our knowledge on higher systematics and division of Palaeodictyopteroida sensu Bechly (1996) is rather complicated and partly confusing. There is no real phylogenetic analysis of this group that we can simply follow. In this case we trace both currently supported systems with additional comments.

First, it is not possible to follow the key of the "Eupalaeodictyoptera" proposed by Riek (1976: 230). For example, this author characterized Homoiopteroidea sensu Riek (1976) by the following characters: "CuA branched"; "MA simple"; "ScP extending almost to wing apex". But the CuA is simple in several taxa currently included in the Homoiopteridae (*Scepasma gigas* Handlirsch, 1911, and *Mazonopterum wolfforum* Kukalová-Peck & Richardson, 1983) (Kukalová-Peck & Richardson, 1983).

Sinitshenkova (2002: Fig. 138) proposed a new phylogeny and system of the superorder Dictyoneurida Handlirsch, 1906 (Palaeodictyopteroida sensu Bechly, 1996). This system is not based on a strict use of the cladistic method. At least in the most basal dichotomy, the clade Dictyoneurina is supported by the alleged synapomorphy "wing wide basally" and its sister clade Frankenholziina is supported by the alleged opposite state of character "wing base narrow", also considered as a synapomorphy. The indication of an outgroup to polarize the characters would be suitable. Thus, Sinitshenkova's classification cannot be considered based on the cladistic method, even if it uses the cladistic terminology.

Nevertheless, we shall provisionally follow Sinitshenkova's classification in this paper. We tentatively include

Paraostrava stanislavi gen. n., sp. n. in the group (Homoiopteroidea + Spilapteroidea) because of the following characters: "wing wide basally"; "wing with enriched venation"; "wing not long and narrow, especially in its apical half"; "ScP extending well beyond wing midlength". Sinitshenkova (2002) added the "CuA branching" to characterize this group, but some Homoiopteridae have a CuA simple, as indicated above. She separated the Homoiopteroidea from the Spilapteroidea after the "archedictyon" lost, veins polymerized' for the former group. But the "archedictyon" of some Spilapteridae (*Spilaptera*, see Carpenter, 1992: Fig. 25.4) is less developed than that of some Homoiopteridae (*Homoioptera*, see Kukalová-Peck & Richardson, 1983: Fig. 19). Thus, this character is difficult to follow. But Riek (1976) proposed a different character to separate the Homoiopteroidea from the Spilapteroidea, i.e. MA simple in the former group and branched in the latter.

Sinitshenkova (2002: 117) indicated that the Homoiopteroidea and the Spilapteroidea differ from Eugereonoidea in multibranched MA. But the Homoiopteridae have MA simple or with very short and weak distal branches (see Kukalová-Peck & Richardson, 1983).

Sinitshenkova (2002: 117) divided the Spilapteroidea into Spilapteridae Handlirsch, 1906, Fouqueidae Handlirsch, 1906, Homothetidae Scudder, 1865, Lamproptilidae Handlirsch, 1906, Mecynostomatidae Kukalová, 1969, and Aenigmatidiidae Rohdendorf, 1961. All these groups have MA with long branches. Note that the type genus of the Aenigmatidiidae, *Aenigmatidia* Rohdendorf, 1961 (type species *Aenigmatidia kaltanica* Rohdendorf, 1961) has no "archedictyon" (see Rohdendorf, 1961: Fig. 34), unlike what Sinitshenkova (2002) indicated for the Spilapteroidea in her classification of the "Dictyoneurida". The same author subdivided the Homoiopteroidea into Homoiopteridae Handlirsch, 1906 and Heolidae Handlirsch, 1906. Both have a MA simple (for Heolidae see Handlirsch, 1906a: Pl. 11, Fig. 6, 1906b: 678, Fig. 5). We attribute *Paraostrava* into this superfamily sensu Sinitshenkova (2002).

First, *Paraostrava* differs from the *Miracopteron* Novokshonov, 1993 (Miracopteridae Novokshonov, 1993 of order uncertain but with "similarities" with the Homoiopteridae, *Miracopteron mirabile* Novokshonov, 1993, based on the base of a hind wing) at least in its position of the M fork clearly distal in *Paraostrava* (Novokshonov, 1993).

Within the Homoiopteroidea, *Homoioptera gigantea* Agnus, 1902, *Homoioptera vorhallensis* Brauckmann & Koch, 1982, *Homioptera woodwardi* Brongniart, 1893, *Homoioptera kortumi* Brauckmann & Herd, 2002, *Thesoneura americana* Carpenter, 1944, and *Heolus providentiae* Handlirsch, 1919 (Heolidae), have the area between RA and RP without numerous long sigmoidal secondary veins (only few in *Homoioptera*), the fork of M into MA and MP distal to the level of the base of RP, and a CuA with 3–4 branches, unlike *Paraostrava* (Kukalová, 1969; Brauckmann & Koch, 1982; Kukalová-Peck & Richardson, 1983; Brauckmann & Herd, 2002). *Homoioptera latipennis* (Handlirsch, 1904) differs from *Paraostrava* in having the area between RA and RP as broad as that between RP and MA (Handlirsch, 1904: Figs 4–5).

Adolarryia bairdi Kukalová-Peck & Richardson, 1983 is based on a nymph, difficult to compare with an adult wing. Nevertheless, it has a CuA divided into long branches, unlike *Paraostrava. Monsteropterum moravicum* Kukalová-Peck, J. 1972 was attributed to Palaeodictyoptera with an uncertain systematic position by Carpenter (1992) and then relocated within Megasecoptera after the presence of the tergal projections by Kukalová-Peck (pers. comm.). It is based on a body with wing bases that cannot be compared with *Paraostrava.* Further three taxa were also considered by Carpenter (1992) as Palaeodictyoptera with uncertain position, although Brauckmann (1991a) listed them in Homoiopteridae (see also Brauckmann & Becker, 1992: 139). *Amousus mazonus* Handlirsch, 1911 and *Ametretus laevis* Handlirsch, 1911 are both based on hind wing bases, with forked CuA, unlike *Paraostrava. Mammia alutacea* Handlirsch, 1906 is based on a very incomplete wing fragment, but differing from *Paraostrava* in its MA strongly curved basally.

Mazothairos enormis Kukalová-Peck & Richardson, 1983 is based on the tergum of a single segment of a thorax. Of course, it is not possible to compare it with the other species of the family. *Turneropterum turneri* Kukalová-Peck & Richardson, 1983 is based on two wing bases. Nevertheless, it differs from *Paraostrava* in its CuA with three branches. *Larryia osterbergi* Kukalová-Peck & Richardson, 1983 has the base of RP in a very distal position, far from that of MA, and has MA distally forked and CuA divided into three main branches, unlike *Paraostrava. Mazonopterum wolfforum* Kukalová-Peck & Richardson, 1983 has no long sigmoidal secondary veins in the area between RA and RP, a long distance between bases of MA and of RP, even if that of RP is in a distal position, unlike *Paraostrava. Mazonopterum* shares with *Paraostrava* the simple MA and CuA.

Parathesoneura Sinitshenkova, 1977 (with two species *P. carpenteri* and *P. anfractuosa*, in Sharov & Sinitshenkova, 1977: 52–54) shares with *Paraostrava* the almost simple MA and CuA, and the presence of long sigmoidal veinlets in the area between RA and RP. However, they have a very long basal part of RP, between its base and first branch, and the base of MA distal to that of RP, unlike *Paraostrava*.

Note that there is a strong similarity between *Parathesoneura* and *Archaemegaptilus* Meunier, 1908 (type genus of the Archaemegaptilidae Handlirsch, 1919), viz. they share a very long basal part to RP, the same organization of MA, MP and CuA, and the presence of long sigmoidal veinlets in RA – RP area (Kukalová, 1969: Fig. 46). There are very few visible differences between the two taxa, in the number of branches of MP. Sinitshenkova (2002: 117) included the Archaemegaptilidae in the Eugereonoidea Handlirsch, 1906 (sensu Sinitshenkova, 2002). She characterized this last superfamily by (1) their wings long and narrow, and (2) the "archedictyon" lost. The first character is not obvious in the type specimen of *Archaemegaptilus kiefferi* Meunier, 1908 because the basal half of its wing is not preserved. The second character is convergently present in the Homoiopteroidea. Thus, a phylogenetic revision of the position of the Archaemegaptilidae would be necessary to clarify this situation.

Scepasma Handlirsch, 1911 (two species, *S. gigas* Handlirsch, 1911 and *S. mediomatricorum* Brauckmann & Becker, 1992) has a simple CuA, but MA with one strong fork, unlike *Paraostrava* (Kukalová-Peck & Richardson, 1983; Brauckmann & Becker, 1992).

Boltopruvostia Strand, 1929 is based on the type species *B. robusta* (Pruvost, 1919), a poorly known taxon, based on two wing bases attached to the thorax. Another species, *B. nigra* (Kukalová, 1960) is based on a nearly complete fore wing, originally attributed to the genus *Ostrava* Kukalová, 1960, later synonymized with *Boltopruvostia* (Kukalová, 1969). In *Boltopruvostia nigra*, the fork of the radius is distinctly basal to that of the median vein, unlike its distinctly distal position in *B. robusta* (Kukalová, 1960: Figs 1–2). This difference is not sufficient for a generic separation of *Boltopruvostia* because Brauckmann (1991b) demonstrated on rich material that a rather important variability occurs in the relative positions of these vein bases in *Homoioptera vorhallensis*. There are no visible differences between *Boltopruvostia robusta* and *Paraostrava* in their comparable preserved parts of wing venation, viz. bases of RP, fork of M, and bases of CuA and CuP (Pruvost, 1919: Pls 1–2). But nothing is known concerning the distal two-thirds of the wing venation of *Boltopruvostia robusta*. Thus, it is not possible to compare it accurately between *Paraostrava* and *Boltopruvostia nigra*.

Furthermore, *Paraostrava* and *Boltopruvostia nigra* differ in the relative widths of the area between RA and RP: about twice broader than that between RP and MA in *Paraostrava*, instead of being of the same width in *Boltopruvostia nigra*. This character is sufficient for a generic separation between these two taxa. But it is unknown in *Boltopruvostia robusta*.

As it is not possible to accurately attribute *Paraostrava* or *Boltopruvostia nigra* to *Boltopruvostia*, we choose better to restore the combination of genus *Ostrava* Kukalová, 1960 with *Ostrava nigra* Kukalová, 1960, to erect a new genus and species for *Paraostrava stanislavi*, and to consider *Boltopruvostia robusta* as Palaeodictyoptera: Homoiopteridae of uncertain position.

CONCLUSIONS

(1) The genus *Ostrava* Kukalová, 1960: 241 (type species *Ostrava nigra* Kukalová, 1960 by monotypy) is restituted.

(2) *Boltopruvostia* Strand, 1929 (type species *Boltopruvostia robusta* (Pruvost, 1919) by monotypy) is considered as Palaeodictyoptera: Homoiopteridae with uncertain position according to the poor state of preservation.

Boltopruvostia Strand, 1929: 20 as nomen novum for *Boltonia* Pruvost, 1919: 284, non Koenig, 1820.

(3) *Paraostrava* gen. n. is established for *Paraostrava stanislavi* sp. n. (type species).

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APPENDIX

List of coding characters used to separate the genera of Homoiopteroidea (Homoiopteridae + Heolidae), see Table 1:

1. "Archedictyon" (reticulate venation after Wootton & Kukalová-Peck 2000): present [0]; absent [1]; uncertain or very strongly reduced [2].

2. ScP: ending in basal position, close to mid wing [0]; ending well distal of mid wing, closer to wing apex [1].

Table 1. Characters matrix used to separate the genera of Homoiopteroidea.

Homoiopteroidea (Homoiopteridae + Heolidae) sensu Sinitshenkova (2002)	Wing	1	2	3	4	5	6	7	8	9	10
Homoioptera woodwardi Brongniart, 1893	yes	2	1	0	1	1	0	0	0	0	1
Homoioptera gigantea Agnus, 1902	yes	2	1	0	0	1	0	0	1	0	1
Homoioptera latipennis (Handlirsch, 1904)	yes	1	1	0	0	1	0	0	1	?	0
Homoioptera vorhallensis Brackmann & Koch, 1982	yes	0	1	0	0	1	0	0	1	0	0
Homoioptera kortumi Brauckmann & Herd, 2002	yes	0	1	0	0	1	1	0	0/1	0	0
Adolarryia bairdi Kukalová-Peck & Richardson, 1983	yes	?	1	?	?	1	?	0	1	1	0
Ametretus laevis Handlirsch, 1911	yes	?	?	?	?	?	?	0	?	0	?
Amousus mazonus Handlirsch, 1911	yes	0	?	?	?	?	?	0	?	?	1
Boltopruvostia robusta (Pruvost, 1919)	yes	0	?	?	?	?	?	?	?	0	1
Larryia osterbergi Kukalová-Peck & Richardson, 1983	yes	2	0	0	0	0	0	0	1	0	0
Mammia alutacea Handlirsch, 1906	yes	0	?	?	?	?	?	?	?	0	1
Mazonopterum wolfforum Kukalová-Peck & Richardson, 1983	yes	0	1	0	0	1	0	1	1	1	0
Mazothairos enormis Kukalová-Peck & Richardson, 1983	no	?	?	?	?	?	?	?	?	?	?
Ostrava nigra Kukalová, 1960	yes	2	1	0	0	1	0	1	1	0	0
Parathesoneura carpenteri Sinitshenkova in Sharov & Sinitshenkova, 1977	yes	2	1	1	0	1	1	1	0	0	0
Parathesoneura anfractuosa Sinitshenkova in Sharov & Sinitshenkova, 1977	yes	2	?	1	0	?	1	1	0	0	0
Scepasma gigas Handlirsch, 1911	yes	0	1	0	0	0	0	1	0	0	0
Scepasma mediomatricorum Brauckmann & Becker, 1992	yes	2	1	0	0	0	?	1	0	0	0
Thesoneura americana Carpenter, 1944	yes	2	1	0	0	1	0	0	0	0	0
Turneropterum turneri Kukalová-Peck & Richardson, 1983	yes	0	?	?	?	?	?	0	?	1	0
Paraostrava stanislavi gen. n, sp. n.	yes	2	1	1	1	1	0	0	1	?	0
Heolus providentiae Handlirsch, 1919	yes	1	1	0	1	1	0	0	0	?	1

3. Secondary veins in area between RA and RP: long sigmoidal veinlets absent or very few [0]; long sigmoidal veinlets numerous [1].

4. Area between RA and RP: nearly of same width as area between RP and MA [0]; distinctly broader than area between RP and MA [1].

5. MA: with at least two long branches [0]; simple or with only short apical weak branches [1].

6. Basal part of RP, basal of first branch of RP: relatively short, shorter than distal part of RP [0]; very long, at least as long as distal part of RP [1].

7. CuA: with at least two long branches [0]; simple or with only short apical weak branches [1].

8. MP: with few branches, less than four [0]; with numerous branches, four or more [1].

9. Basal part of CuA: without a strong anterior curve [0]; with a strong anterior curve [1].

10. Basal part of MA: without a strong anterior curve [0]; with a strong anterior curve [1].

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